

A CLARIFICATION OF THE DISTINCTIONS BETWEEN *PLEUROTHALLIS TALPINARIA* AND *PLEUROTHALLIS TRIMEROGLOSSA* (ORCHIDACEAE: PLEUROTHALLIDINAE) AND AN ALLIED NEW SPECIES FROM ECUADOR

MARK WILSON^{1,9}, LUIS E. BAQUERO R.^{2,3,4}, WIEL DRIESSEN⁵, KATHARINE DUPREE¹,
KAREN GIL⁶, JOSÉ PORTILLA⁷ & MARCOS SALAS GUERRERO⁸

¹Department of Organismal Biology and Ecology, Colorado College, Colorado Springs, CO 80903, U.S.A.

²Carrera de Ingeniería Agroindustrial y Alimentos, Facultad de Ingeniería y Ciencias Agropecuarias. Universidad de Las Américas, Pichincha, Ecuador

³Jardín Botánico de Quito, Ecuador

⁴Instituto Nacional de Biodiversidad, Quito, Ecuador

⁵Loosteeg 7, Panningen, The Netherlands

⁶Universidad de Costa Rica, San José, Costa Rica

⁷Ecuagenera, Km. 2 1/1 Vía a Cuenca Sector Llampasay, Gualaceo, Ecuador

⁸Nature and Culture International, Chachapoyas, Peru

⁹Author for correspondence: email: mwilson@coloradocollege.edu

ABSTRACT. *Pleurothallis trimeroglossa* has long been considered a synonym of *P. talpinaria*. In this study we reviewed types, descriptions, drawings, paintings and living material for both names and concluded that *P. talpinaria* and *P. trimeroglossa* should be recognized as distinct species. An anatomical structure important in the distinction between the two is the large dome-shaped callus at the base of the lip in *P. trimeroglossa*. The approximate distributions and elevational ranges of the two species are discussed. During the study we recognized a novel species, described here as *Pleurothallis jostii*. Labellar morphology of all three species was examined. We speculate on the pollination mechanism of this group of species based on the observations of labellar micro-morphology.

KEY WORDS: labellar morphology, Pleurothallidinae, *Pleurothallis*, pollination, SEM, *Talpinaria*

Introduction. *Talpinaria bivalvis* H.Karst. was described by the German botanist Gustav Karl Wilhelm Hermann Karsten (Karsten 1859). The species was reported to occur in the vicinity of Bogotá, Colombia and Caracas, Venezuela in the northern Cordillera Oriental of the Andes. The holotype of *T. bivalvis* is currently housed in the Herbarium of the Vienna Natural History Museum (W 0075479) (Fig. 1) and an isotype is located in the Harvard University Herbarium (AMES 00287011). The original publication included both very detailed drawings and a painting (Fig. 2). This was not, however, the first recorded observation of the species, since a painting of the species by Vicente Sanchez (Fig. 3) appears among the plants illustrated during the Royal Botanical Expedition to New Granada headed by priest and botanist José Celestino Mutis. More recently the species was illustrated by Schneider (1958) in an article on Colombian orchids;

Dunsterville (Fig. 4) in Venezuelan Orchids Illustrated (Dunsterville & Garay 1961); and by Foldats in Flora de Venezuela (Foldats 1970). In all these illustrations (Figs. 2–4), the morphology of the flower, especially that of the labellum, is consistent and clear, leaving no doubt that all of these collections and illustrations are of the same species. The name for the species, however, did not remain as *T. bivalvis* since Reichenbach (1886) transferred it to the genus *Pleurothallis* R.Br., as *P. talpinaria* Rchb.f., the name *P. bivalvis* Lindl. already being occupied.

In 1921 Schlechter described a similar species, *Pleurothallis trimeroglossa* Schltr., from a plant collected by Weberbauer near Huancayo, Junín, Peru (Schlechter 1921). He did not compare this species to the previously described *P. talpinaria* and the subsequent drawing (Schlechter 1929) did not help to clarify whether *P. trimeroglossa* was distinct

