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PHYLOGENETIC POSITION AND TAXONOMIC DISPOSITION OF TURRAEA BREVIFLORA (MELIACEAE), A HITHERTO ENIGMATIC SPECIES

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SUMMARY

For decades, the rare Malesian shrublet hitherto called *Turraea breviflora*, was the only species of the pantropical family Meliaceae which could not confidently be placed in a genus. Previous morphological re-investigation led to the exclusion of the species from *Turraea* and suggested possibly close links with *Munronia*. In this study, parsimony, maximum likelihood and Bayesian analyses of DNA sequence data from plastid *rbcL* and nuclear ITS rDNA were used to infer the phylogenetic position of *T. breviflora* and its affinities to other representatives of the family. Phylogenetic analyses support Mabberley's (1995a) proposal that the concept of the genus *Munronia* be expanded to accommodate it. The new combination *Munronia breviflora* (Ridl.) Mabb. & Muellner is therefore made.

Key words: Meliaceae, *Munronia*, Sapindales, *Turraea breviflora*, internal transcribed spacer (ITS), *rbcL*, taxonomy.

INTRODUCTION

Turraea breviflora Ridl. (Meliaceae; Fig. 1) is a rather inconspicuous suckering shrublet now restricted to Peninsular Malaysia. It seems that it was first collected by H.N. Ridley at Serangoon, Singapore in December 1897, but the plant has not been recorded from that island since; subsequently it was collected in Selangor and Johor in what is now Peninsular Malaysia.

When Ridley described the plant as a new species in 1922, he provisionally referred it to *Turraea* L., a genus otherwise unknown from the peninsula, or, indeed from the wetter parts of Malesia in general (Mabberley 1995a, b). Since that time it has been collected on only a handful of other occasions and is still known from only a few localities in rather open hill Dipterocarp forest, often associated with bertam, *Eugeissona tristis*, and from limestone rocks. Paradoxically, it is known from some of the most well-worked sites such as Bukit Lagong and Ulu Gombak in Selangor, yet has never been found in fruit, and the number of flowering collections even from those sites is small. No doubt it is frequently overlooked, as it grows amongst tree seedlings and saplings which it greatly resembles. It is like no other Meliaceae and, in the field, sterile material may be readily confused with species of Icacinaceae or other families.

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Fig. 1. *Turraea breviflora* Ridl. a. Habit; b. half flower, with corolla removed. Drawing by Rosemary Wise, reproduced with permission from Flora Malesiana Series I, Vol. 12 / part 1 (1995) 28, f. 2.

Pennington & Styles (1975) noted that the relationships of the species were uncertain, and suggested it had "almost equal affinities with both *Turraea* and *Munronia*". In the early 1980s, when preparing an account for Flora Malesiana Mabberley (1995a: 29), who had collected the plant in the field in 1974, examined herbarium material closely and made a critical morphological analysis, leading him to exclude *Turraea breviflora* from genus *Turraea* because of its habit, indumentum, corolla aestivation, disk and the usual number of ovules in each locule. He pointed out that it resembled the genus *Munronia* Wight, as then understood, in its indumentum, but differed from that in its habit, valvate corolla, the usual number of ovules in each locule and possible dioecy. He thus concluded that it either represented an undescribed genus as Ridley had suspected, or that the concept of *Munronia* had to be enlarged. Today, it is the only species of the pantropical family Meliaceae which cannot confidently be placed in a genus. The writing by the second author of an account of the family Meliaceae for Flora of Peninsular Malaysia has prompted a re-examination of the plant, using molecular methods to augment the earlier morphological analysis, in an attempt to resolve its taxonomic placement.

In this study, therefore, we performed maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses of DNA sequence data from plastid *rbcL* and the internal transcribed spacers (ITS) of nuclear ribosomal DNA (nrDNA), defined as the unit containing the ITS1 spacer, 5.8S rRNA gene, and ITS2 spacer, to infer the phylogenetic position of *Turraea breviflora* and its affinities to other representatives of the family. Based on 46 species of Meliaceae, including a representative sampling for the two subfamilies, all tribes and almost all genera (44 out of c. 50), we focused on the following questions:

- What is the topological position of *T. breviflora* in the family phylogenetic trees derived from MP, ML and Bayesian analyses?
- What are the closest relatives of *T. breviflora*?
- Do the results support either of Mabberley's (1995a) taxonomic proposals?

