



Review article

From DELTA to Genomics: Two decades of Philippine Rubiaceae research progress

Grecebio Jonathan D. ALEJANDRO*

College of Science, Research Center for the Natural and Applied Sciences, and The Graduate School, University of Santo Tomas, España Boulevard, 1008 Manila, Philippines. *Corresponding authors' emails: gdalejandro@ust.edu.ph

(Manuscript received 14 February 2026; Accepted 5 May 2026; Online published 18 May 2026)

ABSTRACT: The coffee family (Rubiaceae) is one of the most diverse angiosperm families found in the Philippines. This review synthesizes two decades of progress in Philippine Rubiaceae systematics, phylogenetics, biogeography, and conservation biology from 2004 to the present. Currently, 94 genera are recognized across 35 tribes within two major subfamilies, Dialypetalanthoideae (51 genera) and Rubioideae (41 genera), with two genera in tribes unclassified as to subfamily. Since 2004, 54 new endemic species and two new endemic genera (*Kanapia* and *Chewlunia*) have been described, with 64.81% facing conservation threats — 23 species (42.59%) classified as Critically Endangered, nine (16.67%) as Endangered, and three (5.56%) as Vulnerable. Major systematic breakthroughs include the resolution of polyphyletic genera, including *Mussaenda*, *Antirhea*, *Morinda*, and *Hedyotis*, and 128 nomenclatural changes addressing century-old taxonomic problems. Endemism rates across the surveyed sites ranged from 46–88%, concentrated in montane ecosystems and edaphically specialized habitats, with *Psychotria* alone comprising 100 or more endemic species. Biogeographic analyses reveal the Philippines as both an evolutionary "crossroads" and "cradle," with Wallace's and Huxley's lines structuring lineage diversification, and molecular dating placing *Ixora* diversification in the Neogene (2.3–2.6 mya). Conservation genomics and bioclimatic modeling have identified montane taxa as the most vulnerable to climate-driven habitat contraction, underscoring the urgent need for climate corridors and assisted colonization. Taxonomic impediment, limited institutional capacity, and insufficient germplasm conservation infrastructure remain the principal barriers to comprehensive biodiversity documentation and the protection of this irreplaceable endemic diversity.

KEY WORDS: biodiversity conservation, biogeography, endemic species, systematics, taxonomic revision.

INTRODUCTION

The coffee family (Rubiaceae) is one of the largest angiosperm families, comprising nearly 14,200 species in approximately 586 accepted genera (Razafimandimbison and Rydin, 2024). Tropical Rubiaceae occur predominantly in forest understories, where they provide habitat and food for numerous organisms while contributing to soil stabilization (Davis *et al.*, 2009; Thureborn *et al.*, 2024). Rubiaceae also exhibit extraordinary morphological and ecological diversity, ranging from minute annuals to giant trees across all terrestrial biomes (Soza and Olmstead, 2010; Ehrendorfer and Barfuss, 2014).

The Philippines is recognized as one of the world's 25 biodiversity hotspots and harbors a unique assemblage of Rubiaceae (Myers *et al.*, 2000; Posa *et al.*, 2008). The complex geoclimatic setting of the archipelago, characterized by tectonic and volcanic activity and fluctuating sea levels, provides ideal conditions for isolation-driven diversification (Hall, 2002; Brown and Diesmos, 2009). Consequently, the flora exhibits exceptional endemism, with species on individual islands or mountain ranges forming distinct assemblages isolated for millennia.

Alejandro and Liede (2003) provided the first updated overview of Philippine Rubiaceae since Merrill (1923). This study counted a total of 80 Rubiaceae genera in the

country, of which six were cultivated and four endemic, *Antherostele* Bremek., *Greeniopsis* Merr., *Sulitia* Merr., and *Villaria* Rolfe, representing at least 12% of the global Rubiaceae genera. Alejandro and Liede (2003) presented a parallel description of 80 genera coded in the Descriptive Language for Taxonomy (DELTA) system, providing the first digital documentation with an interactive key of more than 120 characters. This baseline study subsequently guided the tracing of taxonomic and nomenclatural changes in Philippine Rubiaceae as well as particular genera requiring revision after 1923, as presented by Alejandro (2007).

Philippine Rubiaceae research has advanced considerably since 2007, particularly in molecular phylogenetics, field studies and international collaboration. Consequently, the nomenclatural changes presented by Alejandro (2007) require updating due to numerous generic transfers, new combinations, synonymizations, newly described species, and nomenclatural corrections in the intervening years. The incorporation of next-generation sequencing techniques has illuminated persistent taxonomic questions and revealed previously unknown biogeographic patterns in the cryptic biodiversity of tropical islands (Razafimandimbison *et al.*, 2014; Alejandro *et al.*, 2016; Banag *et al.*, 2017). Complementarily, more focused field studies have provided new information about the distribution of several described and undescribed species (Ordas *et al.*, 2019; Biag



and Alejandro, 2021; Bautista *et al.*, 2024).

Biogeographic analyses and phylogenetic data have revealed the dual role of the Philippine archipelago as a geographical 'crossroads' and 'cradle' of rapid divergence and convergence of lineages from disparate biogeographic regions (Brown and Diesmos, 2009; Siler *et al.*, 2010; Hughes and Eastwood, 2006; Hall, 2002; Lohman *et al.*, 2011). The complex geological history of the Philippine archipelago, characterized by tectonic activity, volcanism associated with the Pacific Ring of Fire, and fluctuating Pleistocene sea levels, has repeatedly fragmented and reconnected dispersal pathways, generating repeated cycles of isolation and colonization that drove in situ adaptive radiation (Hall, 2002; Lohman *et al.*, 2011). Molecular phylogenetic studies on Philippine Rubiaceae, particularly on *Ixora*, have documented multiple independent colonization events from both the Asian and Wallacean biogeographic realms, with Wallace's and Huxley's lines functioning as major barriers structuring gene flow and lineage divergence across the archipelago (Banag *et al.*, 2017). Molecular-dated diversification within Philippine Rubiaceae lineages is concentrated in the Neogene period (2.3–2.6 mya), coinciding with the modern formation of the archipelago and the establishment of tropical forest ecosystems (Hall, 2002). This scenario presents the Philippines as a vast, untamed, and natural laboratory important for the study of the evolution of tropical plants, island biogeography, and conservation biology. The perplexing distribution of Philippine Rubiaceae provides lessons that may be useful for understanding other tropical archipelagos.

Our global flora is currently under great pressure from climate change, deforestation, agriculture, and mining, which are directly attributable to human activity (Sodhi *et al.*, 2004; Hughes, 2017). In the Philippines, the primary forest cover has drastically decreased from 90% historically to under 20% (Mittermeier *et al.*, 1999; Liu *et al.*, 2013). This form of destruction has the most impact on species suffering from a high degree of endemism coupled with stringent dispersal and ecological requirements. For instance, Rubiaceae plants in the Philippines demonstrate the need for active conservation, along with a global perspective of biodiversity.

The years from 2004 to the present are particularly interesting in covering the most important milestones of conservation biology, biogeography, taxonomy, and molecular systematics of the Rubiaceae in the Philippines. The last two decades of work have fit the results in the frameworks of these concepts and have particularly traced the most relevant shifts in the understanding of Rubiaceae in the Philippines. These insights determine the most important lines of conservation research that need to be in place to protect the Rubiaceae diversity in the Philippines. This review considers published works and new techniques expected to influence systematic and

conservation biology in the future.

Scientific Progress and Revolution in Phylogenetics

Molecular systematics has been the major focus of research on Philippine Rubiaceae since 2004, driven by the recognized limitations of morphological traits in resolving relationships at and below the species level (Davis *et al.*, 2009). Early phylogenetic frameworks for the family relied on single plastid genes, such as *rbcL*, across Rubiaceae subfamilies and tribes (Bremer *et al.*, 1995; Bremer and Thulin, 1998), but these produced low resolution and conflicting topologies (Wendel and Doyle, 1998). The transition to multi-gene analyses combining nuclear and chloroplast markers has substantially improved phylogenetic resolution across the family, including Ixoroideae (Andreasen and Bremer, 2000) and the Condamineeae–Rondeletieae–Sipaneeae complex (Rova *et al.*, 2002). Total evidence frameworks integrating molecular and morphological data have further refined tribal and generic delimitations within the Rubiaceae (Wikström *et al.*, 2015). These methodological advances were directly applied to Philippine Rubiaceae: plastid and nuclear markers (*rps16*, *trnT-trnF*, ITS, ETS) resolved the phylogenetic placement of endemic genera, including *Villaria* (Alejandro *et al.*, 2011), *Greeniopsis* (Alejandro *et al.*, 2010; Uy and Alejandro, 2012), and *Ixora* (Banag *et al.*, 2017), while revealing polyphyly in *Antirhea* and driving its reclassification into *Guettardella* (Chavez *et al.*, 2021). Recently, next-generation sequencing approaches, including plastid phylogenomics applied to Rubioideae (Thureborn *et al.*, 2024; Ciborowski *et al.*, 2024), have addressed complex phylogenetic issues, such as incomplete lineage sorting, cytonuclear discordance, and chloroplast capture, which are analytical challenges directly encountered in Philippine *Ixora* (Banag *et al.*, 2017).

Significant phylogenetic studies

Resolving Philippine *Antirhea*: The most extensive generic revision involved the dissolution of Philippine *Antirhea* Comm. ex Juss. All species were transferred to the reinstated genus *Guettardella* Champ. & Benth. (Chavez *et al.*, 2021). This classification adjustment followed extensive molecular phylogenetic analyses and found that *Antirhea* sensu lato (s.l.) was polyphyletic and needed to be subdivided into several genera. All Philippine *Antirhea* taxa formed a well-supported monophyletic group and were more closely associated with *Guettardella* than with true *Antirhea*, which justified their transfer to the resurrected genus. The actions adopted resulted in 12 new combinations that considerably altered the systematics of an important group of Philippine endemics.

The dynamics of evolution in *Ixora*: In 2017, Banag *et al.* used ETS, ITS, *trnT-trnF*, and *rps16* to study 24 species of Philippine *Ixora* and identified five separate



lineages of plants that are geographically unique and have experienced multiple episodes of both recolonization and radiation. There is also evidence of cytonuclear discordance, which has been attributed to a combination of factors, including incomplete lineage sorting, interlineage hybridization, and chloroplast capture through the process of introgression (Wendel and Doyle, 1998). Biogeographic partitioning of lineages based on their geographic distribution was also identified, with one Wallacean-affiliated lineage and four Asian-affiliated lineages supporting this partitioning (Myers *et al.*, 2000). Therefore, it can be inferred that this study demonstrates how geological and climatic events in the Indo-Pacific region have influenced its biodiversity. The presence of the Wallacean-affiliated lineage on all islands except Palawan further supports the notion of ecologically defined barriers to migration, while the presence of multiple Asian lineages may indicate sequential colonization waves into the Philippines by different lineages, followed by in situ speciation (Hall, 2002; Lohman *et al.*, 2011).

Phylogenetic Placement of *Villaria*: Alejandro *et al.* (2011) conducted the first molecular phylogenetic study on the endemic genus *Villaria*. Morphological studies have placed *Villaria* in Gardenieae or Octotropideae, but the phylogenetic affinities remain unclear because of the genus' unique combination of characters, such as unilocular ovaries, parietal placentation, and horizontally oriented ovules (Robbrecht, 1988). Alejandro *et al.* (2011) used *rps16* intron and *trnT-trnF* spacer markers to place *Villaria* within Octotropideae and showed previously unknown relationships with *Hypobathrum* Blume and *Pouchetia* A. Rich., thereby questioning the current tribal classification schemes and showing how there can be discrepancies between the character-based classifications and the phylogenetic relationships (Persson, 2000; Bremer and Eriksson, 2009). In this study, they reduced *Villaria* from seven species to five, described *V. leytenis* Alejandro & Meve as a new species and synonymized *V. philippinensis* Rolfe and *V. rolfei* S. Vidal into *V. odorata* (Blanco) Merr., providing a foundation for studying the evolutionary history of Octotropideae. Subsequent studies further expanded the genus: Arriola and Alejandro (2013) described *V. uniflora*, Arriola *et al.* (2018a) described *V. marinduquensis*, Alejandro and Meve (2016) transferred *Randia lanceolata* as *V. lanceolata*, and Arriola and Alejandro (2020) made three new combinations — *V. coriacea*, *V. multibracteata*, and *V. purpurea* — transferring these Philippine endemics from *Hypobathrum* Blume to *Villaria* based on shared unilocular ovaries with parietal placentation, bringing the total number of recognized *Villaria* species to eleven.

