PHYLOGENETIC SYSTEMATICS OF *ANTIRHEA* AND *TIMONIUS* (GUETTARDEAE: RUBIACEAE)

DISSERTATION

zur Erlangung des akademischen Grades eines
Doktors der Naturwissenschaften (Dr. rer. nat.)
an der Fakultät für Biologie, Chemie und Geowissenschaften
der Universität Bayreuth

vorgelegt von

Jayson Guereña Chavez
aus *Pasay City, The Philippines*
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Die vorliegende Arbeit wurde in der Zeit von Oktober 2016 bis Juli 2020 am Lehrstuhl für Pflanzensystematik der Universität Bayreuth unter Betreuung von Frau Prof. Dr. Sigrid Liede-Schumann und Herrn PD Dr. Ulrich Meve angefertigt.

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This dissertation is submitted as a "Cumulative Thesis" that includes four publications: two published, one submitted and one for submission.

List of Publications

1. Chavez, J.G., Meve, U., Nürk, N.M. & Liede-Schumann, S. Disentangling *Antirhea* (Rubiaceae): Resurrection of *Guettardella* and description of the new genus *Achilleanthus*. In review, Botanical Journal of the Linnean Society (BOTJLS-Feb-2020-3593-ART).

2. Chavez, J.G., Meve, U., Alejandro, G.J.D. & Liede-Schumann, S. Back to the drawing board: Molecular phylogeny challenges the traditional circumscription of *Timonius* (Guettardeae, Rubiaceae). For submission, Taxon.

3. Chavez, J.G., Meve, U. & Liede-Schumann, S. 2020. Taxonomic novelties and changes in Philippine *Timonius* (Rubiaceae, Guettardeae). Nordic Journal of Botany 38: e02730.

4. Chavez, J.G., Alejandro, G.J.D., Tandang, D.N. & Meve, U. 2020. Two new species of *Timonius* (Guettardeae: Rubiaceae) from Samar Island, the Philippines. Botany Letters 167(3): 1–10.

***Publications not included in this thesis*:**

5. Chavez, J.G., Banag-Moran, C.I. & Meve, U. 2020. *Timonius eremiticus* (Rubiaceae), a new species from the Philippines. Blumea 65: 104–106.

6. Chavez, J.G., Liede-Schumann, S. & Meve, U. 2017. On the identity of the rubiaceous *Timonius quadrasii* (Guettardeae: Cinchonoideae): Its typification and transfer to *Rothmannia* (Gardenieae: Ixoroideae). Webbia 72(2): 217–220.

7. Chavez, J.G., Alejandro, G.J.D. & Meve, U. 2017. Lectotypification of *Timonius pachyphyllus* Merr. (Rubiaceae, Guettardeae). Adansonia 39(2): 145–148.

Declaration of contribution to publications

This thesis contains four research manuscripts, for which the works were carried out by myself at the University of Bayreuth under the supervision and assistance of Prof. Dr. Sigrid Liede-Schumann and PD Dr. Ulrich Meve. Some of the sampled Philippine materials were obtained from 2015 to 2018 with the help of the staff and curator of the University of Santo Tomas (UST) Herbarium, and the Plant Sciences Laboratory of UST's Research Center for the Natural and Applied Sciences that is supervised by Prof. Dr. Grecebio Jonathan D. Alejandro. The materials of New Caledonian *Guettarda* were collected by Prof. Dr. S. Liede-Schumann and PD Dr. U. Meve. All manuscripts were prepared by taking into consideration the insights and suggestions of all co-authors.

1st Publication

Chavez, J.G., Meve, U., Nürk, N.M. & Liede-Schumann, S. **Disentangling *Antirhea* (Rubiaceae): Resurrection of *Guettardella* and description of the new genus *Achilleanthus***. In review, Botanical Journal of the Linnean Society (BOTJLS-Feb-2020-3593-ART).

The idea for the manuscript was conceptualized by J.G. Chavez with the guidance of Prof. Dr. S. Liede-Schumann. J.G. Chavez performed the molecular work independently under the assistance of Angelika Täuber at the Department of Plant Systematics, University of Bayreuth. Analyses of the molecular data were conducted by J.G. Chavez while incorporating the evaluative remarks of Dr. N. Nürk. Morphological analysis of herbarium materials was done by J.G. Chavez, and taxonomic implications were assessed together with PD Dr. U. Meve. The manuscript was written by J.G. Chavez recognizing the remarks of the co-authors.

2nd Publication

Chavez, J.G., Meve, U., Alejandro, G.J.D. & Liede-Schumann, S. **Back to the drawing board: Molecular phylogeny challenges the traditional circumscription of *Timonius* (Guettardeae, Rubiaceae)**. For submission, Taxon.

The idea and design of the manuscript were conceived by J.G. Chavez and Prof. Dr. S. Liede-Schumann. Molecular laboratory works and phylogenetic analyses were done by J.G. Chavez. Additional materials for the molecular works were obtained with the assistance of PD Dr. U. Meve and Prof. Dr. G.J.D. Alejandro. Interpretation of the molecular findings was carried out by J.G. Chavez with the support of Prof. Dr. S. Liede-Schumann. Morphological assessments and taxonomic treatments were done by J.G. Chavez with the help of PD Dr. U. Meve. Botanical illustrations were prepared by J.G. Chavez. The manuscript was prepared by J.G. Chavez and all co-authors contributed in its revision.

3rd Publication

Chavez, J.G., Meve, U. & Liede-Schumann, S. 2020. **Taxonomic novelties and changes in Philippine *Timonius* (Rubiaceae, Guettardeae)**. Nordic Journal of Botany 38: e02730.

J.G. Chavez conceptualized the study, examined herbarium specimens and conducted field observations in the Philippines. Taxonomic treatments were prepared by J.G. Chavez under the guidance of Prof. Dr. S. Liede-Schumann and PD Dr. U. Meve. Botanical illustrations and figures were prepared by J.G. Chavez, as well as the preliminary assessment of conservation statuses. J.G. Chavez prepared the manuscript incorporating the comments and suggestions of all co-authors.

4th Publication

Chavez, J.G., Alejandro, G.J.D., Tandang, D.N. & Meve, U. 2020. **Two new species of *Timonius* (Guettardeae: Rubiaceae) from Samar Island, the Philippines**. Botany Letters 167(3): 1–10.

The study was conceived by J.G. Chavez under the supervision of PD Dr. U. Meve. Taxonomic studies were performed by J.G. Chavez with the assistance of D.N. Tandang and Prof. Dr. G.J.D. Alejandro, who also provided materials of *Timonius* species from the island of Samar. Botanical illustrations were prepared by J.G. Chavez. The manuscript was drafted by J.G. Chavez with consideration of the co-authors' comments and suggestions.

Para sa aking minamahal na ina.
(To my beloved mother.)

CONTENTS

SUMMARY

The tribe Guettardeae is well known as an enigmatic group in Rubiaceae-Cinchonoideae when it comes to systematics and taxonomy. It has received limited attention in phylogenetic studies that only provided reference phylogenies with moderate species coverage, which elucidated the expansion of its tribal boundaries, as well as the necessity to re-circumscribe some of its genera. In the Paleotropics, Guettardeae are represented by ca. 260 species that are mostly dioecious (~99%). These dioecious species are currently organized into six genera, two of which, *Antirhea* and *Timonius*, are the focus of this study. The attempt to challenge or further explore the circumscriptions of these genera in a phylogenetic context using two nuclear (ETS, ITS) and three chloroplast (*atpB-rbcL*, *rps16*, *trnT-F*) regions was made to slowly fill the gaps in the current knowledge of tribe Guettardeae.

For over two centuries, the generic circumscription of *Antirhea* has been subject to debate. Its taxonomy has historically been hampered by the varied application of a restricted suite of morphological characters and the different opinions on its geographical provenance. Earlier authors have assumed *Antirhea* to have a trans-Pacific distribution without considering plant sexuality, while most recent workers have restricted the genus to contain only dioecious species that should either be exclusive to the Mascarene Archipelago or to the entire Indo-Pacific region. The results of some phylogenetic studies, however, have still suggested that *Antirhea* is non-monophyletic, despite already applying a more limited generic concept. Guided by this premise, the phylogeny of *Antirhea* was reconstructed with an increased sampling. The findings support its confinement to the Paleotropical Kingdom, but also confirming its unnaturalness. The species of *Antirhea* were recovered in three well-supported clades that were regarded as distinct genera: the much stricter *Antirhea* s.s. with three species, the new genus "*Achilleanthus*" with seven species and the resurrected *Guettardella* with twenty-nine species.

Timonius, with 185 species, is perhaps the easiest to identify among Paleotropical representatives of Guettardeae. The combination of valvate "interlocking type" corolla aestivation and drupes with free pyrenes had been widely accepted as its defining feature for past a century. Regardless, species-rich genera in Rubiaceae that were characterized by limited morphological features were often predisposed to be para- or polyphyletic. To resolve the

uncertainty, a representative selection of species traditionally assigned to *Timonius* was analyzed; and as a result, the genus was retrieved to be strongly polyphyletic which suggested the need to partially redefine its generic concept. The Australian endemic genus *Abbottia* was resurrected with an amended diagnosis to accommodate species previously assigned to *T.* subgen. *Abbottia*. The genus "*Lakapatiphyton*" was proposed to contain species with "leaky" dioecism, adpressed ± foliaceous stipules, monomorphic staminate and pistillate inflorescences having tri- to tetramerous flowers with imbricate corollas.

Lastly, a precursor for a comprehensive revision of Philippine *Timonius* was provided. The taxonomic work was based on herbarium specimens with benefits of *in situ* observations. A total of eight species novelties were recognized (*T. alejandroanus*, *T. dumagat*, *T. noli-tangere*, *T. pseudoarboreus*, *T. ridsdalei*, *T. spes-vitarum*, *T. stevendarwinii* and *T. sulitii*), two species (*T. panayensis* and *T. philippinensis*) were treated as conspecific with other well-defined species, one species (*T. nitidus*) was (re-) excluded from the Philippine flora and one species (*T. quadrasii*) was transferred to the genus *Ridsdalea* of tribe Gardenieae of subfamily Ixoroideae. Furthermore, the phylogenetic results for *Timonius* indicated that two species (*T. appendiculatus* and *T. pachyphyllus*) must be transferred to *Abbottia*, while seven species (*T. auriculatus*, *T. longiflorus*, *T. obovatus* [=*T. rotundus*], *T. oligophlebius*, *T. samarensis*, *T. trichiophorus* [=*T. hirsutus*] and *T. urdanetensis*) have to be accommodated in "*Lakapatiphyton*".

ZUSAMMENFASSUNG

Die Tribus Guettardeae ist im Bezug auf ihre Systematik und Taxonomie als kaum erforschte Gruppe der Rubiaceae-Cinchonoideae bekannt. Diese Pflanzen haben insbesondere in phylogenetischen Studien nur begrenzte Aufmerksamkeit gefunden und die Referenzphylogenien basieren auf einer geringen Anzahl untersuchter Arten, die die Abgrenzung der Tribus erschwerten sowie die Notwendigkeit von Neuumschreibungen einiger ihrer Gattungen verdeutlichen. In der Paläotropis sind die Guettardeae mit ca. 260 Arten vertreten, die zu 99% als diözisch gelten, Diese zweihäusigen Arten sind derzeit in sechs Gattungen klassifiziert, zwei davon, *Antirhea* und *Timonius*, stehen im Mittelpunkt dieser Studie. Der Versuch, mit Hilfe von zwei Kern- (ETS, ITS) und drei Chloroplastenregionen (*atpB-rbcL, rps16, trnT-F*), die bisherige Klassifikation in einem phylogenetischen Kontext zu überprüfen bzw. anzupassen, war vor dem Hintergrund diesess lückenhaften Wissens über die Tribus Guettardeae notwendig geworden.

Seit über zwei Jahrhunderten wird die Gattungsumschreibung von *Antirhea* diskutiert. Ihre Taxonomie wurde historisch durch die unterschiedliche Bewertung einer ohnehin nur begrenzten Anzahl morphologischer Merkmale sowie abweichenden Angaben zu geographischen Herkünften erschwert. Frühere Autoren betonten die Bedeutung einer trans-pazifischen Verbreitung für das Gattungskonzept von *Antirhea*, ohne dabei die Sexualität der Pflanzen zu berücksichtigen. Die meisten aktuelleren Bearbeiter betrachteten *Anthirea* dagegen als eine Gattung die ausschließlich diözische Arten enthält, die entweder ausschließlich im Maskarenischen Archipel oder im gesamten Indopazifik-Raum vorkommen sollen. Die Ergebnisse einiger phylogenetischer Analysen deuteten jedoch bereits darauf hin, dass *Antirhea*, selbst bei Anwendung eines engeren Gattungskonzeptes, nicht monophyletisch ist. Ausgehend von dieser Prämisse wurde die Phylogenie von *Antirhea* mit Hilfe einer höheren Probenzahl rekonstruiert. Die Ergebnisse unterstützen ihre Beschränkung auf das Paläotropische Florenreich und bestätigen gleichzeitig ihre Unnatürlichkeit. Die Arten von *Antirhea* fielen in drei gut unterstützte Kladen, die nun als unterschiedliche Gattungen betrachtet werden: die sehr viel enger gefaßte *Antirhea* mit nur noch drei Arten, die neue Gattung „*Achilleanthus*“ mit sieben Arten und die wieder anerkannte *Guettardella* mit 29 Arten.

Timonius ist mit 185 Arten unter den paläotropischen Vertretern der Guettardeae vielleicht am einfachsten zu identifizieren. Die Kombination von valvat „ineinandergreifendem Typus“ der Aestivation der Blütenkrone und Steinfrüchten mit freien Steinkernen war in den vergangenen hundert Jahren weithin als ihre charakteristische Merkmalskombination akzeptiert worden. Ungeachtet dessen waren artenreiche Gattungen der Rubiaceae, die sich durch eine begrenzte Anzahl morphologischer Merkmale auszeichneten, geradezu prädisponiert dafür, para- oder polyphyletisch zu sein. Um die Unsicherheiten zu beseitigen, wurde eine repräsentative Auswahl von Arten analysiert die traditionell *Timonius* zugeordnet wurden. Im Ergebnis konnte gezeigt werden, dass die Gattung stark polyphyletisch ist, was die Notwendigkeit einer teilweisen Neudefinition ihres Gattungsbegriffs nahelegte. Es wurde die australische endemische Gattung *Abbottia* mit einer abgeänderten Diagnose wiedereingesetzt, um die Arten aufzunehmen, die zuvor in der *Timonius* subgen. *Abbotia* klassifiziert waren. Die Gattung „*Lakapatiphyton*“ wurde für solche Arten eingerichtet, die durch fakultative (unvollständige) Dioezie, angedrückte und wohlentwickelte Stipeln, monomorphe männliche und weibliche Blütenstände mit tri- bis tetrameren Blüten und überlappender Knospendeckung charakterisiert sind.

Schließlich wurde ein Vorläufer für eine umfassende Revision des philippinischen *Timonius* erarbeitet. Die taxonomische Arbeit basierte auf Herbarexemplaren mit ergänzenden In-situ-Beobachtungen. Insgesamt wurden acht neue Arten anerkannt (*T. alejandroanus, T. dumagat, T. noli-tangere, T. pseudoarboreus, T. ridsdalei, T. spes-vitarum, T. stevendarwinii* und *T. sulitii*), zwei Arten (*T. panayensis* und *T. philippinensis*) wurden als Synonyme zweier anderer, gut umschriebener Arten behandelt, eine Art (*T. nitidus*) wurde (erneut) aus der philippinischen Flora ausgeschlossen und eine Art (*T. quadrasii*) wurde in die Gattung *Ridsdalea* der Tribus Gardenieae (Ufam. Ixoroideae) überführt. Darüber hinaus zeigten die phylogenetischen Ergebnisse für *Timonius*, dass auch noch zwei Arten (*T. appendiculatus* und *T. pachyphyllus*) in *Abbottia* übertragen werden müssen, während sieben Arten (T. *auriculatus, T. longiflorus, T. obovatus* [=*T. rotundus*], *T. oligophlebius, T. samarensis, T. trichophorus* [=*T. hirsutus*] und *T. urdanetensis*) nach „*Lakapatiphyton*“ zu übertragen sin

PART A

SYNOPSIS

I

GENERAL INTRODUCTION

A. The Rubiaceae

Rubiaceae Juss., commonly known as the madder or coffee family, is the fourth largest flowering plant family (Davis et al., 2009) that is currently comprised of ca. 600 genera and ~ 14,000 species (Govaerts et al., 2020). The Rubiaceae is morphologically distinct from its sister families, i.e. Apocynaceae, Gelsemiaceae, Gentianacaeae, Loganiaceae, and its monophyly had never been disputed. Members of this species-rich family are unified by opposite-decussate leaves, rarely whorled, presence of interpetiolar stipules, actinomorphic flowers and inferior ovaries (Robbrecht, 1988; Davis et al., 2009). Although cosmopolitan, the bulk of Rubiaceae species are primarily distributed in the tropics and dominate the understorey of forests, where they make up an important component of the vegetation (Robbrecht, 1988). Only few are notable for their socio-economic use, such as *Coffea* L. (crop: coffee), *Cinchona* L. (drug: quinine), *Rubia* L. (dye) and *Ixora* L. as well as *Gardenia* J.Ellis (ornamentals).

The present understanding of the infrafamilial systematics of Rubiaceae at different levels has been greatly influenced by phylogenetic studies published in the past decades, and have provided reasonable and robust definition of the relationships of various lineages in the family (Wikstrom et al, 2020), and have challenged the circumscription of some of its "top twenty" largest genera (Davis et al., 2009), including: *Canthium* Lam. (Lantz et al., 2002; Razafimandimbison et al., 2009; Arriola et al., 2016), *Galium* L. (Ehrendorfer & Barfuss, 2014), *Guettarda* L. (Achille et al., 2006), *Ixora* (Mouly et al., 2009), *Mussaenda* Burm. ex L. (Alejandro et al., 2005), *Oldenlandia* L. (Groeninckx et al., 2009; Guo et al., 2013), *Ophiorrhiza* L. (Razafimandimbison & Rydin, 2019), *Psychotria* L. (Nepokoreff et al., 1999) and *Tarenna* Gaertn. (De Block et al., 2015). However, uncertainties still remain when it comes to the relationships within some of the recognized tribes (Wikström et al., 2020) just like the poorly studied Guettardeae.

B. Tribe Guettardeae

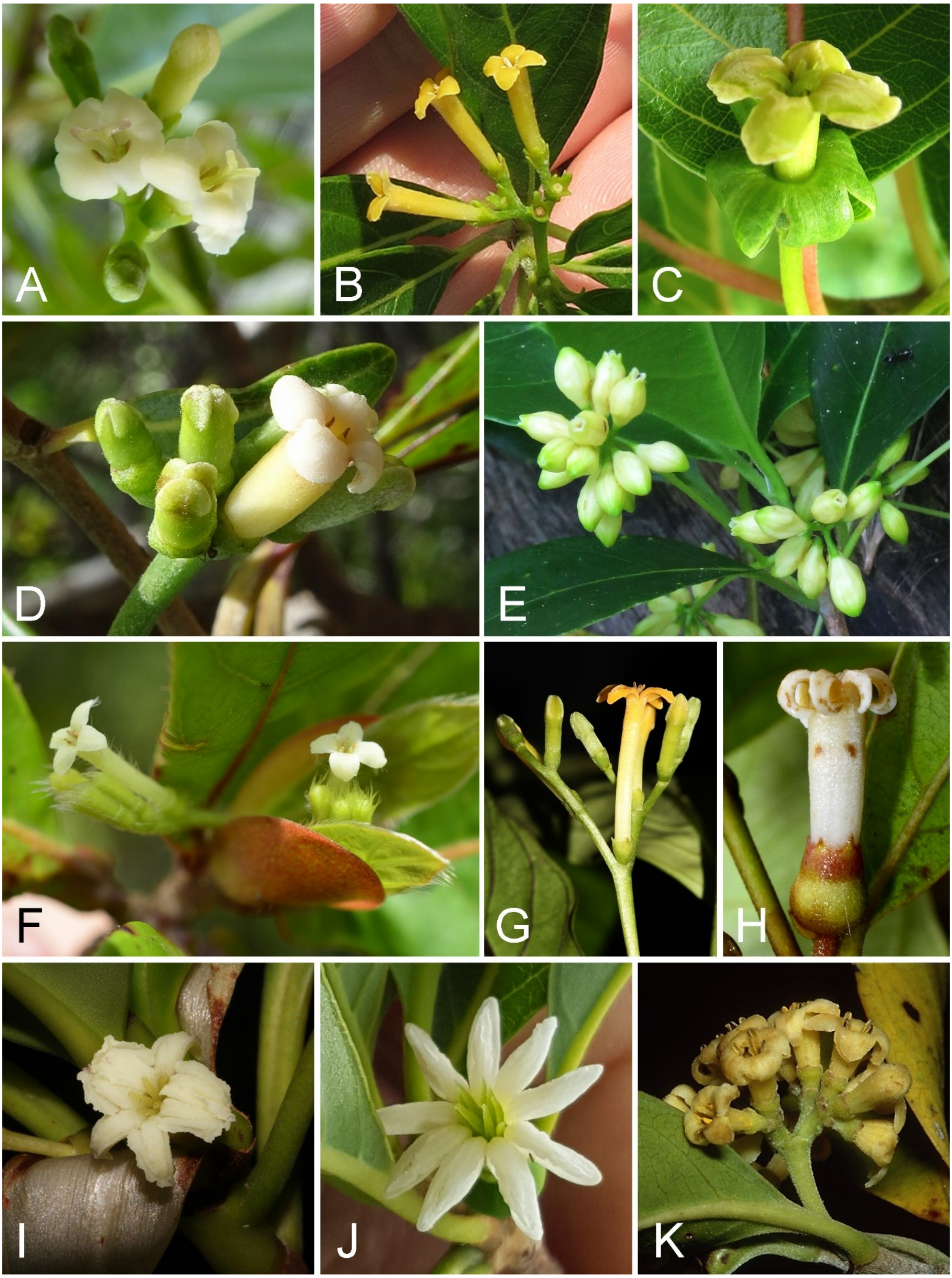
The tribe Guettardeae DC., with ca. 20 genera and ~740 species is one of the controversial groups within the Rubiaceae. Its circumscription has long been a subject of debate (e.g. de Candolle, 1830; Bentham & Hooker, 1873; Schumann, 1891; Verdcourt, 1956; Bremekamp, 1956; Robbrecht, 1988; Bremer et al., 1995; Rova et al., 2002, 2009; Manns & Bremer, 2010) and stability of its taxonomy has been viewed to be far from being achieved (Taylor & Gerau, 2010). This morphologically diverse tribe has a predominantly Neotropical distribution with some taxa reaching the Pacific Islands, Tropical Australia, New Guinea, Southeast Asia, Taiwan, Hong Kong, Southern China, the Indian Ocean and the coast of Tropical East Africa (Manns & Bremer, 2010; Manns et al., 2012). De Candolle (1830) originally circumscribed Guettardeae [= "Guettardaceae"] with two subtribes, Morindeae and Guettardeae, that are united by drupaceous fruits bearing 2 to 10 pyrenes, each with terete seeds. In this scheme, Guettardeae included 27 genera: *Antirhea* Comm. ex A.Juss., *Canthium* Lam. (as *Dondisia* DC.), *Chione* DC., *Coelospermum* Blume, *Cuviera* DC., *Erithalis* P.Browne, *Guettarda* L., *Gynochthodes* Blume (also as *Stigmanthus* Lour.), *Hydnophytum* Jack, *Hypobathrum* Blume, *Ixora* L. (as *Myonima* Comm. ex A.Juss.), *Lasianthus* Jack (as *Litosanthes* Blume, *Mephitidia* Reinw. ex Blume and *Octavia* DC.), *Leptordermis* DC., *Malanea* Aubl., *Mitchella* L., *Morinda* L., *Myrmecodia* Jack, *Nertera* Banks ex Gaertn., *Palicourea* Aubl. (as *Nanotelia* Aubl.), *Psychotria* L. (as *Psathura* Comm. ex A.Juss.), *Pyrostria* Comm. ex A.Juss., *Retiniphyllum* Bonpl., *Spermadictyon* Roxb. (as *Hamiltonia*), *Stenostomum* C.F.Gaertn., *Strumpfia* Jacq., *Timonius* Rumph. ex DC. (including *Bobea* Gaudich.) and *Vangueria* Juss. (also as *Ancylanthos* Desf.). Later, Bentham and Hooker (1873) proposed a different classification and reduced Guettardeae to 11 genera that exhibit imbricate or valvate corollas, inserted stamens, thickened funicle and non-albuminous seeds or only in traces. This redefined concept of Guettardeae was followed by Schumann (1891).

Verdcourt (1956) and Bremekamp (1966), who are the prime-movers for a modern subfamilial classification in Rubiaceae, treated Guettardeae within the monotribal subfamily Guettardoideae, *nom. illeg.* According to these authors, the tribe is without doubt be better treated in a subfamily of its own because of the exalbuminous seeds and presence of calcium-oxalate crystals in the wall of the trichomes. Robbrecht (1988) published a rather more comprehensive systematic treatment of Rubiaceae and treated Guettardeae in subfamily Antirheoideae. This classification was later shown as unnatural by molecular data, transferring

Guettardeae to subfamily Cinchonoideae (Bremer et al., 1995) and was affirmed by subsequent studies (e.g., Robbrecht & Manen, 2006; Bremer & Eriksson, 2009; Manns & Bremer, 2010; Rydin et al., 2017; Wikström et al., 2020).

The phylogenetic studies of Rova et al. (2002, 2009) and Manns and Bremer (2010) have also indicated to extend the tribal limits of Guettardeae to accommodate several genera previously placed by Robbrecht (1988) in the tribes Chiococceae, Isertieae and Rondeletieae (i.e. *Allenanthus* Standl., *Arachnothryx* Planch., *Gonzalagunia* Ruiz & Pav., *Hodgkinsonia* F.Muell., *Rogiera* Planch.). Achille et al. (2006), in a phylogenetic study of *Guettarda* including other core Guettardeae genera (i.e., *Antirhea*, *Bobea*, *Chomelia* Jacq., *Malanea*, *Neolaugeria* Standl., *Ottoschmidtia* Urb., *Pittoniotis* Griseb., *Stenostomum*, *Timonius*), analyzed the ITS nrDNA region for 42 taxa and found that several genera are polyphyletic (i.e. *Antirhea*, *Guettarda*, *Stenostomum*), which casted more problems to an already taxonomically chaotic Guettardeae. It is important to note that these polyphyletic genera play a critical role in the systematics of Guettardeae (Achille et al., 2006), since most of the species circumscribed within the tribe have been associated to these genera by earlier authors (e.g., Lamarck, 1792; Persoon, 1805; Bentham & Hooker, 1873; Baillon, 1879; Schumann, 1891; Guillaumin, 1930, 1948). Thus, their unresolved status is postulated to further slow-down taxonomic progress for the tribe.

In the Paleotropics *sensu* Takhtajan (1986), the ca. 260 species circumscribed within Guettardeae are dioecious, with *Dichilanthe borneensis* Baill., *D. zeylanicus* Thwaites and the trans-Pacific *Guettarda speciosa* L. as exceptions. The dioecious species are further assigned to six genera, namely: *Antirhea*, *Bobea*, *Guettarda* (New Caledonia; *see* Achille et al., 2006), *Hodgkinsonia*, *Timonius* and *Tinadendron* Achille (Fig. 1). These are differentiated based on dioecy-condition, dimorphism of inflorescences and/or flowers, bract/bracteole shape, corolla lobe aestivation, petal fusion, pollen architecture, stigmatic arm shape and pyrene fusion (Table 1; Mueller, 1861; Valeton, 1909; Darwin & Chaw, 1990; Chaw & Darwin, 1992; Darwin, 1993, 1994, 1997, 2010; Achille 2006). These genera (*Hodgkinsonia* not included) were recovered by Achille et al. (2006) in their Paleotropical dioecious clade, while *Bobea* was retrieved as sister to a clade containing *Guettarda crispflora* Vahl. and *G. hirsuta* (Ruiz & Pav.) Pers. Nevertheless, the retrieval of the Paleotropical dioecious clade is very intriguing because of its poor resolution which did not ascertain the naturalness of the included genera.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C. The Genus *Antirhea* Comm. ex Juss.

Antirhea (Fig. 1A–B), in its current circumscription, is distributed from the Mascarene Archipelago, southern China including Hong Kong, Malesia and Melanesia to Tropical Australia and the island of Samoa. Its 37 species are easily delimited from other Paleotropical dioecious Guettardeae by the exclusive combination of imbricate corollas and drupes with fused pyrenes forming a ligneous endocarp referred to as putamen (Chaw & Darwin, 1992). The circumscription of the genus has been a subject of disputes for centuries (Lamarck, 1792; Bentham & Hooker, 1873; Schumann, 1891; Jansen, 1984; Chaw & Darwin, 1992). In its original description (Jussieu, 1789), *Antirhea* was distinguished by whorled phyllotaxy, 4-merous flowers, subsessile and inserted anthers and coronate drupes with 2 single-seeded fused pyrenes. This description was based from the material of "*Bois de losteau*" from Réunion Island that was later named by Gmelin (1791) as *A. borbonica* J.F.Gmel. Lamarck (1792) contradicted the distinctiveness of *Antirhea* and treated it as congeneric with the Neotropical *Malanea*, but de Candolle (1830) opposed this view and reverted to Jussieu's (1789) concept. Bentham (1852) then proposed the genus *Guettardella* Champ. ex Benth. (*G. chinensis* Champ. ex Benth. and *G. philippinensis* Benth.), which also has 4-merous flowers and fused pyrenes. Realizing the close morphological association of his *Guettardella* with *Antirhea* (Bentham, 1867), Bentham and Hooker (1873) synonymized the genus to *Antirhea*, together with the Neotropical *Pittoniotis* and *Stenostomum*. This taxonomic decision gave *Antirhea* a broad definition that encompasses hermaphroditic and dioecious Guettardeae taxa exhibiting 4- to 5-merous flowers with 2- to 3-lobed stigmas and drupes bearing 2 to 10 locular putamen.

← **Fig. 1.** Representative species of the Paleotropical dioecious genera of Guettardeae: **A,** *Antirhea borbonica* J.F.Gmel. (credit: Sophie Leguil); **B,** *Antirhea chinensis* (Champ. ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl. (credit: Nelson So); **C,** *Bobea sandwicensis* (A.Gray) Hillebr. (credit: David Eickhoff); **D,** *Guettarda glabrescens* (Schltr.) Guillaumin (credit: Sigrid Liede-Schumann); **E,** *Hodgkinsonia ovatiflora* F.Muell. (credit: Janis Laraine Cossill); **F,** *Timonius auriculatus* Merr. (credit: Jayson G. Chavez); **G,** *Timonius flavescens* (Jacq.) Baker (credit: Cerlin Ng); **H,** *Timonius lanceolatus* Merr. (credit: Jayon G. Chavez); **I,** *Timonius singularis* (F.Muell.) L.S.Sm. (credit: Andreas Lambrianides); **J,** *Timonius timon* (Spreng.) Merr. (credit: Cameron); **K,** *Tinadendron noumeanum* (Baill.) Achille (credit: Bernard Suprin).

Jansen (1984), who conducted a survey of Paleotropical *Antirhea*, restricted its distribution in the region to the Mascarene archipelago with two species (*A. bifurcata* (Desr.) Benth. & Hook.f., *A. borbonica*), while the remaining species from the Pacific region were accommodated to the resurrected *Guettardella*. Aside from geographical provenance, the redefined circumscription of *Antirhea* presented by Jansen (1984) was based on sexuality (hermaphrodite in *Antirhea* versus dioecious in *Guettardella*), number of flowers per inflorescence (8- to 30-flowered in *Antirhea* versus 3- to 14-flowered staminate inflorescences and 1- to 3-flowered pistillate inflorescences in *Guettardella*) and number of locules per ovary (2 to 3 in *Antirhea* versus 3 to 14 in *Guettardella*). Jansen (1984) also considered two informal groups within *Guettardella*, species with large fruits and species with smaller fruits. Chaw and Darwin (1992) refuted the taxonomic findings of Jansen (1984), and re-lumped *Guettardella* in *Antirhea* and argued that the Mascarene species are actually dioecious. This seminal work of Chaw and Darwin (1992) had also reduced *Antirhea* to the Paleotropics, suggesting that Neotropical species are better placed in *Pittoniotis* or *Stenostomum* because of hermaphroditism and pollen architecture, which was followed by Borhidi and Fernandez (1995). Aside from this, three subgenera were proposed for *Antirhea*, these are: *A.* subgen *Antirhea*, *A.* subgen. *Mesocarpa* and *A.* subgen. *Guettardella* that are differentiated from each other based on the presence of crystals on abaxial leaf venation, branching pattern of staminate and pistillate inflorescences, number of flowers per inflorescence, presence of bracts, mesocarp type and geographical provenance (Chaw & Darwin, 1992). Despite the restriction of *Antirhea* to the Paleotropics, the nrDNA-based phylogeny of Achille et al. (2006) elucidated that the circumscription of the genus remains unnatural, which was also suggested by Manns and Bremer (2010). Nevertheless, these molecular studies were unable to provide taxonomic resolutions.

D. The Genus *Timonius* Rumph. ex DC.

Timonius (Fig. 1F–J) is the largest genus in Guettardeae and one of the species-rich in Rubiaceae (Davis et al., 2009). The genus is comprised of 185 species (Govaerts et al., 2020), while Darwin (2010) and Chen et al. (2015) have estimated it to contain 200 to 300 species. Morphological variation of species circumscribed to the genus is significantly high, but can be straightforwardly identified by the combination of valvate “interlocking-type” corolla aestivation and fruits bearing multiple and free single-seeded pyrenes. The genus has a

Table 1. Some morphological features of Paleotropical dioecious Guettardeae genera (modified from Achille, 2006)

Character	***Antirhea***			***Bobea***	***Guettarda* (N.W.C.)**	***Hodgkinsonia***	***Timonius***	***Tinadendron***
	Antirhea	***Mesocarpa***	***Guettardella***					
Dioecism type	leaky	strict	strict	polygamodioecy	strict	strict	leaky/strict	strict
IInflorescence dimorphism	absent	present	present	present	present	present	variable[+]	absent
Inflorescence type	cyme	cyme	cyme	cyme	cyme	umbel	cyme	cyme
Cyme ramification	simple/ compound	simple	simple/ compound as determinate thyrse	simple	simple	simple	simple	simple
Coroalla aestivation	imbricate	imbricate	imbricate	imbricate	valvate/ imbricate	imbricate	valvate - interlocking	imbricate
Corolla tube shape	salverform	salverform/ infundibular	salverform	salverform/ infundibular	salverform/ infundibular	urceolate	variable[§]	infundibular
Corolla lobes fused	no	no	no	no	no	yes	no	no
Pollen type[*]	*Antirhea*- type	*Antirhea*- type	*Antirhea*- type	*Bobea*-type	*Antirhea*- type	*Antirhea*- type	*Antirhea*- type	*Antirhea*- type
Stigmatic arm shape	linear							
Number of locules	2 to 3 (–4)	6 to 16	3 to 11	(2–) 4 to 10 (–12)	9 to 15	2 to 4	7 to ca. 500	(2–) 3 o 4
Mesocarp type	thinly fleshy	fibrous	fleshy/spongy	fleshy	fleshy/firbous	fleshy	fleshy/fibrous	thinly fleshy
Mesocarp cavities	absent	present	absent	absent	absent	absent	absent	absent
Pyrenes	fused	fused	fused	separate	fused	fused	separate	fused

[*]terminology according to Achille (2006), [*]majority of the species exhibit pistillate inflorescences that are 1– flowered, while some exhibit 3 – to 37– flowered cymes, [§]infundibular, salverform, hypocrateriform.

Paleotropical distribution, with New Guinea, the Philippines and Borneo as its primary centers of diversity. The usage of *Timonius* as a generic name has been compounded in botanical literature (e.g., de Candolle, 1830; Korthals, 1851; Bentham & Hooker, 1873; Schumann, 1891) that led to its conservation against earlier names: *Burneya* Cham. & Schltdl., *Helospora* Jack., *Polyphragmon* Desf. and *Porocarpus* Gaertn. The name of its type species, *T. timon* (Spreng.) Merr., has also been conserved (Rickett & Stafleu, 1960) perhaps due to the discordant opinions surrounding the limits of priority for the epithet. The first extensive treatment for *Timonius* was made by Valeton (1909) with species that are predominantly distributed in the Dutch East Indies. The morphological characterization of *Timonius* presented in this work had survived essentially unchanged up to the present time, and had prompted authors to attribute to the genus all Paleotropical dioecious Guettardeae taxa (excluding Hawaiian species) bearing free pyrenes, without taking into account other phenotypic features (e.g., Wernham, 1916, Merrill, 1923; Merrill & Perry, 1945; Smith, 1957, Darwin, 1983, 1994).

The unquestioned generic boundaries of *Timonius* had also led some authors to define infrageneric groupings, despite the relatively small number of species involved and limited geographic coverage of their studies. Valeton (1909) divided the genus into three sections based on stipule aestivation, pyrene number and orientation. However, he doubted the value of his own infrageneric classification stating: "*Ich lege diesen drei Sectionen keinen großen wissenschaftlichen Wert bei.*" [English translation: *"I do not put too much scientific value on these three sections.*"] (Valeton, 1909: 23), which became evident as it was not utilized in his subsequent work on Papuasian species (Valeton 1927). For his part, Wong (1988) classified *Timonius* from the Malay Peninsula into three informal groups based on leaf venation, corolla aestivation and whether the pyrenes are immersed in a hard matrix or not. Subsequently, Darwin (1993, 1994, 1997, 2010), who was to some extent influenced by the work of Valeton (1909), published a series of seminal studies that partly divided *Timonius* into three subgenera and an alliance of species related to *T. flavescens* (Jacq.) Baker. His works relied on habit, stipule aestivation and leaf venation. It is worth noting that one of his subgenera, *T.* subgen. *Abbottia* (29 species), is typified by *T. singularis* (F.Muell.) L.S.Sm., which is also the type of the Australian and monotypic genus *Abbottia* F.Muell. This genus was recognized to be distinct by Schumann (1891) and Bailley (1900), but treated as congeneric to *Timonius* by Smith (1957). Nevertheless, the infrageneric classifications proposed by these authors may not be widely applicable, since it is important to first ascertain the naturalness of *Timonius*, as currently circumscribed.

Only few species of *Timonius* have been included in phylogenetic studies, and all of those have dealt on other taxonomic issues (Achille et al., 2006; Pessoa, 2016). These studies, however, provided tangential views regarding the phylogenetic status of *Timonius*. Achille et al. (2006) having sampled five species, suggested that *Timonius* is monophyletic, while Pessoa (2016) elucidated that it is polyphyletic despite including only two species. To further complicate the classification of *Timonius*, there are some morphologically odd members of Guettardeae discovered from the Philippines (Publication 2, figure 4) that possess free pyrenes, but exhibit "leaky" dioecism (Baker & Cox, 1984), a character that was never reported to exist in the genus. These enigmatic elements are morphologically allied to a group of *Timonius* endemic to the archipelago (e.g., *T. auriculatus* Merr., *T. samarensis* Merr., *T. trichophorus* Merr.). To obtain a clear view on character evolution and biogeographical history, it is necessary to re-construct the phylogeny of *Timonius* with a larger sampling to evaluate its generic circumscription with more certitude.

E. Aims of the Research

This thesis utilizes taxonomic and phylogenetic information to investigate in detail the circumscriptions of the Paleotropical dioecious genera of tribe Guettardeae, with particular interest on *Antirhea* and *Timonius*. Although it is clear that the current delimitation of *Antirhea* is unnatural, no attempts have been made to resolve its taxonomy. On the other hand, the phylogenetic status of *Timonius* needs to be further explored, since the hypotheses presented by previous studies have relied on limited sampling. The findings of this endeavor will contribute towards a more taxonomically stable Guettardeae. Furthermore, this study will also serve as a basis for further studies regarding the biogeography of the tribe, the evolution of dioecy, and other comparative studies with other monophyletic rubiaceous genera. Hence, this study specifically aims to:

1. re-construct the phylogeny of *Antirhea* and *Timonius* by using molecular sequence data from three chloroplast (*atpB-rbcL*, *rps16*, *trnT-F*) and two nuclear (ETS, ITS) regions, with integration of a greater number of taxa,

2. determine the generic status of two Philippine Guettardeae species that are sexually polymorphic and bear drupes with free pyrenes,

3. evaluate morphological features to produce pragmatic generic re-arrangements for some taxa without contradicting their molecular affinities, and

4. provide a precursor for a comprehensive revision of Philippine *Timonius*.

II

MATERIALS AND METHODS

A. Plant Samples (Publications 1 and 2)

A total of 121 operational taxonomic units (OTUs) were included in the phylogenetic analyses. For tribe Guettardeae, all of its genera (Manns & Bremer, 2010) were included in the ingroup, except for the bitypic and Paleotropical monoecious genus *Dichilanthe* Thwaites, due to difficulties in obtaining DNA material from herbarium accessions. All the Paleotropical dioecious genera of Guettardeae were represented. The entirety of this study represented the Paleotropical dioecious genera with 85 OTUs that include: *Antirhea* (23 OTUs), *Bobea* (3 OTUs), *Guettarda* (New Caledonia, 4 OTUs), *Hodgkinsonia* (1 OTU), *Timonius* (50 OTUs) and *Tinadendron* (2 OTUs). Two additional OTUs ("*Lakapatiphyton*") from the Philippines were also included. Majority of the nucleotide sequences utilized for the phylogeny reconstructions were obtained for the purpose of this study, while a few were drawn from previous works and obtained from NCBI-GenBank (e.g., Achille et al., 2006; Rova et al., 2009; Manns & Bremer, 2010; Paudyal et al., 2018). The OTUs selected as outgroup were based on Manns & Bremer (2010).

B. Molecular Protocols (Publications 1 and 2)

Total DNA was extracted from silica-dried or herbarium materials following the 2x CTAB mini-prep procedure (Doyle & Doyle, 1987) using Carlson lysis buffer (Carlson et al., 1991), and purified with NucleoSpin Extract II (Machery-Nagel, Germany). For recalcitrant materials, the lysis buffer was supplemented with 15% *v/v* β-mercaptoethanol to eliminate secondary metabolites (e.g., tannins and polyphenols) that inhibit downstream reactions. The nuclear (ETS & ITS) and chloroplast (*atpB-rbcL*, *rps16* & *trnT-F*) regions were amplified using previously published primers (Taberlet et al., 1991; Liden et al., 1995; Baldwin & Markos, 1998; Popp & Oxelman, 2001; Razafimandimbison & Bremer, 2002; Shaw et al., 2005; Rydin et al., 2008). The amplification reaction of the nuclear regions was carried out in 25 μL volume (12.15 μL H_2O, 2.5 μL 10x PCR buffer, 1.5 μL 25 mM $MgCl_2$, 1 μL each of 10 mM primers, 1 μL dimethylsulfoxide, 1 μL bovine serum albumin, 2 μL DNA template, 0.35 μL *Taq* polymerase) using the thermocycler profiles of Tosh et al. (2013) and Alejandro et al. (2005). For the chloroplast regions, amplification was performed in 50 μL volume (24.25 μL H_2O, 5 μL 10x PCR buffer, 5 μL $MgCl_2$, 0.5 μL each of 10 mM primers, 5 μL tetramethylammonium chloride, 0.5 μL bovine serum albumin, 5 μL DNA template, 0.25 μL *Taq* polymerase) with an initial denaturation at 94 °C for 2 mins, 35 cycles of 94 °C for 45 secs, 52-59 °C for 1 min, 72 °C for 80 secs, and final extension at 72 °C for 6 mins. Amplicons were cleaned with QIA-quick PCR purification kit (Qiagen, Germany) and sequenced by Eurofins Genomics (Ebersberg, Germany) or Macrogen Europe (Amsterdam, the Netherlands).

C. Phylogenetic Analyses (Publications 1 and 2)

CodonCode Aligner v.7.0.1 (CodonCode Corporation, U.S.A.) was used to evaluate base confirmation of chromatograms and to assemble complementary strands. Automated sequence alignments were performed in MAFFT v.7 (Katoh et al., 2019) with the algorithms Q-INS-I and G-INS-I for the nuclear and chloroplast regions, respectively. The resulting alignments were manually adjusted in PhyDE v.0.997 (Müller et al., 2010) following the homology criteria of Kelchner (2000) and Simmons (2004). For the chloroplast regions, polynucleotide repeats of uncertain length homology and short inversions that were inferred by eye were excluded. Additional ambiguous sites in the sequence alignments were curated in Gblocks v.091b (Castresana, 2000) with the following parameters: –b1 and –b2 half the number of terminals + 1, –b3 8 positions, –b4 5 positions, –b5 half. Binary coding of microstructural characters (i.e., gaps, simple sequence repeats) was conducted for the chloroplast regions following Simmons and Ochoterena (2000) and Ochoterena (2009).

The sequence alignments were concatenated, and the optimal-partioning scheme and models of sequence evolution were identified under the Bayesian Information Criterion (Schwarz, 1978) using PartitionFinder v.2.1.1 (Lanfear et al., 2016). The partitions were assessed for congruence by visual inspection of the tree topologies generated by Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP) (discussed below), prior to the phylogenetic inference of the combined datasets. BI analyses were performed using MrBayes v.3.2.6 (Ronquist et al., 2012) on the CIPRES platform (Miller et al., 2010). Two parallel runs of four Markov chain Monte Carlo (MCMC) chains with sampling every 1000 generations were conducted over a total of 50 (publication 1) or 100 (publication 2) million generations. The first 50% of the sampled trees from each run were discarded as burn-in, and convergence of the runs was evaluated with Tracer v.1.7.1 (Rambaut et al., 2018) and RWTY package (Warren et al., 2017). ML analyses were implemented in RAxML v.8.2 (Stamatakis, 2014) with the trees obtaining the highest likelihood score were estimated with 1000 iterations, and bootstrap support values of the nodes were calculated with 10000 iterations. MP analyses were done in PAUP v.4.0 (Swofford, 2002) using a heuristic algorithm of 1000 random replicates with tree bisection-reconnection (TBR) and multiple trees (MULTREES) options in effect to search for the most parsimonious trees. MP bootstrap values were calculated with the same setting for 10000 replicates, except that there was no retention of multiple trees. The threshold for posterior probabilities and non-parametric bootstrap values to identify well-supported clades followed Hillis and Bull (1993).

D. Morphological Analyses and Taxonomic Treatments (Publications 1, 2, 3 and 4)

Morphological analyses in light of the phylogenies, as well as for the taxonomic treatments including the Philippine species of *Timonius* were based on herbarium specimens deposited in the following herbaria: A, BO, BR, CAHUP, FEUH, GB, GH, L, P, PNH, PPC, PUH, U, UBT, US, USTH and WAG. Additional information were obtained from the curators and staff of BISH, BRI, BRIT, C, CM, CNS, F, FR, HAST, PRC and TAIF, online databases of HBG, K, MO, NY, SING and Z, and from high-resolution digital images in JSTOR Plants and JACQ herbarium management system. All measurements were based on dried materials, while some features of the reproductive structures were documented from specimens that were rehydrated in a solution containing 5:4:1 *v/v/v* water, ethanol and glycerin. Some of the documented features (i.e., plant habit, coloration) were based on the reports of collectors indicated on the herbarium labels. The leaf clearings (Publication 2) were attained by immersing leaf fragments in 10% NaOH solution at 60 °C for 12 to 72 h, replacing the solution when it turned dark. The leaf portions were then rinsed with distilled water, bleached in 2% $NaHClO_3$ solution at room temperature for 10 mins, and finally triple rinsed with distilled water. Cleared leaf tissues were dehydrated in a graded series of ethanol (50%, 70%, 95%) for 15 mins each, stained with Safranin O for 24 h, destained with acid alcohol, and ended with dehydration in absolute alcohol for 24 h. Semi-permanent preparations were made using glycerinated gelatin and were observed under Olympus CX21compound microscope with TOUPCAM™ fixture. Terminologies for indumentum (Publications 3 & 4) were based from Hewson (1988) and the trichomes were measured under Leica S6E stereomicroscope equipped with a micrometer ocular. The morphological features of the taxa presented, especially the genera in Publications 1 and 2, were supplemented by information from both historical and contemporary literature (e.g., genus and species protologues, revisionary works, regional synopses and floras).

E. Conservation Assessments (Publications 3 and 4)

The conservation status of the species novelties presented in this study was evaluated based on geographic range by following the guidelines and criteria of IUCN (2019). Georeferenced data obtained from the herbarium materials were cleaned according to Wieczorek et al. (2004). The measure for extent of occurrence (EOO) and area of occupancy (AOO) was calculated using GeoCAT (Bachman et al., 2011) or the ConR package (Dauby et al., 2017). The AOO was determined with a grid resolution of 2 km, while the number of locations was determined with a grid resolution of 10 km.

III

RESULTS AND DISCUSSION

A. Phylogeny of *Antirhea* and its Re-circumscription (Publication 1)

The delineation of *Antirhea* had been unstable since its establishment (Jussieu, 1789). Many recent workers have restricted the genus to the Paleotropics and adopted a circumscription that is morphologically closer to its dioecious type, *A. borbonica*. This narrow concept, however, had been revealed by phylogenetic studies to still be non-monophyletic (Achille et al., 2006; Manns & Bremer, 2010). To clarify the phylogenetic relationships in *Antirhea*, a total of 318 sequences were analyzed, 205 of which are newly generated for this study. The ingroup (tribe Guettardeae) was represented by 71 accessions with an emphasis on the Paleotropical dioecious genera that were included with 46 accessions.

The topology of the generated tree (Publication 1, figure 1) confirmed that *Antirhea* is non-monophyletic, and that its species are nested in three well-supported clades which also correspond to the three subgenera previously proposed by Chaw and Darwin (1992). The earlier assumption to aggregate other Neotropical genera (*Pittoniotis* and *Stenostomum*) to *Antirhea* (Bentham & Hooker, 1873) is not supported, as all currently recognized species are retrieved within the well-supported Paleotropical Dioecious clade. The first clade (*Antirhea* I, *Antirhea* s.s.) comprises the type species and *A. madagascariensis* Chaw, and is characterized by monomorphic staminate and pistillate inflorescences, presence of crystals-containing cell clusters on the abaxial leaf surface and drupes with 2 to 3 (-4) locular putamen. The second clade (*Antirhea* II, "*Achilleanthus*") consists species of *A.* subgen. *Mesocarpa* and three species of New Caledonian *Guettarda*, and is characterized by dimorphic staminate and pistillate inflorescences, large fibrous drupes with cavities in the well-developed mesocarp and irregularly ribbed putamen with 6 to 16 locules. The third clade (*Antirhea* III, *Guettardella*) includes species of *A.* subgen. *Guettardella*, and is characterized by dimorphic staminate and pistillate inflorescences, small fleshy drupes that are crowned by an unequal-sized calyx and putamen with 4 to 11 locules. The retrieval of these clades is also supported by geographical evidence, *Antirhea* I is restricted to the Indian Ocean, *Antirhea* II in Malesia, Papuasia and

Southwestern Pacific, and *Antirhea* III in a much larger area, the (sub-) tropical Western Pacific. These results allowed to re-circumscribe *Antirhea* with a much stricter concept, recognize the new genus "*Achilleanthus*" and resurrect the genus *Guettardella*.

B. The Fragmentation of *Timonius* (Publication 2)

Although the usage of *Timonius* as a generic name has been compounded by earlier literature (Korthals, 1851; Bentham & Hooker, 1873), its delineation is clear-cut and is widely accepted. The combination of valvate "interlocking type" corolla aestivation and separate pyrenes makes it the easiest to identify among Paleotropical dioecious genera of Guettardeae. However, species of this large genus exhibit high levels of morphological variation that casted doubts on its current circumscription. This study provides the most comprehensive taxon sampling of *Timonius* to date (with 50 accessions, representing 47 species and varieties). The phylogenetic analyses of the combined dataset revealed that *Timonius* is strongly polyphyletic (Publication 2, fig. 2), suggesting that the combination of characters presented above is not enough to differentiate the genus. Here, *Timonius* species are retrieved in three well-supported clades and a branch containing *T. platycarpus* Montrouz.

Abbottia clade is the earliest to diverge and contains all sampled species of *T.* subgen. *Abbottia*. Species in this clade are united morphologically by their hemiepiphytic habit which is sometimes free-standing, strongly imbricate stipules with a single thickened costa, leaves with obscure secondary venation and without free-ending veinlets, truncate calyces and presence of calycine colleters that can be found along the middle or lower half of the calyx tube. Furthermore, the sampled species exhibit a C→A transversion at position 609 of the aligned *rps16* dataset that is absent in all other sampled Guettardeae taxa. The retrieval of this clade clearly shows the necessity to resurrect the genus *Abbottia* F.Muell. to include all species of *T.* subgen. *Abbottia*. Thus, a total of 35 new combinations are proposed for the reinstated genus.

"Lakapatiphyton" clade contains species that are endemic to the Philippines and the two dubious Guettardeae species that possess "leaky" dioecism and free pyrenes. This clade can be easily recognized because of adpressed ± foliaceous stipules with rounded or obtuse apices and monomorphic staminate and pistillate inflorescences. Sampled species also exhibit two defining molecular apomorphies: a 5 bp simple sequence repeat within *atpB-rbcL* (motif 5' TAACA 3',

position 56969-56973 of *Antirhea chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019) and 6 bp simple sequence repeat within *trnT-L* region (motif 5' TATAAA 3', position 48603-48608 of *A. chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019). These morphological and molecular characters permit the recognition of this clade as a distinct genus which is named "*Lakapatiphyton*", presently containing 9 species. The trivial generic name given is in reference to Lakapati, the androgynous diety of ancient Tagalog mythology.

