



<https://doi.org/10.11646/phytotaxa.558.1.4>

An evaluation of the genus *Cyne* (Loranthaceae) including a new species and rediscovery and neotypification of the rare *C. quadriangula*

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Abstract

A new species of *Cyne* (Loranthaceae) from Bucas Grande and Dinagat Islands, Philippines is described and named *C. barcelonae* in honor of the Filipina botanist Julie F. Barcelona. Phylogenetic analysis using the complete nuclear ribosomal DNA cistron confirms it is sister to *C. banahaensis*, the only species among the six in the genus with complete descriptions of floral morphology. The species is similar to the rare *C. perfoliata* of Papua New Guinea by having connate-perfoliate upper leaves but differs from others in the genus by possessing palmate leaf venation, inflorescences lacking an operculum, light green corollas, and stamens with filaments. No type material for *Cyne quadriangula* exists, thus this taxon is only known from the original protologue. It was rediscovered on Bucas Grande Island and that collection was described and used as the neotype for the species. A revised description of the genus and key to the seven species is provided.

Keywords: Caraga region, mistletoe, parasitic plant, Santalales

Introduction

The Loranthaceae is the largest family in the sandalwood order (Santalales) with 76 genera and over 1000 species (Nickrent, 2020). One of the major clades is Elytrantheae that shares the symplesiophorphic base chromosome number in the family of $X=12$ with other early diverging lineages. It was first named as subtribe Elytranthinae (Engler, 1897) but its circumscription as a tribe came later (Barlow, 1964; Danser, 1933a; Nickrent, Malécot, Vidal-Russell, & Der, 2010). Elytrantheae contains 14 genera of Old World mistletoes, five of which are monotypic and one of those (*Trilepidea*) is extinct. As Danser (1931) astutely observed, inflorescence structure is central to the delimitation of genera in the family, and this is particularly exemplified by Elytrantheae. The spectrum of inflorescence types includes single flowers, two-flowered umbels, spikes, racemes, and capitula. Within the tribe, five genera have members with capitate inflorescences: *Cyne*, *Lampas*, *Lepeostegeres*, *Lepidaria*, and *Thaumasianthes*. Despite being in the same tribe and sharing this general inflorescence type, the form and development of these capitula are different among the genera and this has prompted various interpretations (Danser, 1933b; Kuijt, 1981).

The genus *Cyne* currently contains six species distributed from New Guinea to the Moluccas and the Philippines (Barlow, 1997). The genus has had an unstable taxonomic history, with various species previously residing in *Amylothea*, *Decaisnina*, *Lepeostegeres*, *Loranthus*, and *Tetradyas* (Table 1). Three of the species, *C. baetorta* Barlow, *C. papuana* (Danser) Barlow, and *C. quadriangula* Danser are known only from the type specimens and for the latter, no known herbarium specimens are extant. For *C. monotrias* Barlow and *C. perfoliata* (Danser) Barlow, floral material is lacking on the few herbarium specimens that exist, thus their protologues are incomplete. The only species for which good collections and descriptions exist is *C. banahaensis* (Elmer) Danser from the Philippines.

TABLE 1. Currently recognized species of *Cyne* (Loranthaceae).

| Species | Distribution | Synonyms | Publication |
|--|---|---|---|
| <i>Cyne baetorta</i> Barlow | Philippines (Mindoro) | <i>Decaisnina baetorta</i> Barlow | Blumea 38: 103. 1993. |
| <i>Cyne banahaensis</i> (Elmer) Danser | Philippines (Luzon, Tayabas, Lucban, Samar, Mindanao) | <i>Cyne alternifolia</i> Danser, <i>C. capitulifera</i> (Merr.) Danser, <i>Lepeostegeres banahaensis</i> Merr., <i>Lep. alternifolius</i> Merr., <i>Loranthus alternifolius</i> Merr., <i>L. banahaensis</i> Elmer, <i>L. capituliferus</i> Merr., <i>L. lagunensis</i> Merr. | Bull. Jard. Bot. Buitenzorg III, 10: 306. 1929. |
| <i>Cyne monotrias</i> Barlow | Maluku Islands | none | Blumea 38: 105. 1993. |
| <i>Cyne papuana</i> (Danser) Barlow | New Guinea | <i>Amylothecca papuana</i> Danser, <i>Decaisnina papuana</i> (Dans.) Barlow | Blumea 38: 106. 1993. |
| <i>Cyne perfoliata</i> (Danser) Barlow | New Guinea (Papua Sogeri region) | <i>Tetradyas perfoliata</i> Danser | Blumea 38: 106. 1993. |
| <i>Cyne quadriangula</i> Danser | Philippines (Mindanao, Bucas Grande Island) | none | Philipp. J. Sci. 58: 38. 1935. |

Floristic work in the Philippines experienced a lag following the critical work of E. D. Merrill that took place over a century ago, however, more recently activity has increased. Documentation of the existing flora has been continuous and accelerated in the past decade following the emergence of Co's Digital Flora of the Philippines (P.B. Pelser, Barcelona, & Nickrent, 2011 onwards). For Loranthaceae, new Philippine species have been described in *Amylothecca* (Tandang *et al.*, 2021), *Amyema* (P.B. Pelser & Barcelona, 2013); Pelser *et al.* 2018), *Decaisnina* (Tahil, 2021; Tandang *et al.* 2022), *Lepeostegeres* (P. B. Pelser, Nickrent, Reintar, & Barcelona, 2016), and *Macrosolen* (Mazo, Nickrent, & Pelser, 2022). This paper reports a remarkable new species of *Cyne* from Bucas Grande and Dinagat Islands in the southern Philippines. In addition, we review the available material for all *Cyne* species, provide updated descriptive information for *C. banahaensis* and *C. quadriangula*, and neotypify the latter species.

Methods

Specimens of the new *Cyne* species were collected under the following permits: Department of Environment and Natural Resources (DENR) Region XIII Wildlife Gratuitous Permit Nos. R13-2018-30 and R13-2020-08, and the Wildlife Transport Permit No. R13-001-2020. Observations of the plant in its habitat were made and documented photographically. Additional photographs were taken and stereomicroscopy conducted at Central Mindanao University. Type specimens have been deposited at PNH, FEUH and HNUL.

To compare morphological features among *Cyne* species, a matrix of 76 morphological characters was assembled from published information as well as examination of specimen photographs at Naturalis, Paris Herbarium, Kew Herbarium, Herbarium Berolinense, Smithsonian National Museum of Natural History, Harvard University Herbarium, New York Botanical Garden C. V. Starr Virtual Herbarium, and the Natural History Museum London (Supplementary file S1). In some cases, published descriptions were augmented with measurements made from specimen photographs using Adobe Photoshop (version 23.0.2).

The nuclear ribosomal DNA (rDNA) cistron (containing small-subunit rDNA, ITS-1, 5.8S, ITS-2, and large-subunit rDNA) was employed to generate phylogenetic trees for 61 taxa representing 53 of the 76 genera in the family. Accession numbers for all sequences, newly generated and obtained from NCBI Genbank, are listed in Supplementary file S2. All tribes and subtribes as outlined in the classification of Nickrent *et al.* (2010) were sampled. *Nuytsia* has been confirmed as the sister taxon to Loranthaceae (Liu *et al.*, 2018; Nickrent, Anderson, & Kuijt, 2019; Su, Hu, Anderson, & Nickrent, 2015; Vidal-Russell & Nickrent, 2008), thus it was used as outgroup. The molecular methods used to obtain the rDNA sequences were essentially as outlined in Nickrent *et al.* (2021). In brief, genomic DNA was extracted from silica gel dried leaf tissue and the sequences generated using a genome skimming approach (Dodsworth, 2015) at the Roy Carver Biotechnology Center. Shotgun genomic libraries were prepared with the Hyper Library construction kit from Kapa Biosystems (Roche). The libraries were quantitated by qPCR. Samples were multiplexed in one lane

and PCR amplified for 251 cycles from each end of the fragments on a NovaSeq 6000 using a NovaSeq SP reagent kit. Fastq files were generated and demultiplexed with the bcl2fastq v2.20 Conversion Software (Illumina). The adaptors were trimmed from the 3'-ends of the reads which were 250 nt in length.

