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MORE THAN A CENTURY LATER: FIRST MODERN RECORD OF *PTEROGLOSSA MACRANTHA* (ORCHIDACEAE: SPIRANTHINAE) IN ARGENTINA, WITH NOTES ON ITS MORPHOLOGY, DISTRIBUTION, HABITAT, AND CONSERVATION IMPLICATIONS

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Abstract. *Pteroglossa macrantha* (Orchidaceae: Spiranthinae) was previously known in Argentina only from a historical collection made by Ekman in 1908 in the province of Misiones, with no subsequent records confirming its presence in the country. During recent botanical surveys in the province of Corrientes, a new population was discovered, representing the first modern record for Argentina after more than a century and one of the southernmost confirmed occurrences of the species in the country. Detailed morphological observations confirmed its identity and revealed slight variations in leaf proportions compared with specimens from Brazil and Paraguay. The plants of this species grow in seasonally flooded alluvial grasslands on sandy substrates near the Paraná River. The regional conservation assessment, based on IUCN criteria, indicates that *P. macrantha* could be considered Critically Endangered (CR) in Argentina due to its extremely small area of occupancy, its occurrence in a single locality, and ongoing habitat degradation. This finding highlights the importance of the riparian grasslands of Corrientes as biodiversity refuges and priority areas for the conservation of rare and threatened orchids of the Southern Cone.

Resumen. *Pteroglossa macrantha* (Orchidaceae: Spiranthinae) era conocida previamente en Argentina únicamente a partir de una colección histórica realizada por Ekman en 1908 en la provincia de Misiones, sin registros posteriores que confirmaran su presencia en el país. Durante recientes relevamientos botánicos en la provincia de Corrientes, se descubrió una nueva población, lo que representa el primer registro moderno para Argentina después de más de un siglo y uno de los registros confirmados más australes de la especie en el país. Las observaciones morfológicas detalladas confirmaron su identidad y revelaron ligeras variaciones en las proporciones foliares en comparación con ejemplares de Brasil y Paraguay. Plantas de esta especie crecen en pastizales aluviales estacionalmente inundables sobre sustratos arenosos cercanos al río Paraná. La evaluación regional de conservación, basada en los criterios de la UICN, indica que *P. macrantha* podría ser considerada En Peligro Crítico (CR) en Argentina, debido a su área de ocupación extremadamente reducida, su ocurrencia en una única localidad y la degradación continua de su hábitat. Este hallazgo resalta la importancia de los pastizales ribereños de Corrientes como refugios de biodiversidad y áreas prioritarias para la conservación de orquídeas raras y amenazadas del Cono Sur.

Keywords / Palabras clave: Corrientes Province, límite sur de distribución, Paraná River, pastizales ribereños, provincia de Corrientes, río Paraná, riparian grasslands, southern distribution limit

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Introduction. The subtribe Spiranthinae represents one of the most diverse lineages of terrestrial orchids, comprising approximately 40–42 genera and over 500 species (Chase *et al.*, 2015; Guimarães *et al.*, 2019; Salazar, 2003). Recent phylogenetic studies have confirmed its monophyly and recognized several major clades, including the so-called "Stenorrhynchos clade", which encompasses the genera *Buchtienia* Schltr., *Eltroplectris* Raf., *Espinhassoa* Salazar & J.A.N.Bat., *Lyroglossa* Schltr., *Mesadenella* Pabst & Garay, *Nothostele* Garay, *Pteroglossa* Schltr., *Sacoila* Raf., *Skeptrostachys* Garay, *Stenorrhynchos* Rich. ex Spreng., and *Thelyschista* Garay (Batista *et al.*, 2011; Salazar *et al.*, 2003, 2018, 2019).

Pteroglossa shares with the other genera of the "Stenorrhynchos clade" several distinctive floral characters, such as a short, robust, ventrally channeled column, usually a prominent spur, an elongated labellum claw, and a weakly tridentate rostellum (Damián & Salazar, 2017). The genus comprises approximately 11 species distributed from Mexico to Argentina (Buzatto *et al.*, 2014; Chase *et al.*, 2015). In this sense, *Pteroglossa* species are frequently associated with open environments and savannas, growing in moist grasslands or at forest edges (Buzatto *et al.*, 2014).

In Argentina, *Pteroglossa* is represented by five species, mainly distributed in the northeastern and northwestern regions of the country (POWO, 2026; Zuloaga *et al.*, 2025): *P. lurida* (M.N.Correa) Garay, *P. luteola* Garay, *P. rhombipetala* Garay, *P. roseoalba* (Rchb.f.) Salazar & M.W.Chase, and the focus species of the current study, *P. macrantha* (Rchb.f.) Schltr. Hitherto, in Argentina, *P. macrantha* was only known from a single record from the province of Misiones (Posadas, Loreto, San Ignacio), collected by Ekman in 1908, which is the holotype of *Stenorrhynchos regium* Kraenzl., considered here as a heterotypic synonym of *P. macrantha* according to Guimarães *et al.* (2019). Since then, no new collections or evidence had confirmed its presence in the country.

During recent surveys conducted as part of a project on endemic species of the province of Corrientes, a population of *P. macrantha* was found in a small area in the northwest of the province.

The current study aims to document the presence of *P. macrantha* in Argentina, which, together with a record in the Brazilian state of Rio Grande do Sul (Buzatto *et al.*, 2014), represents the southernmost portion of its distribution. A detailed morphological description, information on its ecological preferences, and an assessment of its local conservation status using the IUCN Red List categories and criteria, are provided.

Materials and methods. *Taxonomic treatment.*— The collected specimens, including both vegetative and reproductive structures, were preserved in FAA solution (Formol-alcohol-acetic acid: 5 mL formalin, 5 mL acetic acid, 90 mL 70% ethanol) and deposited in the CTES herbarium (herbarium acronym according to Thiers, 2026). Information on habitat, flowering period, and qualitative traits such as flower color was obtained from direct field observations and from living specimens collected in the field, which were subsequently cultivated and maintained under greenhouse conditions at the *Facultad de Ciencias Agrarias, Universidad Nacional Nordeste (UNNE)*, Corrientes, Argentina, for further observation.

Morphological analyses.— Morphological observations were conducted using both FAA-fixed and fresh material, examined under a Leica MZ6 stereomicroscope. Measurements were taken with a digital caliper. General terminology followed the recommendations of the International Association for Plant Taxonomy (IAPT, 1962) and Simpson (2010), whereas specific terminology was based on Salazar (2003) and Buzatto *et al.*, (2014), who addressed the comparative morphology of *Pteroglossa* and related genera within the subtribe Spiranthinae. The material used for micromorphological studies was derived from specimen *Florentín 389* (CTES).

Geographic distribution and conservation status.— Two expeditions were carried out in 2024 and 2025 in the locality where the species was recorded and in surrounding areas. Geographic coordinates were obtained using a Garmin eTrex 30x GPS. The conservation status of the species for Argentina (regional assessment) was evaluated following the categories and criteria of the IUCN Red List (IUCN, 2012) and its most recent guidelines (IUCN Standards and Petitions Committee, 2024). Regarding Criterion B (geographic range-IUCN 2012, 2024), in order to estimate the extent of occurrence (EOO) and area of occupancy (AOO), the

GeoCAT software (2026) was used, applying a 2 km grid (cell area = 4 km²) as recommended by the IUCN Standards and Petitions Committee (2024). In addition to Criterion B, the species was also evaluated under Criteria C and D; the former considers population size and observed or projected decline in the number of mature individuals, while the latter takes into account very small or restricted populations. Current and potential threats were identified through direct observations during field expeditions. Distribution maps were produced using Google Earth (2018) and QGIS (2018).

Taxonomic treatment

Pteroglossa macrantha (Rchb.f.) Schltr., *Beih. Bot. Centralbl.* 37(2): 450. 1920. Fig. 1–2.

≡ *Spiranthes macrantha* Rchb.f., *Linnaea* 19: 378. 1847 ≡ *Gyrostachys macrantha* (Rchb.f.) Kuntze, *Revis. Gen. Pl.* 2: 664. 1891 ≡ *Stenorrhynchos macranthum* (Rchb.f.) Cogn., *Fl. Bras.* 3(4): 176. 1893–1896. TYPE: Brazil. Minas Gerais: 1839, *Claussen s.n.* (holotype: G00428576 [digital image!]).

= *Spiranthes albescens* Barb.Rodr., *Gen. Spec. Orchid. Nov.* 1: 186. 1877 ≡ *Stenorrhynchos albescens* Barb.Rodr., *Gen. Spec. Orchid. Nov.* 1(Index): x. 1877. TYPE: Brazil. "Hab. *Dans la Serra de Caldas*, *Minas Geraes*", s.d., J. *Barbosa Rodrigues s.n.* [lost]; lectotype (designated by Buzatto *et al*. 2013: 616): Barbosa Rodrigues's original illustration at Biblioteca Barbosa Rodrigues, "Iconographie des Orchidées du Brésil" 1: tab. 52, cited as tab. 375 (then unpublished) in Barbosa Rodrigues (1877: 186), reproduced in Sprunger *et al.* (1996: 105).

= *Stenorrhynchos macranthum* f. *robustior* et *multiflora* Cogn., *Bull. Herb. Boiss.* 3(II): 931. 1903. TYPE: Paraguay. Amambay: "*in campo paludoso*, *in regione cursus superioris fluminis Apa*", December 1901–02, *Hassler 8265*; lectotype (designated by Guimarães *et al*. 2019: 112): G (00009409 [online image!]); isolectotypes: BM (000077495), MO-duplicates (101157383), MO-duplicates (103117938).

= *Stenorrhynchos regium* Kraenzl., *Kongl. Svenska Vetensk. Acad. Handl.*, n.f., 46(10): 20. 1911 ≡ *Pteroglossa regia* (Kraenzl.) Schltr., *Beih. Bot. Centralbl.* 37(2): 451. 1920. TYPE: Argentina. Misiones: Posadas, "*Prope Loreto in clivo umbroso juxta viam*, *quae ad municipium San Ignacio fert*", 30 January 1908, *Ekman 425* (holotype: S-R 5922 5922 [online image!]).

Terrestrial *herbaceous* plant up to *ca.* 50 cm tall, including the inflorescence. *Roots* fleshy, cylindrical, often stipitate, covered with a fine lanuginose pubescence. *Leaves* arranged in a basal rosette, usually present during anthesis, 20–28 cm long, 3–6 cm wide, sessile, coriaceous, lanceolate, acute, with translucent margins; midvein and up to seven parallel secondary veins conspicuous, light green; outer leaves slightly attenuate at the base, inner ones more markedly attenuate. *Inflorescence ca.* 45 cm long, a raceme; scape terete, *ca.* 30 cm long, pubescent, partially covered by 6–9 tubular, acute bracts; rachis *ca.* 15 cm long, pubescent, bearing *ca.* 15 flowers; flowers opening almost simultaneously. *Floral bracts* 3–9 cm long, 1.5–2.0 cm wide, prominent, light green, glabrous, loosely concave, ovate, acuminate. *Flowers* 6.0–7.8 cm long, resupinate, fleshy, pale cream to yellowish; sepals densely pubescent on the outer surface. *Dorsal sepal* 28–39 mm long, 5–9 mm wide, slightly spreading and arched, free from the lateral sepals densely pubescent externally, with nine to ten conspicuous veins, lanceolate, acuminate, with entire margins. *Lateral sepals* up to 67 mm long, 6–10 mm wide, long-connate at their basal portions and adnate to the ovary, forming a short, conical, rounded spur, with four conspicuous veins, elliptic-lanceolate, falcate, acuminate, with entire margins. *Petals* 29–34 mm long, 5–10 mm wide, glabrous, with six and seven conspicuous veins, fusiform, acuminate, with entire margins. *Labellum* 30–42 mm long, 9–11 mm wide, trilobed; blade pubescent externally, glabrous toward the apex, basally adnate to the lateral sepals within the spur, margins adnate to the sides of the column, with *ca.* 30 conspicuous veins, long-unguiculate and narrowly canaliculate below the middle; lateral lobes semi-orbicular; midlobe ovate to obovate-spatulate, acute to rounded. *Column* 15.0–17.5 mm long, 6–10 mm wide, semi-terete, robust, pubescent; base prolonged into a long column foot; clinandrium membranous, with margins partially covered by the base of the anther. *Anther* with brown margins and a whitish central portion, thick, massive, ovate,

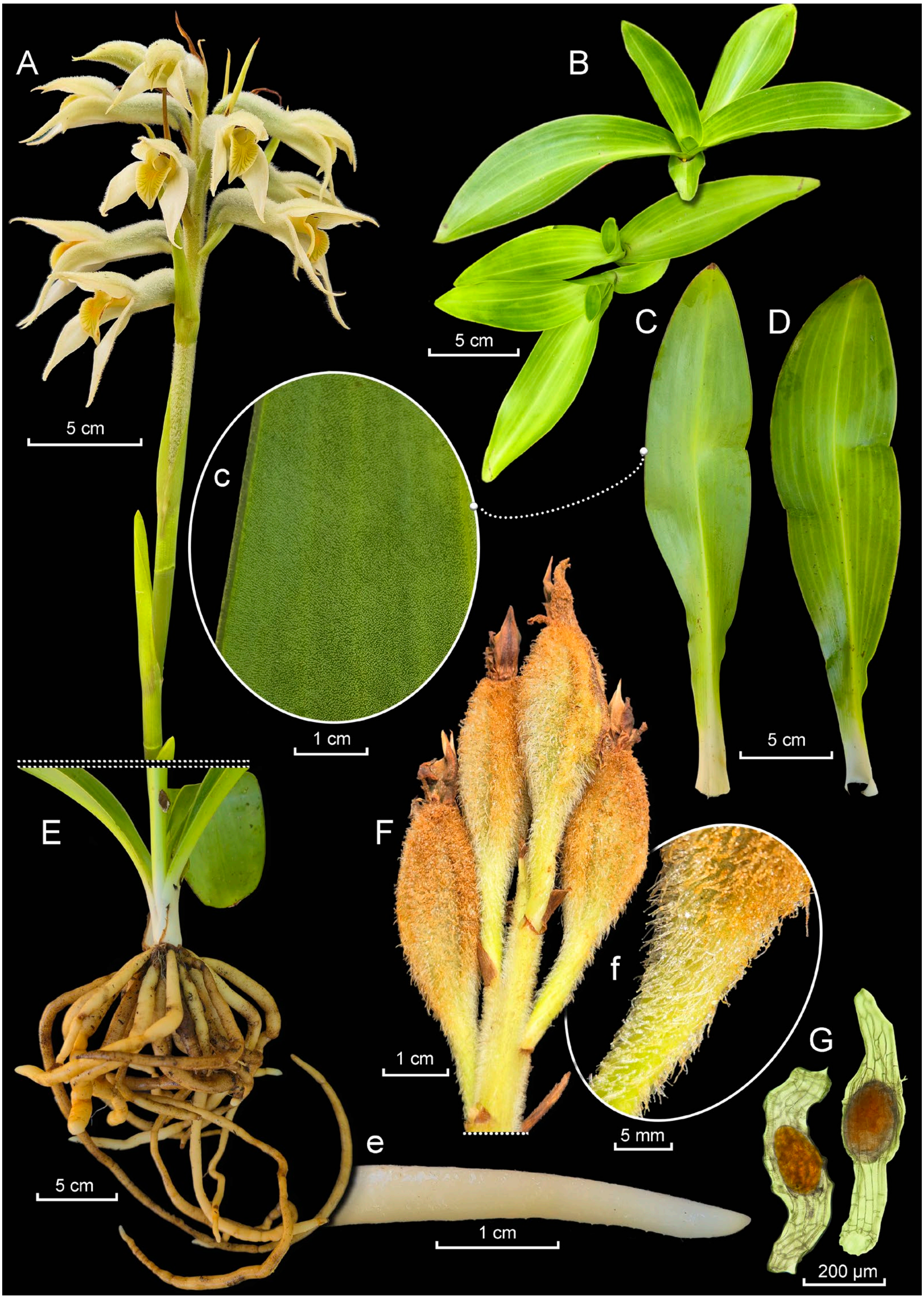

FIGURE 1. *Pteroglossa macrantha*. **A**. General aspect. **B**. Basal rosettes. **C**, **c**. Leaf abaxial surface, entire (C) and detail (c). **D**. Leaf adaxial surface. **E**, **e**. Leaves base, roots (E) and detail of root apex (e). **F**, **f**. Infructescence (F) and detail of fruit basal pubescence (f). **G**. Seeds. Photographs by J.E. Florentín based on *Florentín 389* (CTES).

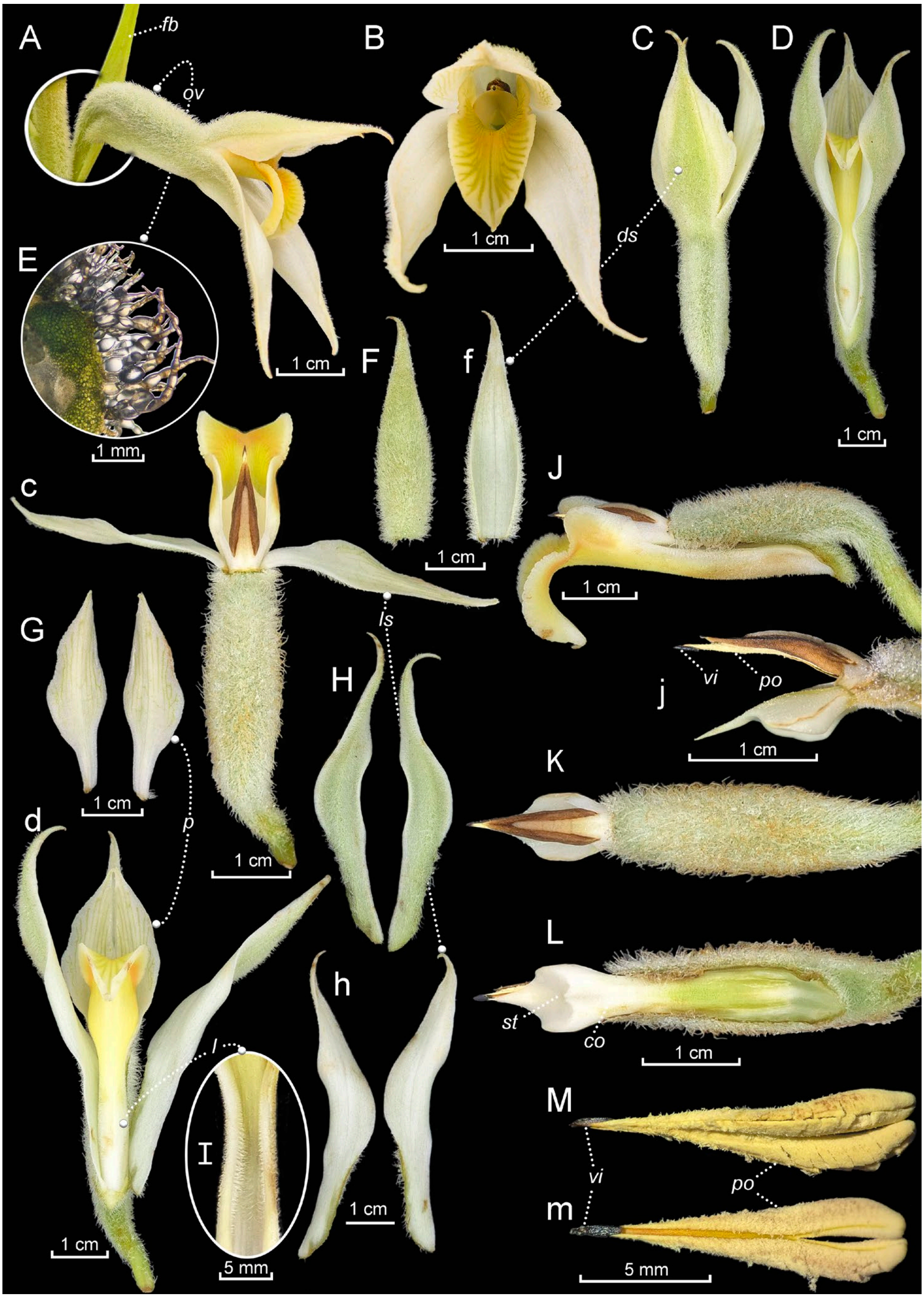

FIGURE 2. Flowers of *Pteroglossa macrantha*. **A**. Flower in lateral view. **B**. Flower in frontal view. **C**, **c**. Flower in dorsal view and detail with lateral sepals and petals removed (c). **D**, **d**. Flower in ventral view and detail showing base of labellum (d). **E**. Ovary's pubescence. **F**, **f**. Dorsal sepal on outer (F) and inner (f) side. **G**. Petals. **H**, **h**. Lateral sepals on outer (H) and inner (h) side. **I**. Labellum inner ornamentation. **J**, **j**. Ovary and column in lateral view and detail with labellum removed (j). **K**. Ovary and column in dorsal view. **L**. Ovary and column in ventral view. **M**, **m**. Pollinia in dorsal (M) and ventral (m) view. Abbreviations: *co*. column. *ds*. dorsal sepal. *fb*. floral bract. *l*. labellum. *ls*. lateral sepals. *ov*. ovary. *p*. petals. *po*. pollinium. *st*. stigma. *vi*. viscidium. Photographs by J.E. Florentín based on *Florentín 389* (CTES).

long-acuminate, with the filament completely adnate. *Pollinarium* 10–12 mm long, 2–3 mm wide, composed of two deeply bipartite, granular, narrowly clavate pollinia, with a ventro-apical, oval, dark gray to black viscidium. *Rostellum* remnant 2.0–2.5 mm long, narrowly triangular, rigid, faintly tridentate in the portion originally covered by the viscidium. *Stigma* slightly bilobed at the base. *Ovary* 23–31 mm long, 8–9 mm wide near the apex, densely pubescent. *Fruit* 5–6 cm long, 1.2–2.0 cm wide, ellipsoid, pubescent, light brown to orangish. *Seeds* 350–820 µm long, 80–140 µm wide, fusiform.

PHENOLOGY: Flowering and fruiting from October to February.

DISTRIBUTION: *Pteroglossa macrantha* was previously known from Brazil (states of Distrito Federal, Goiás, Mato Grosso, Minas Gerais, and Rio Grande do Sul) and Paraguay (Amambay), and Venezuela. In Argentina, its historical record was limited to Misiones (San Ignacio) based on *Ekman 425* (Guimarães *et al.*, 2019). The populations recently identified in Corrientes province occur on sandy riverbanks along the Paraná River, near the city of Empedrado, representing the first modern confirmation of the species in Argentina (Fig. 3). However, according to POWO (2026), the species is also present in Bolivia and Colombia.

ECOLOGY: The Corrientes populations inhabit alluvial grasslands on substrates composed of clay-silt and fine sand. The microhabitats of this species exhibit moderate drainage and direct sun exposure, conditions that appear to favor the presence of *P. macrantha*. Surrounding vegetation includes herbaceous species adapted to periodically inundated conditions, indicating the species tolerance to seasonal variations in soil moisture.

CONSERVATION STATUS IN ARGENTINA: The Empedrado locality harbors high biodiversity and supports extremely localized and fragmented populations of *P. macrantha*. The estimated extent of occurrence (EOO) was 0.012 km² and the area of occupancy (AOO), 4 km², using a 2 km grid, values that fall well below the thresholds for the Critically Endangered (CR) category (kml file available as supplementary material). However, this assessment is currently based on a single locality where the species has recently been recorded. Therefore, a more robust assessment of its conservation status should be conducted in the future. Despite extensive floristic studies and recent species inventories, *P. macrantha* has not been recorded in Misiones for over 100 years. Therefore, we have decided not to include this population in this vulnerability assessment until new records confirm its presence in that area. In Argentina the species meets criteria B1ab(iii)+B2ab(iii), as it is restricted to a single known site and its habitat is projected to undergo continued decline in both quality and extent. It also satisfies criterion C**,** as the known population is extremely small, with a very low number of mature individuals concentrated in a single locality, which increases its susceptibility to stochastic processes and anthropogenic impacts. Finally, it also meets criterion D, due to its very limited area of occupancy and severe spatial restriction.

Multiple threats affect the persistence of the species in the area, including urban expansion along the Paraná River, grazing pressure on natural grasslands, and alterations in the hydrological regime that influences the extent and duration of seasonal flooding. These factors collectively increase the vulnerability of the population and highlight the urgency of implementing *in situ* conservation measures, complemented by *ex situ* cultivation to safeguard the species in Argentina (Fig. 3).

SPECIMENS EXAMINED: Argentina. Corrientes: Empedrado 7 km S de playa de Empedrado. En Barrancas del Paraná, 28 November 2011, *Flachsland & Escobar 175* (CTES); same data, 10 October 2025, *Florentín 389* (CTES).

Discussion. The discovery of *Pteroglossa macrantha* in Corrientes, Argentina, represents an important addition to the knowledge of the Argentine orchid flora. This record confirms the continued presence of the species in Argentina after more than a century without observations and underscores the importance of floristic surveys in poorly explored regions.

The populations identified in Corrientes inhabit marginal alluvial environments along the Paraná River, characterized by seasonally high moisture and sandy soils with a considerable drainage. These habitats are comparable to those described for the species in Paraguay and southern Brazil (Buzatto *et al.*, 2014), suggesting similar ecological conditions throughout its

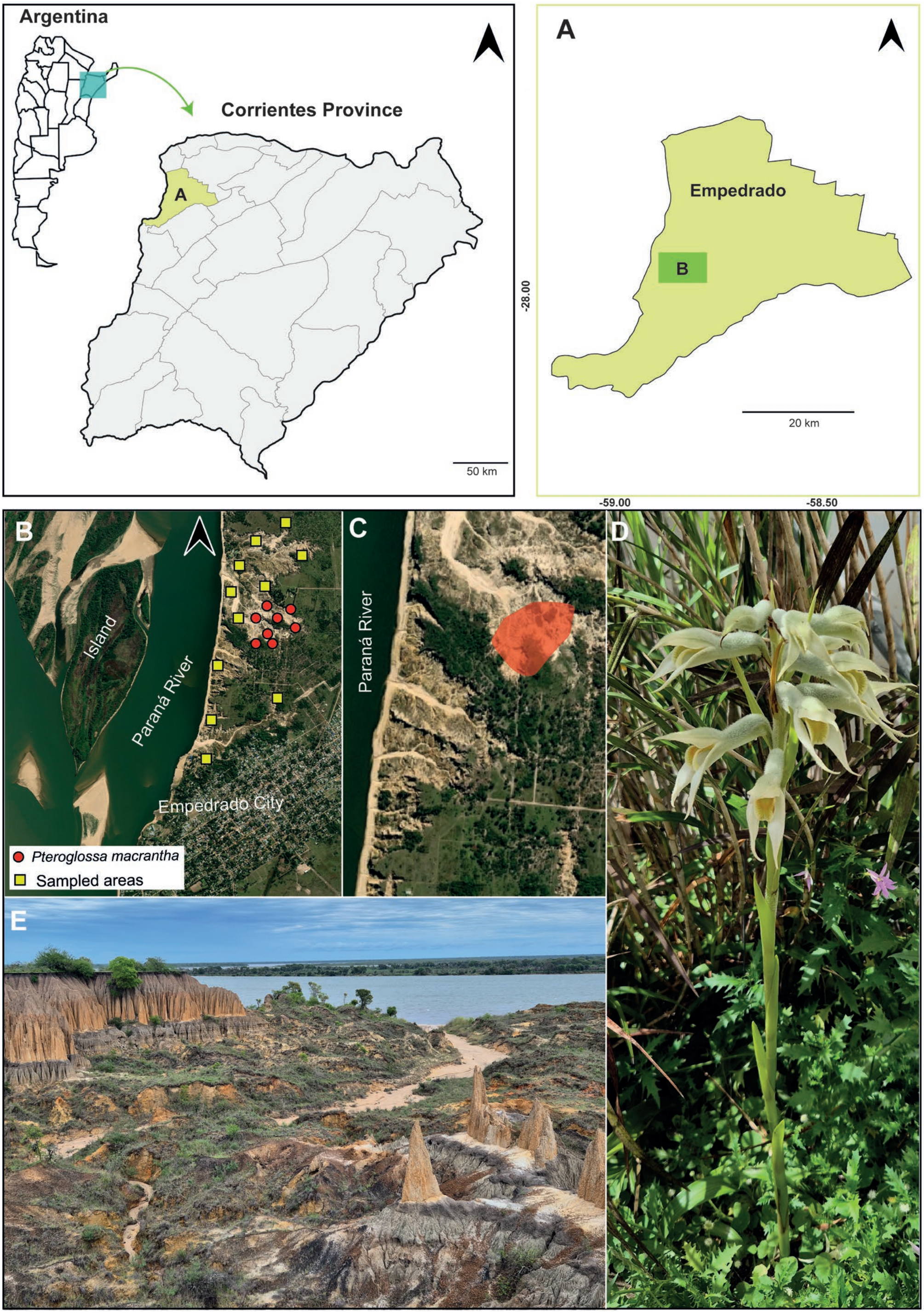

FIGURE 3. Distribution, conservation, and ecology of *Pteroglossa macrantha*. **A**. Location of Empedrado, Corrientes, Argentina. **B**. Satellite image of the study area showing the distribution of *P. macrantha* (red circles) and other sampled sites where the species was not located (yellow square). **C**. Detail of the study area showing the polygon of *P. macrantha* distribution. **D**. Flowering plant in cultivation. **E**. Habitat, ravines of Empedrado. Photographs by J.E. Florentín.

southern distribution. However, the species restricted extent of occurrence and the lack of additional records indicate a very limited distribution in Argentina.

Morphological characteristics of the Corrientes populations are consistent with the diagnostic features of *P. macrantha* as described by Buzatto *et al.* (2014) for Rio Grande do Sul. Plants from Corrientes are slightly taller (up to *ca.* 50 cm) and have narrower leaves (3–6 cm wide in Corrientes *vs.* 5–8 cm). The inflorescence is similar in size but tends to be somewhat laxer and may bear slightly more floral bracts (6–9 in Corrientes *vs.* 6–7). The flowers correspond closely to those reported for the species, though the Corrientes specimens show broader sepals (up to 10 mm), slightly wider petals (up to 10 mm), and a larger labellum (30–42 mm long). The rostellum and pollinarium are also comparatively larger, and the viscidium is dark gray to black rather than grey. These differences are considered quantitative variations within the species and provide additional information on its morphological variety.

Despite extensive floristic surveys in historical localities of Misiones, including areas near Ekman's 1908 collection sites such as Parque Provincial Teyú Cuaré (Misiones province) and its surroundings (Biganzoli & Múlgura, 2004), as well as recent inventories conducted by the Ministerio de Ecología de Misiones (2022), *P. macrantha* has not been recorded in the province. These localities are situated within the same general region as the original records and include habitats with some similarities to those occupied by the Corrientes population, such as seasonally moist grasslands and riverine sandy soils. However, despite these potentially suitable conditions, the species has not been detected in recent surveys, suggesting that it may be extremely rare in Misiones, locally extirpated, or restricted to microhabitats that have not been adequately sampled. This underscores the significance of the population discovered in Corrientes as the first modern and southernmost record of *P. macrantha* in Argentina, highlighting the conservation importance of the Paraná River sandbanks and alluvial grasslands for ensuring the persistence of this critically rare orchid.

At a broader scale, this finding underlines the importance of riverine grasslands and sandbanks as critical habitats for the conservation of rare and threatened Neotropical orchids. Other notable examples include two endemic species from Corrientes Province (Florentín *et al.*, 2025), *Pteroglossa luteola* Garay (Garay, 1980) and *Skeptrostachys correana* Szlach. (Szlachetko, 1996), both restricted to open, moist environments associated with fluvial dynamics. Likewise, *Malaxis irmae* Radins & Salazar, known from only a few records in riverine habitats of Misiones and Uruguay (Radins *et al.*, 2014), represents another remarkable example of highly specialized and poorly documented species in these environments.

Taken together, these cases highlight that remnant populations of species considered extremely rare, locally extirpated, or unrecorded for more than a century may still persist in specific and underexplored microhabitats. Accordingly, our results reinforce the need to continue systematic floristic surveys in northeastern Argentina, with particular emphasis on riverine environments, in order to detect, document, and conserve these vulnerable orchid populations.

SUPPLEMENTARY MATERIAL. KML file (https://figshare.com/s/3eff463171536306bfd5) with occurrence data of *P. macrantha* in Argentina used for EOO and AOO calculations.

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AUTHOR CONTRIBUTION. JEF and EAF conceived the study, designed the research strategy, and carried out the fieldwork and specimen documentation. JEF and NSD performed the morphological analyses and prepared the description and illustrations. JEF wrote the first draft of the manuscript, interpreted the results, and integrated the taxonomic conclusions. NSD and DLS provided critical revisions, contributed to the discussion and interpretation of data, and improved the final version of the manuscript. JEF supervised the overall study and contributed to the final editing and approval of the paper.

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CONFLICT OF INTEREST. The authors declare no competing interests.

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ADDITIONS TO THE ORCHID FLORA OF BHUTAN IV

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Abstract. Five orchid species belonging to four genera, namely, *Bulbophyllum deergongense*, *Bulbophyllum nepalense*, *Liparis sootenzanensis*, *Spiranthes himalayensis* and *Zeuxine gracilis*, are reported for the first time from Bhutan. These findings are based on systematic native floristic diversity field surveys carried out between 2023 and 2025. We provide descriptions, along with information on type, distribution, phenology, habitat, notes, and colour plates to facilitate accurate species identification and support practical conservation efforts.

