The Families and Genera of Vascular Plants

Edited by K. Kubitzki

Volume XI

Flowering Plants. Eudicots

Malpighiales

Springer

THE FAMILIES
AND GENERA
OF VASCULAR PLANTS

Edited by K. Kubitzki

For further volumes see list at the end of the book and:
http://www.springer.com/series/1306

The Families and Genera of Vascular Plants

Edited by K. Kubitzki

XI

Flowering Plants · Eudicots

Malpighiales

Volume Editor:
K. Kubitzki

With 74 Figures

Springer

Editor
Professor Dr. Klaus Kubitzki
Universität Hamburg
Biozentrum Klein-Flottbek und Botanischer Garten
22609 Hamburg
Germany

ISBN 978-3-642-39416-4 ISBN 978-3-642-39417-1 (eBook)
DOI 10.1007/978-3-642-39417-1
© Springer Heidelberg New York Dordrecht London

Library of Congress Control Number: 2013954369

© Springer-Verlag Berlin Heidelberg 2014
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Preface

It is with great satisfaction that, with this volume, the major part of the families of the order Malpighiales is now published within this book series. Malpighiales are a relatively new ordinal concept because the member families have few evident common characters and, therefore, could be recognised as a monophyletic group only after the application of DNA sequence studies. Submission of manuscripts for the families belonging to this order extended over a very long time, and I regret the long delay in publication for those authors who complied early. Now, all but three families of the order (Achariaceae, Malpighiaceae and Salicaceae) are treated in this series and a concise overview of all families is given in the introduction to this volume, including those (the Clusiaceae Alliance and Passifloraceae Alliance) already published in Vol. IX of this series.

My deep thanks go to all authors of this volume for their interesting and scholarly contributions, and to all those who have freely shared additional information and/or have commented on earlier drafts. Dr. C.C. Davis is warmly thanked for permission to prepare a simplified version of his consensus tree of malpighialean families for the introduction of this volume. I am also most grateful to all copyright holders who so kindly gave permission to reproduce illustrations published under their responsibility, including the Director and Board of Trustees, Royal Botanic Gardens, Kew, and the editors of Blumea (Leiden, The Netherlands) and Austrobaileya (Brisbane, Queensland). The artist Bobby Angell, New York, deserves my continued appreciation for her generous authorization to use illustrations published under her authorship.

The volume has greatly profited from the critical eyes of the copy editor, Dr. Monique Delafontaine, whose dedicated work deserves my warmest thanks. I would also like to gratefully acknowledge the pleasant collaboration with Dr. Andrea Schlitzberger from the staff of Springer Verlag, and with SPi Technologies India PvT Limited.

Hamburg
13 October 2013

Klaus Kubitzki

List of Contributors

Amaral, Maria do Carmo E. do	Depto de Biología Vegetal, Instituto de Biología, Universidade Estadual de Campinas, Cx. P. 6109, Campinas SP 13083-970, Brazil, mceamaral2009@gmail.com
Ballard, Jr., Harvey E.	Ohio University, Environmental and Plant Biology, Athens, OH 45701-2979, USA, ballardh@ohio.edu
Bayer, Clemens	Palmengarten der Stadt Frankfurt, Siesmayerstr. 61, 60323 Frankfurt/M., Germany, clemens.bayer@stadt-frankfurt.de
Bittrich, Volker	Rua Mário de Nucci, 500, Campinas SP 13083-290, Brazil, folcar2007@gmail.com
Dickison, William C.†	Formerly at University of North Carolina, Chapel Hill, NC, USA, folcar2007@gmail.com
Dressler, Stefan	Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt/M., Germany, stefan.dressler@senckenberg.de
Kubitzki, Klaus	Biozentrum Klein-Flottbek, Ohnhorststr. 18, 22609 Hamburg, Germany, klaus.kubitzki@gmail.com
Levin, Geoffrey A.	Illinois Natural History Survey, University of Illinois, 1816 South Oak Street, Champaign, IL 61820, USA, glevin@inhs.illinois.edu
Paula-Souza, Juliana de	Universidade de São Paulo, Instituto de Biosciências, Rua de Matão 277, Ed. Sobre as Ondas, São Paulo SP 05508-090, Brazil, jupsouza@gmail.com
Prance, Sir Ghillean T.	Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AS, UK, siriain01@yahoo.co.uk
Repplinger, Miriam	Johannes Gutenberg-Universität, Institut für Spezielle Botanik, Mainz 55099, Germany, siriain01@yahoo.co.uk
Schwarzbach, Andrea	Dept. of Biological Sciences, University of Texas, 80 Fort Brown St., Brownsville, TX 78520, USA, andrea.schwarzbach@utb.edu
Wahlert, Gregory	University of Utah, 257 South 1400 East, Salt Lake City, UT 84112, USA, rinorea@gmail.com
Webster, Grady L.†	Formerly at Section of Plant Biology, University of California, Davis, CA, USA, rinorea@gmail.com

Contents

Introduction to Malpighiales

K. KUBITZKI

Conspectus of Families including those treated in previous volumes and those not received for inclusion into this volume

1. Plants with unclear differentiation of stems, roots, and leaves, or even lacking these completely 2
– Green land plants with stems, roots, and leaves 3
2. Echlorophyllous endophytic stem or root parasites on *Tetrastigma* [Vitac.]; flowers often very large; stamens 12–40 adnate to a central column; ovary inferior; loculi irregular; ovules very many/carpel; embryo undifferentiated. 3/20, SE Asia, W Malesia

   For the time being treated as **Rafflesiaceae** but perhaps to be included into Euphorbiaceae [see **Tribe Rafflesieae** in Vol. II: 560–561]
– Green cataract-dwellers with unclear differentiation of stems, roots and leaves; fertile pollen and fertilisable embryo sacs developed underwater. 49/280, worldwide in tropical and warm-temperate regions **Podostemaceae** [see Vol. IX: 304–344]
3. Monoecious lianes, climbing by leaf tendrils; vessel elements with simple perforations; leaves alternate, serrulate to crenate; stipules knob-like; flowers 5-merous, disk of 5 connate circumgynoecial glands; ovary 5(4)-locular, each locule with 2 apical axile ovules surmounted by small obturator-like appendages; stylodia 5 (4), minute, subulate, stigmatic; fruit 5-winged, 1-seeded, indehiscent. 1/1, from Malay Peninsula to Melanesia **Lophopyxidaceae**
– No lianes climbing by leaf tendrils 4
4. Plants producing glucosinolates, woody; dioecious; vessel elements with scalariform perforation plates; leaves alternate, entire, stipulate; sepals 3–6, petals 0; stamens 2–50; disk intrastaminal or 0; ovary 1–3(–6)-locular, stylodia as many as locules; ovules 2 per locule embedded in massive obturator; placentation axile; fruit drupaceous; seeds 1 per locule (or fruit, by abortion); contain glucosinolates, cucurbitacines. 2/225, pantropical and subtropical, mostly in Africa and Malesia **Putranjivaceae**
– Glucosinolates 0 5
5. Stamen filaments vesiculate towards apex; leaves long-petiolate, trifoliolate, serrate to entire, stipulate, alternate to opposite; plants woody; vessel elements with simple (scalariform) perforations; stamens numerous, inner stamens staminodial; ovary locules and stylodia 4–20; ovule 1 per locule. 1/27, neotropical **Caryocaraceae**
– Stamen filaments not vesiculate; leaves rarely 3-foliolate but then not long-petiolate 6
6. Plants with the combination of epitropous ovules, nucellar beaks and obturators; fruit structure basically a septicidal/loculicidal capsule/schizocarp, also splitting from the persistent columella; mesocarp often splitting from endocarp. **Euphorbiaceae** s. l. [as circumscribed in this volume] 7
– Not this combination of embryological traits and fruit structure [although epitropus ovules are common and nucellar beaks have a scattered occurrence in Malpighiales] 9
7. Ovule 1/locule; laticifers + or 0; stems sometimes succulent; vessel elements mostly with simple perforations; leaves alternate, less often opposite or verticillate; stipules + or 0, with axillary colleters, sometimes transformed into glands or spines; petals 1–8; stamens 1–many; pollen grains usually 3-colporate; inner integument vascularized. 213/c. 5,900. Worldwide **Euphorbiaceae** [s. str., "uniovulate euphorbs"]
– Ovules 2/locule; laticifers 0; stems not succulent ["biovulate euphorbs"] 8
8. Vessel elements usually with scalariform perforation plates; leaves simple and entire (trifoliolate and dentate); petals + or 0; stamens usually 3–8; pollen grains 3–7-colporate (-porate), lacking spines; caruncle mostly 0. 59/1,750, pantropical, most in Malesia, some temperate **Euphorbiaceae** subfam. **Phyllanthoideae** [alternatively: **Phyllanthaceae**]
– Vessel elements usually with simple perforations; leaves simple or palmately compound; petals mostly 0; stamens 2–30; pollen grains 3–7-zono-brevicolporoidate or -porate or 10–40-pantoporate, echinate to verrucose; caruncle mostly +. 26/95, pantropical, preferably S Hemisphere **Euphorbiaceae** subfam. **Oldfieldioideae** [alternatively: **Picrodendraceae**]
9. Carpels sometimes producing false septa; flowers mostly diplostemonous; lamina vernation usually involute 10
– False septa 0, except for some Salicaceae 11

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_1, © Springer-Verlag Berlin Heidelberg 2014

10. Woody; vessel elements with simple perforations; stamen filaments and style folded in bud; nectary disk usually conspicuous; ovary 5(2)-locular; ovules 2 (1) per locule; style simple; seeds winged or arillate. 4/23, pantropical **Ixonanthaceae**

– Herbaceous and woody; vessels with simple or scalariform perforations; stamen filaments not folded in bud; nectary weakly developed; ovary 2–8-locular; stylodia distinct, as many as carpels; ovules 2/locule; seeds sometimes arillate. 13/255, widely distributed in tropical and mostly northern temperate regions **Linaceae**

11. Flowers obliquely monosymmetric; fertile stamens abaxial, ± connate, staminodes adaxial; plants woody; vessel elements mostly with simple perforations; leaves alternate, entire 12

– Flowers not obliquely monosymmetric or only slightly so (Malpighiaceae) 15

12. Flowers with distinctive floral cup lined by a nectary 13

– Flowers lacking distinctive floral cup 14

13. Corolla of 3 petals; androecium with a large anterior pointed staminode flanked by 2 stamen pairs and 2 posterior groups of 2–3 tooth-like staminodes; ovary 3-locular; ovules 2 per carpel, syntropous, collateral, axile; style simple; capsule septicidal. 1/3, northern South America **Euphroniaceae**

– Corolla of 5 (0) petals; androecium of (2–)8–20 to very numerous stamens, abaxially best developed; ovary 1-locular with 2 ovules or 2-locular with 1 ovule in each locule; style ± gynobasic; drupe 1-seeded. 18/531, pantropical, mostly neotropical **Chrysobalanaceae**

14. Inflorescence sometimes adnate to petiole or midvein of leafblade; stamens 5 (4), up to 3 of them sometimes lacking anthers; pollen grains 3-colporate; disk lobate or a ring; ovary 2–5-locular; ovules 2 per locule; stylodia distinct or more often connate into a single style provided with distal style branches; fruit a drupe; plants contain the poisonous fluoracetic acid. 3/170, pantropical, also subtropical regions of India and South Africa **Dichapetalaceae**

– Inflorescence not adnate to petiole or midvein; fertile stamens 4–8 in abaxial part of the flower, staminodes 0 or up to 6 in adaxial part; pollen grains 3–5-porate; nectary glands [staminodial?] at base of standard + or 0; ovary 3(4)-locular; ovules 1–numerous per locule; style simple; capsule septicidal. 5/28, Neotropics, Madagascar, Malesia **Trigoniaceae**

15. Pistillate flowers with the naked ovary surrounded by spirally arranged cupular bracts; staminate flowers in catkins, the perianth reduced to one or several bracts or vestigial perianth lobes; ovary 2–3-locular; ovules 2 per locule, axile, basal; stylodia repeatedly bifurcate; plants woody; dioecious; vessel elements with scalariform perforation plates; leaves alternate, toothed; stipules minute. 1/9, Queensland to Fiji **Balanopaceae**

– The naked ovary not surrounded by spirally arranged cupular bracts 16

16. All or 4 of the 5 calyx lobes with paired abaxial glands producing fat oil [Neotropics] or sometimes nectar [Palaeotropics]; ovary multilocular (inferior), with axile placentas and a solitary ovule in each locule; stylodia mostly distinct, rarely connate into a common style; woody, often lianescent; secondary growth often anomalous; hairs T-, V- or Y-shaped; leaves usually opposite, entire, with paired stipules. $x = 6$ and 9. 68/1,250, worldwide tropical/subtropical, most in America **Malpighiaceae**

[not yet in this volume but see the website of W.R. Anderson et al., Malpighiaceae, http://herbarium.lsa.umich/edu/malpigh/index.html]

– Calyx lobes without glands producing fat oil 17

17. Plants produce a brownish resin which is also excreted as granulous exudate on the stems; annual and perennial herbs or subshrubs; leaves opposite, entire or serrate, with scarious stipules; ovary 2–5-locular; ovules many per locule; placentation axile or basal; stylodia 3–5; capsule septicidal; endosperm scant or 0. $x = 6$. 2/35, nearly worldwide **Elatinaceae**

– Plants lacking superficial granulous exudate 18

18. Leaves opposite or alternate, entire, estipulate, with colleters; schizogenous canals or cavities often + and containing clear, black or coloured exudate; vessel elements with simple perforations 19

– Leaves usually stipulate, plants usually lacking schizogenous canals or cavities containing exudates 22

19. Woody or herbaceous; leaves opposite (alternate); sepals and petals 3–5; stamens distinct or fasciculate; ovary 3–5-locular; ovules 1–many per locule; stylodia distinct, at least distally, or style simple; aril 0; trichomes, if multicellular, stellate. 9/540, worldwide **Hypericaceae** [see Vol. IX: 194–201]

– Strictly woody; leaves opposite or alternate 20

20. Anthers often with complex or simple apical glands; leaves alternate to opposite, entire, often with resin canals; stamens not obviously fasciculate; ovary 1–15-locular; ovules 1–many per locule; style simple, usually long; seeds exarillate, small to large, when large, consisting almost entirely of the huge cotyledons. 13/460, pantropical **Calophyllaceae**

[see Vol. IX under Clusiaceae subfam. Kielmeyeroideae, pp. 48–66]

– Anthers lacking apical glands 21

21. Leaves alternate, supervolute, serrulate-setose; ovary 3–5-locular; stylodia distinct or connate into a simple or distally branched common style; capsule with persistent column. 3/35, SE Asia and Neotropics **Bonnetiaceae** [see Vol. IX: 36–39]

– Leaves opposite, entire, often with resin canals, vernation often flat; stamens sometimes fasciculate; plants mostly dioecious; ovary 1–5-locular; stylodia widely separate or connate into a common short style; seeds arillate or not; hypocotyl much enlarged, cotyledons 1/10 or less length of embryo. 14/595, pantropical **Clusiaceae** (s. str.)

[see Vol. IX under Clusiaceae subfam. Clusioideae and Symphonioideae, pp. 48–66]

22. Placentation axile 23

– Placentation parietal 33

23. Leaves opposite 24

– Leaves alternate 27

24. Style simple; vessel elements with simple and scalariform perforation plates 25

– Common style 0; stylodia as many as carpels; vessel elements mostly with simple perforations 26

25. Leaves often serrate; plants sometimes with subepidermal laticiferous idioblasts; vessel elements with scalariform and/or simple perforations; hairs simple; petals usually with a terminal arista and filiform appendages on two lobes, enwrapping 1–5 stamens; nectary disk intrastaminal, entire or lobed; ovary often ± inferior, 2–20-locular with the locules often incompletely separated at anthesis; ovules 2–6 per locule; style simple. 14/145, pantropical **Rhizophoraceae**

– Leaves opposite, entire; vessel elements with scalariform perforation plates; hairs tufted, stellate and simple; nectary disk extrastaminal; petals unappendaged; ovary 2-locular; ovules 2 per locule, placentation apical; style simple, apically bifurcate; fruit a capsule; seed solitary, persistent on columella, with hairy-papillose arillode. 1/2(3?), W Africa, Malesia **Ctenolophonaceae**

26. Leaves opposite, simple, toothed, stipules 0; phloem stratified; cristarque cells 0; pollen 3-porate; ovary 16–25-carpellate, each carpel with a short stylodium; ovules 2 per locule; fruit capsular, with persistent columella. 1/1, endemic to Mahé, Seychelles Islands **Medusagynaceae**

– Leaves opposite/whorled, simple, sometimes lobed or compound, stipulate; cristarque cells and lysigenous mucilage canals +; tertiary veins parallel or plumose reticulate and very closely spaced; ovary 2–14-locular (gynoecium apocarpous), ovules 2 per locule; fruit baccate (folliculate). 4/51, neotropical **Quiinaceae**

27. Nectary disk 0 28

– Nectary disk + 29

28. Flowers unisexual, actinomorphic; stamens 5–15; plants dioecious; woody, vessel elements with scalariform (simple) perforation plates; leaves alternate, vernation involute; nectary 0; ovary 2–5-locular; ovule strictly 1/locule, pendulous; stylodia 2–5, short, or 0; stigmas spreading; fruit a drupe. 3/15, Old World tropics **Pandaceae**

– Flowers bisexual, actinomorphic to zygomorphic, often polystemonous; woody; vessel elements mostly with simple perforations; cristarque cells +; leaves alternate, ± simple, entire to serrate, stipulate; anthers dehiscing by slits or 1 or 2 pores; nectary 0; ovary 1–15-locular, either entire and provided with a simple apical style, or divided into 5 or more uniovulate lobes and the style gynobasic; ovules 1–many per locule; fruit capsular or drupaceous, or separating into several drupelets. 27/495, pantropical, mostly in Brazil **Ochnaceae**

29. Ovary 2–3-locular 30

– Ovary 4–5(–7)-locular 31

30. Flowers often heterostylous; petals sometimes with fringed bilobed ligule; woody; vessel elements with simple perforations; cristarque cells +; leaves alternate, entire, involute, colleters +, stipules mostly intrapetiolar; nectary glands sometimes on outside of staminal tube; ovary 2-locular; ovule 1(2) per carpel; stylodia distinct or style simple; fruit a 1-seeded drupe or 2–3-seeded capsule; seeds rarely arillate. 4/240, pantropical, especially neotropical **Erythroxylaceae**

– Flowers not heterostylous; petals eligulate; woody; vessel elements with scalariform perforation plates [*Bhesa*]; leaves alternate, stipulate, colleters + or 0; flowers bisexual or unisexual, 5-merous, haplostemonous; disk +; ovary 2- or 3-locular; ovules 2 per locule, collateral, obturator 0; stylodia widely divergent; capsule loculicidal; seed 1 per locule, almost completely enveloped by an exostomal fleshy, sheet-like, coloured aril; seed coat exotegmic, thick-walled, ribbon-shaped; endosperm copious; embryo small. 2/7, West Africa, Indo-Malesia **Centrolepidaceae**

31. Stylodia on outer shoulders of the 5 carpels; woody; vessel elements with scalariform perforation plates; inflorescence umbellate; petals induplicate-valvate, slender; nectary annular; stamens 5, with very short filaments; ovary 5-locular; placentation basal-axile; ovules few per locule; fruit a few-seeded berry; seeds not arillate. 1/3, C and N South America **Goupiaceae**

– Pistil with a single style 32

32. Woody, contains balsamic juice; stamen filaments not folded in bud; vessels elements with scalariform perforation plates; leaves alternate, involute; stamens 10–30+; stamen filaments at base connate into a tube; anthers apiculate or linguiform, thecae with separated superposed loculi; nectary disk intrastaminal; ovary 4–7-locular; ovule 1 (2) per locule; style simple; fruit a drupe; endocarp with "resin"-filled cavities, 1(2)-seeded. 8/50, Central and South America to S Brazil, one sp. in W Africa **Humiriaceae**

– Wood; balsamic juice 0; stamen filaments plicately folded in bud; vessel elements with simple perforations; leaves alternate, vernation involute; stipules very large, intrapetiolar, encircling terminal bud; stamens 10 (9), anther loculi parallel; nectary disk obvious; ovary 5–4(2)-locular; ovule 1 per locule; placental obturator +; style simple, short. 3/10, Old World tropics **Irvingiaceae**

33. Flowers usually strongly monosymmetric; sepals and petals 5; stamens 5 (3), distinct or filaments connate into a tube, anthers commonly bearing a dorsal connective appendage; ovary 1-locular, placentation parietal; ovules 1–many; style simple; fruit capsular, usually 3-valvate; woody (herbaceous, lianescent); vessel elements with simple and scalariform perforation plates; leaves alternate (opposite), with salicoid teeth, stipulate. 22 [+ 9 undescr.]/830, worldwide **Violaceae**

– Flowers polysymmetric; connective appendages 0 34

34. (Andro)gynophore often +; calyx and corolla forming a floral tube 35

– Gynophore and floral tube 0 [the latter + in some Flacourtiaceae] 37

35. (Andro)gynophore 0; petals contorted; floral tube campanulate or funnel-shaped, rarely with weakly developed corona; nectary near base of tube; ovules

1–numerous per placenta (1 basal ovule); seeds arillate, pitted; woody and herbaceous; vessel elements with simple and sclariform perforations; hairs sometimes stellate. 10/205, Africa, America
Turneraceae [see Vol. IX: 458–466]

– [Andro]gynophore usually present; petals cochlear; corona often present and strikingly coloured 36

36. Herbaceous to subwoody; vessel elements usually with simple perforations; stamens 5; pollen grains tricolporate; ovules numerous on parietal placentae; stylodia inserted beneath the top of ovary; seeds exarillate; calyx persistent in fruit; tendrils 0. 1/24, Andean region of N Chile and S Peru
Malesherbiaceae [see Vol. IX: 247–249]

– Woody, vessel elements with simple or scalariform perforation plates; branch tendrils often present; stamens 4, 5, or many; pollen grains 3–12-colporate or -foraminate; ovules numerous; stylodia inserted on top of ovary; seeds arillate; contains often cyanogenic compounds. 17/705, pantropical
Passifloraceae [see Vol. IX: 270–281]

37. Woody; vessel elements with simple or simple and scalariform perforation plates; leaves supervolute-curved or involute, alternate, toothed or serrate, often with the distinctive "salicoid teeth"; flowers 3–6-merous; sepals (0)3–15; petals often 0; nectariferous disk or nectar glands intra-, inter- or extrastaminal; stamens (1 in Lacistemateae) 2–many; placentation parietal (axile); fruit a capsule (berry, drupe); seed coat commonly not vascularized; plants contain benzoylated glacosides but lack cyanogenic glycosides (except *Banara*). 55/1010, pantropical and temperate [not received] **Salicaceae**

– Woody (herbaceous and climbing); vessel element with simple, scalariform or simple and scalariform perforations; leaves alternate, entire, rarely toothed or serrate but then leaf teeth not salicoid; petiole often geniculate; sepals 2–5; petals 4–15 (Acharieae: 3–4 and connate), either whitish and papery or with a gland inside at base; nectary 0; stamens 5–many; anthers sometimes [*Chiangiodendron*, *Kiggelaria*] poricidal; seed coat thick; testa commonly strongly vascularized; plants contain cyclopentenoid cyanogenic glucosides and/or cyclopentenyl fatty acids [gynocardin]. 32/145, pantropical [not received] **Achariaceae**

The Ordinal Concept of Malpighiales. The term Malpighiales had already been created but hardly used by nineteenth century botanists, at a time when family and ordinal concepts most generously were proposed for nearly every characteristic family or even genus. In the 19th and practically the whole 20th century, the allocation of the families presently comprised in the Malpighiales was scattered over many different orders. Even the perspicacious botanists of the 19th century, who had the advantage that the herbaria of that time were limited in size and permitted an easier overview than our vast present collections, recognised hardly any relationship among at least some of the Malpighialean families. It remains enigmatic how Hutchinson, who in his "Families of Flowering Plants" used the Malpighialean concept, in the third edition of this work (Hutchinson 1973) included in it 14 families of which only five did not belong there according to the modern ordinal concept. There were no obvious morphological characters uniting these families, and Hutchinson's finding must have been either fortuitous or perhaps due to his vast experience or instinct, but little attention was paid to it until the advent of molecular systematics.

In the first broad-based molecular systematics analysis of the seed plants by Chase et al. (1993), a clade within their rosids was disclosed which comprised representatives of 11 families previously never found in association. This clade was confirmed and expanded by further work, and the Angiosperm Phylogeny Group (APG 1998) adopted the ordinal name Malpighiales for it. Molecular analyses specifically devoted to this group (Davis et al. 2005; Wurdack and Davis 2009; Korotkova et al. 2009) employed an increasing number of gene regions, eventually of all three genomes, and underpinned its monophyly; they also confirmed or provided evidence for family relationships and revealed suprafamilial clades around the Violaceae/Salicaceae, the Ochnaceae and the Chrysobalanaceae, but failed to resolve deeper relationships among the 16 malpighialean subclades previously identified by Wurdack and Davis (2009). More recently, however, the use of phylogenomic approaches and the inclusion of 82 plastid genes led Xi et al. (2012) to the elaboration of a well-resolved, taxon-rich molecular tree for the Malpighiales, in which 12 additional clades and further increased resolution among its deeper nodes were obtained. This new phylogenetic hypothesis also proved helpful for an understanding of the detailed morphological analyses of the Chrysobalanaceae, Rhizophoraceae, Ochnaceae and their presumed relatives by Matthews and Endress (2008, 2011) and Matthews et al. (2012).

Thus, the concept of Malpighiales is the direct outcome of molecular systematics, which may explain its dearth of easily recognisable distinctive marks. It is only recently that P.F. Stevens (2001 onwards) has succeeded in elaborating a list of possible apomorphies for the whole order and its constituent families and family groups, but the order as a whole is characterised by nothing more than "*leaf margin toothed (teeth with a single vein running into a congested ± deciduous apex); stigma dry; exotegmen fibrous*".

According to classificatory concepts, Malpighiales now comprise 37–42 families, 716 genera and 15,935 species (Stevens 2001 onwards), and within the eudicots are resolved as a member of the Fabidae (Rosidae) where they occupy a sister position to the Oxalidales, both these orders being sister to the Celastrales (Wang et al. 2009; Moore et al. 2010).

Phylogeny. Fig. 1 gives the best resolved consensus tree for malpighialean families available at the time of writing (Jan. 2013), which is redrawn from Xi et al. (2012) and will be used to explain the phylogenetic interrelationships among the families. In it, the previously known subclades of Malpighiales, which hitherto were unresolved in relation to one another, are represented in three well-supported major clades. The first of these is composed of two subclades; one contains the euphorbioids and linoids, the other the Humiriaceae, the parietal clade, and the salicoids. The euphorbioid-linoid clade is remarkable because it brings (albeit with weak support) the uniovulate euphorbs close to the biovulate ones (the phyllanthoids), which traditionally have been included in a single family, Euphorbiaceae (s. l.). Based on early results of molecular systematics, the euphorbs have been split into three families, these being the uniovulate Euphorbiaceae, and the biovulate Phyllanthaceae and Picrodendraceae; the latter share many characters and more recently have been resolved as sister clades. Although the three-family classification for the traditional euphorbs is now generally accepted, the common possession of peculiar capsular fruits (p. 58) and a remarkable combination of embryological characters (p. 55) shared by the uniovulate and biovulate euphorbs is a momentous hint that must not be overlooked; it calls for further inquiry into the deeper nodes of the Malpighialean phylogeny. In this volume, euphorbs are treated in the broad circumscription following the concept of the author of the family. The sister group relationship of the biovulate euphorbs with the linoid clade needs attention because their closeness had been considered by several earlier authors, and a relationship between Linaceae and Ixonanthaceae, already recognised by Hallier (1923), is now strongly supported in the analysis of Xi et al. (2012). Previously, there had been much confusion as to the relationships of the Ixonanthaceae, and both morphological and molecular workers had often associated them with the (equally problematic) Irvingiaceae. The Rafflesiaceae (which are not in Xi's consensus tree) are holoparasites living embedded inside their host plants (species of *Tetrastigma*), and cladistically have been found nested in the Euphorbiaceae between the Peroideae and the rest of the uniovulates (Davis et al. 2007). If one should not wish to incorporate the three rafflesiaceous genera into the euphorbs, the reinstatement of the Peroideae at family rank would allow the intercalation of the Rafflesiaceae between them. More recently, however, Xi et al. (2012, in the SI) have placed the Rafflesiaceae as sister to the Euphorbiaceae + Peroideae, which warns against making premature rearrangements; the loss of plastids and the consequences of horizontal gene transfer in the Rafflesiaceae make the issue very complicated.

The sister clade to euphorbioids and linoids comprises the Humiriaceae with the parietal clade and the salicoids. Support for the placement of the Humiriaceae is low; relationships previously suggested for them were quite diverse but never convincing, and their closest relatives may still remain unknown. In the parietal clade, the Achariaceae, reshaped by Chase et al. (2002), are sister to the Violaceae + Goupiaceae, the latter two being strongly divergent in life form and gynoecium structure, but still sharing other floral traits. Further members of this clade are the closely related Malesherbiaceae, Turneraceae and Passifloraceae, and ultimately the Salicaceae, again reshaped by Chase et al. (2002). I cannot see any cogent reason for maintaining Lacistemataceae, Samydaceae and Scyphostegiaceae separately from the Salicaceae into which, in a future treatment for this series, they would be better integrated.

The second principal clade comprises three subclades in a trichotomy strongly supported

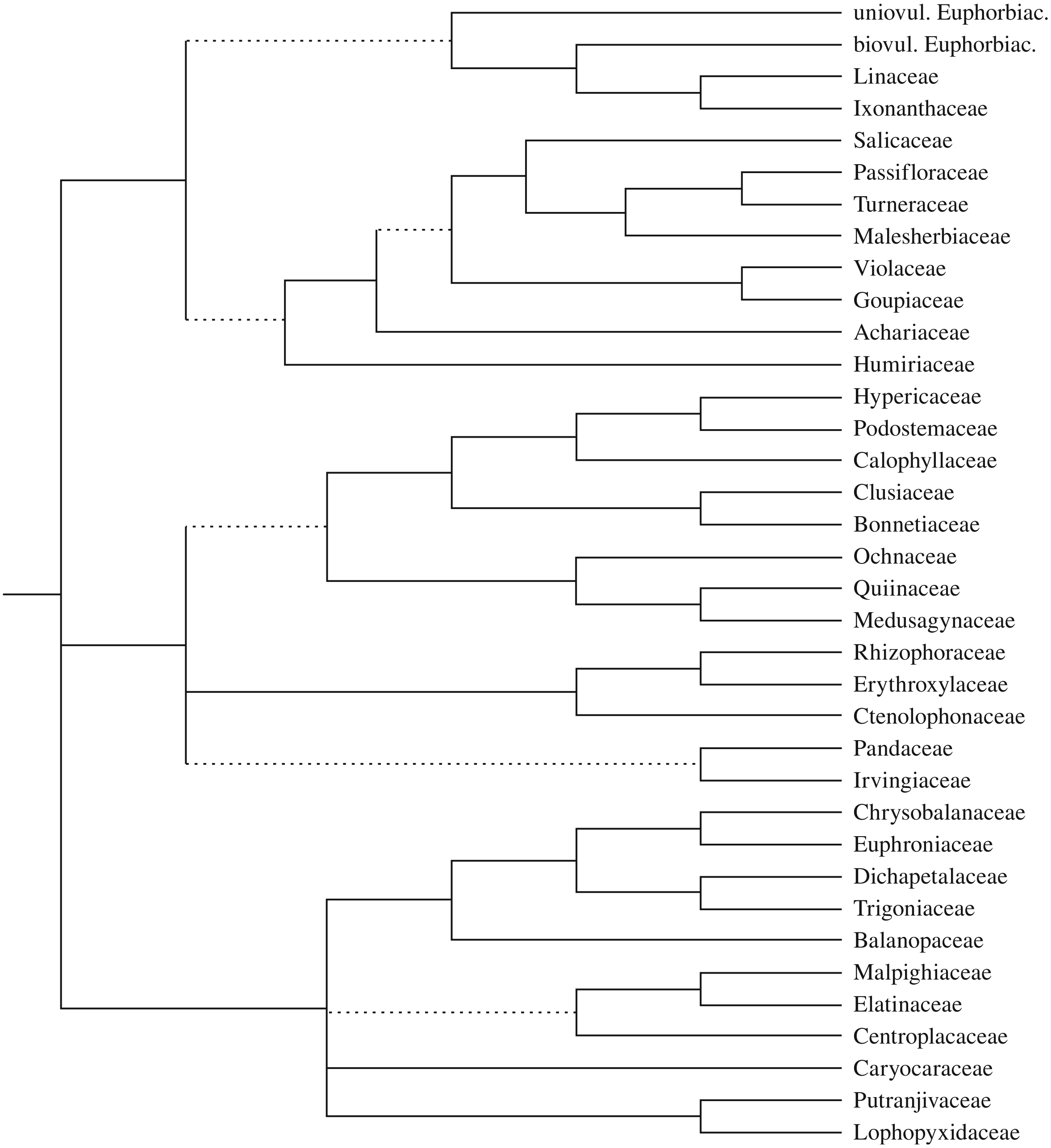

Fig. 1. Maximum likelihood bootstrap consensus tree of the Malpighiales, based on analyses of 82 plastid genes from 58 species added to the existing DNA sequence matrices; redrawn and simplified from Xi et al. (2012) with the kind permission from the authors. Branches with low support hatched.

and characterised by the possession of cristarque cells, with *Medusagyne* as the only exception (elsewhere in Malpighiales, cristarque cells are known from Hugonioideae/Linaceae and Irvingiaceae). The first subclade is composed of the clusioids and the ochnoids, both with a consolidated family classification and containing the interesting association between Hypericaceae and Podostemaceae. Both clusioids and ochnoids usually lack nectar production and are polystemonous; they have brought forth reproductive specialisations like several kinds of floral secretions or simply pollen as reward for pollinators, culminating in buzz pollination. Another subclade, the strongly supported rhizophorids, comprises the Erythroxylaceae, Rhizophoraceae and Ctenolophonaceae, which initially had been recognised as a clade by Wurdack and Davis (2009; see also the morphological work by Matthews and Endress 2011). The third subclade, the pandoids, contains the until recently unplaced Pandaceae, which for lack of a better alternative sometimes had been included in the Euphorbiaceae. They are here in a weakly supported clade with the Irvingiaceae, the latter to date a family of highly controversial placement. This new alliance is backed by several morphological characters listed by Stevens (2001 onwards; see also family treatment of Irvingiaceae).

The third principal clade is composed of four subclades which, except for the position of the Centroplacaceae, had already been recognised by Wurdack and Davis (2009). The five families composing the chrysobalanoids appear in the well-consolidated topology that has already been used as the point of reference for the morphological work by Matthews and Endress (2008). In the malpighioids, Elatinaceae and Malpighiaceae are strongly supported as a clade, whereas their sister position with the Centroplacaceae is only weakly supported. A clade formed by the isolated Putranjivaceae and Lophopyxidaceae and the isolated Caryocaraceae belongs also to the third major clade.

Malpighiales in Time and Space. Davis et al. (2005) used molecular divergence time estimates, calibrated on reliable fossils, to determine the age of the Malpighiales clade. They resolved a much higher age than was expected at that time, i.e. well before the Cretaceous/Tertiary boundary, 112–94 million years ago (Mya) in the Albian and Cenomanian. The extant representatives of this clade are mostly species of shrubs and small trees of the understorey of tropical rain forests, though some of them are tall rain forest trees (*Goupia* and the Irvingiaceae), and various families have extensions into seasonally dry habitats; the Ochnaceae can hardly be seen as a forest family. Davis et al. (2005) extrapolated that the early Malpighiales were shade-tolerant invaders into the understorey of the Cretaceous conifer-dominated forests, where they led to the decline of the light-demanding cycadophytes, pteridophytes and pteridosperms and eventually to the complete disappearance of conifers from tropical biomes. They also suggested that the rise of the Malpighiales might have been paralleled by other tropical clades. Recent broader insights into the age and diversification of the angiosperms have revealed that the Malpighiales were but one part of the vast rosid clade comprising most extant representatives of tropical and temperate tree species (≈70,000 species and 140 families), the lineages of which underwent a rapid diversification within a short period of time in the Cretaceous. The timing of the inferred radiation of the rosids (108 to 91 Mya) and their main branches Fabidae and Malvidae (107–83 Mya) supports a rapid rise of angiosperm-dominated forests in the Cretaceous (Wang et al. 2009; see also Bell et al. 2010; Moore et al. 2010).

With the invasion of modern trees, the habitats of those times underwent profound abiotic and biotic changes. New interactions developed among plants and their substrates, the soil, as well as their pollinators, dispersers, predators, symbiotic partners, etc., thereby triggering an enormous codiversification. The increase of shade reduced the evapotranspiration of the subcanopy including the soil and vegetation, whereas the canopy of the angiospermous forest supplied increased transpiration. This became particularly important for the forest belt of the ever-wet equatorial west wind zone, i.e. the tropical rain forest, the water balance of which is maintained largely by its own transpiration and, to a smaller degree, by the humidity brought by the western winds from the oceans (Salati and Vose 1984). In addition, biogenous aerosol particles in the atmosphere yield condensation nuclei for clouds and precipitation, and sustain the hydrological cycle (Pöschl et al. 2010). Thus, there is an interdependence between vegetation and climate: the equatorial humid west wind zone cannot exist without the humid equatorial forest and vice versa (Kubitzki and Krutzsch 1996; Boyce and Lee 2010).

Very little is known about the place of origin of the Malpighiales and its component lineages. More than half of its families have a pantropical distribution, but in most cases it is unknown whether this is the result of vicariance or dispersal. Lineages that have propagules capable of flotation (Clusiaceae, Chrysobalanaceae and perhaps others) appear prone to long-distance dispersal and, in view of the very many documented intercontinental dispersal events in other groups, it is likely that this may have occurred in the Malpighiales as well. The only pertinent case studies known to me that demonstrate intercontinental dispersal in this plant group are those by Li et al. (2009) on *Bridelia* and by Bardon et al. (2013) on the Chrysobalanaceae. Marked differences in diversification rates among the different Malpighiales clades have been found by Xi et al. (2012), disclosing significant rate decelerations in eight clades, among them Balanopaceae, Ctenolophonaceae, Goupiaceae and Lophopyxidaceae, and rate accelerations in Malpighiaceae, Passifloraceae and three others. Elevated diversification rates may indeed be related to specialised plant–pollinator interactions, as suggested by Xi et al. (2012), whereas each lineage in decline will need its own specific explanation. *Lophopyxis*, for instance, because of its highly specialised shoot morphology and anatomy, may hardly have a chance for further diversification.

To finish this section, the story of *Ctenolophon* (for documentation see family account, this vol.) will demonstrate the value of an ample fossil record for an understanding of extant distribution. By the end of the Cretaceous, *Ctenolophon* appears in West Africa, where it survives to the present with a single species, soon followed by several species in southern Arabia. In the Palaeocene the genus enters into northern South America where its record ends by the Eocene. In the Palaeocene the genus starts also drifting northwards on the Indian Plate and there undergoes its greatest diversification (up to 9 pollen types) but disappears from India in the Neogene, after having spread to SE Asia and Malesia where it has survived to the present day in the Malay peninsula, Sumatra, Borneo, the Philippines, and New Guinea. About 50 years ago my unforgettable mentor, Prof. C.G.G.J. van Steenis, alerted me to look for living *Ctenolophon* in the swamp forests of northern South America and, though I did not see it there, I have pleasure in passing his suggestion onto another generation because it still makes sense!

For references, see under General References.

Balanopaceae

Balanopaceae Benth. in Benth. & Hook., Gen. Pl. 3: 341 (1880), nom. cons. ('Balanopseae').

K. KUBITZKI

Dioecious small to tall evergreen trees; older bark with white, circular, prominent lenticels; hairs simple, unicellular. Leaves basically alternate, dimorphic, shoots with minute scale leaves proximally and foliage leaves distally, the latter sometimes subverticillate and restricted to the shoot tip; foliage leaves petiolate, with prominently to obscurely toothed margins; stipules a pair of minute teeth at the base of the petiole. Inflorescences usually subtended by scale leaves, less commonly by foliage leaves, in staminate plants a catkin; staminate flowers short-pedicellate and axillary to scales on the catkin axis, subtended by one or several bracts or vestigial perianth lobes, these often fewer than stamens; stamens (1–)3–6(−12), filaments short, anthers dehiscing laterally; a vestigial pistil sometimes present; pistillate plants with solitary subsessile or short-pedicellate flowers in the axils of scale leaves, with numerous densely crowded, spirally arranged deltoid "cupular" bracts subtending the naked ovary, or a terminal flower surrounded by further lateral flowers also subtended by cupular bracts; staminodes 0; gynoecium syncarpous, 2(3)-carpellate; ovary 2(3)-locular, the locules imperfectly septate at anthesis but fully septate in fruit; ovules 2 per carpel, collateral, borne axile-basally, bitegmic and intermediate between apotropous and epitropous; stylodia connate at the base and once or twice bifurcate to form ribbon-like lobes stigmatic on the adaxial surface. Fruit a yellow, orange or brown drupe with rather thin fleshy mesocarp, subtended at the base by a cup of numerous imbricate, concrescent bracts; pyrenes 2–3; endosperm fleshy during fruit maturation, but crushed at maturity, and forming only a thin layer around the embryo; embryo large, green, straight. $n = 20$ (21).

A single genus comprising nine spp., distributed across "old lands" in the S Pacific (N Queensland, New Caledonia, New Hebrides and Fiji), and bound to forest and scrub communities; on New Caledonia growing on both serpentine and gneiss.

VEGETATIVE MORPHOLOGY AND ANATOMY. According to the study by Carlquist (1980), the leaves are dimorphic: prior to the fully formed leaves, scale leaves appear on each shoot. In some species (confined to New Caledonia), the foliage leaves form subverticillate clusters at the tips of the shoots only. The leaf margins are toothed to various degrees. The teeth are several cell layers thick, and the cells are filled with a dark content which is thought to be tannins. Both the scale leaves and the foliage leaves are each provided with a pair of lateral, dark-coloured stipules. Hairs are non-glandular, unicellular and early vanishing from the leaves, but persistent in the involucral bracts, which subtend the solitary female flower and fruit and form the "cupule".

Balanops has trilacunar nodes. For leaf anatomy, see Carlquist (1980); a notable anatomical feature is the scattered occurrence of cristarque cells in the leaves. The involucral bracts contain brachysclereids. The wood has no growth rings. The vessel elements are relatively long and possess scalariform or reticulate-scalariform perforation plates. The wood parenchyma is diffuse, and the rays are multiseriate and uniseriate, with a predominance of erect cells.

REPRODUCTIVE STRUCTURES. In contrast to earlier reports to the contrary, Sutter and Endress (2003) have shown that the ovary of *Balanops* is completely septate, that the ovules are weakly crassinucellate, bitegmic with a multilayered inner integument (in contrast to all previous indications), and intermediate between apotropus and epitropous, and that an obturator is not present.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_2, © Springer-Verlag Berlin Heidelberg 2014

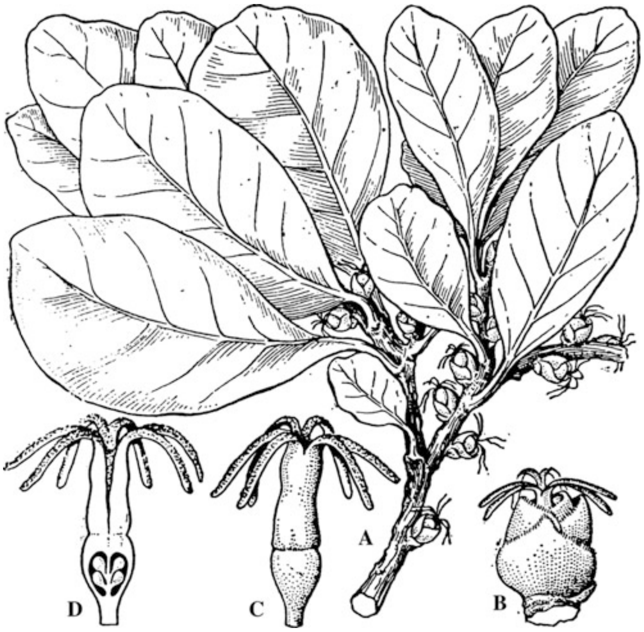

Fig. 2. Balanopaceae. *Balanops sparsiflora*. **A** Branchlet with pistillate flowers. **B** Pistillate flowers enclosed by cupular bracts. **C** Pistillate flower. **D** Same, transversally sectioned. (Takhtajan 1980)

Embryology. Unknown.

Pollen Morphology. The pollen is 3–5-colpate, with colpi that show no sign of an endoaperture. The exine sculpturing consists of small spinules. The exine structure is tectate-granular to columellate. The tectum is traversed by microperforations (Erdtman 1952; Zavada and Dilcher 1986).

Pollination. Probably by wind.

Fruit and Seed. The pericarp consists mostly of thin-walled parenchyma cells, but below the epidermis two or three layers of thick-walled brachysclereids have been observed (Guillaumin 1925; Carlquist 1980). Dispersal is probably by birds (Carlquist 1980).

Phytochemistry. Carlquist (1980) and Sutter and Endress (2003) mention idioblasts containing dark-coloured substances, supposedly tannins, but it is unknown of which type these are. The occurrence of trivial triterpenes gives no clue for affinities (Hegnauer 1964).

Affinities. The affinities of *Balanops* were dubious to early workers such as Engler (1897) and have remained so for a long time. After discussing all taxa that had been suggested as candidates for a relationship to *Balanops*, Carlquist (1980) focused on Hamamelidaceae, Myricaceae, Pittosporales sensu Thorne, and particularly Daphniphyllaceae. Takhtajan (1997) combined Balanopaceae and Daphniphyllaceae in monotypic orders in a superorder Daphniphyllanae, but in sequence analyses of the *rbc*L gene (Litt and Chase 1999; Savolainen, Fay et al. 2000; Chase et al. 2002) Balanopaceae appeared within the Malpighiales in a clade in which they are sister to Dichapetalaceae/Trigoniaceae plus Chrysobalanaceae/Euphroniaceae. In contrast, Sutter and Endress (2003) and Matthews and Endress (2008) argued that features of *Balanops* such as the unisexual flowers, the lack of a perianth, the repeatedly bifurcate stylodia and the weakly crassinucellar ovules would fit much better with a euphorbialean than the chrysobalanoid relationship. However, the multi-gene analyses of Wurdack and Davis (2009), Soltis et al. (2011) and Xi et al. (2012) provide strong support for the earlier molecular findings.

Only one genus:

Balanops **Baill.** Fig. 2

Balanops Baill., Adansonia 10: 117 (1871); Carlquist, Allertonia 2: 191–246 (1980), rev.
Trilocularia Schlechter (1906).

Description as for family. Nine species, for distribution see above.

Selected Bibliography

Carlquist, S. 1980. Anatomy and systematics of Balanopaceae. Allertonia 2(3): 191–246.
Carlquist, S. 1989. Balanopaceae. In: Flora of Australia, vol. 3: 93–95. Canberra: Government Publishing Service.
Chase, M.W. et al. 2002. See General References.
Engler, A. 1897. Balanopsidaceae. In: Engler & Prantl, Nat. Pflanzenfam., Nachtr. I zu T. III, 1. Leipzig: W. Engelmann, pp. 114–116.
Erdtman, G. 1952. See General References.
Guillaumin, A. 1925. Recherches sur l'anatomie et la classification des Balanopsidacées. Rev. Gén. Bot. 37: 433–449.
Hegnauer, R. 1964. See General References.

Hjelmquist, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. Bot. Not. Suppl. 2: 1–171.

Litt, A., Chase, M.W. 1999. The systematic position of *Euphronia*, with comments on the position of *Balanops*: an analysis based on *rbc*L sequence data. Syst. Bot. 23: 401–409.

Matthews, M.L., Endress, P.K. 2008. See General References.

Nemirovich-Dachenko, E.N. 1991. Balanopaceae. In: Takhtajan, A. (ed.) Anatomia seminum comparativa, vol. 3. Leningrad: Nauka, pp. 115–116.

Savolainen, V., Fay, M.F. et al. 2000. See General References.

Soltis, D.E. et al. 2000. See General References.

Soltis, D.E. et al. 2011. See General References.

Sutter, D.M., Endress, P.K. 2003. Female flower and cupule structure in Balanopaceae, an enigmatic rosid family. Ann. Bot. 92: 459–469.

Takhtajan, A.L. 1980. See General References.

Takhtajan, A.L. 1997. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Zavada, M.S., Dilcher, D.L. 1986. Comparative pollen morphology and its relationships to phylogeny in the Hamamelidae. Ann. Missouri Bot. Gard. 73: 348–381.

Caryocaraceae

Caryocaraceae Voigt (1845), nom. cons.

G.T. Prance

Trees or shrubs. Leaves trifoliolate, opposite or alternate, the margins of the leaflets serrate, dentate or crenate or rarely entire, often with stipels at base of leaflets; stipules 2–4, usually caducous, or 0. Inflorescences of terminal racemes; pedicels articulated. Flowers large, hermaphrodite, actinomorphic; sepals 5(6), imbricate; petals 5(6), imbricate, caducous, distinct or rarely slightly connate at base or connate at apex to form a calyptra in *Anthodiscus*; stamens numerous, 55–750; filaments usually connate in a ring at the base, long and slender and usually with some much shorter sterile interior ones which are often recurved, apical portion with numerous vesicles, the sterile filaments often with spirally arranged vesicles along entire length, or the filaments with a row of sterile staminodes at base of interior; anthers basifixed or attached at middle, bilocular; the stamens frequently caducous as a unit together with the petals after pollination; ovary compound, superior, 4(–6)-carpellate in *Caryocar* and 8–20-carpellate in *Anthodiscus*, with as many stylodia as carpels (a common style being absent), each with a distal punctiform stigma; the carpels unilocular each with a single ovule; the ovules basal, erect, anatropous or atropous, bitegmic or unitegmic. Fruit a drupe, with 1–4 seeds developing in *Caryocar* or 8–20 in *Anthodiscus*; mesocarp indehiscent, usually fatty or fleshy; endocarp hard and woody, muricate, tuberculate or spinulose on outer surface, eventually splitting into 1-seeded pyrenes or mericarps. Seeds often reniform, endosperm thin or lacking, the embryo with a straight, arcuate or spirally twisted radicle, a fleshy hypocotyle, and two small cotyledons.

Two genera and 27 spp., in the American tropics from Costa Rica to southern Brazil but not native to the West Indies.

Anatomy and Morphology. A summary of anatomical features with an emphasis on leaf structure is given in Prance and Silva (1973). Brochidodromous and camptodromous nervation are the usual patterns, although *Anthodiscus trifoliatus* is hyphodromous. Branched sclerenchymatous idioblasts are present in the leaf mesophyll and petioles of both genera. The palisade cells frequently contain crystals. Stomata are confined to the abaxial leaf surface, and are usually anomocytic and occasionally either anisocytic or paracytic.

The wood of *Anthodiscus* can easily be distinguished from that of *Caryocar* by the greater abundance (±15/sq. mm) of vessels (3/sq. mm in *Caryocar*), the quantity of gum deposits in the ray cells, and the fibers without septa. The vessels of *Caryocar* vary from 74–577 µm in tangential diameter and are solitary or in radial multiples of 2–5 cells. The vessels of *Anthodiscus* have 50–100 µm mean tangential diameter and are solitary or in multiples of 2–6 cells. Wood of *Caryocar* is described in Barghoorn and Renteria (1967), Loureiro and Silva (1968), Mello (1970) and Araújo and Mattos Filho (1973).

Floral Structure. In *Anthodiscus* the five petals fall as a unit, whereas in *Caryocar* petals and stamens fall as a unit. The floral structure was studied by Dickison (1990) who found that *Caryocar* has bitegmic ovules and simple stylodia, and *Anthodiscus* has unitegmic ovules and compound stylodia (formed by complete coalescence of the upper ventral halves of adjacent carpels). There is also more fusion of major traces in *Anthodiscus*. The gynoecia are richly vascularised by a complex network of wall veins but dorsal or median carpellary bundles are absent. Small prismatic crystals and large deposits of resin-like material are widely distributed throughout all floral parts. The filaments have unique vesicles which are enlarged epidermal cells with numerous membrane-covered wall perforations. Dickison suggests that these cells

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_3, © Springer-Verlag Berlin Heidelberg 2014

function in the rapid release and uptake of water during filament erection and subsequent anther dehiscence.

The inner staminodes and the inner side of the floral tube of *Caryocar* are nectariferous, whereas a nectary has not been found in *Anthodiscus* (Vogel 1968; Dickison 1990; Matthews and Endress 2011). On the outside of the sepals of *Caryocar*, Matthews and Endress (2011) found a glandular structure reminiscent of an oil gland, in which the cuticle is separated from the epidermis and the latter is differentiated into small-celled tissue rich in cytoplasm. It remains unknown whether it is a nectary or an oil gland.

Fig. 3. Caryocaraceae. **A**–**C** *Caryocar harlingii*. **A** Branch with inflorescence. **B** Flower bud. **C** Section of fruit; note spiny endocarp. **D**–**F** *Anthodiscus peruanus*. **D** Flowering branchlet. **E** Petals forming a single caducous unit. **F** Ovary and stylodia. (Orig.)

KARYOLOGY. The chromosome number of three species of *Caryocar* is $2n = 46$ (Ehrendorfer et al. 1984).

POLLINATION. The genus *Caryocar* is bat-pollinated (Vogel 1968), and *C. brasiliense*, which is pollinated mainly by glossophagine bats, is self compatible but sets more fruits when crossed (Barradas 1972; Gribel and Hay 1993). Sphingids may also act as pollinators of *Caryocar* (Gribel and Hay 1993), and *Anthodiscus* is probably insect-pollinated (Prance and da Silva 1973).

FRUIT AND SEED. The fruits are drupes with 1–4 seeds in *Caryocar* splitting into 1-seeded cocci and 8–20 seeds in *Anthodiscus*. In *Caryocar* the mesocarp is soft and fleshy and the endocarp is protected by a layer of spines in most species.

DISPERSAL. Little is known about dispersal of the seeds but agoutis have been reported as dispersers of several species of *Caryocar*. Gribel (1986) found that rheas eat and defecate the stone and seed of *C. brasiliense*, and were the main agent of dispersal before they became so rare.

PHYTOCHEMISTRY. Since the oil of the fruit is comestible, there are many papers about the fatty acid content of *Caryocar* oils, for *C. villosum* Georgi (1929) and Hilditch and Rigg (1935), for *C. brasiliense* Ferreira and Motidome (1962) and Handro and Barradas (1971), and for *C. coriaceum* Sales (1973), Lima et al. (1981) and Alencar et al. (1983). *Caryocar* oils are rich in palmitic and oleic acids, and there is a difference between the mesocarp and kernel oils but little difference between species.

The leaves of *Caryocar brasiliense* contain various triterpenes, ellagic acid (Oliveira et al. 1968) and large amounts of condensed tannins (K. Kubitzki, pers. comm.).

AFFINITIES. Caryocaraceae have been placed in the Theales in most traditional systems of classification and are there still in Takhtajan (2009). Molecular studies have placed the family firmly in the Malpighiales, but no close relatives could be revealed in the vast sequence analyses from many gene regions of Wurdack and Davis (2009) and Soltis et al. (2011). In a 3-gene analysis Soltis et al.

(2007) recovered a clade, albeit with low support, in which Caryocaraceae + [Linaceae + Irvingiaceae] were sister to Erythroxylaceae + Rhizophoraceae. From their careful comparative study of the floral structure of these families, however, Matthews and Endress (2011) concluded that a clade of Linaceae, Irvingiaceae and Caryocaraceae is not well supported by floral morphology, and that Caryocaraceae are morphologically most divergent among these families. This has been confirmed by the analysis of Xi et al. (2012) in which Caryocaraceae are somewhat lost in a moderately supported tetratomy where they stand alongside the chrysobalanoids, malpighioids and putranjivoids.

Distribution and Habitats. Both genera range from Costa Rica to eastern Brazil. *Anthodiscus* occurs in the Guianas and western Amazonia but is absent from central and eastern Amazonia. Most species are found in lowland rainforest and flooded riverside habitats, but species of *Caryocar* occur in other habitats. *C. brasiliense* is common throughout the cerrados of central Brazil and *C. cuneatum* in the arid caatinga of the Brazilian northeast. *C. montanum* occurs at about 1,000 m in the Guayana Highland and *C. gracile* is endemic to white sand areas of north-western Amazonia.

Economic Importance. The uses of *Caryocar* are summarised in Prance (1990). The wood of most species is durable and finishes well, is resistant to insect attack and is much used in boat building. The fruit of most species have an edible mesocarp and a kernel that is used like a nut or for the extraction of a comestible oil rich in oleic acid. The fruit of *C. glabrum* is also used as a fish poison (Prance 1973; Kawanishi et al. 1986), the mesocarp of *C. brasiliense* to prepare a liqueur, and there are many other local indigenous uses.

Conservation. *Caryocar costaricense* has been seriously overexploited for its wood and is listed in Appendix 2 of the CITES Treaty, and therefore requires permits for trade.

Key to the Genera

1. Leaves opposite, calyx deeply lobed; ovary and fruit 4(–6)-locular; stylodia 4; radicle of embryo straight **1. *Caryocar***
– Leaves alternate; calyx truncately dentate and reduced; ovary and fruit 8–20-locular, stylodia 8–15; radicle of embryo spirally twisted **2. *Anthodiscus***

1. ***Caryocar*** L. Fig. 3

Caryocar L., Mant. plantarum 2: 247 (1771); Prance & Silva, Fl. Neotrop. Monogr. 12: 1–75 (1973), rev.

Large trees or rarely shrubs or suffrutices. Leaves opposite, often with 2–4 stipels at base of leaflets; stipules absent or present and soon caducous. Flowers large; calyx distinctly 5(–6)-lobed; petals fused at base together with the base of the filaments and often caducous with the filaments; stamens 55–750, the inner often staminodial and basally with glandular nectar-secreting tissue; ovary 4(–6)-locular; ovules bitegmic. Fruit 4–6-locular, a drupe with 1–4 loculi developing, and dehiscing into 1-seeded cocci; endocarp tuberculate or spinous on exterior. Seeds reniform or subreniform, the embryo with a straight to arcuate radicle.

Eighteen spp., from Costa Rica, Colombia, Peru, Ecuador, Venezuela, the Guianas to central and Atlantic coastal Brazil.

2. ***Anthodiscus*** G.F.W. Meyer

Anthodiscus G.F.W. Meyer, Prim. Fl. Esseq. 193–195 (1818); Prance & Silva, Fl. Neotrop. Monogr. 12: 1–75 (1973).

Trees or shrubs. Leaves alternate; stipels 0; stipules 0. Flowers medium sized; calyx cupuliform with very small, reduced, indistinct dentate lobes; petals circumscissile at base and fused at apex to form a caducous calyptra; stamens 100–280; ovary 8–12(–15)-locular; ovules unitegmic. Fruit an 8–15-locular drupe with most loculi developing. Seeds small, laterally compressed.

Nine spp. in Guyana, Venezuela, Colombia, Peru and western Amazonia, with one sp. in

Costa Rica and Chocó, Colombia and one in Atlantic coastal Brazil.

Selected Bibliography

Alencar, J.W., Alves, P.B., Craveiro, A.A. 1983. Pyrolysis of tropical vegetable oils. J. Agric. Food Chem. 31: 1368–1270.

Araújo, P.A. de M., Mattos Filho, A. de 1973. Estrutura das madeiras de Caryocaraceae. Arch. Bot. Rio de Janeiro 19: 5–47.

Barghoorn, A.W., Renteria, R.M. 1967. Estudio anatomico y fisico-mecanico del cagui (*Caryocar costaricense* Donn. Sm.). Bol. Inst. Forest. Lat.-Amer. Merida 24: 35–57.

Barradas, M.M. 1972. Informação frutificação e dispersão do piqui *Caryocar brasiliense* Camb. (Caryocaraceae). Ciência e Cultura 24: 1063–1068.

Dickison, W.C. 1990. A study of the floral morphology and anatomy of the Caryocaraceae. Bull. Torrey Bot. Club 117: 123–137.

Ehrendorfer, F., Morawetz, W., Dawe, J. 1984. The neotropical angiosperm families Brunelliaceae and Caryocaraceae: first karyosystematical data and affinities. Pl. Syst. Evol. 145: 183–191.

Ferreira, P.C., Motidome, M. 1962: Estudo quimico do óleo de piquí. An. Fac. Farm. Odont. Univ. São Paulo 19: 25–30.

Georgi, C.D.V. 1929. Piqui-a fruit oils. Malayan Agric. J. 17: 166–170.

Gribel, R. 1986. Ecologia da polinização e da dispersão de *Caryocar brasiliense* Camb. (Caryocaraceae) na região do Distrito Federal. M. Sc. thesis, Univ. de Brasília, xii + 109 pp.

Gribel, R., Hay, J.D. 1993. Pollination ecology of *Caryocar brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. J. Trop. Ecol. 9: 199–211.

Handro, W., Barradas, M.M. 1971. Sôbre os óleos do fruto e da semente do pique – *Caryocar brasiliense* Camb. (Caryocaraceae), pp. 110–113. In: III Simpósio sôbre o Cerrado. Ed E. Blücher, Univ. São Paulo.

Hilditch, T.P., Rigg, J.G. 1935. The component glycerides of piqui-a fats. J. Soc. Chem. Indust. 54: 109.

Kawanishi, K., Raffauf, R.F., Schultes, R.E. 1986. The Caryocaraceae as a source of fish poisons in the northwest Amazon. Bot. Mus. Leafl. 30: 247–253.

Lima, M.T., Maia, G.A., Guedes, B.L., Oria, H.F. 1981. Composição de acidos graxos da fração lipidica do piqui (*Caryocar coriaceum* Wittm.). Ciencia Agron. 12: 93–96.

Loureiro, A.A., Silva, M.F. 1968. Catálogo das madeiras do Amazônia 1: 154–164. Belém.

Matthews, M.L., Endress, P.K. 2011. See General References.

Mello, E.C. 1970. Estudo anatômico das madeiras do gênero *Caryocar* Linn. Brasil Florestal 1: 54–62.

Oliveira, M.M. de, Gilbert, B., Mors, W.B. 1968. Triterpenes in *Caryocar brasiliense*. An. Acad. Brasil. Ciências. 40: 451–452.

Prance, G.T. 1973. Ethnobotanical notes from Brazil. Econ. Bot. 26: 221–237.

Prance, G.T. 1990. The genus *Caryocar* L. (Caryocaraceae): an underexploited tropical resource. Adv. Econ. Bot. 8: 177–188.

Prance, G.T., Silva, M.F. da 1973. Monograph of Caryocaraceae. Flora Neotropica 12: 1–75. New York: Hafner.

Sales, F.J.M. 1973. O oleo no fruto de piquizeiro, *Caryocar coriaceum* Wittm. Turrialba 23: 108–109.

Soltis, D.E., Gitzendanner, M.A., Soltis, P.S. 2007. A 567-taxon data set for angiosperms: the challenges posed by Bayesian analyses of large data sets. Int. J. Pl. Sci. 168: 137–157.

Soltis, D.E. et al. 2011. See General References.

Takhtajan, A. 2009. See General References.

Vogel, S. 1968, 1969. Chiropterophilie in der neotropischen flora. Flora 157: 562–602; 158: 195–202, 289–323.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Centroplacaceae

Centroplacaceae Doweld & Reveal (2005).

K. KUBITZKI

Trees. Leaves alternate, stipulate, colleters + or 0. Inflorescences racemose; pedicels articulated. Flowers bisexual or unisexual and then plants dioecious, 5-merous, haplostemonous, stamens antesepalous; gynoecium syncarpous, ovary 2- or 3-locular; stylodia widely divergent, with slightly expanded stigmas; ovules 2 per locule, collateral. Capsule loculicidal. Seed 1 per locule, almost completely enveloped by an exostomal fleshy, sheet-like, coloured aril; seed coat exotegmic, thick-walled, ribbon-shaped; endosperm copious; embryo small.

A family comprising two genera and seven spp., West Africa, Indo-Malesia.

MORPHOLOGY AND ANATOMY. *Bhesa* has vessel elements with scalariform perforation plates and paratracheal parenchyma +; stomata are anisocytic (*Centroplacus*) and laterocytic (*Bhesa*); the ovules are epitropous (*Centroplacus*) and apotropous (*Bhesa*).

POLLEN MORPHOLOGY. The pollen is tricolporate, that of *Centroplacus* tectate and microperforate and very similar to that of (uniovulate!) *Microdesmis* (see also the discussion by Punt 1962: 89), whereas that of *Bhesa* is finely striate (Wurdack and Davis 2009).

FRUIT AND SEED. The loculicidal fruits contain a single seed per locule (one ovule aborts), invested with a coloured, sheet-like, fleshy aril that envelops nearly the entire seed. It is orange or red in *Bhesa* and red in *Centroplacus*; this may be related to bird dispersal. Stuppy (1996) cites a collector's note according to which the valves of the mature fruit of *Centroplacus* fall away completely and leave behind the brown seed wrapped into a fleshy bright orange aril. Wurdack and Davis (2009) believe that the aril arises at the exostome, but Leandri (1957: 207) thought it to be an outgrowth of the "fruit axis".

The seeds of both genera agree in the small size of the embryo, the copious endosperm, and the 1-layered exotegmen of ribbon-like cells (see Corner 1976, figs. 80 and 82; Stuppy 1996: 202 and t. 85; Tokuoka and Tobe 2001). Such a seed coat is also found in genera of the Phyllanthoideae.

RELATIONSHIPS. This family concept is the outcome of recent molecular studies. *Bhesa*, for long considered a strange element within Celastraceae in terms of gross morphology and anatomy, has been recognised as malpighialean by Zhang and Simmons (2006). *Centroplacus*, after having been assigned to Flacourtiaceae and Celastraceae, was referred by Hutchinson (1912) to Euphorbiaceae, where its affinities remained contentious. The absence of an obturator and the minute embryo, together with the presence of an aril may exclude *Centroplacus* from the biovulate Euphorbiaceae. The multi-gene analysis of Wurdack and Davis (2009) provided strong support for a clade consisting of *Centroplacus* and *Bhesa*, which is weakly supported as sister to a clade of Malpighiaceae + Elatinaceae (Xi et al. 2012). These four families share axile placentation, crassinucellar ovules without endothelium, and sepals persistent in fruit (Xi et al. 2012).

KEY TO THE GENERA

1. Flowers unisexual, plants dioecious; leaves denticulate; pistillate flowers apetalous; ovary 3-merous **1. *Centroplacus***
– Flowers bisexual; leaves entire; pistillate flowers petaliferous; ovary 2(1)-merous **2. *Bhesa***

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_4, © Springer-Verlag Berlin Heidelberg 2014

1. *Centroplacus* Pierre

Centroplacus Pierre, Bull. Mens. Soc. Linn. Paris II, 14: 144 (1899); Hutch., Fl. Trop. Afr. 6(1): 629 (1912); Webster, Ann. Missouri Bot. Gard. 81: 54 (1994); Radcl.-Sm., Gen. Euphorb. 78, fig. 8 (2001).

Dioecious trees; indumentum simple. Leaves 2-ranked, denticulate, eglandular; stipules minute, persistent. Inflorescences axillary, paniculate. Flowers unisexual, pedicellate; staminate flowers: sepals and petals 5, imbricate; disk extrastaminal, cupular, its lobes antepetalous; stamens 5, anthers basifixed, introrse, dehiscence oblique-apical; pollen oblate-spheroidal, 3-colporate, tectate-microperforate; pistillode columnar; pistillate flowers apetalous; disk annular; ovary 3-locular; ovules subapical, epitropous; stylodia spreading. Fruits septicidal and loculicidal capsules dehiscing from the base; columella 0. Seeds 1 per locule, carunculate, with black and shining testa, exotegmic cells flattened, elongate at right angles to mesotegmic fibres; cotyledons twice as long as radicle.

A single sp., *C. glaucinus* Pierre, rain forests of West Africa (Cameroon to Gabon).

2. *Bhesa* Buch.-Ham. ex Arn.

Bhesa Buch.-Ham. ex Arn., Edinb. New Philos. Soc. J. 16: 315 (1834); Simmons, this book series vol. VI: 41 (2004).

Buttressed trees, glabrous. Leaves spiral, conduplicate, entire; petioles ± pulvinate apically; stipules with colleters, almost encircling the stem, caducous. Inflorescence axillary, thyrsopaniculate to racemose. Flowers bisexual, 5-merous; calyx contorted; anthers extrorse or introrse; pollen spheroidal, 3-colporate, finely striate; disk lobed or not; ovary 2(1)-locular, ovules basal, erect, apotropous. Fruit capsular, fusiform or deeply 2-lobed, loculicidally dehiscent. Seeds with coloured, sheet-like aril; exotegmic cells fibrous.

Six spp., Indo-Malesia.

Selected Bibliography

Corner, E.J.H. 1976. See General References.

Forman, L.L. 1966. The reinstatement of *Galearia* Zoll. & Mor. and *Microdesmis* Hook.f. in the Pandanaceae, with appendices by C. R. Metcalfe and N. Parameswaran. Kew Bull. 20: 309–321.

Leandri, J. 1957. Notes systématiques sur les Euphorbiacées-Phyllanthées de Madagascar. Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 8: 205–261.

Nowicke, J.W. 1984. A palynological study of the Pandaceae. Pollen Spores 26: 31–42.

Pierre, P.J.L. 1894. Flore forestière de la Cochinchine. Vol. 3. Paris: Octave Doin.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

Stuppy, W. 1996. Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Dissert., Univ. Kaiserslautern.

Tokuoka, T., Tobe, H. 2001. Ovules and seeds in subfamily Phyllanthoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 114: 75–92.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. (2012). See General References.

Zhang, L.-B., Simmons, M.P. 2006. Phylogeny and delimitation of the Celastrales inferred from nuclear and plastid genes. Syst. Bot. 31: 122–137.

Chrysobalanaceae

Chrysobalanaceae R. Br. (1818), nom. cons.

G.T. Prance

Trees, shrubs or suffrutices. Leaves alternate, simple, margins entire, pinnately nerved; stipules small and caducous to large and persistent, sometimes adnate to petiole. Inflorescence racemose, paniculate or cymose. Flowers bracteate and usually with 2 prophylls, actinomorphic to zygomorphic, bisexual or rarely polygamous or unisexual, markedly perigynous; receptacle short to elongate-cylindrical, sometimes gibbous at base; disk always present, forming a lining to receptacle or an annular or shortly tubular structure at its mouth; sepals 5, imbricate; petals 5, imbricate, often unequal, rarely unguiculate, sometimes absent; stamens 2–100 (–300) inserted on margin of disk or basally adnate to it, forming a complete circle or unilateral in zygomorphic flowers; filaments free, connate at base or ligulately connate, included to far exserted; anthers dorsifixed, longitudinally dehiscent; ovary superior, inserted at base, middle or mouth of the receptacle, either unilocular with 2 ovules, or bilocular with 1 ovule in each loculus; ovules erect, epitropous with micropyle directed towards base; style filiform arising from receptacle at base of ovary; stigma distinctly or indistinctly 3-lobed. Fruit a dry or fleshy drupe; endocarp thin and bony to thick and woody, often with a special mechanism for seedling escape, often densely hairy within. Seed erect, almost exalbuminous; cotyledous plano-convex, fleshy, rarely ruminate; germination cryptocotylar or phanerocotylar.

A pantropical family with eighteen genera and 423 of the 531 spp. in the Neotropics, 56 in Africa and Madagascar, and 43 in Asia and the Pacific. Extending beyond the tropics with one species each into the southern U.S.A. and southern Brazil.

Vegetative Morphology. The majority of species of Chrysobalanaceae are leptocaul trees but there are also many savannah shrubs and understorey shrubs, especially in the genus *Hirtella*. At least six species are geoxylic suffrutices, one in Florida, two in the Cerrado region of Brazil and three (*Parinari capensis* and two species of *Magnistipula*) in southern Africa. Many species are tall trees of the rainforest canopy and a few, especially in *Parinari*, are emergents. A few species of *Dactyladenia* and *Hirtella* have scandent branches, but there are no lianas. Those species which have been studied exhibit the architectural model of Troll. Leaves are simple, alternate and usually medium sized, but very large in a few species (up to 50 cm long in *Licania gentryi*). There are frequently glands on the undersurface or on the petioles. Stipules are always present but sometimes very early caducous. They range from minute to quite large in some species of *Licania*, *Parinari* and *Magnistipula*. They are either axillary or, in many species of *Licania*, inserted on the lower portion of the petiole. Seven species of *Hirtella* section *Myrmecophila* have myrmecophilous inflations at the junction of the leaf lamina with the petiole. These are inhabited by ants of the genera *Allomerus*, *Azteca* or *Solenopsis*. *Magnistipula bimarsupiata* also has two small inflations at the base of the lamina, and some internodes are swollen and perforated. It also has the coarse hispid tomentum characteristic of ant plants. The trunks of tree species may be either cylindric or buttressed. The bark of most species chips into small fragments with a sharp metallic ring when hit with a machete, due to the presence of abundant silica grains.

Flower Structure. The flowers are actinomorphic with the ovary inserted at the base of the receptacle in *Chrysobalanus*, *Licania* and *Parastemon* (Fig. 4), and zygomorphic with the ovary inserted at the mouth or middle of the receptacle in the remaining genera (Fig. 5). The

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_5, © Springer-Verlag Berlin Heidelberg 2014

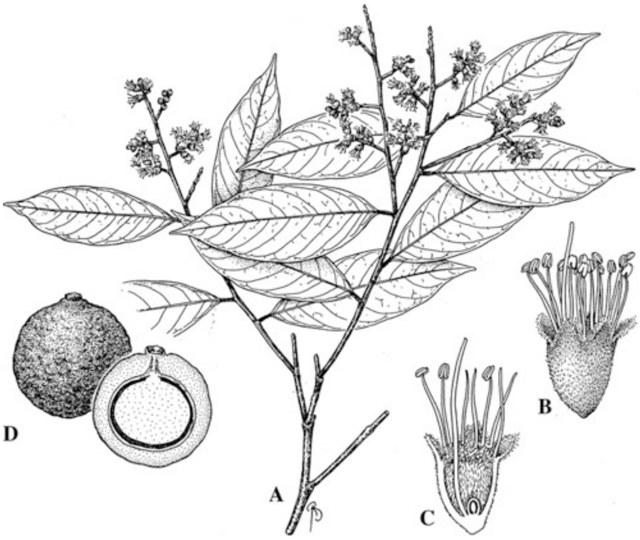

Fig. 4. Chrysobalanaceae. *Licania granvillei*. **A** Flowering branchlet. **B** Flower; note lack of corolla. **C** Medial section of flower showing gynobasic style. **D** Entire and sectioned fruit with attachment scar at top. (Reproduced with kind permission of the artist Bobbi Angell)

calyx is imbricate in bud, 5-lobed, entire; stipitate glands occur in some species of *Dactyladenia* and *Hirtella*. There are usually 5 free, imbricate petals, except in *Licania* subgenus *Licania* and section *Leptobalanus* which are apetalous. In a few species distinctly unguiculate petals occur, especially in *Kostermanthus* where the 2 posterior petals are larger and enclose the stamens in bud. Stamens range from 2 in *Parastemon* to over 300 in some species of *Couepia*. The filaments are usually distinct, but are connate into a unilateral, strap-like ligule in *Acioa*, *Dactyladenia* and *Kostermanthus*; they may be connate for up to half their length in a few species of *Licania* and in *Chrysobalanus*. The stamens may be inserted around a complete circle or unilateral, and the filaments either exserted or included. The anthers are dorsifixed and dehisce laterally. A disk is always present, forming a lining to the receptacle or an annular structure at its mouth. The ovary is superior and inserted at the base, middle or mouth of the receptacle, either unilocular with two ovules or bilocular with one tenuinucellate ovule in each loculus. The ovules are erect and epitropous, with the micropyle directed towards the base. The style is filiform and always arises from the base of the ovary (gynobasic); it usually equals or exceeds the stamens in length.

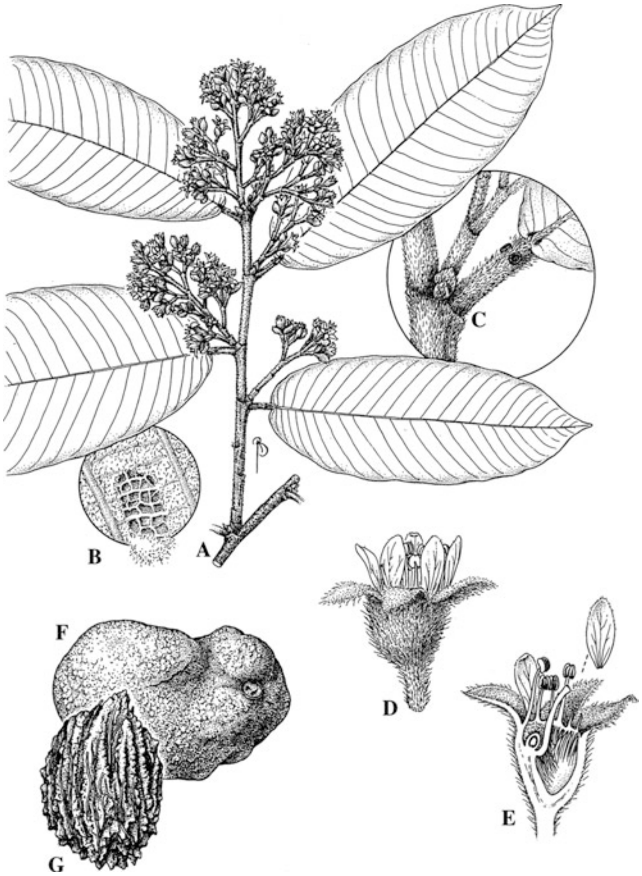

Fig. 5. Chrysobalanaceae. *Parinari montana*. **A** Flowering branchlet. **B** Abaxial leaf surface with part of woolly pubescence removed to show venation. **C** Stipulate node with glandular petiole and base of panicle with prophyll. **D** Flower. **E** Same, medial section, with perched gynoecium, cup-shaped hypanthium and petal. **F** Fruit with attached scar. **G** Seed with corrugated endocarp. (Reproduced with kind permission of the artist Bobbi Angell)

EMBRYOLOGY. The embryology was studied by Tobe and Raven (1984). The tetrasporangiate anthers have five-layered walls including a glandular tapetum with cells two-nucleate. Cytokinesis in the microspore mother cells is simultaneous. The nucellus is very small and the nucellar tissue soon disintegrates, except for the megaspore or embryo sac; antipodal cells are absent. The ovule is bitegmic; the inner integument (ii) and the outer integument (oi) are initiated dermally; the ii is up to five or eight cells thick and the oi more than five cells thick; the inner epidermis of the ii develops into the endothelium, which directly borders the embryo sac and accumulates starch grains; the micropyle is formed by both integuments. Endosperm formation is of the nuclear type and the seed is exalbuminous. The young seed coat is composed of both testa and tegmen.

POLLEN MORPHOLOGY. The pollen of Chrysobalanaceae is very uniform. The pollen is tricolporate but in some species four furrows may occur. There are no special features, excepting equatorial constrictions. The grains are usually distinctly triangular in shape in polar view, except when four-furrowed; they are elliptical to circular in equatorial view and are oblate-spheroidal, prolate-spheroidal or subprolate in shape. The polar length x 100 divided by the equatorial length = 85–150, but the size is quite variable from one genus to another; the polar area is usually small, sometimes medium, but never large. The exine is medium to rather thick with very little patterning on the walls, usually scabrous to verrucose. See Prance and White (1988), and also Barth and Silva (1963), Demchenko (1973), Patel et al. (1983).

KARYOLOGY. The chromosomes have been counted for nine species: $2n = 20$ in *Maranthes* and *Parinari* and $2n = 22$ in *Chrysobalanus*, *Dactyladenia* and *Licania* (Mangenot and Mangenot 1962; de Souza 1979).

POLLINATION. Chrysobalanaceae have a wide range of pollinators. The small-flowered genera *Chrysobalanus*, *Parinari*, *Exellodendron*, *Licania*, etc. are mainly pollinated by a wide variety of small bees. Most species of *Couepia* are night-flowering and are pollinated by hawk-moths, with the exception of the two flagelliflorous species *C. longipendula* and *C. dolichopoda* which are pollinated by bats (Vogel 1968–1969). *Maranthes polyandra* is also bat-pollinated (Lack 1978). *Hirtella* is mainly pollinated by butterflies, except for *H. rugosa* from the mountains of Puerto Rico. The bright red petals of this species do not open fully but form a tube, and it is hummingbird-pollinated. Hummingbirds have also been observed visiting the flowers of several other species of Chrysobalanaceae, especially *Couepia*, but are probably only secondary pollinators. Souza (1979) showed *Chrysobalanus icaco* to be self-compatible.

FRUIT AND SEED. The fruits of Chrysobalanaceae are always drupes and they are quite uniform, yet have become adapted to a wide range of dispersal agents. The fruit may be dry or fleshy, the endocarp thick or thin, fibrous or bony, often with a special mechanism for the seedling to escape, two basal obturators in *Parinari* and lateral plates in *Maranthes*, *Grangeria* and *Parastemon*. There are longitudinal lines of dehiscence in *Chrysobalanus* and *Hirtella*. The seed is erect, exalbuminous, with planoconvex fleshy cotyledons, and ruminate cotyledons in *Atuna*. *Chrysobalanus icaco* and several species of *Atuna* are dispersed by ocean currents. Several riverine species of *Licania* drop their fruit into rivers at flood time, and are eaten and presumably dispersed by fish. Various species including *Licania elaeosperma* and *Acioa guianensis* are water-dispersed by rivers. Species of *Couepia*, *Licania* and *Parinari* are frequently eaten by bats. *Licania splendens* is dispersed by the fruit pigeon, *Ducula aenea*. Various species of *Parinari* are known to be dispersed by bats, elephants, baboons and other primates, a scatter-hoarding squirrel, fruit pigeons, rheas, emus, agoutis and fish. Agoutis have been observed transporting the fruits of two species of *Couepia*. Most species of *Hirtella*, with their small fleshy fruits, are bird-dispersed. *Maranthes corymbosa* is dispersed by fruit pigeons and hornbills.

PHYTOCHEMISTRY. The chemistry of Chrysobalanaceae has been little studied, except for fatty acids in the seeds, including some quite unusual ones: α-elaeostearic acid (η-octadeca-9c, 11t, 13t-trienoic), α-licanic acid (4-keto-α-elaeostearic), α-parinaric acid (η-octadeca-9c, 11t, 13t, 15c tetraenoic) and 4-keto-α-parinaric acid. For details, see Table 2 in Prance and White (1988). As a result, there are several useful oils in Chrysobalanaceae (see section on Economic Importance below). Phenolics have been studied in a few species and the following compounds have been reported: myricetin, delphinidin, quercetin, cyanidin, kaempferol, quercitin 3-O-glycoside, naringenin 7-O-clycoside, quercetin aglycone (Gibbs 1974; Coradin et al. 1985). All species analysed contained kaempferol and quercetin, and only some contained myricetin.

SYSTEMATICS. Prance and White (1988) divided the family into four tribes. More recent molecular work (Yakandawala et al. 2010; C.A. Sothers, in prep.) does not support this tribal division, nor those of other earlier workers. Molecular data show the family as presented here to be a well-defined monophyletic group, but they did not support obvious tribal subdivisions. The tribes of Prance and White were found to be paraphyletic and are not recognised here.

AFFINITIES. Most early classifications regarded the Chrysobalanaceae as a subfamily of the Rosaceae. It is clearly different in terms of many features such as the gynobasic style, erect ovules and wood anatomy. Most later authors who treated Chrysobalanaceae as a family distinct from Rosaceae left it in Rosales. Dahlgren and Thorne (1984) questioned this placement without offering an alternative, but they suggested it might be useful to look at the Myrtales. Tobe and Raven (1984) showed that the embryology does not resemble that of Myrtales, and suggested Theales. Many other placements have been postulated on morphological grounds, including Linaceae, Polygalaceae, Limnanthaceae, Dichapetalaceae, Trigoniaceae, Geraniaceae, Tropaeolaceae, Sapindaceae, Rhizophoraceae, Vochysiaceae and Proteaceae. The Chrysobalanaceae do not even remotely resemble most of these families. However, molecular data suggested that Chrysobalanaceae are a member of Rosidae (rosid group 1) nearest to Trigoniaceae (Chase et al. 1993) in a clade that later became the broadly construed order Malpighiales (APG 1998). Further molecular multigene analyses placed Chrysobalanaceae into a well-supported clade including Chrysobalanaceae + Euphroniaceae and Trigoniaceae + Dichapetalaceae, with Balanopaceae basal to this clade (e.g. Davis and Chase 2004; Wurdack and Davis 2009), a grouping that (without *Balanops*) had been recognised by Hallier (1921) as Chrysobalanaceae (s. l.). The close relationship among these four families is also supported by important traits of their floral structure that have been revealed in the comparative study of Matthews and Endress (2008).

ECONOMIC IMPORTANCE. The fruits of many species are edible and are frequently used by local peoples. Those of *Chrysobalanus icaco* are tinned or bottled in Venezuela and Colombia under the name icacos. Various species of *Couepia*, especially *C. bracteosa* and *C. rufa*, are sold in local markets. Several species of *Parinari* have edible fruits or seeds, and charred kernels of a species of *Parinari* have been found at archaeological sites in Malawi. In Ambuina a dish called *koku koku* is prepared from the mashed seeds of *Atuna excelsa* mixed with fish, ginger, onions, etc. A cooking oil is extracted locally in Amazonia from *Acioa edulis* and *Couepia longipendula*. The oil of *Licania rigida* and *Afrolicania elaeosperma* was formerly used in paints and varnishes as a substitute for tung oil, and *L. arborea* produces a flammable oil which was used for lighting by local people in Mexico. The wood of Chrysobalanaceae is extremely hard to work due to the presence of silica. It has many local uses, especially for marine and river pilings because of its resistance to marine borers. Some species are used locally for fuel and charcoal. Throughout Amazonia the bark of various species of *Licania* and *Couepia* is burnt and the ash mixed with clay to strengthen pottery because of the silica granules. In the Solomon Islands the seeds of *Atuna excelsa*, known as putty nut, is used for caulking boats. The oil from the seed of the same species is used as a hair dressing in the Caroline Islands and as a massage oil in Samoa and Tonga. In Brazil, *Couepia subcordata* and *Licania tomentosa* commonly serve as shade trees.

CONSERVATION. Many species of Chrysobalanaceae are of extremely restricted distribution and grow in highly threatened areas such as the Atlantic coastal forest of Brazil or the lowland forest of Western Ecuador, and are therefore potentially threatened with extinction. The genus *Grangeria* of two species in Madagascar and the Mascarenes must be one of the most endangered, and the states of the monotypic genera *Bafodeya* and *Neocarya* from West Africa is critical.

KEY TO THE GENERA

1. Ovary inserted at or near base of receptacle 2
– Ovary inserted laterally at or near mouth of receptacle 5
2. Endocarp with distinct longitudinal ridges corresponding with lines of dehiscence **5. *Chrysobalanus***
– Endocarp without longitudinal ridges, indehiscent or with two lateral plates 3
3. Flowers unisexual (Africa) **2. *Afrolicania***

– Flowers bisexual (South America and Malesia) 4

4\. Endocarp without lateral plates which allow seedling to escape **13. *Licania***

– Endocarp dehiscing on germination by means of a pair of large lateral plates **16. *Parastemon***

5\. Endocarp with two small basal plugs (obturators); lower leaf surface usually with stomatal crypts 6

– Endocarp without two basal plugs but sometimes germinating by means of two large lateral plates; leaf lower surface rarely with stomatal crypts 7

6\. Receptacle turbinate-campanulate; fertile stamens 6–8 **17. *Parinari***

– Receptacle saccate; fertile stamens 12–17 **18. *Neocarya***

7\. Stamens far exserted beyond calyx lobes 8

– Stamens not or barely exceeding calyx lobes 14

8\. Stamens united into a ligule 9

– Stamens free to base or nearly so, not ligulate 11

9\. Sepals very unequal in size, 3 large, 2 very small, the outer sepals with 1 or 2 large discoid glands **1. *Acioa***

– Sepals subequal, without discoid glands on surface 10

10\. Two posterior petals unguiculate, enclosing stamens in bud **12. *Kostermanthus***

– Posterior petals not unguiculate **7. *Dactyladenia***

11\. Ovary bilocular 12

– Ovary unilocular 13

12\. Fruit dehiscing by two lateral plates; cotyledons not ruminate; exocarp smooth **15. *Maranthes***

– Fruit with no lateral plates; cotyledons ruminate; exocarp warted crustaceous **3. *Atuna***

13\. Stamens 3–9; fruit dehiscing by longitudinal lines; endocarp thin, bony **10. *Hirtella***

– Stamens 15–300; fruit indehiscent; endocarp thick, fibrous **6. *Couepia***

14\. Ovary unilocular 15

– Ovary bilocular 16

15\. Receptacle symmetrical; fruit dehiscing by two lateral plates **9. *Grangeria***

– Receptacle gibbous; fruit indehiscent **14. *Magnistipula***

16\. Leaf undersurface with stomatal cavities; fruit exocarp sparsely lenticellate; receptacle much swollen to one side **4. *Bafodeya***

– Leaf undersurface glabrous or arachnoid pubescent; receptacle symmetrical or only slightly swollen to one side 17

17\. Endocarp opening by lines of weakness which allow seedling to escape **11. *Hunga***

– Endocarp without lines of weakness 18

18\. Receptacle markedly asymmetrical; endocarp thick, hard and bony, not ridged at base **14. *Magnistipula***

– Receptacle only slightly swollen to one side; fruit with hard, bony endocarp thin, with a ridge on one side at the base **8. *Exellodendron***

GENERA OF CHRYSOBALANACEAE

1. *Acioa* Aubl.

Acioa Aubl., Hist. Pl. Guiane 2: 698, t. 280 (1775).

Trees or shrubs. Leaves with 1 or 2 pairs of conspicuous glands at base of lamina and several smaller discoid glands, glabrous on lower surface. Inflorescence a rather lax thyrse with flattened axes; bracts and prophylls not enclosing flower buds, eglandular; receptacle obconic and slightly curved or cyathiform, glabrous within; petals 5, exceeding sepals; stamens 10–20, ligulately connate or free, unilateral, glabrous; ovary unilocular, inserted at mouth of receptacle. Fruit without any special mechanism to allow seedling to escape; endocarp thick, hard, fibrous. Germination phanerocotylar, first two eophylls opposite, otherwise alternate.

Four spp. in Venezuela, the Guianas and Amazonian Brazil.

2. *Afrolicania* Mildbr.

Afrolicania Mildbr., Notizbl. Bot. Gart. Berlin-Dahlem 7: 483 (1921).

Small to medium-sized tree. Leaves usually glabrous, with two glands on petiole. Inflorescence many-flowered terminal and subterminal panicle of racemes; bracts small, membranous, eglandular. Flowers polygamous andro-dioecious; receptacle flattened-turbinate, pubescent within; petals absent; stamens ca. 20, around complete circle, included, free; ovary unilocular, inserted at base of receptacle, absent in male flowers but represented by a slight swelling. Fruit a dry drupe, epicarp warted, without a mechanism for seedling escape. Germination cryptocotylar, eophylls alternate.

One sp., *A. elaeosperma* Mildbr., widespread in W and W Central Africa from Sierra Leone to Gabon.

3. *Atuna* Rafin.

Atuna Rafin., Sylva Tellur.: 153 (1838).

Trees. Leaves with a pair of glands on the midrib at or near base of lower surface, glabrous on lower surface. Inflorescence a raceme or a sparsely branched contracted panicle; bracts and prophylls not enclosing flower buds in groups, eglandular; receptacle obconic, pubescent throughout within; petals 5, shorter than sepals; stamens 10–25; filaments distinct, far exceeding sepals, glabrous, unilateral, tiny denticulate staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit without any mechanism for seedling to escape; endocarp hard and thick, cotyledons strongly ruminate. Germination cryptocotylar, eophylls alternate.

Eight spp. from southern India eastwards to Samoa, and most abundant in the Malay Peninsula, Borneo and Indonesia.

4. ***Bafodeya*** Prance

Bafodeya Prance in F. White, Bull. Jard. Bot. Nat. Belg. 46: 271 (1976).

Small trees. Leaves with stomatal crypts filled with densely matted hairs on lower surface, eglandular. Inflorescence a terminal cymose panicle; bracts and prophylls not enclosing flower buds, eglandular; receptacle obliquely campanulate, markedly zygomorphic, much swollen to one side, pubescent within; petals 5, equalling sepals; stamens ca. 7; filaments more or less equalling sepals, unilateral with 4–10 staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit without special mechanism for seedling to escape; endocarp hard, thin, smooth.

A single sp., *B. benna* (Scott Elliot) Prance, in W Africa in Sierra Leone and adjacent Guinea.

5. ***Chrysobalanus*** L.

Chrysobalanus L., Gen. pl.: 365 (1737); Sp. pl.: 513 (1753).

Shrubs to large trees. Leaves glabrous, usually with two or more glands on lower surface. Inflorescence a few-flowered short raceme of cymules or cymose or a subsessile fascicle; bracts and prophylls not enclosing flower buds, eglandular; receptacle cupuliform, pubescent within; petals 5, longer than sepals; stamens 12–26, filaments ± twice as long as sepals, slightly united in groups at base, around complete circle, hairy; ovary unilocular, inserted at base of receptacle. Fruit longitudinally ridged, with lines of fracture that allow the seedling to escape, endocarp thin and bony. Germination cryptocotylar, eophylls alternate. $2n = 22$.

Three spp., one widespread in tropical Africa, America and the Caribbean, one endemic to the West Indies, and one in submontane forests of Venezuela.

6. ***Couepia*** Aubl.

Couepia Aubl., Hist. Pl. Guiane 1: 519, t. 207 (1775); Prance, Fl. Neotrop. 9: 202 (1972).

Trees or shrubs. Leaves often with 1 or 2 pairs of glands at base of lamina, sometimes with several small marginal glands especially near apex, glabrous or arachnoid pubescent beneath or rarely with stomatal crypts. Inflorescence most often a congested thryse or raceme, rarely flowers solitary or densely crowded in a long-pedunculate compound corymb; bracts and prophylls usually not enclosing buds in small group, eglandular; receptacle turbinate to narrowly cylindric, usually glabrous inside except at throat, hairy throughout in a few species; petals 5, more or less equalling sepals; stamens 15–100 or rarely more; filaments far exceeding sepals, free, glabrous, usually forming a complete circle less frequently unilateral. Ovary unilocular, inserted at mouth of receptacle. Fruit without any mechanism to allow seedling to escape; endocarp hard, thick, granular. Germination cryptocotylar, eophylls alternate.

Seventy one spp., all neotropical, ranging from Mexico to S Brazil, but most abundant in the Guianas and Amazonia.

7. ***Dactyladenia*** Welw.

Dactyladenia Welw., Apont., Ann. Cons. Ultram. 1: 572 (1859); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 133–145 (1988), rev.

Small trees or shrubs occasionally scandent. Leaves glabrous or with stiff appressed hairs, rarely with lanate arachnoid pubescence beneath. Inflorescence a raceme or a panicle of racemes, rarely a subcapitate spike; bracts and prophylls not enclosing flower buds, often with stalked or sessile glands; receptacle elongate cylindrical to obconic-tubular, glabrous within except at throat; sepals more or less equal; petals 5, equalling sepals; stamens 10–75, far exceeding calyx lobes, filaments united into a ligule for most of length, unilateral with short staminodes opposite; ovary unilocular, inserted at mouth of receptacle. Fruit with no plates or lines of dehiscence, endocarp thin and hard. Germination cryptocotylar, eophylls opposite. $2n = 22$.

Thirty spp. in tropical Africa, mostly in the Guineo-Congolian region.

8. ***Exellodendron*** Prance

Exellodendron Prance, Fl. Neotrop. 9: 195, t. 31–32 (1972).

Trees or shrubs. Leaves with a pair of small glands or ill-defined glandular areas on upper surface at junction with petiole, glabrous or lanate pubescent beneath. Inflorescence a simple or branched raceme of small, congested cymes; bracts and prophylls not enclosing flower buds, eglandular; receptacle subcampanulate, slightly swollen on one side, pubescent within; petals 5, equalling sepals; stamens ca. 7; filaments equalling sepals, free, glabrous; ovary bilocular, inserted at mouth of receptacle tube. Fruit without any mechanism for seedling to escape; endocarp thin, smooth, bony.

Five spp. in Amazonia, the Guianas, central and eastern Brazil.

9. ***Grangeria*** Commerson ex Juss.

Grangeria Commerson ex Juss., Gen. pl.: 340 (1789).

Trees or shrubs. Leaves glabrous. Inflorescence a simple, or rarely branched axillary or terminal raceme, bracts and prophylls not enclosing flower buds, often with a single apical gland; receptacle obliquely turbinate, slightly asymmetric, glabrous within; petals 5, slightly shorter than sepals; stamens 7–8 or 15; filaments slightly exceeding sepals, glabrous, distinct, inserted around complete circle or unilateral; ovary unilocular, inserted laterally at mouth of receptacle. Fruit with two large lateral plates which break away on germination and allow endocarp to escape; endocarp thin and bony.

Two spp., one in Mauritius and Réunion, the other in Madagascar.

10. ***Hirtella*** L.

Hirtella L., Sp. pl.: 34 (1753); Prance, Fl. Neotrop. 9: 259 (1972).

Trees or shrubs. Leaves glabrous or with strigose hairs or hirsute, occasionally with 2 large myrmecophilous swellings at base. Inflorescence raceme, thyrse, corymb or panicle; bracts and prophylls with sessile or stipitate glands or eglandular not enclosing flower buds in groups; receptacle subcampanulate to narrowly cylindrical, glabrous within except at throat; sepals usually almost equal; petals 5, not exceeding sepals; stamens 3–9, filaments far exserted, free, glabrous, usually unilateral with short staminodes opposite; ovary unilocular, inserted at mouth of receptacle. Fruit fleshy, usually with longitudinal lines of dehiscence, endocarp thin, bony. Germination cryptocotylar cataphylls ca. 5, minute, eophylls alternate.

107 spp. in tropical America from Mexico to S Brazil, and one sp. in E Africa and Madagascar.

11. ***Hunga*** Pancher ex Prance

Hunga Pancher ex Prance, Brittonia 31: 79 (1979).

Shrubs or small trees. Leaves with a pair of often obscure marginal glands towards base, lower surface glabrous or lanate pubescent. Inflorescence a few-flowered terminal or axillary raceme of cymules; bracts and prophylls not enclosing flower buds, eglandular; receptacle subcampanulate, slightly asymmetric, pubescent within; petals 5, not exceeding sepals; stamens 5–9, filaments shorter than calyx lobes, free, unilateral, glabrous, ovary bilocular, inserted midway up receptacle. Fruit bilocular, with 4–6 longitudinal lines of weakness which allow seedling to escape; endocarp thin, hard, bony.

Eleven spp., three of which occur in Papua New Guinea and eight in New Caledonia and the Loyalty Islands.

12. ***Kostermanthus*** Prance

Kostermanthus Prance, Brittonia 31: 91 (1979).

Large trees. Leaves glabrous and papillate beneath. Inflorescence an unbranched or little-branched terminal or axillary raceme bearing congested cymules proximally and solitary flowers distally; bracts and prophylls eglandular, not enclosing flower buds; receptacle broadly obconic, asymmetric, hairy within, sepals 5, markedly unequal; petals 5, exceeding calyx lobes, markedly unequal, 2 posterior ones larger, unguiculate, enclosing stamens in bud; stamens 30–75, far exceeding calyx lobes, filaments united into a ligule for ¾ length, unilateral with opposite staminodes; ovary unilocular, inserted at mouth of receptacle. Fruit with no lines or plates of dehiscence; endocarp thick, hard. Cotyledons slightly ruminate.

Three spp. in Malesia from the Malay Peninsula to Sulawesi.

13. *Licania* Aubl. Fig. 4

Licania Aubl., Hist. Pl. Guiane 1: 119, t. 45 (1775); Prance, Fl. Neotrop. 9: 21 (1972).

Large to small trees, shrubs or rarely suffruticose. Leaves glabrous, lanate, pulverulent or with stomatal crypts on lower surface. Inflorescence most frequently a panicle of racemes, less often a simple raceme, a spike, a glomerule or a branched panicle of shortly stalked cymules; bracts and prophylls not enclosing flower buds except in *L. licaniiflora*, eglandular; receptacle variable in shape, usually campanulate, cupuliform or urceolate, rarely turbinate or patelliform, always pubescent within; petals either 5, equalling sepals, or absent; stamens 3–40, filaments included to far exceeding sepals, usually glabrous, free in most species, rarely united for half length in groups, usually glabrous, rarely hairy; ovary unilocular, inserted at or near base of receptacle. Fruit with no plates or lines of dehiscence, endocarp thick, hard and woody or thin and fibrous. Germination cryptocotylar, eophylls alternate. $2n = 22$ in two species counted.

218 spp., all but 4 of which are American largely in lowland tropical South America but extend north to Mexico, Florida and (*L. mixauxii*) the Gulf states of the U.S.A., and two in the Malesian region.

14. *Magnistipula* Engl.

Magnistipula Engl., Bot. Jahrb. 36: 226 (1905); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 152–162 (1988).

Trees, shrubs or suffrutices. Leaves glabrous or with few strigose hairs beneath. Inflorescence a simple or branched raceme of cymules or rarely a raceme or sessile glomerule; bracts and prophylls not enclosing flower buds, eglandular or with 1 or 2 pairs of sessile glands or with shortly stipitate glands; receptacle usually curved and gibbous at base, rarely turbinate or campanulate, hairy within; sepals 5, unequal; petals 5, exceeding sepals; stamens 7–9 scarcely exceeding sepals, united towards base, unilateral with staminodes opposite; ovary usually unilocular, bilocular in 1 sp., inserted at mouth of receptacle. Fruit fleshy, with no plates or lines of dehiscence; endocarp usually thin and fibrous, rarely thick and woody. Germination cryptocotylar, cataphylls absent, eophylls opposite or in fours.

Twelve spp. in Africa and Madagascar.

15. *Maranthes* Blume

Maranthes Blume, Bijdr. Fl. Nederl. Ind.: 89 (1825); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 121–129 (1988), rev.

Trees. Leaves with a pair of glands at the junction of the lamina and petiole, glabrous or arachnoid pubescent on lower surface. Inflorescence usually a many-flowered corymbose panicle, rarely a lax few-flowered thryse or a raceme of few-flowered monochasial cymes; bracts and prophylls not enclosing flower buds, eglandular; receptacle obconical, slightly to strongly curved, nearly always solid and almost completely filled by nectariferous tissue, glabrous or glabrous on one side and hairy on the other within; petals 5, more or less equalling sepals; stamens 20–60; filaments free, glabrous, inserted around complete circle, far exceeding sepals in length, usually in a tangled mass; ovary bilocular, inserted at mouth of receptacle. Fruit with two lateral plates which break away on germination to allow seedlings to escape; endocarp very hard, thick, with a rough fibrous exterior. Germination phanerocotylar, first 2 eophylls opposite, the others opposite or alternate. $2n = 20$.

Twelve spp., 10 of which occur in tropical Africa, one each in tropical America (Nicaragua to Panama) and Malesia.

16. *Parastemon* A.DC.

Parastemon A.DC., Ann. Sci. Nat. Bot. II, 18: 208 (1842).

Trees or shrubs. Leaves glabrous, with two small discoid glands at base of lamina. Inflorescence and axillary or rarely terminal simple or little-branched raceme; bracts and prophylls not enclosing flower buds, eglandular; receptacle patelliform or shallowly cupuliform, pubescent within; petals 5, more or less equalling sepals;

stamens 5 around circle or 2 with 3 staminodes opposite; filaments glabrous, free, much shorter than sepals; ovary unilocular, inserted at base of receptacle. Fruit with 2 large lateral plates which break away on germination to allow seedlings to escape; endocarp thin, hard, bony. Germination cryptocotylar, first eophylls opposite.

Three spp. from the Nicobar Islands and the Malay Peninsula to New Guinea.

17. *Parinari* Aubl. Fig. 5

Parinari Aubl., Hist. Pl. Guiane 1: 514, t. 204–206 (1775); Prance, Fl. Neotrop. 9: 178 (1972); Prance & White, Philos. Trans. Roy. Soc. London B, 320: 110–112 (1988), Afr. spp.

Small to large trees or more rarely shrubs or suffruticose. Leaves with two discoid glands on upper surface of petiole and often with small marginal glands along entire length of lamina, usually with stomatal crypts filled with densely matted hairs on lower surface or rarely in two Malesian species glabrous. Inflorescence a many-flowered complex cyme or cymose panicle; bracts and prophylls enclosing small groups of flower buds, eglandular; receptacle subcampanulate, slightly swollen to one side, pubescent within; petals 5, equalling or shorter than sepals; stamens 6–10; filaments shorter than sepals, free, glabrous, unilateral with ca. 6 minute subulate staminodes opposite; ovary bilocular, inserted at mouth of receptacle. Fruit with 2 basal obturators which allow seedling to escape; endocarp thick, hard, with a rough fibrous surface.

Thirty-nine species, pantropical with 19 in tropical America, 6 in tropical Africa and 15 in tropical Asia and the Pacific region extending to Fiji, Tonga and Samoa.

18. *Neocarya* Prance

Neocarya Prance in F. White, Bull. Jard. Bot. Nat. Belg. 46: 308 (1976).

Shrubs or small trees. Leaves with several small, sessile glands near base of lamina, with stomatal crypts filled with densely matted hairs on lower surface. Inflorescence a terminal raceme of almost sessile cymules, sometimes unbranched but more frequently with one or more short to elongate branches at base; bracts and prophylls enclosing one or more flower buds, eglandular; receptacle asymmetric, saccate, gibbous, with reflexed hairs at throat, glabrous towards base within; stamens 12–17; filaments slightly exceeding sepals, unilateral with ca. 6 toothed staminodes opposite; ovary bilocular, inserted at mouth of staminal tube. Fruit with 2 basal obturators which allow seedling to escape; endocarp thick, hard, with a rough fibrous surface. Germination cryptocotylar.

A single species, *N. macrophylla* (Sabine) Prance, in W Africa from Senegal to Liberia.

Selected Bibliography

APG (The Angiosperm Phylogeny Group) 1998. See General References.

Barth, O.M., Silva, A.F. 1963. Catálogo sistemático dos polens das plantas arbóreas do Brasil meridional. IV. Cunoniaceae, Rosaceae e Connaraceae. Mem. Inst. Oswaldo Cruz 61: 411–427.

Chase, M.W. et al. 1993. See General References.

Coradin, L., Giannasi, D.E., Prance, G.T. 1985. Chemosystematic studies of the Chrysobalanaceae. I. Flavonoids in *Parinari*. Brittonia 37: 169–178.

Dahlgren, R., Thorne, R.F. 1984. The order Myrtales: circumscription, variation and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

Davis, C.C., Chase, M.W. 2004. See General References.

Demchenko, N.I. 1973. The pollen morphology of the family Chrysobalanaceae. In: Pollen and spore morphology of recent plants (Proc. 3rd Int. Palynol. Conf. Acad. Sci. USSR.), pp. 60–73. (In Russian).

Gibbs, R.D. 1974. Chemotaxonomy of flowering plants. Vols 1–4. Montreal, London: McGill-Queens University Press.

Hallier, H. 1921. See General References.

Lack, A. 1978. The ecology of the flowers of the savanna tree *Maranthes polyandra* and their visitors, with particular reference to bats. J. Ecol. 66: 287–295.

Mangenot, S., Mangenot, G. 1962. Enquête sur les nombres chromosomiques dans une collection d'espèces tropicales. Rev. Cytol. Biol. Vég. 25: 411–447.

Matthews, M.L., Endress, P.K. 2008. See General References.

Patel, V.C., Skvarla, J.J., Raven, P.H. 1983. Pollen ultrastructure of Chrysobalanaceae. Vidya 26: 1–10.

Prance, G.T. 1972. Flora Neotropica, monograph no. 9 (Chrysobalanaceae). 409 pp. New York: Hafner.

Prance, G.T. 1979. Chrysobalanaceae. Flora of Ecuador (eds. G. Harling & B. Sparre), vol. 10, pp. 1–23.

Prance, G.T. 1979. New genera and species of Chrysobalanaceae from Malesia and Oceania. Brittonia 31: 79–95.

Prance, G.T. 1982. Chrysobalanaceae. Flora de Venezuela, vol. 4(2), pp. 325–482. Carácas: Ediciones Fundación Educación Ambiental.

Prance, G.T. 1983. Chrysobalanacées. Flore da la Nouvelle-Calédonie et dépendances, vol. 12, pp. 105–123. Paris: Muséum national d'Histoire naturelle

Prance, G.T.1988. Flora Neotropica, monograph no. 9 (supplement). New York: The New York Botanical Garden.

Prance, G.T. 1989. Chrysobalanaceae. Flora Malesiana Ser. 1.10: 635–678.

Prance, G.T., Sothers, C.A. 2003. Chrysobalanaceae 1: *Chrysobalanus* to *Parinari*. Species Plantarum: Flora of the World Part 9: 1–319.

Prance, G.T., Sothers, C.A. 2003. Chrysobalanaceae 2: *Acioa* to *Magnistipula*. Species Plantarum: Flora of the World Part 10: 1–268.

Prance, G.T., White, F. 1988. The genera of Chrysobalanaceae: a study in practical and theoretical taxonomy and its relevance to evolutionary biology. Philos. Trans. Roy. Soc. London B, 320: 1–148.

Souza, S. de 1979. Contribution à l'étude biologique et écologique de quelques Chrysobalanacées des genres *Chrysobalanus*, *Parinari* et *Maranthes* au Bénin. Thesis, Université de Bordeaux III.

Tobe, H., Raven, P.H. 1984. An embryological contribution to systematics of the Chrysobalanaceae. I. Tribe Chrysobalaneae. Bot. Mag. Tokyo 97: 397–411.

Vogel, S. 1968–1969. Chiropterophilie in der neotropischen Flora. Flora (Abt. B) 157: 562–602 (1968); 158: 289–323 (1969).

White, F. 1976. The taxonomy, ecology and chorology of African Chrysobalanaceae (excluding *Acioa*). Bull. Jard. Bot. Nat. Belg. 46: 265–350.

White, F. 1976. Chrysobalanaceae. Distributiones plantarum africanarum, vol. 10, maps 281–334.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Yakandawala, D., Morton, C., Prance, G.T. 2010. Phylogenetic relationships of the Chrysobalanaceae inferred from chloroplast, nuclear and morphological data. Ann. Missouri Bot. Gard. 97: 259–281.

Ctenolophonaceae

Ctenolophonaceae Exell & Mendonça (1951).

K. Kubitzki

Buttressed trees with simple and stellately tufted hairs on young shoots, stipules, and the outside of sepals and petals. Leaves opposite, petiolate, entire, simple, pinnately veined; stipules interpetiolar, caducous. Inflorescences thyrso-paniculate, axillary or terminal; bracts present, prophylls 0. Flower buds elongate-ellipsoid; flowers hypogynous, bisexual, 5-merous, diplostemonous, regular, hypogynous; sepals basally shortly connate, quincuncially imbricate, subequal, indurate, swollen and persistent in fruit; petals contorted, caducous, spoon-shaped at the base and often shortly clawed; disk well developed, extrastaminal, cup-like; stamens 10, inserted on inner side of the disk and basally connate into an androecial tube, dorsally surrounded by a 10-lobed corona-like tube; antepetalous stamens shorter than antesepalous ones; anthers dorso-versatile, 2-celled, introrse; connective protruding, acute-triangular; gynoecium syncarpous, 2-carpellate; ovary 2-celled; ovules 2 per cell, axile, collateral, pendant, anatropous, epitropous, bitegmic; style simple, apically ± cleft with 2 capitate stigmas; ovary tube joining near its base the androecial tube to form a short androgynophore. Fruit a 1-celled capsule, the woody pericarp eventually splitting lengthwise into 2 valves. Seed solitary, persisting after falling of the pericarp and pendulous from the top of a filiform columella; aril pectinate-fimbriate, surrounding the lower half of the seed; endosperm copious; embryo straight.

Monogeneric, probably with 2 extant spp., *C. englerianus* Mildbr. in West Africa, *C. parvifolius* Oliv. from Malay Peninsula to New Guinea.

Vegetative Anatomy. *Ctenolophon* differs from its presumed allies in possessing tufted hairs, stellate in appearance, which are found on young vegetative and mature floral parts, and anomocytic to anisocytic stomata. The simple arc of collateral vascular tissue in the midrib and petiole, the scattered occurrence of cristarque cells (crystalliferous cells with a unilaterally thickened and lignified cell wall), and crystals and druses are of a more common occurrence (van Welzen and Baas 1984).

In the secondary xylem, the vessels are exclusively solitary; perforation plates are predominantly scalariform with numerous thick bars; axial parenchyma is paratracheal-abaxial; wood rays are uniseriate, of upright cells, and multiseriate heterogeneous,

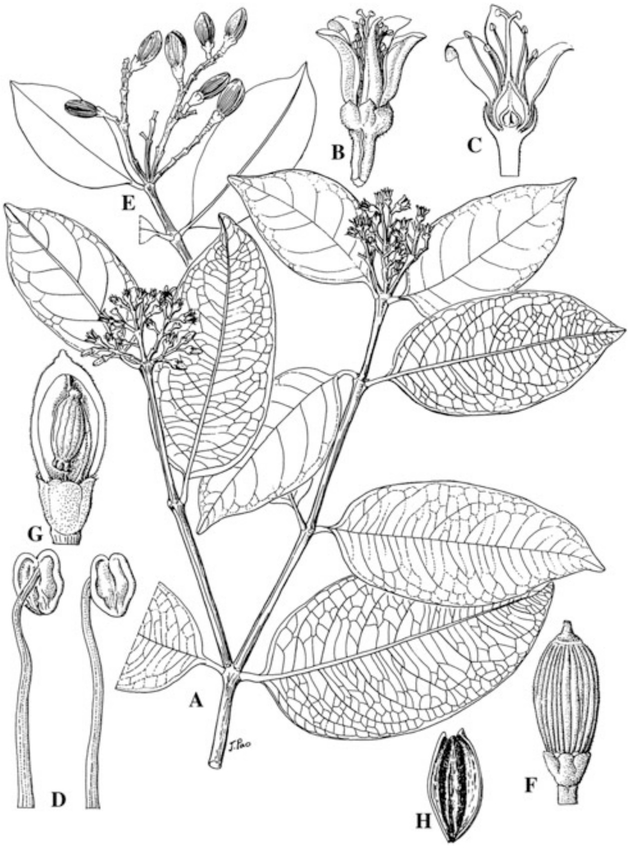

Fig. 6. Ctenolophonaceae. *Ctenolophon parviflorus*. **A** Flowering branchlet. **B** Flower. **C** Same, longitudinal section. **D** Stamens. **E** Fruiting twig. **F** Fruit. **G** Same, longitudinal section. **H** Seed. (Pungga 1996; drawn by J. Pao)

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_6, © Springer-Verlag Berlin Heidelberg 2014

up to 3 cells wide; fibre tracheids have conspicuously bordered pits; solitary crystals occur in chambered parenchyma and ray cells (Heimsch and Tschabold 1972). The heartwood of *C. parvifolius* is reddish to brown, very hard, and heavier than water.

FLOWER STRUCTURE. The flowers of *Ctenolophon* are tubular, as the petals bend outwards only apically. In bud (and later?) the overlapping portions of the petals are postgenitally connected by the indumentum of their dorsal surfaces and margins. In *C. parvifolius* the petals are white to yellow, orange or bright red (van Hooren and Nooteboom 1988). The stamens are basally connate into an androecial tube and are surrounded by a tubular disk, which distally extends into ten lobes that alternate with the stamens (the corona of Matthews and Endress 2011). The disk surrounds the ovary up to three quarters of its height. As the petals bend outwards only apically, the floral tube can retain large amounts of nectar. The tissue of the disk is formed by thin-walled, typical adenoid cells. Close to the margin of both sides of the disk, numerous open anomocytic stomata are diffusely distributed, which may function in the release of the nectar (Link 1992). Due to partial disintegration of the thin septa, the ovary becomes partly unilocular. The ovules have a distinct endothelium (Matthews and Endress 2011).

POLLEN MORPHOLOGY. Pollen morphology of *Ctenolophon* has been studied by, among others, Thanikaimoni et al. (1984) and van der Ham (1989). The pollen is typically zonocolporate, the number of apertures ranging from 3–9. Two main pollen types can be distinguished, which by and large correspond to the two extant species. The parvifolius type has 3–8 apertures and is subspheroidal, whereas the englerianus type has 6–9 apertures and exhibits distinct ridges on the mesocolpia that extend to the polar area, where they fuse into a ring and make the pollen grains characteristically angular and barrel-shaped. Equatorial size ranges from 31 to 66 µm; the thickness of the exine ranges from 3–6 µm, and its stratification is obscure under the light microscope and difficult to determine. The infratectal layer appears labyrinthic and sometimes exhibits granular-columellate structures. The tectum is perforate to foveolate in the parvifolius type, and psilate or finely perforate in the englerianus type. *Ctenolophon* from the Philippines classified as *C. parvifolius* or "*C. philippinensis*" has been found to exhibit a sculpture similar to that of the englerianus type (Thanikaimoni et al. 1984; van der Ham 1989).

Saad (1962) pointed to pollen morphological similarities between *Ctenolophon* and the Malpighiaceae which, however, appeared superficial to van der Ham (in van Hooren and Nooteboom 1988).

POLLINATION. The bright petals and well-developed nectary disk indicate that *Ctenolophon* is entomophilous.

FRUIT AND SEED. The fruit of *C. parvifolius* is yellow to pink and later brown, the seed brown or glossy black, and the aril white to orange or brilliant vermilion. Seeds are exotegmic; the embryo is folded (Boesewinkel and Bouman 2000).

AFFINITIES. *Ctenolophon* had been referred to various families including Oleaceae, Icacinaceae and Celastraceae, until Pierre (1893) suggested a relationship with Linaceae. Winkler (1931) included in it *Ctenolophon* as a subfamily, together with Ixonanthoideae and Humirioideae. These subfamilies have since been elevated to the rank of family; among them, *Ctenolophon* has been considered close to Linaceae s.str., with which it shares the extrastaminal disk. Link (1992) stressed the similarities between Humiriaceae and *Ctenolophon*, particularly the perianth structure, the broadened and markedly elongate anther connectives, and the histology of the disk, including the presence of the marginally distributed nectarial stomata. In this context it appeared less important to him whether the disk is intrastaminal (Humiriaceae) or extrastaminal (*Ctenolophon*), or the filament bases are adnate to the disk (*Ctenolophon*) or distinct (Humiriaceae). Matthews and Endress (2011) identified important structural traits uniting *Ctenolophon*, Rhizophoraceae and Erythroxylaceae. These groups have also been retrieved as a clade [Ctenolophonaceae [Rhizophoraceae + Erythroxylaceae]] by Wurdack and Davis (2009) and Xi et al. (2012).

DISTRIBUTION AND HABITATS. *Ctenolophon englerianus* is known from West Africa, where it grows in riverine forests. *C. parvifolius* is distributed in Malesia from the Malay Peninsula to New Guinea, and grows in primary forest but also swamp and heath forest on a wide variety of soils over peat, sandstone and ultrabasic rocks, commonly in lowland and hill regions and in Borneo up to 1,650 m.

PALAEOBOTANY. The fossil record of *Ctenolophon* is extensive and starts in the Maastrichtian of Central Africa with pollen of the englerianus type, which through a nearly uninterrupted record can be linked with the Recent African distribution of *C. englerianus*. This pollen type is recorded also from the Palaeocene and Eocene of northern South America and the Eocene and Miocene of India but disappeared from these regions in the course of the Tertiary (Krutzsch 1989). The parvifolius type first appeared in the Palaeocene of Africa, but continued there only to the early Eocene. In India (Kutch) it appeared in the early Palaeocene, from where it spread in the course of the Tertiary all over India and, in the Miocene with up to 9 pollen types, attained its greatest diversity (Kar 1985). Erdtman (1955) first described and characterised the fossil pollen from this region. In the course of the Eocene, the parvifolius type became established in Southeast Asia/Malesia, again being linked with the distributional area of its extant name-giving species. Thanikaimoni et al. (1984) and van der Ham (1989) have discovered that populations of *C. parvifolius* from the Philippines exhibit pollen that resembles the pollen of the englerianus type, giving rise to the suggestion (W. Krutzsch, pers. comm., Nov. 2003) that the ridges of the englerianus type pollen are plesiomorphic and have been lost on the pollen grains of *C. parvifolius*, which is supported by rudimentary ridges that have been observed by W. Krutzsch.

Only one genus:

Ctenolophon **Oliver** Fig. 6

Ctenolophon Oliver, Trans. Linn. Soc. 28: 516 (1873); Bullock, Kew Bull. 14: 41 (1960); Badré, Fl. Gabon 21: 43–44 (1973); van Hooren & Nooteboom in Fl. Males. I, 10: 629–634 (1988); R.S. Pungga, Tree flora of Sabah and Sarawak 2: 151–153 (1996).

Two spp., *C. englerianus* Mildbr. from Angola, Zaire, Nigeria and Gabon, and *C. parvifolius* Oliver from the Malay Penisula to New Guinea, but not reported from Java, the Lesser Sunda Islands, Celebes and the Moluccas. The two species are very similar, the only differences being the simple cymose panicle and larger flowers (stamens up to 15 mm long) in *C. englerianus* vs. compound cymose panicles and smaller flowers (stamens up to 10 mm long) in *C. parvifolius*, apart from the differences in pollen morphology.

Selected Bibliography

Boesewinkel, F.D., Bouman, F. 2000. Ctenolophonaceae. In: Takhtajan, A. (ed.) Anatomia seminum comparativa, vol. 6, pp. 13–14. St. Petersburg: Nauka. (In Russian)

Erdtman, G. 1955. Pollen grains of cf. *Ctenolophon* from Tertiary deposits in India. Bot. Not. 108: 143–145.

Heimsch, C., Tschabold, E.E. 1972. Xylem studies in the Linaceae. Bot. Gaz. 133: 242–253.

Kar, R.K. 1985. The fossil flora of Kutch. IV. Tertiary palynostratigraphy. The Palaeobotanist 34: 1–279.

Krutzsch, W. 1989. Paleogeography and historical phytogeography (paleochorology) in the Neophyticum. Pl. Syst. Evol. 162: 5–61.

Link, D.A. 1992. Floral nectaries of the Geraniales and their systematic implication. IV. Ctenolophonaceae Badre. Flora 187: 103–107.

Matthews, M.L., Endress, P.K. 2011. See General References.

Pierre, J.B.L. 1893. Flore forestière de la Cochinchine, IV. Fasc. 18, t. 281. Paris: Doin.

Pungga, R.S. 1996. Ctenolophonaceae. In: Soepadmo, E., Wong, K.M., Saw, L.G. Tree flora of Sabah and Sarawak, vol. 2: 151–153. Kuala Lumpur: Forest Res. Inst. Malaysia.

Saad, S.I. 1962. Pollen morphology of *Ctenolophon*. Bot. Notis. 115: 49–57.

Thanikaimoni, G., Caratini, C., Venkatachala, B.S., Ramanujam, C.G.K., Kar, R.K. (eds.) 1984. Selected Tertiary angiosperm pollens from India and their relationship with African Tertiary pollens. Pondichéry: Institut Français de Pondichéry.

van Hooren, A.M.N., Nooteboom, H.P. 1984. Linaceae and Ctenolophonaceae especially of Malesia, with notes on their demarcation and the relationships with Ixonanthaceae. Blumea 29: 547–563.

van Hooren, A.M.N., Nooteboom, H.P. 1988. Ctenolophonaceae, in: Flora Malesiana I, 10: 629–634.

van der Ham, R.W.J.M. 1989. New observations on the pollen of *Ctenolophon* Oliver (Ctenolophonaceae), with remarks on the evolutionary history of the genus. Rev. Palaeobot. Palynol. 59: 153–160.

van Welzen, P.C., Baas, P. 1984. A leaf anatomical contribution to the classification of the Linaceae complex. Blumea 29: 453–479.

Winkler, H. 1931. Linaceae. In: Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19a. Leipzig: W. Engelmann.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Dichapetalaceae

Dichapetalaceae Baill. (1886), nom. cons.
Chailletiaceae R. Br. (1818).

G.T. Prance

Trees, shrubs or lianas. Leaves alternate, simple, entire, pinnately nerved; stipules often early caducous, entire, lobed, partite or fimbriate. Inflorescences axillary, sometimes on leafless axillary or terminal shoots, cymose, distinctly branched to subcapitate or fasciculate, the peduncle free or adnate to petiole or more rarely the midrib; bracts and prophylls usually small. Flowers small, actinomorphic or zygomorphic, hermaphrodite or unisexual; pedicels usually articulated; sepals 5(4), imbricate, equal to very unequal, free or slightly united or rarely forming a tube; petals 5(4), either free and almost equal or connate into a tube with the lobes equal to very unequal, the lobes usually bifid at apex and most frequently bicucullate or inflexed, often clawed at base; stamens (4) 5, up to 3 of them sometimes lacking anthers, antesepalous, distinct to base of receptacle or adnate to corolla tube, generally with filaments, rarely with anthers sessile; anthers bilocular, introrse, longitudinally dehiscent; 1–5 variously shaped equal or unequal hypogynous glands ("staminodes") or disk lobes alternating with stamens, distinct or connate into a disk; ovary superior, 2–4(5)-locular, with 2 ovules in each loculus, ovules epitropous, anatropous, bitegmic, tenuinucellate, pendulous from top of each loculus, raphe ventral; style usually simple with 2–4(5) lobes, or more rarely 2–4(5) distinct stylodia; stigma punctate. Fruit a dry or fleshy drupe, 1–3(4)-seeded; exocarp most frequently appressed pubescent, sometimes dehiscent; mesocarp thin to thick; endocarp hard or parchment-like, indehiscent, glabrous or pubescent within. Seeds pendulous, with little or no endosperm; embryo large, erect, with plano-convex cotyledons. Germination hypogeal, first leaves opposite or alternate.

Three genera, ± 170 species, tropical Asia, Africa and America extending to subtropics in South Africa and India.

VEGETATIVE MORPHOLOGY. Most species of *Dichapetalum* are lianas, a few are small trees or shrubs. Some species may be either shrubs or lianas or even small trees. Species of *Tapura* and *Stephanopodium* are generally small to medium-sized trees or shrubs but *T. africana* can be a tree of 20 m and 100 cm d.b.h. Two African species of *Dichapetalum* are suffruticose. Tree and shrub forms of variable species tend to occur in shady habitats and lianas in more open, well-lit spaces. Most liana species begin as shrubs and then become lianescent. The lianas are not generally twining and do not have tendrils, but climb by the production of short, hook-like plagiotropic branches. Two models of architecture have been reported, Roux's Model in two African species of *Dichapetalum* and Cook's Model in *Tapura guianensis*. In the latter species with the inflorescences inserted at the distal end of the petiole, a branch-like character occurs on the leaf which is itself part of a leaf-like branch. The stipules in many species are small and early caducous, in *Dichapetalum* they may be fimbriate, pinnatisect or palmately divided into filiform segments. The lower leaf surface is often glandular, but the glands are not arranged in any regular pattern, and less frequently glands also occur on the upper surface. In young leaves the glands are nectariferous.

VEGETATIVE ANATOMY. As is common in many lianas, the wood is often deeply divided by intruding phloem which runs from the exterior in bands towards the centre. The stem is often clearly five lobed because of the intruding phloem, but in some species there are many more strands. The wood has vessels solitary or in small groups, with

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_7, © Springer-Verlag Berlin Heidelberg 2014

simple or scalariform perforation. Parenchyma is predominantly paratracheal around the vessels, with some short irregular wings. Rays are typically 5–6 cells wide, heterogeneous, sometimes uniseriate.

The leaves are dorsiventral, glabrous or with unicellular hairs. The hairs may be long and arachnoid or short, stiff and bristle-like and often barbed or flexible. The leaf indumentum is quite variable. The petiole of species with an axillary inflorescence has the characteristic horseshoe-shaped bundles which are less compact towards the base and are often flanked by small lateral bundles. In species with an epiphyllous inflorescence, the inflorescence usually emerges above the midpoint, but the floral and leaf bundles are separate from near to the base of the petiole. The sterile petioles usually show no trace of the floral bundle, but in a few cases floral bundles have been noted in sterile petioles. The petiolar inflorescence appears to have arisen by a gradual fusion of the peduncle and the petiole, rather than by true epiphylly.

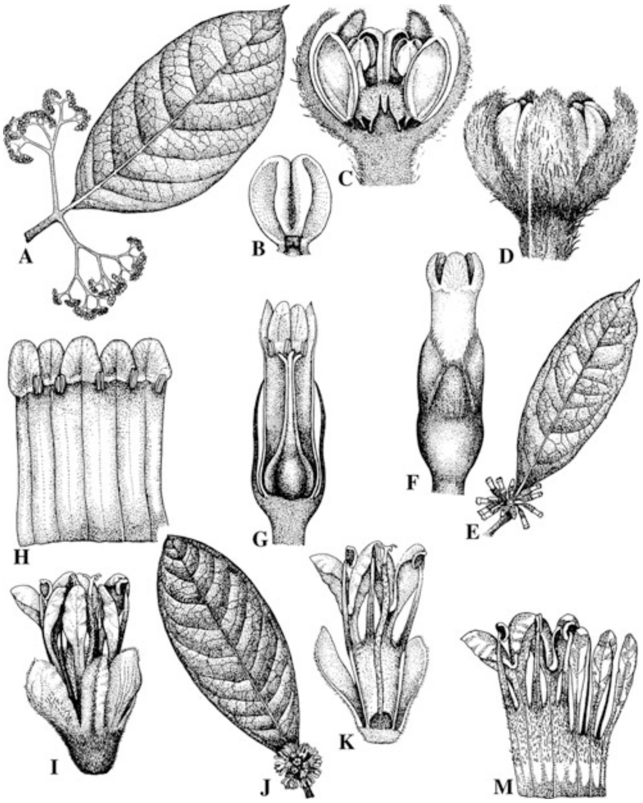

Fig. 7. Dichapetalaceae. **A–D** *Dichapetalum spruceanum*. **A** Leaf and inflorescence. **B** Petal. **C** Flower, vertical section. **D** Flower. **E–H** *Stephanopodium aptotum*. **E** Leaf and inflorescence. **F** Flower. **G** Flower, vertical section. **H** Corolla and stamens. **I–L** *Tapura amazonica*. **I** Flower. **J** Leaf and inflorescence. **K** Flower, vertical section. **L** Corolla and stamens. (Orig.)

The sieve tubes contain non-dispersive protein bodies.

Inflorescence and Flower Structure. The flowers are rather small, seldom exceeding 5 mm in size. Flowers are generally bisexual but unisexual flowers occur in some species of *Stephanopodium* and some Asiatic *Dichapetalum*. In Africa some species with apparently bisexual flowers are functionally unisexual. The inflorescence is always axillary and cymose; it is a fascicle arising from the petiole in *Stephanopodium* and most species of *Tapura*. It is branched and either inserted in the axil or on the petiole in most species of *Dichapetalum*. The petals are distinct almost to their base in *Dichapetalum*, but connate into a tube in *Tapura* and *Stephanopodium*. In the latter genus the anthers are sessile on the tube. The petal lobes are usually cucullate, except in *Stephanopodium*. Breteler (1973) has suggested that the petals are of staminal origin, and that the lobes are homologous with anthers and the lower united part homologous with filaments. This seems quite possible, and the bicucullate lobes strengthens this theory. For convenience in descriptions, however, all authors have termed the tube and lobes petals. At the base of the petals of most species, there are five hypogynous epipetalous structures variously termed glands, disk or staminodes. These staminodes are often bilobed at their apex, one of the reasons for considering them as staminodes rather than disks. It is interesting that within the family a stepwise progression from distinct stylodia through a style with distal style branches to an unbranched style is documented. See also the detailed studies on floral structure of the family and its relatives by Matthews and Endress (2008).

Pollen Morphology. A eurypalynous family in which Punt (1975) distinguished 29 pollen types. The pollen is 3-colporate or in a few species inaperturate, and a small number of 4-colporate grains occur in some specimens. The grains are spheroidal, suboblate or oblate. The longest axis is usually under 20 µm, rarely up to 35 µm. The ornamentation is quite varied from reticulate or microreticulate to pertectate.

KARYOLOGY. A study of 16 African species of *Dichapetalum* (Gadella 1969, 1970, 1972) found all species to have the same basic number $2n = 24$. There is one report of $2n = 20$ in a species where Gadella found $2n = 24$. Arends and van der Laan (1986) gave a summary of all known chromosome numbers in Dichapetalaceae, and reported an octoploid of $2n = 96$ in *D. crassifolium* var. *crassifolium* and a tetraploid of $2n = 48$ in *Tapura africana*. All 50 other counts in 21 species were $2n = 24$. The chromosomes are 1–2 μm in length and have primary constrictions in the median region.

POLLINATION. Very little is known about pollination. The flowers of *Tapura guianensis* are sweet scented and visited by small bees (*Trigona* and *Melipona*). A sweet scent has also been noticed in several African species of *Dichapetalum*.

FRUIT AND SEED. The fruit is a 1–3(4)-seeded fleshy or dry drupe sometimes with pyrenes free from each other, but more often one-seeded. The pyrenes are always 1-seeded, since only one ovule from each loculus develops; they are always free from each other within the fruit pulp. In most species the exocarp is pubescent with a short appressed velutinous pubescence, but in some African *Dichapetalum* long barbed, and irritating *Mucuna* type hairs occur. The endocarp is quite distinct from the exocarp, which may be either leathery or bony. An aril has been observed in two species of *Dichapetalum* but the seeds are normally without arils. The mature seed coat consists only of a tanniniferous exotesta with thickened cell walls, while the mesophyll and inner epidermis of the testa and the tegmen during seed development are compressed and largely resorbed (Boesewinkel and Bouman 1980). The embryo is large and surrounded by a thin endosperm; the cotyledons are plano-convex. Germination of all species examined is hypogeal, the cotyledons remaining within the endocarp and the taproot and epicotyl emerging from a slit at the suture of the endocarp. The first leaves are not markedly different from later leaves but may be either opposite or alternate. Little is known about seed dispersal. Several species have fruits with edible pulp and are presumably dispersed by animals. *Dichapetalum integripetalum* is eaten by chimpanzees. Species with barbed hairs on the exocarp open, exposing the pyrenes covered by brilliantly coloured pulp which may attract birds (Breteler 1973, 1981). Some neotropical species are eaten by bats.

PHYTOCHEMISTRY. Some African species of *Dichapetalum* are extremely poisonous due to the presence of fluoroacetic acid (FCH_2COOH) and fluoro fatty acids. The leaves of *D. toxicarium* contain monofluoroacetate and fluoride ions (Ward et al. 1964; Vickery and Vickery 1972). Species with fluoride compounds are extremely poisonous to cattle and are a problem in some African pastures. The fruits of *D. rudatsii* and *D. toxicarium* are used to kill mice and rats.

AFFINITIES. Many different relationships have been suggested for the family including Geraniales, Rosales, Thymelaeales, Celastrales and Euphorbiales. Although often placed near to the Euphorbiaceae, it does not seem to fit well there. A combined morphological/molecular analysis (Nandi et al. 1998) placed Dichapetalaceae in close proximity with Trigoniaceae and Chrysobalanaceae, and several subsequent molecular studies provided very strong support for a subclade of the Malpighiales in which Dichapetalaceae + Trigoniaceae are in a sister position and together are sister to Chrysobalanaceae + Euphroniaceae (Davis and Chase 2004; Wurdack and Davis 2009; Xi et al. 2012). Matthews and Endress (2008) compared the floral structure of these families and provided support for the close relationship of Dichapetalaceae and Trigoniaceae.

DISTRIBUTION AND HABITATS. In the Neotropics *Dichapetalum* and *Tapura* range from Mexico to C Brazil and *Stephanopodium* from Costa Rica to northern and western South America and Atlantic coastal Brazil but not to Amazonia. In Africa the centre of distribution is in C Africa in Cameroon, Gabon, Zaire, etc. but ranging from West to East tropical Africa, and two species of *Dichapetalum* extend south into subtropical South Africa. There are seven species of *Dichapetalum* in Madagascar, of which six are endemic (Breteler 1986). The Asiatic species of *Dichapetalum* are found in SE Asia, the Philippines, Malaysia, Australia, New Guinea and Melanesia, with one species in Fiji.

The family is found predominantly in forests. Only two African species of *Dichapetalum* are found in semi-arid conditions. Several neotropical species of *Dichapetalum* and *Stephanopodium* are found at altitudes of 2,000 m. One species of *Tapura* is common in the savannas of central Brazil.

ECONOMIC IMPORTANCE. The family is of little economic importance, the only uses being recorded are in a few folk medicines and as a poison.

CONSERVATION. Many species are of very restricted distribution especially in the Neotropics, Africa and Madagascar. The most vulnerable species must be those of the Atlantic coastal forests of Brazil, especially in *Stephanopodium*, and the Madagascan species of *Dichapetalum*.

KEY TO THE GENERA

1. Petals unequal, 1–2 distinctly larger, usually only 2–3 stamens fertile, rarely 5 **3. *Tapura***
– Petals equal, stamens all fertile 2
2. Petals distinctly bilobed, distinct to base or connate into a tube, anthers usually filamentose **1. *Dichapetalum***
– Petals not bilobed, slightly bifid in *S. estellense*, always united into a tube; anthers sessile on tube **2. Stephanopodium**

GENERA OF DICHAPETALACEAE

1. *Dichapetalum* Thouars

Dichapetalum Thouars, Gen. Nov. Madag.: 23 (1806); Prance, Kew Bull. 52: 213–219 (1997), key to Neotrop. spp.; Breteler (1969–1982), rev. Afric. spp.

Lianas, shrubs or rarely small trees. Inflorescence axillary, adnate to petiole or in axil, usually a pedunculate cyme, rarely a sessile glomerule. Flowers usually hermaphrodite, rarely unisexual; petals equal, distinct to base or shortly connate, entire or bilobed at apex; stamens 5, equal, distinct to base or connate at extreme base only, with distinct filaments. $2n = 24$ or 96.

About 135 spp., 90 in Africa, 7 Madagascan, 20 neotropical and 16 in SE Asia, Malesia and the Pacific.

2. *Stephanopodium* Poepp. & Endl.

Stephanopodium Poepp. & Endl., Nov. Gen. et Sp. 3: 40, t. 246 (1842); Prance, Kew Bull. 50: 295–305 (1995), rev.

Small to medium-sized trees or shrubs. Inflorescence a small sessile or shortly pedunculate glomerule, adnate to petiole. Flowers hermaphrodite or polygamo-dioecious; petals united into a long obconical or cylindrical tube, with 5 equal, broadly ovate lobes which are shorter than the tube, lobes entire at apex or slightly bicucullate; stamens 4–5, anthers sessile, adnate to interior of corolla tube.

Thirteen spp. in Costa Rica, N W South America and Atlantic coastal Brazil.

3. *Tapura* Aubl.

Tapura Aubl., Pl. Guiane 1: 126, t. 48 (1775); for revisions, see Bibliography.

Trees or shrubs. Inflorescence usually a small sessile or shortly pedunculate glomerule adnate to petiole, rarely, in Africa, an axillary glomerule borne on a long peduncle free from petiole. Flowers usually hermaphrodite, rarely unisexual; petals connate at base to form a distinct tube or free almost to base, with 1–2 large broad lobes with bicucullate divided apex, the other 2–4 smaller, linear-lanceolate, entire; stamens 2–3 or 5 fertile, adnate to corolla tube or to base of corolla in species with distinct petals, with distinct filaments.

Twenty neotropical spp. and 8 in Africa.

Acknowledgement I am grateful to F.J. Breteler for reviewing this contribution.

Selected Bibliography

Arends, J.C., van der Laan, F.M. 1986. Cytology. In: Breteler F.J. 1986, op. cit.

Barth, F. 1896. Anatomie comparée de la tige et de la feuille des Trigoniacées et des Chailletiacées (Dichapétalées). Bull. Herb. Boissier 4: 497–520.

Boesewinkel, F.D., Bouman, E. 1980. Development of ovule and seed coat of *Dichapetalum mombuttense* Engl. with notes on other species. Acta Bot. Neerl. 29: 103–115.

Breteler, F.J. 1969. The African Dichapetalaceae 1. Acta Bot. Neerl. 18: 375.

Breteler, F.J. 1973. The African Dichapetalaceae (III). A taxonomical revision. Species a–b. Meded. Landbouwhogeschool Wageningen 73-13.

Breteler, F.J. 1978. The African Dichapetalaceae IV. A taxonomical revision. Species c–f. Meded. Landbouwhogeschool Wageningen 78-10.

Breteler, F.J. 1979. The African Dichapetalaceae V. A taxonomical revision. Species g–l. Meded. Landbouwhogeschool Wageningen 79-16.

Breteler, F.J. 1981. The African Dichapetalaceae VII. A taxonomical revision. Species m–q. Meded. Landbouwhogeschool Wageningen 81-10.

Breteler, F.J. 1982. The African Dichapetalaceae VIII. A taxonomical revision. Species r–z. Meded. Landbouwhogeschool Wageningen 82-8.

Breteler, F.J. 1986. The African Dichapetalaceae IX. A taxonomical revision. Agric. Univ. Wageningen Papers 86-3.

Breteler, F.J. 1991. Dichapetalaceae. In: Flore du Gabon 32: 1–221.

Davis, C.C., Chase, M.W. 2004. See General References.

Descoings, B. 1960. Révision de *Dichapetalum* de Madagascar. Mém. Inst. Sci. Madag. B9: 63–120.

De Wildeman, E. 1919. Notes sur les espèces Africaines du genre *Dichapetalum* Thon. Rev. Zool. Afr. 4(2), Suppl. Bot.: 1–75.

Engler, A. 1896. Dichapetalaceae. In: Engler & Prantl, Nat. Pflanzenfam. III, 4: 345–351.

Engler A., Krause, K. 1931. Dichapetalaceae. In: Engler & Prantl, Nat. Pflanzenfam. 2nd ed. 19c: 1–11.

Gadella, Th.W.J. 1969. Chromosome numbers of some angiospermae collected in Cameroun and the Ivory Coast. Proc. Kon. Nederl. Akad. Wet. C, 72: 306–310.

Gadella, Th.W.J. 1970. Chromosome numbers of some Angiospermae collected in Cameroun and the Ivory Coast II. Acta Bot. Neerl. 19: 431–435.

Gadella, Th.W.J. 1972. Cytological notes on some flowering plants collected in Africa. Bull. Jard. Bot. Nat. Belg. 42: 393–402.

Hauman, L. 1958. Dichapetalaceae. In: Flore du Congo Belge et du Ruanda-Urundi 7: 287–348.

Keay, R.W.J. 1958. Dichapetalaceae. In: Flora of West Tropical Africa ed. 2. 1(2): 433–439.

Leenhouts, P.W. 1956. Some notes on the genus *Dichapetalum* in Asia, Australia and Melanesia. Reinwardtia 4: 75–87.

Leenhouts, P.W. 1957. Dichapetalaceae. In: Fl. Malesiana II, 5: 305–316.

Matthews, M.L., Endress, P.K. 2008. See General References.

Nandi, O.I., Chase, M.W., Endress, P.K. 1998. A combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets. Ann. Missouri Bot. Gard. 85: 137–212.

Prance, G.T. 1972. Dichapetalaceae. Flora Neotropica Monograph 10: 1–84.

Prance, G.T. 1995. A synopsis of the genus *Stephanopodium* (Dichapetalaceae). Kew Bull. 50: 295–305.

Punt, W. 1975. Pollen morphology of the Dichapetalaceae with special reference to evolutionary trends and mutual relationships of pollen types. Rev. Palaeobot. Palynol. 19: 1–97.

Vickery, B., Vickery, M.L. 1972. Fluoride metabolism in *Dichapetalum toxicarium*. Phytochemistry 11: 1905–1909.

Vickery, B., Vickery, M.L., Ashu J.T. 1973. Analysis of plants for fluoracetic acids. Phytochemistry 12: 145–147.

Ward, P.F.N., Hall, R.J., Peters, R.A. 1964. Fluoro fatty acids in the seeds of *Dichapetalum toxicarium*. Nature 201: 611–612.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Elatinaceae

Elatinaceae Dumort., Anal. Fam. Pl. 44, 49 (1829), 'Elatinideae', nom. cons.

K. Kubitzki

Perennial or annual herbs of aquatic or moist terrestrial habitats, rarely (*Bergia suffruticosa*) suffrutescent; nodes unilacunar 1-trace (*Elatine*); indumentum of unicellular and multicellular multiseriate capitate trichomes, or plants glabrous; a resinous secretion widely distributed in the tissues and deposited in granular form on the surface of the stems. Leaves opposite and decussate, rarely (*Elatine alsinastrum*) verticillate, entire or coarsely serrate; stipules minute, scarious, distinct or interpetiolar. Inflorescences axillary, dichasial, or flowers solitary. Flowers hermaphroditic, small, actinomorphic, hypogynous, usually inconspicuous, occasionally cleistogamous; sepals 2–5 (6), distinct or connate basally; petals 2–5, distinct, membranaceous, imbricate, persistent; stamens (2)3–6(–10), in 1 or 2 whorls, the outer whorl antesepalous; anthers broadly ovoid, dorsifixed, introrse, dehiscing by longitudinal slits; ovary superior, (depressed-)ovoid, (2)3–5-locular, the partitions not reaching the top of the ovary in some *Bergia*, stylodia 3–5; stigmas capitate, papillate; placentation axile or basal; ovules numerous, anatropous, bitegmic, weakly crassinucellar. Fruit a thin-walled septicidal capsule. Seeds ellipsoid to oblong, 0.5–1.5 mm long, with finely reticulate or smooth surfaces; endosperm reduced to 1–5 cell layers (*Bergia*) or 0 (*Elatine*); embryo straight or less often curved, filling nearly the entire seed; germination epigaeal. $x = 6, 9$.

Two genera and about 35 spp., nearly cosmopolitan.

Vegetative Morphology and Anatomy. *Bergia capensis* has dimorphic roots (D'Almeida 1941): those anchoring the plants in the mud are sparsely ramified but are almost completely covered by roots hairs, whereas the plumose water roots lack root hairs but frequently have chloroplasts in the cortex. Stomata are anomocytic (Tucker 1986). The wood of *Bergia suffruticosa* has been studied by Carlquist (1984). He observed vessel elements with simple perforation plates, vasicentric tracheids and fibriform vessel elements, predominance of uniseriate rays, vertical orientation of scalariform vessel-ray pitting, absence of intraxylary phloem, presence of brownish deposits in the parenchyma, and occurrence of druses and solitary crystals. Stomata have 4–8 irregularly shaped subsidiary cells. In contrast to most other families of Malpighiales, the sieve tube plastids of Elatinaceae lack starch inclusions (Behnke 1991).

Embryology. The tapetum is secretory and micosporogenesis simultaneous. Pollen grains are 2-celled (*Bergia*) or 3-celled (*Elatine*) when shed. The ovules are pendulous apical and epitropous, bitegmic and crassinucellate, and the micropyle is formed by both integuments. The embryo sac is of the Polygonum type; endosperm development is Nuclear. Embryogeny is of the Solanad type (Kajale 1939; Raghavan and Srinivasan 1940; Dathan and Singh 1971).

Pollen Morphology. Pollen is tricolp(oroid)ate with an equatorially constricted colpus but no clearly differentiated endoaperture and finely reticulate (Erdtman 1952; Melikian and Dildarian 1977).

Karyology. Most *Bergia* are based on $x = 6$, most *Elatine* on $x = 9$, up to high polyploid levels (8 x or perhaps higher), but in both genera $x = 10$ is also found (Raghavan and Srinivasan 1940; IPCN, version Feb. 2004).

Reproductive Biology and Pollination. Most *Elatine* species are adapted to reproduce very quickly on the mud of periodically dry

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_8, © Springer-Verlag Berlin Heidelberg 2014

habitats. Salisbury (1967) documented the enormous reproductive capacity of the annual *E. hexandra* and showed that germination is independent from day length but depends on exposure to light of sufficient intensity and duration.

Chasmogamous flowers of *Elatine* have small nectaries but insect visitors are unknown. In Sweden, self-pollination occurs frequently; the filaments elongate and bring the anthers in contact with the stigmas. The same mechanism leads to pollination in cleistogamous underwater flowers known in several species, whereby the pollen tubes germinate in situ and grow through the anther wall into the stigma. In the stamens of cleistogamous flowers, the endothecium may be lacking and the number of microsporangia is reduced (Frisendahl 1927).

Fruit and Seed. The seed coat consists of two thin-walled layers (probably testal), the outer tanniniferous, the inner with annular thickenings (this layer lacking in *Bergia*), and a thick-walled, stellate-undulate layer lignified or not but not fibrous and probably exotegmic, plus the tegmic mesophyll which is early crushed, and thin-walled inner epidermis with tannin (Netolitzky 1926; Dathan and Singh 1971).

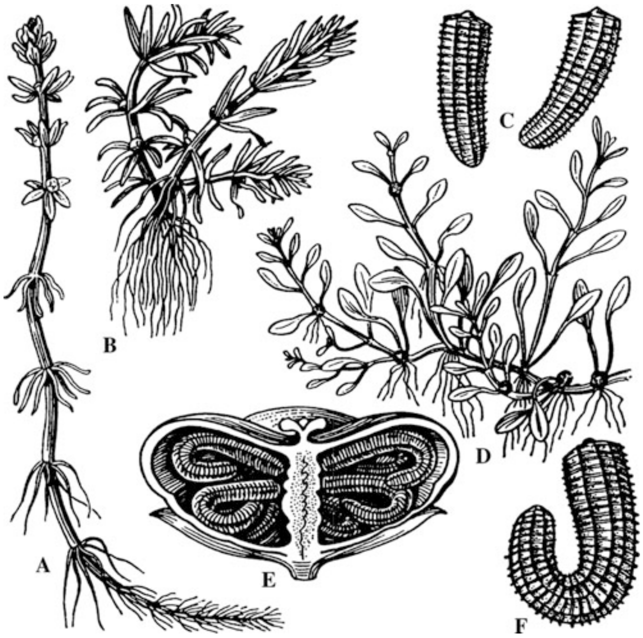

Fig. 8. Elatinaceae. **A–C** *Elatine alsinastrum*. **A** Aquatic plant. **B** Terrestrial plant. **C** Seeds. **D–F** *Elatine hydropiper*. **D** Terrestrial plant. **E** Fruit vertically sectioned. **F** Seed. (Takhtajan 1981, redrawn from Seubert 1845)

Phytochemistry. *Bergia* accumulates resinous substances in parenchymatous cells of the axis and leaf, and these substances are also excreted on the stem surface. From *Elatine*, procyanidin, delphinidin and ellagic acid have been reported, while the search for other compounds remained unsuccessful (Hegnauer 1969, 1989).

Affinities. Previously, Elatinaceae had been considered to be relatives of either the Caryophyllaceae or the Clusiaceae and Hypericaceae; the latter view was still defended by Takhtajan (2009). Features common to them include opposite leaves, distinct stylodia with capitate stigmas, capsular fruits and exotegmic seeds, but Clusiaceae differ from Elatinaceae in the lack of stipules. In the analysis of Savolainen, Fay et al. (2000), *Elatine* was linked with Malpighiaceae, which was strongly corroborated by further studies (Davis and Chase 2004; Wurdack and Davis 2009). Traits such as opposite or whorled stipulate leaves, unicellular and glandular hairs, the production of resin (Elatinaceae) or latex (some Malpighiaceae), the persistent calyx and the base number $x = 6$ may link both families. The problematic Centroplacaceae have recently been included, although with weak support, in the "malpighioid" clade [Centroplacaceae [Malpighiaceae + Elatinaceae]], in turn forming a well-supported clade together with strange companions such as the chrysobalanoids, putranjivoids and Caryocaraceae (Xi et al. 2012).

Distribution and Habitats. *Bergia* is found throughout the warmer regions of the world, with a few species in temperate zones. *Elatine* is almost cosmopolitan, the majority of species occurring in temperate regions. Both genera prefer moist disturbed habitats often on sand bars along rivers, on shores of lakes and ponds, or in mud flats. Several species are weeds in rice fields, those of *Bergia* in the Old World, and some of *Elatine* in California, Java and Japan. About half of the *Bergia* species are aquatic and semiaquatic, while the remainder grow on moist soil. Most *Elatine* thrive in shallow water that seasonally dries out. They are also very common in periodically drained fishponds.

Key to the Genera

1. Plants glabrous; flowers 2–4-merous; sepals obtuse, without visible midrib; capsules globose or depressed-globose **2. *Elatine***
– Plants glandular pubescent throughout; flowers 5-merous; sepals acute, with a conspicuous, thickened midrib; capsules ovoid **1. *Bergia***

1. *Bergia* L.

Bergia L., Mant. Pl. 2: 152 (1771); Leach, J. Adelaide Bot. Gard. 11: 75–100 (1989), Austral. spp.

Annual or perennial, herbaceous or suffrutescent; roots much branched from a conspicuous taproot; stems herbaceous but woody and thickened at base. Leaves (glandular-)pubescent on both surfaces or glabrous; flowers in dichasia or solitary; sepals 5, distinct, mucronate, with a thickened midvein and scarious margins; petals 5; stamens 5 or 10; ovary 5(6)-locular. Seeds oblong, slightly curved. $x = 6$.

About 24 species, most of them native to Old World tropics including Australia; *B. capensis* L. the most widespread species, ranging from southern Africa to India and Indonesia.

2. *Elatine* L.

Elatine L., Sp. pl. 1: 367 (1753).

Small aquatic or emergent annuals or short-lived perennials; stems soft, chlorophyllous, with 5–10 air chambers visible in cross section; flowers solitary, (2)3(4)-merous; sepals inconspicuous; petals as long as sepals, in some spp. with floral nectaries; anthers 4-sporangiate (2–3-sporangiate in cleistogamous flowers); ovaries broadly ovoid, (2)3(4)-locular; placentation basal (axile). Capsules delicate, the seeds visible within; seeds straight or slightly curved. $x = 9$.

About 10 species, in all continents, most of them in North America and Eurasia.

Selected Bibliography

Behnke, H.-D. 1991. See General References.
Carlquist, S. 1984. Wood and stem anatomy of *Bergia suffruticosa*: relationships of Elatinaceae and broader significance of vascular tracheids and fibriform vessel elements. Ann. Missouri Bot. Gard. 71: 232–242.
Corner, E.J.H. 1976. See General References.
D'Almeida, J.F.R. 1941. A contribution to the study of the biology of Indian marsh and aquatic plants. Part II. J. Bombay Nat. Hist. Soc. 43: 92–96.
Dathan, A.S.R., Singh, D. 1971. Embryology and seed development in *Bergia* L. J. Indian Bot. Soc. 50: 362–370.
Davis, G.L. 1966. See General References.
Davis, C.C., Chase, M.W. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. Am. J. Bot. 91: 262–273.
Erdtman, G. 1952. See General References.
Frisendahl, A. 1927. Über die Entwicklung chasmo- und kleistogamer Blüten bei der Gattung *Elatine*. Acta Horti Gothob. 3: 99–142.
Hegnauer, R. 1969, 1989. See General References.
Kajale, L.B. 1939. A contribution to the life history of *Bergia ammanioides* Roxb. J. Indian Bot. Soc. 18: 157–167.
Melikian, A.P., Dildarian, B.I. 1977. Comparative anatomical and palynological study of representatives of Elatinaceae family. Biol. Zhurn. Armenii 30(11): 44–49. (in Russian with Armenian summary)
Metcalfe, C.R., Chalk, L. 1950. See General References.
Müller, F. 1877. Untersuchungen über die Struktur einiger Arten von *Elatine*. Flora 60: 481–496, 519–526.
Netolitzky, F. 1926. See General References.
Niedenzu, F. 1925. Elatinaceae. In: Engler & Prantl, Nat. Pflanzenfam., 2nd edn, 21: 270–276.
Raghavan, T.S., Srinivasan, V.K. 1940. A contribution to the life history of *Bergia capensis* Linn. J. Indian Bot. Soc. 19: 283–291.
Salisbury, E.J. 1967. On the reproduction and biology of *Elatine hexandra* (Lapierre) DC. (Elatinaceae); a typical species of exposed mud. Kew Bull. 21: 139–149.
Savolainen, V., Fay, M.F. et al. 2000. See General References.
Seubert, M. 1845. Elatinarum monographia. Nov. Acta Acad. Caes. Leop.-Carol. Nov. Curios. 21(1): 34–60.
Takhtajan, A. 1981. See General References.
Takhtajan, A. 2009. See General References.
Tucker, G.C. 1986. The genera of Elatinaceae in the southeastern United States. J. Arnold Arb. 67: 471–483.
Wurdack, K.J., Davis, C.C. 2009. See General References.
Xi, Z. et al. 2012. See General References.

Erythroxylaceae

Erythroxylaceae Kunth in H.B.K., Nov. Gen. Sp. 5, ed. 4: 175, ed. f: 153 (1822), nom. cons.
Nectaropetalaceae Exell & Mendonça (1951).

V. Bittrich

Glabrous trees or shrubs, evergreen or deciduous, sap sometimes milky or coloured; alkaloids common. Leaves alternate (opposite), simple, entire, pinnately veined, with intrapetiolar (interpetiolar), often caducous stipules, colleters present. Flowers small, generally bisexual, more rarely unisexual, distylous [*Erythroxylum*], axillary, solitary or in fascicles, rarely in pedunculate subumbelliform cymes. Calyx (4)5-lobed, persistent, lobes valvate or imbricate in bud; petals (4)5, distinct, imbricate in bud, often shortly clawed, early caducous, mostly with a ligular bilobed appendage near the base; stamens 10(–12), biseriate, filaments connate at the base into a cup or tube, generally persistent; anthers basifixed, tetrasporangiate, longitudinally dehiscent; ovary superior, 2–3(–4)-carpellate, all or only one of the locules fertile, bearing 1(2) pendulous crassinucellate ovules; stylodia distinct or a single style. Fruit a monospermous drupe (a 2- or 3-seeded capsule). Seeds with starchy endosperm (absent), embryo straight, aril absent (present).

Four genera and about 240 spp., pantropical/subtropical. The large genus *Erythroxylum* is pantropical, the other genera are restricted to Africa south of the Sahara.

Vegetative Morphology and Anatomy. Growth forms include prostrate shrubs, rosette shrubs, small and tall trees; they are generally correlated with the habitats (Rury 1985); the buds are perulate (Stevens 2001 onwards). The leaves are alternate, opposite in *Aneulophus*, entire, and involute in bud in *Erythroxylum*. This vernation type often results in the presence of two parallel lines on the mature leaf surface. The stipules are mostly intrapetiolar (interpetiolar in *Aneulophus*) and usually more or less connate; they include the terminal bud and are persistent or caducous. In *Erythroxylum* they are often longitudinally striate or ribbed. Unbranched finger- or awl-shaped colleters are present in the axils of the stipules of all genera (Stevens 2001 onwards; Thiebaut and Hoffmann 2005), but easily overlooked. Leaf texture and duration is often correlated with the habitats of the species (Rury 1981). Many evergreen species are sclerophyllous. In *Erythroxylum* persistent cataphylls, which correspond to the stipules of reduced leaf laminas, are common on lateral twigs mainly near their base (Weberling et al. 1980). The aggregation of these cataphylls is often termed "ramenta".

Leaf anatomy was studied by Rury (1981) and van Welzen and Baas (1984). Hairs are absent. A papillose abaxial epidermis occurs in several *Erythroxylum* spp. Mucilage cells in the leaf epidermis are reported from *Erythroxylum* spp. and *Aneulophus*, and crystalliferous epidermis cells containing a solitary crystal of calciumoxalate were found in some *Erythroxylum* (Solereder 1908). The stomatal type is paracytic or parallelocytic. The midrib shows mostly a simple arc of collateral vascular tissue, very rarely more complex vascular systems with pith bundles. Cristarque cells, which are either restricted to the bundle sheath or occur additionally in the ground tissue of petiole and midrib, are reported by van Welzen and Baas (1984). Mesophyll sclereids are common, but typically absent in deciduous and in many mesophytic evergreen leaves (Rury 1981).

Data about stem anatomy were reported by Heimsch (1942), Metcalfe and Chalk (1950), and Rury (1985). Cork develops superficially: epidermal in *Aneulophus*, subepidermal in *Erythroxylum*; secretory cells with gum-like contents are present in the cortex; nodes are unilacunar; cortical bundles are usually present in young stems;

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_9,

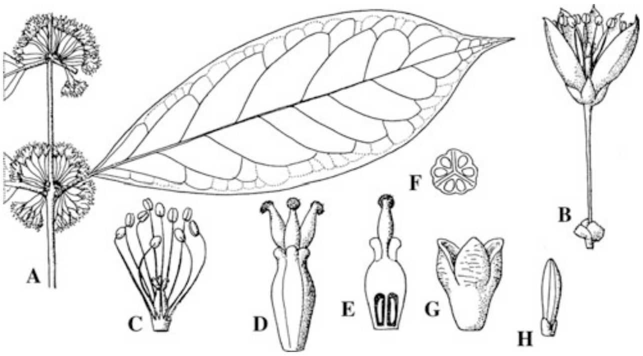

Fig. 9. Erythroxylaceae. *Aneulophus africanus*. **A** Flowering branchlet. **B** Flower with basal bracts. **C** Androecium and gynoecium. **D** Gynoecium. **E** Same, vertically sectioned. **F** Ovary, transversal section. **G** Fruit. **H** Seed. (Badré 1973)

vessel perforations are simple; in most cases evergreen species have longer narrower vessel elements than deciduous species (Rury 1981); the pits to the parenchyma are generally simple. Vasicentric tracheids are present. Fibrous elements consist of fibre tracheids or libriform fibres. The axial parenchyma is predominantly apotracheal-diffuse and paratracheal, rarely with some apotracheal banded parenchyma; rays are uni- to triseriate, rarely pluriseriate (up to 5 cells wide), heterocellular or nearly homocellular. Uni- and biseriate rays show silica grains mainly in species of two neotropical sections of *Erythroxylum*; prisms of calcium oxalate occur in the parenchyma strands of certain *Erythroxylum* spp. and in ray cells of *Nectaropetalum* and *Pinacopodium* (Rury 1981; Chalk 1983). According to Rury (1985) xylem features, life form and leaf structural features are strongly interrelated, reflecting habitat conditions. Wood anatomical specialization within the family may be of xeromorphic as well as of mesomorphic nature. Sieve-element plastids of *Erythroxylum* spp. contain about ten rectangular protein crystals and no starch (type P5c, Behnke 1988).

INFLORESCENCE AND FLOWER STRUCTURE. Single flowers or few- to many-flowered sessile to subsessile fascicles are borne in the axils of leaves or cataphylls, rarely distinctly pedunculate inflorescences are formed axillary or on axillary short shoots (*Pinacopodium*). According to Schulz (1907) the fascicles are cymes with a strongly compressed inflorescence axis. Pedicels are usually present and have two or rarely four (*Aneulophus*) tiny bracteoles at the base; above the bracteoles the pedicel is articulated (Eichler 1878).

The flowers are basically 5-merous, actinomorphic, bisexual or rarely unisexual. The sepals are united below, forming a mostly campanulate and persistent calyx; the lobes are imbricate or valvate in bud. The petals are caducous, alternating with the calyx lobes, imbricate in bud, and mostly shortly clawed; a nectariferous entire or bilobed appendage is inserted at the apex of the claw, more rarely it is absent. Narayana (1960) reports the presence of obdiplostemony for two *Erythroxylum* but its absence for another species. There are 10(–12) stamens, subequal or unequal (then forming two sets) in length, and ± persistent; the filaments are basally united into a sometimes glandular cup or tube of various length and, according to Eichler (1878), a disk participates in their formation; the anthers are basifixed, tetrasporangiate, two-locular, and dehisce by longitudinal slits. The ovary is superior, 2–3-carpellate, 2–3-loculate, with one or two axile pendulous, epitropous ovules per locule, or it has only one uniovulate fertile locule (*Erythroxylum*); the stylodia are free or basally or completely connate; the stigmas are capitate, depressed-capitate or clavate, rarely acute, free or rarely connate and then bilobed (*Pinacopodium*).

EMBRYOLOGY. Both integuments of *Erythroxylum coca* are of dermal derivation (Boesewinkel and Geenen 1980). Embryo sac development is of the Polygonum type, the antipodals degenerate early. The nucellus is partly resorbed by the embryo sac. The inner layer of the inner integument is differentiated into a pigmented endothelium (Tunmann and Jenzer 1910). Endosperm formation is nuclear with later centripetal wall formation. The tapetum is of the secretory type (Narayana 1960). The mature pollen grains are 3-celled.

POLLEN MORPHOLOGY. An overview is given by Oltmann (1968). Pollen grains are suboblate to prolate and generally tricolporate; in *Aneulophus* the colpi are strongly reduced. Pollen size was observed to be significantly different in longer and shorter stamens of the same flower of *Erythroxlum coca*, and pollen from thrum flowers are larger than pollen from pin flowers (Ganders 1979).

Fig. 10. Erythroxylaceae. *Erythroxylum macrophyllum*. **A** Flowering branch with cataphylls and stipules. **B** Cataphyll. **C** Floral bud with floral bract. **D** Flower. **E** Same, with petals and two sepals removed. **F** Adaxial, lateral and medial section of petal. **G** Androecium and pistil. **H** Medial section of androecium and pistil, with cross section of ovary (right) and detail of anther. **I** Pistil. **J** Part of infructescence. **K** Fruit and seed. (Reproduced with the kind permission of the artist Bobbi Angell)

The tectum is finely reticulate or punctate. The colpi are of different length and in some species of *Erythroxylum* united at the pole. The pori are isodiametric or not; in a few species of *Erythroxylum* they are united in a ring in the equatorial zone (zonorate). In various *Erythroxylum* opercula are developed. According to Oltmann (1968) pollen of the Old World representatives is more heterogeneous and shows the basal types within the family.

Karyology. Most counts show that *Erythroxylum* has a chromosome base number of $x = 12$. The counts of Berry et al. (1991) in the agamospermic *E. undulatum* Plowman of $n =$ ca. 18 suggest that this species is a triploid of hybrid origin.

Reproductive Systems and Pollination. Since Darwin (1877) it is known that *Erythroxylum* is often heterostylous. Many species of this genus and of *Nectaropetalum* have dimorphic flowers. There are also reports of three or four different flower morphs (see Payens 1958), but according to Ganders (1979) this is probably a misinterpretation due to continuous variation in the relative lengths of the two sets of stamens in the flowers. As common in heterostylous plants, pin morphs often produce more but smaller pollen grains than the drum morphs (Ganders 1979; Pailler et al. 1998). In *E. coca*, Ganders (1979) found a strong self-incompatibility system linked with floral dimorphism. In the self-compatible pin morph of *E. novogranatense* he observed illegitimate cross-compatibility, whereas Pailler et al. (1998) reported slight illegitimate cross-compatibility in the self-incompatible pin morph of *E. laurifolium*, but without any effect on population structure. Burck (1895, cited in Payens 1958) observed abundant fruiting in introduced plants of *E. novogranatense* in Java, where only the partial self-compatible pin morphs occur. He also discussed the possibility that in some species the heterostyly might have led to dioecy (see Barrett and Richards 1990). In these cases, the flowers of the pin morph possess abortive stamens, the flowers of the drum morph only a rudimentary pistil (Schulz 1907). A dioecious species was also reported by Bawa and Opler (1975) from Costa Rica. As an exception to "Baker's law", Pailler et al. (1998) found distyly in three species of *Erythroxylum* endemic to the Mascarene islands and a heteromorphic incompatibility system in the one species, *E. laurifolium*, studied in detail. In *E. undulatum* the flowers are monomorphic (pin morph) and produce apomictic seeds from sporadically developing aposporous embryo sacs; this species is probably a sterile triploid of hybrid origin (Berry et al. 1991).

Erythroxylum flowers are reported to be fragrant and nectar-producing. The petal appendages may restrict the access of flower visitors to the nectar. Various insects, including Hymenoptera, Diptera and Lepidoptera, with bees or wasps as the most important pollinators, were observed as flower visitor in *Erythroxylum* (Schulz 1907; Domínguez et al. 1997; Barros 1998). Flower visitors of *E. havanense* were found to not distinguish between the two floral morphs, but fruit set of thrum plants was significantly higher than that of pin plants (Domínguez et al. 1997). This difference is probably due to the much higher male sterility of the thrum flowers, leading to a partially gynodioecious system with pin flowers behaving as bisexual flowers. Species of *Erythroxylum* with quite similar flower morphology may occur sympatrically and flower synchronously for months. Such species were observed to partly share the same pollinators (Barros 1998).

FRUIT, SEED AND DISPERSAL. The fruits of *Erythroxylum* and *Nectaropetalum* are drupes, monospermous in *Erythroxylum* and probably bispermous in *Nectaropetalum*. *Erythroxylum* spp. have mostly red drupes with a well-developed endocarp. *Aneulophus* has a 3–4-locular septicidal capsule, with one seed per locule. The mature fruit of *Pinacopodium* is unknown.

The ovule (*Erythroxylum*) is anatropous, bitegmic and crassinucellate with an elongated nucellus (Corner 1976; Boesewinkel and Geenen 1980). The micropyle is formed by the inner integument only. The ventral raphe shows simple or multiple bundles. The tegmen is multiplicative. In *Erythroxylum* the exotegmen with fibre tracheids forms the mechanical layer of the seedcoat; the other layers are crushed during seed development. The embryo is straight, an endosperm is present or absent. The seeds of *Aneulophus africanus* are arillate (Badré 1973).

The drupaceous, reddish, sometimes sweet fruits of most Erythroxylaceae suggest ornithochory. Birds were observed already by Martius to feed on *Erythroxylum* fruits (Schulz 1907).

PHYTOCHEMISTRY. As summarized by Hegnauer (1981, 1989), the present knowledge is restricted to species of *Erythroxylum*. Condensed tannins are common, ellagitannins were very rarely reported. Alkaloids are common, especially tropane and pseudotropane alkaloids, but it is only in *E. coca* and *E. novogranatense* that considerable amounts of cocaine and cinnamylcocain were found. In contrast to tropine alkaloids, hygroline ecgonine alkaloids seem to be restricted to Erythroxylaceae and Rhizophoraceae, ecgonine alkaloids possibly exclusive to Erythroxylaceae, or are very rare in angiosperms. Various esters of tropanols were reported. Phenolic compounds include flavonoids, mainly various flavonols (cf. Johnson et al. 1998) as well as caffeic acid and derivatives and methyl salicylate, which were found in the essential oil of coca leaves. A mixture of essential oils and resins in the wood of *Erythroxylum* contains mono-, di- and sesquiterpenoid metabolites. Triterpenoid compounds were found in the waxes of leaves and fruits. Saponins were reported from a number of species.

SUBDIVISION AND AFFINITIES. *Aneulophus* deviates remarkably in several characters from the other genera. In the cladogram of Schwarzbach and Ricklefs (2000), based on DNA sequence data, it forms the basal branch of the family, and *Nectaropetalum* and *Pinacopodium* appear as sister taxa to *Erythroxylum*. The monophyly of the vast genus *Erythroxylum* would need further confirmation.

Formerly, the family was generally considered as closely related to the Linaceae s.str. from which it differs by traits such as the presence of colleters, mostly appendaged petals, the number of (functional) stamens, mostly drupaceous fruits, and possibly the chromosome base number. Hallier (1923) stressed similarities with Hugoniaceae (Linaceae s.l.), which also have drupacous fruits. A comparison of leaf anatomical characters revealed various similarities with Linaceae, Hugoniaceae, Ixonanthaceae and Humiriaceae (van Welzen and Baas 1984). Boesewinkel and Geenen (1980) listed seed characters common to *Erythroxylum* and *Linum*, but it remains questionable which of these are synapomorphic.

*rbc*L sequences analyzed by Setoguchi et al. (1999), Savolainen et al. (2000) and Schwarzbach and Ricklefs (2000) as well as the multi-gene analyses of Wurdack and Davis (2009), Soltis et al. (2011) and Xi et al. (2012) all resolved a sister group relationship of Erythroxylaceae and Rhizophoraceae and finally a clade comprising [Ctenolophonaceae [Erythroxylaceae + Rhizophoraceae]]. This is also supported by the shared occurrence of hygroline and pyrrolodine alkaloids, sieve tube plastids with protein crystals and involute leaf blades in Erythroxylaceae and Rhizophoraceae. However, the merging of these two families in a broadened family concept, as suggested by APG II (2003), could cause more confusion than it would help to clarify and is not followed here.

Distribution and Habitats. *Erythroxylum* has a pantropical distribution with centres in the Neotropics and on Madagascar. The other genera are restricted to tropical and subtropical Africa south of the Sahara; one species of *Nectaropetalum* was reported from Madagascar.

Nectaropetalum occurs in forest fringes of low altitude and in dry forests. *Erythroxylum* species are found in various habitats, such as the understorey of tropical wet lowland and montane forests, evergreen and deciduous forests, savannah woodland, sandy or rocky shores and hills (Malaysia), and restingas and caatingas (NE Brazil). Deciduous species of *Erythroxylum* are usually found in dry or seasonally dry habitats, whereas evergreen ones occur in a broad range of habitats (Rury 1981). *Aneulophus africanus* occurs in swampy forests and *Pinacopodium* spp. in moist forests of West Africa.

Palaeobotany. Fossils from the Eocene of Argentina are considered to belong to Erythroxylaceae.

Economic Importance. *Erythroxylum coca* and *E. novogranatense* are the source of cocaine, a dangerous narcotic drug. Besides its economic importance for the coca planters in NW South America, it has become notorious for its social, economic and political impact on Central and South America and in the First World. Cocaine has lost its importance as a local anaesthetic to synthetic products. Chewing of coca leaves often with some unslaked lime or ashes of plants as an alkaline catalyst has been a common custom in north-western South America for several thousand years; throughout the northwest Amazon region, powdered coca leaves mixed with ash are slowly dissolved in the mouth (e.g. Rury and Plowman 1983; Davis 1997). Chewing of the leaves confers endurance to hunger and exhaustion. Coca leaves not only contain cocaine, but are very rich in vitamins and minerals. Thus, they are sometimes considered not as a drug but a food with mildly stimulating effects essential for the survival of the native Andean people. These revere coca as a sacred plant, which formerly often played an important role in religious ceremonies (Davis 1997). For this reason, plans for the eradication of coca plants were strongly opposed by ethnobotanists like the late Timothy Plowman. In the last century, coca extracts sometimes mixed with red wine ("Vin Tonique Mariani"), but also in form of candies, cigarettes, soft drinks, etc., became extremely popular as stimulants and for various medicinal purposes. After 1906 cocaine had to be removed from Coca-Cola and similar soft drinks, but the residue of the coca leaf extracts is still used for flavouring (Davis 1997). In Brazil "catuaba", a Tupi name for certain *Erythroxlum* spp. but also used for a few species of other families, is renowned as a tonic and aphrodisiac in form of a tea or alcoholic tincture prepared from the bark. Several species of *Erythroxylum* and *Nectaropetalum* have hard and durable wood used for various purposes. Some local uses of Old World Erythroxylaceae are reported by Hegnauer (1981).

Key to the Genera

1. Leaves opposite **1. *Aneulophus***
– Leaves alternate 2
2. Flowers in pedunculate subumbelliform inflorescences; style bearing a bilobed stigma **2. *Pinacopodium***
– Flowers solitary or in sessile or subsessile fascicles; stylodia distinct or connate into a single style with distinct stigmas 3
3. Stylodia (2)3, distinct or only partly connate; petal appendages large (usually longer than the sepals) **3. *Erythroxylum***
– Style 1, stigmas 2; petal appendages small and hidden by the sepals or absent **4. *Nectaropetalum***

Genera of Erythroxylaceae

1. *Aneulophus* Benth. Fig. 9

Aneulophus Benth. in Benth. & Hook.f., Gen. pl. 1: 244 (1862).

Shrubs with opposite leaves; stipules interpetiolar. Flowers numerous (up to 50) in congested inflorescences; pedicel with 4 minute bracteoles at base; petals much longer than sepals, white, shortly unguiculate, unappendaged, thickened along the midrib; stamens very shortly united at base; stylodia 3(4) united below, ovary 3(4)-locular with two ovules in each locule. Capsule septicidal with one arillate seed in each locule.

One or two spp., tropical West Africa.

2. ***Pinacopodium*** Exell & Mendonça

Pinacopodium Exell & Mendonça, Bol. Soc. Brot. II, 25: 105 (1951).
Morelodendron Cavaco & Normand (1951).

Trees with alternate leaves. Flowers in axillary pedunculate, subumbelliform cymes; sepals valvate; petal appendages indistinct; stamens basally united into a short tube; style 1, very short, stigma capitate, bilobed; ovary two-locular with one ovule in each locule. Fruit unknown.

Two spp. in tropical moist forests of West Africa (Gabon and Mayombé).

3. ***Erythroxylum*** P. Browne Fig. 10

Erythroxylum P. Browne, Civ. Nat. Hist. Jamaica: 278 (1756); Schulz in Pflanzenreich IV, 134: 18–161 (1907).

Evergreen or deciduous shrubs or trees, twigs compressed at apex, often with persistent cataphylls. Leaves alternate, leaf ptyxis involute; stipules united to the apex or bifid, mostly bicarinate and striate, and 2–3-setulose. Flowers in axillary fascicles subtended by bracts, often dimorphic, sometimes unisexual; sepals valvate or imbricate; petals with a usually bifid appendage on the inner face; filaments connate below; stylodia distinct or connate up to the middle; ovary (2)3-locular, usually only one cell fertile; drupe reddish, monospermous.

Ca. 230 spp., tropical, especially Neotropics and Madagascar. *E. coca* Lam. and *E. novogranatense* (Morris) Hieron. (with two varieties) from NW South America are the source of cocaine. The subdivision of the genus in sections by Schulz (1907) is often artificial (Plowman, cited in Rury 1985).

4. ***Nectaropetalum*** Engl.

Nectaropetalum Engl., Bot. Jahrb. Syst. 32: 109 (1902).
Peglera Bolus (1907).

Shrubs or tree. Leaves alternate, with pointed tips or acuminate, stipules mostly completely united. Flowers axillary, single or in small groups; sepals valvate, petals white, clawed or not, with or more rarely without small appendages near the base; filaments united below into a shallow cup, sometimes bearing 5 glands outside; the single style with 2 distinct stigmas; ovary 2-locular, with one ovule in each locule.

Eight spp., South Africa to Kenya, Zaire, Madagascar.

Selected Bibliography

APG II. 2003. The Angiosperm Phylogeny Group. See General References.

Badré, F. 1973. Erythroxylaceae. In: Aubreville, A. et al. (eds.) Flore du Gabon, fasc. 21: 49–54. Paris: Muséum National d'Histoire Naturelle.

Barrett, S.C.H., Richards, J.H. 1990. Heterostyly in tropical plants. Mem. New York Bot. Gard. 55: 35–61.

Barros, M.A.G. 1998. Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P. Br. (Erythroxylaceae) do Brasil. Rev. Brasil. Bot. 21: 159–166.

Bawa, K.S., Opler, P.A. 1975. Dioecism in tropical forest trees. Evolution 29: 167–179.

Behnke, H.-D. 1988. Sieve-element plastids and systematic relationships of Rhizophoraceae, Anisophyllaceae, and allied groups. Ann. Missouri Bot. Gard. 75: 1387–1409.

Behnke, H.-D. 1991. Distribution and evolution of forms and types of sieve-element plastids in the dicotyledons. Aliso 13: 167–182.

Berry, P.E., Tobe, H., Gómez, J.A. 1991. Agamospermy and the loss of distyly in *Erythroxylum undulatum* (Erythroxylaceae) from northern Venezuela. Amer. J. Bot. 78: 595–600.

Boesewinkel, F.D., Geenen, J. 1980. Development of ovule and seed-coat of *Erythroxylum coca* Lamk. Acta Bot. Neerl. 29: 231–241.

Chalk, L. 1983. Axial parenchyma. In: Metcalfe, C.R., Chalk, L. (eds.) Anatomy of the dicotyledons, ed. 2. Vol. II, Wood structure and conclusion of the general introduction. Oxford: Clarendon Press, pp. 15–20.

Corner, E.J.H. 1976. See General References.

Darwin, C. 1877. The different forms of flowers on plants of the same species. London: Murray.

Davis, W. 1997. One river – science, adventure and hallucinogenics in the Amazon basin. London: Simon & Schuster.

Domínguez, C.A., Ávila-Sakar, G., Vázquez-Santana, S., Márquez-Guzmán, J. 1997. Morph-biased male sterility in the tropical distylous shrub *Erythroxylum havanense* (Erythroxylaceae). Amer. J. Bot. 84: 626–632.

Eichler, A.W. 1878. Blüthendiagramme, 2. Teil. Leipzig: Wilhelm Engelmann, pp. 342–343.

Ganders, F.R. 1979. Heterostyly in *Erythroxylum coca* (Erythroxylaceae). Bot. J. Linn. Soc. 78: 11–20.

Hallier, H. 1923. Beiträge zur Kenntnis der Linaceae (DC. 1819) Dumort. Beih. bot. Centralbl. 39: 1–178.

Hegnauer, R. 1981. Chemotaxonomy of Erythroxylaceae (including some Ethnobotanical notes on Old World species). J. Ethnopharm. 3: 279–292.

Hegnauer, R. 1989. See General References.

Heimsch, C. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales", of Wettstein, with reference to taxonomic grouping. Lilloa 8: 83–198.

Johnson, E.L., Schmidt, W.F., Norman, H.A. 1998. Flavonoids as markers for *Erythroxylum* taxa: *E. coca* var. *ipadu* and *E. novogranatense* var. *truxillense*. Biochem. Syst. Ecol. 26: 743–759.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Narayana, L.L. 1960. Studies in Erythroxylaceae - I. Proc. Indian Acad. Sci. 51(6), Sect. B: 270–275.

Oltmann, O. 1968. Die Pollenmorphologie der Erythroxylaceae und ihre systematische Bedeutung. Ber. Deutsch. Bot. Ges. 81: 505–511.

Pailler, T., Humeau, L., Thompson, J.D. 1998. Distyly and heteromorphic incompatibility in oceanic island species of *Erythroxylum* (Erythroxylaceae). Pl. Syst. Evol. 213: 187–198.

Payens, J.P.D.W. 1958. Erythroxylaceae. In: Steenis, C.G. G.J. van (ed.) Fl. Males. I. 5: 543–552.

Rury, P.M. 1981. Systematic anatomy of *Erythroxylum* P. Browne: practical and evolutionary implications for the cultivated cocas. J. Ethnopharm. 3: 229–263.

Rury, P.M. 1985. Systematic and ecological wood anatomy of the Erythroxylaceae. IAWA Bull. n.s. 6: 365–397.

