

The *Timonius* conundrum: Taxonomic deliberations around a complex alliance in the Rubiaceae

Khoon Meng Wong & Junhao Chen*

Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, Singapore 259569, Republic of Singapore; Email: junhao_chen@nparks.gov.sg (*corresponding author)

Abstract. *Timonius* DC., the largest genus of tribe Guettardeae (Rubiaceae) with a previously estimated diversity of 200 species, returned into focus after an earlier revision of Malay Peninsula species in 1988 and following the initiation in 2012 of studies into the Bornean diversity encouraged by Hugh Tan, then major supervisor of the second author. Meanwhile, monographic studies of the genus by Steven Darwin have continued from east Malesia, including New Guinea, through to central Malesia, and recognition of this genus in west Malesia, including Borneo, and beyond has also largely followed Darwin's concept. Following the last Bornean enumerations which accounted for only 16 and 25 species by 1942 and 2014, respectively, subsequent studies in Borneo now reveal close to a hundred species, an astounding diversity that mirrors the landscape, geological and ecological complexity found in Borneo, the world's third largest island. We draw attention to these factors that may encourage insularity and speciation, both ecologically as well as physically (such as with archipelagoes), in fostering such diversification. In dealing with this taxonomic diversity, we have encountered misinterpretations of names and confusion with species boundaries, and the (sometimes) perplexing tasks of matching staminate and pistillate material within a basically poorly understood group. The taxonomy of this genus as presently delimited will be eventually illuminated by a much-needed comparative study of morphological attributes across the wider regional range ascribed to *Timonius*, as well as carefully planned phylogenetic studies. We note the significance of regional floras but highlight the usefulness of focussing on individual geographical units such as Borneo, a large and physiographically complex island.

Key words. Molecular phylogenetics, morphological variation, nomenclature, systematics, taxon sampling

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INTRODUCTION

Found on all continents, the Rubiaceae are widespread but predominantly tropical. With 611 genera and some 13,200 species globally (Davis et al., 2009), they are the fourth largest flowering-plant family after the Asteraceae (Compositae), Orchidaceae and Fabaceae (Leguminosae) (Willis, 2017). A comprehensive, global analysis of the Rubiaceae (Davis et al., 2009) revealed that more than 200 genera in the family are monotypic and over 70% have fewer than 10 species; however, some have many species, e.g., *Psychotria* L. (the largest genus with c. 1,834 species; also the third largest angiosperm genus), *Ixora* L. (c. 530 species), *Pavetta* L. (c. 357 species), *Ophiorrhiza* L. (c. 317 species), and *Timonius* DC. Additionally, they have suggested that many Rubiaceae taxa are vulnerable to extinction because of their highly restricted distributions. In their estimation, Southeast Asia—a region with significant landmass and much edaphic and topographic variation and archipelagos with high degrees of insularity, such as New Guinea, the Philippines and Borneo—appears to have the highest number of endemic Rubiaceae species.

Timonius is placed in the tribe Guettardeae, characterised by axillary and opposite inflorescences, 4–many ovary locules, solitary and pendulous ovules that arise from the locule apex, and exalbuminous seeds. It differs from the key genus *Guettarda* in typically having unisexual flowers on different plants, often 4(–5) (sometimes more) corolla lobes, and pyrenes with separate walls but sometimes immersed in a hard matrix. On the other hand, *Guettarda* has hermaphrodite flowers or is polygamo-dioecious, typically with more than 4 corolla lobes, and pyrene walls fused into a hard stone. The genus *Guettarda* has been revealed to be polyphyletic whereas *Timonius* is shown to be monophyletic (albeit with limited taxon sampling) in phylogenetic studies. The taxonomy of the broader *Timonius* remains complex; in recent years Darwin (1993, 1994, 1997, 2010a, 2010b) has addressed this broad alliance, while KMW worked on the Malay Peninsula representatives (Wong, 1988a; Wong et al., 2019) and some earlier indications on the Bornean species were published (Chen et al., 2014, 2015).