MATERIALS AND METHODS

Plant material

Plant material was collected during field excursions, taken from herbarium specimens, or obtained from the DNA bank at Kew (http:www.dnabank.kew.org). *RbcL* sequences of 44 taxa of Meliaceae (ingroup) and 6 other taxa (outgroup) were available from the first author's previous work on Meliaceae (Muellner et al. 2003, 2006). Our *rbcL* matrix includes representatives of all tribes (Pennington & Styles 1975) of the only two currently recognised subfamilies (Muellner et al. 2003): Melioideae, viz. Turraeeae, Melieae, Vavaeeae, Trichilieae, Aglaieae, Guareeae, and Sandoriceae, and Cedreloideae (Swietenioideae), viz. Cedreleae, Swietenieae, Xylocarpeae, plus representatives of the Sapindalean families Sapindaceae, Rutaceae, and Simaroubaceae. ITS sequences of 32 taxa of Melioideae (ingroup) and four Cedreloideae (outgroup) were available from the first author's previous work on Meliaceae (Muellner et al. 2008a, b). Voucher information and GenBank accession numbers are listed in Table 1.

Isolation of DNA, amplification and sequencing

Total DNA from leaf fragments was extracted using a NucleoSpin Plant kit (Macherey-Nagel, Dueren, Germany). PCR amplification was carried out following Muellner et al. (2003, 2006, 2008a, b). PCR products were cleaned using a NucleoSpin® Extract II kit (Macherey-Nagel, Dueren, Germany). Sequencing reactions were run on a CEQ^{TM} 8800 Genetic Analysis System (Beckman Coulter, Krefeld, Germany), following the manufacturer's protocol.

Table 1. Voucher information and GenBank accession numbers for samples used in this study (in alphabetical order). Voucher specimens are deposited in the following herbaria: ANBG = Australian National Botanic Gardens; FR = Herbarium Senckenbergianum, Senckenberg Research Institute; GC = University of Ghana; KEP FRI = Forestry Institute Malaysia; K = Royal Botanic Gardens, Kew; L = Nationaal Herbarium Nederland, Leiden University branch; LBC = Limbe Botanic Garden; NCU = University of North Carolina; WU = University of Vienna.

