

A NOTE ON *MASDEVALLIA ZAHLBRUCKNERI* AND *M. UTRICULATA* (ORCHIDACEAE)

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Abstract. *Masdevallia utriculata* and *M. zahlbruckneri* are characterized and illustrated based on living plants from Costa Rica. The species are compared with each other on the basis of their general similar morphology. Their taxonomic status is reviewed.

Keywords: *Masdevallia utriculata*, *M. zahlbruckneri*, new record, taxonomy, *Zahleria*

Heinrich Gustav Reichenbach was the first to propose subdivisions of the genus *Masdevallia* Ruiz & Pav.; he published 14 sections in total (Reichenbach f., 1873, 1874a, 1874b, 1875, 1876a, 1876b, 1877, 1878a, 1878b; Woolward, 1896; Luer, 1986), including *Masdevallia* sect. *Amandae* Rchb.f. (Reichenbach f., 1874b). Luer (1986) raised *Amanda* to the rank of subgenus and included five sections within it: *Masdevallia* sections *Amandae*, *Fissae* Rchb.f., *Nidificae* Luer, *Ophioglossae* Luer and *Pygmaeae* Luer. Luer would later elevate these sections to the rank of subgenus (Luer, 2000).

When establishing subgenus *Pygmaeae* Luer, the author united subgenus *Masdevallia* sections *Amaluzae* and *Aphanes* with subgenus *Amanda* section *Pygmaeae* (Luer, 1986). He also clarified that, although the species in subgenus *Pygmaeae* were probably not closely related, he brought them together because of their tufted small habit. In turn, subgen. *Pygmaeae* was divided into four sections: *Amaluzae* Luer, *Aphanes* Luer, *Pygmaeae* Luer, and *Zahlbrucknerae* Luer. Luer (2000) characterized *Masdevallia* sect. *Zahlbrucknerae* as a group of small to medium size herbs with caespitose habit, with a successively flowered raceme borne by an ascending, horizontal to descending, terete peduncle, provided with smooth or slightly costate ovaries and sepals contracted into slender tails. The lips are more or less oblong with a pair of longitudinal calli. The most distinguishing feature of this section is the morphology of the callous petals, which present a distinct, retrorse process at the base, and one or two retrorse teeth above the unguiculate base. In the most recent reclassification of *Masdevallia*, Luer (2006) created the novel generic concept, *Zahleria*, typified by *Z. zahlbruckneri* (Kraenzl.) Luer. *Zahleria* additionally includes, *Masdevallia naranjapatae* (Luer) Luer and *M. vieirana* (Luer & R.Escobar).

Meanwhile, in a very different corner of *Masdevallia*, Reichenbach f. proposed *Masdevallia* sect. *Coriaceae*

Rchb.f. (Reichenbach f., 1874), which in turn Veitch and Sons (1889) reduced to subsection. Luer (1986) retained *Masdevallia* sect. *Coriaceae* and split into subsections *Coriaceae* (Rchb.f.) H.J.Veitch and *Duriae* Luer. In 2000, Luer elevated subsection *Duriae* to the sectional rank, and in 2006 he reduced sect. *Duriae* to the synonymy of his new genus *Regalia* (Luer, 2000, 2006). According to Luer, *Regalia* is a small Andean genus composed of ten species, characterized by large plants with stout ramicauls, thickly coriaceous leaves, and racemes of large, rigid, fleshy, long-lasting, long-caudate flowers produced in slow succession. The petals are thickly cartilaginous, paddle-shaped and truncate, and the lip is oblong and thick, with a pair of concavities at the base (Luer, 2006). *Regalia utriculata* (Luer) Luer (= *Masdevallia utriculata*) is one of its smallest members and lacks the otherwise characteristic long tails of the lateral sepals.

Masdevallia utriculata and *M. zahlbruckneri* share several morphological traits with other species of *Masdevallia* that have not been placed in the same section, subgenus or even genus (Luer, 2006). We here present material of both the species from Costa Rica and discuss their taxonomic status.

Masdevallia zahlbruckneri Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 413. 1921. TYPE: COSTA RICA. Ohne genauem Standort (Endrés) [Endrés 463, collected and illustrated in 1870] (holotype: W 0019499).

Epiphytic, caespitose, small, *herbs*. *Roots* slender. *Ramicauls* slender, erect, 1.0–1.5 cm long, enclosed by 2–3 close, tubular sheaths. *Leaf* erect to suberect, coriaceous, 4.6–8.1 cm long including a petiole, the blade narrowly obovate, obtuse, 1.9–2.0 cm wide, gradually narrowed below into the sub-petiolate base. *Inflorescence* a loose, successively few-flowered raceme borne by a descending to horizontal peduncle 2.7–7.0 cm long, produced from low on the ramicaul, with a bract below the middle. *Floral bracts*

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tubular, 2–5 mm long. *Pedice* 4–10 mm long. *Ovary* curved, 2–4 mm long. *Sepals* glabrous externally, the *dorsal sepal* yellow, often flecked with red or purple, microscopically cellular growths, obovate, 17–22 mm long, 4–6 mm wide including the tails in the natural position, connate to the lateral sepals for 3–5 mm to form a cylindrical tube, the free portion broadly triangular, the obtuse apex contracted into an erect, slender (occasionally thickened distally), yellow tail 12–17 mm long; the *lateral sepals* red-purple, diffusely spotted with darker purple, the spots sometimes raised, with tufts of red hairs, cellular-pubescent to shortly pubescent within, connate 7–12 mm into an ovate, bifid lamina 17–23 mm long, 8–10 mm wide, the acute apices contracted into slender, yellow tails 7–9 mm long; *petals* white, dark red-purple on the labellar half, elliptical-oblong, 4–6 mm long, 2–3 mm wide, the apex obtuse, apiculate or retuse, the labellar half callous, ending in one retrorse teeth above the unguiculate base; *lip* white, diffusely dotted with purple, the dots sometimes raised, oblong-ligulate, 4–7 mm long, 1.7–2.0 mm wide, very slightly narrowed near the middle, the apex subacute, rounded to subtruncate, the disc lightly channeled between a low, longitudinal pair of calli, the base subtruncate, hinged below. *Column* yellow-white to green, the margin purple, semiterete, 4–5.5 mm long, the foot stout with a short, incurved extension.

Distribution: from Costa Rica to Ecuador.

Eponymy: The name honors Alexander Zahlbruckner (Fig. 1) an Austrian botanist who specialized in the study of lichens. He studied at the University of Vienna, and was the grandson of the well-known Austrian botanist Johann Baptist Zahlbruckner (Pisút, 2002). Alexander supplied Fritz Kraenzlin with many specimens from Reichenbach's herbarium.

