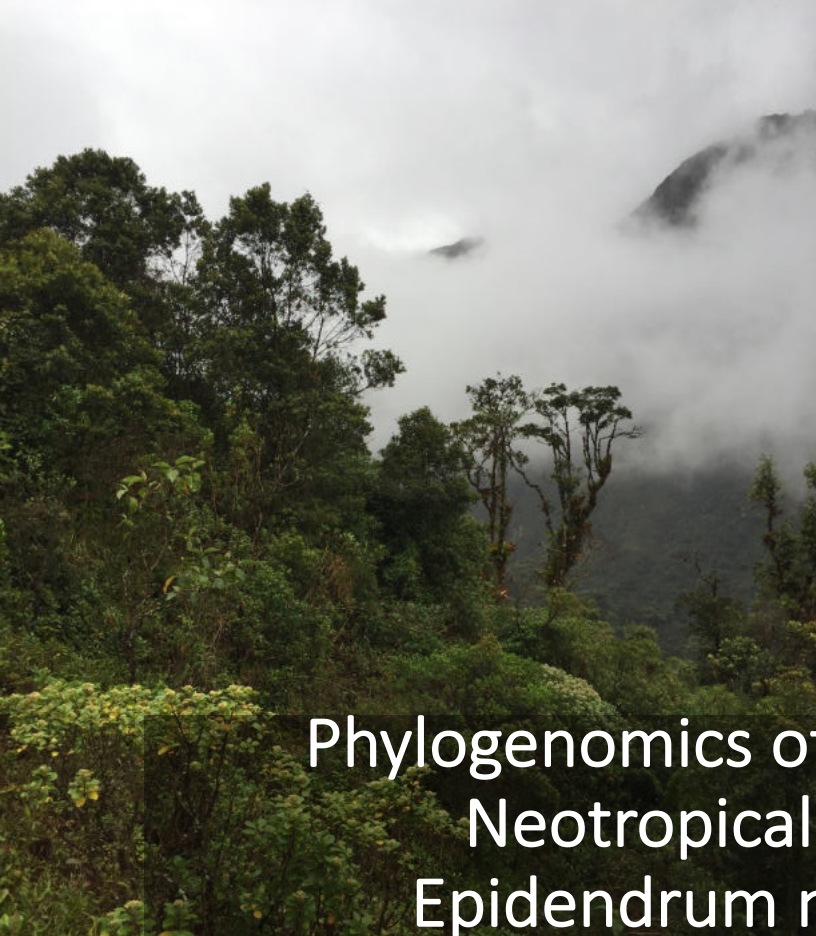
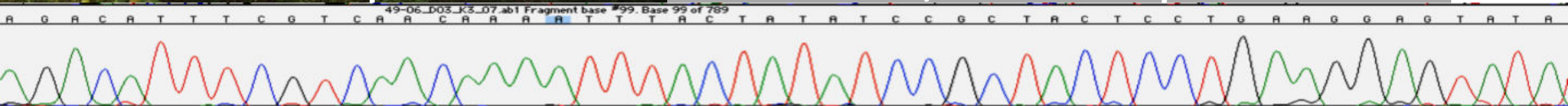




Phylogenomics of *Epidendrum*: untangling a Neotropical mega-diversification: *Epidendrum nocturnum*, an example

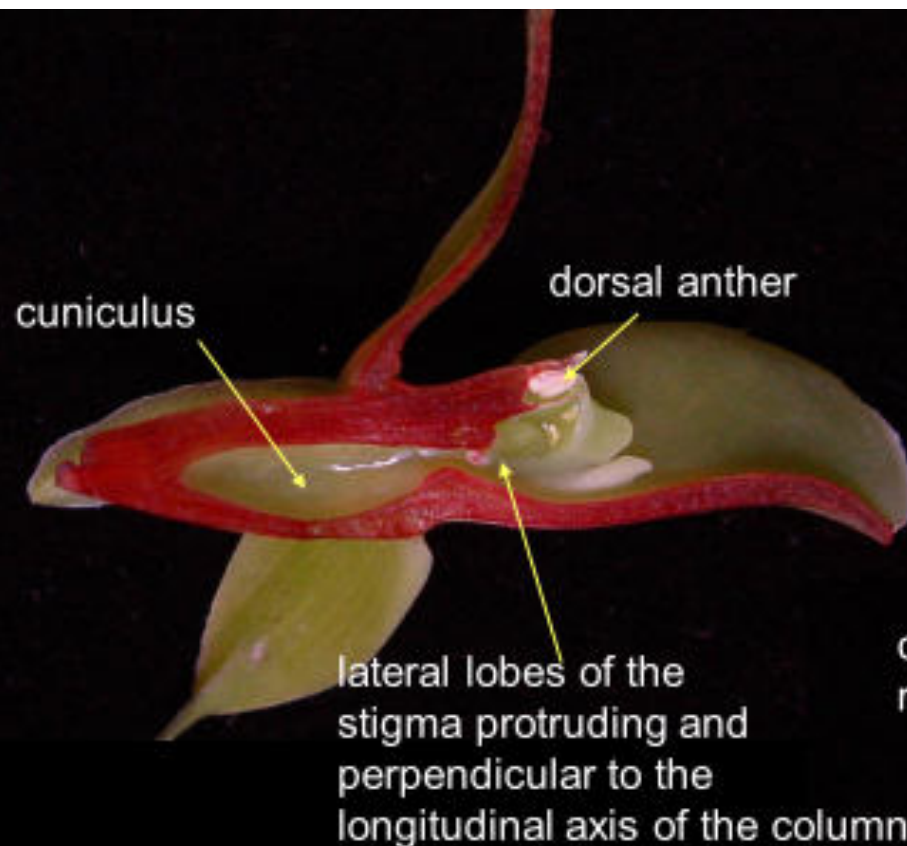


Eric Hágsater, Carolina Granados Mendoza, Gerardo A. Salazar, Elizabeth Santiago A., Gloria Calatayud, Benjamín Collantes, Marcos Salas Guerrero, José Dilmer Edquén, Luis Valenzuela, Rodolfo Vásquez

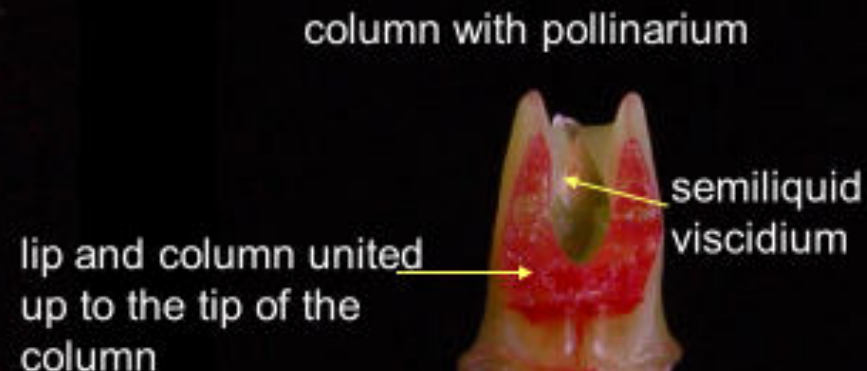


Epidendrum

A collage of various Epidendrum orchid species. The central element is a purple silhouette of the Americas (North and South America) set against a black background. Surrounding this map are numerous images of orchids. Some are whole plants with their roots and leaves, while others are individual flowers or inflorescences. The flowers exhibit a wide range of colors: yellow, pink, red, white, orange, and purple. The shapes of the flowers are diverse, reflecting the variety within the Epidendrum genus. Some flowers have long, slender petals, while others are more compact and star-shaped. The arrangement is artistic, with the plants and flowers appearing to grow out of or around the map.



Floral morphology of *Epidendrum beharorum*



column with pollinarium removed



Lindley, 1853, included **216** species
(excluding Encyclia & Prosthechea)

Dressler, 1993, assigned **1466**
Hágsater & Soto, 2005, ca. **1500**

Hágsater, Santiago &
Rodríguez-Martínez, 2016,
2400 species,

including many still unpublished, but identified
with specimens or digital images

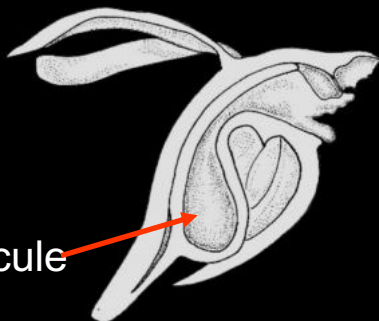


O. Gruss

Nectary-Vesicle

vesicule

E. renzii

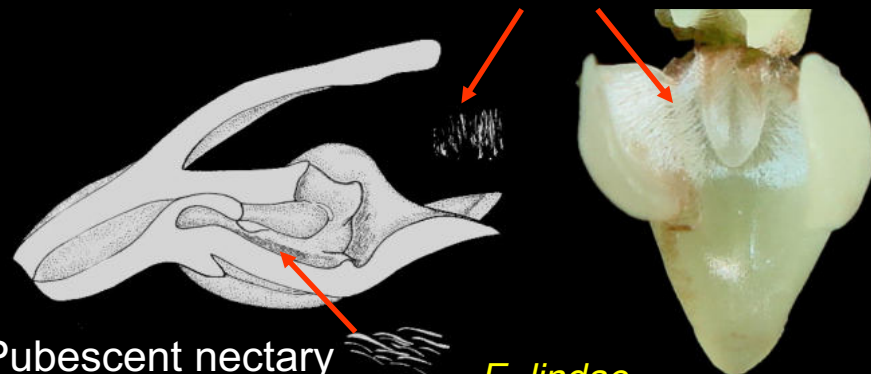


Pubescent labellum

Pubescent nectary

E. lindae

R. Medina

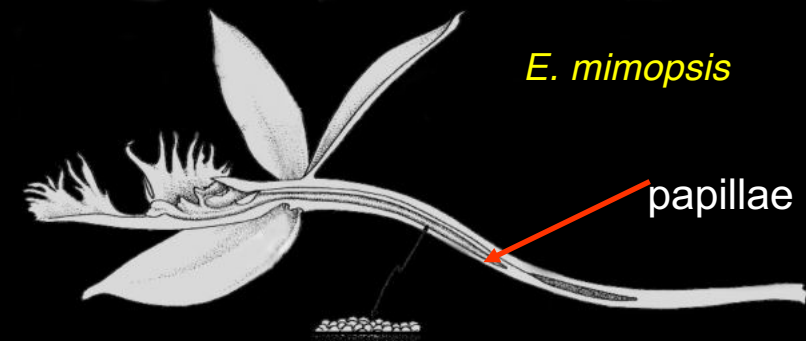


E. mimopsis

papillae

W. & B. Thurston

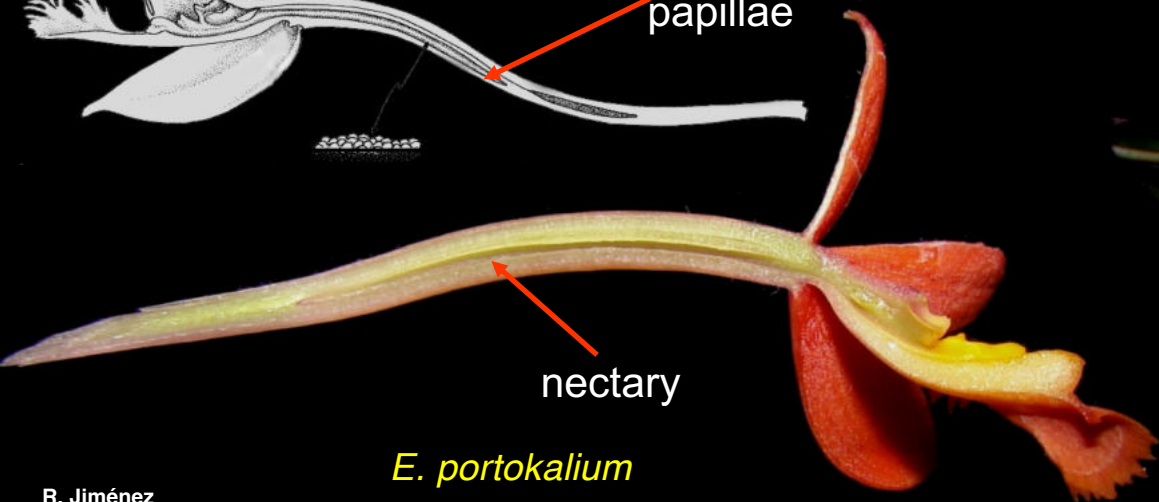
E. macrophorum



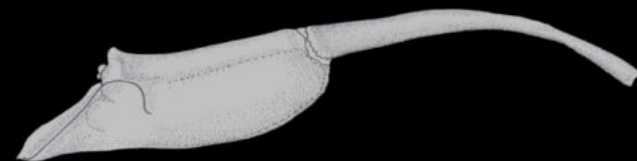
nectary

E. portokali

R. Jiménez



E. ventricosum



Column-labellum union

E. cupreum

Column totally united to the labellum

E. ciliare



M. López

E. oxysepalum

C. Fernández



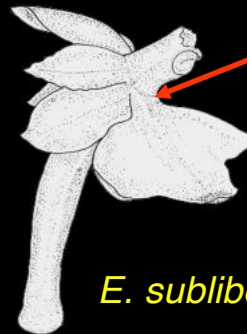
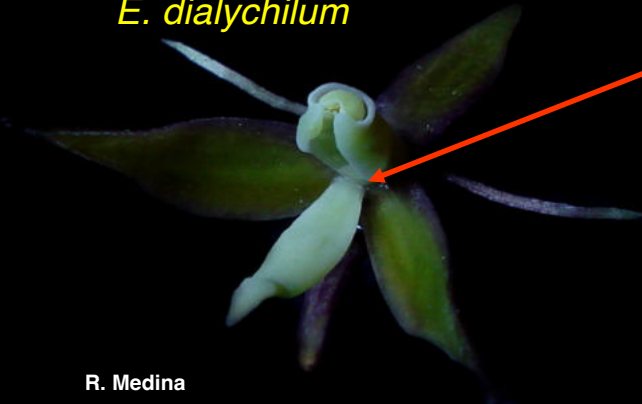
R. Medina

Column partially united to the labellum

Column totally free from the labellum

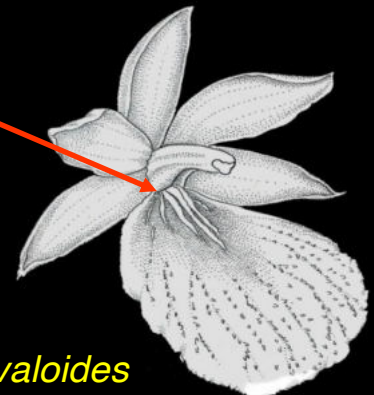
E. dialychilum

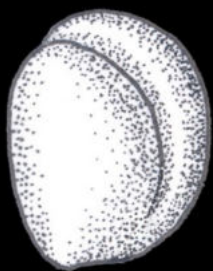
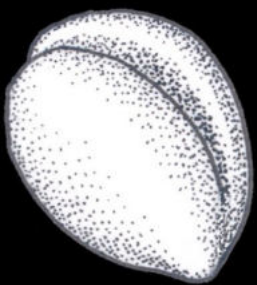
R. Medina



E. subliberum

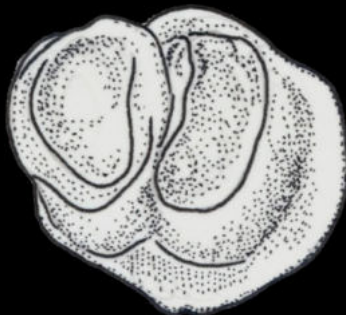
E. arevaloides





2 pollinia

E. rhombochilum



E. candelabrum

E. geminiflorum



E. Hágsater



R. Medina

4 pollinia



E. nora-mesae

O. Pérez

8 pollinia



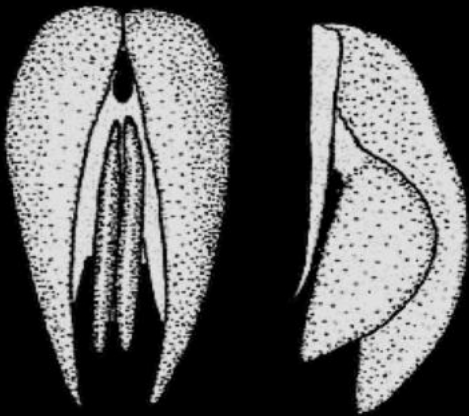
Pollinia and Anthers

O. Pérez



E. bispathulatum

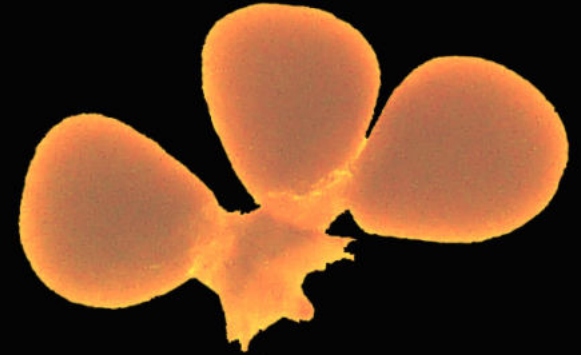
Bird-wing type pollinia,
laminar caudicles