Tribal Placement of endemic *Greeniopsis*: Alejandro *et al.* (2010) clarified the taxonomic status of the endemic genus *Greeniopsis*, which had previously been placed in the tribe *Aleisanthieae* based on morphological

characteristics. Subsequent molecular studies using the nuclear ITS marker (Uy and Alejandro, 2012) and plastid markers (*rps16* intron and *trnT-F* region) across all seven *Greeniopsis* species further supported its taxonomic placement. Through parsimony and Bayesian analyses, Alejandro *et al.* (2010) confirmed the monophyly of *Greeniopsis* in *Aleisanthieae*. Furthermore, their results also supported the sister relationship of *Greeniopsis* with the genera *Aleisanthia* Ridl. and *Aleisanthiopsis* Tange, which has been a subject of research regarding its connection to Southeast Asia, and produced the first molecular evidence for the definition of tribes within Ixoroideae. Additionally, they demonstrated that the woolly abaxial leaf hairs are found in only one *Greeniopsis* species, and these hairy leaves were determined not to be tribal synapomorphies. These findings support the role of molecular data in refining our understanding of character evolution and morphology-based assessments. The study also offered the first thorough taxonomic revision of the genus, providing a robust basis for appreciating the diversity and relationships of this peculiar Philippine endemic group to *Aleisanthieae* systematics and tribal diagnoses.

Polyphyly in *Mussaenda*: Alejandro *et al.* (2005) identified that *Mussaenda* Burm. ex L. s.l. is a polyphyletic group, which was a big step in terms of the taxonomy of the group. Through their use of ITS and *trnT-trnF* DNA sequences, they found that the group had two distinct lineages, which belonged to other groups within the Ixoroideae tribe, and thus were able to completely redefine the generic limits of *Mussaenda*. The diagnostic morphological features of petaloid calyx lobes and large conspicuous inflorescence, evolved separately, on multiple occasions, across different tribes within Ixoroideae, as an example of convergent evolution, due to the selective pressures from pollinators and dispersers, and therefore illustrate the limitations of using morphological characteristics for taxonomic classification (Bremer and Thulin, 1998). In addition to being significant to the study of *Mussaenda*, this study has also been important for understanding the evolution of Ixoroideae characters and for providing key evidence for reconstructing the phylogeny of Rubiaceae, tribal boundaries, and biogeographical origins of tropical woody Rubiaceae (Davis *et al.*, 2009; Wikström *et al.*, 2020).

Tribe and Subfamily Reorganization: Extensive non-monophyly within previously delineated groups of taxa has come to light because of molecular studies, calling for taxonomic restructuring at both the generic and tribal levels. The polyphyly of species-rich genera has been a primary driver of this reorganization: *Psychotria* has been shown to be polyphyletic across multiple continents, demanding either extensive generic reorganization or acceptance of a broadly circumscribed genus encompassing all of Psychotrieae (Davis *et al.*, 2009; Razafimandimbison *et al.*, 2014); *Galium* L. has



been shown to be polyphyletic within tribe Rubieae, challenging generic delimitation across the worldwide circumscription of the tribe (Ehrendorfer and Barfuss, 2014); *Hedyotis* has been demonstrated to be a highly complex, non-monophyletic assemblage in the Asian-Pacific region, necessitating extensive generic re-delimitation within Spermaceae (Wikström *et al.*, 2013; Neupane *et al.*, 2015); and *Ixora* has been shown to comprise multiple geographically and phylogenetically distinct lineages with Asian and Wallacean affinities, reflecting the broader non-monophyly challenges within Ixoreae (Banag *et al.*, 2017). These instances of generic polyphyly collectively illustrate the complexities involved in classifying highly diverse groups and have directly necessitated tribal and subfamily-level reorganization across the family.

The incorporation of temporal data in the form of molecular dating analyses has yielded extremely important and previously elusive information pertaining to the timing of the principal diversification events in the evolution of Rubiaceae. Most studies indicate that the principal lineages diversified during the Paleogene period (65-23 million years ago), while further diversification was enhanced by Neogene period climatic shifts and the development of tropical ecosystems (Wikström *et al.*, 2015; Meseguer *et al.*, 2022). Understanding these temporal patterns is necessary to understand current patterns of biodiversity and the potential impacts of environmental changes in the future. Recent studies involving phylogenomics have deepened the understanding of the family Rubiaceae, describing three subfamilies with well delineated tribal borders (Razafimandimbison and Rydin, 2024). The current classification divides the family into 71 tribes (including three unplaced tribes) within two subfamilies (Dialypetalanthoideae and Rubioideae): Dialypetalanthoideae with 38 tribes, Rubioideae with 30 tribes, and Acranthereae, Coptosapelteae, and Luculieae, which are three unplaced tribes requiring further phylogenetic research.

Following the classification of Razafimandimbison and Rydin (2024), this review paper determines the distribution of 94 Philippine Rubiaceae genera across 35 tribes in two major subfamilies (Table 1). The subfamily Dialypetalanthoideae (formerly Ixoroideae) is more diverse, with 51 genera in 18 tribes. Gardenieae (11 genera) is the most dominant, followed by Naucleaeae (8 genera). The subfamily Rubioideae contains 41 genera in 15 tribes, with Spermaceae being the largest (13 genera), followed by Urophyllaeae (4 genera).

The classification uncovers intricate phylogenetic patterns, such as the monotypic tribes, indicating high phylogenetic divergence. Two genera remain problematic: *Acranthera* Arn. ex Meisn. and *Coptosapelta* Korth., whose tribal affiliations have yet to be assigned to a subfamily. The tribal and subfamilial framework of Razafimandimbison and Rydin (2024) as applied to

Philippine Rubiaceae demonstrates that the Philippines is a significant center of Rubiaceae diversity, harboring representatives of most major lineages within the family and providing essential baseline data for systematic, ecological, and conservation research.

Revolutionary species discoveries and taxonomic breakthroughs

Discovery of new endemic genera: The description of *Kanapia* Arriola & Alejandro represents a major taxonomic breakthrough in the systematics of Philippine Rubiaceae. Extensive phylogenetic analysis using combined nuclear and chloroplast markers revealed that two species previously classified under *Canthium* Lam. represent a distinct evolutionary lineage warranting generic recognition (Arriola *et al.*, 2016). *Kanapia* is distinguished from related Vanguerieae genera by several morphological features: stems lacking aculei, a shorter calyx limb-to-tube ratio, pentamerous corollas, and angular pyrenes with longitudinal crests and associated slits on ventral surfaces (Lantz and Bremer, 2004). Phylogenetic assessments positioned *Kanapia* as a sister to a clade composed of *Afrocanthium* (Bridson) Lantz & B. Bremer, *Keetia* E. Phillips, and other Vanguerieae genera but was found to be genetically divergent and morphologically distinctive enough to warrant generic recognition. The distribution of *Kanapia* species across multiple Philippine islands suggests an ancient origin within the region, followed by allopatric speciation driven by island isolation. This pattern resembles those of other endemic groups and supports the hypothesis that island isolation promotes speciation in organisms in the Philippines (Brown and Diesmos, 2009). The two *Kanapia* species are of concern because they are endemic and subject to habitat destruction and climate change.

The creation of *Chewlunia* P.K.Hoo & Junhao Chen marks the latest generic discovery, bringing the total number of Philippine endemic genera to five. This genus, derived from the monophyletic *Timonius* group, as detailed by Chen *et al.* (2023), includes seven species endemic to the Philippines that were in *Timonius* DC. and *Greenea* Wight & Arn. They are *C. auriculata* (Merr.) P.K.Hoo & Junhao Chen, *C. hirsuta* (Elmer) P.K.Hoo & Junhao Chen, *C. longiflora* (Merr.) P.K.Hoo & Junhao Chen, *C. oligophlebia* (Merr.) P.K.Hoo & Junhao Chen, *C. rotunda* (Merr.) P.K.Hoo & Junhao Chen, *C. samarensis* (Merr.) P.K.Hoo & Junhao Chen and *C. urdanetensis* (Elmer) P.K.Hoo & Junhao Chen. The genera *Timonius* and *Greenea* are more derived, having unique morphoanatomical structures such as unisexual flowers, specialized fruits, 4-merous corollas, and other uniseriate floral elements.

Unprecedented species discovery rate: The rate of new species descriptions has increased dramatically compared to previous decades, likely because of intensified fieldwork and improved taxonomic methods

**Table 1.** Subfamilial and tribal classification of 94 Philippine Rubiaceae genera

| Subfamily/ Tribe | Genera | Count |
|-----------------------------|--|-----------|
| RUBIOIDEAE | | |
| Anthospermeae | <i>Nertera</i> | 1 |
| Argostemmateae | <i>Argostemma</i> , <i>Mycetia</i> | 2 |
| Knoxieae | <i>Knoxia</i> | 1 |
| Lasiantheae | <i>Lasianthus</i> , <i>Paralasianthus</i> | 2 |
| Mitchelleae | <i>Damnacanthus</i> | 1 |
| Morindeae | <i>Coelospermum</i> , <i>Gynochthodes</i> , <i>Morinda</i> | 3 |
| Ophiorrhizeae | <i>Ophiorrhiza</i> , <i>Xanthophytum</i> | 2 |
| Paederieae | <i>Paederia</i> , <i>Saprosma</i> , <i>Serissa</i> | 3 |
| Palicoureeae | <i>Eumachia</i> , <i>Geophila</i> | 2 |
| Prismatomerideae | <i>Prismatomeris</i> | 1 |
| Psychotrieae | <i>Amaracarpus</i> , <i>Chassalia</i> , <i>Psychotria</i> | 3 |
| Rubieae | <i>Galium</i> , <i>Rubia</i> | 2 |
| Schradereae | <i>Schradera</i> | 1 |
| Spermaceae | <i>Debia</i> , <i>Dentella</i> , <i>Dimetia</i> , <i>Exallage</i> , <i>Hedyotis</i> , <i>Involucrella</i> , <i>Leptopetalum</i> , <i>Mitracarpus</i> , <i>Oldenlandia</i> , <i>Oldenlandiopsis</i> , <i>Richardia</i> , <i>Scleromitron</i> , <i>Spermaceo</i> | 13 |
| Urophyllaeae | <i>Antherostele</i> , <i>Praravinia</i> , <i>Streblosa</i> , <i>Urophyllum</i> | 4 |
| | Subtotal | 41 |
| DIALYPETALANTHOIDEAE | | |
| Airospermeae | <i>Boholia</i> | 1 |
| Aleisanthieae | <i>Greeniopsis</i> | 1 |
| Augusteae | <i>Wendlandia</i> | 1 |
| Chiococceae | <i>Badusa</i> , <i>Bikkia</i> | 2 |
| Cinchoneae | <i>Cinchona</i> | 1 |
| Coffeae | <i>Coffea</i> , <i>Diplospora</i> , <i>Discospermum</i> | 3 |
| Dialypetalantheae | <i>Dolicholobium</i> | 1 |
| Gardenieae | <i>Aidia</i> , <i>Atractocarpus</i> , <i>Benkara</i> , <i>Ceriscoides</i> , <i>Gardenia</i> , <i>Oxyceros</i> , <i>Randia</i> , <i>Ridsdalea</i> , <i>Rubovietnamia</i> , <i>Tarennoidea</i> , <i>Vidalasia</i> | 11 |
| Guettardeae | <i>Chewlunia</i> , <i>Guettarda</i> , <i>Guettardella</i> , <i>Timonius</i> | 4 |
| Hydnophyteae | <i>Hydnophytum</i> , <i>Myrmephytum</i> , <i>Myrmecodia</i> | 3 |
| Hymenodictyeae | <i>Hymenodictyon</i> | 1 |
| Ixoreae | <i>Ixora</i> | 1 |
| Mussaendeae | <i>Mussaenda</i> , <i>Pseudomussaenda</i> | 2 |
| Naucleaeae | <i>Adina</i> , <i>Ludekia</i> , <i>Mitragyna</i> , <i>Myrmeconuclea</i> , <i>Nauclea</i> , <i>Neolamarckia</i> , <i>Neonauclea</i> , <i>Uncaria</i> | 8 |
| Octotropideae | <i>Cowiea</i> , <i>Hypobathrum</i> , <i>Villaria</i> | 3 |
| Pavetteae | <i>Pavetta</i> , <i>Tarenna</i> | 2 |
| Scyphiphoreae | <i>Scyphiphora</i> | 1 |
| Vanguerieae | <i>Canthium</i> , <i>Dibridsonia</i> , <i>Kanapia</i> , <i>Psydrax</i> , <i>Pyrostria</i> | 5 |
| | Subtotal | 51 |
| Acranthereae | <i>Acranthera</i> | 1 |
| Coptosapelteae | <i>Coptosapelta</i> | 1 |
| | Subtotal | 2 |
| Total | | 94 |

(Wheeler *et al.*, 2012; Hughes *et al.*, 2021). Between 2004 and 2026, 54 new Rubiaceae species were described in the Philippines (Table 2), all of which are endemic to the archipelago. The conservation status assessment indicated that 64.81% of these newly described species face some level of conservation threat, with 23 species (42.59%) classified as Critically Endangered, nine species (16.67%) as Endangered, and three species (5.56%) as Vulnerable, while 8 species (14.81%) were data deficient, and only 1 species (1.85%) was considered least concerned (Table 2). Taxonomic activity was

concentrated in several genera, with *Timonius* being the most productive (nine species), followed by *Lasianthus*, *Mussaenda* (four species each), and *Villaria*, *Ixora*, *Ophiorrhiza* L. (three species), and *Psychotria* (four species). Publication trends showed peak periods during 2014-2016 and 2020, with the latter year being particularly productive for *Timonius* species descriptions. These findings highlight both the remarkable undiscovered diversity within Philippine Rubiaceae and the urgent need for conservation action, with 64.81% of newly described species facing conservation threats.