Phenology: Apparently flowering all year round.

Additional specimens examined: COSTA RICA. Alajuela: San Carlos, Venecia, without further data collection. It flourished in culture in the Lankester Botanical Garden, *C. Blanco s.n.* (JBL-spirit); Parque Nacional Rincón de la Vieja, rd. to Colonia Grande by Quebrada Rancho Grande, 700 m, 7 July 1978, *C. Todzia 351* (CR); San Ramón, September 1990, *L. Acosta s.n.* (USJ); San Carlos, Venecia, flourished in culture at Lankester Botanical Garden on 20 March 2002 *C. Blanco s.n.* (CR); San Carlos, Reserva Forestal Juan Castro Blanco, November 1992, flourished in culture at Lankester Botanical Garden on April 1993, *Dora E. Mora s.n.* (USJ) Guanacaste: Tilarán, Tierras Morenas, desviación a la izquierda después del Río Cabuyo, camino al Proyecto Geotérmico Tenorio y Cerro Jilguero, ca. 4.5 km norte de Tierras Morenas, ladera sureste del Volcán Tenorio, 10°36'11.6"N, 85°00'05.3"W, 900–1000 m, bosque



FIGURE 1. Portraits of Alexander Zahlbruckner, taken from Pisut (2002).

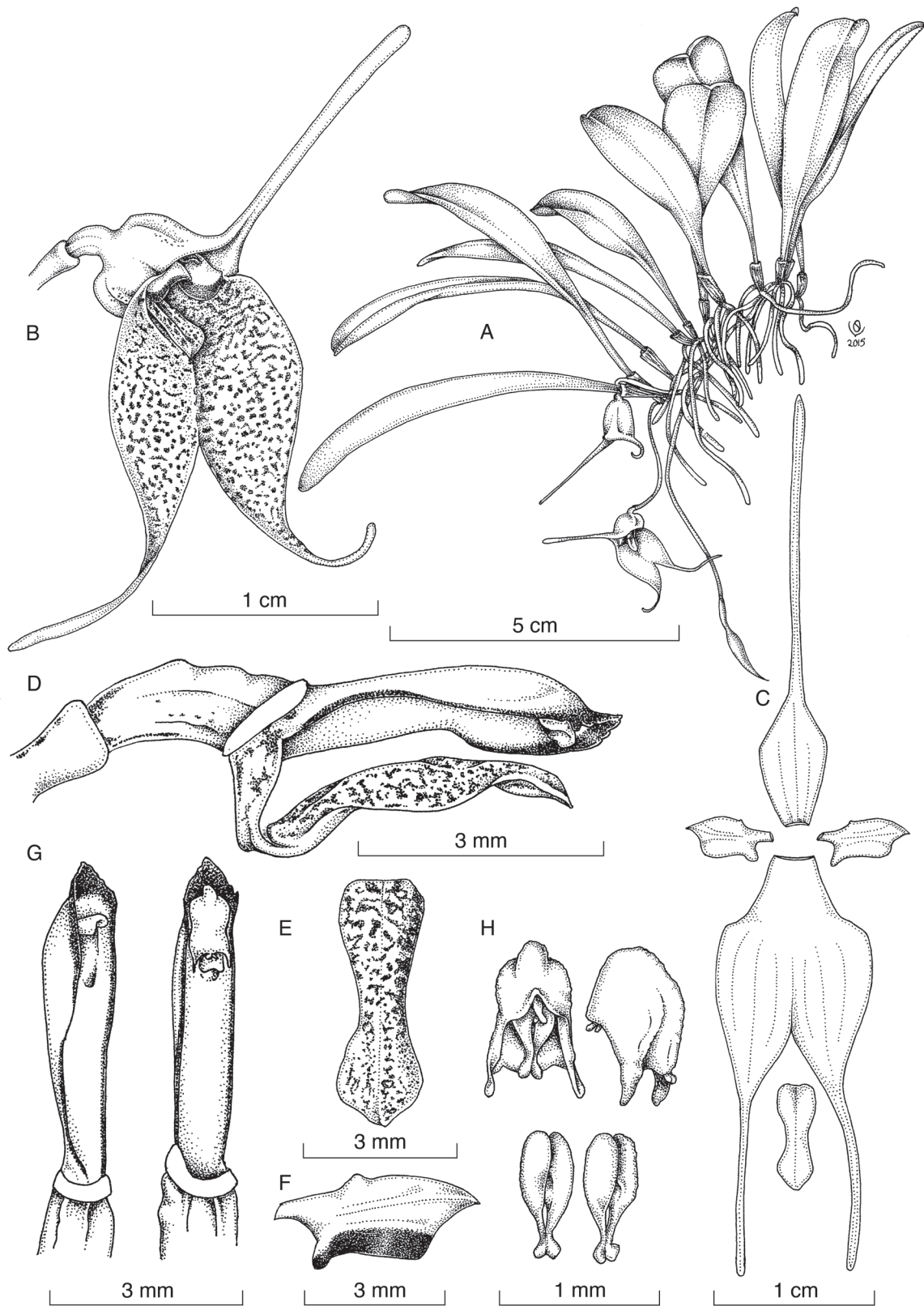


FIGURE 2. *Masdevallia zahlbruckneri*. A, Habit; B, Flower; C, Perianth, flattened; D, Column and lip, side view; E, Lip; F, Petal, ventral view; G, Column, ventral and side views; H, Anther cap and pollinarium. Drawn from Karremans 5873 by L. Oses.

pluvial premontano, epífitas a orillas del camino y en bordes de potreros, 2 February 2006, *D. Bogarín, R.L. Dressler, R. Gomez and A. Rojas 2410* (JBL-spirit); Tilarán, Tierras Morenas, desviación a la izquierda después del Río Cabuyo, entrada al Proyecto Geotérmico Tenorio y Cerro Jilguero, ca. 7 km al noreste de Tierras Morenas, ladera sureste del Volcán Tenorio, 10°36'55.7"N, 85°00'43.1"W, 900–1100 m, bosque pluvial premontano, epífitas a orillas del camino y bosque secundario, 2 February 2006, *D. Bogarín, R. L. Dressler, R. Gómez, and A. Rojas 2413* (JBL-spirit); San José: Pérez Zeledón, San Andrés de Dota, epiphytic plant growth, 10 September 1990, *Victor Gin Lun s.n.* (USJ); Pérez Zeledón, San Ramón Norte, trail to the summit of Cerro Pelón, 1400–1640 m, 3 May 2000, *F. Pupulin, et al. 2405* (USJ); Pérez Zeledón, Paramo, 1420m, 9°29'01"N, 83°45'18"W, Paramo, bosque muy húmedo premontano, sobre la calle principal entre San Ramón Norte y Santa Eduvigis, epífitas al lado de la calle pocos km antes del pueblo, 6 April 2013, *A.P. Karremans, R. Lok, R. Ferreira and V. Ferreira 5873* (JBL-spirit) Fig. 2; Pérez Zeledón, Paramo, Los Ángeles, sobre el camino a San Gerardo de Dota, montañas al norte del río División, en línea con el centro de Los Ángeles, 1700 m, 9°29'55"N, 83°47'46"W, bosque pluvial premontano, a orillas del camino dentro del bosque, 29 May 2014, *A.P. Karremans and G. Meza, L. Oses 6246* (JBL-digital collection); same date and locality *A.P. Karremans, G. Meza and L. Oses 6247* (JBL-digital collection).

