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,

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.

The sieve tubes contain non-dispersive protein bodies.

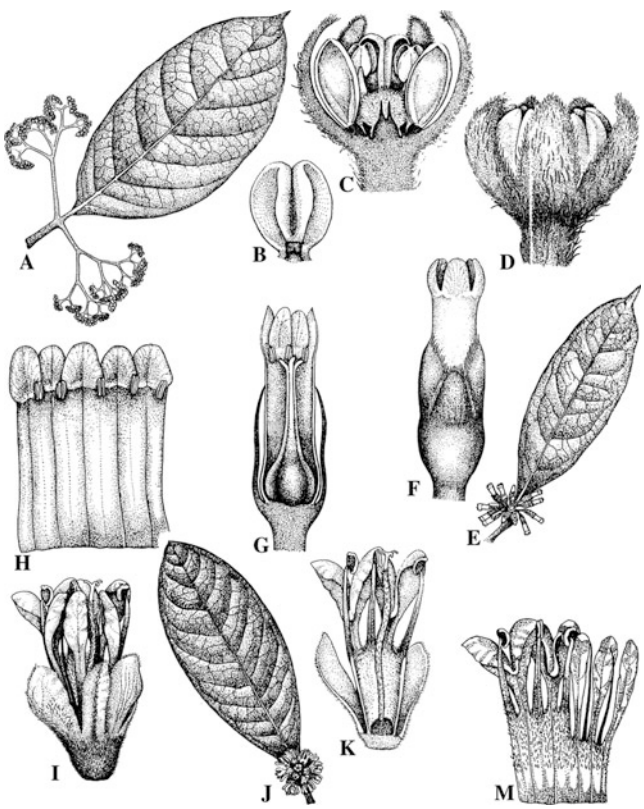

Fig. 7. Dichapetalaceae. **A–D** *Dichapetalum spruceanum*. **A** Leaf and inflorescence. **B** Petal. **C** Flower, vertical section. **D** Flower. **E–H** *Stephanopodium aptotum*. **E** Leaf and inflorescence. **F** Flower. **G** Flower, vertical section. **H** Corolla and stamens. **I–L** *Tapura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

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.