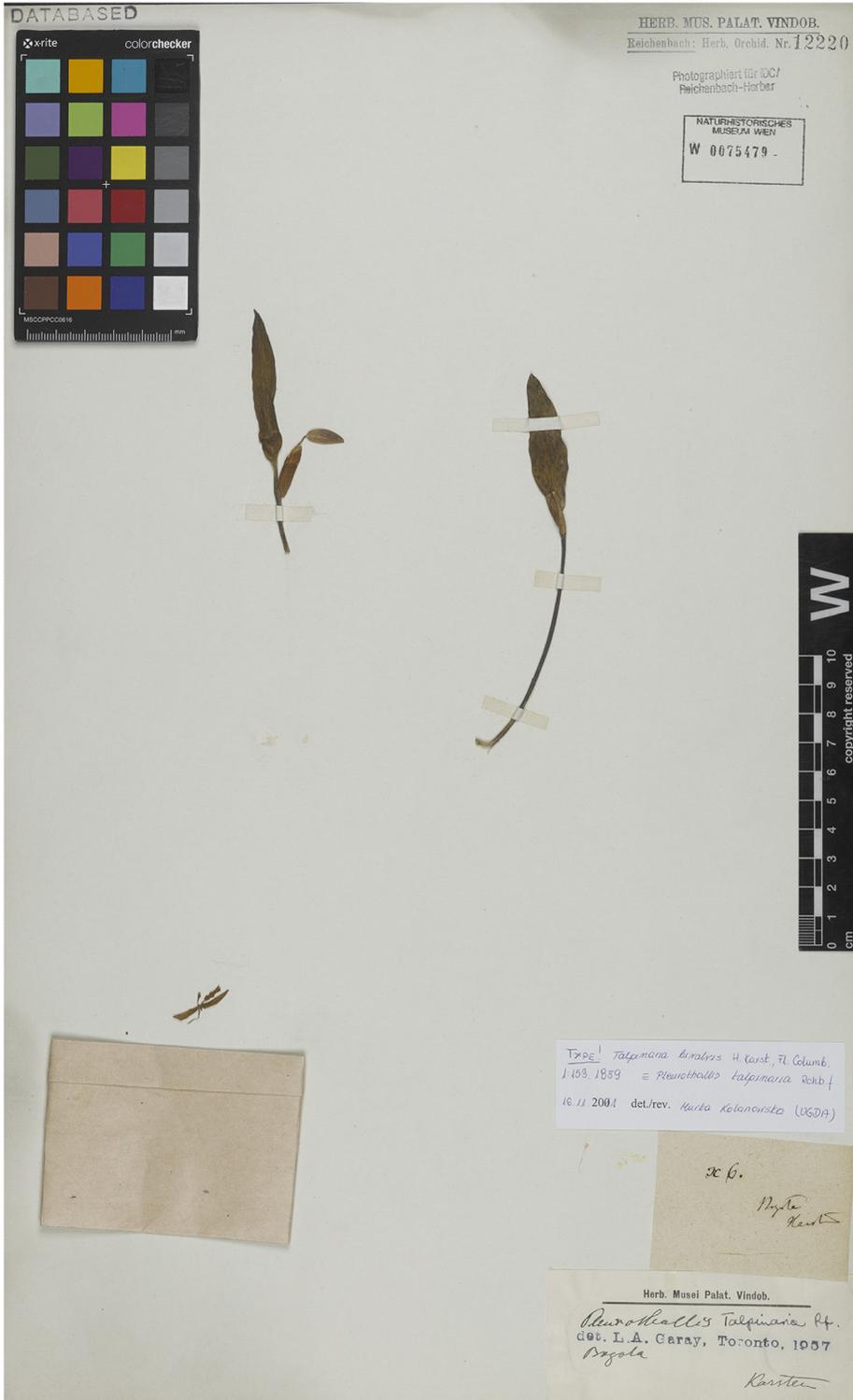


FIGURE 1. Type of *Talpinaria bivalvis*. Courtesy of the herbarium of the Vienna Natural History Museum, Austria (W).



FIGURE 2. Painting of *Pleurothallis talpinaria* (as *Talpinaria bivalvis*). Painting by Gustav Karl Wilhelm Hermann Karsten. From Karsten (1859).



FIGURE 3. Painting of *Pleurothallis talpinaria* (as *Rodriguezia*). Painting by Vicente Sanchez. A. Whole plant. B. Flower (front view). C. Flower (3/4 view). (Courtesy of Royal Botanical Garden of Madrid, Spain. Proyecto de digitalización de los dibujos de la Real Expedición Botánica del Nuevo Reino de Granada (1783-1816), dirigida por José Celestino Mutis: <http://www.rjb.csic.es/icones/mutis> Real Jardín Botánico-CSIC.)

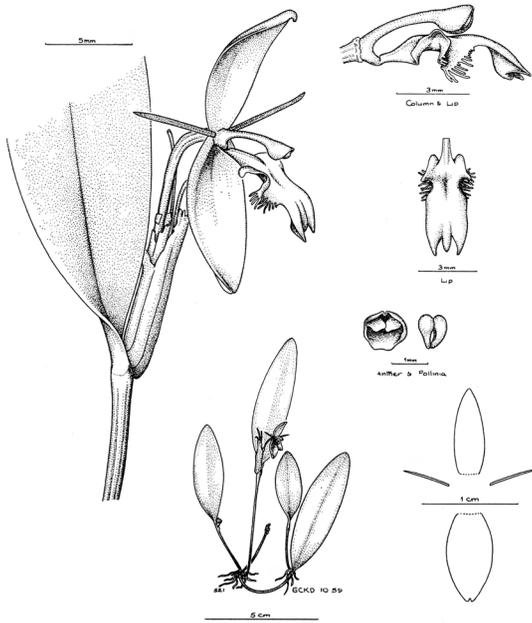


FIGURE 4. Drawing of *Pleurothallis talpinaria*. Drawn by G. C. K. Dunsterville. From Dunsterville & Garay (1961).

from *P. talpinaria*. Unfortunately, the holotype of *P. trimeroglossa* is believed to have been destroyed in Berlin during WWII (Luer 1998). Luckily, however, prior to its destruction, in February 1942, Gordon Dillon drew the lip and column of the type in great detail (Fig. 5) and this drawing is attached to a sheet in the Harvard University Herbarium (AMES 00074793). More recently, a lectotype was designated from Weberbauer's collection 6541 and this is currently housed in the herbarium of the Universidad Nacional Mayor de San Marcos, Lima, Peru (Luer 1998) (Fig. 6). While Schlechter (1921, 1929) did not compare *P. trimeroglossa* with *P. talpinaria*, perhaps because he was unaware of the latter, Schweinfurth (1942) compared the two species and concluded they were one and the same. Following Schweinfurth's lead, Luer (1998) listed *P. trimeroglossa* as a synonym of *P. talpinaria* and illustrated an Ecuadorian specimen presumed to be the latter species (Fig. 7).

