

Studies in Malesian Gentianaceae II: A taxonomic framework for the *Fagraea* complex, including the new genus *Limahlania*

K.M. Wong¹ and M. Sugumaran²

¹Singapore Botanic Gardens,
1 Cluny Road, Singapore 259569
wkm2000@gmail.com

²Rimba Ilmu Botanic Garden,
Institute of Biological Sciences, University of Malaya,
50603 Kuala Lumpur, Malaysia
maran@um.edu.my

ABSTRACT. A molecular phylogenetic study that provided good resolution of the *Fagraea* s.l. complex is the basis for constructing a new taxonomic framework in this group. The lineages identified showed good correspondence with other clades that represent well-established, recently revised genera in the tribe (Potalieae) and subtribe (Potaliinae) in terms of structure and statistical support (monophyly), and possessed recognisable morphological characteristics that were potentially synapomorphic for each monophyletic group. Generic identities are therefore adopted for the clades within this complex, as well as a somewhat isolated lineage, resulting in the definition of *Fagraea* Thunb. s.s.; the reapplication of *Cyrtophyllum* Reinw., *Picrophloeus* Blume, and *Utania* G.Don; and the circumscription of the new genus *Limahlania* K.M.Wong & Sugumaran. A key to the genera of the *Fagraea* complex is presented and nomenclatural notes are provided for each genus, in order to facilitate subsequent revisions. *Limahlania crenulata* (Maingay ex Clarke) K.M.Wong & M.Sugumaran and *U. volubilis* (Wall.) M.Sugumaran are new combinations. Lectotypes are selected for *C. peregrinum* Reinw., *F. ceilanica* Thunb., *Kuhlia morindifolia* Blume, and *P. javanensis* Blume.

Keywords. *Cyrtophyllum*, *Fagraea*, Gentianaceae, *Limahlania*, Malesia, *Picrophloeus*, phylogenetic classification, Potalieae, Potaliinae, *Racemosae*, *Utania*

From clades to genera: taxonomic concepts in the *Fagraea* complex

A new classification for the *Fagraea* Thunb. complex is proposed, based on the results of molecular phylogenetic analyses reported by Sugumaran & Wong (2012). In that study, five distinct lineages were clearly identified within *Fagraea* s.l. that were shown to correspond to other well established genera in the same tribe (Potalieae) (as treated by Struwe & Albert 1997, 2004; Struwe et al. 1994; Struwe et al. 2002), in terms of their monophyly in the molecular phylogenetic analyses as well as circumscription by potentially synapomorphic morphological characters.

The *Fagraea* clade in that study, which includes the type species for the genus, *F. ceilanica* Thunb., is the basis of the 'true' *Fagraea* (*Fagraea* s.s.). *Fagraea*

crenulata Maingay ex Clarke is considered representative of a distinct lineage because in the molecular phylogenetic study, it was only found to associate basally with the *Fagraea* clade by chloroplast gene characteristics, but not in the ITS analysis. It is also morphologically quite well distinguished from *Fagraea* s.s. No special generic name has been associated with this taxon and it is the basis of the new genus *Limahlania* K.M.Wong & M.Sugumaran.

The other clades correspond to genera resurrected from the synonymy of *Fagraea* s.l., and now reapplied to phylogenetically circumscribed entities in the complex. An appropriate name for the Racemosa clade of Sugumaran & Wong (2012) appears to be *Utania* G.Don, which was given to replace the illegitimate name *Kuhlia* Reinw. Don (1838) recognised one species, *U. morindifolia* which was later recombined as *Fagraea morindifolia* by Blume (1838). However *F. morindifolia* is a synonym of *F. volubilis* Wall. (Wong & Sugau 1996), which Sugumaran & Wong (2012: Fig. 5) demonstrated as belonging to their Racemosa clade. This group is consistently monophyletic in all the analyses with different gene regions.