Keywords / Palabras clave: biodiversidad, biodiversity, Orchidaceae, sección *Brachyantha*, sección *Reptantia*, section *Brachyantha*, section *Reptantia*, taxonomy, taxonomía

Introduction. The pioneer work on orchids of Bhutan was done by Pearce and Cribb (2002), who reported 369 orchid species. Since then, there has been a notable increase in the number of orchid species due to recent discoveries of species new to science and new records for Bhutan (Chaida & Tashi, 2020; Dalström *et al*., 2017, 2021; Dechen *et al*., 2020; Dorji, 2008; Dorji *et al*., 2023; Ghalley *et al*., 2022; C. Gyeltshen *et al*., 2019; N. Gyeltshen *et al*., 2017, 2020; P. Gyeltshen *et al*., 2020, 2021, 2023, 2024; Gurung, 2006; Rabgay & Kumar, 2019; Rabgay *et al*., 2021; Tobgay *et al*., 2024; Tshewang *et al*., 2021; Zangpo *et al*., 2019, 2021). Recently, two new species, *Calanthe hastilabia* S.Tobgay, T.Nidup & K.Wangchuck (Tobgay *et al*., 2025) and *Zeuxine drukyulensis* P.Gyeltshen, K.Rabgay & Kumar (Gyeltshen *et al*., 2025) were also added to the orchid flora of Bhutan. With these discoveries, the total number of orchid species in Bhutan now stands at 501, including 12 species reported from unconfirmed localities. Several species reported by Gurung (2006), Dalström *et al.* (2017, 2021), and Chaida & Tashi (2020), are known only from photographs and lack adequate descriptions, therefore, these records require proper documentation and the collection of herbarium specimens.

In continuation with the ongoing surveys and publications, we present here five additional orchid species previously not known from Bhutan. The findings are based on systematic field surveys carried out between 2023 and 2025. With these additions, the orchid flora of Bhutan now comprises 506 species. This increasing species count underscores the significance of continued exploration and research.

Materials and methods. This study was based on floristic assessments conducted in Bhutan between January 2023 and July 2025. Following careful examination of collected specimens, consultation of herbarium materials at CAL, FAFU, KATH, E, K, PE, and THIM (herbarium codes follow Thiers *et al*., 2025, continuously updated), and review of protologues along with other relevant literature (Chen *et al*., 2009; King & Pantling, 1898; Miao *et al*., 2023; Pearce & Cribb, 2002; Raskoti & Ale, 2013; Tetsana *et al*., 2019), we concluded that five orchid species had not previously been reported from Bhutan. We present these five species in this manuscript with their descriptions, distribution maps, habitat notes, and colour photographs to facilitate accurate species identification and support practical conservation efforts.

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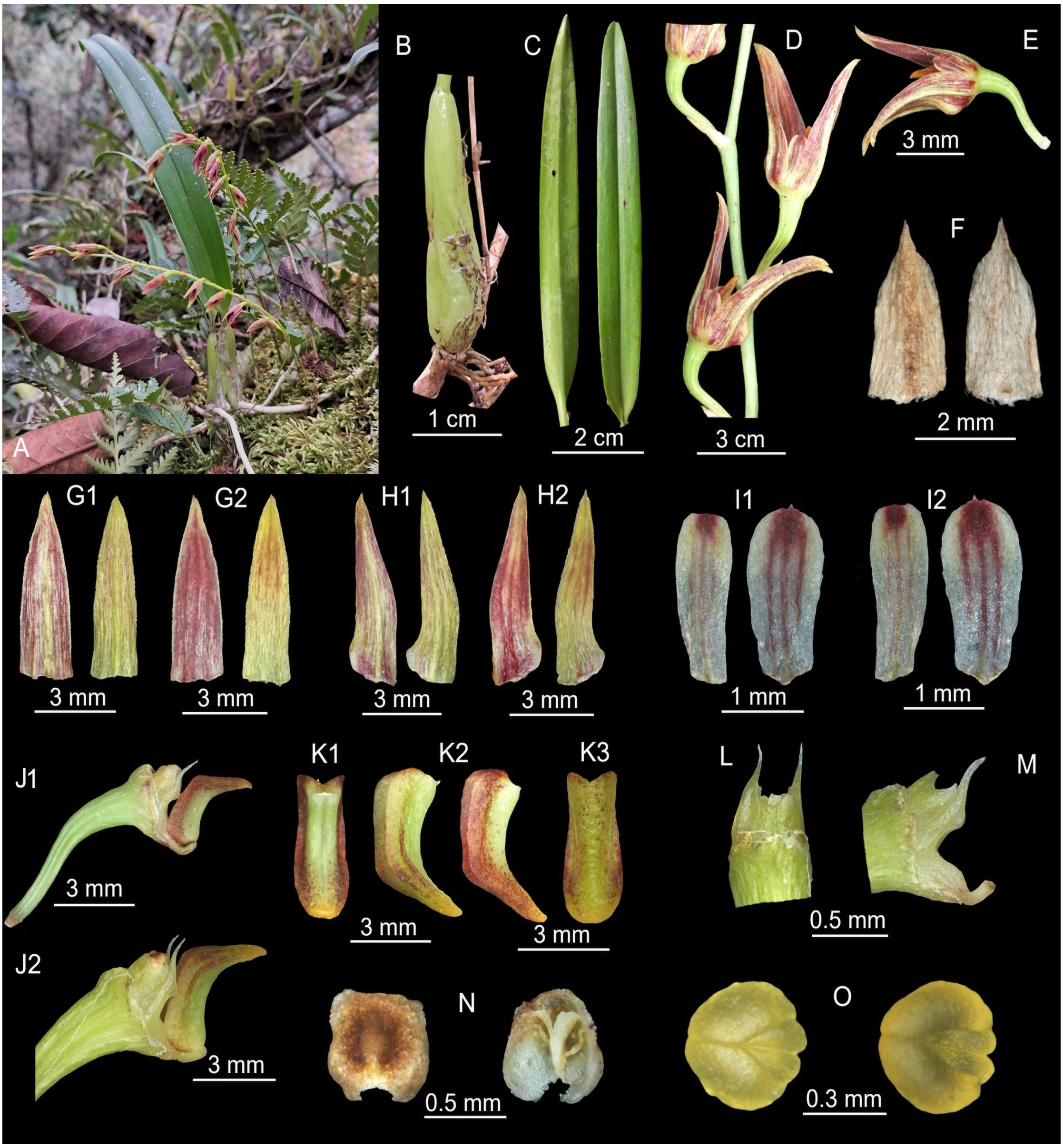

Figure 1. *Bulbophyllum deergongense* J.L.Miao & J.W.Zhai. **A**. Plant in the habitat. **B**. Pseudobulb. **C**. Leaf. **D**. Part of Inflorescence. **E**. Flower, lateral view. **F**. Floral bract, abaxial and adaxial views. **G1–2**. Dorsal sepal, abaxial and adaxial views. **H1–2**. Lateral sepals, abaxial and adaxial views. **I1–2**. Petals, abaxial and adaxial views. **J**. Pedicel and ovary with labellum attached, lateral views. **K1–3**. Labellum, abaxial, lateral and adaxial views. **L-M**. Column abaxial and lateral views. **N**. Anther cap, abaxial and adaxial views. **O**. Pollinia, abaxial and adaxial views. Photographs and illustrations assembled by Phub Gyeltshen based on *Gyeltshen 483* (THIM).

Author abbreviations follow the International Plant Names Index (IPNI, 2025). The circumscription and terminology used in the morphological descriptions follow Pearce & Cribb (2002) and Beentje (2024). Measurements of vegetative and reproductive structures of at least five randomly selected flowers of each species were taken *in situ*. Geographical information, including elevation and geo-coordinates, was recorded using a Garmin GPS (eTrex 40), while photographs were captured with a digital camera. Macro images were obtained using a Z-stacking microscope (ZEISS Stereo Discovery V20, Carl Zeiss Microscopy GmbH) at the National Biodiversity Centre, Thimphu, Bhutan. Coloured plates were prepared and edited using Adobe Photoshop. Distribution data were mapped with QGIS software version 3.38.1 (QGIS Development Team, 2024), and voucher specimens were deposited at the Bhutan National Herbarium (THIM).

Taxonomic Treatment

Bulbophyllum deergongense J.L.Miao & J.W.Zhai, Phytotaxa 619(2): 200. 2023. Fig. 1.

TYPE: China. Tibet, Motuo, Deergong, *Zhai 0180* (holotype: FAFU; isotype: IBSC).

Plant epiphytic, 10–12 cm tall. *Rhizome* thick, covered with fibrous sheaths, (–3) 5–14 (–17) × 2–3 mm. *Roots* emerging from under surface of rhizome throughout it’s length . *Pseudobulbs* oblong-conical, 2.0–4.5 × 0.8–1.2 cm, glabrous, green. *Leaf* solitary, petiolate; petiole 5–10 mm long, obliquely notched on the pseudobulb; lamina leathery, oblong-elliptic to oblong-lanceolate, 8.0–16.5 (–21 cm) × 1.0–1.5 cm (–2 cm), apex subacute, margin entire, base slightly attenuate. *Inflorescence* racemose, 1–2-flowered, erect or sub-erect, emerging from the base of the pseudobulbs or rhizome near the base of the pseudobulbs, 6.5–25.5 cm long; laxly bearing (–3) 5–14 (–16) flowers; peduncle terete, 4.5–10.0 cm long, 2 to 3 sheathing bracts, deflexed at distal portion whilst blooming. *Sheathing bracts* oblong-lanceolate, 6–12 mm long, glabrous; rachis (–2.5) 4–12 (–16) cm. *Flowers* not fully open, 2–5 mm across, yellow to reddish-brown. *Floral bracts* lanceolate, 3–4 × 1.0–1.4 mm, apex acuminate, glabrous; pedicel and ovary, 5–7 mm long, glabrous, yellowish green; *dorsal sepal* oblong, 6.3–7.8 × 2.0–2.2 mm, apex acute, margin entire, yellowish-green to red, 3-veined; *lateral sepals* obliquely oblong-lanceolate, 6.7–8.0 × 1.8–2.1 mm, apex acuminate, margin entire or inconspicuously crenate, more than ½ of the inner margin connate, yellow with red stripes; *petals* broadly oblong-obovate, 2–3 × 1.0–1.2 mm, apex truncate or rounded, apiculate, margin entire, with a red spot in the middle, 3-veined. *Labellum* ovate-oblong, 2.7–3.0 × 1.3–1.5 mm, apex obtuse, papillose, deflexed near the apex, attached to the end of the column-foot by a mobile joint, greenish-yellow abaxially, and yellowish-green with a red tinge or red flush adaxially, margin reddish or yellowish-green with a red tinge, with two high ridges close to the edge. *Column* quadrangular, *ca.* 1.0–1.1 × 0.8–1.0 mm, glabrous, green, with forward and incurved foot; foot rectangular, 1.5 mm long, glabrous, yellow; *stelidia* 2, 0.8–1.0 mm long, with a tooth on the upper margin and round to triangular protrusion on the lower margin; *anther cap* oblong, c. 1 × 1 mm, verrucous abaxially, brown. *Pollinia* 4, 2 pairs, each pair unequal in size, fusiform, 0.3–0.5 mm long, yellow. *Capsules* unknown.

Phenology: Flowering in February–April and fruiting in March–July.

Habitat: *Bulbophyllum deergongense* occurs in warm broadleaved forests at an elevation of 1000–2000 m in association with *Dendrobium nobile* Lindl., *Bulbophyllum hirtum* (Sm.) Lindl., *Bulbophyllum spathulatum* (Rolfe ex E.W.Cooper) Seidenf., *Callostylis rigida* Blume, *Coelogyne articulata* (Lindl.) Rchb.f. and *Coelogyne prolifera* Lindl.

It is epiphytic on *Agapetes variegata* (Roxb.) D.Don ex G.Don, *Lyonia ovalifolia* (Wall.) Drude, *Quercus griffithii* Hook.f. & Thomson ex Miq. and *Rhododendron arboreum* Sm.

Distribution: Bhutan (Wangdue Phodrang, Fig. 2) and China (Tibet Autonomous Region). An additional population has been observed in Zhemgang District; however, due to the absence of a voucher specimen, it has not been included in the distribution map.

Specimen examined: BHUTAN: Wangdue District, Athang Gewog, near Athang Lake, 1270 m, 27.292278°N, 90.108647°E, 08 March 2025, *P. Gyeltshen 483* (THIM21793, THIM21794, THIM21795, THIM21796, THIM21797).

Notes: In the original description, *Bulbophyllum deergongense* was differentiated from *Bulbophyllum reptans* (Lindl.) Lindl. in having cylindrical pseudobulbs with prominent ridges, pseudobulbs distantly placed on the rhizome, 15–20 cm apart; inflorescences with 12–15

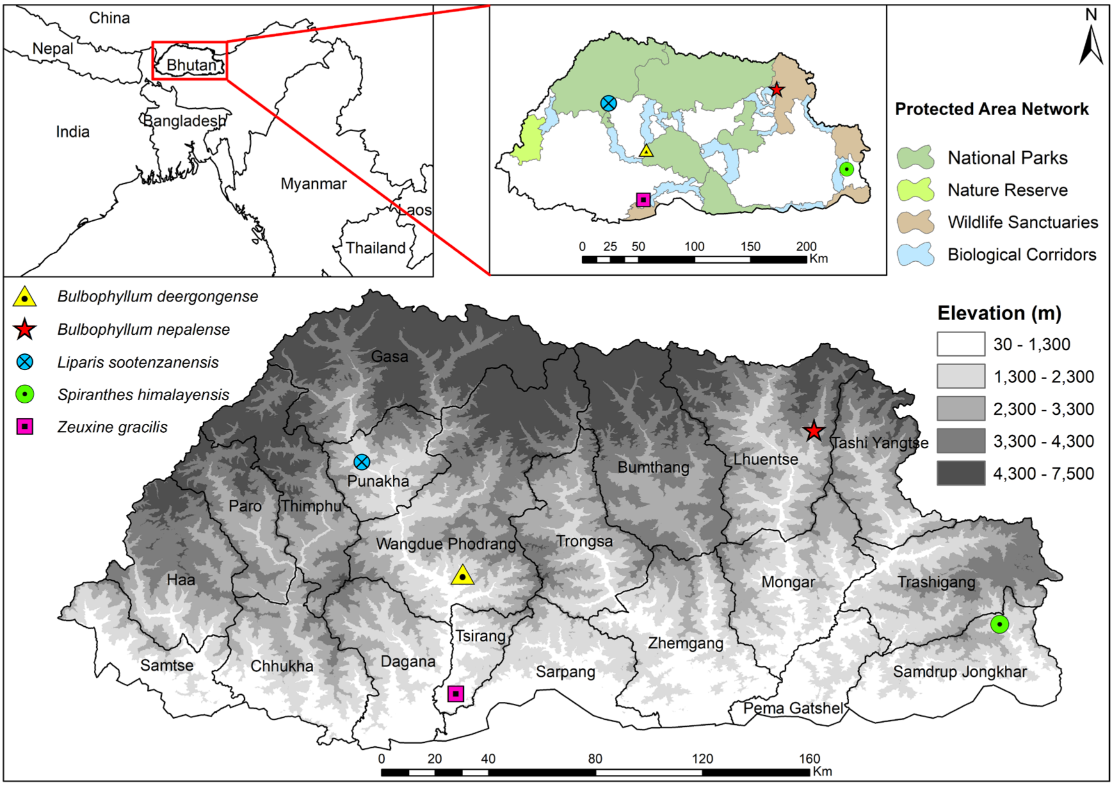

FIGURE 2. Distribution map of *Bulbophyllum deergongense, B. nepalense*, *Liparis sootenzanensis*, *Spiranthes himalayensis* and *Zeuxine gracilis* in Bhutan. Map by Phub Gyeltshen.

flowers (*vs*. 3–6 flowers); flowers yellowish green without stripe, with a purple-brown rounded spot at the apex, dorsal sepal with prismatic projection abaxially and lateral sepals yellowish green, without stripes (Miao *et al.*, 2023). However, specimens of *B. deergongense* from Bhutan have yellowish-green sepals with red striations; petals broadly oblanceolate or spathulate, white with a rounded reddish spot at the apex, 3 prominent veins, margins entire or with a few small teeth towards the apex, apex truncate or rounded, sometimes apiculate; labellum deflexed less in the middle, with papillate hairs towards the apex abaxially. Therefore, *B. deergongense* can be morphologically differentiated from *B. reptans* by floral bracts shorter than pedicel (*vs*. longer floral bracts), and petals broadly oblanceolate or spathulate with rounded reddish spot at the apex, three prominent red veins (*vs*. oblong to oblong-elliptic petals without spot and whitish striations).

Bulbophyllum deergongense has been placed in the *Bulbophyllum* section *Reptantia* J.J.Verm. (Miao *et al.*, 2023) because it has branched and creeping rhizome, pseudobulbs with single persistent leaf, inflorescence an elongate raceme arising from the basal node of the new shoot and with laxly arranged flowers, dorsal sepal 3-veined, lateral sepals spreading, petals half as long as dorsal sepal, labellum mobile, and stelidia almost falcate with a tooth along the lower margin (Pearce *et al.*, 2001; Vermeulen *et al.*, 2014). Section *Reptantia*, as circumscribed by Vermeulen *et al.* (2014), is most similar to *Bulbophyllum* section *Adelopetalum* (Fitz.) J.J.Verm., particularly in having petals that are half as long as, or shorter than, the dorsal sepal. It is distinguished by its inflorescence that arises from the basal nodes of newly developing shoots (Vermeulen *et al.*, 2014). Biogeographically, section *Reptantia* is predominantly distributed across East, South, and Southeast Asia (Chen & Vermeulen, 2009; Pearce & Cribb, 2002), whereas section *Adelopetalum* is largely confined to Australia and New Zealand (Simpson *et al.*, 2024; Vermeulen, 1993).

Bulbophyllum nepalense Raskoti & Ale, Edinburgh J. Bot. 70(2): 381. 2013. Fig. 3.

TYPE: Nepal. Sivapuri National Park, 2300 m, 3 August 2010*, R. Bhakta B.325* (holotype: KATH!).

Plant epiphytic, 10–12 cm tall. *Rhizome* thick, covered with fibrous sheaths, 10–13 × 4–5 mm. *Roots* emerging from all along the rhizome. *Pseudobulbs* narrowly conical, 2.0–3.2 × 0.8–1.1 cm, lightly angular with longitudinal furrows, glabrous, green. *Leaf* solitary, petiolate; petiole 5–6 mm long, obliquely notched on the pseudobulb, green; lamina oblong-elliptic, 5.0–7.7 × 0.8–1.2 cm, leathery, apex subacute, margin entire, base slightly attenuate. *Inflorescence* sub-umbellate, erect or sub-erect, emerging from the base of the pseudobulbs; 5 to 10 flowered; peduncle terete, 4.5–8.0 cm long, covered with 2 to 3 sheathing bracts, green with dark brown streaks, deflexed at distal portion whilst blooming. *Sheathing bracts* oblong-lanceolate, 7–10 mm long, glabrous, upper sheathing bracts lime green, basal bracts brown. *Flowers* resupinate, 2.0–3.2 cm long, golden yellow. *Floral bracts* lanceolate, 5.5–7.0 × 1.0–2.0 mm, apex acuminate, glabrous, pale greenish white or yellowish-green; pedicel and ovary, 5.5–7.0 mm long, glabrous, yellowish green; *dorsal sepal* oblong, 3.8–4.2 × 1.8–2.0 mm, apex obtuse or unevenly dentate, glabrous towards apex and papillate at the base, pinkish with three prominent red veins, margin entire; *lateral sepals* obliquely oblong-lanceolate, 1.4–2.5 × 0.2–0.3 cm, apex acuminate, papillate at base and glabrous towards apex, base yellow with three red stripes and yellow distally, lower margin connate towards the base, upper margin free at the base and connate towards the apex, base oblique; *petals* obliquely oblong, 2.8–3.0 × 1.8–2.0 mm, apex obtuse, margin entire and red, glabrous, pinkish with three red veins. *Labellum* ovate, 2.0–2.5 × 1.0–1.5 mm, apex subacute, deflexed in the middle, attached to the end of the column-foot by a mobile joint, base grooved, maroon abaxially, maroon with golden yellow adaxially. *Column* quadrangular, *ca*. 1 × 1 mm, with forward pointed and incurved foot, glabrous, red; foot rectangular, 1.6–2.0 × 1.0–1.3 mm, glabrous, yellow; *stelidia* 2, narrowly triangular, *ca*. 1 mm long, with adaxial teeth present; *anther cap ca*. 1.1 × 1.0 mm, brown. *Pollinia* 4, fusiform, c. 1 mm long. *Capsules* unknown.

Phenology: Flowering in July–August and fruiting unknown.

Habitat: *Bulbophyllum nepalense* was found growing as an epiphyte on the *Alnus nepalensis* D.Don and *Juglans regia* L. trees in the cool broadleaved forest at 2140 m elevation.

Distribution: Nepal (Shivapuri National Park) and Bhutan (Lhuentse-Bumdeling Wildlife Sanctuary, Fig. 2).

Specimen examined: Lhuentse, Khoma Gewog, Tshango area, 2140 m, 27.77526 N, 91.29000E, 13 August 2023, *K. Sangay 355* (THIM18793).

Notes: *Bulbophyllum nepalense* has been placed in the sect. *Cirrhopetalum* (Lindl.) Rchb.f. (Raskoti & Ale, 2013). It is epiphytic on shrubs growing in the moist humid area in the oak forest at an elevation of 2300 m, and it flowers from July to August in Nepal (Raskoti & Ale, 2013). *Bulbophyllum nepalense* differs from *Bulbophyllum retusiusculum* Rchb.f. by its narrowly ovoid-conical pseudobulbs (Raskoti & Ale, 2013), sepals broader at base, ovate labellum with two ridges with minutely colliculate on the adaxial surface. According to Pridgeon *et al.* (2014), *Bulbophyllum* sect. *Cirrhopetalum* (Lindl.) Rchb.f. has a creeping rhizome, subumbellate inflorescence arising from the base of the one-leaved pseudobulb, pedicellate ovary of the lowermost flower twice as long as rachis or longer, petals (partly) ciliolate, fimbriate or paleate, and stelidia with an antrorse tooth on the adaxial surface. However, the holotype has entire or scabrid petals and stelidia without an antrorse tooth on the adaxial surface (Raskoti & Ale, 2013). The analysis of the same species from Bhutan also suggests that *B. nepalense* has entire petals, sepals twisted proximally, connate along upper margins, stelidia tapering towards the apex, with a triangular tooth along the upper margin, and a labellum undivided. Therefore, we propose , *B. nepalense* to be placed under the *Bulbophyllum* section *Brachyantha* Rchb.f.

Liparis sootenzanensis Fukuy., in Ann. Rep. Taihoku Bot. Gard. 3: 84. 1933. *Liparis macrantha* var. *sootenzanensis* (Fukuy.) S.S.Ying, Coloured Ill.

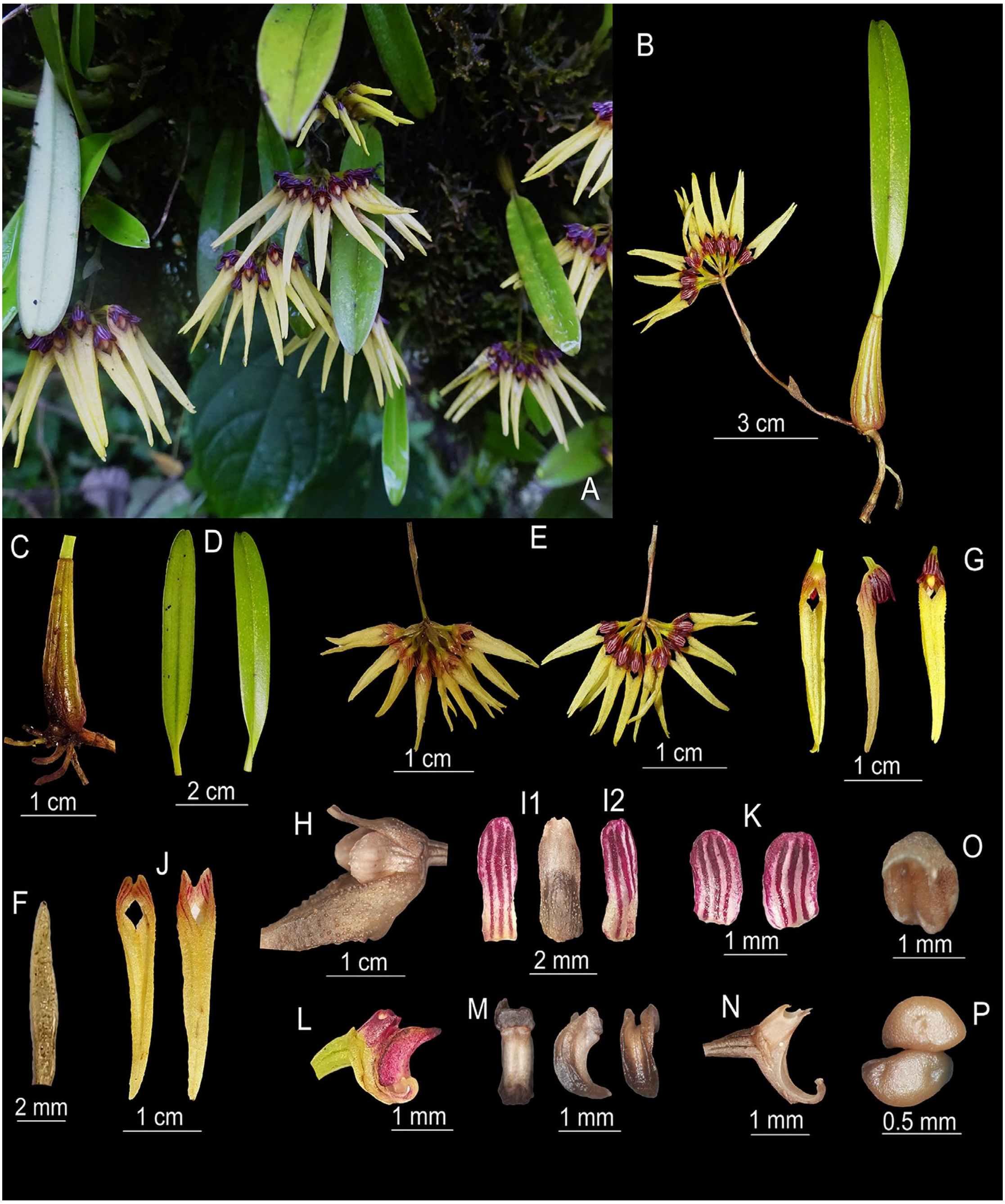

FIGURE 3. *Bulbophyllum nepalense* Raskoti & Ale. **A**. Plant in its natural habit. **B**. Habit. **C**. Pseudobulb. **D**. Leaf, abaxial and adaxial views. **E**. Inflorescence, abaxial and adaxial views. **F**. Floral bract, adaxial view. **G**. Flowers, abaxial, lateral and adaxial views. **H**. Close up flower, lateral view. **I1–2**. Dorsal sepal, abaxial and adaxial views. **J**. Lateral sepals, abaxial and adaxial views. **K**. Petal, abaxial and adaxial views. **L**. Column with labellum attached, lateral view. **M**. Labellum, abaxial, lateral and adaxial views. **N**. Column, lateral view. **O**. Anther cap with pollinia attached, adaxial view. **P.** Pollinia, lateral view. Photographs by Karma Sangay (A–G, J–L) and Phub Gyeltshen (H, I, M–P). Illustration assembled by Phub Gyeltshen based on *K. Sangay 355* (THIM).

Indig. Orchids Taiwan 1(2): 224. 1977; *Liparis nigra* var. *sootenzanensis* (Fukuy.) T.S.Liu & H.J. Su, Fl. Taiwan 5: 1047. 1978; *Diteilis sootenzanensis* (Fukuy.) M.A.Clem. & D.L.Jones, Orchadian 15(1): 41. 2005; *Empusa sootenzanensis* (Fukuy.) T.C.Hsu, III. Fl. Taiwan 2: 20. 2016. Fig. 4.

TYPE: Taiwan. Shinchiku, Minamisooten-zan, May 1933, *N. Fukuyama 4104* (holotype: KPM!).

Plant terrestrial herb, 20–46 cm tall. *Stems* 2–3, borne in tight clusters on short rhizomes, erect, bearing 3–4 leaves clustered at the apex, the older ones leafless. *Pseudobulbs* cylindrical-conoid, 8–12 × 2–2.5 cm, 3–4-noded, enclosed in papery sheaths. *Basal sheaths* triangular, 1.5–8.7 × 2.0–4.6 cm; middle and apex sheaths oblong-lanceolate, 12.5–13.6 × 3.8–4.3 cm, green, 9-veined, prominent. *Leaves* oblique, elliptic 18–23 × 7.5–9.6 cm, plicate, apex acute, margin undulate, sheathing at base, green, 7–10-veined; sheathing base 2.8–4.6 cm long. *Inflorescence* terminal, erect, arising from stem apex between leaf bases, 20.0–33.5 cm long; peduncle 10–15 cm long, with 1 small deltoid sterile bract, 10–12 × 3.5–4.0 mm, abaxial midvein prominent; rachis 10.0–18.5 cm long, bearing 10–34 laxly to sub-densely arranged flowers, ridged, green. *Floral bracts* ovate-triangular, 3–7 × 2–4 mm, apex acuminate, green. *Flowers* 13–20 mm across, petals and sepals spreading backwards and curved, green flushed orange-yellow, becoming orange with age; pedicel and ovary patent, arching upwards at the apex, 8–25 mm long, ridged, green; *dorsal sepal* linear, 13.5–14.0 × 2.8–3.0 mm, arching forwards over column, apex obtuse, margins rolled backwards; *lateral sepals* oblong-lanceolate, 12–14 × 3.8–4.0 mm, apex obtuse, margins rolled backward; *petals* linear, 12.5–13.0 × 1.0–1.1 mm, apex acute; *labellum* flabellate, 13.7–14.0 × 8.6–10.0 mm, slightly notched at apex, strongly decurved above the base and rolling backwards at middle, apical margins serrulate, distinctly longitudinally grooved at centre, bearing 2 bulbous calli near base which give rise to 2 diverging ridges that extend to below the middle, lateral margins cuneate and entire below widest point,. *Column* clavate, arching forwards, 6–7 × 1.0–1.1 mm, winged, with a pair of small triangular stelidia below the apex; anther cape, orbicular, cape c. 1 × 1 mm. *Pollinia* 4 in 2 pairs, clavate, 0.5 mm long, orange. *Capsules* ellipsoid-obovoid, 1.5–2.2 cm long.

Phenology: Flowering occurs from late April to May.

Habitat: *Liparis sootenzanensis* grows in the marshy area in the subtropical forest at 1400 m in elevation.

Distribution: Bhutan (Punakha, Fig. 2), China, India, Japan, Laos, Taiwan, Thailand and Vietnam. An additional population has been observed in Tashiyangtse; however, due to the absence of a voucher specimen, it has not been included in the distribution map.

Specimen examined: Punakha, Goenshari Gewog, Rimchu area, 1415 m, 27.6677N, 89.7688E, 29 May 2024, *P.Gyeltshen & K.Rabgay 267* (THIM22890, THIM22891).

Notes: In Bhutan, *Liparis sootenzanensis* differs from *Liparis nervosa* (Thunb.) Lindl. by large green flowers and with serrulate apical margins of the labellum. *Liparis sootenzanensis* is also similar to *L. gigantea* C.L.Tso, which is widely distributed from the Indo-Myanmar region to Southeastern China and Taiwan. It can be distinguished by the absence of prominent, rounded to triangular wings at the column apex (*vs*. presence of prominent round or triangular-shaped wings).

Spiranthes himalayensis Survesw., Kumar & Mei Sun, PhytoKeys 89: 118. 2017. Fig. 5.

TYPE: India. Manipur, Ukrul district, Imphal-Jessami road, 1 May 2016. *S.Surveswaran 1* (JCB 1001) (holotype: JCB!).

