





Erythrina L. (Phaseoleae, Papilionoideae, Leguminosae) of Brazil: an updated nomenclatural treatment with notes on etymology and vernacular names

Ramon Guedes-Oliveira¹, Ana Paula Fortuna-Perez², Leandro Cardoso Pederneiras³,
Vidal de Freitas Mansano³

- 1 Programa de Pós-graduação em Botânica, Escola Nacional de Botânica Tropical (ENBT), Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (JBRJ), 22460-036, Horto, Rio de Janeiro, State of Rio de Janeiro, Brazil
- 2 Departamento de Biodiversidade e Bioestatística, Instituto de Biociências de Botucatu, (IBB), Universidade Estadual Paulista (UNESP), 18618–970, Botucatu, State of São Paulo, Brazil
- 3 Diretoria de Pesquisas (Dipeq), Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (JBRJ), 22460-030, Jardim Botânico, Rio de Janeiro, State of Rio de Janeiro, Brazil

Corresponding author: Ramon Guedes-Oliveira (guedesoliveira.ramon@gmail.com)

Abstract

Erythrina L. is a genus that comprises ca. 120 to 130 species distributed throughout the tropics and subtropics of the world. Linnaeus established the genus in *Genera Plantarum* (1737) and the first binomial name given to a Brazilian *Erythrina* was *E. crista-galli* L., described by himself in *Mantissa Plantarum* (1767). Vellozo proposed in *Florae Fluminensis* (1790–1881) the first treatment of the genus in Brazil, where he treated three species from the states of Rio de Janeiro and São Paulo. Martins and Tozzi proposed the most recent treatment in 2018, where the authors recognized 11 valid names and presented three new synonyms. Despite extensive efforts already made in the genus, previous works did not treat all names related to the valid ones for Brazilian *Erythrina*. The present work is the most comprehensive and up-to-date nomenclatural treatment for the genus in Brazil, covering all 84 related names found on digital nomenclatural databases. Here we analyze 64 protologues, update typification statuses, propose five new synonyms, 13 new lectotypes (11 first-step, two second-step) and one neotype, linking all protologues and type specimens with their corresponding available digital sources, and make additional notes on etymology and vernacular names.

Key words: Fabaceae, legumes, Linnaeus, nomenclature, papilionoid legume, South America, Vellozo

Introduction

Erythrina L. (Phaseoleae, Papilionoideae, Leguminosae) is a genus that comprises ca. 120 to 130 species (Du Puy et al. 2002; Schrire 2005) distributed throughout the tropics and subtropics of the world in a wide range of habitats. The species can be found in arid tropical deserts or lowland alluvial vegetations to montane forests beyond 3 000 m of altitude, varying from rhizomatous perennial subshrubs to trees measuring more than 40 m high (Neill 1988).



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Linnaeus established the genus in *Genera Plantarum* (Linnaeus 1737), expanded later in *Species Plantarum* (Linnaeus 1753), where he described three species (*E. herbacea* L., *E. corallodendrum* L., *E. piscipula* L.) and two varieties (*E. corallodendrum* var. *occidentalis* L., *E. corallodendrum* var. *orientalis* L.) based on plants mentioned earlier by other authors before the establishment of Linnean binomials. The type species of the genus was designated by Walpers (1853) as *E. herbacea*. The first binomial name given to a Brazilian *Erythrina* was *E. crista-galli* L., described by Linnaeus in *Mantissa Plantarum* (Linnaeus 1767).

The first treatment of the genus in Brazil was proposed by Vellozo's *Florae Fluminensis*, which was done in 1790 but the text was only partially published in 1829, the plates in 1831, and the complete text in 1881 (Vellozo 1829, 1831, 1881; Carauta 1969, 1973). In this work, the author treated three species from the states of Rio de Janeiro and São Paulo: *E. corallodendrum* (which was considered to be a mention of *E. corallodendrum* L. rather than a new publication of this name), *E. verna* Vell., and *E. mediterranea* Vell.

In 1859, Benthams proposed a treatment of Brazilian *Erythrina* in Martius' *Flora Brasiliensis*, where he published two new names (*E. falcata* Benth. and *E. mulungu* Mart. ex Benth.), mentioned five others already validly published (*E. corallodendrum* L. [misspelled as *corallodendron*], *E. crista-galli* L., *E. glauca* Willd., *E. reticulata* C.Presl., *E. velutina* Willd.), and one as a doubtful species (*E. nervosa* DC.).

The subsequent treatment of Brazilian *Erythrina* was proposed by Krukoff (1938), where he published two new names and a form (*E. amazonica* Krukoff, *E. similis* Krukoff and *E. velutina* f. *aurantiaca* (Ridl.) Krukoff), mentioned ten others already validly published (*E. crista-galli*, *E. dominguezii* Hassl., *E. falcata*, *E. flammea* Herzog, *E. glauca* Willd., *E. poeppigiana* (Walp.) O.F.Cook, *E. speciosa* Andrews, *E. ulei* Harms, *E. velutina* Willd., *E. verna*), and three other names as doubtful and unplaced (*E. mediterranea*, *E. nervosa*, *E. secundiflora* Brot.). Krukoff reduced *E. mulungu* and *E. reticulata* to synonyms of *E. verna* and *E. speciosa*, respectively. *E. corallodendrum* was treated as a species that occurs only in Jamaica and Haiti, not Brazil as Benthams (1859) believed.

The most comprehensive revision of the genus to this day was proposed by Krukoff and Barneby (1974), who recognized 11 valid names for Brazilian *Erythrina* (*E. amazonica*, *E. crista-galli*, *E. dominguezii*, *E. falcata*, *E. fusca* Lour., *E. poeppigiana*, *E. similis*, *E. speciosa*, *E. ulei*, *E. velutina*, *E. verna*), published a new hybrid name (*E. × fluminensis* Barneby & Krukoff), maintained two names as doubtful and unplaced (*E. mediterranea*, *E. secundiflora*), and excluded *E. nervosa* as a synonym of *Callichlamys latifolia* (A.Rich) K.Schum. (Bignoniaceae). The authors also considered the previously accepted *E. glauca* as synonym of *E. fusca*, and *E. flammea* as synonym of *E. verna*.

The most recent treatment of Brazilian *Erythrina* was proposed by Martins (2014) in a PhD thesis. In 2015, the author published a taxonomic treatment of the genus in *Flora e Funga do Brasil* (Martins 2023). The nomenclatural treatment was published later in Martins and Tozzi (2018), where the authors also recognized 11 valid names (*E. amazonica*, *E. crista-galli*, *E. falcata*, *E. fusca*, *E. mulungu*, *E. poeppigiana*, *E. similis*, *E. speciosa*, *E. ulei*, *E. velutina*, *E. verna*), designated 12 lectotypes and one epitype, and proposed three new synonyms: the previously accepted *E. dominguezii* as *E. mulungu* (which had

been considered a synonym of *E. verna* since Krukoff [1938]), *E. speciosa* var. *rosea* N.F.Mattos as *E. speciosa*, and *E. velutina* f. *aurantiaca* as *E. velutina*.

However, Martins and Tozzi (2018) did not cover all names related to Brazilian *Erythrina* species. We here present the most comprehensive and up-to-date nomenclatural treatment for Brazilian *Erythrina*, covering all related names found on digital nomenclatural databases. We update typification statuses, propose new synonyms, designate lectotypes and neotypes, linking all protologues and type specimens with its corresponding digital sources when available. We also provide additional notes on etymology and vernacular names for each accepted species.

Methods

Scientific names of *Erythrina* L. were collected from the following digital databases: Global Biodiversity Information Facility (GBIF), International Legume Database & Information Service (ILDIS), International Plant Names Index (IPNI), Legume Data Portal, Plants of the World Online, The Plant List, w3Tropicos, World Flora Online. Original protologues were accessed through the following digital libraries and databases: Biblioteca Digital Real Jardín Botánico, Biblioteca Nacional Digital Brasil, Bielefeld University Library, Biodiversity Heritage Library, Flora Brasiliensis CRIA, Google Books, Google Scholar, Hathi Trust Digital Library, JSTOR Global Plants, Naturalis Biodiversity Center Library, in addition to the more recent articles published in peer-reviewed journals. The authorship and publication dates of protologues were confirmed through the Taxonomic Literature II (TL-2) and the Hunt Institute for Botanical Documentation (BPH) digital databases. The type specimens were analyzed in person only at the herbaria R and RB, the rest of them through digitalized images from the following herbaria: A, B, BAF, BM, BR, E, F, G, GH, HBG, HUEFS, IAN, K, L, LIL, LINN, LP, M, MEL, MG, MO, MPU, NAP, NY, P, S, SI, SP, TCD, U, US, VEN, W and Z, the acronyms following Thiers (continuously updated). Herbarium data were collected through the following digital databases and virtual herbaria: BioPortal, Conservatoire et Jardin botaniques Genève, Field Museum of Natural History, Harvard University Herbaria, Herbarium Berolinense, JABOT, JACQ, JSTOR Global Plants, Kew Royal Botanic Gardens, Meise Botanic Garden, Muséum National d'Histoire Naturelle, Reflora, Smithsonian National Museum of Natural History, speciesLink, Swedish Museum of Natural History, The Natural History Museum, The New York Botanical Garden, w3Tropicos, Zürich Herbaria. The validity of typifications was confirmed through the International Code of Nomenclature for algae, fungi, and plants (ICN) (Turland et al. 2018). Etymology information was based on the original protologues, and vernacular names on herbarium specimens' labels and published studies of the genus.

Results and discussion

From the nomenclatural search in digital databases, 84 names published in a total of 64 protologues were found and analyzed (Suppl. material 1). The nomenclatural revision resulted in the maintenance of 57 synonyms and confirmed the 11 currently valid names for Brazilian *Erythrina*. Here we propose five new synonyms, designate 11 first-step and two second-step lectotypes,

and one neotype. Seven names remained as doubtful synonyms for several reasons explained in the species' commentaries: *E. crista-galli* L. var. *corallina* N.F.Mattos, *E. crista-galli* L. var. *laurifolia* Tod., *E. crista-galli* L. var. *speciosa* Tod., *E. laurifolia* Tod. and *E. speciosa* Tod. as potential synonyms of *E. crista-galli* L.; and *E. atrosanguinea* Ridl. and *E. picta* Blanco as potential synonyms of *E. fusca* Lour. These two accepted species represent the Brazilian *Erythrina* with most names given throughout the years, from 1741 to 2010, being *E. crista-galli* one of the most cultivated *Erythrina* species around the world since the 18th century, and *E. fusca* the most geographically widespread species in the genus (Krukoff and Barneby 1974). Moreover, five names remained unplaced (*E. indica* sensu R.Vig., *E. mediterranea* Vell., *E. moelebei* Vieill. ex Guillaumin & Beauvis., *E. secundiflora* Brot., *E. velutina* Jacq.) and eight were excluded (*Coral-lodendron nervosum* (DC.) Kuntze, *E. adansonii* hort. ex Colla, *E. argentea* Blume ex Miq., *E. compacta* W.Bull., *E. compacta* W.Bull. ex K.Koch, *E. corallodendrum* Vell., *E. fusca* Lour. var. *inermis* Pulle, *E. nervosa* DC.) for several reasons explained in the corresponding section.

Up until the time of this publication, we were unable to access six of the original protologues: i) Index seminum horti regii botanici panormitani, regarding the names *E. laurifolia* and *E. speciosa* by Todaro (1860); ii) Nuovi generi e nuove specie di piante coltivate nel real Orto botanico di Palermo vol. 3, regarding *E. pulcherrima* by Todaro (1861); iii) Catálogo descriptivo de las maderas que se exhibieron en la exposición internacional de agricultura de 1910 in Anales de la Sociedad Rural Argentina, regarding *E. chacoënsis* and *E. crista-galli* var. *inermis* by Spegazzini and Girola (1910); iv) Archives de botanique, mémoires vol. 6, regarding *E. indica* sensu R. Viguier; v) Loefgrenia; Comunicações Avulsas de Botânica vol. 21(1), regarding *E. crista-galli* var. *corallina* by Mattos (1967); and vi) Loefgrenia; Comunicações Avulsas de Botânica vol. 71(3), regarding *E. speciosa* var. *rosea* by Mattos (1977).

Nomenclatural treatment

***Erythrina* L., Gen. Pl.: 216. 1737; Sp. Pl. 2: 706. 1753.**

Generitype. (designated by Walpers 1853, pg. 145): *Erythrina herbacea* L., Sp. Pl. 2: 706. 1753.

1. *Erythrina amazonica* Krukoff, Brittonia 3: 270. 1938.

Fig. 1

Type material. BRAZIL. Amazonas: Basin of Rio Jurua; Near mouth of Rio Embira (tributary of Rio Tarauaca), 8 June 1933, *Krukoff* 4707 (holotype: NY [NY00007986, sheet I; NY00007987, sheet II]; isotypes: A [A00066284], G [G00365285, two sheets], K [K000502766, K000502767]).

Notes. There are no nomenclature issues with *E. amazonica*, as the name was validly published and its type specimen was correctly cited (Fig. 1). However, all databases and studies of the genus state that the protologue was published in 1939. Still, according to the journal's website, the publication date is October 1938.

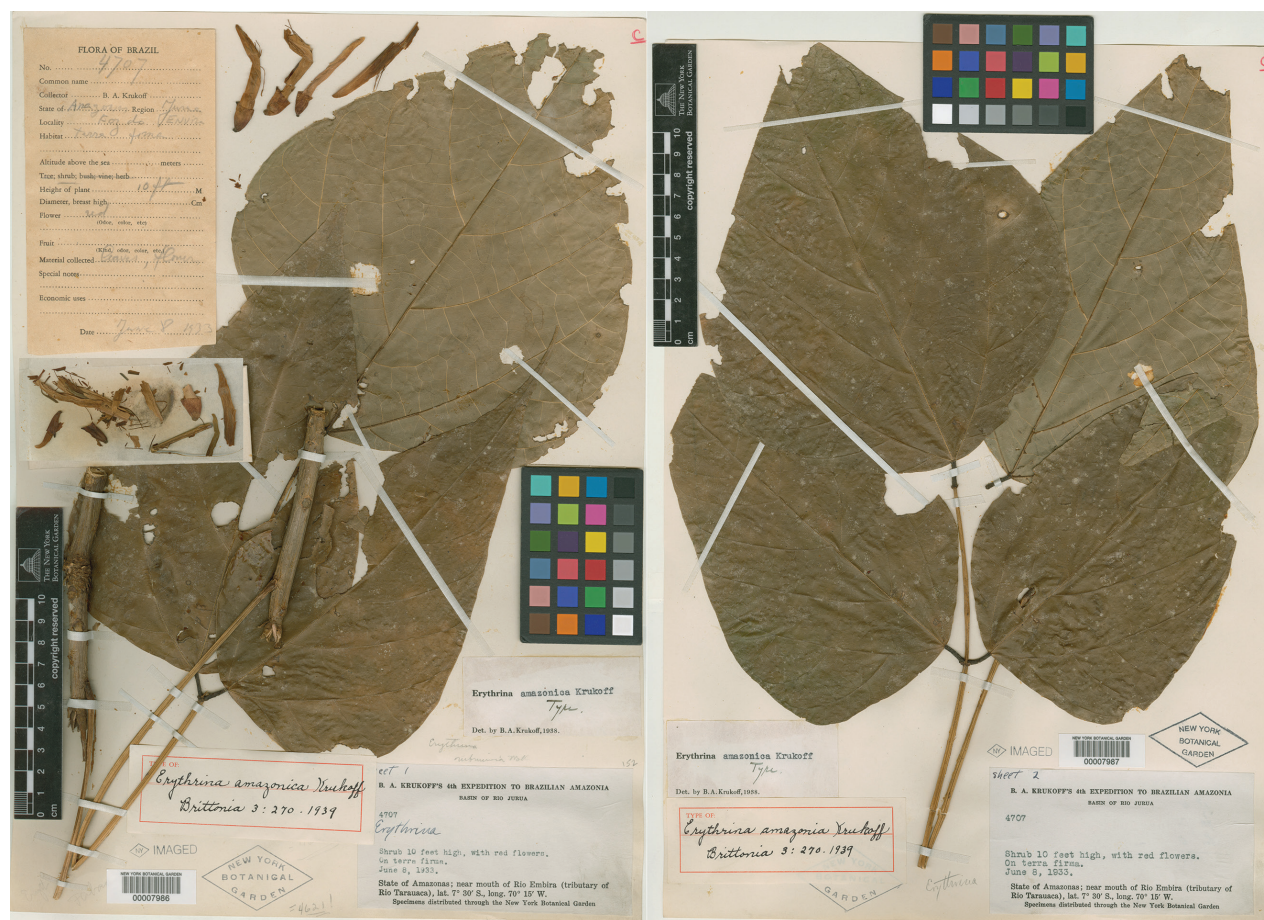


Figure 1. Holotype of *Erythrina amazonica* Krukoff (1938: 270). Source: William and Lynda Steere Herbarium (NY) – The New York Botanical Garden via C. V. Starr Virtual Herbarium, NY00007986, NY00007987.

Etymology. The specific epithet “amazonica” is derived from Latin, meaning “from the Amazon”, and it was chosen due to the species being native to the Amazon Forest domain.

Vernacular names. According to herbaria labels, *E. amazonica* is generally known as “mulungu” in Brazil, and also “açacurana” (and spelling variations) or “mulungu-de-espinho” in the state of **Maranhão**, and “açacurana” (and spelling variations) or “tento” in **Pará**.

2. *Erythrina crista-galli* L., Mant. Pl.: 99. 1767.

Fig. 2

- ≡ *Micropteryx crista-galli* (L.) Walp., in Duchassaing and Walpers, *Linnaea* 23(=7): 740. 1851.
- ≡ *Corallodendron crista-galli* (L.) Kuntze, *Revis. Gen. Pl.* 1: 172. 1891.
- = *Erythrina laurifolia* Jacq., *Observ. Bot.* 3: 1. 1768. Type: Argentina. s.loc., ex hort., s.d., s.leg., s.n. (lectotype, designated by Lozano and Zapater 2010, pg. 181: illustration in Jacquin 1768, tab. 51). (1)
- = *Erythrina graefferi* hort. ex Tineo, *Cat. Pl. Hort. Panorm.*: 278. 1827. Type: Italy. Campania: “ex H. R. Cas. [Parco Reale – Reggia di Caserta]”, ex hort., s.d., *Gussone s.n.* (neotype, designated by Del Guacchio et al. 2019, pg. 119: NAP [image seen]). (2)

- = *Erythrina fasciculata* Benth., Linnaea 22(=6): 517. 1849. Type: Brazil. Minas Gerais: "Ad Caldas", [10 February 1846?], Regnell 1.73 (lectotype, designated by Lozano and Zapater 2010, pg. 183: K [K000674145, sheet I; K000930947, sheet II]; isolectotypes: K [K000930957], MEL [MEL77238], NY [NY01058578], P [P02934611], US [US02338870]). Residual syntype: Brazil. Goiás: "ad Fazenda do Salido ad Rios", s.d., Pohl 763, BR (BR0000013057763), K (K000930946), M (M0240562, M0240563), NY (NY00007993), W (W0027158, W0027159). (3)
- = *Erythrina pulcherrima* Tod., Nuov. Gen. Sp. 3: 70. 1861; Ann. Sci. Nat., Bot. 4(20): 307. 1863. Type: Italy. Sicily: "Jamdudum in horto panormitano [Orto Botanico di Palermo] culta et ut videtur ex Aegypto in Siciliam advecta", ex hort., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 398: illustration in Todaro 1876, tab. XI). (4)
- = *Erythrina crista-galli* var. *hasskarlii* Backer, Voorl. Schoolfl. Java: 87. 1908. Type: Indonesia. West Java: "Cult. in Hort. Bog. [Kebun Raya Bogor]", ex hort., [1904?], s.leg., s.n. (lectotype, designated here: L [L.1951408]; isolectotypes: L [L.1951407, L.1951409]). (5)
- = *Erythrina crista-galli* var. *leucochlora* Lombardo, Flora arborea y arborescente del Uruguay: 69. 1964. Type: Uruguay. Treinta y Tres: "a orillas del río Cebol-latí en "La charqueada"", s.d., s.leg., s.n. (lectotype, designated here: illustration in Lombardo 1964, tab. 66 [as *E. cristagalli*]). (6)
- = *Erythrina crista-galli* var. *longiflora* Zapater & Lozano, in Lozano and Zapater, Darwiniana 48(2): 185. 2010. Type: Argentina. Salta: "Dpto. Gral. Güemes, ruta 9 en autopista de acceso a Salta, al frente de Usina Termo Andes", 10 May 2008, Zapater 2748b (holotype: SI [SI022986]; isotype: MCNS [n.v.]). syn. nov. (7)

Type material. BRAZIL. s.loc., s.d., *Vandelli* s.n. (lectotype, designated by Howard 1988, pg. 488: LINN [LINN-HL888-4]).

Notes. The first known name for the species was published in Linnaeus (1767), who described it from a specimen collected by Vandelli in Brazil. Yet, he did not mention any collection number nor cite any herbarium. Krukoff and Barneby (1974) accessed an exsiccata from the herbarium LINN consisting of a drawing with the inscription "Vandelli" and a single flower that undoubtedly represents the species, considering this to be the original collection. However, this citation cannot be considered a lectotypification of the name, as the authors did not mention it as the type collection. In Flora of the Lesser Antilles, Howard (1988) correctly designated the LINN collection as the type specimen (Fig. 2). Walpers (1851, not 1850) published *Micropteryx* mentioning *E. crista-galli* as a synonym of *M. crista-galli*, but the genus was later synonymized into *Erythrina* in Engler and Prantl (1894). Kuntze (1891) published *Corallodendron* mentioning *E. crista-galli* as a synonym of *C. crista-galli*, but the genus was also synonymized under *Erythrina* in Engler and Prantl (1894).

- (1) Jacquin (1768) published *E. laurifolia* with an illustration of a specimen from a botanical garden in Rome that is morphologically identical to *E. crista-galli*. Lozano and Zapater (2010) correctly designated this illustration as the lectotype, and the name has been synonymized under *E. crista-galli* since Lamarck (1786).



Figure 2. Lectotype of *Erythrina crista-galli* L. (1767: 99), designated by Howard (1988: 488). Source: Linnean Society of London Herbarium (LINN) via JSTOR Global Plants, LINN-HL888-4.

- (2) Tineo (1827) published *E. grafferi*, a name used by gardeners at the Orto Botanico di Palermo (Italy), with a short description resembling *E. crista-galli*. Krukoff and Barneby (1974) doubted that it could represent *E. speciosa* Lamb. ex Andrews, but Del Guacchio et al. (2019) investigated its origin, confirmed its synonymy under *E. crista-galli* and correctly designated a neotype for the name.

- (3) Benthham (1849) published *E. fasciculata* from Brazil, mentioning two collections that can be considered syntypes of the name, one from the state of Minas Gerais (Regnell 1.73) and one from Goiás (Pohl 763). Krukoff and Barneby (1974) recognized those syntypes but did not designate a lectotype, which was then correctly designated by Lozano and Zapater (2010) as the collection from Regnell in herbarium K. Additional material: P (P02934612, photo of K000674145; P02934614, photo of W0027159).
- (4) Todaro (1861) published *E. pulcherrima* based on a cultivated specimen at the Orto Botanico di Palermo (Italy). The original protologue could not be found online, but later publications by himself (Todaro 1863, 1876) also cited this name, including a well-made illustration in 1876 that even mentions the similarity with *E. crista-galli*. Martins and Tozzi (2018) correctly designated his illustration in 1876 as the lectotype, but wrongly considered this publication as the protologue of the name, which is the publication in 1861.
- (5) Backer (1908) published the variety *E. crista-galli* var. *hasskarlii* with a short description from cultivated plants on Java Island (Indonesia), but did not assign any type specimen. Three exsiccatae of a plant cultivated in the “Hortus Bogoriensis” [Kebun Raya Bogor] (Java) were found in herbarium L, with the inscription “*Erythrina crista-galli* Linn. var. *hasskarlii* Backer”, that could represent the original material. One of them was designated here as the presumed lectotype, and the name has been synonymized under *E. crista-galli* since Krukoff and Barneby (1974).
- (6) Lombardo (1964) published the variety *E. crista-galli* var. *leucochlora* from Uruguay with a short description, but did not assign any type specimen. As there are no evident characters that support this variety besides the white flowers, which is a common mutation found in cultivated *Erythrina* species (Guedes-Oliveira et al. manuscript in preparation), the name has been synonymized under *E. crista-galli* since Krukoff and Barneby (1974), and Lombardo’s illustration in the same publication was designated here as lectotype.
- (7) Lozano and Zapater (2010) published the variety *E. crista-galli* var. *longiflora* from Argentina with a full description, an illustration and mentioning the type specimens. However, as there are no evident characters that support this variety besides the size of leaves and flowers, which is a character with well-documented morphological plasticity in *Erythrina* species (Guedes-Oliveira et al. manuscript in preparation), the name was here synonymized under *E. crista-galli*.

Etymology. The specific epithet “*crista-galli*” is derived from Latin, meaning “the crest of the rooster”, and it was presumably chosen after the usual association of the corolla with the shape and color of chicken combs.

Vernacular names. *E. crista-galli* has a variety of vernacular names in many regions where it occurs, either native or introduced and cultivated. According to herbaria labels and Carvalho (2006), the species is generally known as “corticeira” in Brazil, and also “corticeira-de-beira-do-rio”, “corticeira-do-brejo”, “crista-de-galo”, “manequiera”, “mulungu”, “mulungu-de-espinho” or “suinã” (and spelling variations) in the state of **Mato Grosso do Sul**; “crista-de-galo”, “moxoqueiro-do-brejo”, “samaúva” or “samauveira” in **Minas Gerais**; “cortiça”, “corticeira-do-banhado”, “corticeira-do-brejo”, “crista-de-galo”, “flor-de-coral”, “mulungu”, “sananduva” or “suinã” (and spelling variations) in **Paraná**; “cris-

ta-de-galo" in **Rio de Janeiro**; "corticeira-do-banhado", "marrequinha" or "sananduva" in **Rio Grande do Sul**, where it is also the motive for the name of the municipality of Sananduva; "corticeira-do-banhado", "corticeira-bico-de-papagaio", "corticeira-do-brejo", "flor-de-coral" or "marrequeira" in **Santa Catarina**; and "crista-de-galo", "flor-de-coral", "maçã-de-cobra", "muchocho" (and spelling variations), "mulungú", "patinha", "samauveira", "sananduva" or "suinã" (and spelling variations) in **São Paulo**.

Doubtful synonyms of *Erythrina crista-galli*

***Erythrina crista-galli* var. *laurifolia* Tod., Index. Sem. Panorm. 1861: 32. 1862**

≡ *Erythrina laurifolia* Tod., Index. Sem. Panorm. 1860: 11. [1860?], non Jacq., Observ. Bot. 3: 1. 1768.

Type. Unknown.

Notes. As the original protologue for *E. laurifolia* (Todaro 1860) could not be found, it is not possible to determine if this name was validly published and thus illegitimate, as it was already validly published by Jacquin (1768), or it can be considered as a *nomen nudum*. Moreover, the protologue is cited on digital databases as being published in 1860, but according to TL-2 it was published either in 1859 or 1862. Todaro (1862) later published the variety *E. crista-galli* var. *laurifolia* based on his previous *E. laurifolia*, but made no additional informative description that could help confirm the identity of the mentioned specimen.

***Erythrina crista-galli* var. *speciosa* Tod., Index. Sem. Panorm. 1861: 32. 1862**

≡ *Erythrina speciosa* Tod., Index. Sem. Panorm. 1860: 11. [1860?], non Lamb. ex Andrews, Bot. Repos. 7: tab. 443. 1807.

Type. Unknown.

Notes. As the original protologue for *E. speciosa* (Todaro 1860) could not be found, it is not possible to determine if this name was validly published and thus illegitimate, as it was already validly published by Andrews (1807), or it can be considered as a *nomen nudum*. Moreover, the protologue is cited on digital databases as being published in 1860, but according to TL-2 it was published either in 1859 or 1862. Todaro (1862) later published the variety *E. crista-galli* var. *speciosa* based on his previous *E. speciosa*, but made no additional informative description that could help confirm the identity of the mentioned specimen.

***Erythrina crista-galli* var. *corallina* N.F.Mattos, Loeftgrenia 71: 3. 1977**

Type. Unknown.

Notes. As the original protologue (Mattos 1977) could not be found, nor any collection made by Mattos was found in any herbaria, this variety could not be confirmed as a valid name or synonym.

3. *Erythrina falcata* Benth., in Martius, Fl. Bras. 15(1): 172. 1859, nom. cons.
Fig. 3

≡ *Corallodendron falcatum* (Benth.) Kuntze, Revis. Gen. Pl. 1: 172. 1891.

= *Erythrina martii* Colla, Herb. Pedem. 2: 250. 1834, nom. rej. Type: Brazil. Rio de Janeiro: "Campos [Campos dos Goytacazes?]", s.d., s.leg., s.n. (lectotype, designated by Moraes et al. 2013, pg. 200: TO [1793, image seen]). (1)

= *Erythrina crista-galli* L. var. *inermis* Speg. & Girola, Anal. Soc. Rural Argent. 44: 335. 1910. Type: Argentina. Misiones: Puerto León, s.d., *Venturi* 63 (lectotype, designated here: LIL [61285, image seen]; isotype: LP [presumably lost]). (2)

Type material. BRAZIL. Maranhão: "in sylvis ad flumen Itapicurú prov. Maragnanensis", s.d., *Martius* s.n. (lectotype, designated by Krukoff 1938, pg. 233 [first-step]; and Martins and Tozzi 2018, pg. 399 [second-step]: M [M0213337]; isolectotypes: M [M0213336, M0213338]). Residual syntypes: Brazil. Bahia: "in campis prov. Bahiensis australis", s.d., *Wied-Neuwied* s.n., BR (BR0000006584023); Minas Gerais: "in prov. Minarum ad Caxoeira do Campo", 1839, *Claussen* 119, K (K000930965); "prope Barbacena", s.d., *Saint-Hilaire* 155 P (P00758901); 158, P (P00758955); 159, P (P00758954).

Notes. Martius (1859) published *E. falcata* by Bentham mentioning four different collections from Brazil: one from the state of Maranhão (*Martius* s.n.), one from Bahia (*Wied-Neuwied* s.n.), and two from Minas Gerais (*Claussen* s.n. and *Saint-Hilaire* s.n.), but without mentioning any herbaria. Krukoff and Barneby (1974) accessed the collection by Martius in herbarium M and selected it as the type specimen. Because there are three different exsiccatae in the mentioned herbarium, Martins and Tozzi (2018) designated one of them as a second-step lectotype (Fig. 3). Despite not mentioning the herbaria of the other syntypes from Bahia and Minas Gerais, some collections are cited here with what was found in digital herbaria and believed to be the original ones. Kuntze (1891) published *Corallodendron* mentioning *E. falcata* as a synonym of *C. falcatum*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894). Additional material: BR (BR0000013473808, photo n.v.), F (neg. 6301, negative of M0213337), IAN (IAN001758, photo of F neg. 6301), MO (MO-1680376, photo of F neg. 6301), P (P02951457, photo of M0213337).

(1) Colla (1834) published *E. martii* as a doubtful species from Brazil with a short description that resembles *E. falcata*, but without mentioning any collections. Krukoff (1938) already placed it as a doubtful synonym of *E. falcata*, but did not see the type specimen, which he believed could be at herbarium TO. Moraes et al. (2013), in a treatment of Brazilian plants distributed by Martius in 1827 and published by Colla in "*Herbarium Pedemontanum*" (Piedmont, Italy), confirmed the synonymy and designated a collection in herbarium TO, where the original material was deposited, as the lectotype of the name. We got access to an image of the TO collection and agree with the synonymy. Furthermore, as the name *E. martii* had priority over *E. falcata* due to its date of publication, as specified in Article 11 of the ICN (Turland et al. 2018), Martins and Tozzi (2015) proposed to conserve *E. falcata* since it was a very well-established name for the species. The proposal was



Figure 3. Lectotype of *Erythrina falcata* Benth., in von Martius (1859: 172), designated by Krukoff (1938: 233, first-step) and Martins and Tozzi (2018: 399, second-step). Source: Botanische Staatssammlung München (M) via JSTOR Global Plants, M0213337.

approved by the Nomenclature Committee for Vascular Plants of the ICN at the XIX International Botanical Congress (Applequist 2016; Turland et al. 2017; Wilson 2017).

- (2) Spegazzini and Girola (1910) published the variety *E. crista-galli* var. *inermis*, which was doubtfully synonymized under *E. falcata* by Krukoff (1938), who did not see the type specimen. The synonymy was later confirmed by Lozano and Zapater (2010). Furthermore, Gutiérrez et al. (2002) investigated the type collections by Spegazzini in herbarium LP and found that only wood samples were collected for some species. As those samples could not be found anywhere in the LP collections, the holotype for this name is presumably lost. The protologue also could not be found online, but we had access to an image of the isotype's exsiccata at LIL and designated it here as the lectotype.

Etymology. The specific epithet "*falcata*" is derived from Latin, meaning "curved" or "sickle-shaped", and was presumably chosen due to its corolla falcate shape, especially the standard and keel petals.

Vernacular names. According to herbaria labels and Carvalho (2003), *E. falcata* is generally known as "mulungu" or "corticeira" in Brazil, and also "bico-de-papagaio", "bico-de-pato", "canivete", "corticeiro-de-mato", "marrequeira", "mochoco" (and spelling variations), "moxoqueiro" (and spelling variations), "mulungu-coral", "mutuqueiro" (and spelling variations), "pau-cebola", "sanandú" (and spelling variations), "sanandui", "sananduba" (and spelling variations), "sapato-de-judeu", "suinã" (and spelling variations), "suinã-do-brejo" or "sumaúma" in the state of **Minas Gerais**; "bico-de-papagaio", "canivete", "coral", "corticeira-ceboleiro", "corticeira-da-serra", "corticeiro-de-mato", "marrequeira", "mochoco" (and spelling variations), "moxoqueiro" (and spelling variations) or "letuíno" in **Paraná**; "canivete", "mulungú tijolo", "mulungú suinã", "sanandú" (and spelling variations) or "sanandú do brejo" in **Rio de Janeiro**; "bituqueiro" (and spelling variations), "camarão-assado", "ceibo", "corticeira-da-serra" or "corticeira-do-mato" in **Rio Grande do Sul**; "bico-de-papagaio", "bituqueira" (and spelling variations), "corticeira", "corticeira-da-serra", "facãozinho", "mituqueira" (and spelling variations) or "sinhanduva" in **Santa Catarina**; and "bico-de-arara", "bico-de-papagaio", "canivete", "corticeira", "feijão-bravo", "machoco" (and spelling variations), "mulungu-coral", "mutuqueiro" (and spelling variations), "sapatinho-de-judeu", "sanandu" (and spelling variations), "sanandui", "sananduba" (and spelling variations), "suinã" (and spelling variations), "suinã-da-mata", "suinã-da-serra", "suinã-mulambo" or "vermelheira" in **São Paulo**.

4. *Erythrina fusca* Lour., Fl. Cochinch. 2: 427. 1790, based on "*Gelala Aquatica*" Rumph., Herb. Amboin. 2: 235. 1741.

Fig. 4

≡ *Corallodendron fuscum* (Lour.) Kuntze, Revis. Gen. Pl. 1: 172. 1891.

= *Erythrina glauca* Willd., Neue Schriften Ges. Naturf. Freunde Berlin 3: 428. 1801. Type: Venezuela. Caracas: s.loc., s.d., *Hoffmannsegg s.n.* (lectotype, designated here: B [B-W13101-010]). (1)

- ≡ *Duchassaingia glauca* (Willd.) Walp., in Duchassaing and Walpers, *Linnaea* 23(=7): 742. 1851.
- ≡ *Corallodendron glaucum* (Willd.) Kuntze, *Revis. Gen. Pl.* 1: 172. 1891.
- = *Erythrina ovalifolia* Roxb., *Hort. Bengal.*: 53. 1814, nom. nud.; *Fl. Ind.* 3: 254. 1832. Type: India. West Bengal: a scarce tree about Calcutta, s.d., s.leg., s.n. (lectotype, designated here: illustration in Wight 1839, tab. 247). (2)
- ≡ *Duchassaingia ovalifolia* (Roxb.) Walp., in Duchassaing and Walpers, *Linnaea* 23(=7): 742. 1851.
- = *Erythrina patens* Moc. & Sessé ex DC., *Prodr.* 2: 414. 1825; A.DC., *Calques Fl. Mexique* 2: tab. 255. 1874. Type: [the Caribbean?]. s.loc., s.d., Sessé et al. 3693 (lectotype, designated by Krukoff and Barneby 1974, pg. 340 [first-step]; and here [second-step]: MA [MA601534]; isolectotypes: MA [MA601535, MA601536]). (3)
- ≡ *Corallodendron patens* (Moc. & Sessé ex DC.) Kuntze, *Revis. Gen. Pl.* 1: 173. 1891.
- = *Erythrina caffra* Blanco, *Fl. Filip.* 2: 394. 1845, nom. superf. et illeg., non Thunb., *Prodr. Fl. Cap.* 2: 121. 1800. Type: Philippines. s.loc., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 399: illustration in Blanco et al. [1883?], tab. [526?]). (4)
- = *Erythrina ovalifolia* Roxb. var. *inermis* Pulle, *Nova Guinea* 8(2): 651. 1912. Type: Indonesia. Western New Guinea: “am Noord-Fluss in einem verlassenen Dorfe”, 4 September 1909, *Römer* 28 (holotype: L [L 0018975, sheet I; L 0018976, sheet II]). syn. nov. (5)
- = *Erythrina fusca* Lour. var. *inermis* Rock, *Legum. Pl. Hawaii*: 188. 1920. Type: U.S.A. Hawaii, Honolulu: in cultivation on Anapuni Street, s.d., s.leg., s.n. (lectotype, designated here: illustration in Rock 1920, tab. 77). (6)

Type material. INDONESIA. “In Amboina raro occurrit. Arborescens in Lariqua & Hitoe, longa vero feu frutefcens juxta ripas fluminis Elephantis, ubique non longe a mari. Magna vero copia reperitur in Java, Baleya, Borneo & Sumatra, uti & modicum in Ceramæ ora Orientali”, s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 399: illustration in Rumphius 1741, tab. 78).

Notes. Rumphius (1741) published descriptions and illustrations of three species from Ambon Island (Indonesia) that he called “*Gelala*”, before Linnaeus’ binomial system. Then, Loureiro (1790) published *E. fusca* from Vietnam mentioning the name “*Gelala Aquatica*” as a synonym, and Rumphius’ illustration was correctly designated by Martins and Tozzi (2018) as the lectotype of the name (Fig 4). Kuntze (1891) published *Corallodendron* mentioning *E. fusca* as a synonym of *C. fuscum*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894).

- (1) Willdenow (1801) published *E. glauca* from Caracas (Venezuela), but did not mention any type specimen. A collection from Caracas labeled as *E. glauca* was found in Willdenow’s type specimens’ section in herbarium B with the same description given by him, and it was thus designated here as the lectotype. The name has been considered a synonym of *E. fusca* since Krukoff and Barneby (1974). Walpers (1851, not 1850) published *Duchassaingia* mentioning *E. glauca* as a synonym of *D. glauca*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894). Kuntze



Figure 4. Lectotype of *Erythrina fusca* Lour. (1790: 427), designated by Martins and Tozzi (2018: 399). Source: Missouri Botanical Garden – Peter H. Raven Library via Biodiversity Heritage Library, available at <https://www.biodiversitylibrary.org/page/187502>.

- (1891) published *Corallodendron*, mentioning *E. glauca* as a synonym of *C. glaucum*, but the genus was also synonymized into *Erythrina* in Engler and Prantl (1894). Additional material: F (neg. 2372, photo of B-W13101-010), IAN (IAN001757, photo of F neg. 2372).
- (2) Roxburgh (1814) mentioned *E. ovalifolia* from India, but did not describe the species, so this name was first considered a *nomen nudum*. However, he fully described the species in *Flora Indica* (Roxburgh 1832), although no type specimen was assigned. Wight (1839, not 1840) published a re-drawing of Roxburgh's unpublished plates of species described in 1832, and his illustration for *E. ovalifolia* was designated here as the lectotype. The name has been considered a synonym of *E. fusca* since Krukoff and Barneby (1974). Walpers (1851, not 1850) published *Duchassaingia* mentioning *E. ovalifolia* as a synonym of *D. ovalifolia*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894).
 - (3) De Candolle (1825) published *E. patens* based on a plate made by Sessé and Mociño for the *Flora Mexicana*, later published by Alph. De Candolle (De Candolle 1874). As stated by Krukoff and Barneby (1974), the species does not occur in Mexico and must have been collected somewhere in the Caribbean. The authors mentioned a collection by Sessé, Mociño, Castillo and Maldonado as the type, but did not mention any herbaria. Three exsiccatae of this collection were found in herbarium MA and one of them was designated here as the lectotype, in a second-step lectotypification. Kuntze (1891) published *Corallodendron* mentioning *E. patens* as a synonym of *C. patens*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894).
 - (4) Blanco's description (Blanco 1845) of *E. caffra* from the Philippines matches *E. fusca*, but as the name was already validly published by Thunberg (1800), Blanco's publication was considered illegitimate. Martins and Tozzi (2018) correctly designated his illustration in *Flora de Filipinas* 3rd edn. (Blanco et al. 1883?) as the lectotype, but according to TL-2 (Stafleu 1976), both its publication date and plate number remain doubtful.
 - (5) Pulle (1912) published the variety *E. ovalifolia* var. *inermis* from Indonesia based only on the absence of spines, a character with well-documented morphological plasticity in *Erythrina* species (Guedes-Oliveira et al. manuscript in preparation). The exsiccatae found in herbarium L undoubtedly place the name as a synonym of *E. fusca*. The variety was already synonymized in Krukoff and Barneby (1974), but as the authors mistakenly cited it as "*E. fusca* Lour. var. *inermis*", the correct name is designated here as a new synonym.
 - (6) Rock (1920) published the variety *E. fusca* var. *inermis* from a specimen being cultivated in Hawaii after seeds brought from Manila (the Philippines), based only on the absence of spines, which is a character with well-documented morphological plasticity in *Erythrina* species (Guedes-Oliveira et al. manuscript in preparation). His photograph was designated here as the lectotype of the name, which has been considered a synonym since Krukoff and Barneby (1974).

Etymology. The specific epithet "*fusca*" is derived from Latin, meaning "dark" or "dusky", and it was presumably chosen due to the dark-orange color of the petals in some individuals, described as "*fulco-ruber*" in the protologue of the species. It is important to point out that the color of the petals varies a lot in this

species, from shades of light-yellow to dark-orange and even vinaceous-red (Guedes-Oliveira et al. manuscript in preparation).

Vernacular names. According to herbaria labels, *E. fusca* is generally known in Brazil as “mulungu”, and also as “alecrim” in the state of **Acre**; “açacurana” (and spelling variations) or “assacu branco” in **Amazonas**; “assacurana” (and spelling variations) in **Amapá**; “eritrina-da-baixa” or “sumaúma” in **Bahia**; “abobinha” or “flor-de-aboboreira” in **Mato Grosso**; “abobreiro” in **Mato Grosso do Sul**; “assacuhy”, “parica” or “pau angico” in **Pará**; and “assacurana” in **Rio de Janeiro**.

Doubtful synonyms of *Erythrina fusca*

***Erythrina picta* Blanco, Fl. Filip.: 565. 1837, nom. superf. et illeg., non L., Sp. Pl. 2: 993. 1763**

Type. Unknown.

Notes. Blanco (1837) published *E. picta* from the Philippines with a short description but without mentioning any type specimen. However, as Linnaeus (1763) had already validly published it before, it is an illegitimate name. The name was synonymized by Krukoff and Barneby (1974) as *E. fusca*, but could not be confirmed and thus remains here as a doubtful synonym.

***Erythrina atrosanguinea* Ridl., J. Straits Branch Roy. Asiat. Soc. 59: 93. 1911**

Syntypes. Malaysia. Kedah: Lankawi on the sea shore at Kwah; common round Alor Sta; Bukit Pinang, January 1897, *Ridley 15134; 15135*.

Notes. Ridley (1911) published *E. atrosanguinea* from Malaysia with a full description and type specimens, but without mentioning any herbaria. Krukoff (1939) considered this a synonym of *E. fusca*, but he could not see the type specimens. As Ridley described its flowers as “deep red black”, and the type collections were not found on digital databases, it remains as a doubtful synonym.

5. *Erythrina mulungu* Mart. ex Benth., in Martius, Fl. Bras. 15(1): 173. 1859. Fig. 5

≡ *Corallodendron mulungu* (Mart. ex Benth.) Kuntze, Revis. Gen. Pl. 1: 173. 1891.
 = *Erythrina chacoënsis* Speg., in Spegazzini and Girola, Anal. Soc. Rural Argent. 44: 369. 1910; Lillo, Seg. Contr. Arb. Argent.: 20. 1924. Type: Argentina. Formosa, January 1883, *Venturi 281* (holotype: LP [LP010837]). (1)
 = *Erythrina dominguezii* Hassl., Physis 6(21): 123. 1922. Type: Argentina. Formosa: “prope Guayculee”, September 1918, *Jørgensen 3215* (lectotype, designated by Lozano and Zapater 2010, pg. 188: BA [64115, image seen]; isolectotypes: BM [n.v.], G [GH00066286], LIL [n.v.], S [n.v.], US [US00004482]). Residual syntypes: Paraguay. San Pedro: “in silvis ripariis”, December 1916, *Rojas 2061*, BAF (BAF00000133), SI (SI002044, image seen; SI002045, image seen); Alto Paraguay: “Puerto Casado (flum. Paraguay), in silvis”, 1916, *Rojas 2122*, AS (n.v.). (2)

= *Erythrina xinguensis* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 167. 1922. Type: Brazil. Pará: “prope Altamira (Xingú), in silvis secundariis, terries argillosis compactis rufis fertilissimis”, 21 August 1919, *Ducke s.n.* (lectotype, designated here: RB [RB00540259!]; isotypes: B [presumably destroyed], F [V0059282F, frag. and photo of F neg. 2379], K [K000502768], NY [NY00008010, frag. slide, right envelope; NY00008018, frag., top envelope], R [R000043635!], RB [RB00547685!], S [S-R-9685], U [U.1243348]). syn. nov. (3)

Type material. BRAZIL. Minas Gerais: “in silvis Catingas prope Contendas [Águas de Contendas] prov. Minarum”, s.d., *Martius 1582* (lectotype, designated by Krukoff 1938, pg. 241 [first-step]; and Martins and Tozzi 2018, pg. 399 [second-step]: M [M0240565]; isolectotype: M [M0240564]).

Notes. Bentham published a treatment of Brazilian *Erythrina* in *Martius’ Flora Brasiliensis* (Martius 1859). He included the name *E. mulungu*, given by Martius, citing a collection from the state of Minas Gerais but without mentioning any herbaria. Krukoff and Barneby (1974) located a collection by Martius in herbarium M and designated it as the type specimen. However, as there were two different exsiccatae in the mentioned herbarium, Martins and Tozzi (2018) correctly selected one of them as a second-step lectotypification (Fig. 5). Some databases give the authorship of the name only to Martius, but Bentham is the author of this species in *Flora Brasiliensis*. Kuntze (1891) published *Corallogenon* mentioning *E. mulungu* as a synonym of *C. mulungu*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894). Additional material: F (neg. 6302, negative of M0240565), IAN001759 (photo of F neg. 6302).

- (1) Spegazzini published *E. chacoënsis* in Spegazzini and Girola (1910), but the original protologue could not be found online. However, Lillo (1924 [reprint from 1917]) published *Notas sobre el Herbario Venturi*, mentioning the name and the original collection of Venturi in Argentina. An exsiccata from the same location was found at herbarium LP, which has the inscription “*Erythrina chacoënsis* Speg. (n. sp.)” and follows the description given by Lillo; hence it is believed to be the original material cited by Spegazzini. The name has been considered as a synonym of *E. dominguezii* since Krukoff (1938), who believed *E. mulungu* was a synonym of *E. verna* Vell., which was later found to be a different and accepted species by Martins and Tozzi (2018).
- (2) Hassler (1922) published *E. dominguezii* mentioning three collections, one from Argentina (*Jörgensen 3215*) and two from Paraguay (*Rojas 2061* and *2122*), but without citing any herbaria. Lozano and Zapater (2010) then correctly designated the collection from Jörgensen as the lectotype of the name. The name was considered accepted until Martins and Tozzi (2018), who correctly synonymized it under *E. mulungu*. As for the remaining syntypes, some collections are cited here with what was found on digital herbaria and believed to be the original ones. Additional material: MO (MO-1624248, photo n.v.), P (P02934647, photo of GH00066286).
- (3) Ducke (1922) published *E. xinguensis* from Brazil, with a full description and correctly citing the type specimen. However, as there were two exsiccatae in herbarium RB with the same number but without any information regarding a possible division of the same collection in different sheets



Figure 5. Lectotype of *Erythrina mulungu* Mart. ex Benth., in Martius (1859: 173), designated by Krukoff (1938: 241, first-step); and Martins and Tozzi (2018: 399, second-step). Source: Botanische Staatssammlung München (M) via JSTOR Global Plants, M0240565.

(e.g. part 1 of 2), one of them was designated here as the lectotype. This name has been synonymized under *E. ulei* Harms since Krukoff (1938), and it caused much confusion in herbaria as the subsequent taxonomists could not properly identify the species. Ducke's collections, in fact, correctly represent *E. mulungu* (Guedes-Oliveira et al. manuscript in preparation) and the name is thus synonymized here. Additional material: F (neg. 2379, negative of B), IAN001764 (photo of F neg. 2379), MO-1680465 (photo of F neg. 2379).

Etymology. The specific epithet "*mulungu*" is derived from the most common vernacular name applied to all *Erythrina* species in Brazil. The origin is unknown, and it has many different meanings in African languages, most referring to a deity or a god creator of everything, father of all gods (e.g. Frankl 1990).

Vernacular names. According to herbaria labels, *E. mulungu* is generally known as "mulungu" in Brazil, and also "pau-de-tiriça" in the state of **Minas Gerais**; "abobreira" (and spelling variations) or "maleitoso" in **Mato Grosso do Sul**; "açacurana" (and spelling variations) in **Pará**; and "bico-de-papagaio" in **São Paulo**.

6. *Erythrina poeppigiana* (Walp.) O.F.Cook, Bull. Div. Bot. U.S.D.A. 25: 57. 1901. Fig. 6

- ≡ *Micropteryx poeppigiana* Walp., in Duchassaing and Walpers, Linnaea 23(=7): 740. 1851.
- ≡ *Erythrina micropteryx* Poepp. ex Walp., in Duchassaing and Walpers, Linnaea 23(=7): 740. 1851, nom. nud.
- ≡ *Erythrina micropteryx* Poepp. ex Urb., Symb. Antill. 1: 327. 1899.
- ≡ *Erythrina poeppigiana* (Walp.) Skeels, in Galloway, Bull. Bur. Pl. Industr. U.S.D.A. 242: 84. 1912, nom. superf. et illeg., syn. nov.
- = *Erythrina amasisa* Spruce, J. Proc. Linn. Soc., Bot. 3: 202. 1859. Type: Peru. San Martín: "Tarapoto, in sylvis montium inferiorum praecipue secus rivulus", s.d., Spruce 4069 (lectotype, designated by Krukoff 1938, pg. 237 [first-step]; and here [second-step]: K [K000200903, sheet I; K000200905, sheet II]; isoelectotypes: BM [BM000778350], BR [BR0000005196685], E [E00296690], F [V0043470F, V0043471F], G [G00365292, sheet I; G00365293, sheet II], GH [GH00066283], K [K000200906, sheet I; K000200904, sheet II], MPU [MPU023232], NY [NY00007984, NY00007985], P [P00708429, P00708430], TCD [TCD0004415]. (1)
- = *Erythrina pisamo* Posada-Ar., Estudios Cient.: 120. 1909. Type: Colombia. s.loc., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 400: illustration in Molina 1909, tab. s.n.). (2)
- = *Erythrina darienensis* Standl., Contr. U.S. Nat. Herb. 18: 108. 1916. Type: Panamá. Darién: near Boca de Pauarandó, on the Sambú River, southern Darién, February 1912, Pittier 5578 (holotype: US [US00004481]; isotypes: BM [BM000931444], GH [GH00066265], MO [MO-114002, n.v.], NY [NY00007903, frag.; NY00007904]). (3)
- = *Erythrina poeppigiana* (Walp.) O.F.Cook f. *redmondii* Steyererm. & Lasser, Phyto-logia 48: 286. 1981. Type: Veneuela. Miranda: "Los Chorros, Avenida princi-



Figure 6. Lectotype of *Erythrina poeppigiana* (Walpers) O.F. Cook (1901: 57), designated by Martins and Tozzi (2018: 400). Source: William and Lynda Steere Herbarium (NY) – The New York Botanical Garden via C. V. Starr Virtual Herbarium, NY00016336.

pal, Caracas, en frente de la Escuela Hebraica", 9 March 1981, *Redmond s.n.* (holotype: VEN [VEN137030]; isotypes: MO [MO-277140], NY [NY00008000, NY00008001], U [U0003538], US [US00153764]). syn. nov. (4)

Type material. **PERU.** "Peruvia subandina. In sylvis", September 1829, *Poeppig 1306* (lectotype, designated by Martins and Tozzi 2018, pg. 400: NY [NY00016336]; isolectotypes: B [presumably destroyed], F [V0043502F, frag. and photo of F neg. 2373; V0059555F, frag.?).

Notes. Walpers (1851, not 1850) published *Micropteryx* with a new species from Peru (*M. poeppigiana*), which was based on *Erythrina micropteryx*, a name given by Poeppig that was never published. This mention also resulted in the publication of *E. micropteryx* itself, although it is considered a *nomen nudum*. Urban (1899) validly published the name *E. micropteryx* from Poeppig again. As the genus *Micropteryx* proposed by Walpers was later synonymized under *Erythrina* in Engler and Prantl (1894), Cook (1901) published *E. poeppigiana* based on *M. poeppigiana* by Walpers, which is the name that has been used for the species ever since. Krukoff (1938) designated the collection of Poeppig in herbarium B as the lectotype, but it was presumably destroyed in the bombing raid in 1943 (Botanischer Garten und Botanisches Museum Berlin 2022). Thus, Martins and Tozzi (2018) correctly designated the remaining available material in herbarium NY as the new lectotype (Fig. 6). Skeels (Galloway 1912) again published *E. poeppigiana* based on *M. poeppigiana* by Walpers, but as the name was already validly published by Cook (1901), it is considered illegitimate. Additional material: F (neg. 2373, negative of B), IAN001761 (photo of F neg. 2373), MO-1684973 (photo n.v.).

- (1) Spruce (1859) published *E. amasisa* from Peru, but did not mention any type specimen. Krukoff (1938) cited a collection from Spruce in herbarium K as the type, but as there were three different exsiccatae in the mentioned herbarium, one of them was designated here as a second-step lectotypification.
- (2) Posada-Arango (1909) published *E. pisamo* from Colombia but did not assign any type specimen. It was subsequently correctly designated by Martins and Tozzi (2018) as his illustration in the same publication. The name was already synonymized under *E. poeppigiana* by Krukoff (1938).
- (3) Standley (1916) validly published *E. darienensis* from Panama with a full description mentioning the type specimen, and the name was already synonymized under *E. poeppigiana* by Krukoff (1938). Additional material: P (P02951340, photo of US00004481), W (W19390013217, photo of US00004481).
- (4) Steyermarkii and Lasser (1981) published the form *E. poeppigiana* f. *redmondii* from Venezuela based only on some specimens with yellow flowers, and correctly cited the type specimen. As no other known characteristics support the distinction between forms (Guedes-Oliveira et al. manuscript in preparation), nor is this variation reported from elsewhere, it is designated here as a new synonym.

Etymology. The specific epithet "*poeppigiana*" was a homage to Eduard Friedrich Poeppig (1798–1868), a German botanist, zoologist, and explorer who collected the type specimen attributed to the species.

Vernacular names. There are no other known vernacular names for *E. poeppigiana* in Brazil besides the commonly used "mulungu".

7. *Erythrina similis* Krukoff, Brittonia 3: 271. 1938.

Fig. 7

Type material. PARAGUAY. Central: In the region of Lake Ypacaray, February 1913, Hassler 11450 (holotype: MO [MO-2050072]; isotypes: A [A00066288], BM [BM000538332], G [G00381487; G00381504, two sheets; G00381507, two sheets], K [K000502765], L [L0018977], NY [NY00008005, frag. slide, top left envelope; NY00008006], US [US00004504]).

Notes. There are no nomenclature issues with *E. similis*, as the name was validly published and the type was specimen correctly cited (Fig. 7). However, all databases and studies of the genus state that the protologue was published in 1939. Still, according to the journal's website, the publication date is October 1938. Additional material: P (P02960062, photo of MO-2050072).

Etymology. The specific epithet "*similis*" is derived from Latin, meaning "*similar to*", and was chosen due to *E. similis* similarity with *E. amazonica*, especially in dried specimens.

Vernacular names. There are no other known vernacular names for *E. similis* in Brazil besides the commonly used "mulungu".

8. *Erythrina speciosa* Lamb. ex Andrews, Bot. Repos. 7: tab. 443. 1807.

Fig. 8

= *Erythrina poianthes* Brot. ex Tillich & Taylor, Philos Mag. J. 61: 465. 1823; Brotero, Trans. Linn. Soc. Lond. 14: 342. 1824. Type: Portugal. "Colitur in Horto Botanico Olisiponensi [Jardim Botânico de Lisboa] ad Aulam Regiam in Ajuda sito, et alibi in Lusitania", ex hort., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 400: illustration in Brotero 1824, tab. 11). (1)

≡ *Erythrina poianthes* Brot., Trans. Linn. Soc. Lond. 14: 342. 1824, nom. superfl. et. illeg.

≡ *Stenotropis berteroi* Hassk., Retzia 1: 183. 1855.

= *Erythrina poianthes* var. *subinermis* Lindl., Edwards's Bot. Reg. 19: 1617. 1833. Type: England. London: Growing in the stove of his Grace the Duke of Northumberland at Sion, ex hort., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 400: illustration in Lindley 1833, tab. 1617). (2)

= *Erythrina reticulata* C.Presl, Symb. Bot. 2: 22. 1834. Type: Brazil. Rio de Janeiro: "in sepibus", ex hort., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 400: illustration in Presl 1834, tab. 68). (3)

≡ *Micropteryx reticulata* (C.Presl) Walp., in Duchassaing and Walpers, Linnaea 23(=7): 741. 1851.

≡ *Corallodendron reticulatum* (C.Presl) Kuntze, Revis. Gen. Pl. 1: 173. 1891.

= *Erythrina speciosa* var. *rosea* N.F.Mattos, Loefgrenia 21: 1. 1967. Type: Brazil. São Paulo: Cultivada no Jardim Botânico de S. Paulo; proc.: Barra de Una, ao norte de Bertioga, na estrada Bertioga - S. Sebastião, ex hort., s.d., Pires s.n. (holotype: SP [SP000991]; isotype: RB [RB00514374!]). (4)

Type material. ENGLAND. s.loc., ex hort., s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 400: illustration in Andrews 1807, tab. 443).



Figure 7. Holotype of *Erythrina similis* Krukoff (1938: 271). Source: Missouri Botanical Garden (MO) via Tropicos, MO-2050072.



Figure 8. Lectotype of *Erythrina speciosa* Lamb. ex Andrews (1807: tab. 443), designated by Martins and Tozzi (2018: 400). Source: Missouri Botanical Garden – Peter H. Raven Library via Biodiversity Heritage Library, available at <https://www.biodiversitylibrary.org/page/35501082>.

Notes. Andrews (1807) published *E. speciosa*, a name communicated by Lambert from a cultivated specimen in British greenhouses, with a short description and a well-made illustration of a leaf, inflorescence, and flowers. As Andrews did not mention any type specimen, only citing that the species is “supposed to be a native of South America”, Martins and Tozzi (2018) correctly designated his illustration as the lectotype (Fig. 8).

(1) Brotero (1824) published *E. poianthes* from a cultivated specimen in the Jardim Botânico de Lisboa (Portugal), with a complete description and two

very detailed illustrations of leaves, inflorescences, and dissected flowers, but without mentioning any type specimen. However, his description was published in the previous year by Tillich and Taylor (1823) as a resumed version for the Proceedings of Learned Societies. This publication takes place due to the principles of priority as specified in Article 11 of the ICN (Turland et al. 2018), meaning the name published by Brotero is illegitimate. The name has been treated as a synonym since Krukoff (1938), and Martins and Tozzi (2018) correctly designated one of Brotero's illustrations as the lectotype. Hasskarl (1855) published *Stenotropis berteroi* based on *E. poianthes* by Brotero, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894).

- (2) Lindley (1833) published the variety *E. poianthes* var. *subnervis*, with a short description and a well-made illustration of a leaflet and inflorescence from a cultivated specimen in a greenhouse in London (England). The variety was based solely on the absence of spines and the leafy habit in anthesis, which are characters with well-documented morphological plasticity in the species (Guedes-Oliveira et al. manuscript in preparation). The name was already synonymized under *E. speciosa* by Krukoff (1938). Lindley did not assign any type specimen, so Martins and Tozzi (2018) correctly designated his illustration as the lectotype for the name.
- (3) Presl (1834) published *E. reticulata* from a specimen in Rio de Janeiro (Brazil), with a full description and a detailed illustration of leaves, inflorescence and dissected flowers, but without mentioning any type specimen. The name was already synonymized under *E. speciosa* by Krukoff (1938), but as he also did not designate any type specimen, Martins and Tozzi (2018) correctly designated Presl illustration as the lectotype. Walpers (1851, not 1850) published *Micropteryx* mentioning *E. reticulata* as a synonym of *M. reticulata*, but the genus was later synonymized into *Erythrina* in Engler and Prantl (1894). Kuntze (1891) published *Corallodendron* mentioning *E. reticulata* as a synonym of *C. reticulatum*, but the genus was synonymized under *Erythrina* in Engler and Prantl (1894) as well.
- (4) Mattos (1967) published the variety *E. speciosa* var. *rosea* from a cultivated specimen in the Jardim Botânico de São Paulo (Brazil), based on the pinkish color of its flowers. The original protologue could not be found online, but the type specimens were seen. As there are no other morphological characters to support this variety besides the corolla's color, which is a common mutation observed in cultivated specimens of *E. speciosa* (Guedes-Oliveira et al. manuscript in preparation), the name was already synonymized under *E. speciosa* by Martins and Tozzi (2018).

Etymology. The specific epithet "*speciosa*" is derived from Latin, meaning "handsome" or "splendid", and was presumably given by horticulturists who were amazed by the showy appearance of its flowers when the species was introduced to the United Kingdom.

Vernacular names. According to Carvalho (2010) and herbarium records, *E. speciosa* is generally known as "mulungu" in Brazil, and also as "canivete", "eritrina-anã", "mulungu-da-várzea", "mulungu-do-pequeno" or "suinã" (and spelling variations) in the state of **Minas Gerais**; "facãozinho", "mulungu-do-litoral", "suinã" (and spelling variations) or "unha-do-diabo" in **Paraná**; "bico-de-pa-

pagaio”, “candelabro-vermelho”, “corticeira”, “eritrina”, “eritrina-candelabro”, “mulungu-do-litoral”, “suinã” (and spelling variations) or “suinã-reticulata” in **São Paulo**, and “bico-de-papagaio” in **Santa Catarina**.

9. *Erythrina ulei* Harms, in Ule, Verh. Bot. Vereins Prov. Brandenburg 48: 172. 1907.

Fig. 9

Type material. PERU. Loreto: Yurimaguas, August 1902, *Ule* 6300 (lectotype, designated here: K [K000502764]; isoelectotypes: B [presumably destroyed], HBG [HBG519848], L [L0018978], NY [NY00008009, frag., bottom envelope; NY00521212, frag. slide, left envelope], RB [RB00540258!, mixture! fls. in packet are of *E. mulungu* Mart. ex Benth.]). Remaining syntype: Peru. Puno: “Provinz Sandia, Chunchusmayo, in der Nähe des Flusses”, 900 m, July 1902, *Weberbauer* 1249).

Notes. Ule (1907) published a complete description of a species named by Harms mentioning two different collections in Peru (*Ule* 6300 and *Weberbauer* 1249), but without citing any herbaria. Krukoff (1938) correctly designated the collection from Ule in herbarium B as the lectotype, but it was presumably destroyed in the bombing raid in 1943 (Botanischer Garten und Botanisches Museum Berlin 2022). Therefore, here we select one of the remaining available specimens in herbarium K as the new lectotype (Fig. 9). The remaining syntype collection could not be found online. Additional material: F (neg. 2376, photo of B), IAN (IAN001760, photo of F neg. 2376), MG (MG006169, photo n.v.), MO (MO-1680466, photo n.v.; MO-1680467, photo n.v.).

Etymology. The specific epithet “*ulei*” was a homage to Ernst Heinrich Georg Ule (1854–1915), a German botanist who collected one of the syntype specimens attributed to the species.

Vernacular names. According to herbarium records, *E. ulei* is generally known as “mulungu” in Brazil, and also as “mandiocão” in the state of **Mato Grosso**.

10. *Erythrina velutina* Willd., Neue Schriften Ges. Naturf. Freunde Berlin 3: 426. 1801.

Fig. 10

≡ *Chirocalyx velutinus* (Willd.) Walp., Flora 36: 148. 1853.

≡ *Corallodendron velutinum* (Willd.) Kuntze, Revis. Gen. Pl. 1: 173. 1891.