Another interesting result of the study by Sugumaran & Wong (2012) is the parphyly of *Fagraea* section *Cyrtophyllum* (Reinw.) Blume as defined by Leenhouts (1962a), which was consistently resolved as two distinct clades. Wong & Sugau (1996) recognised two complexes within this “section” which they differentiated by the exclusively axillary or terminal flowering habit. Indeed, these two complexes are equivalent to the distinct Gigantea and Elliptica clades, respectively, in the molecular analyses carried out. In the past, Ridley (1918) had regarded this “section” as a separate genus, i.e., *Cyrtophyllum* Reinw., as the species are so different, especially in their habit, in comparison to other epiphytic members of *Fagraea* s.l. For *Cyrtophyllum*, Blume (1826) had included two species, *C. peregrinum* Reinw. and *C. speciosum* Blume. Subsequent classification reduced *C. peregrinum* to a synonym of *F. fragrans* Roxb., and *C. speciosum* to synonymy under *F. elliptica* Roxb. (= *Picrophloeus* Blume now). The molecular analyses of Sugumaran & Wong (2012) show that *F. fragrans* falls within or is closely associated with the Gigantea clade, so that the generic name *Cyrtophyllum* is most applicable to the clade.

In the sectional classification of *Fagraea* s.l. (Leenhouts 1962a), both *Picrophloeus* and *Cyrtophyllum* were reduced to synonymy under *Fagraea* section *Cyrtophyllum*. *Picrophloeus* was established with only one described species, *P. javanensis* Blume that was considered synonymous with *F. elliptica*. Thus, the generic name *Picrophloeus* is applicable to the Elliptica clade.

Characters for clades: circumscription of genera

Sugumaran & Wong (2012) have surveyed the expression of a number of characters in the *Fagraea* complex, in comparison to other members of the Potaliinae (*Anthocleista* and *Potalia*). *Fagraea* s.s. (i.e., the *Fagraea* clade, and excluding *F. crenulata*) (Fig. 1) is distinguished by fruits that produce copious creamy pale yellowish latex in the epidermis and fruit wall. The rest of *Fagraea* s.l. have fruits that have no latex at all



Fig. 1. *Fagraea auriculata*. **A.** Tree with orthotropic complexes of branches. **B.** Each branch segment is potentially terminated by a cyme, here with fruits formed. **C.** A fruit longitudinally cut, revealing how easily the fruit epidermis detaches as a thin peel from the fruit wall, and latex oozing from the cut surface. **D.** Close-up of creamy pale yellowish latex oozing from wound following removal of a fruit calyx lobe. (Photos: K.M. Wong)

(*Utania* or the *Racemosa* clade, equivalent to *Fagraea* section *Racemosae* Benth., and also *Anthocleista* and *Potalia* (Struwe, pers. comm.)), or produce just a translucent gummy sap from the epidermis or wall when bruised (all others in *Fagraea* s.l.). Like *Anthocleista* and *Potalia*, *Fagraea* s.s. has ellipsoid-rounded seeds, contrasting with polygonal seed shapes found in *Cyrtophyllum*, *Limahlania*, *Picrophloeus* and *Utania*. *Fagraea* s.s. includes not only trees, but also species that are epiphytic, hemi-epiphytic and scramblers (life forms that are otherwise not found in the other groups of *Fagraea* s.l. and which are rare in the *Potaliinae* generally).

Limahlania (our new genus represented by *Fagraea crenulata*) has a number of unique characters in the subtribe, such as the development of prickles on the stem or trunk and branches (Fig. 2), and serrulate-crenulate leaf margins. It is also distinguished from all other taxa in the *Fagraea* complex, and also likely in the subtribe, by having Fagerlind's growth architectural model (Hallé et al. 1978; Sugumaran & Wong 2012). This architecture (Fig. 2) is characterised by episodic stem or trunk growth, non-equivalent vegetative axes (i.e., clear differentiation into trunk and branches), and a modular branching system that develops plagiotropically by substitution. In Malesia, the other lineages or clades in the *Fagraea* complex characterised by episodic growth and non-equivalent vegetative axes either develop according to Scarrone's model with orthotropic complexes of branches (*Fagraea* s.s.; the *Elliptica* clade or *Picrophloeus*) (Fig. 1 and 5), or Aubréville's model with branching that is plagiotropic by apposition (Fig. 4) (Hallé et al. 1978; Sugumaran & Wong 2012). These taxa all have a *monopodial* stem or trunk. Other (non-Malesian) taxa in the subtribe are so far documented with *modular* or *sympodial* stem or trunk systems (Hallé et al. 1978); they include the African *Anthocleista* (most species have Leeuwenberg's model) and the American *Potalia* (one species specially analysed corresponds to Chamberlain's model which produces a linear sympodium giving a monocaulous habit; others, including a suite of poorly known species are generally observed to be monocaulous: Struwe & Albert 2004). The apparent exception is a species of *Anthocleista* documented with Scarrone's model (Hallé et al. 1978). Also, Prevost (1978) identifies Koriba's model for the New Caledonian *F. schlechteri*.

