UNIVERSIDAD DE COSTA RICA

SISTEMA DE ESTUDIOS DE POSGRADO

REVISIÓN SISTEMÁTICA DEL GÉNERO *MYOXANTHUS* (ORCHIDACEAE: PLEUROTHALLIDINAE) EN COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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2020

DEDICATORIA

Esta obra está dedica a mis padres Luz y Fernando, quienes siempre me han brindado su apoyo incondicional y a quienes debo mi especial interés y aprecio por la naturaleza, y sobre todo por las orquídeas. También a la familia Orozco Murillo y abuela Celi, a quienes debo su invaluable y especial apoyo durante mis estudios universitarios.

AGRADECIMIENTOS

Agradezco especialmente a mi tutor Adam Karremans, por su gran apoyo y enseñanzas desde el inicio de esta investigación. A Federico Albertazzi su apoyo inicial como tutor temporal, y por su especial ayuda en el trabajo de laboratorio y durante todo el proceso de Maestría. A Mario Blanco por su gran conocimiento transmitido y también por esas buenas retroalimentaciones sobre morfología vegetal. A Franco Pupulin y Diego Bogarín por sus valiosas enseñanzas en todo lo relacionado al mundo de las orquídeas; al último también por sus consejos en la elaboración de ilustraciones botánicas digitales y su ayuda brindada en los análisis filogenéticos. A todo el personal docente de la Escuela de Biología, de los cuales aprendí enormemente en sus clases. También agradezco a los profesores Gustavo Vargas, Luis Jorge Poveda y Rafael Murillo de la Universidad Nacional quienes me transmitieron gran parte de su conocimiento y apoyo durante el proceso de ingreso a la Maestría. Agradezco a Barbara Gravendeel, Richa Kusumawati, Dewi Pramanik y Bertie Joan van Hueven de la Universidad de Leiden, Países Bajos, por permitir el uso, guiar y asistir en la obtención de las imágenes en el microscopio electrónico de barrido.

A Hannia Ramírez del Sistema de Estudios de Posgrado en Biología; en el Jardín Botánico Lankester (JBL) a Karen Barquero, Lizbeth Oses y Maricruz Bonilla del Departamento Administrativo; a Jorge Brenes, Giovanni Meza y Gerson Villalobos del Departamento de Horticultura; a Melissa Díaz y Grettel Salguero del Departamento de Investigación; y a mis compañeros José Esteban Jiménez, Marco Cedeño e Isler Chinchilla por su apoyo durante el proceso de la Maestría, actividades de campo, y aporte de material fotográfico de múltiples herbarios de diferentes países de América. A Jaime Aguilar† del JBL por sus inducciones en la documentación de plantas. Agradezco a los directores y personal de los herbarios USJ, CR, AMES, SEL, AMO, MO, UVAL, KEW, y W por brindar acceso a sus colecciones, aportar y permitir la reproducción de imágenes de especímenes utilizados en esta investigación.

Agradezco también a todos mis amigos y demás personas que de una u otra forma me brindaron su apoyo constante durante esta etapa universitaria. Agradezco especialmente a Vero, una de las personas más importantes para mí y que siempre estuvo en los buenos y malos momentos y nunca dejó darme ánimo para perseguir cada una de mis metas.

"Esta tesis fue aceptada por la Comisión del Programa de Estudios de Posgrado en Biología de la Universidad de Costa Rica, como requisito parcial para optar al grado y título de Maestría Académica en Biología".

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RESUMEN

Desde el siglo XIX se han propuesto sistemas de clasificación para la familia Orchidaceae, una de las más numerosas con alrededor de 28 000 especies, diversidad que la botánica sistemática se ha encargado de organizar. Los primeros sistemas de clasificación para este grupo se basaron principalmente en la morfología discreta; sin embargo, a través de los años, la anatomía, la biología molecular y la química se han convertido en buenas herramientas para esclarecer sus relaciones evolutivas. Dentro de esta familia, la subtribu Pleurothallidinae, distribuida en el neotrópico, con poco más de 5 000 especies, es una de las más diversas y complejas debido a su gran número de especies, muchas de las cuales han diversificado de manera rápida y reciente. Desde sus primeras clasificaciones, muchos han sido los trabajos taxonómicos y sistemáticos realizados en cada uno de sus grupos, y progresivamente los estudios moleculares se han convertido en una de las principales herramientas, los cuales han utilizado de una a varias secuencias de ADN. Sin embargo, debido a la gran diversidad y alto grado de homoplastias las relaciones filogenéticas de muchos grupos aún siguen sin esclarecerse. *Myoxanthus* es uno de los 44 géneros de esta subtribu, comprendiendo 50 especies distribuidas desde el sur de México hasta Bolivia y sureste de Brasil. Su primera especie fue descrita en 1835, pero no fue hasta 1982 que empezó a ser ampliamente aceptado después de estar incluido en *Pleurothallis*. En Costa Rica, tradicionalmente se han reportado siete especies, las cuales se distribuyen aproximadamente desde 300 m hasta 2100 m de altura, tanto en la vertiente del Pacifico como en la del Caribe. Sin embargo, no se ha realizado ningún estudio sistemático de este grupo en el país, ni tampoco uno amplio a nivel genérico que incluya evidencia molecular. Este trabajo presenta una serie de artículos que componen una revisión sistemática de las especies del género *Myoxanthus* en Costa Rica, la cual incluye, la historia del género en el país, una clave dicotómica y descripción de cada especie, incluyendo ilustraciones botánicas, láminas Lankester, láminas de variación de estructuras vegetativas y floreales, mapas de distribución, y discusión taxonómica. Además, se presenta una filogenia molecular donde se incluyen todas las especies costarricenses y se evalúa por primera vez las relaciones filogenéticas dentro del género.

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PREFACIO

La enorme variedad de plantas que existen hace necesaria una organización que le permita al ser humano diferenciarlas; a partir de esto, nace la botánica sistemática, ciencia que se encarga de estudiar la diversidad biológica y su historia evolutiva (Judd *et al*. 2016). Dentro de esa enorme diversidad, la familia Orchidaceae es quizá el grupo de plantas con flores más numeroso, con 736 géneros y aprox. 28 000 especies (Chase *et al.* 2015) que se distribuyen a nivel mundial, excepto en desiertos verdaderos y zonas polares, siendo más diversa en las zonas tropicales y subtropicales (Dressler 1981, Dressler 1993).

Para Orchidaceae se han propuesto sistemas de clasificación desde el siglo XIX, como los aportes de Lindley. Estos sistemas se basaron principalmente en las características morfológicas, que siguieron siendo utilizadas junto con caracteres anatómicos a finales del siglo XX (Dressler 1993, Freudenstein & Rasmussen 1999, Pridgeon *et al.* 1999). En la década de 1990 las técnicas moleculares para inferir relaciones a nivel de familia y subfamilia empezaron a ser utilizados en las orquídeas (Pridgeon *et al.* 1999).

En Costa Rica, los trabajos más recientes para catalogar la diversidad de orquídeas fueron realizados por Mora-Retana & García (1992), Pupulin (2002), Dressler (2003) y Ossenbach *et al.* (2007). En el tratamiento más completo de la familia por Dressler (2003), se reportan 174 géneros y 1328 especies; sin embargo, desde entonces muchas nuevas especies y registros se han documentado para Costa Rica (Bogarín *et al.* 2008, Bogarín 2011, Karremans *et al.* 2012, Fernández *et al*. 2014). Hoy en día al país se le atribuyen alrededor de 1600 especies, superado únicamente por Brasil, Colombia, Ecuador y Perú, pero en relación a su área (51 000 km^2), Costa Rica es quizá el país con mayor número de especies (Karremans & Bogarín 2013).

La subtribu Pleurothallidinae (Orchidaceae: Epidendreae, Epidendroideae) cuenta con más de 5,000 especies y 44 géneros aceptados (Karremans 2016), siendo la subtribu más diversa, representando del 15–20 % de las especies dentro de la familia. Sus especies se distribuyen desde el sur de Florida y México hasta Argentina, con una mayor riqueza de especies en los bosques nubosos de Costa Rica, Panamá, Colombia, Ecuador, Venezuela, Perú y Brasil (Luer 1986). En el sentido tradicional, Pleurothallidinae se distingue por presentar plantas epífitas, litófitas o parcialmente terrestres; con crecimiento simpodial; hojas conduplicadas, desde coriáceas a membranáceas; raíces con velamen; unidades simpodiales con una sola hoja apical; inflorescencias terminales, raramente laterales, flores resupinadas o no, de dos a ocho polinios y con un ovario articulado con el pedicelo (Luer 1986). Esta subtribu presenta un gran número de especies que hace difícil su clasificación. Tiempo atrás, gran parte de las especies descritas se clasificaban dentro del género tipo, *Pleurothallis* R.Br.; incluso Lindley (1859) decidió no dividir este inclusivo género por la gran similitud de características dentro de este extenso grupo. En la misma línea, Luer (1986) mencionó la practicidad de las clasificaciones con subgéneros y secciones en *Pleurothallis*. Algunos intentos de clasificación dentro de la subtribu se basaron en el número de polinios y otras características florales (Garay 1956). Posteriormente hubo intentos por inferir relaciones de parentesco en la subtribu mediante estudios morfológicos (Luer 1986) y anatómicos (Pridgeon 1982). A pesar de ello, debido a la gran diversidad del grupo y las escasas evidencias morfológicas y anatómicas de posibles homologías dificultaron una clasificación filogenética clara (Pridgeon *et al.* 2001). Esto causó que, por mucho tiempo, *Pleurothallis* y Pleurothallidinae fueran tratados prácticamente como sinónimos, excluyendo del primero únicamente algunos géneros muy bien diferenciados morfológicamente (Karremans 2015).

A partir de 1986 en sus monografías “Icones Pleurothallidinarum”, C.A. Luer, el especialista de la subtribu, ha publicado los estudios más amplios y detallados de toda esta subtribu, estableciendo las bases para un adecuado estudio de un grupo tan diverso, y dejando claro que la mejor forma de abordarlo es la documentación detallada de sus especies. Después de esto, muchos han sido los trabajos sistemáticos y taxonómicos que han tratado varios grupos de Pleurothallidinae, y decenas de especies y géneros han sido publicados. Estos estudios han propuesto cambios en su clasificación, que junto con el creciente número de especies aumenta la necesidad de tener una visión más clara de las relaciones filogenéticas dentro de la subtribu (Karremans 2015).

La primera clasificación de la subtribu basada en estudios moleculares de ADN (Pridgeon *et al.* 2001), se basó mayormente en los análisis de tres regiones de ADN de alrededor del 5 % (185) de las especies en la subtribu. La clasificación más reciente de toda la subtribu se publicó en la serie “Genera Orchidacearum” (Pridgeon 2005), tomando como base los estudios moleculares anteriores de Pridgeon *et al.* (2001). Los genes que han sido más utilizados en los análisis filogenéticos de Pleurothallidinae son las regiones intergénicas ITS y el gen plástido *matK*

(Pridgeon *et al.* 2001, Stenzel 2004, Abele 2007, Karremans 2010, Bogarín *et al.* 2013, Karremans *et al.* 2013, Karremans 2014), y también el *rbc*L (Pridgeon *et al.* 2001). A pesar de esto, la aclaración de las relaciones filogenéticas de algunos complejos de especies de linajes muy diversos derivados recientemente, cómo en muchos grupos dentro de Pleurothallidinae (Pérez-Escobar *et al.* 2017), puede resultar difícil utilizando los métodos morfológicos tradicionales o análisis con uno o varios marcadores. Sin embargo, actualmente se han desarrollados nuevos métodos, como la secuenciación de nueva generación (“Next Generation Sequencing” NGS, por sus siglas en inglés), que permite la secuenciación y reconstrucción filogenética con alrededor de 500 loci de "copia única" (típicamente exones largos), del núcleo, mitocondrias y de plástidos en vez de sólo unas pocas regiones como tradicionalmente se han evaluado estos grupos. Esto resulta en inferencias filogenéticas mucho mejor apoyadas y con mayor resolución ya que la cantidad de información analizada es superior a los análisis convencionales mediante secuenciación de Sanger. A pesar de ser muy novedosa, esta técnica ya se ha empezado a utilizar en Pleurothallidinae (Bogarín *et al.* 2018); sin embargo, los costos de secuenciación aún son muy elevados.

El género *Myoxanthus* Poepp. & Endl. comprende 50 especies, distribuidas desde el desde Chiapas, sur de México, hasta Bolivia y sureste de Brasil, siendo más diverso en Ecuador con alrededor de 25 especies. La primera especie de *Myoxanthus* fue recolectada en Perú por Eduard Poeppig, y descrita por primera vez por Poeppig y Endlicher (1835) bajo el nombre *Myoxanthus monophyllus* Poepp. & Endl., que poco tiempo después fue transferido a *Pleurothallis* por Lindley (1836). El segundo intento por establecer un género homólogo lo realizó Karsten en 1847, quien propuso el género *Duboisia* H.Karst., describiendo *D. reymondii* H.Karst. Este género se trató tiempo después como sinónimo de *Pleurothallis* por Reichenbach (1852). Por tercera vez, Barbosa Rodrigues (1882) revivió el género bajo el nombre de *Chaetocephala* Barb.Rodr., el cual nuevamente fue tratado como *Pleurothallis* por Cogniaux (1896). No fue hasta ese momento que se mencionaron dos de las principales características que hoy en día distinguen el género, rizomas y ramicaules con brácteas pilosas (con líneas de tricomas que asemejan escamas) e inflorescencias fasciculadas.

En 1982 Luer restableció el género *Myoxanthus* describiendo una nueva especie y transfiriendo otras 33 especies de *Pleurothallis*, todas con características morfológicas muy distintivas. El establecimiento de este género fue apoyado por estudios anatómicos realizados por

Pridgeon & Stern (1982). En 1986, Luer amplió la circunscripción del género incluyendo en *Myoxanthus* las especies *Pleurothallis aspasicensis* Rchb.f., *Pleurothallis pan* Luer y sus especies afines. Una década después, Luer (1992) presentó la primera revisión taxonómica de *Myoxanthus*, la cual incluye la primera clasificación infragenérica, estableciendo tres subgéneros, *Myoxanthus* (con las secciones *Antenella* Luer, *Myoxanthus* y *Scandentia* Luer), *Satyria* Luer, y *Silenia* Luer, donde las especies fueron acomodadas según su tipo de hábito y número de flores producidas simultáneamente. Sin embargo, poco tiempo después, debido a las diferencias notables de los subgéneros *Satyria* y *Silenia* con el resto del grupo, Luer (1995) decide transferir estos dos a *Pleurothallis*.

Con la evidencia morfológica y anatómica (Pridgeon & Stern 1982) y el apoyo de estudios de ADN, las especies de los subgéneros *Satyria* y *Silenia* se separaron de *Myoxanthus* bajo el nombre genérico *Echinosepala* (Pridgeon *et al.* 2001, Pridgeon & Chase 2001), siendo el más cercanamente emparentado a *Myoxanthus* (Karremans 2016). Con esta última modificación, actualmente se considera a *Myoxanthus* como un género monofilético bien diferenciado dentro de Pleurothallidinae (Karremans 2016). A pesar de ser un género con pocas especies, la actual clasificación infragenérica de *Myoxanthus* nunca ha sido evaluada, ya que, aunque varios estudios filogenéticos han incluido secuencias de este género (Pridgeon *et al*. 2001, Pérez-Escobar *et al.* 2017, Pupulin *et al.* 2017), han sido pocas, y ninguna de ellos han incluido las especies tipo de las tres secciones actualmente reconocidas en el género.

En la revisión taxonómica de Luer (1992) se reportaron cinco especies de *Myoxanthus* en Costa Rica, pero en Pupulin (2002) se citan siete especies. Posteriormente se publicó una nueva especie, *M. sotoanus* Pupulin, Bogarín & Mel.Fernández (Pupulin *et al*. 2010), siendo así la única especie costarricense del género que se ha descrito después del tratamiento de Luer. Aunque es un género con pocas especies en Costa Rica, nunca se ha realizado un estudio sistemático para esclarecer su taxonomía.

El objetivo principal de este trabajo es elaborar una revisión sistemática del género *Myoxanthus* en Costa Rica. Los objetivos específicos son: 1) circunscribir las especies del género presentes en el país, 2) documentar mediante fotografías e ilustraciones las especies del género presentes en Costa Rica, y 3) colocar en un marco filogenético las especies costarricenses del género.

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ARTÍCULO 1: Revision of the Costa Rican species of *Myoxanthus* (Pleurothallidinae: Orchidaceae)

En formato de artículo científico formalmente aceptado para publicación en la revista Phytotaxa el 15 de marzo del 2020

Revision of the Costa Rican species of *Myoxanthus* (Pleurothallidinae: Orchidaceae)

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Abstract: The ten Costa Rican species of *Myoxanthus* are discussed, described and illustrated based mainly on native living material. a key for the species, notes on history, ecology, diagnostic features, taxonomy and distribution maps are included. each species is illustrated with a line drawing and a Lankester composite dissection plate. Photographs of the morphological variation of sheaths, leaves, flowers and lips are provided. the identity of *M. exasperatus* is clarified and recircumscribed to include *M. speciosus*. *Myoxanthus parahybunensis* is reconsidered, and a lectotype is selected.

Resumen: Se discuten, describen e ilustran las diez especies de *Myoxanthus* presentes en Costa Rica, basadas principalmente en mate- rial vivo nativo. Se incluye una clave para las especies, notas sobre la historia, ecología, caracteres diagnósticos, taxonomía y mapas de distribución. Cada especie se ilustra en dibujo y en una lámina de disección compuesta Lankester. Se proveen fotos de la variación de las brácteas, hojas, flores y labelos. Se esclarece y recircumscribe la identidad de *M. exasperatus* para incluir *M. speciosus*. *Myoxanthus parahybunensis* se reconsidera y se selecciona un lectotipo.

Keywords: *Dresslerella, Echinosepala,* Flora of Costa Rica, Pleurothallids, Taxonomy

Introduction

With more than 5 000 species and 44 genera (*sensu* Karremans 2016), subtribe Pleurothallidinae represents 15–20% of all orchid species known worldwide, being one of the most diverse group of plants (Pérez-Escobar *et al.* 2017), which ranges from southern Florida and Mexico to the northern Argentina, with peaks of diversity in the montane rain and cloud forests of Central America and the Andes (Luer 1986). With about 50 species, *Myoxanthus* Poepp. & Endl. as defined by Pridgeon (2005) is an easily recognizable and monophyletic genus within the *Restrepia* Kunth, affinity clade (Karremans 2016). The genus is distributed from southern Mexico and Central America to Bolivia and Brazil (Luer 1982, 1992). The highest diversity is found in Ecuador (25 species), Colombia (18 species), Peru (13 species) and Venezuela (11 species). *Myoxanthus* has one of the broadest elevational distributions in Pleurothallidinae, ranging from 3 m (Brazil) to 3200 m (Colombia; Pridgeon 2005), but most species are found between 1000–2500 m (Luer 1992).

Myoxanthus species are epiphytic, lithophytic, or occasionally pseudo-terrestrial, with caespitose, repent, or scandent habits, characterized by having rhizomes and ramicauls with hispidulous sheaths (Luer 1992) covered by unicellular trichomes arranged in discontinuous lines perpendicular to the axis of the stem (Pridgeon & Stern 1982). Plants of *Myoxanthus* often form large scandent masses, up to 1 m long. The inflorescence is terminal, producing single flowers or fascicles of flowers. The sepals are often pubescent externally, the lateral sepals usually connate; petals are commonly linear and thickened apically. The lip is variously shaped, generally trilobate with a pair of longitudinal lamellae on the disc and delicately hinged to the column foot. The column is variably winged or toothed, and the anther is ventral with a pair of obovoid pollinia brought together by a pair of caudicles. The anther cap is cellular, glandular, often ciliate and fimbriate or papillose on the upper edge (Luer 1992).

The first species assigned to *Myoxanthus* was described by Poeppig and Endlicher (1835) as *M. monophyllus* Poepp. & Endl. on the basis of a plant collected by Poeppig in Peru. The species was transferred to *Pleurothallis* R.Br. by Lindley (1836). Two further proposals to segregate these species from *Pleurothallis* were made, the first by Karsten (1847), who proposed *Duboisia* Karst., and the second by Barbosa Rodrigues (1882) who proposed *Chaetocephala* Barb.Rodr. Both genera suffered the same fate as *Myoxanthus* and were transferred to the synonymy of *Pleurothallis* by Reichenbach (1852) and Cogniaux (1896). The situation would remain virtually unchanged for almost a century, and it is not until 1982 that Luer segregates 33 species from *Pleurothallis* into a newly recircumscribed *Myoxanthus*. This was supported by anatomical studies (Pridgeon & Stern 1982). A decade later, Luer (1992) published the first monograph of *Myoxanthus*, including 47 species in three subgenera, *M.* subgen. *Myoxanthus* with sections *Antenella* Luer, sect. *Myoxanthus* and sect. *Scandentia* Luer (1992: 5), *M.* subgen. *Satyria* Luer and *M.* subgen. *Silenia* Luer. Based on molecular analyses by Pridgeon *et al.* (2001), the last two subgenera were transferred to

Echinosepala Pridgeon & M.W.Chase. As currently defined, with exclusion of the species of *Echinosepala*, *Myoxanthus* is monophyletic (Karremans 2016).

The genus *Myoxanthus* in Costa Rica: Augustus R. Endrés (1838–1874) was probably the first to collect, describe and illustrate a species of *Myoxanthus* from Costa Rica. Endrés' extraordinary botanical contributions during his stay in Costa Rica (Ossenbach *et al.* 2010, Pupulin 2013, Pupulin *et al.* 2014), including specimens, detailed illustrations and descriptions are now preserved at the Herbarium and the archives of the Natural History Museum in Vienna (NHMW). among those materials, there are only eight sheets that correspond to four species of *Myoxanthus*, *M. cereus* (Ames) Luer ex Rojas-Alv. & Karremans (W0019911), *M. congestus* (A.Rich. & Galeotti) Soto Arenas (W0019885), *M. scandens* (Ames) Luer (W0019912, W0019913, W1889-0029903, W1889-0040345, W1889-0076655) and probably *M. parahybunensis* (Barb.Rodr.) Luer (W1889-0030728). accession numbers W0019885 (Fig. 1) and W0019912 (Fig. 2) are the first detailed illustrations of *M. congestus* and *M. scandens*, respectively. None of Endrés' specimens, unfortunately, was used to publish new taxa in *Myoxanthus*, despite several of them being undescribed at the time.

Most of Endrés' specimens at W lack an indication of the year or locality of collection. among his *Myoxanthus* materials, there are only three specimens providing a vague locality. For *M. congestus* (W0019885) Endrés gives the locality *Fajardo*, probably near Cachí, Cartago, considering that other specimens bear the annotation *Fajardo, site north of the Cachí dam on the Reventazón river* (Ossenbach *et al.* 2010). during his stay in Costa Rica, Endrés settled in San Ramón, Alajuela (Pupulin *et al.* 2014), where he collected many orchid specimens, including several of *M. scandens*. one of them (W1889-0076655) was annotated *San Ramón, camino a los Potrerillos, also near Cartago*. this species is still found above 1200 m in the mid to high mountains of Cartago. the specimen of *M. parahybunensis* (W1889-0030728) was annotated as *Near the Desmonte de los Carranzas (Escazú Sn. Rn.)*. If that locality is around San Ramón, Alajuela, then that specimen is the only one of that species collected in that area.

The first decades of the twentieth century were marked by a period of great botanical activity in Costa Rica, thanks to the efforts of important botanists and collectors, including Alberto M. Brenes (1870–1948; Pupulin 2007). Brenes also collected specimens of *M. scandens* in San Ramón. His material collected in 1924 is now preserved at CR. More or less in the same period, the English naturalist Charles H. Lankester (1879–1969) became one of the most important orchid collectors of the first half of the twentieth century in Costa Rica (Ossenbach 2018). Lankester established a fruitful scientific cooperation with Robert A. Rolfe at Kew and, most notably, with Oakes Ames at Harvard university (AMES; Pupulin 2007). Lankester collected a few specimens of *Myoxanthus* around Cartago, including those that would serve as types of *M. cereus* and *M. scandens*, both published by Ames in 1923 as species of *Pleurothallis*. In 1930, Ames and Schweinfurt published another species of *Myoxanthus* from Costa Rica under the name of *P. hirsuticaulis* Ames & C.Schweinf., collected in 1926 by Standley and Valerio in the vicinity of Pejivalle, Cartago. Lankester also sent a specimen of *P. hirsuticaulis* to Ames, a description is attached to the sheet of the type of *P. hirsuticaulis* (upper left side). In 1937, in *Flora of Costa Rica*, Ames listed four species of *Myoxanthus* (under *Pleurothallis*), *M. cereus*, *M. hirsuticaulis* (Ames & C.Schweinf.) Luer, *M. scandens* and *M. trachychlamys* (Schltr.) Luer. the latter was published by Schlechter in 1922 based on a specimen from Panama, but Standley also collected a few individuals in Costa Rica.

During the late twentieth century, several species of *Myoxanthus* were described under *Pleurothallis*, some of them later recorded from Costa Rica. When Luer (1992) published the first monograph of *Myoxanthus*, definitively segregating the genus from *Pleurothallis*, he listed five species for Costa Rica, *M. colothrix* (Luer) Luer, *M. hirsuticaulis*, *M. octomeriae* (Schltr.) Luer, *M. scandens* and *M. speciosus* (Luer) Luer. In the most recent accounts for the country, Pupulin (2002) accepted seven species, whereas Luer (2003) included only five. the difference is that *M. exasperatus* (Lindl.) Luer and *M. trachychlamys*, both included by the former, were only mentioned by the latter. With the addition of *M. sotoanus* Pupulin, Bogarín & Mel.Fernández, a species similar to *M. scandens*, the newly recorded *M. affinis* (Lindl.) Luer and publication of *M. cereus* (Rojas-Alvarado & Karremans 2017), a species described from Costa Rica but commonly placed under the synonymy of *M. octomeriae* or *M. congestus*, the total number of *Myoxanthus* species in Costa Rica is now ten. this is the first complete systematic treatment for those species.

Distribution: Most species of *Myoxanthus* are found at mid elevations, 1200–2500 m. However, some species may grow at extremes, from near sea level, like *M. parahybunensis* in Brazil, to about 3200 m, like *M. gyas* (Luer & R.Vásquez) Luer in Bolivia, which is considered one of the broadest distributions in Pleurothallidinae (Pridgeon 2005). *Myoxanthus trachychlamys* is one of the most widely distributed species, which is found from Nicaragua to Peru and Brazil and from near sea level to 2200 m. In Costa Rica, species of the genus occur from 100 to about 2700 m (Fig. 3), but more frequently at mid elevations. They are well distributed along the Caribbean slopes of the Cordilleras de Talamanca and Volcánica Central, but less commonly on the Pacific side (Fig. 4). *Myoxanthus parahybunensis, M. sotoanus and M. trachychlamys* are the most frequent species, frequently found below 1000 m on the Caribbean slope. Other species like *M. affinis, M. cereus, M. congestus* and *M. scandens* are uncommon. *Myoxanthus colothrix, M. exasperatus* and *M. scandens* are the species typically found above 1500 m.

Materials and Methods

This study was mainly conducted at Lankester Botanical Garden (JBL), University of Costa Rica, in Cartago, Costa Rica. Between 2016 and 2019, plants were collected all over the country, including type localities, and cultivated at JBL. Living plants previously accessioned in the living collection of JBL were also studied. All herbarium material studied was annotated. Dry collections at the Luis Fournier Origgi Herbarium (USJ) and Costa Rica National Herbarium (CR) were examined. Digital images and specimens deposited at AMES, AMO, B, BR, CEPEC, COL, ESA, FLAS, HUA, HUCP, JAUM, K, LPB MBM, MEDEL, MO, NY, PMA, RENZ, SEL, S, QCNE, USM, US, USZ, UVAL and W were studied and annotated.

Vegetative and floral structures of living plants were photographed with a Nikon® 810 camera using a AF-S VR Micro-NIKKOR 105 mm f/2.8G IF-ED lens. Those photographs were used to prepare Lankester composite digital plates (LCDP) using Adobe Photoshop®. For certain species, variable morphological characters were also featured in a composite plate. Plates and illustrations include habit, flower, dissected perianth, column, anther cap and pollinarium, as well as other taxonomically informative characters depending on the taxa illustrated. All photographs are by the authors except if indicated otherwise. When columns without lip do not have scale, it is the same scale as the column with lip. For each documented plant, a spirit specimen, including flowers and stems was prepared and deposited at the JBL-spirit collection. When duplicates were available, they were deposited at CR or USJ as dried specimens. Botanical descriptions were prepared based mainly on living material and the JBL-spirit collection. For the application of names, the documented material and descriptions were compared with protologue descriptions and type specimens or images of the corresponding Costa Rican species.

Maps were made using the geographic information system software ArcGIS 10.1 (ESRI, Inc., California, USA). For plants collected in the field during the course of this study, geographical data were obtained using the software Google Earth PRO. Ecological zones were estimated by using a KMZ layer on Google Earth PRO base on the Holdridge life zone system (Holdridge 1967, 1987). Phenology data were recorded in the field, from cultivated plants and herbarium specimen data.

Taxonomy

Myoxanthus Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 50.

TYPE: Myoxanthus monophyllus Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 50. t.88. 1835.
Heterotypic synonyms:
Pleurothallis poeppigii Lindl., Companion Bot. Mag. 2: 354, 1836.
Humboldtia poeppigii Kuntze, Revis. Gen. Pl. 2: 668. 1891.
Pleurothallis myoxanthus Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 141. 1921, nom. superfl.
Generic synonyms:
Duboisia H. Karst. Allg. Gartenzeitung 15(50): 394. 1847., nom. illeg. Non Duboisia R.Br. Prodr. Fl. Nov. Holland. 448. 1810.
TYPE: Duboisia reymondii H. Karst. Allg. Gartenzeitung 15(50): 394–395. 1847.

Duboisia-reymondia H. Karst., Botanische Zeitung (Berlin) 6(21): 397–*398. 1848.*

TYPE: Duboisia-reymondia palpigera H. Karst., Botanische Zeitung (Berlin) 6(21): 397–398. 1848.
Chaetocephala Barb.Rodr., Gen. Sp. Orchid. 2: 37–38. 1882.
TYPE: Chaetocephala punctata Barb.Rodr., Gen. Sp. Orchid. 2: 37–38. 1882.
Pleurolhallis sect. Chaetocephala (Barb. Rodr.) Cogn., Flora Brasiliensis 3(4): 589. 1896. TYPE: Pleurothallis Chaetocephala Cogn., Flora Brasiliensis 3(4): 590. 1896.

Epiphytic, lithophytic, or occasionally nearly terrestrial herbs, caespitose to repent, frequently with prolific ramicauls. *Roots* velamentous, flexuous, cylindrical, generally branching. *Rhizome* covered by hispidulous sheaths, generally of one or two reduced internodes, infrequently elongate with three internodes. *Ramicauls* erect or spreading, sometimes pendulous, stout to flexible, generally longer than the leaf, with several nodes bearing papery sheaths covered by discontinuous lines of trichomes, basal nodes shorter and sometimes thicker. *Sheaths* tubular, usually imbricating, generally acute, papery, brownish to whitish, the apical sheath generally covering the base of the leaf; when young usually purple, with age frequently disintegrating into fibers or small fragments (Fig. 5). Trichomes arranged in discontinuous lines perpendicular to the ramicaul axis, often deciduous, frequently leaving dark scars; trichomes of younger sheaths generally purple (Fig. 6), becoming papery with age. *Leaves* conduplicate, generally erect, coriaceous, rarely chartaceous, sessile or cuneate into a short petiole, ovate or elliptic, sometimes linear, apex acute to obtuse and generally minutely tridentate (Fig. 7). *Inflorescence* emerging apically on the ramicaul from a small papery spathe, with an obsolete peduncle and extremely abbreviated axis with congested small papery bracts, producing one or several single-flowered branches thus appearing as a fascicle, up to 35 flowers opening simultaneously. *Pseudopeduncle* (structure traditionally misinterpreted as the peduncle) 1–15 mm, sometimes covered by minute trichomes and subtended by a small papery bract usually covered by trichomes. Floral bract tubular to infundibular, acute, generally equal in length to the pedicel and frequently covered by minute trichomes. *Pedicels* glabrous or with minute trichomes with the remainder of the axis adnate and emerging at the end in a form of a filament. *Ovary* cylindrical to subclavate, glabrous or with minute trichomes, slightly sulcate. *Sepals* variously colored, generally ovate, smooth to pubescent abaxially, the apex generally acute and five-veined. Lateral sepals connate to varying degrees, forming a synsepal, sometimes suborbicular. *Petals* variously colored, the base frequently ovate then contracted, frequently irregular in the tapering margin, triveined. *Lip* generally trilobate, sometimes reflexed, base frequently truncate, with a pair of small auricles; lateral lobes erect and irregular; the disc frequently with a longitudinal pair of carinae of lamellae or verrucose, triveined, hinged to column foot by a stalk, apex acute to obtuse, sometimes irregular. *Column* equal to or shorter than the lip, frequently curved and winged, apex with acute teeth, sometimes with broad wings and not toothed, clinandrium sometimes irregular, column foot concave, sometimes with a pair of calli in the middle. *Anther cap* sometimes papillose verrucose to ciliate on the upper edge. *Pollinia* two, yellow, obovoid, with a pair of flat white caudicles. Fruits spherical to ellipsoidal, trivalvate, with the perianth generally persistent (Fig. 8).

Key to the Costa Rican species of *Myoxanthus*

1a. Plants producing chains of prolific ramicauls……………………………………………..………………..…..…2
1b. Plants mostly without prolific ramicauls, not forming chains..…….……….….…..…….………………..……...3

2a. Sheaths of the ramicaul reddish to orange, striped with purple petals, lip purple……….……….…..***M. scandens***
2b. Sheaths of the ramicaul brown to whitish, yellow petals, lip yellow…………………………..…...***M. sotoanus***
3a. Leaves chartaceous, generally with very large plants, ramicauls up to 70 cm long, yellowish flowers….***M. affinis***
3b. Leaves coriaceous, plants small to middle in size, ramicauls up to 50 cm long, whitish flowers, purple or yellowish……………………………………………………………………………………………………..4
4a. Plants short, ≤20 cm tall, repent, yellowish flowers, lip with a conspicuous hump-shape callus basally and lateral lobes small and acute …………..……………………………………….………………………....***M. trachychlamys***
4b. Plants medium to large, ≥25 tall, caespitose to shortly repent, flowers variable colored, lip lacking conspicuous hump-shape callus basally and lateral small acute lobes ……………….………..……..5
5a. Sheaths of the ramicaul smooth, except for a few trichomes or scars on the basal one, whitish flowers, column not toothed, and lip subpandurate with lateral margins purple colored……………….………………..***M. parahybunensis***
5b. Sheaths of the ramicaul with conspicuous trichomes or scars, flowers without above combination of features..…6
6a. Sheaths of the ramicaul whitish, with trichomes soon deciduous leaving scars………..................................……7
6b. Sheaths of the ramicaul brownish to dark, trichomes generally no deciduous……………..……...…………….8
7a. Leaves distinctly petiolate, whitish flowers, lip conspicuously verrucose in the middle, apex apiculate...***M. cereus***
7b. Leaves sessile, whitish to yellowish flowers, lip scarcely verrucose in the middle, apex no apiculate...***M. congestus***
8a. Basal sheaths covered by trichomes, apical sheaths smooth without trichomes nor scars, whitish flowers, lip with margins elevated bellow the middle, and a pair of longitudinal keels emerging in the middle.……….......***M. colothrix***
8b. Basal and apical sheaths covered by trichomes or scars, flowers without above combination of features.......……9
9a. Sheaths densely covered by trichomes, scars not evident, lip yellowish, suffused with purple, entire..***M. exasperatus***
9b. Sheath covered by trichomes, apical sheaths with evident scars, lip purple with white fimbriate margins………………………………………………………………………………….......***M. hirsuticaulis***

1. *Myoxanthus affinis* (Lindl.) Luer, Selbyana 7(1): 35. 1982.

Basionym: *Pleurothallis affinis* Lindl. Companion Bot. Mag. 2: 354. 1836.
TYPE:—PERU. San Martín: lithophytic, province of Chachapoyas, 1835, *Mathews 1899* (holotype: K!).
Homotypic synonym: *Humboldtia affinis* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891.
Heterotypic synonyms: *Pleurothallis rigidifolia* Rchb.f., Bonplandia 3: 224. 1855. *Humboldtia rigidifolia* (Rchb.f.) Kuntze, Revi. Gen. Pl. 2: 668. 1891.
TYPE:—PERU. San Martín: lithophytic near Chachapoyas, 1840, *Mathews 3187* (holotype: G!).
Pleurothallis furfuracea F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 441. 1899.
TYPE:—ECUADOR. Morona Santiago: Andes east of Sigsig, 1887, *Lehmann 6511* (holotype: K!; isotype: AMES!).

Epiphytic, caespitose, erect herbs, up to 75 cm tall. *Roots* flexuous, branching, 1–2 mm in diameter. *Ramicauls* stout, erect, up to 70 cm long, 3–5 mm in diameter, up to 13 internodes with the basal ones shorter, enclosed by hispidulous sheaths. *Rhizome* abbreviated. *Sheaths* of ramicaul tubular, acute, with apical ones generally slightly laterally compressed, light brown to brown, 6–10 cm long, covered by trichomes, often breaking longitudinally into fibres and eventually disintegrating with age, the apical covering up to 3 cm of leaf base; trichomes black to brown, generally deciduous in the apical sheaths leaving few smooth dark scars; sheaths with dark purple trichomes when young. *Leaves* erect, chartaceous, elliptic to ovate, acute to shortly acuminate, 15.0–30.0 × 2.5–10.0 cm, sometimes basally twisted, the abscission layer evident. *Inflorescence* of multiple congested flowers, enclosed during early development by a 6–8 mm long papery spathe that disintegrates when old; producing up to 16 flowers simultaneously. *Pseudopeduncle* generally persistent, 8–12 mm long, with minute purple trichomes, subtended by a 3–5 mm long papery bract covered with minute purple trichomes. *Pedicel* 2–3 × 1 mm, with a few purple trichomes and a 1 mm long filament emerging at the apex. Floral bract papery, 2–5 mm long, enclosing the pedicel, and covered with minute purple trichomes. *Ovary* glabrous, 2 × 1 mm, sulcate. *Flowers* with the perianth yellow to greenish, translucent basally, sepals sometimes with few purple dots abaxially. *Dorsal sepal* narrowly ovate, acute, 7.0–9.0 × 2.5–3.0 mm, 5-veined, margins slightly glandular. *Lateral sepals* narrowly ovate, acute to obtuse, 7.0–9.0 × 1.5–2.0 mm, 4-veined, free to connate at the base forming a mentum covered with few minute white trichomes, margins slightly glandular. *Petals* yellow to greenish, translucent basally, narrowly ovate, acute, 7.0–9.0 × 1.5–2.0 mm, thickened above the middle, conspicuously glandular margins, triveined. *Lip* ovate to oblong, scarcely trilobed, white to yellowish, triveined, 2 × 1 mm, margins purple; lateral lobes elevated below the middle, generally rounded or sometimes acute oblique, entire margin or crenulate, base truncate, hinged to the column foot, disc with a longitudinal purple pair of small parallel lamellae from near the base to above the middle, verrucose to papillose between the lamellae from the base to the near the apex; apex obtuse, irregular, sometimes tridentate. *Column* greenish to white, winged, slightly curved, 2.0–2.5 × 1.0 mm, with a narrowly acute tooth on each side of stigma, the clinandrium purple and denticulate, the anther incumbent, the stigma ventral concave, a 1 mm long column foot straight to slightly concave. *Anther cap* white, mottled with purple in the middle, 0.5 mm wide. *Pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, white caudicles. Fruits not seen.

Distribution: Costa Rica, Colombia, Ecuador, Peru and Bolivia

Habitat and ecology: Reported to grow as an epiphyte at 350–2500 m. In Costa Rica, this large, characteristic species had not been collected until recently in the premontane wet forests of Turrialba and Jiménez in Cartago (Fig. 9A), 700–1100 m at a well botanized area where the species has somehow been overlooked. It flowers in cultivation from December to February.

Specimens examined: COSTA RICA. COSTARICA. Cartago: Jiménez, Pejibaye, La Marta, laderas del Río Gato. Reserva Biológica La Marta, 790 m, 27 Mar 2016, *Karremans 6990 et al.* (JBL-spirit!, CR!; Fig. 10 & 11); Turrialba, Tayutic, Jicotea, Finca La Pradera, 1073 m, 22 Sept 2016, *Rojas-Alvarado 69 et al.* (JBL-spirit!, Fig. 12). BOLIVIA. Santa Cruz: Ichilo, Parque Nacional AMBORO, río Ichilo, elev. ca. 375 m, 20 May 1993, *Vargas et al. 2503* (MO!, USZ!). COLOMBIA. Antioquia: Without data collection, flowers greenish white, lip white, purple toward the base, *Luer 13413* (MO!). ECUADOR. Morona-Santiago: 9–10 km SE of San Juan Bosco, elev. 1600 m, forest edge along stream, epiphyte, flowers yellow; 27 Jan 1981, *Gentry et al. 30883* (MO!); North of Gualaquiza, elev. 1000 m, 4 Feb 1987, *Luer et al. 12631* (MO!, QCNE!); Epiphytic in trees along the road between Mendez and Limon, elev. 1000 m, 7 Feb. 1987, *Luer et al. 12718* (MO!); Cordillera del Condor, east of Chuchumbletza, elev. 1750 m, 21 May 1988, *Luer et al. 13564* (MO!); Cordillera del Condor, east of Chuchumbletza, elev. 1750 m, 21 May 1988, *Luer et al. 13571* (MO!). Esmeraldas: Quininde Cantón, Bilsa Bilogical Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isablel; along Rana Roja Trail, elev. 400–600 m, 5 May 1995, *Clark & Watt 796* (MO!, COL!); Quininde Cantón, Bilsa Bilogical Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isablel; along Rana Roja Trail, elev. 400–600 m, 9 May 1995, *Clark & Watt 813* (MO!, COL!, QCNE!). Napo: El Chaco, elev. 1800 m, Oct. 1984, *Hirtz 1980* (MO!); Cosanga, flowers white, H*irtz &* O*rtega 5404* (MO!); Holling-Loreto road, Km 12–15, elev. 1200 m, May 1993, *Stevenson 93-0309-1* (MO!). Tungurahua: Between Rio Verde and Rio Negro, elev. 1500 m, 12 Apr 1985, *Luer et al. 11181* (MO!, QCNE!). Zamora-Chinchipe: south of Zamora toward Zumba, elev. 1100 m, 3 Feb 1987, *Luer et al. 12607* (MO!, QCNE!); epiphytic in along stream south of Yanzatza, elev. 850 m, 3 Feb 1987, *Luer et al. 12611* (QCNE!). PERU. Cusco: Quispicanchis, Camanti, propiedad privada o bosques de producción permanente del Estado, ubicado en un valle rodeado por montañas boscosas, elev. 800 m, 17 Apr 2008, *Chambi et al.* 950 (BRIT!). Pasco: Yaupi Bajo, elev. 1900 m, 26 Feb 1989, *Aurora & Bennett 4512* (MO!); just above Yuapi Bajo, steep scrub covered slope, ceja montaña; 1550 m, 6 Mar 1989, *Bennett et al. 4531* (MO!). Junin: Tarma, Agua Dulce, in low highland forest, elev. 1900 m, 9 Mar 1948, *Woytkowski 35435* (MO!).

Notes: In Costa Rica, *M. affinis* is easily distinguished from all other species by its outstanding vegetative features. It is the only species with ramicauls that reach up to 70 cm tall, with elliptic to ovate leaves. The less-developed stems of *M. affinis* are rivaled in size only by well-developed plants of *M. cereus*, from which it differs by its brown sheaths of the ramicaul, with persistent trichomes on the basal half sheaths (*vs*. sheaths of the ramicaul whitish with shedding trichomes). It can also be easily distinguished florally; flowers of *M. affinis* (Fig.13, top) are yellowish (*vs*. flowers creamy white), the ovary is 2 mm long (*vs*. 5–6 mm long), pseudopeduncle 8–12 mm long (*vs*. 1–2 mm long), dorsal sepal narrowly ovate and acute (*vs*. oblong-ovate and obtuse-acute), petals with glandular margins (*vs*. smooth), anther cap smooth (*vs*. papillose-verrucose) and lip similar in shape and color. However, in *M. affinis* it is wealy trilobate and slightly verrucose (Fig. 13, bottom) (*vs*. oblong and conspicuously verrucose to the apex).

The type specimen of *M. affinis* was first collected in Chachapoyas, Peru, by Mathews in 1835 and described later by Lindley as *Pleurothallis affinis*. Luer (1992) considered *M. affinis* a variable species and included two other names as synonyms under it. The first, *P. rigidifolia,* was described by Reichenbach in 1855 based on a plant also collected by Mathews in the same locality as the type of *P. affinis*. The second, *P. furfuracea*, was described by Lehmann and Kränzlin in 1899, based on a plant collected in Ecuador.