**Table 2.** Fifty-four endemic Philippine Rubiaceae species published from 2004 to present.

| Species Name | Conservation Status | Reference |
|---|---------------------|---|
| <i>Antherostele samarensis</i> Obico & Alejandro | CR | Obico and Alejandro (2013) |
| <i>Argostemma mirae</i> F.A.Blasco, Tandang & Alejandro | DD | Blasco <i>et al.</i> (2024) |
| <i>Bikkia montoyae</i> Mejillano, Santor & Alejandro | CR | Alejandro <i>et al.</i> (2014) |
| <i>Dibridsonia parvifolia</i> Last., Marcial & Arriola | CR | Arriola <i>et al.</i> (2026) |
| <i>Discospermum philippinensis</i> Arriola & Alejandro | CR | Arriola and Alejandro (2015) |
| <i>Discospermum reyesii</i> Arriola, Valdez & Alejandro | CR | Arriola <i>et al.</i> (2018b) |
| <i>Gardenia ornata</i> K.M.Wong | EN | Wong (2011) |
| <i>Gardenia vulcanica</i> K.M.Wong | CR | Wong (2011) |
| <i>Guettardella surigaoensis</i> (Salamanes & Alejandro) J.G.Chavez* | CR | Salamanes <i>et al.</i> (2015), Chavez <i>et al.</i> (2021) |
| <i>Gynochthodes leonardii</i> J.G.Chavez, Venturina & Alejandro | EN | Chavez <i>et al.</i> (2015) |
| <i>Hedyotis hamiguitanensis</i> Santor, D.D.B.Santiago & Alejandro | DD | Santor <i>et al.</i> (2021) |
| <i>Hedyotis papafranciscoi</i> Alejandro | CR | Alejandro (2015) |
| <i>Ixora alexandroi</i> Banag & Tandang | EN | Banag <i>et al.</i> (2015b) |
| <i>Ixora reynaldoi</i> Banag | CR | Banag <i>et al.</i> (2015b) |
| <i>Ixora silagoensis</i> Manalastas, Banag & Alejandro | CR | Banag <i>et al.</i> (2014) |
| <i>Lasianthus brochidodromus</i> H.Zhu | NA** | Zhu <i>et al.</i> (2012) |
| <i>Lasianthus halconensis</i> Arshed & Alejandro | CR | Arshed and Alejandro (2016) |
| <i>Lasianthus palawanensis</i> H.Zhu | NA | Zhu <i>et al.</i> (2012) |
| <i>Lasianthus ridsdalei</i> H.Zhu | NA | Zhu <i>et al.</i> (2012) |
| <i>Morinda carmosa</i> Venturina, E.E.L.Suarez & Alejandro | CR | Venturina <i>et al.</i> (2017) |
| <i>Mussaenda grandibracteata</i> Alejandro | EN | Alejandro <i>et al.</i> (2016) |
| <i>Mussaenda liedeeae</i> Alejandro | CR | Alejandro <i>et al.</i> (2016) |
| <i>Mussaenda ustii</i> Alejandro | EN | Alejandro <i>et al.</i> (2008) |
| <i>Mussaenda viridiflora</i> Alejandro | NA | Alejandro <i>et al.</i> (2008) |
| <i>Mycetia dagohoyana</i> Dela Bajan, Tandang & Alejandro | DD | Dela Bajan <i>et al.</i> (2017) |
| <i>Mycetia suedixieana</i> Tandang & Ordas | DD | Tandang <i>et al.</i> (2019) |
| <i>Neonauclea connicalycina</i> Ordas, Taradji, Valdez & Alejandro | CR | Ordas <i>et al.</i> (2016) |
| <i>Neonauclea viridiflora</i> Ordas, Banag & Alejandro | EN | Ordas <i>et al.</i> (2017) |
| <i>Ophiorrhiza erythropilosa</i> Alfeche & Alejandro | DD | Alfeche <i>et al.</i> (2020) |
| <i>Ophiorrhiza hamiguitanensis</i> Alfeche & Alejandro | DD | Alfeche <i>et al.</i> (2020) |
| <i>Ophiorrhiza ravifolia</i> Naive & Alejandro | LC | Naive and Alejandro (2024) |
| <i>Paralasianthus zhengyianus</i> H.Zhu | NA | Zhu (2015) |
| <i>Psychotria alexandroi</i> Ordas, Chen & Odulio | CR | Ordas <i>et al.</i> (2025) |
| <i>Psychotria caraballoensis</i> Pajarillaga, Ordas & Moran | EN | Pajarillaga <i>et al.</i> (2025) |
| <i>Psychotria nitidifolia</i> Ordas, Chen & Alfeche | CR | Ordas <i>et al.</i> (2025) |
| <i>Psychotria pendens</i> M.A.Bautista & R.Bustam. | CR | Bautista <i>et al.</i> (2024) |
| <i>Psydrax multiflorus</i> Arriola & Alejandro | CR | Arriola <i>et al.</i> (2017) |
| <i>Psydrax puberulus</i> Arriola & Alejandro | NA | Arriola and Alejandro (2013a) |
| <i>Pyrostria arayatenensis</i> Suba, Arriola & Alejandro | NA | Suba <i>et al.</i> (2020) |
| <i>Pyrostria triflora</i> Arriola, Calaramo & Alejandro | NA | Arriola <i>et al.</i> (2015) |
| <i>Ridsdalea philippinensis</i> R.Bustam. & Pelsler | DD | Bustamante and Pelsler (2022) |
| <i>Rubovietnamia coronula</i> Alejandro & Meve | CR | Alejandro and Meve (2016) |
| <i>Timonius alexandroanus</i> J.G.Chavez, Meve & Liede | EN | Chavez <i>et al.</i> (2020c) |
| <i>Timonius dumagat</i> J.G.Chavez | EN | Chavez <i>et al.</i> (2020c) |
| <i>Timonius eremiticus</i> J.G.Chavez & Banag | CR | Chavez <i>et al.</i> (2020b) |
| <i>Timonius noli-tangere</i> J.G.Chavez, Alejandro & Meve | CR | Chavez <i>et al.</i> (2020a) |
| <i>Timonius pseudoarboreus</i> J.G.Chavez | VU | Chavez <i>et al.</i> (2020c) |
| <i>Timonius ridsdalei</i> J.G.Chavez | EN | Chavez <i>et al.</i> (2020c) |
| <i>Timonius spes-vitarum</i> J.G.Chavez | VU | Chavez <i>et al.</i> (2020c) |
| <i>Timonius stevendarwinii</i> J.G.Chavez | VU | Chavez <i>et al.</i> (2020c) |
| <i>Timonius sulitii</i> Merr. & Quisumb. ex J.G.Chavez & Tandang | CR | Chavez <i>et al.</i> (2020a) |
| <i>Villaria leytenensis</i> Alejandro & Meve | CR | Alejandro <i>et al.</i> (2011) |
| <i>Villaria marinduquensis</i> Arriola & Alejandro | NA | Arriola <i>et al.</i> (2018a) |
| <i>Villaria uniflora</i> Arriola & Alejandro | CR | Arriola and Alejandro (2013b) |

**Guettardella surigaoensis* was originally described as *Antirhea surigaoensis* in 2015; ** NA = not assessed



Recent notable discoveries: *Psychotria pendens* M.A.Bautista & R.Bustam., discovered in the ultramafic soils of Mount Victoria, Palawan, demonstrates specialized adaptations to heavy metal-rich substrates. These include modified root morphology and enhanced physiological tolerance mechanisms that are not observed in closely related species (Bautista *et al.*, 2024). Molecular phylogenetic analysis places *P. pendens* in the Pacific *Psychotria* clade, indicating transoceanic dispersal followed by some form of ecological specialization. The current status of the species is Critically Endangered, largely because of its distributional range and the threats facing its habitat.

Ophiorrhiza ravifolia Naive & Alejandro was collected from the Naga-Kabasalan Protected Landscape Zone. The species is unique in its leaf characteristics and is the only member of the Philippine *Ophiorrhiza* species with silver-grey abaxial leaf surfaces (Naive and Alejandro, 2024). This distribution of new taxa in a protected area supports the need for more systematic biological research in the area.

Argostemma mirae Blasco, Tandang & Alejandro: a new species of the genus *Argostemma*, was described from Surigao del Sur by Blasco *et al.* (2024), which adds to the growing list of the genus in the Philippines. It is found at low elevations in shaded limestone forests, which is unusual for a genus typically found in higher montane regions. This discovery adds to the knowledge of the ecological diversification of the genus and suggests that other limestone karst areas in the archipelago may contain other undescribed species.

Psychotria caraballoensis Pajarillaga, Ordas & Moran, described from the Caraballo Mountain Range, Dupax del Sur, Nueva Vizcaya, northern Luzon, represents a new endemic species allied to the Subalpina species group *sensu* Sohmer and Davis (2007). It can be distinguished from its closest relative, *P. sohotonensis*, by its greater number of lateral veins, inflorescences with verticillate or oppositely branched cymules, puberulous flowers with longer corolla lobes, and smaller globose to subglobose fruits with ruminant endosperms. Notably, it is one of the few Philippine *Psychotria* species documented with dimorphic long- and short-styled flower morphs. The species is assessed as Endangered (EN) due to its restricted distribution and anthropogenic threats (Pajarillaga *et al.*, 2025).

Dibridsonia parvifolia Last., Marcial & Arriola, from Mt. Mariveles, Bataan, Luzon, represents the first endemic species described within the genus *Dibridsonia* for the Philippines, a genus previously known only from widespread Malesian species (Wong *et al.*, 2018). Its discovery at 600 m elevation on Mt Mariveles — an accessible mountain near Manila — underscores that novel species continue to be found even in botanically studied localities and highlights the importance of thorough revisionary work at the genus-level for

accurately documenting Philippine Rubiaceae diversity. This species is assessed as Critically Endangered (CR) (Arriola *et al.*, 2026).

Historical pattern analysis: Analysis of taxonomic and discovery patterns across Philippine Rubiaceae as a whole — encompassing 94 genera distributed across 35 tribes within two major subfamilies, with family wide endemism rates of 46–88% documented through systematic biodiversity surveys (Batuyong *et al.*, 2021a; Ordas *et al.*, 2019) — revealed several significant trends. First, micro-endemism is a pervasive characteristic of Philippine Rubiaceae, not solely of recently described taxa; the dominance of species-rich genera such as *Psychotria* (ca. 100 or more endemic species), *Hedyotis* (33 endemic species), and *Ixora* (30 endemic species) reflects family wide patterns of restricted distribution tied to island geography, elevational zonation, and edaphic specialization (Hughes *et al.*, 2013). Second, cryptic diversity remains substantially under-documented across the entire family, as evidenced by new discoveries even in previously well-surveyed regions, underscoring that inventory gaps are a family wide rather than genus-specific phenomenon. Third, phylogenetic analysis has become indispensable for species delimitation across Philippine Rubiaceae, correcting the systematic underestimation of species diversity that resulted from reliance on morphological characters alone, particularly in phenotypically plastic or convergent lineages (Bickford *et al.*, 2007; De Queiroz, 2007).

Comprehensive generic revisions

Systematic overhaul on *Mussaenda*: Alejandro *et al.* (2016) conducted a detailed systematic review of Philippine *Mussaenda* that encompassed wide-ranging field research, herbarium collections, and morphological analyses to identify Philippine *Mussaenda* species. This resulted in the identification of twenty-four species (three of which are new), four varieties, and the validation of previous nomenclatural issues. In addition, this study provides the first complete morphological descriptions of each taxon, along with distributional data and assessments of their conservation status. Several key taxonomic changes were also made in the course of this work, including the description of *M. grandibracteata* Alejandro, from Occidental Mindoro as having exceptionally large petaloid bracts, *M. liedeeae* Alejandro, from Palawan as the westernmost limit of the genus in the Philippines with unique regional adaptations, and the validation of *M. milleri* Elmer ex Alejandro as a result of resolving the long-standing nomenclatural issues. *Mussaenda milleri*, originally published by Elmer without adequate description or type designation, remained nomenclaturally invalid until Alejandro *et al.* (2016) provided a formal description and designated a proper lectotype, thereby validating the name and recognizing this previously neglected endemic species.



Gardenia species delimitation: Wong (2011) revised Philippine *Gardenia* J.Ellis and provided much-needed clarity to a taxonomically complex group that had suffered from inconsistent species delimitation and nomenclatural confusion. The revision recognized five species, primarily based on calyx morphology, a character system that proved more taxonomically informative than the vegetative and floral characters used in previous treatments. Two new endemic species were described: *G. ornata* K.M.Wong from Mindanao, defined by its calyx structure with elaborate lobe patterns, and *G. vulcanica* K.M.Wong from volcanic and nutritionally poor soils in Luzon, distinguished by its extreme fruit morphology and tolerance of harsh edaphic conditions (Wong, 2011). The revision also elucidated the usage of several problematical names, including *G. pseudopsidium* Blanco, which was determined to be a nomen dubium because of the inadequacy of the original description and the absence of type material.