= *Erythrina aculeatissima* Desf., Tabl. École Bot. 1: 191. 1804, nom. nud. Type: France. Île-de-France: “dans le jardin et dans les serres du Museum d’Histoire Naturelle”, ex hort., s.d., s.leg., s.n. (lectotype, designated by Krukoff and Barneby 1974, pg. 437: P [P02960024]). (1)

= *Erythrina splendida* Diels, Beitr. Veg. Ecuador: 96. 1937. Type: Ecuador. Guayas: Road from Guayaquil to Salinas, km. 89–90 from Guayaquil, just east of village of Buenos Aires. Alt. 35 m. Dry thorn scrub, 17 July 1986, *Plowman* 14314 (neotype, designated here: F [V0448423F]). (2)

= *Erythrina velutina* f. *aurantiaca* (Ridl.) Krukoff, Brittonia 3: 329. 1938. Type: Brazil. Pernambuco: Main island, scattered bushes near the village and in the Sapate. One full-grown tree in the cocoa-nut plantation at Sueste, [1887?],



Figure 9. Lectotype of *Erythrina ulei* Harms, in Ule (1907: 172), designated here. Source: Kew Herbarium – Royal Botanic Gardens (K) via Kew Herbarium Catalogue, K000502764.

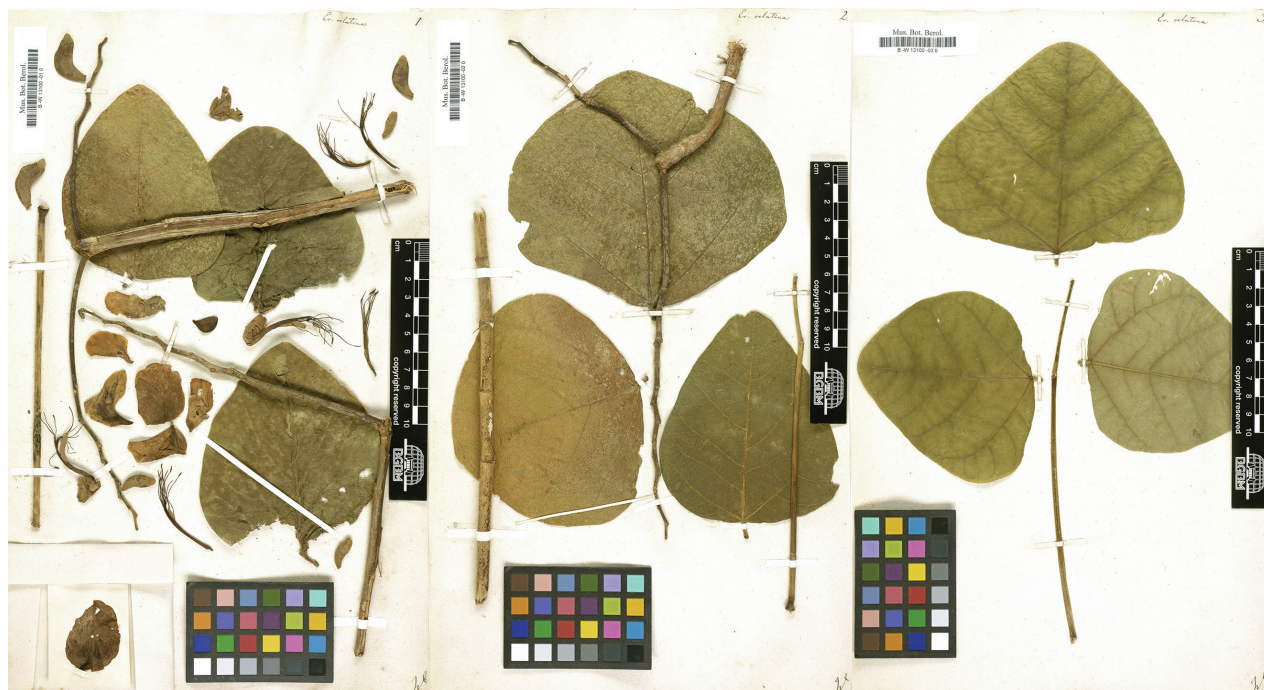


Figure 10. Lectotype of *Erythrina velutina* Willd. (1801: 426), designated by Martins and Tozzi (2018: 400). Source: Herbarium Berolinense (B) – Botanic Garden and Botanical Museum Berlin, BW13100010, BW13100020, BW13100030.

Ridley 35 (holotype: K [K000206207]; isoelectotypes: BM [BM000931431], NY [NY00007988, frag. slide]). (3)

≡ *Erythrina aurantiaca* Ridl., J. Linn. Soc., Bot. 27: 30. 1890.

Type material. VENEZUELA. Distrito Capital: Caracas, s.d., *Humboldt* 653 (lectotype [not holotype], designated by Martins and Tozzi 2018, pg. 400: B [BW13100010, sheet I; BW13100020, sheet II; BW13100030, sheet III]; isoelectotype: P [P00660125]).

Notes. Willdenow (1801) published *E. velutina* with a complete description of a specimen from Venezuela, but without mentioning any type specimen. Martins and Tozzi (2018) then designated, from the Willdenow's type specimens in herbarium B, a collection from Humboldt composed of three sheets as the type of this name. However, as the authors mistakenly stated it as a holotype, the typification is corrected here to lectotype (Fig. 10). Walpers (1853, not 1854) published *Chirocalyx* mentioning *E. velutina* as a synonym of *C. velutinus*, but the genus was later synonymized under *Erythrina* in Engler and Prantl (1894). Kuntze (1891) published *Corallodendron* mentioning *E. velutina* as a synonym of *C. velutinum*, but the genus was also synonymized into *Erythrina* in Engler and Prantl (1894). Additional material: F (neg. 2378, photo of BW13100010), IAN (IAN001755, photo of F neg. 2378), MO (MO-1624337, photo n.v.; MO-1624338, photo n.v.).

(1) Desfontaines (1804) only mentioned the name *E. aculeatissima* in the Tableau de l'École de Botanique du Muséum d'Histoire Naturelle without giving any description, hence it is considered a *nomen nudum*. The name was considered doubtful by Krukoff (1938), but then was treated as a synonym of *E. velutina* by Krukoff and Barneby (1974), where the authors designated a collection in herbarium P as the type specimen.

- (2) Diels (1937) published *E. splendida* from Ecuador mentioning a collection from the province of Guayas in herbarium B (*Diels* 1230) as the type specimen, which was presumably destroyed in the bombing raid in 1943 (Botanischer Garten und Botanisches Museum Berlin 2022). No duplicate or any other collection by Diels could be found on digital databases, so a collection from the same locality was designated as the neotype.
- (3) Ridley (1890) published *E. aurantiaca* from a specimen in the archipelago of Fernando de Noronha (Pernambuco, Brazil), with a full description and an illustration of a leaf, inflorescence, dissected flowers, fruit and seeds. The name was later synonymized under *E. velutina* f. *aurantiaca* by Krukoff (1938) based solely on a different coloring of the seeds of some specimens in the archipelago. As there were no other morphological characters to support this form, as the seeds vary in color both in the archipelago and on the mainland in Pernambuco and other Brazilian states (Guedes-Oliveira et al. manuscript in preparation), the name was synonymized into *E. velutina* by Martins and Tozzi (2018). Additional material: HUEFS (HUEFS000248863, photo of K000206207).

Etymology. The specific epithet “*velutina*” is derived from Latin, meaning “velvety”, and was presumably chosen due to the abundance of trichomes in the species, especially on the petiole, abaxial leaflet surface, peduncle, pedicel, and calyx.

Vernacular names. According to Carvalho (2008) and herbarium records, *E. velutina* is generally known as “mulungu” in Brazil, and also as “mulungu-do-ceará” in the state of **Amazonas**; “bucaré” or “mulungu-da-flor-amarela” in **Ceará**, where it is also the motive for the name of the municipality of Mulungu; “muchôco” or “mulungá” in **Minas Gerais**; and “mulungu-da-caatinga”, “pau-de-coral”, “sanandiú”, “sananduva” or “suinã” (and spelling variations) in **São Paulo**.

11. *Erythrina verna* Vell., Fl. Flumin.: 304. 1829; Fl. Flumin. Icon. 7: tab. 102. 1831.

Fig. 11

= *Erythrina flammea* Herzog, Repert. Spec. Nov. Regni Veg. 7: 57. 1909. Type: Bolivia. Santa Cruz: “Häufiger Baum in den Savannenwäldchen der Hügel von Buenavista”, ca. 400 m, October 1907, *Herzog* 72 (holotype: Z [Z-000022779]). (1)

Type material. Brazil. Rio de Janeiro: “Maritimis habitat”, s.d., s.leg., s.n. (lectotype, designated by Martins and Tozzi 2018, pg. 401: illustration in Biblioteca Nacional Digital Brasil [mss1198656_106]; also in Vellozo 1831, tab. 102); Brazil. Rio de Janeiro: Sta. Maria Magdalena, September 1913, *Constantino* s.n. (epitype, designated by Martins and Tozzi 2018, pg. 401: RB [RB00176986!]; isoepitypes: K [K000931001], NY [NY00600987], U [U.1243354, U.1243356], US [US02339391]).

Notes. Vellozo (1829) published *E. verna* with a complete description, but without mentioning any type specimen. His illustration was published in Vellozo (1831), and Martins and Tozzi (2018) correctly designated it as the lectotype. However, as Vellozo’s illustration was an incomplete drawing of some

inflorescences and dissected flowers that could be easily mistaken for some other *Erythrina* species, Martins and Tozzi (2018) also correctly designated an epitype to represent the species better (Fig. 11).

- (1) Herzog (1909) validly published *E. flammea* from Bolivia with a complete description and mentioning the type specimen. The name was already synonymized under *E. verna* by Krukoff and Barneby (1974).

Etymology. The specific epithet “*verna*” is derived from Latin, meaning “*related to spring*”, and it was presumably chosen due to the association of the flowering period of the species to the beginning of the spring season in the state of Rio de Janeiro, Brazil (September).

Vernacular names. According to Carvalho (2014) and herbarium records, *E. verna* is generally known as “mulungu” in Brazil, and also as “corticeira” in the state of **Bahia**; “bico-de-papagaio”, “corticeira-ceboleiro”, “mulungu-de-flor-branca” or “suinã” (and spelling variations) in **Minas Gerais**; and “mulungú-de-várzea”, “suinã” or “suinã-da-Argentina” in **São Paulo**.

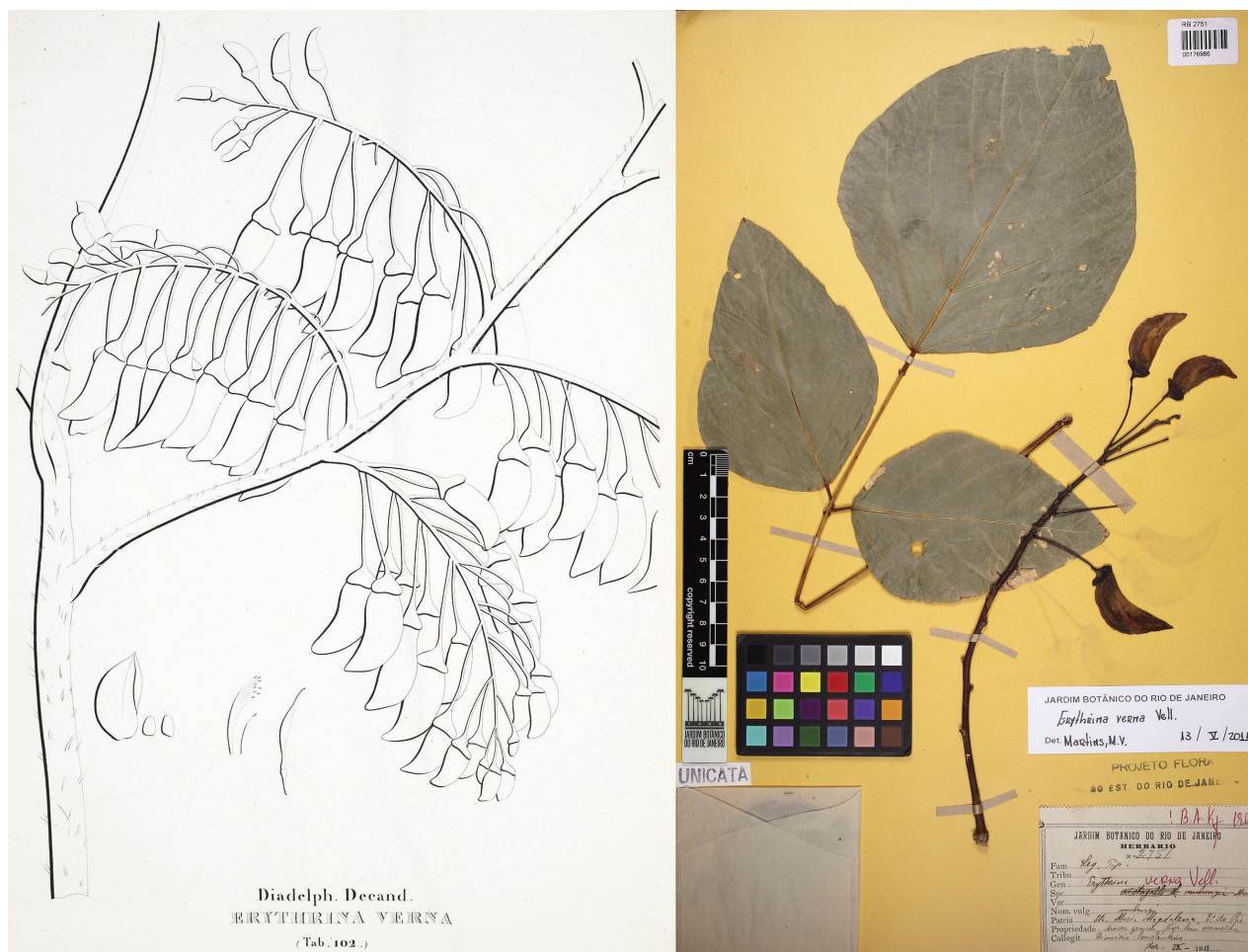


Figure 11. Left: Lectotype of *Erythrina verna* Vell. (1829: 304; 1831: tab. 102), designated by Martins and Tozzi (2018: 401). Source: Biblioteca Nacional Digital Brasil - Fundação Biblioteca Nacional, available at http://objdigital.bn.br/acer-vo_digital/div_manuscritos/mss1198656/mss1198656_106.html; **Right:** Epitype of *E. verna* Vell., designated by Martins and Tozzi (2018: 401). Source: Dimitri Sucre Herbarium (RB) – Botanical Garden of Rio de Janeiro via Reflora Virtual Herbarium, RB00176986.

Hybrid species

***Erythrina × fluminensis* Barneby & Krukoff, in Krukoff and Barneby, *Lloydia* 37(3): 446. 1974.**

Fig. 12

Type material. BRAZIL. Rio de Janeiro: “Guanabara, Horto Experimental do Aterro Glória-Flamengo; Culta de sementes recebidas de Bureau of Plant Introduction (U.S.A.). Cresceu no Horto do Museu Nacional e depois foi transplantada para o Aterro da Glória”, 26 August 1963, *Mello Filho* 2025 (holotype: R [R000117879, two sheets]; isotype: NY [NY00007994]).

Notes. There are no nomenclature issues with *E. × fluminensis*, as the name was validly published, and the type specimen was correctly cited (Fig. 12). The species is a hybrid between *E. fusca* Lour. and *E. speciosa* Andrews (Guedes-Oliveira et al. manuscript in preparation).

Etymology. The specific epithet “*fluminensis*” was based on the Portuguese word “fluminense”, which is derived from Latin meaning “inhabitant of river”. It was presumably chosen as a homage to the denomination of people born in the state of Rio de Janeiro, Brazil, where the hybrid species was first cultivated in the country and still exists to the day of this publication.

Vernacular names. There are no other known vernacular names for *E. × fluminensis* in Brazil besides the commonly used “mulungu”.



Figure 12. Holotype of *Erythrina × fluminensis* Barneby & Krukoff, in Krukoff and Barneby (1974: 446). Source: National Museum Herbarium (R) – Federal University of Rio de Janeiro via speciesLink, R000117879.

Unplaced or excluded names

1. *Erythrina velutina* Jacq., Pl. Hort. Schoenbr. 4: 34. 1804, auct., non Willd., Neue Schriften Ges. Naturf. Freunde Berlin 3: 426. 1801. nom. superfl.

Notes. Jacquin (1804) described *E. velutina* Willd. from a specimen cultivated in Schloss Schönbrunn (Austria), and this mention has been mistakenly considered as a new publication of this name. Moreover, his description matches *E. velutina* and even mentions Willdenow's publication. However, the accompanying illustration represents a different species, so the name authored by Jacquin remains unplaced.

2. *Erythrina secundiflora* Brot., Trans. Linn. Soc. Lond. 14: 346. 1824.

Type. PORTUGAL. Lisbon: "in Horto Regio Olisiponensi [Jardim Botânico de Lisboa], ad Aulam Regiam in Ajuda sitio, et alibi in Lusitania, ubi Martio Aprilique floret. Indigenam e Brasilia esse fertur", ex hort., s.d., s.leg. s.n. (lectotype, designated here: illustration in Brotero 1824, tab. 12).

Notes. Brotero (1824) published the species with a full description and a detailed illustration of leaves, inflorescence and dissected flowers. The description was based on a specimen cultivated at the Jardim Botânico de Lisboa and believed to have a native origin in Brazil. However, according to Krukoff (1938), the calyx as described and illustrated could indicate an association with the African *Erythrina* species, and not the American ones. Still, he pointed out that some characteristics depicted might be incorrect, so the name remains unplaced.

3. *Erythrina nervosa* DC., Prodr. 2: 413. 1825. Type: Unknown.

≡ *Corallodendron nervosum* (DC.) Kuntze, Revis. Gen. Pl. 1: 173. 1891.

Notes. The species was poorly described in De Candolle (1825) and remained as doubtful ever since its publication. Bentham in Martius (1859) believed it could be a native Brazilian species, but still maintained it as doubtful. According to Krukoff and Barneby (1974), this name is better placed as a synonym of *Callichlamys latifolia* (A.Rich) K.Schum. (Bignoniaceae).

4. *Erythrina corallodendrum* Vell., Fl. Flumin.: 304. 1829; Fl. Flumin Icon. 7: tab. 101. 1831, auct., non L., Sp. Pl. 2: 706. 1753.

Notes. Vellozo (1829) included a species called "*E. corallodendrum*" in his treatment of Brazilian *Erythrina* in Florae Fluminensis, with a description and an illustration published later in Vellozo (1831), but without mentioning any type specimen. This citation was then considered to be a record of the occurrence of *E. corallodendrum* L. in Brazil rather than a new publication of the same name. Hence, there is no record of this name in any digital databases.

However, Lima (1995) mentioned this name as being authored by Vellozo and placed it as a synonym of *E. speciosa*. The description and illustration given by Vellozo undoubtedly depict the unique morphological features of *E. speciosa*, but according to Recommendation 50D of Chapter VI of the ICN (Turland et al. 2018), “misidentifications should not be included in synonymies but added after them”, so we exclude the name here.

5. *Erythrina mediterranea* Vell., Fl. Flumin.: 305. 1829; Fl. Flumin Icon. 7: tab. 103. 1831.

Type. Brazil. São Paulo: “silvis mediterraneis transalpinis prope praedium Boavista”, s.d., s.leg. s.n. (lectotype, designated here: illustration in Biblioteca Nacional Digital Brasil [mss1198656_107]; also in Vellozo 1831, tab. 103).

Notes. The species was poorly described in Vellozo (1829) and the accompanying illustration in Vellozo (1831) depicts a sterile branch from a specimen growing in the municipality of Cunha, state of São Paulo (Pastore et al. 2021). According to Krukoff (1938), it could represent either *E. crista-galli* L. or *E. falcata* Benth. As it is impossible to even confirm it as *Erythrina*, the name remains unplaced.

6. *Erythrina adansonii* hort. ex Colla, Herb. Pedem. 2: 249. 1834. nom. nud.

Notes. Colla (1834) mentioned *E. adansonii* Hortul as a doubtful synonym of *E. crista-galli* L. However, as no other valid publication or description of this name was found elsewhere, it was excluded here as a *nomen nudum*.

7. *Erythrina argentea* Blume ex Miq., Fl. Ned. Ind. 1(1): 207. 1855. nom. nud.

Notes. Miquel (1855) mentioned *E. argentea* by Blume as synonym of *E. ovalifolia* Roxb. without any further information. As there was no other valid publication of this name elsewhere, it was excluded here as a *nomen nudum*.

8. *Erythrina compacta* hort. ex W.Bull, Cat. New Beautiful Rare Pl.: 4. 1871, nom. nud.; Carrière and André, Rev. Hortic.: 348. 1882, nom. nud.

≡ *Erythrina compacta* W.Bull ex K.Koch, Wochenschr. Vereines Beförd. Gartenbaues Konigl. Preuss. Staaten 14(20): 159. 1871, nom. nud.

Notes. Bull (1871) briefly described the aesthetic characteristics of a cultivated plant named *E. compacta* by horticulturists. Later in the same year, Koch (1871) mentioned the specimen cited by Bull, but only repeated his description. It was later also described by Carrière and André (1882), who observed that the specimen was just a more compact cultivated variety of *E. crista-galli*. According to Article 38 of the ICN (Turland et al. 2018), a name cannot be effectively published using a description of purely aesthetic features, which is the case for all three publications related to this name, thus all of them are excluded here as *nomen nudum*.

9. *Erythrina fusca* Lour. var. *inermis* Pulle, Nova Guinea 8(2): 651. 1912, auct., non *E. ovalifolia* Roxb. var. *inermis* Pulle, Nova Guinea 8(2): 651. 1912.

Notes. Krukoff and Barneby (1974) mentioned “*E. fusca* var. *inermis*” as a synonym of *E. fusca*, resulting in the publication of this name. However, as Pulle (1912) did not base his variety on *E. fusca* Lour. but on *E. ovalifolia* Roxb., the name is excluded here as misapplied.

10. *Erythrina moelebei* Vieill. ex Guillaumin & Beauvis., Ann. Soc. Bot. Lyon 38: 87. 1914, nom. nud.

Notes. Guillaumin and Beauvisage (1914) cited *E. moelebei* by Vieillard in a list of species from New Caledonia, but without giving any additional information. As there was no description of this name elsewhere and the type specimen cited (Vieillard 60) could not be found, the name remains unplaced. Krukoff (1939) treated it as a “hyponym” of *E. fusca* Lour. without seeing the type specimen as well.

11. *Erythrina dariensis* Standl., Contr. U.S. Nat. Herb. 18: 108. 1916, auct., non *E. darienensis* Standl., Contr. U.S. Nat. Herb. 18: 108. 1916.

Notes. Perkins and Payne (1970) misspelled *E. darienensis* Standl. as “*E. dariensis*”, which resulted in the publication of this name as well, so it is excluded here as misapplied.

12. *Erythrina indica* (sensu R.Vig.), Arch. Bot. Mém. 6. [1944?], auct., in Du Puy et al., Legum. Madagascar: 516. 2002, non Lam., Encycl. 2: 391. 1786.

Notes. This name was mentioned by Du Puy et al. (2002) as a synonym of *E. fusca* Lour. in their treatment of *Erythrina* in The Leguminosae of Madagascar. The protologue is cited by the authors as being published in 1944, but according to BHP these publications by Viguiier ranged only from 1927 to 1936. Moreover, some databases state that this name was used to refer to *E. fusca* Lour. As the original protologue could not be found, it remains unplaced.

Conclusions

The present work highlights the importance of comprehensive and detailed work regarding scientific nomenclature, showing that there are still many issues to address even in a relatively well-known genus like *Erythrina*. Despite the treatments proposed by Krukoff (1938) and Krukoff and Barneby (1974), and the more recent works by Martins (2014) and Martins and Tozzi (2018), in this revision it was possible to designate several new synonyms and type specimens for names related to Brazilian *Erythrina*. We also highlighted the knowledge gaps that remain and should be addressed in future works. Moreover, the ever-growing importance of virtual herbaria, online databases and

digital libraries with up-to-date and reliable scientific information is noteworthy mentioning. Virtually all type specimens and original protologues analyzed in this work were accessed via digital resources, which must remain available to any user through any electronic device with a reasonable internet connection.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Author ORCIDs

Ramon Guedes-Oliveira  <https://orcid.org/0000-0001-8122-0782>

Ana Paula Fortuna-Perez  <https://orcid.org/0000-0003-4977-4341>

Leandro Cardoso Pederneiras  <https://orcid.org/0000-0003-1822-227X>

Vidal de Freitas Mansano  <https://orcid.org/0000-0002-7204-0744>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

***Erythrina* L. of Brazil: nomenclatural revision**

Authors: Ramon Guedes-Oliveira, Ana Paula Fortuna-Perez, Leandro Cardoso Pederneiras, Vidal de Freitas Mansano

Data type: xlsx

Explanation note: Binomials concerning the 11 accepted Brazilian species of *Erythrina* L., chronologically ordered, with protologue information (year: page or illustration), current status, and references (year: page) related to them. See text in Guedes-Oliveira et al. (2023) for details about authorships, typifications and synonymies. In bold the currently accepted names.

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A new species of *Hiptage* (Malpighiaceae) from northwest Yunnan (China) based on molecular and morphological data

Tong-Tong Zhang^{1*}, Shu-Yun Yang^{1*}, Ke Tan², Ming-Xun Ren¹

¹ Key Laboratory of Genetics and Germplasm Innovation of Tropical Special Forest Trees and Ornamental Plants, Ministry of Education, Hainan University, Haikou 570228, China

² Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, Guangxi, China

Corresponding authors: Ke Tan (tank0507@126.com); Ming-Xun Ren (renmx@hainanu.edu.cn)

Abstract

Hiptage stenopterum K.Tan & M.X.Ren, a new species of *Hiptage* collected from a deep valley close to the Nujiang Gorge, northwest of Yunnan Province, China, is described and illustrated based on molecular and morphological data. The new species was found isolated in an entrenched valley of the Laowo River, a tributary of the Nujiang River, at the northern edge of the distribution range of the genus. *H. stenopterum* shares some morphological similarities with the narrowly endemic *H. incurvatum* and *H. lushuiensis*. However, *H. stenopterum* is easily distinguished by its oblanceolate lateral wing of winged mericarp, 10 to 12 calyx glands, and branchlets densely rusty tomentose. The new species status is also supported by molecular phylogenetic analyses based on nuclear ribosome internal transcribed spacer (nrITS), which showed distinct systematic boundaries from the most morphologically similar species, *H. incurvatum* and their morphological relatives, *H. lushuiensis*.

Key words: flora of Yunnan, Hengduan Mountains, *Hiptage*, Malpighiaceae, taxonomy



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Introduction

Hiptage Gaertn. (Gaertner 1791) is a large genus of Malpighiaceae, currently comprising ca. 40 species of woody shrubs or lianas growing at shrub forests or valleys on limestone hills or riverbanks of tropical Asia, such as Indo-China Peninsular, Malay Archipelago and Southern China (Sirirugsa 1991; Hô 1992; Srivastava 1992; Chen and Funston 2008; Ren 2015; Yang et al. 2018; Tan et al. 2019; Dong et al. 2020; Wei et al. 2022). *Hiptage* is derived from the Greek hiptamai, which means “to fly” and refers to its unique three-winged fruit. Such three-winged fruit means it is easily dispersed over long distances, explaining its widespread distribution in tropical Asia (Sirirugsa 1991; Srivastava 1992; Hô 1992; Chen and Funston 2008). Nonetheless, most species of this genus are narrow and endangered endemics, especially in the ravine and mountain peaks, such as *H. multiflora* F.N.Wei, *H. lushuiensis* S.P.Dong, K.Tan & M.X.Ren, and *H. incurvatum* K. Tan & M.X. Ren (Wei 2018; Tan et al. 2019; Dong et al. 2020). In recent years, five new species of *Hiptage* have been described. One species

* The authors contributed equally to this paper.

was found in Southern India (Sujana and Vadhyar 2020), and four were collected in Southwestern China (Yang et al. 2018; Tan et al. 2019; Dong et al. 2020).

Hiptage is currently classified within the Tetrapteroid clade, which is among the ten primary lineages identified for Malpighiaceae (Davis and Anderson 2010). Within that phylogenetic framework, *Hiptage* included six species and was resolved as closely related to *Flabellariopsis* R.Wilczek, a genus endemic to Africa. *Hiptage* and *Flabellariopsis* comprise a clade with weak support, sister to the Neotropical genus *Carolus* W.R.Anderson (Davis and Anderson 2010). Despite relying on a single marker (ITS) and yielding mainly weakly supported clades, recent molecular phylogenies of *Hiptage* indicate that *H. stellulifera* Arènes stands as the basal group within the genus (Tan et al. 2019; Almeida and van den Berg 2022).

During our fieldwork in the Hengduan Mountains, northwest of Yunnan Province, China, we collected specimens from a population of a distinct morphotype of *Hiptage* growing on a hillside in the valley of Laowo River, close to the Nujiang Gorge. After detailed analyses of morphological characters and molecular data of individuals from this population, we found out that this population is most morphologically similar to *H. incurvatum* and *H. lushuiensis*. But it differs in the number of calyx glands and the morphology of mericarp wings, both of which are critical morphological traits for species taxonomy in *Hiptage* (Chen and Funston 2008; Ren 2015). Therefore, we describe it as a new species, depicted and illustrated here.

Materials and methods

Taxonomy

Measurements and observations of morphological characters of the new species were based on fresh and herbarium specimens. Each character was measured across five individuals. Photographs of fresh plants and floral characteristics were taken in the field. The new species was compared with all type specimens of *Hiptage* in morphology from protologues and specimens in the herbarium (at the herbaria IBK, KUN, and IBSC). Images of type specimens of all *Hiptage* species were consulted from JSTOR Global Plants (<http://plants.jstor.org>), the Chinese Virtual Herbarium (<http://www.cvh.ac.cn>), and taxonomic literature (e.g., Yang et al. 2018; Tan et al. 2019; Dong et al. 2020). The morphological terminology follows Niedenzu (1924), Jacobs (1955), Anderson et al. (2006), Chen and Funston (2008), Ren (2015), and Almeida and Morais (2022). The conservation status assessments of the new species *H. stenopterum* were based on the International Union for Conservation of Nature guidelines (IUCN 2022).

Phylogenetic analysis

To verify the taxonomic status of the new species within *Hiptage*, we conducted a phylogenetic analysis using the nuclear ribosomal internal transcribed spacer (ITS) region. We downloaded ITS sequence data for 42 samples from GenBank (Table 1) encompassing 16 species of *Hiptage* and, based on the study of Almeida and van den Berg (2022), four species from the Tetrapteroid

clade serving as outgroups [i.e. *Callaeum psilophyllum* (A.Juss.) D.M.Johnson, *Heteropterys brunnea* R.Sebast. & Mamede, *Niedenzuella multiglandulosa* (A. Juss.) W.R.Anderson and *N. stannea* (Griseb.) W.R.Anderson] (Table 1). Dried leaf material of the proposed new species was collected from the type locality in a valley of the Laowo River, close to Lushui City (Yunnan, China). Five samples from the new species and three samples from *H. lushuiensis* were newly sequenced in this study to provide molecular evidence (Table 1). Total genomic DNA was isolated from dried leaf samples using a CTAB protocol adapted from Doyle and Doyle (1987). PCR amplification, in 25 µl reactions, comprised 1 µl of sample DNA, 12.5 µl of 2× Taq PCR Master Mix (Aidlab Biotechnologies Co. Ltd), 1µl of each primer (10 µmol/ml), with double distilled water making up the remainder. Amplification of the ITS region utilized primers ITS17SE and ITS26SE as per Sun et al. (1994). The amplification regime involved a 5 min initial denaturation at 94 °C, then 35 cycles of 40s at 94 °C, 20s at 69 °C, 1 min at 72 °C, and concluded with a 10 min extension at 72 °C. The resulting PCR products were bidirectionally sequenced on an ABI3730XL platform.

Table 1. Taxa, GenBank accession numbers, voucher numbers of *Hiptage* used in this study.

Species	Locality	GenBank Accession	Voucher Number
<i>Hiptage benghalensis</i> (L.) Kurz	Yangjie, Yunnan, China	MH718400	M. X. Ren & L. Tang 128 (HUTB)
	Menglian County, Yunnan, China	MH718422	S. P. Dong 131 (HUTB)
	Daxin County, Guangxi, China	MH718414	K. Tan & S. P. Dong 95 (HUTB)
	Lekang County, Guizhou, China	MH718415	K. Tan, S. P. Dong, & M. X. Ren 82 (HUTB)
	Singapore	MH718399	T. W. Yam 3334 (HUTB)
	Phatthaya, Thailand	MH718408	K. Tan, S. P. Dong, & M. X. Ren 3344 (HUTB)
	Chiangmai, Thailand	MH718410	K. Tan, S. P. Dong, & M. X. Ren 3336 (HUTB)
<i>H. multiflora</i> F.N.Wei	Nonggang National Nature Reserve, Guangxi, China	MH718424	K. Tan & S. P. Dong 52 (HUTB)
<i>H. stenopterum</i> K. Tan & M.X. Ren	Lushui City, Yunnan, China	OQ968812	tank 190402001 (HUTB)
		OQ968813	–
		OR417356	23tk041401(IBK)
		OR417357	23tk041402(IBK)
		OR417358	23tk041403(IBK)
<i>H. incurvatum</i> K. Tan & M.X. Ren	Pingpo Town, Yunnan, China	MK967956	K. Tan, H. L. Zheng, & M. X. Ren 201903309 (HUTB)
		MK967957	K. Tan, H. L. Zheng, & M. X. Ren 201903310 (HUTB)
		MK967958	K. Tan, H. L. Zheng, & M. X. Ren 201903305 (HUTB)
		MK967959	K. Tan, H. L. Zheng, & M. X. Ren 201903306 (HUTB)
<i>H. monopteryx</i> Sirirugsa	Phatthaya, Thailand	MH718407	K. Tan, S. P. Dong, & M. X. Ren 3337 (HUTB)
<i>H. marginata</i> Arènes	Hue, Vietnam	MH718413	K. Tan & Q. Yang 3363 (HUTB)
<i>H. detergens</i> Craib	KuiBuri, Thailand	MH718404	K. Tan, S. P. Dong, & M. X. Ren 3328 (HUTB)
	Sam Roi Yot, Thailand	MH718405	K. Tan, S. P. Dong, & M. X. Ren 3326 (HUTB)
<i>H. lucida</i> Pierre	Phatthaya, Thailand	MH718406	K. Tan, S. P. Dong, & M. X. Ren 38 (HUTB)
	Xishuangbanna, Yunnan, China	MH718418	Z. N. Qian & S. P. Dong120 (HUTB)
<i>H. subglabra</i> Arènes	Nui Chua National Park, Phan Rang, Vietnam	MH718427	K. Tan & S. J. Ling 3364 (HUTB)
<i>H. bullata</i> Craib	Lampang, Thailand	MH718412	K. Tan, S. P. Dong, & M. X. Ren 3320 (HUTB)

Species	Locality	GenBank Accession	Voucher Number
<i>H. minor</i> Dunn	Lekang County, Guizhou, China	MH718398	K. Tan, S. P. Dong, & M. X. Ren 79 (HUTB)
	Wenshan City, Yunnan, China	MH718423	K. Tan, S. P. Dong, & M. X. Ren 94 (HUTB)
	Lushui City, Yunnan, China	MH718401	K. Tan, S. P. Dong, & M. X. Ren 88 (HUTB)
<i>H. ferruginea</i> Y.H.Tan & Bin Yang	Xishuangbanna, Yunnan, China	MH718402	S. P. Dong 116 (HUTB)
	Xishuangbanna, Yunnan, China	MH718403	S. P. Dong 117 (HUTB)
<i>H. pauciflora</i> Y.H.Tan & Bin Yang	Menglian County, Yunnan, China	MH718420	S. P. Dong 73 (HUTB)
<i>H. umbellulifera</i> Arènes	Caná, Phan Rang, Vietnam	MH718426	K. Tan & S. J. Ling 3386 (HUTB)
	Phan Rang, Vietnam	MH718430	K. Tan & S. J. Ling 3399 (HUTB)
	Núi Chua National Park, Phan Rang, Vietnam	MH718428	K. Tan & S. J. Ling 3385 (HUTB)
<i>H. luzonica</i> Merr.	Luzon Island, Philippines	MH718425	K. Tan, W. Q. Xiang & M. X. Ren 20191181436 (HUTB)
	Palawan Island, Philippines	MH718432	K. Tan, W. Q. Xiang & M. X. Ren 3305 (HUTB)
	Cebu Island, Philippines	MH718431	K. Tan & W. Q. Xiang 3301 (HUTB)
<i>H. candicans</i> Hook.	Chiangmai, Thailand	MH718409	K. Tan, S. P. Dong, & M. X. Ren 3328 (HUTB)
	Chomthong, Thailand	MH718411	K. Tan, S. P. Dong, & M. X. Ren 3330 (HUTB)
<i>H. stellulifera</i> Arènes	NhaTrang, Vietnam	MH718429	K. Tan & S. J. Ling 3376 (HUTB)
<i>H. lushuiensis</i> S.P.Dong, K.Tan & M.X.Ren	Lushui City, Yunnan, China	OR471605	S. P. Dong 176 (HUTB)
		OR471606	S. P. Dong 177 (HUTB)
		OR471607	S. P. Dong 178 (HUTB)
<i>Heteropterys brunnea</i> R.Sebast. & Mamede	–	OK284366	RFAI Meida 579 (HUEFS)
<i>Callaeum psilophyllum</i> (A.Juss.) D.M.Johnson	–	OK268022	RFAI Meida 734 (HUEFS)
<i>Niedenzuella multiglandulosa</i> (A.Juss.) W.R.Anderson	–	OK271417	RFAI Meida 639 (HUEFS)
<i>Niedenzuella stannea</i> (Griseb.) W.R.Anderson	–	OK271412	Pott 1816 (HUEFS)

The sequencing results of ITS fragments were evaluated with PhyDE (Müller et al. 2010) for base confirmation and contiguous sequence editing. All sequences were manually aligned in MEGA v.7 (Kumar et al. 2016). Some erroneous sequencing results were excluded from the alignment range. The Bayesian inference (BI) and Maximum likelihood (ML) analyses were used in Phylosuite (Zhang et al. 2020) to construct the phylogenetic tree of *Hiptage*. The SYM+G4 model and the K2P+G4 model as the best-fit substitution model for ML and BI analysis, respectively, using ModelFinder (Kalyaanamoorthy et al. 2017) with Corrected Akaike Information Criterion (AICc). Bayesian Inference started with a random tree as a simulated tree, used a Markov chain Monte Carlo (MCMC) to run simulations for 10 million generations and sampled every 1000 generations, and was performed using MrBayes v3.2.5 (Ronquist et al. 2012). The first 2500 trees (25% of the total trees) were discarded as burn-in samples. The maximum likelihood (ML) analyses were accomplished with IQ-TREE v.2.0.6 (Nguyen et al. 2015) with 1000 bootstrap replicates. The final constructed phylogenetic tree was visualized in FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Results

The aligned matrix of ITS sequences consisted of 690 bp, of which 466 sites were identical, 132 (19.1%) were parsimony informative, and 92 parsimony-uninformative variable characters. The phylogenetic analysis showed that *Hiptage* is a monophyletic group (PP/BS=1/100), with *H. stellulifera* (PP/BS=1/100) being the first lineage to diverge, consistent with previous studies (Tan et al. 2019; Almeida and van den Berg 2022). The five samples of the proposed new species, *H. stenopterum*, formed a clade with strong support (PP/BS = 0.79/94) sister to a well-supported subclade alongside *H. incurvatum* (PP/BS=0.90/91) (Fig. 3). The results of molecular phylogenetics align with morphological observations, with the new species closely resembling *H. incurvatum* due to the presence of multiple glands. However, *H. stenopterum* is distinguished by its oblanceolate wings, a more significant number of calyx glands, and branchlets that are densely covered with rusty tomentose. Other features, like pedicels, differentiate the two species, as detailed in Table 2. The new species is also similar to *H. lushuiensis* due to the elliptic leaf blade and lanceolate bracteoles. However, there are significant discrepancies between the morphological and molecular phylogenetic findings (Fig. 2, Table 2). Especially in phylogenetics, *H. lushuiensis* was resolved as sister to *H. minor* (PP/BS = 1/99) (Fig. 2).

Table 2. Morphological comparison of key characteristics in *H. stenopterum*, *H. incurvatum*, *H. lushuiensis*, and the most widespread *H. benghalensis*.

Character	<i>H. stenopterum</i>	<i>H. incurvatum</i>	<i>H. lushuiensis</i>	<i>H. benghalensis</i>
Leaf blade	elliptic to oblong, 4.0–12.0 × 2.0–5.0 cm, 2 glands	elliptic, 6–12 × 5–4.5 cm, 10–16 glands	elliptic, 9–16 × 3.5–5.0 cm, 2 or more glands at the base	oblong, elliptic-oblong, or ovate-lanceolate, 9–18 × 3–7 cm, 2 glands
Branchlet	densely rusty tomentose	white to grey sericeous	white to grey sericeous	densely yellowish brown or silver-gray sericeous
Bracteole	lanceolate, ca. 0.5 cm long	lanceolate, 0.3–0.5 cm long	lanceolate, ca. 1.5 mm long	acute, 0.2–0.4 cm long
Pedicel	yellow-brown sericeous, 1.5–2.0 cm long	white sericeous, 1.5–2.5 cm long	white sericeous, ca. 1.5 cm long	sericeous, 0.8–2.5 cm long
Calyx gland	10(–12), two large, ca. 3.0 × 1.0 mm, basally coalescent two smaller adnate to the apex of the two big glands separately, 0.4–0.5 mm diam.; remaining glands 1.8–2.0 × 0.8–1.0 mm, oblong; not decurrent to the pedicel	4(–6), two large, ca. 3.0 × 1 mm, basally connate, remaining glands 0.4–0.5 mm diam., round; not decurrent to the pedicel	2, ca. 1 mm diam., free, sometimes with additional smaller glands on the other sepals, not decurrent along the pedicel	1, very large, oblong, lanceolate to oblanceolate; more or less 1/2 adnate onto the pedicel
Sepal	elliptic to oblong, ca. 0.5 cm long	elliptic to oblong, ca. 0.5 cm long	elliptic, 0.4–0.5 cm long	broadly elliptic or ovate, 0.5–0.6 cm long
Petal	suborbicular, white to light white-pink, 1.0–1.5 × 0.8–1.2 cm	suborbicular, white to light white-pink, ca. 1 × 0.8 cm	suborbicular, pink, ca. 1 cm long	ovate-oblong to suborbicular, white, ca. 1 cm long
Claw	1 mm long, pubescent	1 mm long, pubescent	1 mm long, pubescent	1–2 mm long, glabrous
Posterior lateral wing	oblanceolate, ca. 4.2 × 0.8 cm	ovate, ca. 3.6 × 1.3 cm	ovate, ca. 3.5 × 1.3 cm	oblong, elliptic or obovate-lanceolate, 3–5 × 1–1.6 cm
Anterior lateral wing	lanceolate to linear, straight, ca. 2.5 × 0.4 cm	lanceolate, arcuate back to the middle, ca. 2.3 × 0.7 cm	lanceolate, ca. 2.0 × 0.9 cm	lanceolate-oblong, 1.5–3 cm long

Discussion

The zygomorphic, mirror-image, and floral structure of *Hiptage* represents a distinct evolutionary trait of biological significance that promotes adaptability (Ren et al. 2013; Qian et al. 2016). Currently, the presence, shape, and number of calyx glands, as well as their attachment to the pedicel, are critical diagnostic features for species identification in *Hiptage* (Sirirugsa 1991; Srivastava 1992; Chen and Funston 2008; Yang et al. 2018; Tan et al. 2019; Almeida and van den Berg 2022). However, Almeida and van den Berg (2022) contend that the presence and number of calyx glands in *Hiptage* are highly homoplastic and unsuitable for circumscribing infrageneric ranks. Calyx glands in *Hiptage* might be an evolutionary adaptation to attract myrmecophilous interactions for herbivore defense (Ren et al. 2013; Qian et al. 2016). Therefore, the absence and number of calyx glands may be related to local herbivorous insects, which are a significant factor in promoting speciation (McCall and Irwin 2006; Ramos and Schiestl 2019). Based on long-term field observations, we believe that although there is a slight probability of variation in the number of calyx glands, the overall characteristic remains relatively stable. In summary, we believe that the absence and number of calyx glands still hold significance in the infrageneric classification of *Hiptage*. However, it should be properly carried out in future phylogenetic studies to establish a new monophyletic infrageneric classification system.

Morphologically, *H. stenopterum* shares specific characters with *H. incurvatum* and *H. lushuiensis* in having elliptic leaf blades, lanceolate bracteoles, white to light pink flowers, and suborbicular petals. Based on the phylogeny tree, *H. incurvatum* is closely related to the new species, while *H. lushuiensis* clusters with *H. minor*, which has non-reflexed petals. Not only do the petals differ in posture, but there are also significant morphological differences between *H. lushuiensis* and *H. minor* such as the number of calyx and leaf blade glands, and leaf size (Chen and Funston 2008; Dong et al. 2020). Their clustering together might be due to the limited genetic information from just the ITS region and more comprehensive molecular data will be needed in the future to explain this curious relationship.

Malpighiaceae is characterized by an unparalleled diversity of winged fruits in angiosperms (Anderson et al. 2006; Manchester and O'Leary 2010; Tan et al. 2018). Winged mericarps are an adaption for wind dispersal of fruits (Tan et al. 2018), suggesting that such morphological adaptations have significantly facilitated long-distance dispersal and speciation (Davis et al. 2001, 2002; Tan et al. 2018, 2019). Notably, the wings of *H. stenopterum* distinctly deviate from its phylogenetically proximate taxa, *H. incurvatum*. Moreover, these two taxa are partitioned by the Hengduan Mountains, implying that differing aerodynamic conditions, perhaps governed by localized wind patterns, might have driven morphological divergence. Furthermore, the type localities of *H. stenopterum* and *H. incurvatum*, encircled by high mountains and deep gorges, constitute a distinct isolated habitat, which restricts gene flow and facilitates speciation.

Taxonomy

Hiptage stenopterum K.Tan & M.X.Ren, sp. nov.

urn:lsid:ipni.org:names:77326071-1

Fig. 1

Diagnosis. *Hiptage stenopterum* is most similar to *H. incurvatum* K.Tan & M.X.Ren by branchlets densely rusty tomentose (vs white to grey sericeous), leaf blades with 2 glands near the base (vs 10–16 glands), 10(–12) calyx glands [vs 4 (–6)], the posterior lateral wing oblanceolate (vs ovate), anterior lateral wings straight, lanceolate to linear (vs arcuate back to the middle, lanceolate).

Type. CHINA. Yunnan Province: Lushui City, Laowo River, 25°50'08"N, 98°54'28"E, 1071 m alt., 2 Apr. 2019, K. Tan 190402001 (Holotype: HUTB!; Iso-type: HUTB!, IBK00450922!).

Description. Woody shrubs; young branches densely rusty tomentose, hairs adpressed, older twigs glabrous, with white or greenish lenticels, rounded, coarse warts dotted. **Leaves** opposite; stipules absent; petiole ca. 0.5 cm long, round, tomentose, with yellowish brown hairs, eglandular; leaf blades 4.0–12.0 × 2.0–5.0 cm, coriaceous, elliptic to oblong; young leaves densely rusty tomentose on both surfaces; mature leaves green, glabrous, base obtuse or broadly cuneate, margin plane, apex acuminate, abaxially often with 2 marginal glands near the base; lateral veins in 5–8 pairs, both surfaces prominently. **Thyrses**, terminal or axillary; main axis 4.0–13.0 cm long, rusty tomentose; peduncle 1.0–2.5 cm, rusty sericeous; bracteoles ca. 0.5 cm long, lanceolate. **Flowers** white to slightly pink; pedicels 1.5–2.0 cm long, densely rusty tomentose; sepals 5, 4.5–5.5 × 1.5–2.5 mm, elliptic to oblong, apex obtuse, margin slightly revolute, abaxially densely rusty tomentose, adaxially glabrous. **Calyx glands** 10(–12), prominent, not decurrent to the pedicel, often 1 pair of glands at base abaxially; two large, 2.3–2.8 × 0.8–1.2 mm, connate at the base, two smaller glands, 0.4–0.5 diam., rounded, adnate to the apex of the two larger glands separately; remaining glands small and free, 0.5–0.6 × 0.8–1.0 mm, oblong, attached to the margins of other sepals, occasionally one or two glands lacking. **Petals** 5, 1.0–1.5 × 0.8–1.2 cm, white to light white to pink, basally yellow, extremely reflexed, suborbicular, margin ciliate, claws ca. 1 mm long, base subcordate to rounded, apex roundish, abaxially densely white tomentose, adaxially glabrous. **Stamens** 10, basally fused or free, glabrous, differing in size, pollen sacs rimose; one larger, filament 10–12 mm long, yellowish green, circinate, anther oblong, 1.8–2.0 × 0.7–1.0 mm; 9 smaller stamens, filament 4–6 mm long; anthers oblong, 1–1.3 × 0.7–0.9 mm. **Ovary** ca. 2 mm in diam., ovoid, white to rusty tomentose; style 1, yellowish green, 10–13 mm long, slightly curved upwards, deflected either to the left or right side, glabrous; stigma apical. **Mericarps** 3, wings pink with yellow-green base, rusty sericeous, posterior lateral wing 3.8–4.5 × 0.7–0.9 cm, oblanceolate, apex roundish or lobed slightly, base obtuse, anterior lateral wings 2.4–3.0 × 0.3–0.6 cm, lanceolate to linear; areole ca. 4–6 mm, approximately triangular. **Seeds** angular–globose, 3–5 mm, dark yellow or brown.

Phenology. Flowering in March and fruiting from March to May.

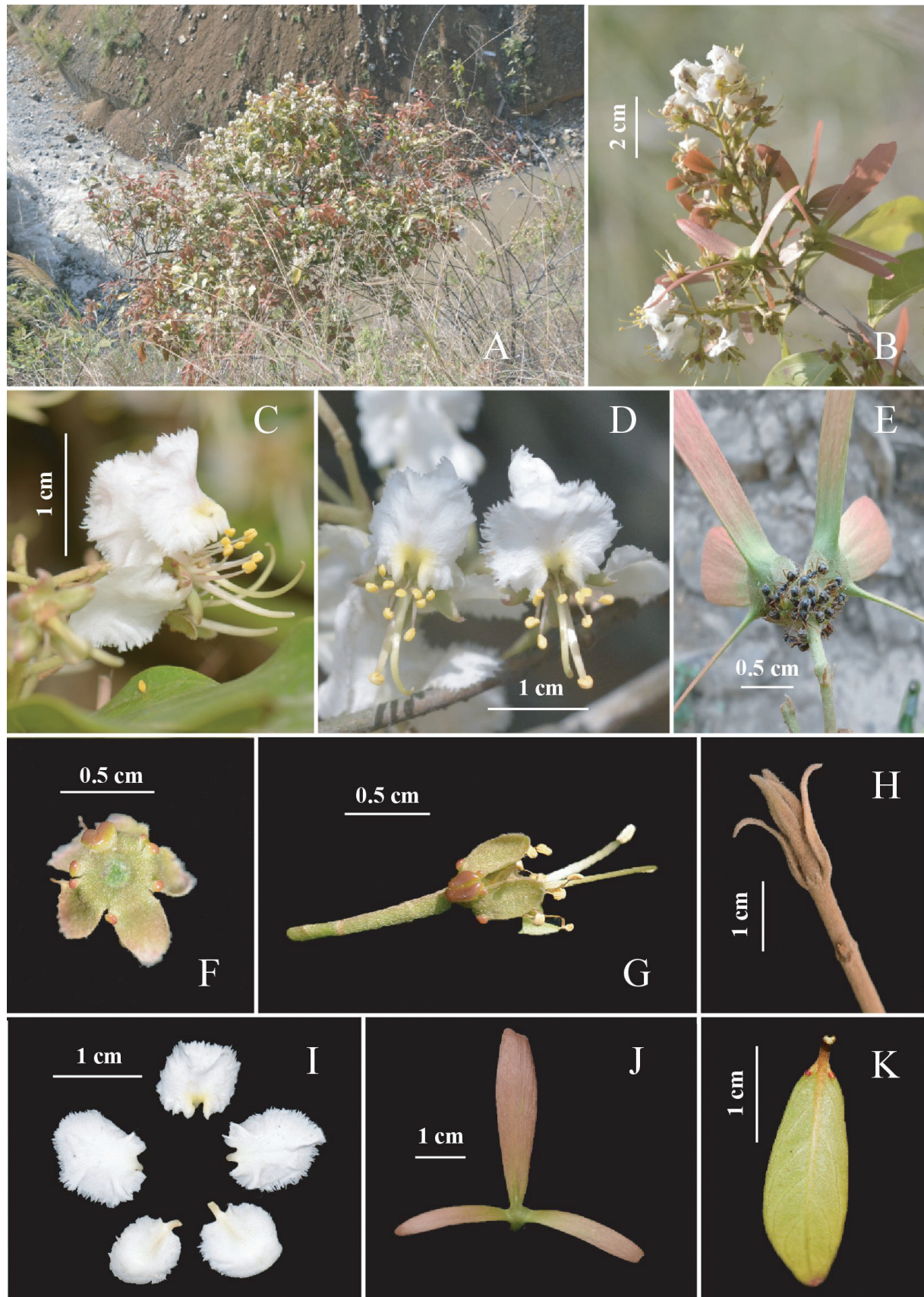


Figure 1. *Hiptage stenopterum* **A** habit **B** flowering branch **C** flower in side view **D** flowers in frontal view **E–G** calyx glands (**E** calyx glands with secretions attracting ants) **H** young branch (showing densely rusty tomentose) **I** petals **J** winged mericarp **K** young leaf. Photos **A**, **B** by M.X. Ren, **E** by T.T. Zhang, and **C**, **D**, **F–K** by K. Tan.

Etymology. Its specific epithet reflects the long and narrow mericarp wings of *Hiptage stenopterum*.

Vernacular name. Chinese: 狭翅风筝果(xiá chì fēng zhēng guǒ). The name 'xiá chì' means its long and narrow wings, and 'fēng zhēng guǒ' is the Chinese name of *Hiptage*.

Habitat and distribution. *H. stenopterum* is only known from a valley of the Laowo River, a tributary of the Nujiang River, at an elevation ca. 1,000 m, near Lushui City, northwest of Yunnan Province, China (Fig. 2).

Conservation status. Since the only known population of *H. stenopterum* is in an entrenched valley of Nujiang River in the northwest Yunnan Province, we have not discovered the wild population outside of the abovementioned place, information known about the population status and natural distribution range of the new species is very limited. Currently, only about 20 individuals are found in the valley. Therefore, we suggest that the new species *H. stenopterum* should be considered Data Deficient (DD) according to current IUCN Red List Categories and Criteria (IUCN 2022).

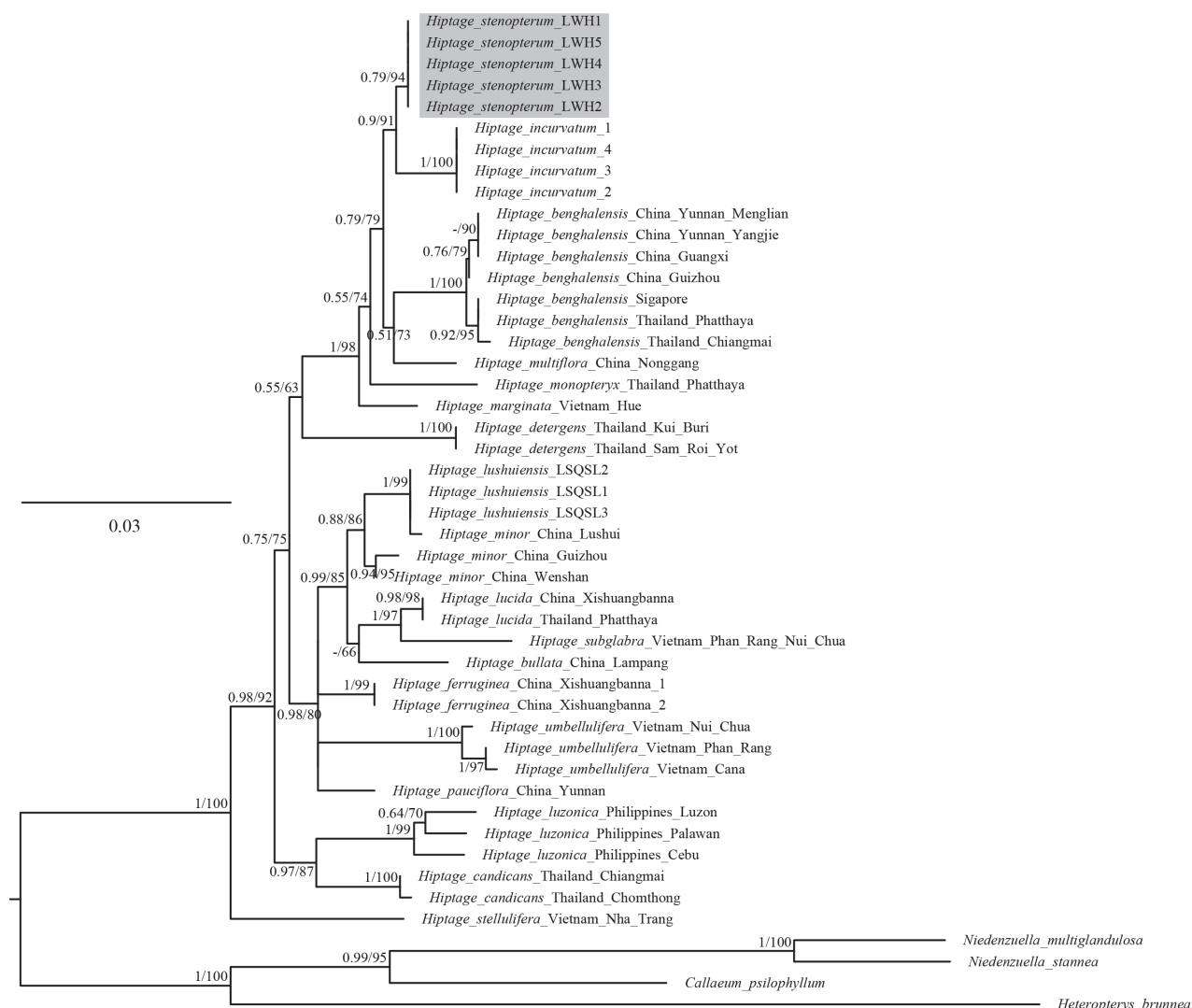


Figure 2. Molecular phylogenetic tree of *Hiptage* based on ITS sequences. Bayesian posterior probability (PP) and ML bootstrap values (BS) are shown above branches as PP/BS (only shown if BS > 50%).

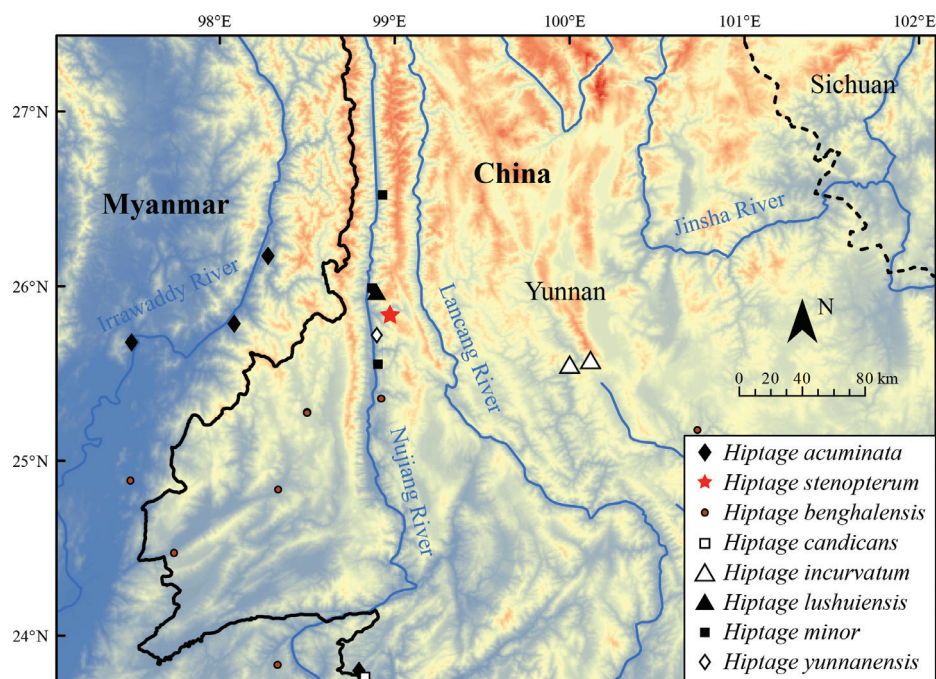


Figure 3. Distribution map showcasing the new species, *Hiptage stenopterum*, alongside the other seven species of the genus found in adjacent regions

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

All authors have contributed equally.

Author ORCIDs

Tong-Tong Zhang <https://orcid.org/0009-0003-9812-2718>

Shu-Yun Yang <https://orcid.org/0009-0000-8129-5194>

Ke Tan <https://orcid.org/0000-0002-9036-163X>

Ming-Xun Ren <https://orcid.org/0000-0002-4707-2656>

Data availability

All of the data that support the findings of this study are available in the main text.

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Stauranthera floribunda, a new species of Gesneriaceae from Yunnan, China

Fan Su^{1,2,3*}, Xiao-Wei Qin^{1,2,3*}, Yun-Lei Wang¹, Ren-Fen Wang^{4,5}, Chao-Yun Hao^{1,2,3}, Ke Tan^{4,5}

¹ Spice and Beverage Research Institute, CATAS, Wanning 571533, Hainan, China

² Ministry of Agriculture Key Laboratory of Genetic Resources Utilization of Spice and Beverage Crops, Wanning 571533, Hainan, China

³ Hainan Provincial Key Laboratory of Genetic Improvement and Quality Regulation for Tropical Spice and Beverage Crops, Wanning 571533, Hainan, China

⁴ Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, Guangxi, China

⁵ Gesneriad Committee of China Wild Plant Conservation Association, National Gesneriaceae Germplasm Resources Bank of GXIB, Gesneriad Conservation Center of China (GCCC), Guilin 541006, Guangxi, China

Corresponding authors: Chao-Yun Hao (haochy79@163.com); Ke Tan (tank0507@126.com)

Abstract

Stauranthera floribunda F.Su, C.Y.Hao & K.Tan, a new species of Gesneriaceae from Yunnan, China, is described and illustrated here. It is morphologically similar to *S. grandifolia* Benth. in the shape of corolla, stigma, leaves and the number of stamens. However, it can be readily distinguished from the compared species by its dense cymes, leaf indumentum, lack of a corolla spur, calyx colour and stamen shape. The description of the new species, photographs, detailed descriptions, notes on etymology, distribution and habitat, as well as comparisons with morphologically similar species, are provided.

Key words: China, Flora of Yunnan, Gesneriaceae, new taxon, *Stauranthera*



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Introduction

Stauranthera Benth. (1835) is a genus of perennial herbs in Gesneriaceae. Originally, this genus was established, based on the species *S. grandifolia* Benth. from the Malay Peninsula. The genus has previously been considered to comprise ca. 13 species distributed in Northeast India and South China throughout Malesia to New Guinea (Willis 1973; Burt 1984). However, the taxonomic delimitation of the genus *Stauranthera* has been revised considerably over time, with *S. brandisii* C.B.Clarke being moved into *Rhynchocheilum* Blume, *Stauranthera johannis-winkleri* Kraenzl. was synonymised with *S. argyrescens* Hallier f., *S. chiritiflora* Oliver and *S. tsiangiana* Hand-Mazz. were transferred to the new genus *Whytockia* W.W.Sm. in which *Stauranthera chiritiflora* is the type of *Whytockia* (Smith 1919; Burt 1984). Merrill (1923) synonymised both *Stauranthera ecalcarata* R.Br. and *S. philippinensis* Elmer with *S. caerulea* (Blume) Merr. (Merrill 1923). Currently, the genus comprises ca. five species recognised by Möller et al. (2016), with two of them being recorded in China, namely *S. umbrosa* (Griffith) C.B.Clarke in Guangxi, Hainan and

* These authors contributed equally to this paper.

Yunnan and *S. grandifolia* Benth. in Yunnan and Hainan (Zhu et al. 1996; Qin and Xing 2006; Wei 2018; Wen et al. 2019; Huang and Liu 2023), respectively. Meanwhile, these two species were also documented in northern Vietnam, a region bordering the distribution area of *Stauranthera* in China (Wei et al. 2022). Additionally, *S. coerulea* (Blume) Merr., a Malesian species, was also introduced to northern Vietnam (Wei et al. 2022).

During a floristic expedition to Yunnan Province in 2022, the authors found an unknown species of Gesneriaceae near the Sino-Vietnamese border at Jinping County, China. Based on features like opposite, unequal leaves, small opposite bracts, a campanulate corolla tube with a basal spur, an indistinctly 2-lipped limb with a 2-lobed adaxial lip and 3-lobed abaxial lip, four included stamens and basifixed anthers connate into a shallow cone, this species appears to belong to the genus *Stauranthera*. However, detailed morphological comparisons to protologues and type specimens of all previously-described *Stauranthera* species revealed it does not match any known species. Thus, we confirmed that it as a new species, described and illustrated here as *S. floribunda* F.Su, C.Y.Hao & K.Tan. We provide a formal description of the new species and an updated key for the genus in China.

Materials and methods

Morphological studies of the new species were based on the type specimens deposited in the Herbaria IBK and NPH and the living plants cultivated in the Spice and Beverage Research Institute, CATAS and Gesneriad Conservation Centre of China (GCCC). All available specimens of *Stauranthera* stored in the Herbaria AU, BM, E, G, HITBC, IBK, IBSC, K, KUN, PE and WU were examined from online specimen images via the Chinese Virtual Herbarium (CVH, <https://www.cvh.ac.cn/index.php>) and JSTOR (<https://plants.jstor.org>). Measurements of morphological characters were based on living plants whose photographs were taken with a Nikon D750 digital camera (Tokyo, Japan) and Dino-Lite digital microscope (Taiwan, China) and the morphological characters described using the terminology presented by Wang (1990) and Wang et al. (1998). Morphological comparison with close species was based on consultation with published literature. The conservation status evaluations of the new species *S. floribunda* were based on the International Union for Conservation of Nature Guidelines (IUCN 2022).

