

INTRODUCTION

1.1 General introduction and taxonomic complexities in *Fagraea sensu lato*: three distinct subgeneric groups; variance in species delimiting concepts

The genus *Fagraea* Thunberg is pantropical, with a distribution from Sri Lanka and India, through tropical South East Asia, reaching as far east to Polynesia (Struwe et al. 2002). The genus is centered in Malesia, where of over 70 species described (Struwe et al. 2002), around 50 species are distributed within Peninsular Malaysia and Borneo (Leenhouts 1962; Wong & Sugau 1996). Species of *Fagraea* have a variety of life forms. They are tall canopy trees, smaller understorey trees reaching only a few meters tall, or are epiphytes and hemi-epiphytes. They occur from sea level to about 3000 m in very moist montane conditions, mostly in forest gaps, forest edges, rocky outcrops, along stream beds in wet tropical forests but less commonly in mesic forests, mangrove swamps and savannas (Motley 2004).

With a large diversity in habit and form, *Fagraea* have species that are both conspicuous and ecologically important in natural landscapes. The widespread *F. fragrans* is a common pioneer on sandy sites, a frequent secondary forest species in the lowlands, and can persist in mature forest. In Peninsular Malaysia, *F. racemosa* is also a common secondary forest species and the large-leaved *F. auriculata* with long-tubed flowers is often conspicuous in coastal sandy sites and on quartz ridges in the lowlands. Throughout the lowland and lower montane forests of Peninsular Malaysia and Borneo, the frequent

presence of *Fagraea* epiphytes or hemi-epiphytes is detected by fallen corollas on the ground at different times during the year. Many species are useful (Motley 2004).

Fagraea is currently placed in the family Gentianaceae within tribe *Potalieae* and subtribe *Potaliinae* (Struwe et al. 2002). In the past, *Fagraea* have been placed within the Loganiaceae (e.g., Leeuwenberg & Leenhouts 1980; Leenhouts 1962) but this classification is now controversial. Subsequent analysis of morphological data (Struwe et al. 1994; Struwe & Albert 1997) and molecular characteristics (Struwe et al. 2002; Downie & Palmer 1992; Olmstead et al. 1993) have demonstrated that *Fagraea* and its tribe *Potalieae* are better placed in the Gentianaceae. Some phytochemical evidence (Jensen 1992; Jensen & Schripsema 2002) also supports the placement of *Fagraea* in the Gentianaceae. The only two clear morphological (non-synapomorphous) characters that make the tribe *Potaliinae* aberrant in Gentianaceae are the occurrence of fleshy berries and occasional large tree habit in some taxa (Molina & Struwe 2009). Other members of the Gentianaceae have dry and capsular fruits and relatively smaller size (Struwe et al. 2002).

Fagraea is closely related to *Anthocleista* Afzel. ex R. Br. and *Potalia* Aublet within the *Potaliinae* (Struwe et al. 2002). Whereas *Fagraea* is a large Indo-Pacific genus, *Potalia* is found in the Central and South American region with nine recorded species and *Anthocleista* is only found in tropical Africa and Madagascar with 14 known species (Struwe et al. 2002). Molecular analyses have consistently shown that the three genera viz., *Anthocleista*, *Fagraea* and *Potalia* form a monophyletic group that justifies inclusion in the same subtribe within Gentianaceae (Struwe et al. 2002; Molina & Struwe 2009).

Within *Fagraea*, three subgeneric groups have been recognized, considered as the sections *Cyrtophyllum*, *Fagraea* and *Racemosae* (Leenhouts 1962). This sectional

classification was adopted by Wong & Sugau (1996), who delimited the sections by inflorescence form and branching, seed form, the nature of fruit epidermis, axillary scale characters and stigma form.

In their review for Borneo, Wong & Sugau (1996) enumerated 42 species, including 20 that they newly described. This was a big contrast to the previous work by Leenhouts (1962, 1984) for Malesia, where he only enumerated 15 species for Borneo. The species concepts of Leenhouts were considered too broad by Conn & Brown (1993) and Wong & Sugau (1996). An example stated by Wong & Sugau (1996) is that Leenhouts (1962) had only one species accepted in the whole section *Racemosae* for Malesia, having reduced many previously described species to synonymy. Wong & Sugau (1996) found many of such taxa morphologically distinct and possible to key out using both vegetative and flower and fruit characters, and resurrected such names from synonymy.

1.2 Scope of work and objectives

The bizarre contrast between the results obtained by Leenhouts (1962) and Wong & Sugau (1996), the demonstration of what appears to be likely impractical species concepts in Leenhouts (1962) by both Conn & Brown (1993) and Wong & Sugau (1996), and the lack of any recent detailed reviews for Malesia other than Borneo, precipitated the present inquiry. Moreover, herbarium holdings of *Fagraea* material would have increased since the accounts by Leenhouts (1962) and Kochummen (1973), the latter being the most recent account for Peninsular Malaysia.

At the fundamental level, the distinctness of the subgeneric groups recognized as *Fagraea* sections *Cyrtothylum*, *Fagraea* and *Racemosae* require further consideration.

This is in view of somewhat conspicuous characters distinguishing them, as summarised by Wong & Sugau (1996), and very preliminary possibilities for generic distinction suggested by limited molecular evidence discussed by Struwe & Albert (1997). This problem is investigated using a molecular analysis of as many taxa as possible from the Malay Peninsula and Borneo, and augmented by molecular results for other taxa in the same subtribe and tribe from other regions.

Parallel to this, a revision of the taxa constituting *Fagraea* sensu lato in the Peninsular Malaysia is conducted. This necessarily draws on herbarium materials and new field studies. Besides allowing a review of species morphological and ecological distinctions, this work would also re-examine the extents of morphological distinction among the so-called sections.

Finally, the merits and intricacies of classifying the several morphologically distinct groups of species within *Fagraea* sensu lato as either sections or distinct genera will be discussed. From this, recommendations would be made for an appropriate classification of the group, including any necessary taxonomic adjustments.

LITERATURE REVIEW

2.1 Taxonomic History of *Fagraea*

2.1.1 Relevant taxonomic documentation

The genus *Fagraea* was originally described by Thunberg in 1782 based on the type species *F. ceilanica* collected from Galle, Sri Lanka. Since then, single to several species have been added piecemeal by Jack (1822), Roxburgh (1824), Blume (1826, 1850), Clarke (1883), Curtis (1894), Ridley (1908, 1918), Merrill (1917), Henderson (1933), Craib & Kerr (1951), Leenhouts (1984), Kochummen (1973) and Wong et al. (1987). On the other hand, a few floristic accounts have attempted summaries of the genus for the Malay Peninsula (King & Gamble 1904, Ridley 1923) and the Malay Archipelago in general (Cammerloher 1923, Leenhouts 1962). More recently, Wong & Sugau (1996) revised the genus for Borneo with remarks on related species elsewhere, and Conn & Brown (1993) reviewed the *F. gracilipes* complex in east Malaysia and Australia.

2.1.2 From Loganiaceae to Gentianaceae: familial classification and taxonomic position of *Fagraea* and the Potalieae

The genus *Fagraea* Thunb. is currently placed within the Gentianaceae, as tribe *Potalieae*, subtribe *Potaliinae*, together with two other genera, *Potalia* Aublet and *Anthocleista* Afzel. ex R. Br. (Struwe et al. 2002). In the past, however, the placement of *Fagraea* has been controversial. In the early classification by Jussieu (1789), *Fagraea* was placed in the Apocynaceae, although other subsequently published works have mostly placed it in the Loganiaceae (e.g., Blume 1826, Ridley 1923, Leenhouts 1962 and Wong & Sugau 1996). Leenhouts (1962) and Leeuwenberg & Leenhouts (1980) used the tribe *Potalieae* for these three genera, but under the family Loganiaceae. Wood anatomical

studies of *Anthocleista*, *Fagraea* and *Potalia* were considered by Mennega (1980) and Jensen & Smets (1998) as providing support for the taxonomic placement of *Fagraea* within the Loganiaceae. *Anthocleista*, *Fagraea* and *Potalia* have also been treated as a separate family, Potaliaceae, by von Martius (1826–1827) and Hutchinson (1973).

The present classification by Struwe (2002) of *Fagraea* and the two allied genera (*Anthocleista* and *Potalia*) within Gentianaceae is not a novel idea as this affinity has been suggested in the past. Earlier works such as by Jussieu (1791), had considered the *Fagraea*-allied genus *Potalia* to be a gentian. Bureau (1856) had formally transferred the tribe *Potalieae* (as "tribu des *Fagraeacées*") from Loganiaceae to Gentianaceae. Bentham (1857) and Gray (1859) also suggested the relationship of the genera *Anthocleista*, *Fagraea* and *Potalia* with other neotropical woody gentians and remarked on the similarity between *Fagraea* and *Lisianthius* (a genus within the same tribe *Potalieae* in the current classification) (see Table 1). Gray (1859) recognised that *Fagraea berteriana* had the bilamellate stigma of *Lisianthius* and Bentham (1857) noted that the only major difference between these taxa was the more developed placentas of *Fagraea*. Fosberg & Sachet (1974, 1980) also suggested including the *Potalieae* in Gentianaceae, although Leeuwenberg & Leenhouts (1980) did not agree (they however, did not provide any evidence to the contrary). Later, Takhtajan (1987), in his *Systema Magnoliophytorum*, also considered this tribe as better placed within the Gentianaceae.

Cladistic analysis of non-molecular and molecular data have also shown that representatives of *Potalieae* (as currently accepted, see Table 1) (Struwe et al. 2002), are consistently positioned within the Gentianaceae. A study by Downie & Palmer (1992) to better understand relationships within the large subclass Asteridae using restriction site

Table 1. Current classification of Gentianaceae subtribes *Potaliinae*, *Faroinae* and *Lisianthiinae* within the tribe *Potalieae* (Struwe et al. 2002).

Subtribe	Genera
<i>Potaliinae</i>	<i>Anthocleista</i> R.Br., <i>Fagraea</i> Thunberg, <i>Potalia</i> Aublet
<i>Faroinae</i>	<i>Congolanthus</i> A. Raynal, <i>Djaloniella</i> P. Taylor, <i>Enicostema</i> Blume, <i>Faroa</i> Welw., <i>Karina</i> Boutique, <i>Neurotheca</i> Salisb. ex Benth. in Benth. & Hook. f., <i>Oreonesion</i> A. Raynal, <i>Pycnosphaera</i> Gilg & <i>Urogentias</i> Gilg & Gilg-Ben.
<i>Lisianthiinae</i>	<i>Lisianthus</i> P. Browne

mapping of chloroplast DNA inverted repeats, placed *Fagraea* in the Gentianaceae clade together with other genera like *Exacum*, *Gentiana*, *Lisianthus* and *Obolaria*, and not within the Loganiaceae clade. A similar study by Olmstead et al. (1993) to circumscribe ordinal-level groups within Asteridae, using sequence analysis of the *rbcL* chloroplast gene, also placed *Fagraea* within a monophyletic Gentianaceae group. A summary of the biochemical characteristics of various groupings within the Gentianaceae, including the distribution of unique compounds such as secoiridoids, corroborated the classification by Struwe et al. (2002) based on chloroplast sequence (*trnL* intron and *matK*) data (Jensen & Schripsema 2002).

Present classification of the tribe *Potalieae* recognises three subtribes including 13 genera and about 154 species (Struwe et al. 2002). The three subtribes are *Potaliinae*, *Faroinae* and *Lisianthiinae*. *Fagraea*, together with *Anthocleista* and *Potalia*, are placed in the *Potaliinae* where together they include about 93 species. *Anthocleista* is found in the African-Malagasy region, *Fagraea* within the Australasian-Pacific region and *Potalia* in the American region. *Fagraea* appears to be the largest genus in this tribe, comprising about 70 species, followed by *Lisianthus*, with about 30 species. *Anthocleista* and *Potalia*

have about 14 and nine species, respectively. The tribe is described in detail in Struwe et al. (2002). Table 1 lists the genera within the three subtribes.

Potalieae members have diverse flower merosity (e.g., 3-merous in the genus *Pycnosphaera*, up to 16-merous in the genus *Anthocleista*) and habit (trees, lianas, shrubs, scramblers and herbs) compared to most other tribes within Gentianaceae. The distribution of *Potalieae* is strictly tropical, mostly found around the equatorial regions (Struwe et al. 2002).

2.1.3 Sectional classification of *Fagraea*

The recognition of infrageneric groups within *Fagraea* has a curious history. Blume (1838) erected *Fagraea* section *Cyrtophyllum*, which included two species he had named as *Cyrtophyllum peregrinum* Reinw. ex Bl. (this is in fact a synonym of the earlier published and better known *F. fragrans* Roxb.) and *C. speciosum* Bl. (a synonym of *F. elliptica* Roxb.). Blume had evidently done this because the many-branched cymes with much smaller flowers in these taxa were rather different from the sparsely branched cymes with larger flowers of *F. ceilanica* Thunb., the type species of the genus.

Later, Blume (1850) included two of his species, *F. kimangu* Bl. and *F. picrophloea* Bl. (both synonyms of *F. elliptica* Roxb., placed in his earlier section *Cyrtophyllum* as above) in his *Fagraea* section *Eufagraea*, with a number of other species that had a very different inflorescence form, where cyme-like clusters of flowers were borne along an elongate main inflorescence axis that superficially resembled a complex raceme (described by Blume as "*cymis in racemum terminalem longissimum*"). In the same

paper, Blume (1850) placed *F. ceilanica* (spelled as *F. zeylanica*) and associated species in "section *Fagraea verae*".

Bentham (1856) appears to be the first person who clearly differentiated three groups within *Fagraea*, as section *Parviflorae* Benth. (= Blume's section *Cyrtophyllum*), section *Racemosae* Benth. (which is that group with raceme-like inflorescences in Blume's section *Eufagraea*), and section *Corymbosae* Benth. (= Blume's section *Fagraea verae*). Subsequent authors who ventured infrageneric names were less thorough. Miquel (1857) considered subgenus *Cyrtophyllum* and subgenus *Eufagraea*, in place of Blume's sections *Cyrtophyllum* and *Fagraea verae*, respectively. Solereder (1892), on the other hand, named section *Pseudoracemosae* and section *Pseudocorymbosae* for Bentham's *Racemosae* and *Corymbosae*, respectively.

In his revision for the Flora Malesiana, Leenhouts (1962) recognised three infrageneric groupings that he called sections *Fagraea* (containing the type and by far the largest number of species), *Cyrtophyllum* (as designated by Blume) and *Racemosae* (as proposed by Bentham). Leenhouts (1962) gave very few characters for sectional distinction, some of which were somewhat inconsistent (see Table 2).

Wong & Sugau (1996) also used these sections as circumscribed by Leenhouts (1962) for their account of *Fagraea* in Borneo, but added more distinguishing characters and provided a key to sections. They used such characters as fruit size, ease of epidermis detachment on drying, seed form, inflorescence branching, characters of the petiole base (including whether scale-like structures develop at the leaf axils), stigma form and the extent of stamen and style exertiveness in open flowers.

Table 2. Diagnostic characteristics of three sections in *Fagraea* according to Leenhouts (1962).

Character / Section	sect. <i>Fagraea</i>	sect. <i>Cyrtophyllum</i>	sect. <i>Racemosae</i>
leaves	auriculate or not	not auriculate	not auriculate
stipules	(<i>not explicitly stated</i>)	(<i>not explicitly stated</i>)	connate in an ocrea
inflorescence form	corymbose, dichasial, glomerulous or with solitary flowers; "usually with a pair of strong branches in the upper leaf axils, therefore the inflorescence as a whole mostly sessile"	corymbose	racemiform, with a number of decussate pairs of small cymes
inflorescence position	always terminal	(<i>not explicitly stated, but including</i> terminal and axillary types in different taxa)	always terminal
flower size	(<i>not explicitly stated</i>)	small	(<i>not explicitly stated</i>)
corolla form	(<i>not explicitly stated</i>)	tubular	(<i>not explicitly stated</i>)
stamens, style	hardly or not exserted	far exserted (except in <i>F. umbelliflora</i>)	not or only slightly exserted
fruit shape, size	(<i>not explicitly stated</i>)	globular, small	(<i>not explicitly stated</i>)

2.1.4 Alternative generic interpretations

Several species placed in *Fagraea* by Leenhouts (1962) and other authors have been the basis of other generic names. Cammerloher (1923) considered *Cyrtophyllum* Reinw. ex Bl. a synonym of *Fagraea*, but Ridley (1923) distinguished the two genera, using the former name for *C. lanceolatum* (Wall.) DC., *C. peregrinum* Reinw. ex Bl. and *C. giganteum* (Ridl.) Ridl. The *Fagraea* equivalents for these names are *F. lanceolata* Wall. (a synonym of *F. wallichiana* Benth.), *F. peregrina* Bl. (a synonym of *F. fragrans* Roxb.), and *F. gigantea* Ridl., respectively.

Leenhouts (1962) suggested that *Cyrtophyllum* and *Picrophloeus* Bl. are synonyms of *Fagraea* section *Cyrtophyllum* (Reinw.) Bl. He also placed the names *Utania* G. Don, *Kuhlia* Reinw. and *Kentia* Steud. (the latter two illegitimate as a later homonym and a name lacking a description, respectively) as synonyms of *Fagraea* section *Racemosae* Benth.

2.1.5 Leenhouts' broad species concepts

Smith (1988) had made the rather cryptic comment that a number of reduced species names (synonyms) in Leenhouts (1962) should be worth recognising at some taxonomic level. Two studies following that of Leenhouts (1962) have provided further insight into the problem of species recognition. In the first, Conn & Brown (1993) demonstrated that Leenhouts' species concepts were too broad when they reviewed the *F. gracilipes* complex. Leenhouts (1962), stating that *F. gracilipes* is a variable species, included many previously described species within *F. gracilipes* but Conn & Brown (1993) were able to recognise good distinguishing characters for a number of these, which they then resurrected as distinct species.

Subsequently, Wong & Sugau (1996) also drew attention to the difficulty of using the generally broad species concepts adopted by Leenhouts (1962), which they consider in many cases to be artificial assemblages of distinct species. They provided some striking examples to support their argument. For instance, they explained that Leenhouts' concept of *F. ceilanica* included specimens from the type provenance (Sri Lanka) with 8–9-cm-long corolla tubes as well as specimens with corolla tubes not more than 3 cm long (from India and Malesia), without any intermediate forms. An even more extreme example was

Leenhout's recognition of only one species, *F. racemosa* for the whole of the section *Racemosae* in the Malesian region, reducing many previously described species to synonymy. In contrast, Wong & Sugau (1996) were able to recognise and key out ten species from Borneo and Malaya, with apparently consistent morphological differences in vegetative and flower or fruit characters. This has given a strong indication that the present classification for Malesia following Leenhouts (1962) may have been oversimplified.

2.1.6 Malayan *Fagraea*

The account by Clark (1883) in Hooker's Flora of British India may be taken as a significant early phase of the documentation of Malayan *Fagraea*, as a number of Malayan taxa are mentioned in that work. In this account, Clark (1883) recognised 10 species of *Fagraea* in the Malay Peninsula. Perhaps to be expected, the number of species documented for the Malay Peninsula increased through the account by King & Gamble (1904), who enumerated 15 species (including four names now considered as synonyms), and Ridley (1923), who enumerated 19 species (including five names now placed in synonymy). This represented a two-fold increase of species enumerated in a 40-year period between Clarke (1883) and Ridley (1923), during a time of active botanical exploration and documentation.

The number of species attributed to the Malay Peninsula was reduced to 15 (including four names now considered to be synonyms) in Leenhouts (1962). This was a direct result of many species names being considered to be applicable to fewer, broadly circumscribed species. The applicability of these broad species concepts have been criticised (see discussion above), and the number of species enumerated for Peninsular

Malaysia later began increasing with the resurrection of species entities from the synonymy in Leenhouts (1962).

Thus, Kochummen (1973), working on the Tree Flora of Malaya project, resurrected *F. gigantea*, for a huge forest tree with a distinctive wavy leaf margin that easily sets it apart from *F. fragrans*, where it had been subsumed. Yet, Kochummen (1973) largely followed Leenhouts (1962) for other species, so that he accounted for a total of 16 species of *Fagraea* in Peninsular Malaysia (including four names now considered to be synonyms). Later, Wong et al. (1987) resurrected another such name, *F. wallichiana*. Wong & Sugau (1996), working primarily on Borneo but also on Peninsular Malaysian taxa that were relevant, resurrected four names (*F. maingayi*, *F. oblonga*, *F. splendens*, *F. volubilis*), and diagnosed two new species previously confused with others (*F. peninsularis*, *F. renae*) applicable to Peninsular Malaysia. In all, Wong & Sugau (1996), recognised 16 species for Peninsular Malaysia in their passing survey.

The number of species enumerated for *Fagraea* in Peninsular Malaysia from the early 20th century until the present study has therefore been dynamic, with additions by earlier authors and a significant reduction by Leenhouts (1962), before re-examination of species concepts led to increased tallies again. These developments have led to the present review of Peninsular Malaysian *Fagraea*, in order to provide an updated inventory and to examine the evidence that could possibly inform on reasonable approaches to classification. Additionally, collections in Peninsular Malaysia would have increased since the last general treatment by Kochummen (1973), both in number as well as in geographical coverage, given greater accessibility into more areas than in the past.

In view of this scenario, it is hardly possible to give the exact size of the genus, since it has been demonstrated clearly how species concepts have changed since Leenhouts (1962), and as yet only parts of the geographical range of the genus has been re-examined in this way. A current estimate of about 70 species of *Fagraea* was given by Struwe et al. (2002).

2.2 Taxonomically important morphological characters

There have been no systematic assessments of taxonomically important morphological characters in *Fagraea*, possibly because most accounts have been floristic in nature and have covered a large group of the genus only in the account for Malesia by Leenhouts (1962). Hence, apart from brief discussions of a few morphological parts in the preamble of the Malesian account of Leenhouts (1962), it is only by an inspection of keys to species and descriptions provided by various authors that many possibly useful characters can be discovered.

2.2.1 Stem prickliness

In *Fagraea* prickles on stems and branches are only present in one species, *F. crenulata* (Clarke 1883, Ridley 1923, Leenhouts 1962, Kochummen 1973, Wong & Sugau 1996).

2.2.2 Leaf shape

Generally, the species known so far have leaf sizes ranging typically from 5 cm to over 20 cm long. Within this range, a number of species characteristically have leaves

within the upper part of the range (such as *F. auriculata*, *F. imperialis*, *F. ridleyi*), whereas some others have typically small leaves (including *F. fragrans* and *F. wallichiana*).

In some species the leaf shape is very distinct such as in the rheophytic *F. stenophylla*, where the leaves are narrowly linear. Leenhouts (1962) regarded this as a variation although other authors, including Wong & Sugau (1996) have recognised this as a good species character; there are also other associated characters that make this species distinct, both ecological (its restriction as a rheophyte) and morphological (floral characters). Cammerloher (1923) appeared to be unaware of the species *F. stenophylla* and proposed his *F. eucalyptifolia* (a synonym of the former) as a new species distinguished by the narrowly linear leaves.

2.2.3 Leaf margin

Fagraea crenulata is the only species in the genus *Fagraea* with crenulate leaf margins and all others species have entire leaf margins. This character has been noted by Clarke (1883), Ridley (1923), Leenhouts (1962), Kochummen (1973) and Wong & Sugau (1996).

2.2.4 Petiole-base appendages

The structures at the petiole base in *Fagraea* species have been discussed by various authors. These structures have been discussed by Leenhouts (1962), who considered the cuplike or sheathing structure as a kind of "vaginae connatae" (connate sheaths) between the petioles of a leaf pair (as typically expressed in *F. salticola* Leenh., where two "axillary scales" meet but are not conspicuously joined along the interpetiolar

median), but can also take the form of an ochrea or completely cuplike structure (as in *F. racemosa*). These structures were considered as stipules by Leenhouts (1962).

Leenhouts (1962) also discussed the taxonomic utility of auricles, which he considered as appendages to the base of the leaf blade, and distinct from the "stipules". He noted how auricles may be only slightly developed in some species, large in others, and reflexed or not, and in some cases harbour ants (Leenhouts 1962).

The term "stipule" was not favoured by Wong & Sugau (1996), who instead accepted the leaf-stalk bases as basally elaborated into axillary scales. They observed that the axillary scales form just above the petiole base and only loosely clasp the node in the section *Fagraea* but, in contrast, form at the very base of the petiole and fuse together as a tightly clasping nodal ochrea in sections *Cyrtophyllum* and *Racemosae*. The auricular structures developing from the sides of the axillary scale or petiole base are considered simply "leaf-stalk auricles" by them. Such leaf-stalk auricles are very conspicuous in species such as *F. auriculata* and *F. imperialis*.

Struwe et al. (2002) consider stipules to be absent in the Gentianaceae (including *Fagraea*) but that interpetiolar lines or sheaths are conspicuous in many cases. They noted that low, interpetiolar sheaths between leaf bases or around stems can be found in *Fagraea*, *Lisianthus*, *Potalia* and several members of tribe Helieae. They also noted that among the tribe Potalieae, auricles are not common although winged petioles are frequent both in that tribe and among gentians in general.

2.2.5 Inflorescence position and form

The position of the inflorescence is terminal in most species but axillary in several, as noted by Cammerloher (1923), Leenhouts (1962) and Kochummen (1973). Ridley (1923) isolated three species with axillary inflorescences known at the time as the genus *Cyrtophyllum*, but described the inflorescences of that genus as "axillary and terminal", probably guided by his misinterpretation of *C. lanceolatum* (Wall.) DC. (a synonym of *C. wallichiana* Benth.; which in fact has axillary inflorescences). Wong & Sugau (1996) considered that section *Cyrtophyllum* included two distinct groups which they called the *F. fragrans* complex (the only species in the genus with axillary inflorescences) and the *F. elliptica* complex (terminal inflorescences).

In *Fagraea*, the inflorescence type has been variously interpreted by Leenhouts (1962) and Wong & Sugau (1996). Leenhouts (1962) states in the generic description for *Fagraea* that the flowers are solitary to paired, or collected in "3-many-flowered cymose inflorescences", and then describes "corymbose" inflorescences for both section *Cyrtophyllum* and section *Fagraea* in the same work. He described the inflorescences of section *Racemosae* as "racemiform, with a number of decussate pairs of small cymes".

Wong & Sugau (1996) stated that the dichasial cyme is the basic structure for all inflorescence types in *Fagraea* (the central flower is oldest, not youngest, among basically three flowers in the ultimate cluster or inflorescence unit). They acknowledged that inflorescence form is a good character for distinguishing the sections *Cyrtophyllum*, *Fagraea* and *Racemosae*. In their diagnosis, section *Fagraea* has an inflorescence without branching (with just a single flower on a very condensed axis, where all branches are entirely suppressed), or that has well-developed primary branches that rebranch 1–3 times.

For section *Racemosae*, they described the inflorescence as developing a comparatively long axis along which are borne pairs (sometimes resembling tiers) of condensed cyme-like branches; they drew attention to the section *Racemosae* inflorescence as an essentially pendulous inflorescence, compared to erect cymes or flower clusters in the other two sections. They characterised the inflorescence in section *Cyrtophyllum* simply as cymes with well-developed primary branches that rebranch to 3–6 orders. In the *Fagraea* context, no one seems to have discussed how both axillary and terminal cymes could have arisen in the same genus or group, or how they are possibly related in an evolutionary context.

Leenhouts (1962) also used the character of "warty-lenticellate" inflorescence axes to separate *F. blumei* in his key to species, but Wong & Sugau (1996) pointed out that this interpretation included several distinct species throughout Southeast Asia. This character is not used by other workers.

2.2.6 Floral size, involucrate bracts, corolla and stamens

Leenhouts (1962) stated that section *Cyrtophyllum* has inflorescences with "many small flowers" but does not use flower size to characterise the other two sections, in particular section *Fagraea*, where he noted species with flowers ranging from small (corolla tubes under 2 cm long), to medium, to large (corolla tubes around 15 cm long). Wong & Sugau (1996) noted that the flowers in section *Cyrtophyllum* are generally small when compared to the other two sections but did not provide further analysis.

Leenhouts drew attention to some species where the floral bracts are enlarged, to an extent that they partly cover the calyx (e.g., the several-flowered *F. auriculata* and the

solitary-flowered *F. involucrata* and *F. macroscypha*). Wong & Sugau (1996) described this enlarged structure formed by such bracts as an involucre.

Ridley (1923) and Kochummen (1973) noted that corolla shape in *Fagraea* is tubular, salver- or funnel-shaped. Wong & Sugau (1996) mentioned that corolla shape is not mutually exclusive among the sections recognised by Leenhouts (1962).

Leenhouts (1962) mentioned in his sectional description that the stamens and styles are only slightly exserted in section *Fagraea* and section *Racemosae* but long-exserted in section *Cyrtophyllum* (except in *F. umbelliflora*). Wong & Sugau (1996) stated that section *Cyrtophyllum* and section *Fagraea* have long-exserted stamens (and styles) in the open flower, but not or only slightly exserted stamens (and styles) in section *Racemosae*. Ridley (1923) also noted that the stamens are long-exserted in *Cyrtophyllum* but not exsert in *Fagraea*. No careful comparisons appear to have been made apart from these general observations.

2.2.7 Palynology

Early observations were made by Erdtman (1952), who described pollens of two species of *Fagraea*, *F. morindaefolia* (a synonym of *F. volubilis*) and *F. imperialis*, and Guinet (1962), who described and illustrated pollen of *F. obovata*. Punt & Leenhouts (1967) recognised three pollen groups (i.e., *F. fragrans*-type, *F. ceylanica*-type and *F. berteriana*-type) within *Fagraea* using aperture, overall shape and exine characters. The *F. fragrans*-type was divided into three subtypes (*F. fragrans* subtype, *F. crenulata* subtype and *F. racemosa* subtype) and the *F. ceylanica*-type was divided into two subtypes (*F. ceylanica* subtype and *F. annulata* subtype). On the one hand, they noted that all species of

Fagraea in their study had reticulate exine except *F. gardenioides* ssp. *borneensis* (a synonym of *F. borneensis*), which had an imperforate tectum. On the other hand, they noted that the species in *Fagraea* show a large range of variation in pollen characters that is generally not seen within a genus. Rao & Lee (1970) have also described the pollen of *F. fragrans*. In a later study, Punt (1978) recognised ten pollen types among the 27 taxa of *Fagraea*.

Nilsson (2002), reviewing pollen characters of the Gentianaceae, suggested alterations to the pollen groups of Punt & Leenhouts (1967), and Punt (1978). Among various changes recommended, Nilsson (2002) noted that *F. elliptica* and *F. fragrans* have the same pollen type and not different types as suggested by Punt (1978). Nilsson (2002) also concluded that pollen morphology in *Fagraea* is consistent with that shown by members of the Gentianaceae generally, but noted that in *Anthocleista* and *Potalia* (i.e., the other two genera within the Potaliinae in the classification of Struwe et al. 2002) the pollen somewhat resembles those of the Loganiaceae.

All members of the *Fagraea* alliance that have been studied by these authors have symmetrical pollen grains issued as monads. Nilsson (2002) notes the following general characters in the groups relevant to *Fagraea sensu lato* in the Malay Peninsula, which indicate considerable variation:

- (a) a group including *F. ceilanica*, *F. involucrata*: 3-porate, coarsely reticulate grains with rounded to angular lumina enclosed by high, narrow and inclined muri;
- (b) a group including *F. racemosa*: 3-colporate to porate grains with markedly sinuous muri; and

(c) a group including *F. fragrans*, *F. elliptica*: 3-colporate grains, striate-reticulate at mesocolpia and striate at poles.

2.2.8 Ovary structure and placentation

Leenhouts (1962) and Kochummen (1973) described ovaries in *Fagraea* as either two-celled with axile placentation or one-celled with two parietal placentas. However, Leenhouts (1962) had remarked that although he could not conduct a thorough study with herbarium specimens, he had observed inconsistent placentation within a single taxon in one case, although he admitted that the single or few sections made for the few taxa surveyed may not be adequate for understanding this character properly. Wong & Sugau (1996) stated that in their observation of ovaries seen in many species of *Fagraea* across the three sections, the ovaries were all unilocular with two parietal placentas.

2.2.9 Stigmatic structure

Leenhouts (1962) stated his suspicion that stigma form (2-lobed or not) could be an important character in further subdivision of section *Fagraea*, which otherwise has an apparently large assemblage of species. He noted a group of species distributed in the Polynesia-Melanesia-Micronesia-New Guinea region (including *F. berteriana*, *F. bodenii*, *F. salticola*) with 2-lobed stigmas apparently associated with linear anthers inserted on a fleshy ring at the corolla throat, but admitted that each character could also occur without the other (as in *F. annulata* and *F. gardenioides*). In the other group, the undivided stigmas were globular, obconic or truncate.

Wong & Sugau (1996) also suggested that stigmatic structure could be important for sectional classification. They regarded that in *Fagraea* the stigma is basically a capitate structure and the uppermost receptive portion is a "slightly 2-lobed shallow dome" which is demarcated from the basal portion by a transverse line. Wong & Sugau (1996) reported that the stigma remains capitate in section *Cyrtophyllum* but its basal part develops a rim as it matures, producing an overall peltate form in sections *Fagraea* and *Racemosae*.

2.2.10 Fruit form and size

The fruit in *Fagraea* is a berry (Leenhouts 1962, Kochummen 1973). The shape of the fruit varies from globular to narrowly elliptic (Leenhouts 1962) and the only confident records of dehiscence upon fruit maturity appear to be for *F. auriculata* (Ridley 1908; also Leenhouts 1962) and *F. imperialis* (Ridley 1930). Ripe fruit colour ranges from pale greenish-grey to mild yellow to red (Leenhouts 1962, Kochummen 1973).

Wong & Sugau (1996) mentioned that fruit size and the nature of the fruit epidermis (whether detaching or not in dried fruits), are important characters for sectional classification. They observed that fruits in section *Fagraea* are typically large at maturity with the epidermis detaching when dry, and smaller in sections *Cyrtophyllum* and *Racemosae*, where the epidermis remains intact and does not detach upon drying.

2.2.11 Seed characters

Leenhouts (1962) merely notes irregularly angular seeds for *Fagraea* as a whole. Wong & Sugau (1996) point out two seed forms: angular in sections *Cyrtophyllum* and *Racemosae*, and ellipsoid-rounded in section *Fagraea*.

2.3 Biological and ecological aspects

2.3.1 Distribution and habitat diversity

Fagraea is distributed from India and Sri Lanka through Myanmar, Thailand, Indo-China, southern China, Hainan, Taiwan, and Malesia, to northern Australia and New Caledonia. The species occupy a wide diversity of habitats. In Peninsular Malaysia, they are present in the lowland forests, where average daily temperature is around 28 °C, to upper montane forests, where average daily temperature can drop typically to between 15 °C and 20°C. They are found on a wide variety of substrates, on sandy sites behind sea beaches, on rocky quartzite and limestone outcrops, on granite-derived soils on ridges, along alluvial riverbanks, and in freshwater and peat swamps. Some species are characteristically secondary forest or pioneer species in relatively open or disturbed areas.

In Peninsular Malaysia, the most widely distributed and commonly encountered taxa are *F. fragrans* and *F. racemosa*. *Fagraea fragrans* and *F. racemosa* are both commonly found establishing in *belukar* (Malay: secondary forest) sites, as well as under the canopy in oil palm (*Elaeis guineensis*) and rubber-tree (*Hevea brasiliensis*) plantations, but they also occur in old-growth lowland forests. In addition, *F. fragrans* also establishes in some open (especially sandy) sites. In contrast, a number of species may show more specialised adaptation, such as being restricted to upper montane forests (e.g., *F. gardenioides*) or limestone rocks (*F. curtisii*). *Fagraea crenulata* establishes in permanently or periodically open swampy conditions, including behind mangrove belts or along rivers.

2.3.2 Growth habit

Species of *Fagraea* have growth habits ranging from free-standing trees, erect or scrambling shrubs, to climbers, epiphytes, and hemi-epiphytes. The term "hemi-epiphyte" has come to refer to initially terrestrial plants, such as some aroids (Araceae), with stems that creep up tree trunks and then lose connection with the ground through breakage or decomposition of the proximal parts, as well as to the growth habits of "strangling" figs (*Ficus* spp., Moraceae; Putz & Holbrook 1989). In the latter case, the fig plants begin life newly germinated on a tree branch, as an epiphyte, and then develop roots that encircle the supporting trunk and at the same time growing down into the forest floor (Corner 1988). As a number of *Fagraea* species have growth habits similar to strangling figs, here the term "hemi-epiphyte" is likewise adopted to refer to their growth habit. In some cases noted for the so-called strangling figs, the 'host' tree eventually dies because the fig develops a crown of its own that shades out that of the "host" and its anastomosing root-lattice presents further "host" trunk thickening. The same effect has been implied for the hemi-epiphytic *F. imperialis*, which Ridley (1930) says, "begins life as an epiphyte on a Palm or other tree, and, eventually killing its host, descends to the ground and forms a widely-spreading shrub or a tree..."

Some species of the section *Fagraea* are scramblers that form untidy tangles and twines, on small trees or on rocky surfaces (e.g., *F. carnosa*). The tree habit includes both small trees (e.g. *F. gardenioides*, *F. racemosa*) as well as gigantic trees with huge crowns, reaching 30 m in height (e.g., *F. gigantea*).

2.3.3 Vegetative growth: architecture, growth rates

Plant architectural analysis has been used to investigate plant form (Hallé et al. 1978). It was originally emphasized (Hallé et al. 1978) that plant architecture is a function of the species and may not be a taxonomically useful tool at higher levels of classification. Nonetheless, whole families or genera are sometimes represented by just a single growth model (e.g., Myristicaceae and *Diospyros* (Ebenaceae) have Massart's growth architectural model). Also, general tree architecture or particular modes of branch architecture may be distinctive of genera or groups of specially related species, such as in the *Gardenieae* (Rubiaceae) (Wong 2004; Zahid & Wong 2004).

In *Fagraea*, architectural investigations have seldom been thoroughly made probably because most species are rare and many are epiphytes that are difficult to observe. Hallé et al. (1978) analysed and identified the architectural models for *F. crenulata* (Fagerlind's model), *F. fragrans* (Aubreville's model) and *F. racemosa* (Roux's model). Apart from these, no architectural analysis has been made for other *Fagraea* species, so the potential usefulness of growth architecture to taxonomy cannot yet be estimated.

Long-term studies of the growth rates of *Fagraea* species are nearly non-existent. Growth observations over 5 years (1999–2004) have shown that *F. fragrans* saplings grow an average of 0.5–0.7 cm per year (Shono et al. 2007). Holttum (1936), Macmillan (1991) and Watson (1935) also described *F. fragrans* as a very slow-growing species. It is not known if all the large tree-forming species are generally slow-growing. There are also no growth observations for the smaller tree species and hemi-epiphytic species.

2.3.4 Myrmecophily and extra-floral nectaries

Leenhouts (1962) recorded that a few species of *Fagraea* have ant-associations, with ants attracted to extra-floral nectaries at the base of the leaves, on the leaf lamina (a drawing of *F. ridleyi* as Fig. 16 in his work illustrates this) and on the calyces. He also stated that the conspicuously developed leaf-base auricles of a few *Fagraea* species housed ants underneath. Elias (1983) lists *Fagraea* under the "hollow nectaries" group among the six extra-floral nectary groups he recognised, based on a classification of Angiosperm extra-floral nectaries by Zimmerman (1932).

2.3.5 Reproductive biology and ecology

Corner (1940) recorded that the flowers of *F. fragrans* open at about sunset and release strong scent which lasts for five to six days. Leenhouts (1962) cites Burck (1892) for the observation that the flowers of species such as *F. auriculata* are protandrous. The flowers of *F. fragrans* have been recorded as mainly pollinated by insects, especially butterflies, moths and wasps (such as *Xylocopa* spp. and *Trigona* spp.) and also by bats (Ridley 1908, Leenhouts 1962). The bat species *Macroglossus minimus* (Pteropodidae) in particular was recorded by Momose et al. (1998) as visiting the flowers of *F. cuspidata* (misidentified as *F. racemosa* in their work) in Sarawak's lowland dipterocarp forest. Hodgkison et al. (2003) recorded that the spotted-winged bat (*Balionycteris maculata*) is an important seed disperser in Peninsular Malaysia and dispersed the seeds of at least 22 species of plants including *F. racemosa*. Endress (1996) discussed the characteristics of bat-pollinated flowers, which include opening at dusk, white or dull colours (such as greenish or brownish), pungent smells and copious production of pollen and mucilaginous

nectar, and notes that the flowers of *F. racemosa* smell strongly of vinegar (his drawing of the inflorescence in his Fig. 7.1 is more reminiscent of *F. cuspidata* from Borneo than *F. racemosa* from the Malay Peninsula). Endress (1996) also notes that the elongated inflorescence of his *F. racemosa* have only 1-few flowers open at a given day.

The small berries of *F. fragrans* do not dehisce and generally turn yellow-green to red upon maturity (Corner 1988), and are eaten mainly by bats (such as giant flying foxes), birds and possibly also by fruit-eating ants (Leenhouts 1962; Ridley 1908). This species is most probably distributed by birds and bats (Corner 1940), but Ridley (1930) records seeing *Polyrachis* ants actually carry a succulent berry of *F. fragrans* for some distance. In *F. auriculata*, the placenta of the fruit often remains erect in the centre following dehiscence and is very attractive to birds and ants, in contrast to the unpleasant bitter fruit pulp (Ridley 1908). Ridley (1930) records bulbuls dispersing the seeds of this species and noted that seeds of *F. imperialis* were also dispersed by birds eating the sweet orange fruit pulp.

2.4 Present and traditional uses

A third to half of some 70 species of *Fagraea* have found use among indigenous peoples (Motley 2004), mainly for wood, medicinal purposes and horticulture. Due to the wide geographical distribution of the genus and many of its species, multiple local names have been applied to a particular species in many cases. The hundreds of local names among cultures, nations and villages indicate that species of *Fagraea* have been utilized for a long time (Motley 2004).

Two species of *Fagraea* have been used to some extent in horticulture in Peninsular Malaysia, namely *F. fragrans* and *F. crenulata*. *Fagraea fragrans*, also known in the Malay language as *Tembusu padang* or just *Tembusu*, has been popularly used as a roadside tree and is also planted in large gardens. At least two trees of *F. fragrans* have been recorded being more than one hundred years old from the Singapore Botanic Gardens (Kojs 2006). The *tembusu* is very slow-growing and takes well to conditions ranging from well-drained sandy soils to swampy sites (Holttum 1936). This broad adaptability and its strong and attractive tree form, conspicuous flowering, and fragrant flowers have made it popular. *Fagraea crenulata* is a tree of moderate height and tiered pagoda-like structure, locally known in Malay as *Malabera* (Corner 1988), and is sometimes planted along roadsides or in open spaces. This has unusually large and attractive leaves that are clustered towards the end of branches, which may have been the basis for its occasionally being called the *cabbage tree* (Corner 1988). Horticulturally not as well known as the two tree species named above is *F. auriculata*, a species with variable habit, ranging from a smallish tree or large shrub to a hemi-epiphyte. This species has large, trumpet-shaped flowers with attractive foliage. This plant is presently under-utilised but has great potential.

The timbers of *F. fragrans*, *F. gigantea* and *F. rugulosa* are classified as heavy hardwood ($640\text{-}1075 \text{ kg/m}^3$ air-dried density) under the Malaysian Timber Council (2006) listing of commercial timbers. Their timber is traded as *tembusu* wood, which is highly valued for its fine-grained texture, durability and yellow-brown colour. The wood seasons very slowly with very minimal degradation or shrinkage and is suitable for many uses, including heavy construction and carvings (Burkill 1936, Leenhouts 1962, Peters 1995, Malaysian Timber Council 2006).

Some species of *Fagraea* have also been reported to have uses in traditional medicine, within the Malesian region such as *F. auriculata*, *F. fragrans*, *F. maingayi* and *F. racemosa*. These include uses among the Malay and indigenous-people cultures in treatment regimes for dysentery, malaria, scabies, fevers, coughs, sciatica, pains, dropsy, rheumatism and colds (Burkill 1936; Perry 1980; Quisumbing 1978).

MATERIALS AND METHODS

3.1 Herbarium materials and studies

The present study is based on specimens from the following herbaria: Royal Botanic Gardens Kew (K), Forest Research Institute Malaysia, Kepong (KEP), Forest Research Centre, Sabah (SAN), Singapore Botanic Garden (SING) and University of Malaya (KLU). Specimens were studied using a handlens ($\times 20$ magnification) and a binocular microscope with magnification up to 40 times. Images from the website of the Nationaal Herbarium Nederland (L) (<http://www.nationaalherbarium.nl/virtual/>) were also consulted.

3.2 Field collections and processing

A number of field trips were made to collect materials for molecular work and herbarium specimens. During the field trips, observations of growth habits as well as architectural construction of various species of *Fagraea* were made. The field trips and collections made during 2004–2009 covered the following localities.

Peninsular Malaysia

Johor, Mawai, Panti Recreational Forest (April 2008)

Johor, Bukit Iban (November 2008)

Kedah, Langkawi Islands (April 2009)

Malacca, Malacca Botanical Garden (March 2008)

Pahang, Cameron Highlands (July 2007)

Pahang, Fraser's Hill (November 2006, October 2007 & January 2008)

Pahang, Genting Highlands, Gunung Ulu Kali & Awana (February & March 2008
& June 2009)

Pahang, Pekan, Menchali Forest Reserve (April 2004 & April 2008)

Penang, Penang Hills (February 2008)

Perak, Temenggor, Belum Forest Reserve (July 2008)

Selangor, Bukit Takun (July & September 2007 & March 2008)

Selangor, Gombak, Sungai Tua Recreational Forest (January 2005, January &
March 2008)

Selangor, Taman Malawati, Klang Gates quartzite ridge (several trips between
2007 & 2008)

Brununei

Andulau Forest Reserve and Muara District area (June 2008)

Sabah

Gunung Alab (May 2007)

Gunung Alab, Mamut Copper mine area, along Papar-Beaufort Road, Forest
Research Centre Sandakan & Ulu Telupid Forest Reserve (August 2008)

For each flowering or fruiting specimen, 3–8 duplicate vouchers were collected but in the case of sterile collections, only 1–2 vouchers were taken. All collections were numbered, trimmed and pressed in the field and sizeable bundles were tied together. In some situations when the trips lasted more than a few days, the bundles were sealed in plastic bags with some methylated spirit. Specimens were oven-dried at 55°C, for 2–4 weeks depending on the size and thickness of the specimens. Flowers, fruits and leafy

branches were also preserved in AWG (70% alcohol + 28% distilled water + 2% glycerol) solution for future reference.

3.3 Photography

General and close-up photographs of various species in the field were taken with a SLR Nikon Coolpix 5700 camera with built-in flash. Photographs of the herbarium sheets were taken with a Nikon D90 with flash and the photographs of the seeds of a few species of *Fagraea* were taken with a Leica DFC 290 digital imaging system.

3.4 Phylogenetic studies

3.4.1 Collection of materials

Leaf materials of 30 taxa of *Fagraea* (Table 3) collected from various locations were preserved in silica gel. *Fagraea cameronensis*, *F. fraserensis* and *F. nervosa* are new taxa diagnosed in the present study (see 4.4), whereas two other unidentified Bornean taxa were labeled as *F. sp 1* and *F. sp 2*. *Fagraea elliptica* is represented by two accessions from Peninsular Malaysia and Borneo.

3.4.2 DNA extraction

Total DNA was extracted from silica dried or fresh leaf tissue samples as listed in Table 3. The extraction was made using the CTAB (cetyltrimethylammonium bromide) method modified from Doyle & Doyle (1987) (Appendix 1) or using the *DNeasy plant* kit (Qiagen) following the manufacturer's protocol (Qiagen 2003–2009).

Table 3. Voucher numbers and collecting localities for *Fagraea* taxa collected for the present study. Vouchers with 'SAN' numbers were deposited in the Forest Research Centre Sandakan, Sabah (SAN) herbarium and all other vouchers were deposited in the University of Malaya herbarium (KLU).

Taxon	Section	Location	Collector's Number / Voucher Number
<i>F. belukar</i>	<i>Cyrtophyllum</i>	Sandakan, Sabah	JM. Postar & A. Sappan, SAN 147987
<i>F. caudata</i>	<i>Cyrtophyllum</i>	Mount Mike, Sarawak	YW Low, LYW 213
<i>F. collina</i>	<i>Cyrtophyllum</i>	Mount Mike, Sarawak	YW Low, LYW 260
<i>F. elliptica</i> 1	<i>Cyrtophyllum</i>	Mount Ulu Kali, Pahang	YW Low, LYW 358
<i>F. elliptica</i> 2	<i>Cyrtophyllum</i>	Mamut coppermine area, Sabah	JM. Postar et al., SAN 147993
<i>F. fragrans</i>	<i>Cyrtophyllum</i>	Muazam–Menchali road, Pahang	M. Sugumaran, SM 212
<i>F. gigantea</i>	<i>Cyrtophyllum</i>	Malacca Botanical Garden, Malacca	M. Sugumaran, SM 193
<i>F. wallichiana</i>	<i>Cyrtophyllum</i>	Penang Hill, Penang	YW Low, LYW 206
<i>F. auriculata</i>	<i>Fagraea</i>	Klang Gates, Selangor	M. Sugumaran, SM 240
<i>F. cameronensis</i>	<i>Fagraea</i>	Cameron Highlands, Pahang	YW Low, LYW 138
(sp. nov.)			
<i>F. carnosa</i>	<i>Fagraea</i>	Bukit Takun, Selangor	KP Lee, DLKP 30
<i>F. crassifolia</i>	<i>Fagraea</i>	Gunung Raya, Langkawi, Kedah	YW Low, LYW 244
<i>F. crenulata</i>	<i>Fagraea</i>	Rimba Ilmu Botanic Garden, Kuala Lumpur	M. Sugumaran, SM 246
<i>F. curtisii</i>	<i>Fagraea</i>	Pulau Dayang Bunting, Langkawi, Kedah	YW Low, LYW 243
<i>F. fraserensis</i>	<i>Fagraea</i>	Jeriau Falls, Fraser Hill, Pahang	M. Sugumaran, SM 164
(sp. nov.)			
<i>F. gardenioides</i>	<i>Fagraea</i>	Mount Ulu Kali, Pahang	M. Sugumaran, SM 170
<i>F. imperialis</i>	<i>Fagraea</i>	Temenggor, Belum, Perak	M. Sugumaran, SM 238
<i>F. oblonga</i>	<i>Fagraea</i>	Jeriau Falls, Fraser Hill, Pahang	M. Sugumaran, SM 165
<i>F. renae</i>	<i>Fagraea</i>	Sungai Tua Recreational Forest, Selangor	M. Sugumaran, SM 177
<i>F. resinosa</i>	<i>Fagraea</i>	Mount Alab, Sabah	JM. Postar et al., SAN 147998

<i>F. ridleyi</i>	<i>Fagraea</i>	Bukit Iban, Johor	YW Low, LYW 227
<i>F. splendens</i>	<i>Fagraea</i>	Gunung Mat Cincang, Langkawi, Kedah	MS Zahid, ZMS 42
<i>F. stonei</i>	<i>Fagraea</i>	Telupid, Sabah	KM Wong et al., SAN 147989
<i>F. sp. 1</i>	<i>Fagraea</i>	Mount Alab, Sabah	JM. Postar et al., SAN 149702
<i>F. cuspidata</i>	<i>Racemosae</i>	Sandakan, Sabah	D. Seligi & U. Lingkong, SAN 145303
<i>F. nervosa</i> (sp. nov.)	<i>Racemosae</i>	Mawai, Johor	M. Sugumaran, SM 201
<i>F. racemosa</i>	<i>Racemosae</i>	Rimba Ilmu Botanic Garden, Kuala Lumpur	M. Sugumaran, SM 248
<i>F. spicata</i>	<i>Racemosae</i>	Sandakan, Sabah	JM Postar & A. Sappan, SAN 147985
<i>F. volubilis</i>	<i>Racemosae</i>	Panti Forest Reserve, Johor	M. Sugumaran, SM 206
<i>F. sp. 2</i>	<i>Racemosae</i>	Papar–Beaufort road, Sabah	JM. Postar, SAN 149705

3.4.3 Gene regions and primers

Sequence data from various gene regions were chosen for the phylogenetic analyses viz., ITS (Internal Transcribed Spacer), *trnL* intron, *trnL*–F spacer and *ndhF*. The ITS is located in the nuclear ribosomal genome whereas *trnL* intron, *trnL*–F spacer and *ndhF* are located in the chloroplast genome. These regions have been widely used to study phylogenetic relationships at the family level and lower (Chassot et al., 2001; Davis et al., 2001; Gielly & Taberlet 1996; Ranker et al., 2003; Struwe et al., 2002; Thiv et al., 1999; von Hagen & Kadereit 2001; Yuan & K  pfer 1995, 1997; Yuan et al., 1996, 2003).

The whole ITS region (ITS1, 5.8S rDNA & ITS2) was amplified with universal primers i.e., ITS 1 (forward) and ITS 4 (reverse), following White et al. (1990). For the *trnL* intron and *trnL*–F regions, universal primer sets (C & D and E & F respectively) given by Taberlet et al. (1991) were used. Two new primer sets for the *ndhF* gene sequence

were constructed at conserved regions following alignment of *ndhF* sequences from three taxa [*Fagraea* sp. (AJ 235830), *Anthocleista grandiflora* (AJ 235829) and *Potalia resinifera* (AJ 235831)] obtained from the GenBank. Each of these two sets of primers (GB1 Fwd & GB1 Rev and GB2 Fwd & GB2 Rev) were estimated amplify about 900–1000 bp of the *ndhF* gene (Appendix 2). Sequences of all primers used in this study are listed in Appendix 3.

3.4.4 Polymerase Chain Reaction (PCR)

3.4.4.1 Conditions used for priming ITS, *trnL*–F and *ndhF* regions

PCR for all the regions were performed in a Whatman Biometra T Gradient or Perkin Elmer GeneAmp PCR System 9600 thermocycler. A total reaction mix of 50 µl was prepared for all samples. The mix contained 25 µl of PCR master mix (2x Go Taq® Green Master Mix), 2 µl (50 mM) each of forward and reverse primer, 1–3 µl of DNA template and RNase free water topped up to final volume of 50 µl. The mix is placed in thin-walled PCR-grade 200 µl microtube and loaded into the thermocycler.

The parameters used for PCR amplification were as follows: 1 cycle of 3 min at 94 °C, linked to 30 cycles of 10 s at 94 °C, 20 s at 55 °C, 90 s at 72 °C, followed by 4 minutes at 72 °C to complete primer extension. The PCR-amplified samples were electrophoresed on agarose gel and samples that had a clear single desired band were selected for sequencing. Purification of PCR products were done by using the QIAquick PCR purification kit (Qiagen) following the manufacturer's protocol.

3.4.4.2 Adjustments and techniques used for 'difficult' specimens

Sometimes multiple bands of different sizes were observed after PCR. In such cases, a gradient PCR (running a few tubes with the same samples at the same time but with different annealing temperatures) were performed to find the optimal temperature that amplified a single desired band. The sample with such band was then selected for purification and subsequently sequencing. Other samples always had multiple bands after PCR despite trying to optimize the annealing temperature. In such cases the PCR product was electrophoresed on agarose gel (1.2–1.5 %) with running time about 60 to 90 minutes. The intended band (estimated by the use of a set of particular primers) was then excised and purified using a Qiaquick Gel extraction Kit (Qiagen) following the manufacturer's protocol. This product was then sequenced.

3.4.4.3 Sequencing PCR products and data authentication

PCR products were sequenced on an Applied Biosystems 3730xl DNA Analyser with BigDye® Terminator ver. 3.1 Sequencing Kit in the following cycle sequencing conditions: 25 cycles of 96 °C for 10 s, 50 °C for 5 s and 60 °C for 4 minutes, at rapid thermal ramp for 1 °C/s. Sequencing were done in both directions with the same primers used for PCR. All sequence data were manually checked by eye with the corresponding electropherograms. Ambiguous base pairs (base pairs with multiple peaks) were cross-checked with the complementary sequence data (i.e. forward sequence was cross-checked with reverse sequence and vice versa). This could be done because the forward and reverse strands that were sequenced had an approximate overlap of about 80 %. Samples that had very noisy sequence data were not used in the analyses.

3.4.5 Phylogenetic analyses

3.4.5.1 Sequence alignment

Sequence data were initially aligned using ClustalX 2.0.10 (Larkin et al. 2007). These aligned sequences were then manually adjusted using the software Bioedit (Hall 1999). The boundaries of the ITS, *trnL* intron, *trnL*–F spacer and *ndhF* were determined by comparison with the published outgroup sequence, *Anthocleista grandiflora*, that was also used in the analyses (see Table 4). The *trnL* intron and *trnL*–F spacer sequences were aligned and combining into a single data matrix (hereby referred to as the *trnL*–F). Numerous single and multibase insertions or deletions (indels) were introduced for the ITS and *trnL*–F data sets but no indels were needed for aligning the *ndhF* data set. The aligned data was then saved in a Nexus file format and phylogenetic analyses were performed using PAUP* version 4.0b4a for Macintosh (Swofford 2001) and MrBayes v.3.1 (Huelsenbeck & Ronquist 2001).

3.4.5.2 Phylogenetic assessments

Two phylogenetic assessments were conducted. The first assessment included analyses with individual data sets (ITS, *trnL*–F or *ndhF*) and a combined data set (ITS + *trnL*–F + *ndhF*). This assessment aims to evaluate if (a) reasonable support can be found for any monophyletic groups forming within the ingroup; (b) if such clades correspond to the sections of *Fagraea* circumscribed by morphological characters; and (c) if these clades are consistent (or congruent) among the topologies representing the different gene regions. The combined data analysis was performed to evaluate whether clades were better resolved in comparison with single-gene analyses. This assessment was performed with 29 taxa of

Fagraea (8 from section *Cyrtophyllum*, 16 from section *Fagraea* and 5 from section *Racemosae*) and one taxon as outgroup (*A. grandiflora*). The 29 DNA sequences of *Fagraea* from all four gene regions included in these analyses are new (details in Table 3). The sequences for *A. grandiflora* were obtained from GenBank (Table 4).