Nomenclatural advances and historical problem resolution

Resolution of century-old nomenclatural problems: Berger (2023) made a major nomenclatural breakthrough — among the significant advances of recent decades — when he resolved the earliest Philippine *Psychotria* description of 1829, *Psychotria philippensis* Cham. & Schltdl. The type specimen of *Psychotria philippensis* has been completely lost, rendering direct morphological re-examination of the original material impossible. Nearly 200 years later, Berger found that this species is conspecific with the resin-producing mangrove species *Scyphiphora hydrophylacea* C.F.Gaertn. Because the type is irretrievably lost, Berger was able to prove that the resin-producing mangrove habitat characteristics of this species excluded it from *Psychotria* s. str., which does not have those characteristics (Sohmer and Davis, 2007), through comprehensive historical research on surviving protologues and early botanical literature alone. The placement of this species within *Scyphiphora* C.F.Gaertn. was supported by all three types of indirect evidence: morphological descriptions, habitat information, and geographic locality data. This example demonstrates the continued value of historical botanical research for nomenclatural stability when physical type material is no longer available, and the importance of preserving historical botanical collections and literature.

Phylogenetically driven taxonomic reassignments: Approximately 128 nomenclatural changes have been documented (Table S1) since Alejandro's 2007 baseline, revealing several major categories of taxonomic revision in Philippine Rubiaceae. The most significant changes involve complete genus transfers, exemplified by the reassignment of all 12 Philippine *Antirhea* species to *Guettardella* (Chavez *et al.*, 2021) and the transfer of four *Rothmannia* Thunb. species to the newly recognized

Ridsdalea J.T. Pereira & K.M.Wong (Wong and Pereira, 2016). The second major category encompasses large-scale generic reassignments driven by molecular phylogenetic studies, including the establishment of the new endemic genus *Chewlunia* in 2023, which accommodates seven species formerly placed in *Timonius* and *Greenea* (Chen *et al.*, 2023), the transfer of eight *Morinda* species to *Gynochthodes* Blume (Razafimandimbison and Bremer, 2011), and the redistribution of ten *Hedyotis* species across multiple genera, including *Oldenlandia* L., *Exallage* Bremek., *Involucrella* (Benth. & Hook.f.) Neupane & N.Wikstr., and *Scleromitron* (Wight & Arn.) Meisn. Species-level changes constitute the third category, prominently featuring extensive synonymizations within *Hydnophytum* Jack where nine species were reduced to synonymy under *H. formicarum* Jack and *H. moseleyanum* Becc. (Jebb and Huxley, 2019), and similar consolidations in *Ixora* involving eight species. Additionally, systematic reassignments have affected entire genera, notably the transfer of all *Borreria* G.Mey. species to *Spermacoce* L. (Cabral and Bacigalupo, 2004) and the relegation of all five Philippine *Randia* L. species to unplaced status, reflecting the ongoing resolution of polyphyletic genera through modern phylogenetic approaches.

Conservation biology and biodiversity assessment advances

Biodiversity documentation: Systematic biodiversity surveys across Philippine regions and habitat types have documented consistently high levels of Rubiaceae endemism, with rates derived from individual site surveys ranging from 46% to 88% across Luzon and Visayas (Biag and Alejandro, 2021; Batuyong *et al.*, 2021a,b; Ordas *et al.*, 2019). Biag and Alejandro (2021) recorded 42 species across 19 genera and 13 tribes of Rubiaceae in the Peñablanca Protected Landscape and Seascape, Cagayan Valley, of which 37 species (88%) were endemic to the Philippines, the highest endemism rate documented among the site surveys, a pattern correlated with the geological complexity of the Sierra Madre Mountains and the area's protected status. Batuyong *et al.* (2021a) documented 39 species in 24 genera and 13 tribes from Mt. Pao Range, Northwestern Luzon, of which 18 (46%) were endemic and two were narrow endemics; notably, both endemic genera of Philippine Rubiaceae, *Antherostele* and *Kanapia*, were recorded at this unprotected site. Batuyong *et al.* (2021b) documented 57 species in 28 genera and 15 tribes across three localities in Ilocos Norte, with the highest species richness in *Psychotria* (nine species), *Ixora* (six species), and *Ophiorrhiza* (four species). Ordas *et al.* (2019) documented 59 species in 31 genera from Eastern Samar, of which 37 (63%) were Philippine endemics. Collectively, these surveys demonstrate that Rubiaceae endemism is consistently high across geographically and



ecologically distinct Philippine localities, while also revealing that many areas (particularly the mountainous regions of Mindanao and surrounding small islands) remain poorly inventoried and likely harbor undescribed diversity (Hughes *et al.*, 2021).

Habitat Specialization of Philippine Rubiaceae: Philippine Rubiaceae exhibit a high degree of habitat specialization that directly underpins their island-specific endemism and conservation vulnerability. Montane forest understory habitats, characterized by distinct soil chemistry, humidity regimes, and altitudinal microhabitat mosaics, support the highest concentrations of endemic Rubiaceae species, with restricted gene flow between populations on separate mountain systems, reinforcing local endemism (Hughes *et al.*, 2013). Edaphically specialized habitats, particularly ultramafic soils and limestone karst formations, harbor unique Rubiaceae assemblages adapted to highly localized and physiologically demanding soil conditions (Proctor, 2003). For instance, *Psychotria pendens* is restricted to the ultramafic soils of Mount Victoria, Palawan, where edaphic-driven divergence from its widespread sister species is supported by molecular phylogenetic analysis (Bautista *et al.*, 2024). Coastal forest habitats support highly specialized taxa, such as *Bikkia philippinensis*, which is confined to small fragments of coastal forests with specific structural and edaphic requirements (Alejandro *et al.*, 2013, 2014). The narrow habitat tolerances characteristic of Philippine Rubiaceae render these taxa acutely sensitive to habitat modification, as even minor changes in soil chemistry, canopy structure, or hydrological regime can exceed their physiological limits.

Threat assessment and conservation status evaluation: The conservation of Philippine Rubiaceae is at severe risk. *Antherostele callophylla* is restricted to small patches of primary forest in Luzon, where low gene flow and inbreeding depression combine to increase the extinction risk from localized catastrophic events. *Bikkia philippinensis* faces mounting pressure from coastal development and projected sea-level rise associated with climate change (Alejandro *et al.*, 2013, 2014). Weak dispersal mechanisms combined with the specialized habitat requirements described above make these species particularly susceptible to environmental changes. Ex situ conservation efforts currently exist; however, long-term sustainability will depend on the implementation of habitat restoration and management plans targeted at the specific requirements of each taxon. Threat assessments are now provided at the time of publication for newly described species, many of which are identified as threatened due to their limited range and habitat destruction. *Psychotria pendens*, described in 2024, was immediately classified as Critically Endangered because of its exclusive association with a single ultramafic locality (Bautista *et al.*, 2024), illustrating the growing

integration of taxonomy and conservation assessment.

Species rediscoveries and range extensions: Targeted field surveys of Philippine Rubiaceae since 2020 have resulted in the rediscovery of several *Psychotria* species not collected since the 1990s, as well as documented range extensions that meaningfully revise the geographic limits and extinction risk of individual taxa. These findings are particularly significant for *Psychotria*, a genus for which extinction estimates have historically been high because of inadequate survey coverage. Koopowitz *et al.* (1998) projected that as many as 50% of Philippine *Psychotria* species might be extinct based on habitat conversion modeling, while the comprehensive monographic treatment of Sohmer and Davis (2007) reduced this estimate to approximately 28% following a more thorough systematic assessment. Recent targeted rediscoveries suggest that actual extinction rates may be lower, although many historical collections remain unverified and systematic survey coverage remains incomplete. Biag and Alejandro (2020) rediscovered multiple *Psychotria* species, subspecies, and varieties collected in the 1990s and presumed lost through targeted surveys in the Northern Sierra Madre Natural Park, Luzon. *Psychotria palimlimensis* Sohmer & A.P. Davis, endemic to Ilocos Norte and considered extremely rare, was rediscovered with updated morphological documentation and a revised conservation status assessment (Batuyong *et al.*, 2021c). Biag and Alejandro (2022) documented a substantial range extension of the threatened *Psychotria catanduanensis* Sohmer & A.P. Davis from its type locality on Catanduanes Island to coastal forests in Palanan, Isabela, greatly expanding its known distribution and demonstrating that Philippine Rubiaceae can occupy coastal habitats previously considered outside their range. Collectively, these findings underscore the importance of continued systematic field surveys, particularly in poorly inventoried regions, for accurately establishing the conservation status of Philippine Rubiaceae.

Conservation genomics applications: Conservation genomics has provided critical tools for assessing the population-level status of the Philippine Rubiaceae. The application of targeted molecular markers to determine genetic diversity within and among populations, identify evolutionarily distinct lineages, and assess the effects of habitat fragmentation on population connectivity forms the foundation of genetic conservation assessments for threatened taxa (Frankham *et al.*, 2014). In Philippine *Ixora*, phylogeographic analyses using nuclear and plastid markers have revealed geographically structured lineages separated by island barriers and mountain ranges, demonstrating that genetically distinct populations have evolved in isolation across the Philippine archipelago. This finding underscores the necessity of preserving genetic variation across multiple localities rather than concentrating conservation efforts on a single population



(Banag *et al.*, 2017). These results identify *Ixora* populations on different islands and mountain systems as independent conservation units warranting separate management considerations. The broader application of population genomic approaches, including RADseq-derived SNP datasets (Baird *et al.*, 2008; Andrews *et al.*, 2016), to other species-rich and threatened Philippine Rubiaceae genera, such as *Psychotria* and *Hedyotis*, remains a priority for establishing baseline genetic diversity data to guide future conservation planning.

Bioclimatic modeling and conservation applications:

Species distribution modeling (Elith *et al.*, 2009; Franklin, 2009) has been directly applied to Philippine Rubiaceae to assess habitat suitability under current and future climate scenarios. Banag *et al.* (2015a) constructed MaxEnt-based bioclimatic models for endemic Philippine *Ixora* species using WorldClim variables with georeferenced herbarium occurrence records, revealing critically narrow climatic envelopes and projecting substantial habitat contraction under climate change conditions. Montane species face the highest extinction risk, as their thermal tolerance limits prevent range shifts at rates sufficient to track climate velocity across the fragmented Philippine archipelago. These findings specifically support the establishment of climate corridors linking ridge systems and the promotion of assisted colonization for the most range-restricted endemic taxa (Banag *et al.*, 2015a). Therefore, the integration of species distribution models with elevation gradient and forest cover data from Philippine landscape surveys is essential for directing conservation resources toward habitats that sustain connectivity among isolated Rubiaceae populations, a priority made urgent by the continuing forest loss across Luzon, Mindanao, and the Visayas.

Biogeographic discoveries and evolutionary insights

Wallace's and Huxley's lines as barriers to dispersal:

Molecular phylogenetics has provided unprecedented insights into both Philippine biogeography and the evolutionary history of Philippine biodiversity. Banag *et al.* (2017) demonstrated that the distributional patterns of Philippine *Ixora* lineages correspond closely with the biogeographic boundaries delineated by Wallace's and Huxley's lines. "Wallace's Line," which marks the faunal and floral discontinuity between Borneo and the western Philippines on one side and Sulawesi on the other (Wallace, 1869), generally places much of the Philippines within the Asian/Bornean biogeographic region. However, the biogeographic position of the Philippine archipelago remains complex and transitional, as the country itself is intersected by both Wallace's and Huxley's lines. This subdivision reflects the mixed biotic affinities of the archipelago, with Philippine Rubiaceae lineages exhibiting both Asian and Wallacean relationships. Huxley's line is a similarly conceptual

boundary delineating a western Philippine zone with Asian biogeographic affinities from an eastern zone with Wallacean affinities (Huxley, 1868). All five Philippine *Ixora* lineages exhibited significant Asian and Wallacean affinities that align with these biogeographic boundaries. The confinement of the Wallacean-affiliated *Ixora* lineage to all Philippine islands except Palawan reflects a distributional pattern consistent with the biogeographic zone described by Huxley's line (Banag *et al.*, 2017), suggesting that the underlying geological and ecological factors associated with this boundary have shaped the separate evolutionary histories of *Ixora* lineages across the archipelago. The biogeographic subdivision of the Philippines is therefore essential for developing conservation plans for tropical flora that evolved through prolonged isolation, as each biogeographic zone harbors its own distinct evolutionary lineage.

