

REVISITING *ASTROCALYX* MERR. (ASTRONIEAE: MELASTOMATACEAE): NEW MORPHOLOGICAL OBSERVATIONS ON THE PHILIPPINE ENDEMIC, ENIGMATIC, ENDANGERED AND MONOTYPIC GENUS

Jeffrey P. Mancera^{1*}, Darin S. Penneys² and Fulgent P. Coritico³

ABSTRACT

The monotypic *Astrocalyx* Merr. (Astronieae: Melastomataceae) was collected in 2015 from the Mount Kitanglad Range Natural Park (Mindanao Island, the Philippines) during a joint expedition conducted by the Central Mindanao University (CMUH) and the California Academy of Sciences (CAS). Since the original publication of the genus, no other detailed account of its enigmatic morphology has been published. Examination of herbarium vouchers revealed discrete variations in morphology, which may be indicative of reproductive isolation or presence of emerging selection pressures among populations of the species across the archipelago. This documentation aims to rekindle interest and initiate approaches toward conservation of this poorly known endemic taxon, already listed as endangered in the Philippine Islands.

Keywords: *Astrocalyx calycina*, conservation, endangered species, Philippine flora, plant diversity

INTRODUCTION

The Astronieae Triana is one of the early-diverging tribes in the Melastomataceae Juss. (VAN VLIET, 1981; MENTINK & BAAS, 1992; RENNER, 1993; CLAUSING & RENNER, 2001; RENNER *ET AL.*, 2001; PENNEYS, 2013). Members of this clade, as traditionally circumscribed (MAXWELL & VELDKAMP, 1990a, b), include *Astrocalyx* Merr., *Astronia* Blume, *Astronidium* A. Gray, and *Beccarianthus* Cogn. The tribe is distinguished from the rest of the core Melastomataceae by a suite of mostly plesiomorphic morphological characters, e.g. woody habit, isomorphic stamens, longitudinally dehiscent anthers, basal-axile placentation, dry capsular fruits, and linear or cuneate seeds (RENNER, 1993; CLAUSING & RENNER, 2001; PENNEYS, 2013).

Astrocalyx comprises a single species, *A. calycina* (S. Vidal) Merr., and is endemic to the primary rainforests of the Philippine Islands. Both genus name and specific epithet allude to its elongated, star-like, calyx lobes (VIDAL, 1886; MERRILL, 1910), a unique feature within the tribe. More noteworthy is the pleiostemonous androecium (with 64 to 96 stamens), a character found sporadically throughout the family (MERRILL, 1910; KADEREIT, 2005; PENNEYS, 2013). A unique characteristic of this taxon is the presence of slender anthers with reduced pollen

¹ Department of Botany, California Academy of Sciences, San Francisco, CA 94118, USA.

² Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC 28403, USA.

³ Center for Biodiversity Research and Extension in Mindanao (CEBREM), Central Mindanao University, Musuan, Bukidnon 8710, Philippines.

*Corresponding author. E-mail: jmancera@calacademy.org

Received 6 October 2016; accepted 15 December 2016.

sacs that have apical, longitudinal slits (WILSON, 1950). This combination of features warrants recognition of *Astrocalyx* as a distinct genus, although its phylogenetic position in the Astroniaceae has yet to be determined (PENNEYS, 2013).

Collections of *Astrocalyx* can be found in the Philippine National Herbarium (PNH), as well as international herbaria with significant holdings of Malesian flora. Sampling of herbarium vouchers indicates that collections have declined significantly since the early 20th Century, which in turn may indicate population declines. Through the 1910s, on average, the taxon was collected annually. Afterwards, approximately two collections per decade were made through the 1960s, with only one additional known collection made in 1983 until the present day. Three decades passed before a small population was encountered in 2015. During a joint botanical expedition conducted by the Central Mindanao University (CMUH) and California Academy of Sciences (CAS) at Mount Kitanglad Range Natural Park, province of Bukidnon, a new specimen of *A. calycina* was collected (Fig. 1). In recognition of its rarity at present, *A. calycina* is included in the list of endangered plant species in the Philippines (FERNANDO ET AL., 2008).

Since the protologs of VIDAL (1886) and MERRILL (1910), no detailed description of the genus has been published. In this paper, we describe morphological observations derived from the examination of herbarium vouchers collected throughout the Philippines since the late 19th Century. The many specimens studied show subtle differences in several aspects of the vegetative and reproductive organs, which may represent outcomes of reproductive isolation at the population level, random mutation, or emerging selection pressures from changing environments. We publish these detailed notes of observation to initiate renewed interest in and contribute to future conservation strategies for this poorly known Philippine endemic and endangered species.

METHODS

Plant materials observed consisted mostly of herbarium vouchers, including an isotype and a paratype. Loans were requested from herbaria with significant holdings of duplicates, most of which were determined by specialists in the group such as Elmer, Merrill, Bakhuizen f., and the latest monographers of the tribe, Maxwell and Veldkamp. Photos of specimens were acquired from other herbaria, while images of types were obtained from virtual databases such as the Kew Royal Botanic Gardens Herbarium Catalogue, Harvard University Herbaria and Libraries Index of Botanical Specimens, and JSTOR Global Plants. A total of 53 vouchers from A, CAS, CMUH, GH, K, L, MA, NY, P, PNH, SING, UC, US, and W were studied.

Additional fresh material was obtained, with permits, from the lowland evergreen rainforest of Mount Kitanglad Range Natural Park, Sitio Kalanganan, Barangay San Vicente, municipality of Baungon, province of Bukidnon in July 2015. Reproductive branches of *Astrocalyx calycina* were collected and preserved as herbarium vouchers following HODGE (1947), leaf tissue for DNA extraction was preserved using silica gel (CHASE & HILLS, 1991), and flower buds were preserved in alcohol for dissection (MILLER & NYBERG, 2011). Notes on habitat and ecology were recorded in the field. Specimens were deposited in CAS, CMUH, and PNH (with 18 duplicates to be distributed), and identification was confirmed using an isotype from L and a paratype from NY.

Gross morphology of branchlets, leaves, and flowers from each collection were observed under a Leica MZ12.5 stereomicroscope (Leica Microsystems, Inc., Deerfield, Illinois, USA) and were photographed and measured using AxioCam ICc5 5-megapixel microscope camera (Carl Zeiss Microscopy GmbH, Oberkochen, Germany) utilizing Zeiss ZEN2012 Lite imaging software, courtesy of the John T. Howell Botanical Laboratory at the California Academy of Sciences. Flowers were rehydrated and dissected in order to observe and measure structures, especially those of the androecium and gynoecium. Finally, trichome morphology and seed surface ultrastructure were observed under the scanning electron microscope (SEM). Pedicels and seeds were selected and attached to stubs using electro-conductive tape, sputter-coated with a mixture of gold-palladium, and examined and imaged using Zeiss/LEO 1450VP SEM (LEO, Cambridge, UK; Carl Zeiss SMT, Peabody, MA, USA) courtesy of CAS. The digital images were further processed in Photoshop CC v. 2015.1.2 (Adobe Systems Inc., San Jose, CA, USA) for optimal image quality. Seed morphology and testa ultrastructure were described following the morphological characterization developed by OCAMPO & ALMEDA (2013).

Finally, analysis of the data in literature and herbarium voucher labels was performed to estimate geographic coordinates to best visualize the distribution of *Astrocalyx*. The distribution map was generated using ArcGIS 10.3.1 (Esri Inc., Redlands, CA, USA) utilizing WGS 1984 geographic coordinate system.