The resulting fastq files were processed using GENEIOUS PRIME 2022.0.1 where paired ends were imported and matched. The Map to Reference function was used to generate the rDNA cistron using "seeds" of ca. 700 bp each from SSU and 200 bp for LSU rDNA developed from highly conserved regions (thereby not biasing the assembly). Ten iterations at Medium-Low sensitivity were performed separately for SSU and LSU with the Geneious Mapper and consensus sequences were imported into ALIVIEW Version 1.28 (Larsson, 2014) where they were trimmed (external transcribed spacers removed), manually aligned, and concatenated. The alignment (Fasta file) is available as Supplementary file S3. Alignment of the 18S, 5.8S, and 26S rDNA regions was straightforward; however, portions of ITS-1 (sites 1833-2415 on the Fasta file) and ITS-2 (sites 2593-3103) were problematic owing to large numbers of substitutions and length variation. Analyses that included and excluded these regions were conducted. Maximum likelihood (ML) analyses were performed using RAxML-HPC2 on XSEDE (8.2.12) as implemented on the CIPRES Science Gateway website. The substitution matrix used was GTR and 100 rapid bootstrap inferences were executed. The likelihood of the final tree was evaluated and optimized under GAMMA (model parameters estimated to an accuracy of 0.1 Log Likelihood units).

Taxonomy

Cyne barcelonae Nickrent & Rule, *sp. nov.*—Figs. 1, 2

Type:—PHILIPPINES. Region XIII (Caraga), Surigao del Norte Province, Bucas Grande Island, Municipality of Socorro, Brgy. Honrado, 17 masl, 9°41.182'N, 125°55.305'E, 22 June 2020, M. G. Q. Rule MGR19-004 (holotype: PNH!; isotypes FEUH!, HNUL!).

Diagnosis:—Similar to *C. perfoliata* by its basally connate upper leaves and to other species by its possession of sessile decussate pairs of triads composed of 6-merous flowers with a style articulated above the base. It differs from these by having palmate (vs. pinnate) leaf venation, inflorescences that lack an operculum (vs. with an operculum), light green corollas (vs. yellow, red, etc.) and stamens with filaments (vs. sessile anthers).

Description:—Glabrous hemiparasitic epiphyte (mistletoe) lacking epicortical runners. Young internodes terete, smooth, yellowish-green, older growth terete, developing reddish-brown bark with conspicuous lenticels, nodes somewhat thickened particularly where the lateral two branches depart from the central stem giving a pseudo-whorled (umbellate) appearance. Leaves opposite, obovate, sessile, upper pairs connate on the margins in the lower 6-12 mm, obovate, (3.4–) 4.3 (–5.3) long × (2.8–) 3.6 (–4.6) wide, base and apex rounded, thick coriaceous, margin entire, brown, adaxial surface somewhat shiny, green to olive green, abaxial surface opaque, light green, nerves ca. 5, palmate (midrib not developed), indistinct, secondary veins invisible; lower leaves obovate or elliptic, not connate. Inflorescence a pseudoterminal capitulum, sessile in the cup formed by the two terminal, connate leaves, arising from a scurfy (furfuraceous), brown, unconsolidated material; flowers all sessile, arranged in mostly two pairs of decussate triads, the inner and outer series difficult to discern owing to compression and unequal development, bracts surrounding triad broadly ovate, margins scarious, brown, apex lacerate, ca. 2 mm long, 1.5 mm wide, bracteoles ovate, tightly pressed against but shorter than ovary, margins scarious, brown, apex lacerate, ca. 1.5 mm long and wide. Ovary (adnate to calyculus) angular from pressure of adjacent ovaries, cylindrical to doliform, 3 mm long by 1.7 mm wide, calyculus limb margin irregularly lacerate 0.6 mm high, brown. Corolla in mature bud stage cylindrical with dilated base, light green overall except for red tips of lobes, straight or very slightly curved, apex obtuse, 20–24 mm long, valvate margins of corolla lobes forming longitudinal ridges, dilated base 5.8 mm long × 2.5 mm wide, corolla lobes 1.1 mm at base, 0.7 mm above, lobes linear, reflexed but not twisted, reflexed part 5.7 mm long. Stamens 6, adnate to lobes and departing from them at reflex point, free filament 2.3 mm long, green; anthers basifixed, 2 mm long, linear, apex acute, locules continuous. Style 19 mm long, articulated ca. 1 mm above a conical base, stigma subcapitate, 0.5 mm wide, green. Fruit obovoid, 10 mm long × 6.5 mm wide, smooth, orange; calyculus limb forming a brown crown 1 mm long by 1.5 mm wide, stylar base forming a brown, nipple-like beak 0.7 mm long. Seeds ca. 2 mm long and wide.

Distribution and ecology:—At present, three populations of *Cyne barcelonae* have been recorded from two islands off the northeast coast of Mindanao in the Caraga Administrative Region (XIII). The first specimens were collected by Fernando Gaerlan in 1995 in the Dinagat Island Province on Dinagat Island, Municipality of Tubajon,

Barangay Navarro at 180 m. In 2013 plants from another population of the species were photographed by Meljan Demetillo at low elevation along the estuary east of Malinao, Municipality of Tubajon. No specimen was collected at this site; however, a photo exists on Phytoimages (DOL66749). Both of these localities are located in lowland evergreen forests over ultramafic rock as defined by Lillo *et al.* (2019); however, no notes on hosts and habitat were reported.