E. aberrans

Types of Pollinia and Caudicles

O. Pérez



E. podocarpophilum

Obovoid pollinia, stacked
or granulose caudicles



E. smithii



Grupo Difforme, 125+ especies

Concept of *Epidendrum*
macrostachyum group
2017: 58 especies



E. dermatanthum



E. bangii



E. orthophyllum



E. sarcostachyum



E. borealistachyum



E. erikae



E. stenobractistachyum



E. lasiostachyum



E. microrigidiflorum



E. retrosepalum



E. puracestachyum



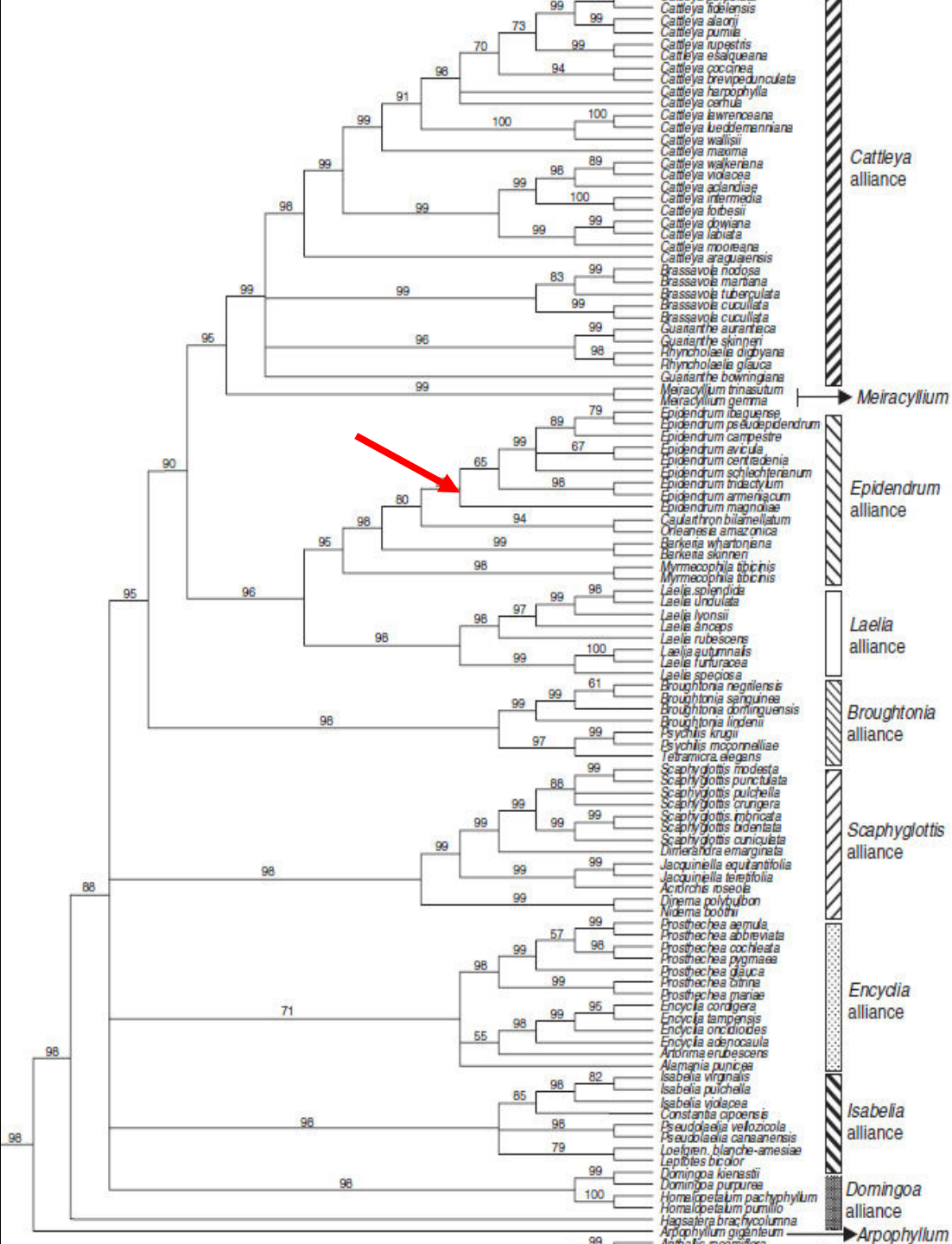
E. porphyrostachyum



E. ariasii

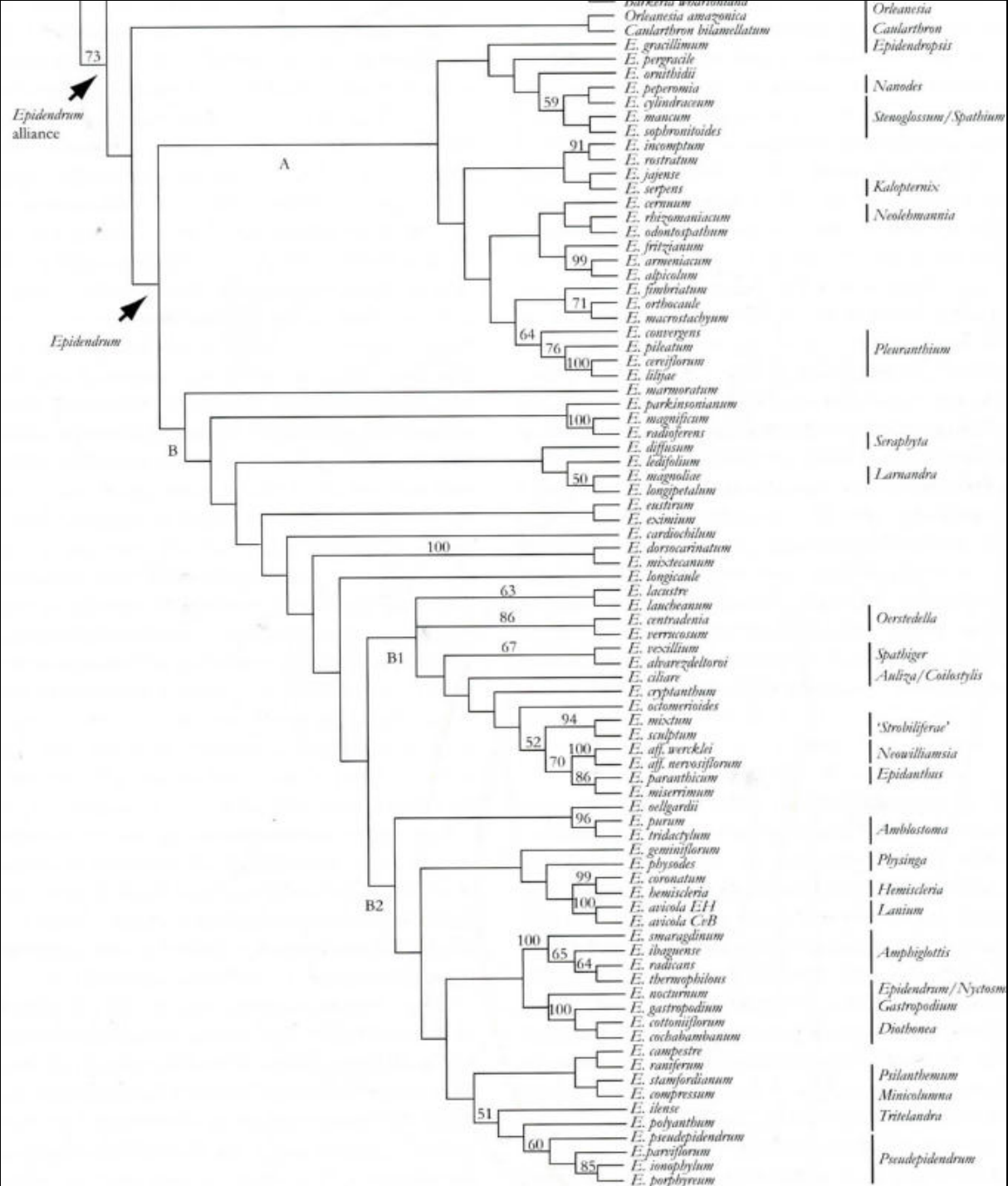


E. bractiacuminatum



0036

0053



0023

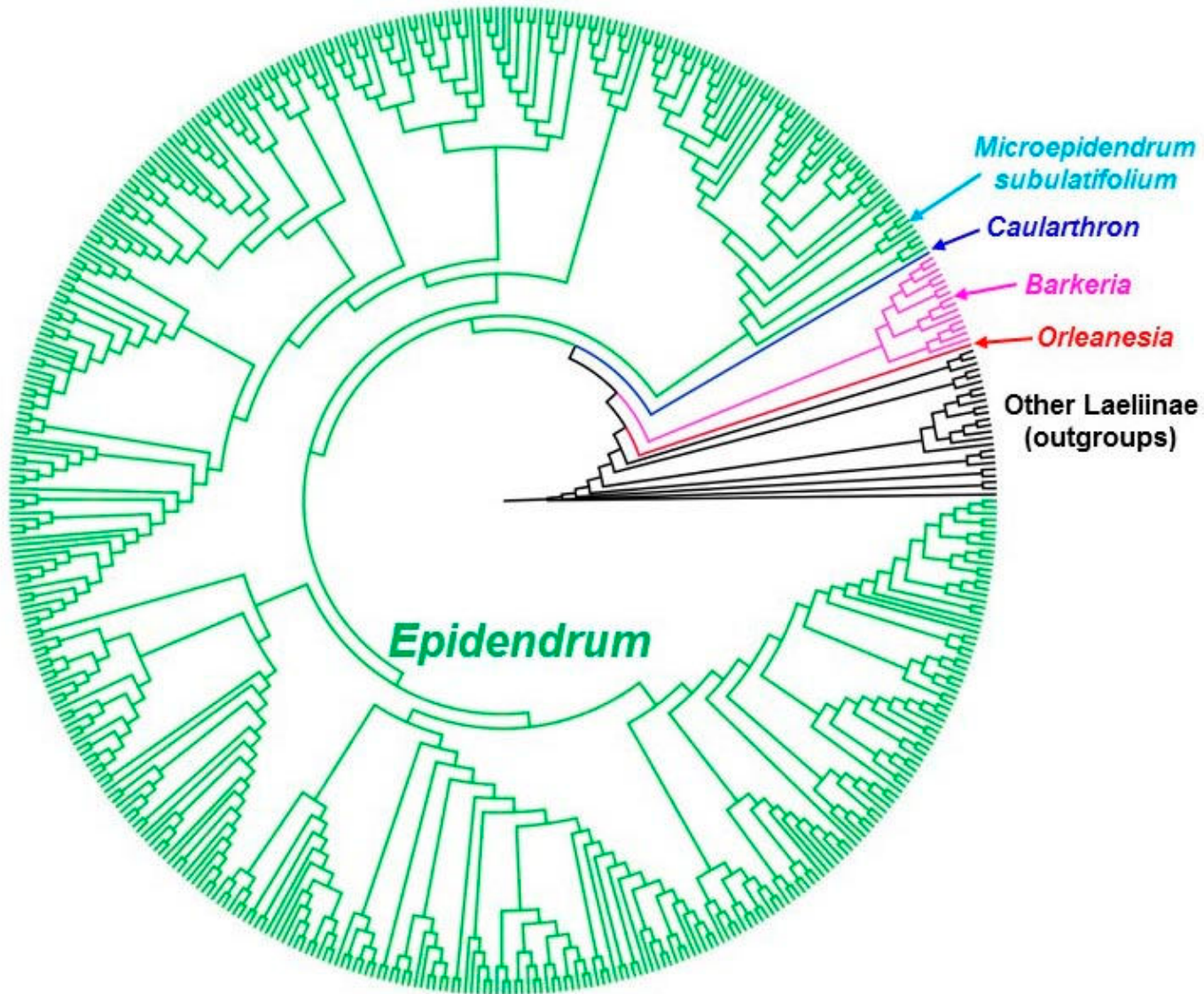
0023

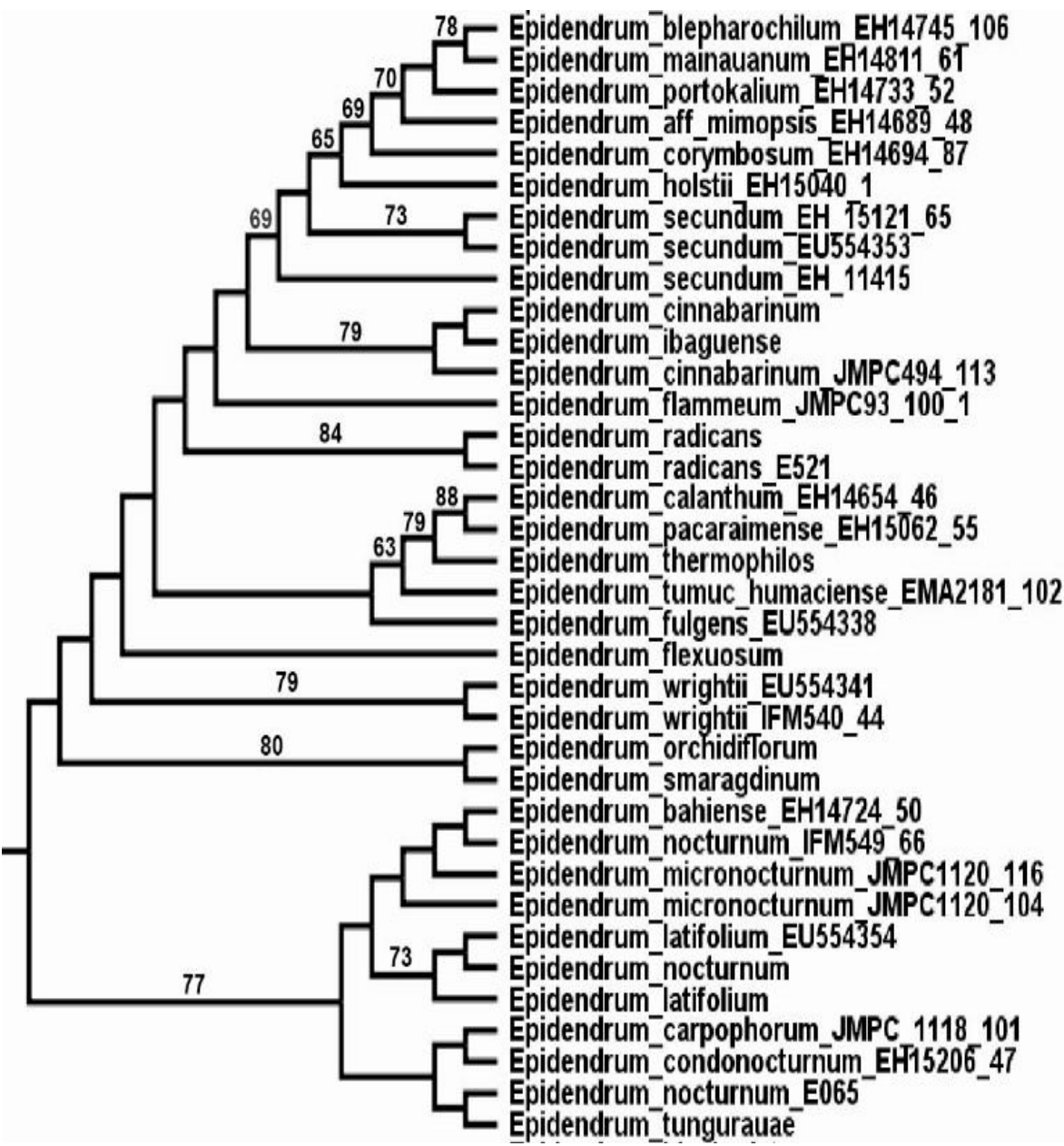
Ongoing research

- 1) Enlarged sample for *matK*/ITS matrix of *Epidendrum* and allies (“baseline” phylogenetic framework guiding subsequent research)
- 2) Phylogenomic approach: genome partition strategy for sequencing hundreds of single-copy nuclear genes



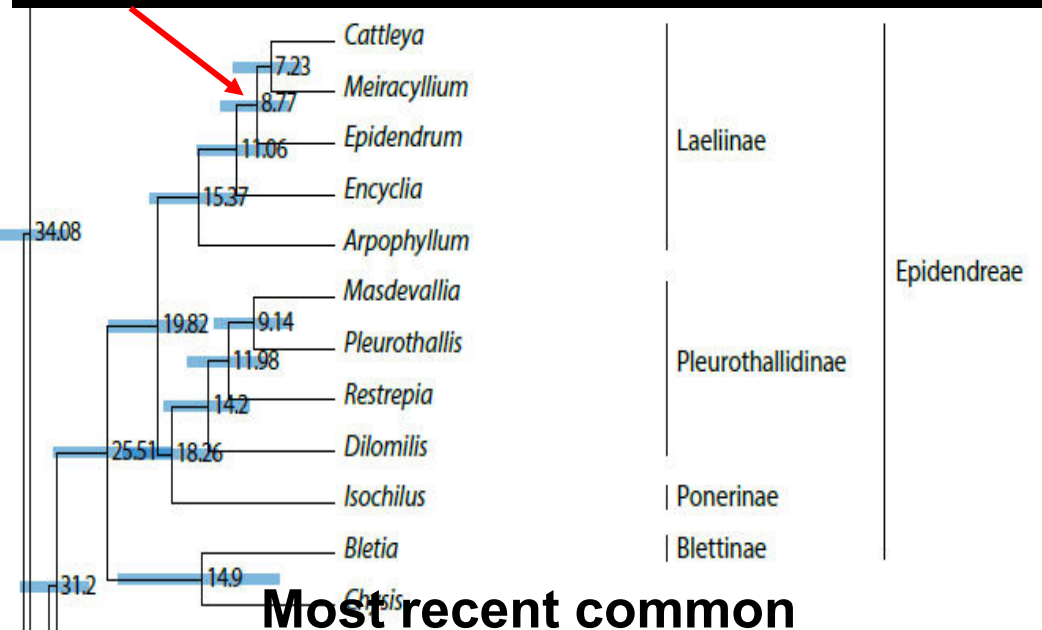
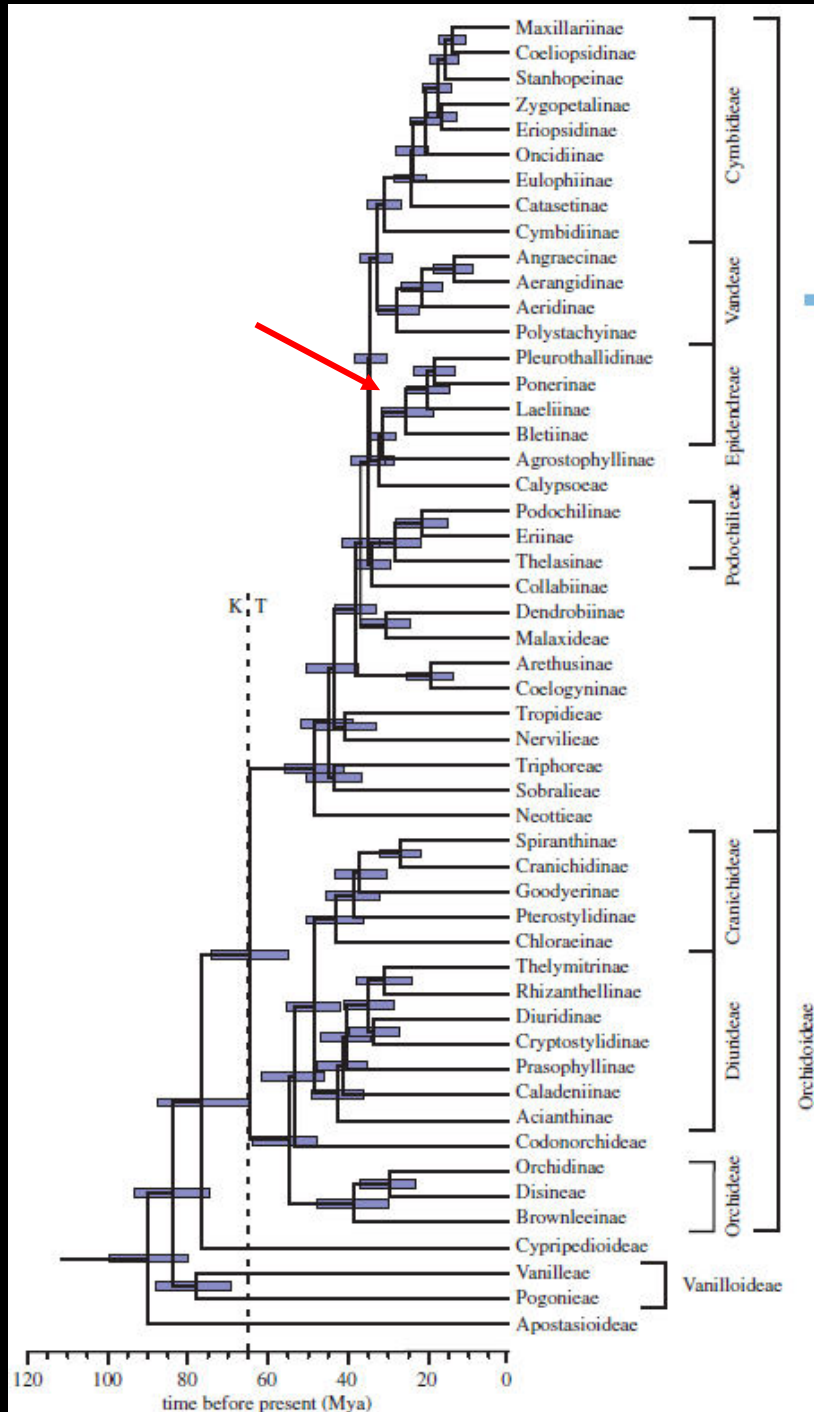
1) Parsimony analysis of plastid *matK* and nuclear ITS DNA sequences from 488 terminals (400+ species of *Epidendrum*)





Schistochilum
group

E. wightii
E. orchidiflorum
NOCTURNUM
GROUP

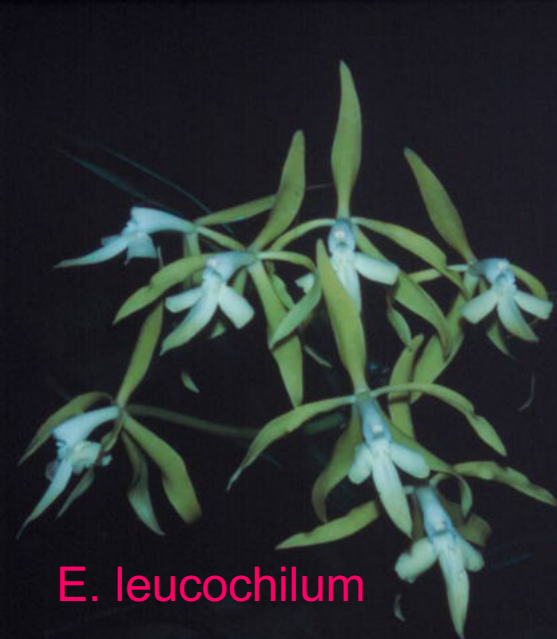


Most recent common

ca. 8.5 Ma

*

Flores en forma de Estrella en Epidendrum



E. leucochilum



E. ciliare



E. lacustre



E. nocturnum



E. steyermarkii



E. parkinsonianum

We have concluded that parallel evolution occurred in different, distinct lineages of the genus in some floral traits, notoriously in those associated with the pollination by Sphingid moths. The big, star-shaped flowers, with narrow, greenish-white segments, and a trilobed lip with a linear mid-lobe, a very long cuniculus (e.g. >3.5 cm), and white, nocturnal fragrances are present in

E. parkinsonianum
E. leucochilum
E. nocturnum
E. ciliare
E. steyermarkii
[*E. apuahuense*]



and their allies. These traits conform the Sphingid pollination syndrome and are undoubtedly adaptive.

These state characters are correlated, often significantly ($p \leq 0.001-0.136$; concentrated changes test, Madisson, 1990; simulation with MAXSTATE).

Therefore, the recent re-installation of the genus *Coilostylis* Raf. (Withner, 2004) must be rejected, since it is not a monophyletic group, rather it is a pollination syndrome.

Ökologische Zusammenhänge anhand von Sammlungsexemplaren erkennen: *Adhemarius sexoculata* GROTE, 1867, als Bestäuber bei der Orchideengattung *Epidendrum* LINNAEUS, 1753 (Lepidoptera: Sphingidae)

● MICHAEL MOOSBURG, ERIC HÄGSATER & MICHAEL OCHSE

Abstract. We describe the identification of pollinaria of the orchid genus *Epidendrum* LINNAEUS on the proboscis of the sphingid moth *Adhemarius sexoculata* GROTE, 1867. Species designation of the plants revealed that the plant species is *Epidendrum nocturnum* JACQUIN, 1760. The potential of ecological pollinator-plant pairings is discussed as a museum-based method for identifying ecological relationships.

Key words. Pollination, ecology, Lepidoptera, Sphingidae, Orchidaceae, *Epidendrum*.

Zusammenfassung. Erstmals wird der indirekte Nachweis des Blütenbesuches von *Adhemarius sexoculata* GROTE, 1867, bei der Orchideengattung *Epidendrum* LINNAEUS dokumentiert.

1867 aus Venezuela (Mérida, Prov. Barinas, Barinitas, 420 m, 9.IV.1997, leg. WENZEL, col. NHMN) und fand an den Rüsseln braune Pollinien. Diese erwiesen sich als der mit etwa 1500 Arten sehr großen und vom Südosten der USA bis ins nördliche Argentinien verbreiteten Orchideengattung *Epidendrum* (Orchidaceae) zugehörig, von der bereits vereinzelt Bestäuber der Sphingidae neben anderen Lepidoptera, Diptera, Hymenoptera und Kolibris dokumentiert wurden (s. Zusammenfassung bei HÄGSATER 2005). Die genauere Untersuchung ergab, dass es sich um die bei Nacht duftende (KAISER 1993) Art *E. nocturnum* handelt, die mit ihren weißen und sternförmigen Blüten und den tiefen Nektarien neben anderen Arten der Gattung die typischen Voraussetzungen für eine Bestäubung durch

Einleitung

Über die Bestäubung von tropischen Orchideen durch Schwärmer (Sphingidae) ist allgemein wenig bekannt. Eine bekannte Ausnahme hiervon bildet ein Beispiel aus der frühen Evolutionsforschung: CHARLES DARWIN und RUSSEL ALFRED WALLACE haben für die in Madagaskar vorkommende Langspornorchidee *Angraecum sesquipedale* (Orchidaceae) einen „Abendfalter“ mit entsprechend langem Rüssel als wahrscheinlichen Bestäuber vorhergesagt (KRITSKY 1991). Es waren schließlich ROTHSCHILD und JORDAN, die 1903 mit der Entdeckung des Schwärmers *Xanthopan morgani praedicta* (praedictus lat. für vorausgesagt) von eben dieser Insel einen wahrscheinlichen Kandidaten benennen konnten. Erst hundert Jahre später wurde von WASSERTHAL (1997) ein indirekter Beweis dafür erbracht indem er den Blütenbesuch im Studio fotografieren konnte.

Die Wechselbeziehungen von Orchideen und Schwärmern sind nach wie vor für die Klärung der Abstammungslinien beider Organismengruppen (KITCHING 2002) sowie für ökologische Betrachtungen von Bedeutung. Da die direkte Beobachtung von Bestäubungsvorgängen im Freiland

aufgrund der nächtlichen Lebensweise der meisten Sphingidae generell schwierig ist, ist der Nachweis von Blütenpollen an den Kopfsegmenten der Schmetterlinge von Bedeutung und soll hier durch ein weiteres Beispiel ergänzt werden.

Identifizierung von Blütenpollen an *Adhemarius sexoculata*

Die von Nordamerika (Texas und Florida) über die Karibik bis nach Südamerika verbreitete Schwärmergattung *Adhemarius* OTTICCA, 1939, umfasst 16 Arten mit drei Unterarten (KITCHING & CADIOU 2000). Kürzlich kam die neu beschriebene Art *Adhemarius roessleri* ERTSCHBERGER, 2002 hinzu. Der Erstautor untersuchte zwei Falter von *Adhemarius sexoculata* GROTE,

nachaktive Schmetterlinge aufweist. Die hier beschriebene Zuordnung eines Schwärmers zu einer Orchideenart als deren Blütenbesucher und damit potentiellen Bestäubers anhand von Blütenpollen an präpariertem Sammlungsmaterial gibt Anlass darüber nachzudenken, inwieweit eine systematische Analyse derartiger ökologischer Paarungen aufschlussreiche weitere Informationen liefern könnte. So ist es denkbar, dass bei hinreichend genügend Datensätzen die Verbreitungsgebiete von ausgewählten Blütenpflanzen mit



Abb. 2. Blütenpollen von *Epidendrum nocturnum* am Rüssel von *Adhemarius sexoculata* GROTE, 1867 (Venezuela, 9.IV.1997).

denen ihrer Bestäuber verglichen werden können und nach biogeographischer Analyse Hinweise auf die evolutionäre Entwicklung der beteiligten Taxa liefern könnten. Falls dabei ausschließlich ein Geschlecht der betroffenen Schmetterlinge mit den Pollen einer Art besetzt ist kann daraus geschlossen werden, dass sich die lockende Blütenpflanze eines nachgeahmten Sexualpheromons bedient. Letzteres wurde bereits mehrfach bei südamerikanischen Orchideen nachgewiesen (s. Zusammenfassung bei HÄGSATER 2005). Da Freilanduntersuchungen zur Blütenbestäubung insbesondere bei Nacht schwie-

rig und sehr zeitaufwändig sind, bei Baumwipfel-bewohnenden Tropenwaldpflanzen sogar nahezu unmöglich, bietet das Studium von Museumsmaterial hierzu eine effektive Alternative.

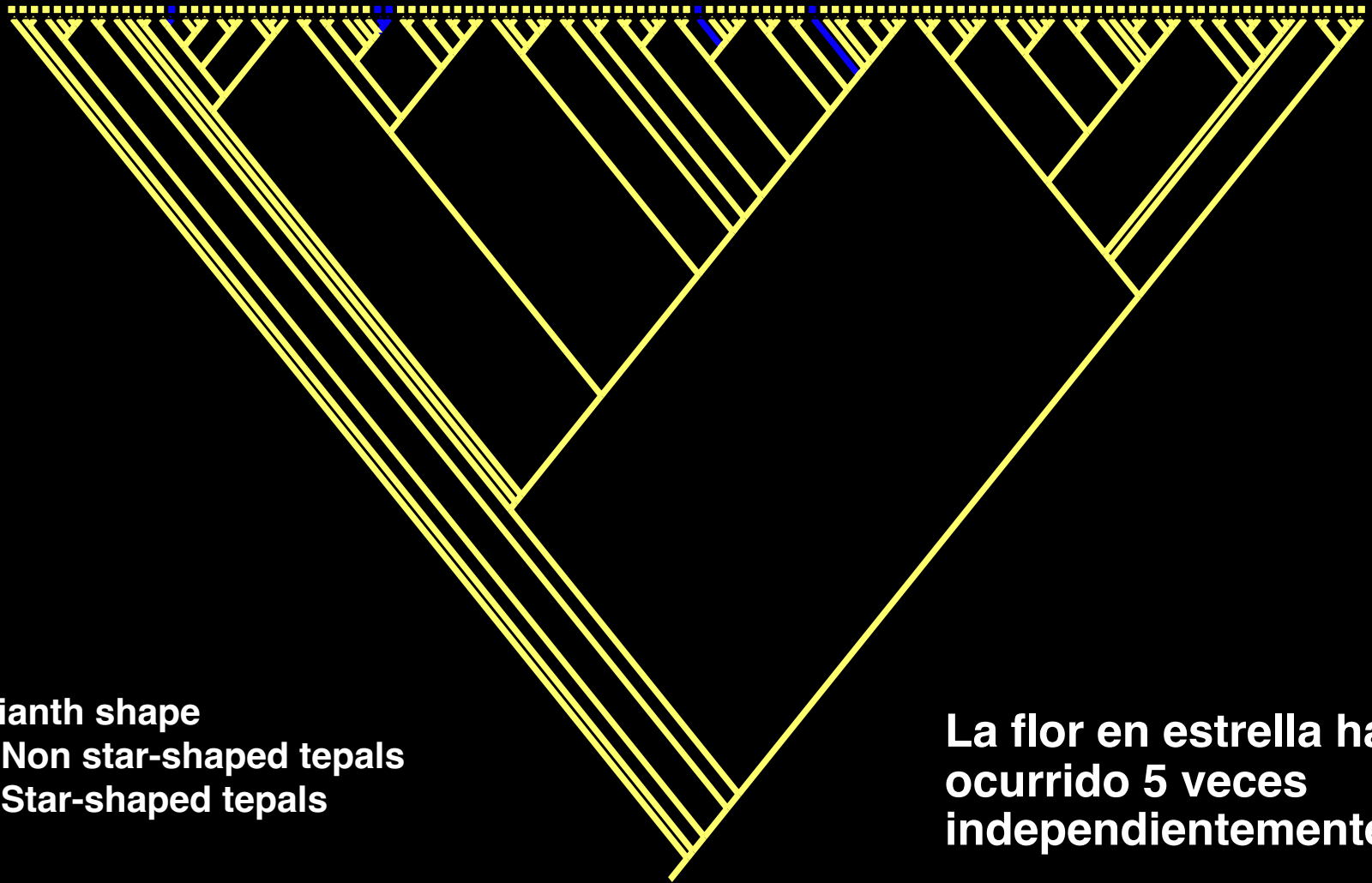
Danksagung. Wir danken BERNHARD WENZEL (Bubikon, Schweiz) für die gesammelten Falter. Bei der ersten taxonomischen Zuordnung der Orchidee half GÜNTHER GERLACH (Botanischer Garten München-Nymphenburg). Für entomologische, fachliche Beratung danken wir IAN KITCHING (Natural History Museum, London).

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- MICHAEL MOOSBURG, Eversbuschstrasse 58, D-80999 München; E-Mail: michael.moosburg@gmx.de
- Dr. ERIC HÄGSATER, AMO Herbarium, Instituto Chinoín, Mexico City; E-Mail: herbamoo@prodigy.net.mx
- Dr. MICHAEL OCHSE, Waldstraße 51, D-67273 Weisenheim am Berg; E-Mail: diehl.ochse@t-online.de



Abb. 1. *Adhemarius sexoculata* GROTE, 1867.



Perianth shape
0 = Non star-shaped tepals
1 = Star-shaped tepals

La flor en estrella ha
ocurrido 5 veces
independientemente

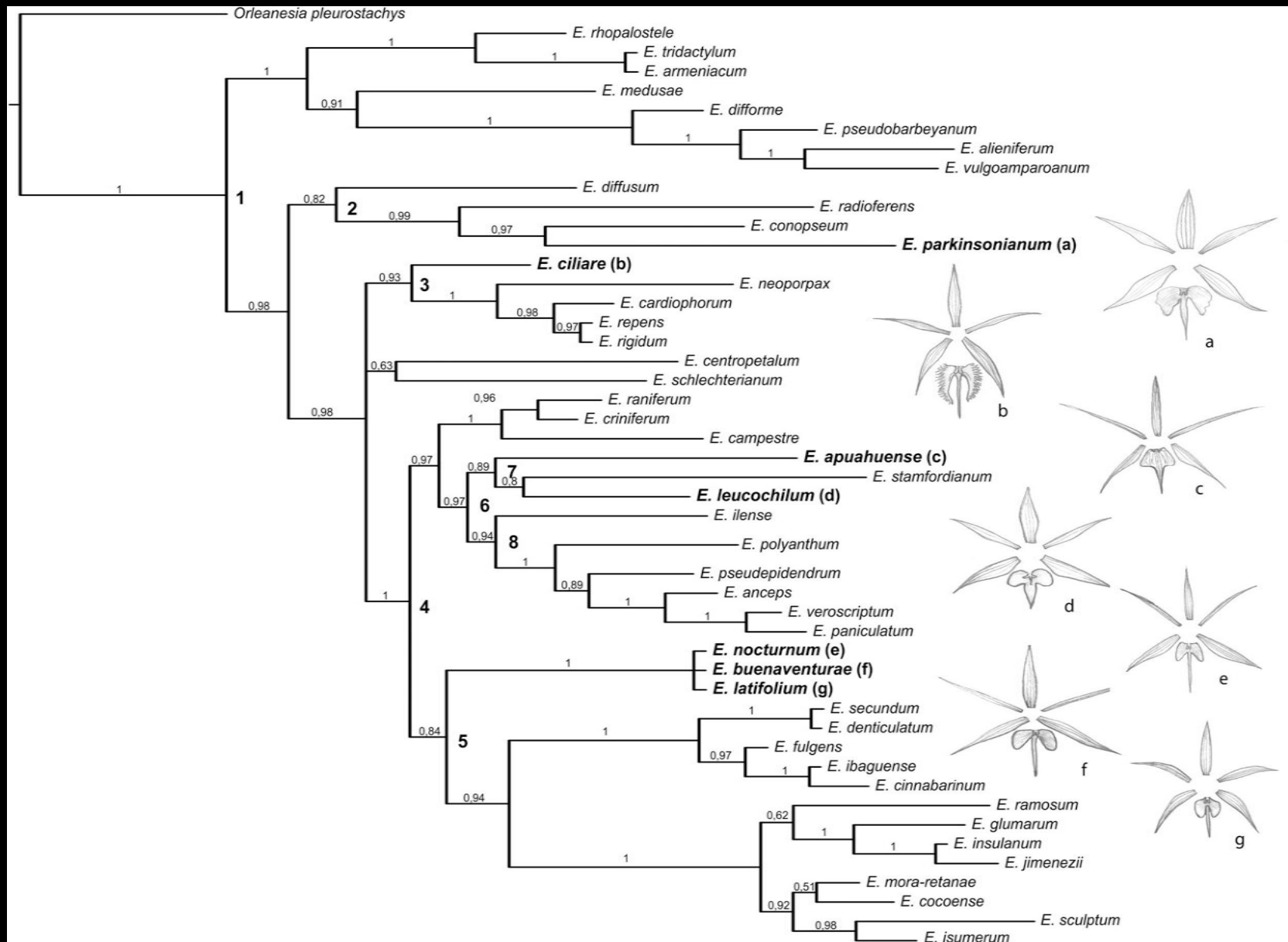
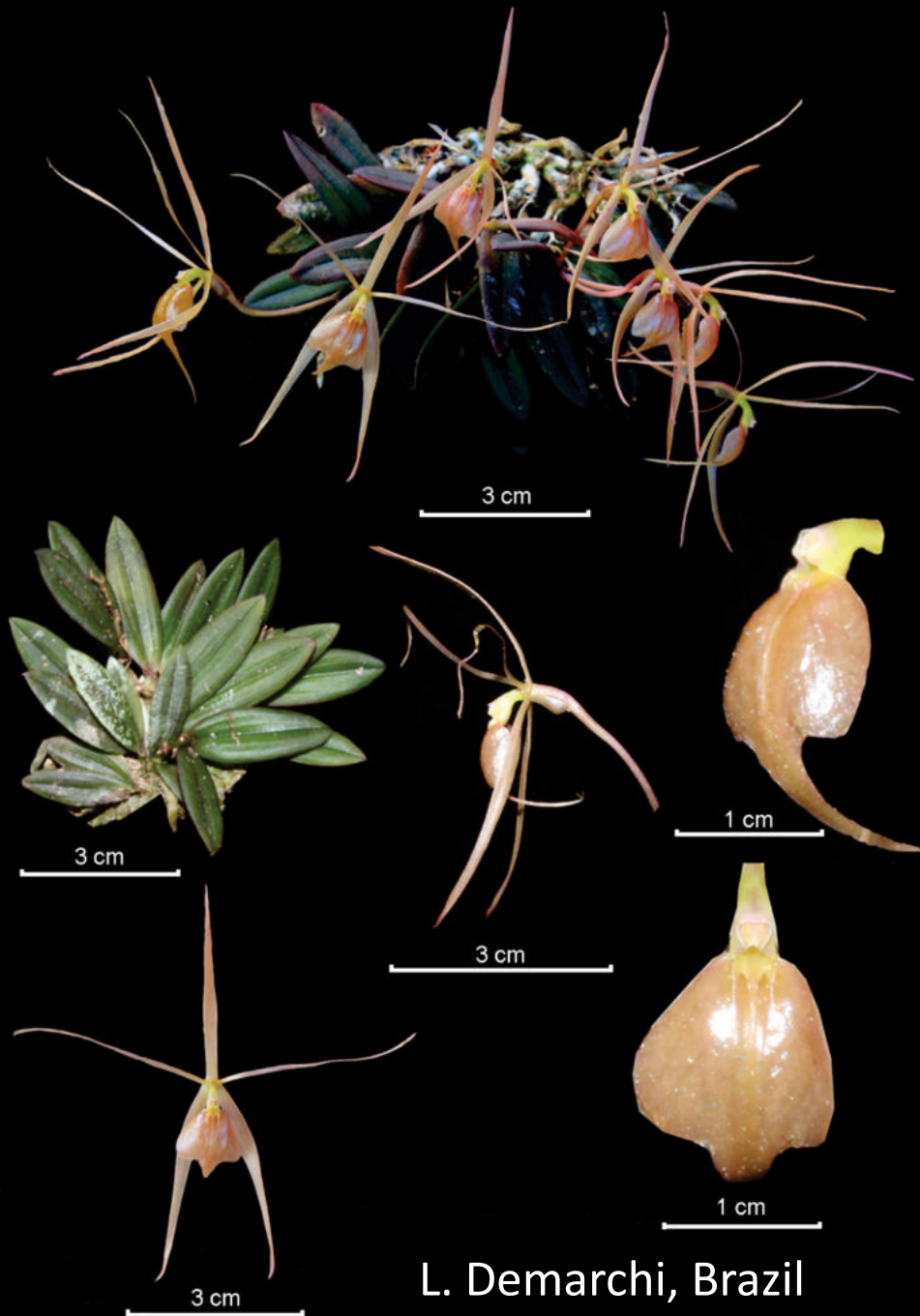


Fig. 4. Phylogenetic relationships of *Epidendrum apuahuense* within *Epidendrum* produced by Bayesian inference based on nuclear ITS sequences. Posterior probabilities (≥ 0.8) are indicated above branches. Taxa in bold represent species with star-shaped flowers, illustrated on the right side.

