



# The asteralean affinity of the Mauritian *Roussea* (Rousseaceae)

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*Roussea*, a monotypic genus endemic to Mauritius, has for a long time been associated with *Brexia* (Celastraceae). Recently, it has been shown that *Roussea* is placed correctly in the mainly Australasian Asterales, but the sister group to *Roussea* has not been unequivocally identified. Cladistic analysis of the chloroplast genes *ndhF* and *rbcL* identifies the sister group to *Roussea* as Carpodetaceae. Recognizing this relationship, the monotypic Rousseaceae is merged with Carpodetaceae into Rousseaceae *s.l.* comprising two subfamilies. This group is characterized by many-locular ovaries and similarities in the appearance of the petals. Rousseaceae *s.l.* exhibit a disjunct distribution in Mauritius, East Australia, New Zealand and New Guinea. © 2001 The Linnean Society of London

ADDITIONAL KEY WORDS: Australia – Carpodetaceae – classification – *ndhF* – *rbcL* – New Guinea – New Zealand.

## INTRODUCTION

In 1789 Sir James Edward Smith described a new genus from Mauritius. He named it *Roussea* Sm. in memory of Jean-Jacques Rousseau, who had died eleven years earlier. *Roussea*, as a single species *R. simplex* Sm., is a climbing shrub endemic to the mountain forests of Mauritius (Takhtajan, 1987; Scott, 1997), where it once was locally abundant, but is now becoming increasingly rare (Scott, 1997). Originally the genus was included in Campanulaceae but, in his monograph of the family, Alphonse de Candolle (1830) excluded *Roussea*. He suggested a relationship with Escalloniaceae (and particularly *Forgesia* Comm. ex Juss.), although he also considered Loganiaceae and Goodeniaceae as possible alternatives. In 1839 Augustin Pyramus de Candolle erected a new monotypic family, Rousseaceae ('Roussæaceæ'), for *Roussea*. Somewhat later (Lindley, 1853), *Roussea* was included in Brexiaceae together with *Brexia* Noronha ex Thouars, *Ixerba* A. Cunn., and *Argophyllum* J. R. Forst. & G. Forst. Since then, *Roussea* has usually been considered closely related to *Brexia* and *Ixerba*, although the rank of this group has varied, as an order (Takhtajan, 1997), a family (Takhtajan, 1966; Thorne,

1992), a subfamily (in Saxifragaceae: Engler, 1928; Schulze-Menz, 1964), a tribe (in Saxifragaceae: Eichler, 1878; in subfamily Escallonioidae in Saxifragaceae: Baillon, 1872) or without formal recognition (in Grossulariaceae: Cronquist, 1981; in tribe Escalloniaceae in Saxifragaceae: Bentham & Hooker, 1862–1867; in Escalloniaceae: Hutchinson, 1967). Other authors have followed de Candolle (1839) and placed *Roussea* in a monotypic family, sometimes considering it rather distantly related to Brexiaceae (e.g. Takhtajan, 1987, with Rousseaceae in Saxifragales and Brexiaceae in Celastrales).

Thouvien (1890) pointed out that, mainly on anatomy, *Roussea* was anomalous within the *Brexia*-alliance. More recently, Hideaux & Ferguson (1976) concluded on palynological grounds that *Roussea* does not have any direct affinities either with *Brexia* or with *Ixerba*. Ramamonjariisoa (1980) came to the same conclusion in her thorough investigation of African saxifragaceous plants, based on data from anatomy and chemistry (as *Ixerba* is a New Zealand plant, it was only superficially treated in her thesis). Acknowledging these differences, Takhtajan (1997) placed *Roussea*, *Brexia* and *Ixerba* in three monogeneric families but in an order of their own, Brexiales, which he considered to be close to Celastrales. The celastralean affinity of the group is mainly due to *Brexia*, which by

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**Table 1.** Previous published molecular studies with *Roussea* included. The analysed genes, number of genera sampled from Asterales (including *Roussea*), the support values obtained for a monophyletic Asterales, the sister group to *Roussea* identified in each analysis, and the support values for this sister group relationship are listed. BrS: Bremer Support, BS: Bootstrap values, JK: Jackknife values. Support values considered as high are in bold face.