Masdevallia utriculata Luer. *Phytologia* 44(3): 169, 1979. TYPE: PANAMA. Chiriquí [Boquete]: epiphytic in cloud forest on Cerro Pate Macho, alt. 2200 m, 27 February 1979, *R. L. Dressler and J. Kuhn s.n.* (holotype, SEL; illustration *Luer 4073*).

Epiphytic, caespitose, *herbs*, small to medium in size. *Roots* coarse. *Ramicauls* slender, erect, 1.0–1.5 cm long, enclosed by 2–3 thin, close, tubular sheaths. *Leaf* erect, coriaceous, 6–10 cm long including an indistinct petiole 1.0–1.5 cm long, narrowly oblong-obovate, 1.2–1.5 cm wide, subacute to obtuse at the apex, narrowed below into the subpetiolate base. *Inflorescence* a congested, few-flowered raceme of successive flowers from low on the ramicaul, borne by a stout, suberect to horizontal peduncle, 1.5–2.0 cm long, with a bract near the middle. *Floral bract* tubular, 4–5 mm long. *Pedical* 4–15 mm long. *Ovary* subverrucose with undulate ribs, 2–5 mm long. *Sepals* fleshy, rigid, the *dorsal sepal* yellow-green, with a few purple verrucosities within, obovate, 12–20 mm long, 4–6 mm wide, connate to the lateral sepals for 5 mm into a cylindrical tube, the apex subacute, contracted into an erect, thick, subclavate, laterally compressed, yellow-green tail ca. 6–11 mm long; the *lateral sepals* yellowish, studded with multiple red excrescences within, connate 15 mm to form an obovate, coarsely verrucose, bifid lamina 15–20 mm long, 9–13 mm wide expanded, with the apices subacute; *petals* yellow, spotted with purple on the labellar half, oblong, 5.0–5.5 mm long, 2 mm wide, the apex truncate-retuse, with a longitudinal callus along both borders, the upper overhanging the apex, the callus of the labellar margin distinct, ending between the basal and middle thirds; *lip* dull yellow, diffusely dotted

with purple, thick, obovate, minutely verrucose, 5.0–6.5 mm long, 2–3 mm wide, the apex broadly rounded, verrucose, the disc shallowly sulcate between a longitudinal pair of oblique calli obtusely angled above the middle, the base bilobed-cordate, each lobe deeply saccate, hinged beneath. *Column* yellow, marked with purple, semiterete, 5 mm long, the foot equally long, spotted with purple, with an incurved 3 mm extension.

Distribution: Known from Western Panama and from Coto Brus and Talamanca in Costa Rica at elevations between 2100–2400 m.

Etymology: From the Latin *utriculatus*, “with small bladders,” referring to the base of the lip.

Phenology: Apparently flowering all year round.

Additional specimens examined: COSTA RICA. Limón: Talamanca, Bratsi, Parque Internacional La Amistad, Valle del Silencio, sendero desde el Jardín (turbera) hacia los Cerros Tararias, cruzando el afluente del Río Terbi (Río de las Plantas), base del cerro conocido como “Ventanas,” 9°08'08.39"N, 82°57'32.58"W, 2400 m, bosque pluvial montano, 19 September 2014, *A. Karremans, M. Díaz, M. Fernández, C. Godínez, J. Godínez, L. Oses, J. Ramírez and D. Villalobos 6365* (JBL-spirit). Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Tablas, Finca Sandí-Hartmann “El Capricho,” camino a El Surá, 8°57'0.63"N, 82°44'59.72"W, 2017 m, bosque pluvial montano bajo, 10 December 2013, *D. Bogarín, A. Karremans, M. Fernández and L. Sandoval 10691* (JBL-spirit); Coto Brus, Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Tablas, en potreros de la Finca Sandí-Hartmann “El Capricho,” 8°58'01.98"N, 82°44'57.42"W, 2162 m, epífitas en árboles aislados en bosque pluvial montano bajo, 11 December 2013, *A. Karremans, D. Bogarín, M. Fernández and L. Sandoval 6169* (JB-spirit); Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 20 April 2012, *A.P. Karremans and J. Geml 5387* (JBL-spirit); Same date and locality *A.P. Karremans and J. Geml 5417* (JBL-spirit); Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, “*ad ager Sandiorum ‘El Capricho,’ supra arbores praecipue quercinis in collibus montibusque et ad margines pascuibus inter flumen Sutú,*” bosque muy húmedo premontano, 6 October 2010, *D. Bogarín, R.L. Dressler, M. Fernández and F. Pupulin 8088* (JBL-spirit); Same date and locality *M. Fernández, R.L. Dressler, D. Bogarín, F. Pupulin 430* (JBL-spirit); Same date and locality *M. Fernández, R.L. Dressler, D. Bogarín, F. Pupulin 431* (JBL-spirit); Coto Brus, Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Tablas, Finca Sandí-Hartmann “El Capricho,” camino a El Surá, 8°57'0.63"N 82°44'59.72"W, 2017 m, bosque pluvial montano bajo, 10 December 2013, *D. Bogarín, A. Karremans, M. Fernández and L. Sandoval 10652* (JBL-spirit) Fig. 3; Same date and locality, *D. Bogarín A. Karremans, M. Fernández and L. Sandoval 10647* (JBL-spirit); Same date and locality *A. Karremans, D. Bogarín, M. Fernández and L. Sandoval 6106* (JBL-spirit).