Our current interest is in the diversity of *Timonius* in Borneo. The third largest island worldwide and situated on the northeastern fringe of the Sunda continental shelf, Borneo is renowned for its spectacularly rich plant life. For instance, the

Borneo lowlands ecoregion is the only one in the world to surpass 10,000 plant species (Kier et al., 2005). Barthlott et al. (2007) consider North Borneo as one of the world's top five biodiversity centres. Recent reviews of the region's biogeography include those by Lohman et al. (2011), Wong (2011) and de Bruyn et al. (2014). The state of biodiversity knowledge of Borneo, however, is still far from satisfactory. Whereas Masamune (1942), largely based on Merrill (1921), recorded just 16 species of *Timonius* for Borneo, Chen et al. (2014) added a further nine species from the Kinabalu Park area alone. Our studies now reveal close to a hundred Bornean species.

The main objectives of this paper are to: highlight the intricate challenges for a morphology-based taxonomy of diverse genera, using *Timonius* as an example; discuss the immense utility of carefully planned, densely sampled phylogenetic studies in elucidating the delimitation of such complex taxa; and propose the usefulness of taxonomic accounts that focus on individual geographical units such as Borneo.

A CHEQUERED TAXONOMIC HISTORY

Timonius DC. (de Candolle, 1830) is a name conserved against four earlier heterotypic synonyms: *Porocarpus* Gaertn. (Gaertner, 1791), *Polyphragmon* Desf. (Desfontaines, 1820), *Helospora* Jack (Jack, 1823) and *Burneya* Cham. & Schltdl. (Chamisso & Schlechtendal, 1829). This is based on a principle in the International Code of Nomenclature for Algae, Fungi, and Plants (ICN; Turland et al., 2018) which allows the name to be used in spite of it having been pre-empted by the others, under certain circumstances. When Janchen (1908) proposed the conservation of *Timonius*, the use of the name had been more prevalent than the others, with about 55 published names, so that conservation obviated the need for a large number of new nomenclatural combinations.

The generic names *Eupyrena* Wight & Arn. (Wight & Arnott, 1834) and *Abbottia* F.Muell. (Mueller, 1875) also apply to *Timonius* but they postdate the generic description of *Timonius* (de Candolle, 1830). Merrill (1937) considered *Nelitris* Gaertn. (Gaertner, 1788) a synonym of *Timonius*, but its type is the superfluous *Nelitris jambosella* Gaertn. which is typified by the type of the cited earlier name *Decaspermum fruticosum* J.R.Forst. & G.Forst. The generic name *Nelitris* is therefore illegitimate under Art. 52 of the ICN.

MORPHOLOGICAL VARIATION AND INCONGRUENCES

Some authors have divided *Timonius* into smaller (formal or informal) infrageneric groups, but none of these have been considered throughout its entire geographic range, owing to the size of the genus.

Valeton's scheme. The earliest infrageneric classification of *Timonius* was by Valeton (1909), recognising three sections based on stipule aestivation, pyrene orientation and pyrene number. In this scheme, *Timonius* sect. *Helospora* (Jack) Valeton usually has obvolute stipules and fruits containing 13–96 pyrenes attached at different levels to an apical placenta; *Timonius* sect. *Polyphragmon* (Desf.) Valeton has valvate (sometimes calyptrate) stipules and fruits containing numerous pyrenes (up to 200 per fruit) attached horizontally to an elongate placenta; and *Timonius* sect. *Pseudobobea* Valeton is characterised by obvolute stipules and fruits containing 8–12 pyrenes attached at the same level to an apical placenta. Valeton's *Timonius* sect. *Helospora* included seven species found in Borneo; *Timonius* sect. *Polyphragmon* included four Bornean species; and *Timonius* sect. *Pseudobobea* comprised only two species, neither of which is found in Borneo.