Timonius platycarpus is retrieved in an isolated position that is sister to *Tinadendron*. The placement of this species in the phylogenetic tree is not surprising because of its fused pyrenes which is already discordant to the current classification of *Timonius*. Nevertheless, it still differs from *Tinadendron* by its monochasial and dimorphic inflorescences, valvate corollas and linear stigmatic arms. The proposal of a new genus for this species will not be made in this study, as the revision of New Caledonian *Guettarda* is still ongoing.

Lastly, the majority of the sampled species of *Timonius* are retrieved within the *Timonius* clade. The morphological characterization presented here is based only on terrestrial species because the attempts to obtain molecular data from 6 epiphytic species from New Guinea and the Philippines (i.e., *T. caudatifolius* Elmer, *T. caudatus* Valeton, *T. epiphyticus* Merr., *T. filipes* Wernham, *T. longistipulus* Merr., *T. minutifolius* Valeton) were futile. The representatives of this clade present variable stipule aestivation (imbricate, valvate or valvate-calyptrate), leaves with prominent secondary nerves and free-ending veinlets, calyces that are toothed or lobed, rarely truncate and calycine colleters that are predominantly absent. The calycine colleters, if present, are distributed on the sinus of calyx teeth or lobes. Furthermore, the sampled species exhibit a 2 bp insertion at position 779 to 780 of the aligned ITS dataset.

C. The Taxonomic Status of Philippine *Timonius* (Publications 3 and 4, and in part, Publication 2)

The Philippines is one of the centers of species diversity of *Timonius*. In the bibliographic consolidation of species from the archipelago, twenty-five species were recognized (Merrill, 1923) and only two species were added afterwards (Merrill, 1925; Wong, 1988). Here, a partial taxonomic treatment of the region's *Timonius* is initialized to eventually provide an extensive revision or synopsis.

Eight new species are described for the archipelago. *Timonius alejandroanus* J.G.Chavez, Meve & Liede (Publication 3, figure 1) that is found in Samar Island, is characterized from the most closely related *T. lanceolatus* Merr. by the combination of pistillate flowers with 5-lobed corollas (vs. 6-lobed), ellipsoid fruits with erect calyx crown (vs. globose and incurved calyx crown) and pyrenes that are arranged in ca. 5 double radiating files (vs. 6 double radiating files). The species is named after Grecebio Jonathan D. Alejandro, for his contributions to the knowledge of Philippine Rubiaceae. The species is here regarded as Endangered EN B2ab(ii,iii,iv) due to habitat degradation and limited area of occupancy.

Timonius dumagat J.G.Chavez (Publication 3, figure 2), a species that is named after the nomadic tribes of dumagat living in the municipalities of Palanan and Divilacan in Isabela, can be differentiated from *T. alejandroanus* with its leaves having 3 to 5 pairs of secondary nerves and smaller fruits that are moderately strigose with long persistent calyx. The long persistent calyx of the fruits of *T. dumagat* is attributed to the elongation of the disk during fruit development. This species also exhibits a high level of polymorphism in its leaf morphology that could have been influenced by its preferred habitat. The species is here assessed as Endangered EN B2ab(ii,iii,iv) due to its limited distribution and futility of current measures to protect the Northern Sierra Madre Natural Park (NSMNP).

Timonius noli-tangere J.G.Chavez, Alejandro & Meve (Publication 4, figure 2) is a species that can only be found in the forest edges on lateritic soils near the tributaries of the Balangiga River in the island of Samar. It is diagnosed against *T. valetonii* Elmer by its peduncles with stramineous trichomes (vs. ferrugineus), reddish and verrucose calyces (vs. green and smooth), cream colored corolla lobes with tawny or amber colored underside (vs. ivory and pink) and smaller fruits with short persistent calyx (vs. large with long persistent calyx). The preferred habitat of *T. noli-tangere* has been greatly damaged by recent natural calamities, i.e. Super Typhoon Haiyan and forest fire. The vegetation in the area is also affected by agricultural and infrastructure expansion. Hence, this species is assigned a provisional conservation status of Critically Endangered CR B2ab(iii).

Timonius pseudoarboreus J.G.Chavez (Publication 3, figure 3) can be easily mistaken for its closest ally, *T. arboreus* Elmer, in the absence of reproductive structures. This species that is distributed in the island of Luzon and the adjacent Polillo Island, can be distinguished with its 8- to 14-flowered staminate inflorescences (vs. 3- to 7-flowered) and ellipsoid to obovoid fruits that are moderately strigose (vs. globose to oblate, glabrous). Despite having a much wider distribution compared with other Philippine species of *Timonius*, *T. pseudoarboreus* is only known to have a 32 km^2 area of occupancy with eight known locations. It is also important to note that the natural landscapes of Luzon and Polillo have been greatly degraded and were converted for urbanization and agricultural use. Hence, *T. pseudoarboreus* is provisionally assigned a conservation status of Vulnerable VUB2ab(ii,iii,iv,v).

Timonius ridsdalei J.G. Chavez (Publication 3, figure 4) is only known from staminate materials collected in Palanan, Isabela, and its description needs to be amended once pistillate individuals are discovered. It is named after Colin E. Ridsdale to posthumously recognize his contributions to the understanding of the Philippine flora. Together with *T. palawanensis* Elmer and *T. ternifolius* (Bartl. ex DC.) Fern.-Vill., *T. ridsdalei* exhibits a predominantly ternate phyllotaxy. It can be recognized from *T. palawanensis* by having coriaceous leaves and staminate flowers with much longer corolla tubes and anthers. It is here assessed as Endangered EN B2ab(ii,iii,iv) despite the fact that its preferred habitat is situated within NSMNP. This is because of the limited area of occupancy (4 km^2) with only two known locations and that the municipality of Palanan is known for illegal logging and land-use change.

Timonius spes-vitarum J.G.Chavez (Publication 3, figure 5) is unique from all Philippine species because of its profoundly lobed calyx. Aside from this, it can be characterized by the combination of its imbricate stipules with glabrous outer surface and glabrous leaves. Based on the available herbarium materials, this species is known to occur in the ultramafic vegetation of Palawan Island, and its population may exhibit a male-sex biased ratio in the wild. This species which is assigned an epithet that will signify hope for the protection of the Philippines' last ecological frontier, is designated a conservation status of Vulnerable B1+2ab(i,ii,iii,iv,v) because of the low extent of occurrence (4797.8 km^2) and area of occupancy (48 km^2) and that the island of Palawan is recognized to experience the highest deforestation rate among terrestrial protected areas in the Philippines during the recent years (Apan et al., 2017). Furthermore, climate change may induce the reduction of mature individuals of *T. spes-vitarum* in the future, as this phenomenon may trigger extreme male-sex biased ratio (Hultine et al., 2016).

Timonius stevendarwinii J.G.Chavez (Publication 3, figure 6) is morphologically more related to the Bornean *T. abanii* Jun H.Chen than any other Philippine species. It can be distinguished from the latter by the combination of valvate stipules, pistillate flowers with 5-lobed corollas and densely strigose fruits. This species which is only known from the island of Palawan is named after Steven P. Darwin to recognize his contributions to the current knowledge on the genus. *Timonius stevendarwinii* has an extent of occurrence of 3679.1 km^2, an area of occupancy of 40 km^2 and is known from 7 locations; thus, is here designated a conservation status of Vulnerable VU B1+2ab(i,ii,iii,iv).

Timonius sulitii Merr. & Quisumb. ex J.G.Chavez & Tandang (Publication 4, figure 3) is a species currently known from a single gathering. The material was collected by Mamerto D. Sulit together with E. Coñese in Mt. Calbiga, Samar. It can be recognized by the combination of chartaceous leaves with silky underside and 8 to 9 pairs of secondary nerves, long pedunculate pistillate inflorescences, tuberculate and costate fruits with schizogenous cavity and pyrenes that are arranged in a U-shaped pattern in longitudinal section of the fruit. *Timonius sulitii* is provisionally assessed as Critically Endangered CR B2ab(iii) because of the low area of occupancy (4 km^2), single location and the declining quality of its preferred habitat.

Aside from these novelties, several taxonomic changes are inferred, these are: 1) synonymy of two species to other well-differentiated *Timonius*, 2) transfer of ten species to other genera and 3) exclusion of one species from the Philippine flora. *Timonius philippinensis* Merr. is treated as conspecific to the widespread *T. finlaysonianus* (Wall. ex G.Don.) Hook.f. The species was earlier recognized by Merrill (1903) as distinct against *T. compressicaulis* (Miq.) Boerl. (= *T. finlaysonianus*) based on the coloration, dimension and indument cover of the branchlets, as well as the length of the corolla tube. However, field and ex-situ observations of the species coupled with examination of herbarium materials indicated that the characters are inconsistent and only reflect phenotypic variations associated with ecological conditions. On the other hand, *Timonius panayensis* Merr. is synonymized to *T. valetonii* Elmer because the diagnostic features provided by Merrill (1920 publ. 1921) falls within the morphological features of the latter.

Timonius appendiculatus Merr. and *T. pachyphyllus* Merr. were treated as members of *T.* subgen. *Abbottia* (Darwin, 1994). Although these were not sampled in the phylogenetic analysis of *Timonius*, their morphology coincides with the features of *Abbottia*, namely: hemiepiphytic, strongly imbricate stipules with a single-thickened costa, leaves without free-ending veinlets and presence of calycine colleters that are distributed along the middle of the calyx tube. Thus, these species are transferred to the resurrected genus.

The retrieval of the "*Lakapatiphyton*" clade in the phylogenetic analysis of *Timonius* (Publication 2, fig. 2) clearly suggests that several species of Philippine *Timonius* must be transferred to the new genus, these are: *T. auriculatus*, *T. longiflorus*, *T. obovatus*, *T. oligophlebius*, *T. samarensis*, *T. trichophorus* and *T. urdanetensis*. All of these species exhibit adpressed ± foliaceous stipules and monomorphic staminate and pistillate inflorescences.

The Philippine endemic *T. quadrasii* Elmer is one of the odd elements in *Timonius*. It is hermaphroditic and exhibits terminal inflorescences that appear axillary because of the presence of brachyblasts bearing a single leaf forming an unequal and ternate phyllotaxy (Appendix 1, figure 1). The species also possesses flowers with left-contorted corollas and two to three locular ovaries that are multi-ovulated. This set of morphological characters allowed its transfer to the genus *Ridsdalea* J.T.Pereira & K.M.Wong from the very distant tribe Gardenieae of subfamily Ixoroideae with the new combination, *R. quadrasii* J.G.Chavez, Meve and Liede.

Timonius nitidus (Bartl. ex DC.) Fern.-Vill. is a species with dubious Philippine origin. The original material used to describe the species was collected by Thaddeus Haenke during the Malaspina Expedition, who indicated that it was obtained from the islands of the Philippines and Marianas. Fernandez-Villar (1880), without having the material in his possession, then reduced its locality to the island of Luzon. This decision of Fernandez-Villar (1880) is perhaps based on mere assumption, because historical records indicate that T. Haenke collected botanical specimens in the North-eastern portion of Luzon. Merrill (1919) started to be suspicious with the provenance of *T. nitidus* in the Philippines, which he later substantiated by excluding the species from the list of Philippine *Timonius* (Merrill, 1923). However, the species was retained to the Philippines by the World Checklist of Rubiaceae (https://apps.kew.org/wcsp) and Co's Digital Flora of the Philippines (https://www.philippineplants.org). Field observations conducted in the island of Luzon and examination of herbarium materials indicate that *T. nitidus* is indeed an extra-Philippine species that was erroneously attributed to the region as a consequence of its colonial history. Thus, *T. nitidus* is now restricted to the island of Guam.

In spite of these taxonomic additions and changes, Philippine *Timonius* still remains a heterogeneous assemblage. Three epiphytic species from the Greater Mindanao ecoregion (*T. caudatifolius*, *T. epiphyticus* and *T. longistipulus*) exhibit a branching pattern that imitates a large compound leaf, which is also found in epiphytic species from the island of New Guinea. This vegetative feature is unique compared to the rest of *Timonius*. It is postulated that this morphological group represents another distinct lineage which might eventually be recognized as another new genus, pending the needed molecular evidences. Furthermore, another Philippine endemic species (*T. gracilipes* Merr.) collected from the island of Cebu has a peculiar association to *Timonius*. The materials for this species all came from a single collection. At first glance, it can be easily mistaken as a species of *Guettardella* because of the imbricate corollas and drupes that are crowned by the unequal sized calyx. However, the pyrenes of this species are separated, unlike that of *Guettardella* which are fused. Acquisition of this species may be challenging because currently, Cebu has less than 1% forest cover that are fragmented, and its specific locality (Buacao) is completely urbanized.

IV

CONCLUSION AND PERSPECTIVES

This study, despite its limits, provides a significant contribution to the understanding of the systematics of the tribe Guettardeae. It highlights the re-delimitation of *Antirhea* and *Timonius*, as well as the current state of the taxonomy of Philippine *Timonius*.

First, the phylogenetic results provide clear evidence that a new circumscription of *Antirhea* is necessary in order to resolve it as monophyletic. This study suggests to restrict *Antirhea* to the Mascarene Archipelago and Madagascar, while its Western Pacific species should be recognized as members of the new genus "*Achilleanthus*" or the resurrected *Guettardella*. It also shows, that some New Caledonian species of *Guettarda* must be transferred to "*Achilleanthus*".

Just like other species-rich genera of Rubiaceae that are characterized by a limited suite of morphological characters, *Timonius* is also revealed to be polyphyletic. The general notion to treat all Paleotropical dioecious species of Guettardeae with valvate "interlocking type" of corolla aestivation and drupes with free pyrenes in *Timonius* is rejected by the phylogenetic results. The application of an increased sampling of *Timonius* in a phylogenetic context provided an interesting picture regarding its systematics, and suggests that one must also look at other possible combinations of morphological characters (e.g. type of dioecism, habit, stipule architecture, leaf venation, inflorescence dimorphism, calycine colleters) to create a more natural classification of the genus. Furthermore, the molecular data suggest that simple sequence repeats and insertion-deletion events can be promising characters that can aid in distinguishing different clades within the Guettardeae.

The topology of the phylogenetic tree that was re-constructed for *Timonius* suggests that the genus *Abbottia* should be resurrected to accommodate species of *T.* subgen. *Abbottia*. The phylogenetic data also indicate that the new genus "*Lakapatiphyton*" should be established. The morphological synapomorphies of this new genus are the adpressed ± foliaceous stipules with obtuse to rounded apices, monomorphic staminate and pistillate inflorescences, tri- to tetramerous flowers and drupes with free pyrenes. In spite of these, an increased amount of data is still needed to resolve the generic boundaries of *Timonius* since this study was unable to include its epiphytic species. Nevertheless, with the current increasing efforts to explore the systematics of *Timonius* that are taking place in Borneo and the Philippines, it is not unlikely that its delineation will be settled in the near future.

Lastly, a partial treatment of Philippine *Timonius* is provided that serves as a base for the completion of a comprehensive account of the genus in the archipelago. This study offers an understanding of features that can be utilized to demystify cryptic species or to unravel species that are yet to be discovered. In addition, to improve the delimitation of species that were described by earlier authors, additional materials must come to light because majority of the extant materials of Philippine *Timonius* are in a poor-state of preservation and only bear fragments of reproductive structures.

V

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PART B

PUBLICATIONS

DISENTANGLING *ANTIRHEA* (RUBIACEAE): RESURRECTION OF *GUETTARDELLA* AND DESCRIPTION OF THE NEW GENUS *ACHILLEANTHUS**

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The Paleotropical genus *Antirhea* (Guettardeae, Rubiaceae) currently comprises 37 dioecious species classified into three subgenera: *Antirhea*, *Mesocarpa* and *Guettardella*. It has a complex taxonomic history with varying generic delineation and variable application of species names. Recent phylogenetic studies have indicated the non-monophyly of *Antirhea*, but the limited sampling neither offered to resolve its circumscription nor to propose nomenclatural changes. Here, we reconcile the generic boundaries of *Antirhea* based on phylogenetic analyses of two nuclear (ETS, ITS) and three plastid (*atpB-rbcL*, *rps16*, *trnT-F*) loci using Bayesian, maximum likelihood and parsimony methods. Our results show that *Antirhea* in its current circumscription is highly polyphyletic, whereas its three subgenera are retrieved as well-supported independent clades. A new generic framework is proposed based on phylogenetic results and supported by morphological evidence. We suppose to restrict *Antirhea* to species native to the Mascarene Islands and Madagascar; reinstate the genus *Guettardella* with emended diagnostic features; and describe the new genus *Achilleanthus* to accommodate the species of subgenus *Mesocarpa* plus *Guettarda glabrescens*, *G. hypoplasia* and *G. ngoyensis*. As a consequence, seven new combinations in *Achilleanthus* and seventeen new combinations in *Guettardella* are made.

Keywords: dioecy, Guettardeae, Indo-Pacific region, Paleotropics, phylogenetic analysis, taxonomy, typification.

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Introduction

The Rubiaceae genus *Antirhea* Comm. ex Juss. includes 37 species of shrubs or trees that are distributed in the Paleotropics from the Mascarene Archipelago, eastward to southern China, Hong Kong, Malesia, Melanesia, Samoa and tropical Australia. In its current circumscription (Chaw & Darwin, 1992), *Antirhea* is characterized by dioecism, tri- to tetramerous flowers with imbricate corolla lobes, inaperturate to 1-porate semitectate pollen grains, coronate drupes, and fused pyrenes that form a ligneous endocarp called putamen. Together with *Timonius* Rumph. ex DC., *Tinadendron* Achille and New Caledonian species of *Guettarda* L., *Antirhea* is phylogenetically positioned within the "Paleotropical Dioecious" (PD) clade of tribe Guettardeae (Achille *et al.*, 2006). However, the generic circumscription of *Antirhea* varied greatly between authors (e.g., Lamarck, 1792; Hooker, 1873; Jansen, 1984; Chaw & Darwin, 1992), and has been a source of considerable taxonomic confusion within the Guettardeae for centuries.

The tribe Guettardeae *s.l.* is a tropical amphi-Pacific group with around 740 species circumscribed in ca. 20 genera (Manns & Bremer, 2010). Its members present a woody habit, axillary or terminal inflorescences, valvate or imbricate corolla lobes, bi- to multi- locular ovaries, single apically attached pendulous ovule per locule, drupaceous or schizocarpous fruits and seeds with little-developed endosperm (Robbrecht, 1988; Taylor & Gereau, 2010). Previous phylogenetic investigations, albeit focused on the reorganization of tribal boundaries (Bremer, 1992; Moynihan & Watson, 2001; Rova *et al.*, 2002; Rova, Delprete & Bremer, 2009; Robbrecht & Manen, 2006; Manns & Bremer, 2010), have improved our understanding of Guettardeae diversity and classification. However, taxonomic stability within the tribe is still projected to be far from being achieved because of problematic applications of generic names (Taylor & Gerau, 2010).

Originally, Jussieu (1789) described *Antirhea* based on Commerson's specimen of *"Bois de losteau*" from the island of Réunion. He initially distinguished the genus with verticillate leaves, tetramerous flowers, included, subsessile anthers, and small calyx-crowned drupes bearing two single-seeded, fused pyrenes. Later, Lamarck (1792) considered *Antirhea* as congeneric with *Malanea* Aubl., but was criticized by Candolle (1830) pointing that *Antirhea* is distinct by its inflorescence architecture, longer corolla tube, and subsessile anthers. Candolle (1830) further associated *Antirhea* with *Stenostomum* C.F.Gaertn. based on floral merosity, and also cited that the flowers of *A. dioica* Bory ex DC. (=*A. borbonica* J.F.Gmel.) are dioecious by abortion, perhaps due to the rudimentary stamens (staminodia) or pistils (pistillodia). Bentham (1852) then formally described *Guettardella* Champ. ex Benth. with two species (*G. chinensis* Champ. ex Benth., *G. philippinensis* Benth.), and later suggested its close relationship with *Antirhea* in view of the polygamous flowers and number of locules per ovary (Bentham, 1867). Afterwards, Hooker (1873) proposed a multi-generic treatment of *Antirhea*, synonymizing *Guettardella*, *Pittoniotis* Griseb., and *Stenostomum*, that was adopted by Schumann (1891) and in various treatments for the New World (e.g., Standley, 1934; Standley & Williams, 1975; Dwyer, 1980). However, Hooker's (1873) wide circumscription had made *Antirhea* a catchall genus for hermaphroditic or dioecious Guettardeae species with tetramerous to pentamerous flowers, 2- to 3- lobed stigma, and 2 to 10 locular putamen.

This broad definition of *Antirhea* (Hooker, 1873) was slowly refuted by morphological investigations focusing on its Paleotropical species. Jansen (1984) divided the Old World *Antirhea* into two genera based on the number of locules per ovary, geographical distribution and a different view of floral sexuality. He re-established *Guettardella* to accommodate the dioecious species from the Tropical Western Pacific, while *Antirhea* was limited to species from the Mascarene Archipelago which according to him are hermaphroditic. His circumscription was accepted by Robbrecht (1988), but did not gain recognition by authors of local floras (e.g., Smith & Darwin, 1988; Wong, 1988; Verdcourt, 1989; Alejandro & Liede, 2003; Salamanes *et al.*, 2015). Chaw & Darwin (1992) found conflicting evidence in Jansen's (1984) generic delimitation, and clarified that the Mascarene *Antirhea* are also dioecious, reducing *Guettardella* to synonymy. Instead, they re-defined *Antirhea* as exclusive to the Paleotropics and suggested that species from the New World are best placed in *Pittoniotis* or *Stenostomum*. Their circumscription was established primarily on sexuality, floral merosity and pollen architecture. Moreover, Chaw & Darwin (1992) presented an infrageneric classification that emphasized on the combination of several traits (i.e., vascular trace, leaf areolation and texture, number of flowers per inflorescence, bracteole type and shape, fruit size, mesocarp type, and distribution), that divided *Antirhea* into three subgenera: *Antirhea*, *Mesocarpa* and *Guettardella*.

The nuclear DNA-based (ITS) phylogenetic study of Achille *et al.* (2006) supported the restriction of *Antirhea* to the Old World, but highlighted that the proposed circumscription of Chaw & Darwin (1992) is unnatural. *Antirhea borbonica* was placed as earliest diverging lineage the “Paleotropical dioecious” (PD) clade, while the sampled species of subgenus *Mesocarpa* and subgenus *Guettardella* appeared in a polytomous clade along with *Tinadendron* and New Caledonian species of *Guettarda*. Nevertheless, they were unable to provide the necessary taxonomic changes, likely because of limited sampling and the poor support or unresolved position of some clades. In this study, we reconstruct the phylogeny of *Antirhea* and its relatives based on an expanded taxon sampling and a larger number of molecular markers (nuclear: ETS, ITS; plastid: *atpB-rbcL*, *rps16*, *trnT-F*). The resulting phylogenetic hypothesis is used to: 1) clarify the circumscription of *Antirhea*, 2) evaluate morphological synapomorphies for well-supported clades, and 3) propose the necessary nomenclatural changes that accommodate the respective clades as monophyletic taxonomic entities for linear classification.

Materials and Methods

Taxon sampling

Our sampling approach gave emphasis to the PD clade of Achille *et al.* (2006), while also considering sequence data from other phylogenetic studies to constitute all lineages of Guettardeae *s.l.* (Manns & Bremer, 2010). For *Antirhea*, we included as many species as possible to represent all subgenera based on the availability of materials suitable for DNA extraction: two out of three species of subgenus *Antirhea*, two out of five species of subgenus *Mesocarpa*, and fifteen out of twenty-nine species of subgenus *Guettardella*. Additionally, four accessions of putative undescribed species of subgenus *Guettardella* were included. Because of the unresolved relationship between Tropical Western Pacific *Antirhea* and New Caledonian *Guettarda* (Achille *et al.*, 2006), we additionally sampled *G. glabrescens* (Schltr.) Guillaumin (two accessions), *G. hypoplasia* Baill., *G. ngoyensis* (Schltr.) Guillaumin and *Tinadendron kajewskii* (Guillaumin) Achille. Furthermore, we expanded the sampling of *Timonius* to fourteen out of *ca.* 200 species (Darwin, 2010). Two outgroup taxa were selected from the subfamily Cinchonoideae based on Manns & Bremer (2010): *Bikkia tetrandra* (L.f.) A.Rich. (Chiococceae), and *Acrosynanthus latifolius* Standl. (Rondeletieae). Details of the sampled taxa, voucher information and NCBI-GenBank accession numbers are provided in Appendix 1.

DNA extraction, amplification and sequencing

Total DNA was extracted from silica-dried leaves (Chase & Hills, 1991) or herbarium materials following the protocol of Doyle & Doyle (1987) using Carlson lysis buffer (Carlson *et al.*, 1991) augmented with 15% v/v β-mercaptoethanol (Merck, Darmstadt, Germany), and subsequently purified with NucleoSpin Extract II (Machery-Nagel, Düren, Germany). The following primers were used for PCR amplification: *atpB-rbcL* (atpB5'R and rbcL5'R; Rydin, Razafimandimbison & Bremer, 2008), ETS (18S-E and ETS-ERIT; Baldwin & Markos, 1998; Negrón-Ortiz & Watson, 2002), ITS (P17F and 26S-82R; Popp & Oxelman, 2001), *rps16* (rpS16F and rpS16R; Shaw *et al.*, 2005) and *trnT-F* (trnT-F_a1F, trnT-F_iR, cF, dR, eF and fR; Taberlet *et al.*, 1991; Razafimandimbison & Bremer, 2002).

The amplification of the nuclear markers included: 2.5 µl 10x PCR buffer, 1.5 µl 25 mM $MgCl_2$, 2.5 µl 10 mM dNTP, 1 µl each of 10 mM forward and reverse primers, 1 µl 5% dimethyl sulfoxide (DMSO), 1 µl 1% bovine serum albumin (BSA), 2 µl template DNA, 0.35 µl *Taq* DNA polymerase and an aliquot of nuclease-free water to obtain a volume of 25 µl. For the plastid markers, PCR were carried out in 50 µl volume containing: 24.25 µl H_2O, 5 µl 10x PCR buffer, 5 µl 25 mM $MgCl_2$, 4 µl 10 mM dNTP, 0.5 µl each of 10 mM forward and reverse primers, 5 µl 10 mM tetramethylammonium chloride (TMAC), 0.5 µl 1% BSA, 0.25 µl *Taq* DNA polymerase and 5 µl DNA template. The PCR conditions for ETS and ITS followed Tosh *et al.* (2013) and Alejandro, Razafimandimbison & Liede-Schumann (2005), respectively. For the plastid markers, the thermocycling profile started with an initial denaturation of 2 min at 94°C, followed by 35 cycles of 45 s at 94°C, 1 min at 52-59°C, 80 s at 72°C and ended with a final extension of 6 min at 72°C. The PCR amplicons were purified with QIAquick PCR purification kit (QIAGEN, Hilden, Germany) and sequenced by Macrogen Europe B.V. (Amsterdam, the Netherlands). Resulting sequences were proofread and assembled using CodonCode Aligner v.7.1 (CodonCode Corporation, Massachusetts, USA).

Sequence alignment, compilation and partitioning

Alignments were first estimated using MAFFT v.7 (Katoh, Rozewicki & Yamada, 2017) with the algorithms Q-INS-i for the nuclear markers and G-INS-i for the plastid markers, and subsequently adjusted in PhyDE1 v.0.997 (Müller *et al.*, 2010) following alignment rules and principals of homology by Kelchner (2000) and Simmons (2004). For the plastid datasets, “informative” microstructural characters (i.e. insertion-deletions, gaps; simple sequence repeats, SSRs) were coded following Simmons & Ochoterena (2000) and Ochoterena (2009). We excluded one poly-T/A string of uncertain length homology in *atpB-rbcL* (positions 382--404 in the aligned dataset) and series of short inversions (in *atpB-rbcL* a 8-bp segment, positions 56447--56454 of *Anitrhea chinensis* chloroplast genome, GenBank accession: MK102723; and in *rps16* a 6-bp segment, 5628-5633 positions of *A. chinensis* chloroplast genome, GenBank accession: MK102723). We utilized Gblocks v.091b (Castresana, 2000) for alignment curation with relaxed conditions: the minimum number of sequences for a conserved position and flank position were half the number of sequences +1, the maximum number of contiguous non-conserved positions was 8, the minimum length of a block was 5 and the allowed gap positions was set to half.

PartitionFinder v.2.1.1 (Lanfear *et al.*, 2016) was used to determine optimal partitioning strategy of the concatenated dataset according to the Bayesian Information Criterion (BIC; Schwarz, 1978). The estimated best partitioning scheme was ETS+ITS and *atpB-rbcL+rps16+trnT-F*, referred to as nuclear and plastid partition in the succeeding text. The General Time Reversible model of sequence evolution (Yang, 1994) was selected for both data partitions, with addition of invariant sites and gamma distribution rates across sites for the nuclear partition, and with gamma distributed rate variation among sites for the plastid partition. Phylogenetic analyses of the individual partitions were conducted, as described below, to check for topological incongruences.

Phylogenetic inference

Phylogenetic reconstructions were carried out using Bayesian Inference (BI), maximum likelihood (ML), and maximum parsimony (MP). BI was conducted using MrBayes v.3.2.6 (Ronquist *et al.*, 2012) on the CIPRES platform (Miller, Pfeiffer & Schwartz, 2010). The analyses comprised two simultaneous independent runs of four Markov chain Monte Carlo (MCMC) for 50 million generations with tree sampling every 1000 generations. Partitions were unlinked to allow each partition to have its own set of parameters. We excluded the initial 50% of the sampled trees as burn-in to obtain the majority-rule consensus tree. To test for convergence, posterior samples of MCMC runs were inspected with Tracer v.1.7.1 (Rambaut *et al.*, 2018) and RWTY (Warren, Geneva & Lanfear, 2017). ML analyses were implemented using RAxML v.8.2 (Stamatakis, 2014) with the GTRGAMMA+I model for the nucleotide partitions and uncorrected BIN model for the microstructural characters. The ML tree was obtained from 1000 search replicates and bootstrap support values were calculated with 10 000 replicates. MP analysis was performed in PAUP v.4.0 (Swofford, 2002) with heuristic searches of 1000 random sequence addition replicates and the tree bisection-reconnection (TBR) and MULTREES options in effect. MP bootstrap values were estimated with 10 000 iterations, TBR branch swapping on, no retention of multiple trees per replicate and 5 random sequence addition. The proportion of bootstrap values ≥ 70% and posterior probabilities ≥ 0.95 were regarded as well-supported following Hillis & Bull (1993).

Results

Sequences characteristic

The concatenated dataset contained 73 terminals with 4109 positions including coded microstructural characters (available from J.G. Chavez). A summary of the alignment statistics is provided in Table 1. For the nuclear partition, 981 bp were used for the analyses after the exclusion of ambiguous sites, 272 bp were phylogenetically informative (PIC) that constitute 57.87% of the total PICs in the concatenated dataset. For the plastid partition, 3105 bp were used for the analyses, of which 175 bp were informative and constitute 37.23% of the total PICs in the concatenated dataset. The coding of microstructural characters for each plastid locus resulted in 23 positions, all are informative (Appendix 2): 3 gaps + 3 SSRs in *atpB-rbcL*, 2 gaps + 3 SSRs in *rps16* and 9 gaps + 3 SSRs in *trnT-F*.

Table 1. Matrix characteristics of each genetic region.

	ETS	**ITS**	***atpB-rbcL***	***rps16***	***trnT-F***
Number of sequences	52	71	70	54	71
Matrix length	476	845	988 + 6 mch[*]	821 + 5 mch	1888 + 12 mch
Number of included characters	386	595	708 + 6 mch	721 + 5 mch	1676 + 12 mch
Number of informative characters	111	161	36 + 6 mch	53 + 5 mch	86 + 12 mch

[*] mch= microstructural characters (i.e., gaps and simple sequence repeats)

Phylogenetic Analyses

Phylogenetic trees estimated using BI, ML and MP are highly congruent with no supported topological conflicts. Analyses of the independent nuclear and plastid partitions (Appendix 3 & 4) resolved the early diverging lineages of Guettardeae, but provided limited resolutions of its core genera, viz. *Antirhea*, *Bobea* Gaudich., *Chomelia* Jacq., *Guettarda*, *Malanea* Aubl., *Neolaugeria* Nicolson*, Ottoschmidtia* Urb., *Pittoniotis* Griseb., *Stenostomum* C.F.Gaertn*.*, *Timonius*, *Tinadendron* (Achille *et al.*, 2006). The MP analysis of the concatenated dataset recovered 17816 most parsimonious trees of 1799 steps. The strict consensus of these trees had a consistency index (CI) of 0.6623 and a retention index (RI) of 0.7240. Figure 1 shows the Bayesian consensus tree of the concatenated data with BI posterior probabilities (PP), ML (MLBS), and MP (MPBS) bootstrap support values.

Guettardeae *s.l.* is moderately supported by BI and received high support from ML and MP (PP= 0.94, MLBS= 84, MPBS= 79). The tribe was resolved into four well-supported principal clades (Fig. 1): A) *Rogiera* Planch. (PP= 1, MLBS= 100, MPBS= 100), B) *Machaonia* Standl. + *Neoblakea* Standl. (PP= 1, MLBS= 100, MPBS= 100), C) *Arachnothryx* Planch. + *Gonzalagunia* Ruiz & Pav. (PP= 1, MLBS= 100, MPBS= 100) and D) the core Guettardeae genera (PP= 1, MLBS= 99, MPBS= 98). The overall topology of core Guettardeae (Achille *et al.*, 2006) is partially resolved, with Neotropical and Hawaiian taxa unresolved in a polytomy, followed by *Chomelia obtusa* as sister to a well-supported PD clade (PP= 1, MLBS= 86, MPBS= 88).

Within the PD clade, the sampled species of *Antirhea* are resolved in three distinct clades: 1) *Antirhea* I (PP= 1, MLBS=98, MPBS= 99), containing accessions of subgenus *Antirhea* (*A. borbonica*, *A. madagascariensis* Chaw), 2) *Antirhea* II (PP= 1, MPBS= 77, MLBS= 71), which includes subgenus *Mesocarpa* represented here by two species (*A. megacarpa*, *A. smithii*) and New Caledonian *Guettarda*, and 3) *Antirhea* III (PP= 1, MLBS= 72), that is formed by representatives of subgenus *Guettardella*. Apart from this, both species of the New Caledonian endemic *Tinadendron* are placed in a well-supported clade (PP=1, MLBS= 99, MPBS= 98). *Timonius platycarpus* Montrouz., indicated as "*Gea"* in Fig. 1 (based on F. Achille's annotations on herbarium materials), is placed as sister to *Tinadendron* with strong support in BI, but low in ML and MP (PP= 1, MLBS= 69, MPBS= 57). On the other hand, the remaining species of *Timonius* are recovered within a strongly supported clade (PP= 1, MLBS= 94, MPBS= 92).

Discussion

The phylogenetic evidence presented here corroborates previous findings on the unnaturalness of *Antirhea sensu* Chaw & Darwin (1992) (Achille *et al.*, 2006; Manns & Bremer, 2010), and confirms the "Paleotropical dioecious" (PD) clade (Achille *et al.*, 2006). Considering a more comprehensive species sampling and an extended molecular dataset, our retrieval of the PD clade provided a more enhanced resolution compared to Achille *et al.* (2006). Since the phylogeny and taxonomy of the PD clade is elaborated in Achille *et al.* (2006), and partly in Achille (2006), the relationships among its genera will not be discussed again. Instead, we will focus on the status of *Antirhea* as indicated by our newly produced phylogenetic evidence.

In spite of the current consensus to restrict *Antirhea* to the Paleotropics, our data reiterate former assumptions that the genus remains polyphyletic even in its narrower circumscription (Achille *et al.*, 2006; Manns & Bremer, 2010). In contrast to Achille *et al.* (2006), our phylogenetic analyses reveal three well-supported clades of *Antirhea* (Fig. 1). These three clades coincide with the subgeneric classification proposed by Chaw & Darwin (1992). However, the sister-group relationships of *Antirhea* II with "*Gea*" + *Tinadendron* (PP= 0.78), and *Antirhea* III with *Timonius platycarpus* ("*Gea*") + *Tinadendron* + *Antirhea* II (PP= 0.83) are poorly supported. *Antirhea* I, instead, is retrieved as sister to the rest of the PD clade with high support (PP= 1, MLBS= 86, MPBS= 88; Fig. 1).

Re-delimitation of Antirhea

The well-supported placement of *Antirhea* I as sister to the rest of the PD clade indicates two options on how to render *Antirhea* monophyletic. One option is to adopt a wide concept of *Antirhea* that is equivalent to the entire PD clade (i.e., including "*Gea*", New Caledonian *Guettarda*, *Timonius*, and *Tinadendron*). This alternative makes *Antirhea* a very heterogeneous group from a morphological standpoint, and would require the transfer of a large number of species. The second option is to retain the three well-supported clades as distinct genera and adopt a narrower concept of *Antirhea*. Our detailed phylogenetic sampling associated with morphology and geographical distribution provides sufficient evidence to favor the latter option, which was also preferred by Achille *et al.* (2006). This division of *Antirhea s.l.* into several genera relies on consistent combination of morphological characters rather than homoplasious features, and presents a more stable classification of the group. The three clades are discussed below.

Antirhea I clade

The *Antirhea* I clade is restricted to *Antirhea* species native to the Madagascan region (Fig. 2), and contains the type species *A. borbonica*. Another Mascarene species, *A. bifurcata* (Desr.) Hook.f., can be unambiguously assigned to this clade based on morphology (see discussion below), but was not included in the molecular study due to the lack of success in extracting DNA from herbarium materials. The most prominent characters of the taxa in *Antirhea* I are the ternate or opposite leaves, monomorphic staminate and pistillate inflorescences and thinly fleshy drupes with two to three fused pyrenes (Fig. 3 a-c). Species in *Antirhea* I also possess small pale elongated or circular clusters containing crystal sand over the abaxial surface of leaf venations (Chaw & Darwin, 1992), which reflect light (Verdcourt, 1983).

The placement of *Antirhea* I clade as a distinct segregate of *Antirhea* II and III clades clearly support Jansen's (1984) decision to limit *Antirhea* to the Madagascan region. However, Jansen's concept of *Antirhea* indicated that it is hermaphroditic, while several authors (Chaw & Darwin, 1992, Achille, 2006; Achille *et al.*, 2006), as well as our observations do not support the presence of this condition, since all species from the Madagascan region are dioecious. This misinterpretation of Jansen (1984) is perhaps due to the plasticity in sex expression of *A. borbonica*. Litrico, Pailler & Thompson (2005) demonstrated that *A. borbonica* exhibits 'leaky' dioecy, indicating that staminate individuals have tendency to bear fruits as a mechanism for habitat colonization. Overall in the PD clade, this phenomenon was only observed in *Antirhea* I and some *Timonius* species occurring on nutrient-depauperate habitats in the Philippines (J.G. Chavez *et al.*, 'unpubl. data'), but not in the clades *Antirhea* II and III.

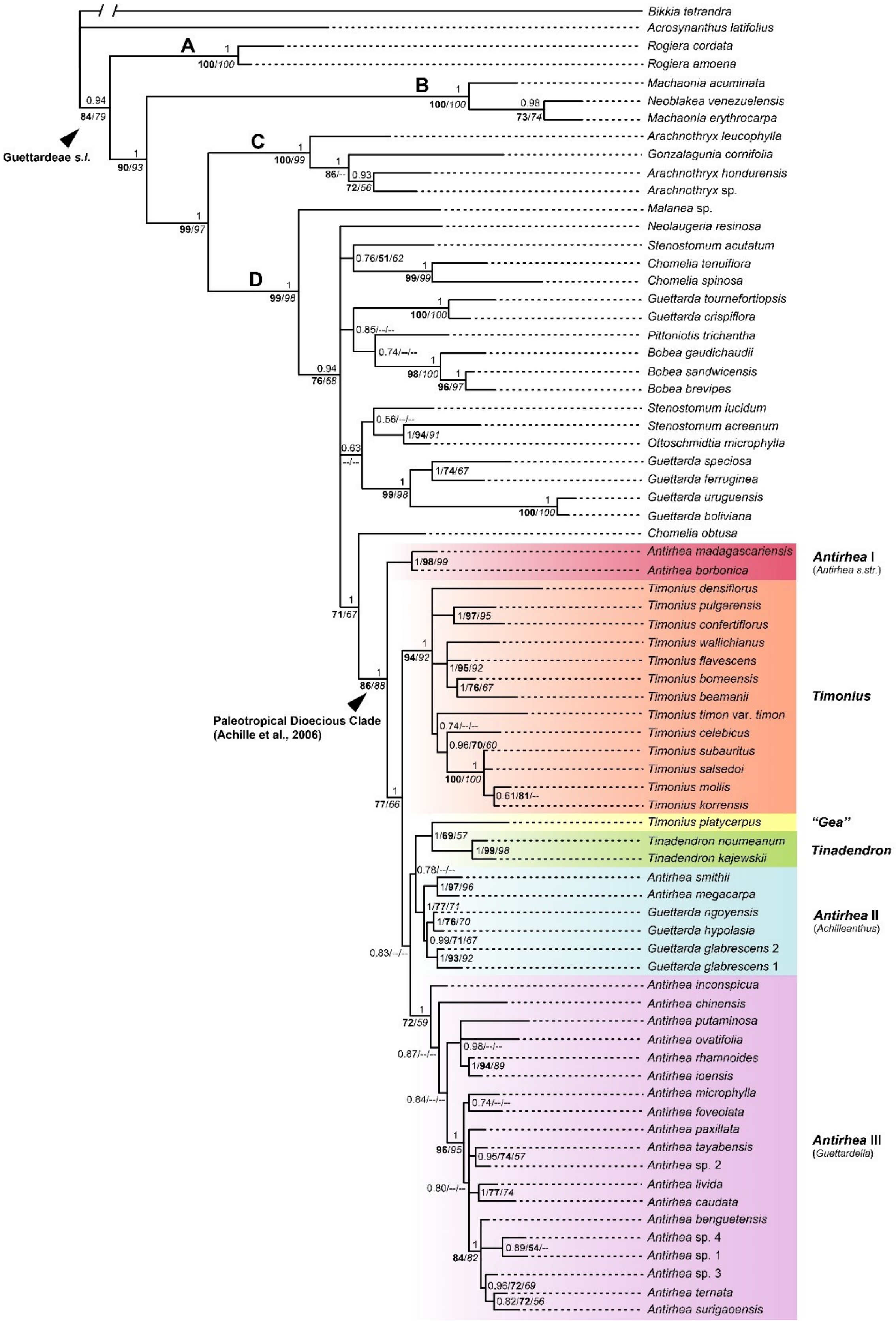

Figure 1. Phylogeny of *Antirhea* within the Guettardeae. Majority-rule consensus tree inferred from Bayesian inference of the concatenated dataset. Numbers on nodes indicate Bayesian posterior probabilities, maximum-likelihood bootstrap values (boldface), and parsimony bootstrap values (italics).

Antirhea II clade

The *Antirhea* II clade contains accessions of *Antirhea* subgenus *Mesocarpa* and three New Caledonian species of *Guettarda*. The placement of the sampled New Caledonian *Guettarda* in this clade is not surprising (Fig. 1), since Achille *et al.* (2006) reported that *Guettarda* species from the region may either belong to subgenus *Mesocarpa* or subgenus *Guettardella*. However, all we may treat here are those that are included in our study; because the revisionary work of New Caledonian *Guettarda* may still be ongoing, and that some species may even belong to a yet undescribed genus (Achille, 2006; Pillon, Barrabé & Buerki, 2017) that is represented here by *Timonius platycarpus* ("*Gea"*, Fig. 1). Species within *Antirhea* II are geographically limited to the Lesser Sunda Islands, Papuasia and the Southwestern Pacific (Fig. 2), and may be distinguished from *Antirhea* I and III by the presence of large drupes (>15 mm long) with sclerenchymatous mesocarp bearing cavities that are almost equivalent to the number of locules (6 to 16) in the putamen (Fig. 3f).

Chaw & Darwin (1992) included *Timonius anodon* (Miq.) Boerl. in their treatment of subgenus *Mesocarpa* based solely on the imbricate corolla lobes of its staminate type material. Although the three clades of *Antirhea* recovered in this study exhibit the same type of corolla aestivation, their taxonomic conclusion seems not appropriate. It is important to note that although *Timonius* is recognized as having valvate corolla aestivation (Achille *et al.*, 2006; Darwin, 1994, 2010), some species exhibit corolla lobe margins that are pressed together and are thinly overlapping giving them an imbricate appearance ("interlocking-type") (J.G. Chavez, *pers. obs.*; also see Wong, 1988; Darwin, 2010). Furthermore, Jansen (1984) recognized that the type of fruit (drupes with fused pyrenes vs. drupes with separate multiple pyrenes) is essential in assigning generic placements of Paleotropical Guettardeae. Our observations of fruiting materials of *T. anodon* (*Endert 1553*, L; *Petrus & Patrick SAN 90641*, L) which are obviously unknown to Chaw & Darwin (1992), indicated that the drupes bear multiple free pyrenes, suggesting that it should be retained in *Timonius*.

Antirhea III clade

This clade includes the majority of *Antirhea* accessions in our study and represents subgenus *Guettardella*. Within the *Antirhea* III clade, we were able to retrieve two well-supported subclades: 1) the New Caledonian clade (PP=1, MLBS= 94, MPBS=89) and 2) the Philippine clade (PP=1, MLBS= 96, MPBS=95). However, we did not recognize shared apomorphic characters that will distinguish these two subgroups, also because morphological characters that differentiate species in subgenus *Guettardella* frequently show reversals (Chaw & Darwin, 1992). Nonetheless, the retrieval of *Antirhea* III as a distinct clade clearly demonstrates the generic distinctiveness of Bentham's (1852) *Guettardella* that was rejected by Hooker (1873) and more recently by Chaw & Darwin (1992), but was at least equivocally accepted by Jansen (1984). Morphologically, members of this clade are characterized by the combination of narrow branchlets (≤ 2 mm broad at apex), dimorphic staminate and pistillate inflorescences and fleshy or spongy fruits bearing three to 11 fused pyrenes (Fig. 3 g-j).

In Jansen's (1984) concept of *Guettardella*, *A. megacarpa* Merr. & L.M.Perry and *A. smithii* (Fosberg) Merr. & L.M.Perry, as well as *A. novobrittaniensis* (M.E.Jansen) Chaw and *A. schmutzii* (M.E.Jansen) Chaw were included in the genus. Although our attempts to obtain molecular data from the latter two species were futile, their fruits are similar to those of *Antirhea* II, thus are excluded from our concept of *Guettardella*.

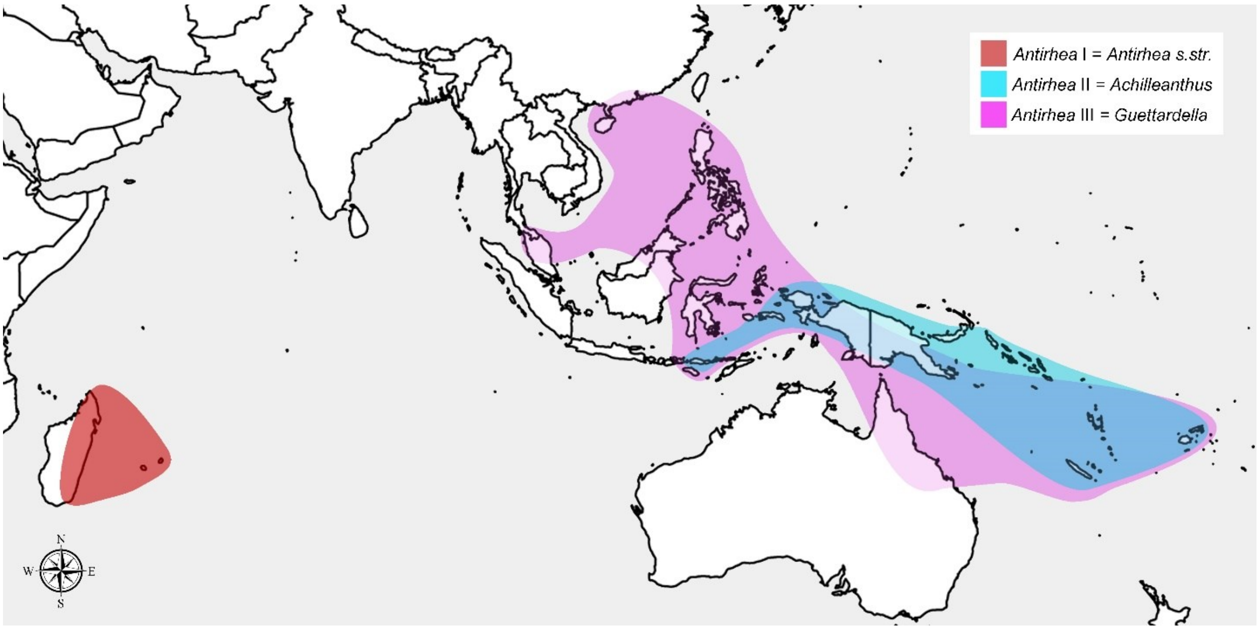

Figure 2. Geographical distribution of the three *Antirhea* clades presented in the study.

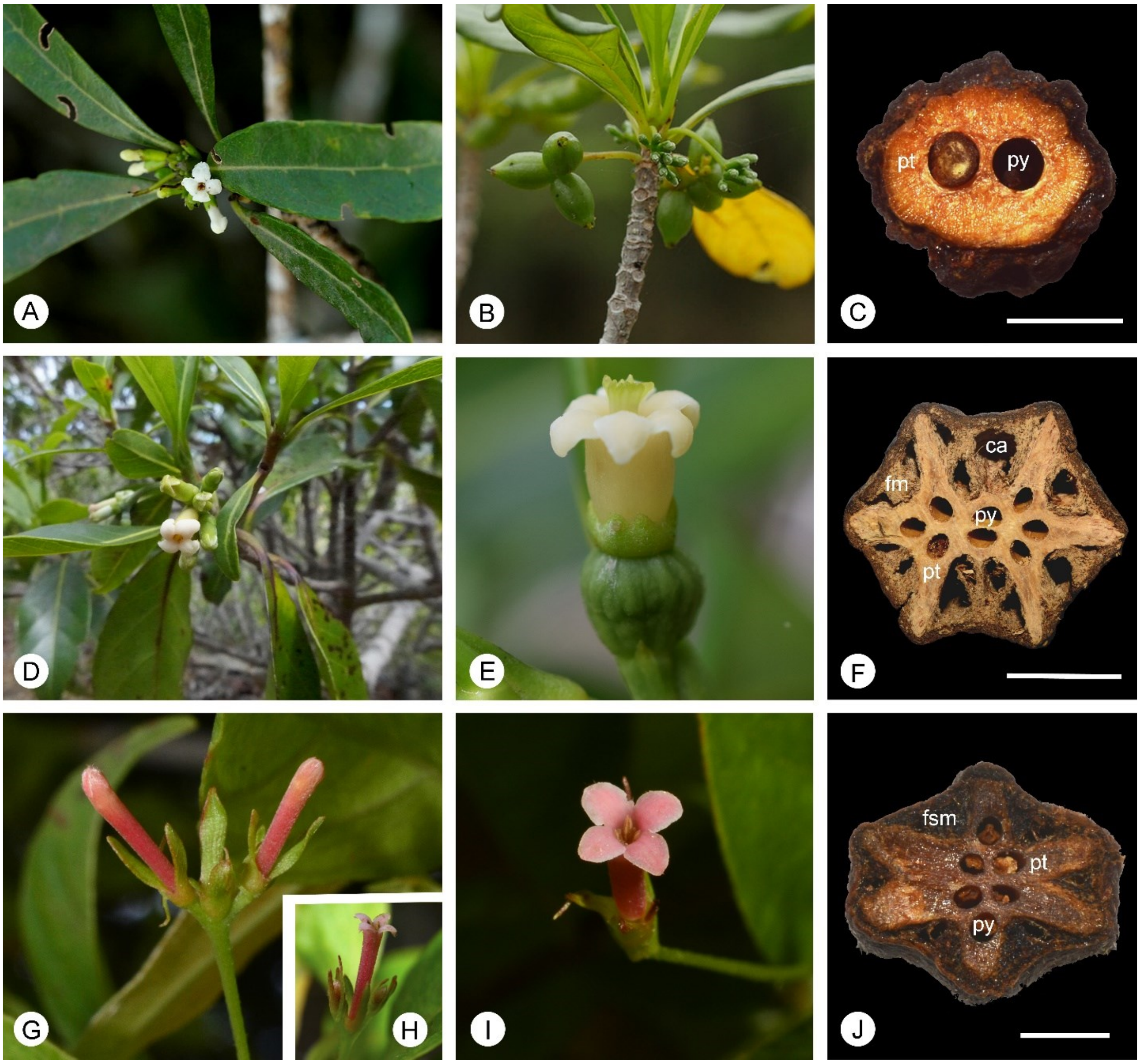

Figure 3. Representative taxa of the three *Antirhea* clades presented in the study. – *Antirhea* I: *Antirhea borbonica* var. *borbonica*, **A**, branch with staminate inflorescence; **B**, branch with infructescence; and *Antirhea borbonica* var. *duplidivisa*, **C**, fruit in cross-section (*Capuron SF18176*). – *Antirhea* II: *Guettarda glabrescens*, **D**, branch with staminate inflorescence; **E**, pistillate flower; and *Antirhea megacarpa*, **F**, fruit in cross-section (*Booer's collectors BSIP7732*). – *Antirhea* III: *Antirhea caudata*, **G**, staminate inflorescence in bud; **H**, staminate flower; **I**, pistillate flower; and **J**, fruit in cross-section (*Dimatatac and Pineda RTJ015*). Scale bars: C, J = 2 mm; F = 1 cm. Legend: ca: cavity; fm: fibrous mesocarp; fsm: fleshy to spongy mesocarp; pu: putamen; py: pyrene. Photographs by: A-B: Max Seyfried; C, F-J: Jayson G. Chavez; D: Ulrich Meve; E: Gildas Gâteblé.

