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MORMODES BENELLIANA (CATASETINAE), A NEW SPECIES FROM MATO GROSSO, BRAZIL

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Abstract. In the present study, we describe and illustrate *Mormodes benelliana*, a new species found in the southwest region of the Brazilian state of Mato Grosso. This species occurs as an epiphyte in the transition between the Amazon and Cerrado domains. *Mormodes benelliana* is similar to *M. hoehnei,* but differs by having smaller pseudobulbs, inflorescences longer than the pseudobulbs, conspicuous peduncle, yellowish-brown and brown-vinous striped flowers, with a large-elliptic to ovate, glabrous lip.

Resumo. No presente estudo descrevemos e ilustramos *Mormodes benelliana*, uma nova espécie encontrada na região sudoeste do estado brasileiro de Mato Grosso, onde ocorre como epífita na transição entre os domínios Amazônia e Cerrado. *Mormodes benelliana* é semelhante a *M. hoehnei* mas difere pelos pseudobulbos menores, inflorescência mais longa que os pseudobulbos, pedúnculo conspícuo, flores listradas de castanho-amarelado e castanho-vinoso, labelo largo-elíptico a ovado, glabro.

Keywords / Palavras chave: Amazon, Amazônia, Cerrado, ecotone, ecótono, epífita, epiphyte, orchid, orquídea, taxonomia, taxonomy

Introduction. The Mato Grosso is the third largest state in Brazil, known for its floristic diversity. The diversity is largely due to its inclusion of the Amazon, Cerrado, and Pantanal domains, as well as their ecotonal areas. This reflects a significant richness of phytophysiognomies and species, with 6247 species of Angiosperms recorded today (BFG, 2015; 2018; 2022; Flora e Funga do Brasil, 2024; IBGE, 2012).

Among the Angiosperms, the Orchidaceae are represented in the state by 83 genera and 326 species (Flora e Funga do Brasil, 2024). Knowledge of this family in Mato Grosso has progressively expanded through the publication of new records, new species, and floristic studies (i.e., Benelli, 2012; Benelli & Pessoa, 2019; Benelli *et al*., 2015; Carpanedo *et al*., 2021; Engels & Ferneda Rocha, 2016; 2017a,b,c; Engels & Smidt, 2021; Engels *et al*., 2017; 2019; Koch & Silva, 2012; Koch *et al*., 2016; Pessoa *et al*., 2015), including representatives of Catasetinae such as *Catasetum* Rich. ex Kunth (i.e., Benelli & Grade, 2008; Benelli & Izzo, 2017; Benelli & Soares-Lopes, 2015; 2017; Engels *et al.* 2016;) and *Mormodes* Lindl. (Campacci & Carr 2015; Engels *et al.* 2020). However, much remains to be investigated, especially in regions with limited sampling (i.e., Zappi *et al.*, 2011; 2016; Zocal *et al*., 2023).

Mormodes comprises 87 species distributed from Mexico to Brazil (Cantuária *et al*., 2019; Chase *et al*., 2015; Malaspina *et al*., 2023; POWO, 2024; Salazar *et al*., 2016). They can be recognized from other genera of Catasetinae by their asymmetrical flowers with a twisted column and perianth (Salazar *et al*., 2016). In Brazil, 30 species are recorded, with seven occurring in Mato Grosso (Cantuária *et al*., 2019; Malaspina *et al*., 2023; Meneguzzo, 2024).

ORCID of the Author: MEE, ECS, CAS, AKK
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The taxonomy of *Mormodes* is complex due to the few diagnostic characters and frequent overlapping of features among the species. Additionally, the rarity in nature results in limited representation in botanical collections and scant information on the morphological variation and autecology of most species (see Engels *et al.*, 2020; Salazar *et al.*, 2016).

During the study of Orchidaceae specimens from the UFMT and TANG herbaria (acronyms according to Thiers, 2024; cont. updated), an undescribed species of *Mormodes* was identified, increasing the number of species for Mato Grosso to eight. In the present study, we propose to describe this new species, providing a comprehensive morphological description, information on the distribution, taxonomy, ecology, and conservation, in addition to images of the new species.

Material and methods. Materials from UFMT and TANG were examined under a stereoscopic microscope, and dried flowers were rehydrated with warm water with the permission from the herbaria curators. Additionally, flowers preserved in spirit at UPCB were examined. Colour data were collected from the labels of specimens and photos of live material. Morphological terminology follows Gonçalves & Lorenzi (2011). Literature on *Mormodes* was consulted for taxonomic comparison (i.e. Castro Neto, 2006; Miranda & Lacerda, 1992; Pabst, 1978).

Taxonomic treatment

Mormodes benelliana Engels & A.K.Koch, ***sp. nov.*** (Fig. 1–3)

TYPE: BRAZIL. Mato Grosso: Reserva do Cabaçal, 16 June 2014 (fl.), *C.B. Freitas APB952* (holotype UFMT 41.445!, isotype UPCB! [spirit]).

Diagnosis: Similar to *Mormodes hoehnei* F.E.L.Miranda & K.G.Lacerda, but it differs with smaller pseudobulbs, inflorescences longer than the pseudobulbs, conspicuous peduncle, yellowish-brown and brown-vinous striped flowers, lip large-elliptic to ovate, glabrous.

Epiphytic *herb*, caespitose, *ca.* 13–14 cm tall. *Roots* 2–3 mm diam., terete, white. *Pseudobulbs ca.* 7.5 × 2.2 cm, heteroblastic, lanceoloid to ovoid, covered by persistent leaf sheaths. *Leaves* 5–8 per pseudobulb, petiolated, caducous during flowering; leaf sheaths tan; blades 19.0–24.8 × 1.0–2.2 cm, narrowly elliptical, base acute, margin entire and sinuate, apex acute, green, concolourous, glabrous. *Inflorescence* 10.4–17.6 cm long, raceme simple, axillary, 9–24-flowered, ascending, produced in the nodes above the base up to the middle of the mature pseudobulb; peduncle 5.3–9.6 × 0.2–0.35 – (0.6) cm, terete, green; *peduncle bracts* 6–7 × 8–10 mm, ovate, amplectives, apex obtuse, brown-greenish; rachis 4.0–10.5 × 0.1–0.2 - (0.6) cm, terete, green; *floral bracts* 3–5 × 1–2 mm, elliptic to elliptic-lanceolate, apex obtuse, brown-greenish. *Flowers* resupinate, glabrous; ovary and pedicel 1.4–2.1 × 0.1–0.2 cm, subterete, sulcate in the carpel welding, brown greenish; perianth brown yellowish with brown-vinous stripes. *Dorsal sepal* 1.7–2.0 × 0.4–0.6 cm, elliptic-lanceolate to lanceolate, base acute, margin entire, apex obtuse to rounded; *lateral sepals* 1.7–2.0 × 0.5–0.8 cm, elliptic-lanceolate to lanceolate, base rounded, margin entire, apex obtuse to sub-rounded with dorsal acute carinae. *Petals* 1.7–2.0 × 0.5–0.8 cm, lanceolate, base acute, margins entire, apex obtuse and apiculate. *Lip* 1.7–2.1 × 0.9–1.4 cm, unguiculate, fleshy, rigid, brown greenish with brown-vinous stripes; claw 4–6 × 2 mm; blade large-elliptic to ovate, entire, base slightly decurrent, margin entire, deflexed in natural position, apex rounded and apiculate, apicule *ca.* 1.0 mm length, acute, deflexed. *Column* 1.0–1.2 × 0.2–0.4 cm, twisted, brown whitish; stigmatic cavity 1.5–3 × 1.5–2.5 mm, elliptical to sub-quadrate. *Anther cap* 4 × 5 mm, transversely elliptic, apiculate, apex acute. *Pollinaria* with viscidium *ca.* 1.5 × 1.7 mm, sub-rounded; stipe *ca.* 5 × 3 mm, oblanceolate, obtuse; pollinia 2, *ca.* 2.0 × 1.25 mm, ellipsoid, cucculate, yellow. *Fruits* and *seeds* not seen.

Additional materials: BRAZIL. Mato Grosso: Tangará da Serra, 20 May 2011 (fl.), *J.Q. Moraes 57* (paratypes TANG 1075! [dried + spirit], UPCB! [spirit]); Reserva do Cabaçal, 16 June 2014 (fl.), *C.B. Freitas nº APB953* (paratype UFMT 41.444!).

Distribution and habitat: Known from the southwest region of Mato Grosso, in the Reserva do Cabaçal and Tangará da Serra municipalities. It occurs as an epiphyte in the ecotone region between the Amazon and Cerrado domains (Fig. 4).

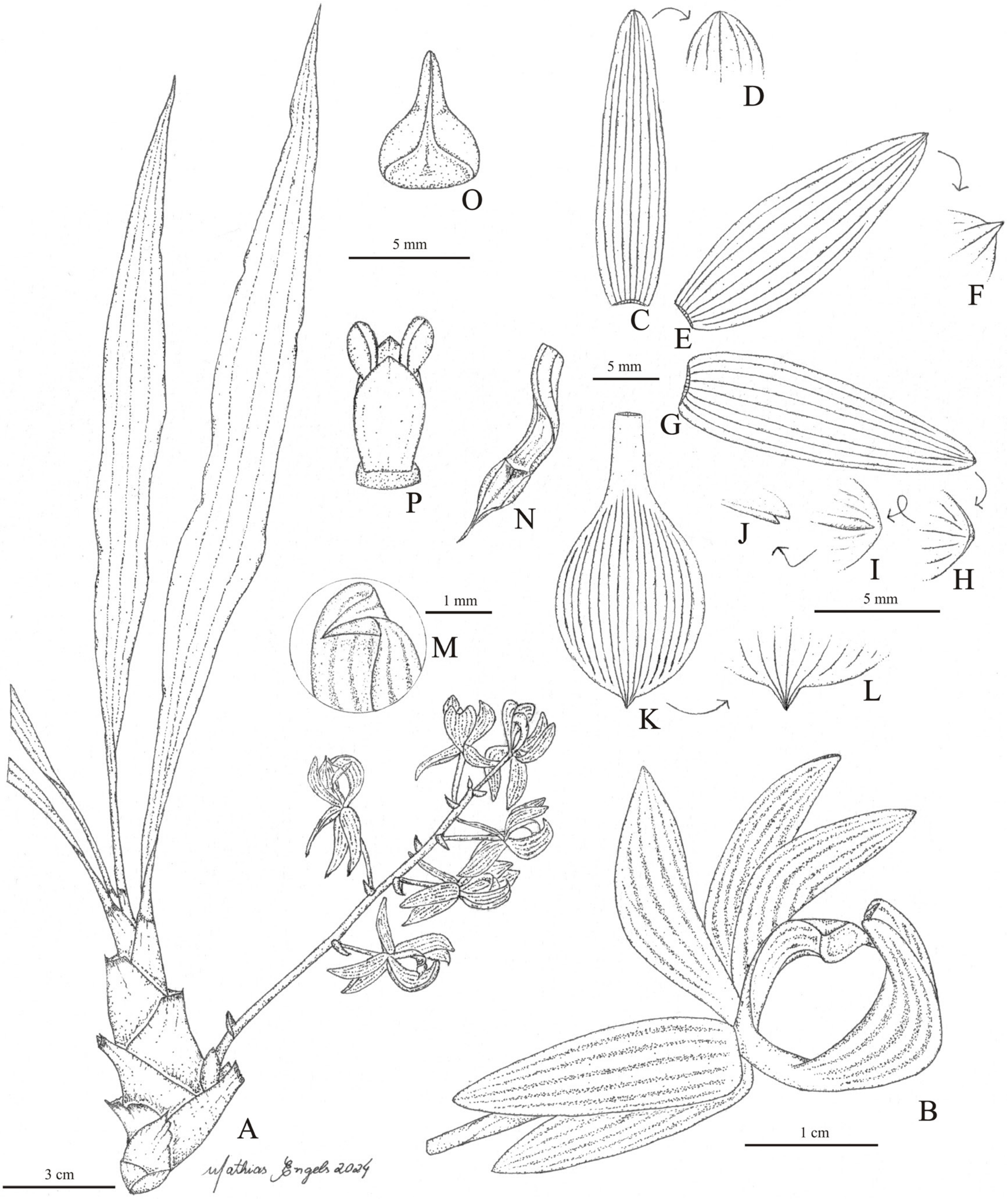

Figure 1. *Mormodes benelliana*. **A**. Habit. **B**. Flower in lateral view. **C–L**. Perianth flattened. **C** and **D**. Dorsal sepal. **D**. Detail of apex. **E** and **F**. Petal. **F**. Detail of apex. **G–J**. Lateral sepal. **H**. Detail of apex in adaxial view. **I**. Detail od apex in abaxial view. **J**. Detail os apex in lateral view. **K–M**. Lip. **L**. Detail of flatteded apex. **M**. Detaisl of apex in natural position. **N**. Column, twisted. **O**. Anther. **P**. Polinarium. **C–G, K–L**. Adaxial view. Drawn by M.E. Engels, based on the type material (**A, O–P**. *J.Q. Moraes 57* [paratype – TANG 1075]. **B–N**. *C.B. Freitas n° APB952* [holotype – UFMT 41.445]).

Figure 2. *Mormodes benelliana.* **A**. Habit. **B**. Inflorescences. **C**. Detail of flowers. **D**. Detail of lip adaxial surface at pickled material. Photos by Celice A. Silva (**A–C**) and Mathias Engels (**D**). **A–C** of *J.Q. Moraes 57* (TANG [dried + spirit]), **D** of *C.B. Freitas n° APB952* (UPCB [spirit]).

UNIVERSIDADE FEDERAL DO PARANÁ

Mormodes sp.

Mathias Erich Engels Data: 10 . 08 . 2023

Projeto: Filogenia de *Catasetum* L.C.Rich. *ex* Kunth (Orchidaceae) e monografia do gênero para a Flora de Mato Grosso, Brasil
Autora: Adarilda Petini Benelli

Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade – UFMT

Coords.: Prof. Dr. Thiago Junqueira Izzo & Prof. Dr. Eric de Camargo Smidt

Família: Orchidaceae Tribo: Epidendroideae Subtribo: Catasetinae
Espécie: ***Mormodes* sp.**
Det.: A. Petini-Benelli, 16/06/2014
Local de coleta: BRASIL. MATO GROSSO. Reserva do Cabaçal. *Ex hort*. Carício Barbosa de Freitas.

Coord.: Elevação:
Data: 16/06/2014 Nº Coleta: APB952 Nº Tombo:
Coletor(es): C.B. Freitas
Habitat: Cerrado
Hábito: Erva epífita Typus ( ) Outro ( )

OBS.: Flores em solução: SPIRIT COLTESE1306; Flores não ressupinadas. Tépalas marrom-amareladas com vênulas longitudinais marrons. Labelo marrom-esverdeado.

FIGURE 3. Holotype of *Mormodes benelliana* (*C.B. Freitas nº APB952* [UFMT 41.445]).

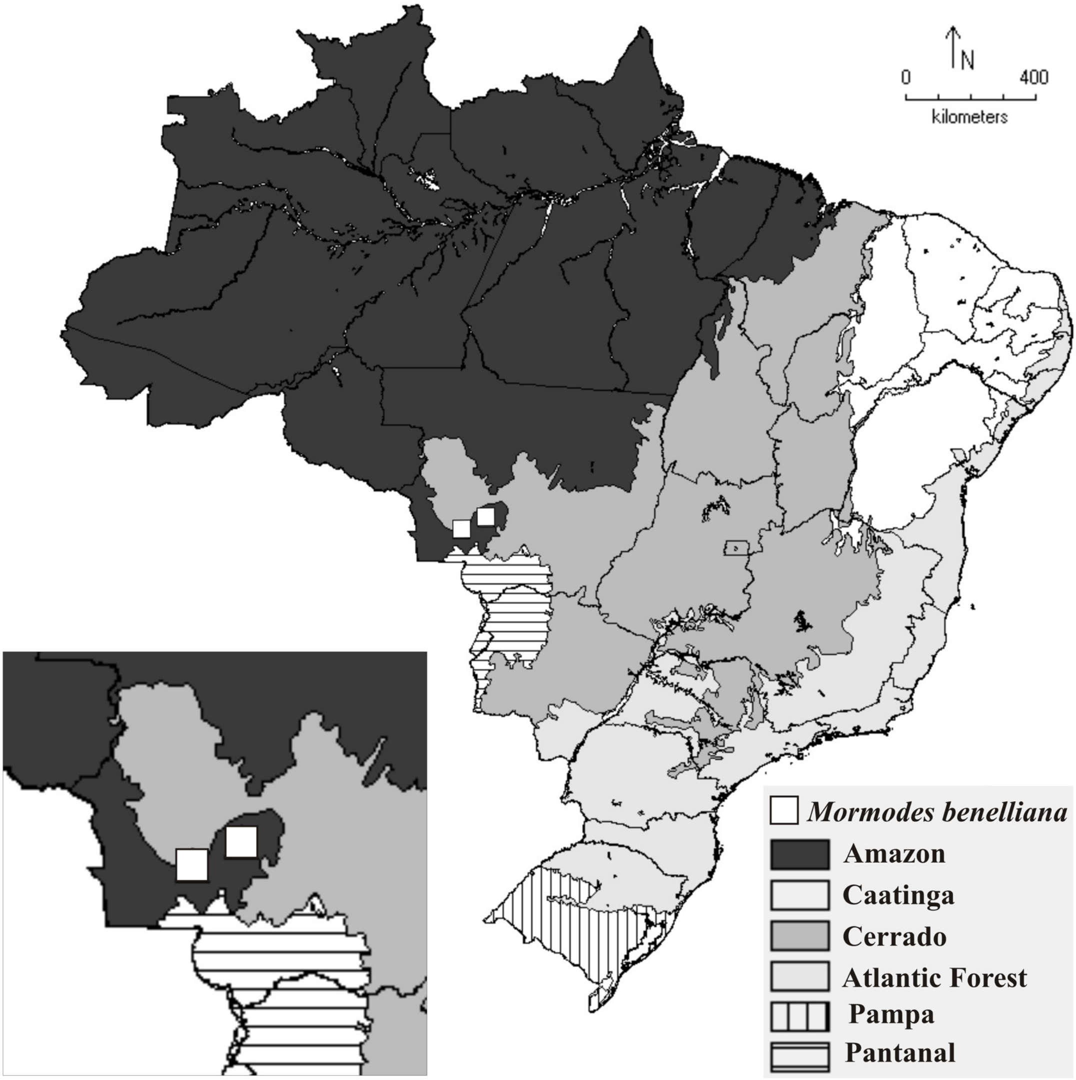

FIGURE 4. Map of Brazil indicating the distribution of *Mormode benelliana*.

ETYMOLOGY: The specific epithet honours Dra. Adarilda Petini Benelli, an orchidologist who has made significant contributions to the knowledge of the genus *Catasetum* (Catasetinae) in the state of Mato Grosso and Brazil (e.g., Benelli, 2024).

CONSERVATION STATUS: According to IUCN, *M. benelliana* falls into the Data Deficient (DD) category. The new species is known from three collections in two municipalities, the exact locations being unknown. With two municipal centroids, calculated at GeoCAT (Bachman *et al.*, 2011), its extent of occurrence (EOO) is 0 km^2 (not calculable with two points) and area of occupancy (AOO) is 8 km^2, being considered as Critically Endangered (CR). However, a more extensive sampling and specific studies on the genus may provide distribution, ecology and abundance data for a better understanding of the species and its threats, providing subsidies for an adequate framework for its conservation.

MORPHOLOGICAL AFFINITIES: *Mormodes benelliana* belongs to *Mormodes* sect. *Mormodes* due to flowering occur after the complete development of the pseudobulbs, after the beginning or complete abscission of the leaves (see Salazar *et al.*, 2016). It is morphologically similar to *Mormodes hoehnei* due to the dimensions of the floral whorls (i.e., *ca.* 2 cm long), the striped flowers and the shape of the lip blade (i.e., entire). However, it is easily differentiated by its entirely glabrous lip (*vs.* densely pilose on the adaxial surface [as *hirsutissimo* or very hirsute]). Additionally, *M. benelliana* has smaller pseudobulbs (*ca.* 7.5 × 2.2 cm, lanceoloid to ovoid *vs.* 28 × 5 cm, eliptic-lanceoloid to fusiform); inflorescence longer than the pseudobulbs (10.4–17.6 cm long, *ca.* 1.5 times longer *vs. ca.* 12 cm long, half the length); conspicuous peduncle, 5.3–9.6 cm long *vs.* peduncle inconspicuous with flowers densely condensed from the base of inflorescence); +fewer flowers (9–24 *vs.* 35+); lip shape (large-elliptic to ovate *vs.* orbicular to transversally sub-elliptic); perianth flowers brown-yellowish with brown-vinous stripes (*vs.* pink to red-vinous flowers with dark red-vinous stripes). Additional characters are presented in Table 1. A detailed description, illustrations and images of *M. hoehnei* are provided in Miranda & Lacerda (1992) and Castro Neto (2006).

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Authors contribution. MEE: Contributed to data analysis, conceptualization and design of the study, preparation and review of the manuscript. ECS: Contributed to data analysis, conceptualization and design of the study and review of the manuscript. CAS: Contributed to data analysis, conceptualization and design of the study and review of the manuscript. AKK: Contributed to data analysis, conceptualization and design of the study and review of the manuscript.

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Conflict of interest. The authors declare no conflict of interest.

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TABLE 1. Morphological comparison between *Mormodes benelliana* and *Mormodes hoehnei*.

Characters	***Mormodes benelliana***	***Mormodes hoehnei***
Habit	epiphyte	epiphyte and rupiculous (dendricolous)
Pseudobulbs		
Size	*ca.* 7.5 × 2.2 cm	28 × 5 cm
Shape	lanceoloid to ovoid	eliptic-lanceoloid to fusiform
Leaves		
Number	5–8 per pseudobulb	12–15 per pseudobulb
Size	19.0–24.8 × 1.0–2.2 cm	*ca.* 25.0 × 5.5 cm
Shape	narrowly elliptical	oblong-lanceolate
Inflorescence		
Size	longer than the pseudobulb (*ca.* 1.5 times longer)	smaller than the pseudobulb (*ca.* half lenght)
Flowers number	9–24	more than 35
Lenght	10.4–17.6 cm	*ca.* 12 cm
Peduncle	conspicuous (5.3–9.6 cm long)	incospicuous (very short)
Flowers		
Position	Resupinate, laxa to agruped	Resupinate, densaly agrupeded
Color	brown-yellowish with brown-vinous stripes	pink to red-vinous flowers with dark red-vinous stripes
Ovary + pedicel		
Size	1.4–2.1 × 0.1–0.2 cm	2.1 × 0.15 cm
Shape	sub-terete	terete
Indument	glabrous	glabrous
Dorsal sepal		
Size	1.7–2.0 × 0.4–0.6 cm	2.2 × 0.4 cm
Shape	elliptic-lanceolate to lanceolate	lanceolate
Indument	glabrous	glabrous
Lateral sepals		
Size	1.7–2.0 × 0.5–0.8 cm	2.0 × 0.7 cm
Shape	elliptic-lanceolate to lanceolate	lanceolate
Indument	glabrous	glabrous
Lip		
Size	1.7–2.1 × 0.9–1.4 cm	2.2 × 1.4 cm
Blade size	1.3–1.6 × 0.9–1.4 cm	1.8 × 1.4 cm
Blade shape	large-elliptic to ovate	orbicular to transversally sub-elliptic
Apex	apicule ca 1.0 mm long	apicule *ca.* 3.0 mm long
Indument	glabrous	very hirsute
Column size	1.0–1.2 × 0.2–0.4 cm	1.5 × 0.15 cm
Anther cap		
Size	4 mm long	8 mm long
Shape	transversely elliptic, apiculate	subtriangular and long apiculate

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A NEW SPECIES OF *TELIPOGON* (ONCIDIINAE) FROM BOLIVIA

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Abstract. *Telipogon minutus*, from the Carrasco National Park in the Bolivian Yungas, is proposed as a new species. Plants of *T. minutus*, which reach up to 4 cm in height, are the smallest known Bolivian *Telipogon*. The new species is characterized by its oblong to ovate labellum, which is weakly sub-auriculate and retuse at the base, with a semi-circular stigma, a column with two lateral lobes and a mammillary protuberance at the apex, and two tufts of setae with trifurcate apices. A description, figures, and a distributional map of the new taxon are provided, along with a discussion of the differences between the new species and morphologically similar *Telipogon* species.

Resumen. *Telipogon minutus*, procedente del Parque Nacional Carrasco en las Yungas de Bolivia, es propuesta como una nueva especie. Las plantas de *T. minutus*, que alcanzan hasta 4 cm de altura, son las más pequeñas de los *Telipogon* conocidos en Bolivia. La especie se distingue por su labelo oblongo a ovado, con la base retusa y ligeramente subauriculada, un estigma semicircular, y una columna con dos lóbulos laterales, una protuberancia mamilar en el ápice, y dos grupos de setas que se trifurcan en el extremo. Se proporciona una descripción detallada, las figuras, y un mapa de su distribución geográfica, así como una comparación con especies de *Telipogon* morfológicamente similares.

Keywords/Palabras clave: Andes, Bolivian Yungas, Los Yungas de Bolivia, miniature *Telipogon*, Orchidaceae, taxonomía, taxonomy, *Telipogon* miniatura

Introduction. *Telipogon* Kunth (Orchidaceae: Oncidiinae) is a diverse neotropical orchid genus, with 255 species (POWO, 2024). It is found from southern Mexico and the Caribbean to Panama and along the Andes from Venezuela to Bolivia (Martel *et al*., 2017), from where 19 species of *Telipogon* have been recorded (POWO, 2024; Vásquez *et al*., 2014). Among these are the so-called miniature *Telipogon* (i.e., those previously included in the former genus *Stellilabium* Schltr.; Martel *et al*., 2017; Reina-Rodríguez *et al*., 2019), six of which are known from Bolivia: *T. boliviensis* (R.Vásquez & Dodson) N.H.Williams & Dressler, *T. calueri* N.H.Williams & Dressler, *T. kukwae* (Szlach. & Mytnik) J.M.H.Shaw, *T. pampatamboensis* (Dodson & R.Vásquez) N.H.Williams & Dressler, *T. perlobatus* (Senghas) N.H.Williams & Dressler, and *T. roberti* N.H.Williams & Dressler (Vasquez *et al*., 2014). The discovery of the new species proposed here suggests that the number of miniature *Telipogon* species recorded for Bolivia could continue to increase in the coming years.

In 2018, during fieldwork in the Carrasco National Park, Cochabamba Department of Central Bolivia, several unidentified specimens of a miniature *Telipogon* were collected. These specimens did not match the descriptions of any known *Telipogon*, and after careful revision, we determined them to represent a new species. The new species resembles *T. huancavelicanus* Collantes & C.Martel, a miniature *Telipogon* from southern Peru (Martel *et al*., 2017). Below, we provide a detailed description, illustration, and distribution map of the proposed taxon.

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Materials and methods. Specimens were collected in the Carrasco National Park during the development of the Ivirizu hydroelectric project in 2018. In the field, photographs were taken with a Canon EOS Rebel T5, equipped with a Canon 100 mm F2.8 lens. Vegetative parts were dried as herbarium vouchers, and flowers were preserved in a solution consisting of glycerin (12 %), ethanol (70 %), and water (18 %). The vouchers were deposited in the "Martín Cárdenas" National Forest Herbarium (BOLV) in Cochabamba. The distribution map was prepared using the software ArcGIS 10.3. The conservation status of the new species was assessed using the IUCN (2017) criteria.

Taxonomic Treatment

Telipogon minutus M.Zárate & C.Martel, ***sp. nov.*** Fig. 1–2.

TYPE: Bolivia. Cochabamba: Prov. Carrasco, Parque Nacional Carrasco, camino de Sehuencas a Yanamayu, 17°24'S 65°14'W, 1320 m, 11 Aug 2018, *M. Zárate et al. 6330* (holotype, BOLV 34911!).

Diagnosis: Similar to *Telipogon huancavelicanus* Collantes & C.Martel, but differing by its obovate petals (vs. oblanceolate petals), the oblong-ovate labellum (*vs*. sub-pandurate), the base of the labellum sub-auriculate and retuse (*vs*. base with two well defined, divergent auricles), the semicircular stigma (*vs*. rectangular) the anterior border of the stigma swollen into a mammillary dome (*vs*. without a mammillary dome), only two tufts of setae emerging from lateral lobes of the column (*vs*. three tufts of setae), and the setae trifurcate at the apex (*vs*. irregularly branched at the apex).

Plant epiphytic, up to 4 cm long (including the inflorescence), erect. *Roots* 1.0–1.2 mm in diameter, adventitious. *Leaves* 3, sub-coriaceous, greenish-yellow, conduplicate at the base, distichous; *blade* 5.3–14.3 × 1.9–3.9 mm, narrowly elliptic to oblong, margin entire, apex acute. *Inflorescence* terminal, a successively 2–4-flowered raceme, up to 3 cm long; peduncle with 1–2 basal bracts. *Floral bracts* 1.5–2.1 mm long, oblong when extended, conduplicate, apex acute. *Ovary* triquetrous, 4.5–7.2 mm long, pedicellate, pedicel nearly 2 mm long. *Flowers* non-resupinate, 9.8 × 10.0 mm, sepals greenish-yellow; petals wine in color at the base and greenish yellow or yellowish towards the apex, veins light maroon; labellum maroon in the basal third, light maroon in the middle third and yellow at the apex, veins light maroon. *Sepals* 5.1–5.4 × 2.1–2.4 mm, retrorse, greenish-yellow, 3-veined, 1-carinate abaxially dorsally, basally concave, apex acute to sub-acute or apiculate, margin entire, *lateral sepals* elliptic; *dorsal sepal* broadly ovate, sub-triangular. *Petals* 6.4–6.5 × 1.9–2.1 mm, 3-veined, incurved in a natural position, lanceolate, apex acute, margin serrulate. *Labellum* 6.1–6.3 × 3.9–4.3 mm, 5–7-veined, oblong to ovate, ecallose, papillose below the middle third, and sub-auriculate at the base, apex acute, margin serrulate below the apical third. *Column* 1.5 × 1.0 mm, stout, maroon, ciliate all over, the anterior of the stigma swollen into a mammillary dome, laterally bilobed from which each tuft of setae is born; *setae* purplish maroon, 1.5–2.0 mm long, three-forked; *stigma* 0.5–0.6 mm, semi-circular; *rostellum* triangular, erect, reflexed when pollinarium is removed. *Anther cap* cordiform, bilocular. *Pollinarium* 1.0 × 0.5 mm; *pollinia* 4, obovoid, complanate, convex-concave, in 2 unequal pairs, the outer pair larger, the inner pair smaller; *caudicles* hyaline; *viscidium* ancistrous.

Etymology: From the Latin *minutus*, meaning "very small," referring to the small size of the plants. *Telipogon minutus* is the smallest species among the Bolivian *Telipogon*.

Ecology and distribution: *Telipogon minutus* is only known from Yanamayu, in the Carrasco National Park (Fig. 3). The vegetation where the plant was found is classified as lower pluvial forest and Yungas palm grove, part of the Peruvian-Bolivian Yungas Province of the Tropical Andean region (Josse *et al.*, 2007; Navarro, 2011).

Individuals of *T. minutus* grow in the tree canopy, between Johansson's zones IV and V, which have high levels of sunlight exposure. Plants of this species flower between July and August, although floral buds can be observed from May. Each flower of *T. minutus* can last approximately three weeks, indicating that some miniature *Telipogon* species may have long-lasting flowers comparable to that of large-flowered *Telipogon* (Martel *et al.*, 2016).

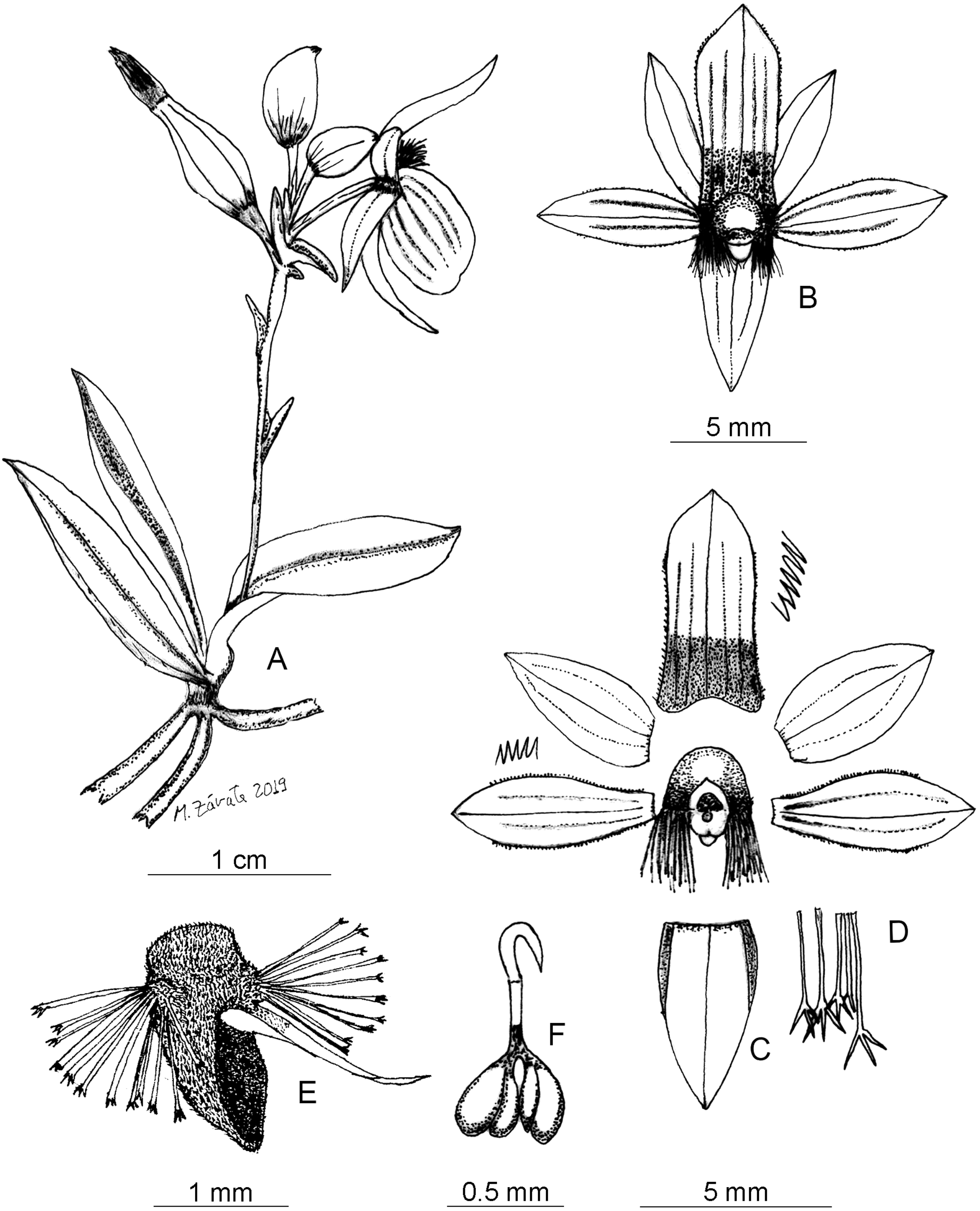

Figure 1. Line drawing of *Telipogon minutus* M.Zárate & C.Martel. **A**. Habit. **B**. Flower, frontal view. **C**. Dissected flower. **D**. Columnar setae. **E**. Column portion, side view. Note that the setae are borne from the columnar lobe and the rostellum are curved because the pollinarium has been removed. **F**. Pollinarium. Drawn by M. Zárate based on *M. Zárate et al. 6330* (BOLV).

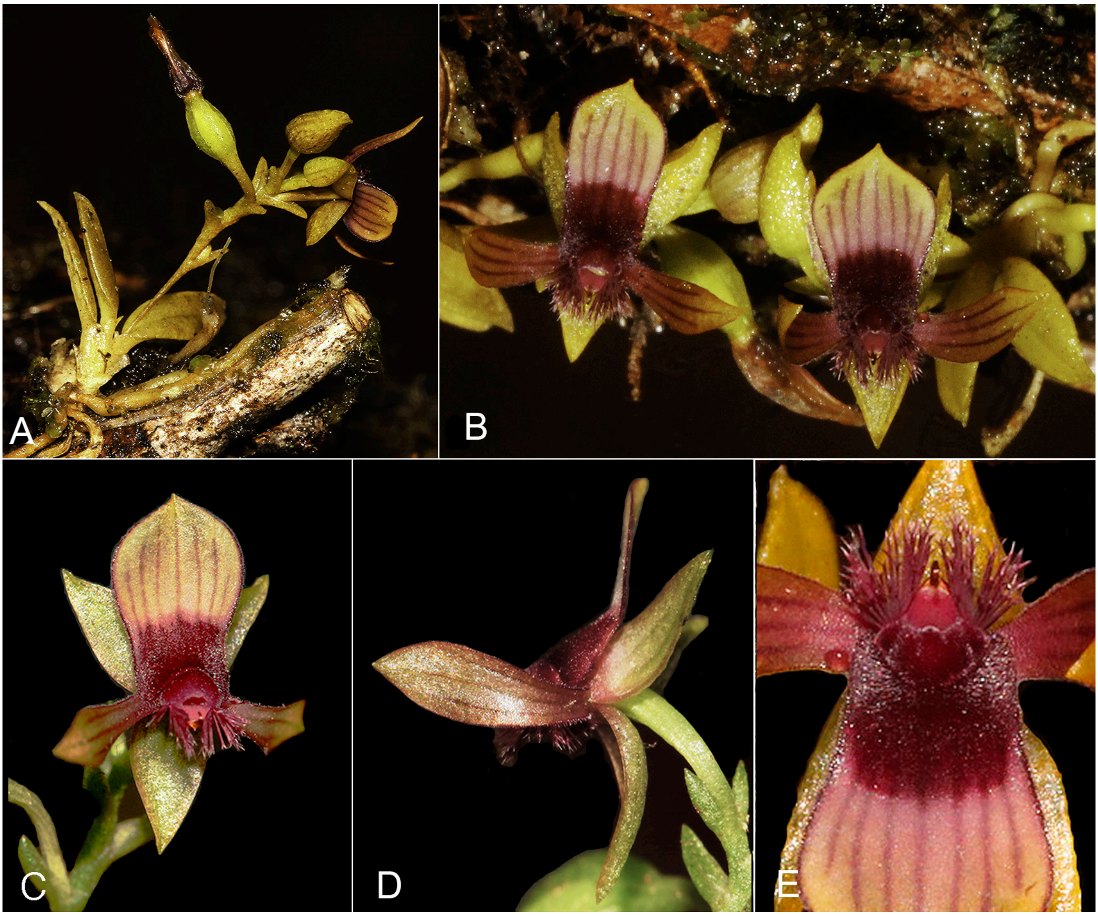

Figure 2. *Telipogon minutus*. **A**. Epiphytic habit on a small tree branch, side view. **B**. Flowers, frontal view. Note the maroon coloration at the labellum base and the two tufts of setae on the column. **C**. Detail of flower. **D**. Flower, side view. **E**. Column, close-up view from above. Photographs by M. Zárate.

Morphological affinities: *Telipogon minutus* is the smallest plant among the *Telipogon* species recorded so far in Bolivia (Fig. 2). The species resembles *T. bennettii* (Dodson & R.Escobar) N.H.Williams & Dressler and *T. huancavelicanus*, particularly in the shape of the labellum and the presence of tufts of setae in the column. However, *T. minutus* is easily distinguished by the absence of pseudobulbs (*vs*. pseudobulbs present in *T. bennettii*), a sub-auriculate labellum (*vs*. developed auricle in *T. huancavelicanus*), a mammillary dome on the anterior area of the column (*vs*. column without a mammillary dome in *T. bennettii* and *T. huancavelicanus*), two tufts of setae on the column (*vs*. three tufts in *T. huancavelicanus*), three-forked setae (*vs*. unbranched setae in *T. bennettii* and cylindrical branched segments in *T. huancavelicanus*) and a semi-circular stigma (*vs*. sub-circular stigma in *T. bennettii* and rectangular in *T. huancavelicanus*). *Telipogon minutus* can also be confused with *T. kukwae*, as both are miniature *Telipogon* species found in central Bolivia and present with furcate tufted setae. However, *T. minutus* has lanceolate, glabrous 3-nerved petals (*vs*. linear-lanceolate, densely ciliate throughout, 1-nerved), a mammillary dome on the dorsal area of the column (*vs*. lacking a mammillary dome), and two tufts of three-forked setae on the column (*vs*. three tufts and biforked in *T. kukwae*).

Conservation Status: The conservation status of *Telipogon minutus* cannot be assessed at this time, as the species is known from only two populations. According to the IUCN Red List criteria (IUCN, 2017), its status must therefore be classified as Data Deficient (DD).