Darwin's scheme. Darwin (2010a) observed that it is unlikely that a comprehensive taxon sampling to better understand infrageneric relationships can be achieved in the near future, and suggests that the delineation of infrageneric groups (representing 'presumed synapomorphies') would serve to guide such sampling in future phylogenetic studies. In Darwin's scheme (Table 1), three subgenera are formally recognised and one alliance is unplaced. In *Timonius* subg. *Timonius*, there are currently eight species with valvate-calyptrate stipules, incompletely dichotomo-reticulate to dendro-reticulate leaf venation and numerous ovules attached to an elongate, columnar placenta (Darwin, 1993). *Timonius* subg. *Abbottia* (F.Muell.) S.P.Darwin comprises 29 species with hemiepiphytic or strangler habit, reticuli-paxillate leaf venation and truncate calyx (Darwin, 1994). *Timonius* subg. *Pseudobobea* (Valeton) S.P.Darwin is represented by 21 known species with corrivate leaf venation, vertically oriented fruit pyrenes and fruits with strongly reflexed or erect calyx lobes (Darwin, 2010a). *Timonius* subg. *Abbottia* includes two species from Borneo (*Timonius avenis* Valeton with a wider distribution that includes Borneo and an unnamed taxon endemic to Borneo); otherwise, the majority of Bornean taxa have not been assigned to any of Darwin's subgenera. In addition, Darwin (1997) coined the unranked '*Timonius flavescens* alliance' which includes 10 species from 'Papuasia' (defined by Darwin as the region extending from Sulawesi to the Solomon Islands although Sulawesi is not usually included in Papuasia by other botanists). This comprises *Timonius flavescens* (Jack) Baker and its close relatives. Members

of this alliance were described as possessing valvate or subvalvate stipules, reticulate leaf venation and pistillate inflorescences that are reduced to a solitary flower (or rarely three flowers). An additional 28 species from Papuaia were not assigned to any of his groups (Darwin, 2010b).

Darwin's *Timonius* subg. *Pseudobobea*, although based on Valetton's *Timonius* sect. *Pseudobobea*, has a considerably different circumscription. Valetton (1909) assigned only two species (*Timonius branderhorstii* Valetton and *Timonius koordersii* Valetton) to his section whereas Darwin (2010a) included 21 species in his subgenus and excluded *Timonius koordersii*; and Darwin's *Timonius* subg. *Pseudobobea* includes one species formerly placed in *Timonius* sect. *Polyphragmon* and two species formerly placed in *Timonius* sect. *Helospora* by Valetton (1909). This discrepancy is due to two additional characters used by Darwin (2010a) in delineating his subgenus: corrivate tertiary leaf venation and strongly reflexed to erect fruit calyx lobes.

The question remains whether these constitute 'acceptable' morphological variation within a widespread genus, or if they reflect incongruences that betray an underlying heterogeneity, grouping together an array of otherwise distinct clades artificially brought together. For example, stipule form in the Rubiaceae is generally consistent within genera, including not a few 'phylogenetically acceptable' clades (Robbrecht, 1988; Wong, 1988b; Wong et al., 2019). Habit, stipule aestivation, leaf venation, pistillate inflorescence morphology, and arrangement of pyrenes in the fruit appear to have much taxonomic utility in distinguishing between Darwin's various groupings in *Timonius* (Table 1).

The valvate to subvalvate stipules, two per node, found in the *Timonius flavescens* alliance (Darwin, 1997) are in stark contrast to the calyprate (hood-like) stipules of *Timonius* subg. *Timonius* (Darwin, 1993). In contrast, stipules tend to be imbricate in *Timonius* subg. *Abbottia* and *Timonius* subg. *Pseudobobea* (Darwin, 1994, 2010a), or else 'obvolute' (when each member of a pair overlaps only one margin of the other). Species of *Timonius* subg. *Abbottia* have a hemiepiphytic habit and reticulipaxillate leaf venation with groups of extremely narrow, parallel areoles granting a fingerprint-like impression on lower leaf surfaces (Darwin, 1994).