Even though there are observable morphological differences between the types of *P. affinis*, *P. rigidifolia* and especially *P. furfuracea*, the original descriptions of the first two are too vague to allow for a robust assessment. Across its wide range, it seems to be variable, and there is apparently little consistency in some of the features that could be used to distinguish specimens. At SEL, there are several sketches of diverse individuals of this species prepared by Luer, and illustrations by other authors have appeared in several local floras. The illustrations clearly show variation in presence/absence of trichomes on the sepals, shape and ornamentation of petal margins, shape of the lip and ornamentation of the column apex. None seems to be consistent, and some of them are similar to the material found in Costa Rica. This variation is notable in plants from South America, along with the color of flowers, from white to yellow and size of pseudopeduncle, sepals and petals. Especially outstanding is variation in the width of the leaf, Rojas-Alvarado &

Karremans (2017) mentioned the broad leaf as consistent in the Costa Rican material, but in 2018 new narrower leaves were produced on same plants. The type specimen of *P. furfuracea* from Ecuador shows a habit much like that of the Costa Rican specimens illustrated here, and we think that they represent the same species. Even though it is possible that more than a single species is currently treated under the name *M. affinis*, at this time it is impossible to separate any of these entities with the available information. Specimens from the type locality of *M. affinis* in Peru need to be examined carefully, and a thorough study of the variation of this species across its distribution is needed to reassess it properly in the future.

2. *Myoxanthus cereus* (Ames) Luer ex Rojas-Alv. & Karremans, Lankesteriana 17(2): 210.

Basionym: *Pleurothallis cerea* Ames, Sched. Orch. 4: 19–20. 1923.
TYPE:—COSTARICA. Cartago: Agua Caliente, *Lankester 358* (holotype: K!, photo AMES, illustration AMES!).

Epiphytic, subcaespitose, erect herbs, up to 60 cm. *Rhizomes* stout, composed of one internode, 1–2 mm, producing roots and covered by sheaths. *Roots* flexuous, branching, 1–3 mm in diameter. *Ramicauls* stout, erect, up to 45 cm long, 3–5 mm in diameter, up to 12 internodes, base of basal internode thicker, enclosed by overlapping, tubular sheaths. *Sheaths* of the ramicaul, papery, whitish, 5–9 cm long, acute, covered by trichomes generally in the basal half, soon deciduous leaving purple to light brown scars; sheaths covered by purple trichomes when young. *Leaves* coriaceous, erect or reclinate when old, elliptic, conduplicate, acute, 17.0–23.0 × 4.5–7.5 cm, cuneate into a distinct 1 cm long petiole, the apex minutely tridentate, nerves adaxially evident, abscission layer evident. *Inflorescence* of multiple congested flowers, enclosed during early development by a 5 mm long papery spathe that disintegrates when old; producing up to 25 flowers simultaneously. *Pseudopeduncle* generally persistent, 1.0–2.5 mm long, glabrous, subtended by a 3–4 mm long papery bract covered with minute purple trichomes to the apex. *Pedicel* glabrous, 3.0–6.0 × 1.0 mm long, with a 1 mm long filament. Floral bract 3–4 mm long with purple trichomes to the apex. *Ovary* subclavate, light green, 4.0–7.0 × 1.0–2.0 mm, glabrous, sulcate. *Flowers* with the perianth white to creamy, glabrous, sepals and petals thickened above the middle. *Dorsal sepal* oblong-obovate, obtuse to acute, 7.0–13.0 × 3.0–4.0 mm, 3–5 veined. *Lateral sepals* free, sometimes connate at the base, oblong-ovate, obtuse to acute, 7.0–11.5 × 2.5–4.0 mm, 3–5 veined. *Petals* glabrous, narrowly oblong-ovate, obtuse, 7.0–11.0 × 2.0–3.0 mm, thickened above the middle, triveined. *Lip* white to yellowish, with dark red to purple shortly elevated margins, oblong sometimes ovate, 2.0–2.5 × 1.0 mm, triveined, the base truncate, hinged to the column foot, the disc with a minute pair of longitudinal lamellae in the middle, papillose-verrucose between from the base to the apex, apex obtuse, apiculate. *Column* white, winged, 2 × 1 mm, apex with a small pair of acute teeth, clinandrium short crenulate to dentate, foot perpendicular to the column or slightly concave, 1 mm long, light purple inside. *Anther cap* dark purple-red with white margins, verrucose to the apex, 0.6 × 0.5 mm, *pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles. *Fruit* not seen.

Distribution: Current only known from a few localities around Cartago in Costa Rica and Coclé Panama.

Habitat and ecology: Epiphytic in lower montane and premontane wet forest (Fig. 9A), 970–1800 m. Flowering in cultivation at JBL October–May and in the field September–October.

Specimens examined: COSTARICA. Without further data collection, *Endrés s.n.* (W-0019911!); 14 Nov 1978, *Mora de Retana s.n.* (USJ!). Cartago: Turrialba, Santa Cruz. Después de La Pastora, desde el puente sobre el Río Turrialba hasta unas cataratas sobre el Río, elev. 1800 m, 31 Jan 2005, *Karremans 754* (JBL-spirit!); Tayutic, Platanillo, en bosque alterado y árboles solitarios en las laderas del Río Platanillo, bosque muy húmedo premontano, elev. 974 m, 11 Aug 2012, *Karremans et al. 5693* (JBL-spirit, CR!; Fig. 14 & 15); Alvarado-Turrialba, Capellades-Santa Cruz, laderas del río Turrialba, epífitas en árboles solitarios en potreros, 1750 m, 30 Mar 2013, *Karremans et al. 5868* (JBL-spirit!; Fig. 16); San Nicolás, Cerros la Carpintera, Campo Iztarú, bosque remanente, 1750 m, 26 Oct 2014, *Cascante et al. 2444* (USJ!); Cerro La Carpintera, 10 Oct, in the private collection of Gerson Villalobos, *Rojas-Alvarado 405* (JBL-spirit!). PANAMA. Coclé: Epiphyte, hills north of El Valle de Antón, trail to Las Minas, elev. ca. 1000 m, 1 Sept. 1941, *Allen 2719* (MO!).

Notes: *Myoxanthus cereus* can be easily distinguished by the whitish sheaths of the ramicaul and the elliptic (>4 cm in wide) leaves with a distinctly petiolate base, flowers creamy white, (Fig. 17), column a little shorter than the lip, with an oblong apiculate lip conspicuously verrucose adaxially (Fig. 18). In Costa Rica, the size and shape leaf of this species is only similar with the huge *M. affinis*, but the latter produces elliptic leaves. The flowers of *M. cereus* are similar to those of *M. congestus*, from which it differs in having an oblong-ovate, obtuse to acute dorsal sepal (*vs.* ovate, acute), lateral sepals oblong-ovate, obtuse to acute (*vs.* ovate, acute), petals oblong-ovate, obtuse (*vs*. ovate, acute) and lip verrucose in the middle with an apicule (*vs*. scarcely verrucose near the apex, without an apicule). *Myoxanthus cereus* has elliptic leaves, >4 cm wide (*vs*. narrower elliptic leaves <4 cm wide) that are cuneate into a 1 mm long petiole (*vs*. leaf sessile). Other similar species are *M. pulvinatus* (Barb.Rodr.) Luer (Fig. 19D), and *M. octomerioides* (Lindl.) Luer (Fig. 19C). The first is found in Brazil and probably Peru, and the second in southern Mexico; both species share the whitish sheaths with *M. cereus*, but the latter is easily distinguished by the petiolate leaf and oblong, distinctly papillose lip.

Even though the type specimen of *P. cerea* Ames was collected by Lankester in Cartago and described by Oakes Ames in 1923, Endrés was the first to collect a specimen of this species in the nineteenth century. Luer (1992) placed *P. cerea* under the synonymy of *M. octomeriae*, a species based on a plant collected by Powell in Panama. Luer noted differences between the two species, and in 1991 annotated the specimen collected by Endrés from Costa Rica as "*M. cereus* (Ames) Luer", a new combination that remained unpublished until Rojas-Alvarado & Karremans (2017). When Soto Arenas (2008) revised the taxonomy of the Mexican *Myoxanthus*, he reduced *M. octomeriae* with all its synonyms to the synonymy of the older *M. congestus*, a name based on material from Mexico. However, he also noted the odd features of *P. cerea*, especially size and shape of the leaf and lip structure.

3. *Myoxanthus colothrix* Luer, Selbyana 7(1): 36. 1982.

Basionym: *Pleurothallis colothrix* Luer, Phytologia 49(3): 202. 1981.
TYPE:—ECUADOR. Morona-Santiago: epiphytic in cloud forest east of Paute, elev. 1700 m, 10 Jul 1977, cultivated at SEL-77-2694, flowered in cult. 26 Mar 1981, *Luer et al. 5991* (holotype: SEL!; isotype: AMES!).

Epiphytic, shortly but distinctly repent, erect herbs, up to 60 cm tall, sometimes forming masses up to 1 m in diameter. *Roots* flexuous, 1.5–2.0 mm in diameter, branching. *Rhizome* stout, up to 1 cm long, composed by 3 internodes, 5 mm in diameter, covered by hispidulous sheaths. *Ramicauls* stout, erect, up to 33 cm long, 2–3 mm in diameter, 4–9 internodes, with the basal ones shorter, enclosed by hispidulous sheaths. *Sheaths* of the ramicaul tubular, papery, brown, covered by trichomes, the upper ones smooth, often breaking longitudinally in fibers and eventually disintegrating with age, overlapping or not up to 3 mm the next internode, the apical one covering up to 1.5 cm the leaf base; trichomes brown to dark; sheaths purple and covered with dark purple trichomes when young. *Leaves* erect, coriaceous, narrowly ovate, conduplicate, acute, 11–27 × 2–

3 cm, margins slightly revolute, base cuneate into a 0.6–1.0 cm long petiole, abscission layer evident, the apex minutely tridentate. *Inflorescence* of multiple congested flowers, enclosed during early development by a 5 mm long papery spathe that disintegrates when old; producing up to 25 flowers simultaneously. *Pseudopeduncle* generally persistent, 5–8 mm long, with minute purple trichomes; subtended by a 3.0–4.5 mm long brown papery bract with scarce minute trichomes at the apex. *Pedicel* 3–5 mm long, glabrous, with a 1 mm long filament. Floral bract papery, whitish, 3.0–4.5 mm long, with the apex frequently brown, sometimes with few purple trichomes at the apex. *Ovary* 1 mm long, glabrous, cellular-glandular, cylindrical, green to brownish. *Flowers* with the perianth whitish to creamy. *Dorsal sepal* ovate, acute, 7–10 × 2 mm, 5-veined, with a few minute warts abaxially. *Lateral sepals* ovate, acute, 6.0–9.5 × 2.0 mm, entire, 4-veined, with a few warts abaxially, free to connate at the base, forming a mentum that may be covered by minute whitish trichomes. *Petals* wider in the basal third, ovate, 6.5–10.0 × 1.5–2.0 mm basally, then linear, sometimes with dentate margins on the tapering margin, triveined. *Lip* oblong-ovate, 2 × 1 mm, whitish to creamy white, hinged to the column foot, triveined, the base truncate, margins erect below the middle, disc with a longitudinal pair of parallel keels emerging in the middle, frequently light purple; apex obtuse to acute, minutely denticulate and sometimes apiculate. *Column* 1.5 × 1.0 mm, winged, slightly arched, with a small acute tooth on each side of the stigma, the clinandrium minutely denticulate, reduced laterally, the anther incumbent, the stigma ventral, with a 1 mm long column foot. *Anther cap* whitish, 0.5 mm wide. Pollinia two, obovoid, with white caudicles. *Fruits* not seen.

Distribution: Costa Rica, Panama and Ecuador.

Habitat and ecology: Generally epiphytic above 1000 m. In Costa Rica, it is common in the mountains along the Pacific slopes of the Talamanca Cordillera (Fig. 9A), 1500–2600 m., epiphytically or terrestrially in humus, forming up to 1 m plant in wet montane forests. Flowering March–October, in cultivation at JBL November–February.

Specimens examined: COSTA RICA. Puntarenas: Buenos Aires, Ujarrás, cuenca superior del río Ceibo, 2200–2600 m, 6 Oct 1989, *Valerio 199* (USJ!); Buenos Aires, Olán, camino entre Sipar y Olán, 1700 m, 24 Sept 1989, *Chacón 410* (CR!, MO!); Coto Brus, Finca Las Alturas, 1550 m, 9 Mar. 1994, *Blanco et al. 1712* (USJ!); Coto Brus, San Vito, Finca Las Alturas, 1500–1600 m, 9 Mar 1994, *Pupulin et al. 1757* (USJ!); Buenos Aires, Cuenca Térraba-Sierpe, Estación Tres

Colinas, 1750 m, 11 Sept 1996, *Alfaro 802* (CR!); Buenos Aires, Parque Nacional La Amistad, Cuenca Térraba-Sierpe, 2200–2300 m, 9 Oct 2000, *Alfaro 3464* (CR!, MO!); Coto Brus, Sabalito, Zona Protectora Las Tablas, 10 km al noreste de Lucha, Sitio Coto Brus, 5 Jun 2010, *Bogarín et al.* 7689 (JBL-spirit!); Coto Brus, Sabalito, Zona Protectora Las Tablas, 10 km al noreste de Lucha, Sitio Coto Brus, camino a la Finca de Sandí Hartmann "El Capricho", 30 Apr 2016, *Rojas-Alvarado et al. 3* (JBL-spirit!; Fig. 20 & 21); Coto Brus, Sabalito, Zona Protectora Las Tablas, 10 km al noreste de Lucha, Sitio Coto Brus, camino a la Finca de Sandí Hartmann "El Capricho", 30 Apr 2016, *Rojas-Alvarado et al. 6* (JBL-spirit!); Buenos Aires, "El arbolado", expedición transtalamanca, 1900 m, 24 Apr 2017, *Rojas-Alvarado et al. 116* (JBL-spirit!). San José: Dota, Copey, Providencia, en potreros a orillas de la Quebrada Garrafa, 3 km después de Providencia hacia Salsipuedes, 1873 m, 30 Jan 2011, *Karremans et al. 3529* (JBL-spirit!).

Notes: This species is recognized by the whitish to yellowish flowers with petals oblong in the first third that contract into a linear apex (Fig. 22) and whitish lip, oblong, with the lateral margins elevated below the middle and a pair of longitudinal keels emerging in the middle (Fig. 23). In Costa Rica, this species is similar to *M. parahybunensis*, from which it can be distinguished by the shortly repent habit (*vs*. caespitose), sheaths of the basal half of the ramicaul completely covered by trichomes (vs. completely glabrous, basal one sometimes with few trichomes), leaves 2–3 cm wide (*vs*. <2 cm wide), bracts of the pedicel without or with few purple trichomes at the apex (*vs*. completely covered by purple trichomes), ovary cylindrical and glabrous (*vs*. subclavate and covered by purple trichomes), column cream with a tooth on each side of the stigma (*vs*. purple wings without teeth), lip oblong-ovate with a pair of longitudinal carinae in the middle, whitish (*vs*. subpandurate with a minute pair of longitudinal lamellae in the middle and both surfaces purple). Petals of *M. colothrix* are commonly found with drops of a liquid, presumably nectar. In Costa Rica, *M. parahybunensis* is commonly found below 1200 m, whereas *M. colothrix* occurs at 1500–2600 m.

Plants of this species were cultivated at SEL, where they flowered in March 1981 showing floral characters that did not match those of any other *Myoxanthus*; the new species was described, illustrated and published by Luer in the same year as *P. colothrix*. The protologue mentions that the flowers are similar to those of *M. affinis*, and they are indeed similar. In Costa Rica, the two species are easily distinguished even without flowers. Dried specimens of *M. colothrix* that have lost their sheaths are almost undistinguishable from *M. parahybunensis*. Luer compared the basal lip callus in *M. colothrix* with that of *M. trachychlamys*, at first the callus is small and in the latter the callus is conspicuously hump-shaped. A photo of this species appears *Las orquídeas de Chiapas* (Beutelspacher & Moreno 2018), being one of two species of the genus recorded in southern Mexico and Central/South America.

4. *Myoxanthus congestus* (A.Rich. & Galeotti) Soto Arenas, Icones Orchidacearum 10: XXII, t. 1053. 2008.

Basionym: *Pleurothallis congesta* A.Rich. & Galeotti, Ann. Sci. Nat., Bot., sér. 3, 3: 17. 1845.

TYPE:—MEXICO. Flor. in hort. bot. Fac. Med. Par., Octubre 1842, *Linden s.n.* (holotype: W-0079480!, drawing annotated by Richard and plant and flower fragment, lectotype published by Soto Arenas in *Icones orchidacearum* 10: t. 1053. 2008; isotype: W-0079482!).

Heterotypic synonyms: *Myoxanthus octomeriae* (Schltr.) Luer, Selbyana 7(1): 47. 1982. *Pleurothallis octomeriae* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 21. 1922.

TYPE:—PANAMA. An Baumen in Schluchten des Chiriquí, c. 5000, *Powell 252* (holotype: B, destroyed, lectotype selected by Christenson, *Lindleyana* 6: 130 (1991): AMES-23789!; isotype: MO-950657!).

Pleurothallis ramentacea Garay & Dunst., Venez. Orchid. VI. 364–365. 1976.

TYPE:—VENEZUELA. Without precise locality, *Steyermark s.n.* (holotype: AMES-spirit, illustration!).

Pleurothallis elongata Klotzsch, Index Seminum [Berlin] App. 1. 1853. *Humboldtia elongata* (Klotzsch) Kuntze, Revis. Gen. Pl. 2: 667. 1891.

TYPE:—Without locality, flowered in the Berlin Garden in 1853 (holotype: BR-0000006574222!).

Epiphytic, caespitose, erect herbs, up to 40 cm tall. *Rhizome* stout, 1.0–3.0 × 0.5 cm, composed of two internodes covered by tubular sheaths. *Roots* flexuous, branching, 1–5 mm in diameter. *Ramicauls* stout, erect, homoblastic, up to 32 cm long, 1–4 mm in diameter, up to 9 internodes, with basal one thicker at the base, covered by tubular sheaths. *Sheaths* of the ramicaul papery, whitish, imbricate or not, overlapping by up to 7 mm the next internode, covered by trichomes, deciduous early leaving light brown scars, upper sheaths without trichomes and scars; or with some light brown scars at the base; sheaths covered by purple trichomes when young. *Leaves* narrowly elliptic, coriaceous, conduplicate, sessile, obtuse, 4.5–19.0 × 1.5–3.7 cm, margins slightly revolute, apex minute tridentate, abscission layer evident. *Inflorescence* of multiple congested flowers, enclosed during early development by a 3 mm long papery spathe that disintegrates when old; producing up to 27 flowers simultaneously. *Pseudopeduncle* generally persistent, 1–2 mm long, glabrous, subtended by a 2.5–3.0 mm long whitish papery bract with minute purple trichomes apically. *Pedicel* glabrous, 4 mm long, with a 1 mm long filament emerging at the apex or near the apex. Floral bract 3.0–3.5 mm long with scarce purple trichomes to the apex. *Ovary* subclavate, light green, 4 × 1 mm, glabrous, sulcate. *Flowers* with the perianth white to yellowish. *Dorsal sepal* ovate, acute, 5.5–7.0 × 2.5–3.0 mm, 3-veined, with few minute warts in the abaxial distal half. *Lateral sepals* free to connate basally, ovate, acute, 5.0–6.0 × 2.5 mm, with few minute warts in the abaxial distal half, 3 to 4-veined. Petals glabrous, ovate, acute to obtuse, 5.0–6.5 × 2.0 mm, triveined. *Lip* oblong, 3 × 1 mm, triveined, hinged to the column foot, the base truncate, yellow longitudinal; with the margins purple, elevated below the middle, acute to rounded becoming into a longitudinal pair of carinae extending from the angle of the acute margins and slightly converging to above the middle, disc minutely verrucose throughout, more conspicuous to the apex, apex acute to obtuse. *Column* whitish, winged, 2–3 × 1 mm, with a narrowly acute to acicular tooth at each side of the stigma, clinandrium short crenulate, stigma ventral, foot 1 mm long light purple inside at the apex. *Anther cap* purple-red with white margins, verrucose-papillose longitudinally, 1.0 × 0.5 mm, *pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles. *Fruits* not seen.

Distribution: Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Venezuela and Colombia.

Habitat and ecology: Epiphytic, in Chiapas, Mexico, commonly collected up to 1000 m. In Costa Rica, it has been collected infrequently in dispersed locations, including Turrialba, Pérez Zeledón, Vara Blanca and Guanacaste (Fig. 9B). It grows in low montane and premontane wet forests, 550–1900 m. Flowered in cultivation at JBL October–January and July. In Costa Rica, this species has an unusual distribution; it is present on both sides of the Talamanca Mountains and the Nicoya Peninsula.

Specimens examined: COSTARICA. Turrialba: CATIE, detrás del edificio Principal del CATIE, sobre el sendero Los Espaveles, 600 m, 02 Aug 2006, *Karremans 1300 & Velásquez Vásquez* (JBL-Spirit!; Fig. 24 & 25). Guanacaste: Hojancha, Huacas, colectada por José Alexis Obregón Carrillo en el 2018, 50 m Ede la plaza deportiva de Huacas, 550 m, floreció en cultivo (Huacas) 27 Aug 2019, *Rojas-Alvarado 401* (JBL-spirit!; Fig. 26). Heredia: Vara blanca, 1900 m, flowered in cultivation at JBL, *Blanco 1683 & Quesada* (USJ!, JBL-spirit!). San José: Pérez Zeledón, Rivas, entre Herradura y Río Blanco, a orillas del río Blanco, 1510 m, 29 Mar 2012, *Karremans 5281 &*

Fernández (JBL-spirit!; Fig. 27); Pérez Zeledón, Platanares, 920 m, flowered in cultivation, 1 Nov 2019, *Rojas-Alvarado 404* (JBL-spirit); without data, flowered in cultivation at JBL, November 1999, *Pupulin 1756* (USJ!); without data, flowered in cultivation at JBL, 23 Jul 1983, *Escobar 3066* (SEL!). GUATEMALA. Alta Verapaz: near Cobán, cultivated by Otto Mittlestaedt, 27 Nov 1990, *Luer 14834* (MO!); Fca Westfalia, La Tinta, en flor 13 Nov 1990, ex: *W. del Pinal, H. Ibañez s.n.* (UVAL-spirit 6639!). MEXICO. Chiapas: Palenque-Ocosingo, Km 18, flores cremas, Dec. 1971, *Hágsater 2361* (AMO!); Ocosingo, entre Bonampak y el Río Lacanjá, 330 m, 1 May 1982, *Soto et al. 4248* (AMO!); Fflores crema, margenes del labelo rojo, fragancia por la mañana a piñones, floreció en cultivo, 22 Nov 1985, *Hágsater 7809* (MO!); Ocosingo, Cañada húmeda entre Nahá y Lacandón, 55 km al SEdel crucero de Chancalá, 800 m, 27 abril 1989, *Soto et al. 5633* (AMO!); Ocosingo, camino Libano-Nahá, apox. 54.4 mi al Ede Ocosingo, 940 m, 7 Aug 1992, *Soto et al. 6884* (AMO!); San Cristobal, rain forest dense mix of trees, flowers yellow light, elev. 950 m, June 2002, *CISCO9402* (AMO!). NICARAGUA. Matagalpa: Cerro Matapalos, (tuma grande), 1200 m, *Heller 2236* (SEL, illustration!). PANAMA. Chiriquí: Boquette, cultivated in Chamblee, Ga, flowers creamy white, lip edged in red-purple, flowered in cultivation, 28 June 1991, *Stevenson 86-723-1* (MO!).

Notes: Flowers of *M. congestus* (Fig. 28) are similar to those of *M. cereus* but can be distinguished by the yellowish lip (Fig. 29), minutely verrucose to smooth axially, acute to rounded apex (*vs*. whitish, conspicuously verrucose, the apex frequently apiculate), a pair of longitudinal carinae extending from the angle of the acute margin to above the middle of the lip (*vs*. a minute longitudinal pair of lamellae on the middle of the lip). Plants of *M. congestus* are easily distinguished from *M. cereus* by the sessile obtuse leaves (*vs*. acute, petiolate). Leaf width of this species seems to be more variable in Central and South America than the material from Mexico. Vegetatively, this species is also similar to *M. octomerioides* (Fig. 19C), from which it differs in yellowish to whitish flowers (*vs*. pink tinged), column with well-developed teeth (vs. teeth absent or scarcely developed). Plants and flowers of *M. congestus* are similar to *M. pulvinatus* (Fig. 19D), from which it differs in a column with aciculate teeth on each side and lip acute to obtuse (*vs*. triangular and frequently bidentate at each side, the lip generally apiculate).

Myoxanthus congestus was first described in 1845 by Richard and Galeotti as *Pleurothallis congesta* based on a plant collected by Jean Linden in Mexico between 1837–1840. The type specimen was prepared from a plant cultivated at the greenhouses of the Faculty of Medicine at Paris in October 1842. However, the name *Pleurothallis congesta* were considered by Lindley (1859) and Luer (1982, 1992) as synonym of *P. octomerioides* Lindl., a species described by Lindley in 1836 based on a plant also collected in Mexico.

In 2008, when Soto Arenas published his studies on *Myoxanthus* of Mexico, he noted that the original material of *Pleurothallis congesta* fitted the concept of *M. octomeriae* better than that of *M. octomerioides,* as previously considered by Luer. The author listed only two species for Mexico, *M. congestus,* with *P. octomeriae*, *P. cerea* and *P. ramentacea* as synonyms, and *M. octomerioides*. *Pleurothallis octomeriae* was described by Schlechter in 1922 from a plant collected in Chiriquí, Panamá. *Pleurothallis ramentacea* was described from Venezuela by Garay & Dunsterville (1976). Although *Pleurothallis cerea* from Costa Rica was suspected by both Luer and Soto Arenas to be a different species, it was later transferred to *Myoxanthus* as *M. cereus* (Rojas-Alvarado & Karremans 2017).

The original material of *P. congesta* is inadequate, but there is an illustration of the flowers by Richard, in which the column teeth are evident. According to the material from Mexico documented by Soto Arenas, *M. congestus* is distinguished from *M. octomerioides* by the less fleshy flowers with sepals and petals creamy white (*vs.* flowers fleshier with sepal profusely tinged with pink) and well-developed column teeth (*vs.* teeth absent or scarcely developed). In Hágsater *et al.* (2005, Fig. 19C) a photo of *M. octomerioides* has flowers with the characteristic pink color. Plants of *M. octomerioides* generally form larger plants with the leaves longer and wider than those of *M. congestus*, but plants with narrower leaves are found. As mentioned by Soto Arenas, the type material of *P. octomerioides* is probably a mixed collection of two species, a plant with a narrow leaf and a few flowers mounted on the right side of the sheet that probably is *P. congesta*. The leaf on the left side with a colored illustration of the flower, lip and pollinia is *P. octomerioides*.

In Costa Rica, *M. congestus* was first described and illustrated by Endrés (1860–1874), based on the plant collected in Fajardo (Fig. 1), which matches the plants of *M. congestus* illustrated and described here, the watercolor illustration by Rafael Lucas Rodríguez (1986, p. 139) identified as *M. octomerioides* and photos in Beutelspacher & Moreno (2018). Based on the material studied here, the width of the leaves appears to be more consistent in Mexico but more variable in Central and South America. Along with *M. colothrix*, they are the only two species of the genus in both southern Mexico and Central/South America.

In 1982, when most of the *Myoxanthus* species were transferred from *Pleurothallis*, Luer included *P. elongata* and *P. congesta* as synonyms of *M. octomerioides*. However, in his monograph, Luer (1992) did not mention *P. elongata*. *Pleurothallis elongata* was described in 1853 by Klotzsch based on a plant from an unknown locality that flowered in cultivation at the Berlin Garden. Based on the narrow leaf and dissected flowers on the specimen, this probably is *M. congestus*. Aspecimen most likely also of *M. congestus* that was apparently collected in Colombia is deposited at the Natural History Museum of Vienna (W0079483).

5. ***Myoxanthus exasperatus*** (Lindl.) Luer, Selbyana 7(1): 36. 1982.

Basionym: *Pleurothallis exasperata* Lindl., Folia Orchidacea. *Pleurothallis*. 15. 1859.

TYPE:—VENEZUELA. Aragua: near Colonia Továr, *Fendler 1490* (holotype: K!; isotype: K!; isotype: AMES!).

Homotypic synonym: *Humboldtia exasperata* (Lindl.) Kuntze. Revis. Gen. Pl. 667, 1891.

Heterotypic synonyms: *Myoxanthus speciosus* (Luer) Luer, Selbyana 7(1): 51. 1982. *Pleurothallis speciosa* Luer, Selbyana 3(3–4): 392–393, f. 296. 1977.

TYPE:—PANAMA. Chiriquí: epiphytic in cloud forest above Guadalupe, elev. ca. 2000 m, 13 Sept 1976, flowered in cultivation 5 Feb 1977, *Luer & Butcher 1371* (holotype: SEL!)

Epiphytic, caespitose herbs, up to 52 cm tall. *Roots* flexuous, 1–2 mm in diameter, branching. *Ramicauls* stout, erect, frequently purple, up to 45 cm long, 1–2 mm in diameter, up to 8 internodes enclosed by hispidulous sheaths, the basal ones shorter and thickened. *Sheaths* of the ramicaul tubular, acute, papery, brown, covered by brown trichomes, often breaking longitudinally in fibres and eventually disintegrating with age, overlapping up to 1.3 cm the next internode, the upper most covering up 1 cm the leaf base; sheaths covered by purple trichomes when young. *Leaves* erect, coriaceous, ovate to elliptic, conduplicate, acute to obtuse, coriaceous, frequently suffused with purple, slightly revolute margins, apex minutely tridentate, 7.0–17.0 × 1.7– 4.0 cm, subpetiolate. Inflorescence of multiple congested flowers, enclosed during early development by a 4 mm long papery spathe that disintegrates when old; producing up to 15 flowers simultaneously. *Pseudopeduncle* 6.0–8.5 × 1.0 mm, with minute trichomes on the distal half, subtended by a 4.5–6.0 mm long papery bract with trichomes to the apex. Pedicel 4.0–4.5 mm long, with a 1 mm long filament emerging at the apex and a longitudinal row of minute trichomes aligned with the filament.

Floral bract tubular, papery, 4.0–5.0 mm long, with minute trichomes, enclosing the pedicel and ovary base. Ovary glabrous, 2.0–3.5 × 1.0 mm, green. *Flowers* yellowish with purple veins. *Dorsal sepal* ovate, acute, 9–11× 4–5 mm, 5-veined, above the abaxially middle with few purple trichomes. *Lateral sepals* ovate, oblique, acute, 8–11 × 4–5 mm, 4-veined, free or basally connate, abaxially with few purple trichomes. *Petals* narrowly ovate, wider at the basal half, then gradually contracted and thickened with the margins often minutely serrate, triveined, 10.0–11.5 × 3.5–4.0 mm wide basally. *Lip* oblong, thick, 4.0–5.0 × 1.5–2.0 mm, yellowish white, suffused with purple longitudinally, yellow across the centre, recurved basally, with two longitudinal thick rounded calli from the base to above the middle; apex revolute, minute irregular, generally cuspidate. *Column* yellowish green, 2.5–3.0 × 1.0 mm, lacking wings and teeth, column foot concave, 1.5–2.5 × 1.0 mm. *Anther cap* granular cellular, white, 0.7 × 0.7 mm. *Pollinia two*, obovoid, yellow, 0.5 mm, with a pair of white caudicles.

Distribution: Guatemala, El Salvador, Costa Rica, Panama, Colombia, Venezuela and Peru.

Habitat and ecology: In Costa Rica, it has been commonly collected along the Pacific slopes of the Talamanca Cordillera (Fig. 9B), 2100–2700 m. Epiphytic or terrestrial in cloud forests. Flowering in cultivation at JBL January–February.

Specimens examined: COSTARICA. Cartago: El Guarco, El empalme, Carretera Interamericana, Cartago to Cerro de La Muerte km 53, in roadside tres, 2335 m. 23 de Jul 2003, *Whitten et al. 2146* (JBL-spirit!); El Guarco, San Isidro, 0.6 km NEde la escuela La Esperanza, Parque Nacional Tapantí, 2560 m, 26 Jul 2016, *Rojas-Alvarado et al. 36* (JBL-spirit!). San José: Dota, Copey, 3 km SEdel pueblo tres de Junio, 2490 m, 26 Jul 2016, *Rojas-Alvarado et al. 42* (JBL-spirit!, Fig. 30 & 31). San José-Cartago: Dota-El Guarco, Jardín, entre La Chonta y Cañón, km 56 carretera Interamericana, Finca Santa María de La Selva, 2450 m, 19 Feb 2005, *Bogarín et al. 1420* (JBL-spirit!). Puntarenas: Coto Brus, Zona Protectora Las Tablas, 2500–2700, 14 Aug 1997, *Gamboa et al. 1773* (CR!); Buenos Aires, Buenos Aires, Olán, ascenso por la falda sur del Cerro Tinuk, 2164 m, 25 Jul 2012, *Bogarín et al. 9715* (JBL-spirit!). COLOMBIA. Cundinamarca: 27 Jul 1941, *Renz 3613* (RENZ!). Bogotá: Chicó, 2800 m, 5 Sept 1943, *Schneider 168* (AMES!). ELSALVADOR. Santa Ana: Cerro Montecristo, antes de llegar a la finca de Freund, árbol solitario, *Hamer 249* (illustration!). GUATEMALA. El Progreso: Sierra de las Minas, 2375 m, 16 Feb 1983, *Dix s.n.* (UVAL9814!). Zacapa: San Lorenzo, Sierra de las Minas, 5 Jan 1992, *Dix s.n.* (UVAL6848!;

specimen erroneously mounted, with the apex of the leaf placed at the apex of the ramicaul); Río Hondo, Sierra de las Minas, 2100 m, 17 Apr 1994, *Dix* (UVAL7378!); Río Hondo, San Lorenzo arriba, bosque nuboso, 2175 m, 19 Jul 1994, *Dix* (UVAL7852!). PANAMA. Chiriquí: Las Cumbres, hogback ridge North of Quebrada Iglesia, near town of Cerro Punta, 22 Jul 1971, *Croat & Porter 16087* (MO!). VENEZELA. Merida: collected at 2700 m elev., 17 Dec 1948, *Renz 5013* (RENZ!); collected at 2300 m elev., 19 Jul 1951, *Renz 7264* (RENZ!); 2000 m elev., *Renz 8093.1* (RENZ!); 2000 m elev., *Renz 8093.2* (RENZ!). Tachira: elev. 2800 m, 30 Nov 1949, *Renz 6239.1* (RENZ!).

Notes: After Luer's (1992) monograph of *Myoxanthus*, *M. exasperatus* had been applied to the species here treated as *M. parahybunensis*. The latter is characterized by caespitose plants with smooth sheaths, narrow ovate leaves frequently laterally flattened apically, white to yellowish flowers with sepals and petals long, narrowly ovate to linear apically, column with purple wings, without teeth, and a whitish subpandurate lip with margins below the middle elevated and purple. However, the type of *M. exasperatus* actually corresponds to what has otherwise been known as *M. speciosus*, which is here thus treated as synonym of *M. exasperatus*, which has priority. The true *M. exasperatus* has been illustrated from Central and South America under diverse other names: in Behar & Tinshert (1998) a specimen from Guatemala as *M. octomerioides*, in Schneider (1958) a Colombian specimen as *P. peduncularis* Lindl. and in Zelenko & Bermúdez (2008) a specimen from Peru as *M. speciosus*.

Myoxanthus exasperatus is recognized by its caespitose habit, fully hispidulous sheaths, ramicaul and narrow ovate leaves frequently purple suffused, flowers yellowish striped with red-purple, a column without teeth and an oblong lip suffused with purple (Fig. 32). In Costa Rica, *M. exasperatus* is vegetatively similar to *M. colothrix*, which is also found at high elevations and from which it differs in being caespitose with ramicauls and leaves frequently purple (*vs.* shortly repent, ramicauls and leaves green) and sheaths of the ramicaul completely covered by trichomes (*vs.* apical sheaths smooth). The habit of *M. exasperatus* is similar to several other species in the genus, but when flowering *M. exasperatus* is easily recognized by its yellowish flowers with red-purple veins, a column without teeth and wings and an oblong lip, slightly reflexed basally and suffused with purple.

In 1859, Lindley described P. exasperata based on a plant collected by Fendler near Colonia Tovar, Venezuela. The original description is vague, but the specimen has well developed fruits, and the flowers are senescent with the lips missing. However, the plant was described as having sheaths completely covered by dark, hard hairs, and that key feature is still evident on the type specimens at K and AMES.

In 1977, Luer published *P. speciosa*, from a plant collected in Chiriqui, Panama. In 1982, Luer transferred *Pleurothallis speciosa* and *P. exasperatus* to *Myoxanthus* without citing any synonyms. In his monograph of *Myoxanthus* in 1992, Luer included *P. peduncularis, Anathallis parahybunensis* Barb.Rodr. and *P. macropus* Schltr. as synonyms of *M. exasperatus*. The author states that "*It is reasonably safe to assume that Lindley's P. exasperata is synonymous with his P. peduncularis. His illustration of P. peduncularis* (Fig. 33A) *from Brazil fits exactly Dunsterville's illustration* (Fig. 33B) *of the same species from near Caracas, Venezuela, from whence Fendler probably collected the specimen described by Lindley as P. exasperata*". This assumption was unfortunately wrong. The species illustrated by Dunsterville from Venezuela is indeed the same as the Brazilian *P. peduncularis*, *P. macropus* and *A. parahybunensis* (Fig. 33C). However, they are not the same as Lindley's *P. exasperata*, which came from a nearby locality in Venezuela. The original material of *P. exasperata* (Fig. 33D) don't fit any of the synonyms included by Luer (1992). The type specimen has sheaths completely covered by trichomes and the upper sheaths covers the base of the leaf, whereas *P. peduncularis, P. macropus* and *A. parahybunensis* bear smooth sheaths, where only the basal one has a few trichomes, and the apical sheath doesn't cover the base of the old leaf, a morphological character that is stable along its wide distribution. This feature was also noted by Luer (1975) when he discussed the *P. peduncularis* from Ecuador.

However, it is specimens of *M. speciosus* that fit the type of *Pleurothallis exasperata*. They are caespitose with ramicauls bearing sheaths completely covered by trichomes, the upper sheaths covering the bases of the narrow leaves. Moreover, fruits of the type of *P. exasperata* are long-ovoid, exactly like those in some specimens of *M. speciosus* collected by Renz around 1950 in the high mountains of Tachira and Merida, Venezuela. *Myoxanthus exasperatus* occurs at elevations above 2000 m. On the other hand, *P. peduncularis, A. parahybunensis* and *P. macropus* have a spherical fruit, like those found in Costa Rica (*Bogarín 10276*; Fig. 8D) and Brazil (*Cadorin et al. 778*, FURB), and plants are frequently found at lower elevations, up to about 2000 m. In summary, *M. exasperatus* and *M. speciosus* are conspecific and differ from *P. parahybunensis* (which includes *P. peduncularis* and *P. macropus* as synonyms).

6. *Myoxanthus hirsuticaulis* (Ames & C.Schweinf.) Luer, Selbyana 7(1): 43. 1982.

Basionym: *Pleurothallis hirsuticaulis* Ames & C.Schweinf., Sched. Orch. 10: 29–30. 1930.
TYPE:—COSTARICA. Cartago: vicinity of Pejivalle, elev. ca. 900 m, 7 Feb 1926, *Standley & Valerio 47052* (holotype: AMES!).

Epiphytic, caespitose, erect herbs, up to 65 cm tall. *Rhizome* composed of two abbreviated internodes. Roots fibrous, flexuous, 1.5–3.0 mm in diameter, branching. *Ramicauls* slender, cylindric, erect-spreading, up to 50 cm long, 1–3 mm in diameter, homoblastic, 8–13 internodes, with the basal ones shorter, enclosed by hispidulous sheaths, overlapping up to 5 mm the next internode. *Sheaths* of the ramicaul tubular, papery, brown to light brown, covered by trichomes, the apical one covering up to 1.5 cm of the leaf base; trichomes dark to brown, generally deciduous on the apical sheaths leaving brown to dark scars, sheaths covered by purple trichomes when young. *Leaves* sub-erect to erect, coriaceous, narrowly ovate, conduplicate, acute, 9.0–18.0 × 0.8–2.5 cm, apex minutely tridentate, base cuneate into 0.5 cm long petiol. *Inflorescence* of few congested flowers enclosed during early development by a 4 mm long papery spathe that disintegrates when old; producing up to 5 flowers simultaneously. *Pseudopeduncle* generally persistent, 2.0–5.0 mm long, with purple trichomes, subtended by a 2.5–4.0 mm long bract covered by minute purple trichomes to the apex. *Pedicel* greenish, 3–6 × 1 mm, sometimes with few minute purple trichomes, sometimes with minute trichomes aligned with the 1 mm long filament. Floral bract papery, 3.0–4.5 mm long, with few purple minute trichomes or their scars. Ovary cylindrical to slightly subclavate, glabrous, 2–3 × 1 mm, cellular-glandular, brownish to purple, frequently arcuate. *Flowers* yellowish, veined and mottled with purple. *Dorsal sepal* generally concave, ovate, acute, 7.5–10.0 × 4.5–5.0 mm, 5-veined. *Lateral sepals* oblique acute, 4-veined, connate to near the apex or completely forming a suborbicular synsepal, with the apex obtuse to rounded, 6.0–7.0 × 6.0–7.0 mm, the base forming a mentum with a subcuadrate callus covered with minute white trichomes. *Petals* ovate, porrect, basally translucent with purple stripes, triveined, 7.0–10.0 × 3.0–4.0 mm in the basal half with denticulate to serrulate margins on the tapering section, then contracted into a 1 mm thickened and distal purple half, obtuse to rounded. *Lip* ovate-oblong, weakly trilobed, slightly recurved, 2.0–3.0 ×1.5–2.0 mm, purple with white fimbriate margins, base subtruncate with a small auricle at each side, lateral margins erect below the middle, the disc with a longitudinal rounded pair of calli at the base extending to near the middle then decreasing and forming lamellae that converge above the middle to form a circular glenium-like structure near the apex of the midlobe; apex rounded to obtuse, hinged to the column foot. *Column* yellowish to white, slightly arched, 2.5–3.5 × 1.0 mm, with narrowly acute tooth on each side of the stigma, clinandrium sharply dentate, wings obtuse forming two calli in the middle of the column foot, anther incumbent, stigma ventral, with a 2 mm long concave column foot. *Anther cap* white with two purple dots at the apex, 0.5 mm wide. *Pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles. Fruits not seen.

Distribution: Costa Rica, Panama, Colombia and Peru.

Habitat and ecology: Epiphyte at 400–1200 m. In Costa Rica, it is found on the Caribbean slopes in Cartago, Alajuela and Limon in premontane wet forests (Fig. 9B). Flowering throughout the year in cultivation at JBL, as also noted by Misas (2005).

Specimens examined: COSTARICA. Alajuela: Upala, Aguas Claras, El Gavilán, 1 km después de la entrada principal del Blue River Resort, al lado del camino, a orillas del río Azul, 424 m, bosque muy húmedo, 21 May 2016, *Karremans et al. 7185* (JBL-spirit!; Fig. 34 & 35). Turrialba: Tuís, Cien Manzanas, ca. 950 m, along a minor tributary of Río Pacuare, 26 May 2003, *Pupulin et al. 4768* (JBL-spirit!); Turrialba, La Suiza, without more data, *M. Blanco 1497* (USJ!); Tayutic, Moravia, 5 km al oeste del centro de Moravia, sobre sendero al lado de la calle hacia Platanillo, 1000–1200 m, 22 Jan 2005, *Karremans et al. 668* (CR!, JBL-spirit!); Jiménez, Pejibaye, Taus, alrededores del Río Pejibaye, 1020 m, 1 May 2008, *Bogarín et al. 4823* (JBL-spirit!); Tayutic, Moravia de Chirripó, 5 Km al oeste del centro de Moravia, cerca de Tsipiri, sobre sendero al lado de la calle que va a Platanillo, 1220 m., 4 Dec 2010, *Karremans et al. 3153* (JBL-spirit!). Limón: Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, 627 m, 3 Dec 2008, *Bogarín et al. 5856* (JBL-spirit!); Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, 627 m, 3 Dec 2008, *Bogarín et al. 5864, 5869, 5872, 5875* (JBL-spirit!). PANAMA. Veraguas: 5 min. west of Santa Fe, on road past Escuela Agricola Alto Piedra on Pacific side, epiphytic, 20 m, leaves violet-purple, elve. 800–1200 m, 18 Mar 1973, *Croat 23084* (MO!); in primary forest 6 miles beyond Escuela Agricola Alto Piedra, elev. 730 m, 4 Apr 1976, *Croat & Folsom 34059* (MO!); mountains west of Alto de Piedras Ciclo Basico School north of

Santa Fe, elev. 2300 ft, 9 Sept 1978, *Hammel 4682* (PMA!). COLOMBIA. Chocó: Serranía del Baudo (Misas 2005: 432–433; photo!, illustration!).