On the other hand, *Limahlania* is related to *Fagraea* s.s. in having petiolar sheaths that do not or only slightly fuse at the edges, and a peltate stigma structure. It also resembles *Fagraea* s.s., *Cyrtophyllum* and *Picrophloeus* in having a fruit epidermis that detaches from the fruit wall easily as a peel, unlike in *Utania*, where the epidermis does not easily detach.

Utania (represented in the phylogenetic analyses of Sugumaran and Wong (2012) by the *Racemosa* clade) has the most potentially synapomorphic morphological characters among the *Fagraea* complex or the *Potaliinae*. These include a plant architecture (Roux's model; Hallé et al. 1978) with continuous stem or trunk growth, and plagiotropic branches with distichous leaf arrangement (Fig. 3); non-resinous terminal vegetative buds, and pendulous inflorescences. In comparison, all other members of the *Fagraea* complex or the subtribe have episodic stem or trunk growth, with either orthotropic complexes of branches, or branching that is plagiotropic by apposition or substitution. Other genera in the *Potaliinae* have resinous terminal vegetative buds



Fig. 2. *Limahlania crenulata*, showing Fagerlind's tree architectural model with episodic trunk development (producing branches in distinct tiers) and modular branch development producing a plagiotropic system by substitution (each segment potentially terminated by a cyme) (Photo: K.M. Wong). *Inset:* Trunk with prickles and developing a lightly fissured bark (Photo: M. Sugumaran).



Fig. 3. Growth architecture and flowering in *Utania*. Arrow indicating continuous orthotropic stem growth in *Utania volubilis* following Roux's model, where the shoot has no marked resting period and stem internode lengths are generally similar; and branches are plagiotropic (Photo: K.M. Wong). *Inset:* The pendulous, elongate terminal inflorescences with very condensed side-branches characteristic of the genus, in another *Utania* species (Photo: M. Sugumaran).



Fig. 4. Aubréville's architectural model in *Cyrtophyllum fragrans*. A series of vertical brackets shows distinct growth episodes on the monopodial trunk along which branching intervals generally alternate as shorter and longer episodes. The brackets along the branch system show repeated branch segments that develop plagiotropically by apposition (Photo: K.M. Wong). *Insets:* (*top*) The inflorescences are axillary and do not terminate the growth of branch segments. (*bottom*) Deeply fissured bark of adult. (Photos: M. Sugumaran).



Fig. 5. *Picrophloeus javanensis*. **A.** The tree architectural model of Scarrone found in this genus is typified by orthotropic branch complexes. **B.** Terminal cymes, with long-exserted stamens and styles in the flowers. (Photos: K.M. Wong)

(Struwe, pers. comm.). In structure, the *Utania* inflorescence is an elongate panicle with cymose branching (branches in several pairs, condensed, and distinctly shorter than the rachis). In other members of the *Fagraea* complex and Potaliinae, solitary flowers, 1–few-flowered cymes and branched cymes in which the basal branches are longest (nearly as long as the rachis, and mostly rebranched) occur. In addition, *Utania* fruits (like those of *Anthocleista* or *Potalia*; Struwe, pers. comm.) do not produce any latex, whereas those of other members of the *Fagraea* complex do. As explained above, *Utania* also has polygonal seeds, as in other members of the *Fagraea* complex except for *Fagraea* s.s. itself (which, like other Potaliinae, have ellipsoid-rounded seeds).