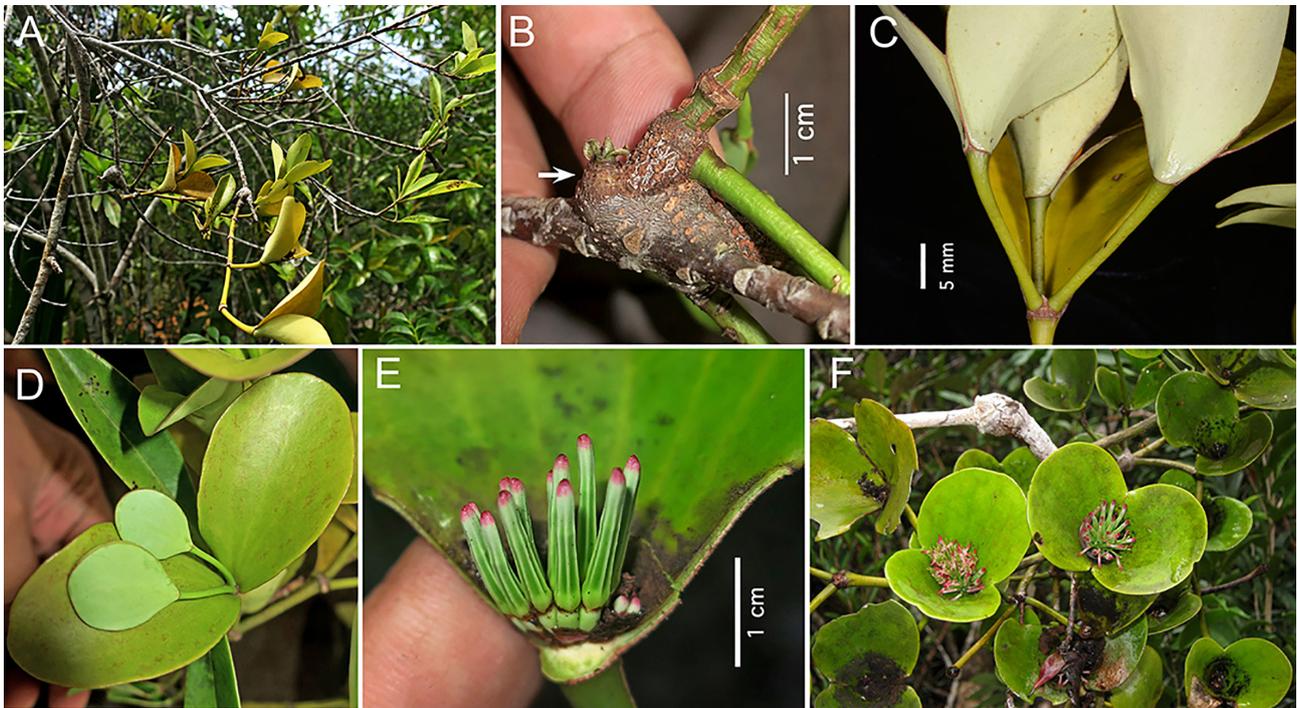


FIGURE 1. *Cyne barcelonae*, sp. nov. A. habit of mistletoe parasitic on *Myrsine* sp. B. A young haustorial connection to host branch. Arrow indicates a new vegetative shoot forming on the flank of the haustorium. Note that no epicortical roots are present. C. Terminal portion of vegetative shoot showing two lateral and the central stems assuming a pseudo-whorled appearance. Note the connation of the leaf bases. D. Non-connate leaves subtending to young shoots with connate leaves, still unopened. E. Young inflorescence with one of the connate leaves removed. Although two pairs of triads can be discerned, their decussate nature is obscure. F. Flowering shoots of plant photographed on Dinagat Island by M. Demetillo. Photos A-E by M. G. Q. Rule.

The third population, the one from which material was obtained for this study, was from Surigao del Norte Province on Bucas Grande Island. The populations of *C. barcelonae* were observed on remnant forests along rocky streams in ultramafic soils at approximately 10 masl. The recorded hosts are *Myrsine* sp., *Sterculia* sp. and *Timonius* sp. The plants were observably concentrated in areas no more than 20 meters away from a nearest stream where its hosts also congregated. They were also observed to share hosts with other mistletoes in the area, i.e., *Cyne quadriangula* Danser, *Decaisnina aherniana* (Merr.) Barlow and *Ginalloa* cf. *angustifolia* (Merr.) Danser.

Phenology:—This species has been observed flowering in the months of November to January, April to May, and August to September and fruiting in February, June, and October.

Etymology:—This species is named in honor of the Filipina botanist Dr. Julie Fenete Barcelona (1972 –) who has made major contributions to our knowledge of the Philippine flora, particularly for pteridophytes and *Rafflesia*.

Conservation Status:—Bucas Grande Island is part of the Siargao Islands Protected Landscape and Seascape (SIPLAS), a protected area as designated by the National Integrated Protected Areas System Act of 1992, RA No. 7586. This island is covered by a management plan (DENR, 2015). This population of *C. barcelonae* was observed in remnant ultramafic forests within the Kanlanuk waterfalls resort operated by a people’s organization. While anthropogenic activities are regulated at this resort, firewood collection and tree cultivation occurs nearby. Flooding that takes place regularly during the rainy season is the most imminent threat because of host tree damage. From observations made 2018–2020 we estimate this population of *C. barcelonae* to be composed of ca. 200 individuals in an area less than a hectare. The status of this population following Typhoon Rai which struck the Caraga region December 2021 is not known.

Dinagat Island is the largest in a series of islands in the Dinagat Islands Province northeast of Mindanao. It is considered part of the Greater Mindanao biogeographic region (Ong, Afuang, & Rosell-Ambol, 2002) and marks the

northernmost landmass in the Eastern Mindanao Biodiversity Corridor (Ibañez & Salvador, 2008). This island boasts a high level of floral and faunal endemism (Ambal *et al.*, 2012; Heaney & Rabor, 1982), with new plant species continually being described (Fernando, Quakenbush, Lillo, & Ong, 2018; Fernando & Wilson, 2021; Maglangit *et al.*, 2021). In a study of plant diversity on Dinagat Island, Lillo *et al.* (2019) reported 432 native species from 87 families and 203 genera from six forest habitat types and with at least 40 island-endemic taxa. However, the island is severely threatened by mining (Nakagawa & Franco, 1995). Approximately half of the island's forest area (over 15,000 hectares) is covered by Mineral Production Sharing Agreements, 58% of which are in lowland forests (De Alban, Bernabe, & de la Paz, 2004). The Dinagat Island Conservation Program initiated by the provincial government, seeks legislation that will exclude some areas from mineral extraction.

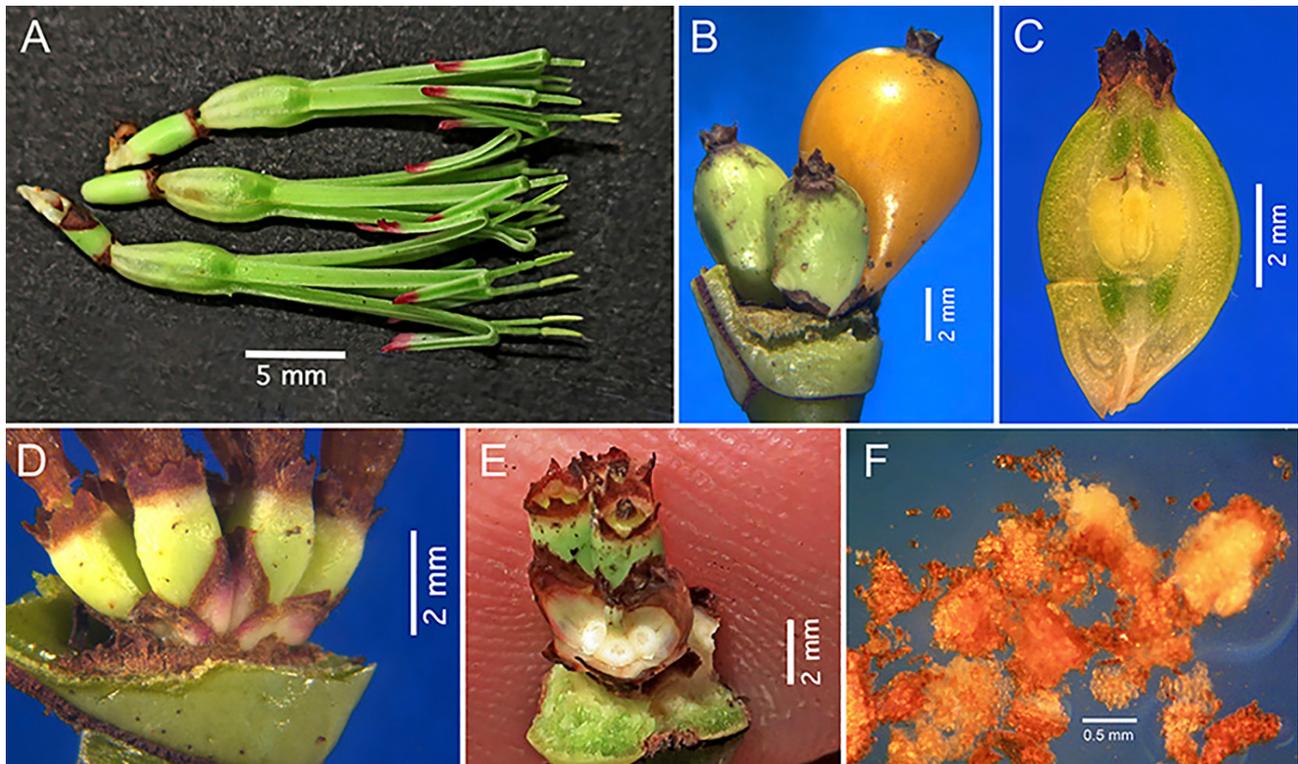


FIGURE 2. *Cyne barcelonae*, sp. nov. A. Flowers at anthesis. Note the green corolla with a dilated base as well as stamens with filaments. B. Fruits young and mature with persistent calyx and style base. C. Young fruit longitudinal section showing seed inside ovary wall. D. Capitulum arising from corky periderm of receptacle. Note the bracts and bracteoles adpressed to calyx / ovary. E. Portion of inflorescence with two triads, one with calyx / ovaries removed to show the lacinate bracts and bracteoles. F. Corky periderm removed from receptacle. Photos A and E by M. G. Q. Rule, the remaining D. L. Nickrent.