Likewise, inflorescence and floral characters also include much variation. Inflorescence bracts are typically much reduced or absent in *Timonius* subg. *Timonius* and *Timonius* subg. *Abbottia* but often involucre and broader in *Timonius* subg. *Pseudobobea*, and easily noticed or even enlarged in species of the *Timonius flavescens* alliance. Corolla lobe number also seems highly variable in the group as presently understood. It is typically just 4 in both males and females in the *T. flavescens* alliance; in *Timonius* subg. *Timonius* it may be (4–)5(–6) in males or 8–10(–12) in females; and *Timonius* subg. *Abbottia* 4(–6) in males and (5–)6–8(–12) in females; however, corollas of *Timonius* subg. *Pseudobobea* are too poorly or not known.

The fruits of *Timonius grandifolius* Valetton (member of *Timonius* subg. *Pseudobobea*) are fleshy but dehiscent at maturity to expose pyrenes embedded in a mucilaginous white pulp (Briggs & Utteridge, 2014); the combination of fleshy and dehiscent fruits has not been documented elsewhere for the genus or the tribe Guettardeae. In the subgenera generally, the pyrenes are pendulous from the ovary apex, apparently from a much-condensed apical placenta. However, pyrene arrangement in *Timonius* subg. *Timonius* is basically along an elongated placenta that may later hollow out in the fruit (Darwin, 1993) but this also occurs in the odd *Timonius finlaysonianus* (Wall. & G. Don) Hook. f. (Wong, 1988a, as *Timonius compressicaulis*) which has not been assigned to any subgenus. Nevertheless, the latter has very different (not calyprate) stipules and a distribution quite disjunct from that of the typical subgenus.

In spite of these, Darwin was not convinced that these subgeneric groups merit recognition as separate genera. Darwin (1994) observes that none of the features that define each subgenus were unique to that subgenus, e.g., the epiphytic habit also occurs in *Timonius epiphyticus* Elmer (currently unassigned to a subgenus) and imbricate stipules occur in both *Timonius* subg. *Abbottia* and *Timonius* subg. *Pseudobobea*.

In addition, three morphological groups were also recognised among Malay Peninsula species by Wong (1988a). Group 1 was characterised by its apparently unique leaf venation with sub-parallel tertiary veins running virtually perpendicular to the midrib, four valvate corolla lobes, and fruits with many separate pyrenes that are not immersed in a hard matrix. Group 2, in the Peninsula solely comprising the Malayan *Timonius wrayi*, also has four valvate corolla lobes but its fruits have many separate pyrenes that are immersed in a hard matrix and its tertiary leaf venation is reticulate. The Bornean *Timonius esherianus* W.W.Sm., *Timonius involucreatus* Valetton and *Timonius palawanensis* Elmer (as *Timonius villamilii* Merr., its synonym) was assigned to this group. Group 3, represented by the Sundaic *Timonius finlaysonianus* (as *Timonius compressicaulis*, its synonym), is unique in having imbricate corolla lobes, with five lobes in staminate flowers and 6–8 lobes in pistillate flowers. In our current understanding, Group 1 of Wong (1988a) appears to correspond closely to the *Timonius flavescens* alliance or Valetton's *Timonius* sect. *Helospora*.

An added, but not minor, intricacy for a morphology-based taxonomy of this rather diverse group is that the species we are dealing with are dioecious, so that collections inevitably capture staminate ('male') or pistillate ('female') material from individuals. The (sometimes) perplexing tasks of matching staminate and pistillate material within a basically poorly understood group can require much effort. This is exacerbated by past misapplications of names and confusion with species boundaries.

In our assessment, it is increasingly clear that *Timonius* as presently accepted is morphologically—and likely to be phylogenetically—disparate. Too many species from Malesia to the Pacific region have not been assessed through Darwin's classification. A molecular phylogenetic study is needed to examine the relationships of the species and test the congruence of morphological characters.