Taxon	Voucher (Herbarium)	GenBank accession number: *rbcL*, ITS.
Aglaia elaeagnoidea (A.Juss.) Benth.	*Samuel 4* (WU)	AY128209
Aglaia odorata Lour.	*Greger 903* (WU)	AY695552
Ailanthus altissima (Mill.) Swingle	*Chase 126* (NCU)	AY128247
Allophyllus cobbe (L.) Raeusch.	*Chase 1306* (K)	AY128248
Anthocarapa nitidula (Benth.) T.D.Penn. ex Mabb.	*Chase 3313* (K)	DQ238056, DQ861616
Aphanamixis polystachya (Wall.) R.Parker	*Chase 2109* (K)	AY128213
	Samuel 14 (WU)	AY695584
Astrotrichilia sp.	*Richard 25* (K)	DQ238060, DQ861621
Azadirachta indica A.Juss.	*Samuel 5* (WU)	AY128215, AY695594
Cabralea canjerana (Vell.) Mart.	*Pennington 17067* (K)	DQ238055, DQ861617
Calodecaryia crassifolia Leroy	*Croat 31521* (K)	AY128216, DQ861631
Capuronianthus mahafalensis Leroy	*Fosberg 52439* (K)	AY128218
Carapa guianensis Aubl.	*Chase 2111* (K)	AY128219
Cedrela odorata L.	*Chase 2112* (K)	AY128220, DQ861606
Chisocheton macrophyllus King	*Chase 1309* (K)	AY128221, DQ861613
Chukrasia tabularis A.Juss.	*Chase 1308* (K)	AY128223
Cipadessa baccifera (Roth) Miq.	*Chase 1310* (K)	AY128224, DQ861627
Dysoxylum gaudichaudianum (A.Juss.) Miq.	*Chase 1312* (K)	AY128227, DQ861619
Ekebergia capensis Sparrm.	*MG 246* (Cynthia Morton)	AY128228, DQ861623
Guarea glabra Vahl	*Chase 336* (NCU)	AY128229, AY695591
Harpullia arborea (Blanco) Radlk.	*Chase 2018* (ANBG)	AY128249
Heckeldora staudtii (Harms) Staner	*Chase 3311* (K)	AY128230, AY695592
Humbertioturraea sp. (*H. labatii* Lescot ined.)	*Bardot-Vaucoulon 160* (K)	DQ238058, DQ861632
Khaya anthotheca C.DC.	*Chase 2859* (K)	AY128231, DQ861608
Lansium domesticum Corrêa	*Chase 2113* (K)	AY128232, AY695586
Lepidotrichilia volkensii (Gürke) J.-F.Leroy ex Styles & F.White	*Hughes 189* (K)	DQ238061, DQ861620
Lovoa sywnnertonii Baker f.	*Chase 2860* (K)	AY128233
Malleastrum mandenense Leroy	*Cheek et al. 3-17-5* (K)	DQ238062, DQ861626
Melia azedarach L.	*Chase 2867* (K)	AY128234, AY695595
Munronia humilis (Blanco) Harms	*Maxwell 75-239* (L)	EU621669, FJ194495/FJ194496
M. pinnata (Wall.) Theob.	*Samuel 6* (WU)	AY128236, DQ861604
Naregamia alata Wight & Arn.	*Kanodia 89603* (K)	DQ238059, DQ861629
Nymania capensis (Thunb.) Lindb.	*Chase 270* (NCU)	AY128238, DQ861633
Owenia vernicosa F.Muell.	*Evans M3071*	DQ238063, DQ861622
Pseudobersama mossambicensis (Sim) Verdc.	*Bidgood, Abdallah & Vollesen 1426* (K)	DQ238064
Pseudocedrela kotschyi Harms	*Asase 008* (GC)	DQ238069/70
Pseudoclausena chrysogyne (Miq.) T.P.Clark	*Muellner 2052* (FR)	DQ238065, DQ861602
Quassia amara L.	*Fernando 1381* (LBC)	AY128250
Quivisianthe papinae Baill.	*Phillipson 1650* (K)	AY128239, DQ861605
Reinwardtiodendron kinabaluense (Kosterm.) Mabb.	*ALFB 112/87* (K)	DQ238054, AY695589
Ruagea pubescens H.Karst.	*Muellner 13* (WU)	DQ238057
	Pennington & Frere 13761 (K)	AY695593
Ruta graveolens L.	*Chase 510* (K)	AY128251
Sandoricum koetjape (Burm.f.) Merr.	*Muellner 2050* (FR)	DQ861600, DQ238068

Schmardaea microphylla (Hook.) H.Karst. ex C.Muell.	*Chase 746* (K)	AY128240
Simarouba glauca DC.	*Chase 124* (NCU)	AY128252
Swietenia macrophylla King	*Chase 250* (NCU)	AY128241, DQ861609
Synoum glandulosum (Sm.) A.Juss.	*Chase 3314* (K)	AY128242
S. glandulosum (Sm.) A.Juss.	*Schodde 5101* (K)	DQ861618
Toona sp.	*Terrazas s.n.* (K)	AY128243, DQ861607
Trichilia emetica Vahl	*Chase 552* (K)	AY128244
	Sieglstetter 15 (FR)	EF136577
Turraea breviflora Ridl.	*Kamarudin KEP FRI 51354* (KEP FRI)	EU621670, FJ194497
Turraea heterophylla Sm.	*Küppers 2212* (FR)	EF136578
Turraea sericea Sm.	*Civeyrel 1336* (K)	AY128245, DQ861630
Vavaea amicorum Benth.	*Katik et al. 74722* (K)	DQ238066/67, DQ861610
Walsura tubulata Hiern	*Chase 1314* (K)	AY128246, DQ861625
Xylocarpus moluccensis (Lam.) M.Roem.	*Sandom 40* (K)	DQ238071

Sequence editing and alignment

Editing and assembly of the complementary strands were carried out with SeqMan^{TM} II version 5.07 (Lasergene, DNASTAR, Inc., Madison, WI, USA). Alignment of *rbcL* sequences was performed by eye. Alignment of ITS sequences was performed following Muellner et al. (2008a, b). New sequences have been deposited in GenBank under the accession numbers EU621669–621670, FJ194495/FJ194496 and FJ194497 (http://www.ncbi.nlm.nih.gov/).