RESULTS AND DISCUSSION

Collection and Documentation

Astrocalyx calycina was found along a trail on a ridge five meters away from a river in a lowland evergreen rainforest at 898 masl, 8.19445°N, 124.7547°E, on the north western slope of Mt. Kitanglad Range. The individual tree collected stood 9 m tall with a stout bole measuring 65 cm DBH, an outlier from the mean ca. 20–30 cm DBH recorded from herbarium vouchers (Fig. 2). The bole was densely covered with bryophytes and hemi-epiphytes. The crown was dense with conspicuous sympodial branching and branchlets and inflorescences ascending. Only five other average-sized individuals, ca. 7–9 m × 20–30 cm, were seen along the trail at 910 masl, 8.19465°N, 124.75455°E.

The associated vegetation consisted primarily of large trees, 20–30 m tall, including *Lithocarpus* spp., *Castanopsis motleyana* King (Fagaceae), *Gymnostoma rumphianum* (Jungb. ex Vriese) L. A. S. Johnson (Casuarinaceae), and *Ficus* spp. (Moraceae). The shrub layer consisted of *Melastoma malabathricum* L., *Medinilla* spp. (Melastomataceae), and the common tree fern, *Sphaeropteris glauca* (Blume) R. M. Tryon (Cyatheaceae), while the ground cover was dominated by more fern species including *Nephrolepis falcata* (Cav.) C. Chr. and *N. biserrata* (Sw.) Schott. (Lomariopsidaceae), *Angiopteris palmiformis* (Cav.) C. Chr. (Marattiaceae), *Asplenium nidus* L. (Aspleniaceae), and several species of Poaceae. It is also noteworthy that the locality was inhabited by the largest flower in the Philippines, *Rafflesia schadenbergiana* Goepp.

Taxonomic History

VIDAL (1886) described one of his collections (mistyped in the protologue as *Vidal 781* – he was actually referring to 780) from Mount Bulusan, province of Sorsogon (formerly

Albay), Bicol Peninsula, Luzon Island. This specimen with five unusually long calyx teeth measuring up to 5 mm was given the name *Astronia calycina*, Vidal mistaking it for a species of the most common and widespread genus of Astronieae in the Philippines. His collection had only floral buds, thus no reproductive parts were described apart from the calyx tube and calyx lobes (Vidal 780, L!).

MERRILL (1910), unaware of Vidal's type, described the peculiar collection made by Aguilar from the province of Camarines Norte in Luzon Island. Alluding to the long calyx lobes and numerous stamens, a combination that is rarely seen within the family, he established a new genus and named it *Astrocalyx*, and the species *A. pleiosandra* (Aguilar FBI4349bis). He assigned the new genus to the Astronieae and hypothesized that it may be most closely related to *Plethiandra*, a pleiostemonous genus found in Peninsular Malaysia, Sumatra, and predominantly in Borneo, which is now properly placed in the Dissochaeteae. *Astrocalyx* and *Plethiandra* are the sole polystaminate genera of Old World Melastomataceae (KADEREIT, 2005), a character that evolved independently in the two lineages (CLAUSING & RENNER, 2001; PENNEYS ET AL., 2015).

Merrill did not know about Vidal's collection until 1911 when Robinson consulted him about *Astronia calycina*. Merrill concluded that the holotype of *Astrocalyx pleiosandra* and Vidal's protologue matched, but believed that the odd features of Vidal's species warranted generic status, prompting him to publish a new combination name, *Astrocalyx calycina* (S. Vidal) Merr. (MERRILL, 1913).

Taxonomy and Description

***Astrocalyx* Merr.**, Philipp. J. Sci., C 5: 203. 1910 [Aug 1910].—Type: *Astrocalyx pleiosandra* Merr. (= *A. calycina* (S. Vidal) Merr.) One species in the Philippines (endemic).

***Astrocalyx calycina* (S. Vidal) Merr.**, Philipp. J. Sci., C 8 (5): 335, t. 11. 1913 [Nov 1913]. = *Astronia calycina* S. Vidal, Revis. Pl. Vasc. Filip. 136. 1866.—*Pharmacum calycinum* (S. Vidal) O. Ktze., Revis. Gen. Pl., 2: 953. 1891.—Type: Mt. Bulusan, province of Albay [Sorsogon], Vidal 780 (holotype, ?; isotype, A, K, L, MA), '781'.

= *Astrocalyx pleiosandra* Merr., Philipp. J. Sci., C 5: 203. 1910.—Type: Luzon, province of Camarines, near Daet, in forest near the Maniba River, Aguilar FBI4349bis (holotype, ?; isotype, K, US; paratype, NY).

Habit

Astrocalyx calycina is a tree 8 to 25 meters tall with bole measuring 27–65 cm in DBH (Fig. 2). The bole and old branches have whitish to gray bark that may be papery, wrinkled, or fissured, and a pale yellowish-brown wood. Abundant, small branchlets with conspicuous sympodial growth ultimately emerge from the bole. An illustration of the species may be found in the Philippine Journal of Science, vol. 8, no. 5, plate XI, page 362 (MERRILL, 1913).

Branches and vestiture

Mature branchlets are whitish to light-gray to brownish, glabrous, and obtusely quadrangular to subterete. Young twigs are green, quadrangular to obtusely quadrangular, covered with minute but conspicuous, sparse, ferruginous vestiture (Fig. 3A). The trichomes consist of reddish brown to brown, heterogeneously elongated, inclined to erect, persistent scales, ca. 0.05–0.2 mm long (Fig. 3B–C), the body conic, densely roughened with irregular, convoluted



Figure 1. Collections of the endangered *Astrocalyx* Merr. (A) Last known herbarium voucher, collected in 1965, Mount Apo National Park, province of Davao del Sur (ANU 1730 Kellman, L). (B) Terminal inflorescence (bud), collected in 2015, Mount Kitanglad Range Natural Park, province of Bukidnon (Mancera 001, CAS).



Figure 2. Habit of *Astrocalyx* at Mount Kitanglad. (A, arrow) Tree standing on a trail adjacent to a river. (B) Massive bole. (C) Ascending, sympodially branching twigs.

protrusions, anchored to the epidermis by a complanate, diminutive stalk (Fig. 3D), a type of trichome found nowhere else in the tribe. The nodes of young branchlets and inflorescences have relatively denser trichomes and are devoid of any lenticel, patch, ridge, swelling, or sub-nodal wart, while the internodes lack grooves or non-glandular peltate scales, all of which may be found in some species of *Astronieae*.

Some collections of *Astrocalyx* exhibit longer and more conspicuous trichomes. For instance, a set of specimens from the province of Laguna (*Elmer 18032*, GH!, L!, UC!) and the lone sample from Catanduanes (*Ramos & Edaño BS75140*, SING!, UC!) are both covered with less erect hairs as long as ca. 0.4 mm (Fig. 4D–F).

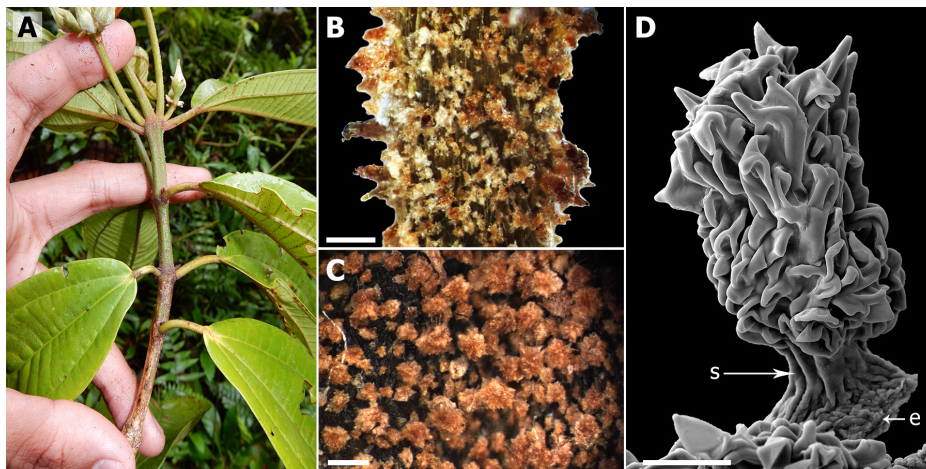


Figure 3. Branchlet morphology and general vestiture of *Astrocalyx*. (A) Young twig. (B) Side view of trichomes on a pedicel (*Stern 2164*, L). (C) Closer top view of trichomes from an inflorescence node and (D) SEM micrograph of an individual trichome from a pedicel (*Mancera 001*, CAS). Abbreviations: s—stalk, e—epidermal fragment. Scale bars = 0.25 mm (B–C), 0.05 mm (D).