Cyrtophyllum (the Gigantea clade in the phylogenetic resolution of the *Fagraea* complex) and *Picrophloeus* (Elliptica clade in the same resolution) have superficial resemblance because of their small flowers and much-protruding stamens and styles (Fig. 5), compared to other groups, which generally have bigger flowers as well as less exerted stamens and styles. The only clear morphological distinction between these two genera is an important one: axillary inflorescences in *Cyrtophyllum* and terminal inflorescences in *Picrophloeus* (Fig. 4 and 5). Wong & Sugau (1996) had recognised these two groups as distinct complexes within the section *Cyrtophyllum* but even earlier, Ridley (1923) had accepted the group with axillary inflorescences (the Gigantea clade) as the distinct genus, *Cyrtophyllum*.

Key to genera formerly placed in *Fagraea* s.l.

- 1a. Inflorescences axillary. Trees with episodic stem / trunk growth, developing a wave-like sympodial branch system with successively higher orders of outwardly directed, then upturned, (indeterminate) branch segments (plagiotropy by apposition) *Cyrtophyllum*
- b. Inflorescences terminal. Trees, shrubs, scramblers or hemi-epiphytes with continuous or episodic stem / trunk growth; branches plagiotropic or orthotropic, if developing a wave-like sympodial branch systems then the branch segments truly modular (determinate) 2
- 2a. Stem / trunk growth continuous. Leaf arrangement on branches distichous. Vegetative terminal buds not resinous. Inflorescence a pendulous flowering cyme with all branches condensed along the rachis. Surface of dried fruits firm and smooth, the epidermis not detaching from the pericarp *Utania*
- b. Stem / trunk growth episodic. Leaf arrangement on branches decussate. Vegetative terminal buds covered with creamy to yellowish resin. Inflorescence without any branching (a solitary flower) or an erect cyme with well-developed branches. Surface of dried fruits wrinkled, the epidermis detaching from the pericarp 3

- 3a. Petiolar sheaths at the base of a leaf pair fully fused to form a cup-like ochrea. Stigma base not expanding conspicuously, the stigma capitate. Stamens and style exerted 40% or more from the corolla mouth *Picrophloeus*
- b. Petiolar sheaths at the base of a leaf pair not fused to slightly fused at the extreme edges and not forming an ochrea. Stigma base expanding into a circular plate-like rim, the stigma appearing peltate. Stamen and style not or only slightly exerted from the corolla mouth 4
- 4a. Stem/trunk bark becoming fissured, densely set with prickles. Leaf margin serrulate-crenulate. Branch system modular, developing plagiotropically by substitution to form a wave-like sympodial system. Seeds polygonal *Limahlania*
- b. Stem / trunk with smooth bark, sometimes becoming cracking-scaly, but never prickly. Leaf margin entire. Branch system non-modular, developing as orthotropic complexes and not wave-like in structure. Seeds ellipsoid-rounded *Fagraea*

Conspectus of genera in the complex

1. *Cyrtophyllum* Reinw.

in Hornschuch, Syll. Pl. Nov. 2 (1825) 8; Blume, Bijdr. Fl. Ned. Ind. (1826) 1022; Ridley, Fl. Malay. Pen. 2 (1923) 421. TYPE SPECIES: *C. peregrinum* Reinw. (= *C. fragrans* (Roxb.) DC.).

Distribution. Bengal, Indo-China, Malay Peninsula, Sumatra, Java, Borneo, Mindoro, Balabac, Palawan, Celebes and north-west New Guinea. Five species known.

NOTES ON TYPIFICATION:

Cyrtophyllum fragrans (Roxb.) DC., Prod. 9 (1845) 31.

Fagraea fragrans Roxb. [Hort. Beng. (1814) 84, *nom. nud.*], Fl. Ind. ed. Wall., 2 (1824) 32; Cammerl., Bull. Jard. Bot. Btzig. III, 5 (1923) 318. TYPE: *Hunter, Wallich Cat. no. 1597E*, “Pullo Penang” (holo K).

Cyrtophyllum peregrinum Reinw. in Hornschuch, Syll. Pl. Nov. 2 (1825) 9; Blume, Bijdr. Fl. Ned. Ind. (1826) 1022. LECTOTYPE (here chosen): *Reinwardt s.n.*, Java (L sheet no. 908.127-246 & barcode L0005030).