Viviane Pagnussat Klein, Edley Max Pessoa, Layon Oreste Demarchi, Mariela Sader, and Maria Teresa Fernandez Piedade, 2019, *Encyclia*, *Epidendrum*, or *Prosthechea*? Clarifying the Phylogenetic Position of a Rare Amazonian Orchid (Laeliinae-Epidendroideae-Orchidaceae) Systematic Botany 44(2): pp. 297–309.





E. esperanza-mejiae

C. Uribe, Colombia



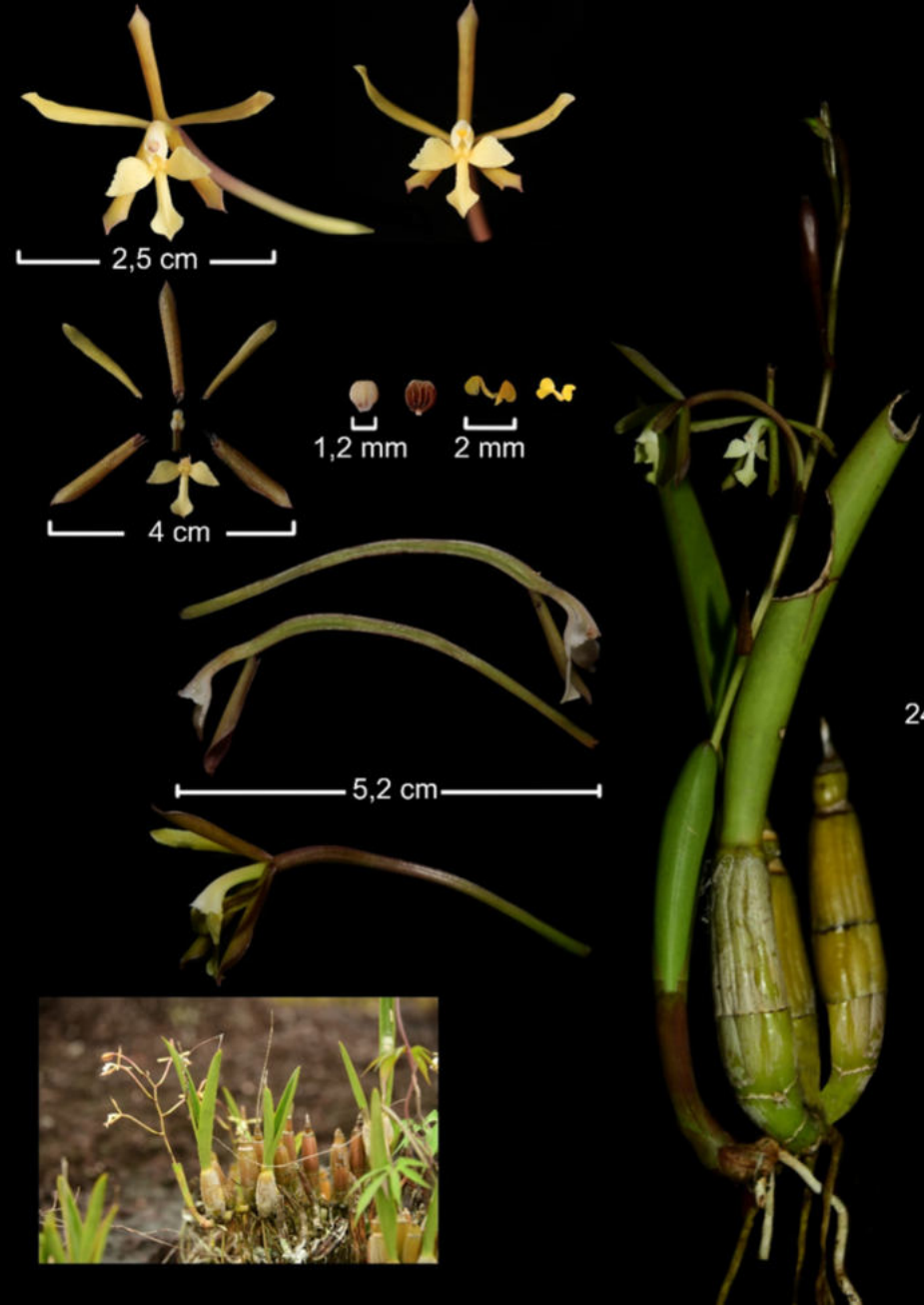
E. ciliare

R. Jiménez, México



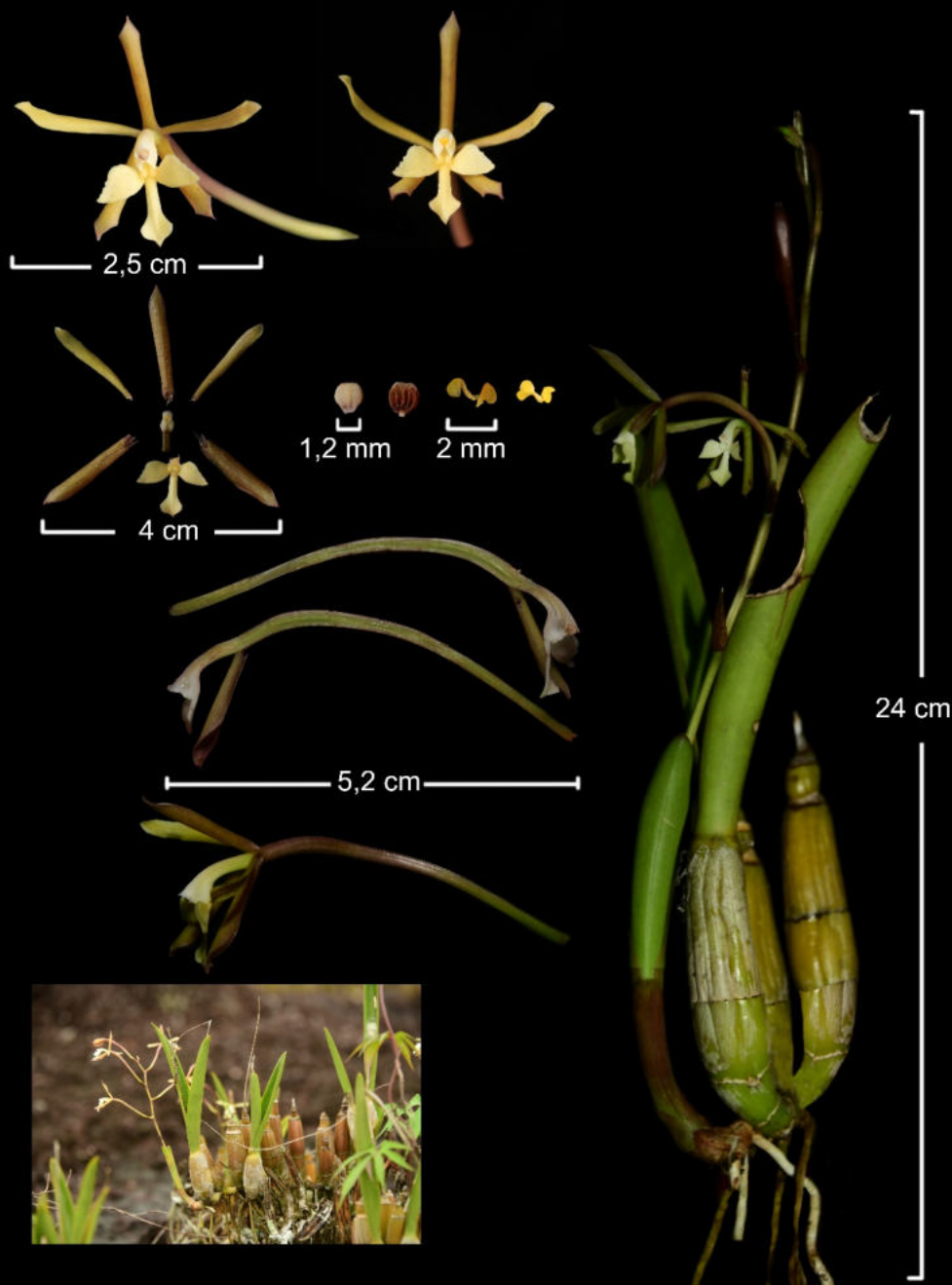
E. viscidum

G. Salazar, México

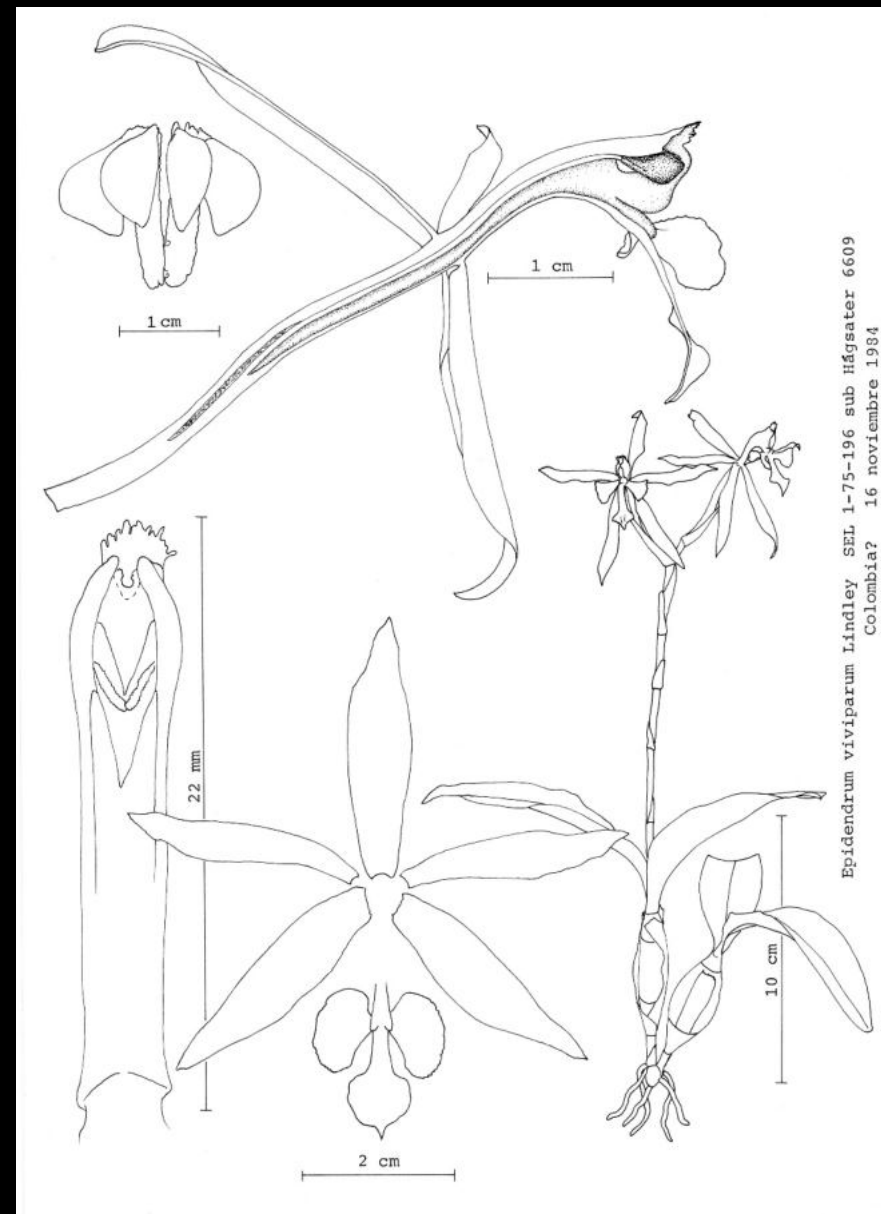


E. hurtadoi

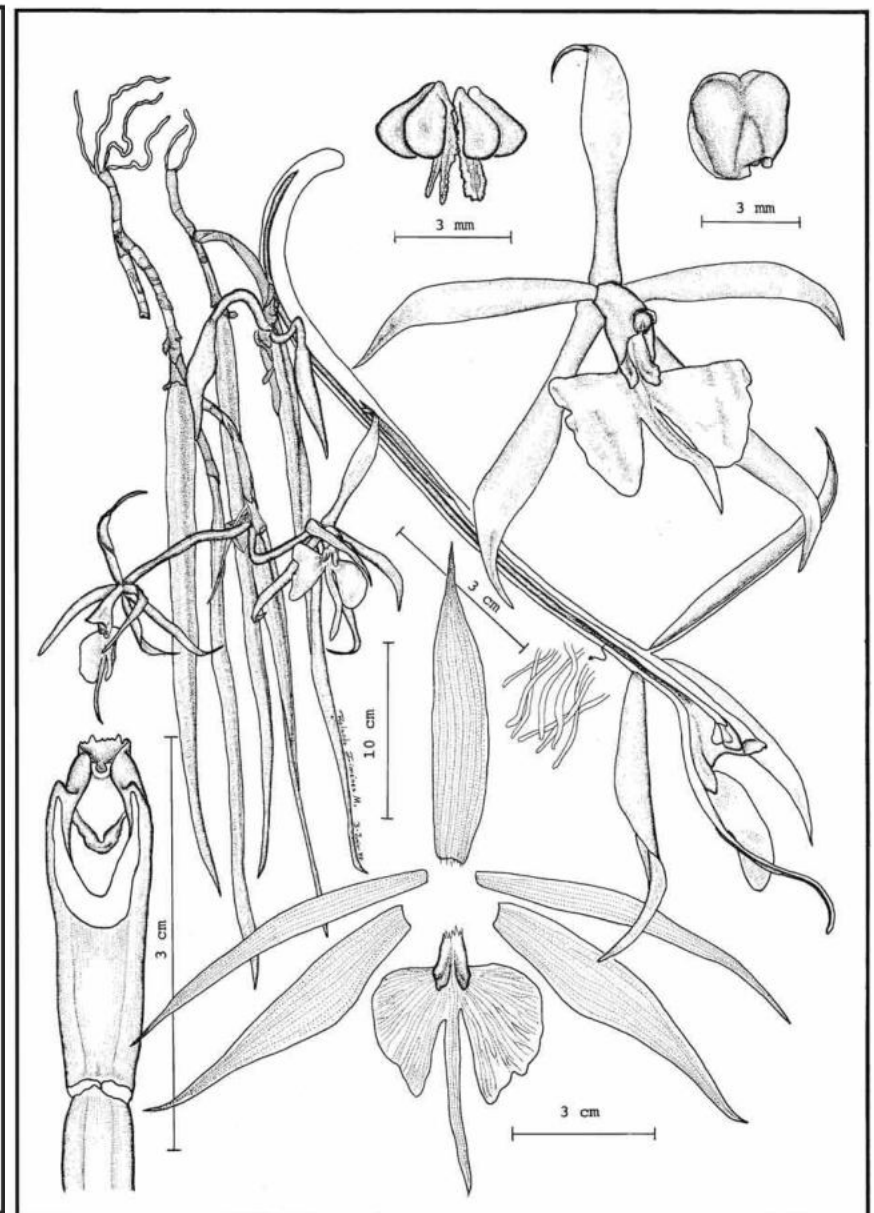
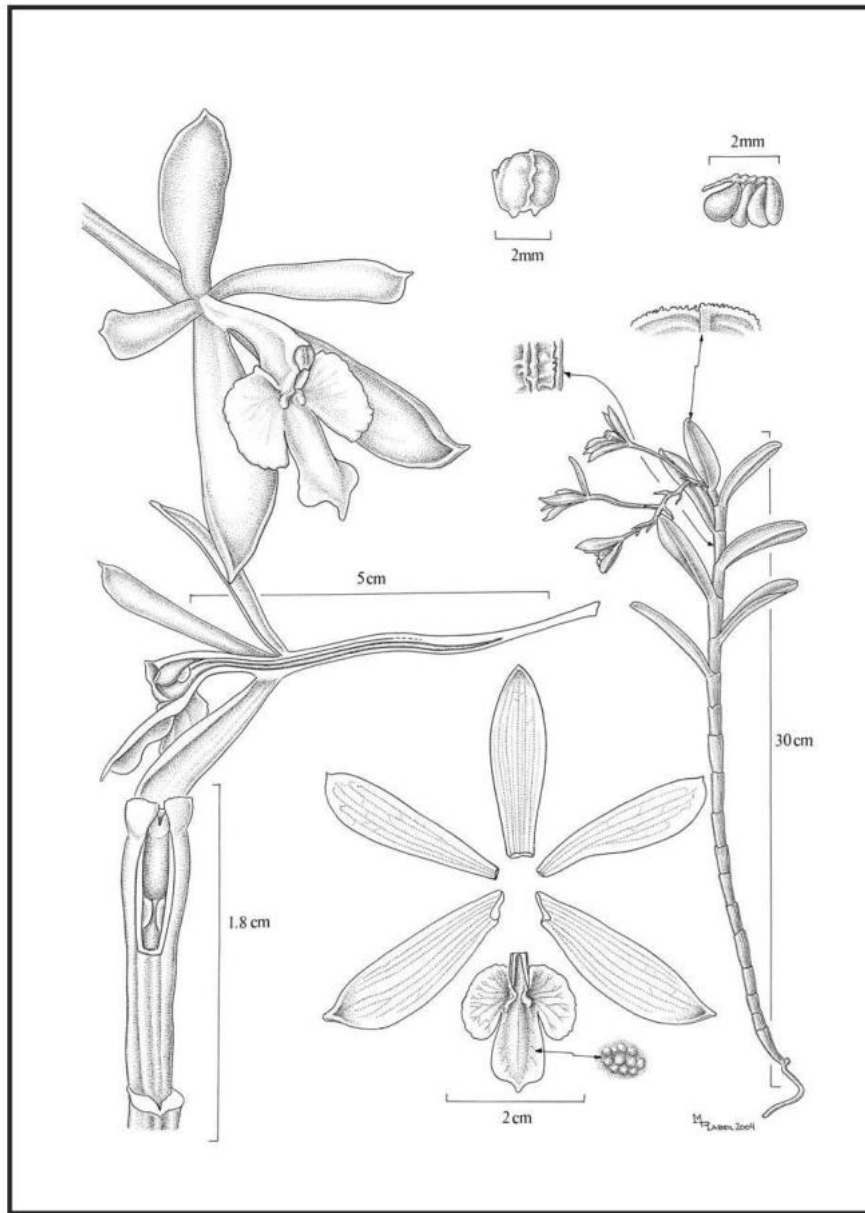
C. Uribe, Colombia



Epidendrum hurtadoi



Epidendrum viviparum



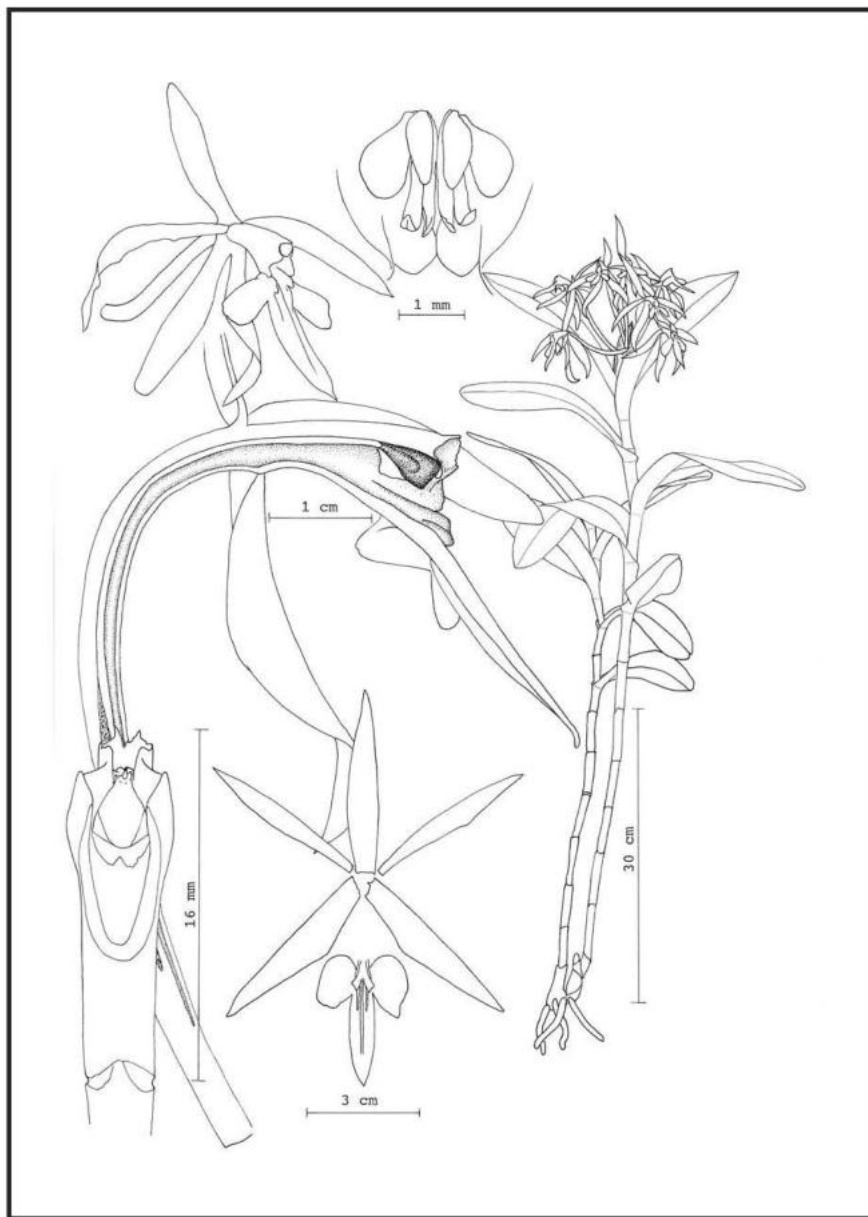
EPIDENDRUM STEYERMARKII A.D.Hawkes

Plate 1294

EPIDENDRUM PARKINSONIANUM Hook.