Taxonomic conclusions

The molecular phylogenetic analysis, along with morphological and geographical evidences detailed above, clearly indicate the need to re-circumscribe *Antirhea*. We are convinced that the three clades of *Antirhea* reflect a more natural concept, and so are worthy to be recognized as distinct genera. Here, we propose to restrict *Antirhea* to (Madagascar and the Mascarenes, erect the new genus *Achilleanthus* to accommodate the *Antirhea* II clade, and incorporate the 29 species of subgenus *Guettardella* into the resurrected genus *Guettardella* (Fig. 4). Brief description and diagnosis of each genus are provided below, the necessary new combinations are presented, and lectotypifications are included and discussed.

Achilleanthus J.G.Chavez, **gen. nov., ined.**
Type species: *A. megacarpus* (Merr. & L.M.Perry) J.G.Chavez (*Basionym*: *Antirhea megacarpa* Merr. & L.M.Perry)

Diagnosis: *Achilleanthus* is distinct from all Paleotropical dioecious Guettardeae with fused pyrenes *viz. Antirhea*, *Guettardella*, and *Tinadendron* by the combination of its dimorphic inflorescences, large fibrous fruits, presence of cavities in the well-developed mesocarp, and irregularly ribbed putamen with 6 to 16 locules.

Dioecious shrubs or trees; branchlets ≥ 2 mm broad toward apex. *Stipules* imbricate, triangular to lanceolate, occasionally twisted at apex. Leaves opposite, rarely ternate, subsessile to petiolate; lamina elliptic to ovate or obovate, chartaceous to (sub-) coriaceous; apex acute to acuminate; base acute to obtuse or subcordate; secondary veins 5-- 12 on each side of the midrib; domatia occasionally present. *Staminate inflorescences* axillary, dichasial, 3-- 31 flowered; peduncle glabrous to densely strigose; bracts or bracteoles absent or triangular; flowers secund, subsessile. Calyx cupular, truncate or undulate to 4-lobed, usually ruptured by expanding corolla, moderately to densely strigose outside. Corolla salverform or infundibular, white to cream-colored, 4-lobed, imbricate, densely strigose outside. Stamens 4, included, anthers (sub-)sessile, linear. Pistillodia bifid. *Pistillate inflorescences* axillary, solitary, pedunculate, rarely sessile; peduncle moderately to densely strigose; bracts triangular. Calyx cupular, truncate or 4- to 6- lobed. Corolla infundibular, white to yellowish, 4- or 5- lobed, imbricate, densely strigose outside. Hypanthium globose to cylindrical. *Fruits* globose, ellipsoid or prolate, 15--45 mm long, crowned by persistent calyx and occasionally by the

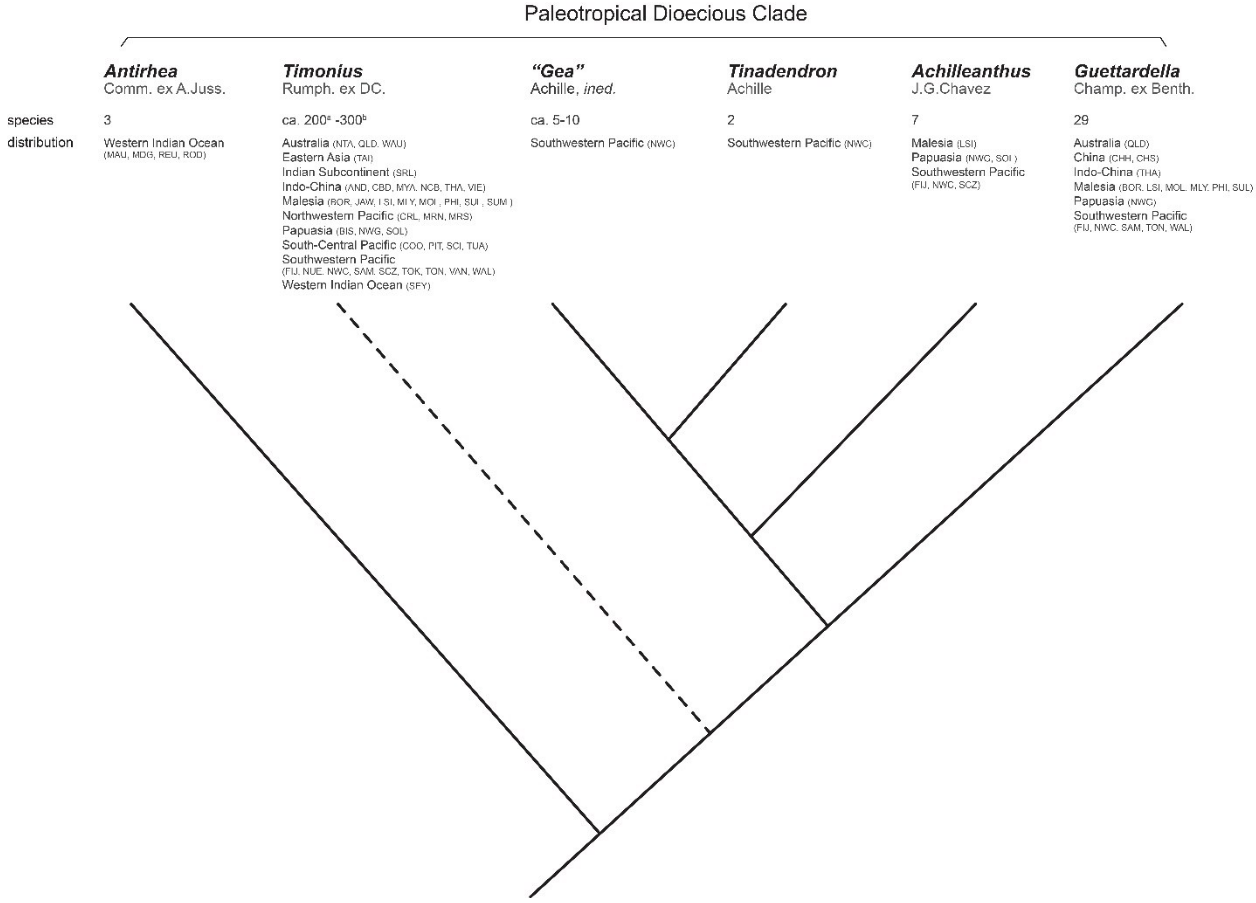

Figure 4. Simplified phylogeny of the PD clade as presented here. Given are the generic names, number of species per genus, and geographical distribution. Species diversity of *Timonius* is based on the estimates of (a) Darwin (2010), and (b) Chen, Tan & Wong (2015), and its monophyly is currently being evaluated. Geographical codes followed TDWG3 (Brummitt, 2001).

expanded disc; mesocarp fibrous, cavities present; pyrenes 6--16, fused forming an irregularly ribbed putamen.

Etymology: The name of the new genus is dedicated to Dr. Frédéric Achille of the Museum of Natural History Paris, in recognition of his contributions that provided significant insights regarding the systematics of the tribe Guettardeae.

Distribution: The genus *Achilleanthus* occurs in Fiji, Indonesia (Papua and Lesser Sunda Islands), New Caledonia, Papua New Guinea and Solomon Islands.

Notes: The species diversity of *Achilleanthus* is projected to increase in the near future. Several species of New Caledonian *Guettarda* fits within the morphological features of *Achilleanthus* (e.g., *Guettarda balansana* Baill., *G. baladensis* Guillaumin, *G. eximia* Baill, *G. heterosepala* Guillaumin, *G. splendens* Baill., *G. wagapensis* Guillaumin); however, the proposal of further nomenclatural changes in this group of species is left for authors working on the revision of the region's *Guettarda*.

1. ***Achilleanthus glabrescens*** (Schltr.) J.G.Chavez, Liede & Meve, **comb. nov., ined.** (Fig. 3 G-E)

   Basionym: ***Timonius glabrescens*** Schltr., Bot. Jahrb. Syst. 39: 257 (1906). ≡ *Guettarda glabrescens* (Schltr.) Guillaumin, Arch. Bot. Mém. 3(5): 17 (1930). *Type*: NEW CALEDONIA. Ngoye, 09 Nov. 1902 (♂), *F.R.R. Schlechter 15256* (**lectotype** HBG HBG520964, **designated here**; isolectotypes BR BR530480, K K000763509, L L0000390, M M0189508, P P00645390).

   Notes: Timonius glabrescens was described based on the collection *F.R.R. Schlechter 15256* (Schlechter, 1906). The holotype at the General Herbarium of B was destroyed in 1943, but six duplicate specimens have been located. Among these, the HBG duplicate (HBG520964) is selected as the lectotype because it possesses more reproductive branches.

2. ***Achilleanthus hypolasius*** (Baill.) J.G.Chavez, **comb. nov., ined.**

   Basionym: ***Guettarda hypolasia*** Baill., Adansonia 12: 240 (1879). *Type*: NEW CALEDONIA. "entre St. Louis et Ounia" (Baillon 1879: 241), 14 Jan. 1869 (♂), *B. Balansa 1138* (**lectotype** P P00645397, **designated here**; isolectotypes K K000763449, MPU MPU021792, P P00645396, P00645398, P00645399).

   Notes: Two syntypes were indicated in the protologue of *Guettarda hypolasia* (Baillon, 1879), *J. Pancher s.n.* and *B. Balansa 1138*; duplicates of both collections are still existent. The collection *J. Pancher s.n.* is from a fruiting individual, but only one of the two duplicates at the Paris herbarium (P) possesses fruit (P00645400). The widely distributed collection *B. Balansa 1138*, on the other hand, is from a flowering staminate individual, and all of the six duplicates are more complete. Among the available duplicates of this collection, the specimen at P (P00645397) is chosen as the lectotype because it bears more flower buds and has an open flower.

3. ***Achilleanthus megacarpus*** (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** (Fig. 3 F) *Basionym*: *Antirhea megacarpa* Merr. & L.M.Perry, J. Arnold Arbor. 26: 234 (1845). ≡ *Guettardella megacarpa* (Merr. & L.M.Perry) M.E.Jansen, Blumea 29(2): 577 (1984). *Type*: NEW GUINEA. Ihu, Vailala River, 12 Feb. 1926 (♀), *L.J. Brass 946* (holotype A A00312892, isotypes BM BM000945300, BRI BRI-AQ0129861, K K000763434).

= *Guettardella erythrocarpa* M.E.Jansen, Blumea 29(2): 574 (1984). *Type*: NEW GUINEA. Monokwari, 27 May 1957 (♀), *C. Versteegh BW 4759* (holotype L L0064551; isotypes A A00312859, CANB CANB86606).

= *Guettardella oriomonense* M.E.Jansen, Blumea 29(2): 582 (1984). *Type*: NEW GUINEA. Western District, Oriemo River, 21 Jan. 1959 (♀), *K.J. White & E. Gray N.G.F. 10439* (holotype L L0443079, isotypes A A00312866, BRI BRI-AQ0129888, CANB CANB68710, SING SING0062101).

= *Guettardella pachyphylla* M.E.Jansen, Blumea 29(2): 584 (1984). *Type*: NEW GUINEA. Madang, Gogol River, 17 Sept. 1969 (♀), *P. Katik N.G.F. 46553* (holotype L L0064561; isotype BRI BRI-AQ0129702).

= *Guettardella solomonense* M.E.Jansen, Blumea 29(2): 586 (1984). *Type*: SOLOMON ISLANDS. East Santa Cruz, 20 Oct. 1969 (♀), *R. Mauriasi et al. B.S.I.P. 17719* (holotype L L0000398).

4. ***Achilleanthus ngoyensis*** (Schltr.) J.G.Chavez, Liede & Meve, **comb. nov., ined.** *Basionym*: ***Timonius ngoyensis*** Schltr., Bot. Jahrb. Syst. 39: 258 (1906). ≡ *Guettarda ngoyensis* (Schltr.) Guillaumin, Arch. Bot. Mém. 3(5): 17 (1930). *Type*: NEW CALEDONIA. Ngoye, 06 Nov. 1902 (♂), *F.R.R. Schlechter 15230* (**lectotype** L L0000394, **designated here**; isolectotypes AMD AMD0000184, BR BR532716, GH GH00312923, HBG HBG520962, K K000763508, L L0000393, M M0189506, S S0510746).

Notes: The description of *Timonius ngoyensis* is based on the collection *F.R.R. Schlechter 15230* (Schlechter, 1906). The holotype at B was destroyed in 1943, but several duplicates of the collection *F.R.R. Schlechter 15230* have been found. Among these, one of the duplicates at L (L0000394) is designated as the lectotype for *T. ngoyensis* because the floral structures are still in good condition.

5. ***Achilleanthus novobrittaniensis*** (M.E.Jansen) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Guettardella novobrittaniense*** M.E.Jansen, Blumea 29(2): 580 (1984). ≡ *Antirhea novobritanniensis* (M.E.Jansen) Chaw, Tulane Stud. Zool. & Bot. 28(2): 64 (1992). *Type*: NEW GUINEA. South New Britain, Eliak Creek, 06 May 1958 (♀), *K.J. White N.G.F. 10058* (holotype L L0064557, isotypes A A00312864).

6. ***Achilleanthus schmutzii*** (M.E.Jansen) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Guettardella schmutzii*** M.E.Jansen, Blumea 29(2): 585 (1984). ≡ *Antirhea schmutzii* (M.E.Jansen) Chaw, Tulane Stud. Zool. & Bot. 28(2): 65 (1992). *Type*: INDONESIA. Lesser Sunda Islands, West Flores, Manggarai, Paku, Apr. 1981 (♀), *E. Schmutz 4820* (holotype L L0000397).

7. ***Achilleanthus smithii*** (Fosberg) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Timonius smithii*** Fosberg, Sargentia 1: 121 (1942). ≡ *Antirhea smithii* (Fosberg) Merr. & L.M. Perry, J. Arnold Arbor. 26: 233 (1945). ≡ *Guettardella smithii* (Fosberg) M.E.Jansen, Blumea 29(2): 585 (1984). *Type*: FIJI. Moala, 20-24 Mar. 1934 (♀), *A.C. Smith 1347* (holotype US US00138435, isotypes GH GH00312922, K K000763426, NY NY00113425, P P00698853, S SG6110, WIS WIS00001041MAD).

Antirhea Comm. ex Juss., Gen. Pl.: 204 (1789).

Type species: *A. borbonica* J.F.Gmel., Syst. Nat. ed. 13[bis]: 244 (1791).

Diagnostic characters: *Antirhea s.s.* can easily be distinguished by the presence of circular or elongated crystal-containing cell clusters over the abaxial surface of leaf venation, valvate stipules, monomorphic staminate and pistillate inflorescences (3—65 flowered), fruits with underdeveloped mesocarp, and 2 or 3 (-4) locular putamina.

Dioecious shrubs or trees, some staminate individuals bear fruits; branchlets ≤ 4 mm broad toward apex. *Stipules* valvate, lanceolate to ovate. *Leaves* ternate, rarely opposite, petiolate; lamina lanceolate to obovate, chartaceous to coriaceous; apex acute to acuminate, rarely rounded; base acute to cuneate; secondary veins 2--7 on each side of the midrib; domatia rarely absent. *Staminate inflorescences* axillary, simple to compound dichasia, 3 --65 flowered; peduncles glabrous to moderately strigose; bracts or bracteoles scale-like to triangular; flowers secund, subsessile. Calyx cylindrical to cupular, 4-lobed, sparsely strigose outside. Corolla salverform, white, 4- or 5- lobed, imbricate, glabrous to sparsely strigose outside. Stamens 4 or 5, included, anthers (sub-)sessile, linear. Pistillodia bifid. *Pistillate inflorescences* similar to the staminate inflorescences. Corolla infundibular, white, 4- or 5- lobed, imbricate, glabrous or sparsely to moderately strigose outside. Hypanthium (sub-)cylindrical. *Fruits* cylindric, ellipsoid to ovoid, 1.5--10 mm long, crowned by persistent calyx; mesocarp thinly fleshy; pyrenes 2 or 3 (4), fused, forming a smooth putamen.

Distribution: As here delimited, *Antirhea* is restricted to Madagascar and the Mascarene Islands.

1. ***Antirhea bifurcata*** (Desr.) Hook.f., in Benth. & Hook.f. Gen. Pl. 2: 100 (1873). ≡ *Malanea bifurcata* Desr. in J.B.A.M.de Lamarck, Encycl. 3: 688 (1792). ≡ *Stenostomum bifurcatum* (Desr.) DC., Prodr. 4: 460 (1830). *Type*: THE MASCARENES (geographical provenance corrected by Verdcourt, 1983: 571). s.loc., s.d. (♀), *M. Dupuy s.n.* (holotype P-LA *n.v.*, isotype P-JU 9792 *n.v.*).

   Notes: In the protologue of *Malanea bifurcata*, Desrousseaux (1792) speculated that the gathering sent by Dupuy to Lamarck came from the Antilles (West Indies). Desrousseaux's (1792) presumption on the type locality of *M. bifurcata* briefly explains the principal area where confusion exists regarding its concept (Grisebach, 1861) and geographical provenance (Hooker, 1873), which have been well-explained by Chaw & Darwin (1992: 53). Nevertheless, the error on the original type locality of *M. bifurcata* was corrected by Verdcourt (1983: 571, 1989: 121) stating that the type specimen of Dupuy sent to Lamarck was clearly wrongly localized to the Antilles and is actually from Mauritius.

= *Tournefortia bifida* Lam., Tabl. Encycl. 1: 417 (1792). = *Antirhea bifida* (Lam.) I.M.Johnst., J. Arnold Arbor. 16: 166 (1935). *Type*: MAURITIUS. s.loc., s.d. (♂), *P. Commerson s.n.* (holotype P-LA *n.v.*, isotype G G00014724).

= *Antirhea frangulacea* DC., Prodr. 4: 459. 1830. *Type*: MAURITIUS. *s.loc.*, *s.d.* (♀), *F.W. Sieber 59* (lectotype G G00190719, designated by Chaw & Darwin (1992: 53), isolectotypes E E00193653, H H1546091, H1633571, HAL HAL0114213, K K000412143, L L2895372, L2895373, LECB LECB 0001523, MEL MEL104991, MO, NY NY00130839, P P00553248, REG REG000879, TUB TUB004580).

2. ***Antirhea borbonica*** J.F.Gmel., Syst. Nat. ed. 13[bis]: 244(1791).

2.a. ***Antirhea borbonica*** var. ***borbonica***. ≡ *Malanea verticillata* Desr., in Lam. Encycl. 3: 688 (1792). ≡ *Antirhea dioica* Bory ex DC., Prodr. 4: 459 (1830). ≡ *Antirhea verticillata* (Lam.) DC., Prodr. 4: 459 (1830). ≡ *Guettarda antirhoea* D.Dietr., Syn. Pl. 1: 788 (1839). *Type*: REUNION. s.loc., s.d. (♀), *Commerson s.n.* (lectotype P P00553237 designated by Chaw & Darwin (1992: 55)). (Fig. 3 A-B).

= *Guettarda acuminata* Sieber ex DC., Prodr. 4: 460. 1830. *pro. syn.* = *Antirhea dioica* var. *acuminata* DC., Prodr. 4: 460. 1830. *Type*: MAURITIUS. s.loc., s.d. (♀), *F.W. Sieber Fl. maurit. 60* (lectotype G G00190721, designated by Chaw & Darwin (1992: 55), isolectotypes E E00193652, GOET GOET010164, HAL HAL091758, K K000412141, L L0000083, L0000084, MEL MEL104993, NY NY00130837, P P03827978, REG REG000877, TUB TUB004579).

= *Guettarda barbinervis* Sieber ex DC., Prodr. 4: 460. 1830. *pro. syn.* = *Antirhea dioica* var. *barbinervis* (Sieber ex DC.) DC. Prodr. 4: 460. 1830. *Type*: MAURITIUS. s.loc., s.d. (♂), *F.W. Sieber Fl. maurit. 61* (**lectotype** HAL HAL0138763, **designated here (or perhaps holotype)**; isolectotypes E E00193651, G G00190722, GOET GOET010165, H H1633572, K K000412137, L L0000087, L0000088, MEL 104994, MEL104995, MO MO391430, NY NY00130835, REG REG000878).

Notes: In the protologue of *Guettarda barbinervis*, Chamisso & Schlechtendal (1829) mentioned the gathering *Sieb. plant. exsic. Ins. Mauritii n. 61*. Several duplicates of this gathering are extant, and it is uncertain whether Chamisso & Schlechtendal (1829) based the description on the HAL duplicate alone or have used the other duplicates that may have been distributed afterwards. Therefore, the duplicate kept at HAL is designated here as the lectotype or perhaps the holotype of *G. barbinervis*.

2.b. ***Antirhea borbonica*** var. ***duplidivisa*** Chaw, Tulane Stud. Zool. Bot. 25: 56 (1992). *Type*: MADAGASCAR. Est, Nord, Environs du Cap-Est, au Sud d'Antalaha, 19-21 Sept. 1967 (♀), *R. Capuron sub Service Forestier de Madagascar SF-27778* (holotype P P00093578, isotype TEF TEF000394). (Fig. 3 C).

3. ***Antirhea madagascariensis*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 57 (1992). *Type*: MADAGASCAR. Mananjary (Sakaitoloho), 26 Feb. 1954 (♀), *Service des Eaux et Forets de Madagsacar SF-9750* (holotype P P00093599, isotype P P00093800, TEF TEF000393).

Guettardella Champ. ex Benth., Hooker's J. Bot. Kew Gard. Misc. 4: 197 (1852).

Type species: ***G. chinensis*** Champ. ex Benth. (designated by Jansen, 1984: 565) (≡ *A. chinensis* Champ ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl.)

Diagnostic characters: *Guettardella* can be easily diagnosed by its narrow branchlets that are ≤ 2 mm broad at apex, dimorphic inflorescences, fleshy drupes that are 4--15 mm long and crowned by unequal-sized calyx lobes, and fused putamen with 4--11 locules.

Dioecious shrubs to trees; branchlets ≤ 2 mm broad toward apex. *Stipules* imbricate or valvate, triangular to lanceolate or ovate. *Leaves* opposite, rarely ternate, petiolate, rarely subsessile; lamina lanceolate to obovate, membranous to chartaceous, rarely subcoriaceous; apex acute to acuminate; base attenuate to rounded or truncate to subcordate; secondary veins 3--10 on each side of the midrib; domatia present (tuft of trichomes, pit- or dome- type, trichomatous pocket), rarely absent. *Staminate inflorescences* axillary, simple to compound dichasia, (2-) 3-- 146 flowered; peduncle strigose, hirtellous, villous or sericeous; bracts and bracteoles filiform or subulate, linear or lanceolate, rarely absent. Flowers secund, sessile to pedicellate. Calyx cupular, 3--5- lobed, rarely truncate, lobes often unequal in size, outer vestiture as in peduncle. Corolla salverform, white, yellow or pink, 3- or 4- lobed, imbricate, outer vestiture as in peduncle. Stamens 3 or 4, included, anthers (sub-)sessile, linear. Pistillodia filiform or bifid. *Pistillate inflorescences* axillary, simple dichasia, 1--19 flowered; peduncle vestiture as in staminate inflorescences; bracts or bracteoles as for the staminate inflorescences. Calyx and corolla as in staminate flowers. Hypanthium globose to ellipsoid. *Fruits* (sub-)globose, ellipsoid or obovoid, 4--15 mm long, crowned by persistent calyx; mesocarp fleshy or spongy, cavities absent; pyrenes 3-- 11, fused, forming a smooth or irregularly ribbed putamen.

Distribution: The genus *Guettardella*, as here defined, is distributed from southeastern China, Hainan Island, Hong Kong, southern Thailand, and Malesia, eastward to Melanesia, tropical Australia and Samoa. The primary center of diversity of *Guettardella* is the Philippines with 14 species.

1. ***Guettardella affinis*** (Zoll.) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Eriosolena affinis*** Zoll., Syst. Verz. Ind. Archip. 2: 116 (1854). ≡ *Antirhea affinis* (Zoll.) Chaw. Tulane Stud. Zool. & Bot. 28(2): 72 (1992). *Type*: INDONESIA. Flores Island, July 1847 (♂), *Zollinger 3209* (holotype P P01001835, isotype L L0064552).

2. ***Guettardella atropurpurea*** (Craib) M.E.Jansen, Blumea 29(2): 571 (1984). ≡ *Timonius atropurpureus* Craib, Fl. Siam. 2: 132 (1932). ≡ *Antirhea atropurpurea* (Craib) Chaw ex Wong, Kew Bull. 43: 493 (1988). *Type*: MALAYSIA. Langkawi, *s.d.* (sterile), *C. Curtis 2544* (lectotype SING n.v., designated by Wong (1988: 493) cf. Chaw & Darwin (1992: 74)).

3. ***Guettardella attenuata*** (Elmer) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Timonius attenuatus*** Elmer, Leafl. Philipp. Bot. 1: 34 (1906). ≡ *Antirhea attenuata* (Elmer) Chaw, Tulane Stud. Zool. & Bot. 28(2): 75 (1992). *Type*: PHILIPPINES. Luzon (Rizal, Bosoboso), Sept. 1904 (♀), *Ahern's collector sub F.B. 1867* (lectotype BO, designated by Chaw & Darwin (1992: 76), isolectotypes K K000763442, NY NY00133415, US US00138413).

4. ***Guettardella benguetensis*** (Elmer) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Timonius benguetensis*** Elmer, Leafl. Philipp. Bot. 1: 35 (1906). ≡ *Antirhea benguetensis* (Elmer) Valeton, Bull. Dép. Agric. Indes Néerl. 26: 32 (1909). *Type*:

PHILIPPINES. Luzon, Benguet, Twin Peaks, May 1904 (♀), *A.D.E. Elmer 6396* (**lectotype** PNH, **designated here**; isolectotypes: BO, G G00436805, K K000763546, P P00836646, NY NY00133416, US US00138415).

Notes: *Timonius benguetensis* is based on the gathering *A.D.E. Elmer 6396* (Elmer, 1906). It is assumed that pre-1945 Philippine type materials kept at the Herbarium of the Bureau of Science, Manila (now known as PNH) were destroyed during the Second World War (cf. Merrill, 1945). However, duplicates of *A.D.E. Elmer 6396* were located in various herbaria, including PNH. The PNH duplicate, which might have been repatriated from foreign herbaria (cf. Barcelona, 2005), is chosen as the lectotype because it shows some intact flowers.

5. ***Guettardella bombysia*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea bombysia*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 78 (1992). *Type*: PHILIPPINES. Palawan, Aborlan, Panacan, 18 May 1950 (♂), *M.D. Sulit Phil. Nat. Herb. 12400* also numbered *M.D. Sulit 3873* (holotype A A00312847, isotype L L0064544).

6. ***Guettardella buruana*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea buruana*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 79 (1992). *Type*: INDONESIA. Moluccas, Fakal, Boeroe, 30 July 1921 (♀), *L.J. Taxopeus 468* (holotype L L0064550).

7. ***Guettardella caudata*** M.E.Jansen, Blumea 29(2): 572 (1984). ≡ *Antirhea caudata* (M.E.Jansen) Chaw, Tulane Stud. Zool. & Bot. 28(2): 80 (1992). *Type*: PHILIPPINES. Palawan, Aborlan, Panacan, 10 May 1950 (♂), *M.D. Sulit Phil. Nat. Herb. 12315* also numbered *M.D. Sulit 3750* (**lectotype** L L0064547, **designated here**; isolectotypes A A00312851, K K000763440, L L0064546). (Fig. 3 G-J).

Notes: Jansen (1984) indicated the holotype of *Guettardella caudata* as *M.D. Sulit Phil. Nat. Herb. 12315* that is kept at L. However, there are two duplicates of the same gathering at L requiring the designation of a lectotype as there is no enough evidence to show which of these was used in the protologue. The specimen chosen as the lectotype of *Guettardella caudata*, L0064547, contains more reproductive branches.

8. **Guettardella chinensis** Champ. ex Benth., Hooker's J. Bot. Kew Gard. Misc. 4: 197 (1852). ≡ *Antirhea chinensis* (Champ. ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl., J. Linn. Soc., Bot. 23: 384 (1888). *Type*: HONG KONG. s.loc., s.d. (♀), *J.G. Champion 113* (**lectotype** K K000763445, **designated here**; isolectotypes K K000763446).

   Notes: *Guettardella chinensis* is based from the collection of Major J.G. Champion from Mt. Gough and Mt. Victoria in Hong Kong (Bentham, 1852). Forbes & Hemsley (1888: 384) then indicated that they have seen Champion's material at K. However, there are two duplicates of Champion's collection deposited at K. The specimen K000763445 possesses more reproductive structures (flower buds and fruits), and is here selected as the lectotype.

9. **Guettardella edanoi** (Chaw) J.G.Chavez, **comb. nov., ined.**
   Basionym: ***Antirhea edanoi*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 83 (1992). *Type*: PHILIPPINES. Sulu Archipelago, Tawi-Tawi Island) July-Aug. 1924 (♀), *M. Ramos & G. Edaño sub B.S. 44015* (holotype W n.v., isotypes A A00312848, B B100294388, K K000763439, NY NY00004685, SING SING0062099, US US01050008).

10. **Guettardella foveolata** (Chaw) J.G.Chavez, **comb. nov., ined.**
    Basionym: *Antirhea foveolata* Chaw, Tulane Stud. Zool. & Bot. 28(2): 85 (1992). *Type*: PHILIPPINES. Luzon, Zambales, Nov.-Dec. 1907 (♂), *M. Ramos sub B.S. 4796* (holotype US US01050009).

11. **Guettardella hexasperma** (Roxb. ex Carey) M.E.Jansen, Blumea 29(2): 575 (1984). ≡ *Pyrostria hexasperma* Roxb., Hort. Beng. 83 (1814), *nom. nud.* ≡ *Pyrostria hexasperma* Roxb. ex Carey, Fl. Ind. 1: 403 (1820). ≡ *Eupyrena hexasperma* (Roxb. ex Carey), Repert. Bot. Syst. 2: 488 (1843). ≡ *Bobea hexasperma* (Roxb. ex Carey) Valeton, Bull. Dép. Agric. Indes Néerl. 26: 7 (1909). *Type*: INDONESIA. Honimoa, Saparua, *s.d.* (♂ & ♀), *Roxburgh s.n.* (holotype *n.v.*).

    Notes: *Pyrostria hexasperma* was first published by Roxburgh (1814) in "*Hortus Bengalensis*" for a species from Honimoa (Saporea, Moluccas) that has not yet been introduced into the Botanical Garden at Calcutta. There is no description nor a diagnosis given to the binomial, so it is a nomen nudum. Later, the brief description of *P. hexasperma* was posthumously published in the first volume of the first edition of "*Flora Indica*" (Roxburgh, 1820). There is no illustration of the species in Roxburgh's Flora Indica drawings at Kew (Sealy, 1956), but the binomial *P. hexasperma* was associated to the gathering Wallich's Catalogue No. 6217: "*Timonius rumphii Dec. (Pyrostria hexasperma Roxb. valde aff. an eadem?)"* (Wallich, 1829: 211). However, Wallich's notes make it clear that his gathering with duplicates at K (K 001123325, K001123326) and PH (PH00023297) refer to a *Timonius* species from Penang (Malaysia) and Singapore, and not specifically Roxburgh's species from Honimoa that is now associated to *Guettardella*. Furthermore, Roxburgh (1820) indicated that his species possesses fruits with six seeds or nuts, which is in contrast to the many-seeded *Timonius*. Jansen (1984: 576) also noted that this observation of Roxburgh may have been from a very young material, in which the ligneous putamen had not yet developed. Nevertheless, if future search for Roxburgh's material remains futile, *P. hexasperma* needs to be neotypified.

= *Bobea hirsutiuscula* Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 29: 247 (1867). = *Antirhea hirsutiuscula* (Teijsm. & Binn.) Valeton, Bull. Dép. Agric. Indes Néerl. 26: 31 (1909). *Type*: INDONESIA. Saparoea, *s.d.* (♀), *Teysmann s.n.* (holotype *n.v.*).

= *Guettardella obscura* M.E.Jansen, Blumea 29: 580 (1984). *Type*: INDONESIA. Borneo,W. Koeta, Kombeng, 29 Nov. 1925 (♀), *F.H. Endert 5397* (holotype L L0064558, isotype A A00112727).

12. ***Guettardella inaequalis*** (Chaw) J.G.Chavez, **comb. nov., ined.**
    Basionym: ***Antirhea inaequalis*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 89 (1992). *Type*: MALAYSIA. Borneo, Kinabantangan, 22 July 1954 (♂), *G.H.S. Wood S.A.N. A4623* (holotype L L0064559, isotype A A00112728, SING SING0062100).

13. ***Guettardella inconspicua*** (Seem.) M.E.Jansen, Blumea 29(2): 576 (1984). ≡ *Guettarda inconspicua* Seem., Fl. Vit. 1: 131 (1866). ≡ *Antirhea inconspicua* (Seem.) Christoph., Bull.. Bernice P. Bishop Mus. 128: 202 (1935). *Type*: FIJI. Ovalau, 1860 (♂), *B. Seeman 257* (lectotype K K000763424, designated by Smith and Darwin (1988: 154), isolectotypes BM BM001040312, G G00389636, GH GH00312860, GH00312899, P P00698855).

14. ***Guettardella ioensis*** (Baill.) J.G.Chavez, **comb. nov., ined.**

    Basionym: ***Guettarda ioensis*** Baill. Adansonia 12: 242 (1879). ≡ *Antirhea ioensis* (Baill.) Chaw, Tulane Stud. Zool & Bot. 28(2): 93 (1992). *Type:* NEW CALEDONIA. Io Valley, 28 Dec. 1869 (♂), *B. Balansa 2392* (**lectotype** P P00645762, **designated here**; isotype P P00645763).

    Notes: Baillon (1879) based the description of *Guettarda ioensis* from the collection *B. Balansa 2392*, and two duplicates were located at P. The duplicate P00645762 is selected as the lectotype because the specimen is particularly rich in floral structures.

15. ***Guettardella livida*** (Elmer) M.E.Jansen, Blumea 29(2): 576 (1984). ≡ *Antirhea livida* Elmer, Leafl. Philipp. Bot. 4: 1327 (1912). *Type*: PHILIPPINES. Palawan, Puerto Princesa, Mt. Pulgar, 1911 (♀), *A.D.E. Elmer 12968* (lectotype P P00789777, designated by Chaw & Darwin (1992: 95), isolectotype BISH BISH1004288, K K000763438, NA NA0026092).

16. ***Guettardella microphylla*** (Bartl. ex DC.) M.E.Jansen, Blumea 29(2): 577 (1984). ≡ *Guettarda microphylla* Bartl. ex DC., Prodr. 4: 457 (1830). ≡ *Antirhea microphylla* (Bartl. ex DC.) Merr., Enum. Philipp. Fl. Pl. 3: 540 (1923). *Type*: PHILIPPINES. Luzon, 1792 (♂), *F.G. Bartling sub T.P.X Haenke s.n.* (holotype PR *n.v*; isotypes isolectotypes GOET GOET010337, HAL HAL0114219, PRC PRC450168).

17. ***Guettardella multiflora*** M.E.Jansen, Blumea 29(2): 578 (1984). ≡ *Antirhea multiflora* (M.E.Jansen) Chaw, Tulane Stud. Zool. & Bot. 28(2): 97 (1992). *Type*: PAPUA NEW GUINEA. Milne Bay, Cape Vogel Peninsula, Menapi, 16 Apr. 1953 (♀), *L.J. Brass 21936* (holotype L L0064556, isotypes K K000763433).

18. ***Guettardella ovatifolia*** M.E.Jansen, Blumea 29(2): 582 (1984). ≡ *Antirhea ovatifolia* (M.E.Jansen) Chaw, Tulane Stud. Zool. & Bot. 28(2): 98 (1992). *Type*: AUSTRALIA. Queensland, Newcastle Bay, 07 May 1948 (♀), *L.J. Brass 18667* (holotype L L0000396, isotypes A A00312863, BRI BRI-AQ0325754, CANB CANB192466, K K000763431).

19. ***Guettardella paxillata*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea paxillata*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 100 (1992). *Type*: PHILIPPINES. Luzon, Cagayan, Mt. Babatngin, May 1930 (♂), *G. Edaño sub B.S. 79440* (holotype A A00312849, isotype BO).

20. ***Guettardella philippinensis*** Benth., Hooker's J. Bot. Kew Gard. Misc. 4: 197 (1852). ≡ *Antirhea philippinensis* (Benth.) Rolfe, J. Linn. Soc., Bot. 21: 312 (1886). *Type*: PHILIPPINES. Bohol, 1841 (♂), *H. Cumming 1827* (holotype K K000763437, isotype BM BM000522433, G G00389630, G00389629, K K000763436).

21. ***Guettardella putaminosa*** (F.Muell.) Benth., Fl. Austral. 3: 419 (1867). ≡ *Timonius putaminosus* F.Muell., Fragm. 4: 92 (1864). ≡ *Antirhea putaminosa* (F.Muell.) F.Muell., Fragm. 9: 183 (1875). ≡ *Guettarda putaminosa* (F.Muell.) F.Muell., Fragm. 9: 183 (1875). ≡ *Matthiola putaminosa* (F.Muell.) Kuntze, Revis. Gen. Pl. 1: 288 (1891). *Type*: AUSTRALIA. "in silvis urbi Rockhampton vicinis", *s.d.* (♀), *A. Thozet s.n.* also numbered *A. Thozet 61* (lectotype MEL, first-step designated by Jansen (1984: 584); **second-step lectotype** MEL MEL2063109, designated here; isolectotypes GH GH00312924, K K000763430, MEL MEL2063110).

    Notes: Jansen (1984) referred to *A. Thozet s.n.* at MEL as the holotype of *Timonius putaminosus*, which can be treated as effective lectotypification under Art. 9.10 of the ICN (Turland *et al*., 2018). However, two duplicates of *A. Thozet s.n.*, which is also numbered as *A. Thozet 61*, were found at MEL. Following Art. 9.17 of the ICN (Turland *et al*., 2018), the duplicate MEL2063109 is here selected as the second-step lectotype.

22. ***Guettardella ramosii*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea ramosii*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 103 (1992). *Type:* PHILIPPINES. Luzon, Cagayan, Peñablanca, Apr. 1926 (♀), *M. Ramos & G. Edaño sub B.S. 46597* (holotype SING SING0062102, isotypes B B100294387, NY NY00004683).

23. ***Guettardella rhamnoides*** (Baill.) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Guettarda rhamnoides*** Baill. Adansonia 12: 241 (1879). ≡ *Antirhea rhamnoides* (Baill.) Chaw, Tulane Stud. Zool. & Bot. 28(2): 105 (1992). *Type*: NEW

CALEDONIA. Daaoui de Oro, 11 Apr. 1869 (♀), *B. Balansa 1128* (**lectotype** P P00645765, **designated here**; isolectotypes P P00645764, P P00645766).

Notes: In the protologue of *Guettarda rhamnoides*, Baillon (1879: 242) cited two collections, *B. Balansa 1128* and *B. Balansa 1976* that were collected from Daaoui Cro and Kougui, respectively. Only the collection *B. Balansa 1128* was located at P with three duplicates. Among these duplicates, P00645764 was annotated by S.P. Darwin (1993) as the "lectotype" of *G. rhamnoides*, something that was likely never effectively published. Here, the duplicate P00645765 is chosen as the lectotype for *G. rhamnoides* as this specimen possess more reproductive structures than P00645764.

24. ***Guettardella sphaerocarpa*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea sphaerocarpa*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 106 (1992). *Type*: INDONESIA. Papua, Djajapura, Rouffaer River, Sept. 1926 (♀), *W.M. Docters van Leeuwen 10353* (holotype A A00312846, isotypes B B100278141, K K000763432, L L0064543).

25. ***Guettardella surigaoensis*** (Salamanes & Alejandro) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea surigaoensis*** Salamanes & Alejandro, Acta Bot. Gallica Bot. Lett. 162(3): 153 (2015). *Type*: PHILIPPINES. Bucas Grande, Socorro, 20 May 2013 (♀), *B. Lemana, J.A. Manaig, J.D. Salamanes & L.S. Santos 13-908* (holotype PNH, isotypes PNH, USTH).

26. ***Guettardella talaudensis*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea talaudensis*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 107 (1992). *Type*: INDONESIA. Talaud, Karakelong, 31 May 1926 (♀), *H.J. Lam 3260* (holotype BO, isotypes K K000763443, L L0064541, SING SING0062103).

27. ***Guettardella tayabensis*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea tayabensis*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 109 (1992). *Type*: PHILIPPINES. Luzon, Quezon, Mt. Binuang, May 1917 (♀), *M. Ramos & G. Edaño sub B.S. 28869* (holotype NY NY00130840, isotypes A A00312850, BM BM000522432, K K000763435, US US01050007).

28. ***Guettardella tenuiflora*** (F.Muell. ex Benth.) M.E.Jansen, Blumea 29(2): 586 (1984). ≡ *Antirhea tenuiflora* F.Muell. ex Benth., Fl. Austral. 3: 418 (1867). ≡ *Guettarda tenuiflora* (F.Muell. ex Benth.) F.Muell., Fragm. 9: 183 (1875). ≡ *Matthiola tenuiflora* Kuntze, Revis. Gen. Pl. 1: 288 (1891). *Type*: AUSTRALIA. Queensland, Rockingham Bay, *s.d.* (♂), *Dallachy s.n.* (lectotype K K000763429, designated by Jansen (1984: 586); isolectotypes BR BR531594, G G00389623, GOET GOET010169, MEL MEL2295609).

29. ***Guettardella ternata*** (Chaw) J.G.Chavez, **comb. nov., ined.**
Basionym: ***Antirhea ternata*** Chaw, Tulane Stud. Zool. & Bot. 28(2): 113 (1992). *Type*: PHILIPPINES. Siargao, June 1919 (♂), *M. Ramos & J. Pascasio sub BS 34916* (holotype SING SING0062104, isotypes BO, NY NY00004682).

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Appendix 1. Accession numbers for included nucleotide sequences, presenting species names, voucher, and genetic markers in the following order: ETS, ITS, *atpB-rbcL*, *rps16*, *trnT-F*. Sequences indicated with * are newly generated in this study. Previously published sequences: a, Manns & Bremer (2010); b, Stranczinger et al. (GenBank, unpubl.); c, Janssens et al. (2016); d, Rova et al. (GenBank, unpubl.); e, Rova et al. (2002); f, Rova et al. (2009); g, Paudyal et al. (2018); h, Motley et al. (2005); i, Achille et al. (2006); j, Andersson & Rova (1999); k, Rydin et al. (2008); l, Robbrecht & Manen (2006); m, Struwe et al. (1998); n, Costion et al. (2016).

Acrosynanthus latifolius Standl., *Rova et al. 2208* (GB), –, GQ852100[a], GQ851966[a], AF242900[b], GQ852457[a]; ***Antirhea benguetensis*** (Elmer) Valeton, *Lola & Lorenzo LL018* (USTH), MT094480[*], MT101691[*], MT113381[*], MT094531[*], MT113420[*]; ***Antirhea borbonica*** J.F.Gmel., *De Block et al. 2004* (BR), MT094481[*], MT101692[*], MT113382[*], KT218828[c], MT113421[*]; ***Antirhea caudata*** (M.E.Jansen) Chaw, *Banag & Hung PP005* (USTH), MT094482[*], MT101693[*], MT113383[*], MT094532[*], MT113422[*]; ***Antirhea chinensis*** (Champ. ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl., *Hu & Kong 005* (L), MT094483[*], MT101694[*], MT113384[*], –, MT113423[*]; ***Antirhea foveolata*** Chaw, *Alejandro et al. 14753* (USTH), MT094484[*], MT101695[*], MT113385[*], –, MT113424[*]; ***Antirhea inconspicua*** (Seem.) Christoph., *Tuiwana et al. 2999* (P), –, GQ852132[a], GQ852024[a], –, GQ852508[a]; ***Antirhea ioensis*** (Baill.) Chaw, *McKee 3961* (L), MT094485[*], MT101696[*], MT113386[*], MT094533[*], MT113425[*]; ***Antirhea livida*** Elmer, *Chavez & Zamudio PL078* (FEUH), MT094486[*], MT101697[*], MT113387[*], MT094534[*], MT113426[*]; ***Antirhea madagascariensis*** Chaw, *De Block et al. 1808* (BR), MT094487[*], MT101698[*], MT113388[*], MT094535[*], MT113427[*]; ***Antirhea megacarpa*** Merr. & L.M.Perry, *Ave 4480* (L), MT094488[*], MT101699[*], MT113389[*], –, MT113428[*]; ***Antirhea microphylla*** (Bartl. ex DC.) Merr., *Calaramo et al. LL084* (USTH), MT094489[*], MT101700[*], MT113390[*], –, MT113429[*]; ***Antirhea ovatifolia*** (M.E.Jansen) Chaw, *Clarkson & Neldner 9265* (L), MT094490[*], MT101701[*], MT113391[*], MT094536[*], MT113430[*]; ***Antirhea paxillata*** Chaw, *Boltron et al. G011* (FEUH), MT094491[*], MT101702[*], MT113392[*], MT094537[*], MT113431[*]; ***Antirhea putaminosa*** (F.Muell.) F.Muell., *Shapcott MGH047* (BRI), MT094492[*], MT101703[*], MT113393[*], MT094538[*], MT113432[*]; ***Antirhea rhamnoides*** (Baill.) Chaw, *McKee 3750* (L), MT094493[*], MT101704[*], MT113394[*], MT094539[*], MT113433[*]; ***Antirhea smithii*** (Fosberg) Merr. & L.M.Perry, *Smith 7685* (L), MT094494[*], MT101705[*], MT113395[*], –, MT113434[*]; ***Antirhea* sp. 1**, *Abad J005* (USTH), MT094495[*], MT101706[*], MT113396[*], MT094540[*], MT113435[*]; ***Antirhea* sp. 2**, *Chavez 001* (FEUH), MT094496[*], MT101707[*], MT113397[*], –, MT113436[*]; ***Antirhea* sp. 3**, *Lola & Lorenzo LL114* (USTH), MT094497[*], MT101708[*], MT113398[*], MT094541[*], MT113437[*]; ***Antirhea* sp. 4**, *Docot & Banag CB16-224* (FEUH), MT094498[*], MT101709[*], MT113399[*], –, MT113438[*]; ***Antirhea surigaoensis*** Salamanes & Alejandro, *Lemana et al. 13908* (USTH), MT094499[*], MT101710[*], MT113400[*], –, MT113439[*]; ***Antirhea tayabensis*** Chaw, *Ong & Luna 1024* (FEUH), MT094500[*], MT101711[*], MT113401[*], –, MT113440[*]; ***Antirhea ternata*** Chaw, *Lemana et al. 13942* (USTH), MT094501[*], MT101712[*], MT113402[*], MT094542[*], MT113441[*]; ***Arachnothryx hondurensis*** (Donn.Sm.) Lorence, *Croat & Hannon 64177* (NY), –, –, –, AF243013[d], AF152716[e]; ***Arachnothryx leucophylla*** (Kunth) Planch., *Rova 2287* (GB, S), MT094502[*], AY730296[f], GQ851977[a], AF242910[f], MT094564[*]+GQ852453[a]; ***Arachnothryx* sp.**, *Rova 2093* (GB), –, AY730297[f], GQ852009[a], AF242934[f], GQ852488[a]; ***Bikkia tetrandra*** (L.f.) A.Rich., *Motley 2451* (NY), KT333180[g], AY763874[h], –, –, –; ***Bikkia tetrandra*** (L.f.) A.Rich., *Curry 1402* (K), –, –, GQ851983[a], GQ852374[a], GQ852467[a]; ***Bobea brevipes*** A.Gray, *Takeuchi 3217* (A), MT094503[*], MT101713[*], MT113403[*], MT094543[*], MT113442[*]; ***Bobea gaudichaudii*** (Cham. & Schltdl.) H.St.John & Herbst, *Motley 2536* (NY), –, DQ063668[i], –, –, –; ***Bobea gaudichaudii*** (Cham. & Schltdl.) H.St.John & Herbst, *Fagerlind 7183* (UPS), –, –, GQ851984[a], –, –; ***Bobea sandwicensis*** (A.Gray) Hillebr., *Takeuchi 3265* (A), MT094504[*], MT101714[*], MT113404[*], MT094544[*], MT113443[*]; ***Chomelia obtusa*** Cham. & Schltdl., *Jansen-Jacobs et al. 4361* (GB), –, GQ852114[a], GQ851998[a], GQ852385[a], GQ852478[a]; ***Chomelia spinosa*** Jacq., *Siegler DS-12793* (MO), –, GQ852115[a], GQ851999[a], –, GQ852454[a]; ***Chomelia tenuiflora*** Benth., *Andersson et al. 2030* (GB, S), –, GQ852116[a], GQ852000[a], –, GQ852479[a]; ***Gonzalagunia cornifolia*** (Kunth) Standl., *Stahl 1407* (GB), MT094505[*], GQ852128[a], MT113405[*], AF242948[d], GQ852501[a]; ***Guettarda boliviana*** Standl., *Persson & Gustafsson 354* (GB), MT094506[*], GQ852130[a], GQ852021[a], AF242962[d], GQ852505[a]; ***Guettarda crispiflora*** Vahl., *Andersson et al. 2081* (GB), MT094507[*], DQ063674[i], GQ852022[a], AF004052[j], GQ852506[a]; ***Guettarda ferruginea*** Griseb., *Rova et al. 2206* (GB), MT094508[*],GQ852131[a], GQ852023[a], GQ852397[a], GQ852507[a]; ***Guettarda glabrescens* 1** (Schltr.) Guillaumin, *Gateble 1079* (UBT), MT094509[*], MT101715[*], MT113406[*], MT094545[*], MT113444[*]; ***Guettarda glabrescens* 2** (Schltr.) Guillaumin, *Mouly 261* (L), MT094510[*], MT101716[*], MT113407[*], MT094546[*], MT113445[*]; ***Guettarda hypolasia*** Baill., *McKee 4196* (L), MT094511[*], MT101717[*], MT113408[*], MT094547[*], MT113446[*]; ***Guettarda ngoyensis*** (Schltr.) Guillaumin, *Gateble 1121* (UBT), MT094512[*], MT101718[*], MT113409[*], –, MT113447[*]; ***Guettarda speciosa*** L., *Motley 2040* (NY), KT333247[g], –, –, –, –; ***Guettarda speciosa*** L., *Achille 661* (P), –, DQ063689[i], –, –, –; ***Guettarda speciosa*** L., *Rova 2492* (GB), –, –, GQ852025[a], –, GQ852509[a];

Guettarda speciosa L., *Persson 141* (GB), –, –, –, AF242964[d], –; ***Guettarda tournefortiopsis*** Standl., *Andersson et al. 2113* (GB), MT094513[*], GQ852133[a], GQ852026[a], MT094548[*], GQ852510[a]; ***Guettarda uruguensis*** Cham. & Schltdl., *Gillis 9575* (FTG), –, AY730294[f], –, EU145489[k], EU145533[k]; ***Guettarda uruguensis*** Cham. & Schltdl., *in cult. Bot. Gard. Lyon*, –, –, DQ131739[l], –, –; ***Machaonia acuminata*** Bonpl., *Bullock 1432* (MO), –, GQ852142[a], GQ852044[a], GQ852408[a], GQ852523[a]; ***Machaonia erythrocarpa*** (Standl.) Borhidi, *Espinoza 520* (GB), –, GQ852103[a], GQ851972[a], MT094530[*], MT094563[*]+GQ852452[a]; ***Malanea* sp.**, *Persson 554* (GB), MT094514[*], MT101719[*], GQ852046[a], GQ852410[a], MT113448; ***Neoblakea venezuelensis*** Standl., *Lieasner et al. 7785* (NY), –, –, –, –, AF152732[e]; ***Ottoschmidtia microphylla*** (Griseb.) Urb., *Ekman H9433* (S), –, GQ852147[a], GQ852061[a], GQ852422[a], GQ852532[a]; ***Pittoniotis trichantha*** Griseb., *Croat 9311* (NY), –, DQ063695[i], –, –, –; ***Rogiera amoena*** Planch., *Rova 2409* (GB), MT094515[*], AM182205[b], GQ852073[a], –, GQ852542[a]; ***Rogiera amoena*** Planch., *Hawkes et al. 1962* (S), –, –, –, AF243000[f], –; ***Rogiera cordata*** (Benth.) Planch., *Gustafsson & Fredriksson 126* (GB), MT094516[*], AY730285[f], GQ852074[a], AF242999[f], GQ852543[a]; ***Stenostomum acreanum*** (K.Krause) Achille & Delprete, *Cornejo et al. 8895* (GB), MT094517[*], MT101720[*], atp, MT094549[*], MT113449[*]; ***Stenostomum acreanum*** (K.Krause) Achille & Delprete, *Andersson et al. 2031* (GB), –, –, GQ852020[a], –, –; ***Stenostomum acutatum*** DC., *Axelrod 3288* (NY), –, DQ063696[i], –, –, –; ***Stenostomum acutatum*** DC., *Stahl & Knudsen 2316* (GB), –, –, –, AF242907[d], AF102378[m]; ***Stenostomum lucidum*** (Sw.) C.F.Gaertn., *Acevedo-Rodriguez 8468* (NY), –, DQ063697[i], –, –, –; ***Stenostomum lucidum*** (Sw.) C.F.Gaertn., *Sanders 1801* (FTG), –, –, GQ852089[a], GQ852447[a], GQ852556[a]; ***Stenostomum resinosum*** (Vahl) Nicolson, *Axelrod et al. 2723* (NY), –, GQ852145[a], GQ852056[a], GQ852417[a], GQ852528[a]; ***Timonius beamanii*** K.M.Wong & Jun H.Chen, *Beaman 8491* (US), MT094518[*], MT101721[*], MT113410[*], MT094550[*], MT113450[*]; ***Timonius borneensis*** Valeton, *Church 2695* (A), MT094519[*], MT101722[*], MT113411[*], MT094551[*], MT113451[*]; ***Timonius celebicus*** Koord., *Ridsdale V.D. 23*, –, GQ852157[a], GQ852095[a], –, GQ852561[a]; ***Timonius confertiflorus*** Merr., *Alejandro et al. 15602B* (USTH), MT094520[*], MT101723[*], MT113412[*], MT094552[*], MT113452[*]; ***Timonius densiflorus*** Valeton, *Takeuchi et al. 4298* (US), MT094521[*], MT101724[*], MT113413[*], MT094553[*], MT113453[*]; ***Timonius flavescens*** (Jacq.) Baker, *Beaman 8720* (US), MT094522[*], MT101725[*], MT113414[*], MT094554[*], MT113454[*]; ***Timonius korrensis*** Kaneh, *Costion 3448-14*, –, KR922357[n], KR922398[n], –, KR922402[n]; ***Timonius mollis*** Valeton, *Costion 3361* (CNS), MT094523[*], KR922360[n], KR922399[n], MT094555[*], MT094565[*]+ KR922403[n]; ***Timonius platycarpus*** Montrouz., *McKee 3441* (US), –, MT101726[*], MT113415[*], MT094556[*], MT113455[*]; ***Timonius pulgarensis*** Elmer, *Chavez & Zamudio PL112* (FEUH), MT094524[*], MT101727[*], MT113416[*], MT094557[*], MT113456[*]; ***Timonius salsedoi*** Fosberg & Sachet, *Costion 3493* (CNS), MT094525[*], KR922359[n], KR922397[n], MT094558[*], MT094566[*]+ KR922401[n]; ***Timonius subauritus*** Valeton, *Costion 3359* (CNS), MT094526[*], KR922365[n], KR922396[n], MT094559[*], MT094567[*]+ KR922400[n]; ***Timonius timon*** (Spreng.) Merr. **var. *timon***, *Dransfield 7707* (A), MT094527[*], MT101728[*], MT113417[*], MT094560[*], MT113457[*]; ***Timonius wallichianus*** (Korth.) Valeton, *Ismail IS436* (A), MT094528[*], MT101729[*], MT113418[*], MT094561[*], MT113458[*]; ***Tinadendron kajewskii*** (Guillaumin) Achille, *Achille 958* (L), MT094529[*], MT101730[*], MT113419[*], MT094562[*], MT113459[*]; ***Tinadendron noumeanum*** (Baill.) Achille, *Achille 662* (P), –, DQ063683[i], –, –, –; ***Tinadendron noumeanum*** (Baill.) Achille, *Mouly 859* (P), –, –, GQ852097[a], –, GQ852563[a].