Luer (1986), in his reorganization of the genus *Pleurothallis*, created subgenus *Talpinaria*, specifying *P. talpinaria* as the type. At the time, he added *P. hitchcockii* Ames, *P. punctulata* Rolfe and *P. sandemanii* Luer to the subgenus, though he admitted that “the flowers of subgenus *Talpinaria*

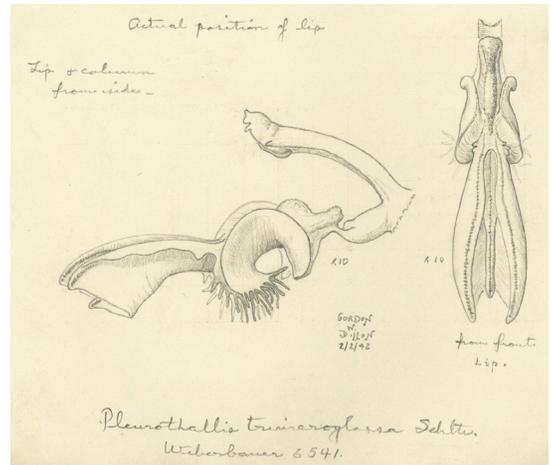


FIGURE 5. Drawing of *Pleurothallis trimeroglossa*. Prepared from the holotype by Gordon W. Dillon 2/2/1942. Courtesy of Harvard University Herbarium.

differ significantly from each other, causing an uneasy alliance” (Luer 1998). Nevertheless, despite the lack of significant morphological similarities, Luer (2004) reinstated the genus *Talpinaria* for the four species *T. bivalvis*, *T. hitchcockii* (Ames) Luer, *T. punctulata* (Rolfe) Luer and *T. sandemanii* (Luer) Luer.

Pridgeon, Solano and Chase (2001) included *P. talpinaria* in their molecular phylogenetic study of subtribe Pleurothallidinae. In their phylogenetic tree of the nuclear internal transcribed spacer (nrITS) sequences, *P. talpinaria* clustered in a clade with *P. ruscifolia* (Jacq.) R.Br., supporting Reichenbach's transfer of *T. bivalvis* to *Pleurothallis*. More recently, Pridgeon, Cribb, Chase and Rasmussen (2005) in *Genera Orchidacearum IV* included subgenus *Talpinaria* in their circumscription of genus *Pleurothallis*. Subsequent phylogenetic studies by Wilson and coworkers (2011, 2013) and Wilson (unpubl. data) have supported the inclusion of the species of this group within *Pleurothallis*. However, the inclusion of the aforementioned species from subgenus *Talpinaria*, including *P. hitchcockii*, *P. punctulata*, *P. sandemanii*, *P. talpinaria* and *P. trimeroglossa*, plus *P. ringens* C.Schweinf., clearly indicate that the subgenus is polyphyletic (Wilson unpubl. data). These observations confirm the “uneasy alliance” comment by Luer (1998) about the subgenus. For this reason, neither genus *Talpinaria* nor subgenus *Talpinaria* are employed further in this paper.



ISOTIPO
Pleurothallis trimeroglossa Schltr.
 Repert. Spec. Nov. Regni Veg. Beih. 9: 78 (1921).
 =*Pleurothallis talpinaria* Rchb.f., Flora 69: 554 (1886).
 Holotipo probablemente destruido en B; isotipo em AMES.

Weberbauer 6541
Pleurothallis talpinaria Reichb. f.
 (= *Pleurothallis trimeroglossa* Schltr.)
 citado en Schweinf. Orch. Perú p.346, 1959

I S O T I P O
 PLANTAS DEL PERU

Depto. JUNIN Prov. Huancayo

Pleurothallis trimeroglossa Schlechter
 Los 2 folíolos laterales del perigonio y el labelo violáceos los demás verdosos con puntos violáceos.
 Localidad: entre Panti y Rocchac, valle del río Pariahuanca

Habitat: Bosque perennifolio
 Fecha: Marzo 31, 1913 Altitud 2400 m.

N. v.:
 Colector: A. Weberbauer 6541

FIGURE 6. Lectotype of *Pleurothallis trimeroglossa*. (Courtesy of the herbarium of the Universidad Nacional Mayor de San Marcos, Peru [USM]).