Phylogenetic analysis

MP analyses of the *rbcL* dataset were performed using PAUP* 4.0b10 (Swofford 2002). Substitutions at each nucleotide position were treated as independent, unordered, multi-state characters of equal weight (Fitch parsimony; Fitch 1971). Heuristic searches were carried out using 1000 random additions of taxa, tree bisection-reconnection (TBR) branch swapping, and the option MulTrees (keeping multiple, shortest trees), but holding only ten trees per replicate to reduce time spent in swapping on large numbers of trees. After 1000 replicates, we then used the shortest trees found as starting trees for a swapping-to-completion search (but with a tree limit of 10 000). Robustness of clades was estimated by bootstrapping (Felsenstein 1985) with 1000 replicates, using simple sequence addition, TBR branch swapping, and MulTrees, again holding ten trees per replicate. We consider 75–84% bootstrap values moderate support and 85–100% strong support. MP analyses of the ITS dataset and the combined *rbcL*/ITS dataset were conducted as described above, except for setting no constraint on the number of trees held per replicate during heuristic searches.

ML analyses were carried out with RAxML version 2.2.1 (Stamatakis 2006; http://icwww.epfl.ch/~stamatak/index-Dateien/Page443.htm) and PAUP* 4.0b10 (Swofford 2002), and Bayesian analyses were performed with MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003; http://mrbayes.csit.fsu.edu/). The substitution models employed in these analyses were found using Modeltest version 3.06 (Posada & Crandall 1998; http://darwin.uvigo.es/software/modeltest.html), which indicated the general time reversible model as best fitting our data with a proportion of invariable sites and a gamma shape parameter alpha to model rate heterogeneity (GTR + I + G). For the Bayesian analyses, model parameters were estimated directly during two parallel runs, using four simultaneous chains and 2 000 000 cycles, sampling one tree every 100 generations. Trees that preceded stabilization of the likelihood value were excluded, and the remaining ones were used to calculate posterior probabilities via the construction of a majority rule consensus tree in PAUP. For the ML searches with RAxML we employed the GTR + G model, using 25 rate categories (instead of four as used in the Bayesian analyses).

RESULTS

The aligned *rbcL* matrix consisted of 1387 characters. For the *rbcL* matrix, 277 (20 %) positions were variable and 166 (12 %) were potentially parsimony informative. With the limits imposed as described above, the parsimony search produced 10 000 most parsimonious trees of 552 steps with a consistency index (CI) = 0.53 and a retention index (RI) = 0.81. The aligned ITS matrix consisted of 785 characters; 480 (61 %) positions were variable and 366 (47 %) were potentially parsimony informative. The parsimony search produced 10 most parsimonious trees of 2072 steps with CI = 0.41 and RI = 0.46. The combined *rbcL*/ITS matrix consisted of 2172 characters; 671 (31 %) positions were variable and 464 (21 %) were potentially parsimony informative. The parsimony search produced 2 most parsimonious trees of 2453 steps with CI = 0.41 and RI = 0.50.

Figures 2 and 3 show results of the ML and Bayesian analyses. *Turraea breviflora* is phylogenetically closest to the two representatives of the genus *Munronia* (Fig. 2, 3; also true for the single *rbcL* and ITS ML and Bayesian trees, trees not shown). Accessions of *T. breviflora* and two species of *Munronia* appear in a clade (Fig. 2, 3). The monophyly of the group is very weakly supported in the Bayesian analysis of the *rbcL* dataset (59 % posterior probability, PP, tree not shown), and receives strong support in the combined *rbcL*/ITS analysis (100 % PP, Fig. 3). Although *T. breviflora* and the two species of *Munronia* are monophyletic in the combined MP strict consensus tree, the clade does not receive > 50 % bootstrap percentage; the latter is also true for the single *rbcL* and ITS analyses (trees not shown). In all three ML analyses, *T. breviflora* and *Munronia* appear in one clade (Fig. 2, and trees not shown).