The second assessment was done with only the ITS data set where sampling was expanded to 45 taxa. This assessment was done to evaluate whether clades formed among so-called *Fagraea* species within the ingroup can be reasonably circumscribed as distinct genera. The selected ingroup taxa are all from the tribe Potalieae and include the recently revised genera *Anthocleista* and *Potalia* (in the same subtribe, Potaliinae, as *Fagraea*) as well as *Lisianthius* (subtribe Lisianthiinae). The two outgroup taxa belong to two other distantly related tribes within the Gentianaceae, namely, Exaceae (*Exacum affine*) and Gentianeae (*Gentiana algida*) (Struwe et al. 2002). The ITS region was chosen because it was relatively more informative than the other two data sets; moreover, many more ITS sequences were available in the GenBank compared to *trnL*–F (intron + spacer) and *ndhF* sequences. Among the 45 taxa, 43 were included as the ingroup and the remaining two were used as outgroup taxa. The ingroup was represented with 35 *Fagraea* taxa, two *Anthocleista* taxa, three *Lisianthius* taxa and three *Potalia* taxa. Of the *Fagraea* sequences used in this assessment, 30 are new sequences, including *F. volubilis* (which was excluded from the first assessment as sequencing results for the *ndhF* region was very poor) (Table 3). All other sequences, including five sequences of *Fagraea* and the outgroup sequences, were obtained from the GenBank (Table 4).

Table 4. List of species included from the GenBank for this study. Current classification in Gentianaceae, voucher information and GenBank accession numbers corresponding to the respective gene regions are given.

Taxa	Current classification in Gentianaceae (Tribe–Subtribe) (Struwe et al. 2002)	Voucher (<i>Herbarium*</i>)	GenBank Number .(respective gene region)
<i>Anthocleista amplexicaulis</i>	Potalia– <i>Potaliinae</i>	Woulhauser PBZT (NEU)	AJ489863 (ITS)
<i>Anthocleista grandiflora</i>	Potalia– <i>Potaliinae</i>	Callmander s.n. (NEU)	AJ489864 (ITS)
		Callmander s.n. (NEU)	AJ490190 (<i>trnL</i> (UAA) intron)
		Callmander s.n. (NEU)	AY251777 (<i>trnL</i> -F spacer)
		Bremer 3098 (UPS)	AJ235829 (<i>ndhF</i>)
<i>Exacum affine</i>	Exaceae	Miller et al. 6201 (E)	AJ489879 (ITS)
<i>F. berteriana</i>	Potalia– <i>Potaliinae</i>	L. Struwe 1219 (NY)	DQ449918 (ITS)
<i>F. ceilanica</i>	Potalia– <i>Potaliinae</i>	L. Struwe 1300 (NY)	FJ23257 (ITS)
<i>F. elliptica</i>	Potalia– <i>Potaliinae</i>	Takeuchi 7122 (NY)	FJ232579 (ITS)
<i>F. macroscypha</i>	Potalia– <i>Potaliinae</i>	Beaman et al. 8867 (US)	FJ232573 (ITS)
<i>F. salticola</i>	Potalia– <i>Potaliinae</i>	Pullen 326 (US)	FJ232571 (ITS)
<i>Gentiana algida</i>	Gentianeae– <i>Gentianinae</i>	Liu 1257 (HNWP)	DQ398659 (ITS)
<i>Lisianthius brevidentatus</i>	Potalia– <i>Lisianthiinae</i>	Ortiz 1664 (F)	FJ32569 (ITS)
<i>Lisianthius cuspidatus</i>	Potalia– <i>Lisianthiinae</i>	Lewis 895 (F)	FJ32567 (ITS)
<i>Lisianthius laxiflorus</i>	Potalia– <i>Lisianthiinae</i>	Struwe & Specht 1153 (NY)	FJ232552 (ITS)
<i>Potalia amara</i>	Potalia– <i>Potaliinae</i>	S. Mori 24123 (NY)	DQ449919 (ITS)
<i>Potalia elegans</i>	Potalia– <i>Potaliinae</i>	P. Berry 7434 (NY)	DQ449920 (ITS)
<i>Potalia resinifera</i>	Potalia– <i>Potaliinae</i>	B. Stahl 1872 (NY)	DQ449921 (ITS)

* E – Royal Botanic Garden Edinburgh, Edinburgh, Scotland, UK; HNWP – Northwest Plateau Institute of Biology, Xining, Qinghai, China; F – Field Museum of Natural History, Chicago, Illinois, USA; NEU – Université de Neuchâtel, Neuchâtel, Switzerland; NY – New York Botanic Garden, Bronx, New York, USA; UPS – Uppsala University, Uppsala, Sweden; US – Smithsonian Institute, Washington, District of Columbia, USA.

Parsimony analyses in PAUP* was performed with heuristic searches where all characters were unordered and unweighted ('Fitch parsimony'; Fitch 1971). All gaps in the sequence were treated as missing data. Starting trees were obtained using simple stepwise addition sequences, with one tree held at each step with tree bisection–reconnection (TBR) branch swapping algorithm, MULTREES option in effect, accelerated transformation (ACCTRAN), branches with zero length were collapsed and topological constraints were not enforced. Separate and combined analyses of the three data sets (ITS, *trnL*–F and *ndhF*) were performed and strict consensus trees were generated. The bootstrap method (Felsenstein 1985) was used in order to estimate the robustness of the various clades revealed in the consensus tree. Bootstrap values were estimated from 1000 replicates of full-heuristic searches using simple addition sequence and TBR branch swapping with a set 'MAXTREES' limit of 10000 trees per bootstrap replicate. Branches less than 50% value were collapsed. The consistency index (CI) (Kluge & Farris 1969), the retention index (RI) and rescaled consistency index (RC) (Farris 1989) as measures of character fit to the phylogenetic trees were also calculated using PAUP*.

For Bayesian inference analyses, an appropriate evolutionary model was selected by using MrModeltest 2.2 (Nylander 2004) together with PAUP* (Swofford 2001). The programme (MrModeltest 2.2) specifically tests the 24 models available common to PAUP* and MrBayes (Huelsenbeck & Ronquist 2001) with a given data set. The Akaike Information Criterion tests selected the General Time Reversible model with gamma distribution of rates for all individual data sets (ITS, *trnL*–F, *ndhF* and ITS-expanded) but for the combined data set (ITS + *trnL*–F + *ndhF*) the invgamma option was selected. Two independent runs of 1.5 million generations were performed each with four MCMC

(Markov Chain Monte Carlo) chains. One tree was sampled every 500 generations and the first 750 trees (burn-in=750) were excluded from the analyses which amounts to 25 % of the trees sampled. A 95% credible set of trees was generated by including all trees with the highest posterior probabilities until the cumulative posterior probabilities (PP) was 95% (Huelsenback et al. 2001). A 50% majority rule consensus of these generated trees was used to estimate the PP of each clade. PP values above $p = 0.95$ were considered to be statistically significant (Huelsenback & Ronquist 2001, Larget & Simon 1999, Lewis 2001, Rannala & Yang 1996, Kauff & Lutzoni 2002).

3.4.5.3 Test of data partition incongruence

The incongruence length difference test (ILD; Farris et al., 1994, 1995) as implemented in PAUP* as the partition homogeneity test (PHP) was employed to test the null hypothesis that the three data sets (ITS, *trnL*-F & *ndh*F) were homogeneous with respect to phylogenetic information. PHP was performed with 100 replicates of heuristic searches, Maxtree=1000 and TBR branch swapping. It has been suggested that PHT p values more than 0.01 indicate that the data sets are congruent and if combined will either improve or will not affect the accuracy of the phylogenetic information (Cunningham et al. 1998).

RESULTS AND DISCUSSION

4.1 Morphology

4.1.1 Growth habits and architecture

As documented earlier (sect. 2.3.2), the species of *Fagraea s.l* investigated in the present work include free-standing trees, epiphytes, hemi-epiphytes and scramblers. The free-standing trees include small understorey or large canopy-sized trees. The smaller trees are usually a few meters tall and grow as understorey plants in the lowlands, such as *F. racemosa*, or plants that establish on ridges in higher elevations, such as *F. gardenioides*. The species that grow into much larger trees reach about 30 meters tall, such as *F. fragrans* and *F. gigantea*.

A number of species of *Fagraea s.l* are hemi-epiphytes (see sect. 2.3.2 for the definition of the term "hemi-epiphyte"), which occur only within *Fagraea* section *Fagraea*, such as *F. imperialis*, *F. oblonga* and *F. splendens*. The seeds of these plants germinate on a 'host' tree and establish initially as epiphytes. The aerial-roots which develop appear to be more stem-like (Putz & Holbrook 1986) and some encircle the 'host' tree, while others grow towards and root in the ground following the trunk of the 'host' tree. The roots that reach the ground will thicken and remain anchored to the ground throughout the life span of the plant. Also, all along these stem-like roots, smaller roots develop to firmly 'attach' the plant to the 'host' tree, as shown in figures 1A–C. The hemi-epiphyte simply stays perched on the 'host' plant, thus it occupies the host only for physical support (Harrison et al. 2003).



Fig. 1. Aerial roots of hemi-epiphytic *Fagraea*. **A.** The initial stage of a very young hemi-epiphytic *Fagraea splendens*, with a few roots around the 'host' tree (black arrow) that bind the plant in place, and some roots growing towards the ground (white arrow). **B.** A mature *F. oblonga* which has developed a large stem-like root (black arrow) that has grown along the 'host' tree trunk and is rooted to the ground (not seen in the image) along with other smaller anastomosing roots (white arrows) that bind the plant to the 'host tree'. **C.** *F. imperialis*, with a woody and large stem-like root (black arrow) eventually reaching and rooted to the ground, and smaller roots (white arrows) that bind the plant to the 'host'.

The species that are scramblers such as *F. carnosa* and *F. larutensis* are found established on ridges or on rocks. Roots of these plants eventually reach and stay attached to the mineral soil for the entire life span of the plant.

Representatives of *Fagraea s.l* from different sections recognised by Leenhouts (1962) can be generally grouped into four plant architectural models, i.e., Aubréville, Fagerlind, Scarrone and Roux, following the description of architectural models for tropical trees by Hallé et al. (1978).

Aubréville's model can be attributed to four species of *Fagraea*, i.e., *F. caudata*, *F. fragrans*, *F. gigantea* and *F. wallichiana*, which are taxa in *Fagraea* section *Cyrtophyllum* with axillary inflorescences. These species are recognised as the *F. fragrans* complex in this section by Wong & Sugau (1996). Fagerlind's model is only represented in *F. crenulata* from *Fagraea* section *Fagraea*. The rest of the taxa from *Fagraea* section *Fagraea* as well as *Fagraea* section *Cyrtophyllum* with terminal flowering taxa, are represented by Scarrone's model. All members from *Fagraea* section *Racemosae* are represented by Roux's model.

The essential architectural similarity and differences of these four models are summarized in Table 5. The pattern of trunk growth is episodic (Fig. 2) in all models except in Roux's model, where trunk growth is continuous (Fig. 3). The leaf arrangement on the branches are decussate in all models except Roux's model, where the leaf arrangement is distichous (Fig. 3 inset). The branch orientation is basically orthotropic in all models except Roux, where the orientation is truly plagiotropic.



Fig. 2. Aubréville's architectural model in *Fagraea fragrans*. A series of vertical brackets shows distinct growth episodes on the monopodial trunk where internode length generally alternate between series of shorter and longer internodes. The brackets along the branch system show the smaller units of repeated branch segments that develop plagiotropically by apposition. (image by K.M. Wong).



Fig. 3. Arrow indicating the continuous orthotropic trunk growth in *Fagraea volubilis* following Roux's model, where the shoots have no marked resting period and as a result there is no obvious difference in stem internode length. **Inset:** A plagiotropic branch showing distichous leaf pairs (images by K.M. Wong).

Table 5. Comparison of key architectural characters among the four tree architectural models found in *Fagraea* s.l.

	Aubréville	Fagerlind	Scarrone	Roux
Species/Group	<i>Fagraea</i> sect. <i>Cyrtophyllum</i> (with axillary flowering taxa) e.g., <i>F. fragrans</i>	<i>F. crenulata</i>	<i>Fagraea</i> sect. <i>Fagraea</i> (except <i>F. crenulata</i>) and <i>F. sect.</i> <i>Cyrtophyllum</i> (with terminal flowering taxa) e.g., <i>F. renae</i> , <i>F. elliptica</i>	<i>Fagraea</i> sect. <i>Racemosae</i> e.g., <i>F. maingayi</i>
Trunk growth & pattern of growth	Orthotropic, Monopodial & Episodic	Orthotropic, Monopodial & Episodic	Orthotropic, Monopodial & Episodic	Orthotropic, Monopodial & Continuous
Leaf arrangement on branches	Opposite & Decussate	Opposite & Decussate	Opposite & Decussate	Opposite & Distichous
Branch orientation	Orthotropic	Orthotropic	Orthotropic	Plagirotropic
Flowering habit	Axillary	Terminal	Terminal	Terminal
Branch construction	Non-modular (branches indeterminate)	Modular (branches ultimately determinate)	Non-modular, branches sympodial; sometimes apparently modular in crown periphery (branches ultimately determinate)	Non-modular (branches ultimately determinate)
Branch extension pattern	Plagirotropic by apposition	Plagirotropic by substitution	Orthotropic complexes	Monopodial or Sympodial growth by substitution after terminal flowering

Branch construction in Aubréville's model is fundamentally non-modular, as the branch-units grow indefinitely, unconstrained by axillary flowering (Fig. 4). Plants represented under Aubréville's model extend their branches rhythmically, so the developing branch system extends plagirotropically by apposition (Fig. 2). In such a branch extension, the smaller repeated branch modules extend in a precise rhythmic wave-like manner. The replacement growth on each of the branch modules is from the lower side of the distal part of the previous branch unit. In Fagerlind's model, the branch is made up of a series of modular units where the units are ultimately determinate due to the terminal flowering habit. Scarrone's model also has essentially non-modular branching as repeating branch



Fig. 4. Axillary flowering on branch segments in *Fagraea fragrans* does not terminate shoot development, but each segment develops a higher-order branch that continues sympodial extension.

units are not clearly formed in a branch system except at the periphery of the crown where the branchlets can be somewhat modular. The trees represented in Scarrone's model have orthotropic branch complexes that extend sympodially after terminal flowering of a segment (Fig. 5). Plants with Roux's model have non-modular branches as the branch extends as a single lateral unit that grows continuously until it is terminated by flowering (Fig. 6). Then axillary, sympodial replacement occurs (Fig. 7).

4.1.2 Vegetative morphology

4.1.2.1 Trunks and stems

The stem and bark characteristics in *Fagraea s.l* are varied. Smooth to lightly scaly bark surfaces which range from pale brown to grey are present throughout *Fagraea* section *Fagraea*, the most speciose group within the complex. In the other two sections of *Fagraea* (*Cyrtophyllum* and *Racemosae*), the bark becomes longitudinally fissured and can be observed especially in older plants. The fissures range from shallow and regularly close, such as in *F. gigantea* (Fig. 8A), to deeply rugged such as in *F. fragrans* (Fig. 8B). However, in some mature individuals of *F. elliptica*, the fissured bark tends to break off in pieces during stem growth, so the character is sometimes less conspicuous. *Fagraea crenulata* is the only species in the whole genus that develops prickles on the trunk and branches. The prickles are generally conical in their shape (Fig. 8C) and usually become sparse in older trees.



Fig. 5. Orthotropic branch-complexes with shoots terminated by cymes.—**A & inset**, *Fagraea fraserensis* (*Fagraea* section *Fagraea*); **B**, *Fagraea elliptica* (*Fagraea* section *Cyrtophyllum* with terminal flowering taxa).



Fig. 6. Plagiotropic branches of the section *Racemosae* are terminated by pendulous compound cymes as shown here in *Fagraea racemosa*.



Fig. 7. The sympodial growth of branches by substitution after terminal flowering of the preceding shoot in *Fagraea nervosa*. Red arrows show old inflorescences, white arrows show substituted branching after terminal flowering (image by KM Wong).



Fig. 8. Bark characteristics of *Fagraea*. — A, Shallow and more regular fissuring in *Fagraea gigantea*, B, Deep and more rugged fissuring in *Fagraea fragrans*, C, Short conically-shaped prickles along with longitudinal fissuring developing on the trunk and branches in *Fagraea crenulata*.

4.1.2.2 Leaves

Leaves within *Fagraea* s.l. vary mainly in their size, shape and texture. *F. crenulata* forms the largest leaf blades within the complex which range by (20–)25–40(–55) cm in their length and by (12–)20–40(–45) cm in their width. The fleshy leaves tend to form rosette-like groups in the distal part of the branches especially in older trees. The smaller leaves are found in *F. fragrans*, *F. gigantea* and *F. wallichiana* measuring 4.4–13 cm long and 1.8–5.3 cm wide.

Leaf shapes are generally elliptic to obovate but as mentioned in section 2.2.2, the rheophytic Bornean endemic, *F. stenophylla*, have conspicuously long, narrow and linear leaf blades. None of the Peninsular Malaysian species specially surveyed in the present account show such a stenophyllous habit. The fresh leaf texture is thin and papery, such as in *F. fragrans* or *F. gigantea*, but others have thick and leathery leaves, such as *F. auriculata* and *F. imperialis*. The secondary veins on the fresh leaves are conspicuously visible in some taxa, such as *F. ridleyi*, but inconspicuous in others such as *F. carnosa* and *F. oblonga*. The leaf margin in all taxa in *Fagraea* s.l. is entire, except in *F. crenulata*, where the margin is finely crenulate (see 2.2.3).

4.1.2.3 Petiolar sheaths

The base of the petiole in *Fagraea* is sheathing, which is an important morphological character. Three terms are used to describe the structures associated with the petiolar sheath. Firstly the term 'ochrea' is used to describe the cup-like structure around the node formed by a pair of petiolar sheaths that completely fuse. This term has

been used in the past (Wong & Sugau 1996) and is only present in sections *Cyrtophyllum* and *Racemosae* (Fig. 9A & 9B).

Secondly, the term 'ligule' may be used for the scale-like adaxial extension at the petiole base (Fig. 9C), when the petiolar sheaths remain essentially separate and thus do not fuse into an ochrea. This structure was referred by Wong & Sugau (1996) as an axillary scale, used to describe each component of the ochrea. However, the structure is not truly axillary, and instead is more properly a part of the elaborated petiolar base. The term ligule is adopted in this study as it is a more established term to describe the inner extension of the adaxial side of the sheathing leaf base, especially in grasses (Dahlgren et. al 1985).

Finally the term 'auricle' is used for the ear-like structure that sometimes develops at each side of the petiole base and thus exists in pairs. This term has also been used in the past by Leenhouts (1962) and Wong & Sugau (1996). The auricles only develop in some species in section *Fagraea* and are completely absent in sections *Cyrtophyllum* and *Racemosae*. The auricles are usually reflexed in most species (Fig. 9D) and in some species such as *F. auriculata* and *F. imperialis*, they are large and often inhabited by ants on the underside (Fig. 9E).

4.1.3 Inflorescence structure

Inflorescence structure is an important character in delimiting sectional divisions within *Fagraea s.l.* The inflorescence in all three sections is terminal, except for a few taxa within *Fagraea* section *Cyrtophyllum* in which they are exclusively axillary. Wong & Sugau (1996) treated these few taxa with axillary inflorescences as the *F. fragrans* complex, in which they recognised four species, i.e., *F. caudata*, *F. fragrans*, *F. gigantea*



Fig. 9. Petiolar sheath characteristics in *Fagraea*. — **A**, Petiolar sheaths of a leaf pair completely fused to form an ochrea (arrow) in *Fagraea fragrans* (section *Cyrtophyllum*), **B**, Petiolar sheaths fused to form an ochrea in *Fagraea racemosa*, **C**, Petiolar sheaths not fully fused in members of *Fagraea* section *Fagraea*, developing ligules (arrows) at the upper edge of the leaf-stalk base in *Fagraea gardenioides*, **D**, Petiolar sheaths at the leaf base in some species of *Fagraea* section *Fagraea* develop ear-like auricles as in *Fagraea auriculata*, **E**, Ants frequently inhabit the space below the reflexed auricles of *Fagraea auriculata*.

and *F. wallichiana*. They treated all the other taxa with terminal inflorescences in *Fagraea* section *Cyrtophyllum* as the *F. elliptica* complex, in which they also recognised four species, i.e., *F. belukar*, *F. collina*, *F. elliptica* and *F. rugulosa*.

As interpreted by Wong & Sugau (1996), the basic inflorescence structure in *Fagraea* is a dichasial cyme, where the primary branches develop in pairs. In *Fagraea* section *Cyrtophyllum*, the cymes are well-developed where the primary branches can rebranch to 3–6 orders. The primary branches can be as long as the rachis. Also, all branch orders typically have well-spaced internodes and due to this, the rachis as well as the branches are clearly visible in the taxa of this section.

In *Fagraea* section *Racemosae*, the cyme branch internodes are very short and condensed, so that the flowering clusters seem to form on the rachis itself. In some taxa, such as *F. racemosa* and *F. nervosa*, the internodes on the rachis are also very short and up to four orders of branches develop. Therefore the flowers or fruits form very closely surrounding the rachis, which remains mostly hidden (Fig 10A & B). In other taxa, such as in *F. maingayi* and *F. volubilis*, the internodes on the rachis are longer and there are only up to three branching orders, supporting fewer flowering or fruiting terminals. Therefore in these taxa the rachis is clearly visible and the flowering or fruiting clusters appear as tiers on the rachis (Fig 10C). The inflorescence is only conspicuously pendulous in this section, as it can develop a comparatively long main axis (Wong & Sugau 1996).

In section *Fagraea*, the inflorescence can be without any branching, i.e., with solitary flowers when the branch nodes are essentially suppressed. In some taxa, there are instances when an extra node (as in *F. latibracteata*) or extra nodes (in other taxa) is (are) present on the peduncle. In some species, these peduncular nodes can develop additional

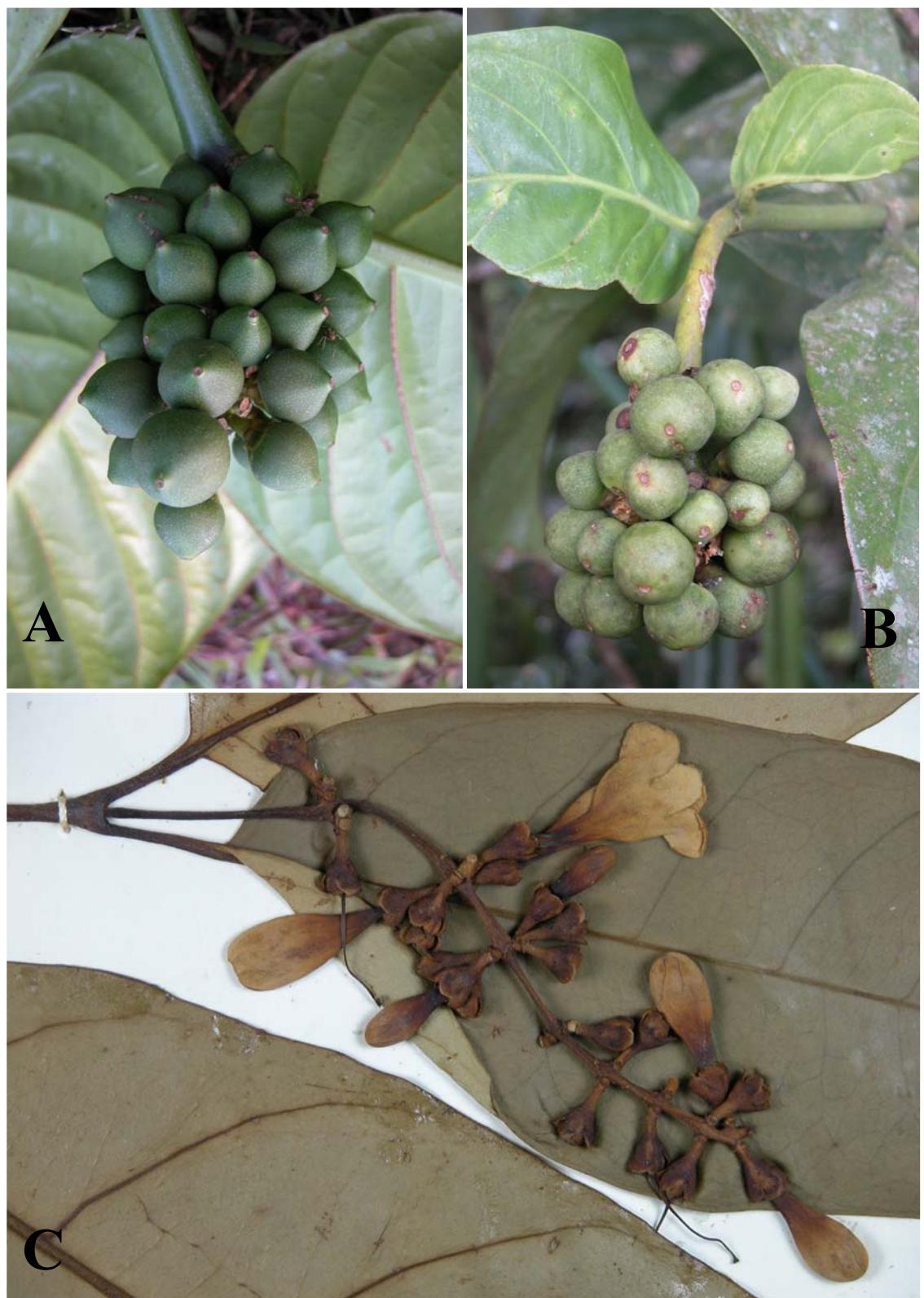


Fig. 10. Inflorescence rachises may be conspicuous or not in *Fagraea* section *Racemosae*. — **A**, *Fagraea nervosa* has a rachis that is not visible due to short rachis internodes and with up to four condensed orders of fruiting (or flowering) terminals, **B**, The rachis is also not entirely visible in *F. racemosa*, except in parts where fruits have detached, **C**, The rachis is clearly visible due to longer rachis internodes and fewer flowering terminals in *F. volubilis*.

pairs of enlarged bracts, such as in *F. resinosa* (Fig. 11), and others which can even form an involucre as in *F. insignis* (Fig. 26). The taxa that develop primary branches typically rebranch only up to one or two orders, such as in *F. fraserensis*. However in a few taxa, primary branches rebranch to three orders, as in *F. renae* or *F. floribunda*. A well-illustrated schematic representation of the inflorescence structure for the genus *Fagraea* was given by Wong & Sugau (1996) (see Fig. 2 in their work).

4.1.4 Flowers

In *Fagraea* s.l., three types of corolla, viz., infundibular (trumpet-shaped), salverform and tubular are found. Infundibular corollas are found in all three sections, the salverform corollas occur only in sections *Cyrtophyllum* and *Fagraea* and tubular corollas are only found among a few species in section *Fagraea*. This has also been observed by Wong & Sugau (1996).

Among the three sections, species in section *Cyrtophyllum* have the smallest corollas measuring up to only 10 mm wide at the mouth. In contrast, species within section *Fagraea* tend to have larger corollas, where the largest measure over 40 mm and up to 80 mm wide at the mouth. The corollas within section *Racemosae* are also small (up to 25 mm wide at the mouth) but generally bigger compared to those in section *Cyrtophyllum*.

The exsertness of the stamen and stigma from the corolla is very pronounced in section *Cyrtophyllum*. More than 70% of the stamen is exserted in *Cyrtophyllum* while the other two sections have stamens reaching only the corolla mouth or only slightly exserted. The styles in section *Cyrtophyllum* are consistently 40% or more exserted from the corolla. The style is at most only slightly exserted from the corolla in the other two sections.

The stigma structure is also of interest as it differs in *Fagraea* section *Cyrtophyllum* compared to the other two sections. The base of the stigma in section *Cyrtophyllum*, does not expand conspicuously, so the structure of the stigmatic head appears knob-like or capitate. In comparison, the stigmatic head in the other two sections appears capitate in younger flowers but as the flowers mature, the base of the stigmatic head expands into a circular plate-like rim, thus appearing generally peltate (Wong & Sugau 1996). This circular plate-like rim around the receptive stigma head is also often undulating in section *Fagraea*.

The stigmatic surface within the section *Cyrtophyllum* forms two shallow distinct lobes which appear as twin mounds on the head in mature and fresh specimens. In section *Fagraea* and *Racemosae*, the stigmatic head is weakly to strongly divided, thus appearing slightly two-lobed.

4.1.5 Fruits

The fruits within section *Cyrtophyllum* are subglobose and are very small, i.e., less than 10 mm in diameter. The fruits in section *Racemosae* are ellipsoid and also in general slightly bigger than in section *Cyrtophyllum*, i.e., not more than 15 mm diameter. In section *Fagraea*, the fruits are narrowly ellipsoid to broadly ovoid to subglobose and generally bigger, measuring more than 40 mm in diameter (except for a few species like *F. crenulata* where the fruits are 10–15 mm across or less).

The fruit epidermis in the sections *Cyrtophyllum* and *Fagraea* can be separated easily from the pericarp as a thin, plastic-like peel in fresh material and in herbarium material the dried epidermis appear wrinkled on the surface of the fruit. This character is

not observed in section *Racemosae* where the epidermis cannot be easily separated from the fruit wall even in fresh material and surface of the dried fruits in herbarium material appears essentially smooth and firm (Fig. 12).

The fruit wall in sections *Cyrtophyllum* and *Fagraea* collapses as it dries and as a result, fruits on herbarium sheets can easily appear flattened or dented. The fruit wall in section *Racemosae* does not collapse or crumble as it dries and retains the original fruit shape (Fig. 12).

Sectioning of very young fruits revealed that placentation in all three sections in *Fagraea s.l* is axile. There are two locules consistently in each flower ovary or fruit. In section *Racemosae*, the older ovaries have tissue tears in their septum, giving the impression of two apparently stalked parietal placentas, which is not the true placentation. Wong & Sugau (1996) had reported in their study that all three sections in *Fagraea* are unilocular with two parietal placentas and Leenhouts (1962) mentioned that the placentation in *Fagraea* is both axile and parietal and in one case inconsistent even within a single taxon.

4.1.6 Seeds

Seeds in *Fagraea* are small, up to about 1–2 mm long and generally ellipsoid-rounded or polygonal. The ellipsoid-rounded seeds (Fig. 13A & B) are found throughout section *Fagraea* with the exception of *F. crenulata*, which has polygonal seeds. The polygonal seed shape is also observed throughout sections *Cyrtophyllum* and *Racemosae* (Fig. 13C & D).



Fig. 11. An assembly of the five calyx lobes (vertical bracket) and two pairs of bracts (larger horizontal bracket) removed from a fresh flower bud of *Fagraea resinosa* (SAN 147998) (image by K.M. Wong). The extra pair of floral bracts (smaller horizontal bracket) are developed from an extra node present between the pedicel and peduncle.

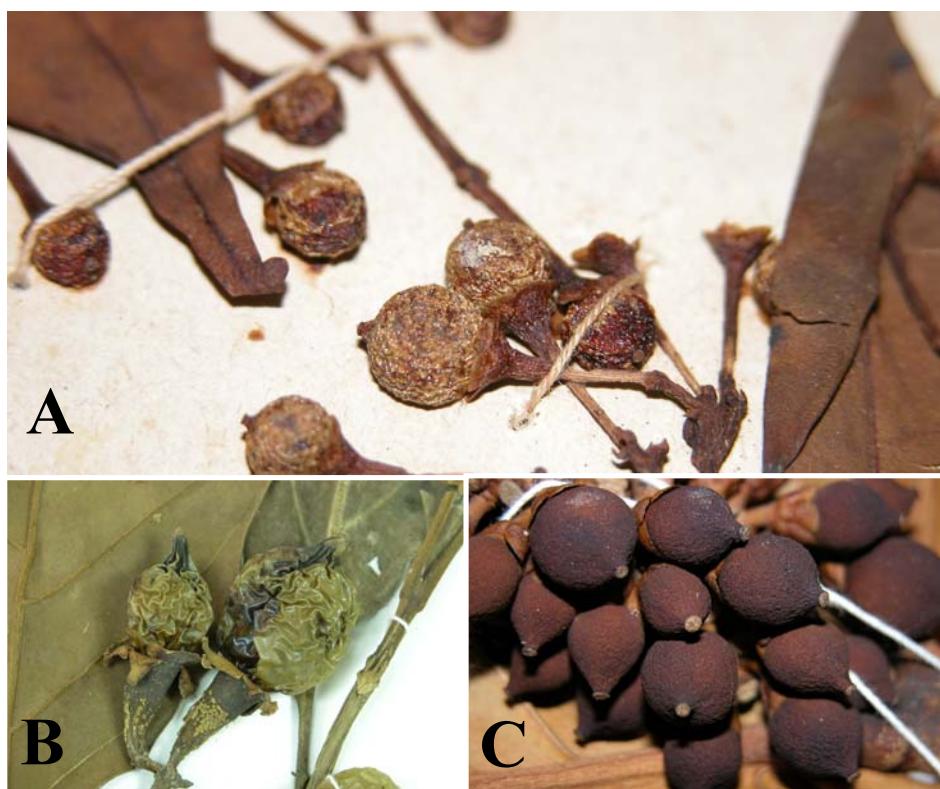


Fig. 12. Fruit surface characteristics of *Fagraea* after drying. — **A**, The surface of the fruit appears crinkled in *Fagraea fragrans* (sect. *Cyrtophyllum*) as the epidermis dries unevenly on the outer surface of the pericarp. **B**, The fruits in *Fagraea* section *Fagraea* also become crinkled and misshapen due to fruit-wall collapse after drying, as seen here in *Fagraea renae*. **C**, The fruit surface is firm and relatively smooth in *Fagraea nervosa* (sect. *Racemosae*) even after drying.

4.1.7 Clonal growth from root suckers

Spontaneous development of root suckers was only observed in *F. auriculata*. Only lateral roots on the ground surface tend to produce sucker shoots (Fig. 14).

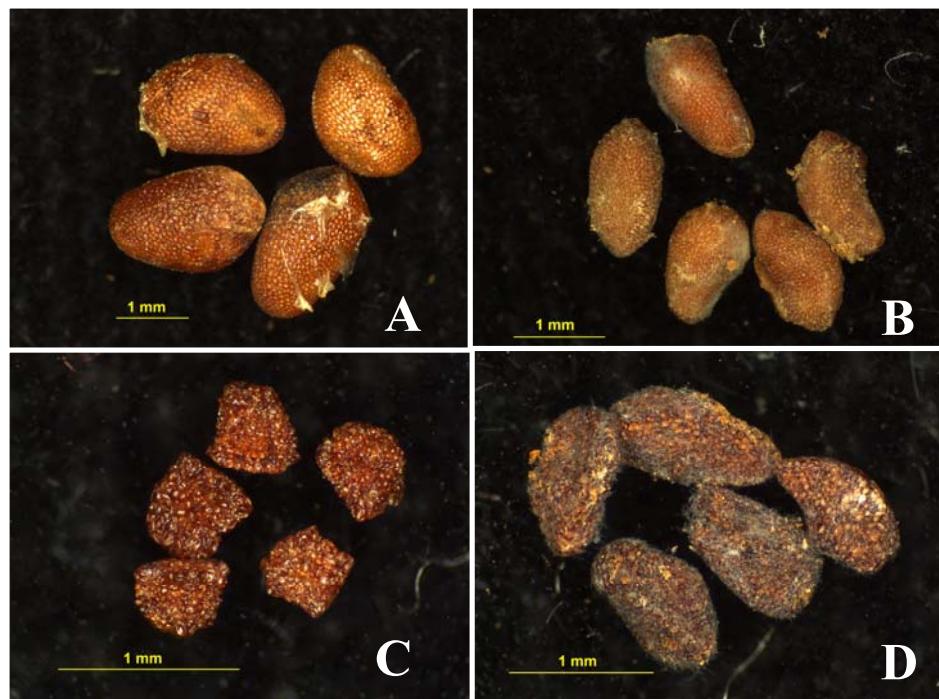


Fig. 13. Seed shapes in *Fagraea*. — A & B Ellipsoid-rounded seeds of *Fagraea imperialis* and *Fagraea splendens* (section *Fagraea*) respectively; C & D Polygonal seeds of *Fagraea elliptica* (section *Cyrtophyllum*) and *Fagraea maingayi* (section *Racemosae*) respectively.



Fig. 14. Root suckers establishing from superficial lateral roots in *Fagraea auriculata*.

4.2 Molecular analysis

4.2.1 Sequence variation

The aligned data matrix of the ITS data set with 30 taxa (Appendix 4) had 639 characters. Out of these, 89 characters were variable but parsimoniously uninformative whereas 64 characters (10% of total characters) were phylogenetically informative. The unaligned length of ITS sequences among the 30 taxa of *Fagraea* (as listed in Table 3) used in this study varied from 622 to 631 bp. These data resulted in uncorrected pairwise sequence divergences ranging from 0 (*F. sp. 1* vs. *F. gardenioides*, *F. curtisii* vs. *F. crassifolia*) to 13.9% (*F. oblonga* vs. *F. sp. 2*).

The individual *trnL*–F sequences (*trnL* intron + *trnL*–F spacer) in *Fagraea* used in this study ranged from 652 to 836 bp. The length varied mainly at several A–T rich regions where alignment could not be readily done due to repeated motifs. These highly variable regions which accounted for 156 bp were excluded from the analyses. The final aligned *trnL*–F data matrix had a total of 811 (Appendix 5) characters where 60 characters were variable and parsimoniously uninformative whereas 49 characters (6% of total characters) were phylogenetically informative. These data resulted in uncorrected pairwise sequence divergences ranging from 0 (*F. auriculata* vs. *F. imperialis*, *F. gigantea* vs. *F. caudata*, *F. wallichiana* vs. *F. caudata*, *F. wallichiana* vs. *F. gigantea*, *F. spicata* vs. *F. cuspidata*, *F. nervosa* vs. *F. cuspidata* and *F. spicata* vs. *F. nervosa*) to 3.5% (*F. stonei* vs. *F. fragrans*).

The two new primer pairs that were used to amplify two partial sequence regions of *ndhF* produced 1832 bp in total. The primer pair "GB1" produced 899 bp whereas the "GB2" pair produced 933 bp. Based on the *ndhF* sequence of *A. grandiflora* (GenBank Acc. AJ235829), the 899 bp sequence data corresponds with positions 161 to 1059

whereas the 933 bp sequence data corresponds with positions 1182 to 2114. The *ndhF* sequences were easily aligned (Appendix 6) and the total 1832 characters had 114 characters that were variable and parsimoniously uninformative whereas 81 characters (4.4% of total characters) were informative. These data resulted in uncorrected pairwise sequence divergences ranging from 0 (*F. racemosa* vs. *F. nervosa*, *F. cuspidata* vs. *F. nervosa*, *F. sp. 2* vs. *F. nervosa*, *F. splendens* and *F. fraserensis* and *F. imperialis* vs. *F. auriculata*) to 2% (*F. resinosa* vs. *F. nervosa*, *F. resinosa* vs. *F. racemosa*, *F. resinosa* vs. *F. spicata*, *F. resinosa* vs. *F. sp. 2*).

The combined data set of ITS, *trnL*–F and *ndhF* resulted in 3282 characters. When combining the data a 5-bp gap was added between data sets for easy reference, however these gaps were excluded from the analyses. The data matrix had 263 variable and parsimoniously uninformative characters whereas 194 characters (5.9% of total characters) were informative.

The aligned matrix of the expanded ITS data set (45 taxa) (Appendix 7) had 697 characters where 131 characters were variable and parsimoniously uninformative whereas 185 characters (26.5% of total characters) were phylogenetically informative. These data resulted in uncorrected pairwise sequence divergences ranging from 0 (*F. ridleyi* vs. *F. gardenioides*, *F. sp. 1* vs. *F. gardenioides*, *F. sp. 1* vs. *F. ridleyi*, *F. curtisii* vs. *F. crassifolia* and *F. macroscypha* vs. *F. auriculata*) to 14% (*F. sp. 2* vs. *F. imperialis*).

4.2.2 Phylogenetic analyses

Data set characteristics are presented in Table 6. In all the analyses, parsimony and Bayesian tree topologies were generally congruent and bootstrap (BS)-supported nodes

mostly also had high support of posterior probabilities (PP). The trees presented were obtained from maximum parsimony analyses and congruent branch support from Bayesian analyses (PP) are stated.

Table 6. Characteristics of the parsimony-based analyses with individual and combined data sets.

Characteristics	ITS	<i>trnL</i> –F (<i>trnL</i> intron + <i>trnL</i> –F spacer)	<i>ndhF</i> (two combined partial regions)	ITS + <i>trnL</i> – F + <i>ndhF</i>	ITS (expanded data set)
Number of taxa	30	30	30	30	45
Total characters	639	811	1832	3282	697
Constant characters	486	702	1637	2825	381
Parsimony informative characters	64	49	81	194	185
Variable characters	89	60	114	263	131
Most parsimonious trees	3520	7224	1	4	2145
Tree length	211	135	242	591	582
Consistency Index, CI (values excluding uninformative sites in parentheses)	0.82 (0.66)	0.85 (0.73)	0.83 (0.68)	0.83 (0.68)	0.73 (0.65)
Retention Index, RI	0.87	0.92	0.91	0.90	0.81
Rescaled Consistency Index, RC	0.71	0.78	0.76	0.74	0.59

4.2.2.1 Analyses of the ITS data set

Parsimony analyses of the 30-taxon ITS data set resulted in 3520 trees with a tree length of 211 (Fig. 15), CI (Consistency Index) of 0.8152 and RI (Retention Index) of 0.8691. Four monophyletic groups can be recognised, referred to as the *Fagraea*, *Racemosa*, *Gigantea* and *Elliptica* clades. In these analyses, all included taxa representing *Fagraea* section *Fagraea* were represented on the *Fagraea* clade except *F. crenulata* which is placed in a tetrachotomy with three other clades. Within the *Fagraea* clade, two

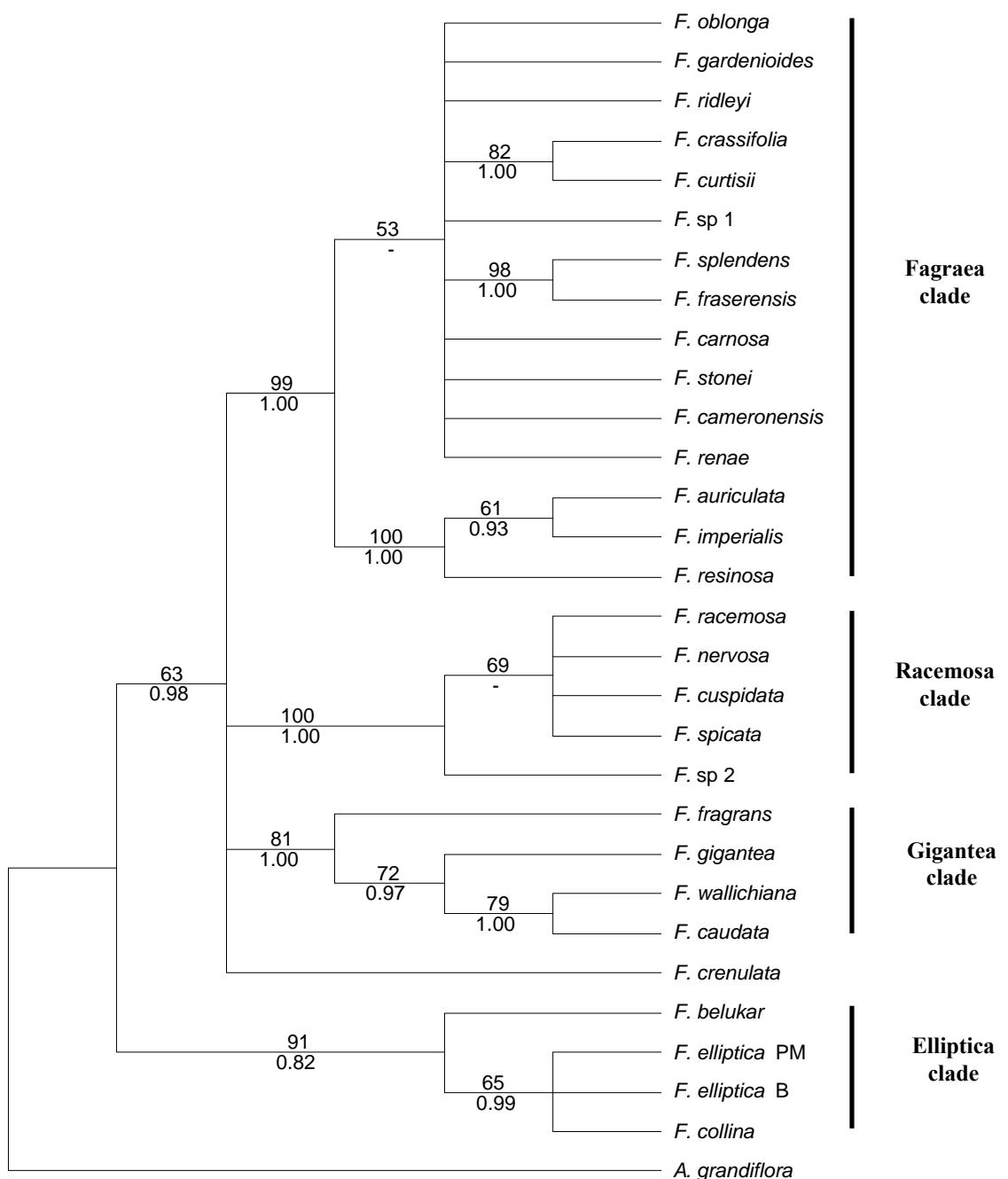


Fig. 15. Strict consensus of 3520 equally parsimonious trees based on the ITS sequence data. The numbers above and below the branches denote Bootstrap and Bayesian Posterior Probability values, respectively. Length (L) = 211; consistency index (CI) = 0.8152; retention index (RI) = 0.8691. *A.* = *Anthocleista*; *F.* = *Fagreae*. Different accessions of *F. elliptica* are indicated (PM = Peninsular Malaysia, B = Borneo).

monophyletic sister groups are formed where one group is smaller consisting of three taxa and the rest form a bigger group with 12 taxa. The three-taxon group is well-supported (BS = 100%; PP = 1.00) with *F. resinosa* is basal to *F. auriculata* and *F. imperialis*. Within the 12-taxon group, there are two smaller well-supported subgroups (*F. crassifolia* and *F. curtisii*; *F. splendens* and *F. fraserensis*) as well as other species whose relationships are unresolved.

Species included in the study representing section *Racemosae* (Racemosa clade) form a strongly supported monophyletic group (BS = 100%; PP = 1.00). Within the Racemosa clade, *F. sp 2* forms the basal taxon to a moderately supported (BS = 69%) and unresolved clade containing four taxa. This relationship however was not observed in the Bayesian analyses.

Section *Cyrtophyllum* is paraphyletic with the eight representative taxa were split into two distinct monophyletic groups. The groups comprising of four taxa each are referred to as the Elliptica and Gigantea clades. The Elliptica clade is basal to the rest of *Fagraea* and well-supported with BS (91%) and moderately supported with PP (0.82) values. Within the Elliptica clade, *F. belukar* is sister to the three other taxa with moderate BS (65%) but strong PP (0.99) support. The Gigantea clade is well supported (BS = 81%; PP = 1.00) and also well resolved where *F. fragrans* is the most basal taxa. The interspecies relationships within this clade received moderate BS and good PP support.

4.2.2.2 Analyses of the *trnL–F* data set

The resulting 7224 most parsimonious trees with the *trnL–F* data set were 135 steps long (Fig. 16) with a CI of 0.8519 and RI of 0.9206. Similar clades observed in the ITS

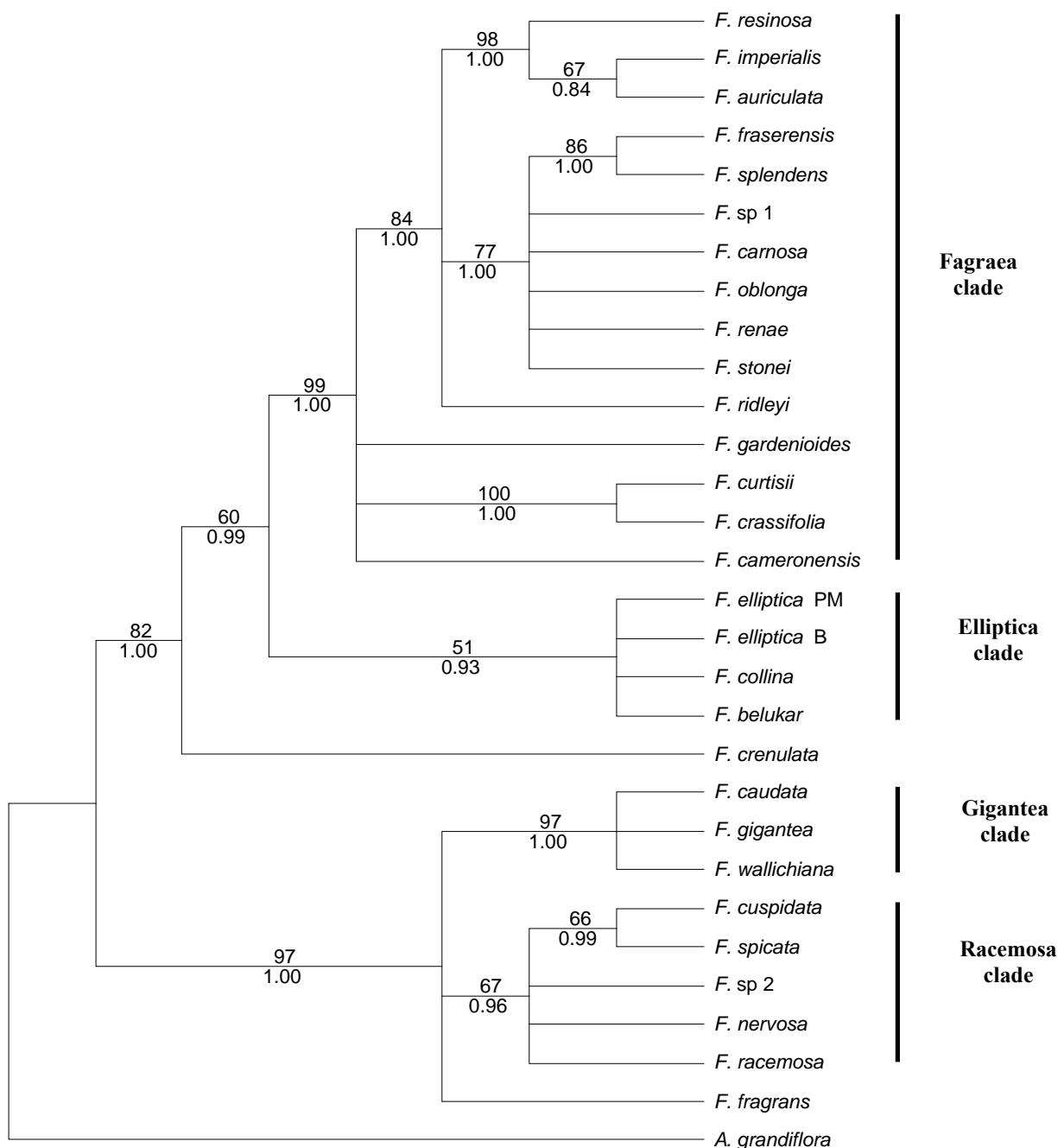


Fig. 16. Strict consensus of 7224 equally parsimonious trees based on the *trnL*-F sequence data. The numbers above and below the branches denote Bootstrap and Bayesian Posterior Probability values respectively. Length (L) = 135; consistency index (CI) = 0.8519; retention index (RI) = 0.9206. *A.* = *Anthocleista*; *F.* = *Fagaceae*. Different accessions of *F. elliptica* are indicated (PM = Peninsular Malaysia, B = Borneo).

tree were also seen in the *trnL*–F tree; however, the interspecific relationships within each clade were less resolved. Again, as in the ITS tree, *F. crenulata* was outside of the Fagraea clade. *Fagraea crenulata* is basal to both the Elliptica and Fagraea clades together and the relationship is well supported (BS = 82%; PP = 1.00). The rest of the species representing *F.* section *Fagraea* (the Fagraea clade) form a strongly supported clade (BS = 99%; PP = 1.00). Within the Fagraea clade, *F. cameronensis* and *F. gardenioides* were unresolved, *F. crassifolia* and *F. curtisii* form a strongly supported group (BS = 100%; PP = 1.00) and the rest also form a well-supported group (BS = 84%; PP = 1.00). In this latter group, *F. ridleyi* is placed in a trichotomy with two well-supported subclades. These subclades have three and seven taxa, respectively. The three-taxon subclade comprising of *F. resinosa*, *F. imperialis* and *F. auriculata* were well resolved where *F. resinosa* was sister to the other two. In the seven-taxon subclade, *F. fraserensis* and *F. splendens* formed a strongly supported group while the rest were unresolved.

Section *Cyrtophyllum* is shown as paraphyletic where four out of its eight species represented formed the Elliptica clade and three other species formed the Gigantea clade. The Elliptica clade was basal to the Fagraea clade and the relationship was moderately supported with BS (60%) but well supported with PP (0.99) values. The Elliptica clade itself was only supported with 51% BS value and a moderate PP support (0.93). The relationship within the Elliptica clade was totally unresolved.

The Gigantea and Racemosa clades plus *F. fragrans* formed a well-supported group (BS = 97%; PP = 1.00). The Gigantea clade received strong branch support (BS = 97%; PP = 1.00) but the interspecies relationships within the clade were unresolved. The remaining taxon, *F. fragrans*, was placed in a trichotomy with the Racemosa and Gigantea

clades. The Racemosa clade, which included all the five representative taxa of section *Racemosae*, was monophyletic with moderate BS (67%) and good PP (0.96) support. The *F. cuspidata* and *F. spicata* subgroup within the Racemosa clade received moderate BS (66%) and good PP (0.99) support and the relationships of the rest were not resolved.

4.2.2.3 Analyses of the *ndhF* data set

Parsimony analysis with the *ndhF* data set produced a single most parsimonious tree with tree length of 242 (Fig. 17), a CI of 0.8347 and RI of 0.9109. The four major clades discussed in the previous two analyses were also observed here and all had good BS and PP support. The *F.* section *Fagraea* (*Fagraea* clade + *F. crenulata*), was a well-supported monophyletic group, with *F. crenulata* basal within the clade. There were two well-supported sister groups, with four and eleven taxa, respectively. The four-taxon group was well resolved with good branch support and *F. gardenioides* basal. The eleven-taxon group has two well supported subgroups: *F. fraserensis* plus *F. splendens*; and a subgroup with *F. resinosa*, *F. imperialis* and *F. auriculata*. These groups were also observed in the analyses with the ITS and *trnL*–F data sets. The relationships among the other taxa in this clade were unresolved.

Section *Cyrtophyllum* was paraphyletic where four out the eight taxa formed the Elliptica clade, while a further three taxa grouped to form the Gigantea clade. The Elliptica clade was sister to the Fagraea clade, both emerging as a group with good branch support (BS = 75%; PP 0.99). The Elliptica clade itself was well supported (BS = 97%; PP = 1.00) and the interspecies relationships within the clade were well resolved with moderate branch support.

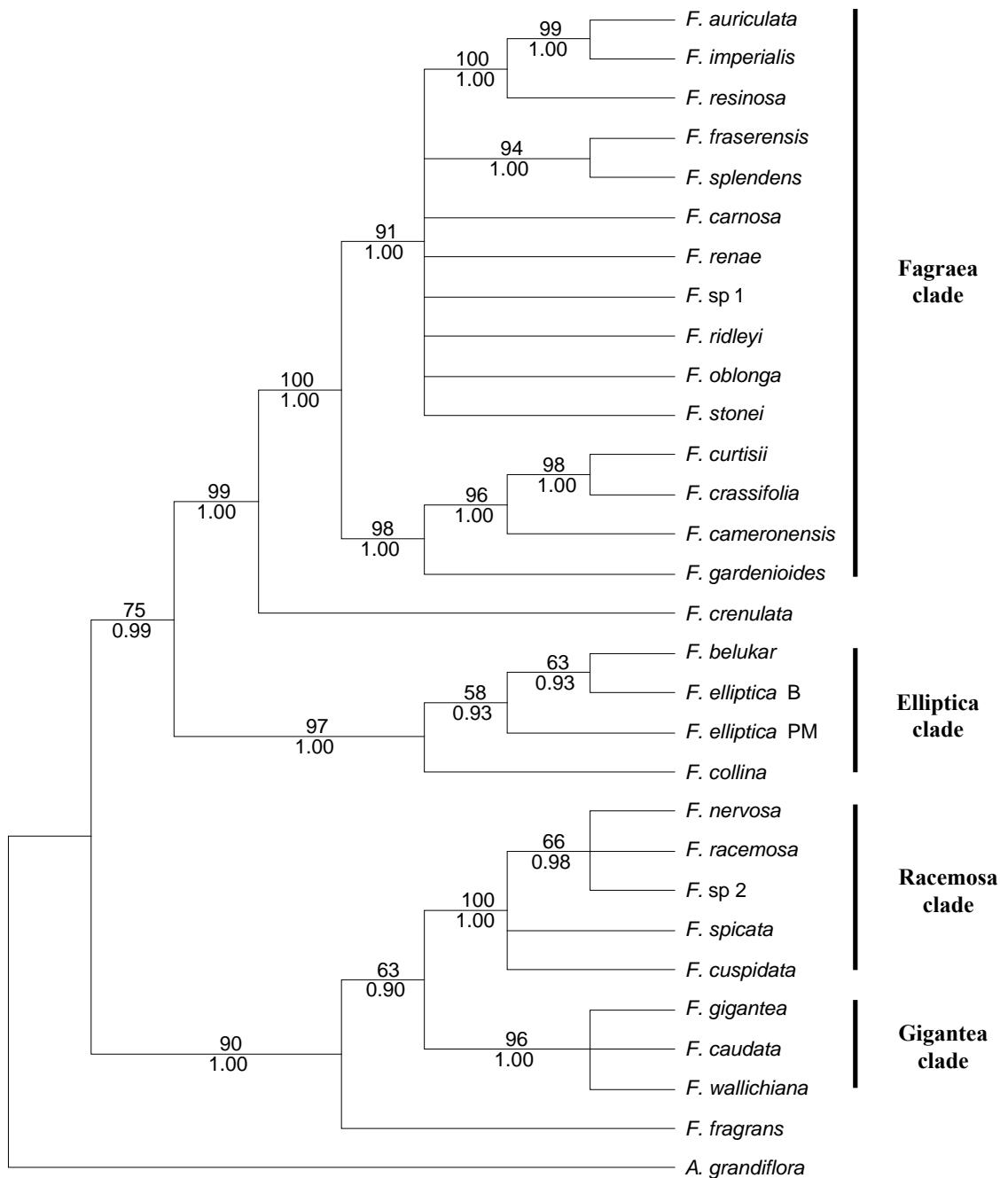


Fig. 17. Single most parsimonious tree based on the *ndhF* sequence data. The numbers above and below the branches denote Bootstrap and Bayesian Posterior Probability values, respectively. Length (L) = 242; consistency index (CI) = 0.8347; retention index (RI) = 0.9109. *A.* = *Anthocleista*; *F.* = *Fagragea*. Different accessions of *F. elliptica* are indicated (PM = Peninsular Malaysia, B = Borneo).