Taxonomy

***Stauranthera floribunda* F.Su, C.Y.Hao & K.Tan, sp. nov.**

urn:lsid:ipni.org:names:77326354-1

Figs 1, 2

Diagnosis. The new species resembles *Stauranthera grandifolia* in leaf blade shape and corolla, but can be easily distinguished from the latter in the flower number of cymes 2–4 bushes (vs. cymes 1–2 bushes), calyx colour white to slightly purple (vs. green), and bract 1, bracteole 1 auriculate connate (vs. bracts 2, linear opposite) and ovary 1-loculed (vs. 2-loculed) (Table 1).

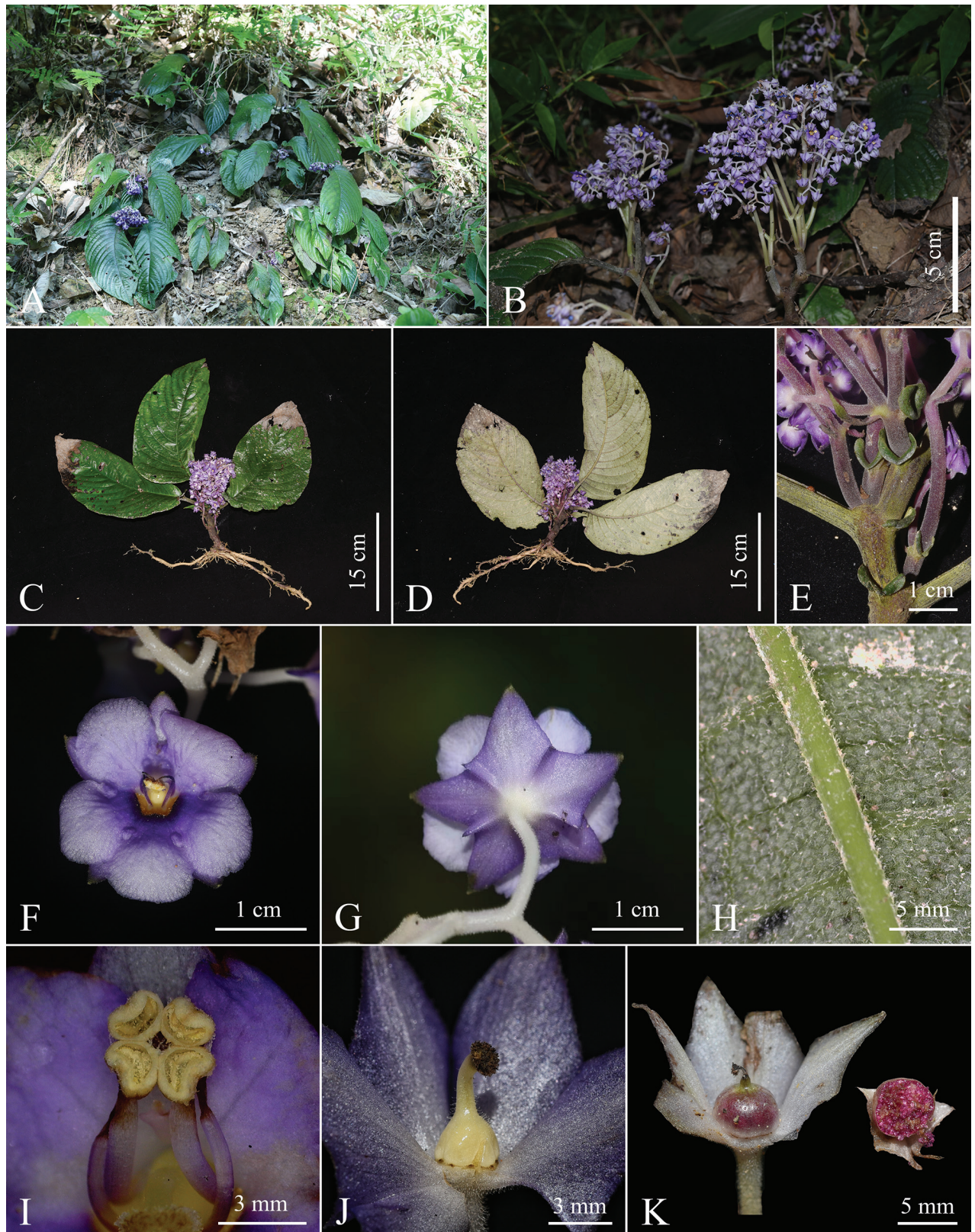


Figure 1. *Stauranthera floribunda* F.Su, C.Y.Hao & K.Tan, sp. nov. **A** habit **B** cymes **C**, **D** adaxial and abaxial views of the whole plant **E** degenerated leaves **F** front view of flower **G** back view of flower **H** detail of abaxial leaf blade **I** detail of stamens **J** detail of pistil **K** ovary and its cross-section view. Photographs by Fan Su.

Table 1. Morphological comparison of key characteristics in *S. floribunda* and *S. grandifolia*.

Characters	<i>S. floribunda</i>	<i>S. grandifolia</i>
Stem	6–28 cm tall, 5–12 mm in diam., puce, pulverulent	10–30 cm tall, 3–10 mm in diam., dark brown, pubescent
Leaf blade	leaves opposite, usually 3–5 pairs, with a normal leaf and a degenerated leaf at the internode, leaf blade strongly oblique, 14–28 cm long, 6–15 cm wide, adaxial surface glabrous, abaxial surface including leaf veins papillose-puberulent	leaves opposite, usually 2–5 pairs, with a normal leaf and a degenerated leaf at the internode, leaf blade strongly oblique, 12–27 cm long, 4–9 cm wide, abaxially pubescent or nearly glabrous, except leaf veins
Leaf vein	lateral veins 10–13 on the narrow side, 13–20 on the wide side	lateral veins 8–11 on the narrow side, 12–14 on the wide side
Petiole	4–6 cm long	1–3 cm long
Degenerated leaves	4–8 mm long	3–4 mm long
Bracts	bract 1, bracteole 1, auriculate connate	bracts 2, linear opposite
Cymes	2–4 bushes	1–2 bushes
Corolla	corolla purple or bluish-purple, throat yellowish; corolla tube ca. 5 mm long, orifice ca. 4 mm in diam.; no short spur	corolla blue-white, throat yellowish; corolla tube ca. 2.1 cm long, orifice ca. 10 mm in diam.; short spur at the base of the corolla
Calyx	white to slightly, purple	green
Stamens	4, adnate to ca. 5 mm above the corolla base, filaments linear, lilac, smooth, outside two ca. 4 mm long, anthers about 1.2 mm long, sides connected to each other.	4, adnate to ca. 3 mm above the corolla base, filaments linear white pilose, outside two ca. 3 mm long, anthers about 1 mm, sides connected to each other.
Pistil	ca. 9 mm long	ca. 5 mm long
Ovary	subuliform, ca. 5 mm long, ca. 4 mm in diam., 1-located, glandular puberulent about the position from the top to 1/3 of the ovary, the rest of ovary glabrous	ovoid. ca. 2 mm long, 2-loculed, glandular puberulent, covering the entire upper portion of the ovary
Style	linear, sparsely glandular-puberulent from the bottom to 2/3 of the style, the rest of style glabrous; stigma 1, covered by densely brownish puberulent hairs.	style sparsely white pilose, short; stigma large-capitate or bilamellate

Type. CHINA. Yunnan Province: Jinping Miao, Yao and Dai Autonomous County, Jinshuihe Town, Nawo, Rubber Forest, 22°37'42.30"N, 103°07'08.89"E, 316 m alt., 1 June 2023, *Fan Su 2023061* (Holotype: IBK! IBK00451428; Isotypes: NPH! NPH 001940, NPH 001941, NPH 001942).

Description. Perennial Herbs, terrestrial, not rhizomatous, up to 35 cm high. **Stem** 6–28 cm tall, 5–12 mm in diam., puce, pulverulent. **Leaves** opposite, usually three pairs, occasionally five pairs, with a normal leaf and a degenerated leaf at the internode, leaf blade strongly oblique, oblong to elliptic obovate, 14–28 cm long, 6–15 cm wide at the middle, apex acuminate, base cuneate on narrow side, broadly cuneate to rounded on wider side, margin nearly entire, adaxially glabrous, abaxially including leaf veins papillose-puberulent, lateral veins 10–13 on the narrow side; 13–20 on the wider side; petiole 4–6 cm long, ca. 4 mm in diam., puberulous; degenerated leaves, sessile, adaxially green, abaxially greenish, pubescent, cordate to auricular-cordate to auricular-reniform, 2–4 mm long, 8–12 mm wide, margin entire, apex retuse or emarginate, leaf vein 3 pairs. **Inflorescence** dichotomous cyme, emerging from the axils of the large leaves, 3–9 cymes per plant, dense flowers, 10–20, rare 5 flowers per cyme, peduncles, pedicels, bracts, calyx densely white pubescent, sticky, peduncle up to 18 cm high; pedicels 1.5–2 cm long; bract 1, bracteole 1, green, auriculate connate; calyx broadly campanulate, ca. 2 cm in diam., white to slightly purple, 5-lobed, lobes deltoid, margin entire, longitudinally wrinkled between lobes. **Corolla** slightly obliquely campanulate, purple or bluish-purple, throat yellowish; corolla tube ca. 5 mm long, orifice ca. 4 mm in diam., upper lip ca. 8 mm long, 2-lobed, lobes suborbicular, ca. 4 mm in diam.,

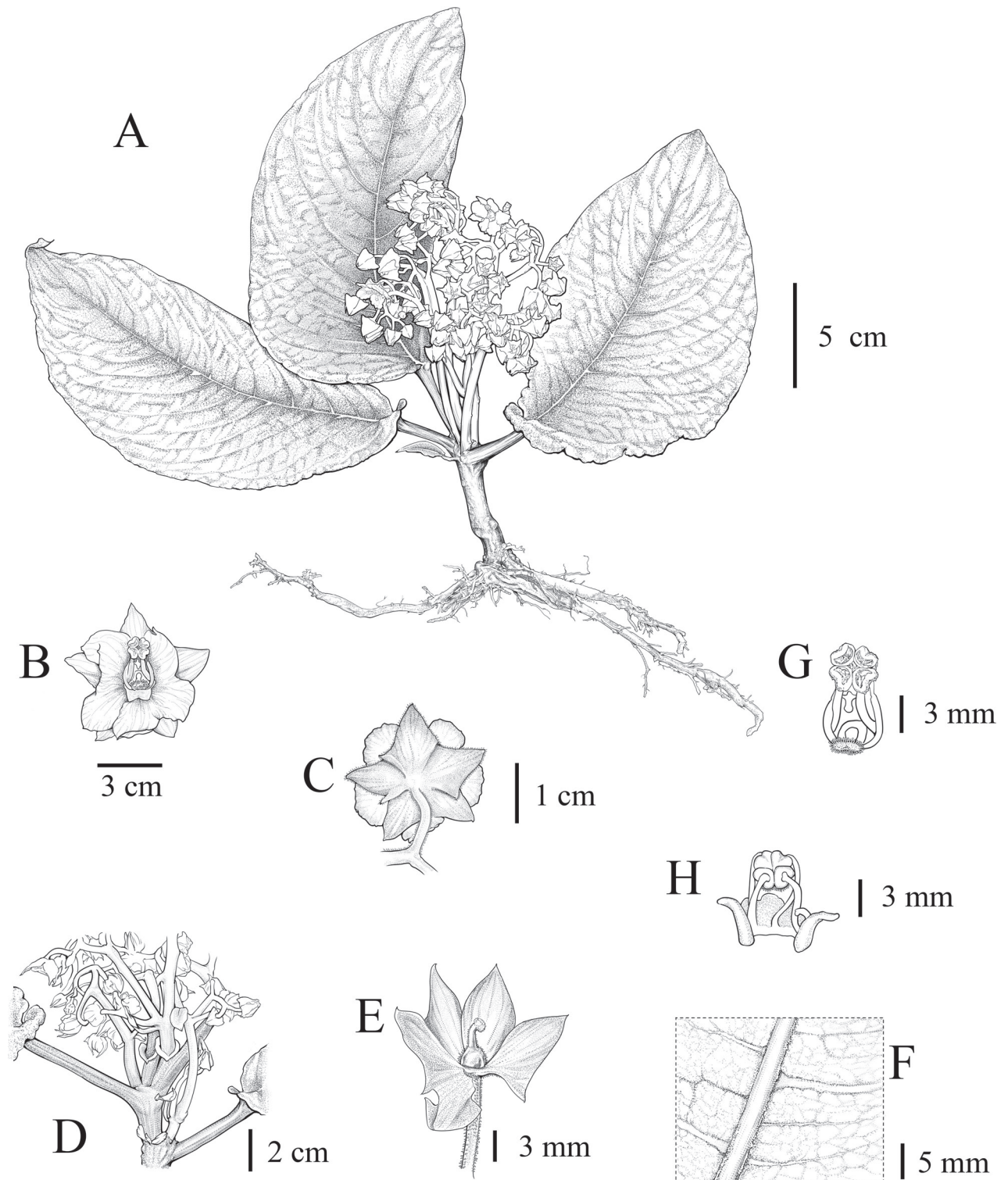


Figure 2. Line drawing of *Stauranthera floribunda* F.Su, C.Y.Hao & K.Tan **A** adaxial view of the whole plant **B** front view of flower **C** back view of flower **D** detail of degenerated leaves **E** pistil **F** hair of abaxial leaf blade **G** frontal view of stamens **H** dorsal side of stamen. Drawn by Di Hu.

lower lip slightly smaller than the upper lip. **Stamens** 4, adnate to ca. 5 mm above the corolla base, glabrous, filaments linear, lilac, smooth, inside two ca. 5 mm long, ca. 0.5 mm in diam., outside two ca. 4 mm long, ca. 0.3 mm in diam.; anthers triangular to cordate, ca. 1.2 mm long, sides connected to each

other, dorsal septum slightly raised. **Pistil** ca. 9 mm; **Ovary** yellowish, subuliform, ca. 5 mm long, ca. 4 mm in diam., 1-located glandular puberulent about the position from the top to 1/3 of the ovary, the rest of ovary glabrous; **Style** ca. 3 mm long, linear, sparsely glandular-puberulent from the bottom to 2/3 of the style, the rest of style glabrous; stigma 1, covered densely brownish puberulent hairs. **Capsule** globose to oblatoid, glabrous, brownish-purple when young, brownish-black when mature.

Phenology. Flowering in May and fruiting from June to July.

Etymology. The specific epithet *floribunda*, which means “many-flowered”, refers the large numbers of the flowers per cyme and the whole plant of the new species. It is noticeably different from the flower numbers of all other known *Stauranthera* species.

Vernacular name. Chinese: 多花十字苣苔 (*duō huā shí zì jù tāi*). The name ‘*duō huā*’ means it has more flowers than other species in this genus and ‘*shí zì jù tāi*’ is the Chinese name of *Stauranthera*.

Habitat and distribution. Up to date, *Stauranthera floribunda* is only known in Nawo of Jinshuihe Town, Jinping County, at an elevation ca. 316 m, near Vietnam, south of Yunnan Province, China. The main companion species were *Alocasia odora* (G.Lodd.) Spach, *Pellionia radicans* (Siebold & Zucc.) Wedd., *Thunbergia grandiflora* (Roxb. ex Rottler) Roxb. and *Oplismenus compositus* (L.) P.Beauv.

Preliminary conservation status. Since the only known population of *Stauranthera floribunda* is in the Rubber Forest of Jinshuihe Town, Jinping County, south Yunnan Province, we have not discovered the wild population expected from the above-mentioned location and information known about the population status and natural distribution range of the new species is very limited. Currently, less than 150 individuals have been found in the Rubber Forest. The new species of population, which grows close to a country road, is potentially threatened by human activities. Although no such habitat destruction is currently occurring, this population will likely be threatened in the foreseeable future under the influences of artificial factors, such as rubber cutting. Considering the known population is surrounded by rubber forests, it might survive under strong man-made intervention. Therefore, we suggest that the new species *S. floribunda* should be considered ‘**Critically Endangered**’ [CR, B2a,b (iii,iv,v)], facing a relatively high risk of extinction in the wild) according to current IUCN Red List Categories and Criteria (IUCN 2022).

Key to the species of *Stauranthera* in China

- 1 Bracts opposite, linear, corolla blue-white, upper lip ca. 7 mm long, 2-lobed, lower lip ca. 13 mm long, 3-lobed, short spur at the base of the corolla.....***S. grandifolia***
- 1 bract, 1 bracteole, corolla white to purple or blue, upper lip ca. 8 mm long, 2-lobed, lower lip ca. 14 mm long, 3-lobed, no short spur at the base of the corolla.....**2**
- 2 Cymes dense, calyx broadly campanulate, white to slight purple.....***S. floribunda***
- Cymes lax, calyx lobes broadly triangular, green.....***S. umbrosa***

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.


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Author contributions

Data curation: YLW. Formal analysis: RFW. Investigation: CYH. Writing - original draft: XWQ, FS. Writing - review and editing: KT, CYH.

Author ORCIDs

Fan Su  <https://orcid.org/0000-0001-7223-6133>

Xiao-Wei Qin  <https://orcid.org/0000-0002-4930-0632>

Ren-Fen Wang  <https://orcid.org/0009-0009-7881-3080>

Chao-Yun Hao  <https://orcid.org/0000-0002-7541-852X>

Ke Tan  <https://orcid.org/0000-0002-9036-163X>

Data availability




All of the data that support the findings of this study are available in the main text.

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Mitreola quanruii (Loganiaceae), a new species from a karst region in Guangxi, China

Renchuan Hu¹, Xiaowen Liao², Binsheng Luo³, Cheng Liu⁴, You Nong¹, Lei Wu²

¹ Guangxi Key Laboratory of Traditional Chinese Medicine Quality Standards, Guangxi Institute of Chinese Medicine and Pharmaceutical Science, Nanning 530022, China

² College of Forestry, Central South University of Forestry and Technology, Changsha 410004, China

³ Lushan Botanical Garden, Jiangxi Province and Chinese Academy of Sciences, Lushan 332900, China

⁴ CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China
Corresponding author: Lei Wu (wuleiibk@163.com)

Abstract

Mitreola quanruii, a new species from Guangxi, China, is described and illustrated in this study. It is morphologically similar to *M. liuyanii* because of the terete stems, creeping and branched at the base, the leaves which are pilose on both surfaces and the bilobed capsules with two erect horns. The new species can be distinguished from *M. liuyanii* by its taller habit, up to 20–50 cm tall, its linear leaves, 4–18 × 0.3–1 cm with acuminate apex and 8–10 pairs of lateral veins, its narrowly triangular stipules, its linear bracts, ca. 1.0 cm long and glabrous and its glabrous calyx. *Mitreola quanruii* is temporarily assessed as data deficient (DD) according to IUCN. The habitat of *Mitreola quanruii* is extremely fragile. Therefore, this species deserves close attention and protection.

Key words: China, Loganiaceae, *Mitreola*, new taxon, taxonomy



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Introduction

Mitreola L. (Linnaeus 1758) is a genus of the family Loganiaceae with pan-tropical distribution (Chen 1995). It is generally characterised by cymose inflorescences, 5-merous flowers, cleft styles, half-inferior and bilocular ovaries and bilobed capsules with two erect or incurved horns (Leeuwenberg 1974; Wang 2018; You et al. 2020). The genus comprises about 17 species distributed in Africa, America, Asia, Oceania and the Pacific islands (Leenhouts 1962, 1972; Leeuwenberg and Vidal 1972; Leeuwenberg 1974; Li and Leeuwenberg 1996; Islas-Hernández et al. 2019; Li 2020; Liu et al. 2022). Some new species of this genus have been discovered and reported in recent years (Shan et al. 2019, 2021; You et al. 2020; Liao and Chen 2021; Liu et al. 2022). Southern and south-western China is the diversification centre of *Mitreola* and ca. 14 species have been recorded in this area so far. Of these, eleven species, most of them found in limestone areas, are endemic to the country (Fang et al. 1995; Li and Leeuwenberg 1996; Ma et al. 2010; Yu et al. 2017; Shan et al. 2019, 2021; You et al. 2020; Liao and Chen 2021; Liu et al. 2022).

Guangxi is located in the south of China. It has geomorphologically diverse landscapes, complex terrain, warm climate, abundant rain, abundant sunshine and other natural conditions, which breed rich and unique plant diversity. A total of 8,892 native plant species have been recorded in Guangxi, including 889 endemic plant species (Wei 2019). As one of the diversification centres of *Mitreola*, Guangxi has a total of seven species, amongst which five species are endemic to Guangxi and are karst obligate species (Yu et al. 2017; Wei 2019).

During our ethnobotanical field survey in Nandan County, northern Guangxi, in 2020, we collected a peculiar population of *Mitreola* with linear leaves, which was quite different from known species in the region. In the following three years, the same species was documented flowering and fruiting regularly at the same site. Careful comparison of the morphological and anatomical features of the collected taxon with other *Mitreola* species led us to believe that the taxon which we collected from Nandan differs from all the previously described species of *Mitreola*.

Materials and methods

Several specimens were collected under evergreen broad-leaved forests in the hill region of Nandan County, Wuai Town, Tonggong Village from 2020 to 2022 and were deposited in the Herbaria CSFI, GXMI, IBK and KUN. The photographs of the plants were taken with a Panasonic LX100 camera. A detailed comparison with all other heretofore known *Mitreola* species was undertaken, including specimens deposited at CSFI, GXMG, GXMI, IBK, IBSC, HIB, KUN, PE, SYS and descriptions from botanical websites (e.g. <http://www.cvh.ac.cn/>, <https://plants.jstor.org/>). Herbarium acronyms follow Thiers (updated continuously). The morphological characters are described according to the terminology presented by Li and Leeuwenberg (1996) and the conservation status is assessed according to the IUCN Red List Categories and Criteria (IUCN 2022).

Taxonomic treatment

Mitreola quanruii L.Wu & R.C.Hu, sp. nov.

urn:lsid:ipni.org:names:77326465-1

Figs 1, 2

Diagnosis. *Mitreola quanruii* is most similar to *M. liuyanii*, but can be distinguished from the latter by its larger plant height up to 20–50 cm tall (vs. up to 9 cm), its linear leaves, 4–18 × 0.3–1 cm (vs. leaves oblanceolate, 0.4–5.6 × 0.2–1 cm) with acuminate apex (vs. apex acute to rounded) and 8–10 lateral veins on each side of the mid-rib (vs. 4–6 pairs), its narrowly triangular stipules (vs. stipules linear), its linear bracts, ca. 1.0 cm long and glabrous (vs. bracts narrowly lanceolate, 2–3 mm long, sparsely pilose on abaxial surface) and its glabrous calyx (vs. abaxial surface of calyx sparsely pilose).

Type. CHINA. Guangxi Zhuang Autonomous Region: Nandan County, Wuai Town, Tonggong Village, growing in limestone areas, under evergreen broad-leaved forests, rare, 24°54'29.65"N, 107°21'43.83"E, 235 m a.s.l., 31 Mar 2021 (fl.), R.C. Hu HRC210331003 (holotype: GXMI051178!, isotypes: CSFI!, IBK!, GXMI051179!).

Description. Perennial herb, up to 20–50 cm tall. Stems terete, creeping, branched at the base, bearing adventitious roots; internodes 1–5 cm long,

shoots sparsely pilose. Leaves opposite, papery, linear, 4–18 × 0.3–1 cm, pilose on both surfaces, base decurrent and narrowly cuneate, apex acuminate, margin ciliate, lateral veins 8–10 on each side of the mid-rib. Petioles 3–8 mm long, sparsely pilose. Stipules narrowly triangular, ca. 1 mm long, interpetiolar. Cymes terminal, 2–3-branched, many-flowered; peduncles slender, 3–8 cm long, glabrous; bracts linear, ca. 1.0 cm long, glabrous; bracteoles narrowly triangular, 1–2 mm long, glabrous; pedicels ca. 1 mm long, glabrous. Calyx lobes 5, ovate, ca. 1.3 × 1 mm, glabrous, margin membranous. Corolla urceolate, white, ca. 2 mm in diam. tube 1.3–1.7 mm long; lobes 5, ovate, 1.0–1.3 × 1.3–1.8 mm, glabrous, except for a ring of long hairs at the throat. Stamens 5, inserted near the middle of the corolla tube, glabrous, filaments ca. 0.8 mm long, anthers broadly ovate, ca. 0.3 mm long. Ovary semi-inferior, bilocular, ca. 0.5 × 1.3 mm, ovules numerous per locule; style ca. 1.2 mm long, free at base, stigma capitate. Capsules glabrous, bilobed, connate for 2/3rds of their length, with two erect horns, 1.2–3 mm long, sepals persistent at the base.

Phenology. Flowering from March to April; Fruiting from May to June.

Distribution and habitat. *Mitreola quanruii* is found growing on a watery stone wall near a rivulet, under evergreen broad-leaved forests in the hill region of Nandan County, Guangxi, China.

Preliminary conservation status. According to currently available data, *Mitreola quanruii* is only found in its type locality and there are only 63 adult plants and 21 seedlings in an area of ca. 450 m² (30 × 15 m). Further detailed investigation of similar habitats is needed to give a better understanding of the species' natural distribution and abundance. *Mitreola quanruii* is temporarily assessed as data deficient (DD) according to IUCN (IUCN 2022). At the type locality of *Mitreola quanruii*, only a small area of native vegetation remains along the creek, surrounded mostly by plantation forests. The habitat of the *Mitreola quanruii* is extremely fragile. Therefore, this species deserves close attention and protection.

Additional specimens examined. CHINA. Guangxi Zhuang Autonomous Region: Nandan County, Wuai Town, Tonggong Village, under evergreen broad-leaved forests, rare, 24°54'29.65"N, 107°21'43.83"E, 235 m a.s.l., 27 May 2021 (fr.), R.C. Hu HRC210527003 (GXMI!); *ibid.*, 28 March 2023 (fl.), Y. Nong NY230328 (GXMI!), *ibid.*, 23 April 2021 (fl.), C. Liu 21CS20379 (KUN!).

Etymology. We dedicate this new species of *Mitreola* to Prof. Quanru Liu for his substantial contributions to botanical research and education in China.

Vernacular name. The Chinese name is proposed as xiàn yè Dù Liáng Cǎo (线叶度量草), which means that the leaves are linear.

Taxonomic notes. *Mitreola quanruii* is most similar to *M. liuyanii* because they share terete stems, creeping and branched at the base, leaves pilose on both surfaces and bilobed capsules with two erect horns. However, *M. quanruii* is well distinguished from *M. liuyanii* by its linear leaves, 4–18 × 0.3–1 cm (vs. leaves narrowly oblanceolate, 0.4–5.6 × 0.2–1 cm), with acuminate apex (vs. apex acute to rounded) and 8–10 lateral veins on each side of the mid-rib (vs. 4–6 pairs); its linear bracts (vs. bracts narrowly lanceolate). Additionally, it is morphologically similar to *M. pingtaoi* in the conspicuous, terete stems, the white corollas, the linear bracts and the capsules with two erect horns, but it differs from *M. pingtaoi* in having linear leaves, 4–18 × 0.3–1 cm (vs. leaves obovate, 2–8 × 1.2–3 cm), glabrous bracts and calices (vs. bracts and calices

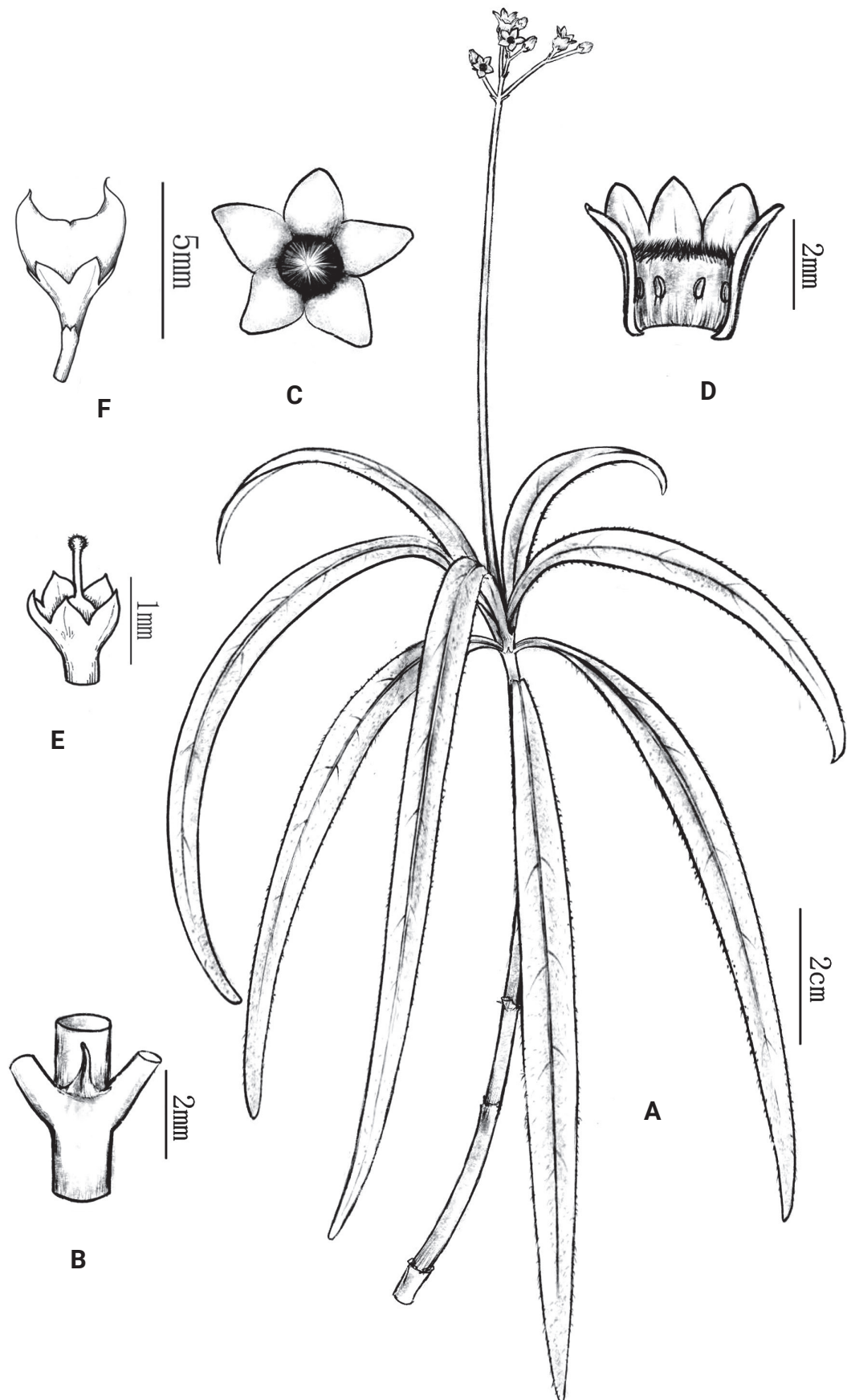


Figure 1. *Mitreola quanruii* L. Wu & R.C. Hu. **A** flowering branch **B** stipule **C** top view of flower **D** longitudinally opened corolla showing the position of the stamens and the hair ring in the throat **E** ovary, calyx, style and stigma **F** lateral view of fruit.

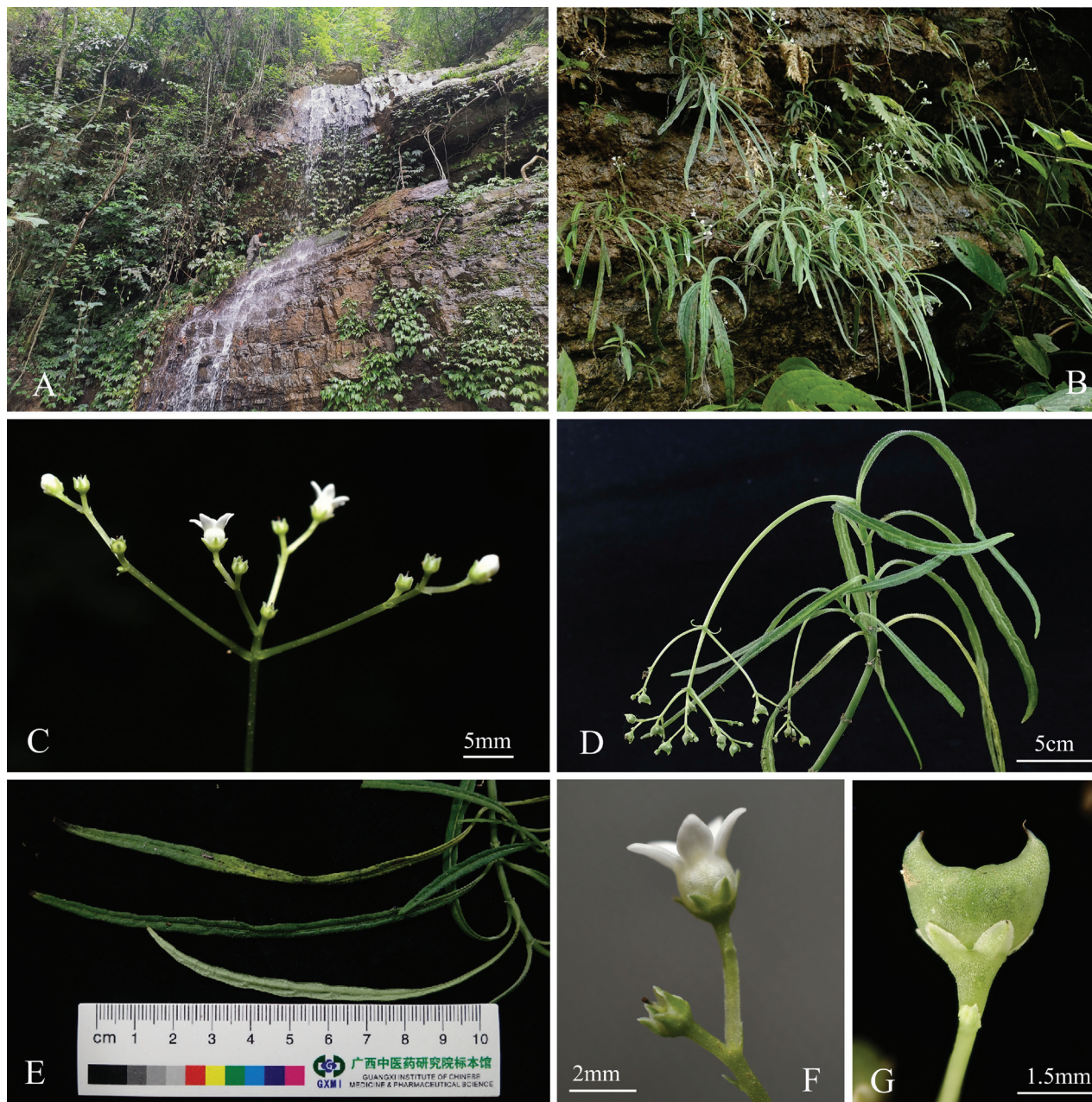


Figure 2. *Mitreola quanruii* L.Wu & R.C.Hu. **A** habitat **B** habit **C** inflorescence **D** fruiting branch **E** leaves **F** lateral view of flower **G** lateral view of fruit.

tomentose). Morphologically, *M. quanruii* is easily distinguishable from other species of *Mitreola* by its linear leaves. A key to the species of *Mitreola* in China is provided below.

Discussion

Karst ecosystems are renowned for their distinct vegetation and high biodiversity, offering exceptional habitats that foster speciation and radiation (Myers et al. 2000; Biswas 2009). The genus *Mitreola* predominantly comprises limestone obligate and narrowly distributed species (Yu et al. 2017; Shan et al. 2019, 2021; Wei 2019; You et al. 2020; Liao and Chen 2021; Liu et al. 2022).

Notably, recent publications have reported new species of *Mitreola* exclusively found in the limestone region of southwest China (Shan et al. 2019, 2021; You et al. 2020; Liao and Chen 2021; Liu et al. 2022). This region boasts the most extensive karst formations globally and is recognised as one of China's three unique floristic centres, as well as a vital area for global biodiversity conservation efforts (Yu et al. 2017). In recent years, scientists have discovered and documented an increasing number of new plant species, including Annonaceae, Gesneriaceae and Magnoliaceae in this area (Hu et al. 2022; Li et al. 2022; Liu et al. 2022; Yang et al. 2023). Consequently, with further advancements in biodiversity surveys, it is expected that numerous additional species of *Mitreola* will be identified and published within the limestone regions of southwest China and northern Vietnam, potentially bringing the total count of species within this genus to thirty.

This highlights the limestone region's ability to support rich plant diversity and endemism, while providing favourable conditions for *Mitreola*. Moreover, the unique landforms in this area have likely accelerated the diversification of *Mitreola*. Consequently, comprehensive surveys and studies on the phylogenetic evolution of *Mitreola* within the limestone areas of southwest China will yield significant scientific insights into floristic geography and the phylogeny of *Mitreola* in this particular region.

Key to species of *Mitreola* in China

- 1 Leaves linear *M. quanruii* L.Wu & R.C.Hu, sp. nov
- Leaves elliptic, ovate, lanceolate or oblanceolate 2
- 2 Stems inconspicuous; leaves in a basal rosette, sessile or subsessile 3
- Stems conspicuous, creeping or erect; leaves opposite, petiolate 5
- 3 Leaves elliptic to oblong-elliptic, 3.5–7 cm long with acute apex and the veins on the lower leaf surface purple; capsule horns incurved
..... *M. purpureonervia* D.Fang & X.H.Lu
- Leaves spatulate or oblanceolate, 7–37 cm long, with obtuse or rounded apex and green veins; capsule horns erect 4
- 4 Leaf blades with 5–7 lateral veins on each side of the mid-rib; bracts narrowly triangular; stamens inserted at the middle of the corolla tube
..... *M. spathulifolia* D.Fang & L.S.Zhou
- Leaf blades with 7–10 lateral veins on each side of the mid-rib; bracts oblong; stamens inserted at the throat *M. macrophylla* D.Fang & D.H.Qin
- 5 Stems 4-angled 6
- Stems terete 9
- 6 Annuals; corolla tube as long as lobes; capsule horns usually curved inwards *M. petiolata* (J.F.Gmel.) Torr. & A.Gray
- Perennials; corolla tube longer than lobes; capsule horns or lobes erect 7
- 7 Corolla lobes blue; stamens inserted at the base of the corolla tube
..... *M. crystallina* Y.M.Shui & W.H.Chen
- Corolla lobes white; stamens inserted at the middle of the corolla tube 8
- 8 Leaves glabrous; stipules with glandular hairs at the margin; peduncles 1–2.5 cm long *M. reticulata* Tirel
- Leaves abaxially pubescent when young; stipules glabrous at the margin; peduncles 3–7 cm long *M. pedicellata* Benth.

- 9 Stems erect; stamens inserted at the base of the corolla tube **10**
- Stems erect or creeping; stamens inserted at or near the middle of the corolla tube **11**
- 10 Annuals; leaf blades ovate, 0.5–2 cm long, apex obtuse ***M. petiolatoides* P.T.Li**
- Perennials; leaf blades not ovate, 1–10 cm long, apex acute ***M. liui* X.L.Du & Z.J.Mu**
- 11 Leaf blades obovate or oblanceolate, with 4–6 lateral veins on each side of the mid-rib **12**
- Leaf blades elliptic, with 7–10 lateral veins on each side of the mid-rib **13**
- 12 Leaf blades narrowly oblanceolate, 0.6–7.4 × 0.2–1 cm ***M. liuyanii* C.Liu & M.Q.Han**
- Leaves obovate, 2–8 × 1.2–3 cm ***M. pingtaoi* D.Fang & D.H.Qin**
- 13 Plant 3.0–8.5 cm tall; leaf blades bullate; calyxes purplish-red; corollas light purple ***M. bullata* Y.S.Chen & J.J.Liao**
- Plant 8–60 cm tall; leaf blades smooth; calyxes green; corollas white **14**
- 14 Leaves 4–10.2 × 1.8–3.8 cm, apex acute; capsules with two erect horns.. ***M. yangchunensis* Q.X.Ma, H.G.Ye & F.W.Xing**
- Leaves 3–5 × 1–1.6 cm, apex pungent; capsules with two horns curved inwards..... ***M. lincangensis* Z.J.Mu, Z.J.Shan & B.Pan**

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Wu Lei and Hu Renchuan conceived of and designed the study. Hu Renchuan, Liao Xi-aowen, Nong You, and Liu Cheng conducted data collection. Hu Renchuan, Nong You and Luo Binsheng integrated the inventory and its analysis. Hu Renchuan wrote the manuscript. All authors read and approved the final manuscript.

Author ORCIDs

Renchuan Hu  <https://orcid.org/0000-0002-0941-7203>

Xiaowen Liao  <https://orcid.org/0000-0003-2652-2862>

Cheng Liu  <https://orcid.org/0000-0001-7146-2542>

Data availability

All of the data that support the findings of this study are available in the main text.

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Craspedostauros nazmii sp. nov., a new diatom species (Bacillariophyta) from the Turkish Coast of the Black Sea

Elif Yılmaz^{1,2}, Andrzej Witkowski¹, Neslihan Özdelice³, Cüneyt Nadir Solak², Romain Gastineau¹, Turgay Durmuş³

¹ Institute of Marine and Environmental Sciences, University of Szczecin, Mickiewicza 16A, Szczecin, PL70–383 Poland

² Department of Biology, Faculty of Science and Art, Kütahya Dumlupınar University, 43000 Kütahya, Türkiye

³ Istanbul University, Faculty of Science, Department of Biology, 34134 Istanbul, Türkiye

Corresponding author: Elif Yılmaz (elif.yilmaz@phd.usz.edu.pl)

Abstract

Craspedostauros E.J. Cox is a diatom genus comprising 17 taxa reported from various regions of the world. While many species of *Craspedostauros* are epibiontic, the taxa have variable ecological preferences. In this study we formally describe *Craspedostauros nazmii* sp. nov., an epilithic species discovered along the Turkish Black Sea Coast, based on light and scanning electron microscopy. *Craspedostauros nazmii* sp. nov. is characterized by valves that are lanceolate to narrowly lanceolate, slightly constricted near the apices with uniseriate, parallel throughout the whole valve, transapical striae and the presence of an apical silica flap. The areolae are distributed over the valve face and the mantle. The differences and similarities between *C. nazmii* sp. nov. and established species of *Craspedostauros* are discussed. Based on shape and morphometrics, the most similar species is *Craspedostauros capensis*, but it is easily distinguished from *C. nazmii* sp. nov. by its lack of an apical silica flap.

Key words: Apical silica flap, Black Sea, *Craspedostauros*, epilithic marine diatom



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Introduction

The genus *Craspedostauros* E.J.Cox, 1999 was established to accommodate several marine species previously included in *Stauroneis* Ehrenberg (Lange-Bertalot and Genkal 1999; Cox 1999). As the latter genus comprised mostly fresh-water species, a separation was proposed by different authors to accommodate the marine species with regards to their autecology and morphological differences. Species strictly conforming with *Stauroneis* Ehrenberg are characterized by naviculoid valves with two girdle appressed chloroplasts and possess a distinct and large central area called stauros (Round et al. 1990). The valves in *Stauroneis* are flat and the girdle is composed of a few plain copulae that is always rather narrow (Krammer and Lange-Bertalot 1986; Round et al. 1990; Cox 1999).

When establishing the genus *Craspedostauros*, Cox (1999) referred to cytological (shape and number of chloroplasts) and ultrastructural characteristics (cribrate occlusions of areolae), also leading her to point out an affinity with *Mastogloia* Thwaites ex W. Smith (1856). With regards to these affinities,

Craspedostauros has been included in Mastogloioaceae with a recommendation to also move *Achnanthes* Bory sensu stricto (Cox 1999; Cox and Williams 2006) there. The molecular phylogeny published by Ashworth et al. (2017) and inferred from a 3 genes dataset (18S, *rbcL* and *psbC* genes) tends to associate *Craspedostauros* to *Achnanthes* and *Staurotropis*, but clearly distinguishes them from *Mastogloia* spp., strongly questioning the monophyly of the Mastogloiales. This group of genera was later referred to as CAS genera, for *Craspedostauros-Achnanthes-Staurotropis* by Mann et al. (2021), whose phylogenetic works surprisingly tended to associate the CAS genera with Bacillariaceae. However, the lack of support at the nodes or strong morphological evidences led the authors to consider this result unlikely, probably resulting from an artefact of genes/species sampling and they emphasized the need for deeper phylogenomic investigations in order to elucidate the position of the CAS genera.

As a genus, *Craspedostauros* is relatively small, with 15 taxonomically accepted species listed on AlgaeBase, to which could be added two recently described taxa from Antarctica (Trentin et al. 2022). Thus, there remains a potential for the description of new species in unexplored habitats such as tropical coasts and biofilms on seaweeds in particular (Risjani et al. 2021; Witkowski unpublished observations).

The Turkish Republic is surrounded by four different seas, namely the Eastern Mediterranean Sea, the Aegean Sea, the Marmara Sea and the Black Sea. *Craspedostauros decipiens* was found in the Sea of Marmara (Witkowski et al. 2000; Akçaalan and Kaleli 2021) but this is so far the only species of *Craspedostauros* discovered in Turkish Black Sea waters. The Black Sea is a semi-closed sea located in southeastern Europe. It is considered an isolated sea since the Dardanelles and Bosphorus straits limit water exchange with the Mediterranean Sea. This semi-closure influences both sea water characteristics (typical salinity) as well as the dispersal potential of aquatic species inhabiting both sides of the straits (Nevrova et al. 2013). Studying the diatoms of the Black Sea may be of additional interest for science in that they may represent flora of an ancient marine basin isolated due to limited water exchange over a fairly long geological time period (Witkowski et al. 2010).

Investigations of the diatom flora of the Black Sea go as far back as the works of Mereschkowsky (1902), whose research resulted in the description of some globally distributed diatom genera and species (e.g. *Catenula* Mereschkowsky, *Licmosphenia* and *Stauronella*). Research on the Black Sea diatom assemblages was continued by Proshkina-Lavrenko (1955, 1963) with several new species and varieties described (e.g., *Amphora inconspicua* and *Nitzschia rupestris*). Later on, Guslyakov et al. (1992) produced an atlas of benthic diatoms for the North-western Black Sea extensively illustrated with electron microscope images. More recently, Witkowski et al. (2010) revised *Navicula pontica* (Mereschkowsky) A.Witkowski, M.Kulikovsky, E.Nevrova and Lange-Bertalot 2010 and *Navicula parapontica*, A.Witkowski, M.Kulikovsky, E.Nevrova and Lange-Bertalot 2010, whereas Witkowski et al. (2014) described *Navicula petrovii* Nevrova, Witkowski, Kociolek and Lange-Bertalot. Nevrova et al. (2013) studied *Lyrella* and described five novel species including *Lyrella abruptapontica*, *L. karayevae* and *L. pontieuxinii*. The Black Sea is inhabited by what seems to be an endemic taxon of the blue-pigment producing diatom, *Haslea karadagensis* Davidovich, Gastineau and Mouget (Davidovich et al. 2012a; Gastineau et al. 2012a, 2012b). An increasing

number of studies on the biodiversity and species richness of the Black Sea diatoms have been published in recent years (Nevrova 2022, 2023; Nevrova and Petrov 2019a, 2019b; Zidarova et al. 2022b). Strains of diatoms from the Black Sea have also been used to investigate either their patterns of auxosporulating (Podunay et al. 2021; Davidovich et al. 2012b, 2017a, 2017b, 2019; Kaczmarzka et al. 2018), physiology (Bedoshvili et al. 2021; Davidovich et al. 2016, 2018; Podunay et al. 2016) or genomic peculiarities (Gastineau et al. 2021).

From the list above, it is obvious that it is mostly the northern part of the Black Sea whose diatom communities have been investigated and in contrast, the Southern Turkish Coasts of the Black Sea only received attention very recently (Baytut 2013). The latter authors investigated the discharge zone of the Kizilirmak River into the Black Sea and among the diatom species list many new records for Turkey were published. Similarly, Kaleli et al. (2017) studied Akliman city in the Sinop area and provided a species list also with new records for Turkish waters.

In this article, we contribute to the expanding list of novel taxa by describing *Craspedostauros nazmii* sp. nov., a new epilithic species from the Turkish Coasts of the Black Sea. The results are based on light and Scanning Electron Microscopy. This is the first and, for now, only species of *Craspedostauros* observed along the Turkish Black Sea coast.

Material and methods

The sample was collected in July 2017 from epilithic substrata in Kastamonu Doganyurt, Southern Black Sea ($42^{\circ}0'29.24''N$, $33^{\circ}27'34.19''E$) (Fig. 1). A sin-



Figure 1. Map of the sampling location **A** shows the Kastamonu Province (red rectangle) on the shores of the Black Sea. The red dot on **B** indicates the exact place where the sampling was conducted in Doğanyurt, north of Kastamonu. Figures obtained from Google Maps, Creative Commons CCO Licence, GNU Free Document Licence.

gle epilithic sample was collected using a toothbrush from the surfaces of submerged stones of this sampling station. Environmental parameters were measured using a Lange Hach HQ40d. No live observations of the samples were conducted as the sample was processed directly and boiled with H₂O₂ and 10% HCl to remove organic matter and calcium carbonate respectively. After washing the diatoms with distilled water several times, permanent slides were mounted with Naphrax synthetic resin. Light Microscope (LM) observations were conducted on an OLYMPUS BX51 Light Microscope with OLYMPUS EP50 camera at Kütahya Dumlupınar University. Scanning Electron Microscope (SEM) observations were made using a FEI Versa 3D at İstanbul University with secondary electron and backscatter excitation, 10 kV and a working distance 10 mm. For this purpose, samples were placed on polycarbonate membrane filters with a 5 µm mesh. The membranes were left to dry and then attached to aluminum stubs with double-sided carbon tape, and sputter coated with ca. 20 nm gold using a Turbo-Pumped Quorum Q 1500T ES coater.

Results

Craspedostauros nazmii E.Yılmaz, Witkowski, Solak, sp. nov.

Figs 2, 3

Type material. Holotype: Slide Number SZCZ 28843, collection of Andrzej Witkowski at the University of Szczecin. Valves representing the holotype population illustrated in Fig. 2F.

Isotype: Slide number TR_Kastamonu_Doganyurt_EPL_Tem2017 deposited in Kütahya Dumlupınar University (Turkey).

Registration. <http://phycobank.org/103900>.

Type locality. TURKEY, Kastamonu Province, seashore in Doğanyurt District, (42°0'29.24"N, 33°27'34.19"E), collected by: Cüneyt Nadir Solak, July 18, 2017.

Description. LM (Fig. 2A–M) valves lanceolate to narrow lanceolate, slightly constricted in the middle and with rostrate to subcapitate apices, 29–42 µm in length, 4.5–5.5 µm in width (n = 50). Valves with a slight constriction in the middle, tapering towards narrowly rostrate to subcapitate apices. Axial area very narrow, but distinct, in the valve middle expanding into a central area in a form of stauros encompassing the whole valve width. Raphe branches in LM resolvable, slightly undulate, external proximal raphe endings distinct, tear-like shaped, external distal raphe endings strongly bent in same direction. Transapical striae well resolvable in LM, parallel in the middle, becoming slightly radiate and finally divergent close to apices, 20–21 in 10 µm (Figs 2A–M, 3A–D).

SEM (Fig. 3A–H). Valve external view (Fig. 3A–D), valve face flat composed of one to two rows of areolae. The valve face margin marked by a distinct, continuous apically oriented siliceous rib (transformed vimineae). The transition from the valve face to valve mantle gradual in the valve middle, becoming abrupt at the apices. Hyaline area becoming larger towards to the margins in the centre. Transapical striae uniseriate, composed of 1–3 areolae on the valve face and 4–6 on the mantle in central area, and decreasing to 4 towards the apical mantle (Fig. 3B–D). The striae of the valve face in the apical part composed of a solitary areola, and increasing towards the valve middle to 2 and finally 3 near the stauros. Areolae variable in size, larger near the raphe with more pores

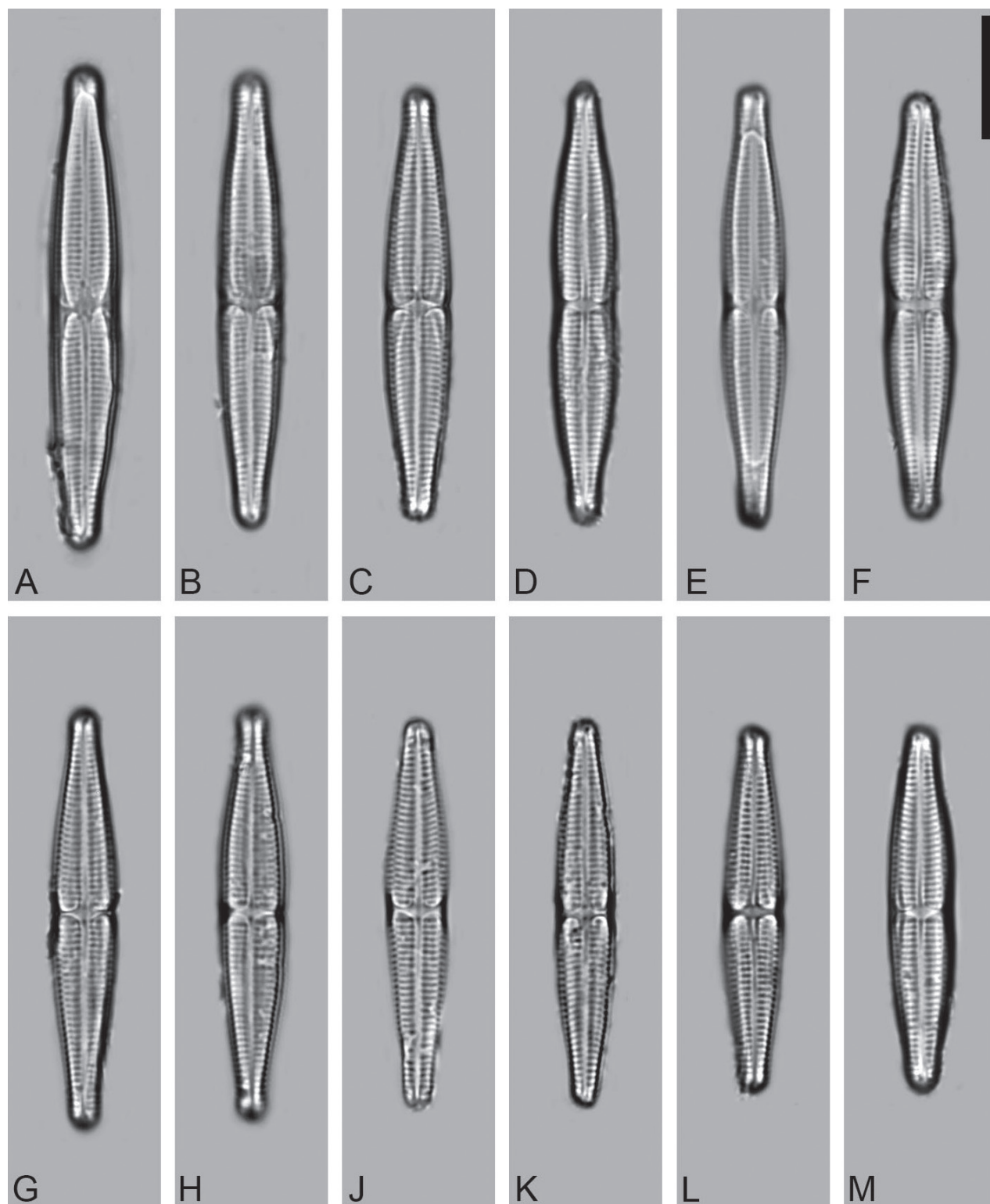


Figure 2. A–M *Craspedostauros nazmii* sp. nov., LM micrographs. Scale bar: 10 μ m.

(up to 17) in the cribrate occlusions (Fig. 3B). Raphe branches slightly undulate with external proximal ends expanded, distant from each other. External apical raphe endings strongly hook-shaped. Prominent wing-like silica flaps partially covering the first row of areolae bordering the raphe sternum present near the apices at valve secondary side (Fig. 3C–D). Valve centre with hyaline area of

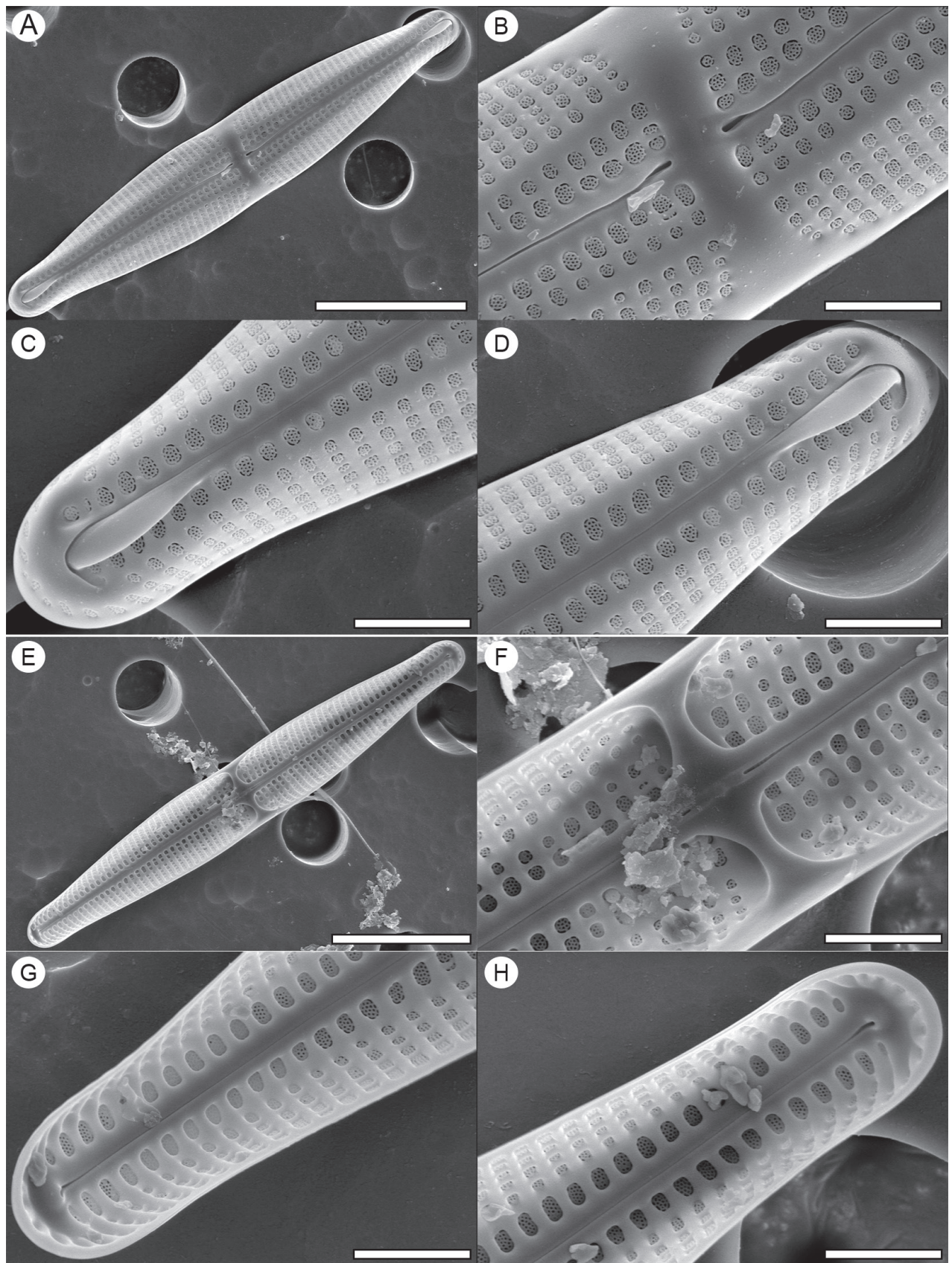


Figure 3. SEM micrographs of *Craspedostauros nazmii* sp. nov. **A** external view of entire valve **B** external view of central area **C, D** external view of valve apex showing wing-like silica flap **E** internal view of entire valve **F** internal view of central area showing raphe terminate **G–H** internal view of valve apex. Scale bars: 10 µm (**A, E**); 2 µm (**B–D, F–H**).

the stauros and symmetric with regular areolae. On one side three and on the other one to two rows of areolae at the beginning. Then, two rows of areolae on both sides and finally one row of areola towards the ends (Fig. 3A–D).

SEM (Fig. 3E–H). Valve surface internally flat, narrow pore-free longitudinal lines running from apex to apex abruptly marking the face-mantle junction (Fig. 3E). Raised stauros distinctly narrower than the fascia (Fig. 3F), broadening and decreasing in thickness close to the valve margins (Fig. 3E–F). Central internal raphe fissures terminate at slight knob of silica onto rectelevatum (Fig. 3F). A flatly ended cylindrical knob present at the central nodule. Apical raphe endings terminating within prominent helictoglossae within a relatively expanded pore-free area (Fig. 3G–H). Areolae externally occluded by cribra, appearing sunken, especially close to the raphe-sternum (Fig. 3F–H).

Etymology. This species is dedicated to Nazmi Yılmaz, father of the first author Elif Yılmaz in appreciation for his dedication to support and encourage her.

Distribution and ecology. The species was observed in Doğanyurt District, Kastamonu Province, Black Sea. The conductivity values at the sampling station were 18.69 mS cm⁻¹, DO values were 8.86 mg L⁻¹, TEMP values were 15.4 °C.

Table 1. Comparison of the main morphological and morphometric characters of *Craspedostauros nazmii* sp. nov. (n = 50) with morphologically similar taxa from the literature.

	<i>Craspedostauros nazmii</i>	<i>C. macewanii</i>	<i>C. capensis</i>	<i>C. britannicus</i>	<i>C. indubitabilis</i>	<i>C. alatus</i>
Valve outline	linear to narrow lanceolate, slightly constricted	linear to linear-lanceolate, slightly constricted	lanceolate, constricted	linear to narrow lanceolate	linear to linear-elliptic	linear to linear-lanceolate, slightly constricted
Valve length (µm)	29.6–41.8	26.0–51.0	25.0–35.0	14.0–60.0	25.0–60.0	20.0–37.0 (16.0–38.0)
Valve width (µm)	4.5–5.4	4.5–5.5	4.5–5.5	5.0–6.0	6.0–7.0	3.0–5.0 (5.0–7.0)
Stria density (in 10 µm)	20–21	28–31	19	~24	25–27	26–28(22–25)
Areolae size	variable	similar	variable	similar	similar	variable
Areolae larger along raphe side	yes	—	Yes	No	Yes	Yes
Average number of cribrum pores	6–17	highly variable	5–13	5(+)	—	3–11
Cribrum shape	rounded	rectangular-rounded	rectangular-rounded	rounded	rounded	rounded
Internal central raphe endings	slightly knob	rectelevatum + knob	knob	double helictoglossae	Knob	rectelevatum
Valve face: mantle junction	abrupt (distinct)	strong (distinct)	gradual	none	strong (distinct)	Strong (distinct)
Valve margin at centre	straight	straight	straight	slightly expanded	straight	very slightly expanded
Apical wing-like silica flaps	present	rudimentary	absent	absent	absent	present
References	this study	Majewska et al. 2021	Cox 1999	Cox 1999	Rivera et al. 2011	Majewska et al. 2018

Discussion

The taxa belonging in *Craspedostauros* originate from various geographic regions of the world with *Craspedostauros britannicus* E.J.Cox 1999 known

from the East and West coast of Great Britain, *C. neoconstrictus* E.J.Cox 1999 from the English Channel coasts, *C. australis* E.J.Cox 1999 from the south coast of Australia, *C. indubitabilis* (Lange-Bertalot and S.I.Genkal) E.J.Cox 1999 from Europe, North America and the Subantarctic Islands, *C. alyoubii* J.Sabir and Ashworth 2016 and *C. paradoxus* Ashworth and Lobban 2016 in the Red Sea and the West coast of Guam respectively, *C. amphoroides* (Grunow ex A.W.F.Schmidt) E.J.Cox 1999 in the Philippines, *C. decipiens* (Hustedt) E.J.Cox 1999 in the English Channel and North Sea coasts, *C. capensis* E.J.Cox 1999 along the West coast of South Africa and *C. laevissimus* (West and G.S.West) Sabbe 2003 in Maritime Antarctic saline lakes (Cox 1999; Sabbe et al. 2003; Rivera et al. 2011; Ashworth et al. 2017). Recently, *C. alatus* Majewska & Ashworth, 2018, *C. danayanus* Majewska & Ashworth, 2021, *C. legouvelloanus* Majewska & Bosak, 2021, and *C. macewanii* Majewska & Ashworth, 2021 were described as epibionts on sea turtles by Majewska et al. (2018, 2021). It is important to note that most of the recent discoveries originated from the Southern Hemisphere (e.g. Majewska et al. 2021; Zidarova et al. 2022a; Trentin et al. 2022).

Based on comparative morphology (Table 1), *C. alatus* in Majewska et al. (2018), *C. britannicus* E.J. Cox (1999), *C. capensis* E.J. Cox (1999), *C. indubitabilis* (Lange-Bertalot and S.I.Genkal) E.J.Cox in Rivera et al. (2011) and *C. macewanii* Majewska and Ashworth in Majewska et al. (2021) are similar taxa. Among them, *C. capensis* is the most similar taxon to *C. nazmii* sp. nov., with similar stria density and valve width. The valve outline and cribrate areolae are also similar (linear to linear-lanceolate), however the apices are not as strongly constricted as in *C. capensis*. When compared with other taxa, the stria density is higher in *C. britannicus* (~24 in 10 µm), *C. indubitabilis* (25–27 in 10 µm) and *C. alatus* (26–28 in 10 µm) than in *C. nazmii* (20–21 in 10 µm). Regarding valve outline, *C. nazmii* sp. nov. resembles the other listed taxa except *C. indubitabilis*. *Craspedostauros indubitabilis* has a markedly elliptic outline with wider apices (Lange-Bertalot and Genkal 1999; Rivera et al. 2011: fig. 1B, C), and a larger valve width (6–7 µm). Moreover, there is no apical wing-like silica flaps (Rivera et al. 2011: fig. 1E, F). *Craspedostauros britannicus* and *C. alatus* also have shorter valves than *C. nazmii* (14.0–60.0, 20.0–37.0 and 29.6–41.8 µm respectively), have no apical wing-like silica flaps (Cox 1999: fig. 26) and the shape of the internal raphe endings are helictoglossae in *C. britannicus* but rectevelatum in *C. alatus*. The valve margin is straight in *C. nazmii* compared to *C. alatus* and *C. britannicus*. The average number of cribrum pores is higher in *C. nazmii* (6–17 in 10 µm) than in the other taxa (5–13 in *C. capensis*, 5(+) in *C. britannicus* and 3–11 in *C. alatus*). Unfortunately, despite numerous attempts, it was impossible to find in our samples any girdle bands that could be used for taxonomy in a similar way that was introduced by Cox (1999).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: EY. Data curation: EY, AW, CNS. Funding acquisition: NÖ. Investigation: EY. Methodology: AW. Project administration: CNS, NÖ. Supervision: CNS. Visualization: EY. Writing - original draft: EY. Writing - review and editing: TD, CNS, RG, NÖ, AW.