LACK OF MOLECULAR PHYLOGENETIC SAMPLING

A fuller understanding of the phylogenetic relationships within *Timonius* and the Guettardeae is not yet obtainable because of extremely limited taxon sampling for *Timonius* (typically one or two species) in the phylogenetic studies thus far available. A sister group relationship between *Timonius* (represented only by *Timonius nitidus* (Bartl. ex DC.) Fern.-Vill. from Guam) and the neotropical genus *Neolaugeria* Nicolson based on nuclear internal transcribed spacer (ITS) sequence data was suggested by Moynihan & Watson (2001) with weak statistical support. From *rps16*, *trnL-F* and ITS sequence data, Rova et al. (2009) suggested that *Timonius* is closely related to the tropical Australian genus *Hodgkinsonia* F.Muell., but again only *Timonius nitidus* was used in their study. Bremer & Eriksson (2009), using five chloroplast regions, retrieved *Timonius* (represented by *Timonius* sp. and the type *Timonius timon*) and the neotropical *Guettarda crispiflora* Vahl (\equiv *Tournefortiopsis crispiflora* (Vahl) Borhidi) in a well-supported clade. The studies of Manns & Bremer (2010), based on five chloroplast markers and ITS sequence data, implied a sister group relationship between *Timonius* (represented by *Timonius timon* and *Timonius celebicus* Koord.) and a clade comprising two *Antirhea* Comm. ex Juss. species (represented by the type *Antirhea borbonica* J.F.Gmel. and *Antirhea madagascariensis* Chaw).

The study by Achille et al. (2006), based on ITS sequence data, had a slightly increased taxon sampling. Five *Timonius* species were sampled, including the type *Timonius timon*. Their results unequivocally indicated the polyphyly of *Guettarda* (a key objective of their investigation) and paraphyly of *Antirhea*, but *Timonius* and *Bobea* were strongly supported as monophyletic in the Bayesian analysis. Their *Timonius–Guettarda–Antirhea* clade was named the Paleotropical Dioecious Clade, consistent with the dioecious sexual system and paleotropical distribution exhibited by its members. The monophyly of *Timonius* was not falsified in this analysis that included a mere five species. However, it can be noted that these five taxa (from Malaysia, Papua New Guinea, Guam and French Polynesia) formed a polytomy, suggesting that there was perhaps a closely related phylogenetic (and taxonomic) complex across different geographical regions.

The most comprehensive taxon sampling in this group, to date, is the study by Chavez et al. (2021), which included 14 species of *Timonius*, but their objective was to re-examine the Paleotropical Dioecious Clade of Achille et al. (2006) and especially the earlier implied non-monophyly of *Antirhea* (represented by 23 species in the 2021 study). The *Timonius* sampling had an odd taxon in a different clade but otherwise mostly clustered as a polytomy, with sub-clades representing geographical groups from the Philippines, Sundaland, Sulawesi, Papua and Micronesia. It is notable that none of the taxa have been treated in Darwin's revisions of his subgenera recognised so far (except for the generic type *Timonius timon*), i.e., representative species of Darwin's subgenera have not been sampled.

Thus, it is not yet possible to gain additional insights into the relationships between Darwin's subgenera from existing phylogenetic data. Clearly, a meaningful taxon sampling of *Timonius* has not yet been attainable. This will form an objective of our future interest in the elucidation of *Timonius* taxonomy, hopefully with collaboration from regional specialists.

TAXONOMIC PROGRESS IN A COMPLEX TAXON

It can be contentious whether plant genera represent evolutionarily real units, i.e., taxa that share both evolutionary history and evolutionary fate through ongoing evolutionary processes (Barraclough & Humphreys, 2015). In a survey by Anderson (1940), twice as many taxonomists believed that plant genera are more natural units than species and that genera and species originated by the same evolutionary processes. However, in the more recent findings of Barraclough & Humphreys (2015), slightly more than half of the respondents regarded species as the most evolutionarily real unit among taxonomic ranks, and about half believed that genera are also real. It was generally agreed that species form via reproductive isolation, but there

was less agreement on the processes that generate genera. Many respondents believed that the only reality of genera is shared evolutionary history but there are no cohesive mechanisms that result in shared evolutionary fate.