The Gigantea clade was well supported and was sister to the Racemosa clade. However, the interspecies relationships within the Gigantea clade were not resolved. The Racemosa clade was monophyletic and received good branch support (BS = 100%; PP = 1.00). Within the Racemosa clade, *F. nervosa*, *F. racemosa* and *F. sp 2* formed a group with moderate BS (66%) but good PP (0.98) support. The remaining two species were unresolved. *F. fragrans* resolved as a basal taxon for the Gigantea plus Racemosa clades.

4.2.2.4 Analyses of the combined ITS, *trnL*–F and *ndhF* data sets

The result of the ILD test was not significant ($p = 0.03$), indicating that the null hypothesis of data set homogeneity could not be rejected. The three data sets were thus combined into a single matrix and parsimony and Bayesian analyses were performed. Parsimony searches on the combined data set produced four trees having a tree length of 591 (Fig. 18) with a CI of 0.8274 and RI of 0.8979. The combined data set tree was most congruent to the tree resulting from the *ndhF* data set. *Fagraea* section *Fagraea* (*Fagraea* clade + *F. crenulata*) was monophyletic with *F. crenulata* strongly placed (BS = 96%; PP = 1.00) as the basal taxon for the clade. *F. crenulata* is then sister to two well-supported groups, one smaller comprising of four taxa and another bigger with eleven taxa. These groups were also observed in the *ndhF* tree but the internal resolutions were slightly better in this tree. The four-taxon group was well resolved and received good branch support. The eleven-taxon group was divided into two subclades with one unresolved taxon (*F. ridleyi*). The *F. resinosa*, *F. imperialis* and *F. auriculata* clade was well resolved with good branch support. *F. resinosa* was sister to the latter two and this clade was also observed in all the single-gene-data analyses. The interspecies relationships among the taxa in the remaining

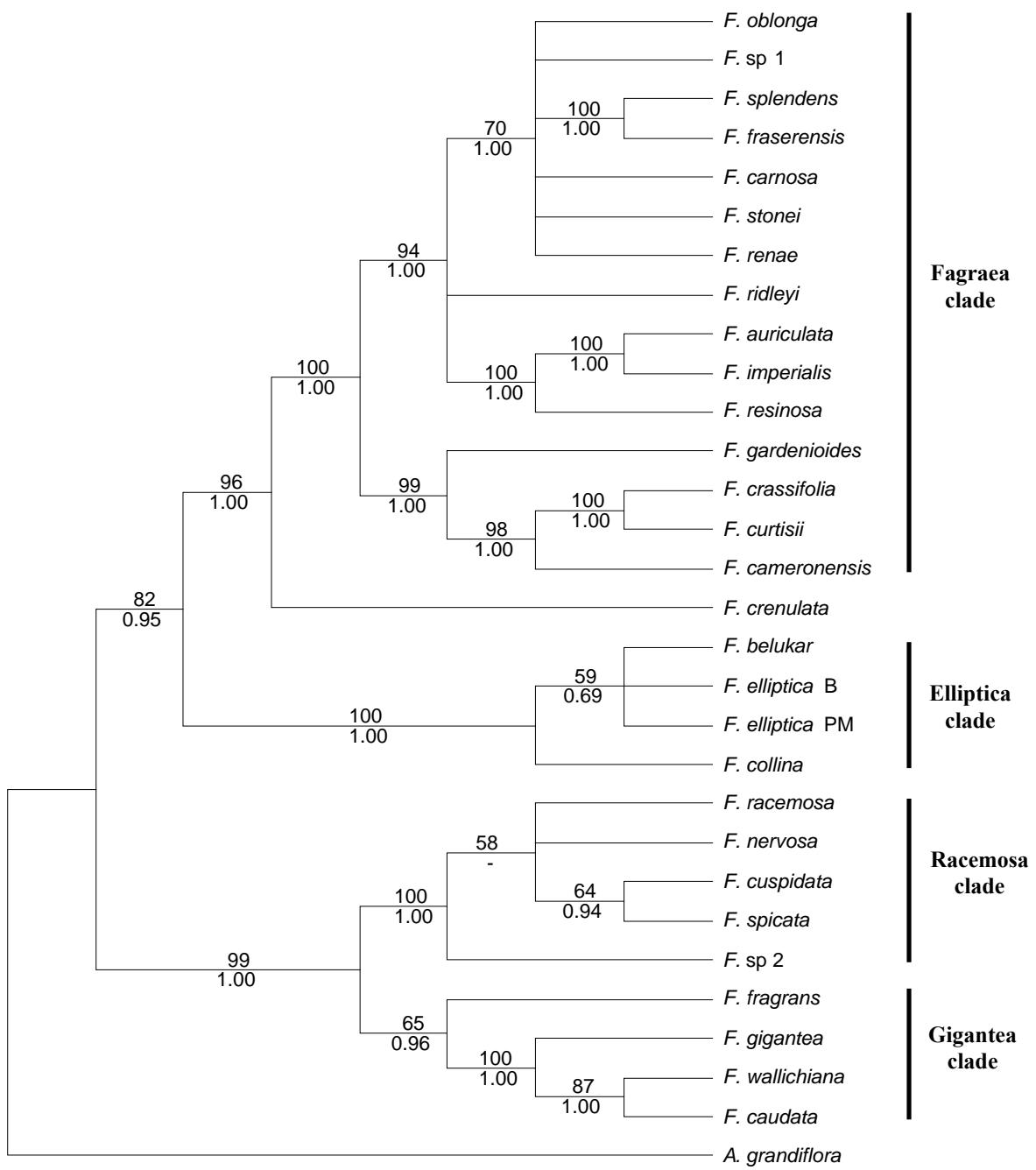


Fig. 18. Strict consensus of four equally parsimonious trees based on the combined ITS, *trnL*-F and *ndhF* sequence data. The numbers above and below the branches denote Bootstrap and Bayesian Posterior Probability values, respectively. Length (L) = 591; consistency index (CI) = 0.8274; retention index (RI) = 0.8979. *A.* = *Anthocleista*; *F.* = *Fagracea*. Different accessions of *F. elliptica* are indicated (PM = Peninsular Malaysia, B = Borneo).

group were not resolved except for two taxa, *F. splendens* and *F. fraserensis*, that formed a well-supported subclade. This subclade was also found in all the single-gene-data analyses.

The section *Cyrtophyllum* was paraphyletic and resolved into two distinct clades (Elliptica and Gigantea) as also observed in all single-gene-data analyses. The Elliptica clade was sister to the Fagraea clade with good support (BS = 82%; PP = 0.95). The Elliptica clade was strongly supported (BS = 100%; PP = 1.00) where *F. collina* was sister to the remaining three taxa in the clade but the relationship received weak support (BS = 59%; PP = 0.69).

The Gigantea and Racemosa clades were sisters to each other with good branch support (BS = 99%; PP = 1.00). The interspecies relationships within the Gigantea clade were well resolved where *F. fragrans* was basal to the remaining three taxa. This relationship received moderate BS support (65%) but good PP support (0.96). The Racemosa clade was well supported (BS = 100%; PP = 1.00) where *F. sp 2* was basal to a weakly formed clade (BS = 58%). Within this clade, *F. cuspidata* and *F. spicata* formed a moderately supported subclade (BS = 64%; PP = 0.94).

4.2.2.5 Analyses of the expanded ITS data set

Parsimony analyses of the expanded ITS data set produced a total of 2145 most parsimonious trees having tree length of 582 with a CI of 0.7337 and RI of 0.8089 (Fig. 19). As seen in the individual and combined data set results, *Fagraea s.l.* was divided into four major clades. *F. crenulata* was placed in a tetrachotomy with the Fagraea, Racemosa and Gigantea clades. This similar pattern was also seen in the 30-taxon ITS tree (Fig. 15).

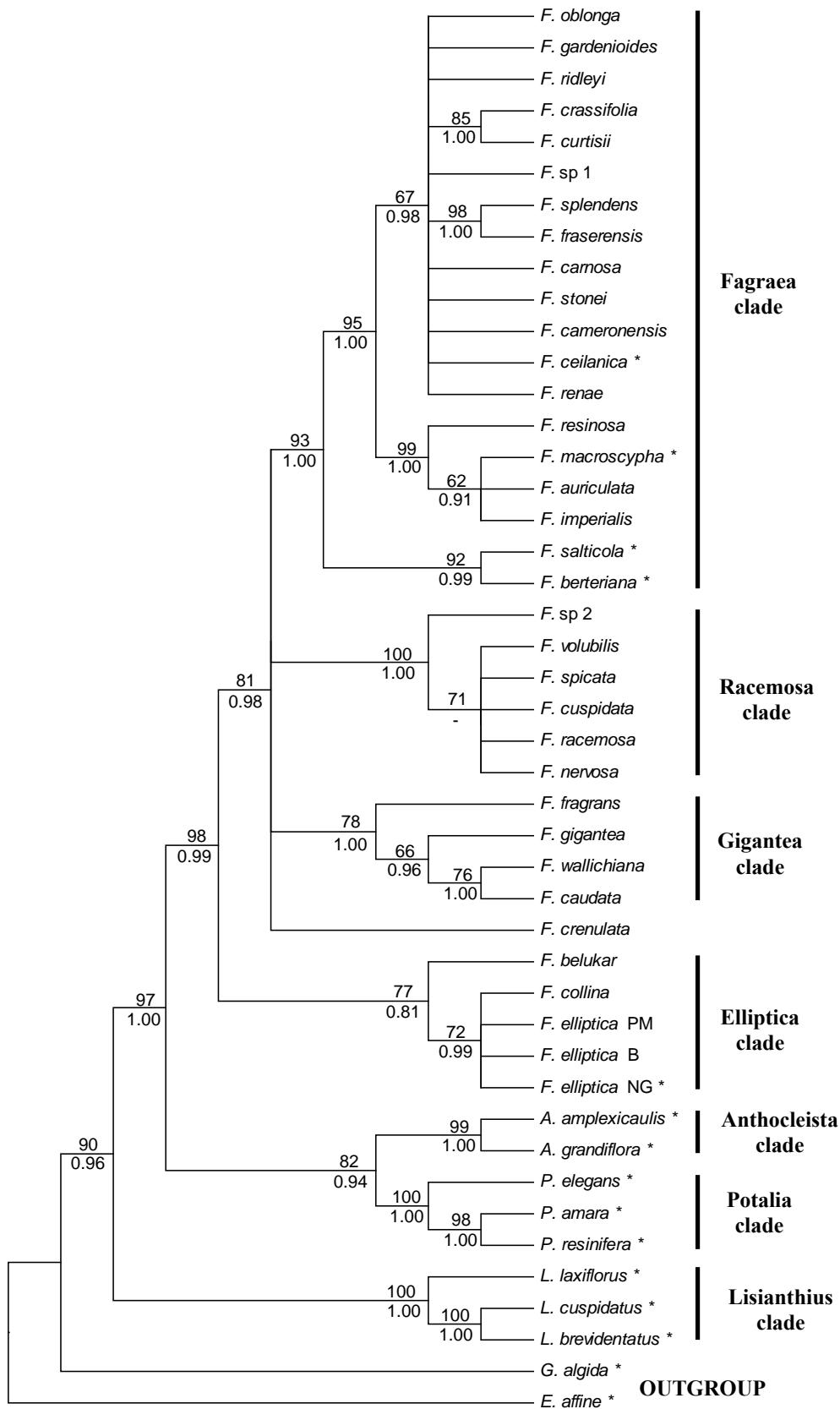


Fig. 19. Strict consensus of 2145 equally parsimonious trees based on the expanded ITS sequence data. The numbers above and below the branches denote Bootstrap and Bayesian Posterior Probability values, respectively. Length (L) = 582; consistency index (CI) = 0.7337; retention index (RI) = 0.8089. *A.* = *Anthocleista*; *E.* = *Exacum*; *F.* = *Fagraea*; *G.* = *Gentiana*; *L.* = *Lisianthus*; *P.* = *Potalia*. Different accessions of *F. elliptica* are indicated (PM = Peninsular Malaysia, B = Borneo, NG = New Guinea). An asterisk after a name indicates the taxon's sequence data obtained from GenBank (see Methods and Materials).

Within the *Fagraea* clade, *F. berteriana* and *F. salticola* are on a well-supported basal branch (BS = 92%; PP = 0.99). These two taxa are sister to two other monophyletic groups where one is larger with 13 taxa and the other is a smaller four-taxon clade. The 13-taxon clade is moderately supported with BS values (67%) but well supported in the Bayesian analyses (PP = 0.98). Within this 13-taxon clade there are two smaller subclades (*F. splendens* and *F. fraserensis*; *F. crassifolia* and *F. curtisii*) with good BS and PP support, as well as several other species whose relationships are unresolved. The four-taxon clade is well supported with both BS and PP values. Within this clade, *F. resinosa* is sister to a moderately supported (BS = 62%; PP = 0.91) subclade.

The Racemosa clade which represents all the taxa selected from section *Racemosae*, is monophyletic and received good support (BS = 100%; PP = 1.00). Within this clade, *F. sp 2* was placed as a basal taxon to the rest of the taxa whose relationships were unresolved. However, this unresolved group was only moderately supported with BS values (71%) and this clade was not present in the Bayesian analysis.

As with all other individual data set analyses, section *Cyrtophyllum* is paraphyletic and was split into two distinct monophyletic groups, viz., the Elliptica and Gigantea clades. The Gigantea clade was moderately supported with BS value (78%) but was well-supported in the Bayesian analyses (PP = 1.00). The interspecies relationships within this clade was well resolved and received moderate BS and strong PP support. The widespread *F. fragrans* was placed as the basal taxon for the Gigantea clade.

The position of the Elliptica clade basal to the rest of *Fagraea* s.l. was well supported (BS = 98%; PP = 0.99). The Elliptica clade received moderate branch support (BS = 77%; PP = 0.81) and within this clade, *F. belukar* was placed as the basal taxon. The

three accessions of *F. elliptica* from Peninsular Malaysia, Borneo and New Guinea along with *F. collina* were clustered together. This subclade was moderately supported with BS (72%) but well supported with PP (0.99) values.

4.3 Implications of the molecular analyses

4.3.1 Correspondence to named sections within *Fagraea* s.l.

Regardless of the genes that were used in the study, including the individual and combined data set analyses as well as the different methods used (MP and Bayesian), the results show *Fagraea* s.l. segregating into four well-supported monophyletic groups. Among these clades, the Fagraea clade and the Racemosa clade closely correspond to the sectional classification, i.e., *Fagraea* section *Fagraea* and *F.* section *Racemosae*, respectively, but *F.* section *Cyrtophyllum* resolved as two distinct clades, i.e., the Elliptica and Gigantea clades.

The position of the bizarre *F. crenulata* basal to Fagraea clade is somewhat doubtful as it unresolved in polytomy in the ITS and the ITS–expanded data sets. It also occupied a position out of the section in the analyses of the *trnL*–F data set. Only the analyses with the *ndhF* and the combined data set supported the placement of *F. crenulata* as a basal taxon to the Fagraea clade. This taxon has a few unique morphological characters within *Fagraea* s.l., such as spiny bark and crenulate leaf margins.

Taxa sampled as *Fagraea* section *Racemosae* were shown to be monophyletic in all the analyses. The clade also received strong BS and PP support in analyses with all the data sets except in the *trnL*–F data set where it received moderate support for BS (67%).

Taxa that represented the *Cyrtophyllum* section resolved as two distinct clades (Gigantea & Elliptica clades) in all the analysed data sets. A position for *F. fragrans* within the Gigantea clade was shown in the analyses with the ITS, ITS-expanded and combined data sets. In the *trnL-F* data set analyses, the position of *F. fragrans* was unclear and in the *ndhF* data set analysis, *F. fragrans* was basal to the Gigantea and Racemosa clades. The analyses clearly show that the section *Cyrtophyllum* is paraphyletic and divides into two distinct clades.

The other related ingroup taxa, i.e. *Anthocleista*, *Potalia* and *Lisianthius*, formed well-supported monophyletic groups (Fig. 19). *Anthocleista* and *Potalia* both formed a group sister to *Fagraea s.l.* with good support (BS = 97%; PP = 1.00), whereas *Lisianthius* was sister to *Anthocleista*, *Potalia* and *Fagraea s.l.* in turn, also with good support (BS = 90%; PP = 0.96).

Thus, there was large but incomplete correspondence between well-formed, well-supported monophyletic groups in the series of analyses conducted with the various molecular data sets and the existing taxonomic "sections" of *Fagraea s.l.* Whereas sections *Fagraea* and *Racemosae* appear well-defined, the section *Cyrtophyllum* appears to be an artificial grouping of two natural groups.

4.3.2 Generic delimitation in *Fagraea s.l.*

The four monophyletic groups of *Fagraea s.l.* are comparable to several well-revised ingroup genera i.e., *Anthocleista*, *Potalia* and *Lisianthius* (Fig. 19) (Struwe et al. 2002, Struwe & Albert 2004). Such a resolution suggests that *Fagraea s.l.*, with clear-cut boundaries delimiting morphologically distinct groups of taxa, could be reasonably

considered as several distinct genera. This is further discussed from the taxonomic standpoint in section 4.4.1 (Generic concepts of *Fagraea* s.l.).

4.3.3 Species concepts in *Fagraea* s.l.

Although the present molecular work was not specially designed to show relationships among species, it reveals some interesting aspects of species concepts adopted in the past. The delimitations by Wong & Sugau (1996) largely contrasted with the broad species concepts adopted by Leenhouts (1962) (see discussion in 2.1.5). The following two examples discussed below are based on the expanded ITS analysis (Fig. 19).

Among the recognised four clades of *Fagraea* s.l., the only clade that had clear interspecies resolution is the Gigantea clade. In this clade, *F. fragrans* was placed as a basal taxon and *F. gigantea* was sister to *F. caudata* and *F. wallichiana*. These relationships received moderate to strong BS support as well as strong PP support.

The structure of these relationships as reflected by molecular data could be explained in terms of distributional range of the four taxa. The basal *F. fragrans* is the most widespread taxon, ranging from Bengal to the west and reaching Sulawesi (Celebes) to the east, as well as being the most commonly encountered among the four taxa. *F. gigantea* is more restricted in distribution, found only in Sumatra, Malaya and Borneo. The last two species, *F. caudata* and *F. wallichiana*, are endemic to Borneo and Peninsular Malaysia, respectively. Also, all these species have clear morphological characters that set them apart as discussed by Wong & Sugau (1996) as well as in the present work (see discussion in section 4.4.3 under *C. fragrans* and *C. wallichianum*). These patterns of distribution, as well as morphological distinctions, reflect on the relationships shown in the

Gigantea clade. Although Leenhouts (1962), in his taxonomic revision for Malesia, included all these taxa under *F. fragrans*, this is highly unlikely because of distinguishing morphological characters that define taxa related in such a way as to suggest later derivation of more restricted taxa from more widespread ancestral taxa. This cannot be an artefact as other species groups of highly distinct species have less cladistic structure in these analyses.

The other example of Leenhouts' (1962) broad species concepts is his definition of *F. ceilanica*. Leenhouts (1962) reduced many species names to synonymy under *F. ceilanica*, however, many of the names have been resurrected and recognised as distinct species by Wong & Sugau (1996), and also in the present study. Three such species (*F. oblonga*, *F. splendens* and *F. crassifolia*) were included in the expanded ITS analysis and the results show them as distinct. The three species emerged in the same clade with *F. ceilanica* but none formed a close alliance with *F. ceilanica*, which should be the case if they are indeed as a single taxon. Furthermore, these three taxa can be differentiated morphologically as described in the present work (see section 4.4.3 under "Key to species" for *Fagraea* Thunb.).

Although more complete sampling of taxa is required for a critical assessment of species delimitations, these two examples above indicate how Leenhouts (1962) has oversimplified species concepts within *Fagraea* at least in these cases.

4.3.4 Morphological characters for identifying phylogenetic clades

An attempt to identify unique, non-molecular characters defining each monophyletic group likely synapomorphies in cladistic terms was made. This is shown in

summary form in Table 7. From this comparison, it can be easily appreciated that the section *Racemosae* appears to have the most number of unique character-states among the sections compared. It is thus highly distinct by morphological characteristics from the other two sections. In section *Fagraea*, *F. crenulata* appears to diverge from all other species in a number of characteristics, including Fagerlind's architectural model with modular branch construction and presence of stem/branch prickles. Likewise, two groups appear well distinguished within the section *Cyrtophyllum*, one with Scarrone's architectural model, terminally flowering and have orthotropic branch complexes; the other with Aubréville's architectural model, axillary flowering and branches that extend plagiotropically by apposition. Likely synapomorphies were found for the Gigantea clade, the Fagraea clade and the Racemosa clade but not for the Elliptica clade, which resolved most basally in the ITS analyses (Fig. 15 & 19).

4.3.5 The Fagraea clade (*Fagraea* s.s., excluding *F. crenulata*)

The growth habits of members in this group are erect, scrambling, climbing or scandent shrubs or smallish trees, which are also facultative hemi-epiphytes. All the other distinguished groups as well as *F. crenulata* are free-standing trees and do not have scrambling, climbing or hemi-epiphytic habit.

Members of *Fagraea* s.s. produce copious amounts of creamy-pale to yellowish latex from the fruit epidermis (visible especially when fresh fruits are cut or bruised). The other groups as well as *F. crenulata* either have small amounts of translucent gummy latex or do not produce latex at all.

The shape of the seeds in this genus are ellipsoid-rounded compared to polygonal in all the other three groups as well as *F. crenulata*.

4.3.6 The Gigantea clade

The general architecture of members of the Gigantea clade follows Aubréville's model in which the monopodial main trunk growth is episodic with opposite decussate phyllotaxis and the branches extend plagiotropically by apposition (sometimes referred to as Terminalian branching) (Halle et al., 1978). The other groups follow Scarrone, Fagerlind or Roux's models. The position of the inflorescence in the Gigantea clade is axillary whereas in all other groups the inflorescence is terminal.

4.3.7 The Racemosa clade

Roux's architectural model applies to all members of the Racemosa clade. Species with this growth model have a monopodial orthotropic trunk with continuous growth. In comparison, all other taxa have episodic trunk stem growth.

The branches in Racemosa clade are opposite and decussate but the leaves on the branches are distichously attached (secondarily distichous) whereas in all the other groups the leaves are arranged in an opposite and decussate pattern. The branches are plagiotropic, ending with a terminal inflorescence whereas the branches in other groups are orthotropic complexes or plagiotropic by apposition. The terminal buds of branches are not conspicuously covered with any resinous substances whereas all the others have creamy to yellowish resin covering the shoot apices.

The inflorescence is generally a pendulous elongate panicle with cymose branching where the branching pairs are condensed and distinctly shorter than the rachis. In comparison, the inflorescences in the other groups bear only a solitary flower or branched cymes where the longest basal branches are nearly as long as the rachis.

The colour of the fruits at maturity in this group are generally pale to dark brown whereas in the other groups they are yellow-orange to red-scarlet or creamy pale grey-green to white. The fruits also do not exude any conspicuous latex, whereas fruits in all the other groups produce a gummy latex. In dried specimens, the outer fruit epidermis does not separate easily from the fruit wall, whereas in all the other groups the epidermis separates easily as a thin, tough and translucent peel. The fruit wall at maturity including in dried herbarium samples retains its rounded structure whereas in other groups the fruit wall breaks down and crumples as it dries.

4.3.8 *Fagraea crenulata* compared with *Fagraea* s.s.

The Fagerlind's tree architectural model is found only in *F. crenulata* in *Fagraea* s.l. The model applies to trees that have a monopodial trunk which with episodic growth as well as branching tiers. The branch modules are terminated by an inflorescence. The other groups have Scarrone's, Aubréville's or Roux's models.

Perhaps the character that makes this species bizarre among *Fagraea* s.l. is the presence of thorns on the stems and branches. Thorns are completely absent in all other species within *Fagraea* s.l. Another aberrant character which unmistakably distinguishes this species is the serrulate-crenulate leaf margin. All other species in *Fagraea* s.l. have

entire leaf margins. In terms of morphology, *F. crenulata* is arguably the most enigmatic species in *Fagraea* s.l.

Notwithstanding, *Fagraea* s.s. and *F. crenulata* do share a number of characters (Table 7), although most of these are not exclusive to them and can be found in the other groups or genera. A possible link is that the petiolar sheaths of a leaf pair in both *Fagraea* s.s. and *F. crenulata* do not fully fuse to form a cup-like structure (ochrea) around the stem. The slight fusion at the extreme edges of the pairing sheaths, do not form an ochrea around the stem as in other taxa of *Fagraea* s.l.

4.3.9 The Gigantea and Elliptica clades share homoplasious character-states

These two clades have several morphological similarities that distinguish them from other taxa in *Fagraea* s.l. The exsertness of the filament is very prominent within these two clades typically more than 70% of the total length of the filament, whereas in the others, the filament is not exerted at all or only slightly to medium exerted. Also, style exsertness in these two clades is typically more than 40% of the total length of the pistil, whereas in the other groups it is either not or only slightly exerted (refer to Appendix 8 for a detailed comparison for filament and style exsertness between all the taxa).

The structure of the stigma in these two clades is knoblike or capitate and the base of the stigma does not expand conspicuously. In *Fagraea* s.s., *F. crenulata* and the Racemosa clade, the stigma structure is peltate due to the base of the stigma expanding conspicuously into a circular plate-like rim.

Further, the fruits in the Gigantea and Elliptica clades turn yellow-orange to red-scarlet upon maturity whereas in the other two clades as well as *F. crenulata*, the fruits

ripen creamy grey-green to white or dark brown. The fruits are also generally smaller in these two clades compared to the others.

Given the distinctness of the Gigantea and Elliptica clades as expressed in the topologies resulting from the molecular analyses (Figs. 15–19), any apparently unique character-states they share must be considered homoplasious in nature (i.e., similarity not due to common ancestry).

4.4 Taxonomic framework

4.4.1 Generic concepts in *Fagraea* s.l.

The respective monophyletic groups of *Fagraea* s.l. shown in the molecular analyses (Fig. 15–19) are represented by the same taxa regardless of the three genetic regions used in the analyses. The analysis with the expanded data set of ITS (Fig. 19) shows that the monophyletic groups are comparable in distinctness to several well-revised ingroup genera, i.e., *Anthocleista*, *Potalia* and *Lisianthius* (Struwe et al. 2002, Struwe & Albert 2004). From the systematic and taxonomic points of view, the respective clades are best recognized as separate genera because regarding *Fagraea* as a single large genus implies including species or groups that are morphologically very divergent.

A new classification for *Fagraea* s.l is thus proposed in this study, based on the results of the molecular analyses obtained. The *Fagraea* clade which includes the type species for the genus, *F. ceylanica*, is the basis of the 'true' *Fagraea* (*Fagraea sensu stricto*) (Fig. 19). *Fagraea crenulata* is considered of uncertain placement as there is only limited evidence showing its close relationship to this group (Fig. 17 & Fig. 18). However, future analyses including more taxa with wider geographical sampling will be needed to reinforce

the placement of this taxon within *Fagraea* s.s. This taxon is provisionally maintained within *Fagraea*.

An appropriate name for the Racemosa clade appears to be *Utania* G.Don, which was given to replace the illegitimate *Kuhlia* Reinw. that had been applied to a different genus. Don (1838) recognised one species, *U. morindaefolia* which was later recombined as *Fagraea morindaefolia* by Blume (1838). However *F. morindaefolia* was reduced to synonymy under *F. volubilis* Wall. (Wong & Sugau 1996). Thus *F. volubilis* is the only name which is represented in the Racemosa clade directly attributable to *Utania* (Fig. 19). As the group is consistently monophyletic, the generic name *Utania* G. Don appears suitable for all members of this clade.

An interesting result of this study is the separation of *Fagraea* section *Cyrtophyllum* as two distinct clades. In the past, Ridley (1918) had regarded this "section" as a separate genus, i.e., *Cyrtophyllum* Reinw. ex Bl., as the species are so different, especially in their habit, in comparison to other epiphytic members of *Fagraea* s.l. Wong & Sugau (1996) recognised two complexes within this "section" which they differentiated by the exclusively axillary or terminal flowering habit. Indeed, these two complexes resolved as the distinct Elliptica and Gigantea clades in the present molecular analyses.

In the sectional classification (Leenhouts 1962), two generic names, *Picrophloeus* Bl. and *Cyrtophyllum* Reinw. ex Bl., have been reduced to synonymy under *Fagraea* section *Cyrtophyllum*. The genus *Picrophloeus* Bl. was recognised with only one described species, *P. javensis* Bl. that was reduced to a synonym under *F. elliptica*. Thus, the generic name *Picrophloeus* is applicable to the Elliptica clade.

The genus *Cyrtophyllum* Reinw. ex. Bl. has two original legitimately published species names, i.e., *C. speciosum* Bl. and *C. peregrinum* Reinw. ex. Bl. Subsequent classification has reduced *C. speciosum* to synonymy under *F. elliptica*, and *C. peregrinum* to a synonym of *F. fragrans*. The molecular analyses show that *F. fragrans* falls within or closely associates with the Gigantea clade, so that the generic name *Cyrtophyllum* is most applicable to the clade.

4.4.2 Key to genera formerly placed in *Fagraea* *sensu lato*

Inflorescences axillary. Trees developing a wave-like sympodial branch system with successively higher orders of outwardly directed, then upturned, (indeterminate) branch segments (plagiotropy by apposition). *Cyrtophyllum*

Inflorescences terminal. Trees, shrubs, scramblers or hemi-epiphytes; branches truly plagiotropic or orthotropic, if developing a wave-like sympodial branch systems then the branch segments truly modular (determinate).

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*

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.

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 exsert from the corolla mouth. *Fagraea*

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. Stamen and style exsert 40 % or more from the corolla mouth. *Picrophloeus*

4.4.3 Enumeration of the Peninsular Malaysian taxa

***Fagraea* Thunb.**

Vet. Acad. Handl. Stockh. 3 (1782) 132. Type: *F. ceilanica* Thunb.

Epiphytes, hemi-epiphytes, scramblers and small to medium sized trees to 20 m tall. **Trunk with** episodic growth; bark smooth to lightly scaly-dimpled (fissured and thorny in *F. crenulata* only). Vegetative shoot tips with creamy yellowish resin. Leaf arrangement on branches decussate; leaf margin entire (serrulate in *F. crenulata* only); **petiolar sheaths** of a leaf pair not to slightly fused at the edges, with scale-like ligules. **Inflorescences**

terminal; of a solitary flower or a many-flowered and branched cyme with basal branches nearly as long as or longer than rachis. **Flowers** small to large (up to 50 mm wide at the mouth); stamens slightly to medium exsert; style not to slightly exsert; stigma peltate. **Fruits** small to big (up to about 40 mm in diameter); colour at maturity creamy pale grey-green; with copious creamy pale yellowish latex in fruit epidermis and fruit wall (small amounts of translucent sticky latex in *F. crenulata* only); epidermis separating as a thin translucent film from pericarp (fruit surface appear crinkled on herbarium specimens). **Seeds** ellipsoid-rounded (polygonal only in *F. crenulata*).

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

Habitat. Lowlands including coastal areas, rocky outcrops, swampy and riverine areas, to upper montane forests.

Key to species

1a. Stems and branches developing prickles. Leaf margins serrulate. Leaf lamina basally decurrent as broad wings 3–5 mm broad or more down to the node, and outer to the petiolar sheath, without any basal elaboration as suddenly broadened rim-like or lobe-like auricles. *F. crenulata*

1b. Stems and branches not developing prickles. Leaf margins entire. Leaf lamina basally terminating above the node and petiole base (not hiding the petiolar sheath) or only very

narrowly decurrent (as 1–2-mm-broad wings) and variously elaborated as broadened rims or auricles.

2a. Leaf base attenuating at the base and forming rounded auricles just above the petiolar sheath. *F. fastigiata*

2b. Leaf base not decurrent to the petiole base and without auricles, or, if decurrent and auricles present, the auricles formed at the petiole base below the petiolar sheath.

3a. Petiole base with narrow, rimlike to broad, rounded, auricular lateral extensions.

4a. Corolla very big, the tube 9.5–17 cm long, the lobes 6.5–7.5(–8) cm long. Leaves located several nodes below inflorescences often very big, to 25–36 cm long. Branch internodes each developing a pair of keels 2–5 mm broad along the inter-petiolar region. *F. imperialis*

4b. Corollas smaller, the tube shorter than 9 cm, the lobes less than 6 cm long. Leaves located several nodes below inflorescences usually smaller, shorter than 25 cm (only exceptionally to 31 cm long). Branch internodes each developing only 2-several ridges at most 1 mm high along the inter-petiolar region, not plate-like keels.

5a. Flowers 2-several in cymes. Floral bracts small, acute, less than 14 mm long and located clearly below the calyx. Petiole base auricles typically large and rounded, to

(3–)8–15(–20) mm broad. Leaves located several nodes below inflorescences 16–22(–31) cm long. *F. auriculata*

5b. Flowers solitary. Floral bracts small to large, rounded, (7–)15–30(–35) mm long, often forming an involucre-like arrangement around the calyx together with a pair of expanded inflorescence bracts (when these are present). Petiole base auricles often smaller, varying from narrow lateral extensions 1–2 mm broad to lobelike structures 2–7 mm broad. Leaves located several nodes below inflorescences 11–18(–22) cm long. *F. insignis*

3b. Petiole base without auricular structures.

6a. Leaf secondary veins distinct and prominent on the lower surface upon drying.

7a. Flower calyx larger, the lobes 13–15 mm long. Cymes little-branched, with 1–2 pairs of primary branches, the basal pair just 10–30 mm long, these typically rebranching just once (exceptionally to 2 orders). Inflorescence rachis thicker, 5–8 mm thick. Leaves very thick-coriaceous, with rounded apices. *F. ridleyi*

7b. Flower calyx smaller, the lobes only 5–10 mm long. Cymes more branched, with 2–3 pairs of primary branches, the basal pair (10–)28–50(–60) mm long, these rebranching 1–2(–3) orders. Inflorescence rachis more slender, 2.5–3(–4) mm thick. Leaves thin-coriaceous, with short-cuspidate apices. *F. renae*

6b. Leaf secondary veins indistinct or, if faintly visible, immersed in the lamina and not prominent upon drying.

8a. Calyx lobes with auriculate bases. *F. fraserensis*

8b. Calyx lobes without auriculate bases.

9a. Leaf surface drying parchment-like, with a smooth surface, and greenish or grayish. Floral bracts inconspicuous, present only as very tiny structures below the calyx base or on the pedicel, measuring less than 0.5 mm long.

..... *F. oblonga*

9b. Leaf surface drying shagreen or grainy, and light brown to dark brown. Floral bracts conspicuously larger and overlapping the calyx base, or small and acute and located below the calyx base, measuring 1 mm or longer in either case.

10a. Flower calyx longer, 15 mm long or more.

11a. Corolla tube essentially cylindrical or slender trumpet-shaped, with only a very gradual increase in width from the base to mouth.

12a. Flowers solitary. Corolla tube 10–14 cm long. *F. carnosa*

12b. Flowers in a 1-2-few-flowered cyme. Corolla tube 4–5.3 cm long.

..... *F. gardenioides*

11b. Corolla tube infundibular with a narrow tubular basal part and widely flared upper portion.

13a. Corolla lobes larger, 35–40 mm long × 25–30 mm wide. Corolla mouth wider, 30–32 mm wide. (Occurring only in limestone outcrops and their vicinity.) (*F. curtisii*)

14a. Floral bracts smaller, 3–5 mm long. (Northwest and west-coast Peninsular Malaysian limestones.) *F. curtisii* var. *curtisii*

14b. Floral bracts larger, 7–18 mm long. (Pahang and east-coast Peninsular Malaysian limestones.) *F. curtisii* var. *calcarea*

13b. Corolla lobes smaller, 15–27 mm long × 9–20 mm wide. Corolla mouth narrower, 16–18 mm wide. (Occurring in lowlands and lower montane forests.)

15a. Flowers solitary. Floral bracts bigger, 17–18 mm long, rounded and overlapping the calyx base. *F. latibracteata*

15b. Flowers in a cyme. Floral bracts smaller, less than 7 mm long, acute, and located below the calyx base.

16a. Calyx smaller, 17–18 mm long × 5–6 mm wide. Corolla lobes smaller, 15–16 mm long × 9–10 mm wide. Corolla tube shorter, 20 mm long or less. *F. larutensis*

16b. Calyx bigger, 20–26 mm long × 9–10 mm wide. Corolla lobes bigger, 20–27 mm long × 15–20 mm wide. Corolla tube longer, 26–30 mm long. *F. crassifolia*

10b Flower calyx shorter, 10 mm long or less.

17a. Inflorescence branches indistinct or extremely short, not longer than 3–4 mm, with few to many flowers crowded together.

18a. Corolla tube slender, essentially cylindrical, not exceeding 6 mm across at the mouth. Leaves ovate. *F. tubulosa*

18b. Corolla tube infundibular, 10–15 mm across at the mouth. Leaves elliptic to obovate. *F. splendens*

17b. Inflorescence branches distinct, the basal branches longer, more than 11 mm long and often much longer, the flowers not tightly bunched together.

19a. Fruits broadly ovoid or subglobose, 13–15 mm in diameter. Mature fruit calyx recurved (folding backwards) away from the fruit base in dried material. Basal inflorescence branch pairs not rebranching. (Coastal areas.)

..... *F. littoralis*

19b. Fruits narrowly ellipsoid, not more than 8 mm across. Mature fruit calyx tightly clasping the fruit base in dried material. Basal inflorescence branch pairs rebranching once. (Highlands.) *F. cameronensis*

1. *Fagraea auriculata* Jack

Mal. Misc. 2, no. 7 (1822) 82; Wallich ex Roxburgh, Fl. Ind. 2 (1824) 34.

Neotype (Wong & Sugau, Sandakania 8 (1996) 51): Wray 2913, Perak (L).

Fagraea auriculata auct. pro parte, excl. *F. imperialis* Miquel in syn.: Clarke in Hooker f., Fl. Brit. Ind. 4 (1885) 83; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 605; Ridley, Fl. Malay. Pen. 2 (1923) 416.

Fagraea auriculata sensu Leenhouts, Fl. Males. I, 6 (2) (1962) 326 pro parte, excl. *F. imperialis* Miq. in syn., ssp. *borneensis* (= *F. borneensis* Scheffer & *F. euneura* Scheffer) & ssp. *parviflora* (= *F. euneura* Scheffer & *F. epiphytica* Elmer).

Fagraea auriculata sensu Kochummen, Tree Fl. Malaya 2 (1973) 270 pro parte, tantum speciminia altitudine infra 1000 m peninsulae Malayensis neque speciminia montium.

Fagraea auriculata sensu Wong & Sugau, Sandakania 8 (1996) 51 pro parte, excl. Fig. 16, Symington KEP 36092, Whitmore FRI 12214, 15551 (= *F. insignis* Sugumaran).

Small tree to large terrestrial shrub or hemi-epiphyte, 5–18 m tall trees or 5–20 m tall on trees as hemiepiphytes; trunk/stems to c. 10 cm diameter; **bark** smooth, grey-brown to reddish brown, smooth becoming scaly-dimpled; branch internodes often with 2-several low ridges 1 mm broad along the inter-petiolar region. **Leaves** elliptic to oblanceolate; (12–)18–27(–31) cm long, (4.5–)5.5–9(–11) cm wide; **base** narrowly decurrent with 1–2 mm broad wings towards the petiole base; **apex** rounded to shortly pointed; **margin** entire, recurved in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** prominent above, more prominent below with a slight median keel upon drying; **secondary veins** 4–6(–7) pairs, faint and immersed in the lamina on both sides; **tertiary and higher-order veins** faint; petioles 15–25(–35) mm long, 3–5 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule (1.5–)2–3 mm high adaxially; **auricles** developing below the petiole base, distinct from the lamina base, typically forming broad, rounded, reflexed lobes (3–)8–15(–20) mm broad (very rarely raised lateral rims just 1–2 mm high).

Inflorescence terminal, a 2-few-flowered cyme, the whole about (1.5–)2–3(–4) cm long; **peduncle** indistinct; inflorescence **rachis** (1.5–)2–3(–4) cm long, 5–7 mm thick, with 1(–2) pairs of primary branches; basal primary **branch pairs** c. 12–22 mm long, 5–8 mm thick and not rebranched. **Flower** fragrant, bisexual; **pedicel** 3–10(–20) mm long, 8–10

mm thick; **floral bracts** small, acute, 8–10(–13) mm long, located below the calyx; **calyx** 27–33 mm long (from the base to the lobe apices), glabrous, not lenticellate, **calyx cup** 15–18 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 20–27 mm long, 12–17 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 30–35(–45) mm long, 10–12(–17) mm wide basally, **upper flared part** of the tube slightly inflated, 30–37 mm long, 40–56(–60) mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 36–42 mm long, 23–31 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 45–60 mm long, protruding to 15–23 mm from the corolla mouth; **anthers** versatile, hastate, 13–15 mm long, 6–8 mm wide, each anther sac somewhat ellipsoid; **style** 70–90 mm long, protruding to 8–10 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive, the whole 3–4 mm across. **Infructescence peduncle** indistinct. **Fruit** narrowly ellipsoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to (65–)80–101 mm long, 25–35(–40) mm wide; the base tightly clasped by the erect calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, c. 1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo, Java, Sumatra, Malay Peninsula, Indo-China.

Habitat. Coastal sites, including behind sea beaches, rocky outcrops, swamp forests; also limestone and quartz outcrops in coastal lowlands.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Batu Pahat, Patani, *Ridley* s.n., FR, no precise date, 1900 (SING!); Pontian, Pengkalan Raja, *Ngadiman* SFN 36752, FL, 3 vii 1939 (SING!); Sedili Kechil, *Corner* s.n., FB, 22 vi 1934 (SING); Sungai Tebrau, *Ridley* 11639, FR, no precise date, 1903 (SING!). **Melaka.** *Alvins* 2053, FL, no date (SING!); Alor Gajah, *Bland* s.n., FR, 24 viii 1902 (SING!). **Pahang.** Bukit Nipah, cliff, *Samsuri* SA 915, FR, 24 ii 1974 (SING!); Kuantan, Baloh F.R. Compt. 1, sandy, *Rahim* KEP 97950, FB, 30 vii 1966 (KEP!), FB, FL (SING!); Menchali Forest Reserve, *Sugumaran* SM 25, FB, FR, 19 iv 2004 (KLU!), *Sugumaran* SM 217, leafy twig only, 4 vi 2008 (KLU!); Nenasi, Merchong, *Sugumaran* SM 13, leafy twig only, 17 iv 2004 (KLU!); Pekan, *Ahmad* AS 119, FR, 9 iii 1973 (SING!), *Ridley* 2170, FB, FL, no precise date, 1891 (SING!); Pulau Tioman, west coast near Kampong Paya, rocky shore, *Ratnasabapathy* s.n., FB, 26 v 1974 (KLU!). **Perak.** Dindings, Bruas, *Ridley* 7998, FB, FL, iii 1896 (SING!); Pangkor, *Foxworthy* CF 1726, FR, 30 iii 1918 (KEP! SING!); Sungai Krian Estate, sea level, *Spare* SFN 36007, FB, FL, 10 vii 1938 (SING!). **Selangor.** Bukit Takun, *Boey* 421, leafy twig only, 19 ix 1971 (KLU!), Bukit Takun, *Stone* 5915, leafy twig only, 11 vii 1965 (KLU!); Klang Gates ridge, *Boey* 398, leafy twig only, 12 ix 1971 (KLU!), *Carrick* 659, leafy twig only, 19 iii 1960 (KLU!), *Mahmud* s.n., FR, vii 1970 (KLU!), *Sugumaran* SM 28, leafy twig only, 20 i 2005 (KLU!), 800 ft alt, *Stone* 14110, leafy twig only, 22 vii 1979 (KLU!), 1000 ft alt, *Henderson* SFN 10490, FB, FL, 6 viii 1923 (SING!). **Terengganu.** Dungun, *Soepadmo* KLU 9103, FR, 30 iv 1968 (KLU!); Gong Balai near beach, *Mohd Shah & Sidek* MS 4045, FR, 24 xi 1978 (SING!); Jambu Bongkok, *Johnson* AJ 4036, FR, 3 iii 1967 (KLU!). **SINGAPORE.** Pulau Ubin, *Ridley* 9582, FB, FL, no precise date, 1898 (SING!). **SUMATRA.** Riouw, Indragiri, Bovenlanden, Kuala Belillas, swampy, *Buwalda* 6774, FB, 29 iv 1939 (SING!).

Jack (1822) had intended a lowland, coastal taxon when he mentioned that his species was collected from Singapore and the west coast of Sumatra at Tapanuly. As there was no type provided (Merrill 1952), a neotype has been designated by Wong & Sugau (1996) which conforms to this. When the Peninsular Malaysian material grouped by both

Leenhouts (1962) and Wong & Sugau (1996) under *F. auriculata* was sorted for the present study, three taxa were distinct.

The first, *F. auriculata* Jack, represented by the neotype, is a coastal species with conspicuous leaf-stalk auricles and medium-sized flowers (corolla tube 30–35(–45) mm long) in cymose inflorescences, with distinct, slender pedicels (8–10 mm thick) and infundibular corolla. Floral bracts are small (8–10(–13) mm long), acute and found on the pedicels. This species also occurs at several other sites, such as limestone hills (e.g., Bukit Takun, Selangor) and quartz ridges (e.g., the Klang Gates ridge outside Kuala Lumpur).

The second species is *F. imperialis*, also with conspicuous leaf-stalk auricles but huge, highly distinctive flowers (corolla tube (40–)90–100 mm long), either solitary or in small numbers in cymes. The corollas are infundibular with overall much larger dimensions than in *F. auriculata* and with a thicker tube. The floral bracts are larger (typically 20–30 mm long) and rounded compared to those of *F. auriculata*. This species is found in (and typified by material from) Sumatra but is now adequately represented by good material recently gathered from Perak, Peninsular Malaysia (*Sugumaran* SM 238) (see under that species), allowing diagnosis of a very few other Peninsular Malaysian collections from both coastal and inland sites. A further difference between *F. imperialis* and *F. auriculata* is the development of strong, sharp keels along the inter-petiolar median of internodes in the former, whereas in *F. auriculata* the internodes are either smooth or at most provided with low ridges without any plate-like keels developing.

The third component of the Peninsular Malayan material (here named *F. insignis*) is distinctive by the strictly solitary flowers with much shorter pedicels (indistinct or to 10 mm long) and a montane provenance (so far documented only from the Peninsular

Malaysian Main Range). The leaf-stalk auricles are poorly developed, ranging from narrow rim-like structures to distinct auricles just several mm wide, not as pronounced as those of *F. auriculata* or *F. imperialis*. The corollas are medium-sized (corolla tube 22–30 mm long), infundibular and similar to those in *F. auriculata*. The floral bracts are large (typically 30 mm long), rounded, and can approach the size of calyx lobes. This species is illustrated in Wong & Sugau (1996) as their Fig. 16, which they placed under *F. auriculata*.

2. *Fagraea cameronensis* Wong & Sugumaran, sp. nov.

Typus: Burkill HMB 818, Pahang, Cameron Highlands, Sungai Uruil, below Golf Course, 4,800 ft., 4 Sep 1956 (holotype SING!).

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad Burkill HMB 818.

(Fig. 20)

Small tree or hemi-epiphyte, usually to 5 m tall or to 17 m high or more on trees; trunk/stems to c. 10 cm diameter; **bark** smooth, grey-brown. **Leaves** elliptic to obovate; (6–)8–11(–13.5) cm long, (2–)3–4(–4.3) cm wide; **base** cuneate, not decurrent; **apex** short blunt cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat to sunken above, prominent below; **secondary veins** 6–9 pairs if visible, otherwise obscure on both sides;

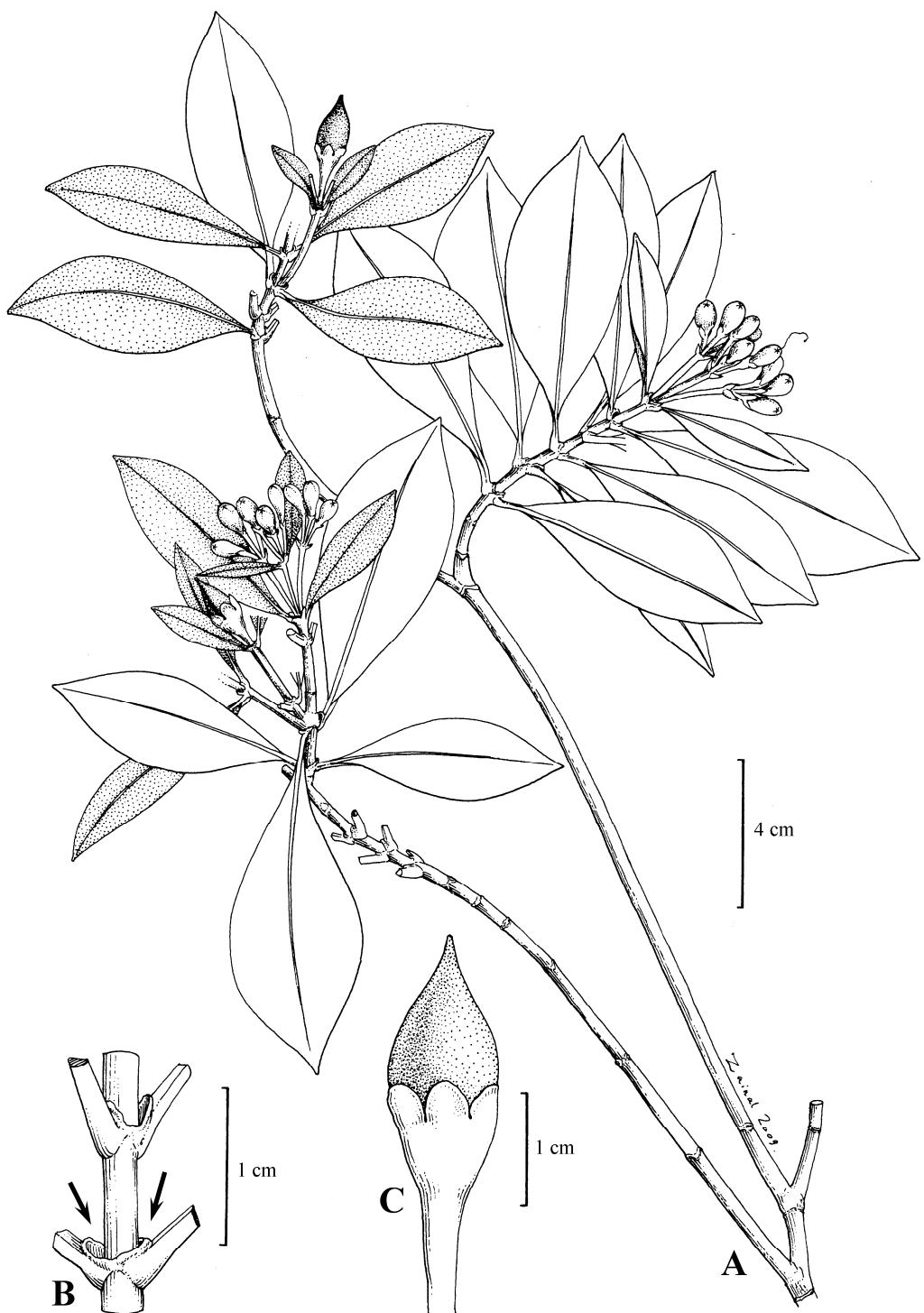


Fig. 20. *Fagraea cameronensis*. A, leafy branch with buds and fruits. B, a portion of stem featuring leaf stalk bases with scale-like ligules (arrows) on adaxial side. C, fruit.
All from Burkhill HMB 818 (holotype, SING).

tertiary and higher-order veins obscure; petioles 8–10 mm long, 1.5–2.5 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 2-few-flowered branched cyme, the whole about 2.1–3.3 cm long; **peduncle** indistinct; inflorescence **rachis** 21–33 mm long, 2–2.5 mm thick, with 1–2 pairs of primary branches; basal primary **branch pairs** 18–26 mm long, 1.5–2 mm thick and rebranched to 1 order, more distal branch pairs not so. **Flower** bisexual; **pedicel** 2–3 mm long, 2–3 mm thick; **floral bracts** small, acute, 1–2 mm long, located below the calyx; **calyx** 8–10 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 3–4 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 3–4 mm long, 4–5 mm wide, margins glabrous, base not auriculate; **corolla** not known; **stamens** not known; **style** not known. **Infructescence peduncle** indistinct. **Fruit** narrowly ellipsoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 12–20 mm long, 5–8 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 1.5–2 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Known only from Peninsular Malaysia (Cameron Highlands).

Habitat. Lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Pahang.** Cameron Highlands, Sungai Uruil, below Golf Course, 4800 ft alt, *Burkill* HMB 818, FB, FR, 4 ix 1956 (SING!); Cameron Highlands, trail to G. Berembun, 5500 ft alt, *Ng* FRI 5930, FR, 1 iii 1968 (KEP! SING!); Cameron Highlands, Gunung Brinchang, *Low* LYW 138, leafy twig only, 29 vii 2007 (KLU!).

This species is similar to *F. rarissima* Wong & Sugau and *F. longipetiolata* Wong & Sugau from Borneo in having relatively small flowers 1-several together in little-branched cymes (without floral bract-involucres), indistinct leaf veins and non-auriculate leaf-stalk bases. It can be distinguished from these species even in the absence of corollas. *F. cameronensis* has smaller flower calyx lobes, 3–4 mm long (4–5 mm long in *F. rarissima*, 6–8 mm long in *F. longipetiolata*). The central inflorescence axis in *F. cameronensis* is 12–24 mm long, whereas in *F. rarissima* it is only up to 10 mm long. The leaf margins are not recurved when dry (unlike in *F. rarissima*), and the leaf apices are acute to cuspidate (unlike in *F. longipetiolata*, where they are consistently caudate).

3. *Fagraea carnosa* Jack

Mal. Misc. 2, no. 7 (1822) 81; Cammerloher, Bull. Jard. Bot. Btzg. III, 5 (1923) 323.

Neotype (here chosen): *Teysmann* HB 998, Sumatra, Sibogo (U acc. no. 38976!; isoneotype L acc. no. 908127-712!).

Fagraea flavidula Ridley, Fl. Malay. Pen. 5 (1925) 322. Type: *Henderson* SFN 11673, Pahang, Cameron Highlands (holotype K; isotype L!SING!).

Fagraea monantha Miquel, Fl. Ind. Bat. 2 (1857) 373. Type: *Teysmann* HB 998, Sumatra, Sibogo (holotype U acc. no. 38976!; isotype L acc. no. 908127-712!).

Fagraea uniflora Merrill, J. Str. Br. R. As. Soc. 77 (1917) 235. Type: *Foxworthy* 114, Sarawak, Santubong (isotype L).

Fagraea rotundifolia Ridley, J. Str. Br. R. As. Soc. 50 (1908) 117. Type: *Rostado*, s.n., Tringganu, Bundi (holotype K!).

Fagraea carnosa sensu Clarke in Hooker f., Fl. Brit. Ind. 4 (1885) 82 pro parte, excl. speciminia origine 'Tenasserim'.

Fagraea carnosa auct. pro parte, excl. speciminia origine 'Burma': King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 604; Ridley, Fl. Malay. Pen. 2 (1923) 416; Leenhouts, Fl. Males. I, 6 (2) (1962) 331; Kochummen, Tree Fl. Malaya 2 (1973) 271.