Major ecological disturbances such as logging and mining pose particularly severe threats to mistletoe populations because they have no seed bank and they require intact, living host trees for survival. The two populations of *Cyne barcelonae* on Dinagat Island were not observed by the authors but based on their locations, the following observations can be made. The population photographed by M. Melijan east of Malinao is near extensive mining operations by Norweah Metals and Mining Company. This region is not currently in protected status. The population collected by F. Gaerlan in 1995 in the Navarro Watershed is also not protected but has been proposed as a conservation site by DENR. At present only three populations of *Cyne barcelonae* are known and its extent on Dinagat and Bucas Grande Islands, as well as the adjacent Siargao Island, is poorly documented. For these reasons we consider this species Data Deficient (DD) (IUCN, 2019).

Additional specimens examined:—This species was originally collected by Fernando Gaerlan (PPI No. 19011) on Dinagat Island January 25, 1995 during the Philippine Plant Inventory, a joint project between the Philippine National Museum and the Botanical Research Institute of Texas (BRIT) headed by D. A. Madulid and S. H. Sohmer. That specimen has been annotated and resides at BRIT (barcode BRIT468437) as well as a duplicate at L (barcode L.3923671).

Phylogenetic analyses:—The results of ML analysis of the complete rDNA dataset show a monophyletic Elytrantheae sister to a strongly supported, monophyletic Loranthaceae (Supplementary file S4). The Elytrantheae portion

of this tree is shown in Fig. 3 and is composed of two major clades, one with the three New Zealand genera (*Alepis*, *Peraxilla* and *Trilepidea*) and other clade with nine genera. The sampled genera in that clade include *Amylotheca*, *Decaisnina*, *Elytranthe*, *Lepidaria*, *Lepeostegeres*, *Loxanthera*, *Lysiana*, and *Macrosolen* (*Lampas* and *Thaumasianthes* were not sampled). *Cyne barcelonae* is strongly supported as sister to *C. banahaensis* and that clade successively sister to *Decaisnina hollrungii* and *Amylotheca duthiana*. The remaining relationships within this subclade of Elytrantheae received comparatively lower bootstrap support. ML analysis of a matrix with ITS-1 and -2 removed yielded the same topology for Elytrantheae genera as the complete matrix.

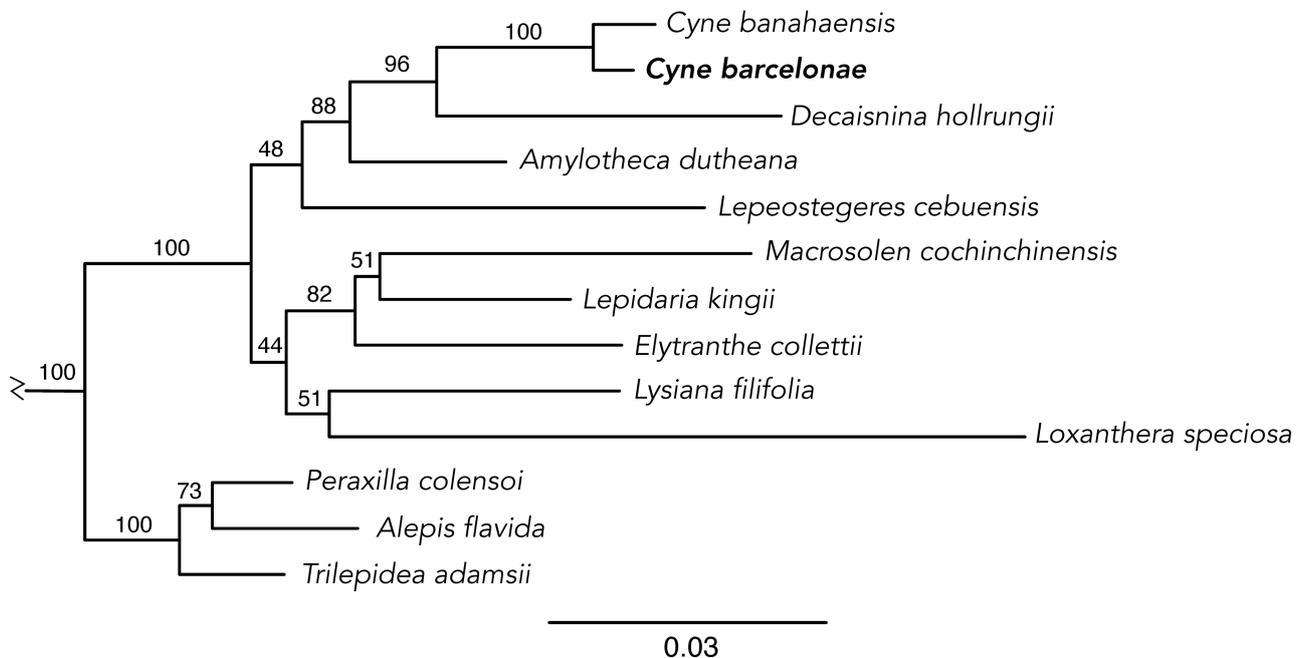


FIGURE 3. Portion of the tree derived from Maximum likelihood analysis of the rDNA cistron from representatives of Loranthaceae, tribe Elytrantheae. Numbers above branches are bootstrap support values. For the full tree that includes 53 genera and 61 taxa, see Suppl. file 4.

Discussion

Since the Flora Malesiana treatment of Loranthaceae by Barlow (1997), no new evidence has been published on the enigmatic genus *Cyne*. Except for *C. banahaensis*, descriptions for the remaining six species are incomplete, often lacking critical features on inflorescences, flowers, and fruits. For this reason, we review here the morphological features of the six named species and compare them with the new species, *Cyne barcelonae*.

When *Cyne barcelonae* was first observed from a photograph taken by Meljan Demetillo on Dinagat Island, the first author immediately recognized it as a new taxon for the Philippine flora, however, its generic placement was uncertain. The only other Loranthaceae with connate leaves of this nature is *C. perfoliata* from Papua New Guinea. This mistletoe was classified in the monotypic genus *Tetradyas* by Danser (1931) who allied it with what is now subtribe Amyeminae composed of *Amyema* (in part), *Dicymanthes*, *Diplatia*, and *Papuanthes*, all of which have capitula surrounded by foliaceous bracts. Those genera are today classified in tribe Loranthae subtribe Amyeminae (Nickrent *et al.*, 2010), not tribe Elytrantheae. Barlow (1974) pointed out that Danser misinterpreted the connate leaves as an involucre surrounding the capitulum and he then correctly assigned *Tetradyas* to Elytrantheae. Later Barlow (1993) combined *Tetradyas* with *Cyne*, noting the presence of an operculum scar at the leaf axils. The presence of an operculum was designated the primary diagnostic feature of the genus *Cyne* (Barlow, 1997). But an operculum was not seen surrounding the inflorescence in the photograph of the undescribed taxon from Dinagat Island, thus its assignment to *Cyne* remained uncertain.