Author ORCIDs


Elif Yılmaz  <https://orcid.org/0000-0001-7939-1814>

Andrzej Witkowski  <https://orcid.org/0000-0003-1714-218X>

Neslihan Özdelice  <https://orcid.org/0000-0001-8030-7480>

Cüneyt Nadir Solak  <https://orcid.org/0000-0003-2334-4271>

Romain Gastineau  <https://orcid.org/0000-0001-8661-5118>

Turgay Durmuş  <https://orcid.org/0000-0002-8242-1823>

Data availability

All of the data that support the findings of this study are available in the main text.

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Ardisia recurvipetala (Primulaceae-Myrsinoideae), a new species from northern Peninsular Malaysia

Avelinah Julius¹, Mat Yunoh Siti-Munirah², Timothy M. A. Utteridge³

¹ Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia

² Forest Research Institute Malaysia, Kepong, Selangor, 52109, Malaysia

³ Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK

Corresponding author: Avelinah Julius (plagiovel80@gmail.com; avelinah.julius@ums.edu.my)

Abstract

Recent fieldwork in Terengganu, Peninsular Malaysia, resulted in the collection of an endemic new species of *Ardisia*, described here as *Ardisia recurvipetala* Julius, Siti-Munirah & Utteridge. The species is a member of subgenus (§) *Crispardisia* on account of its vascularised glands (bacterial nodules) on the leaf margin and the terminal inflorescence on a specialised lateral branch subtended by a normal leaf (rather than a reduced bract-like leaf). *Ardisia recurvipetala* is unique amongst all members of §*Crispardisia* by having leaf margins with both vascularised glands and pustule-like structures and can be further distinguished from other Peninsular Malaysian members of this subgenus by the lamina raised between the leaf venation giving a somewhat bullate appearance, unbranched inflorescences, brownish-red pedicels and recurved corolla lobes, each with a creamy-white apex and a small pink patch at the base. *Ardisia recurvipetala* is known only from a single location in Terengganu and its conservation status is assessed as Data Deficient (DD).

Key words: Ericales, Malesia, Myrsinaceae, subgenus *Crispardisia*, Taman Negeri Kenyir, taxonomy



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Introduction

Botanists at the Forest Research Institute Malaysia (FRIM) are working to produce a more complete and up-to-date Flora for Malaysia, especially by undertaking family revisions for the Flora of Peninsular Malaysia (FPM). To achieve this goal, an ongoing fieldwork programme is being conducted throughout Peninsular Malaysia, especially in areas that are under-explored or have never been botanised, including those that are ecologically significant. This effort has resulted in the discovery of several new species and records for Peninsular Malaysia. For example, four new *Ardisia* Sw. (Primulaceae) species have been discovered since the FPM project launched in 2005 (e.g. Julius and Utteridge (2012, 2021, 2022); Julius et al. (2017)), as well as a new species of *Maesa* Forssk. (Primulaceae; Utteridge (2012)). Other findings include the discovery of the Himalayan genus *Gardneria* Wall. in Pahang and the Neotropical naturalised species *Spigelia anthelmia* L. (both Loganiaceae) in Selangor (Julius et al. 2013).

Many other new species have also been described from various other plant families, including Aristolochiaceae (Yao 2012), Balsaminaceae (Kiew 2016), Capparaceae (Julius 2022), Gesneriaceae (Kiew and Lim 2019; Syahida-Emiza et al. 2020), Orchidaceae (Ong et al. 2020; Ong 2021), Thismiaceae (Siti-Munirah 2021; Siti-Munirah and Dome 2019, 2022; Siti-Munirah et al. 2021) and Zingiberaceae (Sam et al. 2009, 2012; Sam and Ibrahim 2018). This highlights the rich biodiversity of Peninsular Malaysia and opportunities for more discoveries (Middleton et al. 2019).

During a recent botanical survey led by the second author in Taman Negeri Kenyir (Kenyir State Park), Terengganu State, a flowering *Ardisia* plant was documented and collected. The presence of vascularised glands (bacterial nodules) at the incision between the crenatures of the leaf margin and the terminal inflorescence on a specialised lateral branch subtended by a normal leaf (rather than a reduced bract-like leaf) place the taxon within §*Crispardisia*, a well-defined monophyletic group of about 100 species, with a centre of diversity in Asia (Julius et al. 2021; Yang and Hu 2022). After consulting the relevant literature (Larsen and Hu 1991; Hu and Vidal 2004) and specimens of other species in §*Crispardisia*, we confirmed that this is an undescribed species and it is here formally described and illustrated as new to science. It is the only species in §*Crispardisia* that has leaf margins with both vascularised glands and pustule-like structures.

Material and method

Morphological description of the new species was based on both fresh and pressed materials; specimens of *Ardisia* have been studied from BKF, BM, K, KEP, L, SAN and SAR. Specimens of related species from SE Asia, especially *A. crispa* (Thunb.) A.DC and species recorded for Peninsular Malaysia, i.e. *A. crenata* Sims, *A. lankawiensis* King & Gamble, *A. minor* King & Gamble, *A. polysticta* Miq, *A. recurvisepala* Julius & Utteridge, *A. ridlei* King & Gamble, *A. rosea* King & Gamble, *A. sphenobasis* Scheff. and *A. villosa* Roxb. were studied in detail at K and KEP. In addition, specimen images available from JSTOR Global Plants (<http://plants.jstor.org/>), the Kew Herbarium Catalogue (<http://apps.kew.org/herbcat/gotoHomePage.do>) and Plants of the World Online (POWO 2023: <http://www.plantsoftheworldonline.org/>) were examined. Relevant taxonomic literature (e.g. Stone (1982, 1992); Larsen and Hu (1991); Chen and Pipoly (1996); Hu (2002); Hu and Vidal (2004)) was also consulted. The conservation status of the new species was assessed following IUCN Standards and Petitions Committee (2022), including guidelines and procedures developed by FRIM for the Malaysia Plant Red List (Chua and Saw 2006).

Taxonomy

***Ardisia recurvipetala* Julius, Siti-Munirah & Utteridge, sp. nov. (§*Crispardisia*)**

urn:lsid:ipni.org:names:77326762-1

Figs 1–3

Diagnosis. *Ardisia recurvipetala* is the only *Ardisia* species with the following combination of characters: leaf margins with both vascularised glands and pustule-like structures, lamina raised between the venation giving a somewhat

bullate appearance, inflorescences on the main shoot and specialised lateral branches, white flowers with recurved petals with a pink patch at the base of the corolla lobes.

Type. MALAYSIA. Peninsular Malaysia: Terengganu, Hulu Terengganu Distr., Taman Negeri Kenyir, 5°01'00.5"N, 102°32'29.9"E, 201 m elev., 15 June 2022 (fl. & fr.), *Siti Munirah FRI 98670* (holotype KEP!; isotype BORH!).

Woody shrub ca. 1 m tall. **Branches** 5–12.5 cm long. **Indumentum** absent except for short, white or brown, simple eglandular and glandular hairs on reproductive parts. **Leaves** spirally arranged; petioles (0.5–)1–1.5 cm long, winged by the decurrent leaf base, glabrous; lamina chartaceous, with sparse black gland dots throughout abaxially, raised between the venation; usually broadly elliptic, occasionally oblanceolate, (12.5–)17.5–20.5 × 4.5–7.5 cm (excluding reduced leaves subtending inflorescences on specialised lateral branches); young leaves light green, mature leaves dark green above, pale green beneath; base cuneate; margin crenate with vascularised glands (bacterial nodules) at the incision between crenatures and with pustule-like structures along the crenations from projecting venation; apex acute to obtuse; glabrous on both surfaces; mid-rib flat above, raised below; lateral veins 9–14 pairs, irregularly spaced, joining at the marginal vein, distinct on the adaxial surface, prominent on abaxial side; intersecondary veins sometimes present; intercostal veins obscure. **Inflorescences** subsessile, terminal on main shoot and on relatively short specialised lateral branches with 1–2(–3) subtending leaves, condensed racemose, ca. 2 × 3 cm, unbranched, 10–18-flowered. **Flowers** 5-merous; pedicels brownish-red, 1–1.5 cm long, slender, densely glandular hairy with globular tips, covered with dense, brown gland dots; sepals yellowish-green, pale pink at base, not overlapping, covered with dense brown gland dots, triangular-ovate, 1.5–2 × 1–1.5 mm, sparsely glandular hairy abaxially, glabrous adaxially, margin ciliate with laxly spaced, simple, pale brown hairs, apex obtuse; corolla tube ca. 0.5 mm long, lobes 5, white except the creamy-white apex and pinkish base, covered with dense, brown gland dots, lanceolate, 6–7 × 3–4 mm, glabrous on both surfaces, apex acute, strongly recurved at anthesis; stamens 5, yellowish, subsessile, anthers narrowly lanceolate-mucronate, 5–6 × 1.5 mm, glabrous throughout, gland dotted abaxially, thecae not locellate, dehiscent by longitudinal slits; ovary subglobose, ca. 2 × 1.5 mm, glabrous, ovules ca. 9 arranged in 1-series, style and stigma slender, ca. 5.3 mm long, glabrous. **Young fruits** globose, with dense gland dots, 4–6 × 4–6 mm, green, glabrous; pedicels becoming thickened and obconically flared, 1.8–2 cm long. Mature fruits not observed.

Distribution. Endemic to Peninsular Malaysia, Terengganu (Taman Negeri Kenyir); currently known only from the type locality (Fig. 4).

Ecology. Growing in a lowland dipterocarp forest at 201 m elev. in a shaded area not far from a small stream.

Etymology. The species epithet is derived from its recurved corolla lobes.

Conservation status. Data Deficient (DD). *Ardisia recurvipetala* is known from fewer than five individuals in flower and fruit collected from intact forest patches within the Taman Negeri Kenyir. The sites where the taxon was found were previously part of the Tembat Forest Reserve before it was gazetted into Taman Negeri Kenyir in 2018. Further surveys are needed to understand the threats at the type locality and if the species is distributed outside the current area and,

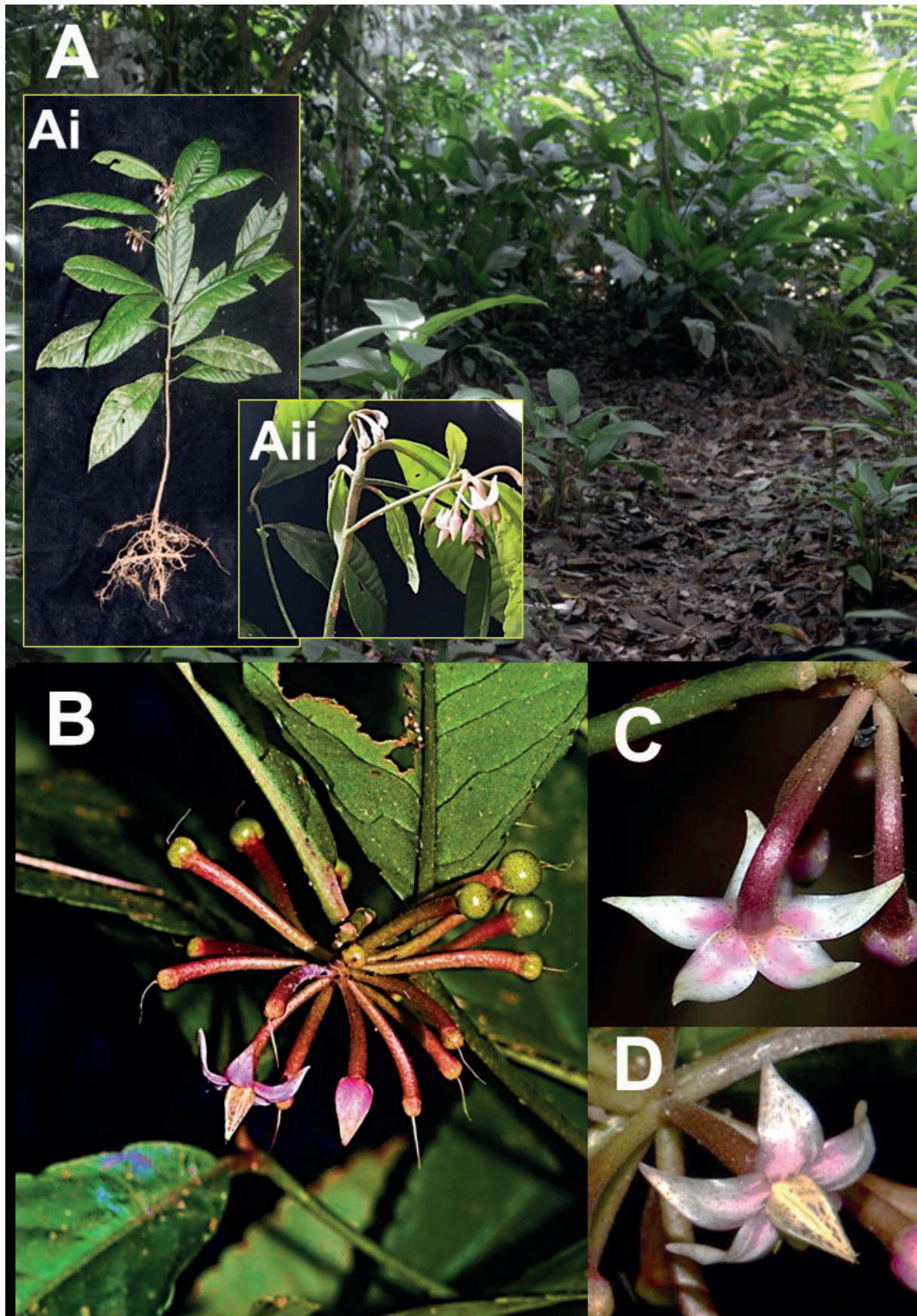


Figure 1. *Ardisia recurvipetala* **A** habitat (inset: **Ai** habit **Aii** inflorescence position on lateral shoot and main stem) **B** lateral branch with flowers and young fruits **C, D** flowers.

until these data are obtained, the species is assessed as Data Deficient (DD) (Chua and Saw 2006; IUCN Standards and Petitions Committee 2022).

Notes. Peninsular Malaysian members of §*Crispardisia* can be placed into two informal groups, based on inflorescence position (Stone 1989; Julius and Utteridge 2021). The first group has inflorescences strictly terminal on specialised lateral leafy branches, while the second group has inflorescences lateral (axillary) and/or terminal on the main stem and/or lateral branches. *Ardisia recurvipetala* falls into the second group, in which the majority of species in §*Crispardisia* belong, including six species from Peninsular Malaysia. Other than characters mentioned in the diagnosis, the new species can be easily recognised by its unbranched and sessile inflorescences terminal on the main shoot and on relatively short specialised lateral branches with 1 to 2(–3) subtending leaves, tiny sepals (1.5–2 × 1–1.5 mm) that are yellowish-green and pinkish at base and corolla lobes that are strongly recurved at anthesis (Figs 1B, 3Bii).

Unlike other members of §*Crispardisia*, the leaf margins of the new species have both vascularised glands at the incisions between the crenatures and pustule-like structures along the crenations (Fig. 2); these result from the venation projecting from the leaf margin and should not be mistaken for bacterial nodules. This combination of vascularised glands and pustule-like structures is not observed in other Peninsular Malaysian members of §*Crispardisia*.

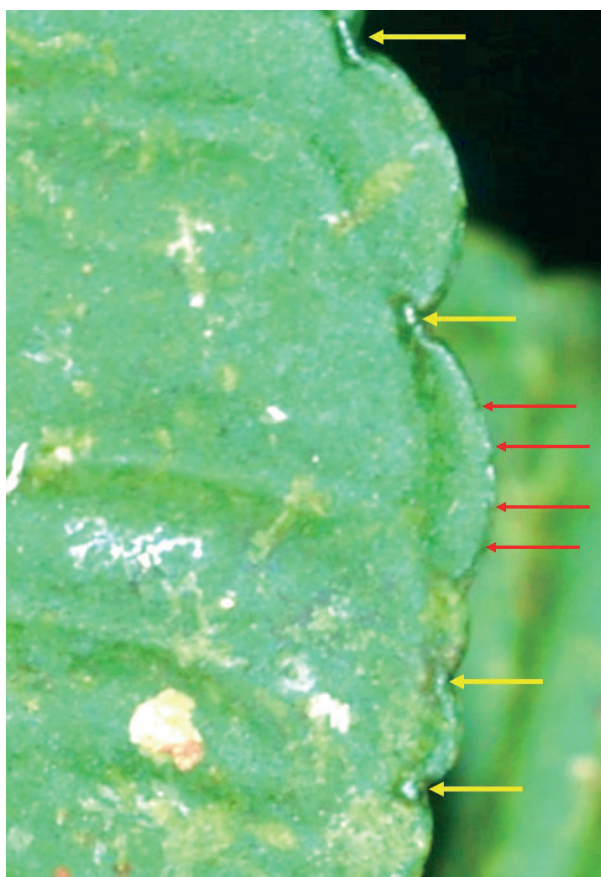


Figure 2. Leaf margin showing vascularised glands (yellow arrow) on the incision between crenation and the pustule-like structures (red arrow) along the crenation.

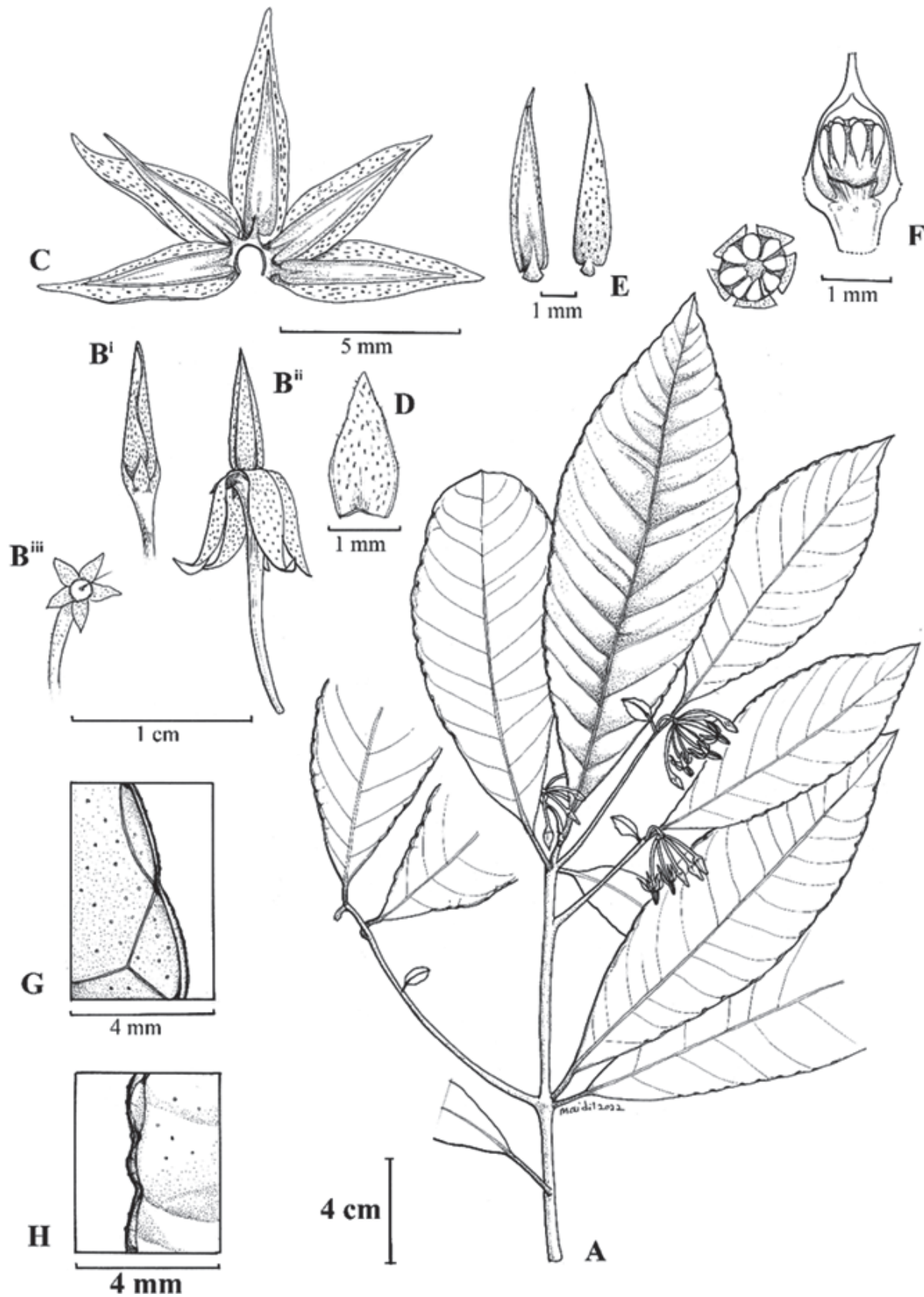


Figure 3. *Ardisia recurvipetala* **A** flowering branches **B** flower bud (i), mature flower (ii) and flower with corolla removed (iii) **C** flower (spread) showing the stamen arrangement **D** adaxial view of sepal **E** ventral (left) and dorsal surfaces (right) of anther **F** anterior (left) and lateral views (right) of ovary **G** leaf margin with venation details and bacterial nodule **H** pus-tule-like structure on leaf margin crenation. Illustration by Mohd Aidil Nordin.

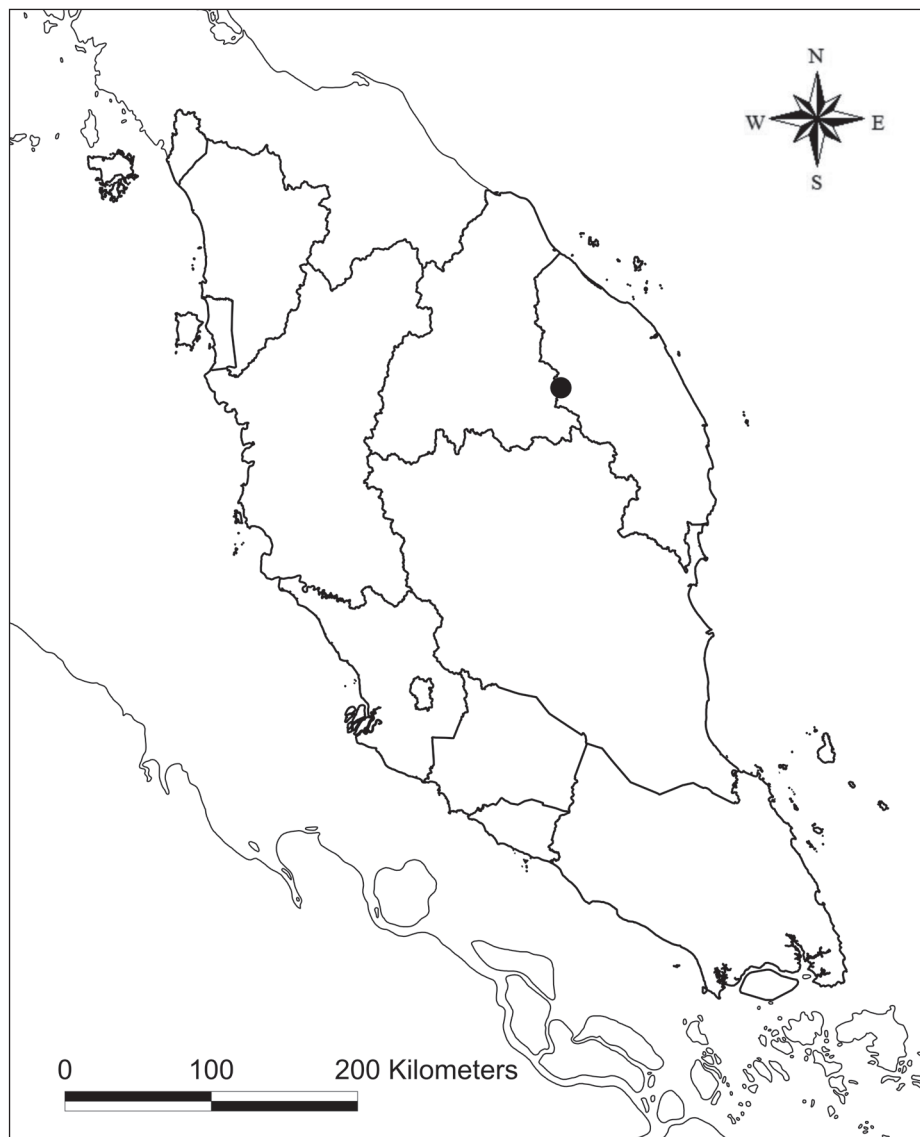


Figure 4. Map showing the type locality of *Ardisia recurvipetala* in Peninsular Malaysia.

The new species is similar to *Ardisia sphenobasis* in having 17.5–23 cm long leaves (excluding reduced leaves subtending inflorescences on specialised lateral branches), but it has inflorescences that are terminal on the main shoot and specialised lateral branches (vs. strictly lateral on main stem). The whitish corollas of the new species are somewhat similar to those of *A. villosa* and *A. crenata*. However, *A. recurvipetala* (Fig. 3) differs in its largely glabrous flowers, except for short, simple eglandular and glandular hairs on the pedicels and calyx (vs. hairy throughout with long, villous hairs in *A. villosa*). Compared to *A. crenata*, a widespread species with a whitish to pinkish corolla, branched and unbranched inflorescences and a flat and coriaceous lamina, the new species has corolla lobes with a creamy-white apex and a pink patch at the base, strictly unbranched inflorescences and chartaceous leaves with the lamina raised between the venation.

This latest addition brings the number of *§Crispardisia* species native to Peninsular Malaysia to ten. Of these, four species, including the new one, are endemic to Peninsular Malaysia: *A. lankawiensis* King & Gamble, *A. minor* King & Gamble, *A. recurvipetala* and *A. recurvisepala* Julius & Utteridge.

We consider species of *Ardisia* as important indicators of tropical and sub-tropical forest quality. Whilst some species are found in a range of habitats (e.g. *A. elliptica* Thunb.), many species have restricted distributions and habitat requirements, including several species of *§Crispardisia*. For example, in Peninsular Malaysia, *A. lankawiensis* is restricted to limestone habitats on Langkawi Islands and, in Thailand, *A. pilosa* H.R.Fletcher is restricted to the subtropical forests found on only Phu Kradeung mountain in north-east Thailand. That this new taxon is currently only found in unlogged areas within the Taman Negeri Kenyir suggests that *A. recurvipetala* is a useful indicator of primary forest within the forest reserve boundary. The discovery and description of new species is important. It contributes to naming and documenting our local biodiversity as part of a revision of the Primulaceae for the FPM, provides a better understanding of botanical distribution patterns and results in information about forest quality in Peninsular Malaysia.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

AJ & TMAU: paper writing, plant identification & examination. AJ & MYSM: conservation assessment. MYSM: Fieldwork.

Author ORCIDs

Avelinah Julius  <https://orcid.org/0000-0003-1991-1915>

Siti-Munirah Mat Yunoh  <https://orcid.org/0000-0002-5062-9988>

Timothy M. A. Utteridge  <https://orcid.org/0000-0003-2823-0337>

Data availability

All of the data that support the findings of this study are available in the main text.

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A new combination and a new synonym of Gesneriaceae in China

Zheng-Long Li^{1,2*}, Zhang-Jie Huang^{3*}, Da-Wei Chen¹, Xin Hong^{1,4,5}, Fang Wen^{2,4}

¹ Anhui Provincial Engineering Laboratory of Wetland Ecosystem Protection and Restoration, School of Resources and Environmental Engineering, Anhui University, CN-230601, Hefei City, Anhui Province, China

² Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006, Guilin City, Guangxi Zhuang Autonomous Region, China

³ Key Laboratory of Resource Biology and Biotechnology in Western China, Ministry of Education, Northwest University, CN-710069, Xi'an, Shaanxi Province, China

⁴ Gesneriad Committee of China Wild Plant Conservation Association, National Gesneriaceae Germplasm Resources Bank of GXIB, The Gesneriad Conservation Center of China, Guilin Botanical Garden, Chinese Academy of Sciences, CN-541006 Guilin, Guangxi, China

⁵ Yunnan Key Laboratory for Integrative Conservation of Plant Species with Extremely Small Populations, Kunming Institute of Botany, Chinese Academy of Sciences, CN-650201, Kunming, Yunnan, China

Corresponding authors: Xin Hong (hongxin1989@vip.qq.com); Fang Wen (wenfang760608@139.com)

Abstract

Didymocarpus subpalmatinervis W.T.Wang was shown to be conspecific with *Petrocodon lithophilus* Y.M.Shui, W.H.Chen & Mich.Möller, by checking original literature, examining specimens, tracing specimen collecting history, and conducting field surveys. The results show morphological characteristics and geographical distribution overlaps between these two species. The transfer of *Didymocarpus subpalmatinervis* to *Petrocodon* as a new combination with *Petrocodon subpalmatinervis* (W.T.Wang) F.Wen & Z.L.Li is proposed here, and *P. lithophilus* is synonymized with *P. subpalmatinervis*. Color photographs and essential information are also provided, including a detailed comparison of description, distribution, habitat, and the proposed IUCN conservation status.

Key words: *Didymocarpus*, Flora of China, Gesneriaceae, new combination, new synonym, *Petrocodon*, taxonomy



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Introduction

Didymocarpus Wall. has a complex taxonomic history, saturated with doubtful taxa (Weber and Burt 1998). Originally, in the taxonomic system of Burt and Wiehler (1995), it was the largest genus in the tribe Didymocarpeae Endl., subfam. Cyrtandroideae, with more than 180 species. Weber and Burt (1998) excluded the section *Heteroboea*, which was considered as part of *Didymocarpus* s. l. (Hilliard and Burt 1995; Weber and Burt 1998). In addition, they considered that 1) *D. hancei* Hemsl. (endemic to China) and *D. bonii* Pellegr. (distributed in Vietnam and East Thailand) should be included in *Calcareoboea* C.Y.Wu ex H.W.Li, as well as *D. mollifolius* W.T.Wang and *D. niveolanosus* D.Fang & W.T.Wang; 2) *D. demissus* Hance should be assigned to the previous genus, *Chirita* Buch.-Ham. ex D. Don (Wei et al. 2010; Wang et al. 2011; Weber et al.

* These authors contributed equally to this work.

2011). Their notion of separating *D. hancei* from *Didymocarpus* Wall. was supported by Li (2007) based on morphological and molecular evidence. Weber et al. (2011) published three new combinations in their revision of the genus *Petrocodon* Hance, viz., *Petrocodon hancei* (Hemsl.) A.Weber & Mich.Möller (\equiv *Didymocarpus hancei* Hemsl.), *Petrocodon mollifolius* (W.T.Wang) A.Weber & Mich.Möller (\equiv *Didymocarpus mollifolius* W.T.Wang) and *Petrocodon niveolanosus* (D.Fang & W.T.Wang) A.Weber & Mich.Möller (\equiv *Didymocarpus niveolanosus* D.Fang & W.T.Wang). *D. subpalmatinervis* W.T.Wang, a species with no collection record after 1905, also has morphological characteristics placing it in section *Heteroboaea*. The taxonomic status of this species remained unchanged because of the difficulty in obtaining type materials. Its problematic taxonomic status has previously been recognized by (Li et al. 2015; Möller et al. 2016; Hong et al. 2018).

The French Catholic priest Francois Ducloux (1864–1945), the head of the Kunming Church from 1889 to 1945, hired people to collect plant specimens extensively in central and northern Yunnan (Qu 2014). In 1905, Ducloux collected a Gesneriaceae-like taxon, perennial and acaulescent in Y-dje, near Loulan, Yunnan, China (collection number *Fr. Ducloux* 3711). He sent three sheets back to the Museum of Natural History in Paris. Since then, those specimens were neglected in P for over 90 years, until in 1996, Wen-Tsai Wang identified Ducloux's specimens as a new species belonging to *Didymocarpus* sect. *Heteroboaea* and published it as *Didymocarpus subpalmatinervis* subsequently a year later (Weitzman et al. 1997).

Petrocodon lithophilus was described at the morphological and molecular level from Naigu Stone Forest, Yunnan Province, where Michael Möller and Yu-Min Shui first discovered it in August 2012. It is placed in *Petrocodon* by some obvious characters of this genus, viz. a rhizomatous rosette with leaves usually rounded or elliptic, mainly in an alternate arrangement, filaments straight, stigma discoid, and fruits dehiscent loculicidally into two valves (Chen et al. 2014).

When sorting out the specimens of *Didymocarpus* sect. *Heteroboaea* of, the type specimen of *D. subpalmatinervis* (*Fr. Ducloux* 3711), morphologically, was found to be extremely similar to *Petrocodon lithophilus*. According to protologue and label information on the type specimen, the type locality of *Didymocarpus subpalmatinervis* is near Lunan Stone Forest, only 13 kilometers away from Naigu Stone Forest. During field investigations near the type locality of *Petrocodon lithophilus*, several populations of *Didymocarpus* aff. *subpalmatinervis* were also found on the hills. The authors concluded that *D. subpalmatinervis* is conspecific with *Petrocodon lithophilus*. Accordingly, it is reasonable to make a new combination *P. subpalmatinervis*, and reduce *P. lithophilus* to a synonym.

Materials and methods

A thorough comparison of the type material of *Petrocodon lithophilus* and *Didymocarpus subpalmatinervis* was made. Their protologues and relevant records were studied intensively. The geographical distribution of the two species was outlined by careful field surveys of the type locality areas. Classical plant taxonomic methods were involved. Major online herbarium databases, including **P** (<https://science.mnhn.fr/institution/mnhn/search>), **E** (<http://www.rbge>).

org.uk/), **K** (<https://www.kew.org/>), **A** (<https://huh.harvard.edu/>), **PE** (<https://pe.ibcas.ac.cn/index.html>) and Chinese Virtual Herbarium (<https://www.cvh.ac.cn/>), et al., were checked. The only recorded specimens of *D. subpalmatinervis* stored at **P** were affirmed and checked, utilizing high-resolution digital images of the type specimen. In addition, the authors observed and recorded morphological characters of *Petrocodon lithophilus* in the field and examined its type specimen at **KUN**.

Results

Comparison and discussion of morphological characteristics of sect. *Heteroboaea*

There are numerous distinct morphological characteristics distinguishing *Didymocarpus subpalmatinervis* from other species within sect. *Heteroboaea*, such as leaves' margins obtusely or doubly dentate (vs. margin irregularly triangular denticulate), triangular lobes (vs. rounded or oblong lobes), straight filaments (vs. curving), separate anthers (vs. confluent anthers). Detailed morphological comparisons with sect. *Heteroboaea* are provided in Fig. 1. Based on the aforementioned, it becomes evident that *D. subpalmatinervis* is not a species within sect. *Heteroboaea*. Additionally, owing to its stemless habit, it does not align with sect. *Didymocarpus* either. Consequently, the taxonomic classification of this species falls outside the scope of the *Didymocarpus* genus. Given its overall vegetative traits, it should be reclassified under the genus *Petrocodon*.

Comparison and discussion of morphological description with *Petrocodon lithophilus*

Comparing the description of *Didymocarpus subpalmatinervis* and *Petrocodon lithophilus* in their protologues, we found consistency in habit, leaves, calyx, corolla, disc, and ovary (indicated by "●" in Table 1). Because Wen-Tsai Wang described *D. subpalmatinervis* (Weitzman et al. 1997) according to the over 90-year-old type specimen, there may be some distortion compared with wild-living plants in morphology. Moreover, terminology may alter to a certain degree among different taxonomists due to personal preference in the use of words. Taxonomic descriptions have evolved over the years, as have identification tools. For example, Wang selected 'puberulous' and Shui picked up 'pubescent' to describe the hair of *Didymocarpus subpalmatinervis* and *Petrocodon lithophilus*, respectively. Such equivalents used by them in the description are marked with "★" in Table 1. The only significant difference appeared in the statement of staminode's number: 2 in *Didymocarpus subpalmatinervis* and 3 in *Petrocodon lithophilus* (indicated by "▲" in Table 1). This feature has already been questioned by Wen et al. (2020). Previous researchers often made mistakes in describing the number of staminodes because 1) they followed generic diagnoses of *Didymocarpus* and paid no attention to the actual staminal condition; 2) staminodes are inconspicuous in many species unless they are carefully observed, but the correct number of staminodes is 3. Detailed morphological comparisons with *P. lithophilus* are provided in Fig. 2.



Figure 1. Morphological comparisons of *Didymocarpus subpalmatinervis* and sect. *Heteroboaea* **A** type specimen of *D. subpalmatinervis* **B** habit of *D. heucherifolius* var. *yinzhengii* **C** habit of *D. cortusifolius* **D** habit of *D. yuenlingensis* **E** habit of *D. heucherifolius* var. *gamosepalus* **F** leaves of *D. subpalmatinervis* **G** leaves of *D. heucherifolius* var. *yinzhengii* **H** leaves of *D. lobulatus* **I** leaves of *D. heucherifolius* **J** opened corolla of *D. subpalmatinervis*, showing lobes and stamens **K** frontal view of *D. yuenlingensis*, showing lobes and stamens **L** frontal view of *D. cortusifolius*, showing lobes and stamens **M** frontal view of *D. sinoprimuminus*, showing lobes and stamens.

The similarity in protologues prompts us to reconsider the circumscription of *Didymocarpus subpalmatinervis* and *Petrocodon lithophilus*.

Locality

In 1905, Ducoux collected *Didymocarpus subpalmatinervis* at the position of Y-dje, near Lou-lan. Lou-lan is the French pronunciation of 路南 (Lùnán) in

Table 1. The description and comparison of the *D. subpalmatinervis* and *P. lithophilus*.

		<i>Didymocarpus subpalmatinervis</i> W.T.Wang	<i>Petrocodon lithophilus</i> Y.M.Shui, W.H.Chen & Mich.Möller	The similarity in description between the two species
Habit		Perennial, stemless herb	Perennial herbs	●
Leaves	shape	leaf blade ovate to oblate	leaf blade rounded or elliptic	★
	hair	adaxially densely appressed puberulous, abaxially appressed puberulous, pilose on veins	pubescent on both surfaces	★
	base	cordate	nearly cordate	●
	margin	obtusely or doubly dentate	shallowly or deeply crenulate	★
	apex	obtuse	rounded	★
Cymes	number	Cymes ca. 2, ca. 2× branched, 2–10– flowered;	about 10 flowers	★
	peduncle	puberulous	pubescent	★
	bracts	2–3, narrowly lanceolate or linear, puberulous	2, linear or lanceolate, pubescent	★
	Calyx	Calyx actinomorphic, 5-sect or nearly so, segments linear-triangular, both surfaces puberulous	Calyx 5-lobed to base, segments linear, pubescent	●
Corolla	color	Yellow	light greenish-yellow	●
	length	2–2.5 cm	2.5–2.8 cm	★
	tube	funnel-form-cylindric, 1.4–1.7 cm	thin tubular, 1.7–1.9 cm	★
	lobes	upper lip 2-lobed, lower lip 3-lobed, all lobes triangular	adaxial lip 2-lobed, lobes triangular, abaxial lip 3-lobed, lobes triangular	●
Stamens	staminodes	2	3	▲
Disc		annular	ring-like	●
Pistil	ovary	ovary linear	ovary linear inflated	●
	hairs	puberulous	pubescent	★
	stigma	depressed capitate	stigma 1, disc-like and undivided	★

● Completely consistent characteristics; ★ Overlapping characteristics; ▲ Different characteristics.

Chinese, and Y-dje corresponds to 维则 (Wéizé). The scope of Lou-lan is not indicated on the type specimens of *D. subpalmatinervis*. China in 1905 was still in the era of the Qing Dynasty. Lunan then refers to Lunanzhou, which is now Shilin County. Naigu Stone Forest is included in Lunan County (now Shilin County). Lunan refers to Lunan Stone Forest. Lunan Stone Forest and Naigu Stone Forest are both in the Stone Forest scenic spot today. Our field survey shows only one species of Gesneriaceae with similar morphological characteristics in these two regions. The distribution of the two species thus overlaps no matter which geographical entity Lunan refers to in the past or present.

In summary, based on literature research, geographical distribution, and morphological analysis, we find no discontinuities and recognize *Didymocarpus subpalmatinervis* and *Petrocodon lithophilus* as conspecific. Therefore, a new combination, *P. subpalmatinervis* (W.T.Wang) F.Wen & Z.L.Li, comb. nov. is proposed here.

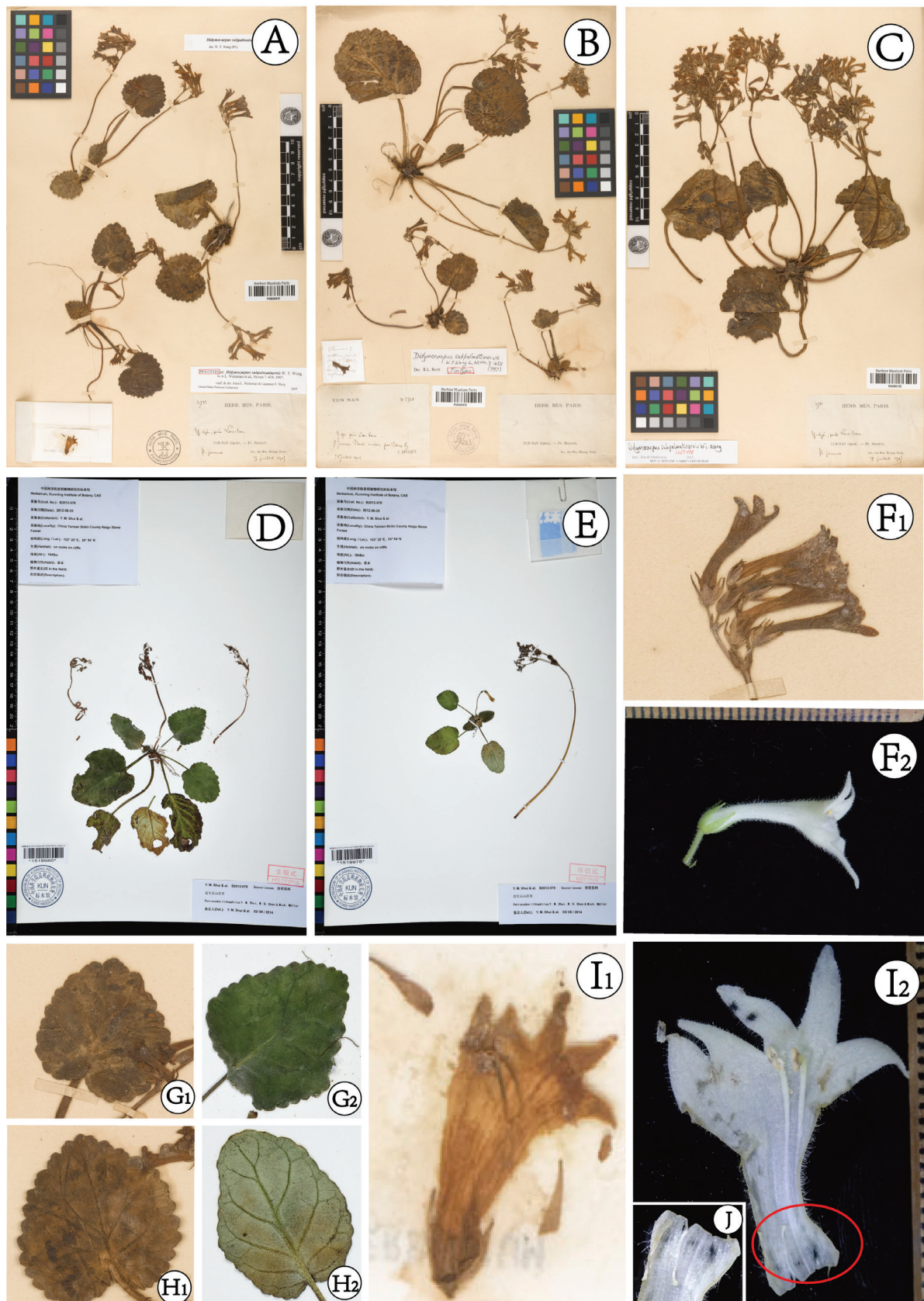


Figure 2. Morphological comparison of *Didymocarpus subpalmatinervis* and *Petrocodon lithophilus* **A–C, F₁–I₁**: *D. subpalmatinervis* **D, E, J, F₂–I₂**; *P. lithophilus* **A** holotype P04060419 **B** isotype P04060165 **C** isotype P04060418 **D** holotype KUN-1519980 **E** isotype KUN-1519978 **F** flower **G** abaxial surface of Leaves **H** adaxial surface of Leaves **I** opened corolla **J** staminodes.

Taxonomic treatment

***Petrocodon subpalmatinervis* (W.T.Wang) F.Wen & Z.L.Li, comb. nov.**

urn:lsid:ipni.org:names:77326781-1

Didymocarpus subpalmatinervis W.T.Wang, *Novon* 7(4): 428–429. 1997. Type: CHINA. Yunnan: Y-dje, near Lou-lan, July 1905, *Fr. Ducloux* 3711 (P: holotype P04060419!; isotypes P04060165!, P04060418!). Basionym.

= *Petrocodon lithophilus* Y.M.Shui, W.H.Chen & Mich.Möller, *Sys. Bot.* 39(1): 325. 2014. syn. nov. Type: CHINA. Yunnan: Shilin County, Naigu Stone Forest, alt. 1848 m, on rocks on cliffs, 29 August 2012, Y.M. Shui et al. B2012–078 (KUN: holotype KUN-1519980!; isotype KUN-1519978!).

Chinese Vernacular name. 掌脉石山苣苔 (Zhǎng Mài Shí Shān Jù Tái).

Distribution and habitat. This species is endemic to Shilin County, Yunnan Province, China, growing in narrow cracks on rocks. Accompanying plants include other shade herbs and trees.

Proposed IUCN conservation status. Naigu Stone Forest is a famous scenic spot for many tourists. The population of *Petrocodon subpalmatinervis* is easily affected by human activities. For example, tourists probably collect the conspicuous flowers of *P. subpalmatinervis* while they visit the scenic spot and walk along the trails among the Karst peaks and hills of Naigu Shilin. As mature individuals are easily damaged, the population will likely gradually decline year by year. According to the results of our field investigation in the type locality and adjacent regions, the EOO and AOO of *P. subpalmatinervis* are about 800 km² and 30 km². Despite the severe drought in the second half of 2022 seriously influencing the plant population, there is still a high number of individuals (more than 5 000) surviving in the scenic spot. In addition, authors also found several small populations (total > 1 000) in the Karst landscape surrounding the type locality, Naigu Shilin. Following the *IUCN Red List Categories and Criteria* (IUCN 2022), this species is evaluated as Endangered [EN B1ab (i, ii, iii, iv)+2ab (i, ii, iii, iv)].

Notes. When Wang published the protologue of *Didymocarpus subpalmatinervis*, the collection date read 1909. But, on the website of **CVH** and the herbarium **P**, the collection date of the information of the specimen we consulted was 1905. Their two different collection years are confusing. We carefully compared the labels of three type specimens of *D. subpalmatinervis* with the collection number '3711' and found that the collector's writing habits might have caused this misunderstanding. Ducloux's personal collection number increased with time like many collectors. For example, the collection number of *Berberis bodinieri* H.Lév. he collected in 1896 was '0004'; in 1904, the collection number of *Potamogeton distinctus* A. Benn. was '2571'; in 1905, he collected *Cornus capitata* Wall. at the same place (Y-dje near Lou-lan) with the collection number '3715'; In 1909, the collection number of *Merremia yunnanensis* (Courchet & Gagnep.) R.C.Fang has reached '6398'. Therefore, it seems likely that the specimens of *D. subpalmatinervis* with the collection number *Fr. Ducloux* 3711 were collected in 1905.

For some species published decades or even a hundred years ago, obtaining molecular materials for systematic analysis is challenging because there may be only one type specimen or a few specimens, or they are stored in a foreign herbarium (Wei 2018; Kong et al. 2021). Despite this complicated background,

it is still reasonable and accurate to conduct an analysis and verification of the type specimen of the dubious species. When combined with the collecting history of the Ducloux, and the current situation of the existing population (Wei et al. 2022), we are confident about the name and status.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

ZL, ZH and DC inspected the specimens of the species. ZL, FW, and ZH performed the data analysis. ZL and ZH wrote the manuscript. FW and XH revised the manuscript. All authors have read and approved the final manuscript.

Author ORCIDs

Zheng-Long Li  <https://orcid.org/0009-0009-8988-5725>

Zhang-Jie Huang  <https://orcid.org/0000-0002-2288-6952>

Da-Wei Chen  <https://orcid.org/0000-0002-8718-8768>

Xin Hong  <https://orcid.org/0009-0003-9477-2414>

Fang Wen  <https://orcid.org/0000-0002-3889-8835>

Data availability




All of the data that support the findings of this study are available in the main text.

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Evolution of connective glands reveals a new synapomorphy for Malpighiaceae and the hidden potential of staminal glands for Malpighiales systematics

Rafael Felipe de Almeida^{1,2}, Gustavo Arévalo-Rodrigues³, Isa L. de Moraes¹,
Poliana Cardoso-Gustavson⁴

¹ Universidade Estadual de Goiás, Quirinópolis, Goiás, Brazil

² Royal Botanic Gardens, Kew, Richmond, Surrey, UK

³ Instituto de Pesquisas Ambientais, São Paulo, São Paulo, Brazil

⁴ Universidade Federal do ABC, São Bernardo do Campo, São Paulo, Brazil

Corresponding author: Rafael Felipe de Almeida (r.felipe_de_almeida@kew.org)

Abstract

Connective glands are important morphological characters for the taxonomy of some genera of Malpighiaceae, with few recent studies having just elucidated these glands' anatomical and ecological functions. In order to test the systematic relevance of connective glands to the currently accepted phylogenetic informal clades of Malpighiaceae, we characterised the anatomy and/or histochemistry of two-thirds of Malpighiaceae genera and ten species from nine families of Malpighiales to test: 1. Do connective glands occur in the flowers of all informal clades of Malpighiaceae?; and 2. Are they taxonomically relevant to characterise those clades? We sampled 25 genera and 26 species of Malpighiaceae, processing their anthers using traditional anatomical methods and characterising their glands using light microscopy and SEM imaging. Selected species were subjected to histochemical tests, and an additional 21 genera and 33 species of Malpighiaceae and nine families (ten species) of Malpighiales were included in our sampling from the literature. Three anatomical characters were scored, coded and mapped using Maximum Likelihood methods onto the molecular phylogeny of Malpighiaceae. All sampled species of Malpighiaceae showed connective glands characterised as epidermal or trichomal elaiophores. Our character-mapping analyses recovered connective elaiophores as a new synapomorphy for Malpighiaceae. Different types of epidermal or trichomal elaiophores were recovered as homoplasies for the *Christianella* and *Banisteriopsis* clades and the genera *Byrsonima*, *Camarea* and *Cottsia*. Our analyses also recovered the glands' place of insertion in the stamen and the exudate type as potential new synapomorphies or homoplasies for the families of Malpighiales sampled. Our results propose the connective elaiophores as a new synapomorphy for Malpighiaceae and hypothesise the role that different staminal glands might play in the systematics of Malpighiales. Further comprehensive anatomical studies are still needed for the staminal glands of most families of this order to shed new light on the patterns recovered in our study.



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Introduction

Malpighiaceae (Malpighiales) are a family of flowering plants comprising 75 genera and 1,350 species of trees, shrubs, subshrubs and lianas distributed across tropical and subtropical regions of the world (Almeida et al. 2020; POWO 2023). The monophyly of this family has been corroborated by several molecular phylogenetic studies of the past two decades (Cameron et al. 2001; Davis et al. 2001; Davis and Anderson 2010; Almeida and van den Berg 2021; Almeida et al. 2023), but the monophyly of its subfamilies, most tribes, and several genera was not supported (Cameron et al. 2001; Davis et al. 2001; Davis and Anderson 2010; Almeida and van den Berg 2021). Since then, several new genera and generic synonymies have been gradually proposed to accommodate these newly identified lineages (Anderson 2006; Anderson and Davis 2007; Almeida and van den Berg 2021). Although no new classification system based on phylogenetic evidence has ever been proposed for Malpighiaceae, the family is currently divided into ten informally named clades: 1. Byrsonimoids, 2. Acridocarpoids, 3. Mcvaughiioids, 4. Barnebyoids, 5. Ptilochaetoids, 6. Bunchosiioids, 7. Hiraeoids, 8. Tetrapteroids, 9. Stigmaphylloids, and 10. Malpighioids (Davis and Anderson 2010; Almeida and van den Berg 2021; Almeida et al. 2023).

Neotropical Malpighiaceae show a conspicuous floral conservatism characterised by monosymmetric (i.e., zygomorphic), monoecious flowers with five sepals adnate at the base, abaxially (i.e., to the flower axis) bearing a pair of oil-secreting glands (i.e., elaiophores) near the base (sometimes absent from the anterior sepal or completely absent in few genera; Fig. 1). The five petals are free, clawed (i.e., narrowed at base), and divided into groups: four lateral petals and a single posterior petal slightly different from the lateral ones (i.e., in size, colour, shaped, posture, or margin; Fig. 1). The androecium comprises two whorls of (1–)5 stamens with eglandular filaments connate at base, connectives frequently glandular and hairy, with anthers basifixed and composed by two, rimose (porate in *Coleostachys* A.Juss.) pollen sacs (Fig. 1). The gynoecium consisting of a 3-carpellate and 3-locular ovary, the ovary showing primordial projections in the genera bearing ornamented mericarps (which will later fully develop into wings, winglets or setae); style (1–)3 usually free and long, cylindrical to flattened, eglandular and usually glabrous, with the apex truncate, rounded, uncinata or expanded (i.e., with a leaf-like projection); and each style with one, capitate or punctate, terminal or lateral stigma (Fig. 1). The fruits vary greatly, ranging from indehiscent fleshy (i.e., drupes), indehiscent dry (i.e., nuts), to dehiscent dry fruits splitting into three fruitlets (i.e., schizocarps) smooth or ornamented (i.e., winged or setose) mericarps (Anderson 1979; Almeida et al. 2020).

The floral conservatism of Malpighiaceae is the result of a 75-million-year mutualism with certain groups of bees that collect the non-volatile oil produced by their elaiophores (Michener 2007; Davis et al. 2014). The solitary female bees collect oil from elaiophores using their posterior legs for larval provisioning and breeding cell lining of their nests (Simpson and Neff 1981; Buchmann 1987; Vogel 1990; Michener 2007; Reis et al. 2007). Malpighiaceae are the oldest and most diversified flowering plants to offer oil as a floral reward to their pollinators (Renner and Schaeffer 2010). Their ancestor emerged ca. 75 million years ago alongside lineages of oil-collecting bees, and both remained on an exclusive

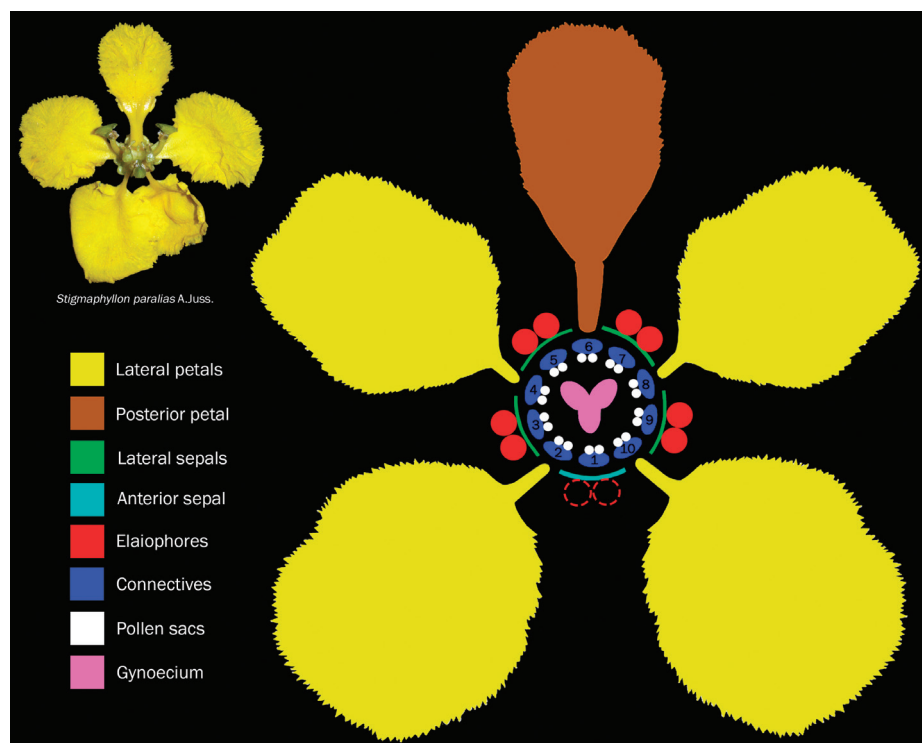


Figure 1. Diagram of a Malpighiaceae flower showing all informative floral organs. Upper left photograph of *Stigmaphyllon paralias* A.Juss. by Marco Pellegrini.

mutualism for at least 40 million years when new lineages of oil-offering angiosperms emerged (e.g., Iridaceae, Krameriaceae, and Plantaginaceae; Renner and Schaeffer 2010; Davis et al. 2014; Martins and Melo 2016). Neotropical species of Malpighiaceae are pollinated mainly by Centridini, Tapinotaspidini, and Tetrapediini bees (Vogel 1974; Alves-dos-Santos et al. 2007; Martins and Melo 2016). On the other hand, the Paleotropical species of Malpighiaceae show a conspicuous change in their pollination syndrome, from oil-offering to pollen-offering, since Centridini, Tapinotaspidini, and Tetrapediini bees are only found in the New World (Davis et al. 2014). These Old-World lineages mostly show actinomorphic, functionally dioecious flowers without oil-secreting glands or with glands reduced to 1–3 large nectaries similar in shape and anatomical structure to the elaiophores of Neotropical species (Anderson 1979; Davis et al. 2014; Guesdon et al. 2019).

Elaiophores are floral glands consisting of a uniseriate and columnar secretory epithelium with a thick cuticle and a parenchyma that is vascularised by xylem and phloem that produce and secrete non-volatile oils as a reward for their pollinators (Vogel 1974). Oil-secreting glands occur in 1500–2400 species of 11 families of monocots and eudicots, including Malpighiaceae. Most of these families only show a single type of elaiophore: 1. epidermal or 2. trichomal (Vogel 1974; Renner and Schaefer 2010). The monocot families Iridaceae and Orchidaceae are currently the only ones showing both epidermal and trichomal elaiophores (Renner and Schaefer 2010).

Over the past three decades, the epidermal elaiophores of Malpighiaceae have been anatomically and ecologically studied by different authors (Lobreaux-Callen 1989; Simpson 1989; Subramanian et al. 1990; Vogel 1990; Cocucci et al. 1996; Carvalho et al. 2005; Araújo and Meira 2016; Possobom and

Machado 2017; Torretta et al. 2018; Avalos et al. 2020; Aliscioni et al. 2022). Nonetheless, elaiophores were only recently found in additional Malpighiaceae floral organs besides their sepals. Possobom et al. (2015) identified epidermal glands in the connectives of *Diplopterys pubipetala* (A.Juss.) W.R.Anderson & C.C.Davis and revealed the non-volatile lipidic nature (i.e., elaiophores) of the exudate of these staminal glands. Possobom et al. (2015) also hypothesised that the function of these staminal elaiophores is to increase pollen transfer efficiency and chemically attract pollinators. The occurrence of glandular projections in stamen's connectives of Malpighiaceae has been noticed by several authors since incredibly early in the taxonomy of several genera of this family (Anderson 1975, 1982, 1987, 1995; Gates 1982; Johnson 1986; Niedenzu 1928; Simpson 1989). Nonetheless, it was only recently that the structure, nature, and occurrence of staminal glands in Malpighiaceae had their systematic relevance properly tested in a phylogenetic context with the study of Arévalo-Rodrigues et al. (2020). These authors described the occurrence of staminal elaiophores for all analysed genera from the Stigmaphylloid clade and the outgroup species *Byrsonima spicata* (Cav.) DC.

Thus, aiming to better characterise the macro-evolutionary patterns of the connective glands of Malpighiaceae, we performed a broad micromorphological study, including 46 genera from nine of the ten informal clades of the family (*sensu* Almeida and van den Berg 2021). Our main goal was to identify the nature of the connective glands of 46 genera and 59 species of Malpighiaceae, from both the New and Old World, by characterising their anatomy, exudate, and tissue histochemistry. More specifically, we intended to answer the following questions: 1. Do staminal connective glands occur in the flowers of all ten informal clades of Malpighiaceae? 2. Are they taxonomically relevant to characterise those clades?

Methods

Plant material

Anthers of flowers at anthesis were sampled from herbarium specimens or collected in the field and fixed in FAA 50 (Johansen 1940) for 25 genera and 26 species of Malpighiaceae (Table 1). Herbarium samples were submitted to a rehydration protocol, being boiled in distilled water for 15 minutes, treated with 2% potassium hydroxide for two hours at room temperature and washed in tap water, being posteriorly dehydrated in an alcoholic series and stored in ethanol 70% (modified from Smith and Smith 1942).

Light microscopy and histochemistry

Fixed or rehydrated samples were embedded using standard methods for Technovit historesin and sectioned at 2 µm thickness (Arévalo-Rodrigues et al. 2020). Sections were stained with toluidine blue/*p*-phenylenediamine (1% aqueous/1% isopropanol: methanol, 1:1) for identification of metachromasy/phenolic compounds and lipid identification, respectively (Feder and O'Brien 1968; Kivimäenpää et al. 2004), and subsequently mounted in water slides for structural analyses under light microscopy.

Table 1. List of species investigated in micromorphological, anatomical, and histochemical studies. **T.** Trichomal elaiophores. **EU.** Epidermal unicellular elaiophores with vacuoles. **EO.** Epidermal overlapping elaiophores without vacuoles. **FA.** Fatty Acids. **Ph.** Phenolic compounds. **Ps.** Polysaccharides. ¹ Species sampled in this study. ² Species sampled by Arévalo-Rodrigues et al. (2020). ³ Species sampled by Lorenzo (1981). ⁴ Simpson (1989). ⁵ Aliscioni et al. (2019). ⁶ Miyashita et al. (1964). ⁷ Sanches et al. (2023). ⁸ Rao (1941). ⁹ Anderson (1980). ¹⁰ Paiva et al. (2019). ¹¹ Stevens (2001, onwards). ¹² Amaral et al. (2017). ¹³ Wurdack and Zartman (2019). ¹⁴ Crockett (2010). ¹⁵ Gama et al. (2016). ¹⁶ Feng (2005). ¹⁷ Bonifácio et al. (2023).