Notes: Costa Rica, *M. hirsuticaulis* is recognized by the flowers striped with purple (Fig. 36) and a suborbicular synsepal, apically purple petals, and a purple lip with white fimbriate margins (Fig. 37). Plants are similar to those of *M. parahybunensis*, from which it can be distinguished by sheaths covered by trichomes or their scars (*vs*. sheaths glabrous, smooth). Flowers of *M. hirsuticaulis* are similar to those of *M. scandens,* from which it can be distinguished by sepals yellowish mottled with purple and suborbicular synsepal (*vs*. purple to greenish, laterals free to connate at the base but not forming a suborbicular synsepal), purple lip with white fimbriate margins (*vs*. purple-yellowish with denticulate margins) and caespitose erect-spreading plants (*vs*. scandent with prolific ramicauls). Moreover, *M. hirsuticaulis* occurs up to about 1200 m, whereas *M. scandens* is found above 1300 m. In South America, *M. hirsuticaulis* is similar to *M. antennifer* Luer & Hirtz in Luer and *M. fimbriatus* Luer & Hirtz. The first differs from *M. hirsuticaulis* in having longer, narrow ovate sepals and petals fimbriate to the apex; the second has much contracted petals, forming a semi-terete linear apex with fimbriate margins and fine long trichomes on the middle of the sepals adaxially.

The type of *M. hirsuticaulis* was collected in Costa Rica by Standley and Valerio in 1926, in the vicinity of Pejivalle, Cartago, and described in 1930 by Ames and Schweinfurt as *P. hirsuticaulis*. A printout of the protologue and illustration of the flower made by Schweinfurt accompanied the type of *M. hirsuticaulis*. The drawing shows the typical petal shape and some other diagnostic features of this species, including a lip with a pair of auricles at the base, fimbriate margins and lamellar disc. Moreover, Ames also added a description (identified by him as *P. hirsuticaulis*) made by Lankester based on a specimen collected in the vicinity of the Pejivalle, Cartago (*Lankester 917*).

Ames considered *M. hirsuticaulis* closely allied to *P. scandens*, they share certain floral features, such as purple-striped petals with a thickened apex, lip with two basal auricles and disc with a pair of longitudinal lamellae, features present also in related species from South America, such as *M. antennifer* and *M. fimbriatus*. After reestablishing the genus, Luer (1992) classified *M. hirsuticaulis* and *M. scandens* in different sections, but DNA analyses (in prep.) support Ames' inference: *M. hirsuticaulis* forms a group with *M. scandens* and *M. sotoanus*.

7. *Myoxanthus parahybunensis* (Barb.Rodr.) Luer, Selbyana 7(1): 47. 1982.

Basionym: *Anathallis parahybunensis* Barb.Rodr., Gen. Sp. Orchid. 2: 76. 1882.

TYPE:—BRAZIL. Minas Gerais: in trees along the River Parahybuna, elev. 680 m, *Barbosa Rodrigues s.n.* (holotype: lost; **lectotype here designated**: illustration tab. 150, in *Iconogr.* O*rchid. Bresil*, vol. 3, at the Library of Rio de Janeiro Botanical Garden, cited as tab. 789 (unpubl.) in Barb. Rodr. loc. cit.; copied and reproduced in black and white in Cogn., *Fl. Bras. (Mart.)* 3(4), tab. 111, fig. II, 1896; reproduced in color in Sprunger *et al.,* 1996, vol. 1: 208; Fig. 28C).

Heterotypic synonyms: *Pleurothallis peduncularis* Lindl., Edwards' Bot. Reg. 29: Mise. 47, 1843, *nom. illeg. hom.* non Hook. 1841. *Humboldtia peduncularis* (Lindl.) Kuntze. (1891: 668). Rev. Gen. Pl. 2. 668, 1891.

TYPE:—BRAZIL. Without locality, imported from Río de Janeiro by Loddiges (holotype: K-000820789!; Fig. 28A).

Pleurothallis macropus Schltr., Repert. Spec. Nov. Regni Veg. 14: 130. 1915.

TYPE:—ECUADOR. San Nicolas: Río Pilaton, June 1886, *Sodiro 30* (holotype: BR!).

Epiphytic, caespitose, erect herbs, up to 60 cm tall. *Rhizome* short, 1 × 2–5 mm, composed of 1 or 2 internodes. *Roots* flexuous, glabrous, 1–3 mm in diameter, branching, the apex usually purple. *Ramicauls* stout, erect-spreading, up to 51 cm long, 1.5–3.0 mm in diameter, 5–12 internodes, enclosed by tubular sheaths. *Sheaths* of the ramicaul papery, whitish to brownish, smooth, often breaking longitudinally into fibres and eventually disintegrating with age, commonly overlapping, up to 4 mm above the next internode, the two basal ones with few trichomes, the apical one covering up to 1 cm of the leaf base; trichomes brown, sheaths covered by purple trichomes when young. *Leaves* erect, coriaceous, narrowly ovate, conduplicate, acute, 15.0–25.0 × 1.4–2.0 cm, shortly cuneate into a subpetiolate base, abscission layer above of the emergence of the inflorescence point, apex frequently laterally flattened. *Inflorescence* with multiple congested flowers, enclosed during early development by a 2 mm long papery spathe that disintegrates when old; producing up to 35 flowers simultaneously. *Pseudopeduncle* 4.0–8.0 mm long, with a few purple trichomes, subtended by a 2.5–4.0 mm long papery bract with minute purple trichomes to the apex. *Pedicel* 2–4 mm long, covered with some purple trichomes, 0.5 mm long vestige at the apex. Floral bract acute, papery, 2.5–3.0 mm, covering the pedicel (sometimes also the ovary), covered with purple trichomes, rarely densely. *Ovary* subclavate, 1 mm long, sparsely to densely covered by purple trichomes. *Flowers* whitish to yellowish. *Dorsal sepal* narrowly ovate, acute, 7.5–11.5 × 2.0–2.5 mm, 5-veined, with few minute purple trichomes abaxially. *Lateral sepals* narrowly ovate, acute, 4-veined, 7.5–11.0 × 1.5 mm, free to connate basally, forming a mentum with white minute trichomes. *Petals* ovate in the basal third, then linear, acute, 7.5–11.0 × 1.5 mm wide basally, triveined. *Lip* white-yellowish, subpandurate, 2.5–3.0 × 1.0 mm, 3-veined, articulate to the column foot, the base truncate, basal half ovate to oblong with margins minutely denticulate, suffused with purple and elevated, the disc sometimes with a pair of small longitudinal lamellae near the middle, the apex generally cuspidate, or acute to obtuse with the margins minutely denticulate. *Column* slightly arcuate, without teeth, white to yellowish, wings purple, 2.0 × 1.0 mm; clinandrium short, exposing the anther, sometimes purple below the stigma, the foot 1 mm long, semi-concave, with few minute purple trichomes on the backside. *Anther cap* white-yellowish, 0.5 mm wide. *Pollinia* two, obovoid, flattened, with a pair of small flat caudicles. *Fruits* spherical, trivalvate, 5 × 6 mm, perianth persistent.

Distribution: Costa Rica, Venezuela, Colombia, Ecuador, Peru, Brazil,

Habitat and ecology: Frequently found epiphytically below 1200 m. However, in Colombia and Ecuador, it has been collected at up to 2200 m. In Costa Rica, it is frequently found in the Caribbean lowlands of the provinces of Alajuela, Heredia, Limon and Cartago (Fig. 9C), in wet premontane forests, up to about 1100 m. It is often found sympatric with *M. sotoanus* and *M. trachychlamys* and sometimes forms large masses. It flowers gregariously *in situ* and in cultivation (at JBL), from October–January, for about one week.

Specimens examined: COSTARICA. Alajuela: Grecia, Rio Cuarto, Refugio Mixto de Vida Silvestre Bosque Alegre, 7 km al noroeste de Cariblanco, 850 m, 20 Mar 2016, *Rojas-Alvarado 1* (JBL-spirit!). Cartago: Jiménez, Pejivalle, La Marta, shores of Río Gato, 750 m, 3 Nov 2006, *Pupulin et al. 6370* (JBL-spirit!); Jiménez, Pejibaye, Taus, alrededores del Río Pejibaye, 1020 m, 1 May 2008, *Bogarín et al. 4824* (JBL-spirit!); Jiménez, Pejibaye, Taus, alrededores del Río Pejibaye, 1020 m, 1 May 2008, *Bogarín et al. 4823* (JBL-spirit!); Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 707 m, 30 Apr 2009, *Bogarín et al. 6924* (JBL-spirit!); Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 707 m, 30 Apr 2009, *Bogarín et al. 6948* (JBL-spirit!); Turrialba, Santa Teresita, Palomo, sobre la calle que va a El Cas, al lado de la calle, 850–900 m, 12 Oct 2009, *Karremans 2616* (JBL-spirit!); Turrialba, Santa Teresita, Guayabo, Monumento Nacional Guayabo, alrededores de los senderos principales, 1128 m, 20 Jun 2015, *Karremans et al. 6661* (JBL-spirit!; Fig. 38 & 38); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de Cariblanco, 900 m, 8 Jun 2017, *Rojas-Alvarado et al. 207* (JBL-spirit!); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de

Cariblanco, 900 m, 5 Jan 2018, *Rojas-Alvarado 302* (JBL-spirit!). Heredia: Sarapiquí, Horquetas, road to Rara Avis, ca. 250 m, 27 Jul 2008, *Pupulin et al. 7078* (JBL-spirit!); Sarapiquí, La Virgen, Reserva Biológica La Tirimbina, ca. 100 m, Jun 2010, *Morales et al. 2331* (USJ!); Sarapiquí, La Virgen, Reserva Biológica La Tirimbina, ca. 150 m, 4 Dec 2012, *Ley-López 230* (USJ!); Horquetas, Colonia Cubujuquí, 200 m, 11 Apr 2016, *Karremans et al. 7022* (JBL-spirit!). Limón: Reserva Indígena Talamanca Sukut, desembocadura del Río Sakut en el Río Uren, camino al sureste, hacia Purisqui, 650 m, 7 Jul 1989, *Hammel et al. 17572* (MO!); Pococí, Guapiles, Finca experimental del CATIE, cerca del Río Corinto, 270 m, 3 May 1995, *Gonzáles et al. 88* (CR); Pococí, Guápiles, Hacienda La Cuenca, falda norte del Volcán Turrialba, , 600 m, 1–3 Jan 2005, *Blanco et al. 2764* (JBL-spirit!); Siquírres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, 627 m, 3 Dec 2008, *Bogarín et al. 5851* (JBL-spirit!); Siquírres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, 627 m, 3 Dec 2008, *Bogarín et al. 5867* (JBL-spirit!); Siquírres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, 627 m, 3 Dec 2008, *Bogarín et al. 5868* (JBL-spirit!;); Pococí Guápiles, Bellavista, 600 m oeste de la Escuela La Guaria de Bellavista, 569 m, 7 Jun 2013, *Bogarín 10276* (JBL-spirit!); without collection data, cultivated and flowered at JBL(JBL-spirit! C0903), *Blanco 1713* (USJ!). Talamanca: Telire, sendero después del Río Coen, antes del cruce hacia San José de Kabecar, expedición transtalamanca, bosque muy húmedo premontano, 29 Apr 2017, *Rojas-Alvarado et al. 113* (JBL-spirit!; Fig. 40). BRAZIL. Bahia: Uruçuca, 250 m, km 25 da ESTR, Uruçuca-Serra Grande, 26 Jul 1979, *Vera L. Gomes 108* (RB!); Uruçuca, Estrada Uruçuca-Serra Grande, próximo ao km 23, elev. 100–200 m, 26 Jul 1979, *Martinelli 6058* (RB!, CEPEC!). Minas Gerais: Carangola, Na minha residencia, 5 Aug 2000, *Leoni 4473* (RB!). Paraná: Panaragua, Rio Gruaraguassú, 10 Dec 1951, *Hatschbach 2733* (MBM!); Guaratuba, Pedra Branca de Araraquara, elev. 150 m, 17 Oct 1964, Hatschbach 11279 (MBM!); Morrestes, mata pluvial as margens de rio, elev. 20–50 m, 14 Aug 1968, *Hatschbach 19611* (NY!, MBM!); Guaraqueçaba, Itaqui, Morro Cunhaporanga, 19 Nov 2003, *Barbosa* 789 (MBM!); Pontal do Paraná, Rio Guaraguaçu, 08 Jul 2007, *Lemos 02* (HUCP!); Paranagua, Pontal do Paraná, Rio Guaraguaçu, 09 Jul 2013, *Silvia 8431* (RA!). Rio de Janeiro: Angra dos Reis, Ilha Grando, enseada do Abraão, subida para o Pico do Papagaio, Parque Estadual da Ilha Grande, s.f., *Braga 208 B* (RB!). Santa Catarina: Ibirama, elev. 100 m, 26 Oct 1953, *Klein 699* (US!); São Bento do Sul, Braço esquerdo, 417 m, 21 Nov 2009, *Cadorin et al. 778* (FURB!); Blumenau, Parque Nacional da Serra do Itajaí-Spitzkopf, elev. 249 m, *Schmitt et al. 30* (FURB!); Blumenau, Área Virgem do

Parque Nacional da Serra do Itajaí, elev. 660 m, 23 Nov 2009, *Cadorin 671* (FURB!). São Paulo: Iguapa, 1918, *Brade 7788* (US!); cultivated at S. Paulo Botanical Garden, 8 Oct 1934, *Hoehne 32096* (NY!); Cananéia, Parque Estadual Ilha do Cardoso, 22 Jul 2002, *Breier 355* (ESA!). COLOMBIA. Antioquia: Guatapé, Represa Miraflores, 1900 m, s.f., Ospina 81 (JAUM!); Guatapé, Verde Santa Rita, bosque pluvial, ca. 1850 m, finca Montepinar, 31 Mar 1983, *Escobar & Folsom 3400* (MO!, HUA!). Cauca: ad. pag. El Tambo, ad La Costa, ca. 1700 m, s.f., *Sneidern 1601* (AMES!). ECUADOR. Carchi: Plateau above Chical, 1800 m, 11 Jan 1993, *Hirtz 5852* (MO!). Morona Santiago: Oeste de la ciudad del Macas, 1600 m, 24 Feb 1986, *Baker 6617* (QCNE!). VENEZUELA. Táchira: 10 km E La Fundación (13–23 km by road), around Represa Dorada 600–1000 m, 10–13 Mar 1981, *Liesner & González 10328* (MO!). PERU. Photo in Zelenko & Bermúdez (2008).

Notes: *Anathallis parahybunensis* was first described and illustrated by Barbosa Rodrigues based on a plant from Brazil collected in Minas Gerais, near the Parahybuna River. In 1982, Luer transferred the name to *Myoxanthus*, including *P. peduncularis* and *P. macropus* as synonyms. In his monograph of *Myoxanthus* (1992), Luer placed *M. parahybunensis*, *P. peduncularis* and *P. macropus* under synonymy of *M. exasperatus*. *Myoxanthus exasperatus sensu* Luer (1992) had been described as having smooth sheaths, narrowly ovate leaves that are frequently adaxially appressed at the apex, white to yellowish flowers with long, narrowly ovate to linear sepals and petals, a winged column without teeth and a whitish, subpandurate lip with the margins below the middle purple and elevated. This concept agrees with *M. parahybunensis*, *P. peduncularis* and *P. macropus*, but not with the type of *M. exasperatus*, which is different and conspecific with *M. speciosus* (see discussion of *M. exasperatus*).

Myoxanthus parahybunensis has priority over the other two names and should replace Luer’s concept of *M. exasperatus*. *Myoxanthus parahybunensis* has been illustrated multiple times under different names. It appears as *P. peduncularis* in Dunsterville & Garay (1961), Foldats (1970) and Dodson & Dodson (1980) and as *M. exasperatus* in Luer (1992) and Chiron & Ximenes (2009). *Myoxanthus parahybunensis* is recognized by its caespitose habit, smooth sheaths on the ramicauls except for the basal one with only a few trichomes or scars; narrowly ovate leaves with the apex frequently laterally flattened; whitish to yellowish flowers (Fig. 41) with narrowly ovate to linear sepals and petals, sepals with few minute purple trichomes abaxially; column with purple wings and without teeth, the lip subpandurate with lateral lobes purple and elevated near the middle (Fig. 42).

A noteworthy variation of *M. parahybunensis* was collected in Talamanca, Limón Costa Rica (*Rojas-Alvarado 113*, Fig. 40). This specimen exhibited features not typical of the variation of this species in Costa Rica, including yellowish flowers (Fig. 43) (*vs*. flowers whitish), pseudopeduncle 2.0–3.0 mm long (*vs*. 4.5–6.5 mm), bract of the pedicel, pedicel and ovary densely covered by bigger dark purple trichomes giving them a dark appearance (*vs*. covered by smaller trichomes not giving a dark appearance), bract of the pedicel generally longer, covering the pedicel and generally the base of the ovary (*vs*. pedicel bract generally shorter than the pedicel, covering only up to the apex). However, plants with yellow flowers are also found in South America. The flowering period also differs in the specimens from this collection, flowering in cultivation several times throughout the year, whereas the other plants of *M. parahybunensis* in the strict sense flowered August–January, but generally in December, and never during the dry season. Although noticeable, we have not regarded these differences as enough to warrant recognition at the species level.

8. *Myoxanthus scandens* (Ames) Luer, Selbyana 7(1): 49. 1982.

Basionym: *Pleurothallis scandens* Ames, Sched. Orch. 5: 18–21, f. 4. 1923.

Type:—Costa Rica. Cartago: La Estrella, *C. H. Lankester & A. Sancho 401*, a delightful scandent species occurring in forest-ridges. Flowers dull raisin purple (holotype, AMES!; isotype, AMES!).

Epiphytic, caespitose, scandent, herbs, up to 1 m long. *Roots* slender, fibrous, 1 mm in diameter, branching. *Ramicauls* slender, cylindrical, flexible, 1.0–1.5 mm in diameter, 0.6–50 cm long, up to 15 internodes with the basal ones shorter, producing up to 10 prolific stems at the apex; enclosed by tubular, hispidulous sheaths. *Sheaths* papery, acute, orange to rusty-red when young, covered by trichomes, imbricate, overlapping by up to 5 mm the next internode, the apical one generally covering the base of leaf up to 1.5 cm; trichomes of the sheaths colored the same, generally deciduous in the apical sheaths. *Leaves* narrowly ovate to linear, coriaceous, conduplicate, acute, 2.5–11.5 × 0.4–1.0 cm, apex minutely tridentate, narrowly cuneate basally, abscission layer evident. *Inflorescence* with 1 or 2 congested flowers, enclosed during early development by a 1–2 mm long papery spathe that disintegrates when old. *Pseudopeduncle* 2.0–2.5 mm long, whitish with minute trichomes, subtended by a 2.0–2.5 mm long papery bract, orange to rusty-red, with trichomes to the apex. *Pedicel* 2.0–2.5 mm long, greenish, with a row of trichomes aligned with the 1 mm long filament. Floral bract, infundibular, papery, 2.0–3.0 mm long, orange to red-rusty, covered with minute trichomes. *Ovary* cylindrical, 1.5 mm long, greenish, sometimes mottled with purple, cellular-glandular. *Flowers* with dark purple sepals, greenish basally, and yellowish translucent purple striped petals. *Dorsal sepal* ovate, acute 4.5–5.5 × 2.0–2.5 mm, 5-veined, apex minutely erose. *Lateral sepals* ovate, acute, 4.5 × 2.0–2.5 mm, oblique, the apex and internal margins commonly minutely erose, 3–4-veined, shortly connate basally, forming a mentum, sometimes with minute trichomes. *Petals* wider in the basal half, then gradually contracted into a purple thickened apex with serrulate to shortly ciliate margin, 5.0–5.5 × 2.0 mm basally, triveined. *Lip* oblong, scarcely trilobed, 1.5–2.0 × 1.0 mm, purple, slightly yellowish on the center, hinged to the column foot, the base subtruncate with an auricle on each side, lateral lobes erect near the middle, with minute denticulate margins, the disc with a small hump-shaped callus at the base becoming a conspicuous longitudinal pair of parallel lamellae from the base to near the apex which becomes frequently crenate-dentate; apex obtuse to rounded. *Column* stout, semiterete, 2.0–2.5 × 1.0 mm, winged, slightly arched, with an acicular to narrowly acute tooth on each side of the stigma, clinandrium denticulate, dorsally elongate; anther incumbent, stigma ventral, with a 1 mm long column foot. *Anther cap* 0.5 mm wide, with purple on each side of the back, yellowish between. *Pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles. Fruits not seen.

Distribution: Only known from Costa Rica.

Habitat and ecology: *Myoxanthus scandens* is found growing epiphytically along the Caribbean slopes of the Central Volcanic Cordillera in montane and premontane rain forests, 1300–1900 m (Fig. 17C). This species had been collected in bloom in September, and November to March, and flowered in cultivation at JBL in March. Luer (1992) cited specimens of *M. scandens* from Panama and illustrated one of them in his monograph. We believe the Panamanian material is a different species.

Specimens examined: COSTARICA. Without locality: *Endrés s.n.* (W!, 0019912, illustration); *Endrés 286* (W!, 1889-0019913); *Endrés s.n.* (W!, 889-0029903); *Endrés s.n.* (W!, 1889-0040345). Alajuela: San Ramón, camino a los Potrerillos, also near Cartago, *Endrés s.n* (W!, 1889-0076655); San Ramón, La Palma de San Ramón, 1300–1500 m, 29 Aug 1924, *Brenes 2291* (CR!);

San Ramón, La Palma de San Ramón, 1300–1500 m, 24 Oct 1924, *Brenes 1536* (CR!). Cartago: 5.6 km of San José, side of road leading to Palmital, steep new dirt road up hill from Pan Am highway, 1700–1800 m, epiphytic on exposed tree near edge of forest, plants to 1 m tall, upright–spreading, flowers extremely dark maroon, almost black, 21 Sept 1979, *Walter 79486* (CR!); near San Cristobal, epiphytic in cloud forest, elev. ca. 1900 m, 22 Sept 1979, *Luer et al. 4252* (SEL!); Turrialba, Torito, 1350 m, 20 Mar 1993, *Blanco 1820* (USJ!); Oreamuno, Cipreses, 1850 m, 23 June 1998, *Pupulin et al. 837* (USJ!; Fig. 44 & 45); Oreamuno, Cipreses, 1850 m, 23 June 1998, *Pupulin et al. 838* (JBL-Spirit!). Heredia: Vara Blanca, en los potreros y partes de bosque secundario pertenecientes al Poás Volcano Lodge cerca del centro de Vara Blanca, 1700–1900 m, 03–04 Aug 2006, *Karremans et al. 1322* (JBL-spirit!).

Notes: Plants of *Myoxanthus scandens* are similar to *M. sotoanus*, but leaves of the former are generally wider (5–10 mm *vs.* 3–8 mm), and sheaths of the ramicaul are generally rusty-red colored in *M. scandens* (vs. brownish). When flowering *M. scandens* is easily differentiated from *M. sotoanus* by its dark purple sepals (*vs.* brownish-yellowish), translucent yellow and purple striped petals (*vs.* yellow translucent), yellowish-purple lip, obscurely trilobed, and disc with a prominent longitudinal pair of lamellae that are irregular (Fig. 46) (*vs.* yellow, trilobed, the disc channeled longitudinal). *Myoxanthus sotoanus* is found below 1200 m, whereas, *M. scandens* has been collected above 1300 m. *Myoxanthus scandens* is also similar to the South American *Myoxanthus antennifer* and *Myoxanthus fimbriatus*. However, the first differs in having non-prolific plants and flowers with longer narrow ovate sepals and the petals fimbriate to the apex; and the latter has sepals with fine, long pubescence on the inner halves bellow the middle and petals that are linear highly contracted at the apex.

Myoxanthus scandens was, like many other Costa Rican Pleurothallidinae, first collected and illustrated by Endrés between 1866–1874 (Fig. 2). However, it was only formally described by Ames in 1923 from a plant collected by Lankester and Sancho in the vicinities of La Estrella, Cartago. Luer (1992) selected *M. scandens* as the type species of his *Myoxanthus* sect. *Scandentia* Luer (1992: 5), an artificial group created to accommodate seven scandent species that produce prolific ramicauls.

Specimens of *M. scandens* cited by Luer (1992) from Panama, along with those preserved at the Herbarium of National University of Panama (PMA) identified as *M. scandens* or *M.*

sotoanus collected in the lowlands of central and eastern Panama probably represent yet another species in this complex. Panamanian specimens have linear leaves more similar to those of *M. sotoanus*, but the sheaths are rusty reddish similar to those of *M. scandens*. According to the collection data, specimens from Panama were generally described as having yellowish or greenish flowers, some with purple spots, and a dark red-purple lip. The illustration labeled *M. scandens* in Luer (1992, t. 34) of a specimen collected in Panama differs from the original type description and illustration of *M. scandens*, the detailed illustration by Endrés (W0019912), and *M. scandens* as documented here, all them based on Costa Rican material. A specimen (*Todzia et al. 1023*, CR) collected in Panama and deposited in the Herbarium of the National Museum of Costa Rica has the same features as Luer's illustration from Panama. Rehydration of a flower revealed translucent sepals and petals similar to those of *M. sotoanus* and *M. scandens*, but the lip was only weakly trilobate with entire, rounded lateral lobes mottled with purple and a pair of purple rounded longitudinal calli extending from the base to near the apex, the base between the longitudinal pair of calli with a small callus extending and converging to near the middle and a retuse apex (*vs.* purple to yellowish lip axially scarcely trilobate, the base with a small callus developing into a longitudinal pair of well-developed lamellae and an obtuse to rounded apex in *M. scandens*) (*vs.* yellow lip, trilobate with acutely serrate, well-developed lateral lobes, the base with a small callus extending into a pair longitudinal calli to above the middle and the apex in *M. sotoanus*). A photo of *Laube et al. SL545* at PMA (Fig. 47) from Panama also agrees with descriptions of collection data on other Panamanian specimens with having greenish translucent sepals and petal with column and lip purple, which are not found in any of the Costa Rican material studied here. Therefore, we believe that the material cited from Panama corresponds to an undescribed entity distinguished by greenish to yellowish sepals and petals, purple column and a weakly trilobed purple lip.

9. *Myoxanthus sotoanus* Pupulin, Bogarín & Mel.Fernández, Lankesteriana 9(3): 470–472. f. 2, 3A–G. 2010.

Type:—Costa Rica. Cartago: Jiménez, Pejibaye, La Marta, shore of Río Pejibaye, 9º47’47”N 83º42’55”W, 690 m, epiphytic in secondary vegetation along the river, premontane wet forest, 10 Jan. 2004, *F. Pupulin 5044, S. Dalström & H. León-Páez* (holotype, CR!, photo and illustration of type!; isotype, JBL-spirit!).

Epiphytic, scandent herbs, up to 1 m long. *Roots* slender, fibrous, 1 mm in diameter, branching. *Ramicaul* slender, flexible, pendent, cylindrical 1.0–1.5 mm in diameter, prolifically producing up to 10 new congested ramicauls at the apex, up to 65 cm long, homoblastic, 4–11 internodes with the basal ones shorter, enclosed by tubular, hispidulous sheaths. *Sheaths* of the ramicaul papery, brown to whitish, covered by trichomes, overlapping up to 1 mm the next internode, the apical one covering up to 1 cm of the leaf base; trichomes brown, generally deciduous in the apical sheaths, leaving brown to black scars; sheaths whitish, covered by pale purple trichomes when young. *Leaves* narrowly elliptic-ovate to linear, coriaceous, conduplicate, acute 4.5–14.5 × 0.3–0.8 cm, cuneate basally. Inflorescence with 1–2 congested flowers, enclosed during early development by a 1–2 mm long papery spathe that disintegrates when old. *Pseudopeduncle* generally persistent, 3 mm long, with purple trichomes to the apex, subtended by a 2.0–2.5 mm long tubular, brown papery bract covered by few minute trichomes to the apex. *Pedicel* 3 mm long, brownish green, with a row of purple trichomes aligned with the 1 mm long filament. Floral bract 2 mm long, rusty, papery, tubular to infundibular, brown, with purple to brown trichomes to the apex. *Ovary* cylindrical to subclavate, 2 mm long, cellular-glandular, purple to greenish, with longitudinal rows of short papillose trichomes. *Sepals* brownish yellowish and petals yellowish, infrequently brownish striped basally. *Dorsal sepal* ovate, acute, 5.0 × 2.0–3.0 mm, entire or minutely erose to the apex, concave, 3–5-veined. *Lateral sepals* ovate, acute, 4.5 × 2.0 mm, entire or the internal margins minutely erose, 2–3-veined, connate at the base forming a papillose mentum sometimes with minute trichomes. *Petals* narrowly ovate, 4–6 × 1–2 mm at the base, serrate on the tapering margin, then gradually contracted into a thickened apex, acute with margins shortly revolute. *Lip* oblong, trilobed, 2.0–2.5 mm long, yellow, hinged to the column foot, the base subtruncate with a small auricle on both sides; lateral lobes erect ovate, oblique, with shortly serrate margins, the apex rounded to acute; the disc with a small callus at the base, becoming a longitudinal pair of calli to above the middle forming a sulcus, the apex obtuse to rounded and minute serrate-denticulate, sometimes shortly cuspidate. *Column* semiterete, 2.0–2.5 mm long, winged, slightly arched, with an acicular tooth on each side of the stigma, the clinandrium denticulate, hooded, completely covering the anther cap; the anther incumbent, the stigma ventral, with a 1 mm long column foot. *Anther cap* 0.5 mm wide, white to yellowish. *Pollinia* two, yellow, obovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles. *Fruits* an ellipsoid capsule, 6 × 4 mm, trivalved, with a persistent dry perianth.

Distribution: Only known from Costa Rica.

Habitat and ecology: Commonly growing epiphytically in the Caribbean lowlands of Alajuela, Heredia, Limon and Cartago (Fig. 5D), in wet, premontane forest from near sea level to about 1000 m. Commonly sympatric with *M. parahybunensis* and *M. trachychlamys*. Flowering continuously March–December.

Specimens examined: COSTARICA. Alajuela: Grecia, Rio Cuarto, Refugio Mixto de Vida Silvestre Bosque Alegre, 7 km al noroeste de Cariblanco, 850 m, 17 July 2016, *Rojas-Alvarado 10* (JBL-spirit!); Upala, Bijagua, en la calle nueva desde el Celeste Moutain Lodge al parque Volcán Tenorio, 680 m, 14 Dec 2016, *Rojas-Alvarado 111* (JBL-spirit!). Cartago: Casa de tejas ridge above Río Gato, 800 m, 28 Dec 1973, *Lent 3710* (CR!, SEL!); Turrialba, La Suiza, 1300 m, 27 Jul 1991, *Blanco 1513* (USJ!); Turrialba, Parque Nacional Barbilla, cuenca del Matina, sendero principal por Río Dantas, 300–400, 11 Nov 2000, *Mora et al. 1655* (CR!); same locality, 20 Nov 2000, *Mora et al. 1722* (CR!, MO!); Jiménez, Pejivalle, El Humo, road to Taus, shores of Río Pejivalle, 740 m, 4 May 2006, *Pupulin et al. 6178* (JBL-spirit!); Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 707 m, 30 abril 2009, *Bogarín et al. 6920* (JBL-Spirit!); Turrialba, Tuis, Cien Manzanas, 1000–1100 m, 15 May 2010, *Karremans 2667* (JBL-spirit!). Heredia: Sarapiquí, Finca La Selva, the OTS field station on the Río Puerto Viejo just Eof its junction with the Río Sarapiquí, 100 m, 22 Aug 1979, *Grayum & Bien 2506* (DUKE, illustration!); Sarapiquí, finca La Selva, OTS field station, 40–101 m, 20 Apr 1992, *Richardson 113* (CR!); Sarapiquí, La Virgen, Magsasay, banks of Río Peje, 110 m, 25 Aug 2007, *Pupulin et al. 6888* (JBL-Spirit!); Sarapiquí, río Peje, 19 Oct. 1984, *Dressler 120* (USJ!); Sarapiquí, Horquetas, ca. 4.7 km del cruce de Río Frío hacia Horquetas, 200 m, 10 Jun 2016, *Karremans et al. 7322* (JBL-spirit!; Fig. 48 & 49). Limón: Cerro Coronel, en Laguna Danto, 20–170 m, 15 Sep 1986, *Stevens 24568* (CR); Pococí, Guápiles, San José-Limón highway, km 47, Molinete, 470–500 m, 9 Jul 2004, *Pupulin & Bogarín 5255* (JBL-spirit!); Pococí, Cuenca del Río Sarapiquí, Guápiles, Finca INBIO, sendero de Las Aves, 300–400, 7 Jun 2007, *Flores et al. 24* (CR!); Siquirres, Guayacán, en potreros bajando el camino frente el bar Guayacán, en las orillas de la Quebrada Quebrador, 477 m, 25 Jan 2008, *Bogarín & Karremans 4049* (JBL-spirit!); Pococí, Guápiles, Bellavista, 600 m oeste de la Escuela La Guaria de Bellavista, 569 m, bosque muy húmedo tropical, epífitas en bosque secundario a orillas de una quebrada, 7 Jun 2013, *Bogarín 10268* (JBL-spirit!). San José: [Vázquez de Coronado], Parque Nacional Braulio Carrillo, sendero La Botella, 750 m, 16 Nov 1990, *Ingram & Farrel 712* (CR!, SEL!).

Notes: *Myoxanthus sotoanus* is recognized by its prolific ramicauls, linear leaves, flowers with brownish sepals (Fig. 50) and yellow petals and lip with serrate margins (Fig. 51). It is similar to *M. scandens* but differs in its narrower leaves, 3–8 mm wide (*vs*. 5–10 mm), brownish young sheaths (*vs*. rusty-red), brownish yellowish sepals (*vs*. dark purple), yellowish to greenish, translucent, entire petals (*vs*. purple striped with shortly ciliate margins), yellow trilobed lip, the disc of which has a pair of longitudinal lamellae (*vs*. purple-yellowish, weakly trilobed, and disc with a prominent pair of longitudinal lamellae irregular at the end). *Myoxanthus sotoanus* is commonly found bellow 1200 m, whereas *M. scandens* has been collected above 1300 m. *Myoxanthus sotoanus* is also similar to *M. epibator* Luer & R.Escobar, which has been only collected in Colombia and differs from *M. sotoanus* by its wider leaves, 8–11 mm (*vs*. 3–8 mm), a dark purple lip with uncinate lateral lobes expanded below the middle (*vs*. yellow with the lateral lobes ovate, acute to rounded).

Myoxanthus sotoanus was described by Pupulin *et al.* (2010) after noticing differences from *M. scandens*. With further examination, the morphology and biogeographic distribution revealed that there was a species that needed to be recognized, a second prolific species described for Costa Rica. The similar prolific habit of *M. sotoanus* and *M. scandens* led to misinterpretation of specimens of the first. The oldest specimen of *M. sotoanus* (identified as *M. scandens*) was collected by Lent in 1973 on a ridge above Río Gato in Cartago. An illustration in Atwood (1989, t. 1373) identified as *M. scandens* is *M. sotoanus*. In Bogarín *et al.* (2014), *M. sotoanus* is reported for Panama. However, as mentioned in the discussion of *M. scandens*, the specimen cited (*Laube et al. 245*, MO), and other material from Panama probably correspond to an undescribed species.

10. ***Myoxanthus trachychlamys*** (Schltr.) Luer, Selbyana 7(1): 51. 1982.

Basionym: *Pleurothallis trachychlamys* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 23. 1922.
TYPE:—PANAMA. On foot-hill, east of Panama City, sea level, *Powell 215* (holotype: B, destroyed; lectotype, AMES 23974!, selected by Christenson 1991; isotypes: AMES!, MO!, illustration of type, AMES!).
Heterotypic synonym:
Pleurothallis cymbicalli Pabst, Arq. Bot. Estado São Paulo 3(5): 268, t. 67. 1962.
TYPE:—COLOMBIA. Amazonas, *Shultes 8584* (holotype: IAN!).

Epiphytic, repent herbs, up to 20 cm tall. *Roots* flexuous, branching, 1 mm in diameter, produced from the rhizome nodes, generally adpressed to the rhizome to about 1 cm. *Rhizome* up to 3 cm long, composed of 3 internodes, 2 mm in diameter, enclosed by scurfy sheaths. *Ramicaul* slender, erect, up to 12 cm long, 1–2 mm in diameter, up to 5 internodes, enclosed by scurfy sheaths. *Sheaths* of the ramicaul tubular, papery, brown to whitish, covered by scurfy trichomes, often breaking longitudinally into fibers and eventually disintegrating with age, overlapping up to 2 mm the next internode, the apical sheaths smooth to the apex; trichomes whitish to brown, sheaths purple, covered by purple trichomes when young. *Leaves* erect, coriaceous, elliptic to narrowly ovate, conduplicate, acute, 4.0–12.0 × 0.8–1.3 cm, slightly glaucous, apex minutely tridentate, cuneate, subpetiolate, abscission layer evident. *Inflorescence* with few congested flowers at the apex of the ramicaul, enclosed during early development by a 4 mm long papery spathe that disintegrates when old, producing 1–3 flowers simultaneously. *Pseudopeduncle* abbreviate, 1 mm long, glabrous, generally deciduous, subtended by a 2–3 mm long papery, whitish to brown bract covered with minute trichomes to the apex. *Pedicel* 2–3 mm long, glabrous, with a 1 mm long filament. Floral bract papery, 2.5–3.0 mm long, with trichomes to the apex. *Ovary* cellular-glandular, greenish, cylindrical, 1 mm long. *Flowers* yellow. *Dorsal sepal* narrowly ovate, obtuse to acute, 5-veined, 5–6 × 2 mm. *Lateral sepals* free, narrowly ovate, acute, 4-veined, 5–6 × 1.5–2.0 mm. *Petals* quadrate to rectangular in the basal third, then contracted and thickened, acute, 5.0–5.5 × 1.5 mm at the base. *Lip* whitish, 2.0–2.5 × 1.0 mm, oblong, the base truncate, hinged to the column foot, lateral margins with an erect small acute lobe in the middle, base with a hump-shaped callus, apex obtuse to acute, frequently revolute. *Column* white to yellowish, 1.5–2.0 mm long, wings broad to the apex, with a narrow acute tooth on both sides of the stigma, anther incumbent, stigma ventral, concave, with a 1 mm long column foot. *Anther cap* yellowish to white, 0.5 mm wide, frequently with yellow in the dorsal and apically parts. *Pollinia* two, yellow, obovoid, with small white caudicles. Fruit a capsule, ovoid-oblong, trivalvate, 9–11 × 5–6 mm, with the perianth persistent.

Distribution: Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru and west of Brazil.

Habitat and ecology: Widely distributed in Central and South America where it is found as a lowland epiphyte, growing from near sea level to about 900 m. In Ecuador, it has been also collected to about 2100 m in Carchi and Pichincha. In Costa Rica, it is commonly found growing in the premontane wet forest on the Caribbean slopes of Alajuela and Heredia, 650–1100 m (Fig. 5D), where it is commonly found sympatric with *M. parahybunensis* and *M. sotoanus*. Plants of this species frequently form large masses up to 1.5 m in diameter, covering trunks and branches. Flowers of *M. trachychlamys* are ephemeral, commonly withering and falling after one day, characterized by a fungal, fetid odor. The species flowers in cultivation at JBL June–December and has been collected with flowers May–August.

Specimens examined: COSTA RICA. Alajuela: Bolívar de San Ramón, flowered in cultivation at Jardín Botánico Lankester, 3 Oct 2001, *Pupulin 3332* (JBL-spirit!); San Carlos, Fortuna, Volcán Chato, sobre el sendero a la laguna de la cima del volcán, 899 m, 27 Jul 2011, *Karremans 4365* (JBL-spirit!); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de Cariblanco, camino al Refugio Mixto de Vida Silvestre Bosque Alegre, 900 m, 17 Jul 2016, *Rojas-Alvarado 27* (JBL-spirit!; Fig. 52 & 53); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de Cariblanco, camino al Refugio Mixto de Vida Silvestre Bosque Alegre, 900 m, 17 Jul 2016, *Rojas-Alvarado 28* (JBL-spirit!); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de Cariblanco, camino al Refugio Mixto de Vida Silvestre Bosque Alegre, 900 m, 16 Jul 2017, *Rojas-Alvarado 168* (JBL-spirit!); Alajuela, Sarapiquí, 4 km al noroeste de Cariblanco, carretera al refugio Mixto de Vida Silvestre Bosque Alegre, 960 m, 5 Nov 2016, *Rojas-Alvarado 79* (JBL-spirit!); Grecia, Rio Cuarto, Los Ángeles Sur de Pata de Gallo, 7 km al noroeste de Cariblanco, camino al Refugio Mixto de Vida Silvestre Bosque Alegre, 900 m, 8 Jun 2017, *Rojas-Alvarado & Fernández 210* (JBL-spirit!); Sarapiquí, 1.5 km al sur de Cariblanco, carretera hacia Vieja Cinchona, 880 m, 5 Aug 2018, *Rojas-Alvarado 220* (JBL-spirit!). BRAZIL. Acre: Cruzeiro du Sul, Río Juruá, 2-5 km west of Cruzeiro du Sul, Varzea forest, 3 Nov 1966, *Prance et al. 2980* (K!, US!, NY!). COLOMBIA. Chocó: Norte de la Costa Pacífica, elev. 100 m, Jul 1988, *Urreta 275* (COL!); Nunquí, quebrada Chanquí, ca. 200 m, Feb–Mar 1994, *Galeano et al. 4840* (COL!); Serranía del Baudo, photo! and illustration! (Misas 2005: 436–437). ECUADOR. Carchi: between Tulcan and Maldonado2050 m, 2–4 Apr 1984, *Luer et al. 9927* (MO!); east of Maldonado, 1900 m, 15 Feb 1989, *Höijer & Dalström 1233* (MO!); above Maldonado, 2000 m, Jan 1989, *Dalström et al. 1148B* (MO!). Pichincha: along the new road to Quito and Santo Domingo, 2100 m, 31 Mar 1984, *Luer et al. 9825* (MO!, QCNE!); Above Tandapi, 2100 m, 31 Mar 1985, *Luer et al. 11058* (MO!, QCNE!); Santo Domingo to Quito via Tandapi, elev. 1800 m, 20 Jun 1985, *C. & T. Dodson 15850* (QCNE!, AMES!). NICARAGUA. Rivas: Ometepe Island, Volcano Maderas, elev. 900 m, *Heller 8303* (SEL!). PANAMA. Panama: on foothills east of city, sea level, *Powell 215* (AMES!, MO!); El Llano-Carthi Road, 10-12 Km from El Llano, 400 m, 17 Sept 1974, *Mass* *et al. 1765* (MO!). Coclé: El Valle de Antón, road to Cerro Gaital, near to Sendero Convento, 815 m, 20 Jan 2005, *Blanco & Penneys 2853* (MO!). PERU. Loreto: Puerto Arturo, lower Río Huallaga below Yurimaguas, 135 m, 24 Aug 1929, *Killip & Smith 27889* (AMES!); Río Ampiyacu, 2 km above Puca Orquill (affluent of Rio Amazonas), 11 Feb 1969, *Plowman 2466* (AMES!). Cusco: La Convención, Echarati, Armihauri well site, 535 m, 14 May 1997, *Percy Nuñez et al. 20051* (USM!). San Martín: Prov. Mariscal Cáceres, Río de la Plata, noreste de Tocache, 500–600 m, 5 May 1975, *Vigo 8377* (MO!). VENEZUELA. Bolivar: Río Icarabú, 450 m, *G. & E. Dunstervillae 722* (illustration VEN!).

Notes: *Myoxanthus trachychlamys* is recognized by the repent plants with scurfy sheaths, yellow flowers (Fig. 54, top) and lip with a basal callus and small acute lateral lobes (Fig. 54, bottom). The long repent habit is shared only with *M. hystrix*, but the other features make this species easily recognizable. Without flowers, small plants of *M. trachychlamys* may be confused with *Octomeria graminifolia* (L.) R.Br., a species with a short repent habit and similar leaves. From *O. graminifolia*, *M. trachychlamys* may be distinguished by the scurfy sheaths of the rhizome and ramicaul (*vs*. sheaths smooth), acute apex of the sheaths (*vs*. sheaths aristate), petals ovate in the basal third and then linear (*vs*. ovate), column winged (*vs*. column unwinged), lip oblong with a hump-shaped basal callus and acute lobes in the margins near the middle (*vs*. lip oblong-trilobed with erose margins apically) and two pollinia (*vs*. eight pollinia). Flowers of *M. trachychlamys* are similar to those of *M. frutex* (Schltr.) Luer, but the latter produces large prolific plants and has a lip with a dentate apex lacking lateral acute lobes characteristic of the former. *Myoxanthus trachychlamys* is one of the few species of the genus that has a well-developed rhizome.