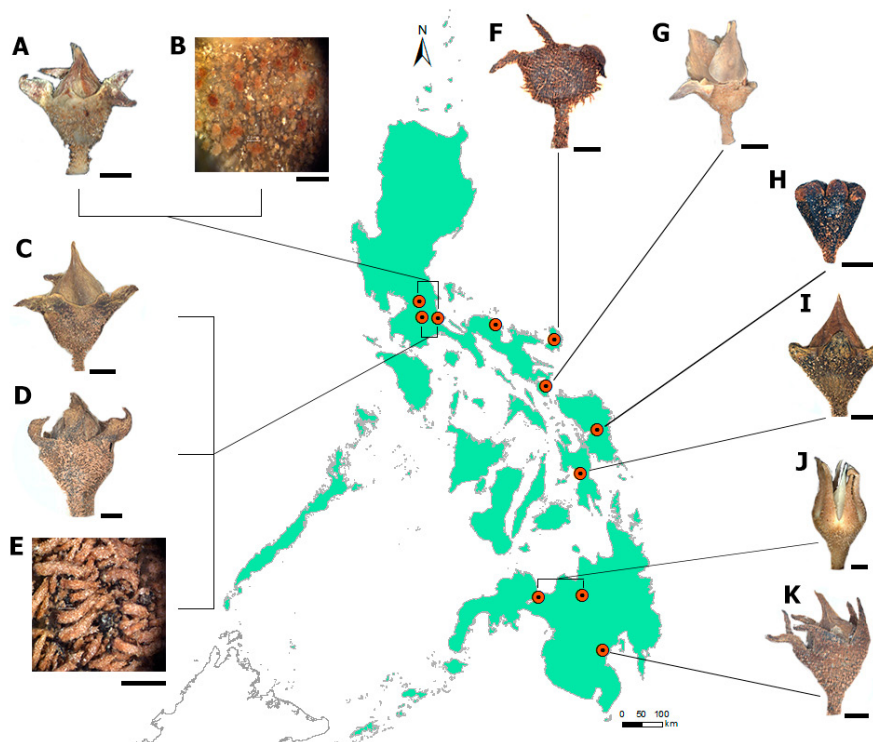


Figure 4. Variation in *Astrocalyx* trichome length and floral bud morphology. (A–B) Representative specimens from the provinces of Rizal and Quezon (*Stern 2164*, L), (C) Laguna (*McGregor BS23063*, L), (G) Sorsogon (*Sulit PNH2669*, L), (H) Samar Island (*Sulit PNH6350*, L), (I) Leyte Island (*Wenzel 327*, GH), (J) Lanao del Norte and Bukidnon (*Mancera 001*, CAS) and (K) Davao del Sur (*Kellman ANU1730*, L). (D–E) Deviant specimens from Mount Makiling and the province of Quezon (*Elmer 18032*, L) and (F) Catanduanes Island (*Ramos & Edaño BS75140*, SING). Scale bars = 2 mm (A, C–D, F–K), 0.50 mm (B, E).

Leaves and venation

The decussate leaves are subcoriaceous and are commonly mistaken for, but are considerably more leathery than, most species of *Astronia* (Fig. 5A). The adaxial surface of mature leaves is glabrous, slightly glossy, and olivaceous green when dry but may be lime green in life, while the abaxial side is always lighter in color (Fig. 5B). They are ca. 10–19.5 × 4.5–9.5 cm, elliptic to oblong-elliptic, the apex moderately acuminate while the base cuneate with traces of trichomes of the above-mentioned type seen on the adaxial side of the base of the midrib. Two pairs of secondary nerves (including the inframarginal nerves) that join the midrib to the apex and the transverse tertiary nerves are markedly depressed on the adaxial surface of the lamina. The inframarginal nerves in particular are conspicuous, ca. 0.21–0.28 mm wide, and maintain ca. 1.2–1.9 mm distance from the margin. The innermost pair of secondary nerves arises ca. 3.5–5 mm from the base of the midrib (Fig. 5C) and forms an oblanceolate to obovate curve towards the apex that is distinctly asymmetric to the outline of the lamina. The midrib and secondary veins on the abaxial side are highly prominent and covered with the same type of hairs as those found on the petiole and branchlets, albeit shorter and scarcer (Fig. 5D). The abaxial epidermis of the lamina is commonly devoid of trichomes but random individuals in various populations may contain few, randomly scattered, stunted, densely roughened, erect scales as with the midrib and secondary veins, or sparse, squamiform, membranous, peltate scales. The petiole is ca. 13.0–27.0 × 1.7–2.6 mm, subterete, non-caliculate, and unlike some species of *Astronieae*, it lacks wings or a sheath, thus the leaf scar is simple and orbicular.

Inflorescence architecture

The inflorescence is a terminal, determinate, paniculate thyrsoid subtended by shorter leaves, and each unit cluster is essentially a simple dichasium of bisexual flowers (Fig. 6). The inflorescence is ca. 8.5–14.5 × 5.0–13.0 cm, green, covered with the same indumentum as described above but conspicuously denser at the nodes, pedicels, and hypanthium. The central rachis is quadrangular with grooves on opposite sides, branching nodes (3–4) 5, branching up to the second order, the ultimate branchlets typically very short thus making the clusters of dichasia appear congested. The lowermost pair of opposite branches is inserted at the base of the peduncle at the same node where the subtending leaves arise, while the next pair of decussate branches is subtended by another pair of leaf-like nodal bracts, albeit smaller. Each cluster of dichasia along the lateral branch is subtended by a pair of narrowly oblong bracteoles at the node, ca. 3.5–8.5 × 0.8–1.3 mm, while each unit flower in each dichasium is subtended by even smaller, linear bracteoles, ca. 3–3.7 × 0.4–0.6 mm.

Perianth

The hypanthium/calyx tube may be funnelliform or cupular, densely covered with the same type of trichomes as vegetative organs, and bears 5(–6) teeth (Fig. 7A). The presence of 6-merous flowers appears to be random across individuals and even among flowers from the same individual, and is not unique to any population (Fig. 8E). Calyx teeth are elongate and keeled or folded at the base of the calyx tube (Fig. 7B), and their shape, size, and orientation vary considerably and seem to characterize discrete populations. For instance, in Luzon Island, all specimens have calyx teeth that are subulate to lanceolate, ca. 3.0–4.0 × 1.0–2.0 mm, laterally flattened, and recurved in bud (Fig. 8A–C, G). The oddly-haired collection from Mount Makiling, province of Laguna (*Elmer 18032*, GH!, L!, UC!) has the widest keel, ca. 1.2–1.5 mm wide, and is distinguished from the rest by having an abruptly narrowed, apiculate

apex (Fig. 8C). All specimens from the islands of Catanduanes and Mindanao have teeth that are slender, ca. $4.5\text{--}6 \times 2\text{--}2.8$ mm, and straight in bud with a less pronounced keel (Fig. 8F, D–E, J). Perhaps the most peculiar of all calyx teeth are those from Samar and Leyte Islands (*Sulit PNH6350*, L!; *Wenzel 314*, GH!; *Wenzel 327*, GH!), which lack elongate limbs and are thus truncate, ca. $1.2 \times 1.5\text{--}2.0$ mm, remarkably obtuse and incurved (Fig. 8H–I). Some species of *Astronia* also possess such keeled calyx lobes but they are usually less pronounced.