Species	Voucher (Herbarium)	Clades	Anatomy	Histochemistry
<i>Caryocar brasiliense</i> Cambess. (Caryocaraceae) ¹⁰	Lombardi s.n. (BHCB53575)	–	EU	FA, Ph, Ps
Celastrales ¹¹	–	–	–	–
<i>Clusia scrobiculata</i> Benoist (Clusiaceae) ¹²	Ribeiro 1838 (INPA)	–	EU	FA, Ph, Ps
<i>Vantanea spiritu-sancti</i> (Cuatrec.) K.Wurdack & Zartman (Humiriaceae) ¹³	Silva et al. 1436 (US)	–	EU	Ph, Ps
<i>Hypericum perforatum</i> L. (Hypericaceae) ¹⁴	–	–	EU	FA, Ph, Ps
<i>Phyllanthus urinaria</i> L. (Phyllanthaceae) ¹⁵	T.S.S. Gama 6 (MFS)	–	–	–
Picrodendraceae ¹¹	–	–	–	–
<i>Anchietea frangulifolia</i> (Kunth) Melch. (Violaceae) ¹⁶	Cuatrecasas 5477 (US)	–	EU	Ph
<i>Bergia perennis</i> F.Muell. (Elatinaceae) ¹⁷	Henshall 1479 (SP)	–	–	–
<i>Elatine gratioloides</i> A.Cunn. (Elatinaceae) ¹⁷	Latz 7536 (SP)	–	–	–
<i>Byrsonima incarnata</i> Sandwith ¹	Lima 05 (HUEFS)	Byrsonimoids	T, EU	FA, Ph, Ps
<i>Byrsonima spicata</i> (Cav.) DC. ²	Rodrigues 277 (SP)	Byrsonimoids	T, EU	absent
<i>Galphimia australis</i> Chodat ¹	Almeida 767 (HUEFS)	Byrsonimoids	EU	absent
<i>Lophanthera lactescens</i> Ducke ¹	Queiroz 5277 (HUEFS)	Byrsonimoids	EU	absent
<i>Pterandra pyroidea</i> A.Juss. ¹	Almeida 838 (JAR)	Byrsonimoids	EU	absent
<i>Verrucularina glaucophylla</i> (A.Juss.) Rauschert ¹	Almeida 606 (HUEFS)	Byrsonimoids	EU	absent
<i>Burdachia duckei</i> Steyerl. ¹	Giulietti 2591 (HUEFS)	Mcvaughoids	EU	absent
<i>Mcvaughia sergipana</i> Amorim & R.F.Almeida ¹	Amorim 8393 (HUEFS)	Mcvaughoids	EU	FA, Ph, Ps
<i>Barnebya harleyi</i> W.R.Anderson ¹	Harley 54284 (HUEFS)	Barnebyoids	EU	FA, Ph, Ps
<i>Dinemandra ericoides</i> A.Juss. ⁴	Simpson 8310141 (TEX)	Ptilochaetoids	EU	absent
<i>Dinemagonum gayanum</i> A.Juss. ⁴	Simpson 831082 (TEX)	Ptilochaetoids	EU	absent
<i>Ptilochaeta bahiensis</i> Turcz. ¹	Almeida 858 (JAR)	Ptilochaetoids	EU	FA, Ph, Ps
<i>Bunchosia pernambucana</i> W.R.Anderson ¹	Mello 10765 (HUEFS)	Bunchosoids	EU	FA, Ph, Ps
<i>Thryallis latifolia</i> Mart. ¹	Almeida 687 (HUEFS)	Bunchosoids	EU	absent
<i>Tristellateia australasiae</i> A.Rich. ⁸	Rao s.n. (JCB)	Bunchosoids	EU	absent
<i>Hiraea hatschbachii</i> C.E.Anderson ¹	Almeida 548 (HUEFS)	Hiraeoids	EU	FA, Ph, Ps
<i>Lophopterys floribunda</i> W.R.Anderson & C.C.Davis ⁷	Sanches s.n. (UFV)	Hiraeoids	EU	FA, Ph, Ps
<i>Alicia anisopetala</i> (A.Juss.) W.R.Anderson ¹	Almeida 890 (JAR)	Tetrapteroids	EO	absent
<i>Callaeum psilophyllum</i> (A.Juss.) D.M.Johnson ¹	Almeida 724 (HUEFS)	Tetrapteroids	EO	absent
<i>Callaeum psilophyllum</i> (A.Juss.) D.M.Johnson ¹	Almeida 734 (HUEFS)	Tetrapteroids	EO	absent
<i>Carolus chasei</i> (W.R.Anderson) W.R.Anderson ¹	Almeida 585 (HUEFS)	Tetrapteroids	EU	absent
<i>Christianella surinamensis</i> (Koesterm.) W.R.Anderson ¹	Almeida 817 (HUEFS)	Tetrapteroids	EO	absent
<i>Dicella bracteosa</i> (A.Juss) Griseb. ¹	Cardoso 273 (HUEFS)	Tetrapteroids	EU	absent
<i>Glicophyllum cardiophyllum</i> (Nied.) R.F.Almeida ¹	Almeida 641 (HUEFS)	Tetrapteroids	EU	FA, Ph, Ps
<i>Heteropterys aenea</i> Griseb. ¹	Almeida 798 (HUEFS)	Tetrapteroids	EU	absent
<i>Niedenzuella lasiandra</i> (A.Juss.) R.F.Almeida ¹	Almeida 891 (RB)	Tetrapteroids	EU	absent
<i>Tetrapteryx phlomoides</i> (Spreng.) Nied. ¹	Almeida 819 (HUEFS)	Tetrapteroids	EU	absent
<i>Tricomaria usillo</i> Hook. & Arn. ⁵	Aliscioni s.n. (CORD)	Tetrapteroids	EU	absent

Species	Voucher (Herbarium)	Clades	Anatomy	Histochemistry
<i>Amorimia rigida</i> (A.Juss.) W.R.Anderson ¹	Almeida 556 (HUEFS)	Malpighioids	EU	FA, Ph, Ps
<i>Aspidopterys concava</i> (Wall.) A.Juss. ¹	Merrill 11601 (US)	Malpighioids	EU	absent
<i>Ectopopterys soejartoi</i> W.R.Anderson ⁹	Soejarto 3399 (US)	Malpighioids	EU	absent
<i>Malpighia glabra</i> L. ⁶	Miyashita 269–2 (HAW)	Malpighioids	EU	absent
<i>Mascagnia sepium</i> (A.Juss.) Griseb. ¹	Almeida 822 (HUEFS)	Malpighioids	EU	absent
<i>Triaspis mozambica</i> A.Juss. ¹	Robertson 6540 (US)	Malpighioids	EU	absent
<i>Aspicarpa harleyi</i> W.R.Anderson ²	Hatschbach 67824 (HUEFS)	Stigmaphylloids	EO	absent
<i>Banisteriopsis adenopoda</i> (A.Juss.) B.Gates ²	Almeida 813 (HUEFS)	Stigmaphylloids	EO	absent
<i>Banisteriopsis argyrophylla</i> (A.Juss.) B.Gates ²	Almeida 808 (HUEFS)	Stigmaphylloids	EO	absent
<i>Banisteriopsis laevifolia</i> (A.Juss.) B.Gates ²	Almeida 658 (HUEFS)	Stigmaphylloids	EO	absent
<i>Banisteriopsis malifolia</i> (Nees and Mart.) B.Gates ²	Francener 1122 (SP)	Stigmaphylloids	EO	absent
<i>Banisteriopsis multifoliolata</i> (A.Juss.) B.Gates ²	Demuner 3629 (SP)	Stigmaphylloids	EO	absent
<i>Banisteriopsis variabilis</i> B.Gates ²	Almeida 815 (HUEFS)	Stigmaphylloids	EO	absent
<i>Bronwenia megaptera</i> (B.Gates) W.R.Anderson & C.C.Davis ²	Almeida 782 (HUEFS)	Stigmaphylloids	EU	absent
<i>Camarea affinis</i> A.St.-Hil. ²	Almeida 760 (HUEFS)	Stigmaphylloids	T	absent
<i>Camarea humifusa</i> W.R.Anderson ²	Pastore 2310 (HUEFS)	Stigmaphylloids	T	absent
<i>Cottisia gracilis</i> (A.Gray) W.R.Anderson & C.C.Davis ²	Sperry 597 (US)	Stigmaphylloids	T	absent
<i>Diplopterys lutea</i> (Griseb.) W.R.Anderson & C.C.Davis ²	Almeida 210 (SP)	Stigmaphylloids	EO	absent
<i>Diplopterys pauciflora</i> (G.Mey.) Nied. ²	de La Cruz 3134 (MG)	Stigmaphylloids	EU	absent
<i>Gallardoa fischerii</i> Hicken ²	Simon 891 (US)	Stigmaphylloids	EU	absent
<i>Gaudichaudia albida</i> Schltdl. & Cham. ²	A.R. Molina 23061 (US)	Stigmaphylloids	EO	absent
<i>Gaudichaudia krusei</i> W.R.Anderson ²	s. col. (US2367483)	Stigmaphylloids	EO	absent
<i>Janusia guaranitica</i> (A.St.-Hil.) A.Juss. ³	Fulvio 164 (CORD)	Stigmaphylloids	EO	absent
<i>Peixotoa hispidula</i> A.Juss. ²	Almeida 818 (HUEFS)	Stigmaphylloids	EO	absent
<i>Sphedamnocarpus galphimifolius</i> (A.Juss.) Szyszyl. ²	Kimp 711 (US)	Stigmaphylloids	EO	absent
<i>Sphedamnocarpus pruriens</i> (A.Juss.) Szyszyl. ²	Strohback 53137 (US)	Stigmaphylloids	EU	absent
<i>Stigmaphyllon abutifolium</i> (A.Juss.) C.E.Anderson ²	Hosaka 3378 (US)	Stigmaphylloids	EU	absent
<i>Stigmaphyllon blanchetii</i> C.E.Anderson ²	Almeida 596 (HUEFS)	Stigmaphylloids	EU	FA, Ph, Ps
<i>Stigmaphyllon grandifolium</i> (A.Juss.) C.E.Anderson ²	Kajwski 803 (US)	Stigmaphylloids	EU	absent
<i>Stigmaphyllon lalandianum</i> A.Juss. ²	Almeida 816 (HUEFS)	Stigmaphylloids	EU	absent
<i>Stigmaphyllon timoriense</i> (DC.) C.E.Anderson ²	Gray 303 (US)	Stigmaphylloids	EU	absent

Regarding herbarium samples, it is possible to perform histochemical analysis of rehydrated samples, except for identifying low-weight lipophilic molecules, including phenolic-based molecules, essential oils, and alkaloids. Connective glands were histochemically characterised in ten genera, representing nine of the ten informal phylogenetic clades currently accepted for Malpighiaceae (Table 1). Additionally, not all rehydrated materials resulted in suitable samples for anatomical/histochemical analyses, aside from the reduced number of flowers in this study. To detect the main classes of compounds in the glands' exudate, we used copper acetate/rubeanic acid for fatty acids (Ganter and Jolles 1969), PAS reaction for total polysaccharides (McManus 1948), and ruthenium red or tannic acid and ferric chloride for mucilage (Gregory and Baas 1989; Pizzolato 1977). The digital images were acquired with an Olympus BX53 compound microscope equipped with an Olympus I-Colour 5 digital camera and Image Pro Express 6.3 software.

Scanning electron microscopy

Fixed anther samples from all 25 genera and 26 species of Malpighiaceae sampled (Table 1) were fully dehydrated using 100% ethanol, rinsed in a hexamethyldisilane (HMDS) series (33.3, 50.0, and 66.6% v/v in 100% ethanol), and then rinsed three times in 100% HMDS for 1 min each to dry the material (Jeger et al. 2009). Chemically dried and herbarium samples were mounted on stubs, sputter-coated with gold using a Leica ACE200 system, and viewed using a JEOL JSM 741F scanning electron microscope at 10 kV. All SEM-analysed specimens were imaged and compared with the micromorphology of the genera analysed for anatomy and histochemistry under light microscopy.

Character coding and mapping

Character coding followed the recommendations of Sereno (2007) for morphological analyses. Primary homology hypotheses (i.e., Ad hoc hypothesis; De Pinna 1991; Ochoterena et al. 2019) were proposed for a total of 46 genera and 59 species of Malpighiaceae: 25 genera and 26 species sampled in this study, and 21 genera and 33 species of Malpighiaceae and nine families of Malpighiales sampled from the specialised literature (Tables 1, 2). Three micromorphological characters were scored, coded, and optimised (i.e. ancestral state reconstruction analysis) using the Maximum Likelihood criterium implemented on Mesquite 2.73 (Maddison and Maddison 2009) on a trimmed consensus tree from the molecular phylogeny of Malpighiaceae published by Davis and Anderson (2010; TreeBase accession 10998), evidencing a single tip per genus and the ten informal clades proposed by de Almeida and van den Berg (2021).

Results

The connectives of all species analysed under light microscopy and SEM showed elaiophores within their lining tissue (Fig. 2A–G, I–K, Table 1). We classified these connectives into three distinct morphotypes: 1. trichomal, composed of secretory papillae in some species of *Byrsonima*, *Camarea*, and *Cottisia* (Fig. 2H, Table 1); 2. epidermal, comprising unicellular globose cells with vacuoles showing polyphenols with different aspects (i.e., granulose, dense, or both), and also the occurrence of many lipid droplets inside them in 33 genera of Malpighiaceae (Fig. 2A–E, Table 1); and 3. epidermal, comprising overlapping globose epidermal cells mainly found in ten genera of Malpighiaceae (Fig. 2F–G, Table 1). The histochemical analyses identified the occurrence of fatty acids (Fig. 2I, Table 1), polysaccharides (Fig. 2J, Table 1), and phenolic compounds (Fig. 2K, Table 1) inside the glandular tissue from the connectives of the analysed genera, and presumably, the secretion of these staminal glands is heterogeneous.

Three micromorphological characters were scored and coded for our sampling (see Table 2). Unicellular globose cells were recovered as the ancestral state in Malpighiaceae connectives, being retained in most lineages of this family (Fig. 3). Secretory papillae were recovered as a homoplasy in the connectives of *Byrsonima*, *Cottisia* and *Camarea* (Fig. 3). Overlapping globose cells were also recovered as a homoplasy for the most recent common ancestor of



Figure 2. Staminal elaiophores of Malpighiaceae species **A** smooth globose cells comprise all the connectives of *Lo-phanthera lactescens* **B** in *Niedenzuella lasiandra*, non-secretory trichomes occur in all the anther epidermis, while in **C** *Carolus chasei*, they permeate only the anther's edge **D** *Pterandra pyroidea*. Detail of the exudate of the globose epi-dermal cells (arrowhead in D, F) **E** the unicellular globose epidermal cells have a dense vacuole in *Amorimia rigida*; note the cuticle detachment (arrow). (**F–I**) *Callaeum psilophyllum*. The latter species have elaiophores formed by overlapping globose epidermal cells with a dense vacuole in the connective **F**, **G** and unicellular trichomal elaiophores in the anther epidermis **H** The unicellular trichomal elaiophores exhibit lipid droplets in the protoplast **H**. **J, K** *Bunchosia pernambucana* **I–K** fatty acids, polysaccharides and phenolic compounds constitute the secretion inside the cell. el = elaiophores; em = endothecium; t = trichomes; va=vacuole. SEM (**A–D**, **F**). TBO+p-phe (**E**, **G–H**). AA (**J**). PAS (**J**). VR (**K**). Scale bars: 250 µm (**B**); 200 µm (**A**, **C**); 100 µm (**D**, **F**); 50 µm (**E**, **G–K**).

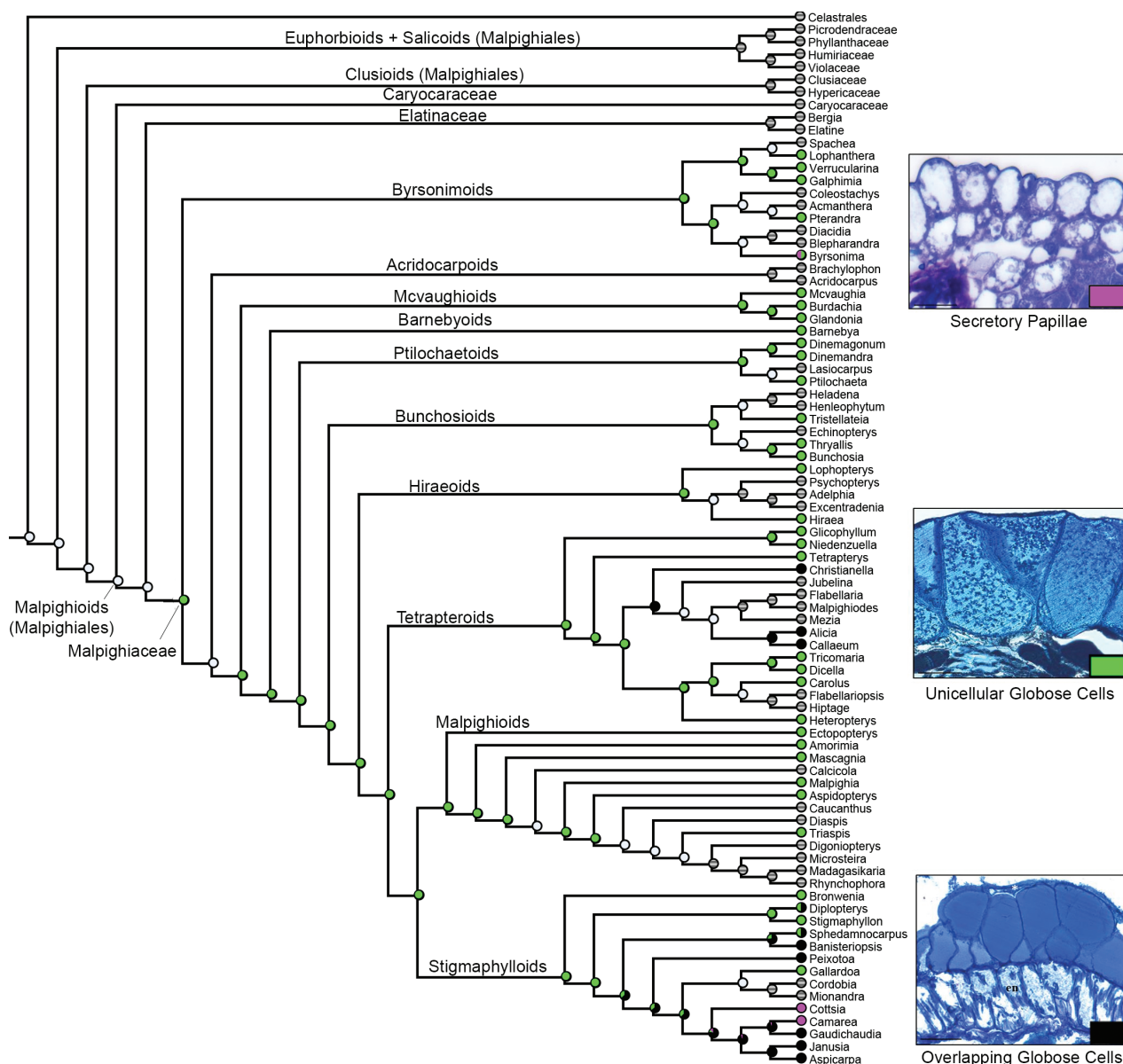


Figure 3. Character-mapping analysis showing the evolution of the three identified types of connective elaiophores by this study in Malpighiaceae. Gray dots represent not applicable (missing data) character states.

the *Christianella* and *Banisteriopsis* clades, within the Tetrapteroids and Stigmaphyllioids, respectively (Fig. 3). Glandular connectives were recovered by us as the ancestral state for Malpighiales (Fig. 4). Glandular filaments were recovered as a synapomorphy for Caryocaraceae (Fig. 4). Eglandular stamens were recovered as homoplastic synapomorphies for Elatinaceae, the Euphorbioids (represented in our analysis by Picrodendraceae + Phyllanthaceae), and Celastrales (Fig. 4). Regarding the nature of the staminal gland exudate, glandular connectives producing non-volatile oils were recovered as a synapomorphy for Malpighiaceae (Fig. 5), while glandular filaments producing non-volatile oils were recovered as a synapomorphy for Caryocaraceae (Fig. 5). Glandular connectives producing resin were recovered as a probable synapomorphy of the Clusioids (Clusiaceae + Hypericaceae; Fig. 5). Finally, glandular connectives producing nectar were recovered as a probable synapomorphy of the Salicoids (Humiriaceae + Violaceae).

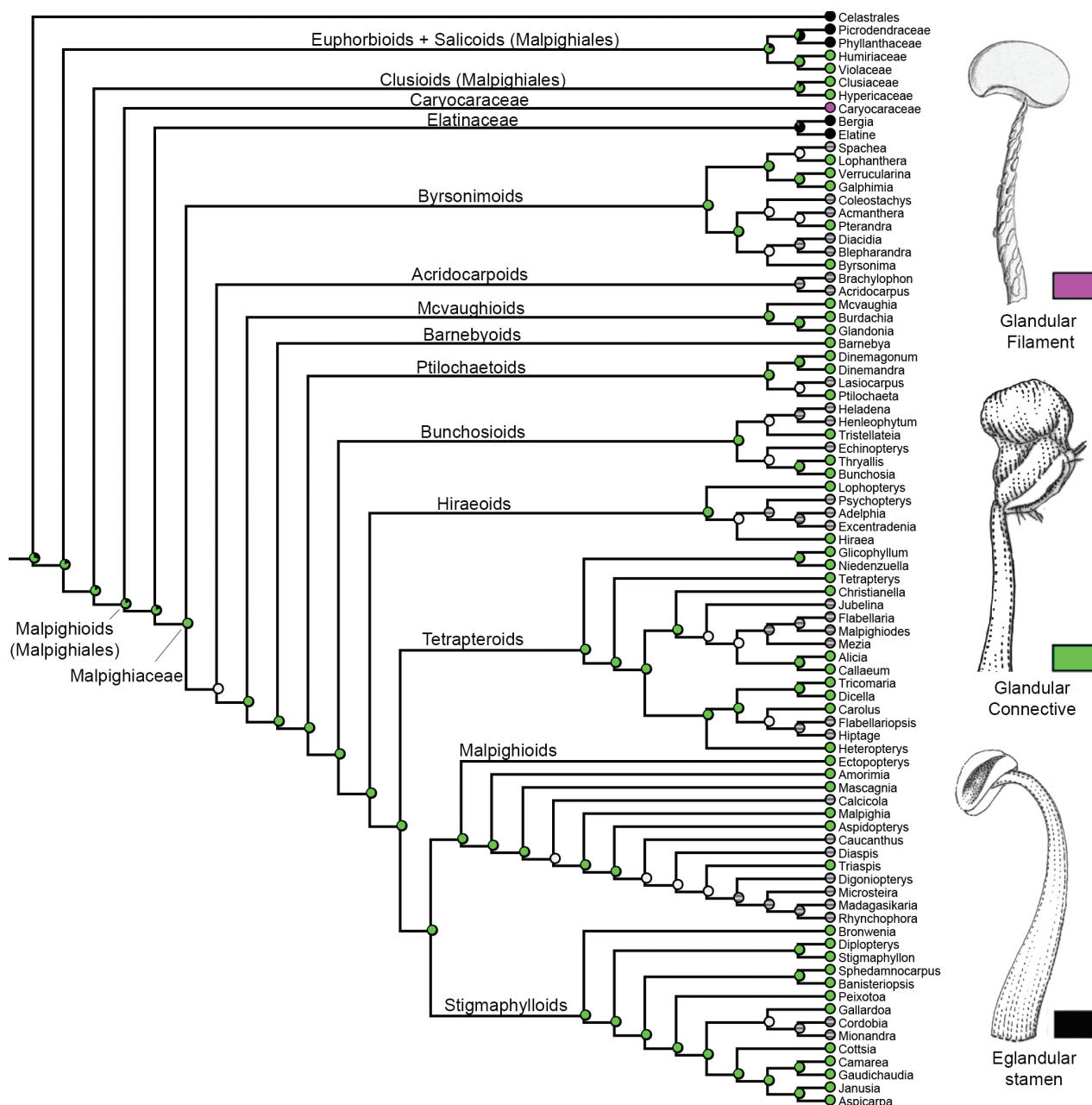


Figure 4. Character-mapping analysis showing the evolution of the three identified types of stamen glands and their respective place of insertion (i.e., on filaments, on connectives or entirely eglandular) by this study in Malpighiaceae. Gray dots represent not applicable (missing data) character states.

Discussion

Evolution of connective elaiophores in Malpighiaceae

The glandular connectives observed in this study in all analysed species of Malpighiaceae were characterised as elaiophores, occurring as epidermal cells or papillae (i.e., trichomal elaiophores). The connective elaiophores described in this study were mainly formed by globose cells, with distinct anatomical features from those found in the sepals, as reported by Arévalo-Rodríguez et al. (2020; Fig. 6). Sepal elaiophores are composed of a palisade

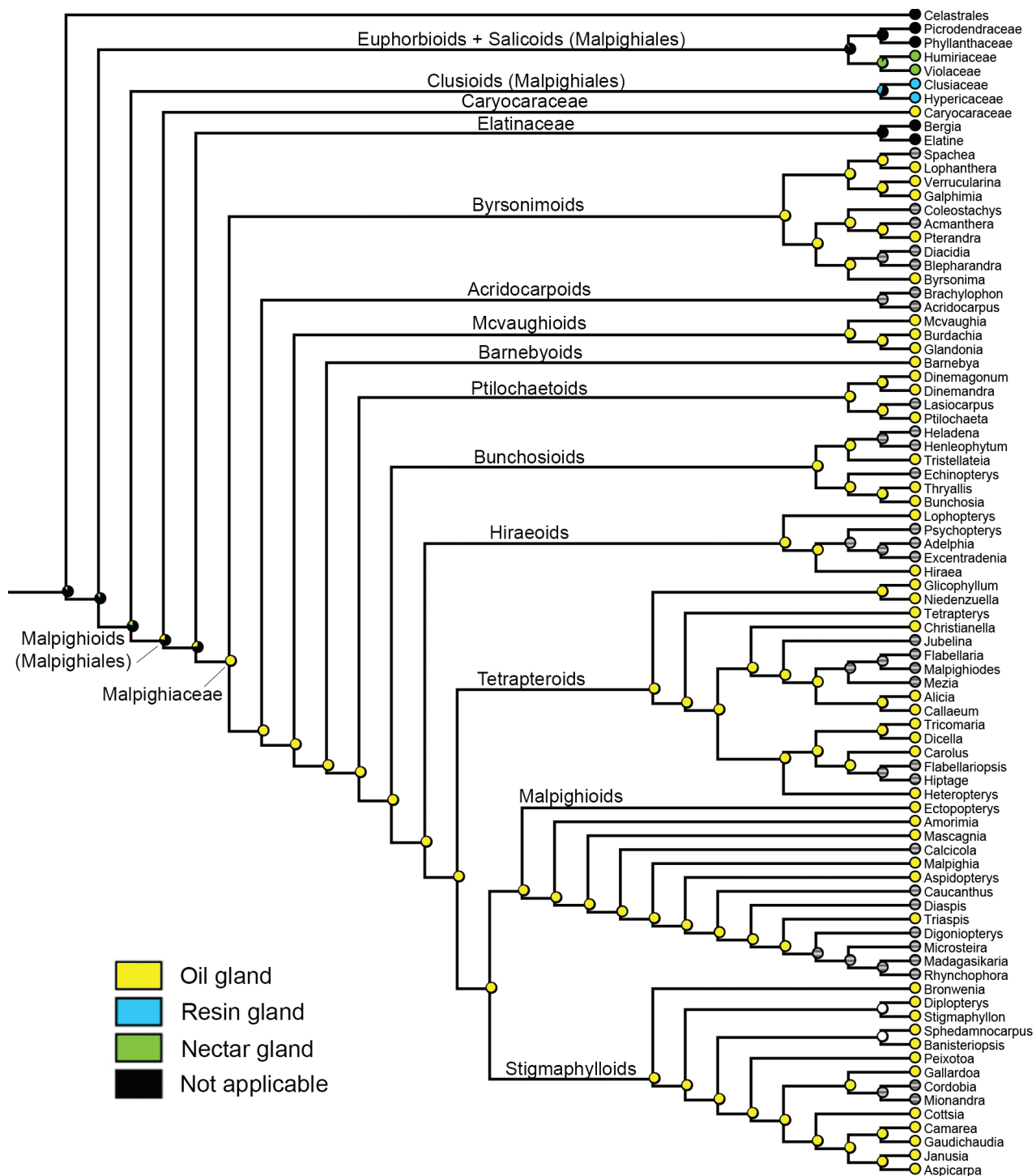


Figure 5. Character-mapping analysis showing the evolution of the four identified types of stamen glands exudate (i.e., oil gland, resin gland, nectar gland or eglandular) in Malpighiales. Grey dots represent missing data, and black dots represent not applicable character state (i.e., taxa with eglandular stamens, which do not produce any exudate, being coded as not applicable).

epidermis bearing a thick cuticle with vascularised parenchyma (Vogel 1974; Castro et al. 2001; Possobom et al. 2015; Araújo and Meira 2016; Possobom and Machado 2017; Aliscioni et al. 2022). Alternatively, connective elaiophores of Malpighiaceae comprise only one or two layers of globose epider-

mal cells or papillae (Possobom et al. 2015; Arévalo-Rodrigues et al. 2020; Avalos et al. 2020; Fig. 6). Nonetheless, trichomal elaiophores (i.e., papillae) in the connectives of Malpighiaceae have only recently been reported (Arévalo-Rodrigues et al. 2020). Despite epidermal and trichomal elaiophores sometimes co-occurring in the same plant organ (Pansarin et al. 2009), their occurrence in the same family is uncommon in flowering plants, being only reported for Malpighiaceae, Iridaceae, Orchidaceae, Plantaginaceae and Scrophulariaceae so far (Vogel 1974, 1984; Vogel and Machado 1991; Cosacov et al. 2009; Renner and Schaefer 2010).

The heterogeneous connective elaiophore secretion produced in Malpighiaceae comprises a mixture of lipids, polysaccharides and phenolic compounds. The same exudate composition was found in the glandular connectives of *Diplopterys pubipetala*, *Stigmaphyllon bonariense* (Hook. & Arn.) C.E. Anderson, and *S. jatrophiifolium* A. Juss. (Possobom et al. 2015; Avalos et al. 2020). A heterogeneous secretion mainly comprising non-volatile oils and polysaccharides is also produced by epidermal cells in the sepal elaiophores of Malpighiaceae (Vogel 1974; Lobreau-Callen 1989; Vinson et al. 1997; Castro et al. 2001; Possobom and Machado 2017; Aliscioni et al. 2022). This heterogeneous composition grants the exudate better fluidity, facilitating its collection by pollinators (Pansarin et al. 2009) being also observed in the nectar and stigmatic secretions of other flowering plant families, including Malpighiaceae (Endress 1994; Fahn 2000; Aliscioni et al. 2018). This fluid exudate of connective glands in Malpighiaceae resembles the fluid resin secreted by the connective glands of Calophyllaceae and the filaments of Clusiaceae and future in depth histochemistry studies should shed some light into their homology (Amaral et al. 2017; Cabral et al. 2021). Additionally, phenolic compounds show a central role as antioxidants and are secondarily astringent and toxic (Bruneton 1999; Simões et al. 2004), protecting floral resources from pathogens. *Monoeca* bees have been reported to collect pollen with the anthers' exudate (Possobom et al. 2015). The connective elaiophores have the primary function of adhering pollen grains to the pollinator's body, but they might also show a secondary chemical attraction function for these oil-collecting bees (Possobom and Machado 2017; Avalos et al. 2020).

The character-mapping analysis recovered unicellular globose cells (i.e., epidermal elaiophores) producing mainly non-volatile oil in the connectives of Malpighiaceae as a new synapomorphy for this family. This result was only possible due to our comprehensive analysis sampling 46 genera (out of 75) from nine of the ten informal phylogenetic clades currently recognised in Malpighiaceae (see Almeida and van den Berg 2021; Almeida et al. 2023). In fact, unicellular 2-branched hairs, conspicuous sepal elaiophores and clawed petals are already recognised as morphological synapomorphies for Malpighiaceae (APG IV 2016; Stevens 2001, onwards), with connective elaiophores proposed here as a fourth morphological synapomorphy for this family. Nonetheless, additional anatomic, histochemical and SEM studies sampling all the remaining genera of Malpighiaceae (see Table 2 for additional information) are still needed to better explore the evolutionary patterns of connective elaiophores structure and exudate composition in this family.

Table 2. Morphological matrix, including two morphoanatomical characters and a single histochemical character, scored and coded based on our results and the specialised literature. **Character 1.** Stamen, connective, elaiophore, type: (0) Trichomal, (1) Epidermal unicellular elaiophores with vacuoles, (2) Epidermal overlapping elaiophores without vacuoles, (?) missing data. **Character 2.** Stamen, gland, position: (0) filaments, (1) connectives, (2) absent. **Character 3.** Stamen, gland, exudate, type: (0) oil, (1) resin, (2) nectar, (-) not applicable, (?) missing data. Taxa highlighted in bold represent phylogenetic outgroups.

Genera/Families	Character 1	Character 2	Character 3
Caryocaraceae	–	0	0
Celastrales	–	2	–
Clusiaceae	–	1	1
Humiriaceae	–	1	2
Hypericaceae	–	1	1
Phyllanthaceae	–	2	–
Picrodendraceae	–	2	–
Violaceae	–	1	2
Bergia L. (Elatinaceae)	–	2	–
Elatine L. (Elatinaceae)	–	2	–
<i>Acmanthera</i> (A.Juss.) Griseb.	?	?	?
<i>Acridocarpus</i> Guill., Perr. & A.Rich.	?	?	?
<i>Adelphia</i> W.R.Anderson	?	?	?
<i>Alicia</i> W.R.Anderson	2	1	0
<i>Amorimia</i> W.R.Anderson	1	1	0
<i>Aspicarpa</i> Rich.	2	1	0
<i>Aspidopterys</i> A.Juss. ex Endl.	1	1	0
<i>Banisteriopsis</i> C.R.Rob.	2	1	0
<i>Barnebya</i> W.R.Anderson & B.Gates	1	1	0
<i>Blepharandra</i> Griseb.	?	?	?
<i>Brachylophon</i> Oliv.	?	?	?
<i>Bronwenia</i> W.R.Anderson & C.C.Davis	1	1	0
<i>Bunchosia</i> Rich. ex Kunth	1	1	0
<i>Burdachia</i> A.Juss.	1	1	0
<i>Byrsonima</i> Rich. ex Kunth	0/1	1	0
<i>Calcicola</i> W.R.Anderson	?	?	?
<i>Callaeum</i> Small	2	1	0
<i>Camarea</i> A.St.-Hil.	0	1	0
<i>Carolus</i> W.R.Anderson	1	1	0
<i>Caucanthus</i> Forssk.	?	?	?
<i>Christianella</i> W.R.Anderson	2	1	0
<i>Coleostachys</i> A.Juss.	?	?	?
<i>Cordobia</i> Nied.	?	?	?
<i>Cottisia</i> Dubard & Dop	0	1	0
<i>Diacidia</i> Griseb.	?	?	?
<i>Diaspis</i> Nied.	?	?	?
<i>Dicella</i> Griseb.	1	1	0
<i>Digoniapterys</i> Arènes	?	?	?

Genera/Families	Character 1	Character 2	Character 3
<i>Dinemagonum</i> A.Juss.	1	1	0
<i>Dinemandra</i> A.Juss.	1	1	0
<i>Diplopterys</i> A.Juss.	1/2	1	0
<i>Echinopterys</i> A.Juss.	?	?	?
<i>Ectopopterys</i> W.R.Anderson	1	1	0
<i>Excentradenia</i> W.R.Anderson	?	?	?
<i>Flabellaria</i> Cav.	?	?	?
<i>Flabellariopsis</i> R.Wilczek	?	?	?
<i>Gallardoa</i> Hicken	1	1	0
<i>Galphimia</i> Cav.	1	1	0
<i>Gaudichaudia</i> Kunth	2	1	0
<i>Glandonia</i> Griseb.	1	1	0
<i>Glicophyllum</i> R.F.Almeida	1	1	0
<i>Heladena</i> A.Juss.	?	?	?
<i>Henleophytum</i> H.Karst.	?	?	?
<i>Heteropterys</i> Kunth	1	1	0
<i>Hiptage</i> Gartn.	?	?	?
<i>Hiraea</i> Jacq.	1	1	0
<i>Janusia</i> A.Juss.	2	1	0
<i>Jubelina</i> A.Juss.	?	?	?
<i>Lasiocarpus</i> Liebm.	?	?	?
<i>Lophanthera</i> A.Juss.	1	1	0
<i>Lophopterys</i> A.Juss.	1	1	0
<i>Madagasikaria</i> C.C.Davis	?	?	?
<i>Malpighia</i> L.	1	1	0
<i>Malpighiodes</i> Nied.	?	?	?
<i>Mascagnia</i> (Bertero ex DC.) Bertero	1	1	0
<i>Mcvaughia</i> W.R.Anderson	1	1	0
<i>Mezia</i> Schwacke ex Nied.	?	?	?
<i>Microsteira</i> Baker	?	?	?
<i>Mionandra</i> Griseb.	?	?	?
<i>Niedenzuella</i> W.R.Anderson	1	1	0
<i>Peixotoa</i> A.Juss.	2	1	0
<i>Psychopterys</i> W.R.Anderson & S.Corso	?	?	?
<i>Pterandra</i> A.Juss.	1	1	0
<i>Ptilochaeta</i> Turcz.	1	1	0
<i>Rhynchophora</i> Arènes	?	?	?
<i>Spachea</i> A.Juss.	?	?	?
<i>Sphedamnocarpus</i> Planch. ex Benth. & Hook. f.	1/2	1	0
<i>Stigmaphyllon</i> A.Juss.	1	1	0
<i>Tetrapterys</i> Cav.	1	1	0
<i>Thryallis</i> Mart.	1	1	0
<i>Triaspis</i> Burch.	1	1	0
<i>Tricomaria</i> Gillies ex Hook. & Arn.	1	1	0
<i>Tristellateia</i> Thouars	1	1	0
<i>Verrucularina</i> Rauschert	1	1	0

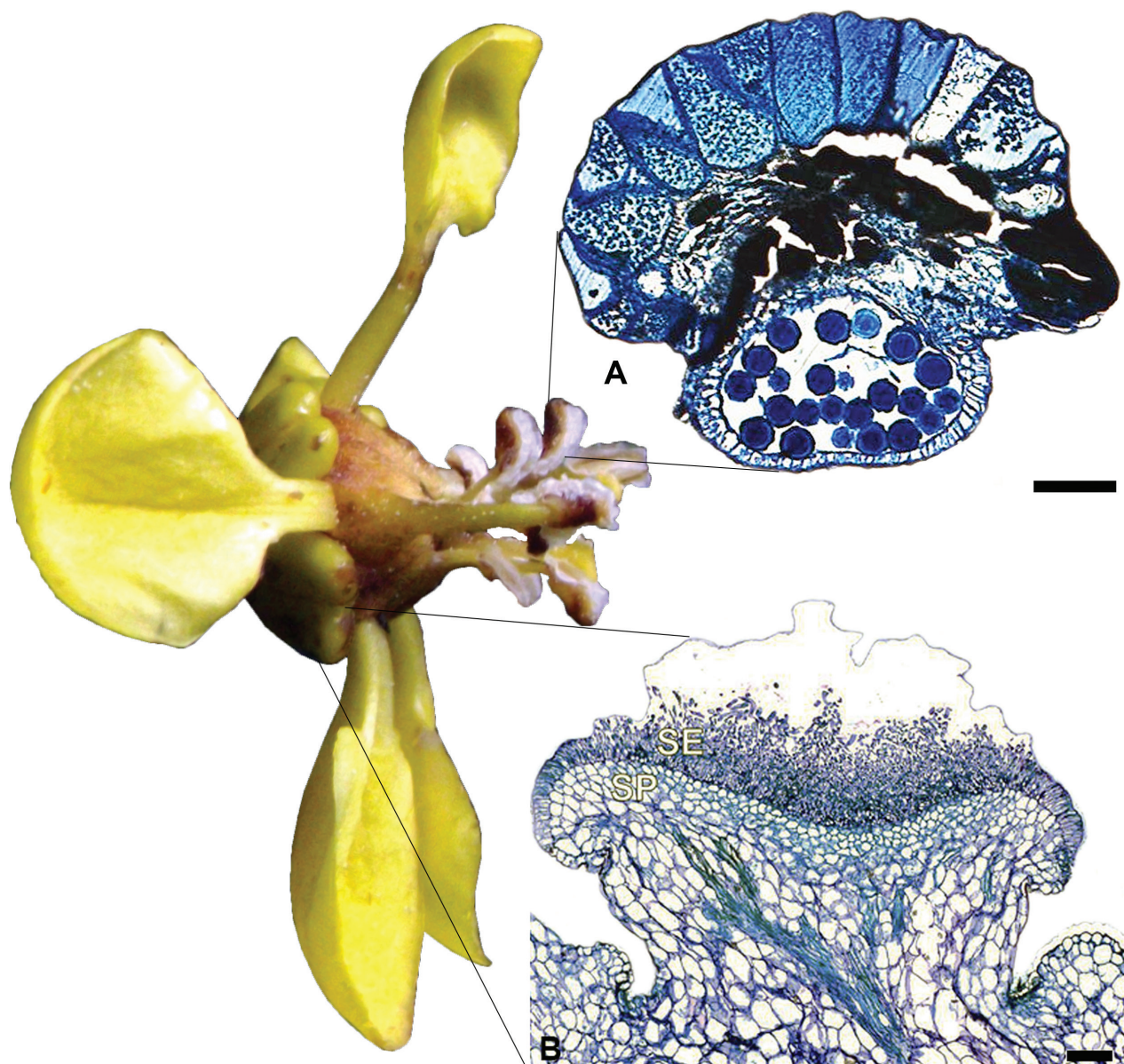


Figure 6. Comparison between staminal and sepal elaiophores of a Malpighiaceae flower **A** transverse section of an anther of *Stigmaphyllon blanchetii* C.E.Anderson **B** longitudinal section of sepal elaiophore of *Mcvaughia sergipana* Amorim & R.F.Almeida. Flower of *Heteropterys oberdanii* Amorim is shown in a side view, evidencing the location of elaiophores in different organs (**A** modified from Arévalo-Rodrigues et al. 2020; **B** modified from Almeida et al. 2019; photograph of *H. oberdanii* by R.F.Almeida).

Evolution of staminal glands in Malpighiales

Based on our sampling, the character-mapping analysis recovered glandular connectives as a possible synapomorphy for Malpighiales, one of Rosids' major extant orders, with 42 families and ~16,000 species with a mostly pantropical distribution, exhibiting remarkable morphological and ecological diversity (Xi et al. 2012). However, further studies focusing on characterising glandular tissue in the stamens of most families comprising Malpighiales are still needed. In fact, we were only able to sample nine out of the 42 families currently accepted in this order (see Table 1). Although strongly monophyletic, relationships between Malpighiales families remain elusive, and no consensus has

been reached even in the phylogenomic era (Davis et al. 2005; Wurdack and Davis 2009; Xi et al. 2012; Cai et al. 2019). Even though unambiguous morphological synapomorphies have not been proposed yet for Malpighiales, the order is generally characterised by a combination of homoplastic characters (i.e., paracytic stomata, leaf-blades with toothed margins, diverse extrafloral glands, ovules with thin, slender nucelli and endothelium, and dry stigmas; Stevens 2001, onwards), possibly including staminal glands.

The character-mapping analysis also recovered different types of staminal gland exudate as possible synapomorphies for some major clades of Malpighiales. This order currently comprises four major clades (i.e., Clusioids, Euphorbioids, Malpighioids, and Salicoids) recognised by different studies (Xi et al. 2012; Cai et al. 2019). However, no synapomorphies have ever been proposed for these four major clades of Malpighiales (Xi et al. 2012; Stevens 2001, onwards). The most recent common ancestor for the Clusioids had resin connective glands recovered in our analysis as a possible synapomorphy for this clade. Several types of exudates are secreted by the connective glands of Clusioids, such as wax and resins in Callophyllaceae (Crockett 2010), Clusiaceae (Crockett 2010; Amaral et al. 2017), and Hypericaceae (Crockett 2010). Currently, the Clusioids only show basifixed anthers as a homoplastic morphological character uniting its members (Silva-Batista et al. 2021).

The Euphorbioids had eglandular stamens recovered as a possible homoplasy shared with Elatinaceae and Podostemaceae in our analysis probably representing a reversal due to the specialised aquatic life form. The Euphorbioids are currently circumscribed by homoplastic characters such as plants often monoecious, flowers small, often imperfect, and 3-merous or not, ovules 1–2/ carpel, inner integument usually thicker than outer, epitropous, fruit a part-septidial + loculicidal capsule/schizocarp, cotyledons longer and broader than radicle (Stevens 2001, onwards). The Euphorbioids comprise five additional families (i.e., Euphorbiaceae, Ixonanthaceae, Linaceae, Peraceae, and Rafflesiaceae) that had never had their stamens anatomically studied, focusing on glandular tissues. In fact, most of these families are pantropically distributed or are difficult to analyse due to their rarity (i.e., Rafflesiaceae; POWO 2023; Stevens 2001, onwards). Further studies are urgently needed in these Euphorbioid families to corroborate the absence of staminal glands in this major clade of Malpighiales.

In our analysis, the Malpighioids (Malpighiales) had oil glandular stamens recovered as a possible synapomorphy. This major clade of Malpighiales had only three (out of 11) of its families anatomically explored regarding staminal glands. Malpighiaceae has already been the subject of staminal glands anatomical studies by several authors (Possobom et al. 2015; Arévalo-Rodrigues et al. 2020; Avalos et al. 2020; this study). On the other hand, Elatinaceae comprises only two genera, *Bergia* and *Elatine*, which were recently sampled in a comprehensive anatomical study by Bonifácio et al. (2023) and seemed to present, indeed, eglandular stamens in most of its species, except for *Elatine lindbergii* Rohrb. These authors performed histochemical tests for *E. lindbergii* indicating the presence of phenolic compounds, but they failed to test the exudate of these glands for lipids. This family is also an aquatic family, just like Podostemaceae, even though not that morphologically specialised and having cleistogamous (sometimes flowering underwater) and/or apomictic flowers. Caryocaraceae have also been anatomically studied by several authors

regarding their staminal glands (Dickison 1990; Matthews and Endress 2011; Sousa-Paiva et al. 2019). In fact, the Malpighioids (Malpighiales) show few circumscribing homoplasies, such as gynoeceium with longitudinal bulges above the placentae, outer integument 3–7 cells across, and inner integument 5–10 cells across (Stevens 2001, onwards). Nonetheless, further studies are still needed on the eight remaining families of the Malpighioids to test the relevance of staminal oil glands as possible synapomorphies or homoplasies circumscribing this major clade of Malpighiales.

Finally, the Salicoids had nectar connective glands recovered as a synapomorphy in our analysis. Nectar connective glands have recently been suggested as a new morphological synapomorphy for Humiriaceae (Wurdack and Zartman 2019). However, this exudate is also recorded in the filament or connective glands of Violaceae within the Salicoids (Feng 2005; Wurdack and Zartman 2019). In fact, only persistent endosperm has ever been proposed as a morphological homoplasy to circumscribe the Salicoids, making the nectar connective glands reported in this study a prominent character to further explore in this group (Stevens 2001, onwards). Classical morphological studies had long suggested that there was a group that included Salicaceae, Achariaceae, Violaceae, Flacourtiaceae, and Passifloraceae and its segregates, Malesherbiaceae and Turneraceae, in part because of their common possession of parietal placentation, some sort of corona or scales in the flower, nectaries outside the stamens, etc. (e.g. Cronquist 1981). However, additional studies in members of Achariaceae, Goupiaceae, Passifloraceae s.lat., and Salicaceae s.lat. are still needed to better explore the presence, structure, and nature of connective glands in these Salicoid families.

Conclusions

Connective elaiophores are proposed, for the first time, as a new synapomorphy for Malpighiaceae based on the characterisation and evolution of 46 genera of this family. Different types of connective glands (i.e., epidermal or trichomal elaiophores) were recovered as homoplasies for the *Christianella* and *Banisteriopsis* clades (i.e., overlapping globose epidermal elaiophores) and the genera *Byrsonima*, *Camarea* and *Cottisia* (i.e., trichomal elaiophores). Their position in the stamens (i.e., connectives or filaments) and exudate type were useful in evidencing evolutionary patterns within the Malpighiales sampling used in this study. Nonetheless, connective and filament glands in Malpighiales are yet to be evolutionarily studied in a broad context or even synoptically surveyed since only nine families (from 36) have any anatomical information available in the literature. Our results only represent the first glance at the potential of these staminal glands in aiding the systematics of Malpighiales and its major clades.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: RFA. Data curation: PCG, GAR. Formal analysis: PCG, RFA. Funding acquisition: PCG, ILM. Investigation: GAR. Methodology: GAR, RFA, PCG. Project administration: PCG. Resources: PCG, ILM. Supervision: PCG. Writing - original draft: RFA. Writing - review and editing: GAR, ILM, PCG.

Author ORCIDs

Rafael Felipe de Almeida  <https://orcid.org/0000-0002-9562-9287>

Gustavo Arévalo-Rodrigues  <https://orcid.org/0000-0002-1860-1707>

Isa L. de Morais  <https://orcid.org/0000-0001-8748-9723>

Poliana Cardoso-Gustavson  <https://orcid.org/0000-0003-0978-9389>

Data availability

All of the data that support the findings of this study are available in the main text.

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A new species of *Lochroma* Benth. (Solanaceae) from the eastern Andes of Colombia

Andrés Orejuela^{1,2}, Stacey D. Smith³, Boris Villanueva², Rocío Deanna^{3,4}

¹ Grupo de Investigación en Recursos Naturales Amazónicos-GRAM, Facultad de Ingenierías y Ciencias Básicas and Herbario Etnobotánico del Piedemonte Andino Amazónico (HEAA), Instituto Tecnológico del Putumayo-ITP, Mocoa, Putumayo, Colombia

² Herbario JBB, Subdirección científica, Jardín Botánico de Bogotá José Celestino Mutis, Bogotá D.C., Colombia

³ Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado, USA

⁴ Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET-UNC, Universidad Nacional de Córdoba, CC 495, 5000, Córdoba, Argentina

Corresponding author: Andrés Orejuela (andres.orejuela@itp.edu.co)

Abstract

Lochroma orozcoae A.Orejuela & S.D.Sm., **sp. nov.** (Solanaceae) is described from the Andean forests of Cundinamarca in the eastern cordillera of Colombia. *Lochroma orozcoae* was first collected by the eminent Spanish priest and botanist José Celestino Mutis in the late part of the 18th century, but the specimens have lain unrecognised in herbaria for over 200 years. The species shares many features with its closest relative, *Lochroma baumii* S.D.Sm. & S.Leiva, but it differs from it in having small flowers with five corolla lobes and few inflorescences per branch, located near the shoot apex with 1 to 4 (–8) flowers, fruits that are greenish-yellow when ripe and its restricted geographic distribution. A description of *L. orozcoae* is provided, along with a detailed illustration, photographs of live plants, a comparison with closely-related species and a key to all Colombian species of *Lochroma* Benth. In closing, we emphasise the value of historical collections for the knowledge of biodiversity.

Resumen

Lochroma orozcoae A.Orejuela & S.D.Sm., **sp. nov.** (Solanaceae) se describe a partir de los bosques andinos de Cundinamarca, en la cordillera oriental de Colombia. *Lochroma orozcoae* fue recolectada por primera vez por el eminente sacerdote y botánico español José Celestino Mutis a finales del siglo XVIII, pero los especímenes han permanecido sin ser reconocidos en herbarios durante más de 200 años. La especie comparte muchas características con su pariente más cercano, *Lochroma baumii* S.D.Sm. & S.Leiva, pero difiere de esta en sus flores más pequeñas con cinco lóbulos de la corola y pocas inflorescencias por rama ubicadas cerca del ápice de la rama, con 1 a 4 (–8) flores por inflorescencia, frutos verde-amarillentos al madurar, y su distribución geográfica restringida. Se presenta una descripción de *L. orozcoae*, junto con una ilustración detallada, fotografías en vivo, una comparación con las especies cercanamente relacionadas y una clave para las especies colombianas de *Lochroma* Benth. Finalmente, enfatizamos el valor de las colecciones históricas para el conocimiento de la biodiversidad.



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Key words: Andes, Colombia, *Lochroma*, lochrominae, IUCN Red List, Solanaceae

Introduction

lochroma Benth. (Solanaceae) is a neotropical genus that comprises approximately 30 species distributed from Colombia to Peru, with the highest concentration of species found in the Peruvian Andes (Smith and Baum 2006). Members of *lochroma* are unarmed shrubs and small trees that display showy, tubular flowers and ovoid berries with an enlarging calyx. These species are typically found in cloud forest clearings and disturbed areas between 1800 and 2800 m altitude. Their flowers are pollinated by hummingbirds and insects (Smith and Baum 2006; Smith et al. 2008). The recently published Catalogue of the Plants and Lichens of Colombia (Bernal et al. 2016) reported three native species for Colombia, the red-flowered *lochroma fuchsoides* Miers and *lochroma gesnerioides* (Kunth) Miers and the white-flowered *lochroma arborescens* (L.) J.M.H.Shaw. Additionally, a recently-described Ecuadorian species, *I. baumii* S.D.Sm. & S.Leiva, has been mentioned for Colombia. Initially documented from a single specimen collected by Cuatrecasas in Caldas in 1946 (Smith and Leiva 2011), its presence has been further confirmed by a subsequent collection in a nearby locality during 2022. In addition to these species, we have made the remarkable rediscovery of an unusual *lochroma* species that was first collected by José Celestino Mutis over 200 years ago during the Royal Botanical Expedition of the New Kingdom of Granada (1783–1816). This species does not correspond to any currently-recognised species within the genus. Recent collection efforts in the Municipality of Lenguazaque, Cundinamarca, located in the eastern Andes of Colombia and herbarium work have provided us with comprehensive material, enabling us to confirm the novelty and relationships of this species. Here, we provide a description of this species, *lochroma orozcoae* A.Orejuela & S.D.Sm., sp. nov. along with a detailed comparison to its closest relatives, based on a phylogenetic analysis. We include an assessment of its conservation status and a dichotomous key for all *lochroma* species distributed in Colombia to aid in identification.

Material and method

All specimens of the genus *lochroma* from the Colombian herbaria COL, PSO, JBB and FMB and Ecuadorian herbaria QCA and QCNE (acronyms follow Index Herbariorum <http://sweetgum.nybg.org/science/ih/>) were revised to understand morphological variation across the genus, as well as major international herbaria that hold representatives from countries across the Andes (BM, E, F, K, MO). Herbarium material of the new species was collected in 2017 and 2021 and deposited at Herbario del Jardín Botánico de Bogotá (JBB) and Herbario Nacional Colombiano (COL). Flowers and fruits were preserved in 70% alcohol to facilitate preparation of taxonomic descriptions and illustrations.

For phylogenetic analysis, DNA was extracted from silica gel dried leaf material and three nuclear markers were sequenced (internal transcribed spacer region (ITS), the granule-bound starch synthase (GBSSI or waxy) gene and the second intron of *LEAFY* (*LFY*)), following Deanna et al. (2019). GenBank accession numbers for these sequences are MH763720, MH796580 and MH82214, respectively. We added these sequences to the dataset of Deanna et al. (2019) and carried out a partitioned Maximum Likelihood phylogenetic analysis in the

RAxML blackbox (<https://raxml-ng.vital-it.ch/>). We chose GTR+gamma as the model of sequence evolution and assessed clade support with automatic bootstrapping (cut-off of 0.03).

To map the distribution of the new species and its close relatives, specimens with coordinates were mapped directly and those lacking coordinates were located using Google Earth, GeoNames gazetteer (<http://www.geonames.org>) and GEOLocate Web service (<https://www.geo-locate.org/default.html>). Distribution maps were created using QGIS (QGIS Development Team 2023). Conservation assessments were made, based on the IUCN Red List Categories and Criteria (IUCN 2012) and the most recent guidelines for using the IUCN Red List Categories and Criteria (IUCN 2022). Herbarium material, field observations and photos were all used to construct the identification key.

Taxonomic treatment

lochroma orozcoae A.Orejuela & S.D.Sm., sp. nov.

urn:lsid:ipni.org:names:77326965-1

Figs 1, 2

Type. COLOMBIA. Cundinamarca: vía Ubate-Lenguazaque, carretera sin pavimentar, antes del sector conocido como las balsas, 5°20'2.5"N, 73°43'23"W, 2600 m elev., 27 August 2017, A. Orejuela & J. Castillo 2942 [holotype: JBB, (accession #JBB30649); isotypes: COL, HUA, HEAA].

Diagnosis. A *lochroma baumii* S.D.Sm. & S.Leiva affinis, sed paucarum inflorescentiae in ramum prope apicem germinis dispositae sunt, quae 1 ad 4 (–8) floribus, flores minores 1.5–2 cm longi; corolla quinque lobis constat, et fructus viridis-flavus colore maturo differt.

Description. Shrub 1.5–3 m tall; young stems pubescent with branched hairs, older stems with corky bark. Leaves alternate, simple, (2.1–) 5.3–11.6 × (1.2–) 2.2–5.5 cm, elliptic; adaxial surface glabrescent; abaxial surface densely pubescent with branched hairs; base cuneate; margins entire; apex acute to attenuate; petioles (0.4–) 0.8–2.5 (–3) cm. Inflorescences axillary on young branches near the shoot apex, 1 to 4 (–8)-flowered; pedicels 1.1–1.7 (–2) cm in flower, 1.6–2.4 cm in fruit, terete, pendulous, densely pubescent with many-branched hairs. Calyx 6–7 × 5–6 mm, tubular to slightly urceolate, green, with few to many-branched hairs, with five broadly triangular lobes, ca. 0.8 × 2–2.5 mm in flower, shallowly divided in flower, deeply divided in fruit, in fruit, the calyx accrescent 9–10 × 10–11 mm, lobes 4–5 × 7–8 mm; corolla 15–20 × 4–4.5 mm at anthesis, tubular, flaring at the mouth, the exterior deep blue-purple, with many simple or occasionally branched hairs, the pubescence increasing towards the mouth, the interior deep blue-purple, glabrous, the lobes 5, 2.6–2.8 × 2.2–2.6 mm, acute to the apex and cucullate; stamens 5, included; filaments with simple and branched hairs, fused to the corolla at 3.8–5.2 mm from the base, with the free portion 7–11.4 mm long; anthers 3.5–5.2 × 1.3–1.7 mm, oblong, cream, longitudinally dehiscent; ovary 3.6–4.8 × 1.7–2.5 mm, pyriform, glabrous, with a yellow nectariferous disc, style 13–15 mm, the stigma green, clavate, bilobed. Berry 12–14 × 9–11 mm, slightly ovoid, greenish-yellow at maturity with 20 to 30 sclerosomes, the basal 3/4 enveloped in the accrescent fruiting calyx; seeds 110 to 170 per berry, 2–2.1 × 1.7–1.9 mm, yellow, reniform.



Figure 1. *Lochroma orozcoae* A.Orejuela & S.D.Sm. **A** flowering branch **B** inner corolla surface, showing the stamens **C** flower. Detail is shown for the simple and branched hairs on the corolla **D** gynoecium **E**, **F** details of the stamens and anthers **G** fruit with persistent calyx **H** seed. Drawn by Omar Bernal from Orejuela & Castillo 2942 & Orejuela et al. 3407.

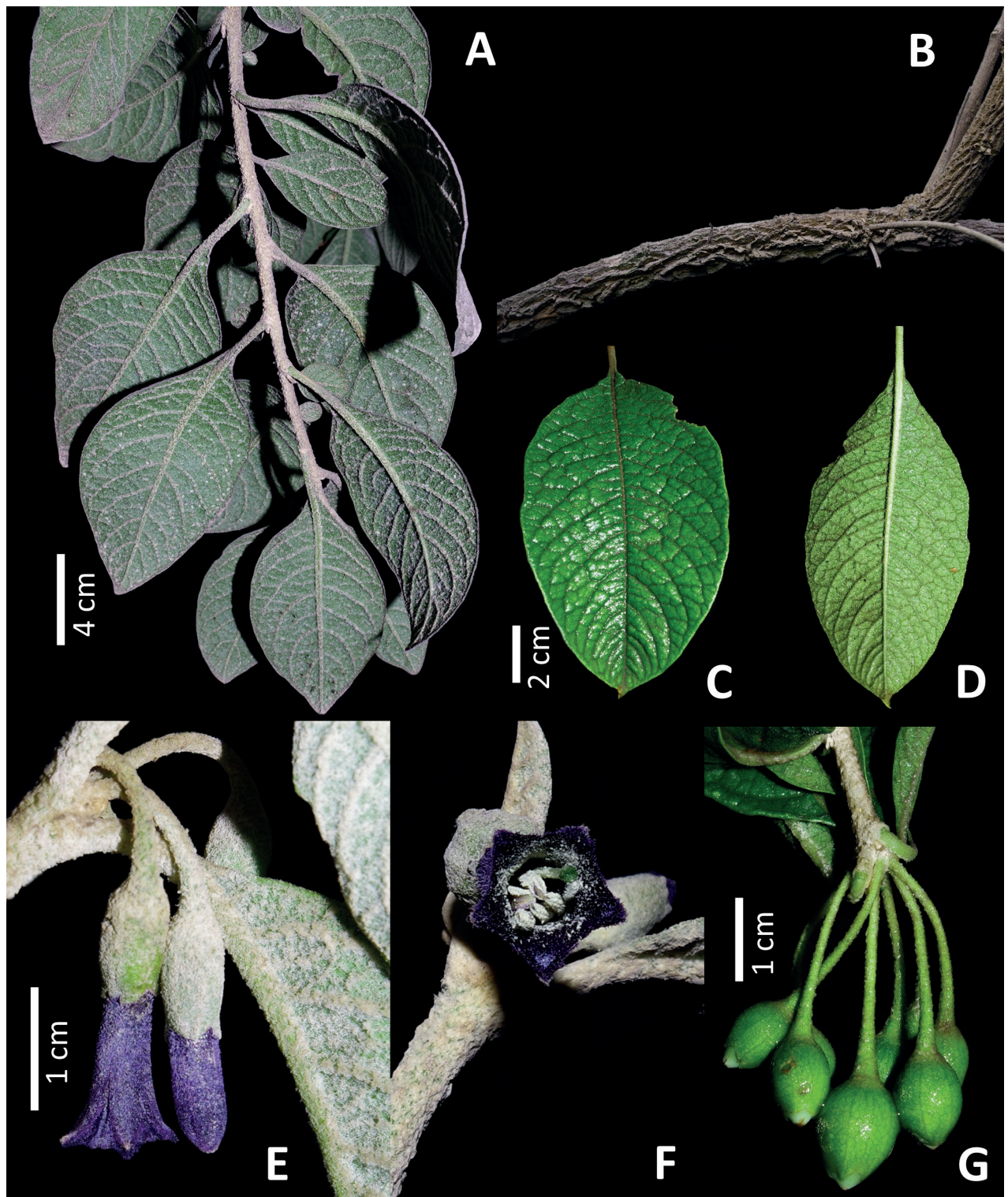


Figure 2. *Lochroma orozcoae* A.Orejuela & S.D.Sm. **A** young branch **B** stem detail **C, D** leaf detail showing the abaxial and adaxial sides **E** floriferous branch with flowers in lateral view **F** floriferous branch with a flower in frontal view **G** fruits showing the accrescent appressed calyx. Photos by Andrés Orejuela.

Etymology. This species is named in honour of Clara Inés Orozco Pardo, an Associate Professor of botany at the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia. Her dedication to the understanding of Colombian flora, particularly in the fields of taxonomy and systematics of

the Brunelliaceae and Solanaceae families, has been remarkable. She has also played a crucial role in mentoring several Colombian botanists, including the first author of this paper.

Distribution and ecology. *Lochroma orozcoae* is found in the Municipality of Lenguazaque, Cundinamarca Department, in the eastern Andes of Colombia, in the surroundings of the rock formation known as the Farallones de Lenguazaque, which is situated at an elevation of 2600 m (Fig. 3). The Farallones de Lenguazaque exhibit a vegetation type characteristic of high-altitude mountain ecosystems. The primary vegetation in this area comprises high Andean forest relicts of native forest, secondary forest, plantations of foreign species, grasslands and subparamo vegetation.

Phylogeny. *Lochroma orozcoae* belongs to the “F” clade (Smith and Baum 2006) containing other northern Andean species (*L. gesnerioides*, *L. fuchsioides*, *L. calycinum* Benth. and *L. baumii*) with high bootstrap support (96%). The red-flowered species (*L. gesnerioides* and *L. fuchsioides*) are separated from the blue-flowered species (*L. calycinum*, *L. baumii* and *L. orozcoae*), but that split is not well supported. Amongst the blue-flowered members of the “F” clade, *L. baumii* and *L. orozcoae* appear as sister taxa with 59% bootstrap support (Fig. 4).

Preliminary conservation status. *Lochroma orozcoae* is classified as a data-deficient species (DD) due to the limited information on its abundance and distribution that is inadequate for comprehensively assessing its conservation status. The species has been collected only on four occasions, suggesting probable local rarity. The initial collection was made by José Celestino Mutis in 1783 from an unknown locality, followed by another by Oscar Haught in 1947 from Lenguazaque, Cundinamarca and a couple of recent collections by the first author from the same locality as Haught’s collection. Despite conducting an extensive search through specialised literature, the drawings of the Royal Botanical Expedition of the New Kingdom of Granada (1783–1816) and Mutis’ journals, the precise location of Mutis’ first collection remains unknown. We infer that the distribution of the species may be highly restricted, based on the small number of known collections from the same locality. Assumptions regarding its scarcity and restricted distribution, however, require further studies. Living plants of *L. orozcoae* originated from seeds, collected at the type locality and are conserved ex situ in the living collections of the Jardín Botánico de Bogotá.

Discussion. Our phylogenetic analyses offer strong support for the placement of *L. orozcoae* in the northern Andean “F” clade from Smith and Baum (2006). However, it differs from all other species in its broader and denser pubescence on both its vegetative and reproductive parts, small corollas and less abundant inflorescences with fewer flowers (Figs 1, 2, 5). The new species shares with *L. baumii* and *L. calycinum* intensely pigmented flowers, which are variously described as purple, violet or blue (Fig. 5). In contrast to *L. baumii* and *L. fuchsioides* which have corollas with ten teeth (five major lobes and five smaller teeth alternating with the lobes), *L. orozcoae* has corollas with five teeth corresponding to the lobes. *Lochroma orozcoae* is morphologically more similar to *L. baumii*. However, the new species is easily separated from *L. baumii* because it presents smaller flowers, 1.5–2 cm long (versus 2.8–4.5 cm long), only a few inflorescences per branch, located near the shoot apex with 1 to 4

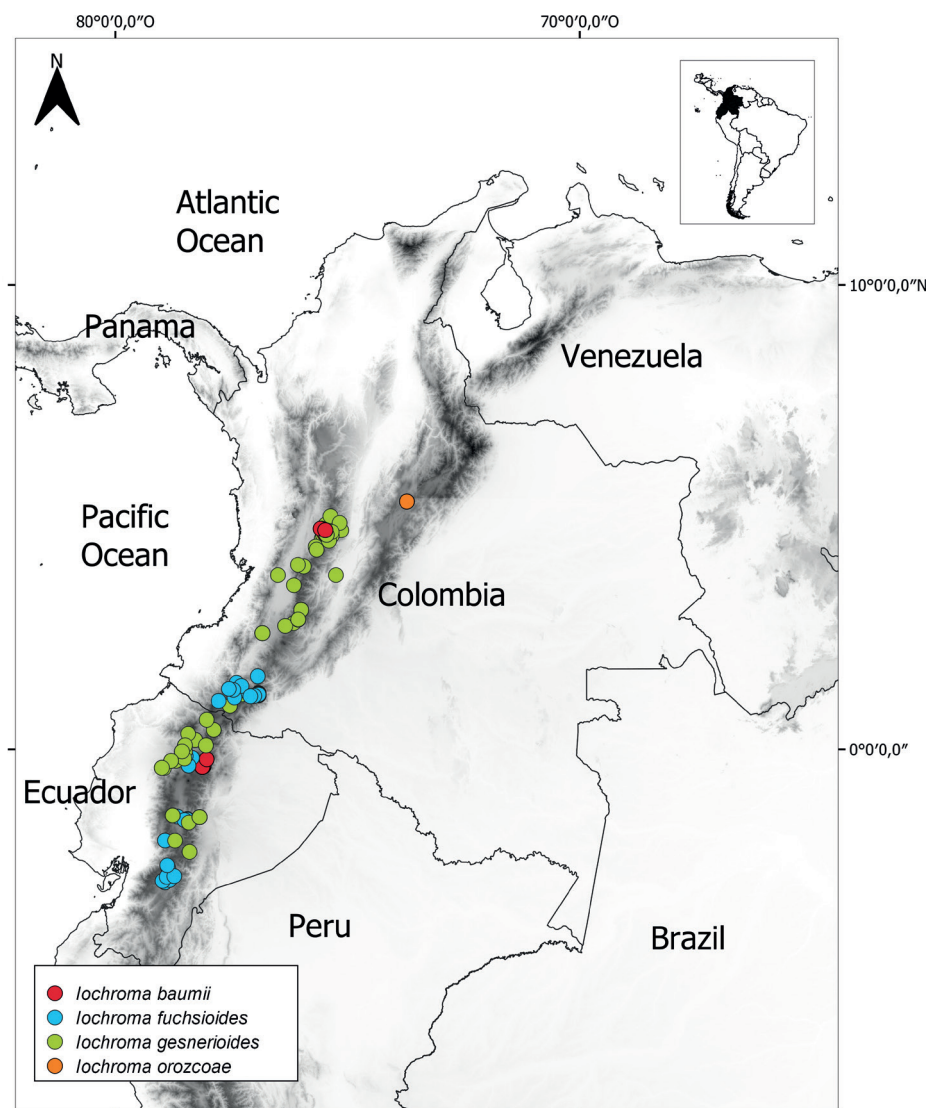


Figure 3. Geographic distribution of *L. orozcoae* (orange circles) and closely-related species in the “F” clade with presence in Colombia, including *L. baumii* (red circles), *L. gesnerioides* (green circles) and *L. fuchsioides* (blue circles).