The species was first described in 1922 by Schlechter based on a plant collected by Powell in Panama. Decades later in 1962, the same species was described by Pabst as *P. cymbicalli* based on a plant collected in the Colombian Amazon. The type of *P. trachychlamys* preserved at the Herbarium of the Botanical Garden of Berlin was destroyed during the WWII. In 1991, Christenson designated a lectotype from an isotype preserved at AMES. When Luer published the monograph of *Myoxanthus* in 1992, he superfluously selected a neotype for *M. trachychlamys*, probably not aware of the earlier lectotypification. This species was illustrated by Foldats (1970), Dunsterville & Garay (1972) and Dodson & Dodson (1980) as *P. trachychlamys*.

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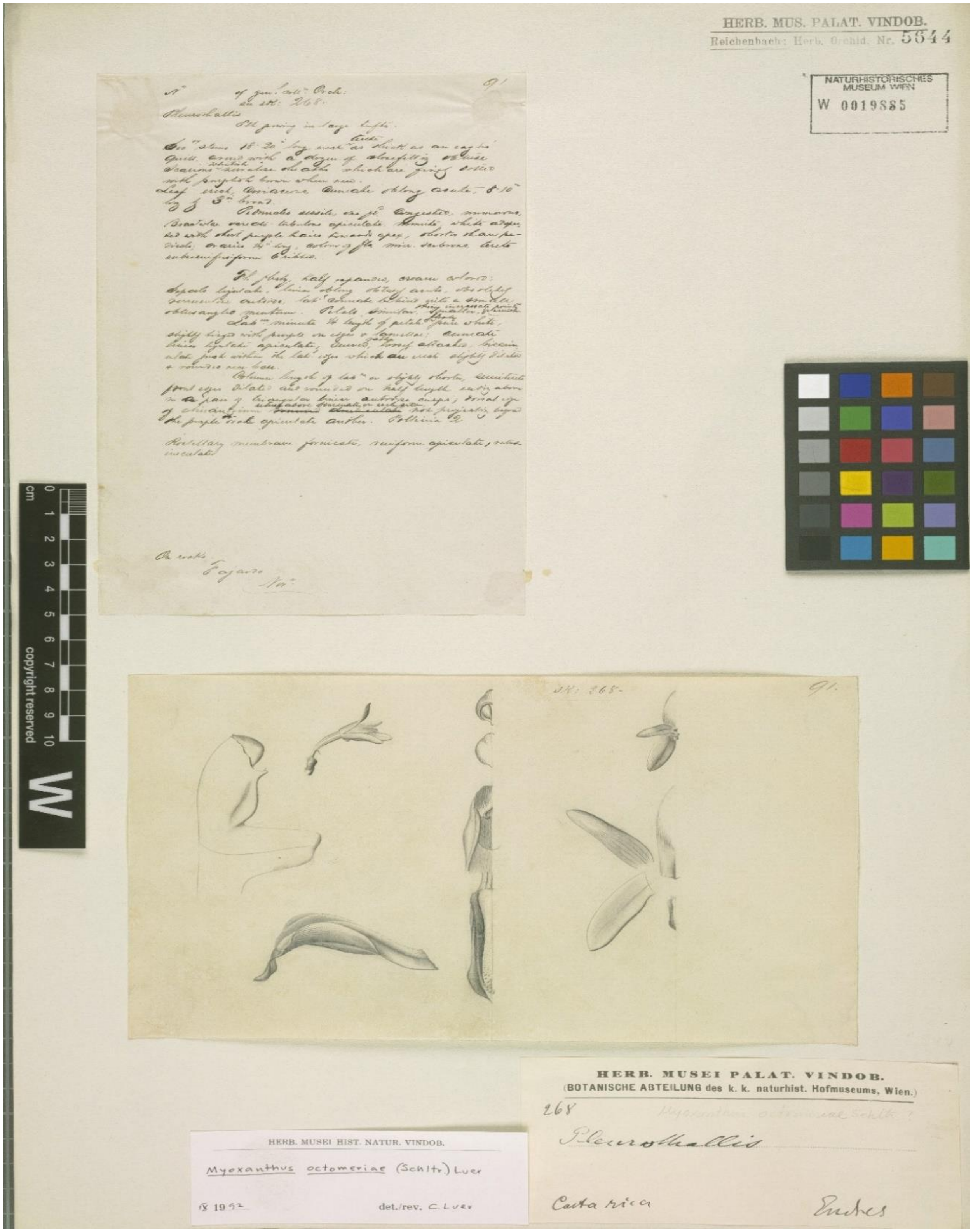

No of gen.l coll.n Orch: 91
in st: 268.

Pleurothallis

Pl. growing in large tufts.

Sec.y stems 18-20'' long, weak, as thick as an eagle's quill, armed with a dozen of closefitting obtuse scarious whitish [illegible] sheaths which are going rotten with purplish brown when new.

Leaf erect, coriaceous, cuneate oblong acute, 8-10'' long & 3'' broad.

Peduncles sessile, [illegible] congested, numerous, Bracteolae [illegible] tubulous apiculate, [illegible] white, adspersed with short purple hairs towards apex, shorter than pedicels; ovaries 1/4'' long, colour of fls. [illegible] scabrous, terete subcuneifusiform 6 ribbed.

Fl. fleshy, half expanded, cream colored; Sepals ligulate, linear oblong obtusely acute, [illegible] verrucose outside, lat.l connate behind into a small obtuse angled mentum. Petals similar, smaller, [illegible]

Lab.m minute 1/4 length of petals, fleshy, pure white, slightly tinged with purple on edges & lamellae; cuneate, basi ligulate apiculate, curved, [illegible] attached, [illegible] fresh within the lat.l edges which are erect, slightly dilated & rounded near base.

Column length of lab.m or slightly shorter, semiterete, front edges dilated and rounded on half length and [illegible] above in a pair of triangular linear antrorse cusps; dorsal edge of clinandrium [illegible] not projecting beyond the purple ovate apiculate anther. Pollinia 2.

Rostellary membrane fornicate, reniform, apiculate, [illegible]

On rocks Fajardo Nov.

Figure 1. Description and drawing of *Myoxanthus congestus* (Rchb. Orch. 5644, 0019885, W) by A. R. Endrés. Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

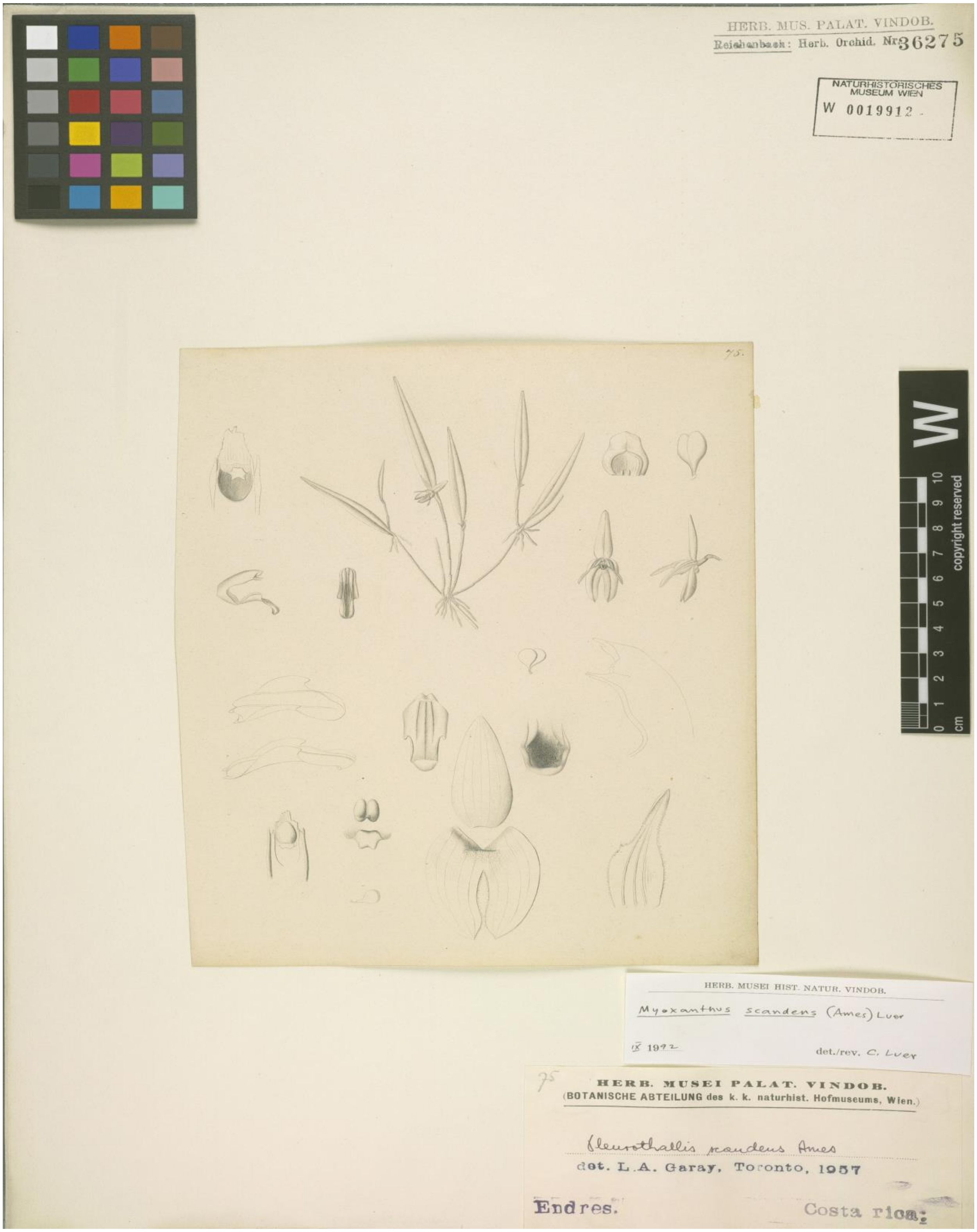

Figure 2. Drawing of *Myoxanthus scandens* (Rchb. Orch. 36275, 0019912, W) by A. R. Endrés. Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

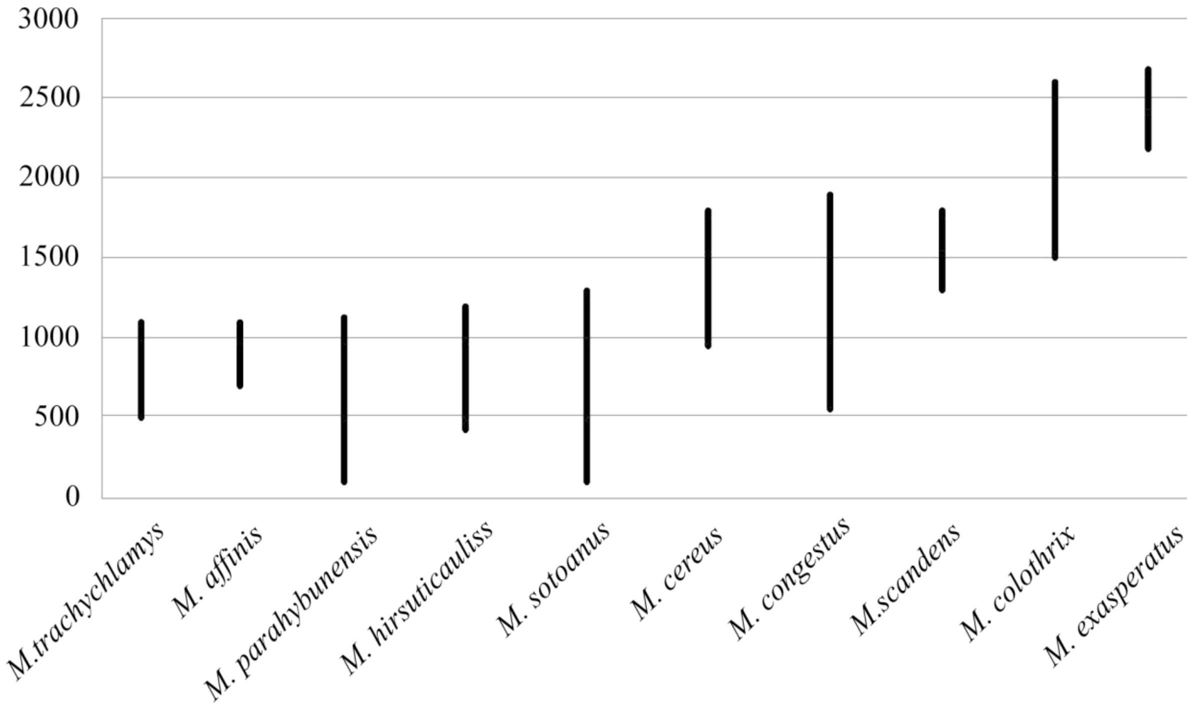

Figure 3. Elevational range of the *Myoxanthus* species in Costa Rica. Vertical axis = meters above sea level, horizontal axis = species.

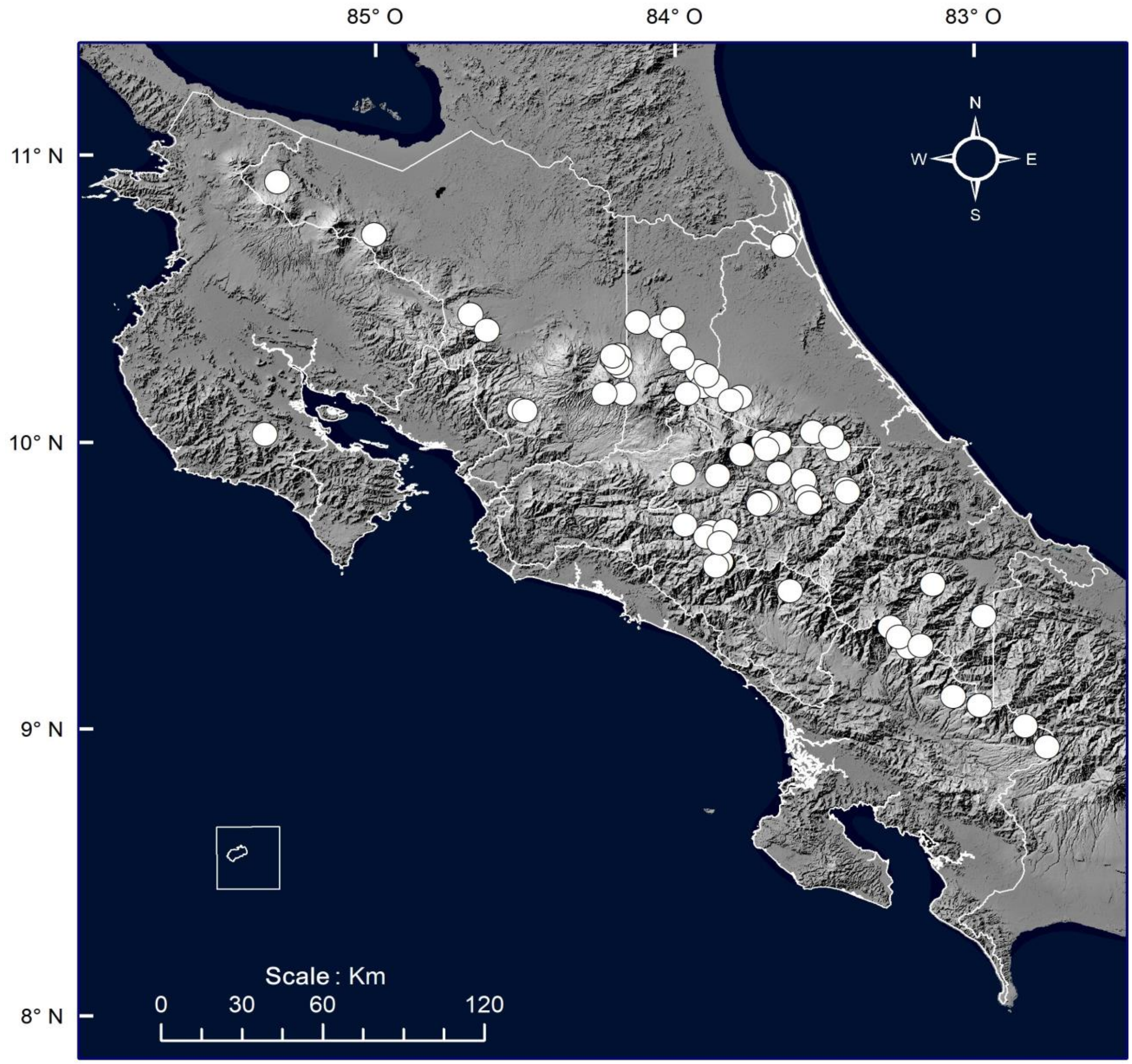

Figure 4. *Myoxanthus* collections sites in Costa Rica.

Figure 5. Basal (bottom) and apical (top) ramicauls' sheaths of the Costa Rican *Myoxanthus*. A. *M. affinis* (*Karremans 6690*). B. *M. cereus* (*Karremans 5693*). C. *M. colothrix* (*Rojas-Alvarado 6*). D. *M. congestus* (*Karremans 5281*). E. *M.* parahybunensis (*Pupulin 7078*). F. *M. hirsuticaulis* (*Bogarín 5872*). G. *M. scandens* (*Pupulin 837*). H. *M. sotoanus* (*Karremans 7322*). I. *M. exasperatus* (*Rojas-Alvarado 42*). J. *M. trachychlamys* (*Rojas-Alvarado 27*).

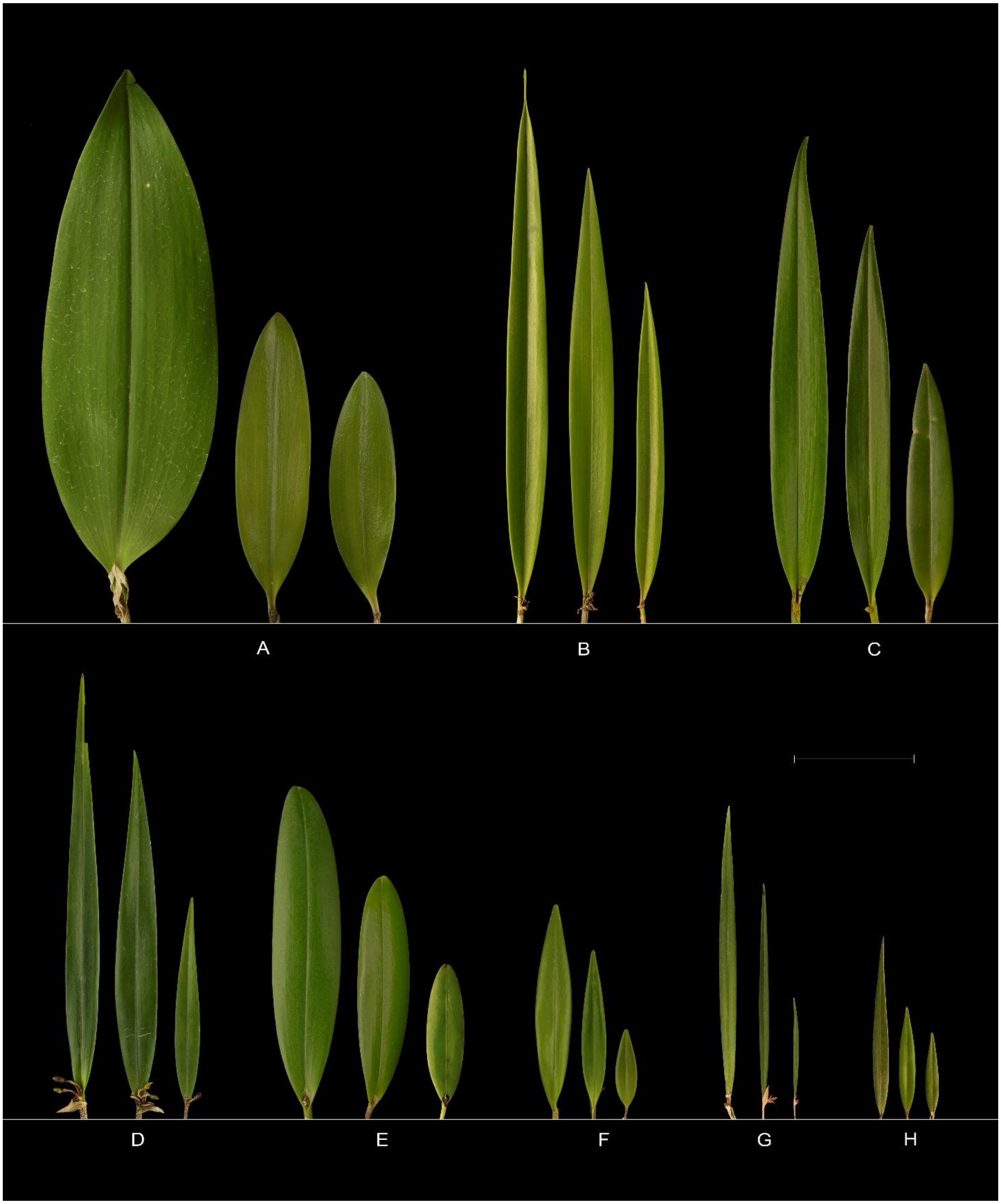

Figure 6. Extremes and intermediate leave variation of the Costa Rican *Myoxanthus*. A. *M. cereus*. B. *M. parahybunensis*. C. *M. colothrix*. D. *M. hirsuticaulis*. E. *M. congestus*. F. *M. trachychlamys* . G. *M. sotoanus*. H. *M. scandens*. Scale bar = 5 cm.

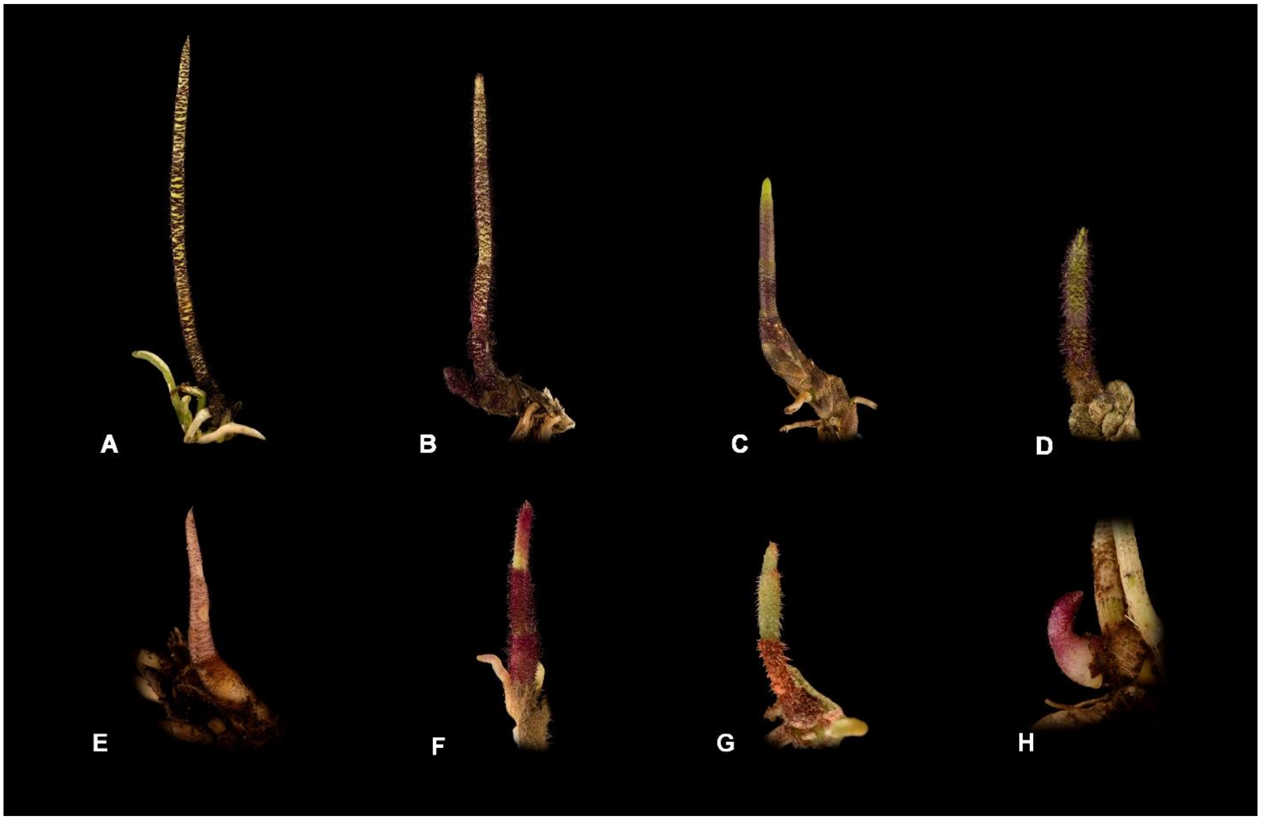

Figure 7. Sheaths over young ramicauls of the Costa Rican *Myoxanthus*. A. *M. affinis* (*Karremans 6990*). B. *M. colothrix* (*Rojas-Alvarado 6*). C. *M. parahybunensis* (*Karremans 6661*). D. *M. exasperatus* (*Rojas-Alvarado 36*). E. *M. sotoanus* (*Karremans 7322*). F. *M. trachychlamys* (*Rojas-Alvarado 79*). G. *M. scandens* (*Pupulin 837*). H. *M. congestus* (*Karremans 1300*).

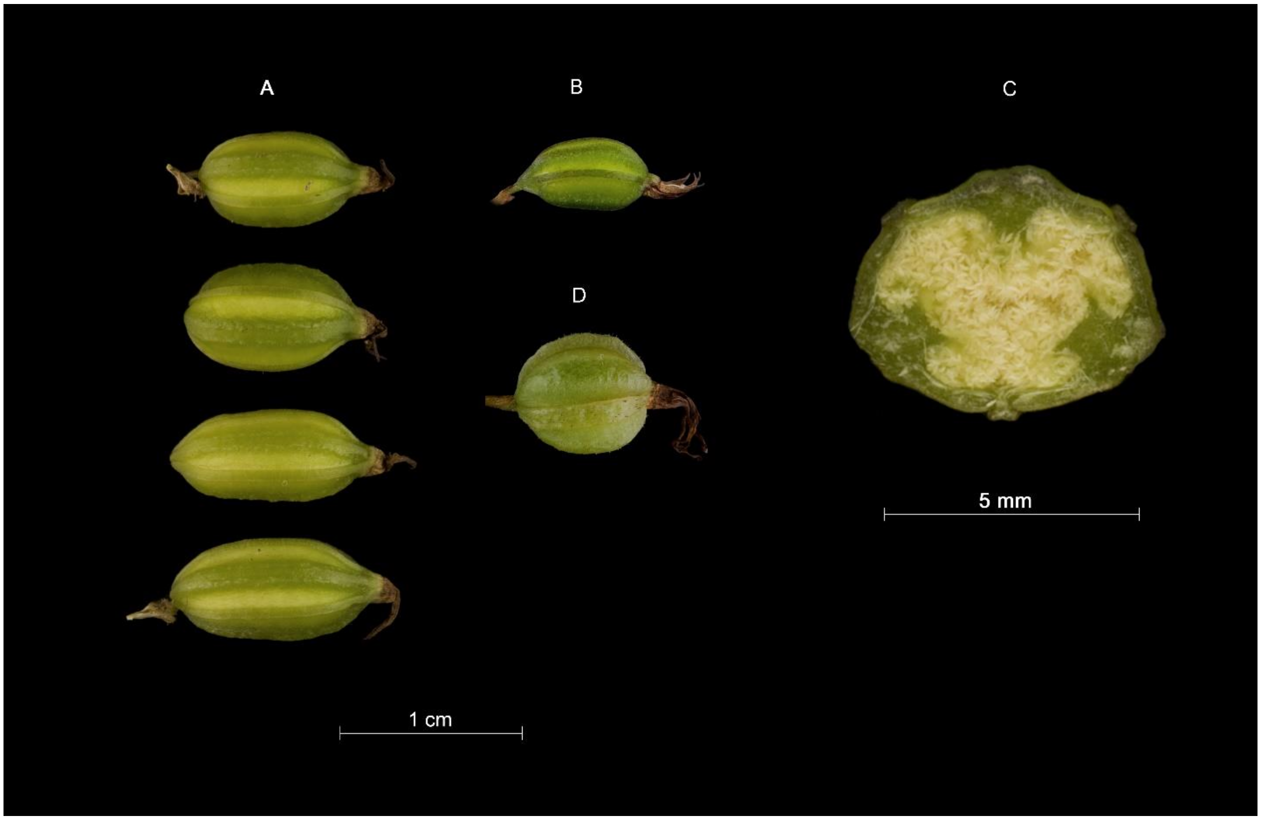

Figure 8. Fruits of *Myoxanthus*. A & C. *M. trachychlamys* (*Rojas-Alvarado 168*). B. *M. sotoanus* (*Karremans 7322*). D. *M. parahybunensis* (*Bogarín 10276*).

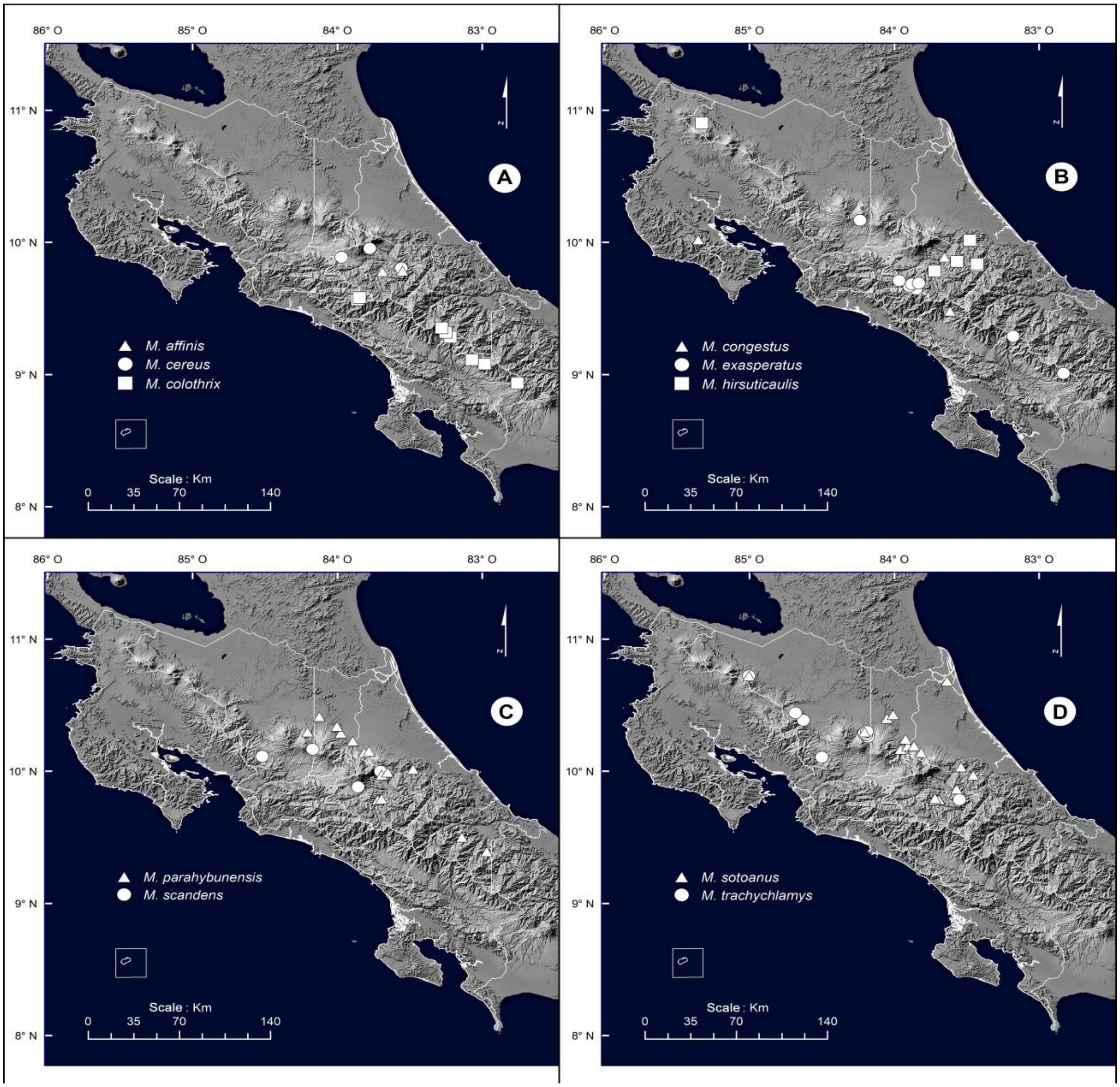

Figure 9. Distribution of *Myoxanthus* species in Costa Rica. A. *Myoxanthus affinis*, *M. cereus* and *M. colothrix*. B. *Myoxanthus congestus*, *M. exasperatus* and *M. hirsuticaulis*. C. *Myoxanthus parahybunensis* and *M. scandens*. C. *Myoxanthus sotoanus* and *M. trachychlamys*.

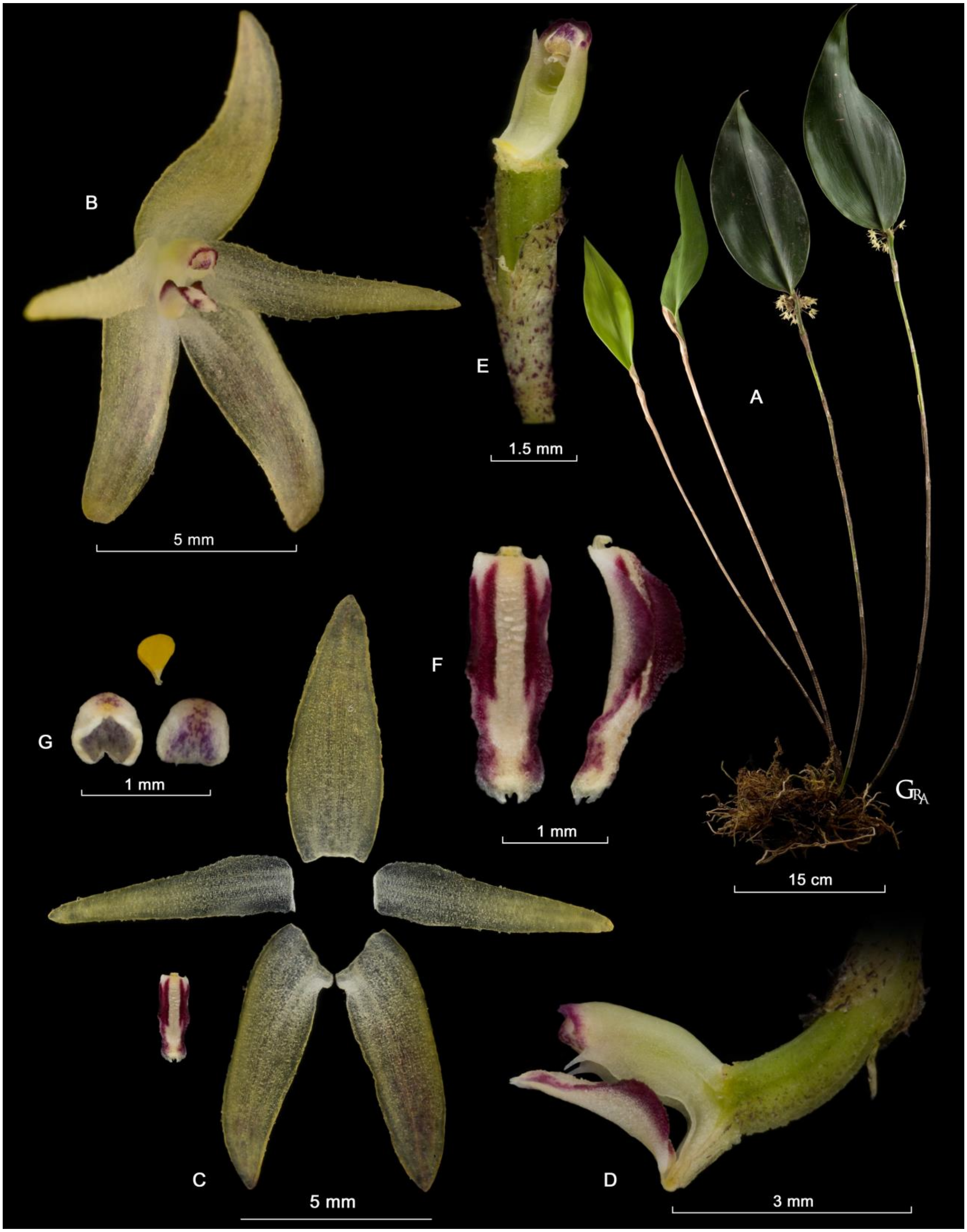

Figure 10. Lankester composite dissection plate (LCDP) of *Myoxanthus affinis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial and lateral view. G. Pollinia and anther cap. Based on *Karremans 6990* (JBL-spirit).

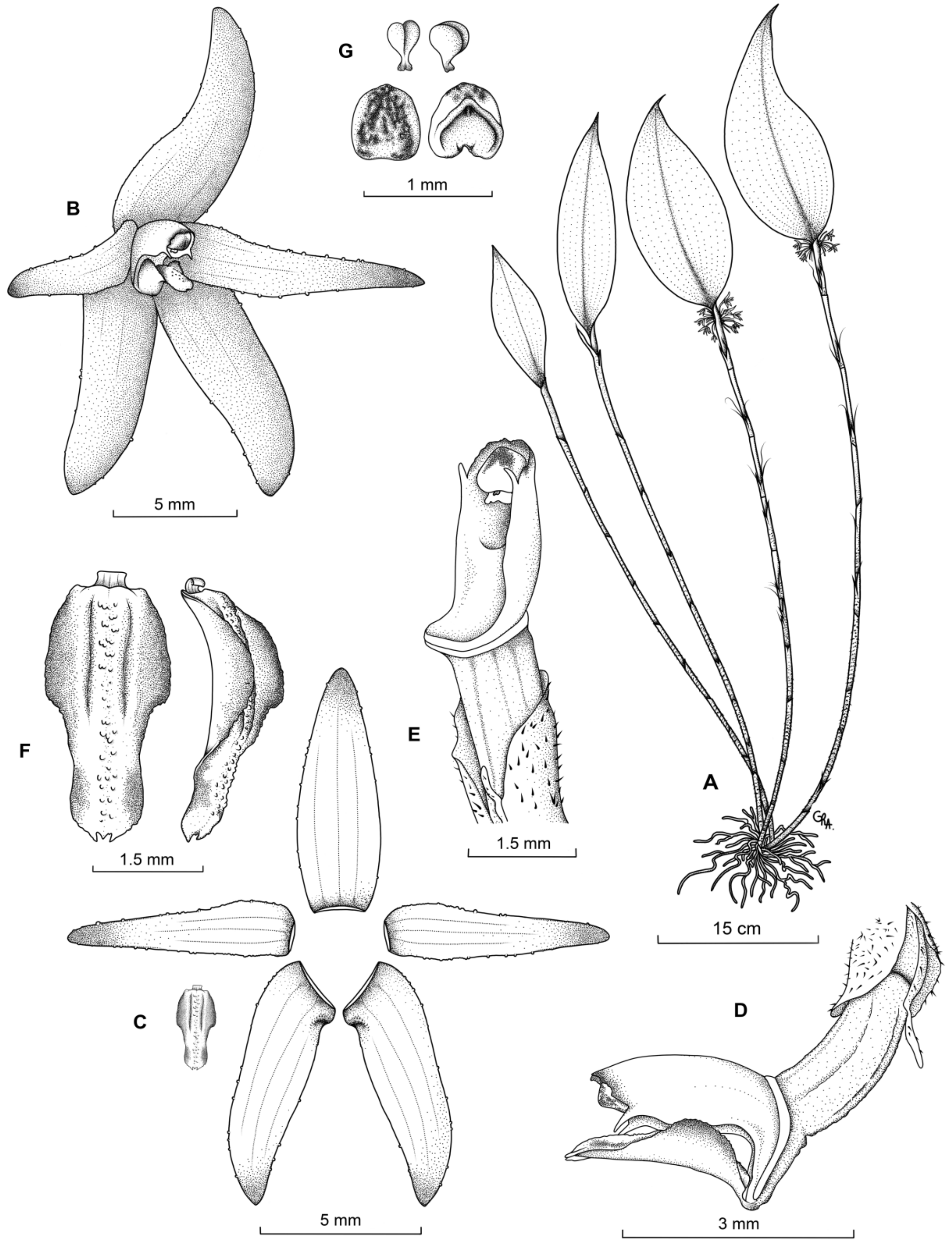

Figure 11. Illustration of *Myoxanthus affinis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial and lateral view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 6990* (JBL-spirit).

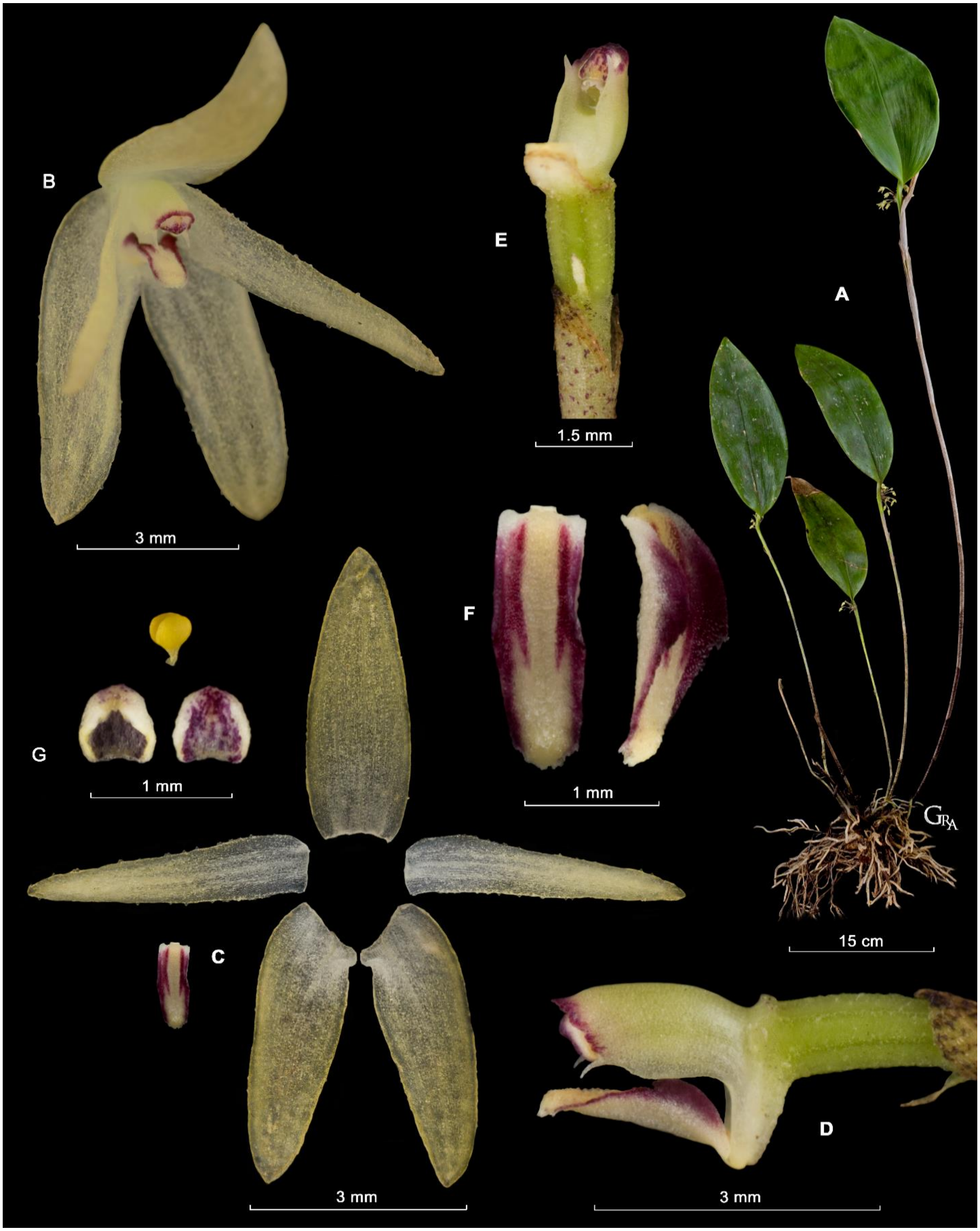

Figure 12. LCDP of *Myoxanthus affinis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial and lateral view. G. Pollinia and anther cap. Based on *Karremans 6990* (JBL-spirit).