Cyrtophyllum was established with a single species, *C. peregrinum*, thus clearly the type. The second species in Blume (1826), *C. speciosum*, is synonymous with *Picrophloeus javanensis* Blume (1826).

The Wallich edition of the *Flora Indica* clearly mentions Hunter’s collection from “Pullo Penang” under *F. fragrans*, so that the no. 1597E at Kew is the actual type. There is also material at De Candolle’s Herbarium (GDC) numbered 1597A (from Martaban, Burma, not taken as type material) and 1597C (from Penang, Malay Peninsula, a possible isotype). There is a specimen at the Brussels Herbarium (BR, barcode 0000006912710) from the Martius Herbarium, which bears an annotation

stating that this was from Roxburgh's Herbarium and was obtained from an auction at the Linnean Society of London; this is not directly attributable to Hunter as collector and its status as type material is uncertain.

For lectotypification of *C. peregrinum*, it is to be noted that although Reinwardt (1825) in Hornschuch (1825–1828) did not explicitly indicate a specimen together with the species, the article in which his taxa were enumerated, *Nova plantarum indicarum genera*, concerned the plants of Java. Thus, we have selected Reinwardt's specimen for this purpose.

2. *Fagraea* Thunb.

Kongl. Vetensk. Acad. Handl. 3 (1782) 132, t. 4. TYPE SPECIES: *F. ceilanica* Thunb.

Distribution. Sri Lanka, India, across Indo-China, S China and Malesia, to northern Australia and Polynesia. Estimated 55 species.

NOTES ON TYPIFICATION:

Fagraea ceilanica Thunb., Kongl. Vetensk. Acad. Handl. 3 (1782) 132, t. 4. LECTOTYPE (here chosen): *Thunberg s.n.*, "e Ceilona" (UPS no. 004308; iso UPS no. 004309, iso S).

The lectotype (UPS 004308) and isolectotype at S have flowering material, the isolectotype at UPS has fruiting material only. The Stockholm duplicate was annotated "Habitat in Ceylona" in 1778, the year Thunberg completed his Ceylon visit. A specimen at the Linnean Society of London Herbarium (LINN barcode no. LINN-HS292-1) without a clear indication of collector but with Thunberg's species name and publication reference for this name written on it, is a possible isotype.

3. *Limahlania* K.M.Wong & M.Sugumaran, **gen. nov.**

Fagraeae Thunb. *sensu stricto similis sed architectura arboris, caulibus aculeis multis brevibus, foliis serrulatis-crenulatis et seminibus polygonalis differt.* TYPE SPECIES: *L. crenulata* (Maingay ex Clarke) K.M.Wong & M.Sugumaran.

Limahlania is distinguished from allied genera in the *Fagraea* complex by its development according to Fagerlind's architectural model (featuring episodic trunk growth and a modular branch system producing a wave-like sympodial series of axes), stem bark bearing prickles that are shed with maturity, serrulate-crenulate leaf margin, and polygonal seed shape. *Limahlania crenulata* (the Malayan *malabera*), like *C. fragrans* (the *tembusu padang* tree), has become a tree of some horticultural note in Southeast Asia, largely due to its ornamental form, beautiful blooms and adaptability to different site conditions. Both are botanically fascinating trees (Corner 1940; Hallé et al. 1978; Gardner et al. 2011, *sub Fagraea*).

This new genus honours Professor Lim Ah Lan, who has taught and supervised numerous students of plant biology at the University of Malaya, and who has been a most encouraging colleague throughout her long career there, completing in 2012.

Distribution. Malay Peninsula, Sumatra, Borneo (southwest and south Kalimantan), south Indo-China (Cambodia, S Vietnam). A single species.

NOTES ON TYPIFICATION:

Limahlania crenulata (Maingay ex Clarke) K.M.Wong & M.Sugumaran, **comb. nov.**

Fagraea crenulata Maingay ex Clarke in Hooker f., Fl. Brit. Ind. 4 (1883) 83; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 610; Cammerloher, Bull. Jard. Bot. Btzig. III, 5 (1923) 321; Ridley, Fl. Malay. Pen. 2 (1923) 420; Leenhouts, Fl. Males. I, 6 (2) (1962) 324; Kochummen, Tree Fl. Malaya 2 (1973) 271; Wong & Sugau, Sandakania 8 (1996) 59. TYPE: *Maingay s.n.*, Malacca (K).