Patterns of multiple colonization and adaptive radiation:

Phylogenetic studies at the genus level have shown that there have been several colonization events followed by in situ adaptive radiations throughout the Philippine archipelago. These results support the "crossroads" and "cradle" concepts for the Philippine archipelago as an old lineage refugium and diversity genesis due to ecological specialization and geographical isolation (Hughes and Eastwood, 2006; Brown and Diesmos, 2009). The timing of colonization and subsequent diversification is believed to coincide with large-scale climatic and geologic changes during the Pleistocene era, including changes in sea levels and volcanism associated with the Pacific Ring of Fire. The fragmentation and reconnection of dispersal pathways have provided a means for periods of divergence and isolation to occur (Hall, 2002; Lohman *et al.*, 2011). Adaptive radiation is supported by rapid morphological and ecological diversification among the endemic lineages of Philippine *Ixora* species. Although phylogenetically related, Philippine *Ixora* species exhibit a variety of floral forms, including differences in flower size, color, and pollination syndromes. Variation in pollination syndromes can be attributed to the rapid adaptation of these species to various pollinator assemblages (Banag *et al.*, 2017). Concentration of molecular-dated diversification occurred during the Neogene period (2.3-2.6 mya), which corresponds with the modern formation of the Philippine archipelago and the development of tropical forest ecosystems (Hall, 2002).

Island-Specific endemism patterns of Philippine Rubiaceae:

Philippine Rubiaceae exhibit remarkably high island-specific endemism, shaped by the interactions among island geography, topographic complexity, and habitat specialization. Luzon harbors the greatest absolute number of endemic Rubiaceae species, reflecting its large area and geological complexity, whereas the smaller islands show proportionally higher endemism per unit area, a pattern consistent with the island biogeographic



effects of isolation and limited gene flow (Ong *et al.*, 2002). The northeastern islands of Babuyan and Batanes, which are physically separated from the main Philippine archipelago, demonstrate particularly strong endemism attributable to prolonged geographical isolation and independent evolutionary divergence. Within individual islands, montane environments generate the highest concentrations of island-specific endemics owing to their mosaic of altitudinally distinct microhabitats that function as ecological isolates, promoting in situ speciation, and restricting gene flow between populations on different mountain systems (Hughes *et al.*, 2013). Edaphic specialization further contributes to island-specific endemism, with ultramafic soils and limestone karst habitats harboring unique assemblages of Rubiaceae that are adapted to highly localized soil conditions (Proctor, 2003). For instance, *Psychotria pendens* evolved its distinctive ultramafic association through edaphically driven divergence from a widespread sister species on Palawan (Bautista *et al.*, 2024). These island-specific processes are reflected in the disproportionate concentration of Philippine Rubiaceae endemism within a small number of species-rich genera: *Psychotria* accounts for 100 or more endemic species, followed by *Hedyotis* (33 species), *Ixora* and *Ophiorrhiza* (30 species each), *Guettardella* and *Pavetta* (14 species each), and *Canthium* and *Villaria* (11 species each) (Table 3). Montane forest lineages consistently dominate lowland taxa across all major islands (Hughes *et al.*, 2013).

Table 3. Top-ranked Philippine Rubiaceae genera by endemic species count.

| Rank | Genus | Number of Endemic Species |
|------|---------------------|---------------------------|
| 1 | <i>Psychotria</i> | 100+ |
| 2 | <i>Hedyotis</i> | 33 |
| 3 | <i>Ixora</i> | 30 |
| 3 | <i>Ophiorrhiza</i> | 30 |
| 4 | <i>Timonius</i> | 24 |
| 5 | <i>Mussaenda</i> | 22 |
| 6 | <i>Tarenna</i> | 21 |
| 7 | <i>Praravinia</i> | 19 |
| 8 | <i>Urophyllum</i> | 16 |
| 9 | <i>Guettardella</i> | 14 |
| 9 | <i>Pavetta</i> | 14 |
| 10 | <i>Canthium</i> | 11 |
| 10 | <i>Villaria</i> | 11 |

Methodological and technological advances in systematic research

Evolution of molecular techniques: Molecular systematic studies of Philippine Rubiaceae have progressed from single-gene approaches to multi-locus and genome-scale analyses in recent years. Early phylogenetic reconstructions employed nuclear ITS sequences and plastid markers (*rbcL*, *matK*, and *trnL-F*) to establish the tribal-level placements of Philippine genera (Bremer and Manen, 2000). Banag *et al.* (2015a, 2017) applied these markers in biogeographic analyses that resolved the distinct Asian and Wallacean affinities

of Philippine *Ixora* lineages relative to Wallace's and Huxley's lines. More recently, whole chloroplast genome sequencing has revealed structural features, including gene loss and pseudogene formation, pertinent to the evolutionary history of Philippine Rubiaceae (Huynh *et al.*, 2024). Target-enrichment phylogenomics and RADseq-derived SNP datasets represent critical untapped tools for resolving cryptic species boundaries and population structures in morphologically complex Philippine genera such as *Psychotria* and *Hedyotis*, where conventional markers have been insufficient (Banag *et al.*, 2015a). Environmental DNA (eDNA) metabarcoding offers a non-destructive means of detecting range-restricted Philippine Rubiaceae in logistically inaccessible forest ecosystems (Thomsen and Willerslev, 2015).

Molecular dating and phylogeographic analysis: Molecular dating analyses using relaxed clock models calibrated with fossil data (Drummond *et al.*, 2006; Ho and Duchene, 2014) have established a temporal framework for Rubiaceae diversification, with principal lineages originating during the Paleogene (65–23 mya) and further diversifying through Neogene climatic shifts (Wikström *et al.*, 2015; Meseguer *et al.*, 2022). For Philippine Rubiaceae, molecular-dated diversification in *Ixora* is concentrated in the Neogene (2.3–2.6 mya), coinciding with the modern formation of the Philippine archipelago (Banag *et al.*, 2017). Phylogeographic analyses, which assess spatial variation in genetic diversity and gene flow in relation to historical climate change and habitat fragmentation (Avice, 2000), are directly applicable to the Philippine context, given the archipelago's complex geological history of repeated island connection and separation. Coalescent methods incorporating gene tree discordance and incomplete lineage sorting (Liu *et al.*, 2009; Bryant *et al.*, 2012) are particularly suited to Philippine Rubiaceae, where cytonuclear discordance has been documented in *Ixora* (Banag *et al.*, 2017). These approaches can identify Evolutionarily Significant Units (ESUs) within Philippine Rubiaceae populations, which are critical for conservation planning. Approximate Bayesian Computation (ABC) provides a framework for testing colonization routes and demographic history (Beaumont *et al.*, 2002; Csilléry *et al.*, 2010), which remains largely unexplored for most Philippine genera.

Digital herbarium resources and data integration: Worldwide, developed digital herbarium resources have changed the ease of accessing and collaborating on specimen data and research of multiple institutions. The Co's Digital Flora of the Philippines project (Pelser *et al.*, 2011 onwards) has almost completely digitized Philippine plants, including remarkable diversity of Rubiaceae, and offers online taxonomic data, specimen images, and distribution data on Philippine flora. Studies have shown that digitized images have enhanced research on fragile specimens while improving access for



education and research (Thiers *et al.*, 2016). The use of 3D scanning and photogrammetry has broadened complex morphology studies. Applied imaging methods facilitate constructive approaches to comparative morphology. Global database initiatives, such as the Global Biodiversity Information Facility (GBIF), have consolidated specimen records for macroecology and large-scale conservation analysis (Edwards, 2004). These resources are now invaluable for geographic and taxonomic knowledge acquisition and prioritization of field research efforts. Automated specimen identification and morphological analyses are being developed with machine learning techniques which may speed up taxonomic work (Wilf *et al.*, 2016; Carranza-Rojas *et al.*, 2017). They would not replace expert taxonomic evaluation, but would aid in first-level sorting and identification, thus relieving taxonomists for more difficult systematic challenges.

Current research problems and existing knowledge gaps

Although much has been accomplished in recent years concerning the study of Rubiaceae in the Philippines, taxonomic impediment continues to be the main barrier to creating a comprehensive inventory of the country's biodiversity and developing conservation plans. This is primarily due to the lack of sufficient trained taxonomists, limited availability of funding, and decreased institutional support for training programs (Wheeler *et al.*, 2004; Kim and Byrnes, 2006). The taxonomic impediment can be clearly seen in several of the many species-rich genera of Rubiaceae. For example, *Psychotria* contains an estimated 100 or more species that are endemic to the Philippines, yet no thorough revisions have been made to this genus because it is highly complex at the level of morphology and contains a large number of synonyms (Sohmer and Davis, 2007). *Hedyotis* includes more than 50 species endemic to the Philippines, which show a great deal of variation in their morphology, and most of these species have insufficient diagnostic characteristics to distinguish them from one another (Terrell and Robinson, 2003). Similar issues exist for *Ixora*.

Due to decreasing university funding for systematic biology since the 1990s, training new taxonomists has become increasingly challenging. One reason for this difficulty is that the skills required by taxonomists are specialized, such as the ability to examine morphology, know nomenclature, and gain experience in the field, which is difficult to include in modern graduate school curricula (Wheeler *et al.*, 2004). There are still unresolved phylogenetic relationships among the principal Rubiaceae clades, and these clades vary greatly in their resolution based upon how many genes were sampled, and what method(s) of analysis were used (Bremer and Manen, 2000; Razafimandimbison and Rydin, 2024).

Phylogenetic analyses have revealed a high degree of paraphyly and polyphyly throughout the Rubiaceae, and therefore, taxonomic reorganization is required, including the reclassification of polyphyletic genera such as *Galium* and *Asperula* L. (Wikström *et al.*, 2013; Ehrendorfer and Barfuss, 2014). Genomic analyses have shown that there are hidden variations in the Rubiaceae, and that populations that appear to be different externally may not necessarily be representative of different evolutionary lineages (De Queiroz, 2007; Shaffer and Thomson, 2007).

There are also significant gaps between the discovery of new taxa and the implementation of conservation efforts for these taxa, with many recently described species lacking effective conservation status (Costello *et al.*, 2013). Much of the taxonomic research has focused on Luzon, leaving other regions of the Philippines, such as Mindanao, relatively unstudied because of geographic and political constraints (Hughes *et al.*, 2021).

Botanical garden *ex situ* conservation programs remain underdeveloped in the Philippines and do not currently possess the specialized botanical gardens and seed banks necessary for long-term conservation efforts (Oldfield, 2009). Habitat corridor climate adaptation strategies remain largely unimplemented (Hannah *et al.*, 2007). There is also a need for increased funding for systematic research relative to its importance (Wheeler *et al.*, 2004; Funk, 2006). Finally, international cooperation to address taxonomic impediments is hindered by complex permitting systems (Prathapan *et al.*, 2018) and limitations in the infrastructure available for integrating molecular techniques (Edwards *et al.*, 2016).

Future research on Philippine Rubiaceae should also address reproductive biology, including pollination ecology, breeding systems, and seed dispersal, as well as systematic plant resource utilization assessments for economically relevant genera such as *Morinda*, *Neonauclea*, *Uncaria*, and *Ophiorrhiza*. The establishment of germplasm conservation infrastructure, including seed banks and DNA repositories for priority endemic taxa, remains an urgent and unaddressed institutional priority (Oldfield, 2009).

CONCLUSION

The study of Philippine Rubiaceae has undergone a complete paradigm transition over the last two decades, now grounded in the integration of molecular phylogenetics, population genomics, and conservation biology. With 94 genera distributed across 35 tribes within two major subfamilies, the Philippines has emerged as one of the global centers of Rubiaceae diversity, harboring representatives of most of the family's genera. The description of 54 new endemic species and two new endemic genera (*Chewlunia* and *Kanapia*) demonstrates that substantial undescribed diversity persists, particularly in montane ecosystems and



edaphically specialized habitats, and that considerable taxonomic knowledge gaps remain.

Philippine Rubiaceae exhibit exceptionally high levels of island-specific endemism, with site survey rates ranging from 46% to 88% across geographically and ecologically distinct localities. *Psychotria* is by far the largest endemic genus, with 100 or more species, followed by *Hedyotis* (33 species) and *Ixora* and *Ophiorrhiza* (30 species each). This endemism is concentrated in montane forest lineages and edaphically specialized habitats — particularly ultramafic soils and limestone karsts — whose high specificity renders Philippine Rubiaceae acutely vulnerable to habitat disturbance. Biogeographic analyses have demonstrated that the Philippines functions as both an evolutionary "crossroads" and "cradle," with multiple independent colonization events from Asian and Wallacean source regions, followed by in situ adaptive radiation. Wallace's and Huxley's lines have operated as major biogeographic boundaries structuring the distribution patterns and lineage diversification of Philippine Rubiaceae, as demonstrated most explicitly in *Ixora* (Banag *et al.*, 2017).

Molecular phylogenetic analyses have fundamentally transformed our understanding of the evolutionary relationships within Philippine Rubiaceae, revealing widespread polyphyly across multiple genera and necessitating 128 nomenclatural changes to resolve long-standing taxonomic problems. Molecular dating places the concentrated diversification of Philippine Rubiaceae lineages in the Neogene period (2.3–2.6 mya), coinciding with the modern formation of the archipelago. Phylogeographic approaches, which assess spatial variation in genetic diversity and gene flow in relation to geological and climatic history, remain largely unexplored for most Philippine genera and represent a critical future research frontier.