In modern taxonomic practice, genera are often delimited based on an inference of monophyly typically hypothesised from morphological data but this may or may not have been tested with molecular phylogenetic data. Notwithstanding, molecular phylogenetics is not a ‘silver bullet’ for this complex task owing to the lack of a common prescription in translating a phylogenetic topology into a generic classification (Humphreys & Linder, 2009). Even if morphological synapomorphies can be identified for multiple clades at different levels of the hierarchy, a taxonomist may choose to recognise a broadly defined genus (with multiple subgenera, sections, subsections, series and subseries) or recognise the smallest clade above the level of species as a genus. In such a situation, we believe that a genus should be diagnosable, predictive and of a moderate size so that it also serves as a convenient memory device for taxonomists as well as other end-users of the taxonomy.

In the case of the broader *Timonius*, there are at least some 300 species in the entire alliance, and despite the systematic studies of Darwin (1993, 1994, 1997, 2010a), very many taxa, notably those in the Philippines, southwest Pacific islands and other Pacific areas, have not yet been assessed or placed in the subgenera recognised. A molecular survey with a comprehensive geographic sampling is not yet feasible.

The taxa in Borneo we address in our current work include just two species in Darwin’s *Timonius* subg. *Abbottia*, and all others would belong to his so-called *Timonius flavescens* alliance. There is some support for the latter to be recognised as a formal group as *Timonius flavescens* (quite widespread throughout the Southeast Asian region), *Timonius wallichianus* Valetton (a Malayan species that has limited occurrence in Borneo), *Timonius beamanii* K.M.Wong & Junhao Chen and *Timonius borneensis* Valetton were shown by the molecular phylogenetic analyses of Chavez et al. (2021) to form a clade. Consistent with Darwin’s concept of subgenera, we consider the *Timonius flavescens* alliance to be another equivalent natural, morphologically distinctive group. Recognition of this group is consistent with the classification developed by Darwin, as well as a practical solution to highlighting features distinguishing the groups or subgroups. As this group is most diverse in Southeast Asia (including Sundaland), this serves a practical purpose in the endeavour towards a useful taxonomy. This will be provided in our upcoming account of *Timonius* in Borneo, now in the final stages of preparation.

Taxonomy and phylogenetics should ideally go hand-in-hand but there is also a real need to discover and identify, as feasible, the as-yet undescribed plant diversity, especially in many tropical areas. Southeast Asia, especially Borneo, is such an area where the plant diversity is very little documented. Thus, bearing in mind the endeavour of matching taxonomy to phylogenetic realities, we must still utilise effective taxonomic handles that can accommodate our slowly advancing but certainly increasing knowledge.

COROLLARY INSIGHTS

The flora of Malesia—the region from Sumatra and the Malay Peninsula eastwards to the New Guinea region, and including the Philippines at its northern extent—is intensely rich in plant life (van Steenis, 1950; Corlett & Primack, 2011). It goes without saying that this richness has not been fully documented, in spite of good efforts regionally (Middleton et al., 2019). The Malesian region includes some of the world’s largest tropical islands (New Guinea, Borneo, Sumatra) and most complex archipelagoes (Indonesia, the Philippines). The astounding plant diversity is a correlate of the insularity granted by the archipelagic setting, as well as geological and ecological complexity in the landscape found on the larger landmasses like New Guinea or Borneo, the world’s two largest tropical islands. New Guinea and Borneo also have the highest mountains in insular Southeast Asia. The insularity, both ecological and physical, as well as intermittently in the geological time frame, can be expected to encourage evolutionary diversification (Ashton, 1972; Beaman, 1996; Morley, 2000; Voris, 2000; Wright, 2002).

Darwin (2010a) estimated that *Timonius* has some 200 species and so would be the largest among the 14 genera placed in tribe Guettardeae (Bremer & Eriksson, 2009). Since then, nine species have been added (Chen et al. 2014, 2015) and here we estimate there are at least 70 more species from Borneo alone. Therefore, the total would be close to 300 species, confirming *Timonius* to be among the largest genera in one of the largest angiosperm families.