Author	Genes	Sampling from Asterales	Support for Asterales	Sister group of <i>Roussea</i>	Support for sister group relationship
Soltis & Soltis (1997)	18S rRNA	5 genera	No support	Campanulaceae	1 (BrS)
Soltis <i>et al.</i> (1997)	18S rRNA	5 genera	No support	Campanulaceae	No support
Savolainen, Spichiger & Manen (1997)	The <i>atpB-rbcL</i> spacer	3 genera	<50 (BS) <b>86 (JK)</b>	Asteraceae/ <i>Phelline</i>	<50 (BS) <63 (JK)
Koontz & Soltis (1999)	<i>rbcL</i> , 18S rRNA	8 genera	No support	Rest of Asterales	No support
Savolainen <i>et al.</i> (2000a)	<i>atpB</i> , <i>rbcL</i>	7 genera	<b>71 (BS)</b>	Campanulaceae	54 (BS)
Savolainen <i>et al.</i> (2000b)	<i>rbcL</i>	20 genera	No support	Carpodetaceae <i>s.l.</i>	<b>80 (BS)</b>
Soltis <i>et al.</i> (2000)	18S rRNA, <i>rbcL</i> , <i>atpB</i>	18 genera	<b>94 (JK)</b>	Campanulaceae	58 (JK)

many researchers has been found to show affinities with Celastraceae (Lindley, 1830, 1853; Verdcourt, 1968; Hegnauer, 1973; Benschel & Palser, 1975; Rammamonjariisoa, 1980; Takhtajan, 1987; Tobe & Raven, 1993). This close relationship between *Brexia* and Celastraceae (Eurosids I *sensu* APG, 1998) has been confirmed by phylogenetic analyses of data sets consisting of *rbcL* (Soltis *et al.*, 1990; Morgan & Soltis, 1993; Chase *et al.*, 1993; Soltis & Soltis, 1997; Savolainen *et al.*, 2000b), 18S rDNA (Soltis & Soltis, 1997; Soltis *et al.*, 1997), or morphological data (Simmons & Hedin, 1999), as well as combined analyses with *rbcL* and 18S rDNA (Koontz & Soltis, 1999), *rbcL* and *atpB* (Savolainen *et al.*, 2000a), and *rbcL*, 18S rDNA and *atpB* (Soltis *et al.*, 2000). *Ixerba* has not yet been placed with any confidence, but seems to be included among the Eurosids (*sensu* APG, 1998), as indicated by Koontz & Soltis (1999), Savolainen *et al.* (2000b), and Soltis *et al.* (2000).

18S rDNA data (Soltis & Soltis, 1997) placed *Roussea* in the Asterales clade (represented by only four other genera), with *Brexia* still close to Celastraceae. The inclusion of *Roussea* in Asterales was also confirmed by Savolainen, Spichiger & Manen (1997) using the *atpB-rbcL* spacer, by Soltis *et al.* (1997) using the 18S rDNA sequence, by Koontz & Soltis (1999) using a combined data set consisting of 18S rDNA and *rbcL* and, recently, by Savolainen *et al.* (2000b) using a broad and dense sampling of *rbcL* sequences, again by Soltis *et al.* (2000) using less dense sampling but combining the three genes, 18S rDNA, *rbcL* and *atpB*, and again by Savolainen *et al.* (2000a) using a combined data set with *atpB* and *rbcL* (Table 1). No analyses

have contradicted a placement of *Roussea* in Asterales, although only a few (i.e. by Savolainen *et al.*, 1997, and Soltis *et al.*, 2000) have received high support values for the Asterales clade.

The position of *Roussea* within Asterales thus needed to be determined with precision, especially as the position of *Roussea* in the cladograms of Koontz & Soltis (1999), Savolainen *et al.* (2000a,b), and Soltis *et al.* (2000) indicated a basal position in Asterales and thus a key rôle for *Roussea* in the understanding of the evolution and biogeography of Asterales as a whole. Using the nucleotide sequences of two chloroplast genes, *rbcL* and *ndhF*, in a phylogenetic analysis, I wanted to obtain a reliable position for *Roussea*. If the sister group of *Roussea* is known with certainty, it will be possible to discuss its relationship to this group from a morphological viewpoint. Furthermore, as a member of a predominantly Australasian Asterales (Bremer & Gustafsson, 1997), *Roussea* has a peculiar distribution, as it is restricted to Mauritius. This disjunct distribution is also in need of attention. The focus of this paper will be on the phylogenetic relationship of *Roussea* and the morphological characterization of this relationship, while the biogeography and position of *Roussea* and its sister group in relation to the rest of Asterales will be treated in future papers.