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Author contribution. MZ found the plants, took photographs *in situ*, collected the plant material, and drew the botanical illustration. MZ and CM identified the taxon as new, prepared the description, and wrote the manuscript.

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Conflict of interest. The authors declare no conflict of interests.

Figure 3. Distribution map of *Telipogon minutus*. Prepared by M. Zárate.

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CORYBAS GEMINIGIBBUS, A NEW ADDITION TO THE ORCHID FLORA OF SUMATRA

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ABSTRACT. *Corybas* is an orchid genus of 154 species distributed from India to South China, the Western Pacific, and New Zealand. Sumatra is home to eight species, five of which are endemic. However, the true diversity is likely underestimated due to limited exploration in some parts of the island. During a recent exploration in the northern Gayo Plateau near the northern tip of the island, a *Corybas* species was discovered that did not match any previously known species. Further identification through specimen comparison and literature review confirmed that the species is *Corybas geminigibbus*. It was found growing in montane bogs. This discovery marks the second bioregion in Indonesia where this species has been recorded and the ninth *Corybas* species on the island. The finding also provides additional evidence of floristic similarities, suggesting past geological connections between northern Sumatra and mainland Asia. A detailed description, discussion, and photographs are provided.

ABSTRAK. *Corybas* adalah genus anggrek dengan anggota berjumlah 154 spesies yang tersebar dari India ke bagian selatan China hingga ke Pasifik bagian barat dan Selandia Baru. Sumatra memiliki delapan spesies yang mana lima diantaranya merupakan spesies endemik, akan tetapi jumlah ini sangat mungkin lebih rendah dari keragaman aslinya karena kurangnya eksplorasi botani di beberapa kawasan di pulau ini. Saat eksplorasi botani di Dataran Tinggi Gayo bagian utara, satu spesies *Corybas* berhasil ditemukan dan tidak cocok dengan spesies yang ditemukan di Sumatra sebelumnya. Identifikasi lebih lanjut melalui perbandingan spesimen dan ulasan literatur mennjukkan bahwa spesies yang diambil adalah *Corybas geminigibbus*. Spesies ini ditemukan tumbuh pada rawa gambut pegunungan. Penemuan ini menandai catatan bioregion kedua di Indonesia dan merupakan spesies *Corybas* ke-9 di Sumatra. Penemuan ini juga menambah bukti kemiripan floristik, menunjukkan koneksi geologi masa lampau antara Sumatra bagian utara dan daratan utama Asia. Deskripsi detail, diskusi, dan foto-foto disajikan.

KEYWORDS/KATA KUNCI: monocots, monokotiledon, montane bogs, gambut pegunungan, taxonomy, taksonomi, West Malesia, Malesia Barat

Introduction. *Corybas* Salisb. (Orchidoideae: Diurideae: Acianthinae) is one of the most distinctive orchid genera, characterized by a single well-developed leaf and one comparatively large flower relative to the plant's size (Dransfield *et al*., 1986). The genus ranges from India and South China to the Western Pacific and New Zealand, comprising approximately 154 species (POWO, 2024).

Sumatra is home to eight species of this genus, five of which are endemic. Some of these species are only known from specimens collected long ago, such as *Corybas bancanus* (J.J.Sm.) Schltr. from Bangka [=Banka] before 1920, and *C. roseus* (Janch.) Janch. ex J.J.Sm. before 1930 from Payakumbuh, Sumatera Barat Province (Comber, 2001). The most recent descriptions of new taxa from Sumatra date back

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nearly three decades, when three endemic species were described: *Corybas karoensis* J.B.Comber & J.Dransf., *C. scutellifer* J.B.Comber & J.Dransf., and *C. stenotribonos* J.B.Comber & J.Dransf. (Comber & Dransfield, 1995).

The number of species known is likely an underestimate. Overall, Sumatra requires more intensive botanical research to uncover new species or other noteworthy findings (Middleton *et al*., 2019). Areas that need further exploration include the northern part of the island (De Wilde & Duyfjes, 1994). So far, only one record of the genus was found from the northern part (i.e., mountainous regions of the Gayo Plateau). The specimen was collected from Mount Ketambe in the southern part of the Gayo Plateau (Dransfield *et al*., 1986).

Recent botanical surveys on the northern Gayo Plateau in North Sumatra have yielded numerous specimens of Orchidaceae, including species of *Corybas*. The collected *Corybas* specimens did not match with any previously known species from Sumatra (Comber, 2001), prompting further identification efforts through specimen comparisons and literature review (Chantanaorrapint & Chantanaorrapint, 2016; Comber, 1990; Dransfield *et al*., 1986; Seidenfaden & Wood, 1992; Truong *et al*., 2020). The results showed that the collected specimens belong to *C. geminigibbus,* which is reported from Sumatra for the first time.

Materials and methods. Fieldwork was conducted in the northern part of the Gayo Plateau, Aceh, Sumatra, Indonesia, in June and September 2023 and August 2024 to explore orchids and other plants in several montane bogs in northern Gayo Plateau, Aceh, Sumatra, Indonesia. Plants in flowers were collected using guidelines from Davies *et al*. (2023). To prepare the morphological descriptions, direct observation and measurement of fresh plants were made in the field, complemented by materials preserved in 70% ethanol stored in LGS and UIDEP. Morphological terminology in the description follows Beentje (2016) and Dransfield *et al*. (1986). The identification was performed using literature (Chantanaorrapint & Chantanaorrapint, 2016; Comber, 1990, 2001; Dransfield *et al*., 1986; Seidenfaden & Wood, 1992; Truong *et al*., 2020) and type specimens accessed from JSTOR Global Plants (2024).

Taxonomic treatment

Corybas geminigibbus J.J.Sm., Mitt. Inst. Bot. Hamburg 7: 13. 1927.

TYPE: Indonesia. Borneo: West Kalimantan, Mt Mulu, *Winkler 496* (HBG500940) (HBG-Holotype n.v.).

Small terrestrial *herb* with underground tuberoids. *Tuberoid* globose, fleshy, 4–5 mm diam. *Stem* erect, whitish-green, *ca*. 8 mm long, *ca*. 1.1 mm diam., with a basal sheath, *ca*. 5.5 mm long, apex filiform; stolons whitish, hairy, 2.0–3.1 cm long, 0.8–1.0 mm diam. *Leaves* sessile, broadly cordate, apex obtuse with short *ca*. 1.25 mm long mucro, glabrous, 13 mm long, 14–15 mm wide at the widest point, slightly undulate especially at the apical margin, light green with paler veins, the veins scarcely conspicuous. *Inflorescence* one-flowered, terminal; bract pale green, narrowly triangular, *ca*. 4.5 mm long, filiform toward the apex, recurved at the base. *Flower* with dorsal sepal pale green, streaked with red from the middle and becoming fully red upwards, with the tip green; lateral sepals pale green at the base, upwards red, and white at the upper 1/3; petals red, whitish at the base and apex; labellum with the lower half mostly transparent white, inside white at the base, white upwards until the apex of the erect part, the reflexed part purple-red with a white apical part. *Dorsal sepal* strongly curved, hood-like, oblanceolate, *ca*. 14 × 3 mm, mucronate at the apex; glabrous. *Lateral sepals* free, narrowly triangular-linear, *ca*. 21.0 × 0.8 mm; glabrous. *Petals* similar to lateral sepals, *ca*. 13–14 mm long, glabrous. *Labellum* 9 mm long, differentiated into two parts, basal half erect, upward strongly reflexed, basal half strongly inrolled, upper half slightly expanded, *ca*. 4.5 × 7.0 mm, spur 2, short, blunt, *ca*. 1 mm long. *Column ca*. 2 mm long, slightly curved; anthers erect, pollinia 2, coarse granulate. *Capsule* and *seed* not seen. (Fig. 1).

Ecology: Terrestrial in montane bogs under trees or shrubs, at elevations from 1410 to 1700 m. The species roots in the acidic organic matter of bogs and grows among mosses. The vegetation is characterized by the presence of several plants from the Ericaceae.

Flowering: June, August and September.

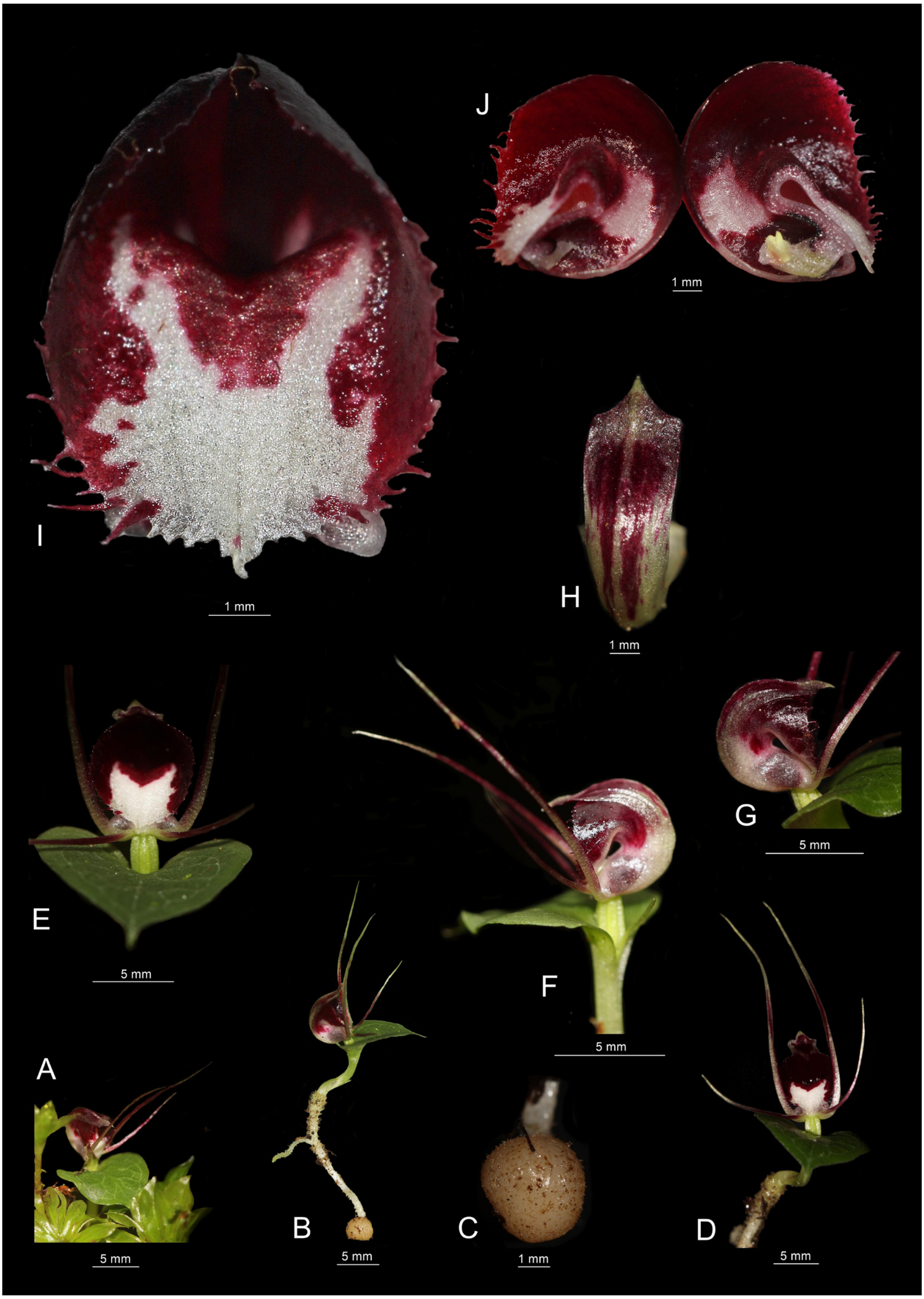

FIGURE 1. *Corybas geminigibbus* from northern Gayo Plateau, Sumatra. **A**. Plant in habitat. **B**. Habit. **C**. Tuber. **D**. Plant with flower. **E**. Flower, frontal view. **F**. Flower, lateral view. **G**. Close up of the flower, lateral view. **H**. Dorsal sepal. **I**. Labellum, frontal view. **J**. Labellum, longitudinal dissection also showing the column. Based on *Mustaqim et al. 3292*. Photos by W. A. Mustaqim.

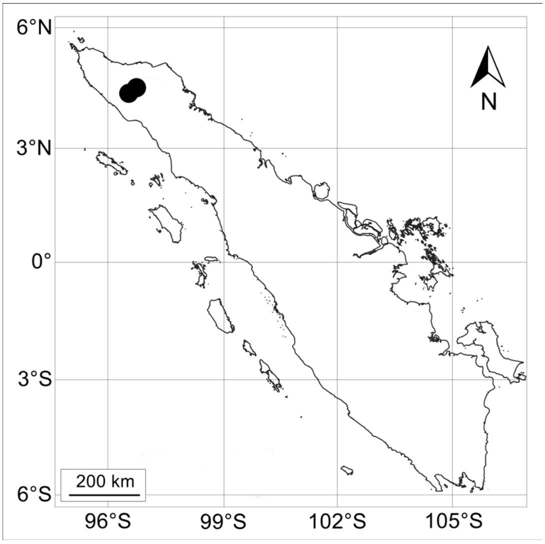

FIGURE 2. Geographic distribution of *Corybas geminigibbus* in the northern Gayo Plateau, Sumatra, Indonesia (●). Map by W.A. Mustaqim.

GENERAL DISTRIBUTION: Thailand (Chantanaorrapint & Chantanaorrapint, 2016), Vietnam (Truong *et al*., 2020), Peninsular Malaysia, Borneo (Dransfield *et al*., 1986), and Sumatra (here recorded, Fig. 1–2). In Sumatra, this species is restricted to the northern Gayo Plateau, with all known locations limited to two sites in Aceh Tengah Regency.

SPECIMENS EXAMINED. **Aceh Province**: Aceh Tengah Regency, Pegasing Subdistrict, *precise location withheld for conservation purposes*, *Mustaqim et al. 2717*, 14 June 2023 (LGS, MEDA); *ibid*. Bebesen Subdistrict, *precise location withheld for conservation purposes*, *Mustaqim et al. 3292*, 17 September 2023 (LGS, MEDA) (Fig. 1); *ibid*. Bebesen Subdistrict, *precise location withheld for conservation purposes*, *Mustaqim 3443*, 4 August 2024 (LGS).

Discussion. *Corybas geminigibbus* is a relatively widespread species in the genus. The species was first collected in Sarawak, Mt. Mulu. Until 1986, it was known only from Peninsular Malaysia and Borneo (Dransfield *et al*., 1986), but more recent records indicate a broader distribution extending to Thailand (Chantanaorrapint & Chantanaorrapint, 2016) and Vietnam (Truong *et al*., 2020). The morphological range of this species is now understood to be considerable, especially in size, as evidenced by the smaller dimensions of plants documented in Thailand (Chantanaorrapint & Chantanaorrapint, 2016).

According to Dransfield *et al*. (1986) and Truong *et al*. (2020), *C. geminigibbus* is characterized by the following combination of floral traits: (1) dorsal sepal that is non-hooded and only slightly longer (nearly subequal) than the lip, with acuminate apex and smooth (not keeled) abaxial side; (2) sepals and petals free at the base; and (3) labellum with straight base, V-shaped throat, a slightly inrolled margin and smooth surface. The specimens collected from the northern Gayo Plateau exhibit a unique color pattern, with a labellum that is predominantly purple with a white apical part. In Sumatra, this species is similar to *C. pictus* but easily distinguished by the acuminate (*vs*. truncate) dorsal sepal (Comber, 2001).

The populations of *C. geminigibbus* in the northern Gayo Plateau are confined to montane bogs (Fig. 3) The first population was found growing on shaded, mossy floors of bogs dominated by Myrtaceae and –Ericaceae vegetation (*Mustaqim et al. 2717*). The second population was found among ericaceous scrub and mixed montane vegetation on boggy ground (*Mustaqim 3292*). The population size in this area is estimated to be more than 250 plants at each site, but many plants have been lost due to illegal collecting by poachers, as happened in other orchid species in this area (Metusala, 2017).

For geographic ranges in Indonesia, this finding expand the distribution of this species to two regions, up from the previously known seven (Midleton *et al*., 2019). Sumatra is the third largest island in Indonesia, as well as the insular Southeast Asia, surpassing the size of neighboring countries like Malaysia or the Philippines. This is the second recorded locality for the species in Indonesia, with the first being in Bukit Mulu, West Kalimantan Province (Dransfield *et al*., 1986).

Conclusions. The record of *C. geminigibbus* in Sumatra is important evidence of past geological connections between mainland Asia and Sumatra. It strengthens the linkage between the two areas based on floristic similarities. The record is also a significant contribution to the future planning of research and conservation activities for Indonesia, e.g., national red-listing with the final aim of a conservation action plan.

Figure 3. Habitat of *Corybas geminigibbus* in the northern Gayo Plateau. **A**. Ericaceae shrubland. **B, D**. *Corybas geminigibbus* in its habitat. **C**. Forest stand with logging trail. Photos by W. A. Mustaqim.

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Author contributions. WAM: Conceptualization (equal); Investigation (equal); Writing – original draft preparation (equal); ZA: Supervision (equal); Writing – reviewing and editing (equal); Investigation (equal); RBG: Data curation (equal); Investigation (equal); TR: Data curation (equal); Investigation (equal); YRY: Supervision (equal); Investigation (equal); Writing – reviewing and editing (equal).

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Conflict of interest. No conflict of interest to declare.

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A NEW GREEN-FLOWERED *AA* (CRANICHIDEAE) FROM PERU

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Abstract. A new species from the Peruvian Andes, *Aa olivacea*, is described and illustrated. Information concerning distribution, habitat, ecology, and conservation status is provided. The new species is similar to *A. hieronymi* by its dense spikes of dark green and brown flowers with translucent whitish floral bracts; but differs from it by its elliptic to lanceolate leaves, 60 to 100-flowered spikes, glabrous rachis, lateral sepals with the margin entire to occasionally minutely erose near the apex, petals with slightly erose to sinuate apical margin, lip unlobed with lacerate to erose margin, and ovary with scarce hairs. Furthermore, *A. tenebrosa* is proposed as a synonym of *A. hieronymi*, *A. nigrescens* is recognized as a distinct species from *A. leucantha*, and *A. lehmannii* is confirmed to be an illegitimate, superfluous name for *A. leucantha.*

Resumen. Se describe e ilustra una nueva especie de los Andes peruanos, *Aa olivacea*. Se proporciona información sobre su distribución, hábitat, ecología y estado de conservación. La nueva especie es similar a *A. hieronymi* en su espiga densa de flores de color verde oscuro con marrón, con brácteas florales blanquecinas y translúcidas, pero se diferencia de ella por sus hojas elípticas a lanceoladas, espiga de 60 a 100 flores, raquis glabro, sépalos laterales con el margen entero y en ocasiones diminutamente eroso cerca al ápice, pétalos con el margen apical ligeramente eroso a sinuado, labelo sin lóbulos con el margen lacerado a eroso y el ovario con escasos pelos. Además, se propone *A. tenebrosa* como sinónimo de *A. hieronymi*, *A. nigrescens* es reconocida como una especie distinta de *A. leucantha* y se confirma que *A. lehmannii* es un nombre ilegítimo, superfluo para *A. leucantha*.

Keywords / Palabras clave: *Aa hieronymi*, *Aa leucantha*, *Altensteinia*, Andes peruanos, Orchidaceae, Peruvian Andes, sinónimo, synonym

Introduction. The Neotropical orchid genus *Aa* Rchb.f. occurs in Costa Rica and throughout the Andean region, from Venezuela to northern Argentina. The genus is characterized by its inflorescences with an elongated peduncle completely enclosed by many hyaline, imbricating sheaths, sub-dense to dense cylindrical spikes of tiny, non-resupinate, protandrous flowers that rarely exceed one centimeter in length (including the ovary). The floral bracts are hyaline to diaphanous, and the ovary may be glabrous to pubescent. The flowers have straight or spreading lateral sepals, a reflexed dorsal sepal and petals, and a calceolate or globose lip

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that conceals the short column with an erose, denticulate, or lacerate margin (Szlachetko & Nowak, 2014; Trujillo & Vargas, 2011).

According to the literature and field notes on herbarium labels, the flower color of *Aa* species has mainly been described as white, whitish, white and green, and brownish white. However, there are also some species with orange or dark green and brown flowers (Martín, Zanotti & Scrocchi, 2020; Trujillo & Vargas, 2011)

Despite several recent studies documenting new populations, describing new species, and transferring species wrongly placed in *Aa* to *Myrosmodes* Rchb.f. (Martín *et al*., 2020; Szlachetko & Kolanowska, 2014; Szlachetko & Novak, 2014; Trujillo & Delgado Rodriguez, 2011; Trujillo & Vargas, 2011), the genus *Aa* remains poorly understood. The taxonomic circumscriptions of most accepted species remain unclear, and several populations may represent undescribed species. So far, excluding the basionyms of species now placed in *Myrosmodes*, 29 names are referable to *Aa*.

Many *Aa* specimens remain unidentified or misidentified in herbaria; for example, in Peruvian herbaria, specimens with different floral features, which clearly represent different species, have been identified as *Aa paleacea* (Kunth) Rchb.f. or *Aa mathewsii* (Rchb.f.) Schltr.

Recent botanical surveys conducted in the departments of Lima and San Martín, Peru, led to the discovery of a new species of *Aa* with dark green flowers (Fig. 1). Additional specimens of the new species were located at USM, and photographic records are also available in iNaturalist (2024).

Based on the revision of type material and the protologues of other species of *Aa* with dark green flowers previously described from Argentina and Colombia, we determined during our studies of the new species of *Aa* from Peru that *Aa tenebrosa* C.M.Martín & Scrocchi is a synonym of *Aa hieronymi* (Cogn.) Schltr., that *Aa nigrescens* Schltr. is a distinct species from *A. leucantha* (Rchb.f.) Schltr. (proposed by Garay, 1978), and that *A. lehmannii* Rchb.f. ex Szlach. & Kolan. is an illegitimate, superfluous name for *A. leucantha* (Shenzhen Code Art. 52.1 in Turland *et al*., 2018).

Material and methods. Fieldwork was carried out in 2023 in Lima and San Martín departments, Peru. Notes on the habitat and phenology, as well as detailed photographs of the vegetative and floral details of the new species, were taken *in situ*. Specimens were deposited at herbaria HOXA, HSP, KUELAP, and MOLF. Additional specimens of *Aa* were examined at USM. Flowers preserved in 70% ethanol or rehydrated flowers from herbarium specimens were examined and drawn under a stereomicroscope. Measurements were made on the herbarium specimens -*exsiccata*- and the alcohol-preserved flowers.

The relevant literature on the genus *Aa* was revised, including the protologues of all previously described species of *Aa*, floristic and taxonomic treatments, and other works that include descriptions and illustrations of this group (e.g., Garay, 1978; Schweinfurth, 1958). Flower sketches were digitized and processed with Paint.NET v 5.0.13. A map was prepared with SimpleMappr and edited with Paint.NET v 5.0.13.

Additionally, specimens were physically reviewed at AMES, K, NY, and W. High-resolution digital images of the specimens housed at CORD, F, G, GOET, and SI were examined through the online platforms *Catalogue des herbiers de Genève* (CHG, 2023), Field Museum's online Botanical Collections Database (F, 2023), JSTOR Global Plants (JSTOR, 2023), and Repositorio Digital UNC Herbarios (UNC, 2023).

The conservation status of the new species was assessed using the IUCN criteria (IUCN, 2012, 2024), based on estimates of the Extent of Occurrence (EOO) and Area of Occupancy (AOO), both calculated through the GeoCat Geospatial Conservation Assessment Tool (Bachman *et al*., 2011).

TAXONOMIC TREATMENT

Aa olivacea D.Trujillo, Rob.Fern. et Edquén, ***sp. nov.*** (Fig. 1–3).

TYPE: Peru. Department of Lima: province Oyón, district Oyón, laderas frente a Oyón, 3740 m, 16–22 May 2023, *R. Fernandez-Hilario, A. A. Wong Sato, I. Revilla. K. Bernabé, & M. Zea 2459* (holotype: HOXA-083298!; isotypes: MOLF000170!, HSP!).

DIAGNOSIS: *Aa olivacea* is similar to *Aa hieronymi* (Cogn.) Schltr., from which it can be distinguished by having elliptic to lanceolate leaves, 60–100-flowered spikes, glabrous rachis, olive green to chestnut brown flowers, lateral sepals with the margin entire to occasionally minutely erose near the apex, petals with slightly erose to sinuate apical margin, lip unlobed, and ovary with scarce hairs.

Plant terrestrial, small, 28–50 cm tall. *Roots* fleshy, fasciculate, to 7 cm long, 3.5–6.0 mm in diameter. *Leaves* withered or green at flowering time, forming a basal rosette; conduplicate, sheathing the stem, blade elliptic to lanceolate, acute, 6.0–6.2 × 1.1–2.5 cm. *Inflorescence* erect, 27.0–48.5 cm long; peduncle terete, 3–5 mm in diameter, enclosed by 10–19 translucent, whitish sheaths with brown veins, these tubular-infundibuliform with ovate to lanceolate, acute to acuminate free apical portion; spike dense, 3–6 cm long, 0.6–1.0 cm in diameter, with 60–100 flowers opening in succession; rachis glabrous. *Flowers* non-resupinate, protandrous; sepals and petals chestnut brown to olive green with cream to light brown apex, lip dark chestnut brown with olive green with a light olive green and creamy white margin, 3–5 mm long (including the ovary). *Floral bracts* translucent brown with cream white apex, broadly elliptic, ovate to lanceolate, acute, distal margin somewhat irregularly erose, 4.2–7.5 × 2.4–3.7 mm, exceeding the length of the flowers. *Ovary* olive green to greenish brown, sessile, obovoid to cylindric, with scarce hairs mainly near its junction with the lateral sepals, 1.2–2.6 × 0.9–1.9 mm. *Dorsal sepal* reflexed, ovate to oblong, obtuse, 1-veined, 1.4–2.9 × 0.9–1.3 mm. *Lateral sepals* spreading almost horizontally in mature flowers, perpendicular to the floral axis, obliquely oblong to lanceolate, obtuse, margin entire to occasionally minutely erose near the apex, shortly connate by <1 mm at base, dorsally with scarce hairs at base, 1-veined, 2.0–3.0 × 0.9–1.0 mm. *Petals* reflexed, ovate to oblong or elliptic, obtuse, distal margin slightly erose to sinuate, 1-veined, 1.6–2.1 × 0.6–1.0 mm. *Lip* globose, oblate in side view, slightly inflexed, shortly unguiculate, unlobed, with a fleshy disc and a narrow opening, the margin lacerate to erose, base with two spherical calli, 1.4–2.4 mm long, 1.8–2.7 × 3.9–4.9 mm when spread out. *Column* short, olive green and brownish, thickened above, straight in young flowers and slightly bent backward in old flowers, 0.75–1.40 × 0.73–1.35 mm. *Anther* dorsally brown with cream-white margins, erect, subquadrate, 0.5–0.8 × 0.60–1.05 mm. *Pollinarium* made up of 4, cream yellow, clavate pollinia, united apically to a translucent white, drop-like viscidium. *Stigma* subrectagular to transversely elongate, 0.45–0.63 × 0.60–1.00 mm. *Fruit* an ellipsoid capsule, 3.0 × 2.5–2.7 mm.

FIGURE 1. Inflorescence of *Aa olivacea* (from *Fernandez-Hilario et al. 2459*, HOXA-083298). **A**. In habitat. **B**. Pressed and dried. Photographs by A. A. Wong Sato (A) and D. Trujillo (B).

PARATYPES: Peru. Departamento de San Martín: provincia de Rioja, distrito Pardo Miguel Naranjos, Bosque de Protección Alto Mayo, sector Chisquilla en orientación al Cerro Campanario o Siete Lagunas, 3348 m, 1 Abr 2023, *J. D. Edquén, K. Edquen, M. Enco & E. Yrigoín 6943* (KUELAP-004023!). Departamento de Lima, provincia de Cajatambo, distrito Copa, Anexo Huayllapa, 3690 m, 2 Ago 2017, *H. Beltrán, S. Castillo & S. Rivera 8220* (USM-305454!). Departamento de Pasco: provincia de Pasco, distrito Huariaca, Fundo Chaprin, 3200 m, 19 May 2012, *S. Baldeón, S. Baldeón & J. Baldeón 7536* (USM-289632!).

OTHER RECORDS: Peru. Department of Ancash: province of Bolognesi, -10.127985° lat., -77.177197° lon., 14

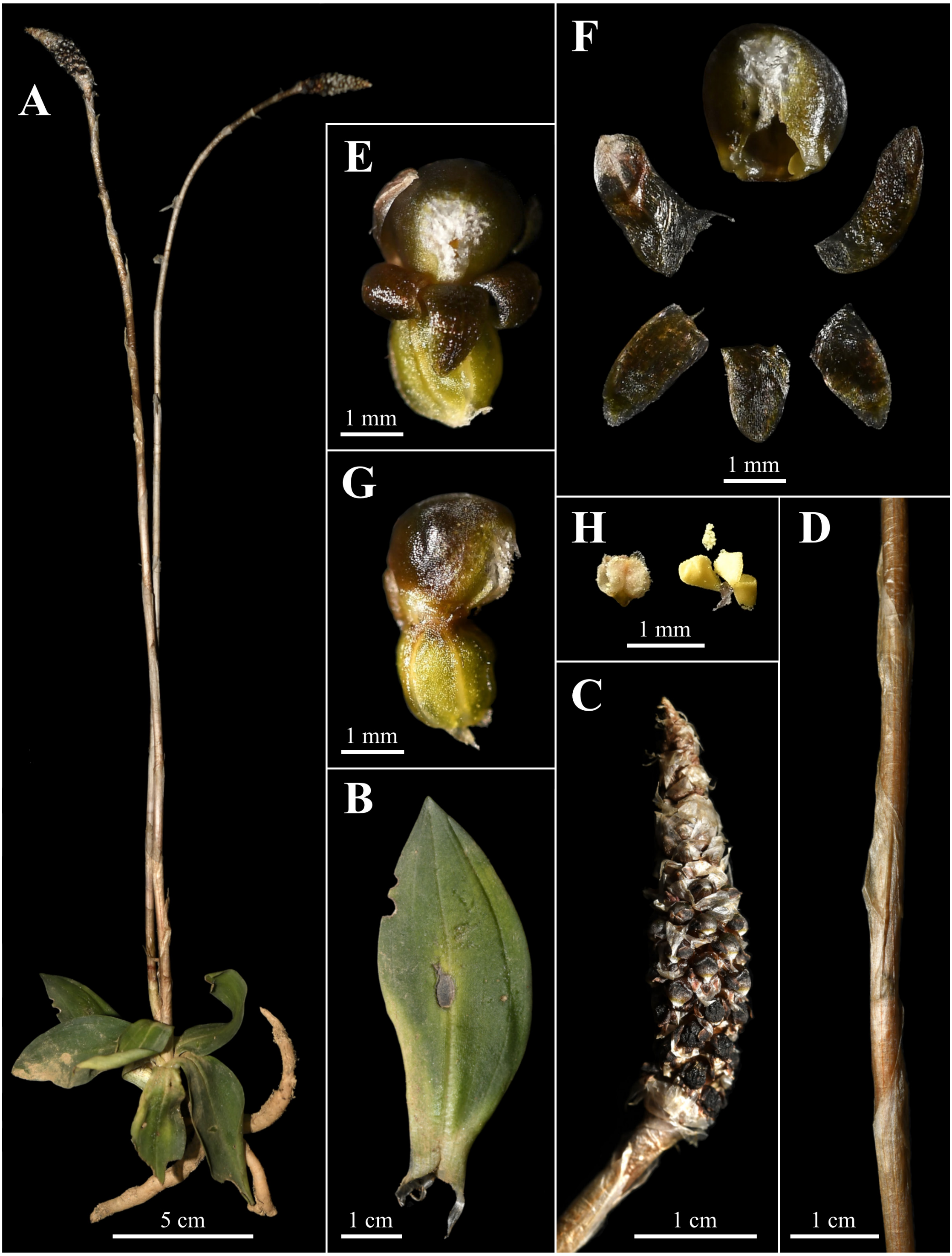

FIGURE 2. *Aa olivacea* (from *Edquén 6943*). **A**. Habit. **B**. Leaf. **C**. Inflorescence. **D**. Peduncle. **E**. Flower, front view. **F**. Dissected perianth. **G**. Lip and ovary, side view. **H**. Anther and pollinarium. Photographs by J.D. Edquén.

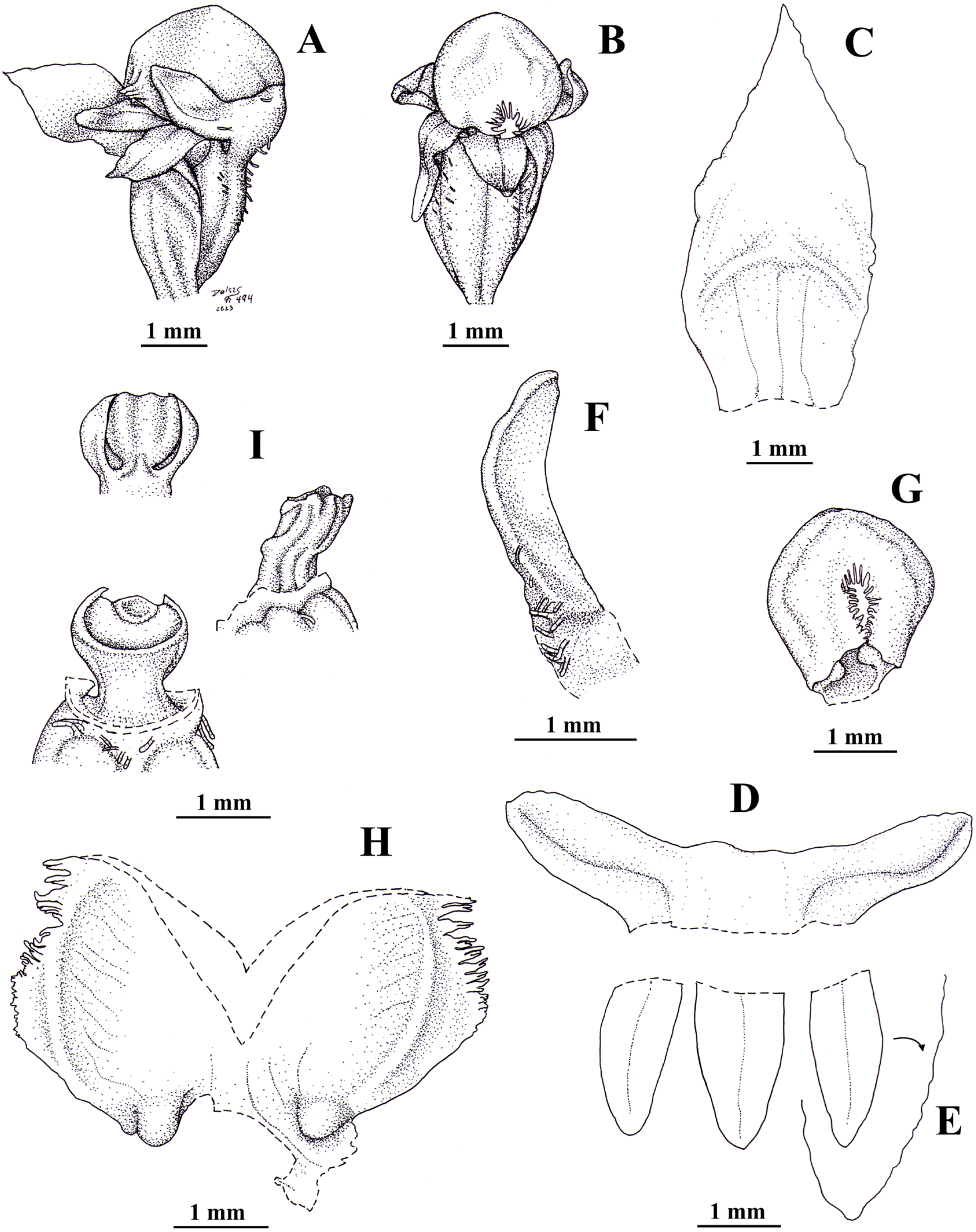

Figure 3. *Aa olivacea*. **A**. Flower, side view. **B**. Flower, front view. **C**. Floral bract. **D**. Dissected perianth. **E**. Detail of petal margin. **F**. Lateral sepal, dorsal view. **G**. Lip, adaxial view. **H**. Lip spread out, adaxial view. **I**. Column, dorsal, side and front view. Drawing by D. Trujillo, based on *Fernandez-Hilario et al. 2459*, MOLF000170.

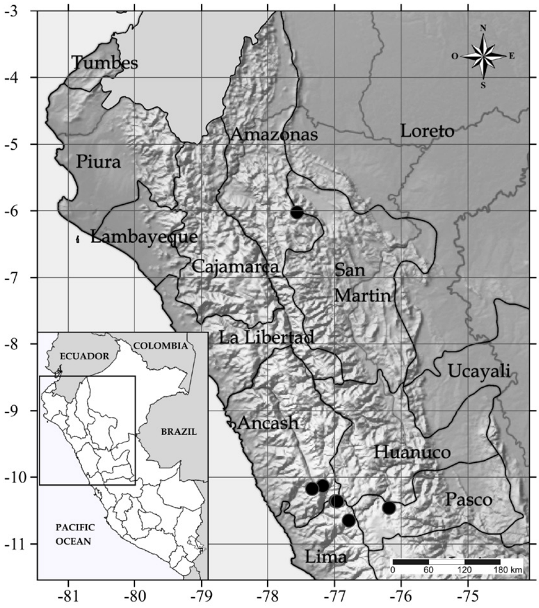

Figure 4. Distribution map of *Aa olivacea* (black circles) in Peru. Created by D. Trujillo.

Jun 2015, *R. Ripley s.n.* (Ripley, 2015a); province of Bolognesi, -10.127963° lat.; -77.177267° lon.,14 Jun 2015, *R. Ripley s.n.* (Ripley, 2015b); province of Bolognesi, -10.17151° lat., -77.337193° lon., 16 Jun 2015, *R. Ripley s.n.* (Ripley 2015c); Department of Lima, province of Cajatambo, -10.359417° lat., -76.961656° lon., 21 Jun 2023, *Chauncey s.n.* (Chauncey, 2023).

Etymology: From the Latin *olivaceus*, referring to the olive-green color of the flowers.

Distribution: Known only from the Peruvian Andes, in the Ancash, Lima, Pasco, and San Martin departments, at elevations of 3200 to 3740 m (Fig. 4).

Habitat and ecology: Terrestrial in wet grasslands (jalca) and shrublands, among rocks on stony hillsides (Fig. 5A–B). In the San Martin location, the grassland reaches 50 cm height, with abundant ferns and *Puya* sp. (Bromeliaceae), scattered shrubs of *Brachyotum* sp. (Melastomataceae), *Senecio* sp. (Asteraceae), and herbs such as *Gentiana* sp. (Gentianaceae), *Rockhausenia nubigena* (Kunth) D.J.N.Hind (Asteraceae), and orchids of the genera *Elleanthus* C.Presl, *Pachyphyllum* Kunth, and *Stelis* Sw. in rocky areas. At Oyón, Lima, the species was recorded in shrublands on slight to moderate slopes dominated by *Alonsoa meridionalis* (L.f.) Kuntze (Scrophulariaceae), *Austrocylindropuntia subulata* (Muehlenpf.) Backeb. (Cactaceae), *Baccharis buxifolia* (Lam.) Pers., *B. tricuneata* (L.f.) Pers. (Asteraceae), *Monnina salicifolia* Ruiz & Pav. (Polygalaceae), *Proustia berberidifolia* (Cuatrec.) Ferreyra (Asteraceae), and *Satureja revoluta* (Ruiz & Pav.) Briq. (Lamiaceae).

In the population of Lima, we observed a cellophane bee, *Colletes* sp. (Colletidae), visiting the flowers of *A. olivacea*. The bee apparently searched for nectar by inserting its proboscis into the lip of the flower (Fig. 5C–D). Celophane bees have also been recorded visiting flowers of *Aa weddelliana* (Rchb.f.) Schltr. in Lomas de Amara, department of Ica, Peru (D. Trujillo, pers. obs.). These floral visits, along with the evidence of protandry from anatomical studies of *Aa erosa* (Rchb.f.) Schltr. (Trujillo, Franke & Agerer. 2011), suggest that *A. olivacea* may be a cross-pollinating species.

Phenology: Flowering occurs in the field from April to August. Developing capsules were observed at the bottom of the spikes in all the specimens examined.