(Fig. 21)

Scrambler or hemi-epiphyte, usually to 2–3 m high or more on trees; stems to c. 5 cm diameter; **bark** smooth, grey-brown. **Leaves** elliptic-obovate to orbicular; (6–)8–13(–16.5) cm long, (2.8–)4–6(–7) cm wide; **base** cuneate to rounded, not decurrent; **apex** short cuspidate to rounded; **margin** entire, recurved in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below; **secondary veins** obscure on both sides; **tertiary and higher-order veins** obscure; petioles (7–)15–22 mm long, 2–4 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 1–3 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, consisting of a solitary flower; **peduncle** distinct, (3–)4–6 mm long, 4–6 mm thick; the rachis internode between peduncle and pedicel inconspicuous. **Flower** very fragrant; bisexual; **pedicel** 3–5 mm long, 4–6(–7) mm thick; **floral bracts** small, acute, 3–5 mm long, located below the calyx; **calyx** 15–21(–34) mm long (from the base to the lobe apices), glabrous, not to sometimes

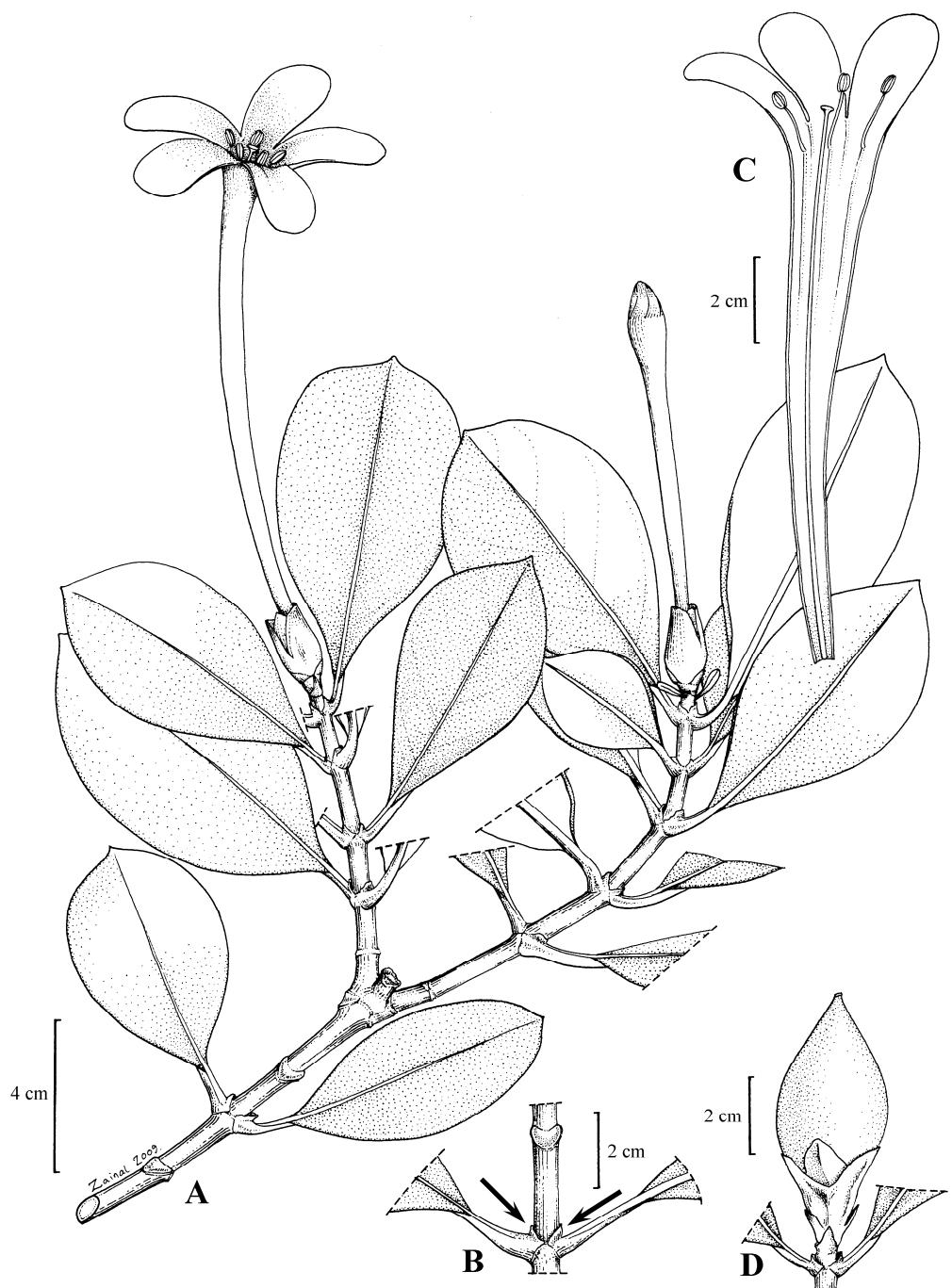


Fig. 21. *Fagraea carnosa*. A. leafy branch with flowers. B. portion of stem with scale like ligules (arrows) on the adaxial side. C. sectioned corolla showing the attachment of stamens. D. fruit.
 A & B from *Chin* 367 (KLU), C from *Yao* FRI 53078 (KEP) and D from *Chin* 566 (KLU).

lenticellate, **calyx cup** 7–10 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 10–12(–16) mm long, 7–10 mm wide, margins glabrous, not auriculate; **corolla** subsalverform (with an elongate narrow lower tubular part and a much shorter upper flared part, spreading to erect lobes); cream to white; **lower subcylindrical part of the corolla tube** 10–13 cm long, 8–10 mm wide basally, **upper flared part** of the tube (when distinct) slightly inflated, 6–10 mm long, 10–15 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 22–35(–46) mm long, 10–18 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 12–15 mm long, protruding to c. 5 mm from the corolla mouth; **anthers** versatile, hastate, 5–6 mm long, 2–3 mm wide, each anther sac somewhat ellipsoid; **style** 12.3–12.6 cm long, not or protruding to 10–17 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 3–4 mm across. **Infructescence peduncle** distinct, 5–7 mm long, 5–6 mm thick. **Fruit** broadly ovoid to ellipsoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 35–50(–57) mm long, 20–28 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1.5–2 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo (Sarawak), Malay Peninsula, Sumatra.

Habitat. Coastal islands, lowland rain forest to lower montane forest; in the lowlands also found on some limestone hills.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kelantan.** Gunung Stong, eastern face, granite cliff, 1000 ft alt, *Whitmore* FRI 12518, FB, FL, 15 viii 1969 (KEP!). **Pahang.** Bukit Serdam, 1300 ft alt, *Henderson* s.n., FL, FR, 6 x 1931 (SING!); Cameron Highlands, 4800 ft alt, *Henderson* SFN 11673, FB, FL, FR, 16 i 1924 (SING!); Cameron Highlands, Tanah Rata, 5000 ft alt, *Henderson* SFN 17729, FR, 17 xi 1925 (SING!); Fraser's Hill, 4000 ft alt, *Md Nur* SFN 11288, FR, 7 ix 1923 (SING!); Fraser's Hill, 'dekat tepi Padang Gof, *Medan* KEP 45409, FL, FR, 9 xi 1937 (KEP!); Pahang, Lesong F.R., *Chan* FRI 25183, FR, 8 vi 1979 (KEP!); Raub, Gua Kechil limestone hill, 350 m alt, *Chin* 1151, leafy branch only, 21 vi 1971 (KLU!).
Penang. Pulau Boetong, *Curtis* 3394, FL, no date (SING!). **Perak.** Dindings, Lumut, *Ridley* 18297, FL 1899 (SING!); Pangkor Island, *Curtis* s.n., FL, ii 1900 (SING!), north coast, rocky headland, *Whitmore* FRI 3009, 17 ii 1967, FR (KEP!), FB (SING!). **Selangor.** Batu Caves, *Wyatt-Smith* KEP 85211, FR, 29 xii 1957 (KEP!), 800 ft alt, *Ng* FRI 1627, leafy branch only, 14 x 1966 (KEP! SING!); Bukit Takun, *Allen* s.n., FL, 27 i 1957 (SING!), *Boey* 422, leafy branch only, 19 ix 1971 (KLU!), *Sinclair* s.n., FL, 27 i 1957 (SING!), *Sow & Tachun* KEP 35092, FB, FL, 17 ix 1940 (KEP!), *Sugumaran & Lee* SM 186, leafy branch only, 20 iii 2008 (KLU!), 500 m alt, *Chin* 566, FR, 31 xii 1970 (KLU!), near summit, 1000 ft alt, *Stone* 11079, FR, 4 iii 1973 (KLU!), summit, *Chin* 367, FB, FL, 27 ix 1970 (KLU!). **Terengganu.** Bundi, *Rostado* s.n., FL, ii 1904 (K!); Dungun, Tanjung Gadong Forest Reserve, rocky seashore, *Yao* FRI 53078, FL, FR, 26 ix 2006 (KEP! KLU! SAN! SAR). **SUMATRA.** Sibogo, *Teysmann* HB998, no precise date FB (L), FB (U!).

In his description, Jack (1822) states only “In the neighbourhood of Bencoolen” with no mention of other localities and so had clearly intended a Sumatran taxon. His description of “Flowers. . . solitary, nearly sessile. . . Corolla. . . tube about four inches long” and “Leaves. . . subrotund with a short reflexed point, entire with reflexed margins, very. . . thick and fleshy” distinguishes the species adequately. However, no original material that could be regarded as typifying Jack’s name could be found. Leenhouts (1962) remarks, “Among the few Sumatran specimens at my disposal none fits his description very well, and there is no later collection from. . . Bencoolen, S. Sumatra” as *Rahmat* 6254

and *Jacobs* 4610 (L) are both fruiting collections without corollas and the meagre flowering material in *Teysmann* HB 998 (also the type of *F. monantha* Miq.) is represented by two half-calyx portions at L and a very young flower bud at U. Neotypification is essential and should be based on Sumatran material, so we choose the Teysmann specimen at U as it is the best, including a good leafy branch and a flower bud.

In the Kew herbarium, the type of Ridley's *F. rotundifolia* has a neotype label for the name *F. carnosa* on it. This should not be accepted as a neotype because it had not been clearly designated by Leenhouts (1962), who, however, stated "The only specimen which is well in accordance with the original diagnosis is Rostado s.n. . . . the type of *F. rotundifolia* Ridl." Although we accept some variation that includes this specimen, it has a flower with a bigger calyx than the Sumatran or other Malayan material and more closely resembles the calyces in Bornean material. In addition to this, the leaves in the Rostado collection are atypically rotund (all other material has elliptic to obovate leaves with mostly rounded apices).

4. *Fagraea crassifolia* Blume

Rumphia 2 (1838) 31, t. 78 f. 1; Mus. Bot. 1 (1850) 166.

Type: Collector unknown, Java (Leiden acc. no. 908127-756) (holotype L!).

Fagraea sparei Henderson, Gard. Bull. S.S. 7 (1933) 114. Type: *Spare* F952, Johore, Sungai Tukong Estate (holotype SING; isotype K!).

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad *F. crassifolia* Blume & *F. sparei* Henderson in syn; Kochummen, Tree Fl. Malaya 2 (1973) 271 pro parte, quoad *F. sparei* Henderson in syn.

Fagraea lanceolata auct. non Blume (1826): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 607, quoad *Kunstler* 6848 & *Wray* 3202.

Hemi-epiphyte, 20–30 m high or more on trees; trunk/stems to c. 15 cm diameter; **bark** smooth, grey-brown. **Leaves** elliptic to subobovate; (5.5–)8–12(–13.5) cm long, (2.3–)3.8–5.5 cm wide; **base** cuneate, not decurrent; **apex** short cuspidate; **margin** entire, recurved in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth under magnification; **midrib** flat above, prominent below; **secondary veins** obscure on both sides; **tertiary and higher-order veins** obscure; petioles 10–20 mm long, 2–3 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 2-few-flowered branched cyme, the whole about 10–15 mm long; **peduncle** indistinct; inflorescence **rachis** 10–15 mm long, 2–3 mm thick, with 1 pair of primary branches; basal primary **branch pairs** 5–15 mm long, 2–4 mm thick and not rebranched. **Flower** bisexual; **pedicel** indistinct or to 7 mm long, to 4 mm thick; **floral bracts** small, acute, 5–6 mm long, located below the calyx; **calyx** 20–26 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 9–10 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 10–13 mm long, 10–12 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 16–17 mm long, 5–6 mm wide basally, **upper flared part** of the tube (when distinct) slightly inflated, 10–13 mm long, 16–18 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 20–27 mm long, 15–20 mm wide, overlapping to

the right; **stamens** not seen (broken off in available material); **style** 28–30 mm long, protruding to c. 2 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 2–3 mm across. **Infructescence peduncle** indistinct. **Fruit** broadly ovoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 40–50 mm long, 25–32 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1.5–2 mm wide; testa surface areolate; placentation axile.

Distribution. Java, Malay Peninsula.

Habitat. Lowland rain forest to lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Kluang State Land, Yeob CF 5849, FR, 17 ii 1922 (KEP! SING!); Sungai Tukang Estate, Spare F952, FB, 13 ix 1931 (K!). **Melaka.** Griffith 3737, FL, no precise date, 1845 (K!). **Pahang.** Ulu Telom, Cameron Highlands, Jaamat & Lasah FMS 27672, FL, FR, 30 viii 1931 (SING!). **Perak.** Maxwell's Hill, Wray 3202, FR, ix 1838 (K! SING!). JAVA. *sine coll.* FB, FR, no date (L!).

Wallich's name *F. obovata* has a number of confusing elements and is not used. In the original description (Roxburgh 1824), Wallich includes material from both Silhet (now Bangladesh) as well as Singapore. Clarke in Hooker (1885) pointed out that the "corolla in Wallich's Silhet example is considerably larger than in his Singapore one." Yet in his description, Wallich appears to describe the flowers of the taxon from Silhet (which Clarke points out has leaves with distinct primary nerves), and leaves that are "fleshy, without

veins or nerves" (that would conform to Peninsular Malaysian material, not the taxon from Silhet). The next oldest name, *F. crassifolia*, is used as there is no conflict of material or description.

5. *Fagraea crenulata* Maingay ex Clarke

in Hooker f., Fl. Brit. Ind. 4 (1885) 83; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 610; Cammerloher, Bull. Jard. Bot. Btzg. 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 (holotype K).

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

Small to medium sized trees, usually to 10–15 m (occasionally to 20 m) tall; trunk to c. 25 cm diameter; **bark** with short stub-like prickles on broadly rounded bases, grey-brown. **Leaves** broadly obovate; (20–)25–40(–55) cm long, (12–)20–40(–45) cm wide; **base** decurrent with (3–)10–20(–25) mm broad wings towards the petiole base and outer to the petiolar sheath; **apex** rounded; **margin** serrulate, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface granular under magnification; **midrib** prominent to flat above, prominent below and sometimes developing a low median keel upon drying; **secondary veins** 5–7 pairs, prominent on both sides; **tertiary and higher-order veins** faint; petioles indistinct, **petiolar sheaths** fusing along the interpetiolar median; petiole base without **auricles**. **Inflorescence** terminal, a branched cyme, the whole

about 7–13 cm long; **peduncle** indistinct; inflorescence **rachis** 6.5–7(–13) mm long, 6–9 mm thick, with 3–4 pairs of primary branches; basal primary **branch pairs** (3–)4.5–6 cm long, (4–)5–7 mm thick and rebranched to 3–4 orders, more distal branch pairs less so. **Flower** fragrant; bisexual; **pedicel** 5–6 mm long, 3–4 mm thick; **floral bracts** small, acute, 2–3 mm long, located below the calyx; **calyx** 8–10 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 3–4 mm wide, **calyx lobes** 5, broad-elliptic to rounded, erect, 5–6.5 mm long, 5–6 mm wide, margins glabrous, base not auriculate; **corolla** slender trumpet shaped (subcylindric and very gradually widening towards the apex), cream to white; **lower subcylindrical part of the corolla tube** 10–11 mm long, 4–5 mm wide basally, **upper flared part** of the tube slightly inflated, 5–7 mm long, 9–10 mm wide at the top; **corolla lobes** 5, broad-obovate, 10–15 mm long, 6–9 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 12–14 mm long, slightly protruding to 7–8 mm from the corolla mouth; **anthers** versatile, hastate, 4–5 mm long, 1–1.5 mm wide, each anther sac somewhat ellipsoid; **style** 15–20(–23) mm long, not to slightly protruding to 5 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive, the whole resembling a somewhat peltate structure 2–2.5 mm across. **Infructescence peduncle** indistinct or to 4.5 cm long, 7–8 mm thick. **Fruit** narrowly ellipsoid, **apex** attenuated; smooth, the epidermis conspicuously wrinkling upon drying; when mature to 20–24 mm long, 12–15 mm wide; the base loosely surrounded by the erect calyx lobes. **Seeds** numerous; polygonal; 1–1.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo (southwest and south Kalimantan), Malay Peninsula, Sumatra, south Indo-China.

Habitat. Swampy and riverine sites in the lowlands.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor**. Batu Pahat, *Teruya* 2399, FR, 6 vi 1933 (SING!); Muar road near Muar, *Sinclair* 8903, FR, 22 x 1956 (SING!). **Melaka**. *Holinberg s.n.*, FB, FL, 30 iv 1891 (SING!), *Maingay* 1032, FB, FR, 3 vii 1868 (K!), FR (L!), Ujong Pasir, *Derry* 1234, FB, 29 iii 1893 (SING!). **Pahang**. Jerantut, cult. ornamental, *Sugumaran & Zulkapli* SM 218, leafy twig only, 6 vi 2008 (KLU!). **Perak**. *Scortechini* 1642, leafy branch only, no date (SING!). **Selangor**. Jugra, *Yeob* CF 3278, FR, 24 vii 1919 (SING!); Klang, *Ridley* 7552, FB, FL, FR, v-vi 1896 (SING!), 2nd mile to Kapar road, *Mohd. Kasim* 687, FR, 18 viii 1964 (KLU!); Klang North, *Gaynar* CF 7072, FB, FL, 8 ii 1922 (SING!); Kuala Lumpur, *Carrick* JC 1548, FR, 20 ii 1967 (SING!); Pantai, University of Malaya, *Stone* 8950, leafy twig only, 17 xii 1969 (KLU!); Port Swettenham, Telok Gadong, *Md Nur* SFN 3008, FR, 17 i 1918 (SING!). PENINSULAR THAILAND. Narathiwat, Bang Nara, Bang Por, along Bangnara river, *Niyomdham et al.* 5920, FL, FR, 5 x 1999 (BKF, SING!). SINGAPORE. Labrador Park, next to Blk. G, *Tang & Sidek* 879, FR, 14 viii 1995 (SING!).

This is the only species developing prickles on the stem and branches and with serrulate leaf margins (the other species are unarmed and have entire leaf margins).

6. *Fagraea curtisii* King & Gamble

J. As. Soc. Beng. 74 (2) (1908) 605; Ridley, Fl. Malay. Pen. 2 (1923) 417; Kerr in Craib, Fl. Siam. En. 3 (1951) 55; Leenhouts, Fl. Males. I, 6 (2) (1962) 332; Kochummen, Tree Fl. Malaya 2 (1973) 271.

Type: *Curtis* 1676, Langkawi, Teluk Woh (holotype K!; isotype SING!).

(Fig. 22)

Fagraea curtisii var. *curtisii*

Small tree or hemi-epiphyte, usually to 13 m tall or 10 m high or more on trees; trunk/stems to c. 30 cm diameter; **bark** smooth, creamy to grey-brown. **Leaves** elliptic to subobovate; (8.5–)10–22(–28) cm long, (3–)5–7.5(–9.2) cm wide; **base** cuneate, not decurrent; **apex** short cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below; **secondary veins** 4–5 pairs if visible, upper side obscure, lower side faint and immersed in the lamina to obscure; **tertiary and higher-order veins** faint to obscure; petioles (1.3–)2–3(–3.5) cm long, 2–3(–4) mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 1–3 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a solitary flowered or 1-2-few-flowered cyme, the whole about 10–20 mm long; **peduncle** indistinct or to 7 mm long, to 5 mm thick; inflorescence **rachis** 10–12 mm long, 4–5 mm thick, with 0–1 pair of primary branches; basal primary **branch pairs** 8–20 mm long, 3–4 mm thick and not rebranched. **Flower** bisexual; **pedicel** indistinct or to 5 mm long, to 5 mm thick; **floral bracts** small, acute, 3–5 mm long, located below the calyx; **calyx** 17–33 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 9–10 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 17–20 mm long, 10–20 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); light orange to cream to white; **lower**



Fig. 22. Holotype of *Fagraea curtisii* King & Gamble var. *curtisii*; Curtis 1676, Teluk Woh, Langkawi (K).

subcylindrical part of the corolla tube 17–25 mm long, 9–10 mm wide basally, **upper flared part** of the tube slightly inflated, 18–30 mm long, 30–32 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 35–40 mm long, 25–30 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 32–40 mm long, protruding to c. 10 mm from the corolla mouth; **anthers** versatile, hastate, 17–20 mm long, 2–3 mm wide, each anther sac somewhat ellipsoid; **style** not seen [*fide* Craib & Kerr (1951): ovary and style c. 6 cm long]; **stigma** not seen [*fide* Leenhouts (1962): stigma peltate, c. 2.5 mm across]. **Infructescence peduncle** indistinct or to 7 mm long, 5–7 mm thick. **Fruit** broadly ovoid to subglobose, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 35–45 mm long, 20–25(–36) mm wide; the base loosely surrounded to tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–3 mm long, 1–2 mm wide; testa surface areolate; placentation axile.

Distribution. Malay Peninsula (including peninsular Thailand, the extreme northwest and west-coast areas of Peninsular Malaysia).

Habitat. Restricted to limestone outcrops and their vicinity.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kedah.** Langkawi, Pulau Dayang Bunting, *Corner* SFN 38129, FR, 13 xi 1941 (KEP! SING!); Langkawi, Pulau Langgon, Tanjong Dalam, *Boey* 528, FR, 4 xi 1971 (KLU!); Langkawi, Pulau Segai, *Haniff* SFN 15584, FR, ii 1911 (SING!); Langkawi, Pulau Timun, *Chia & Chin* LT 372, FR, 13 xi 1979 (KLU!), *Henderson* SFN 29109, FR, 24 xi 1934 (SING!); Langkawi, Pulau Timun, south coast, on limestone, *Whitmore* FRI 15103, FR, 16 xii 1969 (KEP!); Langkawi,

Pulau Timun, sandy beach, *Sim* B-112, FR, 13 xi 1979 (KLU!); Langkawi, Tanjong Sirie, *Curtis* 1696, FB, FL, ix 1890 (SING!); Langkawi, Telok Apau, *Haniff & Md Nur* SFN 7089, FR, 17 xi 1921 (SING!); Langkawi, Teluk Woh, *Curtis* 1676, viii 1888, FL (K!), FB (SING!). **Perak.** Gua Puteri limestone, 500 ft alt, *Samsuri & Mahmud* SA 628, FR, 13 iii 1971 (KLU! SING!); Lenggong, Kampong Gelok, Gua Putri limestone, 100 m alt, *Chin* 967, leafy twig, 13 iii 1971 (KLU!); Padang Rengas, Gua Pondok limestone, 300 m alt, *Chin* 910, FR, 12 iii 1971 (KLU!).

Fagraea curtisii* var. *calcarea (Henderson) Wong & Sugumaran, comb. & stat. nov.

Fagraea calcarea Henderson, Gard. Bull. S.S. 7 (1933) 113, t. 28B; Leenhouts, Fl. Males. I, 6 (2) (1962) 332; Kochummen, Tree Fl. Malaya 2 (1973) 271. Type: *Henderson* SFN 25036, Pahang, Bukit Chintamani (holotype SING! isotype K!).

(Fig. 23)

The only clear morphological difference between this variety and *F. curtisii* var *curtisii* is the larger floral bracts in this variety (7–18 mm long) that are rounded and apically clasping the calyx base. The floral bracts in *F. curtisii* var. *curtisii* are smaller (3–5 mm long), acute and not conspicuously overlapping the calyx.

Distribution. Malay Peninsula (known only from Kelantan and Pahang states in Peninsular Malaysia).

Habitat. Restricted to limestone outcrops and their vicinity.

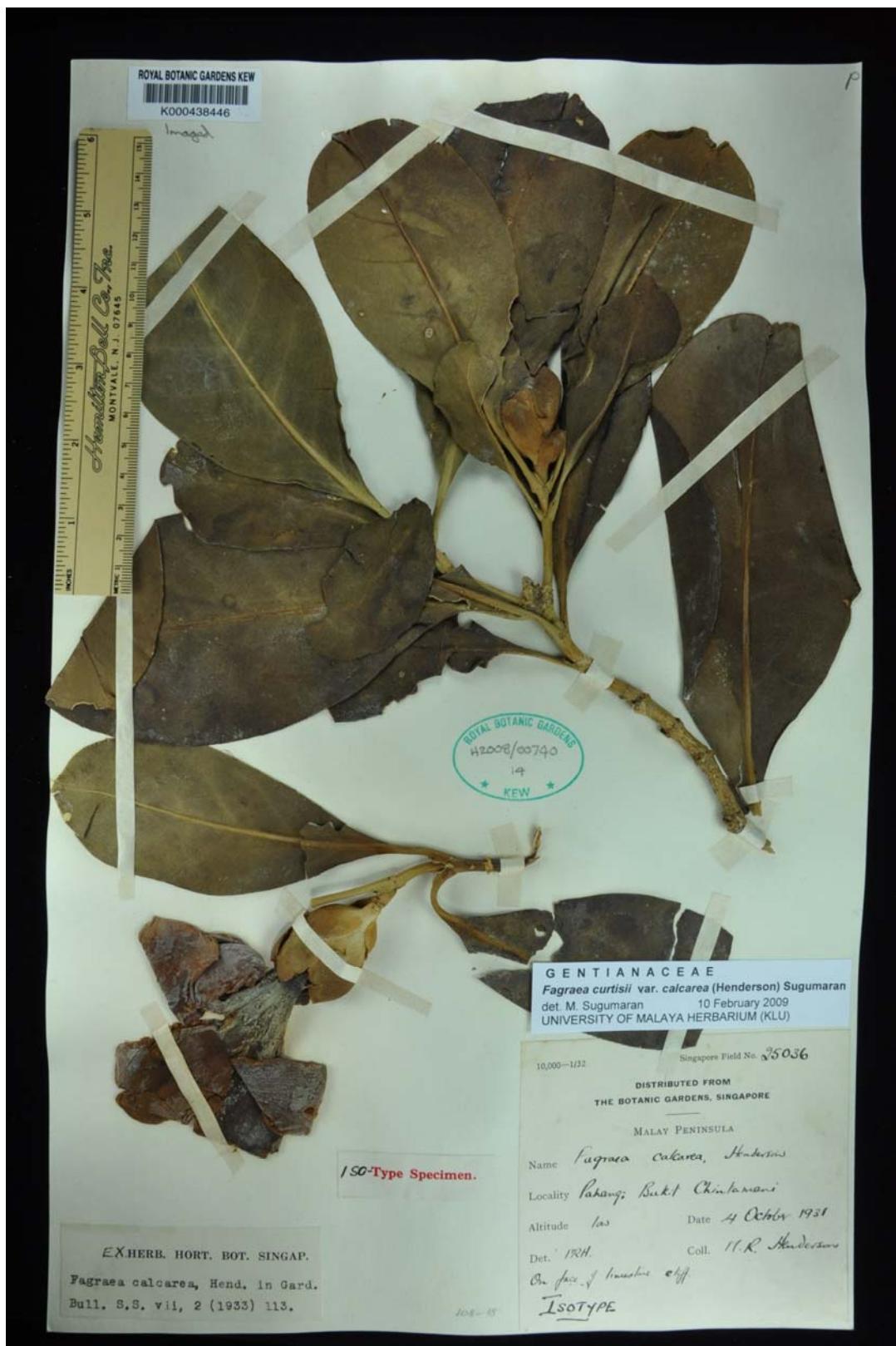


Fig. 23. Proposed holotype of *Fagraea curtisii* var. *calcarea* (Henderson) Wong & Sugumaran, Henderson 25036, Bukit Chintamani, Pahang (K).

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kelantan.** Gua Musang, *Teo & Wintz* KL no. 4819, FL, 7 x 1998 (KEP!); Gua Musang, *Boey* 298, FB, 18 viii 1971 (KLU!); Sungai Nenggiri, Gua Jaya, limestone, *Whitmore* FRI 4243, FB, 27 vii 1967 (KEP! SING!); Ulu Kelantan, Gua Musang, path to Sungai Ketil, *Mohd Shah & Mohd Ali* MS 2855, FR, 30 i 1973 (SING!). **Pahang.** Bukit Chintamani, limestone cliff, *Henderson* SFN 25036, FB, FL, 4 x 1931 (K! SING!); Merapoh, Gua Layang limestone, 100 m alt, *Chin* 1524, FB, 13 viii 1971 (KLU!).

Fagraea curtisii var. *calcarea* differs from the typical variety in having larger floral bracts. It is found on the Pahang and east coast limestones, whereas the typical variety is recorded from limestone in the region including Peninsular Thailand, the extreme northwest of Peninsular Malaysia, Kedah and Perak, i.e., west of the Peninsular Malaysian Main Range.

7. *Fagraea fastigiata* Blume

Rumphia 2 (1838) 30, t. 76 f. 1; Leenhouts, Fl. Males. I, 6 (2) (1962) 324; Kochummen, Tree Fl. Malaya 2 (1973) 270.

Type: Hasselt, s.n., Lesser Sunda Islands (Leiden acc. no. 908127-218) (holotype L!).

Fagraea fastigiata sensu Cammerloher, Bull. Jard. Bot. Btzg. III, 5 (1923) 322 pro parte, tantum speciminia Javanica.

Fagraea fastigiata sensu Ridley, J. Str. Br. R. As. Soc. 30 (1897) 167 pro parte, excl. Ridley 7552 (= *F. crenulata* Maingay ex Clarke).

Hemi-epiphyte, up to 17 m high or more on trees; stems to c. 10 cm diameter; **bark** smooth, grey-brown. **Leaves** elliptic to suborbicular; (10–)18–23(–26) cm long, (4.5)8.5–12(–13.5) cm wide; **base** narrowly decurrent with 1–2 mm broad wings towards the petiole base; **apex** acute; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth under magnification; **midrib** prominent and sometimes keeled upon drying on both sides; **secondary veins** 3–5 pairs, upper side faint and immersed in the lamina, lower side prominent; **tertiary and higher-order veins** obscure; petioles 5–10 mm long, 3–5 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 2–3 mm high adaxially; **auricles** developing above the petiolar sheath, continuous from the lamina base, forming small rounded lobes 4–7 mm broad. **Inflorescence** terminal, a few-many-flowered cyme, the whole about 6–7 cm long; **peduncle** indistinct; inflorescence **rachis** 6–7 cm long, 2–4 mm thick, with 2–3 pairs of primary branches; basal primary **branch pairs** (3.5–)5–6 cm long, 2–3 mm thick and rebranched to 1–2 orders. **Flower** bisexual; **pedicel** c. 5 mm long, c. 2 mm thick; **floral bracts** small, acute, c. 3 mm long, located below the calyx; **calyx** 5–6 mm long (from the base to the lobe apices), glabrous, lenticellate, **calyx cup** 4–5 mm wide, **calyx lobes** 5, broad-elliptic to rounded, apically clasping the corolla tube, 4–5 mm long, 3–4 mm wide, margins glabrous, base not auriculate; **corolla** not seen [*fide* Leenhouts (1962): corolla tube widely funnel-shaped, 3 cm long]; **stamens** not seen [*fide* Leenhouts (1962): anthers ovate-lanceolate, 7 mm long]; **style** not seen. **Infructescence** **peduncle** indistinct. **Fruit** broadly ovoid, **apex** rounded; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 20–30 mm long, 20–28 mm wide; the base loosely surrounded by the erect calyx lobes. **Seeds** numerous;

subovoid (non-angular); 2–2.5 mm long, 1–2 mm wide; testa surface areolate; placentation axile.

Distribution. Java, Malay Peninsula.

Habitat. Lowland rain forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kelantan**. SE border near Trengganu, Ulu Sungai Lebir Kechil, 500 m alt, FR, 17 ix 1967, Cockburn FRI 7121, (KEP!), Whitmore FRI 4386 (KEP! SING!). **Perak**. Ijok Forest Reserve, Sow KEP 48648, FB, 11 ii 1939 (KEP!). INDONESIA. Lesser Sunda Islands, *Hasselt s.n.*, FB, no date (L!).

It is distinctive by its leaf base, which attenuates at the base and forms rounded auricles just above the petiolar sheath. In the other species that have auricular structures associated with the leaves, the leaf base is either not completely decurrent to the petiole base or, if decurrent, the auricles are formed at the petiole base below the petiolar sheath.

8. *Fagraea fraserensis* Wong & Sugumaran, sp. nov.

Typus: Sugumaran & Low SM 163, Pahang, Fraser's Hill, beside path to Jeriau waterfall, 12 Oct 2007 (holotypus KLU!).

(Fig. 24)

Hemi-epiphyte (probably also occasionally a shrub or small tree), usually 1–2 m high (or probably more) on trees; trunk/stems to c. 10 cm diameter; **bark** smooth, dark-brown.

Leaves elliptic to subobovate; (6.8–)10–17(–19) cm long, (3.3–)5.5–7.6 cm wide; **base** cuneate, not decurrent; **apex** short cuspidate; **margin** entire, plane in dried material; thin-



Fig. 24. *Fagraea fraserensis*. **A.** leafy branch with inflorescences. **B.** sectioned corolla showing attachment of stamens. **C&D** stigma. **E.** portion of stem with ligules (arrows) at the adaxial side of leaf stalk base **F.** calyx with lobes auriculate at the base (arrow). **G.** branch with an infructescence. A–F from Sugumaran & Low, SM163 (holotype, KLU). G from Sugumaran et al., SM164 (KLU).

coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth under magnification; **midrib** sunken above, prominent below; **secondary veins** 5–7 pairs if visible, otherwise often obscure on both sides; **tertiary and higher-order veins** obscure; petioles 20–30 mm long, 2–4 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 1–2 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a few-many-flowered branched cyme, the whole about 1.6–1.8 cm long; **peduncle** indistinct or to 6 mm long, to 4 mm thick; inflorescence **rachis** 9–18 mm long, 3–4 mm thick, with 1–2 pairs of primary branches; basal primary **branch pairs** 5–16 mm long, 3–4 mm thick and rebranched to 1 order, more distal branch pairs not so. **Flower** fragrant; bisexual; **pedicel** indistinct or to 4 mm long, to 4 mm thick; **floral bracts** small, acute, 3–4 mm long, located below the calyx; **calyx** 10–12 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 4–5 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 8–10 mm long, 8–10 mm wide, margins glabrous, base auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 16–18 mm long, 4–5 mm wide basally, **upper flared part** of the tube slightly inflated, 10–18 mm long, 13–18 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 9–10 mm long, 8–10 mm wide, overlapping to the right; **stamens** 5, inserted (at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube); **filaments** 20–24 mm long, protruding to 6–10 mm from the corolla mouth; **anthers** versatile, hastate, 4–5 mm long, 2–3 mm wide, each anther sac somewhat ellipsoid; **style** 35–42 mm long, protruding to 6–9 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed,

the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 1–1.5 mm across. **Infructescence peduncle** indistinct or to 5 mm long, to 4 mm thick. **Fruit** narrowly ovoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 20–25 mm long, 15–18 mm wide; the base loosely surrounded to tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–3 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Known only from Peninsular Malaysia (Fraser's Hill area).

Habitat. Lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Pahang.** Fraser's Hill, beside path to Jeriau Waterfalls, *Sugumaran* SM 79, FR, 3 xi 2006 (KLU!), *Sugumaran et al.* SM 164, FR, 3 i 2008 (KLU!), beside path to Jeriau Waterfalls, 3°43'N 101°42'E, 970 m, *Sugumaran & Low* SM 163, FB, FL, FR, 12 x 2007 (KLU!), waterfall, epiphyte, *Kiew RK* 3320, FL, 9 ix 1991 (SING!).

Generally, the auriculate bases of the calyx lobes are highly distinctive and appear to be unique among Peninsular Malaysian species of *Fagraea*. This species also differs from most other *Fagraea* species because of the faint but still discernable secondary veins in the dried leaves. The only other Peninsular Malaysian species with distinct leaf veins in dried material includes *F. auriculata*, *F. imperialis*, *F. insignis* (where flowers are very large in comparison, and large leaf-stalk auricles are present in the former two species), *F. fastigiata* (with leaf blades bearing basal auricles), *F. oblonga* (more pairs of secondary veins, typically more branched inflorescences), *F. renae* (more branched inflorescences),

and *F. ridleyi* (with more robust inflorescence axes, 4–6 mm thick, and even larger calyx lobes, 14–18 mm long).

In the exauriculate leaf-stalk bases, indistinct leaf veins, and relatively small, non-involucrate flowers in small, little-branched cymes, *F. fraserensis* approaches *F. splendens*, but its inflorescence has distinct 1st order branches 3–12 mm long (in *F. splendens* they are only 3–4 mm long). The larger calyces (with lobes 9–10 mm long, 8–10 mm broad) also distinguish it from *F. splendens* (lobes 3–4 mm long and broad). The large, thin calyx lobes wrap tightly around the corolla base or young fruit, giving a spindle-shape to the whole calyx structure, compared to the cup-shaped structure in *F. splendens*, where the calyx lobes are held loosely erect. Also, the fruits of *F. fraserensis* are narrowly ovoid with a long attenuate apex when dry, whereas those of *F. splendens* maintain a broad ellipsoid shape with rounded apex. Other species with similar corolla sizes and generally infundibular shapes, such as *F. littoralis* and *F. oblonga*, are also different in their non-auriculate calyx lobes, among other characters.

9. *Fagraea gardenioides* Ridley

J. Fed. Mal. St. Mus. 5 (1914) 42.

Type: *Robinson*, s.n., 22 Jan 1913, Selangor, Gunung Mengkuang (holotype K!; isotype SING!).

Fagraea gardenioides sensu Leenhouts, Fl. Males. I, 6 (2) (1962) 331 pro parte, excl. ssp. *borneensis* Leenhouts (= *F. havilandii* Wong & Sugau).

Fagraea gardenioides sensu Kochummen, Tree Fl. Malaya 2 (1973) 270 pro parte, excl. specimina origine ‘Borneo’.

(Fig. 25)

Small tree or hemi-epiphyte, usually to 4 m tall or 2 m high or more on trees; trunk/stems to c. 5 cm diameter; **bark** smooth, grey to dark-brown. **Leaves** broad elliptic to obovate; (7.5–)9–13(–15.3) cm long, (4–)5–6(–7.6) cm wide; **base** cuneate to not conspicuously decurrent with up to 1 mm-broad wings towards the petiole base; **apex** rounded; **margin** entire, recurved in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** prominent on both sides towards the leaf base but flat to sunken nearer the leaf apex; **secondary veins** obscure on both sides; **tertiary and higher-order veins** obscure; petioles (3–)7–12(–15) mm long, 2–4 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 3–4 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 1-2-few-flowered cyme, the whole about 1–2.2 cm long; **peduncle** indistinct; inflorescence **rachis** 1–2.2 mm long, 4–6 mm thick, with 1–2 pairs of primary branches; basal primary **branch pairs** 15–21 mm long, 3–5 mm thick and not rebranched. **Flower** fragrant; bisexual; **pedicel** 5–6 mm long, 4–5(–7) mm thick; **floral bracts** small, acute, 7–10 mm long, located below the calyx; **calyx** 22–30 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 10–13 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 14–20 mm long, 10–15 mm wide, margins glabrous, base not auriculate; **corolla** slender trumpet shaped (tubular and very gradually widening towards the apex); cream to white; **corolla tube** 40–53 mm long, 8–15 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 30–42 mm long, 14–25 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments**

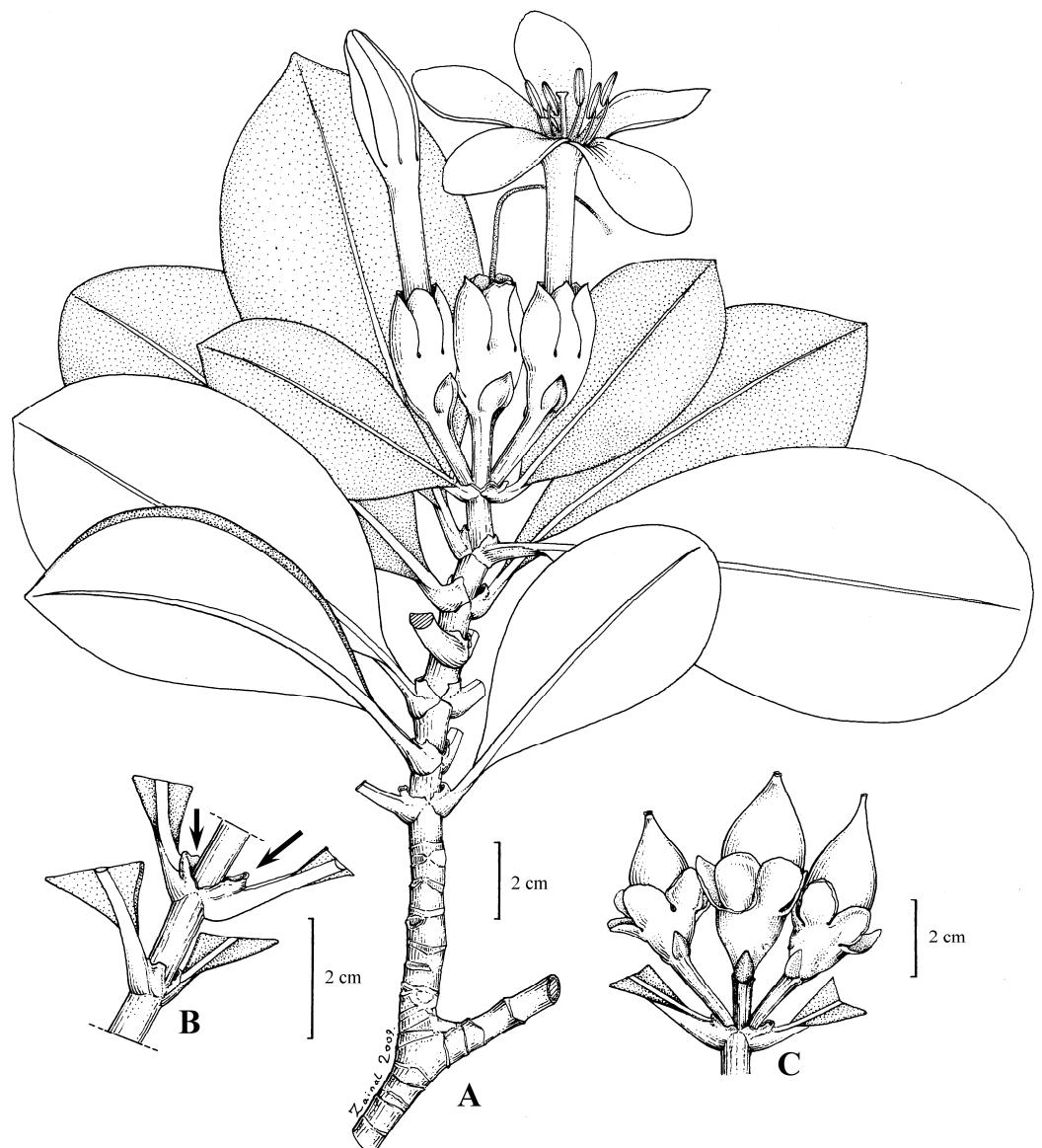


Fig. 25. *Fagraea gardenioides*. A. leafy branch with an inflorescence. B. portion of stem with ligules (arrows) at the adaxial side of the petiole. C. an infructescence.
All from Poore 749 (KLU).

20–27 mm long, protruding to 12–17 mm from the corolla mouth; **anthers** versatile, hastate, 8–10 mm long, 3–4 mm wide, each anther sac somewhat ellipsoid; **style** 50–55 mm long, protruding 2–10 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpetiolate structure 3–4 mm across. **Infructescence peduncle** indistinct or to 6 mm long, to 5 mm thick. **Fruit** narrowly to broadly ovoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 30–40 mm long, 13–20 mm wide; the base loosely to tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–3 mm long, 1–2 mm wide; testa surface areolate; placentation axile.

Distribution. Malay Peninsula (Main Range mountains, Gunung Bubu and Gunung Korbu).

Habitat. Upper reaches of lower montane forest and upper montane mossy forest, common in stunted vegetation on ridges.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Pahang.** Cameron Highlands, Gunung Brinchang, 6000 ft alt, *Poore* 749, FL, 3 vii 1961 (KLU!), 6666 ft alt, *Ng* FRI 5975, FR, 3 iii 1968 (KEP! SING!), 6500 ft alt, *Stone* 7251, FB, FL, 1 viii 1967 (KLU!); Fraser's Hill, Pine Tree Hill, *Symington* KEP 29482, leafy twig, 14 ix 1933 (KEP!), 4750 ft alt, *Burkill*, *Md Shah & Md Noor* HMB 2384, FL, 18 viii 1960 (SING!), 4780 ft alt, *Purseglove* P 4231, FB, FL, 19 iv 1955 (SING!); Pahang/Selangor border, summit of Ulu Kali, 5000-6000 ft alt, *Soepadmo* HUM 9002, FB, FR, 4 iv 1968 (KLU!); Gunung Ulu Kali, 5500 ft alt, *Stone* 14071, FL, 31 iii 1979 (KLU!), 5600 ft alt, *Siew* 144, FL, 18 vi 1977 (KLU!). **Perak.** Gunung Bubu summit, *Symington* KEP 30843, FB, FL, 8 iv 1933 (KEP!); Gunung Korbu, 5500-7000 ft alt, *Symington* KEP 32235, FL, 22 vii 1933 (KEP! SING!); Gunung Raya, 5700 ft alt, *Strugnell & Tachun* KEP 45890, FB, 31 i 1938 (KEP!). **Selangor.** Gunung Mengkuang, 5000-5600 ft alt, *Robinson* s.n., FL, 22 i 1913 (K! SING!); Ulu

Selangor, Genting Highlands, G. Genting Chin-Chin, 1680 m alt, 3°27'N 101°47'E, Chua et al. FRI 40798, FB, FL, 6 v 1999 (KEP!); Ulu Selangor, Gunung Moyang, 5500 ft alt, Symington KEP 56665, FR, 3 xi 1940 (KEP!).

Leenhouts (1962) placed Sarawak material as a subspecies (ssp. *borneensis*) of this species, but that has been distinguished as a different species, *F. havilandii* by Wong & Sugau (1996).

10. *Fagraea imperialis* Miquel

Fl. Ind. Bat. 2 (1857) 372; Wong & Sugau, Sandakania 8 (1996) 68.

Type: Teysmann HB 599, Sumatra, Siboga (Leiden acc. no. 908127-58) (isotype L!).

Fagraea auriculata auct. non Jack (1822), pro parte, quoad *F. imperialis* Miquel in syn.: Clarke in Hooker f., Fl. Brit. Ind. 4 (1885) 83; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 605; Ridley, Fl. Malay. Pen. 2 (1923) 416; Leenhouts, Fl. Males. I, 6 (2) (1962) 326.

Hemi-epiphyte, up to 25 m high or more on trees; stems to c. 15 cm diameter; **bark** smooth, grey-brown; branch internodes typically with a pair of keels 2–5 mm broad along the interpetiolar region. **Leaves** elliptic to subovate; (5–)25–34(–38) cm long, (4–)10–13(–17) cm wide; **base** narrowly decurrent with (0.5–)1–2 mm-broad wings towards the petiole base; **apex** acute to slightly pointed; **margin** entire, recurved in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth under magnification; **midrib** slightly prominent above, more prominent below with a low median keel upon drying; **secondary veins** 5–7(–8) pairs, upper side faint and

immersed in the lamina, lower side prominent; **tertiary and higher-order veins** faint; petioles 5–15(–20) mm long, 5–7(–9) mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 1–2(–4) mm high adaxially; **auricles** developing below the petiole base distinct from the lamina base, forming broad rounded reflexed lobes (0.6–)1–1.8(–2) cm broad (in fresh materials measuring up to 3 cm broad). **Inflorescence** a 2-few-flowered cyme, the whole about 1.5–3.5(–5) cm long; **peduncle** indistinct; inflorescence **rachis** 1.5–3.5(–5) cm long, 1–1.5 cm thick, with 1(–2) pairs of primary branches; basal primary **branch pairs** 2–4 cm long, 1–1.2 cm thick and not rebranched. **Flower** very fragrant; bisexual; **pedicel** inconspicuous; **floral bracts** conspicuous, (1–)2–3(–3.5) cm long, rounded, these and a pair of conspicuous inflorescence-branch bracts forming a loose involucre around the calyx; **calyx** 6.5–7 cm long (from the base to the lobe apices), glabrous, not lenticellate, **calyx cup** 2.5–3(–4) cm wide, **calyx lobes** 5, broad-elliptic to rounded, (4.5–)5–5.5(–5.7) cm long, (3–)3.4–3.7(–4) cm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** (4–)9–10 cm long, (1.5–)2.5–3 cm wide basally, **upper flared part** of the tube slightly inflated, 5–6 cm long, 6.5–7.5(–8) cm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 6.5–7.5(–8) cm long, 4.5–5.5(–7) cm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** (5.5–)8–9 cm long, protruding to (0.5–)2.7–4 cm from the corolla mouth; **anthers** versatile, hastate, 1.5–1.7 cm long, c. 1 cm wide, each anther sac somewhat ellipsoid; **style** 9–10(–11.5) cm long, slightly protruding to c. 5 mm

from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive, 4–6 mm across. **Infructescence peduncle** indistinct. **Fruit** narrowly ellipsoid, **apex** rounded; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to c. 9.5 cm long, c. 4.5 cm wide; the base tightly clasped by the erect calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2.5–3 mm long, 2–2.2 mm wide; testa surface areolate; placentation axile.

Distribution. Sumatra, Malay Peninsula.

Habitat. Swamp forests and lowland terrestrial forests from coastal to inland sites.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. Locality unknown, *Teruya* 2421, FL, vii-viii 1933 (SING!). **Kelantan**. W Kelantan, Sungai Perias at Kuala May, *Whitmore* FRI 4164, leafy twig only, 21 vii 1967 (KEP!); Ulu Kelantan, Gua Musang, summit of limestone hill, Ng FRI 5563, leafy twig only, 22 vi 1967 (KEP!). **Pahang**. Taman Negara, Batu Subuh, summit, *Kiew* 1485, FR, 8 x 1984 (KEP! SING!); Taman Negara, Gua Luas, summit, Ng FRI 27054, leafy twig only, 4 iii 1977 (KEP!). **Perak**. Bubu Forest Reserve, *Symington* FMS 28571, FB, 30 iii 1933 (SING!); Gunung Bubu, banks of Sungai Kenas at dam, 250 ft alt, *Whitmore* FRI 963, leafy twig only, 15 ii 1967 (KEP!); Tasik Temenggor, Sungai Gadong, *Sugumaran et al.* SM 230, FL, 29 vii 2008 (KLU!), SM 238, FB, FL, 5 viii 2008 (KLU!). **Selangor**. Weld Hills F.R., (*Collector name indistinct*) CF 908, FB, FL, 12 viii 1916 (KEP!). SUMATRA. Atjeh, Gunung Leuser Nature Reserve, *deWilde & deWilde-Duyfjes* 14047, FR, 5 vii 1972 (SING!), Oneng Oneng, 1180 m alt, *Steenis* 6583a, leafy branch only, no precise date, 1934 (SING!); Siboga, *Teysmann* HB599, FL (Drawing), no date (L).

This species has often been confused with *F. auriculata* because of the development of large, leathery, rounded auricles at the petiole bases and the generally big,

distinctive creamy flowers. However, the larger flowers of *F. imperialis* and other characters adequately distinguish the two.

11. *Fagraea insignis* Wong & Sugumaran, sp. nov.

Typus: Henderson SFN 23289, Pahang, Cameron Highlands, 4800 ft., 1 Apr 1930 (holotypus SING! isotypus KEP!).

Fagraea auriculata auct. non Jack (1822): Leenhouts, Fl. Males. I, 6 (2) (1962) 331 pro parte, tantum specimina montium peninsulae Malayensis sub 'ssp. auriculata', e.g. Henderson SFN 31081; Kochummen, Tree Fl. Malaya 2 (1973) 270 pro parte, tantum specimina montium peninsulae Malayensis; Wong & Sugau, Sandakania 8 (1996) 51 pro parte, incl. Fig. 16, quoad Symington KEP 36092, Whitmore FRI 12214, 15551.

(Fig. 26)

Small tree or hemi-epiphyte, usually to 5 m tall or 5 m high or more on trees; trunk/stems to c. 5 cm diameter; **bark** smooth to shallowly fissured, grey-brown; branch internodes often developing a pair of low ridges or keels up to 1 mm high in the inter-petiolar region.

Leaves elliptic to subobovate; (7.5–)13–16(–22) cm long, (3.8–)5–6.2(–7.2) cm wide; **base** narrowly decurrent with 1–2 mm broad wings towards the petiole base; **apex** shortly

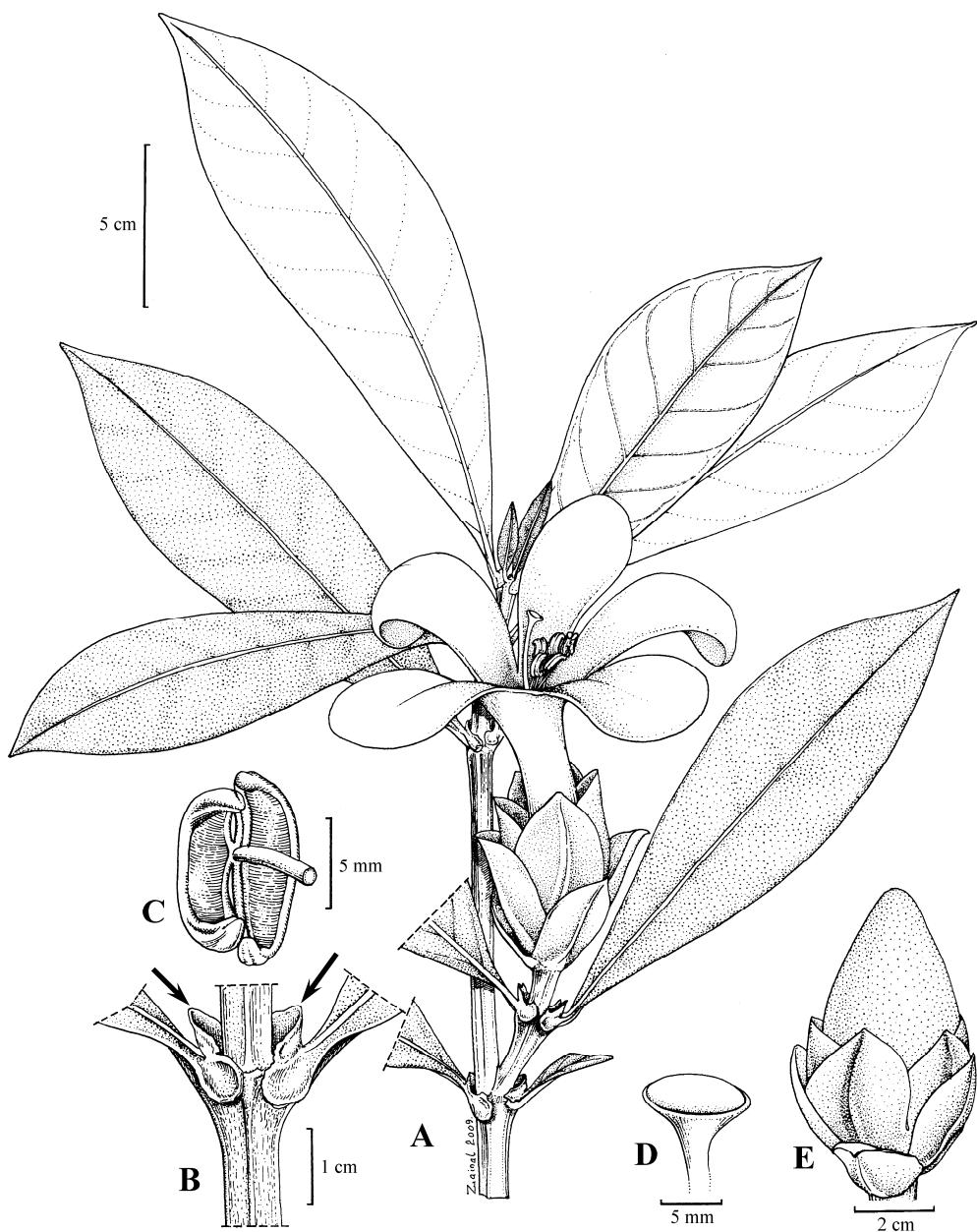


Fig. 26. *Fagraea insignis*. A. leafy branch with an inflorescence. B. portion of stem with ligules (arrows) at the adaxial side of the petiole. C. ventral part of the anther. D. stigma. E. fruit.

A,C & D from Hislop s.n. (SING), B & E from Whitmore FRI 12214 (KEP).

pointed; **margin** entire, recurved in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below and sometimes developing a low median keel upon drying; **secondary veins** 5–7 pairs, upper side faint and immersed in the lamina, lower side faint and immersed in the lamina; **tertiary and higher-order veins** obscure; petioles (1–)5–7(–17) mm long, (2–)3–4 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 2–3 mm high adaxially; auricles developing below the petiolar base, distinct from the lamina base, forming narrow rim-like structures (2–)3–5(–7) mm broad. **Inflorescence** terminal, consisting of a solitary flower, the whole about 5–15 mm long; **peduncle** indistinct or to 5–10(–15) mm long, to 8 mm thick; the rachis internode between peduncle and pedicel indistinct. **Flower** very fragrant; bisexual; **pedicel** indistinct or to 10 mm long, to 10 mm thick; **floral bracts** small to large, rounded, (7–)15–30(–35) mm long, typically overlapping the calyx base and forming a loose involucre around the calyx together with a pair of expanded inflorescence bracts (when the latter are present); **calyx** (30–)35–50 mm long (from the base to the lobe apices), glabrous, lenticellate, **calyx cup** (10–)15–25 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 23–35(–40) mm long, 17–25 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 22–30 mm long, 10–17 mm wide basally, **upper flared part** of the tube slightly inflated, 23–30 mm long, 28–40(–50) mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 32–50(–60) mm long, 30–37 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the

lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 40–50 mm long, protruding to 17–20 mm from the corolla mouth; **anthers** versatile, hastate, 8–10 mm long, 5–6 mm wide, each anther sac somewhat ellipsoid; **style** 65–70 mm long, protruding to 10–22 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive, the whole sometimes resembling a subpeltate structure c. 8 mm across. **Infructescence peduncle** indistinct or to 5 mm long, to 7 mm thick. **Fruit** narrowly to broadly ovoid, **apex** conspicuously attenuated; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 45–55(–60) mm long, 20–35 mm wide; the base tightly clasped by the erect calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, c. 1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Malay Peninsula.

Habitat. Lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Pahang.** Bentong, Fraser's Hill, *Kochummen* KEP 98161, FB, 11 xii 1961 (KEP!); Cameron Highlands, 4800 ft alt, *Henderson* SFN 23289, FL, FR, 1 iv 1930 (KEP! SING!); Cameron Highlands, Mardi Trail 7, 1450 m alt, *Garcia* FRI 32703, FR, 5 iv 1988 (KEP!); Cameron Highlands, route 7 to G. Beremban, 1500 m alt, *Perumal et al.* FRI 41624, FB, 3 iii 1994 (KLU!); Gunung Benom, main NE ridge, boundary of Krau Game Reserve, 4800 ft alt, *Whitmore* FRI 3328, FR, 20 iii 1967 (KEP!); Selangor border, Ulu Kali, *Whitmore* FRI 15551, FL, 2 x 1970 (KEP!), 5000 ft alt, *Whitmore* FRI 12214, FL, FR, 24 viii 1968 (KEP!), FB, FR (SING!); Ulu Telom, *Jaamat* KEP 27295, FR, 29 viii 1931 (KEP!). **Perak.** Birch's Hill, *Fox* s.n., FR, x 1899 (SING!), *Burkill & Haniff* SFN 12861, FR, 29 ii 1924 (SING!); near the Cottage, *Fox* s.n., FB, FL, x 1899 (SING!); Taiping Hill, 4100 ft alt, *Henderson* SFN

11805, FR, 4 iii 1924 (SING!). **Terengganu.** Gunung Padang, *Hislop* s.n., FL, vii 1952 (SING!), 4000 ft alt, *Moysey & Kiah* SFN 31081, FB, FL, vi 1937 (SING!).