Rury, P.M., Plowman, T. 1983 (1984). Morphological studies of archeological and recent coca leaves (*Erythroxylum* spp.). Bot. Mus. Leafl. Harvard Univ. 29: 297–341.

Savolainen, V. et al. 2000. See General References.

Schulz, O.E. 1907. Erythroxylaceae. In: Pflanzenreich, IV. 134: 176 pp. Leipzig: W. Engelmann.

Schwarzbach, A.E., Ricklefs, R.E. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. Amer. J. Bot. 87: 547–564.

Setoguchi, H., Kosuge, K., Tobe, H. 1999. Molecular phylogeny of Rhizophoraceae based on *rbc*L gene sequences. J. Plant Res. 112: 443–455.

Solereder, H. 1908. Systematische Anatomie der Dicotyledonen. Ergänzungsband. Stuttgart: Ferdinand Enke, pp. 54–56.

Soltis, D.E. et al. 2011. See General References.

Stevens, P.F. 2001 onwards. See General References.

Thiebaut, L.E., Hoffmann, P. 2005. Occurrence of colleters in Erythroxylaceae. Kew Bull. 60: 455–459.

Tunmann, O., Jenzer, R. 1910. Zur Anatomie der Blüten von *Pilocarpus pennatifolius* Lem. und *Erythroxylon coca* Lam. Arch. d. Pharmaz. 248: 514–519.

van Welzen, P.C., Baas, P. 1984. A leaf-anatomical contribution to the classification of the Linaceae complex. Blumea 29: 453–479.

Weberling, F., Lörcher, H., Böhnke, E. 1980. Die Stipeln der Irvingioideae und Recchioideae und ihre systematische Wertung nebst Bemerkungen zur Holzanatomie und Palynologie. Pl. Syst. Evol. 133: 261–283.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Euphorbiaceae

Euphorbiaceae Juss. (1789), nom. cons.
Phyllanthaceae Martinov (1833).
Peraceae Klotzsch (1859).
Picrodendraceae Small (1917), nom. cons.

G.L. Webster†[1]

Monoecious or dioecious trees, shrubs, or herbs, sometimes succulent or scandent; stems with or without laticifers; indumentum simple, malphighiaceous, stellate, or lepidote, sometimes glandular or 0. Leaves alternate, spiral or distichous, less commonly opposite or whorled; leaf blades simple to palmately lobed or compound, pinnately to palmately nerved, sometimes with basal, laminar, or marginal glands; stipules persistent or deciduous, sometimes reduced or 0. Inflorescences axillary or terminal, sometimes cauliflorous, thyrsoid, paniculate dichasial, glomerulate or synanthial, or flowers solitary; bracts sometimes colored, glandular, or hypertrophied. Flowers unisexual, usually actinomorphic; perianth segments distinct or connate, imbricate to valvate, rarely obsolete or suppressed; sepals (–)3–6(−10), entire or lobed, sometimes glandular, the pistillate persistent or deciduous in fruit; petals + or 0, greenish to white, yellow, pink, or red; disk + or 0, extrastaminal or less commonly interstaminal, entire to toothed, lobed, or dissected; stamens (1–)3–50 (−400), filaments distinct or connate; anthers mostly 2-locular, dehiscing longitudinally or laterally, extrorse or less commonly introrse; gynoecium syncarpous, ovary (1)2–5(−20)-locular; placentation axile (basal); ovules 1 or 2 per locule, anatropous or hemitropous, epitropous, usually inserted beneath an obturator. Fruits mostly schizocarpic, splitting from the columella, commonly explosively dehiscent, mesocarp often separating from endocarp, sometimes baccate or drupaceous. Seeds often carunculate; seed coat mostly exotegmic; endosperm copious, often fleshy, or 0, sometimes oily; embryo straight, curved or plicate.

---

[1] By the end of 2004 Dr. Grady L. Webster sent me a far advanced version of his treatment of the Euphorbiaceae for this book series and, in June 2005 a few months before his death (Oct. 27, 2005), I received an additional document from him dealing with a review of suprageneric and generic taxa in the family. That year, I could not immediately take care of these documents because I was busy with other volumes of this series. In 2008, through the courtesy of Drs. K.J. Wurdack and P.E. Berry, I received what I thought to be further updated documents left by Grady at the time of his death in his laboratory; contrary to my expectation, however, these did not differ from those supplied earlier by Grady himself. Although the author had made perusal of many taxonomic revisions and publications on pollen morphology and seed anatomy, it was evident that the manuscript needed substantial revision in the light of more recent publications in molecular systematics accrued before and after Grady's death. Regrettably, Dr. Wurdack, the born heir of Grady, did not wish to revise the manuscript so that this task fell onto me, in an effort to not loose Grady's work spanning several years. The paper thus contains many changes introduced by me without being able to secure the author's formal approval, but these were essential for this paper to reflect the high standard that distinguished Dr. Webster's scientific production. Whereas the molecular-cladistic papers on the euphorbs in the widest sense, mainly those by Wurdack and Berry and their co-authors, were of greatest value for me in this task, I must emphasise that the main objective of this series is to give baseline information, whereas further elaboration of a cladistic classification of the family would have been beyond my desire and capacity.

My thanks go to Drs. K.J. Wurdack and P.E. Berry for showing me the manuscripts left by the late Dr. Webster. Prof. W.S. Armbruster is warmly thanked for going through parts of the manuscript lying within his interest and for updating the section on reproductive biology. I am also most grateful to Dr. R. Secco for his comments on Amazonian euphorbs, and to Dr. V.W. Steinmann for advice on subtribe Euphorbiinae.

K. Kubitzki

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_10,

The family is here construed to include 299 genera with 8,000 species; these are grouped into 47 tribes in seven subfamilies, the biovulate Phyllanthoideae and Oldfieldioideae, and the uniovulate Peroideae, Cheilosoideae, Acalyphoideae, Crotonoideae, and Euphorbioideae (see below under CIRCUMSCRIPTION AND SUBDIVISION OF THE FAMILY). Although the family is nominally cosmopolitan (except for the polar regions), it is poorly represented in cool temperate zones and best developed in subtropical and tropical regions.

VEGETATIVE MORPHOLOGY. Euphorbiaceae are highly variable in vegetative structure, with a great range of life forms, including trees, shrubs, and perennial and annual herbs. Sympodial growth related to inflorescence production is common, especially in subfamilies Crotonoideae and Euphorbioideae (Hallé 1971). Scandent life forms are rare in Euphorbioideae (tribe Stomatocalyceae), unknown in Oldfieldioideae and Crotonoideae (except *Omphalea*), but common in Acalyphoideae tribe Plukenetieae. In subfam. Phyllanthoideae the branching pattern tends to be monopodial and inflorescences axillary, and there is a striking tendency toward monopodial plagiotropic branching as in *Flueggea* and *Phyllanthus*. A further specialization of this pattern yields the deciduous, floriferous, phyllomorphic branchlets found in several genera of the Phyllanthinae, including *Breynia*, *Glochidion*, *Phyllanthus*, and *Sauropus*. This highly specialized growth from, first documented by Dingler (1885) and designated as "phyllanthoid branching" by Webster (1956), includes some unique patterns such as the relegation of photosynthetic leaves and flowers to specialized deciduous branchlets in *Phyllanthus* and related genera (Dingler 1885; Webster 1956; Roux 1968; Bancilhon 1971; Rossignol and Rossignol 1985). Subfam. Oldfieldioideae resembles the Phyllanthoideae in having relatively unspecialized monopodial branching patterns. The most divergent life form in the Euphorbiaceae is found in a single neotropical section (*Salviniopsis*) of *Phyllanthus*. Mature plants float unrooted on the surface of white-water streams and lakes in the Amazonian region.

Phyllotaxis in Euphorbiaceae is predominantly alternate (spiral or distichous), but opposite or whorled leaves are common in the Oldfieldioideae and Euphorbioideae. Leaves in the Euphorbiaceae vary in size from scale leaves less than 1 mm long in succulent Euphorbias to the umbracular leaves of *Macaranga gigantea* with blades exceeding 50 cm in diameter. Leaves are usually stipulate, although stipules have been lost in various taxa, notably in *Croton* and *Euphorbia* (Uhlarz 1978). Leaf blades are prevailingly simple or lobed, but palmate/pinnately dissected laminae occur in Oldfieldioideae (*Piranhea*), and Crotonoideae (*Hevea*, *Joannesia*, *Leeuwenbergia*, and species of *Manihot*). There is some variation in ptyxis (leaf blade folding in bud): the study of Cullen (1978), although based on a limited sample, indicates that most of the subfamilies have conduplicate ptyxis, but Euphorbioideae are mainly supervolute. Leaves are persistent in tropical rainforest taxa, but usually deciduous in genera adapted to monsoonal or arid climates. Leaf blade venation is mostly brochidodromous; margins may be entire or toothed with "theoid" or "violoid" teeth (Hickey and Wolfe 1975). An atlas of leaf venation has been published by Klucking (1997, 2003).

The widespread adaptation of Euphorbiaceae to arid habitats has led to characteristic morphological and physiological traits. The succulent life form is well represented in Euphorbiaceae, especially in subfamilies Crotonoideae and Euphorbioideae. Succulent species, mostly caudiciform or geophytic, also occur in African and American *Jatropha*. The immense diversity of the genus *Euphorbia*, which comprises over 2,000 recognized species, is paralleled by enormous structural, ecological and physiological variation; it is the only land plant genus in which the three major photosynthetic pathways are expressed. In a phylogenetic analysis Horn et al. (2012) identify a woody, non-succulent growth form with C_3 photosynthetic pathway as ancestral. Cactiform succulents with CAM photosynthesis amount to nearly 650 species and have arisen in two clades within *Euphorbia*; most of them are concentrated in eastern and southern Africa. An independent evolution of herbs has taken place in the *Esula* Clade and *Chamaesyce* Clade of *Euphorbia*, in the latter accompanied by the acquisition of all three photosynthetic pathways.

VEGETATIVE ANATOMY. Wood anatomy in the Euphorbiaceae was reviewed by Pax (1884) in his first study of the family, and treated in greater detail by students of Radlkofer (Rittershausen 1892; Froembling 1896; Rothdauscher 1896; Herbert 1897), and by Solereder (1908). Metcalfe and Chalk

(1950) synthesized much of these data in their classic work on the anatomy of the dicots. From the studies of Mennega (1987) on Phyllanthoideae and Hayden (1994) on Oldfieldioideae, it appears that the apparently least specialized wood structure is present in Phyllanthoideae tribes Wielandieae and Antidesmateae, evidenced by thick-walled, non-septate fibers, abundant axial parenchyma, and vessel elements with scalariform perforations. In other tribes of Phyllanthoideae, there are trends toward wood with septate, thin to moderately thick-walled fibers, scanty parenchyma, and porous vessel element perforations. In Oldfieldioideae, fibers are non-septate, the rays narrow and heterocellular, axial parenchyma is abundant and diffuse or in wide bands, and vessel perforations are simple with exception of *Podocalyx* (and *Paradrypetes*), which have multiple perforation plates in very long vessel elements. With some exceptions (*Acalypha*, *Clutia*, *Pogonophora*), the basic pattern of wood structure is similar in Acalyphoideae, Crotonoideae and Euphorbieae. Scalariforn vessel perforation plates are lacking; intervascular and vessel/ray pitting is medium to very large; axial parenchyma is apotracheal diffuse or banded; rays are numerous, narrow, heterocellular, and often vertically fused; fibers are non-septate, often wide and thin-walled (Mennega 1987).

Laticifers appear to be completely absent in Phyllanthoideae and Oldfieldioideae but are well-developed in subfamilies Crotonoideae and Euphorbioideae (Rudall 1987). Most laticifers are unicellular (non-articulated) and produce whitish latex, but colored (yellow or red) latex occurs in some Crotonoideae. In the two basal tribes of Crotonoideae (Micrandreae and Manihoteae), the laticifers are mostly multicellular (articulated), with mainly whitish latex. According to Rudall (1994), the multicellular laticifers of *Hevea* and *Manihot* may have evolved from the non-articulated type, and the articulated laticifers reported in *Jatropha* (Dehgan and Craig 1978) may have evolved independently. The latex in tribe Euphorbieae is unusual in containing distinctively shaped (rod- or dumbbell-like) starch grains; the distribution of these starch grain types is considered to be of taxonomic significance (Mahlberg 1975). Latex of Euphorbieae is often toxic, due to triterpenes and diterpenes. Foliar sclereids have been detected in various Acalyphoideae. Rudall (1994) suggests that sclereids (in at least some instances) may be homologous with laticifers.

The indumentum of leaves and stems is highly diverse in the Euphorbiaceae (Metcalfe and Chalk 1950), and has often been used as a diagnostic character. In the biovulate subfamilies it consists usually of simple unicellular or uniseriate trichomes; bifurcate trichomes are known from *Austrobuxus*. Both glandular and branched hairs are common in the uniovulate subfamilies. In *Croton*, there is great diversity in the size, color, and number of rays of branched trichomes (Webster 1993). Dibrachiate (malpighiaceous) trichomes are characteristic of various genera in the Acalyphoideae and Crotonoideae. Particularly notable are the stinging hairs found in Acalyphoideae (Plukenetieae) and Crotonoideae (*Cnidoscolus*). The urticant hairs have clearly evolved independently in the two subfamilies and are basically different in morphology: *Cnidoscolus* stinging hairs are of the *Urtica* type—hollow, with thin walls and deciduous tip (Thurston and Lersten 1969); those of the Plukenetieae represent a unique type, with a central crystalliferous cells forming a kind of hypodermic syringe (Thurston 1976).

Detailed analyses of foliar vention patterns and leaf structure in Phyllanthoideae and Oldfieldioideae have been presented by Levin (1986a, b) and Hayden (1994). Accordingly, stomata are paracytic, brachyparacytic, or anisocytic in Phyllanthoideae, and brachyparacytic (derived) in Oldfieldioideae, with exception of the anomocytic *Podocalyx* (and paracytic *Paradrypetes*). The occurrence of tanniniferous cells in the adaxial leaf epidermis has been confirmed for supertribe Antidesmodae. An atlas of leaf venation in all the subfamilies has been published by Klucking (1997, 2003).

Foliar glands are rare in the Phyllanthaceae, but common in the uniovulate subfamilies. Laminar (embedded) glands appear to be usually derived independently of those at the leaf base or apex of petiole (Bernhard 1966). Inflorescence bracts in the Crotonoideae and especially the Euphorbioideae often have glands that appear homologous to foliar glands, although morphologically divergent. The glands of the cyathium of *Euphorbia* are anatomically similar to and appear to be homologous with those of the thyrses of the Hippomaneae. Although the function of foliar glands may be to attract ants that can deter herbivores, bracteal glands of genera such as *Mabea* appear to be a major source of nectar to attract pollinators (Steiner 1981, 1983).

INFLORESCENCE STRUCTURE. The basic inflorescence pattern in Euphorbiaceae is cymose, as in many angiosperm families. The prevailingly cymose nature of the Euphorbiaceous inflorescence is most explicit in the dichasial inflorescences of genera such as *Cnidoscolus* (Bawa et al. 1982) and *Jatropha* (Dehgan and Webster 1979), where a terminal pistillate flower is subtended by lateral staminate axes. These inflorescences are usually protogynous; the spatial and temporal separation of the staminate and pistillate flowers have the effect of limiting the degree of geitonogamy in pollination. In many genera, the dichasia are reduced to axillary glomerules, and separation of the sexes is commonly achieved by dioecy or by spatial separation. A common modification is a spicate arrangement of cymules (the thyrse). Paniculate and thyrsopaniculate inflorescences, arising from elaboration of dichasia or aggregation of thyrses, appear to represent an end-point in elaboration. Primitively, each flower in an inflorescence is bracteate. Bracts may be deciduous or persistent, and are sometimes distinctively colored, especially in aggregations of flowers into pseudanthia.

Pseudanthia have arisen in all of the subfamilies except for the Cheilosoideae and Crotonoideae. In *Uapaca* (Phyllanthoideae), the pedunculate pseudanthia with 5–10 imbricate colored bracts resemble single flowers (the pistillate flowers are solitary). In Peroideae, the flowers of *Pera* form involucrate capitula enclosed in involucres of 1–2 smaller outer and two larger inner valvate bracts. Most species of *Dalechampia* (Acalyphoideae) have spectacular bisexual, bilaterally symmetrical pseudanthia in which the paired bracts may vary greatly in size, color, and lobing; the pistillate dichasium of three flowers is ventral to a staminate dichasium of mostly 4–21 flowers associated with a resiniferous gland derived from modified bractlets (Webster and Armbruster 1991). Finally, in the Euphorbioideae an entire tribe, the Euphorbieae, is characterized by the pseudanthial cyathium, which closely resembles a bisexual flower and traditionally is interpreted as an inflorescence with a single terminal pistillate flower surrounded by clusters of highly reduced staminate flowers. Hoppe and Uhlarz (1982) and Hoppe (1985) studied the morphogenesis of several species of *Euphorbia* and interpreted their findings within the classical morphological framework. Prenner and Rudall (2007) and Prenner et al. (2008), who included in their study a broader sampling of genera of the Euphorbieae such as *Anthostema*, *Dichostemma*, *Neoguillauminia*, *Calycopeplus*, and *Euphorbia*, suggested several scenarios for a derivation of the cyathium; their findings imply that the nectariferous appendages may not all be of stipulate derivation, as previously believed.

FLORAL STRUCTURE. Since the classic essays on floral structure by Baillon (1858) and Eichler (1875), there have been few comprehensive surveys besides that of Michaelis (1924). Hermaphroditic flowers are rare and sporadic (e.g., in *Jatropha*, and less commonly in *Croton* and *Phyllanthus*), and are not consistently present in any single species. The basic floral pattern is pentamerous, as found in the Phyllanthoideae tribe Wielandieae (e.g., in *Heywoodia*, *Wielandia*). The presumably plesiomorphic and apomorphic states of some of the salient floral characters have been tabulated by Webster (1994a). In virtually all genera, the flowers are hypogynous. Whereas more than half of the genera of the Phyllanthoideae have well-developed petals in at least one of the sexes, nearly all members of the Oldfieldioideae are apetalous. The sepals in some apetalous genera may be distinctly petaloid (e.g., in *Cnidoscolus*, *Manihot*, and *Phyllanthus*). Aestivation of the floral parts, especially the sepals, has been used as a diagnostic character; sepals are imbricate in most of the Pyllanthoideae, whereas in the majority of genera of Acalyphoideae the staminate sepals, at least, are valvate. In pistillate flowers petals are present in some genera of all the subfamilies except the Euphorbioideae; they are usually inconspicuous but can be distinctly showy in some Crotonoideae (e.g., *Aleurites*, *Jatropha*). Except for the Euphorbioideae, a floral disk is generally present although sometimes reduced in pistillate flowers. In the majority of genera, the androecium includes 2–20 stamens, but the stamen number is reduced to 1 in *Dalembertia* and the Euphorbieae, and in some Acalyphoideae and Crotonoideae it has proliferated to 50–100 stamens or more. In many instances, the filaments of the stamens are united into a column, and sometimes (e.g., in *Phyllanthus* and *Omphalea*) the anthers are connate as well. This may also apply to *Androstachys* and *Stachyandra* (Oldfieldioideae), the stamens of which have been interpreted as *spirally* inserted; for details, see under the generic treatment (p. 93). Müller (1866) used anther dehiscence (introrse or extrorse) as a diagnostic character, and it is still a useful indicator of affinity in many cases. Sometimes, there is a rudimentary gynoecium (pistillode) in the center of the staminate flower. The perianth of pistillate flowers is often meristically the same as in staminate flowers, but the sepals often become modified during fruit development to enlargement (accrescence) in some cases, but in other cases the sepals are deciduous in fruit.

The Euphorbiaceous gynoecium is generally described as hypogynous and 3-carpellate. However, carpel number may vary from 2 (sporadically) to 5 or 10, and occasionally the gynoecium may be unilocular or 20-locular (*Hura*). Stylodia vary greatly in configuration, but most commonly are bifid, and often are connate at least at the base; in various taxa they are unbranched (e.g., *Alchornea*, Hippomaneae) or may be repeatedly bifurcate (e.g., in *Croton*). Placentation is axile; Berg (1975) is of the opinion that the Euphorbiaceae show a variation of the axile structure that is linked to the explosive capsular fruit. Each locule contains one or two ovules, which are anatropous and epitropous (i.e., with raphe adaxial) and crassinucellate; the nucellus is extended and may protrude as a nucellar beak far out of the micropyle. There is usually an obturator projecting from the placenta over the micropylar region of the ovule. Epitropous ovules are common among the Malpighiales, and obturators are not restricted to the Euphorbiaceae, but nucellar beaks appear to be very rare elsewhere (only in Malpighiaceae, Polygonaceae). However, the combination of epitropous ovules, obturators and extended nucellar beaks has not been reported for any other angiosperm family, and therefore provides a strong morphological argument for the monophyly of the Euphorbiaceae s.l. (Sutter and Endress 1995; Merino Sutter et al. 2006).

POLLEN MORPHOLOGY. The taxonomic significance of pollen morphology in the Euphorbiaceae, first demonstrated by Erdtman (1952), has stimulated investigations by a number of later workers. Punt (1962), using light microscopy, produced a survey of pollen in the family and established many palynological "types" that were more or less well correlated with phylogenetic position. Köhler (1965), also using LM, proposed a number of taxonomic realignments, notably a new subfamily, the Oldfieldioideae. Detailed palynological surveys using SEM and TEM have been made for the Oldfieldioideae (Levin and Simpson 1994), the Crotonoideae (Nowicke 1994), the Peroideae, the Cheilosoideae, and the Acalyphoideae (Nowicke et al. 1998, 1999, Takahashi et al. 2000; Nowicke and Takahashi 2002). Although no complete atlas of pollen in Phyllanthoideae and Euphorbioideae has been published, there have been a number of studies of infrasubfamilial scope. A detailed survey of pollen morphology in the tribe Plukenetieae has been provided by Gillespie (1994). The genus *Phyllanthus* and its satellites display the most extensive variation of exine sculpturing as well as aperture structure and number, which has led to elevated numbers of colpi (often diploporate) and even to pantoporate grains (Meewis and Punt 1983; Punt 1987; Webster and Carpenter 2002; Sagun and van der Ham 2003).

Pollen features have been used as diagnostic characters to distinguish the seven subfamilies recognized here. The putatively plesiomorphic states are found in the Phyllanthoideae (tribes Wielandieae, Phyllantheae): prolate 3-colporate grains with reticulate (semitectate) exine; transmission electron microscopy has revealed a perforate or discontinuous ektexine with distinct columellae and a continuous homogeneous endexine (Levin and Simpson 1994). In subfam. Oldfieldioideae the grains are mostly oblate-globose and the apertures are contracted, grading from brevicolpate to porate and from zonoporate to pantoporate; basal taxa have at least four apertures, but in the pantoporate condition their number can reach 40; the exine is modified to radially elongate, tapering spines that are continuous with the tectum. The Peroideae are quite diversified palynologically and it is not easy to recognize a common pattern, whereas the Cheilosoideae are characterized by their echinate tectum. In Acalyphoideae the pollen is invariably tricolporate but exhibits a great diversity in structure and sculpture. Although in Crotonoideae colporate, colpate and porate pollen is present, most members of the group have inaperturate grains with an exine sculpture of triangular (−rounded) structures in continuous arrays—now widely known as "Croton pattern". Euphorbioideae have 3-colporate pollen; among them, tribe Euphorbieae appears to have strange conspicuous intine bands bordering the colpi (Suárez-Cervera et al. 2001).

KARYOLOGY. It is apparent from the excellent survey of Hans (1973), and later additions by Urbatsch et al. (1975) and others, that the Euphorbiaceae are quite diversified in chromosome number. There is no single base number from which the chromosomal variation can be derived, although Hans (1973) thought $x = 11$ to be the base number both in the Acalyphoideae and Crotonoideae. However, as 9 and 10 are nearly equally frequent base numbers, the question remains whether these numbers have an aneuploid connection and in which direction this took place. In *Euphorbia* s. l., where very many counts are available, $x = 11$ is rare. It seems that here descending aneuploidy has led to secondary base numbers 10, 9, 8, 7, 6, which were the starting points for effective polyploid speciation. The *Synadenium* clade ($x = 18$) and the *Monadenium* clade ($x = 19, 18, 17, 16$, and 12) apparently represent a mostly decreasing aneuploid series from an ancestral base number of $x = 9$ (Jones and Smith 1969). A similar descending aneuploid series can be found elsewhere in *Euphorbia*, beginning with a base number of $x = 10$ (Hans 1973). The few chromosome numbers known from Hippomaneae are based on 11, 9, and 7. According to the survey of Hans (1973) polyploidy is more frequent in the family than in other woody plant families. *Bischofia javanica* ($2n = 198$, 28-ploid if based on $x = 7$), systematically and geographically isolated, seems to represent the final stage of development in a polyploid complex, i.e., a "relictual polyploid".

REPRODUCTIVE SYSTEMS. In Euphorbiaceae, with open-pollinated strictly unisexual flowers, self-incompatibility is rare, and earlier reports of it appear to be incorrect. Self-incompatibility has been shown to be absent or incomplete in *Chamaesyce* (herbaceous species, Ehrenfeld 1976), *Hevea* (Bouharmont 1962), and *Manihot* (Jennings 1963; George and Shifriss 1967). A documented instance of self-incompatibility is that recorded for some woody Hawaiian species of *Chamaesyce* by Koutnik (1987). The absence of self-incompatibility is also well documented in *Mercurilis annua*. Both hermaphroditic and androdioecious populations are reported, and both exhibit mixed mating (i.e., a mix of self-fertilization and outcrossing; Korbecka et al. 2011). Self-compatibility is also the rule in *Dalechampia* (e.g., Sazima et al. 1985).

It seems likely that primitive Euphorbiaceae were dioecious with binucleate pollen (Webster and Rupert 1973); it is possible that the near-absence of self-incompatibility in the family is a consequence of the evolution of monoecious taxa from dioecious ancestors. Only 19 of the 300 genera of Euphorbiaceae include both monoecious and dioecious species, and the number of monoecious (131) and dioecious (142) genera is nearly equal (Webster 1994a). The Oldfieldioideae are mostly dioecious and the Euphorbioideae are mostly monoecious, but both types are well represented in the other subfamilies. As predicted by Bawa (1980) and others, taxa with ornithochorous dispersal are mainly dioecious, and myrmecochorous taxa are somewhat more likely to be monoecious. Taxa with binucleate pollen grains may be monoecious or dioecious, but it appears that trinucleate grains are produced only in monoecious species.

Prevention of autogamy in the self-compatible monoecious taxa is generally facilitated by spatial separation of the sexes, often in separate inflorescences (e.g., in *Acalypha*), and/or by dichogamy (usually protogyny). In the inflorescences of a number of genera (notably *Cnidoscolus*, *Jatropha*, and *Euphorbia*), the pistillate flowers terminate the main axis or lower dichotomies, and open before the staminate flowers (Bawa et al. 1982). In *Euphorbia*, which has bisexual pseudanthia, monoecious species are self-compatible, but in some species there is functional andromonoecy, with some early-produced cyathia lacking functional pistillate flowers (Narbona et al. 2002). The staminate cyathia are proximal in the inflorescence and open earlier than the cyathia with pistillate flowers, so there is effective protandry, in contrast to the usual protogyny and proximal position of pistillate flowers. As noted by Narbona et al. (2002), andromonoecy appears to be more frequent in perennial species, which are known to have a higher percentage of outcrossing. In *Bridelia tomentosa*, a rarely documented (but possibly frequent, see Sapindaceae in Vol. X of this book series) temporal mating system has been analyzed (Luo et al. 2007), in which each individual produces subsequently staminate, then pistillate, and then staminate flowers, with the resting periods between the flowering phases precluding selfing, and asynchrony among individuals ensuring mating partners (duodichogamy).

Although polyploidy is common in large genera such as *Croton*, *Euphorbia*, and *Phyllanthus*, published records of interspecific hybridization are rare (Webster 1967). Polyploidy is associated with apomixis in some species of *Euphorbia* (Cesca 1961).

POLLINATION. Consistent with their floral and inflorescence diversity, Euphorbiaceae show a great diversity of pollination systems and pollinator species. Pollination occurs abiotically via wind in *Acalypha*, some *Macaranga* and *Mallotus* species, *Mercurialis* (Daumann 1972; Korbecka et al. 2011), *Ricinus* (Alex 1957), and probably many other Acalypheae. Wind pollination has also been reported in *Bernardia* (Bernardieae; Bullock 1994), *Bertya* (Ricinocarpeae; Fatemi and Gross 2009), "*Celaenodendron*" (= *Piranhea*, Oldfieldioideae; Bullock 1994), some *Croton* species (Crotoneae; Bullock 1994) and possibly in two or more species of *Phyllanthus* (Subba-Reddi and Reddi 1984). Anemophilous taxa characteristically have a reduced or lacking perianth and nectary disk combined with a multiplication of stamens, catkin-like inflorescences, and smaller pollen grains than their zoophilous relatives; *Mallotus* may be transitional in this respect (Lock and Hall 1982). The extraordinarily elaborate androecium of *Ricinus*, with branching filaments and hundreds of anthers, doubtlessly reflects adaptation to anemophilous pollination, and is not a primitive character, as claimed by Venkata Rao and Ramalakshmi (1968).

Species with biotic pollination can be divided into two groups: those in which unisexual flowers are visited individually and those in which the flowers operate pseudanthially, i.e., the unisexual flowers are united into generally bisexual blossoms and pollinators visit several flowers (usually of both sexes) simultaneously (with simultaneous or sequential receptivity). Most euphorbs in the former category (visitation of individual flowers) probably have ecologically generalized pollination by a variety of pollinator species seeking nectar, particularly those belonging to the insect orders Hymenoptera and Diptera. These plants include *Croton* (Crotoneae), *Jatropha* (Jatropheae), and *Tragia* (Plukenetieae; see review in Webster 1994). Specialized pollination (by few pollinator species or functional groups) is seen in some species of *Macaranga* (Acalypheae; by thrips, Moog et al. 2002), *Breynia*, *Glochidion*, and some *Phyllanthus* (Phyllantheae; by moths, Kawakita 2010). These four cases represent the recent discovery of the brood-reward systems in the Euphorbiaceae. Here the pollinators lay eggs on or near the flowers and the larvae feed on floral tissues, much as do fig wasps on figs and yucca moths on yuccas. Moderately specialized lepidopteran pollination has been reported in *Cnidoscolus* (Manihoteae; by sphingid moths, butterflies, and even hummingbirds, depending on species). Moderately specialized pollination by mammals has been reported in Central American *Mabea occidentalis* (Hippomaneae; by bats, marsupials, and the woolly opossum, Steiner 1983) and in Central American *Hura* (Hureae; by bats, Steiner 1982). These last two cases are somewhat intermediate between individual-flower and pseudanthial functioning in that mammal pollinators respond to clusters of staminate flowers, although only one or a few pistillate flowers are involved; the less important insect pollinators of *Mabea* presumably respond to individual flowers (Steiner 1983). Incidentally, the primarily bat-pollinated *Mabea fistulifera* in disturbed semi-deciduous forest and woodland of southeastern Brazil has become the meeting point of many forest animals, including more than 30 bird species many of which are frugiverous, two ceboid primates, four frugivorous bat species, the common opossum, and the coati (*Nasua nasua*), the majority of which probably can act as pollinators (Torres de Assumpção 1981; Vieira and Carvalho-Okano 1996; Olmos and Boulhosa 2000). The unspecialized reproductive system of this tree allows its continued existence in biotically impoverished habitats, and at the same time maintains a significant part of the pollinator and frugivore community during a period when fruits are scarce or not available.

Euphorbs with fully pseudanthial inflorescences have either "normal" unisexual flowers (*Dalechampia*, *Pera*) or highly reduced unisexual flowers united in a cyathium (*Euphorbia* and relatives in Euphorbieae). In the latter case the staminate flowers are reduced to a single stamen and the pistillate flowers to a single pistil, with perianth absent in both cases. In both situations, pollinators visit the clusters of flowers as if they were a single flower—hence, application of the term pseudanthium (false flower) or blossom. Pollination of euphorbs with pseudanthial inflorescences is often highly generalized. Pollination by several to many types of insects occurs in some species of Malagasy *Dalechampia* (Plukenetieae; Armbruster and Baldwin 1998), in South American *Pera* (Pereae; Freitas et al. 2011), and many or possibly most species of *Euphorbia*. Other pseudanthiate euphorbs exhibit highly specialized pollination. Most neotropical *Dalechampia* are pollinated by females of one or a few species of resin-collecting bees (Armbruster 1984, 1988). The rewards are oxygenated triterpene resins secreted by modified bractlets borne by the staminate subinflorescence (Armbruster et al. 1997). Specialized pollination by fragrance-collecting, male euglossine bees has evolved independently from resin-reward ancestors at least three times (Armbruster 1993; Armbruster et al. 2009). The fragrance rewards are secreted by the stigmatic surface in two of these clades, and by a modified "resin gland" in one clade (Armbruster 1993). Specialized pollination by hummingbirds is seen in the *Pedilanthus* clade of *Euphorbia*; Cacho et al. 2010).

FRUIT AND SEED. The typical Euphorbiaceous fruit is a 3-locular capsule (schizocarp) that dehisces, often explosively, into three 1- or 2-seeded units (cocci or mericarps). The seeds are released when the cocci separate septicidally and sometimes loculicidally as well; in some genera the cocci remain more or less closed. The axis of the fruit, including the three placentae, persists as a columella, which may be massive or appendaged (e.g., in *Stillingia*), but is sometimes deciduous. However, in a sizeable number of genera scattered through all the subfamilies, the fruit remains indehiscent and the carpellar walls become fleshy, sometimes with a sclerified endocarp. One-seeded fruits are almost always indehiscent. Somewhat counter-intuitively, Stuppy (1996) recorded in biovulate genera only 19 (28%) with 2 seeds per locule in fruit.

The seed coat in Euphorbiaceous seeds, investigated by Netolitzky (1926), Wunderlich (1968), Corner (1976), Stuppy (1996), and Tokuoka and Tobe (1995, 1998, 2001, 2002, 2003), usually consists of two primary layers: the testa, derived from the outer integument of the ovule, and the tegmen, derived from the outer layer(s) of the inner integument. The testa usually has few cell layers, except in seeds with a sarcotesta, which may have 10 cell layers or more (Stuppy 1996). In indehiscent fruits, however, the testa may be thin or even rudimentary. Corner (1976) recognized that the variable structure of the sclerified cells derived from the outer layer of the inner integument (exotegmen) furnished important clues to relationships between genera. In biovulate euphorbs, the exotegmen is often fibrous, but the studies of Stuppy (1996) and Tokuoka and Tobe (2001) have revealed such a great variation in its structure that these authors even considered the exclusion of the aberrant genera *Oldfieldia*, *Picrodendron*, *Hymenocardia* and *Didymocistus* from the family. Among the uniovulate subfamilies, Peroideae (except for the problematic *Pogonophora*) have a peculiar seed coat consisting of only two persistent cell layers, the well-developed exotesta of radially elongated cells and the more weakly developed tracheoidal exotegmen. All remaining uniovulate Euphorbiaceae have the palisadal exotegmen composed of radially elongated cells. Carunculate seeds are lacking in the Phyllanthoideae but occur, though not consistently, in all other subfamilies. The caruncle can function as an elaiosome and, after the ballistic or barochorous ejection of the seeds, attracts ants that are implicated in a further dispersal event (Berg 1975). Bianchini and Pacini (1996) and Lisci et al. (1996) point out that the caruncle may also have functions other than mymecochory, such as facilitation or inhibition of germination.

In Euphorbiaceous seeds, starch as a storage product is replaced by protein and fat oil.

DISPERSAL. The typical Euphorbiaceous fruit (upon drying) dehisces explosively into three 1- or 2-seeded merocarps (cocci). This kind of autochorous dispersal can be quite effective in genera such as *Hevea* or *Hura*, whose seeds may be dispersed as far as 43 m (Swain and Beer 1976). However, in many genera the seed may produce appendages or a sarcotesta, and the primary autochorous dispersal is followed or superseded by animal dispersal. Seeds with fleshy integumental elaiosomes (caruncles) are dispersed by ants. In Australia, myrmecochory is especially prominent, perhaps reflecting the widespread open and xeromorphic vegetation (Berg 1975). As reported by Clifford and Monteith (1989), seed dispersal of Australian *Petalostigma pubescens* implies three distinct phases, beginning with the ingestion and transport of the drupes by migrating emus. Voided endocarps, freed from the fleshy epicarp, upon exposure to the sun dehisce explosively and project the seeds up to 2.5 m from the point of origin, and the seeds can be carried off by ants feeding on the conspicuous elaiosomes. In *Croton*, where myrmecochory is a very widespread mode of dispersal, the typical caruncles have been lost in sect. *Cuneati* with riverine species such as *C. cuneatus* and *C. yavitensis* showing an arillate structure possibly adapted to attract fish (Riina et al. 2010). Dispersal of diaspores by fish during their upstream-directed spawning migrations is a frequent phenomenon in the periodically overflooded river plains of Amazonia, where large fish such as tambaqui (*Colossoma macropomum*) and jatuarana (*Brycon* sp.) show strong preferences for the fruits of *Hevea spruceana* and *H. brasiliensis* (Goulding 1980) but have also been found to disperse the propagules of *Piranhea trifoliata* and *Mabea* sp.

Ornithochory seems to be confined to the tropics, especially in Africa and Asia, but is less common in the Oldfieldioideae and Euphorbioideae (Webster 1994a). Seeds with fleshy coats (sarcotesta), found in all five subfamilies, are generally dispersed by birds. In *Baccaurea*, for example, which has non-explosive fruits, some species have orange arils and are dispersed by birds, whereas other species have berries with sweet pulp and are dispersed by rats, fruit bats, or squirrels (Ridley 1930: 427). The fruits of the shade-intolerant riverine tree *Trewia nudiflora* (= *Mallotus*) are large, hard, and dull-colored upon ripening, unattractive to the usual seed dispersers such as monkeys, bats, and birds, but regularly eaten by the greater one-horned Asian rhinoceros (*Rh. unicormis*). Seeds deposited into the animals' dung on open grassland develop into robust, fast-growing seedlings, providing an interesting example of megafaunal dispersal (Dinerstein and Wemmer 1988).

PHYTOCHEMISTRY. Euphorbiaceae are one of the chemically most diverse angiosperm families (Hegnauer 1966, 1989; Seigler 1994). Many taxa produce toxic or medicinally important compounds (e.g., ricinin in the seed coat and castor oil in the endosperm of *Ricinus* seeds); in the tropics, they have acquired a wide use for many purposes such as for arrow poisons (*Sapium*) or as fish poisons (*Phyllanthus*). A number of genera (*Cnidoscolus*, *Dalechampia*, *Tragia*) are implicated in dermatitis. The sap of several Euphorbioideae (*Euphorbia* subg. *Euphorbia*, *Hippomane*, *Ophthalmoblapton*, *Synadenium*, *Excoecaria agallocha* = "blind-your-eye") is dangerously toxic.

Among the more significant secondary metabolites produced by Euphorbiaceae are tannins, alkaloids, cyanogenic glycosides, diterpenes, glucosinolated lipids, and triterpenes. Both condensed and hydrolysable tannins are present in the family, mostly in woody species. The ellagitannin geraniin has been found in all subfamilies, and in the uniovulate ones it is often accompanied by the similar mallotusinic acid. Alkaloids are particularly diverse in Phyllanthoideae, Crotonoideae (especially *Aleurites*, *Croton*, *Jatropha*) and in some Acalyphoideae (*Alchornea*, *Mallotus*, *Ricinus*), but there is no structural type of alkaloids characteristic for the family. Cyanogenic glycosides are widespread in Phyllanthoideae (*Andrachne*, *Bridelia*, *Flueggea*, *Phyllanthus*) and Crotonoideae (*Aleurites*, *Croton*, *Elateiospermum*, *Hevea*, *Manihot*), but have also been reported from Acalyphoideae (*Acalypha*, *Mercurialis*, *Ricinus*) and several Euphorbioideae. A considerable variety of diterpenes occur in Euphorbiaceae. Cyclic diterpenes are especially prominent in Crotonoideae (*Bertya*, *Croton*, *Jatropha*). Tetracyclic diterpenes isolated from species of *Croton* have been implicated as cocarcinogens. Triterpenes are common in many Euphorbiaceae, especially the Euphorbioideae. In *Euphorbia*, investigations of triterpene composition have produced suggestive evidence for delimiting subgenera and sections (Ponsinet and Ourisson 1965). Terpene-rich latex in many Euphorbiaceae is also accompanied by rubber (polyisoprenes). Although *Hevea* is the best known source of rubber, it is also produced by other Crotonoideae such as *Cnidoscolus*, *Manihot*, and *Micrandra*, as well as *Chamaesyce* and *Euphorbia* (Rizk 1987).

Paleobotany. The Euphorbiaceae, despite their contemporary prominence and broad distribution, do not have an impressive fossil record. Fossil woods, such as the much-cited *Paraphyllanthoxylon* from the Cretaceous of North America (Bailey 1924; Cahoon 1972), cannot be convincingly verified as Euphorbiaceous. Mädel (1962), in a study of Cretaceous fossils from South Africa, plausibly suggested that *Paraphyllanthoxylon capense* is similar to *Margaritaria discoidea*. Mädel's *Securinegoxylon biseriatum* can perhaps be compared with *Heywoodia lucens*, which grows in South Africa today.

There is greater certainty in the relationships of the Eocene fossils of fruits from America and Europe that have been referred to the Hippomaneae by Mazer and Tiffney (1982) and Dilcher and Manchester (1988). Both *Wetherellia* and *Palaeowetherellia*, in fruit morphology and in the depositional facies in which they occur, can be associated with the living genus *Hippomane*; Dilcher and Manchester consider *Crepetocarpon* to be unquestionably close to *Hippomane*.

Fossil flowers of Euphorbiaceae are little known, but the Eocene *Hippomaneoidea* of Crepet and Daglian (1982) is well-preserved, and the pollen suggests a relationship to *Senefeldera*, a neotropical genus considerably less specialized than *Hippomane*.

Dispersed fossil pollen can be hazardous to identify but, according to Muller (1984), genera resembling the Oldfieldioideae, Acalyphoideae, and Crotonoideae are known from the early Tertiary. A notable record of Euphorbiaceous pollen from the Eocene in France (Gruas-Cavagnetto and Köhler 1992) includes a wide range of taxa: *Actephila*, *Antidesma*, *Bischofia*, *Leptopus*, and *Phyllanthus* (Phyllanthoideae); *Austrobuxus* and *Dissiliaria* (Oldfieldioideae); *Alchornea* and *Ricinus* (Acalyphoideae). In Australia, Oldfieldioideae appear in the Paleocene and, in the early Eocene, in greater diversity (Martin 1974, 1978). Because the pollen of most Phyllanthoideae is morphologically unspecialized, it may be difficult to follow the record of fossil pollen of the Euphorbiaceae back into the Cretaceous. Taking the available evidence into account, however, it seems reasonable to surmise that the Phyllanthoideae and Oldfieldioideae, at least, had differentiated by the upper Cretaceous and that the radiation of the subfamilies had occurred by the Paleocene.

Distribution and Habitats. Although Euphorbiaceae are a pantropical family, they also extend into subtropical and warm temperate regions, and some herbaceous species of *Euphorbia* occur in subpolar and alpine areas. Generic diversity for Phyllanthoideae is greatest in Africa, for Oldfieldioideae in Australasia, and for Acalyphoideae and Euphorbioideae in Asia; diversity is approximately equal in American and Asiatic Crotonoideae (Webster 1994a). In total generic diversity, American leads with 111 genera, followed by Asia with 107, Africa with 102, and Australasia with 77. Madagascar, with 51 genera (17 endemic), is the most distinctive subregion.

Among the Phyllanthoideae there are genera—mostly smaller ones—that are restricted to Africa/Madagascar, such as *Wielandia*, *Lachnostylis*/*Securinega*, and *Uapaca*. Some large genera such as the *Meineckia*, *Flueggea*, and *Margaritaria* have a pantropical distribution that includes the African/Malagasy region. There are remarkable disjunctions between closely related genera, such as between the African *Heywoodia* and the neotropical *Chascotheca* + *Astrocasia*. The closest relatives of the strictly African/Malagasy *Wielandia* are the east Asian *Dicoelia* + *Chorisandrachne*, and African *Hymenocardia* is close to neotropical *Didymocistus*. This highly disjunct distribution of the tribes and genera is most likely the result of long-distance dispersal, as has been suggested for *Bridelia*, which very likely dispersed from tropical Africa to Asia and Australia once or twice from 10 million years ago onward (Li et al. 2009).

In the Oldfieldioideae, which are best developed in Australasia, much more compact distribution patterns of the (sub)tribes can be recognized. The whole group is highly disjunct, with the tribally isolated neotropical *Podocalyx* and tribe Picrodendreae disjunct between the New World and Africa/Madagascar. The genera of Mischodontinae, with exception of the Ceylonese *Mischanthus*, all are Madagascan. Tribe Caletieae is a group of 14 genera centered in Australia with a paleontological record dating back there into the Paleocene (Martin 1974, 1978).

Peroideae are utterly disjunct, and Cheilosoideae restricted to the Oriental region. Acalyphoideae are widely distributed in the neo- and paleotropical region including Australia, and only few and smaller tribes are restricted to a single continent, such as neotropical Adelieae, Asian Erismantheae, and Australian Ampereeae;

the large tribes Acalypheae and Plukenetieae are pantropical. Crotonoideae are well represented in the New World, with Crotoneae, Micrandreae, etc., or in the Old World with inclusion of the Australasian region (Codieae, Ricinocarpeae), but have a weak representation in Africa. In Euphorbiodeae the four genera of Stomatocalyceae, two of them monotypes, present a highly disjunct picture, with one genus in the New World, two in Africa, and one in Australasia. A similar trend is evident in the equally relictual basal subtribes of the Euphorbieae, the Anthostematinae and Neoguillauminiinae. Subtribe Euphorbiinae, i.e., *Euphorbia* s. l., is subcosmopolitan, with the *Rhizanthium* clade including mostly southern African xerophytes, the *Esula* clade with predominantly northern hemisphere herbaceous species, the *Euphorbia* clade representing the greatest diversity within the genus formed mainly by African/Madagascan xerophytes, and the mainly New World *Chamaesyce* clade.

Despite their diversity, Euphorbiaceae are predominantly shrubs or short-lived trees adapted to secondary succession in dry to mesic seasonal habitats. In savannas, tropical deciduous forests, and deserts, genera such as *Chamaesyce*, *Cnidoscolus*, *Croton*, *Euphorbia*, *Hymenocardia*, and *Jatropha* are well represented. However, there are also a significant number of genera in lowland tropical rainforest: in America, *Alchornea*, *Amanoa*, *Hevea*, *Hieronyma*, *Micrandra*, and *Richeria*; in Africa, *Maesobotrya*, *Spondianthus*, and other Phyllanthoideae; in Asia and Australasia, *Antidesma*, *Aporosa*, *Baccaurea*, *Glochidion*, *Macaranga*, and *Mallotus*. Adaptation to diverse habitats can be seen even within single genera. For example, while most *Dalechampia* are twining vines or lianas adapted to secondary environments with very high light levels, one clade of 3–4 species, sect. *Cremophyllum*, is a small monopodial shrub largely restricted to the dark understorey of primary rainforests. In tropical regions, some Euphorbiaceae have adopted specialist roles. Along rivers, there are a number of rheophytes adapted to surviving strong currents and submergence, including species of *Phyllanthus* and *Homonoia*. Rooted aquatics are found in *Caperonia* and *Phyllanthus*; the only floating aquatic in the family is the Amazonian *Phyllanthus fluitans*.

Ericoid life forms are common in Australia, especially in *Bertya*, *Beyeria*, *Micrantheum*, and *Pseudanthus*. Ultramafic (serpentinic) outcrops, especially in Cuba and New Caledonia, have housed a spectacular radiation of sclerophyll species of *Phyllanthus*. Sand dunes in subtropical arid regions support psammophile species of *Chamaesyce*, *Chrozophora*, and *Croton*.

CIRCUMSCRIPTION AND SUBDIVISION OF THE FAMILY. The circumscription of the Euphorbiaceae had remained surprisingly stable over a long period of time (Webster 1987), whereas its infrafamilial classification remained contentious (reviewed in Webster 1987, 1994a). Delimitation of infrafamilial taxa was long obfuscated by Müller's unnatural binary division of the family into Platylobeae and Stenolobeae (Müller 1866), which—despite its rejection by Bentham (1880)—was adopted by Pax (1890) and Pax and Hoffmann (1931). Bentham (1880) and later Hutchinson (1969) recognized only the tribal level as the major infrafamilial rank, whereas Pax (1884, 1890) recognized two main subfamilies, Phyllanthoideae and Crotonoideae, for the biovulate and uniovulate taxa, a critical distinction not grasped by Müller and Bentham but accepted since then by most systematists. Nevertheless, the heterogeneity within these two major infrafamilial groups prompted Webster (1975, 1994b) to propose a system of five subfamilies: Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae, and Euphorbioideae. This was generally adopted, notwithstanding the claims by various authors to elevate superficially anomalous genera such as *Hymenocardia*, *Uapaca*, *Bischofia*, etc. to family rank—after closer inspection, these were found to be untenable. In the system of Webster (1994b), the number of tribes was increased from 14 to 49, a number again slightly increased by Radcliffe-Smith (2001).

Corner's (1976) studies in seed coat structure of the dicotyledons led him to question the homogeneity of the family, an opinion that received support from upcoming DNA sequence studies. Molecular systematics, beginning with the work of Wurdack (2002), led to a radical dismemberment of the family into three families, the Phyllanthaceae and Picrodendraceae (= Oldfieldioideae), both biovulate, and the uniovulate

Euphorbiaceae, apart from the hardly disputed expulsion of some extraneous genera relegated to the Putranjivaceae, Centroplacaceae, and Pandaceae. More recently, and not unexpectedly, increased molecular resolution of the deeper nodes of the Malpighiales tree has resolved Phyllanthaceae and Picrodendraceae (Oldfieldioideae) as strongly supported sisters (Tokuoka and Tobe 2006; Wurdack and Davis 2009; Korotkova et al. 2009; Soltis et al. 2011); this means that, for those who want to maintain different families for biovulate and uniovulate euphorbs, there is no longer any compelling necessity for distinguishing between Phyllanthaceae s. str. and Picrodendraceae.

Broad-based molecular phylogenetic analyses of representatives of the traditional uniovulate subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae have recovered the uniovulate euphorbs as monophyletic (Wurdack et al. 2005; Tokuoka 2007; Xi et al. 2012), and have brought to light novel groupings that largely correlate with the distribution of traditional characters such as latex and laticifers, pollen morphology, and ovular and seed coat characters. Two strongly supported basal clades have been proposed as additional subfamilies (Peroideae and Cheilosoideae), whereas the rest of the family is divided into seven major lineages. Among them, the core Acalyphoids and the Euphorbioideae are monophyletic groups, whereas the Crotonoideae are resolved as several distinct and partly not well-supported clades.

Strong molecular evidence supports the monophyly both of the biovulate and uniovulate Euphorbiaceae, whereas molecular proof for the monophyly of the Euphorbiaceae s. l. is still lacking. The most recent analysis (Xi et al. 2012) places the biovulate and uniovulate euphorbs, the latter together with Linaceae and Ixonanthaceae, in a weakly supported clade. There are, however, important similarities in embryological, gynoecial and fruit structures between Phyllanthaceae s. l. and Euphorbiaceae s.str. First, the combination of nucellar beaks, epitropous ovules, and obturators within the angiosperms is restricted to Euphorbiaceae s. l. (Sutter and Endress 1995; Merino Sutter et al. 2006; see above under FLORAL STRUCTURE). Second, the fruit morphology of the Euphorbiaceae s. l., which has attracted the interest of botanists since the time of Baillon (1858; see also Berg 1975), is highly significant; the formation of cocci, separating from a central column, is a characteristic of the family and has been the basis of the earlier ordinal name, Tricoccae. The cocci and their xerochastic sclerenchymatic endocarp tissue instrumental in the explosive dehiscence are the basic elements of the explosive seed release characteristic for the family.

These structural traits support the close relationship between the uni- and biovulate euphorbs, and have led us to retain the broad family concept of the family. Further molecular inquiry into the deeper nodes of the phylogeny of the Malpighiales beyond the interesting findings of Xi et al. (2012) is impatiently expected for a clarification of this issue.

ECONOMIC IMPORTANCE. As a consequence of their chemical diversity, the Euphorbiaceae include a considerable number of economically important species (Schultes 1987). The currently most valuable commodity is probably the starchy tubers of cassava (*Manihot*), widely cultivated in America and Africa. The Pará rubber tree (*Hevea*), the most important Euphorbiaceous crop in the 19th century, is still the major source of non-synthetic commercial rubber. Seed oils of tung (*Aleurites*) and castor bean (*Ricinus*) continue to be widely used, but in South America there is now considerable interest in the seed oil of inchi (*Caryodendron*), which is considered superior to the oil of the African oil palm, *Elais* (Schultes 1987). Waxes from neotropical species of *Sapium* and *Euphorbia* (especially *E. antisyphilitica*) are still a minor source of commercial waxes. Use of the latex of *Euphorbia tirucalli* plants as "gasoline trees", once vigorously advocated by Calvin (1987), appeared not competitive with sugar cane.

As pointed out by Schultes (1987), many Euphorbiaceae have been cultivated in tropical areas for thousands of years. Schultes observed Amerinidians in the Amazon basin exploiting Euphorbiaceae in a variety of ways, including food, medicines, and piscicides. For example, the reddish latex of some neotropical species of *Croton* ("Sangre de Drago") is widely used in South America as a salve applied to cuts and sores. The alkaloids in Sangre de Drago latex appear to be non-toxic to humans, but other species of *Croton* produce phorbol esters that have been implicated in human cancer (Kinghorn 1979). Herbaceous species of *Phyllanthus* have long been used in folk medicine in the tropics to treat kidney and urinary problems and jaundice (Webster 2002), and pharmaceutical research has revealed many useful applications of the antiviral compounds of *Ph. amarus*, which are of potential value in treating the hepatitis B virus.

Because of their generally small inconspicuous flowers, the Euphorbiaceae include relatively few ornamental plants, but species of a few genera are commonly cultivated in tropical gardens or greenhouses for their colorful inflorescences or foliage: *Acalypha*, *Codiaeum*, *Jatropha*, *Euphorbia*. Succulent taxa of *Euphorbia* subgenus *Euphorbia*—e.g., sects. *Monadenium*, *Pedilanthus*, *Synadenium*—are popular in tropical and subtropical gardens. *Dalechampia aristolochiifolia* Kunth is a recently marketed horticultural vine increasingly cultivated in warm temperate regions for its colorful bracts (generally advertised on the internet incorrectly as *D. dioscoreifolia*).

Some Euphorbiaceae have a distinctly negative economic value; the family includes many taxa adapted for secondary succession, and hence there are a number of aggressive weeds. In temperate regions, the most damaging invaders of cultivated fields, especially in North America, are species of *Euphorbia* section *Esula*, especially *E. esula* and related species. Some weedy taxa—species of *Euphorbia*, *Mercurialis*, *Phyllanthus*—are particularly obnoxious because of their toxicity to livestock (Burrows and Tyrl 2001). Recently exotic woody Euphorbiaceae, including species of *Glochidion*, have invaded the southern United States. The most aggressive species is the Chinese tallow tree, *Triadica sebifera* (*Sapium sebiferum*), which has invaded forests and even grasslands from Florida to Texas and has become established in California.

SUBFAMILIES, TRIBES AND GENERA OF EUPHORBIACEAE

In all generic descriptions given below,

- for the sake of briefness it is generally assumed—*if not stated otherwise*—that the plants have alternate simple leaves with entire margins, distinct stipules, lack foliar glands and domatia, have anthers dehiscing longitudinally, and that their petioles are not pulvinate;
- rarely occurring character states are given in parentheses ( ), whereas square brackets [ ] are used in taxonomic descriptions for comments and explanations.

Users of this treatment who want to make determinations of genera of Euphorbiaceae may use this **multichoice key:**

Hoffmann, P., Kirkup, D., Galster, A.M., Challen, G., Radcliffe-Smith, A. 2005. Key to the genera of Euphorbiaceae *sensu lato*. Available at www.kew.org/herbarium/keys/euphorbs

CONSPECTUS OF THE SUBFAMILIES OF EUPHORBIACEAE

1. Locules of ovary each with 2 ovules; milky latex, intraxylary phloem, and stinging hairs 0; indumentum simple (lepidote or dendritic); embedded foliar glands rare; pollen grains binucleate **2**

– Locules of ovary each with 1 ovule; latex + or 0; indumentum various; pollen grains binucleate or trinucleate 3

2. Leaves alternate (opposite), stipulate, simple and unlobed [except in *Bischofia*]; petals + or 0; pollen grains tricolporate to -porate, sexine lacking spines [except in *Amanoa and Croizatia*]; seeds ecarunculate **I. Subfam. Phyllanthoideae** (p. 64)

– Leaves alternate, opposite, or whorled, stipulate or estipulate, simple to trifoliolate; petals 0; pollen grains colporoidate to porate, sexine spiny; seeds carunculate or ecarunculate **II. Subfam. Oldfieldioideae** (p. 90)

3. Ovules with thin integuments [inner integument < 6 cells thick]; seeds arillate; seed coat with tracheoidal exotegmen **III. Subfam. Peroideae** (p. 102)

– Ovules usually [Adenoclineae excepted] with thick integuments [inner integument > 8 cells thick]; seeds arillate or not; seed coat with palisadal exotegmen **4**

4. Pollen exine echinate; flowers apetalous; seeds exarillate **IV. Subfam. Cheilosoideae** (p. 105)

– Pollen exine not echinate; flowers petaliferous or apetalous; seeds arillate or exarillate 5

5. Milky latex 0; laticifers, if present, non-articulate; pollen grains binucleate **V. Subfam. Acalyphoideae** (p. 106)

– Latex + (scanty or 0), milky or colored; laticifers articulate or non-articulate; pollen grains binucleate or trinucleate **6**

6. Latex reddish or yellowish to milky; laticifers articulate or non-articulate; leaves unlobed to lobed or compound; indumentum simple, stellate, dendritic, or lepidote; bracts usually not biglandular at base; sepals imbricate to valvate, usually completely covering anthers in bud; petals mostly + [at least in

pistillate flowers]; pollen grains tricolporate or more often porate or inaperturate, with hexagonal sexinous processes

VI. Subfam. Crotonoideae (p.156)

– Latex whitish (yellow), often caustic or toxic; laticifers non-articulate; leaves usually unlobed; indumentum simple or lepidote (dendritic in some Hippomaneae); bracts often biglandular at base; sepals imbricate to reduced or 0, anthers mostly not covered in bud; petals 0; pollen grains tricolporate, exine mostly perforate-reticulate

VII. Subfam. Euphorbioideae (p. 190)

I. SUBFAM. PHYLLANTHOIDEAE Beilschm. (1833).

Phyllanthaceae Martinov (1820).

Monoecious or dioecious trees, shrubs, or herbs; vessel elements with simple to scalariform perforations; indumentum mostly simple. Leaves alternate (opposite), spiral to distichous, usually stipulate, simple and entire, trifoliolate and dentate in *Bischofia*, without embedded glands, stomata mostly paracytic or anisocytic; petiole eglandular. Inflorescences axillary (terminal), of racemoid or spikelike thyrses or reduced to glomerules or flowers solitary; bracts eglandular. Sepals mostly 4–6, imbricate (valvate), usually ± basally connate; petals and disk + or 0; stamens (2)3–8(−60), filaments distinct or connate; anthers dehiscing horizontally to vertically; pollen grains mostly 3–4(−7)-colporate (−porate), exine mostly semitectate (echinate); male gametophyte binucleate; pistillode + or 0; ovary (1)2–5(−20)-locular, ovules 2 in each locule, anatropous or hemitropous, nucellar beak sometimes prominent; stylodia mostly distinct, usually bifid, sometimes unlobed. Fruit mostly capsular, less commonly baccate or drupaceous; columella often persistent. Seeds ecarunculate [except for *Celianella*]; endosperm + or 0; cotyledons plane, incrassate, or folded. $x = 12$ or 13 (8, 10 or 11).

A diverse subfamily comprising about 59 genera, sometimes recognized as a separate family Phyllanthaceae or Antidesmataceae. Airy Shaw (1965) split off from it four families—Bischofiaceae, Hymenocardiaceae, Stilaginaceae, and Uapacaceae; Meeuse (1990) added one more segregate, Putranjivaceae. Except for *Bischofia*, none of Airy Shaw's proposed segregates is sufficiently aberrant to make its membership in the Phyllanthoideae questionable, and all structural and molecular evidence accrued since 1990 confirms *Bischofia* as a member of Phyllanthoideae. On the other hand, Putranjivaceae have now been excluded definitely from the Euphorbiaceae on the basis of chemical and molecular studies (e.g., Chase et al. 1993; Wurdack 2002), corroborated by Tokuoka and Tobe (1999) in the demonstration of an impressive number of embryological differences between the reinstated Putranjivaceae and Euphorbiaceae and the findings by Xi et al. (2012), which place *Putranjiva* in a clade with *Lophopyxis*.

In the classification of Phyllanthoideae, which largely follows the one given by Hoffmann and Wurdack (2006), the group is subdivided into 10 tribes and 12 subtribes, which correspond with strongly supported clades of the multigene analysis of Kathriarachchi et al. (2005). In spite of this, morphologically they are often utterly disparate and, in extreme cases, determination of species and genera is said to depend on molecular analyses.

KEY TO THE TRIBES OF SUBFAM. PHYLLANTHOIDEAE

1. Leaves simple; inflorescence mainly of glomerules or thyrses; flowers with or without petals; stylodia entire to multifid; fruits capsular, baccate, or drupaceous 2

– Leaves palmately 3–5-foliolate; inflorescence paniculate or racemose; flowers lacking petals and disk; stylodia entire; fruits drupaceous

10. Bischofieae

2. Fruits winged or lobed; petals and disk 0; ovary locules 2; pollen zonoporate

5. Antidesmateae-Hymenocardiinae

– Fruits not winged; inflorescences mostly not amentlike [except in Antidesmeae]; stylodia entire to bifid (multifid); floral disk + or 0; pollen rarely zonoporate 3

3. Stems with resinous exudate; inflorescences paniculate or capitulate 4

– Stems lacking resin; inflorescences not paniculate or capitate 5

4. Petals +; inflorescence terminal, paniculate; pollen not spinulose; fruit capsular **8. Spondiantheae**

– Petals 0; inflorescence axillary, capitate; pollen spinulose; fruit drupaceous **9. Uapaceae**

5. Leaves with tanniniferous cells in upper epidermis; flowers in axillary or terminal spike-like or raceme-like inflorescences, with discernible axes 6

– Leaves without tanniniferous cells in upper epidermis; flowers in axillary glomerules, usually without discernible axes [except in *Flueggea gracilis* and some *Phyllanthus*] 7

6. Thecae usually separate and connective enlarged, anther locules ± pendulous; leaves not glandular **5. Antidesmateae**

– Thecae not separate and connective not enlarged (enlarged in some *Aporosa*), anther locules not pendulous; leaves sometimes glandular **6. Scepeae**

7. Indumentum 0; pistillate sepals persistent; inflorescence sometimes [*Celianella*] pedunculate **7. Jablonskieae**

– Indumentum + or 0; pistillate sepals usually not persistent; inflorescences not pedunculate 8

8. Foliar glands rarely +; sepals distinct or nearly completely connate; petals 0 [+ in *Heterosavia*]; disk + or 0; pistillode + or 0; ovules hemitropous or rarely [*Heterosavia*] anatropous; seeds exarillate or rarely with colored sarcotesta **4. Phyllantheae**

– Foliar glands 0; sepals ± distinct; petals + or 0; disk +; pistillode +; ovules anatropous [hemitropous in *Andrachne*]; seeds exarillate 9

9. Petals + in staminate flowers, 0 in *Chascotheca*, usually equaling the sepals **3. Wielandieae**

– Petals + or 0 in staminate flowers 10

10. Sepals 4–6(7), imbricate (valvate in *Bridelia*, *Cleistanthus*); stamens 4–10(−19); fruit dehiscent or indehiscent **2. Bridelieae**

– Sepals (3)5–6, imbricate; stamens 3–6; anthers rarely poricidal [*Poranthera*]; fruit explosively dehiscent **1. Poranthereae**

IA. Supertribe Phyllanthodae G.L. Webster, **supertrib. nov.**[1]

Subfam. Phyllanthoideae Kostel. (1836).

1. Tribe Porantheraeae Grüning (1913),

recircumscribed by Hoffmann et al., Kew Bull. 61: 41 (2006), Vorontsova et al., Amer. J. Bot. 94: 2026–2040 (2007), mol. syst.; Vorontsova & Hoffmann, Kew Bull. 63: 41–59 (2008), classif.

Staminate disk in distinct parts or extrastaminal-annular, pistillate disk simple; stamens 3–6; filaments distinct or variously connate; anthers longitudinally dehiscing or poricidal; thecae not separate and connective not enlarged; pistillode usually +; ovary 3-locular; stylodia distinct or completely connate; fruits explosively dehiscent; seeds exarillate.

Eight genera, (sub)tropical regions, worldwide. The circumscription of this group of genera was first suggested by Wurdack et al. (2004) and later confirmed by, among others, Vorontsova et al. (2007). The clade comprises genera that formerly belonged to three different tribes, and the group (and even some of its genera!) cannot be recognized on the basis of morphological characters alone. $x = 11, 12$.

Key to the Genera of Porantheraeae (from Voronts. & Hoffm. 2008).

1. Anther dehiscence poricidal; flowers appearing to be in terminal umbels or racemes (in fact in dense aggregations of axillary flowers); fruit deeply 6-lobed; no secondary leaf venation visible with the naked eye. Australia and New Zealand **4. *Poranthera***

– Anther dehiscence longitudinal; flowers clearly axillary, staminate flowers sometimes on short densely bracteate inflorescences; fruit 3(−5)-lobed or globose; secondary leaf venation visible with the naked eye, usually prominent 2

2. Petals in staminate flowers 0 or, if present, less than half the sepal length, if petals longer, then of unequal size or filiform [5(6) perianth segments clearly visible]; petals in pistillate flowers, if present, very similar to those in staminate ones; disk annular, entire or shallowly undulate; stipules usually deciduous 3

– Petals in staminate flowers 5(6), nearly as long as sepals, all equal in size, white [10(12) perianth segments clearly visible]; petals in pistillate flowers, if present, less than half the sepal length, often hidden by the disk; staminate disk glands distinct or fused at the base, bilobed, or almost 10-crenate (*Notoleptopus*) or irregularly crenate (*Pseudophyllanthus*); pistillate disk glands distinct or disk annular, more or less crenate; stipules persistent 4

3. Seeds smooth; endosperm scanty or 0; disk convex, thick and fleshy, becoming thinner toward edge; filaments distinct or connate at base only; petals in staminate flowers 0 or, if present, unequal or filiform; stipules deciduous **2. *Actephila***

– Seeds rugose to fenestrate; endosperm copious; disk concave, slightly cupular, usually thin and chartaceous; filaments connate for 1/4 to 9/10 of their length, rarely (former *Zimmermannia* and *Zimmermanniopsis*) distinct; petals in staminate flowers 0 or rarely (subg. *Petaliferae*) 5, equal, less than half of the sepal length; stipules deciduous or persistent **7. *Meineckia***

4. Plant including branches, leaves, sepals, ovaries and fruit densely covered with hairs about 1 mm long, visible to the naked eye; seed intensely black, rugose **6. *Notoleptopus***

– Plant glabrous, with sparse covering of simple hairs, or rough with gland-tipped hairs not visible to the naked eye; seed whitish to dark brown, smooth to rugose 5

5. Procumbent herbs to subshrubs up to 0.5 m tall (erect in *Andrachne fruticulosa*); ovule adnation hemitropous; seed rough, with star-shaped sculpture visible at high magnification when dry **8. *Andrachne***

---

[1] Supertribe **Phyllanthodae** G.L. Webster, **supertrib. nov.**, floribus cymulis axillaribus, cellulis epidermalibus foliorum non tanniniferis, embryonibus plerumque non chlorophyllosis, fructibus saepe capsularibus. Typus: *Phyllanthus* L.

– Erect shrubs to trees 0.2–6 m tall (*Leptopus clarkei* procumbent); ovules anatropous; seed smooth, rugose or pitted, without star-shaped sculpture 6

6. Staminate disk irregularly crenate to almost lacerate; pistillate disk annular, finely crenulate; filaments usually connate for about one half of their length, rarely distinct. Seed undulate to shallowly rugose; endosperm invaginate independently of seed coat sculpture **5. *Pseudophyllanthus***

– Staminate disk regularly divided into 5 rounded bilobed segments; pistillate disk regularly divided into 5 emarginate segments; filaments distinct; seeds smooth, rugose or pitted; endosperm entire in cross section or with undulations following seed coat curvature 7

7. Stylodia bifid for half their length or less; stigmas acute to dilated; seed smooth **3. *Phyllanthopsis***

– Stylodia bifid to base or almost so; stigmas capitate to dilated; seed smooth, rugose or pitted **1. *Leptopus***

1. *Leptopus* Decne.

Leptopus Decne., Voy. Inde 4 (Bot.): 155 (1836); Voronts. & Petra Hoffm., Kew Bull. 63: 46 (2008) and 64: 627–644 (2009), rev.
Archileptopus P. T. Li (1991).

Monoecious (dioecious) herbs or shrubs; indumentum simple or 0. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate but mostly flowers solitary; staminate flowers sometimes on short bracteate inflorescences. Staminate flowers with pedicels articulate above base; sepals 5(6), petals 5(6), shorter than or as long as sepals; disk of 5(6) contiguous, bilobed segments; stamens 5, filaments distinct; anthers longitudinally dehiscent; pollen prolate to subprolate, exine tectate to microperforate; pistillode of 3 distinct segments or 3-lobed. Pistillate flowers with pedicels apically dilated; perianth as in staminate flowers but petals often minute; disk annular, regularly divided into 5 emarginate segments; ovary 3–4(5)-locular; ovules anatropous; stylodia distinct, bifid to base or nearly so; stigmas apically dilated to capitate. Fruit 3(−5)-lobate to subglobose; columella 4–5 times longer than its narrowest width. Seeds 2 per locule, ecarunculate; endosperm copious, in cross section entire to deeply invaginate; embryo curved to almost straight; cotyledons as long as radicle or longer, wider than radicle. $2n = 22, 24$.

Nine spp., deciduous forests, Caucasus to Malesia.

2. *Actephila* Blume

Actephila Blume, Fl. Ned. Ind.: 581 (1825); Forster, Austrobaileya 7: 57–98 (2005), Austral. spp.; Vorontsova & Petra Hoffm., Kew Bull. 63: 46–47 (2008).

Monoecious trees to subshrubs; indumentum simple or 0. Leaves subverticillate or subopposite, entire or rarely toothed; stipules deciduous. Inflorescences axillary, fasciculate, or flowers solitary; pedicels usually elongated, not articulate. Staminated flowers: sepals 4–6; petals 4–6(0), shorter than sepals; disk annular, entire or shallowly undulate; stamens (3–)5(6), filaments distinct or connate basally with pistillode; anthers introrse; pollen prolate to subprolate, exine reticulate-striate; pistillode apically 3(5)-fid. Pistillate flowers: pedicels longer than staminate ones; sepals and petals as in staminate; disk annular; ovary 3-locular, ovules 2 per locule, anatropous; stylodia short, distinct or nearly so, entire to bifid to base at apex. Fruit capsular, loculicidally 3-valved or separating into 2-valved cocci; columella apically 3-pronged, basally dilated. Seeds 2(1) per locule, sometimes ecarunculate, ovoid, carinate; testa smooth and dry; endosperm scanty or 0; embryo folded, cotyledons thick, fleshy, sometimes plicate.

About 35 spp., Asia, Australia and Melanesia, in rainforest understorey.

3. *Phyllanthopsis* (Scheele) Voronts. & Petra Hoffm.

Phyllanthopsis (Scheele) Voronts. & Petra Hoffm., Kew Bull. 63: 47 (2008).
Phyllanthus subg. *Phyllanthopsis* Scheele (1853).
Andrachne sect. *Phyllantopsis* (Scheele) Müll. Arg. (1866); Petra Hoffm., Bot. Jahrb. 116: 321–331 (1994).

Monoecious or dioecious shrubs; indumentum simple or 0. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate or flowers solitary. Staminate flowers pedicellate; sepals 5; petals 5, slightly shorter than sepals; disk annular, divided into 5 bilobed segments; stamens 5; filaments distinct; anthers longitudinally dehiscent; pistillode of 3 distinct segments. Pistillate flowers pedicellate, sepals 5; petals 5, much shorter than sepals; disk annular, divided into 5 emarginate segments; ovary 3-locular; ovules anatropous; stylodia distinct, bifid for up to half their length; stigmas acute to apically dilated. Fruit rounded to 3-lobed; columella 6 times longer than its narrowest width. Seeds 2 per locule, ecarunculate, smooth; endosperm copious, entire in cross section; embryo curved; cotyledons broad, thin, longer and wider than radicles.

Two spp., Mexico, USA, in dry scrub.

4. ***Poranthera*** Rudge Fig. 11

Poranthera Rudge, Trans. Linn. Soc. London 10: 302 (1811); Halford & Henderson, Austrobaileya 7: 1–27 (2005); Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).
Oreoporanthera (Grüning) Hutch. (1969).

Monoecious (dioecious) annual or perennial herbs, sometimes suffruticose; indumentum 0. Leaves alternate (opposite), sessile or petiolate, entire, 2–20 times longer than wide; stipules pale, scarious. Inflorescences axillary but appearing to be in terminal umbels or racemes, fasciculate or flowers solitary. Staminate flowers: sepals (3)5, not accrescent; petals (3)5 or 0, smaller than sepals; disk of (3)5 distinct globular entire glands, stamens (3)5; filaments distinct; anthers dehiscing by terminal pores; pollen prolate(–spheroidal), exine tectate-perforate to reticulate; pistillode 3-fid. Pistillate flowers: sepals and petals as in staminate; disk annular and divided into (3)5 erose to undular segments; ovary 3-locular, 6-angled; stylodia bifid to base; stigmas rounded to capitate. Fruit deeply 6-lobed; columella 8 times longer than its narrowest width, persistent. Seeds 2 per locule, ecarunculate, smooth, reticulate, rugose or fenestrate; endosperm copious; embryo curved or straight; cotyledons shorter than radicle.

Fifteen spp., Australia, Tasmania, and New Zealand, in temperate grassland and woodland. This is the morphologically most aberrant genus of the tribe.

5. ***Pseudophyllanthus*** (Müll. Arg.) Voronts. & Petra Hoffm.

Pseudophyllanthus (Müll. Arg.) Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).
Andrachne sect. *Pseudophyllanthus* Müll. Arg. (1866), Petra Hoffm., Bot. Jahrb. 116: 321–331 (1994).

Fig. 11. Euphorbiaceae-Phyllanthoideae. *Poranthera obovata*. **A** Flowering branchlet. **B** Staminate flower. **C** Pistillate flower. **D** Branchlet with stipulate leaf. **E** Fruit seen from above. **F** Same from side. (Halford & Henderson 2005, drawn by W. Smith)

Dioecious (monoecious) pubescent shrubs to small trees. Leaves entire; stipules membranaceous. Inflorescences axillary, fasciculate or flowers solitary or in twos, staminate flowers on short densely bracteate inflorescences leaving pedicel stumps ("podia"); pedicels articulate. Staminate flowers: sepals 5; petals 5; disk annular, irregularly crenate to almost lacerate; stamens 5; filaments distinct to connate for about half their length; pollen subprolate, exine tectate-perforate to micro-reticulate; pistillode 3-lobed. Pistillate flowers: sepals and petals as in staminate; disk annular, finely crenulate; ovary 3-locular; stylodia distinct, bifid to base; stigmas capitate. Fruit 3-lobed; columella 2.5–5 times longer than its narrowest width. Seeds ecarunculate; endosperm copious, deeply invaginate independently of outer seed coat sculpture; embryo almost straight; cotyledons longer and wider than radicle.

One sp., *P. ovalis* (E. Mey. ex Sond.) Voronts. & Petra Hoffm., southern Africa, deciduous forests.

6. ***Notoleptopus*** Voronts. & Petra Hoffm.

Notoleptopus Voronts. & Petra Hoffm., Kew Bull. 63: 50 (2008).

Monoecious, densely pubescent shrubs. Leaves entire; stipules persistent. Inflorescences axillary, fasciculate or flowers solitary; pedicels articulate. Staminate flowers: sepals 5; petals 5; disk annular, regularly divided into 5 bilobed segments; stamens 5; filaments distinct; anthers longitudinally dehiscent; pollen prolate, exine tectate-perforate to microreticulate; pistillode of 3 distinct segments.

Pistillate flowers: sepals 5; petals 5, much shorter than sepals; disk annular, regularly and deeply divided into 5 emarginate or erose segments; ovary 3-locular, densely pilose; stylodia distinct, bifid to base; stigmas rounded to apically dilated. Fruit 3-lobed; columella 6 times longer than its narrowest width. Seeds ecarunculate, rounded triquetrous, rugose; endosperm copious, deeply invaginate; cotyledons broad, thin, as long as radicle, wider than radicle.

One sp., *N. decaisnei* (Benth.)Voronts. & P. Hoffm., from Java to New Guinea, Australia, in open forest and savannah. Although habitually very similar to *Leptopus* (see Vorontseva et al. 2007), molecular evidence placed this taxon close to the Southern Hemisphere *Pseudophyllanthus* and *Poranthera*.

7. *Meineckia* Baill.

Meineckia Baill., Étude Gén. Euphorb.: 587 (1858); Webster, Acta Bot. Neerl. 14: 323–365 (1965), rev.; Vorontsova & Petra Hoffm., Kew Bull. 63: 53–55 (2008).
Zimmermannia Pax (1910).
Zimmermanniopsis Radcl.-Sm. (1990).

Monoecious or dioecious shrubs or subshrubs; indumentum simple or 0. Leaves distichous, epeltate or rarely (*M. peltata*) peltate; stipules persistent or deciduous. Inflorescences axillary, fasciculate or flowers solitary; staminate flowers sometimes on short densely bracteate inflorescences, on which the pedicels leave "podia"; pedicels articulate. Staminate flowers: sepals 5 (6); petals 0 (5 small ones in subg. *Petaliferae*); disk annular, entire or shallowly undulate; stamens 5, filaments distinct to connate up to 9/10 of their length; pollen prolate to speroidal, exine reticulate to verrucate; pistillode subentire to 3-lobed. Pistillate flowers: sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3-locular, glabrous or densely pilose; stylodia distinct or connate at base, entire to bifid to base, stigmas apically dilated to capitate. Fruit 3-lobed; columella slender, persistent. Seeds 1 or 2 per locule, ecarunculate; endosperm copious, deeply invaginate; cotyledons much broader than radicle.

Thirty spp., mostly in deciduous forests of Meso-America and South America, Africa, Madagascar and South Asia. Two of them represent ***M.* subg. *Petaliferae*** Voronts. & Petra Hoffm.; these have minute petals and in the molecular analysis of Vorontsova et al. (2007) were found to be basal to the otherwise apetalous species of ***M.* subg. *Meineckia***; morphologically, they are also very close to *Pseudophyllanthus* (see Hoffmann, Adansonia III, 22: 123–133. 2000).

8. *Andrachne* L.

Andrachne L., Sp. Pl.: 1014 (1753); Petra Hoffm., Bot. Jahrb. 116: 321, figs. 1, 2 (1994), Adansonia III, 22: 123 (2000).

Monoecious annual to perennial herbs or subshrubs; indumentum simple, glandular, or 0. Leaves with persistent stipules. Inflorescences axillary, fasciculate, or flowers solitary, the staminate in glomerules, the pistillate solitary; pedicels articulate. Staminate flowers: sepals 5(6), distinct; petals 5, slightly shorter than sepals in staminate flowers; disk in staminate flowers of 5 contiguous bilobed segments or distinct globular glands; stamens 5; filaments distinct to connate up to half of their length; pollen (spheroidal-)prolate, exine striate to micro-reticulate; pistillode of 3 distinct segments or 3-lobed. Pistillate flowers: sepals 5(6), distinct; petals much shorter than sepals to minute or 0; disk either divided into 5 emarginate segments or 5 distinct globular glands; ovary 3-locular; ovules hemitropous; stylodia ± distinct, bifid, stigmas capitate. Fruit rounded to 3-lobed; columella 5–6 times longer than its narrowest width. Seeds ecarunculate, rounded-triquetrous, rough, with star-shaped sculpture visible at high magnification (see illustration in Stuppy 1996: 283); endosperm copious, entire in cross section; embryo curved; cotyledons broader than and about equaling radicle in length. $2n = 24$.

Twenty-two spp., in semi-deserts of South Asia, northern Africa, southern Europe and the Americas; two subgenera, ***A.* subg. *Andrachne***, 16 spp., Old World, and ***A.* subg. *Phyllanthidea*** (Didr.) Voronts. & Petra Hoffm., 6 spp., also in the New World.

2. TRIBE BRIDELIEAE Müll. Arg. (1864), recircumscribed by Hoffmann et al., Kew Bull. 61: 37–53 (2006).

Armature 0 or rarely +; leaves entire or slightly crenate; stipules distinct or rarely intrapetiolar; pedicels sometimes articulated; sepals 4–6 (7), imbricate (valvate); petals (3)4–6 or 0; staminate disk extrastaminal-annular or in distinct parts or 0; pistillate disk simple or double; stamens 4–10 (−19), distinct or variously fused; thecae not separate and connective not enlarged; ovary locules 2–4; stylodia distinct or completely connate; fruit explosively or tardily dehiscent or indehiscent; seeds exarillate.

Twelve genera in five subtribes.

2a. Subtribe Amanoinae Pax & K. Hoffm. (1922).

A monotypic subtribe.

9. *Amanoa* Aubl. (1775).

Amanoa Aubl., Fl. Gui. Fr.: 256 (1775); Hayden, Brittonia 42: 260–290 (1990), Neotrop. spp.

Monoecious (dioecious) glabrous trees or shrubs. Leaves entire; stipules persistent, distinct or intrapetiolar. Inflorescences terminal or axillary, spiciform-thyrsoid; pedicels not articulated. Staminate flowers: sepals 5, imbricate, persistent; petals 5, scale-like; disk extrastaminal-annular; stamens 5, distinct; anthers introrse; pollen oblate, 3-colporate, intectate or tectum widely perforate; pistillode columnar. Pistillate flowers: sepals 5, deciduous in fruit; petals much shorter than sepals or sometimes 0; disk patelliform; staminodes 0; ovary subglobose, 3-locular; ovules anatropous; stylodia connate into a massive column, tips dilated, stigmatiform. Fruit 3-angled, tardily dehiscent; columella massive, dilated toward base and at apex. Seeds usually 1 per locule; endosperm scanty or 0; cotyledons fleshy.

Sixteen spp., 13 in tropical South America, mostly northern, and 3 in west and west-central tropical Africa. This is the only genus of Bridelieae that occurs in both the New World and the Old.

2b. Subtribe Saviinae Müll. Arg. (1865), as 'Savieae'.

Croizatieae G.L. Webster (1994).

Dioecious; pedicels sometimes articulated; sepals imbricate, persistent; staminate disk extrastaminal-annular; pistillate disk simple; staminodes rarely +; stylodia 2-fid or 4-fid; fruit dehiscent.

Five genera, neotropical.

10. *Savia* Willd.

Savia Willd., Sp. Pl. 4: 771 (1805); P. Hoffmann & McPherson, Ann. Miss. Bot. Gard. 94: 519–55 (2007); P. Hoffmann, Brittonia 60: 136–166 (2008), rev.
Kleinodendron L.B. Sm. & Downs (1964).

Dioecious shrubs or trees. Leaves deciduous; stipules deciduous. Inflorescences axillary glomerules, the staminate dense glomerules, the pistillate few- to 1-flowered; bracts obscure; pedicels articulated. Staminate flowers subsessile; sepals 3–5, imbricate; disk annular; petals 5, imbricate, shorter than sepals, or 0; stamens 5, filaments distinct; anthers basifixed, introrse; pistillode 3-fid. Pistillate flowers: sepals 5, distinct, imbricate; petals 5 or 0; ovary 3-locular, sometimes pubescent; stylodia distinct, bifid, branches slender. Fruit capsular; columella 3-angled distally, persistent. Seeds mostly 1 per locule, smooth; endosperm copious, embryo straight; cotyledons much longer than radicle.

Two or three spp., neotropical. Other species formerly included in this genus have been transferred to *Heterosavia* (Tribe Phyllantheae) or *Wielandia* (Tribe Wielandieae) (Hoffmann and McPherson 2007; Hoffmann 2008).

11. *Gonatogyne* Müll. Arg.

Gonatogyne Müll. Arg., Fl. Bras. 11(2): 13 (1873).
Savia sect. *Gonatogyne* (Müll. Arg.) Pax & K. Hoffm. (1922).

Dioecious evergreen trees; indumentum simple. Leaves entire; stipules deciduous. Inflorescences axillary bracteate glomerules; sepals 5, imbricate, the pistillate deciduous in fruit; petals 5, imbricate, as long as sepals; staminate disk fleshy, corrugated; stamens 5, filaments connate into a column; anthers stipitate, erect, introrse; pollen grains 3-colporate, reticulate; pistillode atop column; pistillate flowers pedicellate; staminodes 0; disk multiglandular; ovary 3(4)-locular, sericeous; stylodia twice bifid. Fruit capsular, persistent; seeds smooth; endosperm copious; cotyledons flat, greenish.

One sp., *G. brasiliensis* (Baill.) Müll. Arg., Brazil (São Paulo).

12. *Croizatia* Steyerm.

Croizatia Steyerm., Fieldiana 28: 308 (1952); Webster et al., Syst. Bot. 12: 1–8, figs. 1–8 (1987); Dorr, Sida 18: 831–836 (1999).
Pseudosagotia Secco (1985).

Dioecious trees or shrubs. Leaves alternate to subopposite; stipules deciduous or persistent. Inflorescences axillary, glomerular; bracts inconspicuous. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, very small; disk annular, glabrous; stamens 5, filaments distinct; anthers introrse; pollen grains spheroidal, 3-brevicolporate, sexine tectate-perforate and spinose; pistillode 3–4-lobed. Pistillate flowers pedicellate; sepals 5, distinct, persistent in fruit; petals 5, much shorter than sepals; disk annular, glabrous; ovary 3-locular, pubescent; ovules hemitropous; stylodia distinct, slender, twice 2-fid. Fruits capsular, 3-lobed, cocci reticulate; columella distally expanded in papery wings. Seeds 1 or 2 per locule, ecarunculate; testa smooth; endosperm 0; embryo large, cotyledons thin, contorted.

Four spp., Panama to Venezuela and Ecuador and possibly Peru. Because of its spinose pollen, *Croizatia* was placed in the Oldfieldioideae (Webster 1994; Radcliffe-Smith 2001), but there is now strong molecular support for its inclusion in this subtribe.

13. ***Discocarpus*** Klotzsch

Discocarpus Klotzsch, Archiv. Naturg. 7: 201 (1841); Hayden & Hayden, Ann. Missouri Bot. Gard. 83: 153–167 (1996).

Dioecious trees or shrubs. Stipules deciduous. Flowers in axillary glomerules, the staminate ± compounded. Staminate flowers sessile; sepals 5, basally connate; petals 5, often reduced; disk cupular, lobed or toothed, stamens (4)5; filaments basally connate, exserted from perianth; anthers longitudinally introrsely dehiscent; pollen grains ± oblate, 4- or 5-colporate, exine finely reticulate; pistillode divided into 2 or 3 narrow segments; pistillate flowers subsessile or pedicellate; sepals and petals ± as in staminate; disk slightly lobed, glabrous; ovary 3-locular, densely hirtellous; ovules anatropous; stylodia dilated, bifid or irregularly incised. Fruits capsular, dehiscent into 1- or 2-seeded mericarps; columella massive, 3-winged distally. Seeds subglobose, testa smooth and shiny; endosperm scanty or 0; embryo large, cotyledons thin, contorted.

Four spp., northern South America: Amazon and Orinoco basins, Guayana region, E Brazil.

14. ***Tacarcuna*** Huft

Tacarcuna Huft, Ann. Missouri Bot. Gard. 76: 1080 (1989); Webster, Ann. Missouri Bot. Gard. 81: 130 (1994); Wurdack in Wurdack et al., Amer. J. Bot. 91: 1892 (2004).

Dioecious trees. Stipules deciduous. Inflorescences axillary, glomerular, sessile or subsessile. Staminate flowers pedicellate; sepals 5, imbricate; petals 5, equaling or exceeding sepals; disk obscure; stamens 5 or [*T. amanoifolia* Huft] 14–19, filaments distinct; pollen grains 3-colporate, exine striate- reticulate; pistillode columnar; pistillate flowers pedicellate; sepals 3 and "petals" 3, persistent in fruit, or sepals 5 and petals 0; disk annular (?); ovary 3-locular, sericeous; stylodia bifid. Fruit capsular; columella scarcely winged. Seeds apparently 1 per coccus, angled in cross section, testa smooth; endosperm scant; embryo large; cotyledons thin, contorted.

Three spp., Panama and South America, still unsatisfactorily known.

2c. SUBTRIBE KEAYODENDRINAE P. Hoffm. (2006).

A monotypic subtribe, distinguished by the combination of apetalous flowers, indehiscent, 1-locular and 1-seeded fruits.

15. ***Keayodendron*** Leandri

Keayodendron Leandri, Bull. Soc. Bot. France 105: 517 (1959); Breteler, Bull. Jard. Bot. Nat. Belg. 62: 187–190 (1993).

Dioecious trees; indumentum simple. Stipules deciduous. Flowers in axillary glomerules. Pedicels nor articulated. Staminate flowers subsessile or pedicellate; sepals 5–7, imbricate; petals 0; disk extrastaminal-annular; stamens 5–6; filaments connate; anthers introrse, dehiscing longitudinally; pistillode dilated and subpeltate. Pistillate flowers subsessile or pedicellate; perianth similar to staminate, sepals 5 or 6, persistent in fruit; disk double, minutely pubescent; ovary 2-locular; stylodia 2-fid. Fruit drupaceous, 1-locular. Seed 1 per fruit, linear-compressed, deeply invaginate ventrally; endosperm scanty, embryo curved, cotyledons much longer than radicle.

One sp., *K. bridelioides* Leandri, semi-deciduous forests of west tropical Africa (Ivory Coast to Cameroun).

2d. SUBTRIBE PSEUDOLACHNOSTYLIDINAE Pax & K. Hoffm. (1922).

Armature rarely +; leaves entire, rarely slightly crenate; pedicels sometimes articulated; sepals imbricate or valvate; staminate disk extrastaminal-annular; pistillate disk usually double; stamens 4–7; fruit dehiscent or indehiscent.

Four Old World genera.

16. ***Bridelia*** Willdenow (1806).

Bridelia Willd., Sp. Pl. 4(2): (1806; as *Briedelia*); Webster, Ann. Missouri Bot. Gard. 81: 39 (1994); Dressler, Blumea 41: 263–331 (1996); Radcl.-Sm., Gen. Euphorb.: 19 (2001).

Monoecious (dioecious) trees or shrubs, branches sometimes thorny; indumentum simple. Leaves entire or subentire; stipules persistent or deciduous. Flowers in axillary glomerules, flowering branches sometimes appearing racemose due to reduction of leaves; bracts persistent. Staminate flowers pedicellate or subsessile; sepals 5, valvate; petals 5, erect or inflexed, smaller than sepals; disk annular or somewhat cupular, glabrous or pubescent; stamens 5, filaments basally connate; pollen grains slightly oblate, 3-colporate, exine reticulate with ± striate pattern; pistillode 2–4-lobed or -divided. Pistillate flowers sessile or subsessile; sepals 5, basally connate into a hypanthium, valvate, persistent in fruit; petals as in staminate; disk duplex, outer part annular and adnate to hypanthium, inner part inflexed as cupule surrounding the ovary; ovary 1- or 2-locular; stylodia distinct or basally connate, bifid to subentire. Fruits pseudobaccate with fleshy exocarp but sometimes dehiscent or drupaceous, 1- or 2-locular; columella not persistent. Seeds usually 1 per locule, plano-convex, adaxially grooved [in 2-locular fruits] or ventrally invaginate [in 1-locular fruits]; endosperm copious, excavated adaxially; embryo chlorophyllous, curved, cotyledons broad, not fleshy. $2n = 26$.

About 50 spp. extending from Africa and Madagascar to Australia and the Pacific islands.

17. ***Cleistanthus*** Hook. f. ex Planch. (1848).

Cleistanthus Hook. f. ex Planch. in Hook. Ic. Pl. 8: t. 779 (1848); Kathriarachchi et al., Molec. Phylogenet. Evol. 36: 112–134 (2005); Li et al., Syst. Bot. 34: 529 (2009).

Monoecious (dioecious) shrubs or trees; indumentum simple. Leaves entire; stipules persistent or deciduous. Flowers in axillary, rarely terminal glomerules or axillary thyrses; bracts deciduous. Staminate flowers usually sessile; sepals (4)5(6), valvate; petals (4)5(6), scale-like and shorter than sepals; disk annular or cupulate, entire or lobed; stamens (4)5(6); filaments connate at base; pollen grains subglobose, 3-colporate, exine striate; pistillode at apex of column, 3-lobed. Pistillate flowers sessile or pedicellate; sepals mostly 5, valvate, connate basally, usually persistent in fruit; petals 5, scale-like, adnate to sepalar cup; disk annular or cupular; ovary (2)3(4)-locular; ovules anatropous, rarely hemianatropous; stylodia 1–4-lobate or -fid. Fruit capsular, septicidal or tardily dehiscent to nearly indehiscent [sect. *Chartacei* Jabl.], with subtending podium; columella usually persistent. Seeds 1 or 2 per coccus; testa smooth and shiny; endosperm copious; embryo straight; cotyledons longer and broader than radicle. $2n = 22$.

About 140 spp. distributed from Africa and Madagascar to Malesia, Australia, and Polynesia. The genus is highly variable in various characters including foliar venation, pollen morphology and seed anatomy (Stuppy 1996; Tokuoka and Tobe 2001), is polyphyletic and needs profound taxonomic readjustment.

18. ***Pentabrachion*** Müll. Arg.

Pentabrachion Müll. Arg., Flora 47: 532 (1864); Pax & K. Hoffm., Pflanzenr. 147: XV: 188, fig. 15 (1922); Radcl.-Sm., Gen. Euphorb.: 15 (2001).

Monoecious or dioecious subglabrous shrubs or trees. Leaves entire; stipules persistent. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals (4)5(6), imbricate; petals 4–6, smaller than sepals; disk annular, unlobed; stamens 5(−7), filaments basally connate; pollen grains oblate sphaeroidal, 3-colporate, colpi c. 2/3 length of grain, exine coarsely heterobrochate; pistillode 3-fid, segments laminar. Pistillate flowers long-pedicellate; sepals 5, imbricate; disk annular; ovary glabrous; stylodia twice bifid. Fruits capsular, 3-lobed. Seeds smooth, endosperm copious, embryo with cotyledons longer than radicle.

One sp., *P. reticulatum* Müll. Arg., western equatorial Africa.

19. ***Pseudolachnostylis*** Pax

Pseudolachnostylis Pax, Bot. Jahrb. 28: 19 (1899); Radcl.-Sm., Fl. Trop. E. Afr., Euphorb. 1: 80, fig. 10 (1987), Gen. Euphorb.: 28 (2001).

Dioecious shrubs or trees; buds perulate; indumentum simple. Leaves entire; stipules deciduous. Inflorescences axillary or arising below the leaves, staminate flowers in few-flowered pedunculate or subsessile cymes, pistillate flowers (sub) solitary. Staminate flowers sessile; sepals 5(6), imbricate; petals 0; disk annular-lobed; stamens (4)5–7; filaments adnate to pistillode; pollen grains ± oblate, 3-colporate, coarsely reticulate; pistillode 3-fid. Pistillate flowers: pedicels 2-bracteolate; sepals 5(6), imbricate, deciduous in fruit; petals 0; disk dentate or lobed; ovary 3-locular; ovules hemitropous; stylodia bifid. Fruit a tardily dehiscent woody capsule with fleshy exocarp; columella not persistent. Seeds 1 per locule, ellipsoid, hilum submedian; endosperm copious; cotyledons much longer than radicle. $2n = 26$.

Apparently only one variable sp., *P. maprouneifolia* Pax, distributed from Zaire and Tanzania to South Africa.

2e. Subtribe Securineginae Müll. Arg. (1866).

Two Afro-Madagascan genera without evident similarities, but strongly supported in a subclade that is sister to the remaining four subtribes.

20. *Securinega* Comm. ex Juss. (1789).

Securinega Comm. ex Juss., Gen. Pl.: 388 (1789), nom. cons.; Leandri, Fl. Madag. 111(1): 107–116 (1958); Radcl.-Sm., Gen. Euphorb.: 31 (2001); Schatz, Generic Tree Fl. Madagascar: 164, fig. 171 (2001).

Dioecious shrubs. Leaves entire; stipules deciduous. Flowers in axillary glomerules, the pistillate flowers solitary or few; pedicels not articulated. Staminate flowers pedicellate; sepals 5–7, imbricate, deciduous; petals 0; disk in 5 distinct segments; stamens (4)5(−10), filaments distinct, exserted from calyx; pollen grains subglobose, 3-colporate, colpi long, exine spiny or finely reticulate; pistillode mostly 2–3-fid. Pistillate flowers pedicellate; sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3(4)-locular; stylodia 3 (4), sessile, recurved, 2-fid. Fruit capsular; columella deciduous. Seeds ovoid, testa dark, smooth; hilum submedial, narrowly elliptic; endosperm copious; embryo straight, cotyledons longer and broader than the radicle.

Five spp., Madagascar, Réunion and Mauritius. This genus had been circumscribed to include *Flueggea* by Müller (1866), in which he was followed by Pax and Hoffmann (1931) who added *Meineckia*. This broad circumscription was reduced by the removal of the latter two genera and of *S. congesta* Müll. Arg. (=*Jablonskia*) by Webster (1965–1984), resulting in a core Malagasy group characterized by distinctive spiny pollen and smooth seeds (Wurdack et al. 2004). *Lachnostylis* has a strongly supported relationship with *Securinega capuronii* Leandri, despite the lack of morphological resemblance (Wurdack et al. 2004).

21. *Lachnostylis* Turcz. (1846).

Lachnostylis Turcz., Bull. Soc. Imp. Naturalistes Moscou 19: 503 (1846); Dyer, Gen. S. Afr. Pl. 1: 309 (1975); Radcl.-Sm., Gen. Euphorb.: 12 (2001).

Dioecious shrubs; indumentum simple. Leaves small; stipules deciduous. Inflorescences axillary glomerules; bracts scarious; female flowers often solitary. Staminate flowers pedicellate; perianth abaxially sericeous; sepals 5, distinct, imbricate, persistent; petals 5, equaling the sepals; disk extrastaminal, annular, massive, unlobed, hirtellous; stamens 5, filaments connate below, villous; anthers dehiscing longitudinally; pollen grains subprolate, 3-colporate, exine reticulate; pistillode 3–4-fid, villous, adnate to staminal column. Pistillate flowers pedicellate; perianth similar to the staminate; disk massive, unlobed, villous; ovary 2- or 3-locular, tomentose, ovules hemitropous; stylodia bifid. Fruits capsular, valves tomentose; each coccus with 1(2) seeds. Seeds subglobose, testa smooth, endosperm scanty; cotyledons plicate, longer than the radicle.

One variable or perhaps 2 spp., *T. capensis* Turcz., South Africa.

3. Tribe Wielandieae Baill. ex Hurus. (1954), recircumscribed by Hoffmann et al., Kew Bull. 61: 37–53 (2006).

Monoecious or dioecious; leaf base sometimes peltate; petioles sometimes pulvinate; sepals 4–6 (−8), imbricate, ± distinct; petals 4–6, sometimes reduced or 0; disk + or rarely 0; staminate disk annular or in distinct parts, pistillate disk simple; stamens (3)4–6(−12); filaments distinct or variously connate; ovary 3-6-locular; fruits explosively dehiscent.

Six genera, New and Old World, except Australia.

3a. Subtribe Astrocasiinae G.L. Webster (1992).

Three genera, two New World, one African.

22. ***Heywoodia*** Sim

Heywoodia Sim, For. Fl. Cape Col.: 326, t. 140/1 (1907); Hutchinson, Bull. Misc. Inf. Kew 1922: 115 (1922); G. L. Webster, Ann. Missouri Bot. Gard. 81: 36 (1994); Radcl.-Sm, Fl. Zamb. 9(4): 6, t. 1 (1996), Gen. Euphorb.: 6 (2001).

Dioecious glabrous trees. Leaves of seedlings and sucker-shoots peltate; stipules persistent. Inflorescences axillary bracteate glomerules, staminate flowers many, pistillate 3 or 4. Staminate flowers sessile or nearly so; perianth poorly differentiated, sepals 3(4), distinct, imbricate, unequal; petals (4)5, distinct, longer than sepals, imbricate; disk extrastaminal, lobed, projecting between filaments; stamens 8–12, ± in 2 whorls, filaments distinct, anthers dorsifixed, introrse, muticous, dehiscing longitudinally; pollen 3-colporate-spheroidal; pistillode minute, trifid. Pistillate flowers pedicellate; sepals and petals as in staminate; staminodes 6–8, filiform; ovary 4–5-locular; stylodia 4 or 5, stigmatiform, bilobed. Fruit capsular, 4–5-locular, separating into 4–5 2-valved cocci; columella not persistent. Seeds 1(2) per locule, smooth (minutely striate); endosperm papyraceous, embryo small, cotyledons chlorophyllous, inflexed, much longer than the radicle.

One sp., *H. lucens* Sim, eastern and southern Africa, disjunct along mountain ranges from Tanzania to South Africa (Transkei and Natal). Levin (1986b) suggested a close relationship between *Heywoodia* and *Astrocasia*, which is confirmed by the molecular evidence. Webster (1994) considered *Heywoodia* as an ancient relict genus because he interpreted traits such as dioecy, the poorly differentiated perianth, the variability of stamen and carpel number, and the small embryo as plesiomorphic.

23. ***Chascotheca*** Urb.

Chascotheca Urb., Symb. Ant. 5: 14 (1904); Alain, Fl. Cuba 3: 44, fig. 8 (1953); Radcl.-Sm., Gen. Euphorb.: 26, fig. 3 (2001).
Chaenotheca Urb. (1902; nom. illeg.).

Dioecious shrubs; indumentum simple. Leaves narrowly peltate at base; stipules persistent. Staminate flowers in axillary glomerules, the pistillate solitary and axillary. Staminate flower subsessile; sepals 5, imbricate, somewhat unequal; petals 0; disk annular; stamens 5, filaments connate at base; anthers dorsifixed, dehiscing longitudinally; pollen grains prolate, 3-colporate, exine coarsely reticulate; pistillode 3-fid, adnate to staminal column. Pistillate flower long-pedicellate, sepals and disk as in staminate, persistent, petals 0; ovary 3-locular, ovules anatropous; stylodia short, 2-fid. Fruit capsular, venose; columella slender, persistent. Seeds 1 per locule; testa dry, smooth; reticulate; chalaza appearing dorsal, hilum in depression beneath terminal beak; endosperm copious; embryo deflexed, cotyledons about equaling radicle.

One sp., *Ch. neopeltandra* (Griseb.) Urb., Greater Antilles (Cuba and Hispaniola).

24. ***Astrocasia*** B. L. Rob. & Millsp.

Astrocasia B. L. Rob. & Millsp., Bot. Jahrb. 36, Beibl. 80: 19 (1905); G.L. Webster, Syst. Bot. 17: 311–323 (1992); Jiménez R. & Gordillo, Acta Bot. Mex. 55: 1, fig. 1 (2001).

Dioecious or subdioecious evergreen or deciduous trees or shrubs; indumentum 0. Leaves sometimes peltate or stipellate; stipules ribbed, deciduous. Inflorescences axillary glomerules, pistillate flowers sometimes solitary. Staminate flowers pedicellate; sepals 5, usually unequal; petals 5, longer than sepals, prominently veined; stamens 3–5, filaments connate into a column; anthers extrorse in bud, dehiscing horizontally or deflexed; pollen grains subglobose, 3-colporate, colpi elongated, exine reticulate; pistillode discoid, sessile or stipitate atop the staminal column. Pistillate flowers long-pedicellate [1.5 cm or more in fruit]; sepals and petals similar to staminate, deciduous; disk annular to cupular; ovary 3(4)-locular; stylodia distinct, 2-fid. Fruit capsular, thin-walled; cocci veiny; columella slender, persistent. Seeds 1 or 2 per locule; testa dry, smooth or roughened, raphe conspicuous; endosperm copious; cotyledons much longer and broader than radicle.

Six spp., Cuba and from Mexico south to Bolivia and eastern Brazil.

3b. Subtribe Wielandiinae Pax & K. Hoffm. (1922).

Three genera, western Indian Ocean, East Africa and SE Asia.

25. ***Dicoelia*** Benth.

Dicoelia Benth., Hook. Icon. Pl. 13, 70: t. 1289 (1879); Pax & K. Hoffmann, Pflanzenr. 147 XV: 15, fig. 3 (1922); Airy Shaw, Kew Bull. 36: 285 (1981).

Monoecious trees or shrubs; indumentum simple. Stipules deciduous. Inflorescences axillary, thyrsoid, pedunculate; glomerules often bisexual, staminate flowers several, pistillate 1/node. Staminate flowers pedicellate; sepals 5, valvate, shorter than petals; petals 5, valvate, convex, apically thickened, with 2 paired cavities; disk 0; stamens 5, filaments distinct, basally adnate to pistillode, exserted from perianth; anthers introrse, thecae fitted into paired cavities in the petals in bud; pollen large, prolate, the exine with nearly continuous tectum; pistillode massive, apically 3–5-fid. Pistillate flowers pedicellate; sepals 5, valvate, shorter than petals; disk 0; ovary 3-locular, pubescent; ovules anatropous; stylodia unlobed, elongated, erect. Fruits spheroidal, capsular, thin-walled. Seeds with smooth testa; endosperm copious; cotyledons orbicular.

One sp., *D. beccariana* Benth., Malaya, Sumatra, Borneo. Kathriarachchi et al. (2005) provided molecular support for the relationship of *Dicoelia* to *Chorisandrachne*, and gave a detailed discussion of its peculiar, strongly autapomorphic appearance that, up to very recently, has camouflaged its true relationship.

26. ***Chorisandrachne*** Airy Shaw

Chorisandrachne Airy Shaw, Kew Bull. 23: 40 (1969), 26: 323 (1972), Hooker's Icon. Pl. 38: t. 3707 (1974).

Apparently dioecious trees or shrubs; indumentum simple. Leaves at the base asymmetric, shortly petiolate; stipules subulate, deciduous. Inflorescences axillary, flowers pedicellate, the staminate ones in upper axils of branches solitary or in twos, the pistillate solitary in lower axils. Staminate flowers: sepals 5, broadly obovate, surmounted by the obtuse, unguiculate petals; disk large, flat, subentire; stamens 5, filaments at the base connate, distally distinct, divaricate; anthers small, subglobose; pistillode narrowly cylindric. Pistillate flowers [incompletely known]: sepals 5; petals 5, exceeding the sepals, persistent; disk broadly cupulate, sinuous-pentagonous. Fruits capsular, subtended by persistent disk and calyx; columella persistent. Seeds 2 per locule, orbicular, plano-convex, much flattened.

A single sp., *Ch. diplosperma* Airy Shaw, southwest Thailand. Both Webster (1994) and Radcliffe-Smith (2001) included *Chorisandrachne* in *Leptopus*, but the molecular data (Kathriarachchi et al. 2005: 129) placed it as sister to *Dicoelia beccariana*. Morphologically, *Chorisandrachne* and *Dicoelia* have little in common, and the seed coat of *Chorisandrachne* shows some similarity with that of *Chascotheca* (Stuppy 1996).

27. ***Wielandia*** Baill.

Wielandia Baill., Étude Gén. Euphorb.: 568 (1858); P. Hoffmann, Adansonia III, 20: 333–340 (1998); P. Hoffmann & McPherson, Ann. Missouri Bot. Gard. 94: 519–553 (2007), rev.
Savia Willd. sect. *Wielandia* (Baill.) Müll. Arg. (1863).
Petalodiscus Baill. (1858).
Savia sect. *Petalodiscus* Baill. (1858).
Blotia Leandri (1957).

Monoecious trees or shrubs; indumentum simple and scanty or 0. Petioles channeled or terete; stipules sometimes peltate, persistent or deciduous. Inflorescences axillary or cauline thyrses, or flowers solitary; staminate and pistillate flowers in the same or separate fascicles. Staminate flowers pedicellate; pedicels inarticulate; sepals (4)5 (6); petals (4)5(6), half as long to 3 x as long as sepals; disk extrastaminal, glabrous (pubescent), of antesepalous lobes, crenate, annular, or lacerated, sometimes of different structure in staminate and pistillate flowers; stamens 5(6), filaments distinct or partly connate; anthers introrse; pistillode 3(5)-fid. Pistillate flowers pedicellate, perianth and disk as in staminate, ovary 3 (−5)-locular; stylodia 3(−5), distinct, 2-fid to base, stigmas acute to slightly capitate. Fruits solitary 3(−5)-lobed schizocarps with irregular dehiscence; columellae 3(−5)-angled, base and apex thickened; disk and perianth usually persistent in fruiting stage. Seeds 1 or 2 per locule, usually with ± distinct perichalazal annulus; endosperm very sparse; embryo either with hemispherical to hemi-ovoid cotyledons and short radicle, or with thin and folded cotyledons and prominent radicle.

Thirteen spp., Madagascar (10 endemic), Seychelles, Comoro Islands, and SE Kenya, most in humid forest.

4. TRIBE PHYLLANTHEAE Dumort. (1829).

Monoecious or dioecious trees, shrubs, or herbs; leaves simple, alternate, entire, petioles not pulvinate; inflorescences axillary or rarely on branches; pedicels not articulated; sepals 4–6(7); petals 0 or very rarely +; disk + or 0; stamens 2–15; anthers usually with thecae not separate and connective not enlarged; ovary 2–6(−15)-locular; ovules hemitropous or rarely (*Heterosavia*) anatropous; fruits dehiscent or indehiscent; seeds exarillate.

A tribe of worldwide distribution comprising 10 genera.

Key to the Genera of Phyllantheae

1. Phyllotaxy spiral or distichous on lateral axes but deciduous branchlets not developed; pistillode mostly + in staminate flowers; seeds ventrally invaginated. **4a. Flueggeinae** 2

– Phyllotaxy spiral on penultimate axes, distichous on deciduous branchlets; pistillode 0; seeds with or without ventral invaginations. **4b. Phyllanthinae** 7

2. Petals +; petioles 2-winged to channeled adaxially **31. *Heterosavia***

– Petals 0; petioles terete 3

3. Monoecious; stamens 15–21, inserted on disk; pistillate calyx accrescent **30. *Lingelsheimia***

– Dioecious or monoecious; stamens 2–7, not exserted on disk; pistillate calyx not accrescent 4

4. Monoecious; terminal branches distinctly flattened; stamens 2 **28. *Plagiocladus***

– Dioecious; terminal branches not distinctly flattened (sometime slightly so in *Margaritaria*); stamens more than 2 5

5. Capsule with 1 seed per locule; staminate flowers subsessile; flowers in racemoid paniculate thyrses; seed exotegmen vittate **32. *Richeriella***

– Capsule usually with 2 seeds per locule; staminate flowers pedicellate; flowers in axillary glomerules; seed exotegmen palisadal 6

6. Pistillode + in staminate flowers; seed testa 2-layered, exotegmen 3- or 4-layered, not woody; leaves spiral **33. *Flueggea***

– Pistillode 0; seed testa 6–11-layered, distinctly fleshy; exotegmen 6–14-layered, + bony; leaves distichous **29. *Margaritaria***

7. Floral disk usually +, not completely adnate to calyx; pollen grains 3–4(6)-colporate/monoporate; seeds with dry testa, not ventrally invaginated **34. *Phyllanthus***

– Floral disk 0 or completely adnate to calyx; pollen grains 3–6(−16)-colporate/monoporate or diporate; seeds mostly not ventrally invaginated, with dry or fleshy testa 8

8. Stylodia unlobed; anthers apiculate; pollen grains 3–6-colporate-monoporate; ovary 3–8-locular; seed coat usually fleshy **35. *Glochidion***

– Stylodia bifid or emarginate; pollen grains up to 16-colporate/diploporate; anthers not apiculate; ovary 3-locular 9

9. Seed coat dry; staminate calyx ± discoid, not turbinate; pollen grains 6–16-colporate **36. *Sauropus***

– Seed coat fleshy; staminate calyx turbinate-truncate; pollen grains 4–12-colporate **37. *Breynia***

4a. Subtribe Flueggeinae Müll. Arg. (1865).

Dioecious; branches persistent; flowers in axillary glomerules or thyrses; sepals 4–7, imbricate, the pistillate ± persistent in fruit; petals 0; disk annular; stamens 4–7, filaments distinct, anthers extrorse; pollen grains prolate, 3-colporate, ora circular, exine finely reticulate; pistillode +; ovary 2–6-locular, ovules hemitropous; stylodia bifid; fruits capsular or baccate; seeds ventrally invaginated, testa dry or fleshy; endosperm copious, embryo, curved.

This subtribe of four genera appears closely related to the Phyllanthinae, and earlier (Webster 1994) was more broadly circumscribed to include that group.

28. *Plagiocladus* Brunel ex Petra Hoffm. Fig. 12

Plagiocladus Brunel ex Petra Hoffm., Kew Bull. 61: 45 (2006).

Phyllanthus diandrus Pax (1904); Breteler Bull. Mus. Hist. nat. Paris IV, 12 B Adansonia: 293–295, fig. 1 (1991).

Phyllanthus sect. *Diandri* Pax & K. Hoffm. in Engler & Drude, Veget. der Erde 9 (Pflw. Afr. III, 2): 29 (1921).

Monoecious, glabrous shrub; terminal branches distinctly flattened. Leaves shortly petiolate, entire; stipules unequally subcordate, deciduous. Inflorescences axillary; staminate flowers axillary glomerules; pistillate long-pedicellate, solitary. Staminate flowers: sepals 6; disk flat, annular; stamens 2, filaments distinct; anthers dehiscing longitudinally. Pistillate flower sepals and disk as in staminate; ovary glabrous, 3-locular; stylodia deeply 2-fid. Fruit a 3-carpellate schizocarp; endocarp hard; dehiscence explosive loculicidal, septicidal and septifrague. Seeds deeply invaginated (?).

One sp., *P. diandrus* (Pax) Brunel ex Petra Hoffm., western C Africa, most common in Gabon. *Plagiocladus* is strongly supported as sister to *Margaritaria*, but is easily distinguished from it by the difference in sepal and stamen number and the distinctly flattened terminal branches.

29. *Margaritaria* L. f.

Margaritaria L. f., Suppl. Pl.: 66 (1781); Webster, Ann. Missouri Bot. Gard. 54: 217, fig. 2 (1968), J. Arnold Arb. 60: 403–444, figs. 11–13 (1979), rev.

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves evergreen or deciduous,

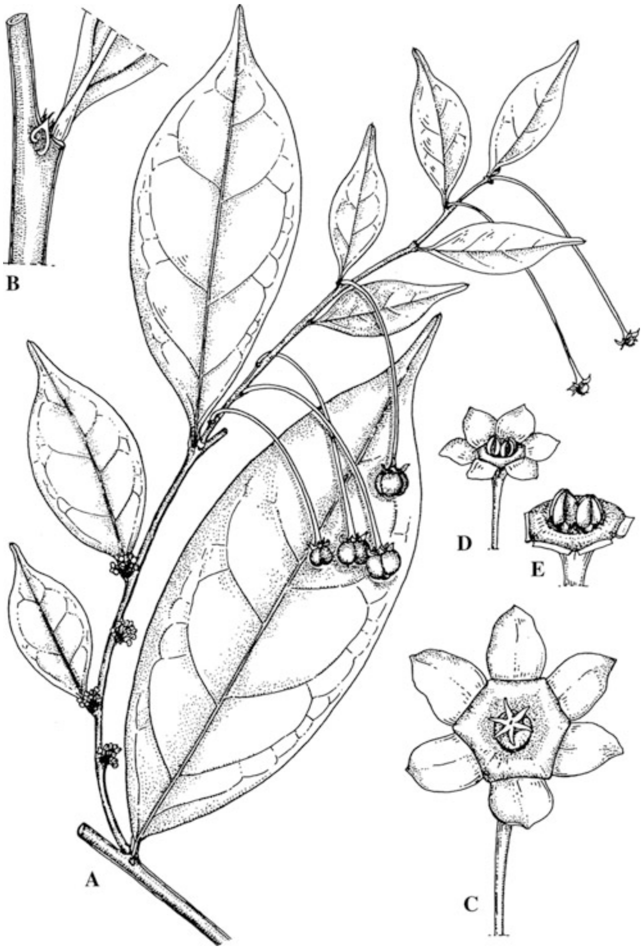

Fig. 12. Euphorbiaceae-Phyllanthoideae. *Plagiocladus diandrus*. **A** Branchlet with glomerules of staminate and single pistillate flowers. **B** Leaf axil with stipule. **C** Pistillate flower. **D** Staminate flower. **E** Same, only disk and stamens. (Breteler 1990; drawn by W. Wessel-Brand)

distichous; stipules deciduous or somewhat persistent. Inflorescences axillary glomerules, the pistillate ones sometimes of solitary flowers. Staminate flowers pedicellate; sepals 4, distinct, biseriate; petals 0; disk annular, sometimes slightly lobed; stamens 4, filaments usually distinct; anthers extrorse; pollen subglobose, 3-colporate, semitectate; pistillode 0. Pistillate flowers pedicellate; sepals 4, persistent in fruit; disk annular; ovary (2)3–4(−6)-locular, ovules hemitropous; stylodia distinct or basally connate, 2-fid, often dilated. Fruit capsular, ± irregularly dehiscent, endocarp papery. Seeds 2(1) per locule, ventrally invaginated; testa fleshy, bluish or greenish; tegmen bony; endosperm copious; embryo straight or curved, cotyledons longer than the radicle. $2n = 26$.

Fourteen spp., extending through most tropical regions from America and the Caribbean through Africa and Madagascar to tropical Asia and N Australia.

30. ***Lingelsheimia*** Pax

Lingelsheimia Pax, Bot. Jahrb. Syst. 43: 317 (1909); Mildbr., Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: t. 54, 55 (1912); Pax & K. Hoffmann, Pflanzenr. 147. XV: 279 (1922); Léonard, Bull. Soc. Roy. Bot. Belg. 84: 49 (1951), Bull. Jard. Bot. État. 32: 513 (1962); Radcl.-Sm., Gen. Euphorb.: 49 (2001).
Danguyodrypetes Leandri (1939).
Aerisilvaea Radcl.-Sm. (1990).

Monoecious shrubs; indumentum 0. Stipules ± persistent. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals (4–)6–7, imbricate; petals 0; disk glandular-lobed and ± intrusive between filaments; stamens 15–35, filaments distinct; anthers basifixed; pollen grains somewhat prolate, 3-colporate, ora circular, exine reticulate; pistillode rudimentary or 0. Pistillate flowers pedicellate; sepals 6, imbricate, persistent and accrescent in fruit; petals 0; disk massive, angled; ovary 3-locular, ovules anatropous [?]; stylodia distinct, 2-fid or -partite. Fruits capsular, dehiscing into three 2-valved cocci or 6 valves. Seeds 1 per locule, ventrally invaginated, testa smooth, dry.

Seven spp., tropical Africa (Zaire, Tanzania), and Madagascar. This genus was placed with *Drypetes* and later with genera like *Meineckia*, but in the molecular analyses of Kathriarachchi et al. (2005, 2006) it has been recovered among the basal genera of Phyllantheae. This placement is also compatible with pollen morphology (Köhler 1965), leaf morphology (Levin 1986b), and seed coat structure (Tokuoka and Tobe 2001).

31. ***Heterosavia*** (Urb.) Petra Hoffm.

Heterosavia (Urb.) Petra Hoffm., Brittonia 60: 152 (rev.: 136–166) (2008).
Savia sect. *Heterosavia* Urb. (1902).

Dioecious trees or shrubs; indumentum simple. Petioles 2-winged to channeled adaxially; stipules persistent. Inflorescences axillary glomerules; staminate flowers 10–25 per inflorescence, subsessile; pistillate flowers solitary, rarely in twos or threes. Pedicels not articulated; staminate flowers: sepals and petals (4)5(6)-merous, sepals imbricate, petals shorter than sepals; disk extrastaminal, annular, crenate to entire, narrow, thick; stamens (4)5(6); filaments distinct or connate for up to half of their length; anthers introrse; pollen 3(long)-colporate, tectate-perforate vermiculate; pistillode 3-fid to base or nearly so, the branches erect; pistillate flowers sepals, petals and disk as in staminate flowers but petals as long as or hardly shorter than sepals; staminodes sometimes +; ovary 3(4) locular; stylodia 3(4), 2-fid to about half of their length; stigmas acute to obtuse. Fruits explosive schizocarps, solitary, rarely in twos, subglobose, 3 (4)-lobed, glabrous to pilose, dehiscence septicidal, loculicidal and septifragous; columella 1.5–2 times as long as wide; perianth persistent in fruit. Seeds 2 per locule, smooth; endosperm copious; cotyledons straight, 3–4 times as long as radicle; radicle 3–4 times as long as wide.

Four spp., Caribbean, from Florida to Swan Islands (Honduras). Recognized as distinct from *Savia* mainly on molecular evidence; distinguishing morphological characters are subtle, and species identification may be problematic unless pistillate material is available.

32. ***Richeriella*** Pax & K. Hoffm.

Richeriella Pax & K. Hoffm., Pflanzenreich 147, XV: 30 (1922); Airy Shaw, Hook. Icon. Pl. 38: t. 3703 (1974), Kew Bull. Add. Ser. 4: 190 (1975).

Dioecious trees; indumentum 0. Stipules deciduous. Inflorescences axillary spiciform thyrses. Staminate flowers sessile or subsessile; sepals 5, imbricate; petals 0; disk-segments 5; stamens 5, filaments distinct, long-exserted; anthers dorsifixed, extrorse; pollen grains subprolate, 3-colporate, coarsely reticulate; pistillode 2–3-fid. Pistillate flowers subsessile in flower but pedicellate in fruit; sepals 5, imbricate; petals 0; disk annular; ovary 3-locular; ovules anatropous?; stylodia distinct, 2-fid. Fruits capsular. Seeds mostly 1 per locule, ventrally invaginated, testa dry, smooth; endosperm scanty; embryo curved, cotyledons thin, longer than the radicle.

One sp., *R. gracilis* (Merr.) Pax & K. Hoffm. [= *Flueggea gracilis* (Merr.) Petra Hoffm.], S and SE Asia from India to Borneo. *Richeriella* and *Flueggea* are similar in leaf anatomy (Levin 1986a) and pollen morphology (various studies), and the molecular results (Kathriarachchi et al. 2005: 127) confirm the close relationship between them but fail to prove that the one is nested in the other. They differ significantly in inflorescence structure and seed anatomy (Stuppy 1996; Tokuoka and Tobe 2001).

33. ***Flueggea*** Willd.

Flueggea Willd., Sp. Pl. 4: 637 (*Flüggea*), 757 (*Fluggea*) (1806); Webster, Allertonia 3: 259–312 (1984), rev.; Hayden, Brittonia 39: 268, fig. 1 (1987).

Dioecious (monoecious) shrubs or trees; branches sometimes spiny; indumentum mostly 0. Stipules persistent or deciduous. Inflorescences axillary glomerules. Staminate flowers pedicellate; sepals 4–7, imbricate; petals 0; disk dissected, or segments ± confluent; stamens 4–7, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains tricolporate, colpi short; pistillode 2–3-fid, rarely rudimentary or 0. Pistillate flowers pedicellate; sepals 4–7, imbricate, persistent in fruit; petals 0; disk annular or lobed; ovary (2)3 (4)-locular; ovules hemitropous; stylodia distinct, 2-fid, sometimes dilated. Fruits capsular or baccate; columella persistent. Seeds usually 2 per locule, ± ventrally invaginated; testa smooth to verruculose; endosperm copious; embryo straight to curved; cotyledons longer than radicle. $2n = 26$.

About fifteen spp. from the West Indies through South America, tropical Africa and southeast Asia to the Pacific islands.

4b. Subtribe Phyllanthinae Pax (1890).

Monoecious or dioecious trees, shrubs, or herbs; branching mostly "phyllanthoid" with main axis distally bearing scale-like leaves that subtend leafy flowering deciduous branchlets; indumentum simple or 0; leaves spiral on main axes, distichous on deciduous branchlets; stipules usually persistent; flowers in axillary glomerules on branchlets, sometimes cauliflorous; staminate sepals (4)5(6), imbricate, entire or dentate; petals 0; disk annular or segmented; stamens (1)2–4 (−10), filaments free or connate; anthers extrorse, dehiscing horizontally to longitudinally; pollen grains prolate to oblate, 3–6-colpate, porate, or panporate, exine reticulate; pistillode 0; pistillate flowers pedicellate; sepals mostly 4–6; disk annular or segmented; ovary 3-locular, ovules anatropous to hemitropous; stylodia bifid or entire; fruits mostly capsular (baccate or drupaceous); columella persistent; seeds usually 2/locule, smooth to striate or ribbed.

This subtribe, with 5 genera and nearly 1,000 species, is the most species-rich taxon in the Phyllanthoideae, due to the large size of *Phyllanthus*. Most of the species, except in some sections of *Phyllanthus*, are characterized by the unique phyllanthoid branching pattern (Webster 1956). The Phyllanthinae appear to have evolved from the Flueggeinae, as suggested by the close relationship between some species of *Flueggea* and *Phyllanthus* subg. *Isocladus*.

34. *Phyllanthus* L. Fig. 13

Phyllanthus L., Sp. Pl. 981 (1753); Müll. Arg. in DC., Prodr. 15(2): 274 (1866), Fl. Bras. 11(2):23, t. 4–10 (1873); Hutch., Fl. Trop. Afr. 6(1): 692 (1912); Fawc. & Rend., Fl. Jam. 4: 251, fig. 85 (1920); Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 60, figs. 28–30 (1931); Alain, Fl. Cuba 3: 44, fig. 9 (1953); Leandri, Fl. Madag. 111(1): 30, t. 7–14 (1958); G.L. Webster, J. Arnold Arb. 37: 91–122, 217–256, 340–357 (1956); 38: 51–79, 170–198, 295–373 (1957); 49–100, 111–212, t. XIII–XXXII (1958), J. Arnold Arb. 48: 332 (1967), Jablonski, Mem. N. Y. Bot. Gard. 17: 85, figs. 17–22 (1967); Webster, Ann. Missouri Bot. Gard.54: 220; fig. 3 (1968); Bancilhon, Boissiera 18: 1–81 (1971); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 9, figs. 2–5 (1987); Santiago, Bradea 5(2): 44 (1988); Howard, Fl. Less. Ant. 5: 70, fig. 34 (1989); Schmid, Fl. Nouv. Caléd. 17: 31, figs. 7–68 (1991); J.R. Wheeler, Fl. Kimberley Reg.: 619, fig. 190 (1992); Webster, Ann. Missouri Bot. Gard. 81: 44 (1994); Friedmann, Fl. Seychelles, Dicot.: 362, figs. 100–103 (1994); Murillo & Franco, Euf. Reg. Araracuara 129, figs. 35–38 (1995); Hunter & Bruhl, Fl. Victoria 3: 74 (2000); Radcl.-Sm., Gen. Euphorb.: 38 (2001); Schatz, Generic Tree Fl. Madag.: 63 (2001); Webster, Contr. Univ. Michigan Herb. 23: 376, fig. 2 (2001), Novon 12: 290, figs. 1, 2 (2002); Li Bingtao & M.G. Gilbert, Fl. China 11: 180–190 (2008).

Niruri Adans. (1763).
Cicca L. (1767).
Kirganelia Juss. (1789).
Cathetus Lour. (1790).
Emblica Gaertn. (1790).
Nymphanthus Lour. (1790).
Epistylium Sw. (1800).
Eriococcus Hassk. (1843).
Macraea Wight (1852).
Hemicicca Baill. (1858).
Reverchonia A. Gray (1880).
Diasperus L. ex Kuntze (1891).
Phyllanthodendron Hemsl. (1898).

Fig. 13. Euphorbiaceae-Phyllanthoideae. *Phyllanthus zornioides*. **A** Flowering branch system. **B** Staminate flower. **C** Stamens with glands. **D** Pistillate flower. **E** Distal (left) and lower leaf. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

Monoecious or dioecious trees, shrubs, or herbs; branching phyllanthoid or unspecialized; indumentum simple, unicellular or multicellular. Leaves on penultimate axes alternate, spiral, those on ultimate axes spiral or distichous on floriferous deciduous branchlets; lamina pinnately veined, often inaequilateral at base; petioles mostly much shorter than blade; stipules persistent or deciduous. Flowers in axillary glomerules on persistent or deciduous branchlets, sometimes cauliflorous. Staminate flowers pedicellate; sepals (4) 5–6, imbricate, entire or dentate; petals 0; disk usually dissected, sometimes annular; stamens (1) 2–4(−10), filaments distinct or connate, anthers dehiscing horizontally to longitudinally, muticous or apiculate; pollen grains prolate to oblate, 3–4 (6)-colporate, rarely diploporate, porate, or panporate, exine patterns various; pistillode 0. Pistillate flowers pedicellate; sepals (4)5–6, imbricate, usually entire, persistent in fruit; petals 0; disk annular or dissected; ovary 3-locular, ovules hemitropous, inner integument thin, 3–5 cell layers; stylodia bifid or entire, sometimes dilated. Fruits capsular, baccate, or drupaceous; columella usually persistent in dehiscent fruits. Seeds usually 2 per locule, trigonous, mostly not ventrally invaginated; testa smooth, striate, ribbed, foveolate, or verruculose; endosperm copious; embryo straight or curved, cotyledons broader than and equal to or longer than the radicle. $2n = 16, 24, 26, 28, 52$.

Over 800 spp., pantropical, and also entering warm temperate regions. Molecular systematic studies (Kathriarachchi et al. 2005, 2006) found three of the eight subgenera of *Phyllanthus* to be polyphyletic, and the genus in its traditional circumscription to be paraphyletic. *Sauropus*, *Breynia* and *Glochidion* are deeply embedded within *Phyllanthus* s. str., and ultimately may be included into an expanded generic concept that would comprise over 1,250 species. At present, however, the nomenclatural changes conforming to the molecular results hardly have been initiated, and the non-monophyletic subtaxa of *Phyllanthus* s. str. and the genera deeply embedded in it will require careful taxonomic revision of the different elements before being amalgamated in the expanded generic concept, as has already been initiated for *Sauropus* by the work of van Welzen (2003), Sagun and van der Ham (2003), and Pruesapan et al. (2008). At present, merging *Phyllanthus* with its embedded genera would displace the lack of a workable taxonomic structure for the expanded genus only to the infrageneric level.

35. *Glochidion* J.R. & G. Forst.

Glochidion J.R. & G. Forst., Char. Gen. Pl.: 57 (1775), nom. cons.; A.C. Sm., Fl. Vit. Nova 2: 467 (1981); McPherson & Tirel, Fl. Nouv. Caléd. 17: 18, t. 4 (1991); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); Florence, Fl. Polynésie Française 1: 66, figs. 9–16 (1997).

Monoecious (dioecious) trees or shrubs; branching phyllanthoid. Leaves alternate, those on penultimate axes spiral and reduced to cataphylls; leaves on deciduous branchlets distichous, often inaequilateral at base, entire; stipules ± persistent. Flowers in axillary glomerules, bracts persistent. Staminate flowers pedicellate; sepals 5–9, imbicate; petals 0; disk 0; stamens 3–8, filaments connate; anthers apiculate, extrorse, dehiscing longitudinally; pollen grains slightly prolate, 3–6-colporate-monoporate, reticulate; pistillode 0. Pistillate flowers pedicellate; sepals usually 6, imbricate, persistent in fruit; petals and disk 0; ovary 3–15-locular, ovules hemitropous; stylodia unlobed, rarely emarginate or bifid, often connivent or connate. Fruit capsular; columella persistent. Seeds usually 2 per locule, ventrally invaginated, testa fleshy; endosperm copius; embryo curved, cotyledons much longer and broader than the radicle. $2n = 26, 52$.

Over 300 spp., Asia and Australasia; the spp. described from Madagascar appear of dubious affinity.

36. *Sauropus* Blume

Sauropus Blume, Bijdr. Fl. Ned. Ind.: 595 (1826); Airy Shaw, Hook. Icon. Pl. 38: t. 3708, 3709 (1974); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); J.T. Hunter & Bruhl, Austrobaileya 4: 661 (1997); Philcox, Fl. Ceylon 13: 99 (1999); Radcl.-Sm., Gen. Euphorb.: 46 (2001); van Welzen, Blumea 48: 319–391 (2003), Males. & Thai spp.; Pruesepan et al., Ann. Bot. 102: 1007–1018 (2008), mol. syst.
Aalius Rumph. ex Lam. (1793).
Ceratogynum Wight (1852).
Diplomorpha Griff. (1854) not Meissn. (1841).
Synostemon F. Muell. (1858).
Breyniopsis Beille (1925).
Heterocalymnantha Domin (1927).

Monoecious shrubs, subshrubs, or herbs; branching phyllanthoid or phyllotaxy entirely spiral; leaves on deciduous branchlets alternate, distichous; lamina pinnately veined, margins entire; stipules persistent. Flowers in axillary glomerules. Staminate flowers pedicellate; sepals 6, connate, the calyx sometimes flattened and discoid; petals and disk 0 but sometime inflexed sepal tips mimicking a disk; stamens 3, filaments connate into a column; anthers sessile, extrorse, dehiscing longitudinally; pollen grains ± oblate, 6–16-colporate-diploporate, reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 6, connate, persistent and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, ovules hemitropous; stylodia bifid. Fruit capsular but pericarp often fleshy; columella persistent. Seeds 2 in each locule, trigonous, hilum linear, within a large ventral invagination, testa dry; endosperm copious; embryo straight or curved, cotyledons broader and longer than radicle. $2n = 24$.

Traditionally comprising about 80 spp. in tropical Asia, Malesia, and Australia except for the widespread *Sauropus bacciformis*. The molecular data of Pruesapan et al. (2008) suggest the splitting of *Sauropus* into two clades, the mainly southeast Asian *Sauropus* s. str., which should be united with *Breynia* under the latter name, and the mainly Australian *Sauropus*, for which the former name *Synostemon* should be reinstated.

37. *Breynia* J.R. & G. Forster

Breynia J.R. & G. Forst., Char. Gen. Pl.: 73 (1775; nom. cons.); Airy Shaw, Kew Bull. Add. Ser. 4: 61 (1975), 8: 38 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 17: 14, fig. 3, 6–10 (1991); Webster, Ann. Missouri Bot. Gard. 81: 46 (1994); Philcox, Fl. Ceylon 11: 238 (1997); Radcl.-Sm., Gen. Euphorb.: 46 (2001).
Foersteria Scop. (1777).
Melanthesa Blume (1826).
Melanthesopsis Müll. Arg. (1863).

Monoecious shrubs; branching phyllanthoid; indumentum 0. Leaves on penultimate axes spiral, reduced to scales, those on deciduous branchlets alternate, distichous; lamina entire; stipules persistent. Flowers in axillary glomerules, the pistillate solitary. Staminate flowers pedicellate; sepals 6, connate into a turbinate cup, sepal tips inflexed; petals and disk 0; stamens 3, filaments connate; anthers basifixed, muticous, dehiscing longitudinally; pollen grains 4–12-colporate-diploporate; pistillode 0. Pistillate flowers pedicellate; sepals 6, nearly distinct to connate, imbricate, persistent and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, rounded to turbinate, ovules hemitropous; stylodia distinct or basally connate, emarginate to bifid. Fruits somewhat fleshy, capsular; columella usually not persistent. Seeds 2 in each locule, trigonous, ventrally invaginated, testa fleshy; endosperm copious; embryo curved, cotyledons equaling or longer than radicle. $2n = 26, 52$.

Traditionally comprising about 35 spp., many difficult to distinguish, east Asia and Australasia. Molecular data suggest a reclassification as indicated under the previous genus.

IB. SUPERTRIBE ANTIDESMODAE G.L. Webster, *supertrib. nov.*[1]

Subfam. Antidesmatoideae Hurus. (1954).
Antidesmatinae Pax (1890), "Antidesminae".

Dioecious or rarely monoecious; leaves simple (compound: *Bischofia*), entire (subentire or toothed); leaf epidermis usually with tanniniferous cells; inflorescences usually thyrsoid with distinct axes; flowers usually apetalous; ovary locules 1–5; ovules anatropous; fruits indehiscent or tardily dehiscent (explosively dehiscent). Tropics and subtropics.

This supertribe corresponds to the tanniniferous clade of Wurdack et al. (2004); in molecular analyses (Kathriarachchi et al. 2005; Samuel et al. 2005), it is placed sister to Phyllanthodae.

5. TRIBE ANTIDESMATEAE Benth. (1873).

Dioecious (monoecious); exudate 0; indumentum simple (lepidote); petioles sometimes pulvinate; foliar glands and domatia 0 or +; sepals (3)4–6 (−8), imbricate to nearly completely connate; petals 0 or [*Thecacoris*] +, small; disk + or 0; stamens 2–8(−13); thecae usually separate and connective enlarged; pistillode + (0); ovary locules (1)2–4(5); ovules anatropous; stylodia + or 0; fruits indehiscent or dehiscent; seeds exarillate, usually albuminous.

Eight genera, pantropical, in five apparently isolated mono- or digeneric subclades (Kathriarachchi et al. 2005; Samuel et al. 2005).

KEY TO THE GENERA OF ANTIDESMATEAE

1. Ovary 2-locular above, appearing 4-locular below; fruits 4-gonous; pollen with atria **42. *Martretia***
– Ovary locules not as above; fruits commonly 1–3-gonous; pollen grains exatriate 2
2. Fruit winged; floral disk 0; tanninferous cells in leaf epidermis 0 3

---

[1] Supertribe **Antidesmodae** G.L. Webster, **supertrib. nov.**, floribus inflorescentiis paniculatis spicatisve, cellulis epidermalibus foliorum saepe tanniniferis, embryonibus plerumque chlorophyllosis, radicula quam cotyledonibus breviore, fructibus plerumque baccatis vel drupaceis. Type: *Antidesma* L.

– Fruit not winged; floral disk + or 0; tanninferous cells in leaf epidermis + 4
3. Fruit capsular; inflorescence paniculate; stylodia lacerate **40. *Didymocistus***
– Fruit samaroid; inflorescence racemoid; stylodia papillose **41. *Hymenocardia***
4. Indumentum lepidote; fruit indehiscent **44. *Hieronyma***
– Indumentum 0 or of simple or stellate hairs 5
5. Ovary 1-locular; fruit indehiscent **38. *Antidesma***
– Ovary 2–5-locular; fruit dehiscent 6
6. Disk 0; pistillode 0; ovary 4–5-locular **45. *Leptonema***
– Disk +; pistillode +; ovary 3–4-locular 7
7. Dioecious; ovary 3-locular; stylodia 2-fid; endosperm copious **39. *Thecacoris***
– Monoecious; ovary 4-locular; stylodia entire; seeds exalbuminous; embryo massive **43. *Apodiscus***

5a. SUBTRIBE ANTIDESMATINAE Müll. Arg. (1865).

Two genera, Old World.

38. *Antidesma* Burm. ex L.

Antidesma Burm. ex L., Sp. Pl.: 1027 (1753); Airy Shaw, Kew Bull. Add. Ser. 4: 207 (1975), 8: 208 (1980); Léonard, Fl. Afr. Centr. Euph. (2): 16–40 (1995); Chakrabarty & Gangopadkyay, J. Econ. Tax. Bot. 24: 1 (2000).
Stilago L. (1767).

Dioecious trees and shrubs; indumentum simple. Leaves sometimes domatiiferous; marginal glands rarely + (*A. vaccinioides*); stipules mostly entire. Inflorescences axillary or terminal, sometimes fasciculate. Flowers in catkin-like, sometimes branched thyrses; bracts 1-flowered. Staminate flowers sessile to pedicellate; calyx cupular or 3–5(8)-lobed, sepals imbricate; petals 0; disk segments distinct or connate; stamens mostly (2)3–5(6); filaments distinct; anthers 2-lobate, thecae distinct, divergent; connective enlarged; pollen grains perprolate, 3-colporate, pores conspicuously lalongate, exine tectate-punctate, scabrate; pistillode small or 0. Pistillate flowers pedicellate; calyx usually cupular-lobed, persistent in fruit; disk annular or cupular; ovary 1(2)-locular; stylodia usually 2, bifid. Fruit drupaceous, asymmetric and flattened, endocarp reticulate or foveolate. Seeds 1(2) per fruit; endosperm fleshy, not copious; embryo flat, cotyledons much longer and broader than radicle. $2n = 26$.

At least 150 spp., mostly from India to Malesia, southern Japan, Australia, and the Pacific islands, only 10 in Africa/Madagascar.

39. *Thecacoris* A. Juss. Fig. 14

Thecacoris A. Juss., Euphorb. Tent.: 12 (1824); Léonard, Bull. Jard. Bot. Nat. Belg. 64: 13–52 (1995).
Cyathogyne Müll. Arg., Flora 47: 536 (1864).

Dioecious or rarely monoecious trees, shrubs, subshrubs or perennial herbs; indumentum simple. Leaves entire or repand; stipules deciduous or persistent. Inflorescences axillary, sometimes fasciculate, racemoid or spiciform; bracts persistent, 1-flowered. Staminate flowers sessile or pedicellate; sepals 5(6), imbricate; petals 5, small or 0; disk segments 5, distinct; stamens 5, filaments distinct; anthers pendent; anther thecae discrete, parallel and pendulous at first, later divaricate and erect; connective enlarged; pollen grains perprolate, 3-colporate, pores lalongate, exine finely reticulate; pistillode massive, dilated. Pistillate flowers pedicellate, pedicel geniculate in fruit; sepals 5, imbricate, persistent in fruit; petals variable in number, sometimes 0; disk annular; ovary 3(4)-locular; stylodia distinct or connate at base, bifid. Fruits capsular, septicidal; columella persistent. Seeds usually 1 per locule; testa dry and shiny; endosperm copious; embryo greenish, cotyledons flat, much longer and broader than radicle.

About 25 spp., four in Madagascar and the rest in tropical Africa from Sierra Leone to Angola and Tanzania. In the concept of Léonard, *Cyathogyne* includes five herbaceous species of Africa and Madagascar. Webster (1994) and Radcliffe-Smith (2001) followed Leandri (in Fl. Madag., 1958) in reducing *Cyathogyne* to a section of *Thecacoris*, with *Th. usambarensis* bridging the gap between the two genera. Léonard's case (1995) for maintaining *Cyathogyne* distinct may find support in the pollen and seed coat structure (Köhler 1965; Stuppy 1996).

5b. SUBTRIBE HYMENOCARDIINAE P. Hoffm. (2006).

Two genera, one neotropical, the other African.

40. *Didymocistus* Kuhlm.

Didymocistus Kuhlm., An. Prim. Reun. Sud-Amer. Bot. 3: 82 (1940); Radcl.-Sm., Gen. Euphorb.: 76, fig. 7 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves with sessile abaxial glands; stipules deciduous. Inflorescences terminal, paniculate; bracts deciduous. Staminate flowers subsessile; sepals 5,

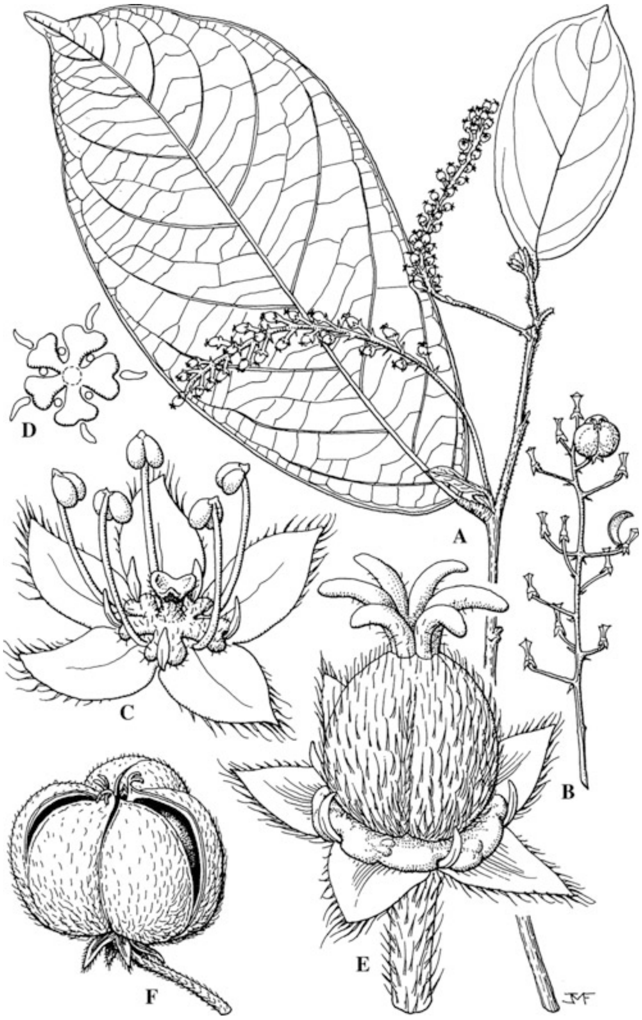

Fig. 14. Euphorbiaceae-Phyllanthoideae. *Thecacoris trichogyne*. **A** Branch tip with pistillate flowers. **B** Infructescence. **C** Staminate flower. **D** Staminate disk glands and petals. **E** Pistillate flower. **F** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

imbricate, distinct; petals 0; disk 0; stamens 5, filaments distinct, exserted, anthers introrse, dorsifixed; pollen grains globose, 3-colporate, exine scabrate, tectum rugulose; pistillode 2–3-lobed; pistillate flowers sessile or subsessile; calyx 5-lobed, petals 0; disk 0; ovary 2-locular, stylodia unlobed, plumose. Fruits capsular, valves thin, inflated, deciduous; columella persistent. Seeds hemitropous, endosperm copious; embryo straight, cotyledons much longer and broader than radicle.

One sp., *D. chrysadenius* Kuhlm., in floodplain forests of Amazonian Brazil, Colombia and Peru; seed dispersal probably hydrochorous (Wurdack et al. 2004).

41. *Hymenocardia* Wall. ex Lindl. Fig. 15

Hymenocardia Wall. ex Lindl., Nat. Syst. ed. 2, 441 (1836); J.G. Adam, Mém. Mus. natl. Hist. Nat., N.S. Bot. 20: 481, t. 174 (1971); Léonard & Mosango, Fl. Afr. Centr., Hymenocardiaceae: 2 (1985); Radcl.-Sm., Fl. Zamb. 9: (4): 113, fig. 18 (1996).

Dioecious trees or shrubs; indumentum simple. Leaves abaxially with domatia and laminar glands; stipules deciduous. Staminate inflorescences axillary, spicate or catkin-like; pistillate flowers solitary or in axillary or terminal, racemoid inflorescences. Staminate flowers subsessile; sepals (4)5(−8), slightly imbricate, connate into a dentate or lobed cup; petals 0; disk 0; stamens usually 5, filaments distinct; anthers introrse in bud, anther sacs discrete, dehiscing longitudinally; pollen grains suboblate, 3-porate or brevicolporate, pores marginate, exine scabrate, tectum rugulose; pistillode cylindric or 2-lobed. Pistillate flowers pedicellate; sepals 5 (4–9), distinct, deciduous; petals 0; disk 0; ovary 2-locular, flattened perpendicular to septum; stylodia 2, unlobed. Fruits samaroid, dehiscing into two 1-seeded winged indehiscent mericarps; columella persistent. Seeds compressed, testa striate, shiny; endosperm copious; embryo flattened, cotyledons longer and broader than radicle. $2n = 26, 28$.

Six or seven spp., all African except one in southeast Asia. A very distinctive genus that has been accepted as a separate tribe or even family by Airy Shaw (1965), Léonard and Mosango (1985), and Meeuse (1990). The ament-like inflorescences and unique samaroid fruits make it one of the more aberrant genera of Phyllanthoideae. However, the pollen evidence weighted so heavily by Léonard must be seen in connection with the complete anemophily found in the genus. In contrast to the pollen data, the wood anatomy of *Hymenocardia*, according to Mennega (1987), is compatible with genera of Antidesmeae, and the foliar venation studies of Levin (1986a, b) show no incompatibility with Phyllanthoideae. The placement of *Didymocistus* with *Hymenocardia* appears strongly supported by the similarities of pollen structure demonstrated by Simpson and Levin (1994), the possession of multicellular

Fig. 15. Euphorbiaceae-Phyllanthoideae. *Hymenocardia ulmoides*. **A** Branchlet with staminate flowers. **B** Staminate flower. **C** Stamen, rear view, showing gland. **D** Branchlet with pistillate flowers. **E** Pistillate flower. **F** Fruiting branch. **G** Fruit. (Radcliffe-Smith 1996; drawn by Pat Halliday).

secretory leaf glands in the absence of tanniniferous leaf epidermal cells, the tanniniferous endotegmic seed coat (Tokuoka and Tobe 2001), and the molecular data of Wurdack et al. (2004) and Kathriarachchi et al. (2005).

5c. Subtribe Martretieae P. Hoffm. (2006).

Two genera held together by strong molecular support; they had been of dubious affinity and have little in common morphologically.

42. *Martretia* Beille

Martretia Beille, C. R. Séances Acad. Sci. Paris 145: 1294 (1907), Bull. Soc. Bot. France 55 (Mém. 8b): 64 (1908); Léonard, Bull. Jard. Bot. Nat. Belg. 59: 319 (1989); Radcl.-Sm., Gen. Euphorb.: 80 (2001).

Dioecious; indumentum 0 on stems and leaves. Tanniniferous epidermal cells 0. Stipules entire, deciduous. Inflorescences axillary, spiciform to racemoid, sometimes compound. Staminate flowers pedicellate; sepals 4 or 5, distinct; petals 0; disk 0; stamens 4–8, filaments distinct; anthers latrorse, dehiscing longitudinally, connective glandular at the apex and pubescent; pollen subspheroidal, 3-colporate, angulaperturate, colpi narrow, unbordered, exine semitectate, vermiculate-rugulose; pistillode 2-fid, pubescent apically. Pistillate flowers pedicellate; sepals 4–6, not persistent in fruit; petals 0; disk of 5 or 6 minute segments; ovary 2-locular, appearing 4-locular below due to intercalary partitions, glabrous or puberulent; stylodia 2, basally connate, unlobed, subulate, elongated. Fruits capsular, 4-gonous, dehiscing into four 1-seeded segments. Seeds albuminous, ellipsoid; testa smooth, fleshy; cotyledons suborbicular.

One sp., *M. quadricornis* Beille, from W and C Africa (Sierra Leone to C.A.R., Congo and Gabon), in swamp and riverine forests. Unique in Phyllanthoideae for its pollen apertures and false-partitioned fruit. Beille (1908) suggested a placement in Antidesmeae, and it was placed in Antidesminae by Pax and K. Hoffmann (1922, 1931).

43. *Apodiscus* Hutch.

Apodiscus Hutch., Bull. Soc. Bot. France 58, Mém. 8: 205 (1912), and in Hook. Ic. Pl. 31: t. 3032 (1915); Keay, Fl. W. Trop. Afr. ed. 2, 1: 373 (1958); Radcl.-Sm., Gen. Euphorb.: 63 (2001).

Monoecious trees; indumentum simple, confined to the inflorescence. Leaves deciduous; stipules deciduous. Inflorescences axillary, spiciform, fasciculate; bracts uniflorous; pistillate flowers 1 or 2 at base of inflorescence. Staminate flowers sessile; sepals 5, imbricate; petals 0; disk segments 5, pubescent; stamens 5, filaments distinct; anthers introrse, thecae subglobose, longitudinally dehiscent, connective slightly produced; pollen prolate, tricolporate, colpus transversalis elongate; pistillode depressed-globose, pubescent. Pistillate flowers pedicellate; sepals 5, imbricate; petals 0; disk 0;

ovary (3)4(5)-locular; stylodia unlobed, recurved. Fruits capsular, septicidally dehiscent into 3 cocci. Seeds exalbuminous; embryo massive, cotyledons much longer and broader than radicle.

One imperfectly known sp., *A. chevalieri* Hutch., from W Africa (Guinea, Liberia and Sierra Leone); it appears aberrant in the Antidesmateae because of its monoecy and exalbuminous seeds.

5d. SUBTRIBE HIERONYMINAE Müll. Arg. (1865).

Monotypic.

44. *Hieronyma* Allemão

Hieronyma Allemão, Pl. Nov. Bras.: 22 (1848); Pax & K. Hoffm., Pflanzenreich 147, XV: 31, fig. 8 (1922); Jablonski, Mem. N. Y. Bot. Gard. 17: 122 (1967); Webster, Ann. Missouri Bot. Gard. 75: 1094 (1988) and ibid. 81: 52 (1994); Franco, Bot. Jahrb. Syst. 111: 297, figs. 1–16 (1990).
Hyeronima Allemão (orth. var.)

Dioecious trees or shrubs; indumentum lepidote or rarely simple. Stipules usually small, cochleate, often soon deciduous. Inflorescences axillary, ± compound racemoid to subspicate thyrses; bracts inconspicuous. Staminate flowers subsessile; calyx 4- or 5-lobed; petals 0; disk pulvinular or cupular; stamens 3–6, filaments distinct; anthers introrse; thecae divergent; anther sacs pendent, dehiscing longitudinally; pollen perprolate, 3-colporate, pores elliptic, exine tectate-perforate or microreticulate; pistillode columnar. Pistillate flowers pedicellate; calyx 4- or 5-lobed, ± persistent in fruit; petals 0; disk cupular; ovary 2(3)-locular, glabrous or lepidote; inner integument thin [2–4 layers]; stylodia very short, stigmatoid. Fruits drupaceous, 1–2-locular by suppression; exocarp fleshy, endocarp hard and bony or fibrous. Seeds usually 1 per fruit by abortion; endosperm fleshy; embryo green, cotyledons much longer and broader than radicle.

Approximately 15(−40?) spp., from S Mexico and Cuba south to Bolivia and S Brazil.

5e. SUBTRIBE LEPTONEMATINAE MüLL. ARG. (1865).

Monotypic.

45. *Leptonema* A. Juss.

Leptonema A. Juss., Euphorb. Tent.: 19 (1824); Leandri, Fl. Madag. 111 (1): 12, fig. IV, 1–6 (1958); Schatz, Generic Tree Fl. Madag.: 157 (2001).

Dioecious (monoecious) shrubs; indumentum simple. Leaves circular to heart-shaped; stipules persistent. Inflorescences axillary, staminate racemoid or corymbiform, pistillate brachyblastic; bracts subulate; flowers 1 per bract. Staminate flowers pedicellate; sepals 5, connate at base, imbricate; petals 0; disk 0; stamens 5, filaments distinct, capillary, exserted; anther connective globose, glandular; thecae separate; pollen sacs pendulous; pollen grains 3-colporate, pores transversely elongate; exine very finely reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, persistent in fruit; petals 0; disk 0; ovary 4–5-locular; stylodia bifid. Fruits capsular, splitting into 4–5 2-valved cocci; columella persistent. Seeds 2 per locule, testa verruculose.

Two spp. endemic to Madagascar, still poorly known.

6. TRIBE SCEPEAE Horan. (1847).

Aporuseae (Lindl. ex Miq.) Airy Shaw (1974).

Dioecious; exudate 0; leaves often with laminar glands; inflorescences axillary or terminal, sometimes cauliflorous; sepals 4–5(−7), distinct; petals 0; disk lobed to dissected or 0; pollen grains 3-colporate, reticulate or tectate; pistillode +; ovary 2–5-locular; stylodia bifid or unlobed; fruit capsular or baccate; seed coat dry or fleshy.

This subtribe of eight genera, all paleotropical except for *Richeria*, was subsumed within the Antidesminae by Pax (1924) and Pax and K. Hoffmann (1922, 1931). Airy Shaw (1974) was the first to formally recognize it, as tribe Aporuseae, which was accepted by Webster (1975) and more recently by Thin (1995).

KEY TO THE GENERA OF SCEPEAE

1. Pistillate disk dissected; stylodia 2-lobate or 2-fid **46. *Protomegabaria***
– Pistillate disk cupular or 0; stylodia 2-fid or unlobed 2
2. Staminate disk +; pistillate disk + or 0 3
– Staminate and pistillate disk 0 6
3. Pistillate disk +; sepals persistent in fruit 4
– Pistillate disk 0; sepals deciduous 5
4. Capsule loculicidal; staminate flowers mostly 1 per bract **51. *Maesobotrya***
– Capsule septicidal; staminate flowers several per bract **47. *Richeria***
5. Staminate sepals distinct, shorter than stamens; staminodes usually 0; stipules narrow **52. *Baccaurea***

– Staminate sepals basally connate, longer than stamens; staminodes + in pistillate flower; stipules broad **53. *Nothobaccaurea***

6. Leaves spiral; stamens 5 or 6; pistillode massive, peltate **50. *Ashtonia***

– Leaves spiral or distichous; stamens mostly 2 [unknown in *Distichirrhops*]; pistillode small or 0 7

7. Leaves spiral; pistillate flowers subtended by 1 bract; pistillate disk + but obscure; pedicels not articulated **48. *Aporosa***

– Leaves distichous; pistillate flowers subtended by 3 bracts; pistillate disk 0; pedicels articulated **49. *Distichirrhops***

46. ***Protomegabaria*** Hutch.

Protomegabaria Hutch., Hook. Icon. Pl. 30: t. 2929 (1911); Léonard, Bull. Jard. Bot. Nat. Belg. 64: 53–63 (1995), Fl. Afr. Cent., Euph. 2: 79, t. 13 (1995).

Dioecious, semipachycaul trees; trunk buttressed and stilt-rooted; indumentum simple or 0. Stipules fugacious. Inflorescences racemose to subspicate, axillary, sometimes cauliflorous, solitary or clustered; pedicels articulate; staminate flowers in clusters partly enclosed by cupular central bractlet; pistillate flowers 1 per bract. Staminate flowers: sepals 5(4), imbricate; petals 0; disk segments usually 5, fleshy; stamens usually 5, distinct; anthers introrse; pollen grains prolate, 3-colporate, pores laterally elongated, exine finely reticulate; pistillode columnar, small. Pistillate flowers: sepals 5, imbricate, persistent in fruit; petals 0; disk annular; ovary 3(4)-locular; stylodia 2-lobate or 2-fid. Fruit capsular, somewhat lignified; columella persistent, dilated at base and clavate distally. Seeds ellipsoid, testa smooth and shiny; endosperm copious; embryo straight. $2n = 26$.

Three African spp. (Guinea to Gabon and Congo), in lowland tropical rainforest.

47. ***Richeria*** Vahl

Richeria Vahl, Eclog. Amer. 1: 30, t. 4 (1797); Secco & Webster, Bol. Mus. Para. Emilio Goeldi, N.S., Bot. 6: 141–158 (1990), rev.

Dioecious trees or shrubs; indumentum simple or 0. Leaves entire or crenulate, sometimes glandular near the base; stipules deciduous. Inflorescences racemoid or spicate, axillary; staminate flowers in dense glomerules; pistillate flowers 1 per bract. Staminate flowers sessile; calyx 3–5-lobed, tips of lobes imbricate; petals 0; disk-segments 3–5; stamens 3–6, filaments distinct and exserted from calyx; anthers introrse, versatile; pollen grains prolate, 3-colporate, semitectate-reticulate; pistillode cylindric, hirtellous. Pistillate flowers pedicellate; calyx 3–5-lobed, sepals imbricate; petals 0; disk cupular; ovary 2–3-locular, sericeous; stylodia 2- or 3-fid. Fruit capsular, tardily dehiscent septicidally; columella flattened, winged, persistent. Seeds 1 per locule, ovoid; testa fleshy, exotegmen vittate; endosperm copious; cotyledons flat, much longer than radicle, both cotyledons and radicle chlorophyllous.

Two or three spp., distributed from the Lesser Antilles and Panama to Bolivia and Brazil.

48. ***Aporosa*** Blume

Aporosa Blume, Bijdr.: 514 (1826; orth. cons.); Airy Shaw, Hook. Icon. Pl. 38: pl. 3701 (1974), Kew Bull. Add. Ser. 4: 30 (1975), ibid. 8: 28 (1980); Schot, Blumea 40: 449 (1995). *Scepa* Lindl. (1836).

Dioecious trees and shrubs [flowers bisexual in four spp.]; indumentum simple. Leaves often with laminar glands, petioles long, often geniculate and distally glandular; stipules mostly persistent, sometimes foliaceous or falcate. Inflorescences usually axillary, often fasciculate, the staminate spiciform and catkin-like, the pistillate racemoid. Staminate flowers sessile or subsessile; sepals 3–6, imbricate; petals 0; disk 0; stamens 2(−5), filaments distinct; anthers subglobose, basifixed; pollen grains subprolate, 3-colporate, pores lalongate, exine semitectate-reticulate; pistillode minute or 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, persistent in fruit; petals 0; disk small; ovary 2(−4)-locular; stylodia usually bipartite, often papillose or laciniate. Fruit capsular; pericarp ± leathery, dehiscing into valves or irregularly; columella persistent. Seeds 1 or 2 per fruit, with colored sarcotesta; endosperm copious; embryo chlorophyllous, straight, cotyledons much longer and broader than radicle. $2n = 26, 52$.

About 75 spp., distributed from India and Sri Lanka to the Philippines and New Guinea.

49. ***Distichirrhops*** Haegens

Distichirrhops (’*Distichirhops*’) Haegens, Blumea Suppl. 12: 193, figs. 3.28, 3.29 (2000).

Dioecious trees; indumentum simple. Leaves distichous, entire, with marginal glands; petioles apically pulvinate; stipules deciduous. Inflorescences axillary or ramiflorous, thyrsoid [only pistillate plants known], unbranched, 10–15-flowered. Pistillate flowers in triads, each subtended by 3 bracts, with articulated pedicels; sepals 4 or 5, deciduous to persistent; petals, staminodes and disk 0; ovary 2–4-locular; ovules 2 per locule; stylodia unlobed to 2-fid. Fruits 0–4-seeded, baccate or capsular and tardily dehiscent, often glandular, 0–4-seeded. Seeds albuminous, with fleshy testa.

Three incompletely known spp., Borneo and New Guinea. According to Haegens, the genus seems to be related to *Aporosa*.

50. ***Ashtonia*** Airy Shaw

Ashtonia Airy Shaw, Kew Bull. 21: 357 (1968), Hook. Icon. Pl. 38: t. 3702 (1974), Kew Bull. Add. Ser. 4: 42 (1975).

Dioecious trees; indumentum 0. Leaves biglandular at base; stipules deciduous. Inflorescences spiciform [staminate] and racemoid [pistillate], solitary; staminate flowers in glomerules, pistillate solitary. Staminate flowers subsessile; sepals 3 or 4, imbricate; petals 0; disk obscure or 0; stamens 5 or 6, filaments distinct, shorter than sepals, anthers latrorse, dehiscing longitudinally; pollen subglobose, 3-colporate, colpi margins broad, exine coarsely reticulate; pistillode massive. Pistillate flowers pedicellate; sepals 3 or 4, deciduous; petals 0; disk 0; ovary 3 or 4(5)-locular; stylodia 2-lobed, stigmatiform. Fruits capsular with fleshy pericarp; columella persistent. Seeds with thin fleshy testa; endosperm layer thin, exotegmen vittate; embryo massive, cotyledons flat, chlorophyllous.

Two spp. from SE Asia: Thailand to Malaya and Borneo.

51. ***Maesobotrya*** Benth.

Maesobotrya Benth., Hook. Icon. Pl. 13, 75: t. 1296 (1879); Léonard, Fl. Afr. Centr., Euph. 2: 46–79, t. 7–12 (1995).

Dioecious trees or shrubs; indumentum simple. Leaves entire or dentate; stipules ± subulate (foliaceous), deciduous or persistent. Inflorescences terminal or axillary, sometimes ramiflorous; staminate flowers in racemoid thyrses, sometimes fasciculate or paniculate; pistillate flowers solitary in axils of bracts on spiciform thyrses; pedicels shortly articulated. Staminate flowers: sepals 4–6, imbricate, distinct or basally connate; petals small, 1–3, or more often 0; disk intrastaminal, segments ± confluent, usually pubescent; stamens 4–6(7), filaments distinct, usually exserted from calyx, anthers introrse, connective not enlarged; pollen grains subprolate, 3-colporate, pores ± elliptic, exine semitectate, finely reticulate; pistillode cylindric or clavate, pubescent. Pistillate flowers: sepals and petals as in staminate; disk cupular, sometimes lobed, rim usually ciliate; ovary 2–3(4)-locular, glabrous or slightly pubescent; stylodia bifid. Fruits capsular, dehiscing loculicidally; pericarp thin; columella not persistent. Seeds 1 or 2 per locule; testa fleshy and often blue; endosperm copious; embryo chlorophyllous, cotyledons flat, much longer than radicle. $2n = 26$.

Some 20 spp., mostly in the West Africa/Congo lowland rainforest area, one in Uganda and another in Zambia.

52. ***Baccaurea*** Lour.

Baccaurea Lour., Fl. Cochinch.: 661 (1790); Haegens, Blumea Suppl. 12: 80–129, figs. 3.1–3.27 (2000).

Dioecious trees; indumentum simple or stellate. Leaves entire to undulate or obscurely crenate, often with laminar and marginal glands; petiole apically and rarely basally pulvinate; stipules deciduous or subpersistent. Inflorescences axillary or ramiflorous, often fasciculate, racemoid to paniculate; staminate flowers mostly in bracteate triads, pistillate 1 per bract. Flowers pedicellate; staminate flowers sepals (3)4 or 5(−8), connate, imbricate; petals 0; disk segments mostly small or obsolete, sometimes confluent; stamens 3–10, filaments distinct; anthers basifixed to dorsifixed, introrse; pollen grains subprolate, 3-colporate, pores lalongate, exine semitectate-reticulate; pistillode massive, sometimes peltate. Pistillate flowers sepals 4–6(−9), deciduous or persistent; petals 0; disk 0; staminodes very rarely +; ovary 2–4-locular; ovules 2 per locule; stylodia unlobed to bifid, often minutely dentate or laciniate. Fruits baccate or capsular, dehiscent or indehiscent; persistent columella lacking. Seeds 0–2 per locule [or capsule]; testa ± fleshy; endosperm copious; embryo straight, cotyledons much longer and broader than radicle. $2n = 26$.

About 45 spp., mainly in southeast Asia and New Guinea, with one sp. in India and two in the Pacific, mostly in rainforest and freshwater swamp forest. Studies of Levin (1986a, b) and

Haegens (2000) indicated that *Baccaurea* is probably most closely related to African *Maesobotrya*, which was confirmed by the molecular data (Kathriarachchi et al. 2005).

53. ***Nothobaccaurea*** Haegens

Nothobaccaurea Haegens, Blumea Suppl. 12: 198, figs. 3.30, 3.31 (2000).

Dioecious trees or shrubs; indumentum simple. Leaves alternate or opposite, often with marginal and laminar glands; petioles apically pulvinate; stipules deciduous. Inflorescences axillary or ramiflorous, solitary or fasciculate, racemoid or spiciform; pedicels articulate or not. Staminate flowers sepals 3–7, fused at base; petals and disk 0; stamens 5–7, longer than sepals, filaments distinct; anthers dehiscing longitudinally or with apical slit; pistillode cylindrical, glabrous. Pistillate flowers: sepals 5 or 6, slightly imbricate, persistent in fruit; petals and disk 0; staminodes +; ovary 2-locular; stylodia bifid. Fruits baccate or tardily dehiscent; pericarp fleshy and glandular. Seed coat fleshy; embryo with cotyledons much longer and broader than radicle.

Two spp., Melanesia: Solomons and Fiji. Appears quite similar to *Baccaurea* and the African *Maesobotrya*.

7. Tribe Jablonskieae Petra Hoffm. (2006).

Monoecious or dioecious; indumentum and exudate 0; inflorescences racemoid or glomerular; sepals 5, imbricate, petals 0; disk +; stamens 5, distinct.

Two neotropical genera, which differ in several traits such as the reproductive system and the structure of the anthers, fruits, and seeds (but see Tokuoka and Tobe 2002), but share similarities in pollen (Webster 1984) and wood structure (Mennega 1987), and appear in a strongly supported sister position (Kathriarachchi et al. 2005).

Key to the Genera of Jablonskieae

1. Monoecious; leaves distichous; flowers in axillary glomerules; fruit dehiscing irregularly **54. *Jablonskia***
– Dioecious; leaves spiral; staminate flowers in pedunculate pseudo-racemes, pistillate ones in few-flowered brachyblasts; fruit septicidal **55. *Celianella***

54. ***Jablonskia*** G.L. Webster

Jablonskia G.L. Webster, Syst. Bot. 9: 232 (1984); Radcl.-Sm., Gen. Euph.: 62 (2001).

Monoecious glabrous shrubs or trees. Leaves distichous, shortly petiolate, with minute pigment streaks and basal laminar glands; tanniniferous cells 0; stipules deciduous. Inflorescences axillary, glomerules bracteate. Flowers sessile or subsessile; staminate flowers sepals 5, imbricate; petals 0; disk segments 5; stamens 5, filaments distinct; anthers introrse, versatile, dehiscing longitudinally; pollen grains prolate, 3-colporate, pores lalongate, exine tectate-perforate; pistillode much shorter than calyx. Pistillate sepals persistent in fruit, petals 0; disk patelliform; ovary 3-locular; stylodia distinct, bifid, erect. Fruit a baccate thin-walled capsule, dehiscing irregularly; columella subpersistent. Seeds 2 per locule; testa thin and fleshy; endosperm copious; cotyledons broader than and about equaling radicle.

One sp., *J. congesta* (Benth. ex Müll. Arg.) G.L. Webster, rainforests of Amazonian South America.

55. ***Celianella*** Jabl.

Celianella Jabl., Mem. New York Bot. Garden 12(3): 176, fig. 28 (1965); Radcl.-Sm., Gen. Euph.: 68 (2001).

Dioecious shrubs; indumentum 0. Leaves subsessile, semisucculent, minutely puncticulate abaxially; stipules deciduous, leaving conspicuous scars. Inflorescences pedunculate, axillary or subterminal, staminate racemoid, pistillate 3–1-flowered brachyblasts; bracts uniflorous, entire, deciduous. Staminate flowers pedicellate; sepals 5, imbricate; petals 0; stamens 5, filaments distinct; anthers introrse, pendulous; pollen grains prolate, 3-colporate, exine finely tectate-perforate; disk central, 5-lobate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, strongly veined, persistent and accrescent in fruit; petals 0; disk annular; ovary 3-locular; ovules 2 per locule, pendulous beneath an obturator; stylodia connate in lower half, 2-fid. Fruits capsular, septicidal; columella persistent. Seeds fusiform, testa reticulate, micropyle with minute caruncle; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *C. montana* Jabl., on sandstone tepuis of southern Venezuela above 1,000 m.

8. Tribe Spondiantheae G.L. Webster (1975).

Dioecious; exudate reddish; inflorescences mostly terminal, paniculate, bracts small; flowers, at least the staminate, petaliferous, subsessile; staminate disk dissected; stamens 5, filaments distinct; pistillode +; pistillate disk lobed; stylodia distinct, bilobed; fruit loculicidally dehiscent; seed testa dry; endosperm scanty; cotyledons much broader than the radicle.

A single, monotypic African genus.

56. *Spondianthus* Engler

Spondianthus Engler, Bot. Jahrb. 36: 215 (1905); Hutchinson, Hook. Icon. Pl. 30: t. 2986 (1911); Léonard & Nkounkou, Bull. Jard. Bot. Nat. Belg. 59: 133–149 (1989).

Dioecious trees; stems with reddish exudate; indumentum simple or 0. Petioles with paired minute glands; stipules deciduous. Inflorescences terminal or subterminal, paniculate; flowers bracteate, staminate in glomerules, pistillate solitary. Staminate flowers subsessile; sepals (4)5, imbricate; petals (4)5, smaller than sepals; disk segments 5; stamens 5, filaments distinct; anthers introrse, connective glandular; pollen subprolate, 3-colporate, pores dumbbell-shaped, exine tectate-perforate; pistillode massive, apically flattened. Pistillate flowers pedicellate; sepals and petals as in the staminate, or petals 0; disk cupular, fleshy; ovary 3(5)-locular; ovules 2 per locule; stylodia 3, distinct, shortly 2-lobate, reflexed; stigmas papillose. Fruit capsular, dehiscing loculicidally; columella persistent. Seeds usually 1 per locule, compressed, testa reddish; endosperm scanty; embryo straight, cotyledons broad, flat.

A single sp., *S. preussii* Engl., widespread in tropical Africa: Guinea to Angola, Uganda and Tanzania. Due to the presence of fluoroacetic acid (Hegnauer 1989; Neuwinger 2000), *Spondianthus* is strongly toxic, and shares with *Uapaca* the unique presence of resinous exudate in the Phyllanthoideae. The molecular data place these genera in a sister position but with low support. The available seed anatomical data are inconclusive.

9. Tribe Uapaceae Hutch. (1969).

Uapacaceae (Müll. Arg.) Airy Shaw (1965).

Dioecious; exudate reddish; inflorescences axillary, capitular, conspicuously bracteate; flowers apetalous, disk 0; sepals 5, connate; stamens 4–6; pistillode large; ovary mostly 3-locular; stylodia laciniate; fruits drupaceous.

A monotypic Afro-Malagasian tribe.

57. *Uapaca* Baill. Fig. 16

Uapaca Baill., Étude Gén. Euph.: 595 (1858); Benth., Hook. Icon. Pl. 13: t. 1287 (1879); Pax & K. Hoffm., Pflanzenr. 147, XV: 298–311 (1922); Leandri, Fl. Madag. 111(1): 163 (1958); Radcl.-Sm., Fl. Zamb. 9(4): 93 (1996).

Dioecious pachycaul trees or shrubs with reddish resinous exudate; trunks often stilt-rooted; indumentum simple or microlepidote. Leaves petiolate or subsessile, entire; stipules deciduous or 0. Inflorescences axillary, pedunculate, globose-capitular, solitary or clustered, bracts 5–12, conspicuous, becoming reflexed, each with 5–10 staminate or solitary pistillate flowers. Staminate flowers sessile; calyx small, truncate to 4–6-lobate, lobes imbricate; petals and disk 0; stamens 4–6, filaments distinct; anthers introrse, erect; pollen grains oblate spheroidal, 3-colporate, angulaperturate, colpi narrow, pore large and rectangular, exine semitectate-reticulate; pistillode clavate to pileiform, sometimes lobate. Pistillate flowers sessile, perianth similar to staminate; disk 0; ovary mostly (2)3(5)-locular; stylodia distinct, dilated, recurving, distally laciniate. Fruit drupaceous with mostly 3 dorsally carinate pyrenes, tardily loculicidal into 2 valves each; columella persistent. Seeds usually 1 per pyrene, compressed; endosperm copious; embryo straight, cotyledons green, flat or slightly plicate, longer and broader than the radicle. $2n = 26$.

About 50 spp. in Madagascar and Africa; growing from humid evergreen to semi-deciduous and sclerophyllous forest and from sea level up to over 2,000 m elevation. The largest number of species are known from the Congo basin and are in need of reevaluation, 12 are endemic to Madagascar. The involucrate heads of disk-less flowers have always set *Uapaca* apart from other Euphorbiaceae, so that Airy Shaw (1965) and similarly Meeuse (1990) removed it to the separate family Uapacaceae. However, the basic floral and fruit structure is clearly euphorbiaceous.

10. Tribe Bischofieae (Müll. Arg.) Hurus. (1954).

Bischofiaceae (Müll. Arg.) Airy Shaw (1965).

Dioecious; exudate 0; indumentum simple, sparse. Leaves palmately 3(5)-foliolate; stipules caducous. Inflorescences axillary, paniculate; flowers apetalous. Sepals 5, imbricate, margins induplicate; disk 0; stamens 5; pollen grains

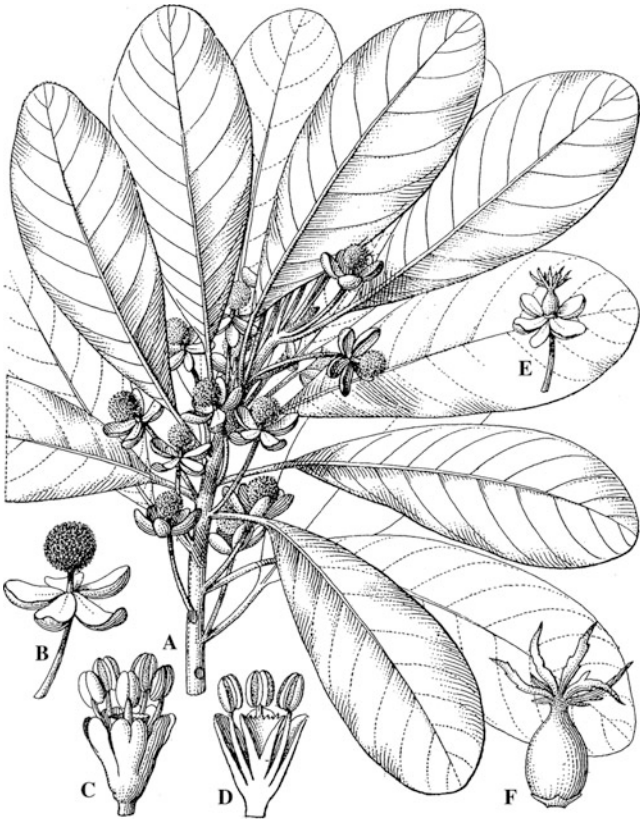

Fig. 16. Euphorbiaceae-Phyllanthoideae. *Uapaca heudelotii*. **A** Flowering branch. **B** Staminate inflorescence. **C, D** Staminate flowers. **E** Pistillate flower. **F** Pistil. (Pax & Hoffmann 1922)

subglobose, 3-colporate; pistillode +; ovary 3(4)-locular; stylodia simple, entire; fruits baccate.

A monotypic paleotropical tribe.

58. ***Bischofia*** Blume

Bischofia Blume, Bijdr.: 1168 (1826); Hook., Icon. Pl. 9: t. 844 (1852); Pax & K. Hoffm., Pflanzenr. 147, XV: 312, fig. 26 (1922); Li Bingtao & Gilbert, Fl. China 11: 217 (2008).

Dioecious (monoecious) trees; vessel element perforations simple and scalariform; wood fibers septate; indumentum simple, very sparse. Leaves palmately 3(5)-foliolate; leaflets petiolulate, crenate-serrate, abaxially with marsupiform domatia and with paired glands on the petiole and the petiolule of the terminal leaflet [interpreted by Wurdack et al. 2004 as stipels]; stipules deciduous. Inflorescences axillary, paniculate, bracts 1-flowered, deciduous; pedicels not articulated. Staminate flowers pedicellate; sepals 5, imbricate, cucullate-concave and enclosing anthers; petals and disk 0; stamens 5, filaments distinct, much shorter than sepals; anthers extrorse, muticous; pollen grains subglobose, 3-colporate, nearly syncolpate, exine tectate-perforate; pistillode peltate. Pistillate flowers pedicellate; sepals 5, imbricate, deciduous; petals and disk 0; staminodes minute or 0; ovary 3(4)-locular; stylodia 3(4), partially connate, subulate, unlobed; stigmas terete, smooth. Fruits oblate, baccate, epicarp thin, mesocarp fleshy, endocarp corneo-pergamaceous; locules 1–2-seeded; columella not persistent. Seeds smooth; endosperm copious; embryo green, curved, cotyledons much broader and longer than radicle. $2n = 196$.

Two spp., *B. javanica* Blume being widespread from India to eastern Asia, Melanesia, and Polynesia (to Samoa and Niue); *B. polycarpa* (Lévl.) Airy Shaw is endemic to China.

The distinctive characters of *Bischofia*, especially the trifoliolate leaves, the marsupiform domatia, and the sepals partly enclosing the anthers led Airy Shaw (1965) to move it to the segregate family Bischofiaceae, but the evidence provided by Bhatnagar and Kapil (1974), Levin (1986a), Mennega (1987), and Tokuoka and Tobe (2001) indicates that *Bischofia* belongs to Phyllanthoideae without showing a clear affinity with any other genus. In the molecular analyses it appears always in basal position within the Tanniniferous Clade.

Incertae sedis:

59. ***Chonocentrum*** Pierre ex Pax & K. Hoffmann

Chonocentrum Pierre ex Pax & K. Hoffmann, Pflanzenr. 147, XV: 205 (1922); Webster, Ann. Missouri Bot. Gard. 81: 37 (1994); Hayden & Hayden, Ann. Missouri Bot. Gard. 83: 165 (1996); Radcl.-Sm., Gen. Euphorb.: 12, fig. 2 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves alternate, entire; stipules persistent. Flowers in axillary glomerules. Staminate flowers subsessile; sepals 4–5, connate, apically pubescent; petals 0; disk cupular; stamens 4–6, filaments distinct; anthers erect, basifixed, longer than filaments, introrse, pubescent, connective not enlarged; pollen grains prolate, 3-colporate, exine apparently tectate; pistillode large, cyathiform, 4- or 5-lobed, glabrous. Pistillate flowers and fruits unknown.

One sp., *Ch. cyanophorum* (Müll. Arg.) Pax & K. Hoffm., Amazonian Brazil, only once collected (Spruce 3781, K, P). Originally described by Müller (1873) as *Drypetes cyatophora*, it was regarded to be related to *Discocarpus* by Pax and Hoffmann (1922). S.M. and W.J. Hayden (1996) have shown that it is not closely related to *Discocarpus* and instead suggested placing it in the Antidesmeae, but there it would be anomalous in its cupular staminate disk and non-versatile anthers.

II. Subfam. Oldfieldioideae Eg. Köhler & G.L. Webster (1967)[1].

Hyaenanchoideae Baillon ex Hassk. (1859) ('Hyaenachneae' [sic!]).
Picrodendraceae Small (1917), nom. cons.