The 5(–6) petals are distinct, glabrous, imbricate in bud, elliptic-ovate to elliptic-oblong at anthesis, inequilateral, and ca. $7.0\text{--}7.3 \times 3.0\text{--}4.5$ mm (Fig. 7C). The petals are reflexed at anthesis along with the calyx teeth and tube, ca. 70° from the vertical, exposing the numerous stamens for the insect (presumed) pollinators. While petals are generally white, some individuals were recorded to be yellowish (*Guerrero 30374*, UC!) or even basally red-tinged (*Stern 2164*, L!).

Androecium

The anisometric, glabrous stamens number from 64 to 96, which is likely the highest number found among all polystaminate species in the Melastomataceae (Fig. 9A). The complanate filaments, ca. $4.0\text{--}6.5 \times 0.2\text{--}0.4$ mm, are densely inserted along the circumference of the torus (Fig. 9B). It had been thought (MERRILL, 1910; MERRILL, 1913; MAXWELL & VELDKAMP, 1990a; RENNER, 1993) that the entire anther thecae are linear-oblong and terete, and that they open through apical collar slits. In reality, the pollen sacs are only restricted to the terminal end, and they open through short, apical, longitudinal slits (Fig. 9C). The long anthers originally described appear to be just a compressed tube that is an extension of the connective (WILSON, 1950). Wilson further described the stamens as lacking a dorsal vascular bundle, instead, possessing a network of vascular bundles in the connective that dichotomously branch at the apex to service the apical pollen sacs. At anthesis, the compressed tube flexes away from the rest of the filament at an obtuse angle, but leaves a relatively flexible fold. Anthers of *Astronieae* open by longitudinal slits and lack an endothecium; the latter character unites the tribe with the rest of the higher Melastomataceae (CLAUSING & RENNER, 2001).

The individual anthers of *Astrocalyx* are slender, ca. $2.5\text{--}4.0 \times 0.5\text{--}0.9$ mm, unappendaged, and generally have compressed, tube-like connectives that are apically bifid, terminating with thecae that dehisce by apical longitudinal slits. However, collections from the province of Laguna in Luzon Island, and the islands of Catanduanes, Leyte, and Mindanao have anther sacs and slits that extend through the anterior lateral margin of the expanded tube and sometimes spread apart, essentially forming a cordate shape (Fig. 10C–E, G–H). The anther shape originally described (MERRILL, 1910) for *Astrocalyx* is found only in a few collections from the provinces of Quezon, Sorsogon (Mount Bulusan), and Laguna (Fig. 10A–B, F).

PleioSTEMONY, a diagnostic feature of *Astrocalyx*, evolved independently in separate lineages of the Melastomataceae and can also be found in species of Dissochaeteae, Henrietteae, and Miconieae (RENNER, 1993; PENNEYS *ET AL.*, 2010; PENNEYS *ET AL.*, 2015). Ontogenetic studies by PUGLISI (2007) and WANNTORP *ET AL.* (2011) show that the condition may result from either of two developmental processes: (1) subdivision of the primordia of antipetalous stamens into multiple, smaller ones, or (2) “dedoublement” or splitting of each stamen into two. The first process is exhibited by a species of *Plethiandra* (Dissochaeteae) (KADEREIT, 2005) while both are seen in many species of *Conostegia* (Miconieae) (KRIEBEL, 2016). PleioSTEMONY has also been reported in other genera of Miconieae such as *Clidemia*, *Miconia*, and *Tococa* (MICHELANGELI, 2000; KRIEBEL, 2016) and in *Llewelynina* (Henrietteae)

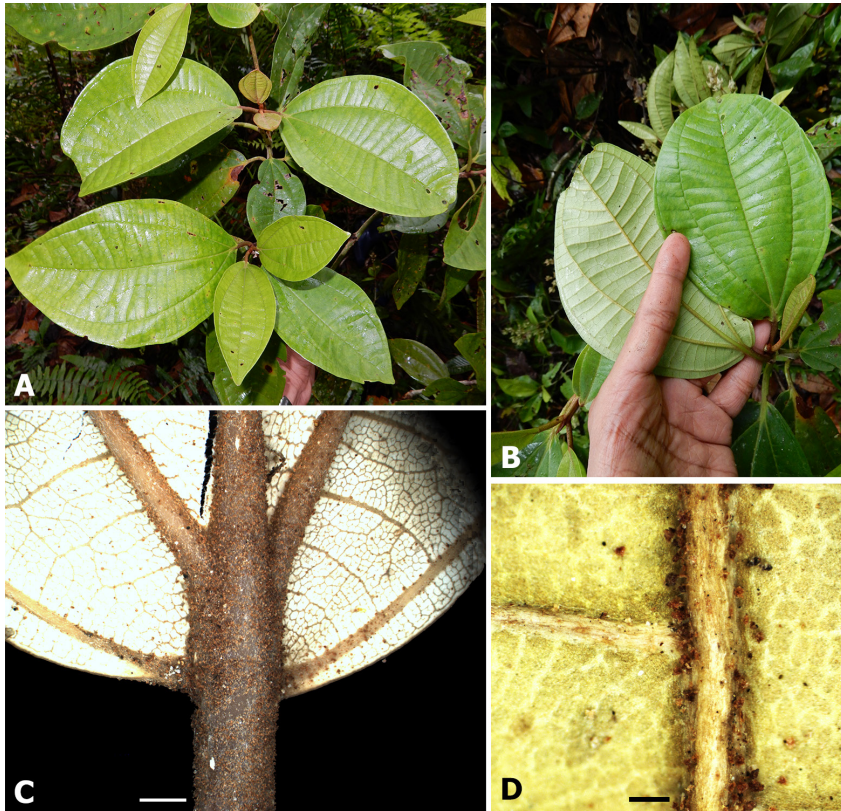


Figure 5. Leaf morphology and venation in *Astrocalyx*. (A) Top view of a twig. (B) Abaxial and adaxial surfaces. (C) Origin of inner secondary nerves. (D) Vestiture of nerves on the abaxial surface. Specimens from *Mancera 001*, CAS. Scale bars = 0.20 mm (C, D).



Figure 6. Inflorescence architecture of *Astrocalyx*. (A) Terminal panicle-like thyrse. (B) Closer view of opposite, simple dichasia on an inflorescence branch. Scale bar = 5 mm (B).

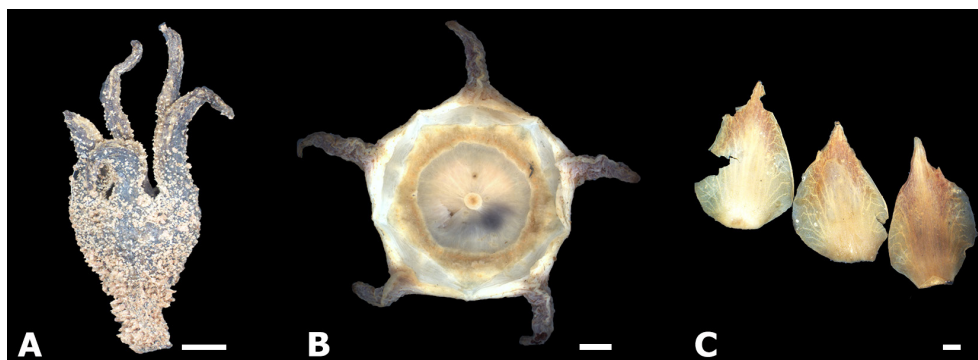


Figure 7. Perianth morphology of *Astrocalyx*. (A) Floral bud (Vidal 780, L, isotype). (B) Top view of hypanthium/calyx tube and calyx teeth with corolla, stamens, and style removed (Ramos BS23537, L). (C) Detached petals, rehydrated (Sulit PNH2669, L). Scale bars = 1 mm.