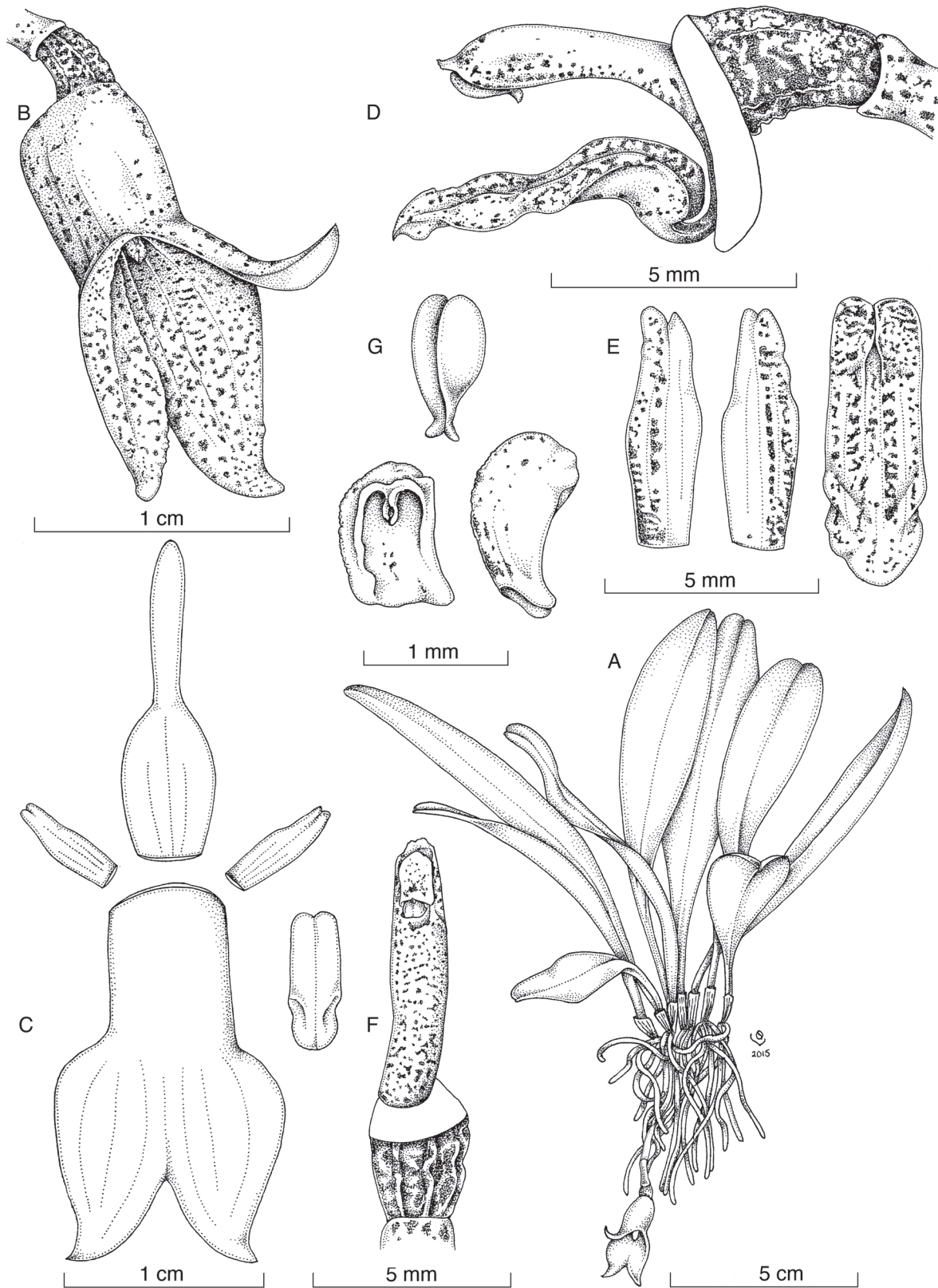


FIGURE 3. *Masdevallia utriculata*. **A**, Habit; **B**, Flower; **C**, Perianth, flattened; **D**, Column and lip, side view; **E**, Petals and lip, ventral view; **F**, Column, ventral view; **G**, Pollinarium and anther cap. Drawn from *D. Bogarín 10652* by L. Oses.

DISCUSSION

Masdevallia zahlbruckneri and *M. utriculata* share features including the relatively small caespitose habit (7–10 cm long tall), a short, horizontal peduncle (horizontal to descending in *M. zahlbruckneri*); a short, successively flowered raceme, the longitudinally convex ovary (slightly steeper in *M. zahlbruckneri*) and a superficial resemblance in the color pattern of the sepals and lip. *Masdevallia crescenticola* F.Lehm. & Kraenzl., *M. descendens* Luer & Andreetta, *M. leontoglossa* Rchb.f., *M. lintrricula* Königer, *M. loui* Luer & Dalström, *M. mascarata* Luer and Vasquez, *M. pyxis* Luer, are also morphologically similar to *M. zahlbruckneri* and *M. utriculata*, sharing a pendulous inflorescence (with exception of *M. mascarata* and *M. pyxis*), the yellow dorsal sepal, and the lateral sepal and lip marked with purple spots.

We can, nevertheless, also find several differences between *M. zahlbruckneri* and *M. utriculata*. In all the examined specimens, there is consistent variation in the length of the tails of each sepal, the tail of the dorsal sepal being up to 12 mm longer, and the one on the lateral sepals up to 7–9 mm longer in *M. zahlbruckneri* versus *M. utriculata*, respectively. The dorsal sepal in *M. utriculata* is prominently thickened apically, whilst the tail of *M. zahlbruckneri* is slender to only slightly thickened. The most important dissimilarity, found in the petals, led Luer (2006) to place the two species in different sections and even different genera. In *M. zahlbruckneri* the laminar half of the lip is callous, ending in an obtuse angle, or into one or two retrorse teeth above the unguiculate base; this characteristic is absent in *M. utriculata*, whose petals are oblong with a callous lower margin. The color pattern of the petals also differs between the two species; they are white and dark red-purple on the labellar half in *M. zahlbruckneri*, whereas in *M. utriculata* the petals are yellow, spotted with purple on the labellar half. The lip is oblong without marginal folds, the disc shallowly sulcate between a longitudinal pair of oblique calli obtusely angled above the middle and the disc lightly channeled between a low, longitudinal pair of calli, the base subtruncate, hinged below in *M. zahlbruckneri*. The yellow-white to green column of *M. zahlbruckneri* has a continuous purple margin, while the column of *M. utriculata* is marked with purple spots along the margins. The pollinaria also differ, although they are hardly noticeable (Fig. 4–6). The two species also have a different pattern of distribution and altitudinal range (Fig. 7–8). According to the known collecting itineraries of Endrés, it can be suspected that the type of *M. zahlbruckneri* came from the area around San Ramón, in the Tilarán mountain range Pupulin et al., 2014).