Monoecious or dioecious trees, shrubs or subshrubs; vessel elements (excepting Podocalyceae) mainly with simple perforations; wood fibers not septate except in *Parodiodendron*; indumentum simple [trichomes unicellular or uniseriate]. Leaves alternate, opposite or whorled; leaf blades simple or palmately compound, venation mostly brochidodromous, margins entire or dentate; stomata mostly brachyparacytic; stipules mostly deciduous or 0. Inflorescences axillary, glomerulate, racemoid, capitulate, or paniculate; bracts eglandular. Flowers mostly apetalous; staminate sepals (3)4–8 (−12), imbricate, usually distinct; disk mostly intrastaminal or 0; stamens (2)3–30, filaments distinct or connate; anthers mostly extorse; pollen spheroidal to oblate, 3–7-zono-brevicolporoidate or -porate or 10–40-pantoporate, microperforate-tectate, mostly with conspicuous spines; male gametophyte binucleate; pistillode + or 0. Pistillate sepals (3)4–8(−13), distinct, imbricate; disk annular to lobed, dissected or 0; ovary 2–4(5)-locular; ovules 2 per locule; stylodia entire, often dilated (2-fid). Fruit capsular (drupaceous). Seeds 1 or 2 per locule, often caruncülate, testa usually smooth and shiny; endosperm usually copious; cotyledons plane or plicate, usually much longer and broader than the radicle. $x = 12$ or 13.

A predominantly Southern Hemisphere group of three tribes with 26 genera and c. 95 species. Relationships within Oldfieldioideae have been greatly clarified by the anatomical and morphological studies of Hayden (1994) and Levin and Simpson (1994), by the analysis of seed structure by Stuppy (1996), and by the molecular analyses of Wurdack (2002) and Wurdack et al. (2004). The latter work suggests the maintenance of three tribes, of which the monotypic Podocalyceae are basal to Picrodendreae and Caletieae, the latter being sister to each other. In Picrodendreae, *Tetracoccus* is first-branching, followed by a subclade in which *Picrodendron* is followed by *Parodiodendron* and then by *Piranhea*. *Hyaenanche* (formerly included in Caletieae) appears sister to *Oldfieldia* and both are sister to Miscodontinae, with which they agree in the whorled leaves and also in seed and general anatomy, but differ from them in the lack of stipules and among themselves in floral traits. Therefore, for these two genera Subtribe Paveusinae is upheld. In Caletieae, from which *Securinega* and *Hyaenanche* have been removed, *Petalostigma* occupies a basal position, whereas the morphologically clearly recognizable Dissilariinae and Pseudanthinae are also supported by the molecular analyses.

Key to the Tribes of Subfam. Oldfieldioideae

1. Pollen grains with 4 apertures; vessel elements at least in part with scalariform perforation plates; staminate disk extrastaminal or 0; leaves simple **1. Podocalyceae**
– Pollen grains [except in *Tetracoccus*] usually with more than 4 apertures, rarely inaperturate; vessel elements with simple perforation plates; staminal disk intrastaminal or 0; leaves simple, unifoliolatae, or palmately compound 2
2. Leaf blades compound [if simple, then lamina stipellate or stipules adnate to petiole]; pollen grains zonoporate [except *Androstachys*]; dioecious trees or shrubs **2. Picrodendreae**

---

[1] Reveal in his Website (since 1995) indicates that the subfamily name Hyaenanchoideae Baill. & Hassk. should have priority over Oldfieldioideae Eg. Köhler & G.L. Webster. Because the latter name has been in use in very many publications during the last four and a half decades, it is exasperating to have to replace it with an obscure, completely unfamiliar and originally misspelled name that obviously never has been used since its proposal by Hasskarl (1859) by taxonomists working on the Euphorbiaceae. For the sake of better communication, we are continuing to use the younger, well-introduced name. This is also so because there is so much still unearthed but nomenclaturally relevant botanical literature especially from the 19th century—e.g., in seed lists and annual reports from botanic gardens or colleges and grammar schools—that there is no end in sight for discoveries of even older botanical names and/or authorships.

- Leaf blades undivided [pseudo-trifoliolate in *Micrantheum*]; pollen grains zonoporate or pantoporate; monoecious or dioecious trees, shrubs, or subshrubs **3. Caletieae**

1. TRIBE PODOCALYCEAE G.L. Webster (1994).

After the exclusion of *Tetracoccus* (to Picrodendreae) and *Paradrypetes* (to Rhizophoraceae), the tribe is monotypic. It is remarkable for its vessel elements, 4-aperturtate pollen and ecarunculate seeds; in the molecular analysis of Wurdack (2002), *Podocalyx* is sister to all other Oldfieldioideae.

60. *Podocalyx* Klotzsch

Podocalyx Klotzsch, Arch. Naturgesch. 7: 202 (1841); Radcl.-Sm., Gen. Euphorb.: 84 (2001).
Richeria sect. *Podocalyx* (Klotzsch) Müll. Arg. (1866).

Dioecious trees; indumentum simple; vessel elements with simple, scalariform, and reticulate perforations. Leaves simple; petioles thickened at both ends, stomata anomocytic; stipules appearing obsolete [precociously deciduous?]. Inflorescences axillary or pseudo-terminal, staminate spiciform with dense pubescent capitular glomerules, pistillate racemoid, often fasciculate. Flowers apetalous; staminate flowers pedicellate, sepals usually 4, scarcely imbricate, basally connate; stamens usually 4, filaments distinct, far exserted above the calyx; anthers extrorse; pollen oblate, 4-zoniporate, echinate; pistillode represented by massive lobed intrastaminal disk. Pistillate flowers pedicellate, sepals 4, entire, distinct, persistent but not accrescent in fruit; disk cupular, 5-lobed; ovary 3-locular, ovules anatropous; stylodia stigmatoid, dilated. Fruiting pedicels massive, lenticellate; fruits capsular, loculicidally and septicidally dehiscent; columella persistent. Seeds 1/locule, hypostase basal, hilum subterminal; testa smooth, blackish, exotegmen cells elongated; endosperm copious; embryo straight, flat, cotyledons much longer and broader than radicle.

A single sp., *P. loranthoides* Klotzsch, widespread and common in Amazonian riparian and inundated forests of Colombia, Venezuela, and Brazil. Treated by Müller (1873) as a section of *Richeria* (Phyllanthoideae-Antidesmateae), *Podocalyx* has spinose pollen grains typical of Oldfieldioideae, but is an isolated genus in the subfamily.

Doubtful genus (for its formal treatment, see under Rhizophoraceae):

60a. *Paradrypetes* Kuhlm.

Formerly included in Oldfieldioideae but, on the basis of molecular findings by Wurdack (2002) and Wurdack and Davis (2009), this genus has been shifted (close) to the Rhizophoraceae. Although there is a general resemblance in habit between *Paradrypetes* and genera such as *Cassipourea*, none of the Rhizophoraceae has echinate pollen, such strongly pronounced unisexual and apetalous flowers, thin, distinct and imbricate sepals, and sessile stigmas (see Levin 1992; Mathews and Endress 2011). Therefore, doubts on the implications of the molecular data persist, and a clarification of the issue would be highly desirable.

2. TRIBE PICRODENDREAE (Small) G.L. Webster (1975).

Picrodendraceae Small (1917).

Monoecious or dioecious; leaves alternate or opposite, simple, unifoliolate or 3–9-parted; stipules fused to petiole or 0; flowers in axillary cymes, racemes, or glomerules; sepals 4–8 or obsolete; disk intrastaminal or 0; stamens 4–50, distinct; pollen [sub]oblate, 4–7-zoniporate, rarely [*Picrodendron*] 5–8-brevicolporate or [*Androstachys*] 5–7-pantoporate, echinate; ovary 2- or 3-locular; fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm usually copious.

This heterogeneous tribe includes 9 genera in 4 subtribes: 2 neotropical and 2 paleotropical.

The West Indian genus *Picrodendron* has been placed by some authors in a separate family Picrodendraceae because of its unusual foliage, flowers, and fruits, but the pollen indicates its membership in the Oldfieldioideae. *Androstachys*, placed in family Androstachydaceae by Airy Shaw (1965) because of its highly specialized flowers, also has pollen typical of the Oldfieldioideae. The tribal position of *Tetracoccus* would merit further inquiry; see the discussion by Stuppy (1996: 172).

KEY TO THE SUBTRIBES OF PICRODENDREAE

1. Pollen grains with 4 apertures, interspinal tectum verrucate ; pistillate sepals persistent in fruit; ovary 2–5-locular; seeds carunculate **2a. Tetracoccinae**
- Pollen grains [at least in part] with 5 apertures or more; pistillate sepals persistent or deciduous; ovary 2–3-locular; seeds carunculate or ecarunculate 2
2. Stipules adnate to petiole and persistent, or intrapetiolar-connate and deciduous; pollen grains with

interspinal tectum psilate; seeds ecarunculate **2b. Mischodontinae**

– Stipules distinct, deciduous or 0; interspinal tectum baculate or verrucate; seeds caruncuIate or ecarunculate 3

3. Leaves alternate; staminate sepals distinct; capsule septicidal or indehiscent **2e. Picrodendrinae**

– Leaves alternate or more often opposite or whorled; staminate sepals connate; capsule loculicidal 4

4. Leaves digitately foliolate; stamen filaments as long as or longer than anthers **2c. Paivaeusiinae**

– Leaves simple, whorled [at least in part]; filaments shorter than anthers **2d. Hyaenanchinae**

2a. SUBTRIBE TETRACOCCINAE G. Levin (1994).

Dioecious; inflorescences racemoid or paniculate; stamens 5–10, distinct; pollen grains 4-zonipororate; ovary 2–5-locular; fruit capsular.

A monogeneric North American subtribe.

61. *Tetracoccus* Engelm. ex Parry

Tetracoccus Engelm. ex Parry, W. Amer. Sci. 1: 13 (1885); Croizat, Bull. Torrey Bot. Club 69: 456 (1942); Dressler, Rhodora 56: 49 (1954), rev.
Halliophytum I.M. Johnston (1923).

Dioecious shrubs; indumentum simple. Leaves alternate, opposite or whorled, 1-veined or pinnately veined, entire or dentate; stipules 0. Staminate inflorescences axillary, racemoid or paniculate, sometimes fasciculate; pistillate flowers axillary, solitary or clustered. Staminate flowers pedicellate; petals 0; sepals 4–10, filaments distinct, exserted; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, zono-4-porate, echinate; disk [pistillode?] intrastaminal, ± lobed. Pistillate flowers pedicellate; petals 0; sepals 5–13, imbricate, persistent in fruit; disk lobed; ovary (2)3–4(5)-locular, ovules anatropous; stylodia distinct, unlobed. Fruits capsular; columella persistent. Seeds carunculate; testa smooth, shiny, blackish, exotegmen tracheoidal; endosperm copious; embryo straight, green; cotyledons flat, much longer and broader than radicle.

Five spp., North America, in deserts of California, Arizona, and northern Mexico.

2b. SUBTRIBE MISCHODONTINAE Müll. Arg. (1865).

Androstachydaceae Airy Shaw (1965).

Monoecious or dioecious; leaves simple or 3–7-foliolate; stipules persistent and adnate to petiole or intrapetiolar-connate; pollen 5–8-zonoporate [*Androstachys* pantoporate]; stylodia ± connate.

This subtribe of 5 genera is African/Madagascan in distribution, except for *Mischodon* in Ceylon.

KEY TO THE GENERA OF MISCHODONTINAE

1. Staminate "flowers" of 30–50 solitary stamens allegedly spirally arranged on an elongated column; stylodia connate into a common style with distal style branches 2

– Staminate flowers compact, with 6–25 stamens and the filaments in 1 or 2 whorls; stylodia distinct or basally connate 3

2. Stipules discrete, adnate to petiole; leaves 3-7-foliolate, leaflets pinnately veined; pollen grains zonoporate **66. *Stachyandra***

– Stipules connate, free from petiole; leaf blade simple, palmately veined; pollen grains pantoporate **65. *Androstachys***

3. Leaves alternate, 1–3-foliolate; staminate disk 0; pistillode + **62. *Aristogeitonia***

– Leaves opposite or whorled, simple; staminate disk and/or pistillode 0 4

4. Staminate disk 0, pistillode +; pistillate sepals deciduous **63. *Mischodon***

– Staminate disk +; pistillode 0; pistillate sepals accrescent in fruit **64. *Voatamalo***

62. *Aristogeitonia* Prain

Aristogeitonia Prain, Kew Bull. Misc. Inf. 1908: 338 (1908); Hook. Icon. Pl. 30: t. 2926 (1911); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 118 (1987).
Paragelonium Leandri (1939).

Dioecious or monoecious trees or shrubs; indumentum simple. Leaves long-petiolate, 1–3-foliolate, leaflets entire; stipules subulate, adnate to petiole. Inflorescences axillary, ± ramiflorous, in glomerules. Staminate flowers pedicellate; sepals 6, distinct, biseriate, imbricate; petals and disk 0; stamens 11–15, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains oblate spheroidal, 5–7-zono-brevicolporate, exine echinate, microperforate; pistillode lobed. Pistillate flowers pedicellate, sepals 6, distinct, biseriate, imbricate, deciduous; petals 0; disk annular, somewhat lobed; ovary 3-locular, slightly pubescent; stylodia short, flat, ± stigmatiform. Fruits capsular, septicidal; columella not persistent. Seeds 1 or 2 per locule; testa shiny, 3–5 cell layers thick, ecarunculate; endosperm copious; embryo straight, cotyledons much longer and broader than radicle.

Seven spp., disjunct in Angola, Kenya/Tanzania, one of them in Madagascar.

63. ***Mischodon*** Thwaites

Mischodon Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 299 (1854); Raju, J. Econ. Tax. Bot. 5: 165 (1984); Philcox, Rev. Handb. Fl. Ceylon 11: 267 (1997).

Dioecious trees; indumentum simple. Leaves whorled, simple, entire; stipules minute, adnate to petiole, deciduous [sometimes obsolete]. Inflorescences axillary, paniculate [pistillate ± reduced to glomerules]. Staminate flowers pedicellate; sepals 5–8, distinct, imbricate; petals 0; disk 0; stamens usually 6(5–10), filaments distinct, exserted; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 5–7-brachycolporate, echinate; pistillode 3-lobed. Pistillate flowers subsessile but pedicels elongating and thickened in fruit; sepals 6, distinct, imbricate, deciduous in fruit; petals 0; disk annular; ovary 3- or 4-locular, glabrous; stylodia stigmatiform. Fruits capsular, thin-walled; columella persistent. Seeds with smooth shiny testa; exotegmen 1-layered; endosperm copious; embryo straight, cotyledons much longer and broader than radicle. $n = 24$.

A single sp., *M. zeylanicus* Thwaites, restricted to Ceylon and southern India.

64. ***Voatamalo*** Capuron ex Bosser

Voatamalo Capuron ex Bosser, Adansonia II, 15: 333 (1976); Radcl.-Sm., Gen. Euphorb.: 108 (2001).

Dioecious trees; indumentum 0 or very sparse. Leaves opposite, simple; stipules intrapetiolar, connate, deciduous. Inflorescences axillary, cymose. Staminate flowers pedicellate; sepals 6 (7), biseriate, distinct, imbricate; petals 0; disk irregularly lobed, partly intrastaminal; stamens 9–14, filaments distinct, exserted; anthers extrorse; dehiscing longitudinally; pollen grains spheroidal, 5- or 6-zonoporate; sexine echinate, microperforate; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, distinct, imbricate, persistent in fruit; petals 0; disk annular; ovary 3–5-locular; stylodia connate in lower half, unlobed, distally dilated. Fruits capsular; columella persistent. Seeds carunculate.

Two spp., endemic to Madagascar, said by Bosser to be related to *Austrobuxus*; however, he also compared *Voatamalo* with *Androstachys*. The distinctive intrapetiolar stipules strongly support a relationship with *Androstachys* and *Stachyandra*.

65. ***Androstachys*** Prain Fig. 17

Androstachys Prain, Kew Bull. Misc. Inf. 1908: 438 (1908); Airy Shaw, Adansonia II, 10: 519 (1970); J.-F. Leroy, C.R. Acad. Sci. D 283: 147 (1976); Radcl.-Sm., Fl. Zambesiaca 9 (4): 120, t. 20 (1996).

Dioecious trees; indumentum simple. Leaves opposite, simple or 3–7-foliolate; stipules intrapetiolar, connate, sheathing, deciduous. Inflorescences axillary; the staminate ones in triad of elongate spikes; pistillate flowers solitary. Staminate flowers subtended by 3–5 distinct, narrow sepals; petals and disk 0; stamens 30–50, allegedly spirally but probably not so inserted on an elongate "receptacle" probably formed by connation of the filaments; anthers extrorse, elongated, connective setose, dehisicing longitudinally; anther connective hispidulous; pollen grains spheroidal, pantoporate; exine echinate; pollen grains spheroidal, 5–7-pantoporate, echinate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, lanceolate, distinct, imbricate, deciduous or persistent in fruit; petals 0; disk 0; ovary 3(−5)-locular; stylodia connate into a long columnar style; stylar branches unlobed. Fruits capsular, depressed-globose; endocarp thin and crustaceous; columella persistent. Seeds 2 per locule, carunculate or not; testa smooth and shiny, 4 or 5 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, cotyledons much longer and broader than radicle.

One sp., *A. johnsonii* Prain, Madagascar and southeast Africa.

In *Androstachys* and *Stachyandra*, the male flowers are usually interpreted as possessing numerous stamens spirally inserted on an elongated column (Radcliffe-Smith 2001), but from the morphological point of view this is unlikely in the extreme, because flowers with numerous spirally arranged stamens on elongate floral axes are unknown in the higher eudicots. It is likely that the androecia of these probably anemophilous plants simply have strongly developed androecia but are not catkin-like pseudanthia, as probably erroneously assumed by Airy Shaw (1965) and Leroy (1976). In all other characters, including the characteristic stipules, fruits and seeds, the two genera agree perfectly with the rest of the subtribe, and there is no need for an elevated taxonomic status.

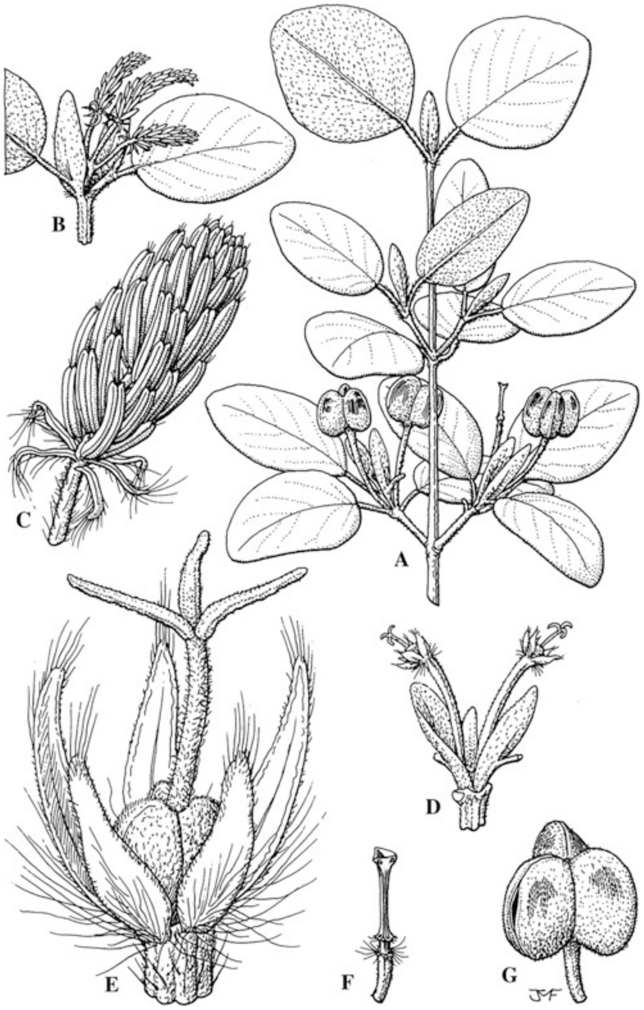

Fig. 17. Euphorbiaceae-Oldfieldioideae. *Androstachys johnsonii*. **A** Distal portion of fruiting branch. **B** Staminate inflorescence. **C** Staminate flower. **D** Pistillate inflorescence. **E** Pistillate flower. **F** Columella. **G** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

66. *Stachyandra* Leroy ex Radcl.-Sm.

Stachyandra Leroy ex Radcl.-Sm., Kew Bull. 45: 562 (1990).

Dioecious trees; indumentum simple. Leaves opposite, 3–7-foliolate; leaflets pinnately veined, entire; stipules intrapetiolar, laterally connate, sheathing, caducous. Inflorescences and staminate floral structures as in *Androstachys*; pollen grains spheroidal, 4–7-zonoporate; exine echinate. Pistillate flowers pedicellate; sepals 6, verticillate, persistent in fruit; disk 0; ovary 3-locular; stylodia connate into a columnar style; tips unlobed. Fruits capsular; apiculate; columella persistent. Seeds 2 per locule, carunculate, testa smooth.

Four spp., endemic to Madagascar. Closely related to *Androstachys* and combined with it by Schatz (2001) on the basis of the close resemblance in floral morphology.

2c. Subtribe Paivaeusinae Pax & K. Hoffm. (1922).

Dioecious; leaves alternate, opposite, or in whorls, long-petiolate, digitately 3–8-foliate, entire; stipules 0; exotegmen 1 or 4–5 cell layers thick.

A single African genus.

67. *Oldfieldia* Benth. & Hook. f. Fig. 18

Oldfieldia Benth. & Hook. f., Hook. J. Bot. Kew Gard. Misc. 2: 184, t. 6 (1850); Pax & K. Hoffm., Pflanzenr. IV, 147: 297 (1922); Léonard, Bull. Jard. Bot. État 26: 338 (1956); Radcl.-Sm., Fl.Trop. E. Afr., Euphorb. 1: 114, t. 21 (1987), Fl. Zambesiaca 9(4): 117, t. 19 (1996).

Paivaeusa Welw. ex Benth. (1867).

Dioecious trees or shrubs; indumentum simple. Leaves alternate, opposite or in whorls of 3, long-petiolate, digitately 3–8-foliolate; leaflets entire; stipules 0. Inflorescences axillary, staminate cymose, ± densely congested, pistillate 1–3-flowered. Staminate flowers pedicellate or subsessile; sepals 5–8, basally connate, imbricate; petals 0; disk intrastaminal; stamens 4–12, filaments distinct, exserted, inserted between lobes of disk; anthers extrorse, dehiscing longitudinally; pollen spheroidal, 5–8-zoniporate or brachycolporate, echinate; pistillode small or 0. Pistillate flowers pedicellate in fruit; sepals 5–8, imbricate, persistent in fruit; petals 0; disk annular; ovary 2- or 3-locular; stylodia unlobed, apically dilated. Fruits capsular, tardily loculicidally dehiscent; columella persistent. Seeds 1 or 2/locule, carunculate, testa fleshy; exotegmen 4 or 5 cell layers thick; endosperm copious; embryo green, cotyledons flat, much longer and broader than radicle.

Four spp., tropical Africa. Stuppy (1996) has questioned the position of *Oldfieldia* in the Oldfieldioideae—and indeed in the Euphorbiaceae—because of its aberrant fruits and seeds. However, the spinose pollen as well as the anatomical and molecular data do not provide any reason to remove *Oldfieldia* from the Euphorbiaceae.

2d. Subtribe Hyaenanchinae Baill. ex Müll. Arg. (1865).

Dioecious; disk 0; pollen grains 6- or 7-zonoporate; stylodia elongated, dilated; seeds carunculate.

A single genus endemic to the Cape region.

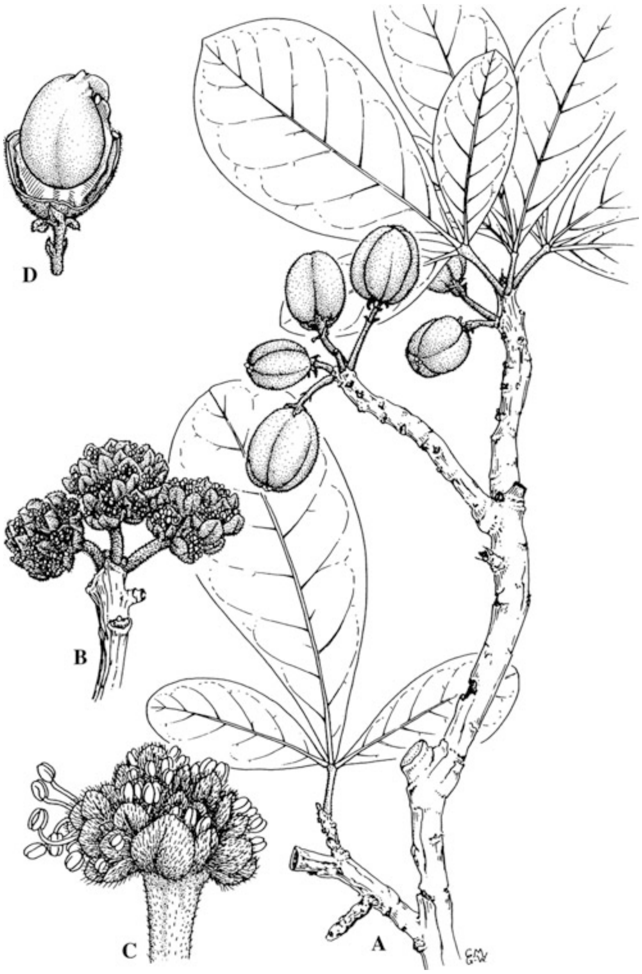

Fig. 18. Euphorbiaceae-Oldfieldioideae. *Oldfieldia dactylophylla*. **A** Fruiting branch. **B** Staminate inflorescence. **C** Staminate flowers. **D** Fruit, partly cut away to show attachment of seed. (Radcliffe-Smith 1987; drawn by Christine Grey-Wilson)

68. *Hyaenanche* Lamb.

Hyaenanche Lamb., Descr. *Cinchona*: 52, t. 10 (1797); Müll. Arg. in DC., Prodr. 15(2): 479 (1866); Connell, Fl. Pl. S. Afr. 21: t. 837 (1941); Dyer, Gen. S. Afr. Pl. 1: 311 (1975); Radcl.-Sm., Gen. Euphorb.: 89 (2001).
Toxicodendrum Thunb. (1796); non *Toxicodendron* P. Miller (1754).

Dioecious shrubs; indumentum simple [inflorescences only]. Leaves opposite or in whorls of 4, simple, entire; stipules 0. Inflorescences axillary, in glomerules or panicles. Staminate flowers pedicellate; sepals 4–8(−12), basally connate; petals 0; disk 0; stamens 8–30, filaments distinct, shorter than anthers, inserted on a convex receptacle; anthers introrse to extrorse, dehiscing longitudinally; pollen oblate, 6–8-zoniporate, echinate; pistillode 0. Pistillate flowers pedicellate; sepals 3–8, distinct, deciduous in fruit; petals 0; ovary 3–4-locular, sericeous; stylodia elongated, ± dilated. Fruit capsular; columella persistent. Seeds caruncluate, caruncule subterminal, hypostase subbasal; testa black, shiny, exotegmen 1 cell layer thick; endosperm copious, embryo green, somewhat bent, cotyledons much longer and broader than radicle.

A single sp., *H. globosa* (Gaertn.) Lamb. & Vahl, Cape region of South Africa. The molecular data (Wurdack et al. 2004) show *Hyaenanche* out of place among the Old World genera of Caletieae, where it had been accommodated, and suggest a place close to *Oldfieldia*, from which it differs in, among other things, its entire, whorled leaves.

2e. Subtribe Picrodendrinae (Small) G.L. Webster (1994).

Dioecious; leaves simple [unifoliolate] or digitately 3-foliolate; pollen 5–8-porate or brevicolporate, echinate; fruit capsular or drupaceous.

This subtribe of three neotropical genera represents the Picrodendraceae of Small (s. str.).

Key to the Genera of Picrodendrinae

1. Leaves simple [unifoliolate], subsessile; pistillate disk 6-lobed **70. *Parodiodendron***
– Leaves mostly 3–5-foliolate, long-petiolate 2
2. Fruits capsular; ovary 3-locular; staminate flowers pedicellate, in spiciform thyrses; disk intrastaminal **71. *Piranhea***
– Fruits indehiscent; ovary 2-locular; staminate flowers sessile or subsessile, in catkins; disk 0 **69. *Picrodendron***

69. *Picrodendron* Planch.

Picrodendron Planch., Hook. London J. Bot. 5: 579 (1846; nom. cons.); Fawcett & Rendle, J. Bot. 55: 268 (1917); Correll, Fl. Bahama Arch. 410, t. 165 (1982); Hayden et al., J. Arnold Arb. 65: 109, t. 1, 2 (1984); M.I. Hakki, Bot. Jahrb. 107: 379 (1985); Radcl.-Sm., Gen. Euphorb.: 103 (2001).

Dioecious (monoecious) trees; indumentum simple. Leaves long petiolate, 3-foliolate, leaflets entire; stipules rudimentary, deciduous. Staminate inflorescences axillary, spicate, catkin-like, flowers 1 per bract; pistillate flowers solitary. Staminate flowers sessile or subsessile; perianth apparently 0; stamens subtended by (1–)3(−7) bracts; disk 0;

stamens (3–)10–15(−55), filaments inserted on convex receptacle, shorter than anthers; anthers slightly extrorse, basifixed, apically puberulent, dehiscing longitudinally; pollen oblate, 5–8-zonibrevicolporate, echinate; pistillode 0. Pistillate flowers long-pedicellate; sepals [bracts?] 4 or 5, valvate, mostly persistent in fruit; petals 0; disk 0; ovary 2-locular, ovules anatropous; stylodia connate c. halfway, distal branches lanceolate, revolute. Fruits drupaceous; exocarp with vesicles. Seeds usually 1 per fruit, labyrinthic, with invaginations of the tegmen into the endosperm that coats the plications of the cotyledons.

One sp., *P. baccatum* (L.) Krug & Urb., endemic to the Greater Antilles, Bahamas, Cayman Islands, and Swan Islands. Stuppy (1996) provided the first correct analysis of the labyrinthic seed of *Picrodendron* and pleaded for its exclusion from Euphorbiaceae, but the anatomical data summarized by Hayden et al. (1984), the typically Oldfieldioid pollen grains, and the molecular data (Wurdack 2002) argue strongly for a position of *Picrodendron* in Oldfieldioideae.

70. ***Parodiodendron*** Hunz.

Parodiodendron Hunz., Kurtziana 5: 331, t. 1–3 (1969); Radcl.-Sm., Gen. Euphorb.: 102 (2001).

Dioecious trees; wood with septate fibers; indumentum simple. Leaves unifoliolate, subsessile, entire; stipules deciduous; apex of petiole with a pair of minute stipels. Inflorescences axillary, staminate flowers in glomerules, the pistillate solitary. Staminate flowers pedicellate; sepals (5)6 (−9), distinct, imbricate; petals 0; disk intrastaminal; stamens 13–19, filaments distinct, inserted in glandular disk, exserted beyond calyx; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 6–8-zonoporate, echinate, tectum smooth; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate, foliose, deciduous; petals 0; disk annular, 6-lobed; ovary 3-locular; stylodia basally connate, short, unlobed, recurved. Fruits capsular, spheroidal; columella persistent. Seeds 1 or 2/locule; hilum subterminal; testa smooth, 5 or 6 cell layers thick, exotegmen 1-layered; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *P. marginivillosum* (Speg.) Hunz., Bolivia and northern Argentina. The minute acropetiolar stipels and the often disarticulated petioles (Hayden 1994: 183) suggest that the leaves are unifoliolate.

71. ***Piranhea*** Baill.

Piranhea Baill., Adansonia 6: 235 (1866); Jablonski, Mem. New York Bot. Gard. 17: 121 (1967); Radcl.-Sm. & Ratter, Kew Bull. 51: 543 (1996), rev.
Celaenodendron Standl. (1927).

Dioecious trees or shrubs; indumentum simple. Leaves 3-foliolate, long-petiolate; leaflets entire; stipules deciduous. Inflorescences axillary, staminate flowers in spiciform thyrses, pistillate flowers solitary or in racemoid thyrses. Staminate flowers pedicellate; sepals 4–6, distinct, imbricate; petals 0; disk intrastaminal, lobed; stamens (3–)6–15, filaments distinct; anthers introrse, dehiscing longitudinally; pollen grains ± spheroidal, 6-zonoporate, echinate; pistillode 0. Pistillate flowers subsessile to long-pedicellate; sepals 4–6, biseriate, imbricate, persistent or deciduous in fruit; petals 0; disk divided into subulate lobes; ovary 3-locular; stylodia unlobed, recurved. Fruits capsular, 3-angled; columella persistent. Seeds 1 per locule, ecarunculate, testa smooth; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

Four neotropical spp., 3 from Brazil, 1 from western Mexico.

3. Tribe Caletieae Müll. Arg. (1865).

Dioecious or monoecious; staminate sepals 4–8 (−13); stamens 4–30; pollen grains spheroidal, zonoporate or pantoporate, exine echinate; pistillate sepals 3–8(−13); seeds carunculate or ecarunculate; endosperm usually copious.

This is the largest tribe of Oldfieldioideae, with 14 genera in 4 subtribes. It is entirely Old World in distribution, confined to Australia and neighboring Melanesia.

Key to the Subtribes of Caletieae

1. Pollen grains pantoporate; capsule dry; cotyledons as broad as or broader than radicle **3b. Pseudanthinae**
– Pollen grains zonoaperturate; capsule dry or fleshy; cotyledons broader than radicle; trees or shrubs 2
2. Leaves opposite; stamens distinct; anthers not apiculate; pistillate sepals persistent in fruit; capsule dry **3c. Dissilariinae**
– Leaves alternate; stamens connate; anthers apiculate; pistillate sepals deciduous; capsule fleshy **3a. Petalostigmatinae**

3a. Subtribe Petalostigmatinae Pax & K. Hoffm. (1922).

Dioecious; stamens 18–40 or more, filaments connate; pollen oblate, 5- or 6- zonoporate, breviechinate; stylodia petaloid-dilated; fruits capsular; seeds carunculate.

A monogeneric Australasian subtribe.

72. *Petalostigma* F. Muell.

Petalostigma F. Muell., Hook. J. Bot. Kew Gard. Misc. 9: 16 (1857); Airy Shaw, Kew Bull. 35: 661 (1980); Forster & van Welzen, Blumea 44: 104–107 (1999).

Dioecious trees or shrubs; indumentum simple. Leaves simple, entire; stipules deciduous. Inflorescences axillary, glomerular. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk 0; stamens 18–85, filaments basally connate into a column; anthers extrorse, dehiscing longitudinally; pollen grains globose, 5- or 6-porate, breviechinate; exine psilate-striate; pistillode usually 0. Pistillate flowers pedicellate, sepals 4–6, imbricate, deciduous; disk 0; ovary (3)4-locular, ovules anatropous; stylodia entire, dilated, petaloid. Fruits capsular, exocarp ± fleshy; columella slender, persistent. Seeds somewhat compressed, carunculate; testa smooth, mostly 4 cell layers thick; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

Five spp., Australia, one of these reaching eastern New Guinea (Papua). The pollen of *Petalostigma* was found to be close to that of *Hyaenanche* (Köhler 1965), while Stuppy (1996) regards the seed structure as suggesting an affinity with subtribe Pseudanthinae. In the analyses of Levin and Simpson (1994), *Petalostigma* appears as the sister group to subtribe Pseudanthinae and in the analyses of Wurdack et al. (2004) as sister to the rest of tribe Caletieae.

3b. Subtribe Pseudanthinae Müll. Arg. (1865).

Monoecious (dioecious) trees, shrubs, or herbs; stamens 3–20; pollen pantoporate. $x = 12$.

An Australasian subtribe of six genera.

Key to the Genera of Pseudanthinae

1. Fruit 1-locular and 1-seeded by abortion 2
– Fruit (2)3-locular with all locules fertile 3
2. Stamens 3–6, ± distinct; staminate flowers with central disk **77. *Pseudanthus***
– Stamens (7–)10–50, variously connate; staminate flowers without central disk **78. *Stachystemon***
3. Stipules foliaceous, appearing as if 2 further leaves per node **76. *Micrantheum***
– Stipules not foliose 4
4. Leaves caudate-acuminate; staminate sepals 4; stamens 10–12 **73. *Kairothamnus***
– Leaves not caudate-acuminate; staminate sepals 4–7; stamens 4–6 5
5. Ovules 1/locule; pistillode columnar; pistillate sepals deciduous in fruit **75. *Scagea***
– Ovules 2/locule; pistillode replaced by intrastaminal disk; pistillate sepals persistent **74. *Neoroepera***

73. *Kairothamnus* Airy Shaw

Kairothamnus Airy Shaw, Kew Bull. 34: 596 (1980), Kew Bull. Add. Ser. 8: 121 (1980); Radcl.-Sm., Gen. Euphorb.: 97 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves alternate; stipules deciduous. Inflorescences axillary, thyrsoid. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk annular; stamens 10–12, filaments distinct, inserted in convex receptacle; anthers extrorse, dehiscing longitudinally; pollen grains 10–12-pantoporate, echinate, tectum granular; pistillode 0. Pistillate flowers pedicellate; sepals 6 , biseriate, distinct, dorsally carinate, deciduous; petals 0; disk 0; ovary 3-locular, strigose; stylodia stigmatoid, ovate. Fruit capsular, stigmas persistent at apex. Seeds ecarunculate, testa dark and smooth, with 2- or 3-cell layers; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One sp., *K. phyllanthoides* (Airy Shaw) Airy Shaw, eastern New Guinea.

74. *Neoroepera* Müll. Arg. & F. Muell.

Neoroepera Müll. Arg. & F. Muell. in DC., Prodr. 15(2): 488 (1866); Airy Shaw, Kew Bull. 35: 658, t. 5, A1–4 (1980); Henderson, Austrobaileya 3: 618, figs. 1–3 (1992); 81: 59 (1994).

Monoecious arborescent shrubs; indumentum simple. Leaves short-petiolate; stipules minute or obsolete. Inflorescences of axillary glomerules, the pistillate flowers often solitary. Staminate flowers pedicellate; sepals (4–)6(−8), biseriate, distinct, imbricate; petals 0; stamens mostly 5 or 6, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 16–25-pantoporate, sexine echinate, tectum granular or psilate; pistillode replaced by central intrastaminal disk. Pistillate flowers pedicellate, sepals usually 6, biseriate, distinct, persistent in fruit; petals 0; disk annular, lobed; ovary 3-locular; ovules 2/locule; stylodia proximally connate, spreading. Fruits capsular. Seeds carunculate, testa smooth and shiny or minutely pitted, 2 cell layers thick; endosperm copious; embryo straight, cotyledons much broader and longer than radicle.

Two spp., Australia (Queensland).

75. ***Scagea*** McPherson

Scagea McPherson, Bull. Mus. Nat. Hist. Nat. Paris, IV B Adansonia 7: 247 (1985); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 90, t. 18 (1987); Radcl.-Sm., Gen. Euphorb.: 97 (2001).

Monoecious trees or shrubs; indumentum simple. Leaves short-petiolate; stipules deciduous. Inflorescences axillary, racemoid, unisexual or bisexual. Staminate flowers pedicellate; sepals (5)6 (−7), distinct, imbricate; petals 0; disk 0; stamens 4–6, filaments distinct, shorter than anthers; anthers extrorse, dehiscing longitudinally; pollen grains spheroidal, 16–20-pantoporate, echinate, tectum rugulose, granular; pistillode usually present. Pistillate flowers pedicellate; sepals 6, distinct, imbricate, deciduous; petals 0; disk segments 3; ovary 3-locular, pubescent; ovules anatropus, 1/locule; stylodia short, erect, thick. Fruit capsular; columella persistent, distally enlarged. Seeds carunculate, testa smooth, 3 or 4 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, cotyledons flat, much longer and broader than radicle.

Two spp. endemic to New Caledonia, originally described in the Crotonoideae because of the (secondarily) uniovulate carpels. However, the pollen is typical for Oldfieldioideae.

76. ***Micrantheum*** Desf.

Micrantheum Desf., Mém. Mus. Hist. Nat. Paris 4: 253, t. 14 (1818); Grüning, Pflanzenr. 147, XV: 21 (1913); Jeanes, Fl. Victoria 4: 70 (1999); Radcl.-Sm., Gen. Euphorb.: 98 (2001).

Monoecious ericoid shrubs or subshrubs; indumentum simple. Leaves pseudo-3-foliate [the stipules as large as the lamina], 1-veined. Inflorescences of axillary glomerules, pistillate flowers often solitary. Staminate flowers pedicellate; sepals 4 or 6, biseriate, distinct, imbricate; petals 0; disk 0; stamens 3–6(−9), filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains prolate-spheroidal, panto[30–40]-porate, pores prominently marginate, exine echinate, tectum granular; pistillode glandular, lobed. Pistillate flowers pedicellate or subsessile; sepals 4–6, distinct, imbricate, persistent in fruit; petals 0; disk + or 0; ovary 2- or 3-locular; ovules anatropous, 2/locule; stylodia connate at the base, unlobed. Fruits capsular; columella persistent. Seeds 1/locule, carunculate, testa smooth, 2 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, straight, cylindric, cotyledons longer than radicle.

Three spp., endemic to Australia. The leaves interpreted by Grüning and Jeanes as ternate clusters seem more plausibly interpreted as spirally arranged leaves with foliose stipules.

77. ***Pseudanthus*** Sieber ex Spreng. Fig. 19

Pseudanthus Sieber ex Spreng., Syst. Veg. 4(2): 22, 25 (1827); Halford & Henderson, Austrobaileya 6: 497–532 (2003), rev.
Pseudanthus Sieber ex Spreng. sect. *Pseudanthus*

Monoecious ericoid shrubs; branchlets longitudinally ridged by decurrent margins of stipules along internodes; indumentum simple, sparse or 0. Leaves alternate or opposite, margins entire and thickened; petioles short; stipules persistent. Flowers in upper leaf axils solitary or 2 or 3; distal branchlet internodes often contracted to produce terminal flower clusters. Staminate flowers pedicellate; sepals (5)6, distinct; petals 0; disk 0; stamens (3–)6, filaments distinct; anthers dehiscing longitudinally; pollen grains spheroidal, panto(6–)10–14 (−25)-porate, brevi-echinate, exine granular; disk generally 3-lobed, fleshy. Pistillate flowers sessile or subsessile; sepals (4–)6, distinct, persistent in fruit; petals 0; disk 0; ovary (2)3-locular; ovules (1)2/locule, anatropous; stylodia connate at the base or to about halfway into a style, the stigmatic branches undivided. Fruits capsular, unilocular by suppression, 1-seeded; splitting at maturity into 3 bivalved segments. Seed solitary, carunculate, testa smooth, 2 cell layers thick, exotegmen uniseriate; endosperm copious; embryo cylindric, cotyledons a little broader than radicle.

Nine spp., eastern Australia.

78. ***Stachystemon*** Planch.

Stachystemon Planch., Hooker's Lond. J. Bot. 4: 471, t. 15 (1845); Halford & Henderson, Austrobaileya 6: 497–532 (2003), rev.

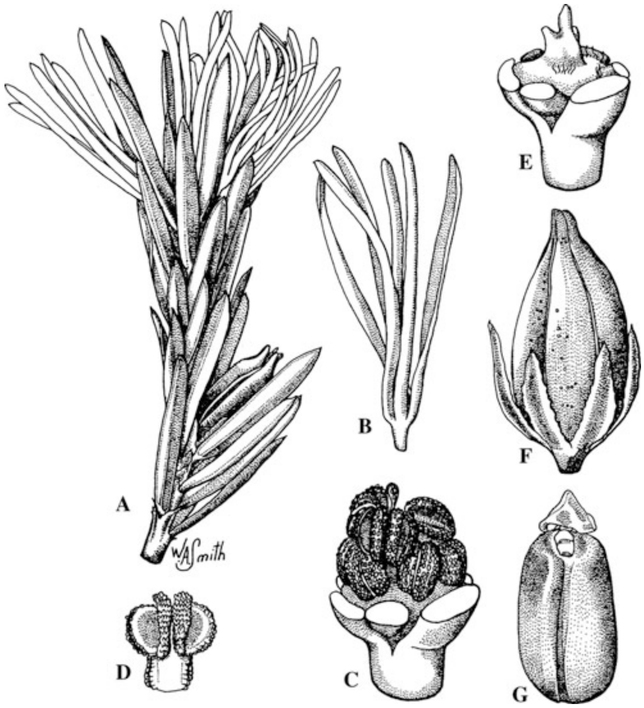

Fig. 19. Euphorbiaceae-Oldfieldioideae. *Pseudanthus ligulatus* subsp. *ligulatus*. **A** Branchlet with flowers and fruit. **B** Staminate flower from side. **C** Staminate flower with sepals removed. **D** Stamen. **E** Pistillate flower with sepals and stamens removed showing central disk. **F** Fruit with persistent sepals. **G** Carunculate seed. (Halford & Henderson 2003; drawn by W. Smith)

Monoecious shrubs; branchlets ridged by decurrent stipular margins; indumentum sparse or 0. Leaves alternate or opposite, thickened along margins; stipules persistent. Flowers few or solitary in upper leaf axils; distal branchlet internodes often contracted to produce terminal flower clusters. Staminate flowers pedicellate or rarely sessile; sepals (3)4–6(−10); receptacle hemispherical to elongated; stamens 7 to numerous; filaments variously connate or distinct, mostly bifid distally; anthers of 2 separate contiguous cells, each transverse on the apex of the filament, dehiscing longitudinally; disk 0. Pistillate flowers sessile or shortly pedicellate, sepals 4 or 6, persistent; disk 0; ovary 2(3)-locular; ovules 2/locule; stylodia 2(3), at the base shortly connate or distinct, entire. Fruit capsular, unilocular by suppression, 1-seeded, splitting at maturity into 2 (3) bivalved segments. Seeds solitary, carunculate, endosperm copious; cotyledons several times broader than radicle.

Nine spp., endemic to southwestern Western Australia.

3c. Subtribe Dissilariinae Pax & K. Hoffm. (1922).

Monoecious or dioecious; stamens 8–50, filaments distinct; pollen grains 5–7-zonoporate, echinate.

Seven Australasian genera with c. 25 species. The subtribe seems clearly monophyletic, but generic boundaries are subject to revision.

Key to the Genera of Dissilariinae

1\. Dioecious 2
– Monoecious 5
2\. Staminate flowers without pistillodes; seeds semielliptic in outline, laterally compressed **80. *Dissilaria***
– Staminate flowers with pistillodes; seeds globose or ovoid, not laterally compressed 3
3\. Stylodia linear in outline; fruit subglobose, strongly tricoccous with remnants of stylodia widely separated **84. *Choriceras***
– Stylodia cordate-ovate in outline; fruit globose, remnants of stylodia in close proximity 4
4\. Ovary 3–4-locular; seeds with arilloid caruncle **79. *Austrobuxus***
– Ovary 2-locular; seeds ecarunculate **81. *Canaca***
5\. Stipules very large, conspicuous, > 8 mm long; pistillate flowers with 3 sepals; receptacle of staminate flowers glabrous **83. *Sankowskya***
– Stipules small, inconspicuous, > 8 mm long, or 0; pistillate flowers with 2+2 or 2+3 sepals; receptacle of staminate flower hairy 6
6\. All flowers with glandular disk; stylodia linear in outline; stamens > 45; pollen spiny **82. *Whyanbeelia***
– All flowers without glandular disk, stylodia cordate-ovate in outline; stamens < 45; pollen smooth **85. *Longetia***

79. *Austrobuxus* Miq.

Austrobuxus Miq., Fl. Ned. Ind. Suppl.: 444 (1861); Airy Shaw, Kew Bull. 29: 303 (1974); A.C. Smith, Fl. Vitiensis Nova 2: 495 (1981); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 193, figs. 40–43 (1987); Forster, Austrobaileya 4: 619–626 (1997).
Bureavia Baill. (1873).
Choriophyllum Benth. (1879).

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves opposite, mostly entire; stipules 0. Inflorescences axillary, cymose, sometimes paniculate. Staminate flowers pedicellate; sepals 4–6, distinct, imbricate; petals 0; disk 0 or represented by convex receptacle; stamens 8–27, filaments distinct, inserted in the raised receptacle; anthers extrorse, dehiscing longitudinally; pollen grains 6–7-zonoporate, echinate, exine between spines rugulose; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 4–6, distinct, imbricate, persistent in fruit; petals 0; disk cupular or 0; ovary 3(4)-locular; stylodia very short, dilated, stigmatiform. Fruits capsular; columella persistent. Seeds smooth, caruncle laciniate; testa smooth, 3 or 4 cell layers thick, exotegmen uniseriate; endosperm copious; embryo green, straight or curved, cotyledons much longer and broader than radicle.

A genus of c. 20 species, from Malaysia and Australia to New Caledonia and Fiji.

80. *Dissiliaria* F. Muell. ex Baill.

Dissiliaria F. Muell. ex Baill., Adansonia I, 7: 366 (1867); Forster, Austrobaileya 5: 9–27 (1997), rev.; Radcl.-Sm., Gen. Euphorb.: 91, fig. 10 (2001).

Monoecious or dioecious trees or shrubs; indumentum simple. Leaves opposite, entire or crenulate; stipules interpetiolar, deciduous. Inflorescences axillary, glomerular. Staminate flowers pedicellate; sepals 3+3, imbricate; petals 0; extrastaminal disk 0; stamens 8–26, filaments distinct, shorter than sepals, inserted on slightly convex receptacle; anthers dehiscing longitudinally; pollen grains 5–7-zonoporate, pores bordered; exine echinate, tectum baculate; pistillode 0. Pistillate flowers pedicellate; sepals 3+3, persistent in fruit; petals 0; disk annular; ovary 2 or 3-locular; stylodia unlobed, shortly connate at the base. Fruits capsular, dehiscing septicidally into 2 or 3 bivalved cocci. Seeds laterally compressed, carunculate; endosperm copious; cotyledons broad, flat.

Six spp., Australia (Queensland).

81. *Canaca* Guillaumin

Canaca Guillaumin, Arch. Bot. Caen 1: 74 (1927); Airy Shaw, Kew Bull. 25: 508 (1971); Radcl.-Sm., Gen. Euphorb.: 91 (2001).

Dioecious trees or shrubs; indumentum of abaxial leaf blades appressed, crystalloid, dark, partly malpighiaceous. Leaves opposite; stipules 0. Inflorescences axillary, dichasial. Staminate flowers pedicellate, sepals 4, imbricate; petals 0; disk 0; stamens (8–)15–26, filaments distinct, inserted on convex receptacle; anthers dehiscing longitudinally; pistillode 0. Pistillate flowers distinctly pedicellate; sepals 4, imbricate, persistent in fruit; petals 0; disk annular; ovary 2-locular; stylodia very short, stigmatoid. Fruits capsular, endocarp thin; columella persistent or deciduous. Seeds suborbicular, compressed tangentially, rugose, pale, ecarunculate; endosperm copious; cotyledons flat, much longer and broader than the radicle.

Seven spp., all endemic to New Caledonia. This genus was combined with *Austrobuxus* by McPherson and Tirel (1987); however, Airy Shaw (1971), who first reduced *Canaca* to synonymy, said that it "almost merits generic recognition" because of the very distinctive seeds. The distinctive indumentum and 2-locular thin-walled capsule with deciduous columella also support the generic distinctiveness of *Canaca*.

82. *Whyanbeelia* Airy Shaw & Hyland

Whyanbeelia Airy Shaw & Hyland, Kew Bull. 31: 375 (1976) and ibid. 35: 691 (1980); Hyland & Whiffin, Austral. Trop. Rain For. Trees 2: 152 (1993).

Dioecious (?) trees; indumentum simple. Leaves opposite, short-petiolate; stipules obsolete. Inflorescences axillary, cymosely paniculate. Staminate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk 0; stamens 50–55, inserted on the pubescent central receptacle; filaments distinct, exserted; anthers subspheroidal; pollen grains oblate, 5–6-zonoporate, echinate, interspinal tectum verrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6; petals 0; disk dissected into subulate segments, glabrous; ovary 3-locular, pubescent; stylodia unlobed, recurved. Fruit capsular. Seeds carunculate, testa 4 or 5 cell layers thick, exotegmen uniseriate; cotyledons green.

A single sp., *W. terra-reginae* Airy Shaw & B. Hyland from Australia (Queensland), with the habit of *Dissiliaria*. Although the genus was first described as monoecious, Airy Shaw (1971) characterized it as dioecious.

83. *Sankowskya* P.I. Forster Fig. 20

Sankowskya P.I. Forst., Austrobaileya 4: 329, fig. 1 (1995); Radcl.-Sm., Gen. Euphorb.: 93 (2001).

Monoecious trees; indumentum simple. Leaves opposite, petiolate; stipules interpetiolar, deciduous. Inflorescences axillary, cymose, bracteate. Staminate flowers pedicellate; sepals 4, biseriate, imbricate; petals 0; disk 0; stamens 12–15, filaments distinct, inserted on convex receptacle; anthers

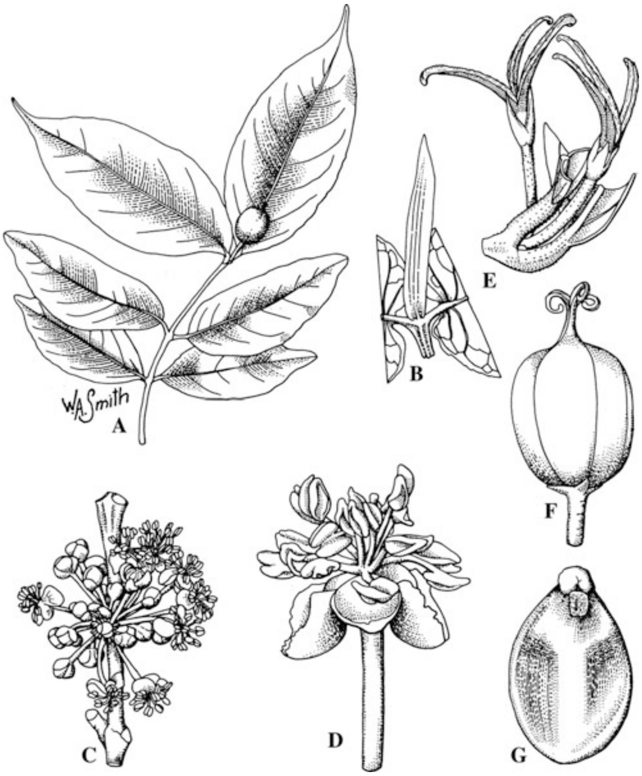

Fig. 20. Euphorbiaceae-Oldfieldioideae. *Sankowskya stipularis*. **A** Fruiting branchlet. **B** Base of leaf pair with interfoliar stipule. **C** Staminate inflorescence. **D** Staminate flower. **E** Pistillate inflorescence. **F** Fruit. **G** Carunculate seed, adaxial view. (P.I. Forster 1995; drawn by W. Smith)

extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers pedicellate; sepals 3, imbricate; petals 0; disk 0; ovary 3-locular; stylodia distinct, unlobed, papillose, recurving. Fruit capsular; endocarp thin. Seeds carunculate, testa smooth.

A single sp., *S. stipularis* P.I. Forst. from Australia, NE Queensland. Forster (1995) suggests that *Sankowskya* may be closest to *Longetia*, with which it shares smooth pollen.

84. ***Choriceras*** Baill.

Choriceras Baill., Adansonia I, 11: 119 (1873); Airy Shaw, Kew Bull. 35: 604 (1961), Muelleria 4: 220 (1980); Hyland & Whiffin, Austral. Rain For. Trees: 310 (1993); Forster & van Welzen, Blumea: 44: 99–101 (1999).

Monoecious trees; indumentum simple. Leaves opposite, subentire or crenulate, short-petiolate; stipules deciduous. Inflorescences axillary, cymose, unisexual or bisexual. Staminate flowers pedicellate; sepals 4–6, biseriate, imbricate; petals 0; disk 0; stamens 4–6, distinct, inserted on the pubescent central receptacle; anthers extrorse, dehiscing longitudinally; pollen grains oblate, 6-zonoporate, exine pilate-wrinkled, scabrate; pistillode small, pubescent. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk of 3 segments; ovary 3(4)-locular, sericeous; stylodia distinct, undivided, recurved. Fruits capsular, apex trifid due to persistent stylodia bases; columella persistent [?], slender. Seeds 1 or 2 per locule, ecarunculate; testa smooth, 2 or 3 cell layers thick, tegmen uniseriate; endosperm copious; embryo straight, cotyledons flat, much longer and broader than radicle.

One or two spp., tropical Australia and New Guinea. Forster and van Welzen (1999) reduced *C. australiana* Benth. to synonymy. Pollen morphology indicates that the genus is closely related to *Longetia*.

85. ***Longetia*** Baill.

Longetia Baill., Adansonia I, 6: 352 (1866); Pax & K. Hoffmann, Pflanzenr. 147, XV: 289 (1922); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 188 (1987).

Monoecious shrubs; indumentum simple, very sparse. Leaves opposite, glabrous, simple, entire; stipules 0. Inflorescences terminal or axillary, cymose-paniculate, unisexual or bisexual. Staminate flowers pedicellate; sepals 6, imbricate; petals 0; disk 0; stamens 9–17, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains zono(5–)6–7-brevicolporate, apertures bordered; exine rugulose, microspinulose; pistillode present. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate; petals 0; disk dissected; ovary 3-locular; ovules anatropous; stylodia short, stigmatoid, stigmas emarginate. Fruit capsular, columella persistent. Seeds 1/locule, tangentially compressed, carunculate; testa smooth; endosperm copious; embryo green, straight, cotyledons flat, much longer and broader than radicle.

A single sp., *L. buxoides* Baillon, endemic to New Caledonia. Pax & Hoffmann (1922) had included several species now placed in *Austrobuxus* within *Longetia*, but the pollen is so different in the two genera that they cannot be very closely related.

III. SUBFAM. PEROIDEAE Baill. & Hassk. (1859), taken up by K. Wurdack & P. Hoffmann in Amer. J. Bot. 92: 1413 (2005).

Dioecious (monoecious) trees, shrubs, or herbs; latex 0; indumentum simple, malpighiaceous, stellate, or lepidote. Leaves alternate (opposite), simple, entire; stipules + or 0. Inflorescences axillary, mostly strongly condensed, rarely [*Pera*] surrounded by involucral bracts; sepals 2–6 [in *Pera* 0 in pistillate flowers and sometimes rudimentary in staminate flowers]; petals + or 0; disk +, 0 in *Pera*; stamens 2–20; pollen prolate to oblate spheroidal, 3(4)-colporate, mostly tectate-perforate; pistillode + [0 in *Pera* but reduced pistillate flowers surrounding staminate flowers in some spp.]; ovary 3(4)-locular; stylodia bifid to bipartite; ovule 1 per locule. Fruit dehiscent (indehiscent); septa membranous, fragile, without visible vascularization. Seeds black, shiny, smooth, carunculate; seed coat with tracheoidal exotegmen [*Pogonophora* excepted]; endosperm usually copious; cotyledons longer and wider than radicle.

Four genera with about 125 spp., pantropical.

Peroideae are characterized by fruits with membranous, fragile septa without visible vascularization, and very peculiar seed coats which in *Clutia*, *Chaetocarpus* and *Pera* have a large tanniniferous exotesta and a tracheoidal exotegmen, whereas *Pogonophora*, like the cheilosoids, acalyphoids, crotonoids, and euphorbioids, has a palisadal exotegmen (Tokuoka and Tobe 2003). Therefore, the inclusion of *Pogonophora* in the Peroideae remained uncertain (Tokuoka 2007), but its inclusion in a strongly supported clade with *Pera* and *Clutia* (Xi et al. 2012) now leaves little doubt of this.

KEY TO THE TRIBES OF SUBFAM. PEROIDEAE

1. Staminate flowers with 5 imbricate sepals and petals; stamens 5; pollen exine tectate-perforate; indumentum simple or malpighiaceous; seeds carunculate; dioecious 2
– Staminate flowers not with 5 imbricate sepals and petals (or if so, cotyledons not broader than radicle); stamen number variable; pollen grains various 3
2. Petals adaxially barbate; filaments distinct; disk segments not glandular-lobed; seeds ecarunculate; leaves not pellucid-punctate **4. Pogonophoreae**
– Petals not adaxially barbate; filaments connate; disk segments glandular-lobed; seeds carunculate; leaves usually pellucid-punctate **1. Clutieae**
3. Flowers in axillary glomerules, not involucrate; stamens 5–15; stylodia bifid, elongated; capsule echinate; leaves stipulate **2. Chaetocarpeae**
– Flowers enclosed in involucres of bibracteolate bracts; stamens 2–6; stylodia very short, stigmatoid; capsule not echinate; leaves exstipulate **3. Pereae**

1. TRIBE CLUTIEAE (Müll. Arg.) Pax (1890).

A monogeneric tribe, containing only the African genus *Clutia*.

86. *Clutia* L.

Clutia L., Sp. Pl.: 1042 (1753); Léonard, Fl. Congo Rwa.-Bur. 8(1): 93, t. 7 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 331, fig. 63 (1987), Kew Bull. 47: 111, figs. 1–3 (1992), Fl. Zambesiaca 9(4): 123, t. 21, 22 (1996).

Dioecious (monoecious) shrubs or perennial herbs; indumentum simple or 0. Leaves alternate, entire, often pellucid-punctate; stipules small or obsolete. Flowers in axillary glomerules, the pistillate often solitary. Staminate flowers pedicellate; sepals and petals 5, distinct, imbricate; disk segments 5 or more, lobed or glandular; disk of numerous glands in 1–3 series at the base of the perianth and staminal column; stamens 5, filaments connate into a column; anthers introrse; muticous; pollen grains prolate, 3-colporate, colpi inoperculate, exine tectate-perforate/reticulate; pistillode inserted on top of staminal column. Pistillate flowers pedicellate; sepals 5, imbricate, entire, persistent in fruit; petals 5, usually persistent in fruit; disk segments 5; ovary 3 (4)-locular, glabrous or pubescent; ovules anatropous, inner and outer integuments thin, mostly 3 or 4 cell layers; stylodia distinct, bifid. Fruits capsular; columella persistent, with deciduous wings in distal half. Seeds carunculate, testa dry, mostly smooth, exotegmen tracheoidal; endosperm copious, cotyledons broader and somewhat longer than radicle.

About 75 African spp., most in South Africa, two in Arabia.

2. TRIBE CHAETOCARPEAE (Müll. Arg.) G.L. Webster (1975).

Dioecious; indumentum simple or 0; leaves entire; flowers in axillary bracteate glomerules; sepals 4 or 5, imbricate; petals + or 0; stamens 5–15; fruits capsular; seeds carunculate, exotegmen tracheoidal.

Two genera; their close relationship is confirmed by Tokuoka (2007).

KEY TO THE GENERA OF CHAETOCARPEAE

1. Petals +; anthers extrorse, subsessile on staminal column; ovary smooth; endosperm 0
87. *Trigonopleura*
– Petals 0; anthers introrse or latrorse, filaments well developed; ovary tuberculate or echinate; endosperm +
88. *Chaetocarpus*

87. *Trigonopleura* Hook. f.

Trigonopleura Hook. f., Fl. Brit. Ind. 5: 399 (1887), Icon. Pl. 18: t. 1753 (1888); Pax & K. Hoffm., Pflanzenr. 147, III: 95, fig. 30 (1911); van Welzen et al., Blumea 40: 363–374, fig. 2 (1995).

Dioecious trees; indumentum simple, scale-like on young growth. Leaves simple, petiolate [petiole adaxially sulcate], entire; stipules deciduous. Flowers in axillary glomerules, the staminate multiflowered, the pistillate 1–3-flowered; bracts minute. Staminate flowers pedicellate, articulate at or above the middle; sepals 5, coriaceous, imbricate, distinct; petals (4) 5, distinct, valvate, pubescent; disk segments 5, erect; stamens (5–) 8–15, biseriate, filaments connate into a column; 5 anthers of lower whorl subsessile on column, 3 upper anthers ± equaling filaments; anthers extrorse; apiculate; pollen grains subprolate, 3-colporate, colpi inoperculate, exine tectate-punctate, tectum psilate; pistillode adnate to staminal column, apically trifid. Pistillate flowers pedicellate, pedicels mid-articulate; sepals 5, imbricate, entire, deciduous in fruit; disk-segments 5; ovary 3-locular, tomentose; stylodia distinct, erect, bipartite, adaxially papillose. Fruits capsular, subglobose, tomentose, carinate-angled, ± reticulate-venose; columella persistent, translucent-winged. Seeds carunculate, the fleshy caruncle partially covering testa; exotegmen tracheoidal, mesotesta vascularized; hilum lobed; endosperm 0.

Three spp., Malay Peninsula and Sumatra to the Philippines and Borneo. According to Nowicke et al. (1998), the pollen of *Trigonopleura* is different from that of *Chaetocarpus*. Although the seeds of *Trigonopleura* are exalbuminous, the genus is resolved as sister to *Chaetocarpus* (Tokuoka 2007).

88. *Chaetocarpus* Thwaites Fig. 21

Chaetocarpus Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 300, t. 10a (1854); Léonard, Fl. Congo Rwa.-Bur. 8(1): 127, fig. 8 (1962); Capuron, Adansonia II, 12: 209–211, t. 2 (1972); Alves, An. Jard. Bot. Madrid 51: 302 (1994); van Welzen, Rheedea 4: 93, fig. 1 (1994); Philcox, Fl. Ceylon 11: 177 (1997); Radcl.-Sm., Fl. Zambesiaca 9(4): 135, t. 23 (1996).

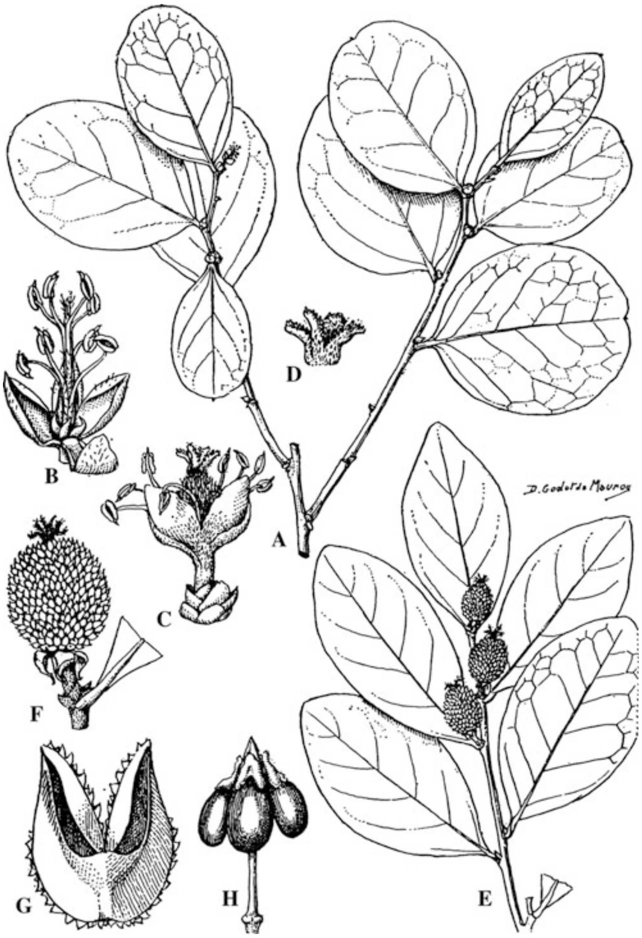

Fig. 21. Euphorbiaceae-Peroideae. *Chaetocarpus rabaraba*. **A** Flowering branchlet. **B** Staminate flower. **C** (Pseudo?)hermaphrodite flower. **D** Stylodia. **E** Fruiting branchlet. **F** Young fruit. **G** Two-valved coccus. **H** Columella with seeds. (Capuron 1972; drawn by D. Godot de Mauroy)

Dioecious trees or shrubs; indumentum simple. Leaves distichous; stipules persistent, sometimes foliose (deciduous). Flowers in axillary glomerules. Staminate flowers pedicellate, pedicels mid-articulate; sepals 3–5, imbricate, distinct or connate; petals 0; disk segments 5; stamens 5–15, filaments proximally connate; anthers introrse or latrorse, basifixed; pollen grains subprolate, 3-colporate, exine tectate-perforate, tectum microrugulose; pistillode distinct from stamens, trifid, villose. Pistillate flowers pedicellate; sepals 3–8, imbricate, distinct, deciduous in fruit; petals 0; disk cupular, lobed; ovary 3(4)-locular, hirsute;

ovules anatropous, inner and outer integuments thin, 3–6 cell layers; stylodia bifid, tips ± laciniate. Fruits capsular, muricate to echinate; columella persistent. Seeds ovoid, compressed, carunculate; testa dry, smooth and shiny; exotegmen tracheoidal; endosperm copious; cotyledons longer and broader than radicle.

Fivteen spp. scattered from the West Indies and South America to Africa, Madagascar, India, and Malesia. The seeds of *Chaetocarpus*, with shiny blackish testa, are strikingly similar to those of *Pera*, and suggest a close relationship between the two genera.

3. Tribe Pereae (Klotzsch & Garcke) Pax & K. Hoffm. (1919).

Monogeneric; represented only by the New World genus *Pera*.

89. *Pera* Mutis Fig. 22

Pera Mutis, Kongl. Vetensk. Acad. Nya Handl. 5: 299 (1784); Pax & K. Hoffm., Pflanzenr. 147, XIII: 2, figs. 1, 2 (1919); Correll, Fl. Bahama Arch.: 834, fig. 347 (1982); L. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 8, figs. 2, 3 (1997); Bigio & Secco, Rodriguésia 63: 163–207 (2012), spp. of Braz. Amazonia.

Dioecious (monoecious) trees or shrubs; indumentum lepidote or stellate (simple). Leaves alternate (opposite), simple, entire, exstipulate. Inflorescences pseudanthial, axillary, fascicled; each pseudanthium usually unisexual, of 3 or 4 flowers subtended by a laterally dehiscing compound involucrate bract [of 2 connate bracts]; petals and disk 0. Staminate flowers sessile, surrounded by "pistillodes" [reduced pistillate flowers]; calyx irregularly lobed; stamens (2)3–4(–8), filaments distinct or connate; anthers introrse to extrorse; pollen grains suboblate to subprolate, 3-colporate, exine intectate or tectate, reticulate to microrugulate. Pistillate flowers sessile or subsessile; perianth and disk 0; ovary 3-locular; ovules anatropous, inner and outer integuments thin, 3–5 cell layers; stylodia very short and connate into a thick peltate stigmatic structure. Fruits capsular, valves woody; columella slender, usually not persistent. Seeds carunculate, testa dry, smooth, dark, shiny, exotegmen tracheoidal.

About 30–35 neotropical spp. In its floral morphology the genus is very distinct from all other Euphorbiaceae, but the seed morphology (Tokuoka and Tobe 2003) suggests a relationship with *Chaetocarpus*.

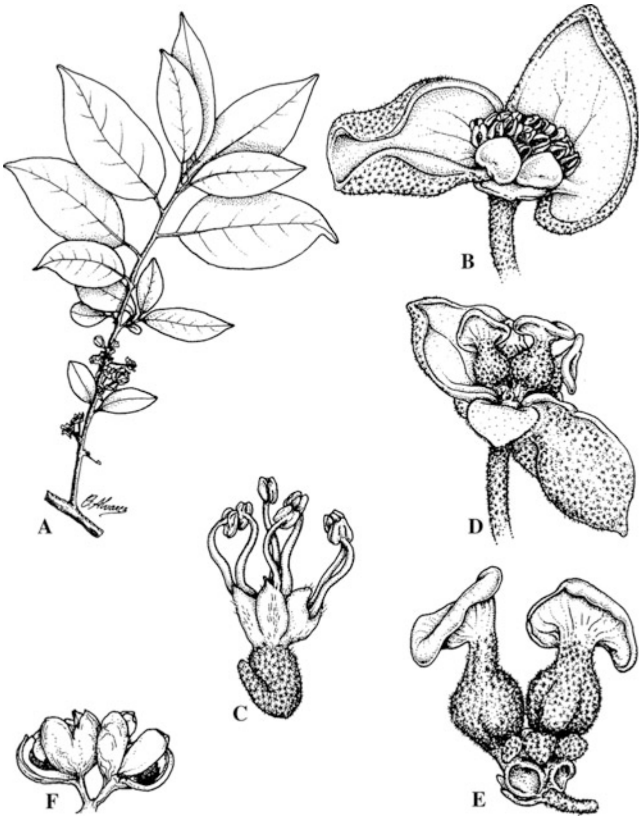

Fig. 22. Euphorbiaceae-Peroideae. *Pera anisotricha*. **A** Flowering branchlet. **B** Staminate inflorescence with involucre. **C** Three staminate flowers. **D** Four pistillate flowers subtended by the opened involucre. **E** Two of these flowers with basal staminodes. **F** Part of infructescence with two septifragal capsules. (Bigio & Secco 2012; drawn by B. Alvarez)

4. Tribe Pogonophoreae (Müll. Arg.) G.L. Webster (1975).

A single genus with a disjunct African/South American distribution.

90. *Pogonophora* Miers ex Benth.

Pogonophora Miers ex Benth., Hook., J. Bot. Kew Gard. Misc. 6: 372 (1854); Letouzey, Adansonia II, 9: 275, fig. 1 (1969); Secco, Revisão dos gêneros *Anomalocalyx* Ducke, *Dodecastigma* Ducke, *Pausandra* Radlk., *Pogonophora* Miers ex Bent. e *Sagotia* Baill.: 88, figs. 26, 27 (1990).

Dioecious trees or shrubs; indumentum simple, alpighiaceous in inflorescence. Leaves alternate; stipules small or obsolete. Inflorescenes of axillary thyrses or spikes; bracts persistent, eglandular. Staminate flowers sessile; sepals 5, distinct, scarious, imbricate, unequal, outer bract-like; petals 5, distinct, imbricate, longer than sepals, barbate adaxially; stamens 5, filaments distinct; anthers introrse, basifixed; pollen grains subprolate, 3-colporate, exine tectate-perforate, tectum psilate; disk intrastaminal, urceolate, enclosing the 2–3-fid pistillode. Pistillate flowers pedicellate; sepals and petals similar to staminate, the calyx persistent in fruit; disk cupular; ovary 3-locular; inner and outer integuments thin, 5 or 6 cell layers; stylodia basally connate, bifid, branches fimbriate-papillate. Fruits capsular, columella slender, persistent. Seeds carunculate; testa smooth or slightly rugulose; exotegmen palisadal.

Three spp., widely disjunct, *P. schomburgkiana* Miers ex Benth. neotropical, the recently described *P. africana* Letouzey and *P. letouzeyi* Feuillet from West Africa (Gabon).

IV. SUBFAM. CHEILOSOIDEAE (Müll. Arg.) K. Wurdack & P. Hoffm. (2005).

Dioecious trees; latex 0; indumentum simple and/or stellate. Leaves alternate, simple, entire or toothed. Inflorescences pseudo-terminal or axillary, thyrsopaniculate. Flowers apetalous; staminate flowers: sepals 4–6, distinct, imbricate; disk with 4 or 5 segments; stamens 5–10, distinct; pollen grains suboblate, 3-colporate, colpi inoperculate, exine echinate; pistillode pubescent; pistillate flowers: sepals 5 or 6, distinct, imbricate, persistent in fruit; disk annular or 0; ovary 2–3-locular; ovules with thick integuments, the outer vascularized; stylodia bifid. Fruits capsular; columella persistent. Seeds with sarcotesta; mesotesta vascularized; exotegmen palisadal; endosperm copious.

Only one tribe:

1. TRIBE CHEILOSEAE (Müll. Arg.) Airy Shaw & G.L. Webster (1975).

Two closely related genera of southeast Asia and Malesia. Cheiloseae are remarkable for their echinate exine sculpture; the seed structure with the fleshy exotesta and vascularized mesotesta (Tokuoka and Tobe 2003) is similar to that of *Trigonopleura*.

Two genera, 7 spp., SE Asia to Melanesia.

KEY TO THE GENERA OF CHEILOSEAE

1. Ovary 3-locular; stamens 8–10, anthers apiculate; leaves without laminar glands; bracts eglandular **91. *Cheilosa***
– Ovary 2-locular; stamens 5–8 (9), anthers muticous; leaves with laminar glands (except *N. kingii*); bracts glandular **92. *Neoscortechinia***

91. *Cheilosa* Blume

Cheilosa Blume, Bijdr.: 613 (1826); Müll. Arg. in DC., Prodr. 15(2): 1123 (1866); J. J. Sm., Meded. Dept. Landb. Ned.-Ind. 10: 604 (1910); Pax & K. Hoffmann, Pflanzenr. 147, XV: 12, fig. 3 (1912); Whitmore, Tree Fl. Malaya 2: 77 (1973); van Welzen et al., Blumea 38: 162, fig. 1 (1993).

Dioecious trees; indumentum simple or fascicled. Leaves dentate to crenate, teeth with abaxial discoid glands; petiole apically pulvinate; stipules deciduous or subpersistent. Inflorescences axillary or terminal, the staminate thyrsoid-paniculate, the pistillate thyrsoid-racemoid; bracts eglandular, persistent, sometimes foliose. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 0; disk annular, ± 5-lobed, pubescent; stamens 9 or 10, ± biseriate, filaments distinct; anthers basifixed, introrse, apiculate; pollen grains suboblate, 3-colporate, colpi inoperculate, tectum echinate and rugulose; pistillode mainly 3-lobed, hirsutulous. Pistillate flowers pedicellate; sepals (4) 5 (6), distinct or nearly so, imbricate, entire, ± persistent in fruit; petals 0; disk annular, pubescent; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments moderately thick, the outer vascularized; stylodia basally connate, unlobed, recurving. Fruits capsular, rugulose; mesocarp woody; columella cylindrical, persistent. Seeds 1–3 per fruit, ovoid, ecarunculate, exotesta fleshy.

A single sp., *Ch. montana* Blume, widespread in western Malesia: Malay Peninsula and Sumatra to Borneo and the Philippines.

92. *Neoscortechinia* Pax

Neoscortechinia Pax, Natürl. Pflanzenfam. Nachtr. 1: 213 (1897); Pax & K. Hoffm., Pflanzenr. 147, XIV: 52 (1919); Whitmore, Tree Fl. Malaya 2: 119 (1973); van Welzen, Blumea 39: 301–320, fig. 3 (1994).

Dioecious trees; indumentum of simple and fasciculate hairs. Leaves usually with 2 raised adaxial basal glands, subentire to glandular-dentate, petioles ± pulvinate; stipules deciduous. Inflorescences axillary or pseudo-terminal, thyrsoid, staminate ± compounded; bracts entire, sometimes glandular; flowers subsessile. Staminate sepals 4–5(6), imbricate; petals 0;

disk dissected; stamens (4)5–9, filaments distinct; anthers basifixed, introrse to latrorse, muticous; pollen grains subglobose, 3-colporate, colpi inoperculate, exine echinate, tectum microrugulose; pistillode 2–3-fid. Pistillate flowers pedicellate, sepals 4 or 5, imbricate, persistent or deciduous in fruit; petals and disk 0; ovary 2-locular, hirsute; ovules anatropous, inner and outer integuments thick, the outer vascularized; stylodia stigmatoid. Fruits capsular, oblong, ribbed; columella persistent or deciduous. Seeds 1 (2) per fruit, exotesta fleshy, endotesta smooth.

Six spp., mainly western Malesian, extending to Burma in the West and Borneo, New Guinea and the Solomons in the East.

V. SUBFAM. ACALYPHOIDEAE Beilschm. (1833).

Subfam. Ricinoideae Baillon ex Hassk. (1859).

Subfam. Dysopsidoideae Baillon ex Hassk. (1859).

Trees, shrubs, or herbs; milky latex 0 [colored exudate in some genera]; indumentum simple, malpighiaceous, or lepidote. Leaves alternate (opposite); lamina simple and pinnately veined, or palmately veined or lobed , often with foliar or petiolar glands. Inflorescences axillary or terminal, racemose, spicate, or paniculate, or reduced to axillary glomerules or solitary flowers; bracts sometimes glandular. Staminate flower: sepals imbricate or valvate [sometimes connate in bud and rupturing at anthesis]; petals and disk + or 0; stamens 2–100+, filaments distinct or connate; pollen grains binucleate, mostly 3- or 4-colporate (3-colpate in some Plukenetieae), exine mostly semitectate-reticulate (echinate); pistillode + or 0. Pistillate flower: sepals mostly 3–6 (2–12), imbricate or open at anthesis; petals and disk + or 0; ovary mostly 2–4-locular, ovules solitary in each locule, anatropous, inner integument non-vascularized; stylodia entire to multifid. Fruit capsular (baccate or drupaceous). Seeds carunculate or ecarunculate; seed coat with palisadal exotegmen; endosperm usually copious; cotyledons longer and broader than radicle [except in Ampereeae]. *x* mostly = 9, 10, 11.

The Acalyphoideae, with 99 genera in 14 tribes and a total of over 3,000 species, are the largest and most complex of the seven subfamilies. They are resolved as monophyletic with exception of the isolated Erismantheae, which may occupy a sister position to the rest of the subfamily.

KEY TO THE TRIBES OF SUBFAM. ACALYPHOIDEAE

1. Leaves opposite; pollen exine reticulate; seeds ecarunculate **1. Erismantheae**
– Leaves alternate; pollen exine rugulose or micropunctate; seeds carunculate or not 2
2. Cotyledons scarcely broader than radicle; monoecious (dioecious) subshrubs with ericoid foliage; seeds carunculate **9. Ampereeae**
– Cotyledons distinctly broader than radicle; foliage generally not ericoid; seeds carunculate or ecarunculate 3
3. Petals +, at least in staminate flowers 4
– Petals 0 6
4. Monoecious (dioecious); indumentum malpighiaceous, stellate, or lepidote [simple in Speranskiinae and *Philyra*]; anther connective not enlarged, sacs not pendulous; pollen sexine often distinctly heterobrochate **11. Chrozophoreae**
– Dioecious; indumentum simple; anther connective enlarged, sacs pendulous; pollen sexine coarsely reticulate, not heterobrochate 5
5. Stylodia bifid; pistillate petals usually present; inflorescences paniculate, racemose, or spiciform; pollen spheroidal; leaves stipulate **3. Agrostistachydeae**
– Stylodia multifid; pistillate petals 0; inflorescences capitellate; pollen prolate; leaves exstipulate **4. Sphyranthereae**
6. Stylodia connate, unlobed; plants often scandent; stinging hairs sometimes present; pollen tectum microverrucate **14. Plukenetieae**
– Stylodia distinct or basally connate; plants rarely scandent; stinging hairs 0; pollen tectum psilate to microverrucate 7
7. Pollen tectum perforate, psilate to scabrate 8
– Pollen tectum usually rugulose, microverrucate 11
8. Staminate disk 0; indumentum stellate **10. Epiprineae**
– Staminate disk + [except in *Adenophaedra*]; indumentum simple 9
9. Pistillate sepals deciduous; staminate disk massive, intrastaminal; stamens 4–15; pistillode + or 0 **2. Caryodendreae**
– Pistillate sepals usually persistent; staminate disk not massive and extrastaminal; stamens (2–)8–100 or more; pistillode usually 0 10
10. Pollen colpi distinctly marginate; indumentum simple or stellate; anthers sometimes 4-locellate **13. Bernardieae**
– Pollen colpi emarginate; indumentum simple; anthers 2-locellate **8. Pycnocomeae**
11. Pollen grains with operculate colpi; seeds mostly ecarunculate, testa not fleshy; stipules deciduous or obsolete 12

– Pollen grains with inoperculate colpi; seeds carunculate or ecarunculate; testa dry or fleshy; stipules deciduous or persistent 13

12\. Leaves without laminar glands; stylodia subentire to multifid; inflorescences axillary; pollen sexine finely perforate-tectate **12. Adelieae**

– Leaves usually with embedded laminar glands; stylodia mostly entire, if divided, then inflorescences terminal; pollen exine rugulose to striate **5. Alchorneeae**

13\. Seeds carunculate; inflorescences terminal; indumentum stellate or 0 **6. Ricineae**

– Seeds mostly ecarunculate; inflorescences axillary or terminal; indumentum simple or stellate **7. Acalypheae**

1. TRIBE ERISMANTHEAE G.L. Webster (1975).

Monoecious trees or shrubs; indumentum simple; leaves opposite, entire or obscurely dentate; stipules interpetiolar; inflorescences axillary, racemoid or spicate; staminate sepals 4 or 5, imbricate (valvate); petals 5 or 0, disk minute or 0; stamens 5–15, filaments distinct; pollen grains 3-colporate, angulaperturate, colpi emarginate, inoperculate, sexine tectate-reticulate; pistillode +; pistillate sepals 5 or 6, imbricate; petals + or 0; disk 0; stylodia distinct or connate, bifid; fruit capsular; seeds ecarunculate, testa smooth and dry.

Three tropical Asian genera with a total of 5 spp. Nowicke et al. (1998) note the anomalous nature of the pollen grains of *Syndyophyllum*, which are operculate and resemble the pollen of *Alchornea*, but in the *rbc*L analysis of Wurdack et al. (2005), *Moultonianthus* and *Syndyophyllum* form a monophyletic group. Later (Wurdack and Davis 2009), *Moultonianthus* has been resolved in a position sister to the rest of subfamily Acalyphoideae s.str., thus confirming the placement of Erismantheae by Webster (1994).

The apetalous flowers of *Erismanthus* (and possibly of *Syndyophyllum* as well) and their elongate stylodia and catkin-like staminate inflorescences are indicative of wind pollination. The opposite leaves are thought to be due to strong shortening of each second internode beginning in the seedling stage (see Radcliffe-Smith 2001: 121).

KEY TO THE GENERA OF ERISMANTHEAE

1\. Pistillode elongated, clavate; staminate inflorescence covered with closely imbricate bracts; staminate pedicel > 1.5 cm long; stamens 12–15; pistillate flowers apetalous **93. *Erismanthus***

– Pistillode deeply trifid into slender branches; staminate inflorescence not closely bracteate; staminate pedicel < 1.5 cm long; stamens 4–11 2

2\. Stipules persistent, foliaceous and cordate at the base; staminate pedicels > 2 mm long; cymules unisexual; pistillate flowers petaliferous **94. *Moultonianthus***

– Stipules deciduous, triangular, not cordate; staminate pedicels < 1 mm long; cymules bisexual; pistillate flowers apetalous **95. *Syndyophyllum***

93. *Erismanthus* Wall. ex Müll. Arg.

Erismanthus Wall. ex Müll. Arg. in DC., Prodr. 15(2): 1138 (1866); Pax & K. Hoffm., Pflanzenr. 147. III: 33, fig. 9 (1911); Airy Shaw, Kew Bull. 36: 294 (1981); van Welzen, Blumea 40: 379, fig. 2 (1995).

Monoecious trees or shrubs, branching sympodially; indumentum simple, often inconspicuous. Leaves opposite, minutely glandular-serrulate, petiole not pulvinate; stipules interpetiolar, subpersistent or deciduous. Inflorescences unisexual or bisexual, staminate flowers in bracteate catkins or capitula, pistillate flowers solitary. Staminate flowers pedicellate; sepals (4) 5, imbricate; petals 5, shorter than sepals; disk 0; stamens 12–15, filaments distinct; anthers biseriate, basifixed, dehiscing latrorsely; pollen grains subprolate, 3-colporate, exine tectate-punctate/reticulate, reticulum slightly vermiculate; pistillode long-exserted, slender, trifid at apex. Pistillate flowers pedicellate; sepals 5, imbricate, subentire, ± foliose, persistent and reflexed in fruit; petals and disk 0; ovary 3-locular, hirsute; stylodia proximally connate, distally bifid, slender, papillose. Fruit oblate, capsular; columella persistent, apically dilated. Seeds 1–3 per fruit, subglobose, ecarunculate, testa smooth.

Two spp., southeast Asia: Vietnam to Sumatra and Borneo.

94. *Moultonianthus* Merr. Fig. 23

Moultonianthus Merr., Phil. J. Sci. Bot. 11: 70 (1916); Pax & K. Hoffm., Pflanzenr. 147, XIV: 41 (1919); van Steenis, Bull. Bot. Gard. Buitenz. III, 17: 404 (1948); van Welzen, Blumea 40: 384, fig. 3 (1995).

Monoecious trees or shrubs; indumentum simple but axes early glabrescent. Leaves opposite, shallowly crenate; stipules interpetiolar, foliose, cordate, persistent. Inflorescences axillary, unisexual, racemiform; bracts small, eglandular. Staminate pedicel articulate; sepals 5, imbricate, biseriate; petals 5 (7), longer than sepals, white, entire; disk rudimentary, 5-lobed; stamens 8–11,

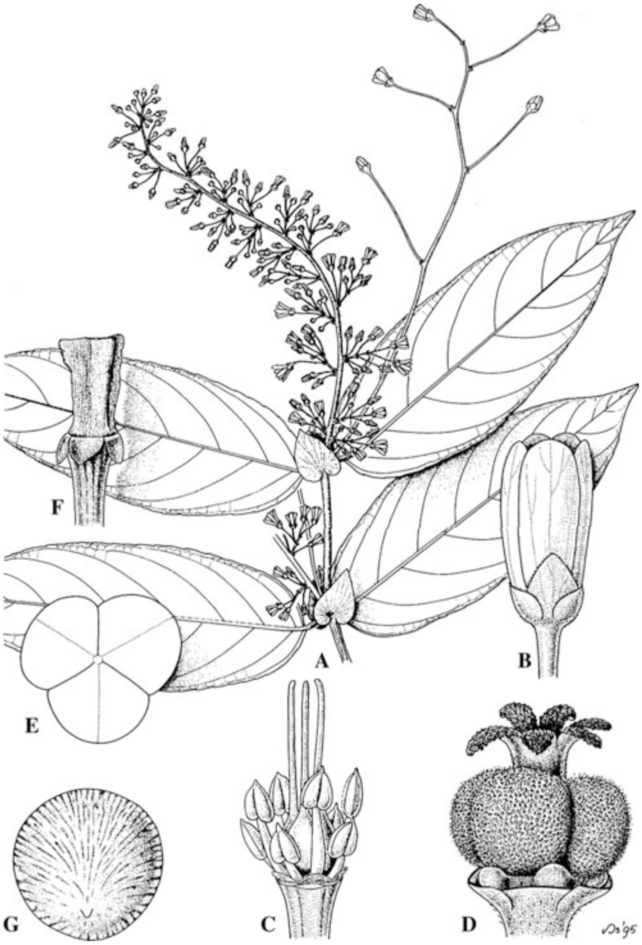

Fig. 23. Euphorbiaceae-Acalyphoideae. *Moultonianthus leembruggianus*. **A** Branchlet with separate staminate and pistillate flowers. **B** Staminate flower. **C** Staminate flower with disk lobes, androecium and pistillode. **D** Pistillate flower with perianth lobes removed, showing disk lobes and pistil. **E** Outline of young fruit. **F** Fruit column after dehiscence. **G** Seed. (van Welzen 1995; drawn by J. van Os)

biseriate, filaments distinct; anthers basifixed, latrorse to introrse, apiculate; pollen grains subprolate, 3-colporate; pistillode deeply trifid, branches slender. Pistillate pedicel articulate; sepals 5, imbricate, entire or glandular-denticulate, persistent in fruit; petals similar to staminate; disk 5-lobed; ovary 3-locular, tomentose; ovules anatropous, inner and outer integuments very thick, the outer vascularized; stylodia basally connate, bifid, branches dilated and papillate. Fruit capsular, spheroidal; columella winged. Seeds 1–3 per fruit, subglobose, ecarunculate; testa smooth.

One sp., *M. borneensis* Merr., Sumatra and Borneo.

95. *Syndyophyllum* Lauterb. & K. Schum.

Syndyophyllum Lauterb. & K. Schum., Fl. Schutzgeb. Südsee: 403 (1901); Pax & K. Hoffm., Pflanzenr. IV. 147: 104 (1911); Airy Shaw, Hook. Ic. Pl. 38(1): t. 3722 (1974); van Welzen, Blumea 40: 388, fig. 4 (1995).

Monoecious trees; indumentum simple, glabrescent. Leaves opposite, distichous, simple, minutely puncticulate, sometimes with abaxial domatia, obscurely crenulate; stipules interpetiolar, deciduous. Inflorescences axillary, bisexual or staminate thyrses, pistillate flowers solitary; bracts minute. Staminate flowers subsessile; sepals 5, imbricate, basally connate; petals shorter than sepals or 0; disk 0; stamens 4–10, filaments distinct, in 1 or 2 series, much longer than anthers; anthers basifixed, apiculate, introrse; pollen grains subspheroidal, 3-colporate, colpi operculate, pistillode deeply trifid, shorter than filaments. Pistillate flowers subsessile; sepals 4 or 5, imbricate, basally connate, entire, persistent and reflexed in fruit; petals and disk 0; ovary 3-locular, hirsute; stylodia connate halfway, tips apically bifid and adaxially papillose. Fruits capsular; columella ± persistent, trigonous and apically dilated. Seeds subglobose, ecarunculate, testa smooth.

Two spp. from Sumatra, Borneo, and New Guinea.

2. Tribe Caryodendreae G.L. Webster (1975).

Dioecious; indumentum simple; leaves with basal laminar glands; inflorescences terminal or axillary, spiciform; staminate sepals 3–5, valvate; petals 0; disk massive, pubescent; stamens 4–15; pollen grains oblate, 3-colporate, colpi not marginate, inoperculate; pistillode + or 0; pistillate flowers sessile, sepals 4–6; disk pubescent; ovary mostly 3-locular; stylodia distinct, unlobed; fruit capsular; seeds ecarunculate, testa dry or fleshy.

As treated here, Caryodendreae comprise three genera, two from the New World, and one African. The group will need a critical revision: in the molecular analysis (Wurdack et al. 2005), *Caryodendron* is resolved in a clade with two bernardioid genera (*Bernardia* and *Adenophaedra*), which is sister to the Plukenetieae, whereas *Alchorneopsis* and, farther away, *Discoglypremna* appear at the base of the "Alchorneoid" grade together with agrostistachyoid genera and *Mareyopsis*.

KEY TO THE GENERA OF CARYODENDREAE

1. Leaves pinnately veined, stipulate; pistillode massive; seed coat dry **96. *Caryodendron***
– Leaves triplinerved, exstipulate; pistillode slender or 0; seed coat fleshy 2
2. Staminate disk dissected; anthers apiculate; pistillode 0; seeds trigonous, testa foveolate **97. *Discoglypremna***
– Staminate disk entire, receptacular; anthers muticous; pistillode +; seeds lenticular, testa reticulate **98. *Alchorneopsis***

96. *Caryodendron* Karsten

Caryodendron Karsten, Fl. Colombiae 1: 91, t. 45 (1860); Müll. Arg., Fl. Brasil. 11(2): 706 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 263 (1914); Ducke, Trop. Woods 76: 18 (1943); Webster, Ann. Missouri Bot. Gard. 54: 287 (1968); Huft, Ann. Missouri Bot. Gard. 76: 1077 (1989); Radcl.-Sm., Gen. Euphorb.: 153, fig. 15 (2001).

Dioecious trees, glabrous except for inflorescences; indumentum simple. Leaves biglandular adaxially near base and with small dispersed glands; stipules lanceolate, entire, deciduous. Inflorescences mostly terminal or subterminal, spiciform, the staminate sometimes compound; bracts eglandular, scarious, rounded to truncate with ciliate margins, multiflorous. Staminate flowers pedicellate; calyx closed in bud, sepals 3 or 4, valvate; petals 0; disk massive, pulviniform, instrastaminal, pubescent; stamens 4–7, filaments distinct; anthers introrse, locules ± pendulous, connective apiculate; pollen grains suboblate, 3-colporate, colpi narrow and emarginate, inoperculate; endoaperture ovate to lalongate, sexine tectate-perforate; pistillode 0. Pistillate flowers with stout pedicels articulated at base; sepals 5 or 6, imbricate, persistent and accrescent in fruit; petals 0; disk annular, sometimes angled; ovary 3-locular, glabrous, ovules with inner integument moderately thick, outer integument thin; stylodia basally connate, unlobed. Fruits thick-walled, (2)3(4)-locular, loculicidally and septicidally dehiscent; columella ± persistent. Seeds ovoid; testa smooth, dry, thin-walled, hilum elliptic.

Three or four closely related neotropical spp., from Costa Rica to Amazonian Brazil. *Caryodendron orinocense* H. Karst., the "inchi", is cultivated for the seed oil in Colombia.

97. *Discoglypremna* Prain

Discoglypremna Prain, Kew Bull. 1911: 317 (1911); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 222, fig. 44 (1987); Léonard, Fl. Afr. Centr. Euphorb. 3: 11, t. 1 (1996).

Dioecious trees; indumentum simple. Leaves often crowded near apices, pinnately veined and triplinerved, subentire, with abaxial embedded glands and biglandular at junction with petiole; stipules deciduous. Inflorescences terminal, paniculate, bracts minute, eglandular; flowers subsessile, the staminate several per axil, the pistillate solitary. Staminate flowers pedicellate, calyx closed in bud, sepals 3–4(5), valvate; disk pubescent, dissected, segments extra- and intrastaminal; petals 0; stamens (5–)8–12(−15), filaments distinct; anthers basifixed, introrse, locules pendulous, connective apiculate; pollen grains subprolate to prolate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate, endoaperture ± circular, sexine tectate; pistillode 0. Pistillate flowers pedicellate, articulate near base; sepals mostly 5, valvate, acute, persistent in fruit; petals 0; disk dissected into 6–8 distally pubescent segments; ovary 3(4)-locular, glabrous or sericeous; inner and outer ovular integuments thick, the outer vascularized; stylodia distinct, unlobed, adaxially fimbriate. Fruit 3-lobed, capsular but exocarp somewhat fleshy; cocci reticulate; columella slender, persistent. Seeds: exotesta fleshy, reddish, endotesta blackish, foveolate, mesotesta vascularized. $n = 11$.

A single sp., *D. caloneura* (Pax) Prain, rainforests of West Africa (including São Tomé) to Uganda.

98. *Alchorneopsis* Müll. Arg.

Alchorneopsis Müll. Arg., Linnaea 34: 156 (1865), and in DC., Prodr. 15(2): 764 (1866); Pax & K. Hoffm., Pflanzenr. 147: 267 (1914); Liogier, Descr. Fl. Puerto Rico 2: 352, fig. 59–4 (1988); Burger & Huft, Fieldiana Bot. n.s. 36: 62 (1995); Radcl.-Sm., Gen. Euphorb.: 156, fig. 16 (2001).

Dioecious trees; indumentum scanty, simple. Leaves triplinerved, biglandular abaxially at base, entire or remotely crenulate; stipules 0. Inflorescences axillary, the staminate often fascicled, spiciform [flowers subsessile or shortly pedicellate]; bracts minute, eglandular; staminate flowers in glomerules, pistillate solitary. Staminate flowers pedicellate, calyx closed in bud; lobes 3 or 4, valvate; petals 0; disk massive, hirsutulous; stamens (5)6(−8), filaments distinct; anthers introrse, locules unequal; pollen grains subspheroidal, 3-colporate, colpi inoperculate, emarginate, endoaperture lalongate; sexine tectate, granulate; pistillode ± 3-lobed, strigose-hirtellous.

Pistillate flowers pedicellate, articulate; sepals 4 or 5, slightly imbricate, acute, persistent in fruit; petals 0; disk annular, pulviniform, hirsutulous; ovary 3-locular; pubescent; inner and outer ovular integuments thin; stylodia unlobed or emarginate. Fruit capsular; columella persistent, broadly 3-winged. Seeds flattened, ecarunculate; exotesta fleshy, endotesta reticulate-striate.

A single sp., *A. floribunda* (Benth.) Müll. Arg., ranging from the Greater Antilles to Costa Rica and Brazil.

3. Tribe Agrostistachydeae (Müll. Arg.) G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; indumentum simple or 0; inflorescences racemoid or spicate; the calyx closed in bud, splitting into 2–5 valvate lobes; petals 3–8, imbricate in bud [except *Cyttaranthus*]; disk receptacular or extrastaminal and dissected; stamens 10–120; anthers introrse, connective ± enlarged or apiculate, thecae often pendulous; ovary 3-locular, often tomentose; stylodia distinct, bifid, sometimes lacerate; fruit capsular; seeds caruncular, not fleshy.

Four genera, two African and two Asian. Nowicke et al. (1999) stated that *Cyttaranthus* and *Chondrostylis* differ in pollen structure from *Agrostistachys* and *Pseudagrostistachys*, implying that the Agrostistachydeae may not be monophyletic. This is confirmed by the molecular data of Wurdack et al. (2005).

Key to the Genera of Agrostistachydeae

1. Petals +; anther connective narrow; flowers in spiciform or racemoid thyrses; anthers extrorse; pistillate disk annular 2
– Petals 0; anther connective flattened, broader than high; flowers in thyrses or panicles; pistillate disk 5-lobed **102. *Chondrostylis***
2. Dioecious; staminate petals imbricate in bud; petals present in pistillate flower 3
– Monoecious; staminate petals not imbricate in bud; pistillate flowers apetalous; leaves with laminar glands **101. *Cyttaranthus***
3. Staminate disk dissected; stamens 8–10; stipules distinct, leaves lacking laminar glands **99. *Agrostistachys***
– Staminate disk receptacular; stamens 20–55; stipules connate, leaving an annular scar; leaves with laminar glands **100. *Pseudagrostistachys***

99. *Agrostistachys* Dalzell

Agrostistachys Dalzell, Hook. J. Bot. Kew Gard. Misc. 2: 41 (1850); Pax & Hoffm., Pflanzenr. 147, VI: 98, figs. 19, 20 (1912); Gagnep., Fl. Indochine 5: 465, t. 57 (7–11), 58 (1–2) (1926); Airy Shaw, Kew Bull. Add. Ser. 4: 25 (1975); Sevilla & van Welzen, Blumea 46: 76–89, figs. 1–3 (2001).

Dioecious (monoecious) trees or shrubs; branches ± resinous; indumentum simple. Leaves alternate, lamina decurrent on the petiole, entire or dentate; stipules deciduous. Inflorescences axillary, racemoid or spicate; bracts glumaceous, indurate, sometimes glandular, persistent, each subtending 1–10 staminate flowers or solitary pistillate flowers. Staminate flowers subsessile or short-pedicellate; calyx closed in bud, dehiscent into 2–5 valvate segments; petals (0)5–8, imbricate; disk segments (4)5(−7); stamens (8)10 (−13), biseriate, filaments distinct or basally connate; anthers basifixed, introrse, minutely apiculate; pollen grains subspheroidal, angulaperturate, 3-colporate, colpi inoperculate with narrow to broad margo, endoaperture lalongate, sexine tectate, intrareticulate; pistillode 2–3-fid or entire (0). Pistillate flowers articulate-pedicellate; sepals (4) 5, imbricate, entire or denticulate, persistent in fruit; petals 5, longer than sepals; disk annular to 5-lobed, sometimes with staminodes; ovary (2)3-locular, glabrous or pubescent; ovules pachychalazal, inner integument thick, outer integument thin; stylodia distinct or basally connate, bifid, papillate. Fruits capsular, thin-valved; columella persistent, narrowly 3-winged. Seeds subglobose, ecarunculate; testa smooth; hilum deltoid-reniform, large.

Ten spp., from India and Sri Lanka to New Guinea, five in Malesia.

100. *Pseudagrostistachys* Pax & K. Hoffm.

Pseudagrostistachys Pax & K. Hoffm., Pflanzenr. 147, VI: 96, fig. 18 (1912); Léonard, Fl. Congo 8(1): 183, fig. 15 (1962); Airy Shaw, Kew Bull. 36: 248, t. 1 A-G (1981); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 166, fig. 30 (1987), Fl. Zambesiaca 9(4): 136 (1996).

Dioecious shrubs or trees; indumentum simple, sparse except in inflorescences. Leaves subentire or somewhat dentate, with dispersed laminar glands and 2–4 glands near junction with petiole; stipules connate, sheathing, deciduous, leaving a circular scar. Inflorescences axillary or ramiflorous, sessile to short-pedunculate, flowers usually 1 per bract; bracts glumaceous, ciliate, persistent, eglandular. Staminate flowers pedicellate, articulate near base; calyx closed in bud, splitting into 2–5 valvate lobes; petals 5–8, distinct, imbricate, longer than sepals; disk receptacular, pubescent;

stamens 20–55, filaments distinct, erect in bud; anthers extrorse, connective thickened and glandular, thecae pendulous; pollen grains subprolate, 3-colporate, colpi inoperculate, emarginate, endoaperture obscure; sexine tectate-reticulate; pistillode small or 0. Pistillate flowers pedicellate; sepals mostly 4 or 5, scarcely imbricate, entire, persistent in fruit; petals 4 or 5; disk thick, annular, pitted; ovary 3-locular, tomentose; stylodia distinct, bipartite, branches papillose. Fruit capsular, 3-lobed, valves crustaceous; columella persistent. Seeds subglobose, ecarunculate, hilum elliptic; testa smooth, shiny.

Two spp., West Africa, one of these reaching Uganda and Zambia.

101. *Cyttaranthus* Léonard

Cyttaranthus Léonard, Bull. Jard. Bot. Brux. 25: 286 (1955); Fl. Congo Rwa.-Bur. 8(1): 180, t. 12 (1962).

Monoecious shrubs; indumentum simple. Leaves subentire to crenate or dentate, trinerved at base and pinnately veined, with scattered discoid glands abaxially, stipellate at junction with petiole; stipules minute, deciduous. Inflorescences axillary, usually unisexual, spiciform; bracts concave, glumaceous, persistent. Staminate flower pedicellate, articulate at base; calyx splitting into 2 or 3 valvate lobes; petals 3(6–8), not imbricate, shorter than calyx lobes; disk segments glabrous, intrastaminal, on the convex receptacle; stamens 25–40, filaments distinct; anthers extrorse, connective apiculate, thecae pendulous; pollen grains prolate spheroidal, 3-colporate, colpi inoperculate, scarcely marginate; sexine irregularly tectate-perforate; pistillode 0. Pistillate flowers pedicellate, pedicel distally dilated and articulate at base; sepals 3, connate into a cup, persistent in fruit; petals 0; disk swollen, appearing as a gynophore; ovary 3-locular, ± pubescent; stylodia slightly connate basally, deeply bifid. Fruit capsular, invaginated between cocci; columella persistent. Seeds oblong to subglobose, ecarunculate, testa smooth.

A single sp., *C. congolensis* Léonard, rainforests and semi-deciduous forests in the Congo.

102. *Chondrostylis* Boerl.

Chondrostylis Boerl., Ic. Bogor. 1: t. 23 (1897); Pax & K. Hoffm., Pflanzenr. 147, VII: 15 (1914); Airy Shaw, Kew Bull. 14: 358 (1960), Kew Bull. Add. Ser. 4: 69 (1975), Kew Bull. 36: 276, fig. 3C (1981); Sevilla & van Welzen, Blumea 46: 89–93, fig. 4 (2001).

Monoecious shrubs; indumentum simple to nearly 0. Leaves subsessile, serrate, usually minutely punctate with dispersed embedded glands and biglandular at base; stipules deciduous. Inflorescences axillary (ramiflorous), paniculate, unisexual; bracts glumaceous, entire, eglandular. Staminate flowers short-pedicellate; calyx splitting into 3 or 4 valvate segments; petals 0; disk of discrete interstaminal segments; stamens 50 +; anthers basifixed, introrse, connective enlarged, thecae divergent; pollen grains spheroidal, angulaperturate, 3-colporate, colpi inoperculate, emarginate, endoaperture lalongate, sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, connate into a cup; petals 0; disk annular, tomentose; ovary 3-locular, pubescent; stylodia distinct, bifid, branches adaxially fimbriate. Fruit capsular, valves thin; columella persistent, slender, trigonous. Seeds spheroidal, ecarunculate, testa smooth.

Two spp., distributed from Thailand to Sumatra and Borneo.

4. TRIBE SPHYRANTHEREAE Radcl.-Sm. (2001).

A monotypic tribe containing only the genus *Sphyranthera*.

103. *Sphyranthera* Hook. f.

Sphyranthera Hook. f., Hook. Ic. Pl. 18: t. 1702 (1887); Chakrabarty & Vasudeva Rao, J. Econ. Tax. Bot. 5: 959 (1984); 6: 429 (1985); Radcl.-Sm., Gen. Euphorb.: 135, fig. 12 (2001).

Dioecious shrubs; indumentum simple, scanty. Leaves glandular; stipules 0. Inflorescences axillary or extraaxillary, sometimes fasciculate, pedunculate and subumbellately capitulate, the staminate many-flowered capitula, the pistillate 1–4-flowered; bracts crowded at apex of peduncle. Staminate flowers pedicellate, basally articulated; sepals (3)4(5), valvate; petals 4, entire to bifid; disk segments 4, apically bilobed; stamens (8–)12–20, filaments distinct; connectives enlarged and minutely bifid, anthers subglobose; pollen prolate, 3-colporate, sexine reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3 or 4 (5), valvate or open in bud, entire, deciduous in fruit; petals 0; disk segments 3 or 4; ovary 3-locular, pubescent; stylodia distinct, bifid, somewhat lacerate. Fruits capsular; columella persistent, emarginate. Seeds globose, ecarunculate, testa smooth.

Two spp., endemic to the Andaman/Nicobar archipelago. The curious malleiform anthers suggest a possible relationship with *Chondrostylis*.

5. TRIBE ALCHORNEEAE (Hurus.) Hutch. (1969).

Dioecious (monoecious) trees or shrubs; wood rays with lysigenous canals; indumentum simple or stellate; leaves entire or dentate, sometimes stipellate or with laminar glands; stipules mostly deciduous or obsolete; inflorescences terminal or axillary; staminate flowers subsessile; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk + or 0; stamens (2–)4–60; pollen grains 3-colporate, colpi operculate; pistillode rudimentary or 0; pistillate flowers subsessile; sepals 3–8, imbricate; petals 0; disk mostly rudimentary or 0; ovary 2–3(4)-locular; stylodia entire to multifid; fruits capsular; columella persistent; seeds carunculate or ecarunculate, testa smooth or tuberculate, not fleshy.

The Alchorneae include 10 genera grouped into 3 subtribes; the monogeneric subtribe Mareyopsinae is added provisionally because *Mareyopsis* is resolved in the Alchorneoid clade of Wurdack et al. (2005).

KEY TO THE GENERA OF ALCHORNEEAE

1. Stylodia bifid; indumentum stellate; stamens 15–60 **109. *Conceveiba***
– Stylodia unlobed (or if bifid then indumentum simple); stamens 2–12; seeds ecarunculate or caruncle, minute 2
2. Indumentum stellate; ovary 2-locular; stylodia unlobed, elongated, slender; pollen exine coarsely rugulose **105. *Alchornea***
– Indumentum simple; ovary 3-locular; pollen exine finely tectate-punctate 3
3. Dioecious or monoecious; stamens 7–12 4
– Monoecious; stamens up to 8 5
4. Dioecious; staminate disk of 8 segments in 4 pairs; stamens 8; fruit indehiscent **111. *Mareyopsis***
– Monoecious; staminate disk 0; stamens 7–12; fruit dehiscent **110. *Aubletiana***
5. Stylodia distinctly bifid; leaf blades pinnately veined, not stipellate; stamens 8 **104. *Orfilea***
– Stylodia entire to emarginate; stamens 2–8; leaf blades pinnately to palmately veined 6
6. Stamens usually 8, distinct; stigmas smooth; pistillate sepals glandular at base; leaf blades spinose-dentate **106. *Coelebogyne***
– Stamens 2–4, filaments basally connate; leaf blades not spinose-dentate 7
7. Stamens 4; stylodia elongated, apically dilated; seeds ecarunculate; leaf blade stipellate; inflorescences terminal **107. *Aparisthmium***
– Stamens 2 or 3; stylodia stigmatiform; seeds minutely carunculate; leaf blade not stipellate; inflorescences axillary or ramiflorous **108. *Bocquillonia***

5a. SUBTRIBE ALCHORNEINAE Hurus. (1954).

Indumentum simple or stellate; staminate inflorescences axillary; stamens 2–10; pollen exine with complex infratectum of columellae; pistillate sepals eglandular; stylodia mostly unlobed, often dilated or stigmatiform; ovary 2–3(4)-locular.

Six genera with c. 70 spp. in both the Neotropics and Paleotropics. Generic limits within the Alchorneae are still controversial; *Orfilea*, *Coelebogyne*, and *Aparisthmium* possibly might be included within *Alchornea* s. lat.

104. *Orfilea* Baill.

Orfilea Baill., Étude Gén. Euphorb.: 452 (1858); Pax & K. Hoffmann, Pflanzenr. 147. VII: 253 (1914, under *Lautembergia*); Coode, Fl. Mascar. 160: 55, fig. t. 11 (1982, under *Lautembergia*); Radcl.-Sm., Gen. Euphorb.: 192 (2001); Schatz, Generic Tree Fl. Madag.: 162, fig. 166 (2001).

Dioecious (monoecious) trees or shrubs; indumentum simple. Leaves entire or crenulate, biglandular at base or eglandular; stipules subulate, subpersistent. Inflorescences terminal and axillary, spiciform or paniculate; pistillate bracts trifid. Staminate flowers subsessile; calyx closed in bud, splitting into 2–4 valvate segments; petals and disk 0; stamens (4)5–10, filaments basally connate; anthers 2-celled; pollen grains prolate spheroidal, angulaperturate, 3-colporate, operculate, emarginate; endoapertures lalongate; tectum microrugulose, microverrucate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 5 (6), entire, persistent in fruit; disk of 5 segments or 0; ovary 3-locular, glabrous; stylodia connate basally, bifid. Fruits capsular; columella persistent. Seeds rounded, ecarunculate, testa smooth.

Four spp. from Madagascar and Mauritius.

105. *Alchornea* Sw. Fig. 24

Alchornea Sw., Prodr.: 98 (1788), Fl. Ind. Occ. 2: 1153, t. 24 (1800); Thin, Tâp Chi Sinh Hoc 6 (3): 26 (1984); Burger & Huft, Fieldiana Bot. II. 36: 59 (1995); Radcl.-Sm., Fl. Zambesiaca 9 (4): 151, t. 31 (1996), Gen. Euphorb.: 192 (2001); Secco, Fl. Neotrop. 93: 55–134 (2004); van Welzen & Bulalacao, Syst. Bot. 32: 803–818 (2007), Males. spp.
Bossera Leandri (1962).

Dioecious (monoecious) trees and shrubs; indumentum simple or stellate. Leaves entire to

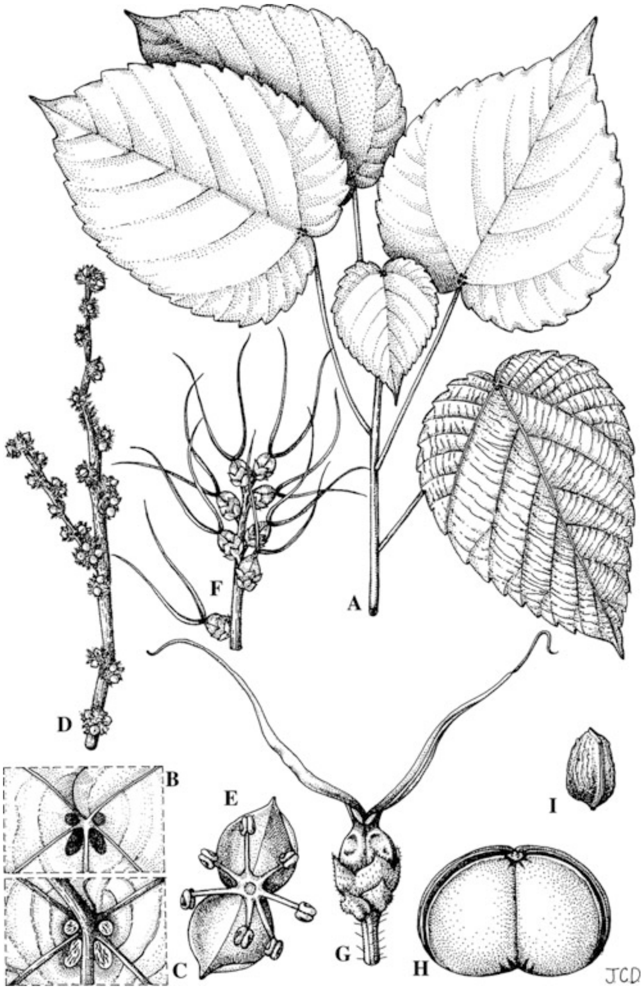

Fig. 24. Euphorbiaceae-Acalyphoideae. *Alchornea cordifolia.* **A** Branchlet. **B**, **C** Base of upper resp. lower leaf surface with extrafloral nectaries. **D** Part of staminate inflorescence, flowers in bud stage. **E** Staminate flower. **F** Tip of pistillate inflorescence, with anthetic flowers. **G** Pistillate flower. **H** Fruit. I Seed. (Radcliffe-Smith 1987; drawn by Judy Dunkley)

dentate, with laminar glands abaxially, sometimes stipellate; stipules persistent to deciduous, sometimes rudimentary. Inflorescences axillary, spiciform, often compound; bracts eglandular. Staminate flowers subsessile, in glomerules; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk receptacular, confluent with base of filaments; stamens (3–)6–8(10), filaments basally slightly connate; anthers introrse or extrorse, muticous; pollen grains ± spheroidal, angulaperturate, 3-colporate, colpi operculate, endoapertures small and obscure, sexine tectate-rugulose, microverrucate; pistillode 0 or rudimentary. Pistillate flowers sessile or pedicellate; sepals usually (3)4(−6), imbricate, entire or denticulate, ± persistent in fruit; petals 0; disk obsolete; ovary 2(−5)-locular, usually pubescent (cristate); ovules with outer integument vascularized; stylodia nearly distinct, unlobed (emarginate). Fruits capsular, smooth or tuberculate; columella persistent. Seeds subglobose or elliptic, ecarunculate (with rudimentary caruncle), testa smooth or tuberculate; mesotesta vascularized. $n = 9, 18$.

About 42 spp., distributed in the Neotropics (23 spp.), Africa and Madagascar, and in Asia and Malesia. The American taxa differ from the Old World taxa in a number of characters such as indumentum and carpel number, and the palynological studies of Takahashi et al. (2000) indicate that the pollen grains of neotropical species have a prominently vermiculate-rugose exine, in distinct contrast with the punctate-spinulose tectum of the paleotropical species. *Bossera* was distinguished by the elevated number of stamens (10) and the cristately ornamented ovary, which is also present in *A. alnifolia.*

106. *Coelebogyne* Js. Sm.

Coelebogyne Js. Sm., Proc. Linn. Soc. London 1: 41 (1839); Baill., Étude Gén. Euphorb.: 416 (1858); Pax & K. Hoffm., Pflanzenr. 147, VII: 255, fig. 38 (1914); Radcl.-Sm., Gen. Euphorb.: 194 (2001).

Dioecious shrubs; indumentum simple. Leaves dentate, with basal and scattered laminar glands; stipules persistent. Inflorescences axillary, spiciform; bracts eglandular. Staminate flowers subsessile; calyx closed in bud, splitting into usually 4 valvate segments; petals and disk 0; stamens 8, filaments distinct; anthers muticous; pollen grains spheroidal, 3-colporate, colpi operculate, sexine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5 or 6, imbricate, entire, basally glandular; petals and disk 0; ovary (2)3-locular; glabrous; stylodia stigmatiform. Fruits capsular; columella persistent. Seeds ecarunculate; testa smooth.

One or two spp., Australia (Queensland, NSW), very similar to the paleotropical spp. of *Alchornea* (*Cladodes*) and often merged with that genus.

107. *Aparisthmium* Endl.

Aparisthmium Endl., Gen. Pl.: 1112 (1840); Webster, Fl. Venez. Guayana 5: 99, fig. 97 (1999); Radcl.-Sm., Gen. Euphorb.: 194 (2000); Secco, Fl. Neotrop. 93: 134–143, fig. 56 (2005).

Dioecious trees or shrubs; indumentum simple. Leaves glandular-crenate, with basal laminar glands, stipellate at junction with petiole; stipules deciduous. Inflorescences terminal; staminate spicate-paniculate, pistillate racemose; bracts biglandular. Staminate flowers glomerulate, subsessile; calyx closed in bud, splitting into 3(4) valvate segments; petals and disk 0; stamens 3–5 (−10), filaments basally connate; anthers latrorse, muticous; pollen grains subspheroidal, 3-colporate, colpi operculate; sexine finely tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate, with 2 basal glands; sepals 4, valvate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, ovules anatropous, smooth, pubescent; inner integuments thick, outer integuments thinner; stylodia thick, dilated, shallowly bifid at tip, papillose. Fruits capsular; columella persistent. Seeds ellipsoid, ecarunculate, testa smooth.

A single sp., *A. cordatum* (A. Juss.) Baill., widespread in tropical South America.

108. ***Bocquillonia*** Baill.

Bocquillonia Baill., Adansonia I, 2: 225 (1862); Airy Shaw, Kew Bull. 29: 321 (1974); McPherson & Tirel, Fl. Nouv. Calédonie 14(1): 114–143, t. 23–29 (1987).

Dioecious (monoecious) trees or shrubs; indumentum simple, but usually very sparse or 0. Leaves dentate, with dispersed laminar glands; stipules persistent but often minute. Inflorescences axillary, spiciform, sometimes reduced to glomerules; bracts ± persistent. Staminate flowers subsessile; calyx closed in bud, splitting into 2 or 3 valvate segments; petals and disk 0; stamens 2–4, filaments basally connate; anthers latrorse or extrorse, muticous; pollen grains suboblate to prolate spheroidal, 3-colporate, colpi operculate, sexine finely tectate-perforate, microverrucate; pistillode vestigial or 0. Pistillate flowers subsessile; sepals 4 or 5, imbricate, entire, ± persistent in fruit but inconspicuous; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner integuments moderately thick, outer thin; stylodia unlobed, ± ovate, dilated. Fruits capsular; columella persistent. Seeds oblong, ecarunculate (?), testa smooth.

Fourteen spp., all endemic to New Caledonia.

5b. SUBTRIBE CONCEVEIBINAE G.L. Webster (1975).

Leaf blades not stipellate; indumentum stellate; floral disk 0; stamens 15–60; pistillate sepals often glandular; ovary 2–3-locular, inner integuments equaling or thicker than outer integuments; stylodia bifid; seeds carunculate.

Two genera, one neotropical, the other African.

109. ***Conceveiba*** Aubl.

Conceveiba Aubl., Hist. Pl. Gui.: 923, t. 353 (1775); Müll. Arg. in DC., Prodr. 15(2): 895 (1866), Fl. Brasil. 11(2): 370, t. 55 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 214, fig. 32 (1914); Macbride, Field Mus. Nat. Hist., Bot. 13 (3A, 1): 152 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 131 (1967); Secco, Fl. Neotrop. 93: 143–177 (2005).
Gavarretia Baill. (1860).
Conceveibastrum (Müll. Arg.) Pax & K. Hoffm. (1914).
Veconcibea (Müll.Arg.) Pax & K. Hoffm. (1914).

Dioecious (monoecious) trees or shrubs; indumentum stellate and sometimes simple as well. Leaves glandular-crenate or entire; stipules persistent or deciduous, or 0. Inflorescences terminal or axillary, the staminate paniculate or racemose, the pistillate racemose or spicate; bracts often biglandular. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments or lobes; petals and disk 0; outer staminodes sometimes +; stamens 7–60, filaments distinct or slightly connate at base; up to 35 inner stamens sometimes infertile; anthers extrorse or introrse, connective sometimes enlarged; pollen grains oblate to prolate spheroidal, 3-colporate, colpi operculate, endoapertures lalongate, sexine finely tectate-perforate, microverrucate; pistillode 0 (+). Pistillate flowers pedicellate; sepals 3–8, distinct or connate, glandular at base, deciduous in fruit; petals and disk 0; ovary 2–3-locular, pubescent; ovules anatropous, inner and outer integuments moderately thick; stylodia usually completely distinct and distally to deeply bipartite. Fruits capsular, smooth to rugose; columella not persistent. Seeds oblong, carunculate, hilum triangular, testa smooth.

About 12 spp., tropical Central and South America.

110. ***Aubletiana*** J. Murillo-A. Fig. 25

Aubletiana J. Murillo-A., Rev. Colomb. Cienc. 24: 360 (2000).
Conceveiba Aubl. quoad Thomas, Ann. Missouri Bot. Gard. 77: 856, fig. 1 (1990) et Breteler & Mennega, Bull. Jard. Bot. Belg. 63: 209–217, t. 1 (1994).

Monoecious trees; indumentum simple. Leaves dentate with often gland-tipped teeth; the blade with two glands at the junction of the petiole;

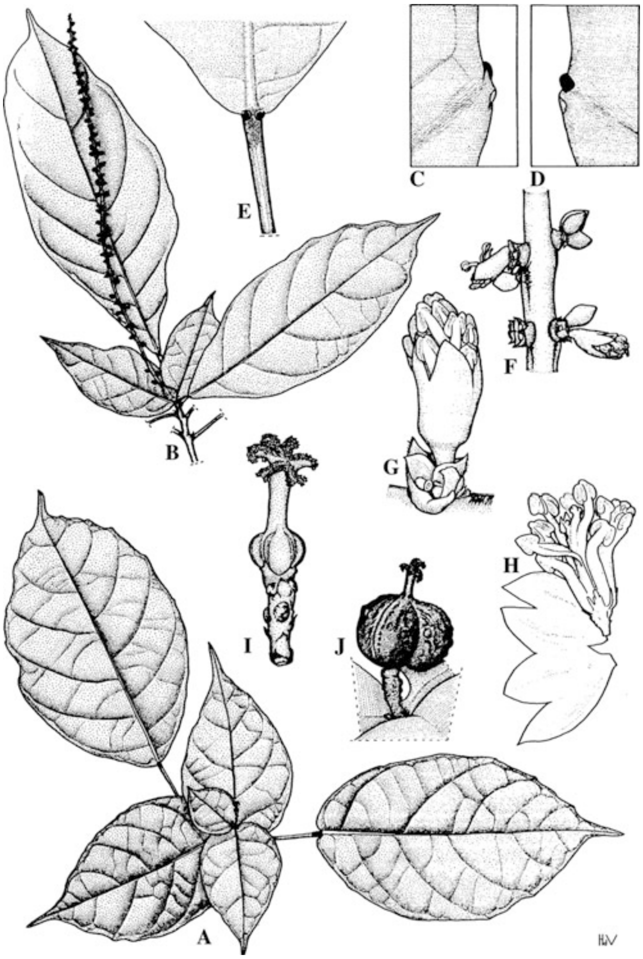

Fig. 25. Euphorbiaceae-Acalyphoideae. *Aubletiana leptostachys*. **A** Branchlet. **B** Same, with staminate inflorescence. **C** Leaf margin with gland seen from above. **D** Same, from beneath. **E** Base of leaf blade with glands. **F** Detail of inflorescence. **G** Staminate flower. **H** Androecium and perianth of staminate flower. **I** Pistillate flower. **J** Fruit. (Breteler 1994; drawn by H. de Vries)

stipules lateral. Staminate inflorescences axillary panicles with contracted 3–4-flowered cymes; pistillate inflorescences terminal spikes or flowers solitary. Staminate flowers: sepals 4 or 5, for lower half connate, valvate; petals and disk 0; stamens 7–12, sometimes with a few staminodes; pollen tricolporate-operculate [Murillo fide Punt]; pistillode +, glabrous or pubescent. Pistillate flowers solitary, sepals sometimes basally glandular; petals and disk 0; ovary 3-carpellate; ovule 1 per locule; stylodia at the base connate into a style provided with 3 undivided or divided style branches. Fruit papillose, 3-lobed, dehiscent, splitting into 3 1-seeded cocci, leaving no column. Seeds ellipsoid, with a triangular hilum, ecarunculate, exarillate.

Two West African spp., Cameroun, Gabon.

5c. Subtribe Mareyopsinae G.L. Webster (2004).

Dioecious; indumentum simple; leaves alternate, lamina puncticulate; inflorescences axillary; flowers subsessile; staminate disk segments and stamens 8; fruits indehiscent, seeds ecarunculate.

A monogeneric African tribe.

111. *Mareyopsis* Pax & K. Hoffm.

Mareyopsis Pax & K. Hoffm., Pflanzenr. 147, XIV: 13 (1919); Léonard, Bull. Jard. Bot. Nat. Belg. 65: 15, fig. 3 (1996), Fl. Afr. Centr. Euphorb. 3: 16, t. 2 (1996); Breteler, Bull. Jard. Bot. Belg. 66: 133, figs. 1, 3 (1997); Radcl.-Sm., Gen. Euphorb.: 223 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves translucent-punctate with scattered embedded glands, ± glandular-dentate; stipules deciduous. Inflorescences axillary, often ramiflorous, generally fasciculate, spiciform; bracts entire, persistent. Staminate flowers subsessile; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk-segments 8, in 4 pairs, extrastaminal; stamens 8, biseriate, filaments distinct, flattened and ligulate; anthers muticous or apiculate, connective somewhat enlarged, thecae pendulous; pollen grains 3-angled, 3-colporate, colpi granulose, neither marginate nor operculate; sexine tectate-perforate and ± rugulose, microverrucate; pistillode prominent, 2- or 3-lobed. Pistillate flowers subsessile; sepals 3–4(5), basally connate, open in bud; petals 0; disk 3- or 4-lobed; ovary 2–3(4)-locular, pubescent; stylodia nearly distinct, unlobed, papillate. Fruits indehiscent, exocarp coriaceous. Seeds ecarunculate, testa smooth.

Two spp. of tropical West Africa. *Mareyopsis* was incorrectly treated by Webster (1994) as a synonym of *Mareya*, but Léonard (1996) conclusively demonstrated that the two genera are not closely related.

6. Tribe Ricineae Bartl. (1830).

Monoecious or dioecious trees or shrubs; indumentum stellate or 0; leaves simple to deeply lobed, dentate; inflorescences terminal or opposite leaves; spiciform or paniculate; staminate calyx closed in bud, splitting into valvate segments; petals and disk 0; stamens 30–1,000, filaments distinct or connate; anthers biloculate; pollen grains spheroidal, 3–5-colpate, colpi inoperculate, emarginate; pistillate sepals 3–5, imbricate; petals and disk 0; ovary 3-locular; stylodia bifid; fruits capsular; seeds carunculate.

The genera comprised in this tribe earlier had been included in two different subtribes of the Acalypheae (Webster 1994), from which they differ in many respects such as the carunculate seeds and terminal inflorescences. The exine structure, which is very similar in both genera (Takahashi et al. 2000), led Webster to unite them in a tribe. The molecular data of Wurdack et al. (2005) place both genera in the alcalyphoid clade A4, but *Ricinus* as sister to *Speranskia*, and *Adriana* as sister to *Monotaxis*, though both with low support. Available data are insufficient for improving this unsatisfactory placement.

KEY TO THE GENERA OF RICINEAE

1. Dioecious; filaments distinct; pistillate sepals persistent in fruit; stipules distinct, glandular **112. *Adriana***
– Monoecious; filaments connate into fascicles; pistillate sepals deciduous; stipules connate, deciduous **113. *Ricinus***

112. *Adriana* Gaud.

Adriana Gaud., Ann. Sci. Nat. Paris 5: 223 (1825); Pax, Pflanzenr. 147, II: 17 (1910); Airy Shaw, Kew Bull. 35: 589 (1980); C.L. Gross & M.A. Whalen, Austral. Syst. Bot. 9: 757, figs. 1–4 (1996); Radcl.-Sm., Gen. Euphorb.: 202, fig. 25 (2001).

Dioecious shrubs; indumentum stellate or 0. Leaves alternate or opposite, petiolate or sessile, pinnately or palmately veined, coarsely dentate; stipules persistent, ± glandular. Inflorescences terminal or opposite the leaves, spiciform, the pistillate shorter and more condensed than the staminate; bracts glandular. Staminate flowers subsessile; calyx splitting into 4–5 valvate segments; petals and disk 0; stamens numerous, filaments distinct; anthers extrorse, linear, much longer than filaments, connective conspicuously apiculate; pollen grains spheroidal, 3–5-colporate, colpi inoperculate, sexine finely tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6–8, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose, sometimes muricate; ovules with outer integuments vascularized, equaling inner integuments in thickness; stylodia bipartite, coarsely papillate. Fruits capsular; columella persistent. Seeds oblong, carunculate, testa pale, rugulose.

Two variable spp., Australia.

113. *Ricinus* L.

Ricinus L., Sp. Pl.: 1007 (1753), Gen. Pl. ed. 5: 437 (1754); Müll. Arg. in DC., Prodr. 15(2): 1016 (1866); Pax & K. Hoffm., Pflanzenr. 147, XI: 119 (1919); Webster, J. Arnold Arb. 48: 379, fig. 4 (1967); Purseglove, Trop. Crops, Dicot. 1: 180, fig. 27 (1968); van Welzen, Blumea 43: 151 (1998).

Monoecious shrub or tree, herbaceous in temperate regions; indumentum simple or 0. Leaves palmately lobed, peltate, denticulate to serrulate; petiole elongated, glandular basally and at junction with blade; stipules connate into a deciduous sheath, leaving a circumaxial scar. Inflorescences terminal, sometimes pseudo-axillary, paniculate; staminate cymules proximal, distal cymules bisexual or pistillate; bracts papery, glandular at base. Staminate flowers pedicellate, articulate in the middle; calyx closed in bud, splitting into 3–5 valvate segments; petals and disk 0; stamens very numerous, to 1,000, filaments partially connate and irregularly branched; anthers introrse, locules distinct and subglobose; pollen grains subspheroidal, angulaperturate, 3-colporate, colpi not operculate, sexine finely tectate-perforate/reticulate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, entire, deciduous; petals and disk 0; ovary 3-locular, prominently echinate, glabrous; ovules pachychalazal, with inner integuments thick, outer integuments thin; stylodia basally connate, bifid, conspicuously papillate. Fruits capsular; columella persistent, distally winged. Seeds ellipsoid-compressed, carunculate, testa smooth. $2n = 20$.

The single sp., *R. communis* L., is probably native originally to east Africa but early dispersed by man to India. It is highly variable due to its cultivation for the oil from the seeds ("castor beans"). The combination of a thick inner integument, a pachychalazal ovule, and an arillate seed makes *Ricinus* unique among Acalyphoids (Tokuoka and Tobe 2003).

7. TRIBE ACALYPHEAE Dumort. (1829).

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple or stellate; leaves simple or lobed, pinnately or palmately veined, glandular or eglandular; inflorescences terminal or axillary, spiciform or racemose to paniculate, unisexual or bisexual; staminate calyx closed in bud, splitting into 2–5 valvate segments; disk intrastaminal, interstaminal, or 0; stamens 4–many; anthers sometimes apiculate, anther sacs sometimes pendulous; pollen grains ± spheroidal, 3–4-colporate, colpi inoperculate; sexine tectate-perforate or rugulose, usually microverrucate; pistillode usually 0; pistillate sepals mostly 3–6, distinct; petals 0; disk cupular or 0; ovary 2–4-locular; stylodia unlobed to multifid or lacerate; fruits capsular or drupaceous; seeds carunculate or ecarunculate; testa dry or fleshy.

This is the largest tribe in the Acalyphoideae, with 9 subtribes including a total of 28 genera, and over 1,000 species. With the removal of subtribes Adrianinae and Ricininae, tribe Acalypheae is somewhat more homogeneous but still remarkably diverse, and further revision of its boundaries will be necessary.

Key to the Subtribes of Acalypheae

1. Filaments connate, distally ramified; stylodia unlobed **7i. Lasiococcinae**
– Filaments distinct or basally connate, not ramified; stylodia bifid or unlobed 2
2. Indumentum stellate and abaxial leaf surfaces with minute beadlike glands [0.1 mm in diam.]; stylodia unlobed, often plumose or laciniate; seed testa often fleshy **7h. Rottlerinae**
– Indumentum mostly simple; abaxial leaf surfaces lacking minute beadlike glands; stylodia lobed or unlobed; seed testa dry or fleshy 3
3. Pollen exine finely reticulate; syles unlobed; seeds carunculate; mostly herbaceous 4
– Pollen exine tectate-perforate to rugulose; stylodia lobed or unlobed; seeds carunculate or ecarunculate; mostly woody 5
4. Staminate sepals discrete; anthers muticous; pollen grains distinctly colporate; cotyledons broader than radicle **7c. Mercurialinae**
– Staminate sepals connate; anthers apiculate; pollen grains with rudimentary colpi; cotyledons scarcely broader than radicle **7d. Dysopsidinae**
5. Anthers apicifixed, thecae divergent from filament; stylodia unlobed, sometimes plumose or laciniate 6
– Anthers basifixed or dorsifixed, thecae adnate to connective, not divergent from filament; stylodia bifid to multifid 7
6. Anthers not vermiform; pollen grains colporate; staminate disk present **7b. Claoxylinae**
– Anthers vermiform; pollen grains pseudo-porate; staminate disk 0 **7f. Acalyphinae**
7. Staminate disk of interstaminal segments, pistillate disk 0; seed testa fleshy **7g. Blumeodendrinae**
– Staminate and pistillate disk 0; seed testa dry 8
8. Stylodia bifid; inflorescences axillary, racemoid or spiciform; staminate flowers pedicellate **7a. Cleidiinae**
– Stylodia unlobed; inflorescences terminal, dichasial; staminate flowers subsessile **7e. Avellanitinae**

7a. Subtribe Cleidiinae G.L. Webster (1975).

Monoecious or dioecious; indumentum simple; leaves with laminar glands, stipulate; inflorescences axillary, spiciform or racemose; staminate flowers without petals or disk, sepals 3 or 4, stamens 25–80, anthers 2(4)-celled, usually apiculate; pollen grains 3-colporate, colpi not operculate, sexine tectate-perforate or rugulose-vermiculate, microverrucate; pistillode 0; pistillate sepals 3–6, imbricate; ovary (2)3-locular; stylodia bifid, branches elongate; fruit capsular; seeds ecarunculate, testa not fleshy.

Three genera, two restricted to southeast Asia and Australia, *Cleidion* widespread. The very graceful, elongate stylodia of *Cleidion* and *Wetria* and their distantly placed pistillate flowers (see our Figs 26 and 27 and Fig. 27 in Radcliffe-Smith 2001) are strongly indicative of anemophily.

Key to the Genera of Subtribe Cleidiinae

1. Staminate flowers subsessile, 1 per bract; stamens 15–25; pollen exine tectate-perforate **115. *Sampantaea***
– Staminate flowers pedicellate, usually 2 or more per bract; stamens 25–80; pollen exine tectate-rugulose 2
2. Pistillate sepals valvate; anthers muticous, 2-celled, dehiscing longitudinally; stamens 25–30 **114. *Wetria***
– Pistillate sepals imbricate; anthers apiculate, 4-celled, dehiscing cruciately; stamens mostly 30–80 **116. *Cleidion***

114. *Wetria* Baill. Fig. 26

Wetria Baill., Étude Gén. Euphorb.: 409 (1858); J. J. Smith, Med. Dept. Landb. 10: 470 (1910); Pax & Hoffm., Pflanzenr. 147,VII: 219 (1914); Forster, Austrobaileya 4: 139–143, fig. 1 (1994); Webster, Ann. Missouri Bot. Gard. 81: 86 (1994); van Welzen, Blumea 43: 156, fig. 5 (1998); Radcl.-Sm., Gen. Euphorb.: 209, fig. 27 (2001).

Dioecious trees; indumentum simple, scanty. Leaves subentire, with several glands near base; stipules deciduous. Inflorescences axillary, slender, the staminate spiciform, nodes with solitary flowers or glomerules, the pistillate racemoid, with solitary flowers; bracts entire, acute, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments;

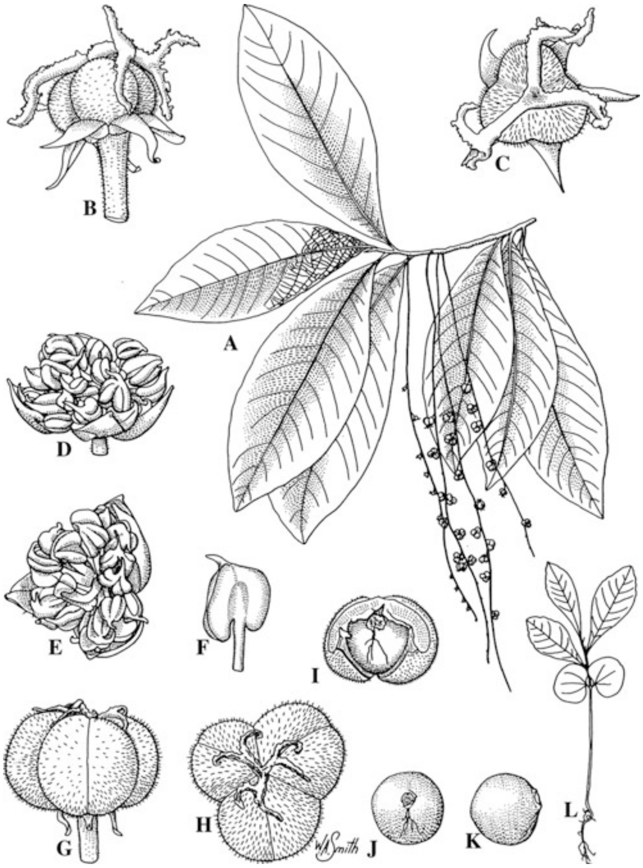

Fig. 26. Euphorbiaceae-Acalyphoideae. *Wetria australiensis*. **A** Branchlet with flowers and fruits. **B, C** Pistillate flower in side and face view. **D, E** Staminate flower in side and face view. **F** Stamen. **G, H** Fruit in side and face view. **I** Capsule with seed. **J, K** Seed in ventral and lateral view. **L** Seedling. (P.I. Forster 1994; drawn by W. Smith)

petals and disk 0; receptacle pubescent; stamens 25–30, filaments distinct; anthers latrorse, muticous or apiculate, 2-celled; pollen grains prolate spheroidal, (3)4-colporate, colpi emarginate, sexine tectate-vermiculate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia bifid, branches thin, elongate. Fruits capsular, 3-lobed; columella persistent, angled and apically dilated. Seeds spheroidal, testa smooth.

Two spp., one in southeast Asia and Malesia, the other in Queensland and New Guinea. In Webster (1994) *Wetria* was placed in subtribe Cleidiinae, a disposition supported by the more recent studies of Fernández-González and Lobreau-Callen (1996) and van Welzen (1998). In the molecular analysis of Wurdack et al. (2005), *Wetria* is resolved in a clade with the African/ Malagasy genera *Argomuellera* and *Pycnocoma* (in the combined analysis) and in a clade with the Thai genus *Sampantaea* (see note under following genus).

115. *Sampantaea* Airy Shaw

Sampantaea Airy Shaw, Kew Bull. 26: 328 (1972), Hook. Ic. Pl. 38: t. 3717 (1974); Radcl.-Sm., Gen. Euphorb.: 212 (2001).

Dioecious trees; indumentum simple. Leaves subsessile or short-petiolate, entire, with 1–3 small glands near base; stipules deciduous. Inflorescences axillary, solitary or fascicled, spiciform, flexuous; bracts persistent, eglandular. Staminate flowers sessile; calyx closed in bud, splitting into 2 (3) valvate segments; petals and disk 0; stamens 15–25, filaments nearly suppressed; anthers subsessile, oblong, minutely apiculate; pollen grains subprolate, 3-colpate or rarely 3-colporate, endoaperture minute; sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, entire; petals and disk 0; ovary 3-loculare, pubescent; stylodia basally connate, erect, thin, elongate. Fruits not seen.

A single sp., *S. amentiflora* (Airy Shaw) Airy Shaw, known from Thailand and Cambodia. In spite of the pollen morphological difference between *Sampantaea* and *Cleidion*/*Wetria* (Fernández-González and Lobreau-Callen 1996), the genus is strongly resolved as sister to *Wetria* in the *trn*L-F analysis of Wurdack et al. (2005).

116. *Cleidion* Blume Fig. 27

Cleidion Blume, Bijdr. Fl. Ned. Ind.: 612 (1826); Leandri, Adansonia II, 12: 193 (1972); A.C. Smith, Fl. Vitiensis Nova 2: 514, fig. 136 (1981); McPherson & Tirel, Fl. Nouv.-Caled. 14: 143–169, t. 30–34 (1987); Webster, Ann. Missouri Bot. Gard. 81: 86 (1994); Philcox, Fl. Ceylon 9: 166 (1997); Kulju & van Welzen, Blumea 50: 197–219, figs. 1–6 (2005); Qiu Huaxing & Gilbert, Fl. China 11: 244 (2008).
? *Polyandra* Leal, Arch. Jard. Bot. Rio de Janeiro 11: 63, fig. 1 (1961); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1087–1144 (1988); Secco, Fl. Neotrop. 93: 13, 178 (2004).

Monoecious or dioecious trees or shrubs; indumentum simple or 0. Leaves often dentate, abaxially with laminar glands; stipules persistent or deciduous. Inflorescences axillary, usually unisexual; staminate spiciform, sometimes compound,

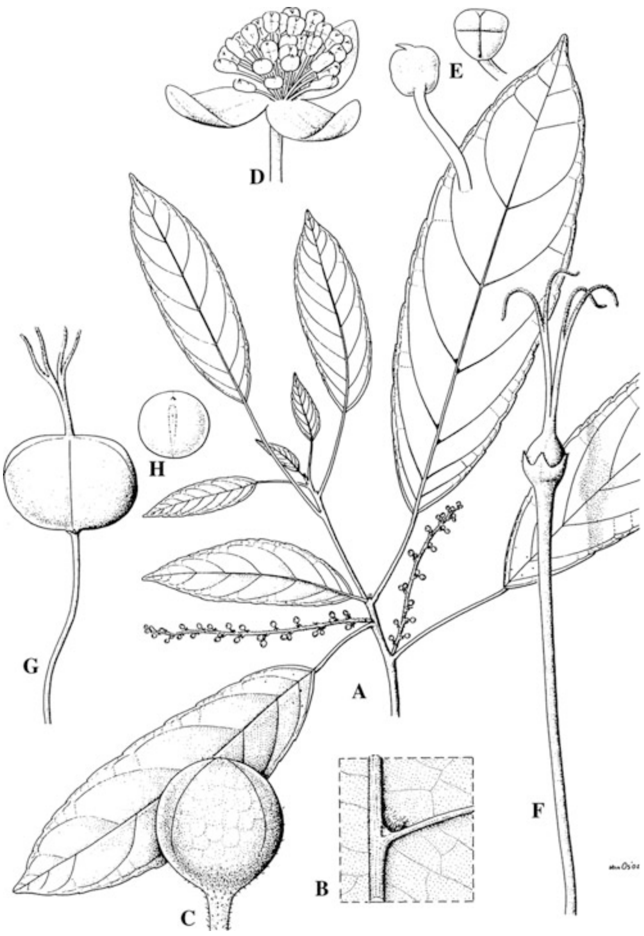

Fig. 27. Euphorbiaceae-Acalyphoideae. *Cleidion javanicum*. **A** Branch of staminate plant. **B** Domatium on lower leaf surface. **C** Staminate bud. **D** Staminate flower. **E** Anthers with cruciate cells. **F** Pistillate flower. **G** Fruit. **H** Seed. (Kulju and van Welzen 2005; drawn by J. van Os)

flowers in glomerules, pistillate racemose, sometimes reduced to 1 or 2 flowers; bracts eglandular, inconspicuous. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments; petals and disk 0; receptacle convex, stamens 20–100, filaments distinct, straight in bud; anthers with enlarged connective, apiculate, 4-celled, on both sides 2 cells above each other, dehiscing introrsely and cruciately; pollen grains oblate to prolate spheroidal, 3-colporate, colpi inoperculate, sexine tectate-punctate, tectum rugulate or microverrucate; pistillode 0. Pistillate flowers long-pedicellate; sepals 3–5, imbricate, entire, persistent in fruit; petals and disk 0; ovary (2)3-locular, pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia basally connate, erect, deeply bifid, branches elongate, thin. Fruits capsular; columella persistent. Seeds subglobose, testa smooth.

About 25 spp., 5 neotropical [except the West Indies], 2 in west Africa and Madagascar, the remainder from India and China to islands in the southwest Pacific, 12 endemic in New Caledonia. In the molecular analysis (Wurdack et al. 2005), *Cleidion* is resolved as basal to *Blumeodendron*, *Macaranga* and *Mallotus*, but lacks the vascular bundles in the outer integuments of those genera.

Polyandra, which is only known from a single staminate specimen collected in central Amazonia, possesses 4-locellate stamens, which led Webster and Huft (1988) to propose a relationship to *Cleidion*. Murillo-A. (2000) synonymised *Cleidion prealtum* Croizat with *Polyandra* and transferred it into *Conceveiba*. The identity of *Polyandra* with *C. prealtum* is still uncertain because the type of the latter species has only solitary pistillate flowers, which would exclude it from *Conceveiba* (Secco 2004). Although both *Polyandra* and the type collection of *C. prealtum* come from the same region of Central Amazonia near Borba, a clarification of the status of *Polyandra* and confirmation of its place in subtribe Cleidiinae would require pistillate material of *Polyandra*.

7b. Subtribe Claoxylinae Hurus. (1954).

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple; inflorescences axillary, racemose or paniculate; staminate sepals 2–5; disk annular and extrastaminal or segmented and interstaminal; stamens 5–40(−200); filaments distinct; anthers extrorse, thecae discrete, ± erect from enlarged connective; pollen grains 3-colporate, colpi inoperculate, emarginate; pistillate sepals 2–4, open or imbricate; disk annular or dissected; ovary mostly 2- or 3-locular; stylodia unlobed, lacerate; fruits capsular, columella ± deciduous; seeds ecarunculate, testa usually fleshy.

Subtribe Claoxylinae is a paleotropical group of 6 genera, best represented in Africa. *Amyrea*, included here in Webster (1994), is now placed in the Pycnocomeae. The systematic position of *Mareya* is still controversial. Baillon (1860) originally noted similarities to *Claoxylon* and *Pycnocoma*, while Müller (1866) saw an affinity with *Alchornea*.

Pax and Hoffman (1919) inserted *Mareya* in their Bernardiiformes [= Bernardieae], but it clearly does not belong in the same taxon as *Bernardia*. Webster (1994) assigned *Mareya* to Acalypheae subtribe Claoxylinae, but Radcliffe-Smith (2001) created a new subtribe Mareyinae to include both *Mareya* and *Mareyopsis*. Pollen evidence (Fernández-González and Lobreau-Callen 1996) indicates that *Mareya*, but not *Mareyopsis*, has pollen characteristic of the Claoxylinae. In the molecular analysis of Wurdack et al. (2005), *Mareyopsis* goes with *Alchorneopsis* and *Alchornea*, and the Old World *Mareya* is in a clade with New and Old World *Acalypha*. Morphological similarities between the two genera include traits such as the laciniate stylodia, the pendulous anther locules, and seed and pollen morphology. It is remarkable that in the molecular analysis *Mercurialis* is basal to the Claoxylinae clade.

KEY TO THE GENERA OF SUBTRIBE CLAOXYLINAE

1. Leaf blades stipellate; seed coat not fleshy **117. *Mareya***
– Leaf blades not stipellate or, if so, then seed coat fleshy 2
2. Indumentum stellate **119. *Lobanilia***
– Indumentum simple 3
3. Stipules usually persistent; buds perulate **122. *Erythrococca***
– Stipules usually deciduous; buds not perulate 4
4. Racemes interrupted; capsules crustaceous; leaf blades stipellate **121. *Micrococca***
– Racemes uniformly floriferous; capsules coriaceous; leaf blades not stipellate 5
5. Staminate disk of interstaminal segments; stamens 10–200 **118. *Claoxylon***
– Staminate disk urceolate, extrastaminal; stamens 6–12 **120. *Discoclaoxylon***

117. ***Mareya*** Baillon

Mareya Baillon, Adansonia 1: 73 (1860); Adam, Mém. Mus. Nat. Hist. Nat. Bot. 20: 495, fig. 184 (1971); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb.:1: 216 (1987); J. Léonard, Fl. Afr. Centr. Euphorb. 3: 18, t. 3 (1996).

Monoecious trees or shrubs; indumentum simple. Leaves abaxially glandular-puncticulate, entire to denticulate, adaxially with 2 or more embedded glands near base; petiole sometimes adaxially stipellate at junction with blade, the stipels deciduous; stipules deciduous. Inflorescences axillary and sometimes terminal as well, spiciform, slender; bisexual; with proximal staminate and distal bisexual glomerules; bracts eglandular, persistent. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into (2) 3 or 4 valvate segments; petals 0; disk of numerous interstaminal segments; stamens (9) 10–40, filaments distinct; anther connective bifurcate, locules pendent; pollen grains subspheroidal, angulaperturate, 3-colp(or)ate, inoperculate, emarginate, endoapertures very narrow; sexine tectate-perforate, microverrucate; pistillode usually 0. Pistillate flowers subsessile or pedicellate; sepals 3–5, imbricate or open in aestivation, entire, persistent in fruit; petals 0; disk annular-lobed; ovary 3-locular, pubescent; ovules with inner integument thick, outer integument thin; stylodia distinct, unlobed, ± plumose or laciniate. Fruits capsular; columella persistent. Seeds subglobose, testa smooth, not fleshy.

Three spp., tropical West and Central Africa.

118. ***Claoxylon*** A. Juss.

Claoxylon A. Juss., Euphorb. Tent.: 43, t. 14 (1824); A.C. Sm., Fl. Vit. Nova 2: 516 (1981); Coode, Fl. Mascar. 160: 58, t. 12, 13 (1982); N. Rani & N.P. Balakr., Rheedea 5: 113, figs. 1–8 (1995); Florence, Fl. Polynésie Française 1: 54, figs. 6–8 (1997); Forster, Austrobaileya 7: 451–472 (2007), Austral. spp.; Qiu Huaxing & Gilbert, Fl. China 11: 245–246 (2008).
Claoxylopsis Leandri (1938); Radcl.-Sm., Kew Bull. 43: 625–647 (1988).

Dioecious (monoecious) trees and shrubs; indumentum simple or 0. Leaves entire or dentate, often purplish when young, abaxially minutely punticulate and eglandular; stipules minute, deciduous. Inflorescences axillary, racemoid; staminate bracts with 1–several flowers, pistillate bracts with 1 flower; bracts eglandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 0; disk of interstaminal segments; stamens (10–)20–30(–200), filaments distinct; anthers extrorse, muticous, connective not enlarged, anther sacs distinct from connective and erect; pollen grains spheroidal, 3–5-colporate, colpi granulose, sexine finely tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals (2)3(4), distinct, imbricate, entire, persistent in fruit; petals 0; disk cupular or deeply lobed; ovary 2–3(4)-locular, glabrous or pubescent; ovules anatropous, inner and outer integuments thin [4–6 cell layers]; stylodia nearly distinct, unlobed, papillose. Fruits capsular or indehiscent, 3-lobed, cocci reticulate; columella sometimes persistent. Seeds globose, exotesta fleshy, endotesta hard and rugose or foveolate. $n = 18, 31, 54$.

About 75 spp., all Asiatic and Australasian except for 10 species in Madagascar. *Claoxylopsis* was accepted as distinct by Webster (1994) and Radcliffe-Smith (1988, 2001), but it does not appear to have any convincing differences. It might be included in *Claoxylon* sect. *Parviflora*.

119. ***Lobanilia*** Radcl.-Sm.

Lobanilia Radcl.-Sm., Kew Bull. 44: 334, t. 1 (1989); Schatz, Generic Tree Fl. Madagascar: 157 (2001).
Claoxylon sect. *Luteobrunnea* Pax & K. Hoffm. (1914).

Dioecious trees; indumentum stellate, sometimes simple as well. Leaves glandular-serrate to entire, densely stellate-pubescent abaxially; stipules deciduous. Inflorescences axillary, racemiform, the staminate elongate, pistillate contracted. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 0; disk segments interstaminal; stamens 15–30, filaments distinct; anthers extrorse, basifixed, 2-celled, thecae erect; pollen grains subspheroidal, 3-colporate, colpi inoperculate, sexine finely tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3, open in bud, reflexed; petals 0; disk annular or of 3 segments; ovary 3–4-locular; stylodia nearly distinct, unlobed, reflexed, papillate-plumose. Fruit capsular, loculicidally dehiscent. Seeds subglobose, extotesta fleshy.

Eight spp., endemic to Madagascar.

120. ***Discoclaoxylon*** (Müll. Arg.) Pax & K. Hoffm.

Discoclaoxylon (Müll. Arg.) Pax & K. Hoffm., Wiss. Ergebn. Deutsche Zentral-Afr. Exped. 2: 452 (1912), Pflanzenr. 147, VII: 137, fig. 19 (1914); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 279, fig. 54 (1987).
Claoxylon sect. *Discoclaoxylon* Müll. Arg. (1864).

Dioecious trees and shrubs; indumentum simple. Leaves abaxially minutely puncticulate, margins glandular-dentate, without laminar glands; stipules deciduous. Inflorescences axillary, staminate racemose, flowers several per glomerule, pistillate spiciform, flowers 1 per node; bracts small, persistent, eglandular or obscurely glandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 or 4 valvate segments; petals 0; disk urceolate or dissected; stamens 6–12, filaments distinct, shorter than anthers; anthers muticous; pollen grains subprolate, 3-colporate, exine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 4, entire, persistent in fruit; disk 2-lipped, segments petaloid; ovary 2-locular, pubescent; stylodia abbreviated, dilated, lacerate. Fruits capsular, deeply 2-lobed, loculicidal; columella not persistent. Seeds globose, exotesta fleshy, endotesta smooth or reticulate.

Four spp., W African, three of them endemic to the São Tomé Islands.

121. ***Micrococca*** Benth.

Micrococca Benth., Niger Fl.: 503 (1849), Gen. Pl.: 309 (1880); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 260, fig. 52 (1987), Fl. Zambesiaca 9(4): 176, t. 37 (1996); Sagun & van Welzen, Blumea 47: 149, fig. 1 (2002).
Claoxylon sect. *Micrococca* (Benth.) Müll. Arg. (1865).

Monoecious or dioecious shrubs or herbs; buds not perulate; indumentum simple. Leaves minutely puncticulate adaxially, entire or dentate; stipules persistent. Inflorescences axillary, sometimes fasciculate, unisexual or sometimes bisexual, ± spiciform; bracts eglandular, ± glumaceous. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 0; disk of interstaminal segments, or 0; stamens 5–50, filaments distinct; anthers extrorse, basifixed, muticous, pollen grains spheroidal, 3–4-colporate, colpi inoperculate, sexine finely tectate-reticulate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3 or 4, imbricate, persistent in fruit, petals 0; disk segments 3, linear; ovary 3-locular, pubescent; ovules anatropous, inner integument thin, outer integument thinner; stylodia distinct, unlobed, plumose-laciniate. Fruits capsular, 3-lobed, scabridulous, sometimes purplish; columella persistent. Seeds subglobose, exotesta thin and fleshy, endotesta rugulose.

Twelve spp., distributed from South Africa and tropical Africa to Madagascar, Arabia, southern Asia, and Malesia.

122. ***Erythrococca*** Benth.

Erythrococca Benth., Niger Fl.: 506 (1849); Gilbert, Kew Bull. 42: 363, fig. 5 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 265, fig. 53 (1987), Fl. Zambesiaca 9(4): 165, figs. 35, 36 (1996).

Dioecious shrubs; buds perulate; indumentum simple. Leaves short-petiolate, without laminar glands, margins glandular-dentate to subentire; stipules entire, persistent, sometimes spinose. Inflorescences axillary, glomerular or racemoid, glomerules sessile or capitellate-pedunculate; bracts minute. Staminate flowers pedicellate, pedicels basally or mid-articulate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk segmented, sometimes segments interstaminal; stamens (2)10–60, filaments distinct; anthers extrorse, 2-celled, locules discrete, erect; pollen grains spheroidal, 3–5-colporate, narrowly operculate, sexine tectate-reticulate, obscurely verrucate; pistillode 0. Pistillate flowers articulate-pedicellate; sepals 2(−4), valvate, entire, persistent in fruit; disk segments 2 or 3, rarely entire; ovary 2(3)-locular, glabrous or pubescent; ovules anatropous; stylodia distinct or basally connate, unlobed, smooth to laciniate. Fruits capsular, deeply lobed, without a persistent columella. Seeds subglobose, exotesta fleshy, endotesta foveolate to nearly smooth.

Forty spp., from southern Africa to Ethiopia, 1 sp. extending into Arabia.

7c. Subtribe Mercurialinae Pax (1890).

Monoecious or dioecious herbs; indumentum simple; leaves alternate or opposite, without embedded laminar glands; inflorescences axillary, mostly unisexual, spiciform, glomerular, or of solitary flowers; stamens (2–)4–20, filaments distinct; anthers extrorse, muticous; pollen grains 3-colpor(oid)ate, sexine tectate-perforate and finely reticulate; ovary 2-locular, smooth or muricate; stylodia unlobed; fruit capsular; seeds ecarunculate.

A problematic alliance of three Old World genera: *Mercurialis* shows a number of characters in common with taxa in the Claoxylinae and is resolved in the same molecular clade (A2), but *Seidelia* and *Leidesia* appear in a different lineage (A5). The pollen grains of the three genera of Mercurialinae are very similar among themselves and to those of *Dysopsis* (Takahashi et al. 2000).

Key to the Genera of Subtribe Mercurialinae

1. Dioecious; stamens 8–20; pistillate disk segments (staminodia) 2; seeds carunculate **123. *Mercurialis***
– Monoecious; stamens 2–7; pistillate disk 0 or rudimentary; seeds ecarunculate 2
2. Capsule smooth; pistillate sepals 3; leaf blades entire or denticulate **124. *Seidelia***
– Capsule setose; pistillate sepals obsolete; leaf blades crenate-dentate **125. *Leidesia***

123. *Mercurialis* (Tournefort) L.

Mercurialis (Tournefort) L., Sp. Pl. 2: 1035 (1753), Gen. Pl. ed. 5: 437 (1754); Zimmermann et al. in Hegi, Ill. Fl. Mitteleur. 5(1): 126, figs. 1746–1750 (1925); Pojarkova, Fl. URSS 14: 295, t. 17.5 (1949); Vindt, Trav. Inst. Sci. Chérifien 6:13, fig. 7 (1953); Webster, J. Arnold Arb. 48: 366 (1967); Tutin, Fl. Europaea 2: 212 (1968); Radcl.-Sm., Fl. Iraq 4(1): 222, fig. 60 (1980); Correll, Fl. Bahama Arch.: 831, fig. 345 (1982); Güemes, Fl. Iberica 8: 201, t. 49, 50 (1997).

Dioecious (monoecious) perennial or annual herbs; rootstocks with purplish pigment; indumentum simple. Leaves opposite, dentate, with minute paired basal glands at junction with petiole; stipules scarious, sometimes glandular, persistent. Inflorescences axillary, unisexual, the staminate spiciform with flowers in glomerules, the pistillate glomerular or on brachyblasts; bracts scarious, persistent. Staminate flowers sessile or subsessile; petals and disk 0; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 8–15 (−20), filaments distinct; anthers extrorse, locules distinct, diverging from connective; pollen grains subprolate, 3-colporate; pistillode 0. Pistillate flowers pedicellate; sepals 3, imbricate, scarious, entire, ± persistent, sexine finely tectate-perforate and densely microverrucate; petals 0; disk segments [staminodia] 2, elongated; ovary 2-locular, glabrous or pubescent, sometimes appendiculate; ovules anatropous, inner integument thin, outer integument thick; stylodia distinct, unlobed, papillose. Fruits capsular; columella membranous-winged, persistent. Seeds ovoid or globose; testa smooth or papillate. $x = 8$.

Eight spp. of temperate Eurasia (Macaronesia to eastern Asia). The genus has been intensely studied in Europe since the 17th century, and biosystematics studies of the European taxa have been made by Durand (1963) and Krähenbühl et al. (2002). *Mercurialis* resembles genera of Claoxylinae in its leaves and flowers with bluish pigment, but its pollen grains are different, and more suggestive of the Ricininae.

124. *Seidelia* Baill.

Seidelia Baill., Étude Gén. Euphorb.: 465 (1858); Prain, Ann. Bot. 27: 398 (1913), Fl. Capensis 5(2): 464 (1920); Dyer, Gen. S. Afr. Fl. Pl., ed. 3: 316 (1975); Radcl.-Sm., Gen. Euphorb.: 206 (2001).

Monoecious (dioecious) annual herbs; indumentum simple. Leaves alternate or opposite below, subentire or denticulate, ± purplish, colliculose, eglandular; stipules minute, deciduous. Inflorescences axillary, glomerular, unisexual or bisexual, with the pistillate at proximal axils, the staminate distal. Staminate flowers pedicellate, pedicels mid-articulate; calyx splitting into 3 valvate segments; petals and disk 0; stamens (1) 2–5, filaments nearly distinct; anthers extrorse, muticous, 2-locular, with locules distinct, opening 4-valved; pollen grains prolate spheroidal, 3-lobed, sexine finely tectate-perforate, microverrucate, muri crested; pistillode 0. Pistillate flowers pedicellate, articulate above the middle; sepals 3 (4), imbricate, entire, persistent; petals and disk 0; ovary 2-locular, glabrous or pubescent, smooth; ovules anatropous, inner and outer integuments thin; stylodia distinct, unlobed. Fruits capsular, 2-lobed; columella slender, persistent. Seeds ovoid; testa smooth or reticulate.

Two spp., South Africa.

125. *Leidesia* Müll. Arg.

Leidesia Müll. Arg., DC. in Prodr. 15(2): 792 (1866); Benth., Hook. Ic. Pl. 13: 66, t. 1284 (1879); Dyer, Gen. S. Afr. Fl. Pl., ed. 3: 316 (1975); Radcl.-Sm., Fl. Zambesiaca 9(4): 159, t. 33 (1996).

Monoecious annual herbs; indumentum simple, very sparse. Leaves alternate or subopposite, pinnately veined or triplinerved, crenate-dentate, minutely puncticulate, eglandular; stipules minute, subulate. Inflorescences terminal, bisexual, racemoid-spiciform, pistillate flower solitary and basal, staminate glomerules distal; occasional axillary pistillate flowers produced as well; bracts entire, gland-tipped. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 4–7, filaments distinct; anthers introrse, muticous, subglobose, discrete and ± pendulous; pollen grains oblate spheroidal, 3-colporoidate, sexine tectate-perforate; pistillode 0. Pistillate flower subsessile; calyx obsolete; disk 0; ovary 2-locular, hispid-muricate; ovules anatropous, inner and outer integuments thin; stylodia nearly distinct, unlobed. Fruits capsular, setose; columella membranous-winged, subpersistent. Seeds subglobose; testa smooth.

A single sp., *L. procumbens* (L.) Prain, in southern Africa, in habit somewhat resembling *Dysopsis*.

7d. Subtribe Dysopsidinae Hurus. (1954).

Monoecious herbs; indumentum simple; leaves alternate, crenate; flowers axillary, mostly solitary; staminate calyx gamophyllous; stamens 3–6; pollen grains globose, colpate, finely reticulate; ovary 3-locular, stylodia unlobed, lacerate; fruit capsular; seeds with obsolete caruncle.

Monogeneric, the single genus *Dysopsis* restricted to Central and South America. It shows clear resemblances with the Mercurialinae in both habit and flowers, but these appear to be superficial, because in the molecular analysis it is resolved as sister to *Caperonia*.

126. *Dysopsis* Baill.

Dysopsis Baill., Étude Gén. Euphorb.: 435 (1858); Pax & K. Hoffm., Pflanzenr. 147, VII (Heft 63): 286, fig. 45 (1914); Burger & Huft, Fieldiana Bot. n.s. 36: 113 (1995); Radcl.-Sm., Gen. Euphorb.: 207, fig. 26 (2001).
Molina Gay (1851; nom. illeg.).

Monoecious herbs; indumentum simple. Leaves ± palmately veined, eglandular; stipules deciduous. Flowers axillary, mostly solitary; bracts minute. Staminate flowers pedicellate; sepals 3 (4), connate; petals and disk 0; stamens 3, or 6 in 2 whorls, the inner filaments connate; anthers introrse, thecae adnate to slender connective; pollen grains subprolate, 3-colpate, colpi narrow, sexine tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3, subvalvate, entire, persistent; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments thin; stylodia unlobed, ± laciniate. Fruits capsular. Seeds subglobose, minutely carunculate, testa smooth; embryo linear.

A single polymorphic sp., *D. glechomoides* (A. Rich.) Muell. Arg., Costa Rica to Chile and Juan Fernandez.

7e. SUBTRIBE AVELLANITINAE G.L. Webster, subtr. nov.[1]

A monotypic subtribe endemic to Chile.

127. *Avellanita* Phil.

Avellanita Phil., Linnaea 33: 237 (1864); Benth., Gen. Pl. 3: 289 (1880); Radcl.-Sm., Gen. Euphorb.: 229, fig. 29 (2001); Barrera et al., Bol. Mus. Nac. Hist. Nat. Chile 30: 7 (2001).

---

[1] Subtribe **Avellanitinae** G.L. Webster, **subtr. nov.**, arbusculae monoicae; indumentum simplex; folia alterna, integra, purpurea; dichasia terminales; flores ♂ subsessiles, stamina > 50; flores ♀ sepalis 6, valvatis, stylodiis integris; fructus capsularis; semina earunculata. Typus: *Avellanita* Philippi.

Monoecious shrubs; indumentum simple. Leaves alternate or distally pseudo-verticillate, entire, eglandular, purplish-tinged; stipules persistent. Inflorescences terminal, pedunculate, dichasial, with 1 central pistillate flower and 2 or 3 lateral staminate flowers. Staminate flowers subsessile; sepals 5, valvate; petals and disk 0; stamens > 50, filaments distinct; anthers small, subglobose, dehiscing horizontally, together forming a globose mass; pollen grains subspheroidal, 3-colporate, sexine tectate-rugulose, microverrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 6, valvate, entire, persistent in fruit; ovary 3-locular, hirtellous; stylodia distinct, erect, elongated, unlobed, papillose. Fruits capsular; columella persistent. Seeds spheroidal, ecarunculate; testa smooth, dry.

A single sp., *A. bustillosii* Philippi, endemic to central Chile. It seems to be correctly placed in tribe Acalypheae (Radcliffe-Smith 2001), but its exact position within this tribe remains to be determined. It shares characters such as the purplish foliar pigment with subtribe Mercurialinae, but differs from that group in its high stamen number, 3-locular ovary, and ecarunculate seeds. It also shares purplish foliar pigments with the Claoxylinae, but differs in stamen morphology and seeds with a non-fleshy testa. Barrera et al. (2001), on the basis of epidermal characters, suggest an affinity with *Chiropetalum* (Chrozophoreae), but this is contradicted by the palynological evidence.

7f. Subtribe Acalyphinae Griseb. (1859).

A monogeneric subtribe, distinctive for its unusual anthers and accrescent fruiting calyx. It appears in some respects most similar to the Claoxylinae, but differs in its very distinctive pollen grains (Nowicke and Takahashi 2002), inflorescence structure, remarkably modified stamens, and flowers lacking a disk.

128. *Acalypha* L.

Acalypha L., Sp. Pl.: 1003 (1753); Pax & K. Hoffm., Pflanzenr. 147, XVI: 12, figs. 1–3 (1924); Wilson, Hook. Ic. Pl. 36: t. 3588 (1962); P.I. Forster, Austrobaileya 4:209–226 (1994); Cardiel, Fl. Colombia, Mon. 15: 23, figs. 1–25 (1995); Qiu Huaxing & Gilbert, Fl. China 11: 251–255 (2008); Sagun et al., Blumea 55: 21–60 (2010), rev. Malesian spp.

Monoecious (dioecious) trees, shrubs, or herbs; indumentum simple or glandular (stellate). Leaves alternate, pinnately or palmately veined, entire or dentate, sometimes gland-dotted but not with embedded laminar glands, rarely stipellate at base; stipules usually persistent. Inflorescences terminal or axillary, unisexual or bisexual, the staminate spiciform with flowers in glomerules, the pistillate spiciform, sometimes racemose or paniculate, the bisexual with proximal pistillate and distal staminate glomerules; staminate bracts minute, subtending several flowers, pistillate bracts ± foliose, entire or dentate, subtending 1–3 flowers, usually accrescent in fruit. Staminate flowers subsessile; calyx closed in bud, splitting into 4 valvate segments; petals and disk 0; stamens 4–8(−16), filaments distinct or basally connate; anthers 2-celled, theca discrete, ± elongated, twisted, vermiform; pollen grains about 10–14 x 12–15 μm, oblate-spheroidal, 3–5-porate, sexine rugulose-tectate, verrucate; pistillode 0. Pistillate flowers sessile or subsessile (pedicellate); sepals 3–4(5), basally connate, imbricate, entire, persistent in fruit; petals and disk 0; ovary (1)2–3-locular, smooth or muricate, often pubescent or papillose; ovules anatropous, inner and outer integuments thin; stylodia nearly distinct, laciniate (bifid or entire). Fruits capsular; columella persistent. Seeds ovoid or ellipsoid, carunculate or not, testa smooth or foveolate. $n = 7, 10, 14, 20$.

Over 450 spp., pantropical, with a few extratropical spp. in the Americas and E Asia, relatively stereotyped morphologically but one section, *Linostachys*, differing in its pedicellate pistillate flowers.

7g. Subtribe Blumeodendrinae G.L. Webster (1975).

Dioecious trees; indumentum simple or minutely stellate; leaves alternate, opposite, or verticillate, long-petiolate; stipules minute or 0; inflorescences axillary, spiciform to racemose or paniculate; staminate flowers pedicellate; calyx splitting into 3–5 valvate segments; disk of interstaminal segments; stamens 15–70, anther connectives enlarged; pollen grains 3-colporate, colpi short, sexine tectate-perforate or coarsely reticulate, tectum thick, with crotonoid sculpture; pistillode

0; pistillate flowers sessile or pedicellate; sepals 3–5, distinct or basally connate; disk annular or pulviniform; ovary 2- or 3-locular; ovules with thick integuments, the outer vascularized; stylodia unlobed; fruits large, thick-walled, indehiscent or tardily dehiscent; seeds ecarunculate, with fleshy testa.

This group of four Asiatic genera was earlier (Webster 1994) included as a subtribe of the Pycnocomeae. Radcliffe-Smith (2001) suggested that they might represent a separate tribe, and this is supported by the pollen evidence of Nowicke et al. (1999). Here they are shifted from the Pycnocomeae, from which they differ in the long petiolate leaves, paniculate inflorescences and large indehiscent fruits, to the Acalypheae, which is also supported by the thick vascularized outer integuments shared by *Blumeodendron*, *Mallotus* and *Macaranga* and by the molecular data (Wurdack et al. 2005).

KEY TO THE GENERA OF SUBTRIBE BLUMEODENDRINAE

1. Anther connective moderately enlarged, not umbraculiform; pistillate disk tenuous or 0; stylodia elongated 2
– Anther connective greatly enlarged, umbraculiform; pistillate disk massive; stylodia stigmatiform **132.** ***Botryophora***
2. Anther locules adnate to connective; fruits not glandular 3
– Anther locules pendent; fruits glandular **131.** ***Podadenia***
3. Anther locules 2; fruits smooth, sometimes carinate, not beaked **129.** ***Blumeodendron***
– Anther locules 4; fruits ± ribbed or spinose, beaked **130.** ***Ptychopyxis***

129. *Blumeodendron* (Müll. Arg.) Kurz

Blumeodendron (Müll. Arg.) Kurz, J. Asiatic Soc. Bengal, Nat. Hist. 42: 245 (1873); J.J. Smith, Meded. Dept. Landbouw 10: 458 (1910); Whitmore, Tree Fl. Malaya 2: 68, figs. 2, 3 (1973); Airy Shaw, Kew Bull. Add. Ser. 4: 57 (1975), Kew Bull. 36: 267, fig. 3A (1981).
Mallotus sect. *Blumeodendron* Müll. Arg. (1866).

Dioecious; indumentum scanty, simple and stellate on new growth. Leaves alternate or more often opposite or verticillate, long-petiolate, pinnately veined or triplinerved, entire, eglandular (obscurely punctate); stipules minute or 0. Inflorescences axillary, the staminate glomerular or racemoid, pistillate spiciform; staminate flowers pedicellate, calyx closed in bud, splitting into 3 or 4 valvate segments, microlepidote abaxially, petals 0; disk receptacular, convex, segments interstaminal; stamens 15–50, filaments distinct, flexed in bud; anthers introrse or latrorse, locules adnate to the enlarged connective, pollen grains oblate spheroidal, 3-colporate, colpi short and narrow, costate, inoperculate; sexine thick, tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate, articulate; sepals 3–5, imbricate, entire, deciduous in fruit; disk annular; ovary 2- or 3-locular, smooth, glabrous; inner integuments very thick, outer integuments thinner, vascularized; stylodia unlobed, papillate. Fruits capsular, dehiscing tardily; columella not persistent. Seeds large, compressed, testa fleshy.

Five spp., ranging from Burma and the Andamans through Indonesia to the Bismarck Archipelago, several spp. in Borneo.

130. *Ptychopyxis* Miq.

Ptychopyxis Miq., Fl. Ned. Ind., Suppl.: 402 (1861); Hook. f., Hook. Ic. Pl. 18: t. 1703 (1887); Croizat, J. Arnold Arb. 23: 47 (1942); Airy Shaw, Kew Bull. 14: 363 (1960), Kew Bull. Add. Ser. 4: 188 (1975), Kew Bull. 36: 340 (1981).

Dioecious trees; indumentum simple or 0. Leaves sometimes clustered at branch tips, entire; petioles pulvinulate at both ends; stipules minute or 0. Inflorescences axillary, racemoid or paniculate; bracts persistent, eglandular. Staminate flowers pedicellate, pedicel articulate above the base; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk of many small interstaminal segments; stamens 35–65, filaments distinct; anthers introrse, connective apiculate; pollen grains oblate spheroidal, 3-colporate, colpi short, narrow, inoperculate; sexine tectate-reticulate; pistillode 0. Pistillate flowers subsessile; sepals 4 or 5, basally connate, entire, ± persistent in fruit; disk annular, glabrous or pubescent; ovary 2–3-locular, pubescent; ovules anatropous, inner integuments very thick, outer integuments thinner and vascularized; stylodia connate, unlobed. Fruits capsular but tardily dehiscent; beaked, smooth to distinctly ribbed. Seeds oblong, exotesta fleshy, endotesta bony.

Thirteen spp., ranging from Thailand through Malesia to New Guinea.

131. *Podadenia* Thwaites

Podadenia Thwaites, Enum. Pl. Zeyl. 4: 273 (1861); Trimen, Handb. Fl. Ceylon 4: 62 (1898); Philcox, Fl. Ceylon 11: 144 (1997); Radcl.-Sm., Gen. Euphorb.: 170, fig. 19 (2001).

Dioecious trees; indumentum simple, glandular on inflorescences. Stipules 0. Inflorescences axillary, paniculate (compound thyrsoid), glandular-pubescent; bracts persistent. Staminate flower pedicellate; calyx closed in bud, splitting into 3 or 4 glandular-pubescent reflexed segments; petals 0; disk of numerous interstaminal segments; stamens 20–30, filaments distinct; anthers latrorse, with enlarged apiculate connective; locules pendent; pollen grains 3-colporate, colpi short and narrow; sexine tectate-punctate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 4–7, imbricate, entire, glandular-pubescent, persistent or deciduous in fruit; disk 0; ovary 3-locular, glandular-pubescent; ovules anatropous, inner integuments moderately thick, outer integuments thinner, vascularized; stylodia nearly distinct, unlobed, papillate. Fruit indehiscent, beaked, covered with gland-tipped setae. Seeds 1 or 2 per fruit, ± compressed; exotesta fleshy, endotesta bony.

A single sp., *P. thwaitesii* (Baill.) Müll. Arg., from Ceylon. Although Philcox (1997) treated it as a species of *Ptychopyxis*, the Ceylonese species appears sufficiently different from the other known taxa of *Ptychopyxis* that its placement in a separate genus is justifiable.

132. *Botryophora* Hook. f.

Botryophora Hook. f., Fl. Brit. Ind. 5: 476 (1888; nom. cons.); Airy Shaw, Kew Bull. 14: 374 (1960), Hook. Ic. Pl. 36: t. 3576 (1962), Kew Bull. 36: 269, fig. 4 (1981).

Dioecious trees; indumentum simple. Leaves sometimes clustered, entire, eglandular; petioles long, pulvinate at both ends; stipules obsolete. Inflorescences axillary, the staminate paniculate (compound spiciform or contracted), the pistillate spiciform; bracts minute. Staminate flowers subsessile; calyx closed in bud, glabrous, splitting into 2 spathaceous segments; petals 0; disk glands receptacular, numerous, several surrounding each stamen; stamens c. 30–60, filaments distinct; anther connective pileiform-peltate, anthers 4-locellate; pollen grains spheroidal, 3-colporate, inoperculate and emarginate, sexine tectate-punctae, microverrucate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 3 or 4, minute, hidden under the massive pulviniform ± segmented disk; petals 0; ovary 3- or 4-locular, smooth and glabrous; stylodia unlobed, thick, shorter than ovary, papillate. Fruit capsular but tardily dehiscent. Seeds somewhat angular, plano-convex, testa smooth and dry.

A single sp., *B. kingii* Hook. f., ranging from Burma to Sumatra, Java and Borneo. Airy Shaw (1960) provided a taxonomic revision of this genus, and was the first investigator to clearly relate it to *Blumeodendron*.

7h. Subtribe Rottlerinae Meisner (1841).

Dioecious (monoecious) trees or shrubs; indumentum stellate (simple); leaves alternate or opposite; blade unlobed or lobed, pinnately or palmately veined; sometimes with embedded laminar glands; stipules deciduous or obsolete; inflorescences terminal or axillary, racemose or paniculate; staminate calyx splitting into valvate segments; petals 0; disk of interstaminal segments or 0; stamens 15–300, filaments distinct; anthers muticous, anther sacs not pendulous; pollen grains 3(4)-colporate, finely to coarsely tectate-perforate and microverrucate; pistillate sepals 3–6(−10), distinct or connate; disk 0; ovary 2–4(−8)-locular, sometimes echinate; stylodia unlobed, ± plumose or lacerate; fruit capsular, baccate, or drupaceous; seeds ecarunculate (carunculate), testa often fleshy.

After the drastic reductions of the satellite genera around *Mallotus*, which were found to be embedded in this genus, subtribe Rottlerinae comprises only three genera, although two very large ones.