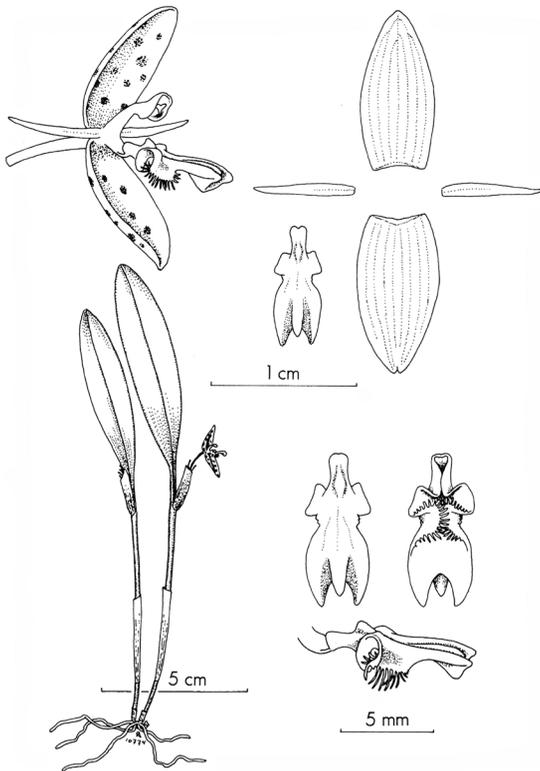


FIGURE 7. Drawing of *Pleurothallis trimeroglossa* (as *Pleurothallis talpinaria*). From Luer (1998). (Courtesy of Missouri Botanical Garden Press.)

Relatively little is known about pollination in *Pleurothallis sensu* Pridgeon *et al.* (2005), but the few studies available suggest that *Pleurothallis* species are pollinated predominantly by Diptera and occasionally by Hymenoptera and Coleoptera (Archila & Chiron 2015, Calderón-Sáenz 2011, Duque 1993, Duque-Buitrago *et al.* 2014). These scant field observations are being supplemented by micro-morphological studies of the labellum using scanning electron microscopy (SEM), which can be used to hypothesize putative pollination mechanisms for future field testing. While a preliminary study of labellar morphology of species in *Pleurothallis* subsection *Macrophyllae-Fasciculatae* (Wilson *et al.* 2016) has been published, this represents the first study of the labellar morphology in the *P. talpinaria* group.

In this manuscript we clarify the distinction between the species *P. talpinaria* and *P. trimeroglossa* and remove the second from synonymy with the first; we describe a new species from Ecuador allied to these two species; and we discuss labellar morphology in

relation to possible pollination mechanisms of these three species.

Materials and Methods

Plant material— Living material of each of the three species was examined by the first author in the collections of Ecuagenera, Gualaceo, Ecuador and Mundiflora, Cuenca, Ecuador. Plants in the collection of Ecuagenera are maintained under the project “Rescate, conservación, reproducción y manejo *ex-situ* de la flora del Ecuador”, authorized by the Ministerio del Ambiente (No 004-2016-IC-FLO-DNB/MA). Photographs of plants in Ecuador were taken with a Canon EOS 40D using a Canon 100 mm f2.8 macro lens and extension tubes as required. These were used for creation of the Lankester composite digital plates (LCDPs). Plants were also imported into the U.S.A. from Ecuagenera and grown in the living collection at Colorado College. Material from these imported plants was used for the creation of herbarium specimens accessioned into the herbarium at Colorado College (COCO). Flowers were preserved in Kew Mix (5% formalin [37.6% formaldehyde], 53% methanol, 5% glycerol, 37% deionized water).

Morphological and taxonomic comparisons— Flowers of *P. talpinaria* and *P. trimeroglossa* were compared in detail to establish that these are two distinct species. Flowers of *P. talpinaria* and *P. trimeroglossa* were then compared to flowers of the putative new species, labeled *P. talpinaria* “purple” in the collection of Ecuagenera, to determine its novelty. To confirm that the species had not been described elsewhere, the new species was compared to descriptions in all pertinent literature, including but not limited to: Bennet and Christenson (1993), Dodson (2003), Dodson and Dodson (1980, 1982), Luer (1975a, 1975b, 1975c, 1976, 1977, 2009, 2011), Luer and Thoerle (2013) and Schweinfurth (1959, 1970). The labella of *P. talpinaria*, *P. trimeroglossa* and the new species were compared in detail by stereo-microscopy, macro-photography and SEM. Flowers for SEM were prepared as described previously (Wilson *et al.* 2016).

DNA sequence comparisons— The nrITS region was sequenced for *P. trimeroglossa* and the new species using methods described previously (Wilson *et al.* 2017).