The process at the base of the petals has been one of the most important criteria to recognize species segregated from *Masdevallia* in different genera (Luer, 2006). Luer's *Acinopetala* differs from *Zahleria* in the petals, which have small process above or along the margin between the middle and basal third in *Acinopetala*, while in *Zahleria* they are provided with a longitudinal callus on the lower

half ending in a retrorse process (Luer, 2006). However, this particular feature is not always evident, and can sometimes vary within a single taxon. *Masdevallia schizopetala*, which has also been placed in *Masdevallia* sect. *Zahlbrucknerae*, was later transferred to the genus *Acinopetala* instead, on the basis of the distinct petals' callus. *Masdevallia humilis* Luer was originally described as a toothless relative of *M. zahlbruckneri*, but was later synonymized. This indicates that this feature does not represent a key character for the recognition of a natural group as species (Fig. 9).

High morphological variation was found in the flowers of *M. zahlbruckneri*, especially in the shape of petals and the length of the dorsal and lateral sepal tails, as was suggested by Luer (2000) where Luer even found that some populations of the species have a clavate dorsal sepal in Central America. *Masdevallia utriculata* is characterized by a broadly cylindrical sepaline tube with the widely expanded, red-verrucose lateral sepals tailless. The tail of the dorsal sepal is clavate. The studied specimens present a slight variation in the arrangement of the tails and the purple dots density of the sepals (Fig. 6).

Due to the overall similarity between the two species, both in terms of vegetative habit and floral shape, we were initially surprised to find out that they had not been associated with each other based on their general morphology, but were assigned instead to different genera, *Regalia* for *M. utriculata* and *Zahleria* for *M. zahlbruckneri* (Luer 2006). Our unpublished DNA analyses of the group confirm, however, that they are not closely related at all. In the sense of *Masdevallia* systematics, it is clear that there is still much to answer and understanding how each species relates to others is one of the most essential questions to resolve.

Flower morphology, most commonly used for the classification of species, has been amply proven to be convergent in many groups of Pleurothallidinae, frequently responding to pollinator adaptations rather than genetic history (Pridgeon et al., 2001; Karremans et al., 2013, 2015). Plant habit, although also under selective pressure due to ecological niche preferences, is however under less influence of the pollinators, and can be more constant amongst close relatives in the Pleurothallidinae. Phylogenetic inferences based on DNA data give us an unbiased view of the relationships amongst species and can be a guide to understand which morphological characteristics have actually converged and which are phylogenetically informative. It is clear now that some of the features used to group species of *Masdevallia* do not convey phylogenetic information and should therefore be revised. It is difficult to place species of *Masdevallia* in subgenera and sections with absolute confidence, and it is not surprising that the genera proposed as segregates of *Masdevallia* are not monophyletic (Abele, 2005, 2007; Pridgeon et al., 2005). We believe a phylogenetic analysis of the entire genus in its broad sense coupled with a morphological characterization of the resulting groups of species is very necessary.

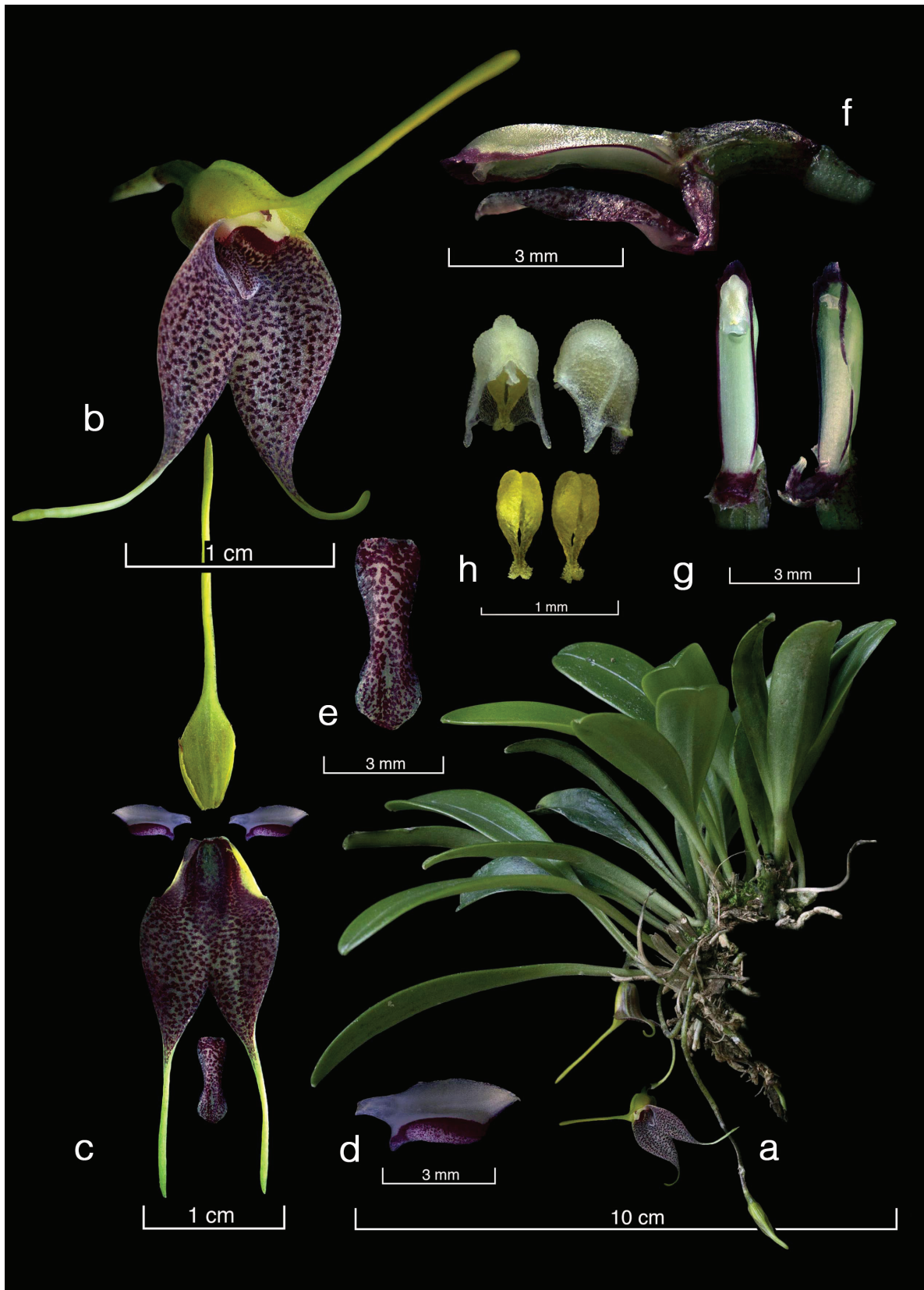


FIGURE 4. Lankester composite dissection plate (LCDP) of *Masdevallia zahlbruckneri*. **A**, Habit; **B**, Flower; **C**, Dissected perianth; **D**, Petal adaxial view; **E**, Lip, adaxial view; **F**, Column and lip, lateral view; **G**, Column, adaxial and three quarters view; **H**, Pollinarium and anther cap. All images from A. P. Karremans 5873, photographs by A. Karremans and L. Oses.