Key to the Genera of Subtribe Rottlerinae

1. Anthers 3- or 4-celled; indumentum simple; leaves alternate **134. *Macaranga***
– Anthers 2-celled; indumentum simple or stellate; leaves alternate or opposite with one member of the pair smaller 2
2. Indumentum of simple and stellate hairs; leaf blades usually granulose-glandular beneath; pollen grains with tectae-microperforate exine; stylodia not particularly elongate **133. *Mallotus***
– Indumentum not stellate but of simple hairs or gland-tipped hairs or sessile peltate-stellate hairs with central cells; leaf blades eglandular; pollen grains with areolate exine sculpture; stylodia often very long [> 20 mm] **135. *Hancea***

133. *Mallotus* Lour. Fig. 28

Mallotus Lour., Fl. Cochinch.: 635 (1790), nom. cons.; Pax & K. Hoffm., Pflanzenr. 147, VII: 145, figs. 23–29 (1914); Airy Shaw, Kew Bull. 21: 379 (1968), Hook. Ic. Pl 38: t. 3715 (1974), Kew Bull. Add. Ser. 4: 160 (1975), 8: 162 (1980);

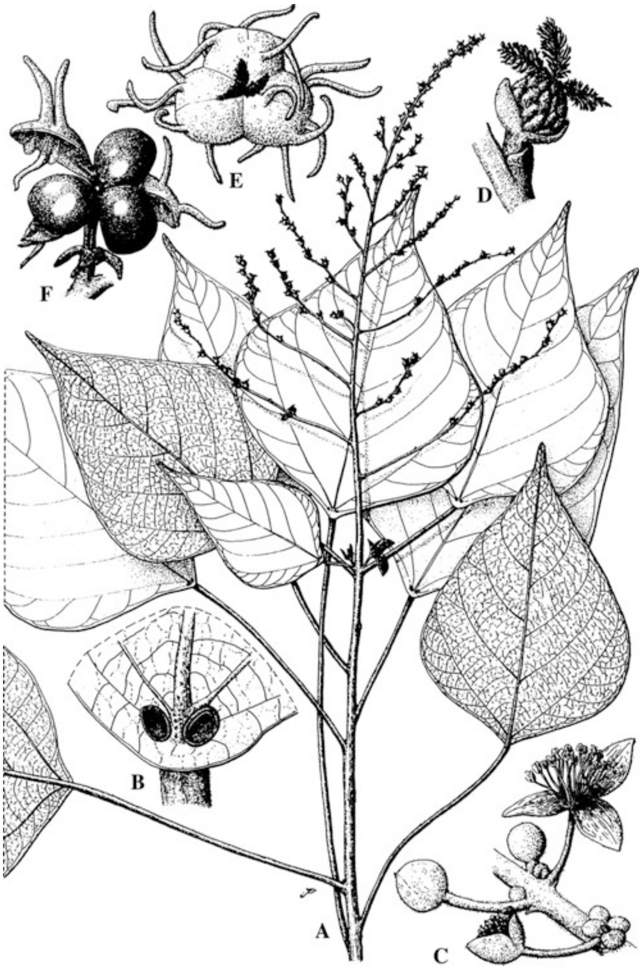

Fig. 28. Euphorbiaceae-Acalyphoideae. *Mallotus paniculatus*. **A** Flowering branch. **B** Base of upper leaf surface with extrafloral nectaries. **C** Staminate flowers and buds. **D** Pistillate flower. **E** Fruit. **F** Dehisced fruit with seeds and apex of column. (Sierra & van Welzen 2005)

McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 104, t. 35, 6–9 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euph. 1: 235 (1987); McPherson, Adansonia III, 17: 169 (1995); Bollendorf et al., Blumea 45: 319, figs. 1–10 (2000); Slik & van Welzen, Blumea 46: 3, figs. 1–22 (2001); Sierra & van Welzen, Blumea 50: 249–274 (2005), tax. sect. *Mallotus*; Kulju et al., Amer. J. Bot. 94: 1726–1743 (2007), mol. syst.; Kulju et al., Blumea 52: 115–136 (2007), *Neotrewia*, *Octospermum* and *Trevia* reduced; Qiu Huaxing & Gilbert, Fl. China 11: 225–237 (2008); Sierra, Kulju, Fiser, Aparicio & van Welzen, Taxon 59: 101–116 (2010), mol. syst.; van Welzen et al., Blumea 55: 285–290 (2011), key to Males. spp.

Trevia L. (1753) (= *Trewia*).

Echinus Lour. (1790).

Rottlera Roxb. (1802).

Coelodiscus Baill. (1858).

Neotrewia Pax & K. Hoffm. (1914).

Octospermum Airy Shaw (1965).

Dioecious (monoecious) trees, shrubs or climbers; indumentum simple and stellate or tufted and glandular. Leaves alternate or opposite, unlobed or palmately lobed, entire to dentate, sometimes peltate, usually with extrafloral nectaries adaxially; stipules persistent, deciduous, or obsolete. Inflorescences terminal or axillary, spiciform to racemoid or paniculate, glomerulate or umbel-like, usually unisexual; bracts eglandular, persistent or deciduous; staminate flowers 1–15 per bract; pistillate flowers 1 per bract, several when umbel-like. Staminate flowers pedicellate; calyx closed in bud, sepals (2)3–5, valvate; petals 0; interstaminal disk glands sometimes +; stamens 15–130, filaments distinct or connate; anthers basifixed, 2-locellate; connective sometimes broadened or apiculate; pollen grains spheroidal, 3(4)-colporate, colpi vestigially operculate, sexine tectate/microperforate; pistillode 0 (+). Pistillate flowers pedicellate; sepals (2)3–6, valvate, ± connate at least at base, sometimes calyx cupular or spathaceous; petals and disk 0; ovary (1)2–3(−9)-locular; ovules anatropous, inner integuments thick, outer integuments thinner, sometimes vascularized; style + or 0; stylodia distinct or basally connate into a common style, stylodia or their distal tips unlobed, papillose to plumose. Fruits capsular (drupaceous), 3(2–5)-locular, very rarely 1-locular [*Neotrewia*] or 7–9-locular [*Octospermum*], smooth or softly spiny; columella persistent. Seeds globose to ovoid, ecarunculate, exotesta sometimes fleshy, endotesta hard, smooth to rugose. $n = 11, 12, 18$.

According to Sierra et al. (2010), *Mallotus* includes about 110 spp. distributed mainly in (sub)tropical Asia, Malesia, Australia, and the southwestern Pacific islands, and only two spp. in Africa/Madagascar, growing in various habitats ranging from the understorey to swamp forest and montane forest, and often in disturbed and secondary vegetation.

134. *Macaranga* Thouars

Macaranga Thouars, Gen. Nov. Madag.: 26 (1806); Gagnep., Fl. Indochine 5: 434, figs. 52–54 (1926); Perrry, J. Arnold Arb. 34: 191 (1953); Whitmore, Tree Fl. Malaya 2: 105, figs. 8, 9 (1973); A.C. Smith, Fl. Vitiensis Nova 2: 500, figs.131–135 (1981); Coode, Taxon 25: 184 (1976), Fl. Mascar. 160: 53, t. 10 (1982); McPherson & Tirel, Fl. Nouv.-Caléd. 14: 172–185, t. 37 (1987); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 239, fig. 49 (1987), Fl. Zambesiaca 9(4): 161, t. 34 (1996); McPherson, Adansonia III, 18: 275 (1996); Florence, Fl. Polynésie Française 1: 104, figs. 17–19 (1997); Slik et al., Gard. Bull. Singapore 52: 12,

figs. 1–24 (2000); Qiu Huaxing & Gilbert, Fl. China 11: 237–240 (2008).
Mappa Juss. (1824).
Pachystemon Blume (1826).

Dioecious trees and shrubs; indumentum of simple (fasciculate) and conspicuous, usually colourful glandular hairs; twigs sometimes hollow, often with reddish exudate. Leaves long-petiolate, unlobed to palmately lobed, pinnately to palmately veined, often peltate, abaxially granulose-glandular; stipules minute to large, persistent or deciduous. Inflorescences axillary, the staminate spiciform or capitulate, the pistillate racemoid, sometimes compound; bracts often conspicuous and glandular. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals and disk 0; stamens (1–)3–20(−30), filaments distinct or basally connate; anthers muticous, 3- or 4-locellate; pollen grains spheroidal, 3-colporate, colpi ± granulate, sexine tectate-microperforate; pistillode 0. Pistillate flower pedicellate; calyx cupular, subentire to 4–6-lobed or -partite, persistent in fruit; petals and disk 0; ovary 1–6-locular, glandular-granulose and sometimes echinate; ovules anatropous, inner integument thick, outer integument thicker, vascularized; stylodia distinct (shortly connate), unlobed. Fruits capsular, (1)2–3(−6)-locular; smooth or spiny, loculicidal; columella not persistent. Seeds globose, ecarunculate; exotesta fleshy, endotesta indurate, often rugose. $n = 11$.

About 260 spp., 26 in Africa, 10 in Madagascar, the rest distributed from India and Ceylon east to Malesia and New Caledonia and the Pacific islands as far east as Polynesia but not Hawaii, usually as forest plants and often as members of secondary vegetation.

135. ***Hancea*** Seem. Fig. 29

Hancea Seem., Bot. Voy. Herald : 409 (1857); Slik & van Welzen, Blumea 46: 3–66 (2001), as *Mallotus* sect. *Hancea*; Sierra et al., Blumea 51: 524–537 (2006), sub *Cordemoya*; Sierra et al., Blumea 52: 361–366 (2007), new comb. under *Hancea*.
Mallotus Lour. sect. *Hancea* (Seem.) Pax & K. Hoffm. (1914).
Boutonia Bojer ex Bouton (1846).
Cordemoya Baill. (1861), Radcl.-Sm., Gen. Euph.: 228 (2001).
Mallotus sect. *Cordemoya* Müll. Arg. (1865).
Deuteromallotus Pax & K. Hoffm. (1914).

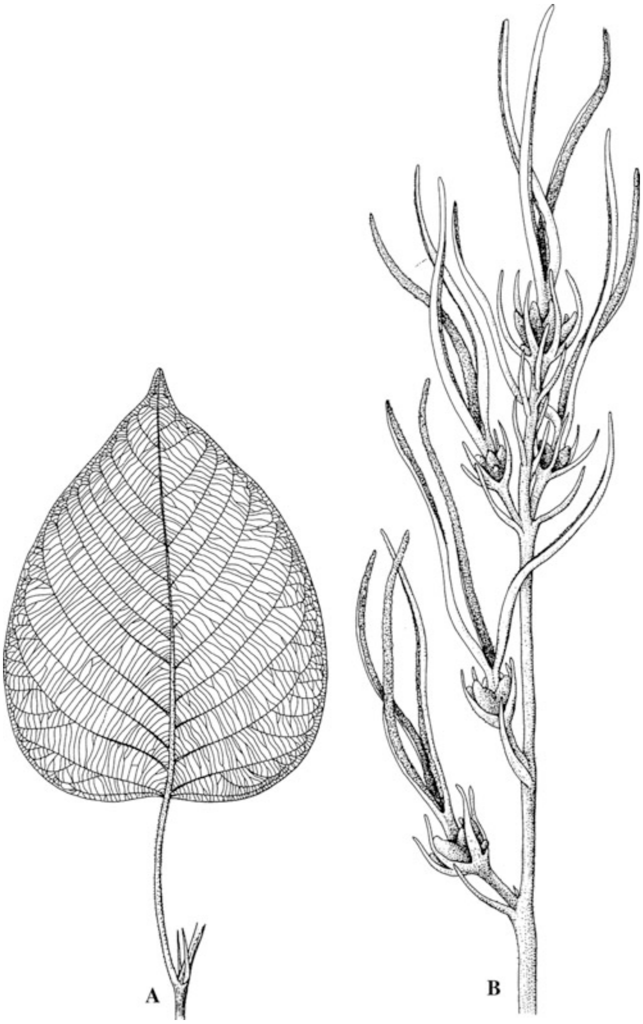

Fig. 29. Euphorbiaceae-Acalyphoideae. *Hancea integrifolia* . **A** Stipulate leaf. **B** Part of inflorescence with pistillate flowers. (Sierra et al. 2006; drawn by A. Walsmit Sachs)

Monoecious or dioecious shrubs or trees; indumentum of simple hairs and gland-tipped hairs or sessile peltate-stellate hairs with central cells; resin sometimes +. Leaves opposite [alternate in *H. subpeltata*], entire, pinnately or palmately 3-veined, with one of each leaf of a pair either slightly smaller than the other [subg. *Cordemoya*] or strongly reduced to appear like a stipule [sect. *Diplochlamys*)]; stipules axillary or intrapetiolar, persistent. Inflorescences axillary, terminal, or ramiflorous, uni- or bisexual, racemes or less often panicles; staminate flowers 1–3 per bract, pistillate flowers 1 per bract. Staminate flowers pedicellate; sepals 2–4, valvate, distinct to basally connate; petals and disk 0; stamens 40–250; filaments distinct; anthers extrorse; pollen grains oblate spheroidal, 3-colporate, sexine areolate, scabrate; pistillode 0. Pistillate flowers pedicellate; sepals (3)4–6(7), valvate or imbricate, distinct; petals and disk 0; ovary 2–3-locular; ovules anatropous, inner integuments very thick, outer integuments thinner, vascularized; stylodia 2–3, unbranched, erect, 5–25 mm long, only basally shortly connate. Fruits capsular, spiny, spines 4–6 or up to 170, sometimes gland-tipped. Seeds subglobose, ecarunculate, testa not fleshy.

A genus of 17 spp., as enumerated by Sierra et al. (2007), four of them in Madagascar and the Mascarenes (subg. *Cordemoya*), the rest (subg. *Hancea*, with 2 sections) distributed from Hong Kong throughout SE Asia to New Guinea. The whole floral structure and particularly the numerous stamens and extremely elongate stylodia are strongly indicative of wind pollination.

7i. SUBTRIBE LASIOCOCCINAE G.L. Webster (1975).

Monoecious or dioecious trees or shrubs; indumentum simple or lepidote; leaves alternate, stipulate; inflorescences axillary, unisexual, racemose or solitary, bracts eglandular; staminate sepals usually 3; disk 0; stamens many, filaments connate and ramified; pollen grains 3-colporate, not operculate, sexine tectate-microperforate or striate-verruculose; pistillode 0; pistillate sepals 5–8, imbricate, persistent or deciduous; disk 0; ovary 3-locular; stylodia unlobed, smooth to papillose or plumose; fruit capsular; seeds ecarunculate, testa usually fleshy.

Three Asiatic genera, originally placed in the subtribe Ricininae by Pax and Hoffmann (1919) because of the ramified filaments, but the totality of characters suggests that the androecial resemblance to *Ricinus* may be due to convergence. Airy Shaw (1974) and van Welzen et al. (1998) thought that the Lasiococcinae may be related to the Malloteae, whereas the molecular signals (Wurdack et al. 2005) place *Homonoia* and *Spathiostemon* with low support close to Acalypheae and Pycnocomeae.

KEY TO THE GENERA OF SUBTRIBE LASIOCCINAE

1. Monoecious; pistillate sepals persistent; indumentum simple; ovary muricate **136. *Lasiococca***
– Dioecious; pistillate sepals deciduous; indumentum simple or lepidote 2
2. Lepidote scales 0; ovary tuberculate; pollen sexine not striate **137. *Spathiostemon***
– Lepidote scales present; ovary smooth; pollen sexine striate **138. *Homonoia***

136. *Lasiococca* Hook. f.

Lasiococca Hook. f., Hook. Ic. Pl. 16: t. 1587 (1887), Fl. Brit. Ind. 5: 456 (1887); Haines, Kew Bull. Misc. Inf. 1920: 70 (1920); Airy Shaw, Kew Bull. 16: 358 (1963), 21: 406 (1968); Whitmore, Tree Fl. Malaya 2: 104 (1973); Thin, J., Biol. Sinh Hoc 8(3): 36 (1986); van Welzen, Thin & Hoai Duc, Blumea 43: 141–144, fig. 3 (1998).

Monoecious trees or shrubs; indumentum simple or glandular. Leaves alternate or subopposite, sometimes pseudo-verticillate, entire, glandular on margins; stipules deciduous. Inflorescences axillary, unisexual; staminate flowers in racemes, bracts uniflorous; pistillate flowers solitary, axillary, bracts deciduous. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens > 100, filaments connate and paniculately branching; anthers introrse, muticous, thecae globose; pollen grains spheroidal, 3-colporate, sexine tectate-perforate, slightly rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5 (−7), foliose, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, tuberculate; stylodia basally connate, unlobed. Fruits capsular, echinate; columella persitent. Seeds ± ovoid, ecarunculate, testa smooth.

Three spp., distributed from India to SE Asia and Malesia.

137. *Spathiostemon* Blume

Spathiostemon Blume, Bijdr.: 621 (1816); Airy Shaw, Kew Bull. 16: 357 (1963), Hook. Ic. Pl. 38: t. 3720 (1974), Kew Bull. 36: 345, fig. 9 (1981); van Welzen et al., Blumea 43: 145–150, fig. 4 (1998).
Polydragma Hook. f. (1887).
Clonostylis S. Moore (1925); still incompletely known; van Welzen (Blumea 43: 150. 1988) argues for its independent generic status.

Monoecious trees or shrubs; indumentum simple. Leaves glandular at base; petioles pulvinate; stipules deciduous. Inflorescences axillary (pseudo-terminal), racemose, not fasciculate, unisexual; bracts entire, eglandular, persistent. Staminate flowers sessile to shortly pedicellate, articulate above the middle; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens > 100, filaments connate into 4–7 ramified phalanges; anthers introrse or latrorse, muticous, 2-celled; pollen grains spheroidal, 3-colporate, sexine coarsely rugulose-tectate and verrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, entire, imbricate, persistent in fruit; petals and disk 0; ovary 3-locular, smooth or papillate; ovules anatropous, inner integument thick, outer integument thin; stylodia distinct, unlobed, acuminate, adaxially papillate. Fruits capsular, smooth or echinate, septicidal and loculicidal; columella sometimes persistent, apically dilated. Seeds obovoid, ecarunculate, hilum triangular, testa smooth.

Two spp., distributed from peninsular Thailand and Indonesia to New Guinea. Pax and Hoffmann (1919) combined *Spathiostemon* with *Homonoia*, and both genera are strongly supported as sisters (*rbc*L only) in the analysis of Wurdack et al. (2005), but their pollen exine ornamentation is very different (Nowicke and Takahashi 2002).

138. *Homonoia* Lour. Fig. 30

Homonoia Lour., Fl. Cochinch.: 636 (1790); Airy Shaw, Kew Bull. 36: 310 (1981); Philcox, Fl. Ceylon 11: 173 (1997); van Welzen, Blumea 43: 136–141, fig. 2 (1998).

Dioecious (monoecious) arborescent shrubs; indumentum simple and lepidote. Leaves eglandular; stipules deciduous. Inflorescences axillary, solitary, spiciform, usually unisexual; glomerules uniflorous. Staminate flowers sessile; petals and disk absent; calyx splitting into 3 valvate segments; stamens > 100, filaments connate into a paniculate androecium; anthers introrse, muticous; pollen grains spheroidal, 3-colporate, colpi narrow and operculate, sexine tectate, striate-beaded; pistillode 0. Pistillate flowers sessile; sepals 5, basally connate, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; ovules anatropous, inner and outer integuments thin; stylodia unlobed, linear, plumose-laciniate. Fruits capsular, loculicidal; columella sometimes persistent, 3-angled. Seeds ovoid, carinate, ecarunculate, exotesta fleshy, endotesta smooth.

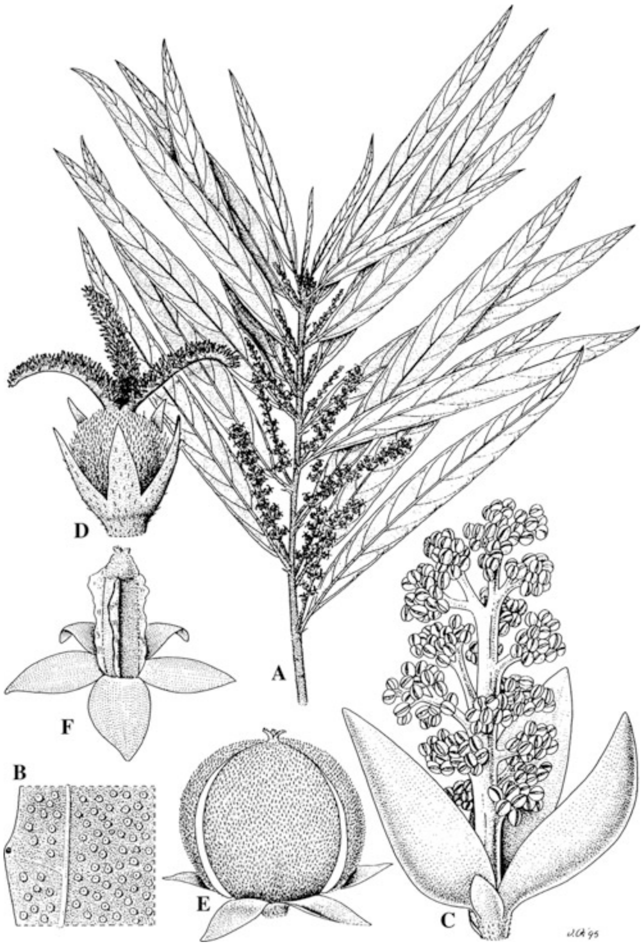

Fig. 30. Euphorbiaceae-Acalyphoideae. *Homonoia riparia*. **A** Flowering branch. **B** Lower leaf surface showing marginal gland and scale hairs. **C** Staminate flower. **D** Pistillate flower. **E** Fruit. **F** Fruit column after dehiscence. (van Welzen et al. 1998; drawn by J. van Os)

Two spp., distributed from India to China and throughout Malesia to New Guinea, growing as rheophytes mainly in and along rivers at low altitudes. The absence of petals and a disk, the numerous stamens united into a "staminate tree", and the plumose, stigmatic stylodia suggest wind pollination.

8. Tribe Pycnocomeae Hutch. (1969).

Monoecious or dioecious trees or shrubs; indumentum simple or 0; leaves alternate, sometimes stipellate or with laminar glands; stipules deciduous or rudimentary; inflorescences axillary, racemoid or spiciform (compounded); staminate calyx splitting into 3–5 valvate segments; petals 0; disk of intrastaminal segments or 0; stamens 8–120, filaments distinct; anthers mostly introrse, sometimes with enlarged connective; pollen grains subspheroidal, 3-colporate, colpi inoperculate and lacking costae; sexine tectate-perforate, or with granules arranged in areoles; pistillode 0; pistillate sepals 3–7, imbricate, persistent in fruit; disk annular, glabrous or 0; ovary 3-locular; ovules usually with inner integuments thicker than the outer; stylodia bifid to unlobed, sometimes laciniate; fruits dehiscent or indehiscent; columella usually persistent; seeds roundish, ecarunculate, testa smooth and dry.

The tribe Pycnocomeae is here redefined from the treatments of Webster (1994) and Radcliffe-Smith (2001) by the expulsion of the Blumeodendrinae and the addition of the Necepsinae, but remains heterogeneous: both *Paranecepsia* and *Necepsia* are resolved as sister taxa to *Pseudagrostis* (Wurdack et al. 2005; Kulju et al. 2008), whereas *Amyrea* is resolved in a clade with *Cyttaranthus* and *Discoglypremna*.

Key to the Subtribes of Pycnocomeae

1. Stylodia bifid; inflorescences mostly unisexual; leaf blades with or without discoid glands **8a. Necepsinae**
– Stylodia unlobed; inflorescences usually bisexual; leaf blades eglandular or minutely punctuate **8b. Pycnocominae**

8a. Subtribe Necepsinae G.L. Webster (2004).

Monoecious or dioecious; leaves alternate, venation mostly eucamptodromous, with scattered laminar glands [except in *Paranecepsia*]; bisexual inflorescences lacking terminal pistillate flower; stamens 10–120; connective sometimes enlarged or apiculate; pistillate disk annular or lobed; stylodia bifid, sometimes lacerate.

Five genera, all African, one extending to Madagascar.

Key to the Genera of Necepsinae

1. Pistillate disk 8–10-lobed; anthers muticous; pollen sexine tectate-striate **141. *Amyrea***
– Pistillate disk annular to crenulate; anthers apiculate; pollen sexine tectate-perforate 2
2. Ovary verruculose; leaf lamina not stipellate at base **139. *Necepsia***
– Ovary smooth; leaf lamina stipellate at base **140. *Paranecepsia***

139. *Necepsia* Prain

Necepsia Prain, Kew Bull. 1910: 343 (1910); Léonard, Fl. Afr. Centr. Euphorb. 3: 32 (1996); Radcl.-Sm., Fl. Zambesiaca 9(4): 23, t. 27 (1996).
Palissya Baill. (1858; nom. illeg.).
Neopalissya Pax (1914).

Monoecious (dioecious) trees or shrubs; indumentum simple. Leaves denticulate, abaxially with embedded scattered glands; stipules persistent or deciduous. Inflorescences axillary, unisexual or bisexual, spiciform, the staminate elongated, the pistillate abbreviated; bracts scarious, persistent. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into (3)4(5) valvate segments; petals 0; receptacle convex; disk of numerous pubescent interstaminal segments; stamens numerous, mostly > 50, filaments distinct; anthers with enlarged ± glandular apiculate connective, locules pendent; pollen grains subprolate, 3-colporate, scarcely marginate, angulaperturate, colpar membrane granulose; sexine tectate-perforate; pistillode 0. Pistillate flowers subsessile; sepals (4)5(6), imbricate, persistent in fruit; petals 0; disk annular; ovary 3-locular, verruculose and pubescent; ovules anatropous, inner integument thick, outer integument thin; stylodia bifid to twice bifid. Fruits capsular, 3-lobed, verruculose; columella winged, persistent. Seeds subglobose, ecarunculate, testa smooth, hilum lunate, conspicuous.

Three spp., tropical Africa. In Webster (1994) and Radcliffe-Smith (2001), *Necepsia* was included in Bernardieae but here has been transferred to Pycnocomeae because of the palynological similarities with that tribe. See also the comments under the tribe.

140. *Paranecepsia* Radcl.-Sm.

Paranecepsia Radcl.-Sm., Kew Bull. 30: 684 (1976), Fl. E. Trop. Afr. Euphorb. 1: 220, fig. 43 (1987); Fl. Zambesiaca 9 (4): 145, t. 28 (1996).

Dioecious trees; indumentum simple. Leaves ± clustered at branch tips, serrate, eglandular, stipellate at base; stipules entire, pubescent. Inflorescences axillary, solitary, lax, racemoid, often aggregated paniculately; staminate glomerules 1–5-flowered, pistillate flowers solitary at each bract. Staminate flowers pedicellate, pedicels articulate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk segments numerous, intrastaminal; stamens 25–40, filaments distinct; anthers dorsifixed, introrse, connective apiculate but not enlarged, thecae pendulous; pollen grains spheroidal, 3-colporate, scarcely marginate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, distinct, unequal, imbricate, accrescent and persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; stylodia basally connate, bifid, papillose. Fruits 3-lobed, septicidally and loculicidally dehiscent; columella persistent. Seeds globose, ecarunculate, testa smooth.

A single sp., *P. alcheornifolia* Radcl.-Sm., East Africa: Tanzania and Mozambique. The stipellate leaf blades suggest a relationship with the Alchorneae, but the inoperculate pollen grains rule out assignment to that tribe. For its possible relationship with *Necepsia*, see above under the tribal description.

141. *Amyrea* Leandri

Amyrea Leandri, Notul. Syst. 9: 168, t. 1, figs. 16–19 (1941); Radcl.-Sm., Kew Bull. 53: 438, t. 1–6 (1998), Gen. Euphorb.: 161 (2001); Schatz, Generic Tree Flora Madag.: 143, fig. 131 (2001).

Dioecious shrubs or trees; indumentum simple or 0. Leaves entire or dentate, eglandular; stipules deciduous. Inflorescences axillary, subterminal, or terminal, spiciform or racemoid, bracts convex, glumiform, subtending solitary flowers. Staminate flowers subsessile to pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk segments interstaminal, pubescent; stamens 20–30, filaments distinct; anthers muticous, latrorse, subpendulous; pollen grains 3-angled, 3-colporate, colpi narrow and not bordered; sexine tectate-striate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, usually persistent; disk fleshy, 8–10-lobed; ovary 3-locular, smooth and glabrous; stylodia bifid, papillose. Fruit capsular; columella persistent. Seeds ovoid, ecarunculate; testa smooth, blackish.

Eleven spp. endemic to Madagascar. In describing the genus, Leandri noted resemblance to *Neopalissya* (*Necepsia*) and to *Mareya*, which furnished the basis of the anagrammatic generic name. See also above under the tribe.

8b. SUBTRIBE PYCNOCOMINAE G.L. Webster (1994).

Monoecious; leaves alternate, lacking dispersed laminar glands, venation brochidodromous; pistillate flowers solitary, terminating inflorescences, rarely so in *Argomuellera*, the staminate glomerules proximal; stamens 15–80, anther connective not enlarged; pollen sexine tectate-perforate or gemmate; pistillate disk + or 0; stylodia distinct or connate, unlobed, apically dilated.

Three genera of Africa and Madagascar.

KEY TO THE GENERA OF PYCNOCOMINAE

1. Pistillate disk +; pistillate flowers usually not terminal in inflorescence **142. *Argomuellera***
– Pistillate disk 0; pistillate flowers terminating inflorescences 2
2. Terminal bud not perulate; pistillate flower solitary and terminal at apex of inflorescence; filaments arcuate in bud; ovary 6-horned, pubescent **143. *Pycnocoma***
– Terminal bud perulate; pistillate flowers not solitary and terminal at apex of inflorescence; filaments straight in bud; ovary unappendaged, glabrous **144. *Droceloncia***

142. *Argomuellera* Pax

Argomuellera Pax, Bot. Jahrb. 19: 90 (1894); Prain, Fl. Trop. Afr. 6(1): 925 (1912); Léonard, Bull. Soc. Roy. Belg. 91: 274 (1959), Fl. Afr. Centr. Euphorb. 3: 56, t. 10, 11 (1996); Radcl.-Sm., Fl. Zambes. 9(4): 147, t. 29 (1996).
Pycnocoma sect. *Wetriaria* Müll. Arg. (1866).
Neopycnocoma Pax (1909).

Monoecious trees or shrubs; indumentum simple. Leaves sometimes apically clustered, simple, subsessile or short-petiolate, entire or denticulate, sometimes with abaxial glands; stipules deciduous. Inflorescences axillary, spiciform (compound); cymules usually bisexual; bracts persistent. Staminate flowers pedicellate, pedicel articulated near base; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk segments interstaminal, pilose; stamens (15–) 25–120, filaments distinct, erect in bud; anthers with enlarged connective, muticous, locules pendent; pollen grains spheroidal, angulaperturate, 3-colporate, emarginate, colpar membrane granulose, sexine tectate-reticulate; pistillode usually 0. Pistillate flowers pedicellate; sepals usually (3–) 5–6(−9), imbricate, entire, persistent in fruit; disk annular; ovary 3(4)-locular, pubescent; ovules pachychazal, inner integument thick, outer thinner; stylodia basally connate, unlobed, tips recurved. Fruits capsular, 3-lobed; columella persistent, apically dilated. Seeds globose, ecarunculate, smooth.

Eleven spp., Africa and Madagascar. The group was first treated by Müller (1866) as a section of *Pycnocoma*. Pax originally regarded *Argomuellera* as related to *Mallotus*, but noted a resemblance in habit to *Pycnocoma*, and Radcliffe-Smith (2001) has included *Argomuellera* in the subtribe Pycnocominae.

143. ***Pycnocoma*** Benth.

Pycnocoma Benth., Niger Fl.: 508 (1849); Léonard, Bull. Jard. Bot. Nat. Belg. 65: 38 (1996), Fl. Afr. Centr. Euphorb. 3: 36, fig. 2, t. 6–9 (1996); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 228; fig. 46 (1987).
Wetriaria (Müll. Arg.) Kuntze (1903).

Monoecious trees or shrubs; indumentum simple. Leaves sometimes pseudo-verticillate, subsessile, entire or dentate, rarely lobed, eglandular but minutely punctate abaxially; stipules deciduous or 0. Inflorescences axillary, bisexual, racemiform or spiciform, staminate flowers in glomerules at proximal nodes, pistillate solitary and terminal; staminate bracts concave. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk receptacular, usually glabrous; stamens > 50, filaments distinct, flexuous in bud, long-exserted; anthers introrse, muticous, connective not enlarged; pollen grains 3-angled, 3-colporate, emarginate, inoperculate but colpar membrane granulose; sexine minutely tectate-punctate, slightly rugulose, with coarse reticulum of granular projections; pistillode 0. Pistillate flowers pedicellate; sepals (4)5–8, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, 6-horned or -winged, pubescent; ovules anatropous, inner and outer integuments moderately thick; stylodia connate into a column, unlobed, apically dilated. Fruits capsular, 3-lobed; columella persistent. Seeds globose, ecarunculate, testa minutely puberulent.

Eighteen spp., tropical Africa. The pollen of *Pycnocoma* is unique in its areolate tectum, which somewhat simulates the pattern in *Croton*.

144. ***Droceloncia*** Léonard

Droceloncia Léonard, Bull. Soc. Roy. Bot. Belge 91: 279 (1959); Webster, Ann. Missouri Bot. Gard. 81: 76 (1994); Radcl.-Sm., Gen. Euphorb.: 167, fig. 18 (2001).

Monoecious shrubs; indumentum simple; terminal buds perulate. Leaves subentire or dentate, eglandular; stipules deciduous. Inflorescences axillary, spiciform, bisexual, staminate flowers in glomerules, pistillate solitary and apical; bracts large, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into several valvate segments; petals 0; disk receptacular, convex, glabrous; stamens c. 40, filaments distinct and straight in bud; anther connective not enlarged; pollen grains subprolate, 3-colporate, inoperculate and emarginate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6 (?), imbricate; petals and disk 0; ovary 3-locular, smooth and glabrous; stylodia distinct, unlobed, apically dilated. Fruit capsular.

A single sp., *D. rigidifolia* (Baill.) Léonard, Madagascar and Comoro I. Although originally included in *Pycnocoma*, its pollen is very different from that genus (Nowicke et al. 1999).

9. TRIBE AMPEREEAE Müll. Arg. (1864).

Monoecious (dioecious) herbs or subshrubs; indumentum simple; leaves alternate, narrow, ericoid, stipulate. Inflorescences glomerular, axillary or terminal; staminate flowers pedicellate; sepals 3–5, basally connate, valvate; petals + or 0; disk dissected or obsolete; stamens 3–10, filaments distinct; anthers biseriate, locules pendulous; pollen grains subprolate to suboblate, 3-colporate, colpi inoperculate; exine reticulate, tectum psilate; pistillode present or 0; pistillate flowers subsessile on a 1(3)-flowered peduncle; sepals (4) 5, imbricate, entire to fimbriate; disk cupular, crenulate; ovary 3-locular, integuments thin; stylodia distinct or nearly so, spreading, bifid; fruits capsular, septicidal; seeds carunculate.

The two Australian genera of Ampereeae have been associated in the taxonomic literature since the treatment of Müller (1866), who placed them in separate subtribes of the tribe Ampereeae. Henderson (1992), on the basis of supposedly intermediate characters in *Amperea spicata* Airy Shaw, has suggested that *Monotaxis* should probably be combined with *Amperea*. However, although Tokuoka and Tobe (2003) did not find any significant differences in ovule and seed anatomy, Nowicke et al. (1998), on the basis of pollen characters, have indicated that there are clear palynological distinctions between the genera. Furthermore, since there are distinct differences in stipules, inflorescences, anthers, and stylodia, amalgamation of the two genera seems premature. The finding of Wurdack et al. (2005) that *Adriana* appears in a clade with the two Ampereeae genera needs attention; also Nowicke et al. (1998) had observed a palynological resemblance between *Amperea* and *Adriana*.

KEY TO THE GENERA OF AMPEREEAE

1. Staminate petals +; sepals imbricate; anther connective not glandular, locules disjunct; pollen grains 3-angled, sexine reticulate; stylodia fimbriate; cymes terminal **145. *Monotaxis***

– Staminate petals 0; sepals ± valvate; anther locules pendulous from a glandular connective; pollen grains 3-lobed, sexine perforate-foveolate; stylodia usually entire; flowers axillary **146. *Amperea***

145. *Monotaxis* Brongn. Fig. 31

Monotaxis Brongn., Voy. Coq. Bot.: 223 (1829); Airy Shaw, Muelleria 4: 239 (1980); Halford & Henderson, Austrobaileya 6: 273–292 (2002), rev.

Monoecious (dioecious) perennial or annual herbs, sometimes suffruticose; indumentum 0. Leaves alternate (subopposite or verticillate), entire (dentate), one-veined, lateral veins obscure; stipules entire or lobed, persistent. Inflorescences glomerular, terminal, each usually with 1–3 pistillate and several staminate flowers subtended by small scarious bracts. Staminate flowers pedicellate; sepals 4 or 5, often petaloid; petals 4 or 5, clawed, basally auriculate; disk segments 4–5; stamens 8–10(11), filaments distinct; anthers 2-celled; anther cells distinct, divergent to pendent on transverse connective; pollen grains subprolate, angulaperturate, 3-colporate, colpi marginate, exine very thick, sexine reticulate, transitional to tectate-perforate; pistillode trifid to subulate or 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, persistent in fruit; petals + or 0; disk segments 3–10, truncate or bifid; ovary 3-locular; ovules anatropous, inner and outer integuments thin; stylodia shortly connate at base, distally distinct, deeply bifid, branches fimbriate. Fruit capsular; columella slender, persistent. Seeds oblong, smooth, carunculate; endosperm copious; embryo cylindrical, straight or curved; cotyledons much longer than radicle.

Eleven spp., endemic to tropical and temperate Australia.

146. *Amperea* A. Juss.

Amperea A. Juss., Euphorb. Tent.: 35 (1824); Henderson, Austral. Syst. Bot. 5: 1, figs. 1–4 (1992); Radcl.-Sm., Gen. Euphorb.: 130 (2001).

Monoecious or dioecious perennial herbs; indumentum scanty or 0. Leaves sessile or petiolate, one-veined, laterals obscure, entire or dentate, often revolute; sometimes scale-like; stipules entire to fimbriate, persistent to deciduous. Inflorescences [except in *A. spicata*] axillary, flowers in dense unisexual or bisexual glomerules, subtended by ± dissected persistent bracts. Staminate flowers pedicellate; sepals 3–5(6), basally connate, entire, ± petaloid; petals 0; disk rudimentary or 0; stamens 3–10, filaments distinct, exserted; anthers with enlarged minutely glandular connective, thecae pendulous; pollen grains oblate spheroidal, 3-colporate and 3-lobed in polar view, colpi inoperculate, with broad margo, sexine tectate-perforate and ± verrucate; pistillode 0. Pistillate flowers subsessile; sepals 4 or 5, nearly distinct, imbricate, entire, persistent in fruit; petals 0; disk annular, tenuous; ovary 3-locular; ovules anatropous, inner and outer integuments thin; stylodia basally connate, bifid. Fruits capsular, valves sometimes with distal appendages; columella ± persistent. Seeds ellipsoidal, somewhat compressed, carunculate; testa smooth (minutely foveolate-striate); embryo cylindrical, cotyledons narrow and longer than radicle.

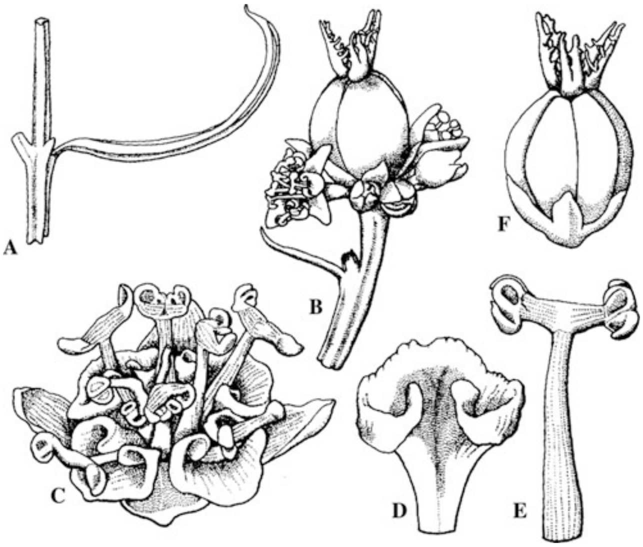

Fig. 31. Euphorbiaceae-Acalyphoideae. *Monotaxis linifolia*. **A** Section of twig with stipulate leaf. **B** Inflorescence. **C** Staminate flower. **D** Auriculate petal. **E** Antepetalous stamen, abaxial view. **F** Fruit. (Halford & Henderson 2002; drawn by W. Smith)

Eight spp., all Australian, 6 of these confined to Western Australia. The 3-lobed pollen with broad margo and verrucate exine of *Amperea* resembles that of *Bernardia*. However, that genus differs in its larger number of pistillate sepals and ecarunculate seeds; the pollen similarity may be homoplasious.

10. TRIBE EPIPRINEAE (Müll. Arg.) Hurus. (1954).

Monoecious; indumentum stellate; leaves alternate (opposite), petiole sometimes with apical paired glands; stipules sometimes glandular; inflorescences terminal or axillary, paniculate, racemoid, or the staminate capitulate; staminate flowers sessile or subsessile; calyx splitting into 2–6 valvate segments; petals and disk 0; stamens 4–15(−50); pollen grains 3-colporate, colpi inoperculate and scarcely marginate, endoaperture large, sexine tectate-perforate or coarsely reticulate; pistillode +; pistillate flowers sessile or pedicellate; sepals (4)5–8, imbricate, entire to lacerate, usually persistent in fruit; petals and disk 0; ovary 3(4)-locular, stellate-tomentose; stylodia distinct or connate, bifid to multifid (unlobed); fruits capsular (indehiscent); columella winged, usually persistent; seeds subglobose, ecarunculate; testa smooth (rugose).

Seven genera, all Asiatic except *Cephalocroton*. Except for the enigmatic *Rockinghamia*, which is added only tentatively, the Epiprineae appear to be a monophyletic group, also in the light of the molecular analysis (Wurdack et al. 2005), although the sampling (4 genera) is limited. *Rockinghamia* has a habit suggestive of *Mallotus*, but the studies of Nowicke et al. (1999) show that its pollen differs from that of all Acalypheae in the lack of microverrucae, whereas it shares with Epiprineae the deeply puntate-microreticulate exine sculpture. In the *rbc*L tree of Wurdack et al. (2005), it is resolved (without support) as basal to the genera of the Epiprineae.

KEY TO THE SUBTRIBES AND GENERA OF EPIPRINEAE

1. Anthers 4-celled; leaves opposite; staminate disk as interstaminate pubescent disk glands; pistillate disk annular. Subtribe **10c. Rockinghamiinae** **154. *Rockinghamia***
– Anthers 2-celled; leaves alternate; staminate and pistillate disk 0 2
2. Pistillate sepals persistent in fruit; staminate calyx of distinct segments; pollen sexine not spinulose. Subtribe **10a. Epiprininae** 3
– Pistillate sepals deciduous; staminate sepals connate; pollen sexine spinulose. Subtribe **10b. Cephalomappinae** **153. *Cephalomappa***
3. Staminate flowers in racemoid or spiciform inflorescences 4
– Staminate flowers in pedunculate capitula 7
4. Pistillate flower sessile, calyx involucrate, accrescent in fruit; stylodia connate into a distinct column; stamens mostly 8–15; leaf blades with paired basal glands at junction with petiole **147. *Epiprinus***
– Pistillate flowers pedicellate, calyx not involucrate; stylodia scarcely connate; stamens (3) 4 or 5; leaf blades eglandular [except *Cleidiocarpon*] 5
5. Filaments straight in bud; staminate sepals connate; stipules persistent **150. *Koilodepas***
– Filaments ± inflexed in bud; staminate calyx of distinct segments; stipules deciduous or obsolete 6
6. Monoecious; fruits capsular; leaves without laminar or petiolar glands **148. *Symphyllia***
– Dioecious; fruits indehiscent; petiole with paired distal glands **149. *Cleidiocarpon***
7. Inflorescences axillary; stamens (2–)4(5); pistillate flowers subsessile, sepals unlobed, accrescent; leaf blades white-tomentose beneath **151. *Cladogynos***
– Inflorescences terminal; stamens 6–10; pistillate flowers pedicellate, sepals pinnately or bipinnately lobed (entire); leaf blades not white-tomentose beneath **152. *Cephalocroton***

10a. SUBTRIBE EPIPRININAE Müll. Arg. (1865).

Leaves pinnately or palmately veined; staminate sepals distinct; stamens mostly 6–8 or more, filaments distinct; pollen sexine not spinulose; pistillate sepals mostly persistent; capsules smooth.

Six paleotropical genera.

147. *Epiprinus* Griffith

Epiprinus Griffith, Notul. Pl. Asiat. 4: 487 (1854); Croizat, J. Arnold Arb. 23: 52 (1942); Thin, Tâp Chi Sinh Vât Hoc 10(2): 30 (1988); Radcl.-Sm., Gen. Euphorb.: 176 (2001).

Monoecious shrubs or trees; indumentum stellate. Leaves alternate or subopposite, clustered at ends of branches, subsessile, subentire, with sparse glands; petiole biglandular at apex; stipules entire, glandular at base, deciduous. Inflorescences terminal, spiciform, bisexual, with 1 or 2 proximal pistillate flowers and distal glomerules or spikelets of staminate flowers. Staminate flowers sessile; calyx splitting into mostly 3 or 4 valvate segments; petals and disk 0; stamens (5–)8–15, filaments distinct, inflexed in bud; anthers introse, minutely apiculate; pollen grains oblate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate; sexine tectate-perforate transitional to reticulate, with microverrucae at angles of lumina; pistillode clavate, pubescent. Pistillate flowers pedicellate; calyx involucrate, bracts glandular at base, deciduous; sepals 5 or 6, imbricate, entire, accrescent and persistent in fruit; ovary

3-locular, stellate-tomentose; ovules with inner integument thin, outer thick; stylodia bifid or unlobed, papillose-lacerate. Fruits capsular, valves thick and woody; columella ± persistent. Seeds roundish, ecarunculate, testa smooth.

Four spp., southeast Asia and Indonesia.

148. *Symphyllia* Baill.

Symphyllia Baill., Étude Gén. Euphorb.: 473 (1858); Gagnep., Fl. Indochine 5: 477, fig. 60, 10–12 (1926); Webster, Ann. Missouri Bot. Gard. 81: 78 (1994); Radcl.-Sm., Gen. Euphorb.: 177, fig. 21 (2001).

Monoecious trees or shrubs; indumentum stellate. Leaves eglandular; stipules glandular, deciduous. Inflorescences terminal or axillary, spiciform or paniculate, usually bisexual; bracts inconspicuous. Staminate flowers subsessile; calyx closed in bud, splitting into 3–6 valvate segments; petals and disk 0; stamens 3–6, mostly 4 or 5, filaments distinct, inflexed in bud; anthers muticous, 2-locellate; pollen grains prolate spheroidal, 3-colporaate, colpi inoperculate and emarginate, sexine tectate-peroratae, heterobrachate; pistillode +. Pistillate flowers subsessile, not involucrate; sepals 5–7, entire, valvate, persistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose; stylodia connate into a column longer than the ovary, bifid or twice bifid. Fruits capsular. Seeds smooth.

Three spp., eastern Asia: India to Hainan and Malaya. Croizat (1942) combined *Symphyllia* with *Epiprinus*, which was followed by Govaerts et al. (2000); however, it differs from that genus in its eglandular leaves and lack of a pistillate involucre. *Symphyllia* is therefore provisionally retained as a distinct genus.

149. *Cleidiocarpon* Airy Shaw

Cleidiocarpon Airy Shaw, Kew Bull. 19: 313 (1965), 32: 410 (1978); Thin, Tâp Chi Sinh Vât Hoc 10(2): 32 (1988); Webster, Ann. Missouri Bot. Gard. 81: 79 (1994); Radcliffe-Smith, Gen. Euphorb.: 179 (2001); Qiu Huaxing & Gilbert, Fl. China 11: 250 (2008).
Sinopimelodendron Tsiang (1973).

Monoecious trees; indumentum stellate. Leaves apically clustered on branches, eglandular; petiole stipellate at apex; stipules deciduous. Inflorescences terminal, spiciform-paniculate, bisexual or sometimes unisexual; bracts and prophylls conspicuous. Staminate flowers subsessile; sepals 4 or 5, valvate; petals and disk 0; stamens 4 or 5, filaments distinct, inflexed in bud; anthers introrse, 4-locellate; pollen grains prolate spheroidal, 3-colporate, colpi inoperculate and emarginate, sexine tectate-punctate; pistillode +. Pistillate flowers subsessile; sepals 4–8, valvate, entire, persistent in fruit; petals and disk 0; ovary 2-locular, stellate-tomentose; stylodia basally connate, distally distinct, multifid. Fruits indehiscent, drupaceous, rugose, beaked. Seed solitary, rugose.

Two spp. from northern Burma, China, western Thailand and Vietnam. Thin (1988) has proposed a new subtribe Cleidiocarpinae for it, and the genus is indeed unusual in the drupaceous fruit.

150. *Koilodepas* Hassk.

Koilodepas Hassk., Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139 (1856), Flora 40: 531 (1857, *Coelodepas*); Croizat, J. Arnold Arb. 23: 50 (1942); Airy Shaw, Kew Bull. 14: 382 (1960), Kew Bull. 36: 310 (1981); Radcl.-Sm., Gen. Euphorb.: 180, fig. 22 (2001).

Monoecious trees; indumentum stellate. Leaves entire or crenate-dentate, abaxially biglandular or with scattered glands; stipules ± dentate, persistent. Inflorescences axillary, spiciform, usually bisexual, with 1 or few proximal pistillate flowers and distal staminate or bisexual glomerules; bracts ovate, ± dentate apically, eglandular. Staminate flowers sessile; calyx closed in bud, splitting into 3 or 4 valvate segments; petals and disk 0; stamens 4–5(−8), filaments basally connate, dilated above the middle, anthers introrse, connective not enlarged, 2-locellate, locules divergent; pollen grains subspheroidal, 3-colporate, colpi narrow, inoperculate and emarginate; sexine tectate-punctate, psilate; pistillode +. Pistillate flowers sessile; sepals 4–10, basally connate, entire; persistent in fruit; petals and disk 0; ovary (2)3-locular, stellate-tomentose; ovules with thick integuments; stylodia bifid to multifid, ± laciniate. Fruits capsular; columella persistent, broadly winged. Seeds subglobose, testa smooth.

Eleven spp., distributed from India to Borneo and New Guinea. Airy Shaw (1960) proposed 2 sections, one (sect. *Hyalodepas* Airy Shaw) including 2 spp. with accrescent fruiting calyx suggestive of *Epiprinus*, and referring the other 9 spp. to sect. *Koilodepas*, with non-accrescent calyx.

151. *Cladogynos* Zipp. ex Span.

Cladogynos Zipp. ex Span., Linnaea 15: 349 (1841); Pax & K. Hoffm., Pflanzenr. 147, VII: 264, fig. 41 (1914); Gagnep., Fl. Indochine 5: 478, fig. 61 (1926); Airy Shaw, Kew Bull. 26: 232 (1972); Radcl.-Sm., Gen. Euphorb.: 182 (2001).

Monoecious shrubs; indumentum stellate. Leaves pinnately veined or triplinerved, double-dentate, peltate or subpeltate at base, eglandular; stipules minute, deciduous. Inflorescences axillary, bisexual, of 1 proximal pedicellate pistillate flower and a distal capitulum of staminate flowers. Staminate flowers sessile; petals and disk 0; stamens (3)4(5), filaments distinct, inflexed in bud; anthers introrse, muticous, locules; pollen grains 3-colporate, colpi narrow, sexine tectate-perforate; pistillode +. Pistillate flowers pedicellate; sepals 5–7, subfoliaceous, basally contracted, subentire, persistent in fruit; petals and disk 0; ovary 3(4)-locular, pubescent; ovules with inner integument thick, outer thin; stylodia basally connate, twice bifid or more, papillose. Fruits capsular, columella persistent, apically dilated. Seeds spheroidal, testa smooth.

A single sp., *C. orientalis* Zipp. ex Span., widespread in southeast Asia and Malesia.

152. *Cephalocroton* Hochst.

Cephalocroton Hochst., Flora 24: 370 (1841); Müll. Arg. in DC., Prodr. 15(2): 760 (1866); Pax, Pflanzenr. 147, II: 7, figs. 3, 4 (1910); Prain, Fl. Trop. Afr. 6(1): 843 (1912); Radcl.-Sm., Kew Bull. 28: 123 (1973); Fl. E. Trop. Afr. Euphorb. 1: 282, fig. 55 (1987); Gilbert, Kew Bull. 42: 365, fig. 6 (1987); Webster, Ann. Missouri Bot. Gard. 81: 79 (1994); Radcl.-Sm., Gen. Euphorb.: 183 (2001).
Adenochlaena Baill. (1858).
Cephalocrotonopsis Pax (1910).

Monoecious shrubs; indumentum stellate and glandular-setose. Leaves palmately veined or triplinerved, usually dentate, eglandular; stipules persistent, sometimes minute or obsolete. Inflorescences terminal (axillary), the staminate flowers in distal capitula, the pistillate flowers proximal, separated by a long internode. Staminate flowers pedicellate (sessile), articulate at base of calyx; sepals closed in bud, splitting into 3–6 valvate lobes; petals and disk 0; stamens (4–) 6–8(−10), filaments distinct, inflexed in bud; anthers dorsifixed, introrse, muticous, 2-locellate; pollen grains prolate spheroidal, 3-colporate, colpi narrow, inoperculate and emarginate, sexine tectate-perforate, muri microverrucate; pistillode 2- or 3-lobed. Pistillate flowers pedicellate, the pedicel usually greatly elongating in fruit; sepals 4–6, pinnately or bipinnately lobed (entire), persistent and accrescent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentose; ovules with inner integuments thicker than outer integuments; stylodia multifid. Fruits capsular, 3-lobed, glandular-verrucate; columella persistent, broadly winged. Seeds roundish, smooth or sparsely pubescent.

About seven spp. in tropical Africa, Madagascar, Socotra and Ceylon.

In Webster (1994), *Adenochlaena* and *Cephalocrotonopsis* were accepted as distinct genera. Radcliffe-Smith (2001) also accepts both genera, even though he earlier sank *Cephalocrotonopsis* into *Cephalocroton*. However, the pollen grains of these taxa are identical (Takahashi et al. 2000), and it now seems preferable to treat both *Adenochlaena* and *Cephalocrotonopsis* as sections of an enlarged genus *Cephalocroton*, distinguished by its unique inflorescence type.

10b. SUBTRIBE CEPHALOMAPPINAE G.L. Webster (1975).

A monotypic subtribe.

153. *Cephalomappa* Baill.

Cephalomappa Baill., Adansonia 11: 130 (1874); Pax, Pflanzenr. 147, II: 16. 1910; Airy Shaw, Kew Bull. 14: 378 (1960); Kosterm., Reinwardtia 5: 413 (1961); Backer & Backh., Fl. Java 1: 486 (1963); Whitmore, Tree Fl. Malaya 2: 75, fig. 4 (1973); Airy Shaw, Kew Bull. 36: 274 (1981); Widuri & van Welzen, Reinwardtia 11: 153, figs. 1–16 (1998); Radcl.-Sm., Gen. Euphorb.: 186, fig. 23 (2001).

Monoecious trees or shrubs; indumentum simple, stellate, and lepidote. Leaves entire to dentate, eglandular or sometimes with abaxial glands; petioles pulvinate; stipules deciduous. Inflorescences terminal or axillary, racemiform, sometimes compounded and corymbose; staminate flowers in pedunculate capitula, pistillate flowers 1–3 at proximal axils; bracts deciduous. Staminate flowers sessile; calyx turbinate, truncate, 2–5-lobed, lobes valvate; petals and disk 0; stamens (2)3–4, filaments connate into a column, tips inflexed in bud; anthers latrorse, connective glandular, muticous, 2-celled; pollen grains oblate spheroidal, 3-brevicolporate, sexine coarsely reticulate and muri spinulose; pistillode clavate, sometimes apically lobed. Pistillate flowers pedicellate; sepals 4–6(−8), imbricate, connate at base, deciduous; petals and disk 0; ovary 3-locular, stellate-tomentose or lepidote; ovules anatropous, inner integuments very thick, outer integuments thick; stylodia connate, tips bifid or palmately incised. Fruits capsular, verrucose, 3-lobed, lepidote. Seeds spheroidal, hilum ovate, testa smooth.

Five spp., southern China, Malay Peninsula, Sumatra and Borneo. The pollen of *Cephalomappa* is so distinctive that Takahashi et al. (2000) suggest the genus should be placed in a separate tribe. However, in other features it appears similar to genera of Epriprineae, and in the molecular analysis of Wurdack et al. (2005) it is resolved in a clade with *Koilodepas* and *Cephalocroton*.

10c. Subtribe Rockinghamiinae G.L. Webster (2004).

A monogeneric Australasian subtribe.

154. *Rockinghamia* Airy Shaw

Rockinghamia Airy Shaw, Kew Bull. 20: 29 (1966), 35: 667, fig. 6 (1980); Hyland & Whiffin, Austral. Trop. Rain For. Trees: 150 (1993); Radcl.-Sm., Gen. Euphorb.: 232 (2001).

Monoecious trees; indumentum simple, sparse. Leaves mostly opposite, often pseudo-verticillate at end of branches, entire or crenate, eglandular; petioles pulvinate; stipules deciduous. Inflorescences terminal (axillary), racemoid or paniculate, bisexual; bracts glandular, entire, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 4 valvate segments; petals 0; disk segments numerous, interstaminal, pubescent; stamens 25–50, filaments distinct; anthers 4-celled, muticous; pollen grains prolate spheroidal, 3-colpor(oid)ate, inoperculate and emarginate, endoapertures indistinct; sexine perforate-tectate to reticulate with narrow muri and deep lumina, sometimes heterobrochate; pistillode + or 0. Pistillate flowers pedicellate; sepals 5, imbricate, subentire, persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; ovules anatropous, inner integument thick, outer thin; stylodia distinct or basally connate, bifid or unlobed. Fruits capsular, 3-lobed, muricate; columella persistent, winged-dilated. Seeds roundish or oblong, hilum deltoid, testa smooth.

Two spp., tropical Australia (Queensland).

11. Tribe Chrozophoreae (Müll. Arg.) Pax & K. Hoffm. (1919).

Monoecious or dioecious trees, shrubs, or herbs; indumentum stellate, lepidote, malpighiaceous, or simple; leaves alternate, unlobed or lobed, entire or dentate, sometimes with laminar glands; stipules persistent or deciduous; inflorescences axillary or terminal, mostly racemoid or spicate; staminate flowers subsessile or pedicellate; calyx splitting into 3–5 valvate sepals; petals (0)4–5(10); disk dissected or 0; stamens 5–many, filaments distinct or connate; connectives generally not enlarged and thecae not pendulous; pollen grains mostly 3–6-colporate, colpi inoperculate, sexine reticulate and often distinctly heterobrochate; pistillode + or 0; pistillate flowers usually pedicellate; sepals 5 or 6, imbricate or valvate, usually entire, persistent in fruit; petals 5 (reduced or 0); disk annular or dissected (0); ovary (2)3-locular; stylodia unlobed to bifid or twice bifid, sometimes lacerate; fruit capsular; columella usually persistent; seeds ecarunculate.

With 11 genera and 125 species or more, tribe Chrozophoreae is widespread and diverse in warm temperate to tropical areas. As the tribal description indicates, the morphological diversity is extreme, and the molecular data of Wurdack et al. (2005) (still with incomplete sampling) point to placements in different clades of the acalyphoids: Ditaxinae as sister to Adelieae, and Speranskiinae and Chrozophorinae into a clade together with Epiprineae. Available data permit, however, the transfer of *Caperonia* from Speranskiinae to Ditaxinae, and to merge Doryxylinae with monotypic Chrozophorinae.

Key to the Subtribes of Chrozophoreae

1. Indumentum stellate; leaves with basal laminar glands **11c. Chrozophorinae**
– Indumentum simple or malpighiaceous, or if stellate then leaves without basal laminar glands 2
2. Inflorescence terminal; indumentum simple; stems not spinose; ovary muricate **11a. Speranskiinae**
– Inflorescence axillary; indumentum malpighiaceous or stellate (entirely simple and stems spinose in *Philyra*) **11b. Ditaxinae**

11a. Subtribe Speranskiinae G.L. Webster (1975).

Monoecious herbs; indumentum simple; leaves glandular-dentate; inflorescences terminal, spiciform; sepals and petals usually 5 in both sexes; stamens 10–15, filaments distinct; pollen grains 3-colporate; pistillate flowers pedicellate or subsessile; disk cupular or 0; ovary usually muricate; inner and outer ovular integuments thin; stylodia distinct, branches lacerate; seed coat dry.

A monogeneric Asian subtribe.

155. ***Speranskia*** Baill.

Speranskia Baill., Étude Gén. Euphorb.: 388 (1858); Pax & K. Hoffmann, Pflanzenr. 147,VI: 14, fig. 3 (1912); Hwang Shu-mei, Bull. Bot. Res. Harbin 9 (4): 37–40 (1989); Radcl.-Sm., Gen. Euphorb.: 138 (2001); Qiu Huaxing & Gilbert, Fl. China 11: 223 (2008).

Monoecious perennial herbs; indumentum simple. Leaves petiolate or sessile, glandular-dentate, without laminar glands, stipellate at base; stipules deciduous or persistent. Inflorescences terminal, spiciform; proximal cymules bisexual or pistillate, distal staminate; bracts eglandular, persistent. Staminate flowers pedicellate; calyx splitting into 5 valvate sepals; petals 5; disk segments 5; stamens 10–15, filaments distinct; anthers in 2 (3) whorls, dorsifixed, extrorse; pollen grains subprolate, 3-colporate, colpi operculate, endoaperture lalongate, exine tectate-punctate to tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, lanceolate, entire, deciduous or persistent; petals 5 or 0; disk cupular; ovary 3-locular, verruculose or tuberculate; inner and outer integuments thin; stylodia distinct, bifid, branches lacerate. Fruits capsular, 3-lobed; columella deciduous or persistent. Seeds globose, testa smooth or foveolate to rugulose.

Two spp., endemic to China.

11b. Subtribe Ditaxinae Griseb. (1859).

Monoecious (dioecious) trees, shrubs, or herbs; indumentum simple, glandular, stellate or malpighiaceous; leaves entire or serrate, stipulate; inflorescences axillary, racemoid or glomerulate; staminate sepals mostly 4 or 5; petals 5, distinct or adnate to staminal column; disk dissected, reduced, or 0; stamens 4–15, filaments connate (almost distinct); anthers introrse, pollen grains 3–4-colporate; pistillode + or 0; pistillate flowers sessile or pedicellate; sepals 5 (6), distinct, imbricate; petals 5 or 0; disk dissected or 0; ovary 3-locular, smooth or muricate; stylodia bifid to laciniate; seeds with dry testa, smooth or ornamented.

As here delimited, subtribe Ditaxinae includes 5 mostly neotropical genera with 110–115 species.

Key to the Genera of Ditaxinae

1. Leaves finely serrate with straight parallel lateral nerves; disk 0; pollen 3–6-colporate; pistillode +; stylodia dissected **160. *Caperonia***
– Leaves not as above; disk +, at least in staminate flowers; pollen 3–4-colporate; pistillode 0 or scarcely developed; stylodia bifid to dissected 2
2. Dioecious; tepals scarious; shrubs or trees, branches often spiny **156. *Philyra***
– Monoecious; tepals not scarious; undershrubs or herbs, not spiny 3
3. Petals 3–7-lobed or -partite; stylodia once bifid; stellate hairs sometimes present; pollen grains 3-colporate **159. *Chiropetalum***
– Petals entire; stylodia twice bifid to multifid; stellate hairs 0 4
4. Stamens 8–10, anthers in 2 whorls; pollen grains mainly 3-colporate, bilaterally symmetrical **158. *Ditaxis***
– Stamens 4 or 5, anthers in 1 whorl; pollen grains stephanocolporate, not bilaterally symmetrical **157. *Argythamnia***

156. ***Philyra*** Klotzsch

Philyra Klotzsch, Arch. Naturgesch. 7(1): 199 (1841); Pax & K. Hoffm., Pflanzenr. 147,VI: 49, fig. 10 (1912); O'Donell & Lourteig, Lilloa 8: 60 (1942); Radcl.-Sm., Gen. Euphorb.: 141 (2001).
Argythamnia sect. *Philyra* (Klotzsch) Müll. Arg. (1865).

Dioecious trees or shrubs; indumentum 0 except for simple hairs on inflorescences. Leaves alternate; stipules persistent, indurate, often associated with long infrastipular spines. Inflorescences axillary, brachyblastic, or the pistillate flowers on expanded tenuous racemes; bracts indurate, persistent. Staminate flowers pedicellate; sepals 3–5, fused in bud, splitting into valvate segments; petals 5, distinct; disk segments 5, adnate to staminal column; stamens (8) 10, filaments connate below into a column; anthers in 2 superposed whorls, extrorse; pollen grains prolate spheroidal to subprolate, 3-colporate, colpi exoperculate and emarginate, endoaperture circular; sexine tectate-punctate; pistillode trifid, at apex of staminal column. Pistillate flowers long-pedicellate; sepals 5, linear-lanceolate, entire, persistent in fruit; petals 5, longer than sepals; disk thickened as gynophore; ovary 3-locular; ovules with inner integument moderately thick, outer thin; stylodia bifid, branches multifid or lobed. Fruits capsular; columella persistent, trifid at apex. Seeds globose; testa smooth.

A single sp., *P. brasiliensis* Klotzsch, from Argentina and Paraguay to northeastern Brazil (Bahia), in deciduous or semi-deciduous tropical woodlands. Although appearing in a clade with three adelioid genera (Wurdack et al. 2005), this petaloid genus differs significantly from them, and the pollen is very distinct.

157. ***Argythamnia*** P. Browne

Argythamnia P. Browne, Civ. Nat. Hist. Jamaica: 338 (1756); Ingram, Gentes Herb. 10(1): 1, figs. 3–19 (1967); Correll, Fl. Bahama Arch. 777, fig. 325 (1982); Howard, Fl. Lesser Ant. 5: 14, fig. 5 (1989); Webster, Ann. Missouri Bot. Gard. 81: 72 (1994); L.J. Gillespie, Fl. St. John 203 (1996); Radcl.-Sm., Gen. Euphorb.: 143 (2001).

Monoecious (dioecious) shrubs or subshrubs; indumentum malpighiaceous. Leaves entire or denticulate, pinnately veined (triplinerved), with steeply ascending laterals; stipules entire, ± persistent. Inflorescences axillary, glomerular or racemiform, pistillate flowers proximal and staminate distal in bisexual inflorescences; bracts 1-flowered, persistent. Staminate flowers subsessile; sepals connate in bud, dehiscing into 4(5) valvate segments; petals 4(5), shorter than sepals, imbricate, entire; disk segments 4(5), adnate to base of staminal column; stamens 4–6, filaments connate at the base, sometimes forming a short column; anthers introrse; pollen grains 4-colporate, colpi inoperculate, sexine tectate-perforate; pistillode rudimentary. Pistillate flowers subsessile; sepals 5(6), distinct, valvate, entire, persistent in fruit; petals 5, distinct, entire, often reduced or rudimentary; disk divided into 5 segments; ovary 3-locular; ovules with inner and outer integuments thin; stylodia bifid or twice bifid. Fruits capsular; columella persistent. Seeds round, testa dry, roughened (alveolate).

About 18 spp., most of which occur in the West Indies, and 8 from S Mexico to Honduras.

158. ***Ditaxis*** Vahl ex A. Juss.

Ditaxis Vahl ex A. Juss., Euphorb. Tent.: 27 (1824); O'Donell & Lourteig, Lilloa 8: 62, figs. 5–10, t. I, III–VII (1942); Wiggins, Fl. Sonoran Desert: 784 (1964); Webster, Jepson Man. Pl. Calif.: 572 (1993); Diggs et al., Fl. North Central Texas: 600 (1999); Radcl.-Sm., Gen. Euphorb.: 142 (2001).
Argythamnia sect. *Ditaxis* (P. Browne) Müll. Arg. (1865).

Monoecious (dioecious) shrubs, perennial herbs, and annual herbs; indumentum malpighiaceous. Leaves entire or dentate, pinnately veined (triplinerved), often with steeply ascending laterals; stipules entire, persistent. Inflorescences axillary, glomerular or racemiform, typically bisexual. Staminate flowers pedicellate; sepals connate, separating into usually 5 segments at anthesis; petals 5, imbricate, distinct but each petal unguiculate and adnate to base of staminal column; stamens (7–)10, filaments connate into a column; anthers biseriate, introrse, dehiscing vertically; pollen grains ± oblate, asymmetrically 3-colporate; colpi inoperculate; sexine tectate-punctate (superreticulate); pistillode at apex of staminal column, divided (0). Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire or denticulate, persistent in fruit; petals 5, imbricate, entire, often persistent in fruit; disk segments 5, often confluent; ovary 3-locular; glabrous or pubescent; ovules with inner integument moderately thick, outer thin; stylodia bifid, branches sometimes emarginate or shortly bifid. Fruits capsular; columella persistent, 3-pronged. Seeds smooth to rugose or foveolate.

About 40–50 spp. ranging from the USA south to Argentina, primarily in subarid regions. The distinct pollen grains furnish the best diagnostic character (Takahashi et al. 1995; Nowicke et al. 1999).

159. ***Chiropetalum*** A. Juss.

Chiropetalum A. Juss., Ann. Sci. Nat. (Paris) 25: 21 (1832); O'Donell & Lourteig, Lilloa 8: 38, figs. 1–3, t. II (1942); Ingram, Gentes Herb. 11(7): 437, figs. 4–9 (1980); L.B. Smith et al., Fl. Ilustr. Catar. EUFO: 154 (1988); Radcl.-Sm., Gen. Euphorb.: 144 (2001).
Argythamnia subg. *Chiropetalum* (A. Juss.) Ingram (1980).

Monoecious shrubs or subshrubs; indumentum malpighiaceous, sometimes also simple or stellate. Leaves alternate, serrate (entire), 3–5-veined from base; stipules entire, persistent. Inflorescences axillary, racemiform, pistillate flowers proximal, staminate flowers distal; bracts 1-flowered, persistent. Staminate flower pedicellate; sepals connate in bud, dehiscing into 5 valvate segments; petals 5, distinct, imbricate, unguiculate, 3–7-lobed or -partite; disk segments 5; stamens 5 (6), filaments connate into a column; anthers stipitate atop column; pollen grains spheroidal to prolate spheroidal, 3-colpate, colpi operculate, emarginate; exine finely tectate; pistillode rudimentary. Pistillate flower pedicellate; sepals 5, valvate, entire, persistent in fruit; petals 5, shorter than sepals, entire (lobed), sometimes obsolete; disk segmented into 5 lobes; ovary 3-locular; ovules with inner and outer integuments thin; stylodia distinct or basally connate, bifid. Fruits capsular; columella persistent. Seeds spheroidal; testa rugose.

About 22 spp., 2 in Mexico and 20 in South America: Peru and Chile to S Brazil. Nowicke et al. (1999) point out that the 3-colpate operculate pollen grains of *Chiropetalum* are very different from the 4-colporate inoperculate grains of *Argythamnia*, contradicting the merging of the two genera by Ingram (1967).

160. *Caperonia* St. Hil.

Caperonia St. Hil., Pl. Remarq. Brésil: 244 (1826); Fawc. & Rendle, Fl. Jam. 4: 288, fig. 93 (1920); O'Donell & Lourteig, Lilloa 8: 54, fig. 4 (1942); Léonard, Fl. Congo 8(1): 166, t. 11 (1962); Webster, J. Arnold Arb. 48: 363 (1967), Ann. Missouri Bot. Gard. 54: 265, fig. 10 (1968); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 163, fig. 29 (1987); Webster, Fl. Venez. Guayana 5: 102, fig. 100 (1999), Fl. Nicaragua: 856 (2001); Radcl.-Sm., Gen. Euphorb.: 140 (2001).

Monoecious annual or perennial herbs, sometimes rhizomatous or fruticose, stems often hollow; indumentum simple, sometimes prickly or glandular. Leaves alternate, serrate, pinnately and strikingly parallel-veined; stipules scarious, persistent. Inflorescences axillary, spiciform, usually bisexual, with 1–5 basal pistillate flowers; bracts entire, persistent, subtending solitary flowers. Staminate flowers with articulate pedicels; calyx of 5 valvate lobes fused in bud; petals 5, often unequal, basally adnate to the staminal column; disk 0; stamens 10, filaments partly connate into a column, anthers in 2 superposed whorls; pollen grains subspheroidal, 3- or 6-colporate, colpi operculate, emarginate, endoapertures obscure, germ pores large, sexine tectate-punctate to -reticulate; pistillode at apex of staminal column. Pistillate flowers subsessile; calyx deeply 5-lobed, with 0–5 smaller supernumerary lobes, persistent in fruit; petals 5, often unequal or reduced; disk 0; ovary 3-locular, usually muricate; ovules anatropous, inner and outer integuments thin; stylodia distinct, laciniate. Fruit capsular, valves thin, usually verrucose; columella persistent, apically dilated. Seeds globose; testa minutely foveolate. $n = 11$.

About 35 spp., mostly American, but a few spp. in Africa and Madagascar, widely spread in marshy habitats.

11c. SUBTRIBE CHROZOPHORINAE Müll. Arg. (1865).

Doryxylinae G.L. Webster (1975).

Monoecious trees, shrubs or herbs; indumentum stellate or lepidote; leaves with laminar glands; inflorescences terminal or axillary, usually bisexual; staminate sepals 3–5; petals 5–10 or 0; disk reduced or 0; stamens (4–)30–250, distinct or partially connate; pollen grains 3(6–9)-colporate, angulaperturate, sexine reticulate; pistillate sepals 5–6, imbricate or valvate, petals rudimentary or 0; disk annular or obsolete; ovary 2–3-locular; stylodia bifid or unlobed; seeds with fleshy exotesta, foveolate endotesta.

An Old World, mainly Asiatic, subtribe of 5 genera.

KEY TO THE GENERA OF CHROZOPHORINAE

1. Petals 0; ovary usually 2-locular; stamens 200 or more **164. *Melanolepis***
– Petals +; ovary 3-locular; stamens 4–100 2
2. Stamens connate; pollen grains stephanocolporate; herbs or subshrubs **165. *Chrozophora***
– Stamens distinct [except in *Thyrsanthera*]; pollen grains 3-colporate; shrubs or trees 3
3. Inflorescences axillary; stylodia unlobed, basally connate; stamens distinct **161. *Doryxylon***
– Inflorescences terminal; stylodia bifid, ± distinct 4
4. Stamens distinct; staminate disk 0; pistillate sepals imbricate **162. *Sumbaviopsis***
– Stamens connate; staminate disk +; pistillate sepals valvate **163. *Thyrsanthera***

161. *Doryxylon* Zoll.

Doryxylon Zoll., Tijdschr. Ned.-Indië 14: 172 (1857); N.P. Balakr., Bull. Bot. Surv. India 9: 56, figs. 1–7 (1967); Webster, Ann. Missouri Bot. Gard. 81: 72 (1994); van Welzen, Blumea 44: 422, fig. 3 (1999).

Monoecious trees or shrubs; twigs often with axillary spines; indumentum simple and stellate. Leaves palmately veined, dentate, whitish-tomentose abaxially; stipules minute, deciduous. Inflorescences terminal, racemoid, often unisexual; bracts uniflorous. Staminate flowers pedicellate or subsessile; sepals 5, valvate; petals 5, shorter than sepals; disk 0; stamens 30–130, filaments distinct, inserted on hairy receptacle; anthers dorsifixed, latrorse; pollen grains oblate spheroidal, angulaperturate, 3-colporate, colpi inoperculate and emarginate, sexine reticulate, heterobrochate; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, imbricate, entire; petals 0; disk annular, glabrous; ovary 3(4)-locular, tomentose; stylodia unlobed, connate below. Fruits capsular; columella persistent. Seeds with fleshy exotesta, foveolate endotesta.

A single Malesian sp., *D. spinescens* Zoll., from the Philippines and Lesser Sunda Islands.

162. *Sumbaviopsis* J.J. Sm.

Sumbaviopsis J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10: 356 (1910); Airy Shaw, Kew Bull. Add. Ser. 4: 197 (1975); van Welzen, Blumea 44: 426, fig. 4 (1999); Radcl.-Sm., Gen. Euphorb.: 148, fig. 13 (2001).

Monoecious trees or shrubs; indumentum mainly stellate. Leaves peltate, palmately veined or triplinerved, subentire or dentate, densely stellate-tomentose abaxially, with small embedded glands; stipules deciduous. Inflorescences terminal (pseudo-axillary), unisexual, staminate thyrsoid, pistillate racemoid; bracts subtending 1–3 staminate flowers or solitary pistillate flowers. Staminate flowers pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 4 or 5, shorter than sepals; disk represented by a convex pubescent torus; stamens 35–45(−75?), inserted on torus, filaments distinct; anthers basifixed, introrse; pollen grains suboblate, 3-colporate, colpi inoperculate, emarginate; sexine coarsely reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5(6), imbricate, entire, persistent in fruit; petals 0; ovary 2- or 3-locular, tomentose; ovules anatropous; stylodia distinct or nearly so, bifid. Fruits capsular, valves laterally corrugated; columella persistent, apically dilated. Seeds spheroidal, exotesta fleshy, endotesta smooth.

A single sp., *S. albicans* (Blume) J.J. Sm., distributed from Thailand and Laos to Java, Borneo, and Palawan.

163. *Thyrsanthera* Pierre ex Gagnep.

Thyrsanthera Pierre ex Gagnep., Bull. Soc. Bot. France 71: 878 (1924); Gagnep., Fl. Indochine 5: 299, figs. 32, 33 (1925); Backer & Backh., Fl. Java 1: 477 (1963); van Welzen, Blumea 44: 431, fig. 5 (1999); Radcl.-Sm., Gen. Euphorb.: 148, fig. 14 (2001).

Monoecious shrubs; indumentum stellate. Leaves palmately veined, entire, at margin with reddish indumentum, stipellar abaxially at junction with petiole; stipules deciduous. Inflorescences terminal, racemoid, bisexual, pistillate flowers proximal; bracts pubescent, 1-flowered (?). Staminate flowers pedicellate; sepals 5, valvate, tomentose abaxially; petals 5, imbricate; disk 0; stamens 40–60, filaments connate into a column; anthers stipitate, basifixed, latrorse; pollen grains suboblate, 3-colporate, exine reticulate; pistillode 0. Pistillate flowers sessile or subsessile; sepals 5, narrow, entire, valvate; disk annular; ovary 3-locular, tomentose; stylodia distinct, unlobed, papillose. Fruits capsular, thin-walled; columella slender, persistent, apically 3-angled. Seeds obovoid, angular, with thin fleshy exotesta, mesotesta vascularized.

A single sp., *Th. suborbicularis* Pierre ex Gagnep., recorded only from Thailand and Cambodia.

164. *Melanolepis* Rchb. f. & Zoll.

Melanolepis Rchb. f. & Zoll., Verh. Natuurk. Ver. Ned. Ind. 1: 22 (1856); Gagnep., Fl. Indochine 5: 347 (1925); Airy Shaw, Kew Bull. Add. Ser. 8: 174, t. 5 fig. 3 (1980); van Welzen, Blumea 44: 438, fig. 1 (1999).

Dioecious trees or shrubs; indumentum mainly stellate or dendritic. Leaves long-petiolate, deltoid, palmately veined, coarsely dentate, often 3-lobed, with raised glandular area at junction with petiole; stipules inconspicuous, deciduous. Inflorescences terminal, paniculate with 2 or 3 elongated racemoid or spiciform axes, usually unisexual; bracts entire, subtending several staminate flowers or 1(2) pistillate flower. Staminate flowers pedicellate; sepals (4)5, valvate; petals 0; disk 0; stamens 200–250, filaments distinct, inserted on convex receptacle; anthers introrse, with glandular connective; pollen grains suboblate, angulaperturate, 3-colporate, colpi inoperculate but with granular membranes, emarginate, endoaperture ovate to lalongate, exine tectate-punctate to reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 5, basally connate, valvate, entire, persistent in fruit; petals 0; disk annular; ovary 2–3-locular, tomentose; ovules anatropous; stylodia unlobed or emarginate. Fruits capsular; leathery, valves and columella ± persistent. Seeds roundish, with thin sarcotesta, foveolate endotesta.

Two Asiatic spp., one endemic to Cambodia, the other distributed from Thailand to Malesia and the Pacific islands (Ryukyus, Micronesia).

165. *Chrozophora* Necker ex A. Juss. Fig. 32

Chrozophora Necker ex A. Juss., Euphorb. Tent.: 27 (1824, nom. cons.); Prain, Kew Bull. Misc. Inf. 1918: 49 (1918); Pojark., Fl. SSSR 14: 288, t. 17, 1–4 (1949); Vindt, Monogr. Euphorb. Maroc. 10, t. 6 (1953); Rech. f. & Schiman-Czeika, Fl. Iranica 6: 5 (1964); Zohary, Fl. Palaestina 2: 266, t. 384–387 (1972); Radcl.-Sm., Fl. Iraq 4(1): 318, t. 59 (1980), Fl. Zambesiaca 9(4): 141, t. 26 (1996); van Welzen, Blumea 44: 418, fig. 2 (1999).

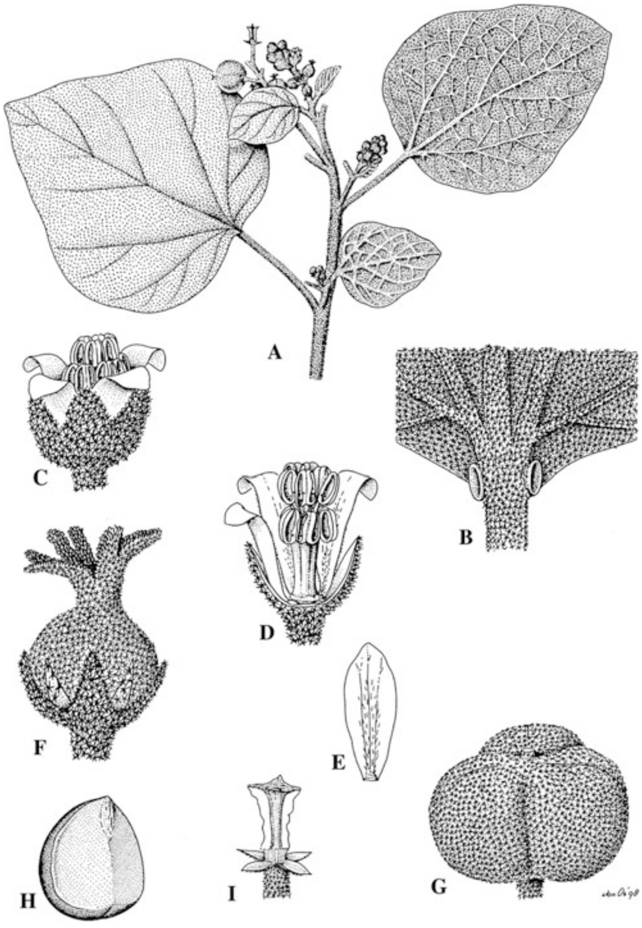

Fig. 32. Euphorbiaceae-Acalyphoideae. *Chrozophora rottleri*. **A** Flowering/fruiting branchlet. **B** Abaxial side of leaf base with extrafloral nectaries. **C, D** Staminate flower. **E** Staminate petal. **F** Pistillate flower. **G** Fruit. **H** Seed. **I** Fruit column after dehiscence. (van Welzen 1999; drawn by J. van Os)

Monoecious herbs or subshrubs; indumentum stellate or lepidote. Leaves subentire or crenate, ± palmately veined, with paired sessile patelliform glands near junction with petiole; stipules deciduous or persistent. Inflorescences terminal or pseudo-lateral, bisexual, racemiform; pistillate flowers proximal, staminate flowers distal; bracts subtending solitary flowers. Staminate flowers subsessile; calyx dehiscing into 5 valvate lobes; petals 5; disk segments 5; stamens 4–16, filaments connate into a column; anthers in 1–3 superposed series, extrorse; pollen grains oblate, 6–9-colporate, colpi short, inoperculate and emarginate, sexine coarsely reticulate, sometimes heterobrochate; pistillode 0. Pistillate flowers pedicellate; sepals and petals 5, narrow, entire, persistent in fruit; disk annular; ovary 3-locular, smooth or muricate, with stellate or lepidote hairs; ovules anatropous; stylodia distinct except at base, bifid. Fruits capsular, valves thin; columella persistent. Seeds ovoid to subglobose, ecarunculate, with thin fleshy sarcotesta, mesotesta vascularized. $n = 11, 22$.

About 10 spp., central and southern Asia, southern Europe to East Africa. The genus appears very different in habit from the other genera of the subtribe, but resembles them by characters of indumentum and seeds, and in the molecular analysis of Wurdack et al. (2005) is resolved in the same clade. The ovules of *Chrozophora* have thin inner and outer integuments, as opposed to the much thicker inner and outer integuments of the remaining genera of the subtribe (Tokuoka and Tobe 2003).

12. Tribe Adelieae G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; indumentum simple or stellate; leaves alternate, simple; lamina pinnately or palmately veined, entire or dentate, eglandular; stipules small; flowers in axillary glomerules or racemes; staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk annular or obsolete; stamens 8–18(–30), filaments distinct or connate at base; anthers introrse, muticous, versatile; pollen grains 3(4)-colporate, ± spheroidal, colpi emarginate, operculate, opercula stratified; sexine tectate-perforate or reticulate, microverrucate, the sculpture crotonoid; pistillode usually +; pistillate flowers pedicellate; sepals 5 or 6, valvate or open at anthesis, persistent in fruit; petals 0; disk annular; ovary 3-locular, pubescent; ovules with inner integuments thick, outer thin to thick; stylodia bifid to multifid; fruits capsular; columella persistent, apically 3-pronged; seeds roundish, ecarunculate, exotegmic, testa smooth.

This American tribe is here expanded to include *Garciadelia*. *Crotonogynopsis* and *Enriquebeltrania*, which were added by Webster (1994) and Radcliffe-Smith (2001), are excluded and treated as unplaced core acalyphoid genera.

Key to the Genera of Adelieae

1. Indumentum simple; stipules deciduous; stylodia lacerate **166.** ***Adelia***
– Indumentum stellate or stellate-lepidote; stipules 0; stylodia bifid to lacerate 2

2. Pistillate disk 0; stylodia aplanate, undivided, apically incised **169. *Garciadelia***
– Pistillate disk conspicuous; stylodia usually not aplanate, bifid or lacerate 3
3. Pistillate disk entire; stylodia bifid or subentire; filaments distinct; pollen 3-colporate; leaves triplinerved, indumentum stellate **167. *Lasiocroton***
– Pistillate disk lobed; stylodia lacerate; filaments ± connate; pollen grains 4-colporate; leaves pinnately veined, indumentum stellate-lepidote **168. *Leucocroton***

166. *Adelia* L.

Adelia L., Syst. Nat. ed. 10, 2: 1298 (1759, nom. cons.); Lourteig & O'Donell, Lilloa 8: 285, fig. 3 (1942); Webster, Ann. Missouri Bot. Gard. 54: 272, fig. 11 (1968); De-Nova, Sosa & Steinmann, Syst. Bot. 32: 583–595 (2007), rev.

Dioecious trees or shrubs; indumentum simple; twigs often spinescent. Leaves often clustered on short shoots, entire or sometimes crenate, beneath domatiiferous; stipules minute, deciduous. Inflorescences axillary, glomerulate; bracts persistent. Staminate flowers pedicellate; sepals 4 or 5, valvate; petals 0; disk annular or 5-lobed, fleshy; stamens 6–30, filaments basally connate; anthers versatile, muticous; pollen grains ± spheroidal, angulaperturate, 3–4-colp(oroid)ate, colpi operculate, operculum fusiform, sexine tectate-perforate, microverrucate; pistillode minute, trifid. Pistillate flowers long-pedicellate; sepals 5–7, narrow, persistent and ± reflexed in fruit; petals 0; disk annular, pubescent; ovary (2)3(4)-locular, pubescent; stylodia 3, multifid-lacerate. Fruits capsular; columella persistent, apically 3-pronged. Seeds spheroidal to oblate, testa smooth.

Nine spp., ranging from North America (N Texas) through Mexico and the Greater and Lesser Antilles to South America (Bolivia/Argentina).

167. *Lasiocroton* Griseb.

Lasiocroton Griseb., Fl. Brit. W. Ind.: 46 (1859), Abh. Königl. Ges. Wiss. Göttingen 9: 20 (1861); Fawc. & Rend., Fl. Jamaica 4: 293, fig. 96 (1920); Alain, Fl. Cuba 3: 87 (1953); Correll & Correll, Fl. Bah. Arch.: 825, fig. 342 (1982); Radcl.-Sm., Gen. Euphorb.: 189 (2001).

Dioecious shrubs; indumentum simple and stellate. Leaves triplinerved or palmately veined, entire; stipules 0. Inflorescences axillary, racemose; staminate flowers in glomerules, pistillate flowers 1 per bract. Staminate flowers pedicellate; calyx closed in bud, splitting into 5 valvate segments; petals 0; disk annular; stamens 7–18, filaments distinct, purplish, pubescent; anthers introrse, versatile, muticous; pollen grains oblate spheroidal, 3-colpate, colpi operculate; sexine tectate-perforate, microverrucate; pistillode minute or 0. Pistillate flowers pedicellate, mid-articulate; sepals 5, aestivation open, persistent in fruit; disk annular-pulvinate, tomentose; ovary 3(4)-locular, pubescent; stylodia bifid or unlobed, tips ± laciniate. Fruits capsular; columella persistent, slender, apically trifid. Seeds roundish, testa smooth.

Six spp., Greater Antilles and Bahamas.

168. *Leucocroton* Griseb.

Leucocroton Griseb., Mem. Amer. Acad. Sci. 8: 160 (1860), Abh. Ges. Wiss. Göttingen 9: 20 (1861); Borhidi, Acta Bot. Acad. Hungar. 36: 13, figs. 1–16 (1990); Jestrow et al., Taxon 59: 1801–1814 (2010).

Dioecious (monoecious) shrubs; indumentum stellate or stellate-lepidote. Leaves pinnately veined or triplinerved, eglandular; stipules 0. Inflorescences axillary, pedunculate, staminate flowers in glomerules on spiciform thyrses, pistillate flowers solitary or paired on shorter bracteate axes; bracts prominent. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk annular or lobed; stamens (5–)7–15(−28), filaments distinct or basally connate; anthers introrse, muticous; pollen grains prolate-spheroidal, 3-colpate, colpi operculate, sexine tectate-perforate, microverrucate; pistillode pubescent. Pistillate flowers pedicellate; sepals 5 or 6, persistent in fruit; disk massive, annular or lobed, pubescent; ovary 2–3-locular, stellate-pubescent; ovules with inner integuments thick, outer thin; stylodia plicate, multifid. Fruits capsular, columella slender, 3-pronged, persistent. Seeds roundish, testa smooth.

About twenty-six spp., all endemic to Cuba where it grows exclusively in serpentine-rich areas. The genus is unique insofar that all spp. have the ability for hyperaccumulation of nickel, having radiated along the fragmented patches of serpentine soils across the island (Jestrow et al. 2010).

169. *Garciadelia* Jestrow & Jiménez Rodr.

Garciadelia Jestrow & Jiménez Rodr., Taxon 59: 1809 (2010).

Dioecious treelets or shrubs; indumentum stellate. Leaves cordate, eglandular; stipules 0. Inflorescences axillary, the staminate subpaniculate, the pistillate racemes. Staminate flowers 5-merous, sepals triangular, valvate; petals 0; stamens twice the number of sepals; anthers dorsifixed; disk weakly lobed; pistillate flowers with perianth as in males; disk 0; ovary 3-locular; stylodia 3, aplanate, undivided but apically incised. Fruit a 3-lobed schizocarp, covered with stellate trichomes. Seeds orbicular.

Four spp., endemic to Hispaniola.

13. TRIBE BERNARDIEAE G.L. Webster (1975).

Monoecious or dioecious shrubs or herbs; indumentum simple or stellate; leaves alternate, entire, often with laminar glands; stipules deciduous; inflorescences terminal to axillary, racemiform or spiciform; flowers pedicellate, the staminate several per bract, the pistillate solitary; staminate calyx closed in bud, splitting into 3–4 valvate segments; petals 0; disk intrastaminal, pulviniform, dissected or obsolete; stamens 3–60, filaments distinct; anthers sometimes appearing 4-locellate; connective sometimes apiculate; pollen grains subspheroidal, 3-lobed, 3-colporate, colpi inoperculate, sexine perforate-tectate; pistillode rudimentary or 0; pistillate sepals 4–6, imbricate; disk annular or dissected; ovary 3-locular, ovules with thick inner and thin outer integuments; stylodia bifid, the branches sometimes lacerate; fruit capsular; seeds roundish, carunculate or ecarunculate, exotegmic, testa smooth.

The circumscription of this tribe is still problematic: in the molecular analysis (Wurdack et al. 2005) *Bernardia* and *Adenophaedra* are resolved with *Caryodendron* in a sister position to Plukenetieae, whereas *Discocleidion*, differing, i.a., in a vascularized outer integument, appears (without support) in a clade with *Ricinus* and *Speranskia*.

KEY TO THE GENERA OF BERNARDIEAE

1. Leaf blades stipellate, palmately veined; seeds carunculate, testa rugose **172. *Discocleidion***
– Leaf blades not stipellate, pinnately veined; seeds ecarunculate, testa smooth 2
2. Stylodia bifid or trifid; staminate disk of interstaminal segments; seeds carinate; stamens (3)4–25; leaf blades usually with abaxial embedded glands **170. *Bernardia***
– Stylodia unlobed and dilated; staminate disk 0; seeds not carinate; stamens 2(3); leaf blades lacking abaxial glands **171. *Adenophaedra***

170. *Bernardia* Houston ex Mill.

Bernardia Houston ex Mill., Gard. Dict. abr. edn (1754); Fawc. & Rend., Fl. Jam. 4: 290, fig. 94 (1920); Lourteig & O'Donell, Lilloa 8: 275, figs. 1, 2 (1942); Allem, Rev. Brasil. Biol. 39: 529, figs. 1–9 (1979); Correll, Fl. Bahama Arch. 781, fig. 327 (1982); Liogier, Fl. Española 4: 85, t. 116–7 (1986); Webster, Fl. Venez. Guayana 5: 101, fig. 99 (1999).
Traganthus Klotzsch (1841).

Monoecious or dioecious shrubs or subshrubs (herbs); indumentum of simple or fasciculate hairs. Leaves often with basal embedded glands, usually dentate; stipules small, persistent. Inflorescences axillary, [pistillate ones sometimes pseudo-terminal], spiciform or racemose; bracts eglandular. Staminate flowers sessile or pedicellate; calyx splitting into 3 or 4 valvate lobes; petals 0; disk of many interstaminal pubescent segments; stamens (2–)5–20(−45), filaments distinct; anthers 4-locellate, introrse to latrorse, connective emarginate to enlarged; pollen grains 3-lobed, 3-colporate, colpi marginate and inoperculate; endoaperture lalongate, sexine tectate-perforate; pistillode rudimentary or 0. Pistillate flowers sessile or subsessile; sepals 4–6, imbricate, entire, ± persistent in fruit; petals 0; disk annular or dissected; ovary 3-locular, pubescent; ovules pachychalazal, inner integument thick, outer thin; stylodia bifid to flabellate. Fruits capsular (indehiscent), 3-angled or -lobed; collumella slender, persistent. Seeds roundish, distinctly carinate, ecarunculate, testa smooth or rugulose; endosperm copious; cotyledons longer and broader than receptacle. $n = 26$.

A genus of over 50 spp., mostly neotropical, one sp. in southwestern USA. Govaerts et al. (2000) list 68 species, some of which may be synonyms. The genus is variable in both vegetative and floral characteristics; Pax & Hoffmann (1914) recognized 7 sections. Section *Traganthus* is distinctive in its herbaceous habit, but has the pollen and seed morphology of other sections; its recognition as a genus would clearly make *Bernardia* excessively paraphyletic.

171. *Adenophaedra* (Müll. Arg.) Müll. Arg.

Adenophaedra (Müll. Arg.) Müll. Arg., Fl. Brasil. 11(2): 385, t. 101 (1874); Pax & K. Hoffm., Pflanzenr. 147, VII: 261 (1914); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1099 (1988).
Bernardia sect. *Adenophaedra* Müll. Arg. (1865).

Dioecious trees or shrubs; indumentum simple. Leaves dentate, abaxial laminar glands + or 0;

stipules deciduous. Inflorescences axillary or the pistillate sometimes appearing terminal, spiciform, the staminate sometimes fasciculate or paniculate-clustered; bracts eglandular. Staminate flowers pedicellate; calyx splitting into 3 valvate lobes; petals and disk 0; stamens 2 (3); anthers longer than filaments, introrse, connective enlarged; pollen grains prolate spheroidal, 3-lobed, 3-colporate, colpi marginate and inoperculate, endoaperture lalongate; sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 6, biseriate, imbricate, ± persistent in fruit; petals 0; disk 3-lobed; ovary 3-locular; ovules anatropous, inner integument very thick, outer integument thin; stylodia contracted into dilated sessile stigmas. Fruits capsular, 3-lobed; columella apically dilated, 3-winged, persistent. Seeds roundish, ecarunculate, testa smooth.

Three neotropical spp., occurring from Costa Rica to Brazil. Although *Adenophaedra* has highly reduced flowers and differs from *Bernardia* in a number of other characters, the similarity in pollen noted by Punt (1962) and Nowicke et al. (1999) supports its inclusion in the Bernardieae.

172. *Discocleidion* (Müll. Arg.) Pax & K. Hoffm.

Discocleidion Pax & K. Hoffm., Pflanzenr. 147, VII: 45, fig. 6 (1914); Webster, Ann. Missouri Bot. Gard. 81: 75 (1994); Qiu Huaxing & Gilbert, Fl. China 11: 241 (2008).

Dioecious trees or shrubs; indumentum simple. Leaves glandular-serrulate, 2–4-glandular abaxially above the stipellate base; stipules persistent. Inflorescences mostly terminal, the staminate paniculate, pistillate spiciform or racemoid (branched); staminate bracts lobed, persistent, eglandular. Staminate flowers pedicellate; calyx splitting into 3–5 valvate segments; petals 0; disk segments interstaminal, on the convex receptacle; stamens 35–60, filaments distinct, longer than anthers; anthers apicifixed, supertrorse to latrorse, muticous, thecae discrete and ± pendulous; pollen grains spheroidal, 3-colporate, colpi with broad margins, inoperculate, sexine tectate-perforate, sometimes with prominent excrescences; pistillode 0. Pistillate flowers pedicellate; sepals 5, entire, imbricate, ± persistent in fruit; petals 0; disk annular, crenulatae, pubescent; ovary 3(4)-locular, sericeous; ovules with inner integument thick, outer thinner and vascularized; stylodia bifid, densely papillose. Fruit capsular; columella slender, persistent. Seeds ovoid, carunculate, caruncle deciduous; exotesta rugulose, purplish-tinged; mesotesta vascularized.

Two spp, China, Ryukyu islands.

14. TRIBE PLUKENETIEAE (Benth.) Hutch. (1969).

Monoecious (dioecious), woody or herbaceous; leaves alternate, unlobed to palmately lobed or parted, pinnately to palmately veined, sometimes glandular or stipellate at base; stipules usually persistent; inflorescences terminal or axillary, usually bisexual, mostly racemoid or spiciform; bracts eglandular; staminate calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk + or 0; stamens (2)3–100, filaments usually distinct; pollen grains mostly 3-colpate with irregular colpar margins, sometimes 3-porate or inaperturate but 3-colporate in *Dalechampia*, sexine intectate to tectate, microverrucate; pistillode 0; pistillate sepals 3–6, imbricate; petals and disk 0; ovary 3- or 4-locular; stylodia unlobed, usually connate into an elongated column, tips smooth to lacerate; fruit capsular; columella persistent; seeds ecarunculate, testa usually smooth and dry.

Sixteen genera in three subtribes, both in the New World and the Old, but the majority of taxa neotropical. Although the tribe appears to be monophyletic (nine genera included in the molecular analysis of Wurdack et al. 2005), palynologically it is the most diverse tribe in subfamily Acalyphoideae (Gillespie 1994). For the position of *Dalechampia* within the tribe, see under Subtribe Dalechampiinae.

KEY TO THE SUBTRIBES OF PLUKENETIEAE

1. Inflorescence pseudanthial, bibracteate; pollen grains prolate, coarsely reticulate, with pronounced costae equatoriales **14c. Dalechampiinae**
– Inflorescence racemoid or spiciform; pollen grains subglobose, 3-colpate, not coarsely reticulate, lacking costae equatoriales 2
2. Stinging hairs 0; fruit winged, crested, carinate, or indehiscent; pollen grains 3-colporate **14a. Plukenetiinae**
– Stinging hair +; fruit usually appendaged; pollen grains 3-colporate or -porate (inaperturate), sexine tectate-perforate to rugulose **14b. Tragiinae**

14a. SUBTRIBE PLUKENETIINAE Benth. (1880).

Trees, shrubs, lianas, or herbaceous vines; indumentum simple, sometimes glandular, never urticant. Leaves alternate, often with embedded laminar glands, sometimes stipellate; inflorescences axillary or terminal; stamens 4–50, filaments distinct; pollen grains tectate-perforate to semitectate-reticulate; ovary 3–4-locular, often appendaged; stylodia partly to entirely connate into a common style; fruit capsular (indehiscent).

Five genera, all neotropical except for a few species of *Plukenetia* in Africa.

KEY TO THE GENERA OF PLUKENETIINAE

1. Ovary 3-locular; pistillate sepals 5 or 6; trees, shrubs, or vines 2
– Ovary 4-locular; pistillate sepals 4; twining vines or lianas **177. *Plukenetia***
2. Stamens 4; staminate disk segments 4 or filament bases forming a pseudo-disk; leaves pinnately veined; trees or shrubs 3
– Stamens 10 or more; staminate disk 0 or of numerous minute segments 4
3. Disk exstrastaminal; ovary horned **173. *Astrococcus***
– Disk 0, the filament bases forming a pseudo-disk; ovary verrucate **174. *Haematostemon***
4. Trees or shrubs; flowers in axillary glomerules; leaves pinnately veined; stamens c. 20; style urceolate **175. *Angostyles***
– Twining vines; flowers in axillary racemes; leaves palmately veined; stamens 10; style apically 3-lobed **176. *Romanoa***

173. *Astrococcus* Benth.

Astrococcus Benth., Hook. J. Bot. Kew Gard. Misc. 6: 327 (1854); Müll. Arg. in DC., Prodr. 15(2): 766 (1866), Fl. Brasil. 11(2): 330, t. 49 (1874); Benth., Gen. Pl. 3: 326 (1880); L.J. Gillespie, Fl. Venez. Guayana 5: 100, fig. 98 (1999).

Monoecious trees or shrubs, branches rib-angled distally; indumentum simple. Leaves subentire (minutely glandular-serrulate), eglandular; stipules minute, deciduous. Inflorescences axillary, spiciform, bisexual; pistillate flowers solitary at the 4 or 5 proximal nodes, staminate in 1- or 2-flowered glomerules at distal nodes, terminal flower pistillate; bracts entire, eglandular, recurved. Staminate flowers short-pedicellate; calyx closed in bud, splitting into 4 valvate segments; petals 0; disk extrastaminal, 4-lobed, lobes enclosing anthers; stamens 4, filaments basally confluent; anthers basifixed, introrse, muticous; pollen grains oblate spheroidal, 3-colpate with very irregular margins; sexine tectate-rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals usually 4, imbricate, narrowly lanceolate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, glabrous, 3-horned; stylodia connate into a clavate hollow column with lobulate rim. Fruits capsular, cocci horned; columella massive, 3-angled, persistent. Seeds turbinate-truncate, testa smooth.

A single sp., *A. cornutus* Benth., Amazonian Brazil and Venezuela.

174. *Haematostemon* (Müll. Arg.) Pax & K. Hoffm. Fig. 33

Haematostemon (Müll. Arg.) Pax & K. Hoffm., Pflanzenr. 147, IX: 31, fig. 11 C, D (1919); Sandwith, Kew Bull. 1950: 133 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 143 (1967); L.J. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 28, fig. 9 (1997); Radcl.-Sm., Gen. Euphorb.: 241, fig. 31 (2001).
Astrococcus sect. *Haematostemon* Müll. Arg. (1865).

Monoecious trees or shrubs; indumentum simple. Leaves crenulate or serrulate, eglandular or obscurely glandular adaxially; stipules minute. Inflorescences axillary, bisexual, spiciform; lower nodes with solitary pistillate flowers or bisexual cymules, distal with glomerules of staminate flowers, terminal flower pistillate; bracts eglandular. Staminate flowers pedicellate; calyx splitting into 4 valvate segments; petals 0; stamens 4, filaments basally dilated and connate into a pseudo-disk; anthers basifixed, introrse, muticous; pollen grains suboblate, 3-colpate, colpi sometimes occluded by sexine, tectum foveolate-rugulose, microverrucate; pistillode 0 or incorporated into pseudo-disk. Pistillate flowers pedicellate; sepals 4–6, imbricate, entire; disk 0; ovary 3-locular, tuberculate; stylodia connate into a cup-shaped hollow column with multidentate rim. Fruits capsular.

Two spp. in northern South America: Venezuela (Guayana Highland) and Guyana.

175. *Angostylis* Benth.

Angostylis Benth., Hook. J. Bot. Kew Gard. Misc. 6: 328 (1854, as *Angostyles*); Müll. Arg. in DC., Prodr. 15(2): 767 (1866), Fl. Brasil. 11(2): 331, t. 50 (1874); Radcl.-Sm., Gen. Euphorb.: 244 (2001).

Monoecious trees or shrubs; indumentum simple, non-urticant. Leaves subsessile, clustered at branch-tips, denticulate, pluriglandular; stipules

Fig. 33. Euphorbiaceae-Acalyphoideae. *Haematostemon guianensis*. **A** Flowering branch. **B** Base of leaf blade, adaxial surface. **C** Pistillate flower, with verrucate ovary lobes and massive truncate style. **D** Staminate flower. (Gillespie & Armbruster 1997; drawn by Cathy Pasquale)

subulate. Inflorescences axillary, glomerular, the staminate 2 or 3 per cymule, the pistillate solitary. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 (4) valvate segments; petals 0; stamens c. 20, filaments distinct; anthers dorsifixed, extrorse, muticous; pollen grains suboblate, angulaperturate, 3-brevicolpate, colpar margins irregular, tectum foveolate-rugulose, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, adaxially glandular; petals and disk 0; ovary 3-locular, muricate; stylodia connate into a hollow infundibiliform column with 6-dentate rim. Fruits capsular, muricate. Seeds subglobose, testa smooth.

A single sp., *A. longifolia* Benth., Brazilian Amazon.

176. *Romanoa* Trevis.

Romanoa Trevis., Saggio Algh. Coccot.: 99 (1848, nom. cons.); Pax & K. Hoffm., Pflanzenr. 147, IX: 28, fig. 9 (1919, under *Anabaenella*); Radcl.-Sm., Kew Bull. 34: 589 (1980); Radcl.-Sm., Gen. Euphorb.: 244 (2001).
Anabaena A. Juss. (1824, nom. illeg.).
Anabaenella Pax & K. Hoffm. (1919).

Monoecious vines; indumentum simple. Leaves palmately veined, biglandular on margins at base; stipules deciduous. Inflorescences axillary, usually bisexual with 1 or 2 basal pistillate flowers and several glomerules of staminate flowers; bracts entire, eglandular. Staminate flowers susbsessile or short-pedicellate, pedicel medially articulate; calyx closed in bud, splitting into 5 segments; petals 0; receptacle ± glandular; stamens 10, filaments distinct; anthers extrorse or introrse, 2-celled but opening into 4 valves; pollen grains oblate spheroidal, angulaperturate, 3-colpate, colpi broad with uneven margins, sexine tectate-perforate, microverrucate; pistillode subulate. Pistillate flowers pedicellate; sepals 5 or 6, narrow, entire, ± persistent in fruit but not accrescent; petals and disk 0; ovary 3-locular, glabrous; stylodia connate into a clavate, apically 3-lobed column. Fruits capsular, valves not veiny; columella persistent, slender, 3-pronged. Seeds carinate-angled, testa smooth.

A single sp., *R. tamnoides* (A. Juss.) Radcl.-Sm., eastern and southern Brazil, Paraguay. Although *Romanoa* appears similar to *Plukenetia* in many respects, the pollen is distinctive (Gillespie 1994).

177. *Plukenetia* L.

Plukenetia L., Sp. Pl.: 1192 (1753), Gen. Pl. ed. 5: 438 (1754); Müll. Arg. in DC., Prodr. 15(2): 768 (1866), Fl. Brasil. 11(2): 232 (1874); Pax & K. Hoffm., Pflanzenr. 147. IX: 12 (1919); Webster, Ann. Missouri Bot. Gard. 54: 293, fig. 15 (1968), ibid. 81: 93 (1994); Huft, Ann. Missouri Bot. Gard. 75: 1105 (1989); Gillespie, Syst. Bot. 18: 575 (1993), Fl. Venez. Guayana 5: 207, figs. 196, 197 (1999); L.J. Gillespie & Armbruster, Smiths. Contr. Bot. 86: 30, figs. 10–12 (1997).
Vigia Vell. (1832).
Apodandra Pax & K. Hoffm. (1919).
Eleutherostigma Pax & K. Hoffm. (1919).
Elaeophora Ducke (1925).

Monoecious (dioecious) lianas or twining vines; indumentum simple. Leaves pinnately or palmately veined, subentire to serrulate, adaxially with embedded laminar basal glands and often stipellate at base; stipules deciduous. Inflorescences axillary or terminal on short shoots, bisexual, racemose; pistillate flowers at proximal nodes, staminate glomerules distally; bracts minute, eglandular. Staminate flowers pedicellate; calyx splitting into 4 or 5 valvate segments; petals 0; disk interstaminal or extrastaminal, sometimes 0; stamens 15–40, filaments distinct, sometimes shorter than anthers, inserted on convex or conical receptacle; anthers extrorse or introrse, muticous, thecae divergent; pollen grains suboblate, angulaperturate, 3-colpate, colpi broad with uneven margins, sexine tectate-perforate to semitectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 4 (5), imbricate, entire, ± persistent in fruit but not accrescent; petals and disk 0; ovary 4-locular, angled or lobed, glabrous; ovules anatropous, inner integument moderately thick, outer thin; stylodia connate into a column, the stigmatic tips entire to bilobed. Fruits capsular or baccate; columella persistent, apically dilated. Seeds lenticular to subglobose, testa smooth.

In the concept of Gillespie (1993), *Plukenetia* includes 13 spp. scattered from tropical America to Africa, Madagascar, and southeast Asia. The genus is very heterogeneous in vegetative, floral, and palynological characters, and it is not surprising that Pax and Hoffmann (1919) recognized a number of segregate genera. Gillespie has in effect included all Plukenetiinae with 4-locular ovaries within *Plukenetia*; although *Eleutherostigma* was maintained as distinct by Webster (1994) and Radcliffe-Smith (2001), it was merged with *Plukenetia* by Gillespie (1993, 1994). The reduction of *Eleutherostigma* and *Vigia*, accepted as generically distinct by Webster (1994), is followed here, but it still appears possible that further analysis will result in redefinition of the generic boundaries of *Plukenetia* and other Plukenetiinae.

14b. Subtribe Tragiinae G.L. Webster (1975).

Monoecious shrubs or herbs, often scandent; indumentum of simple and urticant hairs; leaves simple (lobed), without embedded laminar glands, not stipellate; stipules persistent or deciduous; inflorescences axillary or terminal and opposite leaves; stamens (2) 3–50, filaments distinct or connate; pollen grains 3-colpate, 3-porate, or inaperturate, sexine mostly tectate-perforate and microverrucate; ovary 3-locular; stylodia nearly distinct to completely connate; fruit capsular.

Ten genera with c. 150 species. *Tragia* is pantropical, *Acidoton* and *Platygyna* are neotropical, and the other genera paleotropical.

Key to the Genera of Tragiinae

1. Stylodia usually slender; sepals not adaxially inflexed; anthers extrorse or introrse; stamens 2–many; pollen grains tectate-perforate 2
– Stylodia massive; staminate sepals uually inflexed to form a pseudo-disk; stamens 3 or 4, anthers introrse 7
2. Anthers 2, subsessile; staminate calyx flat with lobes reflexed; stylodia distally recurved and proximally connate into a broad conic-cylindrical base **183. *Pachystylidium***
– Anthers 3 or more, rarely 2, but then not subsessile; staminate calyx concave; stylodia distinct to partly connate into a columnar style 3
3. Anther connective with tuft of stinging hairs; stamens 25–60; dioecious shrubs **182. *Acidoton***
– Anther connective lacking tuft of stinging hairs; stamens (2)3–50; monoecious subshrubs, herbs, or vines 4
4. Stylodia thickened, apically bifid; inflorescences unisexual, contracted [< 1 cm]; pollen grains inaperturate **181. *Platygyna***
– Stylodia slender, entire; inflorescences bisexual, elongated [> 1 cm]; pollen grains 3-colporate 5
5. Stamens 8–40; inflorescences bifurcate, staminate and pistillate flowers on separate axes; pollen sexine coarsely tectate-perforate **178. *Bia***
– Stamens 2–4 (or else pistillate sepals pinnatifid); inflorescences not bifurcate, usually bisexual; pollen sexine finely tectate-perforate-rugulose 6
6. Stamens 2–4, anthers not linear, often shorter than filaments; pistillate calyx entire or pinnatifid **179. *Tragia***
– Stamens 30–50, anthers linear and much longer than filaments; pistillate calyx pinnatifid **180. *Ctenomeria***
7. Pistillate sepals entire or dentate; pistillode 0 8
– Pistillate sepals pinnatifid; pistillode present in staminate flower; stylodia connate into a conical or infundibular column **187. *Tragiella***
8. Pistillate sepals entire; anther connective enlarged, sometimes caudate 9
– Pistillate sepals toothed; inflorescences terminal and leaf-opposed; leaves subglabrous **185. *Sphaerostylis***
9. Stylodia distinct or nearly so, adaxially papillose; inflorescences terminal and leaf-opposed; leaves with stinging hairs **184. *Cnesmone***
– Stylodia connate into a clavate or globose column, not adaxially papillose; inflorescences axillary; leaves subglabrous, not urticant **186. *Megistostigma***

178. *Bia* Klotzsch

Bia Klotzsch, Arch. Naturgesch. 7(1): 189 (1841).
Zuckertia Baillon (1858).
Tragia sect. *Bia* (Klotzsch) Müll. Arg. (1865).

Monoecious vines; indumentum simple (unicellular) and urticant. Leaves palmately veined and usually cordate at base, dentate, eglandular; stipules persistent. Inflorescences axillary, bisexual, eglandular, bifurcate, pistillate branch spiciform, with 5–20 subsessile flowers, staminate branch racemoid, with c. 20–30 glomerules of 1–3 pedicellate flowers; bracts entire, eglandular. Staminate flowers pedicellate; calyx splitting into 3–6 valvate segments; petals 0; disk of interstaminal segments or 0; stamens (5–)8–40, filaments distinct; anthers introrse, muticous, sagittate; pollen grains suboblate or spheroidal, 3-colpate or inaperturate, tectate-perforate to semitectate-reticulate; pistillode 0. Pistillate flowers subsessile; sepals 6, imbricate, entire, persistent in fruit; disk 0; ovary 3-locular, pubescent with simple and urticant hairs; stylodia unlobed, adaxially papillose with complex papillae, basally connate. Fruits capsular; columella persistent. Seeds spheroidal, testa smooth, without distinct microsculpturing.

Five neotropical spp. The genus *Bia* is here reinstated from the synonymy of *Tragia* and construed to include two sections[1]. The work of Nowicke and Takahashi shows great palynological heterogeneity in *Tragia*, and *Bia* appears morphologically distinct from *Tragia* (s. str.) not only in its coarsely tectate-perforate exine, but also in other traits such as the larger stamen number (see key and description above). With the recognition of *Bia* and *Ctenomeria* as distinct genera, *Tragia* becomes less heterogeneous and easier to define, although much more study needs to be given to identifying monophyletic groups.

179. *Tragia* (Plumier) L. Fig. 34

Tragia (Plumier) L., Sp. Pl.: 980 (1753), Gen. Pl. ed. 5: 421 (1754); Müll. Arg. in DC., Prodr. 15(2): 927 (1866); Pax & Hoffm., Pflanzenr. 147, IX: 32, figs. 12–22 (1919); Fawc. & Rendle, Fl. Jam. 4: 304, fig. 100 (1920); Lourteig & O'Donell, Lilloa 6: 347 (1941); Miller & Webster, Rhodora 69: 241, figs. 17–29 (1967); Webster, J. Arnold Arb. 48: 376 (1967), Ann. Missouri Bot. Gard. 54: 291, fig. 14 (1968); Leandri, Adansonia II, 11: 437 (1971); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 291, figs. 57–59 (1987); Radcl.-Sm., Fl. Zambesiaca 9(4): 216, figs. 46–48 (1996), Gen. Euphorb.: 253 (2001).

Monoecious (dioecious) shrubs or herbs, often twining; indumentum simple and urticant, sometimes glandular. Leaves usually petiolate, mostly palmately veined or triplinerved, entire to dentate (lobed or divided), often cordate; stipules usually persistent. Inflorescences usually terminal or opposite leaves, bisexual, spiciform or racemoid, with 1–3 basal pistillate flowers and distal staminate flowers; bracts subfoliose, eglandular, mostly uniflorous. Staminate flowers pedicellate; pedicel articulated just above base to mid-length; calyx closed in bud, splitting into 3–6 valvate segments; petals and disk 0; stamens (2)3–4(−40), filaments distinct or ± basally connate; anthers extrorse or introrse, muticous; pollen grains suboblate to spheroidal, 3-colpate or inaperturate, colpi narrow to broad, sometimes circular; sexine reticulate to tectate-rugulose, sometimes microverrucate; pistillode laminar to globose. Pistillate flowers pedicellate; sepals mostly 6–8, imbricate, entire to pinnatifid, persistent and sometimes accrescent in fruit; petals and disk 0; ovary 3-locular, glabrous or urticant-pubescent; ovules pachychalazal, inner integument thick, outer thin; stylodia unlobed, smooth or papillose, basally connate. Fruits capsular; columella persistent, apically 3-fid. Seeds globose, testa smooth.

About 170 spp., most in America and Africa but extending to Asia and Australia (Govaerts et al. 2000). The genus is quite variable in all

---

[1] A. ***Bia* sect. *Bia*.** Type: *Bia sellowiana* Klotzsch ex Baillon (= *B. alienata* Didrichsen).

Staminate flowers with dissected disk; stamens introrse, 8–20, anthers muticous; style column slender. Four spp.:

1. *B. alienata* Didrichsen (1857) (= *B. sellowiana* Klotzsch ex Baill. 1858).
2. ***Bia fallax*** (Müll. Arg.) G.L. Webster, **comb. nov.** Basionym: *Tragia fallax* Müll. Arg., Linnaea 34: 179 (1865). Type: Peru, *Pavon* (holotype G-Less., photograph F7155). – *Tragia japurensis* Müll. Arg.
3. ***Bia fendleri*** (Müll. Arg.) G.L. Webster, **comb. nov.** Basionym: *Tragia fendleri* Müll. Arg., Linnaea 34: 179 (1865). Type: Venezuela, Biscaina, 3,000 feet, *Fendler* 1208 (holotype G; photograph F7156).
4. *Bia lessertiana* Baillon (1858) [*lesseriana*]. – *Tragia lessertiana* (Baill.) Müll. Arg.

B. ***Bia* sect. *Zuckertia*** (Baill.) Müll. Arg., Linnaea 34: 178 (1865) (as *Tragia* sect. *Zuckertia*).

Zuckertia Baill., Étude Gén. Euphorb.: 495 (1858). Type: *Zuckertia cordata* Baill.

1. ***Bia cordata*** (Baill.) G.L. Webster, **comb. nov.** Basionym: *Zuckertia cordata* Baill, Étude Gén. Euphorb.: 496, t. 10, figs. 10–13 (1858). Type: Mexico, Tabasco: Teapa, *Linden* (holotype P).

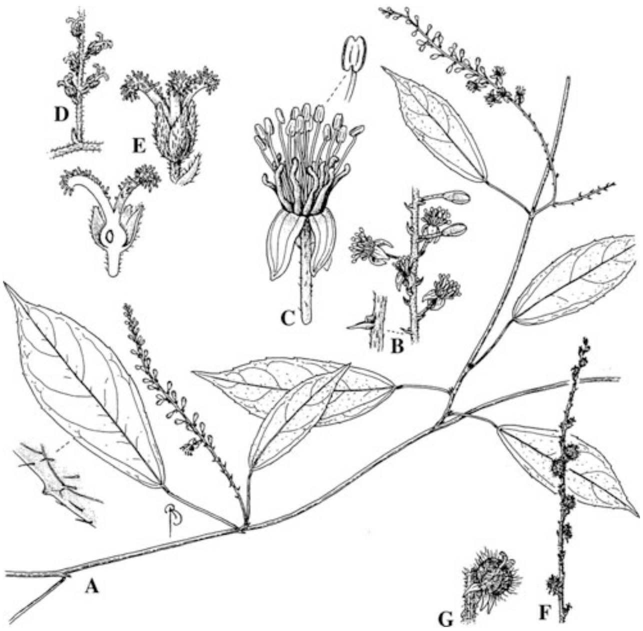

Fig. 34. Euphorbiaceae-Acalyphoideae. *Tragia lessertiana*. **A** Part of stem with leaves and staminate flowers. **B** Part of staminate inflorescence with detail of bract on left. **C** Staminate flower. **D** Part of pistillate inflorescence. **E** Lateral view and medial section of pistillate flower. **F** Part of infructescence. **G** Capsule. (Reproduced with kind permission of the artist Bobbi Angell)

characters and has presented a continuing challenge to systematists. Pax and Hoffmann (1919) recognized 9 sections, and 9 subsections in the African sect. *Tagira*; Gillespie (1994) recognized 5 sections for the Americas. Pollen evidence presented by Gillespie (1994) indicates great heterogeneity within the genus, and suggests that *Tragia* may be an unnatural taxon.

180. *Ctenomeria* Harv.

Ctenomeria Harv., Hook. London J. Bot. 1: 29 (1842); Baill., Étude Gén. Euphorb.: 494 (1858); Prain, Fl. Capensis 5(2): 500 (1920); Dyer, Gen. S. Afr. Fl. Pl. 1: 318 (1975).
Tragia sect. *Ctenomeria* (Harv.) Benth. (1880).

Monoecious twining herbs; indumentum simple and scantily urticant. Leaves palmately veined, sometimes palmately lobed or subpeltate, dentate, eglandular; stipules reflexed, persistent. Inflorescences terminal or leaf-opposed, mostly bisexual, with 1 or 2 proximal pistillate flowers and distal glomerules of staminate flowers; bracts 1-flowered, eglandular. Staminate flowers pedicellate, pedicel articulate and bracteate at or above the base; calyx closed in bud, splitting into 5 valvate segments; petals and disk 0; receptacle convex; stamens 30–60, filaments distinct; anthers longer than filaments, apiculate; pollen grains oblate spheroidal, 3-aperturate, apertures elliptic, occluded by thin exine layer, sexine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6, pinnatifid, imbricate, persistent and ± accrescent in fruit; ovary 3-locular, pubescent; stylodia unlobed, densely papillate-laciniate. Fruits capsular. Seeds globose, testa smooth.

Two spp., southern Africa. Although treated as a synonym of *Tragia* by most recent authors, including Webster (1994) and Radcliffe-Smith (2001), the palynological studies of Gillespie (1994) support the concepts of Prain and Dyer in recognizing *Ctenomeria* as generically distinct.

181. *Platygyna* P. Mercier

Platygyna P. Mercier, Bull. Bot. 1: 168 (1830); Müll. Arg. in DC., Prodr. 15(2): 913 (1866, as *Platygyne*); Pax & K. Hoffm., Pflanzenr. 147, IX: 26 (1919); Alain, Fl. Cuba 3: 100, fig. 28 (1953), Mem. N. Y. Bot. Gard. 21: 132 (1971); Borhidi, Ann. Hist.-Nat. Mus. Nat. Hung. 64: 89 (1972); Radcl.-Sm., Gen. Euphorb.: 255, fig. 33 (2001).
Acanthocaulon Klotzsch (1850).

Monoecious woody vines; indumentum simple and urticant. Leaves dentate, eglandular; stipules ± persistent. Inflorescences terminal, axillary or leaf-opposed, glomerular or contracted-spiciform (< 1 cm long). Staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk pulviniform, strigose-hispid; stamens 5 (4–14), filaments distinct; anthers extrorse, muticous; pollen grains spheroidal, inaperturate, sexine tectate-perforate, sometimes vermiculate, not verrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 6 (5–9), imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, tomentose; ovules pachycaulous, inner integument thick, outer integument thin; stylodia 3 (4), bifid or emarginate, contiguous in a thick, infundibuliform stylar column. Fruits capsular; columella 3-pronged, persistent. Seeds globose, testa smooth.

According to the revision of Borhidi (1972) seven spp., endemic to Cuba. Alain (1971) reduced *Platygyna* to a synonym of *Tragia*, but the pollen evidence of Gillespie (1994) does not support this.

182. *Acidoton* Sw.

Acidoton Sw., Prodr. 6: 83 (1788; nom. cons.), Fl. Ind.. Occid. 2: 952, t. 18 (1800); Müll. Arg. in DC., Prodr. 15(2): 914 (1866); Urb., Symb. Ant. 7: 513 (1913); Pax & K. Hoffm., Pflanzenr. 147, IX: 24, fig. 8 (1919); Fawc. & Rendle, Fl. Jam. 4: 303, fig. 99 (1920); Webster, Ann. Missouri Bot. Gard. 54: 191 (1967), 289, fig. 13 (1968); Liogier, Fl. Española 4: 71 (1986); Webster, Ann. Missouri Bot. Gard. 81: 95 (1994); Burger & Huft, Fieldiana Bot. 36: 56 (1995); Govaerts et al., World Checkl. Bibl. Euporb. 1: 111 (2000); Radcl.-Sm., Gen. Euphorb.: 257, fig. 34 (2001); Webster, Fl. Nicaragua 1: 852 (2001).
Gitara Pax & Hoffm. (1924).

Monoecious or dioecious shrubs, sometimes arborescent; indumentum simple and urticant. Leaves petiolate or subsessile, entire or dentate, eglandular; stipules aristate, persistent. Inflorescences axillary, glomerular or racemoid; unisexual, the pistillate much longer than the staminate; bracts eglandular, persistent, subtending solitary flowers. Staminate flowers pedicellate; calyx closed in bud, splitting into 3–5 valvate segments; petals 0; disk 0 or obscure; stamens 20–60, filaments distinct; anthers extorse, much shorter than filaments, connective with apical tuft of urticant hairs; pollen grains spheroidal or subprolate, 3-colpate or inaperturate, colpi with uneven margins and sexinous islands, sexine tectate-perforate and microverrucate or rugulose and smooth; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, imbricate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, urticant-pubescent; ovules pachycaulous, inner integument moderately thick, outer integument thin; stylodia distally recurved, papillose, and basally connate into acommon style. Fruits capsular, covered with urticant hairs; columella persistent, 3-pronged apically. Seeds spheroidal, testa smooth.

Six spp., 5 in the Greater Antilles, 1 on mainland (Nicaragua to Venezuela). Radcliffe-Smith (2001) has accepted the segregate genus *Gitara* as distinct, based largely on the palynological evidence of Gillespie (1994). It is true that the coarsely dentate leaves and colpate pollen of the mainland *Acidoton* (*Gitara*) *nicaraguensis* considerably differ from the entire leaves and inaperturate pollen of the West Indian species. However, the inflorescences, flowers, and fruits are very similar overall. It seems preferable, therefore, in accordance with the opinion of Govaerts et al. (2000), to maintain *Acidoton* in the broader sense, but retaining *Gitara* at the sectional level.

183. *Pachystylidium* Pax & K. Hoffm.

Pachystylidium Pax & K. Hoffm., Pflanzenr. 147, IX: 108 (1919); Backer & Bakh., Fl. Java 1: 491 (1963); Airy Shaw, Kew Bull. 23: 115 (1969), 26: 310 (1971); Webster, Ann. Missouri Bot. Gard. 81: 95 (1994); Radcl.-Sm., Gen. Euphorb.: 260, fig. 36 (2001).

Monoecious vines; indumentum simple and urticant. Leaves cordate, palmately veined, dentate, eglandular; stipules persistent. Inflorescences terminal or leaf-opposed, pedunculate, bisexual, with proximal pistillate flowers and distal glomerules of staminate flowers; bracts concave, ovate, eglandular. Staminate flowers pedicellate; calyx closed in bud, splitting into 4 or 5 valvate segments; petals 0; disk or pseudo-disk with 2 cavities; stamens 2, filaments distinct; anthers extrorse, longer than filaments, muticous; pollen grains oblate spheroidal, 3-porate, apertures ill-defined with sexinous islands; sexine tectate-punctate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 6, narrow, entire, imbricate; ovary 3-locular, pubescent; stylodia distally recurved, proximally connate into a broad conic-cylindrical base. Fruits capsular; columella persistent, 3-pronged. Seeds globose, testa smooth.

A single sp., *P. hirsutum* (Blume) Pax & K. Hoffm., widespread from India east as far as Sulawesi. *Pachystylidium* is similar in habit to *Cnesmone*, and a close relationship is supported by Gillespie's palynological evidence.

184. *Cnesmone* Blume

Cnesmone Blume, Bijdr.: 630 (1826, as *Cnesmosa*); Croizat, J. Arnold Arb. 22: 427 (1941); Airy Shaw, Kew Bull. 26: 240 (1972); Balakr. & Nair, Gardener's Bull. Singapore 31: 49 (1978); Radcl.-Sm., Gen. Euphorb.: 250 (2001).
Cenesmon Gagnep. (1924).

Monoecious shrubs or lianas; indumentum simple and urticant. Leaves pinnately or palmately veined, often cordate, entire or serrate, eglandular; stipules entire, reflexed, subpersistent. Inflorescences terminal or pseudo-axillary leaf-opposed, spiciform, bisexual, proximal nodes with solitary pistillate flowers, distal with glomerules of staminate flowers; bracts persistent, appearing trifid due to prominent bracteoles, eglandular. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 3 valvate segments; petals and disk 0; stamens 3, filaments basally connate; anthers basifixed, ± introrse, connective enlarged and apiculate, thecae discrete; pollen grains

± spheroidal, weakly 3-colpate, colpi broad and covered with sexinous granules; sexine tectate-perforate and microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–6, imbricate, entire, foliose, persistent in fruit; petals and disk 0; ovary 3-locular, not angled, pubescent with simple and urticant hairs; ovules with very thick integuments; stylodia distally spreading, unlobed, papillate, basally connate. Fruits capsular, endocarp thick and woody; columella persistent. Seeds globose, testa smooth.

Eleven spp., Assam and Andaman Is. to China and Malesia.

185. *Sphaerostylis* Baill.

Sphaerostylis Baill., Étude Gén. Euphorb.: 466 (1858), in Grandidier, Hist. Phys. Nat. Madag. 4 (29): t. 4 (1891); Leandri, Bull. Soc. Bot. France 85: 527 (1939); Croizat, J. Arnold Arb. 22: 430 (1941); Radcl.-Sm., Gen. Euphorb.: 252 (2001); Schatz, Gen. Tree Fl. of Madagascar: 165 (2001).

Monoecious shrubs to vines; indumentum simple and urticant, scanty. Leaves 3-palmatinerved at the base and penninerved above, cordate or peltate at base, entire or dentate; stipules entire, auriculiform, deciduous. Inflorescences terminal or leaf-opposed, unisexual or bisexual, racemoid; bracts uniflorous, eglandular. Staminate flowers pedicellate, pedicel articulate at base; calyx closed in bud, splitting into 3 valvate segments; calyx segments inflexed into a pseudo-disk; petals and disk 0; stamens 2 or 3, filaments distinct, much shorter than anthers, connate; anthers introrse, connective enlarged and apiculate, 2-celled, locules divergent, dehiscing longitudinally/horizontally; pollen grains oblate spheroidal, 3-colpate, exine tectate-perforate, microverrucate; pistillode 0. Pistillate flowers subsessile; sepals 5 or 6, valvate or slightly imbricate, dentate; petals and disk 0; ovary 3-locular, pubescent; stylodia connate into a globose column, tips emarginate. Fruit capsular. Seeds globose, testa smooth.

Two spp., Madagascar, in humid forest.

186. *Megistostigma* Hook. f.

Megistostigma Hook. f., Hook. Ic. Pl. 16: t. 1592 (1887), Fl. Brit. Ind. 5: 466 (1888); Merr., Phil. J. Sci. 16C: 563 (1920): Croizat, J. Arnold Arb. 22: 425 (1941); Backer & Bakh. f., Fl. Java 1: 491 (1963); Airy Shaw, Kew Bull. 23: 119 (1969), 36: 330 (1981); Radcl.-Sm., Gen. Euphorb.: 251 (2001).
Clavistylus J.J. Sm. (1910).

Monoecious shrubs or lianas; indumentum simple and urticant. Leaves palmately veined, often peltate or cordate; stipules persistent or deciduous. Inflorescences axillary, racemoid, unisexual or bisexual, bracts eglandular, persistent, with prominent bracteoles. Staminate flowers subsessile or pedicellate; calyx closed in bud, splitting distally into 3 valvate lobes, proximally connate into a cup; petals 0; receptacular disk 0, pseudodisk at rim of calycine cup; stamens 3, filaments distinct; anthers muticous, introrse, ovate, obtuse, connective enlarged, apiculate; pollen grains spheroidal, irregularly aperturate or inaperturate; sexine tectate-perforate, fissured, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, imbricate, lanceolate, entire, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent; stylar column globose or clavate, broadly 3-lobed distally. Fruits capsular; columella persistent, 3-pronged. Seeds globose, exotesta ± fleshy, endotesta hard, smooth.

Five spp., distributed from Burma to Malesia.

187. *Tragiella* Pax & K. Hoffm.

Tragiella Pax & K. Hoffm., Pflanzenr. 147, IX: 104, fig. 24 (1919); Radcl.-Sm., Kew Bull. 35: 777 (1981), Fl. E. Trop. Afr. Euphorb. 1: 318, fig. 60 (1987), Fl. Zambesiaca 9(4): 212, t. 45 (1996), Gen. Euphorb.: 252 (2001); Webster, Ann. Missouri Bot. Gard. 81: 94 (1994).

Monoecious herbs to twining vines; indumentum of simple and urticant hairs. Leaves palmately veined, denticulate, eglandular; stipules persistent. Inflorescences terminal or leaf-opposed, racemose, bisexual, with 1 or 2 basal pistillate flowers, distal nodes with glomerules of staminate flowers; bracts 1-flowered. Staminate flowers pedicellate; calyx closed in bud, distally splitting into 3 valvate lobes introrsely projecting at top of calyx tube; petals and disk 0; stamens 3 (4), filaments distinct or basally connate; anthers dorsifixed, introrse, muticous, connective enlarged, thecae discrete; pollen grains oblate spheroidal, 3-colpate, colpi narrow with uneven margins; sexine semi-tectate-reticulate, microverrucate; pistillode +. Pistillate flowers pedicellate; sepals 6, imbricate, pinnatifid, persistent in fruit; petals and disk 0; ovary 3-locular, pubescent and sometimes urticant-setose; ovules pachycaulous, inner integument thick, outer integument thin; stylodia united into a conical or infundibuliform column or spherical mass. Fruits capsular, endocarp woody; columella 3-pronged, not persistent. Seeds globose; testa smooth.

Five spp. from east Africa. The genus appears to be linked to *Tragia* by its urticant hairs and pollen morphology, but resembles *Cnesmone* and *Sphaerostylis* in its distinctive staminate flowers and enlarged stylodia. There is also a resemblance to *Ctenomeria* in the pinnatifid pistillate sepals, but the pollen of the two genera is very different.

14c. Subtribe Dalechampiinae (Müll. Arg.) G.L. Webster (1994).

Includes only the genus *Dalechampia*, whose relationships to the Plukenetiinae and Tragiinae remain unclear. The inflorescence of *Dalechampia* has no counterpart in other Plukenetieae, and Gillespie (1994) and Nowicke and Takahasi (2002) have emphasized that its distinctive pollen is strikingly different from that of either Plukenetiinae or Tragiinae. The primitive *Dalechampia* species in sect. *Rhopalostylis* (Armbruster 1996) have the stylar apparatus of Plukenetiinae (especially *Romanoa*) but the persistent stipules and bipartite inflorescence of Tragiinae (*Bia*). Urticant trichomes, which are present in the Tragiinae, from *Dalechampia* are recorded in the more derived sect. *Dioscoreifoliae* (on both vegetative and reproductive parts) but not in the basal sect. *Rhopalostylis*. Obviously, the subtribal classification of the Plukenetieae needs a profound revision. The molecular data available (Wurdack et al. 2005) indicate that *Dalechampia* might be embedded in the Plukenetieae (sister to *Astrococcus*).

188. *Dalechampia* [Plumier] L. Fig. 35

Dalechampia [Plumier] L., Sp. Pl.: 1054 (1753), Gen. Pl. ed. 5: 473 (1754); Müll. Arg. in DC., Prodr. 15(2): 1232 (1866), Fl. Brasil. 11(2): 633, t. 88–91 (1874); Pax & K. Hoffm., Pflanzenr. 147, XII: 3, figs. 1–9 (1919); Gagnep., Fl. Indochine 5: 342, t. 39, 40 (1926); Léonard, Fl. Congo 8 (1): 194 (1962); Webster & Armbruster, Brittonia 31: 352 (1979); Armbruster, Syst. Bot. 9: 272 (1984), 13: 303 (1988); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 285, fig. 56 (1987); Webster, Brittonia 41: 1, figs. 1–3 (1989); Webster & Armbruster, Bot. J. Linn. Soc. 105: 137, figs. 1–5 (1991); Armbruster, Syst. Bot. 21: 209, figs. 5–14 (1996), Smiths. Contr. Bot. 86: 14, figs. 4–8 (1997); Radcl.-Sm., Gen. Euphorb.: 262 (2001).
Cremophyllum Scheidw. (1842).
Rhopalostylis Klotzsch ex Baill. (1858).
Megalostylis S. Moore (1916).

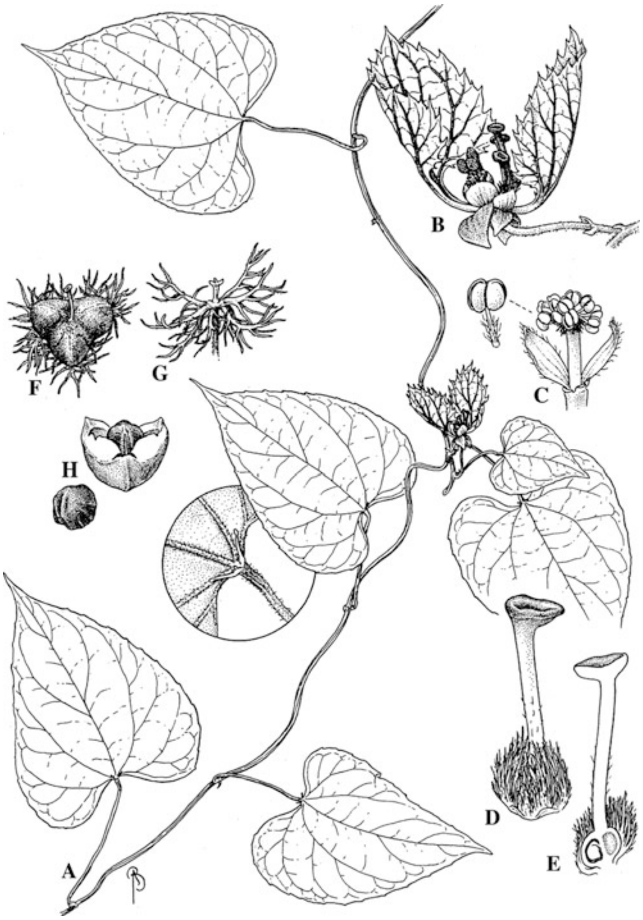

Fig. 35. Euphorbiaceae-Acalyphoideae. *Dalechampia dioscoreifolia*. **A** Part of stem with leaves and inflorescence; note detail of adaxial leaf blade base with stipels. **B** Inflorescence subtended by bracts. **C** Staminate flower; three sepals removed. **D** Pistillate flower. **E** Same, medial section. **F** Fruit. **G** Sepals and column after fruit dehiscence. **H** Fruit segment with seed and isolated seed. (Reproduced with kind permission of the artist Bobbi Angell)

Monoecious undershrubs or vines; indumentum simple and urticant, sometimes scanty. Leaves entire or dentate, unlobed and pinnately veined to lobed and palmately veined, sometimes palmatisect, often stipellate at base; stipules persistent. Inflorescences pseudanthial, pedunculate, axillary or terminating short shoots, mostly bilaterally symmetrical with a pair of subopposite involucral bracts, bisexual; pistillate cymule proximal, 3-flowered, bracteolate; staminate cymule terminal, involucellate, mostly of 8–12 flowers, bractlets subtending staminate flowers resiniferous or odoriferous. Staminate flowers pedicellate, pedicels articulate; calyx closed in bud, splitting into mostly 3–6 valvate segments; petals and disk 0; stamens 5–90; filaments connate into a thick column; anthers latrorse, 2-celled, muticous; pollen grains prolate, 3-colporate, with costae equatoriales of two thickened bands, sexine coarsely reticulate with very large lumina and high muri; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 5–12, imbricate, basally connate, entire or pinnatifid; disk 0; ovary 3-locular, glabrous or pubescent; ovules anatropous, inner integument thick, outer integument thinner, vascularized; stylodia completely connate into an elongate, sometimes clavate or peltate column, stigmatic surface extending down much of the stylar surface. Fruits capsular, usually enclosed by the accrescent urticant calyx, dehiscing explosively by elastic twisting of the dry cocci; columella persistent. Seeds globose, smooth or rugose. $2n = 44, 46, 72, 138$.

About 120 spp., mainly in tropical regions of the Americas, also in tropical Africa/Madagascar and S and SE Asia. The genus was divided into 6 sections by Webster & Armbruster (1991), and Armbruster (1996) has added an additional section. *Dalechampia* had been placed in a separate tribe since Müller (1866) until treated by Webster (1994), who demoted the Dalechampieae to a subtribe of the Plukenetieae.

Three unplaced acalyphoid genera:

189. *Afrotrewia* Pax & K. Hoffm.

Afrotrewia Pax & K. Hoffm. in Engl., Pflanzenreich 147. VII: 14 (1914); Radcliffe-Smith, Gen. Euphorb.: 420 (2001); Kulju, van der Ham & Breteler, Taxon 57: 137–143 (2008).

Shrubs to small trees, presumably dioecious; indumentum minute, stellate to simple. Leaves subentire to shallowly serrate, with extrafloral nectaries on both sides, petiole apically pulvinate; stipules deciduous to somewhat persistent. Inflorescences unisexual, with prophylls at the bases of the inflorescence branches and pedicels; staminate inflorescences axillary to terminal panicles, pistillate inflorescences 2–3-flowered racemes. Staminate flowers: sepals 2 or 3, valvate; petals 0; receptacle conical; disk interstaminal, of hairy glands; stamens 30–40, distinct; anthers basifixed, thecae 2, pendulous, unequally bilobed, latrorse or introrse; connective horizontally enlarged, partly covering the thecae, papillose; pollen grains spheroidal, tricolporate-lalongate, tectate-microreticulate; pistillode 0. Pistillate flowers: sepals 5–6, imbricate?; petals 0; disk annular, thick; ovary 3-locular; stylodia 2. Fruits lobed capsules, dehiscing septicidally, septifragally and loculicidally; column 0?. Seeds subglobose; hilum ± triangular to heart-shaped; testa not fleshy; cotyledons broad, flat.

One sp., *A. kamerunica* Pax & K. Hoffm., Cameroon and Gabon.

In the molecular analysis of Kulju et al. (2008), *Afrotrewia* falls into the core acalyphoid clade basal to clades A2 and A3 of Wurdack et al. (2005).

190. *Crotonogynopsis* Pax

Crotonogynopsis Pax, Bot. Jahrb. 26: 328 (1899); Prain, Fl. Trop. Afr. 6(1): 924 (1912); Pax & K. Hoffm., Planzenr. 147, VII: 14 (1914); Radcl.-Sm., Fl. Trop. E. Afr. Euphorb. 1: 213, fig. 40 (1987); Webster, Ann. Missouri Bot. Gard. 81: 80 (1994); Léonard, Fl. Afr. Centr. Euph. 3: 28, t. 4 (1996); Radcl.-Sm., Gen. Euphorb.: 188 (2001).

Monoecious or dioecious trees or shrubs; indumentum simple. Leaves sessile or subsessile, denticulate, with scattered glands abaxially; stipules deciduous. Inflorescences axillary (ramiflorous), unisexual, racemoid, the pistillate shorter and few-flowered; bracts persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–5 valvate segments; petals 0; disk of many interstaminal glabrous segments; stamens 10–15, filaments distinct; anthers dorsifixed, introrse or extrorse, connective apiculate, not enlarged; pollen grains 3-angled, 3-colporate, colpi granulate, sexine tectate-perforate; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, ± imbricate, persistent in fruit; petals 0; disk annular-lobed; ovary 3(4)-locular, smooth and glabrous; ovules anatropous, inner integument thick, outer integument thin; stylodia nearly distinct, bifid, branches laciniate. Fruit capsular; columella persistent. Seeds subglobose, ecarunculate, testa smooth.

Two spp., tropical Africa. Radcliffe-Smith (2001) referred the genus to the Adelieae, from which it differs in its 3-colporate pollen grains with non-operculate colpi and a complex infratectum with double-layered columellae, otherwise known only from Alchorneinae (*Alchornea*, *Orfila*) (Takahashi et al. 2000). The molecular data (Wurdack et al. 2005) resolve it in the Acalypheae, close to *Mareya* and *Acalypha*.

191. ***Enriquebeltrania*** Rzedowski

Enriquebeltrania Rzedowski, Bol. Soc. Bot. México 38: 75 (1979); Webster, Ann. Missouri Bot. Gard. 81: 80 (1994); Radcl.-Sm., Gen. Euphorb.: 189 (2001); De-Nova et al., Syst. Bot. 31: 533–546 (2006).
Beltrania Miranda (1957; nom. illeg.).

Dioecious shrubs; branches often spinescent; indumentum simple. Leaves fasciculate, distally crenate to dentate, pellucid-punctate; stipules persistent. Flowers in axillary glomerules. Staminate flowers pedicellate; sepals 3 or 4, valvate; petals and disk 0; stamens 20–30, filaments distinct; anthers extrorse, apiculate; pollen grains oblate spheroidal, 3-colporoidate, colpi inoperculate, with obscure margins, sexine tectate-puncate, microverrucate; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, entire, persistent in fruit; disk 0; ovary 2-locular; inner integuments very thick, outer integuments thin; stylodia distinct, unbranched. Fruits capsular, glabrous. Seeds subglobose, caruncualte, testa minutely rugulose.

Two spp., Mexico, Yucatan and Pacific coast. Formerly this genus was included in Adelieae, but Takahashi et al. (2000) found the inoperculate pollen grains of *Enriquebeltrania* very different from the operculate grains of *Adelia*. By molecular studies (Wurdack et al. 2005; De-Nova et al. 2006), no precise placement within the New World acalyphoids could be indicated either.

VI. Subfam. Crotonoideae Beilschm. (1833).

Monoecious or dioecious trees, shrubs, or herbs; laticifers articulated or non-articulated, latex colored or 0; indumentum simple, stellate, or lepidote; leaves alternate or opposite (whorled), stipulate or estipulate, lamina simple to palmately lobed or compound, often with basal laminar glands. Inflorescences axillary or terminal, dichasial to thyrsoid or spiciform. Staminate flowers with imbricate or valvate sepals; petals and disk + or 0; stamens (3–)5–many, filaments distinct or connate; pollen grains binucleate or trinucleate, tricolpate, porate or inaperturate, sexine reticulate to more commonly tectate with triangular or rounded-triangular processes [pillars] frequently forming continuous [triangular] arrays; pistillode + or 0. Pistillate flowers with (2) 3–6 imbricate or valvate sepals; petals and disk + or 0; ovary mostly 3-locular; outer integuments of ovules sometimes vascularized; stylodia bifid to multifid, less often unlobed; ovules solitary in each locule, anatropous. Fruit usually capsular or rarely indehiscent. Seeds carunculate or ecarunculate; exotegmen palisadal, testa sometimes fleshy; endosperm usually copious, often oily.

This subfamily, subfam. Crotonoideae s.l., which comprises 68 genera in twelve tribes, contains lactiferous taxa with crotonoid pollen sculpture and has been resolved to consist of four clades (definition and topology of clades after Wurdack et al. 2005): (I) the Adenoclineae s.l. (tribe 1), (II) the Gelonieae (tribe 2), (III) the articulated crotonoids (tribes 3–6), and (IV) the inaperturate crotonoids (= Crotonoideae s. str.), comprising the remaining tribes 7–12. Members of clades I–III share apetalous flowers, mostly thin integuments (thick in I), and aperturate pollen, whereas clade IV has apetalous flowers, inaperturate pollen, and thick inner integuments that contain vascular bundles. These clades form a grade, in which (I), (II) and (III) subsequently are unsupported sister clades to (IV), the latter comprising two subclades, C1, with tribes 7 and 8, and subclade C2, with tribes 9–12. Subclade C1 is from the New World and the Old, whereas C2 is (nearly) confined to the Old World. Molecular support for subclade C2 is strengthened by a large *trn*L-F spacer deletion.

Key to the Tribes of Subfam. Crotonoideae

1. Pollen grains aperturate; petals 0; laticifers articulated or inarticulated 2
– Pollen grains inaperturate; petals usually present, at least in staminate flowers; laticifers inarticulated (articulated) 5
2. Laticifers articulated; staminate calyx gamophyllous; pollen grains 3-nucleate; plants monoecious or dioecious; chromosome base number $x = 9$ 3
– Laticifers non-articulated; staminate calyx mostly not gamophyllous; pollen grains 2-nucleate; chromosome base number $x = 11$ 4
3. Leaves palmately compound; inflorescences cymose-paniculate, pistillate flowers terminal on lateral axes; calyces gamophyllous; pollen grains colpate; stylodia stigmatiform; seeds ecarunculate, endosperm oily **6. Heveeae**

– Leaves simple to deeply lobed but not compound; inflorescences without terminal pistillate flowers on lateral branches; calyces of distinct sepals; pollen grains pantoporate; stylodia mostly multifid; stylodia mostly multifid; seeds carunculate; endosperm starchy **4. Manihoteae**

4. Pollen grains pantoporate; leaves pellucid-punctate, stipules connate; inflorescences of leaf-opposed glomerules **2. Gelonieae**

– Pollen grains colp(or)ate; leaves not pellucid-punctate, stipules distinct; inflorescences terminal or axillary 6

5. Pollen exine lacking distinct Croton pattern, colpi operculate; monoecious (dioecious); pistillate flowers subsessile **5. Micrandreae**

– Pollen exine with distinct Croton pattern, colpi inoperculate; mostly dioecious; pistillate flowers subsessile to pedicellate **1. Adenoclineae**

6. Leaves simple, unlobed to palmately lobed; inflorescences terminal or axillary; seeds carunculate or ecarunculate 7

– Leaves palmatisect [except *Givotia*]; inflorescences axillary; seeds ecarunculate **11. Ricinodendreae**

7. Staminate sepals distinct or connate but not fused and enclosing petals in bud [except in *Anomalocalyx*]; seeds carunculate or ecarunculate; stipules persistent or deciduous 8

– Staminate sepals joined in bud, splitting into segments valvately or irregularly; seeds ecarunculate **12. Aleuritideae**

8. Indumentum simple or malpighiaceous; pollen grains binucleate; seeds carunculate or ecarunculate 9

– Indumentum stellate or lepidote; pollen grains binucleate or trinucleate; seeds mostly carunculate [except in *Paracroton*] 11

9. Seeds nearly exalbuminous; petals 0; stylodia unlobed; fruits indehiscent **3. Elateriospermeae**

– Seeds albuminous; petals usually present; stylodia mostly bifid; fruits usually dehiscent 10

10. Inflorescences mostly dichasial, terminal, at least in part; usually monoecious; indumentum often glandular; leaf blades often palmately lobed or parted; stamens 5–12, filaments distinct or connate; seeds carunculate **7. Jatropheae**

– Inflorescences racemoid or spiciform to paniculate, terminal or axillary; monoecious or dioecious; indumentum rarely glandular; leaf blades rarely palmately lobed; stamens 7–35, filaments mostly distinct or nearly so; seeds carunculate or ecarunculate **9. Codiaeae**

11. Branches and leaves with resinous glands, or else leaves opposite or verticillate; filaments erect in bud; cotyledons as narrow as radicle or much broader **10. Ricinocarpeae**

– Branches and leaves lacking resinous glands; leaves alternate; filaments erect or inflexed in bud; cotyledons much broader than radicle **8. Crotoneae**

1. Tribe Adenoclineae (Müll. Arg.) G.L. Webster (1975).

Monoecious or dioecious; laticifers non-articulated, latex clear, often colored; indumentum simple, malpighiaceous, or stellate; leaves alternate (opposite), simple; inner integument usually lacking vascular bundles and < 6 cells thick [thick and vascularized in *Klaineanthus*]; stylodia bifid or stigmatiform, rarely completely connate into a column; fruits capsular or drupaceous; seeds ecarunculate.

Unlike the Micrandreae and Manihoteae, tribe Adenoclineae is represented in both the Neotropics and Paleotropics. Subtribe Endosperminae differs markedly in its stellate indumentum, connate stamens, and multilocular ovary, but is linked with *Omphalea* and *Suregada* by the possession of alkaloidal glycosidase inhibitors and/or by being host plants for diurnal uraniine moths (Kite et al. 1991; Wurdack et al. 2005).

Key to the Subtribes and Genera of Adenoclineae

1. Indumentum stellate; stamens connate; fruits baccate, 1–7-locular. **Subtribe 1b. Endosperminae** **197. *Endospermum***

– Indumentum simple or malpighiaceous; stamens distinct, rarely connate; fruits dehiscent or indehiscent; 2- or 3-locular. **Subtribe 1a. Adenoclininae** 2

2. Stylodia completely connate into an obtuse or shortly 2–3-lobate stylar column; stamens 2–3, connate into a short, slender column **195. *Omphalea***

– Stylodia distinct or largely so; stamens > 3, filaments distinct 3

3. Pistillate disk 0; leaves glandular-dentate, without laminar glands **193. *Ditta***

– Pistillate disk +, at least as staminodia; leaves sometimes with laminar glands 4

4. Herbs; seed coat not fleshy; staminate disk segments interstaminal **192. *Adenocline***

– Trees or shrubs; seed-coat fleshy; staminate disk extrastaminal or 0 5

5. Stamens 8–10; anthers 2-locular, not peltate; pollen grains tricolporate; staminate disk of 4 or 5 segments; leaves eglandular, stipules deciduous; indumentum simple; endotesta smooth **196. *Klaineanthus***

– Stamens 3; anthers 4-locular, peltate; pollen grains tricolpate; staminate disk 0; leaves usually with laminar glands, stipules persistent; indumentum [at least in part] malpighiaceous; endotesta foveolate or echinulate **194. *Tetrorchidium***

1a. SUBTRIBE ADENOCLININAE Arg. (1865).

Trees, shrubs, or herbs; indumentum simple or malpighiaceous; stamens 3–30, filaments distinct; ovary 2- or 3-locular; stigmas distinct; fruit capsular or drupaceous.

This subtribe comprises five genera, which are found in the Neotropics and in tropical and temperate Africa.

192. *Adenocline* Turcz.

Adenocline Turcz., Bull.Soc. Imp. Nat. Moscou 16: 59 (1843); Prain, Ann. Bot. 27: 404 (1913), Fl. Cap. 5(2): 488 (1920); Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 1: 315 (1975); Radcl.-Sm., Gen. Euphorb. 279 (2001).

Dioecious (monoecious) annual or perennial herbs, sometimes scrambling; laticifers non-articulated, latex not apparent; indumentum 0. Leaves alternate or opposite, petiolate or sessile, entire or dentate, triplinerved to 1-veined, eglandular or stipellate at apex of petiole; stipules persistent, lanceolate or subulate, ± dentate or lacerate, sometimes foliaceous. Flowers axillary, the staminate in ± umbellate cymes or glomerules at upper axils, sometimes aggregated into terminal panicles; pistillate flowers solitary, leaf-opposed; bracts dissected, persistent, eglandular. Staminate flowers pedicellate; sepals 5, imbricate; petals 0; disk segments interstaminal, sometimes stipitate; stamens mostly (6–)10(–12), biseriate; filaments distinct; anthers basifixed, thecae discrete, globose, dehiscing vertically; pollen grains oblate spheroidal, 3-colpate, colpus margins irregular; sexine tectate, finely clavate; pistillode 0. Pistillate flowers pedicellate; sepals 5, entire, persistent in fruit; petals 0; disk of 3 ± petaloid segments; ovary 3-locular; ovules anatropous; stylodia nearly distinct, bipartite. Fruits capsular. Seeds ecarunculate, testa smooth, rugulose, or foveolate.

Eight spp. in temperate and subtropical South Africa (Dyer 1975; Radcliffe-Smith 2001), but only three in the enumeration of Govaerts et al. (2000).

193. *Ditta* Griseb.

Ditta Griseb., Mem. Amer. Acad. Arts Sci. II. 8: 160 (1861); Urban, Symb. Ant. 7: 261 (1912); Alain, Fl. Cuba 3: 112, fig. 36 (1953); Little et al., Trees Puerto Rico & Virgin I. 2: 400, t. 436 (1974); Liogier, Fl. Española 4: 135, 348, fig. 116–13 (1986), Descr. Fl. Puerto Rico 2: 383, fig. 59–13 (1988); Radcl.-Sm., Gen. Euphorb.: 280 (2001).

Dioecious shrubs; stems with resinous exudate; indumentum simple, scanty. Leaves rigid, subentire or obscurely crenate with embedded marginal glands, ± revolute; stipules persistent, incrassate, dark, resiniferous. Flowers axillary, staminate in few-flowered glomerules, pistillate solitary. Staminate flowers sessile; sepals 3, distinct; petals and disk 0; stamens 3, filaments suppressed; anthers sessile, dorsifixed; pollen grains spheroidal, 3-colpate, sexine tectate with apiculate pillars; pistillode 0. Pistillate flowers sessile; sepals suppressed; petals and disk 0; ovary 2- or 3-locular; ovules anatropous; stylodia distinct, unlobed, incrassate, stigmatiform. Fruits capsular, reddish. Seeds ecarunculate. $n = 11$.

Two spp. described from the Greater Antilles (Cuba, Hispaniola, and Puerto Rico), but Liogier (1986) doubts that *D. maestrensis* Borhidi is distinct from *D. myricoides* Griseb. *Ditta* is morphologically distant from the other genera of Adenoclineae in its resinous axes and highly reduced flowers. However, the pollen is consistent with the Adenoclineae (Nowicke 1994), and in the molecular analysis *Ditta* is sister to *Tetrorchidium*.

194. *Tetrorchidium* Poepp.

Tetrorchidium Poepp., in Poepp. & Endl., Nov. Gen. Sp. 3: 23, t. 227 (1842); Müll. Arg. in DC., Prodr. 15(2): 1132 (1866); Pax & K. Hoffm., Pflanzenr. 147, IV: 29, figs. 8, 9 (1912); Cuatrecasas, Brittonia 9: 76, figs. 1–4 (1957); Léonard, Fl. Congo 8(1): 133, t. 9 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 373, fig. 70 (1987); Breteler, Adansonia III, 21: 97 (1999).
Hasskarlia Baill. (1860).
Tetrorchiopsis Rauschert (1982).

Dioecious trees or shrubs; latex whitish, often scanty or 0; indumentum simple or malpighiaceous. Leaves entire to dentate, eglandular [African spp.] or with raised or stipitate glands at base or laterally on petiole; stipules ± glandular, persistent. Inflorescences axillary or leaf-opposed; staminate spiciform, pistillate racemoid or paniculate; bracts persistent, entire, sometimes glandular. Staminate flowers subsessile, several per bract; sepals 3, distinct, imbricate, adaxially ribbed; petals and disk 0; stamens 3, distinct, filaments shorter than anthers; anthers extrorse, peltate, 4-locular; pollen grains ± spheroidal, 3-colpate, sexine tectate with rounded or angular pillars; pistillode small or obsolete. Pistillate flowers subsessile or pedicellate; sepals 3, distinct, imbricate, entire, persistent in fruit; petals 0; disk cupular or 3-lobed; ovary 2- or 3-locular; ovules anatropous; stylodia distinct, bifid, style branches sometimes dilated. Fruits capsular, thin-walled. Seeds rounded, ecarunculate, exotesta fleshy, endotesta hard, foveolate.

Nineteen spp. in the Neotropics, and four in Africa (Govaerts et al. 2000). In agreement with Radcliffe-Smith (2001), the African *Hasskarlia* is treated as a section of *Tetrorchidium*.

195. *Omphalea* L. Fig. 36

Omphalea L., Syst. Nat. ed. 10: 1264 (1759; nom. cons.); Müll. Arg. in DC., Prodr. 15(2): 1134 (1866), Fl. Brasil. 11 (2): 513, t. 72 (1874); Hemsl., Hook. Ic. Pl. 26: t. 2537 (1897); Croizat, Bull. Jard. Bot. Buit. III, 17: 204 (1941); Alain, Fl. Cuba 3: 109 (1953); P.I. Forst., Austrobaileya 4: 381, t. 1 (1995); Gillespie, Novon 7: 127, t. 1 (1997), Smiths. Contr. Bot. 86: 6, t. 1 (1997).

Monoecious trees, shrubs, or lianas; sap red or pinkish; indumentum simple; foliage evergreen or deciduous. Leaves pinnately or palmately veined or lobed, with paired glands at base or apex of petiole; stipules mostly entire, ± deciduous. Inflorescences terminal, racemoid or paniculate, bisexual or distal nodes staminate; bracts foliose, generally glandular, stipulate. Staminate flowers pedicellate; sepals (3)4–5, discrete, imbricate; petals 0; disk extrastaminal, annular or segmented; stamens 2 or 3, filaments connate into a ± apically dilated column; anthers latrorse; pollen grains oblate spheroidal to oblate, 3-colpate, sexine tectate-foveolate, microverrucate; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals 4 or 5, discrete, imbricate, deciduous; disk 0; ovary 3(4)-locular, glabrous; ovules pachycaulous, inner and outer integuments moderately thick; stylodia completely connate into a stylar column, distally obtuse or very shortly 2–3-lobate. Fruits capsular or baccate; columella not persistent. Seeds subglobose, sometimes compressed or angular, ecarunculate; exotesta fleshy to papery, endotesta hard, smooth.

Seventeen spp. (Gillespie 1997; 22 according to Govaerts et al. 2000), scattered through neotropical and paleotropical regions, except the Pacific islands. In terms of systematics, *Omphalea* is one of the most problematic genera of the family. Müller (1866) assigned it to his subtribe Gelonieae, associated with *Endospermum*, *Elateriospermum*, and other genera now assigned to the Crotonoideae. Pax and Hoffmann first (1919) placed *Omphalea* into the Hippomaneae, and later in a subtribe of the Gelonieae. Croizat (1941) suggested an affinity with the Plukenetieae. The molecular data (Wurdack et al. 2005) place *Omphalea* in the Adenoclineae. Interestingly, *Omphalea*, *Endospermum*, *Tetrochidium* and *Suregada* (Gelonieae) accumulate alkaloidal protease inhibitors, and are host plants for specialist diurnal uraniine moths (Kite et al. 1991; Wurdack et al. 2005).

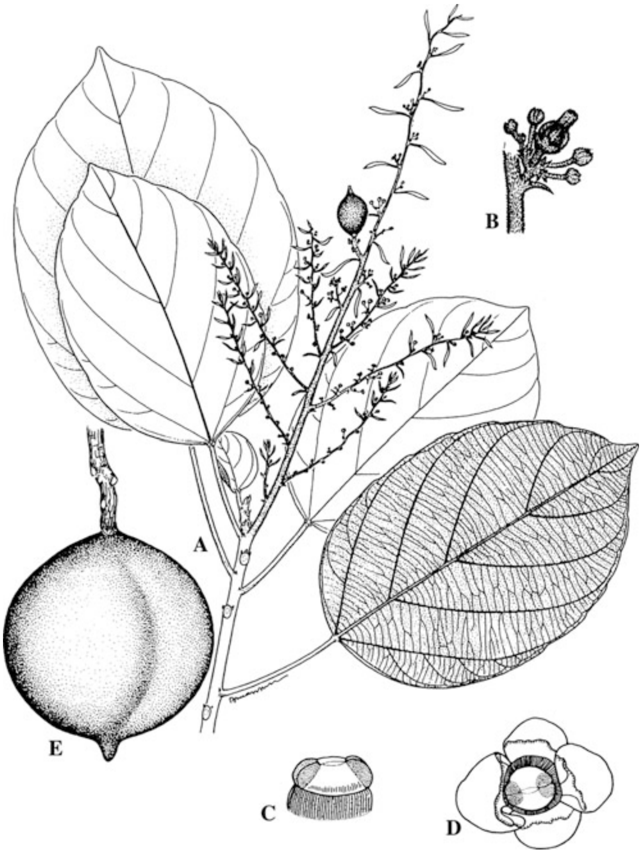

Fig. 36. Euphorbiaceae-Crotonoideae. *Omphalea diandra*. **A** Flowering branch. **B** Partial inflorescence with central pistillate flower and outer staminate flower buds. **C** Androecium above annular nectary. **D** Staminate flower at anthesis. **E** Fruit. (Gillespie 1997)

196. *Klaineanthus* Pierre ex Prain

Klaineanthus Pierre ex Prain, Kew Bull. Misc. Inf. 1912: 105 (1912), Fl. Trop. Afr. 6(1): 963 (1913), Hook. Ic. Pl. 30: t. 2985 (1913); Keay, Fl. W. Trop. Afr., ed. 2, 1: 413 (1958); Léonard, Fl. Congo 8(1): 130 (1962).

Dioecious trees; latex not recorded; indumentum simple. Leaves long-petiolate, eglandular; stipules minute, deciduous. Inflorescences terminal and axillary, the staminate paniculate, the pistillate racemose; bracts deciduous. Staminate flowers pedicellate; sepals (3) 4 or 5, basally connate, imbricate; petals 0; disk segments 4 or 5; stamens 8–10, biseriate, filaments distinct; anthers basifixed, introrse; pollen grains suboblate, 3-colporate, sexine tectate, with clavate pillars; pistillode 2–3-lobed. Pistillate flowers pedicellate; sepals 5 (4), distinct, imbricate, entire, deciduous in fruit; petals 0; disk annular, with 4 or 5 staminodes; ovary 3-locular, glabrous; ovules anatropous, inner integuments with 9–11 cell layers, vascularized; stylodia almost distinct, bipartite, the arms 2-lobulate at their apices. Fruits capsular, with thin papery walls; columella persistent, slender; seeds with fleshy exotesta, endotesta smooth.

A single sp., *K. gaboniae* Pierre ex Prain from West Africa (Nigeria to Gabon). It is anomalous in the Adenoclineae in having a thick, vascularized integument.

1b. Subtribe Endosperminae Pax & K. Hoffm. (1931).

Dioecious trees or shrubs, indumentum stellate; staminate calyx gamophyllous; stamens 6–10, filaments connate; ovary 2–6-locular; inner integuments thin, not vascularized; stylodia stigmatiform, confluent; fruit capsular.

Monotypic, including only the paleotropical genus *Endospermum*.

197. *Endospermum* Benth.

Endospermum Benth., Fl. Hongkong.: 304 (1861; nom. cons.); Beccari, Malesia 2: 45, t. 2 (1884); Pax & K. Hoffm., Pflanzenr.147, IV: 33 (1912); Radcl.-Sm., Gen. Euphorb.: 281 (2001); Guerrero & van Welzen, Edinb. J. Bot. 68:443–482 (2011), rev.

Dioecious trees; latex white, often not evident; indumentum stellate-fasciculate, sometimes scanty. Leaves long-petiolate, sometimes peltate, palmately veined or triplinerved, with abaxial paired sessile patelliform or conical glands at junction with petiole; stipules entire, deciduous. Inflorescences axillary, staminate paniculate, pistillate spicate or racemose, sometimes narrowly paniculate; bracts entire or unidentate, persistent or deciduous, eglandular. Staminate flowers subsessile, basally articulate; calyx 2–4-lobed, often open in bud; petals 0; disk extrastaminal, 4–5-angled; stamens (3–)6–10, filaments connate, anthers nearly sessile on staminal column, didymous and 4-locellate; pollen grains suboblate, 3-colpate, sexine tectate with clavate pillars; pistillode minute or 0. Pistillate flowers subsessile or pedicellate; calyx 5-angled or -lobed; ± persistent in fruit; petals 0; disk patelliform or cupular; ovary 2–6-locular, pubescent; ovules anatropous; stylodia stigmatiform, coalescing into a disk. Fruits separting into indehiscent, sometimes fleshy, cocci; columella not persistent. Seeds spheroidal, ecarunculate, testa rugose or verrucose. $n = 24$.

About 10 spp., distributed from China to northern Australia, Melanesia and Fiji. All Malesian *Endospermum* have extrafloral nectaries on the lower leaf surface, and two New Guinean species are myrmecophilous, of which one, *E. moluccanum* (Teijsm. & Binn.) Kurz, produces food bodies on which the ants feed (Guerrero and van Welzen 2011).

2. Tribe Gelonieae (Müll. Arg.) Pax (1890).

Dioecious trees or shrubs, without evident latex; indumentum simple, usually scanty or 0; leaves alternate, simple; inflorescences leaf-opposed; flowers in glomerules; disk receptacular or extrastaminal; stamens 6–60; pollen grains spheroidal, pantoporate, sexine with Croton pattern; ovules with inner integuments thin, not vascularized.

Two genera, Africa, Madagascar, and tropical Asia.

Key to the Genera of Gelonieae

1. Inflorescences leaf-opposed; pistillode 0; stylodia bifid or multifid, branches terete, not dilated; leaves petiolate, lamina pellucid-punctate, stipules deciduous **198. *Suregada***
– Inflorescences terminal; pistillode present; stylodia dilated, stigmatiform; branches flattened, dilated; lamina not pellucid-punctate; stipules foliaceous, persistent **199. *Cladogelonium***

198. *Suregada* Roxb. ex Rottl.

Suregada Roxb. ex Rottler, Ges. Naturf. Freunde Berlin, Neue Schriften 4: 206 (1803); Baillon, Étude Gén. Euphorb.: 395 (1858); Croizat, Bull. Bot. Gard. Buitenzorg III, 17: 212 (1942); Léonard, Bull. Jard. Bot. Brux. 28: 79 (1958), Fl. Congo 8(1): 124 (1962); Radcl.-Sm., Fl. E. Trop. Afr., Euphorb. 1: 376, fig. 71 (1987), Fl. Zambes. 9(4): 249, t. 53 (1996); Radcl.-Sm. et al., Kew Bull. 58: 965–970 (2003), key Malagasy spp.; Li-Bingtao & Esser, Fl. China 11: 276 (2008). *Gelonium* Roxb. ex Willd. (1806; nom. illeg.).

Dioecious trees or shrubs, without evident latex; indumentum simple, usually scanty or 0. Leaves usually pellucid-punctate, without excavated glands; stipules deciduous. Inflorescences leaf-opposed, glomerular, sessile or subsessile. Staminate flowers subsessile or pedicellate; sepals 5(6), distinct, broadly imbricate; petals 0; disk receptacular or extrastaminal, annular or dissected; stamens (6)10–30(−60), filaments distinct; anthers dorsifixed, introrse, muticous; pollen grains spheroidal, 2-nucleate, 3–6-porate; sexine tectate with clavate pillars in Croton pattern; pistillode 0. Pistillate flowers subsessile or pedicellate; sepals (4)5(−8), distinct, imbricate, entire, persistent in fruit; petals 0; disk annular, tenuous, sometimes with staminodes; ovary (2)3(4)-locular; ovules pachychalazal, inner integuments thin; stylodia bifid or multifid, branches slender. Fruits capsular or sometimes indehiscent; columella persistent. Seeds ellipsoid, ecarunculate, testa smooth. $2n = 22$.

About 30 spp., Africa/Madagascar and tropical Asia.

199. *Cladogelonium* Leandri

Cladogelonium Leandri, Bull. Soc. Bot. France 85: 530, t. 1.15–19bis (1938); Webster, Ann. Missouri Bot. Gard. 81: 131 (1994); Radcl.-Sm., Gen. Euphorb.: 284, fig. 38 (2001).

Monoecious shrubs; branches sympodial, flattened into platyclades similar in texture to the leaves; latex not recorded; indumentum 0. Leaves not pellucid-punctate, obscurely dentate and with abaxial excavated marginal glands; stipules foliaceous, persistent. Inflorescences terminating sympodial axes, glomerulate, unisexual, sessile. Staminate flowers pedicellate; sepals 5, imbricate, distinct, each with an abaxial gland; petals 0; stamens 10, filaments distinct; anthers dorsifixed, extrorse; pistillode 3-fid. Pistillate flowers solitary, pedicellate; sepals 5, distinct, imbricate, each with an abaxial gland; petals 0; disk tripartite [staminodial?]; ovary 3-locular; stylodia stigmatiform. Fruit capsular. Seeds ellipsoid, with minute caruncle, testa foveolate.

A single very rare sp., *C. madagacariense* Leandri, in dry deciduous forest of Madagascar. It appears to be a satellite genus of *Suregada*, from which it differs in details of inflorescence and floral structure. Lobreau-Callen and Suarez Cervera (1997) report 3- or 6-colpate pollen from *Cladogelonium* and a nexine structure similar to *Tetrorchidium*; they suggest the transfer of the genus to Adenoclineae.

3. Tribe Elateriospermeae G.L. Webster (1975).

Monoecious laticiferous trees; leaves biglandular at base; pollen inaperturate; fruits capsular; seeds ecarunculate.

A monotypic paleotropical tribe. Although articulated laticifers are not yet documented for this genus (and not for *Glycydendron* either), the lack of petals, the presence of a vascularized inner integument, and the molecular data safely place them into the articulated crotonoids. For the problematic "inaperturate" pollen grains, see Nowicke (1994).

200. *Elateriospermum* Blume Fig. 37

Elateriospermum Blume, Bijdr.: 620 (1826); Whitmore, Tree Fl. Malaya 2: 91, fig. 6 (1973); Hoang Van Sam & van Welzen, Blumea 49: 427–436 (2004).

Monoecious trees; stems with white latex; indumentum simple or 0. Leaves long-petiolate, biglandular at junction with petiole; stipules deciduous. Inflorescences axillary, dichasial, bisexual, pistillate flower central; bracts minute. Staminate flowers pedicellate; sepals 4–5, distinct, imbricate; petals 0; disk massive, lobed, pubescent; stamens 10–20 or more, filaments distinct; anthers introrse, connective apiculate; pollen grains spheroidal, exine with Croton pattern, muri broad, pillars angular; pistillode minute or 0. Pistillate flowers pedicellate; sepals (4)5(−7), distinct, entire, deciduous (?); disk annular, with subulate staminodia; ovary 2–4-locular, villose; ovules with inner integuments thin, vascularized; stylodia 2–4, massive, stigmas thick, dilated. Fruits capsular, endocarp thick and woody; columella not persistent. Seeds over 3 cm long, testa smooth; endosperm scanty, cotyledons massive.

A single sp., *E. tapos* Blume, distributed in lowland rainforests from peninsular Thailand through Malaya to Sumatra, Java and Borneo.

4. Tribe Manihoteae (Müll. Arg.) Pax (1890).

Monoecious (dioecious); laticifers articulated, latex white; indumentum simple (urticant); leaves mostly palmately lobed or dissected, sometimes unlobed; staminate calyx synsepalous; disk intrastaminal or extrastaminal; stamens 8–10

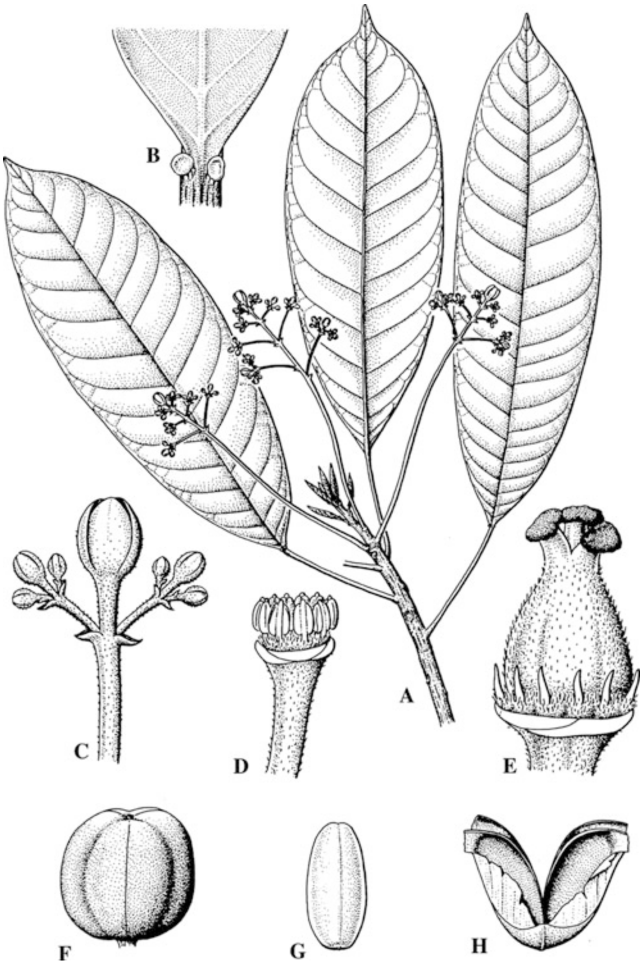

Fig. 37. Euphorbiaceae-Crotonoideae. *Elateriospermum tapos.* **A** Flowering branch. **B** Basal leaf glands. **C** Part of inflorescence with one pistillate and six staminate flower buds. **D** Staminate flower with sepals removed. **E** Pistillate flower with sepals removed, showing pistil and disk lobes. **F** Fruit. **G** Seed. **H** Fruit valves with complete septicidal dehiscence and partly loculicidal dehiscence. (Hoang Van Sam & van Welzen 2004; drawn by J. van Os)

(−25); pollen grains 3-nucleate, pantoporate; inner integuments thick, vascularized.

A small neotropical tribe of only two genera but with over 100 spp., mostly found in deciduous or thorn forests in arid regions of both North and South America.

KEY TO THE GENERA OF MANIHOTEAE

1. Stinging hairs 0; stamens distinct, staminate disk intrastaminal, perianth usually yellowish or greenish; leaf blades stipellate at base; inflorescence racemoid or racemose-paniculate **201. *Manihot***
– Stinging hairs +, very rarely 0; stamens connate, very rarely distinct; staminate disk extrastaminal, perianth whitish; leaf blades glandular at base; inflorescence dichasial-paniculate **202. *Cnidoscolus***

201. *Manihot* Miller

Manihot Miller, Gard. Dict. ed. 4 (1754); Pohl, Pl. Bras. Ic. 1: 17 (1827); Croizat, J. Arnold Arb. 23: 216 (1942); Webster, J. Arnold Arb. 48: 345 (1967); Rogers & Appan, Fl. Neotrop. 13: 1, figs. 9–124 (1973); Allem, Rev. Brasil. Biol. 49: 1 (1989), Genet. Res. Crop Evol. 41: 133 (1994).
Manihotoides C.J. Rogers & Appan (1973).

Monoecious trees or shrubs, sometimes scandent or nearly herbaceous, often with tuberous roots; latex white; indumentum simple or 0. Leaves mostly long-petiolate, simple, mostly palmately lobed, entire (serrulate), stipellate at junction with petiole; stipules mostly deciduous. Inflorescences terminal or pseudo-axillary, racemoid or paniculate, pistillate flowers generally basal, staminate in distal glomerules; bracts entire to laciniatae, mostly deciduous. Staminate flowers subsessile to pedicellate; sepals 5, imbricate, ± connate basally; petals 0; disk central, intrastaminal, entire or 5-lobed, lobes ± bifid; stamens 10, biseriate, filaments distinct; anthers introrse; pollen spheroidal, pantoporatae; pistillode rudimentary or 0. Pistillate flowers distinctly pedicellate; sepals 5, imbricate, deciduous in fruit; disk annular, fleshy, scarcely lobed; ovary 3-locular, glabrous; ovules anatropous, thick, vascularized; stylodia basally connate, branches dilated to lacerate. Fruits capsular, sometimes ribbed or winged; columella often persistent. Seeds carunculate, testa smooth. $2n = 36$.

About 100 spp. in the Neotropics, divided by Rogers and Appan (1973) into 19 sections, plus the proposed segregate genus *Manihotoides*, which could easily be accommodated in *Manihot* adjacent to sect. *Parvibracteatae*.

202. *Cnidoscolus* Pohl

Cnidoscolus Pohl, Pl. Bras. Icon. Descr. 1: 56 (1827); León, Mem. Soc. Cubana Hist. Nat. 15: 235, t. 23, 24 (1941); Lourteig & O'Donell, Lilloa 9: 105, figs. 5–9 (1943); McVaugh, Bull. Torrey Bot. Club 71: 457 (1944); Breckon, Brittonia 31: 125, figs. 3–6 (1979); Fernández Casas, Fontqueria 55: 69 (2002).
Victorinia León (1941).

Monoecious trees, shrubs, or perennial herbs; stems with septate pith; latex white; indumentum simple and urticant. Leaves palmately (pinnately) veined or lobed or sometimes dissected, glandular at junction with petiole; stipules entire to laciniate, ± glandular, mostly persistent. Inflorescences terminal or sometimes pseudo-axillary, pedunculate, dichasial, pistillate flowers at proximal nodes, staminate in clusters at distal nodes; bracts entire to laciniate, sometimes foliaceous, eglandular. Staminate flowers subsessile or short-pedicellate; sepals imbricate, connate, the calyx ± salverform; disk annular, extrastaminal; stamens 8–10(−25), filaments connate into a column or those in the outer whorl distinct [all filaments distinct in *C. urnigerus*]; anthers in 2–3 (4–5) whorls, basifixed to dorsifixed, introrse; pollen grains spheroidal, 3-nucleate, pantoporate, sexine with angular pillars; pistillode of 3 filiform processes atop the column. Pistillate flowers subsessile or pedicellate; sepals 5, distinct or connate, entire, deciduous in fruit; petals 0; disk annular, sometimes with staminodia; ovary 3-locular, often with urticant hairs; ovules anatropous, inner integuments thick, vascularized; stylodia distinct or nearly so, multifid (bifid). Fruits capsular or less often fleshy and tardily dehiscent; columella slender, persistent. Seeds carunculate, testa smooth. $2n = 36$.

About 70 spp. in the Neotropics. McVaugh (1944) recognized 5 sections that have not yet been evaluated by a phylogenetic analysis. Speciation has been most pronounced in Mexico; Breckon (1975) revised sect. *Calyptosolen* and recognized 20 species in Mexico and Central America.