Conservation assessments reveal that 64.81% of the 54 species described since 2004 face some level of conservation threat, with 23 species (42.59%) classified as Critically Endangered, primarily due to habitat loss and restricted distributions. Bioclimatic modeling predicts a disproportionate impact on montane species, whose limited thermal tolerance prevents adequate upward range shifts under projected climate change scenarios, underscoring the urgent need for climate corridors and assisted colonization strategies. High endemism rates (46–88%) across surveyed sites clearly illustrate the evolutionary uniqueness and irreplaceability of Philippine Rubiaceae, necessitating immediate and targeted conservation action.

Currently, taxonomic impediment remains the principal barrier to comprehensive biodiversity documentation. Progress in species-rich genera, such as *Psychotria*, *Hedyotis*, and *Ixora*, requires sustained long-term commitment to taxonomic training, institutional capacity building, and international cooperation. Future

research priorities should integrate phylogenomic approaches with classical systematics, particularly through target enrichment studies and population genomic analyses, alongside investigations into the reproductive biology, germplasm conservation, and plant resource utilization of priority endemic taxa. The documented endemic diversity of Philippine Rubiaceae represents an irreplaceable scientific and conservation resource, the continued loss of which to habitat destruction and climate change constitutes a global biodiversity imperative that requires urgent action.

ACKNOWLEDGMENTS

I am deeply grateful to Prof. Dr. Sigrid Liede-Schumann and PD Dr. Ulrich Meve (University of Bayreuth, Germany), and Prof. Dr. Sylvain G. Razafimandimbison (Swedish Museum of Natural History, Stockholm, Sweden) for their invaluable mentorship in Rubiaceae systematics, which profoundly shaped my research on Philippine Rubiaceae. I also sincerely thank the three anonymous reviewers whose constructive comments substantially improved this manuscript. Financial support from the DAAD, Alexander von Humboldt Foundation, Department of Science and Technology (DOST), and the UST Research Center for the Natural and Applied Sciences is gratefully acknowledged. The contributions of undergraduate and graduate students to the advancement of Philippine Rubiaceae research are also sincerely appreciated.

LITERATURE CITED

- Alejandro, G.J.D. 2007 The current status of the Philippine Rubiaceae. *Philipp. J. Syst. Biol.* **1**(1): 47–60.
- Alejandro, G.J.D. 2015 A new endemic species of Philippine *Hedyotis* L. (Rubiaceae) named after Pope Francis. *Antoninus J.* **1**: 74–78.
- Alejandro, G.J.D., Balete, I.K.C., Caagbay, J.F.C., Cruz, J.M.B., Narciso, C.J.C., Nazareno, D.E., Banag, C.I., Uy, M.M. 2013 Polyphyly of *Bikkia* Reinw. [Rubiaceae] based on multi-locus sequence analysis [ITS, rps16, trnL-F], with emphasis on the endemic *Bikkia philippinensis* Val. including its conservation status. *Acta Manil.* **59**: 49–55.
- Alejandro, G.J.D., Liede, S. 2003 The Philippine Rubiaceae genera: Updated synopsis in INTKEY databases of the DELTA system. *Blumea* **48**(2): 261–277.
- Alejandro, G.J.D., Meve, U. 2016 *Rubovietnamia coronula* sp. nov. (Rubiaceae: Gardenieae) from the Philippines. *Nord. J. Bot.* **34**(4): 385–389.
- Alejandro, G.J.D., Meve, U., Liede-Schumann, S. 2008 Two new species of *Mussaenda* (Rubiaceae) from Panay Island, Philippines. *Bot. J. Linn. Soc.* **158**(1): 87–92.
- Alejandro, G.J.D., Meve, U., Liede-Schumann, S. 2016 A taxonomic revision of Philippine *Mussaenda* (Rubiaceae, Mussaendeae). *Ann. Mo. Bot. Gard.* **101**(3): 457–524.
- Alejandro, G.J.D., Meve, U., Mouly, A., Thiv, M., Liede-Schumann, S. 2011 Molecular phylogeny and taxonomic



- revision of the Philippine endemic *Villaria* Rolfe (Rubiaceae). *Plant Syst. Evol.* **296**(1-2): 1–20.
- Alejandro, G.J.D., Meve, U., Uy, M.M., Mouly, A., Thiv, M., Liede-Schumann, S.** 2010 Molecular support of the classification of *Greeniopsis* Merr. in Aleisanthaceae (Rubiaceae), with a revision of the genus. *Taxon* **59**(5): 1547–1564.
- Alejandro, G.J.D., Razafimandimbison, S.G., Liede-Schumann, S.** 2005 Polyphyly of *Mussaenda* inferred from ITS and trnT-F data and its implication for generic limits in Mussaendeae (Rubiaceae). *Am. J. Bot.* **92**(3): 544–557.
- Alejandro, G.J.D., Santos, L.A.R., Hsu, H.W., Mejillano, M.S.S., Santor, P.J.R., Amoroso, V.B.** 2014 Molecular Phylogeny of the genus *Bikkia* (Rubiaceae) including a new endemic Philippine Inland forest species *Bikkia montoyae*. *Philipp. Sci. Lett.* **7**: 88–96.
- Alfeche, N.K.G., Alejandro, G.J.D., Meve, U., Liede-Schumann, S.** 2020 Two new endemic species of *Ophiorrhiza* L. (Rubiaceae: Ophiorrhizeae) from Davao Oriental, Philippines. *Nord. J. Bot.* **38**(3): e02581.
- Andreasen, K., Bremer, B.** 2000 Combined phylogenetic analysis in the Rubiaceae-Ixoroideae: morphology, nuclear and chloroplast DNA data. *Am. J. Bot.* **87**(11): 1731–1748.
- Andrews, K.R., Good, J.M., Miller, M.R., Luikart, G., Hohenlohe, P.A.** 2016 Harnessing the power of RADseq for ecological and evolutionary genomics. *Nat. Rev. Genet.* **17**(2): 81–92.
- Arriola, A.H., Alejandro, G.J.D.** 2013a A new species of *Psydrax* (Vanguerieae, Rubiaceae) from Luzon, Philippines. *Phytotaxa* **149**(1): 27–30.
- Arriola, A.H., Alejandro, G.J.D.** 2013b A new species of *Villaria* (Octotropideae, Rubiaceae) from Luzon, Philippines including its conservation status. *Phytotaxa* **111**(1): 57–60.
- Arriola, A.H., Alejandro, G.J.D.** 2015 A new species of *Discospermum* (Coffeae, Rubiaceae) from Luzon, Philippines including its conservation status. *Phytotaxa* **206**(1): 43–46.
- Arriola, A.H., Alejandro, G.J.D.** 2020 Three new combinations in *Villaria* (Octotropideae, Rubiaceae), an endemic genus from the Philippines. *Blumea* **65**(1): 86–89.
- Arriola, A.H., Camacho, P.D., Calaramo, M.J.A., Alejandro, G.J.D.** 2015 *Pyrostria triflora*, a new species of Vanguerieae (Rubiaceae) from Luzon, Philippines. *Bangladesh J. Plant Taxon.* **22**(1): 55–58.
- Arriola, A.H., Cobangkiat, A.B., Alejandro, G.J.D.** 2017 *Psydrax multiflorus* sp. nov. (Rubiaceae) from Palawan, Philippines. *Nord. J. Bot.* **35**(2): 182–184.
- Arriola, A.H., Dalit, H.B., Alejandro, G.J.D.** 2018a *Villaria marinduquensis* (Octotropideae, Rubiaceae) a new species from Marinduque, Philippines. *Ann. Bot. Fenn.* **55**(4-6): 325–328.
- Arriola, A.H., Lastimoso, C.D.D., Marcial, M.A.M., Amador, M.L.C., Deguinio, G.A.D., Dimaculangan, C.J.M., Vidallon, S.L. and Mahyuni, R.** 2026 *Dibridsonia parvifolia* (Rubiaceae), a new species from Mt Mariveles, Bataan, Luzon, Philippines. *Blumea* **70**: 195–199.
- Arriola, A.H., Paraguison, L.D., Alejandro, G.J.D.** 2016 *Kanapia* (Vanguerieae): a new endemic genus of Philippine Rubiaceae. *Plant Syst. Evol.* **302**(7): 1231–1240.
- Arriola, A.H., Valdez Jr, M.B., Nievera, E.B., Alejandro, G.J.D.** 2018b *Discospermum reyesii* (Coffeae, Rubiaceae), a new species from Cebu, Visayas, Philippines. *Ann. Bot. Fenn.* **55**(1-3): 155–158.
- Arshed, M.J.C., Alejandro, G.J.D.** 2016 *Lasianthus halconensis* (Rubiaceae), a new species from Mount Halcon, Mindoro, Philippines. *Phytotaxa* **288**(3): 296–300.
- Avise, J.C.** 2000 *Phylogeography: The history and formation of species.* Harvard University Press, Cambridge, USA.
- Axelius, B.** 1990 The genus *Xanthophytum* (Rubiaceae). *Taxonomy, phylogeny and biogeography.* *Blumea* **34**: 425–497. (In supplement)
- Baird, N.A., Etter, P.D., Atwood, T.S., Currey, M.C., Shiver, A.L., Lewis, Z.A., Johnson, E.A.** 2008 Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One* **3**(10): e3376.
- Banag, C.I.** 2014 Systematics of the Philippine endemic *Ixora* L. (Rubiaceae, Ixoreae). [Dissertation]. Universität Bayreuth, Bayreuth, Germany. (In supplement)
- Banag, C.I., Alejandro, G.J.D., Thrippleton, T., Reineking, B., Liede-Schumann, S.** 2015a Bioclimatic niches of selected endemic *Ixora* species on the Philippines: Predicting habitat suitability due to climate change. *Plant Ecol.* **216**(9): 1325–1340.
- Banag, C.I., Manalastas, N.M.B., Alejandro, G.J.D.** 2014 Synonymy of Philippine *Ixora* (Ixoreae, Rubiaceae) and *Ixora silagoensis* sp. nov. *Nord. J. Bot.* **32**(6): 761–764.
- Banag, C.I., Mouly, A., Alejandro, G.J.D., Bremer, B., Meve, U., Grimm, G.W., Liede-Schumann, S.** 2017 *Ixora* (Rubiaceae) on the Philippines – crossroad or cradle?. *BMC Evol. Biol.* **17**: 71.
- Banag, C.I., Tandang, D.N., Meve, U., Liede-Schumann, S.** 2015b Two new species of *Ixora* (Ixoroideae, Rubiaceae) endemic to the Philippines. *Phytotaxa* **202**(2): 155–160.
- Batuyong, M.A.R., Calaramo, M.A., Alejandro, G.J.D.** 2021a Inventory of Rubiaceae species in Mt. Pao Range, Ilocos Norte, Northwestern Luzon, Philippines. *Biodiversitas* **22**(8): 3604–3612.
- Batuyong, M.A.R., Calaramo, M.A., Alejandro, G.J.D.** 2021b Diversity of Rubiaceae in Ilocos Norte, Northwestern Luzon, Philippines: A preliminary checklist, their distribution, and conservation status. *Philipp. J. Sci.* **150**(S1): 487–502.
- Batuyong, M.A.R., Calaramo, M.A., Alejandro, G.J.D.** 2021c Rediscovery and amended description of *Psychotria palimlimensis* (Rubiaceae): a rare species found only in Ilocos Norte, Philippines. *Nord. J. Bot.* **39**(7): e03253.
- Bautista, M.A.C., Chua-Mangussad, V., Cervancia, J., Bustamante, R.A.A.** 2024 *Psychotria pendens* (Rubiaceae, Psychotriaceae), a new ultramafic species from Central Palawan, Philippines. *Phytotaxa* **649**(3): 252–260.
- Beaumont, M.A., Zhang, W., Balding, D.J.** 2002 Approximate Bayesian computation in population genetics. *Genetics* **162**(4): 2025–2035.
- Berger, A.** 2023 Solved at last: The Philippine endemic *Psychotria philippensis* is a synonym of *Scyphiphora hydrophylacea* (Rubiaceae, Scyphiphoreae). *PhytoKeys* **221**: 127–148.
- Biag, R.D., Alejandro, G.J.D.** 2020 Short communication: Rediscovery of *Psychotria* species, subspecies, and varieties collected in the 1990s and new records of *Antirhea benguetensis* (Elmer) Valetton and *Ixora longifolia* Smith (Rubiaceae) in Northern Sierra Madre Natural Park, Luzon, Philippines. *Biodiversitas* **21**(10): 4524–4534.



