Morphological analysis and a resolution of the *Ryparosa javanica* species complex (Achariaceae) from Malesian and Australian tropical rainforests

Bruce L. Webber[A,B] *and Ian E. Woodrow*[A]

[A]School of Botany, The University of Melbourne, Vic. 3010, Australia.
[B]Current address: School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, Norfolk NR4 7TJ, UK. Corresponding author. Email: b.webber@bigfoot.com

Abstract. A study of morphological variation in *Ryparosa javanica* (Blume) Kurz ex Koord. & Valeton *sensu lato* (Achariaceae; Flacourtiaceae *pro parte*) was undertaken after distinct differences were observed between Australian and Bornean populations. The confusing taxonomic history of *R. javanica* is first summarised. Phenetic techniques of agglomerative classification and ordination were used to analyse herbarium and field-collected specimens. Distinct groupings based on vegetative characters were supported by reproductive traits, plant architecture, ant–plant associations and geographical discontinuities. This work demonstrates that the current circumscription of *R. javanica* is a complex of at least nine species: *R. javanica sensu stricto* now confined to Sumatra, Java and Bali; three species that warrant reinstatement: *R. amplifolia* (K.Sch.) Mildbr. from New Guinea, *R. kurzii* King from the Andaman and Nicobar Islands and *R. wrayi* King from southern Myanmar and Thailand, the Malay Peninsula and northern Sumatra; and five new species described as *R. maculata* B.L.Webber from eastern New Guinea, *R. anterides* B.L.Webber from eastern Borneo, *R. milleri* B.L.Webber from New Guinea, *R. maycockii* B.L.Webber from western Borneo and *R. kurrangii* B.L.Webber from northern Australia. A key to the species and commonly mistaken taxa is provided.

Introduction

Ryparosa Blume is a small genus of ∼19 tropical rainforest tree species placed within the relatively homogeneous tribe Pangieae according to all recent treatments (Hutchinson 1967; Lemke 1988; Takhtajan 1997; Chase *et al*. 2002). Pangieae have recently been included in Achariaceae *sens. lat.* (Chase *et al*. 2002) and are distributed largely in the Austro-Malesian region (Sleumer 1954*a*), with the only representatives of the tribe from outside this region being the monotypic genus *Chiangiodendron* T.Wendt (Mexico and Central America; Wendt 1988; Sosa *et al*. 2003) and *Kiggelaria* L. (southern Africa; Dahlgren and van Wyk 1986). *Ryparosa* has its greatest diversity in Borneo and is distributed from Myanmar throughout south-east Asia and New Guinea, with the rainforests of northern Australia forming the south-eastern limits.

Achariaceae *sensu* Chase *et al*. (2002) are united by the presence of cyanogenic glycosides, wood with mostly solitary pores and no tracheids, more petals than sepals (without any specific relative orientation of parts) and typically linear anthers, and differ from the Salicaceae *sensu* Chase *et al*. (2002) in their lack of a disk and

salicoid leaf dentation. Chase *et al*. (2002) emphasised that Flacourtiaceae, in which *Ryparosa* was included, had a reputation as being confusing and largely unrecognisable in the field; specimens of Flacourtiaceae are frequently confused with those of Euphorbiaceae (Sleumer 1954*a*) and are known to have no single character to distinguish them from other families (Lemke 1988). Of the 30 genera previously in Flacourtiaceae incorporated into the revised Achariaceae, 14 are monospecific and *Ryparosa* is the most speciose genus after *Hydnocarpus* Gaertn., a south-east Asian taxon of ∼40 species. *Ryparosa* is similar to other Pangieae in having small, unisexual flowers, sepals and petals in separate whorls distinguishable from each other, and petals with a fleshy scale adaxially (Hutchinson 1967; Chase *et al*. 2002). As a genus, *Ryparosa* is distinguished by its multi-flowered racemes (perhaps with the exception of *R. porcata* P.F.Stevens; Jarvie and Stevens 1998), a lack of stipules and bifurcate T-shaped hairs (often with one branch strongly reduced).

Ryparosa was first found in Australia in the mid-1960s in the Cape Tribulation region in far north Queensland. Based on the descriptions of Sleumer (1954*a*), the specimens

collected were assigned to *R. javanica* (BPM Hyland pers. comm.). This meant that the geographical distribution of *Ryparosa javanica sensu* Sleumer (1954*a*) ranged from southern Myanmar and the Andaman Islands, throughout the Malesian islands and as far east as New Guinea and northern Australia. No other species of *Ryparosa* is known from such a wide region, *R. kunstleri* (Malay Peninsula, Sumatra), *R. hullettii* King (Borneo, Malay Peninsula), *R. acuminata* Merr. (Borneo, Malay Peninsula, Thailand) and *R. caesia* (Java, Sumatra) being the only other species with relatively widespread distributions (Sleumer 1954*a*, 1985; for some of these species this is most likely because of incorrect determinations, BL Webber unpubl. data).

Sleumer's 1954 study (Sleumer 1954*a*) remains the most recent generic revision of *Ryparosa* and only one new species, *R. porcata* from Borneo, has been described in the last 50 years (Jarvie and Stevens 1998). More recently, our interest in the wide geographical range of *R. javanica* was rekindled during fieldwork on the island of Borneo in 2000. Several localities at which *R. javanica* populations were supposed to occur in Brunei Darussalam and the Malaysian state of Sabah were visited, but the plants there differed from those growing in Australia. A preliminary examination of herbarium specimens determined as *R. javanica sens. lat.* indicated that species delimitation in *Ryparosa* was unsatisfactory and based on unsuitable (i.e. poorly described and incorrectly interpreted) characters. Therefore, the objective of this study is to combine a field-based knowledge of vegetative and reproductive characteristics of *Ryparosa javanica sens. lat.* with those acquired from preserved herbarium specimens, and to delimit and describe species in a way that accurately reflects patterns of morphological variation. Since *Ryparosa* individuals in the field generally lack much in the way of reproductive structures, a strong emphasis will be placed on understanding vegetative differences within the species complex.

Historical taxonomy of Ryparosa javanica sens. lat

Ryparosa javanica (Blume) Kurz ex Koord. & Valeton was originally described as *Bergsmia javanica* Blume, based on specimens collected in 1821 in the Bantam region of West Java by Kuhl and van Hasselt (Blume 1848). Kurz (1873) later recognised the similarity between Blume's *Bergsmia* and the genus *Ryparosa,* with the sole taxon at the time, *Ryparosa caesia* Blume (placed in the Euphorbiaceae), described by Blume in 1825. Apparently by inadvertence, in the preface of his Flora Javae, Blume (1828) referred to the genus *Ryparosa* as *Ryparia*, adding more confusion to the already muddled situation. Subsequently, the family alliance of *Bergsmia* and *Ryparosa* (and *Ryparia*) became uncertain, as Bentham and Hooker (1867) listed *Bergsmia* in the Euphorbiaceae but later excluded *Ryparosa* from the same family, as a genus of dubious affinity, making no suggestion as to its most appropriate taxonomic position (Bentham and Hooker 1880).

At around the same time, Kurz (1873) merged *Bergsmia* and *Ryparosa* into the genus *Ryparia*, and was the first person to include the genus in the tribe Pangieae in the Bixaceae (Kurz 1873, 1876, 1877; King 1890). In 1890, King and colleagues (King 1890; Brühl and King 1896) cleared up the confusion between *Ryparia* and *Ryparosa,* using the latter (and original) name in his description of new species from the Malay Peninsula.

All *Ryparosa* specimens from the Andaman and Nicobar islands were originally determined by Kurz as *Ryparia caesia* (Kurz 1876, 1877); however, King (1890) thought that Kurz was mistaken, and described these specimens as *R. kurzii*. In 1900, Koorders and Valeton (1900*a*) redefined *Ryparosa javanica* in relation to two other species of *Ryparosa* – *R. caesia* and *Ryparosa longipedunculata* Boerl. However, Koorders and Valeton expressed a lack of confidence in the diagnostic characters they used to distinguish these species, and shortly afterwards they merged *R. javanica* and *R. longipedunculata* on account of the type specimen for *Ryparia javanica* being somewhat 'abnormal' (Koorders and Valeton 1900*b*). Koorders and Valeton (1900*b*) also merged *Ryparosa kurzii* King and *Ryparosa kunstleri* King with *R. javanica* without any explanation.

The next substantial treatment of the genus (now ascribed to the Flacourtiaceae) was between 1919 and 1925 by van Slooten (1919, 1925), who conducted an extensive revision of the Flacourtiaceae of the Dutch East Indies. In this work, van Slooten resurrected *R. kunstleri* and concluded that the decision of Koorders and Valeton to combine *R. kurzii* with *R. javanica* was most likely incorrect (van Slooten 1919).

By the first half of the 19th century, some 24 species of *Ryparosa* had been described, but there had been no synthesis of the entire genus. As part of the Flora Malesiana series, Sleumer (1954*a*) produced a detailed revision of the genus between 1953 and 1958. During this revision, Sleumer described *Ryparosa baccaureoides* Sleumer and *R. kostermansii* Sleumer (Sleumer 1954*b*), from Bornean material that had been identified as *R. javanica*. Going against the recommendations of van Slooten (1919), Sleumer combined *R. kurzii* with *R. javanica*, but left *R. kunstleri* as a distinct species. Sleumer also decided to merge *Ryparosa wrayi* King, *Ryparosa amplifolia* (K.Sch.) Mildbr. and *R. caesia* from Dutch New-Guinea (van Slooten 1924; based on one specimen) with *R. javanica*, despite these species having several distinct differences from *R. javanica sens. str.* For example, Sleumer recognised that *R. amplifolia* had nearly twice the number of leaf secondary veins to *R. javanica* (Sleumer 1954*a*), yet failed to mention that descriptions of the former species had consistently noted swollen stems with ant domatia and a dense indumentum on the abaxial leaf surface (Schumann and Lauterbach 1901; Gilg 1918; Mildbraed 1928).

Ryparosa wrayi was first described by King (1890) and the species was retained by van Slooten in his

revision of the genus (van Slooten 1919, 1925). *Gertrudia amplifolia* K. Sch., of the monotypic *Gertrudia* described by Schumann and Lauterbach (1901), was originally placed in the Flacourtiaceae–Pangieae–Hydnocarpinae, close to *Trichadenia* because it had 'single ovules on the placenta'. Gilg (1918) questioned this alignment of *G. amplifolia*, based on an examination of flowers that were subsequently shown to belong to *Scleromelum aurantiacum* K. Schum. & Lauterb. (= *Scleropyrum aurantiacum* Pilg.), hardly surprisingly concluding that *Gertrudia* belonged neither to Flacourtiaceae nor Euphorbiaceae. Mildbraed (1928) recognised that Gilg's (1918) description was based on a mixed collection and combined *Gertrudia* with *Ryparosa*, as *Ryparosa amplifolia* (K. Sch.) Mildbr., based on the presence of bifid hairs (unique to *Ryparosa* in the Flacourtiaceae), an irregularly rupturing calyx and petals with a hairy scale adaxially. At the same time he described *Ryparosa calotricha* Mildbr. (Mildbraed 1928).

Sleumer (1954*a*) created a rather broad taxon description to accommodate all the species he merged with *R. javanica*. He described *R. javanica sens. lat.* as being a dioecious tree between 15 and 30 m in height, with small flowers on racemes from cauline tubercles, leaf axils or defoliate branchlets, and leaf blades between 120 and 450 mm long with a glabrous or hairy abaxial surface and between five and nine secondary vein pairs. Unfortunately, to those unfamiliar with *Ryparosa*, it created the situation where almost any specimen could be keyed out to *R. javanica*. Furthermore, the only two images of *R. javanica* (tree *III-F-15* from the Bogor Botanic gardens) included in his account in the Flora Malesiana were not only uninformative in terms of characters used to delineate the species, but the figure legends were also incorrect.

It seems as if Sleumer's decision to unite *R. javanica*, *R. kurzii*, *R. wrayi* and *R. amplifolia* was primarily on account of the staminal column being pilose in the upper half in staminate flowers, in contrast to the glabrous staminal columns described for other *Ryparosa* species (Sleumer 1954*a*). He described the indumentum on the vegetative plant parts as being caducous and placed a low emphasis on the importance of the inflorescence position on a tree, although he noted that the characters used for specific distinctions in *Ryparosa* were difficult. Moreover, Sleumer chose not to describe four apparently new species because the specimens available were inadequate, and instead determined these specimens as *R. javanica*.

Materials and methods

Collections

Material was borrowed from 15 herbaria (BM, BO, BRI, CANB, K, KEP, L, LAE, MEL, MELU, NSW, NY, QRS, SING, UPNG; herbarium abbreviations following Holmgren *et al*. 1990) and comprised 304 specimens currently determined as *Ryparosa javanica sens. lat.*, 19 undetermined *Ryparosa* and 15 specimens of other *Ryparosa* species. These specimens were collected between 1821 and 2003 throughout south-east Asia from southern Myanmar and the Andaman Islands, throughout the Indo-Malesian islands, New Guinea and northern Australia. Many old specimens are in a very poor condition and most of specimens have few flowers or fruits. Most specimens had also been seen by Sleumer in his revision of Malesian Flacourtiaceae in the 1950s (Sleumer 1954*a*). Eight recently collected specimens that had not been seen by Sleumer and that were clearly not *Ryparosa* (five sheets determined as *R. javanica*, three sheets determined as *Ryparosa* sp.), were excluded to eliminate the coding of unnecessary characters. However, two specimens from L that were very unlikely to be *Ryparosa*, but had been clearly determined as *R. javanica* by Sleumer in 1974 (*Balakrishnan & Bhargava, 3465*; *Nair, 3639*), were included.

Specimen mapping

To determine accurately distributions, geographical information for collection locations was collated. Because many specimens had been collected in the first half of last century, very few specimens had latitude and longitude information, and many had poorly written or limited location data. Geographical coordinates for such specimens were collected from associated maps and gazetteers (e.g. Australian Army Royal Australian Survey Corps 1942–1945; United States Army 1943–1946; Royal Army of Great Britain Royal Engineers 1969; Rosenberg 1996–2004; Spot Domain 2000–2005), compared against expedition schedules, itineraries and collecting locality details for early south-east Asian taxonomists (e.g. Koorders-Schumacher 1913; Van Steenis 1958; Van Steenis-Kruseman 1958) and cross-referenced against Google Earth software (Google Inc. 2005).

Morphometric analysis

A list of 68 vegetative and reproductive characters was assembled to code the specimens. These characters were based on observations made during six years of fieldwork on *Ryparosa*, the early works of van Slooten (1919, 1925) and the revision of Sleumer (1954*a*). Several characters used in earlier revisions were deemed inappropriate and excluded, based on field knowledge of the genus and an initial inspection of the material. First, all characters based on specimen colour were confounded by the wide range in specimen age and preservation techniques. Second, stem lenticels are easily confused as food-body scars, eliminating lenticels as a useful character. Food-body production in *Ryparosa* has recently been discovered (Webber 2005) and the ant–plant associations of the genus (including specialised stem domatia, food bodies and hemipteran trophobionts) will be described in detail elsewhere (Webber *et al*. 2006, 2007). Third, several characters have been observed to change during leaf expansion and toughening (Webber 2005), so only specimens with mature foliage were measured. Lastly, reproductive characters were significantly under-represented relative to all others owing to dimorphous flowers and the distinctive reproductive phenology (e.g. widespread flowering only every 2–3 years, staminate and pistillate racemes temporally separated on individual trees; Webber 2005) of *Ryparosa*. Hairs on the fruit epicarp surface were commonly abraded on older specimens and seemed to show strong ontogenetic variation. Standardising the considerable developmental variation in reproductive characters was difficult, and while this was helped by stratification (based on raceme maturity), it only served to further reduce the number of specimens with precisely defined reproductive characters in common.

The final character list contained 65 individual characters and three derived ratios (Table 1). These were composed of 25 continuous quantitative, eight discrete quantitative and 35 discrete qualitative characters. All characters were expressed quantitatively where reasonably possible, to avoid misrepresenting the potential range of variation (Stevens 1991; Thiele 1993). Terminology and character

Table 1.   Characters used for the morphometric analysis of *Ryparosa javanica sens. lat.*

Vegetative characters (1–29) were used for phenetic analysis while reproductive characters (30–68) were reserved for taxon descriptions. Leaf blade width and leaf blade tip were excluded from the final phenetic analyses while some characters could only be measured on staminate and carpellate racemes, respectively

No.	Character	Abbreviation	Description
1	Petiole length	PLength	Petiole length (mm)
2	Leaf blade length	LLength	Leaf blade length (mm)
3	Leaf blade width	LWidth	Leaf blade width (mm)
4	Leaf blade width : length	LeafW : L	Leaf blade width-to-length ratio
5	Widest point of leaf blade	LTWPR	Point of maximum leaf blade width in relation to leaf apex
6	Leaf blade tip	LTip	Leaf tip long-acuminate (1), acuminate (2), acute (3), obtuse (4) or mucronate (5)
7	Leaf blade tip angle	LTipA	Angle of upper 25% of the leaf blade
8	Leaf blade base 1	LBase1	Leaf blade base oblique (0) or not (1)
9	Leaf blade base 2	LBase2	Leaf blade base cordate (0) or acute (1)
10	Leaf blade base 3	LBase3	Leaf blade base cuneate (1), attenuate (2) or rounded (3)
11	Leaf base angle	LBaseA	Angle of lower 25% of the leaf blade
12	Length-vein ratio	LTVR	Distance from leaf tip to its most proximal secondary vein, as a proportion of total leaf blade length
13	2° vein number	SVeinN	Number of secondary veins on right side of the primary vein (abaxial assessment)
14	Lower 2° vein angle	SVeinAL	Angle formed between the primary and secondary veins (Fig. 1, θ_1)
15	Upper 2° vein angle	SVeinAU	Angle (at a point where a secondary vein departs) formed between the primary vein and the leaf edge adjacent to the first anastamosis branching point of the secondary vein (Fig. 1, θ_2)
16	Adaxial 1° vein position	UPVPos	Leaf blade primary vein depressed (1), flat (2) or raised (3) relative to the lamina
17	Adaxial 2° vein position	USVPos	Leaf blade secondary veins depressed (1), flat (2) or raised (3) relative to the lamina
18	2° vein position ratio	SVeinPR	Position of secondary veins on the lamina, relative to the leaf edge [Fig. 1, $a/(a+b)$]
19	2° vein anastamosis 1	SVeinA1	Secondary veins acrodromous (0) or camptodromous (1)
20	2° vein anastamosis 2	SVeinA2	Camptodromous secondary veins distinctly eucamptodromous (1) eucamptodromous (2), brochidodromous (3) or strongly brochidodromous (4)
21	2° vein branching	SVeinBr	Secondary veins branching (1) or not (0)
22	2° vein course	SVCorse	Secondary veins jagged and undulate (0) or distinctly smooth (1)
23	2° vein curvature	SVCurv	Secondary veins strongly curved-ascending (1), moderately curved-ascending (2), or straight for the most part (3)
24	3° venation	TertVein	Pattern of tertiary vein reticulation densely reticulated (1) reticulated (2), somewhat reticulated (3), somewhat percurrent (4), percurrent undulate (5), percurrent straight (6)
25	Lamina texture	LeafTex	Leaf lamina distinctly coriaceous (0) or chartaceous (1)
26	1° vein hair	PVHairD	Primary vein abaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
27	2° vein hair	SVHairD	Secondary veins abaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
28	Lamina hair	LHairD	Lamina abaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
29	Stem swellings	SSwell	Distinctive stem swellings present in branches and/or shoot tips (1) or not (0)
30	Raceme flowers	RacFl	Raceme flowers carpellate (1), staminate (2) or unknown (3)
31	Raceme maturity	RacMat	Raceme with buds (1), flowers (2), immature fruits (3) or mature fruits (4)
32	Raceme position	RacPos	Racemes borne supra-foliate-axillary (1), foliate-axillary (2), defoliate axillary (3), ramiflorous (4), cauliflorous (5) or basi-cauliflorous (6)
33	Raceme length	RacL	Raceme length (mm)
34	Pedicel length	PedL	Pedicel length (mm)
35	Pedicel width	PedW	Pedicel width (mm)
36	Pedicel bract presence	Bracts	Bracts present (1) or absent (0)
37	Pedicel bract length	BractL	Bract length (mm)
38	Calyx lobe number	CalLobeN	Calyx lobe count
39	Calyx division	CalDiv	Calyx division dehiscent (0) or randomly tearing (1)
40	Calyx hair density 1	CalHAd	Calyx adaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
41	Calyx hair density 2	CalHAb	Calyx abaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
42	Calyx width	CalW	Calyx width (mm)
43	Calyx length	CalL	Calyx length (mm)
44	Petal number	PetalN	Petal count
45	Petal hair density 1	PetHAd	Petal adaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
46	Petal hair density 2	PetHAb	Petal abaxially glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs

Table 1.   (*continued*)

No.	Character	Abbreviation	Description
47	Petal width	PetW	Petal width (mm)
48	Petal length	PetL	Petal length (mm)
49	Petal scale width	PetScW	Petal scale width (mm)
50	Petal scale length	PetScL	Petal scale length (mm)
51	Petal scale hair density	PetScH	Petal scale with sparse (1), moderate (2) or dense (3) hairs
52	Stamen number[A]	StamenN	Stamen count
53	Stamen length[A]	StamenL	Stamen length (mm)
54	Filament relationship[A]	FilCon	Filaments free (0) or united (1)
55	Filament hair density[A]	FilHairD	Filaments glabrous, or with sparse (1), moderate (2) or dense (3) hairs
56	Filament hair position[A]	FilHPos	Filaments entirely hairy (1) or hairy only on the upper (2) or lower (3) portion
57	Staminode number[B]	StamndN	Staminode count
58	Staminode length[B]	StamndL	Staminode length (mm)
59	Staminode shape[B]	StamndS	Staminodes stocky and fleshy (0) or thin and stick-like (1)
60	Staminode hair density[B]	StamndHD	Staminodes glabrous (0) or with sparse (1), moderate (2) or dense (3) hairs
61	Staminode hair position[B]	StamndHP	Staminodes entirely covered in hairs (0) or with hair only on the adaxial surface (1)
62	Stigma number[B]	StigmaN	Stigma count
63	Style definition[B]	StyleDef	Styles short with sessile stigmas (0) or stigmas slightly raised on short styles (1)
64	Stigma spacing[B]	StigSpac	Stigmas close together (1) slightly separated (2) or distinctly separated (3)
65	Ovary length[B]	OvaryL	Ovary length (mm)
66	Ovary width[B]	OvaryW	Ovary width (mm)
67	Locule number[B]	LoculeN	Locule count
68	Seed number[B]	SeedN	Seed count

[A]Characters measured on staminate racemes only.
[B]Characters measured on carpellate racemes only.

definitions follow that of Radford *et al.* (1974) and Hickey (1979). Leaf venation characters (14–24, Table 1; after Hickey 1979) and hair density characters (26–28, Table 1) were recorded at a point closest to one-third of the distance from the leaf base. However, these characters were consistent and held for the entire lamina surface, with the exception of the angles of the most apical and basal secondary veins. All measurements were measured in laboratory conditions using a dissecting microscope (magnification 20×) to score hair and food-body characters. The mean value for up to three measurements of each character was recorded for each specimen (less when the specimen did not provide enough material).