Plant terrestrial herbs with tuberous roots, 10.0–30.5 cm tall. *Tubers* terete, 7–13-numbered, 1.5–6.5 cm long, 2–5 mm in diameter, creamy brown. *Stem* erect, 1.5–2.5 cm long, green, leaf clustered towards the base. *Leaf* 5 to 13 per plant; lamina linear-lanceolate, 3.7–7.3 × 0.4–0.9 cm, obscurely 5-veined with depression on the upper surface and elevated lining underneath, mid-vein prominent. *Inflorescence* racemose, up to 28.2 cm long, terete, up to 5 sterile bracts sheathing the peduncle; peduncle terete, 10.5–11.5 cm long, glabrous towards base, glandular-pubescent towards apex; rachis 16.5–17.5 cm long, glandular-pubescent, flowers spirally arranged, flowers evenly distributed along the rachis, flowers opening from the

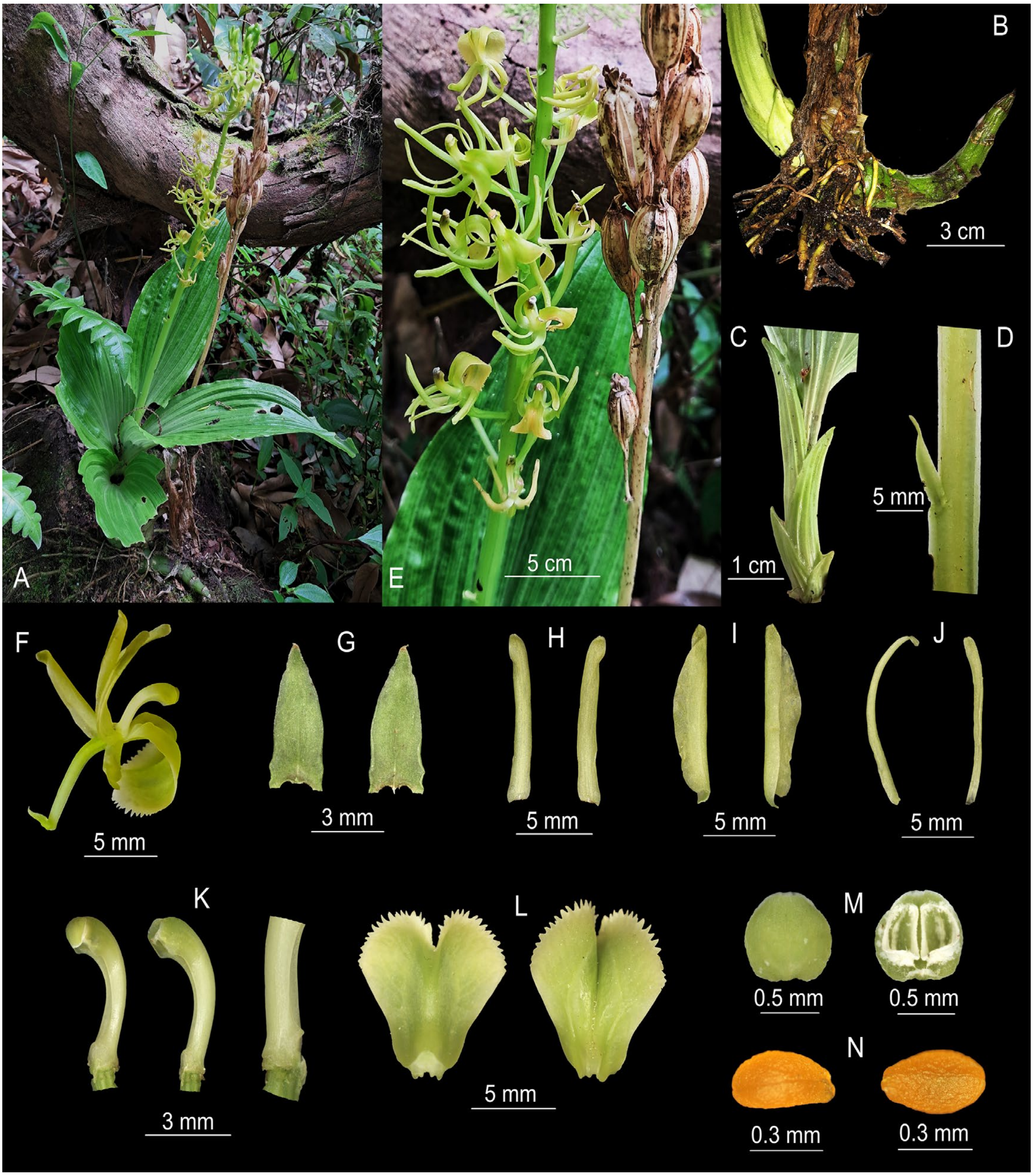

FIGURE 4. *Liparis sootenzanensis* Fukuy. **A**. Habit. **B**. Rhizome. **C**. Basal sheaths, lateral view. **D**. Portion of stem with sterile bract attached. **E**. Inflorescence. **F**. Flower, lateral view. **G**. Floral bracts, abaxial and adaxial views. **H**. Dorsal sepal, abaxial and adaxial views. **I**. Lateral sepal, abaxial and adaxial views. **J**. Petal, abaxial and adaxial views. **K**. Column, lateral view. **L**. Labellum, abaxial and adaxial views. **M**. Anther cap, abaxial and adaxial views. **N**. Pollinia, abaxial and lateral views. Photographs and illustrations assembled by Phub Gyeltshen based on *P.Gyeltshen & K.Rabgay 267* (THIM).

base, pubescent abaxially with glandular hairs. *Sterile bracts* linear-lanceolate, 15–30 × 2.5–3.2 mm, apex acuminate, glabrous, green. *Floral bracts* linear-lanceolate to lanceolate, 5–13 × 1.5–3.0 mm, longer than the combined length of pedicel and ovary, apex acuminate, margin entire, white, green. *Flowers* widely open, re-

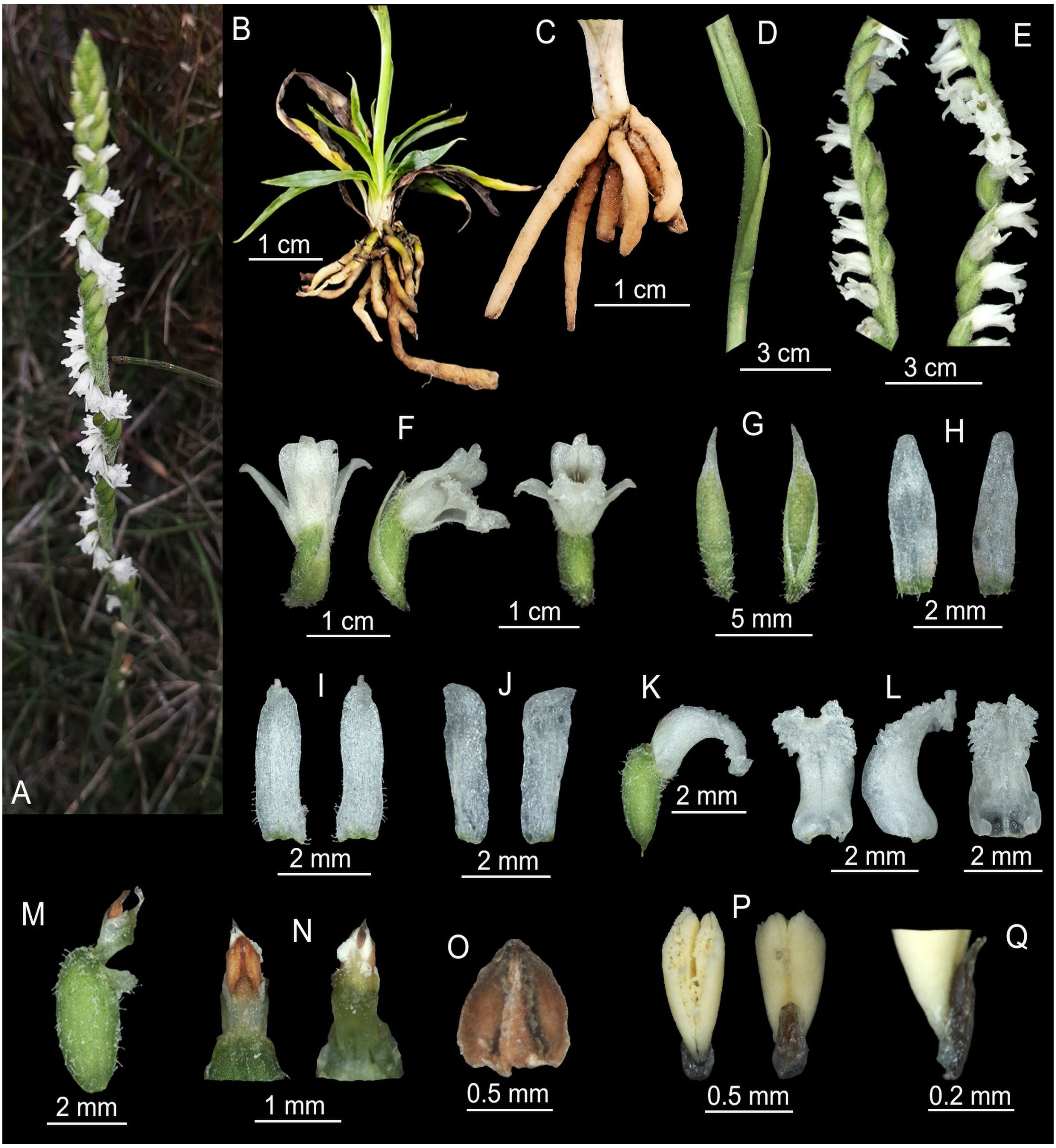

FIGURE 5. *Spiranthes himalayensis* Survesw., Kumar & Mei Sun**. A**. Habitat. **B**. Roots and leaves. **C.** Tubers. **D**. Portion of stem with bract attached. **E**. Portion of Inflorescence. **F**. Flower, abaxial, lateral and adaxial views. **G**. Floral bract, abaxial and adaxial views. **H**. Dorsal sepal, abaxial and adaxial views. **I**. Lateral sepal, abaxial and adaxial views. **J**. Petal, abaxial and adaxial views. **K**. Ovary with labellum attached. **L**. Labellum, abaxial, lateral and adaxial views. **M**. Ovary with column and androecium attached, lateral view. **N**. Column with androecium attached, abaxial and adaxial views. **O**. Anther cap, adaxial view. **P**. Pollinaria with viscidium attached, abaxial and adaxial views. **Q**. Viscidium, lateral view. Photographs by Pema Tobgay (A) and Phub Gyeltshen (B–Q). Illustration assembled by Phub Gyeltshen based on *P.Gyeltshen & P.Tobgay 485* (THIM).

curved, white; *dorsal sepal* oblong-ovate or broadly lanceolate, 3–5 × 1.5–2.0 mm, apex obtuse; *lateral sepals* obliquely oblong to oblong-lanceolate, 3.8–5.0 × 1.5–2.0 mm, apex acute to obtuse; *petals* linear, 3.6–4.0 × 1.0–1.2 mm, apex obliquely rounded, glabrous. *Labellum* distinctly divided into hypochile and epichile with a constriction in the middle, 3.8–4.5 mm; hypochile broadly ovate to suborbicular when flattened, 2.0–3.0 × 2.0–3.0 mm, concave, attached at the base of short foot below the column, saccate, with one semi-globular gland on each side, margin entire and raised upwards till the constriction; epichile oblong or broadly obovate, 1.5–2.0 × 1.3–2.0 mm, margin undulate, dentate with dense papillose hairs adaxially. *Column* obconical, *ca*. 1.0 × 0.5–8.0 mm, with a short foot at the base, *ca*. 0.2 mm long, stigma at the apex on the lower side, green in colour, shiny, filled with viscid liquid. *Rostellum* well developed with two semi-transparent, clavate, rostellum arms projecting in the front above the stigma, 0.5–1.0 mm long. *Pollinarium* elliptic from the side outline, with a deep cleft, *ca*. 1.2 × 0.5 mm, narrower end at both the apex, lobes inside covered with an operculum, with a ligulate viscidium at the narrower end, creamy white; *viscidium* rhombic, 0.4–0.5 × 0.20–0.22 mm, brown. *Operculum* ovate to deltoid, convex, *ca*. 1.0–1.3 × 1.0 mm, yellow-brown coloured, partly embedded on the upper part of the column, not free. *Ovary* subsessile, fusiform, 3.0–5.0 × 1.5–2.0 mm, sparsely to densely glandular-haired, green. *Capsules* unknown.

PHENOLOGY: Flowering occurs from late April to May.

HABITAT: *Spiranthes himalayensis* grows along the stream and river banks at 1000–1300 m elevation in association with *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. (Asteraceae), *Cheirostylis yunnanensis* Rolfe (Orchidaceae) and *Berberis* L. sp. (Berberidaceae).

DISTRIBUTION: The global distribution remains unclear until its taxonomic ambiguity relative to *Spiranthes flexuosa* (Sm.) Lindl. is resolved; see note below. Until then, we consider *S. himalayensis* as a distinct species (Fig. 2).

SPECIMEN EXAMINED: BHUTAN: Samdrup Jongkhar District, Lauri Gewog, Jompa area, left bank of the Jomo river, 1300 m, 27.122069°N, 91.913789°E, *P.Gyeltshen & P.Tobgay 485* (THIM21799).

NOTES: According to Surveswaran *et al.* (2017), *Spiranthes himalayensis* is similar to *Spiranthes hongkongensis* S.Y.Hu & Barretto in having pubescent glandular hairs on the inflorescence and white flowers, but differs in being allogamous (*vs*. autogamous), rostellum well-developed (*vs*. rostellum absent or inconspicuous), basal callosities semi-globular (*vs*. trapezoid), epichile margin is undulate and slightly dentate with papillose hairs (*vs*. margin is undulate and slightly dentate, and glabrous), flowers 4–5 mm wide (*vs*. 1.0–1.2 mm wide). Molecular studies support it as distinct species clade, sister to *S. nivea* T.P.Lin & W.M.Lin (Surveswaran *et al*., 2017).

Recently, Pace *et al.* (2019) synonymised *S. himalayensis* under *Spiranthes flexuosa*. Based on the protologue, *S. himalayensis* differs from *S. flexuosa* by petals oblong (*vs*. lanceolate), semi-circular basal gland (*vs*. conical or obovate basal gland), and column 2.5 mm long (*vs*. 1.7–2.2 mm long). Additionally, based on the present study, *S. himalayensis* differs from *S. flexuosa* by rhombic viscidium (*vs*. linear). Further investigation is needed; for now we retain the two as separate species.

Zeuxine gracilis (Breda) Blume, Coll. Orchid.: 69:1858. *Psychechilos gracilis* Breda in Gen. Sp. Orchid. Asclep. 2: t. 9. 1829; *Monochilus gracilis* (Breda) Lindl. in Fol. Orchid.: 5.1854; *Adenostylis gracilis* (Breda) Merr. in J. Straits Branch Roy. Asiat. Soc. 84: 141. 1921. Fig. 6–7.

TYPE: Breda in Gen. Sp. Orchid. Asclep. 2: t. 9. 1829 (Lectotype [Icon]-designated by Bhattacharjee *et al.* 2011).

Plant terrestrial herbs, 10.5–29.5 cm tall. *Rhizome* 1.0–3.5 cm long, 1.6–4.1 mm thick, pale green, creeping, terete, rooting at nodes. Roots, pale brown, fleshy, with minute root hairs. *Stem* 2.5–10.0 cm long, 1.7–4.0 mm thick, brownish to pale green, erect, glabrous, with few membranous sheaths formed by withered leaf bases. *Leaf* 3–8, scattered along the stem or crowded near apex, glabrous; petiole 6–7 mm long, sheathing at base; lamina ovate to ovate-lanceolate, 1.5–4.1 × 0.7–1.8 cm, acute to acuminate at apex, base cuneate, green, 5–9-veined. *Inflorescence* racemose, terminal, 17.0–19.7 cm long, sub-densely up to 26-flowered, brown, pubescent peduncle 9–12 cm long, with 2–3 sheathing bracts; rachis 6.0–8.3 cm long; *sheathing bracts* ovate-lanceolate, 8.0–13 mm long, clasping at 1/4 to 1/3 of the sheath, apex acuminate, pubescent outside,

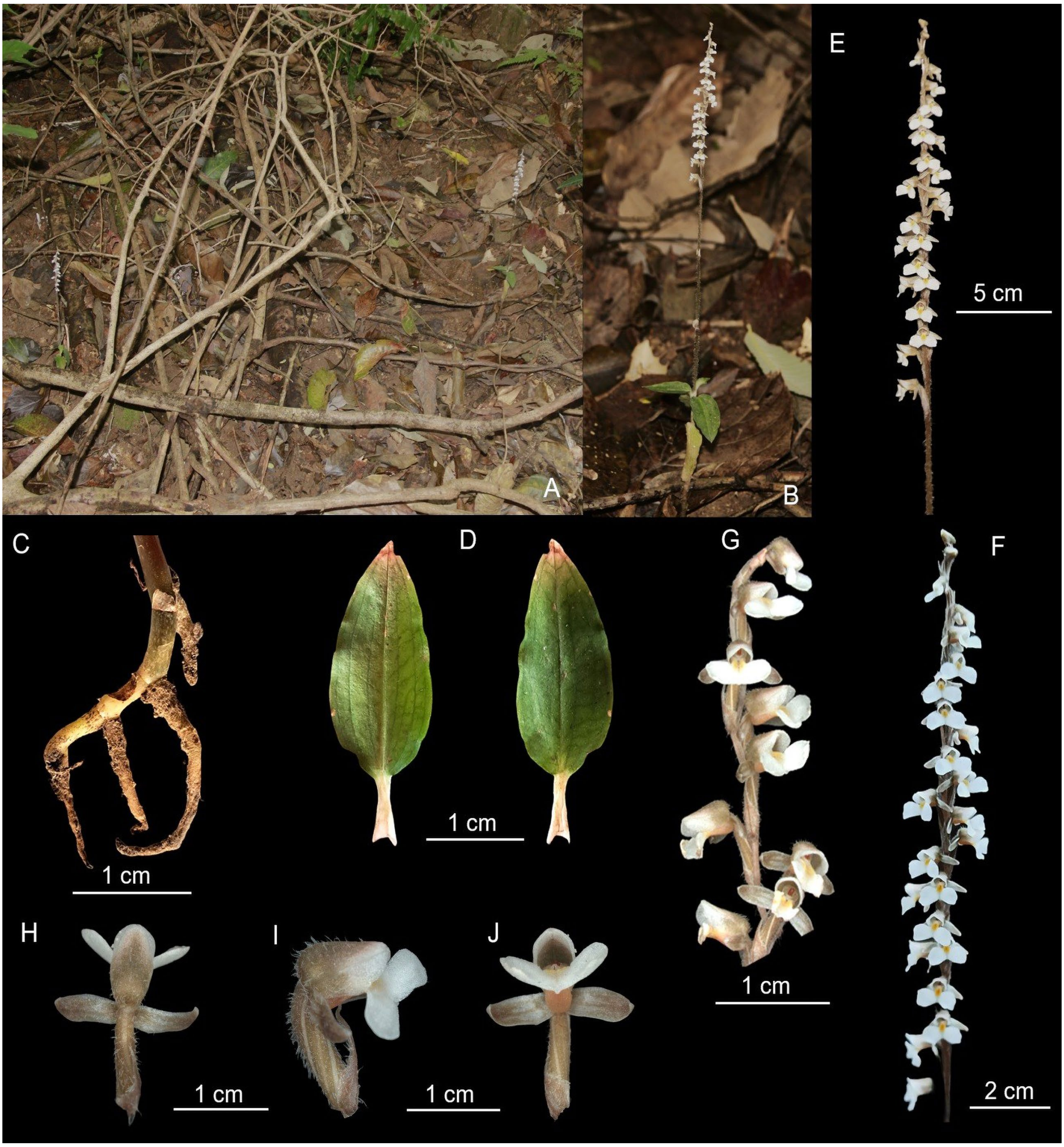

FIGURE 6. *Zeuxine gracilis* (Breda) Blume. **A–B**. Plant in the habitat. **C**. Rhizome. **D**. Leaf, abaxial and adaxial views. **E–F**. Inflorescence. **G**. Upper portion of inflorescence. **H–J**. Flower, abaxial, lateral and adaxial views. Photographs by Kezang Tobgay (A–B, E–F) and Phub Gyeltshen (C–D, G–J). Illustration assembled by Phub Gyeltshen based on *P.Gyeltshen et al. 482* (THIM).

pale brown. *Floral bracts* ovate-lanceolate, 5–8 × 2–3 mm, shorter or longer than pedicel and ovary, apex caudate, pubescent abaxially, pale white. *Flowers* 5–8 mm across, brown, resupinate; pedicel and ovary fusiform, 4–6 mm long, twisted, pubescent, brown; *dorsal sepal* ovate, 3–5 × 2–3 mm, apex obtuse, sparsely pubescent abaxially; *lateral sepals* oblong-ovate to ovate-lanceolate, 4–5 × 1.5–2.0 mm, spreading, apex obtuse, margin incurved, sparsely pubescent abaxially; *petals* obliquely elliptic or oblong-elliptic, 3.0–4.9 × 1.6–2.0 mm, apex obtuse, pale brown base with white apex portion, glabrous, 1-veined. *Labellum* 3.5–5.0 mm long; *hypochile* saccate, sub-globose 1.2–2.0 × 1.0–1.5 mm, pale reddish-orange, with 1 filiform gland

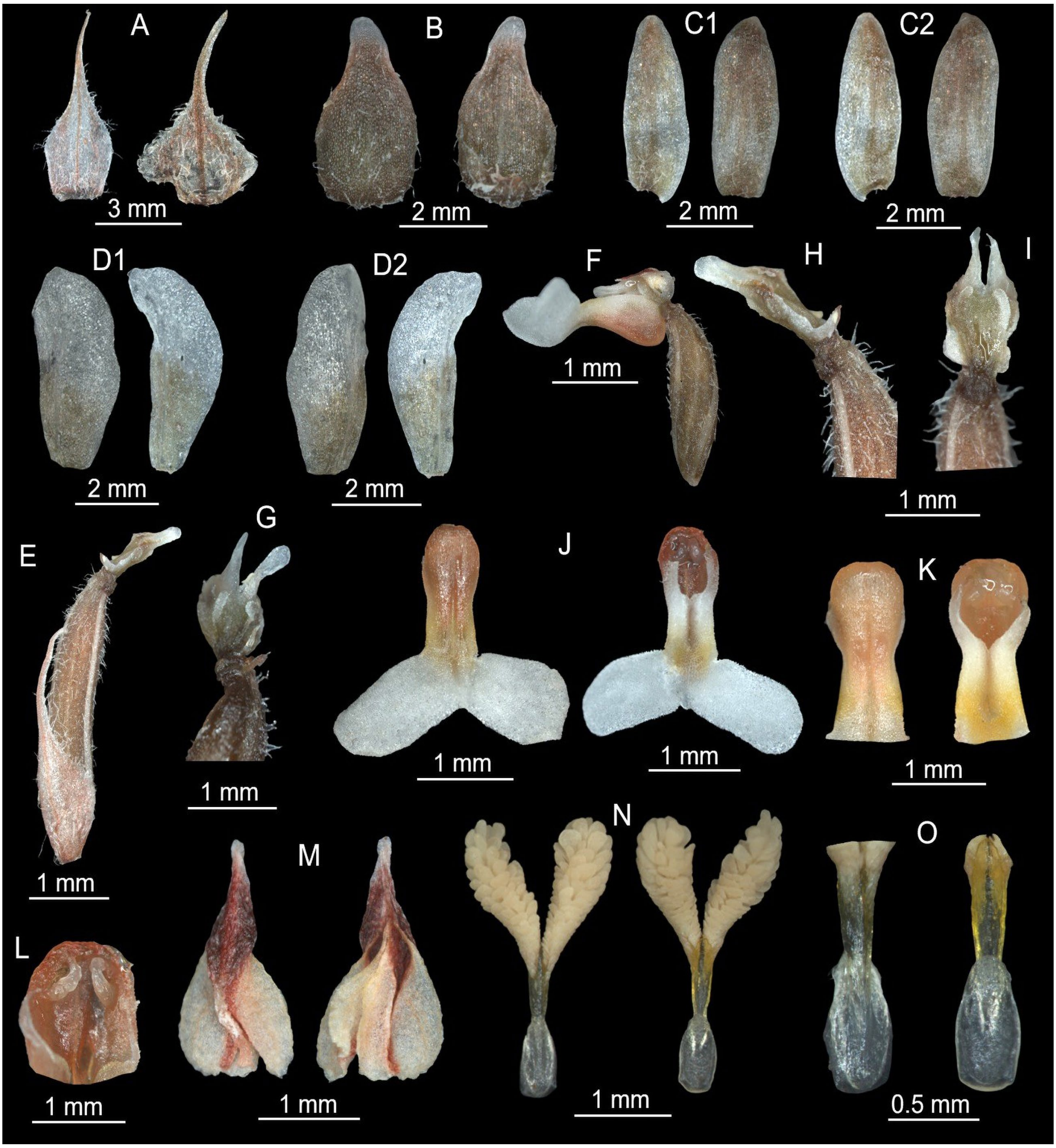

Figure 7. *Zeuxine gracilis* (Breda) Blume. **A**. Floral bracts, abaxial view. **B**. Dorsal sepal, abaxial and adaxial views. **C1–2**. Lateral sepals, abaxial and adaxial views. **D1–2**. Petals, abaxial and adaxial views. **E**. Ovary with floral bract attached. **F**. Ovary with labellum attached. **G–I**. Column, abaxial, lateral and abaxial views. **J**. Labellum, abaxial and adaxial views. **K**. Labellum hypochile & mesochile, abaxial and adaxial views. **L**. Labellum hypochile, adaxial view. **M**. Anther cap, abaxial and adaxial views. **N**. Pollinarium, abaxial and adaxial views. **O**. Stipe and Viscidium, abaxial and adaxial views. Photographs and illustrations assembled by Phub Gyeltshen based on *P.Gyeltshen et al. 482* (THIM).

on each side; *mesochile* oblong, 1.2–1.5 × 0.8–1.0 mm, margin incurved, white with golden yellow adaxially, orange-yellow abaxially; *epichile* 2-lobed, lobes oblong or broadly obovate, 1.5–2.3 × 1.1–2.0 mm, white. *Column* 0.8–1.5 mm long, pale brown, with elongated 2 wings; *stelidia* narrowly deltoid and oblanceolate, 0.7–1.0 mm long, white; without wings but with a seam with 2 upwards oblong process-like below rostellum; *anther cap* lanceolate, 1.5–2.0 × 0.7–1.0 mm, red to white. *Pollinarium* 1.7–2.2 mm long; *pollinia* 2, obovate to obclavate, 1.0–1.3 mm long; *stipe* oblong-elliptic, 0.5–0.7 × 0.2 mm, golden yellow; *viscidium* oblong, 0.4–0.5 × 0.2–0.3 mm, semi-transparent. *Capsules* unknown.

Phenology: Flowering occurs from late April to May.

Habitat: *Zeuxine gracilis* grows in the *Schima wallichii* (DC.) Korth. (Theaceae) forest at 676 m. The associated species are *Nephrolepis cordifolia* (L.) C.Presl (Polypodiaceae) and *Oplismenus* P.Beauv. species (Poaceae).

Distribution: Bhutan (Tsirang, Fig. 2), Borneo, China, India, Indonesia, Malaysia, Thailand and Vietnam.

Specimen examined: BHUTAN: Tsirang District, Mendrelgang Gewog, Kaligon, 676 m, 26.8890°N, 90.0846°E, 23 February 2025, *P.Gyeltshen, K.Tobgay, K.Dechen & S.Dema 482* (THIM21791, THIM21792).

Notes: *Zeuxine gracilis* is similar to *Zeuxine affinis* (Lindl.) Benth. ex Hook.f. but differs by triangular sepals with short ciliate margins (*vs*. lanceolate with entire margins), orange-yellow labellum at base with whitish epichile (*vs*. white), oblong to sub-rectangular epichile, forming an obtuse angle with the axis of the labellum (*vs*. ovate-oblong, with acute angle) (Pearce & Cribb, 2002; Ranjan *et al.*, 2020). Ranjan *et al.* (2020) reported *Z. gracilis* to have oblong-terete pollinia, 0.7–1.0 mm long, whereas, we find that pollinia are obovate to obclavate, 1.0–1.3 mm long.

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Conflict of interest. The authors declare that there is no conflict of interests associated with this publication.

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TEN NEW ORCHID RECORDS FROM THE INDONESIAN ARCHIPELAGO

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Abstract. Orchidaceae is one of the most diverse plant families in Indonesia, yet many species remain poorly documented across the archipelago. Here we report ten orchid species as new national records for Indonesia: *Bulbophyllum nematocaulon*, *Bulbophyllum sanguineomaculatum, Cleisomeria lanatum*, *Corybas calopeplos,* and *Corybas holttumii* from Sumatra; *Acanthophippium bicolor* and *Anoectochilus papuanus* from Java; *Dendrobium teretifolium* from the Lesser Sunda Islands, *Bulbophyllum thiurum* from Kalimantan; and *Aerides agustiana* from Sulawesi. For each species, we provide taxonomic notes, distributional data, type information, phenology, ecological observations, line drawings, and photographs. These new records extend the known geographic ranges of the species and confirm the importance of field exploration and herbarium study for documenting Indonesia's remarkable orchid diversity.

Keywords / Palabras clave: epiphyte, epífita, terrestre, terrestrial, Sundaland, Sondalandia, Islas Menores de la Sonda, Lesser Sunda, Orchidaceae

Introduction. The Indonesian Archipelago is one of the world's major biodiversity hotspots, characterized by exceptionally rich and highly endemic biota (Lohman *et al*., 2011; von Rintelen *et al*., 2017). Based on its biogeographical history, Indonesia formed from a complex collision of Australian Plate margin with Eurasia (Sundaland) and the Philippine Sea Plate (Michaux, 2010). This dynamic evolution of the Indonesian archipelago's geological composition continues to shape its modern landscape and affect the species distribution (Turner *et al*., 2001; Vollering *et al*., 2016). Hence, Indonesia has diverse ecosystems which are natural habitats to 40,000 plant species (Myers, 2000; Sun *et al*., 2024) including 5000 orchid species (Comber, 1990). Despite this recognized importance, the precise number of species in this region remains poorly known. Large parts of the archipelago are still underexplored, and many taxa await formal description and documentation (Middleton *et al*., 2019).

Recent assessments identify Borneo, Sumatra, and New Guinea as "dark spots" of vascular plant diversity, areas predicted to contain the highest number of undescribed or undiscovered species, making them critical targets for future collection efforts (Ondo *et al*., 2024). Extensive initiatives to survey Indonesia's inaccessible regions have been undertaken. However, much of the country's botanical diversity remains insufficiently documented (Sun *et al*., 2024). A series of classical and modern taxonomic investigations on Orchidaceae family have consistently been prioritized in botanical research on five main islands of Indonesia (Sumatra, Java, Borneo, Sulawesi, and Papua) (Comber, 1990, 2001; de Vogel *et al*., 2024; O'Byrne, 1994; Schlechter, 1914; Schuiteman, 2013; Smith, 1905;

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Thomas & Schuiteman, 2002, Tkatchenko & Kami, 2006; Wood, 1997) . However, the species richness in Java and Sumatra is well represented in the literature due to the legacy of continuous floristic assessments that originated during the colonial period and have persisted into the modern era (Sun *et al.*, 2024). Unlike those two regions, Borneo, Sulawesi, Lesser Sunda, Maluku, and Indonesian Papua remain underexplored in contrast with significant number of species new to science that have been published (Vermeulen *et al.*, 2011; Schuiteman & Wanma., 2017).

In addition to these foundational works, several studies have expanded geographic records to include smaller island groups such as the Lesser Sunda and Buru Islands (Atmaja & Tirta, 2019; Margońska *et al.,* 2022; Metusala, 2011; Mustaqim & Astuti, 2019). Here, we report ten new records of Orchidaceae from the Indonesian Archipelago to enhance understanding of the country's orchid diversity. These include the first record for the Lesser Sunda Islands, Kalimantan, and Sulawesi, while two species are recorded as new to Java—one of which was found in Bromo Tengger Semeru National Park—and the remaining five are newly documented for Sumatra.

Materials and methods. Specimens were collected during fieldwork conducted between 2020 and 2024 in Java, the Lesser Sunda Islands, Sumatra, Borneo, and Sulawesi. Whole plants, including roots, pseudobulbs, stems, leaves, flowers, and fruits, were photographed, dissected, and prepared as standard dried herbarium specimens following Forman & Bridson (2000). Spirit collections were prepared using Copenhagen solution (70% alcohol, 29% water, and 1% glycerol) to preserve floral morphology (Forman & Bridson 2000). Coordinate data were recorded during field surveys using a Garmin GPSMap 65s, and map layout creation as well as spatial data processing were carried out with R (version 2026.01.2) using the packages *ggplot*, *sf* and *rnaturalearth*. The final figure layout, minor positional adjustments, and panel arrangement were prepared using Adobe® Photoshop CS 2026. Microphotography was performed using a Nikon D5600 camera equipped with AF-P 18–55 mm VR and Micro AF-S 60 mm f/2.8G ED Nano lenses, and images were processed using Adobe® Photoshop CS6. Dried and spirit specimens were deposited primarily at Herbarium Bogoriense (BO), with duplicates housed at the Herbarium of Andalas University (ANDA) and Herbarium Bandungense (FIPIA). Additional material from major herbaria (BO, ANDA, FIPIA, L, K) was examined for comparative study and species identification. Morphological terminology followed Beentje (2016), and morphological assessments and measurements were based on the original protologues and subsequent taxonomic treatments by Brown (1810), Linden (1889), Dransfield, Comber and Smith (1986), Cribb *et al*. (1988), Vermeulen (1991a, 1991b), Comber (1990, 2001), Wood (2000), and Vermeulen & O'Byrne (2005). Phenology data were collected during fieldwork.

TAXONOMIC TREATMENT

Acanthophippium bicolor Lindl., Edwards's Bot. Reg. 20: t. 1730. 1835. Fig. 1.

TYPE*:* Ceylon, *Watson, s.n. ex Royal Hort. Society* (holotype, likely at K-L, not seen).

EXAMINED MATERIALS: INDONESIA. **Java**: East Java, Lumajang, Pronojiwo, Bromo Tengger Semeru National Park, 800–1200 m 31 January 2023, *T. Artaka 004* (BO!). Unknown locality, without collecting data, 1893 (MNHN! -image P02115508). SRI LANKA. Unknown locality, without collecting data, 09 May 1846 (MNHN! -image P02115507). Unknown locality, 1839 *Martens M, s.n.* (BR! -image BR0000032790801). **Nillaba**: 22 December 1959, *D.M.A. Jayaweera 11* (AMES! -image 88544).

DISTRIBUTION: India to Sri Lanka; extended distribution includes East Java.

HABITAT AND ECOLOGY: In Java, plants grow as clustered terrestrials in mid-montane forest dominated by Dipterocarpaceae, in shaded conditions.

PHENOLOGY: Flowering in the wild from June to September.