- Biag, R.D., Alejandro, G.J.D.** 2021 Diversity, distribution, and conservation status of Rubiaceae species in Peñablanca Protected Landscape and Seascape, Luzon, Philippines. *Biodiversitas* **22(9)**: 3627–3636.
- Biag, R.D., Alejandro, G.J.D.** 2022 Range extension and emended description of the threatened *Psychotria catanduanensis* (Rubiaceae) in the coastal area in Palanan, Isabela, Luzon, Philippines. *Nord. J. Bot.* **2022(4)**: e03422.
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Das, I.** 2007 Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* **22(3)**: 148–155.
- Blasco, F.A., Tandang, D.N., Alejandro, G.J.D.** 2024 *Argostemma mirae* (Rubiaceae) a new species from Tago, Surigao del Sur, Mindanao Island, Philippines. *Phytotaxa* **640(1)**: 65–70.
- Bremer, B., Andreasen, K., Olsson, D.** 1995 Subfamilial and tribal relationships in the Rubiaceae based on rbcL sequence data. *Ann. Mo. Bot. Gard.* **82(3)**: 383–397.
- Bremer, B., Eriksson, T.** 2009 Time tree of Rubiaceae: phylogeny and dating the family, subfamilies, and tribes. *Int. J. Plant Sci.* **170(6)**: 766–793.
- Bremer, B., Manen, J.F.** 2000 Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). *Plant Syst. Evol.* **225(1-4)**: 43–72.
- Bremer, B., Thulin, M.** 1998 Collapse of Isertieae, re-establishment of Mussaendeae, and a new genus of Sabiceae (Rubiaceae); phylogenetic relationships based on rbcL data. *Plant Syst. Evol.* **211(1-2)**: 71–92.
- Brown, R.M., Diesmos, A.C.** 2009 Philippines, biology. In: Gillespie, R.G., Clague, D.A. (eds.), *Encyclopedia of islands*. 723–732pp. University of California Press, Berkeley, USA.
- Bryant, D., Bouckaert, R., Felsenstein, J., Rosenberg, N.A., RoyChoudhury, A.** 2012 Inferring species trees directly from biallelic genetic markers: bypassing gene trees in a full coalescent analysis. *Mol. Biol. Evol.* **29(8)**: 1917–1932.
- Bustamante, R.A.A., Pelser, P.B.** 2022 A new Philippine species of *Ridsdalea* (Rubiaceae, Ixoroideae) from karst vegetation in Palawan. *Blumea* **67(1)**: 15–19.
- Cabral, E.L., Bacigalupo, N.M.** 2004 Novelties in *Borreria* (Rubiaceae-Spermacoceae) from Brazil. *Kew Bull.* **59(2)**: 277–284.
- Carranza-Rojas, J., Goeau, H., Bonnet, P., Mata-Montero, E., Joly, A.** 2017 Going deeper in the automated identification of Herbarium specimens. *BMC Evol. Biol.* **17(1)**: 181.
- Chavez, J.G., Alejandro, G.J.D., Tandang, D.N., Meve, U.** 2020a Two new species of *Timonius* (Guettardeae: Rubiaceae) from Samar Island, the Philippines. *Bot. Lett.* **167(3)**: 365–372.
- Chavez, J.G., Banag-Moran, C.I., Meve, U.** 2020b *Timonius eremiticus* (Rubiaceae), a new species from the Philippines. *Blumea* **65(2)**: 104–106.
- Chavez, J.G., Meve, U., Liede-Schumann, S.** 2020c Taxonomic novelties and changes in Philippine *Timonius* (Rubiaceae, Guettardeae). *Nord. J. Bot.* **38(7)**: e02730.
- Chavez, J.G., Meve, U., Nürk, N.M., Liede-Schumann, S.** 2021 Disentangling *Antirhea* (Rubiaceae): Resurrection of *Guettardella* and description of the new genus *Achilleanthus*. *Bot. J. Linn. Soc.* **197(1)**: 85–103.
- Chavez, J.G., Venturina, R.E.L., Alejandro, G.J.D.** 2015 *Gynochthodes leonardii*: a novel species of Morindeae-Rubiaceae from Palawan, Philippines. *Phytotaxa* **222(1)**: 67–71.
- Chen, J., Hoo, P.K., Wong, K.M.** 2023 *Chewlunia* (Guettardeae: Rubiaceae), a new genus from Borneo and the Philippines. *Sandakania* **24**: 31–38.
- Ciborowski, K., Szczecińska, M., Maździarz, M., Sawicki, J., Paukszto, Ł.** 2024 Decoding evolution of Rubioideae: Plastomes reveal sweet secrets of codon usage, diagnostides, and superbarcoding. *Genes* **15(5)**: 562.
- Costello, M.J., May, R.M., Stork, N.E.** 2013 Can we name Earth's species before they go extinct? *Science* **339(6143)**: 413–416.
- Csilléry, K., Blum, M.G.B., Gaggiotti, O.E., François, O.** 2010 Approximate Bayesian Computation (ABC) in practice. *Trends Ecol. Evol.* **25(7)**: 410–418.
- Davis, A.P., Bridson, D.M.** 2004 A taxonomic revision of the genus *Amaracarpus* (Rubiaceae, Psychotrieae). *Blumea* **49(1)**: 25–68.
- Davis, A.P., Govaerts, R., Bridson, D.M., Ruhsam, M., Moat, J., Brummitt, N.A.** 2009 A global assessment of distribution, diversity, endemism, and taxonomic effort in the Rubiaceae. *Ann. Mo. Bot. Gard.* **96(1)**: 68–78.
- De Queiroz, K.** 2007 Species concepts and species delimitation. *Syst. Biol.* **56(6)**: 879–886.
- Dela Bajan, U.P., Ordas, J.A.D., Tandang, D.N., Alejandro, G.J.D.** 2017 *Mycetia dagohoyana*: a new species of Argostemmatae (Rubiaceae) from Agusan del Norte, Philippines. *Phytotaxa* **292(1)**: 91–96.
- Drummond, A.J., Ho, S.Y., Phillips, M.J., Rambaut, A.** 2006 Relaxed phylogenetics and dating with confidence. *PLoS Biol.* **4(5)**: e88.
- Edwards, J.L.** 2004 Research and societal benefits of the Global Biodiversity Information Facility. *BioScience* **54(6)**: 486–487.
- Edwards, S.V., Potter, S., Schmitt, C.J., Bragg, J.G., Moritz, C.** 2016 Reticulation, divergence, and the phylogeography–phylogenetics continuum. *Proc. Natl. Acad. Sci. USA* **113(29)**: 8025–8032.
- Ehrendorfer, F., Barfuss, M.H.** 2014 Paraphyly and polyphyly in the worldwide tribe Rubieae (Rubiaceae): challenges for generic delimitation. *Ann. Mo. Bot. Gard.* **100(1-2)**: 79–88.
- Elith, J., Leathwick, J.R.** 2009 Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40(1)**: 677–697.
- Frankham, R., Ballou, J.D., Briscoe, D.A.** 2014 *Introduction to conservation genetics*. Cambridge University Press, Cambridge, UK.
- Franklin, J.** 2009 *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge, UK.
- Funk, V.A.** 2006 Floras: a model for biodiversity studies or a thing of the past? *Taxon* **55(3)**: 581–588.
- Govaerts, R.** 2003 World Checklist of Selected Plant Families Database in ACCESS: 1-216203. The Board of Trustees of the Royal Botanic Gardens, Kew, UK. (In supplement)
- Hall, R.** 2002 Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *J. Asian Earth Sci.* **20(4)**: 353–431.



- Hannah, L., Midgley, G.F., Anelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P. 2007 Protected area needs in a changing climate. *Front. Ecol. Environ.* **5**(3): 131–138.
- Ho, S.Y.W., Duchêne, S. 2014 Molecular-clock methods for estimating evolutionary rates and timescales. *Mol. Ecol.* **23**(24): 5947–5965.
- Hughes, A.C. 2017 Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* **8**(1): e01624.
- Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P., Zhu, C. 2021 Sampling biases shape our view of the natural world. *Ecography* **44**(9): 1259–1269.
- Hughes, C., Eastwood, R. 2006 Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci. USA* **103**(27): 10334–10339.
- Hughes, C.E., Pennington, R.T., Antonelli, A. 2013 Neotropical plant evolution: assembling the big picture. *Bot. J. Linn. Soc.* **171**(1): 1–18.
- Huxley, T.H. 1868 On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proc. Zool. Soc. Lond.* **1868**: 294–319.
- Huynh, T.T.T., Quang, M.T., Nguyen, H.D. 2024 Complete chloroplast genome sequence of the medicinal plant *Oxyceros horridus* (Rubiaceae) and phylogenetic analysis. *Mitochondrial DNA B* **9**(12): 1658–1663.
- Jebb, M.H.P., Huxley, C.R. 2019 The tuberous epiphytes of the Rubiaceae 7: A revision of the genus *Hydnophytum*. *Blumea* **64**(1): 23–91.
- Kim, K.C., Byrnes, L.B. 2006 Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. *Ecol. Res.* **21**(6): 794–810.
- Koopowitz, H., Thornhill, A.D., Andersen, M. 1998 A general stochastic model for the prediction of biodiversity losses based on habitat conversion. *Conserv. Biol.* **8**(2): 425–438.
- Lantz, H., Bremer, B. 2004 Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). *Bot. J. Linn. Soc.* **146**(3): 257–283.
- Liu, J., Diamond, J., Raven, P.H. 2013 China's environment in a globalizing world. *Nature* **435**(7046): 1179–1186.
- Liu, L., Yu, L., Pearl, D.K., Edwards, S.V. 2009 Estimating species phylogenies using coalescence times among sequences. *Syst. Biol.* **58**(5): 468–477.
- Löfstrand, S.D., Kruger, Å., Razafimandimbison, S.G., Bremer, B. 2014 Phylogeny and generic delimitations in the sister tribes Hymenodictyeae and Naucleaeae (Rubiaceae). *Syst. Bot.* **39**(1): 304–315. (In supplement)
- Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K.L., Shih, H.T., Carvalho, G.R., von Rintelen, T. 2011 Biogeography of the Indo-Australian Archipelago. *Annu. Rev. Ecol. Evol. Syst.* **42**(1): 205–226.
- Mahyuni, R., Chikmawati, T., Ariyanti, N., Wong, K.M. 2018 The *Psydrax dicoccos* complex (Rubiaceae) in Malesia, with three new species. *Floribunda* **5**: 322–331. (In supplement)
- Mendoza, H., Ramirez, P.B.R., Jimenez, L.C. 2004 Rubiaceae de Colombia: guía ilustrada de generos. Instituto de Investigacion de Recursos Biologicos Alexander von Humboldt, Bogotá, Colombia. (In supplement)
- Merrill, E.D. 1923 An enumeration of Philippine flowering plants. Vol. 3. Bureau of Printing, Manila, Philippines.
- Meseguer, A.S., Michel, A., Fabre, P.H., Pérez-Escobar, O.A., Chomicki, G., Riina, R., Antonelli, A., Antoine, P.O., Delsuc, F., Condamine, F.L. 2022 Diversification dynamics in the Neotropics through time, clades and biogeographic regions. *eLife* **11**: e74503.
- Mittermeier, R.A., Myers, N., Mittermeier, C.G. 1999 Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, Mexico City, Mexico.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**(6772): 853–858.
- Naive, M.A.K., Alejandro, G.J.D. 2024 *Ophiorrhiza ravifolia* (Rubiaceae), a new endemic species discovered in Naga-Kabasalan Protected Landscape (NKPL), Zamboanga Peninsula, southwestern Philippines. *Nord. J. Bot.* **2024**(3): e04311.
- Nandikar, M., Kishor, K. 2019 A new species and a synopsis of the *Hedyotis-Oldenlandia* group (Rubiaceae: Spermaceae) in Andaman & Nicobar Islands, India. *Blumea* **64**(3): 225–230. (In supplement)
- Neupane, S., Dessein, S., Wikstrom, N., Lewis, P.O., Long, C., Bremer, B., Motley, T.J. 2015 The *Hedyotis-Oldenlandia* complex (Rubiaceae: Spermaceae) in Asia and the Pacific: Phylogeny revisited with new generic delimitations. *Taxon* **64**(2): 299–322.
- Obico, J.J.A., Alejandro, G.J.D. 2013 A new species of *Antherostele* (Urophyllaeae, Rubioideae, Rubiaceae) from Mt. Sohoton, Samar, Philippines. *Phytotaxa* **104**(1): 53–57.
- Oldfield, S. 2009 Botanic gardens and the conservation of tree species. *Trends Plant Sci.* **14**(11): 581–588.
- Ong, P.S., Afuang, L.E., Rosell-Ambal, R.G. 2002 Philippine biodiversity conservation priorities: a second iteration of the National Biodiversity Strategy and Action Plan. Department of Environment and Natural Resources-Protected Areas and Wildlife Bureau, Conservation International Philippines, Biodiversity Conservation Program-University of the Philippines Center for Integrative and Development Studies, and Foundation for the Philippine Environment, Quezon City, Philippines.
- Ordas, J.A.D., Banag, C.I., Alejandro, G.J.D. 2017 *Neonauclea viridiflora* (Rubiaceae), a new myrmecophytic species of Naucleaeae from Eastern Samar, with notes on myrmecophytic species in the Philippines. *Syst. Bot.* **42**(2): 364–370.
- Ordas, J.A.D., Chen, Y.T., Odulio, E.J.A., Cortez, G.N.G., Zamudio, S.G.S., Alfeche, N.K.G. 2025 Two new species of *Psychotria* L. (Psychotrieae-Rubiaceae) from Dinagat Island, Philippines. *Webbia* **80**(1): 67–76.
- Ordas, J.A.D., Pinarok, N.A.A., Romero, R.B., Alejandro, G.J.D., Banag-Moran, C.I. 2019 A checklist of Rubiaceae species from Eastern Samar, Visayas, Philippines. *Check List* **15**(2): 295–312.
- Ordas, J.A.D., Taradji, A.J., Valdez, M.B., Banag, C.I., Alejandro, G.J.D. 2016 *Neonauclea connicalycina*: a new myrmecophytic species of Naucleaeae (Rubiaceae) from Cebu, Philippines. *Phytotaxa* **273**(2): 127–132.
- Pajarillaga, J.D., Ordas, J.A.D., Odulio, E.J.A., Venturina, P.J.S., Moran, C.B. 2025 *Psychotria caraballoensis* (Rubiaceae), a new species from northern Luzon, Philippines. *Nordic J. Bot.* **2026**(2): e05026.