Text on the reverse side

Plate 37

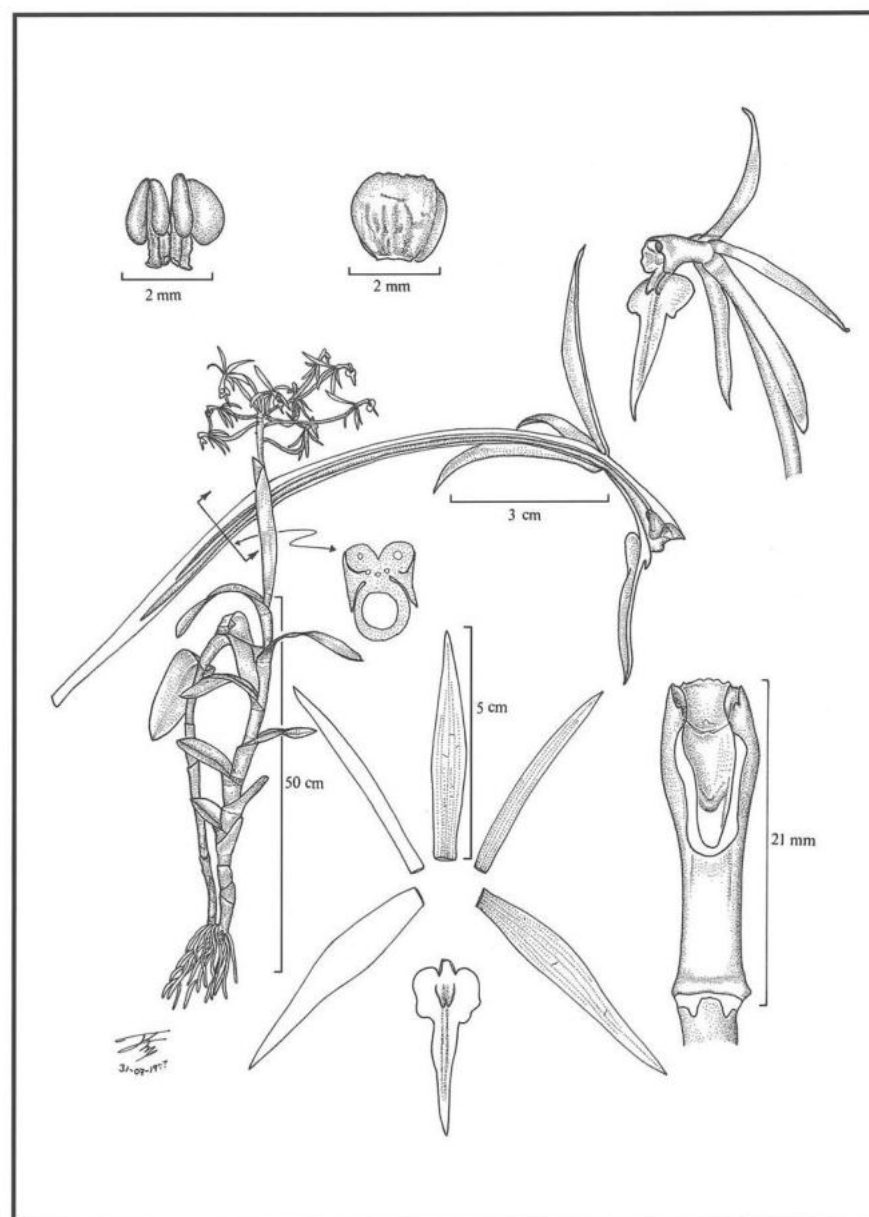


EPIDENDRUM LEUCOCHILUM Link, Klotzsch & Otto

THE GENUS EPIDENDRUM PART 8

Plate 1260

ICONES ORCHIDACEARUM 12. 2009

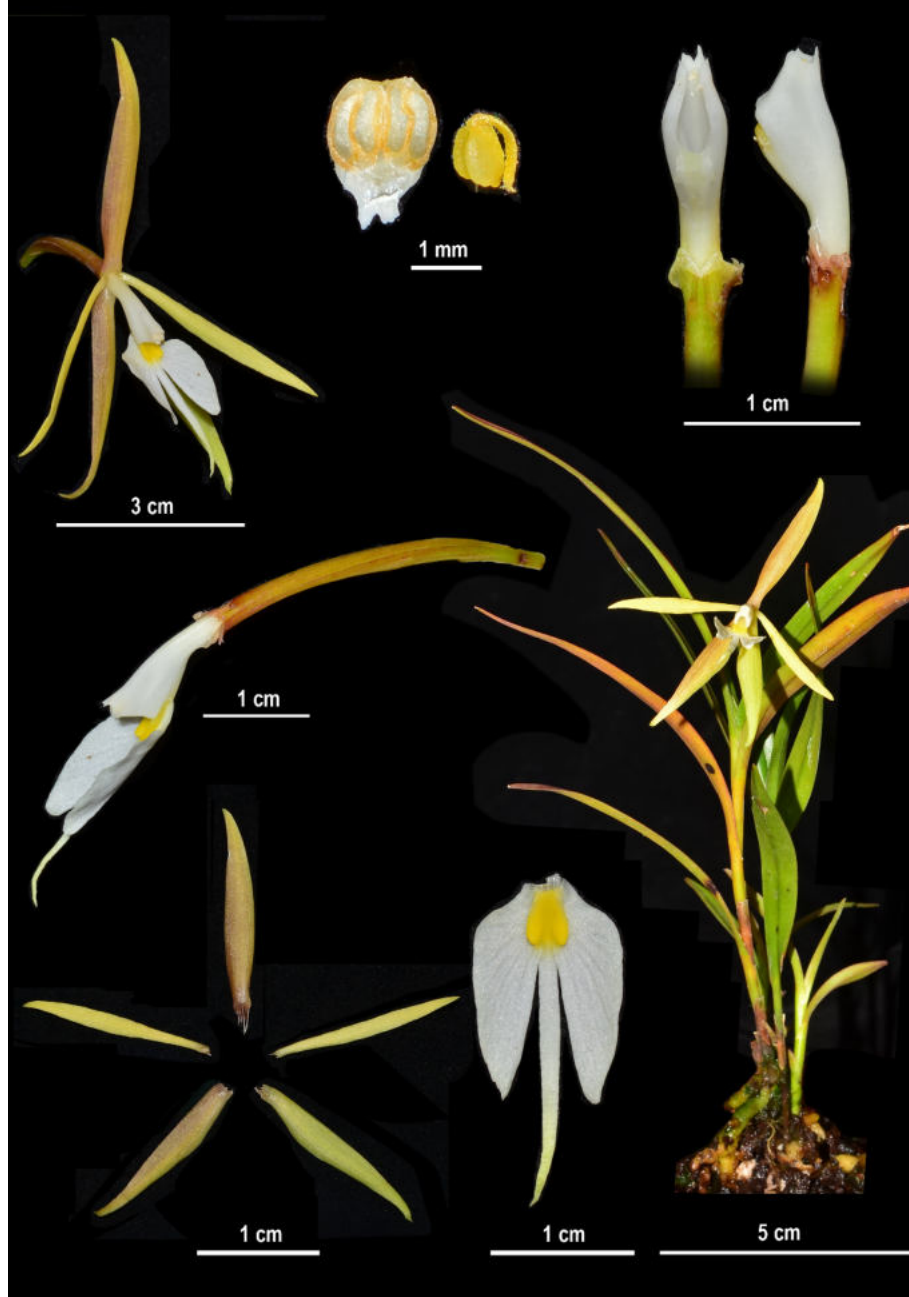


EPIDENDRUM LACUSTRE Lindl.