Fagraea fastigiata auct. non Blume (1838): Ridley, J. Str. Br. R. As. Soc. 30 (1897) 167 *pro parte, quoad Ridley 7552*.

The original description in Hooker's publication only identifies the geographical provenance as "Malacca" for a Maingay collection without indicating number. The unnumbered sheet at K which was accessible to Clarke and Hooker is taken as type. At least two numbered Maingay specimens (1032, 2976) of this species exist at other herbaria (Leenhouts 1962b), so these are not considered type material, although conceivably the notes in Hooker could have meant a representation of this species via a number of Maingay's collections from Malacca, including both numbered and unnumbered material.

4. *Picrophloeus* Blume

Bijdr. Fl. Ned. Ind. (1826) 1019. TYPE SPECIES: *P. javanensis* Blume.

Distribution. Sumatra, Java, Malay Peninsula, Borneo, Celebes, Maluku, New Guinea. Four species.

NOTES ON TYPIFICATION:

Picrophloeus javanensis Blume, Bijdr. Fl. Ned. Ind. (1826) 1020. LECTOTYPE (here chosen): *Blume s.n.*, Java (L: 908.127-201, barcode L0005006).

Blume (1826) provided a brief description in Latin for the genus *Picrophloeus* but not the species *P. javanensis*, which was the sole species listed. A single description, or *descriptio generico-specifica*, for valid publication of both a genus and species, is accepted according to Article 42.1 of the Vienna Code (McNeill et al. 2006), when the genus has but a single species, at least at the time of description. Under the species, Blume stated "*in sylvis altioribus montis Salak*", which is attributable to the specimen *Blume*, Java at the Leiden Herbarium (L: sheet no. 908.127-201). Therefore the genus name *Picrophloeus* and the species *P. javanensis* are to be regarded as validly published.

5. *Utania* G.Don

Gard. Dict. 4 (1838) 663. TYPE SPECIES: *U. morindifolia* (Blume) G.Don (= *U. volubilis* (Wall.) M.Sugumaran).

Kuhlia Reinw. ex Blume, Bijdr. Fl. Ned. Ind. (1826) 777, *nom. illeg.*, non Kunth (1825). *Kentia* Steud., Nomencl. ed. 2 (1840) 845, *nom. illeg.*, non Blume (1838).

Distribution. Indo-China (Cambodia, S Vietnam), the Andaman and Nicobar Islands, Malay Peninsula, Sumatra, Java, Borneo, Celebes, Maluku, the Philippines and New Guinea. Estimated 15 species.

NOTES ON TYPIFICATION:

Utania volubilis (Wall.) M.Sugumaran, **comb. nov.**

Fagraea volubilis Wall. in Roxb., Fl. Ind. ed. Wall. 2 (1824) 36; Wong & Sugau, Sandakania 8 (1996) 40. TYPE: *Jack*, E. Bencoolen (Herb. Wallich, sheet marked "1600. E. Bencoolen" on bottom left) (holo K).

Kuhlia morindifolia Blume, Bijdr. Fl. Ned. Ind. (1826) 777; *F. morindifolia* (Blume) Blume, Rumphia 2 (1838) 32, t. 73; *U. morindifolia* (Blume) G.Don, Gard. Dict. 4 (1838) 663. LECTOTYPE (here chosen): *Anon.* (probably Blume), Java (L: sheet no. 908.127-731, barcode L0005046; isolecto L: sheet no. 908.127-721; isolecto K).

Utania was a new name for the illegitimate *Kuhlia* and was accompanied by a genus description (in English, acceptable under Article 36.1 of the Vienna Code: McNeill et al. 2006). Don listed a single species under his *Utania* as "1. K. MORINDAEFOLIA" (in error for what he should have indicated as "1. U. MORINDAEFOLIA" consistent with the general format of his enumeration of taxa). Under this species, he referred to the locality "Native of Java, at the foot of Mount Salak" and also cited "*Kuhlia morindaefolia* Blum. bijdr. p. 777" (1826), in which there is a description. Thus *Utania* is a validly published genus name and the only one available for use in reference to *Fagraea* section *Racemosae*.