Appendix 2. List of coded microstructural characters and their aligned positions.

I. *atpB-rbcL* intergenic spacer

A. Gaps

1. 151-162
2. 561-564
3. 589

B. Short sequence repeats

1. 190-191: TA
2. 690-694: TAATA
3. 714-736: CTGATTAGTTGATAATATTAGTA

II. *rps*16 intron

A. Gaps

1. 32-34
2. 174

B. Short sequence repeats

1. 327-331: TAGAA
2. 615-620: TTTTTC
3. 698-705: ATTTATTA

III. *trnT-F* region

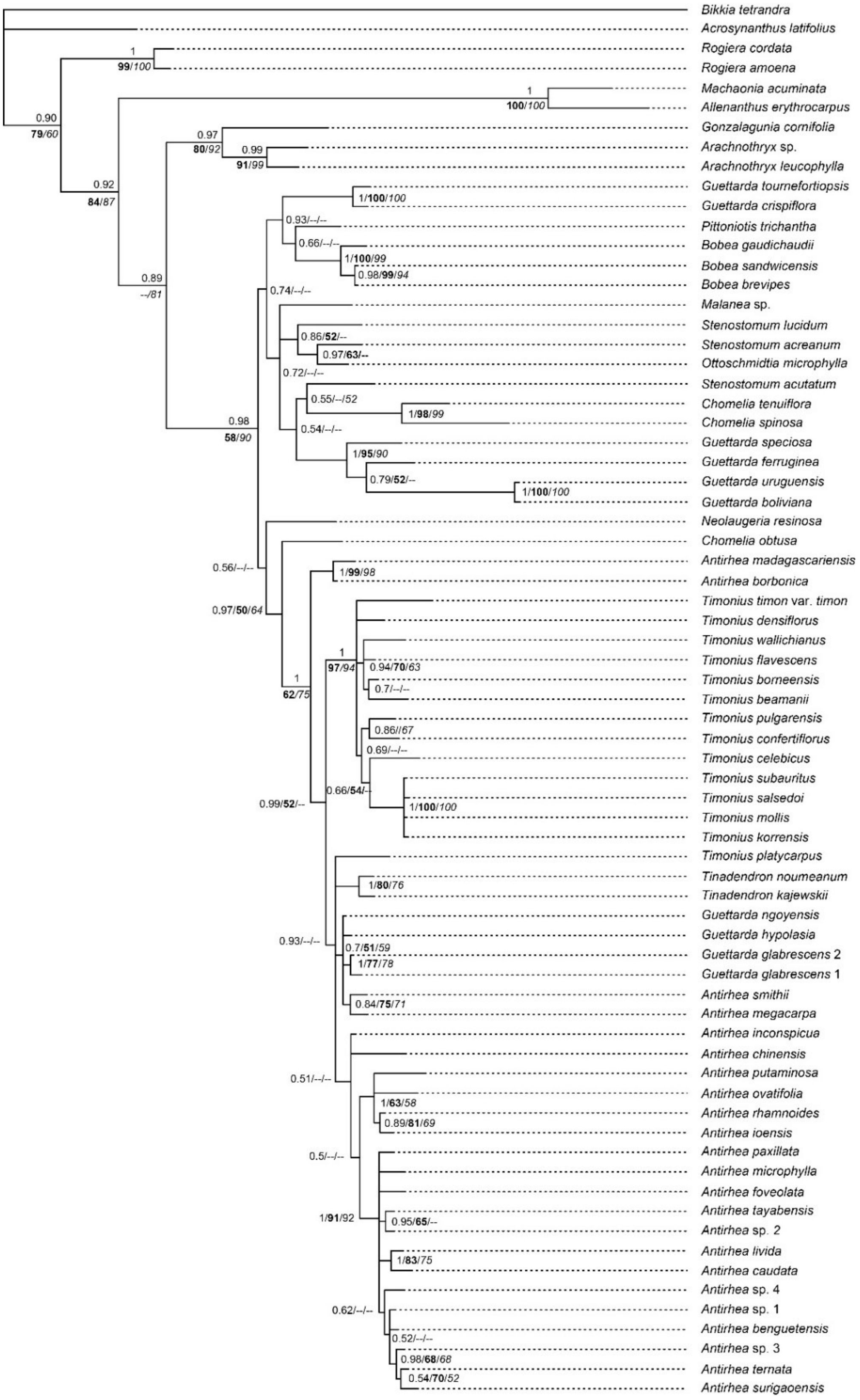
A. Gaps

1. 162
2. 233-238
3. 345-365
4. 662
5. 724-728
6. 818
7. 966-969
8. 1293
9. 1535-1538

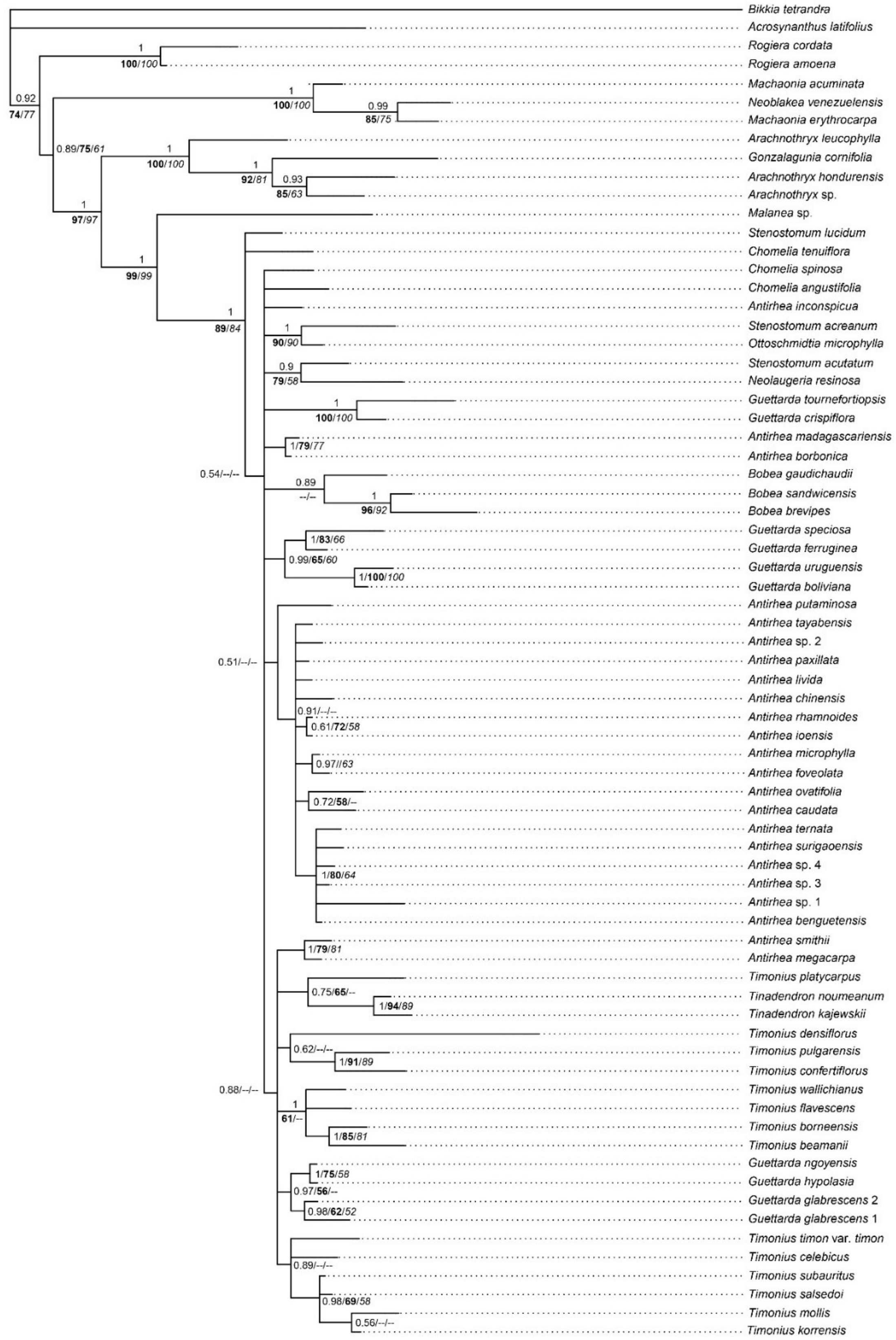
B. Short sequence repeats

1. 20-24: ATTTT
2. 250-255: ATT (doublet)
3. 1142-1146: TGATT

Appendix 3. Majority-rule consensus tree inferred from Bayesian inference of the ETS+ITS dataset. Numbers on nodes indicate Bayesian posterior probabilities, maximum-likelihood bootstrap values (boldface), and parsimony bootstrap values (italics).



Appendix 4. Majority-rule consensus tree inferred from Bayesian inference of the *atpB-rbcL+rps16+trnT-F* dataset. Numbers on nodes indicate Bayesian posterior probabilities, maximum-likelihood bootstrap values (boldface), and parsimony bootstrap values (italics).



Publication II

BACK TO THE DRAWING BOARD: MOLECULAR PHYLOGENY CHALLENGES THE TRADITIONAL CIRCUMSCRIPTION OF *TIMONIUS* (RUBIACEAE)[*]

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The circumscription of the Paleotropical dioecious and species-rich genus *Timonius* has long been based on the restricted combination of morphological features, namely: valvate corolla aestivation and drupes bearing multiple, free, single-seeded pyrenes. Previous studies, albeit focused on different taxonomic problems in tribe Guettardeae, have two contradicting views on the phylogenetic status of *Timonius*. The first is that *Timonius* is monophyletic, but did not encompass the vast morphological variation within the genus. The second is that *Timonius* is polyphyletic, although the hypothesis relied on a limited number of species. A further element that casted doubts on the current delimitation of *Timonius* is the manifestation of cryptic sexual polymorphism ("leaky" dioecism) of some Philippine species. Based on these, the phylogeny of *Timonius* and related genera is here reconstructed using sequences obtained from five molecular loci (ETS, ITS, *atpB-rbcL*, *rps16* and *trnT-F*) to provide a better understanding on its generic boundaries. The phylogenetic results generally affirm the unnaturalness of *Timonius*, and its species are retrieved in three well-supported clades: 1) *Abbottia* clade, containing representatives of *T.* subgen. *Abbottia*, 2) "*Lakapatiphyton*" clade, containing Philippine species with "leaky" dioecism and 3) *Timonius* clade, containing the majority of the sampled species of *Timonius*; whereas the New Caledonian endemic *T. platycarpus* is recovered in an isolated position that is sister to *Tinadendron*. These findings are supported by morphological characters and molecular apomorphies, implying the necessity to resurrect the genus *Abbottia*

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[*] For szbmission, Taxon.

with an amended diagnosis and to establish the new genus *Lakapatiphyton*, so that a more natural concept of *Timonius* could be rendered. Diagnostic morphological characters of *Timonius* clade are also presented for succeeding efforts toward a more stable taxonomy of the genus.

Keywords: *Abbottia*, dioecy, Guettardeae, *Lakapatiphyton*, Paleotropics, phylogeny, *Timonius*

Introduction

The tribe Guettardeae (ca. 20 genera, ~740 spp.) are one of the most taxonomically complex groups within the Rubiaceae. Guettardeae, as a tribe, have their origins in the scheme of Candolle (1807) as "Guettardaceae" that were initially characterized by fruits with several locules. Verdcourt (1958) and Bremekamp (1966), who were concerned with suprageneric classification in Rubiaceae, have placed Guettardeae under the monotribal and illegitimate subfamily Guettardoideae. Later, Robbrecht (1988) modified the subfamilial classification in Rubiaceae and assigned Guettardeae to the subfamily Antirheoideae. However, molecular data contradicted the naturalness of Robbrecht's Antirheoideae, and suggested that Guettardeae are better placed in the subfamily Cinchonoideae (Bremer & al., 1995). Recent phylogenetic studies (Rova & al., 2002, 2009; Manns & Bremer, 2010) have also expanded the tribal boundaries of Guettardeae to include some genera previously classified in Chiococceae (*Allenanthus* Standl., *Hodgkinsonia* F.Muell.), Isertieae (*Gonzalagunia* Ruiz & Pav.) and Rondeletieae (*Arachnothryx* Planch., *Rogiera* Planch.). Whereas the first broad phylogenetic framework of Guettardeae (Achille & al., 2006) had uncovered many taxonomic problems within the group, including the para- or polyphyly of *Antirhea* Comm. ex Juss. *sensu* Chaw & Darwin (1992), *Guettarda* L. and *Stenostomum* C.F.Gaertn., but was unable to draw thorough taxonomic conclusions because of the limited sampling and poor support values of some of the clades.

As currently understood, *Timonius* Rumph. ex DC., *nom. cons.* (Fig. 1) is the most speciose genus in Guettardeae and one of the largest in Rubiaceae (Davis & al., 2009). It is comprised of 185 species (Govaerts & al., 2019), with some authors having a less-conservative estimate of 200 (Darwin, 2010) to 300 (Chen & al., 2015) species. The genus is native to the Paleotropics and its species are distributed from Seychelles and Sri Lanka, eastward to Indo-China, Taiwan, Malesia, Papuasia and Australia, with a few extending to the South-central and South-western Pacific islands. Within this range, the prominent centers of species diversity are New Guinea with 86 species (Govaerts & al., 2019), the Philippines with 33 species (Merrill, 1923; Chavez & al. 2020a, 2020b) and Borneo with 24 species (Puff & Wong, 1993; Chen & al., 2015). *Timonius* is distinguished by the combination of characters, namely: shrubs to tall trees, rarely epiphytic or hemiepiphytic, variable dimorphism of inflorescences and/or flowers, valvate corolla aestivation that occasionally appears imbricate due to the interlocking corolla lobe margins, and calyx-crowned drupes bearing numerous separate single-seeded pyrenes (Gray, 1860; Valeton 1909, 1927; Merrill & Perry, 1945; Jansen, 1984; Fosberg & Sachet, 1987;

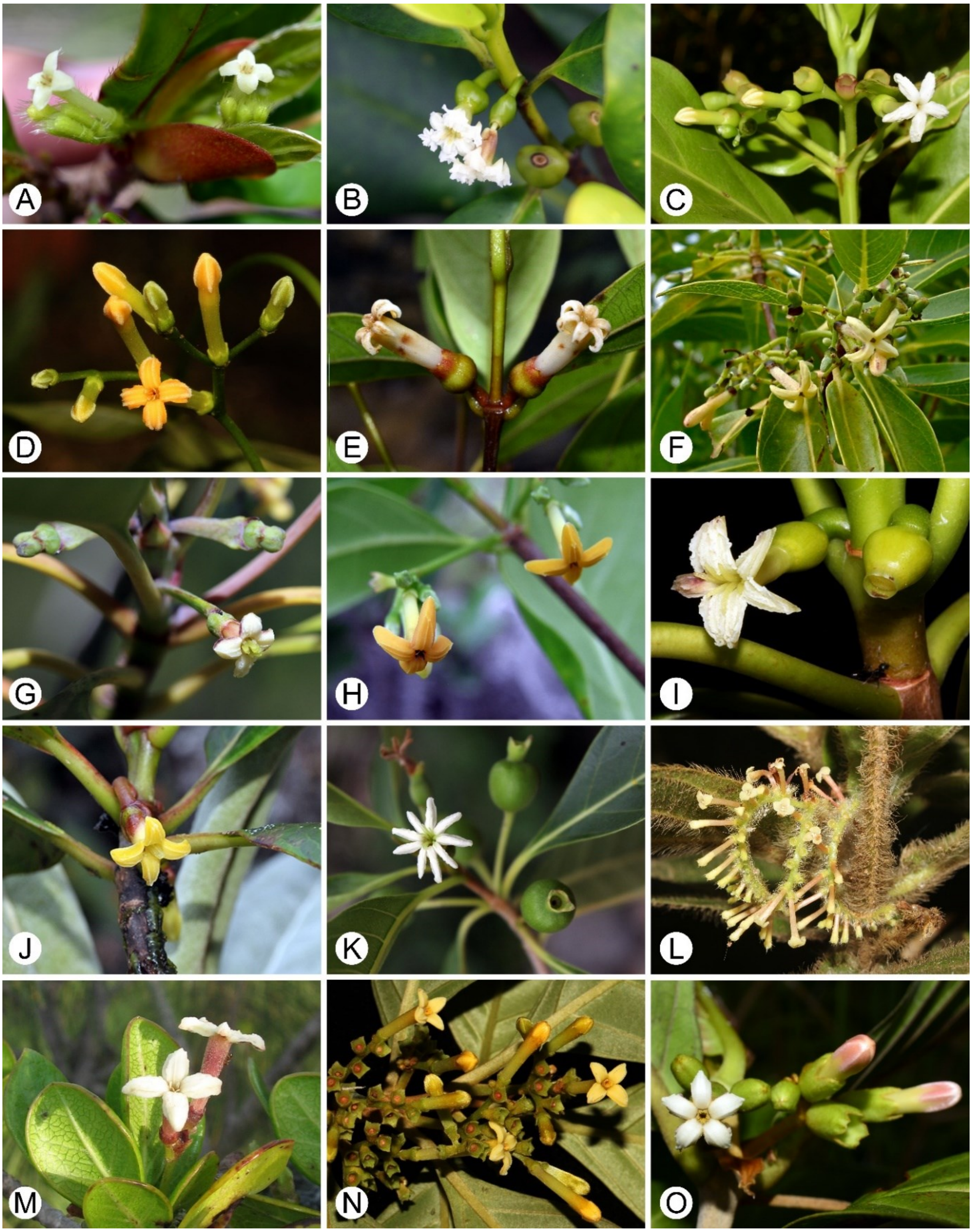
Wong, 1988; Darwin, 1993, 1994, 1997, 2010; Achille, 2006; Achille & al., 2006; Chen & al., 2015; Chavez & al., 2020ab). *Timonius* is also relatively unique within the Rubiaceae due to its large number of locules (Achille & al., 2006) that can reach to more than 80 (Darwin, 1994). This increase in the number of locules was underpinned to the serial fragmentation of each of the primary locules during gynoecium development (Martinello, 1992). Briggs & Utteridge (2014) also reported that certain species of *Timonius*, i.e. *T. grandifolius* Valeton, exhibit dehiscent drupes.

As a genus, *Timonius* has had a confusing taxonomic and nomenclatural history. "Timonius" was first used in the botanical literature by Rumphius (1743) as a Latin vernacular for the "*aytimon*" or "*timon*" that he described from the island of Ambon. Candolle (1830) then validated *Timonius* as a genus, but continued to assign the binomial *T. rumphii* DC. to the Rumphian material (Rumphius 1743: 216, tab CXL) despite his recognition that Sprengel (1813) had already associated for it the name *Erithalis timon* Spreng. This nomenclatural decision of Candolle (1830) was corrected by Britten (1901) with a new combination, *Nelitris timon* (Spreng.) Britten, citing the limits of priority surrounding the two epithets and Trimen's (1894) disposition that *Nelitris* Gaertn*., nom. illeg.* antedated *Timonius*. Afterwards, Merrill (1937) proposed *T. timon* (Spreng.) Merr. (Fig. 1K), which later became the conserved type species of *Timonius* (Rickett & Stafleu, 1960).

Before the formalization of *Timonius* (Candolle, 1830), several genera had been established that were based on different species with drupes containing numerous single-seeded and free pyrenes, these are: *Burneya* Cham. & Schltdl. (Chamisso & Schlechtendal, 1829), *Erithalis* G.Forst., *nom. illeg.* (Forster, 1786), *Helospora* Jack (Jack, 1823), *Nelitris* (Gaertner, 1788), *Polyphragmon* Desf. (Desfontaines, 1820) and *Porocarpus* Gaertn. (Gaertner, 1791). The interpretation of the original descriptions of these genera, as well as their application in various taxonomic treatments compounded the usage of *Timonius* as a generic name. Candolle (1828, 1830) treated these genera, except *Porocarpus*, in three separate tribes within Rubiaceae and one in Myrtaceae. He classified *Polyphragmon* in Hamelieae, *Helospora* in Gardenieae [as "Gardenieaceae"], and *Timonius*, to which *Bobea* Gaudich. and the illegitimate *Erithalis* and its replacement name *Burneya* were at the same time synonymized, in Guettardeae [as "Guettardaceae"] (Candolle, 1830). *Nelitris*, on the other hand, was treated in Myrtaceae (Candolle, 1828) as a probable consequence of the misapplied synonymy of *Decaspermum fruticosum* J.Forst. & G.Forst. to *N. jambosella* G.Forst. [=*T. flavescens* (Jack) Baker] made by

Gaertner (1788) (for a brief discussion, see Scott, 1979; McNeill, 1981). Later, Korthals (1851) recognized the similarity of the then *T. rumphii* to *P. sericeum* Desf. [=*T. timon*] and reduced *Timonius* to a synonym of *Polyphragmon*. Korthals' (1851) opinion was followed by Scheffer (1876), Kurz (1876) and Miquel (1857, 1869), who also synonymized *Helospora* and the post-Candolle genus *Eupyrena* Wight & Arn. (Wight & Arnott, 1834) to *Polyphragmon*. Apparently, Hooker (1873) had a tangential standing on the nomenclature and adopted *Timonius* instead of *Polyphragmon*. It was also in this work (Hooker, 1873) that *Porocarpus* resurfaced in the literature and became a synonym of *Timonius*, although the association of its type species, *P. helminthotheca* Gaertn., remains insufficiently known. The preference of Hooker (1873) for *Timonius* over *Polyphragmon* was followed by Hooker (1882), Boerlage (1891), Schumann (1891) and Warburg (1891). The opposing mainstream opinions of Korthals (1851) and Hooker (1873) may have led to the proposal to conserve the usage of *Timonius* against earlier generic names that was effected in the Vienna rules of botanical nomenclature (Briquet, 1912). However, *Nelitris* was later excluded from the list of rejected names against *Timonius* because it belongs to Myrtaceae (Rickett & Stafleu, 1960; Wong, 1988); while *Bobea* was never formally rejected against *Timonius* since it was earlier recognized as distinct from the genus because of polygamodioecism, imbricate corolla lobes and uniseriate pyrenes (Hillebrand, 1888; Schumann, 1891).

The earliest modern treatment of *Timonius* was carried out by Valeton (1909). His delimitation, including that of Gray (1860), became widely accepted and eventually made *Timonius* a culminating genus for all Paleotropical (excluding Hawaii) dioecious species of Guettardeae with free pyrenes. This concept had led to the description of at least another 150 species and infraspecies names in *Timonius* (e.g., Wernham, 1916; Valeton, 1927, 1930; Kanehira, 1931; Merrill, 1937; Merrill & Perry, 1945; Fosberg & Sachet, 1987; Wong, 1988; Darwin, 1983, 1993, 1994, 1997, 2010a, b; Chen & al., 2014; Chavez & al., 2020a, b) and the reduction of the Australian monotypic genus *Abbottia* F.Muell. as another synonym (Smith, 1957). After the influential work of Valeton (1909), *Timonius* had still received little attention and knowledge of the genus had only been contained in regional treatments for Borneo including Kinabalu Park (Puff & Wong, 1993; Chen & al., 2015, 2020), the Malay Peninsula (Wong, 1988), Palau Islands (Fosberg & Sachet, 1987), Papuasia (Valeton, 1927), the Philippines (Merrill, 1923), Taiwan (Chen & Taylor, 2011) and Thailand (Puff & al., 2005). In addition, Darwin (1997) revised the *T. flavescens* species alliance of Papuasia, while Chavez & al. (2020b) published a short communication for Philippine species. An attempt was also made by Darwin (1993, 1994,



2010a) to infer infrageneric groupings within *Timonius*, but unfortunately his subgeneric classification may not be widely applicable as it was only based on a relatively small number of species and limited geographic coverage.

While some of the "top twenty" largest genera of Rubiaceae (Davis & al., 2009) have already been subjects of molecular phylogenetic studies and their delineations are now understood (Nepokroeff & al. 1999; Alejandro & al., 2005; Achille & al., 2006; Groeninckx & al., 2009; Mouly & al., 2009; Ehrendorfer & Barfuss, 2014; Razafimandimbison & al., 2014; De Block & al., 2015; Razafimandimbison & Rydin, 2019), *Timonius* had only been partly discussed in phylogenetic investigations that addressed different issues (Achille & al., 2006; Pessoa, 2016). In the nrDNA-based phylogeny of Achille & al. (2006), *Timonius* was retrieved as a monophyletic assemblage within their Paleotropical dioecious clade, and is sister to a polytomy containing Western Pacific species of *Antirhea* and New Caledonian *Guettarda* including the recently described *Tinadendron* (Achille, 2006). This monophyly of *Timonius* is, however, uncertain since it was only assessed with five species that did not cover the vast morphological variation within the genus presented by earlier authors (e.g., Valeton, 1909; Merrill & Perry, 1945; Wong, 1988, Darwin, 1994). Pessoa (2016), on the other hand, despite having sampled only two species revealed that the genus is polyphyletic. In her work, Pessoa (2016) retrieved *T. timon* as sister to the New Caledonian endemic *Tinadendron noumeanum* (Baill.) Achille, while *T. affinis* A.Gray was recovered as sister to all Paleotropical dioecious genera of Guettardeae. *Timonius affinis* belongs to a distinct group comprising 28 species that is characterized by hemiepiphytism and reticuli-paxillate leaf venation (subgenus *Abbottia*; Darwin, 1994). Another factor that cast uncertainties on the naturalness of *Timonius* as currently delimited, is the cryptic sexual polymorphism ("leaky dioecism") and ± foliaceous stipules exhibited by some Philippine endemic species, such as: *T. auriculatus* Merr. (Fig. 1A), *T. samarensis* Merr. and *T. trichophorus* Merr. (Fig. 1L). This set of characters was neither considered nor mentioned in the seminal treatments for *Timonius* from the past decades.

←**Fig. 1.** Representative species of *Timonius*: **A,** *T. auriculatus*, staminate; **B,** *T. belensis*, pistillate; **C,** *T. finlaysonianus*, staminate; **D,** *T. flavescens*, staminate; **E,** *T. lanceolatus*, pistillate; **F,** *T. nitidus*, staminate; **G,** *T. platycarpus*, pistillate; **H,** *T. sechellensis*, staminate; **I,** *T. singularis*, pistillate; **J,** *T. tambuyukonensis*, pistillate; **K,** *T. timon*, pistillate; **L,** *T. trichophorus*, staminate; **M,** *T. uniflorus*, staminate; **N,** *T. wallichianus*, staminate; **O,** *T. valetonii*, staminate. — Photos: A, C, E, O by Jayson G. Chavez; B by Wayne Takeuchi; D, N by Cerlin Ng; F by Lauren Gutierrez; G by Guillaume Lannuzel; H by Vit Grulich; I by Andreas Lambrianides; J by Rogier van Vugt; K by John Elliot; L by John Michael M. Galindon; M by Jean François Butaud.

In this study, the first in-depth insights into the phylogeny of *Timonius* based on commonly utilized genetic markers (nrDNA: ETS, ITS; cpDNA: *atpB-rbcL*, *rps16*, *trnT-F*) and a broader sampling of taxa included in the Paleotropical dioecious clade of Achille & al. (2006; 4 genera, 73 species) is provided. This phylogeny is utilized to re-evaluate the current taxonomic circumscription of *Timonius* and propose practical generic re-assignments for some of its species without contradicting their molecular affinities.

Materials and methods

Taxon sampling

To test the phylogenetic status of *Timonius*, the investigation was made to include all Guettardeae genera (Manns & Bremer, 2010) with the exception of the rare *Dichilanthe* Thwaites because of difficulties in obtaining sequenceable material. Sequences which were produced by previous studies (e.g., Achille & al., 2006; Manns & Bremer, 2010) were also incorporated. Sampling of the Paleotropical dioecious clade of Guettardeae plus *Bobea* (Achille & al., 2006) was expanded to represent as many species as possible to cover the morphological variation and geographical distribution of each genus. For this, a total of 85 accessions of Paleotropical dioecious Guettardeae were investigated that includes: *Antirhea* (23 species), *Bobea* (3 species), *Guettarda* (New Caledonia, 3 species), *Hodgkinsonia* (1 species), *Tinadendron* (2 species) and *Timonius* (47 species and varieties). Extraction of DNA from herbarium vouchers of *Timonius* collected in the island of New Guinea, which harbors 46% of the recognized species, was carried out, but only nine species yielded useful amounts of DNA, i.e. *T. belensis* Merr., *T. carstensensis* Wernham, *T. densiflorus* Valeton, *T. kaniensis* Valeton, *T. laugerioides* Wernham, *T. pubistipulus* S.P.Darwin, *T. secundiflorus* S.P.Darwin, *T.* sp. 1 and *T.* sp. 2. The samples *T.* sp. 1 and *T.* sp. 2 were identified as of uncertain affinities following the works of Valeton (1923) and Darwin (1983, 1993, 1994, 1997, 2010a & b), and are hypothesized to be putative novel species. *Timonius* sp. 3 and *T.* sp. 4, both from Borneo, did not complement any of the recognized species from the region (Puff & Wong, 1993; Chen & al., 2015; Chen & Wong, 2020) and constitute undescribed species. Two species from the Philippines, *T.* sp. 5 and *T.* sp. 6, are found to be allied to *T. flavescens* and *T. tambuyukonensis* Jun H.Chen, respectively, but remain morphologically distinct. In addition, two Philippine Guettardeae species of uncertain generic affinity were included. These species, here indicated as *“Lakapatiphyton*” sp. 1 and sp. 2, have free pyrenes that fit the concept of *Timonius* but they exhibit imbricate corollas that cast doubts for their inclusion in the genus. Representatives of tribes Chiococceae (*Bikkia tetrandra* (L.f.) A.Rich), Hymenodictyeae (*Hymenodictyon orixense* (Roxb.) Mabb.), Naucleeae (*Nauclea orientalis* (L.) L.), and Rondeletieae (*Acrosynanthus latifolius* Standl.) were designated as outgroups based on the previous molecular study of subfamily Cinchonoideae by Manns and Bremer (2010). Voucher details and GenBank accessions of the sampled taxa are presented in Appendix 1.

Molecular procedures

Total DNA was isolated from silica-dried or herbarium materials following a modified 2X CTAB mini-prep procedure (Doyle & Doyle, 1987) using Carlson lysis buffer (Carlson & al., 1991) and subsequently cleaned with NucleoSpin Extract II (Machery-Nagel, Germany). For recalcitrant samples, 15% v/v β-mercaptoethanol were added to the extraction buffer. Amplification and sequencing of two nuclear (ETS, and ITS) and three plastid (*atpB-rbcL*, *rps16*, and *trnT-F*) regions were carried out with the primers listed in Table 1. The reaction for the nuclear regions was performed in 25 µl volume containing: 12.15 µl H_2O, 2.5 µl 10x PCR buffer, 1.5 µl 25 mM $MgCl_2$, 1 µl each of 10 mM forward and reverse primers, 1 µl 5% DMSO, 1 µl 1% BSA, 2 µl DNA template and 0.35 µl *Taq*-polymerase. For the plastid regions, amplification was accomplished in 50 µl volume containing: 24.25 µl H_2O, 5 µl 10x PCR buffer, 5 µl 25 mM $MgCl_2$, 0.5 µl each of 10 mM forward and reverse primers, 5 µl 10 mM TMACl, 0.5 µl 1% BSA, 5 µl DNA template and 0.25 µl *Taq*-polymerase. Thermal cycling profile for the ETS and ITS regions followed Tosh & al. (2013) and Alejandro & al. (2005), respectively, while for the plastid regions the program started with an initial denaturation at 94°C for 2 min, followed by 35 cycles at 94°C for 45 s, 52-59°C for 1 min, 72°C for 80 s, and ended with a final extension at 72°C for 6 min. All PCR amplicons were purified with QIAquick PCR purification kit (QIAGEN, Germany) and sequenced by Eurofins Genomics (Ebersberg, Germany) or Macrogen Europe (Amsterdam, the Netherlands).

Phylogenetic reconstruction

Sequences from each genetic region were aligned using MAFFT v.7 (Katoh & al., 2017) and adjusted in PhyDE v.0.997 (Müller & al., 2010) following the criteria of Kelchner (2000) and Simmons (2004). For the plastid markers, three post-alignment approaches were performed

Table 1. Primers used in this study.

DNA region	Primer	Sequence 5‘→3‘	Reference
ETS	ETS-Erit-F	CTTGTATGGGTTGGTTGGA	Negrón-Ortiz & Watson (2002)
	18S-E	GCAGGATCAACCAGGTAGCA	Baldwin & Markos (1998)
ITS	P17F	CTACCGATTGAATGGTCCGGTGAA	Popp & Oxelman (2001)
	P16F	TCACTGAACCTTATCATTTAGAGGA	Popp & Oxelman (2001)
	26S-82R	TCCCGGTTCGCTCGCCGTTACTA	Popp & Oxelman (2001)
	P25R	GGGTAGTCCCGCCTGACCTG	Liden & al. (1995)
atpB-rbcL	rbcl5‘R	CTCTTTAACACCAKCYTTGAATCC	Rydin & al. (2008)
	atpB5‘R	CCGATGATTTGGACAATACG	Rydin & al. (2008)
rps16	rpS16F	AAACGATGTGGTARAAAGCAAC	Shaw & al. (2002)
	rpS16R	AACATCWATTGCAASGATTCGATA	Shaw & al. (2002)
trnT-F	trnT-F_a1F	ACAAATGCGATGCTCTAACC	Razafimandimbison & Bremer (2002)
	c	CGAAATCGGTAGACGCTACG	Taberlet & al. (1991)
	e	GGTTCAAGTCCCTCTATCCC	Taberlet & al. (1991)
	trnT-F_iR	CCAACTCCATTTGTTAGAAC	Razafimandimbison & Bremer (2002)
	d	GGGGATAGAGGGACTTGAAC	Taberlet & al. (1991)
	f	ATTTGAACTGGTGACACGAG	Taberlet & al. (1991)

prior to phylogenetic analyses. First, inferred mononucleotide repeats of uncertain length homology and series of inversions were manually excluded. Second, additional ambiguous sites were eliminated using Gblocks v.091b (Castresana, 2000) with the following conditions: -b1 and -b2 were set to half the number of sequences +1, -b3 was 8, -b4 was 5, and -b5 was set to half. Third, gaps and simple sequence repeats were manually coded following Simmons and Ochoterena (2000) and Ochoterena (2009). The coding of these microstructural characters (mch) was only done if the sites could be unambiguously aligned across the sampled taxa and were flanked by conserved sequence motifs. For the nuclear markers, automated curation of ambiguous sites were also conducted in Gblocks, while coding of microstructural characters were not performed because identified gaps were difficult to align and might increase homoplasy in the nuclear dataset.

The matrices of the five genetic markers and the coded microstructural characters (mch) were concatenated for phylogenetic analyses using Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP). Optimal data-partitioning scheme and best-fitting molecular evolution models were estimated under the Bayesian Information Criterion with PartitionFinder v.2.1.1 (Lanfear & al., 2016). The suggested partitioning scheme was *atpB-rbcL+rps16+trnT-F* and ETS+ITS (hereafter referred as chloroplast and nuclear partition, respectively) with GTR+Γ model of evolution for both partitions, but with proportion of invariable sites for the chloroplast partition. For the coded mch, the restriction site model (F81) was applied to consider ascertainment bias in the BI analyses, while the uncorrected BIN model was used for the ML analyses. Congruence of the chloroplast+mch and nuclear partitions was evaluated by visual inspection of the resulting tree topologies from each separate analyses prior to phylogeny estimations using the concatenated dataset.

BI were employed using MrBayes v.3.2.6 (Ronquist & al., 2012) in the CIPRES Science Gateway platform (Miller & al., 2010). Two independent Bayesian Markov chain Monte Carlo (MCMC) of 50 million generations were carried out, with four chains of incremental heating scheme and sampling every 1000 generations. The first 50% of the sampled trees were discarded as burn-in. For the concatenated dataset, substitution rates, base frequencies and rate of heterogeneity were unlinked across the partitions. To ensure convergence of the MCMC simulations, the behavior of the runs were inspected in Tracer v.1.7.1 (Rambaut & al., 2018) and statistics were assessed using RWTY package (Warren & al., 2017). ML analyses were conducted in RAxML v.8.2 (Stamatakis, 2014), but implemented the GTR+I+Γ substitution model for both nucleotide partitions in the analysis of the concatenated dataset because only one set of parameter can be utilized. The trees with the highest likelihood score were obtained with default parameters and 1000 iterations, while node support values were estimated with 10000 bootstrap iterations. MP analyses were performed in PAUP v.4.0 (Swofford, 2002) with a heuristic search procedure of 1000 random addition replicates, tree bisection-reconnection (TBR) branch swapping, MULTREES option in effect and gaps treated as missing data. Bootstrap analyses of 10000 iterations were conducted to evaluate node support with the same heuristic search settings but with no retention of multiple trees per iteration. Based on Hillis & Bull (1993), we regarded the proportion of Bayesian posterior probabilities (PP) ≥ 0.95, Maximum Likelihood bootstrap values (MLBS) ≥ 70 and Maximum Parsimony bootstrap (MPBS) ≥ 70 as the threshold for well-supported clades.

Results

Sequence characteristics

Table 1 summarizes the number of terminals and basic statistics of the aligned molecular sequences and coded microstructural characters (mch) utilized in the phylogenetic analyses (available from J.G.Chavez). Further details concerning the nature, position and motif of the coded mch is made available in suppl. Appendix 1.

The chloroplast partition (excluding coded mch) consisted 3115 sites out of the 3904 aligned positions. The portions of included sites that comprised the partition were: 728 from *atpB-rbcL*, 721 from *rps16* and 1666 from *trnT-F*. Prior to the automated curation of ambiguous sites present in these markers, four microstructural hotspots were excluded. One of these was a 24 bp poly-A/T segment of uncertain length homology (position 382–405 of *atpB-rbcL* alignment; available from J.G.Chavez), while three were short inversions: 1) 8 bp segment in *atpB-rbcL* (position 56447–56454 of *Antirhea chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019), 2) 6 bp segment in *rps*16 (position 5628–5633 of *A. chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019) and 3) 3 bp segment in *trnT-F* (position 48522–48524 of *A. chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019). Unexpectedly, all the genetic markers comprising the chloroplast partition displayed low sequence variation resulting only to 670 variable sites, of which 293 were informative: 61 from *atpB-rbcL*, 89 from *rps16* and 143 from *trnT-F*. On the other hand, the nuclear partition consisted 977 sites after the automated exclusion of ambiguous characters. The two markers in this partition provided the most number of variable sites with a total of 593 positions, 406 of which were informative. The manual search for mch occurrences from each of the chloroplast markers, as described above, resulted to 41 informative binary-coded positions, 26 of which were gap characters and 15 were SSRs (suppl. Appendix 2). Frequency of coded mch were proportional to the length of the genetic marker: 9 from *atpB-rbcL*, 9 from *rps16* and 23 from *trnT-F*. Gap characters have a length of 1 bp to 21 bp, while SSRs ranged from a 2 bp repeat (motif: 5'-TA-3', position 190–191 of *atpB-rbcL* alignment, suppl. Appendix 1) to a 23 bp repeat (motif: 5'-CTGATTAGTTGATAATATTAGTA-3', position 729–751of *atpB-rbcL* alignment, available from J.G.Chavez).

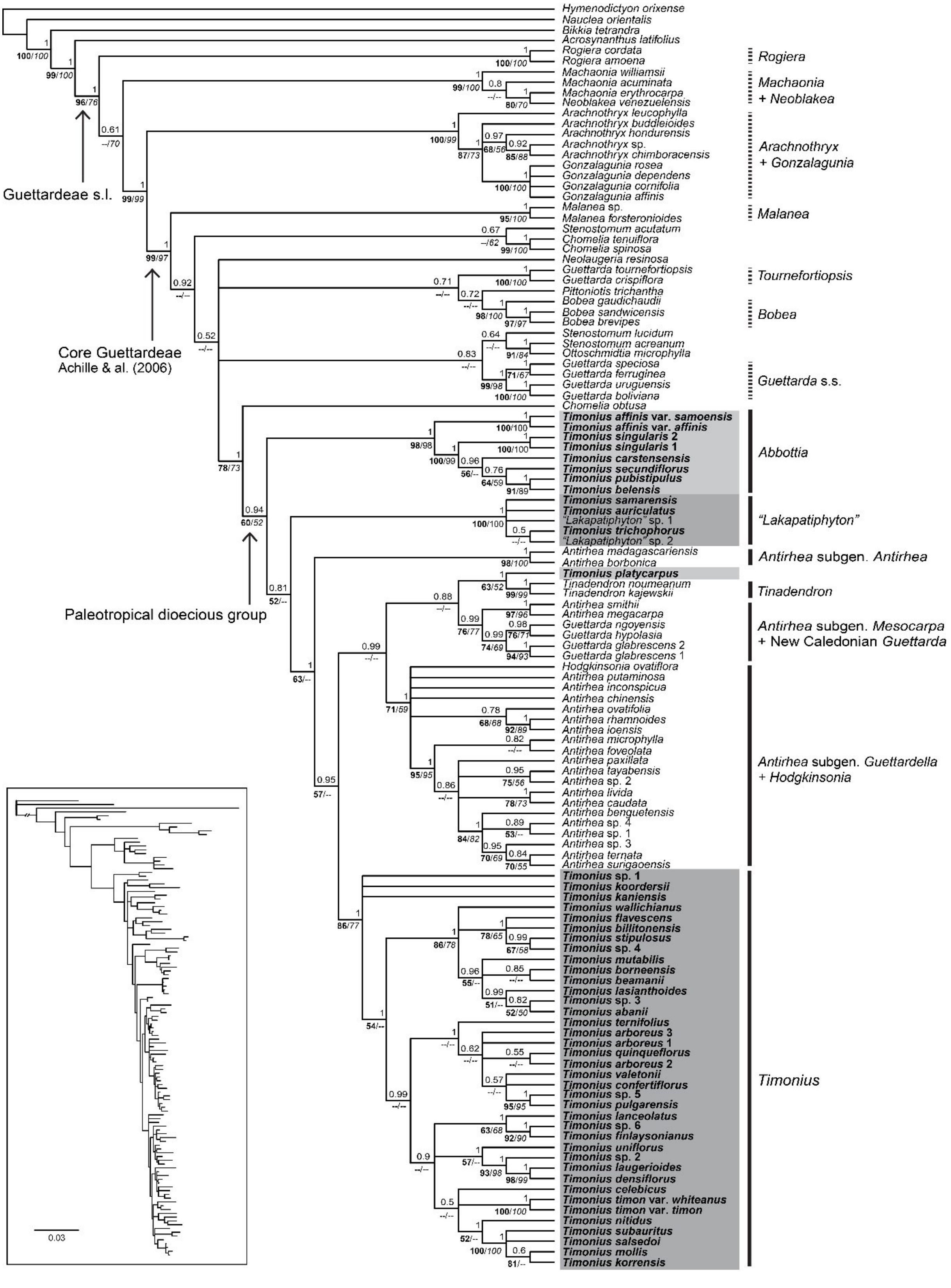


Fig. 2. The Bayesian 50% majority-rule consensus tree based on the combined chloroplast+mch and nuclear partitions. Numbers above branches are BI posterior probabilities, whereas those below branches are ML bootstrap values (boldface) and MP bootstrap values (italics). Dashes indicate bootstrap values < 50. Inset is same tree with BI branch lengths.

Table 2. Characteristics of alignments used in the present study.

Dataset	Nuclear partition		Plastid partition			Combined dataset
	ETS	ITS	*atpB-rbcL*	*rps16*	*trnT-F*	
Number of terminals	88	119	111	97	118	121
Alignment length	498	879	1031	869	2004	5281+41 coded mch
Number of included sites	383	594	728	721	1666	4233+41 coded mch
Variable sites	270	323	131	211	328	1263
Parsimony-informative sites (%)	178 (46.48%)	228 (38.38%)	61 (8.38%)	89 (12.34%)	143 (8.58%)	759+41 coded mch
Coded microstructural characters/ mch	–	–	9 (3 gaps + 6 SSRs)	9 (6 gaps + 3 SSRs)	23 (17 gaps + 6 SSRs)	41

Phylogenetic reconstruction

Comparisons of tree topologies obtained from the separate analyses of the chloroplast+mch and nuclear partitions (suppl. Figs. S1-S2) did not identify well-supported conflicts (PP > 0.95, MLBS > 70, MPBS > 70), although the trees that resulted from the chloroplast+mch partition are less resolved. Thus, these partitions were combined and analyzed in unison. The generated phylogenies from the different tree reconstruction approaches using the combined dataset are concordant and resolutions are enhanced with most of the terminal clades having higher support values than the separate analyses of the two partitions. This suggests that the chloroplast+mch and nuclear partitions simultaneously contribute additional phylogenetic signals. However, the only difference between the three phylogenetic methods is the support values obtained for inter-clade relationships, in which BI provides high to moderate posterior probabilities while ML and MP provide poor bootstrap values (MLBS, MPBS < 70). This is interpreted here as a reflection of the differing approaches in evaluating clade supports by the frequentist technique (bootstrapping) and probabilistic method. In addition, this pattern in the statistical supports within Guettardeae was also observed in the previous study of Achille & al. (2006) where its evolutionary implication was discussed. Given this, the Bayesian consensus tree of the combined dataset is utilized, with ML and MP bootstrap values indicated below branches (Fig. 2). The discussion is only based on this result as it provides the best-supported hypothesis for Guettardeae.

In the topology of the consensus tree (Fig. 2), the core group of Guettardeae (Achille & al., 2006), including *Antirhea*, *Bobea*, *Chomelia*, *Guettarda*, *Malanea*, *Neolaugeria*, *Ottoschmidtia*, *Pittoniotis*, *Stenostomum* and *Timonius*, is retrieved with high support (PP=1.00, MLBS= 99, MPBS= 97). The remaining taxa of the tribe, *Rogiera* (PP=1.00, MLBS= 100, MPBS= 100), *Machaonia* + *Neoblakea* (PP= 1.00, MLBS= 99, MPBS= 100) and *Arachnothryx* + *Gonzalagunia* (PP=1.00, MLBS= 100, MPBS= 99), are indicated as subsequent sisters to this core group. Within the core Guettardeae, a polytomy is inferred constituting Neotropical representatives and *Bobea*. Nevertheless, some of the terminal clades in this polytomy are well-supported, these are: *Bobea* (PP= 1.00, MLBS= 98, MPBS= 100), *Guettarda crispiflora* + *G. tournefortiopsis* ("*Tournefortiopsis*"; PP= 1.00, MLBS= 100, MPBS= 100) and *Guettarda* s.s. (PP= 1.00, MLBS= 99, MPBS= 98). On the other hand, the Paleotropical dioecious genera as interpreted in Achille & al. (2006) are retrieved in a clade, albeit receiving moderate posterior probabilities (PP= 0.94) and low bootstrap supports (MLBS= 60, MPBS= 52). The South American *Chomelia obtusa* is shown as sister to this clade (PP=1.00, MLBS= 78, MPBS= 73).

The Paleotropical dioecious group is divided into seven well-supported clades (Fig. 2), and indicates the polyphyly of *Timonius*, as well as the genus *Antirhea* as understood by Chaw & Darwin (1992). The first clade (*Abbottia*; PP= 1.00, MLBS= 98, MPBS= 99) is formed by *T. affinis*, *T. belensis*, *T. carstensensis*, *T. pubistipulus*, *T. secundiflorus* and *T. singularis*. The second clade (*Lakapatiphyton*; PP=1.00, MLBS= 100, MPBS= 100) contains the two species of *Lakapatiphyton* and three species of *Timonius* from the Philippines (*T. auriculatus*, *T. samarensis* and *T. trichophorus*). *Antirhea* subgen. *Antirhea*, comprised only of species native to the Indian Ocean, is indicated as the third monophyletic group (PP= 1.00, MLBS= 98, MPBS= 100). The New Caledonian endemic and bitypic genus *Tinadendron* represents the fourth clade (PP= 1.00, MLBS= 99, MPBS= 99) to which *Timonius platycarpus* is retrieved as its sister with high support from BI but received low supports in ML and MP (PP= 1.00, MLBS= 63, MPBS= 52). The fifth clade consists of representatives of *A.* subgen. *Mesocarpa* along with three species of New Caledonian *Guettarda* (*G. glabrescens*, *G. hypolasia* and *G. ngoyensis*) (PP= 0.99, MLBS= 76, MPBS= 77). Representatives of *Antirhea* subgen. *Guettardella* and the Australian monotypic *Hodgkinsonia* are retrieved to comprise the sixth clade that is well-supported by BI and ML but poorly supported by MP (PP= 1.00, MLBS= 71, MPBS= 59). Lastly, the remaining accessions of *Timonius* are recovered in a well-supported clade (*Timonius*; PP= 1.00, MLBS= 86, MPBS= 77).

Discussion

The molecular evidence presented here (Fig. 2) conclusively demonstrates that *Timonius* is polyphyletic. Its species are distributed in three well-supported clades: 1) *Abbottia*, 2) *Lakapatiphyton* and 3) *Timonius*, while *T. platycarpus* has an isolated position and was retrieved as sister to *Tinadendron*. Interestingly, the placement of *Abbottia* and *Timonius* clades in the phylogenetic tree reconciles the discordant presumptions of Achille & al. (2006) and Pessoa (2016) regarding the phylogenetic status of *Timonius*. It is important to note that the monophyly of *Timonius* presented in Achille & al. (2006) was based only on five species, i.e. *T. densiflorus*, *T. flavescens*, *T. nitidus* (Bartl. ex DC.) Fern.-Vill., *T. timon* and *T. polygamus* (G.Forst.) B.L.Rob., nom. illeg. [=*T. uniflorus* (Baks ex C.F.Gaertn.) Govaerts], which may have obscured their assertion. Here, these five species, together with the majority of the sampled *Timonius* accessions, emerged within the *Timonius* clade. The retrieval of *Timonius* clade in this study have expanded the clade for the genus presented in Achille & al. (2006: fig. 2). Its placement as sister to the clade composed of Tropical Western Pacific *Antirhea,* New Caledonian *Guettarda* and *Tinadendron* also coincides with the relationship they have inferred. On the other hand, Pessoa (2016), with a more limited sampling of *Timonius*, *T. affinis* and *T. timon*, recovered the former species as the earliest lineage to all Paleotropical dioecious Guettardeae genera. Her findings on the phylogenetic placement of *T. affinis* is congruent with the results presented here, as this species was placed in the early diverging *Abbottia* clade (Fig. 2).