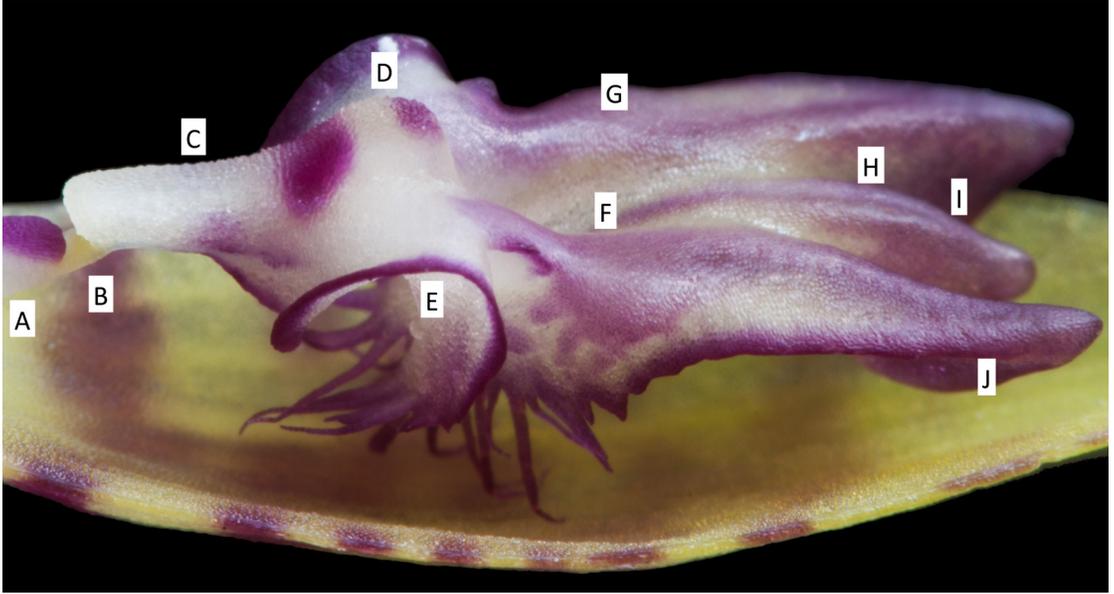


FIGURE 8. Labellum of *Pleurothallis trimeroglossa*. A. Column foot; B. Strap-like attachment; C. Hypochile; D. Callus; E. Auriculate basal lobe; F. Sulcus; G. Mesochile; H. Epichile. I. Central lobe; J. Lateral lobe. Prepared by Mark Wilson.

Results

Morphological and taxonomic comparisons—Specimens of *P. talpinaria* (M. Wilson & J. Portilla PL0946 COCO); *P. trimeroglossa* (M. Wilson & J. Portilla PL0600 and PL0947 COCO; M. Salas Guerrero 129 USM); and the new species of *Pleurothallis* (M. Wilson & J. Portilla PL0314, PL0517 and PL0782 COCO; and PL0974 HA), were examined by macro-photography, stereo-microscopy and SEM.

The labella of *P. talpinaria* and *P. trimeroglossa* are similar consisting of a protuberant, 5-lobed structure. The terete hypochile of the labellum is attached to the column foot via a flexible strap which presumably permits labellar motility; above the hypochile are two

auriculate, revolute, highly fimbriate basal lobes; the mesochile exhibits a distinct sulcus; and the epichile consists of three acute, ridge-like lobes (Fig. 8). The labellum of *P. trimeroglossa* can be distinguished from that of *P. talpinaria* by the presence of a very distinct callus in the shape of a laterally compressed dome (Figs. 8–9), as well as being significantly shorter and narrower (Table 1). The labellum of the new species possesses the same overall architecture as that of *P. talpinaria* and *P. trimeroglossa*, but it is most similar to that of *P. talpinaria*, in that it also lacks the domed callus on the hypochile. In comparison to the labellum of *P. talpinaria* it is significantly shorter and narrower; the terete hypochile is much shorter; the sulcus is less pronounced; and the keel of the central apical lobe is shallower (Figs. 9–10).

TABLE 1. Comparison of dimensions of *Pleurothallis talpinaria*, *Pleurothallis trimeroglossa* and *Pleurothallis justii*.

	<i>Pleurothallis talpinaria</i>	<i>Pleurothallis trimeroglossa</i>	<i>Pleurothallis justii</i>
Whole flower (mm)	23-27 × 23-24	22-24 × 14-15	16-19 × 10-14
Dorsal sepal (mm)	12.8-14 × 5-5.4	10.5-11.3 × 3.4-4	10-10.5 × 5.5-6.7
Synsepal (mm)	12.5-13 × 5.3-6	10.5-11.7 × 4.5-4.8	10 × 6-6.8
Petals (mm)	11-12 × 1.0	5.7-6.0 × 0.6	6-7 × 1-1.4
Column length (mm)	6.8	6.0	4.6-4.8
Labellum (mm)	11 × 4-4.2	7.7-8.5 × 2.8-3	7.5-8 × 3.3-3.9
Callus on labellum	No	Yes	No