NOTES: *Acanthophippium bicolor* was previously known only from India and Sri Lanka. In addition to documenting its natural occurrence in East Java, we identified an undated herbarium specimen labelled "cultivated from Java" and accompanied by brief notes

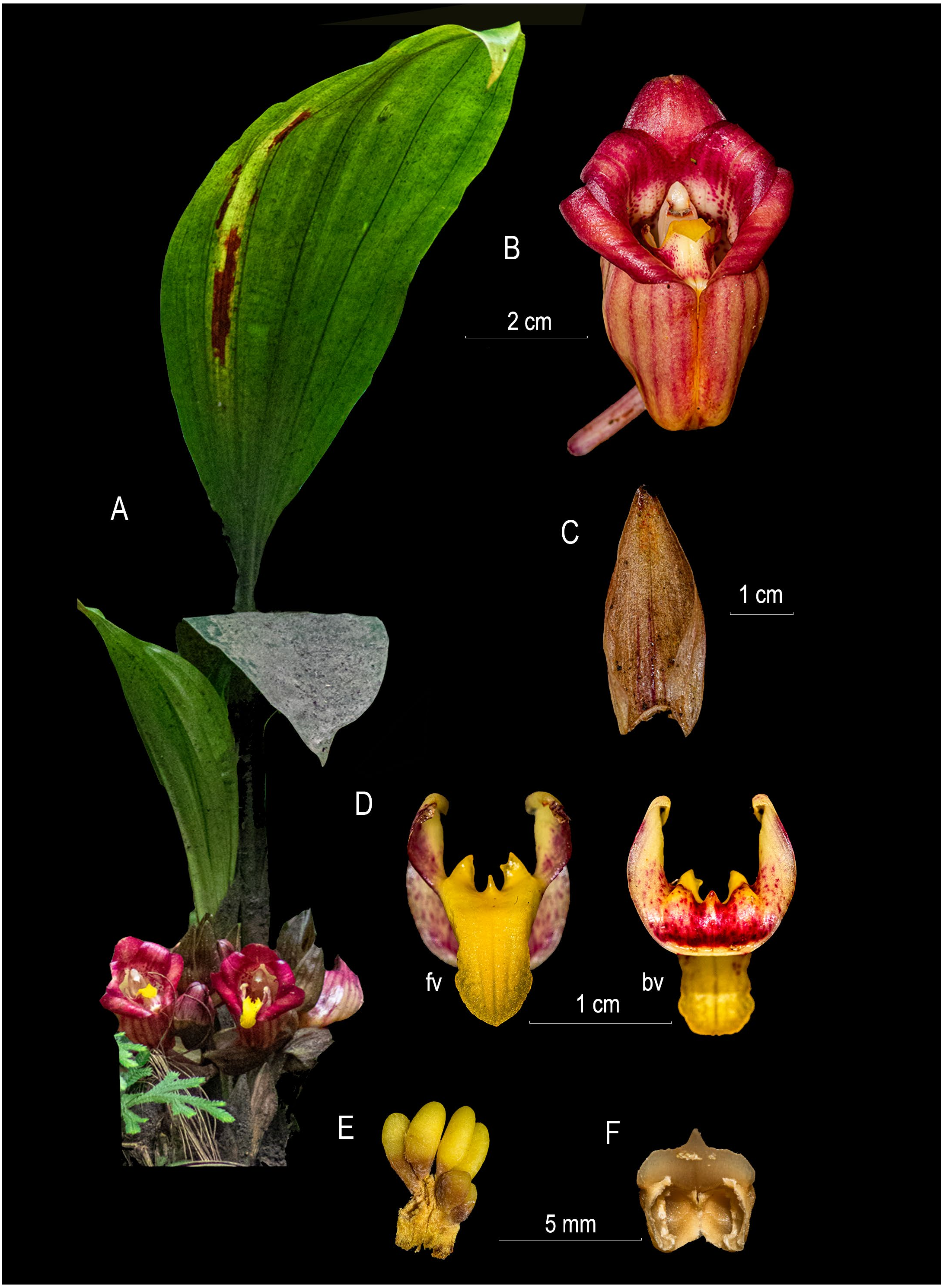

Figure 1. *Acanthophippium bicolor* Lindl. **A**. Plant habit. **B**. Flower. **C**. Bracts. **D**. Labellum, front and back views. **E**. Pollinarium. **F**. Anther cap. Photographed by Y.R. Yudistira based on *T. Artaka 004* (BO).

from 1893, but lacking locality, collector, and number (MNHN, P02115508). The species is easily distinguished by its unguiculate, trilobed labellum, with a callus forming three ridges, the two lateral ridges being larger than the median one. These callus ridges may cause confusion with the common Javan species *A. javanicum* Blume; however, in *A. bicolor,* the lateral callus ridges are slimmer and produce only two spikes, whereas in *A. javanicum,* the lateral callus ridges form four forked spikes (Comber, 1990; Prasad, 2022).

Aerides augustiana Rolfe, Gard. Chron. 9(1): 9. 1890; *ibid*., 232; fig., *ibid.* p. 233. Fig. 2.

TYPE: Philippines. *M.A. Linden, s.n.* (holotype, not located).

Examined materials: INDONESIA. **Central Sulawesi**: Toli-Toli, Baolan, Dadakitan, 500–1000 m. 2 April 2022. *Y.R. Yudistira et al. YRY02042022* (CEB!).

Distribution: Philippines; extended distribution includes Central Sulawesi.

Habitat and ecology: In Central Sulawesi, plants grow as epiphytes higher on tree trunks in lower montane forest, typically in open areas.

Phenology: Flowering in the wild from February to April.

Notes: *Aerides augustiana* is newly recorded from Sulawesi. The species is easily distinguished from the widespread species *Aerides odorata* Lour. by its spur 1.9 cm long, straight and stout *vs.* 1.0—1.2 cm with bending apex almost 90° *in A. odorata*. The Sulawesi specimen bears purple flowers, differing from the protologue, which describes the flowers as pink (Linden *et al*., 1889; Comber, 1990).

Anoectochilus papuanus (Schltr.) W.Kittr., Bot. Mus. Leafl. 30(2): 95. 1985. *Eucosia papuana* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 1: 76. 1911. Fig. 3.

TYPE: Papua New Guinea. Kani Mountains, Feb 1908, *ca*. 1000 m, *R. Schlechter 17361* (holotype, B destroyed; isotype, BO! L! -image L0058586).

Examined materials: INDONESIA. **East Java**: Malang, Pronojiwo, Ranudarungan, 800–1200 m, 14 February 2021, *Y.R. Yudistira et al. ARTAKA0125* (dried and spirit: FIPIA! BO!); Lumajang, South slope of Mount Semeru, *ca*. 1000 m, 5 July 2022, *Y.R. Yudistira et al. ARTAKA0126* (spirit collection: FIPIA!). **Southwest Papua**: Kebar valley, *ca*. 100 km west from Manokwari, southern slope of Mount Nettoti along path from Andjai to Saokorem, *ca*. 1500 m, 28 October 1954, *van Royen, P. 3852* (L! -image L0260519). PAPUA NEW GUINEA. **Southern Highlands**: Kagua district, Aga, near Sumbara market, *ca.* 1500 m, 14 May 1983, *T.M. Reeve 6352* (photo: K001652001). **Eastern Highlands**: Kainantu, Kassam Pass, upper slopes of southeast crest, *ca*. 1700 m, 21 June 1977, *Lae 63413 N.M.U. Clunie et al*. (L! -image L0260520). **Morobe**: Menyamya, Piwi'anga, Menmya-Kaintiba road, *ca*. 1828 m, 11 May 1968, *H. Streiman & A. Kairo NGF35902* (L! -image L0260517).

Distribution: New Guinea, Solomon Islands (Guadalcanal and Santa Isabel); extended distribution includes East Java.

Habitat and ecology: In East Java, terrestrial on the montane forest, in shaded conditions.

Phenology: Flowering in the wild from February to April.

Notes: *Anoectochilus papuanus* is newly recorded for Java. With this addition, the genus now comprises four species in Java (*A. flavescens* Blume, *A. reinwardtii* Blume, *A. papuanus*, and *A. setaceus* Blume). *Anoectochilus papuanus* is distinguished by its shorter inflorescences (8–11 cm) compared with *A. flavescens* (30–32 cm), *A. setaceous* (15–20 cm), and *A. reinwardtii* (15–20 cm), and by having fewer flowers (2–3) *vs. A. flavescens* (5–12)*, A. setaceus* (3–7)*,* and *A. reinwardtii* (2–4). It also differs in labellum morphology: the labellum is lanceolate–elliptic and lacks the hair-like flanges present in the other species (about five short filiform segments in *A. flavescens*; ~7–8 mm long projections in *A. setaceus*; and 10 short segments on each side in *A. reinwardtii*). The flowers of *A. papuanus* do not open widely. Nevertheless, the pink reticulate venation and overall leaf shape may be confused with *A. reinwardtii*, so flowering material is essential for confident identification.

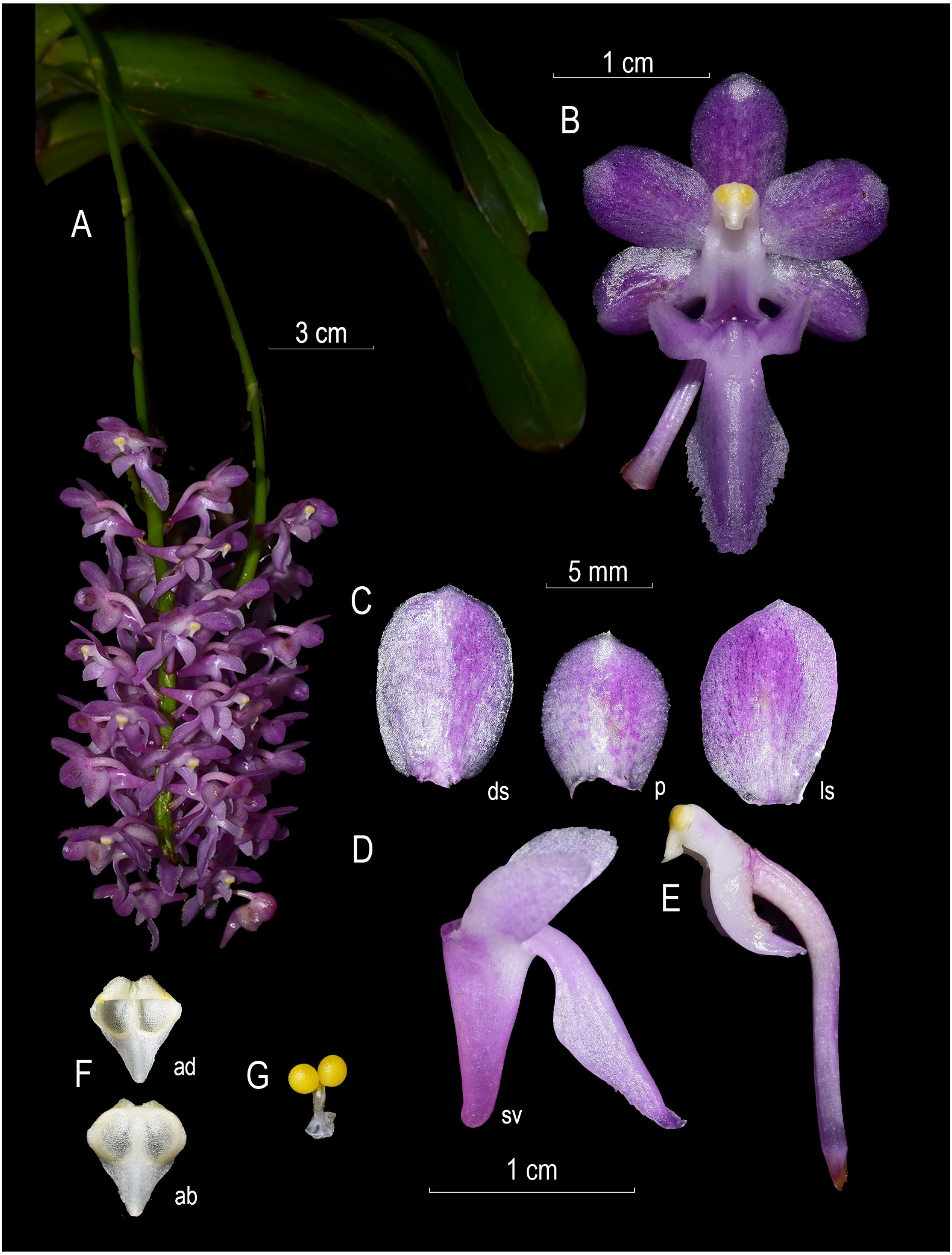

FIGURE 2. *Aerides augustiana* Rolfe. **A**. Plant habit and inflorescences. **B**. Flower, front view. **C**. Dorsal sepal, petal, and lateral sepals. **D**. Labellum with spur, side view. **E**. Column and ovary, side view. **F**. Anther cap. **G**. Pollinarium. Photographed by Y.R. Yudistira based on *YRY0204022* (CEB).

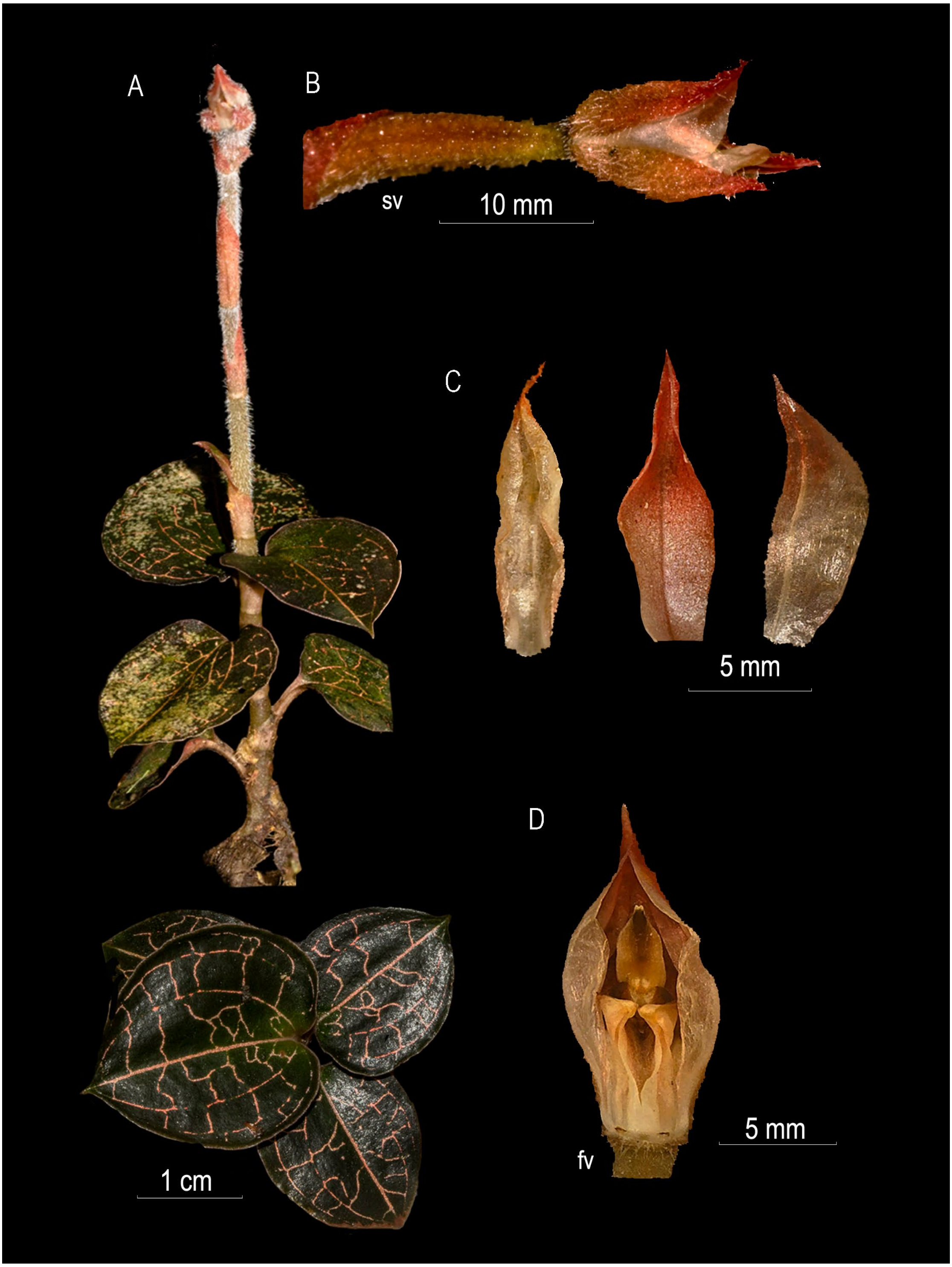

FIGURE 3. *Anoectochilus papuanus* (Schltr.) W.Kittr. **A**. Plant habit. **B**. Flower, side view. **C**. Bract, dorsal sepal and petal. **D**. Column with petals, front view. Photographed by Toni Artaka based on *ARTAKA0125* (BO).

Bulbophyllum nematocaulon Ridl., J. Straits Branch Roy. Asiat. Soc. 82: 197. 1920. Fig. 4–5.

TYPE: Malaysia. Perak, *Scortechini 614*, 16 August 1888 (holotype, K! -image K000829265).

= *Bulbophyllum johannis-winkleri* J.J.Sm., Mitt. Inst. Allg. Bot. Hamburg 7: 59. 1927. TYPE: Indonesia, West-Borneo, auf dem Bukit Raja, 17 December 1924, *H. Winkler 899*, *HBG501375* (holotype, HBG). *Bulbophyllum oreas* Ridl., *Fl. Malay Penins.* 4: 63. 1924. TYPE: Malaysia, Pahang, Gunung Tahan, *Haniff s.n.* (holotype, not seen).

EXAMINED MATERIALS: INDONESIA. **West Sumatra**: Lima Puluh Kota, Payakumbuh, Harau, 800–1400 m, 15 September 2020, *Y.R. Yudistira et al. YRY01372023* (spirit: ANDA!); Padang, Mount Talang, *ca.* 1200 m, 23 July 2023, *Y.R. Yudistira et al. YRY02372023* (ANDA!).

DISTRIBUTION: Vietnam, Peninsular Malaysia, Borneo, the Sumatran record extends the known range to West Sumatra.

HABITAT AND ECOLOGY: In Sumatra, occurring in dipterocarp forest; epiphytic on lower tree trunks in shaded conditions.

PHENOLOGY: Flowering in the wild from June to October.

NOTES: *Bulbophyllum nematocaulon* is placed in sect. *Minutissima* Pfitzer (Engler & Prantl, 1888) based on its creeping, thin rhizome; minute, unifoliate pseudobulbs; persistent leaves; solitary inflorescence; single-flowered, glabrous flowers; free sepals with 1—3 veins; mobile, undivided labellum and minute stelidia (Pfitzer, 1889b; Vermeulen, 1991b; Vermeulen, O'Byrne, & Lamb, 2015). Within section *Minutissima*, *B. nematocaulon* is vegetatively similar to *B. mucronatum* (Blume) Lindl. but differs in having more widely spaced pseudobulbs. Its leaves are elliptic with an acuminate apex, whereas in *B. mucronatum* they are elliptic-ovate, with a cuspidate apex. Differences in the labellum are also clear: in *B. nematocaulon,* the labellum is lanceolate, glabrous, with entire margins and an acuminate apex *vs*. labellum elliptic—ovate—oblong, carinate, curved halfway, margin papillose distally, convex towards apex in *B. mucronatum*. With this new record, *B. nematocaulon* becomes the only member of the sect. *Minutissima* known from Sumatra. In contrast, *B. mucronatum* is recorded from Peninsular Malaysia, Borneo, and Java (Seidenfaden, 1979; Vermeulen, 1991b; Vermeulen *et al.*, 2015).

Bulbophyllum sanguineomaculatum Ridl., J. Linn. Soc. Bot. 32: 265. 1896. Fig. 6.

TYPE: Malaysia. Selangor, Kuala Lumpur, 20 February 1890, *Curtis s.n.*, (holotype, K! -image K001368849).

EXAMINED MATERIALS: INDONESIA. **Aceh**: Aceh Tengah Regency, Jagong Jeget, Jagong village watering area, 4°20'42.6"N 96°46'32.9"E, *ca*. 2150 m, 11 January 2023, *Mustaqim 2586* (LGS.120220135).

DISTRIBUTION: Peninsular Malaysia, Borneo, the Philippines, and Sulawesi; extended distribution includes Sumatra.

HABITAT AND ECOLOGY: In Sumatra, plants grow as epiphytes on tree trunks in upper montane forest.

PHENOLOGY: Flowering in the wild observed in January.

NOTES: This species belongs to section *Beccariana* Pfitz.(Engler & Prantl, 1888), recognized by its creeping rhizome with closely spaced, ovoid pseudobulbs, each bearing a single, elliptic to obovate, acuminate leaf. The inflorescence is solitary, arising from the base of the pseudobulb, up to 6.5 cm long, single-flowered, with spreading sepals and petals. The floral segments are conspicuously marked with irregular reddish to purplish blotches (Ridley, 1896; Vermeulen, 1991b; Vermeulen *et al.*, 2015). *Bulbophyllum sanguineomaculatum* is most similar to *B. membranifolium* Hook.f., which also occurs in Sumatra and belongs to sect. *Beccariana*. *Bulbophyllum sanguineomaculatum* differs from *B. membranifolium* in its irregular and darker blotches on sepals and petals, the free and spreading lateral sepals, and the labellum margins that are erose to denticulate except the base. In contrast, *B. membranifolium* usually shows uniform coloration or lighter spotting, with sepals that are less widely spread and sometimes partially fused at the base, and an entire labellum or slightly erose at the proximal half.

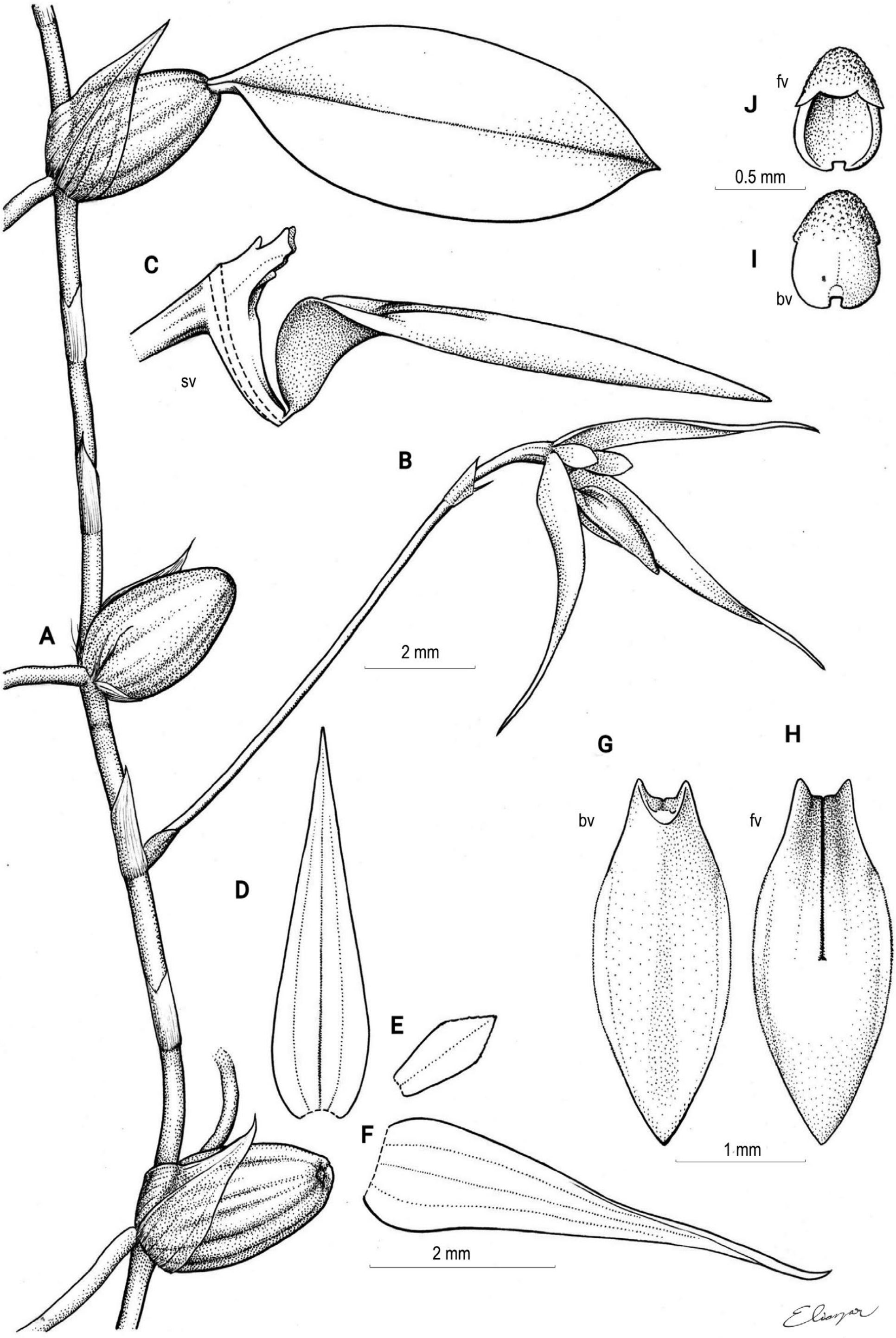

FIGURE 4. Line drawing of *Bulbophyllum nematocaulon* Ridl. **A**. Plant habit. **B**. Flower. **C**. Column and labellum, side view. **D**. Dorsal sepal. **E**. Petal. **F**. Lateral sepal. **G**. Labellum, back view. **H**. Labellum, front view. **I**. Anther cap, back view. **J**. Anther cap, front view. Illustrated by Yuanito Eliazar based on *YRY01372023* (ANDA).

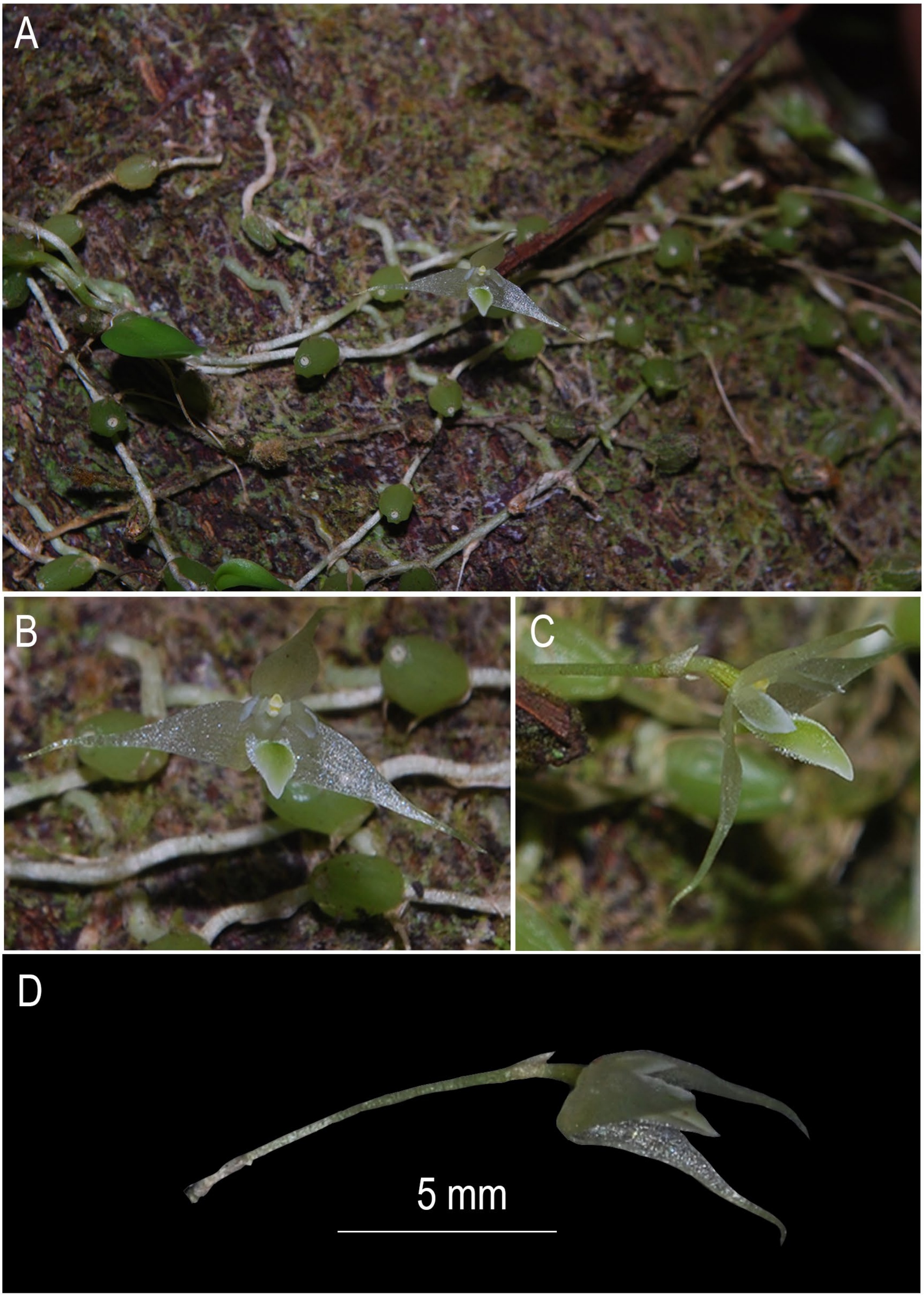

FIGURE 5. *Bulbophyllum nematocaulon* Ridl. **A**. Plant habit *in situ*. **B**. Flower, front view. **C**. Flower, side view. **D**. Flower with pedicel, side view. Photographed by Y.R. Yudistira based on *YRY01372023* (ANDA).

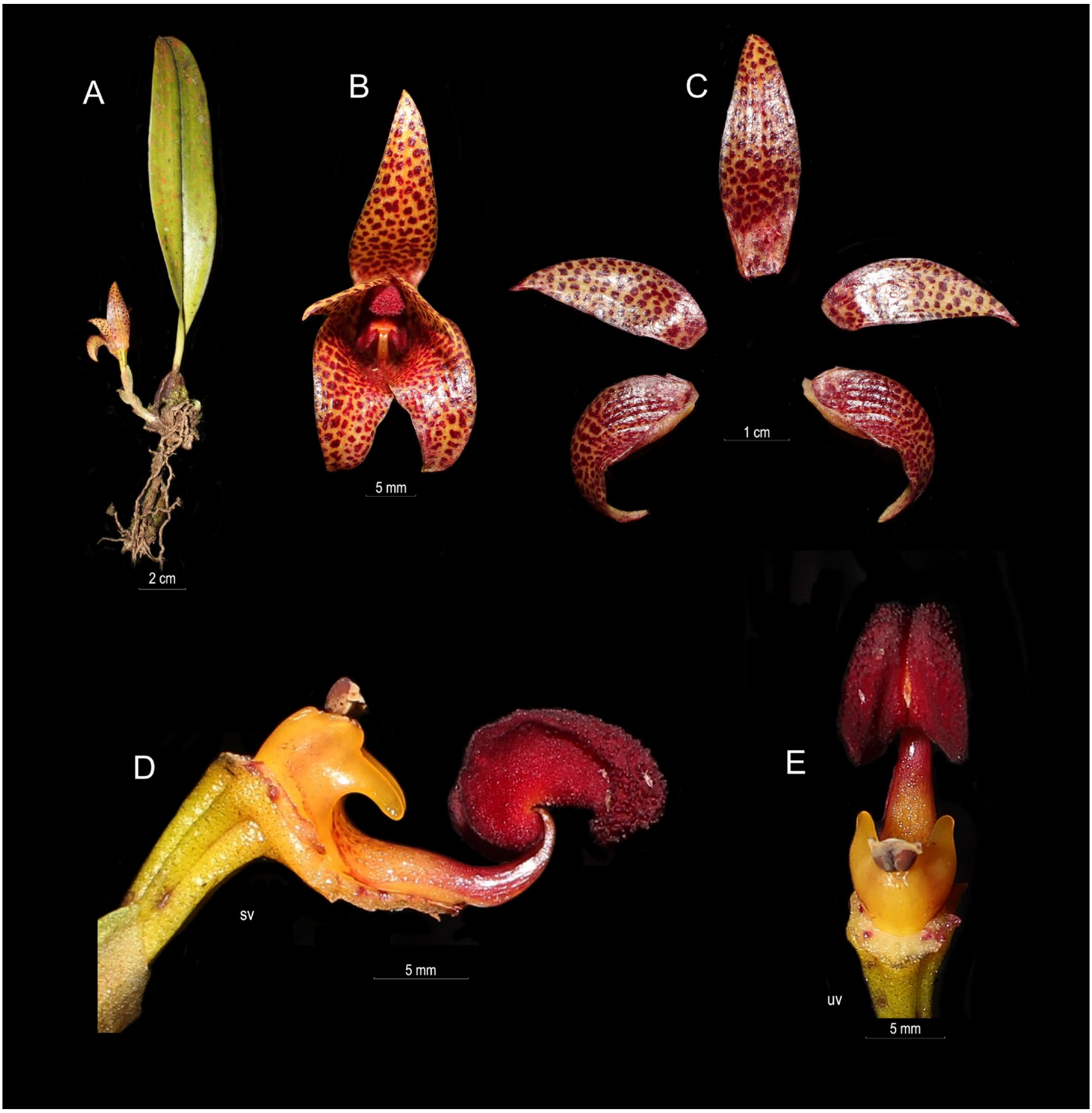

Figure 6. *Bulbophyllum sanguineomaculatum* Ridl. **A**. Plant habit. **B**. Flower. **C**. Perianth, dissected. **D**. Ovary, column, and labellum, side view. **E**. Column and labellum, upper view. Photographed by W. Mustaqim based on *Mustaqim 2586* (LGS).

Bulbophyllum thiurum J.J.Verm. & P.O'Byrne, Gard. Bull. Singapore 57: 136. 2005. Fig. 7.

TYPE: Malaysia. Johore, *SBG-O* 5395 (holotype, SING!).

Examined materials: INDONESIA. **Central Kalimantan:** Murung Raya, Puruk Cahu, 0–100 m asl. 4 October 2023. *Y.R. Yudistira et al. H-SOLEMAN0032023* (ANDA!).

Distribution: Peninsular Malaysia, with an extended distribution that includes Central Kalimantan.

Habitat and ecology: In Central Kalimantan, plants grow as epiphytes in lowland shaded swamp forests.

Phenology: Flowering in the wild all year round.