Phenetic analyses

The final data matrix used in phenetic analyses included 206 specimens (*R. javanica sens. lat.*, $n = 182$; other *Ryparosa* species, $n = 14$; undetermined *Ryparosa*, $n = 10$) measured for 27 characters (characters 1, 2, 4, 5, 6 to 29; Table 1). Leaf width (character 3) was not included as a character as it was highly correlated with leaf length (Pearson correlation 0.77). Moreover, the two ratios leaf width : length (character 4; Table 1) and leaf widest point (character 5; Table 1) gave a better indication of overall leaf shape. Leaf tip shape (character 6; Table 1) was also excluded owing to missing data on many specimens and difficulties in accurately describing the observed variation. Given the extremely limited amount of data that could be collected from the available specimens for reproductive characters, it was decided to remove these characters (characters 30–68; Table 1) from any phenetic analyses and, rather, present this data as supplementary information. The PATN software package (Belbin 1995) and the Gower metric distance measure (Gower 1971) were used to construct a dissimilarity matrix for subsequent cluster and ordination analyses. The Gower metric is a range-standardised coefficient of similarity (Sneath and Sokal 1973), and is applicable to a combination of both continuous and discrete characters, as in this dataset. Both cluster and ordination

analyses were performed with the PATN software package (Belbin 1995). The flexible unweighted pair group method of averaging (UPGMA; Sokal and Michener 1958) was used to produce a hierarchical, agglomerative classification ($\beta = -0.25$; Sneath and Sokal 1973). Ordinations of the dataset were produced in two and three dimensions using the non-metric multidimensional scaling technique (NMDS; Shepard 1962; Kruskal 1964*a*, 1964*b*; Faith *et al.* 1987). Five ordination analyses were performed using random starting configurations and the ordination with the lowest stress value (i.e. the best 'fit') after 100 iterations was used. Correlations of characters with the ordinations were examined by plotting directions of best fit of the character vectors. Correlation coefficients of vectors with the ordinations were calculated to provide an estimation of the fit of each vector to the observed pattern (Belbin 1995).

The interpretation of these phenetic analyses, including designation of groups and clusters, even if somewhat arbitrary, was informed by a detailed appraisal of the available data and how they fit with (1) current species descriptions and those of previously recognised species; (2) observed geographical and morphometric discontinuities in the specimens at hand; and (3) any other supporting data not included in the morphometric analyses (i.e. reproductive data). Thus, the 18-group level was chosen as that at which groups would be recognised in the UPGMA analysis (Fig. 3). For these reasons, also, interpreting the data at any other level created groupings that did not support the clusters apparent in the ordination (Fig. 4).

Results

Vegetative characters of Ryparosa javanica *sensu lato*

The geographical range (Andaman Islands to northern Australia) of *Ryparosa javanica sens. lat.* specimens included in this study covered the entire species distribution described
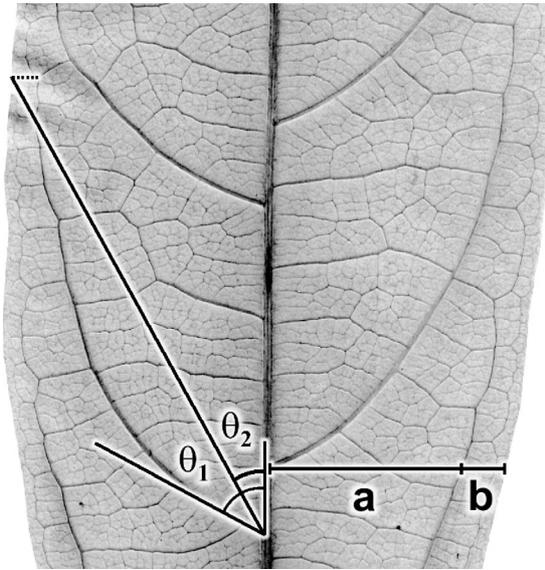
Fig. 1. Nerve descriptor characters used in the morphometric analysis of *Ryparosa javanica sens. lat.*, explained in detail in Table 1.

by Sleumer (1954*a*; Andaman Islands to New Guinea; Fig. 2), over an altitudinal gradient of 5–1450 m, and included trees between 1.2 and 40 m in height that varied considerably in many vegetative attributes (Accessory Publication, Appendix 1; available online at the website of Australian Systematic Botany). Thus, the leaf lamina ranged from being entirely glabrous to densely strigose on the abaxial surface, from 86 to 373 mm in length, and in having between 2 and 11 secondary veins. Venation was acrodromous to camptodromous, with a range of eucamptodromous to clearly brochidodromous types. Leaf blade shape ranged from ovate to distinctly obovate, and lamina bases were oblique, cordate or rounded.

Phenetic classification

An agglomerative classification based on 206 herbarium specimens scored for 27 vegetative characters had a stress level of 0.0147 (merged at a dissimilarity of 0.1; Fig. 3). Specimens were examined at the 18-group level (dissimilarity = 0.25) and the difference between groups was significant ($P < 0.001$). Distinct differences were observed between groups for many measured characters (Appendix 1). Ordination analyses on the same dissimilarity matrix in two dimensions showed distinct (occupying a contiguous area of morphometric space) clustering of specimens (Fig. 4); adding a third dimension resulted in little improvement in the stress values (data not shown). Character vector correlations for the ordinations ranged from 0.22 to 0.86 (Fig. 4). There was no obvious trend between the magnitude of correlation and the type of character for the 27 characters included in analysis (Fig. 4). The clustering of groups in the ordination analysis (Fig. 4) closely corresponded to those groupings generated in the cluster analysis (Fig. 3).

In the UPGMA analysis, there were four distinct clusters of groups – Groups 1–6, Groups 7–9, Groups 10–16 and Groups 17 and 18 (Fig. 3). Group 1, referred to as *R. javanica sens. str.* contained 37 specimens and included the type specimens for *Bergsmia javanica* and *Ryparosa longipedunculata* (Fig. 3). In the ordination analysis, these specimens formed a distinct cluster (Fig. 4). These specimens
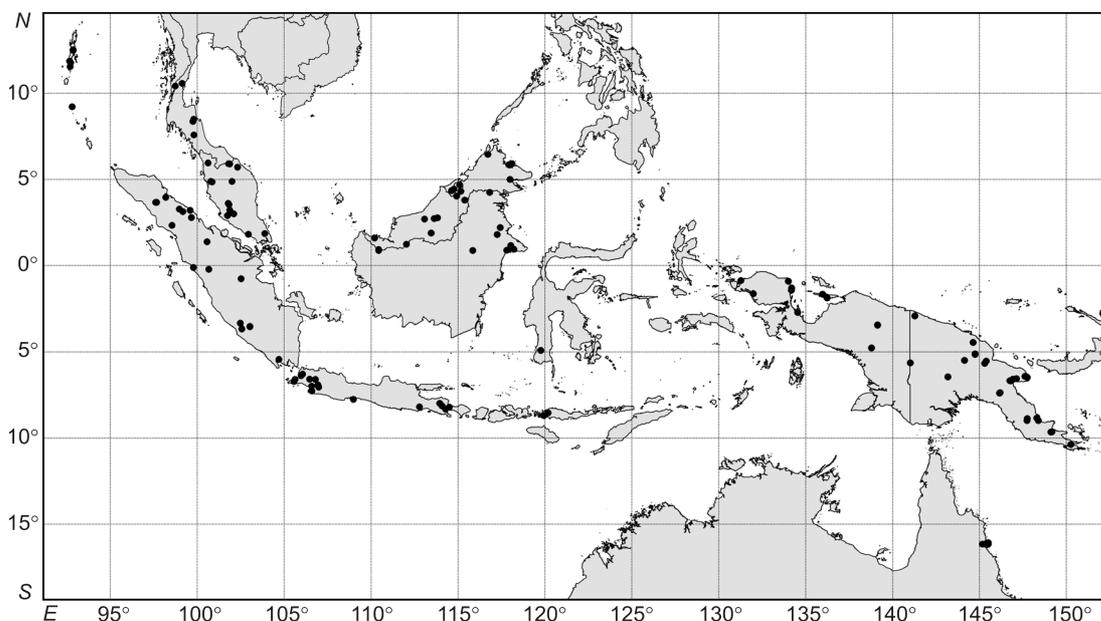
Fig. 2. Collection localities for specimens included in this study ($n = 182$).

covered a geographic range from Bali through Java to Sumatra. Group 1 was the most morphologically variable of the groups; leaf blades varied considerably (mean ± 1 s.e.,
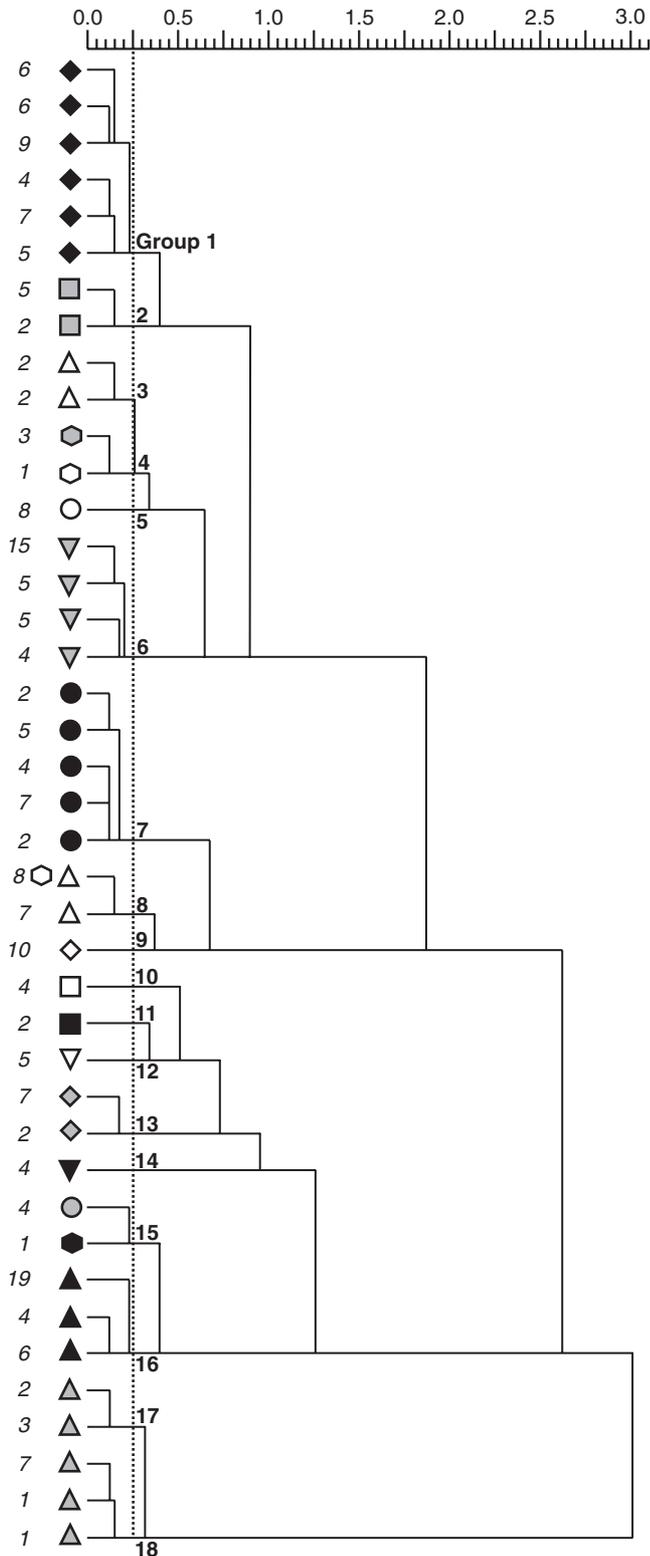
range) in length (241 ± 9.6, 111–317 mm) and width (80 ± 3.3, 37–115 mm), but were elliptic with an attenuate base. Leaf venation was consistently eucamptodromous with six (rarely five or seven) curved-ascending veins, while hairs on the abaxial blade were sparse, particularly away from the veins (Appendix 1).

Group 2 from the cluster analysis, referred to as *R. kurzii sens. str.*, was situated next to, but distinct from, Group 1 in the ordination analysis (Figs 3, 4). Group 2 included seven specimens; all specimens were originally identified as *R. kurzii* and collected from the Andaman and Nicobar Islands. The leaf blades were ovate-elliptic with a base angle of 69–78°. Like *R. javanica sens. str.*, *R. kurzii sens. str.* had curved-ascending, eucamptodromous secondary venation with sparse hairs on the abaxial blade; however, the number of secondary vein pairs was generally six or seven and sometimes eight (Appendix 1).

In the cluster analysis, Group 3 included four specimens from New Guinea; two determined as *R. calotricha*, the other two as *Ryparosa* sp. (Fig. 3). In the ordination analysis, two of these specimens clustered as outliers to specimens corresponding to Group 8, while the other two were aligned near specimens corresponding to Group 7 (hashed data points; Fig. 4). Group 8 from the cluster analysis consisted of 15 specimens; one determined as *R. calotricha* and nine determined as *R.* aff. *javanica*, which also formed a group in the ordination analysis (Figs 3, 4). These specimens were collected in New Guinea, with the exception of one specimen from Sumatra. Group 7 in the cluster analysis consisted of 20 specimens; three determined as *R. amplifolia sens. str.* (including the type specimen for *Gertrudia amplifolia*) from New Guinea and the sole specimen of *Ryparosa* collected from Sulawesi. Also aligning with Group 8 in the ordination were the four specimens from Group 4 in the cluster analysis (Fig. 4). Collected in the 1980s, three of these specimens were from Borneo and determined as '*R.* cf. *javanica* (closest to New Guinea forms)', while the fourth specimen was from Sumatra.

Fig. 3. An agglomerative, hierarchical classification (Gower metric, UPGMA) of 206 herbarium specimens identified as *Ryparosa*, merged at a dissimilarity of 0.1 (β = −0.25, stress = 0.0147). Specimens were scored for 27 vegetative characters (Table 1) and examined at the 18-group level (dotted line; dissimilarity = 0.25). Numbers at left indicate the number of specimens in each terminal, numbers immediately to the right of the symbols are those of specimen groups mentioned in the discussion. Specimen clusters were identified as *Drypetes longifolia* (Putranjivaceae; ■; 11), *Ryparosa acuminata* (◉; 15[1]), *R. baccaureoides* (□; 10), *R. calotricha* (△; 3, 8[1]), *R. glauca* (◇; 13), *R. kostermansii* (▲; 17, 18), *R. multinervosa* (○; 4[1], 8[2]), *R. javanica s. str.* (◆; 1), *R. amplifolia s. str.* (●; 7), *R. kurzii s. str.* (▨; 2), *R. wrayi s. str.* (▽; 6), *R. taxon A* (*R. maculata* sp. nov.; ○; 5), *R. taxon B* (*R. anterides* sp. nov.; ◇; 9), *R. taxon C* (*R. milleri* sp. nov.; ▽; 12), *R. taxon D* (*R. maycockii* sp. nov.; ▼; 14), *R. taxon E* (*R. kurrangii* sp. nov.; ▲; 16), *R.* sp. nov. aff. *acuminata* (●; 15[2]) and *R.* sp. nov. aff. *calotricha* (◉; 4[2]). Numbers refer to specimen groups.

Vector	Character	Correlation	Vector	Character	Correlation	Vector	Character	Correlation
1	PLength	0.28	12	LTVR	0.76	21	SVeinBr	0.52
2	LLength	0.46	13	SVeinN	0.73	22	SVCorse	0.32
4	LeafW:L	0.66	14	SVeinAL	0.85	23	SVCurv	0.85
5	LTWPR	0.30	15	SVeinAU	0.86	24	TertVein	0.80
7	LTipA	0.78	16	UPVPos	0.43	25	LeafTex	0.22
8	LBase1	0.27	17	USVPos	0.51	26	PVHairD	0.76
9	LBase2	0.39	18	SVeinPR	0.73	27	SVHairD	0.84
10	LBase3	0.60	19	SVeinA1	0.67	28	LHairD	0.82
11	LBaseA	0.79	20	SVeinA2	0.77	29	SSwell	0.76

Fig. 4. A two dimensional ordination (NMDS) of 206 herbarium specimens identified as *Ryparosa*, based on 27 vegetative characters (Table 1; stress = 0.1708). Specimen clusters were identified as *Drypetes longifolia* (Putranjivaceae; ■; 11), *Ryparosa acuminata* (⬡; 15[1]), *R. baccaureoides* (□; 10), *R. calotricha* (△; 3, 8[1]), *R. glauca* (◇; 13), *R. kostermansii* (▲; 17, 18), *R. multinervosa* (◯; 4[1], 8[2]), *R. javanica s. str.* (◆; 1), *R. amplifolia s. str.* (●; 7), *R. kurzii s. str.* (▣; 2), *R. wrayi s. str.* (▽; 6), *R. taxon A* (*R. maculata* sp. nov.; ◯; 5), *R. taxon B* (*R. anterides* sp. nov.; ◇; 9), *R. taxon C* (*R. milleri* sp. nov.; ▽; 12), *R. taxon D* (*R. maycockii* sp. nov.; ▼; 14), *R. taxon E* (*R. kurrangii* sp. nov.; ▲; 16), *R. sp. nov. aff. acuminata* (⬢; 15[2]) and *R. sp. nov. aff. calotricha* (◐; 4[2]). Numbers refer to specimen groups from Fig. 3. Hashed *R. calotricha* data points in the ordination space indicate specimens from Group 3 in the cluster analysis; specimens from Sulawesi (S) and Flores (F) are also indicated. Character vector roses show direction of the character vectors in the ordination space, annotated with character numbers. Vector correlations are maximum r-values for character vectors.

Taking into account both cluster and ordination analyses, as well as the condition of the specimens, the following taxon groupings are proposed for the specimens described above. Groups 3 and 8 (with the exception of the Sumatran specimen) from the cluster analysis will be referred to here as *R. calotricha*. Both groups had very similar vegetative

characteristics, differing only in leaf blade width : length (0.46 ± 0.014 for Group 3 compared with 0.35 ± 0.007 for Group 8; mean $\pm$ 1 s.e.) and absence of shoot tip stem swellings (in Group 3; Appendix 1). Leaf blades were elliptic-obovate and generally 155–200 mm in length with (6–)7–8(–9) secondary vein pairs. Venation was

eucamptodromous and secondary venation straight for the most part, with percurrent tertiary venation, and the entire abaxial surface of the leaf blades was densely covered in short adpressed hairs, particularly so on the primary and secondary veins. Moderately swollen hollow stems, sometimes with small round entry holes, were found on some *R. calotricha* specimens (Appendix 1).

Group 7 (*R. amplifolia sens. str.*; containing the type specimen for *G. amplifolia*) from the cluster analysis was characterised by large, distinctly obovate leaf blades, up to 370 mm in length. Specimens generally had acute-mucronate leaf tips and (7–)8–9 pairs of secondary veins. Distinctive hollow stem swellings with small round entry holes were commonly found at shoot tips and in branches (Appendix 1). Similar to *R. calotricha* specimens, the abaxial leaf blade had a dense indumentum of short adpressed hairs.

Vegetatively, the three Bornean specimens from Group 4 were very similar to specimens classed as *R. calotricha*; the most notable difference was that the primary vein was depressed relative to the adaxial leaf blade. Stem swellings were not present in any of these specimens, although non-swollen portions of the stem appeared hollow and had round entry holes. These specimens will be referred to as *R. sp. nov. aff. calotricha*, as given the limited information available, it would be premature to recognise them as a new taxon.