DISCUSSION

Mabberley (1995a) argued, on morphological grounds, that, although *Turraea breviflora* belongs in Turraeeae, it should be excluded from *Turraea* and is most closely related to *Munronia*; this study 1) confirms the position of *T. breviflora* in a clade comprising representatives of Turraeeae and Trichilieae; 2) provides evidence that it is phylogenetically closest to *Munronia*; 3) suggests it indeed be referred to *Munronia*.

It should be noted here, however, that in order to reach a robust phylogenetic appreciation of Turraeeae and Trichilieae, sampling of additional taxa on species level and the collection of additional DNA data will be necessary.

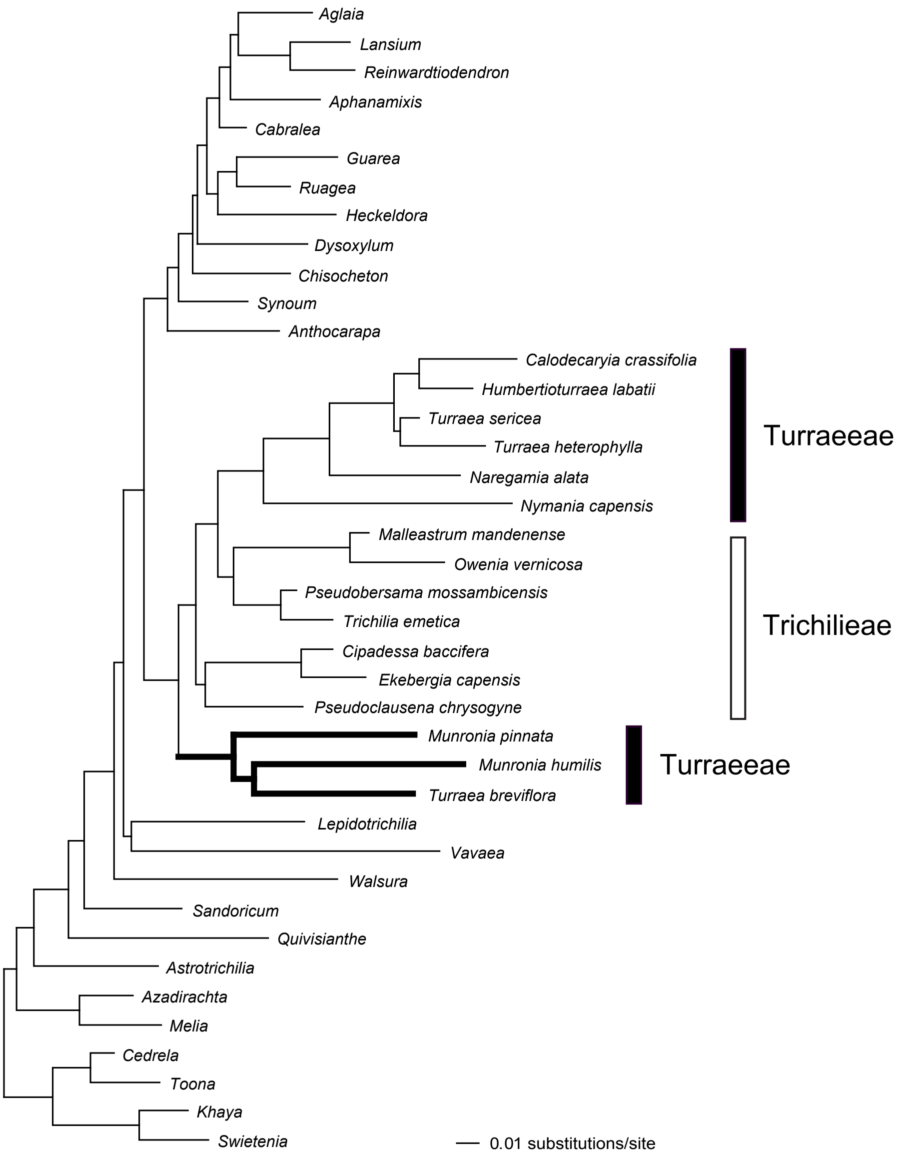

Fig. 2. ML tree obtained from the ML analysis of the combined *rbcL*/ITS dataset of 36 Melioideae ingroup and four Cedreloideae outgroup accessions. Subfamilies after Muellner et al. (2003).