Notes: Our report expands the known range of *B. thiurum*

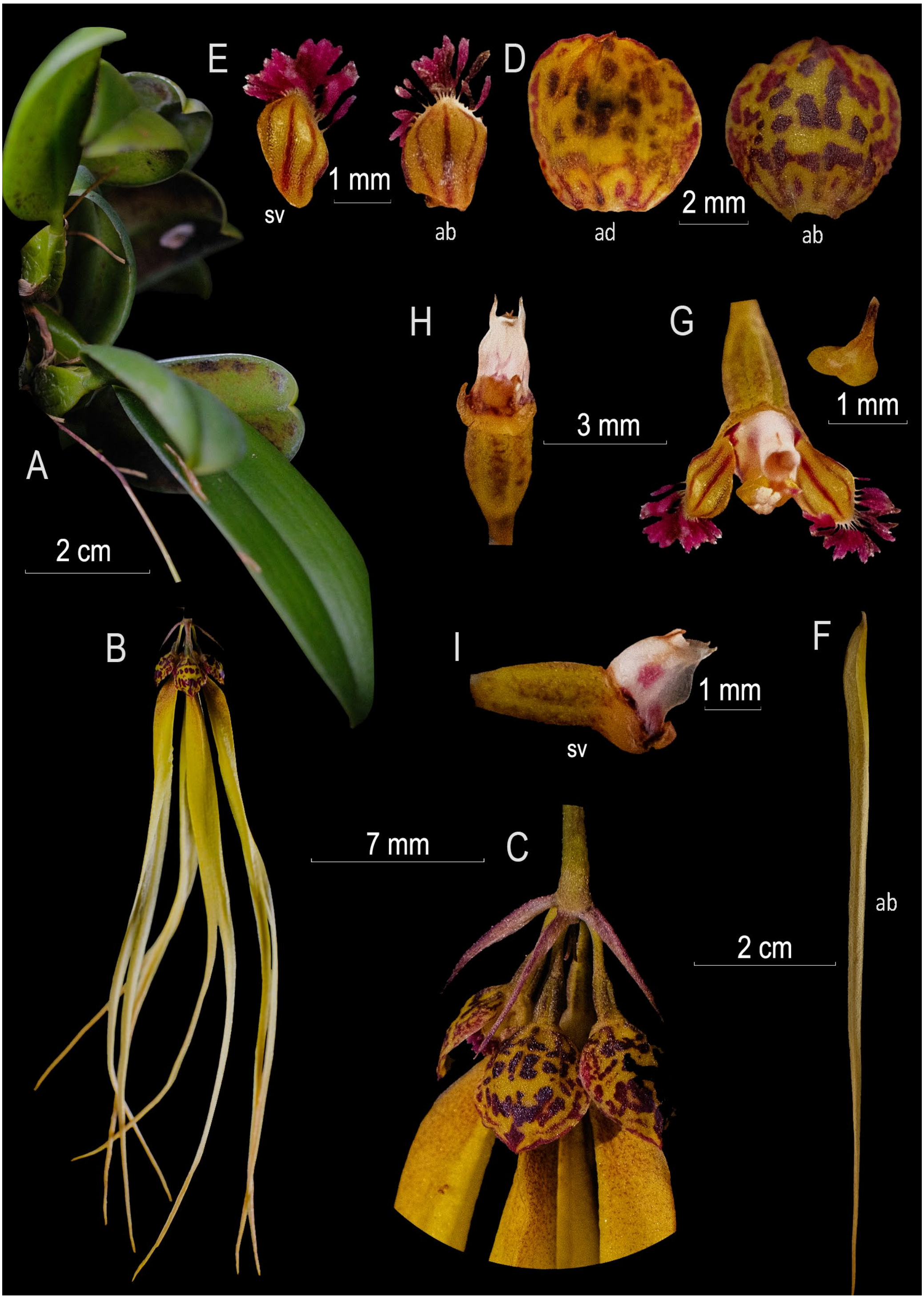

FIGURE 7. *Bulbophyllum thiurum* J.J.Verm. & P.O'Byrne. **A**. Plant habit. **B**. Inflorescence. **C**. Bracts. **D**. Dorsal sepal, adaxial and abaxial. **E**. Petal, side and abaxial views. **F**. Lateral sepal. **G**. Column with petals and labellum. **H**. Column, adaxial view. **I**. Column, side view. Photographed by H. Soleman based on *H-SOLEMAN0032023* (ANDA).

Figure 8. *Cleisomeria lanatum* Lindl. ex G.Don. Photographed by Y.R. Yudistira based on *YRY07112022* (ANDA).

from Johor, Peninsular Malaysia (Vermeulen & O'Byrne, 2005) to Central Kalimantan. Unlike previous reports suggesting it occurs only in primary forests, we found that the species is adapted to lowland swamp forests. *Bulbophyllum thiurum* closely resembles *B. plumatum* Ames and *B. mirum* J.J.Sm in its section placement and its hanging, few-flowered inflorescences. In Kalimantan, prior records of sect. *Plumata* J.J.Verm., Schuit, & de Vogel include only *B. mirum*. *Bulbophyllum thiurum* differs from *B. plumatum* and *B. mirum* by having lateral sepals fused only near the base along both the upper and lower margins, whereas in *B. plumatum* and *B. mirum*, most of the lateral sepals are fused along just the upper margin. The petal appendages are hair-like near the apex, compared to rounded in *B. plumatum* and elliptic and unequal in *B. mirum* (Ames, 1915; Vermeulen & O'Byrne, 2005; Vermeulen *et al*., 2015).

Cleisomeria lanatum Lindl. ex G.Don, J.C. Loudon, Encycl. Pl., new ed., Suppl. 2: 1472. 1855. Fig. 8.

TYPE: East Indies. Without collecting data, 1845 (not seen).

Examined materials: INDONESIA. **West Sumatra**: Bukit Tinggi, Harau 750 m, 07 November 2022, *YR. Yudistira et al. YRY07112022* (ANDA!). *G.H. Pring s.n.* (MO! -image 101306244). THAILAND. **Southeastern**: between Chanthaburi and Trat, *ca*. 3.9 m, 4th Expedition 03 September 1972, Kai Larsen, *Supee S. Larsen, I. Nielsen & T. Santisuk 32415* (L! -image L0267032). **Southwestern**: Kwae Noi basin, Brangkasi, *ca*. 150 m, 19 June 1946, *Hoed, G den, Kostermans, A.J.G.H. Khwae Noi 648* (L! -image L0267033). VIETNAM. **Annam**: Dalat, 1960, *Tixier 6/60* (MNHN! -image P00392647); Dalat, 1953, *C.R.S.T 288* (MNHN! -image P00392648); Lang Nanh, *ca*. 900 m, 05 August 1955, *C.R.S.T 246* (MNHN! -image P00392649).

Distribution: India, Bangladesh, Myanmar, Cambodia, Laos, Thailand, Vietnam, Peninsular Malaysia, and Borneo; extended distribution includes West Sumatra.

Habitat and ecology: In West Sumatra, plants grow as epiphytes in lower montane forest, in shaded conditions.

Phenology: Flowering in the wild from November to December, mean flowering time was recorded in January for specimens maintained in cultivation.

Notes: *Cleisomeria* includes only two species: *C. lanatum* and *C. pilosulum* (Gagnep.) Seidenf. & Garay. *Cleisomeria lanatum* is easily distinguished from *C. pilosulum* by its labellum, which has a 2-lobed apex, each lobe acuminate.

Corybas calopeplos J.Dransf. & Gord.Sm., Kew Bull. 41(3): 584. 1986. Fig. 9–10.

TYPE: Malaysia. Malay Peninsula, Pahang, Cameron Highland, near Tanah Rata, *J. Dransfield 5246* (holotype, K!).

Examined materials: INDONESIA. **North Sumatra**: Padang Lawas, Barumun, Hutarimbaru, Mount Dolok Malea, 1500–2000 m, 17 September 2020, *Y.R. Yudistira et al. YRY17092020* (ANDA!); **Aceh**: Aceh Tengah Regency, Pegasing subdistrict, Berawang Baro village, 4°24’42.8”N 96°39’45.1”E, *ca.* 1420 m, 01 October 2024, *W.A. Mustaqim s.n.* (UIDEP!).

Distribution: Peninsular Malaysia; extended distribution includes North Sumatra.

Habitat and ecology: In Sumatra, plants grow as terrestrials in upper montane rainforest on steep, well-drained, moss-covered banks and flat montane bogs. In North Sumatra Utara, plants grow alongside *C. carinatus* (J.J.Sm.) Schltr., whereas in Central Aceh it is found together with *C. geminigibbus* J.J.Sm.

Phenology: Flowering in the wild from September to October.

Notes: This species is easily distinguished by its translucent green labellum bearing a rounded, eye-like callus. It is morphologically similar to *C. roseus* (Janch.) Janch. ex J.J.Sm., but differs in the coloration and shape of the labellum, which is pale translucent, green to greenish white with radiating crimson blotches line (*vs*. pinkish white with dark purple blotches line in *C. roseus*). Also, the callus in *C. calopeplos* is 1.5 mm wide, white with dark crimson on the center (*vs*. 4 mm wide, light pink in *C. roseus*) (Janchen, 1930; Dransfield *et al*., 1986).

Corybas holttumii J.Dransf. & Gord.Sm., Kew Bull. 41(3): 590. 1986. Fig. 11–12.

TYPE: Malaysia. Selangor/Pahang, Genting Highlands, *Dransfield* 4952 (holotype, K, not seen).

Examined materials: INDONESIA. **West Sumatra**: Payakumbuh, Kelok Sembilan, *ca*. 1400 m asl. 20 June 2022, *Y.R. Yudistira et al. YRY01352023* (ANDA!).

Notes: *Corybas holttumii* is newly recorded from Sumatra and differs markedly from the other *Corybas* native to the island. *Corybas holttumii* resembles *C. taiwanensis* T.P.Lin & S.Y.Leu from Taiwan but differs in the rounded labellum, 10 × 15 mm, flattened papillose with deep crimson color at the middle part *vs*. elliptic-rounded labellum, 1.7 × 1.0 cm, white with dark-red striate dots-line at the middle part (Lin, 1975; Dransfield *et al*., 1986).

Distribution: Peninsular Malaysia, with an extended distribution that includes West Sumatra.

Habitat in Indonesia: In Sumatra, plants grow as terrestrials on moss banks within shaded mossy forests.

Phenology: Flowering in the wild from May to June.

Dendrobium teretifolium R.Br., Prodr. Fl. Nov. Holland.: 333. 1810. Fig. 13.

TYPE: Australia. New South Wales *Brown, R.* 5508 (lectotype, BM! -image BM000990504).

Examined materials: INDONESIA. **East Nusa Tenggara**: Kupang Regency, Leloboko, 500–1500 m, 12 April 2023, *Y.R. Yudistira et al. YRY12042023* (FIPIA!).

Distribution: Australia (New South Wales, Queensland), with extended distribution including East Nusa Tenggara, Indonesia.

Habitat and ecology: In East Nusa Tenggara, plants grow as epiphytes on *Mangifera indica* L. in mid-montane forests on limestone substrates, usually in semi-open areas.

Phenology: Flowering in the wild from August to October.

Notes: The record from East Nusa Tenggara considerably extends the known distribution range of the species. This finding is plausible given the biogeological history of the Lesser Sunda Islands, including East Nusa Tenggara, which is the result of the complex interaction between subduction along the Banda arc and the flora-mobilism of the Timor-Banda Collision (Michaux, 2010). This species is easily distinguished from other members of the *Dendrobi-*

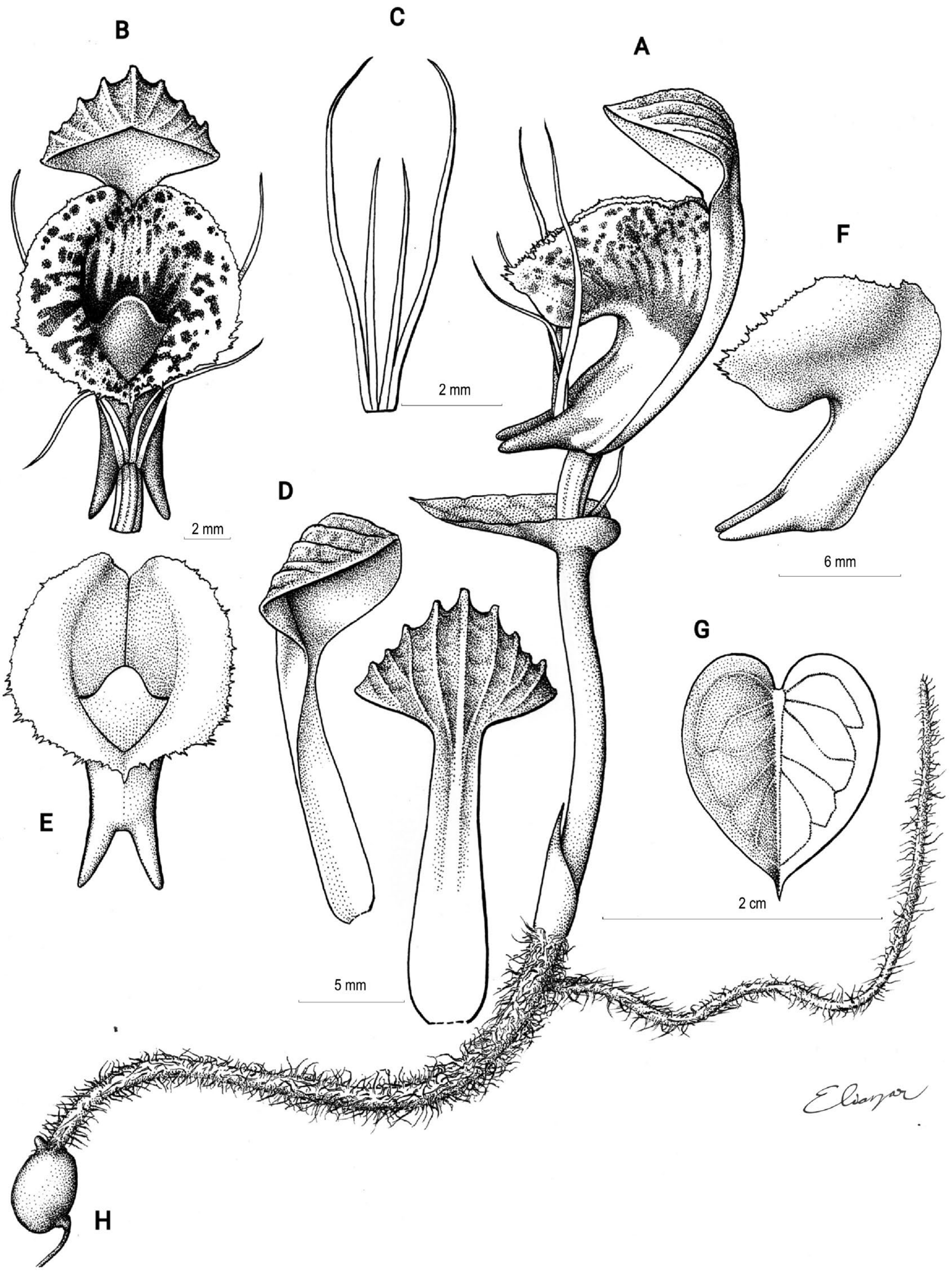

Figure 9. Line drawing of *Corybas calopeplos* J.Dransf. & Gord.Sm. **A**. Plant habit, side view. **B**. Flower, front view. **C**. Lateral sepals and petals. **D**. Dorsal sepal. **E**. Labellum, front view. **F**. Labellum, side view. **G**. Leaves. **H**. Tuber. Illustrated by Yuanito Eliazar based on *YRY17092020* (ANDA).

FIGURE 10. *Corybas calopeplos* J.Dransf. & Gord.Sm. **A**. Plant habit front view. **B**. Plant habit side view. **C**. Plant with tuber and roots. Photographed *in situ* by Y.R. Yudistira based on *YRY17092020* (ANDA).

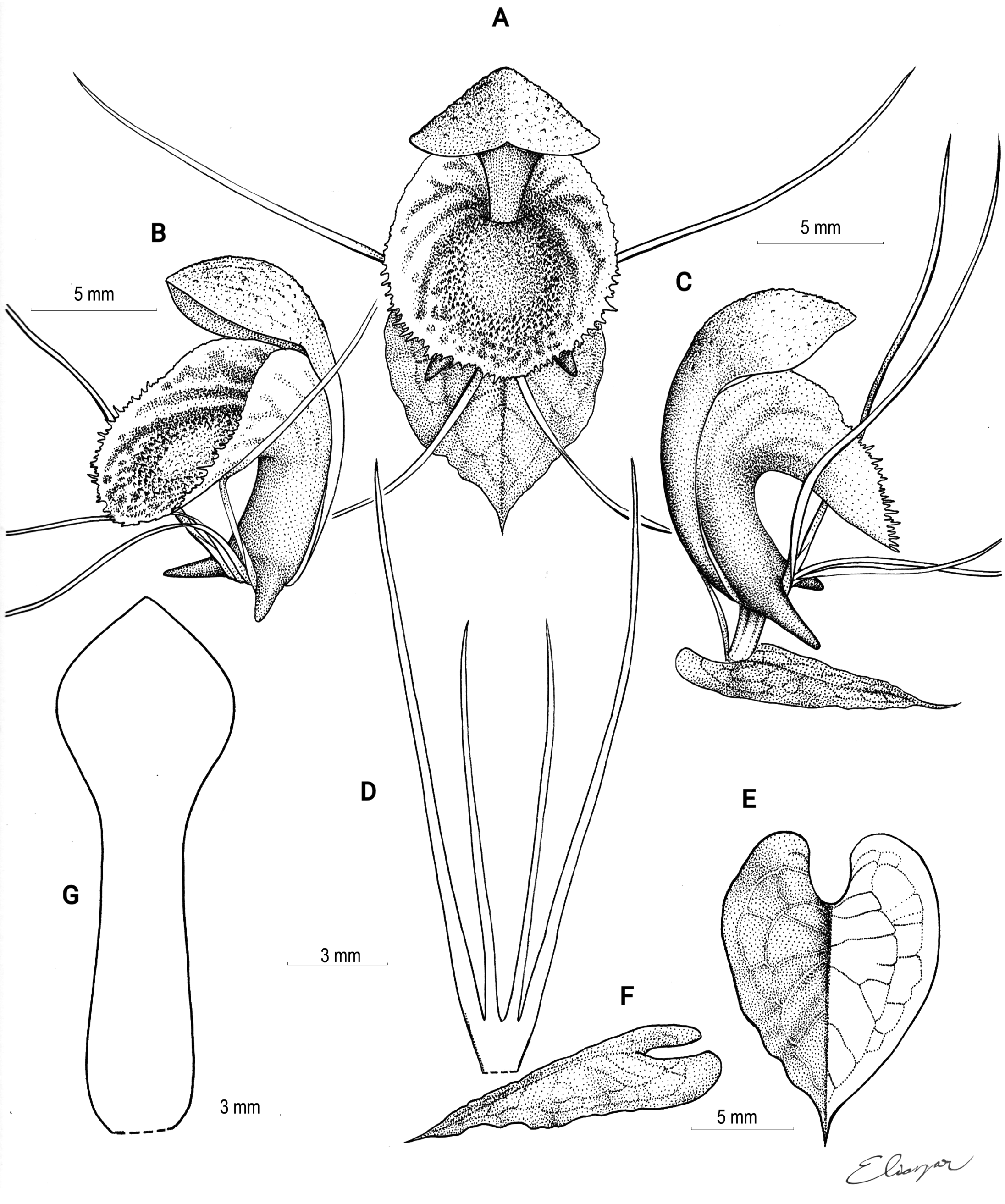

Figure 11. Line drawing and photograph of *Corybas holttumii* J.Dransf. & Gord.Sm. **A**. Plant habit. **B**. Flower, side view. **C**. Flower with leaf, side view. **D**. Lateral sepals and petals. **E**. Leaf venation. **F**. Leaf, side view. **G**. Dorsal sepal. Illustrated by Yuanito Eliazar based on *YRY01352023* (ANDA).

um in section *Rhizobium* Lindl. (Lindley, 1853) by its long, terete leaves. This species is similar to *D. linguiforme* Sw., but differs in its terete leaves *vs.* ovate in *D. linguiforme*. However, the distribution of *D. linguiforme* is restricted to Australia. *Dendrobium teretifolium* is also distinguished by its many-flowered inflorescences, tricarinate labellum, and pleasant floral fragrance.

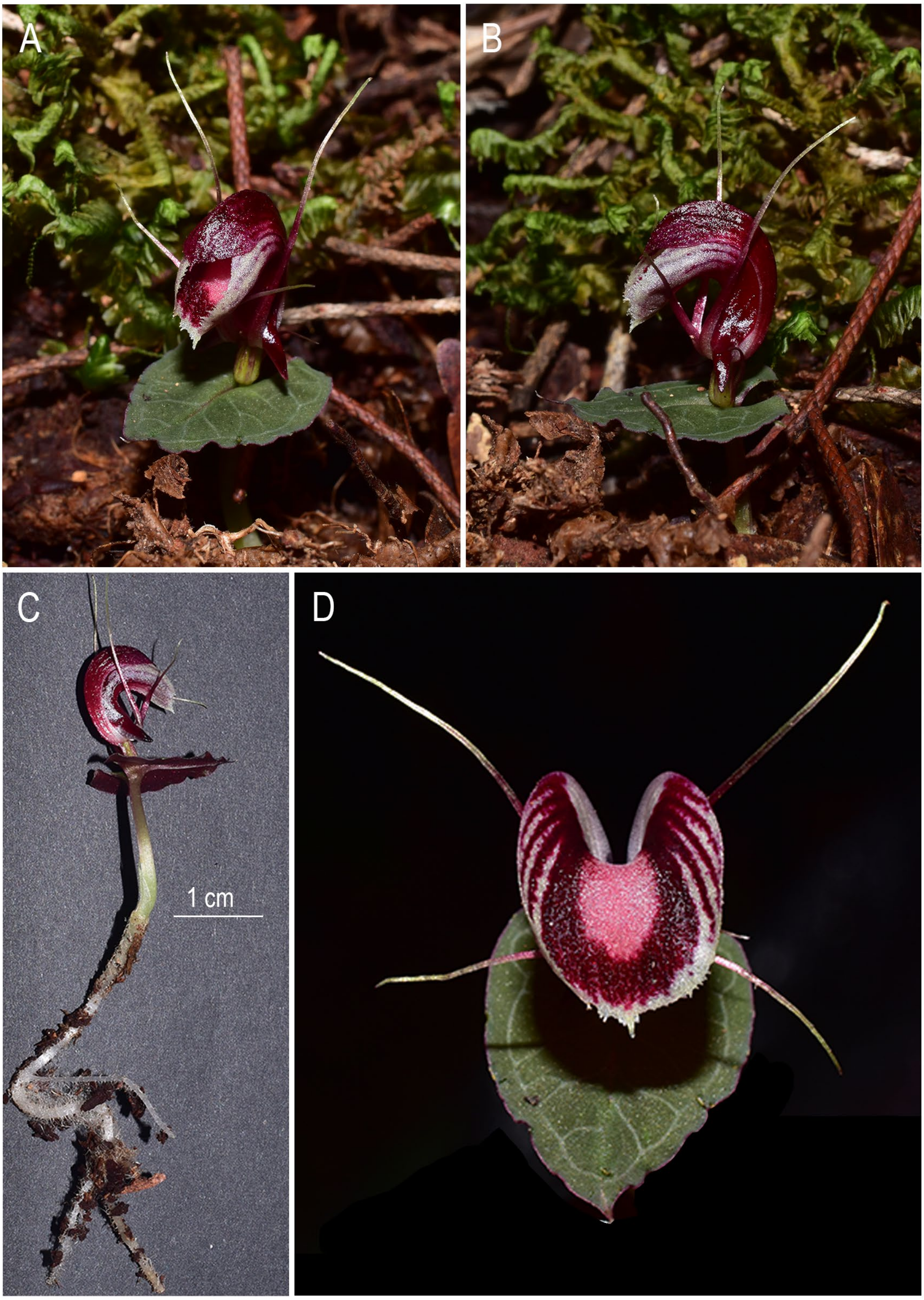

Figure 12. *Corybas holttumii* J.Dransf. & Gord.Sm. **A**. Plant habit, 3/4 view. **B**. Plant habit, side view. **C**. Plant with tuber and roots. **D**. Labellum, front view. Photographed *in situ* by Y.R. Yudistira based on *YRY01352023* (ANDA).

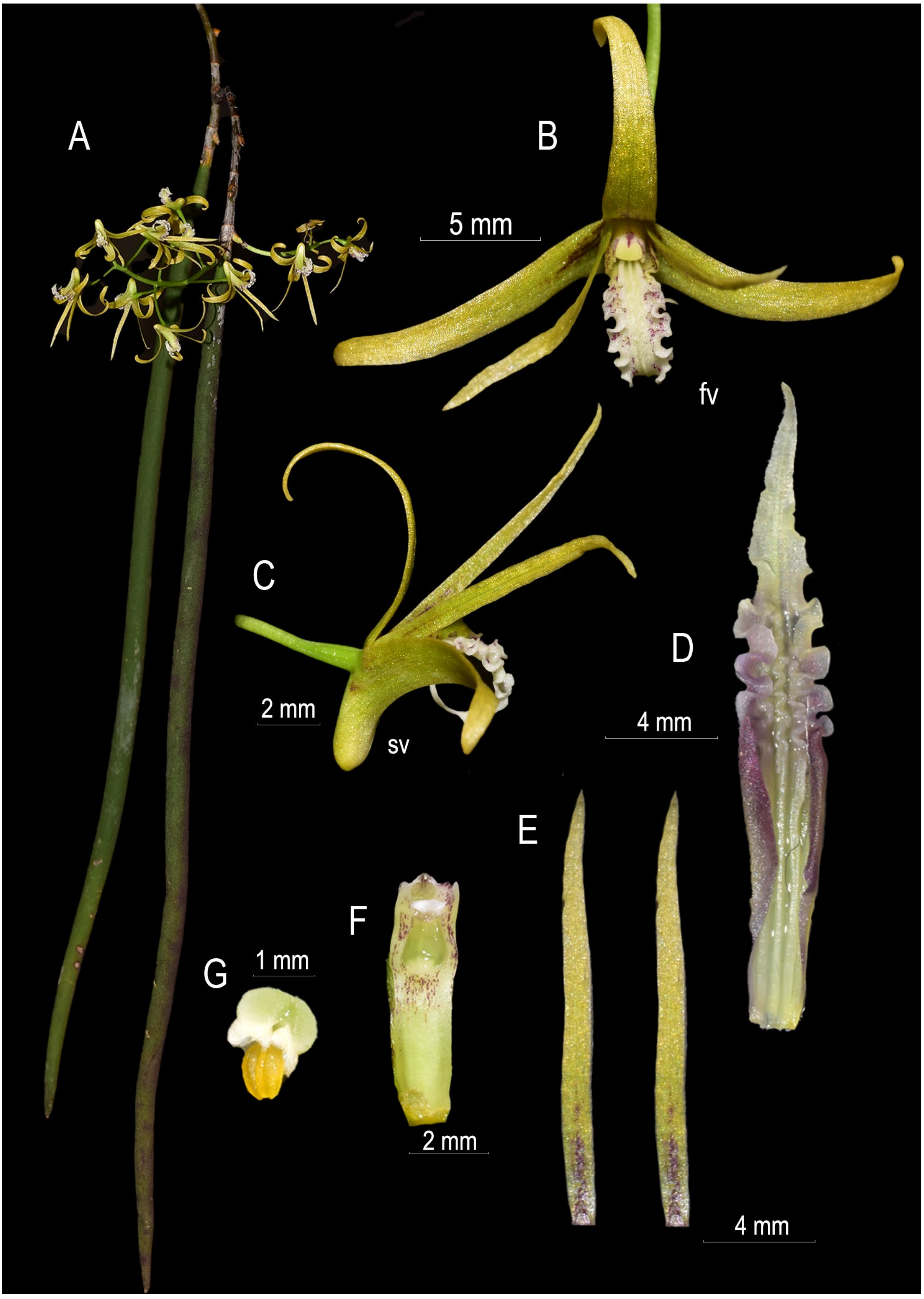

FIGURE 13. *Dendrobium teretifolium* R.Br. **A**. Plant habit. **B**. Flower, front view. **C**. Flower, lateral view. **D**. Labellum. **E**. Petals. **F**. Column. **G**. Anther cap and pollinia. Photographed by Y.R. Yudistira based on *YRY12042023* (FIPIA).

Conclusion. A total of seven species (*Acanthophippium bicolor, Bulbophyllum nematocaulon, B. sanguineomaculatum, B. thiurum, Cleisomeria lanatum, Corybas calopeplos, C. holttumii*) demonstrate a distributional range extending within Sundaland floristic region from mainland Asia (India and Sri Lanka) and peninsular Malaysia to Sumatra, Borneo, and Java. Accordingly, these recent distribution records conform to the phytogeographical boundaries by Van Welzen (2011). Updated distribution patterns of the studied orchid species, including newly documented occurrences, are illustrated in Fig. 14.

In this report, we notice a remarkably expanded distribution from the eastern part of Indonesia for 3 species: *Aerides augustiana, Anoectochilus papuanus,* and *Dendrobium teretifolium.* The expanding distribution of *Aerides augustiana* and *Dendrobium teretifolium* was in line with the floristic affinity area from van Welzen (2011), where Sulawesi and East Nusa Tenggara (Lesser Sunda Islands) fall into the Wallacea group. The Wallacea group shared the flora distribution and affinity with the Philippines and Australia (van Welzen, 2011). The range extension of *Anoectochilus papuanus* from Papua to East Java deviates from predicted biogeographical patterns. While East Java is floristically grouped with the Sunda Shelf and the Philippines within the Wallacean region (van Welzen, 2011), the presence of *A. papuanus* suggests a disjunct distribution that contradicts the floristic affinity area. Such biogeographical anomalies may arise from a paucity of data regarding the flora of Eastern Indonesia, which remains relatively underexplored (Vermeulen *et al.,* 2011; Sun *et al.*, 2024; Schuiteman & Wanma*,* 2017). By presenting these ten novel records, this study contributes to a more comprehensive understanding of orchid diversity in Indonesia, thereby reducing the disparity between documented and undocumented species. However, to address current knowledge gaps, it is essential to prioritize field explorations and the systematic review of herbarium collections across the Wallacea and Sahul bioregions, thereby facilitating a more robust assessment of orchid species richness.

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CONFLICT OF INTEREST. We declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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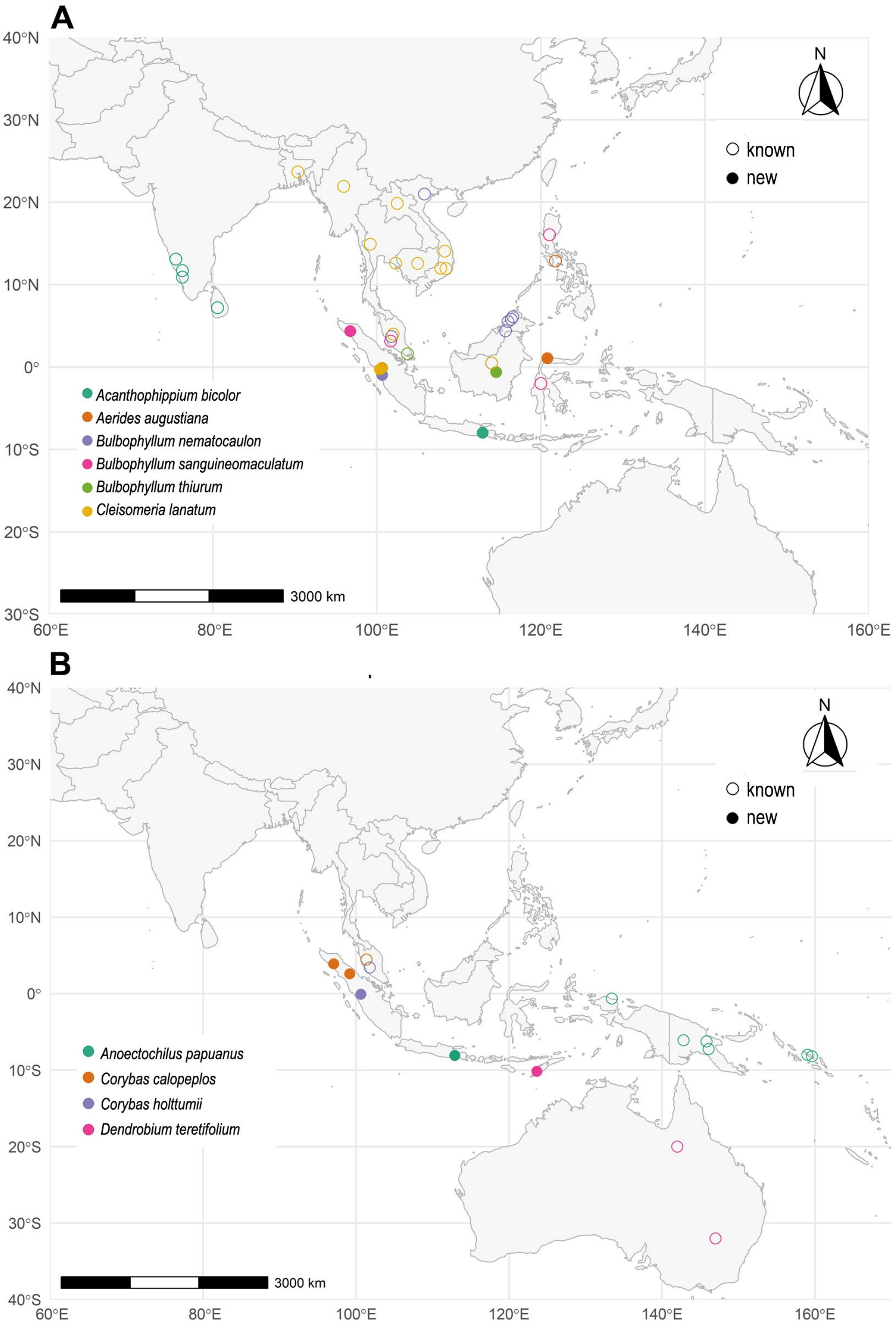

FIGURE 14. Geographic distribution of ten selected orchid species. **A**. *Acanthophippium bicolor, Aerides augustiana, Bulbophyllum nematocaulon, B. sanguineomaculatum, B. thiurum, Cleisomeria lanatum*. **B**. *Anoectochilus papuanus, Corybas calopeplos, C. holttumii, Dendrobium teretifolium*. Filled symbols denote the new distribution records reported in this study, while the open symbols indicate previously known occurrences based on literature and database records. Elaborated by R.K. Wati.