The two Sumatran specimens from Groups 4 and 8 were very similar in vegetative appearance, and may have clustered in separate groups on account of only one specimen (*Laumonier & Torquebiau, TFB 4245*) having swollen shoot tips, the other (*Burley & Tukirin et al., 1223*) not. Leaf blades were again, somewhat shorter than average (150–200 mm) with between six and eight pairs of secondary veins (Appendix 1). The specimens were most clearly defined by their prominent tertiary venation, which was straight percurrent and distinctly perpendicular to the primary vein. This is a character unique to these specimens and was not scored in this study. Based on a detailed analysis of material not included in the phenetic analyses, these Sumatran specimens compare closely to specimens identified as *R. multinervosa* Slooten, and will here be referred to as such.

Group 5 from the cluster analysis consisted of eight specimens from New Guinea, two determined as *R. javanica*, the rest as *Ryparosa* sp. In the ordination analysis, these specimens clustered adjacent to, and somewhat overlapping with, specimens that formed Group 6 (see below) in the cluster analysis (Fig. 4). Group 5 specimens had relatively small (108–172 mm long) obovate leaf blades with five or six secondary vein pairs. Short adpressed hairs on the abaxial leaf blade were moderately dense on the primary and secondary veins and somewhat sparse on the lamina (Appendix 1). Group 5 specimens were distinctly different from all other *Ryparosa* specimens, yet uniform as a group, and will be referred to as *R. taxon A*.

Group 6 from the cluster analysis consisted of 29 specimens from Myanmar, Thailand, the Malay Peninsula and northern Sumatra (Fig. 3). This group included the type specimen for *R. wrayi* and nine specimens originally determined as *R. wrayi*, and will therefore be referred to here as *R. wrayi sens str.* In the ordination analysis, this group of specimens formed a cluster adjacent to, but distinct from, *R. javanica sens. str.* specimens, and overlapped slightly with *R.* taxon A specimens from New Guinea (Fig. 4). Vegetatively, *R. wrayi sens. str.* had elliptic leaf blades (177–336 mm long) with five (rarely four or six) widely spaced secondary vein pairs (the most apical rather distant from the leaf tip) and a moderate covering of short adpressed hairs abaxially. Three specimens were observed to have hollow stems with small round entrance holes; however, these were not associated with specific stem swellings (Appendix 1).

Ten specimens from southern Borneo formed Group 9 in the cluster analysis (Fig. 3) and a discrete group in the ordination analysis (Fig. 4). These included specimens determined as *R. javanica* ($n = 5$), *R.* aff. *javanica* ($n = 3$) and *R.* cf. *javanica* vel sp. nov. ($n = 2$). Specimens were characterised by generally smaller (165 ± 10.7 mm long; mean $\pm$ 1 s.e.) elliptic leaf blades, with a moderate covering of short adpressed hairs abaxially. Secondary veins were straight for the most part and consisted of six (rarely five or seven) pairs, the most apical rather distant from the leaf tip. Shoot tips and stems were commonly swollen and hollow with small round entry holes (Appendix 1). Given the lack of association with known *Ryparosa* taxa and the uniformity of Group 9, these specimens will be referred to as *R. taxon B*.

Group 10 of the cluster analysis, referred to as *R. baccaureoides*, was composed of four specimens from Borneo, none of which had been examined by Sleumer, and one specimen determined as *R. baccaureoides*. These specimens were loosely grouped in the ordination analysis (Fig. 4), but distinct from other clusters. A comparison of these specimens with high-resolution scans of specimens from K supported the link to *R. baccaureoides*. Leaf blades from these specimens were distinctly coriaceous, with eight brochidodromous secondary vein pairs and a sparse scattering of short adpressed hairs abaxially (Appendix 1).

The two specimens that formed Group 11 in the cluster analysis (Fig. 3) were distinct in the ordination space from all other specimens (Fig. 4). One specimen was originally determined as *Hydnocarpus castanea* Hook.f. & Thomson (Achariaceae; Flacourtiaceae *pro parte*), and the distinctly oblique leaf base with ovate-lanceolate leaves indicated that this species was not *Ryparosa*. Leaves were entirely glabrous and had 8–10 pairs of secondary veins that were curved-ascending but distinctly undulate (Appendix 1). A comparison of these specimens to others not included in the phenetic analyses, confirmed that these specimens

were *Drypetes longifolia* Pax & K.Hoffm. (Putranjivaceae, formerly Euphorbiaceae).

Five specimens collected in New Guinea, all determined as *R.* cf. *javanica*, formed Group 12 in the cluster analysis (Fig. 3) and a discrete group in the ordination analysis (Fig. 4). These specimens had leaves with very short petioles (10–11 mm), a distinctly rounded leaf blade base, seven or eight pairs of secondary vein that are distinctly undulate and sometimes branching, and a sparse scattering of short adpressed hairs on the abaxial primary and secondary veins (Appendix 1). These specimens will be referred to as *R.* taxon C, given their lack of association with known *Ryparosa* taxa and the uniformity of the group in analyses.

Group 13 in the cluster analysis comprised nine specimens, seven from Borneo (five determined as *R.* aff. *javanica* and one as *R.* aff. *glauca*) and two from Flores (determined as *R. javanica*). In the ordination this group of specimens was loosely clustered, with those specimens from Flores (having slightly smaller leaf blades than the Bornean specimens) as outliers on one side and a specimen in poor condition from Brunei as an outlier towards *R. baccaureoides* (Fig. 4). Leaves of this group were entirely glabrous, had 8–10(–11) pairs of brochidodromous secondary veins that were strongly curved-ascending and diverging at a wide angle to the primary vein (58–74°; Appendix 1). Given the strong similarity to vegetative characteristics of specimens of *R. glauca* Ridl. not included in the phenetic analyses, Group 13 will be referred to as *R. glauca*.

Group 14 in the cluster analysis consisted of four very distinct specimens from central Borneo (Fig. 3). These specimens separated distinctly in the ordination space (Fig. 4) and had leaves with a shallowly cordate blade base (a character not previously recorded for *Ryparosa*) and seven or eight (rarely nine) brochidodromous secondary vein pairs. The leaf abaxial surface had a dense covering of short adpressed bifid hairs, and smaller branches were commonly hollow with minor swellings (Appendix 1). Given the unique characters seen in these specimens and a lack of association with other known *Ryparosa* taxa, these specimens will be referred to as *R.* taxon D.

Group 15 in the cluster analysis was composed of four specimens from Borneo (currently determined as *R. javanica*) and one specimen from New Guinea (determined as *R.* sp. nov. aff. *javanica*). The four Bornean specimens were loosely clustered adjacent to *R. javanica sens. str.* in the ordination analysis, while the specimen from New Guinea was somewhat isolated in the ordination space (Fig. 4), but closest to specimens identified as *R.* taxon C. The four Bornean specimens were characterised by rather thin leaves with (5–)6 pairs of reasonably straight-ascending secondary veins. Hairs on the abaxial leaf blade were moderately dense on the primary and secondary veins and somewhat sparse on the lamina (Appendix 1). A comparison of the Bornean

specimens to others not included in the phenetic analyses confirmed that these specimens were vegetatively similar to *R. acuminata*, and will be referred to as such here. The sole specimen from New Guinea was in quite poor condition, and due to its uncertain affinities with other *Ryparosa* taxa and a lack of similar specimens for comparison, will be referred to as *R.* sp. nov. aff. *acuminata*.

Group 16 of the cluster analysis comprised 29 specimens from northern Australia, all currently determined as *R. javanica* (Fig. 3), which clustered as a discrete group in the ordination analysis (Fig. 4). Specimens from Group 16 had narrow leaves (W : L 0.21–0.29) with seven or eight (rarely nine) pairs of secondary veins that were brochidodromous and curved-ascending. Hairs on the abaxial leaf blade were moderate in density on the primary and secondary veins and sparse on the lamina (Appendix 1). Given their lack of association with other known *Ryparosa* taxa, and the uniformity of specimens within the group, these specimens will be referred to as *R.* taxon E.

Groups 17 and 18 in the cluster analysis separated at a very low level from the other 16 groups (Fig. 3), and formed an isolated cluster in the ordination analysis (Fig. 4). Vegetatively, the only distinct difference between both groups was the branching of leaf secondary veins in Group 17 specimens and a slightly higher hair density on the abaxial leaf blade (Appendix 1). Specimens from both groups had imperfect, suprabasal, acrodromous venation, small leaf blades 80–160 mm long, short petioles 10–21 mm long and two or three (rarely four) secondary vein pairs (Appendix 1). Group 17 included the type specimen for *R. kostermansii*, and seven specimens currently identified as *R. kostermansii* were divided between both groups; therefore, both groups will be referred to here as such.

Reproductive morphology

In the following section the final groupings of specimens described above will be referred to as 'taxa'. Reproductive material from specimens that formed the basis for this study was severely limited in many aspects. Only three specimens had racemes of both staminate and pistillate flowers, and several specimen labels specifically describe the plant collected as being dioecious. Rather than conducting morphometric analyses on what would be a very small and rather uninformative dataset, we decided to present the available data in tabulated form (Accessory Publication, Appendix 2; available online at the website of Australian Systematic Botany). This information was gathered from 39 reproductive characters and arranged based on the taxa ultimately derived from the phenetic analyses. The description of fruit epicarp characteristics was not included in the final dataset, due to distinct developmental variation observed across all *Ryparosa* taxa: immature fruits were covered in a dense indumentum of adpressed hairs, but were generally glabrous when mature.

The reproductive features of *Drypetes longifolia* specimens were distinctly different from those of *Ryparosa* specimens, with fasciculate inflorescences arising from small ramiflorous tubercles. Fruits from *D. longifolia* had much longer pedicels (13–19 mm), two locules, and slightly stalked stigmas in the shape of a bow tie.

Some of the 39 reproductive characters measured were constant in all *Ryparosa* taxa (Appendix 2). The calyx ruptured irregularly into three (sometimes two or four) segments, often remaining incompletely divided until the flower was fully open. Staminate and carpellate flowers had a flattened scale, densely covered in long hairs, adaxial in each petal. Staminate flowers, for the most part, had filaments united in a column with extrose anthers that undergo dehiscence along a vertical slit. The one exception to this was two specimens identified as *R. kostermansii*, which had three free filaments (Fig. 5*a*). All carpellate flowers had strongly reduced staminodes, almost always without antherode formation. There were, however, several unusual flowers on the racemes of two specimens of *R.* taxon E, which had partially formed, but apparently sterile anthers.

Several distinct differences in reproductive traits were observed between *Ryparosa* taxa. Racemes were found in a range of positions from axillary to arising from large tubercles on the main trunk. *Ryparosa acuminata*, *R. kostermansii*, *R. amplifolia*, *R.* taxon A and *R.* taxon C most commonly had racemes in the axils of leaves, while *R. javanica sens. str.*, *R. calotricha*, *R. kurzii*, *R. wrayi* and *R.* taxa B and D usually had racemes arising from defoliate axils. While several taxa had ramiflorous racemes from small tubercles, this was most common in *R. glauca*. Cauliflorous racemes arising from tubercles on the main trunk were observed in only three species: the lower portion of the main trunk was the predominant

raceme position for *R. baccaureoides* and *R.* taxon E, while some *R. glauca* specimens also had cauliflorous racemes (Appendix 2).

Raceme length was highly variable between specimens within each *Ryparosa* taxon and also differed between staminate and carpellate racemes. Maximum staminate raceme length exceeded 300 mm in *R. javanica sens. str.*, *R. acuminata*, *R. wrayi* and *R.* taxon E, while for *R. baccaureoides*, *R. calotricha*, *R. glauca*, *R. kostermansii* and *R. kurzii* it was between 150 and 300 mm. In *R.* taxa A and B, maximum staminate raceme length did not exceed 150 mm (Appendix 2). In general, carpellate racemes were shorter than staminate racemes, particularly when bearing fruits. Only two species had carpellate racemes exceeding 300 mm (*R. wrayi* and *R.* taxon E); in most they were less than 150 mm long. Indumentum on the raceme and abaxial calyx was generally adpressed puberulent and somewhat sparse. The exceptions to this were *R. acuminata*, which had a densely hirsute indumentum (Fig. 5*b*), and *R.* taxon D, in which the indumentum was densely pilose. Both *R. calotricha* and *R. amplifolia* had racemes in which the flower pedicels appear to be clumped in whorls on the raceme (Fig. 5*c*), a character particularly obvious at the bud stage (Appendix 2).

Perianth parts of carpellate flowers tended to be larger than those of staminate flowers, while overall flower dimensions of *R. kostermansii* specimens were generally smaller than average and those of *R.* taxon E specimens were generally larger than average (Appendix 2). *Ryparosa glauca* and *R. wrayi* had distinctively long pedicels (6.8 and 7.0 mm respectively) in carpellate flowers. Hair density on the filament tubes of staminate flowers showed some variation within species and even between different flowers on the same raceme (Appendix 2). Filaments of *R. acuminata* and *R. kostermansii* were consistently glabrous, while those of
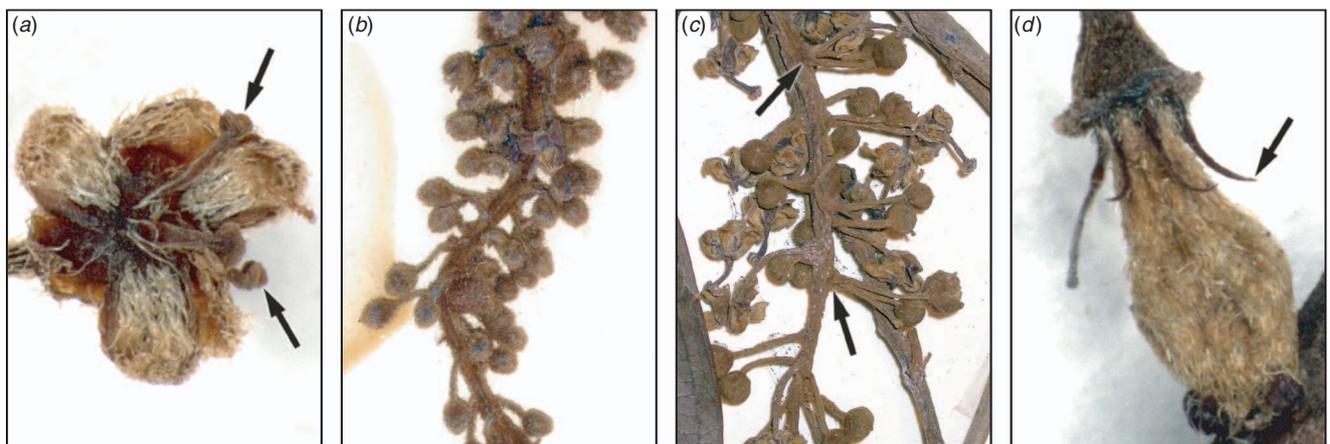
Fig. 5. Distinctive and unusual reproductive features of certain *Ryparosa* specimens examined as part of the morphometric analysis of *R. javanica sens. lat.* (*a*) Free filaments in a staminate flower of *R. kostermansii*; (*b*) distinctly hirsute raceme of *R. acuminata*; (*c*) bunched pedicels on a raceme of *R. calotricha*; (*d*) long filiform staminodes with a pointed tip on a carpellate flower (perianth parts removed) of *R. kurzii*.

R. javanica sens. str., *R. glauca*, *R. kurzii* and *R.* taxon B were sparsely villous. The filaments of *R. baccaureoides* (sparsely villous in the upper portion), *R. calotricha* (entirely glabrous or sparsely villous in the upper portion) and *R.* taxon E (sparsely villous or only in the upper portion) were more or less intermediate.

The staminodes of carpellate flowers varied in length, stature and density of hair coverage (Appendix 2). Staminodes were either thin filiform (*R. javanica sens. str.*, *R. calotricha*, *R. kurzii*, *R. wrayi*, *R.* taxa A and B) or fleshy and stocky (*R. glauca, R. amplifolia, R.* taxa C and E, and *R. javanica sens. str.* specimens from Bali). Staminodes of *R. kurzii* were longer than average (1.1–1.3 mm) and had a distinctively pointed tip (Fig. 5*d*). Most species groupings had staminodes that were pilose on the adaxial surface and glabrous on the abaxial surface. However, *R. calotricha*, *R.* taxa A and E (sometimes entirely glabrous), together with *R. glauca* and *R.* taxon C (entirely pilose) were somewhat intermediate.

Fruits of *Ryparosa* specimens studied commonly contained two seeds in one locule, occasionally divided by a false septum (Appendix 2). *Ryparosa javanica sens. str.*, *R. kostermansii* and *R.* taxon E sometimes had fruits containing one seed, while *R. calotricha* and *R.* taxon A had fruits with three seeds. Stigmas were generally sessile and situated close together on flowers and fruits across all *Ryparosa* species groups. However, *R. wrayi* had stigmas that were slightly stalked, and *R. multinervosa* had stigmas distinctly separated on immature fruits.

Other supporting characters

Information, largely absent from older specimens, was collated from labels according to taxa defined from the phenetic analyses, and there were some obvious differences between species groupings (Table 2). Many of the taxa were collected over a considerable altitudinal gradient, *R. javanica sens. str.*, *R. baccaureoides*, *R. calotricha*, *R. amplifolia* and *R.* taxon A all being collected below 100 m and also above

Table 2.   Descriptive characters on tree habit and location altitude gathered from the labels of herbarium specimens identified as *Ryparosa*

Taxon groupings are based on cluster and ordination analyses (Figs 3 and 4). For each character, the upper line represents mean values (± s.e.) for each group, while the lower line lists the number of specimens on which that character was measured (n*) and the range of values for that character within each taxon group. Values in square brackets indicate the number of specimens for which a value for buttressing was obtained. Alt, altitude (metres above sea level); Hgt, height

Taxon	Alt (m)	TreeHgt (m)	BoleHgt (m)	Trunk buttresses
R. javanica s. str.	562 ± 103	11.8 ± 2.78		
	14, (10–1400)	5, (3.5–18.3)		
R. amplifolia s. str.	267 ± 51	15.9 ± 1.87	11.01 ± 1.66	No buttresses [4]
	21, (5–1006)	15, (6.1–30.0)	8, (6.1–21)	
R. kurzii s. str.	'Sea level'	3.5 ± 0.00		
	2	2, (3.5–3.5)		
R. wrayi s. str.	116 ± 37	14.4 ± 1.47		Buttresses 3.0–3.5 m high [3]
	12, (8–457)	20, (1.8–30.5)		
R. taxon A	334 ± 177	12.2 ± 3.50	6.1 ± 0	Buttresses [1]
(*R. maculata* sp. nov.)	6, (30–1128)	6, (1.8–24.3)	2, (6.1–6.1)	
R. taxon B	182 ± 74	29.2 ± 3.27	17 ± 1	Large thick buttresses 0.5–5.0 m high, up to 3.0 m over the
(*R. anterides* sp. nov.)	5, (10–400)	6, (20.0–40.0)	2, (16–18)	ground [5], sometimes thin concave [1]
R. taxon C	98 ± 48	2.4 ± 0.35[A]		
(*R. milleri* sp. nov.)	2, (50–146)	2, (2.0–2.7)		
R. taxon D		7.0 ± 0.00		
(*R. maycockii* sp. nov.)		2, (7.0–7.0)		
R. taxon E	37 ± 6	15.1 ± 1.11		Thick undulate buttresses 1.0–2.5 m high, up to 0.5 m over
(*R. kurrangii* sp. nov.)	27, (4–100)	20, (6.0–20.0)		the ground [6], somewhat fluted [1]
R. acuminata	101 ± 81	6.1 ± 0.05		
	2, (20–183)	2, (6.0–6.1)		
R. baccaureoides	925 ± 310	5.8 ± 2.09		
	3, (305–1250)	3, (2.0–9.2)		
R. calotricha	631 ± 154	17.6 ± 1.94	12.17 ± 4.67	Buttresses to 1 m high [1]
	15, (20–1402)	15, (5.0–27.0)	3, (3–18.3)	
R. glauca	228 ± 99	4.4 ± 1.03		
	8, (20–800)	8, (1.2–9.1)		
R. kostermansii	407 ± 70	15.0 ± 1.72	9.55 ± 0.45	Buttresses 0.5–1.0 m high [3]
	10, (130–720)	13, (6.1–27.0)	2, (9.1–10)	
Drypetes longifolia	35 ± 15	10.3 ± 2.25		
	2, (20–50)	2, (8.0–12.5)		

[A]Described as a straggling shrub or small tree.

1000 m (with the exception of *R. baccaureoides*; Table 2). *R. javanica*, *R. calotricha* and *R. kostermansii* were collected more commonly above 400 m, while *R. amplifolia*, *R. wrayi* and *R.* taxa A, B and E were more commonly collected below 400 m.

Tree height varied considerably between species groupings, from large trees of 40 m in height to straggling trees of 2 m (Table 2). *Ryparosa* taxon B specimens were distinctly larger than any other species, having an average height of 29 m (maximum of 40 m). Five other species, *R. calotricha*, *R. kostermansii*, *R. amplifolia*, *R. wrayi* and *R.* taxon A, exceeded 20 m in height, although on average, specimens of these species were between 15 and 20 m tall. *Ryparosa acuminata*, *R. baccaureoides*, *R. glauca*, *R. kurzii* and *R.* taxon D specimens were not recorded as being more than 10 m tall, and *R.* taxon C was up to only 3 m tall. The only species that was frequently described as having a distinct bole (between 6–21 m long) was *R. amplifolia*, while buttresses were observed in *R. calotricha*, *R. kostermansii*, *R. wrayi* and *R.* taxa A, B and E (Table 2; Fig. 9). Buttressing was prominent in a large proportion of specimens of *R.* taxa B and E, extending up to 5 m high and 3 m over the ground in the former. Distinctive stem swellings in shoot tips or young stems, commonly hollow with small circular entry holes, were present in *R. amplifolia*, *R. calotricha*, and *R.* taxon B. In *R. amplifolia*, shoot tip swellings and entry holes were usually associated with slit-like prostomata. The extent of ant–plant associations in *Ryparosa* appear to be a critical part of understanding taxonomic groupings in the genus and will be discussed in detail elsewhere (Webber *et al.* 2006, 2007).