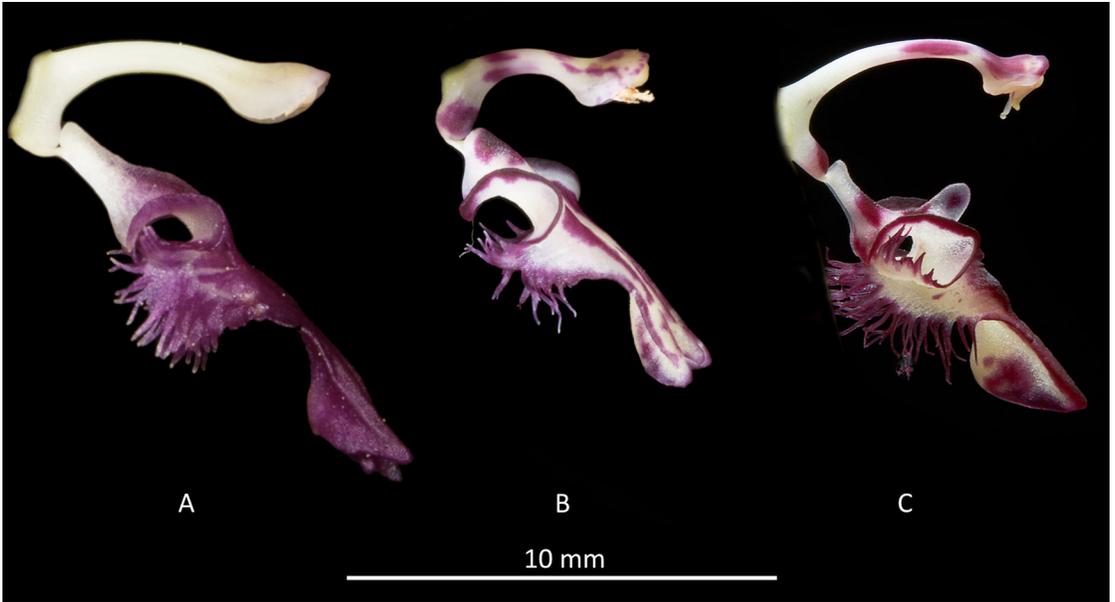


FIGURE 9. Column and labella. A. *Pleurothallis talpinaria* (photo by Wilson); B. *Pleurothallis jostii* (photo by Eric Hunt); C. *Pleurothallis trimeroglossa* (photo by Dale Borders).

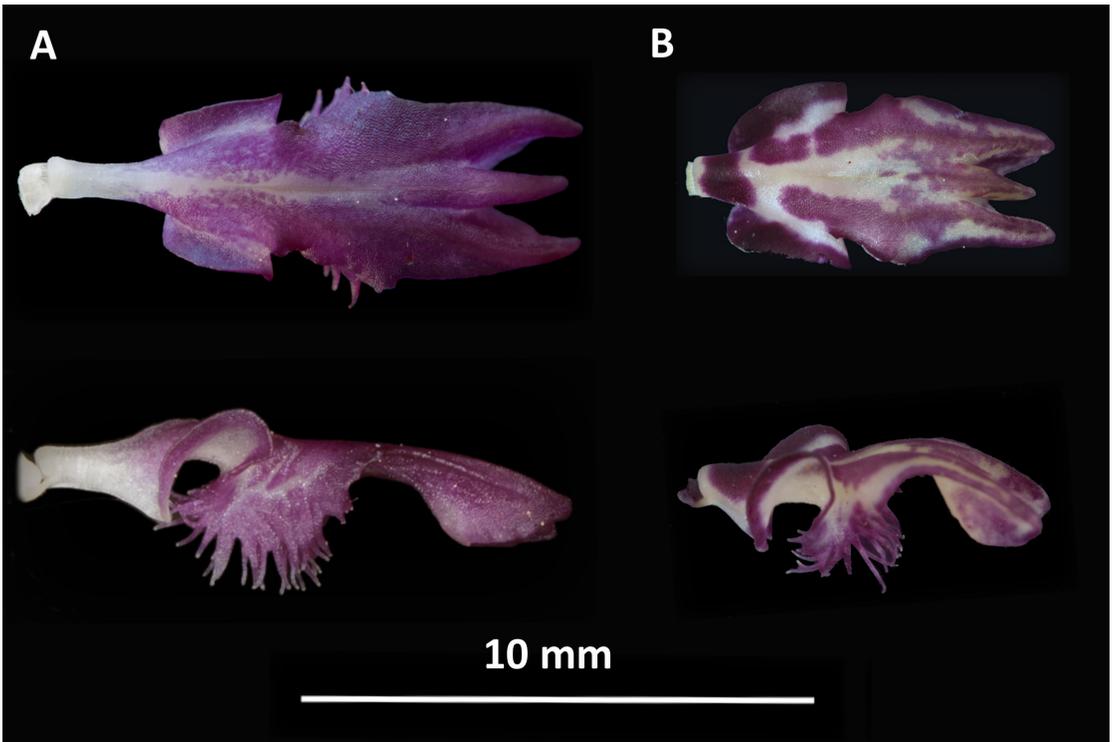


FIGURE 10. Labella of *Pleurothallis talpinaria* (A) and *Pleurothallis jostii*; (B). Prepared by Mark Wilson.

When the labellum of the new species was examined by SEM, no morphology characteristic of secretory tissues

found in other Pleurothallidinae were observed on the adaxial surface (Fig. 11).

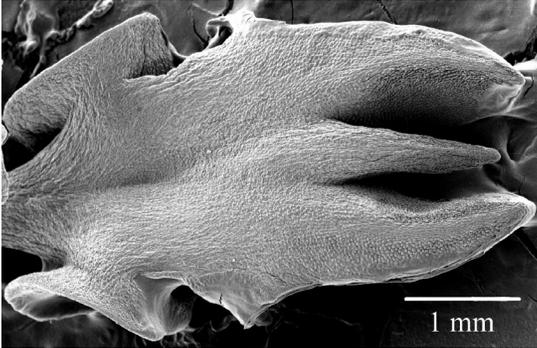


FIGURE 11. Scanning electron micrograph of labellum of *Pleurothallis justii* Electron micrograph by Katharine Dupree.