(–8) flowers (versus masses of inflorescences per branch in clusters typically on older, often leafless branches, rarely near the shoot apex, with 6 to 12 flowers per inflorescence), corolla with five lobes (versus a 10-lobed corolla) and, while the fruits of *L. orozcoae* ripen in greenish-yellow colour, those of *L. baumii* are greenish-purple when ripe. A detailed comparison between *L. orozcoae* and the remaining species in the “F” clade can be found in Table 1.

The rediscovery of *L. orozcoae* over two centuries since the first collection by José Celestino Mutis in 1783 underscores the immense importance of historical collections in documenting and describing botanical diversity and their potential contribution in setting conservation priorities within biodiverse regions. This is a widely-debated topic that is gaining increasing attention over time (Besnard et al. 2018; Albani Rocchetti et al. 2021; Vargas et al. 2023). In the case of *L. orozcoae*, the presence of the long undetermined specimens spurred renewed collecting efforts in the eastern Andean cordillera of Colombia, which continue to be the source for many newly-described taxa, some of which have

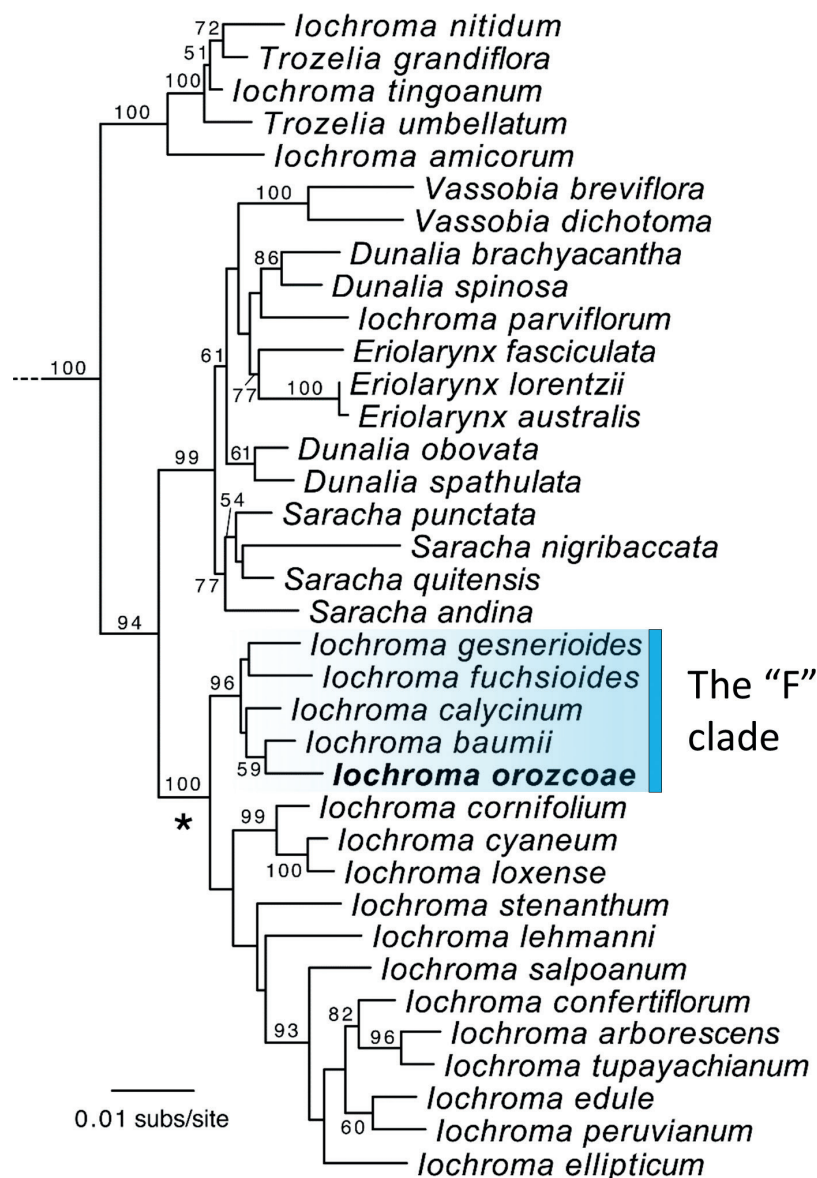


Figure 4. Maximum Likelihood phylogeny of *lochrominae* including the new species, *I. orozcoae*. Relationships based on three nuclear markers with taxon sampling following Deanna et al. (2019). *Physalideae* outgroups from Smith and Baum (2006) (*Physalis peruviana* L., *Leucophysalis grandiflora* (Hook.) Rydb., *Witheringia solanacea* L'Hér., *Tubocapsicum anomalum* (Franch. & Sav.) Makino and *Deprea sachapapa* (Hunz.) S.Leiva & Deanna) were used to root the tree and pruned for visual purposes. Bootstrap values above 50% are shown. Nomenclatural rearrangements are underway for *lochrominae* (Deanna et al., unpublished) given the non-monophyly of the genera. The clade denoted with an asterisk will remain assigned to the genus *lochroma* as it contains the type species (*lochroma cyaneum* (Lindl.) M.L. Green ex G.H.M. Lawr. & J.M. Tucker) and most of the species described in this genus.

remained elusive for many years (e.g. Granados-Tochay et al. (2007)). Given the challenges associated with locating and collecting narrow endemics such as *I. orozcoae*, it will often be necessary to base descriptions on scant material so that perhaps in future, the timespan between additional collections of new species does not span centuries, an important consideration in the context of the ongoing efforts to conserve biodiversity.

Additional specimens examined. Colombia. Cundinamarca: Ubaté – Lenguaque Highway, 2600 m elev., 16 September 1947, O.L. Haught 6188 (COL, US);

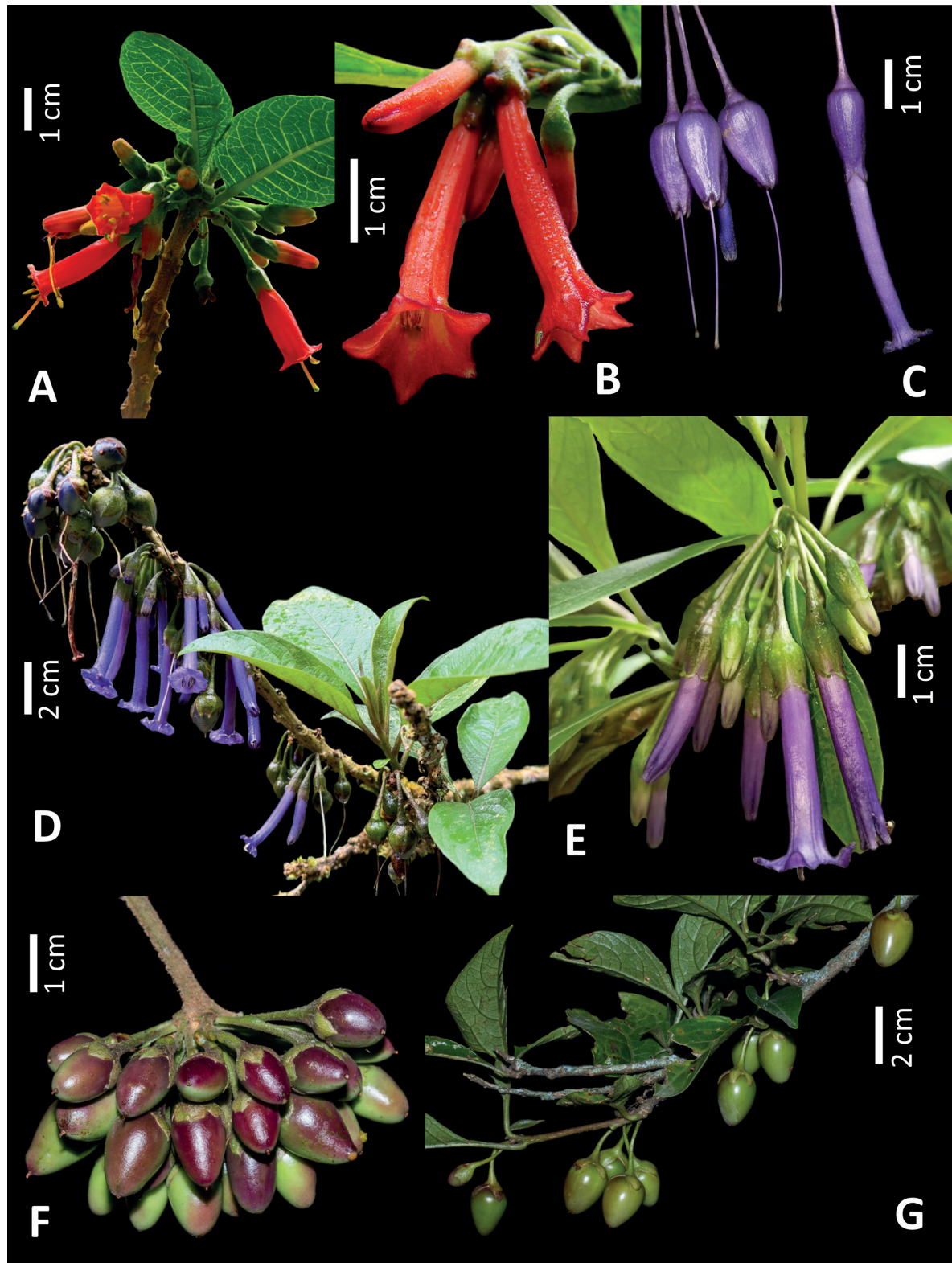


Figure 5. Species within the “F” clade of *Lochroma* that are closely related to *L. orozcoae* **A** flowering branch of *L. fuchsioides* observed at Parque Recreacional y Bosque Protector Jerusalem, Malchingui, Ecuador **B** flowers of *L. gesnerioides* photographed at the Jardín Botánico de Bogotá, Colombia **C** flowers of *L. calycinum* at the reserva Otonga, Sigchos, Cotopaxi, Ecuador **D** flowers and fruits of *L. baumii* observed close to the type locality in Papallacta-Baeza road, Quijos, Napo, Ecuador **E** flowering branch of *L. baumii* from populations from La Pastora, Caldas, Colombia **F** fruits of *L. gesnerioides* photographed at the Jardín Botánico de Bogotá, Colombia **G** fruits of *L. fuchsioides* photographed close to Pasto, Nariño, Colombia. Photos by Andrés Orejuela (**B**, **C**, **F**, **G**), Hal Mitchell (**D**), Nathaly Obregón (**A**) and Juan David Tovar (**E**).

Table 1. A morphological and geographical comparison of *Lochroma* species in the “F” clade (sensu Smith and Baum (2006)), including the new species *L. orozcoae*.

	<i>Lochroma orozcoae</i>	<i>Lochroma baumii</i>	<i>Lochroma gesnerioides</i>	<i>Lochroma fuchsioides</i>	<i>Lochroma calycinum</i>
Geographical distribution	Eastern Colombia	Ecuador and central Colombia	Ecuador and southern and central Colombia	Peru, Ecuador and southern Colombia	Ecuador and Peru
Habitat	Partially altered high Andean forests and roadsides to 2600 m	Disturbed cloud forest habitats, such as pasture hedges, forest gaps and roadsides from 2600 to 3300 m	Common in middle to high elevations in cloud forests, pastures hedges and roadsides from 1800 to 3300 m	Common in middle to high elevations in cloud forests, pastures hedges and roadsides from 2400 to 3500 m	Common in some areas of the wet cloud forest from 2000 to 3350 m
Leaf size (cm)	(2.1–) 5.3–11.6 × (1.2–) 2.2–5.5	(6–) 9–17 × (2.5–) 3–6	12–18 (–30) × 5–7.5 (–12)	3.5–7 (–9) × 1.5–3 (–5)	12–23 × 5–9
Leaf shape	Elliptic	Elliptic to lanceolate	Elliptic to lanceolate	Obovate to elliptic	Elliptic to lanceolate
Inflorescence	Inflorescences axillary on young branches near the shoot apex, 1 to 4 (–8)-flowered	Inflorescences axillary, typically on older, often leafless branches, rarely near the shoot apex, 6 to 12-flowered	Inflorescences axillary, in clusters with masses of flowers (with up ca. 120 flowers) along older or upper leaf nodes	Inflorescences axillary, in small clusters of flowers (1 to 12 flowers) on young branches near the shoot apex or upper leaf nodes	Inflorescences axillary, in small clusters of flowers on young branches near the shoot apex (5 to 12 flowers) or older branches (1 to 6 flowers)
Calyx in flower	Calyx 6–7 × 5–6 mm, slightly urceolate, green, with densely branched hairs	Calyx 4–9 × 3.8–6 mm, tubular to slightly urceolate, purplish-green, with few to many branched hairs	Calyx 3–5 × 4–5 mm, cup-shaped, green, with densely branched hairs	Calyx 7–13 × 4.5–5.5 mm, tubular to campanulate, green, hairless or with a few scattered branched hairs	Calyx 25 × 8–17 mm, inflated, elliptic, purplish, hairless or with a few branched hairs
Corolla	Corolla 15–20 × 4–4.5 mm, deep blue-purple, 5-lobed	Corolla 28–45 × 4–6 mm, deep blue-purple, 10-lobed	Corolla 25–40 × 5–6 mm, red, orange-red, orange to salmon, 5-lobed	Corolla 20–30 × 6–7 mm, red to orange-red, 10-lobed	Corolla 50–65 × 4–8 mm, deep blue to purple, 5-lobed
Fruit	Berry slightly ovoid ca. 1.2–1.4 × 0.9–1.1 cm, greenish-yellow when ripe	Berry markedly ovoid 1.2–1.7 × 1–1.5 cm, green and purple when ripe	Berry markedly ovoid, 1.3–1.8 × 0.9–1.3 cm, green, reddish-brown or purple when ripe	Berry markedly ovoid, 1.6–2.5 × 1.2–1.7 cm, yellow, green or brown when ripe	Berry markedly ovoid to conical, 2.3–3.5 × 1.4–2 cm, white when ripe

Lenguazaque, vía Ubaté-Lenguazaque, antes del sector Las Balsas, en cercanías de los farallones de Lenguazaque 5°20'0.25"N, 73°43'23"W, 2600 m elev., 04 September 2021, A. Orejuela 3407 with H. Mendoza, J. Castillo, V. Luna, C. Luna & M. Mora (JBB, COL, HEAA); Colombia, sin. Loc., 01 January 1783, J.C. Mutis 636 (COL).

Key to the Colombian species of *Lochroma*

- 1 Corolla 15–70 mm long, tubular, flaring at the mouth, red, orange-red, orange, deep blue or purple, calyx conspicuously accrescent in fruit, fruit a slightly to markedly ovoid to conical berry **2**
- Corolla 8–11 mm long, campanulate-infundibuliform, white, greenish or greenish-cream coloured, calyx non-accescent or accrescent to an insignificant degree in fruit, fruit a globose berry..... ***Lochroma arborescens***
- 2 Corolla red, orange-red or orange-coloured **3**
- Corolla deep blue or purple-coloured..... **4**
- 3 Leaves usually pubescent; inflorescences with 30 to 120 flowers; calyx 3–7 mm long, cup-shaped, densely pubescent; corolla pubescent; anthers usually included..... ***Lochroma gesnerioides***
- Leaves usually glabrescent; inflorescences with 1 to 15 flowers; calyx 7–13 mm long, tubular to campanulate, glabrous or with a few scattered hairs; corolla glabrescent; anthers usually exserted or partially exserted... .. ***Lochroma fuchsioides***

- 4 Leaves (2.1–) 5.3–11.6 × (1.2–) 2.2–5.5 cm. Inflorescences few per branch, located near the shoot apex; flowers 1 to 4 (–8) per inflorescence; corolla 1.5–2 cm long, 5-lobed; berry greenish-yellow when ripe *Lochroma orochoae*
- Leaves (6–) 9–17 × (2.5–) 3–6 cm. Inflorescences many per branch, typically in massive clusters on older, often leafless branches, rarely near the shoot apex; flowers 6 to 12 per inflorescences; corolla 2.8–4.5 cm, 10-lobed; berry green and purple when ripe *Lochroma baumii*

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

AO wrote the original draft and prepared the figures; RD and SDS performed the molecular analysis; AO, SDS, BV, and RD reviewed and edited the drafts.

Author ORCIDs

Andrés Orejuela  <https://orcid.org/0000-0002-3511-1478>

Stacey D. Smith  <https://orcid.org/0000-0003-2010-4459>

Boris Villanueva  <https://orcid.org/0000-0002-6929-3572>

Rocío Deanna  <https://orcid.org/0000-0001-8753-7596>

Data availability

All of the data that support the findings of this study are available in the main text.

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New species of *Asclepias* (Apocynaceae), *Baphia* (Leguminosae), *Cochlospermum* (Bixaceae) and *Endostemon* (Lamiaceae) from the Kalahari sands of Angola and NW Zambia, with one new combination in *Vangueria* (Rubiaceae)

David J. Goyder^{1,2}, Nina Davies¹, Manfred Finckh³, Amândio Gomes^{2,4},
Francisco Maiato P. Gonçalves^{2,5}, Paulina Meller³, Alan J. Paton¹

¹ Royal Botanic Gardens, Kew, TW9 3AE, London, UK

² National Geographic Okavango Wilderness Project, Wild Bird Trust, Hogsback, South Africa

³ Institute for Plant Science and Microbiology, University of Hamburg, Hamburg, Germany

⁴ Natural Science Faculty of Agostinho Neto University, Luanda, Angola

⁵ Herbarium of Lubango, ISCED-Huíla, Lubango, Angola

Corresponding author: David J. Goyder (d.goyder@kew.org)



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Abstract

Four new species are described from central and eastern Angola and adjacent NW Zambia. All occur in Kalahari sand savannas rich in endemic and more widely distributed geoxylic suffrutices. Despite being known from very few collections, the conservation status of one of these new species is assessed as Least Concern, as these grasslands are nutrient-poor, are in remote sparsely populated areas, and are not threatened with conversion to agriculture. The remaining three are treated as Data Deficient. In addition, one new combination is provided for *Ancylanthos rubiginosus* Desf. under *Vangueria* as *V. rubiginosa* (Desf.) Lantz is an illegitimate later homonym. We also make orthographic corrections to specific epithets commemorating Ilse von Nolde, a collector who made important collections from Quela in Malange in the 1930s.

Key words: *Ancylanthos*, *Casearia*, Cochlospermaceae, geoxyle, geoxylic suffrutices, Ilse von Nolde

Introduction

Plant diversity in Angola is poorly documented with very uneven geographic coverage – much of the eastern half of the country and some northern provinces are largely devoid of georeferenced plant collections (Sosef et al. 2017; Goyder and Gonçalves 2019). Nevertheless, a Checklist of the plants of Angola was compiled by Figueiredo and Smith (2008), which serves as an invaluable baseline and point of reference for further studies. The indigenous flora of Angola is estimated to comprise 6850 species of vascular plant (Goyder and Gonçalves 2019).

Two initiatives have contributed data to the current publication. Firstly, a series of expeditions under the auspices of the National Geographic Okavango Wilderness Project (NGOWP) focussed initially on the headwaters of the Cuito

and Cuanavale tributaries of the Okavango system in central Angola, then on river catchments further to the east in 2019. Most of these surveys were in Moxico Province, but neighbouring areas of Cuando Cubango with similar rainfall and vegetation were also documented. In parallel, The Future Okavango programme (TFO) of the University of Hamburg initiated a series of ecological studies in *miombo* and grassland sites around Chitembo, Bié Province, just to the west of the core NGOWP study area.

The NGOWP surveys culminated in a Checklist of the Cuito headwaters, documenting 417 species from the region (Goyder et al. 2018) with ten new country records for Angola, 108 new provincial records for Moxico, and nine species potentially new to science. Fieldwork in late 2019 in the Cuito headwater lakes area and further to the east resulted in additional localities for some of the undescribed species, two further undescribed species, and even more new country and provincial records. We here formally describe four of the new species – *Asclepias minutissima* Goyder, *Baphia arenicola* Goyder, F.M.P.Gonçalves & P.Meller, *Cochlospermum adjanyae* Goyder & Amândio Gomes and *Endostemon palustris* A.J.Paton & Goyder. The new *Baphia* had also been encountered in several TFO field surveys. Additional novelties arising from NGOWP fieldwork in the region include two species of *Justicia* (Acanthaceae), *J. cubangensis* I.Darbysh. & Goyder and *J. moorei* I.Darbysh. & Goyder, described by Darbyshire and Goyder (2019), while *Barleria* sp. nov. of Goyder et al. (2018) has since been described as *B. thunbergiiflora* I.Darbysh. (Darbyshire et al. 2021) in a revision of *Barleria* in Angola and Namibia.

Landforms, ecology and endemism of central/eastern Angola

Much of eastern Angola is overlain with deep deposits of Kalahari sand, which in the Cuito headwater zone are white, highly leached, and largely devoid of nutrients (Gröngroft et al. 2013a). The whole area seems to have been uplifted since the middle Miocene, 16 mya (Guillocheau et al. 2015). The plateau in NW Moxico is at an elevation of c. 1500–1600 m and is covered with extensive moist *miombo* woodland, a largely Zambesian vegetation type dominated by the genera *Brachystegia* Benth. and *Julbernardia* Pellegr. in Leguminosae subfam. Detarioideae. Some Congolian elements are also present in the region. Species composition is restricted compared with *miombo* woodlands on richer soils elsewhere in south tropical Africa (Goyder et al. 2018). Dense closed canopy stands of another detarioid legume, *Cryptosepalum exfoliatum* De Wild. subsp. *pseudotaxus* (Baker f.) P.A.Duvign. & Brenan, form patches of *miombo* forest within the more typical open canopy *miombo* woodland of the region. *Julbernardia paniculata* (Benth.) Troupin commonly dominates the steep slopes of the river valleys, with *Brachystegia bakeriana* Hutch. & Burt Davy generally the first woody *miombo* species to establish itself above the water table.

Tributaries of the Cuito River lie in steeply incised valleys around 150 m below the level of the surrounding plateau and their headwaters generally take the form of a wetland or seepage area surrounded by a narrow zone of exposed sand with a herbaceous or suffrutescent flora maintained free of woody vegetation by a combination of fire, frost and high water table (Maurin et al. 2014; Finckh et al. 2016; Goyder et al. 2018; Finckh et al. 2021).

Frequently, a little further downstream, a headwater lake occurs with deep open water and a fringing mat of peat, with its own suite of plants capable of

surviving in this low pH environment. Wetlands are not generally known for high levels of plant diversity or endemism, although some species such as the insectivorous *Genlisea angolensis* R.D.Good appear to be restricted to peaty wetlands on Kalahari sand (Goyder 2016a). Clump or tussock-forming plants such as Eriocaulaceae and Xyridaceae are common, with several species of insectivorous Lentibulariaceae and Droseraceae also present. Cyperaceae are present but appear over-represented in pollen profiles from peat cores taken in the region (Lourenco et al. 2022). Indeed, the extent and significance of Angolan highland peat deposits has only been documented recently (Lourenco et al. 2022).

Further downstream, with the confluence of additional tributaries, the valleys generally become wider and the seasonally burned grassland zones more extensive. This is the habitat that is most significant botanically with many range-restricted and endemic species, including most of the species new to science described below. One notable valley grassland formation consists of extensive sand platforms perched above the level of the current watercourse; it is dominated by grasses and by geoxylic suffrutices, plants with considerable underground woody biomass and seasonal above-ground shoots. These lifeforms are adapted to above-ground disturbances such as fire and frost and were highlighted by White (1977) who, noting the prevalence of this lifeform in central and eastern Angola, referred to them as the underground forests of Africa. The below-ground biomass of these Kalahari sand grasslands rich in geoxylic suffrutices can approach the above-ground biomass of adjacent *miombo* woodlands (Gomes et al. 2021; Huntley 2023). Localities with significant extent of this habitat include the upper reaches of the Lungué-Bungo valley SE of Munhango and N of Chipola; confluences of headwater tributaries below both the Cuito and the Cuanavale River sources; and some of the Cusseque valley system near Chitembo, Bié Province, to the W of the Cuito headwater lake region, sampled extensively by the TFO programme. Three of the four species described here occur in this fire-adapted landscape. The fourth species, *Asclepias minutissima*, was found at a slightly lower elevation in eastern Moxico Province, close to the Zambian border, at the edge of seasonally flooded Kalahari sand savannas on the western fringes of the Barotse floodplain.

Several globally rare species were noted in the high rainfall Kalahari sand savannas of Gabon's Batéké Plateau (Walters et al. 2012; Walters et al. 2022) and our observations in Angola lead us to believe that the same is true here. An analysis of endemism in Kalahari sand floras will be the subject of a future contribution.

Materials and methods

Morphological descriptions are based principally on examination of herbarium specimens at Kew, with smaller organs examined under a Leica MZ12.5 stereo-dissecting microscope fitted with a 10 mm graduated eyepiece graticule. Relevant type material not available for direct observation at K or BM was consulted through the JSTOR Global Plants portal www.plants.jstor.org, or the websites of individual herbaria such as COI www.uc.pt/en/herbario_digital or LISC <https://actd.iict.pt/collection/actd:BIOHERB>. Herbarium abbreviations follow Index Herbariorum (Thiers continually updated) except for the Collections Unit of Angola's National Institute for Biodiversity and Protected Areas which is not listed by Thiers, and is here referred to as INBAC.

Taxonomic treatment

Apocynaceae: Asclepiadeae

Asclepias minutissima Goyder, sp. nov.

urn:lsid:ipni.org:names:77327146-1

Diagnosis. *Asclepias minutissima* appears most similar to *A. aurea* (Schltr.) Schltr. but differs in the campanulate rather than rotate to reflexed corolla, the ascending disposition of the corona rather than radiating from the column in *A. aurea*, the absence of the well-developed distal tongue to the corona of the latter species, and the shorter peduncles (1–3 cm rather than (3)5–14 cm in *A. aurea*).

Type. ANGOLA. Moxico Province: Mussuma plains, 50 km NE of Lumbala, Zambezi drainage, 13°45'49"S, 021°43'25"E, fl. 7 December 2019, D.Goyder & F.Maiato 9204 (holotype: K (K001334259); isotypes: INBAC, LUBA, PRE).

Description. Perennial herb with a single erect stem arising annually from a small napiform tuber, latex white; stems 8–15 cm long, minutely pubescent along two lines. Leaves sessile, 3–7 × 0.05 cm, filiform with inrolled margins, glabrous. Inflorescences terminal or extra-axillary, umbelliform, with 4–5 erect flowers; peduncles 1–3 cm long, minutely pubescent; pedicels c. 1 cm long, minutely pubescent. Sepals 1–1.5 mm long, narrowly to broadly triangular, glabrous. Corolla campanulate, lobes 3.5–4 × 1.5 mm, oblong, green or white, glabrous on both faces. Corona lobes 2–3 mm long, cucullate, lacking an apical tongue, pinkish cream or white. Anther wings 1 mm long. Styler head flat. Follicles not seen. (Fig. 1).

Distribution and ecology. Known from a single collection in eastern Angola and one in NW Zambia. The Angolan population consisted of several scattered individuals on a broad open sandy plain just above the water table. Both the Angolan and the Zambian localities are on Kalahari sand deposits, and the Angolan collection was associated with common geoxyllic suffrutices of the region such as *Parinari capensis* Harv., *Syzygium guineense* (Willd.) DC. subsp. *huillense* (Hiern) F.White, *Eugenia malangensis* (O.Hoffm.) Nied., *Lannea gossweileri* Exell & Mendonça subsp. *gossweileri* and *Cryptosepalum* sp. aff. *mimosoides* Welw. ex Oliv. Altitude 1100–1300 m. (Map 1).

Conservation status. *Asclepias minutissima* is known from two localities some 350 km apart, but is inconspicuous and easily overlooked and is likely to be more common than the herbarium records suggest. Both localities are in nutrient-deficient sandy environments unsuitable for agriculture, and with little threat of habitat transformation as human settlements are few and far between. The new species is therefore provisionally assessed as Data Deficient.

Additional specimens examined. ZAMBIA. Mwinilunga District, 16 km along road from Matonchi Farm, 11°39'S, 24°03'E, fl. 17 November 1962, Richards 17269 (K).

Taxonomic notes. Only three species of *Asclepias* were reported from Angola by Goyder (2008). *Asclepias baumii* Schltr., known only from the type collection which was destroyed in Berlin, is almost certainly synonymous with *A. aurea*, as is *A. radiata* S.Moore (Goyder 2009). *Asclepias randii* S.Moore is also present. Following the transfer of *Odontostelma* Rendle to *Asclepias* by Goyder (2009), *A. minor* (S.Moore) Goyder, also occurs in the country. All of these species occur in scattered populations with few individuals, as is common for *Asclepias* and allied genera in tropical Africa. As a result, they tend to be collected very infrequently and few herbarium records exist for any of them in Angola.

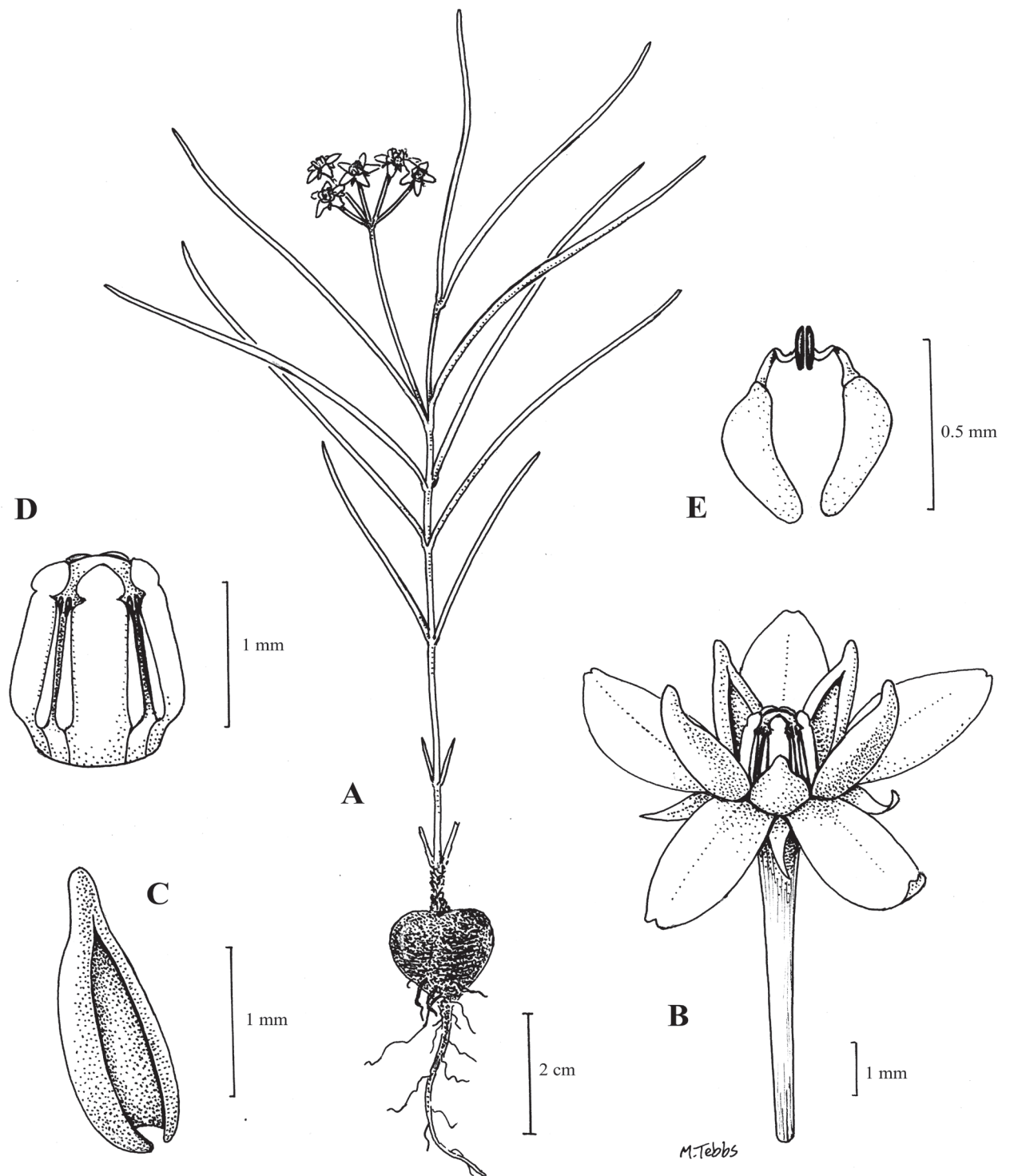
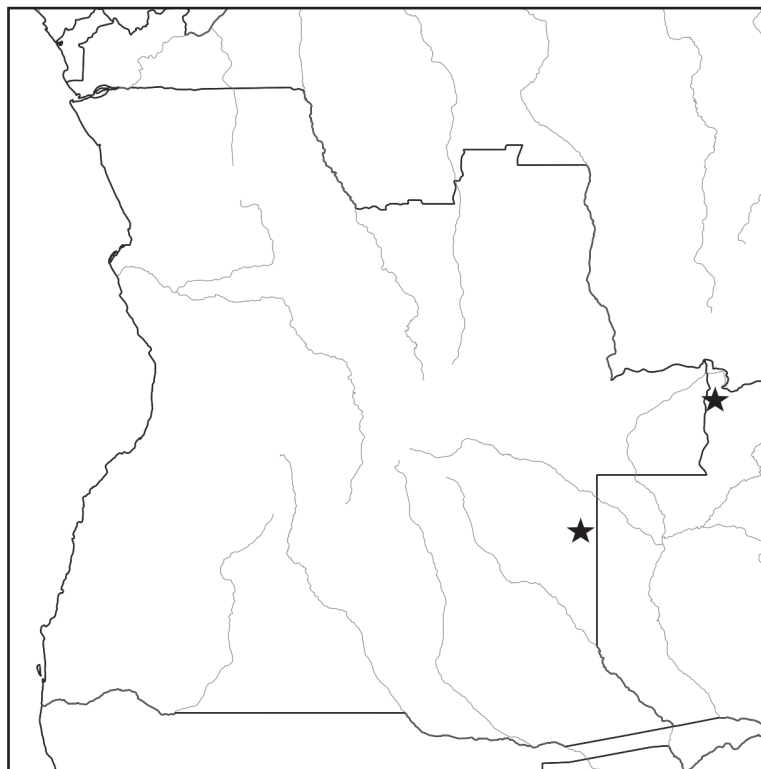


Figure 1. *Asclepias minutissima* **A** habit **B** flower **C** corona lobe **D** gynostegium **E** pollinarium. Drawn by Margaret Tebbs from Richards 17269.

Asclepias randii is a much more robust plant than the other species and has pubescent stems and leaves. *A. aurea* and *A. minor* are glabrous and are slender herbs. *Asclepias minor* has a corona which is much reduced, not even



Map 1. Known distribution of *Asclepias minutissima* (eastern Angola and NW Zambia).

reaching the base of the anther wings and has a short ventral appendage. So the species most similar to our new collection appears to be the highly variable *A. aurea*, which occurs across Namibia, southern Angola, Zambia, the Katanga region of the D.R.Congo, Zimbabwe, northern provinces of South Africa, Eswatini (Swaziland) and Lesotho (Goyder 2009).

Asclepias aurea has rotate to reflexed corolla lobes, corona lobes which radiate from the column and are extended into a long distal tongue, and longer peduncles. In addition to the rather subtle morphological characters that distinguish the new species from *A. aurea*, its ecological requirements, close to the water table on leached Kalahari sand, are probably also significant. *Asclepias aurea* occurs on richer soils. The new taxon was mentioned by Goyder et al. (2020: 276) in a note under the related *A. aurea* but the Angolan (type) collection was cited incorrectly as Goyder & Gonçalves 4809.

Bixaceae: Cochlospermeae

***Cochlospermum adjanyae* Goyder & Amândio Gomes, sp. nov.**

urn:lsid:ipni.org:names:77327147-1

Diagnosis. *Cochlospermum adjanyae* differs from all African species of the genus in possessing palmatisect rather than palmatifid or lobed leaves, with discrete leaflets rather than partially connate lobes.

Type. ANGOLA. Moxico Province: Lungué-Bungo valley, 50 km S of Munchango, near Lungué-Bungo bridge, 12°36'50"S, 018°47'59"E, fl. 20 November 2019, D.Goyder & A.Gomes 9002 (holotype: K (K001334241); isotypes: INBAC, LUBA, PRE).

Description. Geoxylic suffrutex forming diffuse but discrete patches several metres across; above-ground stems 10–20 cm tall, sub-erect, glabrous, burned off in the dry season. Leaves palmate with (4–)5 leaflets; stipules c. 3 mm long, narrowly triangular; petioles (2–)4–6 cm long, glabrous except for a minute rusty pubescence at the junction with the leaflets; leaflets reducing in size from the central leaflet to the lateral and basal ones, central leaflet 3–5 cm long, 1.2–2 cm wide, elliptic to slightly obovate, acute or occasionally obtuse apically, the base somewhat cuneate, margins serrate at least in the upper half, glabrous except for a minute rusty pubescence at the junction with the petiole adaxially. Inflorescences minutely rusty-puberulent, terminal on the leafy shoots, with 1–3 flowers; peduncles 2.5–3 cm long; sepals subequal, 11–15 × 7–8 mm, broadly ovate or elliptic, rounded apically, minutely rusty-puberulent and with occasional dark streaks, the outer pair more deeply coloured than the inner three; petals c. 3 × 2–2.3 cm, obovate, rounded or slightly emarginate, bright yellow with linear red streaks. Stamens numerous (80+), yellow; anthers c. 5 mm long, straight or weakly curved, apical pore 0.5–1 mm long. Ovary c. 2 mm in diameter, glabrous. Fruit not seen. (Figs 2, 3).

Distribution and ecology. Found only once in flower in grassland rich in geoxylic suffrutices on deep Kalahari sand. Material in bud had been encountered, but not collected, the day before in a similar grassland some 15 km to the NW along with the new species of *Baphia* described below and other geoxyles such as *Sclerocroton oblongifolius* (Müll.Arg.) Kruijt & Roebers, *Parinari capensis*, *Entada arenaria* Schinz and *Englerophytum magalismontanum* (Sond.) T.D.Penn. The fact that this conspicuously flowered species was seen only on the November 2019 expedition and not on earlier ones through the same valley system (late rainy season; early and mid-dry season) suggests that populations are highly localised and that the flowering period is short, at the end of the dry season, and perhaps dependent on rainfall following fire. Altitude 1285–1340 m. (Map 2).

Etymology. The specific epithet honours Adjany Costa who was part of the core National Geographic Okavango Wilderness Project headwaters team from the first expedition in 2015 until she left to pursue academic studies at Oxford University in 2019. Initially, she supported freshwater fish specialists Paul Skelton and Ben van der Waal, recording and preserving freshwater fish diversity from the Cuito source to the Delta, before developing the communities programme with Chris and Steve Boyes. She was a National Geographic Young Explorer, starred in the National Geographic documentary film “Into the Okavango”, and was awarded the United Nation’s Young Champions of the Earth Prize for Africa in 2019.

Conservation status. While *Cochlostemum adjanyae* is known from a single locality, these geoxyle-rich grasslands are not currently threatened as this nutrient-poor sandy environment is not conducive to agricultural development. The environment does not support many human settlements, which are few and far between. The species is probably best assessed as Data Deficient.

Taxonomic notes. *Cochlospermum* Kunth is a pantropical genus of around 16 species of trees, shrubs and geoxylic suffrutices, or if expanded to include the herbaceous neotropical genus *Amoreuxia* DC., 20 species. *C. noldeae* Poppend. from NE Angola, *C. macnamarae* Hislop, K.R.Thiele & Brassington and

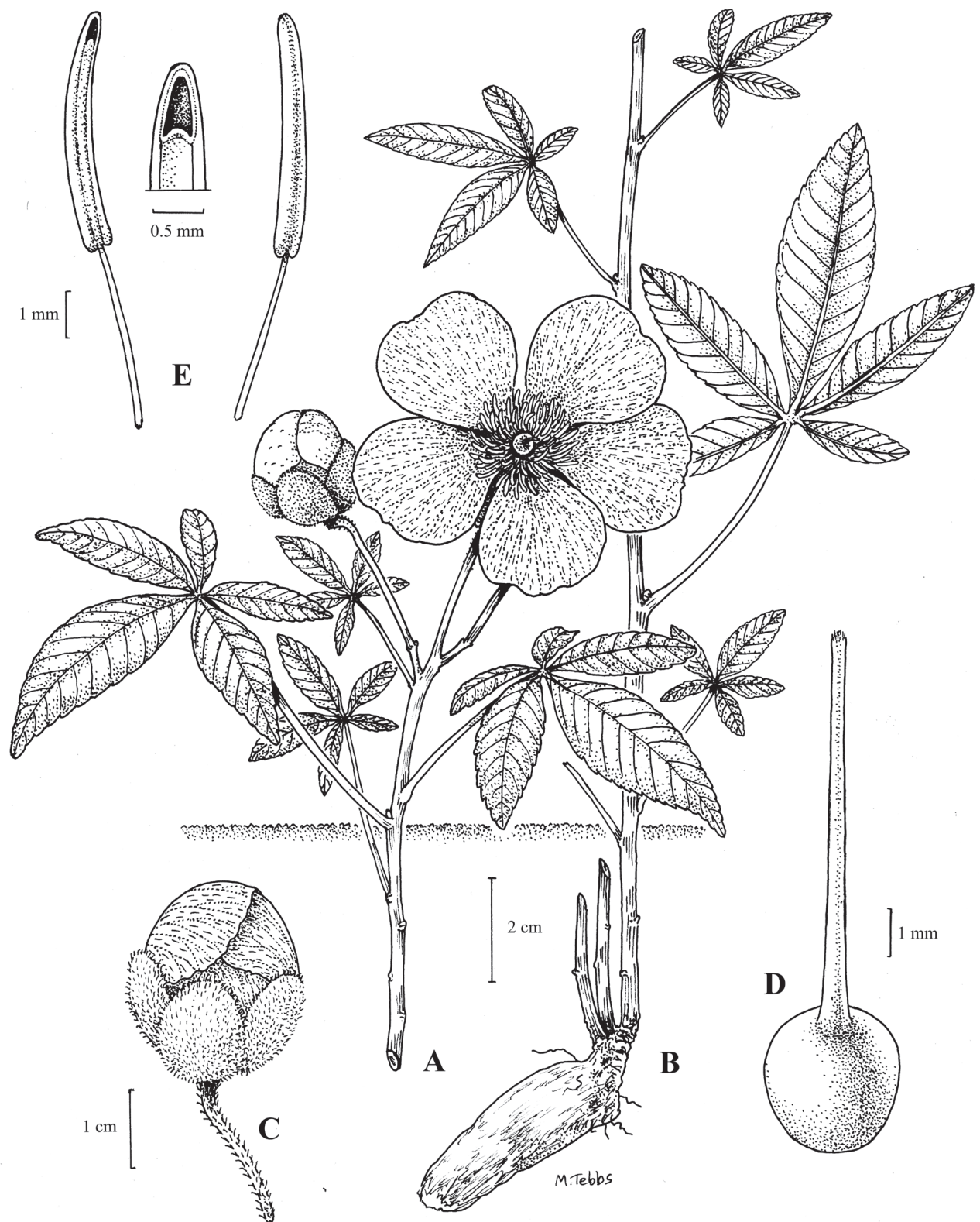


Figure 2. *Cochlospermum adjanyae* **A, B** habit **C** flower **D** ovary and style **E** stamens. Drawn by Margaret Tebbs from Goyder & Gomes 9002.

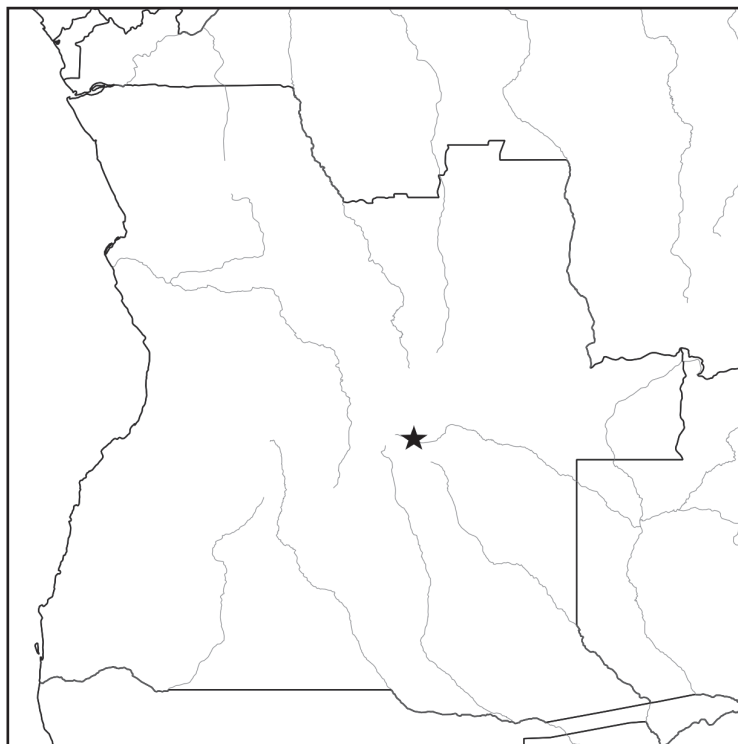
C. arafuricum Cowie & R.A.Kerrigan from Australia (Poppendieck 2004 (see nomenclatural note below), Hislop et al. 2013, Cowie and Kerrigan 2015) were described after Poppendieck's (1980) monograph of the group where he had



Figure 3. *Cochlospermum adjanyae*. Photographed by Chris Boyes at the type locality.

recognised 12 species. Irrespective of the circumscription of the genus, molecular evidence presented by Johnson-Fulton and Watson (2017) supports the monophyly of *Cochlospermum* subgenus *Cochlospermum* sensu Poppendieck (1980), which comprises two species from Central and South America (*C. vitifolium* (Willd.) Spreng. and *C. regium* (Mart. ex Schrank) Pilg.), and all the paleotropical species. Johnson-Fulton and Watson (2017) argue that the geoxylic habit evolved just once from an ancestral arboreal lifeform – all but one of the African taxa are geoxyles, together with a single neotropical species, *C. regium*, from *cerrado* (savanna) regions of Brazil, Paraguay and Bolivia. The remaining species are trees or shrubs.

Species of *Cochlospermum* subg. *Cochlospermum* have a single apical pore to the anthers, and in addition to growth form, can be distinguished by leaf indentation or lobing, indumentum, and the position and timing of flowers on the shoots. A collection made in the geoxyle-rich Lungué-Bungo valley grasslands of Moxico in November 2019 is unique in the African species in having palmatisect leaves, divided to the base rather than being merely lobed. The only other taxon in the subgenus with this leaf character is the nomenclaturally illegitimate *C. gillivrayi* Benth. subsp. *gregorii* (F.Muell.) Poppend., an Australian tree. The Angolan material is described as a new species. It is perhaps closest morphologically to *C. wittei* Robyns from the Upemba region of Katanga. *Cochlospermum wittei* is also associated with savanna and woodland on sand plateaux (Poppendieck 1980) but these are nearly 1000 km to the NE of the Lungué-Bungo grasslands.



Map 2. Known distribution of *Cochlospermum adjanyae*.

Key to African species of *Cochlospermum*

- 1 Trees or shrubs at least 4 m tall ***C. angolense* Welw. ex Oliv.**
- Geoxylic suffrutices or low shrubs with annually produced shoots less than 4 m tall **2**
- 2 Flowering mostly near ground level after fires and before the development of leafy shoots; savanna regions north of the equator ***C. tinctorium* A.Rich.**
- Flowering towards the tip of leafy shoots **3**
- 3 Leaves 3-lobed, the apex of the lobes attenuate; anthers 7 mm long; NE Angola: Malange ***C. noldeae* Poppend.***
- Leaves mostly 5–7-lobed, the apices acute, obtuse or rounded; anthers 4–6 mm long **4**
- 4 Leaves palmately compound with leaflets free to the base; eastern Angola: Moxico ***C. adjanyae***
- Leaves palmately lobed, the lobes connate for at least some of their length **5**
- 5 Leaves with lobes connate for at least half their length, lobes rounded or obtuse apically; leaves generally silvery-white beneath; West African savannas ***C. planchonii* Hook.f. ex Planch.**
- Leaves with lobes connate for less than half their length, lobes obtuse or acute apically; leaf indumentum variable **6**
- 6 Leaves with lobes connate for $\frac{1}{4}$ – $\frac{1}{2}$ of their length; Central African Republic ***C. intermedium* Mildbr.**
- Leaves with lobes connate for less than $\frac{1}{4}$ of their length; DR Congo: Kattanga **7**

* Nomenclatural note on epithets commemorating Ilse von Nolde.

- 7 Leaves glabrous beneath; sepals minutely puberulous; 'forest' understorey ***C. wittei* subsp. *wittei***
- Leaves silvery-white beneath; sepals minutely tomentose, greyish; savanna on Kalahari sand ***C. wittei* subsp. *incanum* (Robyns) Poppend.**

Ilse von Nolde, who lived in Quela, eastern Malange Province where she and her husband farmed coffee, made important collections of plants from the region between 1928 and 1938 (Esdorn 1972; Poppendieck 2004; Figueiredo et al. 2008; Figueiredo et al. 2020). While the top set of her collections in Berlin appears to have been destroyed, some material is duplicated at BM, COI, LISC and MO, and her botanical notes and illustrations are preserved at HBG (Poppendieck 2004). Several species were named after her and while most have the correct termination two, *Cochlospermum noldei* Poppend. and *Casearia noldei* A.Fern. & Diniz, end in -i rather than -ae. -i would be the correct termination for a male collector. We correct these epithets here to *Cochlospermum noldeae* and *Casearia noldeae*, in accordance with Art. 60.8a of the International Code for Nomenclature (Turland et al. 2018).

Lamiaceae: Ocimeae

***Endostemon palustris* A.J.Paton & Goyder, sp. nov.**

urn:lsid:ipni.org:names:77327148-1

Diagnosis. Differs from *E. tubulascens* (Briq.) M.Ashby in the little-branched habit, the sessile rather than petiolate and linear rather than elliptic leaves, the fewer-flowered (4–6-flowered rather than 6–10-flowered) verticils in the inflorescence, the pale violet rather than pinkish white flowers and the longer calyx (fruiting calyx 8–9 mm long rather than 5.5–6 mm).

Type. ANGOLA. Moxico Province: Confluence of Cuito River and its 1st tributary, the Kalua River, c. 65 km SSW of Munhango, 12°44'55"S, 018°21'16"E, fl. 20 Oct. 2016, D.Goyder & F.Maiato 8762 (holotype: K (K001333409); isotypes: INBAC, LUBA).

Description. Aromatic perennial suffrutex with few stems arising from a thick woody rootstock; stems erect, 15–30 cm tall, branched near the base, square in section above, more rounded below, pubescent with both glandular and eglandular hairs. Leaves verticillate, ascending, sessile, linear and folded along the midvein, 2.5–5 cm long, 0.1–0.2 cm wide, pubescent. Inflorescence lax with 4–6-flowered verticils 1.5–2.5 cm apart; bracts lanceolate or narrowly ovate, 3.5–4.5 mm long; pedicels 1–5 mm long, longer in lower verticils. Calyx 5 mm long at anthesis, pubescent with spreading hairs and sessile glands, posterior lip purplish; fruiting calyx 8–9 mm long. Corolla pale violet, 8–10 mm long; tube 6–7 mm long, straight, parallel-sided, dilating at the throat. Filaments c. 0.5 mm long, glabrous or pilose. Ovaries pubescent at apex. (Fig. 4).

Distribution and ecology. Known only from the type collection close to the source of the Cuito River. It was found towards the upper edge of a marsh fringing the river. (Map 3).

Conservation status. Although known from a single locality, *Endostemon palustris* occupies a habitat that is extensive within the upper catchment of the Cuito and its tributaries. The area is not threatened with agricultural

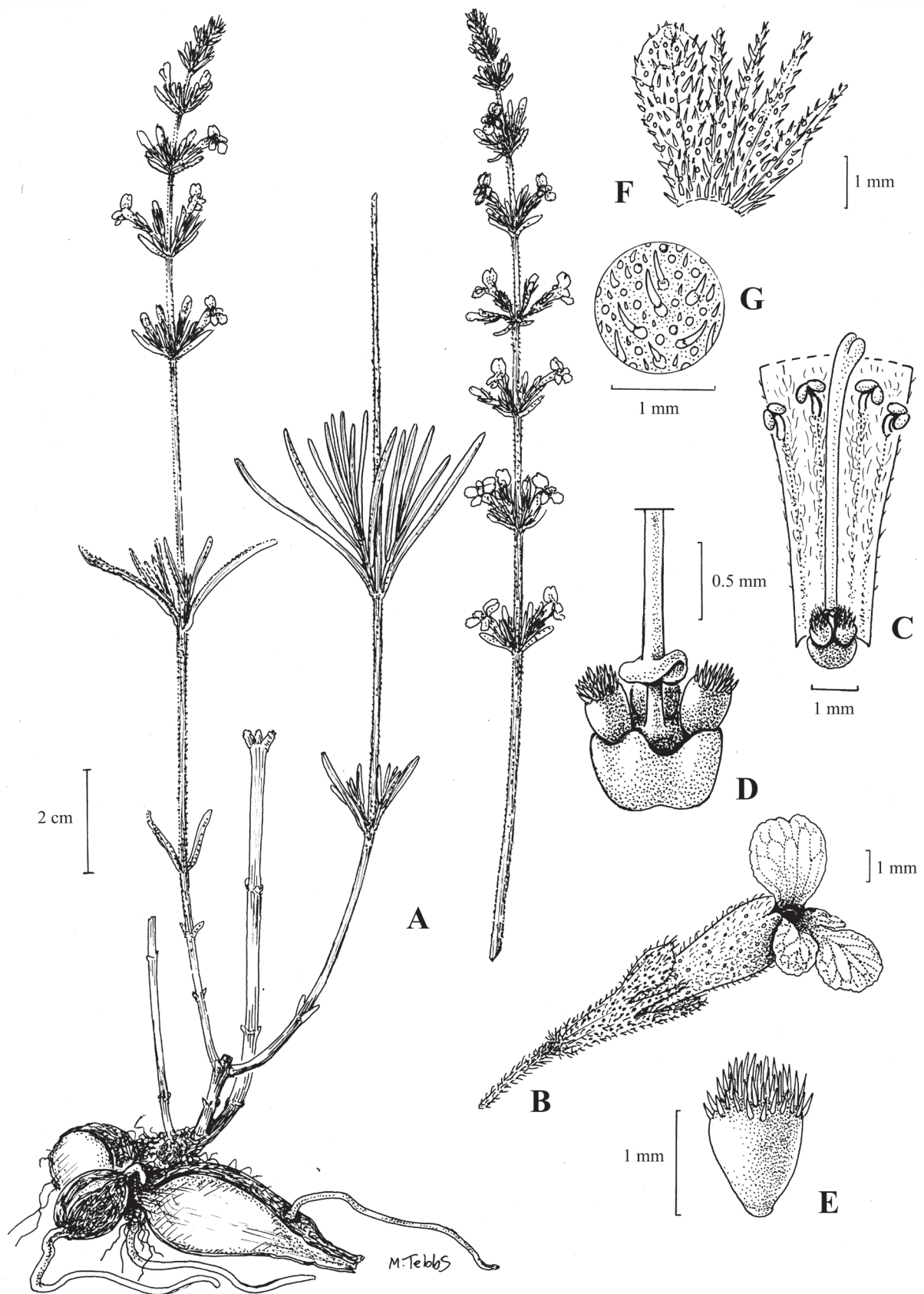
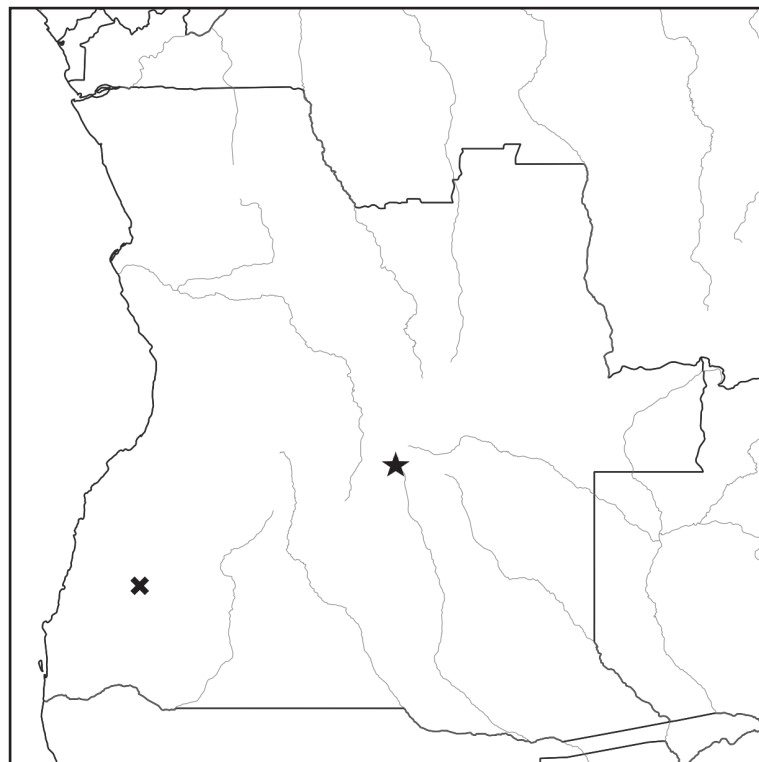


Figure 4. *Endostemon palustris* **A** habit **B** flower **C** opened corolla showing androecium and gynoecium **D** base of gynoecium showing three of the four nutlets and the gynobasic style **E** individual nutlet **F** calyx **G** indumentum. Drawn by Margaret Tebbs from Goyder & Maiato 8762.



Map 3. Known distribution of *Endostemon palustris* (star), and of the related species *E. tubulascens* (cross).

development being both nutrient poor and many kilometres from any human habitation, but with so little information the species is provisionally assessed as Data Deficient.

Taxonomic notes. *Endostemon* N.E.Br. is an isolated genus of 20 species within the tribe Ocimeae, with two centres of endemism – Angola and the Horn of Africa. It can be recognised within the *Orthosiphon* Benth. group of genera by its short, villous staminal filaments, an expanded shield-like base to the style, and pollen with alternating wide and narrow mesocolpia (Paton et al. 1994; Ryding et al. 2003; Paton et al. 2004). With the exception of *E. tereticaulis* (Poir.) M. Ashby which is in *Endostemon* sect. *Oblongi* Ayob. ex A.J.Paton, Harley & M.M.Harley, all of the Angolan species fall within *Endostemon* sect. *Endostemon*. This section is characterised by a relatively short calyx tube with an open glabrous throat, and the form of the lateral calyx lobes – the posterior margins of these lobes are not extended towards the upper lip of the calyx. *Endostemon tubulascens*, to which this new species is compared, appears largely restricted to the high escarpment zone around Lubango, Huíla Province, Angola.

Leguminosae: Papilionoideae

***Baphia arenicola* Goyder, F.M.P.Gonçalves & P.Meller, sp. nov.**

urn:lsid:ipni.org:names:77327149-1

Diagnosis. Most similar morphologically to *B. massaiensis* Taub., from which it can be readily distinguished by its geoxylic lifeform, flowering and fruiting at ground level on short, prostrate above-ground shoots, and the villous suture of the keel petal.

Type. ANGOLA. Moxico Province: tributary of the Lungué-Bungo River 42 km SSE of Munhango, 12°31'34"S, 018°40'13"E, fl. 22 October 2016, *D.Goyder & F.Maiato* 8772 (holotype: K (K001333933); isotypes: INBAC, LUBA).

Description. Geoxylic suffrutex forming large patches; above-ground shoots prostrate, 5–10 cm long, pubescent, arising from extensive woody below-ground stems. Leaves unifoliolate; stipules linear, 3–4 mm long, densely pubescent with silvery hairs; petiole 3–5 mm long, pulvinus barely apparent; leaflet narrowly obovate-oblong and generally folded along the midvein, 4–6 cm long, 1–2 cm wide, obtuse apically, tapering somewhat towards the base, ± glabrous except for the major veins beneath. Inflorescences with an indumentum of greyish or golden hairs; flowers 1–3 in sessile or subsessile axillary fascicles; pedicels 15–20 mm long; bracteoles 1–2 mm below the calyx, caducous. Calyx 7–10 mm long, spathaceous. Petals white, the standard with a yellow triangular mark towards the base; standard 10–12 × 8–10 mm, emarginate; wings c. 10 × 2 mm; keel 10–12 × 2.5–3 mm, lower suture villous distally. Stamens 10, free. Ovary 6–9 mm long, villous, with a glabrous upturned style. Legume c. 7 cm long, c. 1.5 cm wide, brown. Seeds c. 10 mm long, dark brown or black. (Figs 5, 6).

Distribution and ecology. Flowering in October and November in the late dry season or at the onset of the rains; fruiting in February. Known from three sites, the first in the Lungué-Bungo river system of western Moxico Province at an elevation of around 1350 m, the second in the Cusseque River system of Bié Province some 200 km to the SW of the Moxico site at around 1530 m, and the third just over the watershed into the Cacuchi River valley which drains into the Rio Cuchi and is around 1540 m. The three sites are similar topographically, with broad fossil river terraces and sandy alluvial deposits rich in geoxylic suffrutices (Gröngroft et al. 2013b, Revermann et al. 2013, Goyder et al. 2018). (Map 4).

Conservation status. *Baphia arenicola* is known from three localities, two of which have vouchered herbarium collections. TFO project made many unvouchered observations of the plant in the Cusseque and Cacuchi River valleys and it is clear that there are extensive populations of this species. There are no significant threats to these nutrient-poor grasslands rich in geoxylic suffrutices as the environment is not conducive to agricultural development. *B. arenicola* is therefore provisionally assessed as Least Concern.

Additional specimens examined. ANGOLA. Bié Province: Cusseque, TFO core site relevé 23324, 13°41'53"S, 017°06'43"E, fl. 29 October 2011, *Finckh* 132753 (HBG, K); Cusseque, TFO core site relevé 23349, 13°41'53"S, 017°07'48"E, fl. 2 November 2011, *Revermann* 132895 (HBG, K); Cusseque village, Chitembo, 13°43'21"S, 017°05'53"E, fr. 17 February 2014, *Gomes & Maiato* 161 (LUBA); Cusseque 15 September 2019, *Finckh* 145383A (HBG, LUBA); Cusseque, 28 January 2020, *Finckh* 145352B (HBG, LUBA).