This is easily distinguished from both *F. auriculata* and *F. imperialis* by its always solitary flowers, smaller leaves and montane provenance; also in its large floral bracts (different from *F. auriculata*, similar to *F. imperialis*) and smaller flowers (different from the very big flowers of *F. imperialis*, just slightly smaller than those of *F. auriculata*; See discussion under *F. auriculata* for a more detailed comparison for these three species).

Both this and the Bornean *F. resinosa* develop large, rounded floral bracts around the calyx. Both also have a slight auricular structure at the petiole bases. However, this species has a broadly infundibular corolla, unlike the subsalverform corolla with a long narrow tube in *F. resinosa*.

12. *Fagraea larutensis* Sugumaran, sp. nov.

Typus: King's Collector 7518, Perak, Larut, 300–500 ft., April 1885 (holotypus SING!).

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad *Sinclair & Kiah* SFN 38660 & *Burkill & Haniff* 12585.

Fagraea obovata auct. non Wallich ex Roxburgh (1824): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 606 pro parte, quoad *King's coll.* 7578.
(Fig. 27)

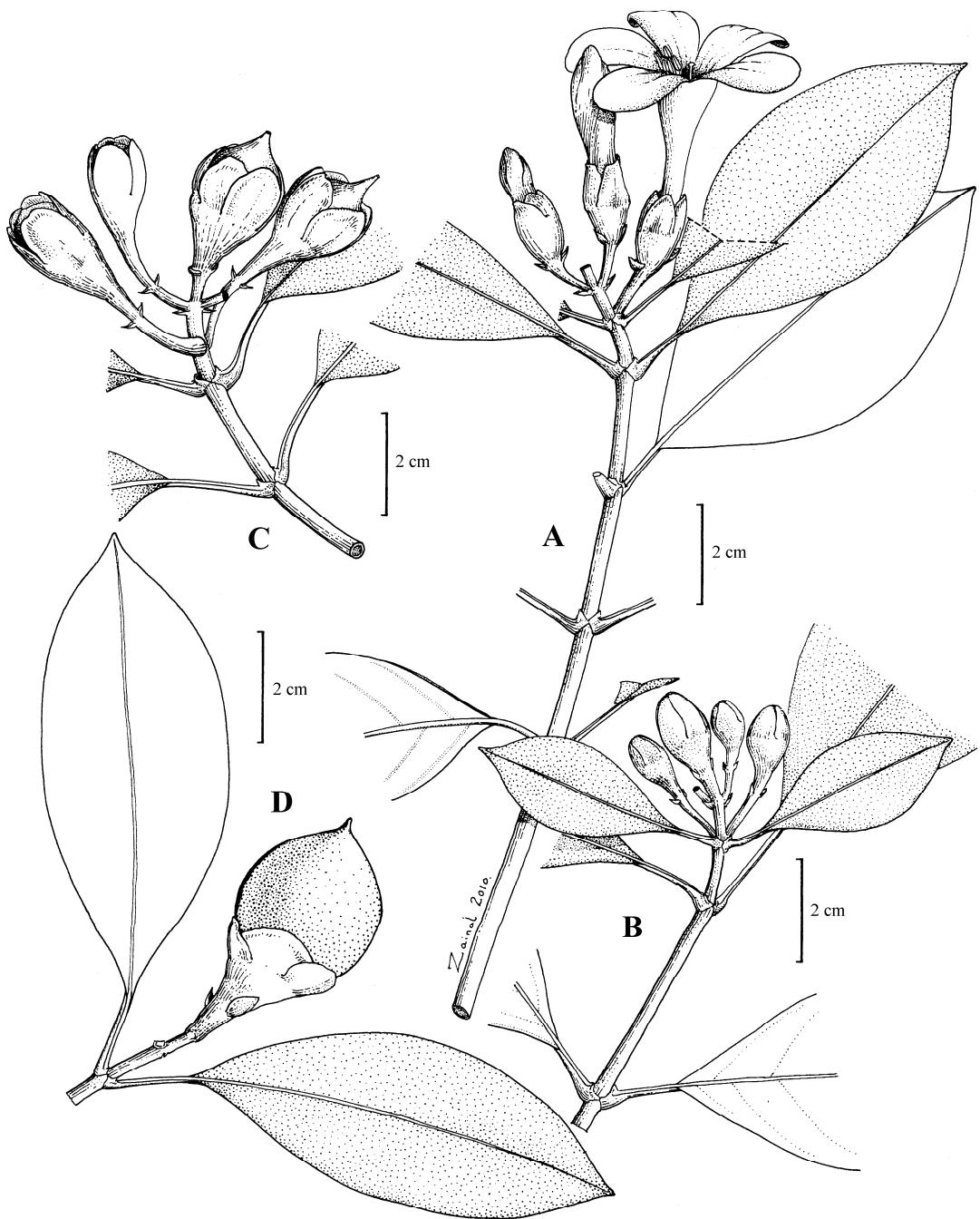


Fig. 27. *Fagraea larutensis*. A. leafy branch with an inflorescence. B. leafy branch with flower buds. C. leafy branch with infructescence. D. leafy branch with a single matured fruit.

A from King's Collector 7518 (Holotype, SING), B Sidek SK 438 (SING), C Sinclair & Kiah SFN 38660 (SING), D from Burkill & Haniff SFN 12585 (SING).

Scrambler or hemi-epiphyte, 10–30 m high or more on trees; trunk/stems to c. 10–15 cm diameter; **bark** smooth, grey-brown. **Leaves** elliptic; (6.5–)8–11(–12) cm long, (2–)3–5 cm wide; **base** cuneate, not decurrent; **apex** short-cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below; **secondary veins** 4–5 pairs if visible, otherwise obscure on both sides; **tertiary and higher-order veins** obscure; petioles 13–20 mm long, 1–2 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a few-many-flowered branched cyme, the whole about 15–25 mm long; **peduncle** indistinct; inflorescence **rachis** c. 10 mm long, c. 4 mm thick, with 2–3 pairs of primary branches; basal primary **branch pairs** 10–12 mm long, 3–4 mm thick and not rebranched. **Flower** bisexual; **pedicel** indistinct or to 3 mm long, to 4 mm thick; **floral bracts** small, acute, 3–4 mm long, located below the calyx; **calyx** 17–18 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 5–6 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 9–10 mm long, 7–8 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); creamy yellow to white; **lower subcylindrical part of the corolla tube** c. 10 mm long, c. 5 mm wide basally, **upper flared part** of the tube (when distinct) slightly inflated, c. 10 mm long, c. 16 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 15–16 mm long, 9–10 mm wide, overlapping to the right; **stamens** not seen; **style** not seen. **Infructescence peduncle**

indistinct. **Fruit** broadly ovoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 30–32 mm long, 20–30 mm wide; the base loosely surrounded by the calyx lobes. **Seeds** numerous; ellipsoid–subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Known only from Peninsular Malaysia (at Maxwell Hill, also known as Bukit Larut).

Habitat. Lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Perak**. Gunung Hijau, 4400 ft alt, *Burkill & Haniff* SFN 12585, FR, 2 iii 1924 (SING!), Larut, 300 to 500 ft alt, *King's Coll.* 7518, FB, FL, iv 1885 (SING!), Maxwell's Hill, between Birch's Hill and the Cottage, *Sinclair & Kiah* SFN 38660, FR, 10 ix 1949 (SING!), Maxwell's Hill, 3000–3700 ft alt, *Sidek* SK 438, FB, 15 ii 1976 (SING!); Taiping Hill, 4100 ft alt, *Henderson* SFN 11807, FR, 4 iii 1924 (SING!).

This species closely resembles *F. crassifolia* Blume and *F. latibracteata* Sugumaran (described here). In *F. crassifolia*, the calyx lobes (20–26 mm long) and corolla lobes (20–27 mm long) are larger and the corolla tube (16–17 mm long) is also shorter. *F. larutensis* has small and acute floral bracts that are located below the calyx base and that are only 3–4 mm long, whereas *F. latibracteata* has larger and rounded floral bracts that overlap the calyx base and 17–18 mm long. Also, *F. larutensis* is confined only to higher elevations in lower montane forests, whereas *F. crassifolia* and *F. latibracteata* are both lowland species.

13. *Fagraea latibracteata* Sugumaran, sp. nov.

Typus: Cockburn FRI 7252, Kelantan, Ulu Kelantan, Relai Forest Reserve, ridge top, 18 Oct. 1967 (*holotypus KEP!* *isotypus SING*).

Fagraea carnosa auct. non Jack (1822): Leenhouts, Fl. Males. I, 6 (2) (1962) 331 pro parte, quoad Sinclair & Kiah SFN 39931.

(Fig. 28)

Small tree or hemi-epiphyte, height not recorded; trunk/stem diameter not recorded; **bark** smooth, grey-brown. **Leaves** narrow elliptic; (5–)6.5–10(–13.2) cm long, (1.5–)2–4 cm wide; **base** cuneate, not decurrent; **apex** short blunt cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat to sunken above, prominent below; **secondary veins** not visible on both sides; **tertiary and higher-order veins** obscure; petioles (8–)10–15 mm long, 1.5–2.5 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, of a solitary flower, the whole about 0.8–1.3 cm long; **peduncle** indistinct or to 6 mm long, to 4 mm thick; the rachis internode between peduncle and pedicel indistinct or to 7 mm long, 5 mm thick. **Flower** bisexual; **pedicel** inconspicuous; **floral bracts** conspicuous, rounded, 17–18 mm long, overlapping the calyx base; **calyx** 20–22 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate,

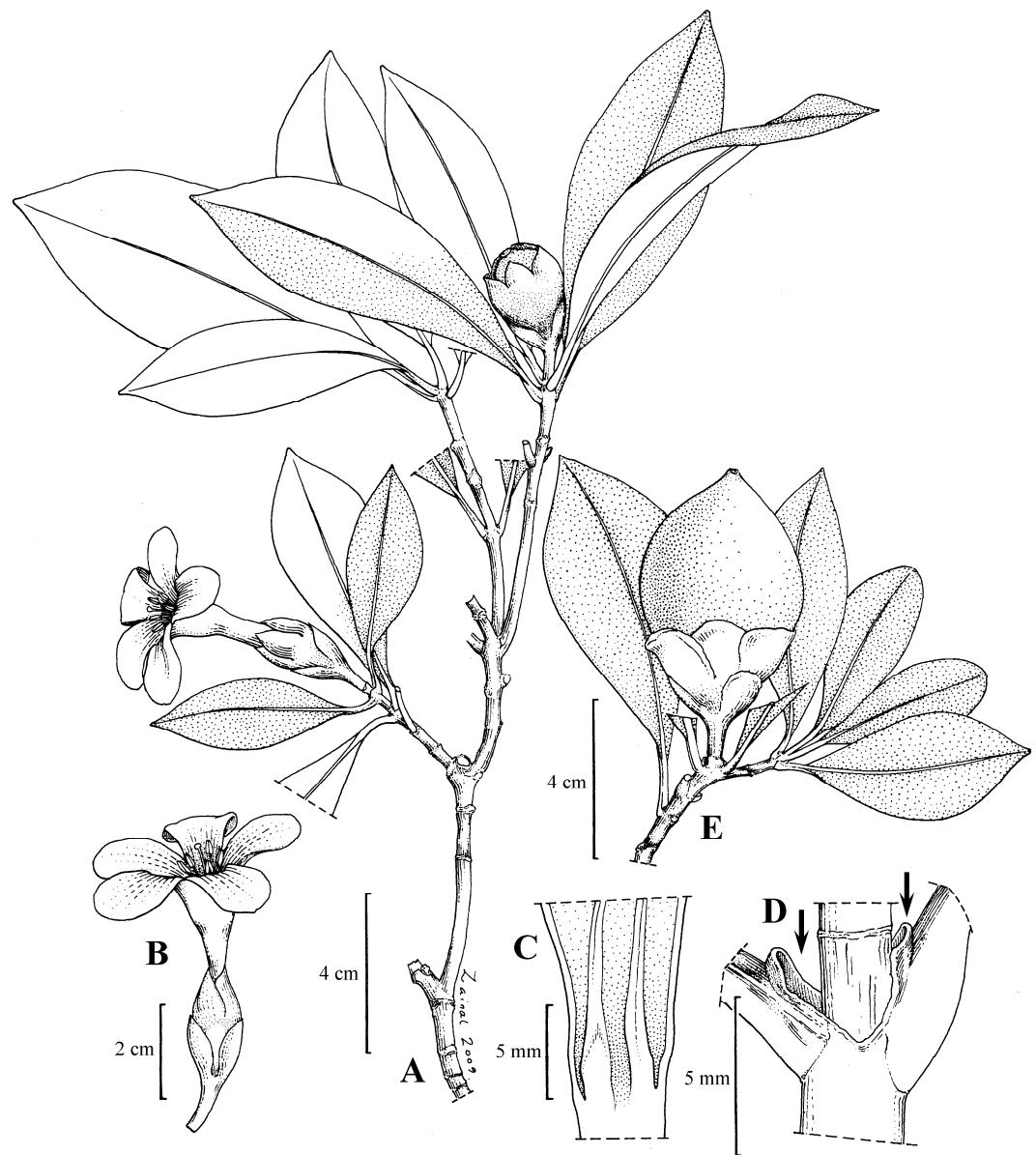


Fig. 28. *Fagraea latibracteata*. A. leafy branch with a flower and a young fruit. B. flower C. a sectioned upper part of the corolla tube showing the attachment of the filament. D. portion of stem with ligules (arrows) at the adaxial side of the petiole. E. leafy branch with fruit.

A, D & E from Cockburn FRI 7252 (Holotype, KEP), B & C from Sugumaran, SM55 (KLU).

calyx cup 8–10 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 10–12 mm long, 10–12 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 13–15 mm long, 5–7 mm wide basally, **upper flared part** of the tube slightly inflated, 10–15 mm long, 16–22 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 16–18 mm long, 13–15 mm wide, overlapping to the right; **stamens** 5, inserted (at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube); **filaments** 16–20 mm long, protruding 5–6 mm from the corolla mouth; **anthers** not seen; **style** not seen. **Infructescence peduncle** indistinct or to 3 mm long, to 3 mm thick. **Fruit** broadly ovoid to subglobose, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 32–55 mm long, 32–40 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. North-eastern part of Peninsular Malaysia, in the states of Kelantan, Pahang and Terengganu.

Habitat. Lowland forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Endau-Rompin, Selai, trail to Takah Tinggi, Sugumaran & Wong SM 55, FL, 18 x 2005 (KLU!). **Kelantan.** Ulu Kelantan, Relai Forest Reserve, Cockburn FRI 7252, FL, FR, 18 x 1967 (KEP!). **Pahang.** Lipis, Taman Negara, K. Relau-K. Juram road, 440 m alt, Saw FRI 44801, FB, 8 viii 1996 (KEP!). **Terengganu.** 23rd mile Trengganu-Besut road, Belara F.R.,

Sinclair & Kiah SFN 39931, FB, 13 vii 1953 (SING!); Ulu Besut, near Bt. Jebak Puyoh, 200 ft alt, *Cockburn* FRI 8279, FR, 2 v 1968 (KEP! SING!).

F. latibracteata closely resembles *F. larutensis* and *F. crassifolia*. The marked difference from these two species is that *F. latibracteata* has larger floral bracts which are 17–18 mm long and overlaps the calyx base. *F. larutensis* and *F. crassifolia* have small and acute floral bracts that are 6 mm long or less and located below the calyx base. Another difference is that both *F. larutensis* and *F. crassifolia* have branched 2-few-flowered cymes, whereas *F. latibracteata* has solitary flowers.

14. *Fagraea littoralis* Blume

Bijdr. (1826) 1021, Rumphia 2 (1838) 28, t. 74; Wong & Sugau, Sandakania 8 (1996) 73.

Type: *Blume*, s.n., Java, Nusa Kambangan (Leiden acc. no. 908127-530) (holotype L!).

Fagraea forstenii Blume, Mus. Bot. 1 (1850) 166. Type: *Forsten*, s.n., Celebes (Leiden acc. no. 908127-228) (holotype L!).

Fagraea littoralis var. *amboinensis* Blume, Rumphia 2 (1838) 28, t. 74. Type: *Zippelius*, Moluccas, Ambon (Leiden acc. no. 908127-67) (L!).

Fagraea littoralis sensu Cammerloher, Bull. Jard. Bot. Btzg. III, 5 (1923) 328 pro parte, excl. *F. crassifolia* Blume in syn.

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad *F. littoralis* Blume & *F. forstenii* Blume in syn.

Fagraea obovata auct. non Wallich ex Roxburgh (1824): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 606 pro parte, quoad *Wray* 2714 & 4269; Ridley, Fl. Malay. Pen. 2 (1923) 418 pro parte, quoad ‘Kamunting’ (= *Wray* 4269).

(Fig. 29)

Hemi-epiphyte, height not recorded; trunk/stems diameter not recorded; **bark** smooth, grey-brown. **Leaves** elliptic to suborbicular; (5–)7–9(–10.5) cm long, (2.5–)3–5(–5.5) cm wide; **base** cuneate to rounded, not decurrent; **apex** short cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface minutely wrinkled under magnification; **midrib** flat above, prominent below; **secondary veins** 7–10 pairs if visible, obscure on both sides; **tertiary and higher-order veins** obscure; petioles 10–15 mm long, 1–3 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 2-few-flowered branched cyme, the whole about 3 cm long; **peduncle** indistinct or to 8 mm long, to 3 mm thick; inflorescence **rachis** c. 22 mm long, c. 2.5 mm thick, with 1–3 pairs of primary branches; basal primary **branch pairs** c. 12 mm long, c. 2 mm thick and not rebranched. **Flower** bisexual; **pedicel** 2–3 mm long, 2–3 mm thick; **floral bracts** small, acute, 1.5–2 mm long, located below the calyx; **calyx** 8–10 mm long (from the base to the lobe apices), glabrous, to sometimes lenticellate, **calyx cup** 2.5–3 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 5–6 mm long, 5–7 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 10–16 mm long, 3–3.5 mm wide basally, **upper flared part** of the tube slightly inflated, 15–16 mm long, 12–14 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 15–22 mm long, 10–13 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower

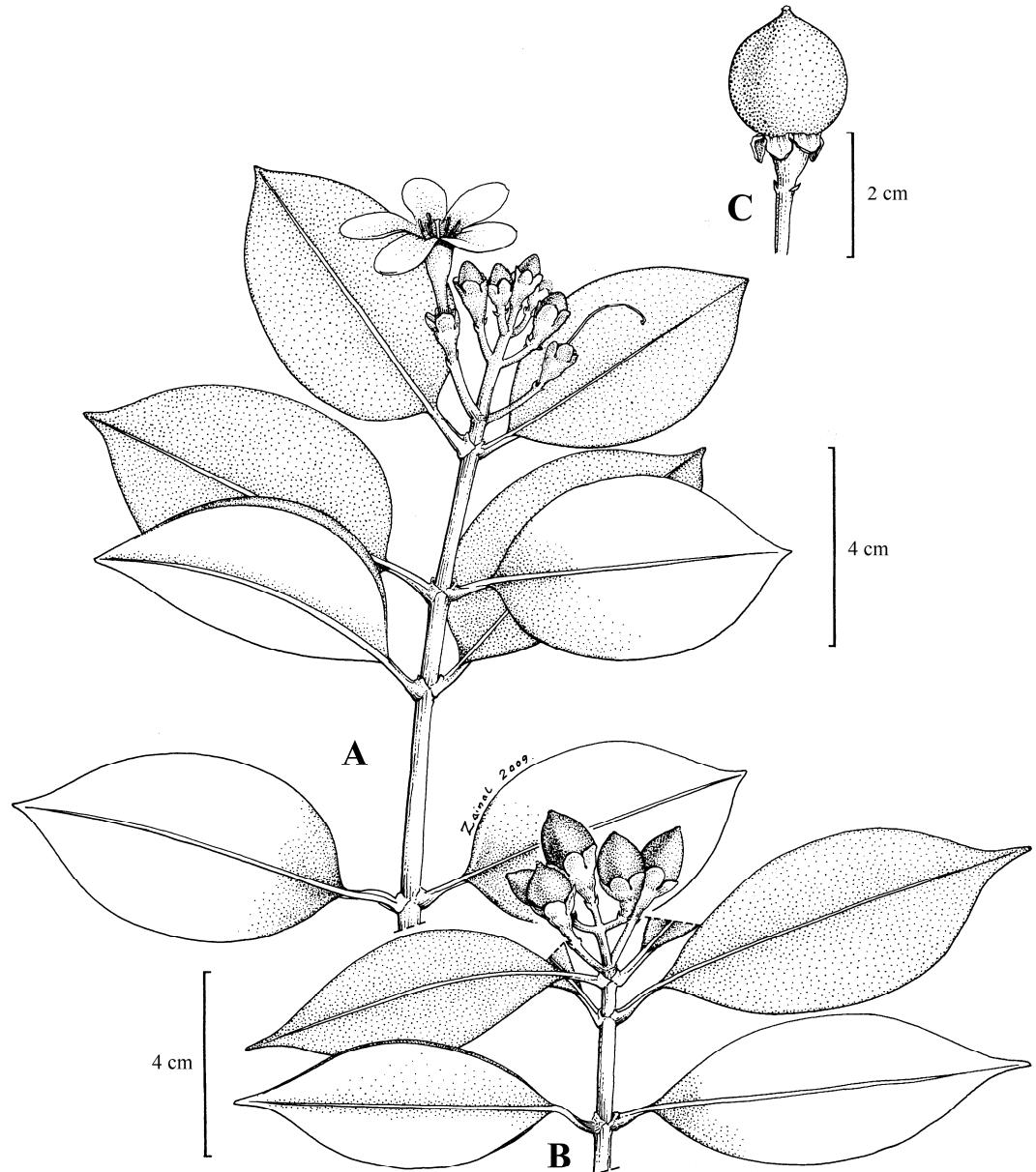


Fig. 29. *Fagraea littoralis*. A. leafy branch with an inflorescence. B. leafy branch with an infructescence. C. fruit.
A from Wray 4268 (SING), B from Wray 2714, C from Spare SFN 36006.

narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 23–25 mm long, protruding to 12–13 mm from the corolla mouth; **anthers** versatile, hastate, 4–5 mm long, 1.5–2 mm wide, each anther sac somewhat ellipsoid; **style** 32–35 mm long, protruding to 3–7 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpetiolate structure 1.5–2 mm across. **Infructescence peduncle** indistinct or to 4 mm long, 3 mm thick. **Fruit** broadly ovoid to subglobose, **apex** slightly pointed to rounded; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 18–20 mm long, 13–15 mm wide; the base loosely surrounded by the calyx lobes (recurved and folding backwards in dried material). **Seeds** numerous; ellipsoid to subovoid (non-angular); 1.5–2 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Java, Malay Peninsula, Sulawesi, Maluku.

Habitat. Coastal sites not far from the sea.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kelantan.** Sungai Kelantan, *Ridley* 9157, FL, xii 1897 (SING!). **Perak.** Larut, Kamunting, *Wray* 4269, FL, 1894 (SING!); Matang, *Wray* 2714, FR, viii 1888 (SING!); Sungai Krian Estate, sea level, *Spare SFN* 36006, FR, 10 vii 1938 (SING!); Simpang, plains, *Wray* 2248, FR, no date (SING!). **Selangor.** Batang Berjuntai, *Ridley* 7551, FB, FR, iii 1891 (SING!). **JAVA.** Nusa Kambangan, *Blume s.n.*, FR, no date (L!). **CELEBES.** Tondano, *Forsten s.n.*, FR, no date (L!).

The taxon in Peninsular Malaysia is the typical variety as represented by Javanese material; Wong & Sugau (1996) described *F. littoralis* var. *borneensis* from Borneo, which

has longer primary branches of the inflorescence (2–6 cm long) and longer calyx lobes (7–10 mm long).

15. *Fagraea oblonga* King & Gamble

J. As. Soc. Beng. 74 (2) (1908) 612; Ridley, Fl. Malay. Pen. 2 (1923) 417; Wong & Sugau, Sandakania 8 (1996) 78.

Lectotype (Wong & Sugau, Sandakania 8 (1996) 78): *King's coll.* 5430, Perak, Larut (K!).

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad *Burkill & Haniff* 12982, *Henderson* FMS Mus. 11128, *Purseglove* P.4141, *Ridley* 12069 & s.n. March 1892 Perak Tea Gardens; Kochummen, Tree Fl. Malaya 2 (1973) 271 pro parte, quoad *F. oblonga* King & Gamble in syn.

Small tree or hemi-epiphyte, usually to 12 m tall or 10 m high or more on trees; trunk/stems to c. 15 cm diameter; **bark** smooth, grey to dark-brown. **Leaves** elliptic-lanceolate to subobovate; (11–)15–28(–36) cm long, 4–8(–10.7) cm wide; **base** cuneate to rounded, not decurrent; **apex** cuspidate; **margin** entire, recurved in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below; **secondary veins** 7–10 pairs if visible, upper side faint and immersed in the lamina, lower side obscure; **tertiary and higher-order veins** obscure; petioles (20–)25–50(–60) mm long, 2–3 mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1.5 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a few-many-flowered branched cyme, the whole about 1.2–3.6 cm long; **peduncle** indistinct or to 4 mm long, to 5 mm

thick; inflorescence **rachis** 1.2–2.7(–3.2) cm long, (1–)3–4 mm thick, with 2–3 pairs of primary branches; basal primary **branch pairs** 8–27 mm long, 1–3 mm thick and not or rebranched to 1(–2) orders, more distal branch pairs less so. **Flower** fragrant; bisexual; **pedicel** 5–10 mm long, 1.5–3 mm thick; **floral bracts** indistinct or present as a very small structure less than 0.5 mm long below the calyx; **calyx** 10–15 mm long (from the base to the lobe apices), glabrous, lenticellate, **calyx cup** 4–5 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 5–7 mm long, 5–6 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 10–20 mm long, 3–4 mm wide basally, **upper flared part** of the tube (when distinct) slightly inflated, 11–16 mm long, 10–15 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 12–18 mm long, 8–10 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 18–22 mm long, protruding to c. 8 mm from the corolla mouth; **anthers** versatile, hastate, 5–6 mm long, 1.5–2 mm wide, each anther sac somewhat ellipsoid; **style** 22–30 mm long, protruding to 1–6 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 1–1.5 mm across. **Infructescence** **peduncle** indistinct or to 3 mm long, to 4 mm thick. **Fruit** broadly ovoid, **apex** rounded; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 32–46 mm long, 20–28 mm wide; the base loosely surrounded to tightly clasped by the

calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo, Malay Peninsula, Sumatra.

Habitat. Lower montane forest, occasionally lowland forest on the foothills of mountains.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Pahang.** Cameron Highlands, 3500 ft alt, *Henderson* SFN 32967, FL, 1 v 1937 (KEP!), 4000 ft alt, *Quaife* s.n., FR, x 1940 (SING!), Boh Plantations, *Md Nur* SFN 32967, FB, 1 v 1937 (SING!), Sungai Bertam, below Robinson's Falls, 3500 ft alt, *Henderson* SFN 11128, FB, FL, 18 vi 1923 (SING!); Fraser's Hill, waterfall, 3800 ft alt, *Manurung* 27, FR, 17 vi 1972 (KLU!), 4000-4370 ft alt, *Burkill & Holttum* FMS 7861, FR, 16-30 ix 1922 (SING!), 4500 ft alt, *Mohd Shah* MS 2730, FR, 30 viii 1972 (KEP! SING!), Bukit Jeriau, *Kochummen* FRI 19451, FL, 11 v 1976 (KEP!), Farm Road, 3800 ft alt, *Purseglove* P 4141, FR, 17 iv 1955 (SING!), Gap, *Hashim* KEP 1084, FR, 3 viii 1917 (KEP!), *Sugumaran & Daniel* SM 176, leafy branch only, 5 iii 2008 (KLU!), Jeriau (Farm) road, 3500-4000 ft alt, *Burkill, Md Shah & Md Noor* HMB 2421, FR, 20 viii 1960 (KEP! SING!), Jeriau Road, *Stone, Mahmud & students* BCS 10804, FR, 17 vi 1972 (KLU!), Jeriau Waterfalls, *Sugumaran et al.* SM 165, FR, 3 i 2008 (KLU!), SM 214, FR, 22 v 2008 (KLU!), Ulu Jeriau, 3500 ft alt, *Loh* FRI 19156, FR, 27 viii 1971 (KEP! SING!); Genting Highlands, around Awana Area, *Sugumaran & Daniel* SM 175, leafy branch only, 4 iii 2008 (KLU!); Telom, *Ridley* 13838, FR (SING!); Ulu Sungai Boh, 3000 ft alt, *Whitmore* FRI 20117, FR, 3 vi 1971 (KEP!). **Perak.** *Scortechini* s.n., FR, no date (K! SING!); Cottage, *Ridley* 5558, FR, vi 1893 (SING!); Maxwell's Hill, *Wray* s.n., FB, FL, no precise date, 1889 (SING!), *Wray* 2992, FR, ix 1888 (SING!); Birch's Hill, 3800 ft alt, *Burkill & Haniff* SFN 12982, FL, FR, 3 iii 1924 (SING!); Larut, 2500 to 3000 ft alt, *King's Coll.* 5430, FR, no precise date, 1884 (K!); Larut Hill, 1100 m alt, *Damahuri* FRI 36505, FR, 18 x 1988 (KEP!); Maxwell's Hill, 3100 ft alt, *Burkill & Haniff* SFN 12685, FR, 6 iii 1924 (SING!), *Sugumaran* SM 4, leafy branch only, 12 ix 2003 (KLU!); Taiping Hill, 3100 ft, *Henderson* SFN 11838, FR, 6 iii 1924 (SING!); Tea Gardens, *Ridley* s.n., FR, iii 1892 (SING!). **Selangor.** Selangor border, Fraser's Hill, *Burkill & Holttum* SFN 7861, FR, 16-30 ix 1922 (KEP!); Semangkok Pass, *Ridley* 12069, FR, viii 1904

(SING!); near Ginting Highlands College site, 3000 ft alt, *Kochummen* FRI 16514, FL, FR, 9 v 1972 (KEP!); Selangor/Pahang, Gunung Ulu Kali, 5200 ft alt, *Mahmud* s.n., FR, iv 1970 (KLU!).

Leenhouts (1962) acknowledges that *F. oblonga* is “a very characteristic form” (of his heterospecific *F. ceilanica*). The generally elongate, clearly petiolate leaves with parchment-like lower surfaces when dried afford ready recognition of this species.

16. *Fagraea renae* Wong & Sugau

Sandakania 8 (1996) 82, excl. *Rena* S.40346 (= *F. ridleyi* King & Gamble).

Type: Anderson S.19121, Sarawak, Bau, Bidi (holotype SAN; isotypes K, L, SAR, SING).

Fagraea vaginata King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 610 pro parte, excl. specimina origine Javae (= *F. blumei* G. Don).

Fagraea blumei auct. non G. Don (1837): Leenhouts, Fl. Males. I, 6 (2) (1962) 320 pro parte, excl. *F. plumeriaeeflora* DC. & *F. vaginata* King & Gamble in syn., excl. specimina origine ‘Java’ & ‘Celebes’.

Small tree or hemi-epiphyte, usually to 10–13 m tall or 10–12 m high on trees; trunk/stems to c. 15 cm diameter; **bark** smooth, grey-brown; branch internodes terete, smooth. **Leaves** elliptic to subobovate; (10–)15–21(–23.5) cm long, (4.5–)6–10(–11.5) cm wide; **base** cuneate, not decurrent; **apex** short cuspidate; **margin** entire, plane recurved in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** flat above, prominent below; **secondary veins** (4–)5–7 pairs, upper side faint and immersed in the lamina, lower side prominent; **tertiary and higher-order veins** obscure; petioles (2–)2.5–3.5(–4) cm long, 2–3(–4) mm thick, **petiolar**

sheaths not fused along the interpetiolar median, each developing a scale-like ligule 1–2 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a few-many-flowered branched cyme, the whole about 3.5–5.5(–6.2) cm long; **peduncle** indistinct; inflorescence **rachis** 3.5–5.5(–6.2) cm long, 2.5–3(–4) mm thick, with 2–3 pairs of primary branches; basal primary **branch pairs** (1–)2.8–5(–6) cm long, 2–4(–5) mm thick and rebranched to 1–2(–3) orders, more distal branch pairs less so. **Flower** fragrant; bisexual; **pedicel** 5–10 mm long, 3–4 mm thick; **floral bracts** small, acute, 2–4 mm long, located below the calyx; **calyx** (from the base to the lobe apices) 15–22 mm long, glabrous, lenticellate, **calyx cup** 5–6 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 5–10 mm long, (6–)14–16 mm wide, margins glabrous, base not auriculate; **corolla** slender trumpet-shaped (tubular and very gradually widening towards the apex); cream to white; **lower subcylindrical part of the corolla tube** 18–22 mm long, 4–6 mm wide basally, **upper flared part** of the tube slightly inflated, (5–)10–12 mm long, 10–15 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 19–27 mm long, 10–15 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 20–26 mm long, protruding to 10–14 mm from the corolla mouth; **anthers** versatile, hastate, 5–6 mm long, 2–2.5 mm wide, each anther sac somewhat ellipsoid; **style** 28–32 mm long, not to slightly protruding to c. 5 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive sometimes resembling a subpeltate structure 1.5–2 mm across. **Infructescence peduncle** indistinct. **Fruit** broadly ovoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating

upon drying; when mature to 35–40(–47) mm long, 2–2.5 mm wide; the base tightly to loosely surrounded by the erect calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo (Sabah, Sarawak), Malay Peninsula.

Habitat. Lowland to lower montane forests, often by streams; also in secondary forests and on limestone outcrops.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Gunung Panti West, 1000 ft alt, *Whitmore* FRI 15697, FB, 13 xii 1970 (KEP!); Pahang border, Labis Forest Reserve, 500 ft alt, *Samsuri & Ahmad* SA 516, FR, 19 ii 1971 (KEP!). **Kedah.** Gunung Inas F.R., compt. 8, 3000 ft alt, *Whitmore* FRI 4661, FR, 7 ii 1968 (KEP!). **Pahang.** Ulu Kuantan, 400 ft alt, *Symington & Kiah* SFN 28923, FB, FL, 17 vi 1934 (SING!). **Perak.** *Wray* 1992, FL, FR, 1885 (SING!); Huks Kenas, *Scortechini* 817, FB, v 1884 (SING!); Larut, 300 ft alt, *King's Coll.* 4238, FL, v 1883 (SING!), 500 to 600 ft alt, *King's Coll.* 3868, FL, FR, ii 1883 (SING!); Slim Hills F.R., banks of Sungai Geliting, 2000 ft alt, *Whitmore* FRI 730, FR, 5 ix 1966 (KEP! SING!); Tapah Hills, Sungai Woh, *Ng* FRI 1373, FB, 14 vii 1966 (KEP!); Ulu Bubong, *King's Coll.* 10124, FB, FL, vi 1886 (SING!). **Selangor.** Bukit Takun, northeast side, 500 ft alt, *Chin* 569, leafy twig only, 31 xii 1970 (KLU!); Genting Sempah ridge, 800 m alt, *Stone* 15168, FR, 21 v 1982 (KLU!); Gunung Ulu Kali, 5200 ft alt, *Mahmud* s.n., FR, v 1972 (KLU!); Rawang, *Ridley* 7607, FL, FR, v 1896 (SING!); Sungai Tua, *Sugumaran, Zahid & Low* SM 26, FR, 20 i 2005 (KLU! SING!), recreation site, *Sugumaran, Lee & Zulkapli* SM 177, FR, 6 iii 2008 (KLU!); Templer Park, Bukit Anak Takun, *Sang JS* 67, FB, FR, 6 xii 1995 (KEP!); Templer Park Country Club Golf Course, stone outcrop 100 m from Bukit Takun, *Sugumaran & Vijayandra* SM 98, FR, 8 vii 2007 (KLU!); Ulu Langat, *Gadoh* KL no. 1592, FR, 8 vii 1959 (KEP! SING!); Ulu Gombak, 2000 ft alt, *Saw* FRI 34065, FB, FR, iv 1985 (KEP!). **Terengganu.** Ulu Brang, Gunung Padang, Camp 1 near K. Lallang, 300 ft alt, *Whitmore* FRI 12610, FB, 16 ix 1969 (KEP! SING!).

A number of specimens of *F. renae* from Peninsular Malaysia have been earlier misidentified by Kochummen in the Kepong herbarium (KEP) as *F. ridleyi*, although this

is not evident through the descriptions in his brief key (Kochummen 1973). These include: *Gadoh* KL no. 1592, *Whitmore* FRI 4661, 12610 and 15697.

Bornean material of *F. renae* available after the account of Leenhouts (1962) were also subsequently misidentified as *F. ridleyi*. These include *Aban* SAN 81130, *Aban* & *Leopold* SAN 80987, *Cockburn* SAN 84984 & 85112, *Dadau* SAN 44903, *Free* & *Sumbing* SAN 79152 and *Muin Chai* SAN 25981 (all at L and SAN).

17. *Fagraea ridleyi* King & Gamble

J. As. Soc. Beng. 74 (2) (1908) 612; Ridley, Fl. Malay. Pen. 2 (1923) 417; Leenhouts, Fl. Males. I, 6 (2) (1962) 320; Kochummen, Tree Fl. Malaya 2 (1973) 271; Wong & Sugau, Sandakania 8 (1996) 87.

Lectotype (Leenhouts, Fl. Males. I, 6 (2) (1962) 320): *Ridley* 5845, Singapore (SING!); isolectotype K!).

Fagraea renae Wong & Sugau, Sandakania 8 (1996) 82 pro parte, quoad *Rena* S.40346.

Small tree or hemi-epiphyte, usually to 6 m tall or up to 30 m high or more on trees; trunk/stems to c. 13 cm diameter; **bark** smooth to lenticellate, dark-brown; branch internodes terete, smooth. **Leaves** broad elliptic to subobovate; (13–)17–22(–25.5) cm long, (7.5–)9–12(–16) cm wide; **base** cuneate, not decurrent; **apex** rounded; **margin** entire, plane in dried material; thick-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth; **midrib** prominent above towards the leaf base but flat to sunken nearer the leaf apex, prominent below; **secondary veins** (3–)4–5, upper side faint and immersed in the lamina, lower side prominent; **tertiary and higher-order veins** obscure;

petioles (1.5–)2–3(–4.3) cm long, 3–5(–6) mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 1–3 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 2-few-flowered branched cyme, the whole about 5–6 cm long; **peduncle** distinct, 2.5–3.5 cm long, 7–9 mm thick; inflorescence **rachis** 25–30 mm long, 5–8 mm thick, with 1–2 pairs of primary branches; basal primary **branch pairs** 20–30 mm long, 3–4 mm thick and rebranched to 1(–2) orders, more distal branch pairs less so. **Flower** bisexual; **pedicel** 15–17 mm long, 3–5 mm thick; **floral bracts** small, acute, 3–4 mm long, located below the calyx; **calyx** 33–35 mm long (from the base to the lobe apices, glabrous, lenticellate, **calyx cup** 8–10 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 13–15 mm long, 13–15 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 18–20 mm long, 3–6 mm wide basally, **upper flared part** of the tube slightly inflated, 14–17 mm long, 14–18 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 17–20 mm long, 10–15 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 25–28 mm long, protruding to c. 10 mm from the corolla mouth; **anthers** versatile, hastate, 8–10 mm long, 2–4 mm wide, each anther sac somewhat ellipsoid; **style** 40–45 mm long, protruding to c. 8 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive, the whole sometimes resembling a subpeltate structure c. 2 mm across. **Infructescence peduncle** distinct, 15–20(–35) mm long, 4–6 mm thick. **Fruit** broadly ovoid to subglobose, **apex** conspicuously attenuated;

smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 40–50(–55) mm long, 20–32(–42) mm wide; the base tightly clasped by the calyx lobes.

Seeds numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo, Malay Peninsula, Lingga.

Habitat. Lowland rain forest (including some *kerangas* forest sites in Borneo).

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor**. Mt. Ophir, 800 ft alt, *Wong* FRI 32191, FR, 19 iii 1981 (KEP!); Ulu Endau, 1200 ft alt, *Cockburn* FRI 8026, FR, 31 iii 1968 (KEP! SING!). **Melaka**. Mt. Ophir, *Ridley* 3785, FR, no precise date, 1892 (SING!). **Pahang**. Bukit Ibam, Muazam Shah, Low Y.W. LYW 227, FR, 29 xi 2008 (KLU!); Jalan Sepadan, Machado s.n., FR, 13 v 1903 (SING!). LINGGA. Sungai Bei, *Hullett* s.n., FB, FR, 23 vii 1893 (SING!). SINGAPORE. Botanic Gardens, *Henderson* SFN 1381, FR, xii 1921 (SING!), Lawn H, *Nur* SFN 18191, FR, 28 ii 1928 (KEP!); Bukit Timah, *Ridley* (no. indistinct), leaves only, 12 viii 1889 (SING!), *Ridley* 2767, FR, no precise date, 1891 (SING!), *Ridley* 5845, FR, no precise date, 1894 (K! SING!), *Ridley* 11363, FL, no precise date, 1902 (SING!); between Sungai Karang and Sungai Morai, *Sinclair* SFN 40176, leafy branch only, 19 xii 1953 (SING!).

The non-auriculate, distinctly petiolate leaves with very coarsely thick-coriaceous texture and prominent secondary veins on the lower surface when dried, and robust inflorescence axes and flower calyces, readily distinguish this species (see Key).

18. *Fagraea splendens* Blume

Mus. Bot. 1 (1850) 168; Wong & Sugau, Sandakania 8 (1996) 87.

Type: *Korthals*, s.n., Borneo (Leiden acc. no. 908127-639) (holotype L!).

Fagraea acuminatissima Merrill, J. Str. Br. R. As. Soc. 77 (1917) 232; Leenhouts, Fl. Males. I, 6 (2) (1962) 319; Kochummen, Tree Fl. Malaya 2 (1973) 271. Type: *Native coll.* 686, Sarawak (isotype L).

Fagraea heterophylla Blume, Mus. Bot. 1 (1850) 168. Type: *Korthals*, s.n., Borneo, Banjermarsing (Leiden acc. no. 908127-518) (L!).

Fagraea ceilanica auct. non Thunberg (1782): Leenhouts, Fl. Males. I, 6 (2) (1962) 315 pro parte, quoad *F. heterophylla* Blume & *F. splendens* Blume in syn.

Fagraea obovata auct. non Wallich ex Roxburgh (1824): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 606 pro parte, quoad *Curtis* 246, *King's coll.* 4878, *Wray* 2115, 3075, 4181; Ridley, Fl. Malay. Pen. 2 (1923) 418 pro parte, quoad specim. *Curtis* (Kuala Lumpur), *Burn-Murdoch* (Gombak), *King's coll.* (Ulu Bubong), *Wray* (Batu Togoh).

Small shrub or hemi-epiphyte, usually to 3 m tall or 10 m high or more on trees; trunk/stems to c. 10 cm diameter; **bark** smooth, grey to dark-brown. **Leaves** elliptic to obovate; (5.5–)10–20(–23) cm long, (2.8–)4–8(–9.3) cm wide; **base** cuneate to rounded, not decurrent; **apex** short cuspidate; **margin** entire, recurved in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface relatively smooth under magnification; **midrib** flat to sunken above, prominent below; **secondary veins** 5–7 pairs if visible, otherwise obscure on both sides; **tertiary and higher-order veins** obscure; petioles (5–)20–35(–47) mm long, (1.5–)2–3(–4) mm thick, **petiolar sheaths** not fused along the interpetiolar median, each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a few-many-flowered branched cyme, the whole about 5–10 mm long; **peduncle** indistinct or to 5 mm long, to 5

mm thick; inflorescence **rachis** 4–8 mm long, 2–4 mm thick, with (1–)2 pairs of primary branches; basal primary **branch pairs** 3–4 mm long, 2–3 mm thick and not rebranched. **Flower** bisexual; **pedicel** 2–4 mm long, 2.5–4 mm thick; **floral bracts** small, acute, 2–3 mm long, located below the calyx; **calyx** 6–10 mm long (from the base to the lobe apices), glabrous, not to sometimes lenticellate, **calyx cup** 3–5 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 4–6 mm long, 4–6 mm wide, margins glabrous, base not auriculate; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 12–18(–20) mm long, 2–4 mm wide basally, **upper flared part** of the tube slightly inflated, 13–17 mm long, 10–15 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 13–20(–23) mm long, 6–12 mm wide, overlapping to the right; **stamens** 5, inserted (at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube); **filaments** 20–25 mm long, protruding to 7–8 mm from the corolla mouth; **anthers** versatile, hastate, 5–6 mm long, 2–2.5 mm wide, each anther sac somewhat ellipsoid; **style** 40–45 mm long, protruding to 8–15 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 1–2 mm across. **Infructescence peduncle** indistinct or to 5 mm long, to 4 mm thick. **Fruit** narrowly ellipsoid, **apex** conspicuously attenuate; smooth, the epidermis conspicuously wrinkling and separating upon drying; when mature to 20–30 mm long, 12–16 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; ellipsoid to subovoid (non-angular); 2–2.5 mm long, 1–1.5 mm wide; testa surface areolate; placentation axile.

Distribution. Borneo, Malay Peninsula, Sumatra.

Habitat. Sea level to lower montane forest; also in peat swamp and freshwater swamp forests.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Kota Tinggi-Mersing road, *Sinclair* SFN 10608, FB, 23 vi 1961 (SING!); Gunung Panti Forest Reserve, 1700 ft alt, *Samsuri* SA 315, FL, 5 vii 1970 (SING!); Gunung Panti, Recreational forest, *Sugumaran* SM 208, leafy twig only, 29 iv 2008 (KLU!); Gunung Panti West, 1684 ft alt, *Stone* 14616, FR, 25 xi 1980 (KLU!), below 1500 ft alt, *Heaslett* 7, FL, 25 vi 1967 (SING!); Mawai-Jemaluang road, *Corner* s.n., FR, 15 v 1935 (SING!); Pontian, Pengkalan Raja, peat forest, *Henderson* SFN 36671, FR, 30 vi 1939 (KEP!); Tanjung Bunga, *Ridley* 6312, FL, 1894 (SING!).

Kedah. Langkawi, Gunung Raya Virgin Jungle Reserve, *Zahid et al.* ZMS 42, FL, 27 iv 2004 (KLU!), road to Ayer Hangat, Kisap F.R., *Allen* KEP 79285, FL, 13 v 1957 (KEP!), Telaga Tujuh, c. 125 m alt, *Stone* 15938, FB, FL, 26 iv 1987 (KEP!); Polo Songsong, *Curtis* s.n., FB, FL, vi 1890 (SING!), *Ridley* s.n., FB, vi 1890 (SING!); Sik, Bukit Enggang, *Mohd Shah & Tan* MS 5051, FR, 5 v 1993 (SING!). **Kelantan.** Jeli F.R., Compt. 20, *Chelliah* FRI 6513, FR, 30 vi 1968 (KEP!). **Melaka.** stream below Gunung Mering, *Ridley* 3182, FL, vi 1892 (SING!). **Pahang.** Fraser's Hill, *Keng, Wee & Honours students* T3/48, FR, 11 xi 1981 (SING!); Gunung Tapis, 1500 ft alt, *Chan* FRI 19905, FR, 29 ix 1971 (KEP! SING!); Jerantut, confluence of Sungai Tekam and Sungai Balol, *Ng & Beltran* FRI 6389, FR, 25 vi 1972 (KEP!); Rompin, Pulau Lang, *Mohamad* KEP 14972, FB, FL, 13 vi 1929 (KEP!); Sungai Bebar, *Sugumaran* SM 38, leafy twig only, 11 iv 2005 (KLU!).

Penang. *Curtis* 346, FB, FL, vii 1885 (SING!); Batu Feringy, *Curtis* 3013, FR, v 1894 (SING!); Penang Hill, Hash trail near Moon Gate to Camp 84 on Jeep track, *Low & Wong* LYW 204, leafy twig only, 6 vii 2008 (KLU!); Penang Hill near Craig Hotel, *Henderson* SFN 21412, FL, 19 vi 1937 (SING!); Penang Hill near Richmond Hotel, *Sugumaran & Vijayandra* SM 167, leafy twig only, 16 ii 2008 (KLU!); Waterfall stone quarry, *Haniff* SFN 3755, FL, 18 vi 1918 (SING!). **Perak.** Assam Kumbang, *Wray* 3075, FB, FL, FR, ix 1888 (SING!), *Wray* 2115, FB, FL, vi 1888 (SING!); Chenderiang, Gunung Bujang Melaka, Sungai Rias, 2000 ft alt, *Mohd Shah & Ahmad* MS 3408, FR, 12 ii 1975 (KEP! SING!); Larut, 300 to 800 ft alt, *King's Coll.* 4878, FR, viii 1883 (SING!), *King's Coll.* 6162, FL, v 1884 (SING!); Larut, 500 to 700 ft alt, *King's*

Coll. 10634, FR, vii 1886 (SING!); Larut, Batu Togoh, *Wray* 4181, FB, vi 1892 (SING!). **Selangor.** Gombak, *Burn-Murdoch* 117, FL, no date (SING!); Kwala Lumpur, *Curtis* 2356, FR, ii 1890 (SING!); Ulu Langat, *Gadoh* KL no. 2167, FR, 1 viii 1960 (KEP!), *Gadoh* KL no. 2215, FL, 16 xi 1960 (KEP!). SINGAPORE. Mandai road, swampy forest, *Henderson* SFN 37739, FR, 12 viii 1940 (KEP!). BORNEO. *Korthals s.n.*, FB, no date (L!); Banjer Manting, *Korthals s.n.*, FR, no date (L!).

This is a very common species in Peninsular Malaysia. The flowers in subsessile, tight clusters, small infundibular corollas and obscure leaf veins distinguish the species quite well.

19. *Fagraea tubulosa* Blume

Mus. Bot. 1 (1850) 167; Miquel, Fl. Ind. Bat. 2 (1857) 373; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 604; Cammerloher, Bull. Jard. Bot. Btzg. III, 5 (1923) 326; Ridley, Fl. Malay. Pen. 2 (1923) 415; Leenhouts, Fl. Males. I, 6 (2) (1962) 320; Kochummen, Tree Fl. Malaya 2 (1973) 270.

Type: *Blume*, s.n., in sylvis montanis insulae Sumatrae (holotype L).

Scrambler to hemi-epiphyte, usually to 5 m high or more on trees; **bark** smooth, grey-brown; branch internodes terete, smooth. **Leaves** ovate; (10–)13–19.5 cm long, 5.5–8 cm wide; **base** rounded not decurrent; **apex** short cuspidate; **margin** entire, plane in dried material; thin-coriaceous; upper and lower **surfaces** glabrous, lower surface minutely wrinkled under magnification; **midrib** flat above, prominent below; **secondary veins** (5–7 pairs if visible), obscure on both sides; **tertiary and higher-order veins** obscure; petioles 20–32 mm long, 2–3 mm thick, **petiolar sheaths** not fused along the interpetiolar median,

each developing a scale-like ligule 0.5–1 mm high adaxially; petiole base without **auricles**. **Inflorescence** terminal, a 2–3-flowered cyme; **peduncle** indistinct or to 3 mm long, to 4 mm thick; inflorescence **rachis** very condensed, with 1 pair of primary branches; basal primary **branch pairs** 1–2 mm long, 3–4 mm thick and not rebranched. **Flower** bisexual; **pedicel** 4–5 mm long, 3–4 mm thick; **floral bracts** small, acute, 1–2 mm long, located below the calyx; **calyx** 5–7 mm long (from the base to the lobe apices), glabrous, not lenticellate, **calyx cup** 3–4 mm wide, **calyx lobes** 5, broad-elliptic to rounded, 4–5 mm long, 4–5 mm wide, margins glabrous, base not auriculate; **corolla** subsalverform (with a long narrow lower tube and patent to erect lobes); cream to white; **lower subcylindrical part of the corolla tube** 70–85 mm long, 2–4 mm wide basally, **upper flared part** of the tube slightly inflated, 5–8 mm long, 5–6 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 10–13 mm long, 5–7 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 15–18 mm long, protruding to c. 10 mm from the corolla mouth; **anthers** versatile, hastate, 3–4 mm long, 1.5–2 mm wide, each anther sac somewhat ellipsoid; **style** 85–88 mm long, protruding 5–10 mm from the corolla mouth in the open flower; **stigma** shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive and the whole sometimes resembling a subpeltate structure 1–2 mm across. **Infructescence** not seen. **Fruit** not seen.

Distribution. Sumatra, Malay Peninsula (collected only once, in Perak).

Habitat. Lowland rain forest.

SPECIMEN EXAMINED – PENINSULAR MALAYSIA. **Perak.** Bujang Malacca, *Ridley* 9738, FL, no precise date, 1898 (SING!). SUMATRA. *sine coll.*, FL, FB, no date (L!), FL, FB, no date (L!).

The slender, non-infundibular corolla shape is shared with *F. gardenioides* and *F. carnosa*. Both these other species have thicker corolla tubes with longer lobes (more than 20 mm long) and also differ by their elliptic to obovate, thick-coriaceous leaves with recurved margins when dry (in *F. tubulosa*, the leaves are ovate, thin-coriaceous and do not have recurved margins).

***Cyrtophyllum* Reinw. ex Bl.**

Bijdr. (1826) 1022. Ridley, Fl. Malay. Pen. 2 (1923) 421.

Type: *C. peregrinum* Reinw. ex Bl. (= *C. fragrans* (Roxb.) DC.).

Medium-sized to large trees usually more than 3 m and often reaching 25 m tall. **Trunk** with episodic growth; bark becoming fissured in older trees. Vegetative shoot tips with light yellowish resin. Leaf arrangement on branches decussate; leaf margin entire; **petiolar sheaths** of a leaf pair fused to form a shallow cup-like ochrea. **Inflorescence** axillary, a many-flowered and multi-branched cyme, basal branches nearly as long as or longer than rachis. **Flowers** small, up to 10 mm wide at the mouth; stamens typically two thirds or more exsert; style typically one third or more exsert; stigma capitate. **Fruits** small, up to about 10 mm in diameter; colour at maturity yellow-orange to bright red; with small amounts of translucent sticky latex in fruit epidermis and fruit wall; epidermis separating as a thin translucent film from pericarp (fruit surface appearing crinkled on herbarium specimen). **Seeds** polygonal.

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

Habitat. Lowland forests.

Key to species

1a. Inflorescence branching to just 1, rarely 2, orders. Corollas 12–25 mm long and 6–10 mm wide at the mouth; styles (34–)42–45(–55) long. *C. wallichianum*

1b. Inflorescence branching to 2–3 orders. Corollas not exceeding 10 mm long and less than 5 mm wide at the mouth; styles not exceeding 25 mm long.

2a. Leaf margin plane in fresh material, with 7–9(–11) pairs of secondary veins forming distinct loops towards the margin; the midrib and secondary veins flat or slightly raised on the upper leaf surface in dried material; lower narrowed part of corolla 1.5–2(–2.5) mm wide. *C. fragrans*

2b. Leaf margin conspicuously wavy in fresh material, with 4–6 pairs of secondary veins forking towards the leaf margin but not forming conspicuous loops; the midrib and secondary veins flat to frequently sunken on the upper leaf surface in dried materials; lower narrowed part of corolla 1–1.5 mm wide. *C. giganteum*

1. *Cyrtophyllum fragrans* (Roxb.) DC.

Fagraea fragrans Roxb., Prod. 9 (1845) 31.

Type: Wallich, Cat. no. 1597E (Coll. Hunter), "Pullo Penang" (K).

[Hort. Beng. (1814) 84. *nom. nud.*] Fl. Ind. ed. Wall., 2 (1824) 32; Cammerl., Bull. Jard.

Bot. Btzg. III, 5 (1923) 318.

Cyrtophyllum peregrinum Reinw., Syll. Pl. nov. Soc. bot. Ratisb. 2 (1826) 9; Blume, Bijdr. (1826) 1022. Syntypes: *Blume*, Java (L!: sheets 908.127-244 & 908.127-126); *Korthals*, Java (L!: sheet 908.127-236).

Fagraea fragrans sensu King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 611 pro parte, excl. *Derry* 272.

Fagraea fragrans sensu Kochummen, Tree Fl. Malaya 2 (1973) 273 pro parte, excl. *Cyrtophyllum lanceolatum* DC., *Fagraea wallichiana* in syn.

Fagraea fragrans sensu Leenhouts, Fl. Males. I, 6 (2) (1962) 304 pro parte, excl. *F. caudata* Ridl., *F. gigantea* Ridl., *F. speciosa* sensu Ridl., non Bl., *F. sororia* J.J. Sm., *F. wallichiana* Benth., *F. lanceolata* Wall in syn.

Fagraea peregrina Bl., Rumphia 2 (1838) 34, t. 80; Mus. Bot. 1 (1850) 172.

Tree, rarely to just 3–4 m tall, more often big, to 30 m tall; trunk to over 1 m in diameter; **bark** deeply fissured, grey-brown to dark brown. **Leaves** elliptic; (5.5–)7.5–11(–13) cm long, (2–)3.5–4.5(–5.3) cm wide; **base** cuneate; **apex** short-cuspidate to caudate; (3–)5–8(–9) mm long; **margin** plane when fresh (in dried specimens sometimes slightly wavy); thin-

coriaceous; upper and lower **surfaces** smooth; **midrib** prominent below, flat to slightly raised above; **secondary veins** (7–)9–12 pairs, upper side faint and immersed in the blade, lower side faint to very slightly prominent; **tertiary veins** faint to inconspicuous; petioles 1–1.3(–1.6) cm long, 1–1.5 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; petiolar base **auricles** absent.