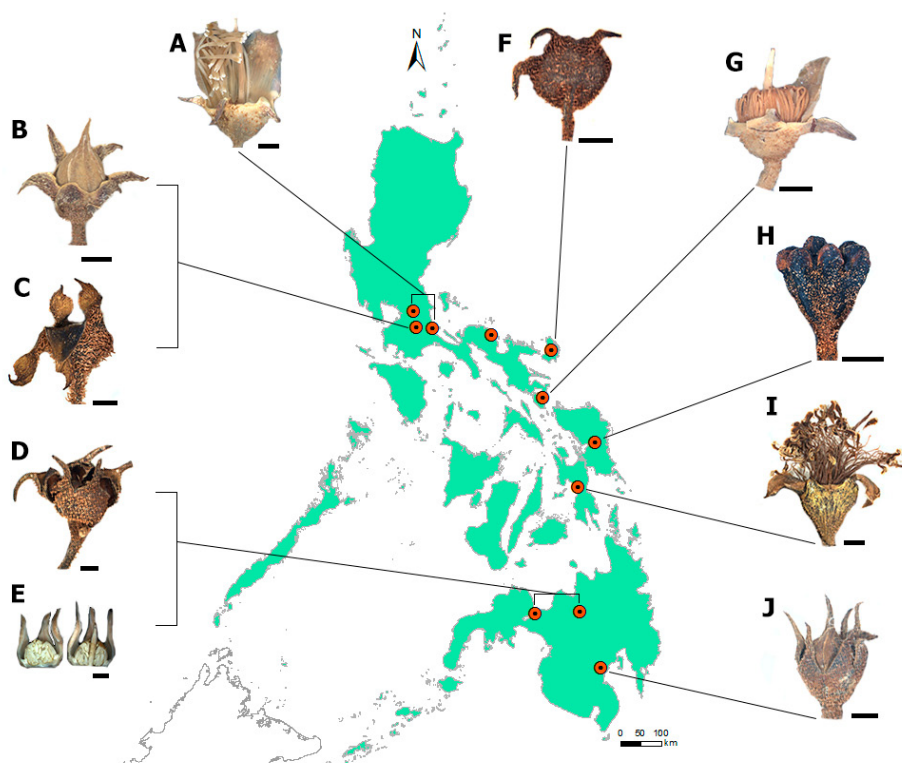


Figure 8. Variation in *Astrocalyx* calyx teeth shape, size, and number. Representative specimens from the provinces of (A) Rizal and Quezon (Stern 2164, L), (B) Laguna (McGregor BS23063, L), and (G) Sorsogon (Sulit PNH2669, L). Deviant specimens from (C) Mount Makiling and the province of Quezon (Elmer 18032, L), (D) provinces of Lanao del Norte and Bukidnon (Sulit PNH9836, L), (F) Catanduanes Island (Ramos & Edaño BS75140, SING), (H) Samar Island, (Sulit PNH6350, L), (I) Leyte Island (Wenzel 327, GH), and (J) province of Davao del Sur (Kellman ANU1730, L). (E) Hexamerous calyx in bud from the province of Bukidnon (Mancera 001, CAS). Scale bars = 2 mm.

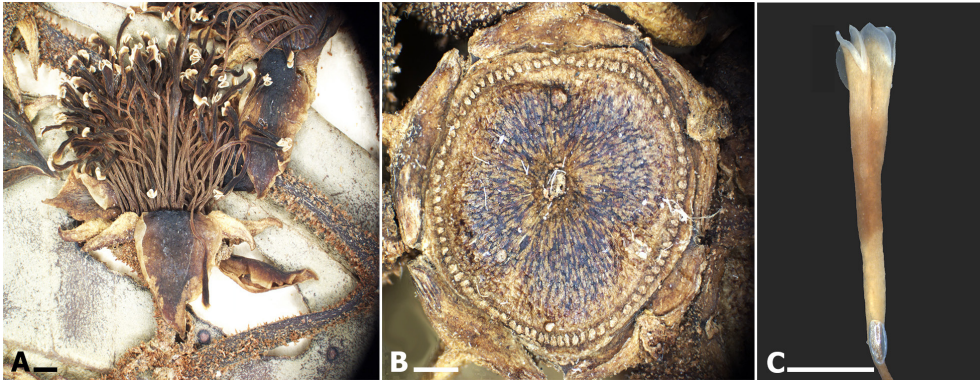


Figure 9. Androecium of *Astrocalyx*. (A) Numerous exserted stamens (*Sulit PNH2669*, L). (B) Top view of a fruit showing staminal scars (*Ramos BS23537*, L). (C) Anther, rehydrated (*Sulit PNH2669*, L). Scale bars = 1 mm.

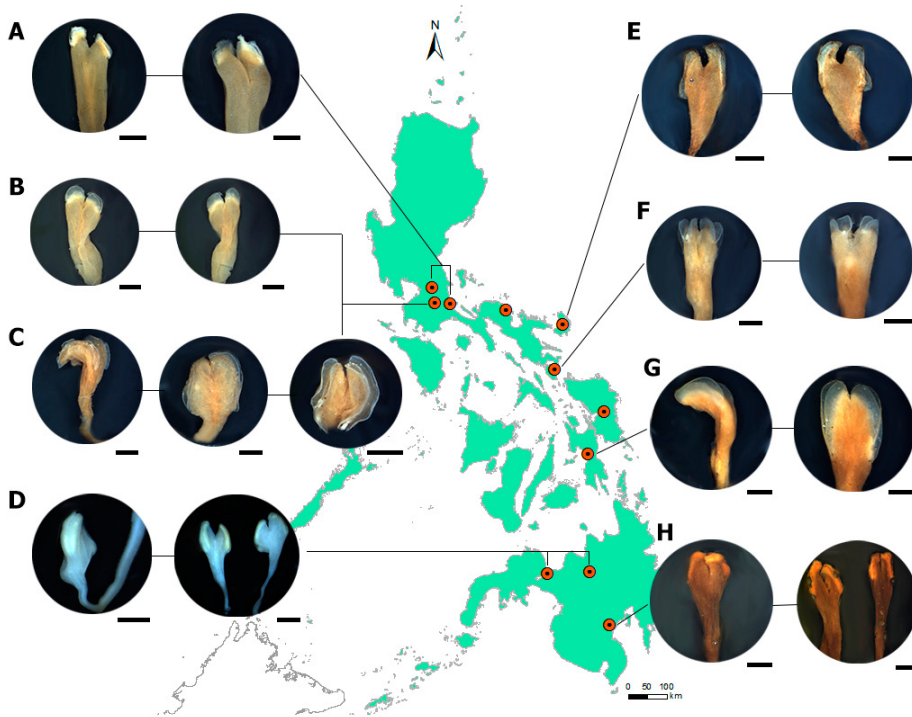


Figure 10. Variation in *Astrocalyx* anther shape. Representative specimens from the provinces of (A) Rizal and Quezon (*Stern 2164*, L), (B) Laguna (*McGregor BS23063*, L), and (F) Sorsogon (*Sulit PNH2669*, L). Deviant anthers from (C) Mount Makiling and the province of Quezon (*Elmer 18032*, L), (D) Lanao del Norte and Bukidnon (*Mancera 001*, CAS), (E) Catanduanes Island (*Ramos & Edaño BS75140*, SING), (G) Leyte Island (*Wenzel 327*, GH), and (H) Davao del Sur (*Kellman ANU1730*, L). Stamens were observed from floral buds (A, B, D, E, H) or flowers at anthesis (C, F, G). Scale bars = 0.5 mm.