Taxonomic notes. *Baphia* Afzel. ex G.Lodd is a genus of around 50 species of woody legumes which has diversified across tropical Africa (Soladoye 1985, Goncharov et al. 2011). A single species extends its distribution to the white sands of NW Madagascar, with a second species endemic to that region (Stirton and Du Puy 1992). Members of the genus are recognised readily by their unifoliolate leaves, free rather than united stamens, and flat, dark brown seeds lacking an aril. Seeds of other genera of the unifoliolate Baphioid clade of Lewis et al. (2005) are globose, arillate, and bicoloured or otherwise brightly coloured (Cheek et al. 2014). *Baphia* species occur in evergreen forest, thick-

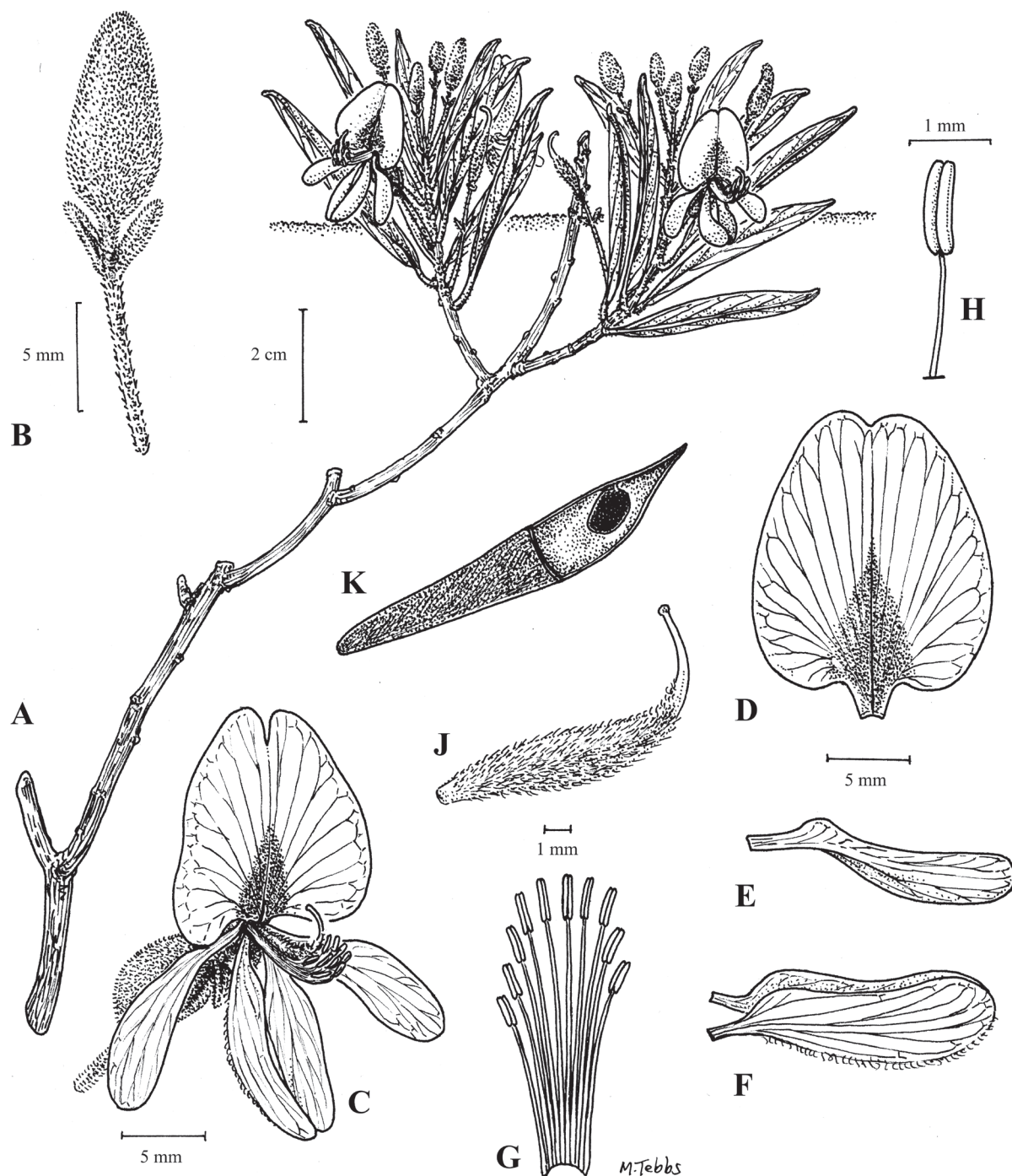
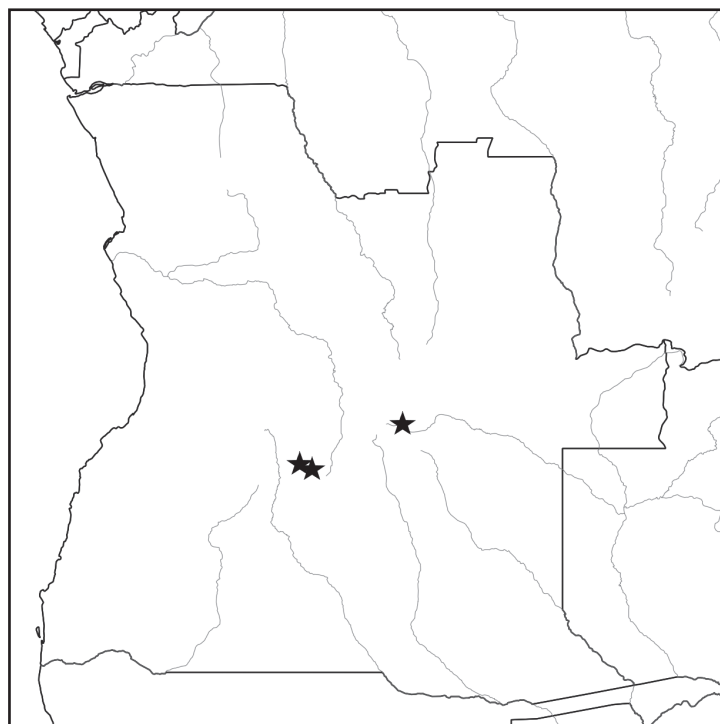


Figure 5. *Baphia arenicola* **A** habit **B** bud **C** open flower **D** standard petal **E** wing petal **F** keel petal **G** androecium **H** stamen **J** gynoecium **K** fruit. Drawn by Margaret Tebbs from Goyder & Maiato 8772 (flowering material) and Gomes & Maiato 161 (fruit).

et and woodland with several species restricted to white sands (Stirton and Du Puy 1992, Brummitt 2007, Mackinder and Clark 2012, Cheek et al. 2014). While most species are shrubs or small trees, *B. aurivellerea* Taub. from NE Angola and western DR Congo can be suffrutescent, but this species still possesses erect woody shoots 20 cm to two metres above ground level. In contrast, an undescribed species encountered in central Angola flowers at ground level on short, prostrate above-ground shoots and is here formally described as *Baphia arenicola*.



Figure 6. *Baphia arenicola*. Photographed by David Goyder at the type locality.



Map 4. Known distribution of *Baphia arenicola* (central Angola).

Most floral characters invite comparison with the locally common woodland species *B. massaiensis*, with its spathaceous calyx split longitudinally down a single line, bracteoles longer than wide and positioned shortly below the apex of the pedicel, glabrous staminal filaments, and pubescent ovary. The keel petal which is somewhat villous along its line of fusion, however, suggests links to *B. bequaertii* De Wild., another *miombo* woodland species of the region. Preliminary molecular analyses by one of us (PM) places the new taxon close to the latter species, with estimated divergence times from *B. bequaertii* less than 1 mya. Divergence times from *B. massaiensis*, on the other hand, are estimated to be between 11 and 27 mya.

Rubiaceae: *Vanguerieae*

***Vangueria fulgida* (Welw. ex Hiern) Goyder & N.M.J.Davies, comb. nov.**

urn:lsid:ipni.org:names:77327150-1

Ancylanthos fulgidus Welw. ex Hiern in Oliv. (ed.), Fl. Trop. Afr. 3: 159 (1877).

Type: Angola, Huíla, Mumpulla to Lopollo, Oct. 1859, *Welwitsch* 3160 (lectotype: LISU (LISU208624) designated here; paralectotypes: BM, K, LISU, P, PRE). (Basionym).

Ancylanthos rubiginosus Desf., Mém. Mus. Hist. Nat. 4: 5 (1818). *Vangueria rubiginosa* (Desf.) Lantz, Pl. Syst. Evol. 253: 181 (2005), non *V. rubiginosa* K.Schum., Bot. Jahrb. Syst. 23: 457 (1897) [= *Rytigynia rubiginosa* (K.Schum.) Robyns, Bull. Jard. Bot. État Bruxelles 11: 209 (1928)]. Type: Angola [without locality or collector, but probably Benguela/Huila Plateau, 1785–1787, *J.J. da Silva* (Exell & Mendonça 1956: IX & XI, following note on specimen at P)] (holotype: P (P00138559)).

Ancylanthos ferrugineus Welw., J. Trav. Nat. Hist. 1: 29 (1868), nomen nudum.

Ancylanthos bainesii Hiern in Oliv. (ed.), Fl. Trop. Afr. 3: 160 (1877). Type: *Baines* s.n. (lectotype: K (K000412071) designated by Robyns 1928: 329).

Taxonomic and nomenclatural notes. *Vangueria fulgida* is a small woody species with conspicuous orange flowers. It can form single-stemmed plants to 1.5 m in height, but over much of its range it behaves as a geoxylic suffrutex, forming patches of much shorter above-ground shoots that are burned off each year. It is found mostly on Kalahari sands and is widely distributed across Angola, western Zambia, Botswana, Namibia and Zimbabwe (Bridson 1998; Figueiredo 2008a, b).

Molecular studies of the tribe *Vanguerieae* A.Rich. ex Dumort. (Lantz and Bremer 2004; Lantz and Bremer 2005; Razafimandimbison et al. 2009) have shown that the species of *Ancylanthos* Desf. are showy members of *Vangueria* Juss., and combinations under the latter were made in Lantz and Bremer (2005). However, *Vangueria rubiginosa* (Desf.) Lantz is a later homonym of *V. rubiginosa* K.Schum. (Schumann 1897: 457) and is therefore illegitimate.

The earliest synonym listed by Bridson (1998), *Ancylanthos ferrugineus* Welw. (Welwitsch 1868a: 29), must be treated as a *nomen nudum* because “very pretty” does not constitute a validating description under the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). No specimen was cited but, as Welwitsch was writing about the Pedras Negras of Pungo Andongo, Angola it can be inferred that *Welwitsch* 3159 from this region

is probably this plant. Welwitsch's second account of the Pedras Negras (Welwitsch 1868b), makes no mention of the plant.

Ancylanthos bainesii Hiern (1877) and *A. fulgidus* Welw. ex Hiern (1877) were published simultaneously and the epithets are both available under *Vangueria*, so either could be used as a basionym for a new combination to replace the illegitimate *V. rubiginosa* (Desf.) Lantz – we have chosen to use *A. fulgidus* described from the Huila Plateau of Angola, a name more widely adopted than *A. bainesii* (Hiern 1898; Schumann 1903: 390; Durand and Durand 1909: 271; De Wildeman 1910: 424, 1913: 153, 1925: 204; Robyns 1928). We designate the LISU specimen bearing Welwitsch's handwritten note as the lectotype of this name.

Hiern (1877) cited two specimens in his description of *Ancylanthos bainesii*. One, without a locality, was just cited as “T.Baines!”. The second is the Chapman & Baines collection labelled “lat. 23°”. Goyder (2016b) drew attention to problems localising Chapman & Baines' collections particularly those labelled lat. 23° – if taken literally, this would imply they were collected near the Namibian coast E of Walvis Bay, but as this is desert and therefore unsuitable habitat for most of the species bearing these labels, it is much more likely that, given the well-documented route of the expedition, they originated in northern Botswana. Robyns (1928: 329) effectively lectotypified the name by citing the unlocalised “T.Baines” collection as the type.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Author ORCIDs


David J. Goyder  <https://orcid.org/0000-0002-3449-7313>

Manfred Finckh  <https://orcid.org/0000-0003-2186-0854>

Amândio Gomes  <https://orcid.org/0000-0002-7812-5490>

Francisco Maiato P. Gonçalves  <https://orcid.org/0000-0002-8859-7491>

Paulina Meller  <https://orcid.org/0000-0001-6711-4385>

Alan J. Paton  <https://orcid.org/0000-0002-6052-6675>

Data availability

All of the data that support the findings of this study are available in the main text.

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Geometric Morphometrics sheds light on the systematics affinities of two enigmatic dwarf Neotropical sedges (*Carex*, Cyperaceae)

Ana Morales-Alonso¹, Tamara Villaverde², Pedro Jiménez-Mejías¹

¹ Área de Botánica, Department of Molecular Biology and Biochemical Engineering, Universidad Pablo de Olavide, ctra de Utrera km 1, Seville 41013, Spain

² Área de Biodiversidad y Conservación, Department of Biology and Geology, Physics and Inorganic Chemistry, Universidad Rey Juan Carlos, Calle Tulipán s/n., Móstoles 28933, Madrid, Spain

Corresponding authors: Ana Morales-Alonso (aimoralons@gmail.com); Pedro Jiménez-Mejías (pjimmej@upo.es)

Abstract

Geometric morphometrics (GM) is a powerful analytical tool that enables complete quantification of shapes. Its use in Botany has a great potential for complementing plant evolutionary and ecological studies. Taxonomic delimitation in *Carex* has been complicated due to reduction of characters and frequent homoplasy. This problem is more marked in cases where the species exhibit dwarfism. South America is the continent with the least understood *Carex* flora. The systematic relationships of some bizarre-looking groups were not unraveled until molecular phylogenetic studies resolved their relationships. In particular, there are two species only known from their type material whose affinities remain uncertain: *Carex herteri* and *C. hypsipedos*. These two taxa are acaulescent plants that respectively grow in the Uruguayan pampa and Peruvian high-altitude meadows. Recently, both species were ascribed to the *Carex phalaroides* group (subgen. *Psyllophorae*, sect. *Junciformes*) due to superficial morphological similarities, such as the androgynous peduncled spikes. However, their character combination is also coincident for its circumscription to sect. *Abditispicae* species. Nevertheless, in the absence of confirmation from molecular analyses, their placement must be considered preliminary until additional data can be provided. In this work we employ for the first time geometric morphometrics (GM) tools to assess the systematic affinities of two taxonomically problematic sedge species based on fruit shape. We compared utricle morphology of *C. herteri* and *C. hypsipedos* with that of *C. phalaroides* group and species in sect. *Abditispicae*. To this end we used GM and traditional morphometric approaches. Utricle shape variation along with other morphological features support the exclusion of these two species from the *C. phalaroides* gr. and, at the same time, show clear affinities of *C. herteri* to sect. *Abditispicae*. *Carex hypsipedos* remains as an *incertae sedis* species. Our work shows the potential utility of GM for the exploration of systematic affinities in sedges and in other graminoids.

Key words: acaulescence, *Carex*, geometric morphometrics, Neotropics, sedges

Introduction

Before the advent of molecular systematics, taxonomic delimitation relied on the evaluation of phenotypic differences. Visible characteristics of organisms have been the basis for classifying the diversity of life within a unifying taxo-



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nomic framework. Analytical advances have allowed the implementation and consequent improvement of tools that can be applied to morphology-based studies (e.g. correlation coefficient (Pearson 1895), analysis of variance (Fisher 1935) or principal components analysis (Pearson 1901; Hotelling 1933). However, certain evolutionary phenomena, such as homoplasy, stasis or recent divergence, may have consequences on morphology of the organisms, hampering the distinction of certain taxa based only on morphological characteristics. Accordingly, these types of tests lose their resolving power, making it necessary to search for additional evidence for its distinction.

One of the less explored analytical tools in plant systematics is geometric morphometrics (GM). GM was developed around 1980 (e.g. Kuhl and Giardina 1982), allowing the analysis of structures shapes and their variation. It uses non-quantitative variables through coordinates of landmarks, which collect geometric information on their relative position (Chen et al. 2018). It enables the visualization of multivariate analyses results as a configuration of landmarks from the original spatial configuration of the organism (Adams et al. 2004). This tool uses as a basis the Procrustes analysis of fixed and sliding landmarks, which extracts a consensus configuration (mean) by standardizing effects of rotation, orientation, and scale among specimens. These effects are translated to the origin, scaled to unit-centroid size, and rotated via a generalized least-squares algorithm that enables their alignment along a common coordinate system (Rohlf and Slice 1990) resulting in the removal of the extraneous information of landmark's size and orientation (Savriama 2018). GM are powerful analytic tools in constant development that offer a new way of studying species evolution (Savriama 2018), systematics (Liu et al. 2018; Menini Neto et al. 2019), and even phylogeography (Terral et al. 2004, 2012) or ecology (García-Jain et al. 2022) and archaeophenomics (Evin et al. 2022) by collecting and comparing the morphology of organisms. GM studies in plants have been implemented with ancient plant organs (Terral et al. 2004, 2012), functional traits (Van der Niet et al. 2010; Neustupa and Nemcova 2022), and floral symmetry (Chen et al. 2018; Savriama 2018).

Carex L. (Cyperaceae) with more than 2000 species, is one of the five largest genera among angiosperms and one of the two largest within monocots (Goovaerts et al. 2022). The genus is largely adapted to temperate-cold climates and has its origin in the Late Eocene (c. 37 mya), probably in southeast Asia from where it spread, reaching currently a nearly cosmopolitan distribution (Martín-Bravo et al. 2019). Traditional taxonomic treatments of *Carex*, as in most plant groups, have been primarily based on morphological data. These classifications' frameworks are known to be affected by morphological homoplasy, which has blurred the systematic relationships among species groups (Jiménez-Mejías et al. 2016a). Among the organs used in the taxonomic delimitation of *Carex*, the utricle is by far the most relevant. It is a bract-derived organ that is modified into a false fruit enclosing the nutlet (see Jiménez-Mejías et al. 2016b). Its morphology is usually conserved among the species of the different natural groups within the genus (see Roalson et al. 2021). All taxonomic treatments of *Carex* use the utricle to circumscribe and identify groups (e.g. Chater 1980; Egorova 1999; Ball and Reznicek 2002; Luceño 2008; Dai et al. 2010).

According to Jiménez-Mejías (2017), about 200 species of *Carex* are native to South America, most of them endemic to the continent where they are mostly

restricted to temperate-cold environments such as steppes, Patagonian forests and pampas and, in tropical latitudes, mountainous areas. An abnormally high number of *Carex* species at these areas exhibit dwarfism, with strong character reduction and acaulescency (Jiménez-Mejías et al. 2021). Such modifications result in diminutive plants with similar homoplastic morphological appearances. This is the case of two South American species, *C. herteri* G.A.Wheeler, an endemic to the pampas of Uruguay, and *C. hysipedos* C.B.Clarke from the dry Andes of central Peru (Wheeler 1996; Poindexter et al. 2017; Fig. 1). Both species are only known from their type collections, from 1920 and 1906 respectively (Fig. 2).

To date, *Carex herteri* and *C. hysipedos* have been included in the group of *C. phalaroides* Kunth (hereafter *C. phalaroides* gr.; subg. *Psyllophorae*, sect. *Junciformes*) due to superficial morphological similarities (Wheeler 1996; Poindexter et al. 2017). The *C. phalaroides* gr. is a taxonomic complex of four to six species depending on the treatment, morphologically characterized by stems usually well-developed, sometimes acaulescent, pedunculate bisexual (androgynous) spikes, utricles with a short beak and an indumentum of hairs

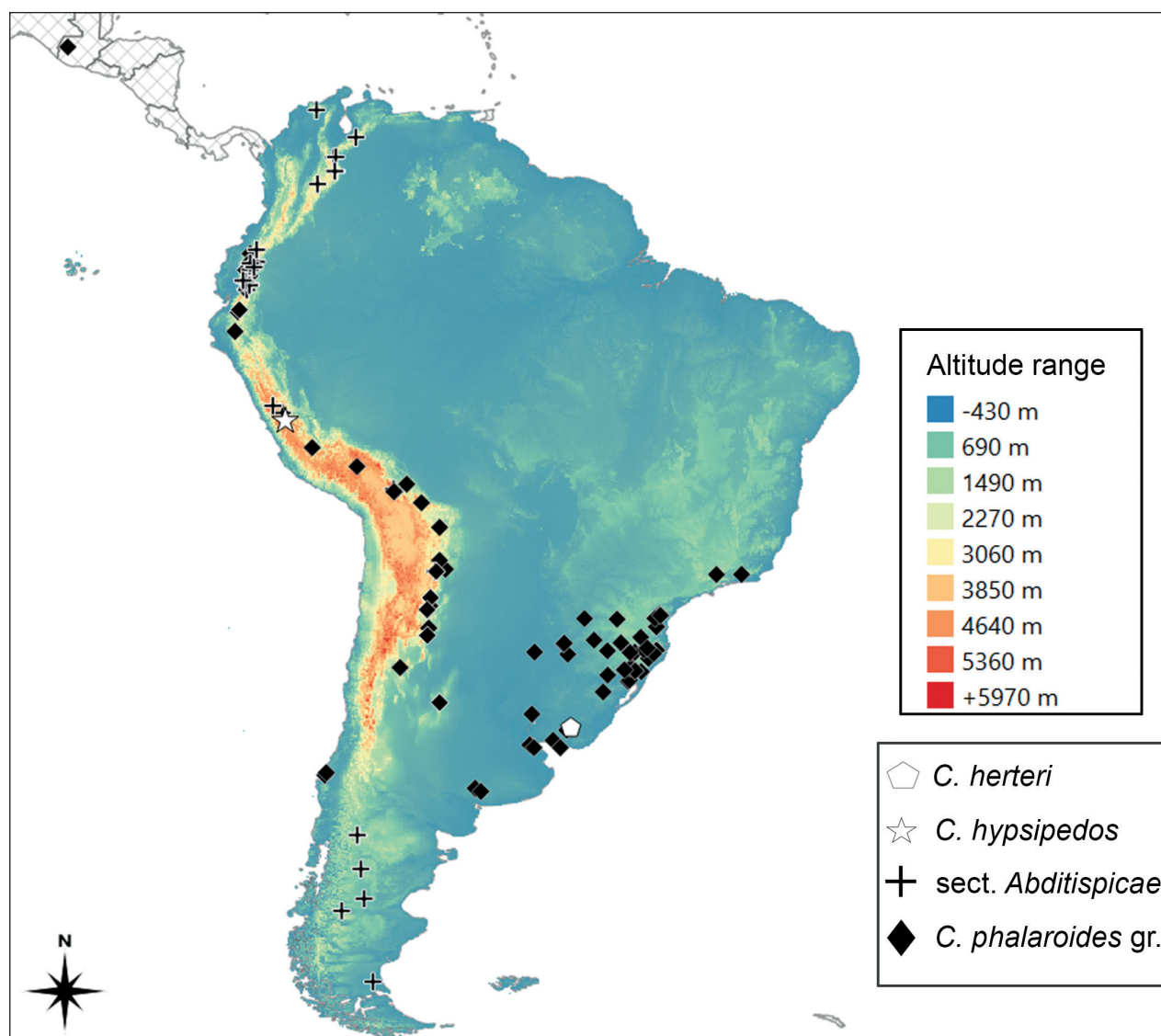


Figure 1. South America elevation map showing known distribution of the taxa considered in this study.

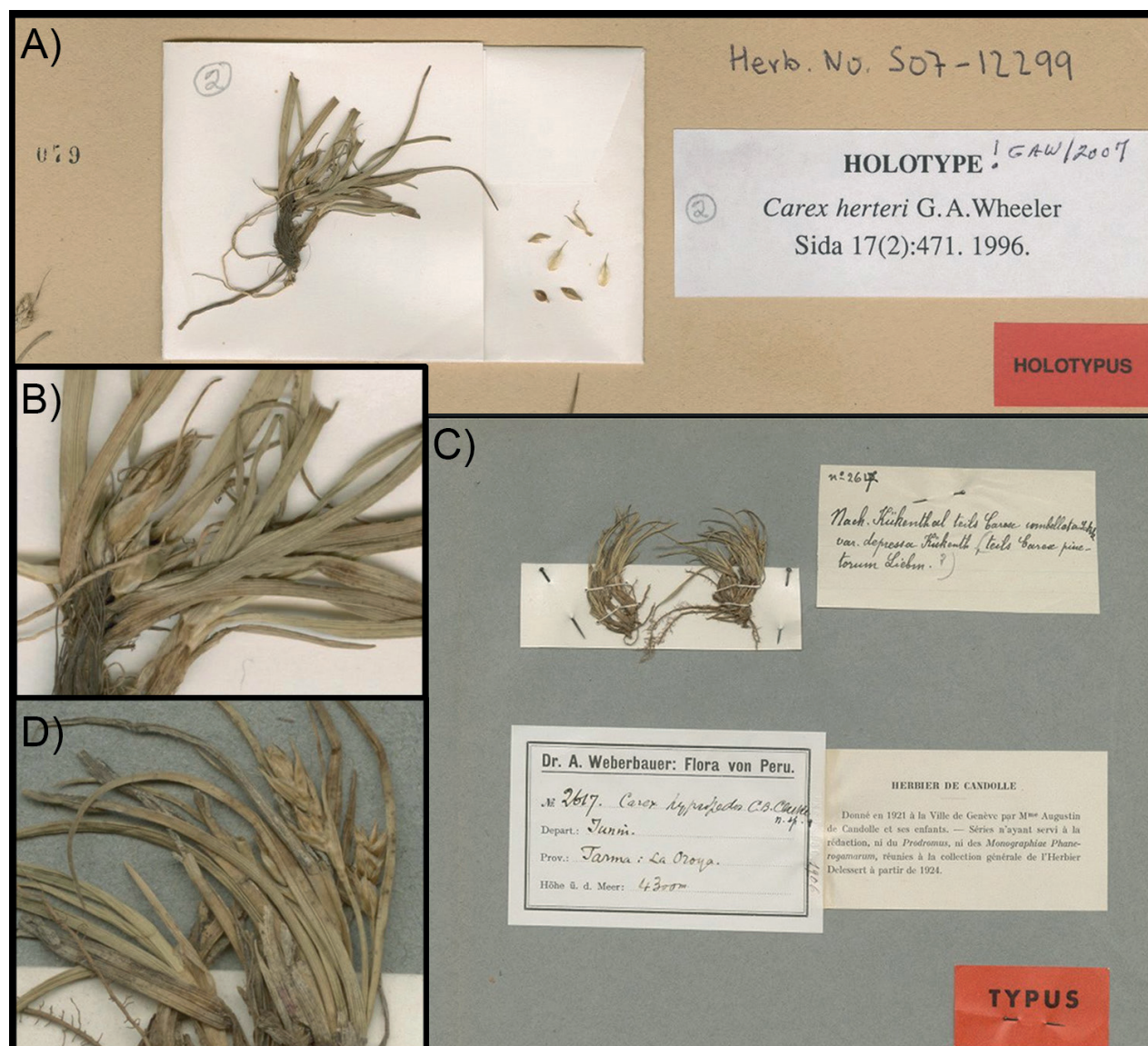


Figure 2. Images of the problematic species type collections **A** holotype of *C. herteri* (Herter 19091, S) **B** zoom in of holotype of *C. herteri* (Herter 19091, S) **C** holotype of *C. hypsipedos* (Weberbauer 2617, G) **D** zoom in of holotype of *C. hypsipedos* (Weberbauer 2617, G).

or papillae, and three stigmas (Hoff-Silveira and Longhi-Wagner 2012; A.M.A. and P.J.-M pers. obs). It is a Neotropical group (Fig. 1) which mainly inhabits temperate and subtropical latitudes of South America, although it reaches tropical areas northwards along the Andes, displaying isolated occurrences in the Central American Cordillera. The *C. phalaroides* gr. species are ecologically atypical among Neotropical sedges as they primarily occur in temperate and subtropical habitats, such as the Atlantic forest and pampas (Benítez-Benítez et al. 2021). Despite their initial attribution to the *C. phalaroides* gr., both *C. herteri* and *C. hypsipedos* display characters that would be deviant within it. On the one hand, *C. herteri* differs from *C. phalaroides* gr. species in its utricle size, presence of a conspicuous beak, and lack of indumentum (Wheeler 1996). On the other hand, *C. hypsipedos* diverges from *C. phalaroides* gr. taxa in the number of stigmas, as it has only two instead of three, and also the utricle with a

conspicuous beak (Poindexter et al. 2017). Therefore, its consideration as part of the *C. phalaroides* gr. is still tentative and pending confirmation.

Among all the remaining South American *Carex* groups, the only other alternative match for these two species would be *Carex* sect. *Abditispicae* G.A. Wheeler (subg. *Carex*). Section *Abditispicae* comprises a group of eight species endemic to South America (Roalson et al. 2021). Its taxa are characterized by acaulescent habit, with lateral female spikes borne at or near the plant base, often hidden among leaves but sometimes with well-developed peduncles, terminal male spike or androgynous, utricles with an indumentum more or less papillose, and with a truncate beak, and two stigmas (Wheeler 1987). This group primarily inhabits Patagonia and Tierra del Fuego, although a few species reach the Tropic of Capricorn and further north through the Andes (Wheeler 2002). The section typically inhabits areas such as moist or wet grasslands, bofedales (Andean bogs), swamps, lake shores, and wet sands and gravels by the sea (Wheeler 1987). The frequent dwarf size of sect. *Abditispicae* species, which makes its collection difficult by non-specialists, in addition to the remote areas they inhabit, might be the cause of the poor representation of species of this group in herbaria (Jiménez-Mejías et al. 2023), with some species known only from a handful of collections or only from their type ones (Wheeler 1987, 1996, 2002).

The taxonomic placement of *C. herteri* and *C. hysipedos* as part of the *C. phalaroides* gr. should be considered tentative, due to the manifest character reduction of the two taxa, the frequent morphological homoplasy in *Carex*, their reported differences with the ascribed group, and the lack of molecular data. Alternatively, sect. *Abditispicae* seems to be a reasonable competitive group for the systematic adscription of the two species. In this study we aim to re-evaluate the attribution of *C. herteri* and *C. hysipedos* to either *C. phalaroides* gr. or sect. *Abditispicae* in absence of available molecular data by analyzing the utricle, an organ of paramount taxonomic relevance in *Carex* together with other morphological characteristics using GM, a tool barely used for taxonomic delimitation in Cyperaceae, and traditional morphometrics, respectively.

Materials and methods

Geometric morphometric sampling

We selected utricles from 11 species (Fig. 3; Suppl. material 1): all four of *C. phalaroides* gr. (representatively covering its entire known morphological and geographical variation), and six from sect. *Abditispicae* (80% of the known species; Roalson et al. 2021). Due to the scarcity of sect. *Abditispicae* herbarium collections (and in particular of specimens bearing ripe utricles), we had to limit our sampling to the few mature specimens we located. After studying *in situ* the full collections of K, QCA, QCNE, and UPOS herbaria, we only managed to obtain 15 utricles: two from *C. acaulis*; three from *C. collumanthus*; one of *C. humahuacaensis*; two of *C. macrosolen*, four from *C. ruthsatzae*, and three of *C. subantarctica*. For *C. phalaroides* gr. we managed to obtain 32 utricle images: 14 of *C. gibertii*, three of *C. moesta*, three of *C. paraguayensis*, and 12 of *C. phalaroides* (Suppl. material 1). Detailed pictures of the utricles were taken with a Nikon stereoscopic microscope (Nikon SMZ745) and an Olympus stereoscopic microscope (Olympus SZX16). We compiled a set of 49 2D-scaled images.



Figure 3. Representative utricles images used for GM analyses. From the top to the bottom, left to right **A** problematic species: *Carex herteri* (Herter, W.G.F., 19091, S), *C. hypsipedos* (Weberbauer 2617, G) **B** *C. phalaroides* gr.: *C. gibertii* (Archavaleta s.n., US), *C. paraguayensis* (L. Pereira-Silva 350, FLOR) and *C. phalaroides* (G. Rodríguez-Palacios 23GERP15, UPOS) **C** *C. sect. Abditispicae*: *C. acaulis* (DM Moore 1240, K), *C. collumanthus* (PJ Grubb 339, K), *C. humahuacaensis* (S. Martín-Bravo et al., 178SMB21, UPOS), *C. ruthsatzae* (G. Rodríguez-Palacios 46GERP15, UPOS), *C. subantarctica* (Marcia Waterway, MW2015.020, UPOS), and *C. macrosolen* (S. Martín-Bravo et al., 11SMB10, UPOS). Scale bar: 4 mm.

Geometric morphometric analyses

Nine fixed landmarks were placed on homologous points within utricles following Jiménez-Mejías and Martinetto (2013) approach to the carpological features of *Carex*. All these fixed landmarks were limited to the beak and utricule base, as homologous structures between species (Suppl. material 2: fig. S1). In addition, to collect as much shape information as possible from the utricule body, we placed eight semi-landmarks equidistantly, on non-homologous points of the utricule body margins. These defined two curves on the right and left side of the utricule, from the base of the beak to the beginning of the substipitate base. Landmarks were digitalized, on images using TPSDig2 (Rohlf 2015) and datasets were created in a .tps format. All fix and sliding landmarks were positioned in the same order in all images.

Main GM analysis was conducted with a complete dataset including all 49 utricule images (from hereinafter referred as "complete GM dataset"). We split this dataset into sect. *Abditispicae* species (15 utricule images) and *C. phalaroides*

gr. species (32 utricle images), creating *Abditispicae* GM dataset and *C. phalaroides* GM dataset two and three, respectively. Datasets two and three excluded problematic species thus we obtained the consensus utricle configuration for each group to allow visual shape comparison with the problematic species. GM analysis was performed four times, first for identifying potential outliers through a PCA scatter plot, second for the complete GM dataset, and third and fourth for shape exploration of sect. *Abditispicae* and *C. phalaroides* gr. datasets, respectively. The GM analysis of the complete dataset revealed that the highly deviant utricle of *C. macrosolen* induced a strong bias to the analysis generating a substantial deviation to the PCA, due to its large peak size (Suppl. material 2: fig. S2), thus, this was removed from all subsequent GM analyses, leaving the complete dataset with only 47 utricle images.

We proceeded to landmark analysis with geomorph, R package v.4.0.2 (Adams et al. 2021). Semilandmarks were set as sliding points with the *geomorph::define.sliders* function. We subsequently performed generalized Procrustes analysis (GPA) using the minimized squared distances method. GPA calculates the consensus configuration of the dataset, along with its shape variation, and makes a separation within size and shape components of the datasets (Viscosi and Cardini 2012). It is here used as a superimposition method because it has been shown to be accurate in sample means estimation (Rohlf 2000a, b, 2003). GPA was performed with the *geomorph::gpagen* function and a maximum of 1000 iterations. The studied utricle morphospace was visualized by performing a principal component analysis (PCA) only for the complete dataset, and the shape variation within the morphospace was depicted with *geomorph::picknplot.shape* function. Subsequently, a Procrustes multivariate analysis of variances MANOVA was carried out with the *geomorph::procD.lm* function to assess statistical patterns of shape variation for a set of Procrustes aligned coordinates between the considered groups (Adams et al. 2021). Accounting for the small size of our dataset, the significance of shape variation between the two major groups was performed against a null model generated by permuted resampling, which uses a residual randomization permutation of 999 replicates (Collyer et al 2015; Renner et al 2018). The mean shape of all sampled utricles for every dataset was visualized with *geomorph::mshape* and *geomorph::plot-RefToTarget* functions. To achieve an objective attribution of the problematic species to either sect. *Abditispicae* or *C. phalaroides* gr. we performed a Discriminant Function Analysis (DFA), more precisely the Linear Discriminant Analysis (LDA) with MASS R package (Venables and Ripley 2002). For this analysis we set a train dataset only with sect. *Abditispicae* and *C. phalaroides* gr. species and prepared two tests, one for *C. herteri* and another for *C. hypsipedos*. These datasets were created from coordinates calculated in the GPA. We checked the coordinates of *C. herteri* and another for *C. hypsipedos* correctly and incorrectly assigned to each of the groups of train dataset through confusion matrices.

Traditional morphometric analyses sampling

Characters to be measured for *C. phalaroides* gr. initially followed the review of *Carex* in Rio Grande do Sul (Hoff-Silveira and Longhi-Wagner, 2012) with slight modifications according to our own observations. The different structures to be measured were selected from the middle zone of each organ, aiming for

homogeneity within the data and to facilitate the comparison between individuals, with the following exceptions (1) the bracts, in which we selected the upper spike bract and the lower spike bract and (2) the length and width of the leaves, for which the longest and the widest leaves of each individual were selected, respectively. A list of 38 potentially diagnostic characters was established, although exploratory PCA analyses retrieved that only 24 characters were diagnostic. Our final dataset was constituted by 24 morphological characters measured on 56 individuals (Suppl. material 3).

Sampling of sect. *Abditispicae* relied on literature data in order to take into account the entire variation span known for each taxon (Suppl. material 3) after contrasting that our own measurements fell within the reported variation intervals.

Principal component analysis

Principal component analysis was carried out on Rstudio v. 1.4.1717 (R Core Team 2022) using 11 morphological variables: two vegetative characters and the rest reproductive-related characters (Table 1) as these were the only characters available for every taxa. For every character in all the considered taxa of sect. *Abditispicae* we included three independent data as detailed on the corresponding taxonomic description (Suppl. material 3): maximum, minimum and the mean. This way we ensured the consideration of the maximum possible span of each species within the morphospace.

Mean comparatives and non-parametric tests

The significance of those characters that allowed the best separation of each of the two morphogroups (*C. phalaroides* gr. and sect. *Abditispicae*; see results) was evaluated by non-parametric Kruskal–Wallis test with Rstudio v. 1.4.1717 (R Core Team 2022). After discarding that the dataset had a normal distribution, we employed Kruskal–Wallis test as a non-parametric alternative to ANO-

Table 1. Summary of the morphological traits analyzed in the two different PCA carried out in this study.

Morphological traits for <i>Carex</i> sect. <i>Abditispicae</i> – <i>Carex phalaroides</i> gr. PCA	
Organ	Character
Leaf	Length (mm)
Leaf	Width (mm)
Lower spike bract	Width (mm)
Inflorescence	Length (mm)
Spike	Length (mm)
Spike	Width (mm)
Scale	Length (mm)
Utricle	Length (mm)
Utricle	Width (mm)
Achene	Length (mm)
Achene	Width (mm)

VA test. As visual support for the test, we performed violin graphic plots to present the comparison between the problem species and the morphogroups we tested them against.

Results

Geometric morphometrics analyses

Procrustes analyses performed for the different datasets recovered the consensus utricles configurations and deviations for every landmark and semi-landmark coordinate (Suppl. material 2: fig. S3). The low utricles shape affinities of the two tested groups were compared and shown at Suppl. material 2: fig. S4. Subsequently, MANOVA results show shape variation is significantly different between the two considered groups (Table 2A) denoting that these are well delimited and can be successfully differentiated using the proposed configuration of landmarks and semilandmarks. For the PCA of the complete dataset, the first three principal components accumulated up to 81.2% of the variance (54.3%, 17%, 10%). PCA scatter-plot for the complete dataset displays the position of the problematic species, *C. herteri* and *C. hypsipedos*, within the morphospace (Fig. 4), illustrating a higher proximity to the sect. *Abditispicae* cluster than to *C. phalaroides* gr one. In the case of *C. herteri*, its affinity was much clearer than for *C. hypsipedos*. LDA model only obtained one linear discriminant and prior probabilities for the main groups were 0.347 for sect. *Abditispicae* and 0.653 for *C. phalaroides* gr. The model obtained a 0.959 of accuracy meaning 95.9% of samples were correctly classified (Table 2 B), only four coordinate samples were misclassified. When testing *C. herteri* dataset in the trained model, both of its coordinates were placed within sect. *Abditispicae* with an accuracy = 1, while *C. hypsipedos* shape information was not clearly positioned in either of the two groups, so the accuracy of the model in this case was only 0.5. Visually, the four graphs comparing the consensus configurations of the sect. *Abditispicae* GM and *C. phalaroides* gr. GM datasets with the problematic species shapes (Fig. 5) assist the results

Table 2. Results of GM statistical analyses.

A) MANOVA test summary table							
	d.f.	Sum Sq	Mean Sq	R Sq	F value	Z	Pr(>F)
Groups	1	0.26965	0.269650	0.46926	41.555	4.8696	9.999e-05
Residuals	47	0.30498	0.006489	0.53074	–	–	–
Total	48	0.57463	–	–	–	–	–
B) Summary of linear discriminant analyses results showing confusion matrices of predicted classes of test dataset within train dataset and its accuracy							
Confusion matrix train dataset	Sect. <i>Abditispicae</i>	<i>C. phalaroides</i> gr	Confusion matrix test dataset	New data			
			Predicted	<i>C. herteri</i>	<i>C. hypsipedos</i>		
Sect. <i>Abditispicae</i>	31	1	Sect. <i>Abditispicae</i>	2	1		
<i>C. phalaroides</i> gr	3	63	<i>C. phalaroides</i> gr	0	1		
Accuracy	0.959		Accuracy	1	0.5		

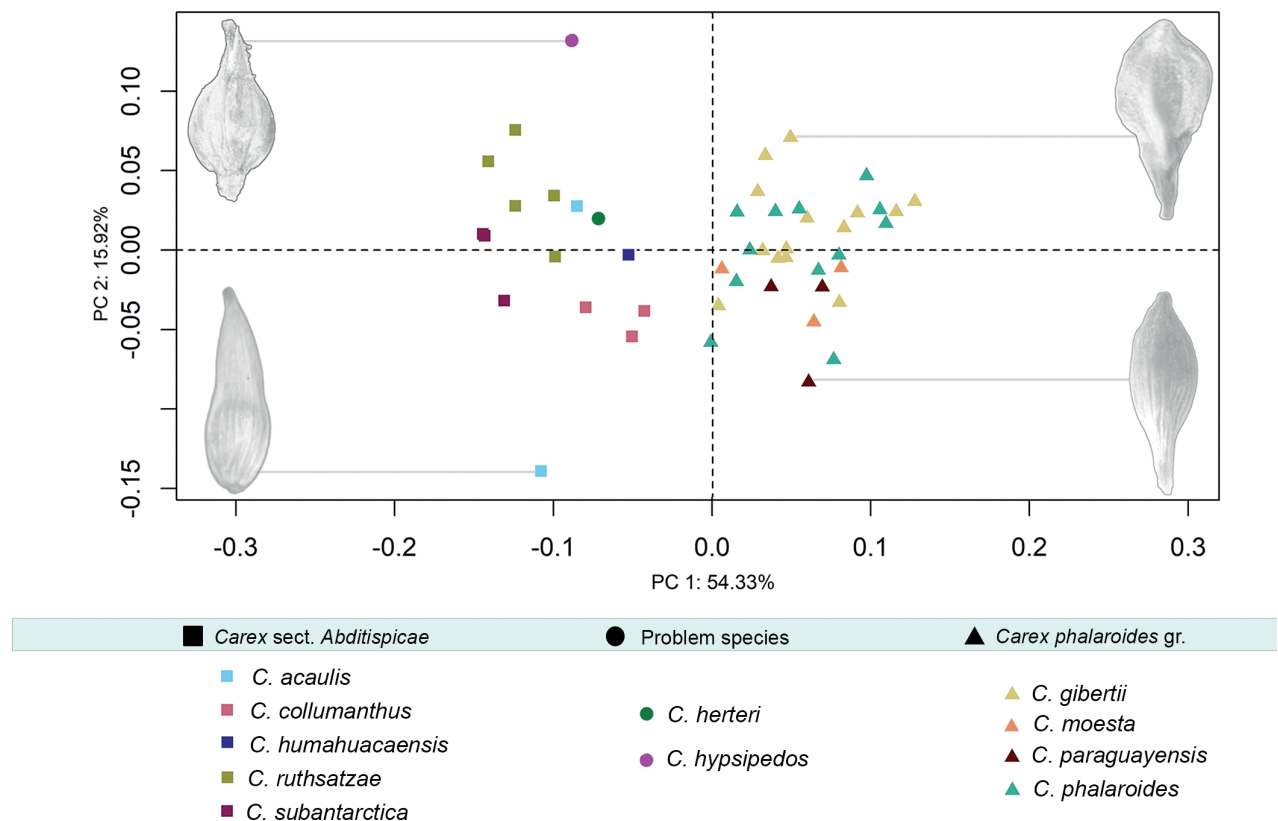


Figure 4. PCA scatter-plot of the geometric morphometric analysis excluding *Carex macrosolen*. Squares represent sect. *Abditispicae* taxa, triangles represent *C. phalaroides* gr. taxa, and circles represent *C. herteri* and *C. hypsipedos* taxa. Utricle shapes at the margins of the graph display the extreme shapes of the morphospace for a better visualization of the utricle morphological features with greater weight within the principal components.

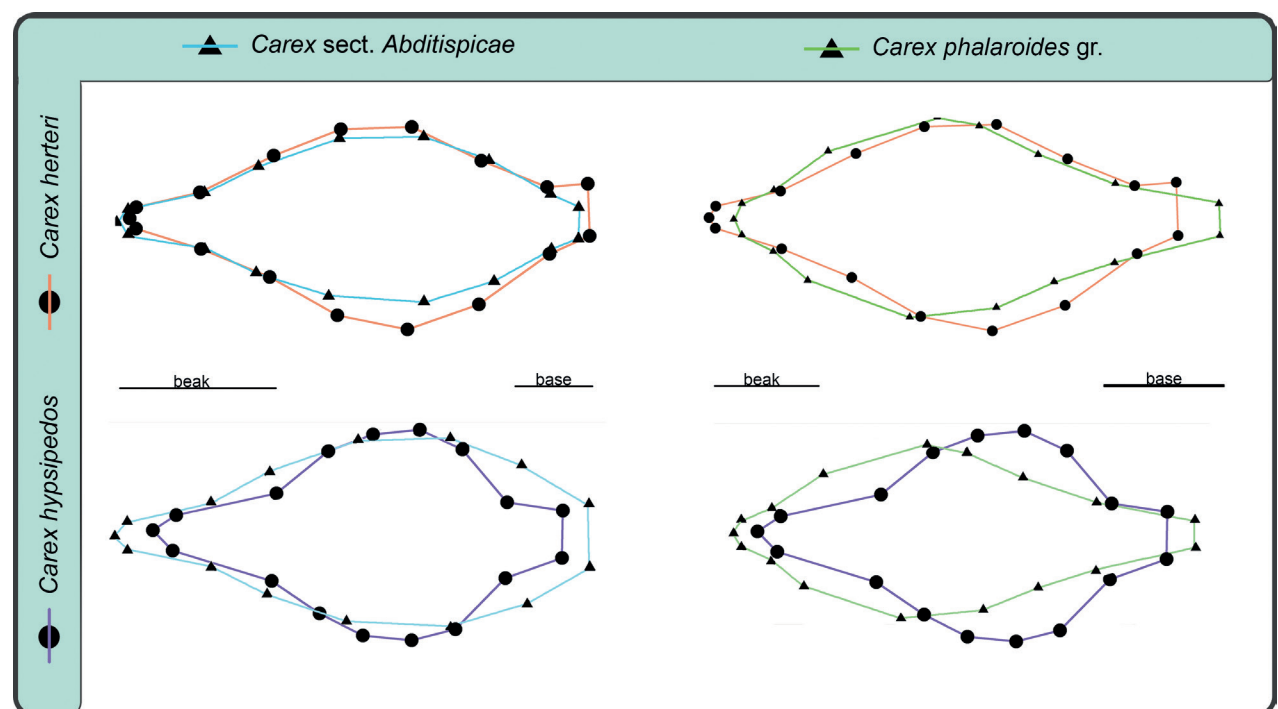


Figure 5. Comparative figures of consensus utricle shapes of both *Carex* sect. *Abditispicae* (triangles and blue line) and *C. phalaroides* gr. (triangles and green line) with *C. herteri* (circles and orange line) and *C. hypsipedos* (circles and purple line).

revealed by PCA and DFA analyses of higher shape affinity of *C. herteri* with sect. *Abditispicae* than with *C. phalaroides* gr., while shape resemblance of *C. hypsipedos* remained uncertain.

Traditional morphometric analyses

PCA performed to assess *C. herteri* and *C. hypsipedos* proximity to major groups included all the available morphological characters (Table 1), since these already allowed the best separations of morphogroups. We only retained principal components with eigenvalues >1. The first two principal components accumulated the 65.9% of the variance and the 75.5% on the first three: PC1 43.1%; PC2 22.8%; PC3 9.7%. PCA values for every character are shown at Table 3. PCA scatter-plot PC1–PC2 (Fig. 6) revealed the existence of two separated clusters,

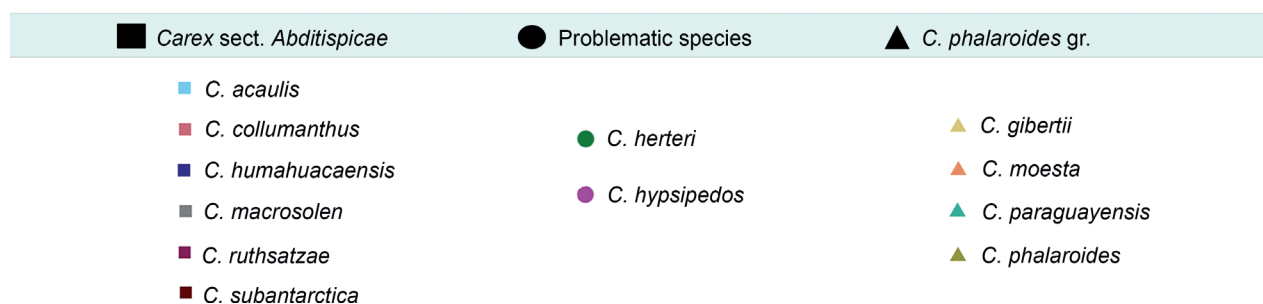
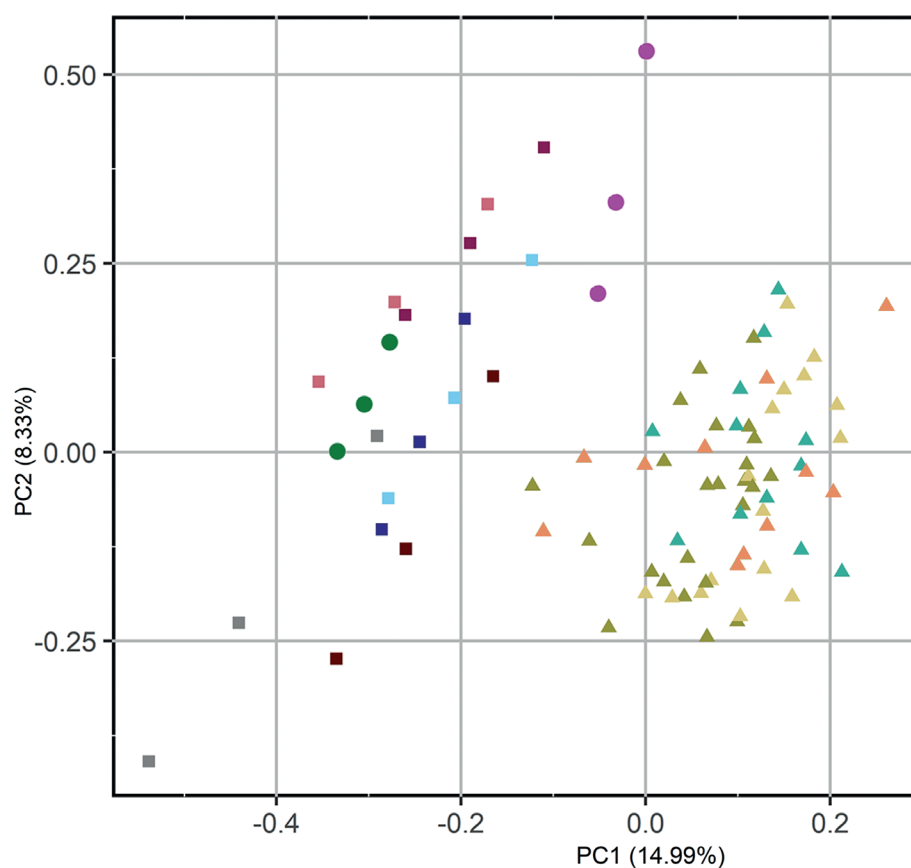


Figure 6. PCA scatter-plot of the traditional morphometric analysis. Squares represents sect. *Abditispicae* taxa, circles represent *C. herteri* and *C. hypsipedos*, and triangles represents *C. phalaroides* gr. taxa.

Table 3. PCA and non-parametric tests results. First two principal component values resulting from the PCA performed for the traditional morphometric study. The *p*-values from the Kruskal-Wallis test are also indicated (* indicate significant results).

Morphological traits	PC1	PC2	Kruskal-Wallis test
Leaf length (cm)	0.370981181	-0.30144017	3.513e-11***
Leaf width (mm)	0.128838175	-0.44318792	0.3196
Lower spike bract width (mm)	0.081672924	-0.46994517	0.01402*
Inflorescence length (cm)	0.29404183	-0.36809907	6.513e-11***
Spike length (cm)	0.338174775	-0.33235128	7.273e-10***
Spike width (mm)	0.006355108	-0.3702008	0.0221*
Scale length (mm)	-0.22673691	-0.18833859	0.4813
Utricle length (mm)	-0.37000759	-0.18041262	1.987e-09***
Utricle width (mm)	-0.3915743	-0.04835903	4.062e-09***
Achene length (mm)	-0.38158338	-0.12137059	2.935e-08***
Achene width (mm)	-0.38857237	-0.15419903	1.218e-07***

one for sect. *Abditispicae* and another for *C. phalaroides* gr. The problematic species were placed close to the first one, indicating morphological similarities for the analyzed characters. The morphological characters which contributed the most to the first principal components were leaf length, utricle length and width and achene length and width, while to the second component important characters were the lower spike bract width, leaf width, spike width and inflorescence length (Table 3). For the Kruskal–Wallis test, eight of the eleven analyzed characters obtained a significant *p*-value < 0.05 (Table 3). Only two of them were vegetative characters (leaf and lower spike bract lengths) while the remaining were reproductive-related characters. Most significant *p*-values were scored by leaf length (3.513e-11), utricle width (4.062e-09), utricle length (1.987e-09), achene length (2.935e-08) and achene width (1.218e-07). Violin plots at Fig. 7 illustrate the distribution differences of the measurement dataset supporting the use of non-parametric tests to assess mean differences between groups.

Discussion

Novel data shed light on the systematic affinities of the two problematic species

Dwarf species *Carex herteri* and *C. hypsipedos* were assigned to *C. phalaroides* gr. by Wheeler (1996) and Poindexter et al. (2017) respectively. This designation was based on morphological affinities not tested under statistical approaches. Given the morphological complexity of the group, its adscription was in need of a revision. *Carex* sect. *Abditispicae* was a major candidate to incorporate these species as these concur on distribution and morphological characteristics (Wheeler 1987, 1989, 2002).

Our GM, DFA and traditional morphometrics results reveal a high statistical support and a close utricle shape resemblance among sect. *Abditispicae* and *C. herteri* for all the analyses performed (Figs 2–4), therefore this species may be better considered as part of this section based on its morphological features.

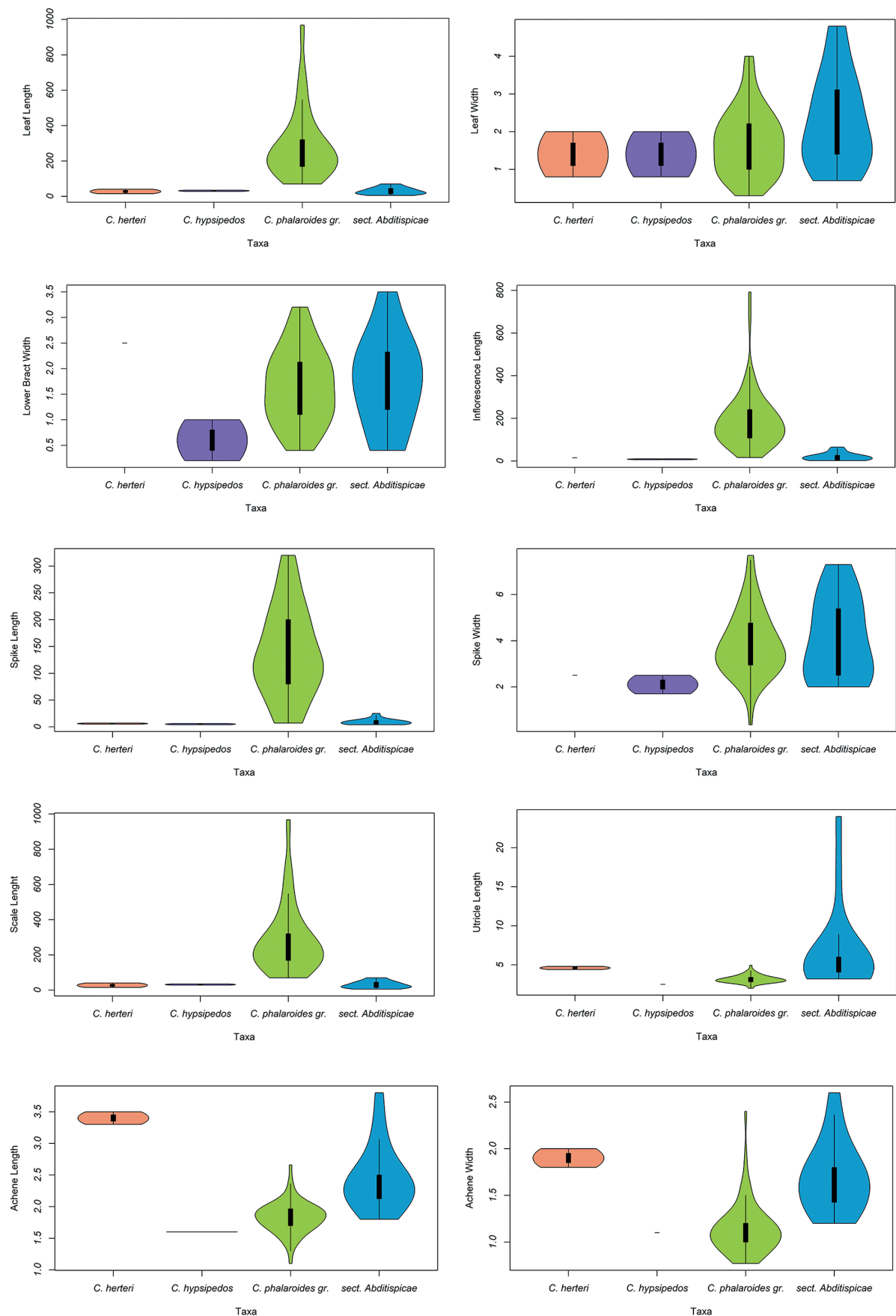


Figure 7. Violin plots; Violin plots illustrating distribution and mean differences for the analyzed characters with traditional morphometrics for the problematic species, *C. phalaroides* gr. and sect. *Abditispicae*.

Contrastingly, *C. hypsipedos* does not display evident statistical affinities, or shape resemblance with either sect. *Abditispicae* or *C. phalaroides* gr. so its affiliation persists unsolved, though it can be excluded as a member of the *C. phalaroides* gr.

Nevertheless, it would be desirable confirmation from procedures such as DNA barcode for two main reasons: (1) The frequent morphological homoplasy that affects the delimitation of infrageneric units within the genus (Jiménez-Mejías et al. 2016a), exacerbated in this particular case by the extreme reduction of such plants (dwarfism, see Jiménez-Mejías et al. 2021), that might further confound their morphological affinities; and (2) The extremely low sampling size of the problematic species (known only from their type collections), thus perhaps no representative of the entire species variation. Ripe utricle morphology is usually fairly constant, as supported by its recurrent use in identification keys (e.g. see keys in Egorova 1999 or Ball and Reznicek 2002). However, variation in utricle size, and also moderately in shape, is also known in *Carex* (Jiménez-Mejías et al. 2017, 2018). Accordingly, we cannot entirely rule out that the included problematic taxa samples were outliers and so could be somehow biasing the inferred affinities of the two problematic taxa, although it would be certainly unexpected because of the consistency in shape variation within each of the detected groups. Dwarfism, acaulescency, and character reduction should be considered the principal cause of the deficiency of herbarium collections and the absence of field citations of these two problematic species, due to their inconspicuousness. Due to the impossibility of performing a destructive sampling on the already poor type collections from which *C. herteri* and *C. hypsipedos* were described, the knowledge of these two taxa would benefit from a focused fieldwork sampling.

The adscription of *C. herteri* to sect. *Abditispicae* would imply an area extension of a thousand km from the Patagonian steppes and high mountainous Andean habitats of the section to the Uruguayan Pampa. This, in turn, implies a much wider ecology for the group, from the cold-dry steppes and high-altitude habitats of the known species to the warm dryness of the pampa. As a common factor, *Carex* sect. *Abditispicae* ecology seems to be linked to stressful environments and may behave as pioneers in colonization processes.

Utility of geometric morphometrics in testing systematic affinities in graminoids

Our approach using GM has assessed fruit shape variation in a non-qualitative way, as it is commonly studied on traditional morphometrics (Chen et al. 2018). Some examples of systematic and taxonomic implications derived from GM have been previously done in Liu et al. (2018) with Chinese oaks leaves, Terral et al. (2012) with the seeds of *Phoenix* genera species, or Van der Niet et al. (2010) assessing flower shape variation. These studies agreed in the application of GM as a useful approach for providing detailed information on the morphological variation of the plant structures with taxonomic value. In addition, research on plant organ shapes and its relationship with other organisms or environmental factors might shed additional light on other fields such biogeography, ecology, and genetics, as we also do when we assign *C. herteri* to sect. *Abditispicae*.

Our study supports the utility of GM on testing systematic affinities in species with graminoid morphology, particularly for Cyperaceae. To this end we used

carpological characters, which have been often ignored in sedges, despite the useful characters for group delimitation residing in such organs (Jiménez-Mejías and Martinetto 2013). Successful differentiation between and within complicated groups such as sect. *Abditispicae* and *C. phalaroides* employing utricle shape sets a landmark for future taxonomic studies in a genus where its general morphology is typically affected by homoplastic processes.

Conclusions

Utricle shape variation along with other morphological features analyzed with GM and traditional morphometric approaches, respectively, support the exclusion of these two species from their traditionally affiliated group (*C. phalaroides* gr.). Moreover, *C. herteri* show clear affinities to sect. *Abditispicae* for both approaches. Besides, *C. hypsipedos* remains an *incertae sedis* species as it did not show affinities with any of these groups, thus further studies are needed for these taxa. Additionally, we employ for the first time geometric morphometrics tools and show its potential utility to approach the systematic affinities of taxonomically problematic sedge species.

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Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

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Author contributions

A. M.-A., T.V., P. J.-M. contributed to study conceptualization. Data preparation was carried out by A. M.-A., P. J.-M. Morphological study was carried out by A. M.-A. Analyses were carried out by A. M.-A. First manuscript draft was written by A. M.-A., P. J.-M. All authors contributed to the following and final version writing, review and editing. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

Ana Morales-Alonso  <https://orcid.org/0000-0003-1497-1070>

Tamara Villaverde  <https://orcid.org/0000-0002-9236-8616>

Pedro Jiménez-Mejías  <https://orcid.org/0000-0003-2815-4477>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

GM material

Authors: Ana Morales-Alonso, Tamara Villaverde, Pedro Jiménez-Mejías

Data type: Excel spreadsheet

Explanation note: Material used in this work for the utricle images. Taxon, botanical country (Brummitt 2001), locality, collection information (herbarium or collector code) and number of utricles is provided for each sample.

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Link: <https://doi.org/10.3897/phytokeys.232.100410.suppl1>

Supplementary material 2

Utricle slide with landmarks; PCA plot with *C. macrosolen*; Consensus configurations; Group comparison

Authors: Ana Morales-Alonso, Tamara Villaverde, Pedro Jiménez-Mejías

Data type: PDF file; fig. S1–S4

Explanation note: Representation of landmark placement within the utricle. Green dots represent landmarks and blue dots semi-landmarks. From the top to the bottom, left to right. A) Problematic species: *Carex herteri* (Herter, W.G.F., 19091, S), *C. hysipedos* (Weberbauer 2617, G). B) *C. phalaroides* gr.: *C. gibertii* Arechavaleta s.n.US), *C. paraguayensis* (L. Pereira-Silva 350, FLOR) and *C. phalaroides* (G. Rodríguez-Palacios 23GERP15, UPOS). C) *C. sect. Abditispicae*: *C. acaulis* (DM Moore 1240, K), *C. columanthus* (PJ Grubb 339, K), *C. humahuacaensis* (S. Martín-Bravo et al. 178SMB21, UPOS), *C. ruthsatzae* (G. Rodríguez-Palacios 46GERP15, UPOS), *C. subantarctica* (Marcia Waterway MW2015.020, UPOS) and *Carex macrosolen* (S. Martín-Bravo et al., 11SMB10, UPOS) utricle was finally excluded from the analysis as it induced a strong bias. Scale bar of 4mm. PCA scatter-plot of the geometric morphometric analysis including *C. macrosolen*. Squares represents sect. *Abditispicae* taxa, triangles represent *C. phalaroides* gr. taxa, and circles represent *C. herteri* and *C. hysipedos* according to the figures legend. Utricles shapes at the margins of the graph display the extreme shapes of the morphospace for a better visualization of the utricle morphological features with greater weight within the principal components. Comparative figure of consensus configurations between datasets: A) representing the utricle consensus configuration (black dots and grey line) and deviations from it (orange dots) for the complete dataset. B) representing the utricle consensus configuration (black dots and blue line) and deviations from it (blue dots) for the sect. *Abditispicae* dataset. C) representing the utricle consensus configuration (black dots and green line) and deviations from it (green dots) for the *C. phalaroides* gr. dataset. Comparative figure for the consensus utricle configuration of *C. phalaroides* gr. (green triangles) with sect. *Abditispicae* (blue dots).

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Link: <https://doi.org/10.3897/phytokeys.232.100410.sup12>

Supplementary material 3

Traditional morphometrics material

Authors: Ana Morales-Alonso, Tamara Villaverde, Pedro Jiménez-Mejías

Data type: Excel spreadsheet

Explanation note: Material used in this work for traditional morphometric analyses. A: measured specimens of *C. phalaroides* gr. Taxa are indicated, the botanical country (Brummitt 2001), the locality and an identification code (herbarium or collector code); B: list the taxonomic treatments from where the representative measurements of sect. *Abditispicae* species were taken.

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A taxonomic synopsis of Heliotropiaceae and new combinations in *Heliotropium* from Thailand

Kanokorn Rueangsawang¹, Pranom Chantaranothai^{2,3}

¹ Department of Biology, Faculty of Science, Ramkhamhaeng University, Bangkok 10240, Thailand

² Applied Taxonomic Research Center, Department of Biology, Faculty of Science, Khon Kaen University, Khon Kaen 40002, Thailand

³ Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

Corresponding author: Pranom Chantaranothai (pranom@kku.ac.th)

Abstract

A synopsis of Heliotropiaceae in Thailand is presented and, as part of this, the taxonomic history, identification keys, distribution maps, herbarium specimen citations and diagnostic characters are provided. Two genera and 12 species are recognised and four new combinations are proposed of *Tournefortia* under the genus *Heliotropium*, namely *H. hookeri*, *H. intonsum*, *H. montanum* and *H. ovatum*. Two species are newly recorded in Thailand: *Euploca ovalifolia* and *H. hookeri*. The neotype and lectotype are designated here for *Tournefortia montana* and *T. boniana*, respectively.