As shown by the molecular phylogenetic analysis (Fig. 3), the new taxon described here is best considered a member of the genus *Cyne* in Elytrantheae. Barlow (1993) hypothesized a phylogenetic relationship between *Cyne* and *Decaisnina* based on an assumed morphocline that transitions the thyrses (racemes of triads) of *Decaisnina* to the

reduced inflorescences in some *Cyne* species. A relationship to *Decaisnina* is also confirmed by the rDNA data (Fig. 3) and is also recovered when complete plastome sequences of these taxa are analyzed (Nickrent, unpublished data).

Given their shared leaf morphology, it could be asked whether *C. barcelonae* is conspecific with *C. perfoliata* or whether it is a new species. Although we were not able to include *C. perfoliata* in our molecular analysis, this species differs from *C. barcelonae* in a number of morphological characters (Suppl. file 1) including leaf blade shape (ovate vs. obovate), leaf length and width, midrib abaxially (prominent vs. not prominent), lateral nerve arrangement (penninerved vs. palmate), inflorescence operculum (present vs. absent), triads (pedunculate vs. sessile), corolla tube base (not dilated vs. dilated), and corolla color (pinkish-yellow vs. green). Moreover, these two species are widely disjunct, separated by 2,500 km on opposite sides of Wallace's line (van Welzen, Parnell, & Slik, 2011). Taken together, these data support that these are two well-differentiated species and that the connate leaf morphology could be convergent evolution or that they are sister species (potentially resolved with a molecular phylogeny of all *Cyne* species).

Before reviewing information available for other *Cyne* species, it is important to provide some discussion of morphological terms used for the genus. The structure here referred to as an operculum was first described by Elmer (1911) who described it as "a large yellowish green rather thick protecting bract or hood-like cover". Although he used the term "bract", he later said "This involucre covering is morphologically different from the numerously imbricated true bracts". Danser (1933b) called the structure a calyptra and he correctly noted that it is not composed of bracts. Despite this, his key entry for *Lepeostegeres* is "capitulum with an involucre of decussate bracts" and the opposing couplet for *Cyne* is "capitulum with hood-shaped involucre in one piece." Botanically, an involucre is composed of bracts (modified leaves) and the operculum clearly is not. In his treatment of Philippine Loranthaceae, Danser (1935) continues this terminology as "inflorescence a capitulum of triads, involucre calyptrate, deciduous or irregularly dehiscent". Barlow (1993) did use the term involucre but added that it derives from the stem periderm. He also introduced the term operculum for this structure; however, later Barlow (1997) reverted to using "calyptra" with no mention of operculum:

There is no involucre of imbricate bracts subtending the entire inflorescence, as in some related genera, and the primary diagnostic character for the genus is the bubble-like or pellicle-like calyptra, developed from the stem periderm, which covers the young inflorescence. As the inflorescence expands the calyptra is displaced or irregularly split.

Given its varied usage, we feel that operculum (a structure that closes an aperture) or calyptra (a membranous, hoodlike structure that covers something, e.g., a moss capsule) are equivalent. To avoid using a term well established in bryology, we choose to use the term operculum. As stated by Barlow (1997), the primary diagnostic character for *Cyne* is the operculum. But this structure is apparently absent from *C. barcelonae* and its phylogenetic position as sister to *C. banahaensis* (Fig. 3) strongly indicates it is a member of this genus. A possible explanation may be found by examining the material that surrounds the base of the sessile capitulum (Figs. 2D, F). We interpret this material as corky periderm tissue, but here it does not form an operculum that is stretched with the developing flowers but simply remains as an unconsolidated mass at the base of the inflorescence.

Cyne banahaensis (Fig. 4) is the most thoroughly documented species in the genus as evidenced by more complete descriptions present in protologues. Despite this, basic information such as fruit color is lacking. *Cyne alternifolia* Danser, *C. capitulifera* Danser, and *Loranthus lagunensis* Merr. were combined into *C. banahaensis* by Barlow (1993) who noted that Danser (1935) was not able to generate a key separating these taxa. Further, he stated that they showed a continuous range of variation and that the combined species was not very polymorphic. Examination of available material shows that leaf size and shape is variable as is corolla color (Suppl. file 1). Accepting that these taxa are conspecific, a composite description that incorporates published information (from Barlow 1993, 1997; Danser 1935; Elmer 1911, and Merrill 1912, 1914), as well as features observed on living plants, is as follows:

Glabrous hemiparasitic epiphyte lacking epicortical runners. Young internodes terete, younger stem apical region slightly flattened, sometimes (in *C. capitulifera*) finely furfuraceous, older growth rugose with conspicuous lenticels, with large round scars of leaves and inflorescences, older nodes thickened. Leaves opposite, subopposite to alternate, petiole acuminate, 1–20 mm long (boundary separating petiole and blade indistinct), blade elliptic, obovate to oblong, 4–17 mm long × 1.5–10 mm wide, base cuneate or attenuate into petiole, apex obtuse or rounded, thinly or thickly coriaceous, margin entire, adaxial and abaxial surfaces opaque to somewhat shiny, green to olive green, penninerved (= pinnate), midrib not prominent adaxially, prominent and raised abaxially, brown (rufous), lateral nerves distinct or not distinct on both surfaces [herbarium specimens may differ from living tissue], veins generally invisible on both surfaces. Inflorescence a sessile capitulum, arising in leaf axils and sometimes adnate to adjacent lateral branch, leaving sunken, ovate, 10–12 mm long scars on branches, receptacle not elevated above surface of branch, inflorescence arising below a bubble-like operculum (derived from periderm) that expands during flower development, later upon

anthesis tearing and dehiscing circumscissally; flowers arranged in three pairs of decussate, sessile triads, bracts and bracteoles suborbicular, adpressed to calyculus / ovary, exterior whorl bracts 2 mm long \times 3 mm wide, interior whorl bracts 1.5 mm long and wide, exterior whorl bracteoles 1.5–2 mm long \times 1.5 mm wide, interior whorl bracteoles 1.5 mm long and wide. Ovary angular from pressure of adjacent ovaries, campanulate, 2–2.3 mm long \times 1.5–2 mm wide, calyculus limb margin irregularly lacerate, 0.1–0.2 mm high. Corolla in mature bud stage 13–20 mm long, weakly dilated at base, gradually tapering from 1/2 to 2/3 its length, and then cylindrical, apex obtuse, corolla lobes lanceolate, reflexed part 3–4 mm long, apex obtuse, subcucullate. Corolla color variable including yellow, orange, red, and purple. Field notes on one isotype of *Loranthus banahaensis* Elmer at NY (barcode 00285115) reads: “corolla at the base orange yellow, dull yellow above the middle, with dark purplish or nearly black tips”. Stamens 6, adnate to corolla lobes, anthers basifixed, sessile (no free part of filament). Style 17–20 mm long, articulated above the base, stigma obtuse, capitate. Fruit globose-ellipsoid, 8 mm long \times 5 mm wide, crowned by the thickened calyculus limb. Elmer’s field notes describe the seed as green with whitish costae.