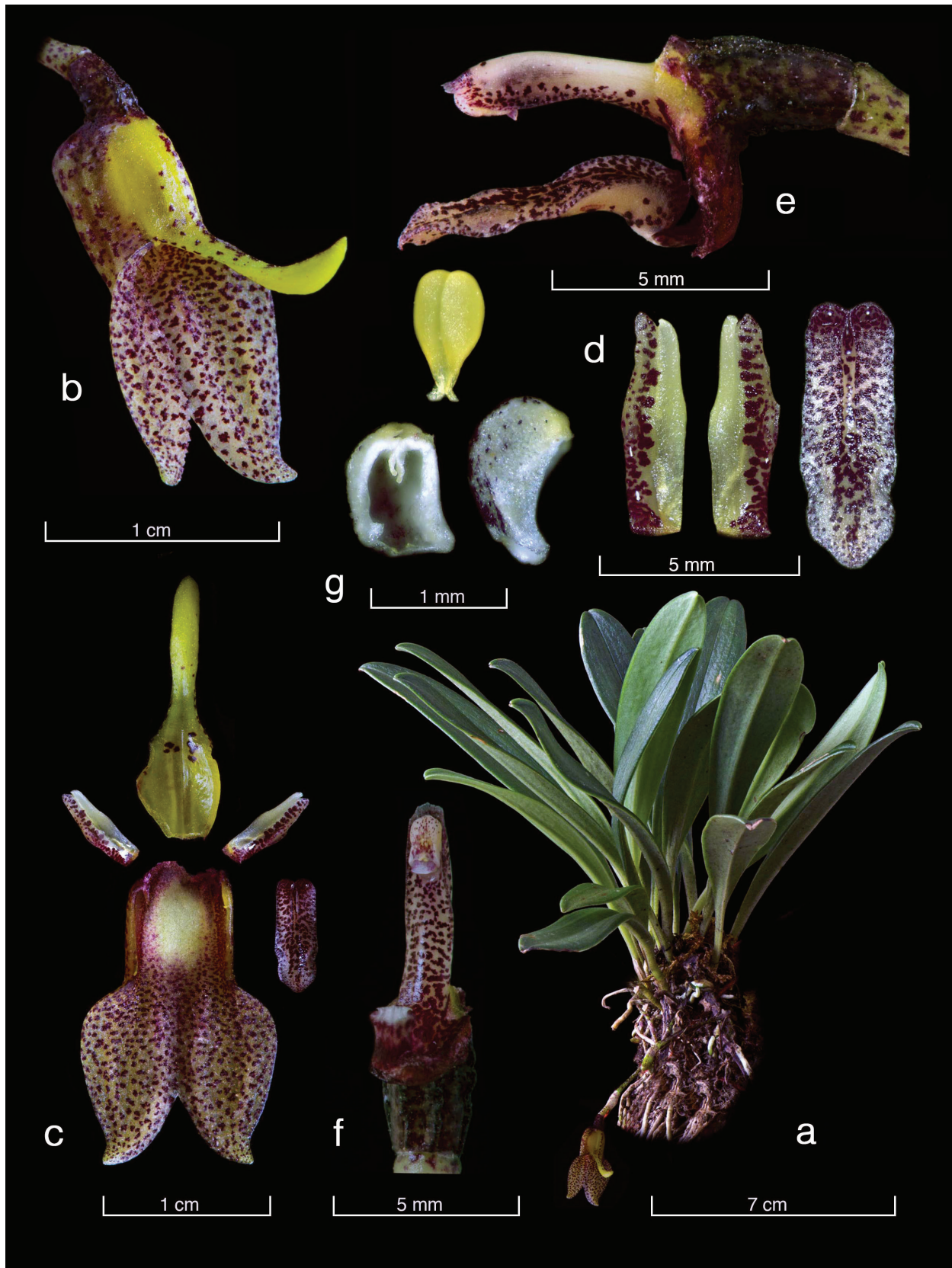


FIGURE 5. LDCP of *Masdevallia utriculata*. A, Habit; B, Flower; C, Dissected perianth; D, Petals and lip, adaxial view; E, Column and lip, lateral view; F, Column, adaxial view; G, Pollinarium and anther cap. All images from *D. Bogarín 10652*, photographs by *D. Bogarín*.