## MATERIAL AND METHODS

### MOLECULAR DATA

Three new sequences were generated as part of this study. These were the *ndhF* gene for *Roussea simplex*,

*Cuttsia viburnea* F. Muell. and *Escallonia rubra* (Ruiz & Pav.) Pers. *Roussea* was sequenced from DNA provided by Soltis & Soltis (1997), while *C. viburnea* and *E. rubra* were sequenced from DNA extracted from herbarium material, according to the methods of Saghai-Marooof *et al.* (1984), as modified by Doyle & Doyle (1987). Voucher specimen data are presented in Table 2. The DNAs were purified with Quiaquick PCR kit (Qiagen) according to the instructions provided by the manufacturer. The primers for the PCR amplifications are described by Oxelman, Backlund & Bremer (1999). The product was purified with the Quiaquick PCR kit (Qiagen) according to the instructions from the manufacturer (using *ddH*<sub>2</sub>O as eluting agent). Cycle-sequencing was with AmpliTaq DNA Polymerase, FS (Perkin Elmer) using the manufacturer's protocol and a GeneAmp PCR System 9600 (Perkin Elmer). Sequence data was collected using an ABI 377 Sequencer (Perkin Elmer).

The sequences were aligned by eye together with 48 previously published *ndhF* and *rbcL* sequences obtained from GenBank/EMBL (Table 2). For a few genera (i.e. *Dampiera* R. Br. and *Cyphia* Bergius), there are no single species sequenced for both *rbcL* and *ndhF*. As it can be assumed that the genera included in the analysis represent monophyletic clades, at least at this level of resolution, the sequences from different species of the same genus for the two genes were pooled into one taxon for the matrix. The resulting *rbcL*–*ndhF* matrix represents 25 taxa, of which 20 (including *Roussea*) are usually considered to belong to the Asterales *s.l.*

After the alignment, indels were removed if they were shared by two or more taxa, and the presence or absence of the gaps were coded in a binary matrix. Out of 20 gaps, only four were informative. The aligned matrix, including the gap matrix, consisted of 3625 characters, of which 760 were parsimony-informative. *Viburnum* L. (Dipsacales: Adoxaceae), *Lonicera* L. (Dipsacales: Caprifoliaceae), *Escallonia* Mutis ex L.f. (Escalloniaceae), *Quintinia* A. DC. (Escalloniaceae), and *Hedera* L. (Apiales: Araliaceae) were used as outgroup.

#### CLADISTIC ANALYSIS

The matrix was analysed using PAUP\* 4.0b4a (Swofford, 2000), using a heuristic search with 100 random addition sequences replicates and the TBR branch swapping algorithm. The internal supports for the clades were tested by a Bremer support analysis (Bremer, 1988) and a Jackknife analysis (Farris *et al.*, 1996) using PAUP (with a proportion of 36.8% of the characters deleted and 10 000 replicates, using the heuristic search option, random addition sequence and TBR branch swapping).

#### MORPHOLOGICAL DATA

Leaf anatomy slides were prepared from *R. simplex* (J. Bosser 22.430 in P). A part of a leaf was rehydrated in boiling water with a trace of detergent, and then dehydrated in an alcohol series (from ethanol to butanol) and embedded in paraffin. Transverse sections *c.* 20 µm thick were cut with a microtome and fixed on slides. After drying, the paraffin was removed and the sections were stained with safranin and Light Green. In a similar way, seeds from *R. simplex* (M. J. E. Coode 4120 in K) were sectioned transversely.

Cleared leaf parts were prepared from *R. simplex* (M. J. E. Coode 4120 in K). A part of a leaf (8 × 12 mm, including margin and apex) was rehydrated as described above, placed in sodium hydroxide solution (5%) for a few days at room temperature, thoroughly washed in distilled water, and mounted in Hoyer's solution on a microscope slide. Seeds from *R. simplex* (M. J. E. Coode 4120 in K) and *C. viburnea* (R. D. Hoogland & H. C. Hayes 8609 in K) were dissected and mounted in Hoyer's solution on microscope slides.

The following specimens of *R. simplex* were studied for morphological features (by dissecting microscope or by naked eye; herbarium abbreviations according to Holmgren, Holmgren & Barnett, 1990): C. Barday 2853 (K), Bernardi 14713 (K), M. Boivin s.n. (P), J. Bosser 22.430 (P), M. J. E. Coode 4120 (K), D. Lorence 2149 (P), and D. D'Urville s.n. (P).