Given the extensive polyphyly of *Timonius* and if its monophyly is to be maintained, the two early diverging clades (*Abbottia* and *Lakapatiphyton*) and *T. platycarpus* need to be recognized as distinct genera, while *Timonius* must be limited to the clade containing its type species, *T. timon*. If the genus is expanded beyond *Timonius* clade., i.e. to include *Antirhea*, *Hodgkinsonia*, New Caledonian *Guettarda* and *Tinadendron*, it will be superseded in priority by the older name *Antirhea* (Jussieu, 1789) as it was not conserved against it (see Achille & al., 2006 for discussion regarding the preference over *Guettarda*). This expanded concept is not taxonomically advisable because it will necessitate the transfer of a great number of species names to *Antirhea* and will make the genus indefinable by any unique combination of morphological characters. In addition, the three well-supported clades of *Antirhea* (Fig. 2) are morphologically distinct and the re-circumscription of these groups will be discussed elsewhere. Fortunately, the splitting approach for *Timonius* is feasible since the three clades and *T. platycarpus* can be distinguished by a suite of phenotypic and molecular characters that is simultaneously consistent with the phylogenetic framework.

Abbottia clade

This clade is comprised of *T. singularis* (Fig. 1I) and of species that are associated to it morphologically (subgenus *Abbottia*; Darwin, 1994). Mueller (1875), initially circumscribed *T. singularis* in his monotypic *Abbottia* that is characterized by truncate calyces, induplicate-valvate corollas, stamens with adnate filaments, anthers that are partly cohering to the corolla tube and unilocular and many-seeded fruits. Baillon (1880), then highlighted the close relation of *Abbottia* to *Timonius* due to their similarities in the structure of their stamens (united) and pyrenes (separate). However, the distinctiveness of *Abbottia* was still retained by Bailley (1900) and Schumann (1891), but was then contradicted by Smith (1957), arguing that Mueller's species is related to *T. avenis* Valeton and reducing *Abbottia* as congeneric to *Timonius*. Later, Darwin (1994), who is focused on inferring a possible useful infrageneric classification scheme within *Timonius*, proposed subgenus *Abbottia* that is typified by *T. singularis*. This subgenus, composed of twenty-nine species, is united by the combination of hemiepiphytism (resembling that of *Ficus* L.; Fig. 3A), individually caducuous imbricate stipules with single-thickened costa and acuminate apices (Fig. 3B), leaves with reticuli-paxillate venation (Fig. 3D–E) and truncate or undulate calyces (Fig. 1) (Darwin, 1994). Another character presented by Darwin (1994) for subgenus *Abbottia* is the obscure or reduced secondary nerves of the leaves (Fig. 3C), but he noted that this is correlated to the thickness of the lamina. A distinguishable secondary venation is observed in *T. bougainvillensis* Merr. & L.M.Perry, as well in some individuals of *T. affinis* Valeton and *T. appendiculatus* Merr.

The retrieval of *Abbottia* clade in this study as a distinct lineage (Fig. 2) clearly illustrates that Mueller's (1875) generic name needs to be resurrected and expanded to include Darwin's (1994) subgenus *Abbottia*. Conversely, the set of morphological characters presented in Darwin (1994) may not be enough to distinguish *Abbottia* because some of the features are found in other Guettardeae taxa, especially in *Timonius*, i.e. epiphytism (*T. caudatifolius* Elmer, *T. caudatus* Valeton, *T. epiphyticus* Merr., *T. filipes* Wernham, *T. longistipulus* Merr., *T. minutifolius* Valeton), reticuli-paxillate venation (*Antirhea paxillata* Chaw: Chaw & Darwin,

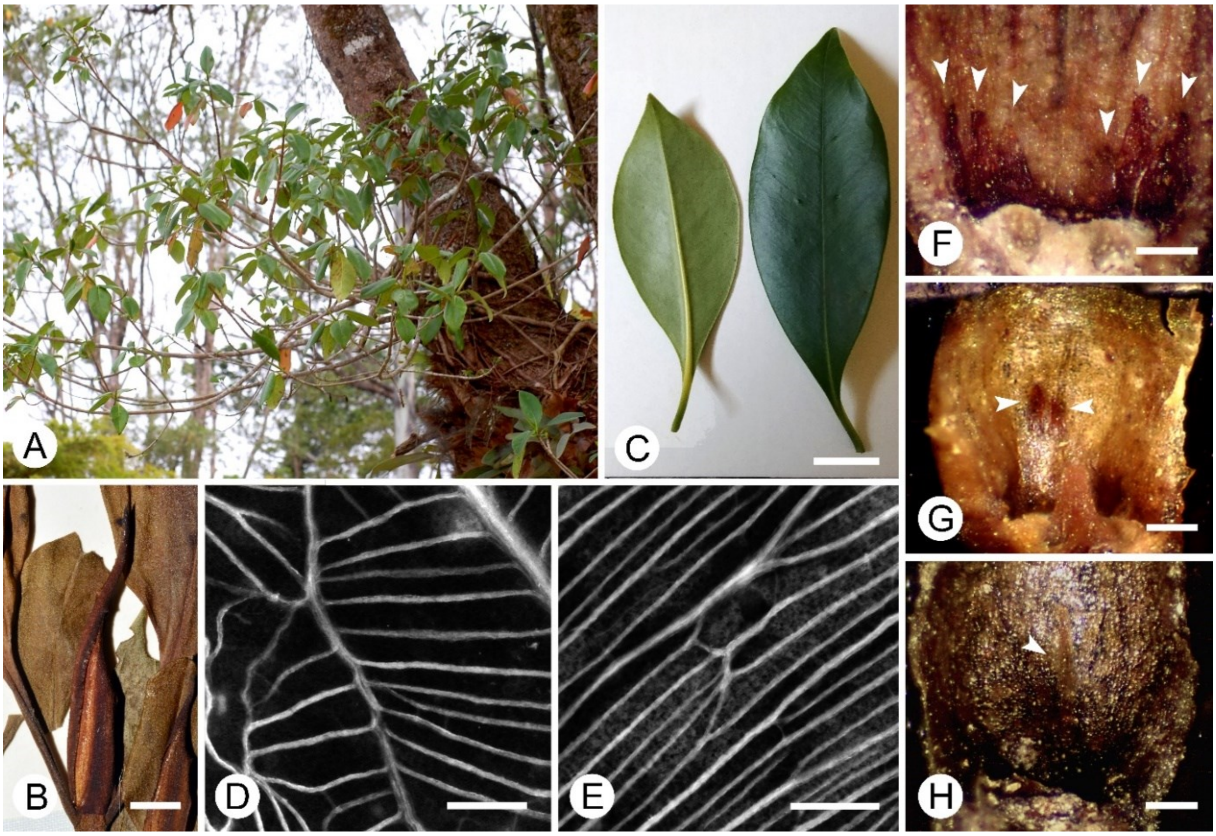


Fig. 3. Key morphological features of *Abbottia* clade: **A,** Hemiepiphytic habit; **B,** Stipules, imbricate with acuminate apex and single thickened costa; **C,** Leaves showing reduced or obscure secondary nerves; **D-E,** Leaf areolation without free-ending veinlets; **F-H,** Calycine colleters along the middle or lower-half of the calyx tube. **A, C, E,** *T. singularis*; **B, D, F,** *T. affinis* var. *affinis*; **G,** *T. belensis*; **H,** *T. secundiflorus*. — Voucher data: B, F, *A.C. Smith 4159*; D, *A.C. Smith 6794*; E, *P.I. Forster 26423*; G, *L. Brass 30619*; H, *R.D. Hoogland & L.A. Craven 10950*. — Scale bars: B, 0.75 cm, C, 1 cm; D-E, 0.5 mm; F-H, 0.25 mm. — Photos: A by David Tng; C by Vhon Oliver S. Garcia; B, D-G by Jayson G. Chavez.

1992; *Stenostomum* C.F.Gaertn.: Moynihan & Watson, 2000) and truncate calyces (*T. rivularis* Merr. & L.M.Perry). The morphological examination of species that are attributed here in *Abbottia* revealed the presence of calycine colleters that was not reported by Darwin (1994). These calycine colleters are distributed along the middle or lower half of the inner surface of calyx tubes (Fig. F–H), an orientation that is not found in *Timonius* (see discussion below and Darwin, 1993). Thus, *Abbottia* is here redefined by the unique combination of characters presented in Darwin (1994) and of the nature of its calycine colleters. In addition, the sampled species of *Abbottia* has a C→A transversion at position 609 of the aligned *rps16* dataset (available from J.G.Chavez) which is not inferred in other Guettardeae taxa.

Lakapatiphyton clade

This clade is composed only of *Timonius* species that are endemic to the Philippines (Fig. 2) and of *Lakapatiphyton* sp. 1 and sp. 2. The apparent unresolved internal relationships within *Lakapatiphyton* clade may be reflected in the low sequence divergence (*Kimura 2-parameter*) for the utilized genetic markers among the species: ETS (< 0.0079), ITS (< 0.0122), *atpB-rbcL* (< 0.0014), *rps16* (< 0.0016) and *trnT-F* (<0.0036), which is in contrast to the high level of morphological variation. This phenomenon could be attributed to rapid radiation that is typical to island genera (e.g.; Baldwin & al., 1990; Jorgensen & Frydenberg, 1999; Kim & al., 1996; Gemmill & al., 2002; Kapralov & Filatov, 2006; Knope & al., 2012).

All of the included species in this clade exhibit a form of leaky dioecism (Baker & Cox, 1984), in which staminate individuals are occasionally labile and produce flowers with functional gynoecia that lead to their capacity to develop fruits and seeds. Such display of inconstant sex expression of staminate individuals had also been reported in *Antirhea borbonica* (Litrico & al., 2005) and other rubiaceous genera, namely: *Coprosma* J.R.Forst. & G.Forst. (Fosberg, 1937; Godley, 1979) and *Nesohedyotis* (Hook.f.) Bremek. (Percy & Cronk, 1997). The most prominent morphological characters of this clade are the adpressed ± foliaceous stipules with obtuse to rounded apices, monomorphic staminate and pistillate inflorescences that are ebracteate (inflorescences are simple to compound dichasial cymes bearing equivalent number of flowers), tri- to tetramerous and ebracteolate flowers and calyces without colleters (Fig. 4). In addition, the grouping of *Lakapatiphyton* can be ascertained by the alignment of the utilized plastid markers which shows two defining molecular apomorphies that are absent in all sampled Guettardeae taxa (available from J.G.Chavez), these are: 1) 5 bp simple sequence repeat within *atpB-rbcL* (motif 5’ TAACA 3’, position 56969-56973 of *Antirhea chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019) and 2) 6 bp simple sequence repeat within *trnT-L* region (motif 5’ TATAAA 3’, position 48603-48608 of *A. chinensis* chloroplast genome, GenBank accession: MK102723; Fan & al., 2019). These phenotypic and genetic features clearly demonstrate that *Lakapatiphyton* clade can be recognized to represent a novel genus. This taxonomic judgment will also necessitate the transfer of four additional Philippine *Timonius* species that were not sampled in the phylogeny to the new genus, since their features fall within the morphological characteristics of this group.

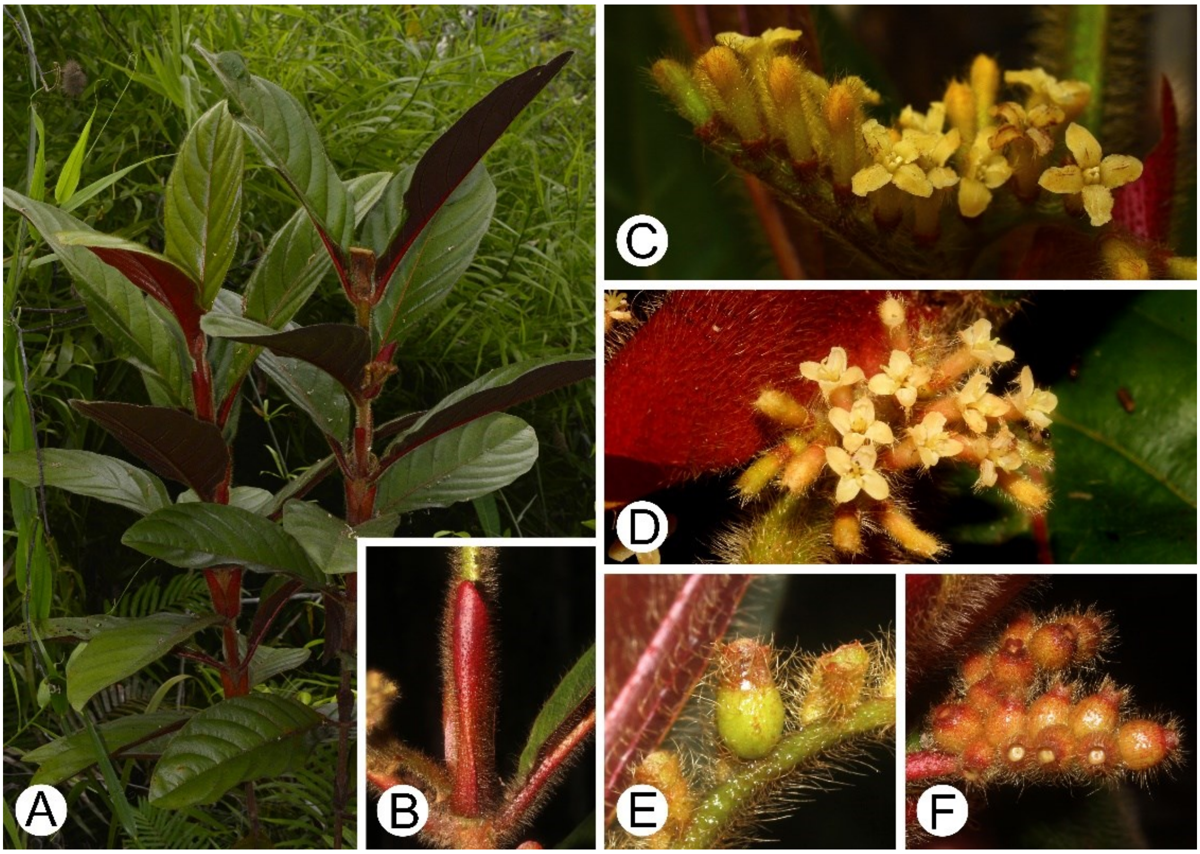


Fig. 4. Key morphological features of *Lakapatiphyton* clade: **A,** Free-standing habit; **B,** Stipules, ± foliaceous with rounded apex; **C-D,** Monomorphic inflorescences: **C,** Staminate inflorescence, **D,** Pistillate inflorescence; **E,** Fruit of "leaky" staminate individual; **F,** Infructescence of pistillate individual. All from: *L. pulcherrimum* sp. nov., the type species of *Lakapatiphyton* gen. nov. Photos: A, C by Jayson G. Chavez; B, D-F by Jay Edneil C. Olivar.

Timonius platycarpus

The New Caledonian endemic *T. platycarpus* (Fig. 1G) has always been a morphologically odd element in the genus because it exhibits drupes with united pyrenes. The treatment of Montrouzier (1860) for this species was supported by Schlechter (1907) who had a broad concept of *Timonius* that includes New Caledonian species of *Guettarda* previously described by Baillon (1879). Guillaumin (1930, 1948) opposed this view, reverting to Baillon's (1879) concept for New Caledonian *Guettarda* and proposed the new combination, *G. platycarpa* (Montrouz.) Guillaumin. In spite of this, Govaerts & al. (2019) only partially adopted the proposal of Gauillaumin (1930, 1948) and still retained the species in *Timonius*. In the phylogenetic analysis (Fig. 2), *T. platycarpus* was recovered in a clade together with *Tinadendron*, where it differs morphologically by its monochasial and sexually dimorphic inflorescences (dichasial and monomorphic in *Tinadendron*), valvate corollas (imbricate) and linear stigmatic arms (flattened or capitate to slightly bilobed). These combination of characters suggests that *T. platycarpus* is best accommodated in a genus of its own. However, the proposal of a new generic name for this species will not be made here as it corresponds to "*Genre nov. A*" presented in Achille (2006) and that a wider sampling of New Caledonian *Guettarda* is required to shed more light on its circumscription.

***Timonius* clade**

This clade constitutes a narrower concept of *Timonius*. It is comprised of the remaining accessions of the genus, including its type species (*T. timon*, Fig. 1K) and the types of two other genera conserved against it, i.e. *Helospora* (*T. flavescens*, Fig. 1D) and *Burneya* (*T. uniflorus*, Fig. 1M). Although this study was also able to sample three species and one variety that are included in the other infrageneric groupings proposed by Darwin (1993, 1997, 2010), i.e. subgenus *Timonius* (*T. timon* var. *timon*, *T. timon* var. *whiteanus* (S.Moore) S.P.Darwin), subgenus *Pseudobobea* (*T. minahassae* Koord.) and *T. flavescens* alliance (*T. flavescens*), the available data is limited and can neither be utilized to confirm nor repudiate the naturalness of his classification scheme. Furthermore, the species relationships within *Timonius* clade reflect geographical provenance rather than morphological similarities, but a more detailed phylogenetic investigation is necessary to establish this pattern of speciation.

All investigated species of *Timonius* in this clade are shrubs or trees. Attempts to obtain DNA from herbarium specimens of epiphytic species (discussed above) were repeatedly unsuccessful. Thus, the morphological features for *Timonius* presented here are constrained by the resolution of the phylogeny and its representatives with terrestrial habit that coincides with the characters of *T. timon*, as well as *T. flavescens* and *T. uniflorus*, so not to over-interpret potential synapomorphic features. The combination of phenotypic characters of *Timonius* as inferred in this study rely on the nature of stipules, leaves, inflorescences, calyx and calycine colleters. The stipules of *Timonius* are imbricate, valvate or calyptrate, without a thickened single costa, while some are slightly or evidently two-ridged with the ridges converging toward the acute to acuminate apex; distinguishing it from the imbricate with triangular thick costa in

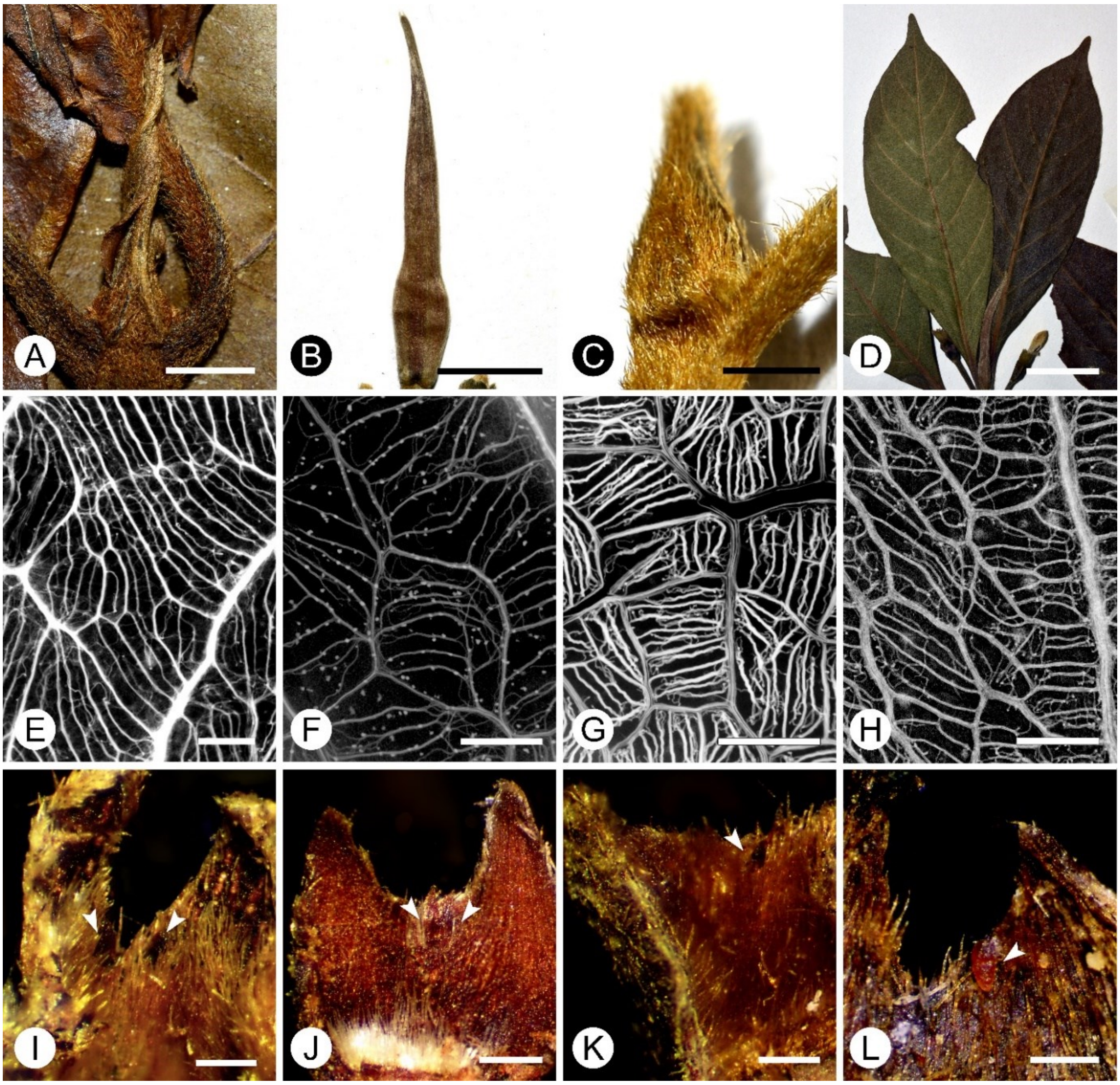


Fig. 5. Morphological features of representative species of *Timonius* clade: **A,** Imbricate stipules, ridges converging toward apex; **B,** Valvate-calyptrate stipules; **C,** Valvate stipules, ridges converging toward apex; **D,** Leaves with evident secondary nerves; **E-H,** Lear areolation with free-ending veinlets; **I-L,** Calycine colleters (if present) along sinus of calyx teeth or lobes. **A,** *T. kaniensis*; **B, D, H,** *T. timon*; **C, K,** *T. mutabilis*; **E,** *T. borneensis*; **F,** *T. finlaysonianus*; **G,** *T. nitidus*; **I,** *T. abanii*; **J,** *T. lasianthoides*; **L,** *T. ternifolius*. — Voucher data: A, *W. Takeuchi & al. 19282*; B, D, *E. Baltisberger & al. 11804*; C, K, *P.J.A. Kessler 632*; E, *A.C. Church & al. 1742*; F, *M. Lorenzo LL063*; G, *G.C. Moore 466*; H, *L.J. Brass 28174*; I, *K.M. Wong 2375*; J, *O. Ismawi 33721*; L, *C.I.Banag LM006*. — Scale bars: A, 0.5 cm; B, 1 cm; C, 2 mm; D, 2 cm; E-H, 0.5 mm; I-L, 0.25 mm. — Photos: Jayson G. Chavez.

Abbottia and adpressed ± foliaceous with rounded apices in *Lakapatiphyton*. The variability of stipule aestivation in *Timonius* was utilized by Darwin (1993, 1997, 2010) as one of the characters to distinguish subgenus *Timonius* (valvate-calyptrate), *T. flavescens* alliance (valvate or subimbricate) and subgenus *Pseudobobea* (strongly imbricate).

The evident secondary nerves and free-ending veinlets (Fig. 5E–H) of *Timonius* differ from *Abbottia*, in which the leaves have obscure secondary venation and have no free-ending veinlets (Fig. 3D–E). The inflorescences of *Timonius* are sexually dimorphic, wherein pistillate inflorescences have fewer flowers and are often reduced to one. This contrasts with *Lakapatiphyton*, which have monomorphic staminate and pistillate inflorescences. Calyces of *Timonius* are toothed or lobed and only reported to be truncate in *T. rivularis* (Merrill & Perry, 1945; Darwin, 1993). Lastly, calycine colleters are predominantly absent in *Timonius* unlike in *Abbottia* where they are present in all species. The calycine colleters in *Timonius*, if present, are located on the sinuses of calyx lobes or teeth (Fig. 5I–L), in contrast to *Abbottia* where the calycine colleters are distributed along the middle or lower half of the calyx tube (Fig. 3F–H). Darwin (1993) has also reported such feature for *Timonius*, but did not emphasize this character since he only observed it in *T. nitens* Merr. & L.M.Perry. Nevertheless, the presence of calycine colleters in *Timonius* as reported here is not correlated with the type of calyx (toothed or lobed) exhibited by its species because it is found on both types. Aside from these morphological characters, the ITS alignment have revealed a 2 bp insertion (position 779–780 of ITS alignment, suppl. Appendix 1) in the sampled species within *Timonius* clade. This molecular apomorphy is unique to this group and cannot be found in other Guettardeae taxa.

In conclusion, this study shows that *Timonius*, as currently delimited, is unnatural and necessitates re-circumscription. The widely accepted combination of interlocking valvate corollas and drupes with free pyrenes is not enough to delimit *Timonius*, as this set of characters has evolved several times within the Paleotropical dioecious Guettardeae. The morphological data and molecular apomorphies are congruent with the results of the phylogenetic study, although the unequivocally identified synapomorphies for the narrower concept of *Timonius* is still precluded by the inadequate sampling. The molecular phylogeny, however, provides strong support for the re-instatement of *Abbottia*, the transfer of species of *Timonius* subgenus *Abbottia* to the resurrected genus and the recognition of the new genus *Lakapatiphyton*. On the other hand, the possible description of the genus that will accommodate *T. platycarpus* is left for authors working on the revision of New Caledonian *Guettarda*, which might still be an ongoing study of Frédéric Achille. These taxonomic decisions for some of the species of *Timonius* gives more constancy in its delineation that is also warranted in providing the much needed stability regarding the application of other Guettardeae genera.

Taxonomic treatment

Abbottia F.Muell., Fragm. 9: 181. 1875. ≡ *Timonius* subgenus *Abbottia* S.P.Darwin, Syst. Bot. Mongr. 42: 17. 1994. – Type: *Abbottia singularis* F.Muell. [≡ *Timonius singularis* (F.Muell.) L.S.Sm.].

Distinguishing features. The diagnostic features of *Abbottia* is amended here to include Paleotropical dioecious Guettardeae species with drupes bearing multiple, free single-seeded pyrenes that are hemiepiphytic to free-standing shrubs or trees with strongly imbricate and individually caducous stipules that have acuminate apices and thickened costa, leaves with obscure or occasionally profound secondary nerves and no free-ending veinlets (reticuli-paxillate), inflorescences with variable sexual dimorphism and flowers with calycince colleters that are distributed on the middle or lower-half of the calyx tube.

Abbottia affinis (A.Gray) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius affinis* A.Gray, Proc. Amer. Acad. Arts. 4: 36. 1860. – Holotype: Fiji. *s. loc.*, 1838, ♀, *Wilkes U.S. Explor. Exped. s.n.* (US barcode US00956410 [image!]; isotype: GH barcode GH00312965 [image!]

a. ***Abbottia affinis* var. *affinis***

b. ***Abbottia affinis* var. *samoensis*** (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius affinis* var. *samoensis* S.P.Darwin, Syst, Bot. Monogr. 42: 28. 1994. – Holotype: Samoa. Savaii, above Sili, 11 Nov 1931, ♀, *E. Christophersen 3246* (BISH barcode BISH1004768 [image!]; isotypes: A barcode A00246686 [image!], BISH barcode BISH1004767 [image!]).

c. ***Abbottia affinis* var. *sapotifolia*** (A.Gray) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius sapotifolius* A.Gray, Proc. Amer. Acad. Arts 4: 35. 1860. ≡ *Timonius affinis* var. *sapotifolius* (A.Gray) Fosberg, Sargentia 1: 121. 1942. – Holotype: Fiji. *s. loc.*, 1838,

♀, *Wilkes U.S. Explor. Exped. s.n.* (US barcode US00956409 [image!]; GH barcode GH00338893, K barcode K000763668 [image!]).

Abbottia amungwiwanensis (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius amungwiwanensis* S.P.Darwin, Syst. Bot. Mongr. 42: 94. 1994. – Holotype: Papua New Guinea. Morobe, Mt. Amungwiwa, 12 Jun 1976, ♀, *P. van Royen 11085* (BISH barcode BISH1004769 [image!]; isotypes L barcode L0001387!, US barcode US01049647 [image!]).

Abbottia appendiculata (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius appendiculatus* Merr., Philipp. J. Sci,, C 4: 327. 1909. – Lectotype, designated here: The Philippines. Luzon, Rizal, Antipolo, Jan 1907, ♂, *M. Ramos sub BS 2164* (US barcode US00138412!; isolectotypes: BO!, NY barcode NY00133413 [image!]).

Abbottia avenia (Valeton) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius avenis* Valeton, Bull. Dép. Agric. Indes Néerl. 26: 46. 1909. – Holotype: Indonesia, New Guinea, Geluksheuvel, 1907, ♀, *G.M. Versteeg 1457* (BO *n.v.*; isotypes: B barcode 100295994 [image!], L barcode L0001391!, U barcode 0006325!).

a. ***Abbottia avenia* var. *avenia***

b. ***Abbottia avenia var. magnifructa*** (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius avenis* var. *magnifructus* S.P.Darwin, Syst. Bot. Monogr. 42: 36. 1994. – Holotype: Indonesia. New Guinea, Manokwari, Vogelkop, Arfak, Angi gita Lake, Sep-Oct 1948, ♀, *A. Kostermanns 2220* (BO *n.v.*; isotypes: A barcodes A00246670 [image!] and A00246671 [image!], K barcode K000763533 [image!], L barcodes L0001392! and L0001393!).

c. ***Abbottia avenia* var. *pubipetala*** (Valeton) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius avenis* var. *pubipetalus* Valeton, Bot. Jahrb. Syst. 61: 37. 1927. ≡ *Timonius pubipetalus* (Valeton) Merr. & L.M.Perry, J. Arnold Arbor. 26: 236.1945. – Lectotype, designated by Darwin (1994: 36): Papua New Guinea. East Sepik, Sepikgebiet, Aug 1913, ♀, *C.L. Ledermann 12678* (L barcode L0001459!).

d. ***Abbottia avenia* var. *vogelkopensis*** (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius avenis* var. *vogelkopensis* S.P.Darwin, Syst. Bot. Monogr. 42: 37. 1994. – Holotype: Indonesia. Vogelkop Peninsula, Lake Ajamaru, 10 Mar 1962, ♀, *W. Vink & M. Vink BW 15269* (A barcode A00246741 [image!]; isotypes: B barcode B100295993 [image!], BRI barcode BRI-AQ0129806 [image!], K barcode K000763532 [image!], L barcode L0001394!).

Abbottia belensis (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius belensis* Merr. & L.M.Perry, J. Arnold Arbor. 26: 236. 1945. – Holotype: Indonesia, New Guinea, Bele River, Nov 1938, ♀, *L.J. Brass 11527* (A barcode A00246742 [image!]; isotypes: BM barcode BM000945299 [image!], BRI barcode BRI-AQ0318309 [image!], L barcodes L0001395! and L0001396!).

Abbottia bismarckensis (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius bismarckensis* S.P.Darwin, Syst. Bot. Monogr. 42: 40. 1994. – Holotype: Papua New Guinea. New Britain, Talasea, south of Cape Ruge, 11 May 1966, ♀, *D. Frodin NGF 26763* (A barcode A00246743 [image!]; isotypes: BRI barcode BRI-A0129735 [image!], L barcode L0001397!, NY barcode NY01288261 [image!], SING barcode SING0058066 [image!], US barcode US01049648 [image!]).

Abbottia bougainvillensis (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius bougainvillensis* Merr. & L.M.Perry, J. Arnold Arbor. 26: 249. 1945. – Holotype: Solomon Islands. Bougainville Island, 10 Apr 1930, ♀, *S.F. Kajewski 1677* (A barcode A00246755 [image!]; isotypes: BISH barcode BISH1004770 [image!], BM barcode BM001040311 [image!], BRI barcode BRI-AQ0318311 [image!], G barcode G00436804 [image!], L barcode L0001398!, S barcode S-G-6105 [image!]).

Abbottia carstensensis (Wernham) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius carstensensis* Wernham, Trans. Linn. Soc. London, Bot. 9: 73. 1916. – Lectotype, designated by Darwin (1994: 43): Indonesia. New Guinea, Utakawa River to Mt. Carstensz, 27 Jan 1913, ♀, *C. Boden Kloss s.n.* (BM barcode BM000945297 [image!]).

Abbottia cryptophlebia (S.Moore) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius cryptophlebus* S.Moore, Proc. Roy. Soc. Queensland 34: 55. 1922. Holotype: Papua New Guinea. Dilava, Jul-

Aug 1918, ♀, *C.T. White 428* (BM barcode BM000945295 [image!]; isotype: BRI barcode BRI-AQ0431392 [image!]).

Abbottia dolichophylla (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius trichanthus* var. *dolichophyllus* Merr. & L.M.Perry, J. Arnold Arbor. 26: 239. 1945. ≡ *Timonius dolichophyllus* (Merr. & L.M.Perry) S.P.Darwin, Syst. Bot. Monogr. 42: 47. 1994. Holotype: Indonesia. New Guinea, Bernhard Camp, Idenburg River, Jan 1939, ♀, *L.J. Brass 12398* (A barcode A00338871 [image!]; isotypes: BM barcode BM000945277 [image!], BRI barcode BRI-AQ0318345 [image!], L barcode L0001407!).

Abbottia heptamera (Wernham) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius heptamerus* Wernham, Trans. Linn. Soc. London, Bot. 9: 73. 1916. – Holotype: Indonesia. New Guinea, Utakwa River to Mt. Carstenz, Feb 1913, ♀, *C. Boden Kloss s.n.* (BM barcode BM000945292 [image!]).

Abbottia lamii (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius lamii* S.P.Darwin, Syst. Bot. Monogr. 42: 49. 1994. – Holotype: Indonesia. New Guinea, Doormantop, 9 Oct 1920, ♂, *H.J. Lam 1572* (L barcode L0001421!; isotypes: A barcode A00338901 [image!], BRI barcode BRI-AQ0431393 [image!], L barcode L0001420!).

Abbottia longifolia (Valeton) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius longifolius* Valeton, Bot. Jahrb. Syst. 61: 44. 1927. – Neotype, designated by Darwin (1994: 50): Papua New Guinea. Sepik, Ambunti, Hunstein River along Yapa, 26 Jul 1966, ♀, *R.D. Hoogland & L.A. Craven 10663* (A barcode A00338903 [image!]; isoneotypes: BRI barcode BRI-AQ0129720 [image!], K barcode K000763531 [image!], L barcode L0001427!, US barcode US01049645 [image!]).

Abbottia longituba (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius longitubus* Merr. & L.M.Perry, J. Arnold Arbor. 26: 241. 1945. – Holotype: Solomon Islands. Ysabell Island, Tiratona, 8 Dec 1932, ♀, *L.J. Brass 3316* (A barcode A00338904 [image!]; isotypes: BISH barcode BISH1004775 [image!], BM barcode BM001040310 [image!], BRI barcode BRI-AQ0318327 [image!], L barcode L0001428!).

a. *Abbottia longituba* var. *longituba*

b. ***Abbottia longituba* var. *pubescens*** (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius longitubus* var. *pubescens* S.P.Darwin, Syst. Bot. Monogr. 42: 54. 1994. Holotype: Papua New Guinea. New Britain, Gasmata, Torlu River, 25 Mar 1965, ♀, *D. Sayers NGF 24225* (A barcode A00338905 [image!]; isotypes: BISH barcode BISH1004776 [image!], BRI barcode BRI-AQ0129746 [image!], L barcode L0001429!, K barcode K000763530 [image!], SING barcode SING0058061 [image!]).

Abbottia meridionalis (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius meridionalis* S.P.Darwin, Syst. Bot. Monogr. 42: 55. 1994. – Holotype: Papua New Guinea. Milne Bay, Goodenough Island, 15-22 Oct 1953, ♀, *L.J. Brass 24773* (A barcode A00338907 [image!]; isotypes: CANB barcode CANB124577 [image!], K barcode K000763529 [image!], L barcode L0001432 [image!], US barcode US01049649 [image!]).

Abbottia modesta (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius modestus* Merr. & L.M.Perry, J. Arnold Arbor. 26: 237. 1945. – Holotype: Papua New Guinea. Fly River, May 1936, ♀, *L.J. Brass 6748* (A barcode A00338909 [image!]; isotypes: BM barcode BM000945284 [image!], BRI barcode BRI-AQ0318331 [image!], L barcode L0001435!)

Abbottia neobrittanica (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius neobritannicus* S.P.Darwin, Syst. Bot. Monogrp. 42: 59. 1994. – Holotype: Papua New Guinea. Morobe, Finschhafen-Umboi Island, Liplip-Mambi River area, 5 Oct 1974, ♀, *B. Conn & P. Katik LAE 66113* (A barcode A00338911 [image!]; isotypes: BRI barcode BRI-AQ0373043 [image!], CANB barcode CANB463215 [image!], K barcode K000763528 [image!], L barcode L0001441!).

Abbottia oktediensis (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius oktediensis* S.P.Darwin, Syst. Bot. Monogr. 42: 60. 1994. – Holotype: Papua New Guinea. Western District, Kiunga, Ok Tedi Headwaters near Kennecott field camp, 29 Oct 1969, ♂, *E.E. Henty, D.B. Foreman & M. Galore NGF 42793* (LAE *n.v.*; isotypes: A barcode A00338878 [image!], BRI barcode BRI-AQ0129770 [image!], K barcode K000763527 [image!], L barcode L0001446!).

Abbottia pachyphylla (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius pachyphyllus* Merr., Philipp. J. Sci. 26: 494. 1925. – Lectotype, designated by Chavez & al. (2017: 146): The

Philippines. Luzon, Rizal, Mt. Angilog, Apr 1922, ♀, *M. Ramos sub BS 40794* (P barcode P03906974!; isolectotypes: A!, K barcode K000763548 [image!]).

Abbottia pseudaffinis (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius pseudaffinis* S.P.Darwin, Syst. Bot. Monogr. 42: 63. 1994. – Holotype: Solomon Islands. Santa Ysabel, Tatamba, 5 Oct 1965, ♀, *P.F. Hunt 2876* (A barcode A00246666 [image!]; isotype L barcode L0001452!).

Abbottia pubistipula (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius pubistipulus* S.P.Darwin, J. Arnold Arbor., 64: 612. 1983. – Holotype: Papua New Guinea. Western Highlands, Minj, 30 Jul 1957, ♀, *R. Pullen 268* (A barcode A00338882 [image!]; isotypes: G barcode G00436801 [image!], L barcode L0001454!, US barcode US00138431 [image!]).

a. ***Abbottia pubistipula*** **var.** ***pubistipula***

b. ***Abbottia pubistipula*** **var.** ***pubescens*** (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius pubistipulus* var. *pubescens* S.P.Darwin, J. Arnold Arbor. 64: 614. 1983. – Holotype: Papua New Guinea. Morobe, Mt. Kaindi near Edie Creek, 9 May 1963, ♀, *T.G. Hartley TGH 11840* (A barcode A00338881 [image!]; isotype: L barcode L0001455!).

Abbottia scabriflora (Valeton) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius avenis* var. *scabriflorus* Valeton, Bot. Jahrb. Syst. 61: 37. 1927. ≡ *Timonius scabriflorus* (Valeton) Merr. & L.M.Perry, J. Arnold Arbor. 26: 238. 1945. – Lectotype, designated by Darwin (1994: 68): Papua New Guinea. Kaiser-Wilelmsland, 24 Mar 1908, ♀, *R. Schlechter 17504* (L barcode L0001464!; isotypes: A barcode A00246740 [image!], BM barcode BM000945281 [image!], BRI barcode BRI-AQ0318321 [image!], C barcode C10018387 [image!], G barcode G00436799 [image!], S barcode S-G-6104 [image!]).

Abbottia secundiflora (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius secundiflorus* S.P.Darwin, Syst. Bot. Monogr. 42: 69. 1994. – Holotype: Papua New Guinea. Sepik, Lumi, Torricelli Mountains, north of Wigote Village, 17 Sep 1961, ♀, *P.J. Darbyshire 455* (A barcode A00338894 [image!]; isotypes: B barcode B100295975 [image!], BISH barcode BISH1004784 [image!], BRI barcode BRI-AQ0129828 [image!], L barcode L0001466!, US barcode US01049650 [image!]).

= *Timonius avenis* f. *triflora* Valeton, Bot. Jahrb. Syst. 61: 38. 1927. – Lectotype, designated by Darwin (1994: 70): Papua New Guinea, Sepik-Gebiet, 1912-1913, ♀, *C.L. Ledermann 9853* (L barcode L0001465!).

Abbottia singularis F.Muell., Fragm. 9: 181. 1875. ≡ *Timonius singularis* (F.Muell.) L.S.Sm., Proc. Roy. Soc. Queensland 68: 50. 1957. Lectotype, designated here: Australia. Rockingham Bay, *s.d.*, ♂, *Dallachy s.n.* (K barcode K000763510 [image!]).

Abbottia subavenia (Valeton) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius scaber* var. *subavenis* Valeton, Bot. Jahrb. Syst, 61: 51. 1927. ≡ *Timonius subavenis* (Valeton) S.P.Darwin, J. Arnold Arbor. 64: 616. 1983. – Lectotype, designated by Darwin (1983: 616): Papua New Guinea. Sepik-Gebiet, 1912-1913, ♂, *C.L. Ledermann 8793* (SING barcode SING0058067 [image!]).

Abbottia trichantha (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius trichanthus* Merr. & L.M.Perry, J. Arnold Arbor. 26: 238. 1945. – Holotype: Papua New Guinea. Morobe, Matap, Feb-Apr 1940, ♀, *M.S. Clemens 11158B* (A barcode A00338870 [image!]; isotypes: E barcode E00438195 [image!], MICH barcode MICH1108316 [image!], US barcode US00679922 [image!]).

Abbottia trichoclada (Merr. & L.M.Perry) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius trichocladus* Merr. & L.M.Perry, J. Arnold Arbor. 26: 239. 1945. – Holotype: Indonesia. New Guinea, Lake Habbema, Aug 1938, ♀, *L.J. Brass 9505* (A barcode A00338872; isotypes: BM barcode BM000945276 [image!], BRI barcode BRI-AQ0318347 [image!], L barcodes L0001474! and L0001475!).

Abbottia wollastonii (Wernham) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius wollastonii* Wernham, Trans. Linn. Soc. London, Bot. 9: 74. 1916. – Lectotype, designated by Darwin (1994: 79): Indonesia. New Guinea, Utakwa River to Mt. Carstenz, 18 Feb 1913, ♀, *C. Boden Kloss s.n.* (BM barcode BM000945272 [image!]).

Abbottia zuckiana (S.P.Darwin) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius zuckianus* S.P.Darwin, J. Arnold Arbor. 64: 611. 1983. – Holotype: Papua New Guinea. Normanby Island, Mt. Pabinama, 2 May 1956, ♀, *L.J. Brass 25653* (A barcode A00338876 [image!]; isotypes: K barcode K000763526 [image!], L barcode L0001481!, US barcode US00138441 [image!]).

Lakapatiphyton J.G.Chavez, **gen. nov., ined.** – Type: *Lakapatiphyton pulcherrimum* J.G.Chavez, sp. nov., ined.

Lakapatiphyton is distinguished morphologically from other dioecious genera of Guettardeae by the combination of adpressed ± foliaceous stipules with obtuse to rounded apices, monomorphic staminate and pistillate inflorescences, 3– to 4–merous flowers and drupes with separate pyrenes.

Shrubs to small trees up to 10 m tall, dioecious ("leaky"). *Branchlets* glabrous, strigose or hirsute. *Stipules* adpressed, ± foliaceous, ovate, elliptic or obovate, apices obtuse to rounded, outer surface glabrous, strigose or hirsute, inner surface glabrous. *Leaves* opposite, petiolate; lamina elliptic, obovate or orbicular, chartaceous to coriaceous, upper and lower surfaces glabrous, strigose or hirsute, apices obtuse to rounded, bases attenuate to rounded or truncate to auriculate; secondary nerves 4 to 15 pairs. *Staminate and pistillate inflorescences* simple to compound dichasial cymes, 5– to 94–flowered; bracts absent; flowers secund, sessile. *Staminate flowers* 3– to 4–merous; calyx truncate to shallowly lobed, cupuliform, outer surface glabrous, strigose or hirsute, inner surface glabous, occasionally strigose at the base; corollas cylindric to infundibular, white, yellow or pink, tube outer surface strigose or hirsute, inner surface glabrous, lobes valvate–interlocking, elliptic to lanceolate or ovate, lower surface strigose or hirsute, upper surface glabrous; stamens 3 to 4; pistillodia with 3 to 4 linear stigmatic arms, glabrous. *Pistillate flowers* same as staminate flowers; stigmatic arms, exserted. *Fruits* globose to ovoid, smooth or costate, crowned by the persistent calyx, glabrous, strigose or hirsute; pyrenes free, 6 to 32, occasionally arranged in double radiating files in transverse section.

Distribution. – *Lakapatiphyton* is endemic to the Philippines.

Etymology. – The plant of Lakapati, deity of the fields and crops in ancient Tagalog mythology, depicted as half-man and half-woman. The trivial generic name was chosen to highlight the tendency of staminate individuals to bear fruits.

Lakapatiphyton auriculatum (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius auriculatus* Merr., Philipp. J. Sci. 17: 480. 1920 publ. 1921 – Lectotype (designated here): The Philippines. Dinagat Island, May 1919, ♂, *M. Ramos and J. Pascasio sub B.S. 35190* (US! barcode US00138414; isolectotypes: A barcode A00312910 [image!], K barcode K000763560 [image!]).

Lakapatiphyton hirsutum (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Greenea hirsuta* Elmer, Leafl. Philipp. Bot. 5: 1857. 1913. ≡ *Timonius hirsutus* (Elmer) Merr., Philipp. J. Sci. 17: 480. 1920 publ. 1921, nom. illeg. – Lectotype (designated here): The Philippines. Mindanao Island, Agusan, Cabadbaran, Mt. Urdaneta, Aug 1912, ♂, *A.D.E. Elmer 13476* (MICH barcode MICH1108160 [image!]; isolectotypes: A barcode A00092934 [image!], BISH barcode BISH1004372 [image!], CAS barcode CAS00123717 [image!], E barcode E00151184 [image!], GH barcode GH00092935 [image!], HBG barcode HBG520963 [image!], K barcode K000763556 [image!], L! barcode L0420045, NY barcodes NY00131648 [image!] NY00131647 [image!], U! barcode U0118297, US! barcode US00137688).

= *Timonius trichophorus* Merr., Philipp. J. Sci., C 9: 388. 1914 publ. 1915 – Lectotype (designated here): The Philippines. Leyte, Buenavista, 20 June 1914, ♀, *C.A. Wenzel 994* (A barcode A00312921 [image!]; isolectotype US! barcode US00138436).

Lakapatiphyton longiflorum (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Greenea longiflora* Merr., Philipp. J. Sci., C 4: 323. 1909. ≡ *Timonius longiflorus* (Merr.) Merr., Enum. Philipp. Fl. Pl. 3: 542. 1923 – Lectotype (designated here): The Philippines. Mindanao Island, Zamboanga, Tibucuy, Feb 1908, ♂, *H.N. Whitford and W.J. Hutchinson sub F.B. 9430* (US! barcode US00137689).

Lakapatiphyton obovatum (Elmer) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius obovatus* Elmer, Leafl. Philipp. Bot. 1: 36. 1906. – Neotype (designated here): The Philippines. Sibuyan Island, Magallanes, Mt. Guiting-Guiting, April 1910, ♀, *A.D.E. Elmer 12359* (GH!; isoneotype: K barcode K000763553 [image!]).

= *Timonius rotundus* Merr., Philipp. J. Sci. 17: 317. 1920 publ. 1921, syn. nov. – Lectotype (designated here): The Philippines. Dinagat Island: May 1919, ♀, *M. Ramos and J. Pascasio sub B.S. 35176* (K barcode K000763540 [image!]; isolectotypes A barcode A00312920 [image!], L! barcode L0001460, P! barcode P03906963, US! barcode US00138434).

Lakapatiphyton oligophlebium (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius oligophlebius* Merr., Philipp. J. Sci., C 11: 34. 1916 – Lectotype (designated here): The Philippines. Luzon Island, Sorsogon, Mt. Kililibong, July-Aug 1915, ♀, *M. Ramos sub B.S. 23367* (PNH!; isolectotypes: A barcode A00312917, BISH barcodes BISH1004778 [image!] BISH1004779 [image!] & BISH1004780 [image!], BRI barcode BRI-AQ0318335 [image!], GH barcode GH00312916 [image!], K barcode K000763552 [image!], L! barcode L0001447, NY barcode NY00133422 [image!], P! barcode P03906973, US! barcode US00138427).

Lakapatiphyton pulcherrimum J.G.Chavez, **sp. nov., ined.** – Holotype: The Philippines. Samar Island, Balangiga, Barangay 01, Sitio Cantinoc, 09 Sept 2017, ♀, *M. Lorenzo & al. LL024* (PNH!; isotypes: L!, USTH!). Figs. 4 & 6.

Lakapatiphyton pulcherrimum is distinct from other species of the genus by the combination of its large stipules, compact arrangement of flowers along the inflorescence branches and shallowly 4-lobed calyces.

Shrubs up to 1.5 m tall. *Branchlets* 4.25–7.25 mm broad toward apex, densely to moderately hirsute. *Stipules* ovate to elliptic, 4.0–7.0 x 1.5–2.5 cm, apex obtuse, outer surface densely hirsute becoming moderately hirsute towards the apex and margin, inner surface glabrous. *Colleters* present, on the inner surface of stipules, distributed along the base. *Leaves* opposite; petioles 6.25–16.90 x 2.20–3.60 mm, densely hirsute; lamina elliptic to obovate, (9.5–) 17.0–33 x (4–) 6.75–12.5 cm, chartaceous to subcoriaceous, upper and lower surfaces moderately to densely hirsute, apex obtuse, base attenuate to cuneate; secondary nerves 6 to 9 pairs; domatia absent. *Staminate inflorescences* 18– to 60–flowered, compactly arranged along the inflorescence branches; peduncles 15.0–43.0 x 1.50–2.50 mm, densely to moderately hirsute. *Staminate flowers* 4–merous; calyx shallowly 4–lobed, outer surface densely to moderately hirsute, inner surface glabrous, except along the base which is moderately strigose, tube 1.75–4.50 x 1.6–2.75 mm, lobes 0.40–0.8 mm long; corolla 4–lobed, infundibular, yellow, tube 5.0–8.50 x 1.70–2.25 mm, outer surface moderately strigose, inner surface glabrous, lobes lanceolate to ovate, 3.25–4.0 x 1.8–3.0 mm, lower surface moderately hirsute becoming glabrous towards the apex and margins; stamens 4, the anthers sessile, linear, 4.0–5.0 x 0.40–0.75 mm; pistillodia with 4 stigmatic arms, inserted. *Pistillate inflorescences* 13– to 18–flowered; peduncles 20.0–50.0 x 1.35–2.50 mm, densely to moderately strigose. *Pistillate flowers* same as staminate flowers, except that the stigmatic arms of the style are exserted. *Fruits* ellipsoid to ovoid, 4.90–9.0 x 4.10–5.50 mm, moderately hirsute, not costate; pyrenes 6 to 12, not arranged in double radiating files in transverse section of fruit.

Etymology. – The epithet is in reference to its magnificent appearance as seen in the wild.

Distribution and habitat. – Lakapatiphyton pulcherrimum is known only from the Municipality of Balangiga in Eastern Samar where it occurs in vegetation on lateritic soils.

Additional specimens examined (paratypes). – The Philippines. Samar Island, Balangiga, Barangay 01, Sitio Cantinoc, 09 Sept 2017, ♂, *M. Lorenzo & al. LL019* (FEUH!, L! [2 sheets], UBT!, USTH!); ibid., ♂, *M. Lorenzo & al. LL020* (A!, USTH!); ibid., ♀, *M. Lorenzo & al. LL020* (US!, USTH!); ibid., ♀, *M. Lorenzo & al. LL021* (L!, USTH!); ibid., ♀, *M. Lorenzo & al. LL022* (FEUH!, USTH!); ibid., ♀, *M. Lorenzo & al. LL023* (L!, UBT!, USTH!).

Lakapatiphyton samarensis (Merr.) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius samarensis* Merr., Philipp. J. Sci., C 12: 165. 1917. ≡ *Timonius macrophyllus* Merr., Philipp. J. Sci., C 5: 246. 1910, nom. illeg. – Lectotype (designated here): The Philippines. Samar Island, Feb 1909, ♀, *R. Rosenbluth sub F.B. 12856* (K barcode K000763551 [image!]; isolectotype US! barcode US00138425).

Lakapatiphyton sancti-thomae J.G.Chavez, **sp. nov., ined.** – Holotype: The Philippines. Dinagat Island, Mt. Paragua, 22 May 2011, ♀, *J.C. Briñas, N.M. Ebisawa and G.J.D. Alejandro 11053* (USTH!; isotypes: USTH! [2 sheets]).

Lakapatiphyton sancti-thomae differs from *L. pulcherrimum* by its shorter stipules, 3.0–4.0 cm long (versus 4.0–7.0 cm long in *L. pulcherrimum*), truncate to auriculate leaf base (versus attenuate to cuneate), 7.5–22.50 cm long peduncles (versus 1.50–5.0 cm long) and lax arrangement of flowers along the inflorescence branches (versus compact arrangement).