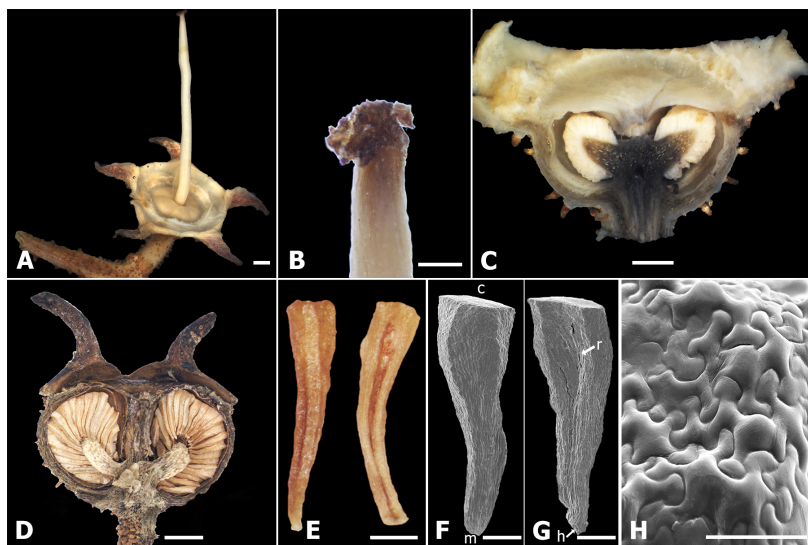


Figure 11. Gynoecium and fruit of *Astrocalyx*. (A) Flower post-anthesis, (B) stigma, and (C) longitudinal section of the hypanthium/inferior ovary, all rehydrated (Stern 2164, L). (D) Longitudinal section of mature capsule and (E) seeds (Sulit PNH9836, L). (F, G, H) SEM micrographs of seed showing anti-raphal, raphal sides and testa relief, respectively. Abbreviations: c—chalazal end, m—micropylar end, r—raphal zone beginning from the pointed depressed region extending down to h—hilum. Scale bars = 1 mm (A, C, D), 0.25 mm (B, E–G), 0.05 mm (H).

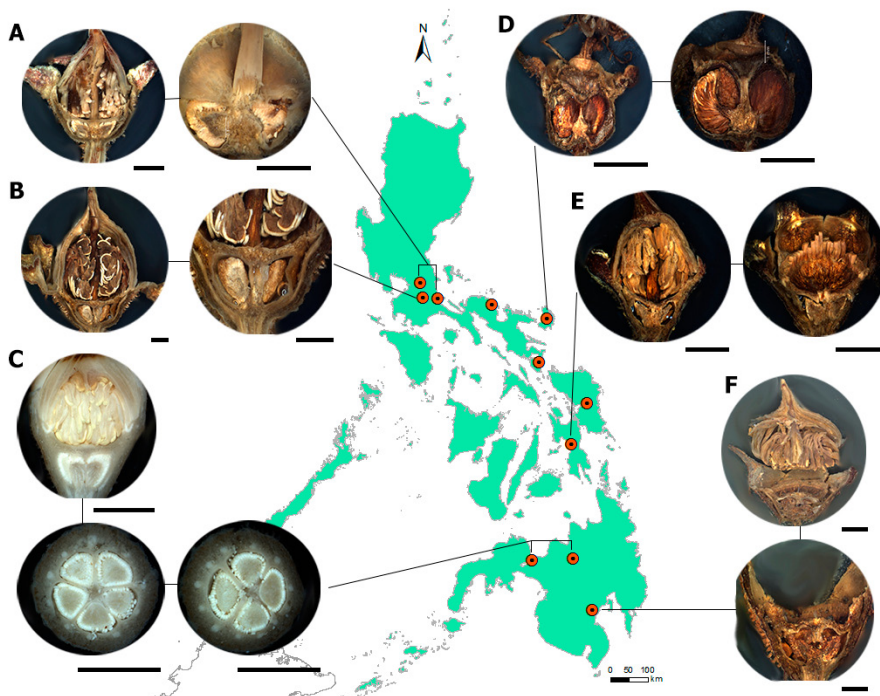


Figure 12. Sections of *Astrocalyx* hypanthium/ovary and variation in locule number. Representative specimens from the provinces of (A) Rizal and Quezon (Stern 2164, L), (B) Laguna (McGregor BS23063, L), (C) Lanao del Norte and Bukidnon (Mancera 001, CAS), (D) Catanduanes Island (Ramos & Edaño BS75140, SING), (E) Leyte Island (Wenzel 327, GH), and (F) Davao del Sur (Kellman ANU1730, L). Scale bars = 5 mm.

(PENNEYS *ET AL.*, 2010), although as in *Astrocalyx*, studies have yet to be conducted to elucidate the ontogenetic mechanisms behind the feature, as well as its significance in the phylogeny and pollination biology of the family.

The peculiar androecial morphology described above at once distinguishes *Astrocalyx* from the rest of the Astronieae, which are diplostemonous. Furthermore, *Astronia* has short, dolabriform anthers, *Beccarianthus* has large, slender anthers with vertical slits, while *Astronidium* has slender anthers, vertical slits, and an elongated dorsal connective appendage (MAXWELL & VELDKAMP, 1990a).

Gynoecium

The ovary of *Astrocalyx calycina* is wholly inferior and has (4–)5(–6) locules, each ca. $1.5\text{--}1.8 \times 1.2\text{--}1.8$ mm. Except for the bluntly-toothed flowers from Leyte Island that are all 4-locular, the number of locules varies across individuals and even among flowers from the same individual, and therefore is not indicative of any population (Fig. 12). Each locule contains a thickened, dorsoventrally flattened, apically bilobed, basal-axile placenta, ca. $0.9\text{--}1.2 \times 0.5\text{--}0.9$ mm, ascending towards the outer wall of the ovary and terminating into acute apices (Fig. 11C–D). The ovary base is convex and the apex concave to planar, cream, glabrous, and lacking ridges. The style is elongate and erect, ca. $6.0\text{--}11.0 \times 0.6\text{--}0.8$ mm, terete, cream, and glabrous (Fig. 11A). The stigma is obliquely truncate to punctiform, ca. $0.2\text{--}0.4 \times 0.3\text{--}0.5$ mm, but the reddish-brown, papillate apex develops a similarly-colored to whitish tuft that can be distinguished from the rest of the style, post-pollination (Fig. 11B).

Fruit shape ranges from funnellform to cupular, and a constriction around the torus (frequently seen in *Astronia*) is lacking (Fig. 11D). The capsules are ca. $3.0\text{--}6.0 \times 4.0\text{--}7.0$ mm and have persistent calyx teeth. The seeds are ca. $0.5\text{--}1.8 \times 0.4\text{--}0.5$ mm (Fig. 11E), very numerous, pyramidal-cuneate, but mostly quadrangular prismatic-cuneate. In the latter case the particular shape may range from rectangular to trapezoid, slightly curved, the micropylar end punctiform and the chalazal side truncate to obliquely truncate, the antiraphal (dorsal) side with two prominent ridges, the raphal zone (ventral) linear-triangular and inappendiculate (Fig. 11F–G). Individual cells of the testa are characterized by anticlinal walls with channeled relief with Ω -type undulations and periclinal walls with low-convex relief lacking any further microrelief (Fig. 11H).

Distribution

Astrocalyx is found in forest edges that are either damp or close to large water sources. Herbarium vouchers also indicate a wide elevational range, of 300–550 m in Luzon to as high as 898–1040(–1700–1830) m in Mindanao.