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THE GENUS *ENCYCLIA* (ORCHIDACEAE, EPIDENDROIDEAE) IN MARANHÃO STATE, BRAZIL: NEW MORPHOLOGICAL DATA AND EXTENT OF DISTRIBUTION

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Abstract. In this study, we report the diversity, geographical distribution, and ecology of the *Encyclia* species from the state of Maranhão, Brazil. For each species treated, we present morphological descriptions, geographic distribution maps, taxonomic and ecological comments, an identification key for the species occurring in the state and photographic plates. Three species were recorded: *E. gonzalezii*, *E. granitica,* and *E. linearifolioides*, with *E. gonzalezii* being endemic to Brazil. *Encyclia granitica* has been locally rediscovered approximately 93 years after its only known collection in Maranhão. We also included new morphological data for this species, for which a description of the fruits had not been available until now. We found that the epicarp of the three species exhibited significant morphological differences, which may aid in their identification and delimitation. Given the complicated taxonomy of the genus, further studies focused on the epicarp may determine the extent to which it can assist in distinguishing additional species and in assessing its phylogenetic signal.

Keywords / Palabras clave: Amazon Forest, Cerrado, fruits, frutos, orchids, orquídeas, Selva Amazónica, taxonomía, taxonomy

Introduction. *Encyclia* Hook. comprises approximately 200 Neotropical species of Orchidaceae, distributed from the southern United States (Florida) to northeastern Argentina (Carnevali *et al*., 2023). It is a monophyletic genus within Laeliinae (Carnevali *et al*. 2023) and its species are epiphytic, lithophytic or occasionally terrestrial on leaf litter, recognized by ovoid, conical or slightly conical pseudobulbs, linear, narrowly oblong, lanceolate or elliptic leaves, an apical inflorescence and flowers with a trilobed lip (Bastos *et al*., 2016, 2018, 2026; Toscano de Brito & Cribb, 2005). The presence/absence of stelidia (column wings) and the surface of the ovary and shape, size, lobes and callosities of the lip are important characters for delimiting species within this genus (Bastos *et al*., 2026; Meneguzzo, 2012).

In Brazil, 48 species of *Encyclia* are recognized, of which 29 are endemic (Bastos *et al*., 2026; Pessoa *et al*., 2025). In the state of Maranhão, three species occur: *E. gonzalezii* L.C.Menezes, *E. granitica* (Lindl.) Schltr. and *E. linearifolioides* (Kraenzl.) Hoehne (Bastos *et al*., 2026; Ferreira *et al*., 2022; Pessoa *et al*., 2022). The state of Maranhão is located in an ecotonal area between the Amazon, Cerrado and Caatinga

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domains (Spinelli-Araújo *et al*., 2016) and harbors a wide variety of natural environments that are suitable for the occurrence of *Encyclia* species (Bastos *et al*., 2026). However, there are still areas of the state that lack botanical collections, especially in the Amazon and Cerrado domains along the southern border of the state. The inclusion of newly documented populations is crucial for improving our understanding of the conservation status of these species, particularly given that Maranhão is one of the Brazilian states that is most affected by the expansion of agriculture and cattle livestock (Nepstad *et al*., 1995).

From a taxonomic perspective, some of these species have incomplete descriptions, as is the case of *E. granitica*, for which the fruit has not yet been described (Lindley, 1841). Although this species was described more than a century ago, detailed information of the fruit remains unknown even in the most recent taxonomic revision of Brazilian *Encyclia* species (Bastos *et al*., 2018). The most common information about fruits relies on their shape and size (Bastos *et al*., 2018, 2026).

Therefore, in view of the limited sampling of *Encyclia* specimens in Maranhão, this study aimed to: (1) provide a taxonomic treatment of *Encyclia* species occurring in the state; (2) expand field sampling to document new populations and refine their known geographic distributions; (3) record ecological aspects and potential threats affecting the conservation of *Encyclia* species; and (4) describe fruit characters of *Encyclia* species as additional diagnostic features for species identification.

Materials and methods. The state of Maranhão (Fig. 1), located in the Northeast region of Brazil, lies between latitudes 1° and 10° S and longitudes 41° and 48° W and occupies an area of 331,983.293 km² (IBGE, 2026). The climate of Maranhão is of the type “Aw”, Tropical with dry winter season, with annual temperatures ranging from 18 to 40 ºC and annual precipitation between 1200 and 1800 mm (Köppen, 1948).

The state comprises three phytogeographic domains as well as transition areas among them, with the Cerrado domain occupying 64% of the territory, followed by the Amazon at 35% and some Caatinga fragments, in addition to coastal phytophysiognomies in the north (IFNMA, 2024; IMESC, 2022; PPCDQ-MA, 2024; Silva *et al*., 2016; Spinelli-Araújo *et al*., 2016). In Maranhão, the Amazon and Cerrado domains have experienced increasing fragmentation due to deforestation and fires. Habitat loss is most pronounced in the Amazon domain, followed by the Cerrado, which has been heavily affected by agricultural expansion in the so-called arc of deforestation (Nepstad *et al*., 1995). Even in protected areas, such as the Gurupi Biological Reserve, Mirador State Park and Chapada das Mesas National Park, fires and illegal deforestation threaten native species (IFNMA, 2024; IMESC, 2022; PPCDQ-MA, 2024; Spinelli-Araújo *et al*., 2016).

Field collections were conducted between January 2020 and October 2025. The collected specimens were photographed and herborized according to Fidalgo & Bononi (1989), and their vouchers were deposited in the MAR and SLUI herbaria (acronyms according to Thiers, 2026). The specimens were identified with the aid of photographs of morphological details observed in the field, based on the original works (Hoehne, 1938; Menezes, 1991; Schlechter, 1919), type specimens available at JSTOR Plants (ITHAKA, 2026) and specialized literature on *Encyclia* (Bastos et *al*., 2018, 2026; Ferreira *et al*., 2022; Meneguzzo *et al*., 2012; Oliveira *et al*., 2021; Pabst & Dungs 1975, 1977; Sambin & Chiron, 2014; Silva *et al*., 1999). The geographic distribution of *Encyclia* species was based on Bastos *et al*., (2018, 2026), Ferreira *et al*., (2022), Flora e Funga do Brasil (2026), and POWO (2026).

Based on the material collected in the field, we provide more detailed information on the fruits of *Encyclia* species from Maranhão. The inclusion of these additional characters does not constitute an emendation of the original descriptions according to Article 47.1 of the International Code of Nomenclature for algae, fungi, and plants (Turland *et al*., 2025).

We also analyzed specimens from Maranhão deposited in the collections of the CEN, COR, ESA, HEPH, HJ, HTO, HUEFS, HUEG, IAN, IBGE, INPA, K, MBM, MG, MO, NY, R, RBR, RB, SLUI, SP, SPF, TEPB, UB and US herbaria, using the virtual collections of Reflora (2026) and SpeciesLink (2026). When images were not available in these repositories, we used the institutions’ own digital platforms.

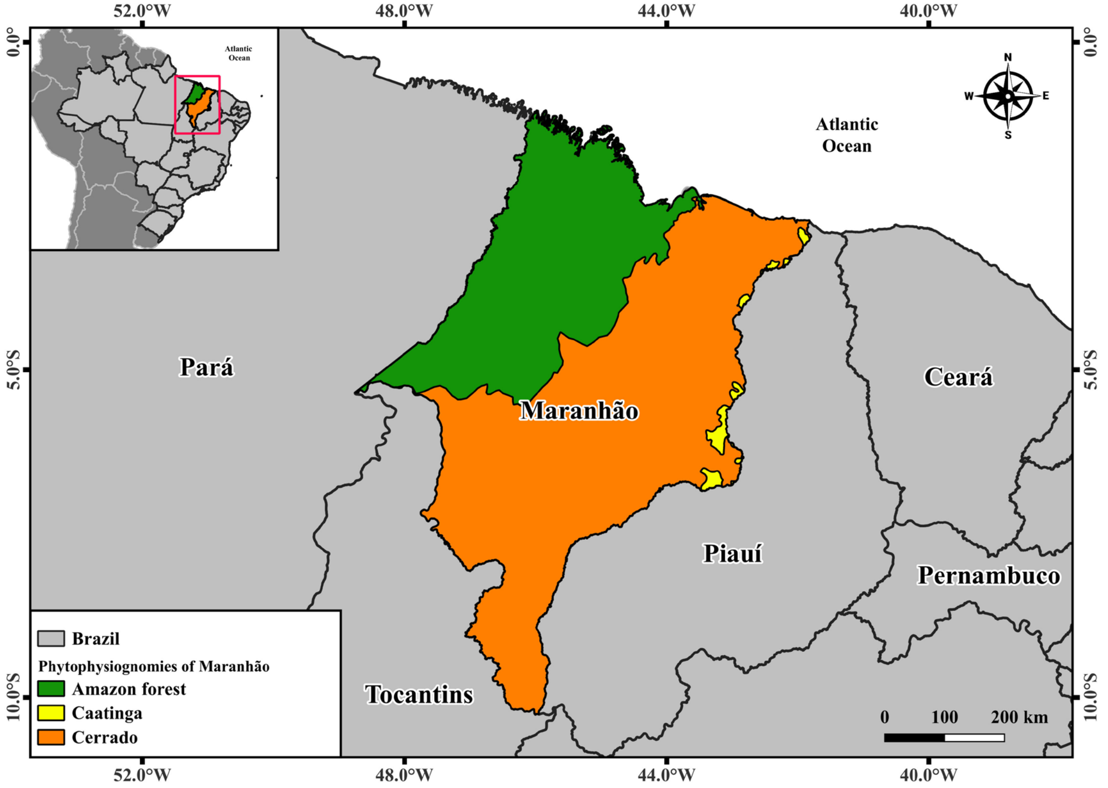

Figure 1. Location of the state of Maranhão, highlighting the Amazon, Cerrado and Caatinga domains. Elaborated by Miguel Sena.

Geographic distribution maps were produced using QGIS v.3.34.1, with the SIRGAS 2000 datum (QGIS Development Team, 2023).

Results. The occurrences of *E. gonzalezii*, *E. granitica*, and *E. linearifolioides* in the state of Maranhão were confirmed. A total of 20 specimens were collected during the field expeditions conducted in this study, comprising two of *E. gonzalezii*, ten of *E. granitica*, and eight of *E. linearifolioides*. Six specimens were located in herbarium collections: two of *E. gonzalezii* (see Ferreira *et al.*, 2022), one of *E. granitica*, and three of *E. linearifolioides*.

Encyclia gonzalezii was found exclusively as an epiphyte, whereas *E. granitica* has occasionally occurred as a terrestrial species in leaf litter, and *E. linearifolioides* was observed as epiphyte and occasionally rupicolous. The only previously recorded sample of *E. granitica* for Maranhão was collected in 1932 (*Fróes 1998* at NY), and the ten new collections mark its rediscovery in the state after approximately 93 years.

The new fertile samples allowed a more detailed characterization of the fruits of the species, with the fruits of *E. granitica* being described for the first time, as they were not included in the original description by Lindley (1841) nor in the most recent revision of Brazilian *Encyclia* (Bastos *et al.*, 2018). In these three *Encyclia* species, the dehiscent fruits were described in greater detail (Fig. 2F, 4F, and 5F). They released anemochorous seeds through three longitudinal keels, which opened approximately 10 months after pollination and the onset of fruit development. The surfaces of the fruits of these three species showed significant differences in size, color, shape and surface texture, which can serve as an aid in their identification and description, as detailed in the morphological descriptions in Table 1. Future studies involving detailed observations of the fruits of other *Encyclia* species may help determine the extent to which these traits can be used to distinguish different species.

TABLE 1. Comparison of characteristics of the fruit of the three *Encyclia* species from Maranhão: *E. gonzalezii, E. granitica,* and *E. linearifolioides.*

Species characteristics	***E. gonzalezii***	***E. granitica***	***E. linearifolioides***
Fruit size (cm)	2.6–2.9 × 0.8	3.0–4.5 × 1.5–2.0	2.5–3.5 × 0.7–1
Fruit shape	Globose-fusiform	Globose–fusiform	Long-fusiform
Fruit coloration	Dark green	Green	Light green
Density of vesicles on the fruit surface	Densely punctuated	Densely punctuated	Sparsely punctuated
Shape and size of vesicles on the fruit surface	Linear–hemielipsoidal, 1 mm	Hemispherical to hemielipsoidal,1–2 mm	Predominantly hemispherical, 0.5 mm
Color of vesicles on the fruit surface	Whitish	Whitish	Translucent

TAXONOMIC TREATMENT

Encyclia Hook., Bot. Mag. 55: t. 2831. 1828.

TYPE: *Encyclia viridiflora* Hook. Bot. Mag. 55: t. 2831. 1828. *Epidendrum viridiflorum* (Hook.) Lindl., Edwards's Bot. Reg. 28 (Misc.): 30. 1842

Epiphytic, terrestrial or lithophytic *herbs*, sympodial. *Rhizome* inconspicuous or conspicuous. *Pseudobulbs* conical, globose, ovoid, ellipsoid or pyriform, usually covered by membranous bracts (paleaceous sheaths). *Leaves* apical on the pseudobulb, 1–4, sessile, with entire margins, obtuse to acute apices and a truncate base; flat or canaliculate, lanceolate, oblong, linear or ovate, fleshy or coriaceous. *Inflorescence*, usually terminal, bearing 1–400 flowers, usually longer than the leaves, arranged in a simple panicle or raceme, lacking spathaceous bracts. *Flowers* bisexual, usually resupinate, with free sepals and free petals, pedicellate, generally fragrant and lacking trichomes or other indumentum. *Sepals* dorsal and lateral symmetrical or asymmetrical, lanceolate, oblanceolate, elliptic, ovate or spatulate, erect, oblong or reflexed, fleshy or membranaceous, cymbiform or falcate, with an attenuate base, entire or undulate margins and an acute, obtuse, mucronate or uncinate apex. *Petals* spatulate, lanceolate or cymbiform, elliptic, erect, reflexed or occasionally pendent, fleshy or membranaceous, with entire, slightly serrate or undulate margins, an acute, obtuse or mucronate apex and an attenuate base. *Lip* trilobed, fused to half of the column or free from the column, usually with an isthmus, base lacking a claw, lateral lobes free or adnate relative to the median lobe; ovate, rectangular, triangular, dimidiate, oblong or falcate, forming an angle of 45° to 90° relative to the median lobe, overlapping it or not, with entire or undulate margins and an obtuse to acute apex; median lobe orbicular to cordate, obovate, rhombic, elliptic, obdeltate, spatulate, conduplicate, reniform, flat or sinuous, with entire, undulate or fimbriate margins, an acute to emarginate or uncinate apex, with an isthmus and a longitudinal callus with a suture in the central part of the lip, cymbiform or dolabriform, with an acute to emarginate apex, truncate, bifid or trifid and flabellate. *Column* clavate, semi-clavate or dolabriform, with or without two arms near the stigma; arms ovate, rounded, quadrate or triangular, with an acute to obtuse apex; clinandrium with a tridentate or unidentate apex, lateral teeth triangular, rounded or corniform, with an acute, truncate or premorse apex; median tooth triangular, with an acute apex, bearing the two arms on the column, s*tigma* ovate, rounded, obovate or triangular, concave, v*iscid*, with or without basal hooks. *Rostellum* apically curved. *Pollinia* 4, waxy, in pairs, of equal size, laterally flattened or ovate to elliptic, parallel, yellow, with a linear and granular caudicle. *Fruit* capsular, fusiform to globose-fusiform, smooth or with verrucose or spiculate vesicles.

KEY FOR THE *ENCYCLIA* SPECIES OF MARANHÃO

1. Adult leaves > 50 cm long and > 2 cm wide; flowers with light beige petals and sepals, with vinaceous striations and spots; callus on the lip acute at the apex .... ***E. granitica***

1a. Adult leaves < 50 cm long and < 2 cm wide; flowers with beige to brownish-beige petals and sepals, without vinaceous striations and spots; callus on the lip trifid or flabellate at the apex 2

2. Lip greenish at the base and pinkish at the apex, lobes with acute apices and trifid apex callus; column with a bidentate apex; fruit dark green, with hemispherical vesicles densely distributed over most of the surface .... ***E. gonzalezii***

2a. Lip beige at the base and white at the apex, lobes with rounded apices and flabellate apex callus; column with a tridentate apex; fruit light green, with hemispherical vesicles sparsely distributed over the surface .... ***E. linearifolioides***

Encyclia gonzalezii L.C.Menezes, Bol. CAOB 3(2): 19. 1991. Fig. 2, 3A.

TYPE: BRAZIL. Distrito Federal: border with Goiás State, Rio Descoberto, July 1990, *Cazelato* sub *Menezes s.n.* (holotype: UB!).

Epiphytic. *Rhizome* inconspicuous. *Pseudobulbs* 2.9–4.9 × 1.1–2.1 cm, conical, elongate, reddish. *Leaves* (1–3) 11.5–41.9 × 0.6–1.7 cm, lanceolate, flattened, coriaceous, with an acute apex. *Inflorescence* 11.4–51.9 × 0.10–0.14 cm, terminal, racemose, cylindrical, glabrous, erect to slightly arched, bearing 8–23 flowers; peduncle 8.4–12.0 cm long; rachis 3.0–39.9 cm long; floral pedicel sparsely verrucose. *Flowers* with greenish-brown sepals and petals and a white lip with brownish-reddish striations; *pedicel* and *ovary* 1.7–3.0 cm long, verrucose. *Dorsal sepal* 1.0–1.1 × 0.3–0.5 cm, lanceolate, with an obtuse apex. *Lateral sepals* 1.0–1.1 × 0.2–0.4 cm, elliptic, falcate, with an acute apex. *Petals* 1.1–1.3 × 0.2–0.4 cm, lanceolate, with an acute apex. *Lip* trilobate, 1.1–1.3 × 0.7–1.0 cm, ungulate (0.14 × 0.20 cm); lateral lobes 0.6–0.7 × 0.2–0.3 cm, rectangular, with rounded lateral margins and straight apices; median lobe rounded, with rounded margins, *callus* cymbiform, apex trifid, 0.4–0.5 × 0.5–0.6 cm, linearly branched with small brownish-reddish spots and veins. *Column* 0.6–0.7 × 0.2 cm, clavate, bidentate at the apex, with a pair of downward-facing arms, rectangular at the base and rounded at the apex (*ca.* 0.1 cm long), *stigma ca.* 0.1 × 0.1 cm, triangular. *Anther cap ca.* 0.1 × 0.1 cm long, elmiform, keeled at the apex, purplish, quadrangular in frontal view, with an emarginate apical portion. *Pollinia* 4, yellow, waxy, ovate, laterally flattened. *Fruit* 2.6–2.9 × 0.8 cm, globose-fusiform, dark green, with six longitudinal sulcate keels (three associated with dehiscence), surface densely marked with linear-hemielipsoidal vesicles (*ca.* 1 mm long), whitish, generally arranged transversely to the fruit.

MATERIAL EXAMINED: BRAZIL. **Distrito Federal**: Brasília, Germplasm bank of the Brasília Botanical Garden. Cultivated in a clay pot, 17 March 2002, *R. Rodrigues Silva 625* (HEPH). Distrito Federal, Floresta do Capão Comprido, 13 November 1998, *Sampaio et al. 257* (CEN). **Goiás**: Campos Belos, Pouso Alto, in a stream by a precast concrete bridge. Cerrado biome, dry forest physiognomy, beside a stream, 11 October 2010, *T.E.C. Meneguzzo et al. 570* (UB). Divinópolis de Goiás, 14 October 2009, *C. Bastos 298* (HUEFS). Guaraíta, Distrito de Guarani de Goiás, at a waterfall. Cerrado biome, gallery forest physiognomy, 9 October 2010*, T.E.C. Meneguzzo et al. 568* (UB). São Domingos, Galheiros River. Cerrado biome, dry forest physiognomy, beside a stream, 10 October 2010, *T.E.C. Meneguzzo et al. 569* (UB). São Domingos, Fazenda São Domingos, deciduous forest physiognomy, 10 March 2004, *A.A. Santos et al. 2297* (CEN). São Domingos, 15 April 1999, (flowered in cultivation in October 2001), *A.A. Santos et al. 410* (CEN). São Domingos (flowered in cultivation from mid-August to mid-September 2003), *A.A. Santos et al. 410A* (CEN, HUEFS). **Maranhão**: Carolina, Rio Farinha, Cachoeira das Mesas, 5 October 2025, *A.W.C. Ferreira 1645* (SLUI). Estreito, near the Carolina border, Cachoeira da Prata, 17 March 2017; (blooming in cultivation on 15 November 2019), *I. Zanandrea et al. s.n.* (SLUI 5945); Ibid., 17 March 2017; (blooming in cultivation on 10 November 2020), *I. Zanandrea s.n.* (SLUI 5946). Estreito, Parque Nacional da Chapada das Mesas, Cachoeira da Prata, 23 November 2021, *M.J.C. Silva & A.V. Scatigna 428* (SLUI).

DISTRIBUTION AND ECOLOGY: *Encyclia gonzalezii* is endemic to Brazil (POWO, 2026), occurring exclusively within the Cerrado domain, with confirmed records from the northern (Tocantins), northeastern (Maranhão) and central-western (Distrito Federal and Goiás) regions. It is typically found in ripar-

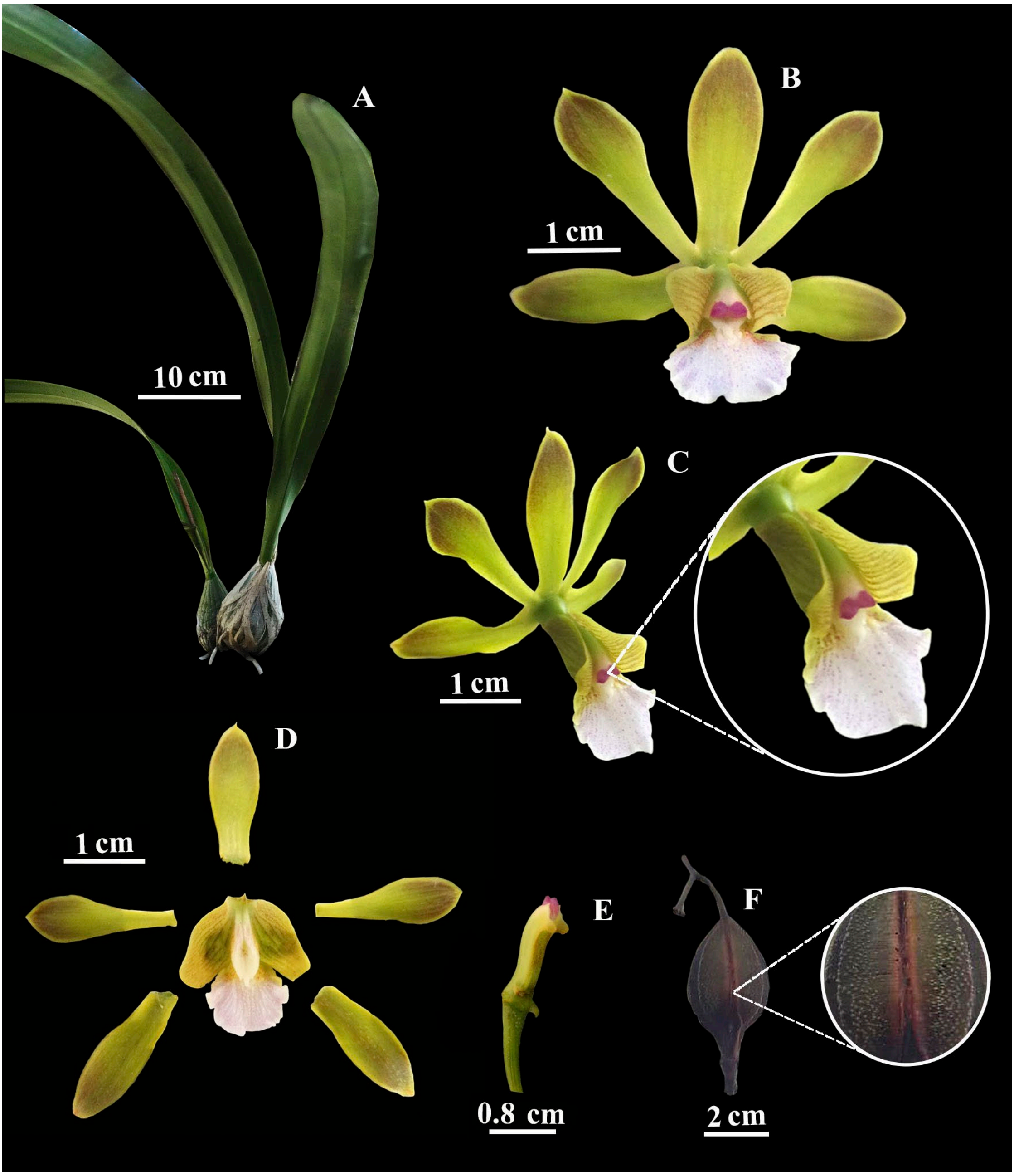

FIGURE 2. *Encyclia gonzalezii*. **A**. Habit, pseudobulbs and leaves. **B**. Flower, frontal view. **C**. Flower, oblique view, highlighting the lip. **D**. Perianth. **E**. Column, lateral view. **F**. Fruit, highlighting the verrucose surface. Photographs by Alessandro Ferreira and adapted from Ferreira *et al*. (2022). Based on *I. Zanandrea et al. s.n.* (SLUI 5945).

ian forests, dry forests with limestone outcrops, near rivers and streams or in small grottos, riparian and gallery forests, and occasionally as a rupicolous species on quartzite rocks (Bastos *et al.*, 2016, 2018, 2026; Ferreira *et al.*, 2022; Meneguzzo, 2012). In Maranhão, *E. gonzalezii* can be found in gallery forests, in rapids and waterfall areas within the Chapada das Mesas National Park region. In

Figure 3. *Encyclia* species in the field. **A**. *Encyclia gonzalezii* **B**. *E. granitica* **C**. *E. linearifolioides*. Photographs by Alessandro Ferreira.

this study area, *E. gonzalezii* was not observed with a rupicolous habit, being found in the canopy of *Terminalia* sp. (Combretaceae) trees (Fig. 3A).

Phenology: *Encyclia gonzalezii* flowers between September and November, during the dry season of the Cerrado in Maranhão (which occurs from May to October) and the beginning of the rainy season (which occurs from November to April). The flowers of *E. gonzalezii* emit a subtle sweet fragrance, noticeable during the day only when approaching the flowers. From 6:00 pm, the fragrance is no longer detectable to the human nose. The flowers last between 18 and 25 days.

NOTES: *Encyclia gonzalezii* is similar to *E. argentinensis* (Speg.) Hoehne, differing by the presence of purple coloration in its vegetative parts, regardless of exposure to sunlight, as well as its floral morphology, in which the median lobe is rounded in *E. gonzalezii*; whereas, in *E. argentinensis*, it is elliptic to ovate or rounded (Bastos *et al.*, 2016, 2018, 2026; Meneguzzo *et al.*, 2012).

Encyclia granitica (Lindl.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 74. 1919. *Epidendrum graniticum* Lindl., J. Bot. (Hooker) 3: 83. 1841. *Epidendrum oncidioides* var. *graniticum* (Lindl.) Lindl., Fol. Orchid. 3: 11. 1853. Fig. 3B, 4.

TYPE: GUYANA. *s. loc.*, 1840, *Schomburgk 195* (holotype: K 583899!; isotype: BM 47557!, BM 47556!, LE, OXF, U).

Epiphytic, occasionally terrestrial in leaf litter or rupicolous. *Rhizome* conspicuous. *Pseudobulbs* 3.0–11.0 × 1.0–4.3 cm, conical, elongate, green. *Leaves* (1–2), 6.5–70.0 × 1.0–3.0 cm, lanceolate to broadly lanceolate, flattened, with an acute apex. *Inflorescence* 32–41.69 × 0.10–0.45 cm, terminal, racemose, cylindrical, glabrous, erect or slightly arched, bearing 4–30 flowers; *peduncle* 24.5–82.0 cm long; *rachis* 8.1–8.7 cm long. *Flowers* with greenish-purple sepals and petals. *Lip* white-purple. *Pedicel and ovary* 0.9–3.1 cm long; floral pedicel sparsely verrucose. *Dorsal sepal ca.* 1.6 × 0.6 cm, lanceolate, with an acute apex. *Lateral sepals ca.* 1.6 × 0.5 cm, lanceolate, with an acute apex. *Petals ca.* 1.5 × 0.6 cm, spatulate, with an acute apex. *Lip* trilobate, *ca.* 1.5 × 2.0 cm, ungulate (0.20 × 0.15 cm); *lateral lobes* 0.6 × 0.3 cm, with undulate margins, obtuse apex; median lobe rounded, white with purple striations, conduplicate, with undulate margins, apex uncinate to mucronate; *callus* cymbiform, acute apex, with the median tooth larger than the lateral ones, *ca.* 0.6 × 0.4 cm, whitish, originating at the isthmus between the median lobes and aligned with the median lobe of the lip, with purple-toned lines. *Column* clavate, 0.8 × 0.3 cm, tridentate at the apex of the clinandrium, lateral teeth short, cordate, premorse apex, median tooth triangular, acute apex; pair of columnar arms downward-facing, rectangular at the base, slightly rounded at the apex and slightly inclined inward; *stigma* with basal hooks, *ca.* 0.2 × 0.2 cm. *Anther cap* elmiform, keeled at the apex, yellow. *Pollinia* 4, yellow, waxy, ovate, laterally flattened. *Fruit* 3.0–4.5 × 1.5–2.0 cm, globose-fusiform, moss green, with six longitudinal sulcate keels (three associated with dehiscence), surface densely marked with hemispherical to hemielipsoidal vesicles (1–2 mm long), whitish, arranged both transversely and longitudinally on the fruit, including along the region of all six keels.