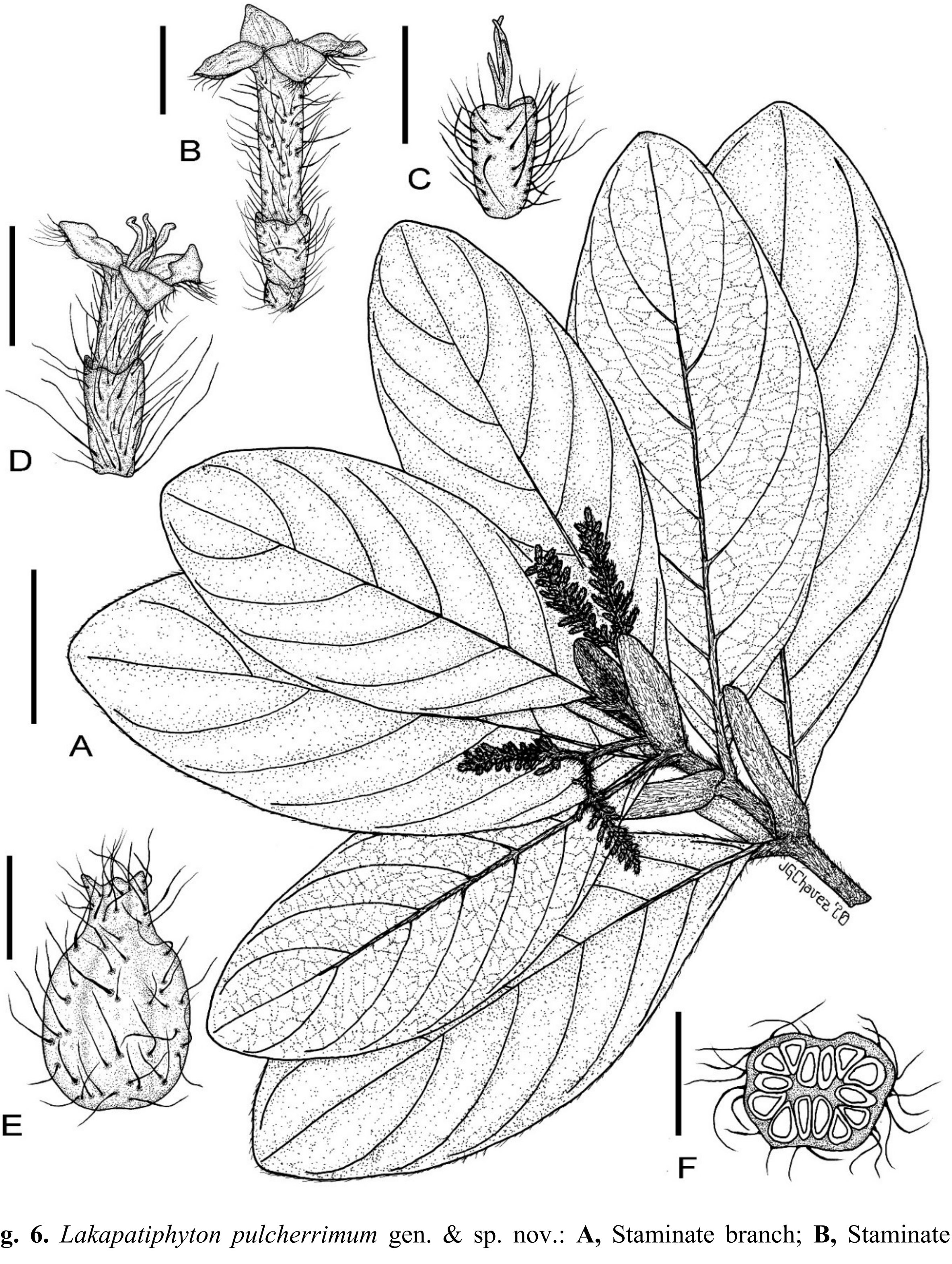


Fig. 6. *Lakapatiphyton pulcherrimum* gen. & sp. nov.: **A,** Staminate branch; **B,** Staminate flower; **C,** Staminate flower showing stigmatic arms of the pistillodium; **D,** Pistillate flower; **E,** Fruit; **F,** Pyrene arrangement in transverse section of fruit. — Voucher data: A, *M. Lorenzo & al. LL020*; B–C, *M. Lorenzo & al. LL019*; D–F, *M. Lorenzo & al. LL024*. — Scale bars: A, 5 cm; B–F, 4 mm. — Drawings: Jayson G. Chavez.

Shrubs to small trees up to 2.0 m tall. *Branchlets* 6.50–7.35 mm broad toward apex, densely to moderately hirsute. *Stipules* obovate, 3.0–4.0 x 1.5–2.5 cm, apex rounded, outer surface densely to moderately hirsute, inner surface glabrous. *Colleters* present, on the inner surface of stipules, distributed along the base. *Leaves* opposite; petioles 18.50–31.0 x 2.50–3.25 mm, densely to moderately hirsute; lamina obovate, 17.50–27.0 x 7.5–11.5 cm, chartaceous to subcoriaceous, upper and lower surfaces moderately to densely hirsute, apex acute to obtuse, base truncate to auriculate; secondary nerves 5 to 10 pairs; domatia occasionally present as tuft of strigose trichomes on axils of secondary nerves. *Staminate inflorescences* 18– to 27–flowered, laxly arranged along the inflorescence branches; peduncles 12.0–22.50 x 0.05–0.13 cm, densely hirsute. *Staminate flowers* 4–merous; calyx shallowly 4–lobed, outer surface densely to moderately hirsute, inner surface glabrous, except along the base which is densely strigose, tube 1.0–2.25 x 1.60–2.75 mm, lobes 0.30–1.0 mm long; corolla 4–lobed, yellow, tube 2.50–3.70 x 1.50-1.75 mm, outer surface densely hirsute, inner surface glabrous, lobes elliptic to ovate, 1.90–2.50 x 1.0–1.5 mm, lower surface densely hirsute, upper surface glabrous; stamens not seen; pistillodia with 4 stigmatic arms. *Pistillate inflorescences* 11– to 15– flowered; peduncles 7.50–14.50 x 0.07–0.17 cm, densely hirsute. *Pistillate flowers* same as staminate flowers, except that the stigmatic arms of the style are exserted. *Fruits* ellipsoid, 5.50–6.10 x 2.0–3.5 mm, moderately hirsute; pyrenes ca. 11, not arranged in double radiating files in transverse section of fruit.

Etymology. – The epithet is treated as a noun in apposition for the patron of the Pontifical University of Santo Tomas–Manila, the institution where the materials of the species are kept.

Distribution and habitat. – Lakapatiphyton sancti-thomae is known only from Mount Paragua in the island of Dinagat, where it occurs on lowland evergreen forests.

Additional specimens examined (paratypes). – The Philippines. Dinagat Island, Mt. Paragua, 22 May 2011, ♀, *J.C. Briñas, N.M. Ebisawa and G.J.D. Alejandro 11054* (USTH!); ibid., ♂, *J.C. Briñas, N.M. Ebisawa and G.J.D. Alejandro 11066* (USTH! [3 sheets]).

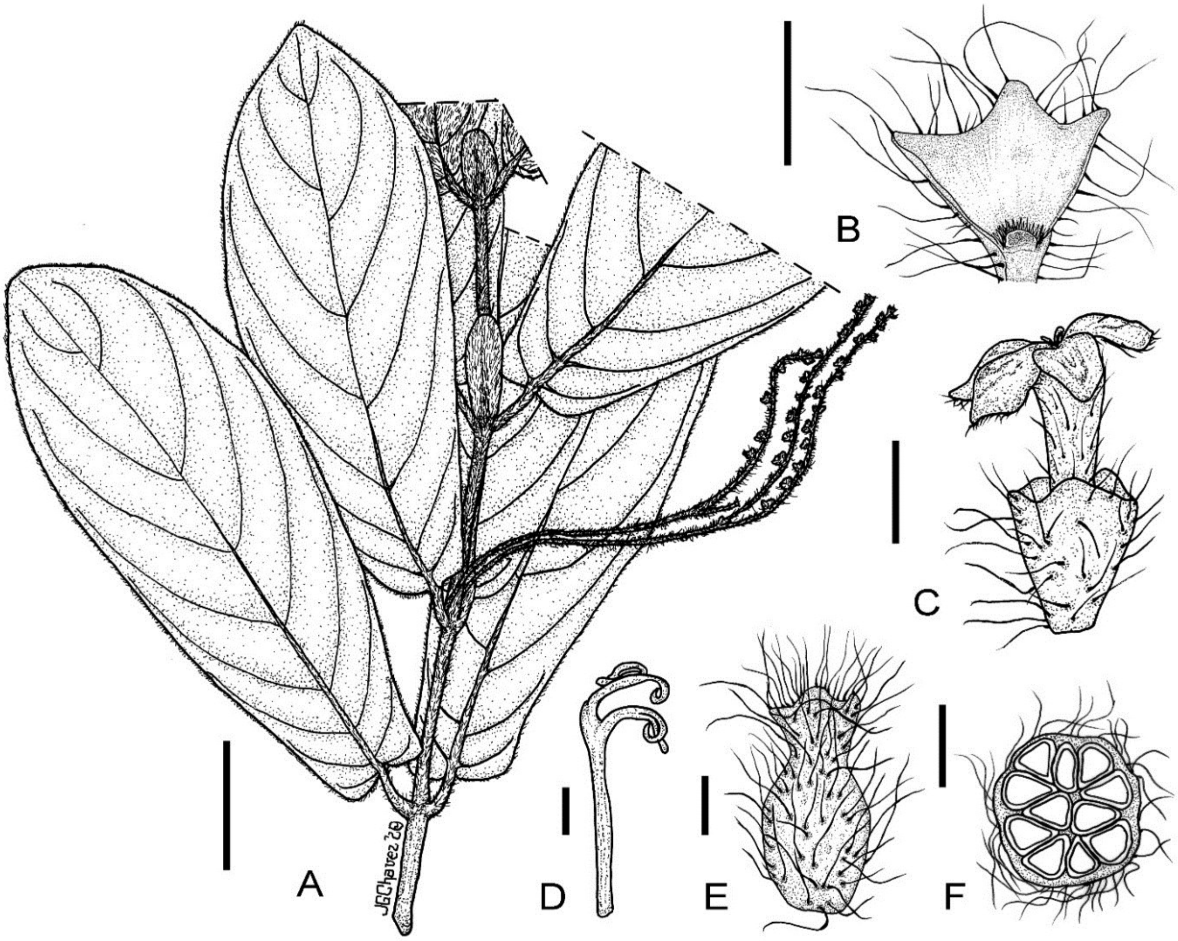


Fig. 7. *Lakapatiphyton sancti-thomae* sp. nov.: **A,** Staminate branch, corollas fallen; **B,** Inner surface of calyx, staminate individual; **C,** Pistillate flower; **D,** Style and stigmatic arms, pistillate individual; **E,** Fruit; **F,** Pyrene arrangement in transverse section of fruit. — Voucher data: A–B, *J.D.C. Briñas & al. 11066*; C–F, *J.D.C. Briñas & al. 11054*. — Scale bars: A, 5 cm; B–F, 2 mm. — Drawings: Jayson G. Chavez.

Lakapatiphyton urdanetensis (Elmer) J.G.Chavez, **comb. nov., ined.** ≡ *Timonius urdanetensis* Elmer, Leafl. Philipp. Bot. 5: 1899. 1913 – Lectotype (designated here): The Philippines. Mindanao Island, Agusan, Cabadbaran, Mt. Urdaneta, Oct 1912, ♀, *A.D.E. Elmer 14197* (GH barcode GH00094666 [image!]; isolectotypes: A barcode A00094667 [image!], BISH barcode BISH1004789 [image!], CAS barcode CAS0005401 [image!], E barcode E00504408 [image!], HBG barcode HBG520959 [image!], K barcode K000763539 [image!], L! barcode L0001477, MICH barcode MICH1108317 [image!], NY barcodes NY00133426 [image!] NY00133427 [image!], U! barcode U0118386, US! barcode US00138437).

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Appendix 1. Accession numbers for included nucleotide sequences, presenting species names, voucher, and genetic markers in the following order: ETS, ITS, *atpB-rbcL*, *rps16*, *trnT-F*. Those marked with ## are newly generated in this study and GenBank accession numbers will be provided as soon as they are made available.

Acrosynanthus latifolius Standl., *Rova et al. 2208* (GB), –, GQ852100, GQ851966, AF242900, GQ852457; ***Antirhea benguetensis*** (Elmer) Valeton, *Lola & Lorenzo LL018* (USTH), MT094480, MT101691, MT113381, MT094531, MT113420; ***Antirhea borbonica*** J.F.Gmel., *De Block et al. 2004* (BR), MT094481, MT101692, MT113382, KT218828, MT113421; ***Antirhea caudata*** (M.E.Jansen) Chaw, *Banag & Hung PP005* (USTH), MT094482, MT101693, MT113383, MT094532, MT113422; ***Antirhea chinensis*** (Champ. ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl., *Hu & Kong 005* (L), MT094483, MT101694, MT113384, –, MT113423; ***Antirhea foveolata*** Chaw, *Alejandro et al. 14753* (USTH), MT094484, MT101695, MT113385, –, MT113424; ***Antirhea inconspicua*** (Seem.) Christoph., *Tuiwana et al. 2999* (P), –, GQ852132, GQ852024, –, GQ852508; ***Antirhea ioensis*** (Baill.) Chaw, *McKee 3961* (L), MT094485, MT101696, MT113386, MT094533, MT113425; ***Antirhea livida*** Elmer, *Chavez & Zamudio PL078* (FEUH), MT094486, MT101697, MT113387, MT094534, MT113426; ***Antirhea madagascariensis*** Chaw, *De Block et al. 1808* (BR), MT094487, MT101698, MT113388, MT094535, MT113427; ***Antirhea megacarpa*** Merr. & L.M.Perry, *Ave 4480* (L), MT094488, MT101699, MT113389, –, MT113428; ***Antirhea microphylla*** (Bartl. ex DC.) Merr., *Calaramo et al. LL084* (USTH), MT094489, MT101700, MT113390, –, MT113429; ***Antirhea ovatifolia*** (M.E.Jansen) Chaw, *Clarkson & Neldner 9265* (L), MT094490, MT101701, MT113391, MT094536, MT113430; ***Antirhea paxillata*** Chaw, *Boltron et al. G011* (FEUH), MT094491, MT101702, MT113392, MT094537, MT113431; ***Antirhea putaminosa*** (F.Muell.) F.Muell., *Shapcott MGH047* (BRI), MT094492, MT101703, MT113393, MT094538, MT113432; ***Antirhea rhamnoides*** (Baill.) Chaw, *McKee 3750* (L), MT094493, MT101704, MT113394, MT094539, MT113433; ***Antirhea smithii*** (Fosberg) Merr. & L.M.Perry, *Smith 7685* (L), MT094494, MT101705, MT113395, –, MT113434; ***Antirhea*** **sp. 1**, *Abad J005* (USTH), MT094495, MT101706, MT113396, MT094540, MT113435; ***Antirhea*** **sp. 2**, *Chavez 001* (FEUH), MT094496, MT101707, MT113397, –, MT113436; ***Antirhea*** **sp. 3**, *Lola & Lorenzo LL114* (USTH), MT094497, MT101708, MT113398, MT094541, MT113437; ***Antirhea*** **sp. 4**, *Docot & Banag CB16-224* (FEUH), MT094498, MT101709, MT113399, –, MT113438; ***Antirhea surigaoensis*** Salamanes & Alejandro, *Lemana et al. 13908* (USTH), MT094499, MT101710, MT113400, –

, MT113439; ***Antirhea tayabensis*** Chaw, *Ong & Luna 1024* (FEUH), MT094500, MT101711, MT113401, –, MT113440; ***Antirhea ternata*** Chaw, *Lemana et al. 13942* (USTH), MT094501, MT101712, MT113402, MT094542, MT113441; ***Arachnothryx hondurensis*** (Donn.Sm.) Lorence, *Croat & Hannon 64177* (NY), –, –, –, AF243013, AF152716; ***Arachnothryx leucophylla*** (Kunth) Planch., *Rova 2287* (GB, S), MT094502, AY730296, GQ851977, AF242910, MT094564+GQ852453; ***Arachnothryx*** **sp.**, *Rova 2093* (GB), –, AY730297, GQ852009, AF242934, GQ852488; ***Bikkia tetrandra*** (L.f.) A.Rich., *Motley 2451* (NY), KT333180, AY763874, –, –, –; ***Bikkia tetrandra*** (L.f.) A.Rich., *Curry 1402* (K), –, –, GQ851983, GQ852374, GQ852467; ***Bobea brevipes*** A.Gray, *Takeuchi 3217* (A), MT094503, MT101713, MT113403, MT094543, MT113442; ***Bobea gaudichaudii*** (Cham. & Schltdl.) H.St.John & Herbst, *Motley 2536* (NY), –, DQ063668, –, –, –; ***Bobea gaudichaudii*** (Cham. & Schltdl.) H.St.John & Herbst, *Fagerlind 7183* (UPS), –, –, GQ851984, –, –; ***Bobea sandwicensis*** (A.Gray) Hillebr., *Takeuchi 3265* (A), MT094504, MT101714, MT113404, MT094544, MT113443; ***Chomelia obtusa*** Cham. & Schltdl., *Jansen-Jacobs et al. 4361* (GB), –, GQ852114, GQ851998, GQ852385, GQ852478; ***Chomelia spinosa*** Jacq., *Siegler DS-12793* (MO), –, GQ852115, GQ851999, –, GQ852454; ***Chomelia tenuiflora*** Benth., *Andersson et al. 2030* (GB, S), –, GQ852116, GQ852000, –, GQ852479; ***Gonzalagunia cornifolia*** (Kunth) Standl., *Stahl 1407* (GB), MT094505, GQ852128, MT113405, AF242948, GQ852501; ***Guettarda boliviana*** Standl., *Persson & Gustafsson 354* (GB), MT094506, GQ852130, GQ852021, AF242962, GQ852505; ***Guettarda crispiflora*** Vahl., *Andersson et al. 2081* (GB), MT094507, DQ063674, GQ852022, AF004052, GQ852506; ***Guettarda ferruginea*** Griseb., *Rova et al. 2206* (GB), MT094508, GQ852131, GQ852023, GQ852397, GQ852507; ***Guettarda glabrescens*** **1** (Schltr.) Guillaumin, *Gateble 1079* (UBT), MT094509, MT101715, MT113406, MT094545, MT113444; ***Guettarda glabrescens*** **2** (Schltr.) Guillaumin, *Mouly 261* (L), MT094510, MT101716, MT113407, MT094546, MT113445; ***Guettarda hypolasia*** Baill., *McKee 4196* (L), MT094511, MT101717, MT113408, MT094547, MT113446; ***Guettarda ngoyensis*** (Schltr.) Guillaumin, *Gateble 1121* (UBT), MT094512, MT101718, MT113409, –, MT113447; ***Guettarda speciosa*** L., *Motley 2040* (NY), KT333247, –, –, –, –; ***Guettarda speciosa*** L., *Achille 661* (P), –, DQ063689, –, –, –; ***Guettarda speciosa*** L., *Rova 2492* (GB), –, –, GQ852025, –, GQ852509; ***Guettarda speciosa*** L., *Persson 141* (GB), –, –, –, AF242964, –; ***Guettarda tournefortiopsis*** Standl., *Andersson et al. 2113* (GB), MT094513, GQ852133, GQ852026, MT094548, GQ852510; ***Guettarda uruguensis*** Cham. & Schltdl., *Gillis 9575* (FTG), –, AY730294, –, EU145489, EU145533; ***Guettarda uruguensis*** Cham. & Schltdl., *in cult. Bot. Gard. Lyon*, –, –, DQ131739, –, –; ***Hymenodictyon orixense*** (Roxb.) Mabb., *Davis*

4087, KC737561, KC737606, –, –, –; ***Hymenodictyon orixense*** (Roxb.) Mabb., *Ridsdale IV.E.107*, GQ852035, GQ852404, GQ852518; **„*Lakapatiphyton*“ sp. 1**, *Lola & Lorenzo LL019* (USTH), ##, ##, ##, ##, ##; **„*Lakapatiphyton*“ sp. 2**, *Briñas et al. 11066* (USTH), ##, ##, ##, ##, ##; ***Machaonia acuminata*** Bonpl., *Bullock 1432* (MO), –, GQ852142, GQ852044, GQ852408, GQ852523; ***Machaonia erythrocarpa*** (Standl.) Borhidi, *Espinoza 520* (GB), –, GQ852103, GQ851972, MT094530, MT094563+GQ852452; ***Malanea* sp.**, *Persson 554* (GB), MT094514, MT101719, GQ852046, GQ852410, MT113448; ***Nauclea orientalis*** (L.) L., *Bremer 3001* (UPS), FN376396, –, –, –, AJ346958; ***Nauclea orientalis*** (L.) L., in cult. NTBG, –, AJ346897, –, –, –; ***Nauclea orientalis*** (L.) L., *c.f. Novotny et al. 2002,* –, –, EU145320, AJ320080, –; ***Neoblakea venezuelensis*** Standl., *Lieasner et al. 7785* (NY), –, –, –, –, AF152732; ***Ottoschmidtia microphylla*** (Griseb.) Urb., *Ekman H9433* (S), –, GQ852147, GQ852061, GQ852422, GQ852532; ***Pittoniotis trichantha*** Griseb., *Croat 9311* (NY), –, DQ063695, –, –, –; ***Rogiera amoena*** Planch., *Rova 2409* (GB), MT094515, AM182205, GQ852073, –, GQ852542; ***Rogiera amoena*** Planch., *Hawkes et al. 1962* (S), –, –, –, AF243000, –; ***Rogiera cordata*** (Benth.) Planch., *Gustafsson & Fredriksson 126* (GB), MT094516, AY730285, GQ852074, AF242999, GQ852543; ***Stenostomum acreanum*** (K.Krause) Achille & Delprete, *Cornejo et al. 8895* (GB), MT094517, MT101720, –, MT094549, MT113449; ***Stenostomum acreanum*** (K.Krause) Achille & Delprete, *Andersson et al. 2031* (GB), –, –, GQ852020, –, –; ***Stenostomum acutatum*** DC., *Axelrod 3288* (NY), –, DQ063696, –, –, –; ***Stenostomum acutatum*** DC., *Stahl & Knudsen 2316* (GB), –, –, –, AF242907, AF102378; ***Stenostomum lucidum*** (Sw.) C.F.Gaertn., *Acevedo-Rodriguez 8468* (NY), –, DQ063697, –, –, –; ***Stenostomum lucidum*** (Sw.) C.F.Gaertn., *Sanders 1801* (FTG), –, –, GQ852089, GQ852447, GQ852556; ***Stenostomum resinosum*** (Vahl) Nicolson, *Axelrod et al. 2723* (NY), –, GQ852145, GQ852056, GQ852417, GQ852528; ***Timonius abanii*** Jun H.Chen, *Beaman 8236* (A), ##, ##, ##, ##, ##; ***Timonis affinis* var. *affinis*** A.Gray, *A.C.Smith 6794* (US), –, ##, ##, ##, ##; ***Timonius affinis* var. *samoensis*** S.P.Darwin, *Whistler 3928* (US), –, ##, ##, ##, ##; ***Timonius arboreus* 1** Elmer, *Ya Yihuang 471* (HAST), ##, ##, ##, ##, ##; ***Timonius arboreus* 2** Elmer, *Ching-I Peng 10726* (HAST), –, ##, ##, ##, ##, ##; ***Timonius arboreus* 3** Elmer, *HVS 395* (L), –, ##, ##, ##, ##; ***Timonius auricularus*** Merr., *Lorenzo et al. LL058* (USTH), ##, ##, ##, ##, ##; ***Timonius beamanii*** K.M.Wong & Jun H.Chen, *Beaman 8491* (US), MT094518, MT101721, MT113410, MT094550, MT113450; ***Timonius belensis*** Merr. & L.M.Perry, *Jensen YUS A11-21* (CNS), ##, ##, ##, ##, ##; ***Timonius billotensis*** Valeton, Ogata et al. OgB908 (L), ##, ##, ##, ##, ##; ***Timonius borneensis*** Valeton, *Church 2695* (A), MT094519, MT101722, MT113411, MT094551, MT113451; ***Timonius carstensensis*** Wernham, *R.J.Johns 10334* (A), ##, ##, ##, –, ##; **Timonius celebicus** Koord., *Ridsdale V.D. 23*, –, GQ852157, GQ852095, –, GQ852561; ***Timonius confertiflorus*** Merr., *Alejandro et al. 15602B* (USTH), MT094520, MT101723, MT113412, MT094552, MT113452; ***Timonius densiflorus*** Valeton, *Takeuchi et al. 4298* (US), MT094521, MT101724, MT113413, MT094553, MT113453; ***Timonius finlaysonianus*** (Wall. ex G.Don) Hook.f., *Banag et al. CB15225* (USTH), ##, ##, ##, ##, ##; ***Timonius flavescens*** (Jacq.) Baker, *Beaman 8720* (US), MT094522, MT101725, MT113414, MT094554, MT113454; ***Timonius kaniensis*** Valeton, *W.Takeuchi 5940* (L), ##, ##, ##, ##, ##; ***Timonius koordersii*** Valeton, *Johansson et al. 597* (L), ##, ##, ##, ##, ##; ***Timonius korrensis*** Kaneh, *Costion 3448-14*, –, KR922357, KR922398, –, KR922402; ***Timonius lanceolatus*** Merr., *Lorenzo et al. LL028* (USTH), ##, ##, ##, ##, ##; ***Timonius lasianthoides*** Valeton, *Ambriansyah & Arifin 1033* (L), ##, ##, ##, ##, ##; ***Timonius laugerioides*** Wernham, *W.Takeuchi 6973* (A), ##, ##, ##, ##, ##; ***Timonius mollis*** Valeton, *Costion 3361* (CNS), MT094523, KR922360, KR922399, MT094555, MT094565+KR922403; ***Timonius mutabilis*** (Korth.) Walp., *Kessler 632* (L), ##, ##, ##, ##, ##; ***Timonius nitidus*** (Bartl. ex DC.) Fern.-Vill., Moore 466 (US), ##, ##, ##, ##, ##; ***Timonius platycarpus*** Montrouz., *McKee 3441* (US), –, MT101726, MT113415, MT094556, MT113455; ***Timonius pubistipulus*** S.P.Darwin, *Hoogland & Schodde 7089* (US), ##, ##, –, ##, ##; ***Timonius pulgarensis*** Elmer, *Chavez & Zamudio PL112* (FEUH), MT094524, MT101727, MT113416, MT094557, MT113456; ***Timonius quinqueflorus*** Merr., *Docot BLSN 002* (FEUH), ##, ##, ##, ##, ##; ***Timonius salsedoi*** Fosberg & Sachet, *Costion 3493* (CNS), MT094525, KR922359, KR922397, MT094558, MT094566+KR922401; ***Timonius samarensis*** Merr., *Lorenzo et al. 18-101* (USTH), ##, ##, ##, ##, ##; ***Timonius secundiflorus*** S.P.Darwin, *Hoogland & Craven 10950* (US), ##, ##, –, ##, ##; ***Timonius singularis*** **1** (F.Muell.) L.S.Sm., *Costion 3246* (CNS),##, ##, ##, ##, ##; ***Timonius singularis*** **2** (F.Muell.) L.S.Sm., *S.J.Worboys 894* (CNS), ##, ##, ##, ##, ##; ***Timonius*** **sp. 1**, *Polak 1071* (L), ##, ##, ##, ##, ##; ***Timonius*** **sp. 2**, *Schodde 21994* (L), ##, ##, ##, ##, ##; ***Timonius*** **sp. 3**, *C.Webb CW3431*(A), ##, ##, ##, ##, ##; ***Timonius*** **sp. 4**, *C.Webb CW3374* (A), ##, ##, ##, ##, ##; ***Timonius*** **sp. 5**, *Chavez & Zamudio PL111* (USTH), ##, ##, ##, ##, ##; ***Timonius*** **sp. 6,** *Lorenzo et al. LL170* (USTH), ##, ##, ##, ##. ##; ***Timonius stipulosus*** Valeton, *T.Laman et al. TL132* (A), ##, ##, ##, –, ##; ***Timonius subauritus*** Valeton, *Costion 3359* (CNS), MT094526, KR922365, KR922396, MT094559, MT094567+KR922400; ***Timonius ternifolius*** (Bartl. ex DC.) Fern.-Vill., *Banag LM006* (USTH), ##, ##, ##, –, ##; ***Timonius timon*** (Spreng.) Merr. **var. *timon***, *Dransfield 7707* (A), MT094527, MT101728, MT113417, MT094560, MT113457; ***Timonius timon*** **var. *whiteanus*** (S.Moore) S.P.Darwin, *Schodde 4261* (US), ##, ##, ##, ##, ##; ***Timonius trichophorus*** Merr., *Lorenzo et al. 18-106* (USTH), ##, ##, ##, ##, ##; ***Timonius uniflorus*** (Banks ex C.F.Gaertn.) Govaerts, *Whistler 6547* (US), ##, ##, –, –, ##; ***Timonius valetonii*** Elmer, *Chavez & Banag SB052* (USTH), ##, ##, ##, ##, ##; ***Timonius wallichianus*** (Korth.) Valeton, *Ismail IS436* (A), MT094528, MT101729, MT113418, MT094561, MT113458; ***Tinadendron kajewskii*** (Guillaumin) Achille, *Achille 958* (L), MT094529, MT101730, MT113419, MT094562, MT113459; ***Tinadendron noumeanum*** (Baill.) Achille, *Achille 662* (P), –, DQ063683, –, –, – ; ***Tinadendron noumeanum*** (Baill.) Achille, *Mouly 859* (P), –, –, GQ852097, –, GQ852563.

Suppl. Appendix 1. List of coded microstructural characters and their aligned positions.

I. *atpB-rbcL* intergenic spacer

A. Simple Sequence Repeats (SSRs)

1. 190–191: TA
2. 430–435: TA
3. 550–557: CTTATTAG
4. 705–709: TAATA
5. 729–751: CTGATTAGTTGATAATATTAGTA
6. 822–826: TAACA

B. Gaps

1. 575
2. 576–579
3. 604

II. *rps16* intron

A. Simple Sequence Repeats (SSRs)

1. 327–331: TAGAA
2. 633–638: TTTTTC
3. 726–733: ATTTATTA

B. Gaps

1. 32–34
2. 174
3. 176
4. 271
5. 700–702
6. 703–711

III. *trnT-F* intergenic spacer

A. Simple Sequence Repeats (SSRs)

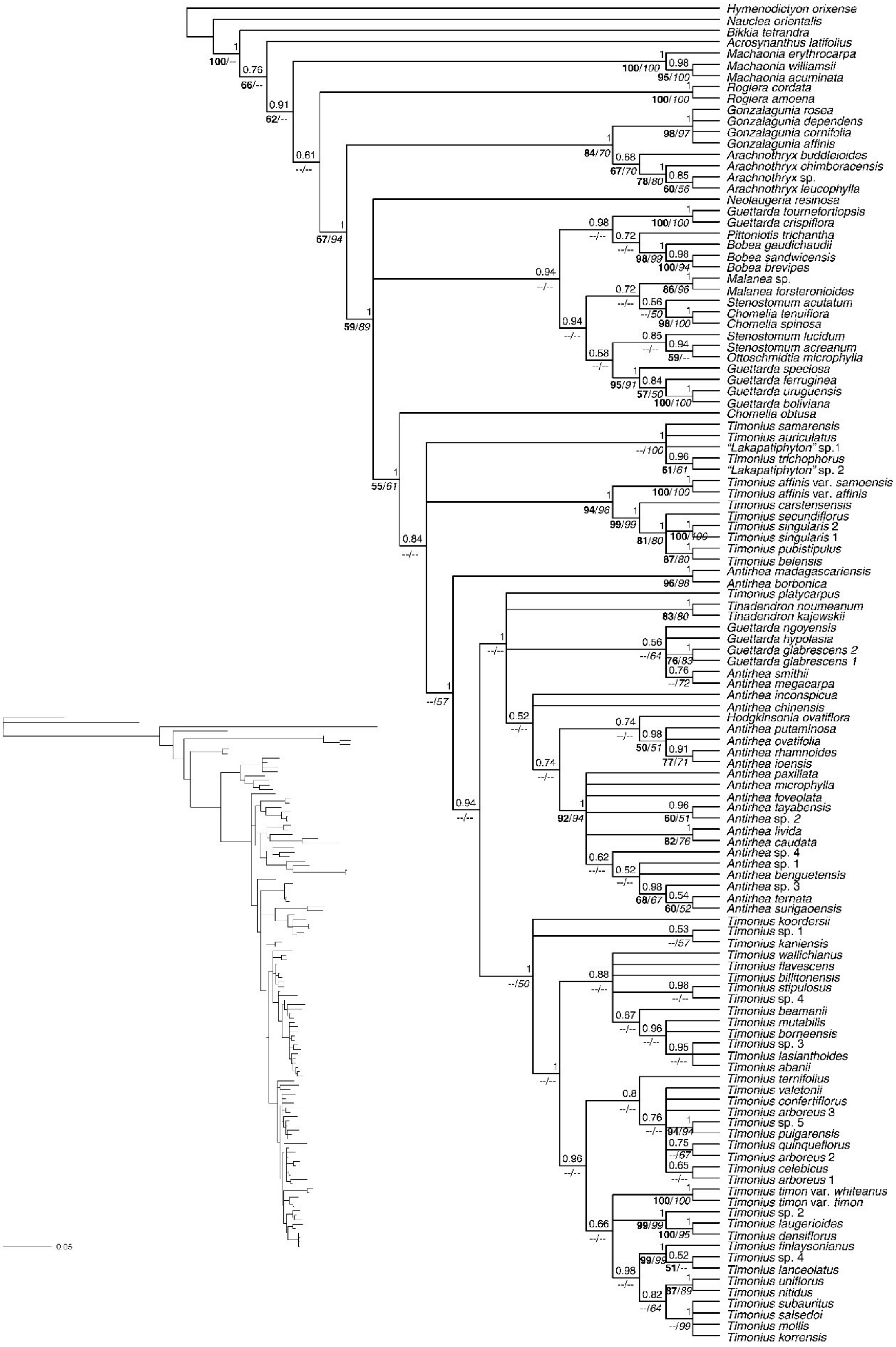
1. 20–24: ATTTT
2. 255–260: ATT

3. 430–448: ATCATATATTTCTAATTAG
4. 811–816: TATAAA
5. 839–842: GACA
6. 1215–1219: TGATT

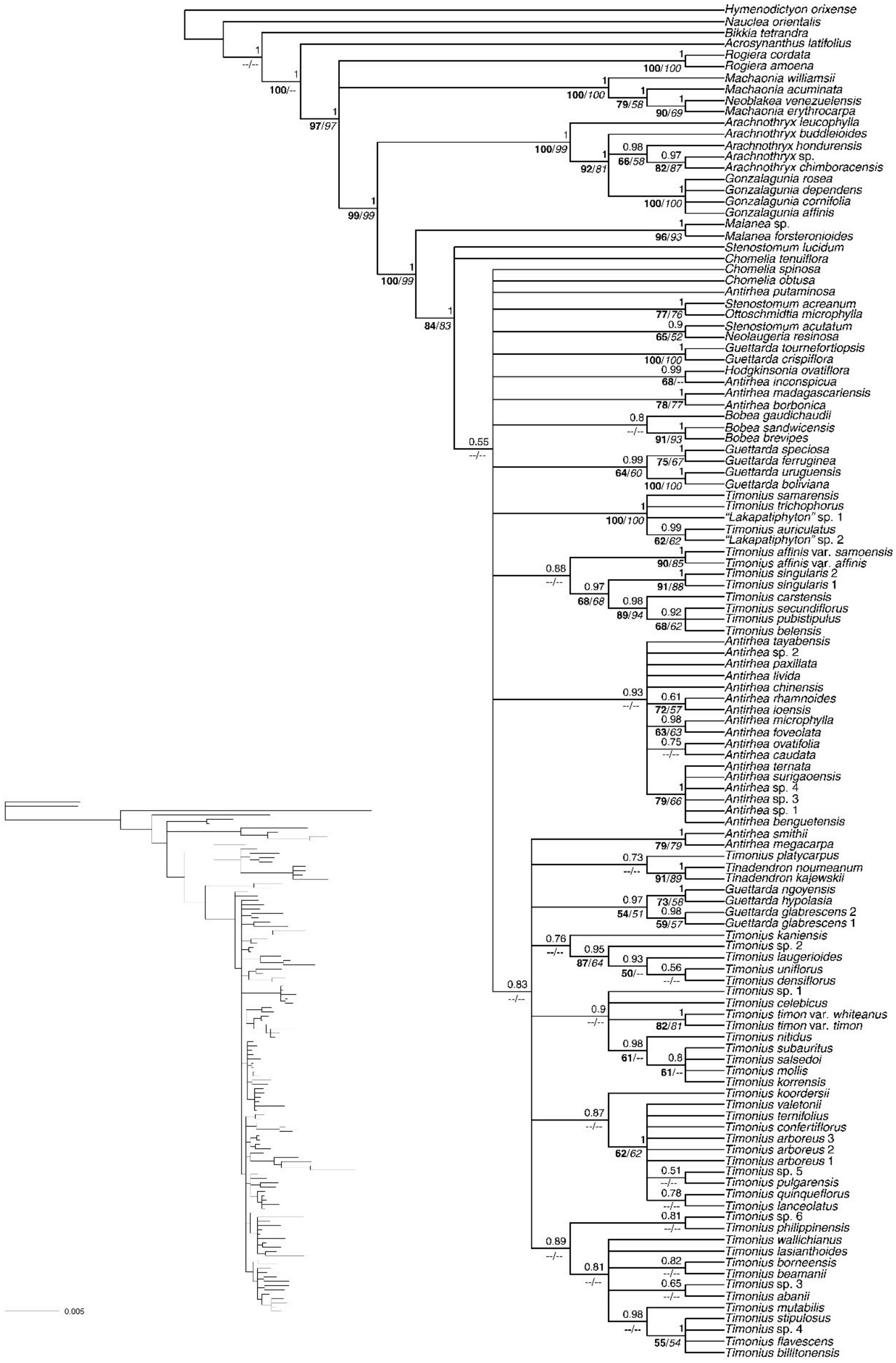
B. Gaps

1. 118–122
2. 155–159
3. 167
4. 238–243
5. 261–265
6. 350–370
7. 370–372
8. 696
9. 715
10. 747–751
11. 777–781
12. 886
13. 995
14. 1034–1037
15. 1372
16. 1614–1617
17. 1890

Supplementary Figure S1. Majority-rule consensus tree inferred from Bayesian inference of the nuclear partition. Numbers on nodes indicate Bayesian posterior probabilities, maximum-likelihood bootstrap values (boldface), and parsimony bootstrap values (italics). Dashes indicate bootstrap values < 50. Inset is same tree with BI branch lengths.



Supplementary Figure S2. Majority-rule consensus tree inferred from Bayesian inference of the chloroplast+mch partition. Numbers on nodes indicate Bayesian posterior probabilities, maximum-likelihood bootstrap values (boldface), and parsimony bootstrap values (italics). Dashes indicate bootstrap values < 50. Inset is same tree with BI branch lengths



Publication III

TAXONOMIC NOVELTIES AND CHANGES IN PHILIPPINE *TIMONIUS* (RUBIACEAE, GUETTARDEAE)*

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The Philippine species of the genus *Timonius* present numerous taxonomic problems resulting from poorly defined species boundaries, misinterpretation of the origin of type specimens, and historical collections that often bear residual reproductive structures. Based on field observations and examination of herbarium materials, the following taxonomic amendments are proposed: conspecificity of *T. philippinensis* with *T. finlaysonianus*, and *T. panayensis* with *T. valetonii*, and transfer of *T. quadrasii* to *Ridsdalea*. This study also describes six new species from the archipelago: *T. alejandroanus*, *T. dumagat*, *T. pseudoarboreus*, *T. ridsdalei*, *T. spes-vitarum*, and *T. stevendarwinii*. Finally, *T. nitidus* is excluded from the Philippine flora.

Keywords: Malaspina expedition, Philippines, *Ridsdalea*, taxonomy, *Timonius*

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Introduction

The Paleotropical genus *Timonius* Rumph. ex DC. is estimated to include about 200 (Darwin 2010) to 300 species (Chen et al. 2015), and is considered as one of the highly diverse genera of Rubiaceae (Davis et al. 2009). Timonius belongs to the tribe Guettardeae s.l. of subfamily Cinchonoideae (Manns and Bremer 2010), and is easily distinguished by the combination of dioecism, dimorphic floral structures, valvate corolla lobe aestivation with some species exhibiting interlocking margins, and drupes with numerous free, single-seeded pyrenes. A modern concept of the genus was presented by Valeton (1909), based primarily on species from the Dutch East Indies. This was subsequently modified by Darwin (1993, 1994, 1997, 2010), who partly divided Timonius into three subgenera and an informal species group, namely: *T.* subgen. *Abbottia* (F. Muell.) S.P.Darwin, *T.* subgen. *Pseudobobea* (Valeton) S.P.Darwin, *T.* subgen. *Timonius*, and *T. flavescens* (Jacq.) Baker alliance. However, this infrageneric classification needs further evaluation before it can be accepted, because the phylogeny of *Timonius* remains insufficiently studied.

After the establishment of *Timonius* in the Philippine flora (Fernandez-Villar 1880), the only comprehensive account for the genus is the bibliographical consolidation of species presented by Merrill (1923). The majority of the ca. 30 species currently recognized are endemic (Merrill 1923, Alejandro and Liede 2003, Pelser et al. 2011, Govaerts et al. 2019), and are principally distributed in the Greater Luzon and Greater Mindanao ecoregions. Species identification is, however, difficult due to obscure species delimitations, incomplete botanical descriptions, dioecism and high levels of morphological variation and plasticity. These problems are further exacerbated by geographical bias and misinterpretations, and the inclusion of several species that are actually misplaced in *Timonius*. Furthermore, our examination of herbarium materials revealed a significant number of species yet to be described, highlighting the remarkable diversity of *Timonius* in the country.

As part of the critical efforts working toward a revision and phylogeny of Philippine *Timonius*, this contribution has been prepared to clarify taxonomic uncertainties and formalize necessary changes. Furthermore, six distinctive species from the archipelago are here described and illustrated as new additions to the genus.

Material and Methods

Assessments were based on observations of living plants, and examined herbarium materials of Guettardeae taxa kept at A, BO, CAHUP, FEUH, GH, L, P, PNH, PUH, WAG, U, US and USTH. Morphological features were observed through a stereomicroscope. Information was also obtained from high resolution images and specimen details provided by BISH, BRIT, C, CM, F, FR, and PRC, as well as those in JSTOR Plants, JACQ, and online databases of HAST, HBG, K, MO, NY, SING, TAIF and Z. A review of historical and fundamental literature was also conducted. Estimations of the extent of occurrence (EOO), area of occupancy (AOO) and number of locations of the species novelties presented here were performed using the ConR package (Dauby et al. 2017). AOOs were calculated with a grid resolution of 2 km, while the number of locations were estimated with a 10 km grid resolution. Conservation status were assessed according to the guidelines and criteria of IUCN (2019).

Results and Discussion

Description of New Species in *Timonius*

***Timonius alejandroanus* J.G.Chavez, Meve and Liede, sp. nov. (Fig. 1)**

A species differing from *T. lanceolatus* Merr. by having pistillate flowers with 5-lobed corollas (versus 6-lobed), ellipsoid fruits crowned by an erect persistent calyx (versus globose fruits crowned by an incurved persistent calyx), and pyrenes arranged in ca. 5 double radiating files in cross-section of the fruit (versus 6 double radiating files).

Type: The Philippines. Samar Island. Taft: Mt. Calbiga, along road km 64, ± 250 m a.s.l., ♀, 25 May 1948, M.D. Sulit Phil. Nat. Herb. 6459 (also numbered M.D. Sulit and E. Coñese 3034) (holotype: PNH; isotype: L 2963914).

Etymology

The adjectival epithet is in reference to Prof. Dr. Grecebio Jonathan D. Alejandro (University of Santo Tomas-Manila) for his significant contributions to the knowledge of Philippine Rubiaceae.

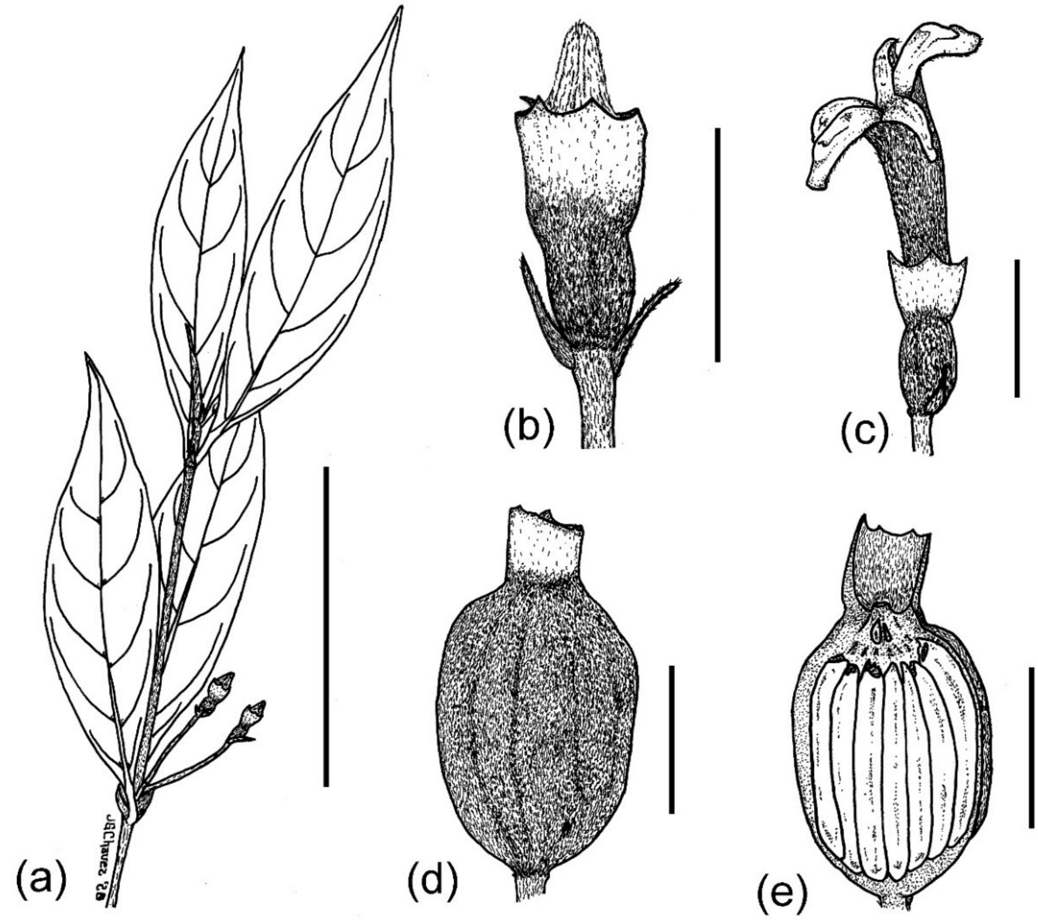

Figure 1. *Timonius alejandroanus* sp. nov. (a) flowering pistillate branch, (b) pistillate flower in bud stage, (c) pistillate flower, (d) fruit, (e) longitudinal section of fruit showing pyrenes. Scale bars: a= 5 cm, b–e= 5 mm. All based on M.D. Sulit Phil. Nat. Herb. 6459.

Description

Shrub or tree up to 5 m tall and 1–15 cm dbh. *Branchlets* 0.7–1.7 mm wide toward apex, densely strigose becoming moderately to sparsely strigose or glabrous when mature, with trichomes 0.05–0.3 mm long. *Stipules* valvate, triangular to lanceolate, 5.1–7.5 x 2.15–3.25 mm, slightly two-ridged, ridges converging toward the apex, outer surface densely strigose, with trichomes 0.13–0.75 mm long, inner surface densely strigose, with trichomes ≥ 1.0 mm long. *Colleters* present on inner surface of stipules and bracts. *Leaves* opposite; petioles 3.0–8.8 x 1.3–1.7 mm, densely to moderately strigose, with trichomes 0.08–0.75 mm long; lamina elliptic, 5.5–11.0 x 1.0–3.0 cm, coriaceous, upper surface glabrous except along the midrib and secondary nerves which are moderately to sparsely strigose, with trichomes 0.25–0.88 mm long, lower surface moderately strigose becoming densely strigose along the midrib and secondary nerves, with trichomes 0.13–0.63 mm long, apex acuminate, base attenuate to cuneate; secondary nerves 5 to 7 pairs; domatia occasionally present as trichomatous pocket, ciliate pit, or intermediate between ciliate pit- and crypt-type in axils of secondary nerves. *Staminate inflorescences* not seen. *Pistillate inflorescences* 1-flowered; peduncles 3.4–19.0 x 0.5–0.9 mm, densely strigose, with trichomes 0.13–0.5 mm long; bracts triangular to lanceolate, 1.8–2.8 x 0.4–0.75 mm, outer surface densely strigose, with trichomes 0.18–0.5 mm long, inner surface densely strigose, with trichomes 0.25–0.5 mm long; calyx cupuliform, usually ruptured by the expanding corolla, 5-toothed, outer surface densely strigose becoming moderately strigose towards the apex, with trichomes 0.08–0.5 mm long, inner surface densely strigose becoming moderately strigose towards the apex, with trichomes ≥ 0.25 mm long, calyx tube 1.6–2.3 x 2.7–3.3 mm, calyx teeth triangular, 0.25–0.75 x 0.25–0.75; corolla infundibular, creamy-white, 5-lobed, corolla tube ca. 8.0 x 2.6 mm, outer surface densely strigose, with trichomes 0.18–0.75 mm long, inner surface not seen, corolla lobes lanceolate, 2.5–4.0 x 1.0–1.5 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.13–0.5 mm long; staminodia not seen; hypanthium ellipsoid, 3.0–3.5 x 2.0–2.6 mm, densely strigose, with trichomes 0.13–0.5 mm long; style not seen. *Fruits* ellipsoid, 7.6–9.3 x 5.7–6.4 mm, neither costate nor tuberculate, densely strigose, with trichomes 0.13–0.5 mm long, persistent calyx 1.7–2.0 mm long; schizogenous cavity absent; pyrenes ca. 20 visible in transverse section of the fruit, arranged in ca. 5 double radiating files, ca. 7 visible in longitudinal section of the fruit, oriented subvertically, cylindric to falcoid, 4.85–7.2 x 1.0–1.5 mm.

Distribution and ecology

At present, *Timonius alejandroanus* is only known from two localities on the island of Samar. It was reported to grow along ridges of dipterocarp forests on Mt. Calbiga, and limestone forests in the municipality of Paranas.

Conservation status

The extent of occurrence (EOO) of *T. alejandroanus* cannot be measured. The estimated area of occupancy (AOO) of 8 km^2 suggests that the species qualifies to the “Critically Endangered” category. Nonetheless, *T. alejandroanus* is currently known in two locations within the Samar Island Natural Park (SINP). The specimen collected in one of the locations (Mt. Calbiga, Taft) dates back 1948; the species has not been recollected in this locality since then, in spite of the extensive botanical explorations made by the Philippine National Herbarium (1948-1996) in Samar and by the team which prepared the checklist of Eastern Samar Rubiaceae (Ordas et al.

2019). The specimen notes indicate that *T. alejandroanus* was found on the ridge of a dipterocarp forest, a type of habitat that was exploited for timber prior to the legal declaration of SINP as a protected area in 2003. On the other hand, the other location (Campo Uno, Paranas), secured as it may seem, is partly a tourism area within SINP. Apan et al. (2017) reported that SINP is one of the protected areas in the Philippines with the highest rate of forest loss. Infrastructure development and impacts of climate change are also seen as threats to *T. alejandroanus*. Because of this information, *T. alejandroanus* is assigned a provisional conservation status of "Endangered" EN B2ab(ii,iii,iv).

Notes

The type material of *Timonius alejandroanus* were initially annotated by Elmer D. Merrill as a form or variety of *T. arboreus* Elmer. However, our examination shows that the two taxa do not exhibit any degree of morphological resemblance. The closest to *T. alejandroanus* is *T. lanceolatus* due to their relatively similar vegetative morphology, while the differences in floral and fruit structures indicated in the diagnosis make the two species easily distinguishable. Furthermore, the disk of *T. lanceolatus* expands horizontally during fruit development, whereas in *T. alejandroanus* the disk neither expands nor elongates.

Additional specimens examined (paratypes)

The Philippines. Samar Island. Paranas: Campo Uno, 400 m a.s.l., 01 May 1996, ♀, Reynoso and Majaducon PPI 24013 (L, BRIT).

***Timonius dumagat* J.G.Chavez, sp. nov. (Fig. 2)**

A species differing from *T. alejandroanus* by having leaves with 3–5 pairs of secondary nerves (versus 5–7 pairs), and 5.5–7.5 mm long, moderately strigose fruits crowned by a 3.5–6.0 mm long persistent calyx (versus 7.6–9.3 mm long, densely strigose fruits crowned by a 1.7–2.0 mm long persistent calyx).

Type: The Philippines. Luzon Island. Isabela: Divilacan, Aubarede Peninsula, west side facing Bicobian, Salniwan Spring, ca. 17 km NNW of Palanan Point, 25 May 1991, ♀, L. Co 3569 (holotype: L 2957184; isotypes: A, CAHUP, PUH, US).