Multicellular, bifurcate hairs were observed on representative specimens from all taxa defined by the phenetic analyses, with the exception of *Drypetes longifolia* (Fig. 6a). *In situ*, these T-shaped hairs were generally adpressed, with one arm distinctly longer than the other (Fig. 6b). Variation in the magnitude of difference between hair arm
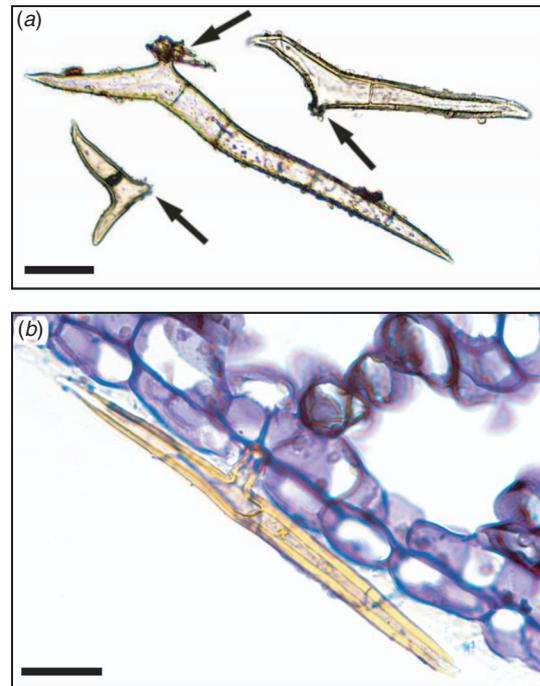
Fig. 6. Multicellular bifurcate hairs from the abaxial leaf lamina and petiole of *Ryparosa* taxon E (*R. kurrangii* sp. nov.). (*a*) Detached hairs (arrows indicate the point of attachment before removal); (*b*) transverse section of hairs *in situ* with base embedded in the epidermis. Scale bar = 50 μm.

lengths differed both within specimens and between taxa. In all *Ryparosa* specimens, hairs on the abaxial leaf blade were very short, up to 0.7 mm in length on the primary and secondary veins and ∼0.2–0.3 mm on the lamina. Hairs were generally visible to the naked eye only when present at a high density, for example, on young shoot tips and unexpanded leaves or on the abaxial leaf blades of *R. amplifolia*, *R. calotricha*, and *R.* taxon D (Fig. 7). In all other taxa, a hand lens of suitable magnification was required to see the hairs.
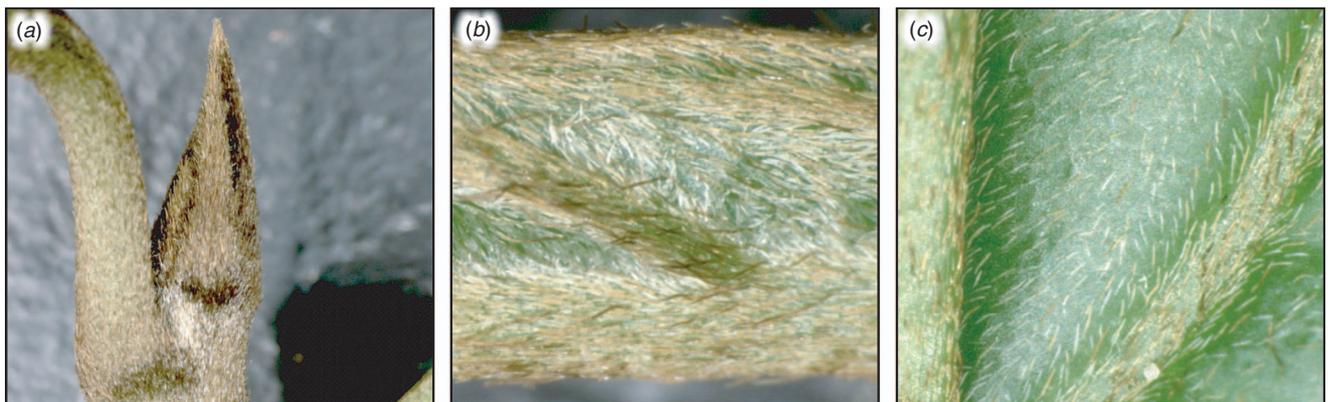
Fig. 7.   Dense hairs protecting shoot tips and expanding leaves in *Ryparosa* taxon E (*R. kurrangii* sp. nov.). The newly formed leaves at the shoot tip (*a*) have a dense indumentum of bifurcate hairs. Hairs are still very dense on leaves undergoing expansion (*b*; abaxial lamina, leaf length 1.5 cm) but become sparser as expansion continues (*c*; abaxial lamina, leaf length 5 cm).

Geographical distribution

The distributions of taxa recognised in the phenetic analyses were geographically circumscribed, incorporating data from additional specimens not used in the phenetic analyses (because they were so poor but nevertheless could be identified to species; *R. amplifolia*, n = 8; *R. calotricha*, n = 2; *R. glauca*, n = 2; *R. javanica sens. str.*, n = 7; *R. wrayi*, n = 3). Importantly, this added data did not extend the distribution range for any taxon. Overall, distinct geographical discontinuities were noted among taxa (Fig. 8).

Ryparosa wrayi is distributed predominantly on the Malay Peninsula and also southern Thailand and Myanmar (Fig. 8*a*). In northern Sumatra it overlaps with the northern limits of *R. javanica sens. str.*, which has a distribution range restricted to Sumatra, Java and Bali (Fig. 8*b*). The two *R. multinervosa*

specimens were both from central Sumatra, while *R. kurzii* is found only in the Andaman and Nicobar Islands (Fig. 8*a*). The island of Borneo, particularly Sabah, contains the highest diversity of species groupings. *Ryparosa acuminata*, *R. baccaureoides*, *R. glauca* and *R. kostermansii* collection locations span Sabah, and most distributions extend south into Sarawak, Brunei and Kalimantan. *Ryparosa* taxon B (Kalimantan), along with *R.* taxon D and *R.* sp. nov. aff. *calotricha* (Sarawak), are also restricted to Borneo and the only Bornean species to extend its range beyond the island is *R. glauca*, with specimens from Flores clustering in the same species group as the Bornean specimens (Fig. 8*b*). The only specimens collected in Australia are those identified as *R.* taxon E, while *R.* taxon A and *R.* sp. nov. aff. *acuminata* are restricted to eastern New Guinea (Fig. 8*d*). *R. amplifolia*, *R. calotricha* and *R.* taxon C extend throughout New Guinea;
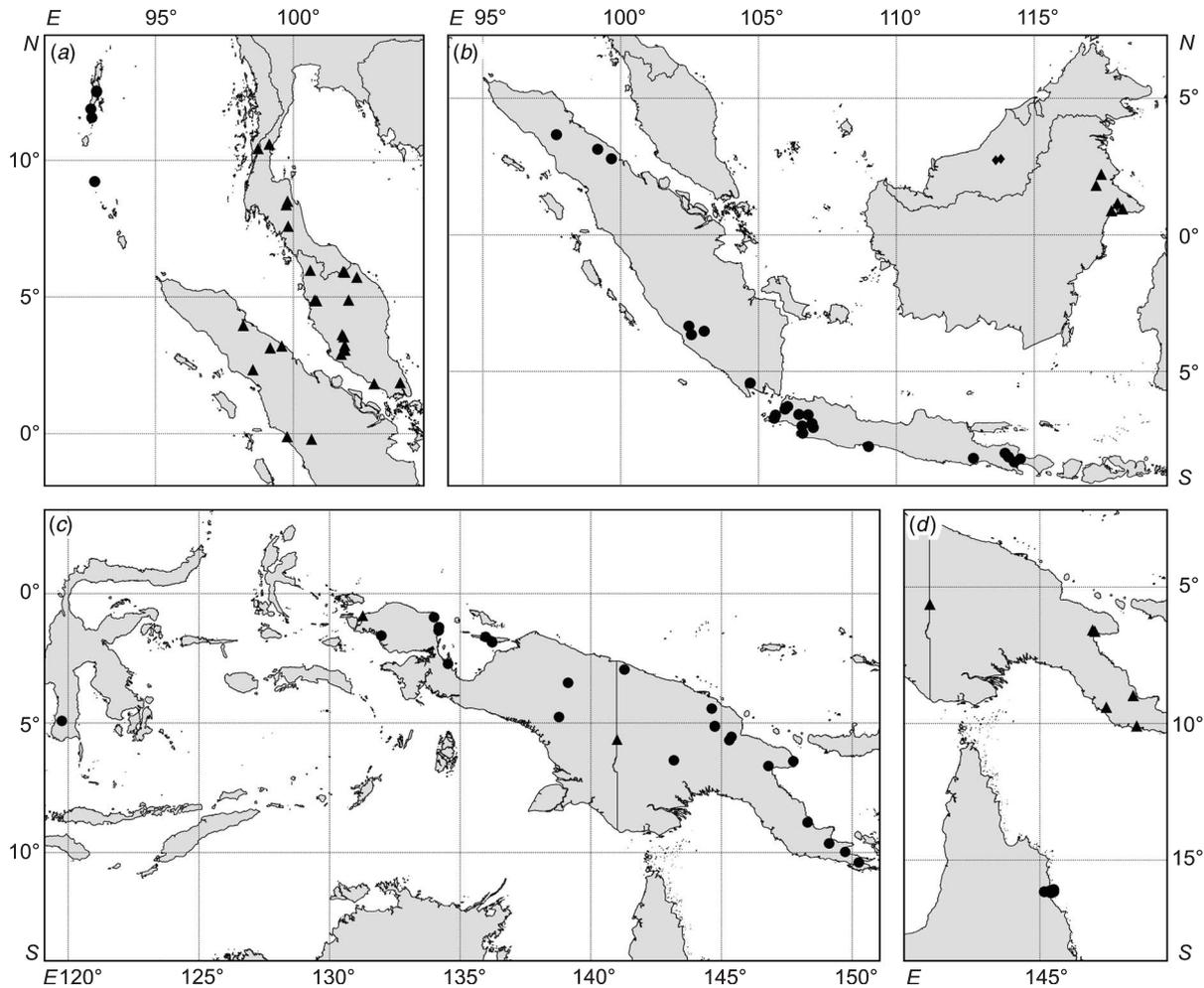
Fig. 8. Distributions of identified taxa within *Ryparosa javanica sens. lat.* (symbols repeated between maps). (*a*) *R. kurzii s. str.* (●; Andaman and Nicobar Islands) and *R. wrayi s. str.* (▲; Myanmar, Thailand, Malay Peninsula, Sumatra). (*b*) *R. javanica s. str.* (●; Sumatra, Java, Bali), *R.* taxon B (*R. anterides* sp. nov.; ▲; Kalimantan) and *R.* taxon D (*R. maycockii* sp. nov.; ◆; Sarawak). (*c*) *R. amplifolia s. str.* (●; Sulawesi, New Guinea) and *R.* taxon C (*R. milleri* sp. nov.; ▲; New Guinea). (*d*) *R.* taxon A (*R. maculata* sp. nov.; ▲; New Guinea) and *R.* taxon E (*R. kurrangii* sp. nov.; ●; Australia).

the former is also known from a single specimen from southern Sulawesi (Fig. 8*c*).

Discussion

Morphological variation and character suitability

As a genus, *Ryparosa* is little studied, poorly known in the field, and has only rarely appeared in the wider scientific literature since it was first described nearly 200 years ago. Taxon delimitation within *Ryparosa* has previously been based largely on a haphazard mix of vegetative qualities and reproductive characters, when they were known. Indeed, staminate or carpellate flowers of many species of *Ryparosa* are still unknown, yet new species have been described taking these limitations into account (e.g. Ridley 1936; Sleumer 1954*b*; Jarvie and Stevens 1998). Herbarium specimens of *R. javanica sens. lat.* are often in poor condition with brief or non-existent label notes and a distinct lack of informative reproductive material. This has not only made correct determinations harder for collectors, but has led to the situation where the genus is widely documented as being dioecious (e.g. Sleumer 1954*a*; Hutchinson 1967; Renner and Ricklefs 1995; Jarvie and Stevens 1998). However, observing tagged individuals in Australian *Ryparosa* populations (*R.* taxon E), made it possible to follow the reproductive biology of individual trees over several seasons, revealing that at least *Ryparosa* taxon E is monoecious (Webber 2005).

In the only monograph on *Ryparosa*, Sleumer (1954*a*) used the presence of hairs on the staminal column and a glabrous berry to distinguish *R. javanica* from other species within the genus. On several specimens, he stated 'filaments pilose' with his determination, and seemed to overlook other significant characters in assigning these specimens to *R. javanica*. Although he stated that hairs seemed to be caducous, he emphasised leaf blade hair density in the species key, but then in individual descriptions gave a wide range of possible densities for some species (Sleumer 1954*a*). He used the position of inflorescences in the first lead of the key, but expressed uncertainty about the robustness of this character. Vegetative features, such as the relative prominence of the leaf primary vein on the adaxial surface and leaf petiole and blade length were also used at times throughout the generic key.

Based on field observations on Australian *Ryparosa* and on herbarium specimens, the importance of Sleumer's (1954*a*) primary defining characters was generally supported. The relative prominence of the leaf primary vein on the adaxial surface, as well as indumentum density on the abaxial leaf blade was consistent between taxon groupings and supported by observations of fresh material. In the original species descriptions of taxa ascribed to *Ryparosa javanica sens. lat.*, many authors make a point of describing the density of bifid hairs on the abaxial surface of the leaf lamina and note that the leaves appear glabrous unless examined

under magnification (e.g. Mildbraed 1928; King 1890). Indeed, the original description of *R. amplifolia* described the leaves as being glabrous (Schumann and Lauterbach 1901), but Mildbraed (1928) recognised that *R. amplifolia* (and *R. calotricha*) had quite dense, adpressed bifid hairs on the abaxial leaf surface. Likewise, van Slooten (1924) recognised the distinct hairiness of the abaxial leaf surface in a *Ryparosa* specimen from New Guinea (*Branderhorst, 327*), and as a result determined it to be *R. caesia*, before Sleumer recognised its affinity to *R. amplifolia sens. str.*, and therefore determined it to be *R. javanica*.

We found that inflorescence position, overall organ dimensions, the number of secondary vein pairs and leaf blade shape were more consistent within species groupings than Sleumer had previously outlined (Sleumer 1954*a*). For example, *R. baccaureoides* and *R.* taxon E produce racemes from large tubercles on the lower portion of the main trunk (e.g. Fig. 9) whereas *R. javanica sens. str.* does not appear to produce trunk tubercles (BL Webber unpubl. data; Dakkus 1957; Astuti *et al*. 2001) and has axillary or fasciculate racemes on small branches. However, racemes on many specimens were detached and had no notes on their position on the tree, which compounded the poor records of this trait. Furthermore, some taxa with large leaves (e.g. *R. amplifolia*) or racemes (e.g. *R. javanica*, *R.* taxon E) are likely to be represented in herbaria by an abundance of specimens with smaller features than might have been observed in the field. While several more recent specimen labels indicated this limitation, this will appear to reduce the differences between similar species. For example, smaller *R. amplifolia* leaves can appear superficially similar to ordinary-sized leaves of *R. calotricha*. In respect to raceme length, maximum length appears to be the best measure.

In contrast, other characters that were emphasised in Sleumer's key and other previous work (e.g. van Slooten 1925) now appear to be somewhat erroneous. For example, *R. scortechinii* and *R. javanica* have been defined as having an entirely glabrous berry (van Slooten 1919, 1925), which is not true for immature fruits – the indumentum of the fruit epicarp had just been lost by fruit maturity. A better understanding of food-body morphology (Webber *et al*. 2006, 2007) has reduced the majority of fruit epicarp variation to developmental differences rather than taxon differences. Indeed, although Sleumer (1954*a*) used lenticels on the branchlets as a defining character separating *R. fasciculata* and *R. glauca*, these distinctive marks (concentrated on young shoots, abaxial leaf surfaces and fruit epicarps) are now known to be the scars remaining after 'Type B' food body (*sensu* Webber *et al*. 2006) removal; they are present in all *Ryparosa* species (Webber *et al*. 2007). Now that a better understanding of plant–ant symbioses in *Ryparosa* is emerging, the inclusion of useful characters associated with ant–plant interactions in taxon delimitation in the future is possible (e.g. Janzen 1974; McKey 2000). These include
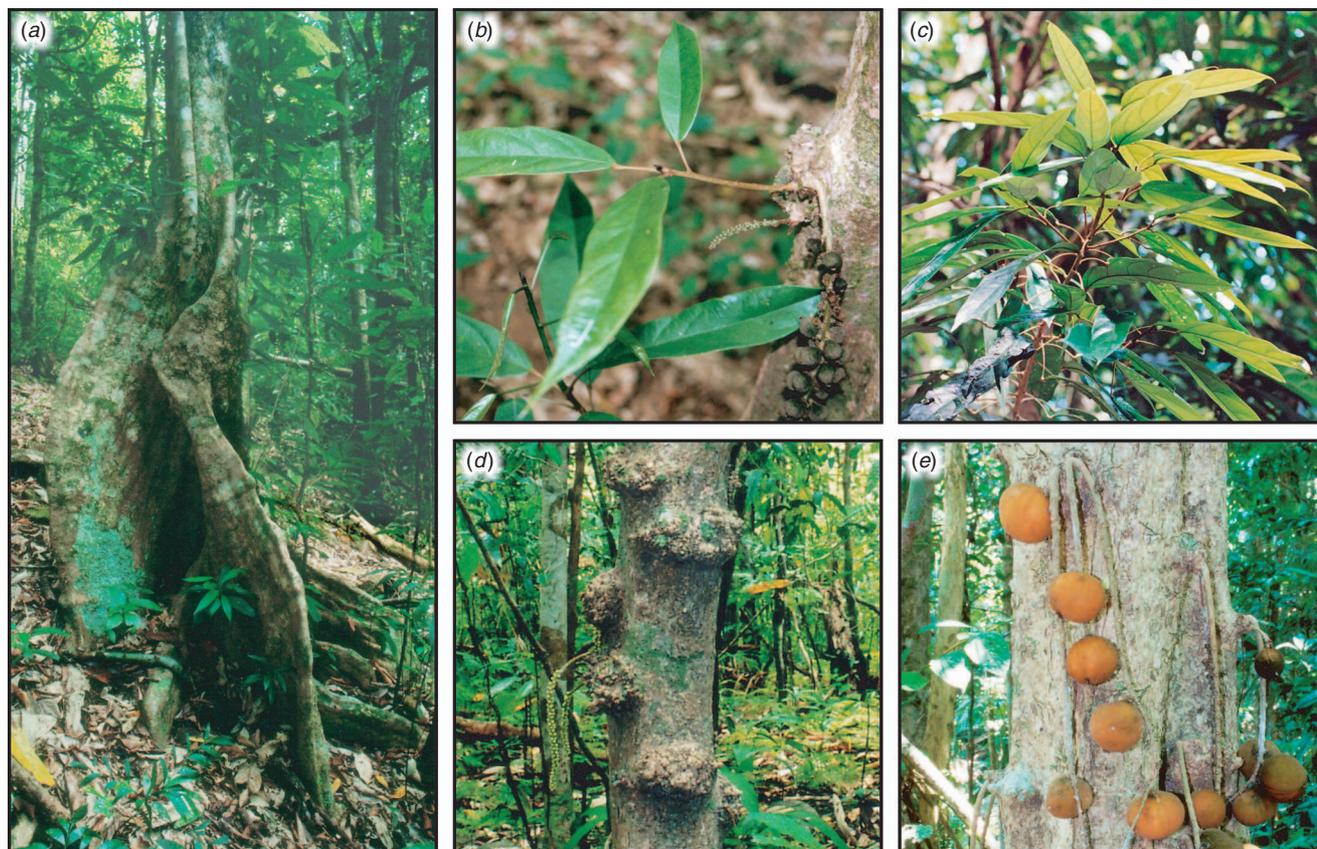
Fig. 9. Distinctive vegetative features of *Ryparosa* taxon E (*R. kurrangii* sp. nov.). The lower trunks of trees become distinctly fluted and often buttressed to 1–2 m (*a*) with inflorescences and small branches borne low near the ground from distinctive tubercles (*b*). Leaves are large and with long petioles (*c*), while the large trunk tubercles (*d*) support fascicles of racemes of flowers and fruits (*e*).

traits such as food-body scars (at a generic level), and at a species level, distinctive stem swellings and prostomata seen on younger branches of certain taxa. Notably, *D. longifolia* is known to have stem domatia and is colonised by the same ant taxa (*Cladomyrma petalae* Agosti and *C. nudidorsalis* Agosti, Moog & Maschwitz) as *R. fasciculata* (Agosti *et al*. 1999; Moog *et al*. 2003). This emphasises the importance of considering myrmecophilic features alongside a suite of other characters in species recognition and delimitation.

Other questionable fruit characters are those described from dried material. Fruits are often described as having little pulp and being quite angular (e.g. Brühl and King 1896; King 1890; Sleumer 1954*a*). By observing changes in pericarp structure during fruit drying, it was clear that the fleshiness of these fruits is difficult to discern from observations of dry specimens (a point also recognised by Sleumer 1954*a*), and that the angularity of dried fruits is not necessarily representative of fresh specimens. There is also considerable conjecture on the number of locules present in *Ryparosa* fruits, with one locule (Koorders and Valeton 1900*a*; Chase *et al*. 2002) and occasionally two locules (Kurz 1873; van Slooten 1919) reported. It will be important to

conduct a more detailed study of flowers at anthesis and fruit development to clarify these disagreements. In some *Ryparosa* taxa, the staminal column is consistently glabrous; however, in those species with filament hairs, noticeable variation in hair presence was observed (even within flowers on the same raceme). Therefore, the use of this character as a taxon-defining trait, particularly in relation to the position of hairs (on the upper or lower part of the staminal column), should be treated with caution.