THE GENUS EPIDENDRUM PART 7

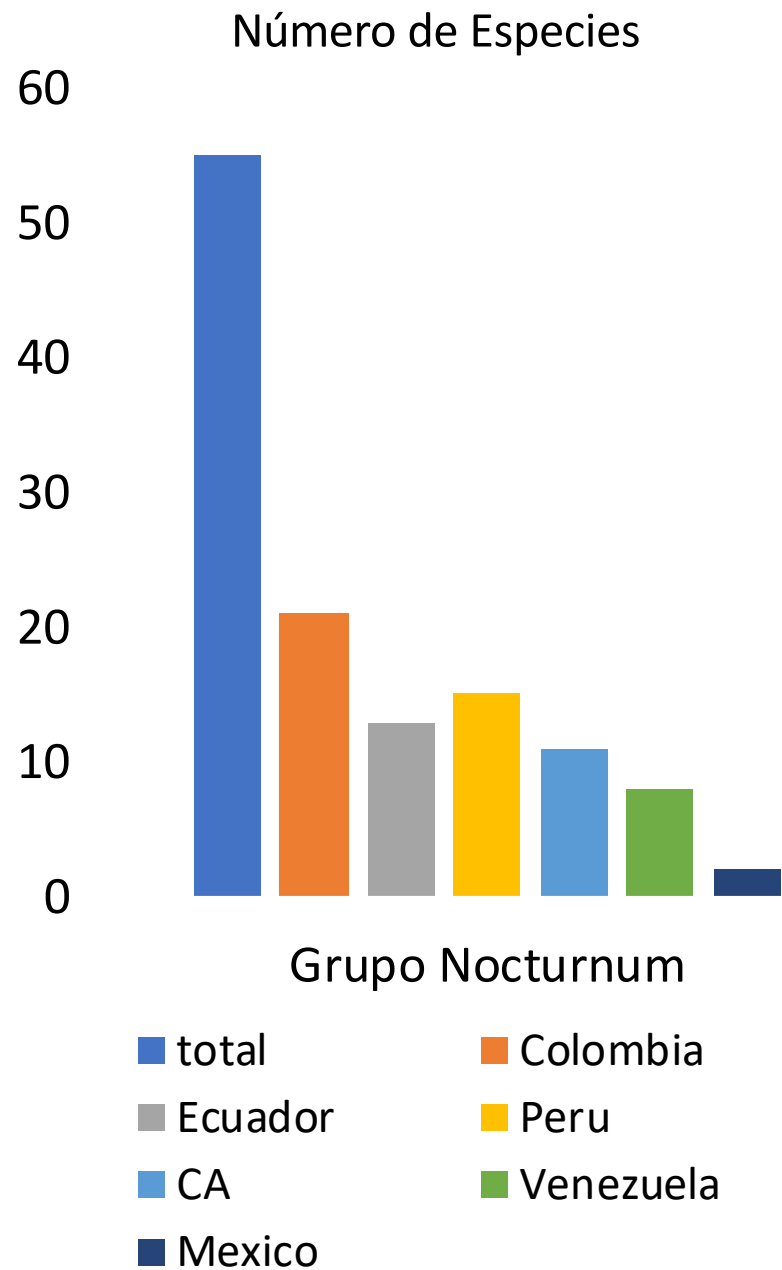
Plate 1135

ICONES ORCHIDACEARUM 11. 2008



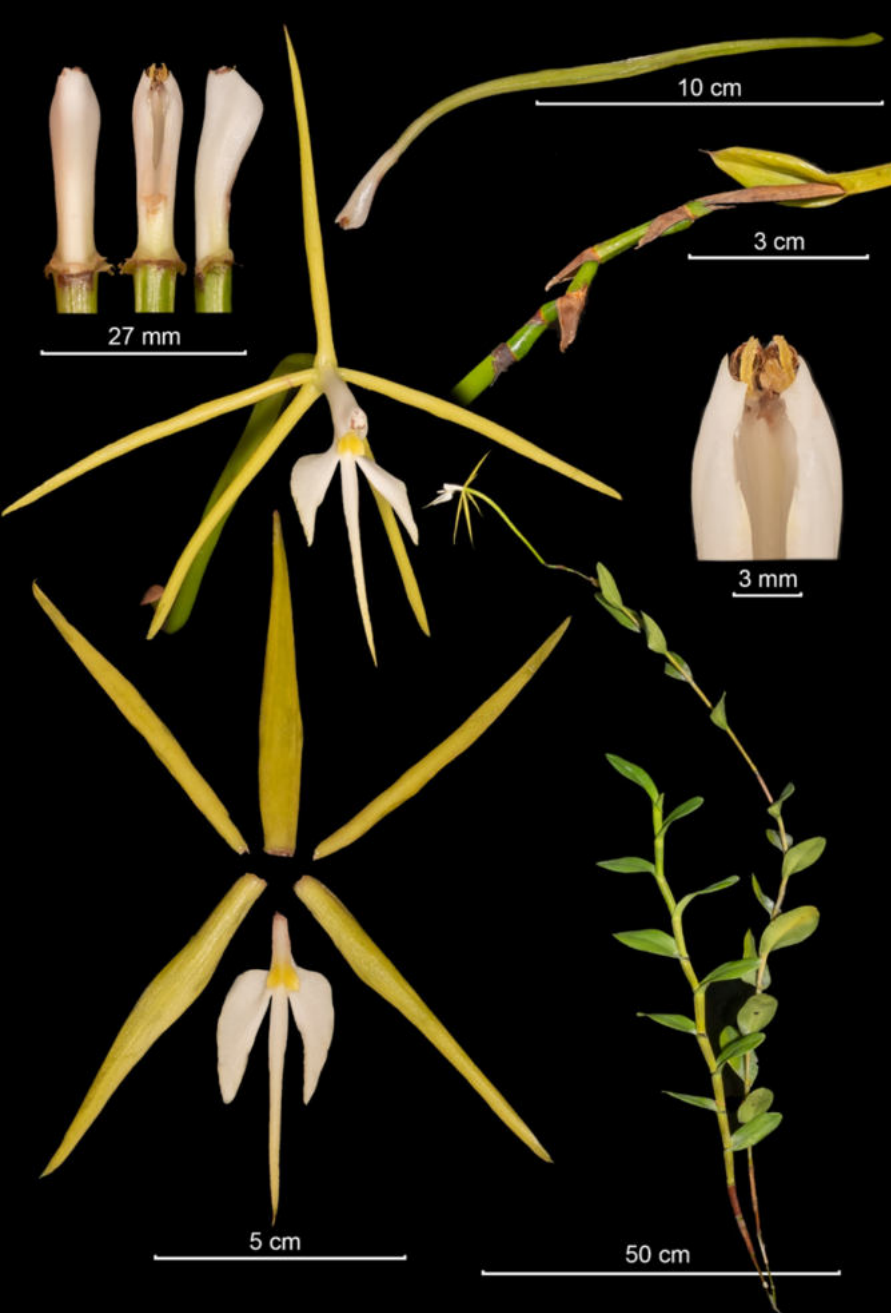
Epidendrum litense

H. Medina, Lita, Esmeraldas, Ecuador



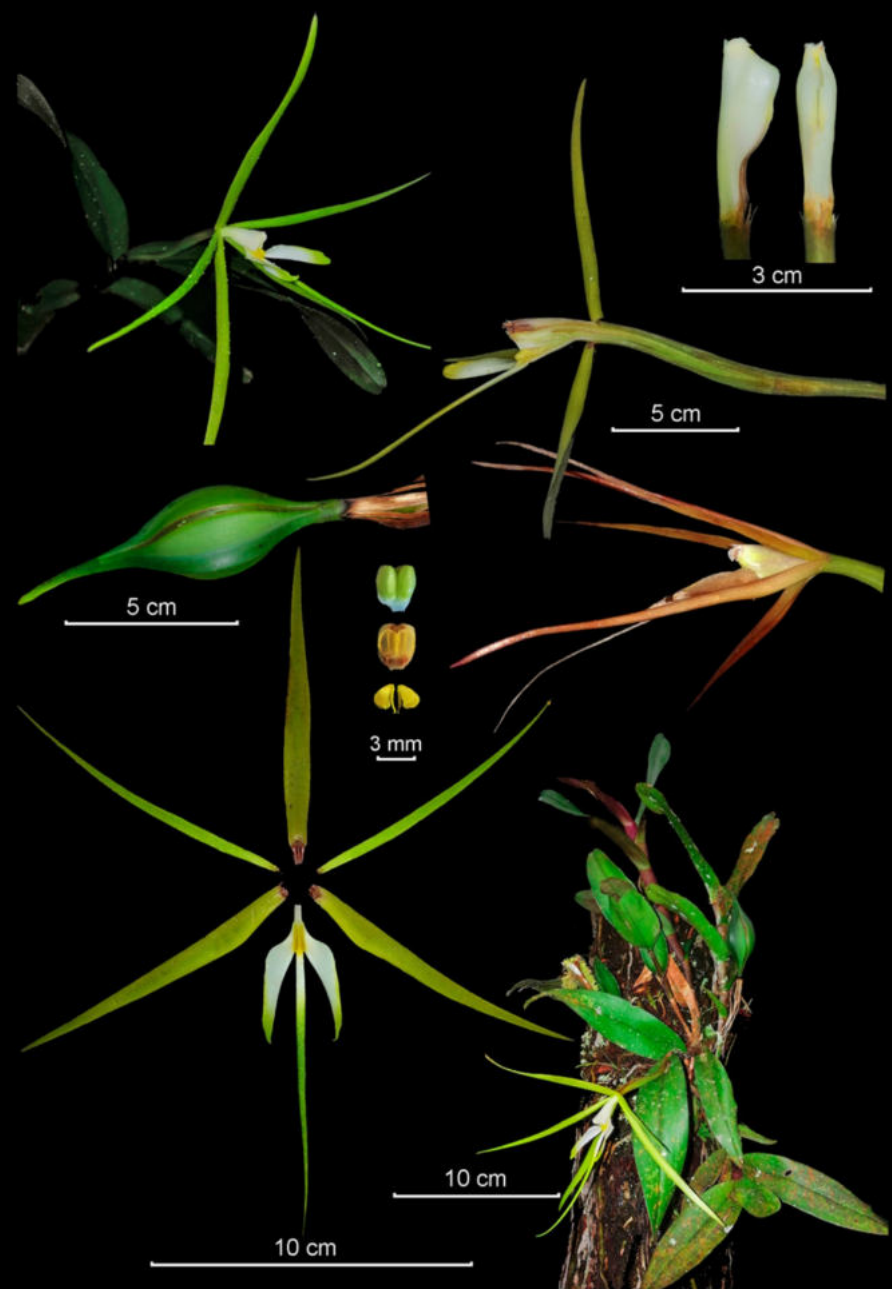


Epidendrum macrophorum
E. Hágsater, Cotopaxi, Ecuador



E. tumuc-humaciense

E. Hágater, Gran Sabana, Venezuela



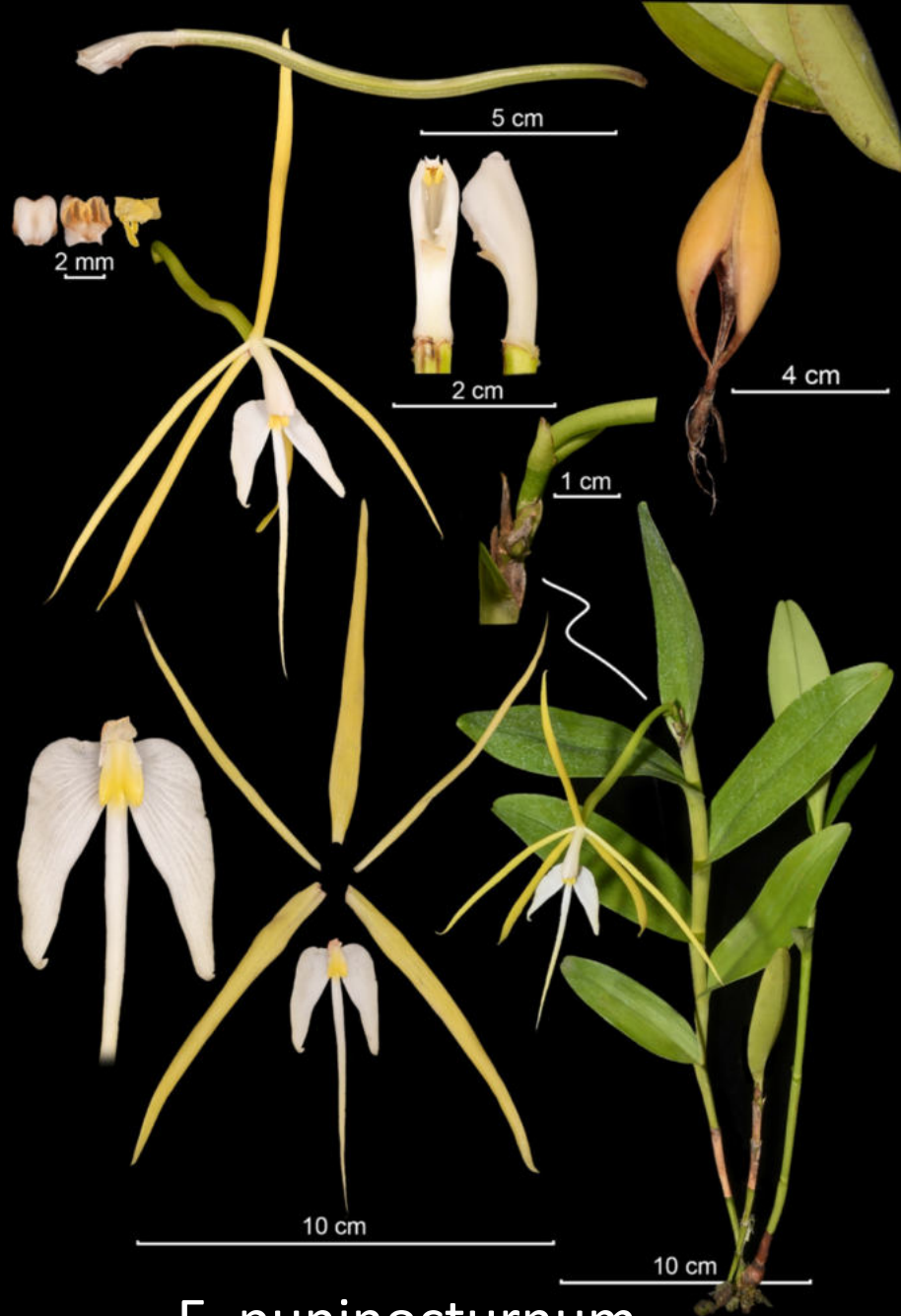
E. noctirufescens

D. Cadena, Santander, Colombia



E. phlebonoctrum

R. Jiménez, Pastaza, Ecuador



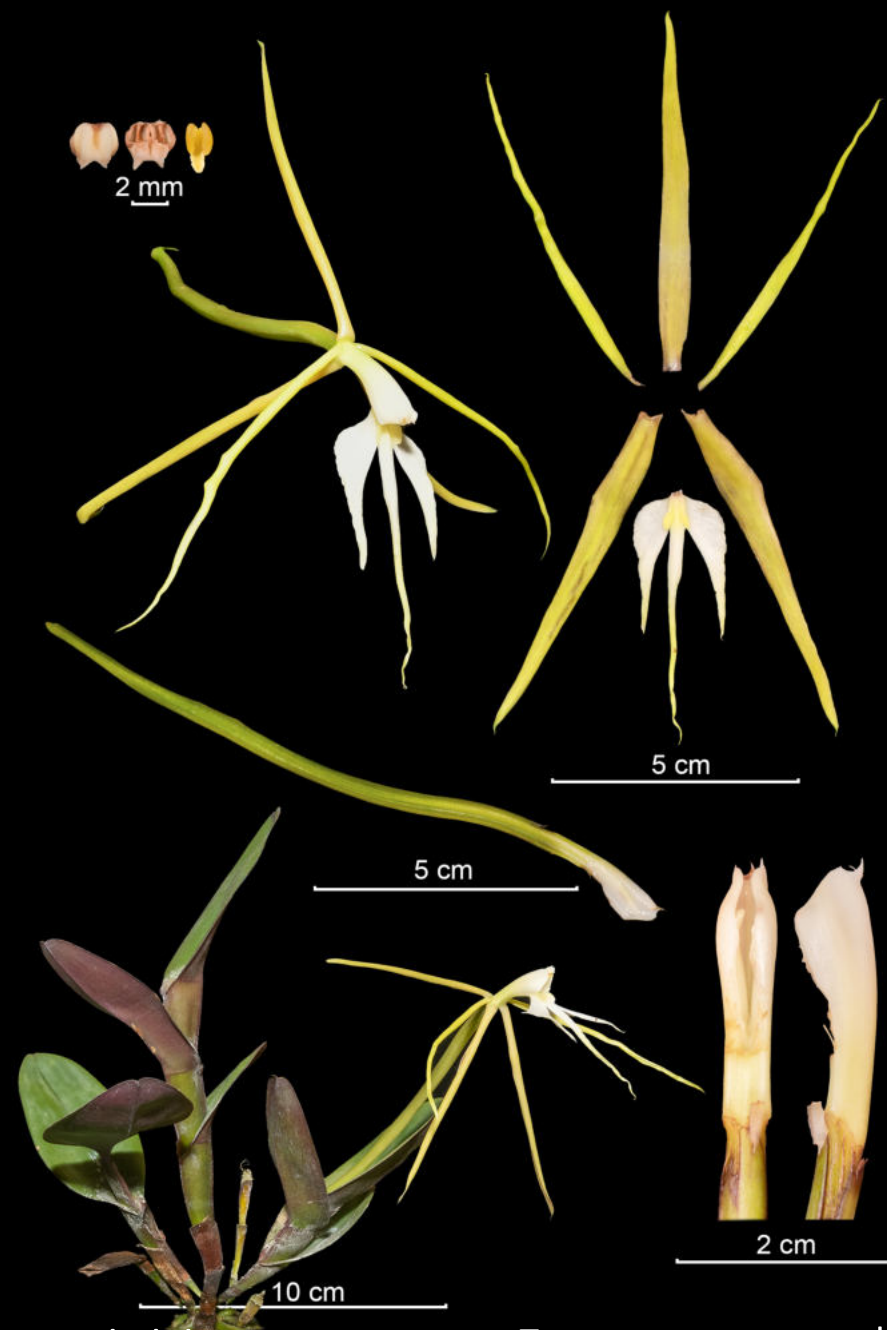
E. puninoctrum

R. Jiménez, Pastaza, Ecuador



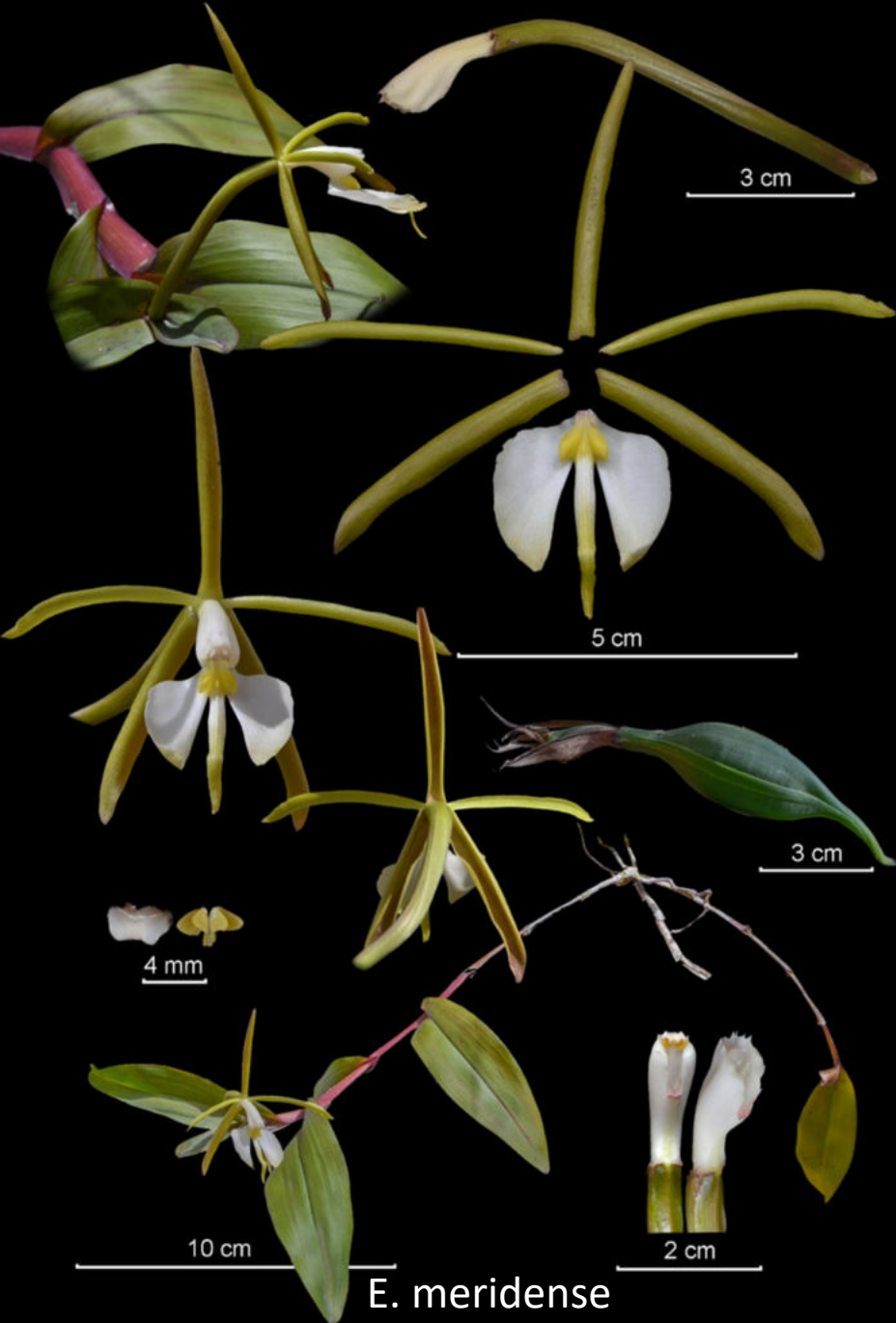
E. trapeziinocturnum

A. Barona-Colmenares, Leticia, Colombia



E. ancipitinocturnum = *E. purpureocaule*

E. Hágsater, Manaus, Brasil



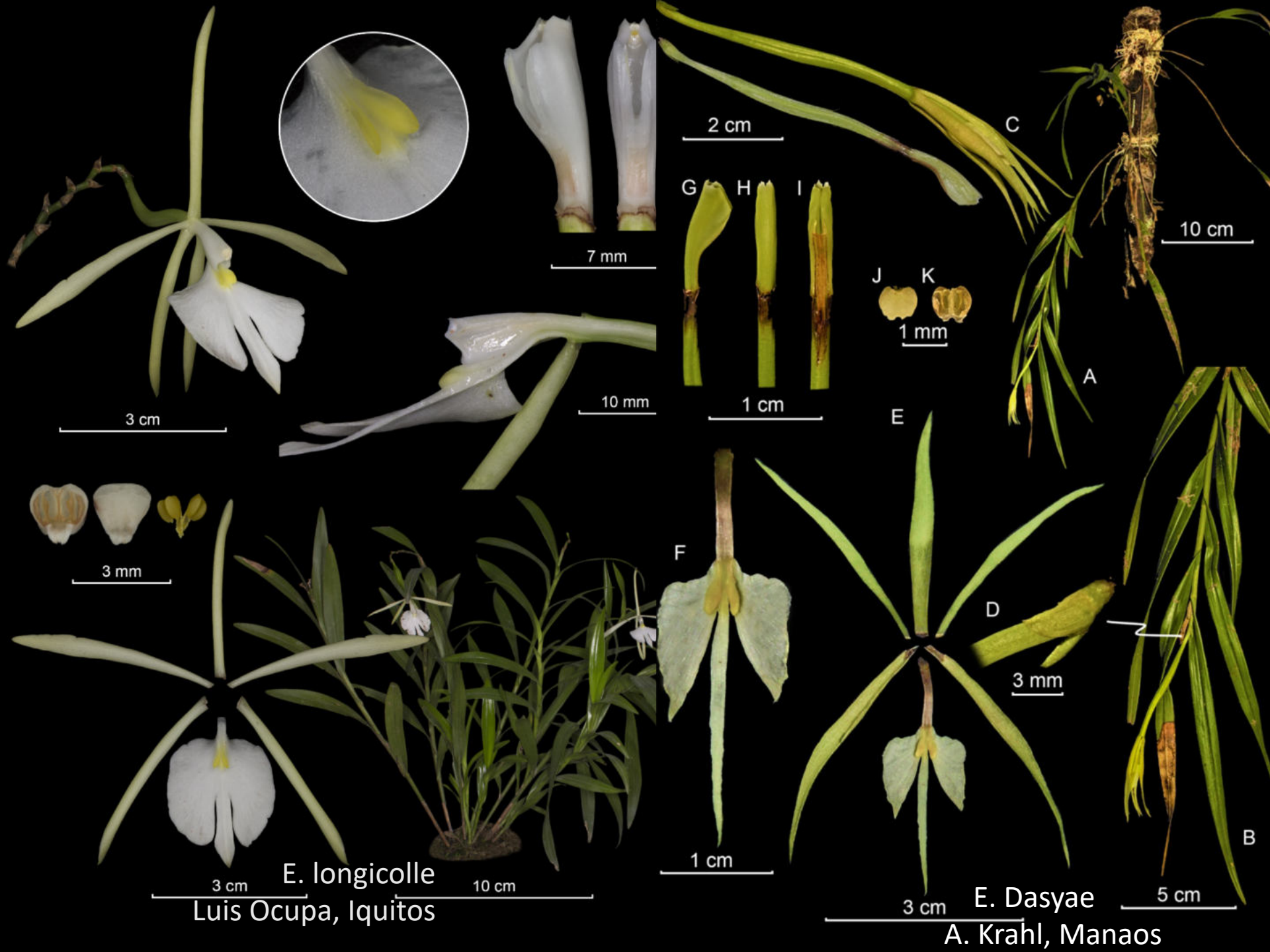
E. meridense

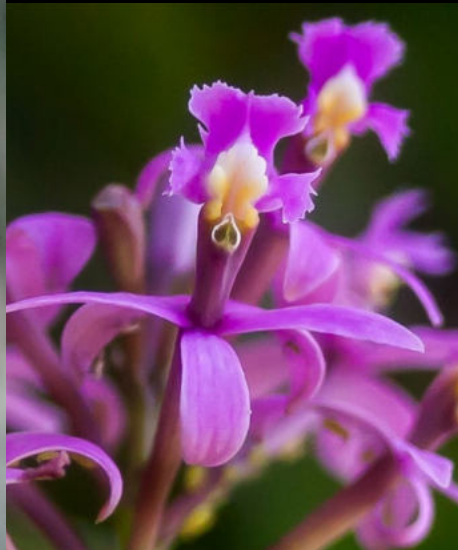
C. Jerez, Mérida, Venezuela



E. platynoctrurnum

R. Jiménez, Pastaza, Ecuador





Epidendrum secundum

Epidendrum x elongatum



Epidendrum x elongatum

Epidendrum cryptopateras

Fotografías: Louison Charly y Pierre Courtinard, Martinica



Epidendrum x elongatum Jacq.



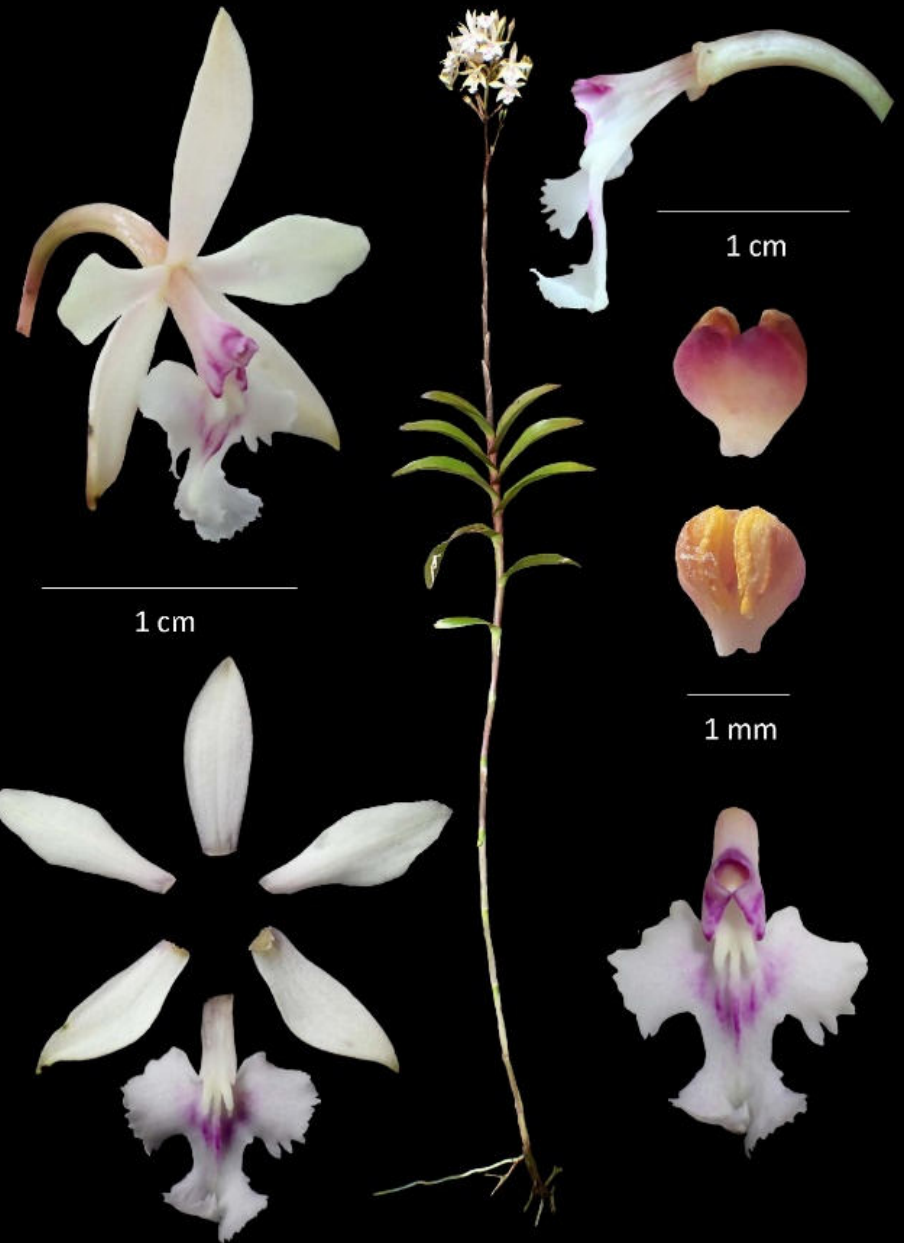


E. x elongatum
var. *album*



Epidendrum revertianum

C et P Guezennec



Epidendrum cyparisii



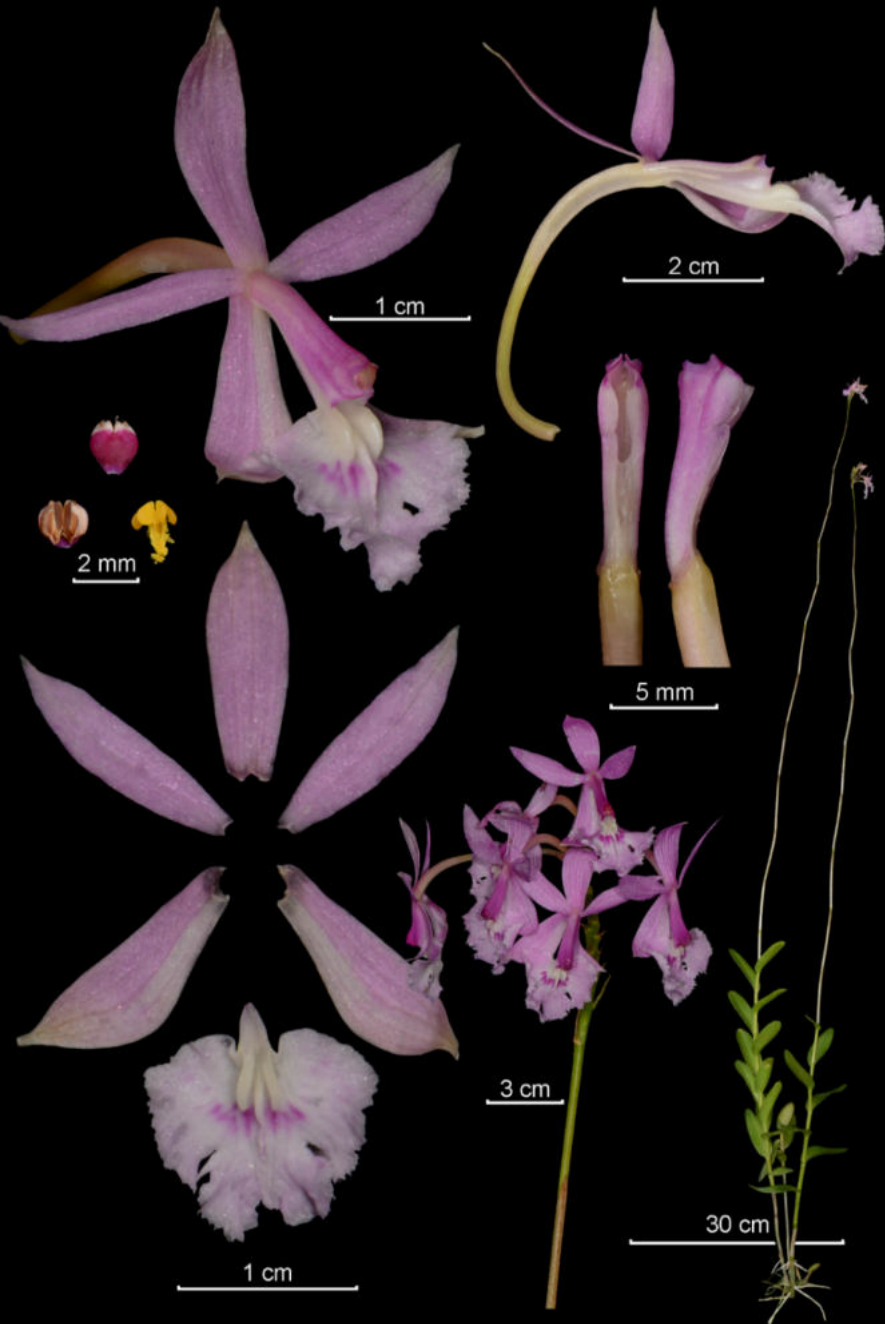
Epidendrum pakaraima x *Epidendrum kamoirán* = *Epidendrum x communis*, ined.



Epidendrum ibaguense
Antioquia, Colombia

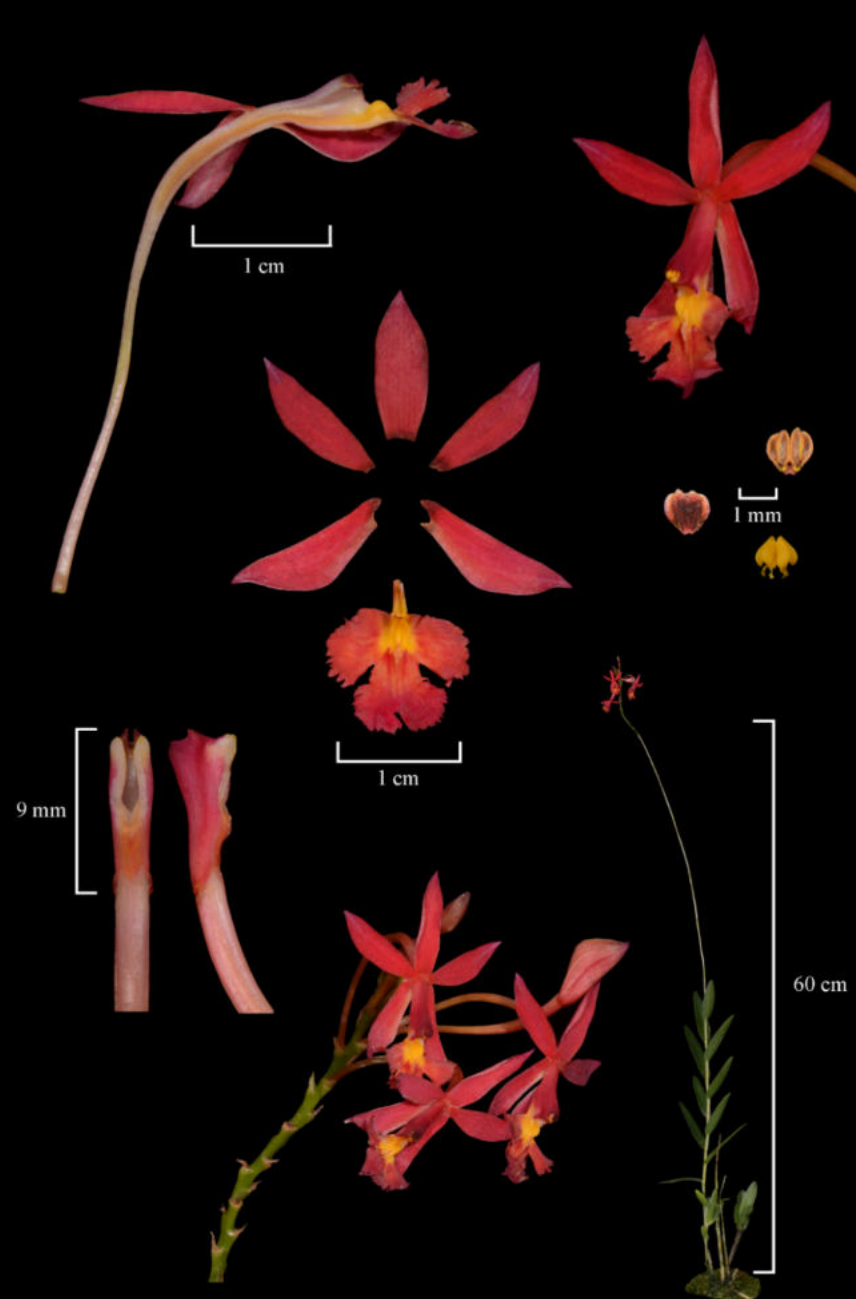
Epidendrum x gransabanenese
Gran Sabana, Venezuela

Epidendrum aff. *secundum*
Roraima tepuí, Venezuela



Epidendrum x communis, ined.

E. Hágater, Tepequém, Roraima, Brasil



E. schomburgkii x kamoirán

E. Hágater, Gran Sabana, Venezuela

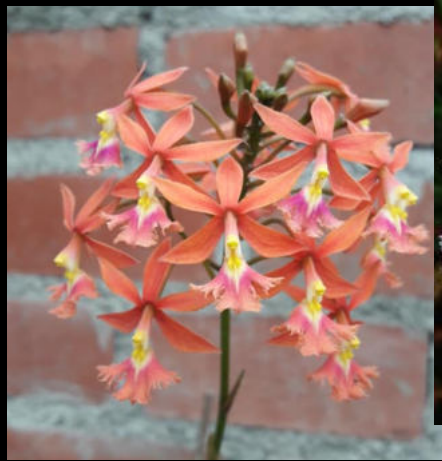
Epidendrum microcarpum rojo
Félix Torres-2013



Epidendrum schomburgkii



?



?

Torres Paucar, Perú



Epidendrum



Epidendrum igneosicium
Río Orinoco, Ven. y Col.



Epidendrum schomburgkii
La Escalera, Bolivar, Ven.



Epidendrum splendens
Ecuagenera, Ecuador



Epidendrum ?

C. Uribe, Colombia

Felix Torres

Uchumbamba

Distribución preliminar de

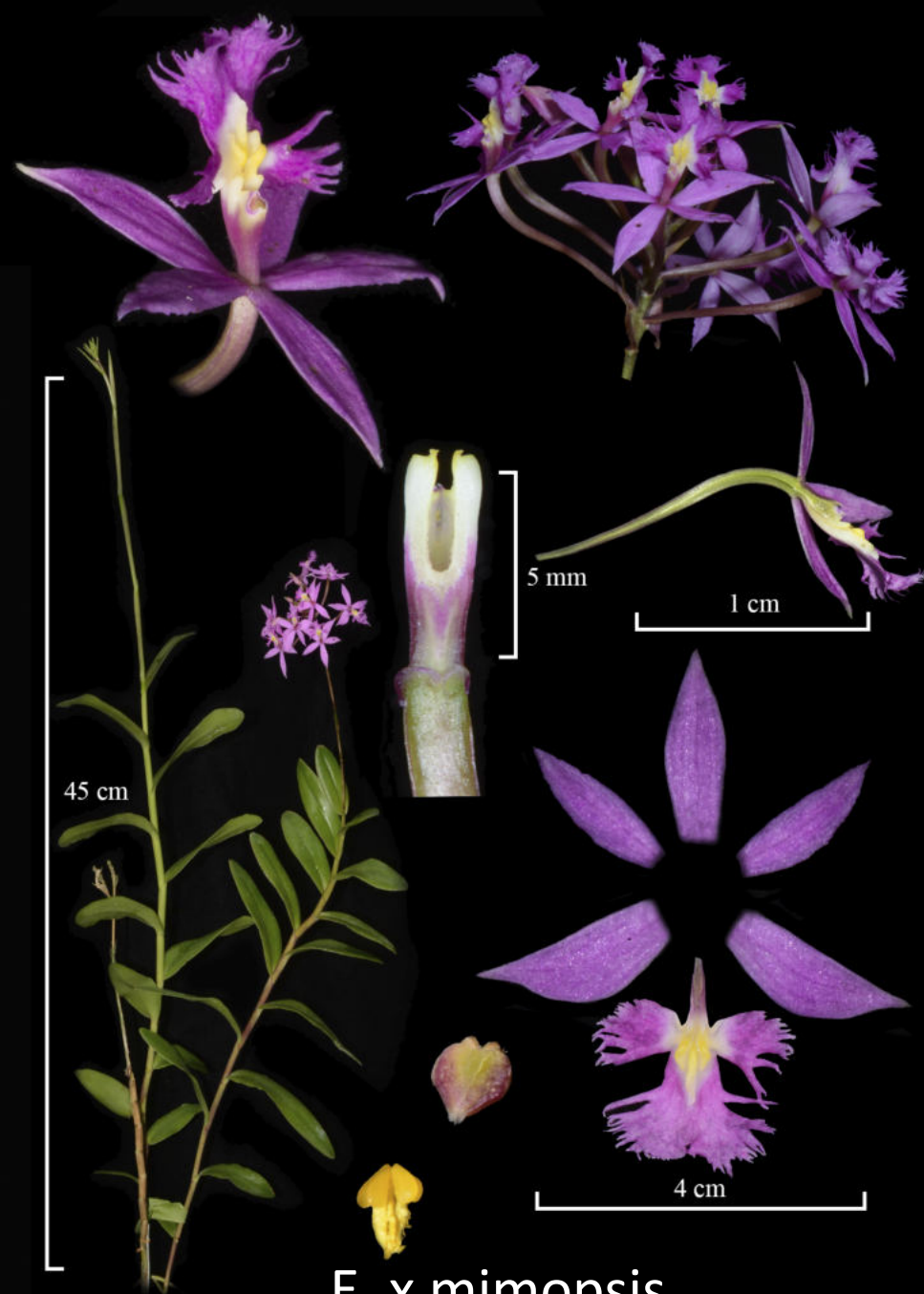
Epidendrum x communis, ined.

Desde Roraima al sur del Escudo Guayanés, hasta La Serranía de la Macarena, Meta, Colombia



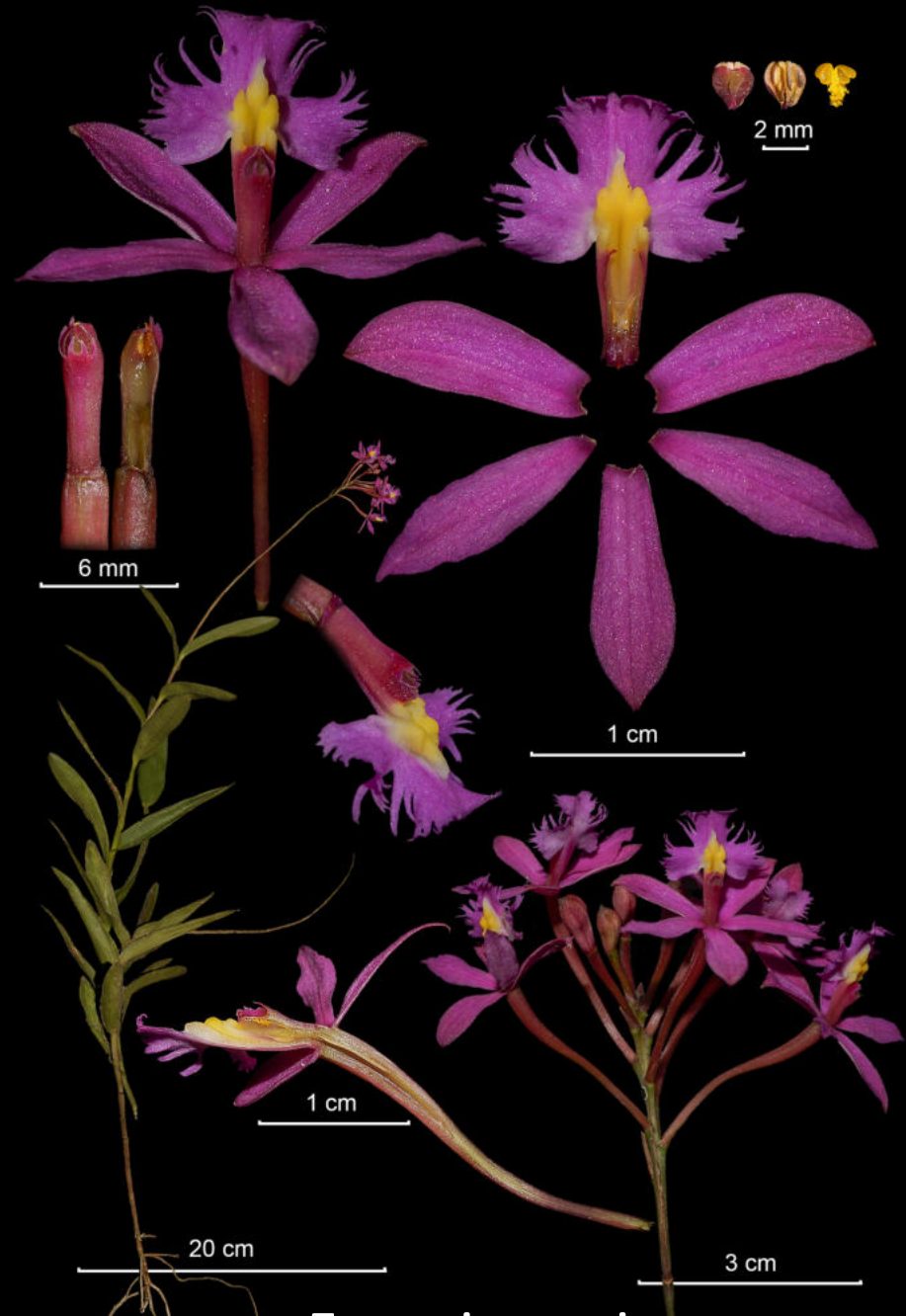
E. splendens x *calanthum*?