Mabberley's (1995a) proposal that the concept of the genus *Munronia* be expanded, is vindicated by our new findings, so that an amended description of the genus is provided below.

The last enigmatic species of Meliaceae has found a home.

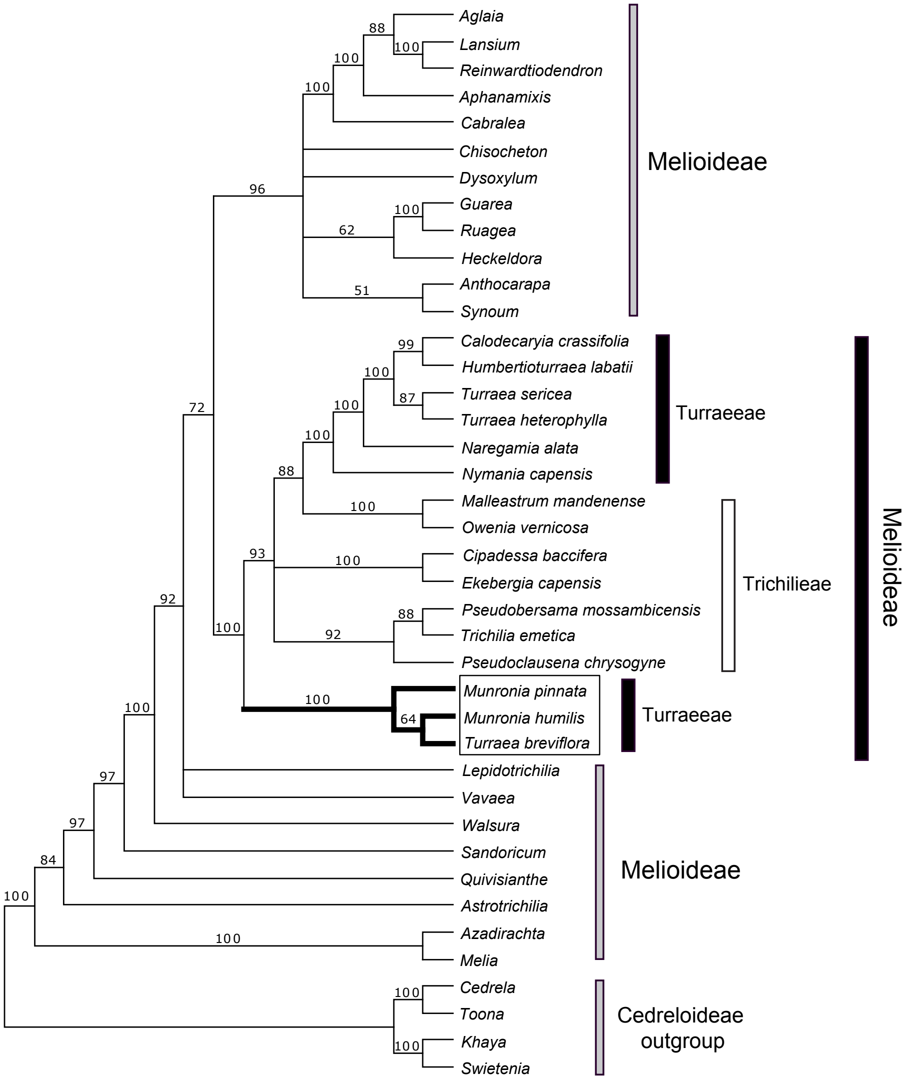

Fig. 3. Bayesian tree (10 000 total trees, burn-in of 1000 trees) of the combined *rbcL*/ITS dataset of 36 Melioideae ingroup and four Cedreloideae outgroup accessions (50 % majority rule consensus tree). Subfamilies after Muellner et al. (2003). Numbers above branches are Bayesian posterior probabilities.

MUNRONIA

Munronia Wight (1838). — Type species: *Munronia pumila* Wight (= *M. pinnata* (Wall.) Theob.).