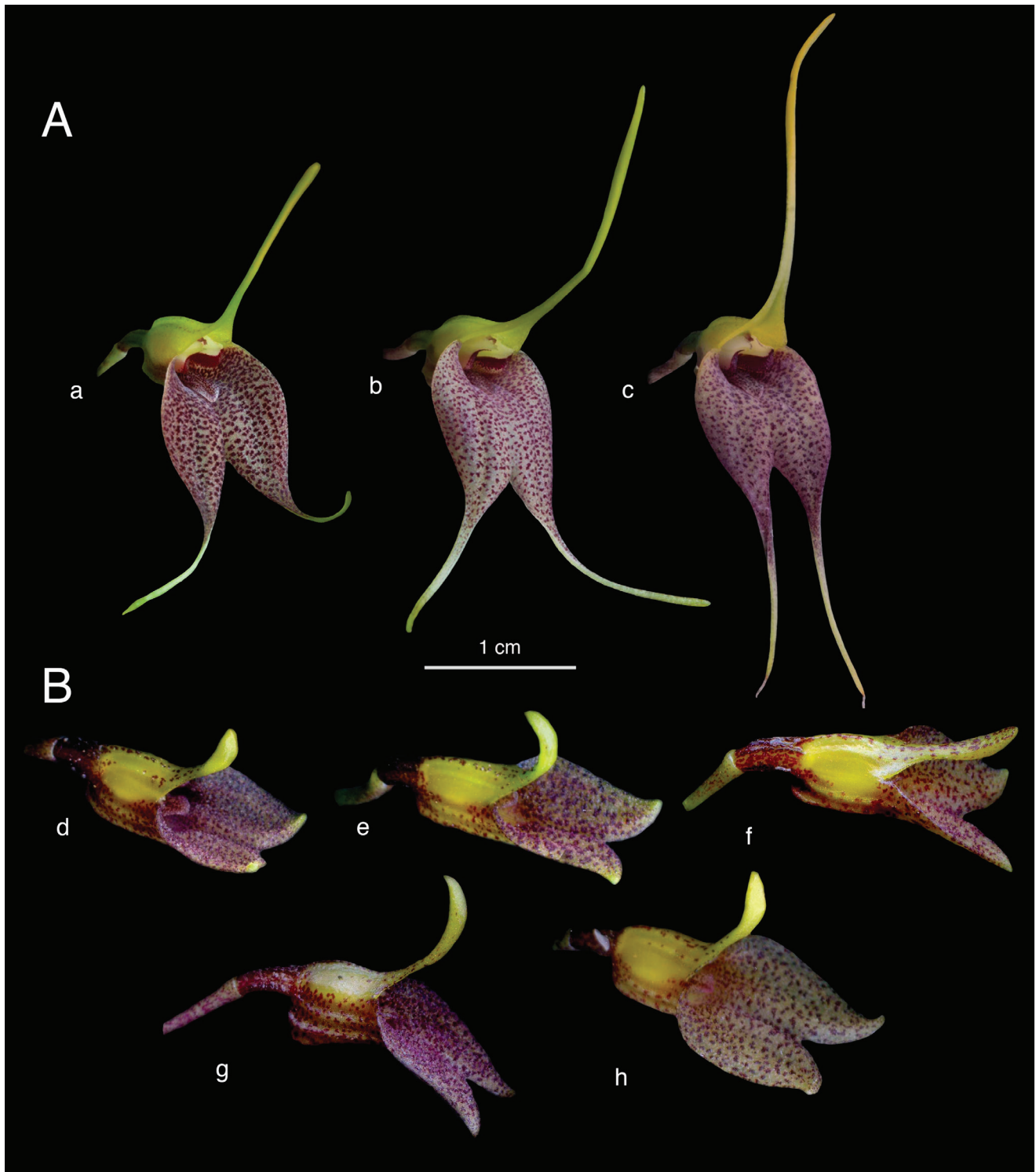


FIGURE 6. Intra-specific variation of floral morphology in different specimens of: **A**, *Masdevallia zahlbruckneri*: **a**, AK5873; **b**, AK6247; **c**, AK6246. **B**, *M. utriculata*: **d**, AK6106; **e**, DB10647; **f**, AK6169; **g**, AK6100; and **h**, DB10652. Photographs by L. Oses (A) and A. Karremans (B) (AK = A. Karremans; DB = D. Bogarín).

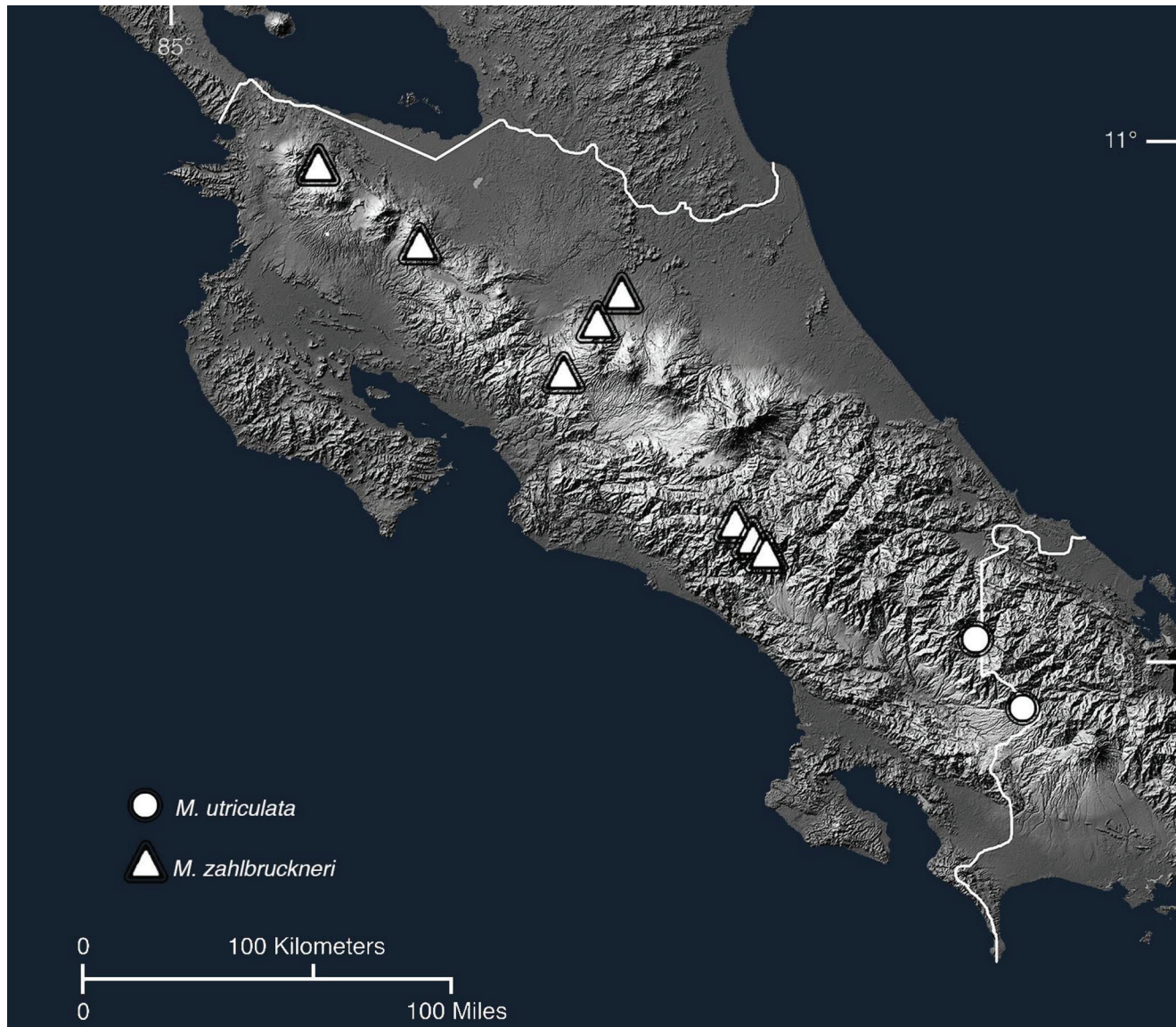


FIGURE 7. Distribution map of *Masdevallia zahlbruckneri* and *M. utriculata* in Costa Rica.