The genus is endemic to the Philippines and is unevenly distributed across the archipelago (Figs. 4, 8, 10, 12). MAXWELL & VELDKAMP (1990a) enumerated the islands of Luzon, Catanduanes, Samar, Leyte, and Mindanao as localities for the genus. Considering the sampled vouchers up to 1965, specific localities in Luzon Island include provinces in Southern Tagalog and the Bicol Peninsula: Laguna (Mount Makiling and other unspecified locations), Rizal (unspecified location), Quezon (along “Dakil River,” municipality of Mauban and other unspecified locations), Camarines Norte (near “Maniba river,” municipality of Daet), and Sorsogon (unspecified locations in Mount Bulusan, but one particularly along the trail from Bulusan Lake to Aguiñgai Valley, Sitio Basud). It was also collected in an unspecified location in the island province of Catanduanes. In the Visayas, the genus was documented

in the municipality of Hinabangan (formerly Concord) in Samar Island and an unspecified location in Leyte Island. Observed specific localities in Mindanao Island include provinces in Northern Mindanao and Davao Region: Lanao del Norte (municipality of Kolambugan), Bukidnon (Mount Kitanglad Range), and Davao del Sur (in the “Gumate District,” eastern slopes of Mount Apo, and in Barangay Baracatan, Davao City).

References to the occurrence of *Astrocalyx* in other localities were also noted, including Laguna Lake Basin (FERNANDO *ET AL.*, 2005) and Mount Banahaw (GASCON *ET AL.*, 2013) in the provinces of Laguna and Quezon, respectively, and Mount Malindang (ARANCES *ET AL.*, 2004) in the province of Misamis Occidental in northern Mindanao Island, although all lack herbarium vouchers for confirmation.

Ecological significance

Astrocalyx, in a study on the Philippine flying lemur (*Cyanocephalus volans*), was found to be a good foraging tree (WISCHUSEN & RICHMOND, 1998). It has also been identified as potential phytoremediation species in heavily metal-polluted habitats (CADIZ, 2005). Pollination biology of this polystaminate species has yet to be elucidated. *Astrocalyx* has already been categorized as Endangered (criterion EN B1ac under the IUCN ver. 2.3) in a biodiversity conservation assessment made by FERNANDO *ET AL.* (2008).

Economic use

A collection from Mount Bulusan (*Sulit PNH2669*, A!) identified *Astrocalyx* as a useful construction material.

Vernacular names

Common names used to refer to *Astrocalyx* are mostly homonyms of the more common genera of Melastomataceae like *Medinilla* and *Astronia*. Its official name is Tanghaw but is called Hantutungaw in Mount Malindang (ARANCES *ET AL.*, 2004), Tunan-tunan in Mount Bulusan (VIDAL, 1886), Tanghau in Mount Banahaw (GASCON *ET AL.*, 2013), Tuñgau in Mount Kitanglad (*Sulit PNH9836*, A!), and Tambis-tambis in Mount Apo (*ANU 1667*, L!).

Specimens examined: Catanduanes Is. Province of Catanduanes: Jul-Sep 1928, *Ramos & Edaño 75140* (SING, UC). LEYTE IS. 25 Jul 1913, *Wenzel 327* (GH); 10 Aug 1913, *Wenzel 314* (GH). LUZON IS. Province of Camarines Norte: Daet, near Maniba river, Jul 1909, *Aguilar FB14349bis* (K, US, isotype). Province of Laguna: Paete, Jul 1909, *Foxworthy BS8983* (NY, undetermined paratype); Jun-Aug 1915, *McGregor BS23063* (A, L, NY); Jun-Dec 1915, *Mabesa FB24888* (UC); Nov 1915, *Amarillas BS24671* (L, SING); Los Baños, Mount Makiling, Jun-Jul 1917, *Elmer 18032* (GH, L, NY, PNH, UC). Province of Quezon: Oct 1915, *Duldulao FB24622* (UC); Jun-Jul 1917, *Cailipan FB26951* (P); Jun-Jul 1929, *Oro FB30987* (NY, UC); Mauban, Maliliit na Bato, drainage of Dakil River, 17 km east of Pangil, 430 masl, 24 Oct 1963, *Stern 2164* (L). Province of Rizal: Aug 1912, *Loher 12574* (UC). Province of Sorsogon: Bulusan, Jan 1884, *Vidal 780* ('781') (A, L, MA, isotype); Jul-Aug 1915, *Ramos BS23537* (L); Irosin, Mount Bulusan, Oct 1915, *Elmer 14509* (CAS, L, NY, UC); Irosin, Mount Bulusan, Jun 1916, *Elmer 16218* (A, L, NY, UC, W); Irosin, Mount Bulusan, Jun 1916, *Elmer 16233* (L, NY, UC); Bulusan, along trail from Bulusan Lake to Aguiñgai Valley, Sitio Basud, Mount Bulusan, 550 masl, Jul-Aug 1947, *Sulit PNH2669* (A, L). MINDANAO IS. Province of Bukidnon: Mount Kitanglad, southern slope of east peak, forest edge above Kantoan, Mar 1949, *Sulit PNH9836* (A, L); Baungon, Brgy. San Vicente, Mount Kitanglad Range Natural

Park, Sitio Kalanganan, 30-min. hike from the village, 898 masl, 18 Jul 2015, *Mancera 001* (CAS, CMUH). Province of Davao del Sur: Davao City, uncleared abaca plantation, Gumate district on the eastern slopes of the Mount Apo, Mindanao, Apr 1964, *ANUI667* (L); Davao City, Gumate district on the eastern slopes of the Mount Apo complex, Jan 1965, *Kellman ANUI730* (L); Barakatan, Davao City, 1830 masl, Sep 1983, *Reynoso et al. 150900* (PNH). Province of Lanao del Norte: Kolambugan, forest, May-Jul 1926, *Guerrero FB30374* (NY, UC). SAMAR IS. Province of Samar: Hinabangan (formerly Concord), Bagacay, Apr–May 1948, *Sulit PNH6350* (L).

ACKNOWLEDGEMENTS

This contribution would not have been possible without the encouragement of Dr. Benito C. Tan, whose desire to pay tribute to the life and works of the late James F. Maxwell (1945–2015), a renowned taxonomist of paleotropical Melastomataceae, resulted in this commemorative issue. He was also key to gaining access to the herbarium collections of *Astrocalyx* at UC and collaborating with colleagues in Mindanao Island, which led to this re-documentation. During the review process, Dr. Tan was diagnosed with brain cancer, to which he succumbed on December 2016. He will forever be remembered as a great mentor, colleague, and friend to the authors and a pillar of bryophyte and pteridophyte taxonomy to the entire east Asian and Malesian botanical community.

We are grateful to Dr. Victor B. Amoroso, Director of the Central Mindanao University (CMU) Center for Biodiversity Research and Extension in Mindanao (CEBREM) who co-organized two productive botanical explorations in Mindanao Island. We also thank the Department of Agriculture (DA) and the Department of Environment and Natural Resources (DENR) of the Republic of the Philippines, the local government unit of the Municipality of Baungon and Barangay San Vicente, as well as the Lumad of Sitio Kalanganan led by their *datu* and *bai* for authorizing the permits of collecting and transporting of specimens and for guiding us in the field. We also express our gratitude to Dr. Pieter Pelser for his guidance in the search for *Astrocalyx*, Mr. Danilo Tandang for his correspondence about the extant deposits at PNH, Dr. Vanessa Handley for her generosity in contributing SEM images, James R. Shevock for his helpful comments and suggestions for improvement of this paper, and the curators and staff at CAS, CMUH, NY, P, PNH, UC, US, and W for access to herbarium specimens. Funding was provided by the National Science Foundation Grant NSF DEB–1146409 and the California Academy of Sciences Lakeside Foundation.