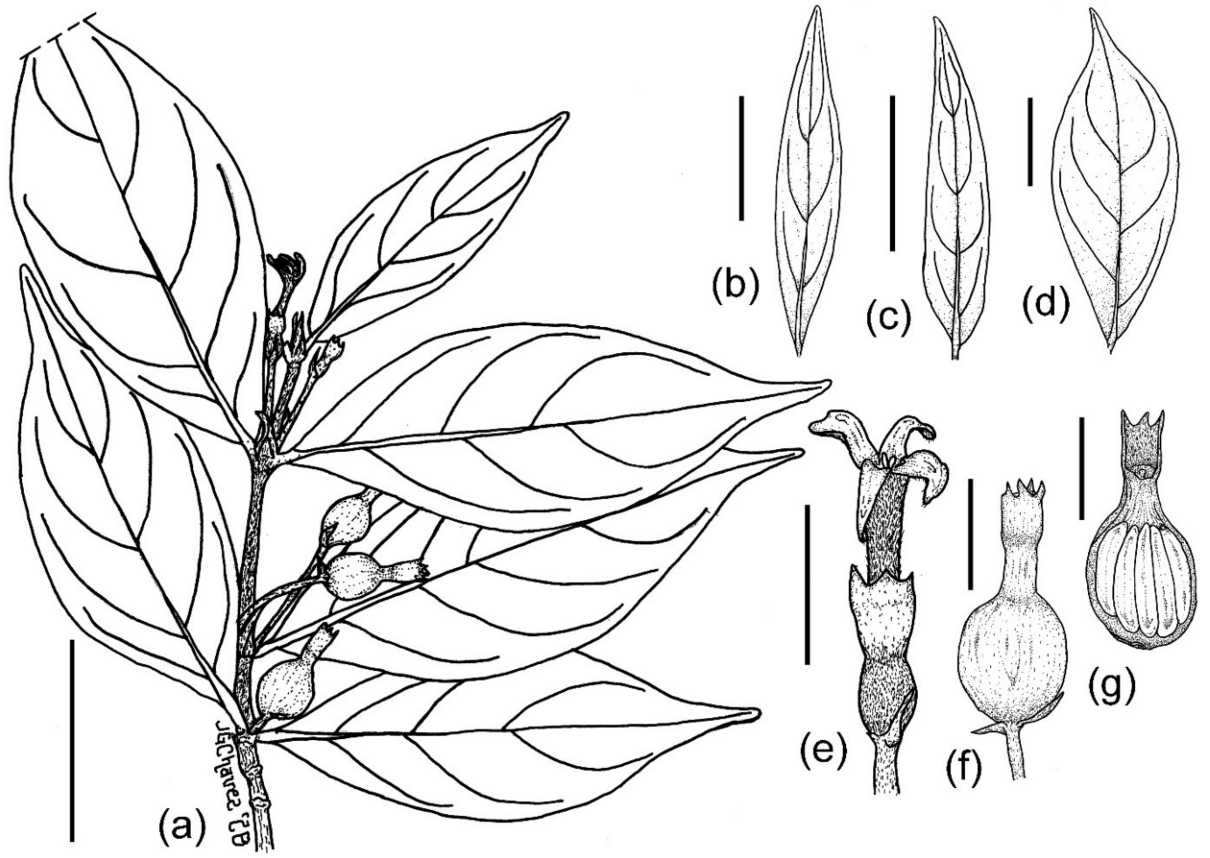

Figure 2. *Timonius dumagat* sp. nov. (a) flowering and fruiting pistillate branch, (b–d) leaf shape variation, (e) pistillate flower, (f) fruit and bracts, (g) longitudinal section of fruit showing pyrenes. Scale bars: a= 2.5 cm, b–d= 2 cm, e–g= 5 mm. Based on (a, d, f–g) L. Co 3569, (b) C.E. Ridsdale, N. Baquiran et al. ISU 416, (c, e) C.E. Ridsdale, V. Dejan and N. Baquiran ISU 121.

Etymology

The epithet is treated as a noun in apposition for the nomadic tribes of the dumagats in Divilacan and Palanan.

Description

Shrub, up to 3 m tall, ca. 4 cm dbh. *Branchlets* 0.75–1.7 mm wide toward apex, densely to moderately strigose becoming sparsely strigose or glabrous when mature, with trichomes 0.08–0.50 mm long. *Stipules* valvate, triangular, 3.6–6.8 x 1.5–2.6 mm, slightly two-ridged, with ridges converging toward the apex, outer surface densely strigose, with trichomes 0.13–0.75 mm long, inner surface densely strigose, with trichomes 0.5–1.25 mm long. *Colleters* present on inner surface of stipules and bracts. *Leaves* opposite, subsessile to petiolate; petioles 1.0–4.3 x 0.9–2.1 mm, densely to moderately strigose becoming sparsely strigose or glabrous when mature, with trichomes 0.08–0.5 mm long; lamina lanceolate to elliptic or obovate, 1.6–8.0 x 0.8–3.6 cm, coriaceous, upper surface sparsely strigose to glabrous, with trichomes 0.2–0.63 mm long, lower surface moderately strigose, with trichomes 0.13–0.75 mm long, apex acute to attenuate or acuminate, base attenuate to cuneate, rarely obtuse or rounded; secondary nerves 3 to 5 pairs; domatia present as tuft of trichomes, trichomatous pocket, ciliate pit or crypt in axils of secondary nerves. *Staminate inflorescences* not seen. *Pistillate inflorescences* 1-flowered; peduncles 2.9–11.8 x 0.55–1.0 mm, densely to moderately strigose, with trichomes 0.18–0.75 mm long; bracts triangular to lanceolate, 1.6–3.5 x 0.35–0.6 mm, outer surface densely strigose, with trichomes 0.13–0.75 mm long, inner surface densely strigose, with trichomes 0.13–0.75 mm long; calyx cupuliform, not ruptured by the expanding corolla, 4- to 5-toothed, outer surface moderately strigose, with trichomes 0.08–0.5 mm long, inner surface densely strigose becoming moderately strigose towards the apex, with trichomes 0.13–0.50 mm long, calyx tube 1.8–2.1 x 1.95–2.85 mm, calyx teeth triangular, 0.25–1.0 x 0.25–1.0 mm; corolla infundibular, white, 4- to 5-lobed, corolla tube 4.0–7.25 x 1.25–1.65 mm, outer surface densely strigose, trichomes 0.13–0.50 mm long, inner surface glabrous, corolla lobes lanceolate, 2.0–3.8 x 0.8–1.0 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.13–0.5 mm long; staminodia 4 to 5, elliptic to lanceolate, 1.60–1.75 mm long, base sagittate, abaxial surface densely strigose, with trichomes 0.25–0.38 mm long; hypanthium globose to (sub-)ellipsoid, 2.0–2.9 x 1.95–2.5 mm, densely strigose, trichomes 0.13–0.5 mm long; style with 4 to 5 unequal stigmatic arms, densely strigose becoming glabrous towards the stigmatic arms, with trichomes 0.25–0.5 mm long. *Fruits* subglobose to ellipsoid, 5.5–7.5 x 5.1–6.2 mm, neither costate nor tuberculate, moderately strigose, with trichomes 0.08–0.18 mm long, persistent calyx 3.5–6.0 mm long; schizogenous cavity absent; pyrenes ca. 18 visible in transverse section of the fruit, arranged in ca. 4 double radiating files, ca. 5 visible in longitudinal section of the fruit, oriented subvertically, cylindric to ovoid or falcoid, 3.8–5.75 x 1.6–1.95 mm.

Distribution and ecology

Timonius dumagat is probably endemic to the province of Isabela. It is reported from lowland riverine forests and open grassy areas on ultramafic substrates. The type material was collected near the coast and was noted to grow with populations of *Machaerina* Vahl. (Cyperaceae) and *Nepenthes* L. (Nepenthaceae).

Conservation status

Timonius dumagat has an EOO of 68.1 km^2 (after exclusion of unsuitable habitat) suggesting a conservation status of "Critically Endangered". However, the estimated AOO is 12 km^2 which fits the threshold for the category "Endangered". The species is known from three locations that are situated within the protected Northern Sierra Madre Natural Park (NSMNP). Satellite imagery indicates that the forest in Aubarede Peninsula remains intact, while the lowland vegetation in the two known locations in Palanan exhibit a decline in quality. Land conversion, logging and charcoal-making will remain as threats to *T. dumagat*. Given these conditions, *T. dumagat* is provisionally assessed as "Endangered" EN B2ab(ii,iii,iv).

Notes

Timonius dumagat exhibits a high degree of variation in its foliage morphology (Fig. 2b–d). Leaf polymorphy is not uncommon in Philippine *Timonius* and is often observed in species growing on ultramafic soil (e.g. *T. gammillii* Elmer, *T. lanceolatus*, *T. pulgarensis* Elmer, *T. valetonii* Elmer). The disk of *T. dumagat* elongates during fruit development, resulting to the long calyx crown of the fruit (Fig. 2f–g). The fruits of *T. dumagat* were also reported to be red when ripe (L. Co 3569), which suggests bird-facilitated seed dispersal.

Additional specimens examined (paratypes)

The Philippines. Luzon Island. Isabela. Palanan: Diguyo, 2 m a.s.l., 22 Apr 1991, ♀, C.E. Ridsdale, V. Dejan and N. Baquiran ISU 121 (CAHUP, L 2 sheets); Digallorin, Divinisa Camp Site, 50 m a.s.l., 08 Apr 1992, ♀, C.E. Ridsdale, N. Baquiran et al. ISU 416 (CAHUP, L, PNH).

Timonius pseudoarboreus J.G.Chavez, sp. nov. (Fig. 3)

A species differing from *T. arboreus* by having 8– to 14–flowered staminate inflorescences (versus 3– to 7–flowered), and ellipsoid to obovoid fruits that are moderately strigose (vs. globose to oblate, glabrous fruits).

Type: The Philippines. Polillo Island: Barangay Amot, Sitio Igad, Burdeos Watershed area, 02 Aug 1995, ♀, Romero, Garcia and Majaducon PPI 15415 (holotype: L 0541981; isotypes: BRIT 42618, GH).

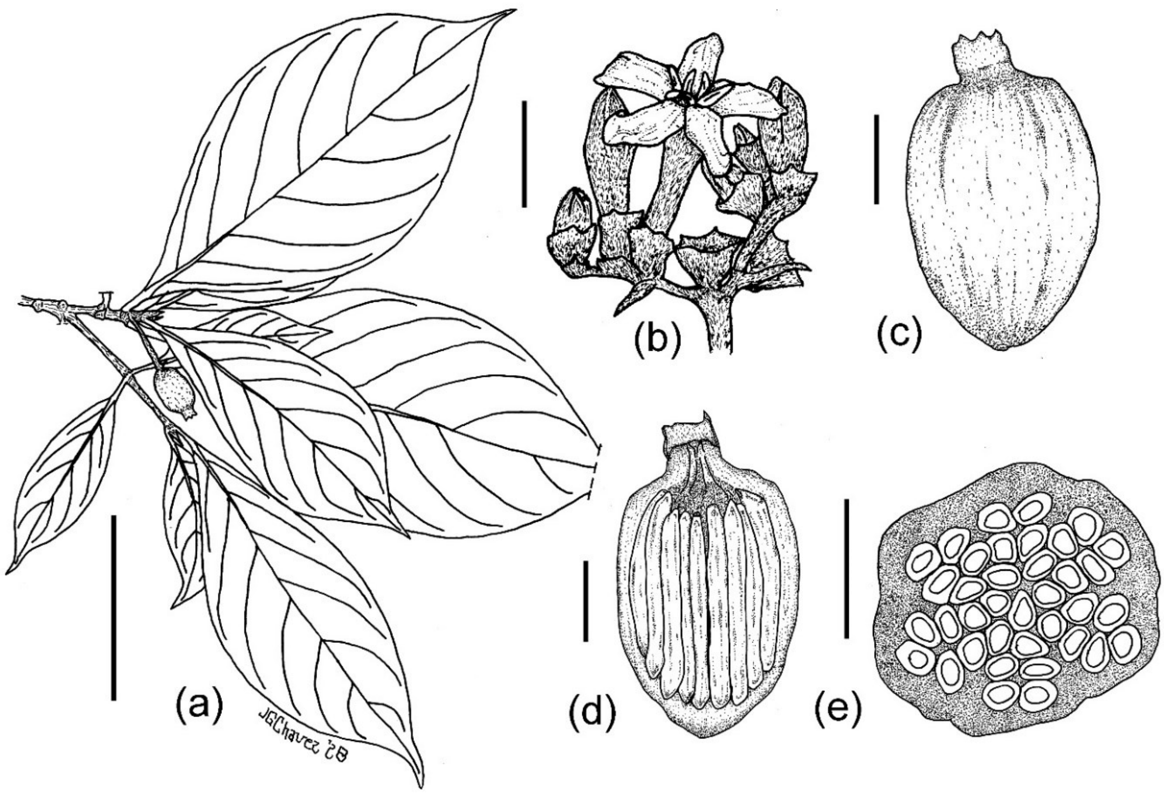

Figure 3. *Timonius pseudoarboreus* sp. nov. (a) fruiting pistillate branch, (b) staminate inflorescence with open flower, (c) fruit, (d) longitudinal section of fruit showing pyrenes, (e) transverse section of fruit showing pyrene arrangement. Scale bars: a= 5 cm, b–e= 5 mm. Based on (a) Romero, Garcia and Majaducon PPI 15415, (b) F. Gaerlan and E. Romero PPI 23645, (c–d) Barbon, Romero and Fuentes PPI 13053, (e) Barbon, Garcia and Fernando PPI 12243.

Etymology

The epithet *pseudoarboreus* is given to this species due to its close resemblance to *T. arboreus*.

Description

Tree up to 12 m tall and 10–12 cm dbh. *Branchlets* 1.65–3.2 mm wide toward apex, densely strigose becoming moderately to sparsely strigose or glabrous when mature, with trichomes 0.08–0.50 mm long. *Stipules* valvate, triangular, 2.1–5.0 x 1.5–2.6 mm, slightly two-ridged, with ridges converging toward the apex, outer surface densely strigose, rarely moderately strigose, with trichomes 0.13–0.63 mm long, inner surface densely strigose, with trichomes 0.5–1.5 mm long. *Colleters* present on inner surface of stipules, bracts and bracteoles of staminate inflorescences, bracts subtending the fruit, and sinus between calyx teeth of staminate flowers. *Leaves* opposite; petioles 3.9–11.0 x 0.8–1.75 mm, densely to moderately strigose, with trichomes 0.08--0.63 mm long; lamina elliptic to oblanceolate or obovate, 5.0–14.5 x 1.8–8.5 cm, chartaceous, upper surface glabrous, lower surface moderately strigose, occasionally becoming densely strigose along the midrib and secondary nerves, with trichomes 0.13–0.75 mm long, apex acuminate to caudate, base attenuate to cuneate, rarely obtuse; secondary nerves 5 to 7 pairs; domatia present as tuft of trichomes, trichomatous pocket, or intermediate between ciliate pit- and crypt-type in axils of secondary nerves. *Staminate inflorescences* 8- to 14-flowered; peduncles 15.5–23.8 x 1.0–1.1 mm, densely to moderately strigose, with trichomes 0.08–0.63 mm long; bracts and bracteoles triangular to lanceolate, 0.5–3.9 x 0.4–0.5 mm, outer surface densely to moderately strigose, with trichomes 0.13–0.63 mm long, inner surface densely strigose, with trichomes 0.38–0.63 mm long; calyx cupuliform, occasionally ruptured at the apex by the expanding corolla, 5-toothed, outer surface densely strigose becoming moderately strigose towards the apex, with trichomes 0.08–0.63 mm long, inner surface densely strigose becoming moderately to sparsely strigose towards the apex, with trichomes 0.18–0.63 mm long, calyx tube 2.5–3.6 x 2.5–3.2 mm, calyx teeth triangular, 0.1–0.4 x 0.1–0.5 mm; corolla infundibular, white, 5-lobed, corolla tube ca. 9.5 x 2.2 mm, outer surface densely strigose, with trichomes 0.4–0.63 mm long, inner surface not seen, corolla lobes lanceolate, 3.6–4.0 x 1.6–1.8 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.13–0.63 mm long; stamens 5; pistillodia bifid, densely strigose becoming glabrous towards the apex, with trichomes 0.18–0.43 mm long. *Pistillate inflorescences* not seen. *Fruits* ellipsoid to obovoid, 11.25–13.75 x 7.8–10.9 mm, 6-costate, not tuberculate, moderately strigose, with trichomes 0.05–0.25 mm long, persistent calyx 1.4–3.3 mm long; schizogenous cavity absent; pyrenes ca. 37 visible in transverse section of the fruit, arranged in ca. 6 double radiating files, ca. 9 visible in longitudinal section of the fruit, oriented subvertically, cylindric to subfalcoid, 9.2–11.4 x 0.75–1.5 mm.

Distribution and ecology

Timonius pseudoarboreus is currently known to occur on the island of Luzon and nearby Polillo Island, where it usually grows along streams in lowland disturbed secondary forests.

Conservation status

The EOO of *T. pseudoarboreus* is 22,775.8 km2 (after exclusion of unsuitable habitat) which is beyond the threshold for any threat category. Nonetheless, the AOO (32 km2) of the species fits in the category “Endangered”. There are eight inferred locations which did not satisfy the subcriterion for the number of locations. Three of the known locations are situated within three protected areas (i.e., Northern Sierra Madre Natural Park, NSMNP; Quezon Protected Landscape, QPL; Unnamed Natural Park, Presidential Proclamation no. 1636 s. 1977). However, many of the remaining forests in the islands of Luzon and Polillo are being degraded for urbanization and agricultural use. With this information, *T. pseudoarboerus* is assessed with a provisional conservation status of "Vulnerable" VU B2ab(ii,iii,iv,v).

Notes

Timonius pseudoarboreus may be easily confused with *T. arboreus* in the absence of reproductive structures. Its differentiating characters occur in the staminate inflorescences, and fruits, which are too constant to be treated as isolated deviations of *T. arboreus*. For this reason, *T. pseudoarboreus* deserves recognition as a distinct species.

Additional specimens examined (paratypes)

The Philippines. Luzon Island. Cagayan. Santa Praxedes: Barangay San Juan, 520 m a.s.l., 11 Aug 1995, ♀, Garcia, Fuentes and Romero PPI 18495 (BRIT, L). Isabela. San Mariano: Barangay San Jose, Sitio Agal, 200 m a.s.l., 05 July 1994, ♀, Barbon, Romero and Fuentes PPI 13053 (BRIT, L). Laguna: Dahican River, Sept 1912, ♀, M. Ramos Phil. Pl. 1290; s.loc., June-Aug 1915, ♀, R.C. McGregor sub B.S. 22943 (US). Quezon. Alabat: Villa Norte to Barangay Bacung, Sitio Canumay, 84 m a.s.l., 22 Mar 1996, ♂, F. Gaerlan and E. Romero PPI 23614 (BRIT, L); Pagbilao: Malikboy, Quezon National Park, 200 m a.s.l., 24 Mar 1996, ♂, F. Gaerlan and E. Romero PPI 23645 (BRIT, L); Real: Barangay Kawayan, Real Watershed area, 02 Sept 1995, ♀, Romero, Garcia and Majaducon PPI 15679 (L); Barangay Kawayan, Real Watershed area, 02 Sept 1995, ♀, Romero, Garcia and Majaducon PPI 15685 (BRIT, L); Tagkawayan: Barangay Bagong Silang II, 08 Sept 1993, ♀, Barbon, Garcia and Fernando PPI 12177 (BISH, BRIT, L); 12 Sept 1993, ♀, Barbon, Garcia and Fernando PPI 12243 (A, BRIT, L).

Timonius ridsdalei **J.G.Chavez, sp. nov. (Fig. 4)**

A species differing from *T. palawanensis* Elmer by having coriaceous leaves (versus chartaceous), staminate flowers with corolla tubes 9.8–10.7 x 1.6–2.0 mm (versus 6.0–9.0 x 2.0–3.0 mm), and 4.75–5.1 mm long anthers (vs. 2.0–3.0 mm long).

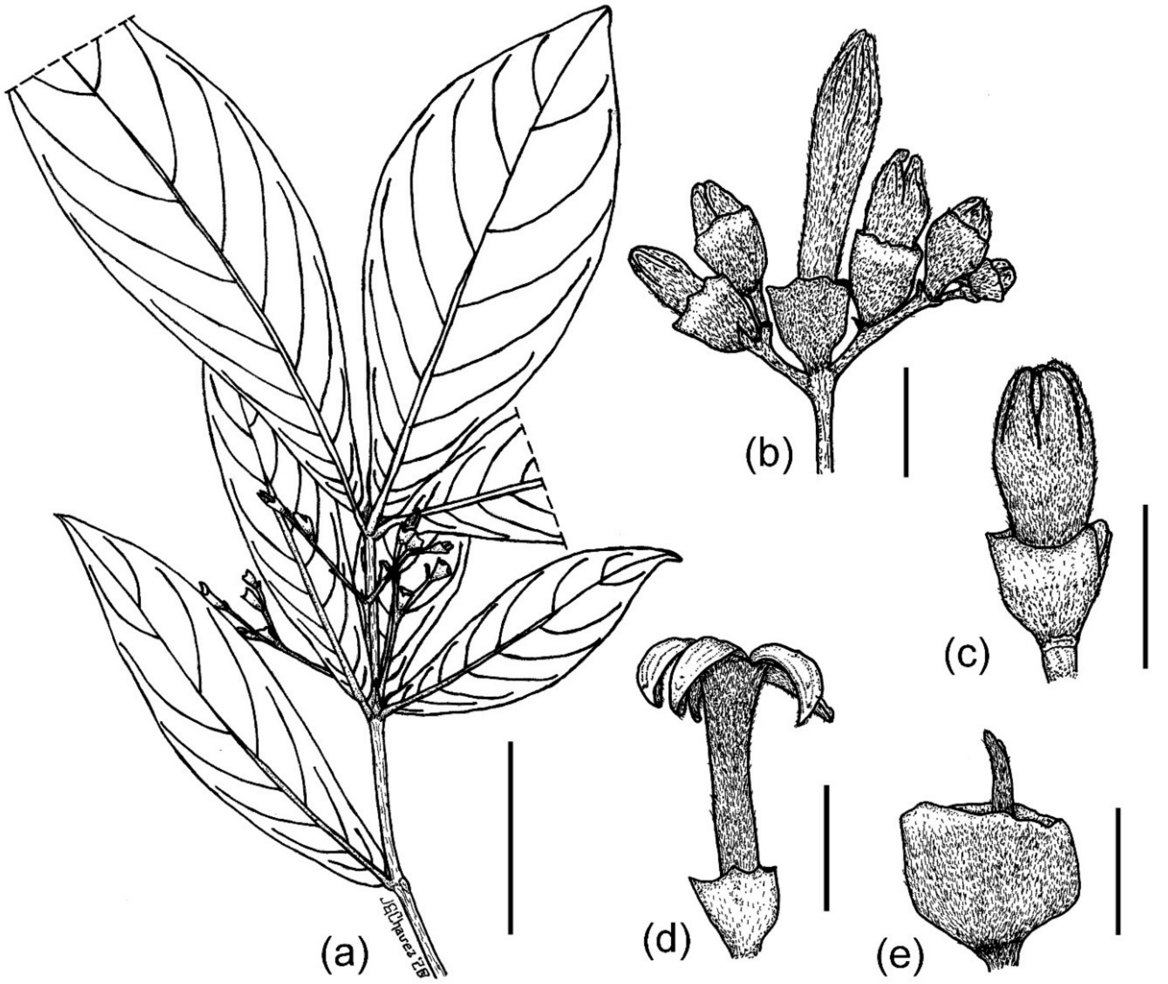

Figure 4. *Timonius ridsdalei* sp. nov. (a) flowering staminate branch, (b) staminate inflorescence in bud, (c) staminate flower in bud stage, (d) staminate flower, (e) calyx with pistillodium. Scale bars: a= 5 cm, b–d= 5 mm, e= 2 mm. Based on (a) C.E. Ridsdale, V. Dejan and N. Baquiran ISU 261, (b-e) C.E. Ridsdale, V. Dejan and N. Baquiran ISU 108.

Type: The Philippines. Luzon Island. Isabela. Palanan: Diguyo, 50 m a.s.l., 22 Apr 1991, ♂, C.E. Ridsdale, V. Dejan and N. Baquiran ISU 108 (holotype: L 2964996; isotypes: A, CAHUP, L 2970012, 2970013).

Etymology

The species is dedicated to the late Dr. Colin Ernest Ridsdale (1944-2017) of the Naturalis Biodiversity Center Leiden, who collected the type material, as well as for his innumerable contributions that helped to provide a better understanding of the Philippines' botanical diversity.

Description

Tree up to 20 m tall and 5–30 cm dbh. *Branchlets* 1.4–3.2 mm wide toward apex, moderately strigose becoming sparsely strigose or glabrous when mature, with trichomes 0.13–0.50 mm long. *Stipules* valvate, triangular to lanceolate, 7.4–10.7 x 3.5–4.6 mm, two-ridged, with ridges converging toward apex, outer surface densely strigose, with trichomes 0.25–0.75 mm long, inner surface densely strigose, with trichomes 0.75–1.75 mm long. *Colleters* present on inner surface of stipules, bracts and bracteoles. *Leaves* ternate, rarely opposite, subsessile to shortly petiolate; petioles 1.1–4.2 x 1.3–3.8 mm, moderately strigose, with trichomes 0.13–0.4 mm long; lamina elliptic to obovate, 8.5–16.75 x 2.75–8.25 cm, coriaceous, upper surface glabrous to sparsely strigose, with trichomes 0.25–0.38 mm long, lower surface moderately strigose, with trichomes 0.13–0.85 mm long, apex acute to shortly acuminate, base obtuse to rounded; secondary nerves 6 to 9 pairs; domatia present as trichomatous pocket or intermediate between ciliate pit- and crypt-type in axils of secondary nerves. *Staminate inflorescences* 3- to 7-flowered; peduncles 8.8–38.0 x 0.75–1.2 mm, moderately strigose, with trichomes 0.08–0.5 mm long; bracts and bracteoles triangular, 1.4–2.75 x 0.6–1.15 mm, outer surface densely strigose, with trichomes 0.13–0.5 mm long, inner surface densely strigose, with trichomes 0.25–0.5 mm long; calyx cupuliform, ruptured at the apex by the expanding corolla, 5-toothed to undulate or truncate, outer surface densely to moderately strigose, with trichomes 0.08–0.63 mm long, inner surface densely strigose, with trichomes 0.13–0.63 mm long, calyx tube 2.5–5.4 x 2.9–3.6 mm, calyx teeth triangular, 0.08–0.25 x 0.13–0.5 mm; corolla infundibular, white to reddish, 5-lobed, corolla tube 9.8–10.7 x 1.6–2.0 mm, outer surface densely strigose, with trichomes 0.08–0.75 mm long, inner surface glabrous, corolla lobes lanceolate, 3.75–6.1 x 0.9–1.7 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.25–0.75 mm long; stamens 5, the anthers elliptic, 4.75–5.1 x 0.50–0.60 mm, base sagittate, abaxial surface densely strigose, with trichomes 0.25–0.38 mm long, the filament glabrous; pistillodia simple or bifid, if divided, with equal lobes, densely strigose, with trichomes 0.13–0.25 mm long. *Pistillate inflorescences* not seen. *Fruits* not seen.

Distribution and ecology

Timonius ridsdalei is probably restricted to Palanan in the Province of Isabela, where it occurs in low stature forests on ultramafic substrates.

Conservation status

The EOO of *T. ridsdalei* cannot be calculated, while its AOO (4 km^2) falls into the "Critically Endangered" category. On the other hand, the species is known from two locations in Palanan which did not satisfy the associated threshold for subcriterion "a" (number of locations) in that threat category. The entire range of Palanan is covered by the protected Northern Sierra Madre Natural Park (NSMNP) but the municipality is recognized as a hotspot for illegal extraction of timber (van der Ploeg et al. 2011). Land-use change especially in one of the two known locations (Diguyo; see van der Ploeg et al. 2016) is also perceived as a threat to *T. ridsdalei*. Taking into account this information, *T. ridsdalei* is assigned a preliminary conservation status of "Endangered" EN B2ab(ii,iii,iv).

Notes

The description of *T. ridsdalei* presented here is based on staminate individuals and needs to be amended upon discovery of pistillate plants. Among Philippine species of *Timonius* that exhibit predominantly ternate phyllotaxy (i.e. *T. palawanensis* and *T. ternifolius* (Bartl. ex DC.) Fern.-Vill.), *T. ridsdalei* is more closely related to *T. palawanensis*. Both species exhibit similar leaf shape and dimensions, while differential characters are the leaf texture and the length of the corolla tube and anthers. It is also important to note that the peduncle length of the staminate inflorescences varies. This variation is not atypical, since it has also been observed in *T. noli-tangere* J.G.Chavez, Alejandro and Meve, *T. spes-vitarum* J.G.Chavez and some Philippine populations of *T. finlaysonianus* (Wall. ex G.Don) Hook.f.

Additional specimens examined (paratypes)

The Philippines. Luzon Island. Isabela. Palanan: Diguyo, 50 m a.s.l., 25 Apr 1991, ♂, C.E. Ridsdale, V. Dejan and N. Baquiran ISU 261 (L 3 sheets); Digallorin Divinisa Camp Site, 05 Apr 1992, ♂, C.E. Ridsdale, N. Baquiran et al. ISU 354 (CAHUP, L 2 sheets, TAIF 2 sheets); Digallorin, Apr 1992, ♂, C.E. Ridsdale, N. Baquiran et al. s.n. (L 2 sheets).

***Timonius spes-vitarum* J.G.Chavez, sp. nov. (Fig. 5)**

Timonius spes-vitarum differs from *T. gammillii* Elmer by its imbricate stipules with glabrous outer surface (vs. valvate, densely strigose), glabrous leaves (vs. moderately strigose on the lower surface), and lobed calyces that are 0.95--5.0 mm long in staminate flowers and 1.40--

8.0 mm long in pistillate flowers (vs. toothed calyces, <1.0 mm long in both staminate and pistillate flowers).

Type: The Philippines. Palawan Island. Narra: Victoria Peaks, Trident Mining Company concession area, along access track, 300-450 m a.s.l., 22 May 1984, ♂, C.E. Ridsdale SMHI 1813 (holotype: PNH; isotypes: CAHUP, L 2964361, 2964362, 2964363).

Etymology

The specific epithet is composed of two Latin words, *spes* (= hope) and *vitarum* (= life), to signify hope for the protection and conservation of biodiversity on the island of Palawan, which is considered as the Philippines' last ecological frontier.

Description

Shrub or tree up to 10 m tall and 10–25 cm dbh. *Branchlets* 1.6–5.0 mm wide toward apex, densely to moderately strigose becoming sparsely strigose or glabrous when mature, with trichomes 0.05–0.13 mm long. *Stipules* imbricate, triangular to ovate, 5.0–12.0 x 2.55–8.5 mm, two-ridged, with ridges converging toward the apex, outer surface glabrous, ciliate, inner surface densely strigose becoming glabrous towards the margin and apex, with trichomes 0.25–1.75 mm long. *Colleters* present on inner surface of stipules, bracts and bracteoles, and sinus between calyx lobes. *Leaves* opposite; petioles 2.8–16.4 x 1.1–4.0 mm, glabrous; lamina elliptic to obovate, rarely orbicular, 4.5–17.0 x 1.5–8.5 cm, chartaceous to coriaceous, upper surface glabrous, lower surface glabrous, apex acute to acuminate, base attenuate to cuneate; secondary nerves 3 to 6 pairs; domatia rarely present as tuft of trichomes in axils of secondary nerves. *Staminate inflorescences* 5- to 24-flowered; peduncles 2.3–25.75 x 1.05–1.8 mm, densely to moderately strigose, trichomes 0.08–0.38 mm long; bracts and bracteoles triangular to lanceolate, 0.5–4.0 x 0.3–1.2 mm, outer surface densely to sparsely strigose, occasionally becoming glabrous, with trichomes 0.05–0.75 mm long, inner surface densely to moderately strigose, occasionally becoming glabrous, with trichomes 0.13–0.75 mm long; calyx cupuliform, not ruptured at the apex by the expanding corolla, 4-lobed, outer surface densely to moderately strigose on the tube, moderately to sparsely strigose on the lobes, with trichomes 0.1–0.5 mm long, inner surface densely strigose on the tube, densely to moderately strigose on the lobes becoming sparsely strigose or glabrous towards the apex and margin, with trichomes 0.08–1.0 mm long, calyx tube 1.5–3.1 x 1.5–2.6 mm, calyx lobes lanceolate to elliptic, 0.95–5.0 x 0.5–2.2 mm; corolla infundibular, white to yellow, 4-lobed, corolla tube 3.25–4.75 x 0.75–

1.35 mm, outer surface densely strigose, with trichomes 0.13–0.4 mm long, inner surface not seen, corolla lobes lanceolate, 1.7–2.75 x 0.95–1.25 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.08–0.5 mm long; stamens 4; pistillodia not seen. *Pistillate inflorescences* 1-flowered, rarely 3-flowered; peduncles 12.3–48.5 x 1.1–1.75 mm, densely to moderately strigose, with trichomes 0.08–0.15 mm long; bracts lanceolate to ovate, 2.5–7.0 x 1.0–2.0 mm, sparsely strigose, with trichomes 0.08–0.18 mm long, inner surface densely strigose, with trichomes 0.25–0.63 mm long; calyx cupuliform, not ruptured by the expanding corolla, 4-lobed, outer surface moderately strigose on the tube, sparsely strigose or glabrous on the lobes, with trichomes 0.08–0.25 mm long, inner surface densely strigose on the tube, moderately strigose or glabrous on the lobes, if moderately strigose becoming sparsely strigose or glabrous towards apex and margin, with trichomes 0.05–0.75 mm long, calyx tube 1.3–2.0 x 2.5–3.0 mm, calyx lobes lanceolate to elliptic, 1.40–8.0 x 0.95--3.0 mm; corolla not seen; staminodia not seen; hypanthium globose 2.4–5.5 x 2.5–5.5 mm, densely strigose, with trichomes 0.08–0.18 mm long; style not seen. *Fruits* globose to ellipsoid, 4.5–7.5 x 7.0–7.5 mm, shallowly 5-costate, not tuberculate, densely to moderately strigose, with trichomes 0.05–0.18 mm long, persistent calyx 1.5–4.7 mm long; schizogenous cavity not seen; pyrenes not seen.

Distribution and ecology

This species is endemic to the island of Palawan, where it occurs in disturbed forests on ultramafic substrates at low to mid altitude.

Conservation status

Timonius spes-vitarum has an EOO of 4,797.8 km^2 (after exclusion of unsuitable habitat) and an AOO of 48 km^2, both are within the "Endangered" category. However, specimen records indicate that *T. spes-vitarum* occurs in nine locations, two of which were affected by ceased mining activities. Intensive efforts to preserve the remaining forests of Palawan are being implemented, but it has been recently recognized as the highest among terrestrial protected areas in the Philippines when it comes to forest loss (Apan et al. 2017). Logging and rapid-urbanization increase pressure to Palawan's natural environment. Furthermore, climate change has been predicted to trigger extreme male-sex biased ratio in populations of dioecious plants (Hultine et al. 2016), which may lead to the reduction of mature individuals of *T. spes-vitarum* in the future. With the above-mentioned facts, *T. spes-vitarum* is assessed with a provisional conservation status of "Vulnerable" VU B1+2ab(i,ii,iii,iv,v).

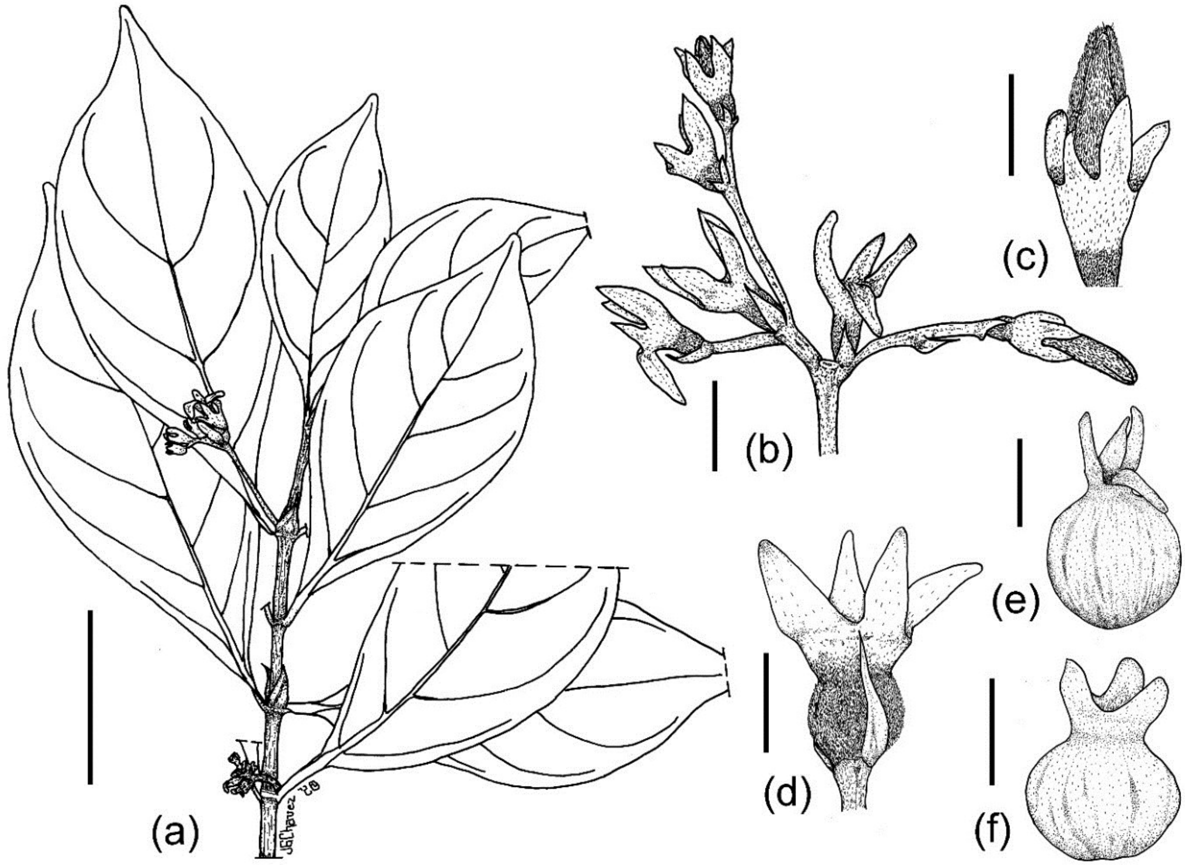

Figure 6. *Timonius spes-vitarum* sp. nov. (a) flowering pistillate branch, (b) staminate inflorescence (corollas mostly fallen), (c) staminate flower in bud stage, (d) bracts, calyx and hypanthium of pistillate flower, (e–f) fruit. Scale bars: a= 3 cm, b, e–f= 5 mm, c–d= 3 mm. Based on (a) D.D. Soejarto and D.A. Madulid 9011, (b–c) A.L. Claustro and R.S. Madulid PCM 182, (d) D.D. Soejarto, F. Gaerlan, E. Sagcal and O. Fernando 8403, (e) J.R. Velasco 9894, (f) C.E. Ridsdale SMHI 1814.

Notes

Although herbarium material of *T. spes-vitarum* bear residual floral structures, its identification is unequivocal. It is the only species of Philippine *Timonius* to date that has a profoundly lobed calyx, while others are toothed to rarely truncate or undulate. Furthermore, the majority of the historical collections of *T. spes-vitarum* are staminate individuals suggesting that this species may present male sex-biased ratios in the wild. This phenomenon has also been observed in certain populations of an undescribed *Timonius* from the province of Aurora on the island of Luzon (digital image DOL: 81116; URL: http://phytoimages.siu.edu).

A flowering staminate specimen collected from the forest along the Karaniogan River in Aborlan (M.D. Sulit 3794, also numbered M.D. Sulit Phil. Nat. Herb. 12354) highly resembles *T. spes-vitarum*. The specimen only differs by its 5-lobed corolla and indument cover on the inner surface of calyx lobes which is densely strigose throughout. We hypothesize that this may represent a new variety, but the limited available materials deter its description.

Additional specimens examined (paratypes)

The Philippines. Palawan Island. Bataraza: Barangay Sumbiling, Sitio Ganayon, 01 Aug 1988, ♂, D.D. Soejarto and D.A. Madulid 9011 (L); Barangay Rio Tuba, Belanjao Range, Gamayon settlement on Rio Tuba-Sumbiling road, 100-200 m a.s.l., 19 June 1994, ♀, D.D. Soejarto, F. Gaerlan, E. Sagcal and O. Fernando 8403 (L). Narra: Victoria Peaks, Trident Mining Company concession area, 490-590 m a.s.l., 19 May 1984, ♂, C.E. Ridsdale SMHI 1753 (CAHUP, L 3 sheets, PNH); Victoria Peaks, Trident Mining Company concession area, along access track, 300-450 m a.s.l., 22 May 1984, ♀, C.E. Ridsdale SMHI 1814 (L 2 sheets); Victoria Mountain Range, vicinity of Trident Mine, 50 m a.s.l., 24 July 1988, ♀, D.D. Soejarto and D.A. Madulid 6171 (A, L); Barangay Calatigas, Dampsite village, logging trail from village to Calatigas Range, 30-200 m a.s.l., 04 July 1994, ♂, D.D. Soejarto, D.A. Madulid, F. Gaerlan, E. Sagcal and O. Fernando 8722 (L). Puerto Princesa: Bacungan, along road, 17 May 1954, ♀, J.R. Velasco 9894 (CAHUP); Bacungan, along road, 17 May 1954, ♂, J.R. Velasco 9895 (CAHUP); Bacungan, along road km 20, 18 May 1954, sterile, J.R. Velasco 10302 (CAHUP); *s.loc.*, 22 Mar 1957, ♂, Y. Kondo and G. Edaño Phil. Nat. Herb. 36555 (L, PNH); Santa Cruz rest house, road km 20 north of Puerto Princesa, 40 m a.s.l., 10 May 1984, ♂, A.C. Podzorski SMHI 2070 (L); along road km 36 to Roxas, 10 m a.s.l., 12 May 1984, ♂, J. Dransfield SMHI 1249 (L 2 sheets, PNH); Nagtabon Hills, above beach, 10-50 m a.s.l., 01 Aug 1988, ♂, D.D. Soejarto and E. Reynoso 6298 (L); Olympic Mines, near Bivouac Point, 26 Jan 1991, ♂, B.C. Stone et al. PPI 185 (BRIT, L); Tagburos, 28 Jan 1991, ♂, B.C. Stone, E.M. Romero and F. Gaerlan PPI 256 (BRIT, L); Bacungan, Oct 1991, ♂, A.L. Claustro and R.S. Madulid PCM182 (USTH).

Timonius stevendarwinii J.G.Chavez, sp. nov. (Fig. 6)

A species differing from *T. abanii* Jun H.Chen by its valvate stipules (versus imbricate), pistillate flowers with 5-lobed corollas (versus 6- to 7-lobed corollas), and densely strigose fruits (versus subglabrous to sparsely pubescent fruits).

Type: The Philippines. Palawan Island. Brooke's Point: Barangay Malis, Magagong settlement at the southern reaches of Mantalingajan Range, 600-700 m a.s.l., 16 June 1994, ♀, D.D. Soejarto, F. Gaerlan, E. Sagcal and O. Fernando 8360 (holotype: A; isotype: L 2957175).

Etymology

This species is named after Dr. Steven P. Darwin, Professor Emeritus at Tulane University (New Orleans, Louisiana), for his remarkable efforts in advancing the knowledge on the systematics of *Timonius*.

Description

Shrub to tree up to 15 m tall and 5–40 cm dbh. *Branchlets* 0.9–2.7 mm wide toward apex, densely to moderately strigose becoming sparsely strigose or glabrous when mature, with trichomes 0.08–0.50 mm long. *Stipules* valvate, triangular, 5.0–8.4 x 2.8–3.2 mm, two-ridged, with ridges converging toward apex, outer surface densely strigose, with trichomes 0.08–0.75 mm long, inner surface densely strigose, with trichomes 0.5–1.13 mm long. *Colleters* present on inner surface of stipules, bracts and bracteoles of both staminate and pistillate inflorescences, and sinus between calyx teeth of pistillate flowers. *Leaves* opposite; petioles 2.4–11.75 x 0.9–2.4 mm, densely to moderately strigose, with trichomes 0.08–0.75 mm long; lamina elliptic, 4.5–14.0 x 1.3–6.9 cm, rarely obtuse, chartaceous, upper surface moderately strigose becoming glabrous, with trichomes 0.25–1.0 mm long, lower surface moderately strigose, with trichomes on the lamina 0.13–0.5 mm long, while those along the midrib 0.25–1.25 long, apex attenuate to acuminate, base attenuate to cuneate; secondary nerves 4 to 6 pairs; domatia present as tuft of trichomes or ciliate pit in axils of secondary nerves. *Staminate inflorescences* 5- to 29-flowered, seen in buds only; peduncles 7.65–32.25 x 0.6–1.0 mm, densely to moderately strigose, with trichomes 0.13–0.75 mm long; bracts and bracteoles triangular to lanceolate, 0.75–2.9 x 0.25–1.25 mm, outer surface densely strigose, with trichomes 0.13–0.4 mm long, inner surface densely strigose, with trichomes 0.25–0.5 mm long; calyx cupuliform, occasionally ruptured at the apex by the expanding corolla, 4-toothed, outer surface densely strigose becoming moderately strigose towards the apex, with trichomes 0.08–0.5 mm long, inner surface densely strigose, with trichomes 0.13–0.5 mm long, calyx tube 1.75–3.0 x 1.25–1.5 mm, calyx teeth triangular, 0.1–0.3 x 0.2–0.5 mm; corolla infundibular, white, 4-lobed, corolla tube outer surface densely strigose, with trichomes 0.25–0.75 mm long, inner surface not seen, corolla lobes lanceolate, upper surface glabrous, lower surface densely strigose, with trichomes 0.38–0.75 mm long; stamens not seen; pistillodia simple, densely strigose, with trichomes 0.18–0.25 mm long. *Pistillate inflorescences* 3-flowered; peduncles 3.0–27.5 x 0.5–1.3 mm, densely to moderately strigose, with trichomes 0.08–0.5 mm long; bracts and bracteoles triangular to lanceolate, 0.4–2.5 x 0.2–0.75 mm, outer surface densely to moderately strigose, trichomes 0.18–0.38 mm long, inner surface densely strigose, trichomes 0.25–0.5 mm long; calyx cupuliform, not ruptured by the expanding corolla, 4- to 5-toothed, outer surface moderately strigose, with trichomes 0.08–0.38 mm long, inner surface densely strigose, with trichomes 0.13–0.38 mm long, calyx tube 0.90–1.5 x 1.5–2.25 mm, calyx teeth triangular to lanceolate, 0.1–1.75 x 0.1–0.6 mm; corolla infundibular, white, 5-lobed, corolla tube 3.5–4.65 x 1.5–1.8 mm, outer surface densely strigose, with trichomes 0.13–0.63 mm long, inner surface glabrous, corolla lobes lanceolate, 1.8–3.24 x 0.95–1.5 mm, upper surface glabrous, lower surface densely strigose, with trichomes 0.13–0.5 mm long; staminodia 5, elliptic to lanceolate, 2.1–2.4 mm long, base sagittate, abaxial surface densely strigose, with trichomes 0.13–0.38 mm long; hypanthium globose to prolate, 2.0–2.5 x 1.7–2.9 mm, densely strigose, with trichomes 0.25–0.5 mm long; style with 5 unequal stigmatic arms, densely strigose becoming glabrous towards the stigmatic arms, with trichomes 0.13–0.5 mm long. *Fruits* globose to sub-ellipsoid, 6.2–7.5 x 5.9–8.75 mm, 5- to 7-costate, not tuberculate, densely strigose, with trichomes 0.08–0.5 mm long, persistent calyx 0.75–3.9 mm long; schizogenous cavity absent; pyrenes ca. 44 visible in transverse section of the fruit, arranged in 5 or probably up to 7 double radiating files, ca. 10 visible in longitudinal section of the fruit, oriented subvertically, cylindric to falcoid, 4.0–5.6 x 1.0–1.6 mm.

Distribution and ecology

Timonius stevendarwinii is known to occur on the island of Palawan, where it grows in slopes of low to mid-elevation forests.

Conservation status

Timonius stevendarwinii has an EOO of 3,673.1 km2 (after exclusion unsuitable habitat) and an AOO of 40 km2, all are within the “Endangered” category. On the other hand, the associated threshold for subcriterion “a” (number of locations) was not met. Based from herbarium records, *Timonius stevendarwinii* is known from seven locations in the island of Palawan. Exploitation of forest resources and infrastructure development especially in the lowland areas of Palawan are seen as threats to *T. stevendarwinii*. Because of this information, *T. stevendarwinii* is provisionally assessed as “Vulnerable” VU B1+2ab(i,ii,iii,iv).

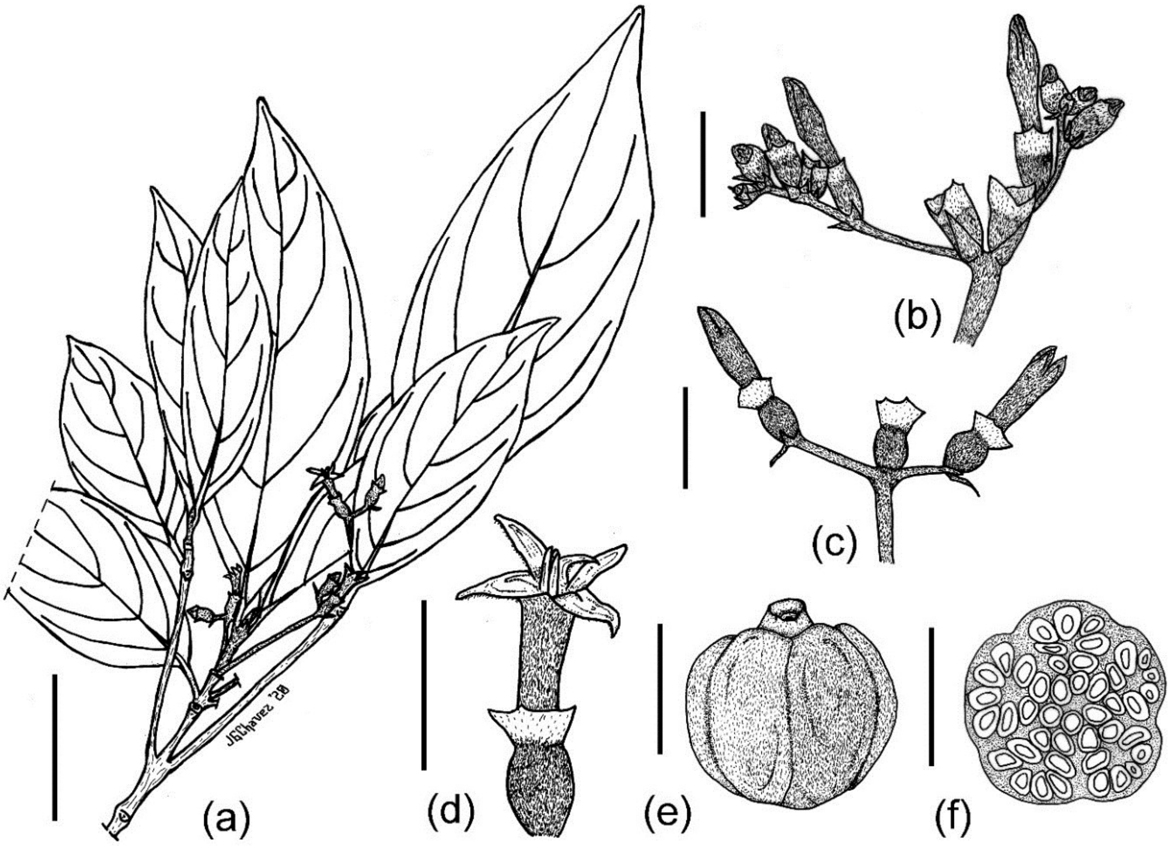

Figure 6. *Timonius stevendarwinii* sp. nov. (a) flowering pistillate branch, (b) male inflorescence, (c) pistillate inflorescence, (d) pistillate flower, (e) fruit, (f) transverse section of fruit showing pyrene arrangement. Scale bars: a= 2.5 cm, b–f= 5 mm. Based on (a, c–d) D.D. Soejarto, F. Gaerlan, E. Sagcal and O. Fernando 8360, (b) B.C. Stone, D. Madulid et al. PPI 32, (e) Pipoly, Romero et al. PPI 38130, (f) A.C. Podzorski SMHI 568.

Notes

Timonius stevendarwinii is phentotypically more closely related to the Bornean *T. abanii* than any other species of *Timonius* in the Philippines. The main differences between the two are in the stipular aestivation, the number of corolla lobes in pistillate flowers, and the indumentum of the fruits. On the other hand, *T. stevendarwinii* is very distinct and can be easily distinguished from all other Palawan *Timonius* by its 3-flowered pistillate inflorescences.