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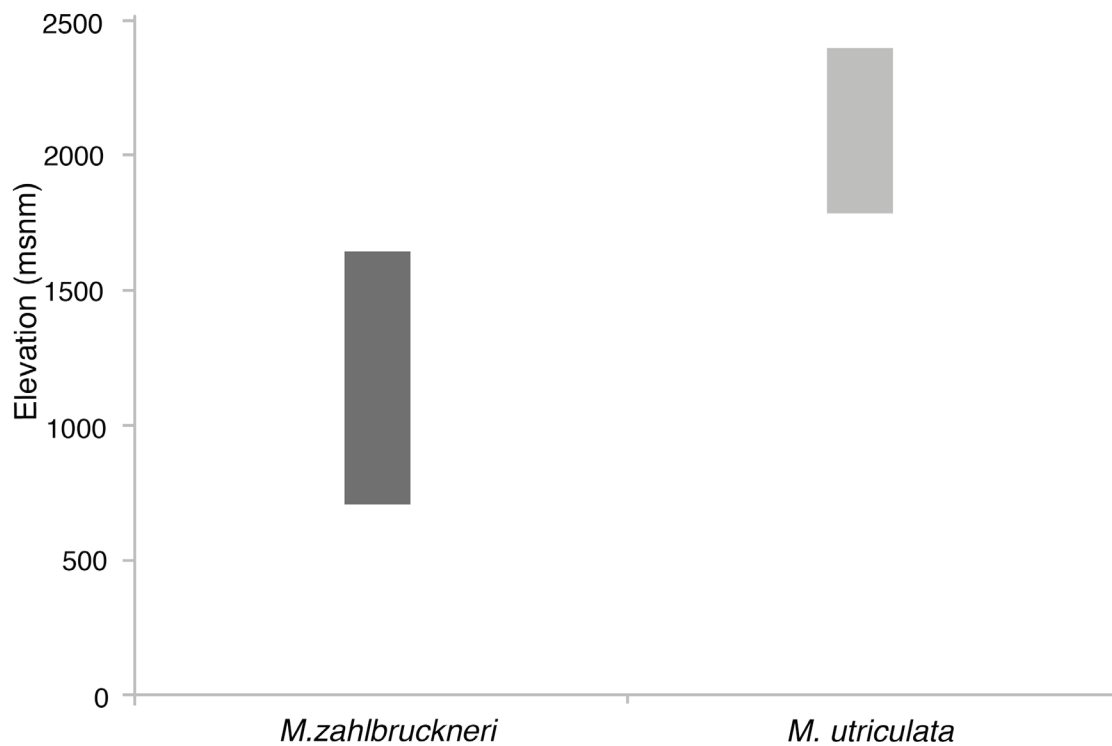


FIGURE 8. Altitudinal range distribution of *Masdevallia zahlbruckneri* and *M. utriculata* in Costa Rica.

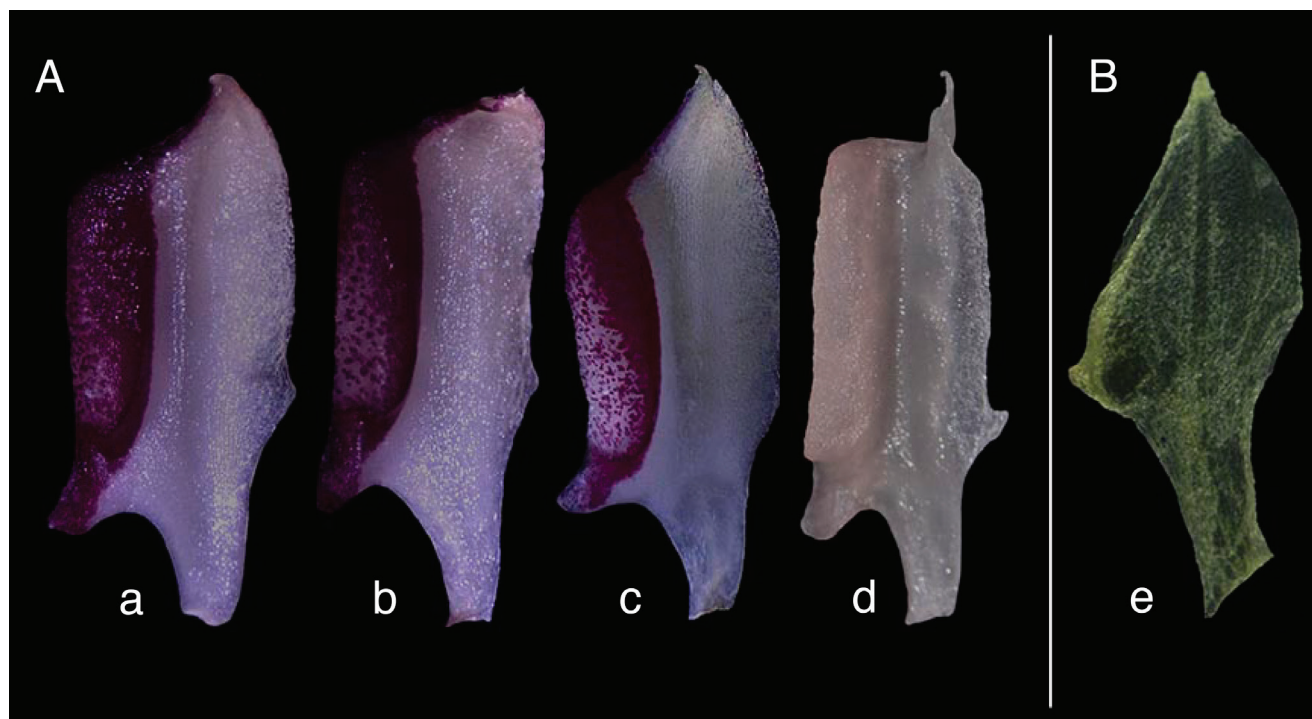


FIGURE 9. Adaxial view of the petal of different specimens. **A**, *Masdevallia zahlbruckneri*: **a**, AK6246; **b**, AK6246; **c**, AK5873; **d**, DB2413 (JBL-Spirit). **B**, *M. schizopetala*: **e**, DB10475. Photographs by L. Oses (AK = A. Karremans; DB = D. Bogarín).

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APPENDIX

INDEX TO NUMBERED COLLECTIONS

- Blanco s.n.* [JBL D2280] (1); *s.n.* [CR](4).
- Todzia 351* (2).
- Acosta s.n.* (3).
- Mora s.n.* (5).
- Bogarín & al.* 2410 (6); 2413 (7); 10691(14); 8088 (18); 10652 (20); 10647 (21).
- Lun s.n.* (8).
- Pupulin & al.* 2405 (9).
- Karremans & Lok* 5873 (10).
- Karremans & Geml* 5387 (16); 5417 (17).
- Karremans & al.* 6246 (11); 6247 (12); 6365 (13); 6169 (15); 6106 (22).
- Fernández & al.* 430 (19); 431 (19).