Inflorescence axillary, a many-flowered, multi-branched cyme, (3.5–)4–7(–7.7) cm long; **peduncle** (2.8–)3–3.5 cm long, 1–1.5 mm thick; with **(2–)3(–4)** **levels** (tiers) of branching on the main axis, the branch tiers (2–)3–5(–6) mm apart, lowest tier typically branched to **2(–3) orders**. **Flower** bisexual; **pedicel** (3–)5–8(–11) mm long, 0.5(–1) mm thick; **calyx** (from the base to the lobe apices) (1.5–)2–2.5 mm long, glabrous, **calyx cup** (1.5–)2–2.5(–3) mm wide, **calyx lobes** 5, erect, 1–1.5(–2) mm long, 1–1.5(–2) mm wide, margins glabrous; **corolla** somewhat infundibular; cream to white; **corolla tube** (4–)6–8 mm long, **lower narrowed part** 1.5–2(–2.5) mm wide, **upper flared part** (3–)4–6(–7) mm wide at the top, the lower narrowed tubular part nearly as long as the upper flared part, inside glabrous to minutely papillate; **corolla lobes** 5, broad-ovate to subobovate, (3–)4–6 mm long, 2–3(–4) mm wide, overlapping to the right; **stamens** 5, inserted at the middle of the upper flared part of the corolla; **filaments** (10–)12–16(–17) mm long, exsert (8–)10–12(–13) mm in the open flower; **anthers** versatile, sagittate, 1–1.5 mm long, 0.5–1 mm wide, each anther sac somewhat narrowly ellipsoid; **style** (14–)18–22 mm long, protruding (8–)10–12(–14) mm from the corolla mouth in the open flower; **stigma** knob-like, c. 0.5 mm across, lobes 2, low and rounded, parting to present two slightly raised, hemispherical, papillate inner surfaces when receptive, not recurving. **Infructescence peduncle** (2.5–)3.5–5(–6.2) cm long, 1–2 mm thick. **Fruit** subglobose; smooth; when mature to 4–6 mm

across; the base loosely to tightly clasped by the calyx lobes. **Seeds** numerous; placentation axile; polygonal; testa surface areolate; 0.5–1 mm across.

Distribution. Bengal, Indo-China, Malay Peninsula, Sumatra, Java, Borneo, Mindoro, Balabac, Palawan, Celebes.

Habitat. Lowland forests, especially in disturbed secondary vegetation patches, also common in *kerangas* (heath forest) type vegetation and coastal or beach forest.

SPECIMENS EXAMINED – BORNEO. **Brunei.** Kuala Belait, Andulau, Taman Rekreasi Hutan Sungai Liang, *Sugumaran et al.*, SM227, FB, FL, 10 vi 2008 (KLU!). **Sabah.** Kuala Penyu, Road to Pantai Tanjung Aru, *Rimi et al.*, SPN 06605, FR, 26 vii 1995 (KEP!); Papar, Mandahan, *Talip Bidin* SAN 80685, FR, 21 vii 1976 (KEP!); Sandakan, Mile ¼ Derby road, *Aban Gibot* SAN 75916, FB, 26 v 1972 (KEP!). **Sarawak.** Kuching, Taman Budaya, *Yahud et al.*, S 57555, FR, 11 v 1991 (KEP!). **PENINSULAR MALAYSIA.** **Johor.** Johore Bharu, *Carrick* 1406, FR, 24 x 1965 (SING!); Tanjung Sedili, *Sugumaran et al.*, SM 209, leafy branch only, 29 iv 2008 (KLU!). **Kedah.** *Rahim* KEP 12386, FR, 31 vii 1929 (SING!). **Melaka.** Merlimau, *Alvins s.n.*, FB, FL, 20 iv 1886 (SING!), *Derry* 53, FR, vii 1888 (SING!). **Negeri Sembilan.** *Cubitt* 706, FR, no precise date, 1916 (SING!); 'Forest Dept.' 697, FR, no date (SING!); Angsi Forest Reserve, *Othman* KEP 23732, FL, xii 1930 (KEP!); Bahau reserve, *Mat Deris* 654, FB, FL, FR, 24 v 1916 (SING!); Port Dickson, Blue Lagoon, *Bremer* 1819, FL, 25 xii 1979 (KLU!); Seremban, *Bain* 18856, FB, FL, 1 v 1924 (KEP!). **Pahang.** *Ridley* 1028, FB, FL, FR, v 1890 (SING!); Kuantan, *Abdul Rahman* FMS 4172, FB, FL, 16 vi 1921 (SING!), *Mahamud* FMS 3729, FB, FL, 26 v 1921 (SING!), *Mohd Soh* 15735, FB, FL, 6 v 1929 (SING!); Muazam Shah-Menchali main road, *Sugumaran et al.*, SM 212, leafy branch only, 2 v 2008 (KLU!); Pulau Berhala, *Burn-Murdoch A.M.* SFN 303, FL, 14 vi 1913 (SING!). **Penang.** *Askey A.M.* FMS 2554, FL, vii 1918 (SING!); Sungai Pinang, Ogata 10344, FL, 10 v 1968 (KEP!); Tasek Gelugor, *Fyfe A.J.* 29321, FR, 8 vi 1932 (SING!); Tulloh Bahang (*sic!* = Teluk Bahang), *Curtis* 314, FL, vi 1892 (SING!), *Curtis s.n.*, FB, FL, v 1893 (SING!), FL, v 1892 (SING!), FR, vii 1892 (SING!). **Perak.** Pangkor Island, Telok Nipah, *Chin* 3137, FR, 19 viii 1981 (KLU!). **Selangor.** Kepong, Forest Research Institute, *Mat Asri* FRI 21839, leafy branch only, 24 ix 1974 (KEP!), *Vethevelu* FRI 29649, FB, 16 iv 1981 (SING!); Gombak,

Klang Gates Quartz Ridge, *Daniel et al.*, s.n., leafy branch only, 18 xi 2006 (KLU!), *Sugumaran* SM 27, leafy branch only, 20 i 2005 (KLU!); Kuala Lumpur, *Ramli* KEP 94100, FR, 1 x 1965 (KEP!), Government Hills, *Kalong* 17463, FR, 19 viii 1929 (SING!), Circular Road, *Omar* 7425, FB, FL, FR, 7 viii 1922 (SING!), University of Malaya campus, *Tan Bee Cheok* s.n., FR, 3 ix 1965 (KLU!), *Zakiah Hassan* s.n., FB, FL, 21 vii 1974 (KLU!), University of Malaya, Rimba Ilmu, *Low KM* 62, leafy branch only, 6 viii 1978 (KLU!).

Terengganu. Kemaman, *Osman* FMS 26996, FB, FL, 13 vii 1971 (KEP!). RIAU ISLANDS. Pulau Kundor, Teruya 1624, FB, FL, ii 1931 (SING!). SINGAPORE. *Cantley's Collection* s.n., FR, no date (SING!); Botanic Gardens, *Henderson* 1329, FL, xi 1921 (SING!); Nature Reserves Sector 17, *Turner et al.*, NRS 269, FR, 9 iv 1992 (SING!); Pulau Pawai, *Sidek* S 99, FR, 8 vi 1967 (SING!); Surrounding reservoir, *Cantley's Collection* s.n., FR, no date (SING!). JAVA. *sine coll.*, FL, FB, FR, no date (L!); *Korthals* s.n., FL, FR, no date (L!). SUMATRA. Palembang. *Endert* 881, FR, iv 1920 (SING!). THAILAND. **Bangkok.** *Marcan* 707, FB, FL, 19 iii 1922 (SING!). **Kraki.** Kraki-Trang Road, *Weerachai Nanakorn* W.N.514, FR, 19 v 1984 (SING!); Jurin?, *Kerr* 8232, FL, 9 i 1924 (SING!); **Surat Thani,** *Prsundej et al.*, 249, FL, 4 vii 1975 (KLU!).

Among all the species in *Fagraea* s.l. for the Malay Peninsula, *C. fragrans* and *U. racemosa* (recognised previously as *F. racemosa*) are probably the most commonly encountered and the most widespread. *Cyrtophyllum fragrans* establishes easily in open areas and secondary forests including along roadsides and around abandoned mining pools. It is known to flower abundantly at least twice a year and the attractive yellow to red fruits are probably dispersed mainly by birds or bats (Corner 1940).

In the past, two other species found in the Malay Peninsula, namely, *C. giganteum* and *C. wallichianum* have been confused with *C. fragrans*. These two species are not as common as *C. fragrans*.

Cyrtophyllum giganteum and *C. fragrans* have very similar flowers that appear only to have consistently different corolla tube widths. However, several vegetative features are very distinctive, such as the distinctively wavy margins in fresh leaves of *C.*

giganteum (*C. fragrans* have leaf margins which are plane). There are more pairs of secondary veins in *C. fragrans* (7–9(–11)) that form distinct loops towards the leaf margin but in *C. giganteum* there are fewer pairs of secondary veins (4–6) that fork towards the leaf margin and do not form conspicuous loops. The vertical fissures on the bark are also notably different between the two, where in *C. fragrans* the fissures are quite rugged, deeper and wider whereas the fissures in *C. giganteum* are neatly formed, shallower and narrower (Fig. 8A & 8B). As for the stature of mature trees, *C. giganteum* grows much taller (more than 50 m) with a very straight and columnar bole just like any other regular lowland forest canopy-reaching species, whereas *C. fragrans* usually reaches up to only 30 m and develops several erect branches that are equally as tall as the main trunk. Finally, *C. fragrans* does not develop buttresses but mature *C. giganteum* trees develop buttresses as also noted by Corner (1940).

C. wallichianum is generally a smaller tree (up to 25 m tall) compared to *C. fragrans*, which can grow taller (up to 30 m tall) and occurs only in hills and ridges whereas *C. fragrans* occurs in the lowlands. *C. wallichianum* is vegetatively quite similar to *C. fragrans* but the floral characters are different. The inflorescence of *C. fragrans* is generally more branched (2 (–3) orders) and so bears more flowers, whereas the inflorescence in *C. wallichianum* is usually less branched (1(–2) orders) with fewer flowers. The corollas of *C. wallichianum* are much bigger (12–25 mm long, 6–10 mm wide) whereas the corollas of *C. fragrans* are smaller ((4–)6–8 mm long, 1.5–2(–2.5) mm wide).

2. *Cyrtophyllum giganteum* (Ridl.) Ridl.

Fl. Malay. Pen. 5 (1925) 421.

Lectotype (Wong & Sugau, 1996): Ridley 8921, Singapore, Garden Jungle (SING).

Fagraea gigantea Ridl., J. Str. Br. R. As. Soc. 79 (1918) 98; Kochummen, Tree Fl. Malaya 2 (1973) 273; Wong & Sugau, Sandakania 8 (1996) 11.

Fagraea sororia J.J. Smith ex Cammerl., Bull. Jard. Bot. Btzg. III, 5 (1923) 319, pl. 5.

Lectotype (Wong & Sugau, 1996): Endert 44E 1P 515, Sumatra, Palembang (L; isolectotypes BO, K, SING).

Fagraea fragrans auct. non Roxburgh (1824): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 611 pro parte, quoad Derry 272; Leenhouts, Fl. Males. I, 6 (2) (1962), pro parte, quoad *Cyrtophyllum giganteum* Ridl. in syn.

Fagraea speciosa auct. non Blume (1826): Ridley, J. Str. Br. R. As. Soc. 50 (1908) 122.

Tree, rarely to just 3–4 m tall, more often big, to 30 m tall; trunk to over 1 m in diameter; **bark** neatly and finely fissured, grey-brown to dark brown. **Leaves** elliptic; (4.4–)5–7(–7.5) cm long, (1.8–)2.2–3(–3.2) cm wide; **base** cuneate; **apex** short-cuspidate to caudate; 4–6 mm long; **margin** conspicuously wavy when fresh and in dried specimens; thin-coriaceous; upper and lower **surfaces** smooth; **midrib** prominent below, flat to sunken above; **secondary veins** 4–6 pairs, upper side faint and immersed in the blade, lower side faint to very slightly prominent; **tertiary veins** faint to inconspicuous; petioles (0.8–)1–1.5(–2.3) cm long, 1–1.5 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; petiolar base **auricles** absent.

Inflorescence axillary, a many-flowered, multi-branched cyme, (3.5)5–6.5(–7.5) cm long; **peduncle** 3.5–5(–5.5) cm long, 1–1.5 mm thick; with **4–5 levels** (tiers) of branching on the main axis, the branch tiers (5)6–10(–12) mm apart, lowest tier typically branched to **(2–)3 orders**. **Flower** bisexual; **pedicel** 3–5 mm long, 0.3–0.5 mm thick; **calyx** (from the base to the lobe apices) 1.5–2 mm long, glabrous, **calyx cup** 1.5–2 mm wide, **calyx lobes** 5, erect, 1–1.5 mm long, 1–1.5 mm wide, margins glabrous; **corolla** somewhat infundibular; cream to white; **corolla tube** 7–8 mm long, **lower narrowed part** 1–1.5 mm wide, **upper flared part** 3–4 mm wide at the top, the lower narrowed tubular part nearly as long as the upper flared part, inside glabrous to minutely papillate; **corolla lobes** 5, broad-ovate to subobovate, 3–4 mm long, 2–2.5(–3.5) mm wide, overlapping to the right; **stamens** 5, inserted at the middle of the upper flared part of the corolla; **filaments** 13–15 mm long, exsert 12–13 mm in the open flower; **anthers** versatile, sagittate, 1–1.5 mm long, 0.5–0.8 mm wide, each anther sac somewhat narrowly ellipsoid; **style** (12)18–22 mm long, protruding (5)12–14 mm from the corolla mouth in the open flower; **stigma** knob-like, c. 0.5 mm across, lobes 2, low and rounded, parting to present two slightly raised, hemispherical, papillate inner surfaces when receptive, not recurving.

Infructescence peduncle (2.5)3–4(–4.8) cm long, 1–1.5 mm thick. **Fruit** subglobose; smooth; when mature to 4–6(–7) mm across; the base tightly clasped by the calyx lobes.

Seeds numerous; placentation axile; polygonal; testa surface areolate; 1–2 mm across.

Distribution. Malay Peninsula, Sumatra, Borneo.

Habitat. Lowland forest.

SPECIMENS EXAMINED – BORNEO. **Sabah**. Sandakan, *Patrick SAN 25509, FB, 26 v 1961 (KLU!)*.

PENINSULAR MALAYSIA. *sine coll.* 16711, FR, no date, (KEP!); **Johor**. Ulu Endau, Labis F.R., Sungai

Jasin, *Ogata* KEP 110427, FB, 28 iii 1968 (KEP!). **Negeri Sembilan**. Kuala Kelawang, Triang F.R., *Lau & Jalil* FRI 18249, FB, 15 v 1981 (KEP!). **Pahang**. Kuantan, *Mohd Soh* FMS 15750, FR, 28 vii 1929 (SING!), *Rahman* 15738, FB, FL, 13 v 1929 (SING!). **Melaka**. Air Keruh Botanical Garden, *Chew s.n.*, leafy branch only, 17 x 2003 (KLU!), *Sugumaran & Lee* SM 193, leaves and stem bark, 18 iii 2008 (KLU!), SM 194, leaves only, 18 iii 2008 (KLU!), SM 195, leaves only, 18 iii 2008 (KLU!); Bukit Saliokor?, *Derry* 272, FL, viii 1889 (SING!). **Selangor**. Ayer Hitam F.R., *sine coll.* KEP 55873, leaves only, 5 ii 1947 (KEP!); Kajang, Banji Reserve, *Foxworthy* 10289, FL, 25 v 1925 (SING!); Sungai Buluh F.R., *Walton* FMS 30770, FL, 8 v 1933 (KEP!). **SUMATRA**. **Palembang**, Lematang Ilir, Semangoes, *Neth. Ind. For. Service* bb. 32270, leafy branch only, 4 vii 1939 (SING!). **Upper Riauw**, Tenajan, Pakanbaru, *Soepadmo* 232, FR, 26 viii 1960 (SING!).

See notes under *C. fragrans*.

3. *Cyrtophyllum wallichianum* (Benth.) Sugumaran & Wong, comb. nov.

Fagraea wallichiana Benth., J. Linn. Soc. Bot. 1 (1856) 98; King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 607; Wong, Saw & Kochummen, Malayan Nat. J. 41 (1987) 267; Wong & Sugau, Sandakania 8 (1996) 12.

Type: *Wallich* Cat. no. 1599, Penang (K).

Cyrtophyllum lanceolatum (Wall.) DC., Prod. 9 (1845) 31, *nom. illeg.*; Ridley, Fl. Mal. Pen. 2 (1923) 421.

Fagraea lanceolata Wall. [Cat. (1829) no. 1599, *nom. nud.*] Schnizl., Iconogr. 2 (1851) t. 131, f. 1, *nom. illeg.*, non Blume (1826); Miquel, Fl. Ind. Bat. 2 (1857) 376.

Fagraea fragrans auct. non Roxburgh (1824): Kochummen, Tree Fl. Malaya 2 (1973) 273 pro parte, quoad *Fagraea wallichiana* Benth. in syn.; Leenhouts, Fl. Males. I, 6 (2)

(1962), pro parte, quoad *Cyrtophyllum lanceolatum* DC., *F. lanceolata* Wall., *F. wallichiana* Benth. in syn.

Tree, rarely to just 3–4 m tall, more often bigger, to 25 m tall; trunk to over 1 m in diameter; **bark** fissured, grey-brown to dark brown. **Leaves** narrow to broadly-elliptic to oblanceolate to obovate; (3.4–)6–10(–13) cm long, (1.4–)2–3(–5) cm wide; **base** cuneate; **apex** acute to short-cuspidate; 2–5(–1.2) mm long; **margin** plane when fresh and in dried specimens; thin-coriaceous; upper and lower **surfaces** smooth; **midrib** prominent below, sunken above; **secondary veins** (4–)5–7 pairs, upper side faint and immersed in the blade, lower side faint to very slightly prominent; **tertiary veins** faint to inconspicuous; petioles (0.3–)0.8–1.2(–1.7) cm long, 1–1.5 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that tightly clasps the stem; petiolar base **auricles** absent. **Inflorescence** axillary, a many-flowered, multi-branched cyme, (2.5–)3–6(–7.8) cm long; **peduncle** (1.9–)2.3–3.5(–5.3) cm long, 1(–1.5) mm thick; with **1(–2) levels** (tiers) of branching on the main axis, the branch tiers 10–14 mm apart, lowest tier typically branched to **1(–2) orders**. **Flower** bisexual; **pedicel** (4–)5–8 mm long, 1–1.5 mm thick; **calyx** (from the base to the lobe apices) (3–)4–5(–6) mm long, glabrous, **calyx cup** 3–4 mm wide, **calyx lobes** 5, erect, 2–3 mm long, 2–2.5 mm wide, margins glabrous; **corolla** somewhat infundibular; cream to white; **corolla tube** (12–)20–25 mm long, **lower narrowed part** 1–2 mm wide, **upper flared part** 6–8(–10) mm wide at the top, the lower narrowed tubular part nearly as long as the upper flared part, inside glabrous to minutely papillate; **corolla lobes** 5, broad-ovate to subobovate, (5–)7–8 mm long, 3–4.5(–5) mm wide, overlapping to the right; **stamens** 5, inserted at the lower end of the upper flared part

of the corolla; **filaments** (27–)30–38 mm long, exsert 20–23(–28) mm in the open flower; **anthers** versatile, sagittate, 1–1.5 mm long, 0.5–1 mm wide, each anther sac somewhat narrowly ellipsoid; **style** (34–)42–45(–55) mm long, protruding 22–25(–30) mm from the corolla mouth in the open flower; **stigma** knob-like, c. 0.5 mm across, lobes 2, low and rounded, parting to present two slightly raised, hemispherical, papillate inner surfaces when receptive, not recurving. **Infructescence peduncle** 2–2.5(–3) cm long, 1–1.5 mm thick. **Fruit** subglobose; smooth; when mature to 7–9 mm across; the base loosely to tightly clasped by the calyx lobes. **Seeds** numerous; placentation axile; polygonal; testa surface areolate; 1–1.5 mm across.

Distribution. Endemic to the Malay Peninsula.

Habitat. Lowland forest on hills and ridges.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor**. Hutan Simpan Labis, Gunung Beremban, Wong FRI 30882, leafy branch only, 4 ix 1985 (KEP!). **Kedah**. Gunung Jerai, Kochummen FRI 18086, FB, 7 vii 1977 (KEP!), FRI 29495, FR, 31 iii 1982 (KEP!), KEP 85027, leafy branch only, 28 iii 1957 (KEP!), KEP 94416, FR, 26 ii 1960 (KEP!). **Kelantan**. Relai Forest Reserve, Cockburn FRI 7251, FL, 18 x 1967 (KEP! SING!), FRI 7280, FL, 21 x 1967 (KEP! SING!), FRI 7411, FB, 22 x 1967 (KEP! SING!). **Penang**. Govt. Hill, *Curtis s.n.*, FL, no precise date, 1899 (SING!), Ridley 7066, FR, xii 1895 (SING!); Moniots Road, Burkhill SFN 3330, FB, 29 ix 1918 (SING!), *Curtis* 375, viii 1885 (SING!); Penang Hill, Ahmad Shukor AS 91, FR, 26 ii 1973 (SING!), Corner SFN 31597, leafy branch only, 21 vii 1936 (SING!), Low et al., LYW 196, FB, 4 vii 2008 (KLU!), LYW 206, leafy branch only, 6 vii 2008 (KLU!), Nauen s.n., FB, 5 viii 1940 (SING!), Samsuri Ahmad SA. 999, FB, FL, 6 x 1974 (KEP! KLU! SING!), Sidek S. 226, FR, 5 iv 1968 (SING!), Sugumaran et al., SM 169, leafy branch only, 16 ii 2008 (KLU!), Symington KEP 28043, FL, 4 ix 1931 (SING!); Western Hill, Nanen s.n., FR, 8 viii 1940 (SING!). **Terengganu**. Ulu Brang, Gunung Padang, Whitmore FRI 12803, FL, 23 ix 1969 (KEP! SING!).

As noted by Ridley (1918), *F. caudata* Ridley (= *C. caudatum*) which occurs only in Borneo (Sarawak and Brunei), closely resembles *C. wallichianum*. *Cyrtophyllum caudatum* differs from *C. wallichianum* by having more coriaceous, lanceolate-caudate leaves and extremely slender peduncles and pedicels, cylindric corolla tubes and shorter stamens.

***Picrophloeus* Bl.**

Bijdr. (1826) 1019. Type: *P. javenensis* Bl. (= *P. elliptica* (Roxb.) Sugumaran & Wong).

Medium-sized to large trees to about 32 m tall. **Trunk** with episodic growth; bark becoming fissured in older trees. Vegetative shoot tips with light yellowish resin. Leaf arrangement on branches decussate; leaf margin entire; **petiolar sheaths** of a leaf pair fused to form a shallow cup-like ochrea. **Inflorescence** terminal, a many-flowered and branched cyme, basal branches nearly as long as or longer than rachis. **Flowers** small, up to 10 mm wide at the mouth; stamens typically two thirds or more exsert; style typically one third or more exsert; stigma capitate. **Fruits** small, up to about 10 mm in diameter; colour at maturity yellow-orange to bright red; with small amounts of translucent sticky latex in fruit epidermis and fruit wall; epidermis separating as a thin translucent film from pericarp (fruit surface appearing crinkled on herbarium specimens). **Seeds** polygonal.

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

Habitat. Lowland forests.

***Picrophloeus elliptica* (Roxb.) Sugumaran & Wong, comb. nov.**

Fagraea elliptica Roxb., [Hort. Beng. (1814) 84, *nom. nud.*] Fl. Ind. ed. Wall. 2 (1824) 32; Cammerloher, Bull. Jard. Bot. Btzg. III, 5 (1923) 316; Kochummen, Tree Fl. Malaya 2 (1973) 272; Wong & Sugau 8 (1996) 21.

Type: not found, see notes below.

Fagraea elliptica sensu Leenhouts, Fl. Males. I, 6 (2) (1962) 303 pro parte, quoad *Cyrtophyllum speciosum* Ridl. var *montanum* Ridl., *F. speciosa* Bl. in syn.

Cyrtophyllum speciosum Bl., Bijdr. (1826) 1022. Type: Blume 1867, Java (L!: sheet no. 908.127-210).

Cyrtophyllum speciosum Ridl. var *montanum* Ridl., Fl. Malay. Pen. 5 (1925) 322. Type: Henderson SFN 10992, Pahang, Cameron Highlands, Gunung Terbakar, 45000 ft. alt., 9 vi 1923 (holotype K; isotype SING).

Fagraea speciosum (Bl.) Bl., Rumphia 2 (1838) 35, t. 81; Mus. Bot. 1 (1850) 172.

Tree, sometimes to 3–4 m tall but more often bigger, to 10–20 m tall; trunk to about 1 m in diameter; **bark** fissured in younger trees, less conspicuously so and dappled-scaly in older trees, grey-brown to dark brown. **Leaves** elliptic; (8–)11–17(–21) cm long, (3–)4–7(–9.5) cm wide; **base** cuneate; **apex** acuminate to short-caudate; 1–3 mm long; **margin** plane when fresh (in dried specimens sometimes slightly wavy); thin-coriaceous; upper and lower **surfaces** smooth; **midrib** prominent below, flat to slightly raised above; **secondary veins** (5–)7–12 pairs, upper side faint and immersed in the blade, lower side faint to very

slightly prominent; **tertiary veins** inconspicuous; petioles (0.5–)1–1.5(–2.2) cm long, 1.5–2(–4) mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; petiolar base **auricles** absent. **Inflorescence** terminal, a many-flowered, multi-branched cyme, (6–)7–10(–12.5) cm long; **peduncle** 0–0.3(–1.8) cm long, 2–4 mm thick; with **(5–)7–8 levels** (tiers) of branching on the main axis, the branch tiers (5–)10–22(–33) mm apart, lowest tier typically most branched, to **(4–)5–6 orders**. **Flower** bisexual; **pedicel** 1–2 mm long, 0.5–0.8 mm thick; **calyx** (from the base to the lobe apices) 1.5–2 mm long, glabrous, **calyx cup** 1.5–2 mm wide, **calyx lobes** 5, erect, 1–1.5 mm long, 1–1.5 mm wide, margins glabrous; **corolla** salverform; cream to white; **corolla tube** 3–5 mm long, not conspicuously flared, 0.8–1 mm wide, inside glabrous to minutely papillate; **corolla lobes** 5, broad-ovate to subobovate, 2–2.5 mm long, 0.8–1 mm wide, overlapping to the right; **stamens** 5, inserted at the upper end of the corolla tube; **filaments** (4–)7–8 mm long, exsert (4–)7–8 mm in the open flower; **anthers** versatile, hastate, 1–1.2 mm long, 0.5–0.8 mm wide, each anther sac somewhat narrowly ellipsoid; **style** (6–)7–9 mm long, protruding 3–4 mm from the corolla mouth in the open flower; **stigma** knob-like, c. 0.5 mm across, lobes 2, low and rounded, parting to present two slightly raised, hemispherical, papillate inner surfaces when receptive, not recurving. **Infructescence** **peduncle** 0–1 cm long, 3–5 mm thick. **Fruit** globose; smooth; when mature to 4–5 mm across; the base tightly clasped by the calyx lobes. **Seeds** numerous; placentation axile; polygonal; testa surface areolate; 0.5–1 mm across.

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

Habitat. Lowland and lower montane forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Kedah**. Kedah Peak, *Kochummen* KEP 94404, FB, 26 ii 1960 (KEP!); Kuala Muda, Jerai F.R., *Abdullah & Motan* 73515, FR, 4 iv 1950 (KEP!), *Gurun* 66405, leafy branch only, 7 viii 1949 (KEP!), plantation Jerai, *Gurun* 59647, FB, FL, 24 iii 1950 (KEP! SING!). **Kelantan**. Sungai Keleh, *Henderson* 19658, FR, 25 x 1927 (KEP! SING!). **Pahang**. Cameron Highlands, Boh Plantations, *Mohd Nur* SFN 32626, FB, 12 iv 1937 (KEP! SING!), Gunung Brinchang, *Teo et al.*, KL 4694, FR, iv 1997 (KEP!); Gunung Terbakar, *Henderson* 31385, FB, FL, FR, 21 v 1936 (KEP!), *Holttum* SFN 31385, FB, FL, 21 v 1936 (SING!), *Symington* KEP 36219, FB, 12 iv 1934 (KEP! SING!); Fraser's Hill, Kiew & Anthony RK 3483, FB, FL, 21 iv 1992 (SING!), Kenari Trail, *Kiew* 3335, FR, 27 ix 1991 (KEP!); Gunung Tapis, *Chan YC* FRI 19906, FR, 29 ix 1971 (KEP!); Ulu Kali, *Siew WH* 156, leafy branch only, 18 vi 1977 (KLU!), 217, leafy branch only, 2 vii 1977 (KLU!), *Stone* 15420, leafy branch only, 1 iv 1983 (KLU!). **SUMATRA**. *Achmad* 58, FB, FL, 5 xi 1917 (SING!), 1515, FB, 21 xi 1919 (SING!), 1616, FR, 14 i 1920 (SING!), *Batten s.n.*, FR, 8 iii 1940 (SING!); *Yates* 2201, FB, no date (SING!). **Asahan**. Loemban Ria, *Rahmat* 7352, FB, FL, 21 xi 1936 (SING!), 7813, FB, FL, 10 iv 1936 (SING!), 7952, FR, 24 xi 1936 (SING!), 7962, FR, 24 xi 1936 (SING!). **Palembang**. Lematang Ilir, Semangoes, *Neth. Ind. For Service* bb. 31728, FB, FL, 3 v 1940 (SING!), bb. 31747, FB, FL, 5 v 1940 (SING!), bb. 32122, FR, 27 vi 1940 (SING!). **Si borong borong**. *Stein* Ba/9/73/7, FB, 13 ix 1973 (SING!). **JAVA**. *Blume* 1867, FB, FL, no date (L!).

Picrophloeus elliptica (= *F. elliptica*) was first described by Roxburgh in 1824 where he gave a very brief description and mentioned that this is a native of Moluccas (Maluku). The sheets in Kew, where most of Roxburgh's collection are kept, do not include collections made from the Moluccas earlier than 1824 which Roxburgh would have seen, and neither are there any in Singapore and Edinburgh (H. Nolte & K.M. Wong, pers. comm.). A search for such material at the Natural History Museum (BM) should still be made before finalizing the case for neotypification (this was not possible prior to conclusion of the present study because of the BM's move to their new Darwin Building

premises. There is also no drawing of this taxon among Roxburgh's Flora Indica illustrations (Sealy 1957).

***Utania* G.Don**

Gard. Dict. 4 (1838) 663. Type: *U. morindaefolia* G.Don (= *U. volubilis* (Wall.) Sugumaran). *Kuhlia* Reinw. ex Bl., Bijdr. (1826) 777 & Reinw. in Syll. Pl. Ratisb. 2 (1828) 6, *nom. illeg.*, non H.B.K.; *Kentia* Steud., Nomencl. ed. 2 (1840) 845, *nom. illeg.*

Small to medium-sized trees usually 1–several m tall, occasionally to 15 m tall. **Trunk** with continuous growth; bark becoming fissured in older trees. Vegetative shoot tips non-resinous. Leaf arrangement on branches distichous; leaf margin entire; **petiolar sheaths** of a leaf pair fused to form a shallow cup-like ochrea; **Inflorescence** terminal, a many-flowered and branched pendulous cyme. **Flowers** small to medium-sized, up to 25 mm wide at the mouth; stamens not to slightly exsert; style not to slightly exsert; stigma peltate. **Fruits** small to medium-sized up to 15 mm in diameter; colour at maturity pale to dark brown; without latex in fruit epidermis or fruit wall; epidermis not separating from pericarp (fruit surface firm and appearing smooth on herbarium specimen). **Seeds** polygonal.

Distribution. Indo-China, the Andaman and Nicobar Islands, Malay Peninsula, Sumatra, Java, Borneo, Celebes, Maluku, the Philippines and New Guinea.

Habitat. Lowlands including secondary forests.

Key to species

1a. Flowers with longer pedicels (6–18 mm long) and bigger calyx lobes (8–11 mm long and 6–10 mm wide); leaf margin distinctly recurved upon drying. *U. maingayi*

1b. Flowers with shorter pedicels (up to 5 mm long) and smaller calyx lobes (up to 6 mm long and 5 mm wide); leaf margin plane even upon drying.

2a. Leaves with 10–16 pairs of secondary veins; peduncle of mature inflorescence (bearing open flowers) thicker (5–7 mm thick) and usually shorter (0.8–1(–2) cm long); infructescence peduncle thicker (5–8 mm thick). *U. nervosa*

2b. Leaves with 3–7 pairs of secondary veins; peduncle of mature inflorescence (bearing open flowers) thinner (1–3(–4) mm thick) and usually longer ((1)3–8(–10) cm long); infructescence peduncle thinner (1–4 mm thick).

3a. Corolla narrowly funnel-shaped (corolla mouth less than to about 3 times the width of the lower narrowed part of the tube); corolla lobes very short, less than 3 mm long, only about 1/4 to 1/5 the length of the broadened upper part of the corolla tube. *U. johorensis*

3b. Corolla broadly funnel-shaped to campanulate (corolla mouth more than 3–4 times the width of the lower narrowed part of the tube); corolla lobes 5

mm long or more, more than half the length of the broadened upper part of the corolla tube.

4a. Inflorescence branching to 1 order only on the lowest branching tier; corolla mouth narrower (7–8 mm wide); leaf with 3–4 pairs of secondary veins, tertiary and higher-order veins not visible in dried specimens. *U. peninsularis*

4b. Inflorescence branching to 2 or more orders on the lowest branching tier; corolla mouth wider (10–17 mm wide); leaf with 5–7 pairs of secondary veins, tertiary and higher-order veins distinct to at least faintly visible in dried specimens.

5a. Rachis in the distal half of the flower-bearing part of the inflorescence and infructescence thinner or as slender as the proximal rachis and peduncle; flowering and fruiting tiers above the basal 1–2 tiers always well-spaced, separated by clearly visible rachis lengths of 0.5 cm or more; calyx lobes spreading out from the corolla or fruit base in dried specimens. *U. volubilis*

5b. Rachis in the distal half of the flower-bearing part of the inflorescence and infructescence conspicuously thicker than

the proximal rachis and peduncle; flowering and fruiting tiers above the basal 1–2 tiers typically closely spaced, without clearly visible rachis lengths between tiers; calyx lobes tightly clasping the corolla or fruit base in dried specimens. *U. racemosa*

1. *Utania johorensis* Sugumaran, sp. nov.

Typus: Ridley 8453, Singapore, Bidadari (April 1897) (*holotypus SING! isotypus K*).

F. peninsularis Wong & Sugau, Sandakania 8 (1996) 33, pro parte, quoad Ridley 2783, 8453.

F. ligustrina auct. non Blume (1838): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 609 pro parte, quoad Ridley 2783 & Ridley 8453; *F. ligustrina* sensu Ridley, Fl. Malay. Pen. 2 (1923) 420 pro parte, quoad Ridley 8453 (Bidadari).

F. racemosa auct. non Jack ex Wall. (1824): Leenhouts, Fl. Males. I, 6 (2) (1962), pro parte, quoad 'F. ligustrina' in King (1908) & Ridley (1923) in syn.

(Fig. 30)

Small tree, c. 2 m tall. **Leaves** elliptic-ovate to elliptic-lanceolate; (4.3–)8–11(–14.7) cm long, (1.2–)3–5.5 cm wide; **base** cuneate rounded; **apex** acuminate-short caudate; **margin** plane; thin coriaceous; upper and lower **surfaces** glabrous; **midrib** prominent below sunken above; **secondary veins** 4–6 pairs, upper side faint, lower side faint to slightly prominent; **tertiary veins** inconspicuous; leaf stalks 8–15 mm long, 1–2 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely

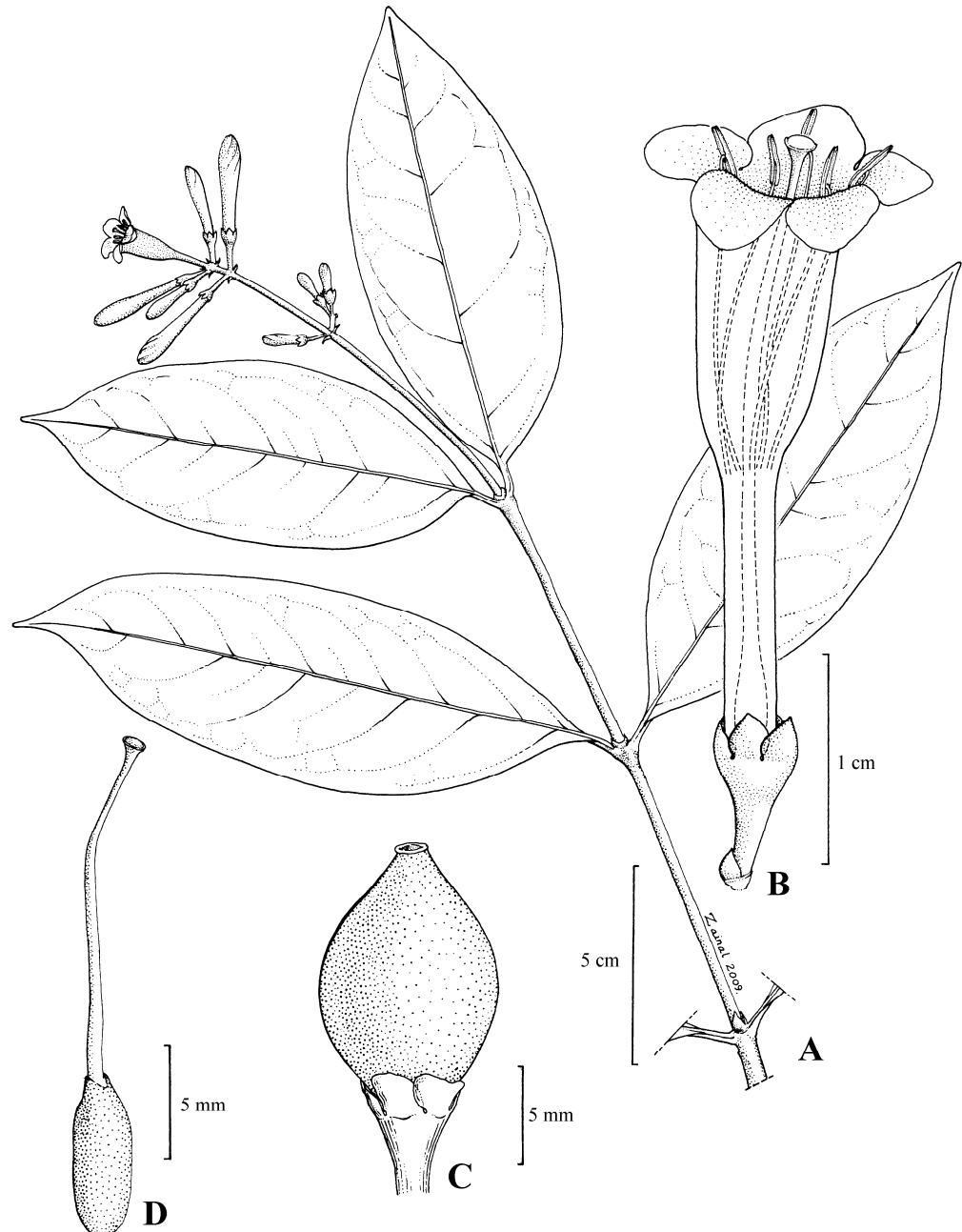


Fig. 30. *Utania johorensis*. **A.** leafy branch with an inflorescence. **B.** flower. **C.** fruit. **D.** stigma with ovary attached.
All drawn from Ridley 8453 (SING).

clasps the stem; leaf-stalk **auricles** absent. **Inflorescence** terminal, a many-flowered panicle, (2.4–)3.5–6(–9) cm long; **peduncle** 2.8–4.5(–6) cm long, 1–1.5 mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence not conspicuously thicker than the proximal part and the peduncle, clearly visible; **branch tiers** closely spaced (except sometimes the lowest two tiers well-spaced, (0.5–)1–2(–2.5) cm apart), the basal 1–2 branch tiers most branched, typically to 1–2 orders, more distal tiers hardly so. **Flower** bisexual; **pedicel** 2–4 mm long, 1–1.5 mm thick; **calyx** (from the base to the lobe apices) 3–4 mm long, glabrous, **calyx cup** 3–3.5 mm wide, **calyx lobes** 5, erect and tightly clasping the corolla tube, 2–3 mm long, 2–2.5 mm wide, margins glabrous to sparsely minute-ciliate or apparently lacinate (the cilia or lacinia just c. 0.1 mm long); **corolla** narrowly infundibular (the mouth less than to about 3 times the width of the lower narrowed part of the tube); white; **lower subcylindrical part of the corolla tube** 10–13 mm long, 2–3 mm wide, **upper flared part** of the tube slightly inflated, 10–12 mm long, 6–7 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 2–2.5 mm long, 2.5–3 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 15–16 mm long, slightly protruding to 5 mm from the corolla mouth in the open flowers; **anthers** versatile, hastate, 1.5–2 mm long, c. 1 mm wide, each anther sac somewhat ellipsoid; **style** 20–28 mm long, not to slightly protruding to 3 mm from the corolla mouth; **stigma** basically shallowly 2–lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure c. 1 mm across). **Infructescence peduncle** 2.2–3.5 cm long, 1–1.5 mm thick; **rachis** in the distal half of the fruit-bearing part of the infructescence not conspicuously

thicker than the proximal part and the peduncle, clearly visible. **Fruit** broadly ellipsoid, **apex** beaked; smooth; when mature to 10–11 mm long, 7–10 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; polygonal and frequently slightly elongated; 1–1.2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

Distribution: Endemic to the southern half of Peninsular Malaysia.

Habitat: Lowland forest understory.

SPECIMENS EXAMINED. PENINSULAR MALAYSIA. **Johor.** Nam Heng, *Teruya* 227, FB, FL, ix 1926 (SING!), *Teruya* 321, FL, ii 1927 (SING!); Pontain, Pengkalan Raja, *Ngadiman s.n.*, FR, 3 vii 1939 (SING!).
Pahang. Tasik Bera, *Soepadmo* KLU 11668, FR, 30 vii 1970 (KLU!). SINGAPORE. *Cantley's Collection*, leafy branch only, no date (SING!); Bidadari, *Ridley* 8453, FB, FL, FR, iv 1897 (SING!); Changi, *Goodenough* 2783, FL, FR, no precise date, 1891 (SING!); Tampinis, *Ridley* 5962, FB, FL, ii 1894 (SING!); Tampinis Road, *Goodenough* 1650, FB, 17 vi 1890 (SING!).

Leenhouts (1962) in his account for Malesian region, adopted a very broad concept for *F. racemosa* (= *U. racemosa*) where he dismissed a number of previously described species. Wong & Sugau (1996), in their account for Borneo, resurrected *F. peninsularis* (= *U. peninsularis*) among various other species from the synonymy of *F. racemosa* (*U. racemosa*). However, their species concept of *F. peninsularis* (= *U. peninsularis*) (Wong & Sugau 1996) was mixed with material here considered to represent a different species (see also *U. peninsularis* below). The essential differences between these two species are as follows.

U. peninsularis has a shorter upper inflated part of the corolla tube than the lower narrowed tubular portion, whereas in *U. johorensis*, the upper inflated part is as long as the

lower narrowed tubular portion. The inflorescence peduncle is only up to 1.6 cm long in *U. peninsularis* but in *U. johorensis* it is 2–6 cm long. The number of leaf secondary veins also differs between these two species, 3–4 pairs in *U. peninsularis* and 4–6 pairs in *U. johorensis*.

2. *Utania maingayi* (Clarke) Sugumaran, comb. nov.

Fagraea maingayi Clarke, in Hook. f., Fl. British India 4 (1883) 84; King & Gamble, J. As. Soc. Beng. 72, 2 (1903) 609; Ridley, Fl. Malay Pen. 2 (1923) 419; Wong & Sugau, Sandakania 8 (1996) 30.

Type: *Maingay* 1033 (holotype K!).

F. racemosa auct. non Jack ex Wall. (1824): Leenhouts, Fl. Males. 1, 6 (2) (1962) pro parte, quoad *F. maingayi* Clarke in syn.

Small to medium-sized tree, usually to 5–15 m (occasionally to 30 m) tall; trunk to c. 15 cm diameter; **bark** slightly to deeply fissured, dark grey to dark brown. **Leaves** elliptic to elliptic-lanceolate; (6–)17–24(–28) cm long, (2.5–)6–9(–10.5) cm wide; **base** cuneate rounded; **apex** acuminate to short-caudate; **margin** recurved (in dried specimens); thick-coriaceous; upper and lower **surfaces** glabrous; **midrib** prominent below, sunken above; **secondary veins** 6–8 pairs, faint on both sides; **tertiary veins** inconspicuous; leaf stalks 1.2–2.4 cm long, (3–)5–7 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; leaf-stalk **auricles** absent.

Inflorescence terminal, a many-flowered panicle, (7–)9–12(–15.5) cm long; **peduncle** (4–)5–8(–9) cm long, 2.5–4(–4.5) mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence not conspicuously thicker than the proximal part and the peduncle, clearly visible; **branch tiers** well-spaced, 1.5–2.5 cm apart, the basal 1–2 branch tiers most branched, typically to (1–)2 orders, more distal tiers hardly so. **Flower** bisexual; **pedicel** (6–)10–18 mm long, 2–4 mm thick; **calyx** (from the base to the lobe apices) 9–13 mm long, glabrous, **calyx cup** 7–12 mm wide, **calyx lobes** 5, erect and tightly clasping the corolla tube, 8–11 mm long, 6–10 mm wide, margins glabrous to sparsely minute-ciliate or apparently laciniate (the cilia or lacinia just c. 0.1 mm long); **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla** 3–4 mm long, 4–6 mm wide, **upper flared part** of the tube slightly inflated, (13–)15–18(–21) mm long, 17–22(–25) mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 12–14 mm long, 10–14 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 19–23 mm long, not to slightly protruding to 3 mm from the corolla mouth; **anthers** versatile, hastate, 3–4 mm long, 1.5–2 mm wide, each anther sac somewhat ellipsoid; **style** 12–23 mm long, not protruding from the corolla mouth; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure 1–2 mm across). **Infructescence** **peduncle** 7–8.5 cm long, 3–4 mm thick; **rachis** in the distal half of the fruit-bearing part of the infructescence not conspicuously thicker than the proximal part and the peduncle, clearly visible. **Fruit** ellipsoid, **apex** beaked; smooth; when mature to 15–18 mm long, 7–

10 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; polygonal and frequently slightly elongated; 1–1.2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

The flowers are fragrant (*Whitmore* FRI 20019).

Distribution: Peninsular Malaysia and Sumatra.

Habitat: Lowland primary and secondary forests.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. *Maingay* 1033, FB, FL, 16 v 1864 (K!); Kedah. Koh Mai F. R., *Kiah* SFN 35105, FB, 1 iv 1938 (SING!); **Melaka**. Sadanan Reserve, *Derry* 573, FL, vi 1890 (SING!); Selandar, *Alvins s.n.*, FB, 29 iv 1886 (SING!); **Negri Sembilan**. Senawang, *Yakim* CF 1986, FB, FR, 24 xi 1918 (SING!); Seremban, *Moorhouse s.n.*, leafy branch only, no precise date, 1904 (SING!); **Pahang**. Aur F.R., Compt. 34, *Whitmore* FRI 3630, FB, 10 v 1967 (KEP!); Bentong, *Ariffin* KEP 92362, detached leaves only, 19 vii 1958 (KEP!); Jerantut, Hutan Simpan Tekai, *Teo & Emmanuel* KL 4892, FB, 5 v 1999 (KEP!), Taman Negara, Sungai Tanum, *Chua et al.*, FRI 40657, FB, FL, 8 v 1997 (KEP! SING!); Kemanson F.R., *Hamid* 10559, leafy branches only, 4 ix 1925 (SING!); Mentakab, Kemasul F.R., *Mohzan* KEP 99591, FB, 17 iii 1962 (SING!); Sungai Telom, Bukit Cheraga, *Whitmore* FRI 20019, FB, 26 v 1971 (KEP!), *Zainuddin* FRI 14737, FB, FL, 26 v 1971 (KEP!); Ulu Krau, Gunung Benom Game Reserve, *Zahir* KEP 99108, FB, 29 iv 1967 (KEP!); **Selangor**. Kajang, Bukit Tunggal, *Harun* 17503, FR, 26 vii 1929 (SING!); Kuala Lumpur, Public Garden, *Foxworthy* FMS 2362, FL, iv 1916 (SING!); Rantau Panjang, *Strugnell* FMS 12787, FB, 10 vi 1927 (SING!). SUMATRA. **Atjeh**. Gunung Leuser Nature Reserve, *de Wilde & de Wilde-Duyfjes* 12685, FL, 7 vi 1972 (SING!).

Among the six Peninsular Malaysian species in this genus, *U. maingayi* is most easily distinguished. It has the largest flowers in this section, where the corolla measures about 3 cm long and 2.5 cm wide at the mouth. The calyx is also the largest within the section, measuring up to 1.2 cm long and up to 1.2 cm wide. It also differs from typical *U.*

racemosa in the following characteristics. The main axis of the inflorescence is clearly seen and not hidden by flowers or flower groups in *U. maingayi* and the flowers or flower groups are in distinct tiers. The leaves of *U. maingayi* are typically oblong to lanceolate or obovate, and the secondary veins are sometimes inconspicuous and fading as they approach the leaf margin. In *U. racemosa*, the main axis of the inflorescence is largely obscured from view by the dense arrangement of flowers or flower groups, the leaves are mostly elliptic-ovate, sometimes lanceolate, and the secondary veins are always prominent on the lower leaf surface, often clearly looping near the margin.

3. *Utania nervosa* Wong & Sugumaran, sp. nov.

Typus: Joseph Lai LJ157 (sheet 2/2), Singapore, Pulau Ubin (1997) (holotypus SING!).

F. racemosa auct. non Jack ex Wall. (1824): Leenhouts, Fl. Males. 1, 6 (2) (1962) pro parte, quoad Burkhill 1961, Corner s.n. 3 June 1936, Goodenough 1146, Kadim & Md. Nur 249, Ngadiman SFN 36894.

(Fig. 31)

Small tree, usually 1–5 m tall; trunk to c. 6 cm diameter; **bark** smooth to slightly fissured, grey-brown to dark brown. **Leaves** elliptic to elliptic-ovate; (13–)20–31(–40) cm long, (6–)11–15(–18) cm wide; **base** cuneate to subcordate; **apex** acuminate-short caudate; **margin** plane; thick-coriaceous, lamina very often strongly bullate between the secondary veins when growing in hot open sites; upper and lower **surfaces** glabrous; **midrib** prominent below, slightly sunken above; **secondary veins** 10–16 pairs, upper side faint, lower side

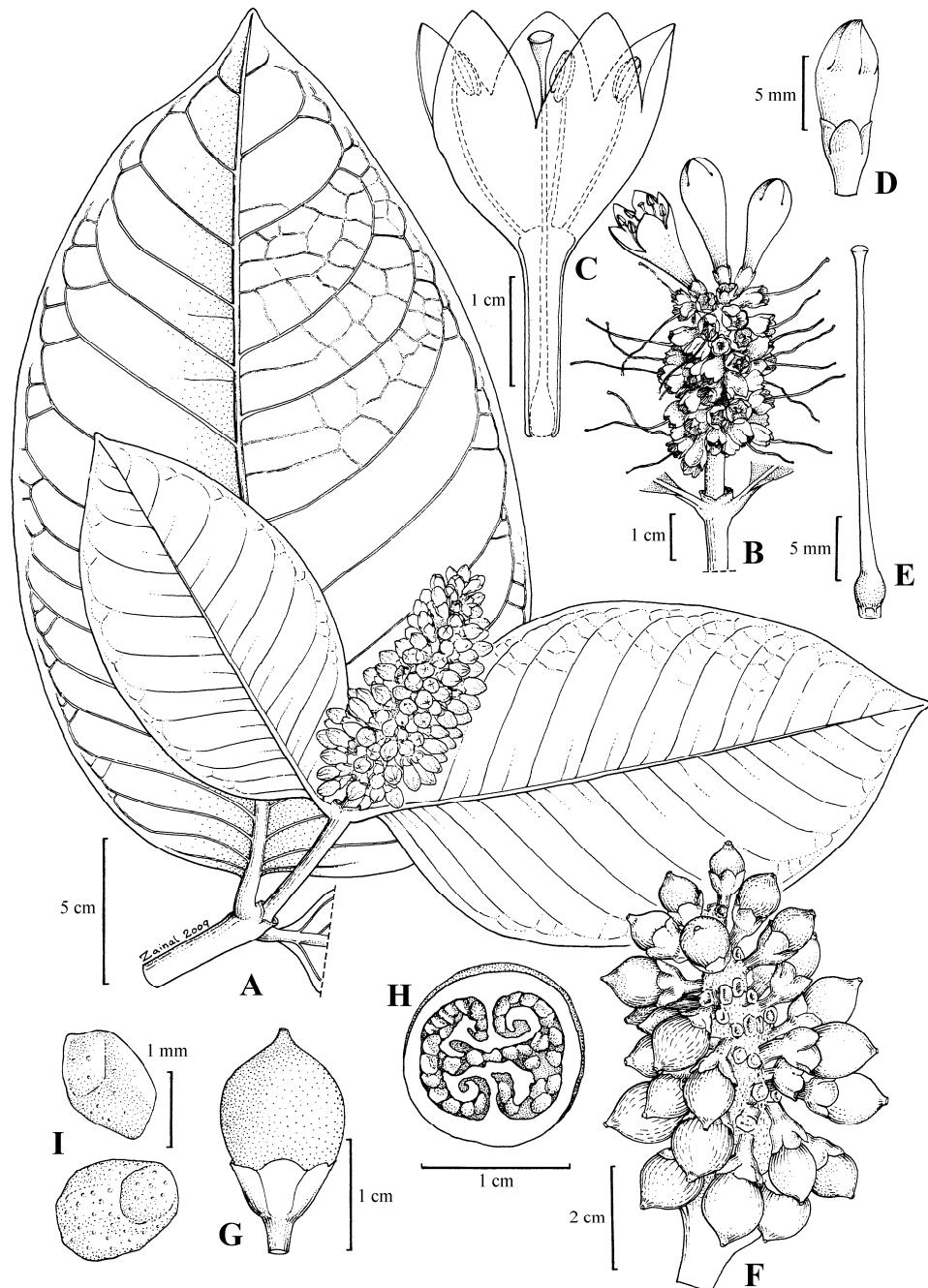


Fig. 31. *Utania nervosa*. **A.** leafy branch with an inflorescence. **B.** an inflorescence. **C.** flower. **D.** flower bud. **E.** stigma with ovary attached. **F.** an infructescence. **G.** fruit. **H.** sectioned matured fruit. **I.** seeds.

A-E from Lai LJ 157 (Holotype, SING), F-I from Sugumaran, SM201.

prominent; **tertiary veins** faint; leaf stalks 5–12 mm long, 4–7 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; leaf-stalk **auricles** absent. **Inflorescence** terminal, a many-flowered panicle, (3.5–)4–8(–10) cm long; **peduncle** 0.8–1(–2) cm long, robust, 5–6(–7) mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence not conspicuously thicker than the proximal part and the peduncle, typically obscured from view by densely crowded flowers; **branch tiers** very closely spaced (except sometimes the lowest two tiers well-spaced, 0.5–1 cm long), the basal 1–2 branch tiers most branched, typically to 3(–4) orders, more distal tiers hardly so. Flower bisexual; **pedicel** 2–3 mm long, 2–3 mm thick; **calyx** (from the base to the lobe apices) 5–7 mm long, glabrous, **calyx cup** 4–6 mm wide, **calyx lobes** 5, erect and tightly clasping the corolla tube, 3–4 mm long, 3–5 mm wide, margins glabrous; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); creamy-yellow to white; **lower subcylindrical part of the corolla tube** 11–15 mm long, 3–4 mm wide, **upper flared part** of the tube slightly inflated, 10–11 mm long, 15–18 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 7–8 mm long, 5–6 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 10–15 mm long, not protruding from the corolla mouth; **anthers** versatile, hastate, 3–4 mm long, 1–2 mm wide, each anther sac somewhat ellipsoid; **style** 22–25 mm long, not to slightly protruding c. 1 mm from the corolla mouth; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure 1–1.5 mm across). **Infructescence peduncle** 0.5–1.6 cm long, 5–7(–8) mm thick;

rachis in the distal half of the fruit-bearing part of the infructescence not conspicuously thicker than the proximal part and the peduncle, typically obscured from view by the very closely spaced fruiting tiers. **Fruit** broadly ellipsoid, **apex** beaked; smooth; when mature to 14–18 mm long, 8–13 mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; polygonal and frequently slightly elongated; 1.5–2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

The flowers are fragrant. The plants are frequently infested with red weaver ants, as noted in the field in Mawai, Johor (*Sugumaran et al.* SM 201), and also in Singapore collections (*Gwee et al.* GAT 339, *Lai* LJ 157).

Distribution: Confined to the southern half of Peninsular Malaysia.

Habitat: Lowlands, in freshwater swamp forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Gunung Panti F.R., *Sugumaran et al.* SM204, leafy branch only, 29 iv 2008 (KLU!); SM205, leafy branch only, 29 iv 2008 (KLU!); Jason Bay, *Carrick* 1411, FR, 25 x 1965 (SING!); Kuala Sedili New Road, *Burkill* HMB 1961, FB, FL, 9 viii 1959 (SING!), *Kadim & Nur* 249, FB, 28 vi 1959 (SING!); Mawai, *Corner s.n.*, FB, 3 vi 1936 (SING!), Batu Piatu, *Sugumaran et al.* SM201, FR, 28 iv 2008 (KLU!); Panti F.R., *Everett* FRI 13851, FB, 24 i 1970 (KEP!); Sungai Sedili, *Ngadiman* SFN 36874, FB, 26 vii 1939 (SING!). **SINGAPORE.** Pulau Tekong, *Gwee et al.* SING 2007-225, FB, FR, 2 iii 2007 (SING!), *Lai* LJ396, FB, FL, no precise date, 1998 (SING!), *Samsuri et al.* 17, FB, FL, 31 x 2001 (SING!), 365, FR, 1 ii 2002 (SING!); Pulau Tekong Kechil, *Gwee et.al.* 23, leafy branch only, 29 xi 2002 (SING!); Pulau Ubin, *Goodenough* 1146, FB, 17 vi 1890 (SING!), *Lai* LJ157, FB, FL, no precise date, 1997 (SING!), Chek Jawa, *Gwee et al.* GAT 217, FB, FL, 28 i 2003 (SING!), GAT 339, FB, FR, 23 ix 2003 (SING!).

U. nervosa described here appears to have resemblances with *F. cuspidata* Bl., (= *U. cuspidata*), *F. racemosa* Jack ex Wall. (= *U. racemosa*) and *F. spicata* Baker (= *U. spicata*) but as discussed below there are clear characters to tell it apart from these three species.