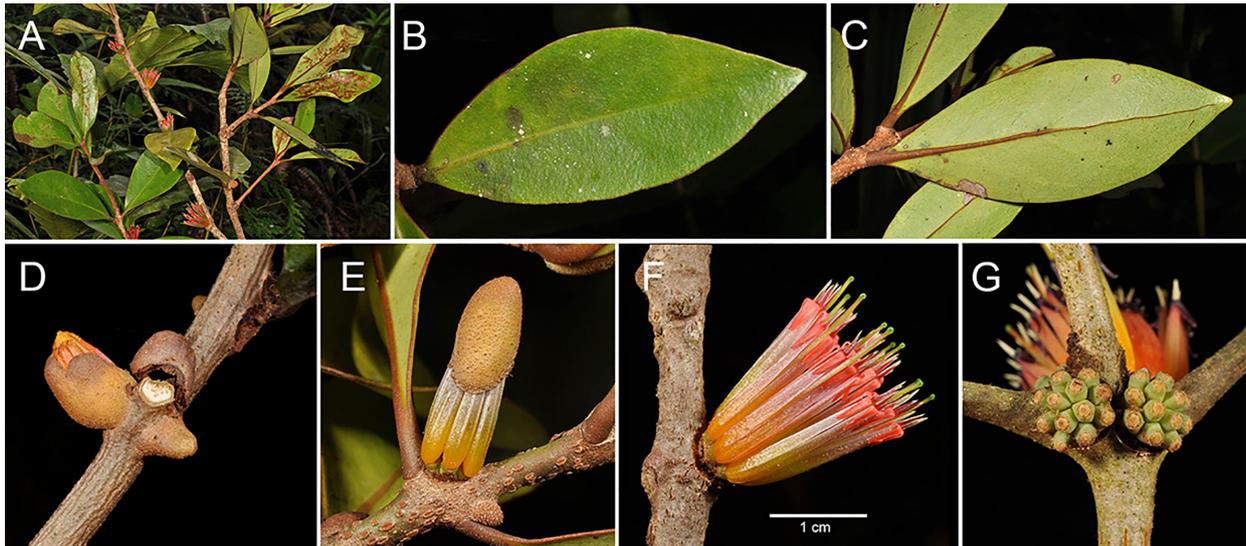


FIGURE 4. *Cyne banahaensis* from Dinagat Island. A. Habit of mistletoe in flower. B. Leaf, adaxial surface. C. Leaf abaxial surface. D. Young inflorescences still enclosed in operculum. E. Inflorescence losing the operculum. F. Inflorescence in full anthesis. G. Young infructescences. All photos by P. Pelsler.

Cyne quadriangula (Fig. 5) is known only from the type and when the protologue was written no flowers were seen. The holotype was likely destroyed in WWII and no isotypes are known to exist. For this reason, there are no historical herbarium specimens of this species to examine. Danser (1935) justified naming it as a new species given its distinctive shiny quadrangular stems and acuminate leaves. The specimen described here was photographed and collected by the second author on Bucas Grande Island, one of the Siargao Islands in Caraga Region of northeastern Mindanao. This is the same general locality as the holotype for the species, Ramos and Pascasio no. 35119 (M). The description, translated from Latin, from Danser (1935) is as follows: “Robust, completely glabrous. The internodes bearing adult leaves quadrangular, base slightly flattened, apex becoming slightly dilated and more flattened, leaf scars terete, 3 to 5 mm long, 3.5 to 4 mm thick at the base, almost twice as broad as the apex, bright and smooth. Leaves opposite, petiole more convex below than above, difficult to distinguish from lamina, 6 to 14 mm long, c. 3 mm wide in the middle, blade elliptic or oblong, often slightly obovate, 8 to 14 cm long, 3.5 to 5 cm broad, base rounded and contracted into the petiole or more attenuate, the apex obtuse becoming shortly acuminate, thinly leathery, almost chartaceous, both surfaces opaque, penninerved, midrib and lateral nerves thick and prominent, finer veins partly distinct. Inflorescences single in the axils of leaves, even in the older nodes growing from both sides of the leaf scars, involucre to 12 mm long and nearly equally wide. Open flowers not seen. Other things, as far as they are known, as in *C. banahaensis*. MINDANAO, Surigao Province, Bucas Grande Island, low altitude, *Bur. Sci.* 35119 Ramos and Pascasio (M) type, calyx green, petals chocolate color.”

The description of *C. quadriangula* from Bucas Grande (Fig. 5) is as follows: Glabrous hemiparasitic epiphyte lacking epicortical runners. Young internodes quadrangular, younger stem apical region dilated and flattened, older growth thickened. Leaves opposite or subopposite, petiole flat on top, rounded below, edges gradually acuminate into blade, 16.5–20 mm long, blade narrowly elliptic, 11–13 cm long \times 3.4–3.6 cm wide, base narrowly cuneate or

attenuate into petiole, apex narrowly acute, thinly coriaceous, margin entire, brown, adaxial and abaxial surfaces opaque, yellowish-green, penninerved, midrib prominent adaxially, abaxially more prominent, brown (ferruginous), lateral nerves distinct on both surfaces, veins indistinct on both surfaces. Inflorescence a sessile capitulum, arising in leaf axils, leaving sunken, ovate, 5–8 mm long scars on branches, inflorescence arising below an operculum 11.5–13 mm long × 9–10 mm wide; flowers arranged in two pairs of decussate, sessile triads, bracts and bracteoles ovate, adpressed to calyculus / ovary, exterior whorl bracts 1–1.5 mm long × 2–2.5 mm wide, interior whorl bracts 1–1.5 mm long × 1.5–2 mm wide, exterior whorl bracteoles 1–1.5 mm long × 1 mm wide, interior whorl bracteoles 1–1.2 mm long × 0.8–1 mm wide. Ovary slightly angular from pressure of adjacent ovaries, cylindrical, 1.5–2 mm long × 2–2.2 mm wide, calyculus limb margin subentire, 0.1 mm high. Corolla in mature bud stage 20–25 mm long, weakly dilated at base and then basically cylindrical, slightly curved, apex acute, corolla tube ca. 5–6 mm long, lobes 1.5 mm wide where they are no longer connate, reflexed part of lobe 4–5 mm long, apex obtuse, subcucullate. Corolla color orange darkening upon maturity to dark red, lobe tips purple on exterior surface. Stamens 6, adnate to corolla lobes, anthers basifixed, sessile, narrowly triangular, 3 mm long with continuous locules. Style 23–25 mm long, the same diameter throughout, articulated just above the base, stigma subcapitate, not much wider than style. Fruit globose, 6 mm long and wide, red, calyculus limb very short.