MATERIAL EXAMINED: BRAZIL. **Amapá**: Calçoene**,** BR 156, near the governmental road camp "Carnot," 10 December 1984, *S.A. Mori et al. 17351* (NY). Macapá: along the Porto Platon–Macapá road, 18 September 1961, *J.M. Pires et al. 51099* (IAN). Amapá, 14 October 1960, *J.M. Pires 48824* (IAN). Oiapoque, Rio Oiapoque, Cachoeira Anauá, 74 m, 11 August 1960, *H.S. Irwin et al. 47421* (IAN). Oiapoque, Rio Oiapoque, low slopes of campina forest, 15 October 1960, *J.M. Pires & L.Y. Th. Westra 48862* (NY). Oiapoque, Rio Oiapoque, large rock, 29 August 2005, *A. Lobão et al. 775* (IAN). Porto Grande, 3 December 1976, *s.c., s.n., 26549* (ESA). **Maranhão**: Boa Vista do Gurupi, Povoado Mariana, near Rio Gurupi, 24 August 2022, *A.W.C. Ferreira 916* (SLUI). Ibid., 26 August 2022, *A.W.C. Ferreira 981* (SLUI); Ibid., 26 August 2022, *A.W.C. Ferreira 982* (SLUI). Carutapera, Povoado Caranandiua, campinarana near Gurupi River, 25 August 2022, *A.W.C. Ferreira 929* (SLUI); Ibid., 13 October 2023, *Silva et al. 190* (SLUI 9063); Ibid., 13 October 2023, *M.S. Silva et al. 194* (SLUI 9067); Ibid., 13 October 2023, *M.S. Silva et al. 212* (SLUI 9085); Ibid., 21 September 2025, *A.W.C. Ferreira 1623* (SLUI); Ibid., 21 September 2025, *A.W.C. Ferreira 1638* (SLUI); Campinarana da Passagem, 14 October 2023, *M.S. Silva et al. 277* (SLUI 9150). Maracaçumé, Mata da Cachoeira, Maracaçumé River region, 20 November 1932, *R.L. Fróes 1998* (NY); Ibid., 20 November 1932, *R.L. Fróes 1998* (AMES). **Minas Gerais**: Medina, BR116 highway, 10–15 km south, 20 November 1985, *G. Hatschbach & J.M. Silva 50012* (RB). Rio Doce, 11 June 1949, *M.G. Magalhães 5139* (IAN). **Pará**: Acará, Guarajá River, 25 September 1964, *Oliveira 3154* (IAN). Belém, 25 May 1957, *J.M. Pires 6587* (IAN). Belém, 10

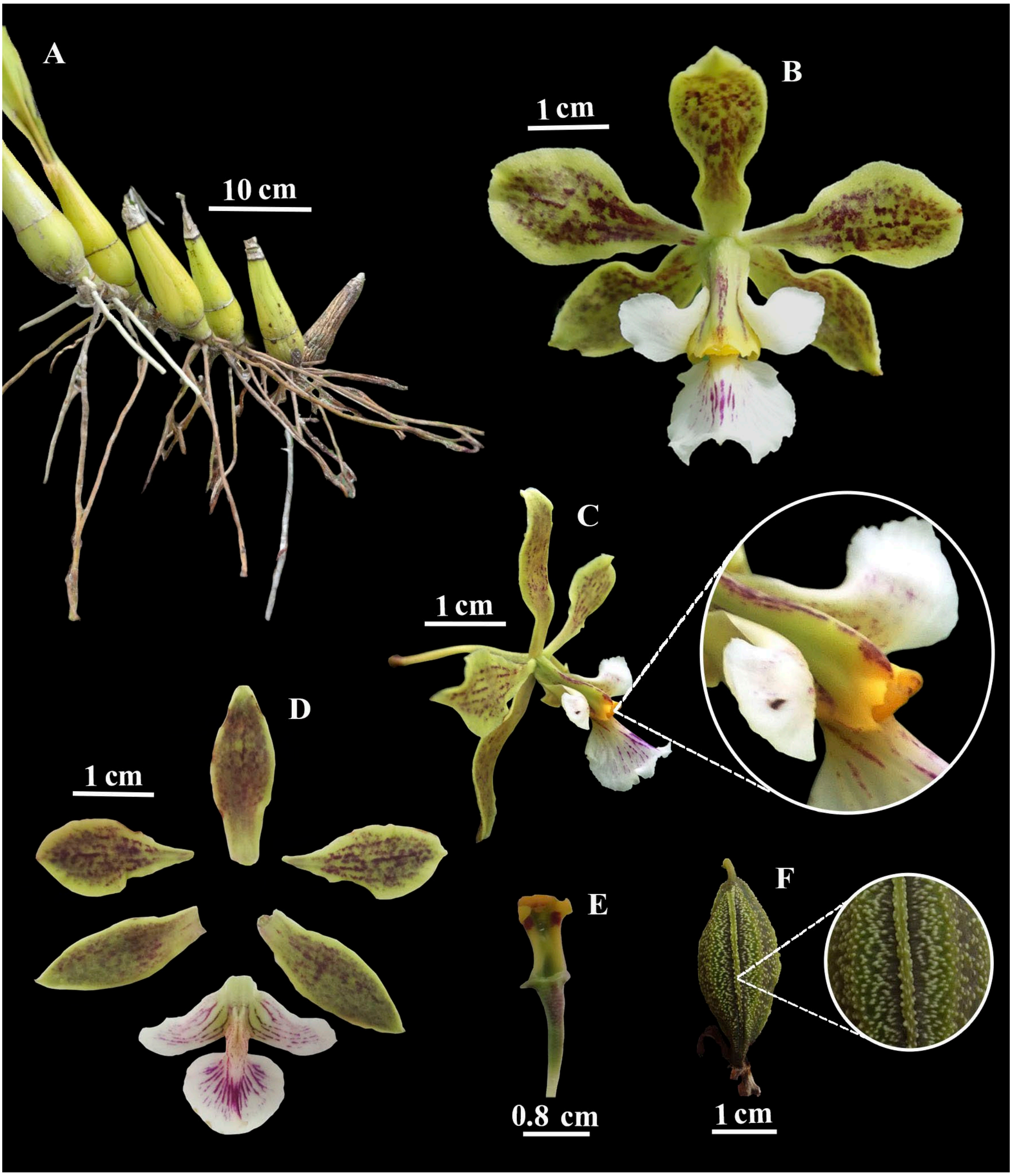

Figure 4. *Encyclia granitica*. **A**. Habit. **B**. Flower, frontal view. **C**. Flower, oblique view, highlighting the lateral lobes of the lip. **D**. Perianth. **E**. Column, frontal view. **F**. Fruit, highlighting the verrucose surface. Photographs by Alessandro Ferreira based on *A.W.C. Ferreira 1638* (SLUI 11628).

July 1961, *J.M. Pires 7833* (IAN). Belém, cultivated at the IAN Botanical Garden, 27 May 1955, *P.V.D. Ledoux 273* (IAN). Belém, cultivated at the IAN Botanical Garden, 31 July 1954, *P.V.D. Ledoux 93* (IAN). Belém, cultivated at the IAN Garden, originating from Campina do Caembe in Vigia, 26 May 1955, (flowered in cultivation in May 1953), *P.V.D. Ledoux 297* (IAN). Belém, south of Belém, 14 August 1986, *Croat 62155* (MG, MO). Bragança, railway, 16 June 1952, *R.L. Fróes 28460* (IAN). Castanhal, 5 May 1994, *Silva 31* (MG). Igarapé Açu, 24 December 1993, *Magalhães s.n.* (MG 147815). Igarapé Açú, cultivated at IAN, pot no. 334, 5 June 1958, *J.M. Pires 6741* (IAN). Irituia, 2 July 1995, *Silva & Silva 425* (MG). Maracanã, Maiandeua Island, 26 October 2000, *Costa et al. 108* (MG). Marapanim, Vila Marudá, 16 July 1991, *Bastos et al. 1045* (MG). Mojú, margins of the Mojú River road, open low campina, sandy soil, 18 August 1983, *J. Revilla et al. 8292* (MO). Ourém, Fazenda Batuíra, 1 May 1994, *Silva 304* (MG). Salinópolis, Marieta Beach, 25 October 2005, *Rocha et al. 321* (MG). Sete Varas airstrip by Curua River, campina or gallery forest along dry stream, 4 August 1981, *J.J. Strudwick et al. 4071* (MO). Tucuruí, Air Force reserve, 19 August 1980, *Braga 3604* (INPA). Vigia, straw campina, 20 March 1991, *Silva & Silva 100* (MG). Vitória do Xingu, 16 September 2013, *C.A.S. Silva, s.n.* (RB). **Roraima**: Cantá, Serra Grande, 12 November 2014, *R.C. Forzza et al. 8320* (RB). Mount Roraima, July 1897, *Quelch & McConnell 279* (K). Mucajaí, *ca.* 50 km south of Boa Vista, 17 July 2002, *L.B. Bianchetti 1721* (CEN).

Distribution and ecology: *Encyclia granitica* is endemic to South America, with confirmed occurrences in Brazil, French Guiana, Guyana, Suriname and Venezuela (POWO, 2026). In Brazil, it occurs exclusively within the Amazonian phytogeographic domain, with confirmed records in the northern (Amapá, Amazonas, Pará and Roraima) and northeastern (Maranhão) regions, typically inhabiting campinarana, gallery forest, restinga and vegetation over rocky outcrops (Bastos *et al.*, 2026). In Maranhão, it was found less frequently as an epiphyte in gallery forests and more commonly as a terrestrial plant in the leaf litter or at the base of phorophytes in sunny sandy campinarana areas in the Gurupi River region, along the border with the state of Pará. Prior to this study, there was only a single record of *E. granitica* for Maranhão, collected in the Maracaçumé River region, likely in the municipality of Governador Nunes Freire, in November 1932 (*Fróes 1998*, NY). Therefore, in this study, *E. granitica* was locally rediscovered approximately 93 years after its first record.

In this campinarana region, individuals growing in shaded environments have light green, elongated and arching leaves (20–70 × 1.2–2.8 cm), whereas those observed in more exposed or full-sun areas have yellowish-green, erect leaves that are shorter (14–30 × 1.0–1.5 cm). The flowers emit a strong, sweet fragrance. The frequent annual fires carried out by cattle ranchers in this sandy campinarana region represent the greatest threat to *E. granitica* and other local plant and animal species. It was common to observe charred *E. granitica* individuals.

In these sunny areas with sandy soils of the campinaranas (Fig. 3B), individuals grow at the base of phorophytes or partially shaded in the leaf litter. This low-to-the-ground positioning at the base of the phorophytes is likely related to the dry season, which occurs from July to December in the study area. Growing at the base of phorophytes protects the plants from sun exposure during the hottest part of the day. Their proximity to the ground and the leaf litter may mitigate the effects of drought, as it creates a cooler microenvironment, especially during the dry season. In the study area, we observed that *E. granitica* occasionally grows in the canopy or mid-trunk of phorophytes, but most often at the base of the phorophytes (near the leaf litter), primarily on yellow ipê, *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore (Fabaceae); murici, *Byrsonima crispa* A.Juss. (Malpighiaceae); *Byrsonima* sp. (Malpighiaceae); *Clusia fockeana* Miq., *Clusia sellowiana* Schltdl. (Clusiaceae); and *Astrocarium* sp. (Arecaceae).

Phenology: *Encyclia granitica* flowers between August and November during the dry season of the Amazon region of Maranhão (which occurs from July to December).

Notes: To date, *E. granitica* is the only species of this genus to have been observed in the Amazon region of Maranhão. Two types of flowers were observed in the study area in regard to lip morphology at the beginning of anthesis: individuals with labella flattened from the outset, and individuals with labella initially shaped like a ridge, with the lateral lobes turned downward. After four or five days, the lip becomes flattened. The flowers of *E. granitica* emit a strong, sweet fragrance, especially during the day. After 6:00 pm, the scent decreases in intensity. The flowers last between 20 and 30 days. Details on the fruits of *Encyclia granitica* were not available either in the original description (Lindley, 1841) or in the most recent revision of *Encyclia* in Brazil (Bastos *et al.*, 2018) and have been included here.

Encyclia linearifolioides (Kraenzl.) Hoehne, Arq. Bot. Estado São Paulo 1: 19. 1938. *Epidendrum linearifolioides* Kraenzl., Kongl. Svenska Vetensk. Acad. Handl., n.f., 46(10): 55. 1911. Fig. 3C, 5.

TYPE: PARAGUAY. *s. loc.*, 1894, fl., *Lindmann, A. 3895* (holotype: HBG!).

Epiphytic or occasionally rupicolous, 10.7–31.0 cm long. *Rhizome* inconspicuous. *Pseudobulbs* conical 1.4–2.9 × 1.0–1.4 cm, usually purplish when exposed to the sun. *Leaves* (1–2), 14–30 × 0.4–0.5 cm, narrow-lanceolate, apex acute, flat, coriaceous, green, with a longitudinal central vein. *Inflorescence* terminal, simple or panicle, 3–30 flowers, erect to slightly arching, glabrescent, 6–20 cm long; *peduncle* 2.5–7.5 cm long and *rachis* 3.5–12.5 cm long; *floral pedicel* sparsely verrucose. *Flowers* with sepals and petals greenish, occasionally yellow, lip yellowish, with an intense, sweet fragrance. *Dorsal sepal* lanceolate, wider in the upper portion and narrower at the base, greenish, reflexed, 1.7–1.8 × 0.4–0.5 cm. *Lateral sepals* lanceolate, greenish, reflexed, membranaceous, apex acute, margin entire, 1.6–1.9 × 0.3–0.5 cm. *Petals* lanceolate, apex acute, margin entire, greenish, reflexed, membranaceous, 1.4–1.7 × 0.4 cm. *Lip* trilobate, *ca.* 1.4 cm long; lateral lobes free from the median lobe, ovate to dimidiate, 0.6–0.8 × 0.3–0.5 cm, yellowish, not overlapping the median lobe and positioned at an angle of about 45 degrees in relation to it, margin entire, apex obtuse; median lobe rounded to elliptic, 0.4–0.7 × 0.5–0.8 cm, yellowish, margin undulate, apex emarginate to obtuse; *callus* cymbiform, apex flabellate, *ca.* 0.8 × 0.4 cm, trifid, apices rounded. *Column* clavate, 0.8–1.0 × 0.2–0.3 cm, apex tridentate, teeth triangular, pair of lateral teeth slightly evident, directed downward, broadly triangular, apex slightly serrulate and rounded; *stigma* rounded. *Anther cap* elmiform, keeled at the apex, dark purple, 0.1 × 0.2–0.3 cm. *Pollinia* 4**,** waxy, yellow, ovate, laterally flattened. *Fruit* 2.5–3.5 × 0.7–1 cm, long-fusiform, light green, with six sulcate longitudinal keels (three of them associated with dehiscence), surface sparsely punctate with predominantly hemispherical vesicles (*ca.* 0.5 mm long), translucent.

Material Examined: BRAZIL. **Distrito Federal**: Brasília, Chapada da Contagem, 1,025–1,150 m, 19 October 2005, *Salles et al. 3815A* (HEPH); APA da Cafuringa, 11 October 2006, *A.C. Amaral & G. Pereira-Silva 36* (CEN); Germplasm bank of Brasília Botanical Garden, cultivated in a clay pot, 17 October 2002, *R. Rodrigues Silva 628* (HEPH); cultivated in the JBB-ORQ nursery, number 1756, 31 October 2005, *A.J.H. Salles 3829* (HEPH); Fercal, 889 m, 12 October 1992, *Bianchetti & Batista s.n. 26615* (CEN). **Goiás**: Alto Horizonte, border between the farms of Mr. Joaquim Bueno and Mr. Jair Eustáquio, 27 November 2009, *J.E.Q. Faria 437* (HUEG, UB). Alto Paraíso de Goiás, Chapada dos Veadeiros, 27 September 1967, *DeHaas et al. 402* (HB). Campo Alegre de Goiás, GO-118 Highway, near the Paranã River, 18 October 1990, *Hatschbach et al. 54733* (MBM). Campinaçu, road to Fazenda Praia Grande, *B.M.T. Walter et al. 2812* (CEN); Serra da Mesa, 28 January 1997, *B.M.T. Walter et al. 3683* (CEN, SP). Cavalcante, Santo Antônio River, 22 May 2002, *G. Pereira-Silva & E. S. G. Guarino 6470* (CEN); Bridge over the Carmo River, 8 November 2000, *B.M.T. Walter et al. 4589* (CEN, HUEFS). Colinas do Sul, riverbank, 11 December 1991, *L.B. Bianchetti & G. Pereira--Silva 1188* (CEN); Serra Negra Lake, 27 February 1997, *S.P. Cordovil-Silva et al. 557* (CEN). Goiânia, 23 November 1964, *Heringer 9955* (UB). Serranópolis, RPPN Pousada das Araras, 26 September 2005, *L.F. Souza 2606* (HJ). Iporá, Fazenda Lage, 11 October 2008, *Meneguzzo et al. 21* (UB); Fazenda Lage, 11 October 2008, *Meneguzzo et al. 23* (UB). Minaçu, Serra da Mesa power plant, 291 m, 1 December 1998, *M.F. Simon 86* (UB). Niquelândia, Dolina, between Uruaçu and Niquelândia, 7 November 1992, *B.M.T. Walter 2033* (CEN); Macêdo, CNT, *ca.* 2.5 km from the nickel mine (gully), 20 October 1996, *M.L. Fonseca 1249* (IBGE); rocky hill, Fazenda Água, 14 August 1996, *M.L. Fonseca et al. 1087* (IBGE). Nova Roma, Ourominas–Nova Roma road, 3 December 2003, *Silva et al. 1211* (HUEFS, RB, SPF and UB). Planaltina, 4 November 2008, *T.E.C. Meneguzzo & L.C. Santos 24* (UB); 4 November 2008, *T.E.C. Meneguzzo & L.C. Santos 26* (UB); Rio Piranha, cultivated at IAN, 25 November 1961, *J.M. Pires 7838* (IAN). Novo Gama, s. loc., 19 October 1963, *J.M. Pires 51157* (UB). Serra Dourada, 9 June 1960, *E.Y. Dawson 15176* (MO). **Maranhão**: Carolina, right bank of the Tocantins River, 24 April 2008, *Pereira-Silva et al. 13402* (CEN); Parque Nacional da Chapada das Mesas. Site 1 – Buenos Aires. Collection point 6, bank of the Farinha River, 20 October 2015, *Sevilha et al. 5420* (CEN). Carolina. Parque Nacional da Chapada das Mesas, waterfall on the Farinha River, 22 November 2021, *Silva & Scatigna 407* (SLUI). Estreito. Road to Cachoeira da Prata, 13 October 2025, *Ferreira 1671* (SLUI). Imperatriz, Arara Azul municipal nursery, 25 July 2023, *Ferreira et al. 1236* (SLUI). Mirador, Parque Estadual do Mirador, 23 August 1998, *G.M. Conceição & J.A. Castro 326* (TEPB). Montes Altos, 11 November 1966, *s. leg., s.n.* (ESA 22505).

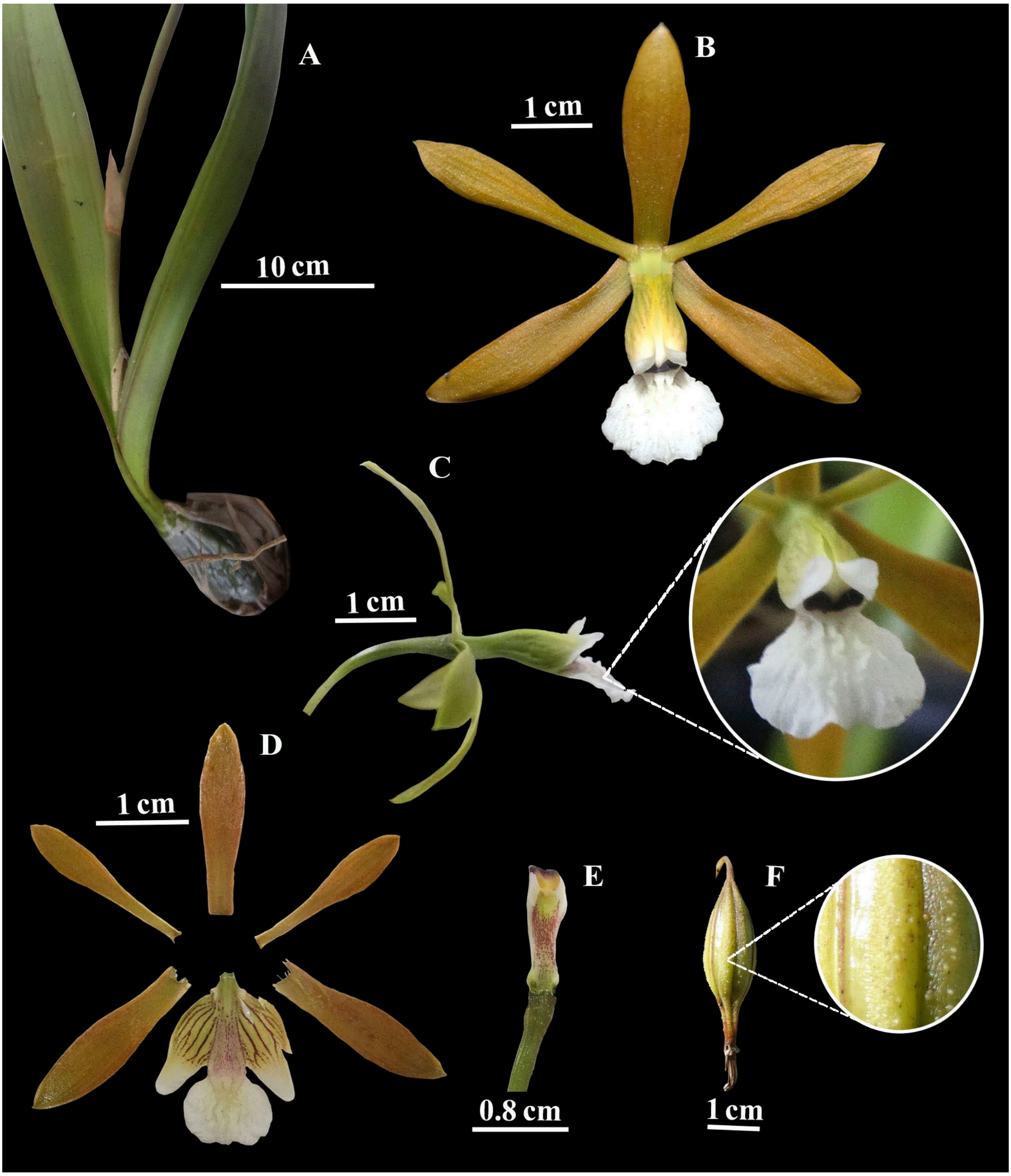

FIGURE 5. *Encyclia linearifolioides*. **A**. Habit, pseudobulb and leaves. **B**. Flower, frontal view. **C**. Flower, oblique view, highlighting the lip. **D**. Perianth. **E**. Column, frontal view. **F**. Fruit, highlighting the verrucose surface. Photographs by Alessandro Ferreira based on *A.W.C. Ferreira 1612* (SLUI 11626).

Ribamar Fiquene, Road to Fazenda 3R, 25 July 2023, *Ferreira et al. 1237* (SLUI). São Pedro dos Crentes, 6 September 2025, *Ferreira 1610*, ibid. *Ferreira 1611*(SLUI), ibid. *Ferreira 1612* (SLUI); ibid, 13 October 2025, *Ferreira 1670* (SLUI). **Mato Grosso**: Aripuanã, Dardanelos, 29 September 1975, *Lisboa et al. 498* (INPA). Barão de Melgaço, Aldeia Perigara, São Lourenço River, 28 November 1973, *s.c., s.n.* (ESA 31053). Cáceres, Fazenda Jacobina, Jaurú River, September–December 1908, *F.C. Hoehne 979* (R). Chapada dos Guimarães, 5 October 1982, *Kautsky s.n. 75231* (HB). Ipiranga do Norte, Fazenda São Luiz, 3 November 1976, *B.C. dos Passos 1190* (RB). Ibid., 29 September 1977, *J.M. Lenies 4* (RB). Ibid., 6 December 1922, s.c. (RB). Nobres, 21 November 1995, *G. Hatschbach et al. 63716* (INPA, MBM and SPF). Paranatinga, 15 July 1990, *Macedo & Assunção 16* (INPA). Paranaíta, Campo Teles Pires, 10 August 1950, *H. Sick 550* (RB). Rio dos Mortos, 1947, *H. Sick 54* (RB). Santo Antônio do Leverger, Mata do Rio Cuiabá, 26 September 1996, *R. Godinho 222* (CEN); Vila Córrego Grande, 24 September 1976, *s.c., s.n.* (ESA 31031). **Mato Grosso do Sul**: Bonito, road Bonito–Campo dos Índios, 8 November 2002, *G. Hatschbach et al. 73908* (MBM, SPF); Bonito–surroundings of Gruta do Lago Azul, 28 November 1999, *G.A. Damasceno Jr. & M.M. Garcia 1781* (COR); road along the edge of Serra da Bodoquena National Park, 4 December 2010, *G. Martinelli et al. 16856* (RB). Chapadão do Sul, Sucuriú River, 24 October 1967, *s.c., s.n.* (ESA 22384). Corumbá, Morro Santa Cruz, 30 July 1999, *D.P. Rodriguez R-09* (COR, SP); Morro do Urucum, 10 November 1995, I.*M. Bortolotto & D.P. Rodriguez 121* (COR). Sidrolândia, Água Rica, 27 January 1979, *M.C. Vianna & H.F. Martins 1401* (R). **Minas Gerais**: Brasilândia de Minas, João Pinheiro road, 11 November 1966, *s.c., s.n.* (ESA 24204). Campina Verde, Fazenda São José do Lajeado, 27 October 2003, *J.F. Santos s.n*. (CEN). Ibid, 25 September 2001, *J.F. Santos 20* (US). Ibid, 20 July 2002, *A. Macedo & R.D. Macedo 0064* (US). Paracatu, riparian forest of the river between Ribeiros and Paracatu, 21 October 1989, *A.J.H. Salles et al. 1380* (HEPH). Paraopeba, 12 November 1960, *Heringer 7741* (UB). Serra da Mesa – Hydroelectric dam region. Cultivated at the GFJP herbarium, November 1997, *L.S. Leoni 3794* (RB). Unaí, Unai–Samboril road, 7 October 1966, s.c., *s.n.* (ESA 23072). **Pará**: São Geraldo do Araguaia, left bank of the Araguaia River, forest of the Foundation, 22 April 2004, *G. Pereira-Silva et al. 8968* (CEN). **Paraná**: Alto Paraíso, Vila Alta, Guarandi Forests, 7 November 2002, *Kozera 1688* (MBM). Porto Rico, Mutum Island, 14 September 1969, *Hatschbach 22176* (MBM). **Tocantins**: Aguiarnópolis, forest of Mr. Francisco do Leite, 22 October 2005, *G. Pereira-Silva et al. 10277* (CEN). Babaçulândia, road to the river mouth, 25 November 2009, *G. Pereira-Silva et al. 14794* (CEN, HUEFS). Conceição do Tocantins, Teleste stream, 12 January 2003, *Curcino 33* (HTO). Dianópolis**,** near the cave, 29 September 2003, *T.B. Cavalcanti et al. 3349* (CEN, HUEFS). Filadélfia, access road to Lagoa do Jacaré, 26 April 2008, *G. Pereira--Silva et al. 13368* (CEN). Itacajá, Vila Pedra Branca, 15 October 2000, *Santos et al. 800* (CEN). Lagoa da Confusão, Ilha do Bananal, 26 March 1999, *R.C. Mendonça et al. 4033* (IBGE). Lajeado, 29 October 1998, *G.F. Árbocz 6258* (HTO, IBGE). Miranorte, Miranorte–Abreulândia road, 5 November 2005, *Lombardi et al. 6202* (HRCB). Nazaré, 15 July 1991, *Silva & Silva 134* (MG). Nazaré, 5 March 1991, *I.V. Lima 20* (HEPH). Palmas, Serra Lajeado, Fazenda Alta Floresta, 25 October 1993, *Santos 551* (HTO); cultivated at ORQ 746–Viveiro–JBB, 10 October 2002, *C.E. Rodrigues Júnior 1506* (HEPH). Palmeirante, old Palmeirante–Tocantins road, 18 November 2010, *J.B. Pereira & J.P. Amaral 301* (CEN, HUEFS). Palmeirópolis, lake of the São Salvador hydroelectric dam, 25 March 2009, *G. Pereira-Silva et al. 14163* (CEN, HUEFS). Paranã, near the dam, 6 July 2006, *G. Pereira-Silva et al. 10427* (CEN, HUEFS).

Distribution and ecology: *Encyclia linearifolioides* is endemic to South America, with confirmed occurrences in Bolivia, Brazil and Paraguay (Meneguzzo, 2012; POWO, 2026). In Brazil, it is found in the Amazon, Cerrado and Pantanal phytogeographic domains, with confirmed records in the northern (Rondônia, Tocantins), northeastern (Maranhão), central–western (Federal District, Goiás, Mato Grosso do Sul, Mato Grosso), southeastern (Minas Gerais) and southern (Paraná) regions, being typical of cerrado vegetation (*sensu lato*), gallery forest, floodplain forest, seasonal semideciduous forest, dry forest and restinga (Bastos *et al.*, 2026; Meneguzzo, 2012; Pessoa *et al.*, 2025).

In Maranhão, it was observed as an epiphyte in gallery forests and adjacent cerrado vegetation. In the study area, individuals of *Encyclia linearifolioides* were associated with the canopy of phorophytes of mirindiba, *Terminalia glabrescens* Mart. (Combretaceae); occasionally on macaúba, *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. (Arecaceae); yellow ipê, *Tabebuia aurea* (Bignoniaceae); jatobá, *Hymenaea courbaril* L. (Fabaceae) and sansão-do-campo, *Mimosa caesalpiniifolia* Benth. (Fabaceae).

Specimens of *Encyclia linearifolioides* exposed to higher solar radiation have erect, yellowish-green and smaller leaves (8–13 × 0.7–1.0 cm), whereas individuals from shaded environments have light green to yellowish, arched and longer leaves (10–30 × 1.0–1.4 cm). Occasionally, rupicolous individuals of *E. linearifolioides* were found near waterfalls, which also have erect, shorter and yellowish-green leaves.

Phenology: *Encyclia linearifolioides* flowers between September and November, during the dry season of the Cerrado in Maranhão (which occurs from May to October) and the beginning of the rainy season (which occurs between November and April). The flowers of *E. linearifolioides* exude a citrus fragrance, perceived during the day when approaching the inflorescences. From 6:00 pm onward, the fragrance decreases in intensity. The flowers last between 20 and 30 days.

Notes: *Encyclia linearifolioides* is often confused with *E. conchaechila* (Barb.Rodr.) Porto & Brade, as they share similarities such as column short. They differ in the overlap of the lateral lobes over the median lobe, which is strictly rounded in *E. conchaechila*; whereas, in *E. linearifolioides,* the lateral lobes are free from the median lobe, which is rounded to elliptic. In addition, *E. conchaechila* has yellowish sepals, petals and lip, whereas *E. linearifolioides* has greenish sepals and petals and a yellowish lip.

Conclusions. Only *Encyclia granitica* occurred in areas of the Amazon domain (forests near watercourses or in campinaranas), within a geographic belt in the western region of Maranhão, delimited by the valleys of the Gurupi River (and its main tributaries) and the Maracaçumé River (and its main tributaries). This geographic distribution in areas of the Amazon domain is consistent with Bastos *et al.*, (2026). The other two species (*Encyclia gonzalezii* and *Encyclia linearifolioides*) occurred in the Cerrado and gallery forests within the geographic belt between Tocantins and Maranhão, along the Tocantins River valley and its tributary, the Farinha River, which crosses Chapada das Mesas National Park.

Taxonomic studies of *Encyclia* do not generally include details of the epicarp of the fruit, and are limited to descriptions of its shape and coloration. In this study, we found that characters of the fruit's surface can serve as complementary features for species identification and for future descriptions of Brazilian species.

When compared with other studies on *Encyclia* in Amazon and Cerrado domains of Brazil, the three species recorded in Maranhão are fewer than the 13 species reported by Bastos *et al*., (2016) for Bahia, in the northeastern region of Brazil, with no species in common with those of the present study. Similarly, Meneguzzo *et al.* (2012) conducted a study in the central-western region (Distrito Federal and Goiás) and in the northern region (Tocantins), where they identified six species, two of which are shared with the present study (*E. gonzalezii* and *E. linearifolioides*). The state of Pará, in the northern region of Brazil and neighboring Maranhão, harbors nine species of *Encyclia* and, so far, *Encyclia granitica* is the only species shared with the three *Encyclia* species recorded for Maranhão (Bastos *et al.*, 2026). Further studies in the remaining forest fragments of the Amazon in Maranhão may reveal new records of *Encyclia*. Likewise, the Cerrado of Maranhão is connected to Cerrado areas in other Brazilian states, which harbor *Encyclia* species that are distinct from those recorded in Maranhão.

The degradation of the Cerrado and the Amazon of Maranhão, mainly due to deforestation and fires, hampers the sampling of new areas in search of additional specimens of *Encyclia* (IFNMA, 2024; PPCDQ-MA, 2024; Sales & Oliveira Neto, 2020). These data highlight the sampling deficiency of *Encyclia* species in Maranhão and the need for the continuation of these studies. Considering that Maranhão is located in an ecotonal region between the Amazon, Cerrado and Caatinga domains, more in-depth studies within forest remnants, especially within conservation units, may contribute to the recording of additional *Encyclia* species not yet collected in Maranhão.

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Conflict of interest. The author declares no commercial, financial, academic, or personal conflicts of interest related to this study.

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ORCHIDS NATURALIZED IN FLORIDA

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ABSTRACT. Florida's naturalized orchids are mostly terrestrials (10/15, 5/10 epiphytes), horticultural escapes (14/15), native to Asia (10/15), tropical America (4/10), and Africa (1/15). Only 3 species are widespread in Florida, *Eulophia graminea*, *Eulophia maculata*, and *Zeuxine strateumatica*, and can be considered invasive based on their spread beyond the areas of their initial establishments. Most of the other orchid species occur in one or two counties and have spread little so are considered naturalized but not invasive. The longest naturalized orchids (5/15) escaped more than 50 years ago, another group (5/10) more than 20 years ago, while the most recently naturalized species (5/10) less than 20 years ago. The 15 naturalized orchids comprise 12% (15/117 species) of Florida's orchid flora, which is higher than most other places except for Hawaii's (18/21) which has only 3 native orchids. Most orchids naturalized in Florida (10/15) have also naturalized elsewhere in the world. Failure to reproduce is the reason why most orchids don't naturalize. To attempt to understand how Florida's 15 naturalized orchids have overcome this barrier, the literature was examined to learn what their breeding systems and pollinators are in their native areas. This enabled predictions to be made about how these orchids reproduce in Florida. Four of the orchids need no pollinators because they are autogamous or apomictic. The native region pollinators of two of the orchids occur in Florida, five of the orchids are probably pollinated by congeneric species of their native area pollinators (*Apis*, *Centris* and *Xylocopa*), Two of the orchids are pollinated by close analogues of their native area pollinators (butterflies and hummingbirds). Overcoming other barriers to their naturalization, such as the lack of suitable mycorrhizal fungi or the inability to deal with abiotic limitations, has occurred but are poorly known and understood.

KEYWORDS / PALABRAS CLAVE: barreras de naturalización, comercio ornamental, *Eulophia*, floras de orquídeas, horticultura, horticulture, naturalization barriers, orchid floras, ornamental trade, pollinators, polinizadores, *Zeuxine*

Florida is famous for being invaded by diverse animals and plants. Burmese pythons (*Python bivittatus* Kuhl, 1820) have adversely impacted mammals in Everglades National Park (Dorcas *et al.,* 2012), while lionfish (*Pterois volitans* L., 1758) and the Asian swamp eel (*Monopterus albus* Zuiew, 1793) threaten native marine and freshwater fish (Sabapathy, 2019; US Fish and Wildlife Service, 2014). Invasive plants such as punk tree (*Melaleuca quinquenervia* (Cav.) S.T.Blake) and Old World climbing fern (*Lygodium microphyllum* (Cav.) R.Br.) have transformed whole wetland environments (Laroche and Ferriter, 1992; Pemberton and Ferriter, 1998). Then there are numerous naturalized species, seemingly more benign species, that are decreasing the proportion of Florida's biota that is native.

Among these are 15 naturalized orchids (Wunderlin *et al*., 2025; Pemberton & Downing, 2025). In this paper, these orchids and their characteristics will be defined. Orchids naturalize much less often than other kinds of plants due to their need for specialist pollinators and mutualistic fungi to enable seed germination (Daehler, 1998). How Florida's naturalized orchids have been able to overcome these barriers to naturalization is explored.