The columns of *P. talpinaria* and *P. trimeroglossa* are similar consisting of a slender, terete, arching structure, with a pronounced column foot at the base and a hood surrounding the clinandrium at the apex (Fig. 9). The column of *P. trimeroglossa*, however, is significantly narrower and more arching; the column foot is longer and more pronounced; and the transition from terete column to hood of the clinandrium is more abrupt (Fig. 9). The column of the new species is shorter and more stout than either of the other species, with the least pronounced column foot (Fig. 9).

In color, *P. talpinaria* is very consistent, with pale cream sepals, petals and column and a pale purple labellum with a white hypochile (Figs. 12–13). *P. trimeroglossa*, on the other hand, exhibits significant color variations (Fig. 14).

DNA sequence comparisons—The nuclear ITS sequences for *P. talpinaria* (GenBank AF262840), *P. trimeroglossa* PL0600 and the new species PL0517 were identical (Wilson *et al.*, unpubl. data). These sequences will be uploaded to GenBank at a later date as part of the ongoing *Pleurothallis* phylogeny project.

Discussion

Pleurothallis talpinaria and *P. trimeroglossa* have been considered to represent a single species since Schweinfurth (1942) examined Peruvian specimens of *P. trimeroglossa*. This taxonomic opinion was followed by Luer (1998, 2004) and has not been challenged until this time. We, however, believe that these are two distinct species, different both in floral morphology and distribution. Indeed, even

Schweinfurth (1942) commented on the differences between the type specimen of Peruvian *P. trimeroglossa* and the description of *P. talpinaria* before erroneously concluding they were the same species. For example: “The flowers are slightly smaller than those described in *T. bivalvis*, while the petals are markedly shorter than the sepals and not almost equalling them as in *T. bivalvis*.”

All the depictions of *P. talpinaria*, from the original drawings and paintings of Karsten (1859, Fig. 2) and Sanchez (date unknown, Fig. 3), to that of Schneider (1958) and that of Dunsterville (in Dunsterville & Garay 1961, Fig. 4) show specimens that are consistent in both morphology with the flowers attached to the holotype and isotype. Specimens observed *in situ* in Cundinamarca, Colombia (Fig. 13) and in collections (Fig. 12) are identical with these earlier drawings and paintings. This species always has cream sepals and petals and a pale pink-purple lip (Figs. 12–13) and, most importantly, never has a domed callus at the base of the lip (Figs. 9, 10A). In contrast, *P. trimeroglossa* has a very distinct, domed callus near the base of the lip (Figs. 5, 8, 9C). The presence of the domed callus on the hypochile of Luer’s drawing of an Ecuadorian specimen identifies that plant as *P. trimeroglossa*. In addition to the morphological differences, color differences and size differences (Table 1), the species also appear to have differing distributions. Because of these differences, we propose that the two species, *P. talpinaria* and *P. trimeroglossa* are distinct and they are removed from synonymy herein.

The new species described herein (Figs. 9B, 10B, 11, 15–17) is distinct morphologically and in size (Table 1) from both *P. talpinaria* and *P. trimeroglossa*. Like *P. talpinaria* it lacks a callus at the base of the lip (Figs. 10B, 11), but it should not be confused with that species because of the marked differences in size (Table 1). In coloration it is more similar to some variants of *P. trimeroglossa*, but it should not be confused with that species due to the presence of the callus on the lip of *P. trimeroglossa* and the very marked differences in flower size (Table 1).

The nrITS region was sequenced for *P. trimeroglossa* and the new species and these sequences were compared to the nrITS sequence for *P. talpinaria* obtained by Pridgeon and coworkers (2001). The