Key words: *Euploca*, *Heliotropium*, morphology, Thai flora, typification

Introduction

Heliotropiaceae (= Boraginaceae s.l., subfamily Heliotropioideae) comprises ca. 450 species in four genera: *Heliotropium* L. (incl. *Tournefortia* L.), *Euploca* Nutt., *Myriopus* Small. and *Ixorhea* Fenzl (Diane et al. 2016; Luebert et al. 2016) and is widely distributed in the tropical, subtropical and temperate zones, with the centre of diversity in the Neotropics (Mabberley 2017). In the previous classification, based on morphology and anatomy, Förther (1998) recognised eight genera: *Argusia* Boehm., *Ceballosia* Kunkel, *Heliotropium*, *Hilgeria* Förther, *Ixorhea*, *Nogalia* Verdc., *Schleidenia* Endl. and *Tournefortia*. The distinct features of the family are based on scorpioid cymes and flowers with a terminal style, undivided, terminal with a conical stigmatic head having a basal ring-shaped stigma (Diane et al. 2016; Luebert et al. 2016). Molecular phylogenetic analyses of Heliotropiaceae, based on *trnL*UAA and ITS1 sequence data, have shown that *Heliotropium* and *Tournefortia* are not monophyletic (Diane et al. 2002; Hilger and Diane 2003). Based on a result of Hilger and Diane (2003), *Tournefortia* sect. *Tournefortia* is nested within *Heliotropium* s.s. which is a sister group to *Heliotropium* l clade and the group has a drupaceous fruit. The species of *Heliotropium* sect. *Orthostachys*, *Hilgeria* and *Schleidenia* are within the *Euploca* clade. This relationship is also supported by morphological features, for example, the presence of bracts at the inflorescences and fruit breaking up



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into four distinct nutlets (Feuillet 2016). According to Hilger and Diane (2003), the molecular and morphological data suggest that a re-arrangement of the current classification is required. More new combinations of *Euploca* and *Heliotropium* have been made (e.g. Craven (2005); Melo and Semir (2009); Luebert et al. (2011); Feuillet (2016); Melo (2017); Frohlich et al. (2020); Antony and Javad (2020)).

In Southeast (SE) Asia, the contributions to the knowledge of *Tournefortia* and *Heliotropium* remain controversial. Many traditional *Tournefortia* species were recognised by Gagnepain and Courchet (1914), Ridley (1923), Johnston (1935), Backer and Bakhuizen van den Brink Jr (1965), Zhu et al. (1995) and Riedl (1997). Fletcher and Kerr (1951) reported the first checklist of the Heliotropiaceae species in the *Florae Siamensis Enumeratio*. The present study aims to: 1) provide a synoptic account of Heliotropiaceae for the Flora of Thailand, 2) present an identification key for species recognition and 3) propose new combinations of *Tournefortia* into *Heliotropium*.

Materials and methods

Extensive collections of herbarium specimens at AAU, ABD, BK, BKF, BM, C, CMU, CMUB, E, K, K-W, KKU, L, QBG and SING (abbreviations follow Thiers 2022, continuously updated) were studied together with living material observations in the field. Species delimitation was based on the examination of original publications including the relevant literature: Clarke (1885); Gagnepain and Courchet (1914); Ridley (1923); Johnston (1935, 1951); Backer and Bakhuizen van den Brink Jr (1965); Zhu et al. (1995); Riedl (1997); Mill (1999). The type collections were observed online in JSTOR Global Plants (<https://plants.jstor.org/>). Most measurements were taken from dried specimens and spirit-preserved material and colour descriptions were studied from living material. Distribution, ecology and flowering and fruiting data were derived from specimen labels. All specimens were imported into SimpleMappr (Shorthouse 2010) to create distribution maps. All collections cited that have been seen by the authors are marked with '!' and those seen as digital images are indicated with 'image'.

The molecular data and morphological species concept (Hilger and Diane 2003; Diane et al. 2016; Luebert et al. 2016) were used in the present study. This concept is consistent with that of previous studies (i.e. de Candolle (1845); Gagnepain and Courchet (1914); Johnston (1935, 1951); Fletcher and Kerr (1951); Förther (1998)). Particular morphological features that were employed to delimit species in *Euploca* species are: stem position and branching, the presence of bracts in the inflorescence, cyme type and floral and fruit structure. For *Heliotropium*, features used include: habit, the presence of bracts in the inflorescence, cyme type and floral and fruit structures. For the generic circumscription, both morphological and molecular data are considered (Diane et al. 2002; Hilger and Diane 2003; Luebert et al. 2016). Morphologically, *Euploca* is separated from *Heliotropium* due to the bracteate inflorescence and fruit breaking up into four distinct nutlets. The terminology used in this present study is adapted from Weberling (1992) and Beentje (2012).

Taxonomic treatment

Heliotropiaceae Schrad., *Commentat. Soc. Regiae Sci. Gött. Recent.* 4: 192. 1819, nom. cons.

Type genus. *Heliotropium* L.

Description. Annual or perennial herbs, climbing shrubs or small trees. Leaves simple, alternate, exstipulate, petiolate or sessile; lamina linear to ovate, apex acute to acuminate, margin entire or revolute. Inflorescences terminal or axillary, spike-like, scorpioid, subcapitate or subcorymbose cymes; with or without bracts. Flowers 5-merous, rarely 4-merous, bisexual, actinomorphic. Calyx 5-lobed, divided almost to the base, lobes linear to ovate, entire, persistent. Corolla white to pinkish-white, purple, pale green or greenish to yellowish, campanulate to funnel-shaped, lobes orbicular. Stamens 5, filaments adnate to the corolla tube. Pistil ovary superior, bicarpellate, usually 4-loculate, 1 ovule per locule, nectar disc at the base surrounds the ovary; style terminal, with a conical stigma structure forming a basal ring around style. Fruit dry or fleshy, separating into four 1-seeded nutlets or two 2-seeded nutlets. Seeds straight or curved, with endosperm.

Two genera and 12 species are found in Thailand.

Key to the genera of Heliotropiaceae in Thailand

- 1 Inflorescence bracteate; fruit separating into four nutlets ***Euploca***
- Inflorescence ebracteate; fruit separating into two nutlets ***Heliotropium***

***Euploca* Nutt., Trans. Amer. Philos. Soc., ser. 2, 5: 189. 1836.**

Heliotropium [unranked] *Orthostachys* R.Br., *Prodr. Fl. Nov. Holland.*: 493. 1810.

Type species: *Heliotropium foliatum* R.Br.

Preslaea Mart., *Nov. Gen. Sp. Pl.* 2: 75. 1827, nom. illeg.

Heliotropium sect. *Orthostachys* (R.Br.) G.Don, *Gen. Syst.* 4: 361. 1838. Type species: Based on *Heliotropium* [unranked] *Orthostachys* R.Br.

Schleidenia Endl., *Gen. Pl.*: 646. 1839. Type species: *Preslaea paradoxa* Mart.

Orthostachys (R.Br.) Spach, *Hist. Nat. Vég.* 9: 32. 1840. Type species: Based on *Heliotropium* [unranked] *Orthostachys* R.Br.

Hilgeria Förther, *Sendtnera* 5: 132. 1998. Type species: *Hilgeria hypogaea* (Urb. & Ekman) Förther.

Type species. *Euploca convolvulacea* Nutt.

Description. Annual herbs. Leaves petiolate or sessile; lamina linear to ovate, apex acute to obtuse, margin entire or revolute, pubescent to strigose or silky silver hairs on both surfaces. Inflorescences terminal or axillary, spike-like, scorpioid or subcapitate cymes, bracteate. Flowers 5-merous. Calyx 5-lobed, lobes linear to lanceolate. Corolla white with a yellow-orange throat inside, tubular or funnel-shaped, lobes orbicular to oblong, throat pubescent inside. Stamens included, sessile or with short filaments; anthers, elliptic-oblong. Ovary divided into 4 lobes. Fruits separating into four 1-seeded nutlets.

Key to the species of *Euploca*

- 1 Inflorescence spike-like or scorpioid cymes 2
- Inflorescence subcapitate cymes 4
- 2 Leaves elliptic to obovate or oblanceolate; cymes 2-rowed scorpioid 3. *E. ovalifolia*
- Leaves linear to narrowly elliptic; cymes unilateral or spike-like 3
- 3 Prostrate much-branched stem; leaves narrowly elliptic with strigose hairs 5. *E. strigosa*
- Erect unbranched to few-branched stem; leaves linear with greyish tomentose hairs 4. *E. paniculata*
- 4 Leaves elliptic with white pubescent hairs 1. *E. bracteata*
- Leaves narrowly lanceolate with stiff bristly white hairs 2. *E. marifolia*

1. *Euploca bracteata* (R.Br.) M.W.Frohl. & M.W.Chase, *Phytotaxa* 434(1): 15. 2020.

Fig. 2A

Heliotropium bracteatum R.Br., Prodr. Fl. Nov. Holland.: 493. 1810. Type: Australia, Northern Territory, Groote Eylandt, 15 Jan 1803, *Brown* 2926 (lectotype, designated by Craven 1996, p. 628: BM [BM001040580!]; isoelectotypes: K [K000998271!, K000998272!]).

Heliotropium marifolium var. *bracteatum* (R.Br.) M.R.Almeida, Fl. Maharashtra 3A: 287. 2001.

Heliotropium bracteatum var. *leptostachyum* Benth., Fl. Austral. 4: 451. 1869. Type: Australia, Cape York, *Daemel* s.n. (holotype K [K000998274!]; isotype BM [BM001040578!]).

Type. Based on *Heliotropium bracteatum* R.Br.

Distribution. Pakistan, India, Sri Lanka, Myanmar, China (Hainan, Kwangtung), Laos, Cambodia, Vietnam, Thailand (Fig. 1A), Malaysia, Java, Australia.

Ecology. Open areas in deciduous forest, dry secondary forest; 50–300 m alt., flowering and fruiting from February to October.

Specimens examined. Thailand, Northern: Nakhon Sawan, 10 km north-west of Nakhon Sawan, 150 m alt., 21 July 1973, *Murata et al.* T-16587 (BKF, L). South-western: Uthai Thani, Tapoh, 4 Jan 1962, *Larsen* 9135 (C, K); Kanchanaburi, Sai Yok, 15 Aug 1967; Khao Pu Maklai, Nong Hoi, 10 July 1978, *Phengklai et al.* 4247 (BKF, K); *ibid.*, 40 m alt., 8 July 1922, *Marcen* 889 (BM, K); Khao Tok, 50 m alt., 13 July 1930, *Kerr* 19547 (BM, BK, K, E); *ibid.*, 50 m alt., 10 July 1930, *Kerr* s.n. (K); Wangpho, 15 Oct 1967, *Chersmsirivathana* 790 (BK). Central: Lop Buri, Lam Narai, 13 Nov 1975, *Smitinand* 12108 (BKF); *ibid.*, 22 Aug 1975, *Boonkurd* 272 (BK); Saraburi, Phraphutthabat, 18 Sept 2004, *Pooma et al.* 4798 (BKF); Phu Khae, 100 m alt., 26 June 1947, *Bunpheng* 147 (BKF, K); Mae Nam Sak, 40 m alt., 29 May 1923, *Kerr* 7020 (BK, K); South-eastern: Sa Kaeo, Aranyaprathet, 9 Apr 1930, *Kerr* 19593 (ABD, BM, BK, BKF, E, K, L); *ibid.*, 20 Oct 1828, *Put* 2073 (BK, BM). Peninsular: Trang, Palian, 20 m alt., 26 May 1976, *Smitinand* 12229 (BKF).

Diagnostic characters. *Euploca bracteata* is suberect, with sparsely white pubescent hairs on both leaf surfaces, subcapitate cyme inflorescence at the end

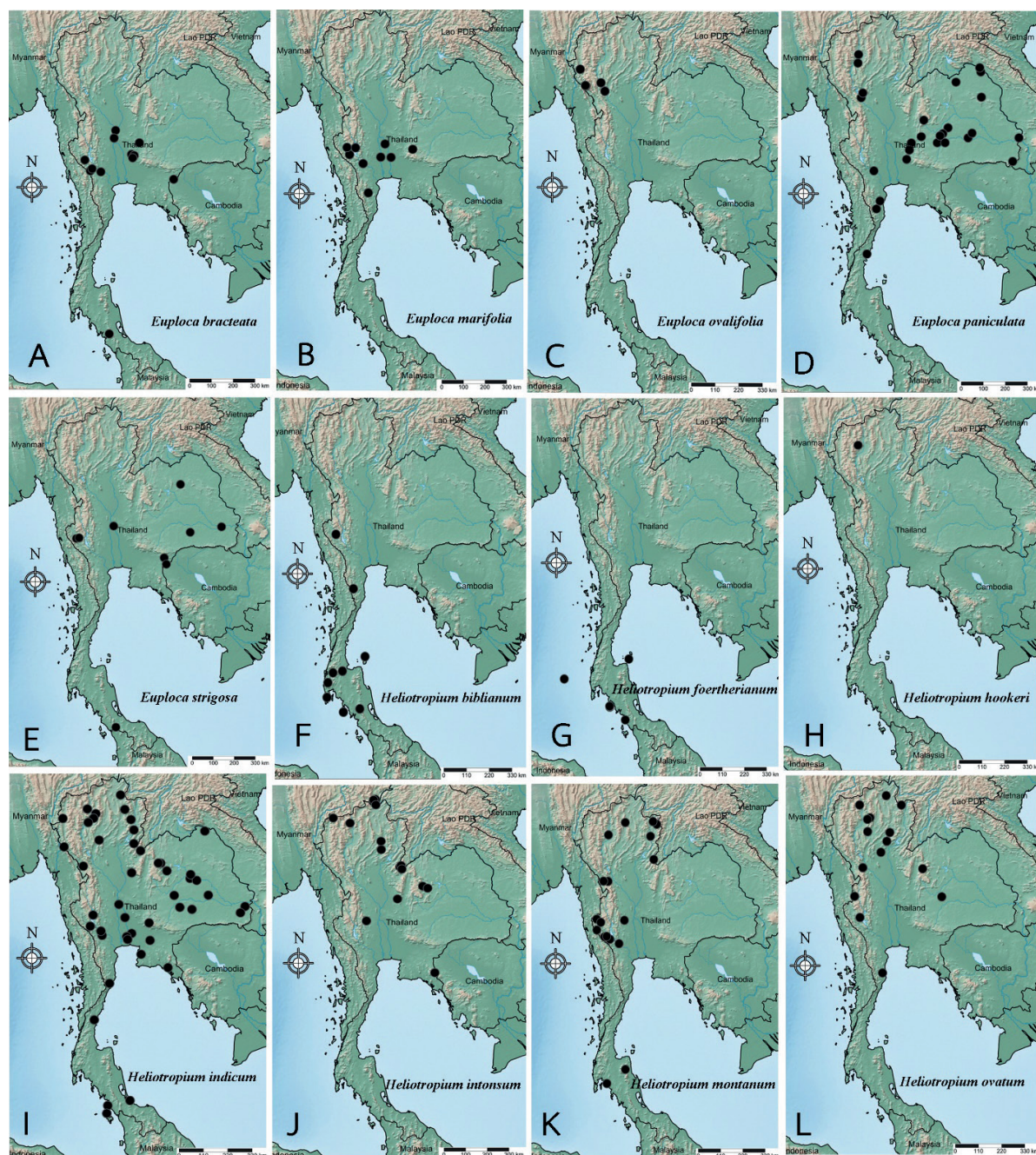


Figure 1. Distribution of Heliotropiaceae from Thailand, based on the specimens examined.

of branches and sessile flower or with pedicels up to 1 mm long. This species is similar to *E. marifolia*, sharing a similar habit, flowers and inflorescence form, but differs in having elliptic leaves (vs. linear to lanceolate leaves in *E. marifolia*).

2. *Euploca marifolia* (J.Köenig ex Retz.) Ancy & P.Javad, Nord. J. Bot. 38(11): 2. 2020.

Fig. 2B

Heliotropium marifolium J.Köenig ex Retz., Observ. Bot. 2: 8. 1781. Type: Asia, 1781, Köenig 7052 (holotype LD [LD1748458 image!]).

Heliotropium scabrum Retz., *Observ. Bot.* 2: 8. 1781. Type: India, Coromandel coast, *Köenig s.n.* ([C10008736!]).

Euploca scabra (Retz.) M.W.Frohl. & M.W.Chase, *Phytotaxa* 434: 19. 2020. Type as above.

Type. Based on *Heliotropium marifolium* J.Köenig ex Retz.

Distribution. Pakistan, India, Sri Lanka, China, Cambodia, Vietnam, Thailand (Fig. 1B), Peninsular Malaysia, Java.

Ecology. In the open deciduous forest, dry secondary forest; 50–300 m alt., flowering and fruiting from January to October.

Specimens examined. Thailand, Eastern: Nakhon Ratchasima, Nong Sarai, 300 m alt., 5 Sept 1963, *Smitinand & Sleumer 8359* (K, L). South-western: Kanchanaburi, Si Sawat, 16 Nov 1917, *van Beusekom et al. 3809* (BKF, L); Sai Yok, 15 Aug 1967; Hin Lat, 50 m alt., 28 Nov 1957, *Smitinand 3875* (BKF); Khao Ai Mao, 15 Nov 1968, *Sangkhachand 1576* (BKF, K); *ibid.*, 40 m alt., 8 July 1922, *Marcant 889* (BM, K); Thong Pha Phum, 215 m alt., 6 Aug 2012, *Middleton et al. 5261* (BKF, E); Phetchaburi, Kaeng Krachan NP, 285 m alt., 11 Aug 2002, *Middleton et al. 972* (BKF, E, K). Central: Sing Buri, Mueang, 5 Jun 1880, *Put 2614* (BM, BK, K, BKF), Suphan Buri, Bang Plama, 22 Sept 1930, *Kerr s.n.* (K); Phra Nakhon Si Ayutthaya, 9 Sept 1922, *Marcant 1000* (ABD, BM, K).

Diagnostic characters. *Euploca marifolia* is characterised by being prostrate, much-branched with stiff bristly white hairs on the stems and leaves, lanceolate leaves (6–17 × 1–4 mm), revolute margin and inflorescence with leaf-like bracts.

3. *Euploca ovalifolia* (Forssk.) Diane & Hilger, *Bot. Jahrb. Syst.* 125(1): 48. 2003. Fig. 2C–E

Heliotropium ovalifolium Forssk., *Fl. Aegypt.-Arab.*: 38. 1775. Type: Yemen, Al-Hadiyah [Hadië], *Forsskål*, 299 (holotype C [C10002362!], isotype BM [BM000795522!]).

Heliotropium coromandelianum J.Köenig ex Retz., *Observ. Bot.* 2: 9. 1781. Type: India, *Köenig s.n.* (holotype C [C10008743!]; isotype BM [BM000795508!]).

Heliotropium gracile R.Br., *Prodr. Fl. Nov. Holland.*: 493. 1810.

Heliotropium ovalifolium ver. *gracile* (R.Br.) Domin, *Biblioth. Bot.* 22(89): 546. 1928. Type: Australia, Northern Territory, North Island, 19 Dec 1802, *Brown 2924* (lectotype, designated by Craven 1996, p. 559: BM [BM001040588!]; isoelectotypes: K [K000998264!, K000998263!] GH [GH00097831]).

Type. Based on *Heliotropium ovalifolium* Forssk.

Distribution. Tropical Africa, Madagascar, Arabian Peninsula, Pakistan, India, Laos, Cambodia, Vietnam, Thailand (Fig. 1C), Australia, Solomon Islands.

Ecology. Open area, sandy soil on riverbanks, rice fields, grassland, along roadsides; ca. 200 m alt., flowering and fruiting from December to May.

Specimens examined. Thailand, Northern: Lamphun, Mae Ping NP, 22 May 2019, *Thammarong et al. 673* (QBG); Tak, Tha Song Yang-Mae Sa Rieng, Moei river, 22 Mar 2006, *Pooma et al. 6220* (BKF, L); Bhumibol Dam, 200 m alt., 29 May 2008, *Pooma et al. 7073* (BKF); Ban Maesong, 23 June 2005,

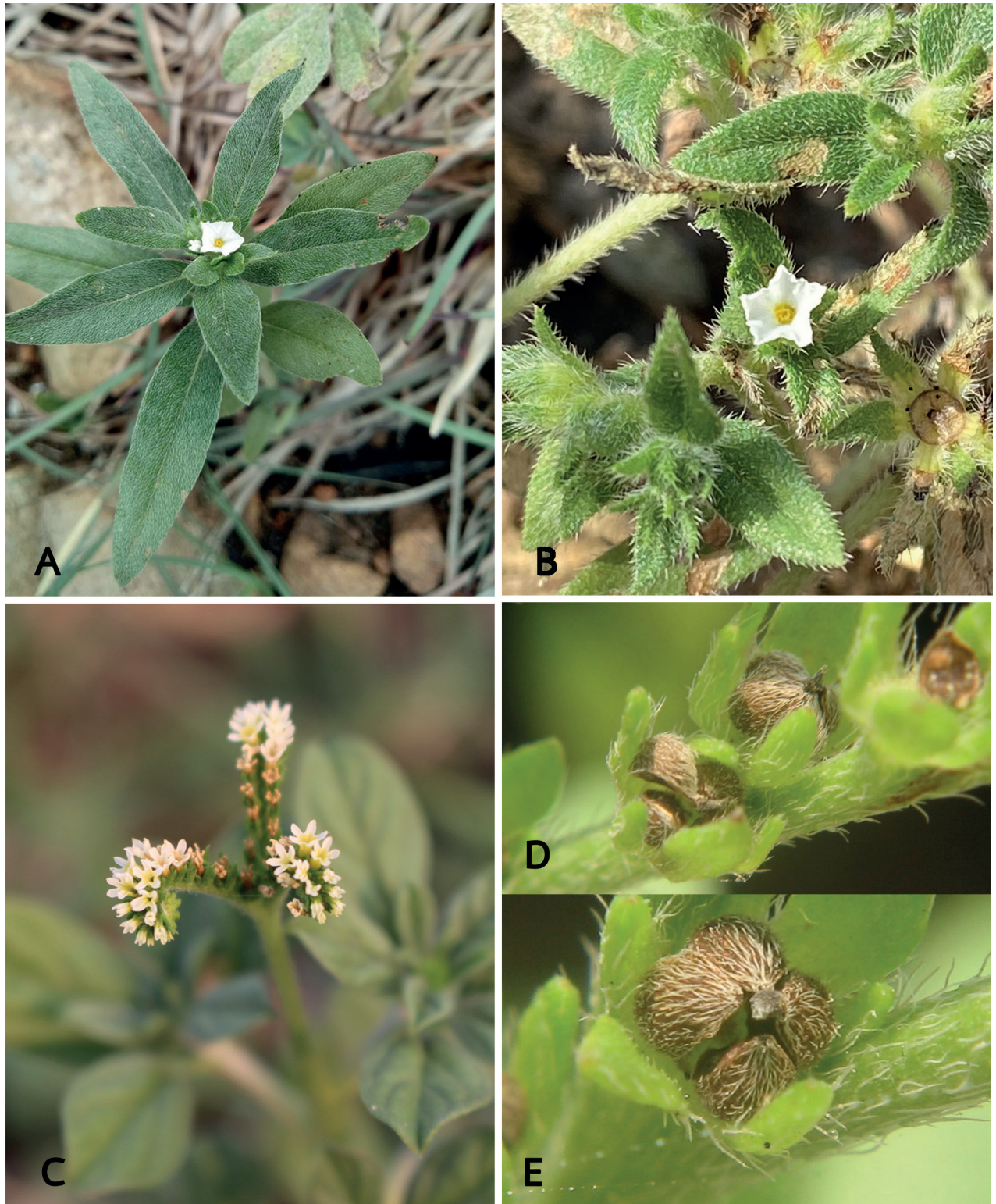


Figure 2. Species of *Euploca* from Thailand **A** *E. bracteata* (R.Br.) M.W.Frohl. & M.W.Chase **B** *E. marifolia* (J.Köenig ex Retz.) Ancy & P.Javad **C–E** *E. ovalifolia* (Forssk.) Diane & Hilger **C** inflorescence **D** dehiscent fruit separating into four nutlets **A** Photo by Pramote Triboun **C–E** Photos by Siriporn Zungsontiporn.

Pooma et al. 5443 (BKF); Mae Sa Riang-Mae Sot road, 15 May 2007, *Pooma et al.* 6786 (BKF, E).

Vernacular. Nguang chang dok khao (งวมช้างดอกขาว).

Diagnostic characters. *Euploca ovalifolia* is newly recorded for Thailand. It is recognised by elliptic to obovate or oblanceolate leaves with silky silver hairs, spike-like or scorpioid cymes inflorescence with pedicels up to 2 cm long and a white corolla with a yellowish to yellow centre. This species is similar to *Heliotropium indicum* in its inflorescence form, but differs in its leaf shape, bracteate inflorescences (vs. ebracteate in *H. indicum*) and fruit breaking up into four nutlets (vs. breaking up into two nutlets in *H. indicum*).

4. *Euploca paniculata* (R.Br.) M.W.Frohl. & M.W.Chase, Phytotaxa 434(1): 18. 2020.

Fig. 3A–C

Heliotropium paniculatum R.Br., Prodr. Fl. Nov. Holland.: 494. 1810. Type: Australia, Queensland: Sweer's Island, 28 Nov 1802, *Brown 2930* (lectotype, designated by Craven 1996, p. 561: BM [BM001040573!]; isoelectotype: K [K000998298!]).

Heliotropium tenunifolium var. *paniculatum* (R.Br.) Domin, Biblioth. Bot. 89: 549. 1928.

Heliotropium zeylanicum subsp. *paniculatum* (R.Br.) Kazmi, J. Arnold Arbor. 51: 156. 1970.

Type. Based on *Heliotropium paniculatum* R.Br.

Distribution. Pakistan, India, Myanmar, Thailand (Fig. 1D), Cambodia, Australia.

Ecology. Open area of bare rock in dry dipterocarp and dry open deciduous forests, roadsides or wheat field; 50–1,000 m alt., flowering and fruiting from June to December.

Specimens examined. Thailand, Northern: Chiang Mai, 300 m alt., 19 Jan 1914, *Kerr 3291* (BM, K); Tak, Ban Tak, 150 m alt., 1 Sept 2016, *Pooma & Pattharahirantricin 7944* (BKF); Nakhon Sawan, 31 km north, 100 m alt., 2 June 1959, *Smitinand 5815* (BKF); Ban Dong Lan, Wang Jan, Sam Ngao, 28 Aug 2010, *Norsaengsri 7030* (QBG); Lamphun, Phra Puttabat Tak Pa, 24 Aug 2010, *Norsaengsri 7205* (QBG). North-eastern: Udon Thani, Ban Phen, 24 Dec 1964, *Chermsirivathana 225* (BK); Sakon Nakhon, Phu Phan NP, 400 m alt., 6 Aug 2004, *Nielsen et al. 1542* (BKF); Bueng Kan, Ban Tong, Seka, 220 m alt., 20 May 2004, *Pooma et al. 4116* (BKF); Tham Noi waterfall, 320 m alt., 30 July 2008, *Pooma et al. 7345* (BKF); Khon Kaen, Mueang Phon, 200 m alt., 5 July 1967, *Smitinand 12385* (BKF). Eastern: Chaiyaphum, Pa Khok Yai Chiu, 190 m alt., 28 Aug 1966, *S.N. 235* (BKF); Nong Bua Deng, 400 m alt., 15 Aug 1972, *Larsen et al. 31869* (AAU, BKF, E, K); Nakhon Ratchasima, Bannot Phattana, Road 226, km 42–41, 14 Sept 2004, *Pooma et al. 4677* (AAU, BKF, E); Phimai, 200 m alt., 26 Aug 1958, *Smitinand 4783* (BKF); *ibid.*, 5 Aug 1968, *Pradit 316* (BK); Bua Yai, 200 m alt., 19 May 1931, *Kerr 20488* (ABD, BK, BKF, BM, K, L); Ban Chum Seng, 22 May 1929, *Noe 153* (BM, E, K); Surin, Chumphon Buri, 8 June 1982, *Paisooksantivatana & Sutheesorn y 913–82* (BK); Roi Et, Kaset Wisai, 150 m alt., 22 June 1969, *Smitinand & Nalamphun 10719* (BKF); *ibid.*, 9 June 1982, *Paisooksantivatana & Sangkhachand y1000–82* (BK); Ubon Ratchathani, Khua Nangnee waterfall, Pha Taem NP, 200 m alt., 22 Aug 2001, *Pooma et al. 2281* (BKF), Phu Chong Nayoi NP, 20 Oct 2009, *Middleton et al. 5196* (BKF, E, K); *ibid.*, 250 m alt., 20 May 1998,



Figure 3. Species of *Euploca* from Thailand **A–C** *E. paniculata* (R.Br.) M.W.Frohl. & M.W.Chase **A** habit and inflorescences **B** inflorescence **C** young fruits **D–F** *E. strigosa* (Willd.) Diane & Hilger **D** inflorescence **E** habit **F** habit and inflorescences. Photos by Kanokorn Rueangsawang.

Suksathan 1043 (QBG) *ibid.*, 100 m alt., 25 Jan 1924, *Kerr 8345* (BK, BM, K). South-western: Kanchanaburi, Khao Meng, 14 Apr 1965, *Chantanamuck 1067* (BK); 50 m alt., 13 Sept 1931, *Kerr 20552* (BK, BM, E, K, L); *ibid.*, 50 m alt., 13 Sept 1931, *Kerr 20553* (E, L); Prachinburi, Huai Saai, Cha-am, 19 Aug 2003, *Puudjaa 1222* (BKF); Wat Luke Chang, Luke Chang Village, Tha Mai Ruak Subdistrict, Tha Yang, 5 July 2007, *Maxwell 07–410* (QBG); Prachuap Khiri Khan, Hua Hin, 31 July 1976, *Maxwell 76–455* (AAU, BK, L); Khao Tao, Hua Hin, *Simitinand 1459* (BKF); *ibid.*, 10 Nov 1928, *Marcen 2450* (BM, K); *ibid.*, 20 m alt., 9 Nov 1928, *Kerr 16164* (AAU, BK, BM, K). Central: Lop Buri, Lam Narai, 50 m alt., 13 Nov 1975, *Smitinand 12102* (BKF); *ibid.*, 50 m alt., 13 Nov 1975, *Smitinand 12109* (BKF); Phatthana Nikhom, Ban Diluang, km 29–30, 100 m alt., 17 May 2004, *Pooma et al. 3989* (BKF); Saraburi, 5 Sept 1954, *Bunnag 10* (BK). Peninsular: Chumphon, Bang Son, Pathio, 20 m alt., 10 Jan 1927, *Kerr 11351* (BK, BM, E, K, L).

Diagnostic characters. *Euploca paniculata* is erect with unbranched to few-branched stems that are woody at the base. The distinguishing features are linear leaves with greyish tomentose hairs, the spike-like inflorescences arranged in one rank that can elongate up to 20 cm and flowers with pedicels up to 2 mm long. The herbarium specimens from Thailand have mostly been confused with *E. strigosa*, but these two species can be differentiated by leaf shape and type of induments that are greyish tomentose (*E. paniculata*) and strigose (*E. strigosa*) on both leaf surfaces.

5. *Euploca strigosa* (Willd.) Diane & Hilger, Bot. Jahrb. Syst. 125(1): 49. 2003.
Fig. 3D–F

Heliotropium strigosum Willd., Sp. Pl., ed. 4, 1(2): 743. 1798. Type: Ghana [Guinea], *Isert s.n.* (holotype B [B-W 219/3253, microfiche], isotypes C [C10003972!], P [P-JU6571 image!]).

Lithospermum chinense Hook. & Arn., Bot. Beechey Voy.: 202. 1837. Type: China, Canton, *Vachell 286* (holotype E [E00369167!]; isotype BR [BR0000006966485 image!]).

Type. Based on *Heliotropium strigosum* Willd.

Distribution. Africa, Afghanistan, Pakistan, India, Nepal, Bhutan, Myanmar, Laos, Cambodia, Vietnam, China (Hainan, Kwangtung), Thailand (Fig. 1E), Malaysia, Australia.

Ecology. Open area of bare rock in dry dipterocarp and dry open deciduous forests; 50–400 m alt., flowering and fruiting from April to November.

Specimens examined. Thailand, North-eastern: Sakon Nakhon, Phu Phan NP, 400 m alt., 6 Aug 2004, *Nielsen et al. 1542* (BKF); Phrae, Ban Nun, Song, 193 m alt., 25 June 2012, *Norsaengsri & Tathana 9480* (QBG). Eastern: Surin, Nadi, 17 May 1965, *Sakol 224* (BK); Ubon Ratchathani, Chiet, 100 m alt., 21 May 1932, *Kerr 21537* (BK, BM, E, K). Central: Chai Nat, Utapao, 20 Sept 1930, *Kerr 19692* (ABD, BM, BK). South-western: Kanchanaburi, 5 km west of Thong Pha Phum Town, 16 Oct 2015, *Tanming 873* (QBG); Thong Pha Phum, along route 323, 4 km, 240 m alt., 29 Nov 1982, *Koyama et al. T-30469* (BKF); Prachinburi, Watanakorn, 23 July 1987, *Paisooksantivatana & Sangkhachand 2109-87* (BK). South-eastern: Sa Kaeo, Aranyaprathet, 50 m alt., 3 Apr 1930, *Kerr 19575* (BM,

BK, K). Peninsular: Songkhla, Padang Besar, 50 m alt., 24 Dec 1927, Kerr 13602 (BM, BK, K).

Diagnostic characters. *Euploca strigosa* is most similar to *E. paniculata* in having spike-like inflorescences arranged in one rank that can elongate up to 10 cm long, but it differs in the stem being a prostrate to many-branched (vs. erect unbranched to few-branched stem in *E. paniculata*), the narrowly elliptic leaves with strigose hairs on both surfaces, 5–10 × ca. 3 mm (vs. linear leaves with greyish tomentose hairs, 7–40 × 1–2 mm in *E. paniculata*).

***Heliotropium* L., Sp. Pl.: 130. 1753.**

Tournefortia L., Sp. Pl.: 140. 1753. Type species. *Tournefortia hirsutissima* L. [= *Heliotropium verdcourtii* Craven].

Argusia Boehm. in Ludwig, Def. Gen., ed. Boehmer: 507. 1760. Type species: *Argusia sibirica* (L.) Dandy.

Messerschmidia L. ex Hebenstr., Nov. Comm. Acad. Sci. Imp. Petrop. 8: 315, t. 11. 1763. Type species: *Tournefortia sibirica* L.

Tetrandra (DC.) Miq., Fl. Ind. Bat. 2: 928. 1858. Type species: *Tetrandra wallichii* Miq. [= *Tournefortia tetrandra* Blume].

Mallotonia (Griseb.) Britt., Ann. Missouri Bot. Gard. 2: 47. 1915. Type species: *Mallotonia gnaphalodes* (L.) Britton.

Type species. *Heliotropium europaeum* L.

Description. Annual herbs, climbing shrubs or small trees. Leaves petiole; lamina ovate, elliptic to obovate or elliptic to lanceolate, apex acute to acuminate, obtuse or rounded, margin entire or irregularly undulate, strigose, stiff hairs or greyish-white tomentose on both surfaces. Inflorescences terminal or axillary, scorpioid cymes, subcorymbose or dichotomously branched, dense 2-rowed scorpioid cymes, ebracteate. Flowers 4–5-merous. Calyx 5-lobed, lobes lanceolate to ovate. Corolla pale green, white to pinkish-white, greenish to yellowish, with a yellow-orange throat inside, funnel-shaped or tube cylindrical, lobes broadly ovate to orbicular, throat glabrous inside. Stamens included, sessile or with short filaments; anthers ovate-lanceolate or elliptic-oblong. Ovary entire. Fruits drupe, deeply bilobed or distinctly lobed, mesocarp thinly fleshy or juicy, endocarp dividing into two 2-seeded nutlets.

Key to the species of *Heliotropium*

- 1 Annual herb or small tree; inflorescence spike-like, scorpioid, subcapitate or subcorymbose **2**
- Climbing shrub; inflorescence dichotomous branched, scorpioid cymes **3**
- 2 Small trees; leaves 8–20 cm long with densely greyish tomentose hairs... **2. *H. foertherianum***
- Annual herbs; leaves 3–6 cm long with strigose and stiff hairs **4. *H. indicum***
- 3 Flower 4-merous; lower surface of leaves pale, brownish-black when dry **1. *H. biblium***
- Flower 5-merous; concolorous leaves, light brown when dry **4**

- 4 Leaves oblong-elliptic to ovate-lanceolate lanceolate, apex acute **5**
- Leaves ovate, apex long acuminate **6**
- 5 Leaves oblong-elliptic; inflorescence dense dichotomous branched; corolla tube angular **5. *H. intonsum***
- Leaves ovate-lanceolate; inflorescence loosely dichotomous branched; corolla tube not angular **6. *H. montanum***
- 6 Leaves with minutely tubercles **7. *H. ovatum***
- Leaves with golden brown tomentose hairs **3. *H. hookeri***

1. *Heliotropium biblianum* Craven, Blumea 50(2): 379. 2005.

Tournefortia tetrandra Blume, Bijdr. Fl. Ned. Ind. 14: 845. 1826. Type: Java, Blume s.n. (holotype L [L0281636!]).

Tournefortia wallichii DC., Prodr. 9: 527. 1845. Type: Singapore, Penang, Wallich Numer. List 911 (holotype K-W [K00111261!]; isotypes K-W [K00111262!, K000998138!], M [M0188731 image!], GZU [GZU000106058 image!], MEL [MEL2502678 image!]).

Tournefortia tetrandra Blume var. *angustifolia* Moritzi, Syst. Verz. 52: 1845. Type: Java, Zollinger 939 (lectotype, designated here: K [K000998147!]; isoelectotypes: K [K000998148!], BM [BM001209066 image!], FI [FI009368 image!]).

Tetrandra zollingeri Miq., Fl. Ind. Bat. 2: 928. 1858. Type: Java, Zollinger 395 (holotype K [K000998149!]).

Type. Based on *Tournefortia tetrandra* Blume.

Distribution. India (Nicobar Islands), Sri Lanka, Cambodia, Vietnam, Thailand (Fig. 1F), Malesia, New Guinea.

Ecology. Deciduous forest, evergreen forest, 40–700 m alt., flowering and fruiting from April to December.

Specimens examined. Thailand, South-eastern: Kanchanaburi, Thong Pha Phum, 700 m alt., 15 Dec 1995, *FRUD & van Welzen 111* (BKF). South-western: Prachuap Khiri Khan, Pa La U. trail, 260 m alt., 20 Jun 2004, *Middleton et al. 2322* (BKF). Peninsular: Ranong, Kaper, 40 m alt., *Shimizu et al. T-26364* (AAU, BKF); *ibid.*, 500 m alt., 19 June 1932, *Kerr 21710* (BK, BM, E, K); Surat Thani, Ko Phangan, 10 Nov 1927, *Put 1247* (BM, BK, E, K); *ibid.*, 50 m alt., 3 Mar 1927, *Kerr 12456* (BK, BM, E, L, K); Bandon, 2 Jan 1935, *Seidenfaden 2089* (K); Phangnga, 500 m alt., 9 Dec 1928, S.N. 3994 (K, SING); Trang, Khao Pap Pa, 13 Mar 1974, *Larsen & Larsen 33277* (AAU); Yan Ta Khao, Sai Roong waterfall, 400 m alt., 26 Apr 1987, *Maxwell 87–434* (BKF, CMU, L); Phuket, Khao Pha Tao Non-Hunting Area, Bang Pae waterfall, 50 m alt., 14 Oct 2004, *Gardner & Sidisunthorn 44268* (QBG).

Vernacular. Fa Ta Hueng (ฟ้าตาทึง).

Diagnostic characters. *Heliotropium biblianum* can be recognised mainly by its tetramerous flower, acute apex leaf, thick leaves with minute tubercles on both leaf surfaces, corolla up to 8–10 mm long and globose fruit up to 8 mm in diameter. According to the label of *Tournefortia tetrandra* var. *angustifolia*, four duplicate specimens were originally collected and are preserved at BM, K and FI. The specimen at K [K000998147] is designated here as the lectotype because it is in the best condition.

2. *Heliotropium foertherianum* Diane & Hilger, Bot. Jahrb. Syst. 125(1): 46. 2003.
Fig. 4A–C

Tournefortia argentea L.f., Suppl. Pl.: 133. 1781. Type: Sri Lanka, *Köenig s.n.* (holotype BM [BM001014452 image!]).

Messerschmidia argentea (L.f.) I.M. Johnst., J. Arnold Arbor. 16: 164. 1935.

Argusia argentea (L.f.) Heine, Fl. Nouv.-Calédonie & Dépend. 7: 109. 1976.

Type. Based on *Tournefortia argentea* L.f.

Distribution. China (Hainan), Taiwan, Japan (Ryukyu), Vietnam, Thailand (Fig. 1G), Malesia, New Guinea, Australia.

Ecology. Sandy beaches, flowering and fruiting from November to February.

Specimens examined. Thailand, Peninsular: Surat Thani, Ban Bua Put, Ko Samui, 14 May 1928, *Kerr 15728* (BK, E, K, TCD); Phangnga, Similan NP, 14 Nov 1996, *Santisuk s.n.* (BKF); Krabi, Lan Ta NP, 7 Jan 1992, *Niyomdham 2854* (BKF); Ko Lan Ta Yai, 20 Mar 1998, *Chamchumroon 37* (BKF); Satun, Adang, La-ngu, 15 Jan 1928, *Kerr 14095* (BK, K).

Vernacular. Nguang chang thale (งวงช้างทะเล).

Diagnostic characters. *Heliotropium foertherianum* is recognised by the combination of a small tree, oblanceolate or obovate leaves that are up to 20 cm long and have densely greyish tomentose hairs, subcorymbose inflorescence with peduncles up to 8 cm long, corollas as long as the calyx and fleshy fruits with a fleshy mesocarp and spongy endocarp.

3. *Heliotropium hookeri* (C.B. Clarke) Rueangs. & Chantar., comb. nov.
urn:lsid:ipni.org:names:77327199-1

Tournefortia hookeri C.B. Clarke, Fl. Brit. India 4: 147. 1883.

Tournefortia viridiflora Gamble, Darjeeling List: 57. 1878. nom. illeg.

Type. Sikkim, Himalayas, *Hooker s.n.* (holotype K [K000998133!]).

Distribution. East Himalaya, Myanmar, Thailand (Fig. 1H).

Ecology. Deciduous forest, flowering and fruiting in June.

Specimens examined. Thailand, Northern: Chiang Mai, Ban Pa Kar, Samoen-gtai, Samoen-g, 1,424 m alt., 26 June 2008, *Jatupol 08-275* (QBG).

Diagnostic characters. *Heliotropium hookeri* is newly recorded for Thailand due to a specimen of this distinctive species seen from QBG. This species is recognisable in the leaves being broadly ovate with dense golden brown tomentose hairs on the lower surface and loosely dichotomous cymose.

4. *Heliotropium indicum* L., Sp. Pl.: 130. 1753.
Fig. 4D–F

Type. India utraque, Herb. Hermann 1: 9, no. 70 (lectotype, designated by Mill in Cafferty and Jarvis 2004, p. 802: BM [BM00061256!]).



Figure 4. Species of *Heliotropium* from Thailand **A–C** *H. foertherianum* Diane & Hilger **A** inflorescence **B** habit **C** flowers **D–F** *H. indicum* L. **D** inflorescences **E** habit and inflorescence **F** young fruits. Photos by Kanokorn Rueangsawang.

Distribution. North America, South America, Pakistan, India, Sri Lanka, China, Myanmar, Taiwan, Japan, Laos, Cambodia, Vietnam, Thailand (Fig. 11), Sumatra, Malaysia, Java, Borneo, Australia.

Ecology. Common on sandy soil near stream or open areas, rice fields, roadsides; 50–1,000 m alt., flowering and fruiting from January to April.

Specimens examined. Thailand, Northern: Mae Hong Son, Mueang, 256 m alt., 10 Sept 2013, *Lakoet 0352* (QBG); 350 m alt., 18 June 1973, *Geesink et al. 5937* (AAU, BKF, E, K, TCD); Chiang Mai, Doi Sa Ket, 12 Dec 2007, *Warintorn 07–105* (QBG); San Kamphang, 325 m alt., 10 July 1996, *Panatkool et al. 37* (BKF); Doi Suthep, 300 m alt., *Hosseus s.n.* (K); *ibid.*, 1,000 m alt., 12 May 1915, *Winit 402* (K, E); *ibid.*, 1,000 m alt., 5 Jan 1911, *Kerr 1845* (BM, K, E); Hod, 8 Sept. 1996, *BGO Staff 28* (QBG); Ban Chang Keong, 488 m alt., 28 May 2019, *Pingyot 276* (QBG); Chiang Rai, Thoeng, 12 Feb 2011, *Norsaengsri & Tathana 7444* (QBG); San Pa Tong, 325 m alt., 26 Apr 1988, *Maxwell 88–521* (BKF, CMUB); Phayao, Ban Khun Kam Lang, Pong, 400 m alt., 19 May 2017, *Pongamorkul 6201* (QBG); Nan, Na Noi, 9 Apr 2018, *Khattiyot et al. 778* (QBG); Huai Haeng, 318 m alt., 26 Apr 2017, *Muaengyen 2011* (QBG); Lampang, Sop Prap, 28 Feb 2012, *Norsaengsri et al. 9055* (QBG); Uttaradit, Nam Pat, 22 Mar 2011, *Romklao Botanical Garden 0224/2554* (QBG); Tak, Mae Sot, 22 July 1959, *Floto 7653* (C); Tha Song Yang, 15 May 2007, *Pooma et al. 6785* (BKF, E, L); Phitsanulok, Tham Pha Phon Non-Hunting Area, 5 Mar. 2012, *Maknoi 4627* (QBG); Wat Hua Khao, 31 Jan 2012, *Maknoi 4565* (QBG). North-eastern: Loei, Na Haeo, Yaa Ngoung Chaang, 31 July 1995, *Nanakorn et al. 4077* (QBG); Phu Kradueng, 27 Aug 1988, *Tamura T-60450* (BKF); Sithan, Huai Yang, 300 m alt., 21 Feb 1958, *Ploenchit 1342* (BKF); Bueang Kan, Mueang, 27 Dec 2011, *Norsaengsri & Tathana 8581* (QBG); Maha Sarakham, Kosum Phisai, 3 May 2001, *Norsaengsri et al. 1440* (QBG); Ban Maong Ai, 130 m alt., 3 Apr 2001, *Norsangsri et al. 1440* (QBG); Chiang Yuen, 14 Apr 2018; Khon Kaen, Chum Phae, 2 Sept 1967, *Shimizu et al. T-8685* (BKF, E, TCD). Eastern: Nakhon Ratchasima, Bua Yai, 18 Mar 2009, *Norsaengsri 5135* (QBG); Ban Chum Sang, 25 May 1929, *Nai Noe 277* (ABD, BM, BK, K); Ubon Ratchatani, Khong Chiam, 170 m alt., 25 May 2001, *Greijmans 90* (BKF); Phibun Mangsahan, 250 m alt., 9 Dec 1982, *Koyama et al. T-30698* (AAU, BKF); Det Udom, 270 m alt., 10 Dec 1982, *Koyama et al. T-30778* (BKF); Buri Ram, 7 Aug 1970, *Sutheesorn 2065* (BK); Ban Na, Suwan Naphum, 16 Aug 1982, *Sutheesorn & Saraphunphichit 5354* (BK). South-western: Kanchanaburi, Si Sawat, 150 m alt., 6 Nov 1971, *van Beusekom et al. 3955* (BKF, C, K); Thum Pha, 13 Dec 1961, *Phengkklai 228* (BKF); Kwae Noi, 30 Apr 1946, *Wichian 304* (K); Na Ta Hom, 23 Apr 1965, *Chantanamuck 1094* (BK); Prachuap Khiri Khan, 18 Aug 1967, *Shimizu et al. T-7689* (AAU, BKF, E, K). Central: Chat Nat, 5 Mar 1958, *Sørensen et al. 1922* (E, C); Pathum Thani, 50 m alt., 12 Mar 1958, *Smitinand 4444* (BKF); Nakhon Nayok, Khao Yai, 1,000 m alt., 5 May 1964, *R.S. 116* (BKF); 40 m alt., 6 Aug 1970, *Phengkklai et al. 3748* (BKF); Nonthaburi, Sai Maa Tai, 14 Apr 1992, *Puudjaa 65* (BKF); Bangkok, 5 July 1920, *Marcan 293* (BM, K); 27 Oct 1919, *Kerr 3840* (ABD, BM, C, K); 19 Apr 1926, *Lakshnakara 52* (BK); Sept 1921, *Smith 49* (BK); 1899, *Zimmermann s.n.* (K); Ang Thong, 30 Dec 1929, *Put 2595* (AAU, ABD, BK, BM, K). South-eastern: Chachoengsao, Phanom Sarakham, 50–100 m alt., 1 Oct 1984, *Murata et al. T-37042* (BKF); Chon Buri, Si Racha, 30 Nov 1927, *Collins 2025* (ABD, BM, BK, K, TCD); Chanthaburi, 8 Apr 1959, *Sørensen et al. 7214* (C).

Peninsular: Chumphon, 31 Jan 1958, *Sørensen et al.* 829 (BKF, C); Ranong, Kapoe, 19 Jan 2016, *Kertsawang* 3937 (QBG); Satun, La-ngu, Ko Kabeng, 11 Apr 2003, *Phengkklai et al.* 13650 (BKF); Songkhla, 21 Aug 1995, *Larsen et al.* 45836 (AAU, BKF); Satun, Terutao, 5 Mar 1966, *Hansen & Smitinand* 12542 (BKF, C).

Vernacular. Ya nguang chang (หญ้าวงช้าง).

Diagnostic characters. *Heliotropium indicum* is likely native to tropical America and introduced in all the tropical regions of the world. This species is also a common weed with medicinal properties (Dash and Abdullah 2013). It is most easily recognised by ovate to elliptic leaves with strigose and stiff hairs on both surfaces, truncate or obtuse leaf base, irregularly undulate leaf margins, white to purple or purplish corollas with a yellow-orange throat inside and fruits are deeply 2-lobed with apical divergent lobes.

5. *Heliotropium intonsum* (Kerr) Rueangs. & Chantar., comb. nov.

urn:lsid:ipni.org:names:77327200-1

Fig. 5A

Tournefortia intonsa Kerr, Bull. Misc. Inform. Kew 1940: 185. 1940.

Type. Thailand, Doi Suteh, ca. 900 m alt., evergreen forest, *Kerr* 2285 (holotype K [K000998142!]; isotypes BM [BM001209041!], E [E00766166!]).

Distribution. Laos, Thailand (Fig. 1J).

Ecology. In deciduous forest, evergreen forest, flowering and fruiting from November to February.

Specimens examined. Thailand, Northern: Mae Hong Son, Pang Mapha, 580 m alt., 26 Feb 1968, *Hansen & Smitinand* 12741 (AAU, BKF, C, E, K); Chiang Mai, Doi Chiang Dao, 20 Mar 1956, *Suvarnakoses* 1121 (BKF, K); *ibid.*, 700 m alt., 18 Feb 1958, *Sørensen et al.* 1312 (BKF); *ibid.*, 23 Dec 1931, *Put* 4570 (BK, E, K); *ibid.*, 600–800 m alt., 14 Mar 1956, *Garrett* 1449 (K, L); *ibid.*, 600 m alt., 14 Mar 1956, *Garrett* 1476 (K, L); *ibid.*, 1,500 m alt., 17 Feb 1958, *Smitinand* 4218 (BKF); *ibid.*, 525 m alt., 26 Feb 1989, *Maxwell* 89–273 (BKF, CMU, CMUB, L); *ibid.*, 550 m alt., 10 Mar 1990, *Maxwell* 90–294 (CMU); Chiang Rai, Doi Tung, 750 m alt., 15 Feb 2012, *van de Bult* 1241 (BKF); Mae Sai, Huai Nam Dang, 612 m alt., 13 Jan 2011, *Norsaengsri & Tathana* 7537 (BKF, QBG); Mae Sai, Ban Phamee, 572 m alt., 15 Feb 2012, *Norsaengsri & Tathana* 9003 (QBG); Hua Yane, Mae Chan, 25 Jan 1970, *Sutheesorn* 1438 (BK); Doi Tung, 1,400 m alt., 29 Jan 1989, *Bragg* 8 (CMU, L); Phrae, Mae Khaen stream, 440 m alt., 5 Jan 1972, *van Beusekom, et al.* 4636 (C, BKF, K); *ibid.*, 22 Mar 1912, *Vanpruck* 454 (K); Mae Yom NP, 400 m alt., 15 Dec 1993, *Maxwell* 93–1509 (CMUB, L)]. North-eastern: Phetchabun, Chon Daen, 15 Jan 1969, *Vacharapong* 304 (BK); Loei, Phu Suan Sai NP, 11 Mar 2008, *Maknoi* 2029 (BKF, QBG); route to Sam Nuck Bab, 15 May 2008, *Maknoi & Srisaga* 2302 (BKF, QBG); Tad Hueang waterfall, 1,000 m alt., 16 May 2006, *Maknoi* 824 (QBG); Na Haeo, 650 m alt., 27 Apr 1995, *Nanakorn et al.* 3239 (QBG); Khon Kaen, Pha Bhroung Cave, Chum Phae, 14 Feb 1963, *Chantanamuck* 295 (BK). South-western: Uthai Thani, Huai Haeng, 27 Apr 1963, *Kasem* 329 (BK). South-eastern: Chanthaburi, Pong Nam Ron, 600 m alt., 12 Jan 1956, *Smitinand* 3192 (BKF).

Vernacular. Ya Nguang Chang Luang (หญ้าวงช้างหลวง).

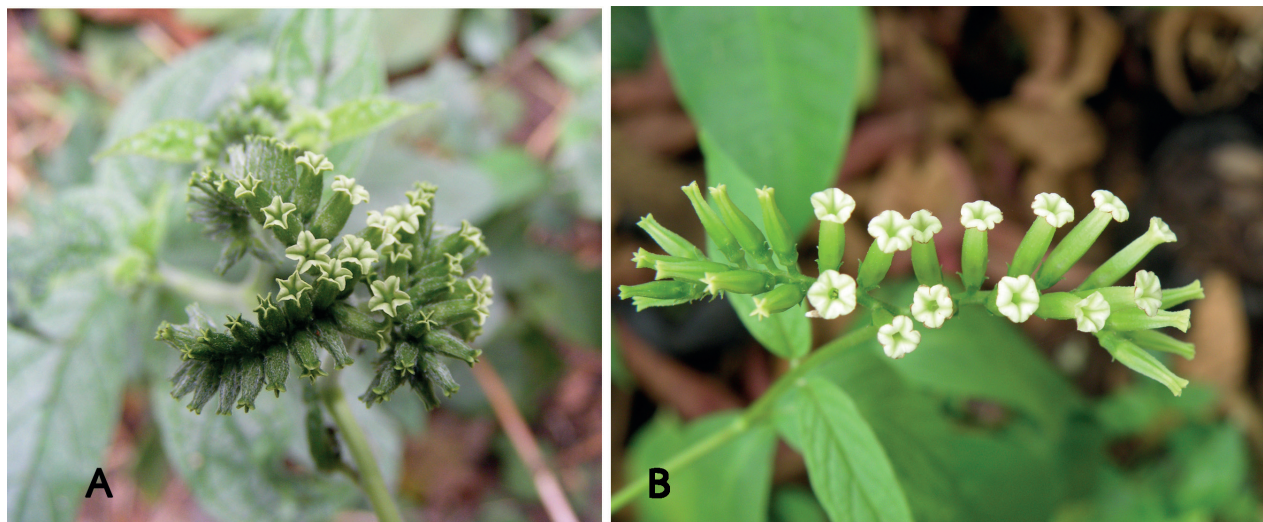


Figure 5. Species of *Heliotropium* from Thailand **A** *H. intonsum* (Kerr) Rueangs. & Chantar. **B** *H. montanum* (Lour.) Rueangs. & Chantar. Photos by Kanokorn Rueangsawang.

Diagnostic characters. *Heliotropium intonsum* is most similar to *H. montanum* in its dichotomous branched inflorescences and subsessile pedicels, but differs in the leaves being oblong or elliptic with densely strigose hairs (vs. glabrous to glabrescent ovate-lanceolate leaves in *H. montanum*) and both the inflorescences and corollas bear densely greyish tomentose hairs (vs. glabrous in *H. montanum*).

6. *Heliotropium montanum* (Lour.) Rueangs. & Chantar., comb. nov.

urn:lsid:ipni.org:names:77327201-1

Fig. 5B

Tournefortia montana Lour., Fl. Cochinch. 1: 122. 1790.

Messerschmidia montana (Lour.) Roem. & Schult. Syst. Veg., ed. 15 bis 4: 544. 1819.

Tournefortia sampsonii Hance, J. Bot. 6: 330. 1868. Type: China, Sai-chii-shan, Cantonesis, *Sampson 13035* (holotype BM [BM001014454!]).

Tournefortia boniana Gagnep., Notul. Syst. (Paris) 3: 33. 1914. Type: Vietnam, Tonkin m ridional, *Bon 1932*, (lectotype, designated here: P [P03897617 image!]; isolectotypes: P [P03897616 image!], K [K000998141!]).

Tournefortia gaudichaudii Gagnep., Notul. Syst. (Paris) 3: 34. 1914. Type: Vietnam, Cochinchine: Tourane, *Gaudichaud 180* (lectotype, designated here: P [P03897604 image!]; isolectotypes: P [P03897602 image!], K [K000998140!]).

Tournefortia brachyantha Merr. & Chun, Sunyatsenia 2: 314. 1935. Type: China, Jiangsu, Hainan, *How70424* (holotype K [K000998121!]).

Type. Vietnam, Cochinchine: Tourane, *Gaudichaud 180* (neotype, designated here: P [P03897604 image!]; isoneotypes: P [P03897602 image!], K [K000998140!]).

Distribution. India (Assam), Bangladesh, southern China, Myanmar, Laos, Vietnam, Cambodia, Thailand (Fig. 1K).

Ecology. Open roadside, along the streams in evergreen forest, bamboo forest, slopes of the hills in evergreen forest and mixed deciduous forests, 250–1,500 m alt., flowering and fruiting from February to December.

Specimens examined. Thailand, Northern: Chiang Rai, Mae Chan, 450 m alt., 17 Mar 2005, *Pooma et al.* 4859 (BKF); Chiang Mai, Mae Hia Thai Literary Botanical Garden, 350 m alt., 13 June 2003, *TLBG* 165 (QBG); 300 m alt., 21 Jan 1921, *Kerr* 4692 (BM, BK, K); Nan [Doi Phu Kha NP 1,500 m alt., 24 Jan 2003, *Srisanga* 2684 (QBG); *ibid.*, 11 Apr 2002, *Srisanga* 1253 (QBG); *ibid.*, 1,200 m alt., 19 Mar 2000, *Srisanga* 1340 (BKF, QBG); Ban Den Thara, Pra That, Chiang Klang District, 346 m alt., 15 Mar 2018, *Khattiyot et al.* 616 (QBG); Tam Paa Toop, Ta Wang Paa, 10 km from Nan, 360 m alt., 24 Feb 1998, *Srisanga et al.* 220 (QBG); Lampang, Doi Luang NP, Wahng Gaye waterfall, 625 m alt., 26 Mar 1997, *Maxwell* 97-753 (BKF); Uttaradit, Phu Soi Dao NP, 1,000 m alt., 18 Mar 2002, *Chamchumroon & Puff* V.C.1438 (BKF); Tak, Doi Muser, Hui Sakulee, 700 m alt. 27 Feb 1987, *Paisooksantivatana* Y2032-87 (BK); Mae Sot to Mae Sariang, 19 Jan 1995, *Pooma* 1007 (BKF, CMUB). South-western: Uthai Thani, Ban Rai, 4 Mar 1977, *Sutheesorn* 4017 (BK); Kanchanaburi, Sangkhla Buri to Thong Pha Phum, 180 m alt., 17 Dec 2009, *Pooma et al.* 7436 (BKF); Sai Yok, Khwae Noi, 21 Dec 1961, *Larsen* 8893 (BKF, C, K); *ibid.*, 21 Dec 1961, *Simitnand* 9500 (BKF); Sai Yok, 23 Dec 1961, *Larsen* 8916 (C); Pompee Village near Khwae Noi, 250 m alt., 26 Mar 1968, *van Beusekom & Phengklai* 129 (BKF, E, K, L); Mae Nam Noi near waterfall, 2 Jan 1962, *Phengklai* 398 (BKF); Huai Banlcae, 8 Nov 1971, *van Beusekom et al.* 3528 (BKF); Thong Pha Phum NP, 260 m alt., 3 Dec 2003, *Sirimongkol* 69-2 (BKF). Peninsular: Krabi, Ban Nai Chong, 17 Dec 1965, *Umpai* 208 (BK); Khap Thong Thai, 19 Jan 1966, *Hansen & Smitinand* 12002 (BKF, C); Nakhon Si Thammarat, Nop Phitum, 80 m alt., 13 Feb 2005, *Williams et al.* 1475 (BKF, E).

Diagnostic characters. *Heliotropium montanum* can be recognised by ovate-lanceolate leaves, glabrous to glabrescent on both surfaces and minute tubercles on the lower surface, loosely dichotomous branched inflorescences and glabrous flowers. The specimens from Thailand have mostly been misidentified as *H. intonsum*. These two species can be differentiated by leaf shape, the type of indument on each of the inflorescences and corollas that are glabrous (*H. montanum*) or densely greyish tomentose hairs (*H. intonsum*).

In the original description of *T. montana* Loureiro (1790) described from ‘*Cochinchina tributarii*’, the type collection of Loureiro has not been found in either P or BM. Therefore, this species is represented by specimens of *Gaudichaud* 180 (K000998140, P03897604, P03897602) from ‘*Cochinchine: Tourane*’, Loureiro’s initial locality. The specimen at P [P03897604] is designated here as a neotype for *T. montana* because it is in the best condition and the characters match the original description.

In the protologue, Gagnepain (1914) described *T. boniana*, based on two different collections (*Bon* 1357 & *Bon* 1932). *Bon* 1932 P [P03897617] is chosen as the lectotype because it is best preserved, with complete inflorescences and numerous flowers and has two duplicates.

Gagnepain (1914) did not specify which of the duplicates of *T. gaudichaudii* was the holotype; therefore, the specimen at P [P03897604] is designated as the lectotype because it is a perfect match for the description in the protologue.

7. *Heliotropium ovatum* (Wall. ex G.Don) Rueangs. & Chantar., comb. nov.

urn:lsid:ipni.org:names:77327202-1

Tournefortia ovata Wall. ex G.Don, Gen. Hist. 4: 369. 1837.

Type. Myanmar, Rangoon, *Wallich Numer. List 908* (holotype K [K001110253!]).

Distribution. India (Andaman Islands, Nicobar Islands), Myanmar, Thailand (Fig. 1L).

Ecology. Open or shaded, slightly disturbed area in mixed evergreen forest 400–500 m alt., flowering and fruiting from November to April.

Specimens examined. Thailand, Northern: Chiang Rai, Tham Luang-Khun Nam Nang Norn NP, Mae Sai, 560 m alt., 27 Mar 2012, *Norsaengsri & Tathana* 9227 (QBG); Mae Tak, 3 Mar 1958, *Sørensen et al.* 1865 (BKF); Chiang Mai, Gnai, Tintok, 500 m alt., 8 Mar 1965, *C.A. & B.S.* 270 (BKF); Doi Chiang Dao, 750 m alt., 29 Mar 1995, *Maxwell* 95–269 (BKF); *ibid.*, 575 m alt., 11 Mar 1989, *Maxwell* 89–317 (BKF, CMU, L); *ibid.*, 550 m alt., 8 Mar 1965, *Hambanond* 270 (BK); Phayao, Doi Pha Dam, Rom Yen Subdistrict, Chiang Kham, 890 m alt., 21 Feb 2013, *La-ongsri et al.*, 2662 (QBG); Lampang, Mae Pukaung, 6 Mar 1925, *Winit* 1282 (BK, K); Nan, Song Khwae, Nam Pan Village, 350 m alt., 12 Jan 2011, *Srithi* 630 (QBG); Tak, Lan Sang NP, 2 Jan 1969, *Cheviwat & Nimanong* 10 (BKF); Phrae, 500 m alt., 22 Mar 1913, *Vanpruck* 454 (BKF, K); Huai Rai, 13 Mar 1961, *Chanthamuk* 6 (BKF); *ibid.*, 13 Mar 1961, *Chanthamuk* 9 (BKF); *ibid.*, 23 Mar 1961, *Phengkklai* 66 (BKF, C, K); 26 Jan 1913, *Vanpruck* 357 (BKF, K); Sukhothai, Srisatchanalai NP, route to Tad Dao Waterfall, 3 Feb 2015, *Maknoi* 7243 (QBG). North-eastern: Phetchabun, Nam Nao NP, 18 Feb 2014, *Maknoi* 6553 (QBG). Eastern: Nakhon Ratchasima, Bua Yai, 400 m alt., 29 Nov 1924, *Kerr* 9487 (BM, BK, E, K, L). South-western: Kanchanaburi, Si Sawat, Dongyai, 50 m alt., 17 Aug 1971, *Phengkklai et al.* 3016 (BKF), *ibid.*, 600 m alt., 17 Jan 1926, *Kerr* 10233 (BM, BK, K, E); Thung Yai Naresuan WS, Sangklaburi, 475 m alt., 11 Apr 1994, *Maxwell* 94–489 (CMUB, L); Prachuap Khiri Khan, Pran Buri, 25 Nov 1929, *Put* 2449 (BM, BK, K).

Vernacular. Liang (เหลียง).

Diagnostic characters. *Heliotropium ovatum* is similar to *H. biblium* in having ovate or ovate-lanceolate leaves, but differs in the 5-merous flower and densely minute tubercles on the lower leaf when dry (vs. 4-merous flowers and minute tubercles on both leaf surfaces in *H. biblium*).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: PC, KR. Data curation: KR, PC. Formal analysis: PC, KR. Funding acquisition: KR. Investigation: KR, PC. Methodology: KR. Writing – original draft: KR. Writing – review and editing: PC.

Author ORCIDs

Kanokorn Rueangsawang  <https://orcid.org/0000-0003-1595-1514>

Pranom Chantaranothai  <https://orcid.org/0000-0002-5065-6169>

Data availability

All of the data that support the findings of this study are available in the main text.

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