#### RESULTS

The PAUP search gave two most parsimonious trees each with a length of 3041 steps, a consistency index of 0.61 and a retention index of 0.51. The two trees differ only in the topology of the outgroup, while the ingroup topology is identical and totally resolved. The strict consensus tree with Bremer support values and Jackknife values is shown in Figure 2.

Several well-supported clades (Fig. 2) are found, many with a Jackknife value of 100%. One of these well-supported clades consists of *Roussea* and the Carpodetaceae (*sensu* Gustafsson & Bremer, 1997); the support is 97%. The position of this clade as sister to the rest of the Asterales is unsupported (receiving a Jackknife value of less than 50%). Basal to the *Roussea*–Carpodetaceae clade is *Roussea* as sister to a highly supported (100%) clade with *Carpodetus* J. R. Forst. & G. Forst., *Cuttsia* F. Muell., and *Abrophyllum* Hook.f. (i.e. Carpodetaceae). Within the Carpodetaceae subclade, *Cuttsia* and *Abrophyllum* shows a sister group relationship with 100% support.

#### DISCUSSION

In 1997, Gustafsson and Bremer published an analysis of relationships of Carpodetaceae using *rbcL* only. They

**Table 2.** The species used in the *rbcL*–*ndhF* data matrix, listed according to family (APG, 1998). Accession numbers and references to previously published sequences extracted from the European Molecular Biology Laboratory (EMBL) and GenBank archives are given. Voucher information is given for the three species sequenced for this study, in addition to the accession numbers. The herbarium abbreviations are according to Holmgren *et al.* (1990). (1) Listed in GenBank/EMBL as *C. ramosa*, but this seems to be a non-existent name, and it is assumed that the correct name should be *C. ramosissima* (Hooker & Jackson, 1895; O. Demker, pers. comm.; Kårehed *et al.*, 1999).

Family/species	<i>rbcL</i>	<i>ndhF</i>
Adoxaceae		
<i>Viburnum rhytidophyllum</i> Hemsl.	X87398 (Gustafsson, Backlund & Bremer, 1996)	AF027273 (Oxelmann <i>et al.</i> , 1999)
Alseuosmiaceae		
<i>Alseuosmia macrophylla</i> A. Cunn.	X87377 (Gustafsson <i>et al.</i> , 1996)	AJ238334 (Kårehed <i>et al.</i> , 1999)
<i>Crispiloba disperma</i> (S. Moore) Steenis	X87382 (Gustafsson <i>et al.</i> , 1996)	AJ238338 (Kårehed <i>et al.</i> , 1999)
Araliaceae		
<i>Hedera helix</i> L.	L01924 (Olmstead <i>et al.</i> , 1992; Albert, Williams & Chase, 1992)	AF130203 (Kim, Jansen & Olmstead, unpublished)
Argophyllaceae		
<i>Argophyllum</i> sp.	X87379 (Gustafsson <i>et al.</i> , 1996)	AJ238335 (Kårehed <i>et al.</i> , 1999)
<i>Corokia cotoneaster</i> Raoul	L11221 (Xiang <i>et al.</i> , 1993)	AJ238337 (Kårehed <i>et al.</i> , 1999)
Asteraceae		
<i>Barnadesia caryophylla</i> (Veill.) S. F. Blake	L13859 (Michaels <i>et al.</i> , 1993)	L39394 (Kim & Jansen, 1995)
Calyceraceae		
<i>Boopis anthemoides</i> Juss.	L13860 (Michaels <i>et al.</i> , 1993)	L39384 (Kim & Jansen, 1995)
Campanulaceae		
<i>Campanula ramosissima</i> Sibth. & Sm. (1)	L13861 (Michaels <i>et al.</i> , 1993)	L39387 (Kim & Jansen, 1995)
<i>Cyphia elata</i> Harv.	L18796 (Cosner, Jansen & Lammers, 1994)	–
<i>Cyphia rogersii</i> S. Moore	–	AJ238339 (Kårehed <i>et al.</i> , 1999)
<i>Lobelia cardinalis</i> L.	–	AF130187 (Kim, Jansen & Olmstead, unpublished)
<i>Lobelia erinus</i> L.	L13930 (Michaels <i>et al.</i> , 1993)	–
Caprifoliaceae		
<i>Lonicera orientalis</i> Lam.	X87389 (Gustafsson <i>et al.</i> , 1996)	AF027274 (Oxelmann <i>et al.</i> , 1999)
Carpodetaceae		
<i>Abrophyllum ornans</i> Hook.f.	X87375 (Gustafsson <i>et al.</i> , 1996)	AJ238333 (Kårehed <i>et al.</i> , 1999)
<i>Carpodetus serratus</i> J. R. Forst. & G. Forst.	Y08461 (Bremer & Gustafsson, 1997)	AJ238336 (Kårehed <i>et al.</i> , 1999)
<i>Cuttsia viburnea</i> F. Muell.	Y08462 (Bremer & Gustafsson, 1997)	AJ277382; this study; Cejje & Williams s.n., UPS
Donatiaceae		
<i>Donatia fascicularis</i> J. R. Forst. & G. Forst.	X87385 (Gustafsson <i>et al.</i> , 1996)	AJ225074 (Laurent, Bremer & Bremer, 1999)
Escalloniaceae		
<i>Escallonia coquimbensis</i> J. Rémy	L11183 (Morgan & Soltis, 1993)	–
<i>Escallonia rubra</i> (Ruiz & Pav.) Pers.	–	AJ277383; this study; A. Backlund s.n., UPS
<i>Quintinia verdonii</i> F. Muell.	X87394 (Gustafsson <i>et al.</i> , 1996)	AJ238344 (Kårehed <i>et al.</i> , 1999)
Goodeniaceae		
<i>Dampiera spicigera</i> Benth.	X87383 (Gustafsson <i>et al.</i> , 1996)	–
<i>Dampiera diversifolia</i> de Vriese	–	L39386 (Kim & Jansen, 1995)