This study has also revealed new characters that have not been used specifically in the past, that are useful in defining taxa within *Ryparosa*. First, patterns of secondary and tertiary venation were distinctly variable between, but consistent within, species (Appendix 1). Patterns of secondary vein anastomosis varied consistently between species and when combined with tertiary venation patterns and the density of abaxial leaf hairs, provide a quick way of discriminating between taxa with otherwise similar vegetative features. Previous authors have alluded to different venation patterns between *Ryparosa* species (e.g. Mildbraed 1928; Sleumer 1954*b*). However, the recent description of *R. porcata* (Jarvie and Stevens 1998) is the only study to specifically refer to

secondary venation patterns as a defining character. Second, while the majority of morphometric flower characters were not consistently different between species, the length and shape of carpellate flower staminodes may be a useful character for species delimitation. Two forms of staminode shape were observed: fleshy and stocky, and thin and filiform, the latter appearing to be distinctly longer and more pointed in *R. kurzii* than in other species. Unlike the extensive reduction in size of petal scales in dried specimens, this variation in staminode form does not seem to be an artefact of specimen preservation or time since collection, as staminode type appeared constant within taxa. Staminode characters were used by Kurz (1873) to highlight the differences between *R. caesia* and *R. javanica* (stipitate and subulate staminodes respectively), although Koorders and Valeton (1900*b*) point out that filiform (not subulate) staminodes were observed on the *R. javanica sens. str.* material they examined.

Species delimitation

Sleumer's work for the 1954 revision of Flacourtiaceae for the Flora Malesiana was conducted on dried herbarium material, and his only chance for field observations on the genus would have been after this monograph was completed, during trips to south-east Asia and New Guinea between 1961 and 1963 (Sleumer 1980). He would have had little opportunity to examine fresh material, or material at known stages of maturity, and so would have not been familiar with developmental variation in reproductive and vegetative tissue. Sleumer's decision to unite *R. kurzii*, *R. wrayi* and *R. amplifolia* with *R. javanica* created a species complex that not only geographically spanned almost the entire known distribution for the genus, but also morphometrically spanned observed differences in many of the other *Ryparosa* species. There is no doubt that this created confusion for subsequent collectors, and specimens collected since 1954 have commonly been determined as *R. javanica* when they were actually other *Ryparosa* species.

Phenetic analyses of variation within *Ryparosa javanica sens. lat.* have allowed us to identify distinct differences in vegetative morphology between numerous groupings of specimens (Appendix 1; Figs 3, 4). While these groupings were not as clearly defined as perhaps may be expected from phenetic analyses of more variable species or data sets that also incorporate reproductive data, they were supported by differences in reproductive characters, tree architecture, and geographical distributions (Appendix 2; Table 2; Fig. 8). In summary, *Ryparosa* species are not readily identifiable by spot characters, but rather each species is distinguished (and defined) by a 'character suite' – a particular combination of characters and / or character states unique to that species (for examples, see bold text in species descriptions). Within *Ryparosa*, there appears to be (based on vegetative characters) only a few characters with widely varying states. Therefore, characters with only very narrowly variable states must be included in phenetic analyses to differentiate and improve the resolution between groups. Although similarities among states for characters used in phenetic analyses will inevitably draw groups together, differences in a few characters and character states will keep them distinct. Across all the species treated here, the range of characters and character states comprising the 'character suite' varies considerably and between any two species the overlap might be great or small. This situation is found also in other 'flacourtiaceous' genera (S Zmarzty pers. comm.).

Ryparosa javanica sensu lato

The three *Ryparosa* taxa included by Sleumer (1954*a*) in *R. javanica sens. lat.* (*R. amplifolia*, *R. kurzii* and *R. wrayi*) are recognisable as distinct from *R. javanica sens. str.* by vegetative characters. Superimposing reproductive traits, habit and geographical data onto these groupings further enhance delimitations between these taxa. Interestingly, unpublished notes made by Sleumer during the 1980s for a revision of the genus indicated that he intended to resurrect these three species (HO Sleumer unpubl. data); however, he died before this was finished. These three taxa warrant recognition at the species level, as originally described, and are separable by a combination of morphological and geographical discontinuities.

As a result, the circumscription of *Ryparosa javanica sens. str.* includes distinctly less variation. *Ryparosa javanica* has leaves with eucamptodromous venation, five or six (rarely seven) pairs of secondary veins and very sparse hairs on the abaxial blade, particularly so on the lamina. Flower racemes are, for the most part, defoliate-axillary and the staminodes of carpellate flowers are thin-filiform in shape. *Ryparosa amplifolia* is most noticeably different from *R. javanica* and more similar to *R. calotricha* than to any other species of *Ryparosa* (see below). Its large, obovate, leaf blades with a dense abaxial indumentum and up to nine pairs of secondary veins contrasts distinctly with *R. javanica sens. str.* Likewise, *R. wrayi* differs from *R. javanica sens. str.* by having a moderately dense indumentum on the abaxial leaf blade and generally fewer pairs of secondary veins, the most apical being quite distant from the leaf apex. Identification of the invertebrate(s) responsible for entry holes in the stems of *R. wrayi* warrants further investigation in light of the discoveries about ant–plant interactions in other species of the genus. Reproductively, *R. amplifolia* differs from *R. javanica sens. str.* in having short racemes with bunched pedicels, while *R. wrayi* appears to have carpellate flowers on rather long pedicels. Lastly, *R. kurzii* is characterised by generally ovate leaf blades and long subulate-filiform staminodes to 1.3 mm in length. The staminodes of *Ryparosa javanica sens. str.* were consistently around 0.7 mm in length (this study), or considerably shorter (0.3 mm; Koorders and Valeton 1900*b*; described from one numbered tree, *1120α*, from Palaboeanratoe, Java). It is anticipated that further

differences will become apparent with a better documentation of reproductive traits from fresh material. For example, Brühl and King (1896) depict considerable differences in fruit shapes between *R. wrayi* (obconic) and *R. kurzii* (globose), while *R. wrayi* is consistently listed as having only one seed per fruit, compared with two seeds in *R. javanica sens. str.* (King 1890; Ridley 1922; van Slooten 1925).

New Ryparosa *taxa*

In addition to those species previously assigned by Sleumer to *R. javanica sens. lat.*, several other groupings within *Ryparosa* were recognisable. Based on morphological and geographical discontinuities and differences in reproductive characters, five of these new taxa deserve specific status. *Ryparosa* taxon A, here described as *Ryparosa maculata* sp. nov., differs from *R. javanica sens. str.* by its small obovate leaf blades with moderately dense hairs on the abaxial lamina, and fruits with two or three seeds. *R.* taxon B, here described as *Ryparosa anterides* sp. nov., is consistently taller than any other known *Ryparosa* species and has prominent buttressing. It is distinctly different from *R. javanica sens. str.* and is more similar to *Ryparosa micromera* Slooten, from Sumatra, than to any other species. Although *R. micromera* has similarly dense hairs on the abaxial leaf surface, it has smaller leaves (60–120 mm long) and shorter racemes (rarely longer than 60 mm) than *R. anterides*, and leaves that appear crowded on the branches. *Ryparosa anterides* is readily distinguished by its eucamptodromous venation, secondary veins that are straight for the most part and diverge at a narrow angle from the primary vein, and moderately dense indumentum on the abaxial blade. The species also has small round entry holes in hollow stems and prominent shoot tip swellings.

R. taxon C, here described as *Ryparosa milleri* sp. nov., is noted as a small tree or straggling shrub by collectors and is recognised from *R. javanica sens. str.* by its broadly rounded leaf base, short petioles and leaves with brochidodromous secondary veins that are curved-ascending but distinctly undulate. Secondary veins in all other *Ryparosa* taxa examined had no undulations (i.e. distinctly smooth) and varied from strongly curved-ascending (e.g. *R. glauca*) to straight for the most part (e.g. *R. calotricha*). Specimens from Borneo, identified as *R.* taxon D and here described as *Ryparosa maycockii* sp. nov. were unique in that they had leaf blades with a cordate base, a character not previously documented in *Ryparosa*. While this character was not consistent on all leaves on all specimens, it was present in the majority of leaves and appears to be unique to the species. Other distinctive characters include dense hairs on the abaxial leaf blade and flower racemes, seven or eight (rarely nine) pairs of brochidodromous secondary veins, and hollow young stems. Lastly, *Ryparosa* taxon E is here described as *Ryparosa kurrangii* sp. nov. and is distinguished from *R. javanica sens. str.* by its long, thin leaf blades, 7–9 pairs of brochidodromous secondary veins and random-reticulate tertiary venation. This

new species compares most closely to *R. acuminata*, from which it differs in respect to leaf shape, raceme position (predominantly basi-cauline compared with foliate-axillary in *R. acuminata*) and indumentum density on racemes (the calyx is distinctly hirsute abaxially in *R. acuminata* rather than adpressed puberulent).

The two unassigned taxa from Borneo (*R.* sp. nov. aff. *calotricha*) and New Guinea (*R.* sp. nov. aff. *acuminata*) were not designated as new species due to limited replication and the poor condition of specimens. Future work on these taxa (listed in other species examined) may elucidate their status, and more work is also needed to clarify the identify of the two specimens from Flores and the single specimen from Sulawesi, tentatively identified in this study as *R.* cf. *glauca* and *R.* cf. *amplifolia*, respectively.

Existing taxa

Specimens of existing *Ryparosa* species incorrectly determined as *R. javanica sens. lat.* were also identified by the phenetic classification (Fig. 3); of the 182 specimens originally determined as *R. javanica*, 18% were incorrectly determined at the species level and belonged to six other *Ryparosa* species. *Ryparosa acuminata* specimens are characterised by their brochidodromous venation, primary venation flat on the adaxial leaf surface, and distinctly hirsute racemes, particularly at the bud stage. Hirsute racemes have previously been used as trait defining *R. acuminata* (e.g. van Slooten 1925), and are indeed characteristic of the species. Two other species from Borneo, *R. baccaureoides* and *R. glauca*, are characterised by having randomly reticulate tertiary venation and distinctly brochidodromous venation; the latter species has secondary veins diverging at a wide angle from the primary vein. Secondary vein pairs are more numerous than *R. javanica sens. str.* (~8 and 8–11, respectively, compared with 5–7) and flowering is generally from branches or cauline. *Ryparosa baccaureoides* and *R. glauca* are distinguished from each other most clearly by the complete lack of indumentum on the leaves of *R. glauca* and the distinctively coriaceous lamina of *R. baccaureoides*. Specimens of another species, *R. multinervosa* are distinguished by their tertiary venation, which is straight percurrent and distinctly perpendicular to the primary vein, and with stigmas separated on immature fruits.

Specimens of *Ryparosa calotricha* (New Guinea) are easily distinguished from *R. javanica sens. str.* by their obovate leaves and dense hairs on the abaxial leaf lamina. However, the similarities between *R. calotricha* and *R. amplifolia sens. str.* seem to be obscured by collections of *R. amplifolia sens. str.* apparently specifically collected with foliage small enough to fit on herbarium sheets. *Ryparosa calotricha* and *R. amplifolia* both had swollen shoot tips (although domatia were far more common in *R. amplifolia*), buds bunched on racemes and leaves with strong percurrent tertiary venation, 7–9 secondary vein pairs and hairs dense

on the abaxial blade. The two species differ in respect to leaf size and the distinctly obovate leaf blades with broadly acute-mucronate tips of *R. amplifolia sens. str*. Lastly, specimens of *R. kostermansii* are easily recognised by their small leaves and flowers[1], and leaf blades with a dense indumentum abaxially, acrodromous venation and two or three secondary vein pairs.

Lastly, two specimens from the Andaman Islands were identified as *Drypetes longifolia* and are immediately separated from *Ryparosa* taxa by their oblique leaf base, 2-locular fruits and bow-tie shaped stigmas. Confusion between specimens from the Euphorbiaceae *sens. lat.* (until recently, *Drypetes longifolia* was assigned to the Euphorbiaceae, but recent work has seen the genus moved to the Putranjivaceae; Savolainen *et al*. 2000) and the Flacourtiaceae is common (e.g. Sleumer 1954*a*), and *D. longifolia* specimens from the Andaman Islands have also frequently been erroneously ascribed to *Hydnocarpus castanea* (e.g. Rao and Chakrabarty 1985; Chakrabarty and Gangopadhyay 1992).

Geographical distributions reconsidered

By resurrecting the three taxa that Sleumer (1954*a*) combined into *R. javanica sens. lat.*, recognising five new species, and assigning erroneously attributed specimens to their correct species, the geographical range of *R. javanica sens. str.* is reduced quite considerably (Fig. 8); it is now restricted to the southern half of Sumatra, Java and Bali. Within the *Ryparosa javanica* complex, *R. kurzii* and *R. amplifolia* are endemic to the Andaman and Nicobar Islands and New Guinea, respectively, while the distribution of *R. wrayi* overlaps with *R. javanica sens. str*. in northern Sumatra. Likewise, the distributions of *R. anterides* and *R. maycockii* overlap in Borneo, and of *R. maculata* and *R. milleri* in New Guinea. This sympatry in newly recognised taxa provides supporting evidence for the existence of these entities. Interestingly, the Australian taxon, *R. kurrangii*,

is not only the sole representative of the genus known from Australia, but one of only two species of Achariaceae recorded from Australia (the other being the monotypic *Baileyoxylon lanceolatum* C.T.White; Sleumer 1954*a*; Chase *et al*. 2002). When specimens from the other six *Ryparosa* species were correctly determined, no collections were from regions outside their previously documented species distribution. It appears that *Ryparosa* species often reflect geographically circumscribed as well as morphologically distinct entities. Moreover, in both species that had specimens that were geographic outliers (*R. glauca* and *R. amplifolia*), these isolated specimens were also outliers in the morphometric analyses.

Conclusions

It is clear that considerable confusion exists in species delimitations within *Ryparosa*, and the groupings of certain taxa in Sleumer's (1954*a*) revision did little to improve the situation. It seems that past species descriptions have not taken into account important identifying characters of the genus, for the primary reason that *Ryparosa* remains little studied and poorly known from field observations. By using a field-based knowledge of the genus to select meaningful characters, along with relevant characters from the previous generic revision (Sleumer 1954*a*), it was possible to delineate distinctive groupings within *Ryparosa javanica sens. lat.* In addition to re-defining *R. javanica sens. str.*, we found that three previously described species should be reinstated and five new taxa deserve recognition at a species level (see species key). Collections of more reproductive material will no doubt improve the resolution of these and new species groupings within *Ryparosa*, and will be a useful supplement for constructing a more detailed species key. In summary, it is clear that a new generic revision of *Ryparosa* is required, combining field observations of live specimens with analyses of dried and wet herbarium collections.

A dichotomous key for species in the *Ryparosa javanica sens. lat.* complex based on vegetative morphology

Quantitative data are presented as an interquartile range followed by the minimum and maximum values (if distinctly different) in parentheses

1. Leaf blade 95–140 (85–160) mm long with imperfect, suprabasal, acrodromous venation, secondary veins 2–3(–4) pairs, sometimes branching, petiole 11–15 (10–21) mm long . . . . *R. kostermansii*
   Leaf blade length variable, 190–265 (110–375) mm, with camptodromous venation, secondary veins 4 or more pairs, rarely branching, petiole 25–39 (9–60) mm long 2
2. Venation brochidodromous, tertiary venation random reticulate 3
   Venation eucamptodromous, tertiary venation perpendicular percurrent, occasionally reticulated 8
3. Leaf blade width : length ratio 0.33–0.41 (0.29–0.45), leaf tip angle 51–65 (43–69)°, leaf base angle 61–77 (49–81)° 4
   Leaf blade width : length ratio 0.24–0.28 (0.21–0.36), leaf tip angle 40–45 (35–58)°, leaf base angle 47–52 (41–63)° 5
4. Leaf blade shallowly cordate at base, abaxial surface with dense short adpressed hairs on primary and secondary veins, subdense elsewhere, secondary veins 7–8(–9) pairs . . . . *R. maycockii*
   Leaf blade acute at base, abaxial surface with short adpressed hairs very sparse (if at all) on primary and secondary veins, glabrous elsewhere, secondary veins 8–10 (7–11) pairs 6

---

[1]The observation of free stamens in staminate *R. kostermansii* flowers is not the first time this has been reported in the genus (see *R. caesia*, van Slooten 1919, 1925; *R. hirsuta*, Sleumer 1954*a*).

5. Secondary veins 5–6 pairs, straight ascending for the most part. Leaf blade width : length 0.31–0.35 (0.30–0.36); leaf tip angle 53–58°, leaf base cuneate
.... *R. acuminata*
    Secondary veins 7–8(–9) pairs, curved–ascending. Leaf blade width : length 0.24–0.27 (0.21–0.29), leaf tip angle 39–43 (35–54)°, leaf base attenuate . .
.... *R. kurrangii*
6. Leaf blade cuneate to attenuate at the base, entirely glabrous, secondary veins diverging at 61–69 (58–74)° from the primary vein, strongly
    curved-ascending .... *R. glauca*
    Leaf blade attenuate to rounded at the base, abaxial surface with sparse hairs at least on midrib, secondary veins diverging at 49–56 (47–61)° from the
    primary vein, curved-ascending 7
7. Leaf blade distinctly coriaceous; petiole 32–45 mm long.. *R. baccaureoides*
    Leaf blade chartaceous; petiole 10–14 mm long.. *R. milleri*
8. Secondary veins curved-ascending; without shoot swellings 9
    Secondary veins straight for the most part; shoot tips (and smaller branches) commonly swollen and hollow with small circular entry holes 12
9. Abaxial surface of leaf blade with subdense short adpressed hairs on primary vein, scattered on secondary veins and lamina 10
    Abaxial surface of leaf blade with sparse short adpressed hairs on primary vein, very sparse on secondary veins and rarely the lamina 11
10. Leaf blades elliptic, at least 180 mm long, width : length 0.27–0.35 (0.23–0.41), tip angle less than 57° .... *R. wrayi*
    Leaf blades obovate, less than 170 mm long, width : length 0.37–0.43 (0.34–0.46), tip angle greater than 57°.......................... *R. maculata*
11. Leaf blades ovate-elliptic; tip angle (58–)62–65°, base angle 69–78(–88)° .... *R. kurzii*
    Leaf blades elliptic; tip angle 52–57 (46–62)°, base angle 57–63 (52–69)° .... *R. javanica*
12. Leaf blades 235–310 (200–373) × 100–125 (85–145) mm, distinctly obovate, tip broadly acute-mucronate, tip angle greater than 65° .... *R. amplifolia*
    Leaf blades up to 210 × 80 mm, obovate-elliptic, tip acute-acuminate, tip angle less than 60° 13
13. Leaf blades obovate-elliptic, width : length 0.33–0.37 (0.29–0.39), tip angle greater than 49°, secondary veins 7–8 (6–9) pairs .... *R. calotricha*
    Leaf blades elliptic, width : length 0.26–0.31 (0.24–0.34), tip angle less than 47°, secondary veins 6 (5–7) pairs .... *R. anterides*

Taxonomic treatment

Place name descriptors were spelled as by the collector (based on best possible interpretations of handwriting on the specimen label), with extra large-scale information (e.g. districts, regencies) and current versions of place names added where necessary (in square brackets) to clarify locations. Dutch and German place name descriptors were changed to their equivalent English version where possible (e.g. Seroei to Serui); however, Malay descriptors (e.g. bukit, gunung) have been retained when used on the original labels. In agreement with the policy of this journal, Australian specimen citations have been deliberately abbreviated for conservation management purposes. Bold text in the descriptions indicates a character trait of importance for the particular species.

Unless otherwise mentioned, for all species described in this treatment plants are most likely monoecious (confirmed for *R. kurrangii* sp. nov.); young twigs and shoot tips are tomentose when young, glabrescent with Type B food-body scars; leaves are borne spirally on the stem, leaf margins are entire (Fig. 9c), the primary vein is distinctly prominent abaxially, the petiole is thickened at both ends, and prominently kneed at the apex; stipules are absent; hairs (sometimes only visible under magnification) are T-shaped bifurcate, and with one branch often reduced, multicellular (Fig. 6); inflorescences are racemes; the calyx splits irregularly and is glabrous adaxially, petals have a basal scale adaxially that is densely villous, the ovary is superior, stigmas are close together both in flower and fruit, and bracts are generally absent from fruit racemes.

Ryparosa javanica (Blume) Kurz ex Koord. & Valeton, *Bijdr. Booms.* 5: 11 (1900), *l.c.* 6: 185 (1900)

Bergsmia javanica Blume, *Rumphia* 4: 23, Tab. 178C, fig. 2 (1848). *Ryparia javanica* (Blume) Kurz, *J. Bot.* 11: 234 (1873). *Typus*: Java,

[West Java, Bantam Region, Gunung Poelasari, 06°20′S, 105°59′E], Kuhl, H. & van Hasselt, J.C., *s.n.*, *1821* (lectotype, here designated: L [*L0011213*]; *likely isolectotype*: L [*L0011214*]).