Conservation status: *Aa olivacea* is endemic to the central-northern Peruvian Andes. It is known from six locations: five in the central departments of Ancash, Lima, and Pasco, and one in the northeastern department of San Martin. The main threats to the species are habitat loss and degradation due to land conversion for agriculture, overgrazing, and the traditional practice of burning of grasses on hillsides by farmers (Roman *et al.*, 2024). Two of the populations were recorded within protected areas: Bosque de Protección Alto Mayo and Private Conservation Area Huallapa, which are expected to effectively protect the habitat of these respective populations. Based on the six known locations, the estimated Extent of Occurrence is 31,176.781 km^2, but the Area of Occupancy is only 28 km^2. However, considering the large areas of potential habitat between the central and northern populations, further research is expected to record new populations in the departments of Amazonas, La Libertad, and northern Ancash. Therefore, the species is assessed as Near Threatened (IUCN, 2012, 2024).

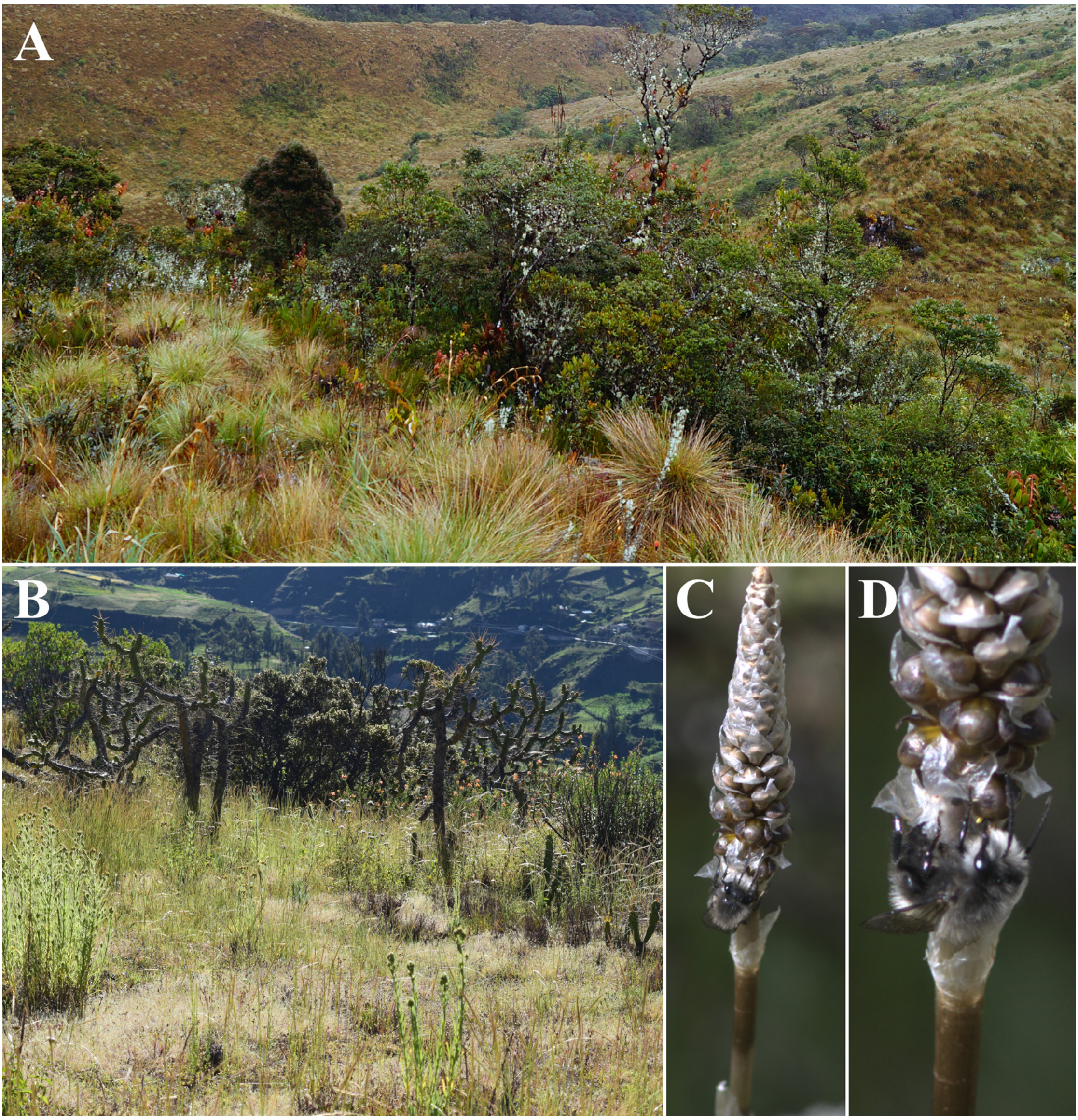

FIGURE 5. *Aa olivacea*. **A**. Habitat in San Martin. **B**. Habitat in Lima. **C**. Cellophane bee visiting flowers. **D**. Cellophane bee inserting its proboscis into the lip. Photographs by J.D. Edquén (A), R. Fernandez-Hilario (B) and A. A. Wong Sato (C, D).

TAXONOMIC COMMENTS: The combination of morphological characteristics with the flower coloration makes specimens of *A. olivacea* readily distinguishable from those of all other species of the genus (Fig. 1–2). The olive green to chestnut brown color of its flowers turns dark brown to black when old and dried (Fig. 1B); whereas other *Aa* species, that have white, white and green or brownish white color flowers turns light brown to brown colors when old and dried; this feature distinguishes the species from others in herbarium collections. The new species is similar to *A. hieronymi* from northern Argentina (Fig. 6). Both species display dense spikes of dark green to brown flowers that turn black in old (and dried) flowers, with translucent, whitish floral bracts, lateral sepals spreading and perpendicular to the floral axis, and a globose, slightly inflexed lip. However, *A. olivacea* is recognized by its elliptic

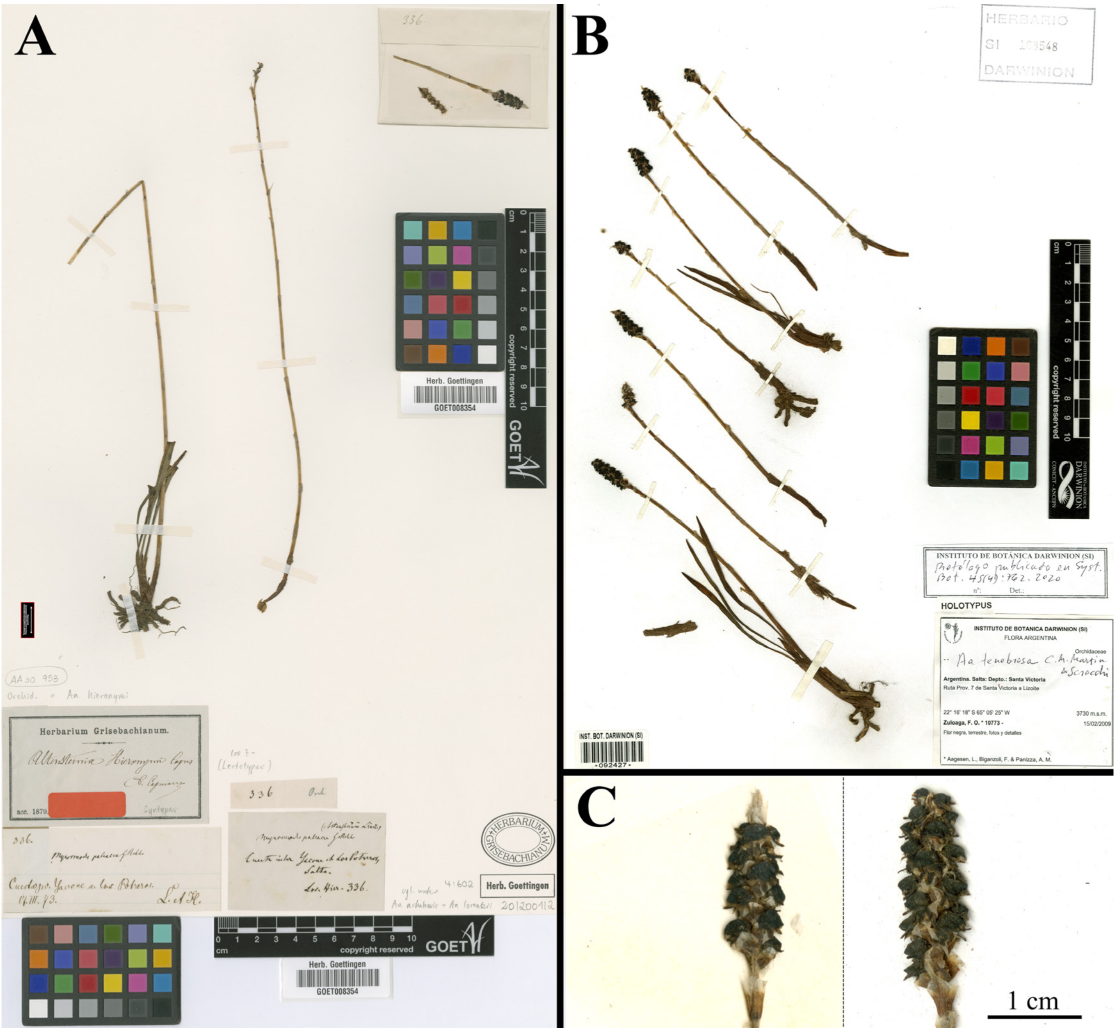

FIGURE 6. Type specimens of *Aa* from Argentina. **A**. Lectotype of *Aa hieronymi* (GOET008354). **B**. Holotype of *Aa tenebrosa* (SI092427). **C**. Close-up of inflorescences of *A. hieronymi* (left) and *A. tenebrosa* (right). Reproduced with the kind permissions of the herbaria of the University of Göttingen (A), and the Instituto de Botánica Darwinion (B).

to lanceolate leaves (*vs*. linear-lanceolate), 60 to 100-flowered spikes, (*vs*. 7 to 25-flowered spikes), a glabrous rachis (*vs*. pubescent), olive green to chestnut brown flowers (*vs*. emerald green to brown), lateral sepals with the margin entire to occasionally minutely erose near the apex (*vs*. apical margin slightly serrate), petals with the apical margin slightly erose to sinuate (*vs*. apical margin slightly serrate), an unlobed lip with lacerate to erose margin (*vs*. obscurely trilobed lip with deeply laciniate margins), and ovary with scarce hairs especially in the distal half (*vs*. many hairs distributed over almost all the ovary).

Aa nigrescens also has a densely many-flowered spike whose flowers turn black upon drying; it was described by Schlechter (1920a) from Cauca, Colombia, based on *Madero 26* (holotype: B destroyed, copy of an analysis based on the type drawing at AMES00000005!). However, this species has narrowly elliptic leaves, larger sepals (3.5–4.0 mm long), erect lateral sepals (*i.e*. not spreading), obliquely ligulate and larger petals (3.5 mm long), and erect, larger lip (*ca*. 4 mm long).

Comments on other *Aa* species with dark green flowers that turn black upon drying

Aa hieronymi (Cogn.) Schltr., Repert. Spec. Nov. Regni Veg. 11: 150. 1912.

Basionym: *Altensteinia hieronymi* Cogn., Fl. Bras. (Martius) 3(4): 245. 1895.

TYPE: Argentina. Province of Salta: cuesta entre Yacone y Potreros, Mar 1873, *P. G. Lorentz & G. Hieronymus 336* (holotype: B, destroyed; lectotype (first step designated by Schlechter 1920c: 438, second step designated by *Martín, Zanotti & Scrocchi* 2020): GOET008354 [mixed] [photo seen]; isolectotype: CORD 00002206 [photo seen]).

Aa tenebrosa C.M.Martín & Scrocchi, Syst. Bot. 45(4): 762. 2020. *syn. nov.*

TYPE: Argentina. Province of Salta: department of Santa Victoria, Ruta Provincial 7, de Santa Victoria a Lizoite, 22°16’18”S, 65°05’25”W, 3730 m, 15 Feb 2009, *F. Zuloaga et al. 10773* (holotype: SI092427 [photo seen]; isotypes: CORD [photo seen], CTES0043314).

Cogniaux (1895) described *Altensteinia hieronymi* citing seven specimens (syntypes): *P. G. Lorentz & G. Hieronymus 336, P. G. Lorentz & G. Hieronymus 617, F. Schickendantz 264, G. Hieronymus s.n., G. Hieronymus s.n.*, *G. Hieronymus 796*, and *O. Schnyder 598.* Later, Schlechter (1912) transferred *Altensteinia hieronymi* to the genus *Aa*, and subsequently, Schlechter (1920b, c) proposed three new species based on various of Cogniaux’s (1895) syntypes: *Aa achalensis* Schltr. (*G. Hieronymus 796*), *Aa lorentzii* Schltr. (*P. G. Lorentz & G. Hieronymus 617*), and *Aa schickendanzii* Schltr. (*F. Schickendantz 264*). Schlechter explicitly designated the specimen *P. G. Lorentz & G. Hieronymus 336* as the (lecto-)type of *A. hieronymi* and emended the species description, including some comments in German (Schlechter, 1920c). In the last lines, Schlechter pointed out: “… It is one of the few species in which the flowers take on a black color when dried”. Duplicates of the specimen *P. G. Lorentz & G. Hieronymus 336* are housed at GOET and CORD, lectotype and isolectotype, respectively, as designated by Martín *et al.* (2020). The herbarium sheet GOET008354 has two attached specimens, with their spikes placed in the envelope in the upper right-hand corner of the sheet, each representing a different species (Fig. 6A). The specimen on the herbarium sheet that agrees with Schlechter’s description and annotation in German of *A. hieronymi* is the inflorescence on the left (the one bearing leaves), and its spike (within the envelope) is the one with a portion of the peduncle.

Martín *et al*. (2020) published a taxonomic revision of the genus *Aa* from the southern central Andes, including the description of *A. tenebrosa*, a new species from Argentina, based on *F. Zuloaga et al. 10773* (Fig. 6B). They indicated that the dark or brownish green flowers of *A. tenebrosa*, in combination with other features, distinguish this species from other members of *Aa.* Nonetheless, it seems that Martin *et al*. (2020) overlooked Schlechter’s comment about the black flowers upon drying of *A. hieronymi*, similar to those of *A. tenebrosa*, as they did not mention it.

Aa tenebrosa shows all the features of *A. hieronymi*, except for having shorter peduncles. Both species have dense and short spikes with relatively few flowers (compared to other species of the genus), pubescent rachis, oblong and obtuse lateral sepals, and lobed, transversely elliptic lip when viewed from the side (in dried flowers; Fig. 6C). The lip of *A. tenebrosa* is 3-lobed (see color photograph of the type in IBODA, 2023), whereas Schlechter (1920c) described the lip of *A. hieronymi* as “sub 5-lobed” (probably and artifact during flower dissection). Due to the similarities noted above, we determined that *A. tenebrosa* is a synonym of *A. hieronymi*.

Aa leucantha (Rchb.f.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 213. 1920.

Basionym: *Altensteinia leucantha* Rchb.f., Flora 69: 548. 1886.

TYPE: [north Ecuador, on moist, boggy ground on the Páramo del Mojanda, 3300 m, 28 Jan 1881. *Lehmann 247*] (holotype: W0302214/W-R 612!) (Fig. 7–8.)

Aa lehmannii Rchb.f. ex Szlach. & Kolan., Ann. Bot. Fenn. 51(5): 330. 2014. *nom. illeg. superfl.*

TYPE: Ecuador. Páramo del Mojanda: 3300 m. 28 Jan 1881, *Lehmann 247* [“*244*” in error] (holotype: W0302214/W-R 612!).

FIGURE 7. Holotype of *Aa leucantha* (W0302214). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum Wien.

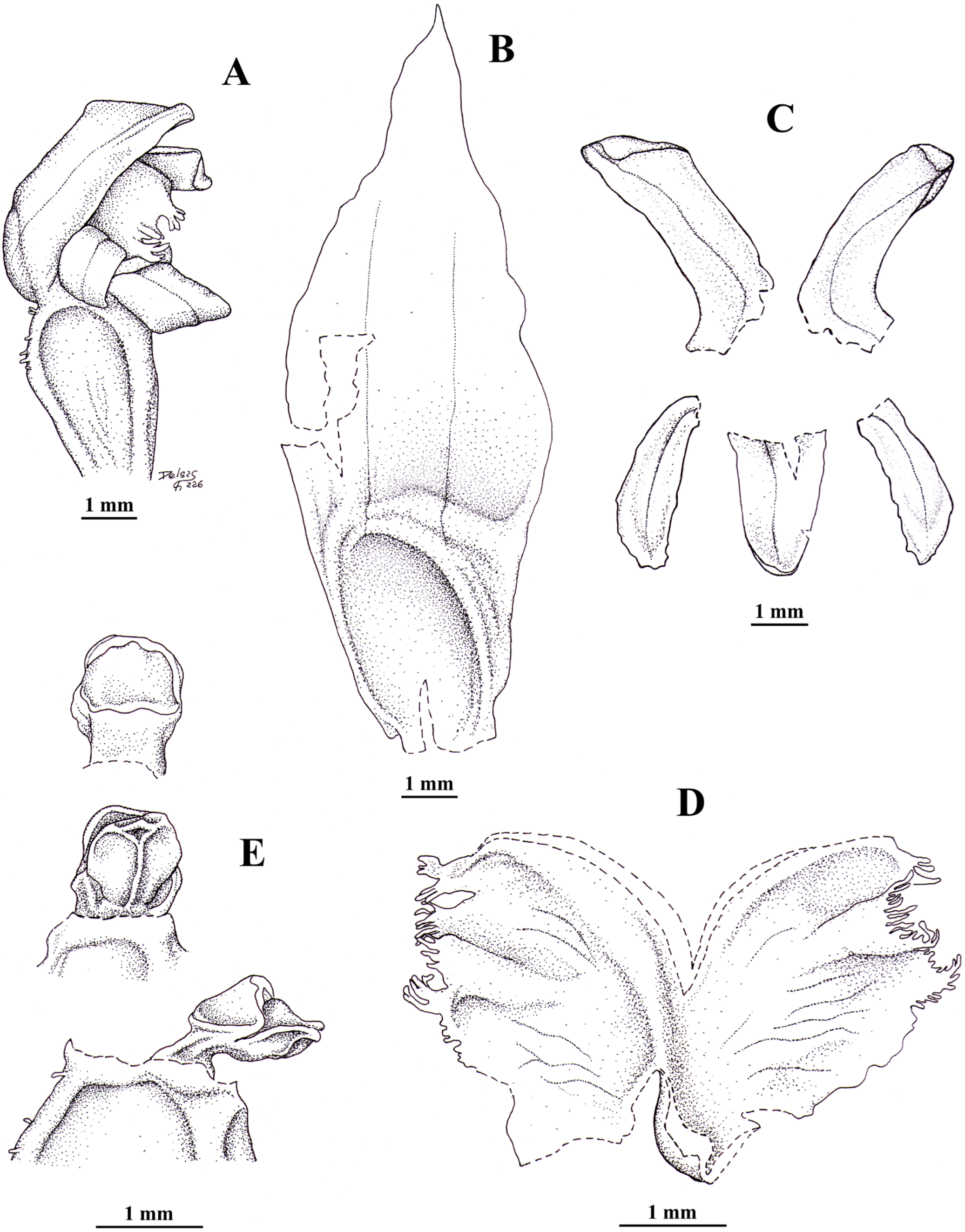

Figure 8. *Aa leucantha*. **A**. Flower, side view. **B**. Floral bract. **C**. Dissected perianth. **D**. Lip, spread out. **E**. Column, front, dorsal, side view. Drawing by D. Trujillo, based on *Lehman 247* (W0302214).

In the protologue of *Altensteinia leucantha* Rchb.f. (the basionym of *A. leucantha*), Reichenbach did not indicate the specimen on which he based the description. However, in the Reichenbach herbarium at W, there is a sheet containing an *Aa* specimen (composed of four inflorescences), a flower illustration, and two (original) labels. One label, in F.C. Lehmann's handwriting, bears the number "*247*" and collection data (Fig. 7). The second label, in Reichenbach's handwriting, indicates: "*Altensteinia* (*Aa*) *lehmanni* […]" followed by a description that agrees with the original description of *Altensteinia* (*Aa*) *leucantha*. Garay, in his work on Orchidaceae in Flora of Ecuador (1978), referred to the specimen *Lehman 247* as the type of *A. leucantha*, and we agree.

Szlachetko and Kolanowska (2014) proposed *Aa lehmannii*, based on *Lehmann 244*, a specimen from Reichenbach's collection at W. The illustration published in their Fig. 1, indicated as having been drawn by A. Kröl, was originally prepared by D. Szlachetko in February 2009. A copy of Szlachetko's drawing, kept at W with collection number 2009-001251 (W-0302213)!, includes an annotation on the upper right-hand corner stating "WR-612"; which is, in fact, the Reichenbach Herbarium's sheet number of specimen *Lehmann 247*, the type specimen of *A. leucantha*. Therefore, *A. lehmannii* is an illegitimate, superfluous name for *A. leucantha* because both names were based on the same specimen (Shenzhen Code Art. 52.1 in Turland *et al.*, 2018).

Garay (1978) considered *A. nigrescens* a synonym of *A. leucantha*; however, we consider them to represent different species. *Aa nigrescens* can be distinguished by its flowers, which are drying black (*vs*. dark brown), an oblong to elliptic dorsal sepal 3.5 mm long (*vs*. ovate, 2.1–3.0 mm long), obliquely lanceolate lateral sepals (*vs*. obliquely obovate to oblong), obliquely ligulate petals with an entire margin (*vs*. obliquely elliptic to lanceolate or oblong with apical margin slightly erose to sinuate), and an obscurely pilose ovary from the middle to the apex (*vs*. sparsely pilose ovary only near its junction with the lateral sepals).

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Author contribution. DT: taxonomic treatment, writing, review and editing. JDE: collection and photography of plant material. RFH: writing, review, editing, collection and photography of plant material. AAWS: review, editing and collection and photography of Celophane bees and plant material. GAS: Taxonomic treatment, writing, review and editing.

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Conflict of interest. The authors declare no conflict of interest.

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PLEUROTHALLIS COP-BIODIVERSITATIS (PLEUROTHALLIDINAE), A NEW SPECIES FROM COLOMBIA

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Abstract. A new species, *Pleurothallis cop-biodiversitatis*, belonging to *Pleurothallis* subsection *Macrophyllae-Fasciculatae*, from the Central Andes of Colombia, is described and illustrated. This new species is compared with *Pleurothallis matudana* and *Pleurothallis tandapiensis*, the most morphologically similar species. *Pleurothallis cop-biodiversitatis* primarily differs from these species in having a lip with erose margins, more pronounced basal lobes, a rounded, apiculate apex, and a sulcate blade with a lanceolate, strongly vesiculate concavity.

Resumen. Una nueva especie, *Pleurothallis cop-biodiversitatis*, perteneciente a la subsección *Macrophyllae-Fasciculatae* de *Pleurothallis*, de los Andes Centrales de Colombia, es descrita e ilustrada. Esta nueva especie se compara con *Pleurothallis matudana* y *Pleurothallis tandapiensis*, que son las especies morfológicamente más similares. *Pleurothallis cop-biodiversitatis* se diferencia principalmente de estas especies por tener un labelo con márgenes erosos, lóbulos basales más pronunciados, un ápice redondeado y apiculado, y una lámina sulcada con una concavidad lanceolada y fuertemente vesiculada.

Keywords / Palabras clave: Andean orchids, COP16, Epidendreae, *Macrophyllae-Fasciculatae*, orquídeas andinas, *Pleurothallis matudana*, *Pleurothallis tandapiensis*, Tolima

Introduction. *Pleurothallis* R.Br. (Brown, 1813) is notable for its remarkable diversity, being the fourth-largest genus in species richness within the subtribe Pleurothallidinae, with more than 528 recognized species (Karremans, 2016; Karremans & Vieira-Uribe, 2020; Sierra-Ariza, 2023). Despite its more refined circumscription (Pridgeon, 2005), the genus' high species diversity and morphological similarity have led to complexes that complicate species delimitation. The monographs on *Pleurothallis* (Luer, 1989, 1998, 1999, 2005) have significantly increased the number of recognized species in recent decades (Karremans & Davin, 2017). However, these works often treated morphological complexes as taxonomic units with consistent morphology and broad geographical ranges, underscoring the need to further clarify species boundaries within the genus (Wilson *et al*., 2017).

Pleurothallis is widely distributed from Mexico to South America, including the Caribbean islands. Colombia is one of the countries with the highest number of species, with 247 recorded (Bernal *et al.*, 2016, Karremans *et al.*, 2023, Ministerio de Ambiente y Desarrollo Sostenible y Universidad Nacional de Colombia, 2015). The genus is generally characterized by epiphytic plants, which are cespitose to creeping, with erect stems—rarely pendant—and sometimes leathery leaves. The inflorescences mostly have an abbreviated peduncle, with single or multi-flowered clusters, either simultaneous or successive, bearing resupinate or non-resupinate flowers (Pridgeon, 2005; Rojas-Alvarado & Karremans, 2024).

The species of the *Macrophyllae-Fasciculatae* subsection are morphologically distinguished by having leaves with rounded or cordate bases, solitary flowers in fascicles, lateral sepals connate into a synsepal similar to the dorsal sepal, a bilobed stigma, and a lip reclined over the synsepal or slightly elevated above it (Lindley, 1859; Luer, 2005; Sierra-Ariza *et al*., 2022; Wilson *et al*., 2018). This subsection is one of the most diverse within the genus and has significantly increased in species numbers in recent decades. Luer (2005) recognized 213 species, and Wilson *et al.* (2018) mentioned between 239 and 309 species depending on the taxonomic treatment.

Here, a new species of the genus *Pleurothallis,* subsection *Macrophyllae-Fasciculatae*, is described and illustrated. It is morphologically similar to *Pleurothallis matudana* C.Schweinf. and *P. tandapiensis*

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(Luer & Hirtz) J.M.H.Shaw. This species was found in a fragment of a highly humid premontane cloud forest in the department of Tolima, Colombia.

Materials and methods. The new species was discovered during an expedition conducted in April 2022 in the municipality of Cajamarca, Tolima, Colombia. During this expedition, a single population of this species was found in its natural habitat. Specimens were photographed in detail to record their morphological characteristics, using a D5300 camera equipped with a NIKKOR AF 105mm f/2.8 D Micro lens. Specimens were stored in a newspaper soaked in 75% ethanol, and floral structures were preserved in 50% glycerol (a mixture of glycerin and 70% alcohol). The collected material was dried in an electric oven at 75°C for 14 hours and deposited into the TOLI Herbarium collection. Floral structures were examined using a Motic Series SMZ 168 LED stereoscope.

To confirm the identity of the new species, the specialized literature on the genus was consulted, including monographs on the systematics of *Pleurothallis*, subsection *Macrophyllae-Fasciculatae* (Luer, 1988, 2005; Wilson *et al*. 2011, 2018; Pupulin *et al*., 2021, Sierra-Ariza, 2023; Sierra-Ariza *et al*., 2022). Additionally, specimens were examined online at the AMES (www.huh.harvard.edu) and KEW (apps.kew.org/herbcat/gotoHomePage.do) herbaria, as well as at the national herbaria TOLI, HPUJ, JBB, and COL (www.biovirtual.unal.edu.co/es/colecciones/búsqueda/plantas/). A Lankester Composite Digital Plate (LCDP) was created using Adobe Photoshop® 2024 (25.3.1), and illustrations were made using the Procreate illustration app on a seventh-generation Apple iPad.

TAXONOMIC TREATMENT

Pleurothallis cop-biodiversitatis Sierra-Ariza ***sp. nov.*** (Fig. 1).

TYPE: COLOMBIA. Tolima: Municipio de Cajamarca, vereda Bolívar, 2690 m, 13 April 2022, *M. A. Sierra-Ariza & J.C. Pavas 429* (holotype: TOLI).

DIAGNOSIS: Species similar to *Pleurothallis matudana* C.Schweinf., but distinguished by the lip with erose margins, more pronounced basal lobes, rounded apex, and longitudinally sulcate with a lanceolate, strongly vesiculose basal concavity.

Plant 9–28 cm tall, erect, epiphytic, caespitose. *Roots* white, slender, flexuous, 0.8–1.2 mm in diameter. *Ramicauls* green, slender, 8.5–27.5 cm long, with two sheaths at the base, papyraceous, light brown. *Leaf* light green, lustrous, coriaceous, ovate to ovate-lanceolate, acuminate, 8–12 × 4–5.5 cm, the base sessile, cordate, deeply 2-lobed, with slightly imbricate lobes. *Inflorescence* with a reduced peduncle, enclosed by a broad, reclining, 1.2 cm long spathe, producing single-flowered; *coflorescences* more than 5 at a time; *pseudopeduncle* terete, green, 7–9 mm long; *floral bracts* tubular, papyraceous, acute, 6–8 mm long. *Ovary* light green with minute black dots, glandular-papillate, cylindrical, longitudinal sulcate, 3.6 mm long, *pedicel* terete, up to 7.5 mm long. *Flowers* resupinate. *Sepals* membranaceous, glandular-papillate on the adaxial surface, margins minutely erose. *Dorsal sepal* yellow with some red hues, broadly ovate, acute, concave, 6.9–7.3 × 3–3.4 mm, 3-veined. *Lateral sepals* yellow, connate into an ovate, rounded, concaves synsepal, 6.0–6.4 × 4.8–5.2 mm, 6-veined. *Petals* yellowish red, linear, slightly glandular-papillose, microscopically denticulate, acute, 3.8–4.2 × 0.5–0.8 mm, 1-veined. *Lip* yellow with white hues due to its texture, oblong-ovate, somewhat curved, papillose, with a subcordate base forming two rounded, prominent defined lobes, slightly concave in the base, margins strongly erose, 3.8–4.2 × 2–2.4 mm; the basal sulcus of the lip forms a lanceolate concavity, which is strongly vesiculated and occupies ¾ of the basal length of the lip, surrounding the glenion; glenion rounded to sub-hexagonal cavity and slightly emarginate at the apex, 0.6 × 0.5 mm. *Column* white with yellow hues, stout, 1.8 ×1.4 mm, the foot thick; stigma apical, bilobed. *Anther cap* red, apical, obovate, minutely papillose, 0.4 × 0.5 mm. *Pollinia* 2, yellow, obovoid. *Capsule* not seen.

ETYMOLOGY: In commemoration of COP 16, held in Cali, Colombia, in 2024, where the importance and status of biological diversity conservation, the adoption of new environmental policies, habitat conservation, climate change mitigation, and international cooperation for nature protection were discussed. The name also honors the nations and people who participated in this significant conference. The specific epithet is derived from the abbreviation COP (Conference of the Parties) and the Latin genitive *biodiversitatis*, which translates to 'of biodiversity,' reflecting the main theme of the event.

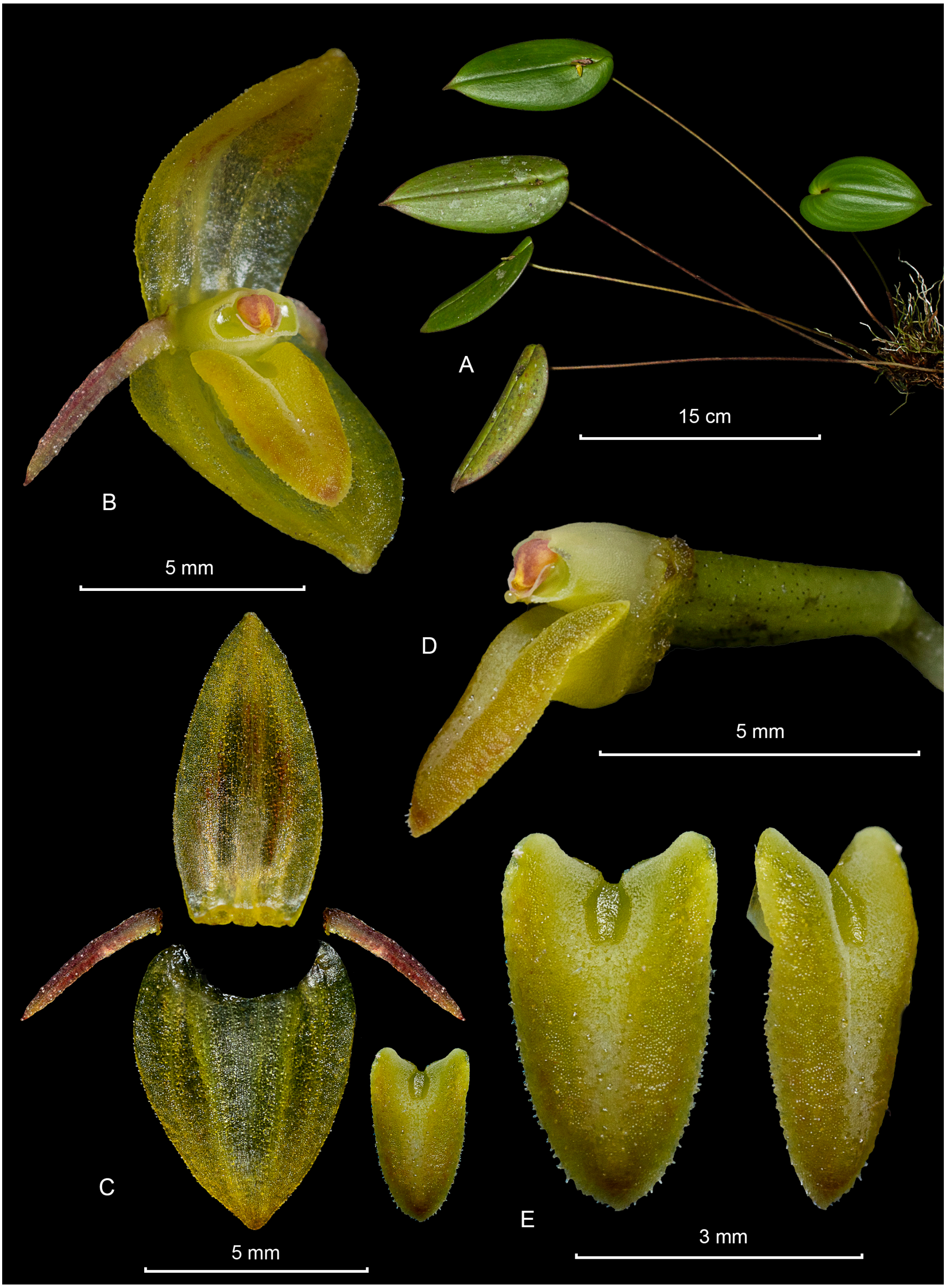

FIGURE 1. *Pleurothallis cop-biodiversitatis* Sierra-Ariza. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Lip and column lateral view. **E**. Lip. LCDP by Sierra-Ariza based on type.

Phenology: The species has been observed blooming in its natural habitat during April and September.

Distribution: To date, this species has only been recorded on the eastern slope of the Central Andes mountain range in Colombia (Pinilla & Pino, 2002), specifically in the forests of the Cajamarca municipality, in the department of Tolima.

Habitat and ecology: The new species was discovered at elevations ranging between 2650 and 2800 m, growing as an epiphyte. It inhabits small remnants of highly humid premontane cloud forests (bmh-PM) (Holdridge, 1967), which are heavily degraded and surrounded by agricultural lands used for livestock and crops. The area has been designated for open-pit gold mining (Contreras-Santos *et al*., 2022; Molina Ríos & Rodríguez Nuñez, 2020; Sánchez-García, 2013).

This zone is characterized by predominantly mountainous terrain, with steep slopes exceeding a 50% gradient. Environmental conditions include annual precipitation of 2500 to 2800 mm, an average yearly temperature of 12 to 18 °C, and an average relative humidity of 83% (Pinilla & Pino, 2002). The higher mountain areas are covered by a fog belt for most of the year, significantly contributing to condensation water and influencing drainage flow and perennial streams. The vegetation is rich in bryophytes and other epiphytic plants (Contreras-Santos *et al.*, 2022; Molina Ríos & Rodríguez Núñez, 2020).

Discussion. *Pleurothallis cop-biodiversitatis* is morphologically similar to *P. matudana* but differs in having sepals with erose margins (*vs*. entire); the dorsal sepal is elliptical, concave, and significantly wider than the synsepal, measuring 3.0–3.4 mm wide (*vs*. ovate, more concave, nearly as wide as the synsepal, 4.0–5.7 mm wide); the petals are straight, inclined toward the ovary, with minutely denticulate margins, measuring 3.8–4.2 × 0.5–0.8 mm (*vs*. falcate, inclined downward, running parallel to the margins of the synsepal, minutely crenulate, 5–7 × 0.5–0.9 mm). The lip is slightly curved, extending parallel to the synsepal, 3.8–4.2 × 2–2.7 mm (*vs*. strongly curved, with the apex directed toward the synsepal, 4–6 × 2.0–2.7 mm), with prominent and well-defined basal lobes (*vs*. short and poorly defined), erose margins (*vs*. minutely crenulate), a rounded apex (*vs*. acute), and a lanceolate, strongly vesiculate sulcus occupying ¾ of the basal length of the lip (*vs*. an oblong, papillose sulcus reaching the apex), and a small, suborbicular glenion (*vs*. larger, oblong).

Pleurothallis cop-biodiversitatis also shares morphological characteristics with *Pleurothallis tandapensis*, but differs in having linear petals that are straight, with microscopically denticulate margins, measuring 3.8–4.2 × 0.5–0.8 mm (vs. linear-oblong, falcate, with strongly denticulate margins, 5.5 × 1 mm); a lip that is the same length as the petals, ovate-oblong, and rounded, measuring 3.8–4.2 × 2–2.7 mm (vs. shorter than the petals, ovate, obtuse, 3.8–4.2 × 2.0–2.7 mm); and a lanceolate sulcus occupying ¾ of the basal length of the lip (vs. subpandurate and partial) (Fig. 2).

Taxonomic note: *Pleurothallis cop-biodiversitatis* belongs to a poorly known species complex characterized by distinctive morphological traits, of which only two species are currently recognized: *P. matudana* and *P. tandapiensis*. The new species could be mistaken for other morphologically distinct species from the Andes, such as *Pleurothallis coriacardia* Rchb.f., *P. phyllocardioides* Schltr., and *P. cordata* (Ruiz & Pav.) Lindl., among others. However, it is distinguished by its lip with erose margins, more pronounced basal lobes, a rounded apex, and a longitudinally sulcate blade with a lanceolate, strongly vesiculate basal concavity.

Acknowledgements. I thank Juan Camilo Pavas for his participation in the field trips during which the new species were discovered; Mark Wilson for his valuable taxonomic insights on the genus *Pleurothallis*; Patricia Harding for her support in writing this manuscript; and Franco Pupulin for his nomenclatural observations. Finally, we extend our gratitude to the University of Tolima for supporting this research under the collection permit granted by resolution #000009 of the National Environmental Licensing Authority (ANLA) and to the TOLI Herbarium for allowing us to deposit the type specimens in their collection.

Author contribution. MSA was responsible for the entire article and figures.

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Conflict of interest. The author declares no conflicts of interest related to this article.