ACKNOWLEDGEMENTS. The Keepers and Curators of the A, BO, K, KEP, KLU, L, NY, US, SAN, SAR and SING herbaria are thanked for loans of, and permission to study, specimens. J.J. Wood, J. Dransfield, N. Martland (Kew), E.F. de Vogel, C.E. Ridsdale, J.-F. Veldkamp, L. Willemse (Leiden), C.C. Davis, D. Boufford, W. Zhang, K. Gandhi (Harvard), L.G. Saw, R.C.K. Chung (Kepong), J.B. Sugau, J.T. Pereira, M. Postar (Sandakan), C.L. Chan (Kota Kinabalu), A.A. Joffre, K. Ariffin (Brunei), R. Kiew (formerly SING), S. Lee, C.J.H. Soh and M.I. Bazilah (SING) are thanked for assisting with a whole range of research matters. Y.W. Low (SING) assisted in fieldwork and research, procurement and assessment of information related to types and specialised collections. Research for, and preparation of, this paper have also benefitted from assistance and comments from L. Struwe (Rutgers University); N. Xia (South China Institute of Botany); C. Puff (University of Vienna), and A.L. Lim (University of Malaya). We thank C. Puff for help with the Latin diagnosis used here. The following are also thanked for their support during the course of the research: M. Sofian-Azirun, Dean of Science, and R. Hashim, Head of the Institute of Biological Sciences, University of Malaya, as well as the previous Deans, A.M. Mohamed and A. Nasrulhaq-Boyce. A University of Malaya Fundamental Research Grant FS 264/2007C helped finance a baseline phylogenetic study, on which the present contribution is partly based.

REFERENCES

- Blume, C.L. (1826) *Bijdragen tot de Flora van Nederlandsch Indië*. Pp. 1020–1022. Batavia: Lands Drukkerij.
- Blume, C.L. (1838) *Rumphia*. Vol. 2. Leiden.
- Cammerloher, H. (1923) Die Loganiaceen und Buddleiaceen Niederländisch-Indiens. *Bull. Jard. Bot. Buitenzorg*. Series III, 5 (4): 295–338.
- Candolle, A.P. de (1845) *Prodromus systematis naturalis regni vegetabilis, sive enumeratio contracta ordinum generum specierumque plantarum huc usque cognitarum, juxta methodi naturalis, normas digesta*. Vol. 9. Paris: Sumptibus Sociorum Treuttel et Würtz.
- Corner, E.J.H. (1940) *Wayside Trees of Malaya*. 2 vols. Singapore: Government Printing Office.
- Don, G. (1838) *A General System of Gardening and Botany* [containing a complete enumeration and description of all plants hitherto known with their generic and specific characters, places of growth, time of flowering, mode of culture and their uses in medicine and domestic economy: preceded by introductions to the linnaean and natural systems and a glossary of the terms used; founded upon Miller's Gardener's dictionary and arranged according to the natural system]. Vol. 4. London: J.G. & F. Rivingston.
- Gardner, S., Sidisunthorn, P. & Lai, E.M. (2011) *Heritage Trees of Penang*. Penang: Areca Books.
- Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) *Tropical Trees and Forests. An Architectural Analysis*. 411 p. Berlin: Springer-Verlag.
- Hooker, J.D. (1883) *The Flora of British India*. Vol. 4. Pp. 82–85. London: L. Reeve & Co.
- Hornschuch, C.F. (1825–1828) *Sylloge Plantarum Novarum Itemque Minus Cognitarum a Praestantissimis Botanicis adhuc Viventibus Collecta et a Societate Regia Botanica Ratisbonensi Edita*. Vol. 2. Ratisbonae: C.E. Brenck.
- King, G. & Gamble, J. S. (1904) *Materials for a Flora of the Malayan Peninsula*. Pp. 813–822. Calcutta: Baptist Mission Press.
- Kochummen, K.M. (1973) Loganiaceae. In: Whitmore, T.C. (ed.), *Tree Flora of Malaya*. Vol. 2. Pp. 296–275. Kuala Lumpur: Longman Malaysia.
- Kunth, K.S. (1825) *Nova genera et species plantarum*. Vol. 7: 234, t. 652. Lutetiae Parisiorum: sumtibus Librariae Graeco-Latino-Germanico.
- Leenhouts, P.W. (1962a) Loganiaceae. In: Steenis, C.G.G.J. van (ed.), *Flora Malesiana*. Series 1 Vol. 6. Pp. 293–336. Groningen: Wolters-Noordhoff Publishing.
- Leenhouts, P.W. (1962b) Identification Lists of Malaysian Specimens, 18. Loganiaceae. Leyden: Foundation Flora Malesiana.
- McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Hawksworth, D.L., Marhold, K. et al. (eds) (2006) International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005. Ruggell: A. R. G. Gantner Verlag KG [Regnum Veg. vol. 146].
- Prevost, M.-F. (1978) Modular construction and its distribution in tropical woody plants. In: Tomlinson, P.B. & Zimmermann, M.H. (eds) *Tropical Trees as Living Systems*. New York: Cambridge Univ. Press.
- Ridley, H.N. (1897) Malay plant names. *J. Straits Branch Roy. Asiat. Soc.* 30: 31–283.
- Ridley, H.N. (1918) New and rare Malayan plants. *J. Straits Branch, Roy. Asiatic Soc.* 79: 97–98.
- Ridley, H.N. (1923) *The Flora of the Malay Peninsula*. Vol. 2. Pp. 415–422. London: L. Reeve & Co.