- Pelser, P.B., Barcelona, J.F., Nickrent, D.L.** 2011 onwards Co's Digital Flora of the Philippines. [www.philippineplants.org]
- Persson, C.** 2000 Phylogeny of the Gardenieae (Rubiaceae) based on chloroplast DNA sequences for the rps16 intron and trnL(UAA)–F(GAA) intergenic spacer. *Nord. J. Bot.* **20(3)**: 257–269.
- Posa, M.R.C., Diesmos, A.C., Sodhi, N.S., Brooks, T.M.** 2008 Hope for threatened tropical biodiversity: lessons from the Philippines. *BioScience* **58(3)**: 231–240.
- Prathapan, K.D., Pethiyagoda, R., Bawa, K.S., Raven, P.H., Rajan, P.D.** 2018 When the cure kills—CBD limits biodiversity research. *Science* **360(6396)**: 1405–1406.
- Proctor, J.** 2003 Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far East. *Perspect. Plant Ecol. Evol. Syst.* **6(1-2)**: 105–124.
- Puttock, C.F.** 1999 Revision of *Atractocarpus* (Rubiaceae: Gardenieae) in Australia and new combinations for some extra-Australian taxa. *Aust. Syst. Bot.* **12(2)**: 271–302. (In supplement)
- Razafimandimbison, S.G., Bremer, B.** 2011 Nomenclatural changes and taxonomic notes in the tribe Morindeae (Rubiaceae). *Adansonia* **33(2)**: 283–309.
- Razafimandimbison, S.G., McDowell, T.D., Halford, D.A., Bremer, B.** 2010 Origin of the pantropical and nutraceutical *Morinda citrifolia* L. (Rubiaceae): Comments on its distribution range and circumscription. *J. Biogeogr.* **37(3)**: 520–529. (In supplement)
- Razafimandimbison, S.G., Rydin, C.** 2024 Phylogeny and classification of the coffee family (Rubiaceae, Gentianales): Overview and outlook. *Taxon* **73(6)**: 673–717.
- Razafimandimbison, S.G., Taylor, C.M., Wikström, N., Pailler, T., Khodabandeh, A., Bremer, B.** 2014 Phylogeny and generic limits in the sister tribes Psychotriaceae and Palicoureae (Rubiaceae): Evolution of schizocarps in *Psychotria* and origins of bacterial leaf nodules of the Malagasy species. *Am. J. Bot.* **101(7)**: 1102–1126.
- Ridsdale, C.E.** 1982 A revision of *Badusa* (Rubiaceae, Condamineae, Portlandiinae). *Blumea* **28**: 145–150. (In supplement)
- Ridsdale, C.E.** 2008 Thorny problems in the Rubiaceae: Benkara, Fagerlindia and Oxyceros. *Reinwardtia* **12**: 289–300. (In supplement)
- Robbrecht, E.** 1988 Tropical woody Rubiaceae. *Opera Bot. Belg.* **1**: 1–271.
- Rova, J.H., Delprete, P.G., Andersson, L., Albert, V.A.** 2002 A trnL-F cpDNA sequence study of the Condamineae–Rondeletieae–Sipaneae complex with implications on the phylogeny of the Rubiaceae. *Am. J. Bot.* **89(1)**: 145–159.
- Salamanes, J.D.P., Chavez, J.G., Arriola, A.H., Alejandro, G.J.D.** 2015 A new species of *Antirhea* (Guettardeae, Rubiaceae) from Surigao del Norte, Philippines. *Acta Bot. Gallica* **162(3)**: 405–408.
- Santor, P.J.R., Santiago, D.D.B., Mataga, C.J.V., Gabriel, E.S., Alejandro, G.J.D.** 2021 *Hedyotis hamiguitanensis* (Rubiaceae: Spermacoceae), a new species from Mt. Hamiguitan, Davao Oriental, Philippines and its systematic position in *Hedyotis*. *Webbia* **76(2)**: 195–202.
- Shaffer, H.B., Thomson, R.C.** 2007 Delimiting species in recent radiations. *Syst. Biol.* **56(6)**: 896–906.
- Siler, C.D., Oaks, J.R., Esselstyn, J.A., Diesmos, A.C., Brown, R.M.** 2010 Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: Cyrtodactylus) contradict a prevailing model of Pleistocene diversification. *Mol. Phylogenet. Evol.* **55(2)**: 699–710.
- Smedmark, J.E.E., Bremer, B.** 2011 Molecular systematics and incongruent gene trees of Urophylleae (Rubiaceae). *Taxon* **60(5)**: 1397–1406. (In supplement)
- Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.** 2004 Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* **19(12)**: 654–660.
- Soejarto, D.D., Delprete, P., Regalado, J.C., Madulid, D.A.** 1996 The true provenance and identity of *Badusa philippica* (Rubiaceae). *Taxon* **45(3)**: 487–492. (In supplement)
- Sohmer, S.H., Davis, A.P.** 2007 The genus *Psychotria* (Rubiaceae) in the Philippine Archipelago. Botanical Research Institute of Texas Press, Fort Worth, USA.
- Soza, V.L., Olmstead, R.G.** 2010 Molecular systematics of tribe Rubiaceae (Rubiaceae): Evolution of major clades, development of leaf-like whorls, and biogeography. *Taxon* **59(3)**: 755–771.
- Suba, M.D.L., Arcangel, N.R.P., Jalipa, J.T., Jurilla, J.G.L., Villaseñor, J.M.J., Arriola, A.H., Alejandro, G.J.D.** 2020 *Pyrostria arayatensis* (Vanguerieae, Rubiaceae), a new species from Mt. Arayat National Park, Pampanga, Philippines. *Ann. Bot. Fenn.* **57(4-6)**: 309–312.
- Tandang, D.N., Ordas, J.A.D., Tadiosa, E.R., Banag-Moran, C.I., Alejandro, G.J.D.** 2019 *Mycetia suedixieana* (Rubiaceae), a new species of Argostemmataeae endemic to the Philippines. *Syst. Bot.* **44(2)**: 371–377.
- Taylor, C.M., Razafimandimbison, S.G., Barrabé, L., Jardim, J.G., Barbosa, M.V.** 2017 *Eumachia* expanded, a pantropical genus distinct from *Psychotria* (Rubiaceae, Palicoureae). *Candollea* **72(2)**: 289–310. (In supplement)
- Terrell, E.E., Robinson, H.** 2003 Survey of Asian species of *Hedyotis*, *Exallage*, and *Oldenlandia* (Rubiaceae) and related genera with capsular fruits. *SIDA* **20**: 1097–1175.
- Thiers, B.M., Tulig, M.C., Watson, K.A.** 2016 Digitization of the New York Botanical Garden Herbarium. *Brittonia* **68(3)**: 324–333.
- Thomsen, P.F., Willerslev, E.** 2015 Environmental DNA in ecology: achievements and prospects. *Biol. Rev.* **90(2)**: 751–777.
- Thureborn, O., Wikström, N., Razafimandimbison, S.G., Rydin, C.** 2024 Plastid phylogenomics and cytonuclear discordance in Rubioideae, Rubiaceae. *PLoS One* **19(5)**: e0302365.
- Turner, I.M.** 2019 A nomenclatural synopsis of *Chassalia* (Rubiaceae) in Asia. *Feddes Repert.* **130(4)**: 215–264. (In supplement)
- Uy, M.M., Alejandro, G.J.D.** 2012 Conservation status and nrITS-supported classification of the Philippine endemic genus *Greeniopsis* Merr. (Rubiaceae). *Asia Life Sci.* **21**: 441–454.
- Venturina, R.E.L., Suarez, E.E.L., Alejandro, G.J.D.** 2017 *Morinda carnososa* (Morindeae-Rubiaceae), a new species from Palawan Philippines. *Phytotaxa* **308(1)**: 141–143.
- Wallace, A.R.** 1869 The Malay Archipelago. Macmillan, London, UK.
- Wang, R.J.** 2019 Taxonomic notes on the genus *Hedyotis* sensu lato (Rubiaceae) in China. *Phytotaxa* **414(3)**: 121–128. (In supplement)
- Wang, R.J., Deng, S.J., Liao, Q.** 2014 Nomenclature clarification of the traditional Chinese medicine



- baihuasheshhecao and its adulterants based on molecular and morphological evidence. *J. Trop. Subtrop. Bot.* **22**: 431–442.
- Wendel, J.F., Doyle, J.J.** 1998 Phylogenetic incongruence: window into genome history and molecular evolution. In: Soltis, D.E., Soltis, P.S., Doyle, J.J. (eds.), *Molecular Systematics of Plants II*. Springer, Boston, USA.
- Wheeler, Q.D., Knapp, S., Stevenson, D.W., Stevenson, J., Blum, S.D., Boom, B.M., Borisy, G.G., Buizer, J.L., de Carvalho, M.R., Cibrian, A., Donoghue, M.J., Doyle, V., Gerson, E.M., Graham, C.H., Graves, P., Graves, S.J., Guralnick, R.P., Hamilton, A.L., Hanken, J., Law, W., Lipscomb, D.L., Lovejoy, T.E., Miller, H., Miller, J.S., Naeem, S., Novacek, M.J., Page, L.M., Platnick, N.I., Porter-Morgan, H., Raven, P.H., Solis, M.A., Valdecasas, A.G., van der Leeuw, S., Vasco, A., Vermeulen, N., Vogel, J., Walls, R.L.** 2012 Mapping the biosphere: Exploring species to understand the origin, organization and sustainability of biodiversity. *Syst. Biodivers.* **10(1)**: 1–20.
- Wheeler, Q.D., Raven, P.H., Wilson, E.O.** 2004 Taxonomy: Impediment or Expedient? *Science* **303(5656)**: 285.
- Wikström, N., Kainulainen, K., Razafimandimbison, S.G., Smedmark, J.E.E., Bremer, B.** 2015 A revised time tree of the asterids: establishing a temporal framework for evolutionary studies of the coffee family (Rubiaceae). *PLoS One* **10(5)**: e0126690.
- Wikström, N., Neupane, S., Kårehed, J., Motley, T.J., Bremer, B.** 2013 Phylogeny of *Hedyotis* L. (Rubiaceae: Spermaceae): Redefining a complex Asian-Pacific assemblage. *Taxon* **62(2)**: 357–374.
- Wikström, N., Razafimandimbison, S.G., Rydin, C., Bremer, B.** 2020 Anthospermeae – a pantropical tribe in the coffee family with an ancient Old World origin. *Mol. Phylogenet. Evol.* **150**: 106879.
- Wilf, P., Zhang, S., Chikkerur, S., Little, S.A., Wing, S.L., Serre, T.** 2016 Computer vision cracks the leaf code. *Proc. Natl. Acad. Sci. USA* **113(12)**: 3305–3310.
- Wong, K.M.** 2011 A revision of Philippine *Gardenia* (Rubiaceae). *Gard. Bull. Singapore* **62**: 233–265.
- Wong, K.M., Low, Y.W.** 2011 A revision of Philippine *Gardenia* (Rubiaceae). *Edinburgh J. Bot.* **68(1)**: 11–31.
- Wong, K.M., Mahyuni, R., Ng, X.Y., Neo, L.** 2018 Flora of Singapore precursors, 8. Systematics of the new Southeast Asian genera *Canthiumera* and *Dibridsonia* (Rubiaceae: Vanguerieae), with notes on plant architecture and reproductive ecology. *Reinwardtia* **17(2)**: 99–119.
- Wong, K.M., Pereira, J.T.** 2016 A taxonomic treatment of the Asiatic allies of *Rothmannia* (Rubiaceae: Gardenieae), including the new genera *Ridsdalea* and *Singaporandia*. *Sandakania* **21**: 21–64.
- Wong, K.M., Turner, I.M., Wang, R.J., Harwood, R., Seah, W.W., Ng, X.Y., Lim, R.C.J., Lua, H.K., Mahyuni, R.** 2019 Flora of Singapore (Gentianales: Rubiaceae). *Flora of Singapore Vol 13*: 1–358. National Parks Board, Singapore.
- Zhu, H.** 2015 *Paralasianthus* (Rubiaceae), a new genus from Southeast Asia. *Phytotaxa* **202(4)**: 273–278.
- Zhu, H., Roos, M.C., Ridsdale, C.E.** 2012 A taxonomic revision of the Malesian species of *Lasianthus* (Rubiaceae). *Blumea* **57(1)**: 1–102.

Supplementary materials are available from the journal website