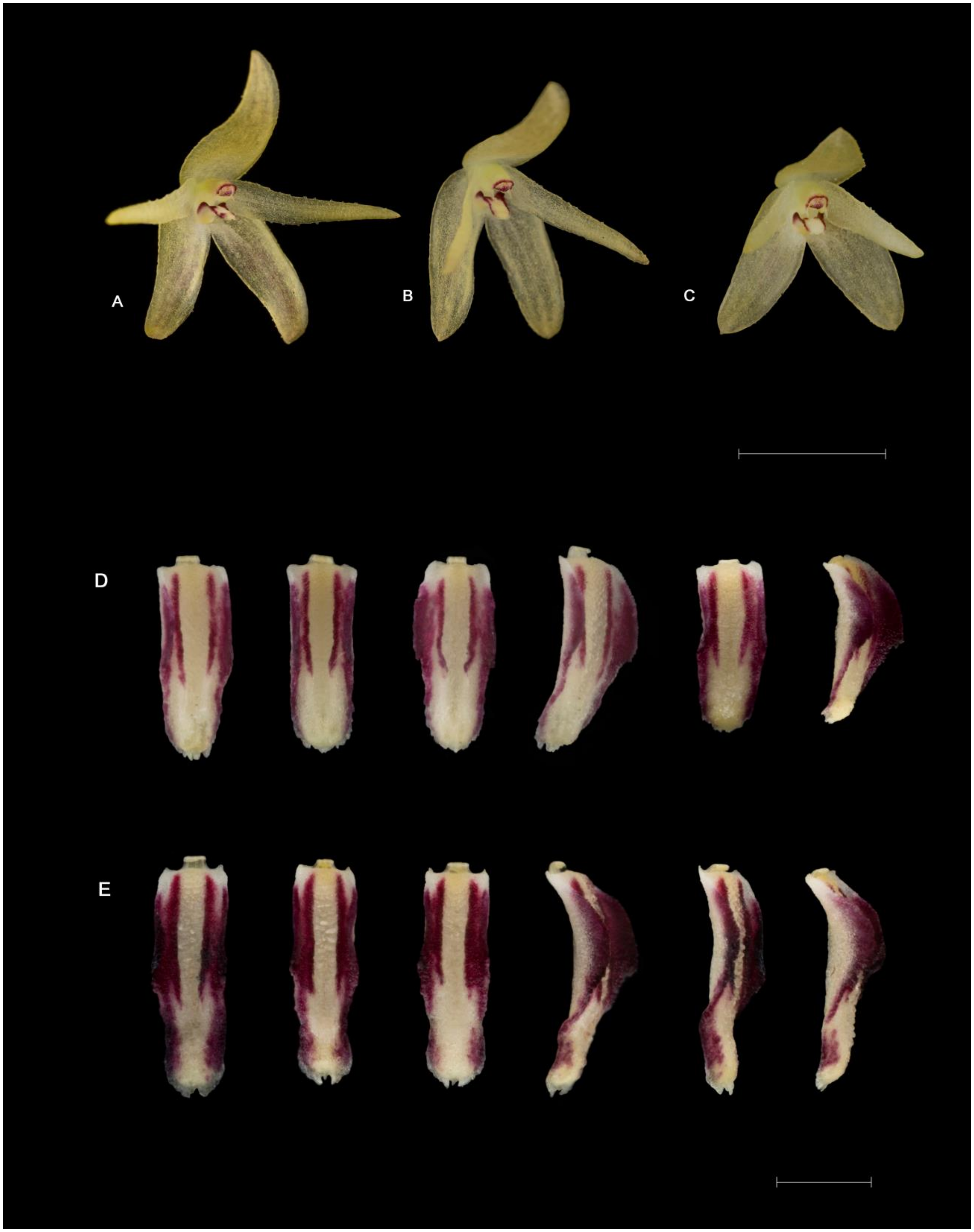

Figure 13. Variation in flower and lip morphology of *Myoxanthus affinis*. A. *Karremans 6990*. B. *Rojas-Alvarado 69*. C. *Rojas-Alvarado 69*. D. *Rojas-Alvarado 69*. E. *Karremans 6990*. Flowers scale bar = 5 mm, lips scale bar = 1 mm.

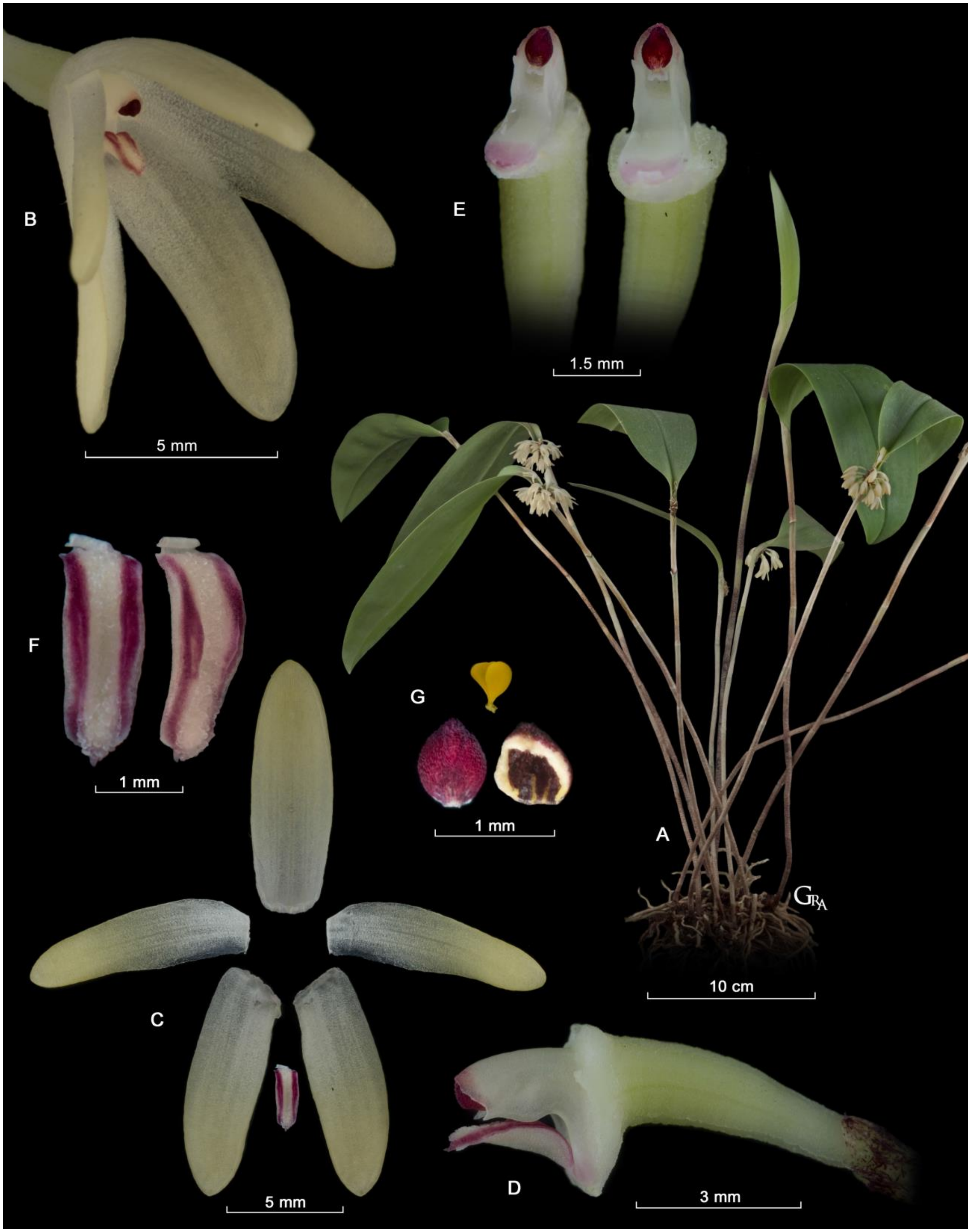

Figure 14. LCDP of *Myoxanthus cereus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Karremans 5693* (JBL-spirit).

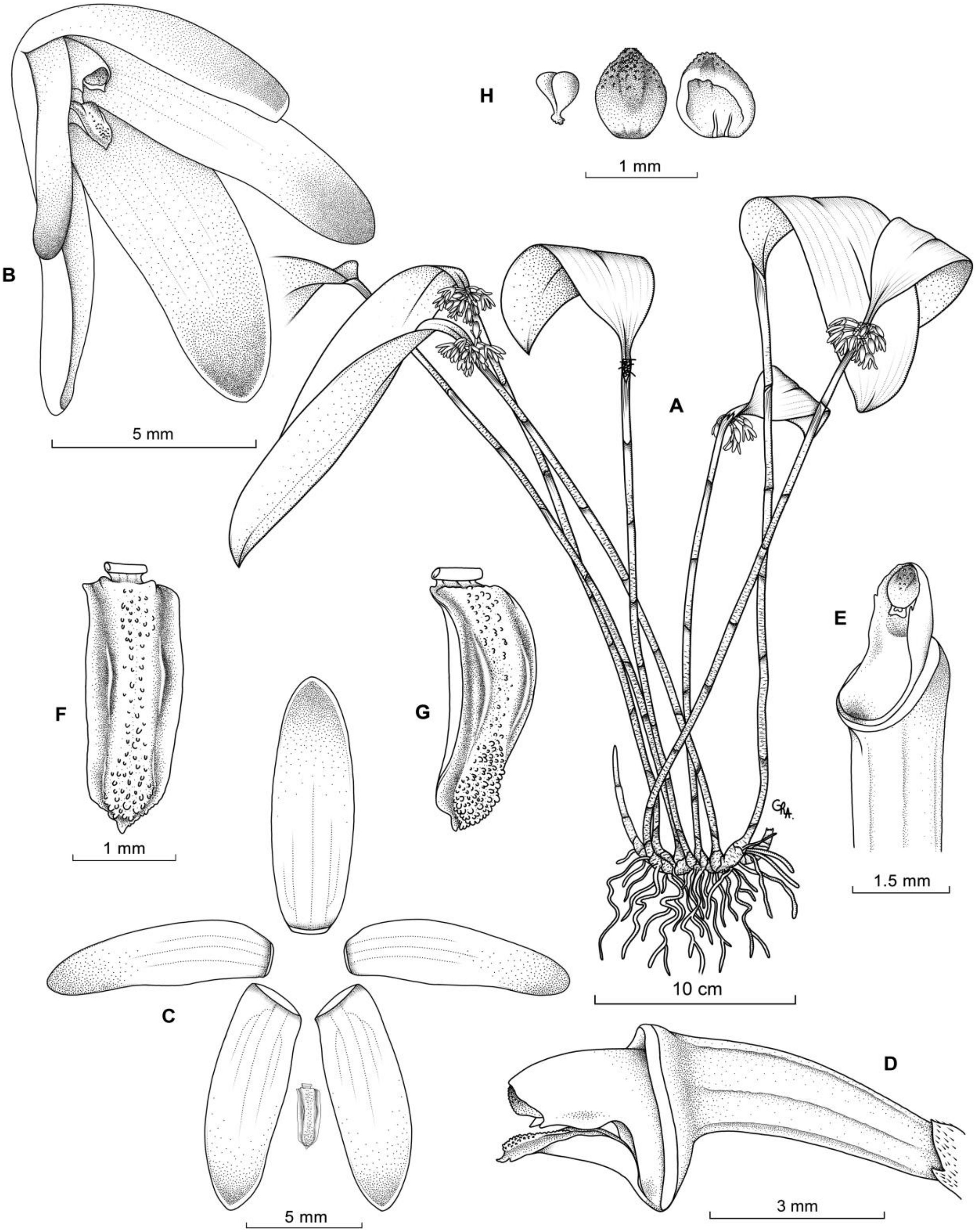

Figure 15. Illustration of *Myoxanthus cereus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F & G. Lip in adaxial view. H. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 5693* (JBL-spirit).

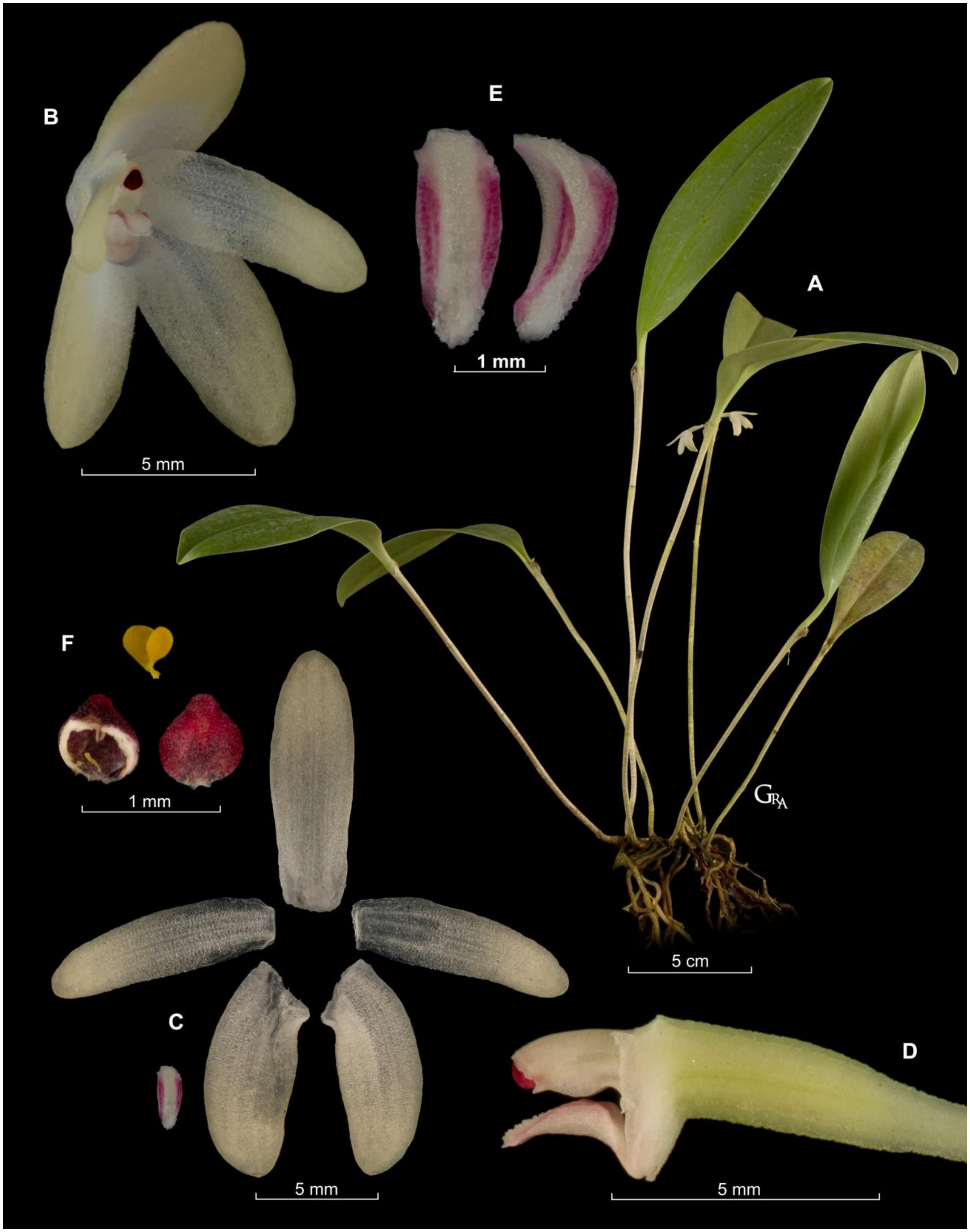

Figure 16. LCDP of *Myoxanthus cereus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Lip in adaxial view. F. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 5868* (JBL-spirit).

Figure 17. Variation of the flowers in *Myoxanthus cereus*. A. *Karremans 5693*. B. *Karremans 5868*. Scale bar = 5 mm.

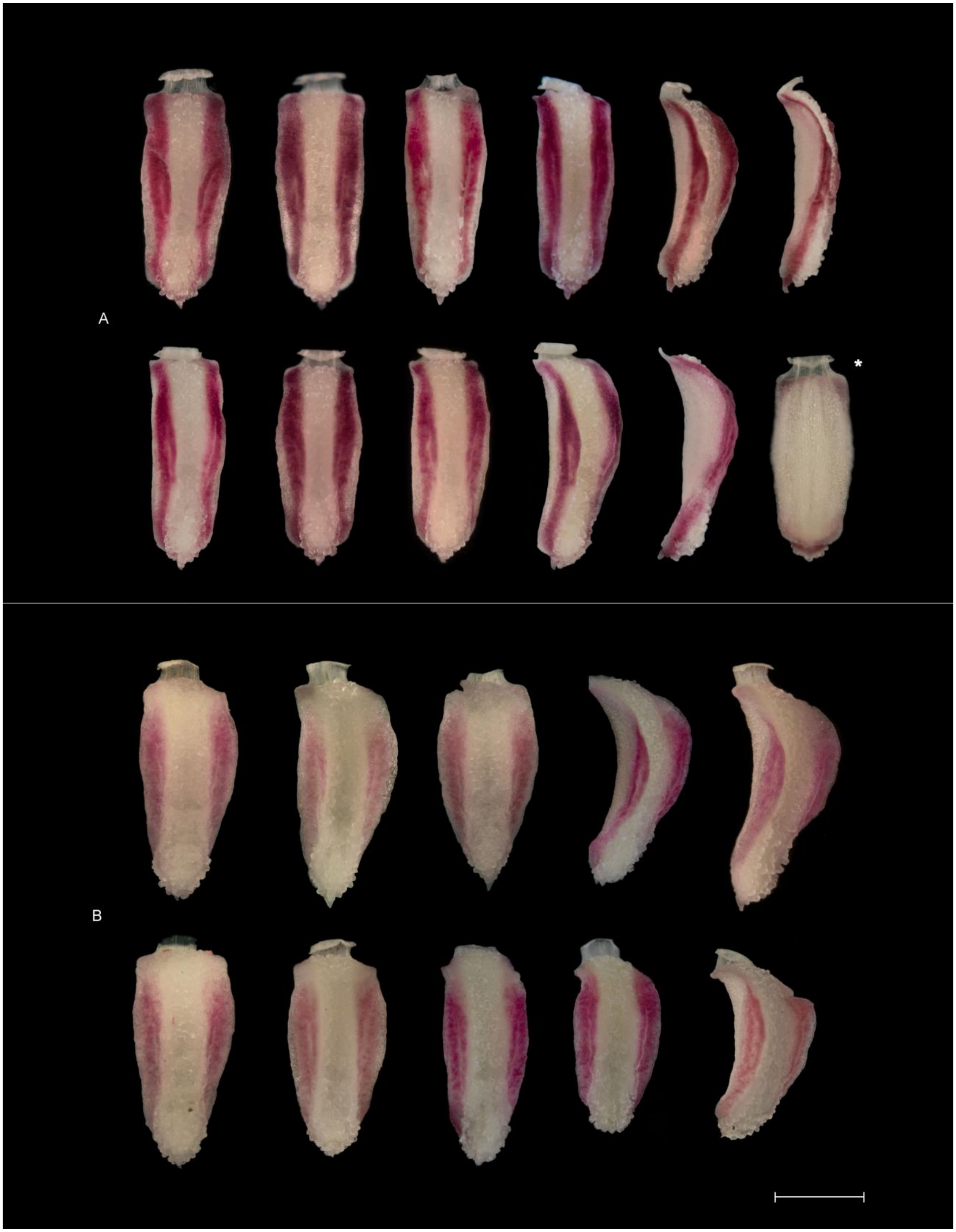

Figure 18. Variation of the lips in *M. cereus*. A. *Karremans 5693*. B. *Karremans 5868*. Scale bar = 1 mm, *abaxial view.

Figure 19. *Myoxanthus congestus* group. A. *Myoxanthus cereus* (Costa Rica). B. *Myoxanthus congestus* (Costa Rica). C. *M. octomerioides* (Mexico). D. *M. pulvinatus* (Brazil). Photographs: A & B, the authors; R. Solano-Gómez (C), M. Rosim (D).

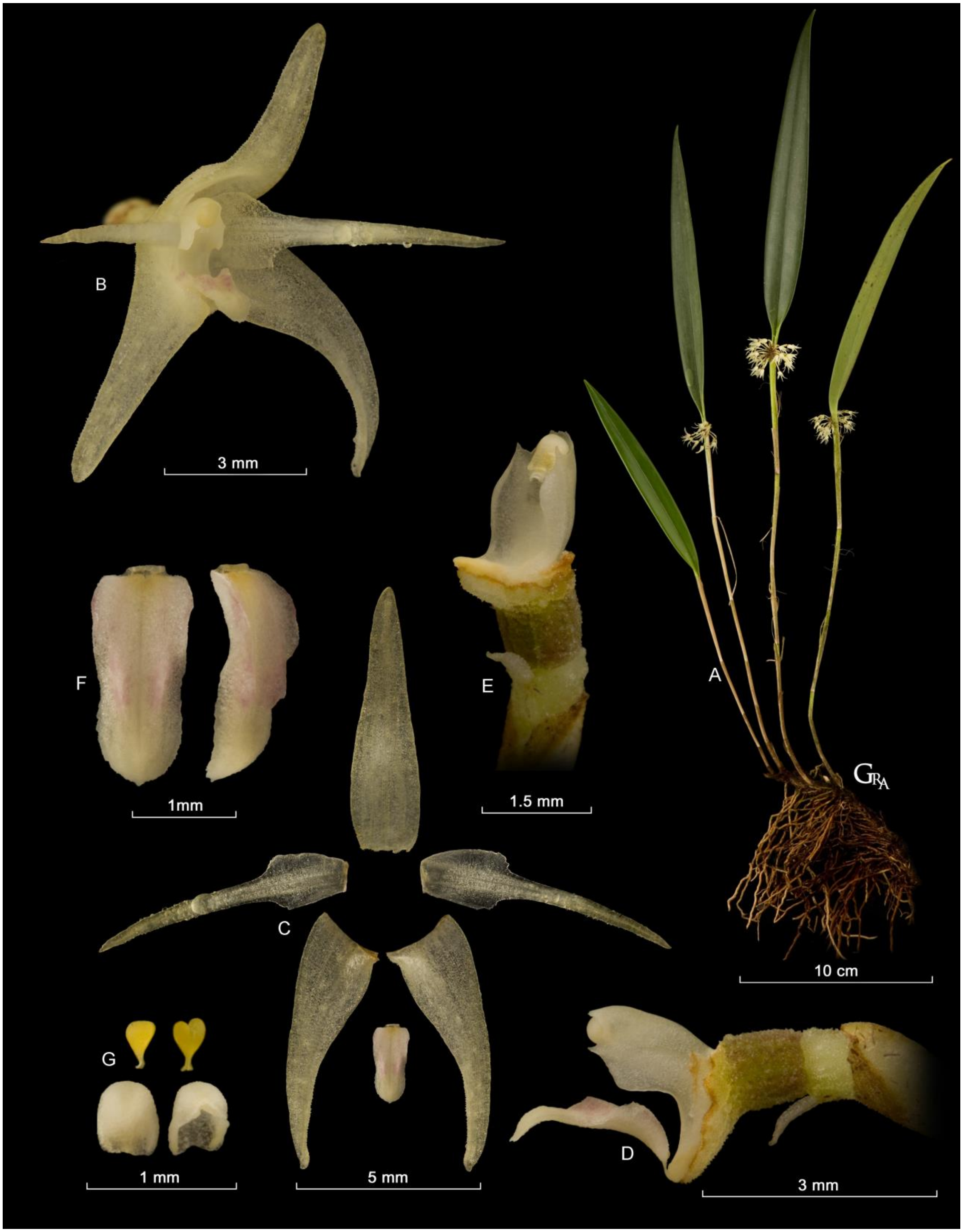

Figure 20. LCDP of *Myoxanthus colothrix*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Rojas-Alvarado 3* (JBL-spirit).

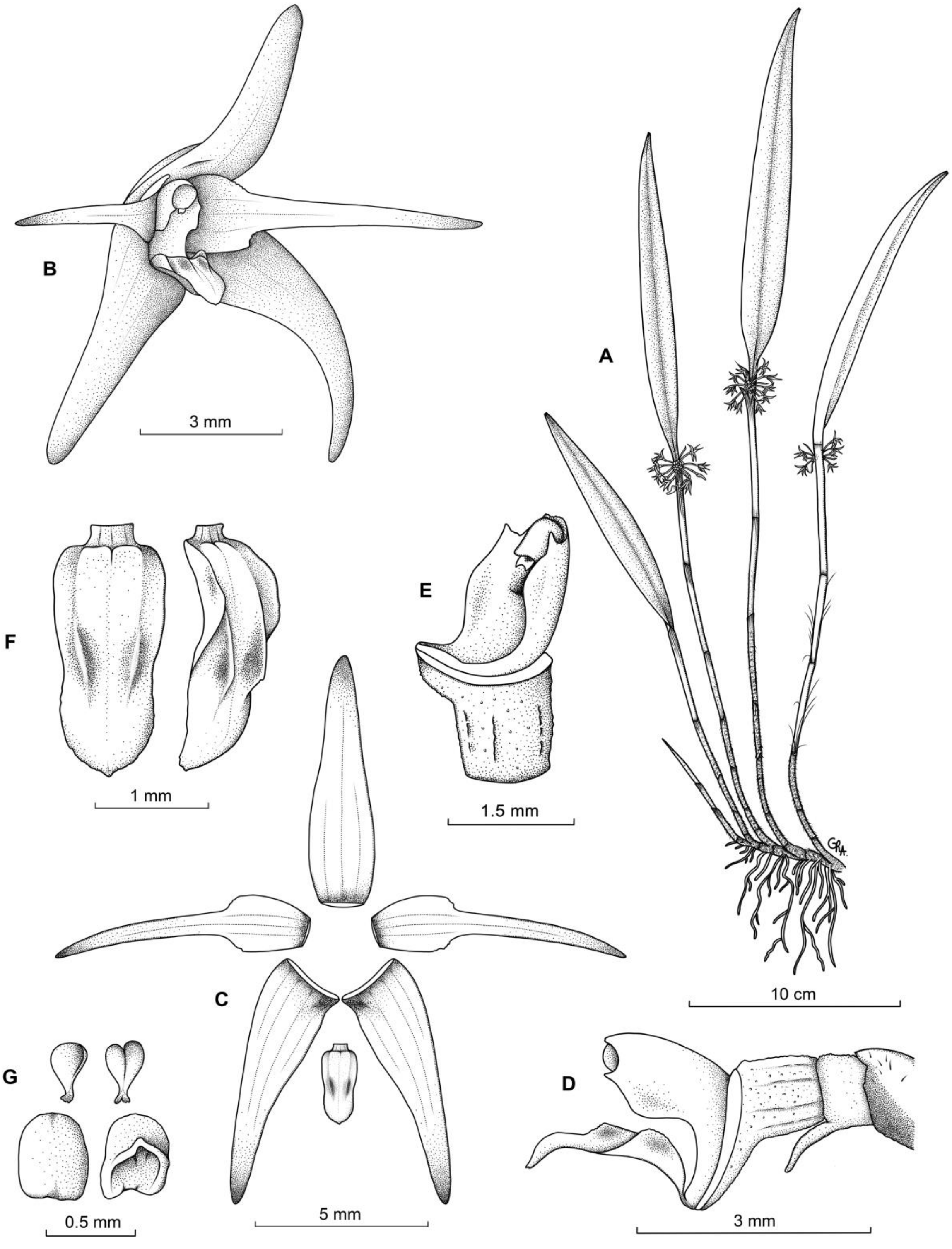

Figure 21. Illustration of *Myoxanthus colothrix*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Rojas-Alvarado 3* (JBL-spirit).

Figure 22. Variation of flowers of *Myoxanthus colothrix*. A. *Bogarín 7689*. B & D. *Rojas-Alvarado 3*. *C. Rojas-Alvarado 6*. Scale bar = 5 mm. Scale bar = 5 mm.

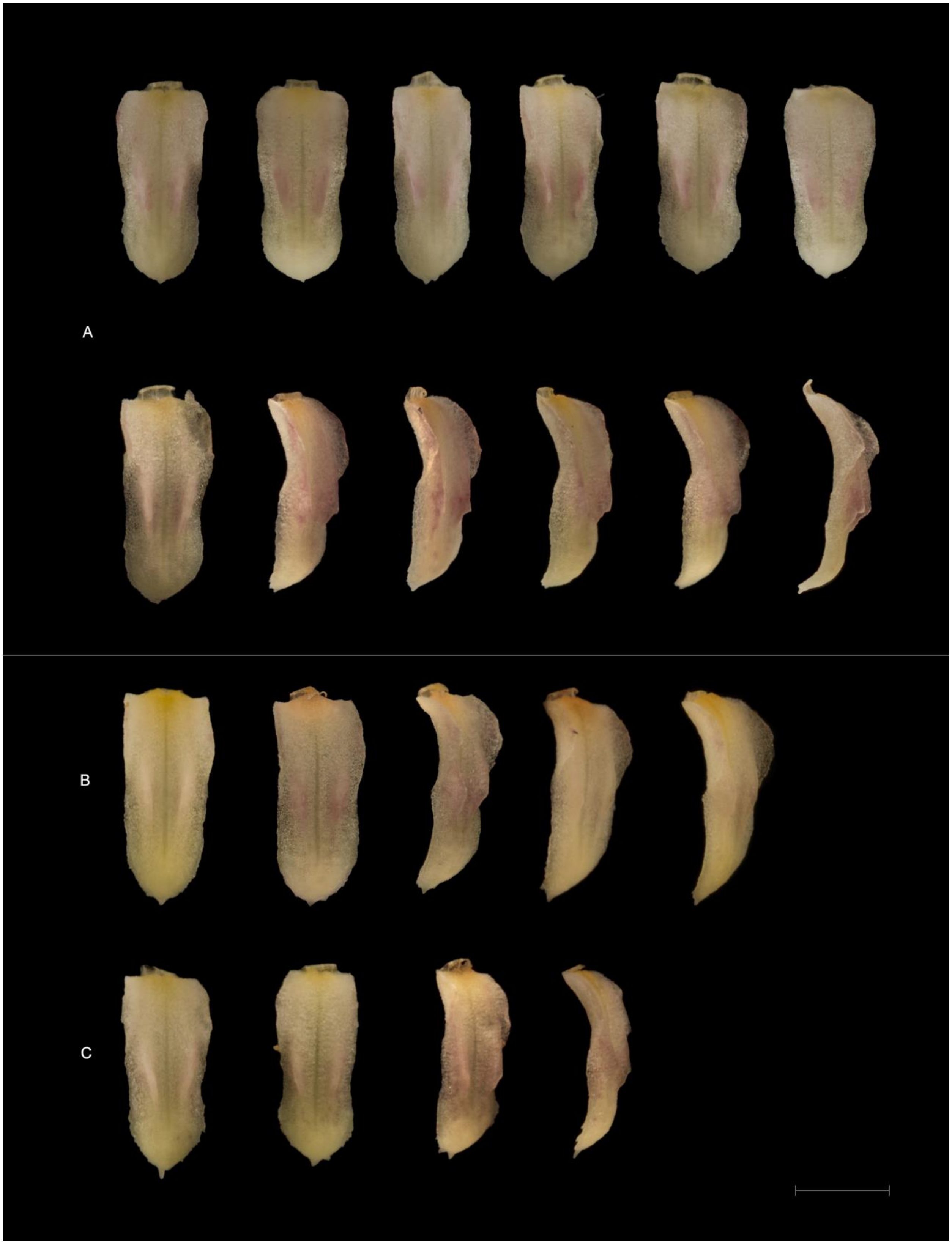

Figure 23. Variation in lips in *Myoxanthus colothrix*. A. *Rojas-Alvarado 3*. B. *Bogarín 7689*. C. *Rojas-Alvarado 6*. Scale bar = 1 mm.

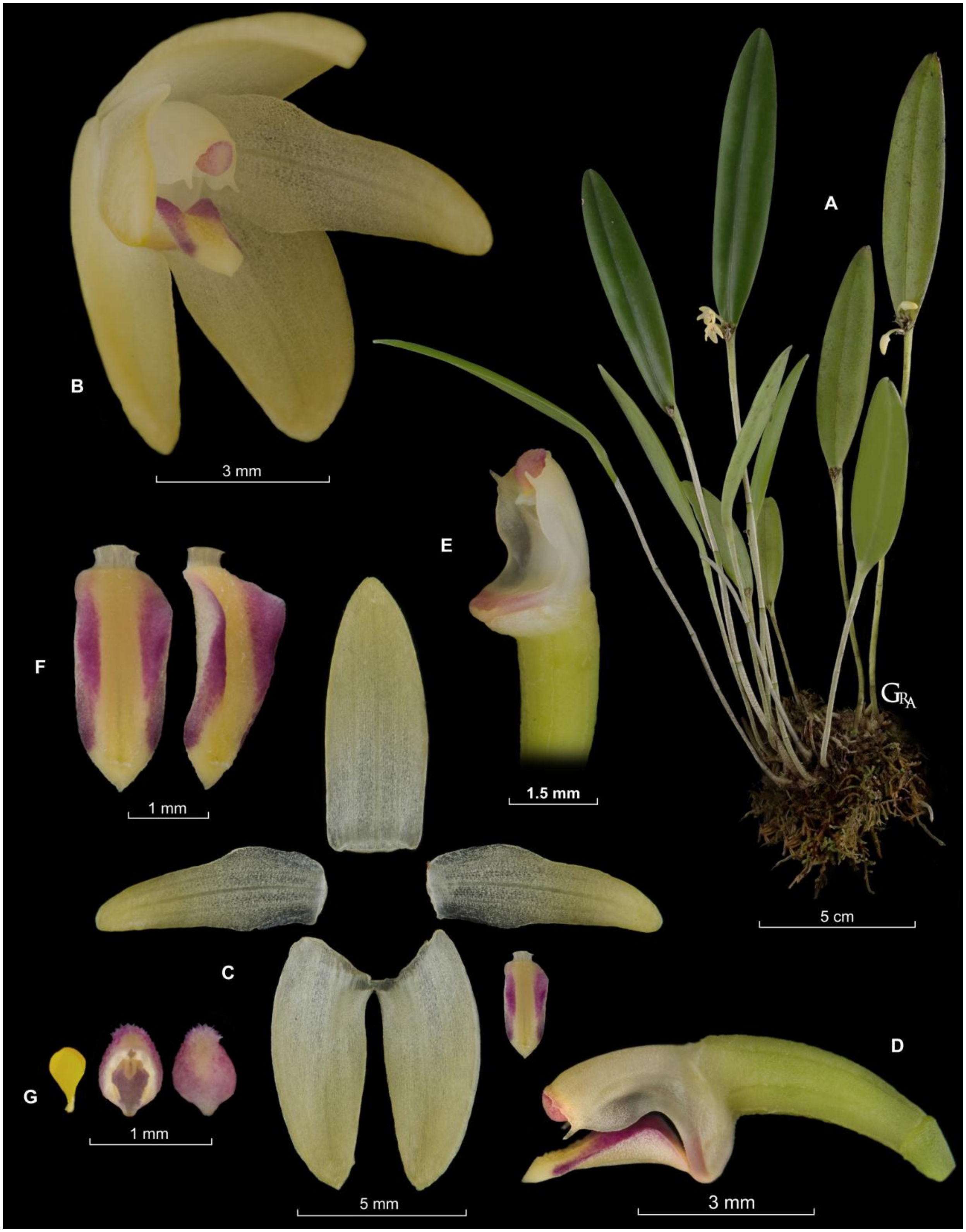

Figure 24. LCDP of *Myoxanthus congestus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Karremans 1300* (JBL-spirit).

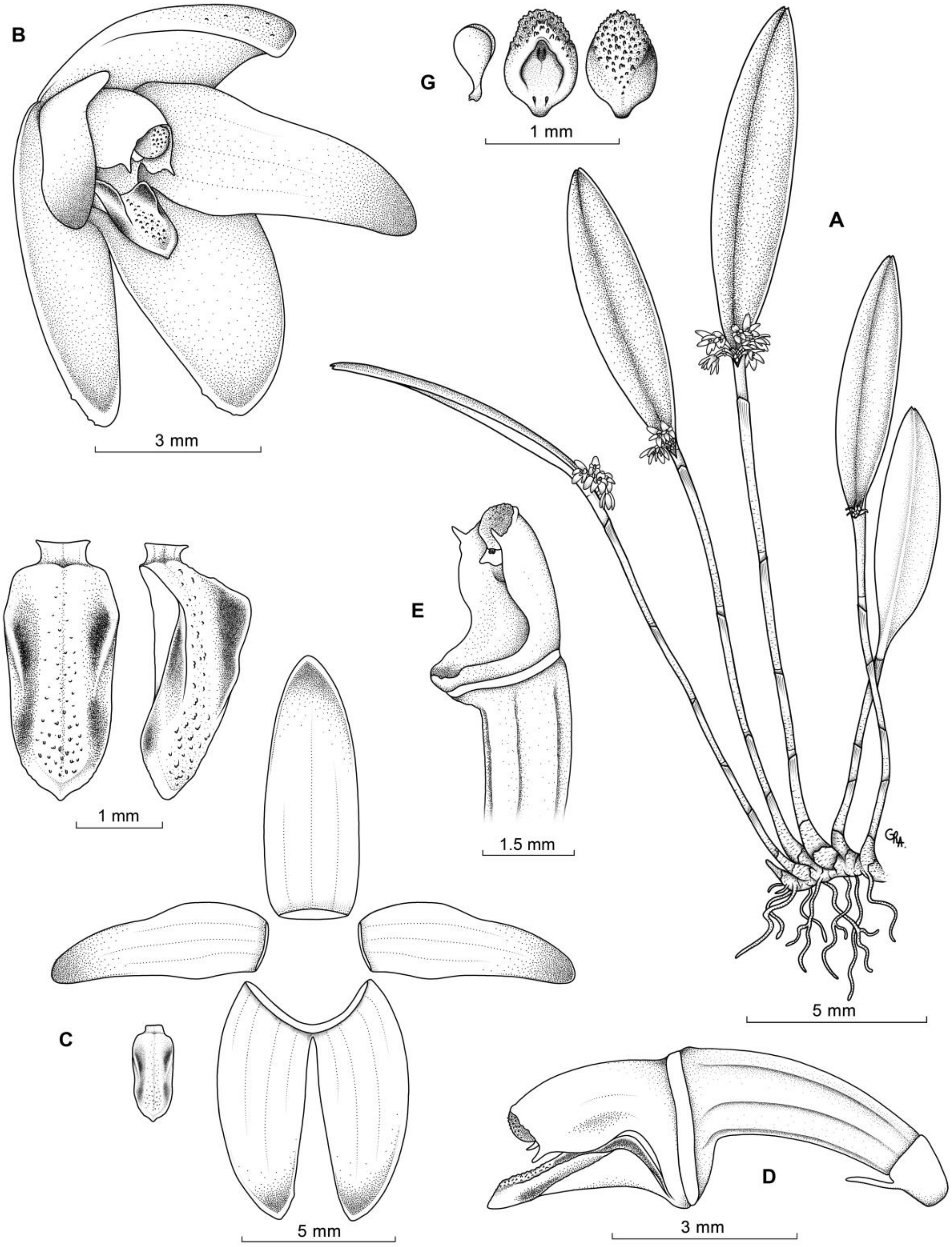

Figure 25. *Myoxanthus congestus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 1300* (JBL-spirit).

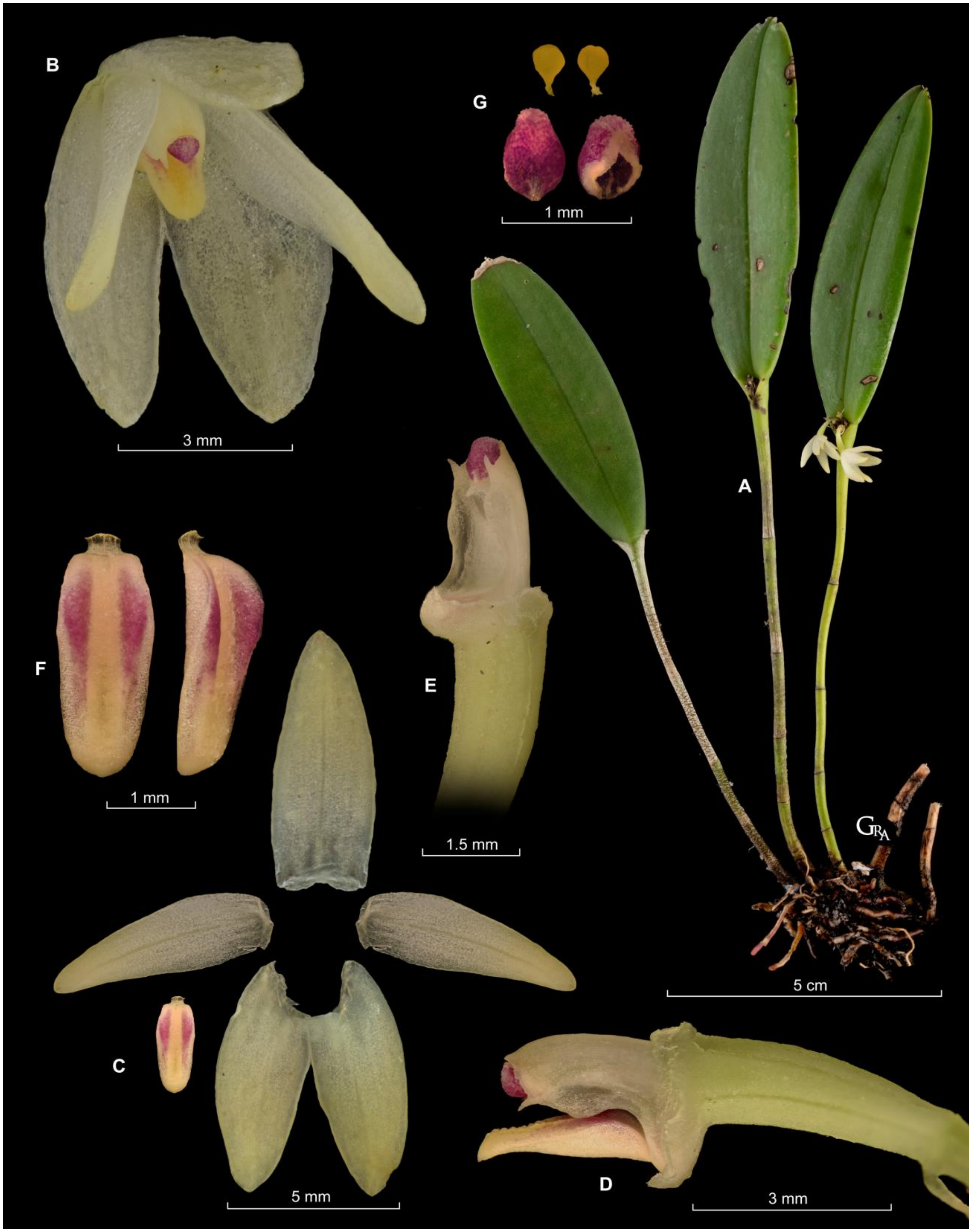

Figure 26. LCDP of *Myoxanthus congestus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Rojas-Alvarado 401* (JBL-spirit).