continued

Table 2 – continued

Menyanthaceae		
<i>Menyanthes trifoliata</i> L.	L14006 (Olmstead <i>et al.</i> , 1993)	L39388 (Kim & Jansen, 1995)
Pentaphragmataceae		
<i>Pentaphragma ellipticum</i> Poulsen	L18794 (Cosner <i>et al.</i> , 1994)	AF130183 (Kim, Jansen & Olmstead, unpublished)
Phellinaceae		
<i>Phelline comosa</i> Labill.	X69748 (Savolainen <i>et al.</i> , 1994)	AJ238342 (Kårehed <i>et al.</i> , 1999)
Rousseaceae		
<i>Roussea simplex</i> Sm.	AF084477 (Koontz & Soltis, 1999)	AJ277384; this study; Herbarium, Mauritius Sugar Industry Research Institute
Stylidiaceae		
<i>Forstera bellidifolia</i> Hook.f.	AJ225056 (Laurent <i>et al.</i> , 1999)	AJ225082 (Laurent <i>et al.</i> , 1999)
<i>Stylidium graminifolium</i> Sw.	L18790 (Cosner <i>et al.</i> , 1994)	AJ225076 (Laurent <i>et al.</i> , 1999)

obtained high support values for a *Carpodetus–Cuttsia–Abrophyllum* clade and the *Cuttsia–Abrophyllum* sister relationship. However, they did not include *Roussea*, as that genus at the time was commonly assumed to be related to *Brexia* and *Ixerba* in the Celastrales. The result of the present investigation, based on both *rbcl* and *ndhF*, also strongly supports a monophyletic Carpodetaceae, but with the addition of the monotypic *Roussea* as the sister taxon to Carpodetaceae.

The morphology of Carpodetaceae was thoroughly discussed by Gustafsson & Bremer (1997), who recognized several characters supporting the monophyly of Carpodetaceae. Of the potential synapomorphies listed by Gustafsson & Bremer (1997), *Roussea* shares the thick petals with a valvate aestivation, as well as pentalocular fruits, while it differs in seed structure and trichome morphology.

The petals of *Roussea* are thick and hairy as in Carpodetaceae and thus similar in appearance but, in contrast to the latter, rather large and also shortly united with each other (e.g. Engler, 1928), and furthermore the indumentum is different (Al-Shammary & Gornall, 1994). The valvate aestivation is a synapomorphy for the Asterales as a whole (Gustafsson & Bremer, 1995; J. Lundberg & K. Bremer, in preparation), and thus cannot be taken as support for the *Roussea–Carpodetaceae* clade.