5. TRIBE MICRANDREAE (Müll. Arg.) G.L. Webster (1975).

Monoecious or dioecious; stems with inarticulated laticifers and usually whitish latex; indumentum simple or stellate; leaves unlobed, entire; disk dissected, lobed, or 0; pollen grains 3-nucleate, 3-colpate, colpi operculate; inner integument thick, vascularized.

This tribe resembles various taxa of subfam. Acalyphoideae; *Micrandra* in particular shows many acalyphoid characters, resembling Cheiloseae in its androecium and Alchorneae in its operculate pollen grains.

KEY TO THE GENERA OF MICRANDREAE

1. Sepals connate; staminate disk 0; stamens 8–10; floral bracts large **204. *Cunuria***
– Sepals distinct; staminate disk +; stamens 5–8; floral bracts small 2
2. Indumentum simple; anthers elliptical; pollen muri smooth **203. *Micrandra***
– Indumentum stellate; anthers linear; pollen muri irregularly appendaged **205. *Micrandropsis***

203. *Micrandra* Benth.

Micrandra Benth., Hook. Kew J. Bot. 6: 371 (1854; nom. cons.); Schultes, Bot. Mus. Leafl. 15: 201, t. 66–73 (1952); Webster, Ann.. Missouri Bot. Gard. 81: 98 (1994); Radcl.-Smith, Gen. Euphorb.: 268 (2001); Berry & Wiedenhoeft, Syst. Bot. 29: 125–133 (2004).

Monoecious trees, often buttressed or with stilt roots at base; laticifers non-articulated; latex copious, white; indumentum simple. Leaves eglandular at base [except *M. elata*]; stipules mostly deciduous. Inflorescences terminal on principal and lateral shoots, pedunculate; staminate flowers in glomerules, pistillate solitary at tips of lateral axes; bracts entire, eglandular, deciduous. Staminate flowers subsessile or pedicellate; sepals 5, valvate or slightly imbricate; petals 0; disk-segments 5; stamens usually 4 or 5, filaments distinct, apically inflexed in bud; anthers subglobose, dehiscing laterally; pollen grains spheroidal, 3-colpate, colpi operculate, sexine [except in *M. elata*] tectate-reticulate, with smooth muri; pistillode much shorter than filaments or obsolete. Pistillate flowers subsessile; sepals 5, entire, distinct, deciduous; petals 0; disk annular; ovary 3-locular, sericeous, ± beaked; ovules anatropous, inner integument thick, vascularized; stylodia distinct, bifid. Fruits capsular; columella slender, subpersistent. Seeds large, > 1 cm long, ecarunculate or with rudimentary caruncle, testa smooth.

Five or six neotropical spp. from lowland Amazonian forests; following Webster (1994) and in contrast to Govaerts et al. (2000) and Berry and Wiedenhoeft (2004), *Micrandra* is here delimited to exclude *Cunuria*. Even in this limited sense, it is heterogeneous: *M. siphonioides* Benth. and *M. minor* Benth. have 3-colpate operculate pollen grains with tectate-reticulate exine very suggestive of pollen grains in the

Acalyphoideae, but *M. elata* has pollen grains with Crotonoid ornamentation distinct from all other Micrandrinae. *M. inundata* P.E. Berry & A.C. Wiedenhoeft is known from the banks of seasonally flooded blackwater rivers in southwestern Venezuela; its trunks consist of very lightweight wood.

204. *Cunuria* Baill.

Cunuria Baill., Adansonia I, 4: 287 (1864); Baldwin & Schultes, Bot. Mus. Harvard Univ. 12: 325, t. 42–46 (1947); Webster, Ann. Missouri Bot. Gard. 81: 98 (1994); Radcl.-Sm., Gen. Euphorb.: 270 (2001).

Monoecious or dioecious trees; laticifers non-articulated, latex white or yellow; indumentum simple. Leaves biglandular at basal juncture with petiole; stipules deciduous. Inflorescences terminal or axillary, pedunculate, dichasially paniculate; staminate flowers in glomerules, pistillate solitary, terminal on axes; bracts entire, eglandular, deciduous. Staminate flowers sessile or subsessile; sepals 5, distinct, imbricate; petals and disk 0; stamens 7–10, distinct; anthers dorsifixed, muticous; pollen grains spheroidal, 3-colpate, colpi operculate, sexine with raised muri and usually regular or irregular processes; pistillode trifid. Pistillate flowers subsessile; sepals 5, imbricate, entire, deciduous; disk cupular or annular, sometimes lobed; ovary 3-locular, glabrous or pubescent; stylodia bifid, branches thickened. Fruits capsular. Seeds ecarunculate; testa smooth and shiny.

Six neotropical spp. This genus was generally accepted by botanists until Schultes (1952) decided to combine it with *Micrandra*, in which he is followed by Berry and Wiedenhoeft (2004). However, if *Micrandra elata* is transferred to *Cunuria*, the remainder of the *Micrandra* species differ from *Cunuria* in having leaf blades without basal glands and very different pollen ornamentation.

205. *Micrandropsis* W.A. Rodrigues

Micrandropsis W.A. Rodrigues, Acta Amazonica 3(2): 5 (1973); Webster, Ann. Missouri Bot. Gard. 81: 98 (1994); Murillo & Franco, Euphorb. Reg. Araracuara 117, fig. 119 (1995); Radcl.-Sm., Gen. Euphorb.: 270, fig. 37 (2001).

Monoecious trees; latex scanty; indumentum minute, stellate. Leaves with 1 or 2 sessile glands at juncture with petiole. Inflorescences terminal on principal and lateral axes, pedunculate, staminate flowers in few-flowered dichasia, pistillate flowers solitary; bracts glandular or eglandular. Staminate flowers subsessile; sepals 5, distinct, imbricate; disk 5-lobed; stamens 5(−7), filaments distinct; anthers linear; pollen grains spheroidal, 3-colpate, tectate-reticulate with irregularly spinose muri; pistillode 0. Pistillate flowers subsessile; sepals 5, distinct, entire, deciduous in fruit; disk annular, tenuous; ovary 3-locular, sericeous. Fruits capsular, valves rugose; seeds carunculate.

A single sp., *M. scleroxylon* (W.A. Rodrigues) W.A. Rodrigues from the lowland rainforest in the vicinity of Manaus, Amazonas, Brazil, but later reported from Amazonian Colombia by Murillo & Franco (1995). The pollen grains of *Micrandropsis* are quite distinct from both *Micrandra* and *Cunuria* in their unique irregularly ornamented muri.

6. TRIBE HEVEEAE (Müll. Arg.) G.L. Webster, stat. nov.[1]

Monoecious; leaves palmately compound; inflorescence with terminal pistillate flower; staminate sepals connate, valvate; stamen filaments connate into a column; pollen grains 3-colpate, colpi operculate, sexine tectate-baculate.

In Webster (1994), *Hevea* was assigned to subtribe Heveinae in the Micrandreae. However, *Hevea* differs from the Micrandreae in a number of characters, such as its articulated laticifers, gamophyllous calyx, connate stamens, very fine pollen exine ornamentation, and palmately compound leaves. It appears that *Hevea* has more in common with the Manihoteae, despite differences in pollen apertures.

206. *Hevea* Aubl. Fig. 38

Hevea Aubl., Hist. Pl. Guiane Fr. 2: 871, t. 335 (1775); Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 217 (1935); Schultes, Bot. Mus. Leafl. Harvard Univ. 25: 243, t. 51, 52 (1977); Bot. Review 36: 197 (1970); Malaysian Rubber Res. Dev. Board Mon. 14: 5 (1990); Murillo & Franco, Euforb. Reg. Araracuara 78, figs. 17, 18 (1995); Hoang Van Sam & van Welzen, Blumea 49: 427–435 (2004).

Monoecious trees; laticifers articulated, latex whitish; indumentum simple. Leaves palmately compound, with 1–3 raised glands at apex of petiole, leaflets entire; stipules entire, deciduous.

---

[1] Tribus **Heveeae** (Müll. Arg.) G.L. Webster, **stat. nov.** Basionym: Subtribus Heveinae Müller Argoviensis, Linnaea 34: 202 (1865). Type: *Hevea* Aubl.

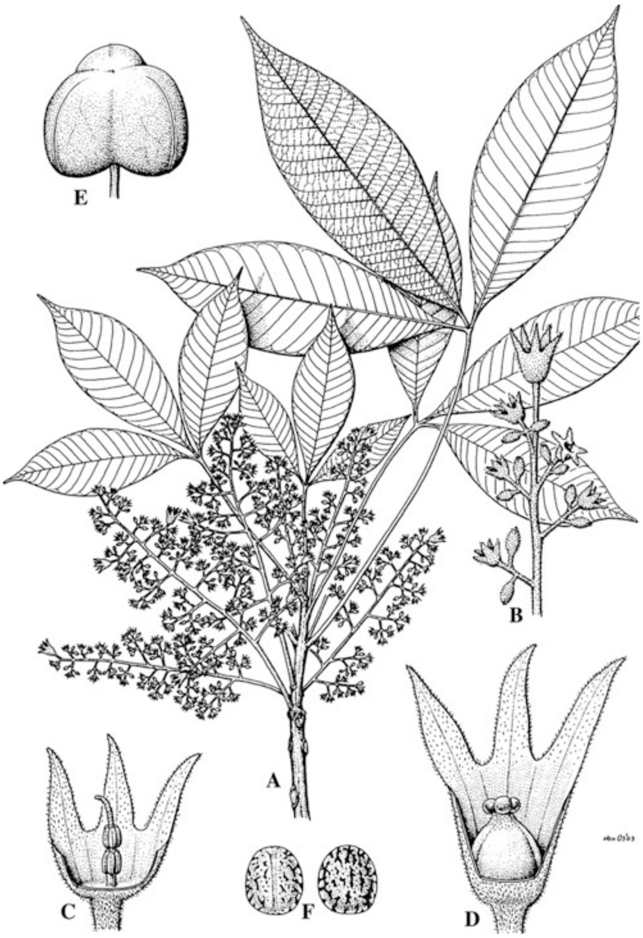

Fig. 38. Euphorbiaceae-Crotonoideae. *Hevea brasiliensis*. **A** Flowering branchlet. **B** Part of inflorescence with a large terminal pistillate flower and smaller staminate flowers. **C** Staminate flower, part of calyx removed. **D** Pistillate flower, part of calyx removed. **E** Fruit. **F** Seed, ventral and dorsal view. (Hoang Van Sam and van Welzen 2004; drawn by J. van Os)

Inflorescences axillary, paniculate with dichasial subunits, the pistillate flowers solitary and terminal on lateral axes; bracts small, entire, deciduous. Staminate flowers pedicellate; sepals connate with valvate lobed; disk segments distinct or connate; stamens 6–9 (10) in 2 irregular whorls; anthers sessile; pollen grains 3-colpate, colpi inoperculate, sexine tectate-reticulate, muri hexagonal or pentagonal, with rounded or angular projections; pistillode represented by terminal appendage of staminal column. Pistillate flowers pedicellate, sepals 5, connate, deciduous in fruit; disk rudimentary or 0; ovary 3-locular; ovules anatropous, inner integuments thick, vascularized; stylodia basally connate, stigmatiform. Fruits capsular; columella fragile, semipersistent. Seeds ellipsoid, smooth, ecarunculate; endosperm oily. $n = 18$.

According to Schultes (1970), *Hevea* includes nine spp. with a total of five varieties that are essentially confined to the Amazon basin, although *Hevea brasiliensis* (A. Juss.) Müll. Arg. is widely cultivated circumtropically. In its compound leaves and connate sepals and stamens, *Hevea* is distinct from the taxa of tribe Micrandreae; however, the pollen grains show some similarities to species such as *Micrandra lopezii*.

Unplaced genus with a strong affinity to the articulated crotonoids:

207. *Glycydendron* Ducke

Glycydendron Ducke, Arq. Jard. Bot. Rio Janeiro 3: 199 (1922), 4: 107, t. 10 figs. a–i (1925); Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 181 (1931, as *Glycynodendron*); Webster, Ann. Missouri Bot. Gard. 81: 100 (1994); Vásquez Martínez, Fl. Res. Biol. Iquitos, Peru: 287, t. 35A (1997); Radcl.-Sm., Gen. Euphorb.: 277 (2001).

Dioecious trees; latex whitish, translucent; indumentum simple. Leaves long-petiolate, deciduous before flowering, simple, entire, triplinerved, with paired adaxial excavated basal glands; stipules minute, deciduous. Inflorescences axillary, staminate also subterminal, sometimes fasciculate, the staminate cymose-paniculate, pistillate racemose; bracts minute, eglandular. Staminate flowers pedicellate; sepals 4, distinct, imbricate; petals 0; disk glands intrastaminal on the pilose receptacle; stamens 25–30, filaments distinct; anthers introrse, basifixed, muticous; pollen grains oblate, 3-colpate, sexine tectate with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4, imbricate, distinct, entire, deciduous; petals 0; disk annular with staminodia; ovary 2-locular, sericeous; ovules anatropous, inner integuments 8–10 cells thick, vascularized; stylodia distinct, bipartite. Fruits drupaceous, 1-seeded, endocarp woody. Seeds ecarunculate.

Probably monotypic, *G. amazonicum* Ducke appears to be common and widespread from Pará in eastern Brazil west to Ecuador, Peru, and Bolivia, with an outlying population in the mata atlántica of eastern Brazil (Espírito Santo). In the molecular analyses (Wurdack et al. 2005; Tokuoka 2007), it is resolved in the articulated crotonoids; in its larger stamen number and drupaceous fruit, it comes close to paleotropical *Elateriospermum*.

7. TRIBE JATROPHEAE (Meisn.) Pax (1890).

Monoecious (dioecious); stems with articulated and/or non-articulated laticifers, the latex white or reddish; indumentum simple, sometimes glandular; leaves simple to deeply palmately lobed or compound; pollen grains spheroidal, binucleate, inaperturate, sexine with Croton pattern; inner integuments thick, vascularized.

Three genera, two of which are neotropical whereas one, *Jatropha*, is well developed in America and Africa and extends to Madagascar and Asia. Among the genera previously placed in this tribe, *Leeuwenbergia* safely belongs to the inaperturate crotonoid clade C2 with the large deletion in the *trn*L-F spacer (Wurdack et al. 2005), whereas molecular data for the Old World *Deutzianthus* and *Oligoceras* are lacking (provisionally placed in Aleuritideae-Grosserinae).

KEY TO THE GENERA OF JATROPHEAE

1. Leaves simple, entire, elobate; stipules infra-axillary, deciduous; seeds ecarunculate **210. *Vaupesia***
– Leaves palmately lobed or palmately compound; stipules not infra-axillary or 0 2
2. Leaves 3- to more palmatilobed or -partite; sepals distinct, covering the petals in bud; fruit capsular; seeds carunculate **208. *Jatropha***
– Leaves compound; staminate calyx open in bud, not covering the petals; fruit drupaceous; seeds ecarunculate **209. *Joannesia***

208. *Jatropha* L.

Jatropha L., Sp. Pl.: 1006 (1753); Müll. Arg. in DC., Prodr. 15(2): 1076 (1866); Pax, Pflanzenr. 147, I: 21 (1910); McVaugh, Bull. Torrey Bot. Club 72: 271, figs. 1–24 (1944); Webster, J. Arnold Arb. 48: 340 (1967); Dehgan & Webster, Univ. California Publ. Bot. 74: 35, t. 1–33 (1979); Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 343, figs. 65–67 (1987).

Monoecious (dioecious or gynodioecious) trees, shrubs, or herbs often with thickened caudices or rhizomes; stems with articulate, inarticulate, or idioblastic laticifers producing yellowish to red latex; indumentum simple, sometimes glandular. Leaves petiolate to subsessile, simple to palmately 3–7-lobed or divided, entire to serrate, lacking paired basal glands; stipules entire to dissected, sometimes glandular or spinose (obsolete). Inflorescences axillary to terminal, often long-pedunculate, of simple to paniculate cymes, sometimes solitary and axillary; pistillate flowers central in bisexual cymules. Staminate flowers pedicellate; sepals 5, imbricate, distinct to basally connate, entire to dentate, sometimes foliaceous; petals 5, distinct to coherent or connate; disk entire to lobed or dissected; stamens (6–)8–10 (−12), filaments distinct or connate; anthers mostly biseriate, dorsifixed; pollen grains spheroidal, binucleate, inaperturate, exine with Croton pattern, pillars rounded or angular, smooth or sulcate; pistillode 0. Pistillate flowers pedicellate; sepals 5, nearly distinct, imbricate, entire or dentate, persistent in fruit; petals 5, distinct to coherent or connate, imbricate; disk annular or deeply lobed; ovary (1–)3-locular, glabrous or pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid, sometimes dilated (multifid). Fruits capsular, sometimes with fleshy exocarp and tardily dehiscent, (1–) 3-seeded; columella generally not persistent. Seeds ellipsoidal to spherical, carunculate; testa thin and smooth; endosperm oily; cotyledons much longer and broader than radicle. $2n = 22$.

Over 180 spp., widely distributed in the tropics and subtropics of America and Africa, rare in Madagascar and Asia. The circumscription of *Jatropha* in the 19th and early 20th century was confused due to the mistaken inclusion of *Cnidoscolus* by Müller (1866) and Pax (1910), but McVaugh (1944) demonstrated that the two genera are not closely related.

209. *Joannesia* Vell.

Joannesia Vell., Alogr. Alkalis: 199 (1798); Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 198, t. 21 (1922); Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 25 (1955); Radcl.-Sm., Gen. Euphorb.: 292 (2001).

Monoecious trees; laticifers non-articulate, branches sometimes with viscid reddish latex; indumentum simple. Leaves palmately compound; leaflets entire; petioles with 2 apical glands; stipules gland-tipped or obsolete. Inflorescences terminal or subterminal, bisexual, cymose-paniculate; bracts entire, deciduous. Staminate flowers pedicellate; calyx cupular-truncate, the 5 sepals represented by minute teeth; petals 5, distinct, imbricate, much longer than calyx, pubescent on both faces; disk segments 5; stamens 7–10, filaments biseriate, the inner longer; anthers basifixed-cordate, introrse or latrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode usually 0. Pistillate flowers subsessile, calyx and petals as in the staminate; disk dissected into 5 segments; ovary 2-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia short, stigmas lobate. Fruits drupaceous or subdehiscent, verrucose, exocarp 1 cm thick. Seeds ecarunculate, endosperm oleaginous.

Three neotropical spp., from Venezuela and Amazonian and coastal Brazil.

210. *Vaupesia* R.E. Schultes

Vaupesia R.E. Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 27, t. 12 (1955); Murillo & Franco, Euforb. Reg. Araracuara 158, fig. 48 (1995); Radcliffe-Smith, Gen. Euphorb.: 290 (2001).

Monoecious trees; latex of trunk whitish, scanty, of branches reddish. Leaves with conspicuous basal glands; stipules deciduous. Inflorescences terminal, bisexual, paniculate; bracts entire, persistent. Staminate flowers pedicellate; sepals 5, imbricate, entire; petals 5, entire; disk segments 5, at base of staminal column; stamens 8, filaments connate into a column; anthers biseriate; pollen grains spheroidal, inaperturate, exine with hexagonal pillars; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, margins fimbriate; petals 5, entire; disk 5-lobed, reddish; ovary 3-locular; stylodia proximally connate, bifid. Fruits capsular, thick-walled; columella not persistent. Seeds ecarunculate, subprolate, compressed, dorsally carinate, with conspicuous hilum.

One sp., *V. cataractarum* R.E. Schultes, from the upper Rio Negro region in SE Colombia and adjacent Brazil.

8. Tribe Crotoneae Dumort. (1829).

Monoecious (dioecious) trees, shrubs, or herbs; laticifers non-articulated, latex clear to yellowish or reddish, sometimes 0; indumentum simple, lepidote, or stellate; leaves simple to palmately lobed with or without basal paired glands; stamens 3–400; anthers extrorse; pollen grains trinucleate, spheroidal, inaperturate, with Croton pattern; ovules with thick vascularized inner integuments; stylodia distinct or basally connate, bifid to multifid; seeds mostly carunculate; cotyledons mostly broader than radicle.

Following the molecular work of Berry et al. (2005) and Wurdack et al. (2005), tribe Crotoneae is here construed to comprise several genera that formerly were included in tribe Codiaeae (*Sagotia*, *Acidocroton* with *Ophellanthe*) and tribe Aleuritideae (*Sandwithia*). The close relationship between *Sagotia* and *Sandwithia* had first been recognized by Secco (1988).

Key to the Genera of Crotoneae

1. Indumentum simple 2
– Indumentum stellate and/or lepidote 4
2. Inflorescences axillary; stipules transformed into spines **213. *Acidocroton***
– Inflorescences mostly terminal; stipules not transformed into spines 3
3. Staminate sepals 2–3, completely connate in bud; disk +; stylodia connate into a common style with distal bifid or entire style branches **211. *Sandwithia***
– Staminate sepals 5(6), distinct; disk 0; stylodia distinct or nearly so, bifid **212. *Sagotia***
4. Stamen filaments not inflexed in bud; stylodia deeply bifid **215. *Brasiliocroton***
– Stamen filaments distinctly inflexed in bud; stylodia bifid to multifid 5
5. Stamens (3)8–20(–400); receptacle usually pilose; seeds terete to compressed; stylodia various **216. *Croton***
– Stamens 8–15; receptacle usually glabrous; seeds quadrangular; stylodia multifid **214. *Astraea***

211. *Sandwithia* Lanj.

Sandwithia Lanj., Kew Bull. 1932: 184 (1933); Jablonski, Mem. N. Y. Bot. Gard. 17: 152 (1967); Secco, Bull. Mus. Par. Emilio Goeldi Bot. 3: 157 (1987), 4: 177 (1988); Fl. Venez. Guayana 5: 217, fig. 203 (1999).

Monoecious or dioecious trees; latex reddish; indumentum simple. Leaves alternate, petiolate (slightly pulvinate at apex), entire, eglandular; stipules deciduous. Inflorescences terminal, flowers in cymose racemes or clusters; bracts deciduous. Staminate flowers pedicellate; sepals 2 or 3, completely connate in bud; petals 3 or 4, distinct, imbricate, s.t. reduced; disk segments 2–4, receptacle pilose; stamens 15–25, filaments distinct; pollen grains spheroidal, inaperturate, exine granular, with Croton pattern, pillars smooth; pistillode 0. Pistillate flowers pedicellate; sepals 4, ± connate, tips imbricate in bud, erect; petals 4, minute, deciduous; disk annular; ovary 3-locular, pilose; stylodia connate into a common style with bifid or entire style branches. Fruits capsular; columella not persistent? Seeds carunculate, testa smooth.

Two spp., Amazonian South America.

212. *Sagotia* Baill.

Sagotia Baill., Adansonia I, 1: 53 (1860; nom. cons.); Jablonski, Mem. N. Y. Bot. Gard. 17: 151 (1967); Secco, Acta Amazonica 15 (1–2, suppl.): 81 (1985); Rev. Gen. *Anomalocalyx*, etc.: 99, figs. 29–34 (1990); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994).

Monoecious trees or shrubs; latex clear, yellowish, or reddish; indumentum simple. Leaves petiolate (pulvinate), entire, eglandular; stipules deciduous, leaving annular scars. Inflorescences terminal, racemoid or thyrsoid-paniculate, unisexual or bisexual; pistillate flowers proximal; bracts deciduous. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 5 (7), distinct, imbricate, longer than the sepals; disk not evident; stamens 20–30, filaments distinct; anthers subsessile, basifixed, latrorse, connective broad; pollen grains spheroidal, inaperturate, exine granular, with Croton pattern, pillars acute or spinose; pistillode 0. Pistillate flowers pedicellate; sepals 5 (6), distinct, recurved, persistent and accrescent in fruit; petals and disk 0; ovary 3-locular, pilose; ovules pachychalazal, inner integuments thick, vascularized; stylodia distinct or early so, bifid. Fruits capsular; columella not persistent. Seeds ellipsoidal, carunculate, testa smooth.

Two spp., Central America and northern South America, in lowland rainforest.

213. *Acidocroton* Griseb.

Acidocroton Griseb., Fl. Br. W. Ind.: 42 (1859; nom. cons.); Müll. Arg. in DC., Prodr. 15(2): 1042 (1866); Pax, Pflanzenr. 147, I: 13 (1910); Urban, Symb. Ant. 7: 513 (1913); Fawc. & Rend., Fl. Jam. 4: 315, fig. 104 (1920); Alain, Fl. Cuba 3: 73 (1953), Fl. Española 4: 69 (1986); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994); Fernández-Alonso & Jaramillo-Mejía, Caldasia 17: 389 (1995); Radcl.-Sm., Gen. Euphorb.: 303 (2001).
Ophellantha Standl. (1924).

Monoecious shrubs; latex not recorded; indumentum simple. Leaves petiolate to subsessile, entire, eglandular; stipules transformed into spines. Inflorescences unisexual, axillary and glomerular or pistillate flowers solitary and subterminal. Staminate flowers pedicellate; sepals 5–6, imbricate; petals 5–7, distinct, imbricate, glabrous, longer than the sepals; disk annular, pubescent; stamens 20–50(−100), filaments distinct; anthers introrse, with enlarged apiculate connective; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode obsolete. Pistillate flowers pedicellate; sepals 5 or 6, ± imbricate, persistent in fruit and sometimes accrescent; petals rudimentary; ovary 3-locular, glabrous or pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia unlobed or bifid, ± dilated and petaloid. Fruits capsular; sepals 5 or 6, distinct, imbricate, entire, persistent in fruit; columella persistent in fruit. Seeds trigonous, carunculate, testa smooth.

Thirteen spp., of which ten in sect. *Acidocroton* are confined to the West Indies, whereas the three of sect. *Ophellantha* occur from Mexico to Colombia. Radcliffe-Smith (2001) rejects the combining of *Ophellantha* with *Acidocroton* by Webster (1994). However, Radcliffe-Smith's characters based on higher stamen number and lower carpel number in *Ophellantha* do not hold, and the only remaining distinction is in the bifid stylodia and somewhat more accrescent pistillate sepals of *Ophellantha*. *Acidocroton* and *Ophellantha* form a monophyletic group (Berry et al. 2005), and there is little to gain in generic subdivision.

214. *Astraea* Klotzsch

Astraea Klotzsch, Arch. Naturgesch. 7: 194 (1841); Baill., Étude Gén. Euphorb.: 363 (1858, as section); Caruzo & Cordeiro, Hoehnea 34: 572 (2007); Cavalari De-Paula et al., Pl. Syst. Evol. 292: 1–14 (2011), floral morph.

Monoecious subshrubs or herbs; indumentum stellate; laticifers non-articulated, latex scanty or apparently 0. Leaves deeply palmately lobed (simple); stipules entire or dissected, sometimes glandular, persistent. Inflorescences terminal, bisexual, racemoid; pistillate flowers solitary at proximal nodes; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals 5, imbricate; petals 5, imbricate, densely pilose at the basis; receptacle glabrous; disk 5-lobate; stamens 8–15, distinct; filaments glabrous, inflexed in bud; anthers basifixed, muticous; pollen grains spheroidal, with Croton pattern; pistillode 0. Pistillate flowers subsessile, elongating in fruit; sepals 5, valvate, ± glandular-dentate; disk segments 5; ovary glabrous or hispidulous with stellate or simple hairs; stylodia distinct, multifid. Fruits capsular; columella persistent. Seeds quadrangular, rugose, carunculate, caruncle reniform-peltate, testa rugulose-costate. $2n = 18$.

About 10 spp. in the Neotropics. This genus has been treated as a section of *Croton* by nearly all 20th century authors. Webster (1967) remarked that *Astraea* had the best claim of any *Croton* section to generic status, and molecular studies (Berry et al. 2005) have resoled *Astraea* as the sister group of *Acidocroton* in the grade leading from *Jatropha* to *Croton* s.str.

215. ***Brasiliocroton*** P.E. Berry & I. Cordeiro

Brasiliocroton P.E. Berry & I. Cordeiro, Syst. Bot. 30: 357, fig. 2 (2005).

Monoecious tree; indumentum stellate. Leaves with two stipitate glands at the junction with the petiole; stipules filiform, deciduous. Inflorescences terminal bisexual panicles, the distal flowers pistillate and opening earliest. Staminate flowers: sepals 5(6), valvate, slightly connate at base; petals 5(6); disk of 5 distinct antesepalous lobes; stamens (20–)25(−30); filaments erect in bud; anthers bilobed, latrorse; pollen inaperturate with Croton pattern, the subunits striate. Pistillate flowers: sepals 5(6), valvate, basally connate for 1/2 to 2/3 their length; petals 0; disk 5-lobate; ovary 3(4)-locular; ovule 1 per locule; stylodia 3, deeply bifid and basally connate into a short column. Fruits schizocarpic, the exocarp separating from the woody cocci; columella 8–12 mm long. Seeds ellipsoid, dorsally angled, with a small caruncle.

A single sp., *B. mamoninha* P.E. Berrry & I. Cordeiro, lowland forests in N and E Brazil.

216. ***Croton*** L. Fig. 39

Croton L., Sp. Pl. 2: 1004 (1753); Müll. Arg. in DC., Prodr. 15(2): 512 (1866); Ferguson, Rep. Missouri Bot. Gard. 12: 33, t. 4–31 (1901); Hutchinson, Fl. Trop. Afr. 6(1): 746 (1912); Gagnepain, Fl. Indochine 5: 256, figs. 28, 29 (1925); Leandri, Ann. Inst. Bot.-Geol. Colon. Marseille V, 7(1): 1 (1939); Webster, J. Arnold Arb. 48: 358, fig. 2 (1967); Leandri, Adansonia II, 10: 191 (1970); Liogier, Fl. Española 4: 108 (1986); Chakrabarty & Balakrishnan, Bull. Bot. Survey India 34: 1–88, figs. 1–16 (1992); Webster, Novon 2: 270 (1992), Taxon 42: 793 (1993); Ann. Missouri Bot. Gard. 81: 111 (1994), Fl. Nicaragua 1: 864–875 (2001), Contr. Univ. Michigan Herb. 23: 353, fig. 1 (2001); Martínez Gordillo, Contr. Herb. UNAM 2: 9 (1995); Berry, Fl. Venez. Guayana 5: 111, figs. 108–125 (1999); Radcl.-Sm., Gen. Euphorb.: 319 (2001); Berry et al., Amer. J. Bot. 92: 1520–1534 (2005) (mol. systematics); Forster, van Ee & Berry, Syst. Bot. 35: 151–167 (2010), mol. syst. sect. *Heptallon*; Riina et al., Syst. Bot. 34: 360–374 (2009), mol. syst. sect. *Cyclostigma*; Riina et al., Taxon 59: 1147–1160 (2010), mol. syst. sect. *Luntia*; van Ee et al., Taxon 60: 791–823 (2011), rev. class. of New World taxa.

Tridesmis Lour. (1790).

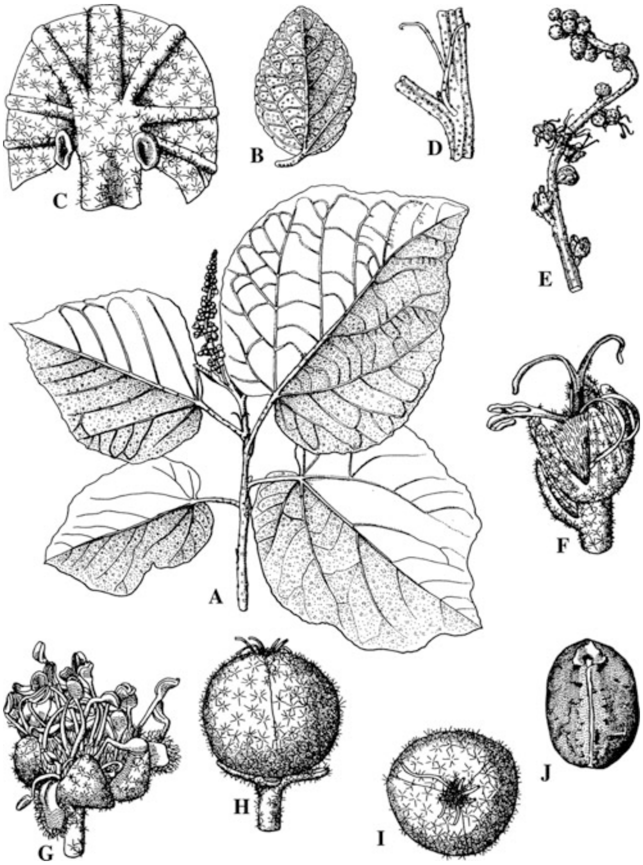

Fig. 39. Euphorbiaceae-Crotonoideae. *Croton arnhemicus.* **A** Flowering branchlet. **B** Undersurface of leaf. **C** Base of leaf lamina showing extrafloral nectaries. **D** Node with stipules. **E** Inflorescence with pistillate flowers in lower half and staminate flowers in upper. **F** Pistillate flower. **G** Staminate flower. **H, I** Fruits. **J** Seed. (P.I. Forster 2003; drawn by W. Smith)

Crotonopsis Michx. (1803).
Julocroton Mart. (1837, nom. cons.).
Eremocarpus Benth. (1844).
Colobocarpos Esser & van Welzen (2001).

Monoecious (dioecious) trees, shrubs, or herbs; laticifers non-articulated (0), latex clear to red or yellow, sometimes resinous; indumentum stellate or lepidote; sessile or stipitate glands sometimes present. Leaves alternate (opposite), simple or lobate, petiolate (sessile), entire, dentate or serrate, usually 2-glandular at the junction of the petiole with the blade; stipules entire or dentate to dissected, persistent or deciduous, sometimes 0. Inflorescences terminal (axillary), usually bisexual, mostly racemoid with solitary pistillate flowers at proximal nodes and glomerules of staminate flowers distally, staminate flowers sometimes 1 per bract; bracts entire to dissected, sometimes glandular. Staminate flowers pedicellate; sepals (4) 5 (6), essentially distinct to connate, imbricate to valvate; petals usually 5(0), distinct, imbricate, glabrous or pubescent; disk entire or dissected; receptacle usually pilose (glabrous); stamens (3–)8–20 (−400), distinct, filaments usually inflexed in bud, glabrous or pubescent; anthers extrorse in bud; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars rounded or angular, mostly sulcate; pistillode 0. Pistillate flowers sessile to pedicellate; sepals (4)5–7 (−10), distinct to connate, imbricate, entire to dentate, usually persistent in fruit and often accrescent; petals 0 (+); disk annular (dissected), sometimes with staminodia [reduced petals?]; ovary 3(−1)-locular; ovules anatropous, inner integuments thick, vascularized; stylodia distinct or basally connate, bifid to multifid. Fruits capsular (indehiscent); columella persistent, usually slender. Seeds terete to compressed, caruncular (arillate), testa smooth. $2n = 20, 28, 64$.

Over 1,200 spp., circumglobal in warm-temperate to tropical regions, 712 spp. recognized for the New World. *Croton* is the second largest genus of Euphorbiaceae and is highly diverse morphologically and cytologically. Not surprisingly, many generic segregates had been proposed in the past but have been brought back to *Croton* again, and those upheld until recently (*Crotonopsis*, *Eremocarpus*, *Julocroton*, *Moacroton*) have been reduced on the basis of extensive molecular studies. There is also evidence pointing to a New World origin of *Croton*, with a subsequent divergence in the Old World, followed, back in the New World, by the principal morphological diversification of the genus (Berry et al. 2005).

Two subgenera:

216a. *Croton* subg. *Croton*

Indumentum mostly stellate; stylodia usually multifid; sepals of pistillate flowers usually valvate.

Contains the bulk of the *Croton* species, which generally show a preference for xeric habitats.

216b. *Croton* subg. *Moacroton* (Croizat) van Ee & P.E. Berry, Bot. Rev. 74: 158 (2008).

Moacroton Croizat (1945); Borhidi, Acta Bot. Acad. Sci. Hung. 36: 7 (1990), rev.
Cubacroton Alain (1960).
Croton sect. *Corylocroton* G.L. Webster (1993).

Indumentum usually lepidote; stylodia bifid or simple; sepals of pistillate flowers usually connate at the base but not valvate.

About 28 or more spp., distributed in North America, Mesoamerica, the Caribbean, and South America, where they generally show a preference for mesic habitats. In addition to the taxa synonymized above, the group comprises a number of South American species of *Croton* hitherto not assigned to a section; they have been revealed as a basal clade of *Croton* by van Ee et al. (2008). The six spp. formerly included in *Moacroton* are endemic to Cuba, where they grow on serpentine outcrops.

9. TRIBE CODIAEAE (Pax) Hutch. (1969).

Monoecious or dioecious trees or shrubs; laticifers non-articulated, latex clear or sometimes reddish; indumentum simple or malpighiaceous; leaves alternate, pinnately veined or triplinerved, usually without laminar glands; stipules deciduous or obsolete; inflorescences terminal or axillary, racemoid-thyrsoid or paniculate; staminate sepals 4–6, distinct or connate, imbricate or valvate; petals 5, distinct, usually imbricate; disk dissected or lobed; stamens (5–)10–100 or more, distinct or basally connate; pollen grains binucleate, spheroidal, inaperturate, exine with Croton pattern; pistillode 0; pistillate sepals 4 or 5, usually imbricate, sometimes accrescent; disk mostly annular; ovary mostly 3-locular; ovules anatropous, inner integuments thick, vascularized; stylodia unlobed to bipartite; fruits capsular; columella usually persistent; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm present.

This pantropical but predominantly Asiatic tribe shows the greatest generic diversity in the Crotonoideae. Further study since the treatment of Webster (1994) has led to the recognition of four subtribes. The geographic distribution of the Codiaeae is distinctive in its primarily South American/Asian concentration (10 genera), with a secondary concentration in Australasia (4 genera), and a single genus (*Pantadenia*) disjunct from southeast Asia to Madagascar; continental Africa is entirely excluded. The treatment of the neotropical taxa adopted here is indebted to the careful work of Secco (1990) on the Amazonian taxa of Codiaeae.

KEY TO THE SUBTRIBES OF CODIAEAE

1. Petals 0 or rudimentary in pistillate flowers **9d. Codiaeinae**
– Petals well-developed in pistillate flowers 2
2. Stamens 3 (5), filaments all connate into a column **9a. Trigonostemoninae**
– Stamens 7 or more, filaments not all connate into a column 3
3. Inflorescences mostly terminal; monoecious (except *Hylandia*); anthers extrorse; seeds carunculate or fruit drupaceous **9b. Baloghiinae**
– Inflorescences mostly axillary; anthers mostly introrse; seeds ecarunculate, fruits capsular **9c. Ostodeinae**

9a. SUBTRIBE TRIGONOSTEMONINAE (G.L. Webster) G.L. Webster[1]

Monoecious; latex reddish; indumentum simple; anthers with enlarged connective; stylodia bifid or twice bifid; fruits capsular. Seeds ecarunculate.

A monogeneric paleotropical subtribe with nearly 100 species. In the molecular analysis (Wurdack et al. 2005), *Trigonostemon* is resolved as the sister group to the rest of the genera forming clade C2.

217. *Trigonostemon* Blume

Trigonostemon Blume, Bijdr. Fl. Ned. Ind. 600 (1825; nom. cons.); Müll. Arg. in DC. Prodr. 15(2): 1105 (1866); Pax & K. Hoffm., Pflanzenr. 147, III: 85 (1911); Gagnepain, Fl. Indochine 5: 309, fig. 35, 3–10 (1925); Airy Shaw, Kew Bull. Add. Ser. 4: 201 (1975), Kew Bull. 35: 352 (1981); Webster, Ann. Missouri Bot. Gard. 81: 108 (1994); Milne, Kew Bull. 50: 23, figs. 1–3 (1995); Radcl.-Sm., Gen. Euphorb.: 307 (2001).
Kurziodendron Balakr. (1966).

Monoecious shrubs or trees; reddish latex sometimes present; indumentum simple. Leaves alternate or opposite, entire, without paired basal glands; stipules entire, ± persistent, sometimes minute. Inflorescences terminal or axillary, usually bisexual, racemoid; bracts entire, eglandular, usually persistent. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, yellow to orange or red, distinct, imbricate, usually longer than calyx; disk dissected or urceolate; stamens 3 (5), filaments connate into a column; anthers extrorse, basifixed, connective enlarged and often apiculate or bifid; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars spinulose; pistillode 0. Pistillate flowers pedicellate; sepals 5, imbricate, entire, persistent in fruit, sometimes accrescent; petals 5, yellow to orange or red, distinct, imbricate, mostly glabrous; disk annular or 5-lobed; ovary 3-locular, glabrous or pubescent; stylodia distinct or nearly so, unlobed to bifid or bipartite. Fruits capsular, cocci thin-walled; columella not persistent. Seeds ecarunculate, testa smooth.

Nearly 100 spp., distributed from India and China south and east to the Philippines, northern Australia (Queensland), New Guinea, and Fiji.

9b. SUBTRIBE BALOGHIINAE G.L. Webster[1]

Dioecious (monoecious); basal laminar glands present or 0; inflorescences terminal or subterminal; pistillate flowers petaliferous; petals longer than sepals; ovary often pubescent; columella usually persistent.

Four Australasian genera. The subtribe is possibly related to subtribe Cocconerioninae in the Ricinocarpeae.

KEY TO THE GENERA OF BALOGHIINAE

1. Indumentum stellate; inflorescences covered with resin **221. *Alphandia***
– Indumentum mainly simple; inflorescences not resinous 2
2. Staminate calyx truncate; fruits drupaceous **220. *Fontainea***
– Staminate calyx distinctly lobed; fruits capsular 3
3. Ovary 3-locular; petals glabrous adaxially **218. *Baloghia***

---

[1] Subtr. **Trigonostemoninae** (G.L. Webster) G.L. Webster, **stat. nov.**, based on Tribe Trigonostemoneae G.L. Webster, Taxon 24: 599 (1975). Type: *Trigonostemon* Blume.

[1] Subtr. **Baloghiinae** G.L. Webster, **subtr. nov.**: plantae dioicae inflorescentiis terminalibus, staminibus 10–100, liberis, antheris extrorsis, seminibus carunculatis vel ecarunculatis. Type: *Baloghia* Endlicher.

– Ovary 2-locular; petals sericeous abaxially
219. *Hylandia*

218. *Baloghia* Endl.

Baloghia Endl., Prodr. Fl. Norf.: 84 (1833); Airy Shaw, Kew Bull. 35: 598 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 43–72, t. 8–13 (1987); Hyland & Whiffin, Austral. Trop. Rain For. Trees 2: 119 (1993).

Monoecious or dioecious trees or shrubs; laticifers non-articulated, latex yellowish to reddish; indumentum simple or 0. Leaves alternate (opposite), pinnately veined, brochidodromous, basal laminar glands mostly 0 [+ on margins near base]; stipules 0. Inflorescences terminal, thyrsoid, unisexual; bracts entire, persistent, uniflorous. Staminate flowers pedicellate; sepals (4)5(6), slightly connate at base, imbricate; petals (4)5(6), white, distinct, usually longer than sepals; disk annular or dissected (0); stamens (10–)40–50(–100), distinct or connate on a ± convex receptacle; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, sexine with Croton pattern, pillars obtuse and slightly sulcate; pistillode 0. Pistillate flowers pedicellate; sepals (4)5(6), imbricate, entire, persistent in fruit; petals (4)5(6), pubescent adaxially; disk annular, sometimes lobed; ovary 3(4)-locular, sericeous; ovules anatropous, inner integuments very thick, vascularized; stylodia bifid to multifid. Fruits capsular; columella persistent. Seeds spheroidal or ellipsoidal, mostly carunculate, testa smooth, exotesta parenchymatous.

Fifteen spp., Australasia, 12 of them endemic to New Caledonia.

219. *Hylandia* Airy Shaw

Hylandia Airy Shaw, Kew Bull. 29: 329 (1974); ibid. 35: 643, fig. 4 (1980); Hyland & Whiffin, Austral. Rain For. Trees 2: 140 (1993).

Dioecious trees; latex viscid, pith reddish; indumentum simple. Leaves with or without raised glands at junction with petiole; stipules 0. Inflorescences terminal, thyrsoid-paniculate; bracts not evident. Staminate flowers pedicellate; sepals 5, distinct, imbricate, unequal; petals 5, white, distinct, imbricate, obovate to spathulate, pubescent adaxially, appressed-sericeous abaxially; disk segments 5, massive, glabrous; stamens 10–16, filaments basally connate; anthers extrorse; pollen grains inaperturate, with Croton pattern; pistillode 0. Pistillate flowers with pedicel articulate near base; sepals 5, distinct, imbricate, entire; petals 5, distinct, whitish, pubescent adaxially and abaxially; disk of 5 lobes or segments; ovary 2-locular, densely hispid-sericeous; stylodia bifid, branches somewhat dilated. Fruits indehiscent, ribbed, exocarp somewhat fleshy. Seeds spheroidal, apparently ecarunculate, testa hard, smooth.

A single sp., *H. dockrillii* Airy Shaw, tropical rainforests of Queensland. *Hylandia* appears to be closely related to the more widely distributed genus *Baloghia*.

220. *Fontainea* Heckel

Fontainea Heckel, Études sur *Fontainea pancheri* (1870); Baillon, Adansonia I, 11: 80 (1873); Airy Shaw, Kew Bull. 35: 632 (1980); Jessup & Guymer, Austrobaileya 2: 112–125, figs. 1–6 (1985); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 74–78 (1987); Forster, Austrobaileya 5: 29–37, figs. 1–3 (1997); Forster & van Welzen, Blumea 44: 101, fig. 2 (1999).

Dioecious (monoecious) trees or shrubs; latex reddish to brown; indumentum simple, scanty. Leaves alternate (opposite), usually with basal or subbasal marginal glands; stipules 0. Inflorescences terminal, sometimes axillary, compound cymose; bracts entire, inconspicuous. Staminate flowers pedicellate; sepals pubescent, connate into a shallowly 3–6-toothed or angled cup; petals 5, white, distinct, densely pubescent, exserted well beyond the calyx; disk obscure; receptacle densely woolly; stamens 18–32 (40), filaments distinct or basally connate; anthers dorsifixed, extrorse, connective sometimes apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars acute, sulcate; pistillode 0. Pistillate flowers pedicellate; sepals connate, dehiscing irregularly, deciduous in fruit; petals 5, white, distinct, exserted from calyx; disk annular, glabrous; ovary (2)3(–6)-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits drupaceous; endocarp bony, angled, sometimes beaked, smooth or rugose. Seeds ecarunculate.

Nine or more spp., distributed from Australia to New Guinea, New Caledonia, and Vanuatu.

221. *Alphandia* Baill.

Alphandia Baill., Adansonia I, 11: 86 (1873); Pax, Pflanzenr. 147, III: 22 (1911); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 86–90, fig. 17 (1987); Airy Shaw, Kew Bull. Add. Ser. 8: 27 (1980).

Monoecious trees or shrubs; stems with yellowish or reddish resinous latex, branches and leaves with resinous exudate; indumentum stellate. Leaves with paired glands at base; stipules 0.

Inflorescences terminal or subterminal, unisexual or bisexual, thyrsoid-paniculate; bracts entire, eglandular. Staminate flowers pedicellate; sepals 5, connate, not closed in bud; petals 5, yellowish, distinct, imbricate, pubescent abaxially; disk segments 5, distinct or confluent; stamens 20–35, inner filaments connate at base, outer distinct, apically deflexed; anthers extrorse; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, connate at base, not imbricate; petals 5, distinct, imbricate, deciduous; disk annular; ovary 3-locular, pubescent and resinous; ovules anatropous, inner integuments thick; stylodia bifid. Fruits capsular, thin-walled; columella persistent. Seeds oblong, apiculate, carunculate or ecarunculate; cotyledons much broader than radicle.

Three spp., Melanesia, 1 in New Guinea and 2 in New Caledonia/Vanuatu. Pax (1911) referred *Alphandia* to the Codiaeinae, where it could be placed except for the stellate indumentum. Although the stellate indumentum of *Alphandia* suggests a relationship with Ricinocarpeae subtribe Cocconeriinae, the pollen exine (Lobreau-Callen in McPherson and Tirel 1987) shows the typical Crotonoid sculpturing of the Baloghiinae and other Codieae, which is very different from the reduced sculpturing of the Cocconeriinae. It seems possible that *Alphandia* may provide a connecting link between the Baloghiinae and Cocconeriinae, and that these Australasian taxa may belong to a single clade.

9c. Subtribe Ostodeinae G.L. Webster[1]

Dioecious; leaves with or without basal paired glands or dispersed laminar glands; stamens 5–35, filaments distinct; anthers mostly introrse; stylodia bifid or multifid; seeds ecarunculate (except in *Pausandra*).

A heterogeneous subtribe of six genera, three paleotropical and three neotropical. *Pausandra* in particular appears aberrant and may prove not to belong to this subtribe.

Key to the Genera of Ostodeinae

1. Staminate calyx cupular, barely lobed; fruiting calyx accrescent **223. *Dimorphocalyx***
– Staminate calyx distinctly lobed; fruiting calyx not accrescent 2
2. Indumentum partly malpighiaceous; flowers subsessile, monoecious **227. *Pausandra***
– Indumentum simple; pistillate flowers distinctly pedicellate; seeds ecarunculate 3
3. Leaf blades dentate, with basal paired glands; anthers not glandular **222. *Ostodes***
– Leaf blades mostly entire, lacking basal paired glands 4
4. Anthers glandular; leaf blades with dispersed laminar glands, inflorescences leaf-opposed **226. *Pantadenia***
– Anthers not glandular; leaf blades with or without dispersed laminar glands; inflorescences terminal or axillary 5
5. Staminate and pistillate flowers externally glabrous; stamens 20+, inserted on convex receptacle; staminate disk and ovary glabrous; stylodia 6-branched **224. *Anomalocalyx***
– Staminate and pistillate flowers externally pilose; stamens 7–16, inserted on an almost plane receptacle; staminate disk pilose, ovary densely pilose; stylodia 10–12-branched **225. *Dodecastigma***

222. *Ostodes* Blume

Ostodes Blume, Bijdr.: 619 (1825); Müll. Arg. in DC. Prodr. 15(2): 1114 (1866); Gagnepain, Fl. Indochine 5: 322, fig. 33, 7–9 (1925); Airy Shaw, Kew Bull. 20: 409 (1967), 35: 334 (1981); Grierson & Long, Fl. Bhutan 1(3): 795, fig. 49 p–r (1987); Chakrabarty & Balakr., Bull. Bot. Surv. India 27: 259 (1987).

Dioecious trees; latex not recorded; indumentum simple. Leaves crenate-serrate, with 2 or more adaxial basal glands at junction with petiole; stipules gland-tipped, entire, deciduous. Inflorescences axillary, unisexual, the staminate thyrsoid, pistillate paniculate; bracts entire, eglandular, persistent. Staminate flowers pedicellate; sepals 5, connate, imbricate, glabrous; petals 5 or 6, white or pinkish, imbricate, concave, glabrous, longer than sepals; disk segments 8–12, massive, puberulent; stamens 30–35, filaments distinct, pilose; anthers dorsifixed, introrse; pollen grains spheroidal, inaperturate, with Croton pattern, pillars rounded; pistillode 0. Pistillate flowers pedicellate, articulate near base; sepals 5, connate, imbricate, entire, deciduous in fruit; petals 5, distinct, imbricate, longer than sepals; disk annular-cupulate, puberulent; ovary 3-locular, sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular, exocarp fleshy, verrucose, endocarp bony; columella persistent. Seeds angular, ecarunculate, exotesta fleshy, tenuous, endotesta bony; cotyledons much longer and broader than radicle. $2n = 20$.

---

[1] Subtr. **Ostodeinae** G.L. Webster, **subtr. nov.**: plantae dioicae inflorescentiis terminalibus, staminibus 5–35, liberis, antheris plerumque introrsis, seminibus plerumque ecarunculatis. Typus: *Ostodes* Blume.

A single polytypic sp., *O. paniculata* Blume, extending from Assam through southeast Asia to Malaya and Java. Partly because of the jumbled treatment of Pax and Hoffmann (1911), the genus has been confused with *Paracroton*, which now is referred to the Aleuritideae.

223. ***Dimorphocalyx*** Thwaites

Dimorphocalyx Thwaites, Enum. Pl. Zeyl.: 278 (1861); Pax & K. Hoffm., Pflanzenr. 147, III: 31, fig. 8 (1911); Airy Shaw, Kew Bull. 23: 123 (1969); Chakrabarty & Balakrishnan, Proc. Indian Acad. Sci. 100: 286, figs. 1–4 (1990); Philcox, Fl. Ceylon 11: 107 (1997); Naithani et al., Forest Fl. Goa 552, t. 118 (1997).

Dioecious trees or shrubs; latex not evident; indumentum simple, scanty or 0. Leaves entire or denticulate, without basal glands; stipules entire, persistent or deciduous. Inflorescences terminal or subterminal, sometimes axillary, pedunculate, cymose or racemoid, pistillate sometimes reduced to solitary flowers; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals 5, connate into a dentate or lobed cup; petals 5, white, distinct, glabrous, equaling or longer than the calyx; disk segments 5, glabrous; stamens (5)8–20(−100), the inner 3–10 filaments connate; anthers basifixed or dorsifixed, introrse; pollen spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire, ± persistent and accrescent in fruit; petals 5, distinct, imbricate, shorter than sepals; disk annular or cupular; ovary pubescent, sometimes rugose; ovules anatropous, inner integuments thick, vascularized; stylodia connate at base (distinct), bifid, branches slender. Fruits capsular; columella persistent. Seeds ellipsoidal, ecarunculate, testa smooth.

Seventeen spp., distributed from India and Ceylon to the Philippines, New Guinea, and northern Australia.

224. ***Anomalocalyx*** Ducke

Anomalocalyx Ducke, Notizbl. Bot. Gart. Berlin 11: 344 (1932), Arq. Jard. Bot. Rio Jan. 6: 60, figs. 7–9 (1933); Secco, Rev. Gen. *Anomalocalyx* et al.: 39, figs. 7, 8 (1990); Webster, Ann. Missouri Bot. Gard. 81: 115 (1994); Radcl.-Sm., Gen. Euphorb.: 338, fig. 43 (2001).

Dioecious trees; latex white; indumentum malpighiaceous but flowers glabrous. Leaves petiolate (pulvinate), adaxially with paired basal glands, abaxially with embedded glands; stipules entire, deciduous. Inflorescences terminal; staminate flowers thyrsoid-paniculate, pistillate flowers solitary; bracts entire, eglandular, deciduous. Staminate flowers pedicellate; sepals 3 or 4, glabrous, connate in the bud, opening in 2 lobes at anthesis; petals 5, distinct, imbricate, adaxially pubescent at base; disk annular, glabrous; stamens 23–30, filaments distinct from the convex receptacle; anthers introrse; pollen spheroidal, inaperturate, sexine with Croton pattern, pillars rounded, sulcate; pistillode 0. Pistillate flowers pedicellate; sepals 3–5, glabrous, connate in bud, splitting into (2) 3 lobes at anthesis, persistent in fruit; petals 5, scantily pilose adaxially at base; disk annular, glabrous; ovary 3-locular, glabrous; stylodia bifid. Fruit capsular, endocarp woody; columella stout, persistent. Seeds rounded, carinate, ecarunculate, testa slightly rugose.

A single sp., *A. uleanus* (Pax) Ducke, Amazonian Brazil, from near Manaus to Amapá. Although it closely resembles *Dodecastigma* in habit, Secco notes that it is immediately distinguishable by its glabrous inflorescences.

225. ***Dodecastigma*** Ducke

Dodecastigma Ducke, Notizbl. Bot. Gart. Berlin 11: 343 (1932); Arq. Jard. Bot. Rio Jan. 6: 58, t. 5 (1933); Sandw., Kew Bull. 1950: 134 (1951); Jablonski, Mem. N. Y. Bot. Gard. 17: 154 (1967); Secco, Rev. Gen. *Anomalocalyx* et al.: 42, figs. 10–12 (1990); Webster, Ann. Missouri Bot. Gard. 81: 106 (1994).

Dioecious trees or shrubs; latex turning reddish; indumentum simple and malpighiaceous, flowers pilose. Leaves petiolate (pulvinate), ± cuspidate, entire with cartilaginous border, abaxially with small dispersed embedded discoid glands but lacking paired basal glands, stipules minute, deciduous. Staminate inflorescences axillary, thyrsoid-paniculate; pistillate inflorescences racemoid, terminal and axillary; bracts entire, inconspicuous, persistent, subtending glomerules of staminate flowers or solitary pistillate flowers. Staminate flowers pedicellate; calyx 3- or 4-lobed, lobes imbricate; petals 3 or 4, green or yellow-green, distinct, imbricate, pilose abaxially; disk annular-crenulate, pilose; stamens 7–16, filaments distinct; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers long-pedicellate; sepals (2) 3–4, imbricate, entire, abaxially pubescent, deciduous in fruit; petals mostly 3 or

4, green or yellow-green, imbricate, pilose abaxially, subpersistent in fruit; disk annular, pilose; ovary 3-locular; densely sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia multifid. Fruits capsular, endocarp wood; columella massive, persistent. Seeds elliptic, ecarunculate, testa smooth and mottled.

Three spp. in Amazonian Brazil and the Guianas. The genus appears to be closely related to *Anomalocalyx*.

226. *Pantadenia* Gagnep.

Pantadenia Gagnep., Bull. Soc. Bot. France 71: 873 (1925); Airy Shaw, Kew Bull. 23: 122 (1969), 26: 312 (1972); Webster, Ann. Missouri Bot. Gard. 81: 106 (1994); Radcl.-Sm., Gen. Euphorb.: 298 (2001).
Parapantadenia Capuron (1972).

Dioecious trees; latex not recorded; indumentum simple. Leaves petiolate or subsessile, abaxially with dispersed scutelliform glands; stipules subulate, ± deciduous. Inflorescences leaf-opposed, the staminate thyrsoid-racemose, pistillate flowers mostly solitary; bracts entire, eglandular. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, distinct, imbricate, with 3 apical marginal glands; disk cupular, undulate; stamens 13–15, filaments distinct; anthers introrse, dorsifixed, connective glandular at apex; pollen grains spheroidal, inaperturate, exine with Croton pattern, lumina large, pillars rounded; pistillode rudimentary. Pistillate flowers pedicellate; sepals 5 or 6, distinct, imbricate, entire, persistent in fruit; petals 2 or 3, apically glandular; disk annular; ovary 2- or 3-locular, hispidulous; stylodia bifid. Fruits capsular or indehiscent and 1-seeded; columella 3-pronged, persistent. Seeds spheroidal, ecaruncular, testa smooth.

Two spp., widely disjunct: Madagascar and Vietnam. Govaerts et al. (2000) and Radcliffe-Smith (2001) uphold *Parapantadenia* as a distinct genus, based on its 2-locular ovary and indehiscent 1-seeded fruit. The question of generic status is problematic, but there is no doubt of a close relationship between the two species despite the considerable geographical disjunction.

227. *Pausandra* Radlk.

Pausandra Radlk., Flora 53: 92, t. 2 (1870); Jablonski, Mem. N. Y. Bot. Gard. 17: 153 (1967); Secco, Bol. Mus. Par. Emilio Goeldi, Bot. 3: 59 (1987); Huft, Ann. Missouri Bot. Gard. 75: 1115 (1989); Secco, Rev. *Anomalocalyx*, etc.: 58, figs. 14–25 (1990); Webster, Ann. Missouri Bot. Gard. 81: 105 (1994); Murillo & Franco, Euforb. Reg. Araracuara: 124, fig. 34 (1995); Radcl.-Sm., Gen. Euphorb.: 296 (2001).

Dioecious trees or shrubs; laticifers non-articulated, latex reddish; indumentum malpighiaceous. Leaves with paired basal glands at junction with petiole; stipules entire, eglandular, subpersistent or deciduous. Inflorescences axillary, spiciform-thyrsoid, staminate flowers in glomerules, pistillate solitary at nodes; bracts inconspicuous, eglandular. Staminate flowers subsessile; sepals 5, distinct, imbricate; petals 5 (6), imbricate, basally connate, adaxially villous; disk extrastaminal, urceolate-lobate, glabrous; stamens (3–)5–7, filaments distinct; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars distinctly sulcate; pistillode 0. Pistillate flowers subsessile; sepals 5, imbricate, entire, persistent in fruit; petals 5, distinct, imbricate, adaxially villous; disk urceolate, sometimes lobate, glabrous; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia distinct, bifid. Fruits capsular; columella persistent. Seeds carunculate, testa smooth.

Six neotropical spp., extending from Nicaragua to Bolivia and southern Brazil (Secco 1990). The status of some species awaits verification. *Pausandra* is isolated within neotropical Codiaeae by a number of features such as the massive petiolar glands or stipels, the subsessile flowers, and the malpighiaceous indumentum; its placement needs reevaluation.

9d. Subtribe Codiaeinae Pax (1911).

Monoecious (dioecious); leaf blades without basal laminar glands; inflorescences terminal or axillary; bracts eglandular; pistillate flowers apetalous or petals rudimentary; seeds mostly carunculate; columella persistent.

Four genera, all paleotropical.

Key to the Genera of Codiaeinae

1. Inflorescences axillary; ovary glabrous 2
– Inflorescences terminal; ovary pubescent 3
2. Staminate flowers apetalous; leaf blades with basal laminar glands; inflorescences bisexual, long thyrsopaniculate **231. *Baliospermum***
– Staminate flowers petaliferous; leaf blades without basal laminar glands; inflorescences unisexual, racemoid **228. *Codiaeum***

3. Pistillate sepals glandular-fimbriate; stipules ± persistent; seeds carunculate **230. *Strophioblachia***
– Pistillate sepals not glandular-fimbriate; stipules deciduous; seeds ecarunculate **229. *Blachia***

228. ***Codiaeum*** Rumph. ex A. Juss.

Codiaeum Rumph. ex A. Juss., Euphorb. Tent.: 33 (1824; nom. cons.); Airy Shaw, Kew Bull. Add. Ser. 4: 88 (1975); 8: 62 (1980); A.C. Smith, Fl. Vitiensis Nova 2: 549 (1981); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 95–101, t. 19 (1987); Howard, Fl. Lesser Antilles 5: 32, fig. 13 (1989); Radcl.-Sm., Gen. Euphorb.: 301 (2001).

Monoecious trees or shrubs; laticifers non-articulated, latex clear; indumentum simple. Leaves alternate (opposite); stipules 0. Inflorescences axillary, unisexual, racemoid; bracts entire, persistent, eglandular. Staminate flowers pedicellate; sepals mostly (3–)5(6), distinct, imbricate; petals 4–6, minute, distinct, imbricate; disk segments 4–6; stamens 10–35, filaments distinct; anthers basifixed, ± latrorse, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars smooth and rounded; pistillode 0. Pistillate flowers pedicellate; sepals mostly 5, distinct, imbricate, entire, usually deciduous in fruit; petals 0; disk cupular; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia slender, unlobed. Fruits capsular; columella mostly persistent. Seeds carunculate, testa smooth. $2n = 48, 72, 96, 120$.

Seventeen spp., distributed from Java and Borneo to the Philippines, New Guinea, tropical Australia and New Caledonia. Müller (1866) construed *Codiaeum* in a very broad sense, to include species of *Austrobuxus*, *Baloghia*, *Blachia*, *Fontainea*, and *Trigonostemon*, but Bentham (1880) reconstituted it in the circumscription that is accepted at present.

229. ***Blachia*** Baill.

Blachia Baill., Étude Gén. Euphorb.: 385 (1858); Pax, Pflanzenr. 147, III: 36 (1911); Gagnep., Fl. Indochine 5: 410, fig. 48, 5–13 (1926); Airy Shaw, Kew Bull. 23: 121 (1969), 26: 223 (1972); Balakrishnan & Chakrabarty, Proc. Indian Acad. Sci. 99 568, figs. 1–4 (1989); Thin, Tap Chi Sinh Hoc 11(3): 16 (1989); Webster, Ann. Missouri Bot. Gard. 81: 107 (1994); Philcox, Fl. Ceylon 11: 105 (1997).
Bruxanellia Dennst. ex Kostel. (1830; nom. rej.).

Monoecious shrubs or trees; latex not recorded; indumentum simple, often 0 or nearly so. Leaves alternate (subopposite), eglandular; stipules deciduous or persistent. Inflorescences terminal [or pistillate terminal and axillary], racemoid, sometimes ± umbellate; bracts inconspicuous or 0 above basal nodes. Staminate flowers pedicellate; sepals 4 or 5, distinct, concave, membranous; petals 4 or 5, distinct, imbricate, shorter than sepals; disk a convex receptacle; disk segments 5; stamens 10–20(−40), filaments distinct; anthers basifixed, extrorse, connective broad, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, entire, usually accrescent and persistent in fruit; petals rudimentary or 0; disk annular; ovary 3–5-locular, glabrous or pubescent; ovules anatropous, inner integuments thick (18–20 cell layers), vascularized; stylodia bifid, branches slender. Fruits capsular; columella persistent or not. Seeds subspheroidal, ecarunculate; testa smooth. $2n = 36$.

Eleven spp., from India to China and Malesia, south to the Andaman Islands. Balakrishnan and Chakrabarty (1989) regard *Pantadenia* as the closest relative of *Blachia*.

230. ***Strophioblachia*** Boerl.

Strophioblachia Boerl., Handl. Fl. Ned. Ind. 3(1): 235 (1900); Pax, Pflanzenr. 147, III: 35, fig. 10 (1911); Gagnepain, Fl. Indochine 5: 408, figs. 47, 8–14, 48, 1–4 (1926); Airy Shaw, Kew Bull. 25: 544 (1971); Thin et al., Blumea 43: 484, t. 1–4 (1998).

Monoecious shrubs; latex not recorded; indumentum simple. Leaves eglandular; stipules entire, pilose, deciduous or persistent. Inflorescences terminal, unisexual, racemoid, few-flowered. Staminate flowers pedicellate; sepals 4 or 5, distinct, imbricate; petals 5, white, dentate; disk segments 5; stamens 15–30, filaments distinct; anthers extrorse, rounded, muticous; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, persistent and with glandular-fimbriate margins in fruit; petals 0; disk annular; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia connate at base, bifid. Fruits capsular, thin-walled; columella persistent. Seeds subspheroidal, carunculate, testa smooth.

Two spp., southern China to Vietnam, the Philippines and Sulawesi.

231. *Baliospermum* Blume

Baliospermum Blume, Bijdr.: 603 (1826); Decaisne in Jacquemont, Voy. Inde Atlas 2: 155 (1844); Müll. Arg. in DC. Prodr. 15(2): 1125 (1866); J.J. Sm., Meded. Dept. Landb. 10: 599 (1910); Pax & K. Hoffm., Pflanzenr. 147, IV: 24, figs. 6, 7 (1912); Gagnepain, Fl. Indochine 5: 429, figs. 51, 6–19, 52, 1–6 (1926); Airy Shaw, Kew Bull. 36: 267 (1981); Long, Fl. Bhutan 1(3): 809, fig. 50 m–o (1987); Chakrabarty & Balakrishnan, Bull. Bot. Survey India 32: 3, figs. 1–8 (1992); Webster, Ann. Missouri Bot. Gard. 81:108 (1994).

Monoecious or dioecious shrubs, sometimes scandent; latex not recorded; indumentum simple. Leaves pellucid-punctate, glandular-dentate or serrate, ± biglandular at base or subbasal on margins; stipules minute, glandular, persistent. Inflorescences mostly axillary, long-pedunculate, thyrsoid-paniculate; bracts entire, eglandular. Staminate flowers pedicellate; sepals 4–5(6), distinct, imbricate, orbicular; petals 0; disk annular, lobed, or segmented; stamens 10–25, filaments distinct; anthers extrorse, muticous, connective narow; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5 or 6, distinct, imbricate, entire or denticulate, persistent in fruit and often accrescent; petals 0; disk annular; ovary 3 (4)-locular, glabrous or pubescent, ovules pachychalazal, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella persistent, distally alate. Seeds carunculate, caruncle apical, discoidal; testa smooth. $2n = 44$.

Five spp., distributed from the Himalayas and Yunnan south to Sumatra and Java. Pax (1912) followed Müller (1866) in placing *Baliospermum* next to *Suregada*; however, the pollen study of Punt (1962) demonstrated that *Baliospermum* has pollen much more similar to genera of Codiaeae than to *Suregada*.

10. TRIBE RICINOCARPEAE Müll. Arg. (1864).

Monoecious (dioecious); latex reddish, often scanty or 0; indumentum stellate, sometimes glandular; sepals 4–6, distinct, imbricate, often petaloid; petals 5 (0); disk dissected or 0; stamens 15–100, filaments mostly connate; pollen grains inaperturate, exine with Croton pattern; stylodia unlobed to multifid; seeds carunculatae.

This strictly Australasian tribe includes seven genera. It has certain characters in common with *Alphandia*, a possible sister group, which is here referred to the Codiaeae.

KEY TO THE SUBTRIBES AND GENERA OF RICINOCARPEAE

1. Embryo with cotyledons much broader than the radicle; pollen exine with reduced pillars; leaves alternate, not ericoid. **10a. Cocconeriinae** 2
– Embryo with narrow cotyledons no broader than radicle; pollen exine with massive pillars (except *Bertya*); leaves opposite or verticillate; shrubs or trees, often with reddish latex. **10b. Bertyinae** 4
2. Leaves opposite; inflorescences terminal, racemoid; stylodia multifid **232. *Myricanthe***
– Leaves verticillate; staminate inflorescences subcapitate or flowers axillary; stylodia bifid or twice bifid 3
3. Sepals 4–7; ovary (2)3-locular; stylodia bifid or twice bifid; flowers axillary, solitary **233. *Cocconerion***
– Staminate sepals 0, pistillate sepals 3; ovary 2-locular; stylodia bifid; staminate inflorescences terminal, subcapitate **234. *Borneodendron***
4. Stylodia dilated, connivent into a pseudo-stigma over the top of the ovary, discoid or rarely with 2 appressed entire limbs or shallowly 3-lobulate **236. *Beyeria***
– Stylodia 3 spreading and divergent limbs, entire or 2–5-lobed 5
5. Stylodia entire; flowers in racemes **237. *Shonia***
– Stylodia deeply 2(–5)-lobed; flowers usually not in racemes 6
6. Petals 0 or rudimentary; calyx strongly recurved at anthesis; disk 0 **238. *Bertya***
– Petals conspicuous, or if 0 then calyx spreading at anthesis; disk + **235. *Ricinocarpos***

10a. SUBTRIBE COCCONERIINAE G.L. Webster, subtrib. nov.[1]

Subtribe Bertyinae sensu Webster (1994), excluding the genus *Bertya*.

Monoecious trees or shrubs; latex reddish or 0; leaves opposite or verticillate; stipules deciduous or 0; inflorescences terminal or axillary, racemoid or flowers solitary; petals and disk 0; stamens 30–100, filaments connate into a column, anthers extrorse, pubescent; pollen grains with minute clavae instead of pillars; ovary 2- or 3-locular; fruits capsular, columella persistent; seeds carunculate, cotyledons broader than radicle.

Three Melanesian genera; these appear to be related to *Alphandia*, and also to the Bertyinae,

---

[1] Subtrib. **Cocconeriinae** G.L. Webster, **subtrib. nov.**, plantae monoicae foliis oppositis vel verticillatis, antheris pilosis, filamentis connatis, pollinis grana exinio microclavato, cotyledonibus quam radicula latioribus. Typus: *Cocconerion* Baillon

although the phylogenetic connections are not yet very clear. In Webster (1994), these genera were included in subtribe Bertyinae.

232. *Myricanthe* Airy Shaw

Myricanthe Airy Shaw, Kew Bull. 35: 390 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 72–73, t. 14, figs. 1–5 (1987).

Monoecious shrubs; latex not recorded; indumentum stellate. Leaves opposite; stipules 0. Inflorescences terminal, unisexual or bisexual, racemoid; bracts deciduous. Staminate flowers pedicellate; sepals 3, distinct, imbricate; petals and disk 0; stamens 60–80, filaments connate into an elongated column; anthers subsessile on column, minutely pilose; pollen grains spheroidal, inaperturate, with Croton pattern, clavae minute and spinulose; pistillode 0. Pistillate flowers pedicellate; sepals 6, distinct, entire, subpersistent in fruit; petals and disk 0; ovary 3-locular, stellate-tomentellous; ovules anatropous, inner integuments very thick, vascularized; stylodia multifid (palmatifid). Fruits capsular; columella persistent. Seeds ± cylindrical, carunculate.

A single sp., *M. discolor* Airy Shaw, confined to ultrabasic substrates in northern New Caledonia.

233. *Cocconerion* Baill.

Cocconerion Baill., Adansonia I, 11: 87 (1873); Airy Shaw, Kew Bull. 25: 503 (1971); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 38–43, t. 7 (1987); Webster, Ann. Missouri Bot. Gard. 81: 110 (1994).

Monoecious trees or shrubs; latex translucent, yellowish to reddish; indumentum stellate-lepidote. Leaves verticillate, 6–10 per node, tapering gradually to an ill-defined petiole, abaxially densely brownish appressed-stellate; stipules 0. Flowers solitary, axillary. Staminate flowers pedicellate; sepals 4–7, imbricate, pubescent on both faces; petals and disk 0; stamens 30–100, filaments connate into a column; anthers pubescent; pollen grains spheroidal, inaperturate, reticulate with micro-clavae; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, imbricate, entire, pubescent on both faces, persistent in fruit; petals and disk 0, staminodes sometimes present; ovary (2)3-locular; ovule anatropous, inner integuments thick, vascularized; stylodia bifid or twice bifid, branches slender. Fruits capsular; columella persistent. Seeds ellipsoidal, carunculate, testa smooth.

Two spp. endemic to New Caledonia.

234. *Borneodendron* Airy Shaw

Borneodendron Airy Shaw, Kew Bull. 16: 359 (1963), Hook. Icon. Pl. 7(2): t. 3633 (1967), Kew Bull. Add. Ser. 4: 60 (1975); Webster, Ann. Missouri Bot. Gard. 81: 110 (1994); Radcl.-Sm., Gen. Euphorb.: 315 (2001).

Monoecious tree; latex reddish; indumentum stellate. Leaves verticillate (ternate), petiolate, without basal paired glands; stipules deciduous. Staminate inflorescences terminal, subcapitate, pedunculate, bracts verticillate; pistillate flowers solitary, axillary. Staminate flowers without perianth or disk; stamens 25–30, filaments connate into a column, anthers basifixed, anther sacs pubescent; pistillode 0. Pistillate calyx 4–5-lobed; petals and disk 0; ovary 2-locular; stylodia bifid. Fruits capsular, endocarp woody; columella persistent. Seeds ellipsoid, carunculate, hilum smooth; cotyledons much broader than radicle.

A single sp., *B. aenigmaticum* Airy Shaw, endemic to northeastern Borneo, in hill forest or *Casuarina* forest on ultrabasic substrate. Radcliffe-Smith (2001) refers to several traits in which it resembles Oldfieldioid genera such as *Aristogeitonia* and *Mischodon*; hence, knowledge of its pollen structure would be highly desirable. The strongly reduced flowers suggest a shift to wind pollination. Unpublished sequence data on *Borneodendron* mentioned by Hoffmann and Wurdack (2007) have not been accessible to us.

10b. Subtribe Bertyinae Müll. Arg. (1865).

Subtribe Ricinocarpinae G.L. Webster (1975).

Monoecious or dioecious; stems and foliage often resinous or with reddish latex; flowers petaliferous; pollen grains with large pillars [except in *Bertya*]; embryo with cotyledons as narrow as radicle.

An entirely Australian subtribe of four genera.

235. *Ricinocarpos* Desf.

Ricinocarpos Desf., Mém. Mus. Hist. Nat. Paris 3: 459, t. 22 (1817); Müll. Arg. in DC., Prodr. 15(2): 203 (1866); Halford & Henderson, Austrobaileya 7: 387–449 (2007), rev.

Monoecious (dioecious) shrubs or small trees; laticifers non-articulated; latex 0 but stems and foliage sometimes resinous; indumentum stellate and simple. Leaves linear, 1-veined, entire, often revolute; stipules 0. Inflorescences terminal or pseudo-axillary, glomerulate or of solitary flowers in upper axils; bracts persistent.

Staminate flowers pedicellate; sepals (4)5(6), nearly distinct; petals (4)5(−7) or 0; disk of distinct alternipetalous segments or forming a continuous ring; stamens numerous, > 15, filaments connate into a column; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, with Croton pattern, pillars massive and spinulose; pistillode 0. Pistillate flowers pedicellate; sepals persistent or deciduous in fruit; petals often marcescent, deciduous or sometimes 0; disk annular or urceolate; ovary 3-locular; ovule 1/locule, inner integument very thick, vascularized; stylodia basally very shortly connate, the distinct branches spreading, deeply 2(3–5)-fid. Fruits capsular, smooth or echinate; columella persistent. Seeds ellipsoidal, carunculate, testa smooth; endosperm copious; cotyledons longer than radicle.

According to the revision of Halford and Henderson, 28 spp., all endemic to Australia.

236. *Beyeria* Miq.

Beyeria Miq., Ann. Sci. Nat. III, 1: 350, t. 15 (1844); Müll. Arg. in DC., Prodr. 15(2): 201 (1866); Halford & Henderson, Austrobaileya 7: 577–635 (2008), rev.

Monoecious (dioecious) shrubs or small trees; stems and foliage resinous; laticifers non-articulated, latex not recorded; indumentum stellate. Leaves petiolate or subsessile, 1-veined, often revolute; stipules 0. Inflorescences axillary, glomerular (racemoid) or the pistillate flowers solitary. Staminate flowers pedicellate; sepals (4) 5 (6), distinct, imbricate, often petaloid; petals (4) 5, sometimes or 0; disk segments mostly 5 or disk 0; stamens 15–40, filaments distinct, shorter than anthers; anthers glabrous, extrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern, pillars massive; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, persistent and sometimes accrescent in fruit; petals 4 or 5; disk obsolete; ovary 2–3-locular; ovules anatropous, inner integuments very thick; stylodia connivent into a conical pseudo-stigma. Fruits capsular; columella persistent. Seeds oblong, carunculate, testa smooth; embryo cylindrical, cotyledons as narrow as radicle.

Twenty-four spp. endemic to Australia recorded by Halford and Henderson (2008).

237. *Shonia* R. Henderson & Halford Fig. 40

Shonia R. Henderson & Halford, Austrobaileya 7: 218 (2005).

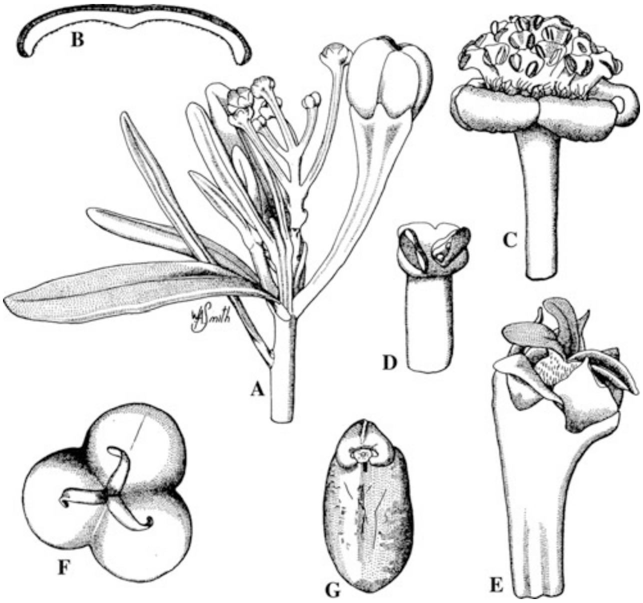

Fig. 40. Euphorbiaceae-Crotonoideae. *Shonia tristigma* subsp. *borealis*. **A** Flowering branchlet. **B** Transverse section of leaf. **C** Side view of staminate flower. **D** Stamen. **E** Side view of pistillate flower. **F** Face view of fruit. **G** Ventral view of seed. (Henderson & Halford 2005; drawn by W. Smith)

Monoecious (dioecious) shrubs or small trees; latex and resin not recorded; indumentum stellate. Leaves shortly petiolate, abaxially pubescent; stipules 0. Inflorescences racemose (paniculate), terminal or apparently axillary, proximally with 1–2 pistillate flowers and few to several staminate flowers distal to them. Staminate flowers with calyx 5(4)-lobed; petals +; disk of distinct alternipetalous glands or a continuous ring; stamens 10–30, erect; filaments distinct; anthers extrorse; pistillode 0. Pistillate flowers with calyx lobes persistent and appressed to ovary; petals +; disk circular; ovary 3-locular; stylodia distinct, entire. Fruit trilobate, capsular, separating into three 2-valved cocci; columellla persistent. Seeds carunculate; endosperm copious; cotyledons narrower than radicle.

Four spp., endemic to Australia (Northern Territory, Queensland).

238. *Bertya* Planch.

Bertya Planch., Hook. London J. Bot. 4: 472 (1845); Müll. Arg. in DC., Prodr. 15(2): 208 (1866); Halford & Henderson, Austrobaileya 6: 187–245 (2002), rev.

Monoecious or dioecious shrubs (trees); laticifers non-articulated, latex not recorded; stems often resinous; indumentum stellate. Leaves alternate (opposite), abaxially densely tomentose, margins revolute; stipules 0. Inflorescences axillary, flowers solitary or in glomerules; bracts forming an involucre at base of calyx. Staminate flowers pedicellate; sepals 5 (4), basally connate, imbricate, sometimes petaloid; petals and disk 0; stamens 15–70; filaments connate into a column, shorter than anthers; anthers dorsifixed, extrorse; pollen grains spheroidal, inaperturate, exine with Croton pattern, clavae reduced; pistillode 0. Pistillate flowers pedicellate or subsessile; sepals 5, distinct, imbricate, entire, persistent and sometimes accrescent in fruit; petals 0 or rudimentary; disk 0; ovary (2)3(−5)-locular, glabrous or stellate-pubescent; ovules anatropous, inner integument very thick, vascularized; stylodia 3(4), proximally shortly connate, distally 2- to several-lobed. Fruits capsular, usually 1-seeded; columella not persistent. Seeds oblong or rounded, carunculate, testa smooth; embryo cylindrical, cotyledons as broad as radicle.

Twenty-eight spp. distinguished by Halford & Henderson (2002), widely distributed in Australia except for the Northern Territory.

11. TRIBE RICINODENDREAE (Pax) Hutch. (1969).

Dioecious or monoecious trees or shrubs; laticifers non-articulated; reddish latex + or not; indumentum stellate, malpighiaceous, or 0; leaves alternate or opposite, simple to lobed or palmatisect, petiole usually glandular at apex; stipules entire, lobed, or 0; inflorescences axillary or the pistillate terminal, cymose-paniculate, glomerular, or reduced to solitary flowers; sepals 4 or 5, distinct or connate; petals 5; disk dissected or lobed; stamens (3–)5–35; pollen inaperturate, with Croton pattern; pistillode 0; ovary 1–3-locular; stylodia bifid; fruits drupaceous or capsular; seeds ecarunculate.

Four paleotropical genera, entirely African/Madagascan except for the New Guinean *Annesijoa* and one Indian species of *Givotia*. In Webster (1994) and Radcliffe-Smith (2001), *Leeuwenbergia* and *Annesijoa* were part of the broadly circumscribed Jatropheae, but in the molecular analysis of Wurdack et al. (2005), *Leeuwenbergia* is resolved (*rbc*L only) in clade C2 together with *Ricinodendron*, *Schinziophyton* and *Givotia*.

KEY TO THE GENERA OF RICINODENDREAE

1. Leaves simple, unlobed to 5-lobed; stipules minute or 0 **239. *Givotia***
– Leaves palmatisect 2
2. Stipules flabelliform; indumentum stellate **240. *Ricinodendron***
– Stipules not flabelliform; indumentum malpighiaceous or 0 3
3. Stylodia slender, bifid; ovary 3-locular; stamens 15–25, anthers muticous; staminate disk dissected; fruit capsular; foliage glabrous **242. *Annesijoa***
– Stylodia dilated, subentire to lacerate; ovary 2-locular; stamens 18–33; anthers apiculate; staminate disk annular and intrastaminal; fruit drupaceous; indumentum malpighiaceous **241. *Leeuwenbergia***

239. *Givotia* Griff.

Givotia Griff., Calcutta J. Nat. Hist. 4: 88 (1843); Müll. Arg. in DC., Prodr. 15(2): 1112 (1866); Pax & K. Hoffm., Pflanzenr. 147, III: 44, fig. 15 (1911); Radcl.-Sm., Kew Bull. 22: 493, fig. 2, t. 5 (1968), Fl. Trop. E. Afr. Euphorb. 1: 329, fig. 62 (1987).

Dioecious trees or shrubs; latex clear; indumentum stellate. Leaves simple to 3–5-lobed, entire to coarsely dentate with sessile discoid glands, base of lamina with or without paired glands; stipules coarsely glandular-toothed or 0. Staminate inflorescences axillary, racemoid, with scattered glomerules; pistillate inflorescences terminal, of solitary or clustered flowers; bracts subulate, entire, deciduous. Staminate flowers pedicellate; sepals 5, distinct, imbricate; petals 5, greenish-yellow, distinct at first, later becoming partially adnate; disk segments 5, sometimes confluent; stamens (3–)8–20, filaments connate at base into a column shorter than the filaments; anthers dorsifixed, extrorse, muticous; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4) 5, distinct, imbricate, entire, deciduous in fruit; petals (4) 5, greenish-yellow, distinct, imbricate; disk annular; ovary 1–3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia bifid, compressed. Fruits drupaceous, 1-seeded; endocarp thin. Seeds ecarunculate, smooth.

Four spp., one in Africa, two in Madagascar, and one in India and Ceylon.

240. *Ricinodendron* Müll. Arg.

Ricinodendron Müll. Arg., Flora 47: 533 (1864), in DC., Prodr. 15(2): 1111 (1866); Benth., Hook. Icon. Pl. 13: t. 1300 (1879); Léonard, Fl. Congo Belge 8(1): 116 (1962); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 325, fig. 61

(1987), Fl. Zambesiaca 9(4): 294, t. 59, 60 (1996); Webster, Ann. Missouri Bot. Gard. 81: 113 (1994); Radcl.-Sm., Gen. Euphorb.: 328 (2001).

Schinziophyton Hutch. ex Radcl.-Sm. (1990).

Dioecious trees; laticifers non-articulated, latex clear; indumentum stellate. Leaves palmatisect, 3–7-foliolate, pellucid-punctate, denticulate; petiole glandular at apex; stipules flabellately dentate, persistent or deciduous. Inflorescences axillary or subterminal, the staminate cymose-paniculate, the pistillate contracted; bracts entire, deciduous, the pistillate foliaceous. Staminate flowers pedicellate; sepals 4 or 5, distinct, imbricate; petals 5, greenish or whitish, imbricate, coherent to form a tube; disk segments 4–6, glabrous; stamens (7–) 10–20, filaments connate basally into a short column, exserted beyond calyx; anthers dorsifixed, versatile, introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4) 5, distinct, imbricate, deciduous in fruit; petals 5, greenish or whitish, imbricate, coherent; disk annular, crenulate, glabrous; ovary 1–3-locular, pubescent, ovules anatropous, inner integuments very thick, vascularized; stylodia bifid. Fruits drupaceous, exocarp fleshy, endocarp woody. Seeds ecarunculate, subspheroidal, testa irregularly ridged. $2n = 22$.

Two spp. widely distributed in tropical Africa. Originally, six African spp. had been described in *Ricinodendron*, of which only a single polymorphic species, *R. heudelotii*, with 3 subspecies was recognized by Govaerts et al. (2000); an additional species was transferred to the segregate genus *Schinziophyton*. However, the key to the Congo spp. of *Ricinodendron* by Léonard contrasts two species that are very distinct, but which in my opinion can easily be accommodated in a single genus; *Schinziophyton* is therefore here relegated to synonymy, and *Ricinodendron* is considered to include at least 2 species.

241. ***Leeuwenbergia*** Letouzey & Hallé Fig. 41

Leeuwenbergia Letouzey & Hallé, Adansonia II, 14: 379, figs. 2, 3 (1974); Webster, Ann. Missouri Bot. Gard. 81: 104 (1994).

Dioecious trees; latex reddish; indumentum malpighiaceous. Leaves palmatisect, petiolate with 1 or 2 large apical glands; leaflets entire; stipules deciduous. Inflorescences axillary or subterminal, unisexual, racemoid-thyrsoid or paniculate; bracts deciduous. Staminate flowers pedicellate; sepals connate, irregularly dehiscent into 2 or 3 lobes, closed in bud; petals 5, white, orbiculate, distinct; disk interstaminal, receptacular; stamens 18–33, distinct, inserted in cavities of the disk; filaments distinct; anthers introrse, apiculate; pollen grains inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calyx and petals as in staminate; disk annular-cupular, hirsute; ovary 2–3-locular, hirsute; ovules anatropous, inner integuments thick, vascularized; stylodia foliose-stigmatiform, crenulate. Fruits and seeds unknown.

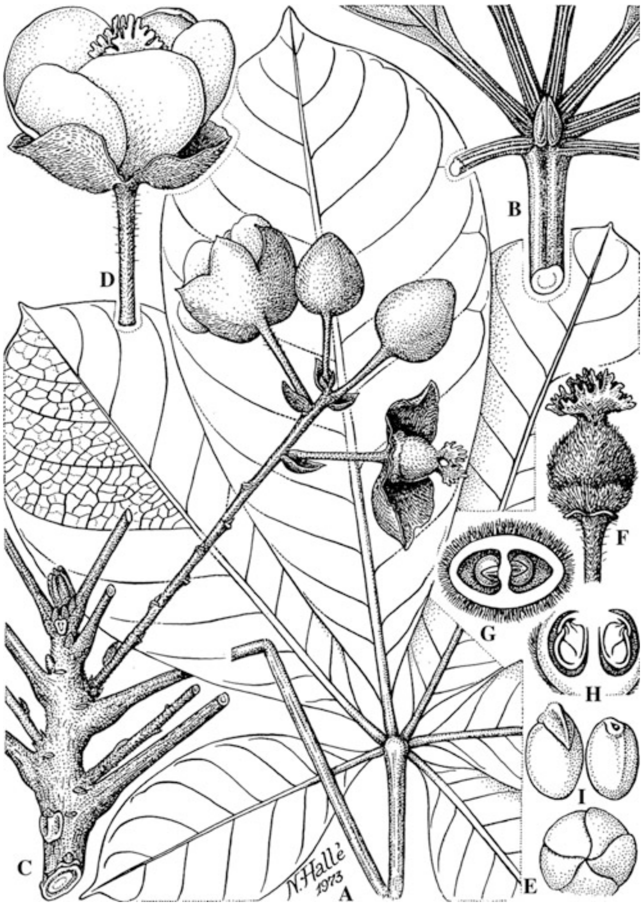

Fig. 41. Euphorbiaceae-Crotonoideae. *Leeuwenbergia africana*. **A** Leaf, seen from below. **B** Glands on petiole apex. **C** Flowering branch. **D** Pistillate flower. **E** Corolla aestivation. **F** Ovary, side view. **G** Same, transversal section. **H** Same, longitudinal section. **I** Ovule with and without obturator. (Letouzey & N. Hallé 1974; drawn by N. Hallé)

Two spp. of west African rainforests: Gabon to Cameroon and Zaire.

242. *Annesijoa* Pax & K. Hoffm.

Annesijoa Pax & K. Hoffm., Pflanzenr. 147, XIV: 9 (1919); Airy Shaw, Kew Bull. 16: 345 (1963), Hook. Icon. Pl. 38: t. 3713 (1974), Kew Bull. Add. Ser. 8: 27, t. 7 (1980); Hoang Van Nam & van Welzen, Blumea 49: 427–437 (2004).

Monoecious trees; latex not recorded; indumentum 0. Leaves palmatisect, petiolate with apical paired stipelliform deciduous glands; leaflets entire; stipules rudimentary. Staminate inflorescences axillary, dichasial-paniculate, pistillate flowers few and subterminal; bracts inconspicuous. Staminate flower pedicellate; calyx cupular, shallowly lobed, of 5 connate sepals, open in bud; petals 5, white, distinct; disk segments 5; stamens 15–25, filaments distinct or coherent in part; anthers ellipsoidal; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct or nearly so, entire; petals 5, distinct, imbricate; disk segments 5; ovary 2-locular, glabrous; ovules anatropous, inner integuments moderately thick, vascularized; stylodia bipartite. Fruits capsular; endocarp woody; columella not persistent. Seeds spheroidal or angled, ecarunculate (?), testa smooth.

One sp., *A. novoguineensis* Pax & K. Hoffm., of rainforests in New Guinea.

12. TRIBE ALEURITIDEAE Hurus. (1954).

Monoecious trees or shrubs; laticifers non-articulated, latex white or reddish; indumentum simple or stellate; leaves alternate, simple, entire (dentate), pinnately to palmately veined or palmately lobed, eglandular or with basal laminar glands; stipules present or 0; inflorescences terminal or axillary, cymose-paniculate or reduced to glomerules; staminate calyx closed in bud, splitting into valvate segments; petals 5(6–13), distinct, imbricate; disk dissected or interstaminal; stamens 7–20(−100); pollen grains spheroidal, inaperturate, with Croton pattern; sepals and petals as in staminate; disk lobed, dissected, or obsolete; ovary 2–5-locular; ovules anatropous, inner integuments thick, vascularized; stylodia bifid; fruit drupaceous or capsular; seeds ecarunculate (carunculate).

As here circumscribed, the Aleuritideae are an exclusively paleotropical group, except for *Garcia*, the affinities of which are dubious. The five subtribes contain a total of 13 genera and 45 species. van Welzen and Stuppy (1999) have shown in a cladistic analysis of the tribe that subtribe Grosserinae as delimited by Webster (1994) is unnatural. *Paracroton*, formerly doubtfully included in the Codiaeae, in the combined and the partial molecular analyses (Wurdack et al. 2005) always goes together with genera of the Aleuritideae and here is shifted to this tribe.

KEY TO THE SUBTRIBES OF ALEURITIDEAE

1. Petals 0; leaves gland-dotted **12e. Neoboutoninae**
– Petals +, at least in staminate flowers; leaves not gland-dotted 2
2. Petals 6–13; stamens 30–100, filaments distinct; inflorescences terminal, glomerular; leaf blades pinnately veined **12b. Garciinae**
– Petals 4 or 5; stamens 6–40, filaments distinct or connate 3
3. Stamens 7–20, filaments connate; monoecious; inflorescences terminal; leaf blades palmately lobed or veined; monoecious; stems with latex **12a. Aleuritinae**
– Stamens 6–40, filaments distinct or connate; dioecious (monoecious); inflorescences terminal or axillary; leaf blades pinnately or palmately veined; stems mostly without latex 4
4. Indumentum simple or 0; inflorescences mostly terminal [axillary in *Tapoides*] **12c. Grosserinae**
– Indumentum stellate or lepidote; inflorescences terminal or axillary 5
5. Staminate petals usually coherent or connate; leaves entire; caruncle 0; dioecious **12d. Crotonogyninae**
– Staminate petals distinct; leaves serr(ul)ate; caruncle + or 0; dioecious or monoecious **12f. Paracrotoninae**

12a. SUBTRIBE ALEURITINAE (Hurus.) G.L. Webster (1975).

Monoecious trees or shrubs; indumentum simple or stellate; leaves palmately veined or lobed, with glands at apex of petiole; inflorescences ± paniculate; bracts eglandular, deciduous; staminate calyx segments 2 or 3; petals 5, distinct, glabrous; disk-segments 5; stamens 7–20, inner filaments connate; ovary 2–3-locular; fruit drupaceous or capsular.

This small paleotropical subtribe includes all of the species traditionally referred to *Aleurites*. The fractionation into 3 genera proposed by Airy Shaw has been widely accepted, but despite the critical study of the Aleuritinae by Stuppy et al. (1999), it seems preferable to combine *Reutealis* with *Vernicia*.

KEY TO THE GENERA OF ALEURITINAE

1. Fruits drupaceous; indumentum stellate; stamens 17–32, anthers in 2 or 4 whorls; leaf blades triplinerved, brochidodromous **243. *Aleurites***
– Fruits capsular; indumentum simple or stellate; stamens 8–12(–14), mostly in 2 whorls; leaf blades palmately veined, eucamptodromous **244. *Vernicia***

243. *Aleurites* J.R. & G. Forst.

Aleurites J.R. & G. Forst., Charact. Gen. Pl.: 111, t. 56 (1776); Müll. Arg. in DC., Prodr. 15(2): 722 (1866); Airy Shaw, Kew Bull. 20: 393 (1967); Webster, J. Arnold Arb. 48: 342 (1967); Walker, Fl. Okinawa: 644, figs. 96–98 (1976); A.C. Sm., Fl. Vitiensis Nova 2: 547 (1981); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 176, fig. 34 (1987); P.I. Forster, Muelleria 9: 6, figs. 1, 2 (1996); Stuppy et al., Blumea 44: 79, fig. 1 (1999).

Monoecious trees; latex not obvious; indumentum simple and stellate. Leaves shallowly 3–5-palmately lobed or unlobed, triplinerved, entire, with paired basal glands at junction with petiole; stipules deciduous. Inflorescences terminal, cymose-paniculate, uni- or bisexual; bracts deciduous. Staminate flowers pedicellate; calyx splitting valvately or irregularly into 2 or 3 lobes; petals 5(6), distinct, imbricate, exserted from calyx; disk segments 5; stamens 17–32, 4-seriate, the filaments of the outer ones distinct, of the inner connate into a column; anthers dorsifixed, introrse, muticous, with dilated connective; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; perianth as in staminate flowers; disk annular, 5-lobed; ovary 2–3(4)-locular, tomentose; stylodia 2 or 3, connate at the base, bilobed. Fruits drupaceous; exocarp fleshy, endocarp thin-walled; seeds massive, subspheroidal, ecarunculate; endosperm copious. $2n = 22$.

Three spp., distributed from Ceylon to SE Asia, Australia, Melanesia and Polynesia, where it is commonly introduced.

244. *Vernicia* Lour.

Vernicia Lour., Fl. Cochinch.: 586 (1790); Hemsley, Hook. Icon. Pl. 29: t. 2801, 2802 (1906, under *Aleurites*); Airy Shaw, Kew Bull. 20: 394 (1967); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 178, fig. 35 (1987); Webster, Ann. Missouri Bot. Gard. 81: 114 (1994); Stuppy et al., Blumea 44: 88, fig. 3 (1999); Radcl.-Sm., Gen. Euphorb.: 331 (2001).
Reutealis Airy Shaw (1967).

Monoecious trees; laticifers non-articulated, latex whitish or reddish, often not apparent; indumentum simple, bifid, or stellate. Leaves unlobed to 3(–5)-lobed, palmately veined, entire, basally with paired glands at junction with petiole; stipules deciduous. Inflorescences terminal, usually bisexual, thyrsoid-paniculate, bracts persistent or deciduous. Staminate flowers pedicellate; calyx splitting into 2 or 3 valvate lobes; petals 5, distinct, contorted-imbricate, adaxially pubescent; disk segments 5, glabrous; stamens 7–12(–15), biseriate, those of the outer stamens distinct to basally connate, of the inner connate halfway or more; anthers basifixed, extrorse or introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; perianth and disk as in staminate flowers; ovary 3(–5)-locular, pubescent; ovules anatropous, inner integuments moderately thick; stylodia bifid. Fruits capsular. Seeds trigonous, ecarunculate, testa thick and woody.

Four spp., SE Asia, Malesia, and extending to Japan.

12b. SUBTRIBE GARCIINAE Müll. Arg. (1865).

Monoecious; indumentum simple; leaves entire, without glands at apex of petiole, estipulate; inflorescences terminal, glomerular; petals 6–13; staminate disk intrastaminal; stamens 30–100, filaments distinct; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick; stylodia bifid; fruits capsular; seeds ecarunculate.

In accord with Webster (1975, 1994), subtribe Garciinae is restricted to *Garcia*, which is very isolated within the Aleuritideae. There are striking resemblances between *Garcia* and *Sagotia* and *Sandwithia*, so that *Garcia* might belong to the Crotoneae.

245. *Garcia* Vahl

Garcia Vahl, Skriv. Naturh. Selsk. Kjöbenh. 2: 217, t. 9 (1792); Müll. Arg. in DC. Prodr. 15 (2): 721 (1866); Pax, Pflanzenr. 147, I: 14 (1910); Lundell, Wrightia 1: 1 (1945); Webster, Ann. Missouri Bot. Gard. 54: 238, fig. 6 (1968); Burger & Huft, Fieldiana Bot. n. s. 36: 122, fig. 21 (1995).

Monoecious shrubs or trees; laticifers non-articulated; latex not recorded; indumentum simple. Leaves petiolate (pulvinate), cartilaginous, without paired basal glands; stipules 0. Inflorescences terminal, glomerular, bisexual, each with 1 or 2 pistillate and several staminate flowers; bracts entire, inconspicuous. Staminate flowers pedicellate; calyx splitting into 2 or 3 valvate segments; petals 6–13, reddish, distinct, narrow, sericeous on both faces, exserted from calyx; disk ill-defined, mainly represented on the convex pilose and glandular receptacle; stamens 30–100, filaments distinct; anthers basifixed, minutely apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calyx splitting into 2 or 3 valvate segments, deciduous; petals as in the staminate flowers; disk deeply lobed; ovary 3-locular, sericeous; ovules anatropous, inner integuments thick, vascularized; stylodia thick, reflexed, bifid. Fruits capsular; columella persistent. Seeds subspheroidal, ecarunculate; testa smooth. $2n = 66$.

Two spp., Mexico south to Colombia.

12c. SUBTRIBE GROSSERINAE G.L. Webster (1975).

Dioecious (monoecious) trees or shrubs; latex usually not recorded; indumentum simple or 0; leaves pinnately veined or triplinerved, with or without basal laminar glands; stipules deciduous or 0; inflorescences terminal, racemoid, or paniculate; staminate petals 4 or 5, distinct or basally connate; staminate disk dissected; stamens 6–40, filaments distinct or connate; pistillate petals 4 or 5, distinct; ovary 3–5-locular; stylodia (twice) bifid; fruit capsular; seeds ecarunculate (carunculate).

Six paleotropical genera, three African/Madagascan and three SE Asian/Malesian. *Deutzianthus* and *Oligoceras*, included by Webster (1994) and Radcliffe-Smith (2001) in the Jatropheae, are here brought to tribe Aleuritidae, in consonance with Thin (1995), and provisionally included in subtribe Grosserinae. Molecular data for this placement are still lacking.

KEY TO THE GENERA OF GROSSERINAE

1. Pollen grains with echinate exinous pillars; leaf blades triplinerved; bracts glandular **249. *Tannodia***
– Pollen grains with rounded exinous pillars; leaves pinnately veined; bracts eglandular 2
2. Leaf blades not pellucid-punctate 3
– Leaf blades pellucid-punctate 5
3. Staminate petals adaxially pubescent **248. *Tapoides***
– Staminate petals glabrous 4
4. Monoecious; glabrous; stylodia 3, connate at the base, bifid **250. *Oligoceras***
– Dioecious; indumentum simple, largely confined to inflorescences and fruits; stylodia 3, ± distinct, twice bifid, or deeply branched and distally bifid, hence appearing as 6 stylodia **251. *Deutzianthus***
5. Bracts small, persistent; inflorescence paniculate; leaf blades denticulate; stipular scars minute; pistillate sepals medianly thickened **247. *Grossera***
– Bracts large, imbricate, deciduous; inflorescence cone-like; leaf blades entire; stipular scars subannular, conspicuous; pistillate sepals not thickened **246. *Cavacoa***

246. *Cavacoa* Léonard

Cavacoa Léonard, Bull. Jard. Bot. Brux. 25: 320, fig. 54 (1955), Fl. Congo Belge 8(1): 191, fig. 16 (1962); Elffers & Taylor, Hook. Icon. Pl. 36: t. 3561 (1956); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 174, fig. 33 (1987); Radcl.-Sm., Fl. Zambesiaca 9(4): 304, t. 63 (1996).

Dioecious trees or shrubs; branches terminating in perulate buds; latex not recorded; indumentum simple. Leaves pellucid-punctate, entire, usually with basal paired glands and scattered embedded glands; stipules deciduous. Inflorescences terminal, racemoid; bracts large, covering flowers in bud, deciduous. Staminate flowers pedicellate; calyx splitting into 2 segments; petals 4 or 5, distinct, imbricate, glabrous; disk segments 4 or 5, glabrous; stamens 15–30, filaments connate into a column [outer filaments ± distinct]; anthers with enlarged connective; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, distinct, imbricate, entire, deciduous in fruit; petals 4 or 5, distinct, imbricate, glabrous; disk annular, glabrous; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella persistent. Seeds ecarunculate, testa smooth.

Three spp. of tropical Africa south to Natal.

247. *Grossera* Pax

Grossera Pax, Bot. Jahrb. 33: 281 (1903); Pax & K. Hoffm., Pflanzenr. 147, VI: 105, fig. 21 (1912); Leandri, Bull. Soc. Bot. France 85: 524 (1939); Cavaco, Bull. Mus. Hist. Nat. Paris 21: 272 (1949); Léonard, Bull. Jard. Bot. Brux. 25: 316 (1955), 28: 118 (1958), Fl. Congo Belge 8(1): 188 (1962); Keay, Fl. W. Trop. Afr. ed. 2, 1: 398 (1958); Radcl.-Sm., Gen. Euphorb.: 337, fig. 42 (2001).

Dioecious shrubs; latex not recorded; indumentum simple. Leaves entire or denticulate, pellucid-punctate, usually with paired basal glands at junction with petiole; stipules deciduous. Inflorescences terminal, cymose-paniculate; bracts entire, eglandular, the pistillate deciduous. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate segments; petals 5, white, distinct, imbricate, glabrous; disk segments 5, glabrous; stamens 13–40, filaments irregularly connate at the base; anthers with enlarged connective; pollen spheroidal, grains inaperturate, exine with Croton pattern, pillars acute, smooth; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, distinct, imbricate, entire, persistent in fruit; petals 4 or 5, distinct, imbricate; disk cupular, lobed, glabrous; ovary 3-locular, glabrous; ovules anatropous, inner integuments thick, vascularized; stylodia bifid. Fruits capsular; columella triquetrous, persistent. Seeds ecarunculate, testa smooth.

Eight spp., C and W Africa and (1) Madagascar.

248. *Tapoides* Airy Shaw

Tapoides Airy Shaw, Kew Bull. 14: 473 (1960), 20: 412 (1966), Hook. Icon. Pl. 37: t. 3632 (1967), Kew Bull. Add. Ser. 4: 200 (1975); Radcl.-Sm., Gen. Euphorb.: 337 (2001).

Dioecious trees; latex reddish; indumentum simple, scanty. Leaves petiolate (pulvinate), crowded at ends of branches, entire, lacking basal glands; stipules subulate, minute. Inflorescences axillary or subterminal, the staminate thyrsoid-paniculate, the pistillate glomerular; bracts entire. Staminate flowers pedicellate; calyx closed in bud, splitting into 3 valvate segments; petals 5, distinct, imbricate, adaxially pubescent; disk segments 5; stamens 6–8, filaments distinct, pubescent; pistillode 0. Pistillate flowers pedicellate; calyx splitting into 3 valvate segments, persistent in fruit; petals and disk unknown; ovary 3-locular, pubescent. Fruits capsular. Mature seeds not recorded.

A single sp., *T. vilamilii* (Merr.) Airy Shaw, endemic to Borneo (Sabah). Airy Shaw (1967) suggested that it is most closely related to *Aleurites* and *Elateriospermum* but also pointed out possible affinities with *Omphalea*. However, the reddish latex, mainly axillary inflorescences, and distinct stamens of *Tapoides* set it apart from the other Grosserinae; this suggests that it may be misplaced.

249. *Tannodia* Baill.

Tannodia Baill., Adansonia I, 1: 251 (1861); Müll. Arg. in DC., Prodr. 15(2): 728 (1866); Pax & K. Hoffm., Pflanzenr. 147, VI: 110 (1912); Léonard, Bull. Jard. Bot. Brux. 25: 300 (1955), Fl. Congo Belge 8(1): 186 (1962); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 172, fig. 32 (1987); Webster, Ann. Missouri Bot. Gard. 81: 115 (1994); Radcl.-Sm., Fl. Zambesiaca 9(4): 306, t. 64 (1996), Kew Bull. 53: 173 (1998), Gen. Euphorb.: 338 (2001).
Tandonia Baillon (1861).
Holstia Pax (1909; nom. illeg.).
Domohinea Leandri (1941).
Neoholstia Rauschert (1982).

Monoecious or dioecious trees; latex not recorded; indumentum simple, scanty [inflorescences only]. Leaves eglandular; stipules persistent or deciduous. Inflorescences terminal, racemoid or spiciform, or the staminate in contracted glomerules, unisexual or bisexual; bracts entire to glandular-lacerate. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–5 valvate segments; petals 4 or 5, white, distinct, imbricate, longer than calyx; disk segments 4 or 5, glabrous; stamens 7–12, filaments connate below, biseriate; anthers dorsifixed, the outer extrorse, inner introrse, connective broad; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, basally connate, imbricate, entire, persistent in fruit; petals 4 or 5, distinct, imbricate, exserted beyond sepals; disk annular; ovary 3-locular, pubescent; ovules anatropous, inner integuments thick, vascularized; stylodia basally connate, erect, bifid. Fruits capsular. Seeds ellipsoidal, ecarunculate, testa smooth.

Nine spp., three in Africa and six in Madagascar (including the Comoros).

250. *Oligoceras* Gagnep.

Oligoceras Gagnep., Bull. Soc. Bot. France 71: 872 (1925); Fl. Indochine 5: 467, fig. 58, 3–9 (1926); Airy Shaw, Kew Bull. 14: 392 (1960).

Monoecious trees; latex not recorded; foliage glabrous. Leaves long-petiolate, lamina ± deltoid, with 2 discoid glands at apex of petiole; stipules 0. Inflorescences terminal, paniculate, bisexual; bracts scale-like, apically fimbriate. Staminate flowers pedicellate; calyx campanulate, sepals 5, connate, each with a cylindric-cornute truncate appendage; petals 5, distinct, imbricate, unguiculate; disk segments 5, connate around the base of the staminal column; stamens and staminodes connate in 2 whorls into a cylindrical column, outer whorl of 5 stamens, inner of 3 staminodes; anthers introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; calycine appendages obtuse, otherwise perianth as in staminate flowers; disk annular; ovary 3-locular, stylodia nearly distinct, bifid, stigmatic portion coiled. Fruits drupaceous. Seeds unknown.

A single sp., *O. eberhardtii* Gagnep., known only from Annam, Vietnam.

251. ***Deutzianthus*** Gagnep.

Deutzianthus Gagnep., Bull. Soc. Bot. France 71: 139 (1924), Fl. Indochine 5: 296, figs. 31, 3–9, 32, 1 (1925); Airy Shaw, Kew Bull. 14: 362 (1960), 16: 346 (1963); Webster, Ann. Missouri Bot. Gard. 81: 104 (1994); Radcl.-Sm., Gen. Euphorb.: 291 (2001).

Loerzingia Airy Shaw (1963).

Dioecious trees; latex yellowish-orange; indumentum simple. Leaves long-petiolate, with 2 adaxial disciform glands at junction with petiole; stipules deciduous. Inflorescences long-pedunculate, terminal or subterminal, of compound unisexual dichasia, bracts linear, eglandular, persistent. Staminate flowers pedicellate; sepals 5, ± connate, the calyx 5-dentate, valvate or subimbricate; petals 5, distinct, entire, adaxially pilose; disk glands 5; stamens 7 or 8, biseriate, 5 outer distinct, 2 or 3 inner connate to halfway; anthers cordulate or sagittate at the base; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0 or rudimentary. Pistillate flowers pedicellate; perianth as in staminate; disk annular or 5-lobed; ovary 3-locular, sericeous; stylodia 3, distally twice bifid, or deeply branched and apically bifid, hence appearing as 6 stylodia. Fruits ± indehiscent or tardily dehiscent. Seeds unknown.

Two species, disjunct in Vietnam and Sumatra. Radcliffe-Smith (2001) maintains *Loerzingia* as a distinct genus on the basis of its deciduous foliar glands, imbricate sepals, and presence of pistillode in the staminate flower. The type species, *D. tonkinensis* Gagnep., does indeed differ in these characters, but the similarities seem more important than the differences.

12d. Subtribe Crotonogyninae G.L. Webster (1975).

Trees or shrubs, sometimes scandent; latex apparently not produced; indumentum stellate or lepidote; leaves pinnately or palmately veined, biglandular at junction with petiole, stipulate; inflorescences axillary, spiciform or racemoid to paniculate; staminate sepals connate in bud, valvately dehiscent; petals coherent or connate; disk dissected; stamens 7–40, distinct or connate; anthers often apiculate; pistillate sepals 4 or 5, imbricate or valvate; ovary 3-locular; stylodia bifid or multifid; fruits capsular; seeds ecarunculate.

A subtribe of three African genera.

Key to the Genera of Crotonogyninae

1. Leaf blades palmately veined; petioles with inflated hairs; stylodia bifid; lianas **254. *Manniophyton***
– Leaf blades pinnately veined; petioles lacking inflated hairs; stylodia bifid or multifid; trees or shrubs 2
2. Stylodia bifid; inflorescences terminal, paniculate; staminate petals distinct; staminate disk receptacular and extrastaminal, of > 10 segments **252. *Cyrtogonone***
– Stylodia multifid; inflorescences axillary, racemoid or spiciform; staminate petals usually coherent or connate; staminal disk extrastraminal, of 5–8 segments **253. *Crotonogyne***

252. ***Cyrtogonone*** Prain

Cyrtogonone Prain, Kew Bull. 1911: 231 (1911), Hook. Icon. Pl. 31: t. 3009 (1915); Pax & K. Hoffm., Pflanzenr. 147, VI: 111, fig. 23 (1912); Keay, Fl. W. Trop. Afr., ed. 2, 1: 399 (1958); Webster, Ann. Missouri Bot. Gard. 81: 116 (1994); Radcl.-Sm., Gen. Euphorb.: 342 (2001).

Dioecious trees; latex not recorded; indumentum lepidote. Leaves entire or dentate, silvery-lepidote abaxially, with paired basal glands at junction with petiole; stipules minute. Inflorescences terminal, cymose-paniculate; bracts inconspicuous. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 5 (6), distinct, contorted, glabrous; disk segments c. 10, receptacle glandular; stamens 12–30, filaments distinct, glabrous; anthers dorsifixed, introrse; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 4 or 5, imbricate, entire; petals 5, distinct, imbricate; disk annular; ovary 3-locular, pubescent; stylodia bifid. Fruits capsular, cocci dorsally verrucate. Seeds subspheroidal, ecarunculate.

A single sp., *C. argentea* (Pax) Prain, W Africa.

253. ***Crotonogyne*** Müll. Arg.

Crotonogyne Müll. Arg., Flora 47: 535 (1864), in DC., Prodr. 15(2): 720 (1866); Pax & K. Hoffm., Pflanzenr. 147, VI: 111, fig. 24 (1912); Prain, Hook. Icon. Pl. 31: t. 3019 (1915); Keay, Fl. W. Trop. Afr., ed. 2, 1: 399 (1958); Léonard, Fl. Congo Belge 8(1): 174, fig. 14 (1962); Webster, Ann. Missouri Bot. Gard. 81: 116 (1994); Radcl.-Sm., Gen. Euphorb.: 342 (2001).

Neomanniophyton Pax (1912).

Dioecious (monoecious); latex not recorded; indumentum simple and stellate or lepidote. Leaves with basal laminar glands at junction with petiole; stipules entire, ± persistent. Inflorescences axillary, racemoid or spiciform, sometimes branched; bracts biglandular at base. Staminate flowers pedicellate; calyx closed in bud, splitting into 2–4 valvate segments; petals 5, mostly ± connate; disk segments 5–8, glabrous; receptacle glabrous; stamens (7–)10–28, filaments distinct; anthers apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals (4)5, slightly connate basally, imbricate, abaxially lepidote, persistent in fruit; petals (4)5(6), distinct, imbricate, glabrous; disk annular-lobed, glabrous; ovary 3-locular, stellate-pubescent or lepidote; ovules anatropous, inner integuments thick, vascularized; stylodia multifid. Fruits capsular; columella persistent, slender, apically dilated. Seeds somewhat compressed, ecarunculate, testa smooth.

Sixteen spp., W Africa, from Sierra Leone to Angola. Pax (1912) separated *Neomanniophyton* from *Manniophyton* on the basis of leaf venation and division of the stylodia. However, further study has shown that *Neomanniophyton* is closer to *Crotonogyne* in its leaf venation and stylar branching. Although generic boundaries in the Crotogyninae need further study, it appears best to follow Webster (1994) and Radcliffe-Smith (2001) in combining *Crotonogyne* and *Neomanniophyton.*

254. *Manniophyton* Müll. Arg.

Manniophyton Müll. Arg., Flora 47: 530 (1864), in DC., Prodr. 15(2): 719 (1866); Benth., Hook. Icon. Pl. 13: t. 1267 (1878); Pax & Hoffm., Pflanzenr. 147, VI: 120, fig. 25 (1912); Keay, Fl. W. Trop. Afr. et. 2, 1: 400 (1958); Léonard, Fl. Congo Belge 8(1): 171, fig.13 (1962); Radcl.-Sm., Gen. Euphorb.: 343 (2001).

Dioecious lianas; latex reddish; indumentum simple to stellate. Leaves simple, sometimes 3–5-lobed, palmately veined, with paired stipels and bottle-shaped glands abaxially near junction with petiole; stipules deciduous. Inflorescences terminal and axillary, often in pairs, ± thyrsoid-paniculate; bracts biglandular at base. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate segments; petals 5, glabrous, connate into an urceolate corolla [lobes much shorter than tube]; disk segments 5 or 6, pubescent; receptacle pilose; stamens 10–20, filaments distinct; anthers basifixed, apiculate, connective enlarged; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, slightly connate at base, imbricate, entire, persistent and somewhat accrescent in fruit, petals 5, yellowish-green, distinct, imbricate, adaxially pubescent; disk annular, pubescent; ovary 3-locular, sericeous-hispid; ovules anatropous, inner integuments moderately thick, vascularized; stylodia bipartite. Fruits capsular, cocci thick and woody; columella persistent. Seeds compressed, ecarunculate, thin and shiny.

A single sp., *M. africanum* Müll. Arg., West Africa, Liberia to Angola.

12e. Subtribe Neoboutoninae (Hutch.) G.L. Webster (1975).

Dioecious trees or shrubs; indumentum stellate or lepidote; leaves unlobed, pinnately or palmately veined, glandular-dotted, stipulate; inflorescences terminal or axillary, racemoid to paniculate; calyx segments 2 or 3; disk dissected or 0; stamens 15–40, filaments distinct, shorter than anthers; anthers with glandular connective; ovary 3-locular; stylodia bifid; fruit capsular; seeds carunculatae or ecarunculate.

Two genera, African and Malagasy.

Key to the Genera of Neoboutoninae

1. Leaf blades palmately veined; stipules persistent; seeds carunculate; indumentum stellate **255. *Neoboutonia***
– Leaf blades pinnately veined; stipules deciduous; seeds ecarunculate; indumentum lepidote **256. *Benoistia***

255. *Neoboutonia* Müll. Arg.

Neoboutonia Müll. Arg., J. Bot. 2: 336 (1864), in DC., Prodr. 15(2): 892 (1866); Benth., Hook. Icon. Pl. 13: t. 1298, 1299 (1879); Pax & K. Hoffm., Pflanzenr. 147, VII: 71 (1914); Radcl.-Sm., Fl. Zambesiaca 9(4): 310, t. 66 (1996).

Dioecious trees and shrubs; latex not recorded; indumentum tufted-stellate and simple. Leaves palmately veined, cordate, with basal laminar stipellate glands and minute dispersed discoid glands; stipules ± foliaceous, entire, persistent. Inflorescences terminal and axillary, cymose-paniculate; staminate bracts entire, eglandular, persistent. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 segments; petals 0; disk segments 8–10, minute; stamens 15–40, filaments distinct; anthers basifixed, introrse, glandular-apiculate; pollen grains spheroidal, inaperturate, exine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5, distinct, imbricate, entire, persistent, sometimes accrescent; petals 0; disk annular; ovary 3-locular, stellate-pubescent or lepidote; ovules anatropous, inner integuments very thick, vascularized; stylodia bipartite, branches slender. Fruits capsular; columella persistent. Seeds subspheroidal, caruncle small, adpressed; testa smooth.

Three spp., widespread in tropical Africa. Pax and Hoffmann (1914) spectacularly misplaced *Neoboutonia* into the Acalypheae-Mercurialinae, assigning it to series Neoboutoniiformes. This was negated by Punt (1962), who showed that the pollen of *Neoboutonia* has the typical Crotonoid pattern of exine ornamentation.

256. *Benoistia* H. Perrier & Leandri

Benoistia H. Perrier & Leandri, Bull. Soc. Bot. France 85: 528 (1938); Radcl.-Sm., Kew Bull. 43: 632 (1988).

Dioecious trees; latex not recorded; indumentum simple and glandular-lepidote. Leaves pellucid-punctate, lacking basal glands at junction with petiole; stipules minute, deciduous. Inflorescences axillary, racemoid or paniculate; pistillate bracts foliose. Staminate flowers pedicellate; calyx closed in bud, splitting into 2 or 3 valvate lobes; petals 0; disk segments interstaminal or 0; stamens 28–30, filaments distinct, shorter than anthers; anthers basifixed, introrse, connective apically glandular; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5–7, imbricate, persistent and ± accrescent in fruit; petals 0; disk annular, pubescent; ovary mainly (2)3(4)-locular, stellate-tomentose; ovules anatropous, inner integuments very thick, vascularized; stylodia bifid. Fruits smooth to tuberculate, dehiscing septicidally; columella trigonous, persistent. Seeds ellipsoidal, ecarunculate, testa smooth; endosperm oily.

Three spp., endemic to Madagascar.

12f. SUBTRIBE PARACROTONINAE G.L. Webster[1]

Monoecious trees or shrubs; leaves ± dentate; sepals and petals 5(6), distinct; staminate disk of distinct glands, pistillate disk annular; stamens 10–32, outer filaments distinct, the inner connate into a column; inflorescences terminal or axillary; seeds carunculate or ecarunculate.

Mildbraedia and *Paracroton* appear to represent sister genera united by a distinctive synapomorphy of the androecium with the outer filaments distinct and the inner connate.

KEY TO THE GENERA OF PARACROTONINAE

1. Dioecious; inflorescences axillary; leaf blades without paired basal glands; seed coat dry **257. *Mildbraedia***
– Monoecious; inflorescences terminal; leaf blades with paired basal glands; seed coat fleshy **258. *Paracroton***

257. *Mildbraedia* Pax Fig. 42

Mildbraedia Pax, Bot. Jahrb. 43: 319 (1909); Pflanzenr. 147, III: 11 (1911), 147, VII: 403 (1914); Léonard, Fl. Congo Belge 8(1): 85 (1962); Radcliffe-Sm., Fl. E. Trop. Afr., Euphorb. 1: 340, fig. 64 (1987), Fl. Zambesiaca 9(4): 273, t. 56 (1996).
Neojatropha Pax (1910).

Dioecious trees or shrubs; latex not recorded; indumentum stellate. Leaves simple, sometimes lobed, triplinerved or pinnately veined, dentate, eglandular; stipules subulate, deciduous. Inflorescences axillary or slightly supraaxillary, pedunculate, dichasial, the pistillate flowers central; bracts minute, deciduous. Staminate flowers pedicellate; sepals 5 (6), distinct, imbricate; petals 5 (6), distinct, imbricate, pubescent abaxially; disk segments 5; stamens 10–25, outer filaments distinct but inner connate into a column, not inflexed in bud; anthers dorsifixed, introrse, muticous; pollen grains spheroidal, inaperturate, eine with Croton pattern; pistillode 0. Pistillate flowers pedicellate; sepals 5 (6), distinct, imbricate, persistent in fruit; petals 5 (6), distinct, imbricate; disk annular, slightly lobed, glabrous; ovary 3-locular, pubescent; ovules pachychalazal, inner integuments thick, vascularized; stylodia nearly distinct, deeply bifid, branches slender. Fruits capsular, cocci thin-walled; columella persistent. Seeds subspheroidal, caruncle subspherical, appressed; testa crustaceous, smooth.

Three or four spp., tropical Africa, from Liberia and Gabon to Kenya and Mozambique.

258. *Paracroton* Miq.

Paracroton Miq., Fl. Ind. Batav. 1(2): 382 (1859); Müll. Arg. in DC., Prodr. 15(2): 1112 (1866); J.J. Sm., Meded. Dept. Landb. 12: 585 (1910); Pax, Pflanzenr. 147, III: 12

---

[1] Subtr. **Paracrotoninae** G.L. Webster, **subtrib. nov.**, monoici; inflorescentiis axillaribus; fructibus capsularis; sepalis foemineis persistentibus; petalis connatis vel liberis. Typus: *Paracroton* Miquel.

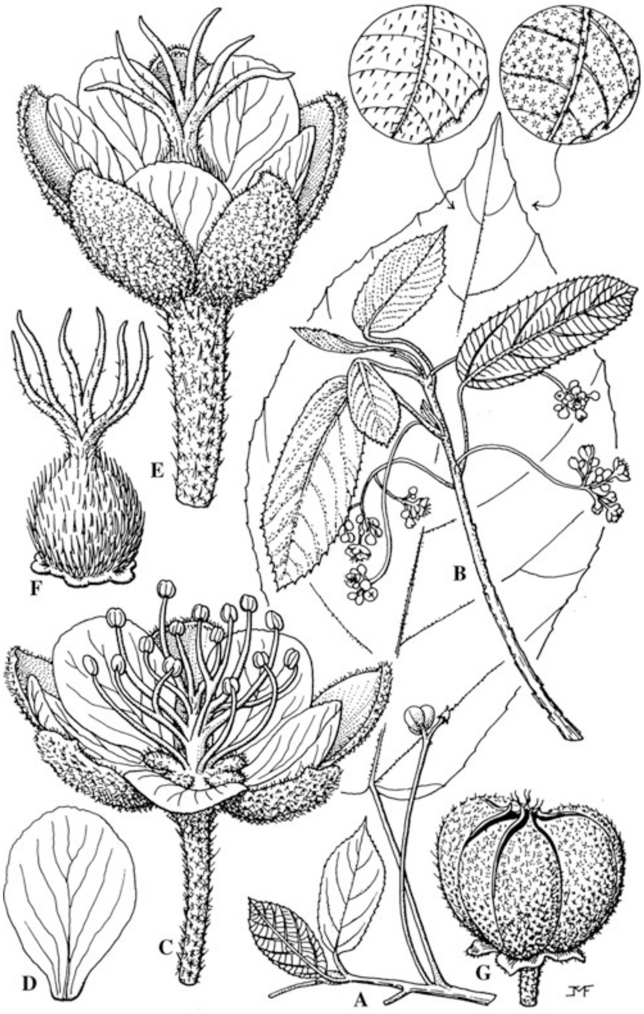

Fig. 42. Euphorbiaceae-Crotonoideae. *Mildbraedia carpinifolia* var. *strigosa*. **A** Distal portion of fruiting branch. **B** Distal portion of branch with staminate flowers. **C** Staminate flower. **D** Petal. **E** Pistillate flower. **F** Pistil. **G** Fruit. (Radcliffe-Smith 1996; drawn by J.M. Fothergill)

(1911); N.P. Balakr. & Chakrab., Kew Bull. 48: 716, figs. 1–3 (1993); Radcl.-Sm., Gen. Euphorb.; 318 (2001).

Fahrenheitia Rchb. f. & Zoll. (1857).

Desmostemon Thwaites (1861).

Monoecious trees; latex not recorded; indumentum stellate or lepidote. Leaves petiolate (pulvinate), glandular-dentate or serrate, biglandular at junction with petiole; stipules represented by sessile glands. Inflorescences terminal, unisexual; staminate inflorescences terminal and axillary, narrowly thyrsoid; pistillate inflorescences terminal, thyrsoid, sparsely branched, flowers 1–3 per node; bracts deciduous. Staminate flowers subsessile; sepals 5, slightly connate, imbricate, dorsally often with knob- or horn-like appendage; petals 5, distinct; disk segments 5, 7 or 10; stamens 12–32, outer filaments distinct, inner ones connate into a column; anthers dorsifixed, extrorse, muticous; pollen grains spheroidal, inaperturate, with Croton pattern. Pistillate flowers pedicellate; calyx as in staminate, persistent in fruit, petals 5, coherent, glabrous, deciduous; disk annular, lobed, pilose; ovary 3-locular, pubescent; stylodia bifid. Fruits capsular. Seeds spheroidal, ecarunculate, testa smooth or striate, slightly fleshy.

Four spp., tropical Asia from Sri Lanka to W Malesia, the Philippines, and New Guinea. Balakrishnan and Chakrabarty (1993) believe that the closest allies of *Paracroton* are *Ostodes* and *Dimorphocalyx*.

Unplaced genus of inaperturate crotonoids:

259. *Radcliffea* P. Hoffm. & K. Wurdack

Radcliffea P. Hoffm. & K. Wurdack, Kew Bull. 61: 194 (2006).

Dioecious shrub or tree, probably latescent; indumentum stellate. Leaves long-petiolate, domatiiferous, at base palminerved, at junction with petiole provided on both sides with minute glands; stipules apparently sometimes replaced by minute glands. Inflorescences terminal, paniculate, with 3–5 orders of branching. Staminate flowers pedicellate, sepals 5, distinct, imbricate, outermost bearing a small abaxial gland; petals 5, distinct, imbricate; disk glands 5, distinct; stamens 5, with the filaments connate for more than half their length into a column; pollen grains spheroidal, inaperturate, with Croton pattern; pistillode +. Pistillate flowers pedicellate, sepals 5, distinct, imbricate, all with abaxial gland; petals 4–7, distinct, imbricate; disk-glands 5, distinct or irregularly connate; ovary 1-locular, asymmetrical; ovule 1, anatropous, inserted subapically; stylodia 3, inserted excentrically, simple, unequal. Fruits and seeds unknown.

A single sp., *R. smithii* P. Hoffm. & K. Wurdack, from deciduous forests on limestone in W Madagascar.

VII. SUBFAM. EUPHORBIOIDEAE

Monoecious (dioecious) trees, shrubs, or herbs (scandent); laticifers non-articulate, latex mostly whitish; indumentum simple or 0, dendritic in *Mabea* and *Senenefelderopsis*. Leaves alternate or opposite, simple, unlobed, entire or dentate, usually pinnately veined, often with basal glands at junction with petiole; stipules often reduced or 0. Inflorescences terminal or axillary, spiciform to racemoid or paniculate or condensed into the pseudanthial cyathium; bracts often biglandular at base. Flowers apetalous, erect or inclinate in bud; staminate sepals (1)3–6, imbricate to valvate, mostly open in bud, commonly minute or 0; disk 0; stamens 1–20(–80), filaments distinct or connate; pollen grains binucleate or trinucleate, 3-colporate, colpi usually marginate, exine usually tectate-perforate; pistillode 0; pistillate sepals 3–6, distinct or connate, imbricate or open in bud, sometimes reduced to obsolete; disk 0; ovary 2–3(–20)-locular; stylodia distinct or connate, nearly always unlobed. Fruits capsular (drupaceous). Seeds carunculate or ecarunculate; testa dry or fleshy, exotegmen palisadal; endosperm copious.

Molecular analyses (Wurdack et al. 2005; Tokuoka 2007) confirm the broad lines of the classification of this subfamily and the inclusion of the Stomatocalyceae, which had been suggested by Webster (1975) and accepted by Radcliffe-Smith (2001); the Stomatocalyceae are resolved as sister to the rest of the subfamily. This is divisible into two subclades, which contain the Hippomaneae and the Euphorbieae, the latter broadened by inclusion of the Hureae and Pachystromateae.

KEY TO THE TRIBES OF SUBFAM. EUPHORBIOIDEAE

1. Pollen exine tectate-reticulate; bracts eglandular, distinct from rachis; stylodia unlobed; seeds ecarunculate; dioecious trees or lianas **1. Stomatocalyceae**
– Pollen exine tectate-perforate; bracts glandular, often adnate to rachis; stylodia bifid or unlobed; seeds carunculate or ecarunculate; monoecious (dioecious) trees, shrubs, or herbs, rarely scandent 2
2. Inflorescences mostly racemoid or spiciform, sometimes capitate but never cyathial; flower buds usually inclinate; staminate calyx usually well developed; stylodia mostly unlobed; intine thickenings along the colpi 0 **2. Hippomaneae** s. l.
– Inflorescences pseudanthial, i.e., cyathial, usually with a single terminal pistillate flower, and 4 or 5 lateral staminate monochasia or dichasia; perianth reduced or 0; stylodia mostly bifid; colpi bordered by two conspicuous intine thickenings **3. Euphorbieae**

1. TRIBE STOMATOCALYCEAE (Müll. Arg.) G.L. Webster (1975).

Dioecious trees, shrubs, or lianas; latex yellowish, often scanty; indumentum simple or 0; leaves alternate, unlobed, pinnately veined, without glands at base of blade; stipules small and caducous or 0; inflorescences axillary, racemoid, bracts eglandular; staminate sepals 4–8, distinct and imbricate or connate; stamens 10–30, distinct, filaments shorter than anthers; pollen grains coarsely reticulate or reticulate-perforate; pistillate sepals 5 or 6, distinct or connate; ovary 2–10-locular; stylodia unlobed, sometimes dilated or stigmatiform; fruit capsular or indehiscent, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

Four genera and about 12 spp., pantropical.

KEY TO THE GENERA OF STOMATOCALYCEAE

1. Fruits indehiscent; stylodia abbreviated; ovary 1–10-locular; pollen grains finely reticulate-perforate 2
– Fruits capsular; stylodia elongated; ovary 2–3-locular; pollen grains coarsely reticulate 3
2. Sepals 6–8, distinct; ovary 1-locular **262. *Plagiostyles***
– Sepals connate, calyx 2-lipped; ovary 2–10-locular **263. *Pimelodendron***
3. Ovary 3-locular; stylodia erect; stamens 18–20; pistillate sepals not glandular; stems ± scandent **261. *Hamilcoa***
– Ovary 2-locular; stylodia spreading; stamens 10; pistillate sepals with large basal glands; stems not scandent **260. *Nealchornea***

260. *Nealchornea* Huber

Nealchornea Huber, Bol. Mus. Goeldi 7: 297 (1913); Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 201, t. 10 (1922); Wallnöfer, Linzer Biol. Beitr. 23(2): 777 (1991); Radcl.-Sm., Gen. Euphorb.: 352 (2001).

Dioecious trees; latex whitish or yellowish; indumentum simple, scanty. Leaves remotely glandular-crenate, with small abaxial basal or submarginal glands; stipules obsolete. Inflorescences axillary and subterminal, the staminate paniculate, the pistillate racemose; bracts eglandular. Staminate flowers pedicellate; sepals 4, biseriate, slightly imbricate, open in bud; stamens 8–15 (–18), distinct; anthers sessile, erect, dehiscing longitudinally; connective enlarged, conspicuously appendiculate terminally; pollen grains oblate spheroidal, 3-colporate, sexine coarsely reticulate. Pistillate flowers pedicellate; sepals 4, basally connate, slightly imbricate, glandular, persistent in fruit; ovary 2-locular; ovules anatropous, inner integuments moderately thick, outer integuments vascularized; stylodia unlobed, thickened, slightly connate at base. Fruits ± baccate, not regularly dehiscent, thin-walled. Seeds ecarunculate.

Two spp., lowland Amazonian forests of Brazil and adjacent Peru and Colombia.

261. ***Hamilcoa*** Prain

Hamilcoa Prain, Kew Bull. 1912: 107 (1912), Fl. Trop. Afr. 6(1): 1000 (1913); Stapf, Hook. Icon. Pl. 31: t. 3990 (1915); Keay, Fl. W. Trop. Afr., ed. 2, 1: 413 (1958).

Dioecious lianas; latex white; indumentum 0. Leaves simple or occasionally lobed, entire or subentire, eglandular; stipules minute, caducous. Inflorescences racemoid, staminate axillary, pistillate terminal; bracts eglandular, 1-flowered. Staminate flowers pedicellate; sepals 5, distinct, imbricate; stamens 18–30, distinct, filaments much shorter than anthers; anthers basifixed, the exterior extrorse, dehiscing longitudinally; pollen grains coarsely reticulate. Pistillate flowers with thick reflexed pedicels; sepals 6, biseriate, imbricate, subentire; ovary 3-locular; stylodia connate at base, erect, dilated, unlobed. Fruits capsular. Seeds with spongy testa.

Only one sp., *H. zenkeri* Prain, from lowland forests in Nigeria and Cameroon.

262. ***Plagiostyles*** Pierre

Plagiostyles Pierre, Bull. Mens. Soc. Linn. Paris 2: 1326 (1897); Prain, Fl. Trop. Afr. 6(1): 1001 (1913); Stapf, Hook. Icon. Pl. 31: t. 3010 (1915); Léonard, Fl. Congo 8 (1): 131 (1962); Radcl.-Sm., Gen. Euphorb.: 348, fig. 44 (2001).

Dioecious trees or shrubs; latex white, scanty; indumentum simple. Leaves eglandular or with small paired adaxial glands; stipules entire, deciduous. Inflorescences axillary, paniculate or racemoid; bracts eglandular, 1-flowered. Staminate flowers pedicellate; sepals 5–8, unequal, imbricate but not covering the stamens in bud; stamens 15–32, distinct, aggregated-capitulate, filaments much shorter than anthers; anthers extrorse, reddish, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 5, unequal, imbricate, entire, persistent in fruit; ovary 1(2)-locular; ovules anatropous, inner integuments moderately thick; stylodia lateral with discoid stigma. Fruit drupaceous; endocarp membranaceous, adherent to seed. Seeds ecarunculate, transversally veined; endosperm yellowish, oily; cotyledons reniform.

Only one sp., *P. klaineana* Pierre, from the rainforests in Nigeria, Gabon, and Congo.

263. ***Pimelodendron*** Hassk.

Pimelodendron Hassk., Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 140 (1856); J.J. Sm., Bull. Jard. Bot. Buit. III, 6: 100 (1924); Airy Shaw, Kew Bull. 36: 339 (1981).

Dioecious trees; latex whitish or yellowish; indumentum 0 on twigs. Leaves subentire or crenate, eglandular; stipules minute, deciduous. Inflorescences axillary, sometimes cauliflorous, racemoid; bracts eglandular. Staminate flowers pedicellate; sepals connate into a 2-lipped calyx; stamens 10–16, distinct or coherent, shorter than anthers; anthers basifixed, extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; calyx cupular, 2–3-lobed, persistent in fruit; ovary 2–10-locular; ovules anatropous, inner integuments thick; outer integuments vascularized; stylodia coalescent into a stigmatoid apex. Fruit indehiscent, fleshy. Seed solitary, carunculate, subspheroidal, testa striate-reticulate.

Six to eight spp. from tropical Asia and Australia.

2. TRIBE HIPPOMANEAE A. Juss. ex Spach (1834).

Hureae Dumort. (1829).
Pachystromateae (Pax & Hoffm.) Pax (1924).

Monoecious, less commonly dioecious trees, shrubs, or herbs; latex usually milky, sometimes toxic; indumentum simple or 0, dendritic in *Mabea*; leaves alternate (opposite), simple and unlobed; lamina pinnately (palmately) veined, commonly with laminar or petiolar glands; stipules sometimes reduced or 0; inflorescences terminal or axillary, racemoid or spiciform (paniculate), usually bisexual with 1 or 2 pistillate flowers at proximal nodes; bracts mostly glandular; flowers usually inclinate in bud; staminate calyx usually open in bud, sepals 0–3, distinct or connate, imbricate to valvate; stamens 1–70, filaments distinct or connate proximally; anthers extrorse; pollen grains 3-colporate, colpi usually marginate, exine tectate-perforate: pistillate sepals 3–6, imbricate, sometimes reduced or 0; ovary 2–3(−10)-locular; stylodia distinct or connate, unlobed, in one genus the stigmas connate into an umbrella-shaped disk; fruits capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious, not oily.

A mainly neotropical tribe of about 30 genera, broadened here to include tribes Pachystromateae and Hureae. In the analysis of Wurdack et al. (2005), the monotypic Pachystromateae are embedded in the Hureae, and the Hureae form part of one of the two strongly supported subclades representing the Hippomaneae. This confirms earlier expectations by Webster (1994b), who doubted the justification of tribal distinctness of *Pachystroma* and pointed to the closeness of the Hureae to the Hippomaneae (which had been included in that tribe as subtribe Hurinae by previous authors). The subtribal division of the Hippomaneae by Webster (1994) and Esser (2001) is not confirmed by the molecular data and their subtribes are not maintained here, but in the molecular analysis two subclades (H1 and H2) are recognized that cannot be characterized morphologically. The classification of the Hippomaneae presents some of the most intractable problems in the family, and both the delimitation of some larger genera such as *Excoecaria*, *Gymnanthes*, *Sapium*, and *Sebastiana* and the justification of several recently described small genera remain controversial. Overall, the preponderance of small genera (five monotypic, five others with only two or three species) is striking and appears as the work of excessive splitting.

KEY TO THE GENERA OF TRIBE HIPPOMANEAE

1. Leaves present only on young branchlets, plants later leafless, succulent, thorny shrubs, flowering when leafless **288. *Spegazziniophytum***
– Leaves present on older branches; flowering with leaves or, if flowering when leafless, then not a succulent thorny shrub 2
2. Floral bracts eglandular, peltate or adnate to the rachis and covering the flowers; seeds ecarunculate 3
– Floral bracts 2-glandular at the base or eglandular, not peltate nor adnate to the rachis 5
3. Ovary 5–20-locular; stamens 10–80, connate; tips of stylodia radiating from apical disk of column; seeds strongly compressed **279. *Hura***
– Ovary 3-locular; stamens 1–3, distinct or connate; stylodia connate but tips not radiating from a disk 4
4. Stylodia connate 1/3 to 2/3 their length, not distally clavate; tips of staminal sepals distinct, imbricate; staminate spikes mostly terminal **280. *Algernonia***
– Stylodia connate their entire length, distally clavate with deltoid apices; staminal sepals completely connate into a cup; staminate spikes axillary **281. *Ophthalmoblapton***
5. Flowers erect in bud; staminate calyx closed in bud, splitting valvately into 2 segments; filaments and anthers connate; seeds ecarunculate; leaves spinose-dentate **282. *Pachystroma***
– Flowers inclinate in bud; staminate calyx open in bud; stamens distinct or filaments connate; seeds carunculate or ecarunculate; leaves mostly not spinose-dentate [Hippomaneae s. str.] 6
6. Staminate calyx laterally compressed or zygomorphic inclinate, with 1 or 2 distinct lobes; stylodia apically glandular and often bifid **271. *Homalanthus***
– Staminate calyx radially symmetric or rarely zygomorphic-inclinate, with 2 or more lobes or completely connate; stylodia apically undivided and eglandular 7
7. Staminate flowers with 5(6) sepals; stylodia usually connate into a long common style with slender branches; leaves and stems with dendritic hairs **275. *Mabea***
– Staminate flowers with 0–3(4) sepals, calyx with more or less connate lobes, or without distinct lobes, or calyx lacking at all 8
8. Ovary 6–10-locular; bracts glandular **283. *Hippomane***
– Ovary 2- or 3-locular; bracts glandular or eglandular 9
9. Seed testa dry [at most with thin fleshy layer] 10
– Seed testa fleshy [arillate] 28
10. Columella 3-horned at base 11
– Columella not 3-horned at base 12
11. Staminate calyx 2-lobed; petiole glandular near apex **289. *Stillingia***
– Staminate calyx 0; petiole eglandular **287. *Adenopeltis***
12. Leaf blades palmately 3–11-lobed; staminate flower with 1 stamen **270. *Dalembertia***
– Leaf blades simple; staminate flower at least with 2 stamens 13
13. Staminate flowers in a glomerulate head; upper part of seed covered by an enlarged caruncle; leaves long-pedicellate **264. *Maprounea***
– Staminate flowers in an elongated inflorescence; caruncle 0 or small on top of seeds 14
14. Pistillate flowers sessile or subsessile, pedicel usually < 5 mm long in fruit; inflorescences mostly terminal, sometimes axillary as well 15

– Pistillate flowers pedicellate, pedicel usually > 5 mm long in fruit, or else ovary appendiculate; inflorescences mostly axillary 27

15. Inflorescences axillary; leaves alternate or opposite; calyx lobes of staminate flowers distinct or nearly so; mostly dioecious **293. *Excoecaria***

– Inflorescences terminal or axillary; leaves mostly alternate, opposite in *Microstachys* and *Colliguaja*, calyx lobes connate; mostly monoecious 16

16. Inflorescences mostly opposite leaves and with staminate flowers distichous; ovary with 2 vertical rows of appendages on each locule; seeds cylindric, truncate, with a stipitate caruncle **272. *Microstachys***

– Inflorescences terminal; staminate flowers spiral on inflorescence axis; ovary not with 2 rows of appendages on each locule; seeds neither cylindric nor truncate, mostly ecarunculate 17

17. Floral bracts with basal glands, or else stipules caducous; fruits capsular or indehiscent 18

– Floral bracts without basal glands; stipules persistent, ovate, ciliate; fruits capsular 23

18. Staminate calyx completely connate without distinct lobes; stamens 4–17 **267. *Senefeldera***

– Staminate calyx of 3 basally connate calyx lobes; stamens 2–3 19

19. Staminate flowers 5–9 per bract 20

– Staminate flowers 1–3 per bract 22

20. Sepals and stamens 2 per flower; ovary 2-locular, not appendaged; fruit drupaceous **278. *Balakata***

– Sepals 3, stamens 2–3 per flower; fruit capsular 21

21. Leaves eglandular above; ovary and fruit with 3 pairs of appendages **274. *Sclerocroton***

– Leaves above often with a pair of petiolar glands at the junction with the blade; ovary and fruit not appendaged **284. *Pleradenophora***

22. Stylodia distinct or nearly so; staminate flowers sessile to subsessile; leaves serrate **276. *Sebastiana***

– Stylodia proximally connate into a style, style branches undivided; staminate flowers shortly but distinctly pedicellate; leaves entire **273. *Ditrysina***

23. Lobes of staminate calyx 2–3, evident though basally connate 24

– Lobes of staminate calyx 1 or 2 and minute or completely reduced 26

24. Inflorescence axillary; ovary 2–3-locular and with 4 or 6 appendages **277. *Anomostachys***

– Inflorescence terminal; ovary 3-locular, unappendaged 25

25. Staminate flowers 6–20 per bract; stamens 2–5, filaments distinct; indumentum simple, often colored **266. *Senefelderopsis***

– Staminate flowers 2–4 per bract; stamens 3, filaments connate into a column; plants glabrous **286. *Grimmeodendron***

26. Inflorescences axillary; leaves (sub)opposite **292. *Colliguaja***

– Inflorescences on lateral short shoots; leaves alternate **285. *Bonania***

27. Inflorescence buds covered by caducous bud-scales; floral bracts irregular and weak, often nearly 0; stamens 4–16 **265. *Actinostemon***

– Inflorescence buds sheathed by the stiff, scaly floral bracts, not by sterile scales; stamens 2–6 **269. *Gymnanthes***

28. Inflorescences unisexual; fruits irregularly dehiscent; seeds whitish arillate **290. *Falconeria***

– Inflorescences bisexual 29

29. Seed aril reddish; flowers sessile or subsessile; leaf blades pinnately veined **291. *Sapium***

– Seed aril whitish; flowers pedicellate; leaf blades triplinerved **268. *Triadica***

264. *Maprounea* Aubl.

Maprounea Aubl., Hist. Pl. Guiane: 895, t. 342 (1775); Pax & K. Hoffm., Pflanzenr. 147, V: 175, fig. 32, 33 (1912); Léonard, Fl. Congo 8(1): 142, fig. 9 (1962); Radcl.-Sm., Fl. Trop. E. Africa, Euphorb. 1: 395, fig. 75 (1987); Webster & Huft, Ann. Missouri Bot. Gard. 75: 1131 (1988); Esser, Novon 9: 32, fig. 1 (1999).

Monoecious (dioecious) trees or shrubs; latex whitish; indumentum 0. Leaves usually with prominent subbasal laminar glands abaxially; petiole eglandular; stipules entire, eglandular, persistent. Inflorescences terminal, usually bisexual, with 1–5 proximal pistillate flowers separated from an ament-like staminate subflorescence; bracts biglandular at base, the staminate subtending 1–3(−5) flowers. Staminate flowers sessile to subsessile; sepals 2–3, connate into a cupular calyx; stamens (1)2–3, filaments connate into a column exserted beyond the calyx; anthers extrorse, dehiscing longitudinally. Pistillate flowers pedicellate, spreading or recurving; sepals 3, discrete, persistent in fruit; ovary 3-locular, smooth; ovules anatropous, inner and outer integuments thin (5 or 6 cell layers); stylodia connate into a common style [except in *M. amazonica*], style branches unlobed. Fruits capsular; columella slender, not persistent. Seeds ellipsoid, with a cap-like caruncle covering the upper half, testa smooth or foveolate.

Five spp., three in South America and two in Africa.

265. *Actinostemon* Mart. ex Klotzsch

Actinostemon Mart. ex Klotzsch, Arch. Naturg. 7: 184 (1841); Pax & K. Hoffm., Pflanzenr. 147, V: 57, figs. 10–14 (1912); Jablonski, Phytologia 18: 213–240 (1969); Burger & Huft, Fieldiana Bot. II, 36: 57 (1995); Berry & Esser, Fl. Venez. Guayana 5: 87, fig. 84 (1999).

Monoecious trees or shrubs; latex scanty; indumentum simple, often scanty. Leaves alternate or pseudo-verticillate, with dispersed glands abaxially; stipules deciduous. Inflorescences terminal and sometimes axillary, racemoid, and in bud ament-like, enclosed by imbricate bud scales, axis glabrous or hirtellous; pistillate flowers proximal, 1–3 per bract; staminate flowers distal, 2 or 3 per bract; bracts biglandular (eglandular) at base, lamina minute or obsolete. Staminate flowers pedicellate; calyx rudimentary or 0; stamens 4–15 or more, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-lobed, 3-colpate, exine tectate-perforate; pistillode 0. Pistillate flowers pedicellate, pedicel elongating in fruit; sepals minute or 0; ovary 3-locular, sometimes appendaged; stylodia unlobed, connate basally. Fruits capsular; columella persistent. Seeds spheroidal, subapically carunculate, testa smooth.

About 15 spp. ranging from the Caribbean to South American. The genus was combined by Webster (1994) with the superficially similar *Gymnanthes* but this is not supported by the molecular evidence.

266. ***Senefelderopsis*** Steyerm.

Senefelderopsis Steyerm., Bot. Mus. Leafl. Harvard Univ. 15: 45, t. 16 (1951); Jablonski, Mem. N. Y. Bot. Gard. 12: 174 (1965); Gillespie, Brittonia 45: 92 (1993); Murillo & Franco, Euforb. Reg. Araracuara 153, fig. 46 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 376 (2001).
Dendrothrix Esser (1993).

Monoecious trees or shrubs; latex white; indumentum simple, on inflorescence axes sometimes dendritic. Leaves with paired adaxial or abaxial glands; stipules caducous. Inflorescences bisexual, terminal, compound, axes thyrsoid; floral bracts eglandular, subtending proximal solitary pistillate flowers and distal cymules of 6–20 staminate flowers on each axis. Staminate flowers subsessile to pedicellate; sepals 2 or 3, basally ± connate; stamens 2–5, filaments distinct or connate, as long as anthers. Pistillate flowers short-pedicellate; sepals 3(−6), basally connate; ovary 3-locular, pubescent; ovules anatropous, inner integuments moderately thick, outer integuments thick, non-vascularized; stylodia undivided, basally connate into a short common style. Fruits capsular, sometimes partly fleshy; columella persistent, distally alate; seeds carunculate or ecarunculate.

Five spp., centered on the Guayana highlands and extending to its southern and eastern foreland. Except for the number of staminate sepals and the dendritic indumentum, *Dendrothrix* does not appear to be strongly different from *Senefelderopsis* s. str., and there seems to be no reason why it cannot be accommodated as a section of that genus.

267. ***Senefeldera*** Mart.

Senefeldera Mart., Flora 24 (Beibl. 2): 29 (1841); Jablonski, Mem. N. Y. Bot. Gard. 12: 171 (1965); Webster, Ann. Missouri Bot. Gard. 75: 1127 (1989); Murillo & Franco, Euforb. Reg. Araracuara 149, fig. 45 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 389 (2001).
Rhodothyrsus Esser (1999).
Pseudosenefeldera Esser (2001).

Monoecious trees; latex white; indumentum simple, dibrachiate or 0. Leaves sometimes pseudoverticillate, abaxially with scattered (sometimes marginal) glands; stipules caducous. Inflorescences axillary, pedunculate, usually bisexual, compound thyrsoid, floral bracts with a pair of elliptic glands; pistillate flowers solitary at 1–4 proximal nodes, glomerules of 1–3 staminate flowers at distal nodes. Staminate flowers pedicellate to sessile or subsessile; calyx completely connate without distinct lobes, sometimes zygomorphic; stamens (2) 4–17, filaments distinct; anthers dehiscing longitudinally. Pistillate flowers pedicellate to subsessile; sepals 3, distinct or basally connate; ovary 3-locular, smooth, glabrous; ovules anatropous, inner integuments moderately thick (8–10 cell layers), outer integuments thin (3–5 cell layers), non-vascularized; stylodia proximally usually connate into a short style with 3 distal stigmatic branches. Fruits spheroidal, capsular; columella triquetrous, distinctly alate, persistent. Seeds subspheroidal, ecarunculate, testa smooth or sculptured.

Six spp., tropical South America from Panama south to Peru. The two segregate genera proposed by Esser have some distinctive characters, but they share a very similar Gestalt and it does not seem necessary to dismember a genus as small as *Senefeldera*. With some modification, the segregate taxa could be fitted into the sectional arrangement of Pax and Hoffmann (1912).

268. ***Triadica*** Lour.

Triadica Lour., Fl. Cochin. 2: 598, 610 (1790); Small, Man. Southeastern Flora 789 (1933); Hurus., J. Fac. Sci. Univ. Tokyo, III. 6: 315 (1954); Kruijt, Bibl. Bot. 146: 7 (1996); Esser, Harvard Papers Bot. 7: 17–21 (2002).

Monoecious trees; latex white; indumentum 0. Leaves entire with submarginal glands and adaxial paired glands at junction with petiole; stipules entire, persistent. Inflorescences terminal, bisexual, spiciform; bracts biglandular at base, subtending solitary pistillate flowers and distal cymules of 3–8 staminate flowers. Staminate flowers pedicellate; sepals 3, basally connate; stamens 2 or 3, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-nucleate. Pistillate flowers pedicellate; sepals 3, basally connate, deciduous in fruit; ovary 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thick; stylodia connate at base, unlobed. Fruits capsular, dehiscing into 6 valves; columella persistent, alate. Seeds ecarunculate, adherent to columella, sarcotesta whitish. $2n = 44$.

Three spp., India, China, and Malesia. The genus has usually been included in *Sapium*, but differs in its pedicellate flowers and the whitish (not reddish) sarcotesta.

269. *Gymnanthes* Sw.

Gymnanthes Sw., Prodr. Veg. Ind. Occ.: 95 (1788); Grisebach, Fl. Brit. W. Ind.: 50 (1859); Bentham, Gen. Pl. 3: 337 (1880); Sargent, Silva N. Amer. 7: t. 309 (1995); Pax & K. Hoffm., Pflanzenr. 147, V: 81 (1912); Fawc. & Rend., Fl. Jam. 4: 329, fig. 111 (1920); Webster, J. Arnold Arb. 48: 387 (1967), Taxon 32: 304 (1983), Ann. Missouri Bot. Gard. 75: 1129 (1989), 81: 122 (1994); Howard, Fl. Lesser Ant. 5: 52, figs. 16, 18 (1989); Esser in Radcl.-Sm., Gen. Euphorb.: 382 (2001); Burger & Huft, Fieldiana n.s. 36: 123 (1995); Berry & Esser, Fl. Ven. Guayana 5: 149 (1999); Webster, Fl. Nicaragua 1: 884 (2001).
Shirakia Hurus. (1954), nom. illeg.
Neoshirakia Esser (1998).
Shirakiopsis Esser (1999).

Monoecious or dioecious trees or shrubs, branches sometimes spinose; latex whitish, sometimes not evident; indumentum simple or 0. Leaves entire or serrate, egandular adaxially, abaxially with marginal (scattered) glands; stipules entire, sometimes glandular. Inflorescences usually bisexual, racemoid, terminal and axillary, solitary, sometimes with minor proximal branches; bracts sometime pedunculate, usually biglandular at base; pistillate flowers solitary at proximal 1–3 nodes, staminate flowers in (1)3–5-flowered cymules. Staminate flowers pedicellate; sepals 1–2, often reduced or obsolete; stamens (2) 3–6, filaments often longer than anthers; anthers basifixed, extrorse, longitudinally dehiscent; pollen grains 3-nucleate. Pistillate flowers pedicellate, often expanding in fruit; sepals 3, distinct or connate; ovary 3-locular, smooth or appendiculate; ovules anatropous, inner integuments moderately thick (8–10 cell layers), outer integuments thin (4–6 cell layers); stylodia distinct or basally connate, simple. Fruits capsular (indehiscent); columella triquetrous, alate, persistent. Seeds elliptic, smooth, caruncle small or 0.

About 45 spp., most in the New World from the southern USA through the Antilles to South America, few spp. in Africa, S and SE Asia, Malesia, and extending to Micronesia, Melanesia and Japan.

Apart from the exclusion of *Actinostemon*, Esser (2001) has modified the circumscription of *Gymnanthes* by including *Sarothrostachys*, *Duvigneaudia*, and *Adenogyne*. In the treatment presented here, *Gymnanthes* is only enlarged by the inclusion of his segregate genera *Neoshirakia* and *Shirakiopsis* (see Esser, Blumea 44: 165–172. 1999). The boundaries of *Gymnanthes* have not yet been established satisfactorily, and it remains to be seen whether they will be decreased to exclude *Neoshirakia*.

270. *Dalembertia* Baill.

Dalembertia Baill., Étude Gén. Euphorb.: 545 (1858); Müll. Arg. in DC., Prodr. 15(2): 1225 (1866); Standley, Contr. U. S. Nat. Herb. 23: 646 (1923); Standley & Steyerm., Fieldiana Bot. 24 (6): 86 (1949); Webster, Ann. Missouri Bot. Gard. 81: 122 (1994); Esser in Radcl.-Sm., Gen. Euphorb.: 391 (2001).

Monoecious herbs or subshrubs, often with tuberous roots; latex white; indumentum simple, multiseriate. Leaves usually palmately 3–11-lobed, entire or distantly serrate; petioles eglandular; stipules persistent. Inflorescences terminal, bisexual, with pedicellate proximal pistillate flowers and a spiciform ament of staminate flowers; bracts biglandular, subtending solitary pistillate flowers and cymules of 1–3 staminate flowers. Staminate flowers pedicellate; calyx completely connate without distinct lobes, zygomorphic; stamen solitary, filament long-exserted; anthers longitudinally dehiscent; pistillode 0. Pistillate flowers with elongated ± recurved pedicels; sepals 3, distinct, entire, deciduous in fruit; ovary 3-locular, smooth; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia connate into a common style with 3 apical unlobed, recurved tips. Fruits capsular; columella 3-angled, persistent. Seeds smooth, ecarunculate.

Four or five spp. native to Mexico and Guatemala, where they grow in deciduous woodland. Their inflorescences, with basal recurved long-pedicellate pistillate flowers subtending an ament of staminate flowers, are strikingly similar to those of *Maprounea.* However, no relationship between the two genera is discernible in the molecular analysis of Wurdack et al. (2005).

271. ***Homalanthus*** A. Juss.

Homalanthus A. Juss., Tent. Euphorb.: 50 (1824) (*Omalanthus*, orth. rej.); Airy Shaw, Kew Bull. 21: 409 (1968), Kew Bull. Add. Ser. 8: 115 (1980); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 25, t. 4 (1987); Forster, Telopea 6: 169 (1994); Florence, Fl. Polynes. Franc. 1: 115, fig. 20 (1997).

Monoecious or dioecious trees or shrubs; exudate watery, innocuous; indumentum simple or 0. Leaves often peltate, without laminar glands; petioles with paired glands at junction with lamina; stipules caducous. Inflorescences terminal and sometimes axillary as well, bisexual or unisexual, spiciform with pistillate flowers at base or at separate axils; bracts uniflorous, biglandular at base. Staminate flowers pedicellate; calyx laterally compressed, sepals 2, cordate, rarely 1, subimbricate; stamens (5–)10–50, filaments distinct; anthers extrorse, dehiscing longitudinally; pollen grains 2-nucleate; pistillode 0. Pistillate flowers long-pedicellate; sepals 2 or 3, deciduous in fruit; ovary 2(3)-locular; ovules anatropous, the inner integuments thin, the outer thick and nonvascularized; stylodia distinct or basally connate, unlobed, often glandular at apex. Fruits capsular or indehiscent; columella persistent. Seeds with hypertrophied arilloid caruncle. $2n = 36, 44$.

About 23 spp., distributed from SE Asia to Australia, New Caledonia, New Zealand, and Polynesia. The resemblance of this genus with the Stomatocalyceae has been noted since the time of Müller (1866), who included *Homalanthus* in *Pimelodendron* (as *Carumbium* sect. *Pimelodendron*), but in the light of the molecular findings (Wurdack et al. 2005), this similarity appears homoplasious.

272. ***Microstachys*** A. Juss. Fig. 43

Microstachys A. Juss., Euphorb. Tent.: 48 (1824); Griseb., Fl. Brit. W. Ind. 1: 49 (1859); Esser, Blumea 44: 173–179 (1999), Gen. Euphorb.: 365 (2001).
Cnemidostachys Mart. & Zucc. (1824).
Sebastiania sect. *Microstachys* (A. Juss.) Müll. Arg. (1866).

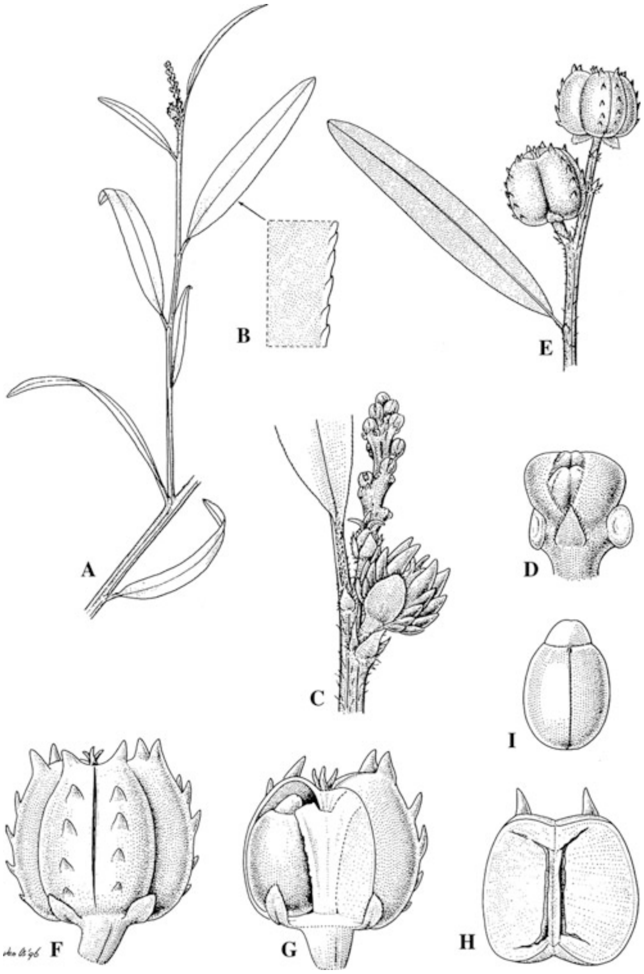

Fig. 43. Euphorbiaceae-Euphorbioideae. *Microstachys chamaelea.* **A** Flowering branchlet. **B** Detail of leaf margin with densely packed glandular teeth. **C** Stipulate node with young fruit and inflorescence. **D** Subsessile staminate flower with large bract glands and distinct sepals. **E** Infructescence. **F** Fruit with excrescences. **G** Partly opened fruit with alate columella. **H** Mericarp with the large septa. **I** Carunculate seed. (Esser 1999; drawn by J. van Os)

Monoecious herbs or subshrubs; latex not evident; indumentum simple or dendritic. Leaves entire or serrulate; stipules scarious, usually obscure. Inflorescences spiciform, mostly opposite the leaves, sometimes terminal or axillary; pistillate flowers proximal, solitary at 1 (2) basal nodes; staminate flowers distichous (spiral), 1–3 per node; staminate bracts biglandular (eglandular) at base. Staminate flowers sessile or subsessile; sepals 3, distinct or basally connate; stamens 3, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers sessile or subsessile; sepals 3, distinct, eglandular or basally minutely glandular; ovary 3-locular, usually with 6 vertical rows of appendages; ovules anatropous, inner and outer integuments thin; stylodia distinct, unlobed. Fruits capsular; columella persistent, alate. Seeds elliptic to cylindrical, often truncate, caruncle discoid, testa smooth.

Approximately 15 spp., mainly neotropical, 3–4 disjunct in Africa and 1 in southwest Asia and Australia. *Microstachys* has previously been classified as part of *Sebastiania* (Webster 1994), but Esser (1994) insisted on generic status for *Microstachys*. In the molecular analysis it is resolved as sister to *Ditrysinia*.

273. ***Ditrysinia*** Raf.

Ditrysinia Raf., Neogenyton: 2 (1825); Esser in Radcl.-Sm., Gen. Euph.: 385 (2001).
Gymnanthes sect. *Ditrysina* Müll. Arg. (1865).
Sebastiana sect. *Stillingiopsis* (Müll. Arg.) G.L. Webster (1967).

Monoecious shrubs; indumentum simple or 0. Leaves entire; stipules undivided. Inflorescences terminal, solitary; bracts with paired elongate kidney-shaped glands, 2–6 proximal ones with 1 female flower, numerous distal ones with 1 male flower; prophylls 0. Staminate flowers shortly pedicellate; calyx 3-lobed, lobes partly connate; stamens 3, filaments short, distinct, anthers basifixed, extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers shortly to moderately pedicellate; calyx 3-lobed, lobes nearly distinct; ovary glabrous, 3-locular; stylodia connate into a short common style with 3 undivided branches. Fruits spheroidal, capsular, columella triquetrous, alate, persistent. Seeds elliptic, smooth, with small caruncle.

A single sp., *D. fruticosa* (Bartram) Govaerts & Frodin (= *D. ligustrina* (Michx.) Raf.), eastern USA. Formerly subsumed under *Gymnanthes* and *Sebastiana*, this genus is resolved as sister to *Microstachys* (Wurdack et al. 2005).

274. ***Sclerocroton*** Hochst.

Sclerocroton Hochst. in C. Krauss, Flora 28: 85 (1845); Kruijt & Roebers, Bibl. Bot. 146: 16–27 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 378 (2001).
Excoecaria sect. *Sclerocroton* Müll. Arg. (1866).
Sapium subg. *Sclerocroton* Pax in Pflanzenr. IV, 147, V: 213–249 (1912).

Monoecious shrubs or trees; latex not evident; indumentum 0. Leaves abaxially with basal or submarginal glands; stipules deciduous. Inflorescences mostly terminal, unbranched, bisexual, 1 or 2 proximal nodes with pistillate flowers, distally with cymules of 5–9 staminate flowers; bracts rounded to acuminate, biglandular at base. Staminate flowers pedicellate; sepals 3, basally connate; stamens 2–3, filaments distinct; anthers dehiscing longitudinally; pollen grains 3-colporate, exine tectate-reticulate; pistillode 0. Pistillate flowers pedicellate; sepals 3, distinct, often with basal glands; ovary 3(4)-locular, each locule with 2 appendages; stylodia basally connate into a short common style with 3 short undivided style branches. Fruits capsular, sometimes with fleshy exocarp, endocarp woody; columella persistent, alate. Seeds ellipsoid to spheroidal, mostly ecarunculate or with small apical caruncle.

Six spp., Africa and Madagascar.

275. ***Mabea*** Aubl. Fig. 44

Mabea Aubl., Hist. Pl. Guiane 2: 867, t. 334 (1775); Müll. Arg. in DC., Prodr. 15(2): 1148 (1866), Fl. Bras. 11(2): 515, t. 73, 74 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 26, figs. 4–6 (1912); Jablonski, Mem. N. Y. Bot. Gard. 17: 164 (1967); Huft, Phytologia 62: 339 (1987), Ann. Missouri Bot. Gard. 75: 1125 (1989); Esser, Syst. Hippom.: 118–221, figs. 7–10 (1994).

Monoecious trees or shrubs; latex whitish; indumentum mostly dendritic. Leaves eglandular [except marginally], entire or denticulate; petiole eglandular; stipules subpersistent or deciduous. Inflorescences terminal or axillary, mostly bisexual racemoid thyrses, sometimes distinctly branched; bracts mostly biglandular, subtending pedunculate glomerules of mostly 3 staminate flowers or solitary pistillate flowers. Staminate flowers long-pedicellate; sepals 5(6), partly connate; stamens (3–)10–80, inserted on the ± convex receptacle; filaments 0 to as long as the extrorsely dehiscent anthers; pollen grains 2-nucleate; pistillode 0. Pistillate flowers distinctly pedicellate; sepals 5(6); ovary 3-locular, finely and densely tomentose; inner integuments moderately thick, outer integuments thick, nonvascularized; stylodia connate into a short to long common style, the distal tips simple, recurved. Fruits capsular; columella alate, persistent. Seeds carunculate.

About 40 spp., restricted to the (sub)humid neotropical lowlands from Mexico to São Paulo, Brazil. Esser (1994) recognized 2 sections: sect.

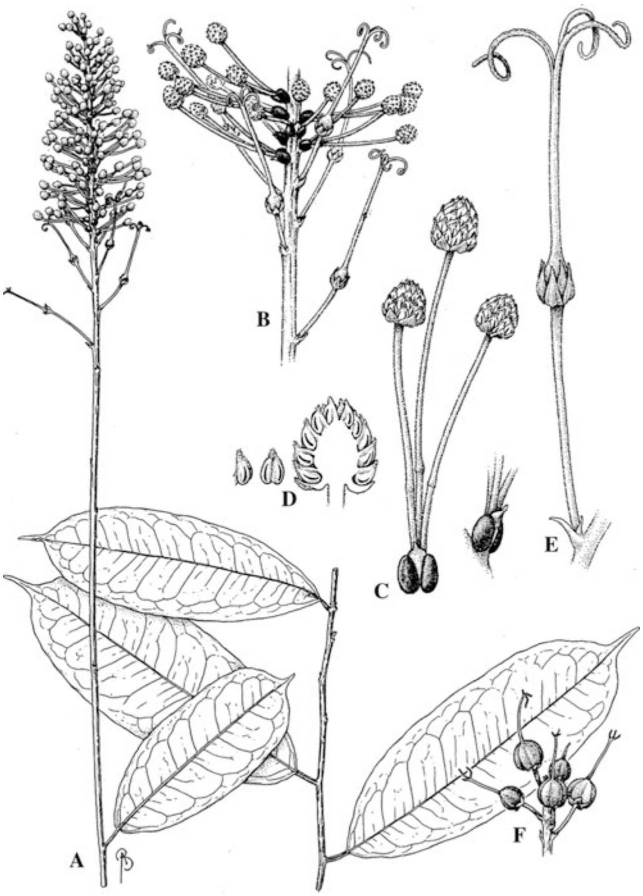

Fig. 44. Euphorbiaceae-Euphorbioideae. *Mabea speciosa*. **A** Inflorescence and part of stem with leaves (right); note that inflorescence is pendent on plant. **B** Proximal portion of inflorescence with pistillate flowers at base and staminate ones above; note glands on bracts subtending staminate flowers. **C** Cluster of staminate flowers subtended by biglandular bract. **D** Medial section of staminate flowers (right) and two views of anthers (left). **E** Pistillate flower. **F** Immature capsules. (Reproduced with kind permission of the artist Bobbi Angell)

Spiculigerae Pax & K. Hoffm., with 2 spp. (one of them the widespread Brazilian *M. fistulifera* Mart.); and sect. *Mabea*, which includes the other sections of Pax and Hoffmann (1912).

276. *Sebastiania* Sprengel

Sebastiania Spreng., Neue Entd. Pflanzenk. 2: 118, t. 3 (1820); Müll. Arg. in DC., Prodr. 15(2): 1164 (1866), Fl. Bras. 11(2): 544 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 88 (1914); figs. 19–22, 26–28 (1912), Natürl. Pflanzenfam. ed. 2, 19c: 192, fig. 103 (1931); L.B. Sm. et al., Fl. Illustr. Catar. EUFO 295, fig. 40 (1988); Webster, Ann. Missosuri Bot. Gard. 81: 121 (1994); Burger & Huft, Fieldiana n.s. 36: 155 (1995); Esser, Syst. Hippom.: 55 (1994), in Radcl.-Sm., Gen. Euphorb.: 363 (2001).
? *Adenogyne* Klotzsch (1841).
Dendrocousinsia Millsp. (1913).

Monoecious (dioecious) trees, shrubs, or herbs; latex whitish, often not evident; indumentum simple or 0. Leaves eglandular except sometimes for marginal glands; margins entire to serrulate or dentate; stipules minute and often dissected. Inflorescences terminal or leaf-opposed, solitary, bisexual; bracts biglandular at base, glands usually flat and elongated or sometimes divided or rugulose; pistillate flowers solitary at proximal nodes, often separated from the distal staminal cymules of mostly 1–3 flowers. Staminate flowers sessile or subsessile; sepals 3, slightly connate at base, sometimes unequal; stamens 3, distinct, filaments longer than anthers; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 3-nucleate. Pistillate flowers sessile to short-pedicellate; sepals 3, discrete, denticulate, ± persistent in fruit; ovary 3-locular, sometimes appendiculate; ovules anatropous, inner and outer integuments thin; stylodia distinct or nearly so, undivided. Fruits capsular; columella persistent, alate, often with adherent caruncles. Seed smooth, carunculate, caruncles ± stipitate and deciduous.

About 25 spp., distributed from Mexico south into tropical South America. The circumscription of this genus has been one of the most contentious issues in the taxonomic history of tribe Hippomaneae. Pax and Hoffmann (1912) followed Müller (1866) in adopting a very broad and patently unnatural circumscription of *Sebastiania*. Esser (1994) has provided a radical solution to the problems of circumscribing *Sebastiania* by transferring sections *Sarothrostachys* and *Adenogyne* from *Sebastiania* to *Gymnanthes*. However, the species of *Adenogyne* assigned to *Sebastiania* by Müller (1866) have terminal inflorescences and pedicellate pistillate flowers, and the species of *Sarothrostachys* have axillary inflorescences and sessile or subsessile pistillate flowers. Both species groups have character combinations that conflict with the characters of *Gymnanthes* and *Sebastiania*, and it is obvious that the current generic boundaries are unsatisfactory. *Sarothrostachys* has axillary branched inflorescences, and its transfer to *Anomostachys* should be considered. *Dendrocousinsia* is treated by Esser as a highly distinct genus, but in fact the diagnostic character—adaxial ciliae or glands in the staminate and pistillate calyx—was described by Müller for a considerable number of species of *Sebastiania*, including the type (*S. brasiliensis* Spreng.). The molecular data of Wurdack et al. (2005) fail to indicate the position of this genus within the Hippomaneae, because the signals of the two species included in the analysis representing the core of *Sebastiana* (S. *klotzschiana* Müll. Arg. and S. *pavoniana* Müll. Arg.) point to different subclades of the Hippomaneae.

277. *Anomostachys* (Baill) Hurus.

Anomostachys (Baill.) Hurus., J. Fac. Sci. Univ. Tokyo, III. Bot. 6: 311 (1954); Kruijt, Biblioth. Bot. 146: 8–12, fig. 2 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 385 (2001).
? *Sarothrostachys* Klotzsch (1841).
Duvigneauia Léonard (1959); Kruijt & Roebers, Biblioth. Bot. 146: 12–15 (1996), rev.

Monoecious trees and shrubs; latex whitish; indumentum 0. Leaves below with marginal glands, otherwise eglandular; stipules caducous. Inflorescences axillary, solitary, ramified, branches racemoid; bracts eglandular, the proximal 2–5 subtending single pistillate flowers and the distal ones subtending cymules of 2–8 staminate flowers. Staminate flowers sessile; sepals 3, basally connate; stamens 3; anthers dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 3, distinct, often bifid; ovary 2- or 3-locular, appendiculate when young but smooth at maturation; ovules anatropous, inner integuments thick [10–20 cell layers], outer integuments thin [3 or 4 cell layers], non-vascularized; a common style short but evident, with 3 undivided distal branches. Fruits indehiscent. Seeds carunculate or not.

Three (or more?) spp., tropical Africa, Madagascar.

278. *Balakata* Esser

Balakata Esser, Blumea 44: 154 (1999), in Radcl.-Sm., Gen. Euphorb.: 378 (2001).
Sapium sect. *Pleurostachya* Pax & K. Hoffm. (1912).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves abaxially with marginal or submarginal glands; stipules entire, eglandular. Inflorescences terminal and axillary, compound, bisexual; bracts biglandular at base, at proximal nodes subtending solitary pistillate flowers, at distal nodes cymules with 5–9 staminate flowers. Staminate flowers pedicellate; sepals 2, connate; stamens 2, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers pedicellate; sepals 2, connate; ovary 2-locular; stylodia 2, basally connate, unlobed. Fruits drupaceous. Seeds oblate-spheroidal, ecarunculate, with thin sarcotesta. $2n = 44$.

Two spp., India to China and New Guinea. *Balakata* appears to be closely related to *Anomostachys*, and the two genera should perhaps be united.

279. *Hura* L. Fig. 45

Hura L., Sp. Pl.: 1008 (1753); Müll. Arg. in DC., Prodr. 15 (2): 1228 (1866), Fl. Brasil. 11(2): 632, t. 86 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 271 (1912); Standl. & Steyermark, Fieldiana Bot. 24(6): 124 (1949); Burch, Ann. Missouri Bot. Gard. 54: 330, fig. 24 (1968); Burger & Huft, Fieldiana n.s. 36: 126, fig. 32 (1995); Esser in Radcl.-Sm., Gen. Euphorb.: 397 (2001).

Monoecious trees, trunk spiny; latex white; indumentum simple. Leaves deciduous, dentate, with paired sessile glands at the junction with petiole; stipules caducous. Inflorescences unisexual, the staminate terminal, pedunculate, compound-spicate, bracts numerous, united into a membranaceous, tunica-like sheath; pistillate flowers solitary, at base of staminate spike or axillary. Staminate flowers pedicellate; sepals connate into a crenulate cup; stamens 10–80, in 2 or more whorls of 12–15 sessile anthers on a stout column formed by the stamen filaments; pistillode 0. Pistillate flowers pedicellate; sepals 5, completely connate into a truncate calyx; ovary 5–20-locular; stylodia connate into a long columnar style with a distal 5–20-lobed discoid stigma. Fruits capsular, dehiscing explosively; columella not persistent. Seeds laterally compressed, suborbicular, ecarunculate. $2n = 44$.

Two neotropical spp., common in lowland deciduous forests. *Hura polyandra* Baill. of Mexico and Central America is replaced in Nicaragua by *H. crepitans* L., which is widely distributed from Nicaragua to the West Indies, Peru, and Brazil. *Hura crepitans* is cultivated throughout most of the Neotropics, and has been introduced into paleotropical regions with monsoonal climates. The unusual floral structure, at first glance very different from that in *Algernonia* and *Ophthalmoblapton*, evidently reflects adaptation for bat pollination (Steiner 1982).

280. *Algernonia* Baill.

Algernonia Baill., Ann. Sci. Nat. IV, 9: 198 (1858), Étude Gén. Euphorb.: 546 (1858); Müll. Arg. in DC., Prodr. 15 (2): 1230 (1866); Fl. Bras. 11(2): 533, t. 87 (1874); Benth., Gen. Pl. 3: 339 (1880); Pax & Hoffm., Pflanzenr. 147, V:

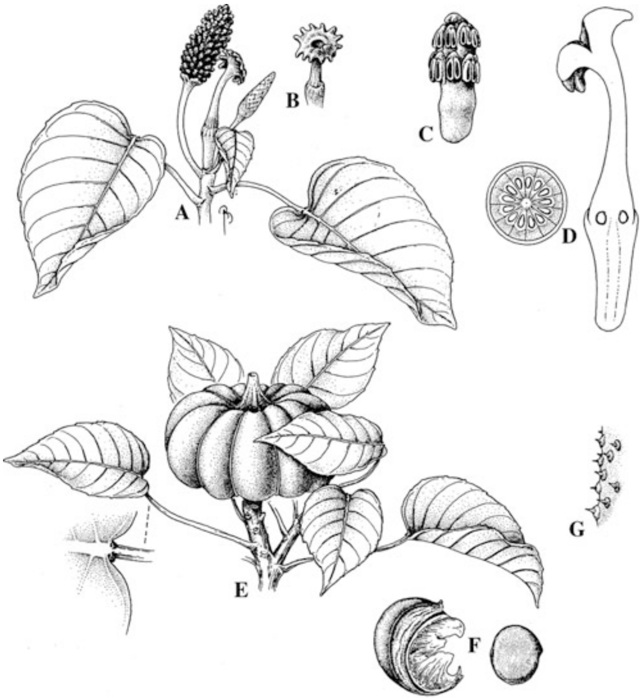

Fig. 45. Euphorbiaceae-Euphorbioideae. *Hura crepitans*. **A** Stem with leaves and staminate inflorescences (left) and pistillate flower (right). **B** Pistillate flower. **C** Androecium with staminal column bearing two rows of anthers. **D** Ovary in transverse section (left) and medial section of pistillate flower (right). **E** Stem with capsule. **F** Segment of capsule and seed. **G** Prickles on trunk. (Reproduced with kind permission of the artist Bobbi Angell)

276, fig. 56 (1912); Emmerich, Arq. Mus. Nac. Rio Janeiro 56: 91–110, t. 1–11 (1981).

Tetraplandra Baill. (1858); Emmerich, l.c.

Monoecious trees or shrubs; latex white; indumentum 0. Leaves entire or obscurely crenulate and occasionally with small abaxial glands, biglandular at base; stipules caducous. Inflorescences terminal, the staminate ones occasionally axillary, bisexual, spiciform; bracts adnate to rachis, eglandular; pistillate flowers solitary at distal nodes, staminate cymules with mostly 3 flowers. Staminate flowers subsessile; sepals 3–5, distinct or connate; stamens 1–3, filaments mostly connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals distinct or connate, persistent in fruit; ovary 3-locular, exappendiculate; stylodia connate c. 1/3 to 2/3 of length into a columnar common style, tips terete, papillose. Fruits capsular; trigonous base of columella persistent. Seeds subspheroidal, smooth, ecarunculate.