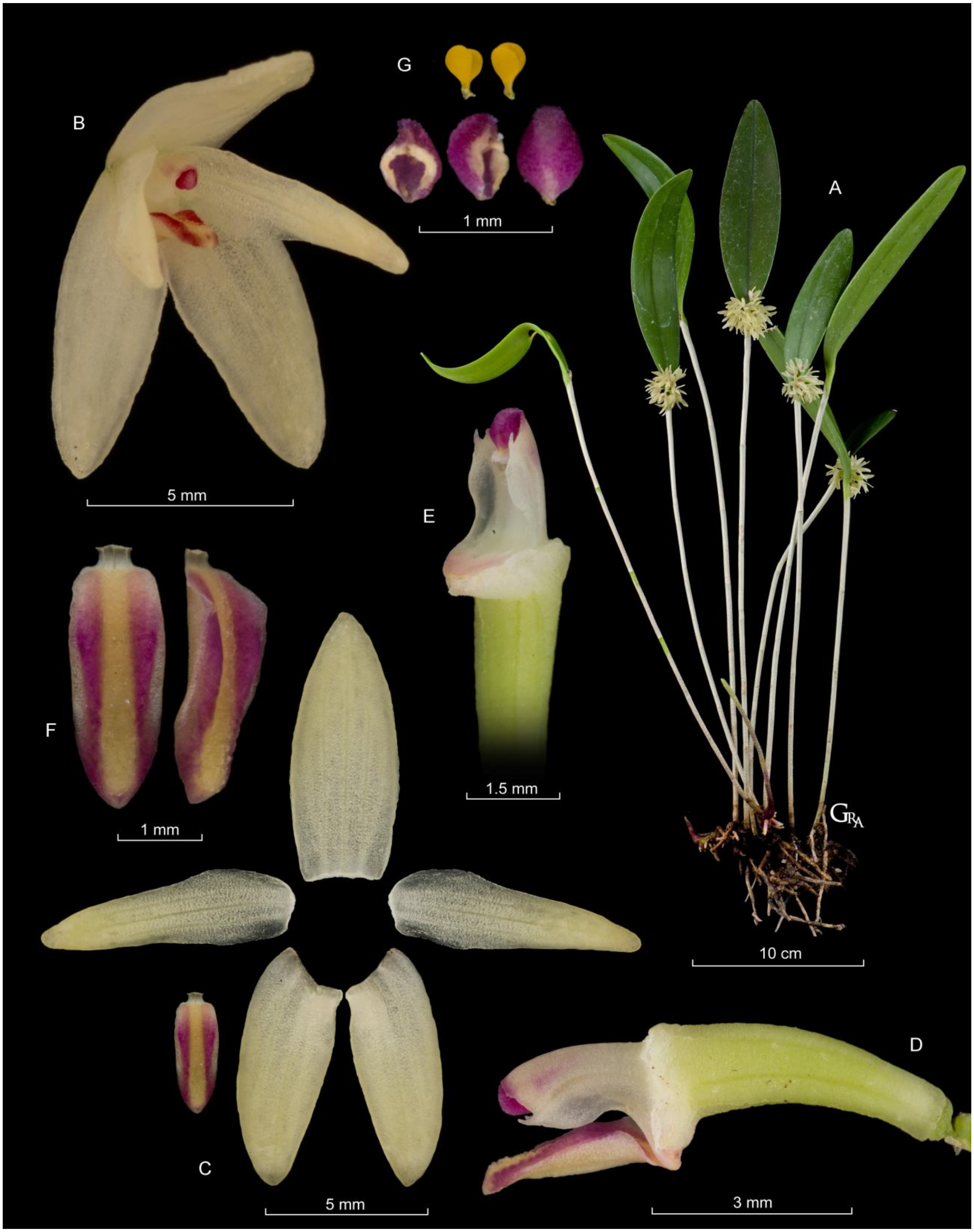

Figure 27. LCDP of *Myoxanthus congestus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Karremans 5281* (JBL-spirit).

Figure 28. Variation in flowers and columns of *Myoxanthus congestus*. A. *Karremans 1300*. B. *Rojas-Alvarado 404*. C. *Karremans 5281*. D. *Rojas-Alvarado 402*. Flowers scale bar = 5 mm; columns scale bar = 3 mm.

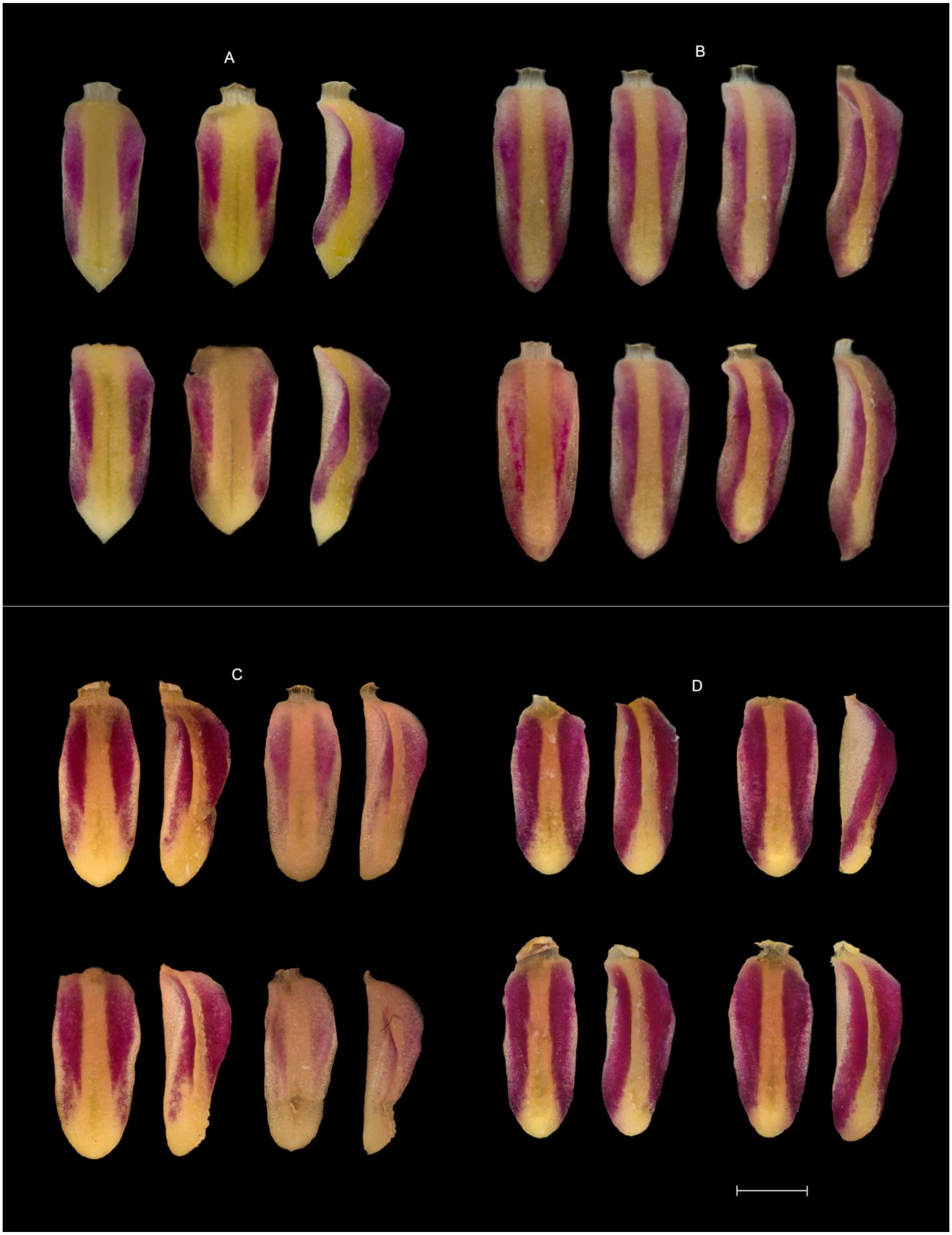

Figure 29. Variation in lips of *Myoxanthus congestus*. A. *Karremans 1300*. B. *Karremans 5281*. C. *Rojas-Alvarado 401*. D. *Rojas-Alvarado 404*. Scale bar = 1 mm.

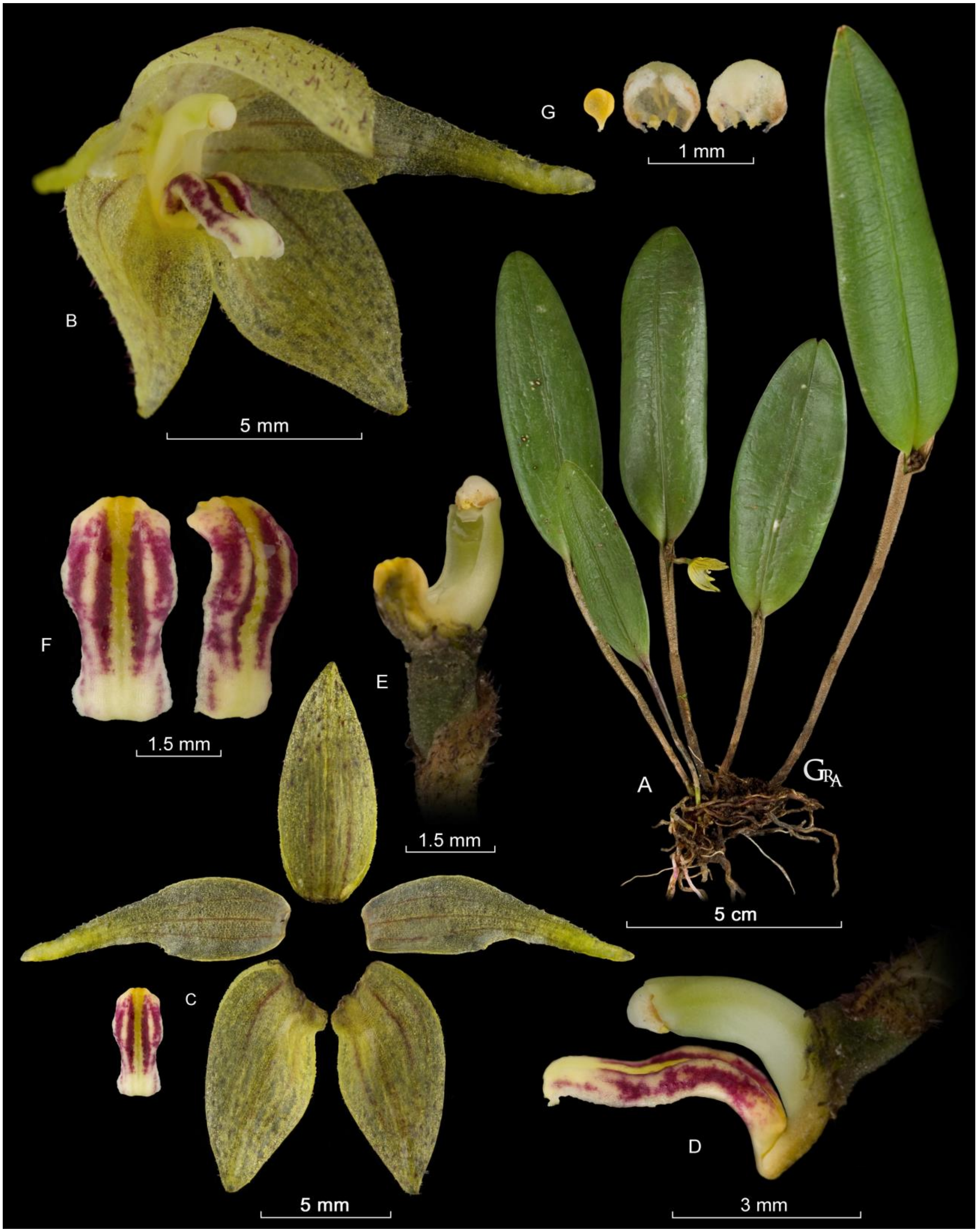

Figure 30. LCDP of *Myoxanthus exasperatus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Rojas-Alvarado 42* (JBL-spirit).

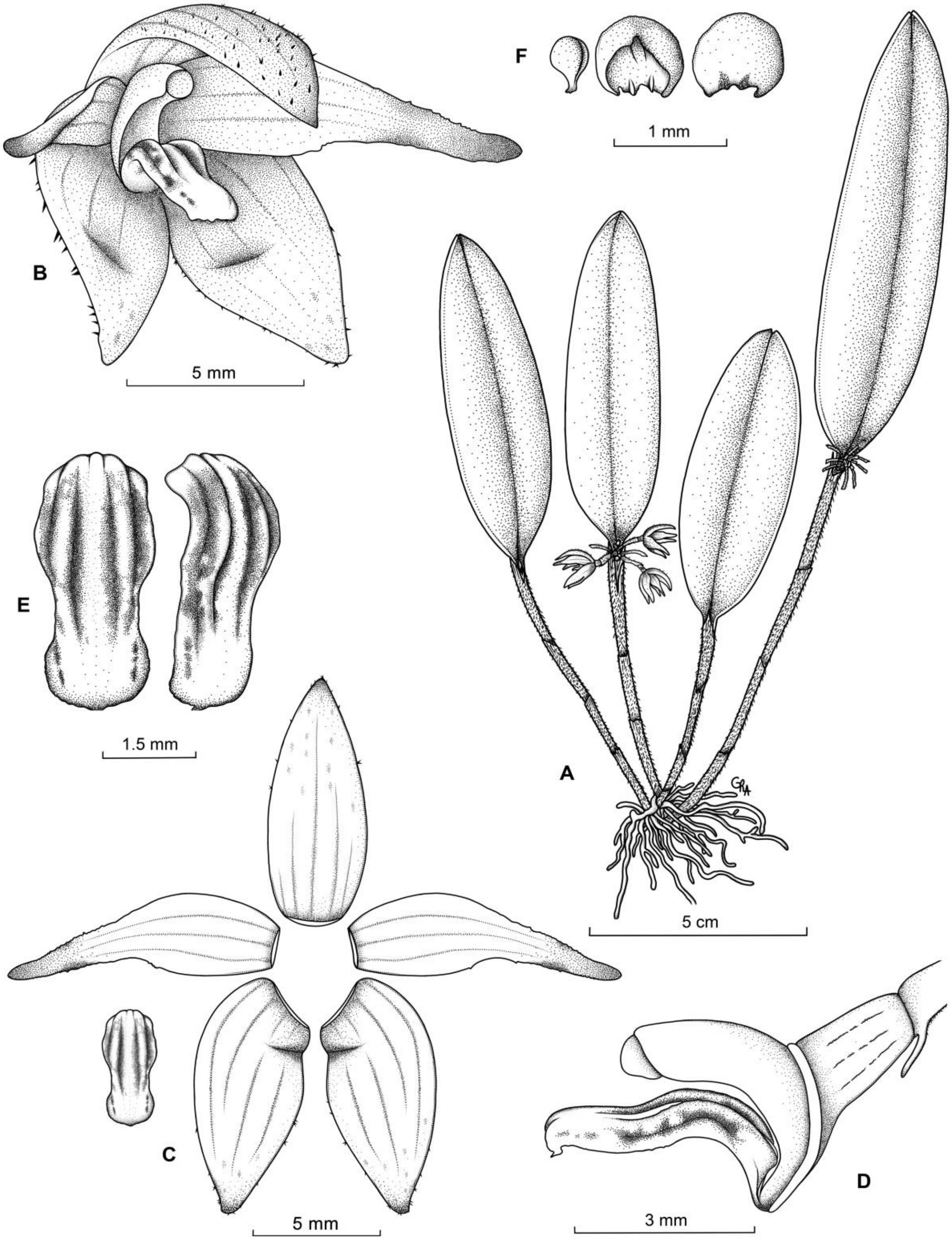

Figure 31. *Myoxanthus exasperatus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Lip in adaxial view. F. Pollinia and anther cap. By G. Rojas-Alvarado based on *Rojas-Alvarado 42* (JBL-spirit).

Figure 32. Variation in flowers and lips of *Myoxanthus exasperatus*. A. *Rojas-Alvarado 42*. B. *Rojas-Alvarado 36*. Flower scale bar = 5 mm; lip scale bar = 1 mm.

Figure 33. A. Type of *Pleurothallis peduncularis* (000820789, K). B. Illustration of *P. peduncularis* in Dunsterville & Garay (1961). C. Lectotype of *Anathallis parahybunensis*. D. Type of *Pleurothallis exasperata* (000820790, K). Reproduced with the kind permission of the of the Director, Harvard University Herbaria, and the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 34. LCDP of *Myoxanthus hirsuticaulis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view and column in ventral view. E. Lip in adaxial view. F. Pollinia and anther cap. Based on *Karremans 7185* (JBL-spirit).

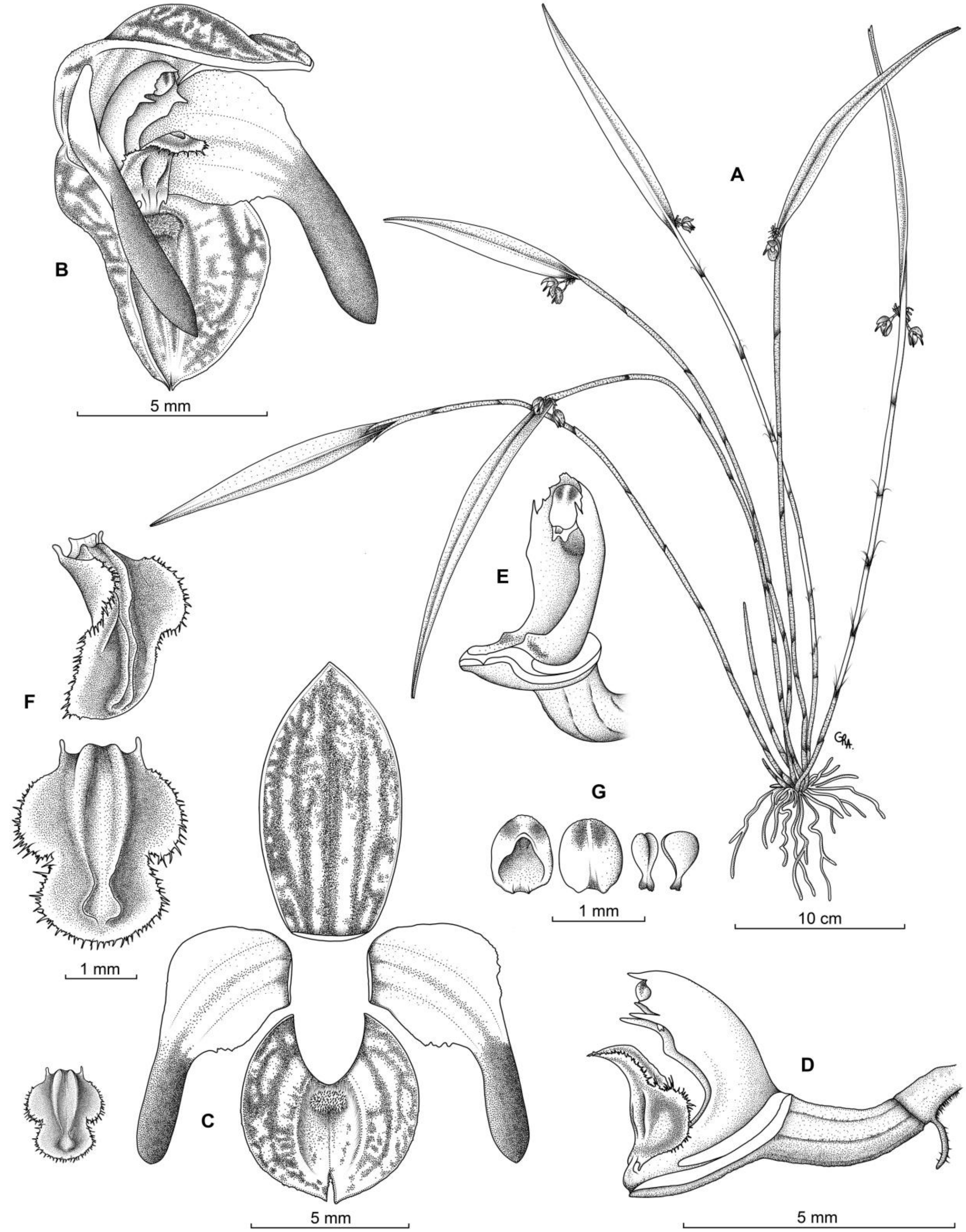

Figure 35. *Myoxanthus hirsuticaulis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 7185* (JBL-spirit).

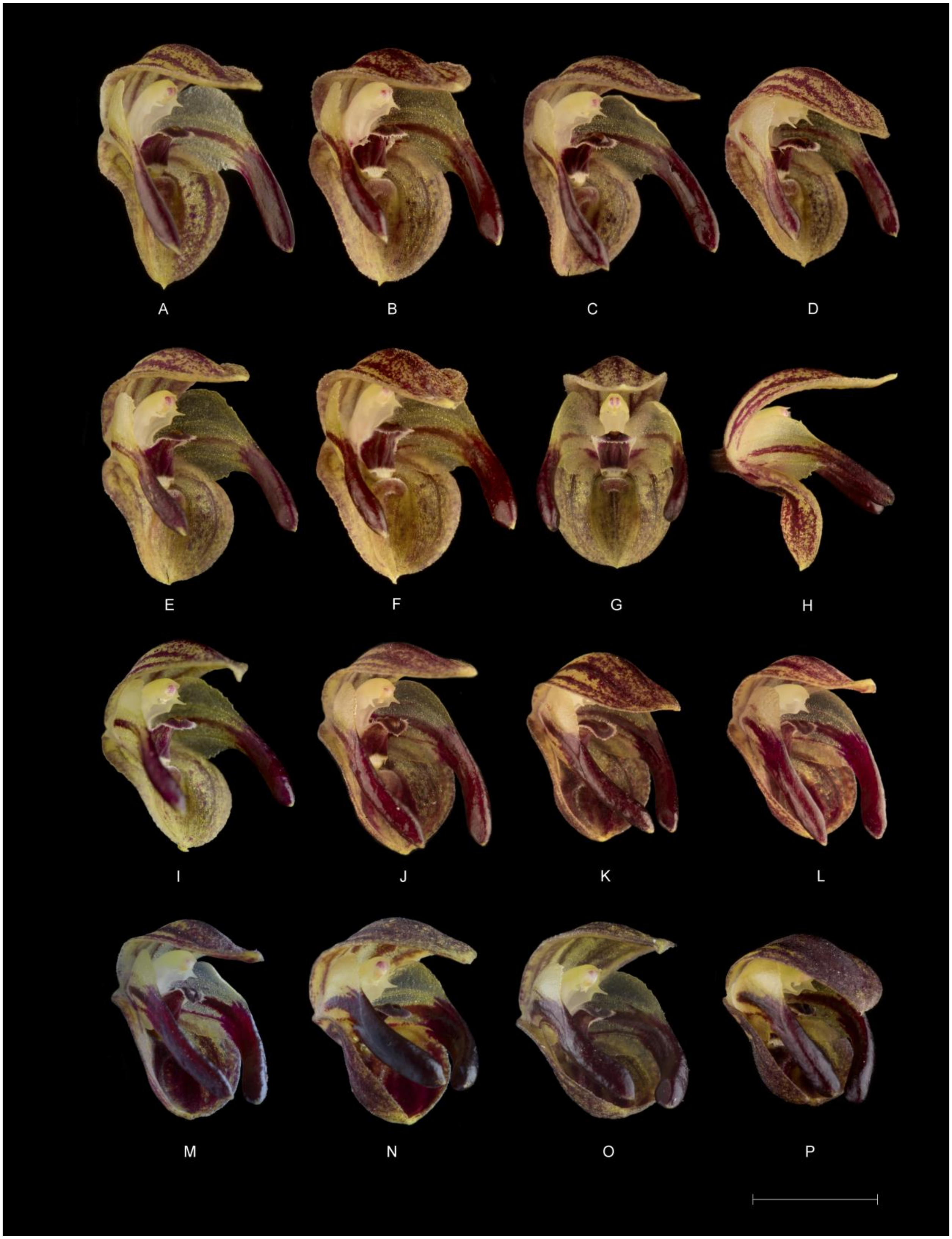

Figure 36. Variation in flowers of *Myoxanthus hirsuticaulis*. A–I. *Karremans 7185.* J–M. *Bogarín 5872*. N. *Bogarín 5869*. O. *Bogarín 5875*. P. *Bogarín 5856.* Scale bar = 5 mm.

Figure 37. Variation in lip of *Myoxanthus hirsuticaulis*. A. *Karremans 7185.* B. *Bogarín 5872*. Scale bar = 1 mm.

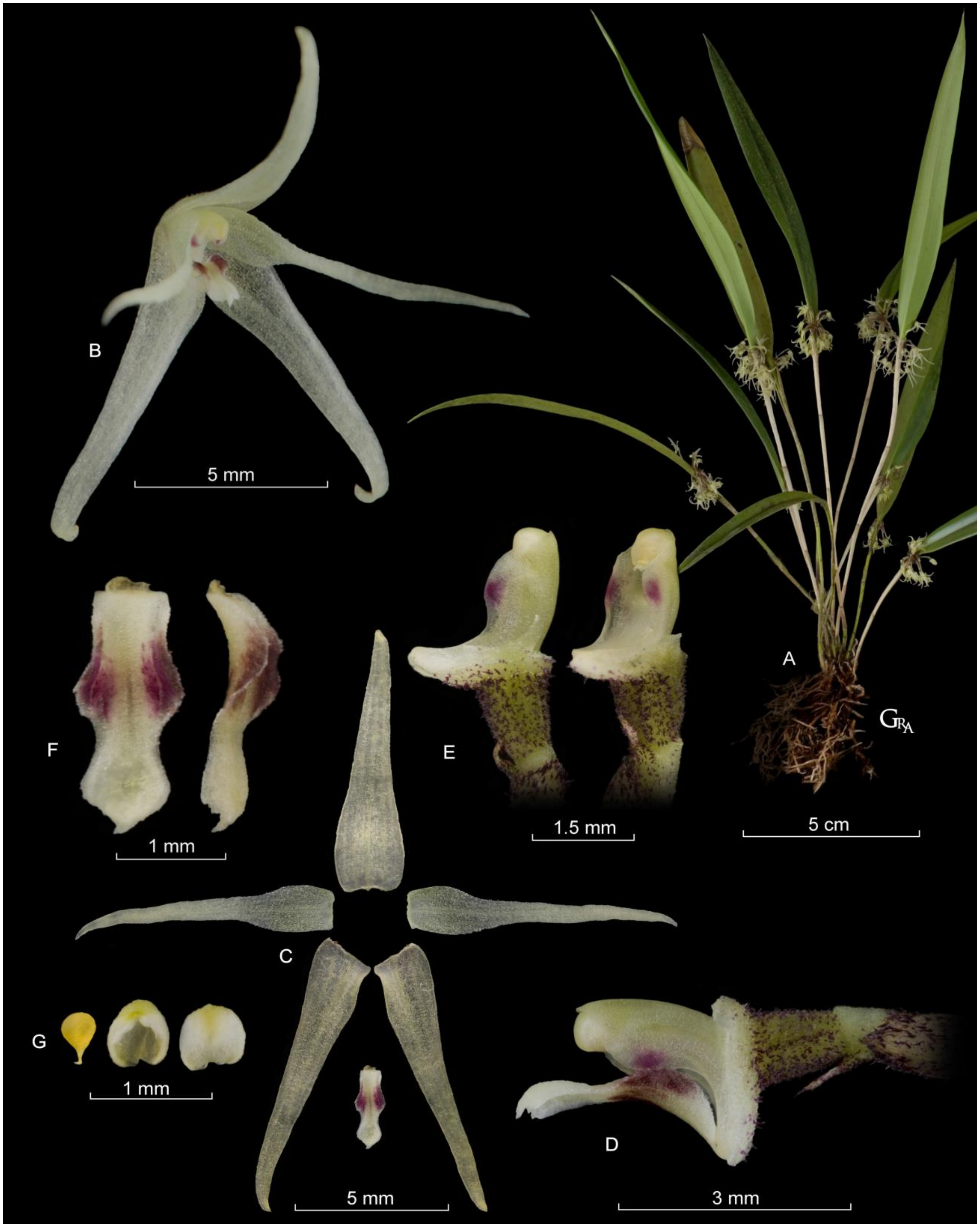

Figure 38. LCDP of *Myoxanthus parahybunensis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in lateral and ventral view. F. Lip in adaxial and lateral view. G. Pollinia and anther cap. Based on *Karremans 6661* (JBL-spirit).

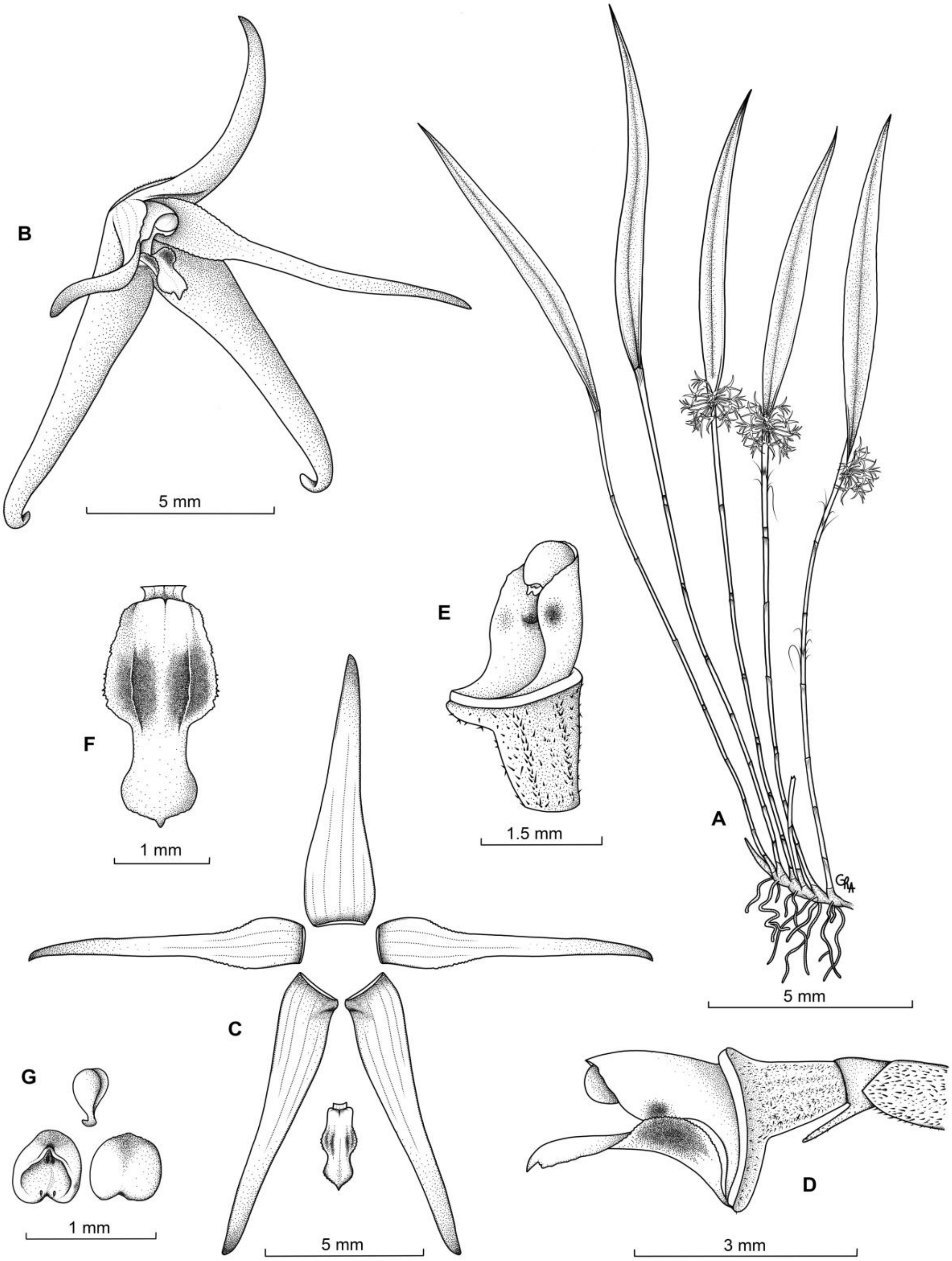

Figure 39. *Myoxanthus parahybunensis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 6661* (JBL-spirit).

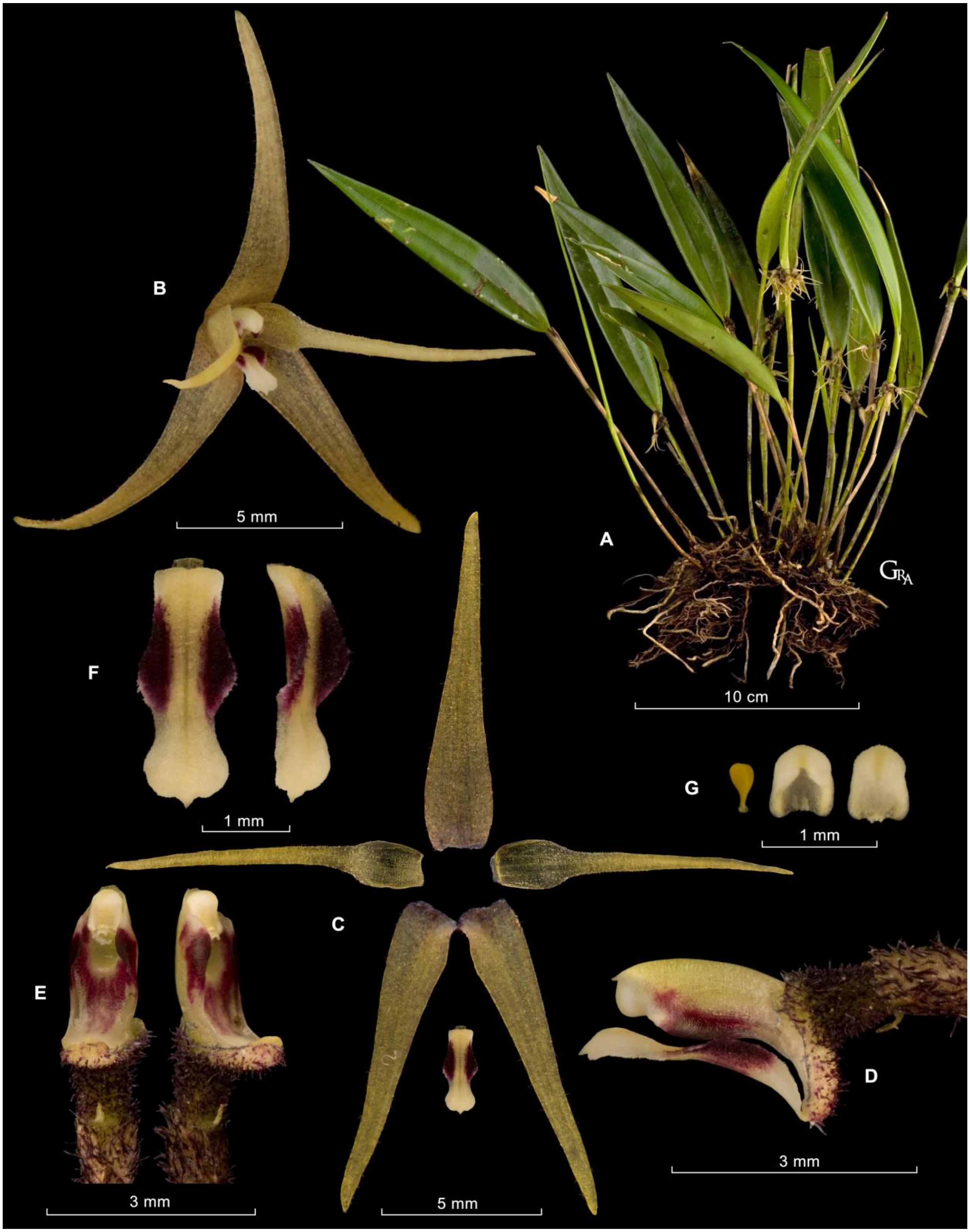

Figure 40. LCDP of the yellow form *of Myoxanthus parahybunensis*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial and lateral view. G. Pollinia and anther cap. Based on *Rojas-Alvarado 113* (JBL-spirit).

Figure 41. Variation in flowers of *Myoxanthus parahybunensis*. A. *Rojas-Alvarado 1*. B. *Bogarín 4823*. C. *Karremans 7022*. D. *Bogarín 5851*. E. *Pupulin 7078*. F. *Karremans 2616*. G. *Karremans 6661*. H. *Rojas-Alvarado 207*. I. *Bogarín 5867*. J. *Bogarín 6924*. K. *Pupulin 6370*. L. *Bogarín 5868*. M. *Bogarín 10276*. N. *Bogarín 4824*. O. *Bogarín 6948*. P. *Bogarín 5867*. Scale bar = 5 mm.

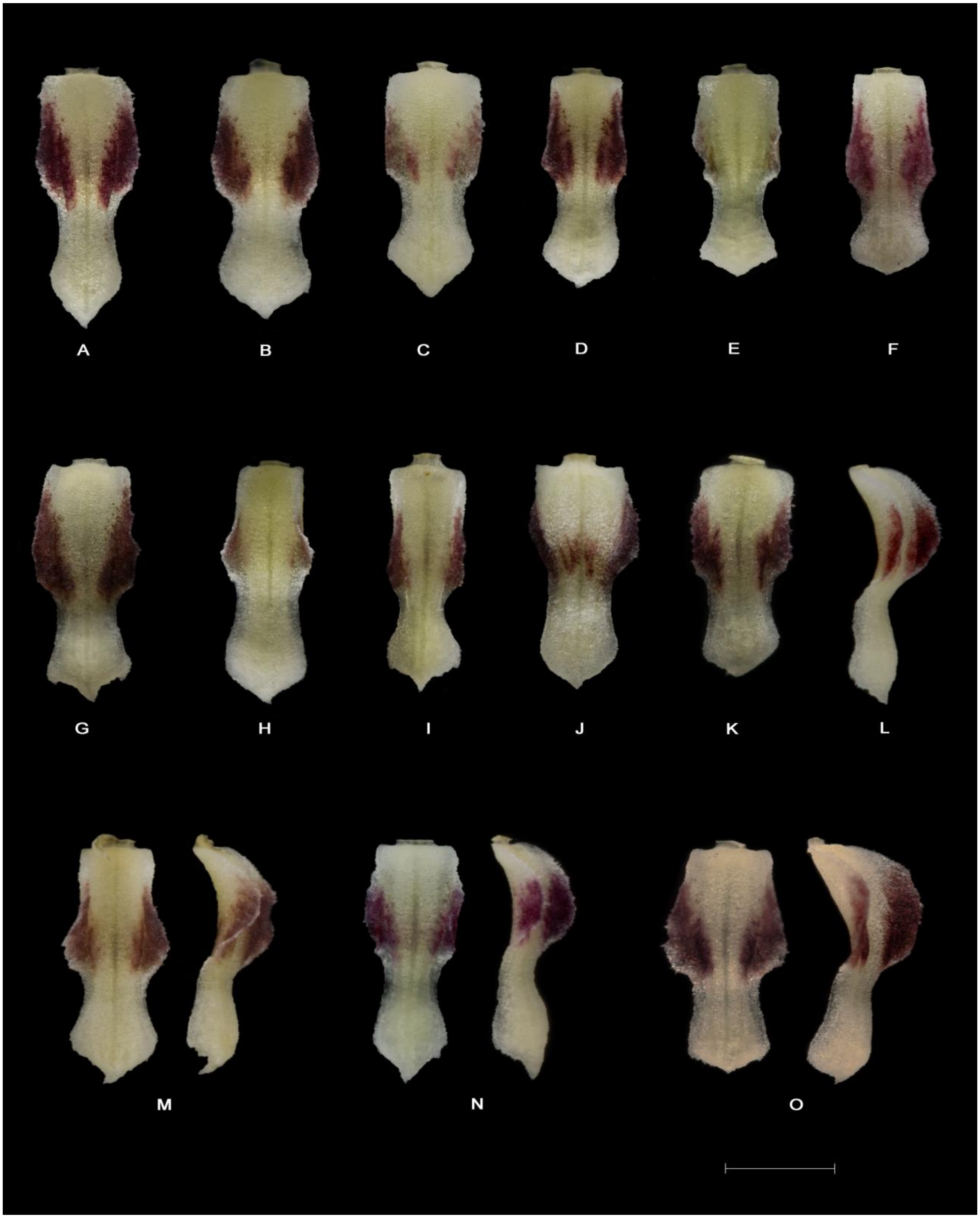

Figure 42. Variation in lips of *Myoxanthus parahybunensis*. A. *Bogarín 6948*. B. *Rojas-Alvarado1*. C. *Bogarín 4823*. D. *Rojas-Alvarado 207*. E. *Bogarín 4824*. F. *Karremans 7022*. G. *Bogarín 5868*. H. *Pupulin 7078*. I. *Karremans 2616*. J– K. *Pupulin* 6370. L. *Bogarín 5851*. M. *Karremans 6661*. N. *Bogarín 5867*. O. *Bogarín 10276*. Scale bar = 1 mm.

Figure 43. Variation in flowers (top) and lips (bottom) of *Myoxanthus parahybunensis*, yellow form. Based on *Rojas-Alvarado 113*. Flower scale bar = 5 mm, lip scale bar = 1 mm.

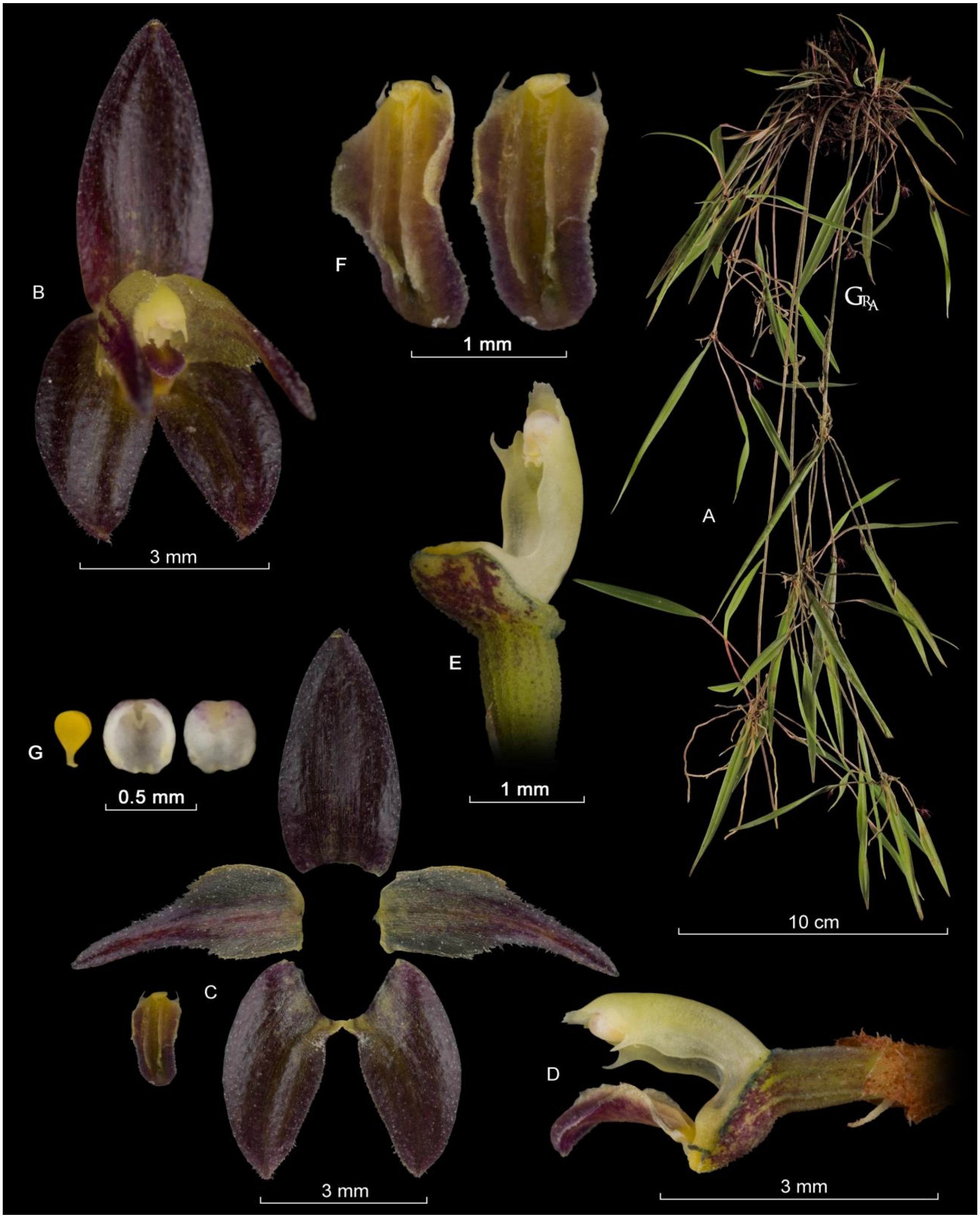

Figure 44. LCDP of *Myoxanthus scandens*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Pupulin 837* (JBL-spirit).