- Roxburgh, W. (1814) *Hortus Bengalensis, or a Catalogue of the Plants Growing in the Honourable East India Company's Botanical Garden at Calcutta*. Serampore, Calcutta.
- Roxburgh, W. (1824) *Flora indica, or, Descriptions of Indian plants, by the late William Roxburgh*. Edited by Dr. William Carey; to which are added descriptions of plants more recently discovered by Dr. Nathaniel Wallich. Vol. 2. Serampore: Mission Press.
- Steudel, E.G. (1840–1841) *Nomenclator botanicus, seu, Synonymia plantarum universalis: enumerans ordine alphabetico nomina atque synonyma, tum generica tum specifica, et a Linnaeo et a recentioribus de re botanica scriptoribus plantis phanerogamis imposita*. Stuttgart: J.G. Cotta.
- Struwe, L., Albert, V.A. & Bremer, B. (1994) Cladistics and family level classification of Gentianales. *Cladistics* 10: 175–206.
- Struwe, L. & Albert, V.A. (1997) Floristics, cladistics and classification: three case studies in Gentianales. In: Dransfield, J., Coode, M.J.E. & Simpson, D.A. (eds.), *Plant Diversity in Malesia, III*. Pp. 321–352. Kew: Royal Botanic Gardens, Kew.
- Struwe, L., Kadereit, J., Klackenberg, J., Nilsson, S., Thiv, M., Hagen, K.B. von & Albert, V.A. (2002) Systematics, character evolution and biogeography of Gentianaceae, including a new tribal and subtribal classification. In: Struwe, L. & Albert, V.A. (eds.), *Gentianaceae—systematics and natural history*. Pp. 21–309. U.K., Cambridge: Cambridge University Press.
- Struwe, L. & Albert, V.A. (2004) A monograph of neotropical *Potalia* (Gentianaceae: Potalieae). *Syst. Bot.* 29: 670–701.
- Sugumaran, M. & Wong, K.M. (2012) Studies in Malesian Gentianaceae I: *Fagraea* sensu lato—complex genus or several genera? A molecular phylogenetic study. *Gard. Bull. Sing.* 64(2): 301–332.
- Thunberg, C.P. (1782) Beskrifning pa et nytt och vackert orte Genus, Kalladt *Fagraea ceilanica*. *Kongl. Vetensk. Acad. Handl.* 3: 132–134, tab. IV.
- Wong, K.M. & Sugau, J.B. (1996) A revision of *Fagraea* (Loganiaceae) in Borneo, with notes on related Malesian species and 21 new species. *Sandakania* 8: 1–93.

