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

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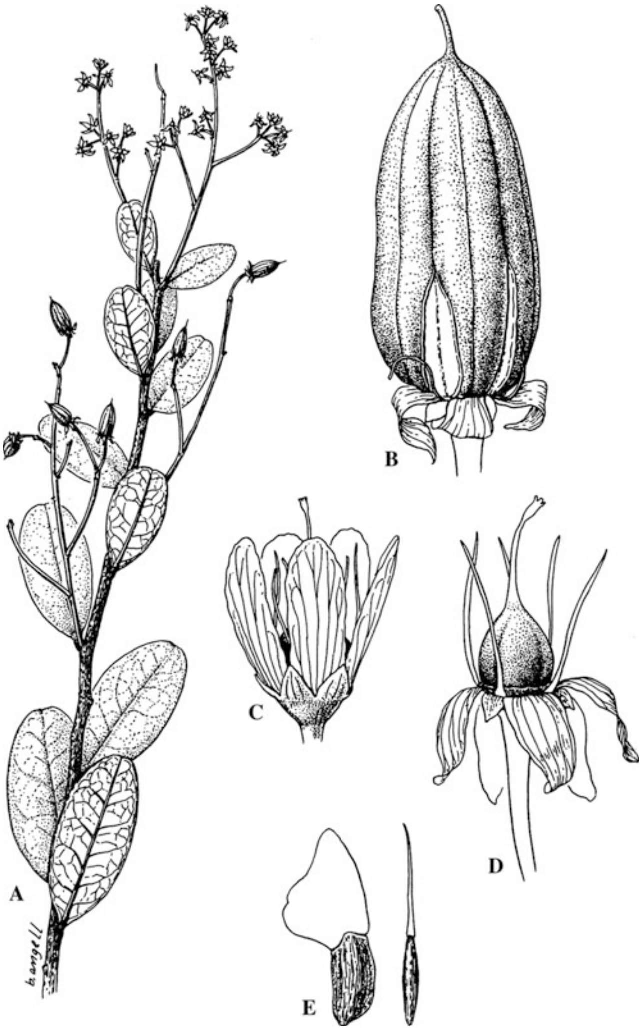

Fig. 52. Ixonanthaceae. *Ochthocosmus longipedicellatus*. **A** Flowering and fruiting branchlet. **B** Mature capsule. **C**, **D** Flowers during progressive stages of anthesis. *O. roraimae* var. *parvifolius*. **E** Winged seed. (Reproduced with kind permission of the artist Bobbi Angell)

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

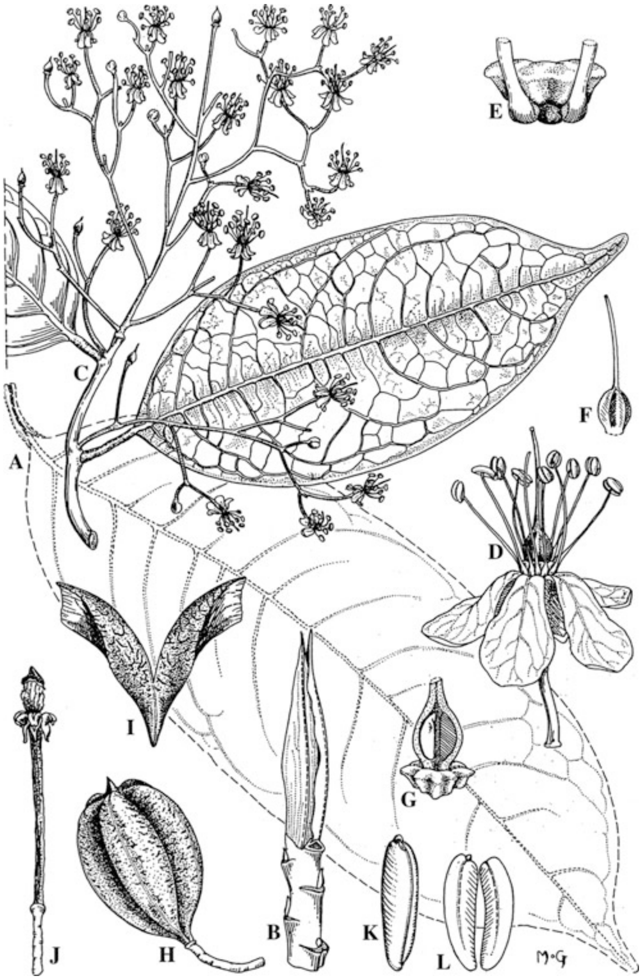

Fig. 53. Ixonanthaceae. *Allantospermum borneense*. **A** Leaf. **B** Leaf-bud with stipules (the lower scars are those of bud-scales). **C** Flowering branch. **D** Flower. **E** Disk with base of filaments (central one removed). **F** Pistil. **G** Vertical section of ovary. **H** Capsule. **I** Valve 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.