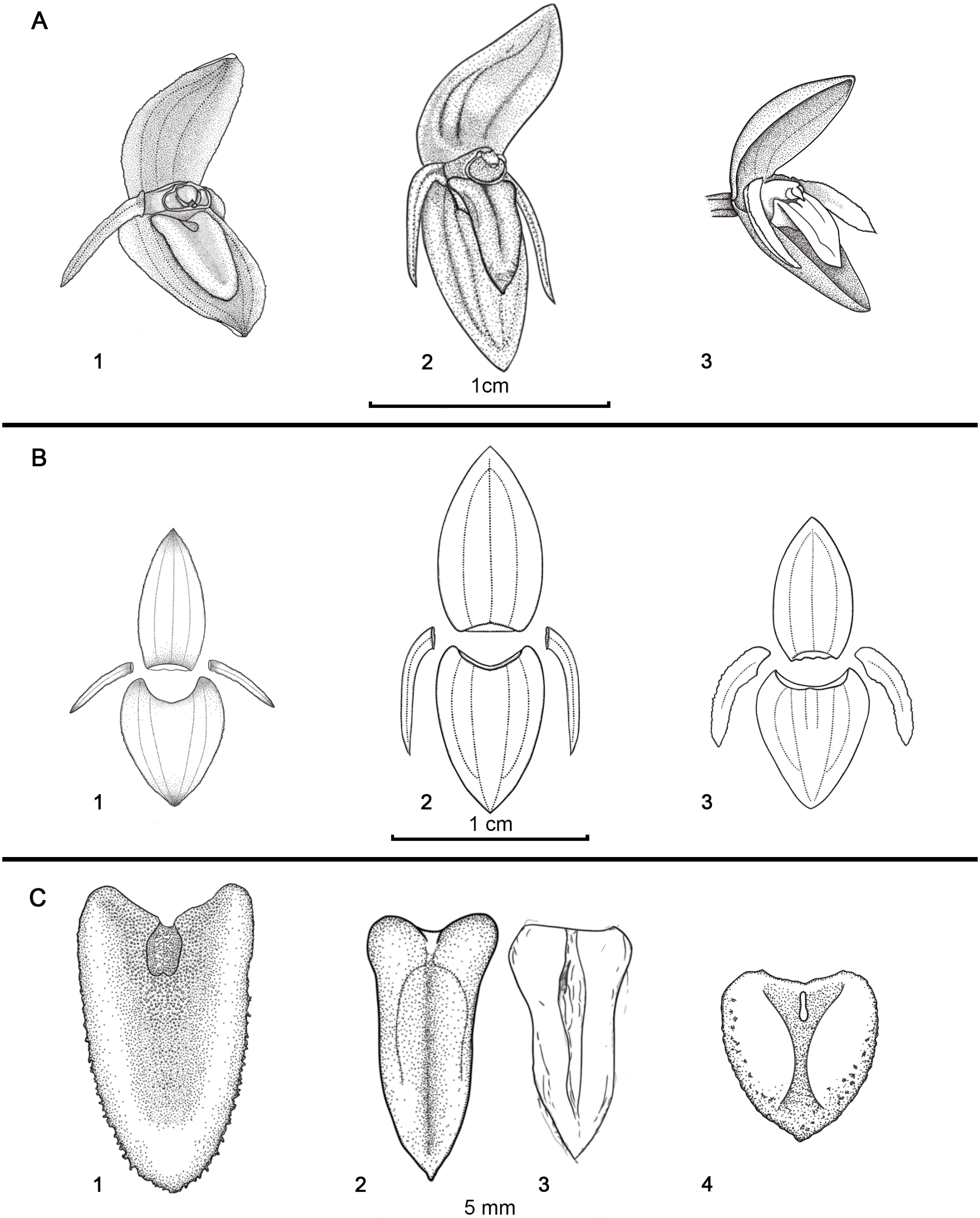

Figure 2. Morphological comparison of the flower (A), sepals and petals (B), and lip (C), between *Pleurothallis copbiodiversitatis* Sierra-Ariza (A1, B1, C1), *Pleurothallis matudana* C.Schweinf. (A2, B2, C2–3), and *Pleurothallis tandapiensis* (Luer & Hirtz) J.M.H.Shaw (A3, B3, C4). Redrawn by Sierra-Ariza: A1, B1, and C1 based on the holotype (TOLI [*M. A. Sierra-Ariza 429*]); A2, B2, and C2 based on a drawing by Rolando Jiménez (AMO [*Soto Arena 3230*]); C3 based on the holotype (AMES [*E. Matuda 1577*]); and A3, B3, and C4 based on a drawing of the holotype by C. Luer (MO [*C. Luer, J. Luer & A. Embree 12066*]).

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NEW DISTRIBUTION RECORDS AND RANGE EXTENSIONS FOR THREE SUMATRAN ORCHID SPECIES IN KALIMANTAN, BORNEO, INDONESIA

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ABSTRACT. Borneo, one of the largest and most biodiverse islands in the world, continues to reveal remarkable biological discoveries. Its unique geological history and the relatively limited extent of botanical exploration have contributed to the island's enigmatic flora. During our expedition across three provinces in Kalimantan, Borneo, Indonesia, we discovered three orchid species previously unrecorded on this mainland. Based on comprehensive specimen examination and literature review, three Sumatran orchid species, *Eria compressoclavata*, *Oxystophyllum cuneatipetalum*, and *Plocoglottis quadrifolia*, are reported for the first time from Kalimantan. This study provides detailed morphological descriptions, notes on the expanded distributional ranges, ecological observations, and high-resolution photographic documentation for each species.

KEYWORDS / PALABRAS CLAVE: Distribución, Distribution, Flora de Malasia, Flora Malesia, New Record, nuevos registros, Orchidaceae

Introduction. Borneo serves as an invaluable natural laboratory for botanists, with Sabatini *et al.* (2022) highlighting the island's extraordinary plant diversity. The geological and geographical conditions of Borneo have contributed to its status as one of the regions with the highest orchid diversity in the world (Hassler & Rheinheimer, 2020; Rafiqpoor *et al.*, 2005; Wood & Cribb, 1994). This island spans three countries: Malaysia, Brunei Darussalam, and Indonesia. According to Juiling *et al.* (2020) the center of orchid diversity and endemicity in Borneo is primarily located in Sabah, Malaysia. Another significant area for orchid exploration is the Heart of Borneo (HOB), a forest management initiative involving the three countries. Besi *et al.* (2020) identified at least 59 genera of orchids in Sarawak, with the highland region serving as a hotspot for diversity. However, this suggests a gap in research on orchid diversity in other parts of Borneo, particularly Kalimantan, Indonesia.

Recent discoveries of new orchid species across various regions of Kalimantan indicate that many areas remain unexplored. Notable new species include *Bulbophyllum pulanense* Yudistira, F.H.Kurniawan & Mustaqim, *B. sapathawungense* Yudistira, R.P.P.Ahmad & Mustaqim, *B. sungaiutikense* F.H.Kurniawan, Yudistira & Mustaqim, *Phalaenopsis kapuasensis* Metusala & P.O'Byrne, and *Trichoglottis najibii* Yudistira & Mustaqim are new species to science found in West and East Kalimantan. Meanwhile, *Bulbophyllum abangjoei* Rusea, Besi & Pungga and *B. lyriforme* J.J.Verm. & P.O'Byrne, previously only known from Sarawak and Papua, have now been recorded in Kalimantan (Kurniawan *et al.*, 2022; Metusala, 2017; Yudistira *et al.*, 2022, 2023, 2024).

Between 2018 and 2024, during field research in the provinces of South, Central, and West Kalimantan, we collected terrestrial and epiphytic orchid specimens from lowland dipterocarp forests and karst areas. Three species previously reported only in Sumatra (Comber, 2001; POWO, 2023) have now been newly recorded from Kalimantan: *Eria compressoclavata* J.J.Sm. (endemic to Sumatra; Sungai Liat, Bangka

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Island, and Jambi), *Oxystophyllum cuneatipetalum* (J.J.Sm.) M.A.Clem. (native to Sumatra), and *Plocoglottis quadrifolia* J.J.Sm. (in Indonesia, it is only known from Sumatra).

Materials and methods. The specimens examined were collected during botanical explorations conducted between 2018 and 2024 in three Kalimantan provinces, Indonesia: South Kalimantan, Central Kalimantan, and West Kalimantan. The comparative morphological study was based on examinations of living plants, dried specimens, and spirit specimens preserved in 70% ethanol, stored at WAN (Herbarium Wanariset, Institute of Research and Development for Natural Resource Conservation Technology, Balikpapan, Kalimantan Timur, Indonesia) and CEB (Herbarium Celebense, Tadulako University). All photographs were taken using a Nikon D5600 body with either a Nikon DX AF-S 40 mm f/1.2, 8G Micro Nikkor lens or a Nikon D3300 AF-P NIKKOR 18–55 mm lens, and images were post-edited for optimization using Adobe® Photoshop CS6. The terminology used for the morphological descriptions follows Beentje (2016). Identification was accomplished by comparing morphometric characters of fresh specimens with those described in *Orchids of Sumatra* by Comber (2001). The original species descriptions and herbarium studies of digital specimens housed at L, P, and MW (following Thiers, 2021, continuously updated) were accessed via GBIF (2023). Distribution data for each specimen were cross-referenced with Comber (2001) and the species distribution map by POWO (2023). The taxonomic account and colour drawings were prepared from recently collected specimens deposited at WAN. Our identifications were confirmed through consultation with relevant literature, original species descriptions, and distribution maps provided by POWO (2023).

Taxonomic treatment

Eria compressoclavata J.J.Sm. Bull. Jard. Bot. Buit. Ser. 3, 12: 129 .1932.

TYPE: Indonesia. Sumatra: Sungai Liat, Bangka,: without locality, *H.A.B.Bunnemeijer s.n., cult. Hort. Bogor. XII B, IX, 130* (holotype, BO! not seen). (Fig. 1).

Epiphytic perennial *herb*, creeping rhizome, branched. *Stems* elliptic at the base, *ca.* 3 cm bearing stem apart, an acute angle, club shape, oblong to elliptic in cross-section, *ca.* 6–38 × 0.5–1.0 cm. *Leaves* exist only at the upper part of stems, carried 1-3 leaves, single formation, *ca.* 1 cm apart, lanceolate, somewhat oblique, acute apex, *ca.* 6–11 × 1.5–2.0 cm, sessile-narrow at the base, short petioles under 3 mm, green to lime green, entire margin, the veins scarcely conspicuous, glabrous. *Inflorescence* spread from the stem close to the apex, nodding, single flowers with very short peduncles, under 3 mm. *Flower bract* single, dark orange, *ca.* 8–9 × 5–6 mm, entire margin, attenuate apex, glabrous, *flower* widely opened, about *ca.* 2.5 cm, concave. *Ovary* straight, grooved, 13–15 mm long, orange to yellowish, darkening toward the base. *Dorsal sepal* oblong, narrow at the base, shortly and obtuse apiculate, concave around *ca.* 10 × 4 mm, reddish to dark red at the base, pale yellow from the middle to the apex. *Lateral sepal* trapezoid, obtuse, about *ca.* 10 × 8 mm, curve close to the base, reddish to dark red at the base, pale yellow from the middle to the apex. *Petals* oblique obovate-oblong, rounded, around *ca.* 10 × 5 mm broad, dark red at the base, yellowish from the middle to the apex. *Lip* trilobed, recurved 90 degrees in the center, with tree ridges between the side lobes, the middle one much taller, mainly white with some pale yellow suffused with red between the side lobes and some purple on the ridges, side lobes erect, narrowly falcate-triangular, acute, much longer, than the mid-lobe, reddish with yellowish close to the margin, 1 cm from the base to their apices, mid-lobe smaller, shallowly trilobed, the lobules rounded, pale yellow and white to the middle, *ca.* 10 × 5 mm. *Column* curved, *ca.* 12 × 3 mm, concave rounded shaped, yellowish to reddish streaks from apex to the base. *Anther cap ca.* 1 mm, bright yellow and pale-yellow inside. *Pollinia* in four pairs, pale yellow, less than 1 mm in size.

Examined materials: INDONESIA. **Bangka**: L!-image L. 0059847; L!-image L. 0059848. **Central Kalimantan**: Palangka Raya, Puruk Cahu, Kelasin, Sapat Hawung Nature Reserve, 800–1000 m, October 2023, YRY018SH (dried and spirit: CEB!). **South Kalimantan**: Tanah Bumbu, HRB-Mangkalapi, Eastern of Mts. Meratus. 77 m, 22 December 2022, ZBA137231222,

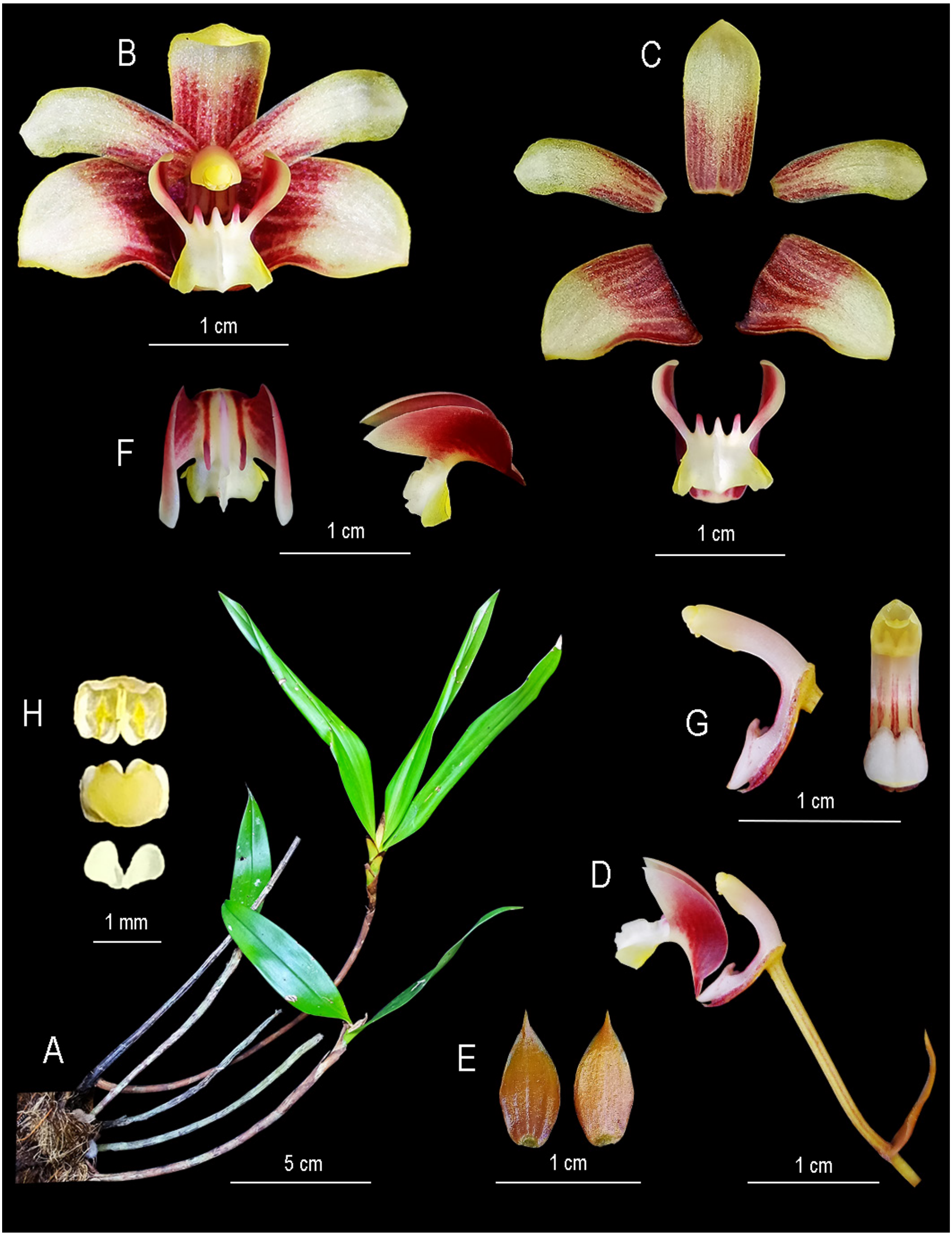

FIGURE 1. *Eria compressoclavata* (J.J.Sm.). **A**. Habit. **B**. Flower (front view). **C**. Perianth dissected. **D**. Column with lip, lateral view. **E**. Floral bract. **F**. Lip, upper-side and lateral view. **G**. Column, lateral and front view. **H**. Anther cap and Pollinarium. Photos taken by Abdul R. Idris, correction and design by Zainudin base on ZBA137231222.

ZBA138231222 (dried specimen: WAN!). **Sumatra**: Bangka Soengai Liat, S. Boei, 27 October 1917 (L!-image L. 1510506). **West Kalimantan**: Bukit Baka Bukit Raya National Park, Sintang, Serawai, Rantau Malam, Soa Tohutung, 1400–1600 m, 02 July 2024, YRY0450BR (dried and spirit specimen: WAN!).

Distribution: Previously known only from Sungai Liat, Bangka Island (500 m), and considered endemic to Sumatra. Range extension includes: Mts. Meratus-HRB Mangkalapi, Tanah Bumbu, South Kalimantan (<100 m), Sapat Hawung Nature Reserve, Central Kalimantan (800–1000 m), and Bukit Baka Bukit Raya National Park, West Kalimantan (1400–1600 m) (Fig. 4).

Habitat and ecology: In Sumatra, it grows at an elevation of 500 m. In Kalimantan, it is found in lowland hill forests, secondary forests, and disturbed dipterocarp forests below 100 m, as well as highland primary forests up to 1600 m. It grows as an epiphyte on *Artocarpus* sp. (Moraceae) and *Garcinia* sp. (Clusiaceae), with most individuals observed growing 5–15 m above the ground in the tree canopy.

Phenology: Flowering in the wild all year round. Seed pods not seen.

Notes: J.J. Smith (Comber, 2001) suggested that this species closely resembled *Eria neglecta* Ridl., a widespread species [Borneo, Malaya, Sumatra, and Thailand] (POWO, 2024), but differed in its thicker stems, number of leaves, larger flowers, and non-lanceolate sepals. He considered it more similar to *Eria nutans* Lindl., though distinguishable by the colour of the flowers and lip shape: *E. nutans* has predominantly pink flowers with obtuse lip side lobes, while *Eria compressoclavata* shows mostly yellowish flowers with acute lip side lobes. Ormerod (2014) proposed placing this species in section *Nutantes* Ridl. along with other seven species, due to its distinct characteristics, such as having one or a few leaves clustered near the stem apex, *vs*. spread along the stem, pseudoterminal *vs*. axillary inflorescence of 1–2 flowers.

Oxystophyllum cuneatipetalum (J.J.Sm.) M.A.Clem., Telopea 10: 277. 2003. *Dendrobium cuneatipetalum* J.J.Sm. Bull. Jard. Bot. Buit, ser. 3, 9: 157. 1927. *Aporum cuneatipetalum* (J.J.Sm.) Rauschert. Repert. Spec. Nov. Regni Veg. 95 (7–8): 439. 1983.

TYPE: Indonesia. Sumatra: West Sumatra, Ranau, G. Pakiwang. Alt. 1300 m. *Steenis*, *3823* (holotype, L!) (Fig. 2).

Rhizomes stem-like, freely branching. *Stems ca.* 2–6 mm apart, flattened, thin basally, leafy to *ca.* 15 cm long, thickened towards the apex. *Leaves* close together, imbricate, the upper edge *ca.* 2.6–3.2 cm, the lower *ca.* 3.1–3.7 × 0.6–0.8 cm broad, their free apices *ca.* 1.5 cm long. *Inflorescence* axillary and terminal, nodding. *Flowers* fleshy, *ca.* 0.8–0.9 cm × 0.7–0.8 cm, pale yellow green. *Floral bract* triangular ovate 0.4–0.5 cm × 0.2–0.3 cm, acute in the apex, pale yellow green. *Ovary* terete, short ca. 0.2–0.3 cm long, green. *Dorsal sepal* recurved in the middle, oblong, obtuse, shortly apiculate, *ca.* 0.5 × 0.2–0.3 cm, suffused with dull purple apically. *Lateral sepals* forming a conspicuous conical, obtuse mentum at the base, which is 4 mm long and obliquely triangular, their apices recurved, *ca.* 0.5–0.6 × 0.5 cm broad at the base, pale yellow to yellowish. *Petals* small, wedge-shaped from the base, obliquely oblong and a slightly undulate, their apices broadly obtuse, erose and dull purple, 0.3–0.4 × 0.1–0.2 cm, dark red to purplish. *Lip* erect, recurved just below the middle, not lobed, oblong, fleshy, 0.5–0.6 × 0.2–0.3 cm, the apical part with thin margins which are strongly recurved, rugose, margins erose and hairy, its surface wrinkled, warty and a small conical tooth underneath, red to brownish. *Column* oblong, 0.5 × 0.15–0.20 cm. *Anther cap* cucullate, 0.1 × 0.1 cm, purple. *Pollinia* not seen.

Examined materials: INDONESIA. **South Kalimantan**: Tanah Bumbu, HRB-Mangkalapi, Eastern of Mts. Meratus. 77 m, 25 December 2022, ZBA207251222 (dried specimen: WAN!). **Sumatra**: Ranau-Mt. Pakiwong, Steenis 07 November 1929 (L!-image L.1498398). **West Sumatra**: Barisan Range-Road Tapa, Sinjai, Vogel 11 March 1974 (L!-image L.1498397).

Distribution: Previously only known native to Sumatra, specifically in Bengkulu and the Barisan Range at an elevation of 1350 m. Distribution extension: Mts. Meratus-HRB Mangkalapi, Tanah Bumbu (<100 m) (Fig. 4).

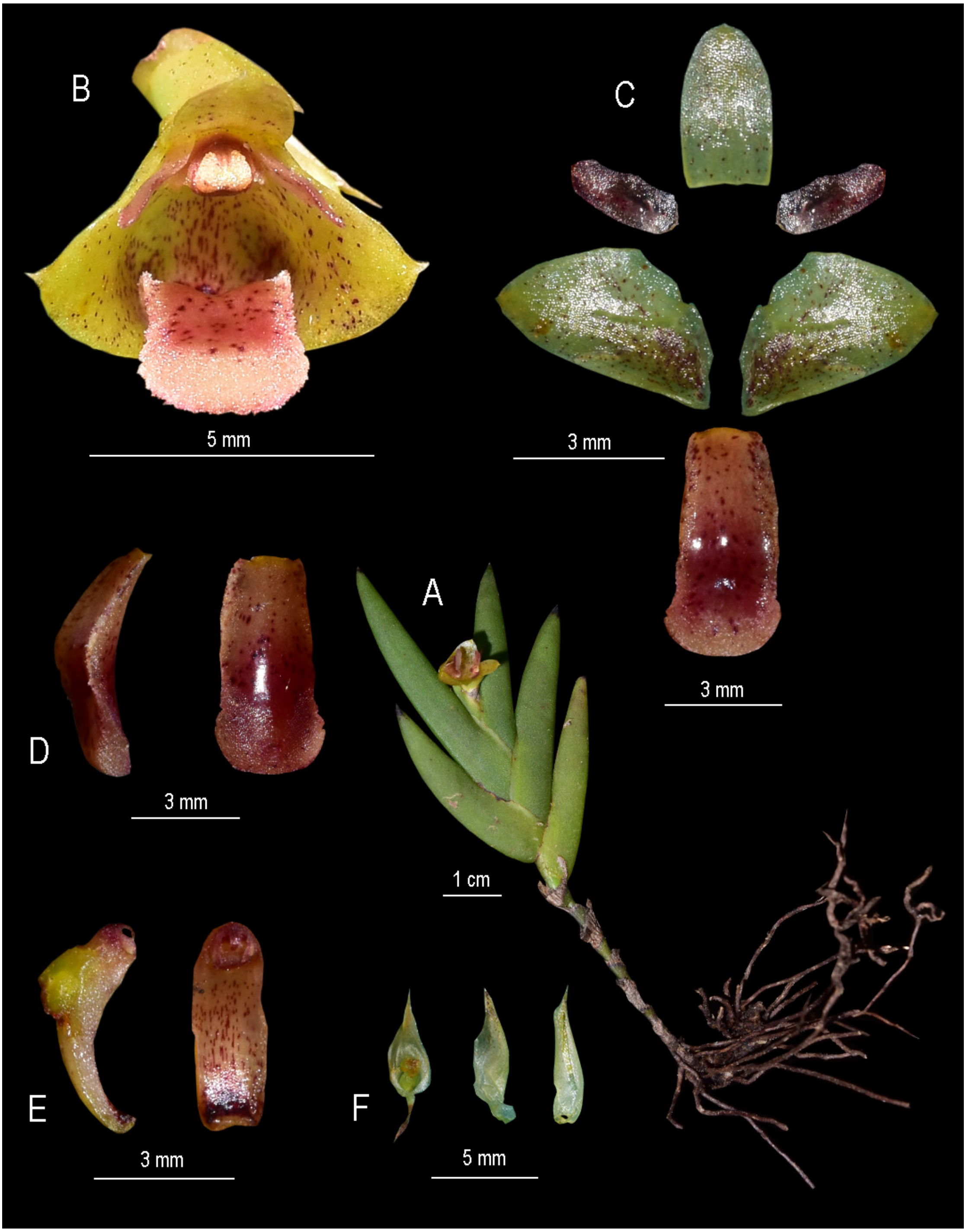

FIGURE 2. *Oxystophyllum cuneatipetalum* (J.J.Sm.). **A**. Habit and Inflorescence. **B**. Flower (front view). **C**. Perianth dissected. **D**. Lip, lateral dan back view. **E**. Column, lateral dan front view. **F**. Floral bract, front, lateral, and back view. Photos taken by Yuda R. Yudistira, correction and design by Zainudin base on ZBA207251222.

Habitat and ecology: In Sumatra, it grows in heavily disturbed montane forest, approximately 35 m high, with an open canopy, abundant rattans (*Calamus* spp.) and undergrowth palms (*Iguanura* spp., & *Pinanga* spp.). It is found on mountain ridges in deep, clayey soil with stones, on steep terrain. In Kalimantan, it occurs in disturbed hill and secondary forests in the eastern part of the Meratus Mountains, at around 100 m elevation, in riparian areas, and as an epiphyte on *Artocarpus* spp. (Moraceae), hanging 8-10 m above the ground in the trees.

Phenology: Flowering all year round. Seed pods not seen.

Notes: J.J. Smith (Comber, 2001) noted that this species is well characterized within the section *Oxystophyllum* Blume, by its flower color, wedge-shaped petals, and the distinctly rugose, erose apical portion with have a tubercle-like projection underneath the apex of the fleshy lip, differentiating it from *D. cuneatipetallum* J.J.Sm., *D. leonis* (Lindl.) Rchb.f., and *D. prostratum* Ridl.

Plocoglottis quadrifolia J.J.Sm. Bull. Jard. Bot. Buitenzorg ser. 3, 8: 36. 1926.

TYPE: Indonesia. Sumatra: Agam, Boekit Batoe Banting, *Groeneveldt 873* (holotype, L!) (Fig. 3).

Terrestrial perennial *herb*, evergreen, cylindrical stems reed-like, 2–4 stem per clump, *ca.* 25–30 × 2–4 cm, *ca.* 1.3–3.0 cm in diameter. *Leaves* exist in the half to the apex of stem, sheathing leaves covered lower stems, 4–6 leaves per stem, lanceolate-elliptic, acute acuminate at the apex, entire margin, glabrous, parallelodromous, blades *ca.*16–23 × 2.5–5.0 cm, short petioles *ca.* 1 cm long, pale green to dark green. *Inflorescence* monopodial, raceme, pubescence cylindrical peduncle *ca.* 50–60 cm × 4–5 mm, carried 10–11 bud flowers, rising from the base of stems, dark-brown with greenish close to the top, brown-black in lower side, taller than leavy shoots, 2–4 sterile bract, clustering, *ca.* 3–4 × 3 mm, concave and openly wide, pale green to reddish, lanceolate-oblong, attenuate at the apex, glabrous to hairy. *Floral bract* ovate to lanceolate, attenuate at the apex, *ca.* 8 × 2 mm, pale green sometimes purplish, rachis *ca.* 1–12 cm long, *flowers* opened from based to the top, 1–3 flowers opened in time, mostly pink-yellowish and bright reddish in some part of lateral sepals and labellum, pubescence. *Ovary* straight, twisted, and grooved, *ca.* 1.5 cm long, densely pubescent, reddish green with a slender shape. *Dorsal sepal* lanceolate, *ca.* 25–27 × 4–5 mm, outside densely pubescence, acute, entire, with 3 dominant veins, pale pink yellow in coloration. *Lateral sepal* ovate-lanceolate, *ca.* 16–19 × 6–8 mm, outside densely pubescence, acute, entire, with 5 dominant veins, pale pink in the abaxial side, pink-bright reddish in the adaxial, and curve at the middle to apex. *Petals* narrowly lanceolate, *ca.* 15 × 5 mm, glabrous, acute, entire, 3 dominant veins, pale pink-yellowish, dark red at the apex. *Lip* quadrangular, narrowed towards the base, 3 lobed in the apical half, midlobe reflexed to apical tooth, sidelobe triangular, *ca.* 12 × 10 mm, united with column, fimbriate margin, glabrous, obtuse, bright yellow-red coloration, in the adaxial side paler in coloration, sometimes with red mart at the base, margin darker with yellow fimbriate. *Column* straight, *ca.* 1 cm long, bright yellow rostellum a short blunt beak.

Examined materials: INDONESIA. **South Kalimantan**: Tanah Bumbu, Teluk Kepayang, Tibarau Panjang, Eastern part of Mts. Meratus. 18 m, 27 February 2022, ZBA256270222 (dried specimen: WAN!). **Sumatra**: W.K. Agam, Boekit Batoe Bintang, Groeneveldt (L!-image L.0062347). THAILAND. Thailand peninsula, Nokhon si Thammarat, Khao Long Foot Hills, Geesink & Santisuk, 16 May 1973 (L!-image L.1531634); Put N., 02 June 1927 (P!-image P00387167); VIETNAM. Nuraliev 30 May 2014 (MW!-image MW0735492).

Distribution: Previously recorded only from a few locations: Bukit Batu Banting, Agam and Kampung Susuk North Sumatra (850 m) Sumatra. Distribution extension: Mts. Meratus, Tibarau Panjang, Teluk Kepayang, Tanah Bumbu (18–59 m), Tabalong-Jaro around 400 m a.s.l. (Fig. 4).

Habitat and ecology: In Sumatra, it is found in rock crevices, disturbed evergreen forests, and along waterfalls, as well as in lower hills up to 500 m. In Kalimantan, it inhabits karst/limestone environments, characterized by warm, dry, evergreen forests. They

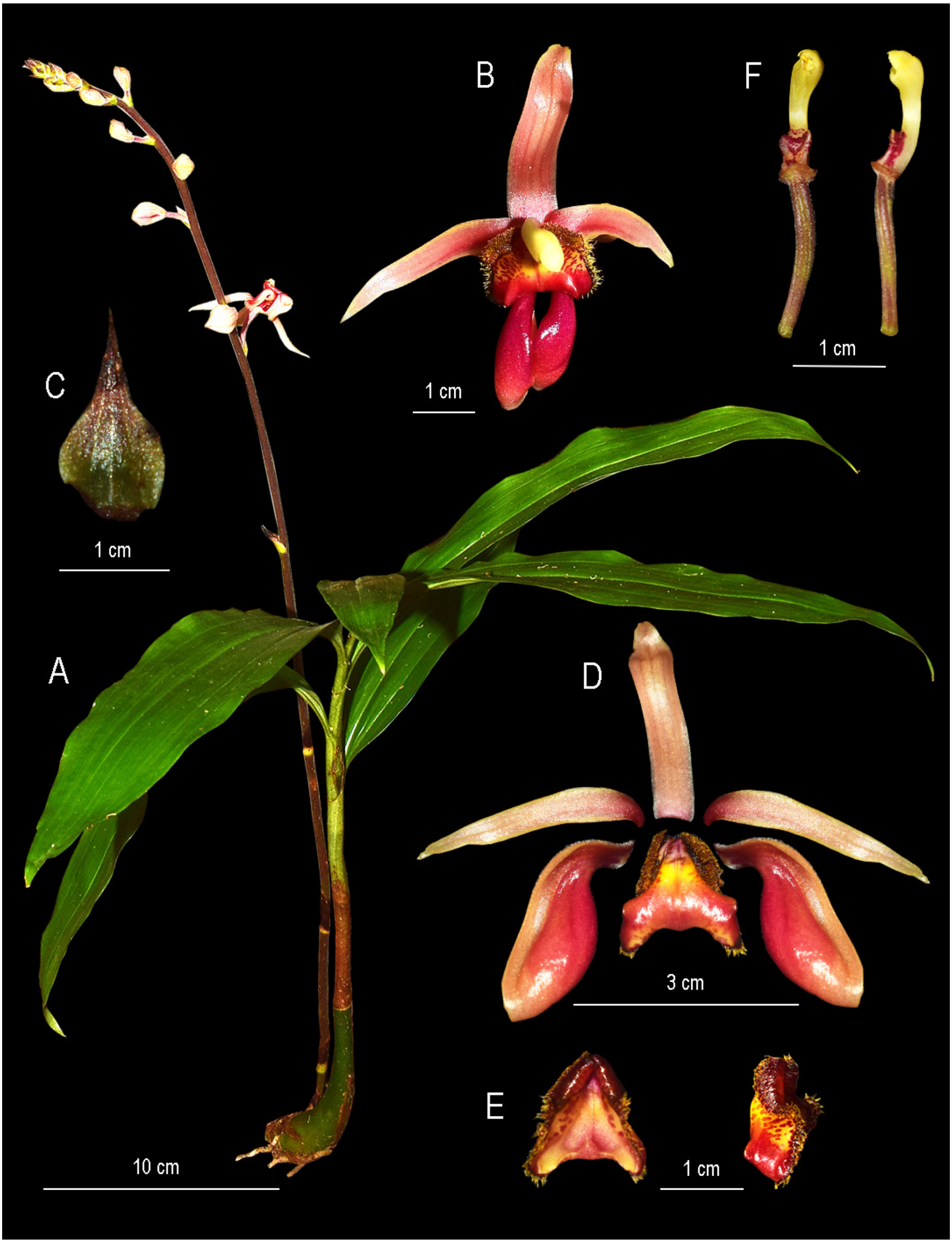

FIGURE 3. *Plocoglottis quadrifolia* (J.J.Sm.). **A**. Habit. **B**. Flower. **C**. Floral bract. **D**. Perianth dissected. **E**. Labellum, adaxial and lateral view. **F**. Column, front and lateral view. Photos, correction and design by Zainudin base on ZBA256270222.

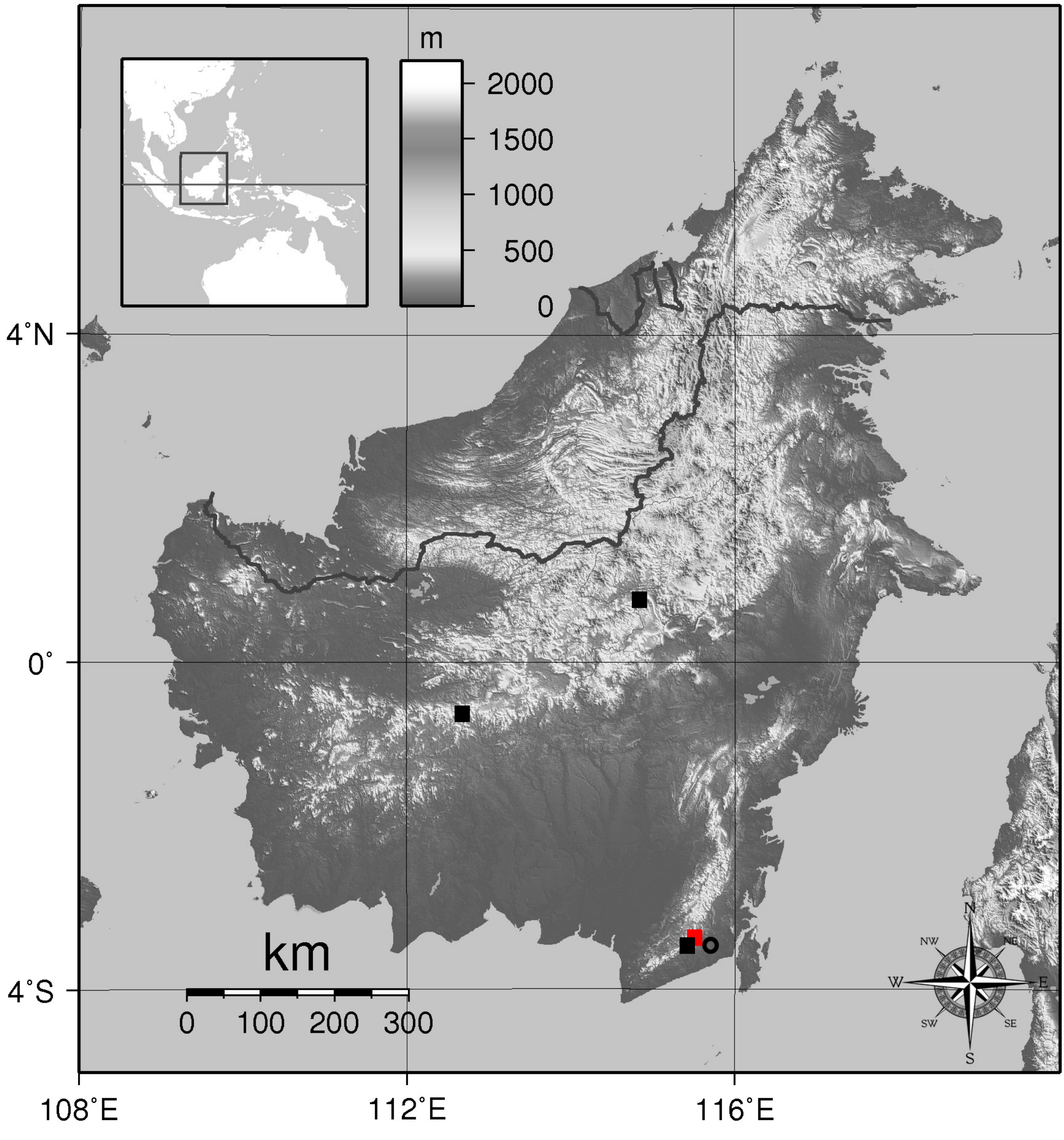

FIGURE 4. Distribution map of three Sumatran orchids in Kalimantan: *Eria compressoclavata* J.J.Sm. (black square), *Oxystophyllum cuneatipetalum* J.J.Sm. (red square), *Plocoglottis quadrifolia* J.J.Sm. (black circle). Map generated from https://commons.wikimedia.org

grow in habitats covered by leaf litter, from 18 to 400 m of elevation.

PHENOLOGY: Previously recorded flowering in May, but we have observed flowering in January, February, and October. Seed pods have not been seen.

NOTES: This species is easily distinguishable from others by its reed-like stems bearing several leaves, long straight dorsal sepal, and fimbriate labellum margins. It is morphologically similar to *Plocoglottis lowii* Rchb.f., but differs vegetatively: reed-like stems versus narrow-conical pseudobulbs, and green versus purple coloration of the plant.

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AUTHOR CONTRIBUTION. Z: Conceptualization (equal); Investigation (equal); Preparing and wrote the original draft (equal); ARI: Investigation (equal); draft reviewing and editing (equal): YRY: Supervision (equal); Data curation (equal); Investigation (equal); draft reviewing and editing (equal).

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CONFLICT OF INTEREST. No conflict of interest to declare.

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CORRESPONDENCE

FEMALE ORCHID BEE *EUGLOSSA DILEMMA* VISITS THE PERFUME ORCHID *CORYANTHES PANAMENSIS* IN FLORIDA

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Abstract. Male orchid bees gather fragrance chemicals from the surfaces of about 700 species of neotropical orchids and pollinate them in the process. The males display the collected chemicals during their courtship, and female orchid bees will mate only with males displaying a species-specific blend of collected chemicals. Given this reality, the discovery of a female *Euglossa dilemma* dead in the bucket trap of a flower of the perfume orchid *Coryanthes panamensis* bearing the orchid's pollinarium is extraordinary. There are no previous reports of female orchid bees visiting a perfume orchid and picking up pollinia of the orchids. Bearing a pollinarium indicates that this female bee made at least two visits to the flowers and that these visits were unlikely to be accidental. The flower in which the bee was found was on a cultivated plant grown in a residential garden in Coral Gables, Florida. Neither the orchid nor the orchid bee are native to Florida and occur in different areas of tropical America. Why this female orchid bee visited this orchid is considered, including the possibility that it may be a gynandromorph. Despite being a morphological female, the bee may have had neurological anomalies that caused it to exhibit a male-like attraction to this perfume orchid.

Resumen. Los machos de las abejas de orquídeas recolectan compuestos químicos fragantes de las superficies de aproximadamente 700 especies de orquídeas neotropicales y las polinizan en el proceso. Los machos presentan los compuestos recolectados durante su cortejo, y las abejas hembras solo se aparean con machos que ofrecen una mezcla específica de estos compuestos. Dada esta realidad, el hallazgo de una hembra de *Euglossa dilemma* muerta dentro de una flor de la orquídea perfumada *Coryanthes panamensis*, que portaba el polinario de la orquídea, es extraordinario. No existen reportes previos de abejas de orquídeas hembras visitando orquídeas perfumadas y recolectando polinios de estas flores. El hecho de que la abeja llevara un polinario indica que esta hembra realizó al menos dos visitas a las flores, lo que hace poco probable que tales visitas hayan sido accidentales. La flor en la que se encontró la abeja pertenecía a una planta cultivada en un jardín residencial en Coral Gables, Florida. Ni la orquídea ni la abeja son nativas de Florida y se encuentran en diferentes áreas de América tropical. Se plantea la cuestión de por qué esta abeja hembra visitó esta orquídea, incluida la posibilidad de que pudiera tratarse de una ginandromorfa. A pesar de que la abeja tiene morfología femenina, podría haber sufrido anomalías neurológicas que le causaron una atracción tipo masculina hacia esta orquídea perfumada.

Keywords / Palabras clave: bucket orchid, fragrance chemicals, ginandromorfismo, gynandromorphism, naturalizada, naturalized, orquídea-balde, químicos fragantes

The estimated 250 species of orchid bees (Hymenoptera: Apidae: Euglossini) pollinate thousands of tropical American plants, perhaps about a third of the plants in this area (Dressler, 1982; Williams, 1982). Male orchid bees are the only pollinators of about 700 so-called perfume orchids in the American tropics (Dressler, 1982; Vogel, 1966). Instead of producing their own pheromones for reproduction, male orchid bees collect volatile chemicals from the surfaces of these orchids and from other sources and expose the chemicals during their courtship (Eltz *et al.*, 2005). Females of each orchid bee species will mate only after their males display particular blends of collected chemicals, unique to each orchid bee

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species (Eltz *et al.*, 2005; Henske *et al.*, 2022; Zimmerman *et al.*, 2009). The bees visiting the orchids are manipulated by their flowers, so their collection of these volatile oils often results in the pollination of their flowers.