Whereas an effort like the Flora Malesiana (van Steenis, 1950; Baas et al., 1989) is laudable (Stone, 1960) and many plant groups might be enumerated and thus serve as a tool towards other practical application, there remain a significant number like the Rubiaceae that will still require much exploration and taxonomic research to unravel. For such highly diverse and complex groups, perhaps the approach is to encourage, support and intensify exploration and study within each unit of Malesia (such as Borneo), and worry about any overlapping nomenclature only when this has been fulfilled to a good degree. There

is no reason why accounts for individual geographical units cannot be useful, contrary to the admonishment of van Steenis (1948: 'The undesirability of compiling. . . local floras. . .'). Clearly, a specimen-based 'revision' has its benefits in the face of a species-diverse group with poorly collected, dioecious taxa and, sometimes, a seemingly unending stream of diversity across the region, such as we highlight here for *Timonius*.

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Table 1. Main characteristics of the subgenera and ‘*Timonius flavescens* alliance’ recognised by Darwin (1993, 1994, 1997, 2010a) as well as additional observations by the authors of this paper (indicated as ‘here’). Characters in italics are those unique to the particular group.

Character	subg. <i>Timonius</i> (Darwin, 1993)	subg. <i>Abbottia</i> (Darwin, 1994)	subg. <i>Pseudobobea</i> (Darwin, 2010a)	‘ <i>Timonius flavescens</i> alliance’ (Darwin, 1997)
Habit	shrubs or trees	<i>hemi-epiphytes</i>	trees or (in one species) initially epiphytic	trees
Stipules	valvate-united and <i>calyptrate</i>	imbricate-obvolute	slightly to strongly imbricate or subvalvate; in one species (<i>Timonius minahassae</i>) foliaceous & slightly connate at base)	subvalvate/ <i>valvate</i>
Leaf venation	incompletely dichotomo-reticulate to dendro-reticulate	<i>reticuli-paxillate</i> (fingerprint-like) formed by narrow and parallel areoles; no free-ending veinlets)	irregularly scalariform or corrivate	reticulate (Darwin, 1997); incompletely dichotomo-reticulate, irregularly scalariform or corrivate (here)
Domatia on lower leaf surface	in axils of secondary (sometimes as well as tertiary) veins	in axils of tertiary as well as secondary veins	present or absent	usually present in axils of secondary (sometimes as well as tertiary) veins
Inflorescence bracts/ bracteoles	minute to absent	highly reduced or absent	highly reduced in male; often broad and involucrate in females	present and distinct
Calyx limb	distinctly lobed/ dentate	<i>truncate-undulate</i>	distinctly lobed/ dentate	distinctly lobed/ dentate
Corolla lobe number	male: (4–)5(–6) female: 8–10(–12)	male: 4(–6) female:(5–)6–8(–12)	corolla not known for many species: 4–5(–6–7 in some females)	male: 4(–5) female: 4(–8)
Corolla lobe aestivation	<i>imbricate</i>	interlocking (Darwin, 1994) but later regarded as valvate (Darwin, 2010)	[corolla not known for many species]	valvate (here)
Pyrene arrangement	<i>arranged around sides and bottom of an elongated, central placenta</i> that may be hollowed in time	pendulous from a condensed apical placenta, some slightly radiating outward but essentially pendulous	vertical to subvertical: essentially pendulous	pendulous from a condensed apical placenta
Distribution	Java, Moluccas, N Guinea, trop. Australia, Solomons	E & C Malesia, trop. Australia, Fiji, Samoa, except <i>T. avenis</i> var. <i>avenis</i> also distributed westward to E Kalimantan (Borneo)	Moluccas to Papua	Seychelles and W Malesia to Papua

Editor’s note: The initial version of this paper contained an error in the DOI number. It was reuploaded with a corrected DOI number on the 10th of November 2022.