Ryparosa longipedunculata Boerl., *Cat. Hort. Bog.* 55 (1899). *Ryparia caesia* var. *macrostachya* Kurz. *nom. nud.*; *nom in sched.* only. *Typus*: [Java, West Java, Bogor Region, Bogor], cultivated in Bogor Botanic Gardens, (06°36′S, 106°48′E), Bogor Botanical Garden, *s.n.* (*III-F-15*), *no date* (lectotype, here designated: L [*L0011217*]).

Tree up to 18 m tall. Outer bark rough, grey-brown, inner bark pink; wood straw yellow. *Leaf* blades elliptic to ovate-elliptic,   (110–)190–290(–320) × (40–)65–95(–115) mm, acute at the apex, (46–)52–58°, sometimes with a short acuminate tip, attenuate at the base, (52–)57–64(–69)°, texture chartaceous, surface glabrous adaxially, abaxially with sparse hairs on the primary (and secondary) veins, **lamina glabrous** (with sparse hairs), primary vein sunken adaxially, secondary veins **eucamptodromous**, **five or six pairs**, slightly raised adaxially and prominent abaxially, diverging at (27–)40–51(–61)° from the primary vein, curved-ascending towards the margin, **tertiary venation subpercurrent**; petiole (22–)30–39(–50) mm long. *Staminate inflorescences* to 325 mm long, single from **foliate or defoliate axils** (solitary or in fascicles of 2 or 3 on branchlets); bracts *c.* 0.5 mm long; pedicels 1.8–3.7 × 0.3–0.5 mm; calyx splitting into two or three lobes, lobes 2.2–2.6 mm long, abaxially sparse adpressed-puberulent; petals 5, 2.7–3.1 × 1.1–1.3 mm, adaxially glabrous, abaxially densely tomentose; scale 1.1–1.4 × 0.5–0.7 mm; filaments five, united, **villous**; stamens 2.3–3.6 mm long. *Carpellate inflorescences* to 185 mm long, single from **foliate or defoliate axils** (solitary or in fascicles of 2 or 3 on branchlets); bracts 0.4–0.5 mm long; pedicels (2.7–)3.9–5.0 × 0.3–0.5 mm; calyx splitting into two or three lobes, lobes 2.3–3.8 mm long, abaxially sparse adpressed puberulent; petals four or five, 3.0–4.4 × 1.2–2.0 mm, glabrous adaxially; abaxially densely tomentose, scale 1.1–1.5 × 0.7–1.0 mm;

staminodes 4 or 5, 0.4–0.9 mm long, **thin filiform** (somewhat fleshy in Bali specimen), pilose adaxially; ovary ellipsoid (obovoid); stigmas 2 or 3, sessile. *Fruit racemes* to 180 mm long; pedicels 3.3–6.2 × 0.6–1.4 mm. *Fruits* globose, 1-locular, 1 or 2-seeded; stigmas 2 or 3, sessile.

Notes

Likely syntypes for *Bergsmia javanica* Blume (*Kuhl & van Hasselt, s.n.*) are currently held by Leiden (*L0351538, L0351539, L0351540, L0351541, L0351542*). *Ryparosa longipedunculata* Boerl. was originally described from three living trees (*III-F-15*, *IX-A-32* and *IX-A-34*) in the Bogor Botanic Gardens, which were grown from seed collected in Sumatra (Boerlage 1899). The lectotype specimen for *R. longipedunculata* (*L0011217*) was taken from the tree *III-F-15*; however, as no date was recorded and the tree died only in 1979, it is possible that the lectotype specimen may have been collected after the species description (e.g. another specimen from *III-F-15* [*L0351617*] was collected on 07.xi.1953). Other designated types (incorrectly indicated by det. slips placed on specimens by H.O. Sleumer; *L0011216, L0011218*) are from another tree (*III-F-15a*), which was grown from seed collected from the same maternal plant as *III-F-15*, but is a separate individual. In their description of *R. longipedunculata*, Koorders & Valeton (1900*a*) cite a synonymy with *R. caesia* var. *macrostachya*, the description of which is attributed to 'Kurz.! msc.' with a specimen lodged in 'Herb. Bog.'. However, no evidence of the specimen or of a published description of *R. caesia* var. *macrostachya* could be found. In western Java, S.H. Koorders collected from permanently tagged trees and some of his 'specimen numbers' refer to individual trees and not true collection numbers (e.g. *2728*β above; van Slooten 1925). The drawing of *Bergsmia javanica* in Blume's description (Tab. 178C, Fig. 2; Blume 1848) depicts the racemes of *R. javanica* far too large relative to the foliage on which they are positioned, while Sleumer (1954*a*) incorrectly labels the staminate racemes of *R. javanica* (figs 18, 19) as carpellate racemes.

Distribution and ecology

Distributed through southern Sumatra, Java and Bali (Fig. 8*b*). In contrast to previous reports, not known from Borneo, the Malay Peninsula or east of Bali. Rainforest habitats up to 500 m, occasionally up to 1400 m, frequently found near streams. Flowering: May–Nov; fruiting: Jul–Jan.

Vernacular

JAVA: Bantam region: *Langit*, *Kisijung* (referring to the scent of the bark; i.e. almond, cyanide); Preanger region: *Kᵢ manjěti*, *Kᵢ měngati*, *Hoeroe gading*, *Hoeroe tangkalak*; Banyumas region: *Langit*, *Wera*, *Selemati*; Besoeki region: *Hendog*, *Boeroe merak*.

Selected specimens (60 specimens examined)

SUMATRA: Aceh Province: [Aceh Tenggara Regency], Gunung Leuser Nature Reserves, Ketambe Research Station and vicinity, Alas River valley (*c*. 35 km NNW of Kutacane), [03°40′N, 97°40′E], *de Wilde, W.J.J.O. & de Wilde-Duyfjes, B.E.E., 18547*, 10.vii.1979 (L). Benkulu Province: Redjang [Rejang Lebong Regency], Konak, 2 km from Kepahiang, [03°40′S, 102°34′E], *Boschproefstation, bb 15438*, 1.iii.1931 (L). Sumatera Selatan Province: [Musi Rawas Regency], Tandjong Ring [cf. Tandjoengning, now Tanjungaing, on the Sungai Saling, 03°32′S, 103°02′E], *Forbes, H.O., 2720*, 1881 (BM, L). Sumatera Utara Province: Asahan [now Simalungun Regency], Silo Maradja [cf. Silomalela], in the vicinity of Taloen Djoring, [*c*. 03°08′N, 99°10′E], *si Toroes, Rahmat* (*with Hamel, C.*), *49*, 1.xii.1927 (SING). JAVA: Central Java: Banjoermas [Banyumas] Region, Nusa Kambangan [Island], near Tjilatjap [Cilacap, 07°45′S, 108°59′E], *Koorders, S.H., 24628β* (*1339c*), 21.ix.1896 (L). East Java: Besuki [Besoeki Region], Gunung Raung, south slope above village Gunungsari, [08°08′S, 114°05′E], *Jacobs, M., 4821*, 17.v.1957 (K, L, SING); Banyumas Prov. [unlikely], Pasoeroean [Region], Tangkill Evidergebergte [cf. Tangkil, 08°11′S, 112°48′E], *Koorders, S.H., 30291β* (*1581x*), 27.vi.1896 (L). West Java: [Bantam Region], foot of Mt Hondje, [06°43′S, 105°34′E], *Kostermans, 19312*, 29.xii.1961 (L); Bantam Region, Gunung Karang, [06°17′S, 106°03′E], *Koorders, S.H., 2763β*, 12.vi.1892 (L); Preanger Region, Palaboeanratoe [Pelabuhan Ratu, 07°00′S, 106°35′E], *Koorders, S.H., 33066β* (*1120a*), 23.iii.1899 (L); Preanger Region, Takoka [now Takokak, 07°03′S, 106°59′E], *Koorders, S.H., 25650β* (*2433a*), 27.x.1896 (L). BALI: [Bakungan Mountains], Gunung Kelatakan, [08°12′S, 114°30′E], *Sarij* (*Maier, R.E.P.*), *110*, 19.vii.1918 (BO, L).

Ryparosa amplifolia (K. Sch.) Mildbr., *Notizbl. Berl.-Dahlem* 10:339 (1928)

Gertrudia amplifolia K. Sch., *Fl. Deut. Schutzgeb.*: 455 (1901). *Typus*: New Guinea, [Papua New Guinea, Madang District], Kaiser Wilhelmsland, Ssigaun [Sigaun, *c*. 05°32′S, 145°23′E], *Lauterbach, C.A.G., 2848*, 11.ix.1896 (*lectotype, here designated*: L [*L0011215*]; *isolectotype*: WRSL). New Guinea [West New Guinea, Papua Province, Yapen Waropen Regency], Jappen-Biak [Yapen] Island, Kaunda, near Seroei [Serui, 01°40′S, 135°59′E], *Aet & Idjan* (*exp. van Dijk, L.J.*), *567*, 19.viii.1939 (*epitype, here designated*: SING [*SING0039126*], *isoepitypes, here designated*: BO [*BO1462938*], L [*L0351597, L0351598*], K).

Tree 14–22(–30) m tall; bole 8–12 m. Outer bark rough, grey-brown, wood straw yellow. **Stem swellings at shoot tips** and younger **internodes commonly hollow with ant domatia**. *Leaf* blades **distinctly obovate, (140–)235–310 (–370) × (70–)95–125(–145) mm**, rounded at the apex, 71–74(–78)°, **generally with a short mucronate tip**, cuneate to attenuate at the base, (67–)72–77(–81)°; texture chartaceous, surface glabrous adaxially, **abaxially with dense hairs on the primary and secondary veins**, **subdense on the lamina**, food-body scars distinct, primary vein sunken adaxially, secondary veins eucamptodromous, **(7–)8 or 9 pairs**, slightly raised adaxially and prominent abaxially, diverging at (36–)43–48(–55)° from the primary vein, reasonably straight ascending towards the margin, tertiary venation undulate, percurrent; petiole 28–38(–50) mm long. *Staminate inflorescences* single from foliate or defoliate axils, or in fascicles of up to 4 from **small tubercles on branchlets**;

buds clumped in distinct bunches on raceme peduncle; mature flowers not seen. *Carpellate inflorescences* to 75 mm long, single from foliate or defoliate axils, or in fascicles of up to 4 from **small tubercles on branchlets**; **buds clumped in distinct bunches** on raceme peduncle; bracts *c.* 0.5 mm long; pedicels 2.4 × 0.7 mm; calyx splitting into three lobes, lobes *c.* 4.1 mm long, sub-dense adpressed puberulent abaxially; petals 5; *c.* 4.7 mm × 1.9 mm, glabrous adaxially, abaxially densely tomentose; scale 2.5 × 1.2 mm; staminodes 0.9 mm long, somewhat fleshy, pilose adaxially; ovary ellipsoid; stigmas 2, sessile. *Fruit racemes* to 85 mm long; pedicels (2.8–)5.8–7.5 × (0.9–)1.3–2.3 mm. *Fruits* globose; stigmas 2, sessile.

Notes

The original type specimen, *Lauterbach, 2848* (lodged at B), appears to have been destroyed during World War II (Zepernick 1978, R Vogt pers. comm.). At some point in his studies, Sleumer created 'kleptotypes' from the B holotype, which are now lodged at Leiden (consisting of one small deformed leaf; *L0011215*) and Wroclaw (consisting of leaf, raceme and fruit fragments). This is all that remains of the original type specimen and it does not allow for the precise application of the taxon name. The only paratype listed by Mildbraed (1928; *Schlechter, 17599*) is also in poor condition and is unidentifiable; therefore, an epitype has been here designated.

Distribution and ecology

Distributed through Indonesian New Guinea and Papua New Guinea (Fig. 8*c*). The correct identity of the single specimen from Sulawesi (*Meijer, 10788*) is uncertain at this stage. Rainforest habitats up to 300 m, occasionally much higher, often found near rivers and streams. Consistently associated with stem-nesting ants (perhaps *Camponotus* sp.; Webber *et al.* 2007). Flowering: Mar–Oct; fruiting: May–Dec.

Vernacular

NEW GUINEA: Sorong Regency, West New Guinea: *Tokahee* (Tehid); Manokwari Regency, West New Guinea: *Bendaang* (Hattam), *Aidia* (Wandammen), *Wobbrijka* (Mamikiong), *Sagoboeatemol* (Colonial Dutch); Madang District, Papua New Guinea: *Abai* (Bilia), *Okabidelo* (Amele), *Papoia* (Dumpu), *Mangu* (Faita); Northern District, PNG: *Sanga*, *Siditoteh* (Orokaiva, Mumuni).

Selected specimens (51 specimens examined)

SULAWESI: SW peninsula, NE of Makassar, within 54–60 km on the road, [04°55′S, 119°45′E], *Meijer, W., 10788*, 4.vii.1976 (L). NEW GUINEA: Papua New Guinea: Madang District, lower slopes of Bismark Range, Ramu Valley, *c.* 5 miles SE of Faita airstrip, [05°40′S, 145°18′E], *Saunders, J.C., 380*, 1.vii.1955 (L); [Madang District], Kaiser Wilhelmsland [NE New Guinea], woods at Djamu [Ramu river, *c.* 04°27′S, 144°38′E], *Schlechter, F.R.R., 17599*, 24.iv.1909 (L); Milne Bay District, Sag Alotau Subprovince, north slopes of Pini Range, [10°23′S, 150°16′E], *Gideon, O., LAE 76985*,

4.iii.1984 (CANB, L, LAE); West Sepik [now Sandaun] District, Vanimo Subdistrict, Ossima, [02°56′S, 141°17′E], *Streimann, H. & Kairo, A., NGF 39271*, 30.i.1969 (L); [Southern Highlands District], 20 km SSW of Kutubu, near Waro airstrip, [06°27′S, 143°11′E], *Jacobs, M., 9159*, 12.x.1973 (L, LAE). Western New Guinea: [Jaya Wijaya Regency], Sabang [Lorentz River, 04°46′S, 138°47′E], *Branderhorst, B., 327*, 2.iv.1908 (L); Hollandia [Jayapura Regency], Bernhard bivak [Bernhardkamp, on the Idenburg River, 03°27′S, 139°08′E], *Neth. Ind. For. Service, bb 25751*, 8.viii.1938 (L); [Manokwari Regency], Wandammen Peninsula, Wondiwoi Mountains, [02°43′S, 134°32′E], *Schram, F.A.W, BW 13455*, 14.iii.1962 (L, LAE); [Yapen Waropen Regency], Eil Japen [Yapen Island], Seroei [Serui, 01°52′S, 136°13′E], *Neth. Ind. For. Service, bb 30610*, 16.ix.1939 (L, SING); [Manokwari Regency], Warmare valley (*c.* 20 km SW of Manokwari), [00°55′S, 134°00′E], *Moll, O., BW 2481*, 4.iv.1962 (L).

Ryparosa kurzii King, *J. As. Soc. Beng.* 59:125 (1890)

Typus: Andaman Islands, South Andaman Island, Mt Harriet, [11°43′N, 92°44′E], *Kurz, S., s.n., 2.ii.1875* (lectotype, here designated: K [*K000186455*]).

  Ryparosa caesia auct. non Blume: Kurz, *J. Bot.* 11:234 (1873); *J. As. Soc. Beng.* 45: 117 (1876); *For. Fl. Br. Burma* 78 (1877).

A rather small *tree* up to 7 m tall. Outer bark rough, grey-brown, inner bark pink; wood straw yellow. *Leaf* blades **distinctly ovate-elliptic**, 200–260 × 95–110 mm, acute at the apex, (58–)62–65°, **attenuate to rounded at the base, 69–78(–88)°**, texture chartaceous, surface glabrous adaxially, abaxially with sparse hairs on the primary and secondary veins and lamina (lamina glabrous), food-body scars distinct, primary vein sunken adaxially, secondary veins **distinctly eucamptodromous, 6 or 7 (rarely 8) pairs**, slightly raised adaxially and prominent abaxially, diverging at 46–55° from the primary vein, curved-ascending towards the margin, tertiary venation somewhat reticulated; petiole 23–28(–33) mm long. *Staminate inflorescences* to 185 mm long, single from foliate or defoliate axils; bracts 0.3–0.5 mm long; pedicels 1.8–2.8 × 0.3–0.4 mm; calyx splitting into three lobes, lobes 2.2–2.6 mm long, abaxially strigose; petals 5, 2.7–3.1 × 0.8–1.0 mm, glabrous adaxially, abaxially densely tomentose; scale 1.0–1.4 × 0.5–0.7 mm; filaments 5, united, villous; stamens 2.8–2.9 mm long. *Carpellate inflorescences* to 120 mm long, single from defoliate axils (foliate axils), or solitary on branchlets; bracts *c.* 0.5 mm long; pedicels 4.2–4.5 × 0.4–0.5 mm; calyx splitting into three lobes, lobes *c.* 3.0 mm long, abaxially strigose; petals 5, 3.3 × 1.2 mm, glabrous adaxially, abaxially densely tomentose, scale 1.6 × 0.6 mm; staminodes **distinctly elongated, 1.1–1.3 mm long, thin filiform with a pointed tip**, pilose adaxially; ovary ellipsoid-obovoid; stigmas 2, sessile. *Fruit racemes* to 110 mm long; **pedicels long, 9.3 × 0.7 mm**. *Fruits* globose; stigmas 2, sessile.

Distribution and ecology

Distribution restricted to the Andaman and Nicobar Islands (Fig. 8*a*). Mixed rainforest habitats at low altitude, noted as being rare by Nair in 1974 (e.g. *Nair, N.G., 1632*). Flowering: Mar–Aug; fruiting: May–Nov.

Selected specimens (7 specimens examined)

ANDAMAN ISLANDS: Andaman Islands, *Parkinson, C.E.*, *336*, 18.ii.1915 (K). Middle Andaman Island: Bom Lung Ta [Bomlungta, 12°30′N, 92°52′E], *Parkinson, C.E.*, *1191*, 14.iv.1916 (BM). South Andaman Island: Dhani Khari, [11°33′N, 92°41′E], *Dr King's Collector, s.n.*, 17.iii.1894 (BM). NICOBAR ISLANDS: North Nicobar Island: Car Nicobar Island, Lapathy District, [Lapate, 09°13′N, 92°48′E], *Nair, N.G.*, *1632*, 14.vi.1974 (L).

Ryparosa wrayi King, *J. As. Soc. Beng.* 59: 126 (1890)

Typus: No location listed [likely to be Malaysia, Peninsular Malaysia, Perak, Taiping region, *c.* 04°51′N, 100°51′E], *Wray, L. Jr.*, *3190*, no date (*lectotype*, *here designated*: K [*K000186444*]; *isolectotypes*: BM [*BM624231*], CAL [*33781*]).

Tree 13–15(–30) m tall; buttressed to 3.0 m. Young twigs rarely with hollow stem internodes and round entry holes. *Leaf* blades elliptic, (175–)200–255(–335) × (45–)55–80(–120) mm, acute at the apex, (42–)47–53°, attenuate at the base, (44–)54–65(–76)°, texture chartaceous, surface glabrous adaxially, **abaxially with hairs moderately dense**, distinct food-body scars, primary vein sunken adaxially, secondary veins **distinctly eucamptodromous**, **(4–)5 or 6 pairs**, **the most apical distinctly distant from the leaf tip**, raised adaxially and prominent abaxially, diverging at (34–)39–48° from the primary vein, moderately curved-ascending towards the margin, tertiary venation percurrent; petiole (20–)26–35(–41) mm long. *Staminate inflorescences* to 550 mm long, solitary from foliate or defoliate axils, or on branchlets; mature flowers not seen. *Carpellate inflorescences* to 305 mm long, solitary from foliate or defoliate axils, or on branchlets; bracts *c.* 0.5 mm long; **pedicels elongated *c.* 7.0 × 0.6 mm**; calyx sparse adpressed puberulent abaxially; petal glabrous adaxially, abaxially dense adpressed puberulent; staminodes 5, thin filiform, pilose adaxially; ovary ellipsoid-obovoid; stigmas 2 (3), somewhat sessile. *Fruit racemes* to 270 mm long; pedicels 5.5–6.5 × 1.1–1.6 mm. *Fruits* globose, 1-locular, 2-seeded; stigmas 2 (3), **slightly stalked** or rarely sessile.

Notes

Specimens from the Malay Peninsula are frequently misidentified as *R. caesia*, most likely due to the hairs on the abaxial leaf lamina. *Ryparosa wrayi* is occasionally associated with stem-nesting ants, although entry holes into hollow internodes do not seem to be associated with swollen stems (Webber *et al.* 2007).

Distribution and ecology

Distributed from southern Thailand and Myanmar through the Malay Peninsula, also in northern Sumatra (Fig. 8*a*). Primary rainforest habitats up to 200 m, occasionally up to 500 m, often found near streams. Flowering: Mar–Oct; fruiting: May–Jan.

Vernacular

THAILAND: Trang Province: *Kluai*; SUMATRA: Sumatera Utara Province: *Tjingkuang, Badja*.