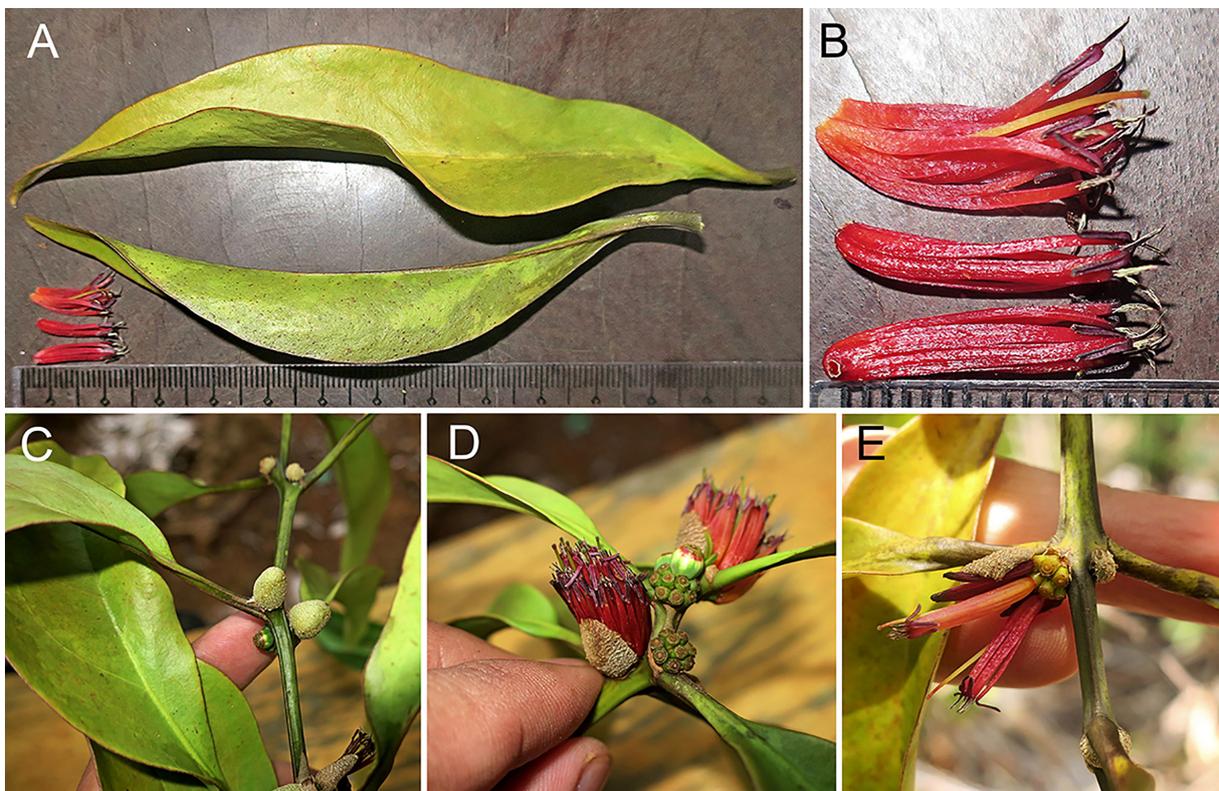


FIGURE 5. *Cyne quadriangula*, from Bucas Grande, one of the Siargao Islands. A. leaves and corollas. B. Corollas. Note the sessile anthers. C. Stem with young inflorescences, still covered by opercula. Note the quadrangular stems. D. Inflorescences emerging from opercula. E. Older inflorescence beginning to form fruits. All photos by M. G. Q. Rule.

The flower color in the protologue was indicated as chocolate (brown?), but given no flowers were seen by Danser and that this color would be very unusual for Loranthaceae, such information is suspect. As shown in Fig. 5, flower color darkens upon maturity, thus this description could have been made from older, senescent flowers.

As shown by the above two descriptions, the mistletoe collected on Bucas Grande conforms well morphologically to the description in Danser (1935). Moreover, the new collection was made from the same island and general region in the Philippines. Database searches of all major herbaria failed to locate any specimens of *Cyne quadriangula*, confirming the statement by Barlow (1997) who said “The holotype (PNH) is apparently not extant, and no isotypes or other specimens referable to this species name have been seen. Whilst the species must be treated as doubtful in this conspectus, the characters noted by Danser (1935) appear to indicate a distinct species.” According to Article 9.13 of the Shenzhen Code (Turland *et al.*, 2018), it is appropriate to designate a neotype because only the original material that constituted the holotype no longer exists.

Cyne quadriangula Danser, Philipp. J. Sci. 58: 38 (1935)

Neotype (designated here):—PHILIPPINES, Region XIII (Caraga), Surigao del Norte Province, Bucas Grande Island, Municipality of Socorro, Brgy. Honrado, 17 masl, 9°41.182'N, 125°55.305'E, 22 June 2019, *M. G. Q. Rule MGR19-001*, (PNH!, FEUH!, HNUL!). Digital images at: <http://www.phytoimages.siu.edu/>.

The protologues of types and later descriptions of the remaining *Cyne* species (*C. baetorta*, *C. monotrias*, *C. papuana*, and *C. perfoliata*) were examined and the character states added to the matrix in Suppl. file 1. Unfortunately, little additional information on these species has been recorded since they were first described.

Cyne baetorta is known from a single fruiting collection (Coode 5651, L) from Mindoro, thus no flowers are available. In 1989 Barlow annotated the specimen as *Decaisnina baetorta* Barlow. Given that this name was never published, it must be considered a *nomen nudum*. Barlow (1993, 1997) was able to discern from this single specimen the basic inflorescence structure composed of a short raceme of 2–3 pairs of pedunculate triads where the central flower is sessile and the laterals on very short (0.5 mm) pedicels. Barlow (1997) continued to apply the term involucre to this species: “inflorescences few in hollows at the nodes, arising through a periderm layer which remains as a basal involucre.” Examination of the holotype shows the large, oval scars left by old, dehisced inflorescences. At one node an infructescence with one fruit can be seen. The structure of the inflorescence, composed of two pairs of triads cannot be discerned, only some indistinct debris. With both the description and the holotype, the existence of a “basal involucre” remains unclear. Although no bubble-like operculum is present on the holotype, the oval scars provide some evidence that they once existed. Finally, the statement in Barlow (1993) “leafy shoots apparently arising from an involucre-like periderm layer” is confusing given that inflorescences, not vegetative shoots, arise in this manner in *Cyne*.

Cyne monotrias is also known only from the holotype (P. J. Eyma 2655, L) collected in 1938 on Seram (formerly Ceram), Maluku (Moluccas) islands, Indonesia. This specimen was annotated by Barlow in 1989 as *Decaisnina cynoides* Barlow, but that name does not appear on any of the plant name indices (IPNI, WFO, etc.) nor is it listed as a synonym in Barlow (1993, 1997). For this reason, the name must be considered a *nomen nudum*. The photograph of the holotype at L shows stems with a few leaves and no reproductive material. As the name implies, the inflorescence is usually composed of one sessile triad (of a pair, the other abortive) on a short (1 mm peduncle). No information on flowers exists.

Cyne papuana was first described as a species of *Amylothea* by Danser (1938) based on the type specimen collected by Carr (no. 15502, BM) in 1936 from southeastern New Guinea. Type material of this species is present at B, BM, HUH, and K, but no additional specimens have been made since. Like *C. barcelonae* and *C. perfoliata*, the leaves are sessile but unlike them not connate at the base. Like *C. baetorta* it has a relatively well-developed inflorescence axis (2–4 mm long) with pedunculate triads where the flowers are very shortly pedicellate. This description, taken from Barlow (1993) differs from Danser (1938) who indicates subsessile triads with all the flowers sessile. It is curious that Barlow (1993, 1997) provides very few details about the flowers in this species, despite more information provided in Danser (1938). Moreover, mature floral buds are present on all the photographs seen of the specimens cited above. Measurements from these specimens show that the mature corolla length averages 18.5 mm, thus agreeing with Danser (1938) who indicated up to 20 mm vs. Barlow (1997) who indicated ca. 30 mm. After examining the available material, Barlow (1993) questioned the existence of an operculum in this species, but the presence of erose flaps of cortical tissue along the margins of the stem hollows suggested to him that an operculum was present. This could also indicate either that the operculum does not exist or that it does not dehisce as a unit but tears irregularly as the flowers mature.

Cyne perfoliata was first named as *Tetradyas perfoliata* Danser by Danser (1931) as a new genus and species based on a collection in 1885 by Forbes (no. 299, holotype BM, isotype MEL) from southeastern Papua New Guinea. This taxon was later collected by Carr (no. 14027) in 1935. No other collections of this species have been made, despite attempts to locate the population by Barlow in 1965 and 1970. Only immature flowers and fruits can be seen on the two specimens, thus only general inflorescence features were described in the protologue by Danser (1931). Danser's misinterpretations of the connate leaves as floral bracts and the vegetative internode as a “peduncle” was corrected by Barlow (1974) such that now it appears the inflorescence is composed of a short axis with nearly sessile flowers formed in dyads and triads. The floral peduncles apparently elongate to 1 mm and the pedicels to 1.5 mm in fruit.