U. nervosa is easily distinguished from *U. cuspidata* and *U. racemosa* in its greater number of leaf secondary veins (10–15 pairs in *U. nervosa*, compared to only 5–7 pairs in *U. cuspidata* and *U. racemosa*). In *U. nervosa*, the inflorescence peduncle is massive, 5–6 mm thick, but more slender in the others (only 2–3 mm thick in *U. cuspidata* and *U. spicata*; 1.5–3(–4) mm thick in *U. racemosa*). It is also much shorter (only 0.5–1.5 cm long) than in *U. cuspidata* (11.5–23 cm long). In *U. nervosa* (and also *U. cuspidata* and *U. racemosa*), the mature fruits are pointed at both ends (spindle-shaped) but in *U. spicata* they are apically more rounded (somewhat top-shaped).

There are other individual differences. *U. nervosa* has branches on the stem which are stiff and ascending compared to long, limply pendulous branches in mature trees of *U. spicata*. *U. nervosa* inflorescences have more branching orders, (2–)3–4 orders, whereas *U. spicata* inflorescences have less, only up to 1–2 orders; consequently the inflorescence in *U. nervosa* typically has a greater number of closely packed flowers than in the other species. Flower pedicels are much shorter (1–3 mm long) in *U. nervosa* but longer (7–20 mm long) in *U. cuspidata*. In *U. nervosa*, the calyx lobes in dried material are tightly clasping the corolla or fruit base but loosely clasping or spreading out in *U. spicata*. In *U. nervosa*, the corolla lobes are much longer and wider (9–10 mm × 7–8 mm) than in *U. spicata* (3–4 mm × 4–5 mm).

4. *Utania peninsularis* (Wong & Sugau) Sugumaran, comb. nov.

Fagraea peninsularis Wong & Sugau, Sandakania 8 (1996) 33, excl. Ridley 2783 (= *Utania johorensis*).

Type: Loh FRI 17131, Peninsular Malaysia, Johor, Segamat Wildlife Reserve, eastern boundary (holotype KEP! isotype K).

F. ligustrina auct. non Blume (1838): King & Gamble, J. As. Soc. Beng. 74 (2) (1908) 609, pro parte, excl. Ridley 2783 & Ridley 8453 (= *Utania johorensis* Sugumaran); Ridley, Fl. Malay. Pen. 2 (1923) 420, pro parte, excl. Ridley 8453 (Bidadari) (= *Utania johorensis* Sugumaran).

F. racemosa auct. non Jack ex Wall. (1824): Leenhouts, Fl. Males. I, 6 (2) (1962), pro parte, quoad '*F. ligustrina*' in King & Gamble (1908, pro parte) & Ridley (1923, pro parte) in syn.

Small tree, c. 2 m tall. **Leaves** elliptic-ovate to elliptic-ob lanceolate; (2.5–)5.5–7(–9.3) cm long, (1–)2.5–3(–4.2) cm wide; **base** cuneate; **apex** caudate; **margin** plane; thin coriaceous; upper and lower **surfaces** glabrous; **midrib** prominent below sunken above; **secondary veins** 3–4 pairs, upper side faint, lower side faint; **tertiary veins** inconspicuous; leaf stalks 10–17 mm long, 1–1.5 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; leaf-stalk **auricles** absent. **Inflorescence** terminal, a many-flowered panicle, 1–2.7 cm long; **peduncle** c. 1.8 cm long, c. 1 mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence not conspicuously thicker than the proximal part and the peduncle,

clearly visible; **branch tiers** closely spaced (except sometimes the basal two tiers well-spaced, 4–5 mm apart), all branch tiers with only 1 branching order. **Flower** bisexual; **pedicel** 3–4 mm long, 1–1.5 mm thick; **calyx** (from the base to the lobe apices) 5–6 mm long, glabrous, **calyx cup** 3–4 mm wide, **calyx lobes** 5, erect and tightly clasping the corolla tube, 2–3 mm long, 2–3 mm wide, margins glabrous; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); white; **lower subcylindrical part of the corolla tube** c. 8 mm long, c. 2 mm wide, **upper flared part** of the tube slightly inflated, c. 6 mm long, c. 7 mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 5–6 mm long, 3–4 mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 6–7 mm long, slightly protruding to 2 mm from the corolla mouth; **anthers** not seen; **style** 17–19 mm long, slightly protruding to 3–5 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure c. 1 mm across). **Infructescence peduncle** 1–1.5 cm long, 1–1.5 mm thick; **rachis** in the distal half of the fruit-bearing part of the infructescence not conspicuously thicker than the proximal part and the peduncle, clearly visible. **Fruit** broadly ellipsoid, **apex** beaked; smooth; when mature to 10–14 mm long, 7–9 mm wide; the base tightly clasped by the calyx lobes. **Seed** numerous; polygonal and frequently slightly elongated; 1–1.2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

Distribution: Endemic to the southern half of Peninsular Malaysia and Banka Island to its south.

Habitat: Lowland forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Segamat Wildlife Reserve, eastern boundary, *Loh* FRI 17131, FB, FL, FR, 1 vi 1970 (KEP!); **Pahang.** Rompin, *Soh* FMS 15425, FR, 15 vii 1928 (SING!).

As mentioned under *U. johorensis*, Wong & Sugau's definition of *F. peninsularis* (= *U. peninsularis*) contained a divergent element (*Ridley* 2783), here taken out of the species definition of the latter.

5. *Utania racemosa* (Jack ex Wall.) Sugumaran, comb. nov.

Fagraea racemosa Jack ex Wall. in Roxb., Fl. Ind. 2 (1824) 35; Wong and Sugau, Sandakania 8 (1996) 37.

Type: *Jack*, Penang (Wallich, Cat. 1601.1) (holotype K).

F. racemosa var. *grandis* DC., Prod. 9 (1845) 29. Type: *Porter*, Penang (Wallich, Cat. 1601.2) (holotype K).

F. racemosa sensu Leenhouts, Fl. Males. I, 6 (2)(1962), pro parte, quoad Roxb., Fl. Ind. 2 (1824) 35 cit. & *F. racemosa* var. *grandis* DC. in syn.

Small tree, usually to 3–4 m (occasionally to 15 m) tall; trunk to c. 18 cm diameter; **bark** smooth to slightly flaky or fissured, grey-brown to dark brown. **Leaves** elliptic-ovate to

elliptic-lanceolate; (6–)13–25(–30) cm long, (4–)6–13(–20) cm wide; **base** cuneate rounded; **apex** acuminate-short caudate; **margin** plane; coriaceous, often bullate when growing in hot open sites; upper and lower **surfaces** glabrous; **midrib** prominent below sunken above; **secondary veins** 5–7 pairs, upper side faint, lower side prominent; **tertiary and higher-order veins** distinct to faint but always visible in dried specimens; leaf stalks 5–12 mm long, 2–5 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; leaf-stalk **auricles** absent. **Inflorescence** terminal, a many-flowered panicle, (2–)9–13(–17) cm long; **peduncle** (1.3–)4–7.5(–10) cm long, 2–3(–4) mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence distinctly thicker than the proximal part and the peduncle, typically obscured from view by the very closely spaced flowers; **branch tiers** very closely spaced (except sometimes the lowest two tiers well-spaced, 0.5–2(–3.5) cm apart), the basal 1–2 branch tiers most branched, typically to (2–)3 orders, more distal tiers hardly so. **Flower** bisexual; **pedicel** 3–4(–5) mm long, 2–2.5 mm thick; **calyx** (from the base to the lobe apices) 4–6(–8) mm long, glabrous, **calyx cup** 4–6 mm wide, **calyx lobes** 5, erect and tightly clasping the corolla tube, 2.5–4(–5) mm long, 2.5–4(–4.5) mm wide, margins glabrous to sparsely minute-ciliate or apparently laciniate (the cilia or lacinia just c. 0.1 mm long); **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to white; **lower subcylindrical part of the corolla tube** 6–9(–10) mm long, (2–)3–4(–5) mm wide, **upper flared part** of the tube slightly inflated, (4–)6–10(–12) mm long, 10–12(–17) mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 5–6(–11) mm long, 4–6(–10) mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost

portion of the upper flared part of the corolla tube; **filaments** 11–17(–20) mm long, slightly protruding to 6–8 mm from the corolla mouth; **anthers** versatile, hastate, 1.5–2 mm long, 0.5–1 mm wide, each anther sac somewhat ellipsoid; **style** 15–20(–25) mm long, slightly protruding to 3–5 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure 0.8–1.2 mm across). **Infructescence peduncle** (2.2–)3.5–7(–8.2) cm long, 2–3(–4) mm thick; **rachis** in the distal half of the fruit-bearing part of the infructescence distinctly thicker than the proximal part and the peduncle, typically obscured from view by the very closely spaced fruiting tiers above the basal 1–2 tiers. **Fruit** broadly ellipsoid, **apex** beaked; smooth; when mature to (7–)10–12(–15) mm long, (8–)9–10(–11) mm wide; the base tightly clasped by the calyx lobes. **Seeds** numerous; polygonal and frequently slightly elongated; 1–1.2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

Distribution: Indo-China, Peninsular Malaysia and Sumatra.

Habitat: Lowland forest, including secondary forest.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. **Johor.** Endau, Kampung Hubong, *Kadim & Noor* KN 350, FB, 18 vii 1959 (SING!); Endau Road, Kampung Hubang, *Burkill* HMB 1883 FB, 14 vii 1959 (SING!); Gunung Panti, *Burkill* HMB 4551, FB, FL, 14 vii 1968 (SING!); Kota Tinggi, *Burkill* HMB 4555, FB, FL, 14 vii 1968 (SING!), Kota Tinggi, *Ridley* 4206 FR, xii 1892 (SING!), Nam Heng, *Teruya* 376, FR, 14 ix 1929 (SING!); Kulai, SM199, leafy branch only, 28 iv 2008 (KLU!); Mawai, *Corner* s.n. leafy branch only, 11 x 1936 (SING!), SM203, FB, FR, 29 iv 2008 (KLU!); Sedili River, *Corner* 25949, FB, FL, 17 vii 1932 (SING!); Serubong, *Kelsall* 4029, FB, FR, 18 x 1892 (SING!); Sungai Kayu, *Kiah* SF32055, FR, 12 x 1936 (SING!); Sungai Labong, *Holttum* 24949, FB, FL, 9 vii 1931 (SING!). **Kedah.** *Haniff & Salleh* 10476 leafy branch only, 5 iv 1924 (SING!); Selama, Sungai Terap, *Henderson* SFN 35437, FB, FL, 21 v 1938

(KEP!); Yan, *sine coll.*, s.n. FB, FR, no date (SING!). **Kelantan.** Chabang Tongkat F.R., *Suppiah* KEP 108868, FB, 19 vi 1968 (KEP!); Gua Musang, Sungai Galas, *Henderson* 29731, FB, FL, FR, 18 vii 1935 (SING!); Pasir Putih, Hutan Lipur Jeram Pasu, *Lim AL et al.*, s.n., FB, 16 vi 2008 (KLU!); Sungai Ketil, *Henderson* 24821, FB, 31 v 1931 (SING!); Sungai Lebir, Kuala Teryna, *Cockburn* KEP 115955, FR, 3 ix 1967 (KEP!), FRI 7032, FR, 6 ix 1967 (KEP!). **Melaka.** *Alvins* 137, FR, no date (SING!), 1764 leafy branch only, no date (SING!); Ayer Panas, *Holinberg* 854 FR, 13 viii 1891 (SING!), *Derry's Collector* s.n. FB, vi 1886 (SING!); Batang Melaka, *Derry* 1111, FR, ix 1892 (SING!), Senda Rub. Est., *Teruya* 3105, FL, 1 vii 1938 (SING!); Bukit Kayu Arang, *Alvins* s.n. leafy branch only, 29 i 1886 (SING!); Chabau, *Alvins* 2344, FB, 27 ix 1885 (SING!), 2345, FR, 27 ix 1895 (SING!); Machap, *Derry* 1062, FB, no precise date, 1892 (SING!); Selandar, *Alvins* s.n., FB, FL, 17 ii 1886 (SING!), 341, FB, 30 i 1885 (SING!). **Negri Sembilan.** Bukit Sutun, *Alvins* 1982, FR, 2 xi 1885 (SING!); Pasir Panjang, *Us of CF* 600, FR, 3 vi 1919 (SING!); Pasoh F.R., *Rogstad* 907, FB, 26 vii 1983 (KEP!); Serting Tengah, Kampung Jawa, *Kochummen* FRI 18427 FR, 3 ix 1976 (SING!); Tampin, *Md Nur* SFN 1313, FB, FL, 28 vii 1915 (SING!). **Pahang.** Bentong, *Burkill & Haniff* SFN 16485, leafy branch only, 4 xi 1924 (SING!), SFN 16613, leafy branch only, 8 xi 1924 (SING!); Beserah, *Burkill & Haniff* SFN 17586 leafy branch only, 6 xii 1924 (SING!), SFN 17640 leafy branch only, 6 xii 1924 (SING!); Bukit Sagu, *Nur* 25168, FR, 15 x 1931 (SING!); Gunung Senyum, *Evans* 13056, FB, FL, vi 1917 (SING!), *Henderson* 22218 FR, 28 vii 1929 (SING!); Jenderok Halt., Sungai Mai Estate, *Kadim & Mahmud* K.60 FR, 29 iii 1959 (SING!); Kuala Lipis, *Burkill & Haniff* SFN 15762, leafy branch only, 22 xi 1924 (SING!); Kuala Tahan, *Keng et al.* 61, FB, FL, 17 vi 1978 (SING!); Kuala Yong, *Everett* FRI 14325, FB, FL, 8 vii 1970 (SING!); Kuantan, Tanjong Pasir, *Mahamud* CF0893, FB, 28 vi 1920 (SING!); Labong Endau, *Evans* 13057, FL, FR, viii 1917 (SING!); Muazam Shah, Menchali, *Sugumaran et al.* SM211, leafy branch only, 2 v 2008 (KLU!); Pahang River, Temerloh, *Hume* 177, FR, 19 x 1983 (KLU! SING!); Pekan, *Ridley* 2169a, FL, FR, no precise date, 1891 (SING!); Raub, Batu Talau, *Burkill & Haniff* SFN 17007 leafy branch only, 14 xi 1924 (SING!), Bukit Serdam, *Chin* 1119, FB, FL, 20 vi 1971 (KLU!); Rompin, *Mohamed* FMS 14981, FB, FL, 25 vi 1929 (KEP!); Tahan River, *Mat s.n.*, FR, 15 vii 1893 (SING!), *Ridley* s.n. FB, 25 vii 1891 (SING!); Taman Negara, Kuala Tahan, *Mohd Shah & Ahmad Shukor* MS 2720, FR, 17 viii 1972 (KEP! SING!); Tasik Bera F.R., *Chan* FRI 16924, FR, 20 vii 1972 (SING!). **Penang.** *sine coll.* 3163, FR, no date (SING!); Botanic Gardens, *Hardial* 654, FR, 9 ix 1968 (SING!), *Md Noor* s.n., FB, FL, 17 vii 1918

(SING!), Lawn A *Abdul Kadir s.n.*, FB, 30 v 1933 (SING!); Govt. Hill, *Curtis* 280, FB, no date (SING!); Muka Head, *Hardial* 660, FR, 10 ix 1968 (SING!); Penang Hill, *Low & Wong* LYW 205, leafy branch only, 6 vii 2008 (KLU!), *Ridley* 9354, FB, FL, vi 1898 (SING!); Tasik Glugor, *Burkill* SFN 6543, FB, FL, 15 vi 1921 (SING!); T. Bahang, *Curtis* 280, FL, vi 1885 (SING!). **Perak.** *Ridley* 14255, FB, FL, FR, viii 1909 (SING!); *Scortechini s.n.*, FB, no date (SING!), 233a, leafy branch only, no date (SING!); Bukit Batu Suloh via Kinta, *Allen & Kadim* 488, leafy branch with inflorescence axis, 12 viii 1959 (SING!); Durian Sebatang, *King's Collector* 388, FR, viii 1880 (SING!); Gopeng, *King's Collector* 4308, FB, FL, vi 1883 (SING!); Grik, *Burkill & Haniff* SFN 13633 leafy branch only, 19 vi 1924 (SING!), SFN 13741 leafy branch only, 18 vi 1924 (SING!), *Burkill* 13841, FB, FL, 17 vi 1924 (SING!); Keledang Siong F.R., *Mohd Shah & Mahmud* MS 4006, FR, 13 vi 1978 (KEP!); Krian, Bukit Semenggol, *Sugumaran* SM 11, FR, 14 ix 2003 (KLU! SING!); Kuala Kangsar, *Ridley* 289, FB, FL, FR, no precise date, 1892 (SING!); Larut, *King's Collector* 3188, FR, viii 1882 (SING!); Matang Jambu, *Wray* 2523, FR, vii 1888 (SING!); Pangkor Island, Telok Gedong, *Burkill & Mohd Shah* HMB 288, FB, FL, 10 vii 1955 (SING!); Selama, *Henderson* SFN 35437, FB, FL, 21 v 1938 (SING!); T. Anson, Durian Sebatang, *Haniff* 15269 leafy branch only, 30 ix 1924 (SING!); Taiping, *Henderson* 10046, FB, FL, FR, 6 i 1922 (SING!), 10218, FR, 8 ix 1922 (SING!), Bukit Tegoh, *Henderson* 11617, FR, 13 xii 1923 (SING!); Taiping Hill, *Haniff* 2400, FR, 17 ii 1917 (SING!); Tapah, *Colomb.* CF 2154, FB, 7 vii 1919 (SING!), *Wray* 1285, FB, FL, no date (SING!); Ulu Bubong, *King's Collector* 10085, FB, FR, no precise date, 1886 (SING!). **Selangor.** Ampang Reserve Well, *Zainuddin* FRI 17994, FB, 1 vi 1972 (KEP!); Bukit Lagong F.R., *Chan* FRI 23951, FB, 5 v 1976 (KEP!); Damansara Road, *Ahmad* C.F. 5421, FB, 22 x 1920 (SING!); Dusun Tuah, *Ridley s.n.*, FB, v 1891 (SING!); Kepong, *Kochummen* KEP 98172, FB, 14 ii 1962 (KEP!), *Vethevelu* FRI 29653, FB, 17 iv 1981 (SING!); Kuala Lumpur, *Ahmad* 2766, FB, no precise date, 1891 (SING!), *Ridley s.n.* FB, v 1896 (SING!), *Ridley* 315, FB, 5 vi 1889 (SING!); Pantai Valley, *Kasim* 1095, FB, FL, 3 vi 1960 (KLU!); Puchong, *Carrick* J.C. 1501, FB, FL, stem bark, 15 vii 1966 (SING!); Sungai Buloh, *Hardial & Sidek* 385, FB, 17 i 1966 (SING!), *Stone* 10765, FB, stem bark, 3 vi 1972 (KLU!); Ulu Gombak, U.M. Field Study Centre, *3rd Year Students 1971 s.n.*, FB, v 1972 (KLU!), *Chin* 1022, FB, 5 v 1971 (KLU!); Ulu Selangor, *Goodenough* 10628, FB, 10 x 1899 (SING!), Gading F.R., *Chan* FRI 11236, FB, 19 vii 1969 (KEP!); University of Malaya Campus, *Stone* 7532, FB, 14 i 1968 (KLU!). **Terengganu.** Besut, Gunung Tebu, *Selvaraj* FRI 13001, FB, 6 vii 1969 (SING!);

Kemaman, Chukai, *Corner s.n.*, FB, FL, 1 ii 1932 (SING!); Kuala Terengganu, Pulau Duyung Besar, *Hume* 107, FB, FL, FR, 27 viii 1983 (KLU!); Sungai Ajil, Kampung Bukit Kolam, *Sinclair & Kiah* SFN 39854, FB, FL, 8 vii 1953 (SING!); Sungai Loh, *Cockburn* FRI 10732, FB, FL, 6 vii 1968 (KEP!); Ulu Brang, *Moysey & Kiah* SFN 33785, FB, FL, vii 1937 (SING!), Tersat, *Moysey & Kiah* SFN 33625, FB, vii 1937 (SING!); Ulu Terengganu, Sekayu, Bukit Lanjut, *Loh* FRI 13478, FR, 18 ix 1969 (SING!), Tasik Kenyir, Sungai Cicir F.R., 1 vii 2007 (SING!). SUMATRA. Asahan, Silo Maradja, Toloen Djoring, *Rahmat* 21, FR, xii 1927 (SING!); East Coast, *Yates* 1024, FR, no date (SING!); Meousola, *Batten Pooll s.n.*, FB, FL, 14 x 1939 (SING!); Riouw, Indragiri, Bovenlanden, Sungai Gangsal, *Buwalda* 6805, FB, 27 vi 1939 (SING!). THAILAND. Takuapah, *Larsen et al.* 30929, FB, FL, 13 vii 1972 (KLU!), FB (SING!); Tranj, Kwan Pra, *Rabil* 253, FR, 30 vii 1929 (SING!).

Fagraea racemosa (= *Utania racemosa*) has been confused with the related *Fagraea volubilis* (= *Utania volubilis*) in different ways. As noted by Wong & Sugau (1996), the material of *U. volubilis* in Wallich's collection in Kew contained both *U. volubilis* and *U. racemosa*, as two separate herbarium sheets with the same number "1600" that have been labelled "*F. volubilis* Jack". They noted that the sheet marked "1600.E Bencoolen" on its bottom left is to be regarded as the type of *F. volubilis* Wall. (= *U. volubilis*), whereas the other sheet marked "1600 Herb. Finl." is in fact *F. racemosa* (= *U. racemosa*) and is to be dismissed from the typification of *F. volubilis* (= *U. volubilis*). Wong & Sugau also pointed out Ridley's earlier comment (Ridley 1894) that some of Jack's specimens distributed by Wallich as from Penang could in fact have originated from Sumatra. They suggested that, as both these species occur in Penang as well as in Sumatra, there could have been some confusion of material during the distribution of Bencoolen (Sumatra) and Penang specimens, or material under "1600" could originally have been a mixed collection.

U. racemosa is a morphologically variable species in its floral as well as leaf characters but nonetheless is clearly distinguishable from the other species here. The leaf sizes are generally big, up to 30 cm long and 14 cm wide, and the shape is elliptic-ovate to elliptic-lanceolate. The typical calyx size is about 4–6 mm long. The internode length between the lowest flowering node (closest to the peduncle) and the following flowering node tends to be variable even within the same plant. All the subsequent internodes are very short so that the inflorescence at the upper part appears to be very condensed. Thus, most of the inflorescence main axis is hidden by the flower clusters and not easily visible. The first internode length expressed as a percentage of the total inflorescence rachis length measured from 15 inflorescences on a single plant growing in the University of Malaya's Rimba Ilmu Botanic Garden showed a range of 11–60%.

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

Fagraea volubilis Wall. in Roxb., Fl. Ind. 2 (1824) 36; Wong & Sugau, Sandakania 8 (1996) 40.

Type: Jack, E. Bencoolen (Herb. Wallich, sheet marked “1600. E. Bencoolen” on bottom left) (holotype K).

U. volubilis var. *volubilis*

F. racemosa var. *pauciflora* K. & G., J. As. Soc. Beng. 74 (2) (1908) 609. Lectotype (here chosen): King's Collector 1926, Perak, Larut (SING, isolectotype K).

F. pauciflora (K. & G.) Ridl., Fl. Malay. Pen. 2 (1923) 419, f. 110. Type as for *F. racemosa* var. *pauciflora*.

F. racemosa auct. non Jack ex Wall. (1824): Leenhouts, Fl. Males. I, 6 (2) (1962), pro parte.

Small tree, usually to 2–4 m (occasionally to 8 m) tall; trunk to c. 6 cm diameter; **bark** smooth to slightly fissured, grey-brown to dark brown. **Leaves** elliptic to elliptic-lanceolate; (8.5–)15–24(–26) cm long, (3.8–)6–8(–10.6) cm wide; **base** cuneate rounded; **apex** acuminate-short caudate; **margin** plane; thin coriaceous; upper and lower **surfaces** glabrous; **midrib** prominent below sunken above; **secondary veins** 5–7 pairs, upper side faint, lower side prominent; **tertiary veins** faint; leaf stalks 1–1.8(–2.2) cm long, (1.5–)2–3 mm thick, **petiolar sheaths** of a leaf pair fused and forming a shallow cup-like ochrea that loosely clasps the stem; leaf-stalk **auricles** absent. **Inflorescence** terminal, a many-flowered panicle, (3–)10–16(–22.8) cm long; **peduncle** (2–)3–5.5(–6.8) cm long, 1.5–2 mm thick; **rachis** in the distal half of the flower-bearing part of the inflorescence not conspicuously thicker than the proximal part and the peduncle, clearly visible; **branch tiers** well-spaced, (1.3–)2–2.8(–3.8) cm apart, the basal 1–2 branch tiers most branched, typically to 2–(3) orders, more distal tiers hardly so. **Flower** bisexual; **pedicel** 2–4(–5) mm long, 1.5–2 mm thick; **calyx** (from the base to the lobe apices) 4–6 mm long, glabrous, **calyx cup** 4–6(–7) mm wide, **calyx lobes** 5, spreading out from the base of the corolla tube, 3–4 mm long, 3–4 mm wide, margins glabrous; **corolla** broadly infundibular (the mouth more than 3–4 times the width of the lower narrowed part of the tube); cream to creamy-yellow; **lower subcylindrical part of the corolla tube** 7–10 mm long, 3.5–4 mm

wide, **upper flared part** of the tube slightly inflated, 8–10(–15) mm long, 12–14(–16) mm wide at the top; **corolla lobes** 5, broad-obovate to suborbicular, 6–7(–10) mm long, 5–7(–8) mm wide, overlapping to the right; **stamens** 5, inserted at the upper portion of the lower narrowed tubular part of the corolla tube or the lowermost portion of the upper flared part of the corolla tube; **filaments** 11–13 mm long, not or slightly protruding to 3 mm from the corolla mouth; **anthers** versatile, hastate, 1.8–2 mm long, 1–1.2 mm wide, each anther sac somewhat ellipsoid; **style** 17–20 mm long, not to slightly protruding to 2 mm from the corolla mouth in the open flower; **stigma** basically shallowly 2-lobed, the lobes broadly suborbicular and recurving when receptive (sometimes resembling a somewhat peltate structure 1–1.2 mm across). **Infructescence peduncle** 4–6 cm long, 1.5–2 mm thick; rachis in the distal half of the fruit-bearing part of the infructescence not conspicuously thicker than the proximal part and the peduncle, clearly visible. **Fruit** broadly ellipsoid, **apex** beaked; smooth; when mature to 11–14 mm long, 9–11 mm wide; calyx lobes spread out and do not clasp the base in dried materials. **Seeds** numerous; polygonal and frequently slightly elongated; 1–1.2 mm long, 0.5–1 mm wide; testa surface areolate; placentation axile.

The flowers are fragrant (*Burkill* 285, *Ridley* 125471, *Whitmore* 0386).

Distribution: Peninsular Malaysia, the Andaman and Nicobar Islands, Sumatra, Java, Borneo, Celebes, Maluku, Philippines and New Guinea.

Habitat: Lowland forests, including secondary forests and forest fringes.

SPECIMENS EXAMINED – PENINSULAR MALAYSIA. *Nauen* SFN 35807, FB, no precise date, 1939 (SING!). **Johor.** Gunung Panti, *Burkill* HMB 3179, FB, 23 vi 1963 (SING!); Gunung Panti Recreational Forest, *Sugumaran et al.* SM206, leafy branch only, 29 iv 2008 (KLU!), SM207, leafy branch only, 29 iv

2008 (KLU!); Tanjong Kopang, *Ridley s.n.* FR, no precise date, 1892 (SING!). **Kedah.** *Nauen* SFN 35807, FB, FL, no precise date, 1939 (SING!); Gunung Jerai, *Whitmore* FRI 386, FB, FL, 12 vi 1966 (KEP!). **Pahang.** Ulu Rompin, *Yeob* FMS 3226, FB, 16 v 1919 (SING!). **Perak.** Maxwell Hill, *Kochummen* FRI 2926, FB, 30 x 1969 (KEP!), FRI 16435, FR, 25 viii 1971 (KEP!); Waterfall Taiping, *Ridley* 14254, FB, FL, viii 1909 (SING!). **SINGAPORE.** Bukit Mandai, *Ridley* 8913, FB, FL, no precise date, 1897 (SING!); Bukit Panjan, *Ridley* 125471, FB, FL, no precise date, 1906 (SING!); Bukit Timah, *Goodenough s.n.*, FB, no precise date, 1891 (SING!), *Ridley* 12434, FB, FL, no precise date, 1906 (SING!); Kranji, *Mat s.n.*, FB, FL, no precise date, 1894 (SING!); Mandai Forest, *Burkill* 285, FL, 31 v 1914 (SING!); Nee Soon, *Maxwell* 82-184, FR, 1 vii 1982 (SING! KLU!); Nee Soon pipeline, *Dahlan* 2005-211, FB, FL, 30 v 2005 (SING!); Nee Soon swamp forest, *Maxwell* 80-178, FR, 31 vii 1980 (SING!), *Samsuri* SA 1506, FB, 29 iv 1981 (SING!); off Mandai Lake Road, *Ibrahim* AI 70, FR, 13 viii 1988 (SING!); Selitar, *Mat s.n.*, FB, no precise date, 1814 (SING!); Sungai Layang, *Ridley* 6692, FR, 1894 (SING!).

No particular specimen was indicated as type by King & Gamble (1904) for their *F. racemosa* var. *pauciflora* (later recombined by Ridley (1923) as *F. pauciflora*), although the specimens cited by them are now regarded as syntypes. Wong & Sugau (1996) correctly referred this name to the synonymy of *F. volubilis* (= *U. volubilis*) but did not lectotypify King & Gamble's name. Here, from among the syntypes of King & Gamble's name, I choose *King's Collector* 1926 (SING) as the lectotype. The long list of synonyms for *F. volubilis* (= *U. volubilis*) is treated in full by Wong & Sugau (1996).

F. volubilis var. *microcalyx* Wong & Sugau (= *U. volubilis* var. *microcalyx*, a new combination needed), Sandakania 8 (1996) 43, is not in Peninsular Malaysia. It is so far known only from Borneo and Maluku. That variety has a smaller calyx (4–5 mm long, 3.5–4.5 mm wide) than var. *volubilis*.

As mentioned by Wong & Sugau (1996), it is somewhat unfortunate that the epithet *volubilis* (Latin, twining) has to be adopted for this species that has the habit of an erect shrub or tree. They surmised that Wallich could have come up with this name due to the long infructescence in Jack's Sumatran (Bencoolen) specimen, which resembles the pendulous blooms common in garden vines.

Nomen nudum

F. malayana Mart., Nov. Gen. Sp. 2 (1826) 91.

Although Leenhouts (1962) listed this name as a synonym under his *F. racemosa*, Martius had not given any formal description of this species but mentioned it only in a note under his treatment of *Potalia resinifera* Mart. (a South American species). No specimen corresponding to this name has been located.

CHAPTER 5

CONCLUSIONS

5.1 *Fagraea*: complex genus or several genera?

Analyses of chloroplast sequence data (*trnL* intron + *trnL*-F spacer and *ndhF*) using the Maximum Parsimony and Bayesian methods consistently resolved the taxonomic sample representing *Fagraea* s.l. into four monophyletic groups. The ITS (nuclear) analysis by the same methods were also largely in agreement, except for *F. crenulata*, which resolved as a solitary branch in polytomy with three other clades. These groupings are not totally in tandem with the current classification with morphological characters into three sections, i.e., *Cyrtophyllum*, *Fagraea* and *Racemosae*. The sections *Fagraea* and *Racemosae* defined according to the concept of Leenhouts (1962) are apparently natural groupings that correspond closely with the Fagraea and Racemosa clades. However the section *Cyrtophyllum* is paraphyletic and divides into two monophyletic groups, the Elliptica and Gigantea clades.

With the expanded ITS data set (*Fagraea* s.l. + *Anthocleista*, *Potalia* and *Lisianthius*), the resulting phylogenetic tree (Fig.19) showed that the four major statistically well-supported clades (*Cyrtophyllum*, *Elliptica*, *Fagraea* and *Racemosa*) comprising *Fagraea* s.l., circumscribed monophyletic groups equivalent to those of *Anthocleista*, *Potalia* and *Lisianthius*, which are well-established New World genera of the same tribe. This lends support for considering the clades in *Fagraea* s.l. as individual genera.

In examining the possible correspondence between morphological character-states and the groups resolving in the molecular analyses, it was possible to ascribe likely

morphological synapomorphies for the four monophyletic groups in *Fagraea* s.l. The Racemosa clade is the group with most morphological synapomorphies. This group is set off from the other taxa by a distinct plant architecture, in which trunk growth is continuous and branches are plagiotropic (with distichous leaf arrangement); pendulous inflorescences; and a firm fruit wall with an epidermis that does not detach and wrinkle upon drying. This group is identifiable with the genus name *Utania* G.Don.

The *Fagraea* clade in these phylogenetic analyses is the 'true' *Fagraea* Thunb. (*sensu stricto*) as the type species for the genus, *F. ceylanica*, is included within this clade. Besides trees, this group also includes species that are epiphytic, hemi-epiphytic and scramblers, life forms that are otherwise not found in the other groups of *Fagraea* s.l. Members of *Fagraea* s.s. also produce copious creamy pale yellowish latex in the fruit epidermis and fruit wall and have ellipsoid-rounded seeds. In comparison, all the other species in *Fagraea* s.l. (including *F. crenulata*) either have no latex or produce small amounts of translucent gummy latex and have polygonal seeds. *Fagraea crenulata* is aberrant in *Fagraea* s.s. by a few more unique (as such, odd) character-states not found elsewhere in *Fagraea* s.l.: Fagerlind's architectural model, thorny bark and crenulate leaf margin; otherwise it resembles *Fagraea* s.s. taxa in having petiolar sheaths that do not or only slightly fuse at the edges and a peltate stigma structure. *Fagraea crenulata* associates basally with the *Fagraea* clade by chloroplast gene characteristics, but not in the ITS analysis. As such, this species is provisionally maintained in *Fagraea* s.s. A review with more representative sampling across to New Guinea and the southwest Pacific islands, as well as with other gene regions that could possibly offer better resolution, would probably improve our understanding of its taxonomic position.

The clear split of section *Cyrtophyllum* as defined by Leenhouts (1962) into the Gigantea and Elliptica clades may be surprising because, morphologically, these two groups tend to look similar with small flowers and much-protruding stamens and styles, and to be generally distinguishable from other groups, which generally have bigger flowers as well as less exserted stamens and styles. The only clear morphological distinction between the two clades is inflorescence position: axillary in the Gigantea clade and terminal in the Elliptica clade. Wong & Sugau (1996) 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* Reinw. ex Bl. Indeed, the earliest applicable generic names for the two groups are *Cyrtophyllum* (as explained here) and *Picrophloeus* Bl. (for the Elliptica clade, with terminal inflorescences).

In summary, *Fagraea* s.l. is morphologically too divergent to be considered as a single genus and even the sectional classification available (Leenhouts 1962) that seems to correspond to rather divergent characteristics (such as different tree architectures, inflorescence form and petiolar sheath fusion) appears to be incompletely delineated. The four monophyletic groups resolved by the molecular phylogenetic analyses presented here correspond to four separate genera, as proposed in the taxonomic framework.

5.2 Limitations of generic concepts

The molecular work in current studies was mainly based from species sampled from Peninsular Malaysia and Borneo (with the type species, *F. ceilanica*, from Sri Lanka). The two species, *F. berteriana* and *F. salticola*, distributed in New Guinea and the

south-west Pacific islands, that were included in the expanded ITS analysis, resolved within the *Fagraea* clade (= *Fagraea sensu stricto*). These species are among several from east Malesia that form a group morphologically distinguished from others in *Fagraea* s.s. by a fleshy ring on the inside of the corolla tube, at the insertion level of the stamens (Leenhouts 1962, Struwe et al. 2002). Better taxon sampling that includes more species from other parts of Malesia and the south-west Pacific islands in future molecular phylogenetic analyses, may give better resolution and confidence about clade relationships. Also, further gene regions should be explored that could bring better resolution or support for the present conclusions. Nevertheless, the proposed generic concepts are clearly applicable to Sundaland species, as these were well-represented in the present analyses.

5.3 Comparison between Borneo and Peninsular Malaysia and biogeographical insights

As suggested by Wong & Sugau (1996), *Fagraea* s.l. is undoubtedly a Malesian centered group. Out of more than 70 species present (Struwe et al. 2002), 42 species were recorded in Borneo where 24 are endemic, whereas with current results, Peninsular Malaysia has 29 species with 11 endemic species. In total both regions have 58 species in *Fagraea* s.l.

A comparison of species numbers between Borneo and Peninsular Malaysia with the new generic concepts is as follows:

- (1) *Fagraea* s.s. in Borneo has a relatively higher number of species as well as endemics (27 species, 18 endemics) than Peninsular Malaysia (19 species, 9 endemics);

- (2) *Utania* is also better represented in Borneo (7 species, 4 endemics) than in Peninsular Malaysia (6 species, 3 endemics);
- (3) *Picrophloeus* in Borneo is better represented (4 species, 3 endemics) than in Peninsular Malaysia (1 species, not endemic);
- (4) *Cyrtophyllum* is equally well represented in both Borneo and Peninsular Malaysia (3 species, 1 endemic in each case).

Borneo (743,330 sq. km) has a much larger land area than Peninsular Malaysia (131,598 sq. km), and also a more complex physiography and varied geology, factors that could be a basis for a greater extent of radiative evolution there, accounting for frequently greater species tallies and endemicities in Borneo than in Peninsular Malaysia (Wong 1998). This is in spite of Borneo being geologically younger in much of its present area above sea level (Morley 2000, Tate 2002). In a group such as *Fagraea* s.s., it could be that evolutionary processes have responded to these factors, resulting in more species and endemics in Borneo than Peninsular Malaysia. This, however, is not so clear for the other three genera, as their species tallies are more-or-less the same between the two areas. All these genera are represented across Malesia (Leenhouts 1962, as sections), so their relative evolutionary antiquity or, alternatively, the relative dispersal abilities of their ancestral forms, cannot be easily compared.

Notwithstanding generally poor resolution within each clade in the molecular analyses conducted, some finer-level biogeographical implications are possible for the *Cyrtophyllum* clade, where all four species in the genus were represented. In this clade, the widespread *C. fragrans* is the basal species and sister to *C. giganteum*, which in turn is

sister to the two endemic species, *C. wallichianum* and *C. caudatum* (Fig. 19). *C. fragrans* is distributed from Bengal and Indo-China through the Malesian region, reaching as far east to north-west New Guinea. Its basal position to the other species suggests it is ancestral to them. Of the younger species, *C. giganteum* has a Sundaland distribution (Sumatra, Malay Peninsula, Borneo), and the others are more narrowly restricted (*C. wallichianum* in Malay Peninsula, *C. caudatum* in north-west Borneo). Thus, it is possible to infer a Pleistocene or pre-Pleistocene origin for *C. giganteum*, as during the Pleistocene ice-ages, lowered sea-levels enabled land contiguity and species dispersal between the Malay Peninsula and Borneo (Morley 2000). Additionally, the more restricted *C. wallichianum* and *C. caudatum* could be postulated to have had a post-Pleistocene origin, as their origin came after *C. giganteum* and their respective endemism to Peninsular Malaysia and north-west Borneo probably represented restriction by the post-Pleistocene South China Sea.

In contrast, the most widespread and most basal species in *Cyrtophyllum*, *C. fragrans*, must have had very good dispersal abilities, in addition to a longer time during which it became distributed widely. This is likely to have been a combination of two forms, dispersal via contiguous land (such as across a Pleistocene Sundaland) and along island chains (such as along the Java-Lesser Sunda islands chain), as well as "island-hopping" (e.g., by long-distance bird dispersal of its fruits or seeds) across the Makassar Strait or across to New Guinea.

5.4 Useful characters for delimiting genera in *Fagraea* s.l.

Tree architectural attributes have some value in group delimitation in *Fagraea* s.l. Roux's model appears unique for *Utania*, Aubreville's model is only found in *Cyrtophyllum*, and Fagerlind's model is specific (so far as is known) to the aberrant *F. crenulata*. However, Scarrone's model is found in both *Picrophloeus* and *Fagraea* s.s., which otherwise are quite unrelated. Thus plant architecture, along with such attributes as branch construction and growth patterns, are only partially useful for larger-taxon delimitation.

Other morphological characters are also useful and should be given further attention in continuing work. These include whether vegetative buds are resinous and the kind of resin exudate found; the nature and fusion of the petiolar sheaths; the exsertness of stamens and styles; stigma form; fruit form and colour at maturity; the copiousness and colour of latex from fruit epidermis and fruit wall; the consistency of the fruit epidermis; and seed shape. In addition, characters noted as consistent for species groups in east Malesia that have not been thoroughly investigated (e.g. a fleshy annulus inside the corolla tube in *F. berteriana* and allies, absent in the *Fagraea* s.s. species assessed for west Malesia) should also be given attention, as inclusion of such taxa in analyses could help make critical assessments about their inclusion as a subgrouping of a genus, or otherwise.

5.5 Summary of future directions

The geographical scope for the present study is centered in Sundaland and molecular studies included only a few species that occur in the Papuan region. The

inclusion of more species from New Guinea as well as form the south-west Pacific would give better insights into species and genus relationships.

Molecular studies with the inclusion of more informative gene regions, in addition to an expanded taxon sampling of *Fagraea* s.s., *Picrophloeus* and *Utania*, could provide better resolution of species relationships within each genus. Also, the biogeographic relationships between New Guinea, Australia and the Southwest Pacific taxa with the Sundaland (west Malesian) species are as yet unclear and require further elucidation with morphological and molecular work.

The enigmatic *F. crenulata*, now provisionally placed within *Fagraea* s.s. with limited evidence, needs further evaluation. Perhaps chromosomal, phytochemical and palynological data could throw some light on the placement of the species.

With the completion of the current studies for Peninsular Malaysia and together with the work done by Wong & Sugau (1996) for Borneo, the taxonomy of *Fagraea* s.l. can be considered well-studied for much of Sundaland. Taxonomic revisions for the rest of Sundaland (Sumatra, Java), the Philippines, New Guinea and the south-west Pacific regions could now proceed on a firmer organization with the present findings.

REFERENCES

- Bentham, G. (1856) Notes on Loganiaceae. *Journal of Linnean Society of London* 1: 52–115.
- Blume, C.L. (1826) *Bijdragen tot de Flora van Nederlandsch Indië*. Lands Drukkerij, Batavia. Pp. 1020–1022.
- Blume, C.L. (1838) *Rumphia*. Vol. 2. Leiden.
- Blume, C.L. (1850) *Stirpium exoticarium novarum vel minus cognitarium ex vivis aut siccis brevis exposito et descriptio*. Lugduni-Batavorum. Pp. 163–173.
- Bureau, L.-É. (1856) *De la famille des Loganiacées, et des plantes qu'elle fournit à la médecine*. Doctoral Thesis, unpublished. Faculté de Médecine de Paris, France.
- Burkill I.H. (1936) *A Dictionary of the Economic Products of the Malay Peninsula*. Fourth print (2002). Ministry of Agriculture and Co-Operatives, Kuala Lumpur. Vol. 1: 1009–1013.
- Cammerloher, H. (1923) Die Loganiaceen und Buddleiaceten Niederländisch-Indiens. *Bulletin Jardin Botanique Buitenzorg*. Series III, 5 (4): 295–338.
- Chassot, P., S. Nemomissa, Y.-M. Yuan, P. Küpfer (2001) High paraphyly of *Swertia* L. (Gentianaceae) in the Gentianella-lineage as revealed by nuclear and chloroplast DNA sequence variation. *Plant Systematics and Evolution* 229: 1–21.
- Clarke, C.B. (1883) XCVI, Loganiaceae. In: J. D Hooker (ed.), *The Flora of British India* Vol. 4. (1885) L. Reeve & Co., London.
- Conn, B. J. & E. A. Brown (1993) Review of *Fagraea gracilipes* complex (Loganiaceae). *Telopea* 5 (2): 363–374.

- Corner, E.J.H. (1988) *Wayside Trees of Malaya*. 3rd edition. Vol. 1. Malayan Nature Society, Kuala Lumpur. Pp. 466–470.
- Craib, W.G. & A.F.G. Kerr (1951) *Florae Siamensis Enumeratio. A list of the plants known from Siam*. Vol. 3, No. 1. Siam Society, Bangkok. Pp. 54–57.
- Cunningham, C.W., K.E. Omland & T.H. Oakley (1998) Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology and Evolution* 13: 361–366.
- Curtis, C. (1894) A catalogue of the flowering plants and ferns found growing wild in the island of Penang. *J. Straits Branch, Roy. Asiatic Soc.* 25: 67–163.
- Dahlgren, R.M.T., H.T. Clifford & P.F. Yeo (1985) *The Family of the Monocotyledons; Structure, Evolution and Taxonomy*. Springer-Verlag, Berlin, Heidelberg, Germany. 520p.
- Davis, C.C., W.R. Anderson & M. J. Donogue (2001) Phylogeny of Malpighiaceae: Evidence from chloroplast *ndhF* and *trnL*–F nucleotide sequence. *American Journal of Botany* 88: 1830–1846.
- Downie, S.R. & J.D. Palmer (1992) Restriction site mapping of the chloroplast inverted repeat: a molecular phylogeny of the Asteridae. *Annals of the Missouri Botanical Garden* 79: 266–283.
- Doyle, J.J. & J.L. Doyle (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
- Elias, T.S. (1983) Extrafloral nectaries: their structure and distribution. In: B. Bentley & T. Elias (eds.), *The Biology of Nectaries*. Columbia University Press, New York. 259 p.

- Endress, P.K. (1996) *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge University Press, U.K. 511p.
- Erdtman, G. (1952) *Pollen Morphology and Plant Taxonomy. Angiosperms*. Almqvist & Wiksell, Stockholm and Chronica Botanica Co., Waltham, MA. 539p.
- Falsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Farris, J.S. (1989) The retention index and the rescaled consistency index. *Cladistics* 5: 417–419.
- Farris, J.S., M. Källersjö, A.G. Kluge & C. Bult (1994) Testing significance of incongruence. *Cladistics* 10: 315–319.
- Farris, J.S., M. Källersjö, A.G. Kluge & C. Bult (1995) Constructing a significant test of incongruence. *Systematic Biology* 44: 570–572.
- Fitch, W.M. (1971) Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* 20: 406–416.
- Fosberg, F.R. & M.-H. Sachet (1974) A new variety of *Fagraea berteriana* (Gentianaceae). *Phytologia* 28: 470–472.
- Fosberg, F.R. & M.-H. Sachet (1980) Systematic studies of Micronesian plants. *Smithsonian Contributions to Botany* 45:1–40.
- Gielly, L. & P. Taberlet (1996) A phylogeny of the European gentians inferred from chloroplast *trnL* (UAA) intron sequences. *Botanical Journal of the Linnaean Society* 120: 57–75.
- Gray, A. (1859) Notes upon some Polynesian Loganiaceae. *Proc. Amer. Acad. Arts Sci.* 4: 319–324.

- Guinet, P. (1962) Pollens d'Asie Tropicale. *Inst. Fr. Pond. Trav. Sect. Scient. Techn. V (1)*.
- Hall, T.A. (1999) Bioedit: a user-friendly biological sequence alignment editor and analyses program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.* 41: 95–98.
- Hallé, F., R.A.A. Oldeman & P.B. Tomlinson (1978) *Tropical trees and forests. An architectural analysis*. Springer-Verlag, Berlin. 411 p.
- Harrison, R.D., A. A. Hamid, T. Kenta, J. Lafrankie, H-S. Lee, H. Nagamasu, T. Nakashizuka & P. Palmiotto (2003) The diversity of hemi-epiphytic figs (*Ficus*; Moraceae) in the Bornean lowland rain forest. *Biological Journal of the Linnean Society* 78: 439–455.
- Henderson, M.R. (1933) *Additions to the Flora of the Malay Peninsula*. Gardens' Bull. Straits Settlements 7 (2): 113–115.
- Hodgkison, R., S.T. Balding, A. Zubaid & T.H. Kunz (2003) Seed dispersal by fruit bats (Chiroptera: Pteropodidae), in the Malaysian lowland rain forest. *Biotropica* 35: 491–502.
- Holmes, E.M. (1892) Malay materia medica. *Bulletin of Pharmacy* 6 (3): 108–117.
- Holtum, R.E. (1936) The flowering of Tembusu Trees (*Fagraea fragrans* Roxb.) in Singapore, 1928–1935. *Malayan Forester* 5: 100–105.
- Hooker, J.D. (1885) *The Flora of British India*. Vol. 4. L. Reeve & Co., London. Pp. 82–85.
- Huelsenback, J.P. & F. Ronquist (2001) MrBayes: bayesian inference of phylogenetic trees. *Biometrics* 17: 754–755.

- Huelsenbeck, J.P., F. Ronquist & B. Hall (2001) MrBayes: A program for the Bayesian of phylogeny (Instruction Manual). <http://golab.unl.edu/teaching/SBseminar/manual.pdf> Assessed September 25, 2009.
- Hutchinson, J. (1973) *The families of flowering plants*. 3rd. edition. Clarendon Press, Oxford.
- Jack, W. (1822) *Descriptions of Malayan Plants. Malayan Miscellanies*. Vol. 2 No. 7. Sumatran Mission Press, Bencoolen. Pp. i–iii, 81–82.
- Jensen, S.R. (1992) Systematic implications of the distribution of iridoids and other chemical compounds in the Loganiaceae and other families of the Asteridae. *Annals of the Missouri Botanical Garden* 79: 284–302.
- Jensen, S.R. & E. Smets (1998) Vestures pits in some woody Gentianaceae. *IAWA Journal* 19 (1): 35–42.
- Jensen, S.R. & J. Schripsema (2002) Chemotaxonomy and pharmacology of Gentianaceae. In: L. Struwe & V.A. Albert (eds.), *Gentianaceae—systematics and natural history*. Cambridge University Press, Cambridge, UK. Pp. 573–631.
- Jussieu, A.L. de (1789) *Genera plantarum, secundum ordines naturales disposita, juxta methodum in Horto regio parisiensi exaratam, anno M.DCC.LXXIV*. Herissant, Paris.
- Kauff, F. & F. Lutzoni (2002) Phylogeny of the Gyalectales and Ostropales (Ascomycota, Fungi): among and within other order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* 25: 138–156.

- King, G. & J. S. Gamble (1904) *Materials for a Flora of the Malayan Peninsula*. Baptist Mission Press, Calcutta. Pp. 813–822.
- Kluge A.G. & J. S. Farris (1969) Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18: 1–32.
- Kochummen, K.M. (1973) Loganiaceae. In: T.C. Whitmore (ed.), *Tree Flora of Malaya*. Vol. 2. Longman Malaysia, Kuala Lumpur. Pp. 296–275.
- Kojs, P. (2006) Successful history of Singapore Botanic Gardens. *Bulletin of Botanical Gardens* 15: 45–52.
- Larget, B. & L. Simon (1999) Markov chain Monte Carlo algorithms in the Bayesian analyses of phylogenetic trees. *Molecular Biology and Evolution* 16: 750–759.
- Larkin, M.A., G. Blackshields, N.P. Brown, R. Chenna, P.A. McGettigan, H. McWilliam, F. Valentin, I.M. Wallace, A. Wilm, R. Lopez, J.D. Thompson, T.J. Gibson & D.G. Higgins (2007) Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947–2948.
- Leenhouts, P.W. (1962) Loganiaceae. In: C.G.G.J. van Steenis (ed.), *Flora Malesiana*. Series 1 Vol. 6. Wolters-Noordhoff Publishing, Groningen. Pp. 293–336.
- Leenhouts, P.W. (1984) A new *Fagraea* from Borneo (Loganiaceae). *Blumea* 29: 423–424.
- Leeuwenberg, A.J.M. & P.W. Leenhouts (1980) Taxonomy. In: A.J.M. Leeuwenberg (ed.), *Engler and Prantl's Die natürlichen Pflanzenfamilien, Angiospermae. Ordnung Gentianales, Fam. Loganiaceae*. Vol. 28b (1). Duncker & Humblot, Berlin. Pp. 8–96.

- Lewis, P.O. (2001) Phylogenetic systematics turns over a new leaf. *Trends in Ecology and Evolution* 16: 30–37.
- Macmillan H. F. (1991) *Tropical Planting and Gardening*. Sixth edition. Malayan Nature Society, Kuala Lumpur. Pp. 115 & 265.
- Malaysian Timber Council (2006) MTC Wood Wizard: Tembusu. <http://woodwizard.mtc.com.my:8888/>.
- Mennega, A.M.W. (1980) Anatomy of the secondary xylem. In: P. Heipko & H. Melchior (eds.), *Die natürlichen Pflanzenfamilien (2 Aufl.) 28bI*. Duncker & Humblot, Berlin. Pp. 112–161.
- Merrill, E.D. (1917) Alabastra Borneensis. *J. Straits Branch, Roy. Asiatic Soc.* 77: 231–237.
- Miquel, F. A. W. (1857) *Flora van Nederlandsch-Indië*. Vol. 2. Amsterdam, Netherlands.
- Molina, J. & L. Struwe (2009) Utility of secondary structure in phylogenetic reconstruction using nrDNA ITS sequences – an example from *Potalieae* (Gentianaceae: Asteridae). *Systematic Botany* 34 (2): 414–428.
- Momose, K., T. Yumoto, T. Nagamitsu, M. Kato, H. Nagamasu, S. Sakai, R. D. Harrison, T. Itioka, A. A. Hamid & T. Inoue (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85: 1477–1501.
- Morley, R.J. (2000) *Origin and Evolution of Tropical Rain Forests*. Wiley, Chichester. 362p.

- Motley T.J. (2004) The ethnobotany of *Fagraea* Thunb. (Gentianaceae): The Timber of Malesia and the scent of Polynesia. *Economic Botany* 58 (3): 396–409.
- Nilsson, S. (2002) Gentianaceae: a review of palynology. In: L. Struwe & V.A. Albert (eds.), *Gentianaceae—systematics and natural history*. Cambridge University Press, Cambridge, U.K. Pp. 377–497.
- Nylander, J.A.A. (2004) MrModeltest 2.2. Evolutionary Biology Centre, Uppsala University. Software programme distributed by the author.
- Olmstead, R.G., B. Bremer, K.M. Scott & J.D. Palmer (1993) A parsimony analysis of the *Asteridae* sensu lato based on *rbcL* sequences. *Annals of the Missouri Botanical Garden* 80: 700–722.
- Perry, L.M. (1980) *Medicinal plants of East and Southeast Asia*. The MIT Press, Cambridge.
- Peters, C.M. (1995) Tembusu (*Fagraea fragrans Roxb.*): *Utilization and management in the Denau Sentarum Wildlife Reserve*. Asian Wetland Bureau, Bogor, Indonesia.
- Punt, W. & P.W. Leenhouts (1967) Pollen morphology and taxonomy in the Loganiaceae. *Grana Palynol.* 7: 496–516.
- Punt, W. (1978) Evolutionary trends in the Potalieae (Loganiaceae). *Rev. Palaeobot. Palynol.* 26: 313–355.
- Putz, F.E. & N.M. Holbrook (1986) Notes on the natural history of hemi-epiphytes. *Selbyana* 9: 61–69.
- Putz, F.E. & N.M. Holbrook (1989) Strangler fig rooting habits and nutrient relations in the Llanos of Venezuela. *American Journal of Botany* 76 (6): 781–788.

Qiagen Sample & Assay Technologies (2003–2009) Handbook for DNA extraction.

<http://www1.qiagen.com/>.

Quisumbing, E. (1978) *Medicinal plants of the Phillipines*. Katha Publishing Co., Inc., Philippines.

Ranker, T.A., J.M.O. Geiger, S.C. Kennedy, A.R. Smith, C.H. Haufler & B.S. Parris (2003) Molecular phylogenetics and evolution of the endemic Hawaiian genus *Adenophorus* (Grammitidaceae). *Molecular Phylogenetics and Evolution* 26: 337–347.

Rannala, B. & Z. Yang (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *Journal of Molecular Evolution* 43: 304–311.

Rao, A.N. & Y.K. Lee. (1970) Studies on Singapore pollen. *Pacific Sci.* 24: 255–268.

Ridley, H.N. (1908) New and Rare Malayan Plants. *J. Straits Branch, Roy. Asiatic Soc.* 50: 117–123.

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. L. Reeve & Co., London. Pp. 415–422.

Ridley, H.N. (1930) *The Dispersal of Plants Throughout the World*. Reeve & Co. Ashford, Kent, England. 744 p.

Roxburgh, W. (1824) *Flora Indica or Descriptions of Indian Plants*. Vol. 2. Mission Press, Serampore. Pp. 31–37.

- Sealy, J. R. (1957) The Roxburgh Flora Indica Drawings at Kew. *Kew Bulletin* 11: 297–399.
- Shono, K., S. J. Davies & Y. K. Chua (2007) Performance of 45 native tree species on degraded lands in Singapore. *Journal of Tropical Forest Science* 19 (1): 25–34.
- Smith, A. C. (1988) Loganiaceae. In *Flora Vitiensis Nova* Vol. 4. Pacific Tropical Botanical Garden, Hawaii. Pp. 5–43.
- Solereder, H. (1892) Loganiaceae. In: A. Engler & K. Prantl (eds.), *Die natürlichen Pflanzenfamilien*. Vol. 4 No. 2. Engelmann, Leipzig, Germany. Pp. 1–50.
- Struwe, L., V.A. Albert & B. Bremer (1994) Cladistics and family level classification of Gentianales. *Cladistics* 10: 175–206.
- Struwe, L. & V.A. Albert (1997) Floristics, cladistics and classification: three case studies in Gentianales. In: J. Dransfield, M.J.E. Coode & D.A. Simpson (eds.), *Plant Diversity in Malesia, III*. Royal Botanic Gardens, Kew. Pp. 321–352.
- Struwe, L., J. Kadereit, J. Klackenberg, S. Nilsson, M. Thiv, K.B. von Hagen & V.A. Albert (2002) Systematics, character evolution and biogeography of Gentianaceae, including a new tribal and subtribal classification. In: L. Struwe & V.A. Albert (eds.), *Gentianaceae—systematics and natural history*. Cambridge University Press, Cambridge, U.K. Pp. 21–309.
- Struwe, L. & V. A. Albert (2004) Monograph of neotropical *Potalia* (Gentianaceae: Potalieae). *Systematic Botany* 29: 670–701.
- Swofford, D.L. (2001) *PAUP**: *Phylogenetic analyses using parsimony and other methods, version 4.0*. Sinauer Associates, Sunderland, Massachusetts.