One orchid bee, *Euglossa dilemma* Bembé & Eltz, has become naturalized in Florida (Pemberton & Wheeler, 2006; Skov & Wiley, 2005) and has spread south to the Keys and north to central Florida (Pemberton & Escalona, 2023). A perplexing discovery was made when a female *E. dilemma* was found dead inside the bucket-shaped flower of a *Coryanthes panamensis* G.Gerlach in Coral Gables, Florida. This female bore the pollinarium of this orchid on her thorax (Fig. 1A). The orchid species was identified to be *C. panamensis* from a photograph of the flowers by the perfume orchid expert Günter Gerlach. The pollinarium on the dead female was determined to be that of a *Coryanthes* species based on its morphology and position on the bee as indicated by a drawing in Roubik and Hanson (2004) and verified by Gerlach. A photograph of the pinned specimen of this bee clearly shows the tibia of its hind leg with its concave morphology (the corbiculae used to carry pollen), verifying that the bee is a female (Fig. 1B). The orchid flower was on a *C. panamensis* plant grown in a basket in the residential garden of a Coral Gables, Florida. The discovery was made when the plant was brought to a meeting of the Orchid Species Coalition, a club of orchid growers, at Fairchild Tropical Garden, also in Coral Gables, on January 8, 2008. A male *E. dilemma* was found dead in the bucket flower of this orchid on a plant also brought to the club's meeting, on November 9, 2008. It did not bear a pollinarium.

Coryanthes orchids have one of the most bizarre flowers and strangest pollination mechanisms of all orchids. The following description of a *Coryanthes* flower and the pollination mechanism is slightly modified from Gerlach and Schill (1989) and is provided to better understand the female's behavior when she visits the orchid. See Gerlach (2016) for more extensive information about these fascinating orchids and their pollination. The fleshy lip of the *Coryanthes* flower (Fig. 2) is composed of three parts- the cup-shaped hypochil (H), the partially covered tubular mesochil (M) and the bucket-like enlarged epichil (E), which is filled with a fluid secreted by two broadly falcate protuberances the pleuridia (P1) at the base of the column (C). Male orchid bees land on the hypochil of the flower and try to get below the hood to collect fragrance compounds. In trying to get a footing on the waxy, smooth mesochil, they slip and fall in the bucket-like epichil, which is filled with a mucilaginous fluid, where their wings are wetted. The only way for a bee to escape is by crawling out through a tunnel formed by the epichil of the lip and the column, which bears the stigma and single anther. Before exiting the tunnel, the bee contacts the stigma, which removes a pollinarium it may bear from its thorax. Then the exiting bee contacts the anther, and its sticky viscidium glues the pollinarium (the viscidium, stipes, and two pollinia –the whole pollen mass) to its thorax.

The female orchid bee paradox. Female orchid bees respond to male orchid bees displaying with particular bouquets of fragrance chemicals and mate. Perfume orchids produce these volatile compounds in higher concentrations and in complex blends to lure male orchid bee pollinators. Female orchid bees, however, don't visit or pollinate the flowers of perfume orchids. Queries with orchid bee-perfume orchid experts James Ackerman, Günter Gerlach, and David Roubik (pers. comm.) confirmed that they have not observed female orchid bees visiting perfume orchids, despite spending many years in the field studying perfume orchids and orchid bees. Furthermore, female orchid bees don't come to, or very rarely come to baits using perfume orchid fragrance chemicals to attract male orchid bees, even when male conspecifics are present at the baits. After checking his records of baiting in Panama, James Ackerman reports that he encountered only a single female orchid bee out of 36,000 orchid bees. This was *Euglossa imperialis* Cockerell that came to a Benzyl Benzoate bait. Günter Gerlach had never seen a female orchid bee at baits, except on occasion when a female flew towards his insect net in which he had captured male orchid bees at baits. That female orchid bees can smell the fragrance chemicals and are attracted to males displaying with them but don't visit perfume orchids or perfume compound baits seems paradoxical. A displaying male orchid bee is, apparently, an essential element in this chemical attraction for females.

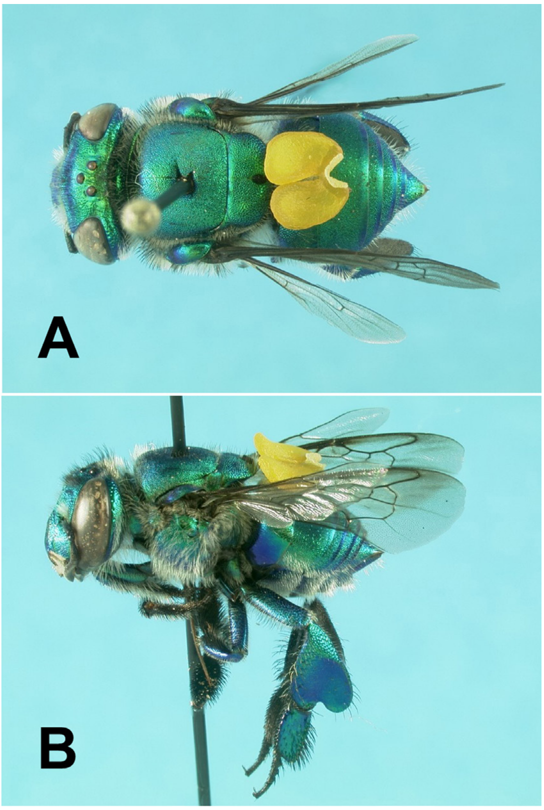

Figure 1. *Euglossa dilemma* female (concave hind tibia) with the pollinarium of *Coryanthes panamensis*. **A**. Dorsal view. **B**. Lateral view. This orchid bee is naturalized in Florida where this specimen was discovered dead in the flower of *C. panamensis,* an uncommon potted plant grown by orchid hobbyists.

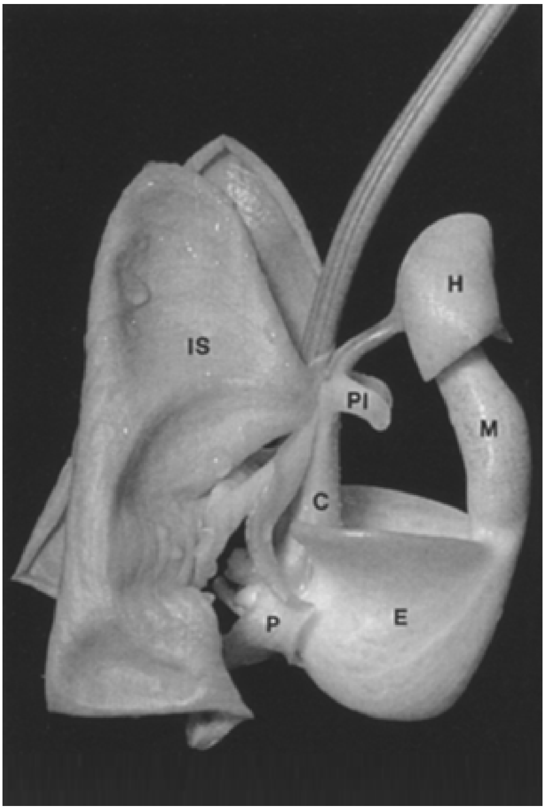

Figure 2. *Coryanthes speciosa* flower, side view. lS, lateral sepalum; P, petalum; lip consisting of a short claw: H, hypochile; M, mesochile; E, epichile; C, column; Pl, pleuridia, ca. life size (Gerlach & Schill, 1989). The flower is shown to illustrate the complexity involved in a female orchid bee's visits to a bucket orchid flower and removing the pollinaria, which *Euglossa dilemma* did twice.

The puzzle of why the female *E. dilemma* visited the flowers of *C. panamensis*. Because this female orchid bee bore the orchid's pollinarium, she either visited the flower she was found in twice, or another flower first and then this flower, where she probably drowned in the viscous liquid it contained. Why did this orchid bee visit this flower intensively enough to be trapped in the bucket, only to escape through liquid through the tunnel and exit with a pollinarium, and then re-enter a flower? Bees do fall into water traps and water-filled pan traps are used to trap and study bees. Other kinds of bees and insects probably fall into the bucket flowers of *Coryanthes* species, but they apparently don't escape with the orchid's pollinarium on them, or re-enter that of another flower. The repeated visitation by the female *E. dilemma* suggests that, although she did have accidents by slipping and falling into the bucket of the flower, her visits were not accidental.

The presence of the pollinarium on the female *E. dilemma* is significant because flower visitors that remove pollen from orchids are considered to be their pollinators (Ackerman, 1983; Dressler, 1981), so by this criterion, this bee is a pollinator of *C. panamensis* (although not a successful one). Plants of this bucket orchid, however, are quite rare in Florida, being non-native pot ornamentals of interest only to specialty orchid hobbyists, suggesting that the trapped bee probably had no or little contact with plants of this species before she visited. With so few plants of this orchid in the environment, this potential pollination has no plant reproductive or plant population level meaning to it. Also, because

Euglossa dilemma and *C. panamensis* are not sympatric in their native ranges in tropical America, there would have been no opportunity for a *E. dilemma* female or male to visit and potentially pollinate the flowers of this species. Male orchid bees of both *Eulaema* and *Euglossa* species associate with *Coryanthes* orchids in Panama (Roubik & Hanson 2004) and *C. panamensis* Friese is pollinated by *Euglossa hemichlora* Cockerell and *Euglossa townsendii* Cockerell (Roubik & Knutson, 2017; G. Gerlach pers. comm.).

What attracted this female *E. dilemma* to make repeated visits to flowers of *C. panamensis*? During 20 years of observing this bee in Florida, I have recorded it to use 259 taxa of plants including 237 different species (Pemberton, 2023). This bee is an extreme generalist concerning the types of flowers it visits to obtain nectar and pollen, although it prefers gullet flowers that it can crawl into, tubular flowers whose rewards it can access with its long tongue, and buzz pollinated flowers for pollen. None of these preferred flowers or the less visited flowers resemble those of *C. panamensis* in terms of morphology or fragrance, so it seems unlikely that a female *E. dilemma* would mistakenly visit *C. panamensis* while seeking food. Females also collect resin rewards from the flowers of the few *Clusia* L. (Clusiaceae) and *Dalechampia* Plum. ex L. (Euphorbiaceae) species (Pemberton, 2024), but these flowers too are extremely different from those of *C. panamensis*. A female *E. dilemma* visited and removed the pollen from the flower of *Vanilla planifolia* L. but this orchid is not perfume orchid (Pemberton *et al.*, 2023).

Perhaps the fragrance of *C. panamensis* attracted this female orchid bee, as it very likely had attracted the male also found dead in a flower of this orchid. Among the fragrance components of the perfume of flowers of *C. panamensis* are methyl cinnamates (Kaiser, 2005). *Euglossa dilemma* males collect these same cinnamates (Pemberton & Wheeler, 2006), and in the process pollinate the perfume orchids offering them, including *Lycaste aromatica* Lindl. (Pemberton, 2023). Male *E. dilemma* have been observed to habitually collect the herbicide triclopyr because the fragrance of its principal breakdown product mimics methyl cinnamate (Pemberton & Kindt, 2024; Ramirez *et al.*, 2010). Methyl cinnamate is used with eugenol as the principal baits to attract *Euglossa viridissima* Friese (Roubik & Hanson, 2004), *E. dilemma*'s sibling species from which it was separated (Eltz *et al.*, 2011). These bees respond to essentially the same chemicals (Brand *et al.*, 2015). Male orchid bees are genetically programed to collect particular odorant chemicals that are essential for their courtship and successful mating (Henske *et al.*, 2022; Zimmerman *et al.*, 2009). Because male *E. dilemma* bees collect and store these cinnamates, they also display with these cinnamates, which are part of their odorant chemical bouquets. This suggests that female *E. dilemma* bees can smell them, which in turn suggests that they can also smell *C. panamensis* flowers. Being able to smell the flower, but not normally visiting it is again the paradox. Female orchid bees, however, are not passive regarding their reproduction. Male orchid bees display with their fragrance bouquets on the tops of ridges or other places with air movement, which facilitates the dispersal of their fragrance, and virgin females fly up these fragrance trails to reach the displaying males (Pokorny *et al.*, 2017). It is possible that the female *E. dilemma* that visited the flower of *C. panamensis* and removed the pollinarium and visited a flower again, was just an aberrant individual female. It could also suggest that female orchid bee behavior is, or potentially is, more plastic than previously thought, but the absence of female orchid bees at perfume orchids and their extreme rarity at baits belies this idea.

Might the female orchid bee's visits to the bucket orchid flowers suggest something about orchid bee evolution? Orchid bees first began to collect volatiles 38 million years ago and subsequently perfume orchids evolved for orchid bee pollination three times (Ramírez *et al.*, 2011). If female orchid bees deviate from their species-specific blend of odor compounds by responding to others or even single odors, such as seen with the female *E. dilemma*'s possible response to methyl cinnamates produced by *C. panamensis*, the reproductive barriers that protect the orchid's and the orchid bee's species integrity could be lost. However, mutations creating new fragrance perceptions and responses in both male and female bees would provide new opportunities for speciation, perhaps like the recent divergence of *E. dilemma* and *E. viridissima* (Brand *et al.*, 2015). The difference in the fragrance blends collected and displayed by male *E. dilemma* and its sibling *E. viridissima* is only a single compound, HNDB (2-hydroxy 6-nona-1,3-dienyl-benzaldehyde), and the bees' difference in degree of preference for HNDB has been traced to a single OR protein that occurs in *E. dilemma* but not *E. viridissima* (Brand *et al.*, 2020). Fragrance perception and response in orchid bees may be more evolutionarily labile than previously thought. Female orchid bee response to specific fragrances is largely unstudied (Thomas Eltz, pers com.).

Although this bee bearing the *Coryanthes* pollinarium appears to be female due to the corbicula on its metatibias, the possibility exists that it could be a gynandromorph. This might explain why an apparent female visited the *Coryanthes* and picked up the orchid's pollinarium. Gynandromorphy is a condition in which bees or other organisms have morphological features of both sexes due to genetic anomalies (Nesbit & Gartler, 1971). Gynandromorphs have been described in at least four *Euglossa* species (Suzuki *et al.*, 2014). The four species discussed by Suzuki *et al*. (2014) were the mixed or mosaic type of gynandromorphy with their sexual characteristics distributed patchily throughout their bodies. Two of these *Euglossa* species gynanders were collected at chemical baits which is an of male behavior. *Euglossa iopoecila* Dressler was collected at a eugenol bait in Brazil (Giannarelli & Sofia, 2011), and *E. pleosticta* Dressler at a cineole bait also in Brazil (Camargo & Gonçalves, 2013). Carmargo and Gonçalves (2013) considered it difficult to predict the behavior of gynanders based on scent attraction. Suzuki *et al.* (2014) did DNA genetic analysis on a gynander of *E. melanotricha* Moure which emerged from a nest collected in southwestern Brazil. The results revealed that the gynandromorph shared several alleles with both normal females analyzed as well as with the two control males. Both the mixed morphology and mixed genetics of this bee led the authors to categorize it as an intersex bee.

To determine if this *E. dilemma* bearing the pollinarium might be a gynander, the external sexual morphology of the specimen was examined and the following characteristics were noted. Both antennae have 12 segments, the scutellum bears an ellipsoid tuft, and the metatibias are corbiculate, all of which are female features. In addition, the specimen lacks male features, including the fore tarsi having brushes, velvet pads on the mesotibias, as well as an inflated hind tibia with a slit on the top. Despite the bee being a morphological female, there may be neurological anomalies that caused the bee to exhibit male-like attraction to and repeat visits to the bucket orchid flowers of *C. panamensis* causing the pollinarium to be placed on its scutellum.

Future research could analyze this *E. dilemma* specimen to determine its genetic gender, which could provide insights into why this apparent female orchid bee behaved, in part, as a male. The specimen will be deposited in the Florida Arthropod Collection in Gainesville. Suzuki *et al.* (2014) extracted DNA from the hind legs of a gynander of *E. melanotricha* Moure to analyze the complementary sex determination gene (sl-CSD), which has been widely accepted as acting in sex determination (Zayed, 2009). DNA can now be routinely extracted from pinned insect specimens, even those of great age through a non-destructive enzymatic method (Santos *et al.*, 2018). Because only one gynander of a *Euglossa* has been genotyped (Suzuki *et al.*, 2014), it would be informative to determine the genders of the others.

It would also be informative to explore the neurological and behavioral responses of female *E. dilemma* and other female orchid bees to fragrance chemicals. There has been no published research on antennograms of female orchid bees, but an unpublished study involving small numbers of bees found that that the antennae of female *E. dilemma* responded to perfume orchid fragrance chemicals, but the response was smaller than that of males (Thomas Eltz, pers. comm.). Antennograms coupled with gas chromatographs record the electrical activity of an insect's antenna in the presence of an odor and have been useful in identifying sex pheromones and pollinator responses to floral fragrances (Cardé & Hayes, 2004; Raguso 2004).

The complex biology and ecology of orchid bees make them fascinating creatures. The extraordinary visitation of a female orchid bee to a perfume orchid is an interesting anomaly of orchid bee behavior.

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REVIEW

ROSTELLUM IN ORCHIDS

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Abstract. The rostellum, a small structure located above the stigma in the gynostemium of monandrous orchid flowers, separates the pollinia from the stigma, can prevent self-pollination, and plays an important role in pollination. It secretes a sticky exudate before and after anthesis, to which the pollinia are attached. Additionally, the viscidium, a sticky disk at the base of the stipe, also connects to the rostellum. This structure varies among species and holds taxonomic significance. For example, in *Catasetum,* the rostellum extends into antennae-like projections. After pollination, emasculation, or injury, the plant hormone ethylene is produced, triggering various post-pollination, post-emasculation, and post-injury processes, including changes in perianth color, senescence, and, ultimately, the death of floral segments that have completed their functions. Although the rostellum plays a significant role, it remains understudied, and many aspects of its function are still unknown. This review highlights current knowledge and explores speculative hypotheses that may invite differing opinions and perspectives, which will likely be revised as future research deepens our understanding of its biological and ecological roles.

Resumen. El rostelo, una pequeña estructura ubicada sobre el estigma en el ginostemo de las flores de orquídeas monandras, separa los polinios del estigma, puede prevenir la autopolinización y juega un papel importante en la polinización. Segrega un exudado pegajoso antes y después de la antesis, al cual se adhieren los polinios. Además, el viscidio, un disco pegajoso en la base del estípite, también se conecta con el rostelo, y esta estructura varía entre especies y posee importancia taxonómica. Por ejemplo, en *Catasetum*, el rostelo se extiende en proyecciones similares a antenas. Después de la polinización, emasculación o lesión, la planta produce la hormona etileno, que desencadena varios procesos posteriores, incluyendo cambios en el color del perianto, senescencia y, finalmente, la muerte de los segmentos florales que han cumplido su función. Aunque el rostelo desempeña un papel significativo, sigue siendo poco estudiado, y muchos aspectos de su función aún se desconocen. Esta revisión destaca el conocimiento actual y explora hipótesis especulativas que pueden invitar a opiniones y perspectivas divergentes, las cuales probablemente se revisarán a medida que futuras investigaciones profundicen en nuestra comprensión de sus roles biológicos y ecológicos.

Keywords/Palabras clave: emasculación, emasculation, ethylene, etileno, floral senescence, ginostemo, gynostemium, pollinia, polinización, pollination, polinios, senescencia floral, viscidio, viscidium

Introduction. Monandrous orchids are distinguished not only by the beauty and intricacy of their flowers but also by the modifications of floral segments, organs, and structures. In these orchids, the style, stigma, and stamens (including anther and filaments) are fused into a single structure known as the gynostemium (Fig. 1: A1–3; B1–3; C1–2; D1–2; F1–3). A key structure within the gynostemium is the rostellum (Table 1). In some species, the rostella can be challenging to observe or recognize (Fig. 1: A1–4, B1–4, C2–4, D1–2, F1–6; 2A–E; 3A–E; 4A–E; 5A–D; 6A–Q; 7: 2, 3, 5; 8A–E, G1; Table 1). The rostellum, located at the base of the pollinarium (which includes the pollinium or pollinia, stipes, and viscidium) and positioned above the stigma, acts as the "roof" of the stigma and the "floor" of the anther, effectively separating the sigma

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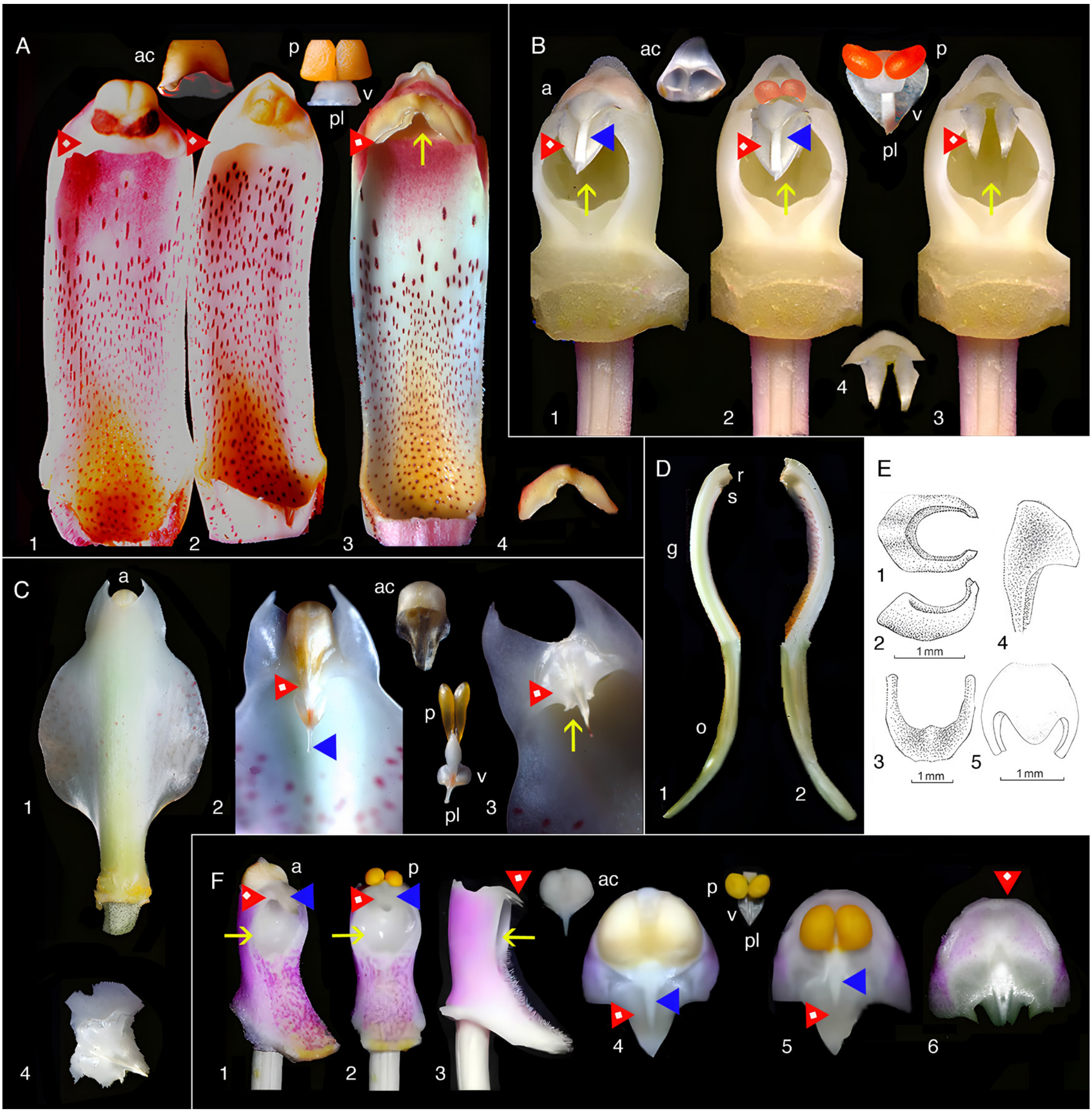
from the pollinia. During the ontogeny of *Bulbophyllum ecornutum* J.J.Sm., the rostellum curves and develops a hook-like shape (Rasmussen, 1986b). In some members of the Pleurothallidinae, the rostellum is prominent and curves downward toward the stigma (Cardoso-Gustavson *et al*., 2017). Although rostella are generally believed to function similarly across all orchid flowers, exceptions do exist (Cheng *et al*., 2009; Darwin, 1904; Nazarov & Gerlach, 1997).

Rostella vary in size and shape (Fig. 1–7; 8A, F, G; 10; 12–16; Table 1), but they are usually small and delicate. For example, a flower of *Cymbidium* Sw. Jungfrau hybrid weighs approximately 8.25 g, measures around 12.5 cm in width, and contains a rostellum weighing 0.02 g, which accounts for 0.24% of the flower's weight and 1.43% of the gynostemium's weight. The rostellum itself measures approximately 1 cm in width (side to side when facing the flower), 1.2 cm in depth (front to back), and 0.2–0.3 cm in height (thickness).

The rostella of *Habenaria* Willd. are even smaller (Fig. 1E: 1–5). In *Pterygodium vermiferum* E.G.H.Oliv. & Liltved, a species native to The Western Cape of South Africa, the rostellum bears "several remarkable, long twisted appendages arising from the



rostellum" (Oliver *et al*., 2008). The specific epithet *vermiferum* refers to these wormlike outgrowths.

Some orchids either lack a rostellum or have one that is not fully developed. In self-pollinating Spiranthinae taxa, a rostellum is absent, allowing pollinia to come into contact with the stigmatic fluid before the flowers open, leading to self-pollination (for a review, see Salazar *et al*., 2016). For example, the self-pollinating *Greenwoodiella micrantha* (Lex.) Salazar & R.Jiménez var. *micrantha* often lacks a rostellum (Salazar *et al.,* 2016). However, this trait is not consistent even within a genus in the Spiranthinae. A good example is the cross-pollinated *Greenwoodiella micrantha* var. *garayana* (R.González) Salazar & R.Jiménez which shows a well-developed rostellum (Salazar *et al.,* 2016).

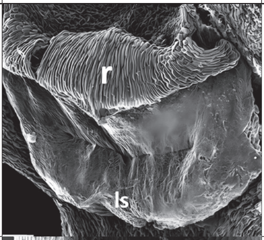
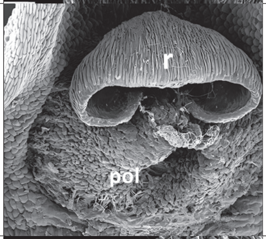
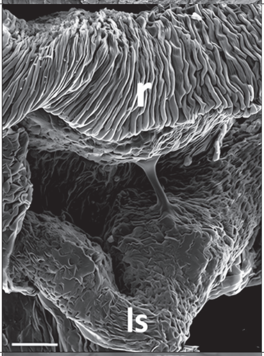
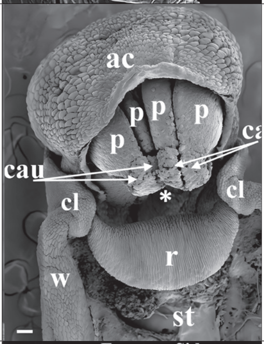
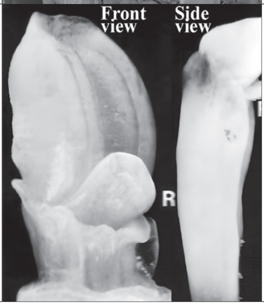
Bletiinae are often characterized as a subtribe of orchids lacking rostella, but *Bletia purpurea* (Lam.) DC., does possess one (Kurzweil, 1987a; Valencia-Nieto *et al*., 2018). In *Chysis laevis* Lindl.*,* the rostellum may be vestigial or absent, whereas *Chysis bractescens* Lindl., and *Chysis limminghei* Linden & Rchb.f., have fully developed rostella (Valencia-Nieto *et al.,* 2018). These examples suggest that the rostellum may be lost in self-pollinating forms, though this trend is not always consistent.

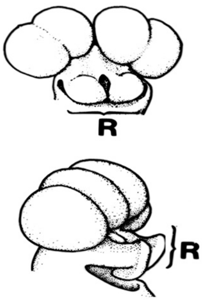
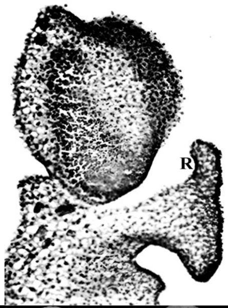
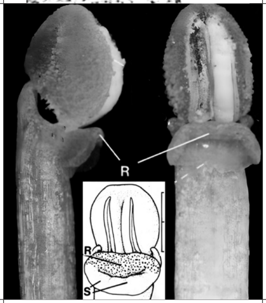
History and nomenclature. The term "rostellum" (meaning "little beak" in Latin; plural "rostella," not "rostellums") was coined by Louis Claude Marie Richard (1754–1821; Fig. 9A), a French botanist, illustrator, and the father of another orchid scientist, Achille Richard (1794–1852). He used the term to describe a small structure found in monandrous orchid flowers. Richard's original definition was likely inspired by the genus *Orchis* L., is "*Supermus stigmatis prossesus ultra gynizum*" a "projection above the stigmas (and) beyond the receptive surface," (translation from Dressler, 1989). Richard was also the first to describe and illustrate the rostella of several orchids (Fig. 3).

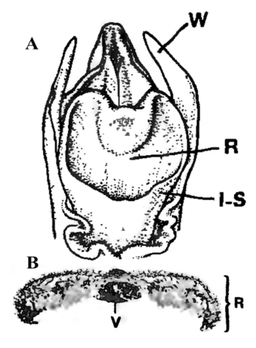
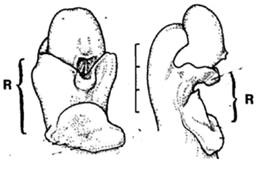
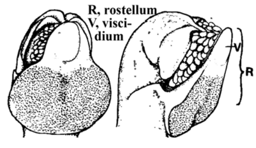
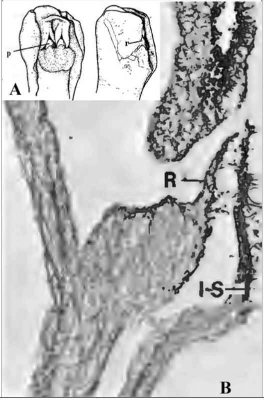
John Lindley (1799–1865; Fig. 9C) and Francis (Franz) Bauer (1758–1840; Fig. 9I) described the orchid stigma as "in most cases it is quite simple, merely terminating in a glandular dilatation of the upper margin, called the rostellum. The glandular dilatation separates from the stigma and adheres to the pollen masses" (Bauer & Lindley, 1830–1838). Interestingly, this is the only instance in which the term "rostellum" appears in their book (Bauer & Lindley, 1830–1838), despite several illustrations depicting structures that can be interpreted, or at least be speculated upon, as rostella (Fig. 10A–D).

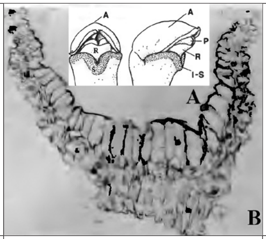
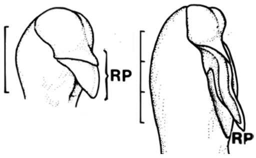
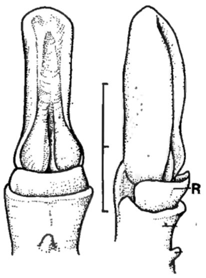
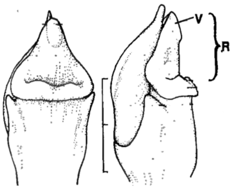
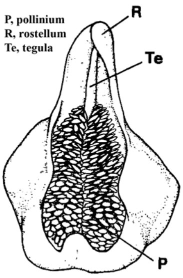
Left, Figure 1. Parts of gynostemia (columns). **A**. *Cymbidium* Sw. hybrid. 1. Intact gynostemium. 2. Anther cap removed showing pollinia in place on the rostellum. 3. Pollinarium removed showing rostellum and stigma. 4. Rostellum. On top, the anther cap and pollinarium (with pollinia and viscidium). **B**. *Phalaenopsis* Blume hybrid. 1. Intact gynostemium showing parts of viscidium, rostellum, and stigma. 2. Anther cap removed showing two pollinia, stipe and viscidium in place on the rostellum. 3. Pollinarium removed showing rostellum and stigma. 4. Rostellum. On top, anther cap and pollinarium (pollinia, stipe and viscidium). **C**. *Stanhopea* J.Frost ex Hook. 1. Dorsal view with yellowish anther cap visible on top. 2. Ventral view with yellowish anther cap in place showing rostellum and viscidium. 3. Ventral view with anther cap and pollinaria removed showing rostellum and stigma. On top, anther cap and pollinarium (pollinia, stipe and viscidium). **D**. *Cymbidium*. Longitudinal section of gynostemium showing side views of rostellum and stigma. **E**. Brazilian *Habenaria* Willd. species showing very small rostella. *Habenaria hipporepica* J.A.N.Bat. & Blanch. 1. Upper view. 2. Lateral view. *Habenaria espinhacensis* 3. Upper view. 4. Lateral view. *Habenaria quadriferricola* J.A.N.Bat. & B.M.Carvalo 5. Upper view. **F**. *Vanda* R.Br. Miss Joaquim, a natural hybrid, which is now the National Flower of Singapore. 1. Gynostemium intact showing anther cap in place and stigma. 2. Anther cap removed showing pollinia, rostellum and stigma. 3. Pollinia removed showing tip of rostellum and side view of stigma. 4. View from above showing anther cap in place, rostellum, and viscidium. 5. View from above after removal of anther cap showing pollinia, rostellum and part of viscidium. 6. View from above with anther cap and pollinaria removed, showing the rostellum. On top, anther cap and pollinarium (pollinia, stipe and viscidium). Explanation of symbols: a, anther; ac, anther cap; g, gynostemium (column); o, ovary; p. pollinia; pl, pollinarium; r, rostellum; s, stigma; v, viscidium; blue wedge, viscidium; red wedge with white dot, rostellum; white or yellow arrow, stigma; Sources: Joseph Arditti (A–D), courtesy of Dr. João A. N. Batista (E), courtesy of Dr. Tim Wing Yam (F).

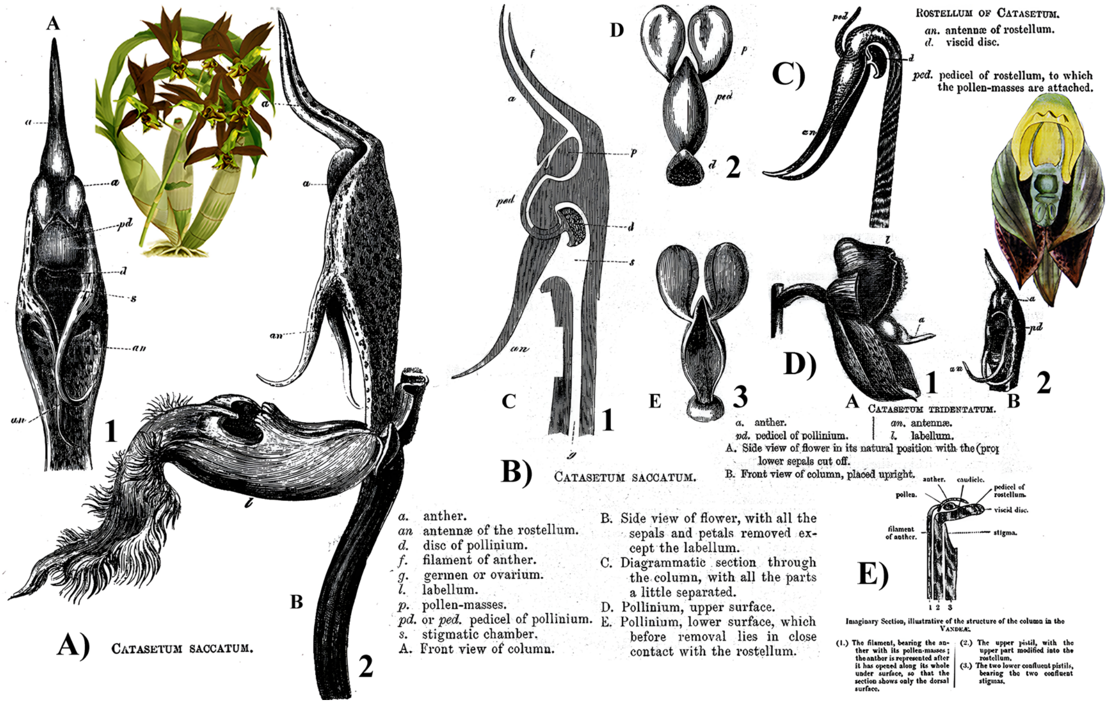
TABLE 1. Morphological features of the gynostemium and rostellum in monandrous orchids.

Species name	Details	Image	Reference
Acianthera aphthosa (Lindl.) Pridgeon & M.W.Chase	Rostella of two species in one genus differ. Symbols: ls, lateral stigma; r, rostellum.		Cardoso-Gustavon *et al.* (2017)
Acianthera fenestrata (Barb. Rodr.) Pridgeon & M.W.Chase	Rostella of two species in one genus differ. Symbols: pol, pollinia; r, rostellum.		Cardoso-Gustavon *et al.* (2017)
Anathallis obovata (Lindl.) Pridgeon & M.W.Chase	Symbols: ls, lateral stigma; r, rostellum.		Cardoso-Gustavon *et al.* (2017)
Bletia purpurea (Lam.) DC.	Rostellum is tongue or semi linate shaped. Shield separates pollinarium from stigma. Symbols: *, anther apex; ac, anther cap; cau, caudicle; cl, clinandrium; p, pollinium; r, rostelum; st, stigma; w, column wing. Scale bar = 100 μm.		Valencia-Nieto *et al.* (2018)
Bletia striata Druce	Median lobe becomes rostellum. Left: Front view. Right: Side view. Symbol: R, rostellum.		Rasmussen (1986b)

Bulbophyllum ecornutum J.J.Sm.	Rostellum swells ventrally, apex reflexes, median stigma becomes the rostellum. Symbol: Ha, hamulus.		Rasmussen (1985)
Bulbophyllum lomsakense J.J.Verm., Schuit. & de Vogel	Rostellar projection is deeply bifid. Symbol: R, rostellum		Rasmussen (1986a) as *Sunipia thailandica* (Seienf. & Smitinand) P.F.Hunt.
Bulbophyllum rimannii (Rchb.f.) J.J.Verm. Schuit. & de Vogel	A deeply bifid rostellar projection. Symbol: R, rostellum.		Rasmussen (1986a) as *Sunipia rimannii* (Rchb.f.) Seidenf.
Photographs: *Cephalanthera longifolia* (L.) Fritsch. Line drawings: *Cephalanthera damasonium* Druce	Rostellum is located above lateral stigmatic lobes. Symbols: R, rostellum; S, stigma. Bar at upper right of drawing: 1 mm.		Rasmussen (1986b)
Cymbidium aloifolium (L.) Sw.	Rostellar projection elongates. Symbol: R, rostellum.		Rasmussen (1982)

A. *Diuris punctata* Sm. B. *Diuris emarginata* var. *pauciflora* (R.Br.) A.S.George	A. Front view of top of column. B. Cross section of rostellum and viscidium. Symbols: I-S, lateral stigma lobe; R, rostellum; V, viscidium; W, wing of column.		Rasmussen (1982)
Epipogium aphyllum Sw.	Front and side view of top of the column showing anther cap, stigma and elongated rostellum. Symbol (only the rostellum is labeled in the original): R, rostellum.		Rasmussen (1982)
Goodyera repens (L.) R.Br.	Rostellum is long, pointed, erect, triangular with large broadly elliptic detachable viscidium.		Kurzweil (1989)
Huttonaea pulchra Harv.	Central lobe of median carpel becomes broadly hemispherical. Symbols: ro, rostellum; stg, stigma.		Rasmussen (1982)
Lecanorchis malaccensis Ridl.	A. Front and side views of column tip showing pollinia. Symbols: r, rostellum; s, stigma; p, pollinia. B. Cross section of rostellum and lateral stigma lobe. Rostellum is hidden behind plate formed by I-S. Symbols: I-S, lateral stigma lobe; r, rostellum.		Dressler (1989); Rasmussen (1982).