Unbranched or sparsely branched shrublets, sometimes suckering with apparently short-lived shoots, sometimes possibly dioecious. *Indumentum* a mixture of simple and bifid or stellate hairs. *Leaves* simple to imparipinnate, often crenate to serrate.

Flowers hermaphrodite, solitary or in few-flowered thyrses, pseudopedicellate, usually white. *Calyx* 5-lobed to near base, lobes often somewhat foliaceous. *Petals* 5, valvate to imbricate, adnate to staminal tube basally, rarely becoming free later. *Staminal tube* narrowly cylindrical or weakly obconical, the margin with 10 entire or bilobed appendages or, rarely, with 10 reflexed filiform appendages recurved some distance below margin; anthers 10, pubescent, inserted on tube rim, alternating with appendages, connective often produced apically forming an appendage, which is rarely filiform. *Disk* 0 or tubular, free or united with base of staminal tube. *Ovary* (3) 5-locular, each locule with 1 or 2 superposed ovules; style-head capitate, sometimes with 5 stigmatic lobes. *Fruit* a 5-valved loculicidal capsule, each locule with 1 or 2 seeds. *Seed* plano-convex with a bony tegmen with an outgrowth enveloping a thick sarcotesta; embryo embedded in thin endosperm.

Distribution — About four species restricted to tropical Asia and subtropical China with two species in Peninsular Malaysia:

Leaves pinnate . . . . ***Munronia pinnata***
(see Mabberley 1995a, b for full descriptions and synonymy)
Leaves simple . . . . **Munronia breviflora**

Munronia breviflora (Ridl.) Mabb. & Muellner, *comb. nov.*

Turraea breviflora Ridl. (1922) 383; M.R.Hend. (1939) 40; Mabb. (1995a) 29, f. 2. — Type: *Ridley 9114* (lectotype, selected here, K!), Singapore, Serangoon, Dec. 1897.

Suckering shrublet to 1 m tall, making stands of branching, whippy, blackish stems 6 mm diam. with distichous leaves; taproots long, tenacious. *Indumentum* of stellate hairs with some simple ones. *Leafy twigs* 2–3 mm diam., densely pubescent. *Leaves* 12–20 by 4–5 cm, simple, elliptic to weakly obovate, somewhat bullate in vivo, subglabrous, pale abaxially, apex gradually long-acuminate, base acute to cuneate; venation prominent on both surfaces in sicco, midrib sparsely pubescent proximally, major veins 7–10 on each side, arcuate and looped at margin. *Flowers* in 3–6-flowered fascicles or cymes, in axils of leaves present or lost; branches 2–4 mm long, pubescent; pedicels 4–9 mm long, pubescent. *Calyx* 2–3 mm tall, very shallowly cupulate, pubescent, green, the lobes triangular to 1.5 mm long. *Petals* 6–7 by 2–3 mm, narrowly ovate, valvate, reflexed at anthesis, white. *Staminal tube* a little shorter than petals, white, bearing filiform appendages alternating with anthers; each anther with an apical appendage. *Disk* cupuliform, short, closely encircling ovary, margin somewhat erose. *Ovary* 5-locular, each locule 1-ovular, or, rarely, apparently 3-locular and some locules 2-ovular, pubescent with upward-pointing simple hairs; style c. 5 mm long, pubescent; stylehead 5-lobed, orange. *Fruit* and *seeds* unknown.

Distribution — Collected from only a few localities in Peninsular Malaysia (Selangor, Johor) and Singapore.

Conservation status — As *Munronia breviflora* has not been collected in its southern sites (Johor, Singapore) for over 70 years and has never been found in fruit anywhere, while its extant populations are very restricted in Selangor, it must be considered very rare and threatened, though Bukit Lagong populations are inside a forest reserve.

Selected specimens:

PENINSULAR MALAYSIA. **Selangor**: Kepong, Bukit Lagong Forest Reserve, above reservoir, *Mabberley 1566* (FHO, K, KEP) & 16th mi, Genting Simpah Road, Selangor Ridge, *Kochummen FRI 2971* (K). **Johor**: Sungei, Kau Ara, *Corner SFN 31470* (K).

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