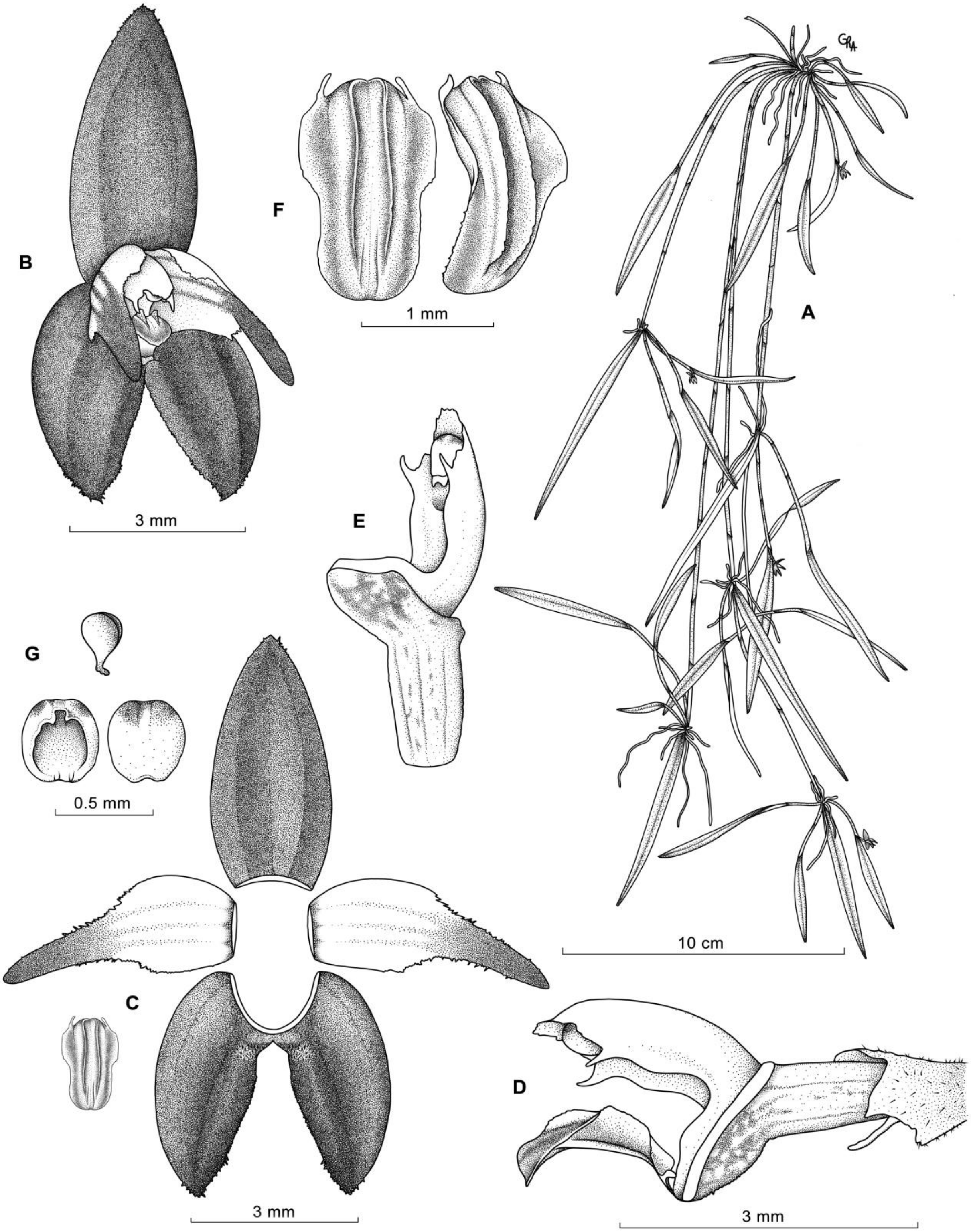

Figure 45. *Myoxanthus scandens*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view, E. column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Pupulin 837* (JBL-spirit).

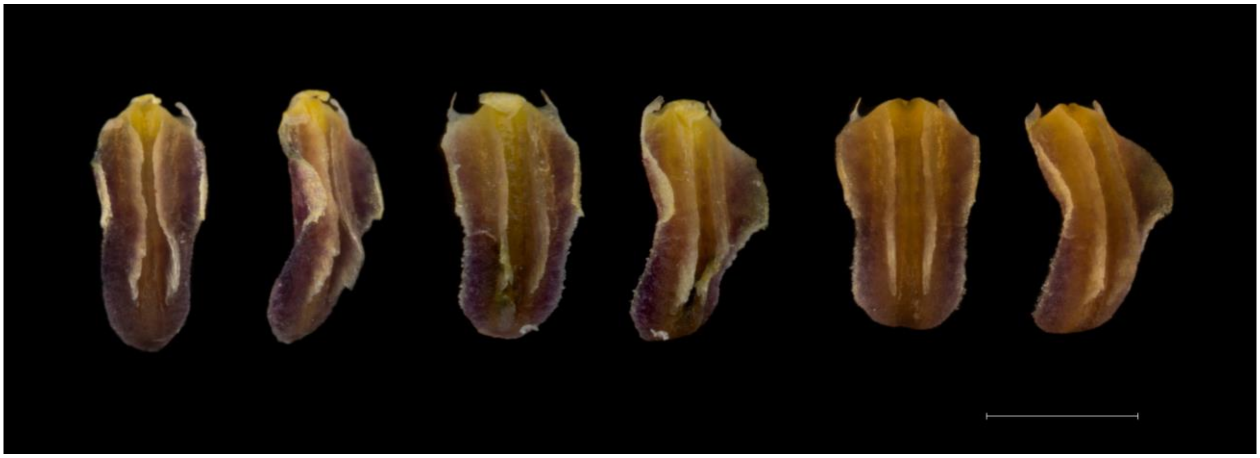

Figure 46. Variation of lips in *Myoxanthus scandens*. Based on *Pupulin 837*. Scale bar = 1 mm.

Figure 47. *Myoxanthus scandens* group in Central America. A & B. *Myoxanthus sp*. from Panama (*S. Laube et al. SL 545*). C. *Myoxanthus scandens* from Costa Rica (*Karremans 1322*). D. *Myoxanthus sotoanus* from Costa Rica (*Karremans 7322*). Photographs: L. Nauheimer (A, B), D. Bogarín (C), G. Rojas-Alvarado (D).

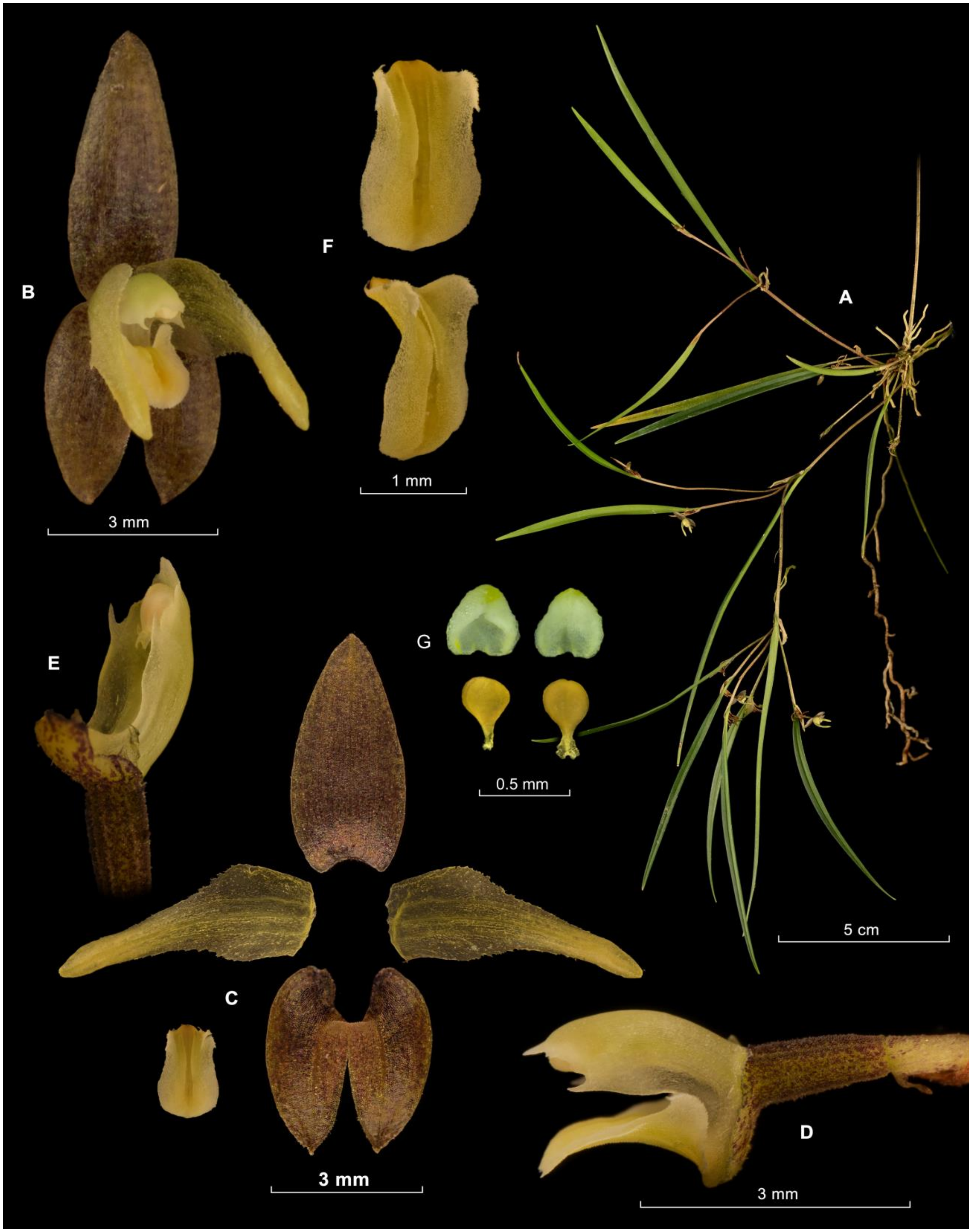

Figure 48. LCDP of *Myoxanthus sotoanus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Karremans 7322* (JBL-spirit).

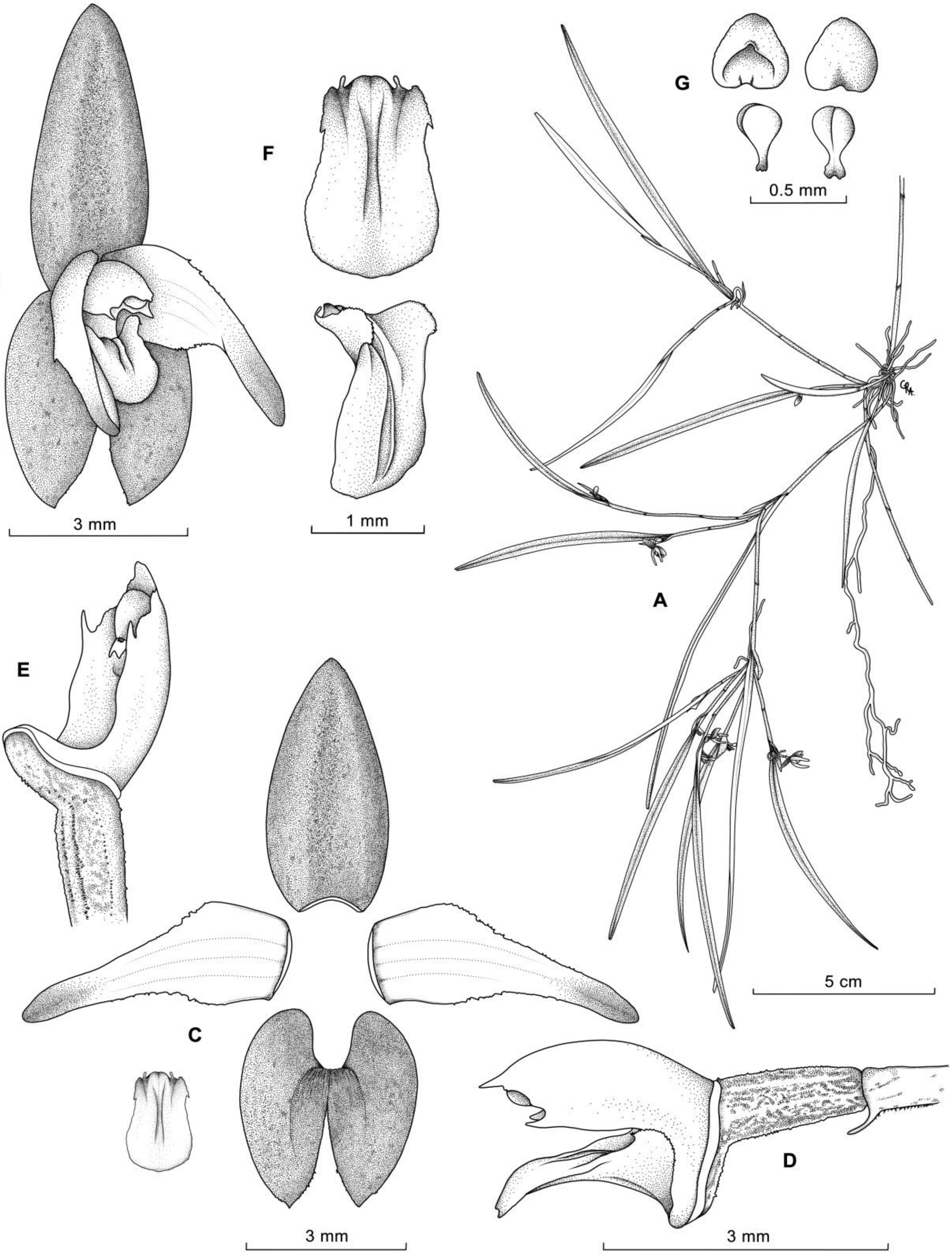

Figure 49. Illustration of *Myoxanthus sotoanus*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Karremans 7322* (JBL-spirit).

Figure 50. Variation of flowers in *Myoxanthus sotoanus*. A–B. *Karremans 7322*. C–F. *Rojas-Alvarado 92*. G–J. *Rojas-Alvarado 111*. K. *Bogarín 10268*. L–M. *Rojas-Alvarado 10*. N. *Blanco 1725*. O. *Bogarín 12404*. Scale bar = 5 mm.

Figure 51. Variation of lips in *Myoxanthus sotoanus*. A. *Karremans 7322*. B. *Rojas-Alvarado 92*. C. *Rojas-Alvarado 111*. D. *Bogarín 10268*. E. *Rojas-Alvarado 10*. F. *Blanco 1725*. G. *Bogarín 12404*. Scale bar = 1 mm.

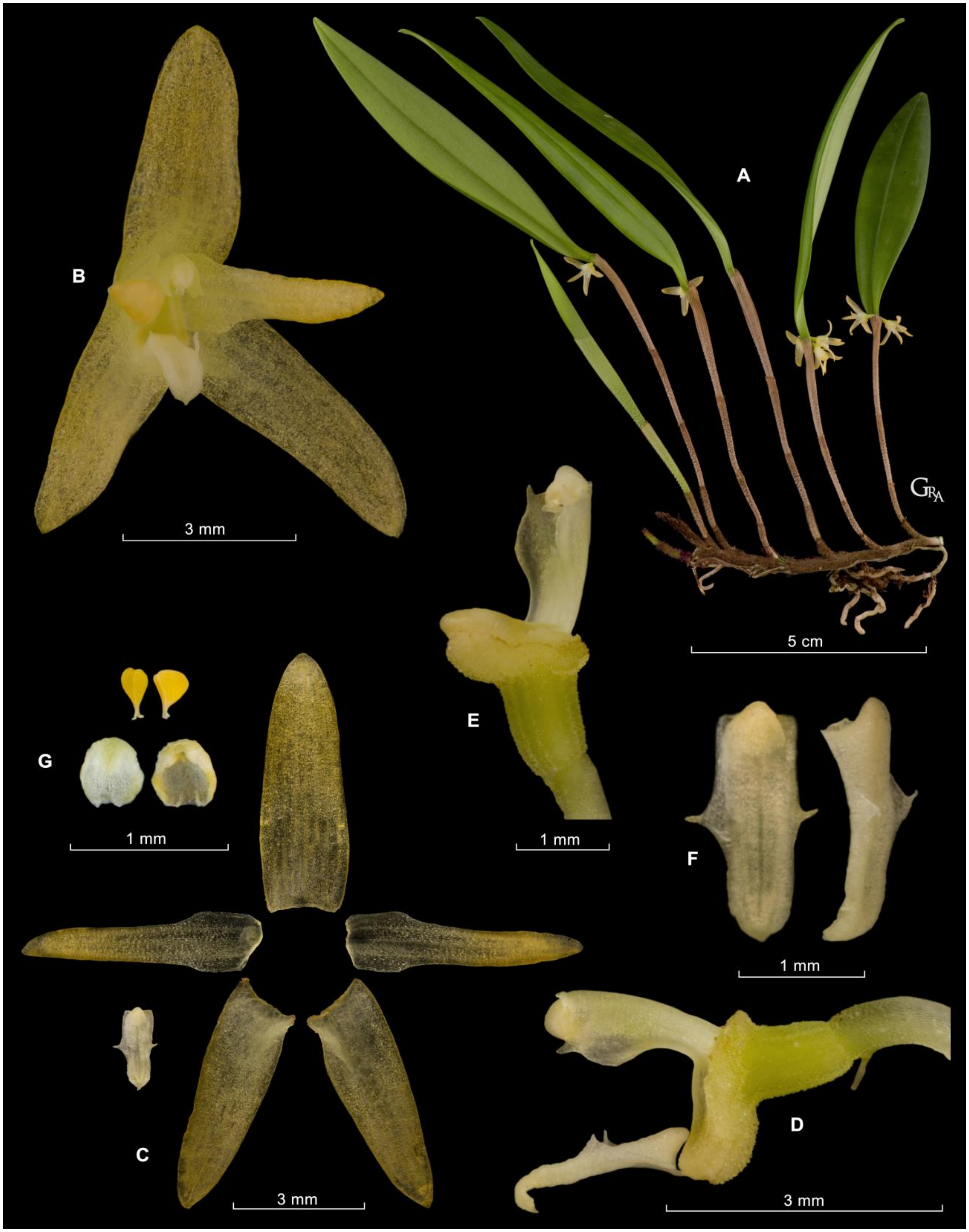

Figure 52. LCDP of *Myoxanthus trachychlamys*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. Column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. Based on *Rojas-Alvarado 27* (JBL-spirit).

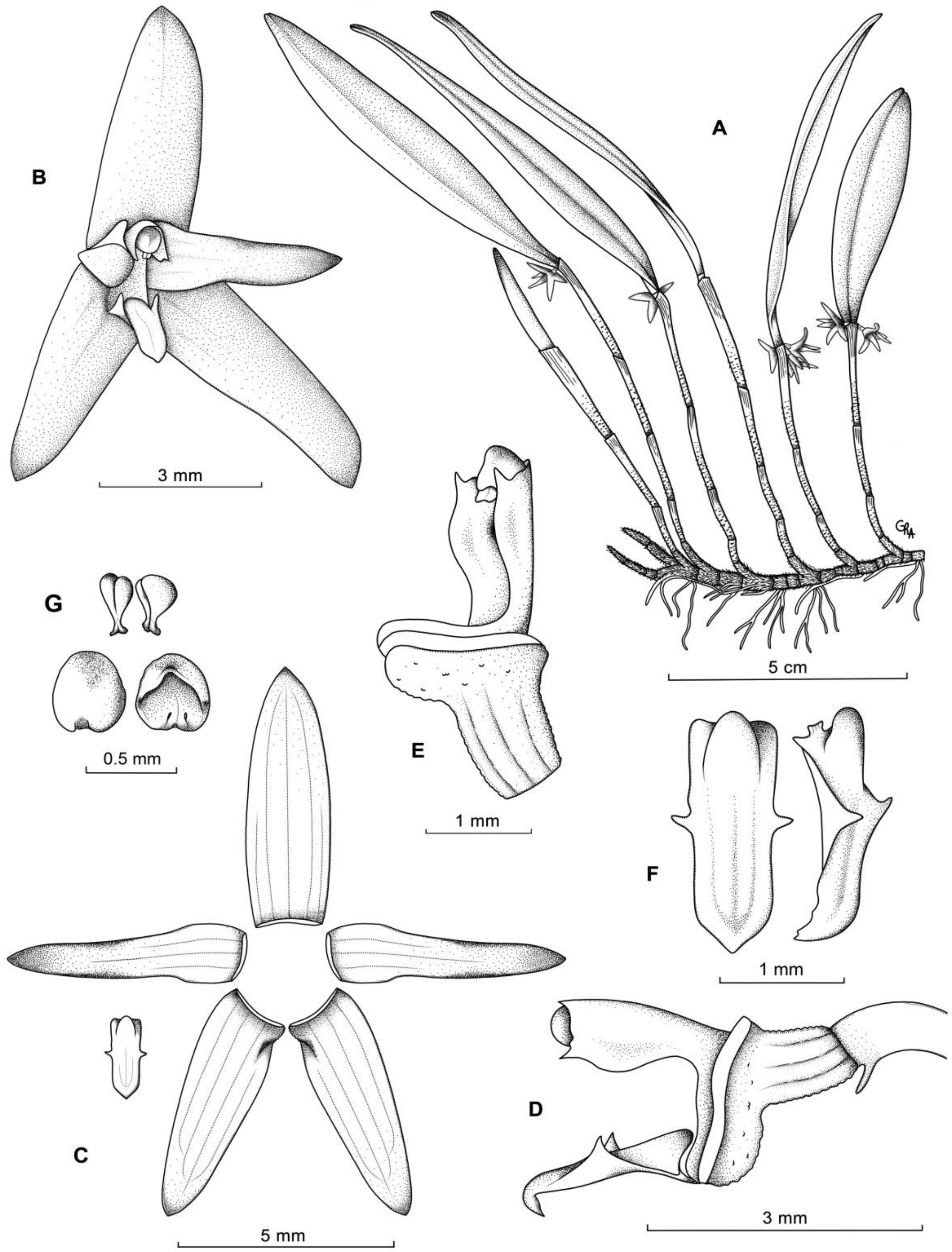

Figure 53. *Myoxanthus trachychlamys*. A. Habit. B. Flower. C. Dissected perianth. D. Column with lip in lateral view. E. column in ventral view. F. Lip in adaxial view. G. Pollinia and anther cap. By G. Rojas-Alvarado based on *Rojas-Alvarado 27* (JBL-spirit).

Figure 54. Variation of flowers (top) and lips (bottom) of *Myoxanthus trachychlamys*. A.–C. *Rojas-Alvarado 27*. D. *JBL-0063*. E–F. *Rojas-Alvarado 210*. G–H. *Rojas-Alvarado 79*. I. *Rojas-Alvarado 27*. J. *Rojas-Alvarado 94*. K. *Rojas-Alvarado* 77. L. *JBL-00631*. M. *Rojas-Alvarado 79*. N. *Rojas-Alvarado 168*. O. *Rojas-Alvarado 210*. Flower scale bar = 5 mm, lip scale bar = 1 mm, * abaxial view.

ARTÍCULO 2: Infrageneric evaluation of *Myoxanthus* (Pleurothallidinae: Orchidaceae)

Infrageneric evaluation of *Myoxanthus* (Pleurothallidinae: Orchidaceae)

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Abstract: The phylogenetic relationships amongst the species belonging to genus *Myoxanthus* are inferred based a combined nuclear region ITS and plastid *matK* gene matrix using Bayesian methods. Sequences of 21 *Myoxanthus* species, including the types of its three currently recognized sections, as well as of closely related genera are included. *Myoxanthus* section *Antenella*, section *Myoxanthus* and section *Scandentia* are not supported as monophyletic; while the exclusion of species previously assigned to *Myoxanthus* subgenus *Satyria* and *Myoxanthus* subgenus *Silenia* into *Echinosepala* is supported. Ten discrete clades are retrieved within *Myoxanthus;* the species belonging to each are characterized and illustrated.

Resumen: Las relaciones filogenéticas en las especies del género *Myoxanthus* son inferidas basadas en una matriz combinada de la región nuclear ITS y el gen plastídico *matK* usando métodos Bayesianos. Se incluyen secuencias de 21 especies de *Myoxanthus*, incluyendo el tipo de las tres secciones actualmente reconocidas, y también de los géneros cercanamente emparentados. *Myoxanthus* sección *Antenella*, sección *Myoxanthus* y sección *Scandentia* no son apoyados como monofiléticos; mientras que, la exclusión de especies previamente asignadas a *Myoxanthus* subgénero *Satyria* and subgénero *Silenia* ahora en *Echinosepala*, es apoyada. Diez clados discretos son retribuidos dentro de *Myoxanthus*; y las especies de cada uno son caracterizadas e ilustradas.

Keywords: *Dresslerella*, *Echinosepala*, Phylogeny, Pleurothallids, systematics, Costa Rican orchids

Introduction

In his monograph of the genus, Luer (1992) proposed the first subgeneric classification of *Myoxanthus* Poepp. & Endl. Recognizing three subgenera based on intuitive morphological features, such as the number of flowers produced at the same time (one, two or several) and the caespitose or scandent habit. *Myoxanthus* subgenus *Myoxanthus*, which includes most of the species (40 species at that time) was further subdivided into three sections, *Myoxanthus* sect.

Antenella Luer, *Myoxanthus* sect. *Myoxanthus* and *Myoxanthus* sect. *Scandentia* Luer. The remaining species were assigned to *Myoxanthus* subgen. *Satyria* Luer and *Myoxanthus* subgen. *Silenia* Luer, with *Pleurothallis pan* Luer and *P. aspasicensis* Rchb.f. as type species respectively, together totaling only seven species at that time. A few years after, Luer (1995) transferred the latter subgenera to *Pleurothallis* subgen. *Acianthera* (Scheidw.) Luer.

Pridgeon *et al.* (2001), in the first molecular-based phylogenetic inference of Pleurothallidinae, found support for the exclusion of *Myoxanthus* subgen. *Satyria* and *Myoxanthus* subgen. *Silenia*, from *Myoxanthus* and segregated them together into a new generic concept, *Echinosepala* Pridgeon & M.W.Chase (2002). *Myoxanthus* was thus recircumscribed to include only the species of subgenus *Myoxanthus*, with its three sections. Anatomically, true *Myoxanthus* species lack the cyclocytic, elevated foliar stomata, which are found in species of *Echinosepala* and *Dresslerella* Luer, a significant synapomorphy not yet found elsewhere in Orchidaceae. Whereas, *Echinosepala* species lack the coralloid raphide clusters found in the foliar epidermis of *Myoxanthus* species, a synapomorphy not found in any other genera within Pleurothallidinae (Pridgeon & Williams 1979, Pridgeon 1982; Pridgeon & Stern 1982).

Even though *Myoxanthus* is highly supported as a monophyletic group, and it clearly belongs to the *Restrepia* Kunth affinity (*sensu* Karremans 2016), its relationships with other genera remains somewhat unresolved. In their combined *matK*, *trnL-F* and nrITS analysis (Pridgeon *et al.* 2001), *Myoxanthus*, *Echinosepala* and *Dresslerella* formed a poorly supported clade (<50% bootstrap support), and in most of the individual analysis they were found in a polytomy with other genera of the *Restrepia* affinity (i.e. *Barbosella* Schltr, *Restrepiella* Garay & Dunst., *Restrepia*, and *Pleurothallopsis* Porto & Brade). In the nrITS phylogenetic inference published by Chiron *et al.* (2012), *Myoxanthus* is found sister to the remaining members of the *Restrepia* affinity, whereas in that of Pupulin *et al.* (2017), also using nrITS data, *Myoxanthus* is found sister to *Echinosepala* with low support (54% p.p.). Finally, in Pérez-Escobar *et al.* (2017), *Myoxanthus* is retrieved monophyletic, and, together with *Echinosepala,* forming a sister clade to the rest of the *Restrepia* affinity.

Myoxanthus is a well differentiated genus within the *Restrepia* affinity. Today it includes 51 species (Rojas-Alvarado *et al.* in press) distributed from southern of Mexico through Central America to Bolivia and southern Brazil. Previous DNA-based studies included accessions of up to five *Myoxanthus* species (Pridgeon *et al.* 2001, Chiron *et al.* 2012, Pupulin *et al*. 2017), or about 10% of the members of the genus, making it impossible to evaluate the subgeneric classification currently in use (Luer 1992). In an attempt to evaluate the phylogenetic relationships of *Myoxanthus,* we have inferred a phylogeny using sequences of about half of the species recognized for the genus, including the type species of all three sections of *Myoxanthus*, as well as representative members of the all genera of the *Restrepia* affinity.

Materials and methods

DNA extraction: DNA was obtained from 1 cm^2 fresh leaves cuttings. Each individual sample was placed into a polypropylene bag with silica gel, and dried for about a week. Then, about 20–100 mg of each dried sample were pulverized in liquid nitrogen by shaking them in mortar using a pestle. DNA extractions were performed by following the protocol DNeasy Plant Kit extraction protocol (QIAGEN Biotechnology).

ADN amplification and sequencing: The nuclear ribosomal internal transcribed spacer (nrITS) region was amplified using methods and primers for sequencing and amplification described by Sun *et al.* (1994). The plastid *matK* partial gene was amplified and sequenced using the Kew primers 2.1af and 5R. PCR was performed in a 50 µL mixtures containing 25 µL Dream Taq PCR Master Mix (2x), 1 µL of each primer, 5 µL DNA, and 18 µL PCR water. Samples were amplified in a 2720 Thermal Cycler (Applied Biosystems, Inc.) using a temperature profile with an initial pre-melt at 95°C for 5 min (94°C for 3 min in *matK*), 35 cycles of denaturation at 94°C for 30 sec (40 cycles, 94°C for 30 sec in *matK*), annealing at 58°C for 45 sec (50°C for 40 sec in *matK*), extension at 72°C for 1 min in both, and a final extension at 72°C for 7 min (72°C for 5 min in *matK*). All DNA samples (5 µL of sample DNA with 1.5 µL of 6× loading dye) were checked on a 1.2 % agarose gel in 1× TBE (Tris-borate-EDTA) buffer running for 8 min at 220 V with a size ladder of 100 bp–1000 bp fragments. Purification and Sanger sequencing was done commercially by Macrogen on a 96-capillary 3730xl DNA Analyzer automated sequencer (Applied Biosystems, Inc.) using standard dye-terminator chemistry (Macrogen, Inc.).

Editing of sequences and analysis: The Staden *et al.* (2003) package was used for sequence editing. Contigs were exported as fasta files and opened in Mesquite v3.61 (Maddison and Maddison, 2007), where they were checked for base calling errors; the ITS and *matK* matrices were aligned separately using MAFFT version 7.4 (Katoh & Standley 2013) available on the CIPRES Science Gateway V. 3.3. The ends of each matrix were trimmed to eliminate possible misreads, and gaps were regarded as missing data. *Arpophyllum giganteum* Hartw. ex Lindl. was used as the outgroup, as it was found to be one of the most distantly related of all included species in this phylogenetic analysis (Pridgeon *et al.* 2001). Accessions of the *Restrepia* affinity available on GenBank were also included. If any of both sequences were no available, it was included by filling in missing positions with Ns. The trees were produced analyzing a combined nrITS + *matK* dataset (tab. 1) using the Bayesian inference with the software BEAST v1.10.4. (Drummond *et al.*, 2012). Parameters were set to preset, except for substitution model GTR with 10 categories for ITS and 8 categories for *matK*, clock models uncorrelated lognormal and exponential respectively, tree prior Yule process, and number of generations 30,000,000, with samples frequency of 3000. The resulting trees were combined using TreeAnnotator v1.8.0., where the first 20% of the trees were used as burn-in to get a final maximum clade credibility tree. FigTree v1.4.4. (Rambaut 2009) and Adobe Illustrator CS6 (Adobe Systems Inc., California, USA) were used to edit the resulting tree. Posterior probabilities (p.p.) values were plotted for each clade on nodes.

Scanning electron microscopy (SEM): Micrographs were taken from flowers fixed in FAA. The samples were dehydrated in a series of ethanol solutions (70–96%– ≥ 99.9%) and twice in fresh acetone ≥ 99.8%. Critical point drying was performed in the Automated Critical Point Dryer Leica EM CPD300 (Leica Microsystems, Wetzlar, Germany) with ≥ 99.8% acetone and liquid CO_2 as exchange fluids following the manufacturer procedures. Samples were mounted and sputter-coated with 20 nm of Pt/Pd in a Quorum Q150TS sputter-coater and observed with a JEOL JSM-5300 scanning electron microscope at an accelerating voltage of 10 kV.

Results

The phylogenetic inference presented here (Fig. 1) shows a highly supported *Restrepia* affinity (pp=1). Also very well supported is genus *Myoxanthus* (pp=1), with *Echinosepala* as its sister genus, with low support (pp=0.42). They form a clade sister to *Dresslerella*, with low support (pp=0.35). Together all three genera are sisters to a highly supported clade (pp=1) including the remaining species of the *Restrepia* affinity. It is composed of two very well supported subclades, on one hand *Restrepia* and *Pleurothallopsis* (pp=0.99), and on the other hand *Barbosella* and *Restrepiella* (pp=1).

Within *Myoxanthus*, six major clades with very high support were retrieved (Fig. 2). Clade A includes *Myoxanthus ruschii* as sister (pp=1) to a group comprised by *M. punctatus* as sister to *M. lonchophyllus*, *M. reymondii* and *M. seidelii*. In clade B three subclades are retrieved, a highly supported subclade made up of *Myoxanthus congestus* and *M. cereus*, that is sister to the *M. serripetalus* subclade (pp=0.96). Together they are sisters to the *Myoxanthus uxorius* subclade, with low support (pp=0.5). Clade C includes all accessions of *Myoxanthus colothrix*, clustered with high support. Clade D include two subclades, one comprised by the highly supported group of *Myoxanthus ceratothallis* and *M. georgei*, as sister to *M. exasperatus*, with moderate support (pp=0.73). The second subclade, comprised by *Myoxanthus monophyllus* and *M. gyas* showed low support (pp=0.6) as sister to the first. Clade E includes a highly supported group comprised by *Myoxanthus scandens* as sister to *M. sotoanus*, both in turn sisters to *M. hirsuticaulis*. Clade F includes two subclades, the highly supported *Myoxanthus affinis* and *M. parahybunensis* subclade as sister, with low support (pp=0.45), to the *Myoxanthus trachychlamys* subclade.

Only two major clades, clade A and the monospecific clade C, have members of only one of the three *Myoxanthus* sections. All remaining clades included species assigned to different sections, one of them (clade D) with taxa belonging to all three sections. Clade A is sister to all other groups in the genus and is represented by several species mostly endemic of southeast Brazil and the Andean *Myoxanthus reymondii*. Clade C grouped the accessions of *Myoxanthus colothrix*, which formed an isolated lineage. In clade D, *Myoxanthus monophyllus*, type species of *Myoxanthus* sect. *Myoxanthus*, and *Myoxanthus ceratothallis*, type species of *M.* sect. *Antenella* are clustered with low support (pp=0.5) in sister subclades, each one intermingled with members of other sections. *Myoxanthus scandens*, type species of *Myoxanthus* sect. *Scandentia* is found in a clade together with *M. hirsuticaulis*, assigned to *Myoxanthus* sect. *Antenella*. The latter was found to be a sister, with low support (pp=0.45), to clade F, which does not include any species assigned to *Myoxanthus* sect. *Scandentia*.

Discussion

In agreement with previous DNA-based studies (Pridgeon *et al.* 2001, Pérez-Escobar *et al.* 2017, Pupulin *et al.* 2017) the phylogenetic inference presented here, based on the analyses of a combined nuclear ITS and plastid *matK* datasets, shows high support for the monophyly of the *Restrepia* affinity (*sensu* Karremans 2016). The group includes the genera *Restrepia* and *Pleurothallopsis* in a highly supported clade that is sister to the genera *Barbosella* and *Restrepiella*, both highly supported as well. Sisters to these genera is low supported clade comprising the genus *Dresslerella* as sister to *Echinosepala* and *Myoxanthus*, also with low support. As previously reported, and despite the broader dataset, the relationships between these three genera remain unresolved, even though they themselves are highly supported as monophyletic.

Within *Myoxanthus*, the relationships among species groups has become much clearer. Luer (1992) recognized three sections, *Myoxanthus* sect. *Antenella*, *Myoxanthus* sect. *Myoxanthus and Myoxanthus* sect. *Scandentia*. *Myoxanthus* sect. *Antenella* featured caespitose, shortly repent or long repent habits, producing one, two or sometimes three flowers at a time, with the apices of the petals commonly thickened or clavate. This sections were found as non-monophyletic in this study. Its type species, *Myoxanthus ceratothallis* grouped with members of both *Myoxanthus* sect. *Scandentia* and *Myoxanthus*. sect. *Myoxanthus*, including the type species of the latter (Fig.2, clade D). *Myoxanthus* sect. *Myoxanthus* characterized by having caespitose to shortly repent habits, producing few to many flowers at a time, was also found as non-monophyletic. Its type species, *Myoxanthus monophyllus* formed a highly supported group with *M. gyas*, which belong to *Myoxanthus* sect. *Scandentia* (Fig. 2, clade D). The *Myoxanthus* sect. *Scandentia* also showed to be non-monophyletic. This section was created to accommodate seven species with a scandent habit, producing fascicles of ramicauls from the apex of the preceding ramicaul, with few to many flowers produced at a time. *Myoxanthus scandens*, type species of the section formed a highly supported group together with *Myoxanthus sotoanus* and *M. hirsuticaulis*, the latter a member of *Myoxanthus* sect. *Antenella* (Fig. 2, clade E).

Characterization of discrete groups

Clade A

***Myoxanthus lonchophyllus* group:** This highly supported group is represented in the analysis by *Myoxanthus lonchophyllus, M. ruschii, M. punctatus, M seidelii,* and *M. conceicionensis* M.Frey & N.Sanson, the latter not included in the analysis but likely part of it based on morphology, which is similar to *M. punctatus*, but with different habit and light purple flowers. This group is characterized by having fleshy flowers with dark purple warts on sepals and petals, a conspicuous pair of calli internally in the column foot, a hispid-hirsute anther cap, a fleshy lip with a pair of auricles at the base and margins generally revolute to the apex (Fig. 3). The hispid-hirsute anther cap and the fleshy lip revolute to the apex are the main diagnostic characters of this. The first character is also present in *Myoxanthus serripetalus,* but floral morphology is completely different. Species of the *Myoxanthus lonchophyllus* group are endemic from the southeast Brazil, had been collected only in the low lands of Espirito Santo and Minas Gerais.

Myoxanthus reymondii showed to be embedded within *M. lonchophyllus* group as sister to *M. seidelii*, but with low support (pp=0.7). However, this species lacks of main diagnostic characters of *Myoxanthus lonchophyllus* group, but present characters consistently shared with other unsampled species, including *Myoxanthus cymex*, *M. melittanthus*, and *M. hystrix*. A reevaluation of the phylogenetic relationships of this clade including relatives of *Myoxanthus reymondii* is needed. *Myoxanthus reymondii* group is recognized by having short pubescent-abaxially sepals, a non-toothed column with broad rounded wings, petals mottled-spotted with red-purple, basally triangular to quadrated then contracted ending in a fleshy clavate apex, and a distinct recurved lip above the middle (Fig. 4). Species of this group are mainly distributed along the northern Andes, from Venezuela to Ecuador, generally above 1500 m in elevation. *Myoxanthus mejiae*, which is found only in western Venezuela, probably represent a member of this group, but still conserving some features of the *Myoxanthus lonchophyllus* group. The habit and the big fleshy lip with the margins revolute to the apex and the auricles at the base are similar to that found on *Myoxanthus lonchophyllus* group, whereas morphology of sepals, petals and column is similar to the *M. reymondii* group. In Luer´s (1992) classification, all species found in Clade A were placed under the *Myoxanthus* sect. *Antenella*.

Clade B

***Myoxanthus congestus* group:** It is represented on the analysis by *Myoxanthus congestus* and *Myoxanthus cereus*, and based on morphology it likely includes *M. octomerioides* (Lindl.) Luer and *M. pulvinatus* (Barb.Rodr.) Luer. This group showed to be highly supported as sister to *Myoxanthus serripetalus*, a completely different morphological species. *Myoxanthus congestus* group is well characterized by having caespitose plants with sheaths of the ramicaul whitish covered by trichomes soon deciduous leaving smooth scars, multiple flowers produced simultaneously, fleshy creamy white to yellowish flowers sometimes suffused with rose or purple (Fig. 5), the lip oblong with purple margins frequently elevate below the middle and the anther cap papillose-verrucose to the apex (Fig. 6A–C), which appear to be a synapomorphy of the group. Species of this group are generally found at mid elevations, from 800–1800 m, distributed from Mexico through Central America, to Colombia, Venezuela, Peru and the southeast Basil, probably the most widely distributed group within the genus. Members of this group were included in *Myoxanthus* sect. *Myoxanthus* (Luer 1992).

***Myoxanthus serripetalus* group:** It is represented only by *Myoxanthus serripetalus*, which is the most aberrant species of the genus, having not morphological similar species. It produces the largest flowers on the genus, with big sepals (up to 3 cm long) and small petals (1 cm long), both densely verrucose adaxially; the lip is long ovate with fringed margins and elevated bellow the middle, and the column is long scarcely winged with the anther cap hispid-hirsute (Fig. 7D & E). *Myoxanthus serripetalus* in found in the Ecuadorean and Peruvian Andes generally above 2000 m of elevation. This species was placed under *Myoxanthus* sect. *Myoxanthus* (Luer 1992).

***Myoxanthus uxorius* group:** It is also only represented by one species, *Myoxanthus uxorious*, which showed to be sister (with low support, pp=0.48) to the *M. serripetalus* and *M. congestus* groups. *Myoxanthus uxorious* also tended to form an isolated linage when running others analysis with the same data and parameters, but low supported. This species has yellow flowers with a big lip having basal auricles and the disc with a pair of thick smooth rounded calli and the column with ovate lobular wings above the middle (Fig. 7A–C). Shape of the lip and column of *Myoxanthus uxorius* is more similar to what is found in the *M. lonchophyllus* group, but lacking the calli on the column foot. Flowers of *Myoxanthus uxorious* resemble those of *M. ruschii* of the *M. lonchophyllus* group. *Myoxanthus uxorius* in found generally above 1800 m of elevation along the Andes in Colombia and Ecuador. This species was included in *Myoxanthus* sect. *Antenella* (Luer 1992).

Clade C

***Myoxanthus colothrix* group:** All accessions of *Myoxanthus colothrix* formed an isolated high supported clade (pp=0.97). This group is recognized by the shortly but distinctly repent habit, ramicauls erect with narrow ovate acute leaves, producing multiples whitish flowers with a narrow ovate membranaceous perianth, and the lip ovate-oblong with the margins elevate bellow the middle and with a small pair of calli emerging in the middle frequently suffused with light purple (Fig. 6D; Fig. 8D & E). *Myoxanthus colothrix* had been reported in southern Mexico, Costa Rica, Panama and Ecuador, at high elevation above 1500 m. Luer (1992) included this species in *Myoxanthus* sect. *Myoxanthus*.

Clade D

***Myoxanthus monophyllus* group:** Represented on the analysis by the type species of the genus, *Myoxanthus monophyllus* and *M. gyas*, and likely includes *Myoxanthus frutex* (Schltr.) Luer, *M. chloe* (Luer & R.Vásquez) Luer, *M. gorgon* Luer, and *M. montanus* P.Ortiz. This group is characterized by having or not scandent plants, the sepals and petals narrow elongate and the pubescent floral bract covering the pedicel, ovary and the base of the perianth, which id the main diagnostic character of the group (Fig. 9). This group is distributed mainly at high elevation, above 1800 m, along the Andes, from Ecuador to Bolivia. With the exception of *M. monophyllus*, all species of this group were placed under *Myoxanthus* sect. *Scandentia* (Luer 1992).

***Myoxanthus ceratothallis* group:** It includes the highly supported group of *Myoxanthus* ceratothallis (type species of *Myoxanthus* sect. *Antenella*) and *M. georgei*, as sister to M. *exasperatus*, with moderate support (pp=0.73). Together, they are low supported as sister to the *Myoxanthus monophyllus* group. *Myoxanthus ceratothallis* and *M. georgei* share only the basal auricles on the lip and a pair of longitudinal keels on the disc, which is also present in species of Clade E. However, with the inclusion of *Myoxanthus exasperatus* diagnostic characters of theis groups becomes unclear due to the inconsistency of the floral morphology. With the available information it is impossible to characterized this group. Species of this group were placed under *Myoxanthus* sect. *Antenella* (Luer 1992).

Clade E

***Myoxanthus scandens* group:** It is represented in the analysis by *Myoxanthus scandens*, the type species of *Myoxanthus* sect. *Scandentia*, *M. sotoanus* and *M. hirsuticaulis*. They share a lip with shortly oblique acute lateral lobes, a pair of auricles at the base, the disc with a pair of longitudinal keels or lamellae from the base to near the apex, the column with acute teeth and the clinandrium long hooded. Base on morphology, the *Myoxanthus scandens* group likely include *M. eumeces* (Luer) Luer, *M. fimbriatus* Luer & Hirtz, *M. merae* (Luer) Luer, *M. epibator* Luer & Escobar, *M. antennifer* Luer & Hirtz, *M. ephelis* (Luer) Luer, *M. panamense* Rojas-Alv. & Karremans, and *M. pennellius* (Luer) Rojas-Alv. & Karremans, representing the most diverse group among the clades. This group is characterized by having scandent and not scandent species with narrow, frequently linear (<2 cm) leaves, the perianth generally purple or purple striped, less common yellowish colored, the petals are generally wider basally then gradually or abruptly contracted forming a narrower and sometimes fleshy apex, but never clavate; the lip is scarcely trilobate, with an auricle basally on each side, the lateral lobes generally acute oblique and elevate, and the disc with a longitudinal pair of lamellae or keels from the base of the lip to near the apex, and frequently with shortly dentate margins. The column is curved, always winged with acute teeth at the apex and the clinandrium long hooded (Fig. 10). The fimbriate margins on petals and lip is present in this group, as in *M. fimbriatus* and *M. hirsuticaulis*, but not elsewhere in the genus (Fig. 6E). Species of this group are distributed in central America and south America, had been collected between 1000–2500 m of elevation, in Costa Rica, Panama, Guyana and the northern Andes, Venezuela, Colombia, Ecuador and Peru, however, most of the species of this group are present in Ecuador. This group include species of the sect. *Antenella* and sect. *Scandentia* (Luer 1992).