Neottia Guett. (no species listed in original)	Unique . . . described as a gland (Dressler, 1989). Symbols: A, anther cap, R, rotellum; P, pollinia; I-S, lateral stigma lobe		Rasmussen (1989b)
Phalaenopsis pulcherrima (Lindl.) J.J.Sm.	Rostellar projection (RP) is elongated. Scale bar = 3 mm		Rasmussen (1982)
Stereosandra javanica Blume	Rostelum is shorter than the anther. It projects beyond the lateral lobes. Has no viscidium. Symbol: R, rostellum.		Rasmussen (1982)
Tropidia curculigoides Lindl.	Erect rostellum is as long as anher. Removal of viscidium leaves a V-shaped scar. Symbols: R, rostellum; V, viscidium. Scale bar = 2 mm		Rasmussen (1982)
Vanilla imperialis Kraenzl.	Column and labellum are fused. Rostellum is extended.		Rasmussen (1986b)
Zeuxine affinis (Lindl.) Benth. ex Hook.f.	Rostellum errect, triangular, retuse apex with ridge.		Rasmussen (1982)



CATASETUM SACCATUM.

a. anther.
an antennæ of the rostellum.
d. disc of pollinium.
f. filament of anther.
g. germen or ovarium.
l. labellum.
p. pollen-masses.
pd. or ped. pedicel of pollinium.
s. stigmatic chamber.
A. Front view of column.
B. Side view of flower, with all the sepals and petals removed except the labellum.
C. Diagrammatic section through the column, with all the parts a little separated.
D. Pollinium, upper surface.
E. Pollinium, lower surface, which before removal lies in close contact with the rostellum.

ROSTELLUM OF CATASETUM.

an. antennæ of rostellum.
d. viscid disc.
ped. pedicel of rostellum, to which the pollen-masses are attached.

CATASETUM TRIDENTATUM.

a. anther.
pd. pedicel of pollinium.
an. antennæ.
l. labellum.
A. Side view of flower in its natural position with the (pro
lower sepals cut off.
B. Front view of column, placed upright.

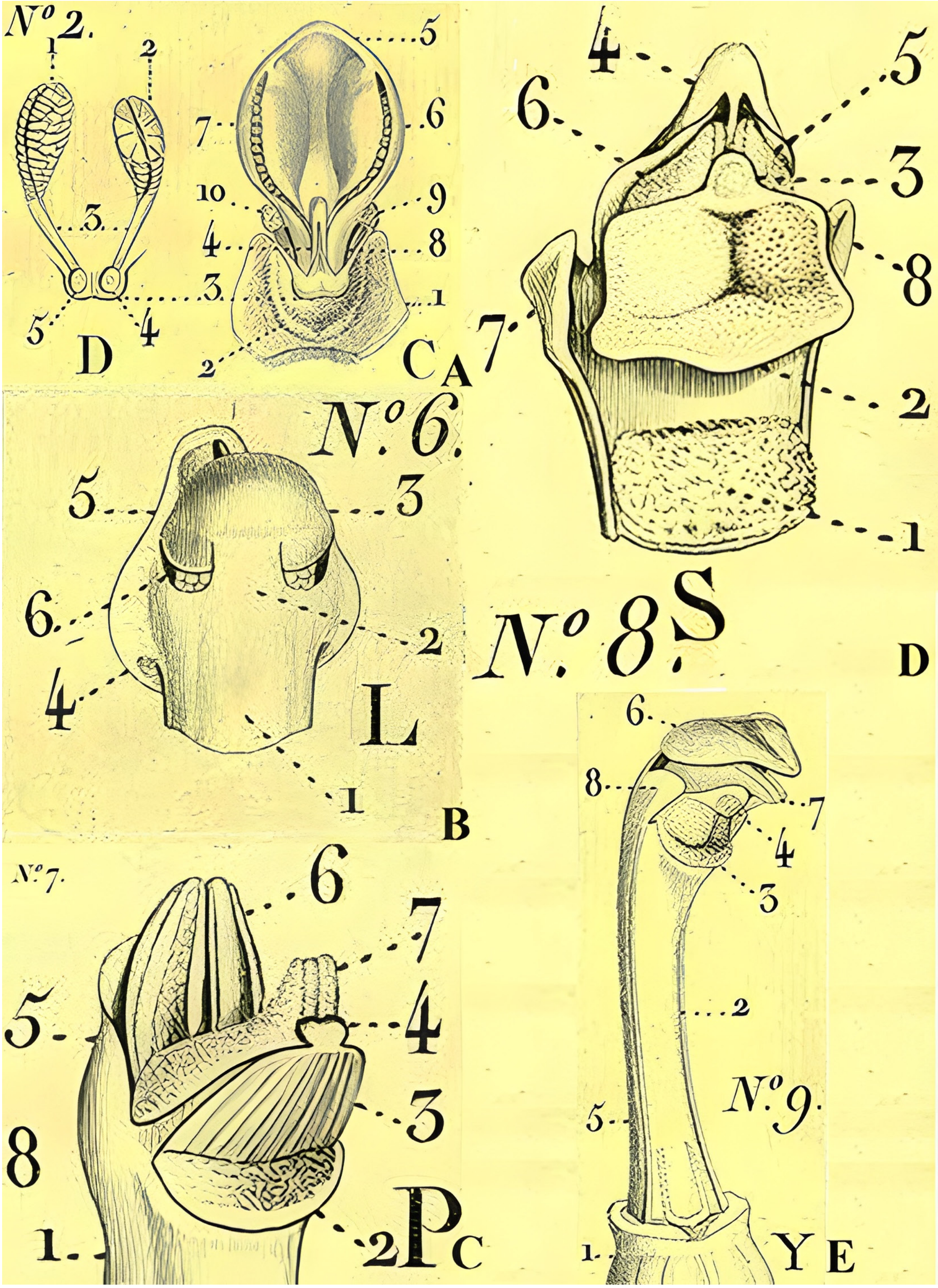
Imaginary Section, illustrative of the structure of the column in the VANDEÆ.

(1.) The filament, bearing the anther with its pollen-masses; the anther is represented after it has opened along its whole under surface, so that the section shows only the dorsal surface.
(2.) The upper pistil, with the upper part modified into the rostellum.
(3.) The two lower confluent pistils, bearing the two confluent stigmas.

FIGURE 2. Drawings and illustrations of *Catasetum saccatum* Lindl. (**A–B**), *Catasetum tridentatum* Hook., currently *Catasetum macrocarpum* Rich. ex Kunth (**C–D**), and *Vanda* Jones ex R.Br. (**E**). The captions and labels are those in the original publication, except for the bold numbers and letters, which were added for clarity. What Darwin labeled as pedicel of the pollinium is now called stipe. The stipe is connected to the viscidium (Darwin's term is viscid disk). Black and white drawings by Charles Darwin (Darwin, 1904). Color illustrations: A) Painting by John Nugent Fitch of *Catasetum saccatum*, plate 83 in the *Orchid Album* (1882–1897). D) *Catasetum tridentatum*, currently *C. macrocarpum*, plate 3329, volume 61 (1834) of *Curtis' Botanical Magazine*.

The British botanist Robert Brown (1773–1858; Fig. 9B), who discovered the cell nucleus while working with orchids, also suggested a stigmatic origin of the rostellum. He proposed that it arose from the median stigma lobe, stating, "The result of my examination of this point satisfies me that Orchideae have in reality three stigmata, generally more or less confluent, but in some cases, manifestly distinct, and two of which are in several instances furnished with styles of considerable length" (Brown, 1833). The third, anterior lobe, "manifestly differs from the other two. To this. . . lobe. . . the glands [now referred to as viscidium or viscidia] always belong to which the pollen-masses become attached" (Brown, 1833; Fig. 1: A1–4, B1–4, D1–2, F1–3; 10: A1, 3, 5, B6, 7). The statement that the viscidium (a sticky pad) "originates from a part of the rostellum" (Rasmussen, 1985) further supports Brown's hypothesis regarding the origin of the viscidium.

RIGHT, FIGURE 3. *Orchidearum Genitalia* (term used in the original source) as drawn by L. C. Richard. Only some of his drawings are presented here. **A**. *Loroglossum* Rich. **B**. *Nigritella* Rich. **C**. *Gymnadenia* R.Br. **D**. *Platanthera* Rich. **E**. *Herminium* L. Generic names are those used by Richard. The numbers (N°2, N°6, N°7, N°8, N°9 and those pertaining to every structure as well as letters C, D, L, P, S, Y), in black or blue are as in the original. Letters in modern bold Times Roman font (**A**, **B**, **C**, **D**, and **E**) at bottom right of the figures were added. Only numbers pertaining to rostella in the figures are noted here. **A**. In N°2 the rostellum is labeled as 3 in C and D. **B**. The rostellum in N°6, L is labeled as 5. **C**. Number for the rostellum in N°7, P is 3. **D**. Designation for the rostellum in N°8, S is 3. **E**. Rostellum is 4 in N°9, Y. Numbering and lettering is somewhat confusing in the original, and therefore, also here. The sepia cast is due to aging of the original. Source: Richard (1818).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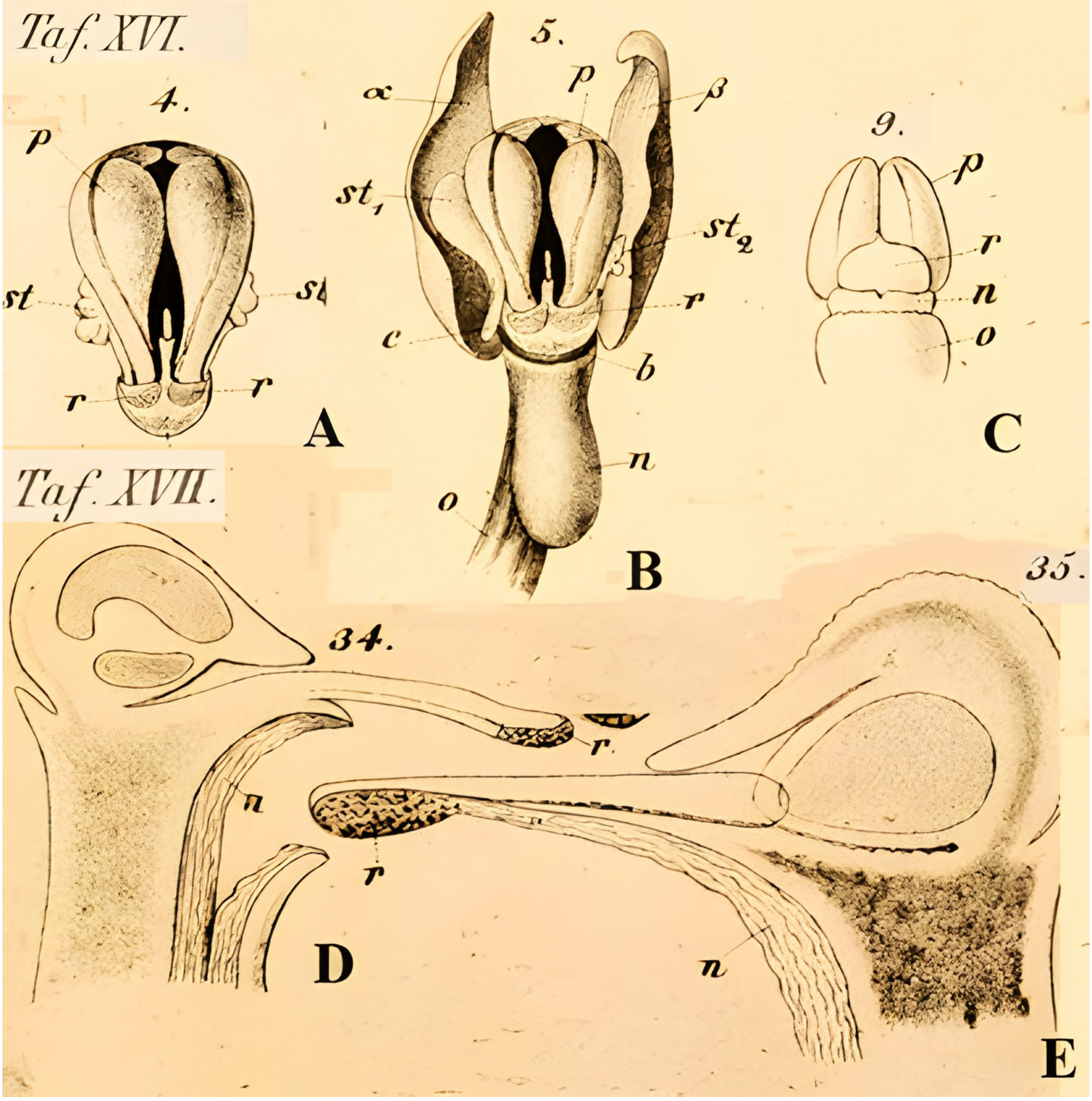


FIGURE 4. Early detailed drawings of the rostellum by Theodor Franz Wolf (1841–1925) in his Taf. XVI and Taf XVII. **A**. Taf. XVI, 4. Mature pollinia of *Orchis mascula* (L.) L. **B**. Taf. XVI, 5. Position of rostellum in the column of *O. mascula*. **C**. Taf. XVI, 9. Pollinia of *O. mascula*, on the rostellum. **D**. Taf. XVII, 34. Positions of stamen, pollinia, stigma and rostellum in *Lycaste aromatica* (Graham) Lindl. in a longitudinal section. **E**. Taf. XVII, 35. Longitudinal section through the gynostemium of *L. aromatica*. Names and lettering used here are those in the original. Only letters pertaining to the rostellum and associated structures are noted here: p, pollinia; n, stigma; r. rostellum; rounded shaded areas on r in A and B, viscidium; st, stamen. Source: Wolf (1865–1866). Sepia cast and low contrast are due to aging of the original.

These interpretations were widely accepted by many subsequent researchers, including renowned orchid scientists and illustrators such as Francis (Franz) Bauer, George Bentham (1800–1884; Fig. 9J), Olaf Hagerup (1889–1961; Fig. 9K), John Stevens Henslow (1796–1861; Fig. 9L), Joseph Dalton Hooker (1817–1911; Fig. 11G), and Charles Darwin (Fig. 1D) (Bauer & Lindley, 1830–1838, Bentham, 1881; Darwin, 1904; Hagerup, 1952; Henslow, 1858; Hooker, 1854, 1855; for reviews

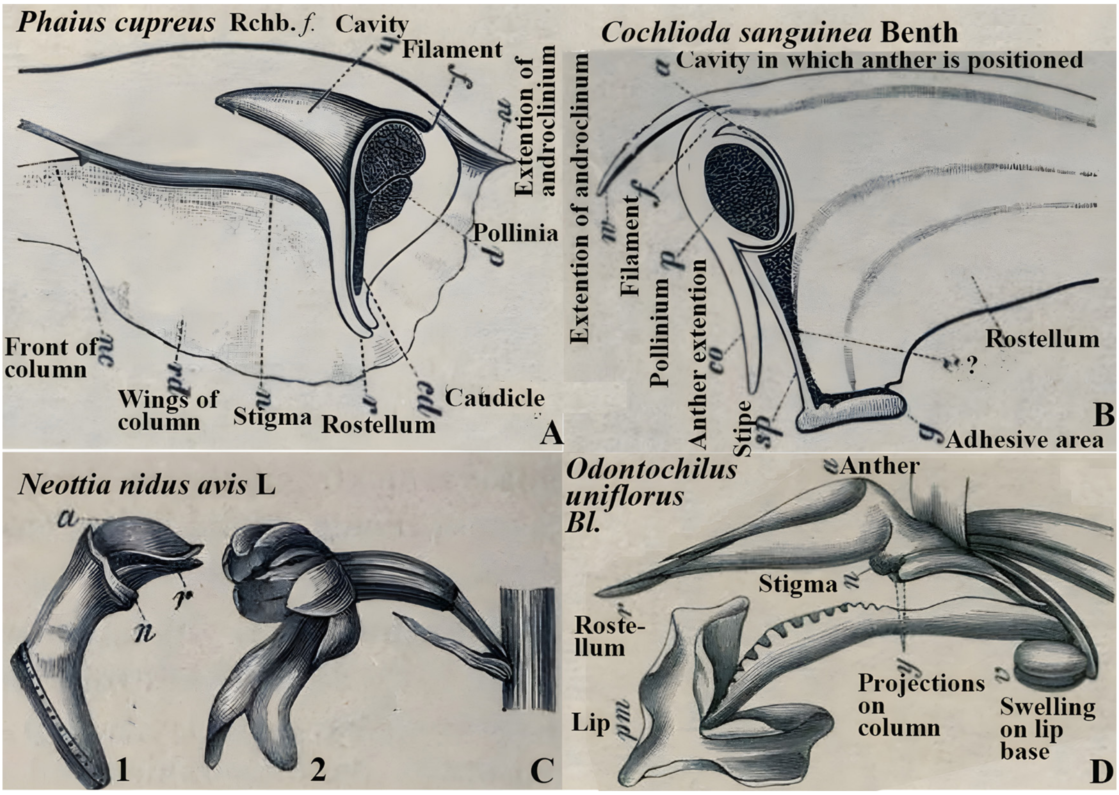


Figure 5. Drawings of orchid gynostemia (columns) showing different sizes and shapes of rostella in the first major taxonomic treatment of the Orchidaceae, which considered the rostellum. Symbols: Most labeling is on the original illustration except in C1 were a, anther; n, stigma; r, rostellum. In A and B, androclinium is a collective name for stamens, which is hard to explain because orchid flowers do not have separate stamens. Also, in A and B, stipe and caudiculum seem to be used for the same structure. The question mark (?) In B refers to a symbol, which could be a sideways Z, but not deciphered with certainty. Source: Pfitzer, 1889. The grey cast is due to the aging of the original.

see Arditti & Flick, 1974; Cardoso-Gustavson *et al*., 2017; Strauss & Arditti, 1984).

Pioneering studies of orchid flower vascularization by Bengaluru Gundappa Lakshminarayana Swamy (1916–1980; Fig. 11I) provided further anatomical support for the stigmatic origin of the rostellum. In *Habenaria* Willd., for instance, the compound stigma has three vascular strands, though one fails to develop when the dorsal stigma fails to form (Garay, 1960; Swamy, 1948).

The Reverend Professor John Stevens Henslow (1796–1861), Darwin's mentor and friend, suggested that the rostellum produces an adhesive substance and speculated that it might function as an anterior stigma (Henslow, 1858). This was later confirmed by George Bentham (1881), Joseph Dalton Hooker (1854, 1855), and Olaf Hagerup (1952). Heinrich Gustav Reichenbach (1823–1889; Fig. 11H) observed that this adhesive (viscid) substance accumulates in *Cattleya* Lindl. and *Laelia* Lindl. (Reichenbach, 1885).

Charles Darwin (1809–1882; Fig. 9D) studied the rostella of several orchids, including *Catasetum* Rich. ex Kunth (Fig. 2A–D, black and white; captions in the figures are those in the original) and *Vanda* R.Br. (Fig. 2E). He provided a clear description, detailed illustrations (Fig. 2), and a convincing hypothesis (Darwin, 1888, 1904): "The rostellum strictly is a single organ, formed by the modification of the dorsal stigma and pistil. . . In. . . the Orchideae there are three confluent pistils; of these the dorsal one forms the rostellum. . . " and "there is every reason to believe that the whole of this upper stigma, and not merely a part, has been converted into the rostellum; for there are plenty of

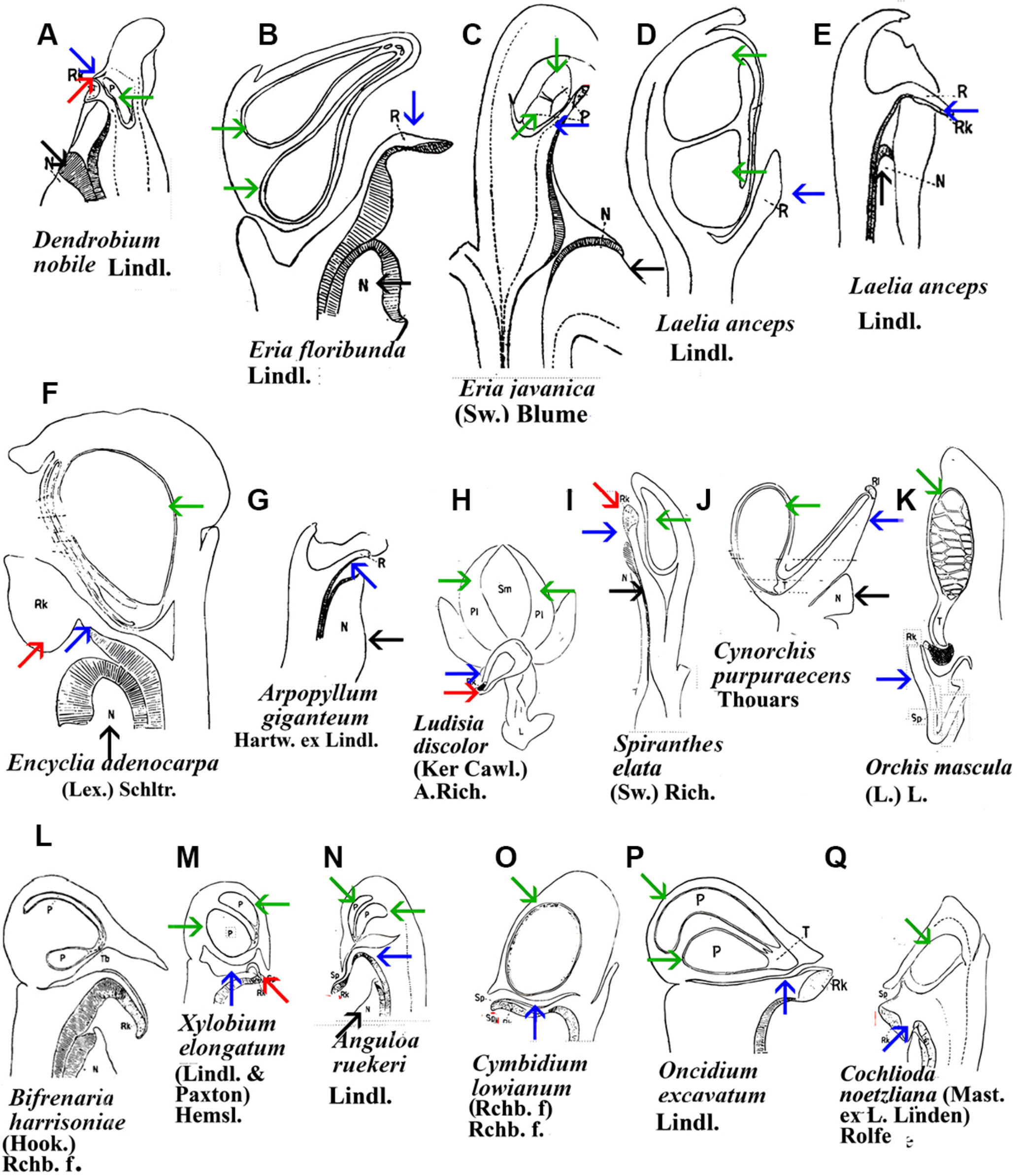


FIGURE 6. Drawings of parts of the gynostemium, stigmas and rostella in one the best structural studies of the rostellum. Symbols: Black arrows, stigma; Blue arrows, rostellum; Green arrows, pollinium or pollinia; N, stigma; R or r, rostellum; P, pollinium or pollinia; Rk, viscidium or area containing adhesive substance; Sp, stipe. Source: Hirmer, 1920, courtesy of Thomas Zuhr of Hirmer Verlag and the Hirmer family.

cases of two stigmas, but not one of three stigmatic surfaces being present in these Orchids which have a rostellum." This concept has since gained general acceptance (Vermeulen, 1959).

Darwin's special interest in the rostellum of *Catasetum* led him to suggest that the antennae (Fig. 2A1, B1, C, D2), which trigger the ejection of pollinaria (Fig. 2B1, B2) are part of this structure. He described them as "are prolongations of the sides of the anterior face of the rostellum" (Darwin, 1904). His drawings show this clearly (Fig. 2A1, B1, C, D2).

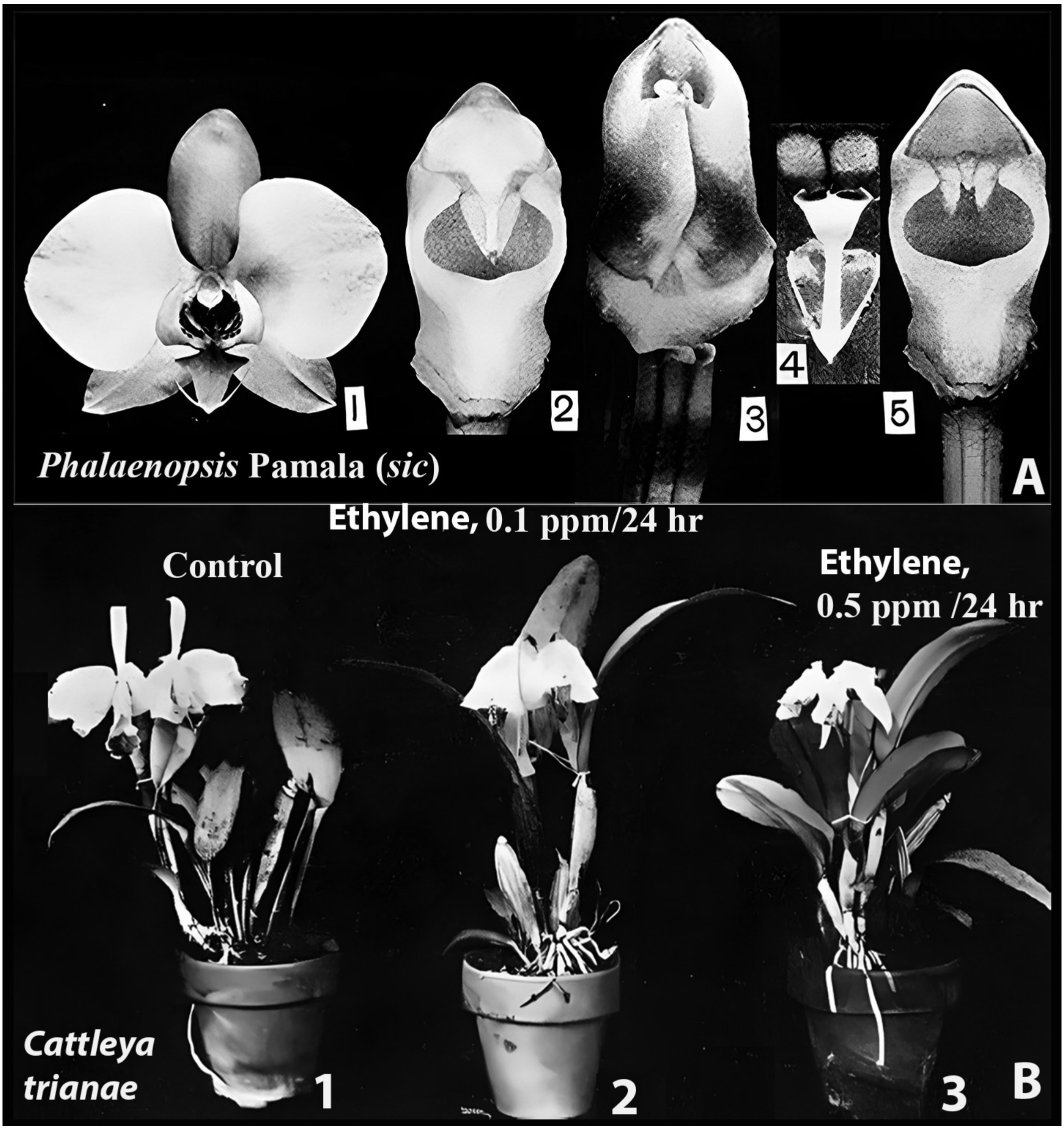


Figure 7. Pollination and ethylene effects on orchid flowers. **A**. *Phalaenopsis* Blume Pamala (*sic*). **1**. Unpollinated flower. **2**. Gynostemium (column) of unpollinated flower. Light grey horizontally elliptical area is the stigma. **3**. Gynostemium following pollination. **4**. Pollinarium. **5**. Gynostemium after removal of the pollinia. Light grey triangular area on top is where the pollinarium was located. The barely visible thin dark line at the base of the light grey area is part of the rostellum; two horn like structures pointing down are also parts of the rostellum; dark grey horizontally elliptical area is the stigma. This figure duplicates parts of Fig. 1B. It is included here intact with no additional labels because of its historical value. The black numerals on white background are as in the original. **B**. Effects on ethylene on *Cattleya* flowers. Exposure to the gas causes wilting. Sources: A. Curtis (1943). He spelled the grex name as "Pamala," but the correct name is "Pamela." B. Davidson (1949) with notations added.

One of the preeminent orchid systematists during the last half century, Robert Louis Dressler (1927–2019; Fig. 9H) noted that since Darwin, "most authors. . . defined the rostellum. . . as the median stigma lobe" (Dressler, 1989). However, since "the boundaries between the stigma lobes are often unclear, . . . authors used the term as Richard did" (Dressler, 1989). Dressler's well-reasoned perspective defined the ros-

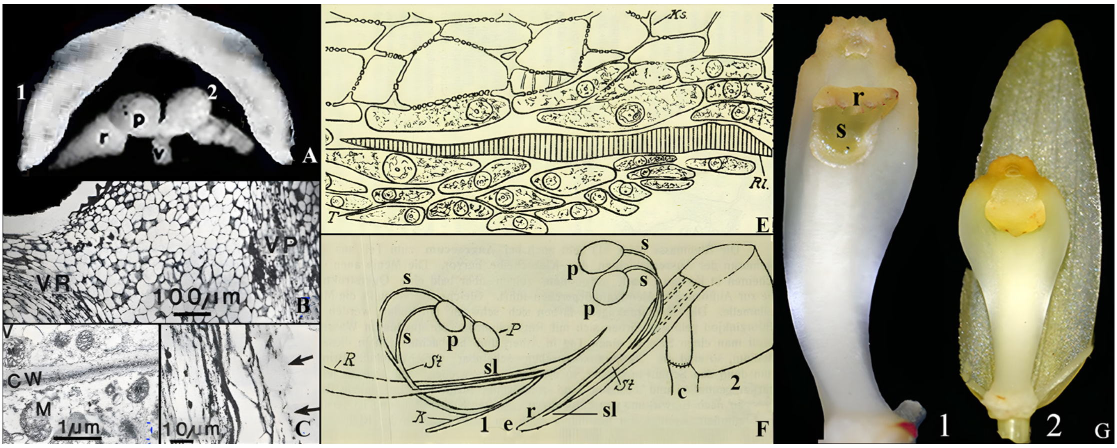


FIGURE 8. Rostella: intact and microscopy. **A**. Excised rostellum of *Cymbidium* Jungfrau. **1**. Rostellum only. About 9–10 mm wide (side to side), 12 mm wide (front to back), 2–3 mm thick. **2**. Rostellum with pollinaria in place. Lettering: p, pollinia; r, rostellum; v, viscidium. **B**. Light microscope photograph of *Phalaenopsis* Blume gynostemium showing vascular strands leading to the rostellum (VR) and pollinia (VP). **C**. Electron microscope photograph of rostellum cells showing numerous mitochondria (M), cell wall (CW), and vacuole (V). **D**. Light microscope photograph of the wounded outer edge of the rostellum where the viscidium was attached, showing wound where cells are degenerating (arrows). **E**. Separation layer between the viscidium and rostellum in *Vandopsis lissochiloides* Pfitzer. Lettering as in the original: Ks, viscidium; Rt, separation area, break or crack where wounding occurs; T, separation tissue consisting of loosely packed cells. **F**. Column, pollinarium and rostellum of *Cyrtorchis chailluana* Schltr. 1. Lower end of rostellum with detached pollinarium. The stipe is bifurcated about half the distance above the viscidium, with every branch carrying a single pollinium. 2. Column following the removal of the anther cap. The stipe is detached from the rostellum. Dotted line indicates he original position of the stipe. When the pollinarium is removed a slit (wound) forms on the rostellum. Lettering: Cursive letters are on the original. Modern Times Roman font letters were added. c, column; e, tip of the extension of the rostellum; K, viscidium; p, pollinium; R and r, rostellum; s, branch of the stipe; sl, slit; St, unbranched part of stipe. Light grey cast in E and F is due to aging of the original. **G.** *Coelogyne fimbriata* Lindl. 1. Column showing stigma and rostellum before pollination. 2. Rostellum (yellow, nearly oval) covering stigma after pollination. Sources: Joseph Arditti (A), Dr. Michael S. Strauss (B–D), a graduate student in JA's laboratory at the time; Gellert, 1923 (E–F), and courtesy of J.-C. Cheng and Y.-B. Luo (G). The yellowish and greyish cast of E and F are due to the aging of the original.

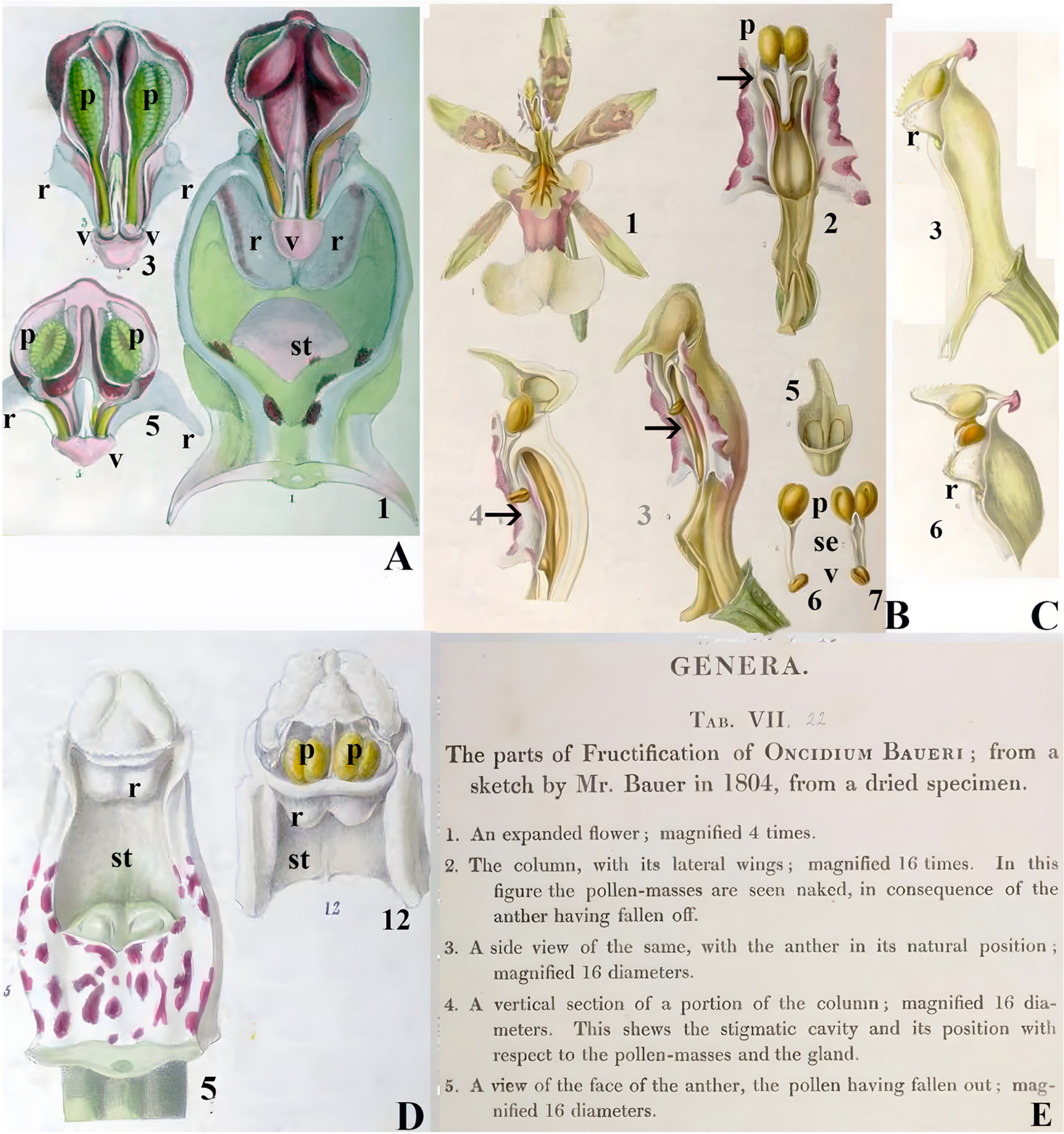
tellum as the "modified portion of the median stigma lobe" (Dressler, 1961). Developmental studies on *Bletia purpurea* (Lam.) DC., *Malaxis commelinifolia* (Zoll. & Moritzi) Kuntze, *Calanthe* × *veitchii* R.H.Torr and other Epidendroid species "conformed that the rostellum is the upper part of the median stigma" and originates entirely from the primordium of the median carpel (Kurzweil, 1987a). In Orchidoid species, the rostellum is three-lobed and originates "entirely from the median carpel" (Kurzweil, 1987b). The rostellum in Neottioideae develops completely from the upper part of the median stigma lobe (Kurzweil, 1988). In the Australian *Genoplesium fimbriatum* (R.Br.) D.L.Jones & M.A.Clem. (*Prasophyllum fimbriatum* R.Br.), the rostellum is likewise formed from the median carpel (Kurzweil *et al*., 2005).

Leslie Andrew Garay (1924–2016; Fig. 11C), a distinguished orchid systematist of the 20th century, described the rostellum as "the median stigma [which] during reorganization of the flower has evolved into a new organ. . . with a specific function. It is the controlling and ensuring device for fertilization" (Garay, 1960). Although he did not address the antennae of *Catasetum* as Darwin did, his definition appears broad enough to include them.

It has been suggested that "the term 'rostellum' is used in various senses, sometimes referring to the entire median stigma-lobe and *sometimes* (emphasis added) to the extension only" (Rasmussen, 1985). In fact, the term "rostellum" is generally applied for all parts of this structure.

The rostella of *Himantoglossum hircinum* (L.) Spreng. (*Loroglossum hircinum* (L.) Rich.; Heusser,

Figure 9. Students of the rostellum. **A.** Ludovico (Louis) Claudio (Claude) Marie Richard (1754-1821). **B.** Robert Brown (1773-1858). **C.** John Lindley (1799-1858). **D.** Charles Robert Darwin (1809-1882). **E.** Max Hirmer (1893-1981). **F.** Ernst Hugo Heinrich Pfitzer (1846-1806). **G.** Peter Vermeulen (1899-1981). **H.** Robert Dressler (1927-2019). **I.** Francis (Franz) Andreas Bauer (1758-1840). **J.** George Bentham (1800-1884). **K.** Olaf Hagerup (1889-1961). **L.** John Stephens Henslow (1796-1861), friend and mentor to Darwin. Sources: A, https://images.shoutwiki.com/roses/6/6c/Richard%2C_Louis_Claude_Marie.jpg and https://archives.somme.fr/https://archives.somme.fr/ark:/58483/j39p-8wr04cq6. B-D, F, I-L, Wikipedia; E. Courtesy Thomas Zuhr, Hirmer Verlag and the Hirmer family; G, Joseph Arditti; H, *Orchids*.



GENERA.

TAB. VII. 22

The parts of Fructification of ONCIDIUM BAUERI ; from a sketch by Mr. Bauer in 1804, from a dried specimen.

1. An expanded flower ; magnified 4 times.
2. The column, with its lateral wings ; magnified 16 times. In this figure the pollen-masses are seen naked, in consequence of the anther having fallen off.
3. A side view of the same, with the anther in its natural position ; magnified 16 diameters.
4. A vertical section of a portion of the column ; magnified 16 diameters. This shews the stigmatic cavity and its position with respect to the pollen-masses and the gland.
5. A view of the face of the anther, the pollen having fallen out ; magnified 16 diameters.