Additional specimens examined (paratypes)

The Philippines. Palawan Island. Aborlan: Barangay Apis, 18 Feb 1992, ♀, M.A.O. Cajano and B.F. Hernaez 1538 (CAHUP). Narra: Trident Mining concession area, April 1987, ♀, R.S. Madulid et al. 054 (USTH). Puerto Princesa: Mt. Beaufort, north-northwest spur, east side, 550 m a.s.l., 14 Mar 1984, ♀, A.C. Podzorski SMHI 537 (L, PNH); Mt. Beaufort, north spur, west side, 370 m a.s.l., 19 Mar 1984, ♂, A.C. Podzorski SMHI 568 (L); Irawan River Valley head, north side, ± 170 m a.s.l., 21 Mar 1984, ♀, C.E. Ridsdale SMHI 176 (L); Irawan River Valley, Mt. Venture slopes, vicinity of Benguet Mining Compound, 400-500 m a.s.l., 4 Apr 1989, ♂, D.D. Soejarto, E. Reynoso, E. Sagcal and R. Rutz 6392 (L, US); Irawan River Valley, Tatanarom, vicinity of Benguet Mine, 500 m a.s.l., 4 Apr 1989, ♀, D.D. Soejarto, E. Reynoso, E. Sagcal and R. Rutz 6396 (U); Irawan River Valley, north slope of Mt. Beaufort, ca. 3 km from Irawan River crossing at Tatanarom, 9°51', 118°38' E, 650 m a.s.l., 26 Mar 1990, ♀, D.D. Soejarto, E. Reynoso, E. Sagcal and R. Edrada 7092 (L); Irawan, Tatanarum, 20 Jan 1991, ♂, B.C. Stone, D. Madulid et al. PPI 32 (BISH, BRIT, L); on ridge above camp two towards Cleopatra's Needle, 590 m a.s.l., 19 Jan 1998, ♂, G.C.G. Argent, Q. Cronk, M. Mendum, D.J. Middleton, P. Wilkie, R. Fuentes and R.V. Chavez 25367 (L). Quezon: Sumindap River, Barangay Bundog, 225 m a.s.l., 21 Aug 1996, ♀, Pipoly, Romero et al. PPI 38130 (BRIT, GH, L). Rizal: Ransang, Kumaraka, 22 Jan 1994, ♀, Gaerlan, Romero and Sagcal PPI 13204 (BRIT, GH, L).

Synonymies in Philippine Timonius

Timonius finlaysonianus (Wall. ex G.Don) Hook.f. (1880 p. 127) (Fig. 7)

Basionym: *Guettarda finlaysoniana* Wall. ex G.Don. (1834 p. 552).
Based on the same type: *Timonius jambosella* Thwaites var. *finlaysoniana* (Wall. ex G.Don) King and Gamble (1904 p. 54).
Type: Singapore. s.loc., s.d., ♀, N. Wallich s.n. (holotype K 000950289-6823).

Taxonomic synonym: *Timonius compressicaulis* (Miq.) Boerl. (1891 p. 133).
Basionym: *Polyphragmon compressicaule* Miq. (1857 p. 235).
Type: Indonesia. Sumatra. Ciboga, s.d., ♂, Teijsmann s.n. (lectotype K 000763579, first-step designated by Wong, 1988 p. 514; isolectotype K 000763578, second-step designated by Wong et al., 2019 p. 312).

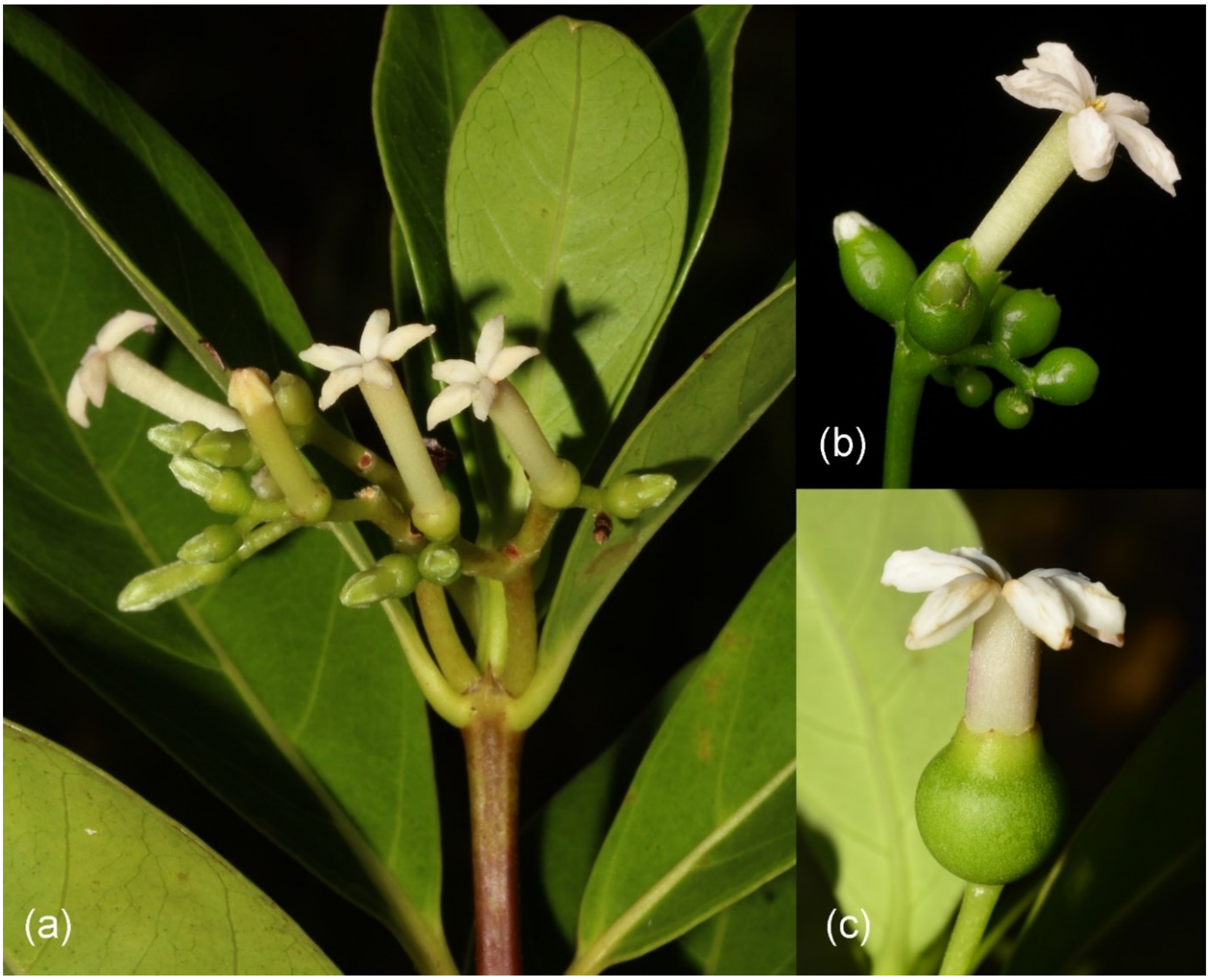

Figure 7. *Timonius finlaysonianus* (a) flowering staminate branch, (b) staminate flower, (c) pistillate flower. Based on (a, c) individuals from the type locality of *T. philippinensis*, no vouchers, (b) cultivated at University of Bayreuth, Lorenzo LL063, voucher in UBT.

Taxonomic synonym: *Timonius philippinensis* Merr. (1903 p. 54), syn. nov.
Type: The Philippines. Dinagat Island. s.loc., ♂, G.P. Ahern 463 (lectotype HBG, HBG520960, designated here; isolectotypes K 000763547, NY 00133424, US 00138430).

Timonius finlaysonianus is a widespread species distributed in Java, Peninsular Malaysia, the Philippines, Singapore, and Sumatra (Wong 1988; Wong et al. 2019). Its occurrence in the Philippines was first reported by Wong (1988) based on a staminate specimen of *T. philippinensis* from the island of Dinagat (M. Ramos and P. Convocar sub B.S. 84095). Merrill (1903) described *T. philippinensis* from two specimens collected in that same locality: Capt. G.P. Ahern 463 and 456. In the protologue (Merrill 1903 p. 54), *T. philippinensis* is distinguished from *T. compressicaulis* (then treated as distinct from *T. finlaysonianus*) by its thicker, purplish, glabrous, and terete branchlets, glabrous calyx, and longer corolla. Our field and ex-situ observations, as well as examination of herbarium materials revealed that these characters are inconsistent and only reflect phenotypic variations associated with ecological conditions (e.g., soil type, canopy open or closed). Also, the floral and fruit traits of *T. philippinensis* fall within the range of *T. finlaysonianus*. Therefore, the distinctiveness of *T. philippinensis* claimed by Merrill (1903) cannot be supported and the species should be treated as a synonym.

Timonius valetonii **Elmer (1911 p. 1012) (Fig. 8)**

Type: The Philippines. Sibuyan Island. Magallanes: Mt. Guiting-Guiting, Apr 1910, ♀, A.D.E. Elmer 12342 (lectotype NY 00133428, designated here; isolectotypes A 00094669, GH 00094668, HBG 520958, K 000763538, L 0001478, U 0118385, US 00138438, Z 000023247).

Taxonomic synonym: *Timonius panayensis* Merr. (1920 publ. 1921 p. 317), syn. nov.

Type: The Philippines. Panay. Capiz: Libacao, May-June 1919, ♀, A. Martelino and G. Edaño sub B.S. 35445 (lectotype US 00138429, designated here; isolectotypes A 00312919, K 000763550, L 0006229).

Elmer (1911) based the description of *T. valetonii* on a fruiting specimen collected from Mt. Guiting-Guiting on the island of Sibuyan. In the protologue, Elmer (1911 p. 1013) mentioned two additional gatherings: A.D.E. Elmer 12292 and A.D.E. Elmer 12120. The former is a pistillate specimen which he associated with *T. arboreus*, but based on our examination, the specimen represents *T. gammillii*. A.D.E. Elmer 12120 is from a staminate plant of *T. valetonii*, from which the diagnosis of the species was derived. Later, Merrill (1920 publ. 1921) described *T. panayensis* based on specimens from Libacao on the island of Panay, a locality that is close to Sibuyan Island (ca. 100 km). This species is distinguished by its variable leaf morphology, elongated staminate flowers and ellipsoid fruits that are crowned by a cylindric and elongated calyx (Merrill 1920 publ. 1921 p. 318). However, there are no significant morphological differences between *T. valetonii* and *T. panayensis*. The features of the vegetative and staminate floral structures of *T. panayensis* are within the range of morphological variations of *T. valetonii*. Additionally, the description of fruit characteristics for both taxa provided by Elmer (1911) and Merrill (1920 publ. 1921) were based on materials at different stages of maturity. Field observations also show that the persistent calyx crown of the fruits of *T. valetonii* is

Figure 8. *Timonius valetonii* (a) flowering staminate branch, (b–c) fruits showing length variation of the persistent calyx. Based on (a) J.G. Chavez and C.I. Banag SB055, (b–c) J.G. Chavez and C.I. Banag SB 052.

elongated, but sometimes appears short and truncate (Fig. 8b–c) due to deterioration or damage caused by canopy soil or foraging insects. We therefore consider the two taxa as conspecific, and *T. valetonii* should be retained as the correct name based on priority of publication.

New Combination in Ridsdalea J.T. Pereira and K.M. Wong

Ridsdalea quadrasii **(Elmer) J.G.Chavez, Meve and Liede, comb. nov.**

Basionym: *Timonius quadrasii* Elmer (1906 p. 36).
Based on the same type: *Rothmannia quadrasii* (Elmer) J.G.Chavez, Liede and Meve (2017 p. 218), *syn. nov.*

Type: The Philippines. Mindanao Island. Zamboanga: Tetuan, May-June 1901, J.F. Quadras sub G.P. Ahern 245 (also numbered G.P. Ahern 545) (lectotype: US 00138432, designated by Chavez et al. (2017 p. 218)).

Timonius quadrasii Elmer is a singleton species that is endemic to the island of Mindanao (Merrill, 1923). This hermaphroditic species shows 3:3 nodal pattern of leaves, left-contorted corolla lobes, pseudo-axillary inflorescences, bilocular ovaries, and ovules with axile placentation, which prompted Chavez et al. (2017) to transfer it to *Rothmannia* Thunb. of tribe Gardenieae without knowing of the newly described genus *Ridsdalea*. The genus *Ridsdalea* is treated as a segregate of the *Rothmannia* complex, and contains Asian species with left-contorted corolla aestivation (Wong and Pereira 2016, Khammongkol et al. 2018). The morphological features of *T. quadrasii* are within the limits of *Ridsdalea*; thus, we here formalize the transfer of this species to the genus. This taxonomic act is necessary to correct the oversight that was made (Chavez et al., 2017) on the current circumscription of *Rothmannia* and its restriction to Africa (Wong and Pereira 2016). Furthermore, the transfer of *T. quadrasii* to *Ridsdalea* makes Philippine *Timonius* a less heterogeneous assemblage.

Occurrence of Timonius nitidus (Bartl. ex DC.) Fern-Vill.

The provenance of *T. nitidus* in the Philippine flora remains dubious, due to complex interpretations of its *locus classicus*. De Candolle (1830) originally described the species as belonging to the genus *Petesia* P. Browne (now recognized as a heterotypic synonym of *Rondeletia* L.), based on a specimen collected by Thaddeus Haenke [T.P.X. Haenke s.n., s.d., ♂ (GOET 2 sheets, HAL)] during the Malaspina expedition (1789-1794). In the protologue, de Candolle (1830 p. 395) stated that the origin of Haenke's material is "*in insulis Philippicis et Marianis*". Later, Fernandez-Villar (1880 p. 109) transferred de Candolle's species to *Timonius* and reduced its locality to the Philippine island of Luzon, perhaps knowing of Haenke's route during the exploration (see Madulid 1983, 1988 for discussion). In contrast, Merrill (1919 p. 544) assumed that the Philippine locality was erroneous and that the specimens used by de Candolle may have originated from the island of Guam. He then formally excluded *T. nitidus* from the Philippines, stating that: "… *recently collected Guam material exactly matches the type, a fragment of which is before me, while the species has not been found in the Philippines*" (Merrill 1923 p. 543). This emendation was substantiated by Fosberg et al. (1993), who provided a comprehensive morphological description of *T. nitidus* and treated it as endemic to the island of Guam. In spite of this, *T. nitidus* was re-listed as a member of the Philippine flora in the online checklists of Govaerts et al. (2019) and Pelser et al. (2011).

It is important to note that although several botanical collections from the Malaspina Expedition are accompanied by field labels with erroneous localities, *T. nitidus* is not included in the list of extra-Philippine species that were attributed to the archipelago (Merrill, 1915, Madulid 1988). The confusion, however, whether to include the Philippines in the range of distribution of *T. nitidus*, is based on the indeterminate locality in Haenke's exsiccates and the concept of Spain's colony in the Philippines. "Spain's colony in the Philippines" (ca. 16th to 19th century) includes the present-day Marianas, Guam, and Caroline Islands, which justifies the locality presented by de Candolle (1830) during his time. On the other hand, to accept the interpretation of Govaerts et al. (2019), and Pelser et al. (2011), one must assume the out of date geopolitical demarcation, which is inadvisable. Furthermore, our careful morphological comparison between *T. nitidus* and available herbarium material of Philippine and Guam *Timonius*, coupled with field observations in the island of Luzon, provide clear indications that this species is not found in the Philippines, supporting the assumptions of Merrill (1919, 1923). Based on this, we (re-)exclude *T. nitidus* from the Philippine flora.

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Publication IV

TWO NEW SPECIES OF *TIMONIUS* (GUETTARDEAE: RUBIACEAE) FROM SAMAR ISLAND, THE PHILIPPINES*

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Two new Philippine endemic species of *Timonius* are described and illustrated: *T. noli-tangere* J.G.Chavez, Alejandro and Meve, and *T. sulitii* Merr. and Quisub. ex J.G.Chavez and Tandang; both have been found on the island of Samar. *Timonius noli-tangere* is characterized by its opposite to whorled phyllotaxy, variable leaf blade morphology, reddish and verrucose calyces and subsessile pistillate inflorescences; while *T. sulitii* can be easily recognized by its widely ovate to suborbicular chartaceous leaves with silky underside, costate and tuberculate fruits with schizogenous cavity, and U-shaped orientation of pyrenes in longitudinal section of the fruit. The distribution, ecology and consertvation status of the two species are discussed.

Keywords: conservation, flora, Guettardeae, Samar, taxonomy, *Timonius*

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Introduction

Samar (Figure 1) is the fourth largest island in the Philippine archipelago with a land area of 12,849 km2 (Bouquet 2017). The island is geologically characterized by gray marls, siltstone, sandstone and pebble conglomerates on its northern region; volcanic soils on its south-eastern part; and low-lying coralline deposits on the Guiuan Peninsula (Madulid and Agoo 1999). Its natural vegetation includes mangrove forests, beach forests, old- and second-growth tropical lowland evergreen forests, forests over limestone and forests over ultramafic rocks. Samar's flora belongs to the Greater Mindanao ecoregion (Ong et al. 2002) but shares a strong affinity with the island of Luzon (Madulid and Agoo 1999). Although the flora of Samar is still insufficiently known, the island is recognized as a key center of plant diversity in the Philippines and Malesia, with about 400 endemic species of flowering plants that are classified in ca. 200 genera and 65 families (Madulid and Agoo 1999). Many of its lowland habitats were revealed as sources of recent novel angiosperm taxa that often have restricted distributions (Hay and Yuzammi 2000; Slik and van Welzen 2001; Wang and Saunders 2006; Ormerod 2008; Gutierrez et al. 2010; Wong and Low 2011; Aurige et al. 2013; Cheek and Jebb 2013; Obico and Alejandro 2013; Banag et al. 2015; Ordas et al. 2017). Nonetheless, the remaining contiguous forest of Samar is in danger of losing much of this richness due to habitat loss and degradation driven by illegal logging and land conversion. Apan et al. (2017) reported that in the past decade the rate of forest loss in this IUCN category II protected area is high. Thus, considerable efforts are needed to record floristic diversity as a fundamental aspect in developing conservation policies that will secure its future.

Timonius Rumph. ex DC. (Rubiaceae), a genus within the tribe Guettardeae of subfamily Cinchonoideae, is recognized to contain about 190 species (Govaerts et al. 2018). The phylogenetic analysis of Achille et al. (2006) placed Timonius within their "Paleotropical Dioecious Clade" as a natural assemblage, but this monophyly is still uncertain due to the limited sampling that certainly did not cover the morphological range of variation within the genus. A general account of the morphology of *Timonius* is found in the seminal works of Valeton (1909) and Darwin (1993, 1994, 1997, 2010a), but the major characteristics that distinguish it from other Paleotropical dioecious Guettardeae are the dimorphic inflorescences and flowers, valvate corolla lobes and drupaceous fruits with many free pyrenes (Achille et al. 2006; Achille 2006). Most of the centers of diversity of *Timonius* have been the subject of extensive modern treatments, viz.: Borneo including Kinabalu Park (Puff and Wong 1993;

Chen et al. 2015), the Malay Peninsula (Wong 1988), Palau (Fosberg and Sachet 1987) and Papuasia (Darwin 1983, 1993, 1994, 1997, 2010a, 2010b); but no particular attention has been given to Philippine species since Merrill (1923). The current knowledge of Philippine *Timonius* is based only on species protologues with incomplete descriptions, and on historical types that frequently lack floral parts or are in a poor state of preservation. The genus was first recorded in the Philippines by Fernandez-Villar (Naves and Fernandez-Villar 1880) who recognized two species, viz. *T. nitidus* (Bartl. ex DC.) Fern.-Vill. and *T. ternifolius* (Bartl. ex DC.) Fern.-Vill. However, Merrill (1923) excluded *T. nitidus* from the Philippine flora noting that the specimen used in the original description (Candolle 1830) was collected from Guam and that no Philippine specimen matches the co-type.

After the account of Fernandez-Villar (Naves and Fernandez-Villar 1880), numerous species novelties of Philippine *Timonius* were proposed in the floristic contributions of Elmer (1906, 1911, 1912, 1913) and Merrill (1903; 1909, 1913, 1914, 1915, 1916a, 1917, 1920). These species were subsequently included in Merrill's (1923) "*Enumeration of Philippine Flowering Plants*", in which he recognized 25 species, with only two species added afterwards, viz. *T. pachyphyllus* Merr. (Merrill 1925) and *T. finlaysonianus* (Wall. ex G. Don) Hook. f. [=*T. compressicaulis* (Miq.) Boerl. sensu Wong (1988)]. All except three species (*T. arboreus* Elmer, *T. caudatifolius* Elmer, T. *finlaysonianus*) are endemic. Nevertheless, our analysis of recent collections revealed that some of the species recognized in Merrill (1923) display high degree of morphological plasticity, making his taxonomic interpretations equivocal. It seems that Merrill (1923) treated distinct species as conspecific, while he regarded morphologically similar species as different. In addition, some of the species he treated in *Timonius* possess characters that contrast with the current delineation of the genus. Hence, the diversity of Philippine *Timonius* is still uncertain, awaiting the findings of an ongoing revision and phylogenetic study (Chavez, in prep.). During our examination of herbarium vouchers of *Timonius*, a number of specimens collected on Samar Island stood out; exhibiting a combination of characters that cannot be matched to any known Philippine or Malesian *Timonius* species. Two of these are found in habitats prone to anthropogenic pressure and are described here as new to science.

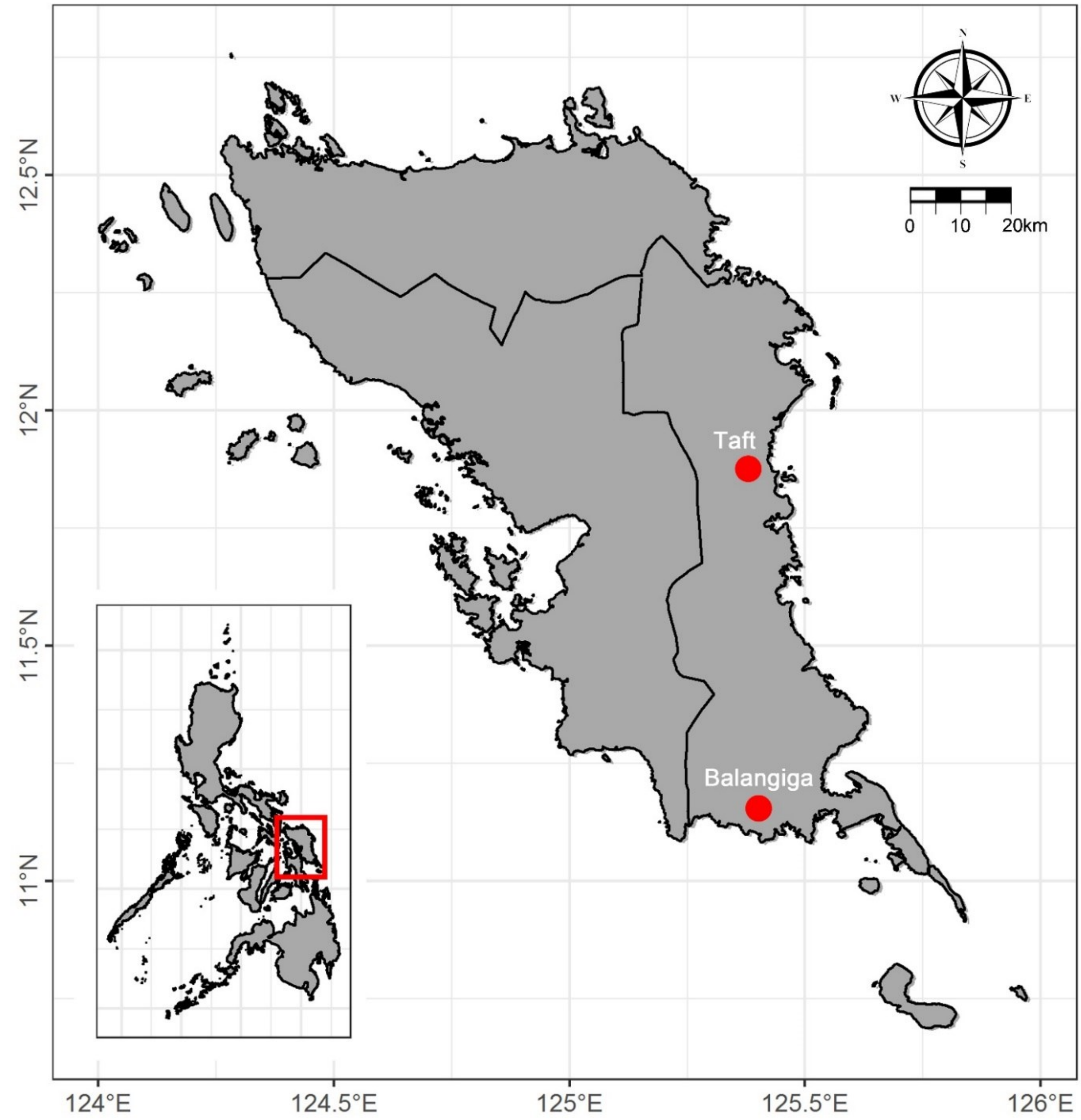

Figure 1. Map of Samar Island showing the collection localities of the two *Timonius* species described in this study (marked in red circles).

Materials and Methods

This study is based on historical and contemporary literature on Timonius, and herbarium specimens from A, BO, CAHUP, FEUH, GH, L, P, PNH, PUH, WAG, U, US and USTH. Additional information was obtained from digital images and specimen details provided by BISH, BRIT, C, CM, FR, and PRC (herbarium codes according to Thiers 2019), and those curated in JSTOR Global Plants and in JACQ. Micromorphological features of vegetative and rehydrated reproductive structures were observed through a Leica S6E stereomicroscope. Indumentum terminology follows Hewson (1988). For structures where only single measurements could be made, the abbreviation ca. was added. The conservation status of the species was assessed applying the IUCN Red list categories and criteria (IUCN 2019).

Descriptions of New Species

Timonius noli-tangere J.G.Chavez, Alejandro and Meve, sp. nov. (Figures 2, 3a–b)

Diagnosis

Timonius noli-tangere resembles *T. valetonii* Elmer (Figure 3c-d) but is distinct by its leaves opposite to whorled (vs. strictly opposite in *T. valetonii*), peduncles with stramineous indumentum (vs. ferruginous), calyces reddish and verrucose (vs. green and smooth), corolla lobes cream colored on the upper side, amber or tawny on the underside (vs. ivory, pink), and fruits 13.5–22.0 x 16.5–19.0 mm with persistent calyx crown up to 2.0 mm long (vs. 25.0–28.0 x 24.0–26.0 mm, persistent calyx crown 5.0–7.5 mm long).

Type

THE PHILIPPINES. Eastern Samar: Balangiga, Barangay Sta. Rosa, ♀, 23 May 2012, *B. Lemana BC012* [holotype PNH; isotypes L, USTH (2 sheets)].

Description

Trees up to 10 m tall. Bark dull brownish yellow. *Branchlets* 2.0–5.0 mmwide toward apex, angular, densely strigose becoming sparsely strigose to glabrous when mature, trichomes 0.08–0.50 mm long. *Stipules* valvate, lance-ovate to ovate, 6.0–10.0 x 3.5–6.0 mm, 2-ridged, outer surface densely strigose, trichomes 0.13–0.88 mm long, inner surface densely strigose, trichomes 0.25–1.75 mm long. *Colleters* present on inner surface of stipules, bracts and bracteoles, and sinuses of calyx teeth. *Leaves* opposite or in whorls of three or four; petioles 5.0–22.0 x 1.5–4.0 mm, densely to moderately strigose becoming sparsely strigose to glabrous with age, trichomes 0.13–0.63 mm long; lamina elliptic to oblance-ovate or lance-ovate to widely ovate, 10.0–22.5 x 4.0–12.0 cm, apex attenuate to acuminate, base cuneate to obtuse or rounded, coriaceous, adaxial surface glabrous or sparsely strigose becoming moderately strigose along the midrib and lateral nerves, trichomes 0.05–0.25 mm long on the lamina, 0.25–

0.63 mm long on the midrib and lateral nerves, abaxial surface moderately strigose becoming densely strigose along the midrib and lateral nerves, trichomes 0.08–0.38 mm long on the lamina, 0.08–0.75 mm long on the midrib and lateral nerves; secondary nerves (4-) 5 to 7 pairs; domatia present as dome-excavations or intermediate between ciliated pit or crypt-type in the axils of secondary nerves. *Staminate inflorescences* 3- to 7-flowered, pedunculate or rarely subsessile; peduncle 3.5–13.5 x 1.0–1.5 mm, densely strigose, trichomes 0.08–0.5 mm long; bracts and bracteoles lance-ovate to ovate, 1.75–3.60 x 0.75–1.5 mm, outer surface densely strigose, trichomes 0.08–0.5mmlong, inner surface densely strigose, trichomes 0.13–0.75 mm long; calyx cupuliform to suburceolate, 5-toothed, apex often ruptured by the expanding corolla, outer surface densely strigose, trichomes 0.08–0.38 mm long, inner surface densely strigose, trichomes 0.25–2.0 mm long; tube 3.25–5.5 x 2.75–3.75 mm; teeth, triangular, 0.38–1.5 x 0.5–1.5 mm; corolla 5-lobed, seen in buds only; tube outer surface densely strigose, trichomes 0.13–0.5 mm long, inner surface glabrous to sparsely strigose, trichomes 0.13–0.25 mm long; lobes adaxial surface glabrous, abaxial surface densely strigose, trichomes 0.13–0.5 mm long; stamens 5, elliptic, abaxial surface densely strigose, trichomes 0.2–0.63 mm long; pistillodia bifid, equal, densely strigose, trichomes 0.05–0.25 mm long. *Pistillate inflorescences* 1-flowered, subsessile; peduncle up to 2 mm long, densely strigose, trichomes 0.08–0.25 mm long; bracts lance-ovate, 1.5–6.0 x 1.20–2.0 mm, outer surface densely strigose, trichomes 0.05–0.25 mm long, inner surface densely strigose, trichomes 0.38–0.88 mm long; calyx tubular to subcupuliform, 6-toothed, outer surface moderately strigose, trichomes 0.08–0.43 mm long, inner surface densely strigose, trichomes 0.13–1.25 mm long; tube 1.8–3.0 x 4.0–5.0 mm; teeth triangular, 0.75–1.0 x 1.5–1.65 mm; corolla infundibular, cream colored, amber or tawny on the underside of the lobes, 8-lobed; tube ca. 8.0 × 4.0 mm, outer surface densely strigose, trichomes 0.08–1.0 mm long, inner surface glabrous; lobes lanceolate, 3.5–4.5 x 1.0–1.5 mm, adaxial surface glabrous, abaxial surface densely strigose, trichomes 0.08–0.5 mm long; staminodia 8, lanceolate, up to 2 mm long, abaxial surface densely strigose, trichomes 0.13–0.25 mm long; hypanthium globose to suboblate, 2.5–5.0 x 4.0–7.0 mm, densely strigose, trichomes 0.05–0.25 mm long; disk densely strigose, trichomes 0.10–0.25 mm long; style with 8 unequal stigmatic arms, densely strigose becoming glabrous towards the apex of the stigmatic arms, trichomes 0.13–0.25 mm long. *Fruits* globose to suboblate, neither costate nor tuberculate, 13.5–22.0 x 16.5–19.0mm, densely strigose, trichomes 0.08–0.5 mm long, persistent calyx crown 1.0–2.0 mm long, incurved or ruptured by the expanded disk; schizogenous cavity absent; pyrenes ca. 62 visible in transverse section of fruit, 11 to 13 visible in longitudinal section of fruit, arranged in 8 double radiating lines in transverse section (Figure

2j), arranged in a ± horizontal line and oriented subvertically in longitudinal section (Figure 2i), cylindrical to falcoid, 6.5–9.25 x 1.0–2.50 mm.

Etymology

The epithet is derived from the Latin "do not touch", since it is presently known to a single location, and its population is estimated to decline due to land conversion and habitat clearance.

Distribution and ecology

Timonius noli-tangere is apparently endemic to the island of Samar and is currently known only from Balangiga (Figure 1). It grows along edges of disturbed mixed dipterocarp forests on lateritic soils near the tributaries of Balangiga River at 20 to 60 m altitude. Associated species found in its habitat include: *Greeniopsis multiflora* (Elmer) Merr. (Rubiaceae*), Melastoma malabathricum* L. (Melastomataceae), *Nepenthes samar* Jebb and Cheek (Nepenthaceae), *Swietenia macrophylla* King (Meliaceae), *Timonius finlaysonianus* (Rubiaceae) and *Utania volubilis* (Wall.) Sugumaran (Gentianaceae).

Provisional assessment of IUCN conservation status

The extent of occurrence of *Timonius noli-tangere* cannot be calculated. The area of occupancy is estimated to be 4 km^2 (calculated in GeoCAT with 2 km defined cell-width, Bachman et al. 2011), which complies with criterion B2 for the Critically Endangered category. The species is only known from a single location, which complies with subcriterion "a" of the Critically Endangered category B2. The locality is situated within the buffer zone of the Samar Island Natural Park (SINP), but *T. noli-tangere* occurs on a vegetation near human settlement areas where agricultural and infrastructure expansion were observed. Furthermore, Stibig et al. (2007) reported that illegal logging on secondary and degraded forests is an ongoing concern for Eastern Samar, confirming that it remains a threat to the sustainability of forest ecosystems and biodiversity conservation in the region (Carandang et al. 2012). Collection of firewood and illegal artisanal small-scale gold mining are also seen as threats to its habitat and population. This human-induced habitat degradation is further aggravated by recent natural disturbances. The vegetation of Balangiga has been damaged by the Category-5 typhoon Haiyan (locally known as Super Typhoon "Yolanda") in 2013 and the habitat of *T. noli-tangere* was severely affected (A. Canillas pers. comm.). The typhoon was followed by a wildfire that scourged most of the protected forest area in Balangiga (Granath 2014). Because of the above-mentioned facts, we assess *T. noli-tangere* as Critically Endangered CR B2ab(iii).

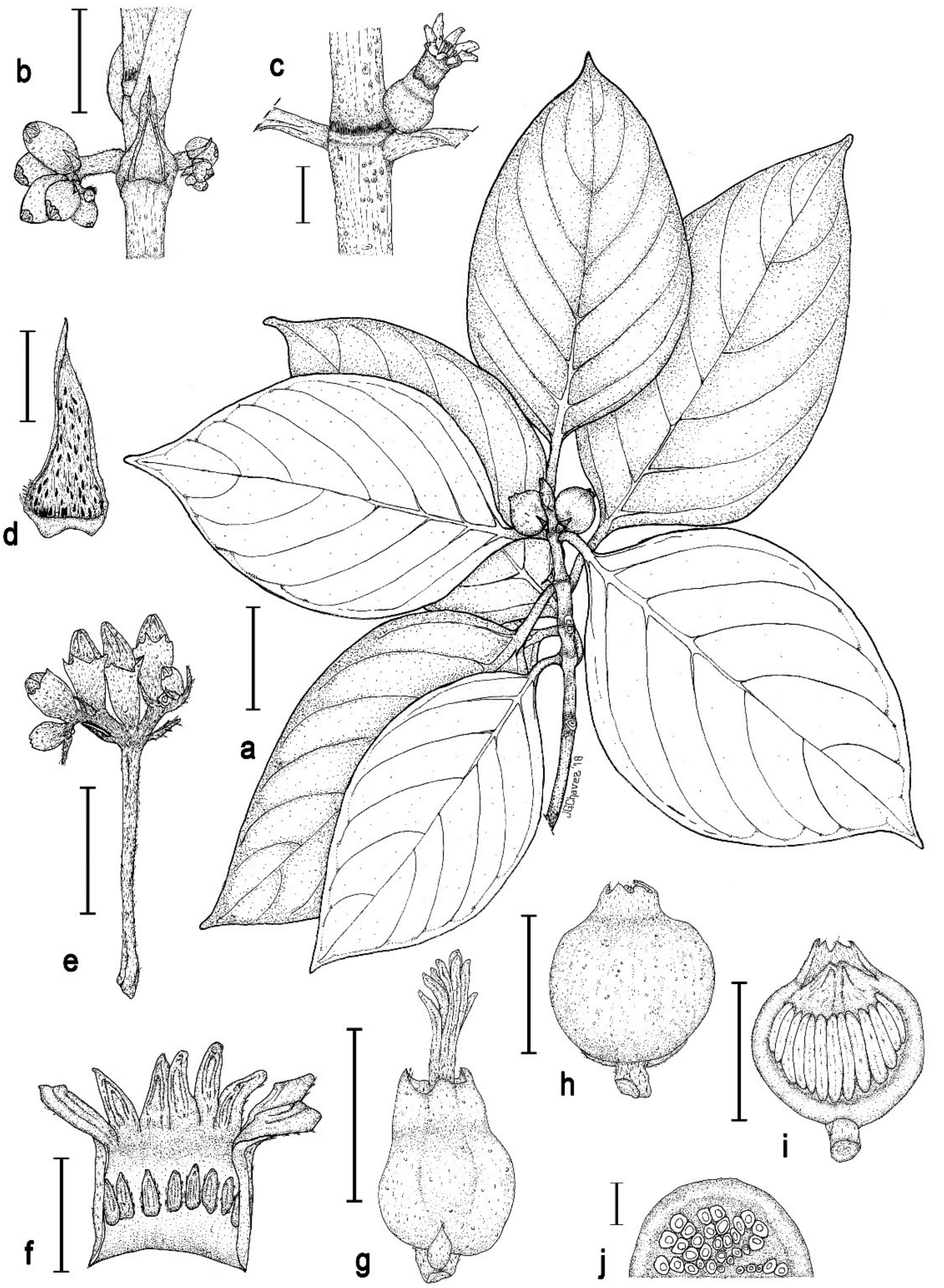

Figure 2. *Timonius noli-tangere.* (a) fruiting branchlet; (b) staminate branchlet; (c) pistillate branchlet; (d) stipule, inner surface showing colleters; (e) staminate inflorescence; (f) corolla, opened pistillate flower; (g) hypanthium and style; (h) fruit; (i) fruit, longitudinal section; (j) fruit, cross-section. Scale bars: a = 3 cm; b = 15 mm; c, f–g = 7 mm; d, j = 4.5 mm; e = 12 mm, h–i = 17 mm. All drawn by Jayson G. Chavez, based from (a, h–j) B. Lemana BC012; (b, d) A. Lola and M. Lorenzo LL003; (c, f–g) A. Lola and M. Lorenzo LL004; (e) A. Lola and M. Lorenzo LL006.

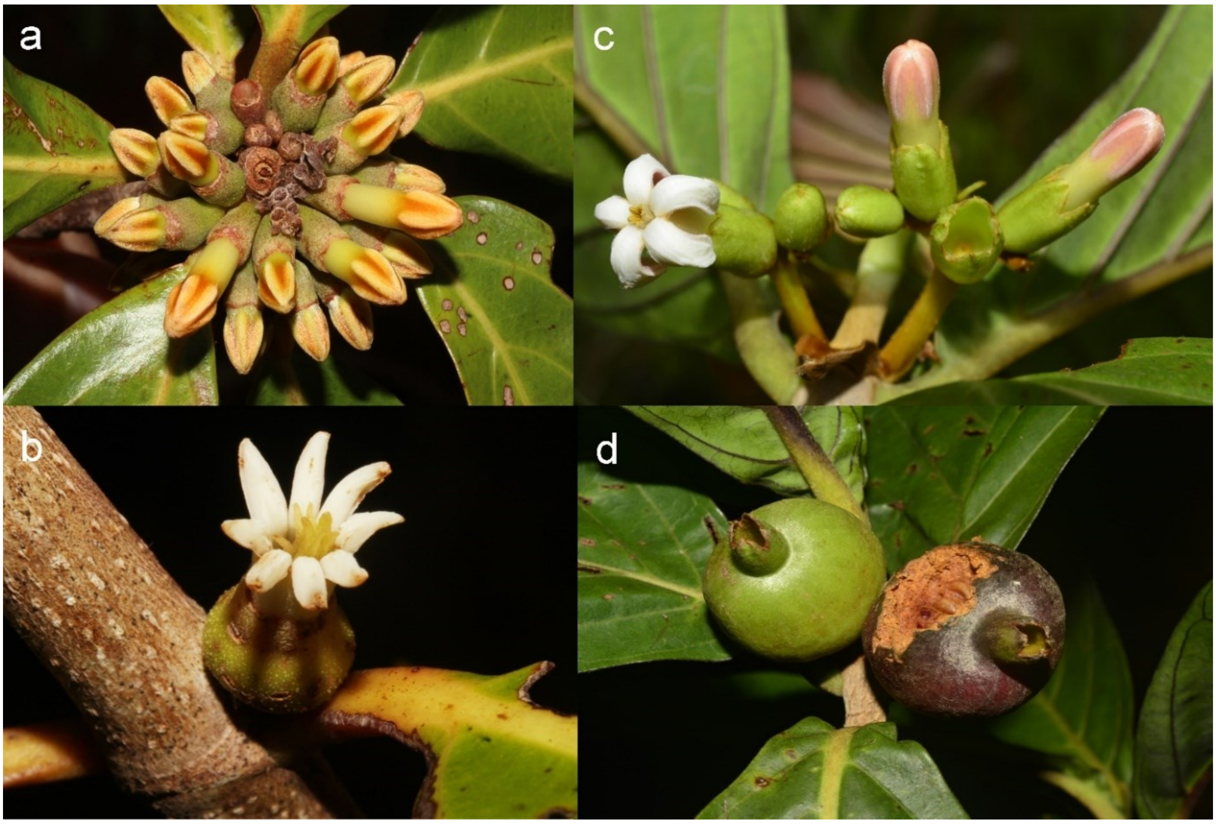

Figure 3. *Timonius noli-tangere*. (a) staminate inflorescences; (b) pistillate inflorescene. – *Timonius valetonii*. (c) staminate inflorescences; (d) infructescence. Photographs by Jay Edneil C. Olivar (a–b) and Jayson G. Chavez (c–d).

Remarks

Timonius noli-tangere exhibits leaves with variable phyllotaxy (opposite or in whorls of three or four) and leaf shape (elliptic to oblance-ovate or lance-ovate to widely ovate with apex shortly acuminate to attenuate and base cuneate or obtuse to rounded). Also, variable is the length of the peduncle and the number of flowers in the male inflorescences. *Timonius noli-tangere* is noted here as one of the Philippine *Timonius* that has a high degree of morphological plasticity, even within an individual. However, it can be easily distinguished by the combination of opposite to whorled leaves, reddish and verrucose calyces, subsessile fruits with dense trichomes crowned by the short persistent calyx. The indumenta of *Timonius noli-tangere* are often covered by wax or crystal-like substances or are even ruptured (those on the branchlets) especially on specimens infected by scale insects. Furthermore, some specimens have hollow branchlets with porate openings that are inhabited by ants, viz.: *B. Lemana BC001* (USTH) and *A. Lola and L. Lorenzo LL003* (USTH). Such an ant-plant association was also observed in *T. papuanus* Merr. (Darwin 2010a).

Additional specimens examined (paratypes)

The Philippines. Eastern Samar: Balangiga, Barangay Sta. Rosa, ♂, 22 May 2012, *B. Lemana BC001* (USTH); same location, ♂, 7 September 2017, *A. Lola and M. Lorenzo LL002* [L (2 sheets), UBT, USTH]; same location, ♂, 7 September 2017, *A. Lola and M. Lorenzo LL003* [A, L (3 sheets), UBT, USTH]; same location, ♀, 7 September 2017, *A. Lola and M. Lorenzo LL004* [L (2 sheets), PNH, USTH (2 sheets)]; Barangay 01, Sitio Cantinoc, ♂, 8 September 2017, *A. Lola and M. Lorenzo LL006* [L (2 sheets), US, USTH].

***Timonius sulitii* Merr. and Quisumb. ex J.G.Chavez and Tandang, sp. nov. (Figure 4)**

Diagnosis

Timonius sulitii is related to *T. noli-tangere*, but differs from it by having chartaceous leaves with silky underside and 8 to 9 pairs of lateral nerves (vs. coriaceous, dull, 4 to 7 pairs in T. noli-tangere), long pedunculate female inflorescences 22.0–34.5 mm long (vs. subsessile, up to 2.0 mm long), 10.5–11 x 10.0–10.5 mm, tuberculate and costate fruits with schizogenous cavity (vs. 13.5–22 x 16.5–19.0 mm, neither tuberculate nor costate, absent) and by the U-shaped orientation of the pyrenes in longitudinal section of the fruit (vs. subvertical orientation).

Type

THE PHILIPPINES. Eastern Samar: Taft, Mt. Calbiga, along road km 64, ♀, 18 May 1948, *M. Sulit sub. Phil. Nat. Herb. 6429* (also numbered *M. Sulit and E. Coñese 2938*) (holotype PNH; isotype L).

Description

Trees up to 7 m tall, ca. 6 cm dbh. *Bark* unknown. *Branchlets* 3.0–3.5 mm wide toward apex, angular, moderately strigose becoming glabrous when mature, trichomes 0.10–0.4 mm long. *Stipules* lance-ovate to ovate, 8.0–11.0 x 4.0–8.0 mm, slightly two ridged converging towards the apex, outer surface densely strigose becoming glabrous towards the margin, trichomes 0.13–0.5 mm long, inner surface densely strigose-pilose, trichomes 0.38–2.0 mm long. *Colleters* present on inner surface of stipules, bracts and sinuses of calyx teeth. *Leaves* opposite; petiole 10.5–16.0 x 2.5–3.0 mm, moderately strigose, trichomes 0.05–0.75 mm long; lamina ovate to suborbicular, 13.5–15.5 x 11.5–16.0 cm, apex mucronate, base cuneate to rounded, chartaceous, upper surface moderately strigose, trichomes 0.08–0.38 mm long, lower surface moderately silky-strigose becoming densely silky-strigose along the midrib and secondary nerves, trichomes 0.13–0.38 mm long along the lamina while 0.38–1.25 mm along the midrib and secondary nerves; secondary nerves 8 to 9 pairs; domatia present as tuft of trichomes on axils of secondary nerves, occasionally as crypt-type in axils of tertiary nerves. *Staminate inflorescences* unknown. *Pistillate inflorescences* 1-flowered; peduncle 22.0–34.5 x 1.5–2.0 mm, moderately strigose, trichomes 0.08–0.5 mm long; bracts triangular, 1.5–2.0 x 1.0–1.25 mm, outer surface densely strigose, trichomes 0.13–0.25 mm long, inner surface densely strigose-pilose, trichomes 0.13–0.25 mm long; calyx tubular to cupuliform, 5- to 6-toothed, outer surface moderately strigose, trichomes 0.05–0.5 mm long, inner surface densely strigose, trichomes 0.38–0.75 mm long; tube 2.1–2.5 x 3.3–3.4 mm; teeth triangular, recurved, 0.75–1.9 x 0.75–1.75 mm; corolla seen in buds only, 5-lobed; tube outer surface densely strigose, trichomes 0.13–0.38 mm long, inner surface glabrous; lobes adaxial surface glabrous, abaxial surface densely strigose, trichomes 0.13–0.5 mm long; staminodia not seen; hypanthium cupuliform, ca. 5.0 × 4.5 mm, moderately strigose, trichomes 0.05–0.18 mm long; disk densely strigose, trichomes 0.18–0.63 mm long; style not seen. *Fruits* (sub-) globose, 5-costate, tuberculate, 10.5–11.0 x 10.0–10.5 mm, moderately strigose, trichomes 0.08–0.38 mm long, persistent calyx crown 2.5–3.0 mm long, recurved; schizogenous cavity present; pyrenes 8 to 9 visible in transverse section of fruit, 11 to 15 visible in longitudinal section of fruit, not arranged double radiating files in transverse section (Figure 4j), arranged in a U-shaped pattern and oriented horizontally to vertically in longitudinal section (Figure 4i), ovoid, 2.50–3.5 x 1.0–2.0 mm.

Etymology

The substantival epithet is adopted from the unpublished name of Elmer D. Merrill (1876–1956) and Eduardo A. Quisumbing (1895–1986) as indicated on the herbarium label of the type materials. The name is in reference to Mamerto D. Sulit (1915–1953), who collected the specimens during the rehabilitation of the Philippine National Herbarium (PNH) after the Second World War.

Distribution and ecology

Timonius sulitii is apparently rare and only known from the type locality. It is reported to occur in a dipterocarp forest along roadsides at about 250 m altitude. However, the type locality of *T. sulitii* should be treated with caution, since the geopolitical boundaries of some municipalities in the Philippines may have changed after the Second World War.

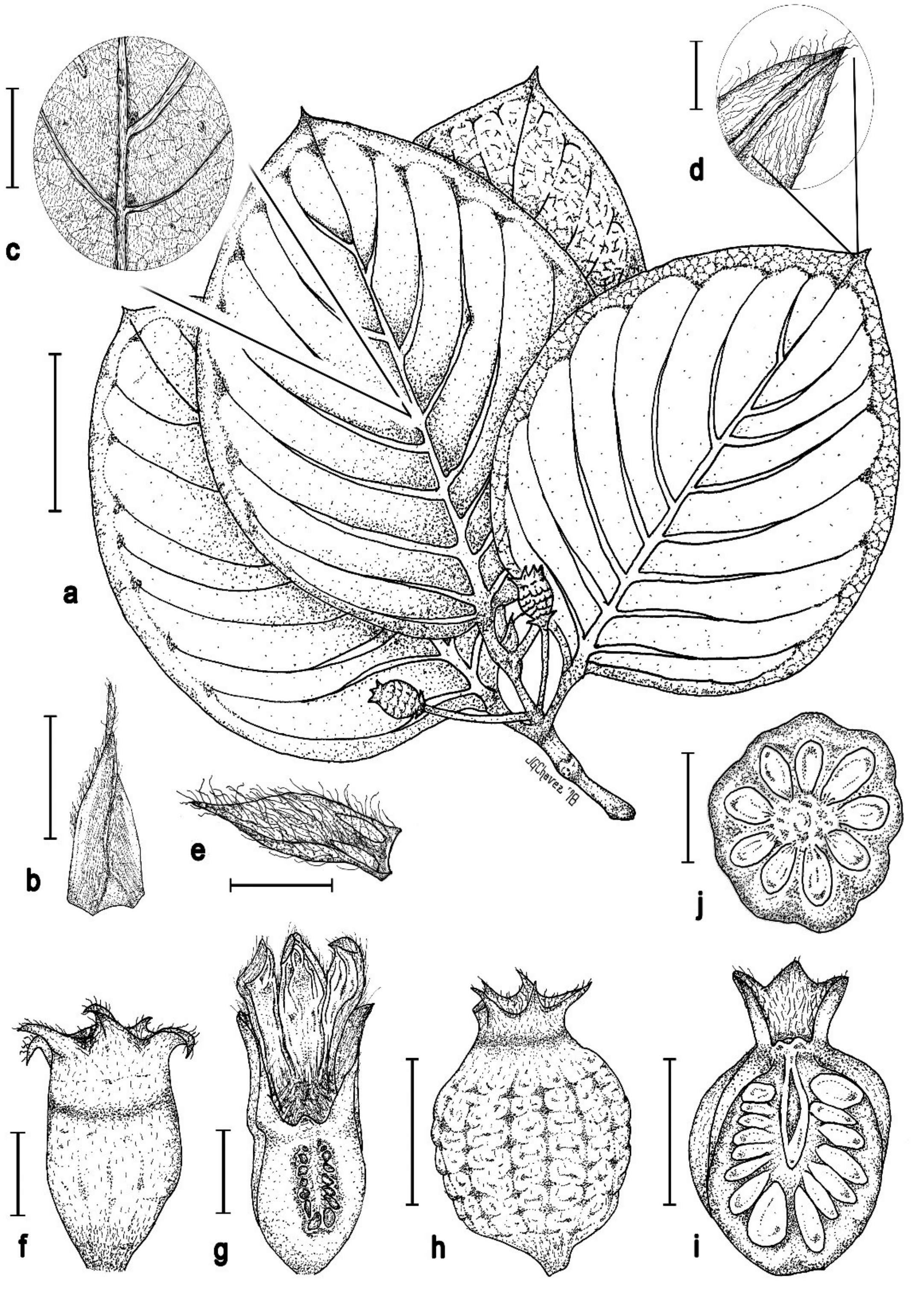

Figure 4. *Timonius sulitii.* (a) fruiting branchlet; (b) stipule, outer surface; (c) leaf lamina, abaxial surface; (d) leaf apex, abaxial surface; (e) bracts, inner surface showing two colleters; (f) hypanthium with calyx limb, outer surface; (g) hypanthium with corolla, longitudinal section; (h) fruit; I: fruit, longitudinal section; (j) fruit, cross-section. – Scale bars: a = 4 cm; b, j = 5 mm; c = 20 mm; d = 2 mm; e = 1 mm; f, g = 2.5 mm; h, i = 6.5 mm. – All drawn by Jayson G. Chavez from the type material.

Provisional assessment of IUCN conservation status

The extent of occurrence (EOO) for *Timonius sulitii* cannot be calculated because the species is only known from a single specimen. The area of occupancy (AOO) is estimated to be 4 km^2, which complies with criterion B2 for the Critically Endangered category. The species is known from a single specimen and a single location, which complies with subcriterion "a" of criterion B2 for the Critically Endangered category. The species occurs in a vegetation type that Madulid and Agoo (1999) considered as heavily exploited for important timber trees. Furthermore, extensive habitat clearance in the Philippines was observed in the post-war period (Kummer 1992). We therefore infer a reduction in the extent and quality of the habitat of *Timonius sulitii*. The species was never re-collected since 1948 despite extensive botanical expeditions conducted in Samar (1948–1996). Because of the low AOO, the single location, the inferred reduction in the quality and extent of its habitat and the fact that the species was not collected since 1948, we assess it here as Critically Endangered CRB2ab(iii).

Remarks

Timonius sulitii is readily distinguished from all Philippine *Timonius* by the combination of chartaceous and widely ovate leaves with silky pubescence on the underside, recurved calyx teeth and the tuberculate and costate fruits with schizogenous cavity. Among Philippine *Timonius*, a schizogenous cavity can only be observed in *T. sulitii* and the coastal *T. finlaysonianus*. This air-filled chamber appearing as a central locule is hypothesized by Darwin (1993) to provide buoyancy to the fruits.

The type specimen of *T. sulitii* has two different collection numbers that are found on different labels mounted on the sheets. The first is the herbarium label of PNH indicating that it belongs to the collection of M. Sulit Phil. Nat. Herb. 6429, and the second is the field label containing the original notes about the plant and that it was collected by M. Sulit and E. Coñese with the number 2938. The practice of placing these two labels on mounted sheets from Philippine collections was proposed by Merrill (1916b), who acknowledged the importance of field notes in providing valuable data for plant identification.

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