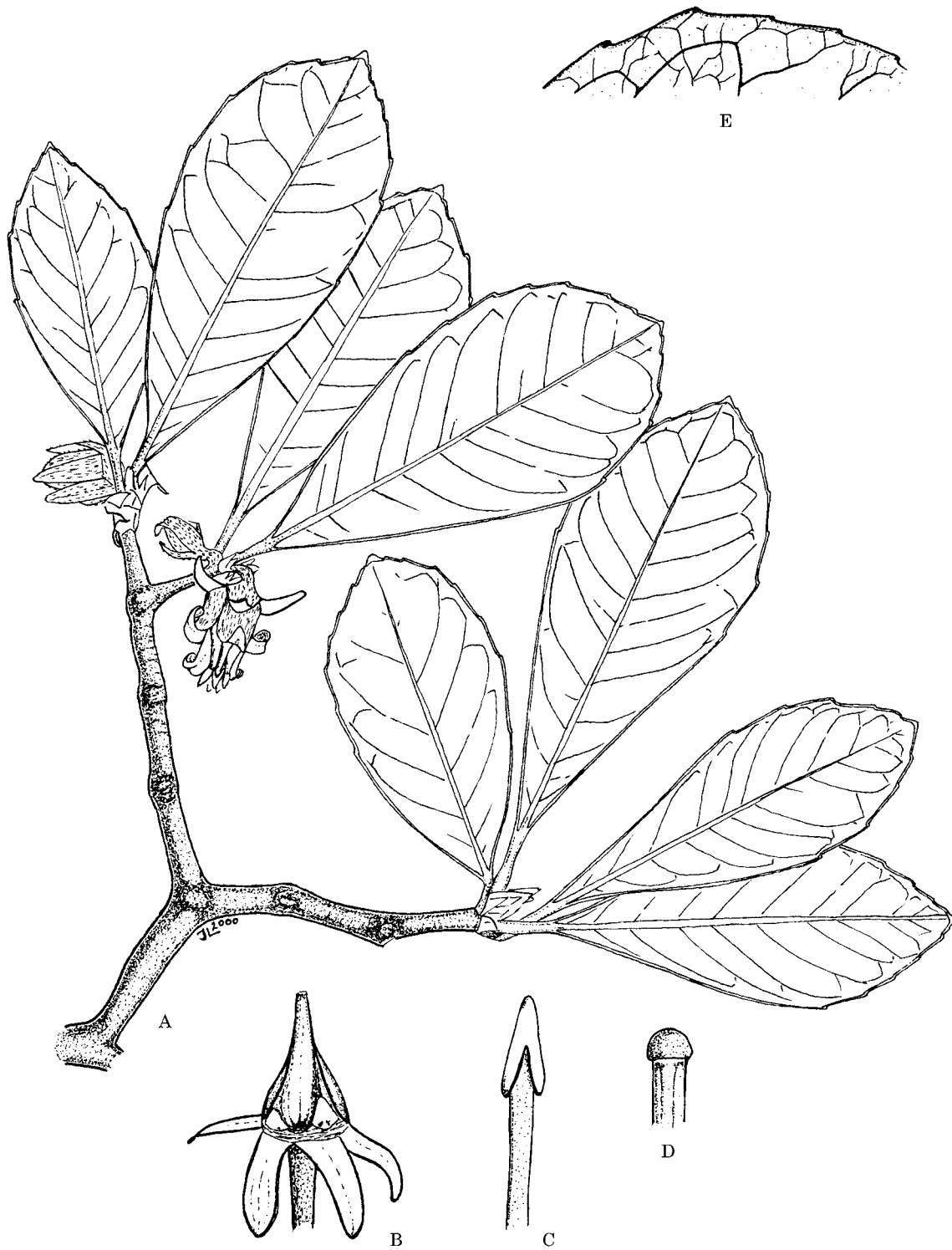
The fruits of *Roussea* are rather large pale green berries with four to five (up to seven) locules (Baillon, 1872; Engler, 1928; Scott, 1997), while the fruits of the Carpodetaceae are variable in shape, size and fleshiness (small, black berries in *Abrophyllum*, small, leathery berries in *Carpodetus*; and loculicidal capsules in *Cuttsia*; Baillon, 1872; Engler, 1928; van Royen, 1983; Gustafsson & Bremer, 1997; Takhtajan, 1997). However, in all genera the fruits are multilocular, a

state not commonly encountered elsewhere in Asterales. Outside the *Roussea–Carpodetaceae* clade they are found in some Campanulaceae, some Argophyllaceae and *Phelline*. These occurrences are most parsimoniously interpreted as parallelisms (J. Lundberg & K. Bremer, in preparation), and the presence in the *Roussea–Carpodetaceae* clade is thus a likely synapomorphy for this clade.