. Torres, Tarma-San Ramón



E. x mimopsis

E. Hágsater, Zumba, Chinchipe, Ecuador



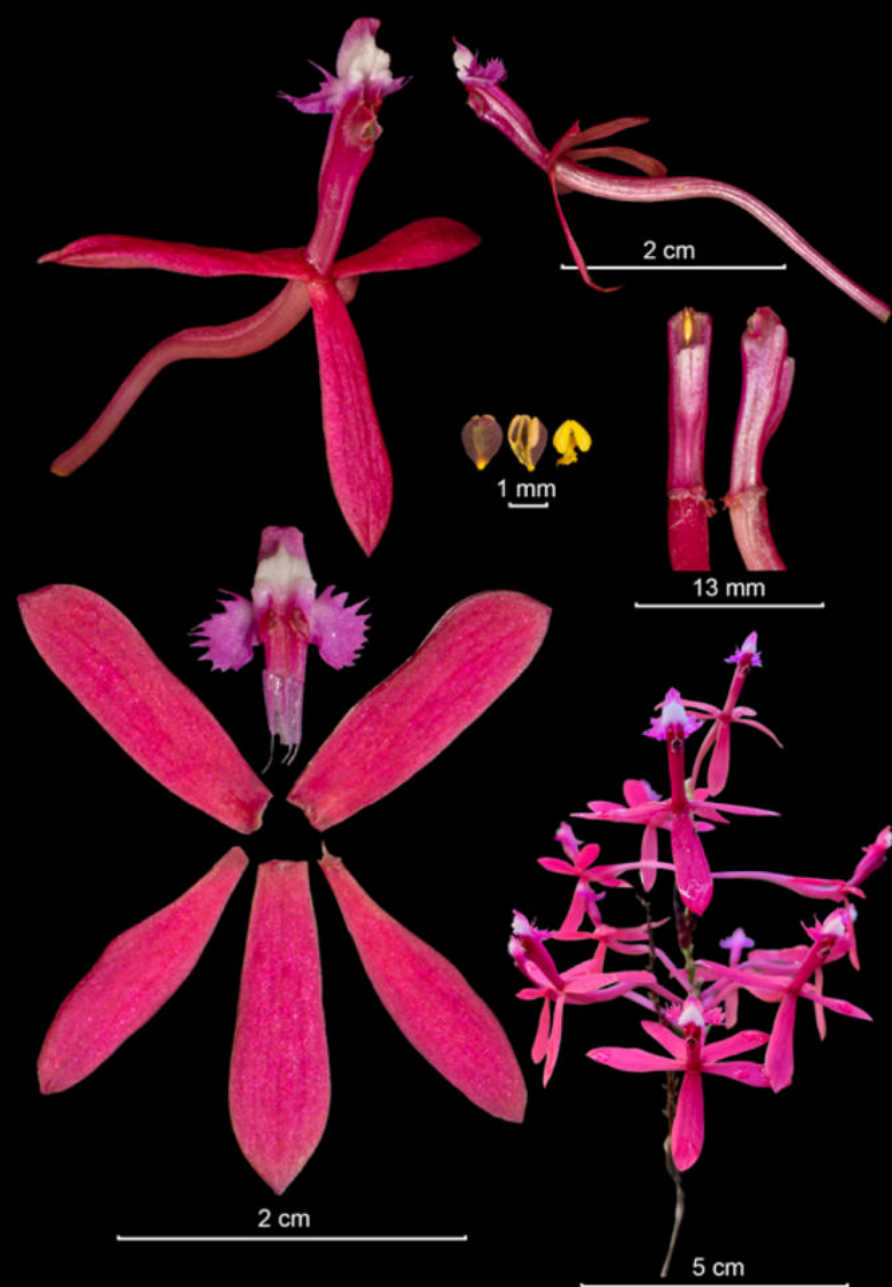
E. x mimopsis

J. Edquén, Venceremos, San Martín



E. x inauditum

B. Zambrano, El Oro, Ecuador



E. vinosum

E. Hágster, Moyobamba, San Martín

ICONES ORCHIDACEARUM

Fascicle 17(1)
THE GENUS EPIDENDRUM
Part 13
“Species New & Old in Epidendrum”

Editors: Eric Hágsater & Elizabeth Santiago

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ICONES ORCHIDACEARUM

Fascicle 17(2)
THE GENUS EPIDENDRUM
Part 13
“Species New & Old in Epidendrum”

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ICONES ORCHIDACEARUM

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THE GENUS EPIDENDRUM
Part 14
“Species New & Old in Epidendrum”

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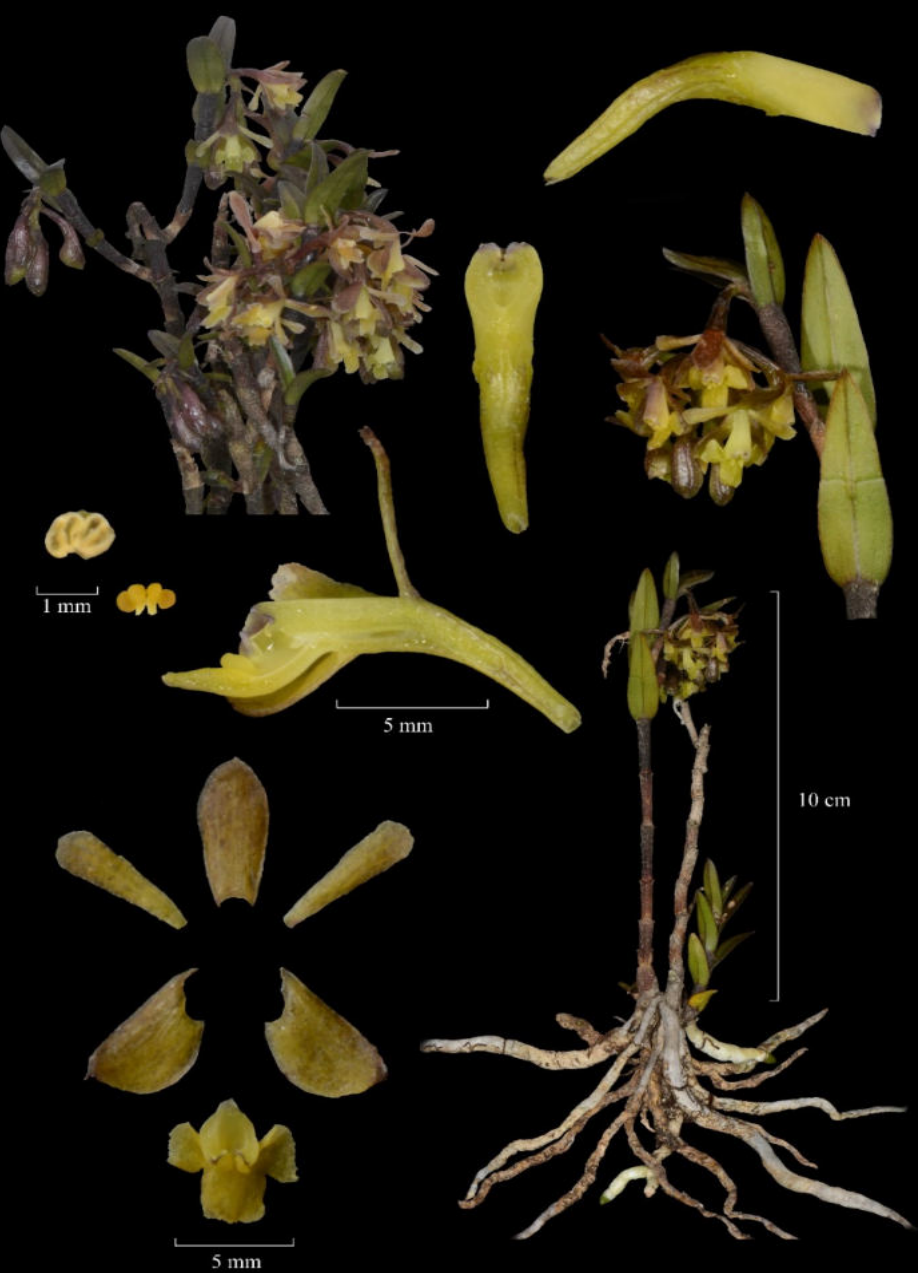


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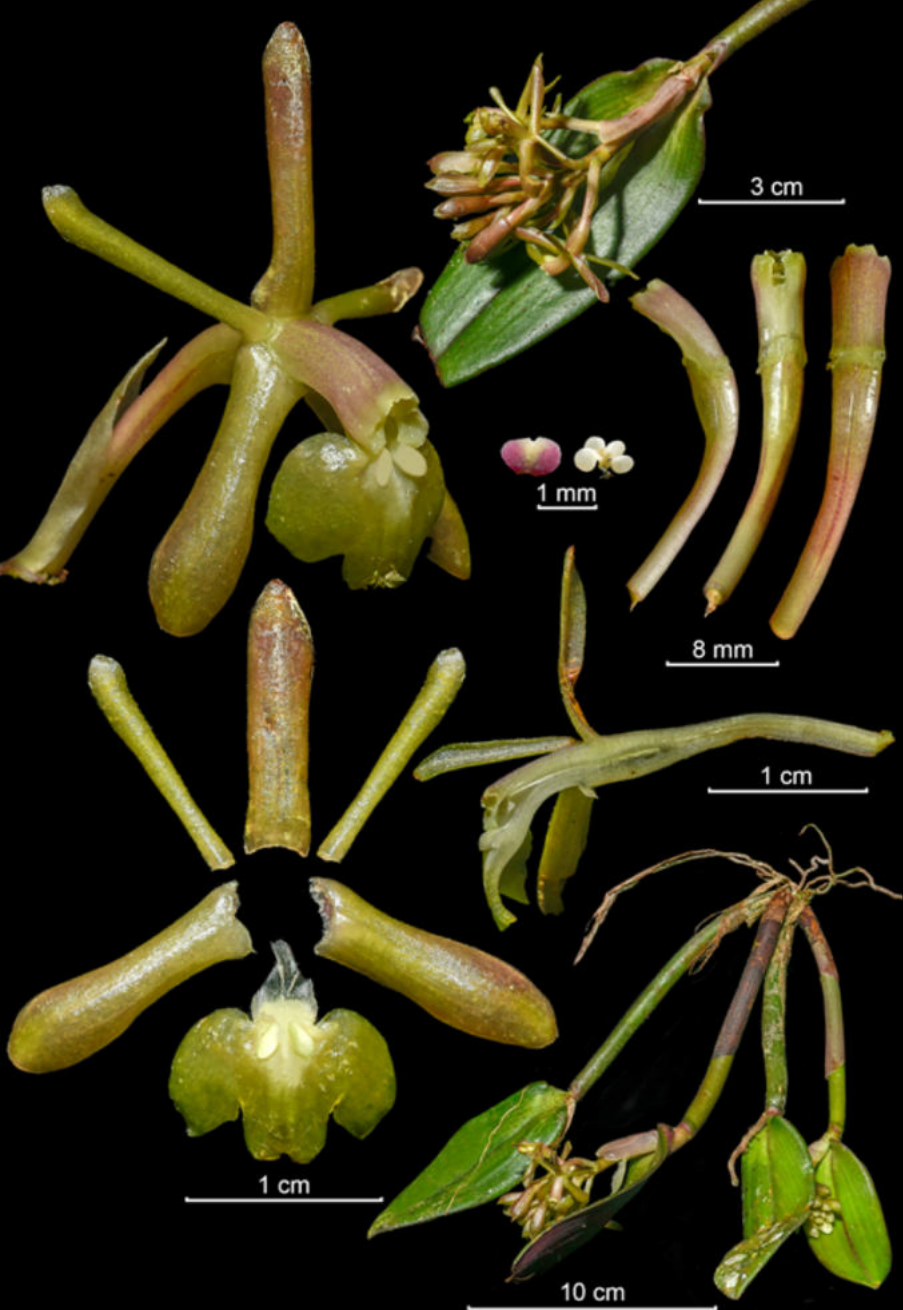
E. acrolithophilum