About 10 spp., ranging from E Brazil to Peru. Baillon (1858) described both *Algernonia* and *Tetraplandra* simultaneously, and Bentham (1880) selected the former on joining the two genera, in which he is followed here. Pax and Hoffmann (1912) distinguished the genera by the more gamophyllous staminate calyx in *Algernonia*, but in both floral and vegetative structures the two taxa appear similar overall. Emmerich (1981) provided detailed descriptions and excellent illustrations of both genera, and the entire reliance on vegetative characters in her generic key is revealing.

281. ***Ophthalmoblapton*** Allem.

Ophthalmoblapton Allem., Pl. Novas Brasil: 4 (1849), Ann. Sci. Nat. Bot. III, 13: 119 (1849); Müll. Arg. in DC., Prodr. 15(2): 1155 (1866), Fl. Bras. 11(2): 531 (1874); Benth., Gen. Pl. 3: 333 (1880); Pax & K. Hoffm., Pflanzenr. 147, V: 278, fig. 58 (1912); Emmerich, Bol. Mus. Nac. Rio de Janeiro, Bot. 62: 1, t. 1 (1981); L.B. Sm. et al., Fl. Illustr. Catar. EUFO 325, t. 41 figs. h–m (1988); Howard, Fl. Lesser Ant. 5: 57 (1989).

Monoecious trees; latex white, highly toxic; indumentum 0. Leaves entire or dentate, adaxially with basal glands at junction with petiole; stipules caducous. Inflorescences axillary, bisexual or staminate, spiciform; pistillate flowers basal and solitary, ± separated from crowded staminate flowers; bracts eglandular, staminate bracts subtending 3–12 flowers. Staminate flowers sessile, sometimes laterally confluent; calyx closed in bud, splitting into 2 or 3 lobes or segments; stamen solitary, exserted from calyx; anther dehiscing longitudinally. Pistillate flowers sessile or subsessile, becoming somewhat pedunculate in fruit; sepals 5 or 6, discrete, imbricate, persistent in fruit; ovary 3-locular; stylodia basally connate into a columnar style with distal stigmatic style branches. Fruits capsular; endocarp woody; columella deciduous. Seeds ovoid, ecarunculate, testa smooth.

Four spp. of the mata atlântica region in eastern Brazil (Bahia to Santa Catarina).

282. ***Pachystroma*** Müll. Arg. Fig. 46

Pachystroma Müll. Arg., Linnaea 34: 177 (1865), in DC., Prodr. 15(2): 893 (1866), Fl. Bras. 11(2): 387, t. 54 (1874); Pax, Pflanzenr. 147, II: 99 (1910); Senna, Bradea 3 (48): 421 (1983).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves eglandular, usually spinose-

Fig. 46. Euphorbiaceae-Euphorbioideae. *Pachystroma longifolium*. **A** Flowering branchlet. **B** Staminate flower. **C** Same, longitudinally sectioned. **D** Transversal section of androecium. **E** Pistillate flower. **F** Ovary medially sectioned. **G** Fruit locule. **H** Columella after seed dehiscence. (Pax 1910)

dentate; petioles eglandular; stipules caducous. Inflorescences terminal, spiciform, bisexual; bracts biglandular, basally up to 2 with 1 pistillate flower, apically numerous ones with cymules of 1–3 staminate flowers. Staminate flowers sessile; calyx cupular, 2-lobed; stamens 3, filaments connate into a column; anthers basifixed, extrorse, dehiscing vertically, exserted from calyx. Pistillate flowers subsessile; sepals 3, distinct, imbricate, persistent in fruit; ovary 3-locular; stylodia connate into a columnar style, style branchlets unlobed, compressed. Fruits capsular, valves woody and thick-walled; trigonous base of columella persistent. Seeds ovoid, somewhat compressed, ± cordate at base, ecarunculate.

A single sp., *P. longifolium* (Nees) I.M. Johnston of SE Brazil, Bolivia and Peru. Müller (1866) misplaced the genus among the Acalyphoideae, and Pax (1910) placed it in the Adrianeae, although noting its resemblance in habit to Hippomaneae. Pax and Hoffmann (1931) created a tribe for it, but still placed it between the Acalypheae and Dalechampieae. In the molecular analysis of Wurdack et al. (2005), *Pachystroma* is embedded within the Hureae, which are part of one of the hippomanoid subclades, as foreseen by Webster (1994a).

283. *Hippomane* L.

Hippomane L., Sp. Pl.: 1191 (1753); Müll. Arg. in DC., Prodr. 15(2): 1199 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 261, fig. 51 (1912); Fawc. & Rend., Fl. Jam. 4: 327, fig. 110 (1920); Webster, J. Arnold Arbor. 48: 393 (1967); Webster, Ann. Missouri Bot. Gard. 81: 124 (1994).
Mancanilla Miller (1754).

Monoecious trees or shrubs; latex white, toxic; indumentum 0. Leaves ± cordate at base, entire or obscurely crenulate to spinose-dentate, with a single adaxial gland at junction with petiole; stipules lanceolate, caducous. Inflorescences terminal, bisexual, spiciform, bisexual; bracts biglandular at base, subtending 1 or 2 proximal solitary pistillate flowers and distal cymules of 8–15 staminate flowers. Staminate flowers subsessile; sepals 2 or 3, connate; stamens 2, filaments connate into a column; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals 3, distinct, persistent in fruit; ovary 5–10-locular; stylodia basally connate into a short style, branches unlobed, densely papillate adaxially. Fruits drupaceous with bony endocarp. Seeds smooth, ecarunculate. $2n = 22$.

Three Caribbean spp., two of which are endemic to Hispaniola, while *H. mancinella* L., the noted highly toxic "manchineel", is widely distributed along littoral zones from Florida to northern South America and the Galapagos. In the molecular analysis of Wurdack et al. (2005), Hippomane is resolved in a clade with *Pleradenophora*, *Bonania*, and *Grimmeodendron*.

284. *Pleradenophora* Esser

Pleradenophora Esser in Radcl.-Sm., Gen. Euph.: 377 (2001).

Monoecious shrubs or trees; indumentum 0; latex white. Leaves serrate, below sometimes with marginal glands, often with a pair of disk-shaped petiolar glands on the junction of the petiole with the blade; stipules small. Inflorescences terminal or laterally displaced, solitary; floral bracts with several pairs of disk- or cup-shaped glands, 1–3 basal ones with 1 pistillate flower, numerous apical ones with 5–10 staminate flowers. Staminate flowers shortly pedicellate; calyx 3-lobed, partly connate; stamens 2–3(5), filaments distinct, anthers basifixed, extrorse, longitudinally dehiscent; pistillode 0. Pistillate flowers (sub)sessile; calyx 3-lobed, lobes distinct; ovary smooth, 3-locular; stylodia undivided, basally connate or not into a short common style. Fruit subglobose, smooth, dehiscing septicidally into 3 mericarps, columella 3-quetrous, alate, persistent. Seeds ovoid-globose, smooth, often maculate, ecarunculate.

Three spp., Mexico, Guatemala, Belize; formerly treated as part of *Sebastiana* (*S. longicuspis* Standl.).

285. ***Bonania*** A. Rich.

Bonania A. Rich., Hist. Fis. Cuba 2, 11: 201, t. 68 (1853); Benth., Gen. Pl. 3: 335 (1880); Pax & K. Hoffm., Pflanzenr. 147, V: 259 (1912); Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305 (1976); Webster, Ann. Missouri Bot. Gard. 81: 123 (1994); Esser in Radcl.-Sm., Gen. Euphorb.: 369 (2001).

Monoecious shrubs; latex not recorded; indumentum 0. Leaves distichous, subsessile, eglandular, margins glandular-crenate; stipules persistent. Inflorescences terminal on axillary branches, unbranched, bisexual, pistillate flower solitary at base, staminate flowers in numerous distal 1–3-flowered cymules; bracts eglandular. Staminate flowers subsessile; calyx nearly completely connate, without distinct lobes; stamens 2 or 3, filaments about as long as anthers, distinct or basally connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile, calyx urceolate, 2–3-lobed or toothed; ovary 3-locular, smooth; ovules anatropous, inner integuments moderately thick [8–10 cell layers], outer integuments thin [3–5 cell layers]; stylodia incrassate, recurved, papillate adaxially. Fruits capsular; columella persistent, alate. Seeds spheroidal, ecarunculate, testa smooth.

Seven spp., endemic to the Greater Antilles and Bahamas but not in Jamaica.

286. ***Grimmeodendron*** Urb.

Grimmeodendron Urb., Symb. Ant. 5: 397 (1908); Pax & K. Hoffm., Pflanzenr. 147, V: 258, fig. 50 (1912); Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305 (1976); Esser in Radcl.-Sm., Gen. Euphorb.: 368 (2001).

Monoecious trees or shrubs; latex white; indumentum 0. Leaves serrulate, adaxially biglandular at base at junction with petiole; stipules deltoid or lunate, the fimbriate scarious tip deciduous, the lunate base persistent. Inflorescences terminal, bisexual; bracts eglandular, subtending 1 or 2 solitary proximal pistillate flowers and several distal staminate cymules with 2 or 3 flowers. Staminate flowers subsessile; sepals 3, valvate, distinct or basally connate, entire; stamens 3, filaments connate into a column ± exserted from the calyx; anthers extrorse, dehiscing longitudinally. Pistillate flowers sessile; sepals 3, deltoid, entire, persistent in fruit; ovary 3-locular; stylodia united at base into a short style, tips unlobed, recurving. Fruits capsular; columella alate distally, persistent. Seeds ovoid-subspheroidal, smooth, ecarunculate.

Two spp., Greater Antilles except Puerto Rico and Bahamas.

287. ***Adenopeltis*** Bert. ex A. Juss.

Adenopeltis Bert. ex A. Juss., Ann. Sci. Nat. I, 25: 24 (1832); Müll. Arg. in DC., Prodr. 15(2): 1164 (1866); Pax & K. Hoffm., Pflanzenr. 147, V: 264, fig. 52 (1912); Esser in Radcl.-Sm., Gen. Euphorb.: 369 (2001).

Monoecious shrubs; latex not recorded; scabrid emergences on stems and inflorescence axes. Leaves short-petiolate or subsessile, eglandular, glabrous, margins prominently glandular-denticulate; stipules small, divided into several ciliae, eglandular. Inflorescences terminal and axillary, solitary, bisexual, spiciform; bracts ovate, entire, with a pair of stipitate, disk-shaped glands, the 0–2 basal ones subtending solitary pistillate flowers, and numerous apical ones with 1–3 staminate flowers. Staminate flowers subsessile; calyx 0; stamens 2 or 3, connate at base; anthers basifixed, dehiscing longitudinally; pistillode 0. Pistillate flowers pedicellate; sepals 0; ovary 3-locular; stylodia distinct or basally connate, slender. Fruits capsular, 3-lobed; columella not persistent, base of cocci persistent as three lobes. Seeds subspheroidal, ecarunculate, testa smooth.

A single sp., *A. serrata* (Ait.) G.L. Webster, Chile and Peru.

288. ***Spegazziniophytum*** Esser

Spegazziniophytum Esser in Radcl.-Sm., Gen. Euporb.: 371 (2001).

Monoecious, succulent shrubs, branches transformed into thorns. Leaves present only on young branches, subsessile. Inflorescences axillary, solitary, catkin-like; bracts with a pair of cup- to disk-shaped glands; pistillate flowers 1 per bract, staminate flowers 2 or 3 per bract. Staminate flowers sessile; calyx 2-lobed, connate; stamens 2, filaments distinct; pistillode 0. Pistillate flowers subsessile; calyx 3-lobed, lobes nearly distinct; ovary smooth; stylodia entire. Fruit 2-locular, dehiscent; columella alate but lacking a carpidiophore. Seeds 2 per fruit, subglobose, with minute apical caruncle.

A single sp., *S. patagonicum* (Speg.) Esser, Argentinian Patagonia. Formerly included in *Colliguaja*, but in the molecular analysis (Wurdack et al. 2005) resolved in a clade with *Stillingia* and *Adenopeltis*, from which it differs by the lack of a carpidiophore.

289. ***Stillingia*** Garden ex L.

Stillingia Garden ex L., Syst. Nat. ed. 12, 2: 637 (1767); Müll. Arg. in DC., Prodr. 15(2): 1155 (1866); Fl. Bras. 11 (2): 537 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 180 (1912); Rogers, Ann. Missouri Bot. Gard. 38: 207, figs. 1–3, 6–16 (1951); van Steenis, Blumea Suppl. 5: 302 (1966); Webster, J. Arnold Arb. 48: 388, fig. 5 (1967); A.C. Sm., Fl. Vit. Nov. 2: 565, fig. 161 (1981); Esser in Radcl.-Sm., Gen. Euphorb.: 370 (2001).
Gymnostillingia Müll. Arg. (1863).

Monoecious arborescent shrubs, subshrubs, or herbs, sometimes with succulent stems; latex white; indumentum 0. Leaves alternate or opposite, entire to glandular-serrulate, with paired basal glands at junction with petiole; stipules ± laciniate-dissected. Inflorescences terminal, unbranched, spiciform, bisexual; bracts biglandular at base; with distal cymules of 1–3 staminate flowers. Staminate flowers subsessile; sepals 2, connate; stamens 2 (3), filaments distinct, exserted from calyx; anthers basifixed, extrorse, dehiscing longitudinally; pollen grains 2-nucleate. Pistillate flowers subsessile; sepals 3, sometimes reduced or 0; ovary 2- or 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin, vascularized; stylodia connate basally, unlobed. Fruits capsular; columella alate, usually persistent, with 3 horn-like projections from base; seeds subspheroidal, carunculate (caruncle reduced). $2n = 22, 30, 36$.

About 30 spp., most of them in the New World (North, Central and South America), a few spp. with scattered distribution in the Old World (2 in Madagascar, 1 in Malesia, and 1 or 2 on Pacific islands extending to Fiji). The Old World species ascribed to *Stillingia* would merit critical revision. Also the inclusion of *Adenopeltis* and *Spegazziniophytum* in *Stillingia* should seriously be considered; it is not formally proposed here only because not all new combinations are available.

290. ***Falconeria*** Royle

Falconeria Royle, Ill. Bot. Himal.: 354 (1839); Wight, Ic. Pl. Ind. Or. 5(2): 20, t. 1866 (1853); Esser, Blumea 44: 160–165 (1999), rev.
Sapium sect. *Falconeria* (Royle) Hook. f. (1888); Pax & K. Hoffm., Pflanzenr. IV: 147, V: 241, fig. 45 (1912).

Monoecious trees; latex white; indumentum 0. Leaves deciduous, sometimes apically clustered, serrate, abaxially with paired basal glands at junction with petiole; stipules dissected. Inflorescences terminal, unisexual, spiciform; bracts biglandular at base with discoid glands, subtending solitary pistillate flowers or cymules of 10–15 staminate flowers. Staminate flowers subsessile; sepals 2, connate; stamens 2, filaments distinct; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers subsessile [short-pedicellate in fruit]; sepals 2 or 3, connate below, eglandular; ovary 2- or 3-locular, smooth; stylodia distinct or basally connate, unlobed. Fruits spheroidal, dehiscing irregularly, pericarp fleshy becoming papery; columella 2- or 3-angled, alate, caducous. Seeds spheroidal, ecarunculate, testa pale, arillate. $2n = 32$.

A single sp., *F. insignis* Royle, E Asia from India to SW China and peninsular Malaysia. *Falconeria* is distinctive due to its unisexual spikes and irregularly dehiscing fruits enclosing seeds with whitish aril. It seems to be closer morphologically to *Sapium* (s. str.) than to other Asiatic Hippomaneae.

291. ***Sapium*** Jacq.

Sapium Jacq., Enum. Syst.: 9 (1760), nom. cons.; Pax & K. Hoffm., Pflanzenr. 147, V: 199 (1912); Webster, J. Arnold Arb. 48: 391 (1967), pro parte; Kruijt & Zijlstra, Taxon 38: 320 (1989); Kruijt, Bibl. Bot. 146: 27–91, figs. 10–31, 33–35 (1996), rev.; Esser in Radcl.-Sm., Gen. Euphorb.: 373 (2001).

Monoecious or dioecious trees or shrubs; latex white, often viscous; indumentum 0. Leaves entire to serrulate; petioles usually biglandular; stipules ovate, persistent. Inflorescences terminal and axillary, solitary or clustered, spiciform; bracts biglandular, discoid to oblong, subtending solitary proximal pistillate flowers and distal cymules of (2–)5–10(–15) staminate flowers.

Staminate flowers mostly subsessile; sepals 2, connate; stamens 2, distinct or basally connate; anthers basifixed, extrorse, dehiscing longitudinally. Pistillate flowers sessile or subsessile; sepals 2 or 3, basally connate; ovary (1)2–3-locular, unappendaged; ovules anatropous, inner and outer integuments moderately thick; stylodia distinct to basally connate into a common style, distally unlobed. Fruits capsular; columella persistent. Seeds spheroidal, ecarunculate, testa covered with red aril. $2n = 22, 44$.

About 25 spp. from the Neotropics. The classical circumscription of the genus of Pax and Hoffmann (1912), which has been followed in most floristic works until recently, was much more inclusive, but Kruijt (1996) has excluded all taxa lacking an aril, so that *Sapium* appears restricted to the New World.

292. ***Colliguaja*** Molina

Colliguaja Molina, Saggio Chile: 158 (1781); Müll. Arg. in DC., Prodr.15(2): 1226 (1866), Fl. Bras. 11(2): 630, t. 85 (1874); Pax & K. Hoffm., Pflanzenr. 147, V: 265, fig. 53 (1912); L.B. Smith et al., Fl. Illustr. Catar. EUFO: 326 (1988).

Monoecious shrubs, sometimes arborescent; latex not recorded; indumentum 0. Leaves mostly opposite or subopposite, short-petiolate, glandular-denticulate or entire; stipules entire, minute, deciduous. Inflorescences terminal, bisexual, spiciform, bracts ovate, eglandular, subtending 1 or 2 proximal solitary pistillate flowers and several cymules of 3 staminate flowers. Staminate flowers subsessile; sepals 1 or 2 and minute or 0; stamens 2–4 (12–18 in *C. brasiliensis*), filaments distinct or connate; anthers basifixed, extrorse, longitudinally dehiscent. Pistillate flowers subsessile; sepals 3, minute; ovary 2–3(4)-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia basally connate into a short style, the distinct branches recurved, adaxially papillate. Fruits capsular, trigonous; columella triquetrous, alate apically, persistent. Seeds subspheroidal, ecarunculate, testa smooth. $2n = 36$.

Four spp., three in C Chile and one in S Brazil and adjacent Paraguay and Uruguay; *C. brasiliensis* is rheophytic.

293. ***Excoecaria*** L.

Excoecaria L., Syst. Nat. ed. 10: 1288 (1759); F.M. Bailey, Queensl. Fl. 5: 1456 (1902); Pax & Hoffm., Pflanzenr. IV, 147, V: 157, figs. 29–31 (1912); Airy Shaw, Kew Bull. 16: 268 (1971), Add. Ser. 4: 112 (1975), 8: 88 (1980); Radcl.-Sm., Fl. E. Trop. Afr. Euphorb. 1: 382, fig. 72 (1987); Chakrab. & Gangop., J. Econ. Tax. Bot. 18: 193 (1994); Radcl.-Sm., Fl. Zamb. 9(4): 315, t. 68 (1996); Esser in Radcl.-Sm., Gen. Euphorb.: 360 (2001).
Commia Loureiro (1790).
Spirostachys Sond. (1850).
Conosapium Müll. Arg. (1863).
Taeniosapium Müll. Arg. (1866).
Glyphostylus Gagnep. (1925).

Dioecious or monoecious trees or shrubs; latex milky, toxic; indumentum 0. Leaves alternate or opposite, entire or crenulate, eglandular, rarely with basal glands; stipules deciduous or ± persistent. Inflorescences axillary or terminal on brachyblasts, solitary, spiciform; bracts usually biglandular at base, subtending 1–3 staminate flowers or single pistillate flowers. Staminate flowers sessile or subsessile; sepals 3(2), distinct; stamens 3(2), filaments distinct; anthers extrorse, dehiscing longitudinally; pistillode 0. Pistillate flowers subsessile or short-pedicellate; sepals 3, distinct or basally connate; ovary 3-locular; ovules anatropous, inner integuments moderately thick, outer integuments thin; stylodia distinct or slightly connate at base. Fruits capsular; columella persistent, alate. Seeds subglobose, ecarunculate or the caruncle persistent on top of the columella.

About 40 spp. distributed from Africa to Australia and Melanesia. Esser (2001) has redefined the genus by excluding some elements retained by Pax and Hoffmann (1912) and synonymizing *Glyphostylus*. There is still considerable uncertainty about the monophyly of *Excoecaria*; for example, the study of ovular structure by Tokuoka and Tobe (2002) indicates that *E. bussei* differs greatly from other species and may not be congeneric. Although Esser maintains *Spirostachys* as a distinct genus, it is included within *Excoecaria* here (and was resolved as the strongly supported sister to *E. agallocha*; Wurdack et al. 2005), where it will probably survive as a well-marked subgenus or section. *Conosapium* from Madagascar, although generically accepted by Esser (2001) and Schatz (2001), can probably be accommodated as a distinctive section.

3. TRIBE EUPHORBIEAE

Monoecious (dioecious) trees, shrubs, or herbs, sometimes succulent; latex milky, sometimes toxic; indumentum simple or 0; leaves alternate, opposite, or whorled, mostly unlobed and pinnately veined, sometimes reduced, without laminar or petiolar glands; stipules + or 0; inflorescences pseudanthial with connate bracts forming a cyathium that encloses a single terminal pistillate flower and 4 or 5 lateral staminate dichasia or monochasia; cyathia often aggregated in compound inflorescences; staminate flowers with calyx reduced or 0, the solitary stamen articulating with the pedicel; pollen grains 3-colporate, colpi bordered by conspicuous intine bands, exine perforate-tectate; pistillate flowers ± pedicellate, calyx 3–6-lobed or reduced or 0; ovary (2)3(4)-locular; stylodia distinct or basally connate, bifid, rarely entire; fruit capsular, rarely drupaceous; seeds carunculate or ecarunculate; testa dry.

This tribe includes 3 subtribes grouped into 5 genera and > 2,000 spp., the vast majority in the genus *Euphorbia* s.l. In many molecular analyses (e.g., Steinmann and Porter 2002; Wurdack et al. 2005; Horn et al. 2012), Euphorbieae are resolved as monophyletic with the Anthosteminae as the earliest diverging group, followed by the Neoguillauminiinae and Euphorbiinae in a sister position. Genera until recently kept separate from *Euphorbia* s. str. but now found to be deeply embedded and sunk into it (see below under *Euphorbia* s. l.) are not formally accepted here but are keyed out in order to demonstrate on which characters they had been based; this is also because they have been in wide use in general and phytogeographic writings until recently, and may still be so until a full infrageneric classification of *Euphorbia* s. l. becomes available and accepted.

KEY TO THE SUBTRIBES AND GENERA OF EUPHORBIEAE

1. Staminate calyx +; involucre of 4 partially or fully connate bracts; cyathial glands commissural, not on rim of cyathium. **3a. Anthosteminae** 2
– Staminate calyx 0; involucral bracts usually 5, connate into a cup or tube; cyathial bracts different 3
2. Inflorescences axillary; cyathia bisexual; involucral bracts partially connate into an open 4-lobed involucre; cyathial glands at margins of involucral bracts; ovary 3-locular **294. *Anthostema***
– Inflorescences terminal; cyathia mostly unisexual; involucral bracts connate into a closed cup; cyathial glands connate by pairs into 4 lobes alternating with the involucral bracts; ovary 4-locular **295. *Dichostemma***
3. Petaloid appendages bracteal [dilated involucral lobes], opposite the staminate dichasia; cyathial glands commissural; bracts of staminate dichasia large, imbricate, enclosing staminate flowers; pistillate sepals 5 or 6, large, imbricate. **3b. Neoguillauminiinae** 4
– Petaloid appendages interbracteal [opposite cyathial glands], alternate with staminate monochasia; cyathial glands on rim of cyathium; bracts of staminate monochasia small or obsolete; pistillate sepals + or 0. **3c. Euphorbiinae (298. *Euphorbia* s. l.)** 5
4. Cyathial glands 8 or 10, massive; petaloid involucral bracts c. 1 cm long; leaves spiral **296. *Neoguillauminia***
– Cyathial glands 4, small; petaloid bracts < 1 cm long; leaves opposite **297. *Calycopeplus***
5. Cyathia bilaterally symmetrical; glands enclosed within a nectar spur; stylodia connate into a long column. 17 spp., most in Mexico *Euphorbia* **'*Pedilanthus*'**
– Cyathia ± radially symmetrical, glands not enclosed within a nectar spur; stylodia distinct or nearly so 6
6. Involucral glands distinct, (1–)4–5(8), alternating with involucral lobes on rim of cyathium; bracts subtending cyathium distinct or connate 7
– Involucral glands not 4 or 5 alternating with lobes; bracts subtending cyathium often connate into a cup 8
7. Leaves alternate, opposite, or whorled, but if opposite then not inaequilateral at base; veins of leaves not chlorenchyma-sheathed; stipules + or 0; main [embryonic] axis not abortive *Euphorbia* s.str.
– Leaves opposite, stipulate, inaequilateral at base; veins chlorenchyma-sheathed; main axis abortive above cotyledons. About 250 spp., mostly in trop. America and Africa *Euphorbia* **'*Chamaesyce*'**
8. Pistillate flower calyculate; involucral lobes connate; glands 2, connate into a shield; seeds ecarunculate; stems not succulent. 3 spp., Cuba, Hispaniola *Euphorbia* **'*Cubanthus*'**
– Pistillate flower naked; involucral lobes and glands connate into a ring; seeds mostly carunculate; stems succulent 9
9. Cyathium somewhat bilaterally symmetrical; gland-ring with a gap on one side. 70 spp., trop. Africa *Euphorbia* **'*Monadenium*'**
– Cyathium radially symmetrical, without a gap on one side 10
10. Involucral glands connate, conspicuous; ovary without angular crests. 19 spp., E and S trop. Africa *Euphorbia* **'*Synadenium*'**
– Involucral glands distinct, inconspicuous; ovary with prominent double angular crests. 1 sp., Angola *Euphorbia* **'*Endadenium*'**

3a. SUBTRIBE ANTHOSTEMINAE (Klotzsch & Garcke) G.L. Webster (1975).

Monoecious or dioecious; leaves with dispersed and submarginal glands; stipules caducous;

cyathia in axillary inflorescences; cyathial involucre of 4 bracts subtending or enclosing 4 staminate partial inflorescences; staminate flowers in dichasia ± enclosed by prophylls; pistillate flower solitary, central and terminal or apparently lateral; cyathial glands projecting inward from infolded margins of involucral bracts; staminate and pistillate flowers with gamophyllous calyx; ovary 3–4-locular; stylodia emarginate to bifid; fruit capsular; seeds caruncular or ecarunculate.

Two genera of Africa and Madagascar.

294. *Anthostema* A. Juss.

Anthostema A. Juss., Euphorb. Tent.: 56 (1824); Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207, fig. 11 a, b (1931); Keay, Fl. W. Trop. Afr. ed. 2, 1: 416 (1958); Berhaut, Fl. Ill. Sénégal 3: 379 (1975); Schatz, Gen. Tree Fl. Madag.: 145, fig. 134 (2001).

Monoecious trees; latex white; indumentum 0. Leaves distichous, with minute punctiform glands and larger abaxial submarginal glands. Inflorescences axillary, of contracted cymes of cyathia; cyathia with involucre of 4 bracts connate laterally; each bract with 2 marginal glands. Staminate flowers enclosed by 4 prophylls; calyx 3- or 4- dentate; pollen grains oblate-spheroidal, 3-colporate, colpi marginate, exine reticulate; pistillate flowers pedicellate; calyx 3- or 4-dentate; ovary 3-locular, sessile; stylodia for lower half connate into a column, distally clavate or bifid. Fruits capsular; endocarp thick and woody; columella trigonous-alate, clavate, persistent. Seeds laterally compressed, caruncular. $2n = 22$.

Three spp., 2 in west Africa and 1 in Madagascar.

295. *Dichostemma* Pierre

Dichostemma Pierre, Bull. Mens. Soc. Linn. Paris 1 (159): 1259 (1896); Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207 (1931); Keay, Fl. W. Trop. Afr. ed. 2, 1: 416 (1958), Trees Nigeria 151 (1989); Radcl.-Sm., Gen. Euphorb.: 400, fig. 46 (2001).

Monoecious or dioecious trees, sometimes climbing; latex white; indumentum pruinose on inflorescence axes. Leaves eglandular. Inflorescences terminal with the cyathia in a panicle; cyathia mostly unisexual, bilateral, with involucre of paired connate bracts; glands connate in pairs alternating with involucral bracts. Staminate flowers 5–12; calyx 4-lobed; pistillate flower pedicellate; calyx cupular or obscurely 4-lobed; ovary 4-locular; stylodia distinct, entire or obscurely bifid. Fruits capsular; endocarp woody but thin; columella 4-angular, persistent. Seeds trigonous-rounded, ecarunculate, testa smooth.

Two spp. from W Africa.

3b. Subtribe Neoguillauminiinae Croizat (1938).

Monoecious; indumentum 0; leaves alternate or opposite, entire; stipules 0; cyathia in axillary or subterminate pedunculate cymes; involucral bracts 4(−6), basally connate, distally dilated or petaloid; staminate dichasia opposite the involucral bracts; nectary glands in 4 or 5 pairs, sometimes small, or 0; pistillate flower central. Staminate flowers in bracteate dichasia; staminate calyx 0; pistillate sepals 5 or 6, imbricate; ovary 3-locular; stylodia unlobed, dilated; seeds smooth, caruncular.

This Australasian subtribe of 2 genera (1 in Australia and the other in New Caledonia) appears to bridge the gap between the Anthosteminae and Euphorbiinae.

296. *Neoguillauminia* Croizat Fig. 47

Neoguillauminia Croizat, Phil. J. Sci. 64: 398 (1938), Bull. Jard. Bot. Buit. III, 17: 206 (1941); Guillaumin, Fl. Anal. Syn. Nouv-Caléd.: 182 (1948); McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 22–25, t. 3 (1987).

Monoecious trees or shrubs; latex white; indumentum 0, young stems pruinose. Leaves alternate or opposite, eglandular. Inflorescences axillary and subterminal, long-pedunculate; cyathia mostly 3 in a terminal dichasium; involucral bracts 4–6, basally connate into a cup and distally with 4–6 petaloid appendages reddish without and white within; staminate dichasia opposite the involucral bracts, bracteate, each surrounded by broad, erose, rectangular bracts, 10–28-flowered; nectary glands 8–12, stipitate, fleshy, pair-wise partitioning the staminate partial inflorescences; pistillate flower central. Staminate flowers pedicellate; perianth 0; pollen grains 2-nucleate; pistillate flower subsessile; calyx annular, persistent in fruit; anther introrse with respect to the cyathium; ovary 3-locular; stylodia recurved, basally connate, distally bifid. Fruits capsular, endocarp woody; columella apically dilated, deciduous except for conical base. Seeds ellipsoid, caruncular, testa smooth.

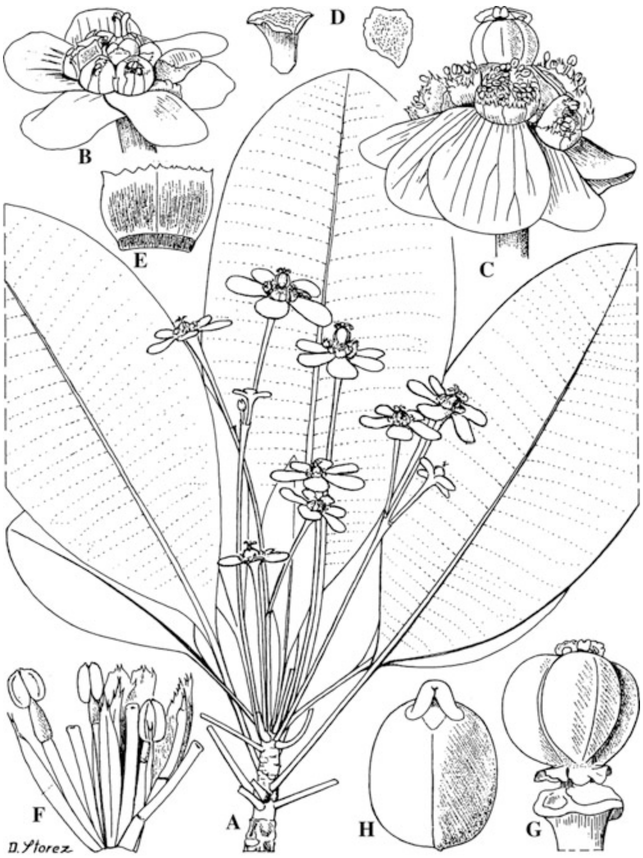

Fig. 47. Euphorbiaceae-Euphorbioideae. *Neoguillaumia cleopatra*. **A** Flowering branchlet. **B** Young cyathium. **C** Cyathium at anthesis. **D** Nectar gland seen from the side and from below. **E** Involucral bract. **F** Bracteate staminate flowers. **G** Fruit. **H** Carunculate seed. (McPherson & Tirel 1987; drawn by D. Storez)

Only one sp., *N. cleopatra* (Baill.) Croizat, endemic to New Caledonia. The showy and fragrant cyathia resemble those of species of *Euphorbia*, but the petaloid appendages may not be homologous.

297. *Calycopeplus* Planch.

Calycopeplus Planch., Bull. Soc. Bot. France 8: 30 (1861); Boissier, Ic. Euphorb.: t. 120 (1866); Airy Shaw, Kew Bull. 35: 603 (1980); P.I. Forster, Austrobaileya 4: 418, t. 1, 2 (1995).
Euphorbia sect. *Calycopeplus* (Planch.) Boiss. (1862).

Monoecious shrubs, sometimes arborescent, or subshrubs; stems and branches virgate; latex white. Leaves opposite or verticillate, petiolate to sessile, eglandular, soon deciduous. Inflorescences axillary, rarely terminal, the cyathia solitary or paired, subsessile; involucral bracts 4, connate, their distinct lobes small, petaloid, white or greenish; nectary glands 4 between the lobes, sometimes reduced; staminate partial inflorescences opposite the lobes in 3–7-flowered bracteate dichasia; pistillate flower solitary, central. Staminate flowers pedicellate; perianth 0; anther introrse in relation to pistillate flower. Pistillate flower pedicellate; calyx cupular, 4–6-lobed; ovary 3-locular, sessile or subsessile; stylodia distinct or basally connate. Fruit capsular, 3-lobed, endocarp thin and crustaceous; columella persistent, clavate. Seeds subspheroidal or oblong, carunculate, testa smooth.

Five spp., all endemic to Australia, which differ by a xeromorphic habit from *Neoguillauminia* but share with it the cyathial structure.

3c. Subtribe Euphorbiinae

Monoecious (dioecious) trees, shrubs, or herbs; latex milky; indumentum simple or 0; leaves alternate, opposite, or whorled, usually unlobed and pinnately veined, stipulate or exstipulate; inflorescences terminal or axillary, cyathia often subtended by paired bracts; cyathium distinctly cupulate with (1–2)4–5 interbracteal glands on the rim; glands with or without petaloid appendages; pistillate flower central, staminate flowers in 4 or 5 monochasia [usually cincinni] (rarely 1-florous) with ± reduced prophylls; staminate calyx 0; stamen 1; pollen grains 2- or 3-nucleate; pistillate calyx 3–6-lobed, often vestigial or 0; ovary 3-locular; stylodia distinct or connate, bifid (entire); fruit capsular (drupaceous); seeds carunculate or ecarunculate.

Only one genus, *Euphorbia* (s. l.).

298. *Euphorbia* L.

Euphorbia L., Sp. Pl.: 450 (1753); Boissier in DC., Prodr. 15(2): 7 (1862), Icon. Euphorb.: t. 27–119 (1866); Carter, Fl. E. Trop. Afr., Euphorb. 2: 409 (1988); Carter & Leach, Fl. Zambesiaca 9(5): 339, t. 71–84 (2001); Radcl.-Sm., Gen. Euphorb.: 405, figs. 47–50 (2001).
Tithymalus Gaertn., Fruct. 2: 115 (1790), nom. cons.
Pedilanthus Necker ex Poit., Ann. Mus. Nat. Hist. 19: 388 (1812), nom. cons.; Dressler, Contr. Gray Herb. 182: 1–188 (1957).
Chamaesyce S. F. Gray, Nat. Arrang. Brit. Pl. 2: 260 (1821); Koutnik, S. Afr. J. Bot. 3: 262 (1984); Ya Yang & Berry, Amer. J. Bot. 98: 1486–1503 (2011).
Poinsettia Graham, Edinburgh New Phil. J. 20: 412 (1836).
Synadenium Boiss. in DC., Prodr. 15(2): 187 (1862); S. Carter, Fl. E. Trop. Afr., Euphorb. 2: 534, fig. 101 (1988), Fl. Zambes. 9(5): 434, t. 85 (2001).

Monadenium Pax, Bot. Jahrb. 19: 126, fig. (1895); P.R.O. Bally, Genus *Monadenium*: 14, figs. 1–34, t. I–XXXII (1961).
Elaeophorbia Stapf, Hooker's Icon. Pl. 29: t. 2823 (1906).
Cubanthus (Boiss.) Millsp., Field Mus. Nat. Hist. Bot. 2: 371 (1913); Steinmann et al., Ann. Jard. Bot. Madrid 64: 123–133 (2007).
Endadenium Leach, Garcia de Orta 1: 31 (1973).

Monoecious (dioecious) trees, shrubs, or herbs, often succulent and/or spiny; stems erect to procumbent, rarely plants acaulescent; latex whitish; indumentum simple or 0. Leaves alternate, opposite, or whorled, persistent or deciduous, simple (deeply lobed), sessile to petiolate, entire or variously toothed, mostly pinnately veined, eglandular; stipules small and inconspicuous or 0, often glandular, sometimes modified into spines. Inflorescences bisexual (unisexual), contracted into pseudanthial cyathia; cyathia in terminal or axillary dichasia or pleiochasia, sometimes solitary, each subtended by 2 variously colored distinct or connate modified leaves, composed of a single central terminal pistillate flower and 5 or 4 staminate cincinnate monochasia with their associated prophylls, the monochasia alternating with 5 or 4 involucral bracts connate into a radially or isobilaterally symmetrical campanulate to hemispherical involucre; the tips of the involucral bracts alternating with (0)1–5(20) glands situated on the rim of the opening (enclosed in a zygomorphic-spurred involucre); glands sometimes forming a ± continuous rim on the outer wall of the involucre but usually distinct and entire, bicornute, cupular, bilabiate, or sometimes highly divided, usually with dorsal appendages, these often flat and petaloid, sometimes glandular or branched. Staminate flowers monandrous; perianth usually 0 or very rarely developed; anthers dehiscing longitudinally and introrsely in relation to the vertical axis of the cyathium; pollen grains 2- or 3-nucleate, subspheroidal, tricolporate, reticulate to finely tectate-perforate; pistillate flower pedicellate, pedicel often becoming reflexed; sepals (0)3–6, ± connate basally; ovary (2)3(4)-locular, glabrous or pubescent, often angled or carinate; stylodia distinct or connate at base, 2-fid (unlobed). Fruits capsular (drupaceous); columella ± persistent. Seeds carunculate or ecarunculate, testa smooth, ridged, pitted, or tuberculate. $x = 6$–10; many spp. based on $x = 7$ or $x = 10$.

With > 2,000 spp., this is the largest genus in the Euphorbiaceae and one of the five largest angiosperm genera. It is subcosmopolitan in distribution and is extremely variable in habit; Hallé et al. (1978), in their architectural analysis, reported from it 12 of the 23 recognized structural types ("models"). Horn et al. (2012) analyzed the major structural traits in a phylogenetic context, which revealed an extreme parallelism in the evolution of the xeromorphic growth forms within the genus.

Delimitation of the genus *Euphorbia* always has been strongly contentious, and in the 260 years that elapsed since Linnaeus treated the then-known 56 spp. of *Euphorbia*, more than 75 satellite genera have been proposed. Most of them, however, have fallen into synonymy, and until very recently, only six or seven generally have been maintained, as by Webster (1994) and Radcliffe-Smith (2001). Molecular phylogenetic research by Steinmann and Porter (2002) demonstrated that *Chamaesyce*, *Pedilanthus*, *Monadenium*, *Synadenium*, and *Endadenium* are all deeply nested within paraphyletic *Euphorbia*, and that most of the historically recognized subgenera and sections of *Euphorbia* s.str. are either paraphyletic or polyphyletic. Further work (Steinmann 2003; Bruyns et al. 2006; Steinmann et al. 2007; Zimmermann et al. 2010; Horn et al. 2012) confirmed and extended these findings, and led to the broadly construed generic concept of *Euphorbia* that is gaining increasing acceptance. Steinmann and Porter (2002) also recovered four major lineages within *Euphorbia*, designated as clades A–D; with one exception, these do not correspond to any previously known taxon but are composed of various sections or subgenera of *Euphorbia*; only a single clade, by and large, is congruent with subg. *Esula*. Bruyns et al. (2006), in their study of southern African *Euphorbia*, confirmed the existence of these clades; they used the names of some of the existing subgenera with which the clades showed partial overlap for designating and formally treating them as the four subgenera of *Euphorbia*: A = subg. *Rhizanthium*, B = subg. *Esula*, C = subg. *Euphorbia*, and D = subg. *Chamaesyce*. This proposal has also been taken up by, i.a., Horn et al. (2012), who have provided the hitherto most comprehensive overall phylogenetic analysis of the genus and its structural traits. Although these clades are strongly supported and, as such, valuable for further phylogenetic understanding of

Euphorbia, they seem hardly acceptable to us as taxa because they are very heterogeneous, are not distinguishable on the basis of morphology, and rather are the mere product of the algorithm. A taxonomic subdivision of *Euphorbia*, which is a great desideratum, favorably would have to be built upward from clearly circumscribed entities of lower rank such as sections. This has been accomplished for the Chamaesyce Clade by Yang et al. (2012)[1].

A brief characterization of the four clades reads as follows:

A. **Esula Clade**. Annual and perennial herbs, shrubs, and trees, some are stem succulents; inflorescence terminal, pseudo-umbellate; branching sympodial; cyathial glands 4; stipules 0; caruncles +. About 480 spp., mainly in temperate Northern Hemisphere, outside this area woody as trees or stem succulents in the Canary Isl., Africa, Madagascar, and Arabia; very few in tropical America.

B. **Rhizanthium Clade**. Woody and succulent xerophytes, morphologically diverse, often cactiform and sometimes with spines derived from persistent, indurated bases of inflorescence peduncles; some geophytic; often with stem tubercles on the tips of which the leaves are borne; inflorescences terminal, rarely lateral; cyathial glands 5; stipules glandular, filamentous, or 0; caruncles 0. About 200 spp., most of them in southern Africa but also in Madagascar and extending north to Arabia.

C. **Euphorbia Clade**. The clade with the greatest diversity in taxa and growth forms, ranging from trees up to 30 m high to low "pencil plants" and cactiform succulents many of which, unlike cacti, maintain the possibility to develop large foliage leaves. In some caudiciform shrubs, the stems bear at the nodes spine-shields subtending pairs of stipular spines accompanied by supernumerary spines associated with the leaf bases (Uhlarz 1974). Inflorescences terminal or more often lateral with concomitant transition from sympodial to monopodial growth. Cyathial glands 5(4); stipules + or 0; caruncles often +. The extreme xerophytic subg. *Euphorbia* is nested within this large clade. About 700 spp., pantropical, but with greatest diversity in Africa/Madagascar.

D. **Chamaesyce Clade**. Herbs, subshrubs, or shrubs, sometimes succulent; leaves alternate or opposite; stipules + or 0; inflorescences terminal; cyathial glands 5, 4, or 2–1, glands sometimes with petaloid appendages; caruncles rarely +. About 600 spp. with mostly C_3 or CAM photosynthesis in the Old World including Africa/Madagascar and Australia, and 350 New World spp. of mostly C_4 photosynthetic herbs.

Selected Bibliography

Airy Shaw, H.K. 1965. Diagnoses of new families, new names, etc. for the seventh edition of Willis's "Dictionary ". Kew Bull. 18: 249–273.

Airy Shaw, H.K. 1968. Notes on Malesian and other Asiatic Euphorbiaceae, XCVI. Kew Bull. 21: 409–418.

Airy Shaw, H.K. 1974. Noteworthy Euphorbiaceae from tropical Asia. Hooker's Icon. Plant. 38 (1): t. 3701–3725.

Alex, A.H. 1957. Pollination of some oil seed crops by honey bees. Texas A. & M. College Agr. Exp. Stat. Progr. Rep. 1960.

Alvin, K.L. 1987. Leaf anatomy of *Androstachys johnsonii* Prain and its functional significance. Ann. Bot. 59: 579–591.

Armbruster, W. 1984. The role of resin in pollination: Ecological and chemical considerations. Amer. J. Bot. 71: 1149–1160.

Armbruster, W.S. 1988. Multilevel comparative analysis of the morphology, function, and evolution of *Dalechampia* blossoms. Ecology 69: 1746–1761.

Armbruster, W.S. 1993. Evolution of plant pollination systems: hypotheses and tests with the neotropical vine *Dalechampia*. Evolution 47: 1480–1505.

Armbruster, W.S. 1994. Early evolution of *Dalechampia* (Euphorbiaceae): insights from phylogeny, biogeography, and comparative ecology. Ann. Missouri Bot. Gard. 81: 302–316.

Armbruster, W.S. 1996. Cladistic analysis and revision of *Dalechampia* sections *Rhopalostylis* band *Brevicolumnae* (Euphorbiaceae). Syst. Bot. 21: 209–235.

Armbruster, W.S., Baldwin, B.G. 1998. Switch from specialized to generalized pollination. Nature 394: 632.

Armbruster, W.S., Webster, G.L. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11: 278–283.

---

[1] Added in proof: Attention is directed to the following recently published systematic treatments of the Euphorbia Clade and the Esula Clade (as "subgenera"), which provide detailed sectional classifications:

- Dorsey, B.L., Haevermans, T., Aubriot, X., Morawetz, J. J., Riina, R., Steinmann, V.W., Berry, P.E. 2013. Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*. Taxon 62: 291–315.
- Riina, R., Peirson, J.A., Geltman, D.V., Molero, J., Frajman, B., Pahlevani, A., and further 7 authors. 2013. A worldwide molecular phylogeny and classification of the leafy spurges, *Euphorbia* subgenus *Esula* (Euphorbiaceae). Taxon 62: 316–342.

Armbruster, W.S., Howard, J.J., Clausen, T.P., Debevec, E., Loquvam, J., Matsuki, M., Cerendolo, B., Andel, F. 1997. Do biochemical exaptations link evolution of plant defense and pollination systems? – Historical hypotheses and experimental tests with *Dalechampia* vines. Amer. Nat. 149: 461–484.

Armbruster, W.S., Lee, J., Baldwin, B.G. 2009. Macroevolutionary patterns of defense and pollination in *Dalechampia* vines: adaptation, exaptation, and evolutionary novelty. Proc. Natl. Acad. Sci. USA 106: 18085–18090.

Bailey, I. W. 1924. The problem of identifying the wood of Cretaceous and later dicotyledons: *Paraphylanthoxylon arizonense*. Ann. Bot. 38: 439–452.

Baillon, H. 1858. Étude générale du groupe des Euphorbiacées. Paris: Victor Masson.

Bally, P.R.O. 1961. The genus *Monadenium*. Bern: Bentelli.

Bancilhon, L. 1971. Contribution à l'étude taxonomique du genre *Phyllanthus*. Boissiera 18: 1–81.

Barrera, M.E., Meza, P.I., Serra, V.M.T. 2001. Epidermis foliar de Euphorbiaceae presentes en Chile, aporte a la ubicación sistemática de *Avellanita bustilosii* Phil. Bol. Mus. Nac. Hist. Nat. Chile 50: 7–19.

Bawa, K.S. 1980. Evolution of dioecy in flowering plants. Ann. Rev. Ecol. Syst. 11: 15–39.

Bawa, K.S., Webb, C.J., Tuttle, A.F. 1982. The adaptive significance of monoecism in *Cnidoscolus urens* (L.) Arthur (Euphorbiaceae). Bot. J. Linn. Soc. 85: 213–223.

Bentham, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc. Bot. 17: 185–267.

Bentham, G. 1880. Euphorbiaceae, pp. 239–340. In: Bentham and Hooker, Genera Plantarum, vol. 3. London: L. Reeve.

Berg, R. 1975. Fruit, seed and myrmecochorous dispersal in *Micrantheum* (Euphorbiaceae). Norw. J. Bot. 22: 173–194.

Bernhard, F. 1966. Contributión à l'étude des glandes foliaires chez les Crotonoidées (Euphorbiacées). Mém. Inst. Fond. Afr. Norire 75: 71–156.

Bhatnagar, A.K., Kapil, R.N. 1974. *Bischofia javanica* – its relationships with Euphorbiaceae. Phytomorphology 23: 264–267.

Bianchini, M., Pacini, E. 1996. The caruncle of *Ricinus communis* L. (castor bean): its development and role in seed dehydration, rehydration, and germination. Int. J. Plant Sci. 157: 40–48.

Blattner, F.R., Weising, K., Bänfer, G., Maschwitz, U., Fiala, B. 2001. Molecular analysis of phylogenetic relationships among myrmecophytic *Macaranga* species (Euphorbiaceae). Mol. Phylogen. Evol. 19: 331–344.

Boissier, E. 1862. Euphorbiaceae subordo I.Euphorbieae. DC. Prodromus 15(2): 3–188.

Bouharmont, J. 1962. Fécondation et développement de la graine après croisement et autopollinisation chez *Hevea brasiliensis* Muell. Arg. Cellule 62: 119–130.

Breckon, G. 1975. *Cnidoscolus*, Section *Calyptosolen* (Euphorbiaceae) in Mexico and Central America. Ph. D. diss., University of California.

Brunell, J.F. 1975. Contribution à l'étude de quelques *Phyllanthus* africains et à la taxonomie du genre *Phyllanthus* (Euphorbiaceae). Strasbourg: Université Louis Pasteur de Strasbourg.

Bruyns, P.V., Mapaya, R.J., Hedderson, T. 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and *psb*A-*trn*H sequence data. Taxon 55: 397–420.

Bullock, S.H. 1994. Wind pollination of neotropical dioecious trees. Biotropica 26: 172–179.

Burger, W., Huft, M. 1995. Flora Costaricensis: Euphorbiaceae. Fieldiana Bot. n.s. 36: 1–169.

Burrows, G.E., Tyrl, R.J. 2001. Toxic plants of North America. Hoboken (NJ): Wiley.

Cacho, N.I., Berry, P.E., Olson, M.E., Steinmann, V.W., Baum, D.A. 2010. Are spurred cyathia a key innovation? Molecular systematics and trait evolution in the slipper spurges (Pedilanthus clade: *Euphorbia*, Euphorbiaceae). Amer. J. Bot. 97: 493–510.

Cahoon, E.J. 1972. *Paraphyllanthoxylum alabamense*—a new species for fossil dicotyledonous wood. Amer. J. Bot. 59: 5–11.

Call, V.B., Manchester, S.R., Dilcher, D.L. 1993. *Wetherellia* fruits and associated fossil plant remains from the Paleocene/Eocene Tuscahoma-Hatchetigbee interval, Meridian, Mississippi. Mississippi Geol. 14: 10–18.

Calvin, M. 1987. Fuel oils from euphorbs and other plants. Bot. J. Linn. Soc. 94: 97–110.

Carter, S. 1994. A preliminary classification of *Euphorbia* subgenus *Euphorbia*. Ann. Missouri Bot. Gard. 81: 368–379.

Carter, S., Leach, L.C. 2001. Flora Zambesiaca, Vol. IX, 5. Euphorbiaceae-Euphorbioideae-Euphorbieae. Kew: Royal Botanic Gardens Kew.

Cesca, G. 1961. Ricerche cariologiche ed embriologiche sulle Euphorbiaceae. 1. Su alcuni biotipi di *Euphorbia dulcis* L. della toscana. Caryologia 14: 79–96.

Chase, M.W. et al. 1993. See General References.

Clifford, H.T., Monteith, G.B. 1989. A three phase seed dispersal mechanism in Australian quinine bush, (*Petalostigma pubescens* Domin). Biotropica 21: 284–286.

Corner, E.J.H. 1976. The Seeds of Dicotyledons. Cambridge: Cambridge University Press.

Cremers, G. 1977. Architecture végétative de quelques espèces malgaches du genre *Euphorbia* L. Bull. Jard. Bot. Nat. Belg. 47: 55–81.

Crepet, W.L., Daglian, C.P. 1982. Euphorbioid inflorescences from the Middle Eocene Claiborne formation. Amer. J. Bot. 69: 258–266.

Croizat, L. 1938. Notes on Euphorbiaceae, with a new genus and a new subtribe of the Euphorbieae. Philip. J. Sci. 64: 397–411.

Croizat, L. 1941. The Tribe Plukenetieae of the Euphorbiaceae in eastern tropical Asia. J. Arnold Arbor. 22: 417–431.

Croizat, L. 1973. Les Euphorbiaceées vues en elles-mêmes, et dans leur rapport envers l'angiospermie en général. Mem. Soc. Broteriana 23: 5–207.

Cronquist, A. 1981. See General References.

Cullen, J. 1978. A preliminary survey of ptyxis (vernation) in the angiosperms. Notes Roy. Bot. Gard. Edinburgh 37: 161–214.

Daumann, E. 1972. Zur Blütenmorphologie und Bestäubungsökologie von *Mercurialis* L. Preslia 44: 308–315.

Davies, S.J., Lum, S.K.Yl, Chan, R., Wang, L.K. 2001. Evolution of myrmecophytism in western Malesian *Macaranga* (Euphorbiaceae). Evolution 55: 1542–1559.

Dehgan, B., Craig, M.E. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 345–352.

Dehgan, B., Webster, G.L. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.

Dilcher, D.L., Manchester, S.R. 1988. Investigations of the angiosperms from the Eocene of North America: a fruit belonging to Euphorbiaceae. Tertiary Research 9: 45–68.

Dinerstein, E., Wemmer, C.M. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. Ecology 69: 1768–1774.

Dingler, H. 1885. Die Flachsprosse der Phanerogamen. Erstes Heft: *Phyllanthus* sect. *Xylophylla*. Munich: T. Ackermann.

Domínguez, C.A., Bullock, S.H. 1989. La reproducción de *Croton suberosus* (Euphorbiaceae) en luz y sombra. Rev. Biol. Trop. 37: 1–10.

Domínguez, C.A., Dirzo, R., Bullock, S.H. 1989.On the function of floral nectar in *Croton suberosus*. (Euphorbiaceae). Oikos 56: 109–114.

Dressler, R.L. 1957. The genus *Pedilanthus* (Euphorbiaceae). Contr. Gray Herb. 182: 1–188.

Durand, B. 1963. Le complexe *Mercurialis annua* L. s.l.: une étude biosystématique. Ann. Sci. Nat. Paris, Bot. 12: 579–736.

Ehrenfeld, J. 1976. Reproductive biology of three species of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). Amer. J. Bot. 63: 406–413.

Eichler, A.W. 1875. Blüthendiagramme. Leipzig: W. Engelmann.

Emmerich, M. 1981. Revisão taxinômica dos gêneros *Algernonia* e *Tetraplandra*. Arq. Mus. Nac. Rio de Janeiro 56: 91–110.

Erdtman, G. 1952. See General References.

Esser, H.-J. 1994. Systematische Studien an den Hippomaneae Adr. Jussieu ex Bartling (Euphorbiaceae), insbesondere den Mabeinae Pax & K. Hoffm. Hamburg: Dissertation, Universität Hamburg.

Esser, H.J. 2002. A revision of *Triadica* Lour. (Euphorbiaceae). Harvard Pap. Bot. 7: 17–21.

Esser, H.-J., van Welzen, P., Djarwaningsih, T. 1997. A phylogenetic classification of the Malesian Hippomaneae (Euphorbiaceae). Syst. Bot. 22: 617–628.

Fatemi, M, Gross, C.L. 2009. Life on the edge - High levels of genetic diversity in a cliff population of *Bertya ingramii* are attributed to *B. rosmarinifolia* (Euphorbiaceae). Biol. Conserv. 142: 1461–1468.

Fernandez-González, D., Lobreau-Callen, D. 1996. Le pollen de la tribu des Acalypheae (Acalyphoideae, Euphorbiaceae). Grana 35: 266–284.

Freitas, J.R. de, Figueiredo, R.A., Nadai, I.C., Hardman, L. 2011. Aspects of *Pera glabrata* (Schott) Poepp. ex Baill. (Euphorbiaceae) reproductive ecology in a cerrado area in São Paulo State. Revista Arvore 35: 1227–1234.

Froembling, W. 1896. Anatomisch-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. Bot. Centralbl. 65: 129–139, 177–192, 242–249, 321–329, 369–378, 407–421, 433–442.

George, Jr., W.L., Shifriss, O. 1967. Interspersed sexuality in *Ricinus*. Genetics 57: 347–356.

Gilbert, M.G. 1994. The relationships of the Euphorbieae. Ann. Missouri Bot. Gard. 81: 283–288.

Gillespie, L.J. 1994. Pollen morphology and phylogeny of the tribe Plukenetieae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 317–348.

Gillespie, L. 1997. *Omphalea* (Euphorbiaceae) in Madagascar: a new species and a new combination. Novon 7: 127–136.

Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaita, Amazonia. Biotropica 10: 170–183.

Goulding, M. 1980. The fishes and the forest. Berkeley: Univ. of California Press.

Govaerts, R., Frodin, D.G., Radcliffe-Smith, A. 2000. World Checklist and Bibliography of Euphorbiaceae. 4 vols. Kew: Royal Botanic Gardens.

Gruas-Cavagnetto, C., Köhler, E. 1992. Pollen fossiles d'Euphorbiacées français. Grana 31: 291–304.

Hakki, M.I. 1985. Studies on West Indian plants 3. On floral morphology, anatomy, and relationships of *Picrodendron baccatum* (L.) Krug & Urban (Euphorbiaceae). Bot. Jahrb. Syst. 107: 379–394.

Hallé, F. 1971. Architecture and growth of tropical trees exemplified by the Euphorbiaceae. Biotropica 3: 56–62.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B. 1978. Tropical trees and forests: an architectural analysis. Berlin: Springer.

Hans, A.S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hayden, W.J. 1994. Systematic anatomy of Euphorbiaceae subfamily Oldfieldioidae. I. Overview. Ann. Missouri Bot. Gard. 81: 180–202.

Hayden, W.C., Hayden, S.M. 2000. Wood anatomy of Acalyphoideae (Euphorbiaceae). IAWA J. 21: 213–235.

Hayden, W.J. , Gillis, W.T., Stone, D.E., Broome, C.R., Webster, G.L. 1984. Systematics and palynology of *Picrodendron*: further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arb. 65: 105–127.

Hegnauer, R. 1966, 1989. See General References.

Herbert, H. 1897. Anatomische Untersuchung von Blatt und Axe der Hippomaneen. Dissertation: Munich.

Hickey, L.J. 1983. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–32.

Hickey, L.J., Wolfe, J.A. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hoang Van Sam, van Welzen, P.C. 2004. Revision of *Annesijoa*, *Elateriospermum*, and the introduction of species of *Hevea* in Malesia. Blumea 49: 425–440.

Hoffmann, P. 2008. Revision of *Heterosavia*, with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). Brittonia 60: 136–166.

Hoffmann, P., McPherson, G. 2007. Revision of *Wielandia*, including *Blotia* and *Petalodiscus* (Phyllanthaceae; Euphorbiaceae s.l.). Ann. Missouri Bot. Gard. 94: 519–553.

Hoffmann, P., Wurdack, K.J. 2006. *Radcliffea*, a new genus of Euphorbiaceae sensu stricto from Madagascar. Kew Bull. 61: 193–197.

Hoppe, J.R. 1985. Die Morphologie der Cyathiendrüsen und ihrer Anhänge, ihre blattypologische Deutung und Bedeutung. Bot. Jahrb. Syst. 105: 497–581.

Hoppe, J., Uhlarz, H. 1982. Morphogenese und typologische Interpretation des Cyathiums von *Euphorbia*-Arten. Beitr. Biol. Pflanzen 56: 63–98.

Horn, J.W., van Ee, B.W., Morawetz, J.J., Riina, R., Steinmann, V., Berry, P.E., Wurdack, K.J. 2012. Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). Mol. Phylogen. Evol. 63: 305–326.

Hurusawa, I. 1954. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Bot. 6: 209–342.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Jablonski, E. 1967. Euphorbiaceae. Botany of Guayana Highland—Part VII. Mem. New York Bot. Gard. 17: 80–190.

Jennings, D.L. 1963. Variation in pollen and ovule fertility in varieties of cassava, and the effect of interspecific crossing on fertility. Euphytica 12: 69–76.

Jones, K., Smith, J.B. 1969. The chromosome identity of *Monadenium* Pax and *Synadenium* Pax (Euphorbiaceae). Kew Bull. 23: 491–493.

Jussieu, A. 1824. De Euphorbiacearum generibus medicisque earumdem tentamen. Paris: Didot.

Kapil, R.N., Bhatnagar, A.K. 1972. Endosperm in Euphorbiaceae—a critical appraisal. Pp. 376–393. In: Murty, Y.S., Johri, B.M., Mohan Ram, H.Y., Verghese, T.M. (eds.) Advances in Plant Morphology. Meerut: Rustogi Publs.

Kapil, R.N., Bhatnagar, A.K. 1994. The contribution of embryology to the systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 145–159.

Kathriarachchi, H., Samuel, R., Hoffmann, P., Mlinarec, J. Wurdack, K.J., Ralimanana, H., Stuessy, T. F., Chase, M.W. 2006. Phylogenetics of tribe Phyllantheae (Phyllanthaceae; Euphorbiaceae sensu lato) based on *nr*ITS and plastid *mat*K DNA sequence data. Amer. J. Bot. 93: 637–655.

Kathriarachchi, H., Hoffmann, P., Samuel, R., Wurdack, K.J., Chase, M.W. 2005. Molecular phylogenetics of Phyllanthaceae inferred from five genes (plastid *atpB*, *matK*, 3'*ndhF*, *rbcL*, and nuclear *PHYC*). Mol. Phylogen. Evol. 36: 112–134.

Kato, M., Takimura, A., Kawakita, A. 2003. An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). Proc. Natl. Acad. Sci. USA 100: 5264–5267.

Kawakita, A. 2010. Evolution of obligate pollination mutualism in the tribe Phyllantheae (Phyllanthaceae). Plant Sp. Biol. 25: 3–19.

Kawakita, A., Kato, M. 2004a. Obligate pollination mutualism in *Breynia* (Phyllanthaceae); further documentation of pollination mutualism involving *Epicephala* moths (Gracillariidae). Amer. J. Bot. 91: 1319–1325.

Kawakita, A., Kato, M. 2004b. Evolution of obligate pollination mutualism in New Caledonian *Phyllanthus* (Euphorbiaceae). Amer. J. Bot. 91: 410–415.

Kinghorn, A.D. 1979. Carcinognic irritant Euphorbiaceae. In: Kinghorn, A.D. (ed.) Toxic plants, pp. 137–159. New York: Columbia Univ. Press.

Kite, G.C., Fellows, L.E., Lees, D.C., Kitchen, D., Monteith, G.B. 1991. Alkaloidal glycosidase inhibitors in diurnal Uraniine moths and their respective foodplant genera *Endospermum* and *Omphalea*. Biochem. Syst. Ecol. 19: 441–445.

Klucking, E.P. 1997. Leaf Venation Patterns, vol. 8, Euphorbiaceae Part I: Phyllanthoideae and Oldfieldioideae. Berlin: J. Cramer.

Klucking, F.P. 2003. Leaf Venation Patterns, vol. 9, Euphorbiaceae Part II: Acalyphoideae, Crotonoideae, and Euphorbioideae. Berlin: J. Cramer.

Köhler, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palyn. 6: 26–120.

Korbecka, G., Hamilton, A., Pannell, J.R. 2011. Mixed mating in androdioecious *Mercurialis annua* inferred using progeny arrays and diploid-acting microsatellite loci in a hexaploid background. Ann. Bot. 107: 1057–1061.

Korotkova, N. et al. 2009. See General References.

Koutnik, D.L. 1987. A taxonomic revision of the Hawaiian species of the genus *Chamaesyce* (Euphorbiaceae). Allertonia 4: 331–388.

Krähenbühl, M., Yuan, Y.-M., Küpfer, P. 2002. Chromosome and breeding system evolution of the genus *Mercurialis* (Euphorbiaceae): implications of ITS molecular phylogeny. Plant Syst. Evol. 234: 155–169.

Kruijt, R.C. 1996. A taxonomic monograph of *Sapium* Jacq., *Anomostachys* (Baill.) Hurus., *Duvigneudia* J. Léonard and *Sclerocroton* Hochst. (Euphorbiaceae tribe Hippomaneae). Bibl. Bot. 146: 1–109.

Kulju, K.K.M., van der Ham, W.J.M., Breteler, F.J. 2008. Rediscovery and phylogenetic position of the incertae sedis genus *Afrotrewia* (Euphorbiaceae): morphological, pollen and molecular evidence. Taxon 57: 137–143.

Lees, D.C., Smith, N.G. 1991. Foodplant associations of the Uraniinae (Uraniidae) and their systematic, evolutionary, and ecological signficance. J. Lepidopt. Soc. 45: 296–347.

Léonard, J. 1962. Euphorbiaceae. Fl. Congo & Rwanda-Burundi 8(1): 1–214.

Léonard, J. 1989. Révision du genre africain *Martretia* Beille (Euphorbiaceae) et la nouvelle tribu des Martretieae. Bull. Jard. Bot. Nat. Belg. 59: 319–332.

Léonard, J. 1995. Euphorbiaceae, Fl. Afr. Centr. 8(2): 1–115.

Léonard, J. 1996. Euphorbiaceae, Fl. Afr. Centr. 8(3): 1–74.

Léonard, J., Mosongo, M. 1985. Hymenocardiaceae. Fl. Afrique Centrale.

Leroy, J.-F. 1976. Recherches sur la nature et l'origine de la fleur angiospermienne: interprétation des structures dans un groupe singulier d'Euphorbiaceae. Compt. Rend. Séanc. Acad. Paris, Sér. D, 283: 147–150.

Levin, G.A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae), I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

Levin, G.A. 1986b. Systematic foliar morphology of Phyllanthoideae III. Cladistic analysis. Syst. Bot. 11: 515–530.

Levin, G.A. 1992. Systematics of *Paradrypetes* (Euphorbiaceae). Syst. Bot. 17: 74–83.

Levin, G.A., Simpson, M.G. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae

(Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 239–244.

Li, Y., Dressler, S., Zhang, D., Renner, S.S. 2009. More Miocene dispersal between Africa and Asia—the case of *Bridelia* (Phyllanthaceae). Syst. Bot. 34: 521–529.

Lisci, M., Bianchini, M., Pacini, E. 1996. Structure and function of the elaiosome in some angiosperm species. Flora 191: 131–141.

Lobreau-Callen, D., Suarez Cervera, M. 1997. Le pollen des Crotonoideae Apétales (Euphorbiaceae): Ultrastructure de l'exine. Rev. Palaeobot. Palynol. 98: 257–291.

Lobreau-Callen, D., Pons, D., Malécot, V. 2001. Pollen aperturé des Crotonoideae apétales actuelles et fossiles. Contr. to Geol. and Palaeontol. of Gondwana in honour of H. Wopfner, pp. 303–323. Cologne.

Lock, J.M., Hall, J.B. 1982. Floral biology of *Mallotus oppositifolius* (Euphorbiaceae). Biotropica 14: 153–155.

Luo, S., Zhang, D., Renner, S.S. 2007. Duodichogamy and androdioecy in the Chinese Phyllanthaceae *Bridelia tomentosa*. Amer. J. Bot. 94: 260–265.

Maedel, E. 1962. Die fossilen Euphorbiaceen-Hölzer mit besonderer Berücksichtigung neuer Funde aus der Oberkreide Süd-Afrikas. Senckenbergiana leth. 43: 283–321.

Mahlberg, P.G. 1975. Evolution of the laticifer in *Euphorbia* as interpreted from starch grain morphology. Amer. J. Bot. 62: 577–583.

Mansfeld, R. 1928. Beitrag zur Morphologie des *Euphorbia*-Cyathiums. Ber. Deutsch. Bot. Ges. 46: 674–677.

Martin, H.A. 1974. The identification of some Tertiary pollen belonging to the family Euphorbiaceae. Austral. J. Bot. 22: 271–291.

Martin, H.A. 1978. Evolution of the Australian flora and vegetation through the Tertiary: evidence from pollen. Alcheringa 2: 181–202.

Matthews, M.L., Endress, P.K. 2011. See General References.

Mazer, S.J., Tiffney, B.H. 1982. Fruits of *Wetherellia* and *Paleowetherellia* (? Euphorbiaceae) from Eocene sediments in Virginia and Maryland. Brittonia 34: 300–333.

McPherson, G., Tirel, C. 1987. Euphorbiacées. Fl. Nouv. Caléd. 14(1): 1–226.

Meeuse, A.D.J. 1990. The Euphorbiaceae auct. plur.: an unnatural taxon. Delft: Eburon.

Meeuse, A.D.J., Vinkenoog, S., Vroege, P.W. 1989. Anthecology of *Euphorbia*—preliminary studies. Acta Bot. neerl. 38: 493–502.

Meewis, B., Punt, W. 1983. Pollen morphology and taxonomy of the subgenus *Kirganelia* (Jussieu) Webster (genus *Phyllanthus*, Euphorbiaceae) from Africa. Rev. Palaeobot. Palynol. 39: 131–160.

Mennega, A.M.W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily. Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.

Merino Sutter, D., Forster, P.I., Endress, P.K. 2006. Female flowers and systematic position of Picrodendraceae (Euphorbiaceae s.l., Malpighiales). Pl. Syst. Evol. 261: 187–215.

Metcalfe, C.R., Chalk, L. 1950. Anatomy of the Dicotyledons. Oxford: Clarendon Press.

Michaelis, P. 1924. Blütenmorphologische Untersuchungen an den Euphorbiaceen. Bot. Abh. Jena 3: 1–150.

Moog, U., Fiala, B., Federle, W., Maschwitz, U. 2002. Thrips pollination of the dioecious ant plant *Macaranga hullettii* (Euphorbiaceae) in southeast Asia. Amer. J. Bot. 89: 50–59.

Muller, J. 1984. Significance of fossil pollen for angiosperm history. Ann. Missouri Bot. Gard. 72: 419–443.

Müller, J. 1866. Euphorbiaceae [except Euphorbieae]. DC. Prodr. 15(2): 189–1261.

Müller, J. 1873–1874. Euphorbiaceae. In: Martius, Fl. Brasiliensis 11(2): 1–750. Leipzig: Fleischer.

Narbona, E., Ortiz, P.L., Arista, M. 2002. Functional andromonoecy in *Euphorbia* (Euphorbiaceae). Ann. Bot. 89: 571–577.

Netolitzky, F. 1926. See General References.

Neuwinger, H.D. 2000.African traditional medicine: a dictionary of plant use and application. Stuttgart (Germany): Medpharm Scientific.

Nowicke, J.W. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.

Nowicke, J.W., Takahashi, M. 2002. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 4. Rev. Palaeobot. Palynol. 121: 231–336.

Nowicke, J.W., Takahashi, M., Webster, G.L. 1998. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 1. Rev. Palaeobot. Palynol. 102: 115–152.

Nowicke, J.W., Takahashi, M., Webster, G.L. 1999. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae), Part 2. Rev. Palaeobot. Palynol.105: 1–62.

Olmos, F., Boulhosa, R.L.P. 2000. A meeting of opportunists: birds and other visitors to *Mabea fistulifera* (Euphorbiaceae) inflorescences. Ararajuba 8: 93–98.

Pax, F. 1884. Die Anatomie der Euphorbiaceen in ihrer Beziehung zum System derselben. Bot. Jahrb. 5: 384–421.

Pax, F. 1890. Euphorbiaceae. In: Engler, K., Prantl, K. (eds.) Die natürl. Pflanzenfam. III, 5: 1–119. Leipzig: W. Engelmann.

Pax, F. 1924. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. Syst. 59: 129–182.

Pax, F., Hoffmann, K. 1912. Euphorbiaceae—Hippomaneae. Das Pflanzenreich, IV, 147. V: 1–319.

Pax, F., Hoffmann, K. 1919 Euphorbiaceae-Acalypheae-Plukenetiinae, Epiprininae, and Ricininae, in: Engler, A., Das Pflanzenreich, IV 147, IX, X, XI, Heft 68.

Pax, F., Hoffmann, K. 1931. Euphorbiaceae. In: Engler, K., Prantl, K. (eds.) Die natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233. Leipzig: W. Engelmann.

Perkins, G., Estes, J.R., Thorp, R.W. 1975. Pollination of *Cnidoscolus texanus* (Euphorbiaceae) in south-central Oklahoma. Southw. Nat. 20: 391–396.

Ponsinet, G., Ourisson, G. 1965. Étude chimiotaxonomique dans la famille des euphorbiacées—I. Phytochemistry 4: 799–811.

Prenner, G., Rudall, P.J. 2007. Comparative ontogeny of the cyathium in *Euphorbia* (Euphorbiaceae) and its allies: exploring the organ-flower-inflorescence boundary. Amer. J. Bot. 94: 1612–1629.

Prenner, G., Hopper, S.D., Rudall, P.J. 2008. Pseudanthium development in *Calycopeplus paucifolius*, with particular reference to the evolution of the cyathium in Euphorbieae (Euphorbiaceae-Malpighiales). Austr. J. Bot. 21: 153–161.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

Punt, W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Bot. J. Linn. Soc. 94: 127–142.

Radcliffe-Smith, A. 1987. Segregate families from the Euphorbiaceae. Bot. J. Linn. Soc. 94: 47–66.

Radcliffe-Smith, A. 1996. Euphorbiaceae, Pt. 1. In: Flora Zambesiaca 9(4): 1–337. Kew: Royal Botanic Gardens.

Radcliffe-Smith, A. 1997. Flora of tropical East Africa. Euphorbiaceae (Pt. 1). Rotterdam/Boston: A.A. Balkema.

Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Kew: Royal Botanic Gardens.

Reddi, E.U.B., Subba-Reddi, C. 1983. Pollination ecology of *Jatropha gossypifolia* (Euphorbiaceae). Proc. Indian Acad. Sci. (Plant Sci) 92: 215–231.

Reveal, J.L. 1995 onward. Index nominum supragenicorum plantarum vascularium. http://www.life.umd.edu/emeritus/reveal/pbio/WWW/supragen.html

Ridley, N.H. 1930. The dispersal of plants throughout the world. Ashford: Reeve.

Riina, R., van Ee, B., Wiedenhoeft, A.C., Cardozo, A., Berry, P.E. 2010. Sectional rearrangement of arborescent clades of *Croton* (Euphorbiaceae) in South America: evolution of arillate seeds and a new species, *Croton domatifer*. Taxon 59: 1147–1160.

Rittershausen, P. 1892. Anatomisch-systematische Untersuchung von Blatt und Axe der Acalypheen. Inaugur.-Diss., Munich.

Rizk, A.M. 1987. The chemical constituents and economic plants of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 292–326.

Rossignol, L., Rossignol, M. 1985. Architecture et tendences évolutives dans le genre *Phyllanthus* (Euphorbiaceeae). Bull. Mus. Nat. Hist. Nat. IV. 7: 67–80.

Rothdauscher, H. 1896. Über die anatomischen Verhältnisse von Blatt und Axe der Phyllantheen (mit Ausschluss der Euphyllantheen). Inaug.-Diss., Cassel (also publ. in Bot. Centralbl. 68).

Roux, J. 1968. Sur le comportement des axes aériens chez quelques plantes à rameaux végétatifs polymorphes; le concept des rameaus plagiotropes. Ann. Sci. Nat. Bot. XII. 9: 109–256.

Rudall, P.J. 1987. Laticifers in the Euphorbiaceae—a conspectus. Bot. J. Linn. Soc. 94: 143–163.

Rudall, P.J. 1994. Laticifers in Crotonoideae (Euphorbiaceae): homology and evolution. Ann. Missouri Bot. Gard. 81: 270–282.

Sagun, V.G., van der Ham, R.W.J.M. 2003. Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). Grana 42: 193–219.

Sahagún-Godiñez, E., Lomelí-Sención, J.A. 1997. *Pedilanthus diazlunanus* (Euphorbiaceae): pollination by hymenopterans in a bird-pollinated genus. Amer. J. Bot. 84: 1584–1587.

Samuel, R., Kathriarachchi, H., Hoffmann, P., Barfuss, M. H.J., Wurdack, K.J., Davis, C.C., Chase, M.W. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plastid *mat*K and nuclear PHYC sequences. Amer. J. Bot. 92: 132–141.

Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Weston, P., Whitten, M., Wurdack, K.J., Chase, M.W. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull.55: 257–309.

Sazima, M., Sazima, I., de Carvalho-Okano, R.M. 1985. Biologia floral de *Dalechampia stipulacea* (Euphorbiacaea) e sua polinização por *Euglossa melanotricha* (Apidae). Rev. Bras. Biol. 45: 85–93.

Schatz, G.E. 2001. Generic Tree Flora of Madagascar. Kew, Royal Botanic Gardens and Missouri Botanical Garden.

Schultes, R. 1952. Studies in the genus *Micrandra* I. The relationship of the genus *Cunuria* to *Micrandra*. Bot. Mus. Leafl. Harvard Univ. 15: 201–222.

Schultes, R. 1970. The history of taxonomic studies in *Hevea*. Bot. Rev. 36: 197–276.

Schultes, R.E. 1987. Members of Euphorbiaceae in primitive and advanced societies. Bot. J. Linn. Soc. 94: 79–95.

Secco, R. 1989. Dialissepalia do gênero *Sandwithia* Lanjouw: Uma novidade botânica do alto Rio Negro e da Venezuela. Bol. Mus. Paraense Emilio Goeldi, n.s., Bot. 4: 177–185.

Secco, R. 1990. Revisão dos gêneros *Anomalocalyx* Ducke, *Pausandra* Radlk., *Pogonophora* Miers ex Benth. e *Sagotia* Baill. (Euphorbiaceae-Crotonoideae) para a América do Sul. Belém: Museu Paraense Emílio Goeldi.

Seigler, D.S. 1994. Phytochemistry and systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 380–401.

Simpson, M.G., Levin, G.A. 1994. Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Plant Sci. 155: 313–341.

Slik, J.W.F. 2001. *Macaranga* and *Mallotus* (Euphorbiaceae) as indicators for disturbance in the lowland Dipterocarp forests of east Kalimantan, Indonesia. Wageningen: The Tropenbos Foundation.

Solereder, H. 1908. Systematische Anatomie der Dicotylen. Ergänzungsband. Stuttgart: Enke.

Soltis, D.E. et al. 2011. See General References.

Steiner, K.E. 1981. Nectarivory and potential pollination by a Neotropical marsupial. Ann. Missouri Bot. Gard. 68: 505–513.

Steiner, K.E. 1982. Mistake pollination of *Hura crepitans* (Euphorbiaceae) by frugivorous bats. Doctoral dissert., University of California, Davis.

Steiner, K.E. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Syst. Bot. 8: 105–117.

Steinmann, V.W. 2003. The submersion of *Pedilanthus* into *Euphorbia* (Euphorbiaceae). Acta Bot. Mexic. 65: 45–60.

Steinmann, V.W., van Ee, B., Berry, P.E., Gutiérrez, J. 2007. The systematic position of *Cubanthus* and other shrubby endemic species of *Euphorbia* (Euphorbiaceae) in Cuba. Ann. Jard. Bot. Madrid 64: 123–133.

Steinmann, V.W., Porter, J.M. 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and *ndh*F sequence data. Ann. Missouri Bot. Gard. 89: 453–490.

Stuppy, W. 1996. Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Dissert., Univ. Kaiserslautern.

Suárez-Cervera, M., Gillspie, L., Arcalis, E., Le Thomas, A., Lobreau-Callen, D., Seoane-Camba, J.A. 2001. Taxonomic significance of sporoderm structure in pollen of Euphorbiaceae: tribes Plukenetieae and Euphorbieae. Grana 40: 78–104.

Subba-Reddi, C., Reddi, E.U.B. 1984. Wind-pollination in two tropical tree species of Euphorbiaceae. Proc. Indian Natn. Sci. Acad. B 50: 66–80.

Sutter, K., Endress, P.K. 1995. Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. Bot. Jahrb. Syst. 116: 517–536.

Swaine, M.D., Beer, T. 1976. Explosive seed dispersal in *Hura crepitans* (Euphorbiaceae). New Phytol. 78: 695–708.

Takahashi, M., Nowicke, J.W., Webster, G.L. 1995. A note on remarkable exines in Acalyphoideae. Grana 34: 282–290.

Takahashi, M., Nowicke, J.W., Webster, G.L., Orli, S.S., Yankowski, S. 2000. Pollen morphology, exine structure, and systematics of Acalyphoideae (Euphorbiaceae), part 3. Rev. Palaeobot. Palynol. 110: 1–66.

Thin, N.N. 1995. Euphorbiaceae of Vietnam. Hanoi: Publishing House "Agriculture".

Thurston, E.L. 1976. Morphology, fine structure and ontogeny of the stinging emergences of *Tragia ramosa* and *T. saxicola* (Euphorbiaceae). Amer. J. Bot. 63: 710–718.

Thurston, E.L., Lersten, N.R. 1969. The morphology and toxicology of plant stinging hairs. Bot. Rev. 35: 393–412.

Tokuoka, T. 2007. Molecular phylogenetic analysis of Euphorbiaceae sensu stricto based on plastid and nuclear DNA sequences and ovule and seed character evolution. J. Plant Res. 120: 511–522.

Tokuoka, T., Tobe, H. 1995. Embryology and systematics of Euphorbiaceae sens. lat.: a review and perspective. J. Plant Res. 108: 97–106.

Tokuoka, T., Tobe, H. 1998. Ovules and seeds in Crotonoideae (Euphorbiaceae): structure and systematic implications. Bot. Jahrb. Syst. 120: 165–186.

Tokuoka, T., Tobe, H. 1999. Embryology of tribe Drypeteae, an enigmatic taxon of Euphorbiaceae. Pl. Syst. Evol. 215: 189–208.

Tokuoka, T., Tobe, H. 2001. Ovules and seeds in subfamily Phyllanthoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 114: 75–92.

Tokuoka, T., Tobe, H. 2002. Ovules and seeds in subfamily Euphorbioideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 115:361–374.

Tokuoka, T., Tobe, H. 2003. Ovules and seeds in Acalyphoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 116: 355–380.

Tokuoka, T., Tobe, H. 2006. Phylogenetic analyses of Malpighiales using plastid and nuclear DNA sequences, with particular reference to the embryology of Euphorbiaceae sens. str. J. Plant Res. 119: 599–616.

Torres de Assumpção, C. 1981. *Cebus apella* and *Brachyteles arachnoides* (Cebidae) as potential pollinators of *Mabea fistulifera* (Euphorbiaceae). J. Mamm. 62: 386–388.

Uhlarz, H. 1974. Entwicklungsgeschichtliche Untersuchungen zur Morphologie der basalen Blatteffigurationen sukkulenter Euphorbien aus den Subsektionen Diacanthium Boiss. und Goniostema Baill. Trop. Subtrop. Pflanzenwelt 9: 575–639.

Uhlarz, H. 1978. Ueber die Stipularorgane der Euphorbiaceae, unter besonderer Berucksichtigung ihrer Rudimentation. Trop. Subtrop. Pflanzenwelt 23: 1–65.

Urbatsch, L.E., Bacon, J.D., Hartman, R.L., Johnston, M. C., Watson Jr., T.J., Webster, G.L. 1975. Chromosome numbers for North American Euphorbiaceae. Amer. J. Bot. 62: 494–500.

van Ee, B.W., Berry, P.E., Riina, R., Gutiérrez-Amaro, J.E. 2008. Molecular phylogenetics and biogeography of the Caribbean-centered *Croton* subgenus *Macrocroton* (Euphorbiaceae). Bot. Rev. 74: 132–165.

Venkata Rao, C. 1971. Anatomy of the inflorescence of some Euphorbiaceae. Adv. Pl. Morphol. 1972: 85–91.

Venkata Rao, C., Ramalakshmi, T. 1968. Floral anatomy of the Euphorbiaceae—I. Some non-cyathium taxa. J. Indian Bot. Soc. 47: 219–235.

Vieira, M.F., Carvalho-Okano, R.M. de 1996. Pollination biology of *Mabea fistulifera* (Euphorbiaceae) in southeastern Brazil. Biotropica 28: 61–68.

Vogel, C. 1986. Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae; Beiträge zur infrafamiliären Gliederung und zu Beziehungen im extrafamiliären Bereich. Dissert. Bot. 98: 1–124.

Vorontsova, M.S., Hoffmann, P., Maurin, O., Chase, M. W., 2007. Molecular phylogenetics of tribe Porantheraeae (Phyllanthaceae; Euphorbiaceae sensu lato). Amer. J. Bot. 94: 2026–2040.

Warmke, H.E. 1952. Studies on natural pollination of *Hevea brasiliensis* in Brazil. Science 116: 474, 475.

Webster, G.L. 1956. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 37: 91–122, 217–268, 340–359.

Webster, G.L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arb. 48: 303–430.

Webster, G.L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

Webster, G.L. 1986. Irritant plants in the spurge family (Euphorbiaceae). Clinics Dermatol. 4: 36–45.

Webster, G.L. 1987. The saga of the spurges: a review of the classification and relationships of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 3–46.

Webster, G.L. 1993. A provisional synopsis of the sections of the genus *Croton* (Euphorbiaceae). Taxon 42: 793–823.

Webster, G.L. 1994a. Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 3–32.

Webster, G.L. 1994b. Synopsis of the genera and suprageneric taxa of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

Webster, G.L. 2002. A synopsis of the Brazilian taxa of *Phyllanthus* section *Phyllanthus* (Euphorbiaceae). Lundellia 5: 1–26.

Webster, G.L., Armbruster, W.S. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). Bot. J. Linn. Soc. London 105: 137–177.

Webster, G.L., Carpenter, K. 2002. Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae). Bot. J. Linn. Soc. 138: 325–338.

Webster, G.L., Rupert, E. 1973. Phylogenetic significance of pollen nuclear number in Euphorbiaceae. Evolution 27: 524–531.

Webster, G.L., Brown, W.V., Smith, B.N. 1975. Systematics of phytosynthetic carbon fixation in *Euphorbia*. Taxon 24: 27–33.

Webster, G.L., Rupert, E., Koutnik, D. 1982. Systematic significance of pollen nuclear number in Euphorbiaceae, tribe Euphorbieae. Amer. J. Bot. 69: 407–415.

Welkie, G.W., Caldwell, L. 1970. Leaf anatomy of species in some dicotyledon plant families as related to the C3 and C4 pathways of carbon fixation. Can. J. Bot. 48: 2135–2146.

Welzen, P.C. van. 1995. Taxonomy and phylogeny of the Euphorbiaceae tribe Erismantheae G. L. Webster (*Ersimanthus*, *Moutonianthus*, and *Syndyophyllum*). Blumea 40: 375–396.

Welzen, P.C. van. 1999. Revision and phylogeny of subtribes Chrozophorinae and Dorylinae (Euphorbiaceae) in Malesia and Thailand. Blumea 44: 411–436.

Welzen, P.C. van, Bulalacao, L.J., Ôn, T.V. 1995. A taxonomic revision of the Malesian genus *Trigonopleura* Hook. f. (Euphorbiaceae). Blumea 40: 363–374.

Welzen, P.C. van, Stuppy, W. 1999. Phylogenetic considerations of Euphorbiaceae tribe Aleuritidae. Ann. Missouri Bot. Gard. 86: 894–903.

Wheeler, L.C. 1943. The genera of living Euphorbieae. Amer. Midl. Nat. 3: 456–503.

Wunderlich, R. 1968. Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 301–311.

Wurdack, K.J. 2002. The molecular systematics and evolution of Euphorbiaceae *sensu lato*. Doct. dissert., Univ. North Carolina at Chapel Hill. Chapel Hill. UMI number 3047094.

Wurdack, K.J., Chase, M.W. 1999. Spurges split: molecular systematics and changing concepts of Euphorbiaceae. Abstr. XVI Int. Bot. Congress 142.

Wurdack, K.J., Davis, C.C. 2009. Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. Amer. J. Bot. 96: 1551–1570.

Wurdack, K.J., Hoffmann, P., Samuel, R., de Bruijn, A., van der Bank, M., Chase, M.W. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid *rbc*L DNA sequences. Amer. J. Bot. 91: 1882–1900.

Wurdack, K.J., Hoffmann, P., Chase, M.W. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbc*L and *trn*L-F DNA sequences. Amer. J. Bot. 92: 1397–1420.

Xi, Z. et al. 2012. See General References.

Yang, Y., Riina, R., Morawetz, J.J., Haevermans, T., Aubriot, X., Berry, P.E. 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). Taxon 61: 764–789.

Zimmermann, N.F.A., Ritz, C.M., Hellwig, F.H. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and *trnL-trnF* IGS sequence data. Plant Syst. Evol. 286: 39–58.

Euphroniaceae

Euphroniaceae Marcano-Berti in Pittiera 18: 16 (1989).

K. KUBITZKI

Medium-sized savannah trees or shrubs with conspicuous arachnoid tomentum of unicellular hairs; branches terete, lanuginose, glabrescent. Leaves alternate, simple, entire or revolute, pinnately veined; stipules minute, caducous. Inflorescences terminal and subterminal racemes or thyrses; bracts minute; prophylls 0. Flowers bisexual, perigynous, obliquely monosymmetric; calyx with 5 subequal, imbricate sepals connate at the base and inserted on a campanulate or campanulate-turbinate cup, the two outer sepals shorter and narrower than the inner ones, the inner surface of the floral cup lined by a smooth unlobed nectary; petals 3, distinct, all of same size, contorted in bud, unguiculate; androecium with a large anterior pointed staminode with sterile anther flanked by two stamen pairs and two posterior groups of 2–3 tooth-like staminodes; each stamen pair with a longer outer antesepalous stamen and a shorter inner antepetalous stamen, these fused with the dilated bases of their filaments; anthers dorsifixed, dithecal, slightly apiculate, introrse, dehiscing with longitudinal slits; filaments of fertile stamens apically glabrous, of the large staminode retrorsely pilose throughout; gynoecium posteriorly positioned, syncarpous; ovary partly inferior, 3-locular; ovules apotropous, bitegmic, incompletely tenuinucellar, 2 per locule, axile, nearly collateral but one pendant, the other erect and shorter; style antrorsely pilose; stigma capitate. Fruit a 3-valved capsule with fleshy exocarp and persisting calyx and androecium, dehiscing septicidally from apex towards base. Seeds 1 per locule, with thin endosperm, slightly winged.

A single genus comprising 3 spp., distributed on white sand savannahs and heath forests in northern South America (Brazil, Venezuela).

ANATOMY. Year rings obvious; vessels solitary, with simple perforations and alternate intervascular pitting; wood parenchyma paratracheal-aliform; rays uniseriate and biseriate, heterocellular Type II and III, containing gum; fibre tracheids thick-walled, non-septate (Espinoza de Pernia 1989). The indumentum consists of unicellular lignified and unlignified hairs, the latter dense and woolly, and oxalate druses and tanniniferous tissue is found in all floral parts (Matthews and Endress 2008).

FLOWER STRUCTURE. The turbinate-campanulate floral tube seems to be glandular inside and may secrete nectar (Marcano-Berti 1989). The fertile stamens appear to belong to two different cycles. The ovules are bitegmic, incompletely tenuinucellar, anatropous and apotropous. The obliquely monosymmetric floral plan fits well with that of related families (Chrysobalanaceae, Dichapetalaceae, Trigoniaceae; see Matthews and Endress 2008, the INTRODUCTION TO MALPIGHIALES, and Fig. 48).

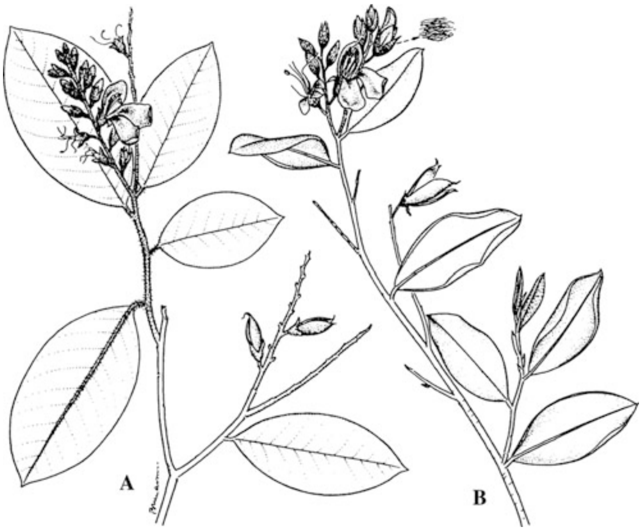

Fig. 48. Euphroniaceae. **A** *Euphronia hirtelloides*. **B** *E. acuminatissima*. (Steyermark & Marcano Berti 1999; drawn by Bruno Manara)

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_11, © Springer-Verlag Berlin Heidelberg 2014

POLLEN MORPHOLOGY. The pollen of *Euphronia* is tricolporate-oblate with a triangular amb and a rugulate exine (Lleras 1976).

AFFINITIES. Originally placed in Rosaceae or Vochysiaceae, more recently the genus has been considered a member of Trigoniaceae. Lleras (1976, 1978) recognised some differences between *Euphronia* and Trigoniaceae and, in spite of the lack of a well-developed spur in *Euphronia*, opted for its vochysiaceous affinity. Although both Trigoniaceae and Vochysiaceae traditionally were included in the order Polygalales, molecular studies did not confirm a link between them. Litt and Chase (1999) provided strong support for a clade of *Euphronia* + Chrysobalanaceae sister to Dichapetalaceae + Trigoniaceae, a relationship that since has been confirmed by several multigene analyses and the comparative floral morphological study by Matthews and Endress (2008).

Thus, the notion of Marcano-Berti (1989), who had disagreed with the view of Lleras, is fully justified.

A single genus:

Euphronia Mart. Fig. 48

Euphronia Mart. ex Mart. & Zucc., Flora 8: 32 (1825); Steyermark, Ann. Missouri Bot. Gard. 74: 89–94 (1987); Steyermark & Marcano-Berti, Fl. Venezuel. Guayana 5: 228–230 (1999). *Lightia* Schomb., Linnaea 20: 753 (1847).

Characters as for family.

Selected Bibliography

Espinosa de Pernia, N. 1989. Estudio xilologico del genero *Euphronia*. Pittieria 18: 57–61.

Litt, A., Chase, M.W. 1999. The systematic position of *Euphronia*, with comments on the position of *Balanops*: an analysis based on *rbc*L sequence data. Syst. Bot. 23: 401–409.

Lleras, E. 1976. Revision and taxonomic position of the genus *Euphronia* Martius ex Martius & Zuccarini (Vochysiaceae). Acta Amazonica 6: 43–47.

Lleras, E. 1978. Trigoniaceae. Flora Neotropica Monograph 19: 1–73.

Marcano-Berti, L. 1989. Euphroniaceae: una nueva familia. Pittieria 18: 15–19.

Matthews, M.L., Endress, P.K. 2008. Comparative floral structure and systematics in Chrysobalanaceae s. l. (Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, Trigonaceae; Malpighiales). Bot. J. Linn. Soc. 157: 249–309.

Steyermark, J.A., Marcano-Berti, A. 1999. Euphroniaceae. In: Berry, P. et al. (eds.) Flora of the Venezuelan Guayana, vol. 5. St. Louis: Missouri Bot. Gard. Press.

Goupiaceae

Goupiaceae Miers, Ann. Mag. Nat. Hist. III, 9: 292 (1862).

K. KUBITZKI

Evergreen aluminium-accumulating trees. Leaves alternate, distichous, petiolate, subtriplinerved and transversely venose, sometimes domatiiferous; stipules narrow, rather long, caducous. Inflorescence an axillary, umbel-like, pedunculate raceme. Flowers bisexual, regular, (4)5-merous; pedicels slender; bracts short and triangular, hairy; sepals connate, lobes imbricate; petals very long and subulate, concave, induplicate-valvate, the upper third sharply inflexed in bud and sometimes geniculate or sigmoid at anthesis; nectary disk large, cupular, thin-walled, sinuate on the margin; stamens 5, alternating with petals, inserted on the inner edge of the nectary disk, filaments very short, anthers small, ovoid, lengthwise dehiscing, with a thickened and apically setose-pilose connective and ellipsoidal, separate, introrse locules; pollen grains small, 3-colporate; gynoecium syncarpous, partly enclosed by disk but free from it, ovary depressed-globose, 5-locular; stylodia 5, subulate, stellately divergent; stigmas diminutive; ovules several in each locule, basal, axile, ascending. Fruit a small, globose drupe, 1–3-locular, hard. Seeds 1–4 per fruit, erect, obovoid, with axile straight embryo in fleshy endosperm; testa reticulate, pitted inside. $n = ?$

A monogeneric family with four or perhaps five spp. from tropical America.

MORPHOLOGY AND ANATOMY. *Goupia glabra*, the most frequent species, is a vast, buttressed tree corresponding with Roux's architectural model. The upper leaf epidermis is underlain by a hypodermis. Stomata are laterocytic or rarely anisocytic. The palisade tissue is two-layered. The spongy tissue is crossed by branched scelerenchymatous elements and veinlets, the ends of which are in close contact with vesiculose sclereids that do not contain any visible contents (Rao and Bhattacharya 1975). Cork originates superficially. The nodes are unilacunar. The wood contains vasicentric tracheids; vessel perforation is always scalariform with 3–10 thick bars, and the fibres have distinctly bordered pits. The rays are heterogeneous and have elongate ends. The axial parenchyma is apotracheal and paratracheal.

FLOWER STRUCTURE. The following account of the flower structure of *Goupia* reviews the excellent, well-illustrated description given by Miers (1862) and his interpretation. The cup-shaped calyx is deeply divided into five acute lobes that have an imbricate aestivation. The petals are linear-oblong and fleshy and more than six times the length of the calyx. Their straight margins are introflexed and valvate in bud; their appendiciform apices, measuring half their length, are inflected and united together by their valvate margins. At anthesis, the petals become horizontally expanded, with the inflected apices standing erect at right angles with them. The disk forms a notable structure, being nearly the size of the calyx, and has five very short teeth that alternate with the stamens. The five stamens are erect and stand within the disk, free from it as well as from the ovary; their linear connectives extend beyond the anthers and are truncated at their summit, where they are furnished in front with a horizontal tuft of long hairs, whereas their margins, behind the anthers, are ciliated with similar hairs. The anthers are bilobed and introrse, each theca dehiscing by a longitudinal and somewhat oblique fissure. One half of each anther rises above the margin of the disk, and their long apical horizontal tufts of hairs meet in the middle of the ovary, passing between the stylodia and serving as collectors to convey their pollen to them. An illustration of Baillon (1877, p. 10) shows a *Goupia* flower at the beginning of the anthesis, in which the petals not yet spread and the setose hairs at the anther tips are directed

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_12, © Springer-Verlag Berlin Heidelberg 2014

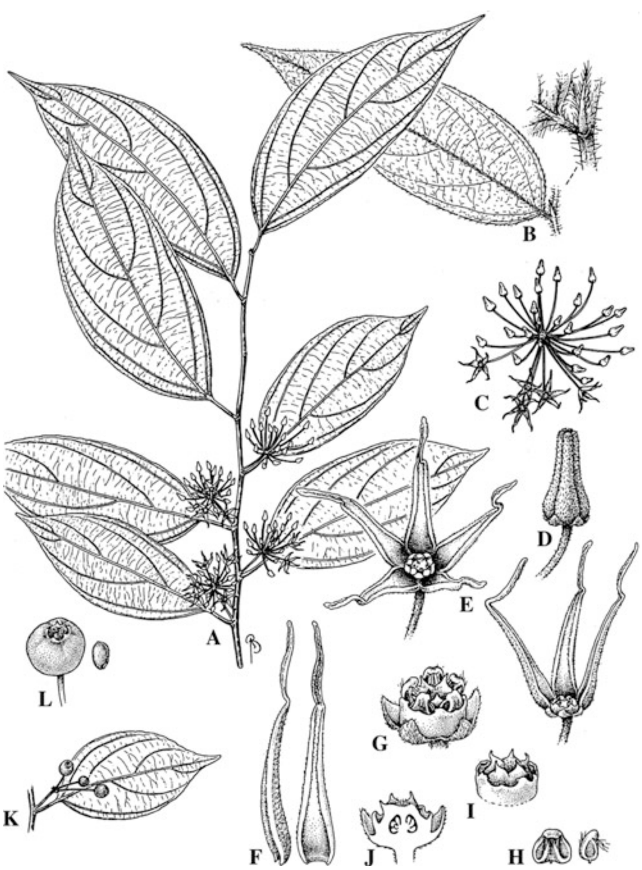

Fig. 49. Goupiaceae. *Goupia glabra*. **A** Flowering branch. **B** Leaf of young plant and stipule. **C** Umbellate inflorescence. **D** Floral bud. **E** Apical (left) and lateral (right, with two petals removed) views of flowers. **F** Petals. **G** Flower, petals removed, nectary disk surrounding the stamens. **H** Adaxial and lateral views of stamens. **I** Nectary disk surrounding pistil with distinct stylodia, petals removed. **J** Same, medial section. **K** Leaf with infructescence. **L** Fruit and seed. (Reproduced with the kind permission of the artist Bobbi Angell)

upwards. This strange floral structure certainly calls for live observations of the floral biology.

POLLEN MORPHOLOGY. The pollen is suboblate, very small (11 x 12–13 µm), and tricolporate, the amb is circular to convex triangular, and both the ectoapertures and the transversal endoapertures are very straight; the ectexine is microreticulate or finely perforate to foveolate (Lobreau-Callen 1977; Furness 2011).

FRUIT AND SEED. The fruits are probably bird-dispersed. The endocarp is heavily sclerified. The testa is about six cells thick and the subepidermal layer is sclerified. The outer epidermis of the tegmen is moderately thickened, but otherwise it is crushed (Melikian and Savinov 2000).

AFFINITIES. Traditionally incorporated in Celastraceae, Miers (1862) raised this aberrant taxon to family rank, whereas Loesener (1892) retained it in Celastraceae as a distinct subfamily. Molecular work (e.g. Simmons et al. 2001) confirmed the exclusion of *Goupia* from Celastraceae, and subsequent work resolved it as member of the broadly circumscribed order Malpighiales, as sister to Achariaceae (Davis et al. 2005), in an unsupported position in the 'parietal clade' (Violaceae/Passifloraceae) (Wurdack and Davis 2009; Soltis et al. 2011), and finally, with moderate support, in a sister position with Violaceae (Xi et al. 2012), with which it shares appendages on the stamen connectives and haplostemony, among other traits, but the differences are significant.

DISTRIBUTION AND HABITATS. *Goupia* is a genus of rain forest trees from northern South America and Central America (Guatemala).

USES. *Goupia glabra* is a frequent and important timber tree in the Guyanas and Pará, Brazil. Its light red-brown wood has a disagreeable smell and has been used in carpentry and for railway sleepers.

A single genus:

Goupia **Aubl.** Fig. 49

Goupia Aubl., Hist. Pl. Gui. 1: 295, tab. 116 (1775); Miers, Contr. Bot. 2: 131–137, t. 74 (1862); Oliver, Ic. Pl. III, 6, t. 1590 (1897).

Description as for family.

Four or perhaps five spp. from northern South and Central America.

Selected Bibliography

Araujo, P.A.M., Filho, A.M. 1973. Estrutura da madeira de *Goupia glabra* Aubl. (Goupiaceae). Arq. Jard. Bot. Rio de Janeiro 19: 149–153.

Baillon, H. 1877. Histoire des plantes, vol. 6. Paris: Hachette.

Davis, C.C. et al. 2005. See General References.

Furness, C.A. 2011. Comparative structure and development of pollen and tapetum in Malpighiales, with a focus on the parietal clade. Int. J. Pl. Sci. 172: 980–1011.

Lobreau-Callen, D. 1977. Les pollen des Celastrales: illustrations, commentaires. École Pratique des Hautes Études, Institut de Montpellier.

Loesener, T. 1892. Celastraceae. In: Engler & Prantl, Nat. Pflanzenfam, III, 5. Leipzig: W. Engelmann, pp. 189–222.

Lundell, C.L. 1986. *Goupia guatemalensis* (Celastraceae), a genus and species new to Mesoamerica. Phytologia 57: 238–239.

Melikian, A.P., Savinov, I.A. 2000. Goupiaceae. In: Takhtajan, A. (ed.) Anatomia seminum comparativa, vol. 6. St. Petersburg: Nauka, pp. 135–136.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Miers, J. 1862. Contributions to Botany 2: 131–137. London, Edinburgh: Williams and Norgate (repr. in Ann. Nat. Mag. Hist. Soc. III, 9: 289).

Rao, T.A., Bhattacharya, J. 1975. On foliar terminal vesiculose sclereids in *Goupia glabra* Aubl. Curr. Sci. 44: 132–134.

Simmons, M.P., Clevinger, C.C., Savolainen, V., Archer, R.H., Mathews, S., Doyle, J.J. 2001. Phylogeny of the Celastraceae inferred from phytochrome B gene sequence and morphology. Am. J. Bot. 88: 313–325.

Soltis, D.E. et al. 2011. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Humiriaceae

Humiriaceae Juss. in St.-Hil., Fl. Bras. mérid. 2: 87 (1827), nom. cons.

K. KUBITZKI

Evergreen trees or shrubs; wood often with balsamic juice; cork subepidermal; indumentum of simple hairs, usually sparse or 0. Leaves alternate, simple, involute, often distichous, penninerved, entire, crenulate or slightly serrate, petiolate or rarely sessile, sometimes decurrent along branches; stipules very small, lateral, caducous or 0. Inflorescences axillary or terminal, paniculate, often corymbiform, dichotomous or trichotomously branched, branchlets often articulate; bracts and prophylls small, amplectant, persistent or caducous. Flowers hermaphroditic, actinomorphic, pedicellate; sepals 5, ± connate, quincuncially arranged or imbricate, all of same size or 2 outer ones smaller; petals 5, caducous or sometimes persistent, distinct, white (red), contorted, cochlear or quincuncial; stamens numerous or in definite number of 10–30 and 1–2-seriate, alternating in length, sometimes the 5 antepetalous ones trifurcate at apex; filaments at base connate in a ± long tube; anthers dorsifixed or subbasifixed; thecae 2, bilocular and each cell dehiscing by longitudinal slit, or else 4 or 2, unilocular, dehiscing by detachment or sometimes by a slit; connective thick, fleshy, most commonly produced in an apiculum or linguiform appendix, or obtuse; some stamens occasionally staminodial; disk intrastaminal, girding the ovary, membranaceous or subcoriaceous, tubular or cupular, dentate, lobate, laciniate or composed of 10–20 distinct scales; gynoecium syncarpous, (4)5(−7)-carpellate, carpels opposite the sepals or rarely alternating with them; ovary ovoid or ellipsoid, (4)5(−8)-locular; placentation axile; ovules 1 or 2 per cell, pendulous, anatropous, epitropous, with the micropyle facing upwards and the raphe ventral, when 2 then superposed and the lower hanging from the longer funicle; style entire; stigma capitate, 5-lobate or 5-radiate. Fruit drupaceous; exocarp varying from pulpy to fibrous; endocarp woody, usually very hard, compact or containing many round, resin-filled cavities, rarely spongious-woody, (4)5 (−7)-septate, with 1–2(−5) seeds developed; dehiscence germinal with longitudinal valves at the back of each carpel; subapical foramina alternating with valves often present. Seeds oblong, germinating enclosed in the fruit, retaining some nucellar remnants; embryo straight or slightly curved; endosperm fleshy and oily. $x = 12$.

A family of 8 genera and about 50 species, from Costa Rica through tropical America to southern Brazil, one sp. in coastal West Africa.

VEGETATIVE MORPHOLOGY AND ANATOMY. Branching is from the previous flush. The leaves are often distichously arranged; the buds on growing points are long-pointed and elongate while still rolled up and often have longitudinal lines down the blade (Stevens 2001). The leaf blade is usually coriaceous, and the margin varies from indistinctly entire to crenulate and dentate.

Stomata are anomocytic in *Endopleura*, *Humiria*, *Humiriastrum* and *Sacoglottis*, and paracytic in *Vantanea*. Sclerenchymatous idioblasts extending from the upper to the lower epidermis are found in *Sacoglottis*. Clustered and solitary crystals are found in the mesophyll. Vessels are solitary and their elements have simple or scalariform perforations and their members are extremely long. Axial parenchyma is predominantly diffuse and somewhat vasicentric or ranging to confluent. Rays are uniseriate or 2 (−4) cells wide and have conspicuous marginal rows of upright or square cells which are filled with a gum-like substance. Fibres are very long and have bordered pits (Metcalfe and Chalk 1950; Queiroz de Vilhena 1978).

The sieve element plastids contain protein crystalloids and starch (P5cs type, Behnke 1991).

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_13, © Springer-Verlag Berlin Heidelberg 2014

FLOWER STRUCTURE. Floral structure including anatomy has been studied by Narayana and Rao (1969–1977). Sepals are 3-traced; aestivation is quincuncial throughout, and their degree of fusion varies; in one *Vantanea* (*V. parviflora*), the limbs of the sepals are completely reduced. Aestivation of the corolla varies from quincuncial to contorted; petals are 3-traced in *Vantanea* but 1-traced in probably all other genera. The stamen filaments are basally more or less connate into a shorter or longer tube, which in *Humiria* extends up to one third or a half of their entire length. From its peripheral part the staminal traces separate, while the inner part of the tube forms the disk. In the fully differentiated flowers, however, vascular bundles have only been observed in the disks of *Vantanea*, *Humiria* and *Schistostemon*.

The multistaminate androecium of *Vantanea* has been interpreted as 3-whorled by Cuatrecasas (1961) but the floral anatomical studies of Narayana and Rao (1969) show that the densely packed stamens do not form distinct whorls. In genera such as *Humiria* and *Humiriastrum*, the biseriate androecium consists of 20 stamens with an outer antesepalous whorl of 15 stamens arranged in five groups each of three and an inner whorl of five antepetalous stamens. The bundle supply of the triplets indicates that they are stamen fascicles. In *Sacoglottis* there are ten stamens in two whorls, and in *Duckesia* among the numerous stamens the five antepetalous ones are usually fertile and in *Schistostemon* the antesepalous stamens are trifurcate. Thus, to my mind, the androecium of the family appears to be built upon a basically (ob)diplostemonous plan extended by lateral dédoublement and further reduction, rather than being basically multistaminate.

The complete 4-sporangiate anther is only found in *Vantanea*. In the two superposed pairs of thecae of *Endopleura*, the outer pair of sporangia is sterile in the upper thecae and the inner part in the lower (Rao and Narayana 1965). Further reduction leading to the complete loss of sporangia is met with in the rest. The outer pair of sporangia is sterile in *Humiria* and *Schistostemon*, whereas in *Humiriastrum* and *Sacoglottis* it is the inner ones (Narayana and Rao 1969–1977).

Whereas the androecium shows a great variability, the ovary is nearly always 5-carpellate and always syncarpous. Orientation of the carpels is usually antesepalous; only in *Humiria* are they constantly antepetalous, as first observed by Urban (1877); there is no explanation for this anomaly. There are two superposed ovules per carpel in *Vantanea* and *Humiria*, each of the marginal placentae bearing one ovule; locules of the remaining genera are uniovulate. The common style has a stylar canal lined by transmitting tissue and is traversed by the dorsal carellary bundles; in *Endopleura*, the common median lateral bundles extend into the style (Rao and Narayana 1965).

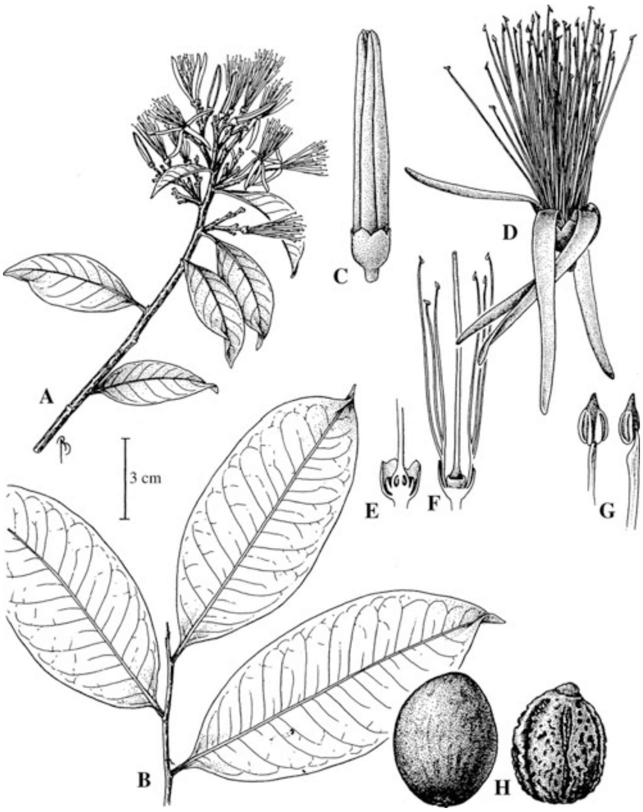

Fig. 50 Humiriaceae. *Vantanea guianensis*. **A** Flowering branchlet. **B** Leafy apex of flowering stem. **C** Flower bud. **D** Flower. **E** Vertical section of base of flower, petals and stamens removed. **F** Longitudinal section of flower with petals removed; note connate stamen filaments and cupular disk. **G** Adaxial and lateral view of stamens showing expanded connective. **H** Entire fruit and endocarp. (Reproduced with the kind permission of the artist Bobbi Angell)

EMBRYOLOGY. The ovule is anatropous and epitropous with the micropyle facing upwards, bitegmic and crassinucellate (Netolitzky 1926). In *Humiria balsamifera*, which has been studied by Boesewinkel (1985), the nucellus is large and persistent and an endothelium is lacking; the outer integument is mainly 2-layered and contains tannins. The inner layer of the 3-layered inner integument contains also tannins and is not endothelial. The micropyle is formed by both integuments. The embryo sac is 8-nucleate and the endosperm in *Vantanea* is probably nuclear (Mauritzon 1934).

POLLEN MORPHOLOGY. Pollen is suboblate to subprolate, 26–58 x 25–47 µm and 3–4-colporate; in LM, the tectum appears punctitegillate or more rarely faintly reticulate, the colpi are provided with sexinous thickenings, and the ora are lalongate to lolongate. Pollen of the Vantanea type (all genera except *Humiria*) has long ectocolpi and a thick columellar infratectum, whereas the Humiria type (*Humiria* only) has short ectocolpi and a thin columellar infratectum (Erdtman 1952; Suryakanta 1974; Bove and Melhem 2000).

KARYOLOGY. The chromosome number of *Sacoglottis gabonensis* was determined as $2n = 12$.

FRUIT AND SEED. The drupaceous fruit varies in size from the size of a pea to that of a hen's egg. The coriaceous, juicy or fibrous mesocarp encloses the woody fruit stone (pyrene), which in the five locules contains usually only 2–5 seeds. *Humiria* has two fertile seeds per locule, whereas all other genera have single-seeded locules. The endocarp is usually very hard and in some genera contains many round, resin-filled cavities which may contribute to the buoyancy of the fruits. At germination the seedlings seem to push away the valves which cover every locule or alternatively may seek exit through the apical foramina of the pyrene, which are present in the endocarp of some genera.

After fertilisation, a nuclear endosperm develops and continues to resorb the nucellus and eventually becomes cellular, fleshy and oily. In the mature seed there remains always a thin layer of nucellar tissue (perisperm) bordering the seed coat. The outer integument remains 2- or 3-layered but its outer epidermis (exotesta) is fortified by thick-walled cells with lamellate and lignified, pitted cell walls. The inner integument divides further and becomes 4–6-layered, and its outer epidermis develops into a fibrous exotegmen with heavily thickened, lignified cells (Boesewinkel 2000). The development of the seed coat of *Humiria* shows much resemblance to that of Linaceae and Erythroxylaceae, which differ, however, in having less strongly fortified seed coats, lacking nucellar remnants in the mature seed and having an endothelium.

PHYTOCHEMISTRY. The composition of the balsamic juice is unknown. Bergenin and gallate are present in the bark of *Sacoglottis*. The seeds of *Sacoglottis gabonensis* contain considerable amounts of palmitinic, oleic and linolic acids (Hegnauer 1966, 1990).

AFFINITIES AND SUBDIVISION OF THE FAMILY. Humiriaceae were considered as part of Engler's Geraniales and Hutchinson's Malpighiales, in both groupings together with Linaceae (including *Ixonanthes* and *Ctenolophon*) and Erythroxylaceae. Of the two large-scale molecular analyses of Wurdack and Davis (2009) and Soltis et al. (2011), the former placed the family in an unresolved position in Malpighiales, whereas the latter found strong support for its sister relationship with the rest of the Malpighiales clade. In the analysis of Xi et al. (2012), Humiriaceae are resolved in a sister position to the families of the pariatal clade.

A cladistic analysis of 40 morphological characters (Herrera et al. 2010) confirmed the obvious placement of *Vantanea* as sister to the rest of the family, followed by *Humiria* and the other genera, and with *Sacoglottis* and *Schistostemon* in the latest diverging subclade, as also anticipated by Cuatrecasas (1961).

DISTRIBUTION, HABITATS AND DISPERSAL. Humiriaceae are members of the neotropical rain forests and sometimes of woodland and savannahs up to an elevation of 1,400 m. They grow mostly in upland (non-flooded) forest, some species also along creeks. In the Guyana Highland, *Humiria balsamifera* is rich in local varieties and is an important constituent of scrub, savannah and woodland communities on rocks and yellow and white sand and grows up to an altitude of 2,300 m.

Only one species, *Sacoglottis gabonensis* (Baill.) Urb., is found outside tropical America, on the West African coast, where it is a tall tree growing in inundated forest.

Humiriaceous fruits or endocarps are often found in drifts and drift deposits of the Amazon and Magdalena rivers. Particularly those of *Sacoglottis amazonica* have been carried by currents from the Orinoco and Amazon deltas to the shores of the West Indies and Central America without having been established there, and even across the Atlantic to the British Islands (Cuatrecasas 1961). The age and means of the establishment of *Sacoglottis gabonensis* in West Africa are unknown.

FOSSIL RECORD. The fossil record of the family was evaluated by Cuatrecasas (1961), who excluded from it all finds from outside of South America. More recently, Herrera et al. (2010) reinvestigated and listed all fossil endocarps which, with the exception of one from Bahia (Selling 1945), are from the Andean countries between Costa Rica and Bolivia. The majority are of Neogene age (Miocene/Pliocene); *Vantanea* dates back to the Eocene. The fossil pollen of *Psilabrevitricolporites devriesii* (Lorente) Silva-Caminha et al., which is similar to extant *Humiria*, has been observed in beds dating back to the Early Miocene along the northern Andes and from western Amazonia (Herrera et al. 2010).

USES. Local use is made of the oil content of the seeds. Schultes (1979) gives details of interesting uses of the family by indigenous people in the north-western Amazon.

KEY TO THE GENERA

1. Stamens numerous (30–180) and pluriseriate; anthers with 2 bilocular thecae dehiscing longitudinally **1. *Vantanea***
– Stamens 10–30; anthers with unilocular, distinct thecae dehiscing by detachment 2
2. Carpels 2-ovulate, ovary locules opposite petals; thecae of anthers hirsute **2. *Humiria***
– Carpels 1-ovulate, ovary locules opposite sepals; thecae of anthers glabrous 3
3. Anthers 4-thecate; stamens 20–30 4
– Anthers 2-thecate; stamens 10–30 5
4. Usually only 5 stamens fertile; endocarp spongy-lacunose, evenly costate with long valves **4. *Duckesia***
– Most stamens fertile; endocarp not resinous-lacunose, at the base with 5 elevated prominent ribs each divided into 2 higher up **3. *Endopleura***
5. Stamens 20–30, only 5–15 fertile; endocarp prominently 5-costate, not resinous **5. *Hylocarpa***
– Stamens 10–20 6
6. Stamens 10; endocarp resinous, often bullate, shallowly or inconspicuously furrowed; valves broad, alternating ribs thin, inconspicuous **8. *Sacoglottis***
– Stamens 20 7
7. Stamens all with a single anther, 10 longer ones alternating with 10 shorter ones; thecae basally attached; endocarp with 5 elliptic, short valves in the upper half of fruit alternating with small apical foramina **6. *Humiriastrum***
– Five antesepalous stamens distally trifurcate and triantheriferous, 5 antepetalous stamens shorter, with a single anther, and the remaining 10 shortest, between sepals and petals; endocarp resinous-lacunose, valves broad, apical foramina usually lacking **7. *Schistostemon***

GENERA OF HUMIRIACEAE

1. TRIBE VANTANEEAE Cutrec. (1961).

Stamens numerous; anthers with 2 basal-lateral bilocular thecae; anther locules longitudinally dehiscing; carpels opposite sepals, 2-ovulate.

1. *Vantanea* Aubl. Fig. 50

Vantanea Aubl., Pl. Guiane 1: 572, t. 229 (1775).

Trees. Bracts caducous; stamens 50–120(–180), in 3 indistinct series, anthers 2-thecate, bilocular. Drupe medium-sized to large, ovoid or ellipsoid, the exocarp carnose; endocarp woody, not resinous, dehiscent at seed germination by oblong valves. Seeds usually only 1 per fruit.

About 15 spp., from Costa Rica and throughout northern South America southwards to Bolivia and Brazil (Santa Catarina).

2. TRIBE HUMIRIEAE Cuatrec. (1961).

Stamens 10–30, in 1–2 series; anthers with 2–4 unilocular thecae; carpels opposite sepals or alternating with them, 2- or 1-ovulate.

2. *Humiria* St.-Hil.

Humiria St.-Hil., Exp. Fam. 2: 374 (1805); Cuatrecasas, Contr. US Nat. Herb. 35: 67–122 (1961), rev.

Trees or shrubs. Leaves often decurrent on branchlets. Bracts persistent; stamens 20, uniseriate, united into a tube for about halfway up from base, longer and shorter alternating; filaments glandular; thecae inserted at base, hirsute; disk annular, of 20 linear, thick, united scales; carpels opposite petals; ovary cells with 2 superposed pendulous ovules. Drupe small (<16 mm), ovoid, ellipsoid or oblong; exocarp thin, mesocarp fleshy, palatable, endocarp woody, with 10 equidistant striae marking 5 narrow germinal valves alternating with 5 small apical foramina. Seeds commonly 4–1.

Four spp. in rain forests, woodland and savannah vegetation of tropical South America, *H. balsamifera* (Aubl.) St.-Hil. widespread with numerous varieties and forms, an important constituent of scrub or thicket communities in savannahs and the Guayana sandstone massif.

All other Humiriaceae:

Anther sacs glabrous; carpels opposite sepals; ovary cells 1-ovulate.

3. *Endopleura* Cuatrec.

Endopleura Cuatrec., Contr. US Nat. Herb. 35: 80 (1961).

Trees. Bracts persistent; stamens biseriate, 20–30, united in lower half or third, the largest opposite the petals; anthers dorsifixed; thecae 4, 2 basal and 2 apical or lateral, sometimes 2 thecae or rarely all 4 sterile; disk of 10 triangular-ovate scales, united at base. Drupe large, ellipsoid, exocarp coriaceous; mesocarp fleshy; endocarp woody, not resinous, with 5 strongly elevated ribs at the base each divided into two higher up; germinal valves inconspicuous between the unbranched ribs; apical foveola 5. Seeds usually 2–3 per fruit.

One sp., *E. uchi* (Huber) Cuatrec., Brazilian and Venezuelan Amazonia.

4. *Duckesia* Cuatrec.

Duckesia Cuatrec., Contr. US Nat. Herb. 35: 76 (1961).

Trees. Bracts persistent; stamens biseriate, 20–25, plus occasionally some shorter staminodes; anthers glabrous, usually only 5 fertile; connective lanceolate, carnose; thecae 4, 2 attached at base of connective, 2 laterally in the middle; disk of 10 subulate distinct scales surrounding the ovary. Drupe large, ovoid; exocarp thick, coriaceous; endocarp verrucose, resinous-lacunose; germinal valves 5, alternating with 5 apical foramina. Seeds few, oblong.

One sp., *D. verrucosa* (Ducke) Cuatrec., Brazilian Amazonia.

5. *Hylocarpa* Cuatrec.

Hylocarpa Cuatrec., Contr. US Nat. Herb. 35: 84 (1961).

Trees. Bracts caducous; stamens 30, biseriate, only 5–15 with fertile anthers; connectives thick, club or hammer shaped; thecae 2, basal; disk of 10 distinct, thick scales. Drupe large, fusiform, exocarp thick; endocarp woody, not resinous, prominently 5-costate, with germinal valves between the furrows. Seeds oblong, 1–3(5) per fruit.

Only one sp., *H. heterocarpa* (Ducke) Cuatrec., in the upper Rio Negro region of Brazil.

6. *Humiriastrum* (Urb.) Cuatrec.

Humiriastrum (Urb.) Cuatrec., Contr. US Nat. Herb. 35: 122–146 (1961).
Sacoglottis subg. *Humiriastrum* Urb.

Trees. Stamens 20, of alternating length, in 1 series; thecae 2, basal; disk a dentate ring or of distinct scales. Drupe medium sized to small, ellipsoid to subglobose, exocarp carnose; endocarp woody, usually without resinous cavities; germinal valves in upper half of fruit, oblong, alternating with 5 apical foramina. Seeds 1–2(−5) per fruit.

About 16 spp. spread from Costa Rica throughout tropical South America from the eastern to the western coast southwards to Rio de Janeiro.

7. *Schistostemon* (Urb.) Cuatrec.

Schistostemon (Urb.) Cuatrec., Contr. US Nat. Herb. 35: 146–161 (1961).
Sacoglottis subg. *Schistostemon* Urb.

Trees. Bracts persistent; stamens 20, in one series, the longest 5 antesepalous, trifurcate at apex and triantheriferous, 5 a little shorter, antepetalous, entire and with single anthers, 10 short, between sepals and petals, also with single anthers; disk cupular, dentate, or rarely of 10 distinct scales. Drupe rather large, exocarp carnose, endocarp woody, resinous-lacunose, the surface rugose or bullate, valves broad, separating ribs thin, apical foveola usually 0.

About nine spp. in northern South America southwards to Peruvian and Brazilian Amazonia.

8. *Sacoglottis* Mart.

Sacoglottis Mart., Nov. Gen. Spec. Pl. 2: 146 (1827).

Trees. Bracts persistent or deciduous; stamens 10, 5 antesepalous and longer than the 5 antepetalous ones; thecae 2, attached dorsally near base; disk cupular, dentate; drupe of medium to large size, exocarp carnose, endocarp woody, globose, bullate, resinous-lacunose, valves broad, apical foramina rare.

About eight species, seven in northern South America and one, *S. gabonensis* (Baill.) Urb., in coastal West Africa.

Selected Bibliography

Behnke, H.-D. 1991. See General References.

Boesewinkel, H.-D. 1985. The ovule and seed of *Humiria balasamifera* (Aubl.) St. Hil. Acta Bot. Neerl. 34: 183–191.

Boesewinkel, F.D. 2000. Semeistwo Humiriaceae, pp. 16–18. In: Anatomia Seminum Comparativa, vol. 6. St. Petersburg: Nauka.

Bove, C.P. 1997. Phylogenetic analysis of Humiriaceae with notes on the monophyly of Ixonanthaceae. J. Comp. Biol. 2: 19–24.

Bove, C.P., Melhem, T.S. 2000. World Pollen and Spore Flora 22: 1–35. Humiriaceae Juss.

Cuatrecasas, J. 1961. A taxonomic revision of Humiriaceae. Contr. US Nat. Herb. 35, 2: 24–214.

Cuatrecasas, J., Huber, O. 1999. Humiriaceae, pp. 623–641. In: Berry, P.E., Yatskievych, K., Holst, B.E. (eds.) Flora of the Venezuelan Guayana, vol. 5. St. Louis: Missouri Bot. Gard. Press.

Erdtman, G. 1952. See General References.

Hallier, H. 1923. Beiträge zur Kenntnis der Linaceae. 9. Die Humiriaceen. Beih. Bot. Centralbl. 39, Abt. 2: 56–62, 174.

Hegnauer, R. 1966, 1990. See General References.

Herrera, F., Manchester, S.R., Jaramillo, C., MacFadden, B., Silva-Caminha, S.A. da 2010. Phytogeographic history and phylogeny of the Humiriaceae. Int. J. Pl. Sci. 171: 392–408.

Mauritzon, J. 1934. Etwas über die Embryologie der Zygophyllaceae sowie einige Fragmente über die Humiriaceen. Bot. Notiser 1934: 409–422.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Narayana, L.L., Rao, D. 1969. Contributions to the floral anatomy of Humiriaceae 1. J. Jap. Bot. 44: 328–335.

Narayana, L.L., Rao, D. 1973. Contributions to the floral anatomy of Humiriaceae 2. J. Jap. Bot. 48: 143–146.

Narayana, L.L., Rao, D. 1973. Contributions to the floral anatomy of Humiriaceae 3. J. Jap. Bot. 48: 242–246.

Narayana, L.L., Rao, D. 1976a. Contributions to the floral anatomy of Humiriaceae 4. J. Jap. Bot. 51: 12–15.

Narayana, L.L., Rao, D. 1976b. Contributions to the floral anatomy of Humiriaceae 5. J. Jap. Bot. 51: 42–44.

Narayana, L.L., Rao, D. 1977. Contributions to the floral anatomy of Humiriaceae 6. J. Jap. Bot. 52: 145–153.

Netolitzky, F. 1926. See General References.

Queiroz de Vilhena, R.C. 1978. Anatomia foliar de très espécies da família Humiriaceae. Acta Amazonica 8: 25–43.

Rao, D., Narayana, L.L. 1965. Vascular anatomy of Humiriaceae. Curr. Sci. 34: 383–384.

Record, S. 1944. Random observations on tropical American timbers; Humiriaceae in Central America. Trop. Woods 77: 8–9.

Reiche, K. 1890. Humiriaceae. In: Engler & Prantl, Die natürl. Pflanzenfam. III, 4: 35–37. Leipzig: W. Engelmann.

Schultes, R.E. 1979. Interesting uses of the Humiriaceae in the northwestern Amazon. J. Ethnopharmacol. 1: 89–94.

Selling, O.E. 1945. Fossil remains of the genus *Humiria*. Sv. Bot. Tidskr. 39: 258–269, figs. 1–24.

Soltis, D.E. et al. 2011. See General References.

Stevens, P.F. 2001 onwards. See General References.

Suryakanta 1974. Pollen morphological studies in the Humiriaceae. J. Jap. Bot. 49: 112–122.

Urban, I. 1877. Humiriaceae. In: Martius, Flora Brasiliensis XII, 2: 425–454, pl. 92–96.

Urban, I. 1878. Die Begrenzung der Gattungen in der Familie der Humiriaceae. Sitz.-Ber. Ges. Naturf. Freunde 1878: 2–5. Berlin.

Winkler, H. 1931. Unterfam. IV, Humirioideae. In: Engler & Prantl, Die natürl. Pflanzenfam. ed.2, 19a, pp. 126–129, figs. 58, 59. Leipzig: W. Engelmann.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Irvingiaceae

Irvingiaceae Exell & Mendonça (1951), nom. cons.

K. Kubitzki

Glabrous trees; wood extremely hard; leaves sometimes papillate underneath; mucilage cells in leaf and stem epidermis; secretory canals containing mucilage in leaves and stems. Leaves alternate, simple, entire, petiolate, pinnately veined, coriaceous; stipules very large, unequal, intrapetiolar, encircling the terminal bud, early caducous and leaving a very distinct scar. Inflorescences paniculate, axillary or terminal. Flowers small, hermaphroditic, regular, pedicels articulated; sepals 5, small, imbricate; petals 5, free, imbricate, exceeding the sepals; stamens 10 (9), distinct, exceeding the petals, inserted below the large intrastaminal nectary disk, filaments plicately folded in bud; anthers subbasifixed, 2-locular, ± globular, dehiscing by slits; gynoecium syncarpous, 5–4(2)-carpellate; ovary superior, 5–4(2)-locular; ovule 1 per locule, epitropous, anatropous, bitegmic and crassinucellar, pendulous from the top of the central axis; obturator present; style terminal, short; stigma punctiform. Fruit a drupe with 1 or (5)4 pyrenes or a broadly winged samara. Seeds with large embryo; cotyledons flattened, cordate; endosperm fatty, almost 0 to copious.

Three genera and about 11 spp. mainly from W and C Africa, one of them from SE Asia and W Malesia.

Vegetative Morphology and Anatomy. Most species are vast, buttressed forest trees often with fluted boles; *Desbordesia glaucescens* is reported to grow up to 55 m tall and to develop buttresses up to 8 m high. The young stem of *Klainedoxa* is often heavily armed with blunt spines up to 12 cm long. In *Klainedoxa* the bark is dark brown, and there are no fibres at the centre of the slash. In *Desbordia* and *Irvingia* the bark is white to pale brown, and in the slash of the latter genus prominent fibres are present towards the centre of the slash. Leaves are involute. Stipules are intrapetiolar and folded to form a cone around the terminal bud; they are early caducous and leave circular scars on the twig. In *Klainedoxa* they are of enormous size, fall almost at once and then are found in large numbers beneath the tree; in *Desbordesia*, they are usually less than 1 cm long but in *Irvingia grandifolia* occasionally up to 8 cm long.

The leaves are completely glabrous but sometimes papillate on the undersurface, and mucilage cells are present in the leaf and stem epidermis. Stomata are paracytic. Mucilage cells, mucilage spaces and cristarque cells are found in the leaf mesophyll and the stem. Vessel elements have simple perforations; lateral pitting is alternate; axial parenchyma is in continuous bands; rays are homogeneous.

Floral Structure and Biology. The flowers of Irvingiaceae have a prominent, fleshy nectary disk, which surrounds the base of the ovary and pre-soaks among the bases of the filaments. Along a circular line on the crest of the disk of *Klainedoxa*, Link (1992) observed 10–15 stomata deeply sunken each at the bottom of a trumpet-shaped duct and underlain by a voluminous cavity. The disk in an *Irvingia* was similar but the stomata were fewer in number and less concealed. In all three genera the disks attract attention through their size relative to the dimensions of the flowers, and their bright yellow colour and strong nectar production (Harris 1996); however, details about pollinators and the diurnal rhythm of nectarial secretion remain unknown.

Matthews and Endress (2011) gave a detailed description of the floral morphology of one species of *Irvingia*, and compared it with that of putatively related families, but could not find good support from floral morphology for the clade Linaceae, Irvingiaceae and Caryocaraceae.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_14, © Springer-Verlag Berlin Heidelberg 2014

POLLEN MORPHOLOGY. Pollen is quite uniform, ± spheroidal, 17–23 x 18–24 µm, tricolporate, prominently triangulaperturate with plane or concave intercolpia and emarginate apertural angles, ectoaperture 6 (7.5) µm long, endoaperture nearly rectangular; tectum continuous, appearing granular in LM but either verrucose or striate-rugulate in SEM (Sabatier 1974).

KARYOLOGY. For *Irvingia gabonensis* $2n = 28$, and for *Klainedoxa* $2n = 26$ have been reported.

FRUIT AND SEED. The pericarp anatomy of *Irvingia* and *Klainedoxa* has been studied by Fernando and Quinn (1992). The exocarp comprises up to 20 layers of thickened, but unlignified, mostly tangentially elongated cells; also the epidermis is unlignified. The mesocarp is very broad and mostly composed of thin-walled parenchyma with numerous large secretory canals, isolated fibres, fibre bundles and vascular bundles ensheathed by fibres. The endocarp consists of a complex pattern of elongated sclereids in tangential or longitudinal orientation and an inner epidermis that is strongly lignified. The pericarp structure of *Allantospermum* (see Ixonanthaceae, this volume) was found to be very different.

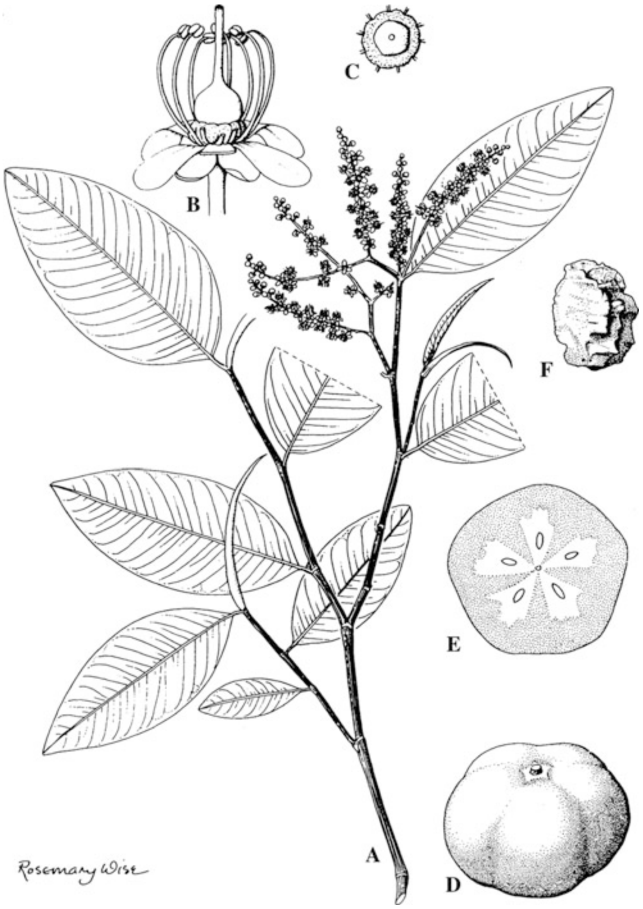

Fig. 51. Irvingiaceae. *Klainedoxa gabonensis*. **A** Flowering branch, the shoot tips with stipules clasping the terminal bud. **B** Flower. **C** Disk and ovary. **D** Fruit. **E** Same, transverse section. **F** Pyrene after remainder of fruit has rotted. (Harris 1996; drawn by Rosemary Wise)

The seeds (*Desbordesia* and *Klainedoxa* studied by Netolitzky 1926, *Irvingia* by Tobe and Raven 2011) have a fibrous exotegmen, whilst the mature testa is sclerotic throughout and traversed by post-chalazal branches of the raphe bundle. Tobe and Raven (2011) found no similarity with the seed structure of other Malpighiales families but rather with Huaceae and Connaraceae (Oxalidales).

Germination is epigeal and phanerocotylar throughout.

DISPERSAL. The following interesting details are taken from Harris (1996). The fruits of *Klainedoxa gabonensis* and various *Irvingia* are swallowed whole by elephants. The pyrenes separate in their digestive tract and are passed out in the dung, from where they have been observed germinating. Lowland gorillas usually eat the mesocarp but do not swallow the pyrenes. Yellow backed duikers (*Cephalophus sylvicultor*) also swallow these fruits and regurgitate the pyrenes after digesting the mesocarp. Squirrels and other rodents occasionally open pyrenes and eat the seeds. The fresh fruits of *Irvingia smithii*, which grows in seasonally flooded and riparian forest, develop slimy air bubbles in the meocarp and are then carried by the current; when the mesocarp starts to rot, the fruits lose their buoyancy and sink. The fruits are also eaten by a wide variety of fish. The samaras of *Desbordesia* are blown by the wind.

PHYTOCHEMISTRY. *Irvingia* contains gallic acid and ellagic acid (Nooteboom 1967).

AFFINITIES. Mainly on account of the presence of the mucilage spaces and mucilage cells mistaken as secretory ducts, Irvingiaceae have been considered close to, or included in, Simaroubaceae, which differ profoundly in having compound, estipulate leaves, scales on the filaments, distinct stylodia and more or less distinct carpels, and in containing the rutalean nortriterpenoid bitter principles. Hallier (1923) included *Irvingia* in his broadly construed Linaceae, which comprised, i.a., Erythroxylaceae, Ixonanthaceae and Humiriaceae. Hutchinson (1973) placed the latter three families with Irvingiaceae in his Malpighiales. Forman (1965) supported the inclusion of the Ixonanthoideae into the Irvingiaceae. In DNA sequence analyses, *Irvingia* was resolved as sister to the Linaceae, although with low support (Tokuoka and Tobe 2006; Korotkova et al. 2009), and without support as sister to Ixonanthaceae in the clusoid clade (Soltis et al. 2011). In a 4-gene analysis, Ruhfel et al. (2011) found *Irvingia* highly supported as sister to *Bruguiera* (Rhizophoraceae) and *Cyrillopsis* (Ixonanthaceae). In the phylogenomic analysis of Xi et al. (2012), the Irvingiaceae are placed, although with moderate support, in a clade together with the Pandaceae; see there (this volume) for possible synapomorphies.

Distribution and Habitats. The family is restricted to the humid zone of West and Central Africa with the exception of one species (*Irvingia malayana*) in SE Asia/W Malesia. Most of the African species and *Irvingia malayana* grow in non-inundated lowland forest; some enter into dry or flooded forest, savannah or secondary forest.

Palaeobotany. A fossil wood, *Irvingiaceoxylon dechampsii*, is reported from the upper Pliocene/lower Pleistocene of Ethiopia (Gros 1983), testifying to the extension of humid forests to this region by that time. *Irvingioxylon taibaense*, described by Koeniguer (1970) from the Eocene of Senegal, has been excluded from Irvingiaceae.

Uses. The seeds of species of all three genera are eaten by humans, either raw or cooked. The juicy mesocarp of *Irvingia gabonensis* is eaten as a dessert fruit; the tree is often planted (Harris 1996).

Key to the Genera

1. Ovary 5-celled; fruit a drupe with 5 pyrenes; stipules, covering terminal buds, 3.5–12(−25) cm long **1. *Klainedoxa***
– Ovary 2-celled; fruit a drupe with a single pyrene or fruit a samara; stipules, covering terminal buds, to 4 (very rarely 8) cm long 2
2. Fruit a 1-seeded drupe **2. *Irvingia***
– Fruit a 2-seeded samara, broadly winged all around **3. *Desbordesia***

1. ***Klainedoxa*** Pierre ex Engler Fig. 51

Klainedoxa Pierre ex Engler in Engler & Prantl, Nat. Pflanzenfam. III, 4: 227 (1896); Harris, Bull. Jard. Bot. Nat. Belg. 65: 152–166 (1996), rev.

Tall trees; stipules massive, ribbed, very long. Leaves not papillose on undersurface. Inflorescences terminal. Flowers congested on lateral branches of the panicles; ovary 5-locular; ovule 1 per locule. Fruit a hard drupe; exocarp thin, fleshy; mesocarp firm but mucilaginous, fibrous, pyrenes 5, oblong with very hard endocarp, fibrous outside. Seeds oblong, with copious endosperm.

Two spp. are recognised by Harris, widely distributed in the forested regions of W and C Africa.

2. ***Irvingia*** Hook. f.

Irvingia Hook. f. in Trans. Linn. Soc., Bot. 23: 167 (1860); Harris, Bull. Jard. Bot. Nat. Belg. 65: 166–196 (1996), Afric. spp., rev.

Trees, often vast. Leaves sometimes papillose on under surface; stipules large. Inflorescences axillary and terminal panicles or compound racemes. Flowers inserted at regular intervals or in fascicles on main branches of inflorescence; ovary 2-locular; ovules 1 per locule. Drupes large, edible, thick and fibrous, rounded-oblong in outline, compressed, 1(2)-locular and 1(2)-seeded; pyrene(s) with thick wall covered with fibres. Seeds oblong, embryo fatty, straight with flat cotyledons; endosperm copious to 0.

Seven spp., six in the humid zone of W and C Africa, and one in SE Asia/Malesia.

3. ***Desbordesia*** Pierre ex van Tiegh.

Desbordesia Pierre ex van Tiegh., Ann. Sci. Nat. IX, 1: 289 (1905); Harris, Bull. Jard. Bot. Nat. Belg. 65: 147–151 (1996), rev.

Tall trees. Leaves matt on undersurface. Inflorescences usually much branched. Flowers inserted on short lateral branches of the panicle (occasionally lateral branches fasciculate); ovary flattened, 2-locular; ovules 1 per locule. Fruit a samara with (1)2 fatty seeds; endosperm scanty.

A single sp., *D. glaucescens* (Engler) van Tiegh., confined to the lower Guinean block of the Central African forest from Nigeria to Zaire.

Selected Bibliography

Fernando, E.S., Quinn, C.J. 1992. Pericarp anatomy and systematics of the Simaroubaceae sensu lato. Austral. J. Bot. 40: 263–289.

Forman, L.L. 1965. A new genus of Ixonanthaceae with notes on the family. Kew Bull. 19: 517–526.

Gros, J.-P. 1983. *Irvingiaceoxylon dechampsii* n.g. et n.sp. du Cénozoique d'Éthiopie, et *Simaroubaceoxylon* (*Irvingioxylon*) *taibaense* n.g. et n.comb. de l'Yprésien du Sénégal. Rev. gén. Bot. 90: 153–171.

Hallier, H. 1921. Beitäge zur Kenntnis der Linaceae (DC. 1819) Dumort. Beih. Bot. Centralbl. 39, II: 1–178.

Hallier, H. 1923. See General References.

Harris, D.J. 1996. A revision of the Irvingiaceae in Africa. Bull. Jard. Bot. Nat. Belg. 65: 143–196.

Hutchinson, J. 1973. The families of flowering plants. 3rd edn. Oxford: Clarendon Press.

Koeniguer, J.-C. 1970. Sur deux bois fossiles de l'Éocène du Sénégal. 95ème Congr. Soc. Sav., Reims 1970, Sci., 3: 39–77.

Korotkova, N. et al. 2009. See General References.

Link, D. 1992. The floral nectaries in the Irvingiaceae. Pl. Syst. Evol. 180: 235–242.

Matthews, M.L., Endress, P.K. 2011. See General References.

Netolitzky, F. 1926. See General References.

Nooteboom, H.P. 1967. The taxonomic position of Irvingioideae, *Allantospermum* Forman, and *Cyrillopsis* Kuhlm. Adansonia II, 7: 161–168.

Rojo, J.P. 1968. The wood anatomy of *Allantospermum borneense* Forman and *Allantospermum multicaule* (Capuron) Nooteboom. Adansonia II, 8: 73–83.

Ruhfel, B.R. et al. 2011. See General References.

Sabatier, B. 1974. Contribution de la palynologie à l'étude des Irvingiacées d'Afrique tropicale. Adansonia II, 14: 277–289.

Soltis, D.E. et al. 2011. See General References.

Tobe, H., Raven, P.H. 2011. Embryology of the Irvingiaceae, a family with uncertain relationships among the Malpighiales. J. Plant Res. 124: 577–591.

Tokuoka, T., Tobe, H. 2006. See General References.

Verdcourt, B. 1984. Ixonanthaceae. In: Polhill, R.M. (ed.) Flora of Tropical East Africa. 9 pp. Rotterdam: Balkema.

van Welzen, P.C., Baas, P. 1984. A leaf anatomical contribution to the classification of the Linaceae complex. Blumea 29: 453–479.

Winkler, H. 1931. Linaceae. In: Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19a. Leipzig: W. Engelmann.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Ixonanthaceae

Ixonanthaceae Planch. ex Miquel (1858), nom. cons.
Ixonantheae Benth. (1862).

K. Kubitzki

Trees or shrubs. Leaves spiral, usually involute, entire or glandular-serrate; stipules small, lateral or rarely intrapetiolar. Inflorescences lateral, corymbose. Flowers small, mostly hermaphroditic, regular or nearly so, commonly 5-merous; sepals connate at the base or free, imbricate; petals free, imbricate or contorted; stamens 5, 10 or 20; filaments folded in bud, widened at the base, free or basally adnate to the conspicuous annular or cupular nectary disk (lacking in neotropical *Ochthocosmus*); gynoecium 5(2)-carpellate; style slender; stigma capitate or discoid; ovary sometimes apically unilocular and sometimes the locules divided into locelli by incomplete secondary septa; style and filaments folded in bud; ovules 2 or rarely 1 per locule, apical. Fruits septicidal capsules, sometimes also loculicidal by secondary septa; columella persistent or not; seeds with obvious basal wing or suprahilar arillode; embryo straight with large cotyledons; endosperm scanty or 0.

A family comprising four genera including the controversial *Allantospermum* and about 23 spp. from tropical America, tropical Africa, the Himalayas and NE India, SE Asia and Malesia to New Guinea.

Vegetative Morphology and Anatomy. Ixonanthaceae differ from Irvingiaceae in the absence of mucilage cells and mucilage cavities and the occasional presence of mesophyll sclereids (*Ochthocosmus*) and tracheoidal idioblasts; cristarque cells, which are present in both the ground tissue and the bundle sheath, are found in *Ochthocosmus* and, more prominently, in Irvingiaceae and Linaceae-Hugonioideae. Stomata are paracytic, as usual in the Linaceae complex; petiole bundles are arcuate (van Welzen and Baas 1984). Cuticle waxes are present as variously arranged platelets. Sieve-element plastids are S-type.

Vessels have simple perforations. *Allantospermum* differs from both Ixonanthaceae and Irvingiaceae in its heterogeneous rays and minute, half-bordered vessel-ray pits (Rojo 1968).

Extrafloral epithelial nectaries were described from the ventral side of the sepals of *Ixonanthes icosandra* (Narayana and Rao 1966; Link 1992) and from the leaf margins of the same species (Belin-Depoux 1978), where they are functional in juvenile stages of leaf development.

Flower Structure. Articulate pedicels with prophylls are reported from *Cyrillopsis*. Narayana and Rao (1966) and Link (1992) studied the prominent intrastaminal disk of *Ochthocosmus africanus* and *Ixonanthes*; the margin of the latter was found to bear 20–25 nectarial stomata over stomatal cavities. In *Ochthocosmus barrae*, a disk is lacking but the filament bases are connected by a glandular staminal tube secreting nectar through the numerous open nectarial stomata.

Pollen Morphology. Pollen is (spheroidal-) subprolate-prolate, tricolporate and 27–52 μm long. The tectum and nexine are thin, and the infratectal layer is columellate. The sculpture is usually scabrate, in *Cyrillopsis* rugulate or striate. The pollen of *Ixonanthes* is spheroidal, large (up to 45 μm diameter) and has distinct supratectal spines (Metcalfe et al. 1968).

Fruit and Seed. The seeds of *Ixonanthes* are exotegmic (Corner 1976; Boesewinkel and Bouman 2000). The American and African species of *Ochthocosmus* (*O.* s.str versus '*Phyllocosmus*') differ in seed structure: the former have seeds with an apical wing pointing upwards in fruit and the latter

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_15, © Springer-Verlag Berlin Heidelberg 2014

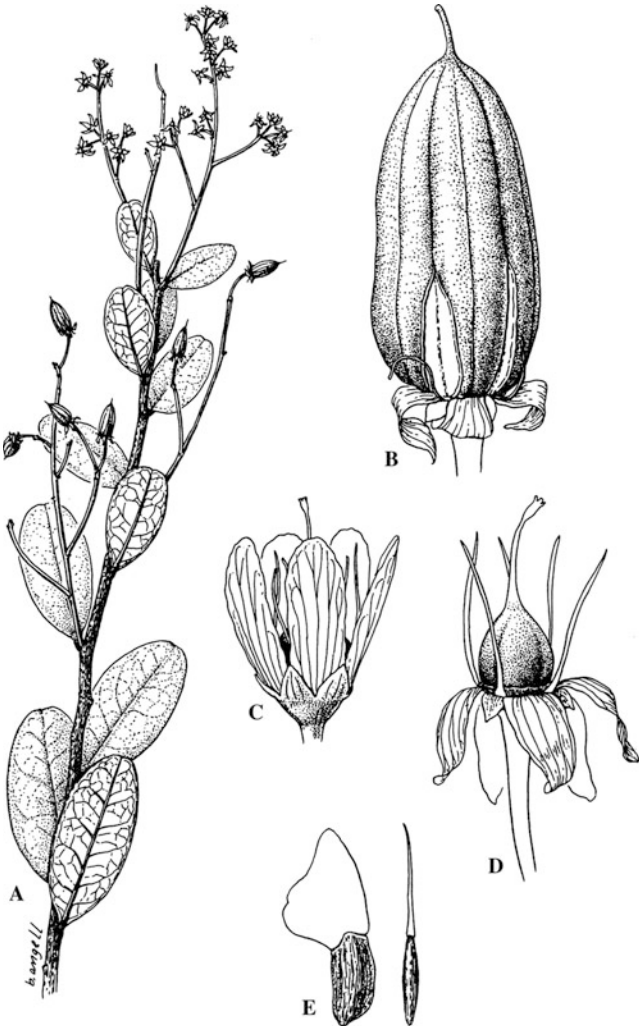

Fig. 52. Ixonanthaceae. *Ochthocosmus longipedicellatus*. **A** Flowering and fruiting branchlet. **B** Mature capsule. **C**, **D** Flowers during progressive stages of anthesis. *O. roraimae* var. *parvifolius*. **E** Winged seed. (Reproduced with kind permission of the artist Bobbi Angell)

an apically attached aril(lode) that is turned down and clasps the upper part of the seed. Both the wings and arillodes are anatomically very similar; they develop from the micropylar region and appear homologous (Kool 1988), just following the reasoning of Corner in his durian theory (1954) "that all winged seeds are *prima facie* indications of arillate ancestry". (See also the comments on winged vs. arillate seeds in Rhizophoraceae under that family, this vol.) In *Ixonanthes* one species, *I. icosandra* Jack, has a (funicular?) aril attached to the seed between the micropyle and the hilum, whereas the two other species of the genus (sectionally different) have seed wings that are said to be inserted at the chalazal end and vascularized, and having a texture like the rest of the testa (Corner 1976; Kool 1988).

PHYTOCHEMISTRY. Seed oils contain predominantly lauric and myristic acids, in which they differ from those in Simaroubaceae. In hydrolysates of *Allantospermum*, Nooteboom (1967) found ellagic and gallic acid, which are lacking from the other three genera.

CLASSIFICATION. *Ochthocosmus* and *Phyllocosmus* have sometimes been kept separate (see Forman 1965) but, as Hallier (1923) and Kool (1988) have explained, if this course is to be followed, then a third genus must be distinguished. *Ochthocosmus*, *Ixonanthes* and *Cyrillopsis* are clearly related but the position of *Allantospermum* is problematic because the intrapetiolar stipules, the caducous petals and the solitary ovules seem to fit better with Irvingiaceae than with Ixonanthaceae, where *Cleistanthopsis* (a synonym of *Allantospermum*) originally had been placed. Forman (1965) considered the central columella of *Allantospermum* as equivalent to five splinters into which the central tissue of the fruit in Ixonanthaceae separates and which remain attached to the edges of the valves. After considering all characters, however, Forman was inclined to place the genus into Ixonanthaceae. A different interpretation of the fruit structure of *Allantospermum* led Nooteboom (1967) to keep *Allantospermum* in Irvingiaceae. Wood anatomically, *Allantospermum* differs from both Irvingiaceae and Ixonanthaceae (Rojo 1968).

AFFINITIES. Forman (1965), Corner (1976) and others combined Irvingiaceae and Ixonanthaceae in spite of their morphological differences, and Takhtajan (2009) placed Ixonanthaceae in the Linales, together with, i.a., Erythroxylaceae/Rhizophoraceae and Ctenolophonaceae. Molecular datasets have led to a confusing picture. Initially, *Ochthocosmus* and *Ixonanthes* remained unplaced or in vacillating positions within the Malpighiales. Wurdack and Davis (2009) provided support for a clade of (*Ixonanthes* (*Ochthocosmus* + *Cyrillopsis*)) but left it unplaced

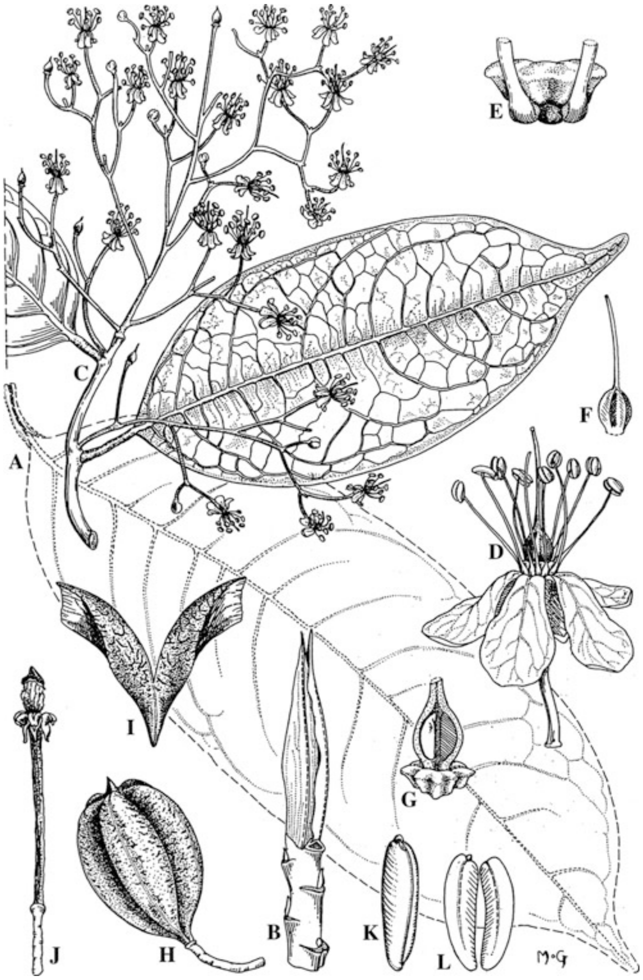

Fig. 53. Ixonanthaceae. *Allantospermum borneense*. **A** Leaf. **B** Leaf-bud with stipules (the lower scars are those of bud-scales). **C** Flowering branch. **D** Flower. **E** Disk with base of filaments (central one removed). **F** Pistil. **G** Vertical section of ovary. **H** Capsule. **I** Valve of capsule. **J** Columella of capsule bearing arilloid processes. **K** Seed. **L** Embryo. (Forman 1965)

within Malpighiales. Ruhfel et al. (2011) reported a relationship between *Cyrillopsis* and *Bruguiera* (Rhizophoraceae), which in turn are sister to *Irvingia* (Irvingiaceae). The 7-gene analysis of Soltis et al. (2011) resolved *Ochthocosmus* in an unsupported clade with Irvingiaceae as part of the clusioid clade. Strong support for the family pair Linaceae and Ixonanthaceae was provided by Xi et al. (2012), which makes sense in view of their common possession of mostly diplostemonous flowers, a contorted corolla, carpels with false septa, a placental obturator, etc.

DISTRIBUTION AND HABITATS. The family is bound to the tropical lowland forests including heath forests and swamp forests of Africa and Asia/Malesia, and in South America mainly occurs in upland white sand savannahs of the Roraima formation in southern Venezuela.

Ixonanthes, today considered a typical Malesian element, appeared in the fossil pollen record of India in the Palaeocene, along with other originally African elements such as *Durio* and *Gonystylus* (Kar 1985). These are thought as having rafted from Africa on the Indian Plate and having dispersed eastwards with subsequent range reduction in Africa and India.

KEY TO THE GENERA

1. Capsule valves splitting away from a central column; ovules 1 per cell; stamen filaments distinct from disk; stipules intrapetiolar; stamens 10 **4. *Allantospermum***
– Capsule without a central column; ovules 2 per cell; stamen filaments attached at the base to the disk; stipules lateral; stamens 5–20 2
2. Ovary 2-celled; capsule 2-valved; pedicel articulated and provided with prophylls; stamens 5 **3. *Cyrillopsis***
– Ovary 5(or spuriously 10)-celled; capsule 5-valved; pedicel not articulated; prophylls 0; stamens 5–20 3
3. Trees of SE Asia and Malesia; stamens 10, 15 or 20; (sepals with extrafloral nectaries) **1. *Ixonanthes***
– Trees and shrubs of N South America and tropical Africa; stamens 5 or 10 **2. *Ochthocosmus***

1. *Ixonanthes* Jack

Ixonanthes Jack, Mal. Misc. 2, 7: 51 (1822); Kool, Blumea 26: 191–204 (1988).

Evergreen, buttressed trees or treelets. Inflorescences pedunculate, pleiochasial-corymbose. Flowers pedicellate; sepals and petals quincuncial, the sepals with extrafloral nectaries on the ventral side; stamens 10 or (15–)20, apparently in one whorl, filaments inserted outside and against the disk; anthers (basi-)dorso-versatile; disk annular or cup-shaped; ovary 5-locular; ovules 2 per locule, collateral, pendulous; style simple; stigma discoid. Capsule septicidal and septifragal, 5-valvate. Seeds 1 or 2 per locule, either with a basal wing or a supra-hilar arillode; endosperm oily; embryo straight.

Three spp., SE Asia and Malesia but lacking from Java, the lesser Sunda Islands and the

Moluccas. The arillode of *I. icosandra* Jack (sect. *Brewstera*) is attached between the hilum and the micropyle, whereas the remaining two species have chalazal wings.

2. *Ochthocosmus* Benth. Fig. 52

Ochthocosmus Benth. in Hook., London J. Bot. 2: 266 (1843); Robson, Fl. Zambes. 2, 1: 100–102; Badré in Fl. Cameroun 14: 57–63 (1972) and Fl. Gabon 21: 55–62 (1963); Steyermark & Luteyn, Brittonia 32: 128–143 (1980), rev. neotr. spp.

Phyllocosmus Klotzsch (1857).

Trees. Inflorescences in racemes. Flowers pedicellate or sessile; sepals lacking extrafloral nectary; petals imbricate or contorted; stamens 5 or 10; anthers dorsifixed; ovary 5-locular; locules with 2 ovules, sometimes with incomplete false septum; style simple, stigmas 5, free or fused. Capsule septicidal, 1–3(–5)-seeded. Seeds obliquely oblong, either with a conspicuous thin wing or an arillode attached to the distal end.

About 16 spp., 7 of them in northern South America and 9 in tropical Africa. Three sections were distinguished by Hallier (1921); see also Kool (1988).

3. *Cyrillopsis* Kuhlm.

Cyrillopsis Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4: 356, t. 29 (1925); Ramírez & Berry, Fl. Venez. Guayana 5: 665–666 (1999).

Small trees. Stipules very small, fugacious. Inflorescence a fascicle of racemes. Pedicels articulate, with prophylls beneath articulation. Flowers pentamerous; sepals and petals imbricate, persistent; stamens 5, alternipetalous; anthers basifixed, introrse; ovary 2-locular; ovules 2 per locule, pendent from apex of axile placenta; style filiform. Capsule 2-valved. Seeds with a distal flat triangular arillode.

Two spp., northern South America, in woodland on white sand and in altitudinal savannahs.

4. *Allantospermum* Forman Fig. 53

Allantospermum Forman, Kew Bull. 19: 517 (1965); Nooteboom, Adansonia II, 7: 161–168 (1967).

Cleistanthopsis R. Capuron (1965).

Buttressed or polycormic trees. Leaves entire; stipules intrapetiolar. Inflorescences thyrso-paniculate; sepals and petals 5, imbricate, caducous; stamens 10; disk intrastaminal; ovary 5-locular, with 1 pendulous ovule per locule; style simple; stigma capitellate. Capsule 5-valvate, septicidal, with persistent columella bearing near apex 5 arilloid processes from which the seeds break away. Seeds cylindric-ellipsoid, up to 2.5 cm long, shining and waxy, distally with a arillode sometimes adherent to the columella.

Two spp., one in Sarawak, the other in Madagascar.

Selected Bibliography

Belin-Depoux, M. 1978. Contribution à l’étude des glandes foliaires d’*Ixonanthes isosandra* Jack (Ixonanthaceae). Rev. gén. Bot. 85: 371–382.

Boesewinkel, F.D., Bouman, F. 2000. Ixonanthaceae. In: Takhtajan, A. (ed.) Anatomia seminum comparativa, vol. 6. Nauka: St. Petersburg. (In Russian).

Corner, E.J.H. 1954. The durian theory extended. 2. Phytomorphology 4: 152–165.

Corner, E.J.H. 1976. See General References.

Forman, L.L. 1965. A new genus of Ixonanthaceae with notes on the family. Kew Bull. 19: 517–526.

Hallier, H. 1923. See General References.

Kar, R.K. 1985. The fossil floras of Kachchh - IV. Tertiary palynostratigraphy. Palaeobotanist 34: 1–279.

Kool, R. 1988. A taxonomic revision of the genus *Ixonanthes* (Linaceae). Blumea 26: 191–204.

Link, D.A. 1992. The floral nectaries of the Geraniales and their systematic implications: VI. Ixonanthaceae Exell and Mendonça. Bot. Jahrb. Syst. 114: 81–90.

Metcalfe, C.R., Lescot, M., Lobreau, D. 1968. A propos de quelques caractères anatomiques et palynologiques comparés d’*Allantospermum borneensse* Forman et d’*Allantospermum multicaule* (Capuron) Nooteboom. Adansonia II, 8: 337–351.

Narayana, L.L., Rao, D. 1966. Floral morphology of Linaceae. J. Jap. Bot. 41: 1–10.

Nooteboom, H.P. 1967. The taxonomic position of Irvingioideae, *Allantospermum* Forman, and *Cyrillopsis* Kuhlm. Adansonia II, 7: 161–168.

Ramírez, N., Berry, P.E. 1999. Ixonanthaceae, pp. 665–666. In: Flora of the Venezuelan Guayana, vol. 5. St. Louis: Missouri Bot. Gard. Press.

Robson, N.K.B., Airy Shaw, H.K. 1962. A note on the taxonomic position of the genus *Cyrillopsis* Kuhlmann. Kew Bull. 15: 387–388.

Rojo, J.P. 1968. The wood anatomy of *Allantospermum borneense* Forman and *Allantospermum multicaule* (Capuron) Nooteboom. Adansonia II, 8: 73–83.

Ruhfel, B.R. et al. 2011. See General References.

Soltis, D.E. et al. 2011. See General References.

Takhtajan, A. 2009. See General References.

van Welzen, P.C., Baas, P. 1984. A leaf anatomical contribution to the classification of the Linaceae complex. Blumea 29: 453–479.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Linaceae

Linaceae DC. ex Perleb, Vers. Arzneikr. Pfl.: 107 (1818), nom. cons.
Hugoniaceae Arn. (1834).

S. Dressler, M. Repplinger, and C. Bayer

Herbs, shrubs, trees, or lianas, sometimes with climbing hooks. Leaves alternate (more rarely opposite or whorled), sometimes distichous, simple, sessile or petiolate, the lamina usually involute; stipules present or reduced, sometimes dentate or incised. Inflorescences terminal or axillary thyrsoids or botryoids, exceptionally flowers solitary. Flowers perfect, actinomorphic, 5(4)-merous; sepals quincuncially imbricate, distinct or connate at the very base, sometimes persistent; petals usually contorted, often clawed, distinct or almost so, usually caducous; stamens usually twice the number of petals or antesepalous stamens and staminodia [these sometimes reduced] as many as petals, connate at base, usually with glands outside the tube; ovary superior, (2)3–5(–8)-carpellate; ovules 2 per carpel, sometimes more, anatropous, epitropous; locules sometimes divided into 2 one-seeded portions by complete or incomplete false septae; stylodia as many as carpels, usually distinct; stigma capitate to filiform. Fruit a septicidal capsule, sometimes schizocarpic or a drupe. Seeds sometimes arillate; seed coat often mucilaginous; endosperm usually scanty, sometimes copious; embryo straight or slightly curved.

A family of 13 genera with ca. 255 species, mostly from northern temperate to tropical regions.

Vegetative Morphology. The Old World Hugonioideae are woody climbers with hooks that correspond to modified shoots. Such hooks are often found as lowermost branches of inflorescences. Rhizomes are unknown in Linaceae; perennial herbs form persistent primary roots (Troll and Weberling 1989). *Cliococca* has an extensively branched underground rootstock. Stipules are sometimes pectinate (Hugonioideae), in Linoideae absent or sometimes reduced to glands. In contrast to Ctenolophonaceae, tufted hairs are absent.

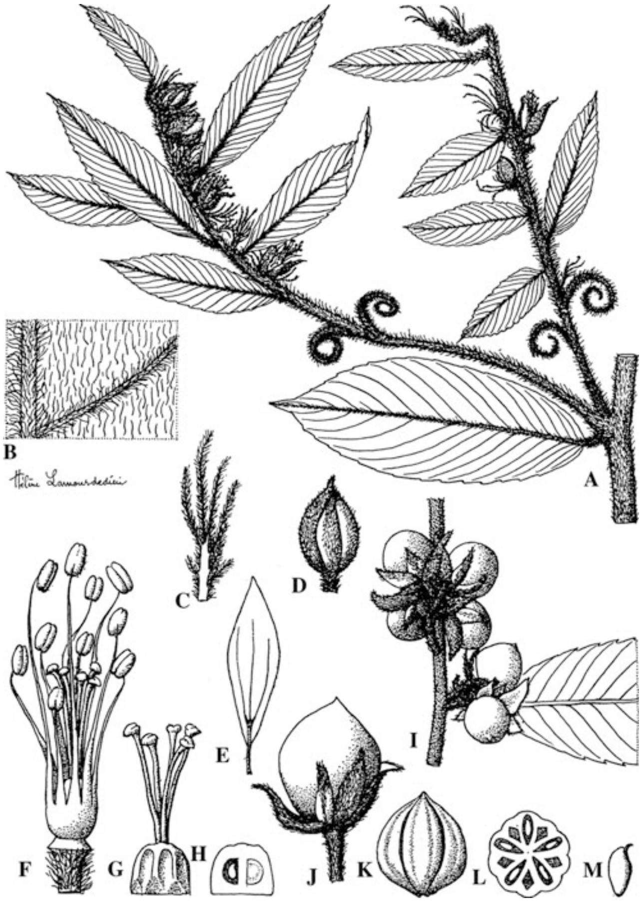

Fig. 54. Linaceae. *Hugonia villosa*. **A** Flowering branchlet. **B** Detail of lower leaf surface. **C** Stipule, adaxial side. **D** Flower bud. **E** Petal. **F** Androecium and gynoecium. **G** Gynoecium. **H** Vertical section of ovary. **I** Part of fruiting branch. **J** Fruit. **K** Pyrene. **L** Same, transverse section. **M** Seed. (Badré 1973, drawn by Hélène Lamourdedieu)

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_16, © Springer-Verlag Berlin Heidelberg 2014

VEGETATIVE ANATOMY. Winkler (1931) and Metcalfe and Chalk (1950) provide anatomical overviews of the family. Leaf anatomy was studied in detail by van Welzen and Baas (1984).

The indumentum usually consists of narrow and unicellular trichomes, in *Hesperolinon* combined with glandular hairs with multiseriate stalk (van Welzen and Baas 1984). The leaves are generally dorsiventral and hypostomatic. Especially herbaceous members (e.g. *Linum*, *Radiola*, *Hesperolinon*) are sometimes amphi- or even epistomatic. Stomata are of the paracytic type. (Sub)epidermal cells are often mucilaginous (all Linoideae and most Hugonioideae); their absence is reported for *Hebepetalum neblinae* (Jardim and Berry 1999) and three *Roucheria* spp. studied by van Welzen and Baas (1984), whereas Metcalfe and Chalk (1950) mentioned them for the latter genus. Hugonioideae are well defined by regular sinuously lobed subsidiary cells and lignified guard cells (missing in *Indorouchera*). Mesophyll contains idioblasts in *Hugonia* (Metcalfe and Chalk 1950, not confirmed by van Welzen and Baas 1984) and *Roucheria* (van Welzen and Baas 1984). Crystals are present as druses or solitary ones (rarely clustered) in woody members of the family only. Hugonioideae are well defined by the occurrence of cristarque cells in the ground tissue of petiole and midrib (van Welzen and Baas 1984).

Stems of *Linum* have large, well-defined bast fibres in the pericycle or phloem (see Economic Importance), where they sometimes form a continuous ring, but these are absent from *Reinwardtia trigyna* (Metcalfe and Chalk 1950). The pith disintegrates in *Linum*.

The wood is characterised by mostly solitary vessels (but a few radial multiples of 2–3 occur in *Hugonia* or *Linum*), scalariform to simple or only simple perforations, predominantly apotracheal parenchyma, multiseriate rays, and fibres with distinctly bordered pits (whole family). Crystals are reported in *Hebepetalum*. Linoideae are interpreted as being more advanced than Hugonioideae in having reduced axial parenchyma, homogeneous rays, short vessel elements and a tendency towards vessel aggregation but they show vestiges of primitive characters such as tracheidal fibrous elements and vestiges of scalariform vessel perforations in *Linum* spp. (Heimsch and Tschabold 1972). *Indorouchera* has the most primitive wood with exclusively scalariform perforations and spiral thickenings (van Hooren and Nooteboom 1984). Sieve element plastids are of the Ss-type.

REPRODUCTIVE STRUCTURES. Although little is known on the woody Hugonioideae, it is likely that the family has basically monotelic synflorescences (see Troll and Weberling 1989). Terminal flowers are easy to detect in herbaceous Linaceae, and the basic structure appears to be a thyrsoid. Further branching of the inflorescence is restricted to the distal portion (e.g. *Linum* spp., but see also *Anisadenia*; Troll and Weberling 1989). The paracladia can be restricted to a single flower with both prophyllar nodes, which may lead to cymose branching (e.g. dichasia in *Radiola*; Troll 1964), or produce more nodes, leading to thyrso-paniculate systems. Reduced ramification leads to determinate raceme-like inflorescences (botryoids, e.g. *Anisadenia*), cincinnate sympodia (e.g. *Linum austriacum*) or single-flowered inflorescences (some *Linum* spp.; Troll and Weberling 1989).

The bases of stamens and, where present, staminodia are connate to form a short tube. Nonetheless, the androecium is originally diplostemonous or obdiplostemonous (Ströbl 1925; Narayana and Rao 1978). The exterior side of the tube often bears distinct glands, which in some Hugonioideae may form a continuous disk (Narayana and Rao 1973). In some Linoideae, small nectary glands external to the stamens or at the inner base of the petals are reported to exist.

Floral anatomy of several Linaceae has been studied by Narayana and Rao (1978, summarizing and discussing numerous previous works). Matthews and Endress (2011) described floral morphology and anatomy for several Linaceae, and reported gynophores in *Linum* and *Reinwardtia*.

Some species of *Hugonia*, *Linum*, *Tirpitzia* and *Reinwardtia* are heterostylous; dimorphic pollen and stigmas are reported for some species (Heitz et al. 1971; Dulberger 1973, 1974; Bahadur et al. 1984, 1996; Lloyd et al. 1990; Sugawara et al. 2002; see also McDill et al. 2009). *Hugonia serrata* is reported to be tristylous (Thompson et al. 1996). The stigma is wet or dry with unicellular papillae (Sutter and Endress 1995). In *Linum pratense*, the persistent sepals move inwards after the fall of the petals, leading to self-pollination (Uno 1984).

Some *Linum* have been reported to be pollinated by bees or flies; bee pollination is also known for *Hugonia mystax* (Heitz 1980; Kearns and Inouye 1994; Aluri et al. 1997).

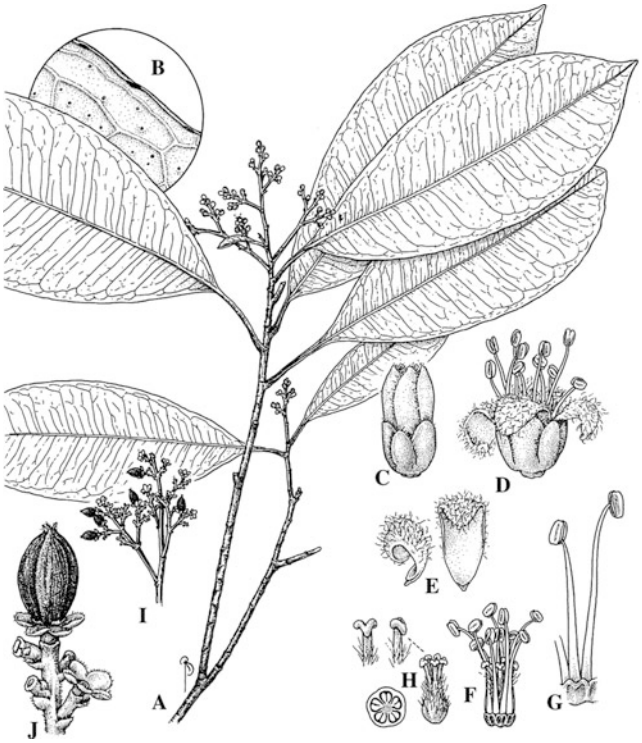

Fig. 55. Linaceae. *Hebepetalum humiriifolium*. **A** Branch with flower buds. **B** Lower leaf surface showing punctuations. **C** Opening flower bud. **D** Flower. **E** Petals. **F** Flower with perianth removed. **G** Stamens with basal nectaries. **H** Pistil, with detail of stigmas and cross section of ovary. **I** Part of infructescence. **J** Fruit. (Reproduced with the kind permission of the artist Bobbi Angell)

EMBRYOLOGY. The anther wall is 5-layered with an innermost layer of secretory tapetum of binucleate cells. Pollen is 3-cellular when shed (Narayana 1964). Most embryological information refers to *Linum usitatissimum* and few other species (for *Linum*, *Hugonia* and *Reinwardtia*, see especially Narayana 1964). Ovules are bitegmic, crassinucellar to tenuinucellar, and epitropous. The endothelium is one- or two-layered (Sutter and Endress 1995); its ultrastructure was described by Vazart and Vazart (1965). The micropyle is formed by the inner integument; an obturator is often present (Narayana 1964; Matthews and Endress 2011; absent in *Radiola*: Crété 1937). Embyro sac development conforms to the Polygonum type. One of the synergids degenerates (Vazart 1971). The endosperm develops according to the Nuclear type; embryogeny follows the Solanad type (Souèges 1937; Narayana 1964; Erdelská 1967; Johri et al. 1992). For ultrastructure of the embryo sac of *Linum*, see Vazart and Vazart (1966), Vazart (1969) and D'Alascio Deschamps (1973, 1981).

POLLEN MORPHOLOGY. Erdtman (1952) considered Linaceae to be eurypalynous, which was based on a broad circumscription of the family, including genera now placed in Humiriaceae, Erythroxylaceae, Rhizophoraceae, Ixonanthaceae and Ctenolophonaceae. Palynological characters agree with the narrow circumscription of Linaceae followed here. Pollen grains are suboblate to prolate and 3-colpate or -colpor(oid)ate, occasionally with more apertures (Erdtman 1952; Rogers and Xavier 1971). *Anisadenia*, *Tirpitzia* and *Reinwardtia*, earlier reported to have inaperturate pollen grains (Erdtman 1952), proved to have pantoporate ones with similar bacula covering pores and exine alike; *Indorouchera*, however, is reported to have inaperturate pollen ("tritenuate"; Saad 1962). Unlike representatives of the other families mentioned above, Linaceae-Linoideae have more or less verrucose or spinose pollen, sometimes with verrucae of different sizes (Erdtman 1952; Saad 1961; Xavier et al. 1980; Rogers 1985); in Hugonioideae, the exine is baculate or tectate(-reticulate) (Saad 1962).

Dimorphic pollen is known from heterostylous species of *Linum* (Rogers 1980; Dulberger 1981; Grigorieva 1989) and *Reinwardtia* (Sugawara et al. 2002).

KARYOLOGY. Diploid chromosome numbers have been reported for *Hugonia* as $2n = 12$, 24, 26, for *Radiola linoides* 18, for *Reinwardtia trigyna* 20, 22, for *Cliococca selaginoides* 36 (Bolkhovskikh et al. 1969; Robertson 1971), for *Hesperolinon* 34, 36 (Rogers et al. 1972) and for *Sclerolinon* as 12 (Rogers et al. 1972) or 16 (Raven 1959).

Within the diverse genus *Linum*, diploid chromosome numbers range mostly between 16 and 60 (Rogers et al. 1972; Diederichsen and Richards 2003; Muravenko et al. 2010). There are, however, also reports of counts of $2n = 12$ (*L. hypericifolium*), 68 (*L. bahamense*), 72 (*L. suffruticosum*) and 84, 86? (*L. monogynum*; all from Bolkhovskikh et al. 1969). Basic numbers of $n = 9$ and 15 predominate (Chennaveeraiah and Joshi 1983).

FRUIT AND SEED. Drupaceous fruits are found in Hugonioideae; in some species, the fruits split into indehiscent mericarps. Most Linoideae have capsular fruits; each carpel is usually divided into two one-seeded portions. Capsules in *Linum usitatissimum* are described in detail by Roth (1977).

The seed coat is formed by both integuments with thick-walled cells in the outer epidermis of the inner integument (Narayana 1964). Structure and development of seeds have been studied in detail in *Linum* (Boesewinkel 1980). The mature seed coat consists of five layers: an innermost, pigmented layer derived from the inner cells of the inner integument; a layer of compressed cells; a sclerenchymatic layer derived from the outer layer of the inner integument; the cells of the inner layer of the outer integument; and the outermost layer of mucilage cells. Upon soaking, the mucilage swells, ruptures the cell walls of the epidermis and penetrates through lesions in the cuticle. For production and composition of linseed mucilage, see Heinze and Amelunxen (1984). In contrast to *Linum* and *Reinwardtia*, the seeds of *Radiola* lack mucilage in the outer epidermis (Crété 1937).

Roucheria and *Hugonia* with hard endocarp in their drupaceous fruits seem to deviate from the exotegmic state of the family by modification of this layer from slightly lignified to mostly unlignified (Corner 1976). Instead, there are abundant sclerotic cells. Furthermore, no mucilage is formed.

The straight to slightly curved embryo with flat cotyledons is embedded in a nuclear, oily endosperm.

PHYTOCHEMISTRY. Knowledge on the phytochemistry of the family is limited. Known phenolic compounds include C-glycosyl flavones (only in *Linum usitatissimum*), lignans, and cinnamic acid derivatives. *Roucheria griffithiana* contains a saponin; pyrrolizidin alkaloids are known from *Hugonia*; *Linum* spp. and *Reinwardtia* are cyanogenic, containing linamarin and lotaustralin monoglucosides. Mucilage of *Linum usitatissimum* is restricted to the seed coat epidermis of mature seeds; it consists of a mixture of neutral and acid heteropolysaccharides mixed with peptides (Hegnauer 1966, 1989).