FIGURE 10. Rostella painted by Francis (Franz) Bauer with captions by John Lindley. **A.** Fructification. Plate 3. Illustration 1, original caption, "A front view of the column of *Orchis mascula* with the base of the labellum, shewing the position of the anther with its pouch, the cells of the former being partially open, so as to shew the pollen within; on each side of the anther are the two glandular tumors, which are the rudiments of stamens; magnified 15 times." Illustration 3, original caption. "A front view of the anther with the cell opened, so as to exhibit the pollen masses inside in their natural position; magnified 15 times. The pouch in the glands of the pollen-masses are confined is forced a little down." Illustration 5. "A transverse section of fig 3; magnified 15 times. In this the inner structure of the cells of the anther is exhibited, and the pouch is in its natural position." Illustrations numbers (except for modern bold face letters and numbers, which were added for clarity), spellings, lack of italics for species names, and spaces before semi colons are as in the original. "Gland" seems to refer in illustration 3 to what is currently called "viscidium." It is not clear to what "glandular tumors" refers to. Both the location of the "pouch" and the attachment of the "gland"

(viscidium) to it in illustrations 1, 3 and 5 indicate that it is the rostellum. Numbers 1, 3 and 5 refer to illustration numbers in the original plate 3 (which contains 16 illustrations). Lettering: ac, anther cap; p, pollinia; r, rostellum; st, stigma; v, viscidium. **B, E**. Genera Plate 7. Parts of the fructification of *Oncidium baueri* Lindl. Illustration 1. Expanded flower. Illustrations 2-6. See caption in E. In all illustrations anther refers to the anther cap, caudicula is the stipe (se), gland is the viscidium (v) and pollen-masses is the pollinia (p). In 2, 3 and 4 the arrows point to what seems to be the rostellum. Both B and E are fully reproduced to show the language, terminology, descriptions and spellings as they were used by Lindley. **C.** Genera plate 8. Fructification of *Galeandra baueri* Lindl. Illustration 3. Side view of column. Illustration 6. Side view of the apex of the column with the anther cap raised up to show pollinia, their stipes and the viscidium. What seems to be the rostellum (r) was painted by Bauer, but not identified. **D.** Genera Plate 6. Parts of fructification of *Dendrobium speciosum* Sm. Illustration 5. Front view of the column. Illustration 12. Apex of the column with the anther cap removed to show pollinia, the rostellum is shown, but not identified. **E.** Original captions for B. Lettering: p, pollinia; r, what seems to be the rostellum; st, stigma. Source: A-E, Bauer and Lindley, 1830-1838. Some of the images are not sharp due to the aging of the original.

1914) and *Cattleya labiata* Lindl. (Rotor & MacDaniels, 1951) are formed by the invagination of part of the stigma and subsequent forward growth. Because of these and similar observations, the rostella of these and other orchids, such as *Cymbidium*, were thought to represent a third stigma (Gellert, 1923; Heusser, 1914; Hirmer, 1920; Rotor & MacDaniels, 1951; Wolf 1865–1866). In *Herminium monorchis* (L.) R.Br., the rostellum originates from “the middle lobe (apex) of the median carpel lobe” (Rudall *et al*., 2013). In the Pleurothallidinae, the median stigmatic lobe of the carpel serves as the origin of the rostella, with this lobe differentiating before the lateral lobes (Cardoso-Gustavson *et al*., 2017). Thus, “the rostellum is accepted as a modified. . . portion of the median stigma lobe” (Cardoso-Gustavson *et al*., 2017).

There is a general agreement that rostella produces a viscid substance (Cardoso-Gustavson *et al*., 2017), which supports the theory of their stigmatic origin since stigmas typically produce sticky substances. However, other glands in plants produce similar secretions. *Spiranthes* Rich. provides evidence supporting the stigmatic origin of this sticky substance. In these orchids, two functional stigmas are located below an elongated third stigma, the rostellum, whose underside has been described as a functional, presumably sticky, stigma (Garay, 1960).

Theodor Franz Wolf (1841–1924; Fig. 11B), a theologian, geologist, and botanist, studied the rostella of European, Asian, and American orchids in the late 1800s (Fig. 4) and recognized the taxonomic significance of the rostellum. He observed that rostella can vary in size and form, consist of parenchyma cells along with spiral vessels, and produce adhesive in pads of various shapes.

Ernst Hugo Heinrich Pfitzer (1846–1906; Fig. 9F), Professor of Botany and Director of the Botanical Garden at the University of Heidelberg, and a leading German orchid biologist of the late 1800s, was the first to use the rostellum as a taxonomically descriptive feature extensively. In his contributions to Adolf Engler (1844–1930) and Karl Anton Eugen Prantl’s (1849–1893) *Die Natürlichen Pflanzenfamilien* (published from 1844 until 1930), Pfitzer produced 605 illustrations and 192 figures of the Orchidaceae, many of which depict the rostellum’s variability in size and shape (Fig. 5).

The most detailed and impressive early study of the rostellum was conducted by Max Hirmer (1893–1981; Fig. 9E), a German botanist, photographer, publisher, archaeologist, historian, and art student, who was dismissed as a professor by the Nazis in 1936 for political reasons. Hirmer studied the rostellum because, as he noted, “Darwin left open the organographic connection between the rostellum and the anther [and he studied them] in greenhouses in England and not in [the natural habitat] of the orchids . . . and the visiting [pollinators]” (Hirmer, 1920). He created longitudinal sections of numerous flowers, illustrating the differences in size and shape among rostella (Fig. 6). His drawings confirmed both the morphological variability of rostella and their consistent location within the gynostemium. Hirmer was also the first to include photomicrographs of the gynostemium in a publication, offering an unparalleled study of these intriguing yet somewhat mysterious organs in orchid flowers.

Hirmer reviewed previous research and statements on the function and taxonomy of the rostellum, reaching conclusions (beyond physiological aspects) that re-

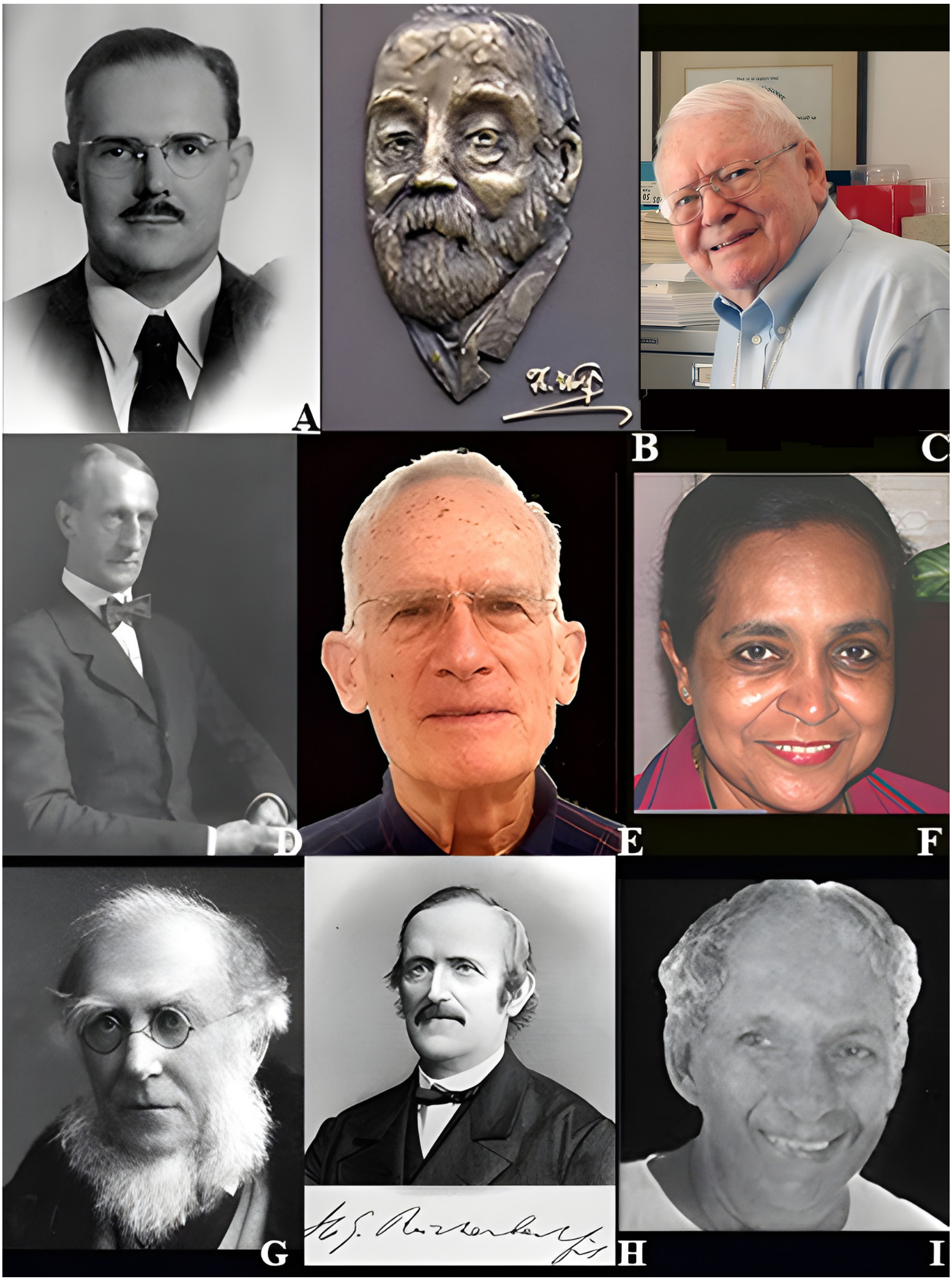


FIGURE 11. Rostellum investigators. **A**. John Thomas Curtis (1913-1961). **B**. Theodor Franz Wolf (1841-1924). **C.** Leslie Andrew Garay (1924-2016). The original photograph was out of focus and required sharpening with Photoshop. No other photograph was available. **D**. Oakes Ames (1874-1950). **E**. Arthur V. Chadwick (1943-). **F.** Helen Nair (Mrs. James Bonney) (No year here?). **G**. Joseph Dalton Hooker (1817-1911). **H**. Heinrich Gustav Reichenbach (1823-1889). **I**. Bangalore Gundappa Lakshminarayana Swamy (1918-1980). Sources: A, courtesy Dr. Kenneth Cameron; B, D, G-I, (1874-1950) Wikipedia; C, courtesy Bill Thoms; E, Courtesy Dr. A. V, Chadwick; F, Joseph Arditti.

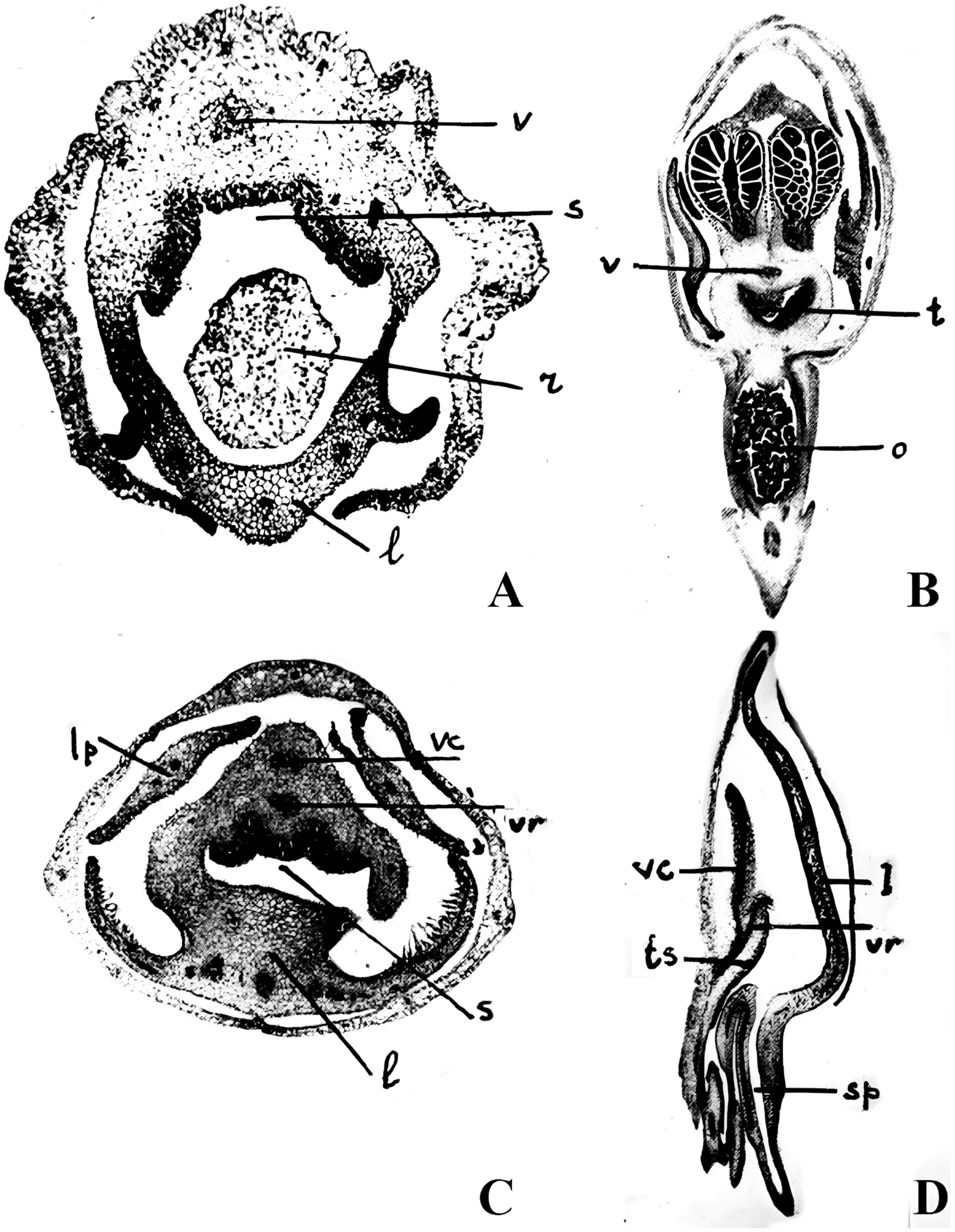


Figure 12. Stigmas with three lobes. **A**. Transverse section of *Himantoglossum* Spreng., flower. **B**. *Ophrys* L., no species listed in the original. **C**. Transverse section of *Ophrys* L., flower. **D**. *Galeeis spectabilis* (L.) Raf. [*Galeorchis spectabilis* (L.) Rydb.] Lettering, handwritten as in the original: l, lip; lp, lateral petal in C; r, part of the rostellum in A; s, sigma with three separate lobes in A, C; sp, spur in D; t, third tongue shaped stigmatic lobe in B; ts, third stigmatic lobe in D; v, vascular bundle in A; vc, vascular bundle of anther in C; vr, vascular bundle of rostellum in C, no explanation given in the original for D; vs, vascular bundle for anther in D. Source: Vermeulen, 1955.

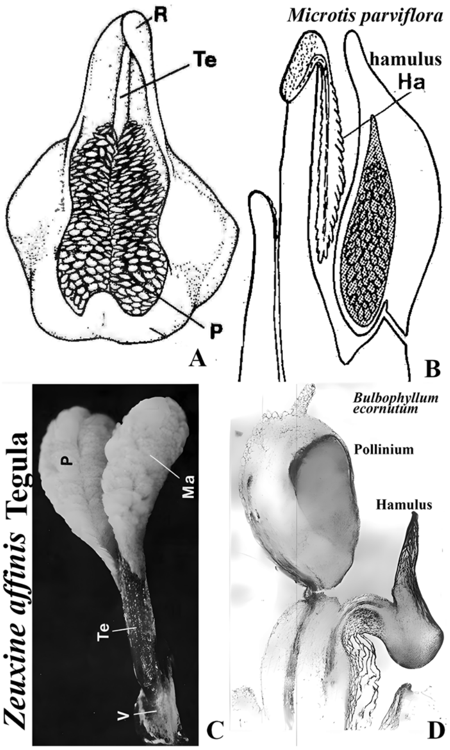


FIGURE 13. Tegula and hamulus. **A**. Line drawing of *Zeuxine affinis* (Lindl.) Benth. ex Hook.f., tegula. **B**. Line drawing of *Microtis parviflora* R.Br. hamulus. **C**. Photograph of *Zeuxine affinis* (Lindl.) Benth. ex Hook.f., *tegula*. **D**. Longitudinal section of *Bulbophyllum ecornutum* (J.J.Sm.) J.J.Sm., hamulus. Explanation of symbols: Ha, hamulus; Ma, massula; P, pollinium; R, rostellum; Te, tegula; V, Viscidium. Sources: A, B, Rasmusen (1982); C, D, Rasmussen (1986a).

main valid regarding the rostellum's role, its functions, and its relationship with the pollinia and their adhesive pad, the viscidium. His comprehensive discussion spans anatomy, morphology, microscopy, pollen, pollinia, pollination, taxonomy, and evolution. One of his key conclusions was that the rostellum originates from the median stigma, which "no longer retains the function of pollen reception, but at least in its apical part functions in pollen transmission through the formation of an adhesive mass" (Hirmer, 1920 and see above). Hirmer's meticulous and insightful work deserves more recognition than it has received.

In his study of rostella in the Ophrydeae (now Orchideae) and Neottiae (now Neottieae), Dutch botanist Peter Vermeulen (1899–1981; Fig. 9G) observed structural differences in the rostellum between these groups (Vermeulen, 1959). He also noted that "in many Ophrydeae [and] several Neottiae," the stigma has three lobes (Fig. 12), which is "contrary [to] the opinion of Darwin (Vermeulen, 1959)." Vermeulen believed that in Neottieae with three stigmas, the rostellum forms "in connection with, or above the median stigma lobe." At the same time, in the more primitive Orchideae, it originates from the lateral stigma lobes. He suggested that rostella may not have a single origin.

Existing rostellum nomenclatural and origins questions. Despite extensive discussions (Arditti, 1992; Arditti & Flick, 1974; Cardoso-Gustavson *et al.*, 2017; Dressler, 1981, 1993; Rasmussen, 1982, 1985, 1986a, 1986b, Valencia-Nieto *et al.*, 2018; van de Pijl & Dodson, 1966; Vermeulen, 1955; Yam *et al.*, 2009), questions remain surrounding the rostellum's structure and classification due to insufficient information (Cardoso-Gustavson *et al.*, 2017). For example, in species with three stigmas (Fig. 12A–D), such as *Coeloglossum* Hartm. (a synonym of *Dactylorhiza* Neck. ex Nevski), *Dactylorchis* (Klinge) Verm. (a synonym of *Dactylorhiza*), *Galeorchis* Rydb. (a synonym of *Galearis* Raf.), *Himantoglossum* Spreng., *Ophrys* L., *Orchis*, and *Platanthera* Rich., what is assumed to be the rostellum may, in fact, represent a different organ.

According to Garay (1960 and personal communication to J. Arditti around 1973), this structure "must be given a different name or it is merely connective tissue between the two thecae of the anthers." These interpretations suggest that the definition of the rostellum might need broadening to encompass variations in its position, origins, and functions, indicating a need for further research.

In any case, if the rostellum or rostellar structures originated strictly from stigmas, then no orchids would possess both a rostellum and three stigma lobes. However, contrary to Darwin's view, there are cases where such lobes exist (Fig. 12), as seen in *Orchis*, *Galeorchis*, *Ophrys*, *Himantoglossum*, *Dactylorchis*, *Coeloglossum*, and *Platanthera* (Vermeulen, 1955, 1959). This suggests two possibilities. The first is an independent origin for some rostellar structures, as Vermeulen

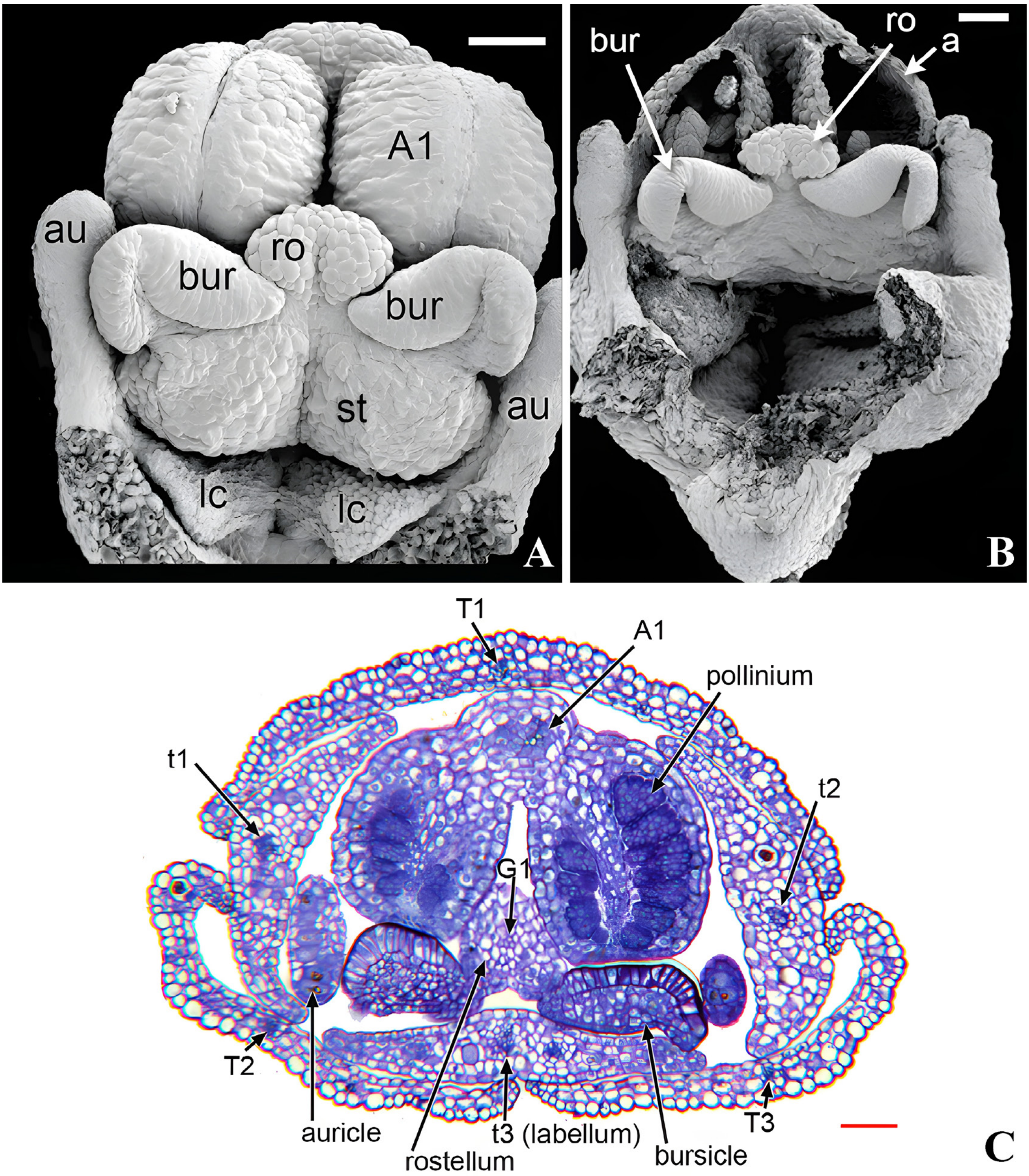


Figure 14. Development of rostellum in *Herminium monorchis* (L.) R.Br. **A**. Scanning electron microscope of a stage in rostellum and bursicle development. **B**. Scanning electron microscope of dissected gynostemium of anthetic flower showing developed rostellum. **C**. Light microscope photograph of a serial transverse section of a pre-anthetic bud early state of rostellum development and vasculature. Explanation of symbols: A1, putative vascular bundle of outer whorl stamens; a, fertile anther; au, auricle; bur, bursicle; lc, lateral carpel; ro, rostellum; st, stigmatic surface, T1, T2, stamens; t1, t2, petals; t3, labellum; Scales, bar in A, B, C, 100 µm. Source: Rudall *et al*. 2013.

(1959) proposed. The second is that the origin of the rostellum in orchidoids may be the same as that in epidendroids, as suggested by Kurzweil (1987a, b).

Leslie A. Garay also suggested that if the term "rostellum" is used strictly according to its original definition, a different term might be required for these rostellar structures (personal communication, ca. 1973, to J. Arditti from the late L.A. Garay, then at the Botanical Museum, Harvard University). Alternatively, what appears to be a rostellum could be connective tissue between the anthers. These interpretations highlight the complexity of the rostellum's origins and functions and suggest that the traditional definitions may need to be broadened to reflect its diverse structural forms and potential variations in origin.

Rostellum and taxonomy. As previously stated, the rostellum has long been used in the description and/or revision of orchid species (Batista *et al*., 2016, Eftimov, 2022; Jakubska-Busse *et al*., 2020; Pfitzer, 1889). Significant morphological differences in rostellum structure can be observed even between species within the same genus, such as *Acianthera aphthosa* (Lindl.) Pridgeon & M.W.Chase and *Acianthera obovata* (Lindl.) Pridgeon & M.W.Chase (see Table 1; Cardoso-Gustavson *et al*., 2017), justifying its use in taxonomic classification. In the predominantly African genus *Satyrium* Sw., the rostellum structure was deemed taxonomically and phylogenetically significant enough to aid in establishing phylogenetic relationships (Johnson & Kurzweil, 1998; Kurzweil & Linder, 1999); however, this was later contradicted by molecular data (personal communication to J. Arditti, 2023, from Hubert Kurzweil, now retired from the Singapore Botanic Gardens).

At one time, subtribe Calypsoinae (= Corallorhizinae) was considered potentially paraphyletic, partly due to the presence of hamulus or tegula (Freudenstein, 1994). The hamulus (Fig. 13B, D) is a stalk formed by the distal section of the rostellum, while the tegula (Fig. 13A, C) is a cuticular strap originating from the dorsal epidermis of the rostellum. Hamuli are present in *Aplectrum* (presumably *Aplectrum* Nutt., not *Applectrum* Blume), *Corallorhiza* Gagnebin, *Cremastra* Lindl., and *Oreorchis* Lindl. Based on a cladistic analysis of morphological features, it was suggested that these genera form the core of Calypsoinae and are closely related to a clade that includes *Tipularia* Nutt., *Calypso* (presumably *Calypso* Salisb., not *Calypso* Thouars), and *Yoania* Maxim. *Govenia* Lindl. is likely most closely related to Cymbidieae, such as *Eulophia* R.Br., due to its cellular epidermal pollinium stalk and *Cymbidium*-type velamen. *Dactylostalix* Rchb.f. and *Ephippianthus* Rchb.f. appear to represent earlier diverging lineages within the Epidendroideae.

In summary, the size and morphology of rostella are sufficiently variable (Fig. 1–6, 10, 12) to be useful in orchid taxonomy, as has been discussed by Valencia-Nieto *et al*. (2018).

Development and formation of the rostellum. Extensive studies of the development and formation of the rostellum have been undertaken only more recently (Cardoso-Gustavson *et al.,* 2017, Freudenstein *et al*., 2002; Rasmussen 1982, 1985, 1986a, 1986b; Rudall *et al*., 2013, Valencia-Nieto *et al.,* 2018).

Extensive studies on the development and formation of the rostellum have only recently been conducted (Cardoso-Gustavson *et al*., 2017; Freudenstein *et al*., 2002; Rasmussen, 1982, 1985, 1986a, 1986b; Rudall *et al*., 2013; Valencia-Nieto *et al*., 2018). In the early stages of rostellum ontogeny in *Bulbophyllum lomsakense* J.J.Verm., Schuit. & de Vogel (Table 1), whose synonymy with *Sunipia thailandica* (Seidenf. & Smitinand) P.F.Hunt is debated, the rostellum's lobes appear as mere knobs, later becoming hammer-shaped at the apex (Rasmussen, 1986a). Just before anthesis, the rostellum lobe differentiates into a pollinium stalk and a "supporting tray" (Rasmussen, 1986a).

Pollinium stalks that arise from the rostellum are referred to as stipes (singular: stipe; Rasmussen, 1986a). Gene-derived stalks from the rostellum have been termed tegulae (singular: tegula; Rasmussen, 1986a; Fig. 13). Tegulae are found in epidendroid (formerly vandoid) orchids and in the Australian genus *Prasophyllum* R.Br. (see Rasmussen 1986a for a review). Upon removal, tegulae leave a scar on the rostellum, which is physiologically significant but likely not taxonomically relevant. In *Phalaenopsis pulcherrima* (Lindl.) J.J.Sm. (*Doritis pulcherrima* Lindl.), the rostellum is a long, pointed projection (Rasmussen, 1986a; Table 1).

Observations indicate a lack of strict uniformity in the development, shape, and precise positioning of rostella. In the musk orchid, *Herminium monorchis* R.Br., a European terrestrial species, the rostellum differentiates through "deep trilobing of the apex of the median carpel, which is highly reminiscent of the trilobing of the

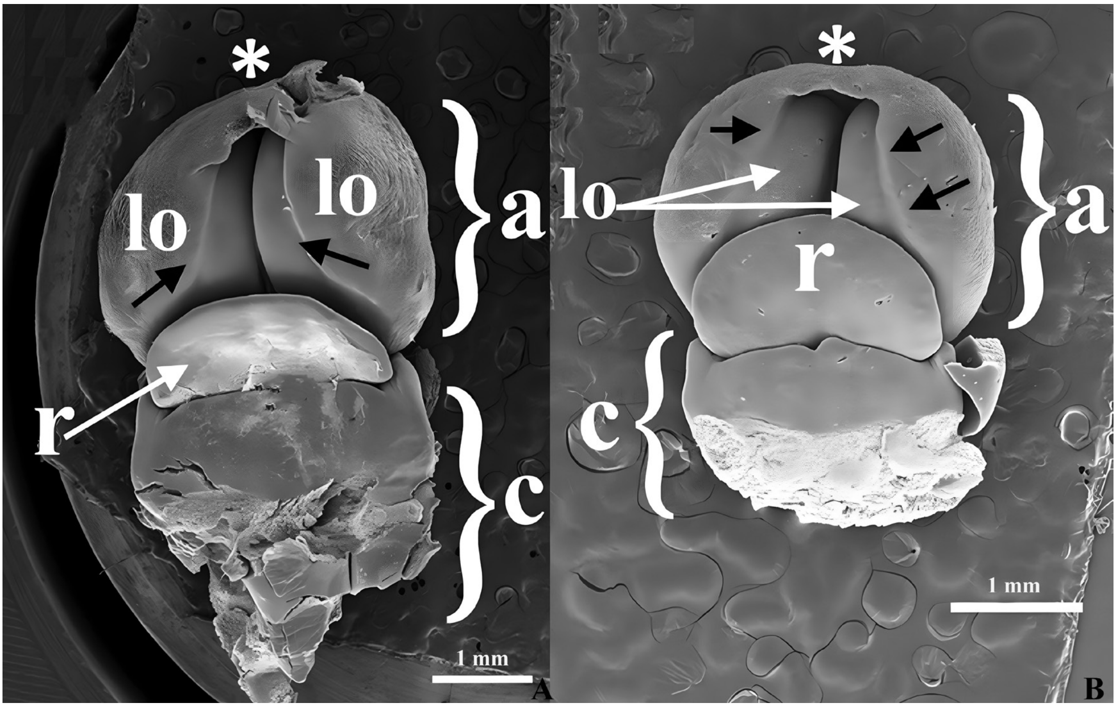


Figure 15. Scanning electron microscope photographs of early stages of rostellum and anther development in *Chysis*. **A**. *Chysis bractescens* Lindl. **B**. *Chysis limminghei* Linden & Rchb.f. Explanation of symbols: *, apex of anther; black arrows, longitudinal lines in epidermal tissue; a, anther; c, column; lo, lobule; r, rostellum. Source: Valencia-Nieto *et al*. 2018.

labellum. Such carpel lobing also suggests differential-perhaps prolonged-timing of gene expression during floral ontogeny" (Rudall *et al*., 2013; Fig. 14).

Significant diversity in floral morphology and pollination systems is evident in the Epidendreae (Valencia-Nieto *et al*., 2018). A comparative study of rostellar development and other floral organs in six subtribes of Epidendreae at the late anther stage recorded notable differences. For example, the developing rostellum in *Coelia triptera* (Sm.) Mutel (subtribe: Calypsoinae) is transverse, with rectangular cells that form many intercellular connections in the lower tissue layer. A layer formed by the mature rostellum separates the stigmatic surface (Valencia-Nieto *et al*., 2018).

Despite mentioning a "lack of rostellum in Bletiinae" (Valencia-Nieto *et al.,* 2018), the development of the rostellum in *Bletia purpurea* (Lam.) DC., is described as beginning with a transverse ridge, which forms a "defined rostellum" that projects "as a well-developed tongue shaped structure with rectangular epidermal cells" (Valencia-Nieto *et al.,* 2018; Table 1). Underneath it "is the stigmatic surface covered by the well-developed rostellum" (Valencia-Nieto *et al.,* 2018).

In *Chysis bractescens* Lindl. (Fig. 15) and *Chysis limminghei* Linden & Rchb.f., the developing rostellum at the anther's base is semi-lunate in shape and points upward, a position retained through later stages. In contrast, *Chysis laevis* Lindl. shows only two underdeveloped, inconspicuous projections (Valencia-Nieto *et al*., 2018).

In *Ponera juncifolia* Lindl., a species of Ponerinae, the obtriangular rostellum consists of two cell types and projects forward. One cell type is slender and elongated longitudinally, extending from the front to the middle part, while the other is glandular and produces abundant secretions (Valencia-Nieto *et al*., 2018).

Exudate production by the rostellum. In unopened flowers, the rostellum produces a mucilaginous exudate, described as visually resembling stigmatic exudate (Arditti & Flick, 1974; Cardoso-Gustavson *et al*.,

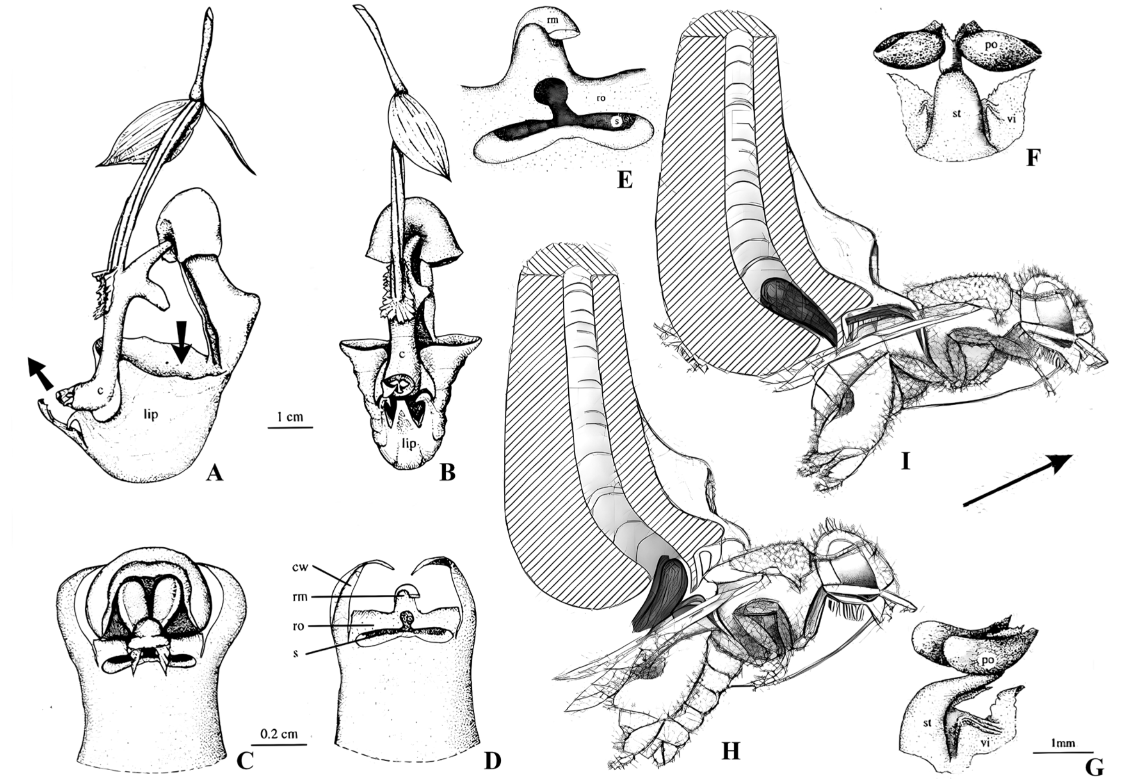


FIGURE16. *Coryanthes senghasiana* G.Gerlach, flower and its pollination. **A**. Lateral view of flower with one column wing, petals and sepals removed. **B**. Dorsal view of flower with one column wing, petals and sepals removed. **C**. View from above of apex of column before first visit by pollinator. **D**. View from above of apex of column after first visit by pollinator, which removed the pollinarium. **E**, **F**, **G**. Rostellum and pollinarium. **H**, **I**. Pollination, scraping of pollinia from pollination by the rostellum. Explanation of symbols: arrows in a, path of pollinator, which falls into the bucket (arrow on right) and escapes through narrow tunnel (arrow on left); c, column; cw, column wing; po, pollinarium; rm, rostellum mid lobe; ro, rostellum; s, stigma; st stipe; vi, wing. Source: Nazarov and Gerlach, 1997.

2017). This exudate is "copious and viscous" similar in appearance to the stigmatic exudate of *Zootrophion atropurpureum* (Lindl.) Luer and *Acianthera fenestrata* (Barb.Rodr.) Pridgeon & M.W.Chase (Cardoso-Gustavson *et al*., 2017), although its precise chemical composition and physical state remains unknown. In many orchid taxa, the pollinaria contain an "adhesive secreted by the. . . rostellum" (Freudenstein *et al*., 2002). In the Pleurothallidinae, the rostellum has a palisade epidermis that secretes a mucilaginous exudate resembling that of the stigma, released through cell walls and the cuticle (Cardoso-Gustavson *et al*., 2017).

In *Acianthera fenestrata*, pollinia and pollen tubes adhere to the rostellum, which has been interpreted to suggest that the rostellar exudate "assists adherence of the pollinia and the germination and growth of pollen tubes" (Cardoso-Gustavson *et al*., 2017). This adherence may be due to the physical properties of the exudate. At the same time, the germination and growth of pollen tubes suggest that the chemical compositions of rostellar and stigmatic exudates are likely similar or identical. However, while Cardoso-Gustavson *et al*. (2017) study was of high quality, it is important to note that it: a) included only a few orchid species, and b) did not involve detailed chemical and physical analyses of rostellar and stigmatic exudates. Consequently, its findings may not be representative of all taxa. Given the diversity within orchids, additional research could reveal findings that either support, expand upon, or challenge current knowledge.

In many orchids, the rostellum contains "a sharply defined body made up of rostellar glue and usually

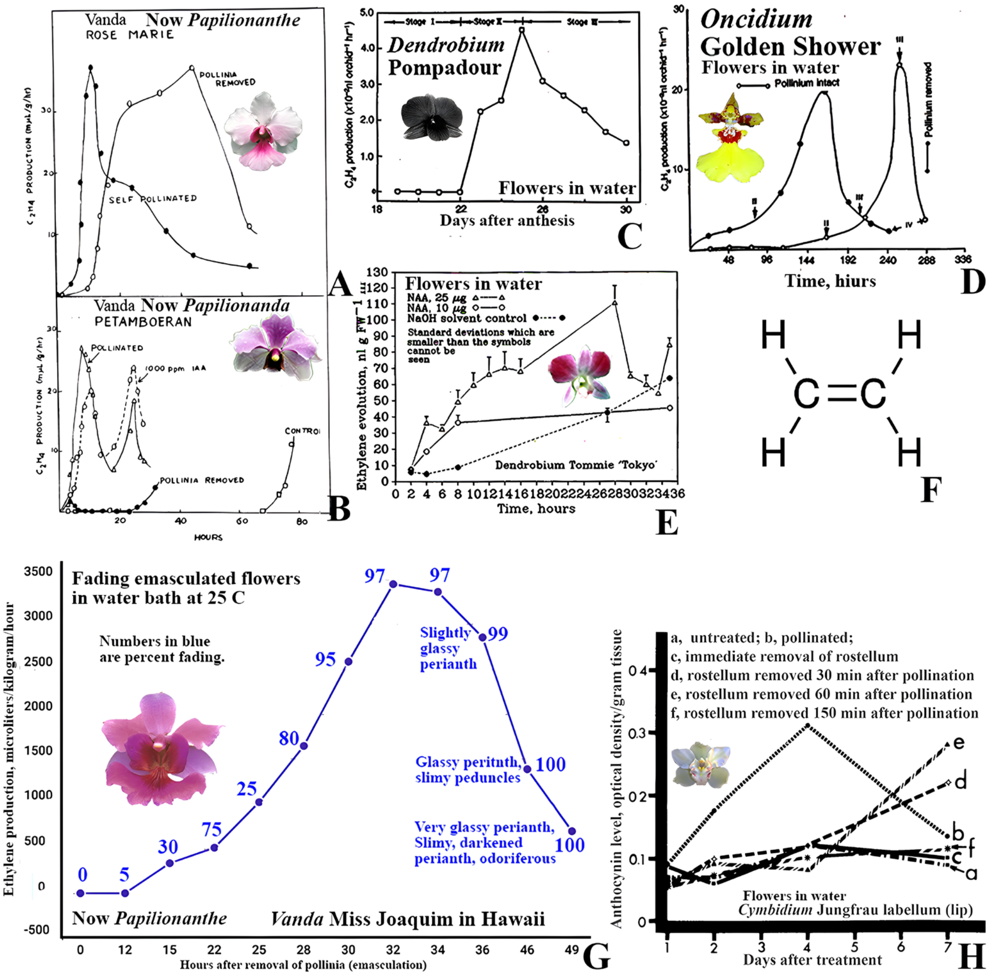


Figure 17. Ethylene evolution and its effects. **A**, **B**. First graphic presentation of ethylene evolution by orchid (*Vanda*) flowers following pollination, emasculation (removal of pollinia), and auxin (indoleacetic acid, IAA) treatment. **C**. Ethylene evolution by senescing untreated cut *Dendrobium*, flowers in water. **D**. Ethylene evolution by intact and emasculated *Gomesa* R.Br. Golden Shower flowers. **E**. Ethylene evolution by flowers of *Dendrobium*. Tommie 'Tokyo' after auxin application (naphthaleneacetic acid, NAA) to stigmas. **F**. Ethylene. **G**. Ethylene evolution by fading flowers of *Vanda* R. Br. Miss Joaquim, a natural hybrid, which is now the National Flower of Singapore. **H**. Effects of pollination and removal of the rostellum (all of which are known to produce ethylene) on anthocyanin production by the labellum (lip) of *Cymbidium* Jungfrau flowers. Patterns of ethylene evolution by all orchids (A-E, G, and H) are similar.Timing and level of ethylene evolution differ. Source: A, Burg and Dijkman, 1967 with permission from Dr. Yunde Zhao, Editor in Chief of *Plant Physiology*; C, D, courtesy Dr. Helen Nair; E, Nair *et al.*, 1991; F, Wikipedia; G, graph prepared for this article from data in Akamine, 1963; H, Arditti & Flick, 1974. Sources of photographs: A, D, G, courtesy Dr. Tim Wing Yam; B, E, H, Joseph Arditti; C, courtesy Dr. Helen Nair.

some cellular tissue" (Dressler, 1989). Early literature often refers to this area as a gland or glandular structure, even though it is not strictly a gland. Other terms include retinaculum, proscollum, viscid disc, and viscidium, with Dressler (1989) favoring "proscolla". At anthesis, pollinia attach to this area "directly or by a stipe" (Dressler, 1989). To avoid confusion, Dressler and Salazar (1991) proposed the term "viscarium" to denote "the glue and glue-producing area in those orchids that do not have a distinct (removable) viscidium" because "it is better to use a special term in place of rostellum for a structure that is only part of the rostellum" (Dressler & Salazar, 1991).