Conspectus of the genus *Cyne*

The presence of an operculum was considered a diagnostic character for the genus *Cyne* by Barlow (1997). With the addition of *Cyne barcelonae*, this character now applies only to some of the species. Aside from this character, there are few features that differentiate *Cyne* from the closely related genus *Decaisnina*. As pointed out by Barlow (1997), both genera have racemes of triads, which can also be described as conflorescences or thyrses (Nickrent *et al.* 2019). For *Decaisnina*, the inflorescences are well-developed and the weakly decussate triads are usually secund. For *Cyne*, these thyrses are highly contracted, sometimes to the point where the triad peduncles and lateral flower pedicels are absent leaving the flowers sessile in a capitulate arrangement (*C. barcelonae*, *C. perfoliata*, *C. banahaensis*, *C. quadriangula*). That these flowers in capitula represent an endpoint of axis contraction is an interpretation based on an assumed morphological reduction series. This hypothesis might best be tested using developmental and anatomical data.

Barlow (1997) indicates that epicortical runners are present in the genus; however, none of his individual species descriptions mention this feature. Although most herbarium specimens did not include basal portions of the plant, no epicortical roots were seen nor did labels indicate they were present. Three species, *Cyne banahaensis*, *C. barcelonae* and *C. quadriangula* have been thoroughly documented photographically and all species show only single, quite bulbous haustorial connections (holdfast according to Calvin and Wilson 2006) to the host. Although other species have not been so examined, we feel it is prudent to not indicate the presence of epicortical roots.

Given the information presented above, a revised description of the genus and key to the species of *Cyne* are provided:

Aerial parasites (mistletoes) with swollen holdfasts. Younger internodes terete, weakly angular or quadrangular (*C. quadriangula*); older nodes thickened or not; leaves opposite or subopposite, petiolate or sessile; lower margins of leaf pairs connate or not; midrib prominent adaxially (*C. quadriangula*) or not; lateral veins palmate (*C. barcelonae*) or pinnate (penninerved). Inflorescences terminal, in leaf axils, or from depressions in older nodes, developing beneath a corky operculum (calyptra) that expands and splits irregularly or dehisces in one piece upon anthesis; operculum absent in *C. barcelonae* but the sessile capitulum arises from unconsolidated corky periderm tissue; inflorescence of 1-3 decussate pairs of triads (rarely dyads); triad peduncles and floral pedicels present or absent, sometimes enlarging only in fruit; central flower of triad subtended by a bract and each lateral flower by a bracteole; corolla 6-merous, actinomorphic, 17-30 mm long in mature bud, petals sympetalous only in a short (2-6 mm) tube at the base, otherwise choripetalous, base inflated or not, apex obtuse or acute, lobes reflexed; anthers basifixed, sessile or filaments present (*C. barcelonae*); style simple, articulate above the base, projecting beyond the reflexed corolla lobes; stigma capitulate. Fruits globose, ellipsoid or obovoid, orange or red (in species recorded), calyculus and style base often persistent, containing a single viscid seed.

1. Leaves (at least the upper pair) connate along margins
2. Leaves (upper) obovate, leaves (lower) elliptic, lamina 3.4-5.3 cm long, lateral nerves palmate, inflorescence operculum absent, mature bud corolla tube base inflated. Philippines, Bucas Grande and Dinagat Islands *C. barcelonae*
2. Leaves ovate, lamina 7.5-12 cm long, lateral nerves pinnate, inflorescence operculum present, mature bud corolla tube base not inflated. Papua New Guinea *C. perfoliata*
1. Leaves not connate along margins
3. Leaves sessile, base rounded, corolla base not inflated. Papua New Guinea *C. papuana*
3. Leaves petiolate, base cuneate or attenuate, corolla base weakly inflated. Philippines and Indonesia
4. Older nodes thickened, leaves generally longer (4-17 cm), lateral nerves adaxially distinct, inflorescence a sessile head, triad peduncle absent
5. Young internodes terete, lamina apex obtuse or rounded, lateral nerves abaxially indistinct, corolla tube less than 5 mm long. Philippines, Luzon, Samar, and Mindanao Islands *C. banahaensis*
5. Young internodes quadrangular, lamina apex narrowly acute, lateral nerves abaxially distinct, corolla tube more than 5 mm long. Philippines, Bucas Grande Island *C. quadriangula*
4. Older nodes not thickened, leaves generally shorter (4-7 cm), lateral nerves adaxially indistinct, inflorescence a contracted raceme, triad peduncle present
6. Petiole 4-7 mm long, leaf lamina larger (5-7 X 3.5-5 cm), triad pairs 2-3. Philippines, Mindoro Island *C. baetorta*
6. Petiole 8-12 mm long, leaf lamina smaller (4.5-6 X 2.5-3 cm), triad pairs 1-2. Indonesia, Maluku Islands *C. monotrias*

Conclusions

It appears that the presence of an operculum cannot now be used as a diagnostic feature of all *Cyne* species. Despite this, corky periderm tissue subtending the inflorescences, whether it enlarges upon flower maturation or not, may

be present among all the species. The well-documented floral features of *C. barcelonae*, *C. banahaensis*, and *C. quadriangula* reported here expand the range of morphological character states known for the genus. It is clear that for the remaining species much more morphological information, obtained from living material, is required to fully understand interspecific relationships and to confirm placement within *Cyne* (e.g. *C. monotriasis*). Although it is encouraging that new populations of the three Philippine *Cyne* species have been discovered, continuing environmental degradation, from both natural and anthropogenic causes, decreases the prospect of rediscovering and documenting the exceptionally rare *C. baetorta*, *C. monotriasis*, *C. papuana*, and *C. perfoliata*. Because of their complex life histories and existence at higher trophic levels, these mistletoes are extremely sensitive to environmental perturbation, thus their conservation should be of high priority. In fact, the presence of such rare mistletoes could be used to monitor overall ecosystem health.

Data Availability

Supplementary files associated with this paper are as follows:

- S1:—The morphological character matrix (74 chrs.) used to compare six previously recognized *Cyne* species to the new species (Excel file)
- S2:—Full scientific names for the 61 Loranthaceae taxa sampled for phylogenetic analysis, as well as NCBI Genbank numbers for their rDNA cistrons (Excel file)
- S3:—Multiple sequence alignment of the rDNA cistron for the 61 Loranthaceae taxa (fasta file)
- S4:—The Maximum Likelihood tree obtained from analysis of the alignment in file S3 (pdf file)

Acknowledgements

We acknowledge the Department of Environment and Natural Resources (DENR) Region XIII at Ambago, Butuan City and SIPLAS Protected Area Management Board for the issuance of permits to collect and transport the specimens; and the local government unit of Socorro for allowing the authors to conduct the study in their jurisdictional areas. We thank Meljan Demetillo from Caraga State University for providing information on the distribution of *C. barcelonae* populations on the Dinagat Islands. We would also like to thank Rudolph Valentino A. Docot of FEUH for his assistance in managing the vouchered specimens. Thanks go to Dr. Pieter Pelser who provided a silica gel sample of *Cyne banahaensis* and to Dr. Kurt Neubig for allowing laboratory access. The professional services provide by Dr. Alvaro Hernandez and his skilled staff at the Roy J. Carver Biotechnology Center are gratefully acknowledged. Finally, the manuscript was greatly improved by the comments and suggestions of an anonymous reviewer and Dr. Marcos Caraballo.

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