Clade F

***Myoxanthus trachychlamys* group:** This group is only represented by *Myoxanthus trachychlamys*, which showed to be sitter to the *Myoxanthus affinis* group, but with low support (pp=0.48). When running other analysis, it tended to form a low supported group with the *Myoxanthus scandens* group as sister. *Myoxanthus trachychlamys* has a combination of characters not found in any other *Myoxanthus*, having small long repent plants with yellow flowers, the lip with small acute lateral lobes, and the base with a hump-shaped callus backwards oriented (Fig. 7A–C, Fig. 6F). The long repent habit is elsewhere only in *M. hystrix*, but flowers are completely different. This species was included in sect. *Antenella* (Luer 1992). The most similar species with a similar hump-shaped callus basally on the lip are those of the caespitose species *M. priapus*, and *M. ortizianus*, but the callus is upwards oriented and the remain parts of the lip and flowers are completely different.

Myoxanthus affinis **group:** Is represented on the analysis by *Myoxanthus affinis* and *M. parahybunensis*, these species share caespitose plants, producing multiple simultaneous flowers, with narrow elongate sepals and petals, frequently in yellowish to whitish colors, the perianth is frequently covered by minute trichomes abaxially, the lip is ovate with purple margins elevated below the middle and the disc with a small longitudinal pair of calli, sometimes purple. These characteristics are also present in *Myoxanthus neillii* Luer & Dodson, which is quite similar to *M. parahybunensis*, but with small flowers and a toothed column; *M. herzogii* (Schltr.) Luer, and *M. dasyllis* Luer & Hirtz, which are similar to *M. affinis*, but with a short pseudopeduncle and few differences on lip´s shape. The *Myoxanthus affinis* group is characterized by producing multiple simultaneous yellowish to whitish flowers, with floral bracts, pedicels, ovary and abaxial surface of sepals frequently covered by minute red-purple trichomes, petals narrow elongate, and the lip frequently with purple margins (Fig. 11). This group is found from Costa Rica to Peru and southeast Brazil, between 1000–2500 m of elevation, but *M. parahybunensis* may be also found lower in Costa Rica and Brazil. All species of this group were place under *Myoxanthus* sect. *Myoxanthus* (Luer 1992).

Morphology

Luer´s sections were distinguished from each other essentially by the plant habit (caespitose, shortly repent, long repent, scandent) and number of flowers produced at a time (one, tow, few to many), however, these characters are not phylogenetically informative. Most of the clades include species with different habit, even within subclades, except for clade C, which include only one species with shortly repent plants. About numbers of flowers produced simultaneously, in clades A and E, species always produced few simultaneous flowers (<5), whereas, production of multiple (10–40, or more) flowers is consistently in clade C and in a subclade within clade B and F. Moreover, a correlation of numbers of simultaneous flowers and color perianth is noted on the genus. Species with white-yellowish flowers produce multiples flowers, while these with red-purplish colors (stripped, mottled or completely colored) always produce few simultaneous flowers.

A synapomorphy share by all *Myoxanthus* species is the discontinuous lines of trichomes covering sheaths of the ramicauls, which is not found in any other Pleurothallidinae (Fig. 6G). Different ornamentation of these trichomes are found, some of them taxonomically value, but not phylogenetically informative. Leave morphology, as narrow ovate leaves (<2 cm wide) generally linear grouped species of clade E. With the exception of the latter, vegetative characters are not phylogenetically informative.

A fasciculate inflorescence as a result of peduncle and rachis reduction is consistently among the clades. This type of inflorescence is apparently an synapomorphy of Pleurothallidinae not mentioned yet on literature, presenting variation of single or multi-flowered coflorescences in some genera, however, it is consistently single-flowered in *Myoxanthus* and *Restrepia* affinity. The floral bract covering the ovary and base of the perianth is shared by all species of *Myoxanthus monophyllus* group (Fig. 9D). The trichomes covering part of the inflorescence is also consistently among the clades. Also is consistently the remain of the coflorescence axis in form of a vestige adnate to the pedicel (Fig. 6H), which is also share by some related genera with Restrepia affinity, which is also found adnate or not.

Genus *Myoxanthus* present a wide variation in floral morphology, however, some floral characters are not phylogenetically informative, and most groups among clades are recognized by a combination of petals and lip characters, and just few groups may be recognized by a single one. Connation at different levels on lateral sepals are common among different clades, however, these forming a suborbicular synsepal is only found in *Myoxanthus hirsuticaulis*, clade E, and in two unsampled species, *M. priapus* Luer and *M. ortizianus* Kolan. & Szlach. Among the different clades, petals are generally wider basally then contracted with an elongate sometimes thickened apex, however, the clavate apex share by all species of the *Myoxanthus reymondii* affinity, in clade A, is not present in any other group. Also, the serrate petals of *Myoxanthus serripetalus* are unique to this group. Lip is also wide variable among clades, but there are some generalized characters features, as the basal auricles at the base of the lip, presented in clades A, B, D and E (Fig. 6I). Another generalized character is that of a pair of longitudinal callus, keels or lamellae on the disc of the lip, which is found in all clades, just absent in the *Myoxanthus trachychlamys* group within clade F (Fig. 6A, D, E, F, I). A fleshy lip with revolute margins to the apex is unique in *Myoxanthus lonchophyllus* group (Fig. 3), clade A. In the same clade, another unique lip morphology is found, the small ovate lip highly revolute above the middle present in the *Myoxanthus reymondii* affinity (Fig. 4), in clade A. The column morphology is generally consistently among clades, but with some variation in length and wide of wings, most notoriously the broad wing shared by all species of clade A. About pollinarium, it presents a consistently tow obovoid yellow flattened pollinia with white flat caudicles. In the other hand, there are three discrete type of anther caps. The hispid-hirsute anther cap, which is restricted to the *Myoxanthus lonchophyllus* (Fig. 3) and *M. serripetalus* groups, in clades A and B respectively. This type of anther cap is related with the presence of circular warts over sepals and petals. A papillose-verrucose anther cap is shared by all species of the *Myoxanthus congestus* group in clade B. The remain groups present a smooth anther cap.

Discrete groups representation

Most of the morphological discrete groups of *Myoxanthus* were represented on the analysis by one or more species, however, there are three groups with no representation, including *Myoxanthus parvilabius* (C.Schweinf.) Luer, *M. xiphion* Luer, *M. priapus* Luer, *M. ortizianus* Kolan. & Szlach., *M. sarcodactylae* (Luer) Luer, *M. simplicaulis* (C.Schweinf.) Luer and *M. werneri* Luer species. The group of *Myoxanthus parvilabius* and *M. xiphion* is characterized by the dorsal sepal somewhat projected towards the column covering the latter, the lateral sepals spread flat and connate basally, the lip oblong with a small bilobed callus at the base, a pair of small longitudinal keels emerging on the middle, and the lateral margin with shortly acute angles. The *Myoxanthus priapus* and *M. ortizianus* group have lateral sepals connate forming a suborbicular synsepal, petals contracted at the apex, and the lip with a thick erect callus near the base. The *Myoxanthus simplicaulis* and *M. sarcodactylae* share the shortly pubescent-abaxially sepals, the petals thickened at the apex with revolute margins, and the lip with the base subtruncate, oblong, scarcely trilobate with the lateral lobes elevated with the margins erose-dentate, the midlobe rounded with the apical margins erose-dentate and the disc with a pair of longitudinal calli extending towards the midlobe. *Myoxanthus werneri* is probably relative to the latter group, the sepals are shortly pubescent abaxially and lip is similar but strongly recurved in the middle. We consider these three groups may be close related to any of the *Myoxanthus scandens* or *M. ceratothallis* groups than any other, however, they must be evaluated.

Conclusions

The three currently recognized section within *Myoxanthus* (Luer 1992) showed to be non-monophyletic. The characters used by Luer for delimitating the three section, as the habit and number of flowers produced at a time, were not phylogenetically informative, however, there is correlation between numbers of flowers produced simultaneously and flowers color. The sister group to all the other species of the genus is formed by the *Myoxanthus lonchophyllus* group, all of them endemic from southeast Brazil, including the Andean *M. reymondii*. Considering that not all evident morphological groups within *Myoxanthus* were included in the analysis, the low supported support of some subclades, and that others must be reevaluated with the inclusion of unsampled species, none infrageneric classification was proposed here. However, most of the subclades are well characterized, mainly by a combination of floral character.

Acknowledgements

The authors are thankful to the directors and staff of the herbaria AMES, AMO, CR, JBL, K, SEL, W, UCR, USJ, and UVAL which provided information, images, access to their collections. Alexander Hirtz, the Atrium Biodiversity Information System, Brayan Coral Jaramillo, Diego Bogarín, Ecuagenera, Eerika Schulz, Emerson Luiger, Eric Hunt, Gerrit Verhellen, Gilberto Merino, H. Richard Ellis, Joost Riksen, Jorge Gastin, Luis Enrique Godo Yupanqui, Luis Felipe Varella, Lars Nauheimer, Linda & Mikael Karlbom, Lourens Grobler, Maruro Rosim, Nova de Jong, Rene Stalder, Ron Parsons, Rubén Velázquez, Sebastian Moreno, Sebastian Vieira-Uribe, the Swiss Orchid Fundation, Tomas Karrer and Yéri Dewèvre are thanked for providing photographic material. José Esteban Jiménez, and Marco Cedeño Fonseca are also thanked for provided images of *Myoxanthus* specimens at MO and several South American herbaria. Franco Pupulin, Diego Bogarín, Isler Chinchilla, Lizbeth Oses, Grettel Salguero part of the Lankester Botanical Garden staff, are thanked for their support and diversely assisting this project. Barbara Gravendeel, Richa Kusumawati, Dewi Pramanik and Bertie Joan van Heuve are thanked for provided use and assinting on taking SEM micrographs. The authors also wish to thank to the Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC) of Costa Rica for issuing the scientific passports under which wild species treated in this study were collected.

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Table 1. List of vouchers and GenBank accession numbers used in the phylogenetic analyses.

Taxon	Voucher collector and number	ITS	*matk*	Source
Arpopjhyllum giganteum Hartw. ex Lindl.		AF266742		Pridgeon *et al*. 2001
Barbosella australis (Cogn.) Schltr.	*Karremans 5758*	KY988808	KY988628	Pérez-Escobar *et al*. 2017
Barbosella cogniauxiana (Speg. & Kraenzl.) Schltr.	*Van der Berg 2124*	JQ306503		Chiron *et al*. 2012
Barbosella cucullata (Lindl.) Schltr.	*Chase 1334*	AF262815	AF265483	Pridgeon *et al*. 2001
Barbosella dolichorhiza Schltr.	*Heidelberg 123410*	EF079370	EF079328	Górniak *et al*. 2016
Barbosella gardneri (Lindl.) Schltr.	*Van der Berg 2001*	JQ306335		Chiron *et al*. 2012
Barbosella geminata Luer	*Bogarín 2011*		EU214308	Lehaye *et al*. 2008
Barbosella handroi Hoehne	*Chase 1436*	AF262813		Pridgeon *et al*. 2001
Barbosella miersii (Lindl.) Schltr.	*Chase 6809*	AF262816		Pridgeon *et al*. 2001
Barbosella orbicularis Luer	*Chase 1444*	AF262814		Pridgeon *et al*. 2001
Barbosella prorepens (Rchb.f.) Schltr. (1)	*Cuellar 19*		JN589956	Sosa *et al*. 2013
Barbosella prorepens (Rchb.f.) Schltr. (2)	*Chase 17835*		EU214140	Lehaye *et al*. 2008
Barbosella sp	*Karremans 5121*		KP012451	Karremans *et al*. 2015
Barbosella spiritu-sactensis (Pabst) F. Barros & Toscano	*Chiron 09437*	JQ306334		Chiron *et al*. 2012
Dresslerella elvallensis Luer (1)	*Chase 1279*	AF262901	AF265477	Pridgeon *et al*. 2001
Dresslerella elvallensis Luer (2)	*Karremans 5741*	KY988812	KY988632	Pérez-Escobar *et al*. 2017
Dresslerella hirsutissima (C.Schweinf.) Luer	*Chase 1306*	AF262902		Pridgeon *et al*. 2001
Dresslerella hispida (L.O.Williamns) Luer (1)	*Bogarín 10001*	KY988815	KP012428	Pérez-Escobar *et al*. 2017
Dresslerella hispida (L.O.Williamns) Luer (2)	*Karremans 5738*	KY988813	KP012427	Pérez-Escobar *et al*. 2017
Dresslerella hispida (L.O.Williamns) Luer (3)	*Karremans 6435*	KY988814	KY988633	Pérez-Escobar *et al*. 2017
Dresslerella pertusa (Dressler) Luer (1)	*Karremans 5787*	KY988817		Pérez-Escobar *et al*. 2017
Dresslerella pertusa (Dressler) Luer (2)	*Chase 1326*	AF262903		Pridgeon *et al*. 2001
Dresslerella pilosissima (Schltr.) Luer	*Bogarín 6243*	KY988818	KP012446	Pérez-Escobar *et al*. 2017
Dresslerella sp	*Karremans 6478*	KY988819	KY988635	Pérez-Escobar *et al*. 2017

Echinosepala aff. tomentosa (Luer) Pridgeon & M.W.Chase	*Karremans 5957*		KP012435	Karremans *et al*. 2015
Echinosepala aspasicensis (Rchb.f.) Pridgeon & M.W.Chase (1)	*Chase 971*	AF262905	AF302645	Pridgeon *et al*. 2001
Echinosepala aspasicensis (Rchb.f.) Pridgeon & M.W.Chase (2)	*Bogarín 8211*	KP012468		Karremans *et al*. 2015
Echinosepala aspasicensis (Rchb.f.) Pridgeon & M.W.Chase (3)	*Bogarín 1945*	KP012469	EU214340	Karremans *et al*. 2015
Echinosepala expolita Pupulin & Belfort	*Bogarín 1871*	KP012479		Karremans *et al*. 2015
Echinosepala lappiformis (A.Heller & L.O.Williams) Pridgeon & M.W.Chase	*Bogarín 9554*	MT556803	MT571342	This study
Echinosepala longipedunculata Pupulin & Karremans (2)	*Bogarín 5449a*	KP012480		Pupulin *et al*. 2017
Echinosepala longipedunculata Pupulin & Karremans (1)	*Bogarín 5449b*	KP012481		Pupulin *et al*. 2017
Echinosepala pan (Luer) Pridgeon & M.W.Chase (2)	*Bogarín 1913*	KP012471	KP012429	Pupulin *et al*. 2017
Echinosepala pan (Luer) Pridgeon & M.W.Chase (1)	*JBL859*	KP012470		Karremans *et al*. 2015
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (1)	*Bogarín 10716*	KP012474		Karremans *et al*. 2015
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (2)	*Bogarín 4678*		KP012434	Karremans *et al*. 2015
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (3)	*Karremans 3199*		KP012431	Karremans *et al*. 2015
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (4)	*Bogarín 10717*		KP012433	Pupulin *et al*. 2017
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (5)	*Bogarín 7137*	KP012472		Pupulin *et al*. 2017
Echinosepala sempergemmata (Luer) Pridgeon & M.W.Chase (6)	*Bogarín 5775*	KP012473	KY988637	Karremans *et al*. 2015
Echinosepala sp(1)	*Karremans 5986*	KP012477		Karremans *et al*. 2015
Echinosepala sp(2)	*Karremans 5985*	KP012478	KP012436	Karremans *et al*. 2015
Echinosepala stonei (Luer) Pridgeon & M.W.Chase (1)	*Bogarín 7190*	KP012484		Pupulin *et al*. 2017
Echinosepala stonei (Luer) Pridgeon & M.W.Chase (2)	*Bogarín 5777b*	KP012483		Pupulin *et al*. 2017
Echinosepala stonei (Luer) Pridgeon & M.W.Chase (3)	*Bogarín 5777a*	KP012482		Pupulin *et al*. 2017
Echinosepala tomentosa (Luer) Pridgeon & M.W.Chase	*Bogarín 5622*	KP012485		Pupulin *et al*. 2017

Echinosepala uncinata (Fawc.) Pridgeon & M.W.Chase (1)	*Chase 1321*	AF262904	AF265478	Pridgeon *et al*. 2001
Echinosepala uncinata (Fawc.) Pridgeon & M.W.Chase (2)	*Bogarín 5871a*	KP012486		Karremans *et al*. 2015
Echinosepala uncinata (Fawc.) Pridgeon & M.W.Chase (3)	*Bogarín 5871b*	KP012487		Pupulin *et al*. 2017
Echinosepala vittata (Pupulin & M.A.Blanco) Luer	*Blanco 1324*	KP012488		Karremans *et al*. 2015
Myoxanthus affinis (Lindl.) Luer (1)	*Rojas-Alvarado 69_3*		MT571349	This study
Myoxanthus affinis (Lindl.) Luer (2)	*Rojas-Alvarado 69*	MT556806	MT571347	This study
Myoxanthus affinis (Lindl.) Luer (3)	*Rojas-Alvarado 69_2*	MT556805	MT571348	This study
Myoxanthus affinis (Lindl.) Luer (4)	*Karremans 6990*	MT556804	MT571346	This study
Myoxanthus ceratothallis (Rchb.f.) Luer	*Karremans 8071*	MT556817	MT571350	This study
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (1)	*Karremans 5868_AK1*	MT556808	MT571340	This study
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (2)	*Karremans 5693_AK2*	MT556807	MT571351	This study
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (3)	*Karremans 5693_GRA1*	MT556809	MT571352	This study
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (4)	*Karremans 5693_AK1*		KP012444	Karremans *et al*. 2015
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (4)	*Karremans 5693_AK1*	KY988920		Pérez-Escobar *et al*. 2017
Myoxanthus cereus (Ames) Luer ex Rojas-Alv. & Karremans (5)	*Karremans 5868_GRA1*	MT556810	MT571353	This study
Myoxanthus colothrix (Luer) Luer (1)	*Rojas-Alvarado 6*	MT556816		This study
Myoxanthus colothrix (Luer) Luer (2)	*Bogarín 7689*	MT556813	MT610367	This study
Myoxanthus colothrix (Luer) Luer (3)	*Rojas-Alvarado 5*	MT556815	MT610365	This study
Myoxanthus colothrix (Luer) Luer (4)	*Bogarín 7680*	MT556814	MT610366	This study
Myoxanthus congestus (A.Rich. & Galeotti) Soto Arenas (1)	*Karremans 1300*	MT556812	MT571365	This study
Myoxanthus congestus (A.Rich. & Galeotti) Soto Arenas (2)	*Karremans 5281*	MT556811	MT571354	This study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (1)	*Chase 1323*	AF262882		Pridgeon *et al*. 2001
Myoxanthus parahybunensis (Barb.Rodr.) Luer (10)	*Karremans 5257*	MT556819	MT571356	this study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (2)	*Karremans 5953*	KY988922	KP012440	Pérez-Escobar *et al*. 2017
Myoxanthus parahybunensis (Barb.Rodr.) Luer (3)	*Karremans 5952*	KY988918		Pérez-Escobar *et al*. 2017
Myoxanthus parahybunensis (Barb.Rodr.) Luer (3)	*Karremans 5952*		KP012439	Karremans *et al*. 2015

Myoxanthus parahybunensis (Barb.Rodr.) Luer (4*)*	*Chiron 9155*	JQ306343		Chiron *et al*. 2012
Myoxanthus parahybunensis (Barb.Rodr.) Luer (5)	*Rojas-Alvarado 115_2*	MT556821	MT571344	This study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (6)	*Rojas-Alvarado 115*	MT556822	MT571360	This study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (7)	*Rojas-Alvarado 1*		MT571359	This study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (8)	*Bogarín 6948*	MT556820	MT571358	this study
Myoxanthus parahybunensis (Barb.Rodr.) Luer (9)	*Bogarín 6924*	MT556818	MT571357	this study
Myoxanthus georgei (Luer) Luer	*Karremans 8078*	MT556825		This study
Myoxanthus gyas (Luer & R.Vásquez) Luer	*Karremans 8075*	MT556826		This study
Myoxanthus hirsuticaulis (Ames & C.Schweinf.) Luer (1)	*Bogarín 5875*	KY988919		Pérez-Escobar *et al*. 2017
Myoxanthus hirsuticaulis (Ames & C.Schweinf.) Luer (1)	*Bogarín 5875*		MT571343	this study
Myoxanthus hirsuticaulis (Ames & C.Schweinf.) Luer (2)	*Bogarín 5872*	MT556824	MT571355	this study
Myoxanthus lonchophyllus (Barb.Rodr.) Luer	*Chase 1332*	AF262884		Pridgeon *et al*. 2001
Myoxanthus monophyllus Poepp. & Endl.	*Karremans 8077*	MT556827		This study
Myoxanthus punctatus (Barb.Rodr.) Luer (1)	*Van denBerg 2049*	JQ306349		Chiron *et al*. 2012
Myoxanthus punctatus (Barb.Rodr.) Luer (2)	*Chase 1324*	AF262885		Pridgeon *et al*. 2001
Myoxanthus reymondii (H.Karst.) Luer	*Karremans 8070*	MT556828	MT571338	This study
Myoxanthus ruschii Fraga & L.Kollmann	*Van den Berg 2005*	JQ306352		Chiron *et al*. 2012
Myoxanthus scandens (Ames) Luer (1)	*Pupulin 837*	MT556829	MT571345	This study
Myoxanthus scandens (Ames) Luer (2)	*Karremans 1322*	KY988921		Pérez-Escobar *et al*. 2017
Myoxanthus scandens (Ames) Luer (2)	*Karremans 1322*		KP012443	Karremans *et al*. 2015
Myoxanthus sotoanus Pupulin, Bogarín & Mel.Fernández (2)	*Pupulin 5044*		EU214413	Lahaye *et al*. 2008
Myoxanthus seidelii (Pabst.) Luer	*Van den Berg 2054*	JQ306350		Chiron *et al*. 2012
Myoxanthus serripetalus (Kraenzl.) Luer (1)	*Heidelberg 124228*	EF079369	EF065600	Gorniak *et al*. 2006
Myoxanthus serripetalus (Kraenzl.) Luer (2)	*Chase 1329*	AF262883		Pridgeon *et al*. 2001

Myoxanthus sotoanus Pupulin, Bogarín & Mel.Fernández	*Blanco 1725*	MT556832	MT571337	This study
Myoxanthus exasperatus (Lindl.) Luer (1)	*Bogarín 1240*		EU214414	Lahaye *et al*. 2008
Myoxanthus exasperatus (Lindl.) Luer *(2)*	*Rojas-Alvarado 36*	MT556830	MT571339	This study
Myoxanthus exasperatus (Lindl.) Luer (3)	*Rojas-Alvarado 42*	MT556831	MT571341	This study
Myoxanthus trachychlamys (Schltr.) Luer (1)	*Karremans 8074*	MT556833	MT571361	This study
Myoxanthus trachychlamys (Schltr.) Luer (2)	*Rojas-Alvarado 94*	MT556823	MT571362	This study
Myoxanthus uxorius (Luer) Luer (1)	*Karremans 8079*	MT556834	MT571364	This study
Myoxanthus uxorius (Luer) Luer (2)	*Karremans 8072*	MT556835	MT571363	This study
Pleurothallopsis microptera (Schltr.) Pridgeon & M.W.Chase	*Karremans 5742*	KY988958	KY988765	Pérez-Escobar *et al*. 2017
Pleurothallopsis nemorosa (Barb.Rodr.) Porto & Brade (1)	*Bock s.n. none*	AF291099	AF291104	Pridgeon *et al*. 2001
Pleurothallopsis nemorosa (Barb.Rodr.) Porto & Brade (2)	*Rodrigues 516*	KT599880	KT709650	unpublished
Pleurothallopsis reichenbachiana (Endrés & Rchb.f.) Pridgeon & M.W.Chase	*Bogarín 111*	KY988959	KY988766	Pérez-Escobar *et al*. 2017
Pleurothallopsis striata (Luer & Escobar) Pridgeon & M.W.Chase (1)	*Karremans 5744*	KY988960	KY988767	Pérez-Escobar *et al*. 2017
Pleurothallopsis striata (Luer & Escobar) Pridgeon & M.W.Chase (2)	*Chase 1103*	AF262910	AF265480	Pridgeon *et al*. 2001
Pleurothallopsis tubulosa (Lindl.) Pridgeon & M.W.Chase	*Bogarín 7618*	KY988961	KY988768	Pérez-Escobar *et al*. 2017
Pleurothallopsis ujarrensis (Rchb.f.) Pridgeon & M.W.Chase	*Karremans 2704*		KP012450	Karremans *et al*. 2015
Restrepia antennifera Kunth	*Chase 982*	AF262906		Pridgeon *et al*. 2001
Restrepia aristulifera Garay & Dunst.	*Chase 1109*	AF262907	AF265481	Pridgeon *et al*. 2002
Restrepia chocoensis Garay	*Karremans 4872*	MT556836		this study
Restrepia muscifera (Lindl.) Rchb.f. ex Lindl. (1)	*Pupulin 3921*		EU214438	Lahaye *et al*. 2008
Restrepia muscifera (Lindl.) Rchb.f. ex Lindl. (2)	*Rodrigues 512*		KT709651	unpublished
Restrepia muscifera (Lindl.) Rchb.f. ex Lindl. (3)	*Bogarín 9208*	KY988965	KP012449	Pérez-Escobar *et al*. 2017
Restrepia muscifera (Lindl.) Rchb.f. ex Lindl. (4)	*Chase 308*	AF262908		Pridgeon *et al*. 2001
Restrepia sp	*AD7LJ60*	MF349131	MF349936	Zúñiga *et al*. 2017
Restrepia trichoglossa F.Lehm. ex Sander (1)	*Heidelberg 23495*		EF079329	Gorniak *et al*. 2006

Restrepia trichoglossa F.Lehm. ex Sander (2)	*JBL02309*		KP012448	Karremans *et al*. 2015
Restrepia xanthophthalma Rchb.f.	*Chase 308*		AY370654	Freudenstein *et al*. 2004
Restrepiella lueri Pupulin & Bogarín	*JBL18696*	KY988966	KY988769	Pérez-Escobar *et al*. 2017
Restrepiella ophiocephala (Lindl.) Garay & Dunst.	*Chase 291*	AF262909	AF265482	Pridgeon *et al*. 2001
Restrepiella ovatipetala (Chiron & Xim.Bols.) Rojas-Alv. & Karremans	*Van den Berg 2024*	JQ306351		Chiron *et al*. 2012

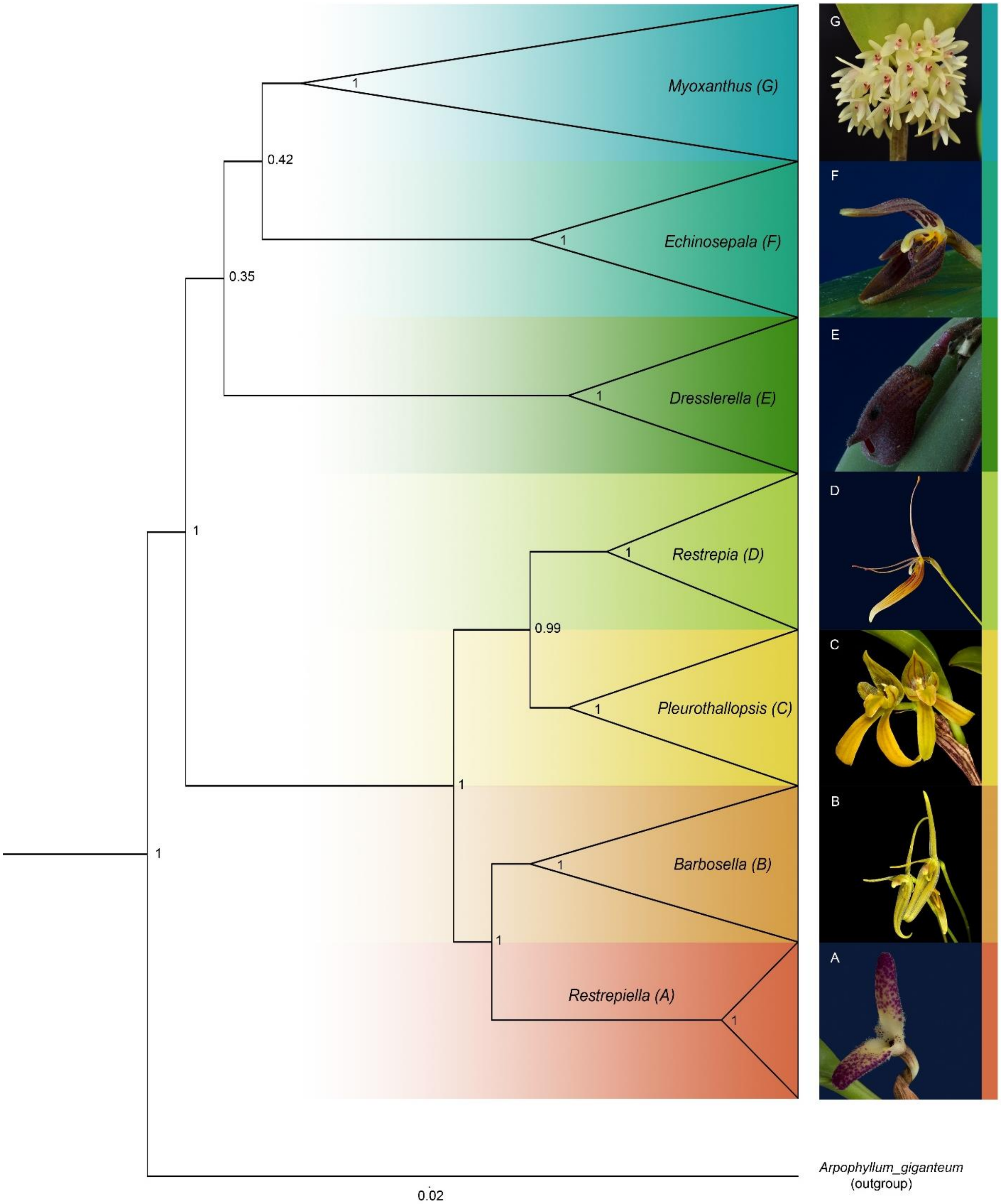

Figure 1. Phylogenetic Bayesian inference based on the concatenated dataset (nrITS+*matK*) of *Restrepia affinity* in collapse clades. Values on nodes represent Bayesian posterior probability (pp). Photograph by: G. Salguero (A). R. Parsons (B & C). M. Díaz (D–F). M. Rosim (G).

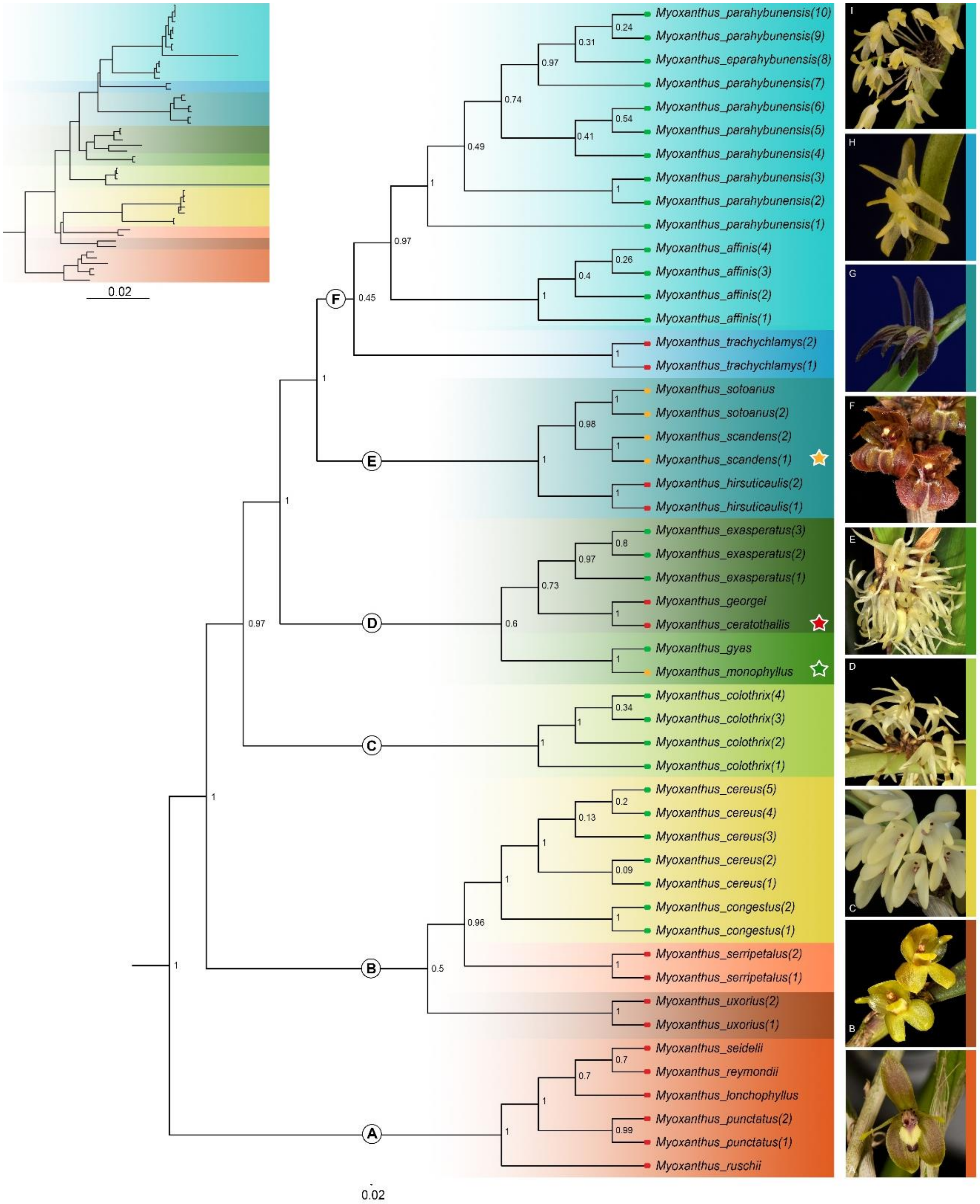

Figure 2. Expanded phylogenetic Bayesian inference of *Myoxanthus* clade based on nrITS+*matK* data. Node values=Bayesian posterior probability (pp). Letters on circles=major clades. Subclades represented by colors. Terminal color tips=currently section of each species, red=*Myoxanthus* sect. *Antenella*, green=*M*. sect. *Myoxanthus*, yellow=*M*. sect. *Scandentia*, with stars indicating its type species. Photograph by: Ron Parsons (A, B, E, F). Authors (C, D, H, I), D. Bogarín (C).

Figure 3. Species of the *Myoxanthus lonchophyllus* group. A. *M. conceicionensis*. B. *M. lonchophyllus*. C–E. *M. punctatus*. Photographs by: D. Holland (A). R. Parsons (B–E). Arrow indicate the hispid-hirsute anther cap. Arrow indicate the hispid-hirsute anther cap.

Figure 4. Species of the *Myoxanthus reymondii* group. A. *M. cimex*. B. *M. hystrix*. C. *M. reymondii*. D. *M. melittanthus*. Photographs by: S. Vieira-Uribe (A). R. Parsons (B–D).

Figure 5. Species of the *Myoxanthus congestus* group. A. *M. cereus*. B. *M. pulvinatus*. C. *M. octomerioides*. D–C. *M. congestus*. Photographs by: Authors (A, D, E). M. Rosim (B). P. Mannens (C).

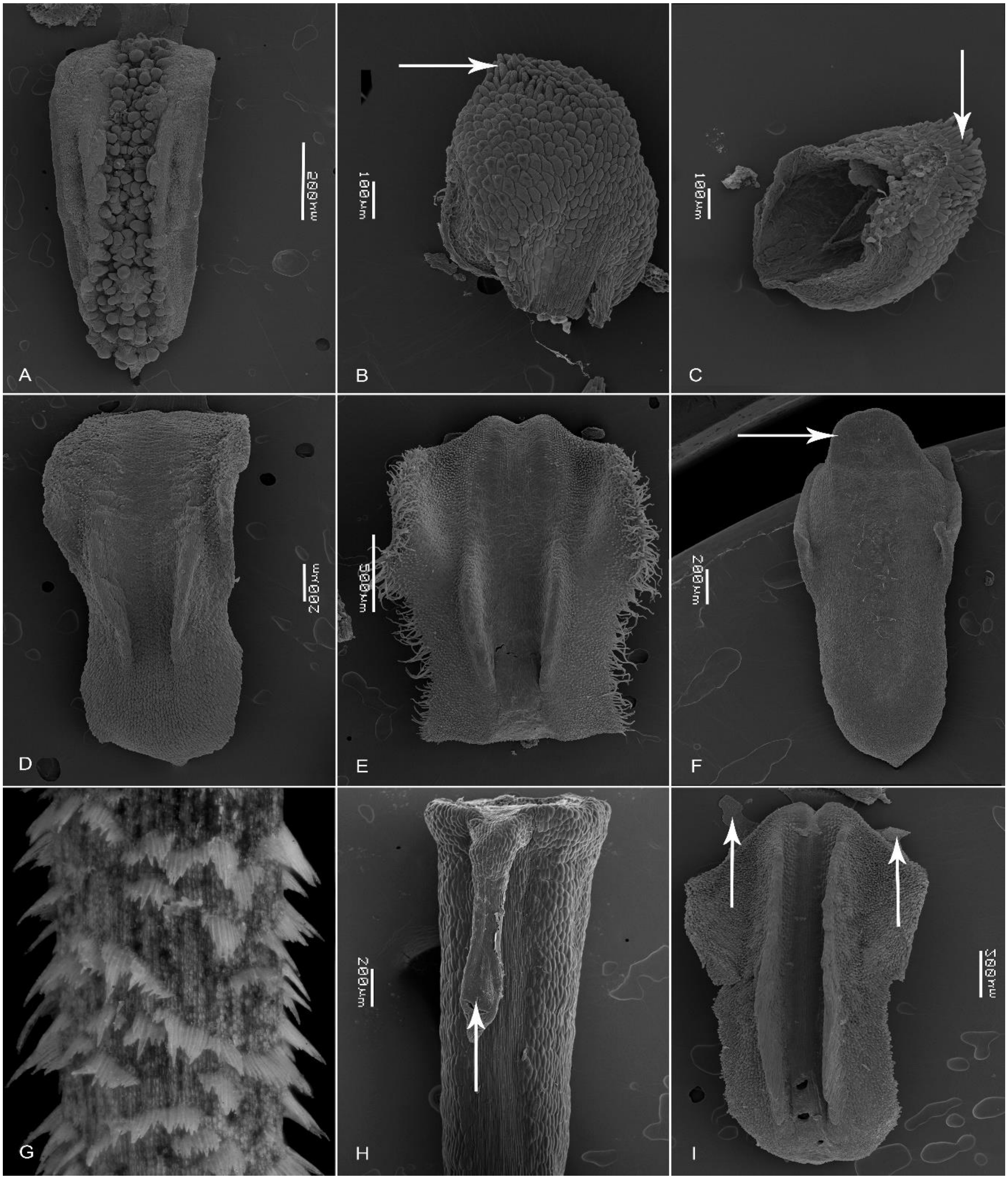

Figure 6. Scanning electron microscopy. A. lip of *Myoxanthus cereus*. B. Anther cap of *M. cereus* (arrow indicate the papillose-verrucose apex). C. Anther cap of *M. congestus* (arrow indicate the papillose-verrucose apex). D. Lip of *M. colothrix*. E. Lip of *M. hirsuticaulis*. F. Lip of *M. trachychlamys* (arrow indicate the basal callus). G. Sheaths' trichomes on *M. trachychlamys*. H. Pedicel of *M. congestus* with the remain of the axis as a vestige (arrow indicate the vestige). I. Lip of *M. scandens* (arrows indicate the basal lobes).

Figure 7. Species of the *Myoxanthus uxorius* and *M. serripetalus* group. A–C. *M. uxorius*. D–E. *M. serripetalus*. Photographs by: S. Vieira-Uribe (A). R. Parsons (B, C). G. Verhellen (D). A. Phillip (E).

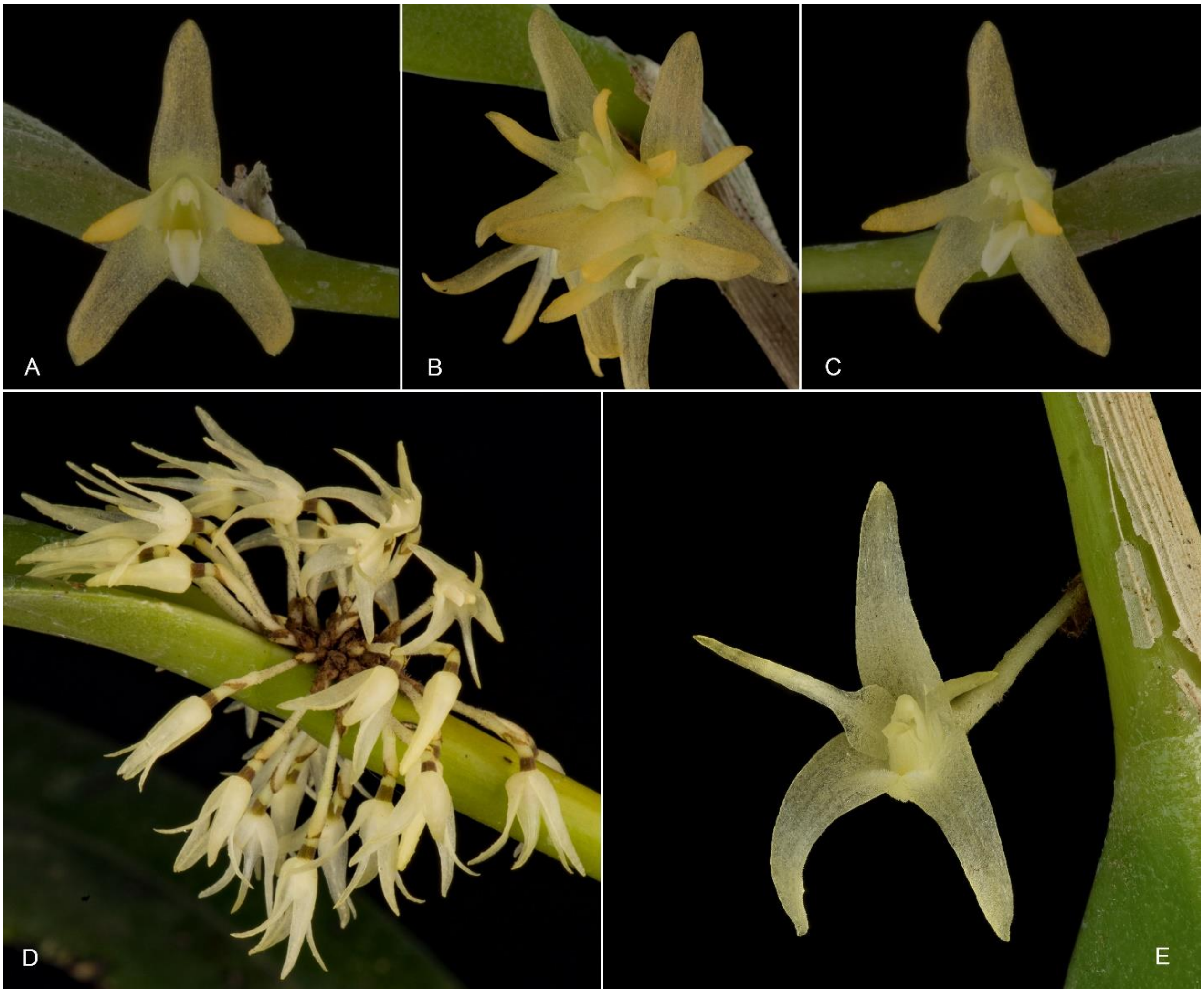

Figure 8. Species of the *Myoxanthus trachychlamys* and *M. colothrix* group. A–C. *M. trachychlamys*. D–E. *M. colothrix*. Photographs by: Authors.

Figure 9. Species of the *Myoxanthus monophyllus* group. A. *M. chloe*. B. *M. frutex*. C. *M. gyas*. D–E. *M. monophyllus*. Photographs by: Authors (A). R. Repasky (B, C). R. Gelis (D). R. Parsons (E). Arrow indicate the floral bract.

Figure 10. Species of the *Myoxanthus scandens* group. A. *M. scandens*. B. *M. antennifer*. C. *M. sotoanus*. D. *M. hirsuticaulis*. E. *M. fimbriatus*. Photographs by: D. Bogarín (A). A. Hirtz (B). Authors (C, D). P. Mannens (E).

Figure 11. Species of the *Myoxanthus affinis* group. A–B. *M. affinis*. C. *M. parahybunensis*. D–E. *M. aff. herzogii*. Photographs by: R. Parsons (A). B.R. Chambi (B). Autors (C). L.E. Yupanqui Godo (D, E).