SUBDIVISION AND AFFINITIES. Linaceae can readily be subdivided into subfamilies Hugonioideae (trees, climbers or shrubs, stamens twice the

Fig. 56. Linaceae. **A–C** *Linum grandiflorum*. **A** Plant with flowers and young fruit. **B** Stamens and pistil. **C** Pistil. **D–G** *Linum usitatissimum*. **D** Plant with flowers and a capsule. **E** Dehiscing capsule. **F, G** Different growth forms of cultivated flax. **H** *Tirpitzia sinensis*, flower. **I** *Anisadenia saxatilis*, flowering branch with rhizome. (Takhtajan 1980)

number of petals, staminodia 0, fruit drupeacous) and Linoideae (herbaceous to shrubby, stamens and staminodia as many as petals, fruit capsular or schizocarpic). Linoideae are poorly resolved so far. Recent molecular studies conducted by McDill and colleagues (McDill et al. 2009; McDill and Simpson 2011) indicate that *Linum* is paraphyletic in relation to *Radiola*, *Hesperolinon*, *Cliococca* and *Sclerolinon*. At present five sections are recognized within *Linum*: *Linum*, *Dasylinum*, *Syllinum*, *Linopsis* and *Cathartolinum*, with *Linum* and *Dasylinum* being sister to the remaining sections/genera. *Hesperolinon*, *Cliococca* and *Sclerolinon* are nested within a paraphyletic sect. *Linopsis*. This clade is sister to the monotypic sect. *Cathartolinum*, being again sister to the monophyletic sect. *Syllinum*. *Radiola* is sister to all this. Taxonomic consequences, however, have not yet been addressed.

Some genera formerly thought to be related to Linaceae had to be excluded and are now referred to Erythroxylaceae and Ixonanthaceae (van Hooren and Nooteboom 1984; APG II 2003; Davis and Chase 2004). Linaceae belong to Malpighiales (eurosid I clade sensu APG II 2003). Within Malpighiales, Linaceae are resolved in an unsupported sister position with the chrysobalanoid clade (Davis and Chase 2004; Soltis et al. 2011), whereas the analysis of Xi et al. (2012) places Linaceae in a well-supported clade with Ixonanthaceae, this latter clade being sister to the phyllanthoids.

Distribution and Habitats. Hugonioideae occur in rain forests or periodically inundated savannahs in the tropical belt of northern South America, Africa, southern India and Papuasia. The neotropical representatives are trees or shrubs, whereas lianas or more rarely shrubs predominate in the palaeotropics. The range of the mostly herbaceous Linoideae extends into the temperate zones of both hemispheres, except for the large deserts. Many species are typical of steppe vegetation.

Palaeobotany. Megafossils formerly assigned to this family (*Wetherellia*, *Decaplatyspermum*) proved to belong elsewhere (Mazer and Tiffney 1982; Collinson et al. 1993). Pollen of the *Linum* type was found from the upper Miocene of Spain and the Pliocene of Germany (Muller 1981). Boesewinkel (1984) compared recent with fossil linseed samples, which are frequently found in archaeological remains.

Economic Importance. *Linum usitatissimum* has been under cultivation for more than 7,000 years in Europe, the Near East and western Asia (Pengilly 2003). Today, special varieties are grown for their oil seeds or their excellent fibre (Marchenkov et al. 2003). Linseed (in American English flaxseed) oil is used for paints, varnishes and coatings, as well as an edible condiment. The seed itself provides a dietary complementary food, its mucilage facilitating digestion and excretion. Several linseed compounds (e.g. α-linolenic acid, lignans) have proven to have positive pharmacological effects on cardiovascular diseases and cancer (Cunnane 2003; Prasad 2003; Rickard-Bon and Thompson 2003). Flax fibre is flexible, strong, durable and absorbs water, making it very useful for towels and table cloths. Usually the fibres are 2–4 cm long, in rare instances they may reach up to 12 cm. Some other *Linum* species are cultivated as ornamentals.

Key to the Genera

1. Trees or lianas with hooks, rarely shrubs, all ligneous; petals not or hardly clawed; stamens twice as many as petals; ovary (1–)3–5-celled; fruit a drupe, rarely splitting finally into indehiscent mericarps (**subfam. Hugonioideae**) 2
– Erect herbs or small shrubs; petals usually long-clawed; stamens as many as petals, alternating with the same number of staminodes; ovary 6–10-celled (4 in *Sclerolinon*); fruit usually a capsule (**subfam. Linoideae**) 6
2. Trees or shrubs of the Neotropics 3
– Lianas with hooks, rarely shrubs (New Caledonia) of the Old World tropics 4
3. Secondary veins arching near the margin (brochidodromous) and reticulately veined in between; petals villous on inner surface and basally clawed; stylodia usually 5 **5. *Hebepetalum***
– Secondary veins fine and closely parallel, running into a marginal vein, no reticulate veins in between; petals glabrous on inner surface; stylodia 3 **4. *Roucheria***
4. Indumentum present, at least on the calyx; stylodia 5(6); ovary 5(6)-celled, locules all distinct in the fruit; drupe with 2–4(5) developed seeds **1. *Hugonia***
– All parts glabrous; stylodia 3–4(5); ovary 3(4)-celled, only one, rarely two locules distinct in fruit; drupe usually one-seeded 5
5. Buds and stipules often covered with resin; leaves distichous; flowers in axillary fascicles, subtended by often densely packed, imbricate bracts **3. *Indorouchera***

– Resin absent; leaves spiral; flowers in rather lax racemes or panicles **2. *Philbornea***

6\. Leaves petiolate 7

– Leaves sessile 9

7\. Low shrubs or subshrubs; sepals without stalked glands; fruit a 6–10-seeded capsule 8

– Perennial herbs; sepals with conspicuous long-stalked glands; fruit indehiscent, 1-seeded nut **6. *Anisadenia***

8\. Flowers white or pink; capsule splitting into 4–5 two-seeded valves **7. *Tirpitzia***

– Flowers yellow; capsule splitting into 6–8 one-seeded valves **8. *Reinwardtia***

9\. Locules, stylodia and stigmas 2 or 3 10

– Locules, stylodia and stigmas 4 or 5 11

10\. Leaves alternate; stipular glands present (sometimes minute); petal base with appendages; stigmas as wide as stylodia; stylodia 2 or 3 **12. *Hesperolinon***

– Leaves opposite; stipules 0; petals without well-defined appendages; stylodia wider than stigma; stylodia and stigmas 2 **11. *Sclerolinon***

11\. Petals and stylodia 4 12

– Petals and stylodia 5 13

12\. Flowers small, white **10. *Radiola***

– Flowers yellow (*Linum keniense*) **9. *Linum***

13\. Flowers few, terminal on densely leaved branches; petals imbricate, shorter than sepals, whitish or pale pink **13. *Cliococca***

– Inflorescense cymose; petals contorted, usually larger than sepals **9. *Linum***

GENERA OF LINACEAE

I. SUBFAM. HUGONIOIDEAE Planch. ex Hooren & Noot. (1984).

Trees or lianas, rarely shrubs; leaves alternate; petals without claw; stamens twice the number of sepals; fruit drupaceous, rarely splitting into indehiscent mericarps; pantropical.

1. *Hugonia* L. Fig. 54

Hugonia L., Sp. Pl.: 675 (1753); Badré, Adansonia II, 11: 95–106 (1971), reg. rev.; van Hooren & Nooteboom, Fl. Males. 10(3): 609–613 (1988), reg. rev.

Durandea Planch. (1847).

Lianas, rarely shrubs, often hooked, indumentum present. Leaves spiral; stipules entire to palmatifid. Inflorescences axillary or terminal, racemes or panicles, or axillary cymes, rarely solitary flowers; bracts and prophylls present or missing; sepals somewhat unequal, distinct; disk + or 0; ovary 5(6)-locular, stylodia 5(6); drupe (pseudo-) indehiscent, stone 5(6)-locular with as many interlocular sterile cavities (sect. *Hugonia*) or splitting into 5 mericarps (sect. *Durandea*). Seeds 1 per locule, exarillate, but with woody chalaza; embryo straight; endosperm fleshy. $2n = 12$, 24, 26.

About 40 spp. from Africa, Madagascar, tropical Asia eastwards to Solomon Isl., Queensland, New Caledonia and Fiji. *Hugonia* including *Durandea* is paraphyletic with respect to *Indorouchera* and *Philbornea* (McDill and Simpson 2011), but taxonomic consequences remain to be addressed. Resurrection of the generic status of *Durandea* might be the appropriate action.

2. *Philbornea* Hallier f.

Philbornea Hallier f., Arch. Néerl. Sci. Exact. Nat. III, 1: 110 (1912); van Hooren & Nooteboom, Fl. Males. 10(3): 614–615 (1988).

Liana with hooks, glabrous. Leaves spiral; stipules entire. Inflorescences axillary or terminal, raceme-like [probably botryoids], bracts and prophylls present; sepals somewhat unequal, connate at the very base; exterior side of connate filament bases glandular; ovary 3-locular, stylodia 3; drupe little fleshy, 1-seeded. Seeds arillate; embryo straight; endosperm fleshy, scarce.

One sp., *P. magnifolia* (Stapf) Hallier f., Sumatra, Borneo, Palawan.

3. *Indorouchera* Hallier f.

Indorouchera Hallier f., Beih. Bot. Centralbl. 39(2): 50 (1921); van Hooren & Nooteboom, Fl. Males. 10(3): 615–619 (1988), rev.

Lianas with hooks, glabrous, young leaves and buds often covered with resin. Leaves distichous; stipules entire or toothed. Flowers in dense axillary clusters or solitary, pedicel with numerous bracts; nectaries 0; ovary 3(4)-locular; stylodia 3–5, connate at base or distinct; stigmas discoid. Drupe 1(2)-seeded. Seeds arillate; endosperm oily, copious; embryo straight to curved.

Two spp., SE Asia, mostly in rain forests.

4. *Roucheria* Planch.

Roucheria Planch., London J. Bot. 6: 141 (1847); Jardim, M.Sc. Thesis Univ. of Missouri, St. Louis (1999), rev.;

Ramírez et al., Fl. Venez. Guayana 5: 620–623 (1999), reg. rev.; Jardim & Berry, Novon 9: 520–523 (1999), key.

Shrubs or trees. Leaves alternate, secondary veins parallel; petiole sometimes indistinct; stipules small. Inflorescences axillary or terminal, paniculate or fasciculate; sepals connate at base; petals glabrous or pubescent on margins; stamens 10(15); nectaries 10; ovary 1–5-locular, ovule 1–2 per locule, subapical; stylodia (2)3(–5); stigmas discoid. Fruits drupaceous, subglobose, 1–5-locular, little fleshy, endocarp 3–5-angled. Seeds 1 or 2 per locule, embryo somewhat curved.

Seven spp., tropical South America.

5. *Hebepetalum* Benth. Fig. 55

Hebepetalum Benth. in Bentham & Hooker, Gen. Pl. 1: 244 (1862); Jardim, M.Sc. Thesis Univ. of Missouri, St. Louis (1999), rev.; Ramírez et al., Fl. Venez. Guayana 5: 618–620 (1999), reg. rev.; Jardim & Berry, Novon 9: 520–523 (1999), key.

Small to tall trees. Leaves alternate, pedicel distinct; stipules small. Inflorescences terminal, paniculate; sepals somewhat connate at base; petals with short claw, adaxially pubescent; androecium with 5 nectaries; ovary 4–5-locular, stylodia 5, connate at base, with thickened stigmas; locules 1–2-ovulate. Drupe ovoid, 1–5-locular, mesocarp black. Seeds 1(2) per locule; embryo somewhat curved.

Three spp. from tropical South America, in lowland evergreen forests, often on white sand.

II. SUBFAM. LINOIDEAE Arn. (1832).

Herbs, subshrubs or shrubs; leaves alternate or opposite; stipules sometimes reduced to glands or 0; petals clawed; stamens as many as sepals, connate at base; staminodia usually present, antesepalous; ovules 2 per locule, locules usually divided into 1-seeded portions; fruit usually a capsule; mostly northern hemisphere.

6. *Anisadenia* Wall. ex Meisn. Fig. 56I

Anisadenia Wall. ex Meisn., Pl. Vasc. Gen. 2: 96 (1838).

Perennial herbs; stems simple or little branched. Leaves alternate, petiolate, lanceolate, entire or slightly denticulate; stipules present, ovate-lanceolate. Inflorescences thyrsoid or botryoid; sepals 5, with 1 or 2 rows of glandular hairs near margin and numerous parallel nerves; petals 5, contort, purple or white; stamens 5; nectaries 3, at base of staminal tube; staminodia 5, filiform; ovary 3-locular without false septae; stylodia 3; stigmas discoid. Fruit a 1-seeded nut. Seeds oblong.

Two spp., C China, Himalaya, Thailand.

7. *Tirpitzia* Hallier f. Fig. 56H

Tirpitzia Hallier f., Beih. Bot. Centralbl. 39(2): 5 (1921).

Densely branched shrubs. Leaves alternate, petiolate, obovate-spathulate, nerves pinnate; stipules minute, caducous. Inflorescences cymose; sepals 5; petals 5, white, claw about three times as long as limb; stamens 5; 5 nectaries at base of staminal tube present; staminodia 5; ovary 4–5-locular; false septae incomplete; stylodia 4–5, connate at base; stigmas pear-shaped. Capsule splitting into 4–5 two-seeded valves.

Three spp., S China, Thailand, Vietnam.

8. *Reinwardtia* Dumort.

Reinwardtia Dumort., Comment. Bot.: 19 (1822).

Erect or prostrate, glabrous shrubs or subshrubs; branches erect and prostrate, the latter with adventitious roots. Leaves alternate, petiolate, base attenuate, elliptic-oblong to lanceolate-obovate, nerves pinnate; stipules minute, caducous. Inflorescences thyrso-paniculate, umbelliform, rarely flowers solitary; flowers heterostylous; sepals 5; petals 5, yellow; stamens 5; nectaries at base of staminal tube 2 or 3; staminodia 5; ovary 3–4-locular; false septae present; stylodia 3–4, connate at base; stigmas capitate. Capsule splitting into 6–8 one-seeded valves. Seeds compressed, reniform. $2n = 20, 22$.

One sp., *R. indica* Dumort. [syn. *R. trigyna* (Roxb.) Planch.], N India, China, SE Asia.

9. *Linum* L. Fig. 56A–G

Linum L., Sp. Pl.: 277 (1753); Rogers, Brittonia 15: 97–122 (1963), rev. E North Am.; Rogers, Brittonia 20: 107–135 (1968), rev. C & W North Am.; Mildner & Rogers, Phytologia 39: 343–390 (1978), rev. South Am.; Rogers, Nord. J. Bot. 1: 711–722 (1981), rev. South Afr.

Perennial or annual herbs or rarely shrubs, glabrous or hairy. Leaves alternate, rarely opposite, sessile, often lanceolate or sometimes spathulate at base, entire, nerves parallel; stipular glands present or absent. Inflorescences cymose. Flowers homostylous or heterostylous; sepals 5, sometimes with glandular hairs; petals 5, contort, usually yellow, blue, white or pinkish, distinct or connate at base; stamens 5; nectaries at base of staminal tube 0–5; staminodia 5 if present; ovary 5-locular; false septae incomplete or complete; stylodia 5, distinct or connate; stigmas linear or capitate. Capsule splitting into 10 one-seeded valves, 5 two-seeded valves or indehiscent with 10 one-seeded segments. Seeds compressed. $2n = 12, 16, 18, 20, 24, 26, 28, 30, 32, 34, 36, 40, 42, 52, 54, 60, 62, 68, 72, 84, 86(?)$.

About 180 spp., widely distributed in temperate and subtropical regions, esp. Mediterranean region; five sects. *Cathartolinum*, *Dasylinum*, *Linopsis*, *Linum*, *Syllinum*. *Linum* is paraphyletic with respect to *Radiola*, *Hesperolinon*, *Cliococca* and *Sclerolinon* (McDill et al. 2009; McDill and Simpson 2011), but taxonomic consequences remain to be addressed.

10. ***Radiola*** Hill

Radiola Hill, Brit. Herb.: 227 (1756).

Small annual, glabrous herbs; leaves opposite, sessile, ovate to lanceolate, 1-nerved; stipules 0. Inflorescences dichasial. Flowers homostylous; sepals 4, apically (2)3(4)-toothed; petals 4, contort, white, small; stamens 4; nectaries indistinct; staminodia minute or absent; ovary 4-locular; false septae incomplete; stylodia 4, distinct; stigmas capitate. Capsule splitting into 8 1-seeded valves. Seeds irregularly ovate. $2n = 18$.

One sp., *R. linoides* Roth, temperate Asia, Europe, the Mediterranean region and montane tropical Africa.

11. ***Sclerolinon*** C.M. Rogers

Sclerolinon C.M. Rogers, Madroño 18: 182 (1966).

Annual, glabrous herbs, simple or occasionally branched below. Leaves opposite throughout or alternate above, sessile; stipular glands absent. Inflorescences densely cymose. Flowers homostylous; margins of upper floral bracts and sepals lacerate; sepals 5, gland-toothed; petals 5, yellow; stamens 5, diminutive; staminodia absent; nectaries 0(?); false septae nearly complete; stylodia 2, distinct or faintly connate, very short; stigmas capitate. Fruit splitting into 4 one-seeded nutlets. Seeds narrowly ovate, wedge-shaped in cross-section. $2n = 12, 16$.

One sp., *S. digynum* (A. Gray) C.M. Rogers, W North America.

12. ***Hesperolinon*** (A. Gray) Small

Hesperolinon (A. Gray) Small in N. Amer. Fl. 25: 84 (1907); Sharsmith, Univ. Calif. Publ. Bot. 32: 235–314 (1961), rev.

Ephemeral erect annuals. Leaves alternate, opposite or whorled, sessile, filiform to linear, caducous; stipular glands present or absent. Inflorescences cymose. Flowers homostylous; sepals 5, glabrous or hairy; petals 5, yellow to orange or white to pink/lavender, base with adaxial (glandular?) appendages; stamens 5; staminodia absent; nectaries present (?); ovary 2–3-locular; false septae incomplete; stylodia 2-3, distinct; stigmas minute. Capsule splitting into 4–6 one-seeded valves. Seeds oblong to clavate, triangular or wedge-shaped in cross-section. $2n = 34, 36$.

Thirteen spp., California and Oregon.

13. ***Cliococca*** Bab.

Cliococca Bab., Proc. Linn. Soc. Lond. 1: 90 (1841), Trans. Linn. Soc. 19: 33 (1842); Rogers & Mildner, Rhodora 73: 560–565 (1971), rev.

Perennial, glabrous herbs with extensively branched underground rootstock. Leaves alternate, linear, 1-nerved; stipular glands absent. Solitary flowers terminal on branches, homostylous; sepals 5, margins entire; petals 5, imbricate, whitish, shorter than sepals; stamens 5; staminodia sometimes present; nectaries present (?); ovary 5-locular; false septae complete; stylodia 5, distinct, very short; stigmas capitate. Capsule indehiscent, 10 one-seeded segments. Seeds elliptic. $2n = 36$.

One sp., *C. selaginoides* (Lam.) Rogers & Mildner, temperate South America.

Selected Bibliography

Aluri, R.J.S., Rama Das, K., Aluri, J.B., Subba Reddi, C., Bahadur, B. 1997. Sexual system and pollination in distylous *Hugonia mystax* L. (Linaceae). J. Palynol. 33: 185–202.

APG II (The Angiosperm Phylogeny Group) 2003. See General References.

Badré, F. 1973. Linaceae. Flore du Gabon 21: 23–39. Paris: Muséum Natl. d'Hist. Nat.

Bahadur, B., Reddy, N.P., Rao, M.M., Farooqui, S.M. 1984. Corolla handedness in Oxalidaceae, Linaceae and Plumbaginaceae. J. Indian Bot. Soc. 63: 408–411.

Bahadur, B., Reddy, N.P., Ramaswamy, N. 1996. Heterostyly and pollen dimorphism in *Reinwardtia indica* Dum. (Linaceae). J. Palynol. 32: 67–77.

Boesewinkel, F.D. 1980. Development of ovule and testa of *Linum usitatissimum* L. Acta Bot. Neerl. 29: 17–32.

Boesewinkel, F.D. 1984. A comparative SEM study of the seed coats of recent and of 900-1100 years old, subfossil linseed. Ber. Deutsch. Bot. Ges. 97: 443–450.

Bolkhovskikh, Z. et al. 1969. See General References.

Chennaveeraiah, M.S., Joshi, K.K. 1983. Karyotypes in cultivated and wild species of *Linum*. Cytologia 48: 833–841.

Collinson, M.E., Boulter, M.C., Holmes, P.L. 1993. Magnoliophyta (Angiospermae). In: Benton, M.J. (ed.) The fossil record 2. London: Chapman & Hall, pp. 809–841.

Corner, E.J.H. 1976. See General References.

Crété, P. 1937. Développement et structure du tégument séminal chez le *Radiola linoides* Roth. Bull. Soc. Bot. France 84: 655–659.

Cunnane, S.C. 2003. The contribution of α-linolenic acid in flaxseed to human health. In: Muir, A.D., Westcott, N.D. (eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 150–180.

D'Alascio Deschamps, R. 1973. Organisation du sac embryonnaire du *Linum catharticum* L., espèce récoltée en station naturelle; étude ultrastructurale. Bull. Soc. Bot. France 120: 189–200.

D'Alascio Deschamps, R. 1981. Embryologie du *Linum catharticum* L. Le zygote: étude ultrastructurale. Bull. Soc. Bot. France 128: 269–278.

Davis, C.C., Chase, M.W. 2004. See General References.

Diederichsen, A., Richards, K. 2003. Cultivated flax and the genus *Linum* L. In: Muir, A.D., Westcott, N.D. (eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 22–54.

Dulberger, R. 1973. Distyly in *Linum pubescens* and *L. mucronatum*. Bot. J. Linn. Soc. 66: 117–126.

Dulberger, R. 1974. Structural dimorphism of stigmatic papillae in distylous *Linum* species. Amer. J. Bot. 61: 238–243.

Dulberger, R. 1981. Dimorphic exine sculpturing in three distylous species of *Linum* (Linaceae). Pl. Syst. Evol. 139: 113–119.

Erdelská, O. 1967. Type of endosperm of the species *Linum austriacum* L. Biologia (Bratislava) 22: 172–176.

Erdtman, G. 1952. See General References.

Grigorieva, V.V. 1989. O dimorfizme pyl'tsy nekotorykh distil'nykh vidov roda *Linum* (Linaceae) [On pollen dimorphism in some distylous species of the genus *Linum* (Linaceae)]. Bot. Zhurn. 74: 65–73.

Hegnauer, R. 1966. See General References.

Hegnauer, R. 1989. See General References.

Heimsch, C., Tschabold, E.E. 1972. Xylem studies in the Linaceae. Bot. Gaz. 133: 242–253.

Heinze, U., Amelunxen, F. 1984. Zur Schleimbildung in *Linum*-Samen. Elektronenmikroskopische und chemische Analysen. Ber. Deutsch. Bot. Ges. 97: 451–464.

Heitz, B. 1980. La pollinisation des lins hétérostyles du groupe *Linum perenne* L. (Linacées). Compt. Rend. Acad. Sci. Paris D 290: 811–814.

Heitz, B., Jean, R., Prensier, G. 1971. Observation de la surface du stigmate et des grains de pollen de *Linum austriacum* L., hétérostyle. Compt. Rend. Hébd. Séances Acad. Sci., D 273(25): 2493–2495.

Jardim, A., Berry, P.E. 1999. A new species of *Roucheria* and a new species of *Hebepetalum* (Hugoniaceae) from the Venezuelan Guayana. Novon 9: 520–523.

Johri, B.M. et al. 1992. See General References.

Kearns C.A, Inouye, D.W. 1994. Fly pollination of *Linum lewisii* (Linaceae). Amer. J. Bot. 81: 1091–1095.

Kumar, P.V., Bahadur, B. 1978. Structure of the epidermis and ontogeny of stomata in *Reinwardtia indica* Dum. (Linaceae). Indian J. Bot. 1: 127–131.

Lloyd, D.G., Webb, C.J., Dulberger, R. 1990. Heterostyly in species of *Narcissus* (Amaryllidaceae) and *Hugonia* (Linaceae) and other disputed cases. Pl. Syst. Evol. 172: 215–227.

Marchenkov, A., Rozhmina, T., Uschapovsky, I., Muir, A. D. 2003. Cultivation of flax. In: Muir, A.D., Westcott, N.D. (eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 74–91.

Matthews, M.L., Endress, P.K. 2011. See General References.

Mazer, S.J., Tiffney, B.H. 1982. Fruits of *Wetherellia* and *Palaeowetherellia* (?Euphorbiaceae) from Eocene sediments in Virginia and Maryland. Brittonia 34: 300–333.

McDill, J.R., Repplinger, M., Simpson, B.B., Kadereit, J.W. 2009. The phylogeny of *Linum* and Linaceae subfamily Linoideae, with implications for their systematics, biogeography, and evolution of heterostyly. Syst. Bot. 34: 386–405.

McDill, J.R., Simpson, B.B. 2011. Molecular phylogenetics of Linaceae with complete sampling and data from two plastid genes. Bot. J. Linn. Soc. 165: 64–83.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Muller, J. 1981. See General References.

Muravenko, O.V., Bolsheva, N.L., Yurkevich, O.Y., Nosova, I.V., Rachinskaya, O.A., Samatadze, T.E., Zelenin, A.V. 2010. Karyogenomics of species of the genus *Linum* L. Russ. J. Genet. 46: 1182–1185.

Narayana, L.L. 1964. A contribution to the floral anatomy and embryology of Linaceae. J. Indian Bot. Soc. 43: 343–357.

Narayana, L.L., Rao, D. 1973. Contributions to floral anatomy of Linaceae 5. J. Jap. Bot. 48: 205–208.

Narayana, L.L., Rao, D. 1978. Contributions to the floral anatomy of Linaceae (14). J. Jap. Bot. 53: 300–312.

Pengilly, N.L. 2003. Traditional food and medicinal uses of flaxseed. In: Muir, A.D., Westcott, N.D. (eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 252–267.

Prasad, K. 2003. Flaxseed in the prevention of cardiovascular diseases. In: Muir, A.D., Westcott, N.D. (eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 204–213.

Raven, P. 1959. Documented chromosome numbers of plants. Madroño 15: 49–52.

Rickard-Bon, S.E., Thompson, L.U. 2003. The role of flaxseed lignans in hormone-dependent and independent cancer. In: Muir, A.D., Westcott, N.D.

(eds.) Flax – The genus *Linum*. London, New York: Taylor & Francis, pp. 181–203.

Robertson, K.R. 1971. The Linaceae in the southeastern United States. J. Arnold Arbor. 52: 649–665.

Rogers, C.M. 1980. Pollen dimorphism in distylous species of *Linum* sect. *Linastrum* (Linaceae). Grana 19: 19–20.

Rogers, C.M. 1985. Pollen morphology of the monotypic genus *Cliococca* (Linaceae). Grana 24: 121–123.

Rogers, C.M., Xavier, K.S. 1971. Pollen morphology as an aid in determining relationships among some widely separated Old World species of *Linum*. Grana 11: 55–57.

Rogers, C.M., Mildner, R., Harris, B.D. 1972. Some additional chromosome numbers in the Linaceae. Brittonia 24: 313–316.

Roth, I. 1977. Fruits of angiosperms. Handbuch der Pflanzenanatomie, ed. 2, vol. 10(1). Berlin, Stuttgart: Bornträger, pp. 233–235.

Saad, S.I. 1961. Pollen morphology and sporoderm stratification in *Linum*. Grana 3: 109–129.

Saad, S.I. 1962. Palynological studies in the Linaceae. Pollen Spores 4: 65–82.

Soltis, D.E. et al. 2011. See General References.

Souèges, R. 1937. Développement de l'embryon chez le *Radiola linoides* Roth. Bull. Soc. Bot. France 84: 297–306.

Ströbl, F. 1925. Die Obdiplostemonie in den Blüten. Bot. Archiv 9: 210–224.

Sugawara, T., Tanaka, N., Murata, J., Zaw, K.M. 2002. Dimorphism of pollen grains and stigmas in the heterostylous subshrub, *Reinwardtia indica* (Linaceae) in Myanmar. Acta Phytotax. Geobot. 53: 173–180.

Sutter, D., Endress, P.K. 1995. Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. Bot. Jahrb. Syst. 116: 517–536.

Takhtajan, A.L. (ed.) 1980. See General References.

Thompson, J.D., Pailler, T., Strasberg, D., Manicacci, D. 1996. Tristyly in the endangered Mascarene Island endemic *Hugonia serrata* (Linaceae). Amer. J. Bot. 83: 1160–1167.

Troll, W. 1964. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers, I. Jena: Fischer.

Troll, W., Weberling, F. 1989. Infloreszenzuntersuchungen an monotelen Familien. Stuttgart, New York: Fischer.

Uno, G.E. 1984. The role of persistent sepals in the reproductive biology of *Linum pratense* (Linaceae). Southwest. Nat. 29: 429–433.

Vazart, J. 1969. Organisation et ultrastructure du sac embryonnaire du Lin (*Linum usitatissimum* L.). Rev. Cytol. Biol. Veg. 32: 227–240.

Vazart, J. 1971. Dégénérescence d'une synergide et pénétration du tube pollinique dans le sac embryonnaire de *Linum usitatissimum* L. Ann. Univ. A.R.E.R.S. 9: 89–97.

Vazart, B., Vazart, J. 1965. Infrastructure de l'ovule de lin, *Linum usitatissimum* L. L'assise jaquette ou endothélium. Compt. Rend. Hébd. Séances Acad. Sci. Paris 261: 2927–2930.

Vazart, B., Vazart, J. 1966. Infrastructure du sac embryonnaire du lin (*Linum usitatissimum* L.). Rev. Cytol. Biol. Vég. 29: 251–266.

van Hooren, A.M.N., Nooteboom, H.P. 1984. Linaceae and Ctenolophonaceae especially of Malesia, with notes on their demarcation and the relationships with Ixonanthaceae. Blumea 29: 547–563.

van Welzen, P.C., Baas, P. 1984. A leaf anatomical contribution to the classification of the Linaceae complex. Blumea 29: 453–479.

Winkler, H. 1931. Linaceae. In: Engler, A., Harms, H. (eds.) Die natürlichen Pflanzenfamilien, ed. 2, 19a. Leipzig: Engelmann, pp. 82–130.

Xavier, K.S., Mildner, R.A., Rogers, C.M. 1980. Pollen morphology of *Linum*, sect. *Linastrum* (Linaceae). Grana 19: 183–188.

Xi, Z., Ruhfel, B.R., Schaefer, H., Amorim, A.M., Sugumaran, M., Wurdack, K.J., Endress, P.K., Matthews, M.L., Stevens, P.F., Mathews, S., Davis, C.C. 2012. Phylogenomics and a posteriori data partitioning resolve the Cretaceous angiosperm radiation Malpighiales. Proc. Natl. Acad. Sc. (PNAS) 109(43): 17519–17524.

Lophopyxidaceae

Lophopyxidaceae (Engl.) H.H. Pfeiffer in Rev. Sudamer. Bot. 10: 4 (1951).
Lophopyxidoideae Engler in Engler & Prantl, Nat. Pflanzenfam. III, 5: 257 (1893) (in Icacinaceae).

K. KUBITZKI

Monoecious climbing shrubs or small trees with watch-spring tendrils; branches with lateral bud at the base; cork superficial. Leaves spiral, simple, serrulate to crenulate, domatiiferous; stipules small, knob-like. Inflorescence a loose axillary panicle with flowers in distant glomerules, the basal bracts often transformed into completely coiled tendrils. Flowers regular, sessile, small, 5-merous; sepals basally connate, valvate, persistent; petals distinct, much smaller than sepals; disk yellowish; staminate flowers: stamens 5(6), antesepalous, with filiform filaments and subglobose, introrse, almost basifixed anthers, alternating with 5(6) antepetalous cordate glands ± adnate to the petals; pollen grains subprolate, 3-colporate, exine reticulate; pistillode subglobose, hairy; pistillate flowers: glands concrescent into a 5(6)-lobed disk with the glands or lobes opposite the ovary cells; gynoecium 5(4)-carpellate, carpels antepetalous; ovary superior, 5(4)-locular, ovoid-oblong, shallowly ribbed; ovules 2 per locule, pendulous, apical-axile, anatropous, epitropous, each surmounted at the micropyle by a small obturator-like appendage originating from the funicle; stylodia 5(4), minute, subulate, stigmatic. Fruit indehiscent, fusiform, 1-locular and 1-seeded, with 5 broad stramineous wings. Seed oblong, albuminous; embryo erect, with oblong cotyledons and a short erect radicle.

A single genus and sp., *Lophopyxis maingayi* Hook. f., in forests from the Malay Peninsula through Malesia to the Solomon and Caroline islands.

VEGETATIVE MORPHOLOGY AND ANATOMY (Information from Handa 1940 and Baas in Sleumer 1971). Axillary branchlets are metamorphosed into strong woody tendrils, which distally are coiled and often bear a bud. The petiole shows a strongly incurved arc of separate bundles; the vascular system of the midrib forms a closed flattened cylinder. Stomata are paracytic. Crystals are present as solitary rhomboids and clusters. Hairs are unicellular. The young stem has five ribs with a continuous xylem cylinder, which encloses a pentagonal pith with a central portion of thick-walled parenchyma cells and a marginal area of thin-walled cells; Engler (1893) erroneously interpreted it as intraxylary phloem. Between the ribs the secondary xylem has numerous vessels; in the ribs the vessels are narrower and scarcer. Vessel element perforation is simple. Through anomalous activity of the cambium, five phloem strands become enclosed within the xylem in the young shoot. Later intraxylary phloem is formed as continuous bands alternating with secondary xylem. The phloem is stratified into soft and fibrous portions. Axial parenchyma is scarce and paratracheal. The ground tissue of the xylem consists of fibres with numerous minutely bordered pits. Rays vary from 1–6-seriate in the young stem. The outer phloem is surrounded by a cylinder of fibres and stone cells. Cork arises in the subepidermal layer.

EMBRYOLOGY. The ovule is bitegmic and weakly crassinucellate (Mauritzon in Sleumer 1942).

POLLEN MORPHOLOGY. Pollen is 3–4-colporate, subprolate, 26 μm long (Erdtman 1952) or foveate, 39 × 30 μm (Dahl 1955).

ECOLOGY. Sleumer (1971) reports *Lophopyxis* as a straggling climber at the edge or in the canopy of primary lowland forests, both in well-drained and swamp forest, in littoral forest and even sometimes in mangroves, from sea level up to ca. 300 m.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_17,

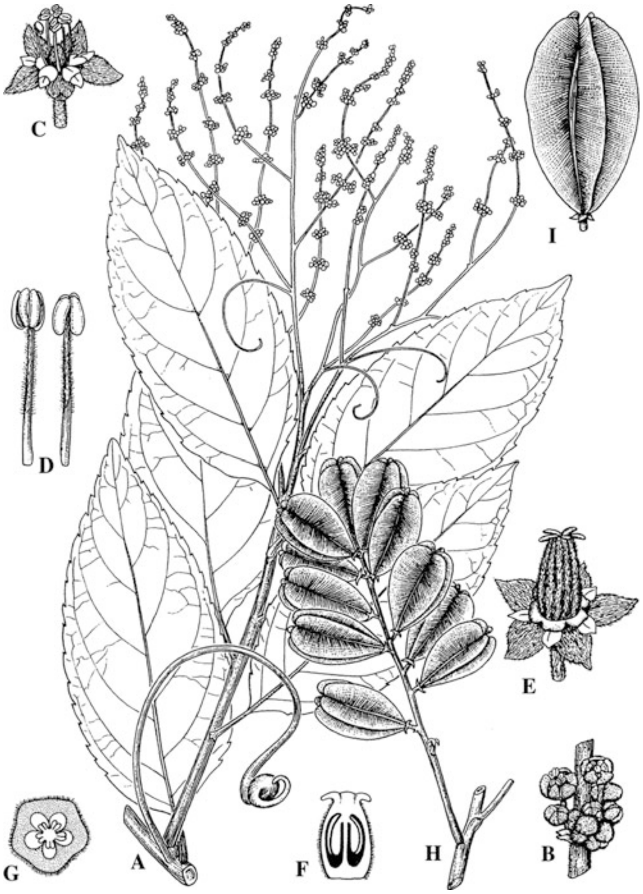

Fig. 57. Lophopyxidaceae. *Lophopyxis maingayi*. **A** Habit. **B** Staminate flower buds. **C** Staminate flower. **D** Stamens, front and back view. **E** Pistillate flower. **F** Pistil vertically sectioned. **G** Ovary, cross section. **H** Infructescence. **I** Fruit. (Sleumer 1971)

AFFINITIES. Formerly (and sometimes still recently) *Lophopyxis* was placed in or close to Euphorbiaceae, Icacinaceae or Celastraceae, plus four further families (see Sleumer 1968 for details), but Pfeiffer (1951) found neither position defendable and suggested family rank for it. Lophopyxidaceae are resolved as the strongly supported sister to Putranjivaceae (Wurdack and Davis 2009; Soltis et al. 2011) with which they share paracytic stomata, unisexual 5-merous flowers with a disk or disk segments, 2 apical epitropous ovules per carpel, and 1-seeded fruits (Stevens 2001 onwards). The clade of Lophopyxidaceae and Putranjivaceae, the "putranjivoids", has now been resolved as part of a well-supported tetratomy that otherwise includes the chrysobalanoids, the malpighioids and the Caryocaraceae (Xi et al. 2012).

A single genus:

Lophopyxis **Hook. f.** Fig. 57

Lophopyxis Hook. f. in Hook., Icon. Pl. 18: t. 1714 (1887).

Description as for family.

Selected Bibliography

Dahl, A.O. 1955. The pollen morphology of several genera excluded from the family Icacinaceae. J. Arnold Arbor. 36: 159–163, 1 pl.
Engler, A. 1893. S.-B.Preuss. Akad. Wiss. Berlin 18: 265–266 (a note on *Lophopyxis* in an article about anatomical characters of Icacinaceae).
Erdtman, G. 1952. See General References.
Handa, T. 1940. Anomalous secondary growth in the axis of *Lophopyxis pentaptera* (K. Schum.) Engler. Bot. Mag. Tokyo 54: 41–47, figs. 1–6.
Pfeiffer, H. 1926. Das abnorme Dickenwachstum. In: Linsbauer, H., Handbuch der Pflanzenanatomie, vol. 9. Berlin: Borntraeger.
Pfeiffer, H.H. 1951. *Lophopyxis* als Typus einer eigenen Familie. Rev. Sudamer. Bot. 10: 3–6.
Sleumer, H. 1942. *Lophopyxis*. In: Engler & Prantl, Nat. Pflanzenfam. ed. 2, 20b, pp. 392–396. Leipzig: W. Engelmann.
Sleumer, H. 1968. The genus *Lophopyxis* Hook.f. (Lophopyxidaceae). Blumea 16: 321–323.
Sleumer, H. 1971. Lophopyxidaceae. In: Flora Males. I, 7: 89–92. Leyden: Nordhoff.
Soltis, D.E. et al. 2011. See General References.
Stevens, P.F. 2001 onwards. See General References.
Wurdack, K.J., Davis, C.C. 2009. See General References.
Xi, Z. et al. 2012. See General References.

Medusagynaceae

Medusagynaceae Engler & Gilg (1924), nom. cons.

W.C. Dickison† and K. Kubitzki[1]

Small tree with a rounded crown. Leaves opposite, simple, elliptic or elliptic-oblong, glabrous, with a retuse apex and apical sinus, an attenuate base, and fine, widely spaced marginal glandular teeth, apical sinus contains a colleter on either side of the depression and a single one at the base of the cavity; stipules 0. Inflorescences lax, multiflowered, paniculate. Flowers regular, hypogynous, bisexual and male, the plants andromonoecious; staminate flowers without evidence of an abortive gynoecium; sepals 5, connate at the base, quincuncial in their distinct apices; petals 5, contort, at first spreading, later reflexed; stamens numerous, filaments distinct, slender, anthers basifixed, bithecate and tetrasporangiate, latrorse, dehiscing by slits; connective shortly protruding as apical extension; carpels numerous, 16–25, attached to central axis, each on its outer shoulder with a short stylodium and capitate stigma; ovules anatropous, epitropous, bitegmic, 2 per locule, on separate axile placentas, one ascending, the other descending; endosperm cellular. Fruit a septicidal capsule, each carpel separating acropetally from the central column along its entire margin, the dehisced carpels only maintaining a distal connection to the persistent columella. Seeds winged, with a thin layer of endosperm and a straight embryo.

A single genus and sp., *Medusagyne oppositifolia* J.G. Baker, endemic to Mahé of the Seychelles Islands, where it occurs at middle altitudes in pockets of soil between granite masses (Hemsley 1905).

Vegetative Morphology and Anatomy. *Medusagyne* grows to about 10 m in height; its trunk is up to 20 cm in diameter with dark, fibrous, striated bark (Robertson et al. 1989). Vegetative anatomy was described by Beauvisage (1920) and Dickison (1990a). Leaves are subcoriaceous with pinnate and brochidodromous venation. Veins are surrounded by a double sheath, a dense inner fibrous zone and an outer, parenchymatous layer. The petiole contains numerous small collateral bundles having various orientations and arranged in an arc. The mesophyll contains mucilaginous and crystalliferous cells. Cristarque cells have not been found. Nodal anatomy is multilacunar, multitrace, an infrequent pattern in dicotyledons with opposite leaves (Dickison 1990a). As described by Dickison (1990a), the wood contains solitary vessel elements with simple perforations. Intervascular pitting is opposite to predominantly alternate. Tracheids are present. Rays are heterogeneous with both uniseriates and multiseriates; axial parenchyma is diffuse and diffuse-in-aggregates, also paratracheal scanty. Tanniniferous tissue is present throughout the plant body. Sieve-tube plastids are of the S-type (H.-D. Behnke, pers. comm.).

Floral Morphology and Anatomy. The actinomorphic flowers are either bisexual or staminate (Robertson et al. 1989; Dickison 1990a). Nothing is known of the pollination biology or breeding system. Bisexual flowers possess numerous, distinct stamens that surround the gynoecium in layer-like groups that differ in length and are vascularized by the breakup of individual stamen fascicle traces (stamen trunk bundles). The biovulate carpels

---

[1] In his paper on *Medusagyne* (Dickison 1990a) and in the manuscript to this contribution, the late Dr. Dickison had ascribed spiral phyllotaxis to the androecium of *Medusagyne*, which definitely does not exist there; I have deleted this from the manuscript, and also added some recent information on the family.

K. Kubitzki

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_18, © Springer-Verlag Berlin Heidelberg 2014

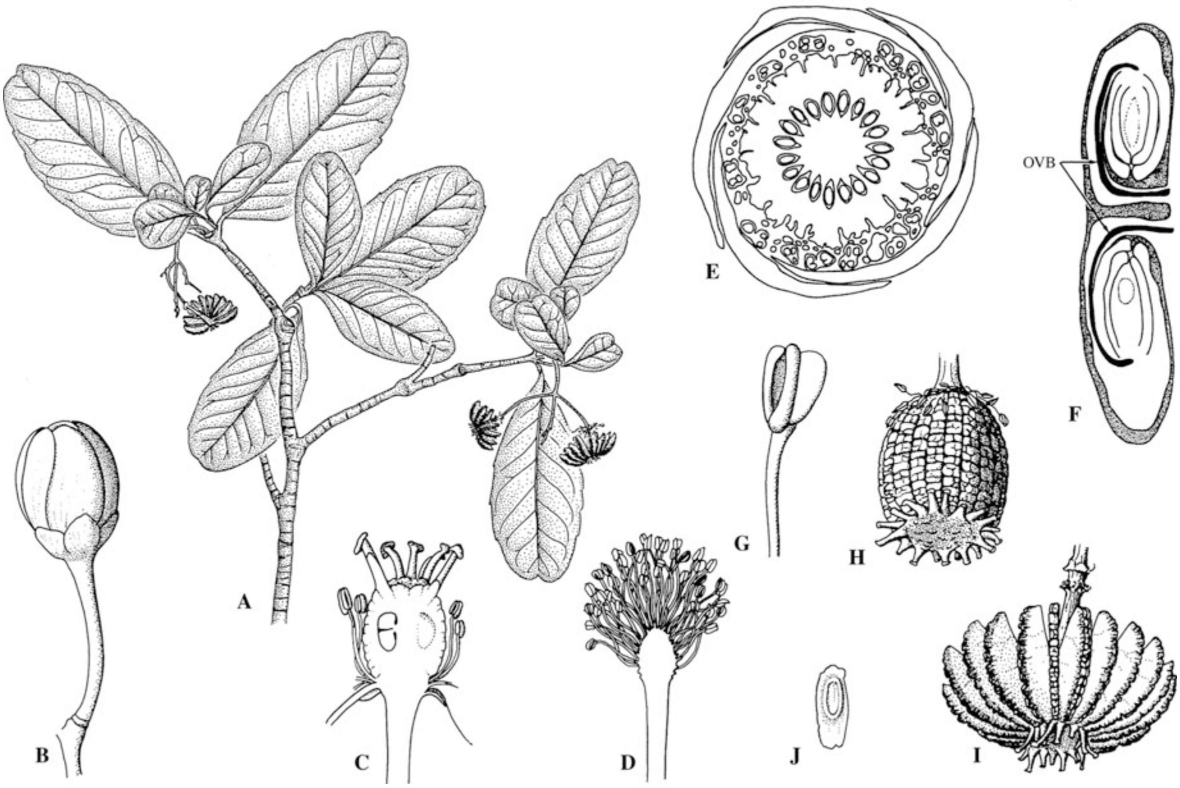

Fig. 58. Medusagynaceae. *Medusagyne oppositifolia*. **A** Fruiting branching. **B** Flower bud. **C** Bisexual flower, vertical section. **D** Staminate flower, vertical section. **E** Bisexual flower, transverse section. **F** Carpel locule, vertical section showing biovulate condition and ovulary vascular supply (OVB). **G** Stamen. **H** Fruit. **I** Open fruit. **J** Seed. (**A** original; **B**–**D** Robertson, Wise & White 1989; **E**, **F** Dickison 1990a)

occur in a single whorl and are borne on the sides of a broad, elongated torus that represents the upward extension of the receptacle. In a manner somewhat comparable to *Dillenia* (Dilleniaceae), carpels show pronounced ontogenetic adaxial deformation, during which the upper ventral surfaces become expanded, greatly extending the ventral margins and forming a domelike cushion of carpel-derived tissue over the summit of the torus (Dickison 1990b). Details of floral vascularization were presented by Dickison (1990a, b).

EMBRYOLOGY. The anther wall contains a subdermal endothecial layer with cells having well-developed bands of secondary thickenings and an inner tapetal layer. Each carpel locule contains a pair of superimposed ovules attached separately on axile placentae. Funiculi are long and curved. The upper ovule of the pair is ascending or erect, micropyle below, raphe dorsal. The micropyle is straight. The inner integument is 3–4 cells thick, and the outer epidermal cells of the inner integument differentiate into a fibrous layer in the seed. Ovules are weakly crassinucellate and vascularized by a single bundle that extends unbranched from the funiculus to the chalaza. Embryo sac and embryo development are unknown.

POLLEN. Pollen is subisopolar, i.e. the distal and proximal faces are unequal, one being very convex, the other less convex, triporate, semiangular, small (13–15 x 14–17 μm). Apertures protrude. Sculpture striate, intertwined at different levels. At the TEM level, pollen is tectate-columellate with a massively developed foot layer (Dickison 1990a).

Fruit and Seed. As the fruit matures, carpels unfold on a radial frame from the base upwards in a manner resembling the ribs of an umbrella. In mature pericarps an inner region of thick-walled, lignified cells lines the locules. Seeds are small, c. 3.0 mm in length, compressed, winged and exarillate with reduced endosperm. The mature seed coat is exotegmic-exotestal with 4 or 5 layers of cells with thickened and suberized walls and a tegmic layer of thick-walled, lignified fibres. The endosperm is represented by a narrow, cellular zone without starch. The embryo is straight. See the detailed study of the fruit and seed anatomy by Doweld (1998).

Affinities. The totality of the structural evidence confirms the view that *Medusagyne* is a very distinct genus. Cladistic analyses based on the plastid gene *rbc*L by Fay et al. (1997) place *Medusagyne* in a clade with Quiinaceae and Ochnaceae, and Xi et al. (2012) resolve it with moderate support in a sister position with Quiinaceae. With these families, *Medusagyne* shares various characters including multilacunar nodes, mucilage cells and dentate leaves, but differs in, i.a., the organisation of the petiolar vascular supply.

Distribution and Habitats. *Medusagyne oppositifolia* is endemic to Mahé, the largest island in the Seychelles group. It occurs as a very rare component of the intermediate forest zone.

Conservation. The genus was once feared extinct, and even today only very few individual plants remain alive in scattered populations. One locality is now a national park nature reserve, although the area is threatened by a proposed dam construction. Attempts to cultivate *Medusagyne* have met with somewhat limited success.

One monotypic genus:

Medusagyne J.G. Baker Fig. 58

Medusagyne J.G. Baker, Fl. Mauritius Seych.: 17 (1877).

Characters as for family.

Selected Bibliography

Baker, J.B. 1877. Flora of Mauritius and the Seychelles: a description of the flowering plants and ferns of those islands. London: L. Reeve & Co.

Beauvisage, L. 1920. Contribution a l'étude anatomique de la famille des Ternstroemiacées. Doctoral diss., Univ. de Poitiers. Tours: E. Arrault et Cie.

Dickison, W.C. 1990a. The morphology and relationships of *Medusagyne* (Medusagynaceae). Pl. Syst. Evol. 171: 27–55.

Dickison, W.C. 1990b. An additional note on the floral morphology and affinities of *Medusagyne oppositifolia* (Medusagynaceae). Brittonia 42: 191–196.

Doweld, B. 1998. On the phylogenetic relationships of *Medusagyne* (Medusagynaceae) as evidenced by the structure of its fruits and seeds. Bot. Zhurn. 83: 54–68.

Fay, M.F., Swensen, S.M., Chase, M.W. 1997. Taxonomic affinities of *Medusagyne oppositifolia*. (Medusagynaceae). Kew Bull. 52: 111–120.

Hemsley, W.B. 1905. *Medusagyne oppositifolia* J. G. Baker. Hook. Icon. Plant. IV, 8: 1–3, pl. 2790.

Hickey, L.J., Wolfe, J.A. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Matthews, M.L. et al. 2012. See General References.

Robertson, A., Wise, R., White, F. 1989. *Medusagyne oppositifolia*. Kew Mag. 6: 166–171.

Soltis, D.E. et al. 2011. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Ochnaceae

Ochnaceae DC., Nouv. Bull. Sci. Soc. Philom. Paris 2: 209 (1811), nom. cons.

M.C.E. Amaral and V. Bittrich

Trees, shrubs or shrublets, generally evergreen, rarely herbs, mostly glabrous. Leaves alternate, generally simple, often coriaceous, entire, serrate, ciliate or with persistent or caducous teeth, secondary veins often numerous and densely parallel; stipules distinct or more rarely basally intrapetiolarly connate, persistent or caducous, entire or laciniate. Inflorescences terminal or axillary, cymose or racemose, more rarely flowers solitary in leaf axils. Flowers on articulated pedicels, generally bisexual, actinomorphic or zygomorphic; sepals generally 5, mostly distinct, imbricate or nearly valvate, caducous or persistent, sometimes accrescent, enveloping the mature bud or not; petals generally 5, mostly distinct, imbricate, contort (cochlear or quincuncial), caducous; stamens 5–10–∞, rarely 1, with sometimes persistent filaments, generally distinct, anthers basifixed, bithecate, tetrasporangiate, dehiscing latrorsely with longitudinal slits or with one or two apical or subapical pores; staminodes present or absent, distinct or ± connate, petaloid or not, sometimes completely enveloping stamens and gynoecium; nectary absent; ovary superior, (2)3(4) or 5(–15)-carpellate, syncarpous at least at the basal part of the ovary, and either entire with one apical style or deeply and apparently completely divided into five to several uniovulate lobes with one gynobasic style; style distinct from or continuous with the ovary apex; androgynophore and gynophore usually present, often inconspicuous; placentas (2) 3(4) or 5(–15) basal, axile or parietal, stigmas distinct or connate. Fruit generally a septicidal capsule, rarely a nut or drupe, or separating into 2 to several blackish drupelets on an accrescent reddish receptacle. Seeds exarillate, albuminous or exalbuminous, winged or not; embryo straight or curved.

A pantropical family of 27 genera with about 500 spp., divided into three subfamilies.

Vegetative Morphology. The great bulk of the Ochnaceae are evergreen shrubs or small trees. Annual or perennial herbs are restricted to a few *Sauvagesia* spp., larger trees occur in *Lophira* and some species of *Brackenridgea*. The leaves are often coriaceous and glossy, petiolate, alternate and stipulate. Phyllotaxy is generally distichous on plagiotropic branches and spiral on orthotropic branches. The young shoots of *Perissocarpa* are densely covered with cataphylls (Wallnöfer 1998). The stipules are distinct or more rarely at base intrapetiolarly connate (*Campylospermum*, *Rhabdophyllum*, *Idertia*, *Testulea*), entire, toothed or laciniate, persistent or caducous, leaving small or conspicuous scars. Stipules in *Ouratea* sometimes form extrafloral nectaries (Oliveira and Leitão Filho 1987).

The leaves are simple, with the exception of *Rhytidanthera*. The margins are straight, crenate, serrate or serrulate, and mostly denticulate, ciliate in some *Luxemburgia* spp. Many genera of all subfamilies show leaves with rather closely spaced, rigidly parallel secondary veins, with the tertiary veins perpendicular or more rarely nearly parallel to these. Secondary veins curving strongly near the margin and continuing more or less parallel to it are typical for *Ouratea* and related genera (Fig. 59A).

Vegetative Anatomy. Most information of the literature is summarized in Solereder (1899 and 1908), Metcalfe and Chalk (1950), Carlquist (1988) and Amaral (1991). Cristarque cells with a solitary sphaerocrystal are a typical feature of the family (Solereder 1899), and not only for the Ochnoideae as assumed by Van Tieghem (1902a) and Metcalfe and Chalk (1950). Details about petiole vascularization were reported (partly contradictory) by Metcalfe and Chalk (1950), Decker (1967) and Schofield (1968). A simple arc

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_19, © Springer-Verlag Berlin Heidelberg 2014

with two lateral traces occurs in *Sauvagesia* p.p. and *Tyleria*. The bundles may form a solid siphonostele in the upper part of the petiole or in the blade (e.g. *Elvasia*, *Lophira*, *Luxemburgia*, *Ochna*, *Wallacea*), sometimes with medullary bundles (Schofield 1968), or they remain separate throughout the leaf partly forming a dissected siphonostele with some medullary bundles (e.g. *Ochna*, *Ouratea*, *Sauvagesia* p.p.). According to Decker (1967), the latter condition is also characteristic for *Euthemis* and a group (probably a clade) formed by *Cespedesia*, *Godoya*, *Rhytidanthera* and *Krukoviella*. According to Metcalfe and Chalk (1950), however, the petiole of *Lophira* shows isolated bundles. Hairs are very rare (*Ouratea* spp., *Elvasia* sp.), they are unicellular or uniseriate multicellular. The epidermis has commonly some mucilage cells (e.g. *Elvasia*, *Ochna*, *Ouratea*, *Luxemburgia*), not rarely the cell walls become lignified. Stomata are paracytic, sometimes with three subsidiary cells (*Sauvagesia*, *Lophira*). They are mostly restricted to the abaxial side, more rarely they occur on both sides (*Ouratea* spp., *Lophira lanceolata*), in *Cespedesia* they are restricted adaxially to the midrib (Sastre 1975a). Hydathodes were reported by Sastre (1975b) from *Sauvagesia erecta* and *Cespedesia*. Thick glandular hairs, probably colleters, occur on the inner stipule base in *Cespedesia*. The sepals of *Godoya* and *Rhytidanthera* have very similar glandular hairs at their inner base, while marginal glands are found in several genera of Sauvagesioideae s.str.

The mesophyll is generally dorsiventral. Cristarque cells with druses are common in the region of the midrib and the lateral veins. A hypodermis was observed in *Lophira* and *Elvasia*. Spicular cells occur as a layer under the upper epidermis in a few genera (e.g. *Blastemanthus*, *Cespedesia*). Distinct fibres in the mesophyll occur in *Cespedesia* and *Rhytidanthera*, and mucilage-filled cavities in the mesophyll of *Euthemis* (Schofield 1968).

Cortical vascular bundles are distributed throughout the family (lacking in, e.g. *Krukoviella* and *Poecilandra*), while medullar bundles are rare (e.g. *Godoya*, *Rhytidanthera* and *Cespedesia*). Nodes are multilacunar with many leaf traces (e.g. *Cespedesia*, *Rhytidanthera*), or trilacunar with generally three (e.g. *Schuurmansiella*, *Sauvagesia* p.p.) or, more rarely, many leaf traces (*Blastemanthus*, *Poecilandra*, *Wallacea*). Growth rings are sometimes evident. Stone cells are common in the cortex. The initiation of cork development is superficial, sometimes even starting in the epidermis (e.g. *Ochna*, *Godoya*). *Euthemis*, *Sauvagesia* and *Schuurmansia* are characterized by large mucilage cells in the cortex and medulla (data from Decker 1966; Schofield 1968).

Wood anatomy in Sauvagesioideae is rather homogeneous, with the exception of *Tyleria* and *Testulea*, while the Ochnoideae are more heterogeneous. The pericycle is formed by small isolated fibre bundles, rarely the cells between the fibre bundles become sclerified (*Ouratea*). Vasicentric tracheids are rare (*Lophira*), septate fibre tracheids are common, and libriform fibres were found in a few genera (*Tyleria*, *Wallacea*). Vessels elements occur solitary or rarely in multiples, their perforation in most species is simple or more rarely both simple and scalariform. Diagonal aggregation of vessel elements was observed in *Lophira*. As regards vestured pits, first reports indicated that they are characteristic only for the Ochnoideae and absent in the Sauvagesioideae (Bailey 1933). Jansen et al. (2001), however, found vestured pits also in various genera of Sauvagesioideae s.str. (e.g. *Testulea*, *Wallacea*) and in *Luxemburgia* (Luxemburgioideae). They were absent only in *Sauvagesia* (one sp. investigated). Helical thickenings in vessels are sometimes present. According to Decker (1966), unilateral compound pitting between parenchyma and vessel elements (which show the large pits) is typical for the Sauvagesioideae (except *Testulea*) and absent in the Ochnoideae. It is unclear, however, in how many genera this was actually observed. Rays are mostly of the heterogeneous type (mainly Kribs type IIA), but homogeneous in *Lophira* and *Testulea*; they are (1)2–5(–8)-seriate. Axial parenchyma is scanty, it is paratracheal to vasicentric (*Blastemanthus*, *Cespedesia*) or diffuse apotracheal (e.g. most Ochnoideae), while in *Lophira* it forms broad distinctive metatracheal bands (Decker 1966). A chambered crystalliferous axial parenchyma is present in *Elvasia*, *Lophira* and *Cespedesia*. The tissue of the pith often becomes early lignified. That of *Lophira* contains chambered crystalliferous fibres.

Inflorescence and Flower Structure. Most species have cymose or racemose terminal, determinate or indeterminate inflorescences, only a few have single axillary flowers. Inflorescence types comprise racemes (e.g. *Luxemburgia*), panicles (e.g. *Schuurmansia*) and thyrses (e.g. *Cespedesia*) with dichasial or monochasial branching. The pedicels are always articulated, generally near the base, more rarely in the middle or near the apex of the pedicel. The receptacle of the flowers of all genera of Ochnoideae with gynobasic styles enlarges during fruit development and becomes red-coloured.

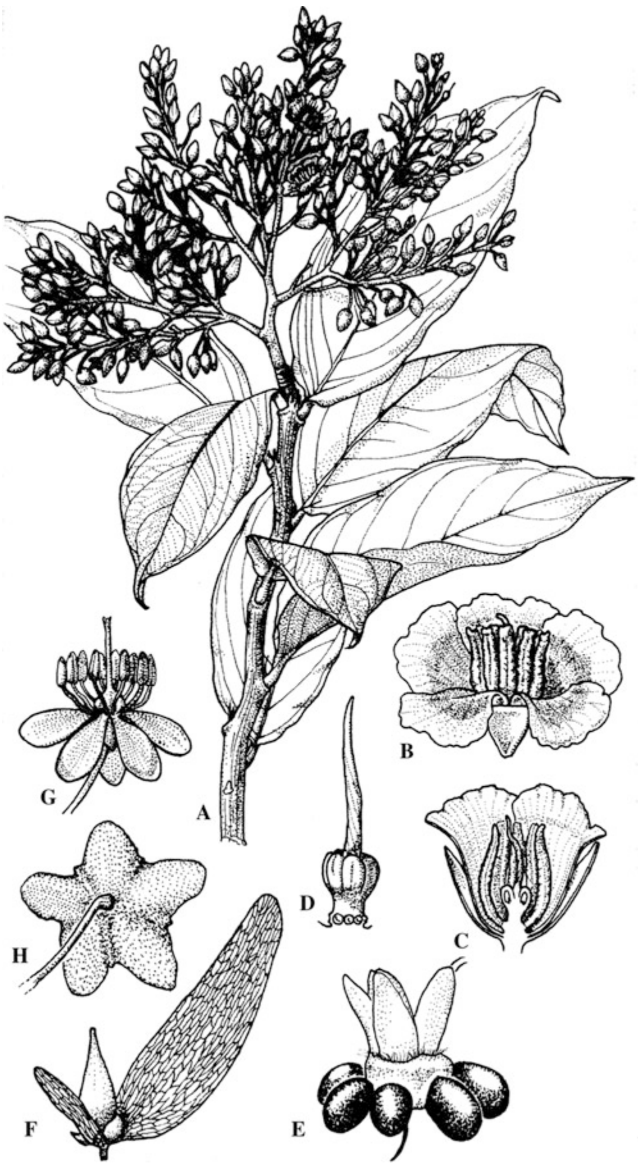

Fig. 59. Ochnaceae. **A–H** Subfam. Ochnoideae. **A–D** *Ouratea spectabilis*. **A** Flowering branch. **B** Flower. **C** Longitudinal section of flower; note gynobasic style. **D** Pistil, gynophore and very short filaments. **E** *Ochna serrulata*. Fruit with drupaceous mericarps on enlarged receptacle. **F** *Lophira alata*. Fruit with two enlarged sepals. **G**, **H** *Elvasia calophyllea*. **G** Flower. **H** Fruit. (**A–D** redrawn from Engler 1876, all others orig.)

A detailed comparative floral morphological and anatomical study of the Malpighiales family clade Ochnaceae/Quiinaceae/Medusagynaceae was undertaken by Matthews et al. (2012). Flowers are actinomorphic or zygomorphic. The Ochnoideae are characterized by actinomorphic flowers while, in Luxemburgioideae and Sauvagesioideae s.str., 7 of the 14 genera have zygomorphic flowers. Calyx and corolla, however, are always basically actinomorphic. In several genera (e.g. *Cespedesia*, *Blastemanthus*) zygomorphy develops only during anthesis, with stamens shifting to the adaxial side of the flowers and the ovary to the abaxial side (Fig. 60G). Only in three genera does zygomorphy exist already before anthesis: In Luxemburgioideae the androecium surrounds the ovary only on the adaxial side of the flowers (Fig. 60H), while *Testulea* (Sauvagesioideae) has only one adaxial stamen. Sepals are generally distinct, rarely they are congenitally united at the base and in *Perissocarpa* connate for most of their length. In *Ouratea* and segregated palaeotropical genera and in *Brackenridgea nitida*, the margins of the inner sepals are cleaved and clasp the margins of the outer ones ("quinconciale engrainée", Van Tieghem 1902b). Most genera of the Ochnaceae have five sepals; only *Testulea* with four, *Elvasia* with 2–6 and *Blastemanthus* with 10–15 sepals show deviating numbers. The outer sepals of some genera (e.g. *Poecilandra*, *Godoya*) are much smaller than the inner sepals. In *Blastemanthus*, the outer sepals are small and distichous (possibly bracts rather than sepals) and the inner ones are larger and spirally arranged. Aestivation of the sepals is mostly imbricate (quincuncial or more rarely cochlear) or, more rarely, nearly valvate. Sepals in most genera envelop the mature bud completely, in a few genera only its basal part (e.g. *Euthemis*, *Schuurmansia*, *Cespedesia*). Sepals are caducous or persistent. In most Ochnoideae with gynobasic styles, the sepals are accrescent and become red during fruit development like the receptacle. In *Lophira* the two outer sepals are prolonged and form the wings of the samaroid fruit (Fig. 59F). Marginal glands (*Adenarake*) and basally adaxial (*Godoya*, *Rhytidanthera*) colleters-like glands on the sepals are of unknown function.

Petals are usually distinct, but very short sympetaly occurs in *Cespedesia* and *Euthemis*. Postgenital fusion of the upper parts of the early caducous petals occurs in *Perissocarpa* (Wallnöfer

Fig. 60. Ochnaceae. **A–G** Subfam. Sauvagesioideae. **A** *Sauvagesia ericoides*, flower. **B** *S. alpestris*. Flower with partially removed petals showing the connate petaloid staminodes. **C–F** *S. racemosa*. **C** Habit. **D** Staminodes. **E** Capsule with persistent sepals, staminodes and stamens. **F** Separated carpel of a capsule showing the placenta. **G** *Blastemanthus gemmiflorus*, flower. **H–J** Subfam. Luxemburgioideae. **H** *Luxemburgia ciliosa*, flower. **I** *L. octandra*, capsule, dehiscence starts apically. **J** *Philacra auriculata*, capsule, dehiscence starts basically. (**A–F** redrawn from Eichler 1871, **G, H** redrawn from Engler 1876, all others orig.)

1998). The vast majority of genera are characterized by five petals. In *Elvasia* the petal number varies within a species or even within an inflorescence. Aestivation is either imbricate quincuncial (*Blastemanthus*), cochlear (*Luxemburgia* spp.) or usually contort. For the contort condition there exists in some genera a variation called "préfloraison cloisonnée" (Van Tieghem 1902b), whereby the margins of the petals enter between the stamens and spirally enclose the style (*Ouratea* and segregated genera, *Perissocarpa* (Ochnoideae) and *Euthemis* (Sauvagesioideae)). Petals have one (e.g. *Luxemburgia*, *Philacra* (Luxemburgioideae), Ochnoideae, *Sauvagesia*) or three (part of Sauvagesioideae s.str., e.g. *Blastemanthus*, *Cespedesia*) vascular traces.

The number of stamens varies between one (*Testulea*) and more than 50 (*Lophira*), common are five or ten stamens. Filaments are distinct except in *Philacra* and *Luxemburgia*, were they are congenitally connate and persistent. Persistent filaments are also characteristic for the genera of Ochnoideae with gynobasic styles, in some other genera the persistent stamens are enclosed by the persistent sepals (e.g. *Sauvagesia*). Anthers are basifixed, bithecate and tetrasporangiate; at the transition from filament to anther, a complete or incomplete pit may be formed (Matthews et al. 2012). In Ochnoideae, the dorsal pollen-sacs are sometimes smaller than the ventral ones which, according to Eichler (1878: 257), led some earlier authors to the erroneous conclusion that these anthers are monothecate. The anthers dehisce by longitudinal slits of variable length or more commonly by one or two pores. The latter condition is probably primitive within the family (Amaral 1991). Generally, in the poricidal anthers an endothecium is present in the whole anther wall, not only around the pores. This has probably facilitated the evolutionary reversal from poricidal dehiscence to dehiscence by slits. In *Sauvagesia* both dehiscence types occur. In *Luxemburgia*, some Ochnoideae (*Elvasia*, *Campylospermum*) and Sauvagesioideae (*Blastemanthus*, *Tyleria*), however, the endothecium is restricted to the level of the pores. Anthers with one pore are frequently characterized by uneven growth of their apex. The poricidal anthers of *Ouratea* spp. show regular circular constrictions or wrinkles along the thecae (Fig. 59B, C), a condition typical for various buzz-pollinated flowers in the angiosperms. In some species of *Sauvagesia* the connective is prolongated at the anther apex. The anthers of a few genera are covered with wax crystals (e.g. *Wallacea*, *Poecilandra*). In Luxemburgioideae, some Ochnoideae (*Elvasia*, *Ochna*) and Sauvagesioideae (e.g. *Cespedesia*), the anthers are caducous after anthesis. They are generally persistent, however, in flowers with staminodes around the fertile stamens (e.g. *Sauvagesia*).

Staminodes occur in several genera of the Sauvagesioideae s.str., always outside the fertile stamens, both are sometimes united at base (*Sauvagesia*, *Tyleria*). Two types, petaloid and filamentous, can be distinguished. Both may occur in the same flower, with the smaller filamentous staminodes surrounding the petaloid ones (Fig. 60D). Petaloid staminodes are highly variable in size and form. They are distinct or connate at base (*Tyleria*) or connate for more or less their whole length (*Sauvagesia* p.p., Fig. 60B). Often large petaloid staminodes completely envelop the stamens and the gynoecium, leaving only a pore-like opening at the apex (Fig. 60B). Filamentous staminodes are either subulate (*Blastemanthus*, *Schuurmansiella*, *Wallacea*) or markedly broadened at the apex (*Sauvagesia* p.p.). The latter type may occur combined with petaloid staminodes, the broadened tips possibly mimicking anthers. In *Philacra auriculata* several small staminode-like filamentous structures occur on the same side as the fertile stamens, they are slightly broadened apically and possibly glandulous here.

The androecial ontogeny of *Ochna atropurpurea* was studied by Pauzé and Sattler (1978). On five primary androecial primordia, stamina primordia development was observed to follow a centripetal pattern. Flowers of the Luxemburgioideae and Sauvagesioideae, however, show a typical centrifugal development of the androecium (Amaral and Bittrich 1998). An androgynophore occurs in all Ochnaceae (Matthews et al. 2012), it is mostly very short, but conspicuous in *Indosinia* and *Adenarake*.

Detailed studies of the gynoecium morphology in the family were provided by Guédès and Sastre (1981) and Matthews et al. (2012). The ovary is superior and syncarpous at least at the base, with angiospermy type 2, 3 and 4. A short and broad gynophore is present in *Ouratea* (Fig. 59C, D) and *Elvasia* (cf. Sastre 2004); in some other genera (e.g. *Blastemanthus* and *Wallacea*) the ovary shows a sterile basal zone in longitudinal section, but without being stipitate. A comparative study of Ochnaceae, Quiinaceae and Medusagynaceae showed that at least an inconspicuous gynophore is usually present (Matthews et al. 2012). The gynophore becomes swollen and fleshy in fruit in some Ochnoideae (*Brackenridgea*, *Ochna*, *Ouratea*).

In part of the Ochnoideae (*Ochna*, *Campylospermum*, *Brackenrigea* and related genera) the ovary is deeply lobed and for its major part apocarpous (contra Baum 1951), with each lobe containing only one ovule. The degree of apocarpy varies in this subclade of Ochnoideae: the placenta may be part of the basal synascidiate region (*Campylospermum*), or the synascidiate zone ends below the placenta and the placenta belongs already to the plicate region (*Brackenridgea*, *Ochna*). The ovary in this group lacks a symplicate region completely. *Elvasia* (also Ochnoideae), on the other hand, is synascidiate up to above the placenta, then symplicate in the upper part except for the apocarpous stigmas. The gynoecium of the Luxemburgioideae and Sauvagesioideae s.str. is entirely syncarpous with a basal synascidiate region that may reach only the mid-region or the basal part of the placenta or end even below it. Most of the ovary is thus symplicate. In the Ochnoideae group with mostly apocarpous gynoecium, the styles are inserted gynobasically (Fig. 59C) and united completely postgenitally (e.g. *Ouratea*, *Campylospermum*) or are distinct near the apex (*Ochna* spp.). The stigma is punctiform in most genera, either non-papillate (e.g. *Elvasia*, *Luxemburgia*, *Philacra*, *Wallacea*) or papillate (*Campylospermum*, *Blastemanthus*, *Sauvagesia*, *Tyleria*), but more or less suction-cup-shaped in *Ochna* and *Brackenridgea* (and in Medusagynaceae and Quiinaceae; Matthews et al. 2012). Pollen-tube transmission tissue is present in the styles and the ovary. A compitum is present in the symplicate zone in Luxemburgioideae and Sauvagesioideae, in the uppermost part of the unilocular ovary in *Elvasia* (Ochnoideae), and at a short one in the transition from the synascidiate to the apocarpous zone in the Ochnoideae with a mainly apocarpous gynoecium. In *Campylospermum* additionally a compitum may be present in the closely associated papillae of the stigmas.

In several genera of Sauvagesioideae s.str. and in the Ochnoideae with gynobasic styles, the ovary is plurilocular, the placentation axile. In *Elvasia* (Ochnoideae) the ovary is unilocular above the synascidiate zone (Matthews et al. 2012). In other genera of Sauvagesioideae s.str. and in *Lophira* (Ochnoideae), the ovary is either more or less unilocular with parietal (e.g. *Sauvagesia* p.p., *Schuurmansia*) or basal (*Sauvagesia* p.p., *Lophira*) placentation, or it is bi- to plurilocular at base and unilocular or incompletely plurilocular in the upper part. The latter condition is also typical for the Luxemburgioideae. In these cases the placentation is axile at the base and parietal at the apex. Sometimes the placenta is inserted on deeply protruding and postgenitally fused septa (e.g. *Blastemanthus*). In *Wallacea* the ovary is unilocular and the placentation is laminar diffuse. Tanniferous tissue in floral organs is abundant in all Ochnaceae and in the closely related families Quiinaceae and Medusagynaceae (Matthews et al. 2012).

FLOWER BIOLOGY. The predominance of poricidal anthers or of the "poricidal system", where the pore is formed by staminodes (Fig. 60B; Kubitzki and Amaral 1991), suggests that pollination by bees capable of vibrating the anthers or the staminodes around the stamens to collect pollen ("buzz-pollination") is common in the family. Observations on *Luxemburgia* spp., *Ouratea* spp., and *Poecilandra retusa* with poricidal anthers and on *Sauvagesia* spp. with a poricidal system in Brazil and Venezuela confirmed this prediction: Small to large bees of various taxonomic groups were observed to act as pollinators (pers. obs.; Nadia and Machado 2005). The apically elongated connective on anthers with longitudinal dehiscence observed in some *Sauvagesia* spp. might, similarly as in some *Ternstroemia* spp., transmit the vibrations from the staminodes directly to the anthers (cf. Bittrich et al. 1993). In *Perissocarpa*, the inner lobes of the apically bilobed petals stick firmly together and the thereby formed cap-like structure is thought to protect the anthers of the buzz-pollinated flowers from the permanent moisture in the natural habitat (Wallnöfer 1998). The wax covering the anthers of some species (*Wallacea*, *Blasthemanthus*) seems to have rather a protective function. Wax-collecting bees were observed much more rarely than pollen-collecting bees and they were less effective as pollinators (*Poecilandra* sp., pers. obs.). Nectaries are apparently always absent. The report of a sweet mucilaginous secretion in the flowers (from sepal colleters?) of *Rhytidanthera mellifera* attracting bees (Schultes 1949) begs for further investigations. Reports that the flowers of *Lophira lanceolata* are a source of honey in Nigeria (Mapongmetsem 2007) also need confirmation. Self-compatibility (in the weedy *Sauvagesia erecta*) as well as self-incompatibility (e.g. *Ouratea spruceana*) was observed. Few species have unisexual flowers (*Sauvagesia serrata*, *Euthemis minor*, *Schuurmansiella angustifolia*, *Schuurmansia henningsii*).

EMBRYOLOGY. The tapetum is secretory, division of the pollen mother cells is simultaneous and the pollen grains are two-celled when shed (except in *Ochna kirkii*, Davis 1966; Narayana 1975). Ovules are incompletely tenuinucellate (*Luxemburgia*, *Philacra*, *Sauvagesia*, *Tyleria*, *Wallacea*) or weakly crassinucellate (*Blastemanthus*) and anatropous or campylotropous, syntropous (curved into the same direction as the carpel closure), rarely additionally a few ovules are antitropous. Ovules are bitegmic in Luxemburgioideae and Sauvagesioideae s.str., but in Ochnoideae appear as mostly (*Campylospermum*, *Elvasia*, *Ochna*) or completely (*Brackenridgea*, *Lophira*) unitegmic due to fusion of the integuments. The micropyle is formed either by both integuments and often zigzag (*Blastemanthus*, *Luxemburgia*, *Philacra*, *Sauvagesia*, *Tyleria*) or more rarely straight (*Cespedesia*, *Wallacea*), or only by the inner (*Campylospermum*, *Ochna*, also in *Wallacea*), and by the apparently only integument in *Brackenridgea* and *Lophira* (Ochnoideae) (Narayana 1975; Matthews et al. 2012). The embryo sac is of the Polygonum type, endosperm formation is nuclear becoming cellular throughout. Apospory was found in two species of *Ochna*.

POLLEN MORPHOLOGY. Pollen is tricolporate (rarely tetracolporate), the exine is laevigate (Luxemburgioideae and part of the Sauvagesioideae s.str.) or variously sculpted. A striate-rugulate exine characterizes the Ochnoideae and most Sauvagesioideae s.str., which have petaloid staminodes. The presence of a baculate exine suggests sister-group relationship of the former genera *Neckia* and *Indovethia*, today both included in *Sauvagesia* (Amaral 1991).

KARYOLOGY. Nearly all chromosome counts reported are from members of the Ochnoideae: *Idertia*: $n = 12$, *Rhabdophyllum*: $n = 12$, *Campylospermum*: $n = 10, 12, 24$, *Ouratea*: $n = 13$, *Ochna*: $n = 12, 14$, *Lophira*: $n = 14$, $2n = 24$. The only count of a member of Sauvagesioideae s.str., *Sauvagesia erecta*, was reported with $2n = 38$. It seem thus probable that the basic chromosome number for the Ochnoideae is $n = 12$ but, in the absence of more counts from the Luxemburgioideae and Sauvagesioideae s.str., currently no further conclusions can be drawn.

FRUIT AND SEED. Many-seeded capsules are common in the Luxemburgioideae and Sauvagesioideae s.str. These are always septicidal, but the dehiscence may start apically (e.g. *Sauvagesia*, *Luxemburgia*, Fig. 60I) or basally (e.g. *Cespedesia*, *Philacra*, Fig. 60J). A columella is present or absent. In *Wallacea* the two or three valves separate completely. Dry indehiscent monospermous fruits occur in *Elvasia* (Fig. 59H), *Perissocarpa* (nut-like) and *Lophira* (samaroid, Fig. 59F). Drupaceous fruits with one or two seeds per locule occur in *Euthemis* while, in all genera of Ochnoideae characterized by deeply lobed and for their major parts apocarpous ovaries (see above), the carpels separate completely during fruit development ("ecological apocarpy", Baum 1951), forming monospermous drupelets inserted on the accrescent fleshy receptacle (Fig. 59E).

The wings of the seeds of many capsular fruits develop from the outer epidermis of the outer integument. These wings may be restricted to one (e.g. *Luxemburgia*) or both ends (e.g. *Schuurmansiella*) of the seeds or surround the seed completely (e.g. *Poecilandra*). Wings can be much longer than the seed body (e.g. *Cespedesia*, *Schuurmansia*) or much shorter (e.g. *Luxemburgia*, *Schuurmansiella*). Endosperm is absent in the ripe seeds of Ochnoideae, and present in those of Luxemburgioideae and Sauvagesioideae s.str. The cuticle of the testa may be smooth or variously sculpted (Amaral 1991). The cells of the inner epidermis of the outer integument in Luxemburgioideae and almost all Sauvagesioideae contain small crystals. The embryo is straight or curved, isocotylar or rarely heterocotylar.

According to Farron (1985) and Sastre (1975b), germination is epigeal (*Sauvagesia*, *Ouratea*, *Rhabdophyllum* spp., *Campylospermum* spp.) or hypogeal (*Elvasia*, *Ochna*, *Idertia*, *Campylospermum* spp., *Rhabdophyllum* spp.).

DISPERSAL. In several genera with capsular fruits the seeds are provided with wings of various form and size. The species with such seeds, which are probably wind-dispersed, occur generally in open vegetation. Anemochory must also be assumed for the samaroid fruits of *Lophira* spp., which form large trees of rainforests or medium-sized trees in savannas. Species which occur in inundated forests (igapós or várzeas) show adaptations to hydrochory: the epidermis of the seeds of *Wallacea* is formed by large, dead, air-filled cells. The indehiscent fruits of *Elvasia elvasioides* have an aerenchyma and are hydrochorous (pers. obs.). The white or red drupes of *Euthemis* contrasting with the dark red sepals (Kanis 1971) and the blackish drupelets inserted on an accrescent red-coloured receptacle of the group with apparently apocarpous gynoecia are ornithochorous. Species characterized by ornithochory occur commonly in more or less closed forests, but many species of *Ouratea* occur in savannah-like vegetation.

PHYTOCHEMISTRY. Relevant data are reported in Hegnauer (1969, 1990) and Mbing et al. (2003). Condensed tannins are present, ellagi- and gallotannins absent. C-glycoflavones, flavones, biflavones and other biflavonoids (lophirone and related substances in subf. Ochnoideae) were more or less regularly found, triterpenes (*Ouratea*) and alkaloids are rare (*Testulea*, *Lophira*). The pericarp of species of *Ochna* and *Ouratea* and of the seeds of *Ochna* and *Lophira* are rich in fat oil (see Mapongmetsem 2007 for information about the fatty acid composition of the seed oil of *L. lanceolata*).

SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY. The subdivision of the Ochnaceae into two monophyletic subfamilies, as already proposed by Engler (1874), seemed to be well-supported by several morpho-anatomical characters (Amaral 1991). Chloroplast DNA sequence data showed, however, that *Luxemburgia* and *Philacra* form a basal clade within the family, thus rendering the Sauvagesioideae in the traditional circumscription paraphyletic (Amaral et al., unpubl. data; Wurdack and Davis 2009). Consequently, these two genera are transferred to subfamily Luxemburgioideae in the present treatment. It is unclear at present which morpho-anatomical characters support the clade of Ochnoideae + Sauvagesioideae s.str. and the subclade of Sauvagesioideae s.str. Even the detailed analysis of flower structure by Matthews et al. (2012) did not reveal possible synapomorphies of these clades. Lack of knowledge about the infrafamilial phylogeny currently impedes safe conclusions. Thus, possibly the striate-rugulate pollen surface is synapomorphic for the former clade, but it may also have evolved independently in both subfamilies. The exclusion of *Lophira* from the family, as suggested by Takhtajan (1997), is supported neither by the cladistic analysis of Amaral (1991), as the genus shares various derived characters with other members of subfamily Ochnoideae, nor by molecular data (Wurdack and Davis 2009). Within the Ochnoideae the genera with a more or less apocarpous gynoecium most probably form a monophyletic subgroup. The relationship of this group to the other genera of this subfamily is still unsettled, however, so that a further subdivision of the Ochnoideae is premature. Also a subdivision of the Sauvagesioideae s.str. in monophyletic tribes is still not possible, although some monophyletic groups within the subfamily are well supported by the cladistic analysis of Amaral (1991).

AFFINITIES. For some time the Ochnaceae were generally but not unanimously accepted as part of the Theales. Guédès and Sastre (1981) proposed its inclusion together with the major part of the Theales in the Violales. Based on the presence of cristarque cells, petiole anatomy and trilacunar nodes, Schofield (1968) considered Quiinaceae as the most closely related family. A few taxonomists believed that Ochnoideae and Sauvagesioideae are only distantly related and belong to different parts of the dicotyledons. Thus, Corner (1976) in the tradition of Bentham and Hooker (1862) suggested that the Ochnoideae are closely related to the Simaroubaceae while the Sauvagesioideae would be close to the Violaceae. This suggestion was based on a superficial character analysis (see Eichler 1878; Amaral 1991), however, and not supported by new data. There are numerous differences between the subfamilies, including the fact the androecial development in the Ochnoideae and the other two subfamilies seems to be different. The monophyly of the Ochnaceae, however, is today settled. Possible synapomorphies of the family are the poricidal anthers (reversed in *Brackenridgea* spp., *Ochna* spp., *Sauvagesia* spp., *Schuurmansia*, *Schuurmansiella*) and the crystal layer in the endotesta (reversed in the Ochnoideae probably due to the development of indehiscent fruits). Recent phylogenetic analyses based on DNA sequence data clearly support the inclusion of the Ochnaceae in a clade with Medusagynaceae and Quiinaceae, the "ochnoids", in which Quiinaceae and Medusagynaceae are sister taxa and Ochnaceae the sister group to the clade formed by both (Schneider et al. 2005; Wurdack and Davis 2009; Soltis et al. 2011; Xi et al. 2012). This clade is also morphologically characterized by stratified phloem, mucilage cells, contorted petal aestivation, lack of nectaries, and tenuinucellate ovules (Stevens 2001 onwards), and several floral characters support the sister-group relationship of Quiinaceae and Medusagynaceae (Matthews et al. 2012). APG II (2003) suggested the inclusion of all three families in an expanded family Ochnaceae as optional and APG III (2009) prefers this lumping, but we see little advantage of it, besides the risk of confounding non-specialists. The phylogeny of Xi et al. (2012) shows the clusioids as the moderately supported sister of the ochnoids.

DISTRIBUTION AND HABITATS. The Ochnaceae have a pantropical distribution. Fourteen genera are restricted to the New World. Seven genera occur in the Indo-Malaysian region and nine genera in tropical Africa; three of these, *Ochna*, *Brackenridgea* and *Sauvagesia*, are common to both regions. Only one genus, *Sauvagesia*, occurs in all three tropical regions. The weedy *Sauvagesia erecta* occurs in the New World and, probably due to human transport, in Africa. Central America is poor in genera (mainly species of *Ouratea* and *Cespedesia spathulata*); possibly this region was colonized via long-distance dispersal by birds or only after the formation of the Isthmus of Panama. Vicariant distribution patterns of Ochnaceae in the Guyanas were studied by Sastre (1992).

The majority of the species occurs in open vegetation, mainly savannas; a few are pioneers (*Cespedesia spathulatha*, *Schuurmansia*). Some genera with hydrochorous fruits or seeds are known from inundated forests of northern South America. *Lophira alata* is a member of the upper canopy in lowland rainforests. Species of Ochnoideae with bird-dispersed drupelets occur in the understories of forests and in savannas.

ECONOMIC IMPORTANCE. Only *Lophira alata* has some economic importance. The hard and durable wood is used for construction purposes.

The seed oil is used for cooking and soap production, also in *L. lanceolata* (Mapongmetsem 2007). The South African *Ochna serrulata* (Hochst.) Walp. is widely cultivated in gardens in the tropics.

KEY TO THE GENERA

1. Styles gynobasic; carpels apparently distinct; receptacle enlarging during fruit development, often becoming red 2
– Styles apical; carpels completely connate; receptacle not enlarging during fruit development 7
2. Anthers usually opening by longitudinal slits; stipules laciniate or striate; drupelets with an internal projection of the endocarp **4. *Brackenridgea***
– Anthers opening by pores, or if by longitudinal slits, stipules entire and not striate and drupelets without internal projection of the endocarp 3
3. Stamens 12–∞, filament length at least 1/3 of the length of the anther **3. *Ochna***
– Stamens 10, anthers sessile or subsessile 4
4. Sepals persistent; embryo curved 5
– Sepals caducous or rarely persistent; embryo straight 6
5. Leaves with more than 30 secondary veins; petals as long as the sepals **7. *Rhabdophyllum***
– Leaves generally with ca. 10–25 secondary veins; petals longer than sepals **8. *Campylospermum***
6. Leaf margin without bristles; flowers in terminal or rarely axillary generally multi-flowered inflorescences; sepals generally caducous (Neotropics) **5. *Ouratea***
– Leaf margin with persistent bristles; flowers in 1–4-flowered axillary inflorescences; sepals persistent (Africa) **6. *Idertia***
7. Locules uniovulate; fruits indehiscent, dry, not winged 8
– Locules with 2–∞ ovules; fruits capsular, drupaceous, or samaroid 9
8. Sepals distinct; petals yellow, patent; carpels 2–7 **9. *Elvasia***
– Sepals distinct or connate for most of their length; petals white or cream-yellow, sticking together apically and forming a cap-like structure; carpels 2(3) **10. *Perissocarpa***
9. Flowers tetramerous; stamen 1; leaf nervation brochidodromous **16. *Testulea***
– Flowers pentamerous; stamens (4–)5–∞; leaf nervation craspedodromous 10
10. Petals shortly connate at the base; apex of the anthers beaked; locules bi-ovulate; fruits drupaceous, 5-locular **21. *Euthemis***
– Petals distinct; apex of the anthers not beaked; locules with 4–∞ ovules; fruits 1–5-locular, capsular or indehiscent 11
11. Outer sepals longer than inner sepals; fruits indehiscent, winged by the accrescent two outer sepals, 1-seeded **11. *Lophira***
– Outer sepals smaller than inner sepals or ± of equal length; capsules with several to many seeds 12
12. Carpels 5 13
– Carpels 2–3 17
13. Leaf apex emarginate; secondary veins closely parallel; marginal teeth absent; stamens 5 **17. *Fleurydora***
– Leaf apex obtuse; secondary veins separated by 7–11 areoles; marginal teeth present; stamens 10–∞ 14
14. Stipules deeply bifid, persistent; sepals basally connate, much smaller than the flower bud **15. *Cespedesia***
– Stipules entire, caducous; sepals distinct, at least half as long as the flower bud 15
15. Leaves compound; stamens ∞; flowers white **13. *Rhytidanthera***
– Leaves simple; stamens 10; flowers yellow 16
16. Sepals enclosing the mature flower bud, centripetally becoming larger, adaxial with clavate hairs at the base; anthers biporate **12. *Godoya***
– Sepals not enclosing the mature flower bud, all of ± the same size; clavate hairs 0; anthers uniporate **14. *Krukoviella***
17. Stamens ∞, rarely 4–10, located adaxially already in bud 18
– Stamens 5 or 10, regularly distributed around the ovary or moving only during anthesis to the adaxial side 19
18. All secondary veins ending in marginal teeth; anther apex straight; capsule dehiscence starting at the apex (Brazil south of the Amazon) **1. *Luxemburgia***
– Only part of the secondary veins ending in marginal teeth; anther apex recurved; capsule dehiscence starting at the base (northern Brazil and southern Venezuela) **2. *Philacra***
19. Sepals 10–15; stamens 10; fruits with 1–2 seed per locule **18. *Blastemanthus***
– Sepals and stamens 5; locules of fruit many-seeded 20

20. Flowers becoming zygomorphic during anthesis 21
– Flowers actinomorphic 22
21. Petals yellow; placentation parietal; capsule opening apically by 3 valves; seed winged **19. *Poecilandra***
– Petals white to pink; placentation laminar; capsules splitting completely into 2–3 valves; seed not winged **20. *Wallacea***
22. Capsule dehiscence starting at the base; seeds with long wings at both ends **22. *Schuurmansia***
– Capsule dehiscence starting at the apex; seeds shortly winged or unwinged 23
23. Staminodes filiform; seeds short-winged at both ends **23. *Schuurmansiella***
– Staminodes ± spathulate, petaloid; seeds on the whole surface with short irregular wing-like folds or unwinged 24
24. Staminodes keeled; seeds winged **24. *Tyleria***
– Staminodes not keeled; seeds unwinged 25
25. Stipules auriculate with marginal glands; testa finely tuberculate **25. *Adenarake***
– Stipules triangular, margins ciliate or with long bristles; testa not tuberculate 26
26. Stipules shortly ciliate; seeds reniform, longitudinally canaliculate, testa cells rectangular; carpels 2 **26. *Indosinia***
– Stipules with long bristles; seeds globose or ovate, not canaliculate; testa cells hexagonal; carpels (2)3 **27. *Sauvagesia***

GENERA OF OCHNACEAE

I. SUBFAM. LUXEMBURGIOIDEAE Planch. ex Endl. (1850) ('Luxemburgieae').

Pitting between vessel elements and parenchyma generally unilaterally compound. Flowers obliquely zygomorphic already in bud with the stamens surrounding the ovary only adaxially; filaments fused congenitally at least at the base, anthers partially fused postgenitally or rarely distinct, staminodes 0 or very small (in adaxial position outside the fertile stamens); pollen laevigate. Seeds albuminous, shortly winged, endotesta with small crystalliferous cells.

1. ***Luxemburgia*** A. St.-Hil. Fig. 59H, I

Luxemburgia A. St.-Hil., Mém. Mus. Hist. Nat. 9: 352 (1822).

Shrubs or small trees. Leaves with closely parallel secondary veins all ending in marginal, sometimes ciliate teeth; stipules deeply 3-partite, ciliate. Sepals 5(6); petals 5(6), yellow, imbricate; stamens numerous, filaments connate at base, persistent, anthers partially connate, opening by 2 apical pores; staminodes 0; ovary 3-carpellate, 1-loculate above, placentation parietal. Capsule with many shortly winged seeds.

18 spp., mountainous regions of SE, NE and central Brazil.

2. ***Philacra*** Dwyer Fig. 59J

Philacra Dwyer, Brittonia 5: 124 (1944); Sastre, Flora Venez. Guayana 7: 146–148 (2003).

Small trees or shrubs. Leaves with closely parallel secondary veins with fewer persistent marginal teeth; stipules persistent. Sepals 5; petals 5, imbricate, yellow; stamens numerous, rarely 4–10; filaments very short, connate, persistent, anthers partially connate or distinct, strongly curved at their apex and opening by two pores; staminodes, if present, very small, broadened at the apex, possibly glandular; ovary 3-carpellate, unilocculate above, placentation axile to parietal. Capsule with many, shortly winged seeds.

Four spp. in Venezuela and northern Brazil.

II. SUBFAM. OCHNOIDEAE Burnett, Outl. Bot.: 886, 1093, 1125 (1835) ('Ochnidae').

Pitting between vessel elements and parenchyma not unilaterally compound. Flowers actinomorphic, filaments distinct, staminodes 0, pollen striate/rugulate. Ripe seeds without endosperm, testa poorly differentiated, unitegmic.

3. ***Ochna*** L. Fig. 59E

Ochna L., Sp. Pl.: 513 (1753); Kanis, Blumea 16: 22–40 (1968); Robson, Fl. Zambes. 2(1): 225–251 (1963).

Trees, shrubs or shrublets. Leaves with serrate, ciliate or entire margins; stipules entire or not, caducous. Sepals (4)5, persistent, enlarging and becoming coloured in fruit; petals 5(–12), contort, mostly yellow; stamens numerous, distinct, with persistent filaments; anthers dehiscing by longitudinal slits or terminal pores; ovary deeply divided into (3–)5–10(–15) uniovulate lobes with gynobasic style. Fruit separated into one to several black drupelets on an accrescent reddish receptacle. Embryo straight or curved. $n = 12, 14$.

About 85 spp. in the tropics and subtropics of Africa and Asia. The separation of *Brackenridgea* is dubious, and possibly makes *Ochna* paraphyletic.

4. *Brackenridgea* A. Gray

Brackenridgea A. Gray, Proc. Amer. Acad. Arts 3: 51. 1853 (sero) (1853); U.S. Expl. Exped. Bot. Phan. 1: 361, t. 42 (1854); Kanis, Fl. Males. I, 7: 101–104 (1971); Robson, Fl. Zambes. 2(1): 252–255 (1963).

Trees, shrubs or shrublets often with yellow pigment under the bark. Leaves with entire or glandular serrulate margin; stipules and bracts longitudinally striate, laciniate, persistent on the first year shoots. Sepals (4)5, white or pink in flower, accrescent and red in fruit; petals (4)5, contort, white to pink, rarely yellow; stamens usually (8–)13–20(–22), anthers usually dehiscing by longitudinal slits; ovary deeply divided into (3) 5–10 uniovulate lobes, style gynobasic. Fruit separated into one to several black drupelets on an accrescent red receptacle. Seeds with an intrusion of the endocarp, embryo curved.

About seven spp. in tropical Africa, Madagascar, Malaysia, and the Philippines.

5. *Ouratea* Aubl. Fig. 59A–D

Ouratea Aubl., Hist. Pl. Guiane: 397 (1775), nom. cons.; Sastre, Adansonia III, 1: 47–67 (1988); Maguire & Steyermark, Mem. N.Y. Bot. Gard. 51: 56–102 (1989); Sastre, Flora Venez. Guayana 7: 131–143 (2003).

Gomphia Schreb., Gen. Pl. ed. 8, 1: 291 (1789); Bittrich & Amaral, Taxon 43: 89–93 (1994), nomencl.

Trees or shrubs, glabrous or rarely with hairs. Leaf margin entire, serrate to ciliate, secondary veins generally curving strongly near the margin; stipules entire, distinct, scale-like and caducous, or rarely setaceous and persistent. Sepals 2–5, mostly caducous; petals 5, contort, generally yellow; stamens 10, filaments very short, anthers transversely wrinkled or rarely smooth, poricidal; ovary 5–10-carpellate, on a short broad gynophore. Fruit separating into 1–10 black drupelets on a red accrescent receptacle. Embryo straight. $n = 13$.

About 200 spp. in tropical or subtropical regions of the New World. The separation of *Campylospermum*, *Idertia* and *Rhabdophyllum* from *Ouratea* is dubious and needs further investigation.

6. *Idertia* Farron

Idertia Farron, Ber. Schweiz. Bot. Ges. 73: 212 (1963).

Small trees or shrubs. Leaf margin with persistent bristles; stipules membranaceous, intrapetiolarly united at base. Inflorescences axillary, short, 1–4-flowered; sepals 5, accrescent and red in fruit; petals 5, contort, yellow; stamens 10, anthers smooth, subsessile, poricidal; ovary deeply 5–6-lobed with completely connate gynobasic style. Fruit separating into 1–6 black drupelets on an accrescent red receptacle. Embryo straight. $n = 12$.

Four spp. in West Africa, São Tomé.

7. *Rhabdophyllum* Tiegh.

Rhabdophyllum Tiegh., J. Bot. (Morot) 16 17: 201 (1902); Sosef, Andansonia III, 30: 119–135 (2008), rev.

Small trees or subshrubs. Leaf secondary veins numerous, dense, margin sometimes toothed; stipules intrapetiolarly united at base, caducous or persistent. Inflorescences axillary, many-flowered. Sepals 5, accrescent and reddish in fruit; petals 5, yellow, contort, of the same length as the sepals; stamens 10, anthers subsessile, transversally wrinkled, poricidal; ovary deeply 5-lobed with completely connate gynobasic style. Fruit separating into 1–5 brown or black drupelets on an accrescent receptacle. Embryo curved. $n = 12$.

Eight spp. in tropical moist forests of West Africa.

8. ***Campylospermum*** Tiegh.

Campylospermum Tiegh., J. Bot. (Morot) 16: 35, 40 (1902).

Small trees, shrubs or subshrubs. Leaves entire or with caducous teeth; stipules intrapetiolarly united at base. Inflorescence terminal (axillary). Sepals 5, accrescent and yellow or reddish in fruit; petals 5, contort, longer than the sepals; stamens 10, anthers sessile or subsessile, often transversely wrinkled, poricidal; ovary deeply 5-lobed with completely connate gynobasic style. Fruit separating into 1–5 black drupelets on a red accrescent receptacle. Embryo curved. $n = 10, 12, 24$.

About 65 spp. in the Old World, the majority in tropical Africa, Madagascar, Ceylon to SE Asia.

9. ***Elvasia*** DC. Fig. 59G, H

Elvasia DC., Ann. Mus. Natl. Hist. Nat. 17: 422, t. 20 (1811); Sastre, Flora Venez. Guayana 7: 129–130 (2003).

Small trees or shrubs, glabrous or with indument on young shoot. Leaves with closely parallel secondary nerves and caducous marginal teeth; stipules deltoid, persistent. Sepals 2–6, caducous; petals 3–8, imbricate, yellow; stamens 5–20, anthers opening by two apical pores; ovary on a short broad gynophore, basically unilocular, but strongly 2–5(–7)-lobed with one ovule per carpel; placentation median and axile at the ovary base. Fruits indehiscent, coriaceous or woody, globular or star-shaped, 1(2)-seeded.

About 15 spp. in South America, mainly Guayana Highland and Amazonia, one sp. in NE Brazil, and one in Central America.

10. ***Perissocarpa*** Steyerm. & Maguire

Perissocarpa, Steyerm. & Maguire, Ann. Missouri Bot. Gard. 71: 319 (1984); Wallnöfer, Ann. Naturhist. Mus. Wien 100B: 683–707 (1998), rev.

Small trees or shrubs. Leaves with closely parallel secondary nerves and caducous marginal teeth; stipules deltoid, caducous or persistent. Sepals 5, distinct or connate for most of their length, caducous; petals 5, contort, cream-yellow, white or greenish-white, basally distinct, bilobed with the inner lobes inflexed and sticking firmly together, corolla thus forming a cap-like structure; stamens 5(6), ± persistent, anthers opening by 2 apical pores; ovary with 2(3) uniovulate locules, placentation axile. Fruit 1-seeded, globular, indehiscent.

Three spp. in Venezuela, Peru, and northern Brazil, in mountain forests and savannas.

11. ***Lophira*** Banks ex C.F. Gaertn. Fig. 59F

Lophira Banks ex C.F. Gaertn., Suppl. carp.: 52 (1805).

Small to large deciduous trees up to 50 m. Leaves with closely parallel secondary nerves. Flowers actinomorphic; sepals 5, imbricate, persistent; petals 5, contort, white; stamens numerous, anthers opening with 2 subapical pores; ovary 2-carpellate, ovules numerous, placentation basal. Fruit 1-seeded, winged by the two outer accrescent sepals. $n = 14$, $2n = 24$.

Two vicariant spp. in lowland rainforests and savannas of West and Central Africa to Sudan. *Lophira alata* Banks ex C.F. Gaertn. is the source of excellent heavy timber. The seeds of both species are used for the extraction of an edible oil.

III. SUBFAM. SAUVAGESIOIDEAE Beilschm. (1833) ('Sauvagesieae').

Pitting between vessel elements and parenchyma generally unilaterally compound. Flowers zygomorphic as regards androecium and ovary (in most cases the zygomorphy developing only during anthesis) or actinomorphic; stamen filaments distinct, staminodes often present, sometimes 2 different types (filamentose and petaloid) in the same flower. Seeds albuminous, often winged, endotesta generally with small crystalliferous cells.

12. ***Godoya*** Ruiz & Pav.

Godoya Ruiz & Pav., Fl. Peruv. Prodr. 1: 58 (1794).

Trees or shrubs. Leaves with distant secondary nerves, margin strongly crenate and toothed; stipules caducous. Flowers becoming zygomorphic during anthesis; sepals 5, adaxially with long clavate hairs at base; petals 5, imbricate, yellow, inside basally with long clavate hairs; staminodes 0, stamens 10, anthers opening by 2 apical pores; ovary with 5 locules and numerous ovules, placentation axile. Capsule with numerous winged seeds.

Two spp., north-western South America.

13. ***Rhytidanthera*** Tiegh.

Rhytidanthera Tiegh., Ann. Sci. Nat. Bot. VIII, 19: 43 (1904).

Trees or shrubs. Leaves 4–5-pinnate with distant secondary nerves and marginal teeth; stipules caducous. Flowers becoming zygomorphic during anthesis; sepals 5, adaxially with glandular hairs (colleters?) at base; petals 5, contort, white; staminodes 0, stamens numerous, anthers opening by 2 subapical pores; ovary 5-loculate, pluriovulate, placentation axile. Capsule with numerous winged seeds.

Five spp. in Colombia and Venezuela.

14. ***Krukoviella*** A.C. Sm.

Krukoviella A.C. Sm., J. Arnold Arbor. 20: 295 (1939).

Scandent shrubs. Leaves with distant secondary nerves and marginal teeth; stipules caducous. Flowers becoming zygomorphic during anthesis; sepals 5, caducous; petals 5, contort, yellow; staminodes 0, stamens 10, anthers opening by 1 apical pore; ovary 5-loculate, pluriovulate, placentation axile. Capsule with numerous winged seeds.

One sp., *K. disticha* (Tiegh.) Dwyer, in western Amazonia.

15. ***Cespedesia*** Goudot

Cespedesia Goudot, Ann. Sci. Nat. Bot. III, 2: 368 (1844); Sastre, Cespedesia 4: 191–214 (1975).

Trees. Leaves up to 1 m long with distant secondary nerves and marginal teeth; stipules persistent, inside with glandular hairs (colleters?) at base. Flowers becoming zygomorphic during anthesis; sepals 5, small, connate at base; petals 5, contort, yellow, shortly connate at base; staminodes 0, stamens numerous, anthers covered with wax crystals, opening by 2 subapical pores; ovary 5-carpellate, apically incompletely septate, placentation axile to parietal. Capsule with numerous winged seeds.

One to six spp. from Nicaragua to Bolivia and central Brazil.

16. ***Testulea*** Pellegr.

Testulea Pellegr., Bull. Soc. Bot. France 71: 76 (1924).

Trees. Leaves with distant secondary nerves, without marginal teeth; stipules intrapetiolarly connate, persistent. Flowers zygomorphic; sepals 4, petals 4, imbricate, white to pink; staminodes filamentose, connate for 2/3 of their length; fertile stamen 1, adaxial, anther opening by two apical pores; ovary bicarpellate, unilocular in the upper part, placentation axile to parietal. Capsule with numerous winged seeds.

One sp., *T. gabonensis* Pellegr., Gabon. This genus shows several aberrant characters and deserves further investigation.

17. ***Fleurydora*** A. Chev.

Fleurydora A. Chev., Bull. Mus. Hist. Nat. (Paris) II, 5: 158 (1933).

Small trees or shrubs. Leaves with closely parallel secondary veins, without marginal teeth; stipules caducous, margins glandular. Flowers becoming zygomorphic during anthesis; sepals 5; petals 5, imbricate, yellow; staminodes 0, stamens 5, anthers opening by 2 subapical pores; ovary with 5 locules, placentation axile. Capsules with numerous winged seeds.

One sp., *F. felicis* A. Chev., Guinea.

18. ***Blastemanthus*** Planch. Fig. 60G

Blastemanthus Planch., London J. Bot. 5: 644 (1846).

Small trees or shrubs. Leaves with closely parallel secondary veins and caducous marginal teeth; stipules persistent. Flowers becoming zygomorphic during anthesis; sepals 10–15, caducous; petals 5, imbricate, yellow; staminodes numerous, linear; stamens 10, anthers covered with wax crystals, opening with one pore; placentation axile to parietal; ovary tricarpellate. Capsule with 1–2 unwinged seeds per locule.

About three spp., northern South America.

19. *Poecilandra* Tul.

Poecilandra Tul., Ann. Sci. Nat. Bot. III, 8: 342 (1847); Sastre, Flora Venez. Guayana 7: 148–150 (2003).

Shrubs or small trees. Leaves with closely parallel secondary veins, caducous marginal teeth, and caducous stipules. Flowers becoming zygomorphic during anthesis; sepals 5, imbricate, caducous; petals 5, contort, yellow; staminodes numerous, linear or spathulate; stamens 5, anthers covered with wax crystals, opening by one pore; ovary tricarpellate with parietal placentation. Capsule with numerous winged seeds.

Three spp., northern South America.

20. *Wallacea* Spruce ex Benth. & Hook. f.

Wallacea Spruce ex Benth. & Hook. f., Gen. Pl. 1: 320 (1862); Sastre, Flora Venez. Guayana 7: 160–161 (2003).

Small trees. Leaves with closely parallel secondary veins, caducous marginal teeth, and caducous stipules. Flowers becoming zygomorphic during anthesis; sepals 5, imbricate, caducous; petals 5, contort, white or pink; staminodes numerous, linear or 0; stamens 5, anthers covered with wax crystals, opening by longitudinal slits; ovary 2–3-carpellate with laminar placentation. Capsule splitting completely into 2–3 valves; seeds numerous, unwinged.

Two spp., northern South America.

21. *Euthemis* Jack

Euthemis Jack, Malayan Misc. 1(5): 15 (1820); Kanis, Blumea 16: 62–66 (1968), rev.

Shrubs. Leaves with closely parallel secondary veins, persistent marginal teeth, and caducous stipules. Flowers actinomorphic, bisexual or unisexual; sepals 5, imbricate, persistent, purplish-red in fruit; petals 5, connate at base, white or pink; staminodes 5, linear or absent; stamens 5, anthers beaked, opening by one pore; ovary 5-carpellate, placentation axile with two ovules per locule. Fruit drupaceous, white or red, with 1(2) seeds per locule.

Two spp., southeast Asia.

22. *Schuurmansia* Blume

Schuurmansia Blume, Mus. Bot. 1: 177 (1850); Kanis, Blumea 16: 74–80 (1968), rev.

Trees or treelets. Leaves up to 85 cm long, with closely parallel secondary veins, persistent or caducous marginal teeth, and caducous stipules. Flowers actinomorphic, bisexual or unisexual; sepals 5, imbricate, persistent or caducous; petals 5, contort, white to pink; staminodes petaloid or linear, distinct or connate at base, persistent; stamens 5, persistent, anthers opening by slits; ovary 3-carpellate with parietal placentation. Capsule opening from the base, seeds numerous with long wings at both ends.

Three spp., New Guinea to the Philippines.

23. *Schuurmansiella* Hallier f.

Schuurmansiella Hallier f., Recueil Trav. Bot. Néerl. 10: 344 (1913); Kanis, Blumea 16: 73–74 (1968), rev.

Small trees or shrubs. Leaves with closely parallel secondary veins, persistent marginal teeth and persistent stipules. Flowers actinomorphic, unisexual; sepals 5, valvate, persistent; petals 5, white to pink, contort; staminodes numerous, linear, connate at base, persistent; stamens 5, persistent, anthers opening by apical slits; ovary (2)3-carpellate, placentation parietal. Capsule with numerous seeds shortly winged on both ends.

One sp., *S. angustifolia* (Hook. f.) Hallier f., in NW Borneo.

24. *Tyleria* Gleason

Tyleria Gleason, Bull. Torrey Bot. Club. 58: 391 (1931); Sastre, Flora Venez. Guayana 7: 125, 157–160 (2003).
Adenanthe Maguire, Steyerm. & Wurdack (1961).

Trees or shrubs. Leaves with closely parallel secondary veins, marginal teeth or bristles, and persistent or caducous stipules. Flowers actinomorphic; sepals 5, imbricate or valvate, persistent; petals 5, contort, white to pink; staminodes 10, dimorphic, those opposite the sepals often laciniate, petaloid, basally generally connate, those opposite the petals keeled adaxially; stamens 5, persistent; anthers opening by slits or pores; ovary (2)3(5)-carpellate, with parietal placentation. Capsule with numerous short-winged seeds.

13 spp., Guayana Highland.

25. *Adenarake* Maguire & Wurdack

Adenarake Maguire & Wurdack, Mem. New York Bot. Gard. 10: 15 (1961).

Shrubs. Leaves with closely parallel secondary veins and persistent marginal teeth; stipules auriculate with marginal glands, caducous. Flowers actinomorphic with conspicuous androgynophore; sepals 5, valvate, with marginal glands; petals 5, contort, white to pink; staminodes 15, the inner 5 larger, enclosing the 5 stamens; anthers opening by apical slits; ovary tricarpellate, placentation axile. Capsule with numerous unwinged, tuberculate seeds.

Two spp., northern Brazil and southern Venezuela, at higher elevations.

26. *Indosinia* J.E. Vidal

Indosinia J.E. Vidal, Bull. Soc. Bot. France 111: 405 (1965); Kanis, Blumea 16: 68–69 (1968), rev.

Shrubs. Leaves with closely parallel secondary veins, persistent marginal teeth, and caducous lacerate stipules. Flowers actinomorphic with conspicuous androgynophore; sepals 5, valvate, with glandular hairs; petals 5, contort, white; staminodes 10, petaloid, enclosing the 5 persistent stamens; anthers opening by apical slits; ovary bicarpellate, placentation axile. Capsule with numerous reniform, unwinged seeds.

One sp., *I. involucrata* (Gagnep.) J.E. Vidal, from southern Vietnam at 1,700 m.

27. *Sauvagesia* L. Fig. 60A–F

Sauvagesia L., Sp. Pl. 1: 203 (1753); Kanis, Blumea 16: 69–73 (1968), part. rev. (*Neckia*); Sastre, Sellowia 23: 9–44 (1971); Sastre, Flora Venez. Guayana 7: 150–157 (2003).

Lauradia Vell. ex Vand. (1788).
Neckia Korth. (1848).
Leitgebia Eichler (1871).
Vausagesia Baill. (1890).
Indovethia Boerl. (1894).
Sinia Diels (1930).
Pentaspatella Gleason (1931).
Roraimanthus Gleason (1933).

Treelets, shrubs or herbs, rarely small trees. Leaves with closely parallel secondary veins, persistent teeth, and persistent, pectinate stipules. Flowers actinomorphic, bisexual or very rarely unisexual; sepals (4)5, imbricate or valvate, sometimes glandulose-ciliate, persistent; petals (4)5, contort, white to pink; 5(10) petaloid staminodes generally enclosing the stamens, sometimes connate (*Lauradia*), outside of these 1–2 series of smaller staminodes sometimes present; stamens 5, persistent; ovary (2)3-carpellate, placentation parietal to basal. Capsule with many unwinged, alveolate seeds. $2n = 38$.

One sp. endemic in SE China, two spp. endemic in Malaysia, one sp. endemic in Africa, and ca. 35 spp. in the Neotropics; *S. erecta* L. is a pantropical weed.

Selected Bibliography

Amaral, M.C.E. 1991. Phylogenetische Systematik der Ochnaceae. Bot. Jahrb. Syst. 113: 105–196.

Amaral, M.C.E., Bittrich, V. 1998. Ontogenia inicial do androceu de espécies de Ochnaceae subf. Sauvagesioideae através da análise em microscopia eletrônica de varredura. Rev. brasil. Bot. 21: 269–273.

APG (Angiosperm Phylogeny Group) II. 2003. See General References.

APG (Angiosperm Phylogeny Group) III. 2009. See General References.

Bailey, I.W. 1933. The cambium and its derivative tissues. VIII. Structure, distribution and diagnostic significance of vestured pits in dicotyledons. J. Arnold. Arbor. 14: 259–273.

Baum, H. 1951. Die Frucht von *Ochna multiflora*, ein Fall ökologischer Apokarpie. Österr. Bot. Zeitschr. 98: 383–394.

Bentham, G., Hooker, J.D. 1862. Genera plantarum 1(1). London: Reeve.

Bittrich, V., Amaral, M.C.E., Melo, G.A.R. 1993. Pollination biology of *Ternstroemia laevigata* and *T. dentata* (Theaceae). Pl. Syst. Evol. 185: 1–6.

Carlquist, S. 1988. Comparative wood anatomy. Berlin, Heidelberg, New York: Springer.

Chase, M.W. et al. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Corner, E.J.H. 1976. See General References.

Cronquist, A. 1981. See General References.

Davis, G.L. 1966. See General References.

Decker, J.M. 1966. Wood anatomy and phylogeny of Luxemburgieae (Ochnaceae). Phytomorphology 16: 39–55.

Decker, J.M. 1967. Petiole vascularization of Luxemburgieae (Ochnaceae). Amer. J. Bot. 54: 1175–1181.

Eichler, A.W. 1871. Sauvagesiaceae. In: Mart., Fl. bras. 13 (1): 397–420, t. 81–85. München: Typographia regia.

Eichler, A.W. 1878. Blüthendiagramme, 2. Teil, pp. 257–262. Leipzig: Wilhelm Engelmann.

Engler, A. 1874. Über die Begrenzung und systematische Stellung der natürlichen Familie der Ochnaceae. Nova Acta Acad. Leop.-Carol. German. Nat. Cur. 37: 1–28.

Engler, A. 1876. Ochnaceae. In: Mart., Fl. bras. 12(2): 298–366, t. 62–77. München: Typographia regia.

Farron, C. 1985. Les Ouratinae (Ochnaceae) d'Afrique continentale. Cartes de distribution et clés de détermination de tous les genres et espèces. Bot. Helvetica 95: 59–72.

Guédès, M., Sastre, C. 1981. Morphology of the gynoecium and systematic position of the Ochnaceae. Bot. J. Linn. Soc. 82: 121–138.

Hegnauer, R. 1969. See General References.

Hegnauer, R. 1990. See General References.

Jansen, S., Baas, P., Smets, E. 2001. Vestured pits: their occurrence and systematic importance in eudicots. Taxon 50: 135–167.

Kanis, A. 1971. Ochnaceae. In: Van Steenis, C.G.G.J. (ed.) Flora Malesiana I, vol. 7: 97–119.

Kubitzki, K., Amaral. M.C.E. 1991. Transference of function in the pollination system of the Ochnaceae. Pl. Syst. Evol. 177: 77–80.

Mapongmetsem, P.-M. 2007. *Lophira lanceolata* Tiegh. ex Keay. In: van der Vossen, H.A.M., Mkamilo, G.S. (eds.) PROTA 14: Vegetable oils/Oléagineux. [CD-Rom]. PROTA, Wageningen. http://database.prota.org/PROTAhtml/Lophira%20lanceolata_En.htm

Matthews, M.L. et al. 2012. See General References.

Mbing, J.N., Bassomo, M.Y., Pegnyemb, D.E., Tih, R.G., Sondemgam, B.L., Blond, A., Bodo, B. 2003. Constituents of *Ouratea flava*. Biochem. Syst. Ecol. 31: 215–217.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Nadia, T.D.L., Machado, I.C. 2005. Polinização por vibração e sistema reprodutivo de duas espécies de *Sauvagesia* L. (Ochnaceae). Rev. Brasil. Bot. 28: 255–265.

Narayana, L.L. 1975. A contribution to the floral anatomy and embryology of Ochnaceae. J. Jap. Bot. 50: 329–336.

Oliveira, P.S., Leitão Filho, H.F. 1987. Extrafloral nectaries: their taxonomic distribution and abundance in the woody flora of cerrado vegetation in Southern Brazil. Biotropica 19: 140–148.

Pauzé, F., Sattler, R. 1978. L'androcée centripète d'*Ochna atropurpurea*. Can. J. Bot. 56: 2500–2511.

Sastre, C. 1975a. Etude du genre *Cespedesia* Goudot (Ochnacées). Cespedesia 4: 191–214.

Sastre, C. 1975b. L'importance des caractères anatomiques dans la systématique des Ochnacées. C. R. 100ème Congrès National Soc. Sav. 2: 185–196.

Sastre, C. 1992. Vicariance et distribution géographique de quelques Ochnacées des Guyanes. C. R. Soc. Biogéogr. 68: 35–45.

Sastre, C. 2004. In: Smith, N., Mori, S.A., Henderson, A., Stevenson, D.Wm., Heald, S.V., Flowering plants of the neotropics. Princeton: Princeton University Press, pp. 274–275.

Savolainen, V. et al. 2000. See General References.

Schneider, J.V., Swenson, U., Zizka, G. 2005. Phylogenetic relationships of Quiinaceae (Malpighiales): insights from trnL-trnF sequence data. Abstracts XVII International Botanical Congress, Vienna, p. 425, abstract P1181.

Schofield, E.K. 1968. Petiole anatomy of the Guttiferae and related families. Mem. New York Bot. Gard. 18: 1–55.

Schultes, R.E. 1949. Plantae colombianae XII. Botanical Museum Leaflets 14: 21–47.

Solereder, H. 1899. Systematische Anatomie der Dicotyledonen. Stuttgart: F. Enke.

Solereder, H. 1908. Systematische Anatomie der Dicotyledonen. Ergänzungsband. Stuttgart: F. Enke.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M. and 10 further authors. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linnean Soc. 133: 381–461.

Soltis, D.E., Soltis, P.S., Endress, P.K., Chase, M.W. 2005. Phylogeny and evolution of angiosperms. Sunderland, Mass.: Sinauer Associates.

Soltis, D.E. et al. 2011. See General References.

Stevens, P.F. 2001 onwards. See General References.

Takhtajan, A. 1997. See General References.

Van Tieghem, P. 1902a. Le cristarque dans la tige et la feuille des Ochnacées. Bull. Mus. Hist. nat. Paris 8: 266–273.

Van Tieghem, P. 1902b. Sur les Ochnacées. Ann. Sci. Nat. Bot. sér. 8, 16: 161–416.

Wallnöfer, B. 1998. A revision of *Perissocarpa* Steyerm. & Maguire (Ochnaceae). Ann. Naturhist. Mus. Wien 100B: 683–707.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Pandaceae

Pandaceae Engl. & Gilg (1913), nom. cons.

K. KUBITZKI

Dioecious trees or shrubs; indumentum simple. Leaves alternate, simple, entire or dentate, pinnately veined, eglandular; stipules small, inserted at different levels on the axis, generally persistent. Inflorescences terminal or cauliflorous and pseudoracemose-thyrsiform, or axillary and fasciculate, or flowers solitary; bracts minute. Flowers unisexual; sepals 5, distinct or connate; petals 5, ± imbricate or valvate; disk 0; stamens 5–15, filaments distinct; anthers bilocular, usually introrse, dehiscing longitudinally; pollen grains prolate to oblate spheroidal, 3-colporate, inoperculate (operculate), sexine tectate-punctate or reticulate; pistillode columnar, non-lobate, sometimes peltate; gynoecium syncarpous; ovary 2–5-locular; ovules 1 per locule, pendulous, bitegmic, anatropous and epitropous or less often orthotropous; obturator 0; stylodia 2–5, short, or 0; stigmas 2–5, stigmatoid, sometimes branched. Fruits drupaceous, exocarp fleshy, hard, thick, sculpted; endocarp bony, entire to perforate or ruminate, containing (2)3(4) one-seeded locules, dehiscing by valves at germination. Seeds ecarunculate; embryo flattened, truncate apically, cordate basally; endosperm copious, oily. $2n = 30$ (*Microdesmis*).

Three genera, tropical Africa and SE Asia through Malesia to the Solomon Islands.

VEGETATIVE ANATOMY. Stomates are anomocytic or paracytic, in *Panda* also encyclocytic. Solitary or clustered crystals of calcium oxalate are present in parenchymatous tissue of the shoot; vessel segments have scalariform or both scalariform and simple perforations; imperforate trachaeary elements have bordered pits and occasionally some are true tracheids; wood rays are heterocellular, 4–6-seriate, some uniseriate, mostly of procument cells, the uniseriate of upright or square cells; wood parenchyma is mainly diffuse or in uniseriate apotracheal bands (Metcalfe and Parameswaran in Forman 1966; Hayden and Hayden 2000).

SHOOT MORPHOLOGY INCLUDING INFLORESCENCES. A very conspicuous feature of the family are the dorsiventral lateral shoots with a distichous leaf arrangement which superficially can be mistaken as pinnate leaves. However, the shoots terminate in a claw-like bud which appears capable of producing a further flush of leaves; they are borne in the axil of a reduced leaf and bear a bud in their axil. As a result of the strongly dorsiventral shoot organisation, the petioles are turned almost 90° and the stipules are inserted at different levels. Whereas in *Microdesmis* the leaves subtend staminate flower-fascicles or solitary pistillate flowers, in *Galearia* and *Panda* the leaves have completely lost their axillary buds.

In contrast to the condensed leaf-axillary inflorescences of *Microdesmis*, in *Galearia* and *Panda* the inflorescences are thyrsiform, with the staminate flowers arranged in cymose clusters along the elongate axis and the pistillate flowers solitary or paired in pseudoracemes. In *Galearia* subgen. *Galearia* they are produced at the tip of the leafy shoots, and in *G.* subgen. *Orthopetalum* the inflorescences are borne both on bracteose dorsiventral shoots and on bosses of old wood of branches and trunks. *Panda* has only cauliflorous inflorescences.

FLORAL STRUCTURE. The calyx of *Microdesmis* is clearly 5-partite or 5-lobed, whereas in *Galearia* and *Panda* it is increasingly cup-shaped; in *Panda*, the cup bears only five minute teeth. Petal aestivation is imbricate, though weakly so in staminate *Panda*, but usually valvate in *Galearia*. To my knowledge, the structure of the ovule has directly been observed only in *Panda*, and

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_20,

Forman (1966) has inferred its anatropy in the other genera from the position of the embryo in the seed. In *Microdesmis* and most *Galearia*, the seeds develop with the radicle pointing laterally, i.e. as a result of an anatropous ovule. In one *Galearia* (*G. maingayi*) and in *Panda* the radicle of the seed points downwards. This suggests that the ovule is orthotropous.

PALYNOLOGY. The pollen grains have been studied by Nowicke (1984) and Nowicke et al. (1998). Those of *Galearia* and *Microdesmis* are very similar: 3-colporate, prolate spheroidal to prolate, small, 10–23 µm long, with a punctate-perforate or microreticulate tectum; *Panda* differs in being suboblate, up to 28 µm long, and having a deeply reticulate tectum, with a notable range of lumina size and muri height—large and high at the mesocolpia and poles, but smaller and shallower at the colpi margins.

SEED AND FRUIT. The fruits are drupes of very different size and shape, but transverse sections of them reveal a common pattern (Fig. 61). Those of *Panda* are subglobose, provided with a massive endocarp, and about 7 cm long, whereas those of *Galearia* are bilaterally flattened and transversely elongate or depressed-angular. The drupes of *Microdesmis* are rounded and rarely more than 5 mm long, although in *M. magellanensis* they are laterally compressed similar to those of *Galearia* subgen. *Galearia*. At germination in all genera, valves break off from the stony endocarp to release the germinating seed (Hill 1937; Forman 1966).

The seed coat anatomy of the three genera is very similar (Vaughan and Rest 1969; Corner 1976; Tokuoka and Tobe 2003). The outer epidermis is underlain by one or several layers of longitudinal, pitted, lignified fibres and an inner epidermis. It is uncertain whether this structure is tegmic (as usually interpreted) because there is no indication of a presumably testal layer.

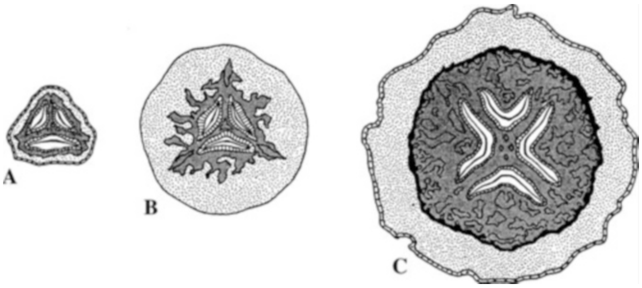

Fig. 61. Pandaceae. Fruits in transverse section. **A** *Microdesmis magellanensis*. **B** *Galearia maingayi*. **C** *Panda oleosa*. (Forman 1966)

FAMILY CIRCUMSCRIPTION AND AFFINITIES. On the basis of vegetative and reproductive characters, Forman (1966) proposed the inclusion of the tribe Galearieae (*Microdesmis* and *Galearia*) into the then monotypic family Pandaceae. This was accepted by Webster (1987), but later (1994) he returned to including these three genera as an emended tribe Galearieae in subfamily Acalyphoideae. Since then, however, it has been found that the genera of Galearieae display a number of features discordant within the Acalyphoideae and, indeed, within the Euphorbiaceae as a whole. These include divergent floral and wood structural features, a seed coat with tracheoidal rather than palisadal mechanical layer, and the lack of obturators. Also molecular data (e.g. Wurdack and Davis 2009; Soltis et al. 2011) firmly support the treatment of the Pandaceae as a separate family. These data are inconclusive, however, in regard to the closest relatives of the family. Wurdack and Davis (2009) left Pandaceae unresolved, and in Soltis et al. (2011) they appeared in an unsupported sister position to Centroplacaceae + Linaceae. Xi et al. (2012) resolve Pandaceae in a clade with Irvingiaceae, though with low support. This would make sense, because Pandaceae and Irvingiaceae share involute vernation, a single apical ovule per carpel, axile placentation, indehiscent fruits, and palaeotropical distribution (Stevens 2001 onwards; Xi et al 2012).

KEY TO THE GENERA

1. Inflorescences axillary, flowers solitary or in glomerules; staminate petals imbricate; leaves usually pellucid-punctate **1. *Microdesmis***
– Inflorescences terminal or cauliflorous, thyrsiform; staminate petals valvate or ± imbricate; leaves not pellucid-punctate 2
2. Endocarp mostly thin-walled; ovules usually anatropous; petals valvate; inflorescences mostly terminal **2. *Galearia***
– Endocarp thick-walled; ovules orthotropous; petals ± imbricate; inflorescences cauliflorous **3. *Panda***

1. ***Microdesmis*** Planch. Fig. 61A

Microdesmis Planch., Hook. Ic. Pl. 8: t. 758 (1848); Pax & K. Hoffm., Pflanzenr. 147. III (Heft 47): 105, fig. 34 (1911); Léonard, Fl. Congo 8(1): 102, t. 8 (1962); Whitmore, Tree Fl. Malaya 2: 118 (1973); Radcl.-Sm., Gen. Euphorb.: 126 (2001).

Dioecious trees or shrubs; indumentum simple. Leaves alternate, distichous, simple, entire or dentate, minutely pellucid-punctate; stipules small, linear, persistent. Inflorescences axillary (supraaxillary), glomerular. Staminate flowers pedicellate; sepals 5, slightly imbricate; petals 5, contorted or imbricate in bud; disk 0; stamens 5 or 5 + 5, filaments dilated, broader than anthers, distinct from or ± adherent to lobes of the pistillode; anthers basifixed, introrse or latrorse, sometimes apiculate, dehiscing longitudinally; pollen subprolate, angulaperturate, 3-colporate, colpi operculate or inoperculate, sexine tectate-perforate; pistillode columnar or pentagonal in the lower half and cylindric at the apex; pistillate flowers pedicellate; sepals and petals 5, imbricate, the sepals ± persistent in fruit; disk 0; ovary 2–5-locular; ovule pendulous, solitary, anatropous; stylodia 2–5, short, deeply bipartite, papillose, spreading. Fruit a drupe, ovoid-subglobose, not or scarcely lobed; mesocarp fleshy, endocarp woody, tubercled or muricate, (1)2–5-locular. Seeds compressed-ovoid, testa smooth; cotyledons broad, flat.

Ten spp., 8 in tropical Africa, and 2 in Asia.

2. ***Galearia*** Zoll. & Moritzi Fig. 61B

Galearia Zoll. & Moritzi, Syst. Verz.: 19 (1846); Pax, Pflanzenr. 147. III (Heft 47): 97, figs. 31, 32 (1911); Forman, Kew Bull. 26: 153–165, fig. 1, 2 (1971), rev.; Airy Shaw, Kew Bull. 36: 365 (1981); Radcl.-Sm., Gen. Euphorb.: 127 (2001).

Dioecious trees or shrubs; buds in shoot-axils, not in leaf-axils; indumentum simple. Leaves alternate, distichous, simple, entire (crenulate towards the apex), eglandular; stipules entire to pinnatifid, persistent or deciduous. Inflorescences terminal or cauliflorous, pseudoracemose-thyrsiform (the pistillate ones racemose), elongate, often pendulous, sometimes in cymose fascicles and then pistillate ones solitary. Staminate flowers sessile or pedicellate; sepals 5, free or connate, entire, imbricate; petals 5, concave or flat; disk 0; stamens 10, biseriate, or 15 in 1 whorl; filaments basally connate, thickened, the exterior inflexed; anthers introrse, muticous; pollen grains prolate spheroidal to prolate, 3-colporate, operculate or inoperculate, sexine tectate-perforate; pistillode apically dilated, pubescent; pistillate flowers pedicellate; sepals 5, entire, imbricate, persistent; petals 5, imbricate; disk 0; ovary 2–5-locular; ovule pendulous, anatropous or orthotropous; stigma sessile, variously lobed or laciniate into several arms. Fruit a drupe, small, bilaterally flattened and transversely elongate, or larger, depressed-(sub)globose, usually 1-seeded; exocarp fleshy or bony, endocarp crustaceous, thin and entire or thick and much perforated and channelled, 1–5-celled. Seeds compressed.

Six spp., SE Asia, from Myanmar through Malesia to the Solomon Islands. Two subgenera: **subgen. *Orthopetalum***, petals straight and flat, fruits 3–4-angled or circular; **subgen. *Galearia***, petals in staminate flowers concave or cucullate, fruits laterally compressed.

3. ***Panda*** Pierre Figs. 61C, 62

Panda Pierre, Bull. Mens. Soc. Linn. Paris: 1255 (1896); Engl., Notizbl. Kgl. Bot. Gart. Mus. 5 (49): 274–276, with fig. (1912); Aubrév., For. Fl. Côte d'Iv. 1: 300 (1959); Forman, Kew Bull. 20: 309–321 (1966).

Dioecious trees; buds in axils of leafy short-shoots, not in leaf-axils; indumentum simple. Leaves alternate, distichous, simple, subentire to shallowly toothed; stipules minute, deciduous. Inflorescences ramiflorous to cauliflorous, the staminate in up to 25 cm long thyrsiform pseudoracemes fascicled on bosses on the trunk and branches, the pistillate flowers solitary or paired on elongate racemes; bracts minute. Staminate flowers pedicellate; sepals completely connate into a truncate 5-toothed cup open in bud; petals 5, valvate below, weakly imbricate above; disk 0; stamens 10, biseriate; filaments distinct, the outer much longer than the inner; anthers basifixed, introrse, dehiscing longitudinally, connective somewhat enlarged; pollen grains oblate spheroidal, 3-colporate, sexine coarsely reticulate, distinctly heterobrochate; pistillode columnar; pistillate flowers pedicellate; sepals connate into a truncate cup; petals 5, imbricate; disk 0;

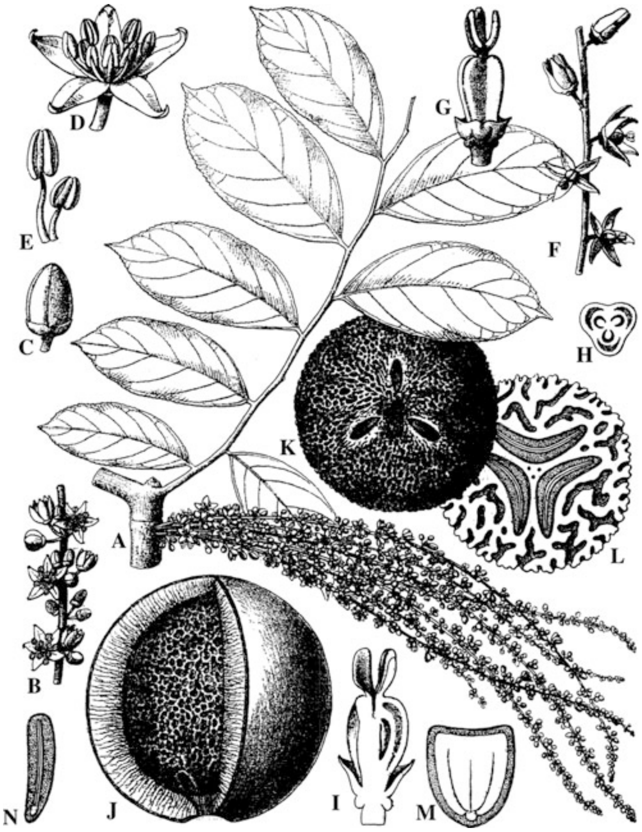

Fig. 62. Pandaceae. *Panda oleosa*. **A** Branch with staminate inflorescences. **B** Part of staminate inflorescence. **C** Flower bud. **D** Staminate flower. **E** Outer and inner stamen. **F** Part of pistillate inflorescence. **G** Calyx and pistil of pistillate flower. **H** Ovary in cross section. **I** Pistil in longitudinal section. **J** Fruit, part of exocarp removed. **K** Endocarp, seen from below. **L** Cross section of endocarp and locules. **M** Seed with cotyledon in longitudinal section. **N** Seed in radial length section. (Engler 1912)

staminodes 0; ovary (2)3–4-locular; ovule pendulous, orthotropous; stigmas (2)3–4, entire, erect at first, later reflexed. Fruit a drupe, subglobose, c. 6.5 cm diam., (2)3–4-seeded; exocarp thick, tartareous; endocarp massive, bony, pitted, (2) 3–4-sutured, tardily dehiscent along these sutures into (2)3–4 valves, leaving a large capped tri- or tetrapterygoid columella. Seeds flattened, obtriangular; cotyledons cordate, truncate.

A single sp., *P. oleosa* Pierre, restricted to West African rain forest areas (Côte d'Ivoire to the Congo). The seed oil is regionally used for cooking. The fruits are said to be dispersed by elephants.

Selected Bibliography

Corner, E.J.H. 1976. See General References.
Engler, A. 1912. *Panda oleosa*, ein Ölsamenbaum Westafrikas. Notizbl. Königl. bot. Gart. Mus. Berlin 5: 274–276.
Forman, L.L. 1966. The reinstatement of *Galearia* Zoll. & Mor. and *Microdesmis* Hook.f. in the Pandaceae, with appendices by C. R. Metcalfe and N. Parameswaran. Kew Bull. 20: 309–321.
Hayden, W.C., Hayden, S.M. 2000. Wood anatomy of Acalyphoideae (Euphorbiaceae). IAWA J. 21: 213–235.
Hill, A. W. 1937. The method of germination of seeds enclosed in a stony endocarp. II. Ann. Bot. II, 1: 239–256, fig. 7.
Nowicke, J.W. 1984. A palynological study of the Pandaceae. Pollen et Spores 26: 31–42.
Nowicke, J.W., Takahashi, M., Webster, G.L. 1998. Pollen morphology, exine structure and systematics of Acalyphoideae (Euphorbiaceae) Part 1. Rev. Palaeobot. Palynol. 102: 115–152.
Radcliffe-Smith, A. 2001. See General References.
Soltis, D.E. et al. 2011. See General References.
Stevens, P.F. 2001 onwards. See General References.
Tokuoka, T., Tobe, H. 2003. Ovules and seeds in Acalyphoideae (Euphorbiaceae): structure and systematic implications. J. Pl. Res. 116: 355–380.
Vaughan, J.G., Rest, J.A. 1969. Note on the testa structure of *Panda* Pierre, *Galearia* Zoll. et Mor. and *Microdesmis* Hook. f. (Pandaceae). Kew Bull. 23: 215–218.
Webster, G.L. 1987. The saga of the spurges: a review of the classification and relationships of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 3–46.
Webster, G.L. 1994. Synopsis of the genera and suprageneric taxa of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.
Wurdack, K.J., Davis, C.C. 2009. See General References.
Xi, Z. et al. 2012. See General References.

Putranjivaceae

Putranjivaceae Endl., Ench. Bot.: 174 (1841).

G. Levin

Trees or shrubs, with simple trichomes or sometimes stellate on fruits. Leaves alternate or rarely opposite, spirally arranged but often appearing distichous, simple, petiolate, pinnately veined, base usually oblique, margins entire or dentate, the teeth sometimes spinose; stipules deciduous or persistent. Flowers in axillary or cauliflorous clusters, sometimes solitary, rarely cymes, pedicellate, actinomorphic, generally unisexual and the plants dioecious, but occasionally polygamodioecious or monoecious; sepals (3)4–5(6), distinct, imbricate or the pistillate rarely open in bud; petals 0. Staminate flowers: stamens (2) 3–20(−50), filaments distinct, anthers erect, dithecal, introrsely or less frequently latrorsely or extrorsely dehiscent by longitudinal slits; disk intrastaminal or absent; pistillode small or absent. Pistillate flowers: sepals deciduous or persistent; disk annular or absent; ovary superior, syncarpous, 1–3(−6)-locular, placentation axile; ovules 2 per locule, anatropus, bitegmic, embedded in a massive obturator; stylodia as many as the locules, usually short, stigmas subpeltate, reniform, discoid, bilobed, or petaloid; fruit drupaceous; seeds 1 per locule or fruit by abortion, albuminous, embryo large, straight.

Two genera and c. 225 spp., tropical and subtropical Asia, Africa, America, Australia, and western Pacific islands.

Vegetative Anatomy. The leaves are dorsiventral. Druses may be found in the mesophyll, and prismatic crystals in the mesophyll and vein bundle sheathes. Venation is brochidodromous or sometime eucamptodromous; higher order venation patterns are variable and may be systematically informative. Stomata are restricted to the abaxial side and are brachyparacytic, with the subsidiary cells overlying the guard cells (Levin 1986).

Wood is ring or diffuse porous with the vessels solitary or in radial multiples. Perforation plates are scalariform, simple, or both; intervascular and ray/vessel pitting is minute and alternate. Axial parenchyma is diffuse or apotracheal in numerous short, often interrupted bands one cell wide. Rays are uniseriate and multiseriate, heterocellular. Fibers are non-septate and very thick-walled. Prismatic crystals are found in the axial and ray parenchyma (Smith and Ayensu 1964; Hayden 1980; Mennega 1987).

Embryology and Seed Anatomy. Readers are referred to the detailed descriptions by Stuppy (1996) and Tokuoka and Tobe (1999). Systematically significant features include glandular anther tapetum; two-celled pollen grains (when shed); anatropous, bitegmic, crassinucellate ovules; a two- or three-celled archesporium; a thin, two cell-layered parietal layer in the nucellus; Polygonum type embryo sac; no nucellar beak or cap; early disintegrating nucellar tissue; a massive funicular obturator; thick, multiplicative inner and outer integuments; an endothelium; Nuclear endosperm formation; abundant endosperm in the seeds; a large, straight embryo; and generally a fibrous exotegmen.

Pollen Morphology. Pollen is spheroidal to prolate, 3-colporate with transversely elongate ora and often with elongate colpi, and tectate-reticulate (Punt 1962; Köhler 1965). Punt (1962) assigned the pollen of *Drypetes* and *Putranjiva* to different types based on grain shape and exine thickness, whereas Köhler (1965), who sampled a more diverse set of *Drypetes* species, assigned the two genera to the same type and recognized a second pollen type in *Drypetes* based primarily on aperture length. A broader survey could reveal

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_21, © Springer-Verlag Berlin Heidelberg 2014

that variation in shape, apertures, exine thickness, and sculpture is systematically informative.

KARYOLOGY. Chromosome numbers have been reported for only five *Drypetes* species, four African (Hans 1973) and one southeast Asian (Oginuma et al. 1998), and they are consistently $n = 20$. In contrast, counts of $n = 7$, 19, 20, and 21 have been reported from *Putranjiva roxburghii* (Hans 1973; Sanjappa 1979; Chattopadhyay and Sharma 1988). It is possible that the base number for the family is $x = 7$, with polyploidy and aneuploidy accounting for the other numbers. It is also possible that the counts other than $n = 20$, particularly those of $n = 7$, are in error. Broader surveys are indicated.

FRUIT AND DISPERSAL. Although all fruits of Putranjivaceae are drupaceous, there is considerable variation in the exocarp. It may be fleshy, leathery, or somewhat woody, and colors at maturity include red, orange, yellow, brown, and white. Tomlinson (1980) reported that the red fruits of *Drypetes lateriflora* are removed rapidly, whereas the white fruits of *D. alba* persist on the trees for long periods. There are almost no detailed studies of fruit dispersal in the family, but various doves and pigeons have been reported to disperse the fruits of *D. deplanchei* (Floyd 1989; Forster 1997).

PHYTOCHEMISTRY. Putranjivaceae is noteworthy for producing glucosinolates (mustard oil glucosides). Phylogenetic studies demonstrate that this evolved independently here and in the Brassicales (Rodman et al. 1998). In addition, sesquiterpene lactones and friedelanes are known from the family (Wandji et al. 2003).

PHYLOGENY. Putranjivaceae traditionally have been included in Euphorbiaceae subfamily Phyllanthoideae (Phyllanthaceae) as tribe Drypeteae, along with the African genus *Lingelsheimia* Pax (Webster 1994; Radcliffe-Smith 2001). Meeuse (1990), focusing on embryology, seed anatomy, and especially chemistry, removed the tribe from the Euphorbiaceae and placed it as a family in Brassicales. Molecular phylogenies clearly show that *Drypetes* and *Putranjiva* are closely related, belong outside the Euphorbiaceae, and are members of the Malpighiales rather than the Brassicales (Rodman et al. 1998; APG II 2003). *Lingelsheimia* has not been included in molecular studies, but its morphology is quite different from Putranjivaceae (Léonard 1962) and consistent with Phyllanthoideae.

Affinities within Malpighiales place Putranjivaceae with strong support as the sister of *Lophopyxis* (Wurdack and Davis 2009; Soltis et al. 2011), and Xi et al. (2012) have resolved Putranjivaceae and Lophopyxidaceae, the "putranjivoids", within a larger clade, elsewhere comprising Caryocaraceae, "malpighioids" (Malpighiaceae, Elatinaceae, Centroplacaceae) and the "chrysobalanoids". For morphological traits shared by Putranjivaceae and Lophopyxidaceae, see under Lophopyxidaceae, this volume.

Various efforts have been made to fragment *Drypetes* into smaller genera. The only commonly accepted segregates are *Sibangea* and *Putranjiva*. The former, which has three African species, is distinguished by having the pistillate sepals open in bud and persistent in fruit, in contrast to imbricate and deciduous in *Drypetes* s.s. (Radcliffe-Smith 2001). Phylogenetic analysis of DNA sequence data place *Sibangea* within *Drypetes* (Wurdack et al. 2004), a placement that is adopted here. Although Hurusawa (1954) reduced *Putranjiva* to a subgenus of *Drypetes*, a treatment that has been widely followed, molecular phylogenetic studies show them to be sister taxa (Wurdack et al. 2004) and here they are treated as distinct.

DISTRIBUTION AND HABITATS. *Drypetes* grows primarily in tropical and subtropical lowland forests, woodlands, and savannas. A few species are found in tropical montane forests or warm temperate areas. Its greatest diversity is in Asia, with about 120 species. About 75 species grow in Africa and Madagascar, with only about 20 species, many of them undescribed, found in the Americas. *Putranjiva* is found in forests of tropical Asia from the Indian subcontinent to Indonesia, south China, Taiwan, and the Ryukyu Islands. Most species are narrowly distributed, but *P. roxburghii* is found in seasonal forests from Pakistan to Indonesia.

ECONOMIC IMPORTANCE. Fruit of some species of *Drypetes* are eaten locally, and the hard wood is locally used in construction. Bark extracts from several *Drypetes* species and *Putranjiva roxburghii* are used medicinally in central Africa and India; these may have pharmacological value (Chungag Anye et al. 2003). *P. roxburghii* is widely cultivated as an ornamental tree in tropical to warm temperate regions.

CONSERVATION. Although many species of Putranjivaceae are common, in some cases dominant forest trees, others are of conservation concern. This is particularly true of some island endemics, notably *Drypetes glabra* and *D. henriquesii* from São Tomé, *D. andamanica* from the Andaman Islands, *D. leiocarpa* from the Nicobar Islands, and *D. riseleyi* from the Seychelles.

KEY TO THE GENERA

1. Disk present; stamens mostly 4 or more; stigmas somewhat swollen and subpeltate, reniform, discoid, or bilobed, but not petaloid **1. *Drypetes***
– Disk absent; stamens mostly 2 or 3; stigmas conspicuously dilated and petaloid **2. *Putranjiva***

1. ***Drypetes*** Vahl Fig. 63

Drypetes Vahl, Eclog. Amer. 3: 49 (1810); Pax & K. Hoffm., Pflanzenreich 147. XV: 229–279 (1922), rev.; Airy Shaw, Kew Bull. Addit. Series 4: 97–108 (1975), rev. Borneo spp.; Airy Shaw, Kew Bull. 36: 286–292 (1981), rev. Sumatra spp.; Radcl.-Sm., Fl. Trop. E Africa, Euphorbiaceae I: 88–103 (1987), rev. E Afric. spp.; Radcl.-Sm., Fl. Zambes. 9(4): 87–93 (1996), rev. SE Afric. spp.; P.I. Forster, Austrobaileya 4: 477–494 (1997), rev. Australian spp.; T. Chakrab et al., J. Econ. Taxon. Bot. 21: 251–280 (1997), rev. S Asian spp.; McPherson, Adansonia III, 22: 205–209 (2000), rev. Madag. spp.; L. Phuphathanaphong and K. Chayamarit. Flora of Thailand, 8(1); 231–253 (2005), rev. Thai spp.

Sibangea Oliv. (1883).

Trees or shrubs, usually dioecious. Leaves alternate or rarely opposite, spiral but sometimes appearing distichous, petiolate, stipulate, pinnately veined, usually oblique at the base, margins entire or spinose-dentate. Flowers in axillary clusters or cauliflorous; sepals 4–5, imbricate or the pistillate rarely open in bud; petals none. Staminate flowers: stamens 3–20(–50); disk intrastaminal; pistillode small or none. Pistillate flowers: disk annular; ovary 1–3(–6)-locular; stigmas subpeltate, reniform, discoid, or shallowly bilobed. Fruit drupaceous. Seeds 1 per locule or fruit. $n = 20$.

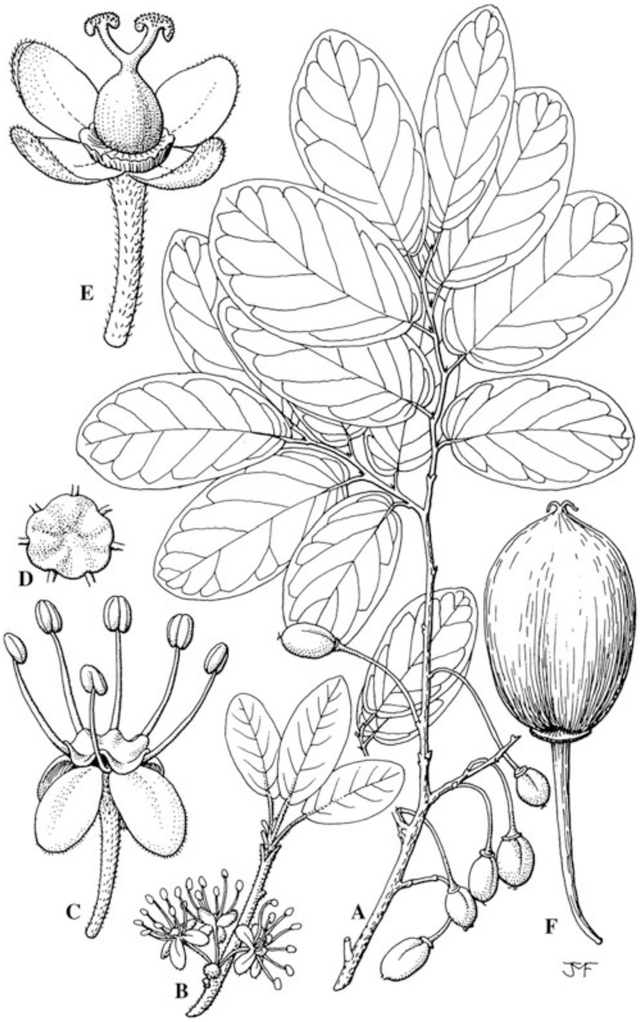

Fig. 63. Putranjivaceae. *Drypetes mossambicensis*. **A** Part of distal branch with immature fruits. **B** Staminate inflorescence. **C** Staminate flower. **D** Disk thereof. **E** Pistillate flower. **F** Fruit. (Radcliffe-Smith 1996; drawn by J-M. Fothergill)

About 220 spp.; subsaharan Africa, southern and eastern Asia, Australasia, and tropical America.

2. ***Putranjiva*** Wallich

Putranjiva Wall., Tent. Fl. Napal.: 61 (1826); Hurus., J. Fac. Sci. Univ. Tokyo III, Bot. 6: 335–338 (1954), reg. rev.

Trees, dioecious. Leaves alternate, spiral, petiolate, stipulate, pinnately veined, usually oblique at the base, margins entire or dentate. Flowers in axillary clusters or the pistillate solitary; sepals 3–6, imbricate; petals none; disk none. Staminate flowers: stamens 2–3(–4), anthers extrorsely dehiscent; pistillode none. Pistillate flowers: ovary 2–3-locular; stigmas dilated, petaloid. Fruit drupaceous. Seed 1. $n = 20$ (and possibly 7, 19, and 21).

Four spp., tropical Asia, from Pakistan and Ceylon to Taiwan and Ryukyu Islands.

Selected Bibliography

APG II. The Angiosperm Phylogeny Group. 2003. See General References.

Chattopadhyay, D., Sharma, A.K. 1988. Sex difference and chromosomes in *Putranjiva roxburghii* Wall. Curr. Sci. 57: 1017–1019.

Chungag Anye, N.B., Njamen, D., Wandji, J., Fomum, Z.T., Dongmo, A., Nguelefack, T.B., Wansi, D., Kamanyi, A. 2003. Anti-inflammatory and analgesic effects of Drypemolundein A, a sesquiterpene lactone from *Drypetes molunduana*. Pharmaceut. Biol. 41: 26–30.

Floyd, A.G. 1989. Rainforest Trees of Mainland Southeastern Australia. Melbourne & Sydney: Inkata Press.

Forster, P.I. 1997. A taxonomic revision of Drypetes Vahl (Euphorbiaceae) in Australia. Austrobaileya 4: 477–494.

Govaerts, R., Frodin, D.G., Radcliffe-Smith, A. 2000. World Checklist and Bibliography of Euphorbiaceae (and Pandaceae). Kew: Royal Botanical Gardens, pp. 591–614, 1381–1383, 1471–1473.

Hans, A.S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hayden, W.J. 1980. Systematic anatomy of Oldfieldioideae (Euphorbiaceae). Ph.D. dissertation. College Park: University of Maryland, pp. 202–219.

Hurusawa, I. 1954. Eine nochmalig Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo III, Bot. 6: 209–342.

Köhler, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

Léonard, J. 1962. Notulae systematicae XXXIII. Sur les limites entre les genres *Drypetes* Vahl et *Lingelsheimia* Pax (Euphorbiacées). Bull. Jard. Bot. État 32: 513–516.

Levin, G.A. 1986. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

Meeuse, A.D.J. 1990. The Euphorbiaceae auct. plur., an unnatural taxon. Delft: Eburon.

Mennega, A.M.W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.

Oginuma, K., Kiaptranis, R., Damas, K., Tobe, H. 1998. A cytological study of some plants from Papua New Guinea. Acta Phytotax. Geobot. 49: 105–114.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

Radcliffe-Smith, A. 1996. Euphorbiaceae. In: Pope, G.V. (ed.) Flora Zambesiaca 9, Pt. 4. Kew: Royal Botanic Gardens.

Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Richmond: Royal Botanic Garden, Kew, pp. 48–55.

Rodman, J.E., Soltis, P.S., Soltis, D.E., Sytsma, K.J., Karol, K.G. 1998. Parallel evolution of glucosinolate biosynthesis inferred from congruent nuclear and plastid gene phylogenies. Amer. J. Bot. 85: 997–1006.

Sanjappa, M. 1979. IOPB chromosome number reports LXIII. Taxon 28: 274–275.

Smith, A.C., Ayensu, E.S. 1964. The identity of the genus *Calyptosepalum* S. Moore. Brittonia 16: 220–227.

Soltis, D.E. et al. 2011. See General References.

Stuppy, W. 1996. Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Ph.D. dissertation. Kaiserslautern, Germany: Universität Kaiserslautern.

Tokuoka, T., Peng, C.-I. 1997. Floral morphology and its systematic implications in *Drypetes integerrima* (Koidz.) Hosok. (Euphorbiaceae, tribe Drypeteae) from Bonin Islands, Japan. Acta Phytotax. Geobot. 48: 159–166.

Tokuoka, T., Tobe, H. 1999. Embryology of tribe Drypeteae, an enigmatic taxon of Euphorbiaceae. Pl. Syst. Evol. 215: 189–208.

Tomlinson, P.B. 1980. The Biology of Trees Native to Tropical Florida. Alston, Massachusetts: Harvard University Printing Office.

Wandji, J., Tillequin, F., Mulholland, D.A., Temgoua, A.D., Wansi, J.D., Seguin, E., Fomum, Z.T. 2003. Phenolic constituents from *Drypetes armoracia*. Phytochemistry 63: 453–456.

Webster, G.L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Wurdack, K.J., Hoffmann, P., Samuel, R., de Bruijn, A., van der Bank, M., Chase, M.W. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid *rbc*L DNA sequences. Amer. J. Bot. 91: 1882–1900.

Xi, Z. et al. 2012. See General References.

Quiinaceae

Quiinaceae Engl. (1888), nom. cons.

K. Kubitzki

Usually (andro)dioecious trees of moderate size with lysigenous mucilage-containing spaces and ducts. Leaves opposite or whorled, serrate to entire, simple, lobed or pinnately compound (often pinnately compound on young plants, simple on adults), usually glabrous, petiolate, secondary veins pinnate, craspedodromous to brochidodromous, tertiary parallel or plumose reticulate and very closely spaced; stipules interpetiolar, foliaceous and with midrib and pinnate venation or setaceous, distinct or sometimes pairwise connate. Inflorescences axillary or (*Froesia*) terminal thyrsoids or botryoids. Flowers bisexual or more often unisexual and then dioeciously distributed (the pistillate with stamens producing sterile pollen), hypogynous, regular; sepals 3–5(6), small, unequal, imbricate; petals (3)4–5(–8), contorted or imbricate, basally sometimes joining with neighbouring petals and sepals to form a short floral cup; stamens 15–numerous, sometimes forming 5 indistinct fascicles; filaments distinct, slender; anthers basifixed to slightly dorsifixed, bithecate, dehiscing by slits; gynoecium syncarpous, 2–14-carpellate, longitudinally ribbed, with as many locules and stylodia as carpels, or (*Froesia*) apocarpous and 3-carpellate; ovules 2(–4) in each locule, on basal-axile placentas, epitropous, anatropous, ascending. Fruit berry-like, fleshy or leathery, but often dehiscent at full maturity, longitudinally ribbed. Seeds with or without endosperm, villous or (*Froesia*) glabrous; the embryo straight, with short hypocotyl and thick cotyledons, or with thin cotyledons and thick endosperm (*Lacunaria*, *Touroulia*).

Four genera and about 51 spp., centred in the humid lowlands of northern South America and extending to Belize and S Brazil.

Vegetative Morphology. Quiinaceae are small to midcanopy trees. In *Froesia*, the unbranched stem bears a rosette of huge leaves and is terminated by the inflorescence; it is unknown whether *Froesia* is hapaxanthous or, by continued growth of the stem apex after fructification or by sympodial branching, can flower repeatedly. Phyllotaxis is generally decussate; whorls with preferably four leaves occur in most species of *Lacunaria* and a single *Quiina*, *Q. pteridophylla*. Leaves on juvenile plants and coppice shoots are often pinnatisect or pinnately lobed (Fig. 64); this leaf form persists in adult *Froesia* and *Touroulia*. Some species of *Quiina*, such as *Q. leptoclada*, *Q. indigofera* and *Q. obovata*, have simple seedling leaves. The leaves have interpetiolar stipules which, by virtue of a midrib and pinnate venation, often appear leaf-like and can vary from leafy to setose, and caducous to persistent; they can be deeply dissected with several setose lobes (*Froesia*) or united through pairwise fusion as in *Touroulia* (Foster 1950a, b, 1951). Leaves can be very large and may reach a length of 1.5 m, the stipules 10 cm.

Vegetative Anatomy. Gross venation of leaves and leaflets is craspedodromous or brochidodromous, but last order veinlets produce a peculiar, closely spaced parallel to plumose-reticulate pattern characteristic of the family. The veinlets originating from adjacent lateral veins anastomose straightway or, as in *Touroulia guianensis*, meet to form a "geniculate" arch (Fig. 65; Foster 1950a, b, 1951). Hallier (1911) believed that this regular venation pattern might reflect the product of fusion in an originally bipinnate leaf, but there is little evidence in support of this.

Stomata are paracytic. The mesophyll of *Froesia* and *Touroulia guianensis* contains masses of crystalliferous cells with U-shaped thickening (cristarque cells). They form more or less continuous strands, often one abaxially and another

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_22,

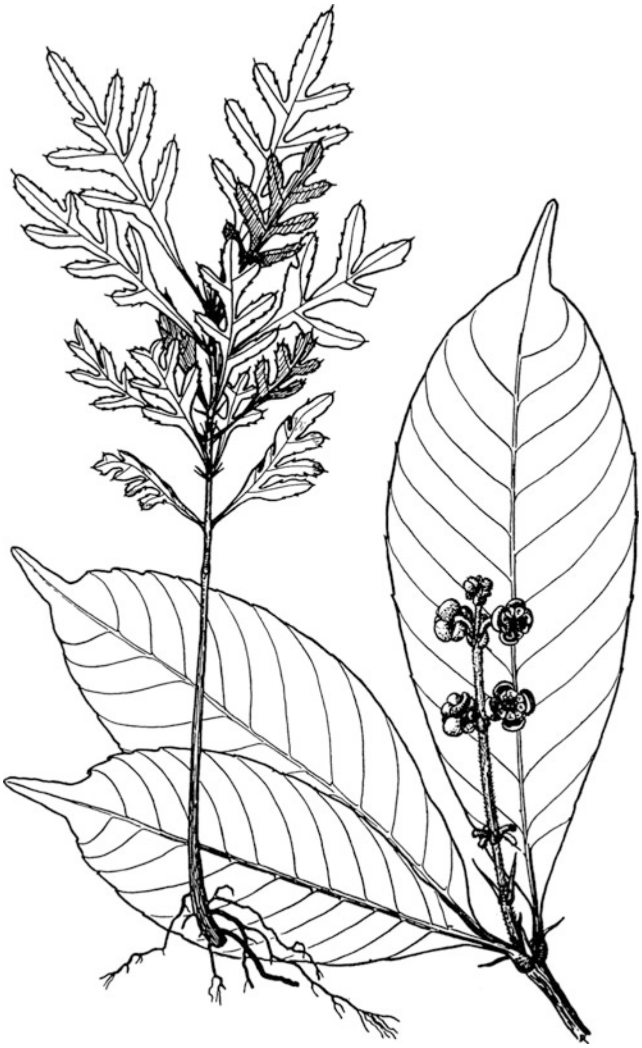

Fig. 64. Quiinaceae. *Lacunaria crenata*. Leaf dimorphism, a seedling with decussate stipulate pinnatified leaves, and shoot tip of adult tree with simple leaves. (Foster 1951)

adaxially, which occur in direct contact with the fibres flanking the vascular tissue of the veinlets. *Quiina negrensis* is noteworthy for containing abundantly small branched sclereids in the leaf mesophyll (Pires 1950).

Lysigenous intercellular spaces and ducts filled with mucilage are generally found in the medulla and vascular strands of the midrib and petiole. Their occurrence distinguishes the family from the Guttiferae in which Quiinaceae formerly were included. An extensive study of the anatomy of the wood and bark of the family revealed a uniform pattern (Gottwald and Parameswaran 1967). There is broad agreement in features such as diameter and simple perforations of vessels, small vestured intervascular pits, and fibriform vessel members. Apart from this general pattern, some noteworthy special features include rays containing silica and scalariform vessel perforations in *Lacunaria*, and banded parenchyma in *Froesia*. The nodes are trilacunar. Among the numerous families that have been compared with Quiinaceae, Ochnaceae and Medusagynaceae are similar in wood anatomy.

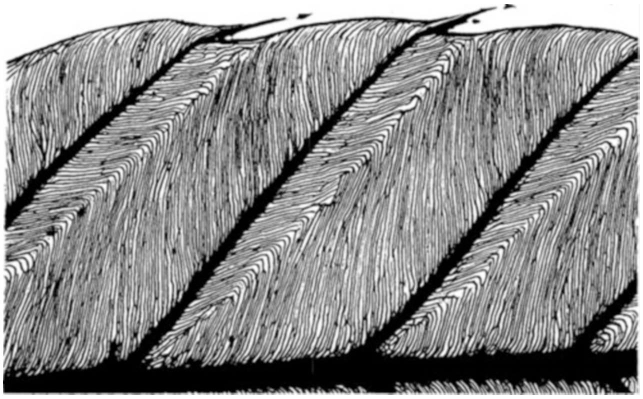

Fig. 65. Quiinaceae. *Touroulia guianensis*, geniculate venation pattern of seedling leaflet. (Foster 1950b)

INFLORESCENCE STRUCTURE. The basic type seems to be a determinate thyrse (i.e. a thyrsoid) with richly flowered dichasial cymes (*Froesia*, *Touroulia*). Often several basal partial inflorescences are present per leaf axil, forming a pleiothyrsoid. Possible progressions include (a) the transition from decussate to dispersed phyllotaxis of bracts subtending partial inflorescences (*Quiina*, *Lacunaria*); (b) a reduction in number of flowers per partial inflorescence down to 1 (leading to botryoids, as in some *Quiina*); and (c) the reduction in number of basal special thyrsoids (pleiothyrsoid → thyrsoid).

FLOWER STRUCTURE AND REPRODUCTIVE SYSTEMS. Although there is some meristic variation in the flowers of Quiinaceae, pentamery and an imbricate calyx originating in quincuncial sequence and a contorted corolla (as found in *Froesia* and *Touroulia*) seem to represent the basic condition. In *Touroulia* the androecium originates on a ring wall in centrifugal direction (C. Bayer, pers. obs.), although fascicled androecia are known as well (*Lacunaria coriacea*). The

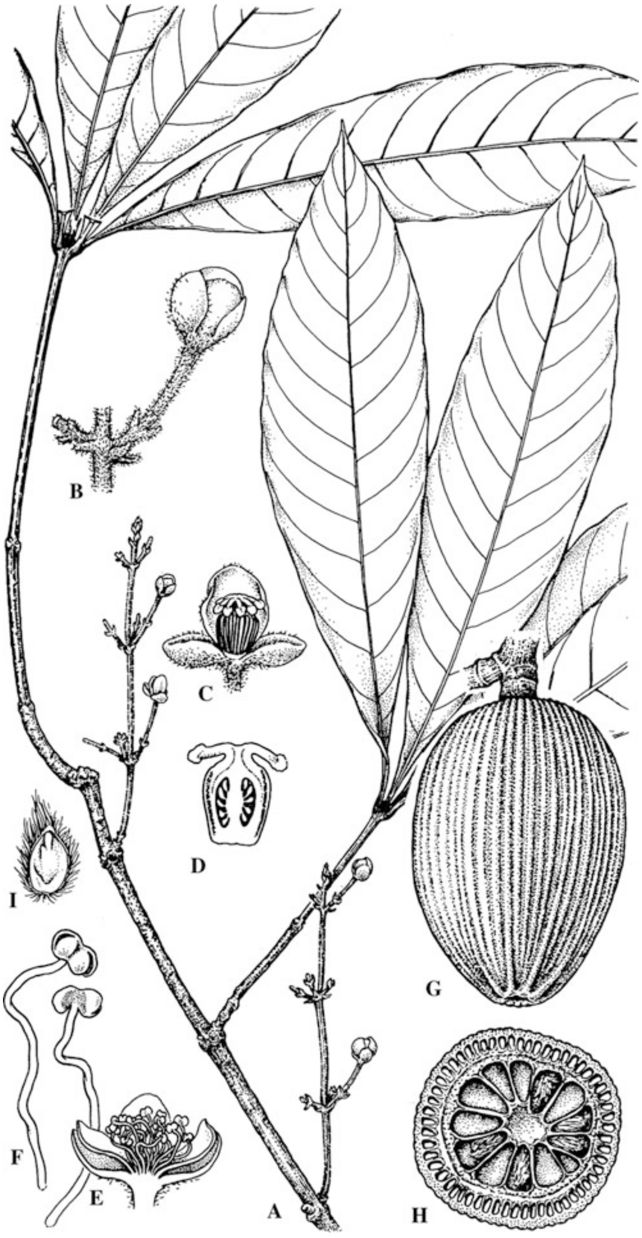

Fig. 66. Quiinaceae. *Lacunaria jenmani.* **A** Branchlet with pistillate inflorescences. **B** Detail of pistillate inflorescence. **C** Pistillate flower with one sepal and three petals removed. **D** Vertical section of pistil. **E** Vertical section of staminate flower. **F** Stamens. **G** Fruit. **H** Same, transversal section, showing cavities in pericarp. **I** Vertical section of seed. (Reproduced with the kind permission of the artist Bobbi Angell)

apocarpy of *Froesia* raises the question of whether it is a primary or secondary condition, but applying the criteria of Endress (1982) for evolutionarily secondary apocarpy fails to indicate a secondary origin, and molecular data place *Froesia* as sister to the rest of the family (see below).

Froesia is the only genus with bisexual flowers (but see *Touroulia amazonica*); *Lacunaria* is truly dioecious with no vestiges of the opposite sex in its staminate and pistillate flowers. *Touroulia guianensis* and all species of *Quiina* are also functionally dioecious with probably strictly staminate or (morphologically) bisexual flowers on different individuals, with significantly less stamens in the bisexual than in the staminate flowers. The bisexual flowers of *Quiina* are reported to produce sterile pollen, in contrast to the staminate ones (Baillon 1877; pers. comm. of the late J.M. Pires to the author). This issue needs further investigation because Schneider (1996) observed in six species pollen dimorphism with inaperturate grains in the staminate flowers, whereas my own preliminary tests with carmin acetic acid treatment of two species of *Quiina* revealed stainable and, hence, probably viable pollen in the staminate flowers. Because nectar does not seem to be produced, the pollen of these flowers may be a (deceptive?) attractant; relevant field observations would be of great interest.

Affinities and Phylogeny. Traditionally, Quiinaceae have been considered to form part of a broadly delineated order Theales (Engler 1925), where they were supposed to be close to Ochnaceae. Both families agree in wood anatomy (Gottwald and Parameswaran 1967), the possession of cristarque cells (Amaral 1991), tenuinucellate ovules, and the lack of nectaries, but in a revised ordinal classification (APG 1998) they were included in Malpighiales. Within this vast alliance, multi-gene sequence analyses (Wurdack and Chase 2009; Soltis et al. 2011; Xi et al. 2012) place Quiinaceae sister to *Medusagyne* and these as sister to Ochnaceae s. str.

The obvious basal position of *Froesia* within the family is confirmed both by a morphologically based (Schneider et al. 2002) and a DNA-based cladistic analysis (Schneider et al. 2006).

Distribution and Habitats. The family is centred in the lowlands and colline belt of Amazonia and Guyana, with some extensions to the Atlantic rain forest of E and SE Brazil, the cloud forests of northern Venezuela, the lowlands of Central America up to Belize, and Jamaica.

Key to the Genera

1. Leaves of adult plants pinnate or pinnatifid 2
– Leaves of adult plants simple 3
2. Stipules distinct, setaceous; gynoecium apocarpous; seeds glabrous **1. *Froesia***
– Stipules connate; gynoecium syncarpous; seeds villous **2. *Touroulia***
3. Leaves mostly verticillate, rarely opposite; pistillate flowers without staminodes; ovary with 4–14 locules and stylodia **3. *Lacunaria***
– Leaves mostly opposite, rarely verticillate; pistillate flowers with staminodes; ovary with 1–3(–5) locules and stylodia **4. *Quiina***

Genera of Quiinaceae

1. *Froesia* Pires

Froesia Pires, Bol. Técn. Inst. Agron. Norte 15: 22 (1948); Steyermark & Bunting, Brittonia 27: 172–178 (1975), rev.; Schneider & Zizka, Novon 7: 406–412 (1997), key.

Shrubs or small trees; trunk unbranched, ending in a terminal rosette of leaves. Leaves very large (up to 1.5 m long), opposite, imparipinnate, 11–27-foliolate, the leaflets opposite to alternate; veins prominent, lined with series of cristarque cells; stipules distinct, setaceous. Inflorescence terminal, thyrsoid. Flowers bisexual; sepals (4)5, petals 5, yellow to roseate; stamens very numerous; carpels (2)3, distinct; stylodia filiform. Mericarps 1–3-seeded. Seeds exalbuminous (?), glabrous.

Six spp., lowland of northern South America and cloud forests of Venezuela.

2. *Touroulia* Aubl. Figs. 64, 65

Touroulia Aubl., Hist. Pl. Gui. 1: 492 (1775); Pires, Bol. técn. Inst. Agron. Norte 20: 48–50 (1950); Zizka & Schneider, Willdenowia 29: 227–234 (1999).

Small trees, androdioecious (*T. amazonica* with bisexual flowers?). Leaves opposite, imparipinnate, sometimes with alate rachis in distal part, 7–17-foliolate, leaflets sessile, serrate-crenate; stipules subulate, caducous or persistent. Inflorescences terminal, slender thyrsoids. Flowers either morphologically bisexual or staminate but the plants probably dioecious; sepals 5, distinct or basally connate; petal (4)5; stamens in staminate flowers and staminodes in pistillate flowers numerous; ovary with 4–11 locules and stylodia. Fruit baccate, 4–8(–11)-celled; stylodia persistent. Seeds 1(2) per cell, compressed, ferrugineous-villous; endosperm copious.

Two spp. in the lowlands of northern South America. *T. amazonica* Pires differs considerably from *T. guianensis* Aubl. in larger flowers, distinct sepals, persistent and not resinous petals, non-geniculate tertiary veins, and absence of cristarque cells in the mesophyll, and time and again, generic status has been suggested for the former.

3. *Lacunaria* Ducke Fig. 66

Lacunaria Ducke, Arch. Jardim Bot. Rio de Janeiro 4: 139 (1925), and Arch. Inst. Biol. Veg. 2: 168–171 (1935); Rocha & Secco, Acta Amazonica 34: 425–433 (2004), rev.

Small or medium-sized trees, dioecious. Adult leaves simple, in whorls often of 4, or rarely opposite (*L. oppositifolia* Pires), medium-sized to large; stipules linear-subulate or -lanceolate, distinct to connate. Inflorescences axillary thyrsoids. Flowers unisexual; sepals 4–5, petals 4–8, imbricate or contort, staminate flowers: stamens 20–170; pistillate flowers: ovary globose-pyriform, striate, with 4–14 locules and stylodia, each locule with 2 ovules. Fruit a 5–13-celled, lignescent berry; pericarp fleshy with well-developed mucilage-containing cavities; septa dissolving. Seeds albuminous, compressed, embedded in pulp; testa ferrugineous-villous.

Eight (–10) spp., humid forests of Central (Costa Rica, Panama) and northern South America, one species in C Brazil.

4. *Quiina* Aubl.

Quiina Aubl., Hist. Pl. Gui. Suppl.: 19 (1775); Schneider, Acta Bot. Venez. 21: 1–74 (1998), Venez. spp.

Trees or shrubs, sometimes climbing, androdioecious. Leaves opposite, rarely verticillate, simple, entire or dentate, stipulate, the stipules leafy or setose, distinct or connate. Inflorescences axillary (pleio)thyrsoids or botryoids. Flowers either morphologically bisexual or staminate but the plants probably largely functionally unisexual; sepals 3–6 and petals 3–5(–7); stamens 14–62 (staminate flowers) or 12–20 (morphologically bisexual flowers); ovary with 2–3(–5) locules and stylodia. Fruit a 1–3-seeded, lignescent berry with fibrous pericarp; cavities in the pericarp small to inconspicuous. Seeds ferrugineous-villous or velutinous; cotyledons thick; endosperm 0.

About 34 spp., centred in northern S America, extending with one species to coastal S Brazil and with another to Belize.

Selected Bibliography

Amaral, M.C.E. 1991. Phylogenetische Systematik der Ochnaceae. Bot. Jahrb. Syst. 113: 105–196.

APG 1998. The Angiosperm Phylogeny Group. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85: 531–553.

Baillon, H.E. 1877. Histoire des plantes, t. 6. Clusiaceées – Quineae. Paris: Librairie Hachette.

Endress, P.K. 1982. Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive angiosperms. Taxon 31: 48–52.

Engler, A. 1925. Quiinaceae. In: Engler & Prantl, Die natürlichen Pflanzenfamilien, 2nd edn, 21: 106–108.

Foster, A.S. 1950a. Morphology and venation of the leaf of *Quiina acutangula* Ducke. Amer. J. Bot. 37: 159–171. [Note that this sp. has been renamed *Q. pteridophyllea* (Radlk.) Pires]

Foster, A.S. 1950b. Venation and histology of the leaflets of *Touroulia guianensis* Aubl. and *Froesia tricarpa* Pires. Amer. J. Bot. 37: 848–862.

Foster, A.S. 1951. Heterophylly and foliar venation in *Lacunaria*. Bull. Torrey Bot. Club 78: 382–400.

Gottwald, H., Parameswaran, N. 1967. Beiträge zur Anatomie und Systematik der Quiinaceae. Bot. Jahrb. Syst. 87: 361–381.

Hallier, H. 1911. L'origine et le système phylétique des angiospermes exposés à l'aide de leur arbre généalogique. Arch. Néerl. Sci. exact.et nat. Sér. III B, 1: 146–234.

Matthews, M., Amaral, M., Endress, P.K. 2012. See General References.

Pires, J.M. 1948. Quiinaceae. Bol. técn. Inst. Agrón. Norte 15: 22–31.

Pires, J.M. 1950. Contribuição para a flora Amazónica. Bol. técn. Inst. Agrón. Norte 20: 41–51, pl. V–XV.

Schneider, J. 1996. Morphologische, anatomische und mikromorphologische Untersuchungen zur Taxonomie der Gattung *Quiina* (Quiinaceae). Diplomarbeit, Fachbereich Biologie, Joh. Wolfg. Goethe Universität, Frankfurt/Main.

Schneider, J.V., Swenson, U., Zizka, G. 2002. Phylogenetic reconstruction of the neotropical family Quiinaceae (Malpighiales) based on morphology with remarks on the evolution of an androdioecious sex distribution. Ann. Missouri Bot. Gard. 89: 64–76.

Schneider, J.V., Swenson, U., Samuel, R., Stuessy, T., Zizka, G. 2006. Phylogenetics of Quiinaceae (Malpighiales): evidence from *trn*L-*trn*F sequence data and morphology. Pl. Syst. Evol. 257: 189–203.

Soltis, D.E. et al. 2011. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Rhizophoraceae

Rhizophoraceae Pers. (1806), nom. cons.

A.E. SCHWARZBACH

Shrubs or trees, sometimes with aerial roots. Leaves opposite or verticillate, decussate or bijugate, simple, toothed, crenate, or entire, marginal teeth of a distinctive Macarisioid type; stipules interpetiolar, valvate and pubescent or imbricate and glabrous, always bearing colleters. Inflorescences axillary, cymose, dichasial, or fasciculate. Flowers regular, bisexual or rarely unisexual, with articulated pedicels; the sepals valvate, basally usually congenitally connate and above with (3)4–5(−16) lobes postgenitally connected by interdigitation of their papillose margins; petals equalling the number of sepals, contorted or infolded in bud, usually with both a terminal arista and filiform appendages on the two lobes, rarely entire, usually each petal enwrapping 1–5 stamens; androecium diplostemonous or obdiplostemonous or polyandrous, the filaments sometimes connate at base, borne around the base of or on an intrastaminal entire or lobed nectary disk; anthers tetrasporangiate or (*Rhizophora*) multisporangiate, dehiscent by a longitudinal valve; gynoecium syncarpous, ovary superior to inferior, (2)3–5(−20)-carpellate, the locules often incompletely or not at all separated by septae at anthesis; ovules 2–6 per carpel, epitropous, anatropous or less often hemianatropous or campylotropous, bitegmic and crassinucellate or rarely tenuinucellate, usually apically inserted; style simple, stigma capitate or with pronounced lobes, generally papillate. Fruit capsular, baccate, or hard-walled and indehiscent. Seeds 1–many, nonappendaged, arillate, or winged; seed coat exotestal or exotestal-exotegmic or undifferentiated; endosperm well-developed, oily; embryo green, usually straight, with laminar cotyledons and epigeal germination, or with thick cotyledons or thick cotyledonary body and viviparous germination. $n = (13), 14, 16, 18, 21$.

Fourteen genera and about 145 spp. with a pantropical distribution, dominant in tidal swamps or growing in non-inundable forests.

VEGETATIVE STRUCTURES. Aerial stilt roots are well known from the mangrove genera but are found also in inland genera (*Gynotroches*, *Crossostylis* and *Carallia*). These roots are initiated from aerial parts of the plants and in *Rhizophora* develop as a series of sympodial loops, whereas in *Ceriopos tagal* and species of *Bruguiera* as well as in the inland genera they are formed on the hypocotyl and base of the trunk. In *Bruguiera* and *Ceriops* there are also knee-like pneumatophores that develop by looping of horizontal roots. In the mangrove genera, trunk axes are monopodial but may branch continuously or diffusely, and the branches may repeat the structure of the parent axis (Attim's model). Little is known in this respect about the inland genera, but *Carallia* and *Gynotroches* may also correspond with Attim's model.

Leaves are opposite and have interpetiolar stipules, which bear colleters that secrete gummy substances onto the buds. However, strictly decussate phyllotaxis (with right angles between successive leaf whorls) is restricted to tribe Macarisieae and *Pellacalyx*, whereas in Gynotrocheae (except *Pellacalyx*) and Rhizophoreae successive leaf pairs are offset by angles of 70–80° (bijugate phyllotaxis; Tomlinson and Wheat 1979). This arrangement reduces shading and provides more flexibility of orientation in the branch systems as compared to the decussate arrangement. The stipules of the genera with bijugate leaves are imbricate, whereas those of genera with decussate leaves are valvate. Juvenile and usually also adult leaves are variously toothed or crenate in most inland Rhizophoraceae, but consistently entire in the mangrove genera. The latter

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_23,

have also a succulent hypodermal layer and often abundant sclereids. Leaf texture varies with habitat, those of tribe Rhizophoreae being leathery to somewhat fleshy, glabrous and with well-developed hypodermis (Keating and Randrianasolo 1988). Laticiferous cells occur in more or less continuous subepidermal layers in sepals and ovaries; in *Gynotroches* and *Pellacalyx*, the laticifers appear modified into idioblastic secretory cells. Root hairs are absent from the family, with the exception of seedlings of *Cassipourea*. The nodes are trilacunar or multilacunar with split-lateral traces.

Wood anatomically, both the Macarisieae and Rhizophoreae are quite homogeneous, whereas Gynotrocheae appear less uniform (van Vliet 1976). Rhizophoreae stand out in having exclusively scalariform vessel perforations and scalariform inter-vessel pits, while otherwise vessel perforations are mixed scalariform/simple, and scalariform inter-vessel pits are nearly always absent; libriform fibres are restricted to Rhizophoreae, and fibre tracheids are constantly present in Macarisieae and Gynotrocheae. Rays are heterogeneous with scanty uniseriates.

The narrow, relatively short vessel elements and their scalariform perforations of the Rhizophoreae are an unexpected trait and may be related to the high negative pressures induced by the saline environment of the mangrove (Tomlinson 1986).

Sieve element plastids of Rhizophoraceae contain numerous rectangular or irregular protein crystals, which represents the P5c-type of Behnke (1988) otherwise known only in Erythroxylaceae.

INFLORESCENCE AND FLORAL STRUCTURE. Inflorescences are basically cymose, in other words, branching is consistently from prophylls, and pairs of prophylls also subtend each flower. Branching is mostly dichasial, usually with suppression of the terminal flower ("pseudodichotomous" branching), and the cymes are pedunculate or more or less sessile. Open-branched and condensed fasciculate inflorescences occur in all three tribes.

Flowers are mostly bisexual, but *Gynotroches* and some *Sterigmapetalum* are functionally dioecious (Juncosa and Tomlinson 1988b), and some *Crossostylis* and *Blepharistemma* are reported to be polygamodioecious.

Petals are basically bifid, provided with a prominent terminal arista, and each encloses one or several stamens in a very unusual kind of petal vernation. Many filamentous appendages appear on the distal lobes of the petals, which abort early in development in *Crossostylis* and *Anopyxis* and are never initiated in *Rhizophora*. Petals of *Bruguiera* and *Ceriops* are postgenitally connected not only with their neighbours but also among themselves, and the release of this bond is instrumental in the explosive pollen dispersal of these flowers.