E. Hagsater, El Oro, Ecuador



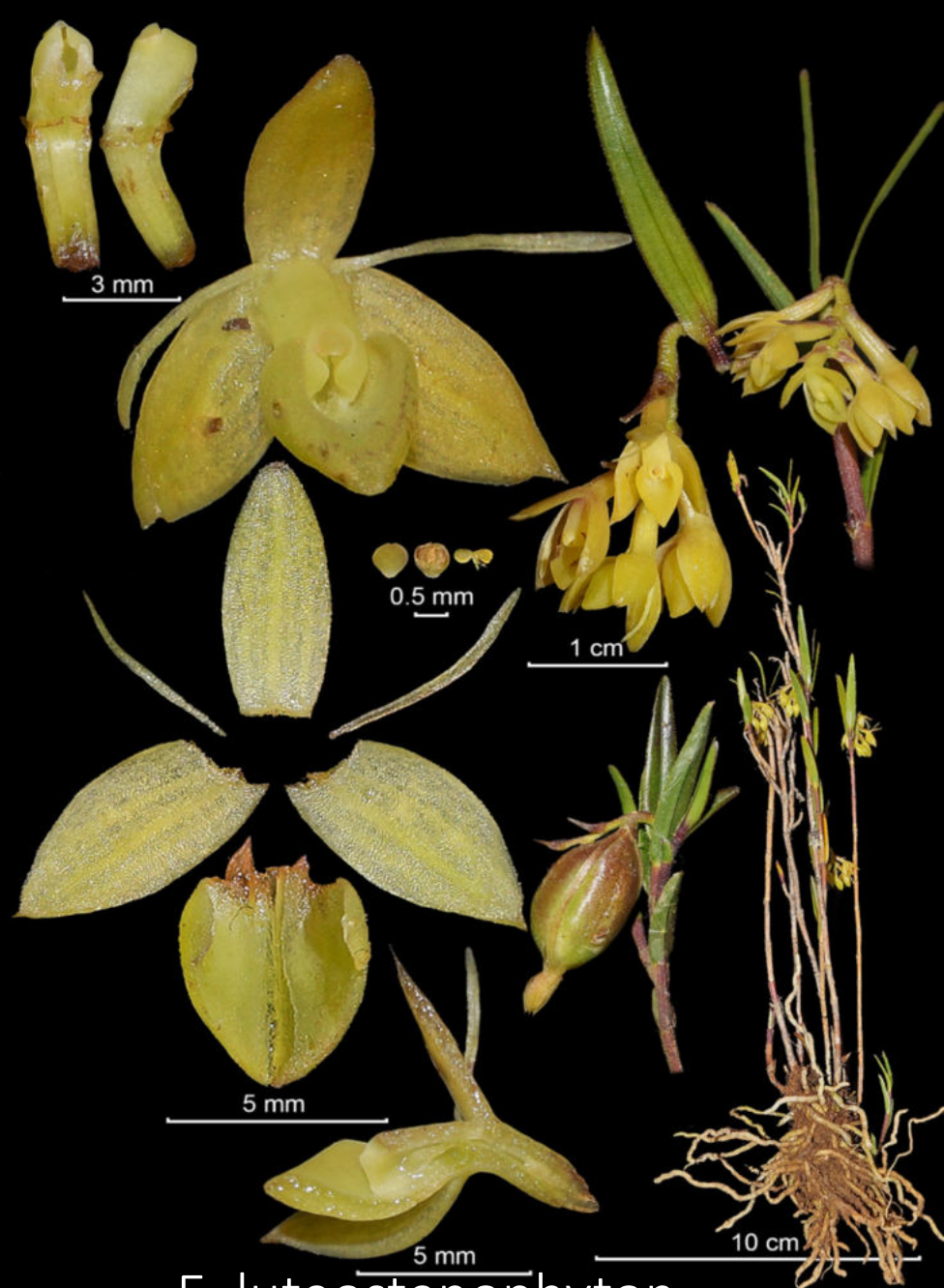
E. caranquii

M. Salas, Leimebamba, Perú



E. unifolium

J. Edquén, Venceremos, San Martín



E. luteostenophyton

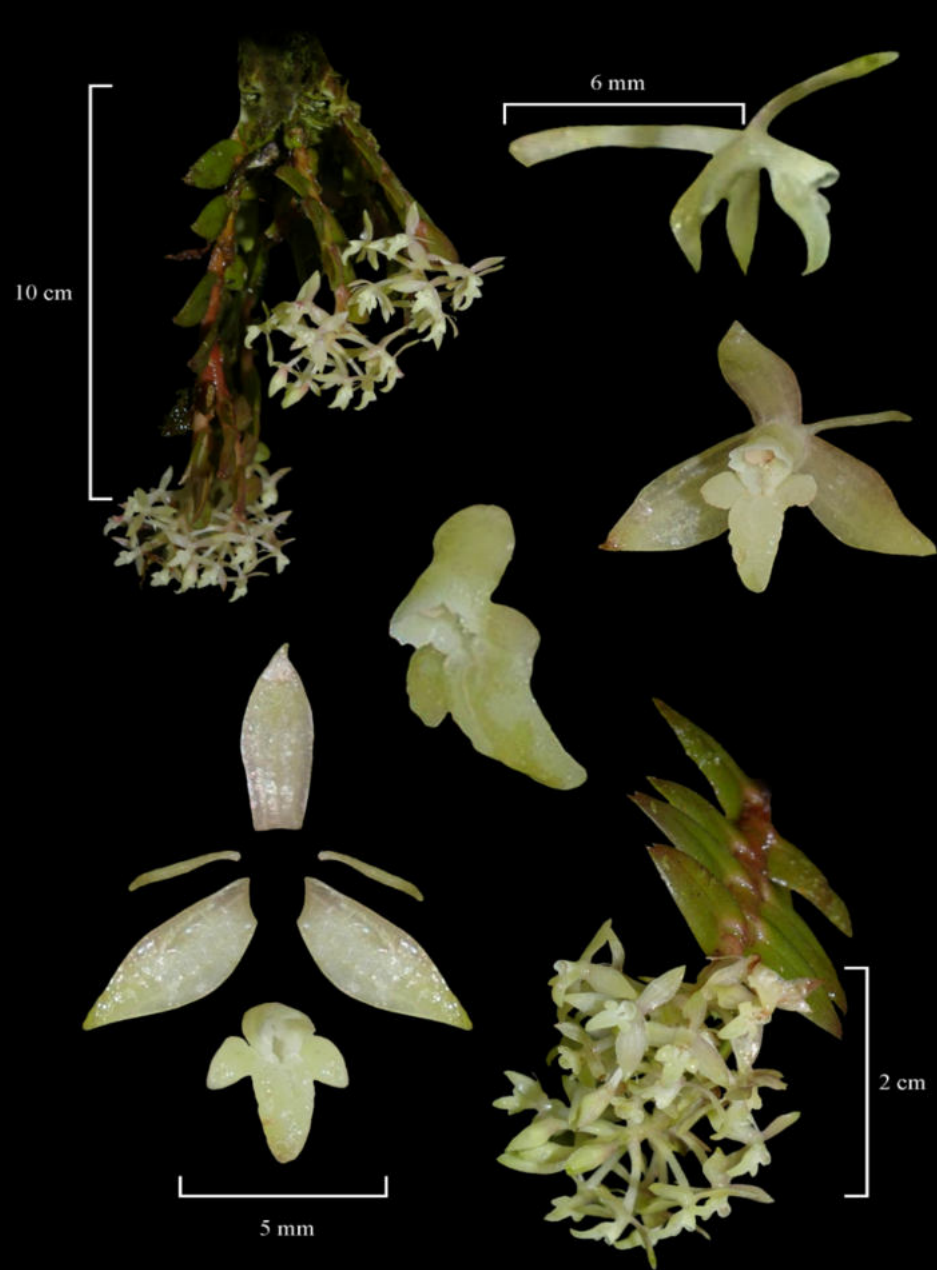
J. Edquén, Chachapoyas, Perú

R. Vásquez, Oxapampa

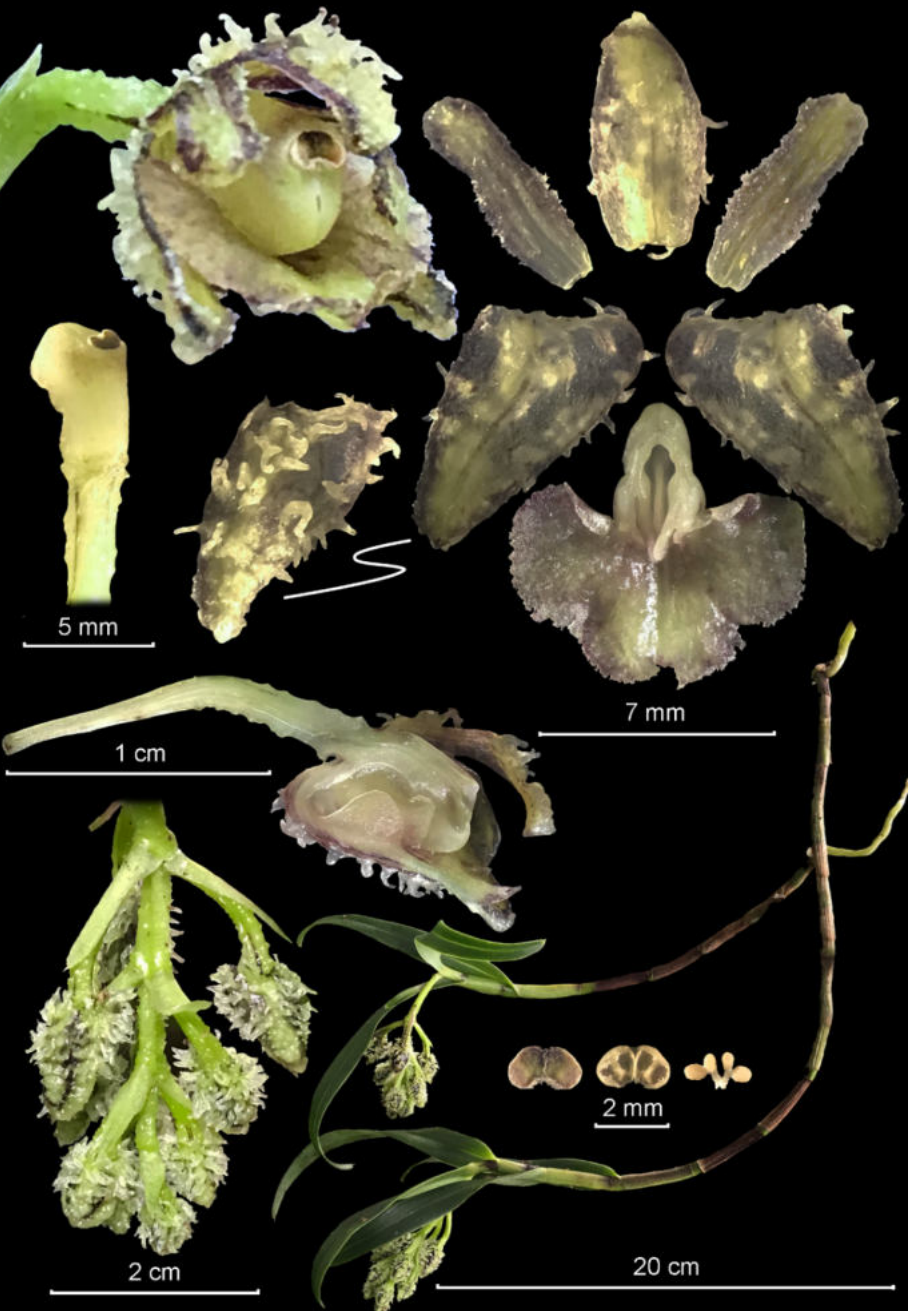
Hágsater, Ayabaca, Piura



E. vesicinanum
L. Valenzuela, Oxapampa



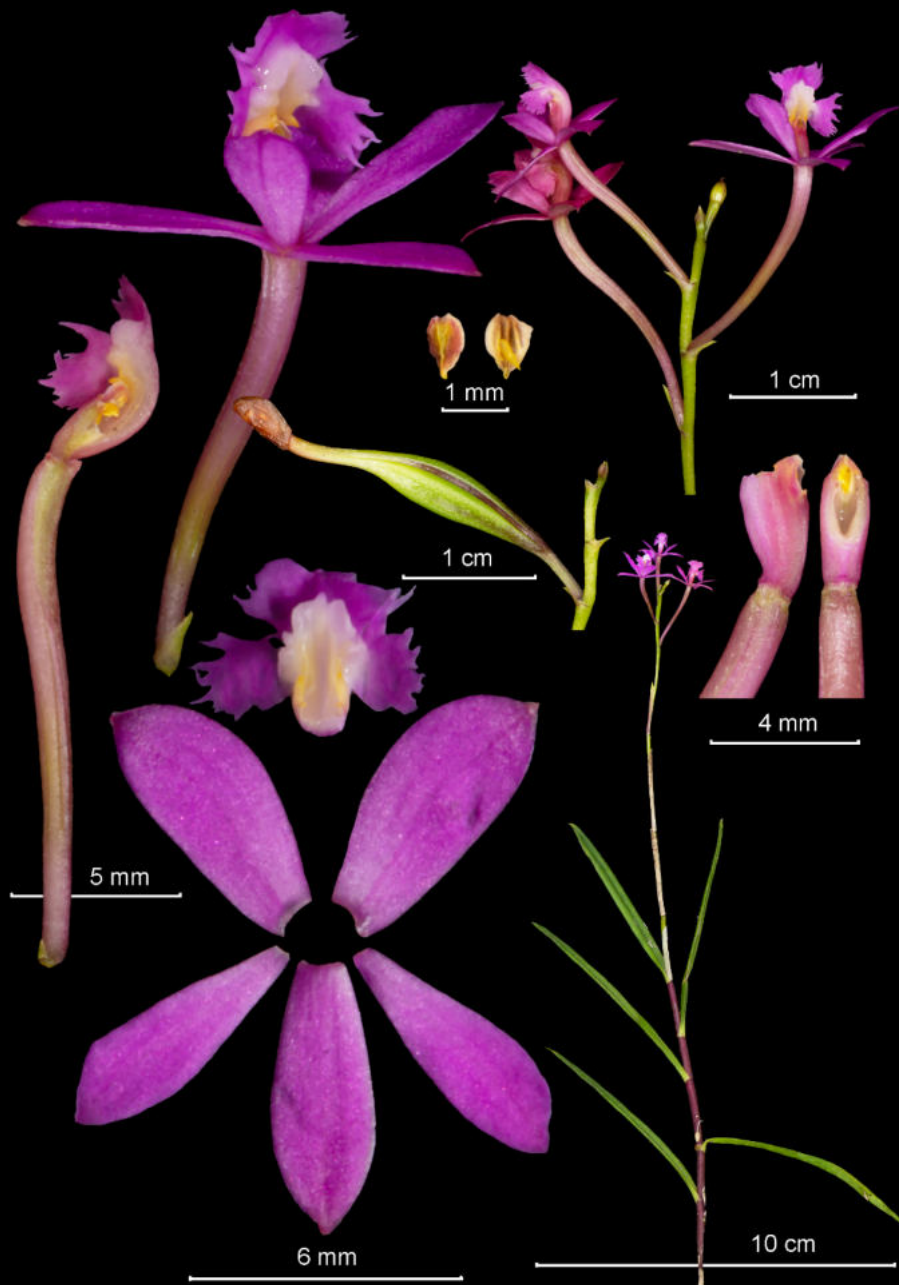
E. leuconanum
R. Vásquez, Oxapampa



Epidendrum camilae
B. Collantes, Machu Picchu

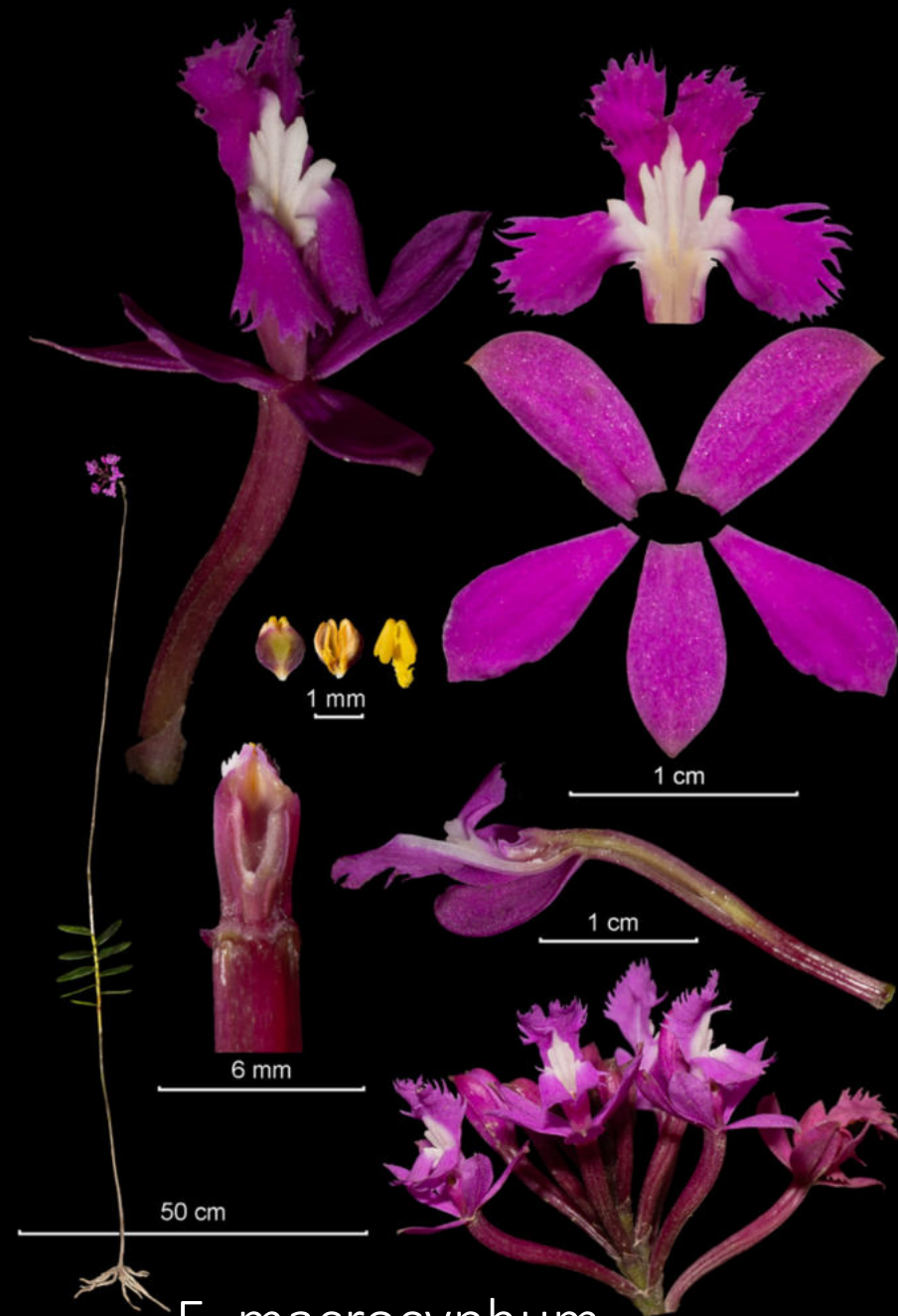


Epidendrum tundaycirrhatum
F. Tobar, Cordillera del Condor, Ecuador



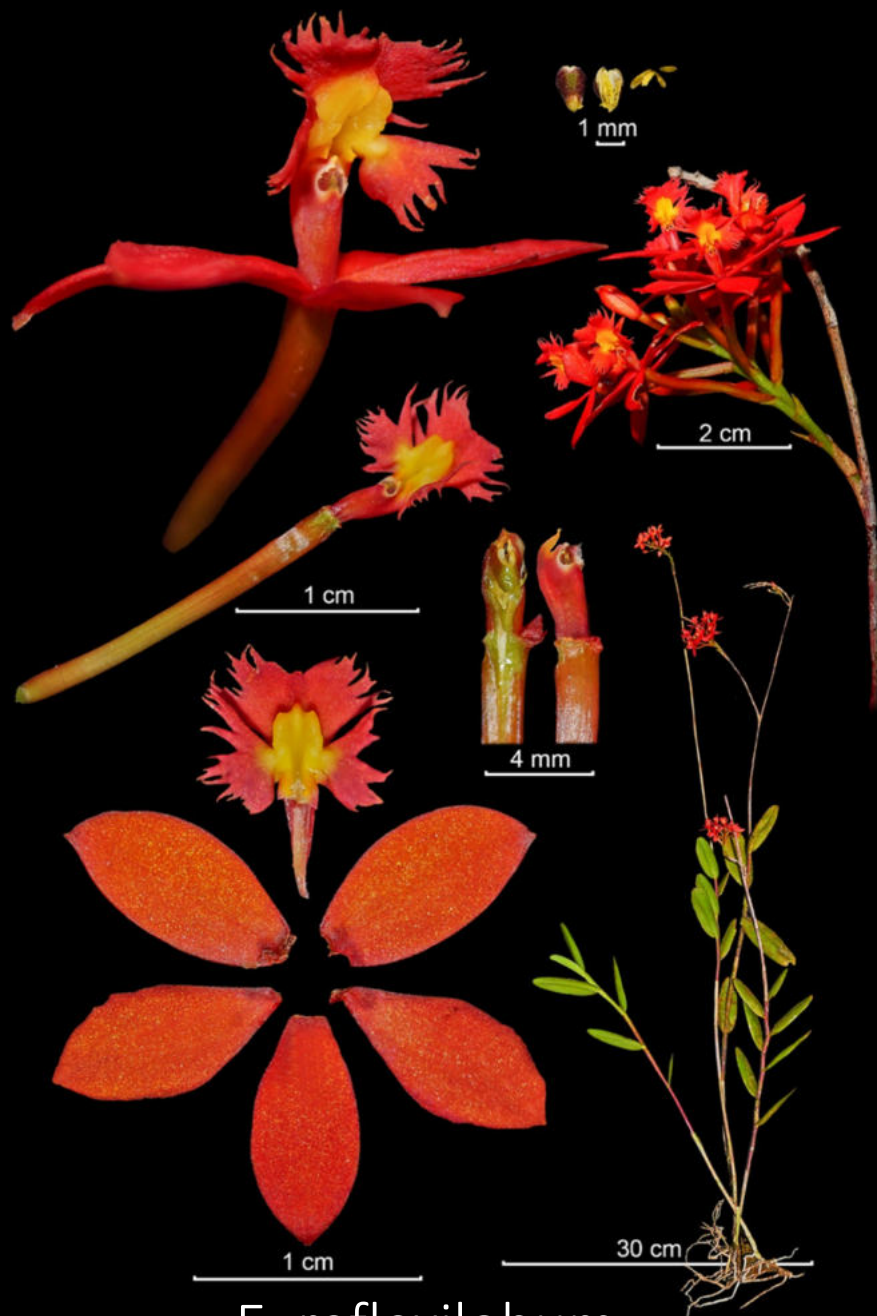
E. Azulensis

Hágsater, San Martin, Perú



E. macrocyphum

Hágsater, Huambos, Cajamarca



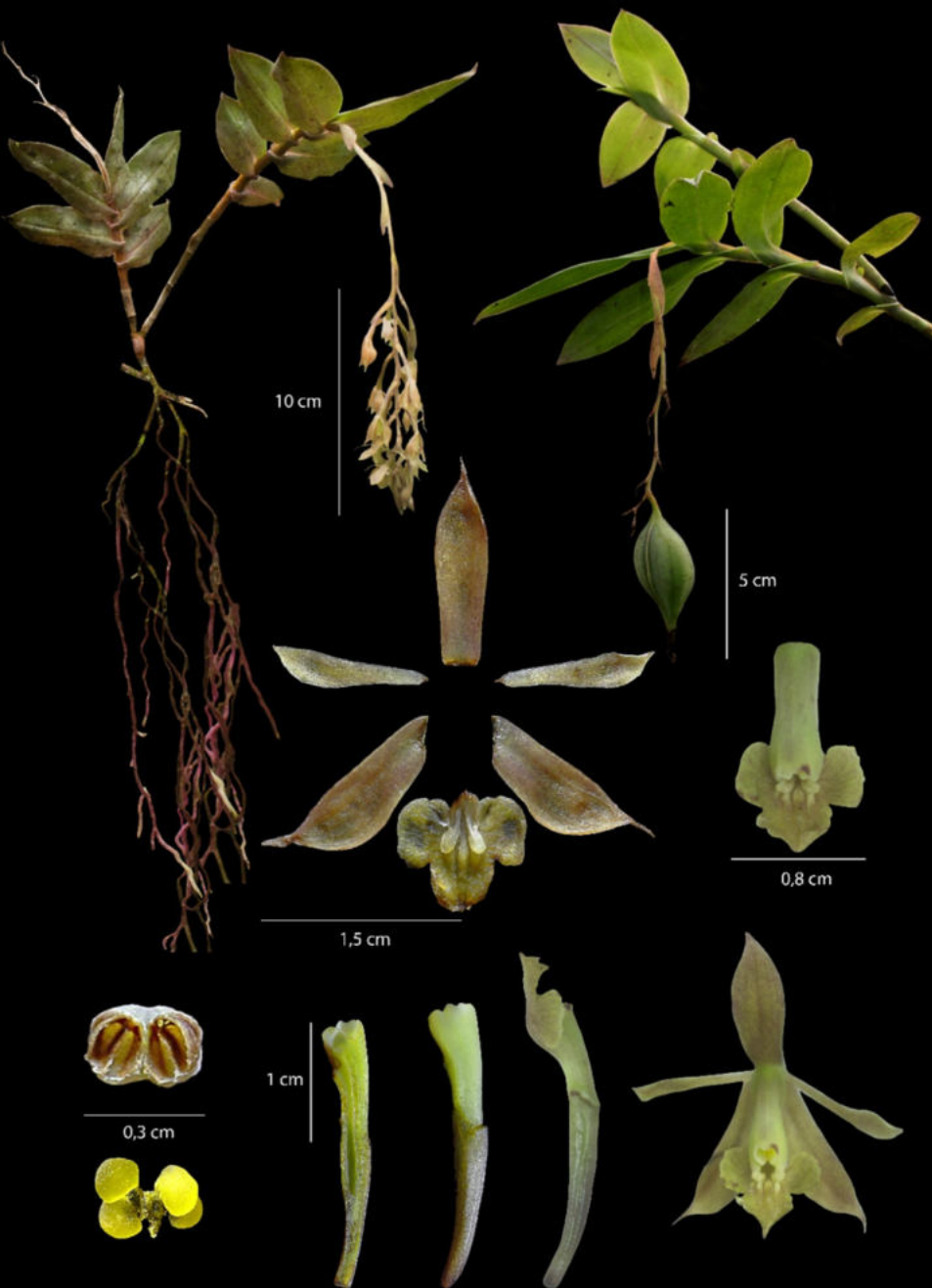
E. reflexilobum

J. Edquén, Venceremos, San Martín



E. microsecundum

Hágsater, Cuenca, Azuay y San Martín



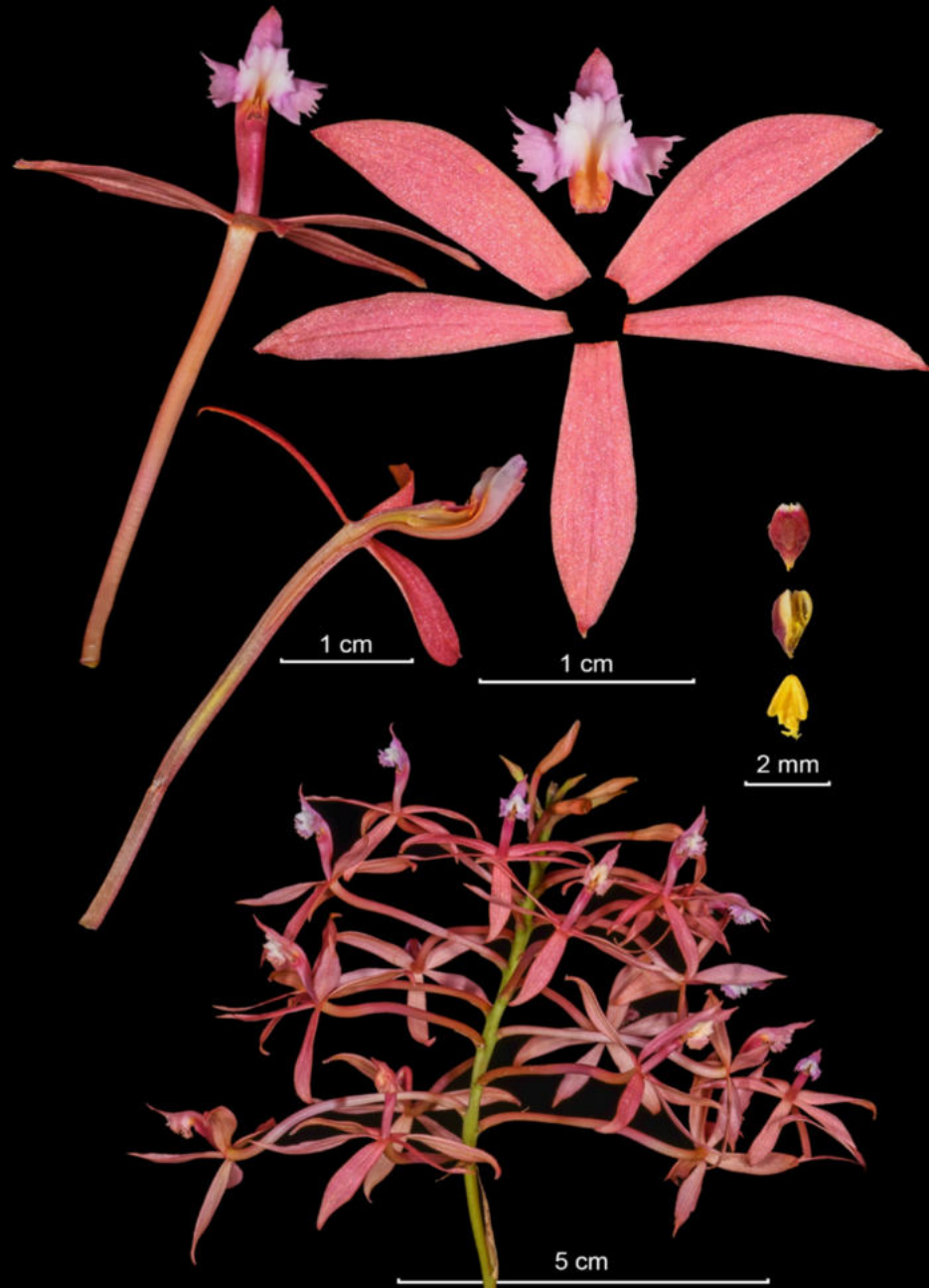
E. curimarcense

H. Quispe, Jauja, Junín



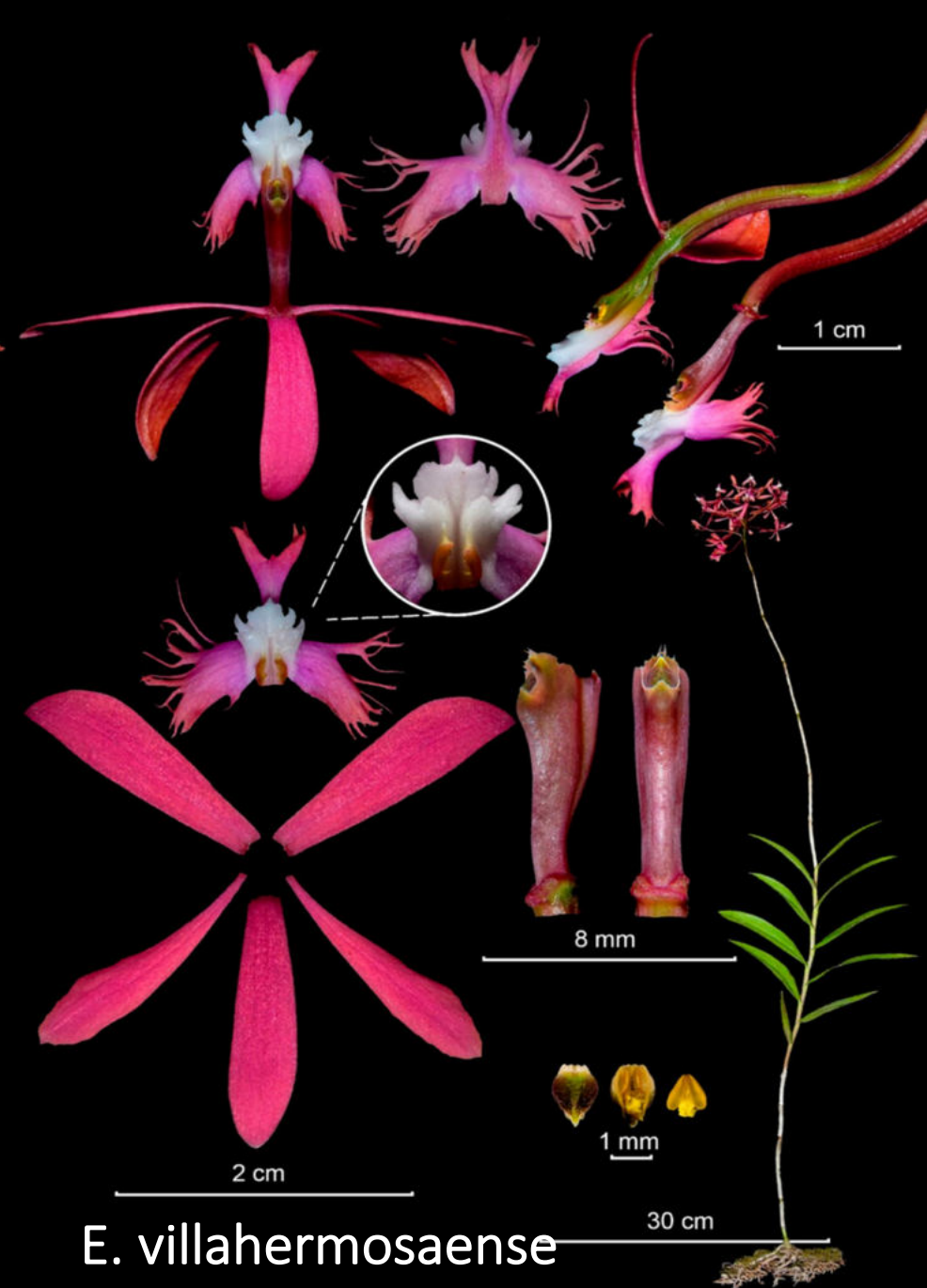
E. huaytianum

A. Huayta, Oxapampa



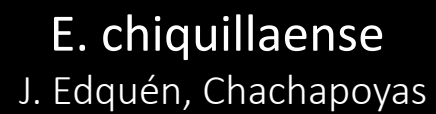
E. acutilobum

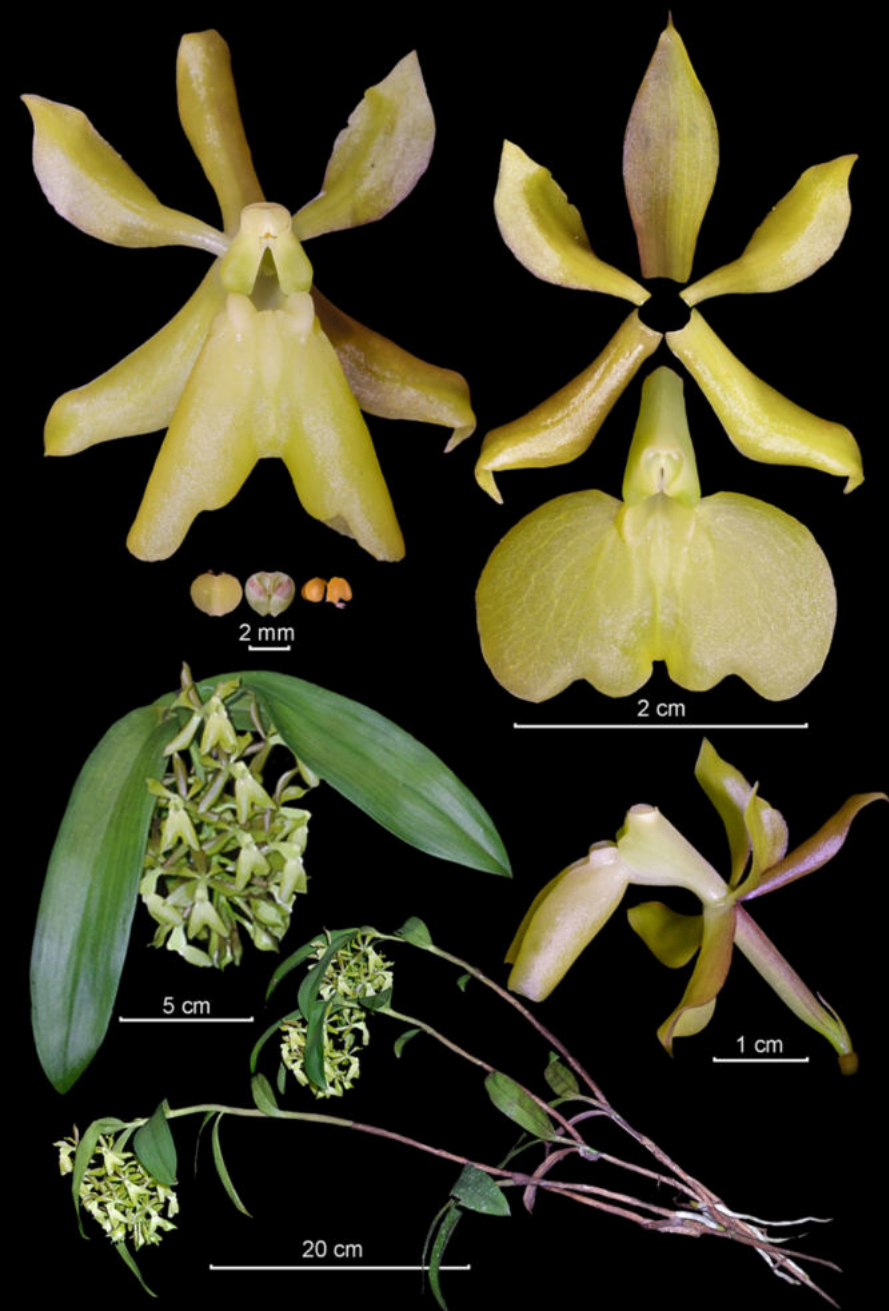
C. Uribe, Huila, Colombia



E. villahermosaense

M. Sierra-Ariza, Tolima, Colombia





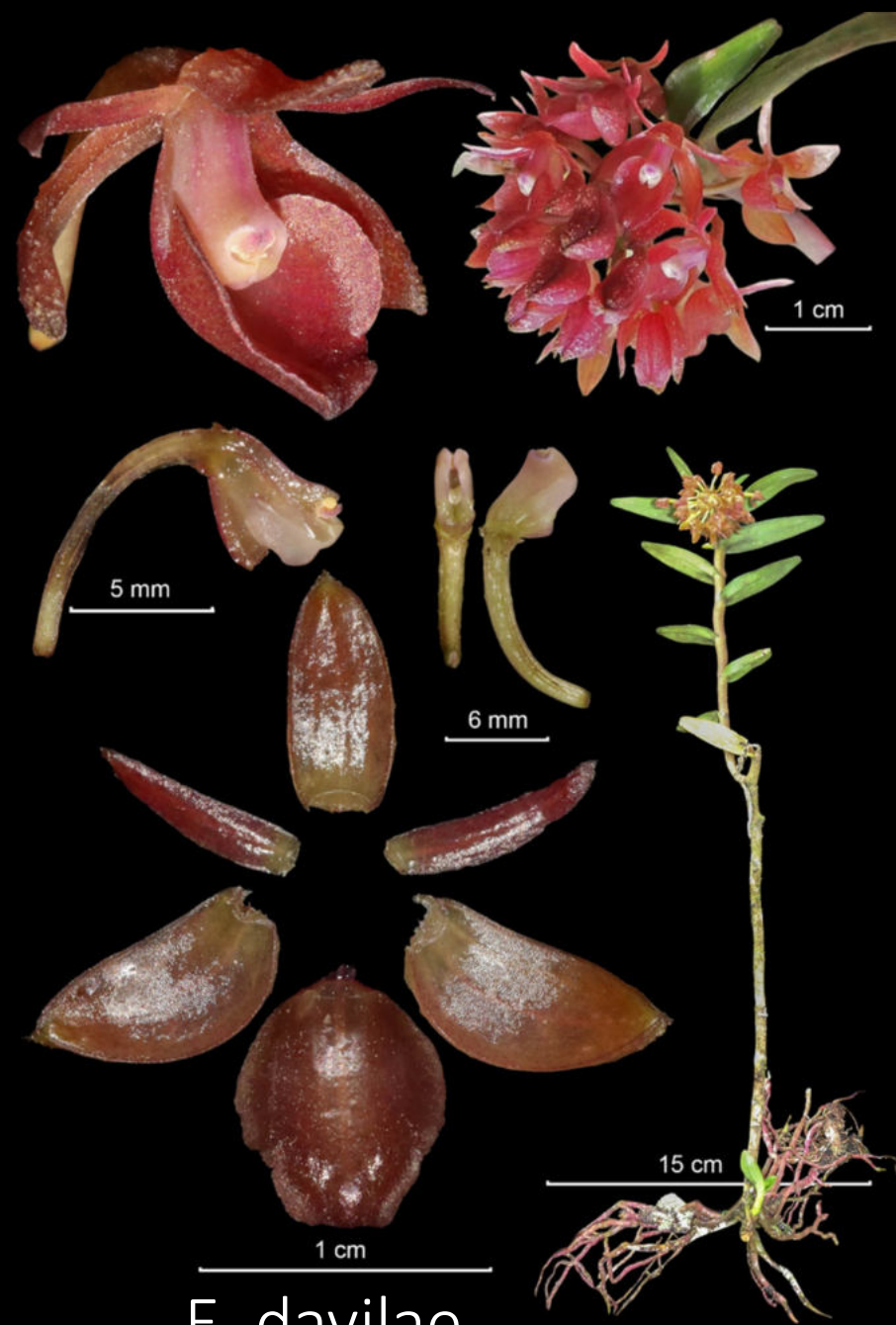
E. Ulcumanoae

G. Gerlach, Oxapampa



E. kockii x kymatochilum

A. Gutierrez, Yambrasbamba, Amazonas



E. davilae

R. Caverio, Chugur, Cajamarca