Selected specimens (36 specimens examined)

MYANMAR: Tenasserim [now Tanintharyi] Division: Hui Sai Kao, [*c.* 10°26′N, 98°44′E], *Kerr, A.F.G.*, *21650*, 1.vi.1932 (K). PENINSULAR THAILAND: Chumphaun [Chumphon] Province: Tha Sae District, Ta San [cf. Tha Sae, 10°35′N, 99°08′E], *Kerr, A.F.G.*, *16252*, 22.xii.1925 (BM, L). Nakhon Si Thammarat Province: Lansagah [probably Phrom Khiri] District, Khao Luang NP, Prom Loke falls, [08°30′N, 99°47′E], *Maxwell, J.F.*, *87–191*, 24.ii.1987 (L). Narathiwat Province: Waeng, [05°54′N, 101°52′E], *Phusomsaeng, S.*, *41198*, 1.v.1968 (L). Trang Province: Na Yong District, Khao Chong F.R., [07°35′N, 99°49′E], *Phusomsaeng, S. & Pinnin, S.*, *315*, 10.xii.1969 (K, L). PENINSULAR MALAYSIA: Johore: Kota Tinggi, Medang, Panti FR, No. 72, (01°51′N, 103°53′E), *Baker, F.G.A.*, *93640*, 8.vii.1961 (KEP). Kelantan: [Tanah Merah], Ulu Sat FR, [05°43′N, 102°19′E], *Suppiah, T.*, *KEP 104565*, 16.vi.1968 (L). Perak: Larut, (04°53′N, 100°47′E), *Dr King's Collector*, *6642*, ix.1884 (BM, L). Selangor: Kajang, Sungai Lalang FR, Sungai Seningoh river valley, [03°03′N, 101°53′E], *Symington, C.J.*, *22668*, 6.iii.1930 (SING); Ulu Langat, Bukit Tangkol [Bukit Tunggul], [02°54′N, 101°45′E], *Gadoh anak Unbai (for Millard, A.H.), KL 2181*, 2.x.1960 (KEP). SUMATRA: Sumatera Barat Province: Pasaman Regency, Batang Mandiangin, [00°07′S, 99°47′E], *Laumonier, Y.*, *TFB 3528*, 21.iii.1982 (L). Sumatera Utara Province: East Coast, Longkat [Lankat] Regency, Telaga Said, [03°57′N, 98°12′E], *Boschproefstation, bb 9376*, 10.xi.1925 (L).

Ryparosa maculata B.L.Webber, *sp. nov.*

A *R. javanica* (Blume) Kurz ex Koord. & Valeton in laminis minoribus (125–160 mm longis) obovatis indumento paginis abaxialibus praeditis, et fructibus 2–3-seminibus differt.

Typus: New Guinea, [Papua New Guinea], Northern District, S slopes of Hydrographers Range, Managalase area, near Siurane [cf. Siurani] village, [08°59′S, 148°23′E], *Pullen, R.*, *5479*, 28.vii.1964 (*holotype*: LAE [*75752*]; *isotype*: L [*L0351604*]).

Tree up to 24 m tall (butressed). Outer bark rough, light brown-grey, wood straw yellow. *Leaf* blades **obovate**, **(110–)125–160(–170) × (40–)45–65(–70) mm**, acute-acuminate at the apex, 59–64°, with a well defined **acuminate tip to 15 mm**, attenuate at the base, 60–65°, texture subcoriaceous, surface glabrous adaxially, abaxially with hairs **moderately dense on the primary and secondary veins**, sparse on the lamina, food-body scars, **distinctive circular pellucid spots in the lamina abaxially**, primary vein sunken adaxially, secondary veins **eucamptodromous, 5 or 6 pairs**, slightly raised adaxially and prominent abaxially, diverging at 38–43° from the primary vein, curved-ascending towards the margin, tertiary venation **percurrent undulate**; petiole (9–)17–23 mm long. *Staminate inflorescences* to **120 mm long**, solitary from foliate or defoliate axils; bracts 0.5–0.6 mm long; pedicels *c.* 0.5–1.3 × 0.4 mm; calyx lobes *c.* 2.2 mm long, abaxially sparse adpressed puberulent; petals four or five, 2.0–2.3 × 0.9–1.1 mm, glabrous adaxially, abaxially densely tomentose, scale *c.* 1.0 × 0.4–0.6 mm;

filaments four or five, united, villous (glabrous); stamens 1.9–2.7 mm long. *Carpellate inflorescences* to 35 mm long, solitary from foliate or defoliate axils; bracts *c.* 0.5 mm long; pedicels *c.* 1.2 × 0.5 mm; calyx splitting into three lobes, lobes *c.* 2.3 mm long, abaxially sparse adpressed puberulent; petals *c.* 3.1 × 1.9 mm, glabrous adaxially, abaxially densely tomentose, scale *c.* 1.1 × 0.7 mm; staminodes 5, *c.* 1.1 mm long, thin filiform, pilose adaxially or entirely glabrous; ovary ellipsoid (obovoid); stigmas two, sessile. *Fruit racemes* to 65 mm long; pedicels **stocky,** *c.* **1.8 × 1.6 mm**. *Fruits* globose, 1 locule, **2 or 3 seeds**; stigmas 2, sessile.

Distribution and ecology

The species is only known only from the rainforests of eastern New Guinea (Papua New Guinea; Fig. 8*d*) where it has been collected at altitudes from 30 to 1100 m. Flowering known from Feb to Sep and fruiting from Aug to Dec.

Etymology

From the Latin, *maculatus*, spotted, referring to the conspicuous circular pellucid spots in the abaxial leaf lamina.

Additional specimens examined

NEW GUINEA: Papua New Guinea: Central District, *c.* 15 km NE of Cape Rodney, Mori River, [10°06′S, 148°31′E], *Pullen, R., 8189*, 1.ix.1969 (LAE); Central District, Ilolo, [09°25′S, 147°25′E], *Streimann, H. & Kairo, A., NGF 26185*, 3.ii.1966 (LAE); Morobe District, ~7 miles N of Lae, between Busu and Butibum rivers, [06°38′S, 146°59′E], *Hartley, Thomas G., TGH 11443*, 20.iii.1963 (CANB, LAE); Morobe District, Lae, end of Sunkwep Logging Rd, [06°35′S, 146°55′E], *Katik, P. & Steven, F., NGF 46786*, 23.vii.1971 (CANB, L, LAE); Western District [Kiunga Subdistrict], near Ingembit village, [05°39′S, 141°01′E], *Henty, E.E., Ridsdale & Galore, NGF 31863*, 10.vi.1967 (LAE).

Ryparosa anterides B.L.Webber, *sp. nov.*

A *R. micromera* Slooten in statura (ad 40 m), trunco anteridibus praedito, nervis eucamptodromis pro parte maxima rectis a costa angulis angustis divergentibus, et caulibus tumoribus myrmecophilis distinctis ornatis, differt.

Typus: East Borneo [East Kalimantan], East Kutei, Sangkulirang Subdivision, Sungai Susuk region, [00°57′N, 118°13′E], *Kostermans, A.J.G.H., 5481*, 27.vi.1951 (*holotype*: L [*L0351551 & L0351552*]; *isotypes*: BM [*BM756086*], CAL, K, NY, SING [*SING0039112*]).

A **large** *tree* **up to 25–35(–40) m tall**; bole fluted, 16–18 m; **large thick buttresses** up to 5.0 m high, 3.0 m over the ground. Outer bark smooth, light-brown; wood pale brownish-yellow. **Distinctive stem swellings at shoot tips and young stem internodes** commonly hollow with circular entry holes formed by ants. *Leaf* blades elliptic, **135–195(–215) × 40–50(–55) mm**, acute at the apex, (39–)43–46°, without a sharply acuminate tip, attenuate at the base, 54–60(–64)°, texture chartaceous, surface glabrous adaxially, **abaxially with hairs moderately dense,**

distinct food-body scars, primary vein sunken adaxially, secondary veins **distinctly eucamptodromous**, 5 or 6(–7) pairs, slightly raised adaxially and prominent abaxially, diverging at (27–)30–38(–41)° from the primary vein, **rather straight-ascending at a distance from the margin**, tertiary venation undulate percurrent; petiole (20–)26–30(–35) mm long. *Staminate inflorescences* to **120 mm long**, solitary from foliate or defoliate axils; bracts *c.* 0.6 mm long; pedicels *c.* 1.7 × 0.3 mm; calyx splitting into two or three lobes, lobes *c.* 2.2 mm long, abaxially sparse adpressed puberulent; petals five, *c.* 2.1 × 0.9 mm, glabrous adaxially, abaxially densely tomentose, scale *c.* 0.6 × 0.3 mm; filaments 5, united, villous; stamens *c.* 2.5 mm long. *Carpellate inflorescences* solitary from foliate or defoliate axils; bracts *c.* 0.5 mm long; pedicels *c.* 4.5 × 0.4 mm, calyx splitting into two or three lobes, lobes 2.4–2.6 mm long, abaxially sparse adpressed puberulent; petals 4 or 5, *c.* 3.2–3.7 × 1.3 mm, glabrous adaxially, abaxially densely tomentose, scale 1.6–2.3 × 1.0–1.1 mm; staminodes 5 (4), 0.7–0.8 mm long, thin filiform, pilose adaxially; ovary ellipsoid; stigmas 2, sessile. *Fruit racemes* to 125 mm long; pedicels 5.0–6.0 × 1.4–1.9 mm. *Fruits* globose; stigmas 2, sessile.

Notes

The mature fruits of *R. anterides* are said by Kostermans (*Kostermans, 13720*) to be brown and edible (mature fruits are not known from the vegetatively similar *R. micromera*).

Distribution and ecology

Known only from the rainforests of east Kalimantan (Fig. 8*b*), sometimes on sand or loam soil containing limestone rocks and in wet or periodically inundated areas; noted as uncommon to rare by Kostermans in the 1950s (e.g. *Kostermans, A., 13440*). *Ryparosa anterides* is consistently associated with stem-nesting ants (identity unknown). Habitat altitude 10–400 m. Flowering: May–Oct; fruiting: Jul–Nov.

Vernacular

BORNEO: Berau Region, Kalimantan: *Rukun* (Bassap).

Etymology

The epithet is a noun in apposition, from the Latin, *anterides*, buttresses, referring to the distinctive large buttresses formed by this taxon.

Selected specimens (15 specimens examined)

BORNEO: East Kalimantan: Berouw [Berau] Region, foot of Mt Ilas Bungaan, [02°13′N, 117°26′E], *Kostermans, A., 13720*, 8.ix.1957 (K, L); Berau Region, Sungai Kelai, base of Mt Njapa, [01°48′N, 117°16′E], *Kostermans, A., 21216*, 11.x.1963 (L); East Kutei, S of Sangkulirang, Gunung Sekrat, [00°53′N, 117°49′E], *Kostermans, A, 5923*, 28.vii.1951 (BM, L, SING); [East Kutei], Sangkulirang District, north of Sangkulirang, Mt Medadam [Gunung Madadem, 01°09′N, 118°02′E], *Kostermans, A., 13424*, 9.viii.1957 (K, L, LAE, SING).

Ryparosa milleri B.L.Webber, *sp. nov.*

A *R. javanica* (Blume) Kurz ex Koord. & Valeton foliis in basin late rotundatis, petiolis brevibus (12–14 mm longis), nervis foliorum brochidodromis curvati-ascendentibus undulatis differt.

Typus: Netherlands New Guinea [West New Guinea, West Irian Jaya Province], Sorong District, hills S of Radio Sorong, [00°52′S, 131°16′E], *van Royen, P., 3332*, 7.iv.1954 (*holotype*: L [*L0351582*]; *isotypes*: BRI [*BRI376716*], LAE [*20341*], SING [*SING0039128*]).

Small *tree* (straggling *shrub*) up to 3.0 m tall. Outer bark brown, wood straw yellow. *Leaf* blades distinctly oblong-elliptic, 170–205(–215) × 60–75 mm, acuminate at the apex, 52–57°, generally with a **well defined tip to 15 mm**, **rounded at the base**, **74–79°**, texture chartaceous, surface glabrous adaxially, abaxially with sparse hairs on the primary vein (secondary veins), lamina glabrous, food-body scars; primary vein sunken adaxially, secondary veins **brochidodromous (undulate)**, seven or eight pairs, slightly raised adaxially and prominent abaxially, diverging at 51–57° from the primary vein, curved-ascending close to the leaf margin, tertiary venation reticulated; **petiole short, 12–14 mm long**. *Staminate inflorescences* not known. *Carpellate inflorescences* to 100 mm long, solitary from foliate, **somewhat supra-foliate** or defoliate axils; bracts 0.5–0.6 mm long; pedicels 1.9–2.2 × 0.3–0.4 mm; calyx splitting into two or three lobes, lobes 1.7–1.9 mm long, sparse adpressed puberulent abaxially; petals 4 or 5, 2.1–2.7 × 1.1–1.5 mm, glabrous adaxially, abaxially densely tomentose, **scale *c.* 0.8 × 0.6–0.7 mm**; staminodes 0.2–0.3 mm long, **thick fleshy, pilose on both sides**; ovary ellipsoid; stigmas 2, sessile. F*ruit racemes* to 65 mm long; pedicels *c.* 2.0 × 1.6 mm. *Fruits* globose, stigmas 2, sessile.

Distribution and ecology

Ryparosa milleri is known from two widely-separated locations in New Guinea (Fig. 8*c*). Primary rainforest habitats sometimes on swampy ground up to 150 m. A flowering specimen was collected in July and a specimen with immature fruit in April.

Etymology

The specific epithet honours Dr J.R.M. (Roy) Miller O.B.E., pioneering surgeon in Kenya, grandfather and source of inspiration to the first author throughout the course of his studies.

Additional specimens examined

NEW GUINEA: Papua New Guinea: Western District [Kiunga Subdistrict], near Ingembit village, [05°39′S, 141°01′E], *Henty, E.E., Ridsdale & Galore, NGF 31883*, 12.vi.1967 (L, LAE).

Ryparosa maycockii B.L.Webber, *sp. nov.*

A *R. javanica* (Blume) Kurz ex Koord. & Valeton in laminis basin leviter cordatis, paginis abaxialibus racemisque indumento denso praeditis, laminis nervis 7–8 paribus brochidodromis valde curvato-ascendentinus et undulatis, et petalis adaxialibus indumento subdenso praeditis, differt.

Typus: [Borneo, Malaysia, Sarawak], 7th Division, Ulu Sungai Belaga, [02°46′N, 113°49′E], *Othman et al., S 43823*, 3.xi.1981 (*holotype*: K; *isotypes*: KEP [*K56075*], L [*L0351547*], SAN?, A?).

Tree up to 7 m tall. *Leaf* blades elliptic, 230–280 × 80–120 mm, acuminate at the apex, 52–65° (acuminate for up to 20 mm), **cordate to a depth of 2–3 mm at the base**, 70–80°, texture chartaceous, adpressed hairs scattered on the primary vein adaxially, otherwise glabrous, abaxially with **hairs dense on the primary and secondary veins, subdense on the lamina**, food-body scars, primary vein level with the lamina adaxially, secondary veins **distinctly brochidodromous**, 7–8(–9) pairs, raised adaxially and prominent abaxially, diverging at 52–57° from the primary vein, strongly curved-ascending towards the margin, tertiary venation **random reticulate**; petiole **48–55 mm long**. *Staminate inflorescences* not known. *Carpellate inflorescences* to 90 mm long, solitary from foliate or defoliate axils; bracts *c.* 0.4 mm long; pedicels *c.* 1.0 × 0.7 mm; calyx splitting into three or four lobes, lobes *c.* 2.9 mm long, **densely pilose abaxially**; petals 5, *c.* 3.3 mm long, **moderately puberulent adaxially**, abaxially densely tomentose, **scale small relative to the petal**; staminodes pilose adaxially; ovary ellipsoid; stigmas 2, sessile. *Fruit racemes* to 125 mm long; pedicels 2.8–3.0 × 1.7–2.5 mm. *Fruits* globose, stigmas 2, sessile.

Notes

Although a complete description of reproductive material is lacking for this taxon, it agrees with *Ryparosa* owing to the presence of racemose flowers, an irregularly splitting calyx, a lack of stipules and bifurcate hairs on the leaves and stems. The presence of hairs on the adaxial petals of carpellate flowers (staminate flowers are unknown) and the shallowly cordate base of leaf blades appear to be unique in the genus.

Distribution and ecology

Ryparosa maycockii is known from two locations in mixed Dipterocarp rainforest in the Sungai Belaga region of Sarawak, Borneo (Fig. 8*b*). A flowering specimen was collected in October and specimens with immature fruits in October and November.

Etymology

The specific epithet honours Dr Colin Maycock, a plant ecologist and colleague with considerable knowledge of the Bornean rainforests.

Additional specimens examined

BORNEO: Sarawak: 7th Division [actually 4th Division], Belaga, Ulu Sungai Semawat, [02°43′N, 113°38′E], *Othman et al., S 43553*, 17.x.1981 (KEP, L).

Ryparosa kurrangii B.L.Webber, *sp. nov.*

A *R. acuminato* Merr. foliis longis (240–280 mm), tenuibus (58–73 mm), nervis binatis 7–9 paribus curvato-ascendentibus, racemis e tubercularis grandis in trunco principali ortis, et racemis inflorescentiarum juvenium sine indumento denso, differt.

Ryparosa sp. nov. 1 (*sensu* Webber & Curtis *BW-017*) in Webber & Woodrow, *Func. Pl. Biol.* 31:506 (2004).

Typus: Australia, Queensland, Cook District, Daintree NP, Mt Hutchinson [description abbreviated], (16°12′S, 145°25′E), *Webber, B.L. & Curtis, A.S.O., BW 017*, 12.iv.2003 (*holotype*: MELU [*D102277*]; *isotypes*: BO, CANB, K, L, QRS).

Understorey *tree* 15–20(–23) m tall, larger specimens with **fluted trunks and undulate buttresses** up to 2.5 m high, 0.5 m over the ground (Fig. 9*a*), some branching near the ground from **large distinctive tubercles** (Fig. 9*b*). Outer bark rough, grey-brown, inner bark bright pink; wood straw yellow. *Leaf* blades elliptic, **(210–)240–280 (–320) × (55–)60–75(–85) mm**, acuminate at the apex, (35–)39–43(–54)°, with a well defined tip to 17 mm, **attenuate at the base, (41–)47–51(–56)°**, texture chartaceous, surface glabrous adaxially, abaxially with hairs moderately dense on the primary vein, sparse on the secondary veins and abaxial lamina (rarely glabrous on the abaxial lamina), distinct food-body scars, primary vein somewhat sunken or level with the lamina adaxially, secondary veins brochidodromous, **7 or 8 (rarely 9) pairs**, raised adaxially and prominent abaxially, diverging at 47–56(–63)° from the primary vein, curved-ascending close to the leaf margin, tertiary venation reticulated; **petiole (34–)40–50(–60) mm long**. *Staminate inflorescences* to **300–400 mm long**, in fascicles of up to 5 (solitary), **cauliflorous from large tubercles on the lower main trunk** (Fig. 9*d, e*; rarely from smaller branches); unopened flower buds globose; bracts 0.5–0.9 mm long; pedicels 1.3–2.3 × 0.3–0.5 mm; calyx splitting into 3 or 4 (2) lobes, lobes 2.3–4.0 mm long, sparse adpressed puberulent abaxially; petals (4–)5, 3.1–4.2 × 1.0–2.1 mm, glabrous adaxially, abaxially densely tomentose; scale fleshy (when fresh), 0.8–1.4 × 0.5–1.0 mm (dried); filaments (4–)5, united, sparsely villous beneath the anthers or entirely villous; stamens 3.1–3.9 mm long, extrorse anther dehiscence. *Carpellate inflorescences* to **250–350(–570) mm long**, generally shorter than the staminate inflorescences, in fascicles of up to 5 (solitary), **cauliflorous from large tubercles on the lower main trunk** (very rarely from smaller branches); unopened flower buds pyriform; bracts

0.5–0.8 mm long; pedicels (0.8–)2.2–4.7 × 0.4–0.7 mm; calyx splitting into (2–)3(–4) lobes, lobes 3.0–4.0 mm long, sparse adpressed puberulent abaxially; petals (4–)5, 3.3–4.8 × 1.4–2.5 mm, glabrous adaxially, abaxially densely tomentose, scale fleshy (when fresh), 1.0–2.2 × 0.6–1.3 mm (dried); staminodes (4–)5, 0.3–0.7 mm long, **fleshy stocky**, pilose adaxially or entirely glabrous; ovary ellipsoid (obovoid); stigmas 2(3), sessile. F*ruit racemes* to 260 mm long with extensive secondary thickening of racemes and pedicels. *Fruits* ellipsoid-oblate to globose drupes, 30–60 mm diameter when ripe, indehiscent, epicarp *c.* 1 mm thick, mesocarp fleshy, dark green when immature changing to bright yellow-orange when ripe, 1 locule; stigmas 2(–3), lateral in 1-seeded fruits, terminal in 2-seeded fruits, sessile. *Seeds* (1–)2, flattened-globose (2-seeded) or globose (1-seeded), 20–30 × 15–20 mm, containing copious endosperm surrounded by a thin, dark chartaceous layer and a protective woody layer (*c.* 0.6 mm thick with no lines of dehiscence). *Germination* cryptocotylar epigeal with fleshy haustorial cotyledons and a significant endosperm reserve.

Notes

Further collections (lodged at MELU) from several permanently tagged trees (including the tree from which the type specimen was collected) have both staminate and carpellate racemes and also fruits, so documenting the monoecious nature of *R. kurrangii*.

Distribution and ecology

Ryparosa kurrangii is restricted to a small strip of coastal rainforest between the Alexandra range and Cape Tribulation in the Daintree World Heritage area of northern Queensland, Australia (Fig. 8*d*). Typically a sub-canopy understorey tree, *R. kurrangii* is found at low altitudes (only once observed at an altitude above 240 m) in lowland tropical rainforests (Type 1a, 2a; *sensu* Tracey 1982), where it consistently grows near creeks and ephemeral streams. Young leaves flush in distinctive bursts during the late dry and early wet seasons (Oct–Dec). Peak flowering is during Jun–Sep (staminate and carpellate flowering times are generally separated by 3–4 weeks on individual plants), while fruiting is concentrated in Oct–Dec. Flowers are strongly scented (sickly sweet with overtones of wet-dog and body odour) with heavy nocturnal nectar production. Flower pollination is most likely carried out by small, unspecialised invertebrates (Webber 2005). Extant seed dispersal vectors are most likely restricted to scatter-hoarding animals (short distances) and the cassowary (between populations and over long distances; Webber and Woodrow 2004). The species is highly cyanogenic, with cyanogenic glycosides detected in all plant tissues (Webber 2005). Petiolar and leaf lamina tissue sections were found to contain crystal idioblasts with druse crystals (Webber 2005).