The diplostemonous condition with the initiation of antesepalous stamens before the antepetalous ones occurs in genera of each tribe and is considered as ancestral (Juncosa and Tomlinson 1988b). Modifications thereof have arisen in all tribes; for instance, in *Carallia* and *Pellacalyx*, the antepetalous stamens are initiated first. (See the comments for the occurrence of obdiplostemony and diplostemony within the same family in Matthews and Endress 2011: 389.) There are also different pathways to polyandry in the family, with antepetalous position of the supernumerary stamens in *Kandelia* and *Cassipourea*, and antesepalous in *Crossostylis*. The nectarial disk develops after and independently from the androecium.

The ovaries are typically 3–5-carpellate with 2 ovules per carpel, but both the number of carpels (*Crossostylis*, up to 20) or the number of ovules per carpel (*Gynotroches*, up to 8) or both the number of carpels and of ovules (*Pellacalyx*) is increased. The single style has a stigma that sometimes bears rather long stigmatic lobes. Most Macarisieae have superior ovaries, but two genera of this tribe and most genera of the other tribes have half-inferior or inferior ovaries.

EMBRYOLOGY. Relevant traits can be summarized as follows: Anthers tetrasporangiate, tapetum glandular, its cells binucleate, cytokinesis simultaneous or successive (in *Gynotroches*, *Pellacalyx* and *Crossostylis*, simultaneous and successive even in the same anther); pollen tetrads tetrahedral or decussate; pollen binucleate; ovules epitropus, bitegmic, crassinucellate or (*Gynotroches* and *Pellacalyx*) tenuinucellate; integuments two cell layers thick at inception or

(*Carallia* and Rhizophoreae) multiseriate; endothelium absent in Rhizophoreae; ovule archesporium multicelled in Macarisieae, 1-celled in Gynotrocheae and Rhizophoreae; embryo sac Polygonum type; endosperm initially free-nuclear; mature seeds with abundant non-starchy endosperm; embryo chlorophyllous (Juncosa and Tobe 1988b; Tobe and Raven 1987, 1988).

These data support the sister position of *Gynotroches* and *Pellacalyx* and add evidence in favour of the placement of *Crossostylis* in the Gynotrocheae (for more details, see Juncosa and Tobe 1988). The presence of an endothelium in Macarisieae and Gynotrocheae is unusual for a moderately crassinucellar and bitegmic lineage because an endothelium is usually associated with unitegmic tenuinucellate ovules. However, Matthews and Endress (2011: 401) comment that the nucellus in the Rhizophoraceae is long and slender and almost completely disintegrates at the flanks by the expansion of the embryo sac, so that in the absence of an endothelium the embryo sac locally would come into direct contact with the inner integument.

POLLEN MORPHOLOGY (see Vezey et al. 1988). Pollen in Rhizophoraceae is usually spheroidal, (2)3(4)-colporate and has a punctate-psilate or rugulate tectum; in Macarisieae and less so in Gynotrocheae the intercolumellar space contains granular matrix. There are clearly defined endoapertures, which particularly in tribe Gynotrocheae are fused laterally. Palynologically tribe Macariseae appears intermediate between Gynotrocheae and Rhizophoreae. Overall, pollen morphology of the family is so generalized that it hardly offers clues for assessing relationships with other families.

FRUIT AND SEED. Fruit and seed structure in the family varies greatly and includes (1) dehiscent capsular fruits with arillate or winged seeds, (2) baccate fruits that contain nonappendaged seeds, and (3) indehiscent hard-walled fruits that contain viviparous seeds (Tobe and Raven 1988). The seeds of all Rhizophoreae contain ample endosperm, which in the mangrove genera (except *Bruguiera*) is formed so abundantly that it extrudes from the micropyle and fills up the space between the fruit wall and the seed.

The genera with a superior ovary (Tribe Macarisieae and *Crossostylis*) have arillate or winged seeds, whereas the baccate Gynotrocheae genera lack any sort of seed appendage. Both the aril and the wing develop as an outgrowth of the exostome and are regarded as homologous (Tobe and Raven 1987). All inland groups (Macarisieae and Gynotrocheae) basically have a similar mature seed coat structure, including a well-developed exotesta and mostly also a fibrous exotegmen; their seed coat is either exotestal or exotestal-exotegmic. It is significant that the seed coat of arillate seeds is thicker than that of winged seeds (c. 0.2 mm vs. less than 0.1 mm thick). The thinner seed coat of the latter may be adaptive in facilitating their wind dispersal.

The seeds of the Rhizophoreae are included in indehiscent, hard-walled fruits and their seed coat comprises only a thick testa that is histologically undifferentiated but contains profusely branched vascular strands. Although the inner integument is present at ovular stage, the mature seeds completely lack a tegmen.

POLLINATION AND DISPERSAL. Little is known about the floral biology of terrestrial taxa, even though there is a range from plants with perfect flowers to polygamous or dioecious plants. Flowers are generally small and individually inconspicuous (but up to 6 cm diameter in *Crossostylis grandiflora*), although their frequent aggregation and appendaged petals increase their visibility. They may be associated with generalist flower visitors (small insects). Members of the mangrove tribe Rhizophoreae, on the other hand, have been well studied and show a considerable range of floral mechanisms (Tomlinson et al. 1979). *Rhizophora* is presumed to be wind-pollinated; it has a high pollen-ovule ratio and pollen is discharged within the bud and presented by expansion of the usually hairy, but ephemeral petals. The style, however, is unelaborated for the reception of pollen. In *Bruguiera* and *Ceriops tagal* there is an explosive discharge of pollen, triggered by the flower visitor of appropriate behaviour and size in relation to that of the flower. In this process, birds act as visitors of the large-flowered Bruguieras, whereas day-flying insects such as butterflies visit the smaller-flowered Bruguieras, and small night-flying moths search the nocturnally scented *Ceriops* *tagal*. *Kandelia* seems generalized in its floral biology (Tomlinson 1986; Kondo et al. 1987).

Direct observations on seed dispersal of the terrestrial taxa are not known to us, but it is obvious that the arillate genera will be dispersed by animals (Tobe and Raven 1988 think of ants and possibly birds) and the winged ones by wind. The distribution of *Crossostylis*, which is scattered in Polynesian islands, has very likely been dispersed by birds from one island to the other. The small, hard seeds of the capsular Gynotrocheae (*Carallia*, *Gynotroches* and *Pellacalyx*) appear endozoochorously dispersed by flying vertebrates.

The most distinctive characteristic of the mangrove Rhizophoraceae is the viviparous seedling in which the embryo lacks a dormant phase (Sussex 1975) and develops on the parent plant, the hypocotyl protruding from the fruit (Fig. 68H, I). The propagule is thus a seedling, not a seed. In *Bruguiera*, the seedling disperses initially with the fruit (Tomlinson 1986), whereas in *Kandelia*, *Ceriops* and *Rhizophora* only the seedling disperses.

Most of the elongated viviparous seedlings of the mangrove Rhizophoraceae are not “self-planting” by falling vertically into the soft mud below the parent tree but are carried away from it. For their survival they need habitats where the tidal range is small and where they can raise the plumule above the tidal influence so that gas exchange becomes possible for the seedling, which is hindered by the thick, cutinized and stomata-free epidermis of the hypocotyl. Erection of the horizontally stranded seedling with the exposition of the plumule into the air is achieved by an eccentric secondary growth of the xylem in the distal pole of the seedling, which produces a distinct hook at its distal end (Tomlinson and Cox 2000).

KARYOLOGY. Chromosomes of Rhizophoraceae are very small, usually about 1 μm long. *Crossostylis* has $n = 14$; *Anopyxis* $n = 32$; for *Cassipourea*, $n = 18$ and $n = 21$ have been reported, and the Rhizophoreae genera uniformly have $n = 18$ (see listing in Juncosa and Tomlinson 1988).

AFFINITIES AND SUBDIVISION. Although sometimes referred to as the "mangrove family", this appellation is misleading since the majority of taxa are terrestrial, a point established by Brown (1814) in his circumscription of the family since he included both mangal (*Rhizophora*) and terrestrial taxa (*Carallia*). Consequently, the monophyly of this group has been accepted independently of the sharp ecological contrasts within it. The place of the family in the natural system has been extensively debated but molecular studies have clarified its relationships (Schwarzbach and Ricklefs 2000): Rhizophoraceae are the sister family to the Erythroxylaceae, and both are sister to the Ctenolophonaceae, all in the order Malpighiales (Wurdack and Davis 2009; Soltis et al. 2011; Xi et al. 2012). Anisophylleaceae that have been considered close relatives of or even been included in Rhizophoraceae (according to molecular analyses; Schwarzbach and Ricklefs 2000; Zhang et al. 2007) are placed in the Cucurbitales.

Traditionally the family has been divided into three tribes that, with slight modifications, persist to the present day. The molecular analyses (Setoguchi et al. 1996; Schwarzbach and Ricklefs 2000) support the monophyly of the recircumscribed tribes and show Gynotrocheae in a sister position with Rhizophoreae and both sister to Macarisieae.

By and large, the tribes can be characterised by fruit characters (capsular fruits, berries, and indehiscent fruits with viviparous seeds, see above under FRUIT AND SEED); their flowers are usually (ob)diplostemonous, and ovaries are mostly superior in Macarisieae and inferior in the other two tribes. In view of its arillate seeds, *Crossostylis* has often been considered as belonging in Macarisieae but the molecular data resolve it firmly in the Gynotrocheae clade. Indeed, apart from its arillate seeds (perhaps a convergent development?), *Crossostylis* shares many characters with Gynotrocheae, such as the (semi)inferior gynoecium developing into a capsule that opens with only short slits (see Schwarzbach and Ricklefs 2000: 557, and above under EMBRYOLOGY).

PHYTOCHEMISTRY AND USES (see Hegnauer 1973). The bark of all mangrove species is rich in tannin, which can amount up to 45 % of the dry weight. The tannins are mainly of the condensed type, based mainly on procyanidin, but prodelphinidin is also present; there are also some records of myricetin and ellagic acid from bark and leaf extracts. The bark of *Bruguiera*, *Ceriops* and *Rhizophora* contains also large amounts of mucilage (11–35 %), which is based on arabinose, rhamnose and galactose. Alkaloids have been found in some species from all tribes; they belong to the tropin, hygrolin and necin type, and sometimes contain sulphur.

The main use of the family is mangrove timber and bark, the former for fire wood and charcoal, and the latter for tanning (formerly important) and dyeing (batik), but now seems to have been superseded by synthetic products or persists rather on a regional/local scale.

PALAEOBOTANY. Macrofossils are known only from the mangrove genera, representing *Ceriops* and a *Bruguiera*-like form from the early Eocene in the London Clay (Collinson 1983), followed by *Kandelia* from the middle Eocene of Alaska (Wolfe 1972). Pollen ascribed to *Rhizophora* from strata older than middle Eocene that have frequently been reported was rejected by Graham (2006) but relatively unambiguous palynological records show the genus widespread in coastal habitats of the Old and New World tropics from the late Eocene onwards. For the history of *Rhizophora* in the New World mangrove, see Graham (2006).

DISTRIBUTION AND HABITATS. The family as a whole is virtually limited to the tropics and the tribes themselves all have a considerable range, but each with one relatively large and widely distributed genus (indicated in parenthesis). Macarisieae (*Cassipourea*, 55 spp.) extend from South America to India, but not to SE Asia; Gynotrocheae (*Carallia*, 10 spp.) are Old World and range from Madagascar to the South Pacific (*Crossostylis*); Rhizophoreae (*Rhizophora*, 8 spp.) are pantropical but concentrated in the Indo-Pacific region. The most widely distributed species is probably *Bruguiera gymnorrhiza*, a common component of the tidal environment (mangal) from East Africa to Samoa.

Rhizophoreae, which may collectively be referred to as "the mangrove Rhizophoraceae", are restricted to coastal communities on muddy substrate away from strong wave action and tidal currents. *Rhizophora* species constitute the typical element of this distinctive tropical vegetation type, but where other genera co-occur there is often a distinct zonation, with *Ceriops* the most landward and salt-tolerant, *Bruguiera* and *Kandelia* less so and *Rhizophora* the least. *Rhizophora* commonly dominates the seaward fringe of the mangal, sometimes associated with *Avicennia* (Avicenniaceae) and *Sonneratia* (Sonneratiaceae). In some areas *Rhizophora* forms extensive forests with trees up to 30 m tall; since there is little understorey and the trees are supported by massive stilt roots, such forests have a distinctive physiognomy. The ecological status of the Rhizophoreae suggests that they combine features of pioneer and mature phases in vegetation development because of the species poverty of the mangal, i.e. they have adapted to establish communities as pioneers and maintain them as mature-phase species (Tomlinson 1986). Typically, such plants are shade intolerant, not establishing under their own canopy, and *Rhizophora* regenerates most conspicuously in open areas like forest gaps and along shifting coastlines. Although it has the reputation of being a landbuilder, it is probably not efficient in the consolidation of highly mobile substrates shifted by water action and tidal scour.

The terrestrial taxa of the family are much less well studied ecologically but are typical of lowland rain forest. Consequently, the presumed ecological origins of the Rhizophoreae within the family as a whole have been little discussed.

KEY TO THE GENERA

1. Plants of mangrove forests; seeds germinating in the fruit while this is still attached to the tree; hypocotyl protruding from the fruit 2
– Plants of inland habitats; seeds not germinating in the fruit when this is still attached to the tree; hypocotyl not protruding 5
2. Calyx always 4-lobed; petals entire, without appendages; anthers multi-locellate, eventually dehiscing with a large ventral valve **14. *Rhizophora***
– Calyx 5–16-lobed; petals 2-lobed, multifid or with apical appendages; anthers 4-locular, dehiscing with lengthwise slits 3
3. Flowers polymerous, diplostemonous; calyx 8–16-lobed, lobes subulate-lanceolate, pointed; petals bilobed or emarginate **11. *Bruguiera***

– Flowers 4–5-merous, diplostemonous or polyandrous; calyx lobes ovate or linear-oblong, acuminate or obtuse; petals fringed with apical appendages or multifid 4

4. Flowers 5-merous, diplostemonous; calyx lobes ovate, 2.5–3.5 mm long; petals less than 0.5 cm long; hypocotyl ridged **13. *Ceriops***

– Flowers 4–5-merous, polyandrous; calyx lobes linear-oblong, about 15 mm long; petals c. 1.5 cm long; hypocotyl smooth **12. *Kandelia***

5. Fruit baccate; seeds nonappendaged 6

– Fruit capsular; seeds appendaged (arillate or winged) 8

6. Leaves with indumentum of stellate and simple hairs; free part of the calyx forming a distinct tube divided into the calyx lobes only at the upper part, lower part of tube hairy within; disk 0; stamens attached to mouth of the calyx tube; stipules flat, not imbricate **10. *Pellacalyx***

– Indumentum not stellate; free part of calyx divided to the base, inside glabrous in lower part; disk annular or cupular-shaped, surrounding the base of the style; stamens attached to disk; stipules imbricate and overlapping 7

7. Young branches solid; leaves black dotted beneath; stipules accompanied by stalked extrastipular glands; flowers usually in peduncled (rarely in sessile) cymes, 5–8-merous; petals erose or fimbriate; calyx lobes persistent and terminating the fruit **7. *Carallia***

– Young branches hollow; leaves not black dotted; extrastipular glands 0; flowers in fascicles, 4–5-merous; petals fringed with filamentous appendages; calyx lobes persistent at the base of the fruit **9. *Gynotroches***

8. Seeds arillate, the aril not exceeding the seed 9

– Seeds winged, the wing usually exceeding the wing 12

9. Ovary inferior or semi-inferior, 3–28-locular; stamens 2, 3 or more times the number of petals **8. *Crossostylis***

– Ovary superior or semi-inferior, 2–5-locular 10

10. Hermaphrodite; flowers 4-merous, diplostemonous; ovary 2-locular **3. *Comiphyton***

– (Polygamo-)dioecious; flowers 4–6-merous, stamens 2 or more times the number of petals 11

11. Flowers 4-merous, diplostemonous; ovary 3-locular **1. *Blepharistemma***

– Flowers 4–6-merous, stamens 2, 3, or more times the number of petals; ovary 2–5-locular **2. *Cassipourea***

12. Flowers unisexual, plants dioecious **6. *Sterigmapetalum***

– Flowers perfect, plants hermaphrodite 13

13. Leaves mostly in whorls of three, stamen filaments connate into a tube **4. *Anopyxis***

– Leaves in pairs, stamen filaments distinct **5. *Macarisia***

TRIBES AND GENERA OF RHIZOPHORACEAE

I. TRIBE MACARISIEAE Baill. (1876).

Shrubs or trees of moist or dry forest; stilt roots 0 or poorly developed. Leaves toothed, verticillate or opposite; stipules valvate, pubescent. Inflorescences lax-cymose or fasciculate. Flowers bisexual except in *Sterigmapetalum* and *Blepharistemma* (?), diplostemonous (polyandrous in *Cassipourea*); ovary usually superior, 2–6-locular. Fruit a capsule, sometimes indehiscent. Seeds arillate or winged.

A group of six genera, centred in Africa, extending to Madagascar, Sri Lanka and India and to South and Central America. Detailed information lacking for several genera.

1. *Blepharistemma* Wall. ex Benth.

Blepharistemma Wall. ex Benth., J. Proc. Linn. Soc., Bot. 3: 73, 78 (1858); Gamble, Fl. Madras 1: 460 (1997, re-edn); Sasidharan, Biodivers. documentation for Kerala, Flowering Plts 6: 169 (2004); Saldanha, Fl. Karnatka 2: 57 (1996).

Polygamo-dioecious shrubs or small trees. Leaves opposite, apically crenate; stipules caducous. Inflorescences axillary, condensed cymes; prophylls 0 (?). Flowers small, white, 4-merous, diplostemonous, somewhat dimorphic; petals fringed apically, shorter in pistillate flowers; disk 8-lobed; ovary 3-locular, superior, with 2 ovules in each locule; the stigma somewhat 3-lobed. Fruit subglobose, fleshy, variously described as indehiscent or not. Seeds with aril attached to upper half of seed.

A single sp., *B. serratum* (Dennst.) Suresh, SW India (Western Ghats, North Malabar and South Kanara), in the understorey of wet evergreen forest up to 700 m.

2. *Cassipourea* Aubl. Fig. 67

Cassipourea Aubl., Pl. Guian.: 528, t. 211 (1775); Alston, Kew Bull. 1925: 241–276 (1925), rev.; Floret, Bull. Mus. Natl. Hist. Nat. B, Adansonia 10: 25–45 (1985); Breteler, Edinb. J. Bot. 65: 407–424 (2008), synopsis of and key to subgenera.

Weihea Spreng. (1825).

Dactylopetalum Benth. (1858).

Petalodactylis Arènes (1954).

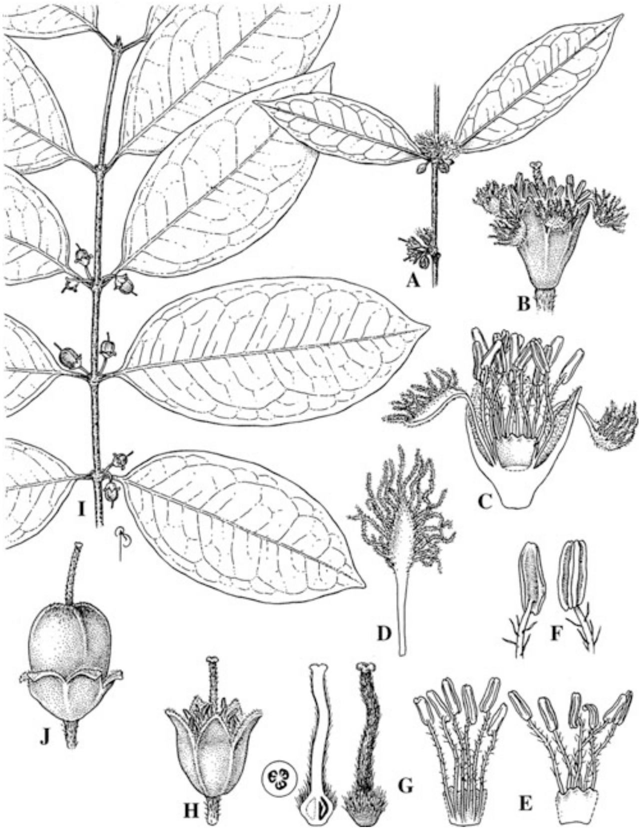

Fig. 67. Rhizophoraceae. *Cassipourea guianensis*. **A** Flowering branchlet. **B** Flower. **C** Same, transversal section with pistil removed. **D** Petal, adaxial view. **E** Part of androecium and disk in adaxial and abaxial view. **F** Abaxial and adaxial views of anthers. **G** Pistil with vertical section and transverse section of ovary. **H** Flower past anthesis, the petals have fallen. **I** Part of axis with immature fruits. **J** Immature fruit. (Reproduced with kind permission of the artist Bobbi Angell)

Shrubs or trees, dioecious or hermaphrodite. Leaves decussate or rarely whorled, entire to serrate in apical half; stipules caducous. Inflorescences axillary condensed cymes, or flowers solitary. Flowers subsessile, (4)5(6)-merous; calyx lobes valvate; petals white, inflexed in bud, linear or spathulate, caducous, with laciniate-fimbriate margins; stamens 2, 3 or more times the number of petals, inserted outside or on the annular disk; ovary superior to half-inferior, the base sometimes somewhat fused with the calyx tube, often hairy, 2–5-celled; ovules 2 per locule, pendulous and apically inserted; style filiform or stout, the stigmas enlarged and obscurely lobed. Fruit a somewhat fleshy capsule, with septifragal dehiscence. Seeds 2–6, compressed or angular, nearly completely covered by an aril.

About 64 spp., ranging from tropical America through tropical Africa to Madagascar, Sri Lanka and S India; most spp. concentrated in West Africa. Many occur in humid lowland forest, but some grow in drier habitats and there is also a considerably altitudinal range (to 2,500 m on Mt. Ruwenzori).

For the division into seven subgenera, see Floret (1985) and Breteler (2008). The justification of the inclusion of *Dactylopetalum* in *Cassipourea* by Alston (1925) has been doubted by Floret (1976) and the genera are held distinct by Juncosa and Tomlinson (1988a, b), but the morphological separation is not clear cut and molecular data are contradictory (Setoguchi et al. 1996 vs. Schwarzbach and Ricklefs 2000); see the discussion in Breteler (2008).

3. *Comiphyton* Floret

Comiphyton Floret, Adansonia II, 14: 501 (1974), ibid. 16: 39–49 (1976).

Shrubs to tall trees. Leaves opposite, decussate, distally denticulate; stipules interpetiolar. Inflorescences axillary shortly pedunculate contracted cymes. Flowers perfect, small, 4-merous, diplostemonous; calyx campanulate, with 4 short triangular teeth, other floral parts shortly exserted; petals distinct, linear, expanded apically into 5–6 pointed lobes; stamens inserted on a lobed disk, inner (antepetalous) stamens longer than the outer; anthers bilocular; ovary superior, 2-locular, each locule with 2 pendulous ovules inserted near the apex of the septum; style long, exserted, with a bilobed capitate stigma. Fruit probably dehiscent, 1(2)-seeded. Seeds arillate, the aril 2–3-lobed, attached to top of seed.

A single sp., *C. gabonense* J.-J. Floret, Equatorial Africa (Gabon and Zaire), mainly of the forest understorey. Apparently not sharply differentiated from *Dactylopetalum*.

4. ***Anopyxis*** (Pierre) Engl.

Anopyxis (Pierre) Engl. in E.-P., Nat. Pflanzenfam., Nachtr. II–IV, 2: 48 (1900).
Macarisia sect. *Anopyxis* Pierre (1898).

Vast trees to 50 m or more. Leaves ternate or verticillate, entire, glabrous but young leaves sometimes covered with long hairs; stipules small, linear. Inflorescences axillary or terminal contracted cymes on long peduncle. Flowers perfect, 5-merous, obdiplostemonous; calyx campanulate with 5 bluntly pointed lobes; petals entire or toothed, somewhat longer than the calyx lobes; the stamen filaments connate over their entire length into a long, slightly exserted tube with the 10 small anthers at the top; disk 0; ovary superior, flask-shaped, 5-locular; each locule with 2 ovules inserted axially or apically; style slender, the stigma slightly enlarged. Fruit a 5-valved woody hairy capsule with septicidal dehiscence. Seeds up to 10, with a membranous wing on the micropylar top.

A single sp., *A. klaineana* (Pierre) Engl., West Africa from Sierra Leone to Zaire and Angola (Cabinda).

5. ***Macarisia*** Thouars

Macarisia Thouars, Hist. Vég. Isles Austr. Afr.: 49, pl. 14 (1806); Arènes, Fl. Madagascar Comores, Rhizophoraceae: 21–31 (1954); Schatz, Generic Tree Fl. Madagascar: 314 (2001).

Trees, with young parts hairy. Leaves entire or glandular dentate; stipules caducous. Inflorescences axillary, few-flowered pedunculate cymes, or flowers solitary. Flowers 5(6)-merous, diplostemonous; calyx at the base short tubular, the lobes persistent; petals slightly longer than the calyx lobes, caducous, distally with 4–13 spoon-shaped imbricate appendages; disk annular, 10-toothed; stamens inserted between the teeth of the disk; filaments distinct; ovary superior, shortly stalked, 5-locular but with incomplete septa; ovules 2 per locule; style filiform; stigma capitate to obscurely lobed. Fruit a septicidal capsule, somewhat woody. Seeds usually 10, with a membranous wing on the micropylar top.

Seven species, restricted to Madagascar, in humid and semidry vegetation from lowland to 200 m above sea level.

6. ***Sterigmapetalum*** Kuhlm.

Sterigmapetalum Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4: 359 (1925); Steyermark & Liesner, Ann. Missouri Bot. Gard. 70: 179–193 (1983), rev.

Dioecious trees to 30 m. Leaves decussate or in whorls of 3–4, entire or serrate; stipules glabrous or sericeous. Inflorescence pedunculate, congested cymes with few to many flowers. Flowers unisexual, 4–6-merous, diplostemonous; calyx campanulate, the lobes valvate; petals linear and usually with 3 lobes elaborated in various ways; disk 0; stamens in staminate flowers alternately long and short and inserted on a membranous staminal tube within the petals; ovary rudimentary; pistillate flowers with reduced staminodial tube; ovary superior, 5–6-celled, with 2 ovules per cell; style short, expanded distally into a radially symmetrical discoid stigma. Fruit a septicidal 5–6-celled capsule. Seeds oblong, with a membranous wing on the micropylar top.

About nine spp., northern South America from E Colombia to Suriname and Brazilian Amazonia. Two subgenera, distinguished by the presence or absence of a resinous exudate on the buds and flower buds, this feature correlated with whorled versus opposite leaves (Steyermark and Liesner 1983).

II. Tribe Gynotrocheae Engl. (1892).

Shrubs and trees, some in disturbed vegetation; prominent aerial roots in all genera but *Pellacalyx*. Leaves crenate, bijugate or (*Pellacalyx*) decussate. Flowers bisexual except in *Gynotroches*, diplostemonous; ovary inferior (superior in *Gynotroches*), 5- or many-carpellate; ovules 2 or many per carpel (locules incompletely separated). Fruit ± baccate, 1–many-seeded, unappendaged (arillate in *Crossostylis*).

Four genera, centred in Malesia, but extending to Madagascar, India, northern Australia, and Fiji.

7. ***Carallia*** Roxb.

Carallia Roxb., Pl. Corom. 3: 8, t. 211 (1811), nom cons.; Ding Hou, Fl. Males. II, 5: 481–488 (1958).

Shrubs or trees to 50 m, sometimes with small buttresses or stilt-roots. Leaves bijugate, black-dotted beneath, entire to dentate or serrate; stipules large, lanceolate, caducous, accompanied by large stalked glands. Inflorescences resinous, sessile or peduncled, lax-cymose or condensed, di- or trichotomously branched, or sometimes reduced to 2 or 1 flowers; prophylls distinct and caducous or connate and persistent. Flowers sessile or pedicelled, small, perfect, 5–8-merous, obdiplostemonous; calyx deeply divided into deltoid lobes; petals caducous or persistent, narrowed below but the margins and apex of the expanded distal portion lobed or fimbriate; stamens distinct or shortly connate into a tube, persistent; disk within the stamens, annular, sometimes lobulate, fleshy; ovary inferior, either 5–8-celled and each cell 2-ovulate, or 1-celled with 10–12 ovules; style filiform or slightly conical, stigma discoid, capitate, or obscurely lobed. Fruit a globose to obovoid berry, 1-celled, 1(−5)-seeded. Seeds ellipsoid or reniform.

Eleven spp., Madagascar, India, Nepal, Indochina, S China, Malesia, Solomon Islands, and N Australia, in (sub)humid forest up into the mountains to c. 1,800 m. *Carallia brachiata* (Lour.) Merr. has the widest range of the genus from Madagascar to the Solomons; its timber is commercially valuable.

8. ***Crossostylis*** J.R. & G. Forst.

Crossostylis J.R. & G. Forst., Char. Gen. Pl.: 44 (1775); Setoguchi et al., J. Plant Res. 109: 7–19 (1996), floral morph.

Trees up to 20 m or shrubs, sometimes polygamodioecious. Leaves bijugate, glabrous, entire or serrulate. Inflorescences axillary condensed cymes with usually few (2–12) flowers. Flowers perfect or sometimes pistillate, sometimes large (to 6 cm diam.), 4–6-merous, diplostemonous to polyandrous; petals apiculate, entire or slightly lobed or few-toothed; stamens 8–28, apparently arranged in one whorl; disk lobed, the lobes opposite to or alternate with the stamens (formerly interpreted as staminodia); ovary half-inferior or inferior, 3- to 28-locular and incompletely septate; ovules 2 per locule; style exserted, stigma discoid or 4–many-lobed with linear to filiform stigmatose lobes. Fruit a conical capsule, enclosed by the calyx, dehiscence tardy with distal slits or an operculum. Seeds numerous, arillate, the aril attached to the micropylar top of the seed.

About 12 spp., six of them in the Solomon Islands, Vanuatu and Fiji, and the others in New Caledonia and Polynesia. With emphasis on seed morphology, Tobe and Raven (1988) suggest the erection of a monotypic tribe to accommodate this genus.

9. ***Gynotroches*** Blume

Gynotroches Blume, Bijdr.: 218 (1825); Ding Hou, Fl. Males. II, 5: 488–489 (1958).

Dioecious shrubs or trees up to 40 m; young branches hollow. Leaves bijugate, entire to denticulate; stipules lanceolate. Inflorescences fasciculate or flowers solitary. Flowers unisexual by abortion, 4–5-merous, diplostemonous; calyx deeply lobed; petals unguiculate, with distal filamentous appendages; stamens distinct, inserted at the margin of the calyx cup and outside the shallowly lobed disk, sterile in pistillate flowers; ovary superior (pistillate flowers), 4–6-celled, each cell with 3–8 ovules, or half-inferior, with sterile ovules (staminate flowers); style simple, very short in staminate flowers, stigma discoid or 4–6-lobed; staminate flowers with a reduced gynoecium. Fruit a globose to oblong berry. Seeds few to many.

One sp., *G. axillaris* Blume (or perhaps several ones: Ding Hou 1958; Juncosa and Tobe 1988), in non-seasonal parts of southeast Asia from Myanmar through Malesia to northern Australia, the Solomon Islands and into Micronesia, in forests and along rivers, occasionally in secondary forests, up to c. 2,000 m.

10. *Pellacalyx* Korth.

Pellacalyx Korth., Tijd. Nat. Gesch. Phys. 3: 20 (1836); Ding Hou, Fl. Males. I, 5: 490–493 (1958).

Trees up to 45 m; young branches hollow. Leaves decussate, entire, serrulate or serrate, pubescent with stellate or simple hairs, or glabrous; stipules flat, valvate. Inflorescences axillary, few-flowered, scarcely pedunculate glomerules, or flowers occasionally solitary; pairs of prophylls fused into a toothed cup. Flowers perfect, 4–5-merous, obdiplostemonous, small; calyx deeply tubular, hairy inside, apically with deltoid lobes; petals distinct, inserted on the margin of the calyx tube, denticulate or fringed; stamens attached to mouth of calyx tube with very short filaments in two series or one; ovary inferior, with 9–10(−12) locules, each locule with 8–25 ovules in a cluster on the axile placenta; style columnar, not or scarcely exserted, with a capitate, slightly lobed stigma. Fruit a few- to many-seeded berry. Seeds small.

About 7 spp., distributed from Myanmar to S China and Malesia. The genus seems to fall naturally into one group of species with predominantly tetramerous and small flowers (e.g. *P. lobbii* (Hook. f.) Schimp.) and another with predominantly pentamerous and larger flowers (e.g. *P. axillaris* Korth.).

III. Tribe Rhizophoreae Bartl. (1830).

Mangrove shrubs or trees. Aerial stilt roots always present but prominent only in *Rhizophora*. Leaves bijugate, entire. Inflorescences cymose. Flowers 4–16-merous, mostly diplostemonous; petals usually enclosing one to several stamens; ovary half to fully inferior, 2–3-carpellate; ovules 2 per carpel. Fruit baccate, fibrous, 1-seeded; germination viviparous, the huge seedling axis (up to 1 m) emerging from both the seed coat and the fruit up to 9 months before abscission.

Four genera, the tribe pantropical.

11. *Bruguiera* Savigny Fig. 68

Bruguiera Savigny, Encycl. (Lamarck) 4: 696 (1798); Ding Hou, Nova Guinea II, 8: 163–171 (1957), Fl. Males. II, 5: 457–468 (1958); Duke & Ge, Blumea 56: 36–48 (2011), hybridization.

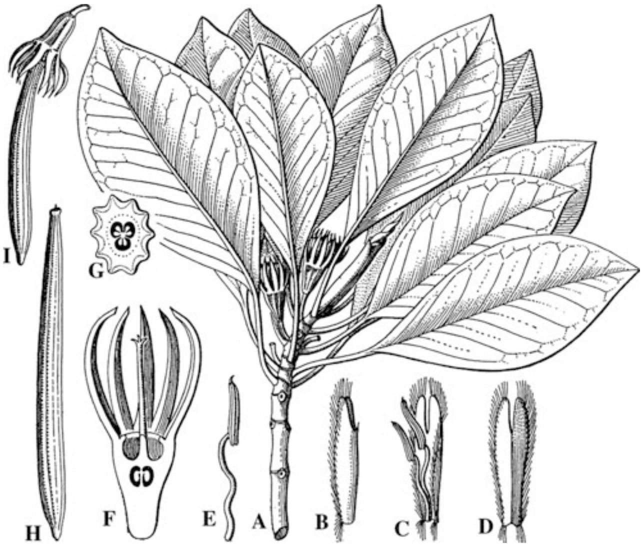

Fig. 68. Rhizophoraceae. *Bruguiera exaristata*. **A** Flowering branchlet. **B–D** Petals, lateral, ventral (with 2 stamens), and dorsal. **E** Stamen. **F** Flower, vertical section, petals and stamens removed. **G** Ovary, transversal section. **H, I** Hypocotyls. (Ding Hou 1958; drawn by Ruth van Crevel)

Trees with trunks with sturdy basal buttresses and with knobby pneumatophores produced from horizontal roots, and sometimes with aerial roots when young. Leaves bijugate, entire; stipules lanceolate, glabous, to 4 cm long. Inflorescences cymose with numerous small flowers or reduced to 1–3 large flowers, then often without prophylls. Flowers bisexual, 4–16-merous, diplostemonous; petals 2-lobed, often with reduced distal appendages, each embracing a pair of stamens that are released explosively when stimulated by a probing pollinator, the petals being held together by marginal interlocking hairs that unzip instantly to allow pollen discharge; disk cup-shaped, adnate to calyx tube; ovary deeply inferior, adnate to lower part of calyx tube, 2–4-celled, each cell with 2 ovules; style filiform; stigma obscurely 2–4-lobed. Fruit usually 1-celled. Seeds 1(2); hypocotyl terete or obscurely ribbed, perforating the apex of the fruit and falling with it.

Six spp., from south-east Africa through Malesia to northern Australia and the Pacific Islands (Samoa). The genus has been divided into "large-flowered" (e.g. *B. gymnorrhiza*) and "small-flowered" (e.g. *B. cylindrical*) species, obviously in relation to the size of the pollinators (birds vs. insects).

12. ***Kandelia*** (DC.) Wight & Arn.

Kandelia (DC.) Wight & Arn., Prodr. Fl. Ind. Orient.: 310 (1834); Ding Hou, Fl. Males. II, 5: 472–473 (1958).

Small trees to 7 m; buttresses and pneumatophores 0. Leaves decussate or bijugate, entire; stipules linear. Inflorescences axillary, long pedunculate, 4–9-flowered. Flowers perfect, pentamerous, polyandrous; calyx deeply lobed, subtended by a cuplike prophyllar involucre, lobes long and reflexed at anthesis; petals bilobed, with long seta in the sinus, each lobe multifid; stamens numerous (30–40) and inserted on the rim of the calyx cup, the filaments uneven in length and with minute anthers; ovary inferior below a well-developed nectar cup with a pronounced intrastaminal rim; ovary half-inferior, 1-celled; ovules 6, attached apically to a pronounced basal extension of the ovary wall; style filiform, the stigma minutely 3-lobed. Fruit pedunculate with persistent reflexed sepals. Seed 1, viviparous; hypocotyl up to 40 cm long.

Two spp., one distributed from Bangladesh to Borneo, the other from China to S Japan (Kyushu), typically growing in back-mangrove communities and on banks of tidal rivers.

13. ***Ceriops*** Arn.

Ceriops Arn., Ann. Mag. Nat. Hist. 1: 363 (1838); Ding Hou, Fl. Males. I, 5: 468–472 (1958).

Small to moderate-sized trees with a characteristic basal cone of appressed aerial stilt roots and sometimes with knobby pneumatophores produced from horizontal roots. Leaves bijugate, entire; stipules lanceolate. Inflorescences subsessile to shortly peduncled trichasial to monochasial cymes. Flowers 5(6)-merous, diplostemonous, their prophylls partly connate; calyx deeply lobed; petals keeled, emarginate or truncate, fringe-like divided or with 3 clavate appendages, enwrapping 2 stamens or not; disk shallowly lobed, lobes antesepalous; stamens inserted in the sinuations of the disk; ovary half-inferior, 3-celled, each cell with 2 ovules; style simple; stigma simple or obscurely 2–3-lobed. Fruits conical, mainly by extension of the upper part of ovary. Seed solitary, viviparous, hypocotyl up to 20 cm long, terete or ridged, released from the cotyledon at dispersal.

Two spp., both wide-ranging from E Africa to Queensland, Melanesia and Micronesia north to Hong Kong; they are strongly salt-tolerant and grow preferentially in the back-mangal, often at the margins of saltpans in the higher tidal reaches. The species differ in the non-explosive and explosive methods of pollen discharge, the latter presumably evolved independently from that in *Bruguiera*.

14. ***Rhizophora*** L.

Rhizophora L., Sp. Pl.: 443 (1753), Gen. Pl. ed. 5: 202 (1754); Salvoza, F.M., Nat. Appl. Sci. Bull. Un. Philipp. 5: 179–237 (1936); Ding Hou, Fl. Males. II, 5: 448–457 (1958), Blumea 10: 625–634 (1960).

Trees; stems supported by numerous branched stilt roots; most vegetative parts contain trichosclereids. Leaves bijugate, with numerous microscopic black cork-warts below; stipules lanceolate. Inflorescences peduncled and di- or trichotomously branched cymes. Flowers 4-merous, stamens 2(3) times the number of petals; calyx deeply lobed, subtended by cup-shaped prophylls; petals inserted at base of disk, entire, ephemerous, the edges barely enclosing the single antepetalous stamen; stamens (sub)sessile, multilocellate, dehiscing introrsely; ovary half-inferior, 2-celled; ovules 2 per cell; style obscure or distinct; stigma 2-lobed. Fruit ovoid. Seeds 1(2, 3), viviparous; hypocotyl maturing on tree to 15–30 (70) cm; cotyledons fused to form an emergent collar from which the seedling abscises at maturity. Wind-pollinated.

About 8 spp. of which at least two appear to be hybrids. The genus as a whole is pantropical but there is an almost complete geographic separation between Old World and New World species (Tomlinson 1986), with the exception of the western Pacific (Fiji and New Caledonia).

Doubtfully attached:

14a. ***Paradrypetes*** Kuhlm.

Paradrypetes Kuhlm., Arq. Inst. Biol. Veg. Rio Jan. 2: 84 (1935); Levin, Syst. Bot. 17: 74–83 (1992); Webster, Ann. Missouri Bot. Gard. 81: 56 (1994); Radcl.-Sm., Gen. Euphorb.: 87 (2001).

Dioecious trees; indumentum 0. Leaves opposite, simple, spinulose-dentate or subentire; stipules sheathing, interpetiolar, with colleters. Inflorescences cymose, ebracteate, the peduncle in both sexes adnate to subtending petiole or not. Flowers apetalous; staminate flowers pedicellate; sepals 3 or 4, distinct, imbricate; disk 0; stamens 10–12, filaments suppressed; anthers extrorse, dehiscing longitudinally; pollen grains oblate, 4-brevicolporate, exine echinate, tectum psilate-wrinkled; pistillode 0; pistillate flowers solitary or in 3-flowered dichasia; sepals 4, caducous; disk annular; ovary 3-locular, ovules anatropous; stigmas 3, dilated, sessile. Fruits drupaceous with crustaceous endocarp, 1-seeded. Seeds ecarunculate; testa reticulately veined; endosperm abundant; cotyledons chlorophyllous, plicate, much longer and broader than radicle.

Two Brazilian spp., one in central Amazonia, the other in the Atlantic coastal forests.

Hutchinson (1969) was the first to refer *Paradrypetes* to the Oldfieldioideae, and Levin's placement in tribe Podocalcyeae was supported by the palynological study of Levin and Simpson (1994). *Paradrypetes* shares with *Podocalyx* the unique synapomorphy of the absence of distinct columellae in the interstitium between endexine and ectexine. However, molecular studies by Wurdack et al. (2004) and Wurdack and Davis (2009) vindicate the placement of *Paradrypetes* in Rhizophoraceae. There is a general resemblance in habit between *Paradrypetes* and genera such as *Cassipourea*, and the opposite leaves, interpetiolar stipules with colleters and chlorophyllous embryos are rhizophoraceous rather than euphorbialean, but none of the Rhizophoraceae has echinate pollen, such strongly pronounced unisexual and apetalous flowers, thin, distinct and imbricate sepals, and sessile stigmas as *Paradrypetes* (see Levin 1992; Matthews and Endress 2011). All this calls for continued observance of this enigmatic genus.

Selected Bibliography

Alston, A.H.G. 1925. Revision of *Cassipourea*. Kew Bull. 1925: 241–276.

Behnke, H.-D. 1988. Sieve-element plastids and systematic relationships of Rhizophoraceae, Anisophylleaceae and allied groups. Ann. Missouri Bot. Gard. 75: 1387–1409.

Bentham, G., Hooker, J.D. 1865. Genera Plantarum, Vol. 1, Part 2. London: L. Reeve.

Brown, R. 1814. General remarks, geographical and systematical, on the botany of Terra Australis. Appendix III. Pp. 533–613. In: M.A. Flinders, Voyage to Terra Australis. London: G. & W. Nicol.

Collinson, M.E. 1983. Fossil plants of the London Clay. A field guide to fossils. No. 1. London: The Palaeontological Association.

Ding Hou 1957. A conspectus of the genus *Bruguiera* (Rhizophoraceae). Nova. Guinea, n.s. 8: 163–171.

Ding Hou 1958. Rhizophoraceae. Flora Malesiana I, 5: 429–493.

Ding Hou 1960. A review of the genus *Rhizophora* with special reference to the Pacific species. Blumea 10: 625–634.

Duke, N.C. 2010. Overlap of eastern and western mangroves in the south-western Pacific: hybridization of all three *Rhizophora* (Rhizophoraceae) combinations in New Caledonia. Blumea 55: 171–188.

Floret, J.-J. 1974. *Comiophyton*, genre nouveau gabonais Rhizophoraceae-Macarisieae. Adansonia II, 14: 499–506.

Floret, J.-J. 1976. A propos de *Comiophyton gabonense* (Rhizophoraceae). Adansonia II, 16: 39–49.

Graham, A. 2006. Paleobotanical evidence and molecular data in reconstructing the historical phytogeography of Rhizophoracae. Ann. Missouri Bot. Gard. 93: 327–334.

Hegnauer, R. 1973. .See General References.

Hisahi, Y. et al. 1984. Karyomorphological studies in five species of mangrove genera in the Rhizophoraceae. La Kromosomo II, 35/36: 1115–1116.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Juncosa, A.M. 1982. Developmental morphology of the embryo and seedling of *Rhizophora mangle* L. (Rhizophoraceae). Amer. J. Bot. 69: 1599–1611.

Juncosa, A.M. 1984a. Embryogenesis and seedling development in *Cassipourea elliptica* (Sw.) Poit. (Rhizophoraceae). Amer. J. Bot. 71: 170–179.

Juncosa, A.M. 1984b. Embryogenesis and developmental morphology of the seedling in *Bruguiera exaristata* Ding Hou (Rhizophoraceae). Amer. J. Bot. 71: 180–191.

Juncosa, A.M., Tobe, H. 1988. Embryology of the tribe Gynotrocheae (Rhizophoraceae) and its developmental and systematic implications. Ann. Missouri Bot. Gard. 75: 1410–1424.

Juncosa, A.M., Tomlinson, P.B. 1987. Floral development in mangrove Rhizophoraceae. Amer. J. Bot. 74: 1263–1279.

Juncosa, A.M., Tomlinson, P.B. 1988a. A historical and taxonomic synopsis of Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1278–1295.

Juncosa, A.M., Tomlinson, P.B. 1988b. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1296–1318.

Keating, R.C., Randrianasolo, V. 1988. The contribution of leaf architecture and wood anatomy to the classification of the Rhizophoraceae and Anisophylleaceae. Ann. Missouri Bot. Gard. 75: 1343–1368.

Kondo, K., Nakamura, T., Tsuruda, K., Saito, N., Yaguchi, Y. 1987. Pollination in *Bruguiera gymnorrhiza* and *Rhizophora mucronata* (Rhizophoraceae) in Ishigaki Island, The Ryukyu Islands, Japan. Biotropica 19: 377–380.

Lersten, N.R., Curtis, J.D. 1974. Colleter anatomy in red mangrove, *Rhizophora mangle* (Rhizophoraceae). Can. J. Bot. 52: 2277–2278.

Levin, G.A. 1992. Systematics of *Paradrypetes* (Euphorbiaceae). Syst. Bot. 17: 74–83.

Levin, G.A., Simpson, M.G. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

Matthews, M.L., Endress, P.K. 2011. See General References.

Prance, G.T., da Silva, M.F., Albuquerque, B.W., Jesus da Silva Araujo, I. de, Medeiros Carreia, L.M., Marinho Nogeira Braga, M., and six further authors. 1975. Revisão taxonómica das especies amazônicas das Rhizophoraceae. Acta Amazonica 5: 5–22.

Salvoza, F.M. 1936. *Rhizophora*. Nat. Appl. Sci. Bull. Univ. Philipp. 5: 179–237.

Schimper, A.F.W. 1892. Rhizophoraceae. In: A. Engler & K. Prantl (eds.) Die natürl. Pflanzenfam. III, 7:42–56. Leipzig: W. Engelmann.

Schwarzbach, A.E., Ricklefs, R.E. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on Chloroplast DNA, nuclear ribosomal DNA, and morphology. Amer. J. Bot. 87: 547–564.

Setoguchi, H., Ohba, H., Tobe, H. 1996. Floral morphology and phylogenetic analysis in *Crossostylis* (Rhizophoraceae). J. Plant Res. 109: 7–19.

Soltis, D.E. et al. 2011. See General References.

Sprague, T.A., Boodle, L.A. 1909. Kokoti (*Anopyxis ealaensis* Sprague). Bull. Misc. Inform. (Kew Bull.) 1909: 309–312.

Sussex, I.M. 1975. Growth and metabolism of the embryo and attached seedling of the viviparous mangrove, *Rhizophora mangle*. Amer. J. Bot. 62: 948–953.

Tobe, H., Raven, P.H. 1987. The embryology and relationships of *Cassipourea* and *Sterigmapetalum* (Rhizophoraceae-Macariseae). Opera Bot. 92: 253–264.

Tobe, H., Raven, P.H. 1988. Seed morphology and anatomy of Rhizophoraceae, inter- and infrafamilial relationships. Ann. Missouri Bot. Gard. 75: 1319–1342.

Tomlinson, P.B. 1986. The Botany of Mangroves. Cambridge: Cambridge University Press.

Tomlinson, P.B., Cox, P.A. 2000. Systematic and functional anatomy of seedlings in mangrove Rhizophoraceae: vivipary explained? Bot. J. Linn. Soc. 134: 215–231.

Tomlinson, P.B., Wheat, D.W. 1979. Bijugate phyllotaxis in Rhizophoreae (Rhizophoraceae). Bot. J. Linn. Soc. 78: 317–321.

Tomlinson, P.B., Primack, R.B., Bunt, J.S. 1979. Preliminary observation on floral biology in mangrove Rhizophoraceae. Biotropica 11: 256–277.

Vezey, E.L., Shah, V.P., Skvarla, J.J., Raven, P.H. 1988. Morphology and phenetics of Rhizophoraceae pollen. Ann. Missouri Bot. Gard. 75: 1369–1386.

Vliet, G.J.C.M. van 1976. Wood anatomy of the Rhizophoraceae. Pp. 20–75. In: Baas, P., Bolton, A.J., Catling, D.M. (eds.) Wood structure in biological and technological research. Leiden: Leiden University Press.

Wolfe, J.A. 1972. An interpretation of Aaskan Tertiary floras. Pp. 201–233. In: Graham, A., Floristics and paleofloristics of Asia and eastern North America. Amsterdam: Elsevier.

Wurdack, K.J, Davis, C.C. 2009. See General References.

Wurdack, K.J., Hoffmann, P., Samuel, R., de Bruijn, A., van der Bank, M., Chase, M.W. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid *rbc*L DNA sequences. Amer. J. Bot. 91: 1882–1900.

Xi, Z. et al. 2012. See General References.

Yin, G.S., Keng, H. 1974. Morphological studies on some inland Rhizophoraceae. Gard. Bull. Straits Settlem. 27: 183–220.

Zhang, L.-B., Simmons, M.P., Renner, S.S. 2007. A phylogeny of Anisophylleaceae based on six nuclear and plastid loci: ancient disjunctions and recent dispersal between South America, Africa, and Asia. Mol. Phyl. Evol. 44: 1057–1067.

Trigoniaceae

Trigoniaceae A. Juss. in Orbigny, Dict. univ. hist. nat. 12: 670 (1849), nom. cons.

V. BITTRICH

Trees, shrubs, scandent shrubs or lianas, glabrous or with indumentum of unicellular hairs, sometimes with glands. Leaves opposite or alternate, simple, entire, venation pinnate; stipules simple or bifid, interpetiolar when leaves opposite, often conspicuous, mostly caducous. Inflorescences panicles, racemes, cymes, or thyrses. Flowers hermaphrodite, small, papilionaceous, obliquely zygomorphic, 5-merous; sepals ± unequal, imbricate, connate at base or partly distinct; petals distinct, the posterior forming a saccate or spurred standard; stamens and staminodes connate basally into a tube that is more strongly developed on the anterior part of the flower by the 4–8 fertile stamens, staminodes 0 or up to 6 in the posterior part, anthers opening longitudinally; nectary glands 1–2(–4) opposite to the standard petal or 0; ovary superior or partly inferior, 3(4)-locular, rarely unilocular, pubescent, each locule with 1–numerous ovules; style simple. Fruits septicidal capsules or indehiscent 3(4)-winged, sometimes easily splitting into 1-winged samaras. Seeds hairy or not, embryo straight, endosperm + or 0.

A pantropical family of five genera and about 30 species, centred in South America, but also in Malesia and Madagascar.

VEGETATIVE MORPHOLOGY AND ANATOMY. The available information is summarized mainly in Lleras (1978). The species of *Humbertiodendron*, *Isidodendron*, *Trigoniastrum* and *Trigoniodendron* form middle-sized or large trees, while treelets, shrubs, scandent shrubs or lianas are typical for *Trigonia*. The branches are generally terete and lenticellate. Inconspicuous pilose domatia occur on the leaf blades of *Isidodendron*. Leaf margin and the abaxial surface of the bracts have impressed glands in *Trigoniastrum*; Stevens (2001) mentions marginal glands towards the leaf bases for *Humbertiodendron*; glandular papillae or hairs on the leaf, stipule, bract and bracteole margins also occur in some *Trigonia* species (e.g. *T. reticulata*).

Trichomes are reported mainly as simple, unicellular; sometimes a more or less dense arachnoid indumentum of twisted hairs is found, especially on the lower leaf surface; 2-armed unicellular trichomes, similar as in Malpighiaceae, were reported by Rao and Sharma (1992). Mucilaginous cells are common in the epidermis, which is uniseriate in *Trigonia* and two-layered in *Humbertiodendron* and *Trigoniastrum*. The paracytic stomata are restricted to the abaxial leaf surface. Branched sclereids are distributed in the mesophyll of *Humbertiodendron* and *Trigoniastrum*. Rhomboid or irregularly shaped crystals are common.

Information on stem anatomy is found in Metcalfe and Chalk (1950), Bridgwater and Baas (1982), and Carlquist (1988). The cork of the stem is derived from a subepidermal phellogen. Cortical sclereids are especially common in *Humbertiodendron* and *Trigoniastrum*. Vessels are solitary or in radial bands, the perforations simple or rarely scalariform, the parenchyma generally apotracheal and irregular (*Trigoniastrum*) or banded (*Trigonia*); scanty paratracheal parenchyma was reported from *Trigoniastrum*. Petersen (1896) described medullar vascular bundles with internal phloem forming an interrupted ring from an unidentified *Trigonia* species. Crystals occur in chambered axial and ray parenchyma. The vessels have bordered pits to the ground tissue of the xylem; Carlquist (2007) reported bordered pits from the axial parenchyma of *Trigoniastrum hypoleucum*, evident especially on the cross-walls. True tracheids and fibre tracheids are present, but libriform fibres and intraxylary phloem are absent. The rays are 1–5-seriate

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_24, © Springer-Verlag Berlin Heidelberg 2014

and heterogeneous (Kribs' type II). Sieve element plastids contain starch grains (type Ss, Behnke 1991).

FLOWER STRUCTURE. The flowers are united in panicles, racemes, cymes or thyrses, the pedicels are articulate. The buds of the short branches bearing the simple racemes of *Isidodendron* are protected by perulae. A detailed analysis of the flower structure of *Trigonia rugosa* and *Trigoniastrum hypoleucum* is provided in Matthews and Endress (2008), who also compared the results with their data from closely related families. The flowers are obliquely zygomorphic with the plane of symmetry through the third sepal, hypogynous or slightly perigynous (Eichler 1878). The sepals are unequal (the inner larger) with quincuncial aestivation, congenitally united at base or two sepals free on the posterior side of the flower, and generally have a strigose indumentum. Their margin is glandular in *Trigoniodendron*. The corolla is papilionaceous and consists of five petals, which are contorted in bud. The posterior (standard) and the wing petals are mostly hairy at base, but glabrous in *Trigoniodendron*. The standard petal is saccate or shortly spurred and bulges outwards between the two free posterior sepals (observed by Matthews and Endress 2008 in *Trigonia* and *Trigoniastrum*); the two anterior petals are often saccate and form a keel. The petal epidermis is epithelium-like in *Trigonia* and *Trigoniastrum* (Matthews and Endress 2008). The filaments of the four to eight fertile stamens and the one to six staminodes, if present, are fused into an unequally developed tube, much higher so in the anterior part of the flower, where the fertile stamens are positioned; studying young buds, Matthews and Endress (2008) concluded that the fertile stamens are basically arranged in two series; the anthers are tetrasporangiate, nearly basifixed and with a dorsal pit at the insertion of the filament, they open introrsely by longitudinal slits; the endothecium is continuous over the dorsal side of the connective (Matthews and Endress 2008). Staminodes are long and pointed or more rudimental, the latter become incorporated into the nectary glands; anthers rudiments are always lacking. The one or two nectary glands (or up to four according to Eichler 1878), possibly of staminodial origin, are inserted opposite the standard, they are sometimes lobed or laciniate, often puberulous. Such nectary glands are absent in *Isidodendron*, possibly the swollen bases of its staminodes secrete nectar. The ovary is superior or partly inferior, hairy, 3(4)-locular or 1-locular by reduction of the septa, placentation axile or axile-apical or in unilocular ovaries parietal on more or less deeply intruding placentas with a central column absent; the ovules are epitropous or antitropous and horizontal (*Trigonia*), pendulous (*Trigoniastrum*) or erect (*Humbertiodendron*). The style is terminal, simple, sometimes pubescent, the stigma capitate or rarely trilobate or circular, rarely punctate, its surface papillate. The ovary and lowest part of the common style were found to be completely synascidiate in *Trigoniastrum*, with the carpel tips in the style distinct or postgenitally connate for most of their length; in *Trigonia*, however, only the lower 2/3 of the ovary is synascidiate, but symplicate above; in the locules of *Trigonia* an obturator is formed by unicellular papillae protruding from the funicle, while in *Trigoniastrum* long, unicellular hairs are present on top of the locule (Matthews and Endress 2008).

EMBRYOLOGY. Only a few species of *Trigonia* were studied embryologically (Mauritzon 1936; Boesewinkel 1987). The ovule primordium is trizonate. Endosperm formation of *Trigonia* is initially nuclear, becoming cellular throughout. The nucellus becomes resorbed by the ovule and the mature ovules are bitegmic, anatropous, and epitropous or rarely apotropous, and tenuinucellate (the report of crassinucellate ovules by Mauritzon (1936) is dubious and needs confirmation). The embryo sac is probably of the Polygonum type. The integuments are of dermal origin, the inner is strongly multiplicative.

POLLEN MORPHOLOGY. Pollen grains are 3–4 (5)-porate, 25–60 µm long with the pollen size being highly variable within the same species; the exine is tenui-exinous and psilate (Lleras 1978).

KARYOLOGY. *Trigonia virens* has $2n =$ ca. 20.

POLLINATION. The basically papilionaceous flower typical for the family suggests insect-, probably bee-pollination, but observations are nearly completely lacking. Also the glands in the flowers suggest nectar as reward, but Lleras (1978) was unable to find any traces of it in flowers of *Trigonia* spp.

FRUIT AND SEED. *Trigonia* and *Trigoniodendron* have septicidal capsules, which are hairy outside and sometimes inside, the hard endocarp generally separates from the exocarp at maturity; *Isidodendron*, *Humbertiodendron* and *Trigoniastrum* have 3-winged fruits which easily split into 1-winged samaras in *Humbertiodendron* and *Trigoniastrum*. The seed coat is mostly covered with long often silky unicellular hairs, but is glabrous in *Humbertiodendron* and probably *Isidodendron*, the seeds of which are reported to be alate. Only the seed anatomy of *Trigonia* and *Trigoniastrum* was studied in detail (Boesewinkel 1987; Matthews and Endress 2008). The seeds are bitegmic. The outer integument is 2–3 cell layers, and the inner 3–6 layers thick. The exotegmen is fibrous and lignified, the endotegmen tanniniferous. The micropyle was described as zigzag for *Trigonia cipoensis* (Boesewinkel 1987); in *Trigoniastrum* it is formed by the inner integument only (Matthews and Endress 2008). The raphal bundle is amphicribral and complex. An endosperm rich in fat is present in *Trigonia* but absent in *Humbertiodendron* and *Trigoniastrum*. The embryo is straight and positioned longitudinally or transversely to the length of the seed, the cotyledons are flat but rather thick in *Trigoniodendron*.

DISPERSAL. The species with winged fruits are probably anemochorous. Nearly all species with capsular fruits have long-haired seeds which may be adapted to anemochory as well as to hydrochory. The seeds of two *Trigonia* species (*T. spruceana* and *T. hypoleuca*) have echinate trichomes and are possibly hydrochorous. Hydrochory and anemochory match with the typical habitats of *Trigonia* species.

PHYTOCHEMISTRY. The plants are often tanniniferous (stem and seeds); they show no accumulation of aluminium (Hegnauer 1973).

SUBDIVISION AND AFFINITIES. Most probably the palaeotropical genera *Humbertiodendron* and *Trigoniastrum*, with 3-winged fruits and various anatomical characters in common, form a monophyletic subgroup.

A couple of families including Polygalaceae, Chrysobalanaceae, Dichapetalaceae, Sapindaceae and Vochysiaceae were considered as next related to Trigoniaceae. *Trigoniastrum* was sometimes included in Polygalaceae. Based on ovule and seed structure, Boesewinkel and Venturelli (1987) suggested a close relationship of Trigoniaceae with the families of Linales (Malpighiales), but also Vochysiaceae (Myrtales). Vochysiaceae were most often considered as the closest relatives, and various differences in flower morphology between the two families were already discussed by Petersen (1896). Lleras (1978) mentioned anatomical evidence, like a simple petiole epidermis, general lack of libriform fibres and pith without sclereids in Trigoniaceae. The genus *Euphronia* was formerly often considered a member of Trigoniaceae, but *rbc*L sequence data revealed *Euphronia* as sister to Chrysobalanaceae (Litt and Chase 1999). The analysis based on combined *rbc*L and non-molecular datasets by Nandi et al. (1998) depict Chrysobalanaceae and Dichapetalaceae as the closest relatives of Trigoniaceae within Malpighiales. The cladogram of Litt and Chase (1999) shows Trigoniaceae as sister group of Dichapetalaceae, both together forming the sister group of Euphroniaceae + Chrysobalanaceae, a topology confirmed by Wurdack and Davis (2009), Soltis et al. (2011) and Xi et al. (2012). This family group, first proposed by Hallier (1921), was object of a careful study of floral structures revealing numerous characters of taxonomic importance (see Matthews and Endress 2008). The four families share the occurrence of obliquely zygomorphic flowers, sepals congenitally united at base, tenuinucellate ovules, and the occurrence of a zigzag micropyle (*Trigonia*). Trigoniaceae and Dichapetalaceae also share various floral characters, such as special mucilage cells in the mesophyll of the sepals, ovary and lower style sometimes completely synascidiate (*Trigoniastrum*), nectary semi-annular and with distinct scales or lobes.

DISTRIBUTION AND HABITATS. The family shows an interesting amphipacific distribution: *Humbertiodendron* is restricted to Madagascar, *Trigoniastrum* to Indonesia and Malaysia, and *Isidodendron*, *Trigonia* and *Trigoniodendron* to the Neotropics, with *Trigoniodendron* being endemic in coastal Espírito Santo (Brazil) and *Isidodendron* in the Rio Magdalena valley in central Colombia. Possible scenarios to explain the distribution pattern of *Trigonia* species are discussed by Lleras (1978). With exception of *Trigonia*, the genera occur in moist tropical forests. *Trigonia* species are found in periodically flooded riverine forests, gallery forests, edges of wet forests, and disturbed sites.

Economic Importance. The family has little economic importance. The hard wood of *Trigoniastrum hypoleucum* is used for furniture making.

Key to the Genera

1. Leaves alternate 2
– Leaves opposite 4
2. Leaves and bracts with impressed marginal glands; stamens 6. Malesia **2. *Trigoniastrum***
– Leaves and bracts glandless; stamens 7. South America 3
3. Flowers in panicles; staminodes 0; fruit a capsule **4. *Trigoniodendron***
– Flower in racemes; staminodes 4–6; fruit 3-winged, indehiscent **5. *Isidodendron***
4. Floral gland 1; ovule 1 per locule; fruit 3-winged dehiscing into1-winged samaras; seeds glabrous. Madagascar **1. *Humbertiodendron***
– Floral glands 2; ovules more than one per locule, fruit a 3(4)-valvate capsule; seeds hairy. Neotropics **3. *Trigonia***

Genera of Trigoniaceae

1. ***Humbertiodendron*** Leandri

Humbertiodendron Leandri, Compt. Rend. Hebd. Séances Acad. Sci. 229: 848 (1949).

Small trees. Leaves opposite, stipules connate. Flowers in axillary triflorate cymes, bracts eglandular; petals slightly strigose externally; stamens 6; 1 fleshy pilose gland adpressed to the ovary; ovary pubescent, 3-winged, trilocular, with 1 ovule per locule. Fruit 3-winged, dehiscing into 1-winged samaras. Seeds glabrous.

One sp., *H. saboureaui* Leandri, from coastal forests of E Madagascar.

2. ***Trigoniastrum*** Miq.

Trigoniastrum Miq., Fl. Ned. Ind., Eerste Bijv.: 394 (1861), nom. cons.

Trees up to 30 m; bark with a yellowish gummy juice. Leaves alternate, acuminate, with margins and acumen generally glandular, thinly arachnoid pubescent below; stipules caducous. Flowers in axillary or terminal panicles, bracts with marginal glands; standard slightly pilose externally; stamens 6, rudimental staminodes +; glands 1–2, puberulous; ovary hairy, 3-locular with 2 ovules per locule. Fruit 3-winged, splitting into 1-winged samaras. Seeds velutinous.

One sp., *T. hypoleucum* Miq., from tropical rainforests of Indonesia, Malaysia, Singapore and Brunei.

3. ***Trigonia*** Aubl. Fig. 69

Trigonia Aubl., Hist. Pl. Guiane: 387 (1775); Lleras, Fl. Neotrop. Monogr. 19: 29–62 (1978), rev.

Treelets, shrubs, scandent shrubs, or lianas. Leaves opposite, often with white indument below, stipules interpetiolar, entire or apically bifid, caducous or rarely persistent. Flowers in thyrses or panicles, bract margins glandular or eglandular; standard and wing petals mostly hairy at base; fertile stamens 4–8, staminodes up to 6 or 0; glands 2(–4), pilose or glabrous; ovary 3–4-carpellate, sometimes 1-locular due to reduction of the septa; ovules few to numerous per locule. Fruit a septicidal, often trigonous, outside mostly pilose capsule. Seeds pilose.

24 spp., trop. and subtrop. America, temporarily inundated forests, gallery forests, open forest edges, and disturbed areas.

4. ***Trigoniodendron*** E.F. Guim. & Miguel

Trigoniodendron E.F. Guim. & Miguel, Rev. Brasil. Biol. 47: 559 (1987).

Trees. Leaves alternate, stipules entire, caducous. Flowers in terminal panicles; margin of sepals glandular, petals glabrous, stamens 7, filaments connate in the lower half, staminodes 0, glands 2; ovary lanuginose. Capsule globose, septicidal, 3-valvate. Seeds hairy, cotyledons thick.

One sp., *T. spiritusanctense* E.F. Guim. & Miguel, known only from the Atlantic rainforest of Espírito Santo state, Brazil.

5. ***Isidodendron*** Fern. Alonso, Pérez-Zab. & Idagarra

Isidodendron Fern. Alonso, Pérez-Zab. & Idagarra, Revista Acad. Colomb. Ci. Exact. 24: 348 (2000).

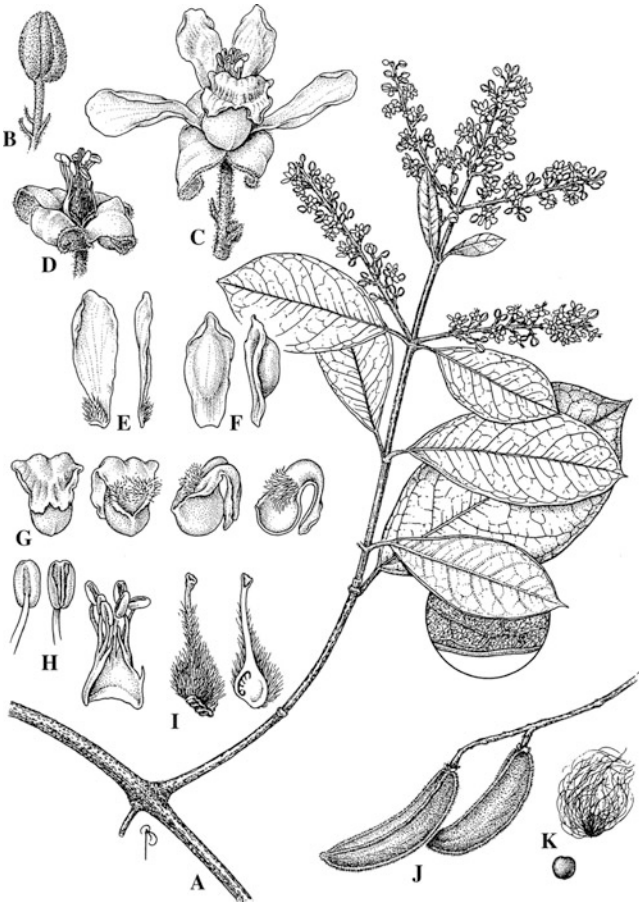

Fig. 69. Trigoniaceae. *Trigonia villosa*. **A** Flowering branch. **B** Flower bud. **C** Flower, oblique-apical view. **D** Flower after petals have fallen. **E** Adaxial and lateral views of lateral petal. **F** Adaxial and lateral views of anterior petal. **G** Three views and medial section of saccate posterior petal. **H** Abaxial and adaxial views of anthers and entire androecium. **I** Lateral view of pistil with basal nectary and medial section thereof. **J** Fruits. **K** Seed with hairs and with hairs removed. (Reproduced with kind permission of the artist Bobbi Angell)

Trees. Leaves alternate. Flowers in racemes on perulate short branches; petals glabrous, stamens 7, filaments connate in the lower half, staminodes 4–6, carnose at base, glands 0; ovary lanuginose. Fruit 3-winged. Seeds winged.

One species, *I. tripterocarpum* Fern.-Alonso, Pérez-Zab. & Idagarra, known only from the moist forests of the Rio Magdalena valley, central Colombia.

Selected Bibliography

Behnke, H.-D. 1991. See General References.

Boesewinkel, F.D. 1987. Ovules and seeds of Trigoniaceae. Acta. Bot. Neerl. 36: 81–91.

Boesewinkel, F.D., Venturelli, M. 1987. Ovule and seed structure in Vochysiaceae. Bot. Jahrb. Syst. 108: 547–566.

Bridgwater, S., Baas, P. 1982. Wood anatomy of *Xanthophyllum* Roxb. IAWA Bull. n.s. 3: 115–125.

Carlquist, S. 1988. Comparative wood anatomy. Berlin, Heidelberg, New York: Springer.

Carlquist, S. 2007. Bordered pits in ray cells and axial parenchyma: the histology of conduction, storage, and strength in living wood cells. Bot. J. Linn. Soc. 153: 157–168.

Chase, M.W. et al. 1993. See General References.

Eichler, A.W. 1878. Blüthendiagramme, 2. Teil. Leipzig: Wilhelm Engelmann, pp. 343–345.

Hallier, H. 1921. Beiträge zur Kenntnis der Linaceen (DC. 1819) Dumort. Beihefte Bot. Centralbl., Abt. 2, 39: 1–178.

Hegnauer, R. 1973. .See General References.

Litt, A.J., Chase, M.W. 1999. The systematic position of *Euphronia*, with comments on the position of *Balanops*: an analysis based on *rbc*L sequence data. Syst. Bot. 23: 401–409.

Lleras, E. 1978. Trigoniaceae. Fl. Neotrop. Monogr. 19: 1–73.

Matthews, M.L., Endress, P.K. 2008. See General References.

Mauritzon, J. 1936. Zur Embryologie und systematischen Abgrenzung der Reihen Terebinthales and Celastrales. Bot. Notiser (1936): 161–212.

Metcalfe, C.R., Chalk, L. 1950. See General References.

Nandi, O., Chase, M.W., Endress, P.K. 1998. A combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets. Ann. Missouri Bot. Gard. 85: 137–212.

Petersen, O.G. 1896. Trigoniaceae. In: Engler & Prantl, Natürl. Pflanzenfam. 3(4): 309–311.

Rao, S.R.S., Sharma, V. 1992. Morphology of 2-armed trichomes in relation to taxonomy: Malpighiales. Feddes Repertorium 103: 55–565.

Soltis, D.E. et al. 2011. See General References.

Stevens, P.F. 2001 onwards. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Violaceae

Violaceae Batsch, Tab. Affin. Regni Veg.: 57 (1802), nom cons.

H.E. Ballard, J. de Paula-Souza, and G.A. Wahlert

Trees, treelets, shrubs or subshrubs, infrequently lianas or herbs, sometimes stoloniferous. Leaves alternate, sometimes opposite, distichous or pseudo-whorled, pinnately or rarely palmately veined, entire or rarely lobed or dissected, with conspicuous persistent or sometimes deciduous stipules, petiolate or sometimes subsessile, epulvinate; plants glabrous or variously pubescent with unicellular or multicellular hairs. Inflorescences thyrso-paniculate, botryoids (pseudoracemes, compound or simple cymes), fascicles or condensed “short shoots”, or flowers solitary; inflorescences subtended by a commonly persistent bract; pedicels commonly articulated, almost always bearing a pair of prophylls; flower buds in *Viola* and some other strongly zygomorphic genera becoming resupinate at anthesis, with saccate or spurred petal lowermost. Flowers bisexual (unisexual), actinomorphic to strongly zygomorphic, hypogynous (slightly perigynous); sepals 5, free, typically quincuncially arranged, persistent through fruiting, equal in actinomorphic flowers, slightly unequal or rarely strongly unequal in zygomorphic ones; petals 5, free, rarely persistent into fruit, equal in actinomorphic flowers, the anterior slightly to much longer and saccate or spurred in zygomorphic flowers, aestivation commonly apotact sensu Hekking (1988b), sometimes quincuncial or rarely convolute; stamens 5(3), free or filaments weakly to strongly connate into a tube; anthers dithecal, introrse, rarely extrorse, commonly bearing a dorsal sterile connective appendage, occasionally with two ventral connective appendages; in zygomorphic flowers 2 filaments and/or dorsal surfaces of the anthers bearing individual or fused nectariferous glands enclosed by a sac or spur at the base of a differentiated petal; ovary superior, (2)3(4–5)-carpellate, unilocular with parietal placentas; ovules 1–many, anatropous, bitegmic, crassinucellate; style filiform or sometimes clavate, straight, curved or sigmoid; stigma often simple, less often rostrate, orifice porrect or bent downward especially in zygomorphic flowers. Fruits commonly a capsule dehiscing with (2)3(4–6) coriaceous to woody, rarely elastic or papery valves, sometimes fleshy, rarely a nut. Seeds in most genera uniform, globose to narrowly ellipsoid, compressed to strongly flattened and often with an intermittent to entire wing in a few genera, rarely of two types (spindle-shaped and discoid), in some genera bearing elaiosomes; endosperm nuclear, oily; embryo flat, straight.

A predominately tropical family consisting of up to 1,100 species in 22 currently recognized genera, plus ten additional generic segregates to be extracted eventually from polyphyletic *Hybanthus* and *Rinorea* (Wahlert et al., accepted). The largest genus, *Viola*, is cosmopolitan in temperate and mountainous regions; the second and third largest genera as currently circumscribed, *Rinorea* and *Hybanthus*, are mainly pantropical.

Characters Occurring in Relatively Few Genera and Species. Roots tuberous in *Viola arborescens*, xylopodiferous in a few *Hybanthus*. Climbing or scrambling habit in *Agatea*, *Anchietea*, *Calyptrion* and *Hybanthopsis*; entirely herbaceous habit in a few *Hybanthus* and most *Viola*, acaulescent habit in some *Viola*, stolons produced in some acaulescent *Viola*; annual duration in a few *Viola*. Thorns in a few *Hybanthus* and one *Melicytus*. Domatia in some *Rinorea*. Leaves opposite in some *Rinorea*, a few *Hybanthus*, pseudo-whorled in *Allexis*; pellucid-punctate in *Leonia*. Leaf blades lobed or dissected in a few *Viola*; stipules lacerate or lobed in some *Viola*. Flowers cauliflorous in *Allexis*, one *Leonia*, rarely in *Melicytus* and *Paypayrola*, basally cauliflorous in

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_25,

Hekkingia; flowers unisexual in some *Anchietea* and *Melicytus*. Inflorescence a spiciform botryoid in *Paypayrola*, solitary flower in a condensed "short shoot" in *Isodendrion*; flowers consistently solitary in some *Hybanthus* and nearly all *Viola*. Some flowers in a spiciform botryoid aborting early and apparently secreting nectar in *Paypayrola*. Racemoid with large and emarginate bracts in *Hekkingia*. Pedicels not articulated in *Viola*. Sepals strongly unequal in size and shape in *Hybanthus heterosepalus*, *H. lehmannii*, and *Schweiggeria*, auricled at base in *Viola*. Petal aestivation convolute in *Fusispermum*, quincuncial in *Hekkingia*, *Leonia*, some *Gloeospermum*, and rarely in *Rinorea*. Corolla persistent into mature fruit in *Noisettia*. Lateral petals "bearded" with tufts of hair on inner surfaces near throat in some *Viola*, bottom petal pubescent within in some *Hybanthus* and some *Viola*. Stamens three in one *Leonia* species. Filaments fully connate into a tall tube and anthers slanting or horizontal in *Hekkingia*, *Leonia* and *Paypayrola*. Ring of stamens with internal basal finger-like projections in a few *Rinorea*. Dorsal connective scales lacking in *Fusispermum* and *Leonia*, minute or lacking in *Hekkingia*, some *Isodendrion* and *Paypayrola*. Ventral connective scales large in *Allexis* and a few *Rinorea*. Ovary 5-carpellate in some *Leonia*, 4-carpellate in some *Anchietea*, 2-, 4- or 5-carpellate in some *Melicytus*. Ovary disintegrating early, with seeds maturing naked on placental traces in *Decorsella*; fruit a nut in most *Leonia* and fleshy in one *Leonia* and a few *Rinorea*, all *Gloeospermum* and *Melicytus*; semidehiscent and woody in *Calyptrion*, and dehiscing by six sutures in one *Agatea* species and by one suture in *Hybanthopsis*; capsule tuberculate in *Amphirrhox*, *Hekkingia*, *Orthion*, and a few *Rinorea*; capsule thin-walled and elastic in *Hybanthopsis* and a papery "bladder" in *Anchietea*. Seeds strongly flattened in *Agatea*, *Anchietea* and *Calyptrion*, winged in *Agatea* and most *Anchietea* and with basal expansions in *Hybanthopsis*; seeds ellipsoidal and with longitudinal ridges and/or foveolae in Old World *Hybanthus enneaspermus* group; seeds fusiform or discoid in *Fusispermum*; seeds pubescent in *Hybanthopsis*, some *Rinorea* and a few *Viola*; seeds bearing elaiosomes in *Allexis*, *Fusispermum*, *Hekkingia* and *Viola*, very reduced in *Hybanthus*.

VEGETATIVE ANATOMY. Extensive detail of wood and leaf anatomy are provided by Metcalfe and Chalk (1972). Leaf laminas are typically dorsiventral (centric in a few *Hybanthus*) and lack secretory cavities. Most species have sparse to dense or irregularly distributed vegetative indumentum of unicellular, uniseriate or rarely stellate trichomes (these occasionally gland-tipped), and also commonly have marginal serrations or crenations tipped by a small hard gland. The cuticle is usually thin and sometimes striated, and may lie beneath a thin wax layer. The inner walls of the epidermal cells are often mucilaginous, with mucilage cells showing up as transparent dots in anatomical cross sections; various species of several genera also produce reddish to yellow resin cells. The mesophyll varies with 1 to a few palisade layers, with layer number being species-specific and apparently correlated with degree of light intensity in Hawaiian *Viola* species (C. Havran and H.E. Ballard, unpubl.). Secretory cells containing a brown unidentified substance (tannins?) have been noted in the mesophyll but not in the epidermis of some Hawaiian *Viola* species. Vascular bundles in herbaceous species (largely confined to *Viola*) lack sclerenchyma while sclerenchyma strands are well developed around bundles in woody genera. An adaxial hypodermis is rarely present (some *Melicytus*). Leaves of all genera contain calcium oxalate crystals: irregular discoid crystals dispersed throughout the cytoplasm (almost entirely restricted to phylogenetically basal genera), uniform prismatic crystals restricted to veins (restricted to phylogenetically derived genera), and rarely, spinose druses (thus far found only in *Hybanthus concolor*, H.E. Ballard, unpubl.). Minor leaf veins lack phloem transfer cells, at least in *Viola*. Stomata are primarily or entirely confined to the abaxial surface, being anisocytic or paracytic.

Taylor (1972) found considerable variability in wood structure across the genera that he interpreted as largely supporting the traditional classification, except for endemic island groups. The nodes of caulescent taxa are trilacunar. Primary vascular tissue forms a cylinder, with secondary tissue derived from a cylinder of cambium. Libriform fibers are present or absent associated with vessels, depending on the genus. Wood-rays are heterocellular or homocellular, mixed uniseriate and pluriseriate. Crystals are common in ray cells. Imperforate tracheary elements are present. Wood parenchyma is sparse and paratracheal or lacking. Vessel members have angular pores, thin walls and uniform diameter.

The more basal genera, specifically *Fusispermum* in subfamily Fusispermoideae, as well as subfamily Leonioideae and subfamily Violoideae tribe Rinoreeae, have very elongate vessels with tapering end walls and scalariform perforation plates. The endemic island genera *Isodendrion* and *Melicytus*, traditionally placed in tribe Rinoreeae, and all genera in previously circumscribed tribe Violeae have short vessels with perpendicular to oblique end walls and simple perforation plates. Taylor (1972) argued that the insular Rinoreeae experienced accelerated rates of xylem evolution and were therefore anomalous in their "non-primitive" vessel morphologies. Recent phylogenetic reexamination of the family using multiple plastid and nuclear DNA sequences (Hodges et al. 1995; Tokuoka 2008; Wahlert et al., accepted) has dramatically revised our view of relationships among genera and provided the foundation for a new intrafamilial classification (see AFFINITIES below). Nevertheless, all more-basal genera in the family within this new phylogenetic framework possess elongate "primitive" vessels, whereas more derived genera possess shorter "advanced" vessels as described by Taylor. The anomalous endemic island groups are phylogenetically placed as highly derived among other derived taxa, thus demonstrating the significant correspondence of vessel element morphology with phylogenetic position.

Taylor (1972) also found similarities between the three lianescent genera then known, which he interpreted as the product of convergence. He believed an affinity between Indo-Pacific *Agatea* on the one hand and Latin American *Anchietea* and *Calyptrion* on the other to be highly unlikely. Chloroplast DNA data have confidently placed these lianescent genera and the more recently described herbaceous twining genus *Hybanthopsis* into an exceptionally well-supported "lianescent" clade (Paula-Souza and Souza 2003; Wahlert et al., accepted), revealing the unusual scandent to vining habit as a phylogenetically meaningful trait and supporting the surprising southern amphi-Pacific disjunction.

INFLORESCENCE STRUCTURE. The fundamental inflorescence form, found in the most basal genera *Fusispermum*, *Leonia* and *Rinorea*, is the thyrsoid, also loosely referred to as a panicle. According to Hekking (1988b), from this type depauperation (reduced ramification) leads to the thyrsoid, the botryoid and the spiciform botryoid, but also to the compound cyme, found in many genera, and the simple cyme, the latter found principally in some *Hybanthus*. A fascicle, found in several genera, may be derived from a compound cyme by condensation of the secondary and primary axes, or from a simple cyme or racemoid through drastic shortening of the primary axis. A short shoot with solitary flowers is found in *Isodendrion*. Solitary axillary flowers are almost ubiquitous in *Viola*, frequent in *Hybanthus* and occasionally occur in otherwise typically dichasial or fasciculate *Gloeospermum*. The simple "cymes" in some Hawaiian species of *Viola* are derived from initially branched stems through loss of leaves and telescoping of internodes (Skottsberg 1940).

FLORAL STRUCTURE AND ANATOMY. Pedicels are articulated except in *Viola*, and always bear a pair of prophylls. Flowers are hypogynous or slightly perigynous and perfect except in some *Melicytus* and rare *Rinorea*. Petals are spreading or somewhat recurved distally, rarely strongly reflexed in *Allexis*, persistently tightly closed in most *Gloeospermum*. Flowers have 5 equal or slightly unequal sepals, dramatically unequal in *Schweiggeria*, with auricles in *Viola*. Corollas in approximately half of the genera, namely, in currently recognized tribe Rinoreeae, have been customarily interpreted as actinomorphic, but numerous floral dissections across taxa of nearly all genera in the family by the authors (unpublished data) have revealed no instances of true actinomorphy in which all petals are identical in size and shape (*Allexis*, excluding *A. zygomorpha*, approaches this). Conversely, nearly all members of the family express at least weak zygomorphy in the corolla, or the whole perianth, and often also in the androecium and gynoecium. While Arnal's (1945) characterization of the "transitional" genera *Amphirrhox*, *Decorsella*, *Paypayrola*, and *Isodendrion* as groups with one petal slightly to noticeably broadened in the apical portion relative to the others but essentially the same length has remained accurate, about half of the reportedly actinomorphic genera in the family nevertheless show noticeably zygomorphic features in calyx, corolla, androecium, gynoecium or combinations of these, and the remainder of the family is moderately to strongly zygomorphic in floral morphology.

Zygomorphic flowers within tribe Violeae have the anterior petal moderately to strongly differentiated in shape, often into a slender claw and abruptly widened blade, commonly also longer than the others, saccate or spurred at the base. The sac or spur encloses two free or fused slightly or greatly prolonged staminal glands functioning as nectaries (Fig. 73G). In *Calyptrion*, *Noisettia*, *Schweiggeria* and some *Viola* the spur is long. In *Allexis zygomorpha*, some *Hybanthus*, some *Viola* and some *Rinorea*, the bottom petal blade is pubescent on the inner surface near the throat, or over both surfaces. The lateral petals are pubescent on the inner surface near the throat in some *Viola*.

The androecium in perfect flowers is composed of 5 fertile antesepalous stamens (3 in *Leonia triandra*). Anthers and dorsal connective appendages are often connivent or tightly coherent around the slightly to moderately exserted style, forming a "pollen cone" especially well developed in zygomorphic flowers and in some species of *Melicytus*. Filaments are weakly to moderately connate in *Fusispermum*, genera in the traditional tribe Rinoreeae and some Violeae to very strongly so, and form a tall staminal tube in *Hekkingia*, *Leonia* and *Paypayrola*. Small glands are borne on or at the base of the filaments or on the filament tube in the traditional subfamily Violoideae, in tribe Violeae two of them enlarged, and sometimes fused, to form nectaries. Thecae are vertical, slanting in *Hekkingia* and *Paypayrola* or horizontal in *Leonia*. Stamens terminate in a membranous connective appendage, which is large and conspicuous in most genera but rudimentary in some *Isodendrion* and *Rinoreocarpus* and absent or rudimentary in *Fusispermum*, *Hekkingia*, *Leonia*, and *Paypayrola*. Broadly attached ventral connective appendages are present in *Fusispermum*, and small linear or bicuspidate ventral processes are found in some *Allexis* and a few *Rinorea* species.

Current investigations into floral development, details of sepal and petal aestivation, and androecial morphology (especially staminal gland features) are providing many additional overlooked characteristics with which to distinguish segregate lineages of polyphyletic *Hybanthus* and *Rinorea* as separate genera, and to create a more natural classification expressing recognizable taxonomic diversity in the Violaceae (Wahlert et al., accepted).

Violets (mainly *Viola*) provide examples of the evolutionarily successful mixed chasmogamous/cleistogamous breeding system (Ballard et al. 2011). Cleistogamous flowers have been documented in a few *Hybanthus* and most *Viola* species. The few exceptions in *Viola* lacking cleistogamous flowers are inhabitants of xeric, desert or grassland environments in a number of disparate groups, suggesting multiple independent losses of cleistogamy in these particular cases. In cleistogamous flowers, stamen and pistil development is accelerated relative to the sepals and petals in the very young bud (Mayers and Lord 1983). The reproductive organs remain somewhat rudimentary in form and sometimes fewer stamens are formed; comparatively fewer pollen grains are shed than in the typical chasmogamous flower. The style in some species curves around within the tightly coherent pollen cone, and pollen grains, which have germinated within the top of the anthers, penetrate the anther walls and contact the stigmatic orifice in situ. Thus, cleistogamous capsules are easily distinguishable from chasmogamous ones by the tightly curled, rudimentary style commonly persisting at the tip of one of the valves. In European *Viola odorata* the production of chasmogamous vs. cleistogamous flowers is determined by the photoperiod; plants receiving 11 hours or less of daylight produce chasmogamous flowers, whereas those receiving 14 hours or more produce cleistogamous ones (Mayers and Lord 1983). Similar observations hold for New Zealand *Viola cunninghamii* (Holdsworth 1966). At least some tropical montane *Viola* species, however, produce both types simultaneously.

Embryology. The vast majority of embryological information comes from studies of various *Viola* species, in a genus which is anomalous in many ways and quite derived in the family (for summary see Johri et al. 1992). The anther is tetrasporangiate and four- to six-layered; the endothecium is fibrous, middle layers are ephemeral in some *Viola* species, and Ubisch granules stud the inner walls of tapetal cells in certain *Hybanthus*. Pollen is shed at the two-celled stage. In *Viola riviniana*, the generative cell has been documented dividing either in the pollen grain or in the pollen tube.

Ovules are anatropous, bitegmic, and crassinucellate; the inner and outer integuments forming a zigzag micropyle in *Viola* and some *Hybanthus*, whereas only the inner integument forms the micropyle in *Hybanthus concolor*. Embryo sac development follows the Polygonum type. Antipodals are small and ephemeral in some, relatively large in other *Hybanthus* and *Viola*. Endosperm development is of the Nuclear type with centripetal wall formation; the endosperm is massive and persistent. Embryogeny corresponds to the Asterad type. The mature embryo is chlorophyllous, straight and spatulate, with flat cotyledons embedded in the endosperm.

POLLEN MORPHOLOGY. As with embryological information, very few other genera besides *Viola* have been adequately examined and documented; information summarized here is derived from Erdtman (1952). In several *Viola* species as well as a few *Hybanthus*, *Leonia*, *Melicytus* and *Rinorea*, pollen grains are 3–4(5)-colporate and suboblate to prolate or prolate-spheroidal. The exine is tectate, with a psilate tectum. Pollen exine micromorphology appears to be approximately similar across genera but this demands further scrutiny. Preliminary observations of a few other genera indicate greater diversity to be found than previously appreciated; e.g., *Hekkingia* pollen is cylindrical and monocolpate (H.E. Ballard, unpubl.). Recent Malpighiales-wide studies of pollen morphology and tapetum (Furness 2011) revealed potential palynological synapomorphies defining the loosely phenotypically circumscribed order and also suggestive of shared traits uniting sister families Passifloraceae and Violaceae, namely, a thick bilayered or channeled apertural intine, and pollen (in *Viola*) with more than 3 colporate apertures.

Pollen heteromorphism is known from *Viola*, where specifically the number of pores generally increases as polyploidy increases (Nadot et al. 2000). Similarly, in the *Viola nuttallii* complex (Fabijan et al. 1987) and in *Viola adunca* (McPherson and Packer 1974), pollen size has been found to increase with each higher ploidy level.

KARYOLOGY. Most counts in the family are for *Viola* (over 1,200), but several other genera have at least one (see Ballard 1996). Relatively few chromosome counts exist for members of tribe Rinoreeae, and none for *Fusispermum* and *Leonia*. The lowest regularly confirmed number yet counted is $n = 5$ for *Viola mercurii* and *V. parvula*, two small annual Mediterranean pansies of section *Melanium*; the largest number is $n =$ ca. 120 for *V. bubanii*, another pansy in Mediterranean Europe. Counts for some Rinoreeae (e.g., *Rinorea*) but also certain Violeae (*Viola*, African and Australasian *Hybanthus*, North American *Hybanthus concolor*) have diploid and polyploid numbers conforming to a base number of $x = 6$, whereas Hawaiian *Isodendrion*, Indo-Pacific *Agatea*, Australian-Oceanic *Melicytus* and other New World *Hybanthus* have diploid and polyploid numbers arising from a base of $x = 8$ (Beuzenberg 1961; Bennett 1972; Kellogg and Weitzman 1985). While the affinities suggested by chromosome numbers do not correspond well with the traditional intrafamilial classification, they closely match the affinities of genera portrayed by plastid DNA sequence data (Wahlert et al., accepted): basal genera possess $2n = 24$ or 48 (potentially polyploids on $x = 6$), while more derived genera have the higher base number ($x = 8$). However, Marcussen et al. (2012) have argued from *Viola* and other genera with more abundant counts that the basal number in the genus may in fact be $x = 7$. Chromosome numbers support molecular systematic evidence for extreme polyphyly of the genus *Hybanthus*; unfortunately, little cytological evidence is yet available for the large and heterogeneous genus *Rinorea*. On the contrary, the genus *Viola*, largest in the family, is demonstrably monophyletic and yet shows extensive polyploid speciation (Ballard et al. 1999). Using a molecular phylogeny of *Viola* groups worldwide based on the nuclear Internal Transcribed Spacer DNA region, Ballard et al. (1999) proposed that all but one of several aneuploid groups have arisen from euploid progenitors through loss of one or more chromosomes. Exceptionally, the three species assigned to the Asian *Viola* subsect. *Diffusae* were inferred to have each gained a chromosome relative to their nearest sister group. Subsequent studies by Marcussen et al. (2012) recently applied genetic information from a single-copy nuclear gene, glucose phosphate isomerase (GPI), to demonstrate that all polyploid groups in North America and Hawaii are allopolyploid, with two to several genomes from different diploid and tetraploid ancestral groups. Results documented a primary allopolyploid 10x level common to all five high-polyploid groups, and secondary allopolyploidization with additional tetraploid ancestors in three of the five groups.

POLLINATION. Most members of the family, including the most primitive genera, are undoubtedly entomophilous, displaying chasmogamous floral syndromes appropriate for attracting butterflies, bumblebees, solitary flees, hawkmoths or, in the tiniest flowers of some Andean *Viola* species, perhaps even small flies. A few taxa, including the red-flowered South American scandent shrub or liana *Viola arguta*, with flowers bearing an inflated spur, may in fact be pollinated by birds. A diversity of *Viola* species with different corolla color patterns and divergent floral morphologies, including members of the same subsection, have been shown to attract largely different classes of insect pollinators, resulting in a significant degree of pollinator partitioning, not to mention some level of ethological or mechanical isolation between closely related species (Beattie 1974). In *Viola*, a yellow corolla has been inferred to be a generalist syndrome, whereas a blue or white corolla (depending also on the petal morphology and flower architecture) solicited a narrower and more specific suite of pollinators, usually bee and butterfly, or moth, respectively.

The basic flower structure in zygomorphic groups of the Violaceae fits that of "nectar flowers", the pollination reward for most species being the secretion of nectariferous glands located on or at the base of the anther's filaments, which is stored inside the anterior petal's sac or spur. However, some species produce very scanty nectar or none at all (although nectaries are present, as in some species of *Viola* sect. *Leptidium*) and pollination is effected by pollen-collecting insects instead (Freitas and Sazima 2003; Braun et al. 2012).

The generalized pollination process in *Viola* relies in part on the tightly coherent ring of dorsal connective appendages of the stamens surrounding the style to form a "pollen cone", and in part on the elastic flexibility of the style on the pistil. This is also echoed in some species of *Melicytus* that have tightly coherent stamens and well-developed anther connectives. The head or proboscis of the insect forcing its way into the flower displaces the style from the center of the pollen cone. As the style is displaced, a drop of viscous fluid exudes from the stigmatic orifice, collecting pollen grains from neighboring conspecific flowers that are scraped off the insect's body. Concomitantly, the displacement of the style opens a gap in the pollen cone, permitting pollen of the present flower to fall onto the insect (Beattie 1969). When the insect withdraws its head, the style snaps back into position, drawing in the viscous drop with collected pollen grains and also closing off the gap in the pollen cone. In some weakly zygomorphic genera (e.g., *Amphirrhox*, *Paypayrola*), the dorsal connective appendages are rudimentary and do not form a "pollen cone", and the floral structure (stigmas hidden in the long, narrow corolla tubes and anthers located on short filaments near the base of the corolla) suggests pollination through the mouthparts of long-tongued insects. Therefore, pollen-release mechanisms do not occur as observed in *Viola* and possibly most species of the family, in which pollen placement on the insect body is trigged by the manipulation of the style (Braun et al. 2012). Further study of other zygomorphic genera is required, to determine whether the classic "*Viola*" strategy or another pollination mechanism is employed in other zygomorphic flowers, and what pollination mechanism(s) predominate in genera with actinomorphic flowers.

Floral syndromes of certain species have become quite specialized for their preferred pollinators. Several studies have been conducted on floral variation and reproductive success of the extraordinarily long-spurred *Viola cazorlensis*, narrowly endemic to the limestone hills of the Cazorla region of Spain (see Herrera 1988). Short of exceptional morphological specializations, closely related species in the same group of *Viola* have been found to attract modally different classes of pollinators (Beattie 1970). A substantial degree of ethological isolation through pollinator partitioning is accomplished among simultaneously flowering species by virtue of the evolution of a few seemingly minor floral differences (Beattie 1974). During nectar feeding in *Viola*, flowers with comparatively large bottom petals, tufts of hairs ("beards") on lateral petals and absence of strong corolla color contrast or heavy nectar guides encourage insect approaches in the prone (head up) position for all insect pollinators, leaving pollen deposited on the top of the head and upper thorax. Conversely, flowers with small bottom petals, glabrous lateral petals and presence of strongly contrasting corolla color patterns (including heavy nectar guides or eyespot) foster visitation in the supine (head down) position for some insects, particularly bumblebees and solitary bees, leaving pollen deposited on the face and lower thorax.

The anthesis in Violaceae is mostly diurnal (Beattie 1969, 1974; Augspurger 1980; Powlesland 1984; Munzinger and Pauly 2003), although recent studies have reported a nocturnal flowering in *Anchietea* (Hoffmann et al. 2010), *Amphirrhox* and *Paypayrola* (Braun et al. 2012). Two phases of anthesis have been inferred, at least in *Viola*, from changes in petal position and flower orientation (Beattie 1969): shedding of pollen from anthers into the pollen cone, and deposition of pollen from the cone onto the bottom petal. The first is believed to be effective only for pollinators properly operating this primary pollination mechanism, whereas the second is a "failsafe" secondary pollen presentation mechanism in which a wider range of insects may accomplish pollination.

In *Hybanthus enneaspermus*, flowers not successfully cross-pollinated roll up their enlarged bottom petal longitudinally and orient the rolled petal downward, permitting pollen to fall onto the style within. Pollen tubes will often germinate, effecting self-fertilization (J. Munzinger, unpubl.). Some pansy species of *Viola* sect. *Melanium* are purportedly primarily or exclusively selfers, perhaps aided by the same mechanism. The tightly closed corollas of most *Gloeospermum* species suggest that selfing might be common in that genus as well.

For cleistogamy, see Floral Structure and Anatomy above.

Fruit and Seed. Most genera produce a characteristic thick-walled, three-valved capsule; *Hybanthopsis* bears a very thin-walled elastic capsule. The capsules of most genera have a smooth to slightly rugulose surface but those of *Amphirrhox*, *Hekkingia* and most *Orthion* are strongly tuberculate. In *Rinorea anguifera* of tropical Asia, as well as a few species of Brazilian *Hybanthus*, the capsule produces a dense indumentum of long shaggy multicellular, multiseriate hairs. *Leonia* bears indehiscent nuts in most species and a berry-like nut with a thin, edible pericarp in *L. glycycarpa*. Neotropical *Gloeospermum* and Australian-Oceanic *Melicytus* produce soft fleshy berries, edible in at least some species of the first genus. The capsule of extra-Amazonian *Anchietea* is paper-thin and bladder-like (Fig. 73). The seeds of most genera are narrowly ovoid to obovoid or globose; those of the lianescent genera *Agatea*, *Anchietea* and *Calyptrion* are distinctly to strongly flattened and in *Anchietea* and *Agatea* are typically bordered by an intermittent to continuous thin wing. The twining herb *Hybanthopsis*, phylogenetically allied with these lianescent genera, has a compressed seed with two basal processes which are presumably homologous to the flattened ridge or marginal wing found in related genera. A few genera with ovoid or ellipsoid seeds, namely *Allexis*, *Fusispermum*, *Hekkingia*, a few *Hybanthus* and *Rinorea* species, and all *Viola* species, possess an elaiosome which originates as an outgrowth of the micropyle or the raphe base (in *Hybanthus* and *Viola*) or from the woody annulus surrounding the apex of the funicle (*Rinorea*) (Corner 1976). The testa is made of tabular or radially elongate cells with a thin to strongly thickened outer wall, sometimes with stomata, and scattered sclerotic cells. The mesophyll is thin- or thick-walled, sometimes somewhat lignified and with crystal-cells. The exotegmen consists of longitudinally oriented flat lignified fibers laid down in 1 to 4 layers (few and short in *Hybanthus* and *Viola*, more and elongate to sinuous in *Rinorea*). Seeds of all genera have well-developed nuclear oily endosperm. The two cotyledons are flat. The embryo is chlorophyllous and straight (in several species of *Viola*). Seed shape, size and color provide taxonomically significant traits in *Viola* sect. *Leptidium* (Ballard, unpubl.) and seed coat microsculpturing diverges recognizably among species in certain *Viola* groups, e.g., subsect.

Boreali-Americanae, and provides some taxonomic potential for inferring relationships or hybrid origin (Gil-ad 1995, 1998). Sculpturing of the seed coat and size, shape and color of the mature seeds have proven to be of great taxonomic utility (together with androecial and inflorescence morphology) in supporting the recognition of several phylogenetically distinct lineages currently lumped under the polyphyletic assemblage *Hybanthus*.

Significant seed predation by infesting microlepidoptera and depressed seed set due to reduced pollinator visitation in temporally isolated flowering individuals of *Hybanthus prunifolius* may have been key factors in selection for synchronous flowering time in that species (Augspurger 1982).

DISPERSAL. Seed dispersal in most capsule-bearing representatives of *Viola* is of the diplochorous, or explosive, type (Beattie and Lyons 1975), and this is presumably the case with other dehiscent capsule genera, too. This is characterized by readily dehiscing capsules, usually green and commonly on upright, well-elevated peduncles. At maturity, the fruit dries and the expanding seeds force open the capsule valves, which spread wide; the valves complete the drying process and the side walls squeeze together, forcibly ejecting the seeds up to 2 (or more) meters away. Seeds are located by ants and secondarily removed further from the parent plant.

Species of some acaulescent groups of *Viola* produce small, globose, purple-blotched cleistogamous capsules on short, prostrate or burrowing peduncles conforming to the myrmecochorous mode of seed dispersal. In these species, the capsule dehisces slowly or gradually disintegrates, spilling the seeds onto the ground surface or burying them under the soil. In the former event, ants are attracted to the elaiosome on the seeds and may carry them some distance away from the parent plant. This latter dispersal syndrome may represent a fairly high degree of coevolution with particular ant species (Beattie and Lyons 1975). Generally, diplochorous species occupy open sites with presumably greater environmental change, whereas myrmecochorous species are characteristically woodland inhabitants.

The genera *Gloeospermum*, *Melicytus* and the species *Leonia glycycarpa* produce berries and are presumably dispersed by birds or other animals. The indehiscent "nuts" of most *Leonia* species are likely dispersed by animals as well. The winged seeds of *Anchietea* and the soft, floating seeds of the riverine species of *Calyptrion* suggest that hydrochory and anemochory play a major role in the distribution patterns within these genera (Paula-Souza et al. 2011).

The germination ecology of seeds in temperate species of *Viola* is complex. Many species (e.g., *Viola egglestonii*) display true dormancy immediately following dispersal, and will not germinate until after a period of cool temperatures or cold stratification (Baskin and Baskin 1975). Contrariwise, the winter annual *V. bicolor* (as *V. rafinesquii*) requires high temperatures such as would be passed during summer dormancy, to foster germination (Baskin and Baskin 1972). The seed ecophysiology of other genera remains unknown.

REPRODUCTIVE BIOLOGY. All except some dioecious *Anchietea* and *Melicytus* species produce bisexual flowers; most genera are presumably facultatively self-compatible, and perhaps occasional to frequent selfers through allogamy. The vast majority of species in *Viola* and at least one *Hybanthus* (*H. concolor*) produce cleistogamous flowers in addition to the normal chasmogamous ones and are at least intermittently autogamous. Studies of such species suggest that cleistogamy serves as an important stopgap measure to compensate for losses of outcrossed seeds during environmentally stressful periods (Redbo-Torstensson and Berg 1995). Contrary to theoretical expectations, fitness in *Viola canadensis* is not significantly reduced in plants derived from cleistogamous versus chasmogamous seeds, suggesting that high levels of selfing are tolerated well by this species (Culley 2000). Slight responses interpreted as low-level inbreeding depression occur in the offspring of cleistogamous flowers of other *Viola* species but this cost is likely outweighed by the lesser effort required to produce cleistogamous flowers (Redbo-Torstensson and Berg 1995).

PHYTOCHEMISTRY. Whereas hydrolysable tannins are absent from Violaceae, the occurrence of condensed tannins (proanthocyanin and proanthodelphinidin) in the leaves of very many species of the herbaceous genus *Viola* is remarkable (Hegnauer 1973). A wide variety of flavones, flavonols and related flavonoids and their derivatives have been isolated and identified in leaves of several *Viola* species particularly of the yellow-flowered subsect. *Nuttallianae* (Fabijan et al. 1987). Various volatile compounds have been isolated in leaves of *Viola odorata* (Cu et al. 1992), and violaxanthin esters have been shown to occur in *Viola tricolor* flowers (Hansmann and Kleinig 1982). Leaves and flowers harbor considerable quantities of acidic mucilage, which is typically found in epidermal cells. Many Violaceae thus far tested (e.g., *Hybanthus enneaspermus*, Anago et al. 2011) possess saponins and/or alkaloids, flavonoids, and often resinous secretory cells with yellowish to brownish contents. Methyl salicylate has been identified in rhizomes of the pansies *Viola arvensis* and *V. bicolor* (Hayden and Clough 1990) as well as the branchlets of *Rinorea*, and pentacyclic triterpenes as well as putatively anti-allergic aliphatic hydrocarbons and methyl esters of fatty acids have been extracted from *Anchietea salutaris* (= *A. pyrifolia*) (Di Stasi et al. 1999). Unfortunately, the chemistry of the Violaceae has never raised much interest; the basalmost woody genera have been neglected in this respect, and the nature of the alkaloids of the family appears to remain unknown.

Aluminum accumulation is known to occur in *Allexis* and *Amphirrhox* (Chenery 1948), and nickel uptake has been demonstrated in New Caledonian *Agatea deplanchei* (Jaffré 1980), in Australian and South Pacific *Hybanthus* species (Severne and Brooks 1972; Cole 1973; Jaffré and Schmid 1974; Brooks et al. 1974, 1977a; Kelly et al. 1975; Lee et al. 1977), in Indo-Malayan *Rinorea bengalensis* (Brooks and Wither 1977) and *R. javanica* (Brooks et al. 1977b), and accumulation of zinc and other heavy metals is done by *Viola calaminaria* (Jedrzejczyk et al. 2002) and other European pansies, as well as by the New World *V. cuneata* (Reeves et al. 1983).

Cyclopeptides were first detected and isolated as metabolites earlier in the last century and later ascribed a role in plant defense (Craik 1999). Their recently recognized medical promise, with some types showing high levels uterotonic, anti-HIV, antimicrobial and insecticidal activity, has catalyzed intensive scrutiny by phytochemists to determine their taxonomic distribution across families and lineages of angiosperms as well as their overall diversity. These proteins are especially abundant in the Cucurbitaceae, Rubiaceae and Violaceae (see review by Craik 2010). A population- and species-level study of cyclopeptides in Australian *Hybanthus* demonstrated that the distribution of characterized proteins correlated well with morphological similarity of species and characterized 246 new proteins in this class, bringing the total for the family to more than 9,000 types (Simonsen et al. 2005).

Subdivision of the Family. The Violaceae are currently subdivided into three subfamilies, the Fusispermoideae (with *Fusispermum*), the Leonioideae (with *Leonia*), and the Violoideae (with the remaining 20 genera). Subfamily Violoideae consists of two tribes, with an approximately equal number of genera in each. Tribe Rinoreeae bears more or less actinomorphic or very scarcely zygomorphic flowers, and the staminal glands lack any further elaboration, although they may be fused to each other or to any existing filaments. Tribe Violeae possesses distinctly zygomorphic, saccate or spurred flowers, with two staminal glands elaborated to form nectaries, which may be free or conjoined. Due primarily to the efforts of Hekking and others with the actinomorphic woody genera, tribe Rinoreeae has been divided further into subtribes, principally on the basis of androecial characters. Relatively little change has taken place since de Candolle's time (De Candolle 1844), aside from the addition of new genera and further grouping of genera into an intrafamilial framework. The only comprehensive treatment of genera in the family and their relationships has been that by Melchior (1925a, 1925b). The classification presented below follows that of Hekking (1988b), who provided the most recent research on many Neotropical woody genera and gave a useful synopsis of the family in his treatment on *Rinorea* and *Rinoreocarpus*. Newly described or recognized genera have been inserted in their most logical positions based on morphological characters.

Recently initiated cladistic studies using morphological and anatomical characters (Ballard et al., unpubl.) support basal positions for subfamilies Leonioideae and Fusispermoideae, and place some genera of tribe Rinoreeae basal to those of tribe Violeae except for *Isodendrion*, which is embedded within a clade of Neotropical *Hybanthus*, and *Melicytus*, which is associated with zygomorphic genera. However, the relationships among genera are evidently more complex than the simplistic portrayal implied by the traditional classification. Molecular phylogenies from plastid DNA *trn*L intron, *trn*L–*trn*F spacer and *rbc*L sequences (Tokuoka 2008; Wahlert et al., accepted) are congruent in revealing several independent derivations of zygomorphic-flowered genera from within broader actinomorphic lineages, dramatic polyphyly in *Hybanthus* and *Rinorea* suggesting the need to distinguish an additional 10 lineages as recognized genera, and *Gloeospermum* and *Leonia* as sister taxa in a non-basal clade. Recent comparative anatomical and micromorphological studies of *Fusispermum*, *Rinorea* and other basal groups have supported molecular systematic inferences on relationships and provided their own additional illumination on the distinctive taxonomic and phylogenetic status of Hekking's "Apiculatae" group as a small transitional lineage between the first-mentioned genera (Hoyos Gomez 2011). Although macromorphological, micromorphological, anatomical and palynological research proceeds apace across the family to characterize each distinct genus and clade more precisely, it is premature to segregate the several additional genera deserving of formal recognition.

AFFINITIES. On morphological and embryological grounds, among them salicoid teeth, parietal placentation and a primitive actinomorphic pentamerous floral condition, Violaceae have traditionally been allied with a number of other "Parietalean" families including Passifloraceae (now including Malesherbiaceae and Turneraceae) and Salicaceae (including Flacourtiaceae in part). All recent molecular data (Wurdack and Davis 2009; Korotkova et al. 2009; Xi et al. 2012) support this broader assemblage with the addition of *Goupia*, now segregated from Celastraceae into its own family (Goupiaceae). Results from numerous plastid sequences by Xi et al. (2012) show an unexpected sister relationship between Goupiaceae and Violaceae, with this clade sister to one containing Salicaceae s.l. (including Scyphostegiaceae, Samydaceae and Lacistemataceae) and Passifloraceae s.l. The violet family (plus Goupiaceae) is nevertheless relatively isolated and divergent from other higher Rosidae from a morphological and molecular standpoint.

DISTRIBUTION AND HABITATS. The family as a whole is nearly cosmopolitan, owing primarily to the widely distributed genus *Viola*. Generally, phylogenetically basal genera occupy low-elevation wet or dry forests, whereas more derived genera range into a greater diversity of habitats, often reaching higher elevations, temperate or boreal latitudes and more extreme environmental conditions. Except for a few *Hybanthus* and *Viola*, nearly all members of the family are restricted to subtropical and tropical regions. The three largest genera, *Viola*, *Rinorea* and *Hybanthus* are found in both the New and Old Worlds and represent approximately 93% of the species diversity (ca. 1,020 species) in the family. Whereas species of *Rinorea* worldwide are relatively restricted to lower elevation humid or seasonally dry forests, representatives of *Hybanthus* and *Viola* are found in a wide range of habitats, with the latter ranging from snowmelt lines of permanent glaciers above 6,000 m down to mid-elevation cloud forests at 1,200 m or in low-elevation deserts in both the New and Old World. Centers of species diversity lie in the Amazon Basin, Indonesia, western Africa and Madagascar for *Rinorea*; in central Mexico, northern South America and Australia for *Hybanthus*; and in the Andes, central Mexico, Rocky Mountains and Appalachians of North America, mountainous Asia and southwestern Europe for *Viola*. Of the remaining genera, five are confined to the Old World: *Allexis* and *Decorsella* inhabit seasonally dry forests of western Africa, and *Agatea* and *Melicytus* are distributed in monsoon forests and coastal or montane habitats, respectively, in the South Pacific region. The remaining 15 genera are Neotropical, with *Amphirrhox*, *Calyptrion*, *Fusispermum*, *Gloeospermum*, *Leonia*, *Orthion* and *Paypayrola* found in both Mesoamerica and South America (all but *Orthion* best represented in South America); *Mayanaea* restricted to Guatemala in Mesoamerica; and *Anchietea*, *Hekkingia*, *Hybanthopsis*, *Noisettia*, *Rinoreocarpus* and *Schweiggeria* confined to South America. Most Neotropical genera inhabit low-elevation rainforests or the low montane slopes delimiting the Amazonian basin.

Exceptionally, *Viola* in the tropics often reaches exceedingly high altitudes, and in the Andes of South America reaches its greatest species diversity and its most divergent morphologies in the Western Hemisphere.

ECONOMIC IMPORTANCE. Certain *Viola* species are cultivated and bred as ornamentals, but many more wild species have been distributed as novelties for specialty gardeners. Flowers of commonly cultivated *Viola odorata* and a few wild species are used for condiments, jellies and syrups, and candies (see MacNicol 1967). Young leaves of various *Viola* species are occasionally eaten as a potherb rich in vitamin C, and syrup from the flower has been used medicinally. Fresh leaves of *Leonia glycycarpa* have been used in bird-lime.

CONSERVATION. Several polytypic genera (*Agatea*, *Hybanthus*, *Rinorea* and *Viola*) harbor narrowly endemic species, some of which are threatened with extinction; in some cases these are protected in nature reserves or on municipal or federal lands. Some *Rinorea* species in Madagascar are now believed extinct (e.g., *R. microphylla*, *R. verticillata*). All species in the endemic Hawaiian genus *Isodendrion* are now imperiled and are currently listed as "threatened" or "endangered" at the state and federal levels. A few genera are also highly localized in distribution, e.g., *Mayanaea* has not been collected around Lake Izabal in Guatemala for decades, and *Hybanthopsis* is known from a small area of Bahia state in easternmost Brazil.

KEY TO THE GENERA

1. Flowers and capsules to 2 mm long; connective of stamens lacking a dorsal scale but bearing a broad ventral scale; seeds of two types, spindle-shaped or discoid **1. *Fusispermum***
– Flowers or capsules longer than 2 mm; connective of stamens usually bearing a well-developed dorsal scale (rudimentary in *Isodendrion*, *Melicytus* and *Rinoreocarpus*, absent in *Hekkingia*, *Leonia* and *Paypayrola*), lacking a broad ventral scale; (*Rinorea* sometimes with a linear or bicuspidate process); seeds uniformly globose to obovoid, or strongly flattened 2

2. Filaments fused into a tall tube much longer than the anthers, anthers sessile; connective of stamens lacking a dorsal scale 3
– Filaments fused into a short continuous or intermittent tube distinctly shorter than the anthers, with anthers borne on a free portion of filament, or anthers sessile on receptacle; connective of stamens with a rudimentary to well-developed dorsal scale, this broadly attached to the apex in most genera (extending down the sides in most *Rinorea*) 5

3. Leaves pellucid- or dark-punctate; thecae of anthers horizontal **2. *Leonia***
– Leaves lacking punctae. Thecae of anthers slanting 4

4. Inflorescence a basally cauliflorous long-pedicellate raceme; bracts subtending pedicels persistent, deeply emarginate; capsule tuberculate **11. *Hekkingia***
– Inflorescence a ramiflorous (cauliflorous) spicate raceme; bracts subtending pedicels deciduous, acute; capsule smooth **12. *Paypayrola***

5. Corolla actinomorphic or weakly to distinctly zygomorphic, all petals similar in size or different but one not substantially larger and dramatically different in shape than the others, nor conspicuously saccate or spurred at base; staminal glands never elaborated into prolonged nectarines 6
– Corolla strongly zygomorphic, at least one petal ("bottom" petal) considerably longer or shorter than the others and conspicuously saccate or spurred; two staminal glands commonly prolonged or differentiated into nectaries enclosed by sac or spur 13

6. All petals essentially or quite identical 7
– One petal slightly differently shaped from the others, gradually or abruptly expanded in the apical half, commonly clawed 12

7. Fruit a three-valved capsule 8
– Fruit a berry 11

8. Corolla white to violet or yellow, very rarely pink 9
– Corolla red to red-orange 10

9. Inflorescence various but not a short shoot with a solitary flower; dorsal connective appendage of stamens conspicuous, completely covering top, and often sides, of stamen **3. *Rinorea***
– Inflorescence a short shoot with a solitary flower; dorsal connective appendage of stamens a small prickle or lacking **9. *Isodendrion***

10. Petals porrect or weakly spreading; dorsal connective appendage a tiny linear or deltoid prickle tipping the stamen; seeds not arillate **4. *Rinoreocarpus***
– Petals strongly reflexed; dorsal connective appendage of stamens large, completely covering top of stamens; seeds arillate **6. *Allexis*** (most spp.)

11. Petals connivent with one petal clasping around others, rarely spreading at anthesis; dorsal connective appendage large and conspicous, commonly covering top of anthers completely; flowers strictly bisexual **5. *Gloeospermum***
– Petals widely spreading to recurved at anthesis; dorsal connective appendage a tiny slender prickle tipping the anthers; flowers bisexual or unisexual **8. *Melicytus***

12. Bottom petal emarginate at the apex; dorsal connective appendage a conspicuous linear prickle tipping the stamens; ovary persistent in maturing fruit, enclosing seeds **10. *Amphirrhox***

- Bottom petal narrowly rounded at apex; dorsal connective appendage ovate, completely covering top of anthers; ovary disintegrating early, seeds maturing naked on spreading placental traces **7. *Decorsella***

13. Bottom petal saccate or with very short cylindrical spur, the blade at least one and one-third times longer than lateral and upper petals, commonly much longer, often distinctly differentiated into a claw and abruptly expanded blade 14
- Bottom petal distinctly spurred or greatly distended and gibbous at base, the blade slightly longer or shorter than lateral and upper petals, not strongly differentiated into a claw and blade 17

14. Plant a liana or scandent shrub; seeds moderately to strongly flattened, bordered by one or two roughened ridges or a wing 15
- Plant a tree, treelet, erect shrub or herb; seeds obovoid to globose, lacking ridges or wings 16

15. Liana or scandent shrub; capsule thick-walled and firm, dehiscing by 3 or 6 sutures; seeds strongly flattened, encircled by an interrupted or broad membranous wing **16. *Agatea***
- Twining herb; capsule thin-walled and elastic, dehiscing by 1 suture; seeds obovoid, with a pair of lateral expansions only at base **15. *Hybanthopsis***

16. Plant a full-sized tree; inflorescence a long-pedunculate compound cyme; capsule usually tuberculate **13. *Orthion***
- Plant a herb or shrub (a treelet); inflorescence a raceme, simple cyme, fascicle or solitary flower, rarely a short-pedunculate compound cyme; capsule smooth **14. *Hybanthus***

17. Plant a herb, rarely a subshrub or shrub; pedicels not articulated; sepals auricled at base **22. *Viola***
- Plant a tree, liana or shrub; pedicels articulated; sepals not auricled at base 18

18. Plant a liana or scandent shrub; seeds strongly flattened (with an intermittent or broad, entire or erose wing in *Anchietea*) 19
- Plant an erect shrub or tree; seeds obovoid to globose, lacking a wing 20

19. Spur less than one-half as long as petal blades; capsule very thin-walled, bladder-like; seed margins bearing an intermittent or rudimentary to broad wing **18. *Anchietea***
- Spur at least twice as long as the petal blades; capsule thick-walled, firm and semi-dehiscent; seed margins lacking a wing **19. *Calyptrion***

20. Plant a tree or treelet; spur under 3 mm long 21
- Plant a shrub; spur 5–20 mm long 22

21. Flowers ramiflorous, in a long-pedunculate compound cyme, glabrous within; bottom petal with short, cylindrical spur; capsule unspotted **17. *Mayanaea***
- Flowers cauliflorous, in a fascicle, heavily pubescent within; bottom petal with hugely distended gibbous spur; capsule red-spotted **6. *Allexis* (*A. zygomorpha*)**

22. Sepals uniformly linear-lanceolate; spur slender, less than 2 mm thick; corolla orange with yellow throat, persistent into fruit **21. *Noisettia***
- Three sepals much larger and broader than the other two, ovate-triangular; spur stout, 4–8 mm thick; corolla white, caducous **20. *Schweiggeria***

GENERA OF VIOLACEAE

I. SUBFAM. FUSISPERMOIDEAE Hekking (1984).

Corolla aestivation in bud convolute; stamens 3, filaments weakly connate, dorsal connective appendage lacking, ventral appendage present; fruit a three-valved capsule; seeds discoid or fusiform.

1. *Fusispermum* Cuatrec.

Fusispermum Cuatrec., Fieldiana Bot. 27: 94 (1950); Hekking, Proc. Kon. Ned. Akad. Wetensch. C 87: 121–130 (1984).

Trees; leaves oblanceolate. Flowers in axillary paniculate cymes or pseudoracemes; corolla white, actinomorphic; stamens 5, filaments weakly connate, dorsal connective appendage absent; pistil 3(4)-carpellate, style filiform. Fruit a thick-walled 3-valved capsule. Seeds 30–50 per carpel, fertile seeds fusiform, sterile ones discoid.

Three spp., southern Central America, northern South America.

II. SUBFAM. LEONIOIDEAE Melch. (1925).

Corolla aestivation in bud imbricate or quincuncial per Hekking (1988b); stamens 3 or 5, fused into a tall tube, dorsal connective appendage lacking; fruit a nut or berry; seeds oblong-ovoid.

2. *Leonia* Ruiz & Pav. Fig. 70

Leonia Ruiz & Pav., Fl. peruv. 2: 69 (1799).

Trees; leaves oblanceolate. Flowers in short-pedunculate, cauliflorous or ramiflorous compound cymes or racemoids, actinomorphic; corolla yellow to orange; thecae oriented horizontally and dehiscing laterally ("apically"); pistil 3–5-carpellate, style filiform. Fruit a nut with thick woody pericarp, one sp. (*L. glycycarpa*) with thin juicy pericarp (a "berry"). Seeds numerous per carpel, oblong-ovoid. Chromosome number unknown.

Five to six spp., southern Central America, northern South America.

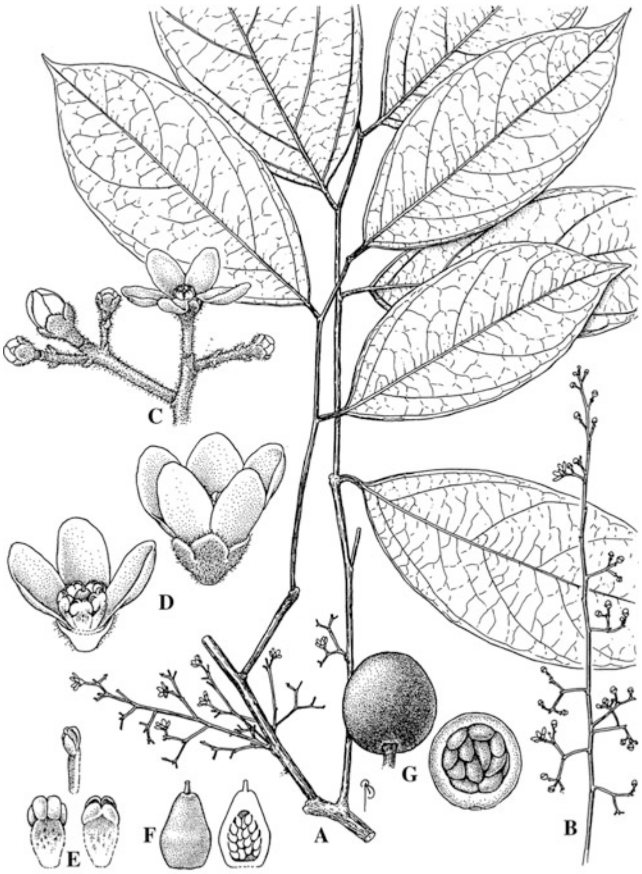

Fig. 70. Violaceae. *Leonia glycocarpa* var. *glycocarpa*. **A** Branchlet with inflorescence. **B** Part of inflorescence. **C** Detail thereof. **D** Flowers, at left two petals removed. **E** Lateral, adaxial and abaxial views of stamens. **F** Pistil in lateral view and vertically sectioned. **G** Fruit, entire and sectioned. (Reproduced with kind permission of the artist Bobbi Angell)

III. SUBFAM. VIOLOIDEAE Burnett (1835).

Leaves alternate or sometimes in pseudo-whorls, or sometimes opposite in *Rinorea*; bud aestivation mostly apotact sensu Hekking (1988b), sometimes imbricate in *Gloeospermum*; dorsal connective appendage commonly large, linear to deltoid-ovate, entire to lacerate, but obsolete in *Paypayrola*, inconspicuous or obsolete in *Isodendrion*; fruit a thick-walled 3-valved dry capsule in most genera, very rarely a fleshy 3-valved capsule in *Rinorea*, a paper-thin "bladder" in *Anchietea*, a thin-walled follicle in *Hybanthopsis*, or berry in *Gloeospermum* and *Melicytus*; seeds narrowly ovoid to globose, or flattened in a few lianescent genera.

1. Tribe Rinoreeae Reiche & Taub.

Corollas actinomorphic or weakly zygomorphic, lacking a spur and calcarate stamens; filaments weakly to strongly connate or stamens fused into a tube (*Hekkingia*, *Paypayrola*), dorsal connective appendage entire or erose to lacerate, thecae vertically oriented (diagonally on tube in *Hekkingia* and *Paypayrola*), dehiscing introrsely (laterally in *Hekkingia* and *Paypayrola*).

1a. Rinoreeae subtribe Rinoreinae Melch. (1925).

3. *Rinorea* Aubl. Fig. 71

Rinorea Aubl., Hist. pl. Guiane 1: 235 (1775), nom. cons.; Hekking, Fl. Neotrop. 46 (1988b).
Alsodeia Thouars (1806).

Trees, treelets or shrubs; leaves alternate or opposite, linear to orbicular leaves. Flowers in axillary compound cymes, racemoids, short-pecunculate compound cymes, fascicles or solitary; corolla white to yellow, scarcely to notably zygomorphic with one petal scarcely to somewhat longer, sometimes this and nearest petals also somewhat different in shape from the remaining pair; filaments weakly to strongly connate, dorsal connective appendage large, linear-oblong to ovate, entire or erose to lacerate; style filiform to rostellate. Capsule smooth to tuberculate or scaly thick-walled. Seeds 1–4 per carpel, globose to obovoid. $2n = 24, 48$.

230–280 spp., pantropical.

4. *Rinoreocarpus* Ducke

Rinoreocarpus Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 144 (1925); Hekking, Fl. Neotrop. (1988b).

Trees or treelets with oblong-lanceolate leaves. Flowers in axillary, short-pedunculate compound cymes; corolla caducous, reddish-orange, actinomorphic; filaments free, dorsal connective appendage small, apiculate; style truncate. Fruit a thick-walled three-valved capsule. Seeds 2–4 per carpel, obovoid.

One sp., *R. ulei* (Melch.) Ducke, northern South America.

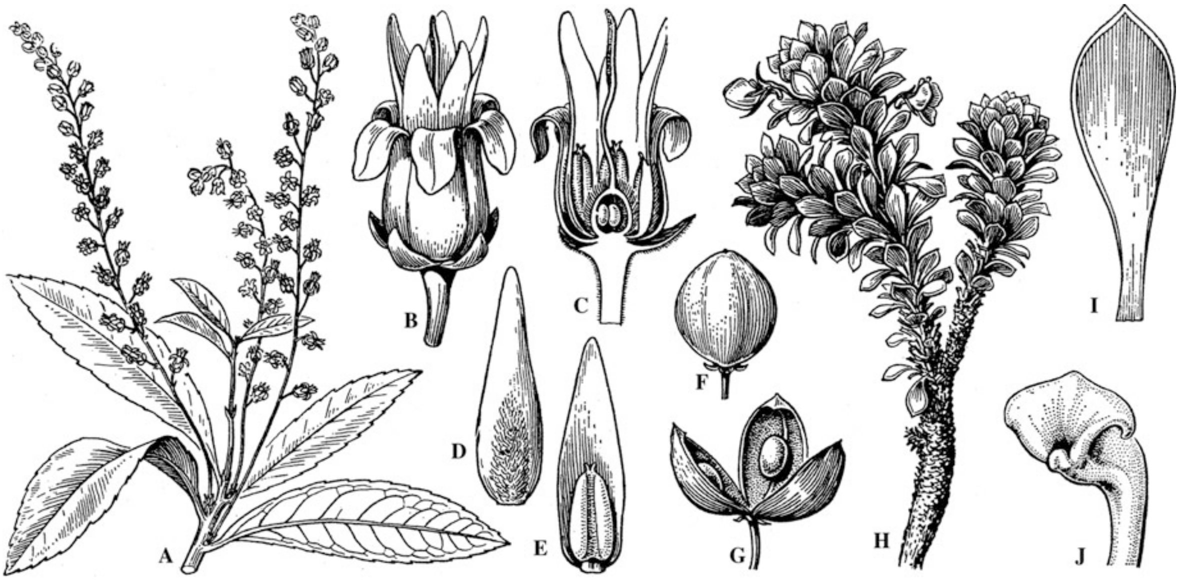

Fig. 71. Violaceae. *Rinorea physiphora*. **A** Flowering branch. **B** Flower. **C** Same, vertically sectioned. **D** Abaxial view of petal with nectary. **E** Same adaxially, with stamen. **F** Capsule. **G** Same, dehisced. *Viola cotyledon*. **H** Habit. **I** Leaf. **J** Stigma with orifice. (Takhtajan 1981)

5. ***Gloeospermum*** Triana & Planch. Fig. 72

Gloeospermum Triana & Planch., Ann. Sci. Nat. IV, 17: 128 (1862).

Trees or treelets; leaves (oblong-)lanceolate. Flowers in axillary short-pedunculate compound cymes, fascicles or solitary; corolla caducous or briefly persistent, white, essentially actinomorphic; filaments weakly to strongly connate, dorsal connective appendage large, deltoid to oblong, erose to lacerate; style filiform. Fruit a dryish fleshy berry. Seeds 7–22 per carpel, globose.

About 12 spp., Central America, northern South America.

6. ***Allexis*** Pierre

Allexis Pierre, Bull. Soc. Linn. Paris II, 1: 25 (1898).

Treelets or shrubs; leaves pseudo-whorled, oblanceolate. Flowers in compound, cauliflorous cymes; floral forms of two dramatically different types: a) corolla nearly actinomorphic with petals narrowly lanceolate and reflexed, stamens erect and exserted, dorsal connective appendages large, linear-attenuate, entire; or b) corolla hypocertoid, stamens short and included, dorsal connective appendages short, ovate, erose (*A. zygomorpha*); corolla in all cases pink to red; filaments free; style filiform. Capsule thick-walled. Seeds 1–2 per carpel, obovoid, arillate.

Ca. four spp., W Africa.

7. ***Decorsella*** A. Chev.

Decorsella A. Chev., Bull. Soc. Bot. Fr. 61, Mém. 8: 297 (1917).

Gymnorinorea Keay (1953).

Treelets or shrubs; leaves oblanceolate. Flowers in axillary, short-pedunculate compound cymes; corolla yellow to reddish, slightly zygomorphic, one petal slightly longer and distinctly widened distally; filaments strongly connate, dorsal connective appendage large, ovate, apical and lateral, entire; style filiform; ovary wall disintegrating early, leaving seeds to mature naked on spreading placental traces. Seeds 1–2 per placenta, drupe-like with thin fleshy testa, globose. $2n = 20$.

One sp., *D. paradoxa* A. Chev., W Africa.

1b. Rinoreeae subtribe Hymenantherinae Melch. (1925).

8. ***Melicytus*** J.R. Forst.

Melicytus J.R. Forst., Char. Gen.: 123, t. 62 (1776).

Hymenanthera R. Brown (1818).

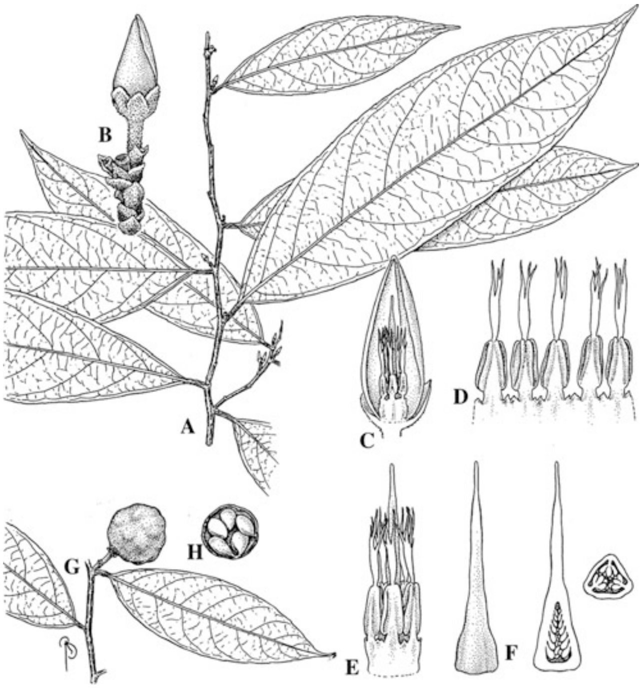

Fig. 72. Violaceae. *Gloeospermum sphaerocarpum*. **A** Branchlet with flower buds. **B** Part of inflorescence with flower bud. **C** Flower, two petals removed. **D** Adaxial view of upper part of androecium opened out; note laciniate connective extensions on apices of anthers. **E** Androecium surrounding the gynoecium. **F** Pistil with medial transverse section of the ovary. **G** Part of branch with dried fruit. **H** Fruit in transverse section showing parietal attachment of seeds. (Reproduced with kind permission of the artist Bobbi Angell)

Treelets or shrubs; leaves alternate or pseudowhorled, linear to ovate; branches occasionally thorny. Flowers unisexual or bisexual, in ramiflorous, rarely caulifolorous racemoids, fascicles or solitary; corolla white or yellow to blue, actinomorphic; filaments strongly connate, dorsal connective appendage large, deltoid to oblong-ovate and lacerate in bisexual flowers (lacking in unisexual ones); style filiform to trilobate. Fruit a juicy berry. Seeds 2–3 per carpel, obovoid. $2n = 32, 64, 96$.

Ca. 10 spp., Australia, New Zealand, South Pacific islands.

1c. Rinoreeae subtribe Isodendriinae Melch. (1925).

9. *Isodendrion* A. Gray

Isodendrion A. Gray, Proc. Am. Acad. 2: 324 (1852).

Treelets to shrubs; leaves lanceolate to ovate. Flowers solitary in axillary short shoots; corolla caducous, blue, weakly zygomorphic, petals prolonged into a "tube" with bottom petal slightly longer than others and weakly differentiated, scarcely saccate at base; filaments free, anthers dehiscing laterally, dorsal connective appendage a minute prickle or obsolete; style filiform or rostellate. Capsule thick-walled. Seeds 2(–4) per carpel, obovoid. $2n = 16$.

Four to ten spp., Hawaiian Islands.

1d. Rinoreeae subtribe Paypayrolinae Melch. (1925).

10. *Amphirrhox* Spreng.

Amphirrhox Spreng., Syst. veg.: 51 (1827).
Spathularia A. St.-Hil. (1824), non *Spathularia* Pers. (1797).

Trees, treelets or shrubs; leaves oblanceolate, alternate at branch tips, opposite below. Flowers in subterminal or terminal long-pedunculate simple cymes, rarely in compound cymes; corolla white, actinomorphic, one petal twice as broad as others, differentiated into claw and blade and emarginate; filaments weakly connate, dorsal connective appendage large, linear, entire; style filiform. Capsule thick-walled, tuberculate. Seeds 3–6 per carpel, obovoid.

One sp., *A. longifolia* (A. St.-Hil.) Spreng., Mesoamerica, northern South America.

11. *Hekkingia* H.E. Ballard & Munzinger

Hekkingia H.E. Ballard & Munzinger, Syst. Bot. 28: 345 (2003).

Trees or shrubs; leaves lanceolate to oblanceolate. Flowers in long-pedicellate racemoids, basally cauliflorous; corolla yellow, actinomorphic, one petal scarcely broader than others, all petals emarginate, spreading to strongly recurving; filaments connate into a tall tube with anther tissue distinct, dorsal connective minute and apiculate, thecae oriented diagonally on tube and dehiscing laterally; style filiform. Capsule strongly tuberculate, thick-walled. Seeds 5–8 per carpel, obovoid, arillate.

One sp., *H. bordenavei* H.E. Ballard & Munzinger, northern Brazil, French Guiana.

12. ***Paypayrola*** Aubl.

Paypayrola Aubl., Hist. pl. Guiane 1: 249 (1775).

Trees or shrubs; leaves lanceolate to oblanceolate. Flowers in axillary or terminal spiciform racemoids; corolla white to yellow, actinomorphic, one petal twice as broad as others, differentiated into claw and blade and emarginate; filaments connate into a tall tube continuous with anther tissue, dorsal connective minute or obsolete, thecae slanting and dehiscing laterally; style filiform. Capsule smooth, thick-walled. Seeds 5–8 per carpel, globose.

Eight spp., southern Central America, northern and eastern South America.

2. **Tribe Violeae** Reiche & Taub.

Corollas weakly to strongly zygomorphic, the anterior ("bottom") petal distinctly longer than others, commonly shorter in *Viola*, weakly to strongly differentiated from the others, saccate or inflated into a spur at the base; filaments free or scarcely connate, either all stamens distinct and with separate glands at the summit of their filaments, or the bottom two stamens only with a separate gland each on the filament or the bottom of the connective (or both), or the glands fused to form one ridge or shield-like structure across the base of the two stamens; thecae vertical, dehiscing introrsely; dorsal connective appendage large, entire; seeds narrowly ovoid to obovoid or globose, strongly flattened in *Agatea*, *Anchietea*, *Calyptrion* and *Hybanthopsis*, then with a membranous wing or ridge in many species.

2a. **Violeae subtribe Hybanthinae** Melch. (1925).

13. ***Orthion*** Standl. & Steyerm.

Orthion Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 249 (1940)

Treelets to shrubs; leaves lanceolate to oblanceolate. Flowers in terminal, long-pedunculate compound cymes; corolla white, weakly zygomorphic, bottom petal slightly longer than others and somewhat differentiated, bottom petal saccate at base; filaments weakly to strongly connate (occasionally entire stamens connate), dorsal connective appendage large, oblong-ovate, entire; style rostellate. Capsule thick-walled, typically tuberculate. Seeds 3 per carpel, broadly obovoid.

Six spp., Mesoamerica and northern South America.

14. ***Hybanthus*** Jacq.

Hybanthus Jacq., Enum. Pl. Carib.: 2 (1760).

Treelets, shrubs or herbs; leaves alternate to opposite, linear to orbicular; branches occasionally thorny or very rarely twining. Flowers in axillary racemoids, simple cymes or solitary, rarely in short-pedunculate compound cymes or fascicles; corolla greenish-white to white, yellow or blue, the throat commonly yellow to orange within, weakly zygomorphic with bottom petal slightly longer and scarcely differentiated, or strongly zygomorphic with bottom petal much longer and differentiated into claw and blade, bottom petal saccate at base; filaments free or rarely strongly connate, dorsal connective appendage large, oblong-ovate, entire; style filiform. Capsule thick-walled. Seeds 1–several per carpel, narrowly ovoid to globose, rarely with a small (non-functional?) aril. $2n = 8$, 12, 16, 24, 32, 48.

Ca. 120 spp., most pantropical, desert SW North America (three spp.), temperate E North America (one sp.).

15. ***Hybanthopsis*** Paula-Souza

Hybanthopsis Paula-Souza, Brittonia 55: 210 (2003).

Twining herbs; leaves ovate-lanceolate. Flowers solitary; corolla violet, strongly zygomorphic, bottom petal very large and differentiated into claw and blade, saccate at base; filaments weakly connate, two lowest anthers weakly calcarate, dorsal connective appendage large, oblong-ovate, entire; style filiform-rostellate. Fruit thin-walled, elastic, "follicle" dehiscing by only one longitudinal suture. Seeds several per carpel, obovoid with a pair of basal-lateral expansions.

One sp., *H. bahiensis* Paula-Souza, eastern Brazil.

16. ***Agatea*** A. Gray

Agatea A. Gray, Proc. Am. Acad. 2: 323 (1852).

Lianas or reclining shrubs; leaves lanceolate to ovate. Flowers in terminal pseudo-racemes or racemoids; corolla white, strongly zygomorphic, bottom petal very large and differentiated into claw and blade, saccate at base; filaments weakly connate, two lowest anthers weakly calcarate, dorsal connective appendage large, oblong-ovate, entire; style filiform to clavate. Capsule thin- to thick-walled, 3(6)-valved. Seeds 2–several per carpel, strongly flattened with broad thin wing. $2n = 16$.

Ca. eight spp., New Guinea, S Pacific islands.

17. *Mayanaea* Lundell

Mayanaea Lundell, Wrightia 5: 58 (1974).

Trees; leaves lanceolate. Flowers in terminal, long-pedunculate compound cymes; corolla blue to white, strongly zygomorphic, bottom petal much longer than others and differentiated into a claw and blade, spur well exserted; filaments weakly connate, two lowest stamens calcarate, dorsal connective appendage large, oblong-ovate, entire; style filiform. Capsule thick-walled. Seeds 1–2 per carpel, broadly obovoid.

One sp., *M. caudata* (Lundell) Lundell, Guatemala.

2b. Violeae subtribe Violinae Melch. (1925).

18. *Anchietea* A. St.-Hil. Fig. 73

Anchietea A. St.-Hil., Ann. Sci. Nat. I, 2: 252 (1824).

Lianas or reclining shrubs; leaves oblong-lanceolate to ovate. Flowers unisexual or bisexual, in axillary racemoids or fascicles; corolla white to orange, strongly zygomorphic, bottom petal longer than others and weakly differentiated, spur well exserted; filaments strongly connate, two lowest stamens calcarate, dorsal connective appendage small, ovate, entire; style rostellate. Capsule very thin-walled, bladder-like. Seeds many per carpel, orbicular in outline, strongly flattened and encircled by a low interrupted ridge or uniformly broad wing.

Five spp., South America.

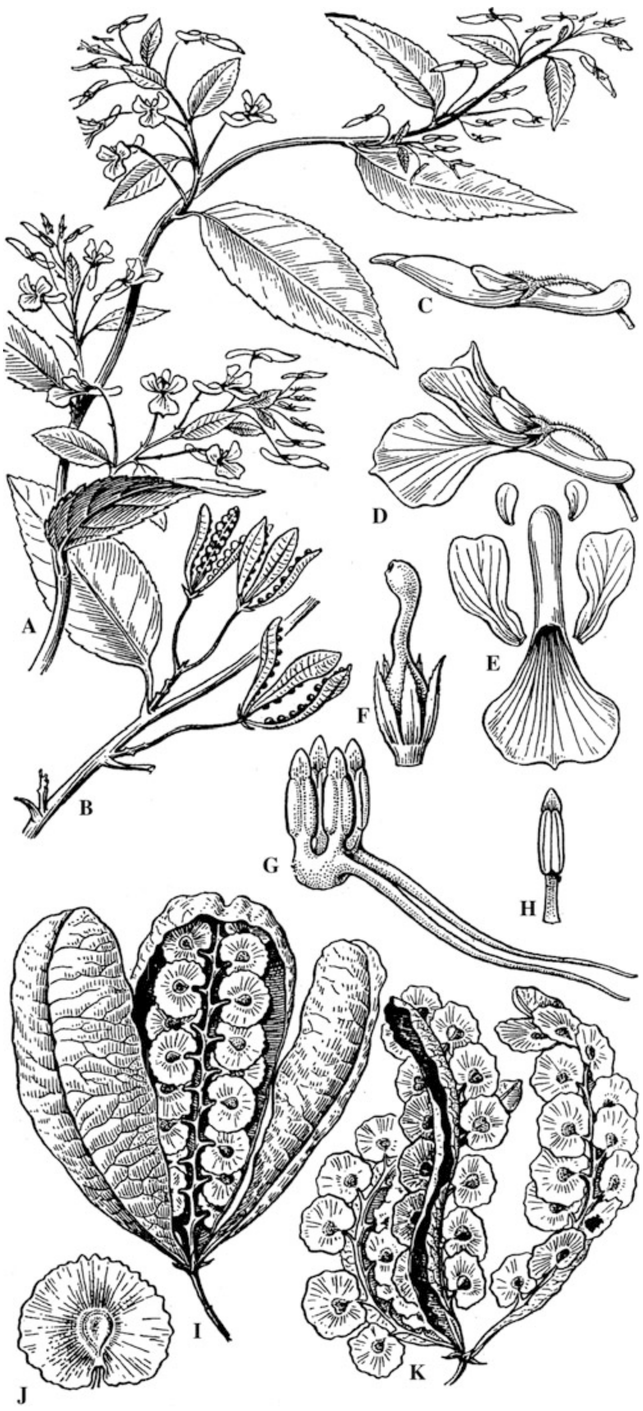

Fig. 73. Violaceae. *Anchietea pyrifolia*. **A** Flowering branch. **B** Fruiting branchlet with torn capsule valves. **C** Floral bud. **D** Flower. **E** The petals: 2 small posterior ones, 2 clawed lateral ones, and the anterior spurred one. **F** Gynoecium with calyx. **G** Androecium, the two anterior stamens calcarate. **H** Adaxial view of stamen. **I** Capsule, with seed maturation continuing when valves are torn. **J** Seed. *A. pyrifolia* var. *pyrifolia*. **K** Capsule, the bladder-like valves withered but seed maturation continues. (Takhtajan 1981)

19. *Calyptrion* Ging.

Calyptrion Ging., Mém. Viol.: 5 (1822).

Corynostylis Mart. & Zucc., Nov. Gen. Sp. Pl. 1: 25–26 (1824).

Lianas; leaves oblong-lanceolate to ovate. Flowers in axillary or terminal racemoids, rarely solitary; corolla white, strongly zygomorphic, bottom petal slightly longer than others and weakly differentiated, spur very long; filaments free, two lowest stamens calcarate, dorsal connective appendage large, oblong-ovate, entire; style filiform. Capsule thick-walled, semi-dehiscent. Seeds numerous per carpel, asymmetrically orbicular in outline, strongly flattened.

Four spp., Mesoamerica, South America.

20. *Schweiggeria* Spreng.

Schweiggeria Spreng., Neue Entdeck. 2: 167 (1821).

Shrubs; leaves oblanceolate. Flowers in axillary fascicles, rarely solitary; corolla caducous, white, strongly zygomorphic, bottom petal longer than others, clawed, spur well exserted; filaments free, two lowest stamens calcarate, dorsal connective appendage large, oblong-ovate, entire; style rostellate or lobed. Capsule thick-walled. Seeds 3 per carpel, obovoid.

One sp., *S. fruticosa* Spreng., eastern Brazil.

21. *Noisettia* Kunth

Noisettia Kunth in H.B.K., Nov. Gen. Sp. (quarto edn) 5: 382, t. 499b, f (1821).

Shrubs; leaves oblanceolate. Flowers in axillary fascicles; corolla initially persistent as a covering around fruit, orange with yellow throat, strongly zygomorphic, bottom petal much longer than others and clawed, spur very long; filaments free, two lowest stamens calcarate, dorsal connective appendage large, oblong-ovate, entire; style rostellate. Capsule thick-walled. Seeds 3–4 per carpel, obovoid, papillate.

One sp., *N. orchidiflora* (Rudge) Ging., northern and eastern South America.

22. *Viola* L.

Viola L., Sp. Pl.: 933 (1753).

Annual or perennial acaulescent or caulescent herbs, shrubs or very rarely treelets; leaves linear to reniform. Flowers axillary and solitary, rarely in cymes; corolla white to yellow, orange or blue or multicolored with or without yellow throat, strongly zygomorphic, bottom petal slightly to much shorter than others and weakly differentiated, spur scarcely exserted to very long; filaments free, two lowest stamens calcarate, dorsal connective appendage large, oblong-ovate, entire; style filiform or clavate and globose to rostellate at tip. Capsule thick-walled. Seeds few to many per carpel, obovoid to globose, typically arillate. $2n = 10, 12, 14, 16, 18, 20, 22, 24, 26, 32, 34, 36, 40, 44, 46, 48, 52, 54, 58, 60, 70, 72, 74, 80, 100, 104, 128$.

Ca. 525 spp., temperate regions and montane areas in the tropics worldwide.

Selected Bibliography

Achoundong, G., Onana, J.-M. 1998. *Allexis zygomorpha* (Violaceae): a new species from the littoral forest of Cameroon. Kew Bull. 53: 1009–1010.

Anago, E., Lagnika, L., Gbenou, J., Loko, F., Moudachirou, M., Sanni, A. 2011. Antibacterial activity and phytochemical study of six medicinal plants used in Benin. Pakistan J. Biol. Sci. 14: 449–455.

Arnal, C. 1945. Recherches morphologiques et physiologiques sur la fleur des Violacées. PhD dissertation, University of Dijon, Dijon.

Augspurger, C.K. 1980. Mass-flowering of a tropical shrub (*Hybanthus prunifolius*): influence on pollinator attraction and movement. Evolution 34: 475–488.

Augspurger, C.K. 1982. Reproductive synchrony of a tropical shrub: experimental studies on effect of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62: 775–788.

Ballard, H.E., Jr. 1996. Phylogenetic relationships and infrageneric groups in *Viola* (Violaceae) based on morphology, chromosome numbers, natural hybridization and Internal Transcribed Spacer (ITS) sequences. PhD dissertation, University of Wisconsin, Madison, WI.

Ballard, H.E., Jr., Sytsma, K.J. 2000. Evolution and biogeography of the woody Hawaiian violets (*Viola*, Violaceae): Arctic origins, herbaceous ancestry and bird dispersal. Evolution 54: 1521–1532.

Ballard, H.E., Jr., Sytsma, K.J., Kowal, R.R. 1999 ("1998"). Shrinking the violets: phylogenetic relationships of infrageneric groups in *Viola* (Violaceae) based on internal transcribed spacer DNA sequences. Syst. Bot. 23: 439–458.

Ballard, H.E., Cortes-Palomec, A.C., Feng, M., Wang, Y., Wyatt, S. 2011. The chasmogamous/cleistogamous mixed breeding system, a widespread and evolutionarily successful reproductive strategy in angiosperms. In: Thangadurai, D., C.A. Busso, M. Hijri (eds.) Frontiers in biodiversity studies. Bioscience Publications, Agrobios, India, pp. 16–41.

Baskin, J.M., Baskin, C.C. 1972. Physiological ecology of germination of *Viola rafinesquii*. Am. J. Bot. 59: 981–988.

Baskin, J.M., Baskin, C.C. 1975. Observations on the ecology of the cedar glade endemic *Viola egglestonii*. Am. Midl. Naturalist 93: 320–329.

Beattie, A.J. 1969. The floral biology of three species of *Viola*. New Phytol. 68: 1187–1201.

Beattie, A.J. 1970. Pollination mechanisms in *Viola*. New Phytol. 69: 343–360.

Beattie, A.J. 1974. Floral evolution in *Viola*. Ann. Missouri Bot. Gard. 61: 781–793.

Beattie, A.J., Lyons, N. 1975. Seed dispersal in *Viola* (Violaceae): adaptations and strategies. Am. J. Bot. 62: 714–722.

Bennett, E.M. 1972. A revision of the Australian species of *Hybanthus* Jacquin (Violaceae). Nuytsia 1: 218–241.

Beuzenberg, E.J. 1961. Observations on sex differentiation and cytotaxonomy of the New Zealand species of the Hymenantherinae (Violaceae). New Zealand J. Sci. 4: 337–349.

Braun, M., Dötterl, S., Schlindwein, C., Gottsberger, G. 2012. Can nectar be a disadvantage? Contrasting pollination natural histories of two woody Violaceae from the Neotropics. Int. J. Plant Sci. 173: 161–171.

Brooks, R.R., Wither, E.D. 1977. Nickel accumulation by *Rinorea bengalensis* (Wall.) O. K. J. Geochem. Explor. 7: 295–300.

Brooks, R.R., Lee, J., Jaffré, T. 1974. Some New Zealand and New Caledonian plant accumulators. J Ecol 62: 493–499.

Brooks, R.R., Wither, E.D., Zepernick, B. 1977a. Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. J. Geochem. Explor. 7: 49–77.

Brooks, R.R., Wither, E.D., Zepernick, B. 1977b. Cobalt and nickel in *Rinorea* species. Plant Soil 47: 707–712.

Chenery, E.M. 1948. Aluminium in the plant world. Part I. General survey in dicotyledons. Kew Bull. 3: 173–183.

Cole, M.M. 1973. Geobotanical and biogeochemical investigations in the sclerophyllous woodland and scrub associations of the eastern Goldfields area of western Australia with partial reference to the role of *Hybanthus floribundus* (Lindl.) F. Muell., a nickel indicator and accumulator plant. J. Appl. Ecol. 10: 269–320.

Corner, E.J.H. 1976. See General References.

Craik, D.J. 1999. Plant cyclotides: a unique family of cyclic and knotted proteins that defines the cyclic cystine knot structural motif. J. Mol. Biol. 294: 1327–1236.

Craik, D.J. 2010. Discovery and applications of the plant cyclotides. Toxicon 56: 1092–102.

Cu, J., Perineau, Q.F., Gaset, A. 1992. Volatile components of violet leaves. Phytochemistry 31: 571–573.

Culley, T.M. 2000. Inbreeding depression and floral type fitness differences in *Viola canadensis* (Violaceae), a species with chasmogamous and cleistogamous flowers. Can. J. Bot. 78: 1420–1429.

De Candolle, Alph. 1844. Prodromus systematis naturalis regni vegetabilis. Vol. 8. Paris: Treuttel & Würtz.

Di Stasi, L.C., Gomes, J.C., Vilegas, W. 1999. Studies on anti-allergenic constituents in the leaves and stems of *Anchietea salutaris* var. *martiana* (Violaceae). Chem. Pharmac. Bull. 47: 890–893.

Erdtman, G. 1952. See General References.

Fabijan, D.M., Packer, J.G., Denford, K.E. 1987. The taxonomy of the *Viola nuttallii* complex. Can. J. Bot. 65: 2562–2580.

Freitas, L., Sazima, M. 2003. Floral biology and pollination mechanisms in two *Viola* species – from nectar to pollen flowers? Ann. Bot. 91: 311–317.

Furness, C.A. 2011. Comparative structure and development of pollen and tapetum in Malpighiales, with a focus on the parietal clade. Int. J. Plant Sci. 172: 980–1011.

Gil-ad, N.L. 1995. Systematics and evolution of *Viola* L. subsection *Boreali-Americanae* (W. Becker) Brizicky. Doctoral dissertation, University of Michigan, Ann Arbor, MI.

Gil-ad, N.L. 1998. The micromorphologies of seed coats and petal trichomes of the taxa of *Viola* subsect. *Boreali-Americanae* (Violaceae) and their utility in discerning orthospecies from hybrids. Brittonia 50: 91–121.

Hansmann, P., Kleinig, H. 1982. Violaxanthin esters from *Viola tricolor* flowers. Phytochemistry 21: 238–239.

Hayden, W.J., Clough, J. 1990. Methyl salicylate secretory cells in roots of *Viola arvensis* and *Viola rafinesquii* (Violaceae). Castanea 55: 65–70.

Hegnauer, R. 1973. Chemotaxonomie der Pflanzen. Vol. 6. Basel: Birkhaeuser.

Hekking, W.H.A. 1984. Neotropical Violaceae: the genus *Fusispermum*. Proc. Kon. Nederl. Akad. Wetensch. C 87: 121–130.

Hekking, W.H.A. 1988a. Studies on Neotropical Violaceae 2. Arrangement of leaves, inflorescences and branchlets in Neotropical *Rinorea*. Flora 180: 345–376.

Hekking, W.H.A. 1988b. Flora Neotropica Monograph 46: Violaceae Part I - *Rinorea* and *Rinoreocarpus*. Bronx, New York: New York Botanical Garden.

Herrera, C. 1988. Biology and ecology of *Viola cazorlensis* I. Variability in floral traits. An. Jard. Bot. Madrid 45: 233–246.

Hodges, S.A., Ballard, H.E., Jr., Arnold, M.L., Chase, M.W. 1995. Generic relationships in the Violaceae: data from morphology, anatomy, chromosome numbers and rbcL sequences. Am. J. Bot. 82: 136.

Hoffmann, M.H., Paula-Souza, J., Flaschendräger, A., Röser, M. 2010. The gynoecium of male *Anchietea pyrifolia* (Violaceae): preserved structure with a new function. Flora (Jena) 205: 429–433.

Holdsworth, M. 1966. The cleistogamy of *Viola cunninghamii*. Trans. Roy. Soc. New Zeal., Bot. 3: 169–174.

Hoyos Gomez, S.E. 2011. Towards an understanding of the basal evolution of Violaceae from an anatomical and morphological perspective. MSc thesis, University of Missouri-St. Louis, St. Louis, MO.

Jaffré, T. 1980. Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie. Paris: O.R.S.T.O.M.

Jaffré, T., Schmid, M. 1974. Accumulation du nickel par une Rubiacée de Nouvelle Calédonie, *Psychotria douarrei* (G. Beauvisage) Däniker. C. R. Acad. Sci. D 278: 1727–1730.

Jedrzejczyk, M., Rostanski, A., Malkowski, E. 2002. Accumulation of zinc and lead in selected taxa of the genus *Viola* L. Acta Biol. Cracov. Bot. 44: 49–55.

Johri, B.M. et al. 1992. See General References.

Kellogg, E.A., Weitzman, A.L. 1985. A note on the Oceanic species of *Melicytus* (Violaceae). J. Arnold Arbor. 66: 491–502.

Kelly, P.C., Brooks, R.R., Dilli, S., Jaffré, T. 1975. Preliminary observations on the ecology and plant chemistry of some nickel-accumulating plants from New Caledonia. Proc. Roy. Soc. London B 189: 69–80.

Korotkova, N. et al. 2009. See General References.

Lee, J., Brooks, R.R., Reeves, R.D., Boswell, C.R., Jaffré, T. 1977. Plant-soil relationships in a New Caledonian serpentine flora. Plant Soil 46: 675–680.

MacNicol, M. 1967. Flower cookery: the art of cooking with flowers, pp. 223–235. New York: Fleet Press.

Marcussen, T., Jakobsen, K.S., Danihelka, J., Ballard, H.E., Jr., Blaxland, K., Brysting, A.K., Oxelman, B. 2012 ("2011"). Inferring species networks from gene trees in high-polyploid North American and Hawaiian violets (*Viola*, Violaceae). Syst. Biol. 60: 1–20.

Mayers, A.M., Lord, E.M. 1983. Comparative flower development in the cleistogamous species *Viola odorata*. I. A growth rate study. Am. J. Bot. 70: 1548–1555.

McPherson, G.D., Packer, J.G. 1974. A contribution to the taxonomy of *Viola adunca*. Can. J. Bot. 52: 895–902.

Melchior, H. 1925a. Violaceae. In: Engler, A., Prantl, K. (eds.) Die natürlichen Pflanzenfamilien, 2nd edn, vol. 21. Leipzig: W. Engelmann. pp. 329–377.

Melchior, H. 1925b. Die phylogenetische Entwicklung der Violaceen und die natürlichen Verwandtschaftsverhältnisse ihrer Gattungen. Rep. spec. nov. regni veg. 36: 83–125.

Metcalfe, C.R., Chalk, L. 1972. Anatomy of the dicotyledons, leaves, stem, and wood in relation to taxonomy with notes on economic uses, pp. 102–109. Oxford: Clarendon Press.

Morton, C.V. 1944. Taxonomic studies of Tropical American plants: the genus *Hybanthus* in continental North America. Contr. US Natl. Herb. 29: 74–82.

Munzinger, J.K., Ballard, H.E., Jr. 2003. *Hekkingia* (Violaceae), a new arborescent violet from French Guiana, with a key to genera in the family. Syst. Bot. 28: 345–351.

Munzinger, J.K., Pauly, A. 2003 Mechanism of self-pollination in *Hybanthus enneaspermus* (L.) F. Muell. and notes on the floral biology of some *Rinorea* species (Violaceae) in Ivory Coast. Acta Bot. Gallica 150: 155–166.

Nadot, S., Ballard, H.E., Jr., Creach, J.B., Dajoz, I. 2000. The evolution of pollen heteromorphism in *Viola*: a phylogenetic approach. Plant Syst. Evol. 223: 155–171.

Paula-Souza, J., Souza, V.C. 2003. *Hybanthopsis*, a new genus of Violaceae from eastern Brazil. Brittonia 55: 206–210.

Paula-Souza, J., Pirani, J.R., Feliciano, C.D. 2011. Taxonomic and geographic notes on the *Hybanthus lanatus* (A.St.Hil.) Baill. complex (Violaceae). Candollea 66: 367–375.

Powlesland, M.H. 1984. Reproductive biology of three species of *Melicytus* (Violaceae) in New Zealand. New Zealand J. Bot. 22: 81–94.

Redbo-Torstensson, P., Berg, H. 1995. Seasonal cleistogamy: a conditional strategy to provide reproductive assurance. Acta Bot. Neerl. 44: 247–256.

Reeves, R.D., MacFarlane, R.M., Brooks, R.R. 1983. Accumulation of nickel and zinc by western North American genera containing serpentine-tolerant species. Am. J. Bot. 70: 1297–1303.

Severne, B.C., Brooks, R.R. 1972. A nickel-accumulating plant from western Australia. Planta 103: 91–94.

Simonsen, S.M., Sando, L., Ireland, D.C., Colgrave, M.L., Bharathi, R., Goransson, U., Craik, D.J. 2005. A continent of plant defense peptide diversity: cyclotides in Australian *Hybanthus* (Violaceae). Plant Cell 17: 3176–3189.

Skottsberg, C. 1940. Observations on Hawaiian violets. Bot. Tradgard. Meddel. 13: 451–528.

Takhtajan, A.L. 1981. See General References.

Taylor, F.H. 1972. The secondary xylem of the Violaceae: a comparative study. Bot. Gaz. 133: 230–242.

Tokuoka, T. 2008. Molecular phylogenetic analysis of Violaceae (Malpighiales) based on plastid and nuclear DNA sequences. J. Plant Res. 121: 253–260.

Wahlert, G.A., Ballard, H.E., Jr. 2012. A phylogeny of *Rinorea* (Violaceae) inferred from plastid DNA sequences with an emphasis on the African and Malagasy species. Syst. Bot. 37: 964–973.

Wahlert, G.A., Marcussen, T., Ballard, H.E., Jr., de Paula-Souza, J., Feng, M. accepted. A phylogeny of the Violaceae (Malpighiales) inferred from plastid DNA sequences: implications for generic diversity and intrafamilial taxonomy. Syst. Bot.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Addition to Peridiscaceae

C. Bayer and S. Dressler

The placement of the problematic genus *Medusandra* in Peridiscaceae reported by Wurdack and Davis (2009) motivates us to the following addition to the treatment of the family in Vol. IX of this series, pp. 297–300.

Peridiscaceae

syn. Medusandraceae Brenan, Kew Bull. 1952: 228 (1952), nom. cons.

Medusandra Brenan Fig. 74

Medusandra Brenan, Kew Bull. 1952: 228 (1952).

Trees up to 20 m, exuding a yellowish to reddish sap when cut; young parts pubescent. Leaves spiral, simple, elliptic to ovate, pinnatinerved, faintly toothed, minutely pubescent below; petiole long, with proximal and distal pulvinus; stipules small, caducous. Inflorescences axillary, often paired (rarely 3 per axil), racemose, more or less lax and pendulous, or condensed, with caducous bracts. Flowers hermaphroditic, actinomorphic, pentamerous, small, scented; sepals distinct or almost so, persistent, aestivation apert; petals distinct, imbricate, white to greenish; fertile stamens antepetalous, distinct but adnate to base of petals, anthers tetrasporangiate, introrse, dehiscing by valves; staminodia antesepalous, pubescent, folded in bud, at anthesis much longer than stamens, with rudimentary anther; ovary superior, 3–4-carpellate, unilocular, with central column and apical placenta; ovules 2 per carpel, pendulous, anatropous; stylodia 3–4, short, distinct. Fruit a globose, 3–4-valved, one-seeded capsule. Seed large, albuminous, somewhat ruminate; embryo small, straight, peripheral.

Two species, *M. richardsiana* Brenan and *M. mpomiana* Letouzey & Satabié, trop. W Africa.

When he described *Medusandra*, Brenan (1952) placed it in a unispecific family and order of its own, which was thought to be related to Olacales or Santalales. In 1954, he added *Soyauxia* (formerly in Passifloraceae or Flacourtiaceae) to that family, a view that was followed by many but rejected by Hutchinson (1959). *Medusandra* differs from *Soyauxia* in the presence of secretory canals, a more condensed inflorescence, and floral characters such as the apert aestivation of the sepals, stamen number, the presence of (at anthesis) elongate, finely pubescent staminodia, and the lack of a disk; the latter traits, together with the catkin-like inflorescences, call for observations of the mode of pollination. Based on molecular studies, *Soyauxia* was placed in Peridiscaceae (Davis and Chase 2004), and *Medusandra* remained in an unigeneric family related to Passifloraceae in the Malpighiales (Soltis et al. 2005). However, Wurdack and Davis (2009) received strong support for its placement in Saxifragales as sister to *Peridiscus* and *Soyauxia*. This is corroborated by floral features (unilocular ovary with central placentation and pendulous ovules as well as distinct stylodia), similar seed coat structure, small embryo and an insertion in 18S rDNA considered unique in Saxifragales. Nevertheless, Peridiscaceae differ from the bulk of Saxifragales by syncarpy of three (to five) carpels and hypogyny.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_26, © Springer-Verlag Berlin Heidelberg 2014

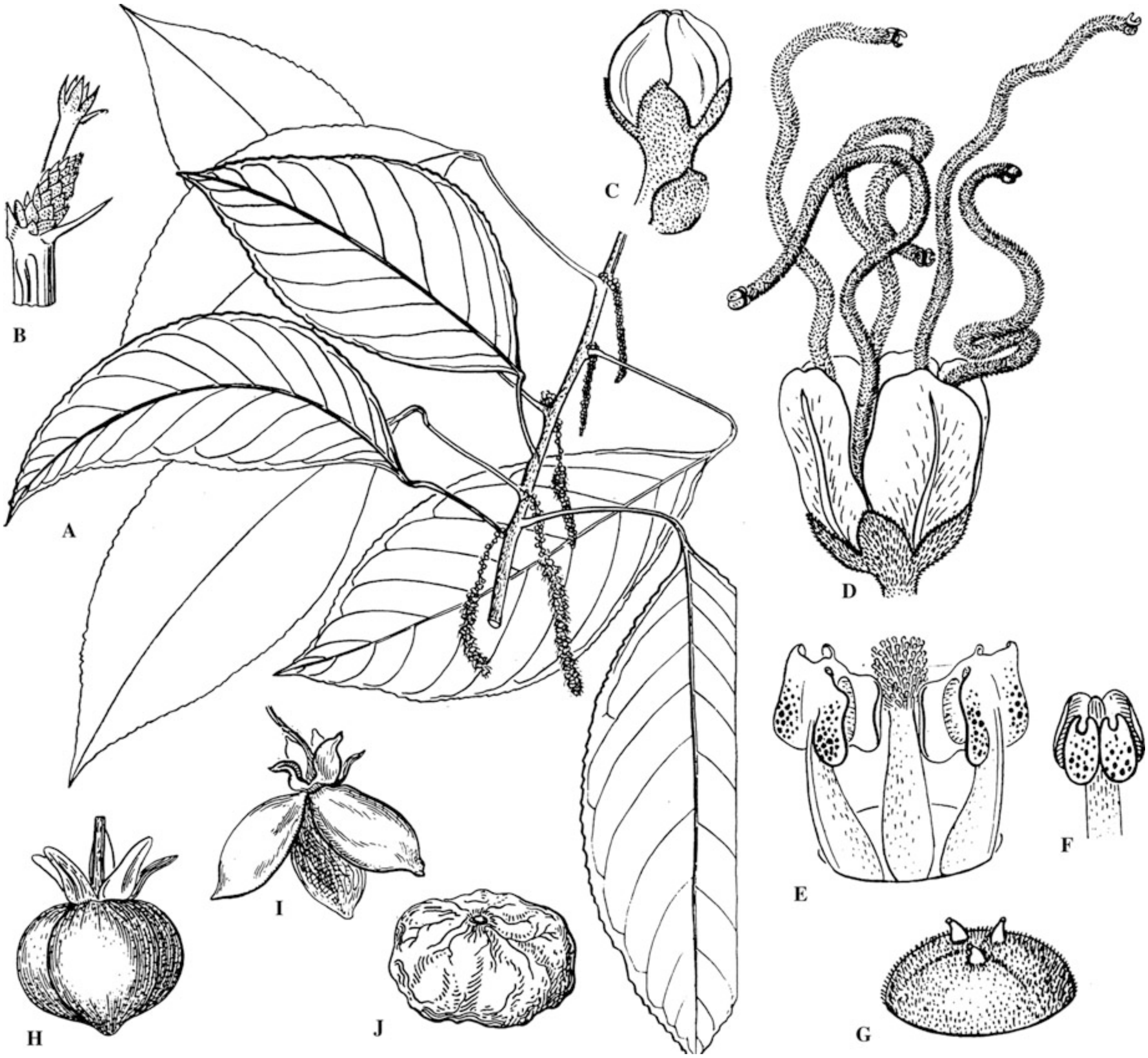

Fig. 74. Periidiscaceae. *Medusandra richardsiana*. **A** Flowering twig. **B** Stipule and bud. **C** Flower bud with bract. **D** Anthetic flower. **E** Two fertile dehisced anthers and base of staminode. **F** Dehisced fertile anther. **G** Ovary with stylodia. **H** Mature fruit. **I** Same, dehisced. **J** Seed. (Brenan 1952)

Selected Bibliography

Brenan, J.P.M. 1952. Plants of the Cambridge expedition, 1947–1948: II. A new order of flowering plants from the British Cameroons. Kew Bull. 1952: 227–244.

Brenan, J.P.M. 1954. *Soyauxia*, a second genus of Medusandraceae. Kew Bull. 1954: 507–511.

Burkill, H.M. 1997. The useful plants of west tropical Africa, ed. 2, vol. 4, Families M-R. Kew: Royal Botanic Gardens.

Davis, C.C., Chase, M.W. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. Amer. J. Bot. 91: 262–273.

Hutchinson, J. 1959. The families of flowering plants, 2nd ed., vol. I. Oxford: Clarendon.

Letouzey, R., Satabié, B. 1974 Une seconde espèce du genre *Medusandra* Brenan (Medusandracées). Adansonia II, 14: 63–68.

Metcalfe, C.R. 1952. *Medusandra richardsiana* Brenan. Anatomy of the leaf, stem and wood. Kew Bull. 1952: 237–244.

Metcalfe, C.R. 1962. Notes on the systematic anatomy of *Whittonia* and *Peridiscus*. Kew Bull. 15: 472–475.

Miller, R.B. 1975. Systematic anatomy of the xylem and comments on the relationship of Flacourtiaceae. J. Arnold Arb. 56: 20–102.

Nyananyo, B.L. 1987. Systematic survey of the leaf epidermis in the Medusandraceae (Rosidae). Feddes Repert. 98: 595–598.

Soltis, D.E., Soltis, P.S., Endress, P.K., Chase, M.W. 2005. Phylogeny and evolution of angiosperms. Sunderland, MA: Sinauer.

Stevens, P.F. 2001 onwards. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

General References

APG (Angiosperm Phylogeny Group). 1998. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85: 531–553.

APG (Angiosperm Phylogeny Group) II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linnean Soc. 141: 399–436.

APG (Angiosperm Phylogeny Group) III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linnean Soc. 161: 105–121.

Bardon, L., Chamagne, J., Dexter, K.G., Sothers, C.A., Prance, G.T., Chave, J. 2013. Origin and evolution of Chrysobalanaceae: insights into the evolution of plants in the Neotropics. Bot. J. Linn. Soc. 171: 19–37.

Behnke, H.-D. 1991. Distribution and evolution of forms and types of sieve-element plastids in the dicotyledons. Aliso 13: 167–182.

Bell, C.D., Soltis, D.E., Soltis, P.S. 2010. The age and diversification of the angiosperms revisited. Am. J. Bot. 97: 1296–1303.

Bolkhovskikh, Z., Grif, V., Matvejeva, T., Zakharyeva, O. 1969. Khromosomnye chisla tsvetkovykh rastenii [Chromosome numbers of flowering plants]. Leningrad: Nauka.

Boyce, C.K., Lee, J.-E. 2010. An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity. Proc. Roy. Soc. B 277: 3437–3443.

Chase, M.W. et al. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Chase, M.W., Zmarzty, S., Lledó, M.D., Wurdack, K.J., Swensen, S.M., Fay, M.F. 2002. When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid *rbc*L DNA sequences. Kew Bull. 57: 141–181.

Corner, E.J.H. 1976. The seeds of dicotyledons. 2 vols. Cambridge: Cambridge University Press.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Davis, G.L. 1966. Systematic embryology of the Angiosperms. New York, London, Sydney: Wiley.

Davis, C.C., Chase, M.W. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. Am. J. Bot. 91: 262–273.

Davis, C.C., Webb, C.O., Wurdack, K.J., Jaramillo, C.A., Donoghue, M.J. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. Am. Naturalist 165: E36–E65.

Davis, C.C., Latvis, M., Nickrent, D.L., Wurdack, K.J., Baum, D.A. 2007. Floral gigantism in Rafflesiaceae. Science 315: 1812.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Stockholm: Almqvist and Wiksell.

Hallier, H. 1923. Beiträge zur Kenntnis der Linaceae (DC. 1819) Dumort. Beih. bot. Zbl., Abt. 2, 39: 1–178.

Hegnauer, R. 1962–1992. Chemotaxonomie der Pflanzen. Basel: Birkhaeuser (Vol. 1: 1962; Vol. 2: 1963; Vol. 3: 1964; Vol. 4: 1966; Vol. 5: 1969; Vol. 6: 1973; Vol. 7: 1986; Vol. 8: 1989; Vol. 9: 1990; Vol. 10: 1992).

Huber, H. 1991. Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer. Stuttgart: G. Fischer.

Hutchinson, J. 1973. The families of flowering plants. 3rd edn. Oxford: Clarendon Press.

Johri, B.M., Ambegaokar, K.B., Srivastava, P.S. 1992. Comparative embryology of angiosperms. 2 vols. Berlin, Heidelberg, New York: Springer.

Korotkova, N., Schneider, J.V., Quandt, D., Worberg, A., Zizka, A., Borsch, T. 2009. Phylogeny of the eudicot order Malpighiales: analysis of a recalcitrant clade with sequences of the *pet*D group II intron. Plant Syst. Evol. 282: 201–228.

Kubitzki, K., Krutzsch, W. 1996. Origins of east and southeast Asian plant diversity. In: Zhang, A., Wu, S. (eds.) Floristic characteristics and diversity of east Asian plants, pp. 56–70. Beijing: China Higher Education Press, Berlin: Springer.

Li, Y., Dressler, S., Zhang, D., Renner, S.S. 2009. More dispersal between Africa and Asia – the case of *Bridelia* (Phyllanthaceae). Syst. Bot. 34: 521–529.

Matthews, M.L., Endress, P.K. 2008. Comparative floral structure and systematics in Chrysobalanaceae s.l. (Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, Trigoniaceae; Malpighiales). Bot. J. Linn. Soc. 157: 249–309.

Matthews, M.L., Endress, P.K. 2011. Comparative floral structure and systematics in Rhizophoraceae, Erythroxylaceae and the potentially related Ctenolophonaceae, Linaceae, Irvingiaceae and Caryocaraceae (Malpighiales). Bot. J. Linn. Soc. 166: 331–416.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1, © Springer-Verlag Berlin Heidelberg 2014

Matthews, M.L., Amaral, M.C.E., Endress, P.K. 2012. Comparative floral structure and systematics in Ochnaceae *s. l.* (Ochnaceae, Quiinaceae, and Medusagynaceae; Malpighiales). Bot. J. Linn. Soc. 170: 299–392.

Metcalfe, C.R., Chalk, L. 1950. Anatomy of dicotyledons. 2 vols. Oxford: Clarendon Press.

Moore, M.J., Soltis, P.M., Bell, C.D., Burleigh, J.G., Soltis, D.E. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. Proc. Natl. Acad. Sci. U.S.A. 107: 4623–4628.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47: 1–142.

Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. Handbuch der Pflanzenanatomie II, 2, Vol. 10. Berlin: Borntraeger.

Pöschl, U., Martin, S.T., Sinha, B., Chen, Q., Gunthe, S.S., Huffman, J.A., and 18 further authors. 2010. Rainforest aerosols as biogenic nuclei of clouds and precipitation in the Amazon. Science 329: 1513–1516.

Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Kew: Royal Botanic Gardens.

Ruhfel, B.R., Bittrich, V., Bove, C.P., Gustaffson, M.H.G., Philbrick, C.T., Rutishauser, R., Xi, Z., Davis, C.C. 2011. Phylogeny of the clusioid clade (Malpighiales): evidence from the plastid and mitochondrial genome. Am. J. Bot. 98: 306–325.

Salati, E., Vose, P.D. 1984. Amazon basin: a system in equilibrium. Science 255: 129–138.

Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M. C., Soltis, D.E., Soltis, P.S., Weston, P., Whitten, W. M., Wurdack, K.J., Chase, M.W. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull. 55: 257–309.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S. B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C., Farris, J.A. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Soltis, D.E., Smith, S.A., Cellinese, N., Wurdack, K.J., Tank, D.C. and 23 further authors. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. Am. J. Bot. 98: 704–730.

Stevens, P.F. 2001 onwards. Angiosperm Phylogeny Website, Version 12, July 2012.

Takhtajan, A.L. (ed.) 1980. Plant Life. Vol. 5(1). Leningrad: Proswjestschenije.

Takhtajan, A.L. (ed.) 1981. Plant Life. Vol. 5(2). Leningrad: Proswjestschenije.

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Takhtajan, A. 2009. Flowering plants. 2nd edn. Heidelberg: Springer.

Tokuoka, T. 2007. Molecular phylogenetic analysis of Euphorbiaceae sensu stricto based on plastid and nuclear DNA sequences and ovule and seed character evolution. J. Plant Res. 120: 511–522.

Tokuoka, T., Tobe, H. 1995. Embryology and systematics of Euphorbiaceae sens. lat.: a review and perspective. J. Plant Res. 108: 97–106.

Tokuoka, T., Tobe, H. 2006. Phylogenetic analyses of Malpighiales using plastid and nuclear DNA sequences, with particular reference to the embryology of Euphorbiaceae s. str. J. Plant Res. 119: 599–616.

Wang, H., Moore, M.J., Soltis, P.M., Bell, C.D., Brockington, S.F., Alexandre, R., Davis, C.C., Latvis, M., Manchester, S.R., Soltis, D.E. 2009. Rosid radiation and the rapid rise of angiosperm-dominated forests. Proc. Natl. Acad. Sci. U.S.A. 106: 3853–3858.

Winkler, H. 1931. Linaceae. In: Engler & Prantl, Nat. Pflanzenfam., 2nd edn, 19a. Leipzig: W. Engelmann.

Wurdack, K.J., Davis, C.C. 2009. Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. Am. J. Bot. 96: 1551–1570.

Xi, Z., Ruhfel, B.R., Schaefer, H., Amorim, A.M., Sugumaran, M., Wurdack, K.J., Endress, P.K., Matthews, M.L., Stevens, P.F., Mathews, S., Davis, C.C. 2012. Phylogenomics and a posteriori data partitioning resolve the Cretaceous angiosperm radiation Malpighiales. Proc. Natl. Acad. Sci. U.S.A. 109: 17519–17524.

Index

References to accepted names in **bold-faced** print, to synonyms in upright print, to illustrations in *italics*.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1, © Springer-Verlag Berlin Heidelberg 2014

Volumes published in this series

Volume I	Pteridophytes and Gymnosperms Edited by K.U. Kramer and P.S. Green (1990) Date of publication: 28.9.1990
Volume II	Flowering Plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families Edited by K. Kubitzki, J.G. Rohwer, and V. Bittrich (1993) Date of publication: 28.7.1993
Volume III	Flowering Plants. Monocotyledons: Lilianae (except Orchidaceae) Edited by K. Kubitzki (1998) Date of publication: 27.8.1998
Volume IV	Flowering Plants. Monocotyledons: Alismatanae and Commelinanae (except Gramineae) Edited by K. Kubitzki (1998) Date of publication: 27.8.1998
Volume V	Flowering Plants. Dicotyledons: Malvales, Capparales and Non-betalain Caryophyllales Edited by K. Kubitzki and C. Bayer (2003) Date of publication: 12.9.2002
Volume VI	Flowering Plants. Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales Edited by K. Kubitzki (2004) Date of publication: 21.1.2004
Volume VII	Flowering Plants. Dicotyledons: Lamiales (except Acanthaceae including Avicenniaceae) Edited by J.W. Kadereit (2004) Date of publication: 13.4.2004
Volume VIII	Flowering Plants. Eudicots: Asterales Edited by J.W. Kadereit and C. Jeffrey (2007) Date of publication: 6.12.2006
Volume IX	Flowering Plants. Eudicots: Berberidopsidales, Buxales, Crossosomatales, Fabales p.p., Geraniales, Gunnerales, Myrtales p.p., Proteales, Saxifragales, Vitales, Zygophyllales, Clusiaceae Alliance, Passifloraceae Alliance, Dilleniaceae, Huaceae, Picramniaceae, Sabiaceae Edited by K. Kubitzki (2007) Date of publication: 6.12.2006
Volume X	Flowering Plants. Eudicots: Sapindales, Cucurbitales, Myrtaceae Edited by K. Kubitzki (2011) Dates of publication: 10.12.2010 (online); 10.1.2011 (print)
Volume XI	Flowering Plants. Eudicots: Malpighiales Edited by K. Kubitzki (2014)