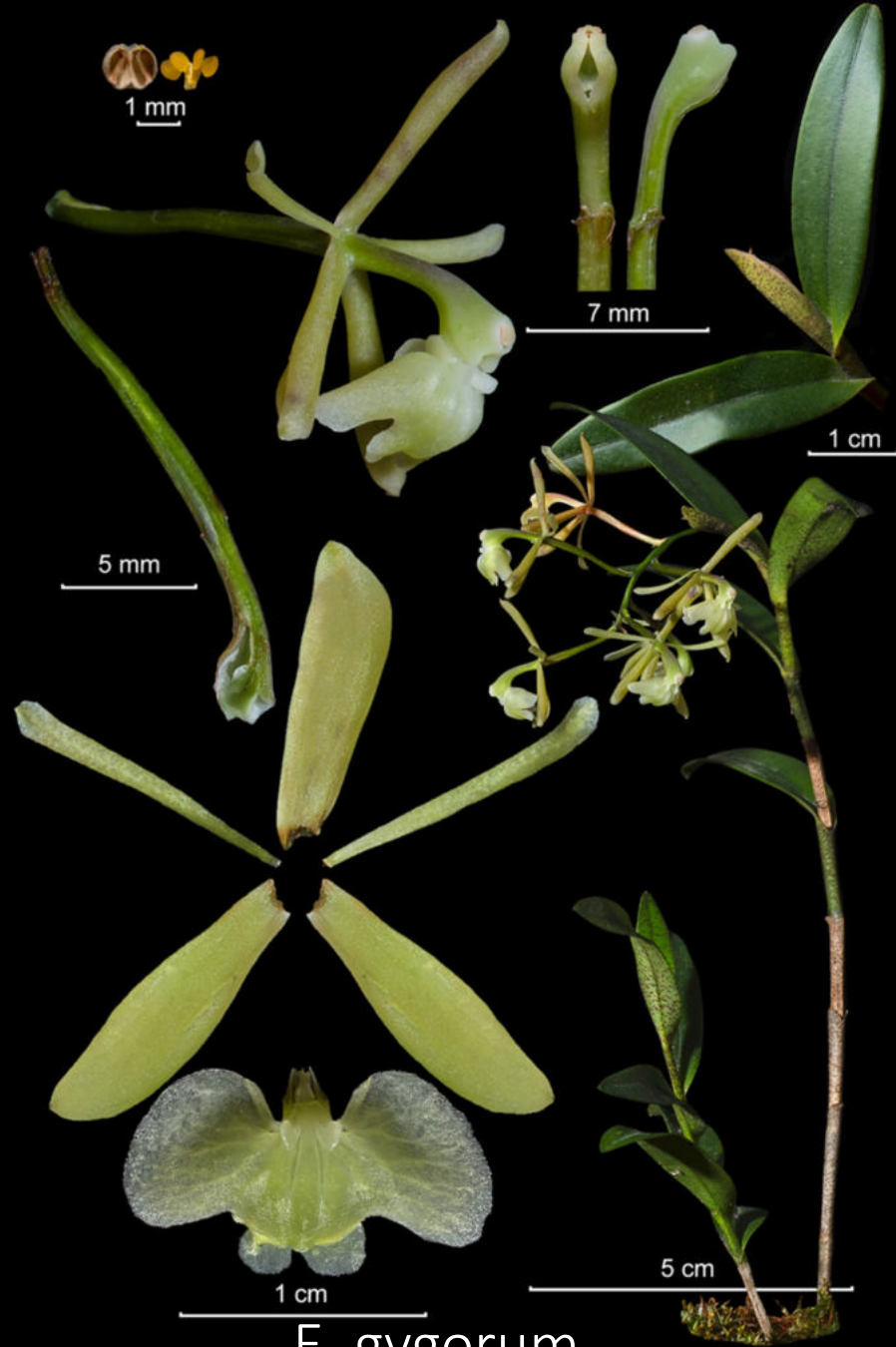
E. davilae

L. Dávila, Chugur, Cajamarca



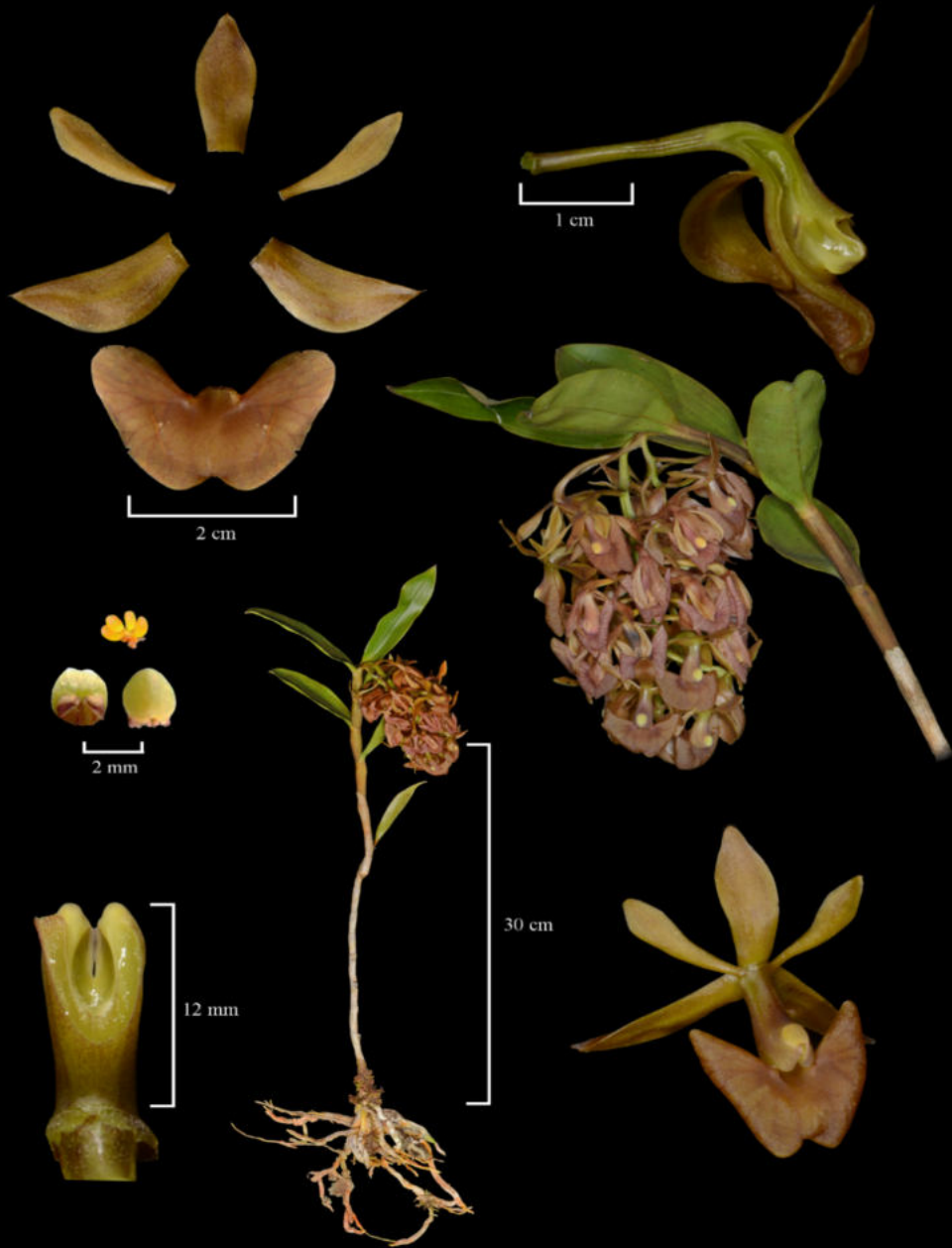
E. liguliferum

Yupanqui & Ocupa, Mito, Huánuco



E. gygorum

A. Goicochea, San Martín



E. coroshaense

E. Hágsater, Bongara, Amazonas



E. deorsus

E. Hágsater, Oxapampa



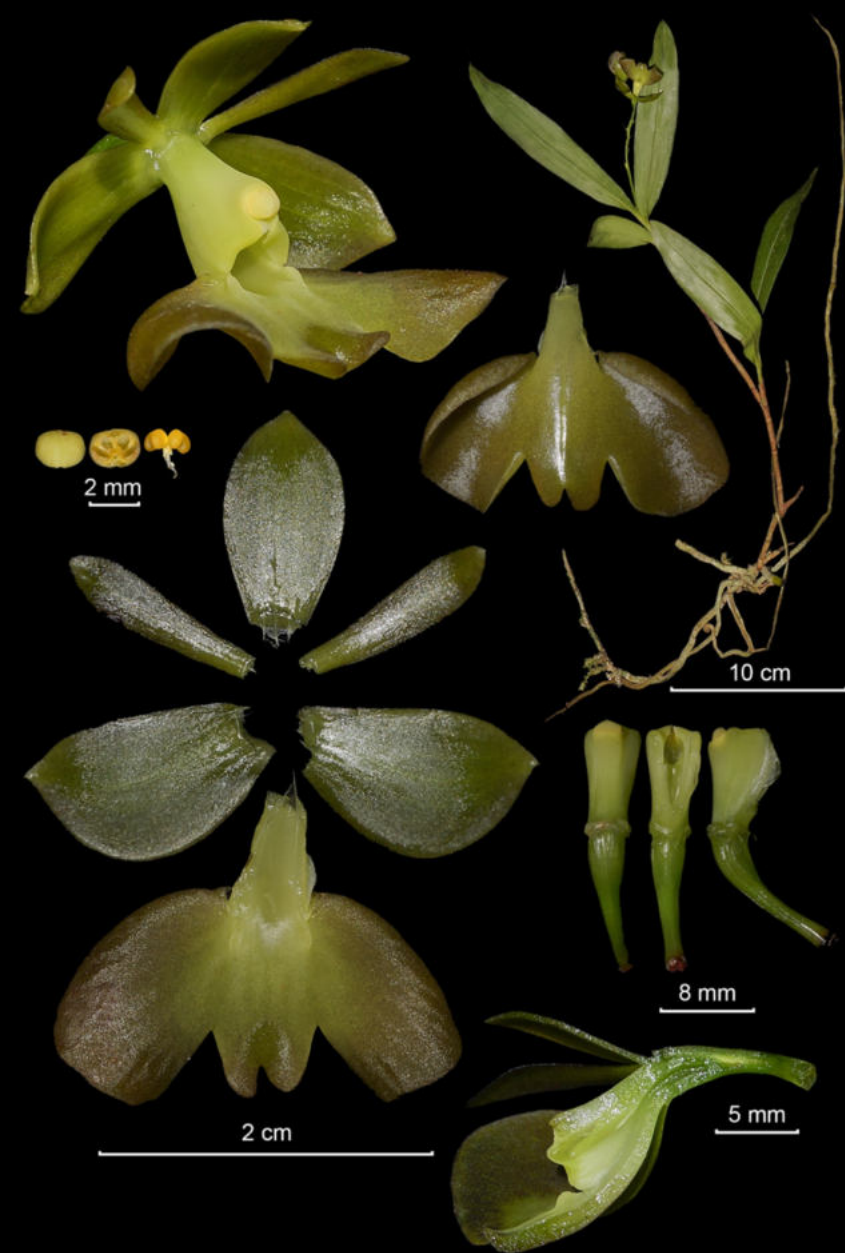
E. rimarachinii

E. rimarachin, San José de Lourdes



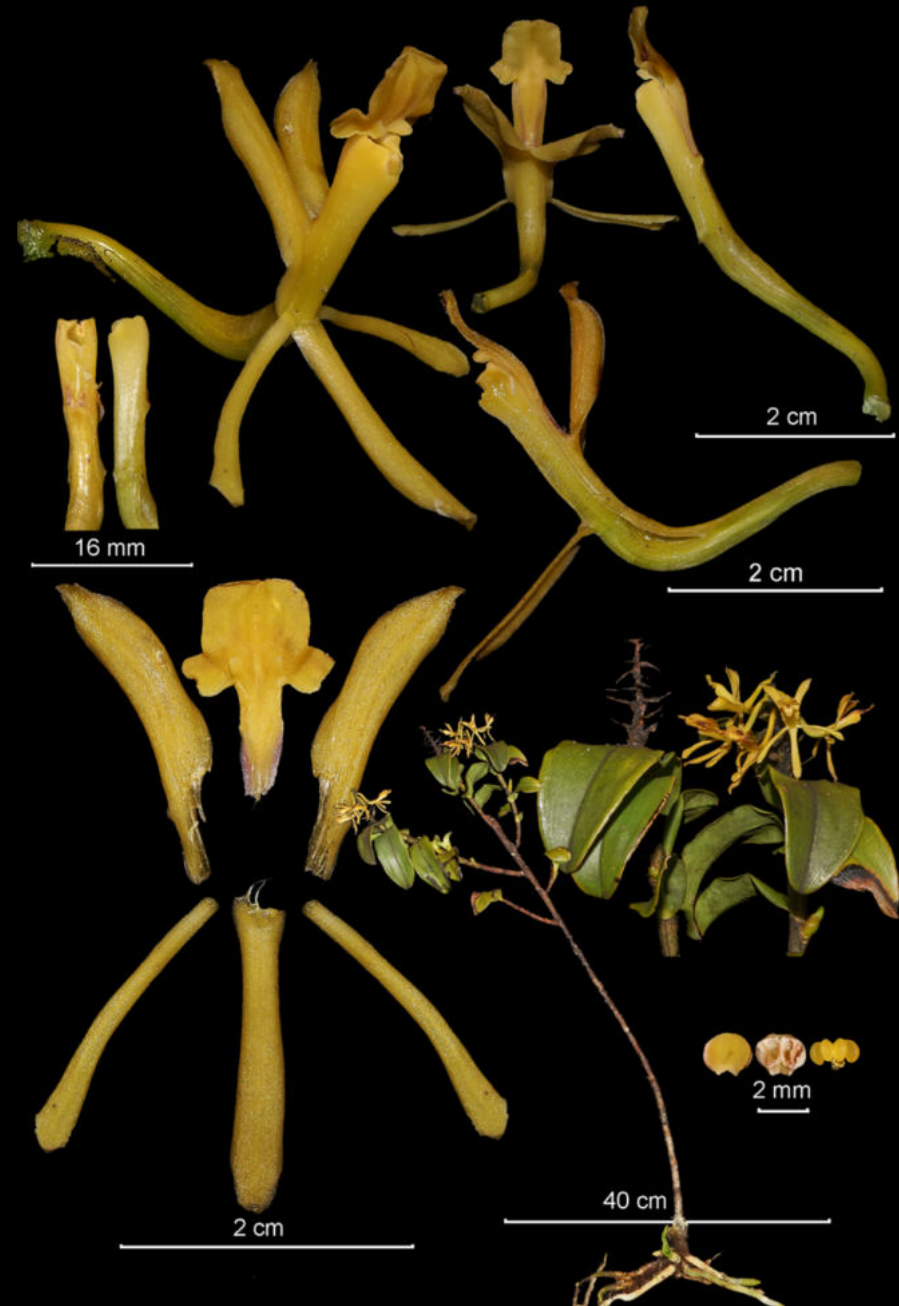
E. xelidorimarachinii

E. rimarachin, San José



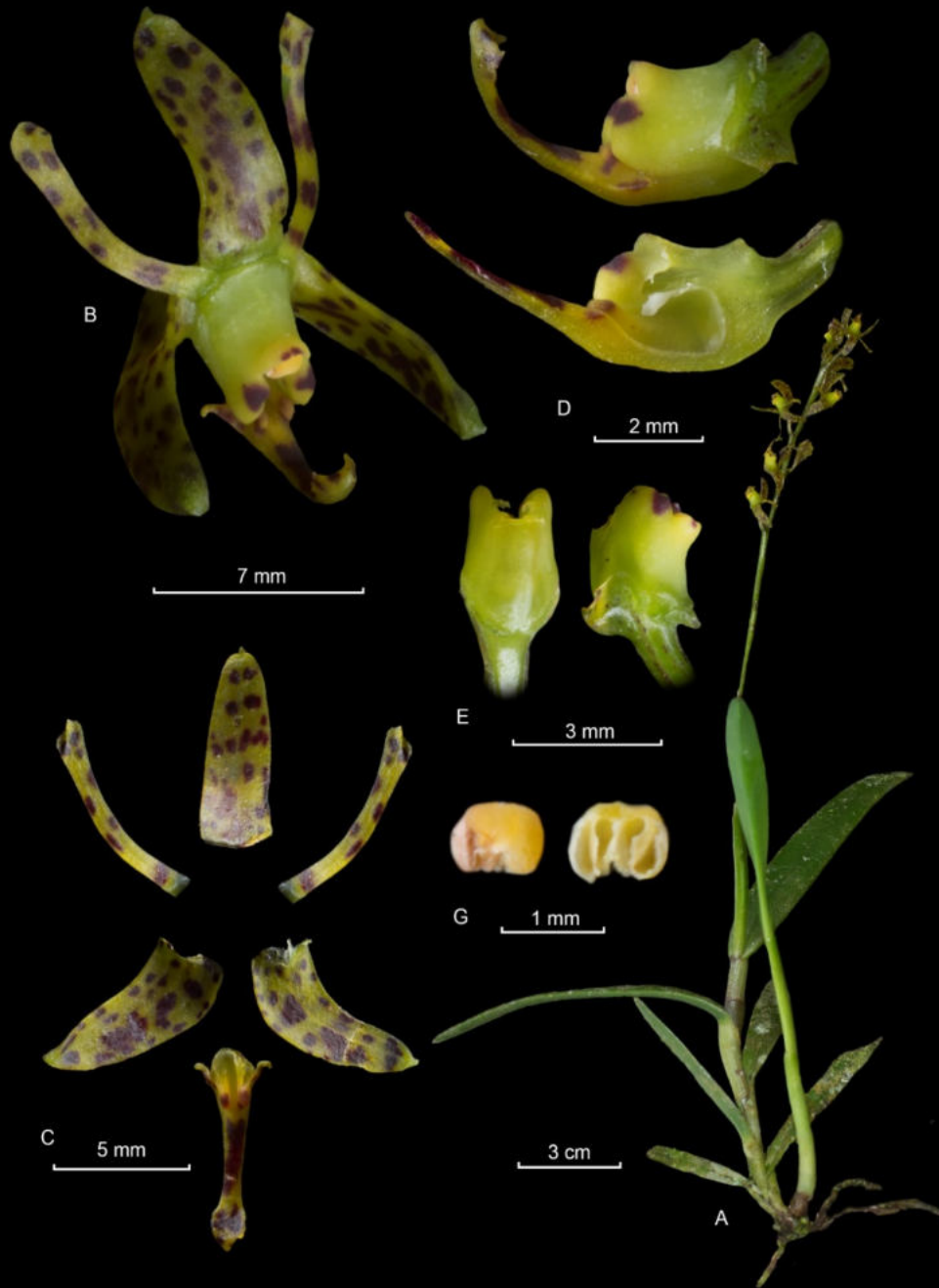
E. posticorevolutum

J. Edquén, Granada, Chachapoyas



E. quadratilobum

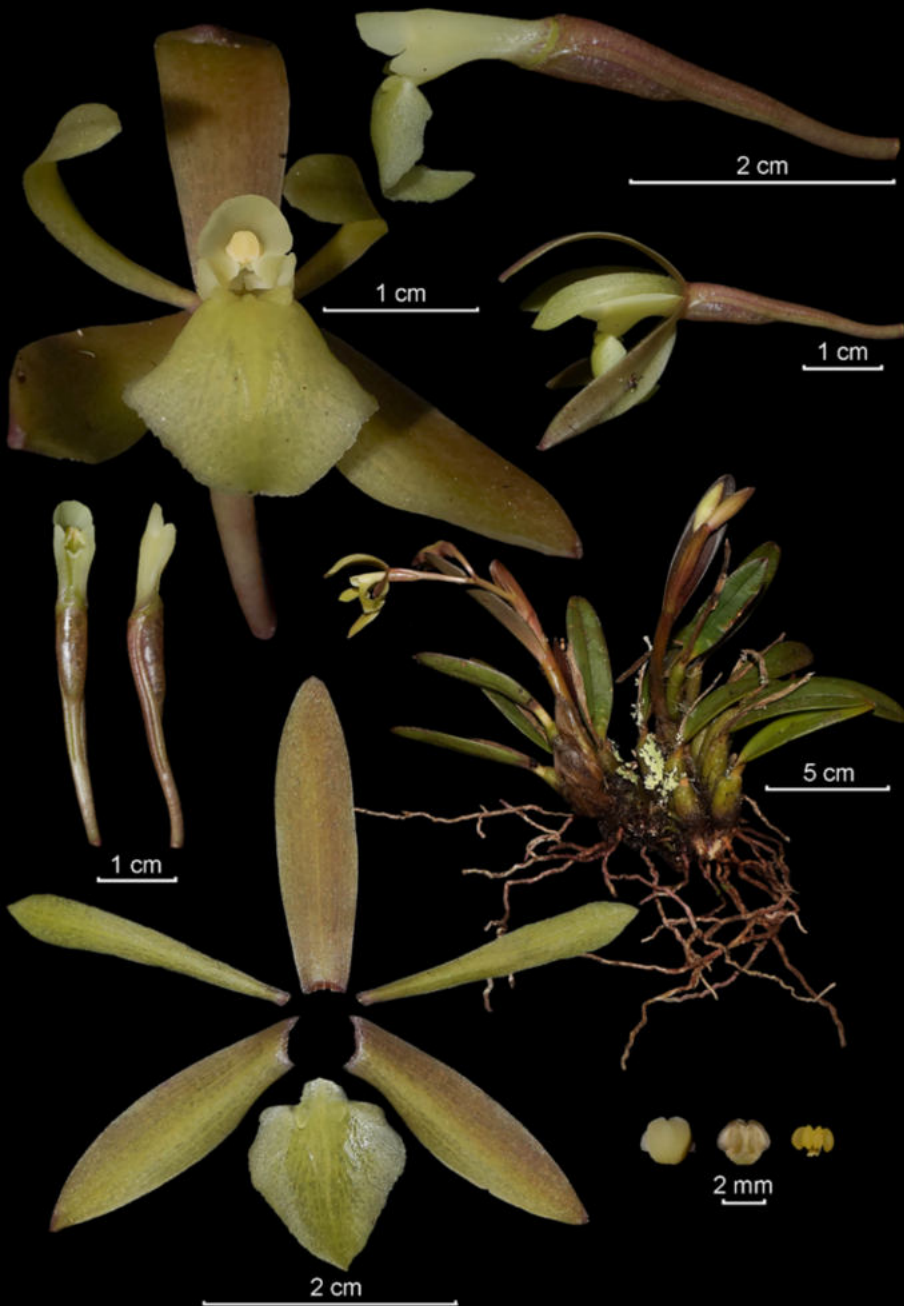
J. Edquén, Granada, Chachapoyas



E. leopardihamatum
E. Domínguez, Antioquia, Colombia



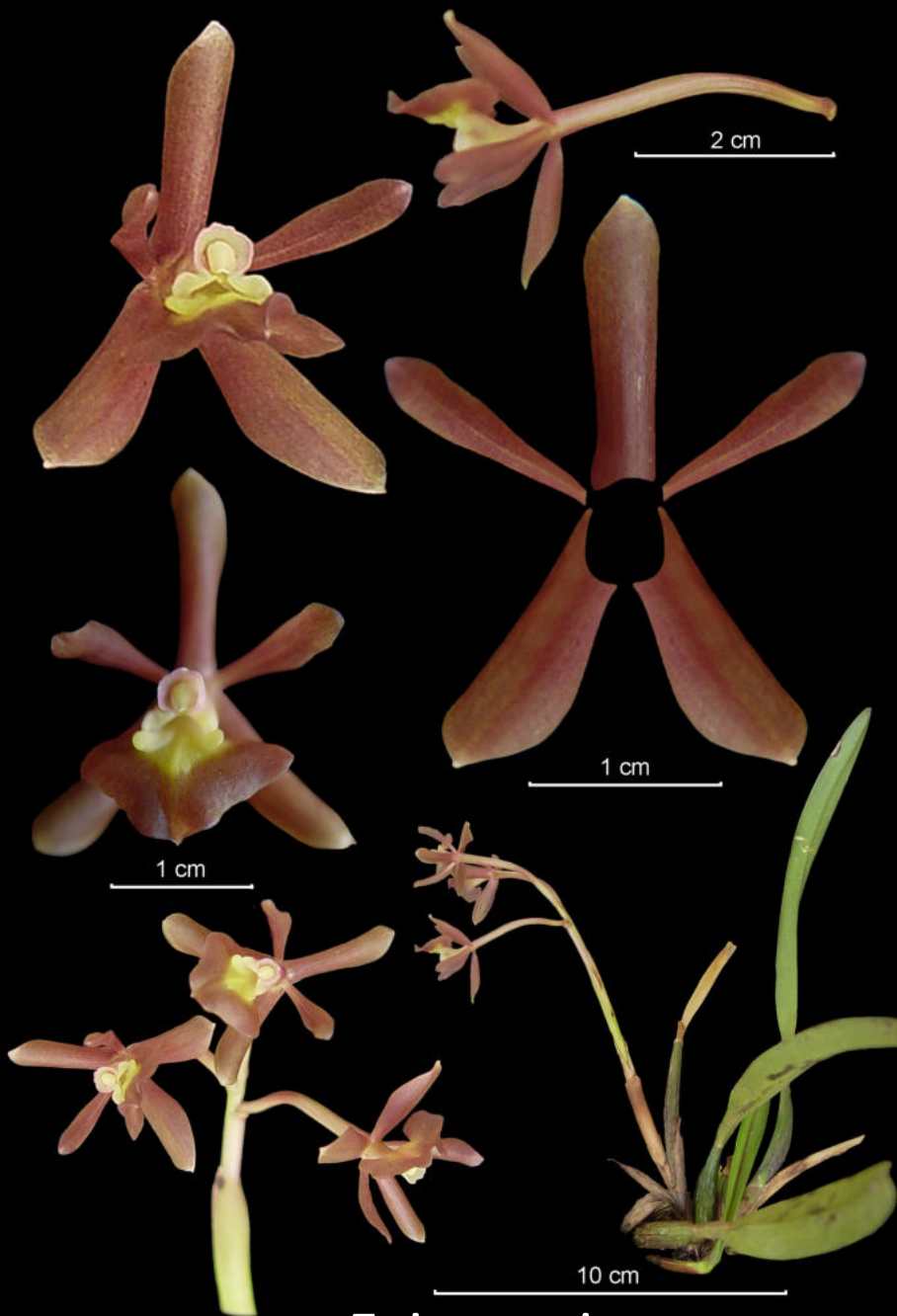
E. chugurense
C. Chilón, Chugur, Cajamarca



E. magnisaxicola
J. Equén, Chachapoyas



E. milpoense
R. Vásquez, Oxapampa



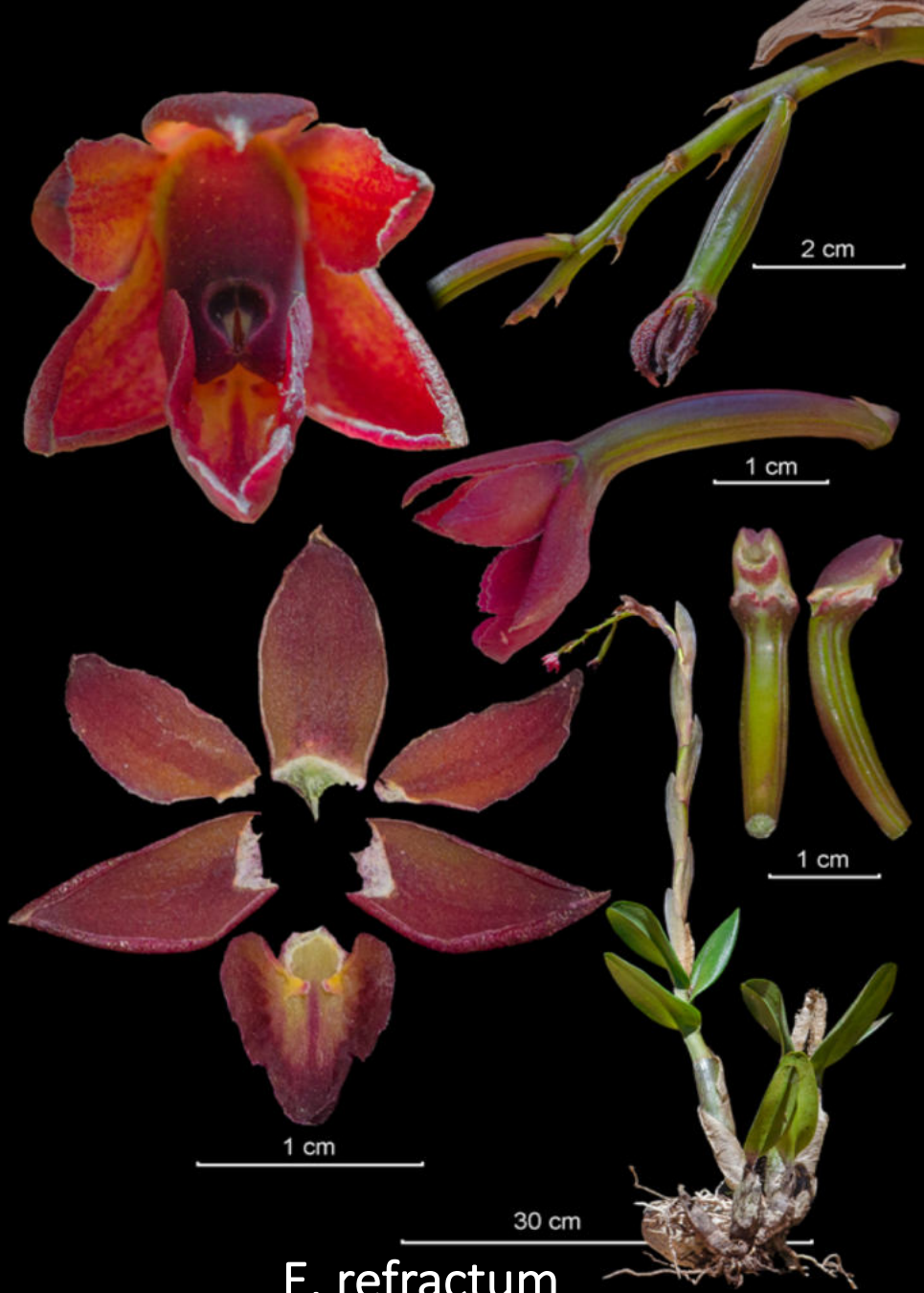
E. incognitum

E. Hágsater, Ecuagenera, Azuay



E. kosnipataense

I. Huamantupa, Kosñipata, Cusco



E. refractum

C. Jerez, Sierra Nevada, Mérida, Venezuela



E. palidovirens

R. Repasky, Kosñipata, Cusco



E. wayquechaense

R. Repasky, Kosñipata, Cusco



E. repaskyae

R. Repasky, Kosñipata, Cusco



E. Naviculare

E. Ortiz, Oxapampa, Pasco



E. pepeportillae

H. Medina, Cutucú, Ecuador



E. villenae

K. Villena & L.A. Velásquez, Yambrasbamba, Amazonas



E. quisayanum

G. Salazar, Imbabura, Ecuador