Conservation status

A significant proportion of the remaining *R. kurrangii* populations are on private land, outside the boundaries of protected reserves. Continued settlement and development in the Daintree region is threatening current populations and introduced animals are having a detrimental effect on potential seed vectors, which, in turn, has a negative effect on population recruitment (Webber 2005). Based on detailed knowledge of the distribution and age structure of current populations, the number of individuals in reserved areas and on freehold land, and known processes threatening the most flourishing of the remaining populations (Webber and Woodrow 2004; Webber 2005), an upgraded conservation code of vulnerable 2VCi (Briggs and Leigh 1996) is strongly recommended for this species.

Indigenous use

Kuku Yalangi elders said that the fruit of *R. kurrangii* were eaten during hunting and fishing trips in the lowlands region (B Walker, R Harrigan, pers. comm.). Fruits were gathered and taken back to more permanent camps in the nearby uplands region (e.g. Thornton Peak, Roaring Meg Creek), but the seeds did not grow at these camps when the Yalangi tried to establish trees for use as an uplands food source (R Harrigan pers. comm.). Flowers are reported as being used as a water infusion for 'clearing the head' (A Small pers. comm.). Flower racemes were soaked in hot water when heavy with nectar, and the resulting steam from the solution was inhaled deeply.

Etymology

From the local Kuku Yalangi dialect, *kurrangi* (cassowary), referring to the traditional name for a prominent coastal feature of the restricted taxon distribution (Cape Tribulation), as well as the apparent mutualism between *R. kurrangii* and cassowaries (Webber and Woodrow 2004).

Selected specimens (45 specimens examined)

AUSTRALIA: Queensland, Cook District: [Daintree lowlands region], Arsenic Creek, [16°10′S, 145°25′E], *Stocker, G.C.*, *1617*, 2.xi.1977 (QRS); [Daintree lowlands region], Cooper Creek, [16°10′S, 145°24′E], *Nicholson, D.I.*, *AFO 5078*, 1.x.1980 (QRS); Daintree lowlands region, Mt Sorrow Valley, [description abbreviated, 16°07′S,145°27′E], *Webber, B.L.*, *BW 008*, 14.vii.2002 (MELU); Daintree NP, Mt Hutchinson [description abbreviated, 16°12′S, 145°25′E], *Webber, B.L. & Curtis, A.S.O.*, *BW 018*, 12.iv.2003 (MELU); [Daintree NP], Oliver Creek, *c.* 1 km upstream from Cape Tribulation road, [16°08′S, 145°26′E], *Hind, P. & Healey, D.*, *KHILL 2080*, 8.viii.1986 (NSW); [Daintree Region], Noah Creek, [16°10′S, 145°25′E], *Hyland, B.*, *1080 RFK*, 11.x.1967 (BRI).

Other specimens examined (selection only)

Ryparosa sp. nov. aff. acuminata

NEW GUINEA: Papua New Guinea: Morobe District, Sattelberg, Yuinzaing [Yunzain, 06°25′S, 147°37′E], *Clemens, M.S.*, *6461*, 21.vi.1937 (K, L, NY).

Ryparosa sp. nov. aff. calotricha

BORNEO: Sarawak: Matang (proposed NP), SW slope of Gunong Bawang, [01°35′N, 110°10′E], *Burley, J.S. & Lee, Bernard*, *317*, 1.x.1987 (L, SING). West Kalimantan: G. Bentuang area, 150 km NE of Pontiank, 5–10 km N of Masa village, [00°52′N, 110°26′E], *Burley, J.S. & Tukirin et al.*, *2303*, 6.vi.1989 (K).

Ryparosa acuminata *Merr.*

BORNEO: East Kalimantan: North Borneo Conomisi, Bukit Sungai Toelit [Tulit, near Tenampak, 04°15′N, 116°49′E], *Amdjah (with van Genderen Stort, Capt. P)*, *705*, ix.1912 (BO, K). Sabah: North-East Borneo, Sandakan Bay, southern part of Nunukun [Nunuyan] Island, [05°55′N, 118°07′E], *Kostermans, A.*, *9205*, 1.i.1954 (BO, BRI, K, SING); Papar District, Simpangan., [06°27′N, 116°43′E], *Burgess, P.F.*, *SAN 28428*, 28.v.1962 (K).

Ryparosa baccaureoides *Sleumer*

BORNEO: Sabah: Mt Kinabalu FR, [Naradaw area], intersection of Ulu Liwagu and Ulu Mesilau, [05°58′N,116°37′E], *Chew, W.L., Corner, E.J.H. & Stainton, A.*, *RSNB 2926*, 10.ix.1961 (CANB). Sarawak: Kuching District, Matang, Ulu China, [01°36′N, 110°12′E], *Ashton, P.S.*, *S 16699*, 22.xi.1962 (MEL); 4th Division, Bario, route to Batu Lawi, [03°48′N, 115°23′E], *Awa, Dayang et al.*, *S 50477*, 1.viii.1985 (KEP, L).

Ryparosa calotricha *Mildbr.*

NEW GUINEA: Papua New Guinea: Morobe District, Oomsis (near Lae), [06°41′S, 146°48′E], *White, K.J.*, *NGF 10484*, 5.iii.1959 (BRI, CANB, L, LAE, SING); Milne Bay District, Rabaraba Subdistrict, junction of Ugat and Mayu rivers, near Mayu 1, [09°39′S, 149°10′E], *Streimann, H. & Katik, P.*, *NGF 28904*, 15.vii.1972 (BO, L, LAE); [Northern District, Owen Stanley Range], Isuarava, [09°00′S, 147°44′E], *Carr, C.E.*, *CEC 15169*, 4.ii.1936 (K, L, NY, SING). Western New Guinea: [West Irian Jaya Province] Sorong Regency, Sausapor, [00°32′S, 132°06′E], *Versteegh, Chr.*, *BW 4617*, 19.x.1956 (CANB).

Ryparosa glauca *Ridl.*

BORNEO: Brunei: Temburong, Bukit Biang, [04°41′N, 115°06′E], *Forman, L.L.*, *LLF 924*, 17.x.1989 (K). Sarawak: 4th Division, Gunung Mulu NP, Ulu Sungai Berar, [04°02′N, 114°55′E], *Chai, Paul, S 39626*, 11.i.1978 (KEP); Tau Range, Sungei Mayeng, [02°42′N, 113°05′E], *Purseglove, J.W., P 5331*, 4.vi.1956 (NY, SING). LESSER SUNDA ISLANDS: Flores: Manggarai Regency, [Laboehanbadjo District], Naga, [08°42′S, 119°56′E], *Schmutz, Fr. E.*, *4135*, 6.v.1978 (L); Manggarai Regency, Palie [cf. Reo District, Palit, *c.* 08°32′S, 120°11′E], *Schmutz, Fr. E.*, *4818*, 3.iii.1981 (L).

Ryparosa kostermansii *Sleumer*

BORNEO: East Kalimantan: Peak of Balikpapan, (Gunung Beratus), Beoul, [01°02′N, 116°20′E], *Kostermans, A.*, *7564*, 16.vii.1952 (L). West Kalimantan: [Bukit Raya NP], Bukit Raya, [00°45′S, 112°47′E], *Nooteboom, H.P.*, *4886*, 6.ii.1983 (L). Sabah: Lahad Datu, Kennedy Bay, Takun (Section 42), [05°00′N, 118°00′E], *Chai, Nuin, SAN 26079*, 6.ix.1961 (BO). Sarawak: 1st Division, Lundu District, Gunung Pueh, [01°48′N, 109°41′E], *Mamit, James et al., S 34417*, 14.vi.1974 (L); 5th Division, Limbang, path to Bukit Pagon, [04°18′N, 115°09′E], *Awa, Dayang & Lee, B., S 47569*, 29.vii.1984 (L).

Ryparosa multinervosa *Slooten*

SUMATRA: Sumatra, Riau Province: [Indragiri Hulu Regency], Tigapuluh Mountains, 5 km W of Talanglakat on Rengat–Jambi Rd, Bukit Karampal area, [00°46′S, 102°32′E], *Burley, J.S. & Tukirin et al., 1223*, 6.xi.1988 (L); North of Kampar Regency (not far from North Sumatra), River Mahato Hulu (kiri) area, [01°23′N, 100°34′E], *Laumonier, Y. & Torquebiau, E., TFB 4245*, 13.iv.1983 (L).

Drypetes longifolia *Pax & K.Hoffm.*

ANDAMAN ISLANDS: South Andaman Island: Wrightmyo, [11°47′N, 92°43′E], *Balakrishnan, N.P. & Bhargava, N., 3465*, 14.iii.1976 (L); Dhani Khari, [11°33′N, 92°41′E], *Nair, N.G., 3639*, 27.iii.1976 (L).

References

Agosti D, Moog J, Maschwitz U (1999) Revision of the Oriental plant–ant genus *Cladomyrma*. *American Museum Novitates* **3283**, 1–24.

Astuti IP, Soewilo LP, Said TD, Kosasih RNA (2001) 'An alphabetical list of plants species cultivated in the Bogor Botanic Garden.' (Botanic Gardens of Indonesia, Indonesian Institute of Sciences: Bogor)

Australian Army Royal Australian Survey Corps (1942–1945) New Guinea one inch series. In 1:63,360. (Australian Army Topographic Survey Corps: Canberra)

Belbin L (1995) 'PATN: pattern analysis package.' (Division of Wildlife and Ecology, CSIRO: Canberra)

Bentham G, Hooker JD (1867) 'Genera Plantarum.' (Lovell Reeve & Co.: London)

Bentham G, Hooker JD (1880) 'Genera Plantarum.' (Lovell Reeve & Co.: London)

Blume CL (1828) 'Flora Javae.' (J. Frank: Bruxellis)

Blume CL (1848) 'Rumphia, sive, Commentationes botanicae imprimis de plantis Indiae Orientalis, tum penitus incognitis tum quae in libris Rheedii, Rumphii, Roxburghii, Wallichii aliorum recensentur.' (Prostat Amstelodami Apud C. G. Sulpke: Lugduni Batavorum)

Boerlage JG (1899) 'Catalogus plantarum phanerogamarum quae in horto botanico Bogoriensi coluntur herbaceis exceptis.' (Typis Officinae Publicae: Bataviae)

Briggs JD, Leigh JH (1996) 'Rare and threatened Australian plants.' Revised edition. (CSIRO Publishing: Melbourne)

Brühl P, King G (1896) A century of new and rare Indian plants. *Annals of the Royal Botanic Garden, Calcutta* **5**, 71–170

Chakrabarty T, Gangopadhyay M (1992) The Flacourtiaceae of Andaman–Nicobar islands. *Journal of Economic and Taxonomic Botany* **16**, 715–722.

Chase MW, Zmarzty S, Lledo MD, Wurdack KJ, Swensen SM, Fay MF (2002) When in doubt, put it in *Flacourtiaceae*: a molecular phylogenetic analysis based on plastid *rbc*L DNA sequences. *Kew Bulletin* **57**, 141–181.

Dahlgren RMT, van Wyk AE (1986) Structures and relationships of families endemic to or centered in southern Africa. *Monographs in Systematic Botany from the Missouri Botanical Garden* **25**, 1–94.

Dakkus PMW (1957) 'An alphabetical list of plant species cultivated in the Hortus Botanicus Bogoriensis.' (Pertjetaken Archipel: Bogor)

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance: a theoretical model and computer simulations. *Vegetatio* **69**, 57–68. doi: 10.1007/BF00038687

Gilg E (1918) Die bis jetzl aus Neu-Guinea bekannt gewordenen Flacourtiaceen. *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie* **55**, 273–294.

Google Inc. (2005) Google Earth: http://earth.google.com. (Google Inc.: Mountain View) (verified 7 September 2006)

Gower JC (1971) A general coefficient of similarity and some of its properties. *Biometrics* **27**, 857–871. doi: 10.2307/2528823

Hickey LJ (1979) A revised classification of the architecture of dicotyledonous leaves. In 'Anatomy of the dicotyledons (2nd ed. Vol. I), systematic anatomy of the leaf and stem'. (Eds CR Metcalfe, L Chalk) pp. 25–39. (Clarendon Press: Oxford)

Holmgren PK, Holmgren NH, Barnett LC (1990) 'Index Herbariorum. Part 1. The herbaria of the world.' (New York Botanical Gardens: New York)

Hutchinson J (1967) 'The genera of flowering plants.' (Clarendon Press: Oxford)

Janzen DH (1974) 'Swollen-thorn Acacias of Central America.' (Smithsonian Institution Press: Washington)

Jarvie JK, Stevens PF (1998) New species and notes on Violaceae and Flacourtiaceae from Indo-Malesia. *Harvard Papers in Botany* **3**, 253–262.

King G (1890) Materials for a flora of the Malayan Peninsula. *Journal of the Asiatic Society of Bengal, Calcutta* **59**, 113–206.

Koorders SH, Valeton T (1900*a*) Bijdrage No. 5 tot de Kennis der Boomsoorten op Java. Additamenta ad cognitionem Florae arboreae Javanicae. *Mededeelingen uit 'sLands Plantentuin* **33**, 1–464.

Koorders SH, Valeton T (1900*b*) Bijdrage No. 6 tot de Kennis der Boomsoorten op Java. Additamenta ad cognitionem Florae arboreae Javanicae. *Mededeelingen uit 's Lands Plantentuin* **40**, 1–193.

Koorders-Schumacher A (1913) 'Systematisches Verzeichnis der zum Herbar Koorders gehörenden, in Niederländisch-Ostindien, besonders in den Jahren 1888–1903 gesammelten Phanerogamen und Pteridophyten nach den Original-Einsammlungsnotizen und Bestimmungs-Etiketten, unter der Leitung von Dr. S.H. Koorders.' (Selbstverlag: Buitenzorg)

Kruskal JB (1964*a*) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* **29**, 1–27. doi: 10.1007/BF02289565

Kruskal JB (1964*b*) Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**, 115–129. doi: 10.1007/BF02289694

Kurz S (1873) On the affinity and position of *Ryparia*, Bl. *Journal of Botany* **11**, 233–234.

Kurz S (1876) A sketch of the vegetation of the Nicobar Islands. *Journal of the Asiatic Society of Bengal, Calcutta* **XLV**, 105–164.

Kurz S (1877) 'Forest flora of British Burma.' (Superintendent of Government Printing: Calcutta)

Lemke DE (1988) A synopsis of Flacourtiaceae. *Aliso* **12**, 29–43.

McKey D (2000) *Leonardoxa africana* (Leguminosae: Caesalpinioideae): a complex of mostly allopatric subspecies. *Adansonia* **22**, 71–109.

Mildbraed J (1928) *Gertrudia* K. Schum. = *Ryparosa* Bl. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* **10**, 338–340.

Moog J, Fiala B, Werner M, Weissflog A, Saw LG, Maschwitz U (2003) Ant–plant diversity in Peninsular Malaysia, with special reference to the Pasoh Forest Reserve. In 'Pasoh: ecology of a lowland rainforest in southeast Asia'. (Eds T Okuda, N Manokaran, Y Matsumoto, K Niiyama, SC Thomas, PS Ashton) pp. 459–494. (Springer Press: Tokyo)

Radford AE, Dickison WE, Massey JR, Bell CR (1974) 'Vascular plant systematics.' (Harper & Row: New York)

Rao MKV, Chakrabarty T (1985) *Drypetes longifolia* (Euphorbiaceae) in Andamans. *Journal of Economic and Taxonomic Botany* **6**, 445.

Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants. *American Journal of Botany* **82**, 596–606. doi: 10.2307/2445418

Ridley HN (1922) 'The flora of the Malay Peninsula.' (L. Reeve & Co.: London)

Ridley HN (1936) Notes on Malay Flacourtiaceae. *Journal of Botany* **74**, 221–225.

Rosenberg C (1996–2004) World index global gazeteer: http://www.fallingrain.com/world. (Falling Rain Genomics: Palo Alto) (verified 7 September 2006).

Royal Army of Great Britain Royal Engineers (1969) Joint operations graphic (air) map of Indonesia. In 1 : 250,000. (Survey Production Centre: United Kingdom)

Savolainen V, Fay MF, Albach DC, Backlund A, van der Bank M, Cameron KM, Johnson SA, Lledó MD, Pintaud JC, Powell M, Sheahan MC, Soltis DE, Soltis PS, Weston P, Whitten WM, Wurdack KJ, Chase MW (2000) Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequence. *Kew Bulletin* **55**, 257–309.

Schumann K, Lauterbach K (1901) 'Die Flora der Deutschen Schutzgebiete In der Südsee und Nachträge.' (Gebrüder Borntraeger: Leipzig)

Shepard RN (1962) The analysis of proximities: multidimensional scaling with an unknown distance function. *Psychometrika* **27**, 125–140. doi: 10.1007/BF02289630

Sleumer HO (1954*a*) Flacourtiaceae. In 'Flora Malesiana. Series 1 (Spermatophyta). Vol. 5'. (Ed. CGGJ Van Steenis) pp. 1–106. (Noordhoff-Kolff N V: Djakarta)

Sleumer HO (1954*b*) Florae Malesianae Precursores. VII. New Malaysian Flacourtiaceae. *Blumea* **7**, 484–497.

Sleumer HO (1980) 'Flora neotropica. Monograph number 22. Flacourtiaceae.' (The New York Botanical Garden: New York)

Sleumer HO (1985) The Flacourtiaceae of Thailand. *Blumea* **30**, 217–250.

van Slooten DF (1919) Bijdrage tot de kennis der Combretaceeën en Flacourtiaceeën van Nederlandsch-Indië. PhD thesis, Universiteit Utrecht.

van Slooten DF (1924) Flacourtiaceae. *Nova Guinea* **14**, 190–194.

van Slooten DF (1925) Contributions à l'étude de la Flore des Indes Néerlandaises—the Flacourtiaceae of the Dutch East Indies. *Bulletin du Jardin Botanique Buitenzorg. Series III* **7**, 291–421.

Sneath PAH, Sokal RR (1973) 'Numerical taxonomy. The principles and practice of numerical classification.' (W. H. Freeman and Company: San Francisco)

Sokal RR, Michener CD (1958) A statistical method for evaluating systematic relationships. *University of Kansas Science Bulletin* **38**, 1409–1438.

Sosa V, Chase MW, Barcenas C (2003) *Chiangiodendron* (Achariaceae): an example of the Laurasian flora of tropical forests of Central America. *Taxon* **52**, 519–524.

Spot Domain (2000–2005) Geographic and geospatial information: http://www.earthsearch.net. (Spot Domain LLC: Denver) (verified 7 September 2006)

Stevens PF (1991) Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* **16**, 553–583. doi: 10.2307/2419343

Takhtajan A (1997) 'Diversity and classification of flowering plants.' (Columbia University Press: New York)

Thiele K (1993) The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* **9**, 275–304. doi: 10.1111/j.1096-0031.1993.tb00226.x

Tracey JC (1982) 'The vegetation of the humid tropical region of North Queensland.' (CSIRO: Melbourne)

United States Army (1943–1946) Great East Residency Moluccas (New Guinea), prepared and reproduced from Dutch map printed by Topografische Dienst (Topographic Service). In 1 : 250,000. (Base Map Plant: Washington DC)

Van Steenis CGGJ (1958) Introduction. In 'Flora Malesiana. Series 1 (Spermatophyta). Vol. 1'. (Ed. CGGJ Van Steenis) pp. xi–xliv. (Noordhoff-Kolff N V: Djakarta)

Van Steenis-Kruseman MJ (1958) Malaysian plant collectors and collections. In 'Flora Malesiana. Series 1 (Spermatophyta). Vol. 1'. (Ed. CGGJ Van Steenis) pp. 1–598. (Noordhoff-Kolff N V: Djakarta)

Webber BL (2005) Plant–animal interactions and plant defence in the rainforest tree, *Ryparosa*. PhD thesis, The University of Melbourne.

Webber BL, Woodrow IE (2004) Cassowary frugivory, seed defleshing and fruit fly infestation influence the transition from seed to seedling in the rare Australian rainforest tree, *Ryparosa* sp. nov. 1 (Achariaceae). *Functional Plant Biology* **31**, 505–516. doi: 10.1071/FP03214

Webber BL, Abaloz BJ, Woodrow IE (2006) Myrmecophilic food body production in the understorey tree, *Ryparosa kurrangii* (Achariaceae), a rare Australian rainforest taxon. *New Phytologist*, in press.

Webber BL, Moog J, Curtis ASO, Woodrow IE (2007) The diversity of ant–plant interactions in the rainforest understorey tree, *Ryparosa* (Achariaceae): food bodies, domatia, prostomata and hemipteran trophobionts. *Botanical Journal of the Linnean Society*, in press.

Wendt T (1988) *Chiangiodendron* (Flacourtiaceae: Pangieae), a new genus from southeastern Mexico representing a new tribe for the New World flora. *Systematic Botany* **13**, 435–441. doi: 10.2307/2419305

Zepernick B (1978) Typen und Typoide der Flacourtiaceae im Generalherbar des Botanischen Museums Berlin-Dahlem. *Willdenowia* **8**, 409–424.