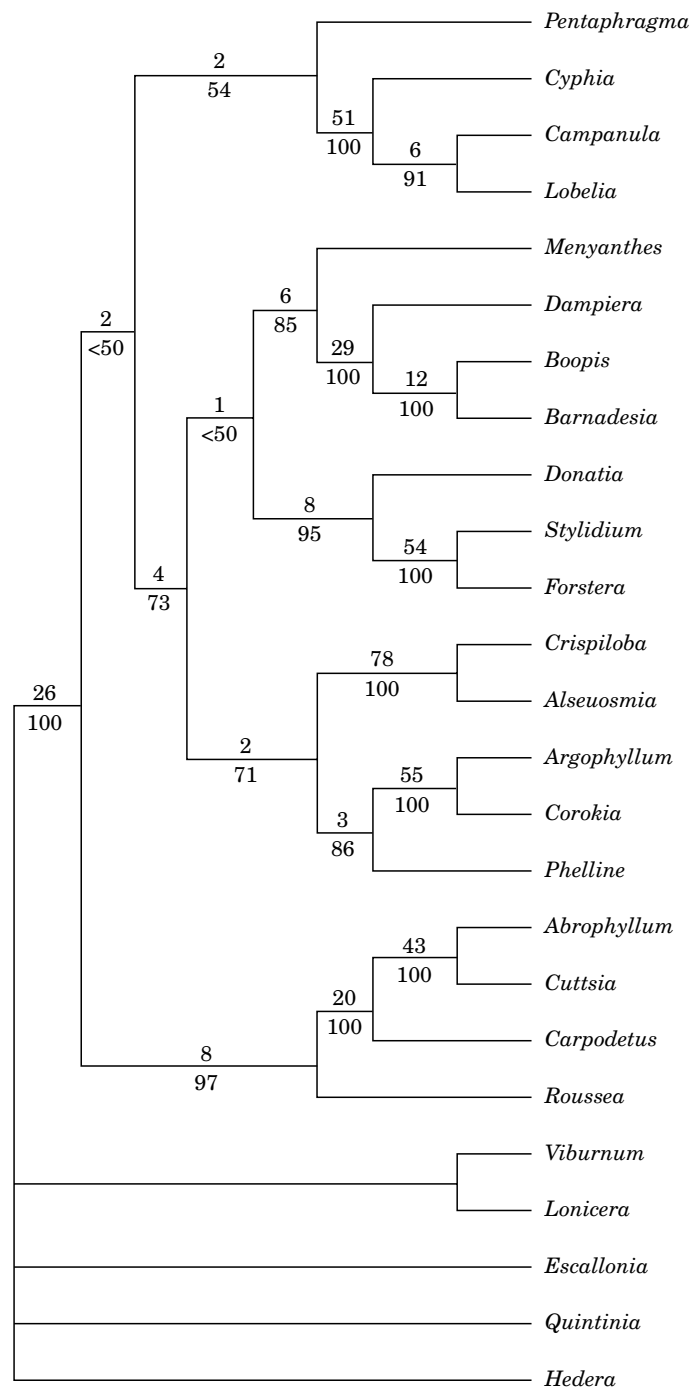
#### ONE FAMILY OR TWO?

The family Rousseaceae is monogeneric (and monospecific) with a single family, Carpodetaceae, as its sister group. As this sister group relationship is well supported, both by the molecular data set and by supposed morphological synapomorphies, a merging of these two families into one seems to be desirable (for a discussion on the topic, see Backlund & Bremer, 1998). The two clades also merit formal recognition in order to highlight the differences in morphology and distribution. The subfamily rank seems best fitted for this purpose, as this will give the clades a formal rank without giving too much emphasis to them. Although this will create a monotypic and thus redundant subfamily, Rousseoideae, the alternative not to recognize the two clades will only obscure the close relationships between *Abrophyllum*, *Carpodetus* and *Cuttsia*.

The family name Rousseaceae, validly published in 1839 (de Candolle, 1839), has priority over Carpodetaceae, validly published in 1841 (Fenzl, 1841). Thus, the merged family should be named Rousseaceae. In this new circumscription it contains four genera and six species. For the formal classification of Rousseaceae *s.l.*, refer to Appendix 1, and for a description of subfamily Rousseoideae, see Appendix 2. Subfamily Carpodetoideae (as 'family Carpodetaceae')



**Figure 1.** *Roussea simplex*. A, habit, branch with flower and flower buds. B, fruit with attached calyx. C, stamen with anther. D, style with stigma. E, leaf margin. (Original drawing by J. Lundberg from herbarium material, C. Barday 2853, K.)