REFERENCES

- ARANCES, J. B., V. B. AMOROSO, W. SM. GRUEZO, C. RIDSDALE, L. VISSER, B. C. TAN, L. V. RUFILA, J. B. GALVEZO, G. S. OPISO, R. COMILAP, C. LUMARAY, C. COMILAP, N. PACUT, B. MONTIMAR, AND S. SACAL. 2004. *Development of a Participatory Methodology for Inventory and Assessment of Floral Resources and Their Characterization in the Montane Forests of Mt. Malindang*. College, Laguna. 94 pp.
- CADIZ, N. M. 2005. *Plant Diversity in Selected Mine Tailing Areas [from the following mining corporations in the Philippines: United Paragon Mining Corp., Paracale, Camarines Norte, Atlas Consolidated Mining Corp., Toledo City, Cebu, Balatoc Mine-Benguet Mining Corp., Itogon, Benguet, VICLODE Mining Corp., a subsidiary of APEX, (Ayala-Puyat Exploration) Mining Corp., Compostela Valley, Maco, Davao*

- del Norte*]. Food and Agriculture Organization of the United Nations. Available from: <http://agris.fao.org/agris-search/search.do?recordID=PH2014001049> (accessed 4 Dec. 2015)
- CHASE, M. W., AND H. H. HILLS. 1991. Silica gel: An ideal material for field preservation of leaf samples for DNA studies. *Taxon* 40: 215–220.
- CLAUSING, G., AND S. S. RENNER. 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. *Amer. J. Bot.* 88: 486–498.
- FERNANDO, E. S., D. A. LAGUNZAD, N. A. D. MALLARI, AND P. L. ALVIOLA III. 2005. Biodiversity. Pages 153–166 in R. D. Lasco, and M. V. O. Espaldon (eds.), *Ecosystems and People: The Philippine millennium ecosystem assessment (MA) sub-global assessment*. University of the Philippines Los Baños, Laguna.
- FERNANDO, E. S., L. L. CO, D. A. LAGUNZAD, W. S. M. GRUEZO, J. F. BARCELONA, D. A. MADULID, A. B. LAPIS, G. I. TEXON, A. C. MANILA, AND P. M. ZAMORA. 2008. Threatened plants of the Philippines: A preliminary assessment. 47 pp. Available from: <http://www.nationalredlist.org/species-information/?speciesID=178427> (accessed 4 Dec. 2015)
- GASCON, C. N., R. C. GARCIA, F. N. BELTRAN, W. C. FALLER, AND M. A. R. AGUIDILLA. 2013. Biodiversity assessment of Mt. Banahaw de Dolores, Philippines. *Asian J. Biodivers.* 4: 23–45.
- HARVARD UNIVERSITY HERBARIA & LIBRARIES INDEX OF BOTANICAL SPECIMENS. 2016. *Astrocalyx calycina* (S. Vidal) Merr., det. J. F. Maxwell, 1983. Digitized collections. Available from: <http://kiki.huh.harvard.edu/databases>
- HODGE, W. H. 1947. The use of alcohol in plant collecting. *Rhodora* 49: 207–210.
- JSTOR GLOBAL PLANTS. 2016. *Astrocalyx calycina* (S. Vidal) Merr. Digitized collections available from: <http://plants.jstor.org/> (accessed 4 Jan. 2016)
- KADEREIT, G. 2005. Revision of *Plethiandra* Hook. f.: A polystaminate, East Asian genus of Melastomataceae. *Edinb. J. Bot.* 62: 127–144.
- KRIEBEL, R. 2016. A monograph of *Conostegia* (Melastomataceae, Miconieae). *PhytoKeys* 67: 1–326.
- MAXWELL, J. F., AND J. F. VELDKAMP. 1990a. Notes on the Astronieae (Melastomataceae) – I. *Astrocalyx*, *Astronia*. *Blumea* 35: 71–114.
- MAXWELL, J. F., AND J. F. VELDKAMP. 1990b. Notes on the Astronieae (Melastomataceae) – II. *Astronidium*, *Becarianthus*. *Blumea* 35: 115–165.
- MENTINK, H., AND P. BAAS. 1992. Leaf anatomy of the Melastomataceae, Memecylaceae, and Crypteroniaceae. *Blumea* 37: 189–225.
- MERRILL, E. D. 1910. New or noteworthy Philippine plants VIII. *Philipp. J. Sci.* 5: 203–204.
- MERRILL, E. D. 1913. Studies on Philippine Melastomataceae II. *Philipp. J. Sci.* 8: 345–362.
- MICHELANGELI, F. A. 2000. A cladistics analysis of the genus *Tococa* (Melastomataceae) based on morphological data. *Syst. Bot.* 25: 211–234.
- MILLER, A. G., AND J. A. NYBERG. 2011. Chapter 27: Collecting herbarium vouchers. Pages 1–9 in L. Gaurino, V. Ramanatha Rao and E. Goldberg (eds.), *Collecting Plant Genetic Diversity: Technical guidelines, 2011 update*. Biodiversity International, Rome.
- OCAMPO, G., AND F. ALMEDA. 2013. Seed diversity in the Miconieae (Melastomataceae): morphological characterization and phenetic relationships. *Phytotaxa* 80: 1–129.
- PENNEYS, D. S. 2013. Preliminary phylogeny of the Astronieae (Melastomataceae) based on nuclear and plastid DNA sequence data, with comments on the Philippine endemic genus, *Astrocalyx*. *Philippine J. Sci.* 142: 159–168.
- PENNEYS, D. S., F. ALMEDA, F. MICHELANGELI, AND P. W. FRITSCH. 2015. Progress towards a revised classification of the Melastomataceae. Paper presented at the Botany 2015 Conference of the Botanical Society of America, Edmonton, Alberta. Abstract. Available from: <http://2015.botanyconference.org/engine/search/index.php?func=detail&aid=1211> (accessed 4 Jan. 2016)
- PENNEYS, D. S., F. A. MICHELANGELI, W. S. JUDD, AND F. ALMEDA. 2010. Henrietteae (Melastomataceae): A new Neotropical berry-fruited tribe. *Syst. Bot.* 35: 783–800.
- PUGLISI, C. 2007. *Multiplication of Floral Parts in the Genus Conostegia (Melastomataceae)*. Ph.D. thesis, University of Edinburgh.
- RENNER, S. S. 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nord. J. Bot.* 13: 519–540.
- RENNER, S. S., G. CLAUSING, AND K. MEYER. 2001. Historical biogeography of Melastomataceae: The roles of tertiary migration and long-distance dispersal. *Amer. J. Bot.* 88: 1290–1300.
- THE HERBARIUM CATALOGUE, ROYAL BOTANIC GARDENS, KEW. 2016. Melastomataceae – *Astrocalyx calycina* (S. Vidal) Merr. Digitized collections. Available from: <http://www.kew.org/herbcat> (accessed 4 Jan. 2016)
- VAN VLIET, G. J. C. M. 1981. Wood anatomy of the paleotropical Melastomataceae. *Blumea* 27: 395–462.

- VIDAL, S. S. 1886. *Revision de Plantas Vasculares Filipinas*. Estab. tipo-litográfico de M. Perze, Manila. vi + 454 pp.
- WANNTORP, L., C. PUGLISI, D. PENNEYS, AND L. P. RONSE DE CRAENE. 2011. Multiplications of floral organs in flowers: a case study in *Conostegia* (Melastomataceae, Myrtales). Pages 218–235 in L. Wanntorp and L. P. Ronse de Craene (eds.), *Flowers on the Tree of Life, Systematics Association Special Volume Series*. Cambridge University Press, England.
- WILSON, C. L. 1950. Vasculature of the stamen in the Melastomataceae, with some phyletic implications. *Amer. J. Bot.* 37: 431–444.
- WISCHUSEN, E. W., AND M. E. RICHMOND. 1998. Foraging ecology of the Philippine flying lemur (*Cyanocephalus volans*). *J. Mammal.* 79: 1288–1295.