Rostellum and pollination. Darwin's studies, along with those of other researchers (for a review, see Arditti, 1992), led to the conclusion that the rostellum plays a major role in orchid pollination. This conclusion is well supported, as indicated by the examples below.

As previously mentioned, Charles Darwin developed a keen interest in the rostellum (for a review, see Yam *et al*., 2009), studied it extensively (Darwin, 1904), and wrote: A) "Pollen masses are never retained on the rostellum except by accident.", B) in some orchids, such as *Vanda* (with some species now under *Papilionanthe* Schltr.), pollinaria are attached to the rostellum (Fig. 2A). C) the rostellum of *Catasetum* ([presumably *Catasetum* Rich ex Kunth, not *Catasetum* Blind.; (Fig. 2B) has "lost the normal [stigmatic] function of being fertilized" and "its shape is most singular with the upper end thickened, bent over and produced into two long. . . antennae", D) additionally, variations in the structure of rostella can be found across different orchid species.

In *Cyrtorchis chailluana* (Hook.f.) Schltr., the column is very short, the rostellum is long and extended, and the pollinia are positioned on two separate, elongated stalks that merge into a single stipe near the rostellum (Fig. 8F). When pollinaria (i.e., pollinia, stipe, and viscidium) are removed from the rostellum, a long tear or slit forms in its extension, facilitating detachment (Gellert, 1923; Fig. 8F).

In *Oncidium wentworthianum* Bateman ex Lindl. and *Oncidium otogaya* (an unverified taxon not listed in IPNI, Plants of the World Online, or the RHS List of Orchid Hybrids), pollinaria removal involves a two-stage process. The mechanical resistance of this detachment process has been measured (Thielen *et al*., 2021). The first stage involves the removal of the anther cap, which protects the pollinia and prevents the premature detachment of young, immature pollinaria. Once the pollinaria mature, the anther cap sheds, initiating the second stage: a detachable bond forms between the pollinarium and the rostellum. Pollinators can overcome this bond by applying a force of at least 10.8 mN (in *O. otogaya*) or 12.6 mN (in *O. wentworthianum*) to the viscidium, thereby breaking the connection and allowing for pollinarium removal.

Some orchids, such as species of *Catasetum* (Darwin, 1904), do not display stigmatic functionality in their rostella. However, certain autogamous species retain or reacquire the rostellum. In an auto-pollinating variant of *Bulbophyllum bicoloratum* Schltr., rostellum penetration and pollen tube growth have been observed, suggesting that the non-vascularized parts of its rostellum may contain stigmatic tissue (Gamisch *et al*., 2013). Rostellum penetration has also been documented in *Eulophia nyasae* Rendle, though this may not result from self-pollination (Gamisch *et al*., 2013; Williamson, 1984). Despite these observations, some rostella are considered unsuitable for pollen germination (Cardoso-Gustavson *et al*., 2017), potentially due to orchids' specific pollen germination requirements, which appear more stringent than those of other plants (Kemeç-Hürkan *et al*., 2015; Pritchard & Prendergast, 1989; Rao & Lee, 1973; Sanford *et al*., 1963).

This inability of the rostellum to support pollen germination has evolutionary advantages. In orchid pollination, pollen germinates on the stigma in a position that allows the pollen tubes to reach the ovary and fertilize ovules, leading to seed formation. In contrast, pollen tubes germinating on the rostellum may be unable to reach the ovary, thus preventing successful fertilization and reproduction.

In *Neottia ovata* (L.) Bluff & Fingerh. [*Listera ovata* (L.) R.Br.], pollinia adhere to the pollinator's face with the "help of the explosive mechanism of the rostellum" (Nazarov & Gerlach, 1997). When the pollinator visits another flower, the pollinia are inserted into the stigma (Nilsson, 1981). In *Cephalanthera longifolia* (L.) Fritsch., pollinia attach to the thorax of the pollinating vector, *Halictus* Latreille. Upon a subsequent visit to a flower, the rostellum scrapes the pollinia of the pollinator (Nazarov & Gerlach, 1997). Species of *Coryanthes* Hook. are pollinated when the pollinator passes through a narrow tunnel between the labellum and the gynostemium while escaping from a liquid-filled bucket. As the pollinator moves through the tunnel, the rostellum removes the pollinia (Nazarov & Gerlach, 1997; Fig. 16).

An intriguing and unique function of the rostellum has been observed in the self-incompatible, food-mimicking orchid *Coelogyne fimbriata* Lindl. in China. This orchid has a large rostellum that "projects beyond and between the stigma and the anther"

(Cheng *et al*., 2009) and forms a flap over the stigma (Fig. 8G1). Within 24 hours after pollination, the flap bends down, covering the stigma (Fig. 8G2). This prevents additional pollen deposition and causes visiting wasps, which might otherwise attempt to pollinate, to back away (Cheng *et al*., 2009). Orchids have evolved various mechanisms that prevent, or at least discourage, repeat visits by pollinators to flowers that have already been pollinated.

Pollinia typically adhere to pollinators via the viscidium, which is named for the viscid substance produced by the rostellum. In most orchids, pollinia are attached to a stalk bearing the viscidium at its base, an important feature in orchid taxonomy (for discussions, see Rasmussen 1985, 1986a). One type of these stalks, the caudicula, originates from the tapetum and pollen mother cells (Rasmussen, 1985, 1986a). Orchids lacking caudiculae have viscidia originating from the rostellum (Freudenstein *et al*., 2002). Another type of stalk, the stipe, is formed from the rostellum (Freudenstein *et al*., 2002). Stipes are found in epidendroid and other orchid subdivisions and are formed by a strap of rostellar epidermis in epidendroid orchids (Rasmussen 1985, 1986a; Fig. 13).

Rostellum and post pollination phenomena. It is important to emphasize that the removal of pollinaria causes wounding of the rostellum (Fig. 8D–F). While this wound has no role in the transfer of pollen, it plays a significant physiological role in inducing post-pollination phenomena (discussed below). For a long time, pollination was thought to be the primary, perhaps sole, biological function of the rostellum. Oakes Ames (1874–1950; Fig. 11D) poetically described the rostellum as having “resigned itself to the altruistic function of bringing to its fertile sisters the fertilizing pollen of an anther” (Ames, 1946), a statement that is both teleological and anthropomorphic. While the rostellum indeed supports reproduction, it also initiates the senescence and eventual death of floral segments that have completed their functions once a flower is pollinated or emasculated (for reviews, see Arditti, 1979, 1992, Avadhani *et al*., 1994).

For over a century after its naming, the rostellum was studied primarily for its structural, taxonomic, and pollination-related characteristics. During this period, no one—not even Darwin—suspected it had an important physiological function. Given the state of plant physiology knowledge at the time (the discovery of the first plant hormone, auxin, was still about 65 years away) and the limited understanding of orchid physiology in particular, this oversight is neither surprising nor scientifically disappointing.

The definitions and descriptions discussed above do not address the physiological function of the rostellum (for reviews, see Arditti, 1992; Arditti & Flick, 1974; Avadhani *et al*., 1994). Although it was known that orchid flowers produce ethylene by the time Vermeulen, Dressler, and Garay formulated their definitions, the physiological role of the rostellum and its involvement in producing this gaseous plant hormone had yet to be discovered.

The effects of ethylene on plants were first identified in 1901 by Russian scientist Dimitry Nikolayevich Neljubov (1879–1926). In 1934, Richard Gane demonstrated that plants biosynthesize ethylene, but research on this gas as a plant hormone remained limited between 1930 and 1960, and none of it involved the rostellum. Extensive knowledge about ethylene as a plant hormone—including its effects on orchids—accumulated between 1960 and 1980 and has continued to expand since (Abeles, 1973; Abeles *et al*., 1992; Burg & Dijkman, 1967; Dijkman & Burg, 1970).

Dr. John Thomas Curtis (1913–1961; Fig. 11A), Professor of Botany at the University of Wisconsin, Madison, was the first to suggest that rostella might have a physiological function. In his study of fruit development in *Phalaenopsis* Blume, Curtis observed that pollination caused wilting of the perianth in *Phalaenopsis Pamela* [Fig. 7: A1; Curtis 1943 wrote “Pamala” but the correct name is *Pamela* (Phalaenopsis *Elisabethae* × P. *Fontainebleau*)] and swelling of the column (Fig. 7: A2, A3). Curtis found that removal of the pollinia (Fig. 7: A4), emasculation (Fig. 7: A5), and even “merely stroking the rostellum with a needle” (likely causing a wound) also triggered perianth wilting (Curtis, 1943). Although Curtis could not provide a “satisfactory explanation of the physiological reactions” he hypothesized that these effects involved a substance similar to the plant hormone auxin, specifically indoleacetic acid (IAA) (Curtis, 1943).

Curtis’s suggestions about the involvement of the rostellum and a regulatory substance were prescient, as

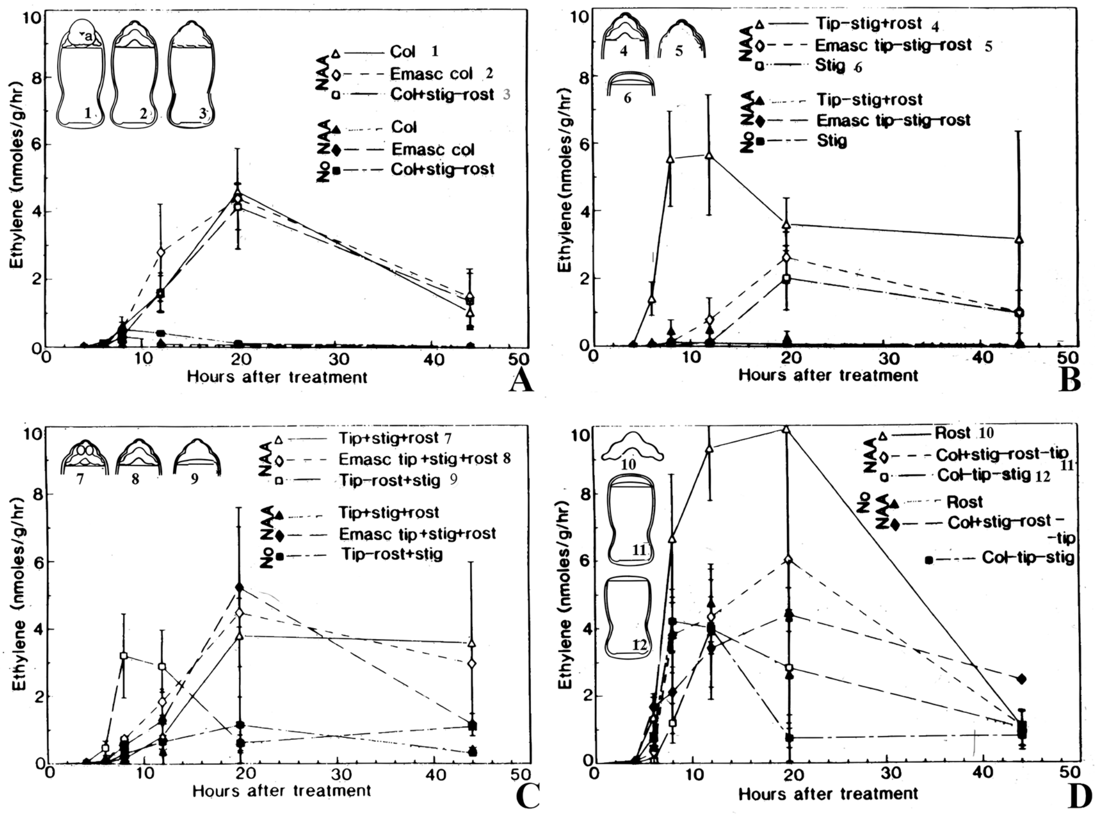


FIGURE 18. Effects of auxin applications (naphthaleneacetic acid, NAA) and surgical treatments of gynostemia on ethylene evolution by the column and its parts of *Cymbidium* Jungfrau (for a photograph see Fig. 17H). **A**. Auxin application following emasculation or excision of the rostellum. **B**. Auxin application following excision of the stigma. **C**. Auxin application following excision of the rostellum. **D**. Auxin application following excision of rostellum and gynostemium tip or the gynostemium tip and stigma. Explanation of symbols: a, anther cap; Col, column (gynostemium); Emasc, emasculation; rost, rostellum; stig, stigma; tip, tip of the gynostemium. Numbers following captions (upper right of A-D) correspond to the numbers of surgical treatment (upper left of A-D). Bars at data points are standard deviations, some of which are large. Source: Chadwick *et al*., 1986.

the effects of IAA (indoleacetic acid) and ethylene on orchid flowers are similar. IAA, a plant hormone, can initiate ethylene production. However, at the time, little was known about the connection between IAA and ethylene or the roles of these plant hormones in orchid flower physiology. Additionally, ethylene was not yet considered a plant hormone, and its effects on orchid flowers were unknown. Curtis continued his research on post-pollination phenomena, but not specifically on the rostellum. One of his students later published the first substantial report on post-pollination phenomena in orchid flowers (see Avadhani *et al*., 1994 for a review and reminiscences by the student).

Six years after Curtis's findings on the role of the rostellum in post-pollination phenomena in *Phalaenopsis*, Dr. O. Wesley Davidson (ca. 1904–1991) demonstrated at Rutgers University that exposure of *Cattleya* Lindl. flowers to atmospheric ethylene caused injury and wilting (Davidson, 1949; Fig. 7B2, B3). At that time, ethylene was not yet recognized as a plant hormone, and no connection was made between ethylene and the rostellum.

Today, it is well established that the rostellum is involved in inducing post-pollination phenomena in *Angraecum* Bory (Strauss, 1976, Strauss & Koopowitz, 1973), *Cymbidium* (Arditti & Flick, 1974, Chadwick *et*

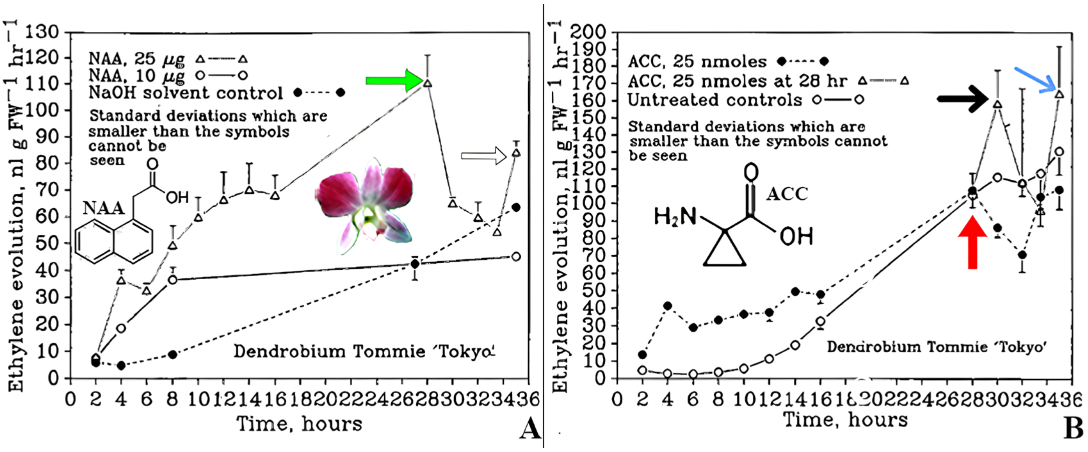


Figure 19. Ethylene production by flowers of *Dendrobium* Sw. Tommie 'Tokyo'. **A**. Evolution of ethylene after application of auxin (naphthaleneacetic acid, NAA) to the stigma. Green arrow points to peak of evolution 28 hours after treatment. The open arrow points to a secondary peak at 35 hours. **B**. Production of ethylene after application of the ethylene precursor, 1-aminocyclopropane-1-carboxilic acid (ACC). Red arrow points to the initial peak of ethylene production at 28 hours, and the time at which additional ACC was applied to the stigma. The black arrow points to a peak resulting from the application of the additional ACC. A secondary peak resulting from the application of ACC is marked with a blue arrow. Source: Graphs, Nair et al, 1991; photograph, Joseph Arditti.

al., 1980; 1986; Duncan & Schubert, 1947), *Dendrobium* Sw. (Nair *et al*., 1991), *Phalaenopsis* (Curtis, 1943; Duncan & Schubert, 1943), *Vanda* (Burg & Dijkman, 1967; Dijkman & Burg, 1970), and other orchids (for reviews, see Arditti, 1979, 1992; Avadhani *et al*., 1994). In *Cymbidium*, rostellum injury induces anthocyanin synthesis—a known effect of ethylene (Fig. 17F)—but does not trigger stigmatic closure, which is instead induced by auxins. Ethylene production by the rostellum, a modified stigma, aligns with reports that stigmas in other plants produce ethylene as well (for a brief review, see Strauss & Arditti, 1984).

Research on the interactions between ethylene, the gaseous plant hormone (Fig. 12F), and orchid flowers began in the 1940s (for reviews, see Akamine, 1963; Arditti, 1979, 1992; Avadhani *et al*., 1994; Burg & Dijkman, 1967; Chadwick *et al*., 1986; Davidson, 1949, Dijkman & Burg 1970; Duncan & Schubert, 1943; Hew & Yong, 1997, 2004; Hew *et al*., 2002). This research led to the discovery that the following factors trigger the autocatalytic production of ethylene (Fig. 19B): pollination (Fig. 17A, B), emasculation (Fig. 17A, B, D), application of auxin (IAA or its analog NAA) (Fig. 17B, E, H), aging of flowers (Fig. 17C, fading of blossoms (Fig. 17G), injury to blooms (Fig. 17H), and application of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC).

Ethylene production triggered by auxin application and pollination follows the same pattern: it begins, peaks, and then declines after a similar period (Fig. 17B). This parallel timing is likely due to post-pollination ethylene synthesis being initiated by auxin from the pollinia.

In contrast, ethylene production following emasculation takes longer to start and reach its peak than ethylene induced by pollination (Fig. 17A, B, D), possibly because emasculation triggers the production of wound-induced ethylene, which has a delayed onset. Emasculated flowers also tend to have a longer lifespan than pollinated ones, which is evolutionarily advantageous since they remain receptive to pollen and can produce seeds if pollinated later. In nature, emasculation often occurs when pollinators remove the pollinaria.

A suggestion that rostellum desiccation is "responsible for post-emasculation phenomena in orchid flowers" is supported by data showing higher levels of ethylene production in emasculated *Cymbidium* and *Phalaenopsis* flowers at 60% relative humidity (RH) compared to 100% RH (Woltering & Harren, 1989). However, further studies have not been conducted on *Cymbidium*, *Phalaenopsis*, or other orchids. While this suggests a role for desiccation, it seems intuitively unlikely to play as significant a role as plant hormones like ethylene and auxin.

Structural, color, and vegetative differences between different clones within the same grex may result from mutations or genetic variation within seedling populations. *Papilionanthe* Schltr. (formerly *Vanda*) 'Rose Marie' (Fig. 17A) and *Vanda* (now *Papilionanthe*) 'Miss Joaquim' (Fig. 17G), the National Flower of Singapore and a natural hybrid [*Papilionanthe teres* (Roxb.) Schltr. var. *andersonii* × *Papilionanthe hookeriana* (Rchb.f.) Schltr.], share the same parentage (Arditti & Hew, 2007). As a result, the patterns of ethylene production following emasculation in these orchids are similar, though not identical (Fig. 17A vs. Fig. 17G). Any differences likely stem from varietal characteristics or different cultivation conditions in Florida (Fig. 17A) and Hawaii (Fig. 17G).

Papilionanda R.E.Schult. & Pease 'Petamboeran' (Fig. 17B) was originally hybridized and cultivated in Indonesia. Its parentage includes *Vanda foetida* J.J.Sm. × *Papilionanthe* 'Miss van Deun' [*Papilionanthe* Schltr. 'Miss Joaquim' (*Papilionanthe teres* (Roxb.) Schltr. var. *andersonii* × *Papilionanthe hookeriana*)] × *Papilionanthe teres* (Roxb.) Schltr. The overall plant architecture, with its thin upright stems and terete leaves, is strongly influenced by *Papilionanthe teres* (Roxb.) Schltr., which is also evident in the similarity of the initial peak of ethylene production after pollination in *Papilionanthe* 'Rose Marie' (Fig. 17A) and *Papilionanda* 'Petamboeran' (Fig. 17B).

Altogether, it is reasonable to assume that the similarities and differences in ethylene production, timing, levels, and patterns in the rostellum, stigmas, and other parts of the gynostemium are genetically determined. More research is needed to clarify these aspects of rostellum and orchid flower physiology, as the rostellum is clearly a more complex organ than its small size suggests. Ethylene evolution begins: A) within an hour or less after pollination (Fig. 17A, B, D). B) Following emasculation, between one and 96 hours later (Fig. 17A, B, D, G, 18). C) Two to five hours after the application of auxin (indole- or naphthalene-acetic acid) (Fig. 17B, 18). D) Twenty-two days after the opening of intact, uninjured, unpollinated, and untreated flowers in *Dendrobium* 'Pompadour' (Fig. 17D) and earlier in *Cymbidium* 'Jungfrau' (Fig. 17H).

Despite speculation that ethylene is produced and released by rostella and stigmas (for reviews, see Arditti 1979, 1992; Arditti & Flick 1974; Avadhani *et al*., 1994), experimental evidence was lacking until Dr. Arthur V. Chadwick (1943– Fig. 11E, then at Loma Linda University in California), the late Dr. Leslie P. Nyman (a postdoctoral fellow in Joseph Arditti's laboratory; for a photograph, see *Orchid Biology, Reviews and Perspectives* Vol. VI), Dr. Helen Nair (Fig. 11F, now retired from the University of Malaya in Kuala Lumpur), and Dr. Joseph Arditti conducted the necessary experiments (Chadwick *et al*., 1986; Nair *et al*., 1991). Emasculation and surgical experiments, combined with applications of naphthalene acetic acid (NAA), demonstrated that in *Cymbidium* 'Jungfrau' (Chadwick *et al*., 1986): A) regardless of any other treatment, NAA (an IAA analog) induces or enhances ethylene evolution (Fig. 18A1–3, B4–6, C7–9, D10–12). B) The stigma and rostellum are the primary sites of ethylene evolution (Fig. 18A3, B6, C7–9, D10–11). C) An excised rostellum produces the highest levels of ethylene per-weight basis (Fig. 18D10). D) The gynostemium can still produce ethylene even after the stigma and rostellum are removed (Fig. 18B4, B5).

Besides pollination, another event that induces ethylene evolution by the rostellum in nature is emasculation (i.e., pollinia removal by a pollinator; Fig. 18B5). To investigate how pollinia removal triggers ethylene evolution, Dr. Michael S. Strauss (then a graduate student in JA's laboratory) used light and electron microscopy (Strauss & Arditti, 1984, Strauss & Koopowitz, 1973). The structure of the *Phalaenopsis* rostellum made the experimental process challenging, as fixation, embedding, sectioning, and staining were difficult for both light and electron microscopy. Images of the *Phalaenopsis* rostellum revealed elongated, prosenchymatous (soft and succulent) vacuolated cells (Fig. 8B, C), with a strand of vascular tissue extending through the rostellum. These cells are rich in mitochondria with easily visible cristae (Fig. 8C), which may be associated with the metabolic regulation of xylem and/or phloem functions and could provide the energy required for ethylene synthesis.

Pollinia removal causes wounding along a tear in the rostellum (Fig. 8D, arrows; Fig. 8E, F). Previous studies, which were mainly structural, reported similar wounding in other orchids (Gellert, 1923; Table 1). As is typical in plants, tissue damage induces wound ethylene production. Because ethylene production is autocatalytic, the wound ethylene initiates a subsequent increase in gas production.

Experiments conducted by others (Burg & Dijkman, 1967; Fig. 17B) and in J. Arditti's and Chadwick's laboratories (Chadwick *et al*., 1986; Fig. 17) confirmed that pollen induces ethylene evolution by providing auxin, which is known to be present in high concentrations in orchid pollen (see Avadhani *et al*., 1994 for a review). Additionally, the enzyme responsible for ethylene production is present in orchid flowers before pollination, and its levels increase after pollination or auxin treatment (Bui & O'Neil, 1998).

An unanswered question at the time was why ethylene production drops sharply after reaching its peak (Fig. 17A–E, G, H; 18A–D; 19A, B). To investigate this phenomenon, the auxin naphthalene acetic acid (NAA; Fig. 19A) and the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC; Fig. 19B) were applied to the stigmas of *Dendrobium* 'Tommie Tokyo' (Nair *et al*., 1991; Fig. 15A, B). For the first six hours following treatment, ethylene evolution was similar for both NAA and ACC applications, although ethylene production was higher after NAA application. Both treatments peaked at 28 hours, after which ethylene production decreased substantially. Similar patterns were observed in other orchids (Fig. 17), though with differences in timing, ethylene levels, and curve shapes.

Adding ACC at 28 hours restored ethylene evolution, resulting in a peak at 30 hours, a drop at 32 hours, and a second peak at 34 hours (Fig. 19B). Both new peaks were higher than the initial peak at 28 hours (Fig. 19B). These findings suggest that either the ethylene production pathway becomes temporarily impaired at 28 hours and is restored by ACC, or that the decrease in ethylene production is due to ACC depletion.

Conclusions. Despite its small size and often concealed position, the rostellum plays a crucial role as a floral organ because it: A) Separates the pollinia from the stigma, and with few exceptions, prevents self-pollination. B) Produces an adhesive, facilitating pollination. C) Develops the antennae in *Catasetum*, enabling a unique pollination mechanism. D) Varies in size and shape, making it useful in orchid systematics. E) Plays an important role in orchid pollination phenomena by producing ethylene, which induces the senescence and death of floral organs that are no longer needed, thereby conserving energy and allowing the reutilization of substances and resources (Harrison & Arditti, 1976).

Despite its significance in orchid biology, the rostellum has not been extensively studied, and much remains to be discovered. This lack of information required several speculations and assumptions in this review, which may lead to differing opinions and may need revision as more is learned about the rostellum.

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Dedication. This paper is dedicated to Jean Ikeson for being excellent at what she does.

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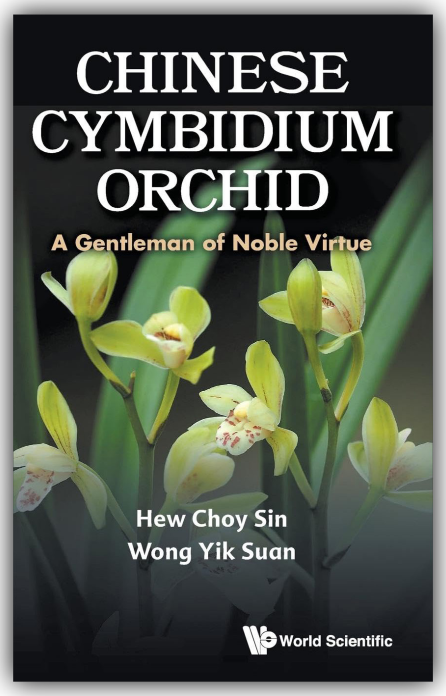
BOOKS

Chinese Cymbidium Orchid, A Gentleman of Noble Virtue, by Hew Choy Sin and Wong Yik Suan. World Scientific Publishing Co.,Pte., Singapore, 2023. ISBN 9789811263361. 180 pages, color photos. Hardbound. Price: US$78; GBP 70. Ordering: https://www.worldscientific.com



Orchids have been cultivated and appreciated in ancient China for at least 3,000 years. The renowned Chinese philosopher Confucius (551–479 BC) referred to *Lan* (Chinese cymbidiums) as the "*Gentleman of Noble Virtue*". In ancient China, *Lan* symbolized refinement, elegance, integrity, modesty, nobility, and purity. Early Chinese writings that mention *Lan* include:

- Shi-Jing (Book of Songs), the earliest collection of Chinese poetry, dating back to the 11th–7th centuries BC.
- References (p. 3 in book) from the Spring and Autumn (770–476 BC).
- Mentions in the Book of Rites (Li-Ji) during the Western Han era (206 BC–25 AD; p. 3).
- Poems from approximately 2,000 years ago (p. 3).
- Yong Lan by Tang Yanqian, composed late in the Tang Dynasty (ca. 900 AD; p. 8).
- References during the Song Dynasty (960–1279 AD; p. 8).
- Poems by the Song poet Huang Tingjian (1045–1127; p. 8).
- Accounts from the Ming Dynasty (1368–1644; p. 8).
- Descriptions from the Qing Dynasty (1644–1911; p. 8).

Additional information about *Cymbidium* cultivation in ancient China can be found in Table 1.1. There is some confusion regarding the dates due to differing uses of the terms "ni" and "lan" for orchids and cymbidiums. This book addresses and clarifies this confusion in Chapter 1, titled "History of Chinese *Cymbidium*" which is well-written, detailed, and engaging without being overwhelming. The authors demonstrate a profound interest in the history and cultivation of orchids in ancient China, as evidenced by their earlier works (Hew, 2001; Hew, Arditti & Lin, 1997; Hew & Yong, 2006; Pan, Ye & Hew, 1997). Their scholarly expertise in both orchid research and library science is prominently displayed throughout the book.

It is impressive that the Chinese valued and cultivated orchids as far back as the 11th century BC, possibly even earlier. For context, other significant events around 1000 BC include:

- 1040 BC: Birth of David, future King of Israel.
- 1026 BC: Saul becomes King of Israel.
- 1020 BC: Destruction of Troy.
- 1000 BC: Advent of the Phoenician alphabet.
- 970–931 BC: King Solomon's reign.
- 371–287 BC: Theophrastus gave orchids the name we use today.

If evidence showing that orchids were cultivated in Greece at the same time as in China, it is yet to be discovered.

Cymbidium orchids have played a significant role in Chinese calligraphy, literature, paintings, and poetry. Chapter 2, titled "*Chinese Cymbidium and Chinese Culture*," explores these connections. For example, it discusses the *Doctrine of Modesty*, which states that Chinese cymbidiums must possess a fragrance that is "moderate, pure, and delicate" (p. 19). Additionally, there are specific color requirements for these orchids.

The book examines the influence of Confucianism, Buddhism, and Taoism on the selection, judging, and naming of Chinese cymbidiums. It presents this information in a way that is accessible to Western readers.

The enduring presence of *Lan* in Chinese poetry is exemplified by a poem by Zhang Heng (78–139 AC), a poet and astronomer. A translation (Hu, 1971, pp. 22–23) reads:

How elegant, O orchid of autumn!
The sweet smell, the yellow bud.
Though confined in shade;
Your beauty is beyond comparison.
As afar as the cloud. I suffer; O what!

At first glance, paintings of Chinese cymbidiums may seem simple, but this is far from the truth. To excel at painting these orchids, artists must deeply study and understand the plants and their ecology. A painting can only be considered excellent when there is a balance among the leaves, flowers, plants, and their environment. The book effectively clarifies this concept.

Additional factors to consider include whether the paintings are done on silk or paper, and if they are in color or black and white. The personality of the painter and their social or political activism also play a significant role. Much of Chapter 2 is dedicated to discussing the finer points and appreciation of *Lan* paintings, making this section both enlightening and engaging.

Like Ai Weiwei (b. 1957) today, several past painters clashed with high-ranking officials. The most famous among them is Zheng Banqiao (1693–1765), who wrote, "*My paintings of Lan, bamboo, and boulder are meant to comfort the hard-working masses, not to please those who lead a comfortable and leisurely life*." Zheng was not the only rebellious or politically active painter of *Lan* in ancient China, and Chapter 2 discusses several such artists.

Chapter 2 also covers calligraphy associated with *Lan*, its role in Chinese customs, its significance as a cultural symbol, and its representation on postage stamps. Much insight can be gained from this profusely illustrated and well-written chapter (pp. 17–52). However, I found it challenging to read because the presence of Chinese characters interspersed among the English text disrupted the flow of thought.

Modern taxonomy is introduced in Chapter 3, where the authors describe and discuss several species, including *C. ensifolium* (L.) Sw., *C. faberi* Rolfe, *Cymbidium goeringii* (Rchb.f.) Rchb.f., *C. kanran* Makino, and *C. sinense* Willd.

Western taxonomists named four of these species without acknowledging their Chinese origins and heritage. Combining their Chinese history with modern taxonomy offers a fascinating and instructive perspective.

- The type specimen of *Cymbidium goeringii*, found at elevations of 300–2200 m above sea level in China and one of the earliest known Chinese cymbidiums, was actually collected in Japan. It was named in 1852 by Gustav Reichenbach filius (1823–1889) in Germany, in honor of the German-Dutch botanist, chemist, and plant collector Philipp Friedrich Wilhelm Goering (1809–1876).

- *Cymbidium faberi*, originating from Jiangzhe, was named by Robert Allen Rolfe (1855–1921), founder of *The Orchid Review* in the UK, after the German plant collector Ernst Faber (1839–1899). This species produces nine flowers per inflorescence, which earned it the old Chinese name "Nine Children Lan."
- Despite being described in the West, *Cymbidium sinense*, from humid inland forests in China, is aptly named to reflect its origins.
- *Cymbidium ensifolium*, found at elevations of 600–1800 m on temperate forest slopes in China, was popular in ancient China but named in Europe.
- The "Linnaeus of Japan", Tomitaro Makino (1862–1957), named *C. kanran* in 1902. Known as "The Cold Lan" because it blooms in the cold season, the name combines *kan* (cold in Japanese) and *ran* (orchid in Japanese). Another Japanese name for *C. kanran* is *Syunran,* as it also blooms in the warm spring. The species was brought into cultivation from southern China around 2,500 years ago.
- Each of these species has multiple forms and varieties. Their descriptions and illustrations (pp. 53–86) complete this well-rounded chapter.

The biology of Chinese cymbidiums is explored in Chapter 4 (pp. 87–120). The chapter begins by stating: "...Appreciation of Chinese cymbidiums can be summarized in four words 'Scent, Colour, Form, and Charm' " highlighting their distinction in leaf and flower structure, color, form, beauty, and fragrance. This sentiment was expressed as early as 1247 by the poet Wang Gui Xue in his book *Wang Shi Lan Pu,* published during the Song dynasty (960–1279):

> "*Bamboo has integrity but is short of flowers.*
> *Mei* [*plum blossoms*, Prunus mume] *has flowers but is short of leaves during flowering time.*
> *Pine has leaves when in flower but is short of fragrance.*
> *Orchid* (Cymbidium) *has leaves, flowers, and fragrance all at the same time*."

This excellence stems from the unique biology and physiology of cymbidiums, which share some characteristics with other orchids and *Cymbidium* species but also exhibit distinct differences. For example:

- Flowers are fragrant, but the intensity of the fragrance varies between species and cultivars (Zhang *et al.*, 2014).
- Leaves are often variegated, and plants are frequently selected for this trait.
- The structure of leaves and stomata is similar to other monocotyledonous plants, though variations in color and length can occur within a single species.
- Pseudobulbs are shorter than those of many other orchids.
- Roots are fleshy, unlike the roots of most terrestrial orchids.

The biological characteristics of Chinese cymbidiums are well-described, discussed, and explained in this chapter. The ancient Chinese do not appear to have propagated cymbidiums from seeds. It is unclear whether they recognized orchid seeds for what they were, as no ancient writings, paintings, or drawings depicting seeds, seed germination, or seedlings have been discovered to date. I hope that a thorough investigation of ancient Chinese texts about orchids will reveal relevant information.

Chapter 4 provides detailed information about fruits (referred to as pods on pages 108 and 109; they are technically capsules), as well as seeds and seed germination in Chinese cymbidiums.

In the past, the clonal propagation of Chinese cymbidiums was primarily achieved by dividing existing plants. This traditional method is still practiced today, alongside modern propagation techniques that are described in detail. The chapter effectively combines ancient and contemporary knowledge, resulting in a well-balanced and informative discussion.

Ancient Chinese *Cymbidium* growers were not aware of orchid mycorrhiza, but they recognized that the natural substrates where cymbidiums thrived contained elements that enhanced plant growth. Historical texts suggest that when collecting cymbidiums from the wild, it was important to also gather substrate debris, as this was deemed essential for successfully establishing the collected plants (for more information on ancient cultivation methods, see Hew, 2001). This practice continues to be relevant today.

At present, Chinese cymbidiums are extensively cultivated using modern methods. Chapter 5 (121–142) illustrates and discusses these methods and information on pests and diseases.

Chapter 6 (pp. 143–148) addresses the current prospects of Chinese cymbidiums. References are provided on pp. 149–154, and an index is provided on pp. 155–159.

I have several concerns to address. First, references numbered 44–89 on pages 152–154 are listed only in Chinese characters, making it impossible for those who do not read Chinese to understand their significance. Providing English translations would have been very helpful. Responsibility for this issue lies with the authors.

Second, the publisher opted for a page size of only 15 × 23 cm, which results in illustrations that are too small to discern details. For example, the 12 illustrations on page 100 measure only 3.3 × 2.5 cm each. The 18 illustrations on page 101 vary in size: 3.3 × 1.8 cm, 3.3 × 2.1 cm, 3.3 × 2.6 cm, 3.3 × 2.4 cm, and 3.3 × 2.5 cm. A larger page size, such as 21.6 × 27.9 cm, with fewer but larger illustrations per page, would have been preferable.

Third, not all illustrations in the book are printed or cropped well. For instance, an illustration on page 109 supposedly shows seeds measures only 5.5 × 5.2 cm, which is not large enough for clarity. The pinkish-purple background makes the white seeds appear like small pieces of string. On page 108, two fruits take up only 6.4 × 6.2 cm of an 8.9 × 7.0 cm image, wasting the remaining space with a black background. Similarly, a statue in Figure 2.26 on page 118 measures just 2.8 × 1.3 cm within a 4.8 × 5.9 cm photograph, leaving much of the image area unused. Better cropping could have provided larger and clearer details.

Lastly, on page 141, an image of a virus-infected leaf appears as indistinct bands of green and white, likely due to poor color printing. This is surprising and disappointing for a book published in Singapore, a country known for its high-quality publishing standards.

Professor (retired) Choy Sin Hew from the Department of Biological Sciences at the National University of Singapore is a laureate of the 1997 Singapore National Science Award, the country's highest honor for research scientists. Ms. Yik Suan Wong (Mrs. Hew), who holds a BSc in Biological Sciences and a Postgraduate Diploma in Librarianship, served as a librarian at the National University of Singapore before her retirement. The authors' expertise in their respective fields is evident throughout this book, making it a valuable resource for anyone interested in Chinese orchids.

ACKNOWLEDGMENTS: I thank my friend of over 30 years, Professor Syoichi Ichihashi (retired) from Japan, for translating and clarifying the nomenclature of *Cymbidium kanran*, and editor Dr. Diego Bogarín for editing this review (at age 92, my writing needed a good editor).

DISCLOSURE: Professor C. S. Hew and I have known each other for approximately 50 years due to my frequent visits to the Botany Department at the National University of Singapore. During these visits, I collaborated on orchid research and publications with Professor Hew, Professor P. N. "Dhani" Avadhani (now retired), Professor A. N. Rao (the long-time excellent department head).

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