**Figure 2.** Strict consensus tree of the two equally parsimonious trees obtained by parsimony analysis of *rbcL* and *ndhF* sequences from the Asterales and five outgroups from related orders (*Viburnum* through *Hedera*).

have been described in a similar way by Gustafsson & Bremer (1997).

#### A NOTE ON THE DISTRIBUTION

Rousseaceae, in its new wider circumscription, has a wide and peculiar distribution. Carpodetoideae conform with the general Australasian distribution of Asterales (Bremer & Gustafsson, 1997), with *Cuttsia* and *Abrophyllum* restricted to eastern Australia (New South Wales and Queensland) and *Carpodetus* more widely distributed in New Zealand, New Guinea and the Solomon Islands. Rouseoideae with its single genus *Roussea*, in contrast, is confined to Mauritius, an island located some 7700 km west of the Australian east coast. Mauritius is a volcanic island, with an estimated subaerial age of about 8 Myr (Upton, 1982). A direct dispersal to Mauritius of the ancestor of *Roussea* from the Australasia must thus have been taken place not earlier than Pliocene. However, there are other possibilities, involving migrations and subsequent extinctions from areas where Rouseaceae today are absent. Madagascar is one possibility, India is another. As the biogeography of the Indian Ocean area still is insufficiently known, a further analysis of the biogeography of Rouseaceae must be postponed.

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## APPENDIX 1

## CLASSIFICATION OF ROUSSEACEAE S.L.

Rousseaceae A. P. de Candolle (1839: 521, as 'Ordo CVIII. Roussæaceæ')

Carpodetoideae (Fenzl) J. Lundberg, stat. nov. Basionym: Carpodetaceae Fenzl, Denkschr. Königl.-Baier. Bot. Ges. Regensburg 3(1841): 155. Type: *Carpodetus* J. R. Forst. & G. Forst.

*Abrophyllum* Hook.f.

*Carpodetus* J. R. Forst. & G. Forst.

*Cuttsia* F. Muell.

Rousseoideae Horaninow (1847)

*Roussea* Sm.

## APPENDIX 2

## ROUSSEOIDEAE, A BRIEF DESCRIPTION

The following description is based on original observations and on data from Agababian (1964), Al-Shammary & Gornall (1994), Hideaux & Ferguson (1976), Ramamonjarisoa (1980), Scott (1997), Stern, Brizicky & Eyde (1969), Swamy (1954) and Watari (1939).

Climbing shrub, sometimes strangler, up to 4 m in height. Trichomes of two types: glandular, peltate hairs with multicellular heads, and eglandular, uniseriate (up to four cells tall) or unicellular, borne either solitary or in clusters. Vessels with very oblique end walls and scalariform perforation plates with an average of 20 (up to 49) bars; lateral pitting scalariform or occasionally transitional; spiral thickenings absent. Imperforate tracheary elements (tracheids and fibre-tracheids) with bordered pits and without septa. Wood-rays tri- to multi-seriate, heterogenous. Axial parenchyma scanty paratracheal. Nodes trilacunar. Leaves opposite and sometimes in pseudo-whorls, simple, petiolate, and stipulate with serrate-glandular margins and semi-craspedodromous venation; petiole and lamina with radially elongated, schizogynous resin canals. Leaf epidermal and hypodermal cells often filled with an unknown, smooth substance (staining with safranin). Stomata anomocytic. Flowers solitary or few, borne in the leaf axis. Calyx parts 4–5, united at the base; calyx lobes rather large, light green, thick, as young with eglandular hairs on both sides but later more or less glabrous, valvate in bud, persistent. Corolla parts 4–5, united at the base; petals rather large, yellow to orange, thick, with eglandular hairs outside, valvate in bud, persistent. Stamens isomerous and alternating with petals, inserted within the lobes of the nectary disc. Anthers large, oblong-sagittate, tetrasporangiate and dithecal, extrorse, opening by longitudinal slits, basifixed. Pollen grains isopolar, polyporate, with smooth and complete tectum, dispersed in monads; collumella reduced, not branched. Style glabrous, thick, unbranched, persistent. Stigma capitate, 4–5-lobed, revolute at margins. Ovary superior, pyramidal, 4–5-angular and gradually tapering into the style, 4–5(–7)-locular with many, distinctly two-ranked ovules on thick, axile placentas. Fruit an angular, 4–5(–7)-locular, fleshy berry with a dilated base. Seeds numerous, flattened, ovoid, exotestal. Testa with elongated epidermis cells with a strongly undulating outline and thickened and lignified cell walls. Endosperm copious, embryo straight, minute. Tannins absent.