- Taberlet, P., L. Gielly, G. Pautou & J. Bouvet (1991) Universal primers for amplification of the three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Takhtajan, A. (1987) *Systema Magnoliophytorum*. Nauka, Leningrad.
- Tate, R.B. (2002) *Geological map of Borneo*. Geological Society of Malaysia.
- Thiv, M., L. Struwe & J.W. Kaderiet (1999) The phylogenetic relationships and evolution on the Canarian laurel forest endemic *Ixanthus viscosus* (Aiton) Griseb. (Gentianaceae): evidence from matK and ITS sequences, and floral morphology and anatomy. *Plant Systematics and Evolution* 218: 299–317.
- Thunberg, C.P. (1782) Beskrifning pa et nytt och vackert orte Genus, Kalladt *Fagraea ceilanica*. *Kongl. Vetenskamps Acad. nya Handlingar Stockh.* 3: 132-134, tab. IV.
- von Hagen, K.B. & J.W. Kadereit (2001) The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the Southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. *Organisms Diversity and Evolution* 1: 61–79.
- von Martius, C.F.P. (1826–1827) *Nova genera et species plantarum quas in itinere per Brasiliam*. Vol. 2. V. Wolf, München.
- Watson J.G. (1935) Tembusu. *Malayan Forester* 4: 136–137.
- White, T.J., T. Burns, S. Lee & J. Taylor (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: M.A. Innis, D.H. Gelfand, J.J. Sninsky & T.J. White (eds.), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, San Diego, pp. 315–322.

- Wong, K.M., L.G. Saw & K.M. Kochummen (1987) Some new and interesting plant species from Ulu Endau, Johore, Malaysia. *Malayan Nature Journal* 41: 267–273.
- Wong, K.M. & J.B. Sugau (1996) A revision of *Fagraea* (Loganiaceae) in Borneo, with notes on related Malesian species and 21 new species. *Sandakania* 8: 1–93.
- Wong, K.M. (1998) Patterns of plant endemism and rarity in Borneo and the Malay Peninsula. In: C.-I. Peng & P.P. Lowry (eds.), *Rare, Threatened and Endangered Floras of Asia and the Pacific Rim*. Institute of Botany, Academia Sinica Monograph Series No. 16. Pp. 139–169.
- Wong, K.M. (2004) *Bungarimba* (Rubiaceae), a new genus distinguished from *Porterandia* and other allies. *Sandakania* 15: 25–54.
- Yuan, Y.-M. & P. Küpfer (1995) Molecular phylogenetics of the subtribe Gentianinae (Gentianaceae) inferred from the sequences of the internal transcribed spacer (ITS) of nuclear ribosomal DNA. *Plant Systematics and Evolution* 196: 206–226.
- Yuan, Y.-M., P. Küpfer & J.J. Doyle (1996) Infrageneric phylogeny of the genus *Gentiana* (Gentianaceae) inferred from nucleotide sequences of the internal transcribed spacer (ITS) of nuclear ribosomal DNA. *American Journal of Botany* 83: 641–652.
- Yuan, Y.-M. & P. Küpfer (1997) The monophyly and rapid evolution of *Gentiana* sect. *Chondrophyllae* Bunge s.l (Gentianaceae): evidence from the nucleotide sequences of the internal transcribed spacer of nuclear ribosomal DNA. *Botanical Journal of the Linnaean Society* 123: 25–43.

- Yuan, Y.-M., S. Wolhauser, M. Möller, P. Chassot, G. Mansion, J. Grant, P. Küpfer & J. Klackenberg (2003) Monophyly and relationships of the tribe Exaceae (Gentianaceae) inferred from nuclear ribosomal and chloroplast DNA sequences. *Molecular Phylogenetics and Evolution* 28: 500–517.
- Zahid, M.S. & K.M. Wong (2004) Tree architecture in *Porterandia* (Rubiaceae) from Borneo and Sulawesi. *Sandakania* 15: 79–91.
- Zimmerman, J. (1932) Über die extrafloralen nektarien der Angiospermen. *Bot. Cent. Beih.* 49: 99–196.

APPENDICES

Appendix 1

CTAB DNA extraction protocol for both silica dried and herbarium quality material (modified from Doyle & Doyle 1987).

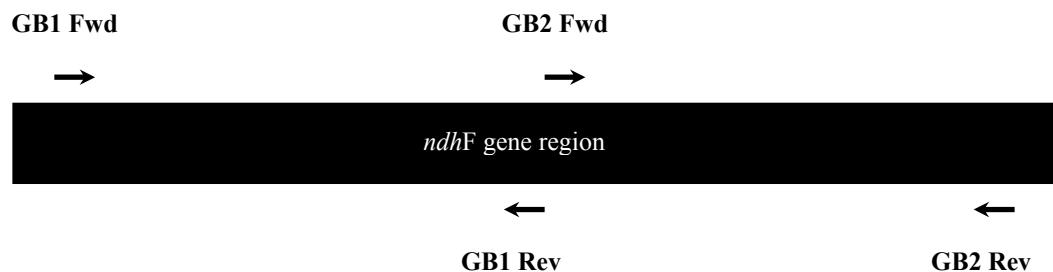
Extraction buffer

100 mM Tris-HCl
1.4 M NaCl
20 mM EDTA
2% (wt/vol) CTAB
0.4% (vol/vol) β -mercaptoethanol
1% (wt/vol) PVP 360,000
Buffer finally adjusted to pH 8.0

1. Grind 0.1g fresh or 0.02g dried frond material with 500 μ L extraction buffer and incubate in 50–65 °C for 15–30 minutes (Retain samples on ice until placing them into the hot water bath).
2. Add 500 μ L of Sevag (24:1 chloroform : isoamyl alcohol) and shake tube for 10–20 minutes or vortex on a low setting. Then centrifuge tubes for 10 minutes @ 15, 000 x g and transfer aqueous layer (a.k.a. supernatant) to a fresh tube.
3. Precipitate the DNA by adding an equal volume of cold isopropanol and 0.5 volumes of 5 M NaCl to the supernatant and let sit at room temperature for 30 minutes.
4. Recover DNA by centrifugation @ 15, 000 x g for 20 minutes. Retain pellet and discard aqueous layer.
5. Wash pellet with 700 μ L 70% cold ethanol and centrifuge at maximum speed for 5 minutes.
6. Suspend pellet in 180 μ L TE (pH 8.0) and add 2 μ L of 1 mg/mL Rnase and incubate in 37 °C for 30 min.
7. Add cold 7.5 M NH₄O aqueous to reach a final concentration of 2.5 M (this is 60.6 μ L).
8. Add two volumes of 95–100% ethanol and put in the freezer (-20 °C) overnight or in the deep freezer (-80 degrees C) for 1 hour.
9. Recover DNA by centrifuging tubes with maximum speed for 20 minutes.
10. Wash pellet with 700 μ L of 70% ethanol and centrifuge for 10 minutes.
11. Dry off excess ethanol in the lamina flow.
12. Resuspend in ddH₂O (20–50 μ L). Allow to resuspend for 1 hour at 55 °C or overnight in the fridge.

Appendix 2

Approximate positions of the two primer sets used for amplifying the partial *ndhF* gene region.



Appendix 3

Sequences of primers used in PCR for amplifying ITS, *trnL* intron, *trnL*–F spacer and *ndhF* regions.

PCR Amplified Regions	Primer Names	Sequences (5' — 3')	Approximate Size of Amplification in PCR	Source
ITS	ITS 1	TCC GTA GGT GAA CCT GCG G	700–750 bp	White et al. 1990
	ITS 4	TCC TCC GCT TAT TGA TAT GC		
<i>trnL</i> intron	'C'	CGA AAT CGG TAG ACG CTA CG	300–400 bp	Taberlet et al. 1991
	'D'	GGG GAT AGA GGG ACT TGA AC		
<i>trnL</i> –F spacer	'E'	GGT TCA AGT CCC TCT ATC CC	300–400 bp	Taberlet et al. 1991
	'F'	ATT TGA ACT GGT GAC ACG AG		
<i>ndhF</i>	GB 1 Fwd	CTT TCA TTC CAC TTC CAG TTC CT	900–1000 bp	In this study
	GB 1 Rev	TAT AGG GTG AAT AGC CAA GAA GCC		
	GB 2 Fwd	AAA GCC AAA ATA TGG TTC TTA TGG G	900–1000 bp	In this study
	GB 2 Rev	AAA TAA ATA GAA GAA AAT ATA AGA AGA AAT GCG		

Appendix 4

The aligned ITS data matrix (30 taxa).

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F_OBLONGA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_GARDENIOIDES TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_RIDLEYI TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_CRASSIFOLIA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_SP_1 TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_SPLENDENS TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_AURICULATA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCGGG ACCGGCGCC
F_IMPERIALIS TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGTC
F_RESINOSA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGTC
F_CARNOSA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_STONEI TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_CAMERONENSIS TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_FRASERENSIS TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_RENAE TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_CURTISII TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_BELUKAR TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_ELLIPTICA_1 TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_ELLIPTICA_2 TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_COLLINEA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_RACEMOSA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_NERVOSA TCGAATCTG CGAACAGAC GACCCGTGAA CATGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_CUSPIDATA TCGAATCTG CGAACAGAC GACCCGTGAA CATGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_SP_2 TCGAATCTG CGAACAGAC GACCCGTGAA CATGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_SPICATA TCGAATCTG CGAACAGAC GACCCGTGAA CATGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_FRAGRANS TCGAATCTG CGA-GCAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GGAACCTGGG ACCGGCGCC
F_GIGANTEA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGAAAGTGG GGAACCGGG ACCGGCGCC
F_WALLICHIANA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGAAAGGG GGAACCGGG ACCGGCGCC
F_CAUDATA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
F_CRENULATA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGT CGGGACGTGG GAAACCGGG ACCGGCGCC
A_GRANDIFLORA TCGAATCTG CGAACAGAC GACCCGTGAA CTTGTTAAC CCACGGCGC CGGGACGTGG GAAACCGGG ACCGGCGCC

F_OBLONGA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_GARDENIOIDES CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_RIDLEYI CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_CRASSIFOLIA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_SP_1 CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_SPLENDENS CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_AURICULATA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_IMPERIALIS CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_RESINOSA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_CARNOSA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_STONEI CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_CAMERONENSIS CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_FRASERENSIS CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
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F_CURTISII CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_BELUKAR CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_ELLIPTICA_1 CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_ELLIPTICA_2 CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_COLLINEA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_RACEMOSA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_NERVOSA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_CUSPIDATA CACGCACCGC GTCGGCCATT GTTCGCTCGT CGGGCGAGAA ACTAAACCCG GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_SP_2 TGTGACCGGC ATCGGCCATT GGTCGATCGT CGGGCGAGAA ATTAACCCC GGCGCAGAAA AGGCCAAGG AAAACGAGAA
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F_WALLICHIANA CGCGCACCGC GTCGGCCATT GGTCGATCGT CGGGCGAGAA ATTAACCCC GGCGCAGAAA AGGCCAAGG AAAACGAGAA
F_CAUDATA CGCGCACCGC GTCGGCCATT GGTCGATCGT CGGGCGAGAA ATTAACCCC GGCGCAGAAA AGGCCAAGG AAAACGAGAA
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A_GRANDIFLORA CGCGCACCGC GTCGGCCATT GGTCGATCGT CGGGCGAGAA ATTAACCCC GGCGCAGAAA AGGCCAAGG AAAACGAGAA

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F_GARDENIOIDES AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_RIDLEYI AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_CRASSIFOLIA AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_SP_1 AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_SPLENDENS AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_AURICULATA AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
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F_RESINOSA AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_CARNOSA AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_STONEI AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_CAMERONENSIS AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_FRASERENSIS AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_RENAE AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_CURTISII AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_BELUKAR AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC
F_ELLIPTICA_1 AAGGATGGCC TGCCCTCTGA CGCCCCGTAC CGGGTGTGCA CGAGGGGAGC ACAGGCACCT GTACAAAAGT AAAACGACTC

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Appendix 5

The aligned *trnL*–F data matrix (30 taxa).

F_NERVOSA GAGGAAAAGC CTATTTTACT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_RACEMOSA GAGGAAAAGC CTATTTTACT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_SPICATA GAGGAAAAGC CTATTTTACT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_BELUKAR GAGGAAAAGC CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_WALLICHIANA GAGGAAAAGC CTATTTTACT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_CRENULATA GAGGAAAAGC CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_FRASERENSIS GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_SPLENDENS GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_SP_1 GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_CARNOSA GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_OBONGA GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_CAMERONENSIS GAGGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_RENAE GAAGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_STONEI GAAGAAAAGA -TTTTTATT TCCCCGCCCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
F_RIDLEYI GAGGAAAAGT CTATTTTATT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC
A_GRANDIFLORA GAGG----- TACT TCCCCGACCT TTTTGCCAT CCCCTTTTG TTAGAGGTG AAAATTCTG ATGCATCCGC

F_RESINOSA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA TTTTAGAAAG AGATCTGGC AGAAATGCC TTCTCTTATT
F_IMPERIALIS CCT----AT ATTCTATTG ATT---CGT TTAGTTTA TTTTAGAAAG AGATCTGGC AGAAATGCC TTCTCTTATT
F_AURICULATA CCT----AT ATTCTATTG ATT---CGT TTAGTTTA TTTTAGAAAG AGATCTGGC AGAAATGCC TTCTCTTATT
F_CAUDATA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA TTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_GARDENIOIDES CCTATTCTAT ATTCTATTG ATT---CAT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_ELLIPTICA_1 CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_ELLIPTICA_2 CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_CURTISII CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
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F_SP_2 CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_NERVOSA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
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F_SPICATA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_BELUKAR CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
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F_SP_1 CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_CARNOSA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_OBONGA CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_CAMERONENSIS CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_RENAE CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT
F_STONEI CCTATTCTAT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGACATGCC TTCTCTTATT
F_RIDLEYI CCTATTCTCT ATTCTATTG ATT---CGT TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGACT TTCTCTTATT
A_GRANDIFLORA CC-----T ATTCTATTG ATTGATTG TTAGTTTA GTTTAGAAAT AGATCTGGC AGAAATGCC TTCTCTTATT

F_RESINOSA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_IMPERIALIS A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CGTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_AURICULATA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTAAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_CAUDATA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_GARDENIOIDES A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_ELLIPTICA_1 A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_ELLIPTICA_2 A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_CURTISII A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_CRASSIFOLIA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_GIGANTEA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_COLLINA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_CUSPIDATA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GATCTCGAAT
F_FAGRANS A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_SP_2 A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_NERVOSA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_RACEMOSA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_SPICATA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GATCTCGAAT
F_BELUKAR A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_WALLICHIANA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCGAAT
F_CRENULATA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_FRASERENSIS A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_SPLENDENS A-CATGTTAT --ATATA-----
F_SP_1 A-CATGTTAT ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_CARNOSA A-CATGTTAT --ATATATGA TAATATATAC AAATGAACAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_OBONGA ATCATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT GAACCTGAAC GACCTCAAAT
F_CAMERONENSIS A-CATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_RENAE A-CATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_STONEI A-CATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
F_RIDLEYI A-CATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT
A_GRANDIFLORA A-CATGTTAT --ATATATGA TAATATATAC AAATGAGCAT CTTTGAGAAA AACCCCATTT G-----AAC GACCTCAAAT

F_RESINOSA CGATATCATC CCTCATACTG AAATAAAAA A-----AAAA TG----- ----- --AATACCA AGAGCTTCTA
F_IMPERIALIS CGATATCATC CCTCATACTG AAATAAAAA -----AAAT TT----- ----- --AATACCA AGAGCTTCTA
F_AURICULATA CGATATCATC CCTCATACTG ATACTGAAAT AAAA-----TT----- ----- --AATACCA AGAGCTTCTA
F_CAUDATA CGATATCATC CCTCATACTG ----- -----AAAT TG-----AAAAA GTTTTT----- --AAGACCA AGAGTTTCCA
F_GARDENIOIDES CGATATCATC CCTCATACTG ----- -----AAAT TT-----AAAAA GTTTTTACT TTAATACCA AGAGCTTCTA
F_ELLIPTICA_1 CGATATCATC CCTCATACTG ----- -----AAAT TG-----AAAAA GTTTTT----- --AATACCA AGAGCTTCTA
F_ELLIPTICA_2 CGATATCATC CCTCATACTG ----- -----AAAT TT-----AAAAA GTTTTT----- --AATACCA AGAGCTTCTA
F_CURTISII CGATATCATC CCTCATACTG ----- -----AAAT TT-----AAAAA GTTTTTGATT TTAATACCA AGAGCTTCTA
F_CRASSIFOLIA CGATATCATC CCTCATACTG ----- -----AAAT TT-----AAAAA GTTTTGATT TTAATACCA AGAGCTTCTA

F_GIGANTEA CGATATCATT CCTCATACTG ----- AAAT TG-AAAAA- GTTTTT-- --AACACCA AGAGTTTCA
 F_COLLINA CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AATACCA AGAGCTTCA
 F_CUSPIDATA CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_FRAGRANS CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_SP_2 CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_NERVOZA CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_RACEMOSA C-----T CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_SPICATA CGATATCATT CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_BELUKAR CGATATCATC CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AATACCA AGAGCTTCA
 F_WALLICHIANA CGATATCATT CCTCATACTG ----- AAAT TG-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_CRENULATA CGATATCATC CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_FRASERENSIS CGATATCATC CCTCATACTG ----- AAAT TT-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_SPLENDENS ----- ----- ----- ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_SP_1 CGATATCATC CCTCATACTG ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_CARNOSA CGATATCATC CCTCATACTG ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_OBLONGA CGATATCATC CCTCATACTG ----- AAAT TAAAAAAAC GTTTTT-- --AACACCA AGAGCTTCA
 F_CAMERONENSIS CGATATCATG CCTCATACTG ----- AAAT TA-AAAAA- GTTTTTTATT TTAATACCA AGAGCTTCA
 F_RENAE CGATATCATC CCTCATACTG ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_STONEI CGATATCATC CCTCATACTG ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 F_RIDLEYI CGATATCATC CCTCATACTG ----- AAAT TA-AAAAA- GTTTTT-- --AACACCA AGAGCTTCA
 A_GRANDIFLORA CGGTATCATT CCTCATACTG ----- AAAT TG-AAAAA- GTTTTT-- --AACACCA AGGGCTTCA

 F_RESINOSA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAGAT TAGGGTATA
 F_IMPERIALIS GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT TAGGGTATA
 F_AURICULATA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT GAAGATGATA
 F_CAUDATA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT GAAGATGATA
 F_GARDENIOIDES GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT TAGGGTATA
 F_ELLIPTICA_1 GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT TAGGGTATA
 F_ELLIPTICA_2 GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT GAGGTGATA
 F_CURTISII GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTAATAAAAT GAGGTGATA
 F_CRASSIFOLIA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_GIGANTEA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_COLLINA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_CUSPIDATA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_FRAGRANS GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_SP_2 GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_NERVOZA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_RACEMOSA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_SPICATA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAAGATGATA
 F_BELUKAR GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_WALLICHIANA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_CRENULATA GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_FRASERENSIS GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_SPLENDENS GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_SP_1 GGACCTAGAT AAAACTTGTG AATCTCTTT CGTACTGTTA ATTGACAAG ACCCGTTCT CTCATAAAAT GAGGTGATA
 F_CARNOSA CATTGGGACT G
 F_OBLONGA CATTGGGACT G
 F_AURICULATA CATTGGGACT G
 F_CAUDATA CATTGGGACT G
 F_GARDENIOIDES CATTGGGACT G
 F_ELLIPTICA_1 CATTGGGACT G
 F_ELLIPTICA_2 CATTGGGACT G
 F_CURTISII CATTGGGACT G
 F_CRASSIFOLIA CATTGGGACT G
 F_GIGANTEA CATTGGGACT G
 F_COLLINA CATTGGGACT G
 F_CUSPIDATA CATTGGGACT G
 F_FRAGRANS CATTGGGACT G
 F_SP_2 CATTGGGACT G
 F_NERVOZA CATTGGGACT G
 F_RACEMOSA CATTGGGACT G
 F_SPICATA CATTGGGACT G
 F_BELUKAR CATTGGGACT G
 F_WALLICHIANA CATTGGGACT G
 F_CRENULATA CATTGGGACT G
 F_FRASERENSIS CATTGGGACT G
 F_SPLENDENS CATTGGGACT G
 F_SP_1 CATTGGGACT G
 F_CARNOSA CATTGGGACT G
 F_OBLONGA CATTGGGACT G
 F_CAMERONENSIS CATTGGGACT G
 F_RENAE CATTGGG-CT G
 F_STONEI CATTGGGACT G
 F_RIDLEYI CATTGGGACT G
 A_GRANDIFLORA CATTGGGACT G

Appendix 6

The aligned *ndhF* data matrix (30 taxa).

F_CARNOSA
F_RENAE
F_SP_1
F_RIDLEYI
F_OBLONGA
F_AURICULATA
F_IMPERIALIS
F_RESINOSA
F_GARDENIOIDES
F_CRENULATA
F_BELUKAR
F_CURTISII
F_CRASSIFOLIA
F_CAMERONENSIS
F_ELLIPTICA_2
F_STONEI
F_COLLINA
F_ELLIPTICA_1

A_GRANDIFLORA
F_NERVOSA
F_RACEMOSA
F_SPICATA
F_CUSPIDATA
F_SP_2
F_GIGANTEA
F_CAUDATA
F_WALLICHIANA
F_FRAGRANS
F_FRAZERENSIS
F_SPLENDENS
F_CARNOSA
F_RENAE
F_SP_1
F_RIDLEYI
F_OBLONGA
F_AURICULATA
F_IMPERIALIS
F_RESINOSA
F_GARDENIOIDES
F_CRENULATA
F_BELUKAR
F_CURTISII
F_CRASSIFOLIA
F_CAMERONENSIS
F_ELLIPTICA_2
F_STONEI
F_COLLINA
F_ELLIPTICA_1

A_GRANDIFLORA
F_NERVOSA
F_RACEMOSA
F_SPICATA
F_CUSPIDATA
F_SP_2
F_GIGANTEA
F_CAUDATA
F_WALLICHIANA
F_FRAGRANS
F_FRAZERENSIS
F_SPLENDENS
F_CARNOSA
F_RENAE
F_SP_1
F_RIDLEYI
F_OBLONGA
F_AURICULATA
F_IMPERIALIS
F_RESINOSA
F_GARDENIOIDES
F_CRENULATA
F_BELUKAR
F_CURTISII
F_CRASSIFOLIA
F_CAMERONENSIS
F_ELLIPTICA_2
F_STONEI
F_COLLINA
F_ELLIPTICA_1

A_GRANDIFLORA
F_NERVOSA
F_RACEMOSA
F_SPICATA
F_CUSPIDATA
F_SP_2
F_GIGANTEA
F_CAUDATA
F_WALLICHIANA
F_FRAGRANS
F_FRAZERENSIS
F_SPLENDENS
F_CARNOSA
F_RENAE
F_SP_1
F_RIDLEYI
F_OBLONGA
F_AURICULATA
F_IMPERIALIS
F_RESINOSA
F_GARDENIOIDES
F_CRENULATA
F_BELUKAR
F_CURTISII
F_CRASSIFOLIA
F_CAMERONENSIS
F_ELLIPTICA_2
F_STONEI
F_COLLINA
F_ELLIPTICA_1

A_GRANDIFLORA
F_NERVOSA
F_RACEMOSA
F_SPICATA
F_CUSPIDATA
F_SP_2
F_GIGANTEA
F_CAUDATA
F_WALLICHIANA
F_FRAGRANS
F_FRAZERENSIS
F_SPLENDENS
F_CARNOSA
F_RENAE
F_SP_1
F_RIDLEYI
F_OBLONGA
F_AURICULATA
F_IMPERIALIS
F_RESINOSA
F_GARDENIOIDES
F_CRENULATA
F_BELUKAR
F_CURTISII
F_CRASSIFOLIA
F_CAMERONENSIS
F_ELLIPTICA_2
F_STONEI
F_COLLINA
F_ELLIPTICA_1

A_GRANDIFLORA
F_NERVOSA
F_RACEMOSA
F_SPICATA
F_CUSPIDATA
F_SP_2
F_GIGANTEA

F_IMPERIALIS TGGAGTTTTT TCCGGTAGTT TATCTTAATT CGGAATACTT CTAGGCTTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_RESINOSA TGCAGTTTT TCCGGTAGTT TATCTTAGTT CGGAATAATT CTAGGCTTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_GARDENIOIDES TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_CRENULATA TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_BELUKAR TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_CURTISII TGGAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT CTAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_CRASSIFOLIA TGGAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT CTAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_CAMERONENSIS TGGAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT CTAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_ELLIPTICA_2 TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_STONEI TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT CTAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_COLLINA TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA
F_ELLIPTICA_1 TGCAGTTTT TCCGGTAGTT TATCTTATT CGGAATAATT ATAGGCTCT TTATATATAA AGCCCCCTAT TGCTCTTAA

A_GRANDIFLORA TCAAGTTTG A TTTCATCAA TCACTGGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_NERVOSEA TAAATTTG A TTTCATTAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_RACEMOSA TAAATTTG A TTTCATTAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_SPICATA TAAATTTG A TTTCATTAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CUSPIDATA TAAATTTG A TTTCATTAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_SP_2 TAAATTTG A TTTCATTAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_GIGANTEA TAAATTTG A TTTCATCAAT TTAGTTGTTT AAAAGAGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CAUDATA TAAATTTG A TTTCATCAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_WALLICHIANA TAAATTTG A TTTCATCAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_FRAGRANS TAAATTTG A TTTCATCAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_FRAESERENSIS TAAATTTG A TTTCATCAAT TTAGTTGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_SPLENDENS TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CARNOSA TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_RENAE TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_SP_1 AAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_RIDLEYI TAAATTTG A TTTCATAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_OBONGA TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_AURICULATA TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_IMPERIALIS TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_RESINOSA TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_GARDENIOIDES TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CRENULATA TAAATTTG A TTTCATTAAT TCGGGTTT AAAGAGGTCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_BELUKAR TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CURTISII TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CRASSIFOLIA TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_CAMERONENSIS TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_ELLIPTICA_2 AAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_STONEI TAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_COLLINA AAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT
F_ELLIPTICA_1 AAAATTTG A TTTCATCAAT TCGGGTTT AAAGAGGCC TAATAGAATG TTGGGAAA ATGGATAAA TCATATTTAT

A_GRANDIFLORA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_NERVOSEA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_RACEMOSA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_SPICATA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CUSPIDATA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_SP_2 AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_GIGANTEA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CAUDATA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_WALLICHIANA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_FRAGRANS AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_FRAESERENSIS AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_SPLENDENS AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CARNOSA AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_RENAE AATTGGTCG ATAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_SP_1 AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_RIDLEYI AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_OBONGA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_AURICULATA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_IMPERIALIS AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_RESINOSA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_GARDENIOIDES AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CRENULATA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_BELUKAR AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CURTISII AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CRASSIFOLIA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_CAMERONENSIS AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_ELLIPTICA_2 AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_STONEI AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_COLLINA AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT
F_ELLIPTICA_1 AATTGGTCG AAAATCGTG TTACATGAT TCTTTTATA CAACACCTT AACTAGAGGA GTAAGAGGAT TAGCGGAATT

A_GRANDIFLORA AACTATTTT TTTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_NERVOSEA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_RACEMOSA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_SPICATA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA AG
F_CUSPIDATA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_SP_2 AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_GIGANTEA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_CAUDATA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_WALLICHIANA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_FRAGRANS AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_FRAESERENSIS AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_SPLENDENS AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG
F_CARNOSA AACTCATTT TTGATCGAC GTCTAATTGA TGGATTACCA ATGGGGTTG GTTTTTTAG TTCTTGTGA GG

F_RENAE	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_SP_1	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_RIDLEYI	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_OBLONGA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_AURICULATA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_IMPERIALIS	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_RESINOSA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_GARDENIOIDES	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_CRENULATA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_BELUKAR	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_CURTISII	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_CRASSIFOLIA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_CAMERONENSIS	AACTCATTTC	TTTGATCGAC	GTCTAATAGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_ELLIPTICA_2	AACTCATTTC	TTTGATCGAA	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_STONEI	AACTCCTTC	TTTGATCGAC	GTCTAATTGA	AGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_COLLINA	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTAC	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG
F_ELLIPTICA_1	AACTCATTTC	TTTGATCGAC	GTCTAATTGA	TGGAATTACG	AATGGGTTT	GTTTTTTTAG	TTTCTTTGTA	GG

Appendix 7

The aligned ITS-expanded data matrix (45 taxa).

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P_AMARA CGAAGCGGAC GACCCGGG C--TTGTTTA ACCGACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
P_RESINIFERA TCGAATCCCG CGAACGGAC GACCCGGG C--ATGTTTA ACCGACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
P_ELEGANS TCGAATCTG CGAACGGAC NACCCGGG C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_OBLONGA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_GARDENIOIDES TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_RIDLEYI TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CRASSIFOLIA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_SP_1 TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_SPLENDENS TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_AURICULATA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_IMPERIALIS TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_MACROSCYPHA TCGAATCTG CGACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_RESINOSA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CARNOSA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_STONEI TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CAMERONENSIS TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_FRASERENSIS TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CEILANICA --AAT-CG CGAACGGAC GACC-TGAA C--TTGTTTA ACCCACGGG- -CGT-CGAA CGTGGGAAC CG--CGGAC
F_RENAE TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CURTISII TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_SALTICOLA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_BERTERIANA YNGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_BELUKAR TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_ELLIPTICA_1 TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_ELLIPTICA_2 TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_ELLIPTICA_3 TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_COLLINA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_RACEMOSA TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_NERVOSEA TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_CUSPIDATA TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_SP_2 TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC TG--CGGAC
F_SPICATA TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_VOLUBILIS TCGAATCTG CGAACGGAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
F_FRAGRANS TCGAATCTG CGA-GCAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA AGTGGGAAC TG--CGGAC
F_GIGANTEA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA AGTGGGAAC CG--CGGAC
F_WALLICHIANA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA AGCGGGGAAC TG--CGGAC
F_CAUDATA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA AGCGGGGAAC CG--CGGAC
F_CRENLATUM TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGTAAC CG--CGGAC
A_AMPLEXICAULIS TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CN--CGGAC
A_GRANDIFLORA TCGAATCTG CGAACGGAC GACCCGTAA C--TTGTTTA ACCCACGGG- -CGT-CGGGA CGTGGGAAC CG--CGGAC
L_LAXIFLORUS TCGAATCTG CAAAGCAC GACCCGTAA C--ATGTTTA ACCCACGGG- -CAT-CGAGA CGTGGTAAC CACACGGAC
L_CUSPIDATUS TCGAATCTG CGAACGGAT GACCCGGAA C--ATGTTTA ACACCGGGG -CAT-CGGGA CGTGGCAAC CG--CGGAC
L_BRIDENTATUS TCGAATCTG CGAACGGAC GACCCGGAA CATATGTTTA ACACACGGG GCAT-CAGGA CGTGGTAAC CG--CGGAC
E_AFFINE TCGAATCTG CGAACAGAC GACCCGGAA C--ATGTTTA ACTCACGGG- -CGT-CGGGA CGGGGGAAAC CA--CGGAC
G_ALGIDA TCGATTCTG CGAACGGAC GACCCGAGAA C--ATGCTA ACGCACGGG- -CGTCCGGGA CGAGGGAAAC CA--CGGAC

P_AMARA CG-TGCCCG CC--GCACGG CGTCGATCTC C----GGTC CTCGT-CGTG TTGAAACCTA AACCGGGCG CGAAAAGCG
P_RESINIFERA CG-TGCCCG CC--GCATGG CGTCGATCTC C----GGTC CTCGT-CGTG CTAAAACCTA AACCGGGCG CGAAAAGCG
P_ELEGANS CG-GGCCCG AC--ACACGG CGTCGATCTC G---GGTC CTCTNT-CGTG TTGAAACCTA AACCGGGCG CGAAAAGCG
F_OBLONGA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_GARDENIOIDES CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_RIDLEYI CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_CRASSIFOLIA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_SP_1 CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_SPLENDENS CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_AURICULATA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_IMPERIALIS CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_MACROSCYPHA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_RESINOSA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_CARNOSA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_STONEI CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_CAMERONENSIS CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_FRASERENSIS CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_CEILANICA CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_RENAE CG-GGCCCG AC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_CURTISII CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_SALTICOLA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_BERTERIANA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_BELUKAR CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_ELLIPTICA_1 CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_ELLIPTICA_2 CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG TGGAAAAGCG
F_ELLIPTICA_3 CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_COLLINA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_RACEMOSA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC CTCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_NERVOSEA CG-GGCCCG GA--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_CUSPIDATA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_SP_2 CT-GCACCT GT--GCACGG CATCGGCCAT T---GGTC ATCGT-CGAG CGAGAAACTA AACCGGGCG CGAACACAGCA
F_SPICATA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_VOLUBILIS CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CGAAAAGCG
F_FRAGRANS CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG
F_GIGANTEA CG-GGCCCG GC--GCACGG CGTCGGCAT T---GGTC ATCGT-CGGG CGAGAAACTA AACCGGGCG CAGAAAAGCG

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<i>F_WALLICHIANA</i>	CG-GGCC	GC--GCACGG	CGTCGGCCAT	T---GGCG	CTCGT-CGGG	CGAGAAA	ACTA	AACCGGGCG	CAGAAAAGCG
<i>F_CAUDATA</i>	CG-GGCC	GC--GCACGG	CGTCGGCCAC	T---GGTG	CTCGT-CGGG	CGAGAAA	ACTA	AACCGGGCG	CAGAAAAGCG
<i>F_CRENULATA</i>	CG-GGCC	GC--GCACGG	CGTCGGCCAT	T---GGTG	CTCGT-CGGG	CGAGAAA	ACTA	AACCGGGCG	CGGAAAAGCG
<i>A_AMPLEXICAULIS</i>	CG-GN	GCACGG	CGTCGATCTC	T---GGTG	CTCGT-CGGG	CGAAA	AACTA	AACCGGGCG	TGGAAGAGCG
<i>A_GRANDIFLORA</i>	CG-GGCC	GC--GCACGG	CGTCGATCTC	Y---GGTG	CTCGC-CGGG	CGAGAAA	ACTA	AACCGGGCG	CGGAAAAGCG
<i>L_LAXIFLORUS</i>	CGTG	CCCC	CCCTGCA	CATCGATCTG	CCATCGGT	ATCGT-CGGG	CAA	AACTCA	ACTCGGGCG
<i>L_CUSPIDATUS</i>	CGTG	CCCC	CC--GCGCG	CATCGATCTG	CCGGCGGT	ATCGT-CGGG	CGAAA	AACTCA	ACTCGGGCG
<i>L_BREVIDENTATUS</i>	CGTG	CCCC	C--GCGCG	CATCGATCTG	CCGGCGGT	ATCGT-CGGG	CGAAA	AACTCA	ACTCGGGCG
<i>E_AFFINE</i>	CG-TG	CCCC	GC--GCACGG	CGTCGGCC	A---CGCC	GTTGACCT	CAGAAA	AC-A	AACCGGGCG
<i>G_ALGIDA</i>	CG-AT	CCCC	GA--GCACGG	CGTCGACCAC	C---GGTG	CTCGT-CGTG	CAA	ACAACCA	AACCGGGCG
<i>P_AMARA</i>	CCAAGGAA	--ATCGAGA-A	AAGGACGCC	TGCCC	TGCGC	AGGAGCG	GGGAGCG		
<i>P_RESINIFERA</i>	CCAAGGAA	--ATCGAGA-A	AAGGACGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>P_ELEGANS</i>	CCATGGAA	--ATCGAGA-A	ANNGACGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_OBLONGA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_GARDENIOIDES</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_RIDLEYI</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CRASSIFOLIA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_SP_1</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_SPLENDENS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_AURICULATA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_IMPERIALIS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_MACROSCYPHA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_RESINOSA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CARNOSA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_STONEI</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CAMERONENSIS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_FRAZERENSIS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CEILANICA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_RENAE</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CURTISII</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_SALTICOLA</i>	CCAAGGAA	--AACTAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_BERTERIANA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_BELUKAR</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_ELLIPTICA_1</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_ELLIPTICA_2</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_ELLIPTICA_3</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_COLLINA</i>	CCAAGGAA	--TACTAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_RACEMOSA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_NERVOSA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CUSPIDATA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_SP_2</i>	CCAAGGAA	--AACAAAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_SPICATA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_VOLUBILIS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_FRAGRANS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_GIGANTEA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_WALLICHIANA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CAUDATA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>F_CRENULATA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	TGCCC	TGCGC	AGGAGC	ACAGG		
<i>A_AMPLEXICAULIS</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	CGCC	CGCG	AGGAGC	ACAGG		
<i>A_GRANDIFLORA</i>	CCAAGGAA	--AACGAGA-A	AAGGATGCC	CGCC	CGCG	AGGAGC	ACAGG		
<i>L_LAXIFLORUS</i>	CCAAGGACT	TAATCGA	TGGGTG	TTCT	-GATG	CGT	AGTC	TGTCGAT	AGGAGCATCG
<i>L_CUSPIDATUS</i>	CCAAGGACT	TAACCGA	ATGGGTG	TCTCG	TGAC	CGT	CGT	TGCGCT	AGGAGCATCG
<i>L_BREVIDENTATUS</i>	CCAAGGAA	TAACCGA	TGGGTG	TCTTG	ATG	CGT	CGT	TGCGCT	AGGAGCATCG
<i>E_AFFINE</i>	CCAAGGAA	--AACGAA-A	GA-GATTGCT	GGCCT	-GGCG	-CGT	CGT	CGC	AGGAGCATCG
<i>G_ALGIDA</i>	CCAAGGAA	--AACGAA-A	AAGGATGCC	TGCCC	TGCGC	-AGT	CGT	TGCGC	AGGATCACCG
<i>P_AMARA</i>	GCGCC	-CATA	AAAA-CCG-A	AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>P_RESINIFERA</i>	GCGCC	-TGTG	AAAA-CCG-A	AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>P_ELEGANS</i>	GCGCC	-TGTN	AAAA-CCG-A	AACGACTCTC	GGCAACNGAT	ATCNCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_OBLONGA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_GARDENIOIDES</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_RIDLEYI</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CRASSIFOLIA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_SP_1</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_SPLENDENS</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_AURICULATA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_IMPERIALIS</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_MACROSCYPHA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_RESINOSA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CARNOSA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_STONEI</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CAMERONENSIS</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_FRAZERENSIS</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CEILANICA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_RENAE</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CURTISII</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_SALTICOLA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_BERTERIANA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_BELUKAR</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_ELLIPTICA_1</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_ELLIPTICA_2</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_ELLIPTICA_3</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_COLLINA</i>	GCACC	-TGTA	CAAAACT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_RACEMOSA</i>	GCTCC	-CGTA	AAA-CT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_NERVOSA</i>	GCACC	-CTTA	AAA-CT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_CUSPIDATA</i>	GCACC	-CTTA	AAA-CT	AA AACGACTCTC	GGCAACGGAT	ATCTCGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAC
<i>F_SP_2</i>	GCACC	-CGTC	AAA-CT	AA AACGACTCTC	GACAGGGAT	ATCTGACTC	TCACATCAAT	AAAGAACGCA	GAGAAC

F_SPICATA	GCACC-CGTA	CAAA-CT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_VOLUBILIS	GCACC-CGTA	CAAA-CT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_FRAGRANS	GCACC-TGTA	CGAAACT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_GIGANTEA	GCACC-TGTA	CGAAACT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_WALLICHIANA	GCACC-TGTA	CGAAACT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_CAUDATA	GCACC-TGTA	CGAAACT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
F_CRENULATA	GCACC-TGTA	CGAA-CT-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
A_AMPLEXICAULIS	GCGCC-TGTA	GAAA-CC-GA	TACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
A_GRANDIFLORA	GCGCC-TGTA	GAAA-CT-GA	TACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
L_LAXIFLORUS	ACGCC-TCTA	AAA--CA-AA	AACGACCCCC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
L_CUSPIDATUS	GCGCCCTCTA	AAA--CG-GA	AACGACCCCC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
L_BREVIDENTATUS	GCGCCCTCTA	AAA--CG-GA	AACGACCCCC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
E_AFFINE	GCG--TCTG	TCGAAAAGAA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCAAACACTCG
G_ALGIDA	GCGCC-TAAA	GAAA-CA-AA	AACGACTCTC	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAACACTCG
P_AMARA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
P_RESINIFERA	ATACTTGGTG	TGAATTGCAN	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
P_ELEGANS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_OBLONGA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_GARDENIOIDES	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_RIDLEYI	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CRASSIFOLIA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_SP_1	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCC-A
F_SPLENDENS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCATA
F_AURICULATA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	GTCCGGCCGA
F_IMPERIALIS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	GTCCGGCCGA
F_MACROSCYPHA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	GTCCGGCCGA
F_RESINOSA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	GTCCGGCCGA
F_CARNOSA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_STONEI	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CAMERONENSIS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	TTCCAGCATA
F_FRAZERENSIS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CEILANICA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_RENAE	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CURTISII	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_SALTICOLA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_BERTERIANA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCRGCCGA
F_BELUKAR	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_ELLIPTICA_1	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_ELLIPTICA_2	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_ELLIPTICA_3	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_COLLINA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_RACEMOSA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_NERVOSA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CUSPIDATA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	TTCCGGCCGA
F_SP_2	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_SPICATA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_VOLUBILIS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_FRAGRANS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_GIGANTEA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_WALLICHIANA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CAUDATA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
F_CRENULATA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
A_AMPLEXICAULIS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
A_GRANDIFLORA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
L_LAXIFLORUS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCCGGCCGA
L_CUSPIDATUS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCAGGCTGA
L_BREVIDENTATUS	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATCAGGCTGA
E_AFFINE	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	GTCAAGGCCGA
G_ALGIDA	ATACTTGGTG	TGAATTGCAG	AAT-CCCGTG	AACCAT-CGA	GTCTTTGAAC	-GCAAGTTGC	GCCCGAAGCC	ATTAGGCCA
P_AMARA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	C-AAGCCC--	---GTGCC	TCCGTGTT	GCAGGCG--G
P_RESINIFERA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	C-ATCCCC--	---GTGCC	TCCGTGTT	GCAAGCG--G
P_ELEGANS	GGGCACGTCT	GCCTGGGGT	CANGCATCGN	GTCGCGCNNC	C-AAGCCC--	---GTGCC	TCTATCCGTT	GCGGGTG--G
F_OBLONGA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_GARDENIOIDES	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_RIDLEYI	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_CRASSIFOLIA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_SP_1	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_SPLENDENS	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_AURICULATA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_IMPERIALIS	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_MACROSCYPHA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_RESINOSA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_CARNOSA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_STONEI	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_CAMERONENSIS	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_FRAZERENSIS	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_CEILANICA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_RENAE	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_CURTISII	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_SALTICOLA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_BERTERIANA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	T-AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_BELUKAR	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	--AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_ELLIPTICA_1	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	--AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_ELLIPTICA_2	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	--AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_ELLIPTICA_3	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	--AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A
F_COLLINA	GGGCACGTCT	GCCTGGGGT	CACGCATCG	GTCGCCCCCCC	--AACCCC--	---GTGCC	TCCATCGTT	GCGGGCG--A

F_RACEMOSA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GCGTGC TCCATTGTT GCGGGCG--A
F_NERVOSEA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GCGTGC TCCATTGTT GCGGGCG--A
F_CUSPIDATA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GCGTGC TCCATTGTT GCGGGCG--A
F_SP_2 GGGCACGTCT GCCTGGG-GT CACGCATCGC ATCACCCC --AACCC-- ---GTGTGC TCCATTGTT GCAGGCA--A
F_SPICATA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GCGTGC TCCATTGTT GCGGGCG--A
F_VOLUBILIS GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GCGTGC TCCATTGTT GCGGGCG--A
F_FRAGRANS GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC CCAACCC-- ---GTGACC TCCATCGTT GCGGGTG--A
F_GIGANTEA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GTGACC TCCATCGTT GCGGGTG--A
F_WALLICHIANA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GTGACC TCCATCGTT GCGGGTG--A
F_CAUDATA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GTGACC TCCATCGTT GCGGGTG--A
F_CRENULATA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC CAAACCC-- ---GTGACC TCCATCGTC GCGGGGG--A
A_AMPLEXICAULIS GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC CAAACCC-- ---GTGACC TCCATCGGT GCGGGGGGG--A
A_GRANDIFLORA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC CAAACCC-- ---GTGACC TCCATCGGT GCGGGGGGG--A
L_LAXIFLORUS TGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC A-AACCC-- ---GTGACC TCCATCGGT GCGGGGGGG--A
L_CUSPIDATUS TGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC ACAGCCTT-- ---GCGC GC-----GC GCGC-----A
L_BREVIDENTATUS TGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC CTCCCACGAC ACCGTCACA GCCGTG--TC -CGGGTC--A
E_AFFINE GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GTGACC GATATCA-T GCC-----G
G_ALGIDA GGGCACGTCT GCCTGGGCGT CACGCATCGC GTCGCCCCCCC --AACCC-- ---GTGACC GATATCA-T GCC-----G

P_AMARA CTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GT TGGCGGAAT -----G CGAGTCCCTC
P_RESINIFERA CTGGA---- GGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GT TGGCGGAAT -----G CGAGTCCCTC
P_ELEGANS CTGGA---- GAGGGTGG-A AAATGGCTTC CCATGCCCTT GGC-GT TGGCGGAAT -----G CGAGTCCCTC
F_OBLONGA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_GARDENIOIDES CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_RIDLEYI CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_CRASSIFOLIA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_SP_1 CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_SPLENDENS CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_AURICULATA TTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_IMPERIALIS TTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_MACROSCYPHA TTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_RESINOSA TTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_CARNOSA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_STONEI CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_CAMERONENSIS CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_FRASERENSIS CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_CEILANICA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_RENAE CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_CURTISII CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_SALTICOLA CCGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_BERTERIANA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_BELUKAR CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_ELLIPTICA_1 CTCGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_ELLIPTICA_2 CTCGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_ELLIPTICA_3 CTCGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_COLLINA CTCGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G CGAGTCCCTT
F_RACEMOSA TTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_NERVOSEA TTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_CUSPIDATA TTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_SP_2 TTAGA---- GGGGACGG-A AAATGGTTT CCGTGCCTT AGCTG---GGC TGGCTTAAT -----G AGAGTCCCTT
F_SPICATA TTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_VOLUBILIS TTGGA---- GGGGACGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_FRAGRANS CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_GIGANTEA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_WALLICHIANA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_CAUDATA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----G AGAGTCCCTT
F_CRENULATA CTGGA---- GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAT -----T CGAGTCCCTT
A_AMPLEXICAULIS CTGAA---GG GGGGGCGG-A AAATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----A CGAGTCCCTT
A_GRANDIFLORA CTGAA---GG GGGGGCGG-A AGATGGCTTC CCGTGCCTT GGC-GC---GGC TGGCTTAAT -----A CGAGTCCCTT
L_LAXIFLORUS AAGCT-TGT GGGGGCGG-A GGATGGCTTC CTGTCCTT GGTGC---GGC TGGCTGAAT -----G CGAGTGCCTT
L_CUSPIDATUS AAAGGGCGGA GGGGGCGG-GA GGATGGCTTC CCGTGCCTT ---C-C---CCC GGGCGCGCT GGCCCCAAACG CGAGCAGCGT
L_BREVIDENTATUS AT-GGGCGGA GGGGGCGG-A GGATGGCTTC CCGTGCCTT ---CCC---CCC TGGCGCGCT GGCACAAACG CGAGCAGCGT
E_AFFINE GT-GGTC-GC GGGGGCGG-A AATGGCTTC C-GTGGCC-- GGTGCGG-GC TGGCTTAAT -----G CGAGTCCCTC
G_ALGIDA GT-CGTCGA-G GGGGGCGG-A TATGGCTTC CCGTGCCTT GGTGC---GGC TGGCTTAAC -----G CAAGTCCCTT

P_AMARA GCGACGGAGC CGACGACGGG TGTTGGTTGA ATCCCTCGGC TCGAGCGC-C GTCGCGCAG TCCCCGTC-G GAAGAGGAGA
P_RESINIFERA GCGACGGAGC CGACGACGGG TGTTGGTTGA ATCCCTCGGC TCGAGCGC-C GTCGCGCAG TCCCCGTC-G GAAGAGGAGA
P_ELEGANS GCGACGGAGC CGACGACGGG TGTTGGTTGA ATCCCTCGGC TCGAGCGC-C GTCGCGCAG TCCCCGTC-G GAAGAGGAGA
F_OBLONGA GCGACGGAGC CGACGACGGG TGTTGGTTGA ATCCCTCGGC TCGAGCGC-C GTCGCGCAG TCCCCGTC-G GAAGAGGAGA
F_GARDENIOIDES GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG TCCCCGTT-G AAAGAGGAGA
F_RIDLEYI GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_CRASSIFOLIA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_SP_1 GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_SPLENDENS GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_AURICULATA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_IMPERIALIS GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_MACROSCYPHA -CGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_RESINOSA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_CARNOSA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_STONEI GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_CAMERONENSIS GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_FRASERENSIS GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_CEILANICA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_RENAE GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_CURTISII GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_SALTICOLA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_BERTERIANA GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTT-G AAAGAGGAGA
F_BELUKAR GCGACGGAGC CGACGACGG TGTTGGTTGA TTGTCCTAAC TCGAATGC-T GTCGCGCAG GCCCCGTC-C AAAGAGGAGA

F_ELLIPTICA_1 GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_ELLIPTICA_2 GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_ELLIPTICA_3 GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_COLLINA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_RACEMOSA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_NERVOSEA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_CUSPIDATA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G ATAGAGGAGA
F_SP_2 GCGACGGTA- CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_SPICATA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_VOLUBILIS GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG AACCCGTC-G AAAGAGGAGA
F_FRAGRANS GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_GIGANTEA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_WALLICHIANA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_CAUDATA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
F_CRENULATA GCGACGGAGC CGACGACAAG TGGTGGTTGA TTGTCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCGTC-G AAAGAGGAGA
A_AMPLEXICAULIS GTGACGGATG CGACGACAAG TGGTGGTTGA ATGCCAAC TCGGGTGC-T GTCGCGCGAG GCCCCGTC-A GGAGAGGAGA
A_GRANDIFLORA GCGACGGAGC CGACGACAAG TGGTGGTTGA ATGCCAAC TCGGGTGC-T GTCGCGCGAG GCCCCGTC-G GGAGAGGAGA
L_LAXIFLORUS TCGACGGGTG CGACGACAAG TGGTGGTTGA TTGCTCAAC CGCTGAGG-T GTCGCGCGAG GTCCCCGTC-G AGAGGAGA
L_CUSPIDATUS TCGACGGCG CGACGACAAG TGGTGGTTGA CCGCTCAAC TCGAGAGC-T GTCGCGCGAG GTCCCCCACCG AAAGAGGATG
L_BREVIDENTATUS TCGACGGCG CGACGACAAG TGGTGGTTGA TTGCTCAAC TCGAGGCGCT GTCGCGCGAG GTCCCCCACCG AAAGAGGATG
E_AFFINE CGGGCGGAG CGACGACAAG TGGTGGTTGA TTGCTCAAC TCGAGTGC-T GTCGCGCGAG GCCCCCCC-G ACGTAGGAGA
G_ALGIDA GCGACGGACA CGACGACAAG TGGTGGTTGA TTTT-TCAAC TAAGGTGC-T GTCGCGCGTT GCCCCGTC-G GATGAGGAGA

P_AMARA CTG--CCCCG ACCCT---GG A-GCATGCGT CCCCA--CGA CG-CGTGCCA CGACCGA
P_RESINIFERA CTG--CCCCG ACCCT---GG A-GCATGCGT CCCCA--CGA CG-CGTGCCA CGACCGC
P_ELEGANS CTG--CCCCG ACCCT---GG A-GCATGCGT CCCCA--CGA CG-CGTGCCA CGACCGC
P_OBLONGA F_GARDENIOIDES CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F RIDLEYI CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CRASSIFOLIA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_SP_1 CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_SPLENDENS CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_AURICULATA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_IMPERIALIS CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_MACROSCYPHA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_RESINOSA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CARNOSA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_STONEI CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CAMERONENSIS CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_FRASERENSIS CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CEILANICA CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_RENAE CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CURTISII CTCTCCCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_SALTICOLA CTC--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_BERTERIANA CTC--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_BELUKAR CTG--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_ELLIPTICA_1 CTG--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_ELLIPTICA_2 CTG--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_ELLIPTICA_3 CTG--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_COLLINA CTG--CCCCG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_RACEMOSA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_NERVOSEA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CUSPIDATA CTT--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_SP_2 CTT--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_SPICATA CTT--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_VOLUBILIS CTT--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_FRAGRANS CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_GIGANTEA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_WALLICHIANA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CAUDATA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
F_CRENULATA CTG--CCTTG ACCCT---AC A-GCATGTGT CGCCA--TGA CG-CATGTCA CGACCGC
A_AMPLEXICAULIS CTG--CCCCG ACCCT---AC A-GCATGTGT CGGCC-TGA CG-CATGCCA CGACCGC
A_GRANDIFLORA CTG--CCCCG ACCCT---GT AAGCGTGCCT CGCCG--TGA CG-CATGCCA CGACCGC
L_LAXIFLORUS CTG--CCCCG ACCCT---C A-TCATGGCT CGTCA--CGA CG-TGTGCCA CGGCCG
L_CUSPIDATUS CTG--CCCCG ACCCT---GC A-CCATGGCT CGTACACCA CG-CATGCCA CGGCCG
L_BREVIDENTATUS CTG--CCCCG ACCCT---GC A-CCATGGCT CGTCA--CGA CG-CATGCCA CGGCCG
E_AFFINE CCT---ACCG ACCCTTT-GC A-C---GGT CGAAA--GGA CGAAGTGCCA CGACCGC
G_ALGIDA CTT--CCTTG ACCCTAACCG A---A-GCGT CGTCA--CGA CG-TGTGCCA CGACCGC

Appendix 8

Style and filament exsertness from the corolla tube in selected species of *Fagraea* s.l., representing sections *Cyrtophyllum*, *Fagraea*, and *Racemosae*.

Species	Section	Total Corolla Tube Length (mm)	Style Length (mm)	Extent of Style Protrusion (mm)	% of Style Protrusion	Filament Length (mm)	Extent of Filament Protrusion (mm)	% of Filament Protrusion
<i>F. fragrans</i>	<i>C</i> (AI)	(4–)6–8	(14–)18–22	(8–)10–12(–14)	57–64	(10–)12–16(–17)	(8–)10–12(–13)	76–80
<i>F. gigantea</i>	<i>C</i> (AI)	7–8	(12–)18–22	(5–)12–14	42–64	13–15	12–13	87–92
<i>F. wallichiana</i>	<i>C</i> (AI)	(12–)20–25	(34–)42–45(–55)	22–25(–30)	55–65	(27–)30–38	20–23(–28)	73–74
<i>F. elliptica</i>	<i>C</i> (TI)	3–5	(6–)7–9	3–4	44–50	(4–)7–8	(4–)7–8	100
<i>F. auriculata</i>	<i>F</i>	60–82	70–90	8–10	11–12	45–60	15–23	33–38
<i>F. carnosia</i>	<i>F</i>	106–140	123–126	0–17	0–13	12–15	5	33–41
<i>F. crassifolia</i>	<i>F</i>	26–30	28–30	0–2	0–7	-	-	-
<i>F. crenulata</i>	<i>F</i>	15–18	15–20(–23)	0–5	0–22	12–14	7–8	57–58
<i>F. curtisii</i>	<i>F</i>	35–55	c. 60	c. 5	c. 8.3	32–40	c. 10	c. 25
<i>F. fraserensis</i>	<i>F</i>	26–36	35–42	6–9	14–26	20–24	6–10	30–42
<i>F. gardenioides</i>	<i>F</i>	40–53	50–55	2–10	4–18	20–27	12–17	60–63
<i>F. imperialis</i>	<i>F</i>	90–160	90–115	0–5	0–4	(55–)80–90	(5–)27–40	9–44
<i>F. insignis</i>	<i>F</i>	43–60	65–70	10–22	15–31	40–50	17–20	40–43
<i>F. latibracteata</i>	<i>F</i>	22–30	-	-	-	16–20	5–6	30–31
<i>F. littoralis</i>	<i>F</i>	25–32	32–35	3–7	9–20	23–25	12–13	c. 52
<i>F. oblonga</i>	<i>F</i>	21–36	22–30	1–6	5–20	18–22	c. 8	36–44
<i>F. renae</i>	<i>F</i>	23–34	28–32	0–5	0–16	20–26	10–14	50–54
<i>F. ridleyi</i>	<i>F</i>	32–37	40–45	c. 8	18–20	25–28	c. 10	36–40
<i>F. splendens</i>	<i>F</i>	25–37	40–45	8–15	20–33	20–25	7–8	32–35
<i>F. tubulosa</i>	<i>F</i>	75–93	85–88	5–10	6–12	15–18	c. 10	56–67
<i>F. johorensis</i>	<i>R</i>	20–25	20–28	0–3	0–11	15–16	4–5	27–31
<i>F. maingayi</i>	<i>R</i>	16–25	12–23	0	0	19–23	2–6	11–26
<i>F. nervosa</i>	<i>R</i>	21–26	22–25	0–1	0–4	10–15	0	0
<i>F. peninsularis</i>	<i>R</i>	c. 14	17–19	3–5	18–26	6–7	1–2	17–28
<i>F. racemosa</i>	<i>R</i>	10–22	15–20(–25)	3–5	20	11–17(–20)	6–8	40–55
<i>F. volubilis</i>	<i>R</i>	15–25	17–20	0–2	0–10	11–13	0–3	0–23

The three blocks of species from top to bottom in the Table, correspond to *Fagraea* sections *Cyrtophyllum*, *Fagraea* and *Racemosae*, respectively. Flowering material of *F. cameronensis* was not available in this study. Filaments were not observed in *F. crassifolia*, *F. fastigiata* and *F. larutensis* and styles were not observed in *F. fastigiata*, *F. latibracteata* and *F. larutensis*. *C* (AI) = *Cyrtophyllum* (Axillary Inflorescence), *C* (TI) = *Cyrtophyllum* (Terminal Inflorescence), *F.* = *Fagraea*, *R.* = *Racemosae*.