General characteristics and occurrence of the naturalized orchids. These 15 orchids are taxonomically diverse and limited, belonging to different genera, except for two genera *Eulophia* R.Br and *Cymbidium* Sw. that have three and two naturalized species respectively (Table 1). Ten of the orchids are native to Asia, five native to tropical America and one [*E. maculata* (Lindl.) Rchb.f.] is native to Africa. Ten of the orchids are terrestrials while five are epiphytes. Almost all (14/15) of these orchids are likely horticultural escapes except for *Zeuxine strateumatica* (L.) Schltr. which is thought to have been introduced with grass seed (Ames, 1938).

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The commonness of these orchids in Florida is indicated by the number of counties in which the orchid has been collected (Wunderlin *et al*., 2025; Table 1). Only three of the naturalized orchids are widespread in Florida (Fig. 1). *E. graminea* Lindl., also collected from 25 counties, was first found in South Miami in 2007 (Pemberton *et al*., 2008) and has spread widely in the state (Pemberton, 2013; Fig. 1A–B). Beyond Florida, *E. graminea* has spread through the West Indies reaching Puerto Rico (Ackerman & Gónzález-Orellana, 2021) and in Texas where it appears to be very common in the Houston area due to more than 279 iNaturalist posts of it there (iNaturalist, 2026). *E. maculata* collected from 25 counties, is an African species that has spread slowly northward after it appeared in Brazil, reaching Florida by 1974 (Wetterer & Wetterer, 2022) (Fig. 1C–D). *Zeuxine strateumatica* first found in Indian River County on Florida's east coast in 1936 (Ames, 1938), has been collected from 48 counties (Fig. 1E–F).

Most of the others, such as *Phaius tankervilleae* (Banks) Blume (Robinson *et al*., 2011), are limited to one or two counties (Wunderlin *et al*., 2025). The greater naturalization of terrestrial orchids may be due to the large array of mycorrhizae in the soil and mulch environments in which they grow, or a widespread fungus that the orchid is able to exploit. Naturalized terrestrial orchids are probably also better able to survive the variable weather of subtropical Florida because their subterranean parts of these orchids may survive periodic freezes.

Of the five epiphytic orchids that have naturalized in Florida, the persistence of two of these species is questionable. *Laelia rubescens* Lindl. was found growing on Southern live oak trees (*Quercus virginiana* Mill.) in Miami-Dade County in 1990 by Roger Hammer (pers. com.). This author's search for the orchid at that site failed to find it; however, there is a 2019 iNaturalist post (iNaturalist, 2019) of the orchid in the Big Cypress National Wildlife Preserve in Collier County *ca*. 80 km west of where it was first found. The other, *Encyclia rufa* (Lindl.) Britton & Millsp., was collected from Brevard County on the east coast in 1926, but this orchid has not been seen in the last 10 years. One naturalized terrestrial orchid, *Bletia florida* (Salisb.) R.Br., appears to have disappeared from where it was first reported in Dade County, but has been found in Everglades National Park in 2022 (iNaturalist, 2022).

The year, if known, when these orchids were first detected or reported to be naturalized in Florida is given in Table 1. These dates are from the literature, and herbarium specimens cited by Wunderlin *et al*., (2025). The first orchid to naturalize in Florida is apparently *E. rufa* in 1926 followed by *Z. strateumatica* in 1936 (Ames, 1938). *Cymbidium aloifolium* (L.) Sw. and *C. dayanum* Rchb.f. are the most recent orchids reported to be naturalized in Florida (Pemberton & Downing, 2025; Pemberton & Downing, unpublished data). Large old plants of both species were found among naturalized populations of these plants, suggesting that they were naturalized much earlier than when they were reported.

When Roger Hammer made the first collection of *Cyrtopodium flavum* (Nees) Link & Otto ex Rchb. at the Boystown Preserve in Miami in 1997, hundreds of plants were growing at the site including large ones (R. Hammer, pers. com.), indicating that the population began much earlier than in 1997. The longer horticulture plants are marketed, the greater the chance of their naturalization and invasion (Pemberton & Liu, 2009). The longer naturalized plants have been established, the greater chance for them to become invasive (Gallagher *et al*., 2015). It is not known how long these orchids were naturalized before they were detected and reported, but five were first collected more than 50 years ago, another five more than 20 years ago, while the other five less than 20 years ago.

I have used the word naturalized for these orchids through this paper because of the absence of evidence of impact that these orchids have on Florida's environment. A widely accepted definition for an invasive species, which does not include impact, is that an invasive species is one which has spread beyond the population of their initial establishment (Blackburn *et al*., 2011). Only three of the naturalized orchid species readily meet this definition, *E. graminea, E. maculata*, and *Z. strateumatica*, which are widely distributed in Florida (Table 1). Seven of the naturalized species occur in single counties so have spread very little. Five of the orchid species occur in two or three counties, including counties that are geographically separated from one another, but the occurrences of these orchids in one or three separated counties could easily be due to separate naturalizations rather than spread. The populations of the five orchids that occur in two or three counties tend to be small and isolated,

Table 1. Naturalized orchids in Florida, USA. The species are from Wunderlin *et al.*, 2026, plus 1 (Pemberton & Downing, 2025), minus 5 species: *Epidendrum blancheanum* Urb. (= *E. acunae* Dressler), *Bulbopyllum pinelianum* (A.Rich.) Ormerod [= *B. pachyrachis* (A.Rich.) Griseb.], *Leochilus labiatus* Kuntze, and *Trichocentrum carthagenense* (Jacq.) M.W.Chase & N.H.Williams (Rogert Hammer, pers. com) which were collected only once; and *Ludisia discolor* which was found in the Fakahatchee Strand in 2010 but was removed by park officials (McCartney, 2010). Herbarium specimens were consulted in SERNEC (2026).

Scientific name **Common name**	**Native region**	**Epiphyte or terrestrial**	**No. Counties found in**	**Year first found**	**References & Herbarium Specimens**
Bletia florida Slender pinepink	Cuba, Jamaica	Terrestrial	1	2002	Brown, 2002
Bletilla striata Chinese ground orchid	China	Terrestrial	1	1979	FLAS136675
Cymbidium aloifolium Aloe leaved cymbidium	Asia	Epiphyte, Lithophyte	1	2025	Pemberton & Downing, 2025
Cymbidium dayanum Day's cymbidium	Asia	Epiphyte	3	2023	FLAS290648; Pemberton & Downing, unpublished data
Cyrtopodium flavum Yellow cowhorn orchid	Brazil	Terrestrial, Lithophyte	3	1997	USF220833
Encyclia rufa Rufous butterfly orchid	Bahamas	Epiphyte	1	1926	NY468306
Epidendrum radicans Star orchid	Tropical America	Terrestrial	1	1956	GH02029670
Eulophia andamanensis Andaman crown orchid	Southeast Asia	Terrestrial	1	2018	USF297837
Eulophia graminea Chinese crown orchid	Asia	Terrestrial	25	2007	Pemberton *et al.,* 2008; Pemberton, 2013
Eulophia maculata Monk orchid	Africa	Terrestrial	25+	1974	Wetterer & Wetterer, 2022
Laelia rubescens Pale laelia	Central America	Epiphyte	1	*ca.*1990	R. Hammer pers. com.
Phaius tankervilleae Nun's hood orchid	Asia	Terrestrial	2	1965	Robinson *et al.*, 2011
Spathoglottis plicata Philippine ground orchid	India to Australia	Terrestrial	2	2001	USF230623
Vanilla planifolia Commercial vanilla	Tropical America	Epiphyte	3	1933	Small, 1933
Zeuxine strateumatica Lawn orchid	China	Terrestrial	48+	1936	Ames, 1938

while *E. graminea. E. maculata* and *Z. strateumatica* are not only geographically widespread but are often common where they occur. The relatively small body sizes and low densities of naturalized orchids may limit their abilities to compete with and displace other vegetation so their direct impacts are limited. However, indirect ecological impacts can occur as in the interesting case in Puerto Rico reported by Recart *et al.* (2013). The invasive orchid *Spathoglottis plicata* Blume is a host of a flower feeding native weevil which also used the native orchid *Bletia patula* Hook. as a host. When *S. plicata* grows near *B. patula*, the native *B. patula* has more weevils and lower fruit set. *Spathoglottis plicata* has no impact on its own but when it grows near *B. patula* and hosts the weevil, it indirectly negatively impacts *B. patula*.

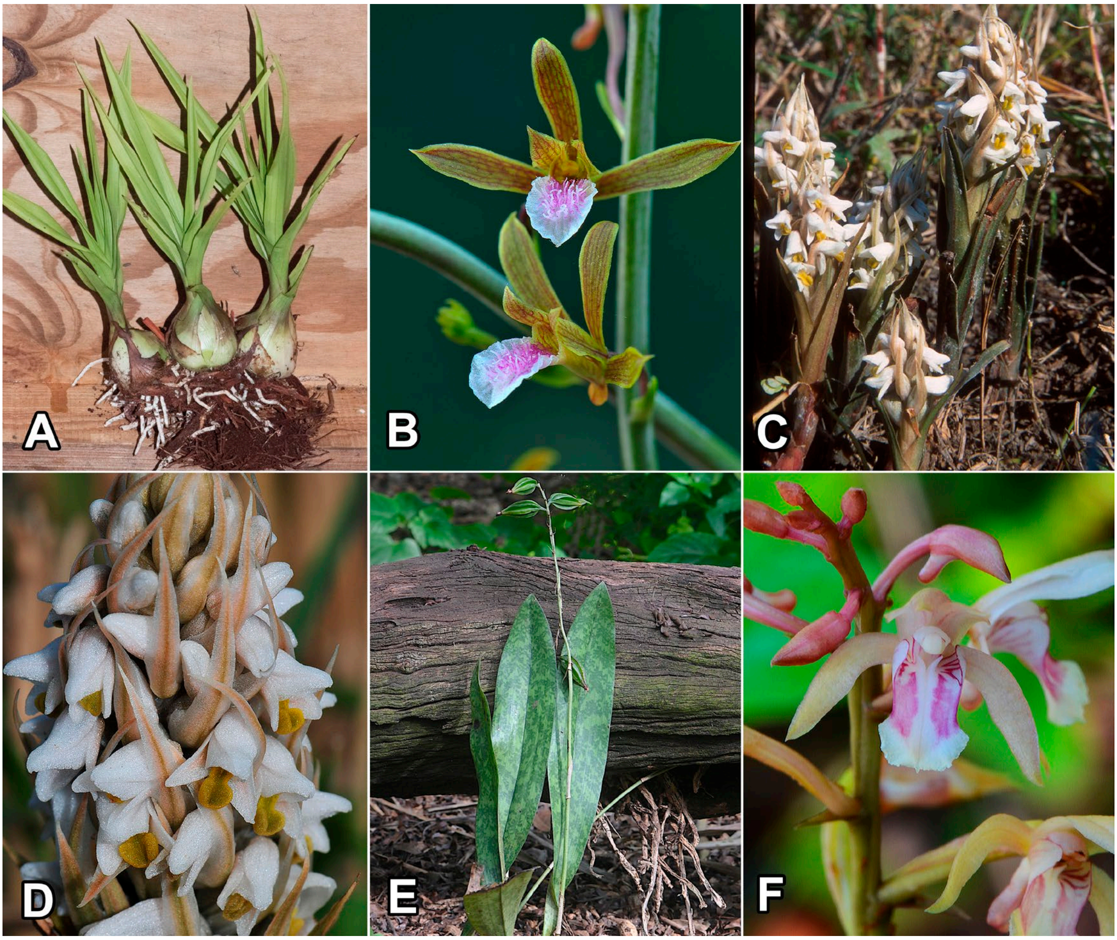

FIGURE 1. The three most widespread naturalized orchids in Florida. The Chinese crown orchid, *Eulophia graminea* (**A**. habit. **B**. single flowers), first found in 2007 (Pemberton *et al.,* 2008). The lawn orchid *Zeuxine strateumatica* (**C**. habit. **D**. inflorescence), first found in 1936 (Ames, 1938). Photographs by Roger Hammer. The monk orchid, *Eulophia maculata* (**E**. habit. **F**. single flower), first found in 1974 (Wetterer & Wetterer, 2022).

Overcoming barriers to naturalization: need for pollinators. The inability to reproduce is an important barrier to orchid naturalization, which is a major reason why orchids naturalize less frequently than other plants (Daehler, 1998). Most orchids have single pollinators (Ackerman *et al*., 2023), and these pollinators rarely occur in the regions beyond the native areas where orchids are grown as ornamentals. To attempt to understand how these 15 naturalized orchids have overcome this critical barrier, the scientific literature was examined to learn what their breeding systems and pollinators are in their native regions (Table 2). This enabled predictions to be made about their probable pollination in Florida.

The pollination of only a few of these orchids has been studied in Florida. *Cyrtopodium flavum* is pollinated by a naturalized oil-collecting bee (*Centris nitida* Smith, 1874) in Florida (Liu & Pemberton, 2010), similar to its *Centris* spp. pollinators in its native Brazil (Pansarin *et al*., 2008). *Vanilla planifolia* Andrews was found to be infrequently visited during a study in Florida but was pollinated by the honeybee (*Apis mellifera* L., 1758) and a female of the naturalized orchid bee (*Euglossa dilemma* Bembé & Eltz, 2011) (Pemberton *et al*., 2023). The pollinators of this orchid are unknown in its native tropical America (Lubinsky *et al*., 2006; Quezada-Euán *et al*., 2024).

The predicted pollinators of the other 13 orchids fall into a number of categories. There are four orchids that do not need pollinators to set fruit. *Eulophia graminea, E. maculata,* and *S. plicata* are autogamous, while *Z. strateumatica* is apomictic (Ackerman, 2007). *Eulophia andamanensis* Rchb.f. has not been studied but because *Eulophia* species usually lack nectar (C. Peter, pers com.) it is probably a deceit orchid, or autogamous like the other two naturalized *Eulophia* spp. in Florida. There are the pollinators of two orchids in their native area which also occur in Florida. The common honeybee (*A. mellifera*) which pollinates *Bletilla striata* (Thunb.) Rchb.f. (Chung & Chung, 2005) in South Korea was introduced to both South Korea and Florida. The polka-dot wasp moth (*Syntomeida epilais* Walker, 1854), the pollinator of *Encyclia rufa* in its native Bahamas (Esperón & Sauleda, 2012), also occurs in Florida (Bug Guide, 2026).

Then there are congeneric species of orchid pollinators in the native area which occur in Florida. *Cymbidium aloifolium* and *C. dayanum* are pollinated by an Asian honeybee (*Apis cerana* Fabricius, 1793) in their native Asia (Adit *et al*. 2022, Matsuda & Sugiura 2019), so they are predicted to be pollinated by the similar-sized common honeybee (*A. mellifera*) in Florida. As mentioned above, *Cyrtopodium flavum* is pollinated by *Centris* species in Brazil, is pollinated by *C. nitida* in Florida (Liu & Pemberton, 2010). *Phaius tankervilleae* is pollinated by *Xylocopa violacea* L., 1758 in its native area (Buragohain *et al*., 2016), is probably pollinated by *Xylocopa virginica* L., 1771 in Florida.

In addition, there are analogs, pollinators that are taxonomically and morphologically similar to the orchid's pollinators in their native regions. *Epidendrum radicans* Pav. ex Lindl., pollinated by butterflies in its native tropical America (Bierzychudek, 1981), is probably pollinated by butterflies in Florida as well. *Laelia rubescens* is pollinated by hummingbirds in Costa Rica (Trapnell & Hamrick, 2004) and a social wasp (*Polybia* sp.) in Mexico (Cen, 2016). This suggests pollination by hummingbirds or social wasps in Florida. Finally, the pollinators of the two remaining orchids, *Bletia florida* and *Eulophia andamanensis*, are unknown in their native regions so their pollinators in Florida are less predictable. Peter (2009) studied the pollination of 11 *Eulophia* species in South Africa and found that five are pollinated by bees, two by beetles, while four are autogamous.

Although orchids have a wide variety of breeding systems (Sun, 1997), outcross deception is more common in these naturalized orchids than in orchids overall (Neiland & Wilcock, 1998). Deception occurs in 100% (11/11) of the outcrossing naturalized orchids in Florida (Table 2), compared to about *ca*. 30% of orchids overall (Neiland and Wilcock, 1998), and 44.6% of the orchids in the Ackerman *et al*. pollination database (Ackerman *et al*., 2025). Nectarless orchids have fewer visitors but higher outcross rates (Neiland & Wilcock, 1998). This phenomenon occurs because visitors to nectarless orchids spend shorter times on these plants before abandoning them and moving to the flowers of other plants while carrying the pollen from the flowers of plants previously visited. Visitors to rewarding (nectar bearing) orchids spend longer times on the same plant, moving from flower-to-flower, causing more pollination with self pollen (getionagamy). Also, having more outcrossing in these 11 naturalized orchids may have made them better adapted to Florida's environment.

Overcoming the need for mycorrhizal associations. The absence of suitable mycorrhizal fungi is thought to be another important barrier to orchid naturalization (Daehler, 1998). The mycorrhizal associates of orchids are mostly unknown, both in their native and introduced regions. The fungi associated with a few naturalized orchids (*Cyrtopodium flavum* and *Eulophia graminea*) in Florida appear to be common saprophytes (Downing *et al*., 2020). This suggests that either there is less specificity in fungal associates of naturalized orchids than with their pollinators, or they are more widely available than their pollinators. The lack of needed fungi may be less of a barrier to orchid naturalization than has been presumed. However, Bayman *et al*. (2016) found many orchid mycorrhizae in the roots of *Eulophia* (as *Oeceoclades*) *maculata*, but only one widespread fungus was successful in germinating the seed.

Influences of polyploidy and self-compatibility. There are other biological characteristics that are associated with plant naturalization. Self-compatibility is one of these characteristics (Kinlock *et al*., 2025), and orchids usually have a high degree of self-compatibility. Ackerman *et al*. (2023) reported

TABLE 2. Naturalized orchids in Florida and their reproduction.

Scientific name **Common name**	**Pollinator in native region**	**Reference**	**Breeding System**	**Reference**	**Predicted pollinator in Florida**
Bletia florida Slender pinepink	unknown	-	deceit?	Sosa, 1992	*Apis mellifera*
Bletilla striata Chinese ground orchid	*Tetralonia nipponensis*	Sugiura, 1995	deceit	Sigiura, 1995	*Apis mellifera*
	Apis mellifera	Chung & Chung, 2005	deceit	Ackerman *et al.,* 2025	-
Cymbidium aloifolium Aloe leaved cymbidium	*Apis cerana*	Adit *et al.*, 2022	deceit	Adit *et al.,* 2022	*Apis mellifera*
Cymbidium dayanum Day's cymbidium	*Apis cerana*	Matsuda & Sugiura, 2019	deceit	Matsuda & Sigiura, 2019	*Apis mellifera*
Cyrtopodium flavum Yellow cowhorn orchid	*Centris* spp., rain assisted selfing	Pansarin *et al.,* 2008	deceit	Liu & Pemberton, 2010	*Centris nitida*[1]
Encyclia rufa Rufous butterfly orchid	*Syntomeida epilais* (polka-dot moth)	Esperón & Sauleda, 2012	deceit?	-	*Syntomeida epilais*
Epidendrum radicans Star orchid	Butterflies	Bierzychudek, 1981	deceit	Ackerman, 2007	butterflies
Eulophia andamanensis Andaman crown orchid	unknown	-	deceit?	-	unknown
Eulophia graminea Chinese crown orchid	autogamy	-	autogamy	Ackerman, 2007	autogamy
Eulophia maculata Monk orchid	autogamy	-	autogamy	González-Díaz & Ackerman, 1988	rain assisted, autogamy
Laelia rubescens Pale laelia	hummingbirds	Trapnell & Hamrick, 2004	deceit	Trapnell & Hamrick, 2004	hummingbirds
	Polybia	Cen, 2016	deceit	Ackerman *et al.,* 2025	social wasps
Phaius tankervilleae Nun's hood orchid	*Xylocopa violacea*	Buragohain *et al.,* 2016	deceit	Ackerman, 2007	*Xylocopa virginica*
Spathoglottis plicata Philippine ground orchid	autogamy	Ackerman, 2007	autogamy	Ackerman, 2007	autogamy
Vanilla planifolia Commercial vanilla	unknown	Lubinsky *et al.,* 2006	deceit	Pemberton *et al.,* 2023	*Apis mellifera*[2]
					Euglossa dilemma[2]
Zeuxine strateumatica Lawn orchid	apomixis	Ackerman, 2007	apomixis	Ackerman, 2007	apomixis

[1] Liu & Pemberton, 2010. [2] Pemberton *et al.,* 2023.

that only 12% of 1076 orchid species are self-incompatible. Polyploidy is known to increase plant naturalization (Te Beest *et al*., 2012), and orchids show a remarkable amount of polyploid and aneuploid variation (Givnish *et al*., 2015). Polyploidy is known in some of the 15 naturalized orchids in Florida, including *E. maculata* (Dematteis and Daviña, 1999) and *V. planifolia* (Bory *et al*., 2008), and may occur in some of the other species as well.

Proportion of naturalized orchids in Florida and other orchid floras. The 117 orchid species in Florida, including the 15 naturalized species, means that the naturalized orchids comprise 13% of the state's orchid flora. To put this proportion in perspective, the numbers of naturalized orchids in various other places were sought through the literature and correspondence with orchid specialists in those places. Table 3 gives the proportions of

TABLE 3. Proportion of naturalized orchids in the orchid floras.

Place	Number of orchids	Number of naturalized	Percent of naturalized	Reference
Florida	117	15	12.82	Wunderlin *et al.*, 2025; Pemberton & Downing, 2025
Bhutan	462	0	0	S. Dalstrom, pers. com.
California	34	1	2.94	Jepson's eflora, 2026
Cuba	312	6	1.92	Mujica & González, 2015
Hawaii	21	18	85.7	Gallaher *et al.*, 2020
Panama	1360	4	0.029	Bogarín *et al.*, 2014; D. Bogarín, pers. com
Puerto Rico	147	11	7.5	J.D. Ackerman, pers. com
South Africa	470	1	0.02	C. Peter, pers. com.
Sri Lanka	188	4	2.23	Fernando & Omerod, 2008
Taiwan	497	4	0.8	Lin & Liu, 2025; T.P. Lin, pers. com.

the orchid floras that naturalized species comprise. Naturalized orchids comprise 85.7% of Hawaii's orchid flora because it has 18 naturalized orchids but only 3 native orchids. Its 18 naturalized orchids are the most similar to the number of species (15) naturalized in Florida, but a much larger proportion than Florida's 13% (Table 3). At the other end of the spectrum is Bhutan which has 462 native orchids but no naturalized orchids. Close to this are Panama with 1360 orchids including 4 naturalized species (0.29%). and South Africa with 470 orchids including just one naturalized species (0.2%). The percentage of orchid floras that naturalized orchids comprise depends on the number of native species as well as the number of alien orchids. Both the number of naturalized orchids in Florida (15) and the proportion of the orchid flora that they comprise is 13% (15/118), which is much higher than all other orchid floras examined except Hawaii.

Occurrence of naturalized orchids elsewhere. Two thirds, 10/15, of the orchids naturalized in Florida have naturalized elsewhere. These places (the countries, islands, and U.S. states) are shown in Table 4. Five of these 10 orchids have naturalized widely and occur on multiple continents. These are *Eulophia maculata*, *Phaius tankervilleae*, *Vanilla planifolia* and *Zeuxine strateumatica*. *Vanilla planifolia* occurs in 40 places, followed by *E. maculata* in 30 places and *S. plicata* in 14. Only 3/15 occur within the continental United States in addition to Florida: *Bletilla striata* in Maryland, *E. graminea* in Texas, and Z. *strateumatica* in California and six states in the southeastern United States. Hawaii and Puerto Rico share the most naturalized orchids with Florida, numbering 5 and 7 species respectively. The naturalization of many tropical orchids in Florida, Hawaii and Puerto Rico is due to the intensity of horticultural marketing in these areas which are climatically suitable for these orchids. In Panama most orchids in cultivation are mostly local species so there are fewer foreign orchids to naturalize, hence the low orchid naturalization percentage.

Limiting abiotic factors. The lack of suitable pollinators and mycorrhizal fungi may be the reason for orchids not naturalizing, but it could also be due to abiotic factors. The Ackerman *et al*. (2024) study used the Maxent Model to predict suitable areas for *Arundina graminifolia* (D.Don) Hochr. Florida was not predicted to be climatically suitable for this orchid.

Biological characteristics that promote naturalization. There are other biological characteristics that are associated with plant naturalization. Self-compatibility is one of these characteristics (Kinlock *et al*., 2025), and orchids usually have a high degree of self-com-

TABLE 4. Naturalized orchids in Florida, USA, that are naturalized elsewhere.

Scientific name Common name	No. USA States	No. places	Places naturalized beyond Florida	Reference
Bletia florida Slender pinepink	1	2	Trinidad	POWO, 2026
Bletilla striata Chinese ground orchid	2	2	Maryland	POWO, 2026
Cymbidium aloifolium Aloe leaved cymbidium	1	1	None	Pemberton & Downing, 2025
Cymbidium dayanum Day's cymbidium	2	2	Hawaii	POWO, 2026
Cyrtopodium flavum Yellow cowhorn orchid	1	1	None	
Encyclia rufa Rufous butterfly orchid	1	1	None	
Epidendrum radicans Star orchid	1	3	Cuba, Puerto Rico	POWO, 2026
Eulophia andamanensis Andaman crown orchid		1	None	None
Eulophia graminea Chinese crown orchid	4	6	Bahamas, Cuba, Mexico, Puerto Rico, U.S.A (Texas)	POWO, 2026; Ackerman *al.*, 2021
Eulophia maculata Monk orchid	1	30	Central & South America, West Indies	POWO, 2026
Laelia rubescens Pale laelia	1	1	None	
Phaius tankervilleae Nun's hood orchid	2	7	Cuba, Jamaica, Mauritius, Panama, Puerto Rico, U.S.A (Hawaii)	POWO, 2026
Spathoglottis plicata Philippine ground orchid	2	14	Cayman I., Comoros, Cuba, Dominican Rep., Leeward I., Marquesas, Nauru, Panama, Puerto Rico, Reunion, Seychelles, Society I., U.S.A (Hawaii), Windward I.	POWO, 2026
Vanilla planifolia Commercial vanilla	2	40	Bangladesh, D.R. Congo, Dominican Rep., Indonesia, Madagascar, Papua NG, Puerto Rico, Reunion, S. Amer-part, U.S.A (Hawaii), and others	POWO, 2026
Zeuxine strateumatica Lawn orchid	5	17	Argentina, Bahamas, Bermuda, Brazil, Cuba, Jamaica, Puerto Rico, Saudi Arabia, Türkiye, U.S.A. (Alabama, Calif., Georgia, Hawaii, Louisiana, Mississippi, Texas)	POWO, 2026

patibility (Neiland & Wilcock, 1998). Polyploidy is known to increase plant naturalization (Te Beest *et al.* 2012), and orchids show a remarkable amount of polyploid and aneuploid variation (Givnish *et al.*, 2015). Polyploidy is known in some of the 15 naturalized orchids in Florida, including *E. maculata* (Dematteis & Daviña, 1999) and *V. planifolia* (Bory *et al.*, 2008), and may occur in some of the other species as well.

Most orchids prefer ephemeral habitats which they reach by producing numerous wind-borne seed (Ackerman, 2007). This suggests preadaptation to Florida habitat types was not needed by these naturalized orchids. In Brazil *Cyrtopodium flavum* grows on rock outcrops (Pansarin *et al*., 2008), whereas the biggest population in Florida is in a Pine Rockland at Boystown Preserve in Miami, but it also occurs in many other habitats (Pemberton & Liu, 2011). *Laelia rubescens* occurs largely in anthropogenically altered habitat (Trapnell & Hamrick, 2004). *Eulophia graminea* often grows in mulch (Pemberton *et al*., 2008) which has become extensively used in recent years. The orchid was introduced to Puerto Rico with mulch imported from Florida (Ackerman & Gónzález-Orellana, 2021).

Nonnative ornamental orchids that fail to naturalize in Florida. It is of interest to note that some very commonly grown non-native ornamental orchids that are well-pollinated in Florida have not naturalized. *Guarianthe skinneri* (Bateman) Dressler & W.E. Higgins was pollinated by the naturalized orchid bee *Euglossa dilemma* (Pemberton, 2007). The orchid bee quickly discovered and visited newly exposed flowers and removed more than half of the pollinaria of this orchid. *Oncidium sphacelatum* Lindl. was pollinated by the naturalized oil-collecting bee *Centris nitida*, whose pollination induced a much higher fruit set than has been recorded in the native area (Pemberton, 2008). *Arundina graminifolia* is pollinated by the common honeybee, which caused half of the flowers to set fruit (Pemberton, unpublished), which is much higher than has been recorded in places like Hawaii, Mauritius, and Puerto Rico, where it has naturalized (Ackerman *et al*., 2024). These orchids have overcome the pollination barrier yet have not naturalized. The lack of suitable mycorrhizal fungi may be the reason for their failure, but it could also be due to abiotic factors. The Ackerman *et al*. (2024) study used the species distribution modeling program Maxent to predict suitable areas for *Arundina graminifolia*. Florida's climate was not predicted to be suitable for this orchid.

Influence of orchid clubs and commerce. But this is the story of a small number of orchids that have naturalized in Florida, which are relatively numerous compared to smaller numbers of orchids that have naturalized in other places. Marketing brought most of these foreign orchids to Florida, which is driven by the popularity of growing orchids as a hobby. An indication of this is the large number of orchid clubs in the state. For instance, in the three heavily populated counties of southeastern Florida there are 25 orchid clubs affiliated with the American Orchid Society and additional unaffiliated clubs. The ability of these naturalized orchids to reproduce is a primary factor for their success, but the other important factors are as yet unknown.

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- Cite authors of all names at the rank of genus and below when first used in the text, without repeating citations after the first name’s use. Refer to the International Plant Names Index (IPNI) for correct abbreviations (https://www.ipni.org).
- Italicize all scientific names at the generic level or below.
- Spell out the genus and species the first time used in a paragraph and abbreviate the generic name by the first initial thereafter in that paragraph. Do not abbreviate the genus name at the beginning of a sentence.
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- Acknowledgments: Keep acknowledgments brief and focused, crediting those who contributed to the study and explaining the reasons for acknowledgment. List all grant numbers or funding sources.

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Lankesteriana uses APA Reference Style 6th edition. See the style manual for guidance on using this Reference Style. Consider using citation management tools like Zotero, Mendeley, or EndNote for efficient referencing.

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- Begin each new page for figures and tables, continuing the page number sequence.
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- Double-space the legends and group them according to figure arrangements. Avoid using a separate page for each group of legends.
- Number figures consecutively with Arabic numerals.
- Format legends in paragraph style and label plant illustrations according to the order of their taxonomic description. For example: Figure 1. *Pleurothallis inedita*. A. Habitat. B. Flower. C. Flower dissection. D.

Outer floral bract. E. Inner floral bract. F. Petal. G. Column, profile view (left) and 3/4 dorsal view (right). H. Pollinarium. (Drawn from the holotype). Illustration by Who Nobody. Figure 2. *Luisia inedita*. A. Habit. B. Fruit (Somebody 567, CR). Illustration by Who Nobody. Note that labels on the figure ("A") should be in upper case and match that on the legend. Italicize the collector's name and number.

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LANKESTERIANA, the International Journal on Orchidology, has been dedicated to publishing articles focused mainly (today exclusively) on orchid science, spanning a wide variety of topics, including anatomy, ecology, evolution, history, physiology, phylogenetics, and systematics. Founded in 2001, LANKESTERIANA is hosted by the University of Costa Rica. The first issue published on the 15th of May, 2001, with the support of Jorge Warner, former Director of Lankester Botanical Garden, and Franco Pupulin, its inaugural Editor in Chief, was funded by Brian Holley from Cleveland Botanical Garden. The journal's early years were marked by enthusiasm and rapid growth despite initial challenges in distinguishing itself from other botanical journals. However, it quickly gained recognition within the scientific community, largely due to contributions from prominent figures in orchid science, including James Ackerman, Germán Carnevali, Phillip Cribb, Stig Dälstrom, Mark Chase, Calaway H. Dodson, Robert L. Dressler, Eric Hágsater, Günter Gerlach, Alec Pridgeon, Gerardo Salazar, and Norris H. Williams.

Initially not exclusively focused on orchids, LANKESTERIANA shifted its scope to solely cover orchid-related research in 2007, filling a gap in orchidology left by the discontinuation of other recognized journals in the field, such as Lindleyana, Orquídea, Orquideología, and Selbyana. With the continuous support of the Vice-Rectorate for Research at the University of Costa Rica and the incorporation of Diego Bogarín, Adam P. Karremans, and Melissa Díaz as Associate and Managing Editors and Noelia Belfort-Oconitrillo as Technical Editor, the journal maintained a steady flow of high-quality publications. Today, LANKESTERIANA is the only scientific journal dedicated exclusively to publishing original research articles on orchid science, along with correspondence, comments, corrigendum, opinions, obituaries, special issue contributions, conference proceedings, checklists, and reviews.

The journal continues to assert its influence within the field of orchidology, evidenced by its high citation in orchid-related literature worldwide and its inclusion in well-recognized indexes such as Scimago and Scopus. LANKESTERIANA is a peer-reviewed, electronic, open-access journal that still distributes printed copies to over 50 institutions worldwide.

Aims and scope: LANKESTERIANA, the International Journal on Orchidology, is an international scientific journal published by the Lankester Botanical Garden Research Center – University of Costa Rica. The journal is globally recognized for its specialization and contributions to the knowledge of the orchid family. In addition to research articles, LANKESTERIANA is dedicated to facilitating scholarly communication and exchange by publishing a comprehensive array of content, including book reviews, checklists, comments, conference proceedings, correspondence, corrigendum, obituaries, opinions, reviews, and special issue contributions.

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