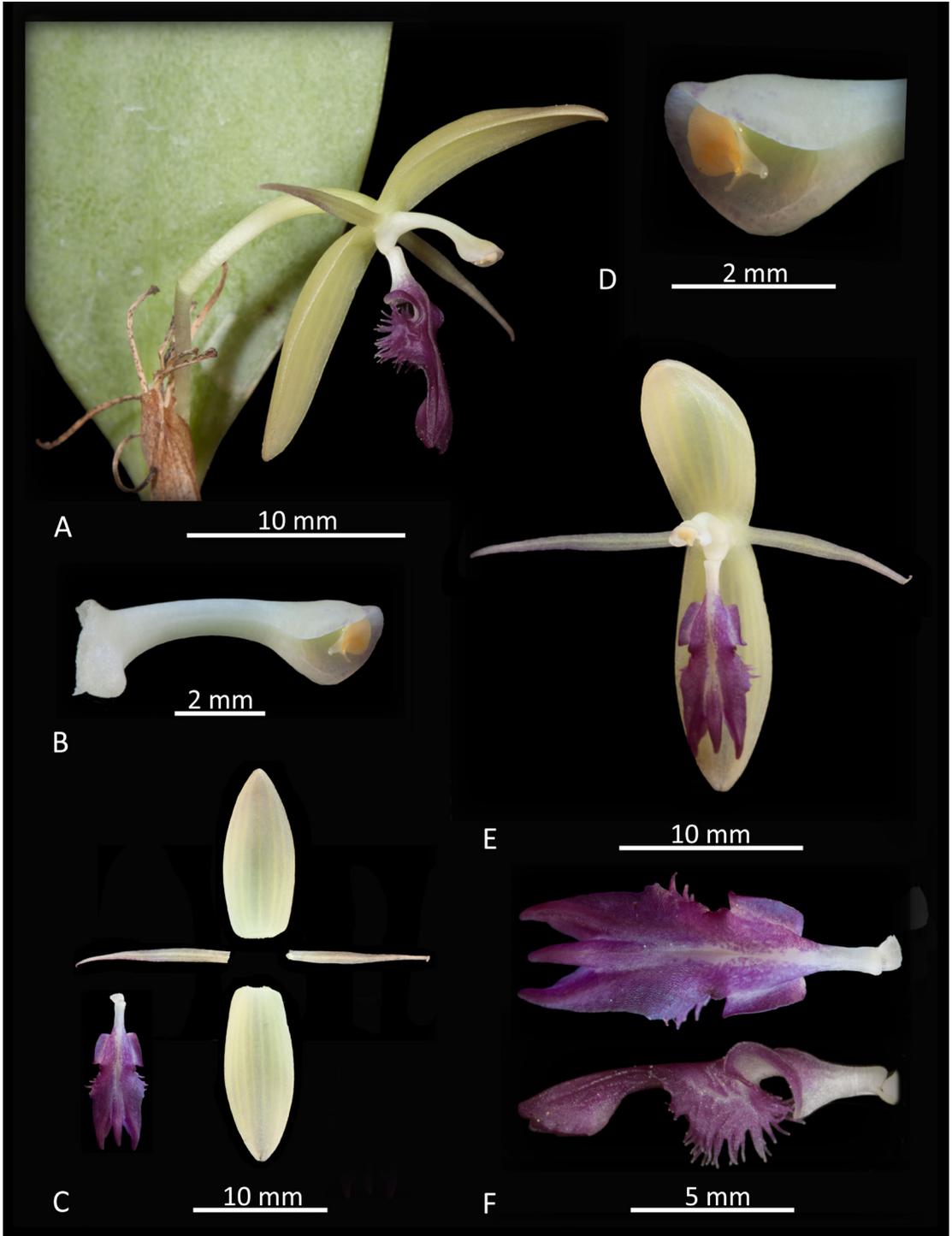


FIGURE 12. Lankester composite digital plate of *Pleurothallis talpinaria*. A. Whole flower, ovary, pedicel and spatheous bract; B. Column (3/4 ventral view); C. Floral dissection; D. Column tip and anther; E. Whole flower (front view); F. Labellum (dorsal and lateral views). LCDP prepared by Mark Wilson from *M. Wilson & J. Portilla PL0946*.



FIGURE 13. *Pleurothallis talpinaria* in situ in Reserva Biológica El Encenillo, Guasca, Cundinamarca, Colombia. Photographs by Karen Gil.

nrITS sequences were invariant and not useful for discriminating among the three species. This situation is not at all uncommon in the species-rich genus *Pleurothallis* (Wilson *et al.* unpubl. data) and does not imply that *P. talpinaria*, *P. trimeroglossa* and the new species are one and the same. To find a sequence-based method of species discrimination, future sequencing will focus on the more variable regions 3' *yef*, *trnL-F* and *trnH-psbA*.

Unfortunately, the distribution data for *P. talpinaria* reported by Luer (1998) and Tropicos (2017) represent the combined distributions of *P. talpinaria* and *P. trimeroglossa*. Full characterization of the geographic and elevational distributions of *P. talpinaria* and *P. trimeroglossa* will require extensive field work. Although it will be useful to examine collections in herbaria in Venezuela, Colombia, Ecuador, Peru and Bolivia, *P. talpinaria* and *P. trimeroglossa* are vegetatively indistinguishable and the majority of herbarium specimens do not have a flower on the sheet or preserved in spirit. However, we can infer approximate distributions for the two species from the information available.

The type locality for *P. talpinaria* is in the Department of Cundinamarca, Colombia. Based upon recent photos taken *in situ* by Colombian botanists, the species also occurs in the Departments of Caldas and Santander. We believe that the Venezuelan collections all represent this species. Therefore, tentatively, pending further examination of herbarium collections and field work, one could characterize the distribution of *P. talpinaria* as the Cordillera Oriental of the Andes, from central and northeastern Colombia into southwestern Venezuela. In this study, *P. talpinaria* was observed *in situ* growing epiphytically in a subparamo forest of *encenillo* (*Weinmannia tomentosa* L.f.) in the Reserva Biológica El Encenillo, Guasca, Cundinamarca, Colombia (Fig. 13).

Inferring a distribution of *P. trimeroglossa* is more challenging because less information is available. The type locality for *P. trimeroglossa* is near Huanuco, Department of Junin, Peru. However, the species was observed by author Salas growing epiphytically on the trunks of palm trees in Chachapoyas Province, in the Department of Amazonas, Peru, much closer to Ecuador. Examination of specimens from the herbarium at Selby Botanical Gardens (SEL) suggests that this species has been collected in the Ecuadorian provinces of Loja, Zamora-Chinchiipe, Morona-Santiago, Pastaza and Napo, all on the eastern slope of the Andes. *Pleurothallis trimeroglossa* does not appear to have been collected further west than these provinces, or further north than Napo. The report of *P. talpinaria* in Bolivia (Jiménez-Pérez 2011), possibly represents the most southerly populations of *P. trimeroglossa*, but this needs to be verified. It also remains to be determined whether the color variants of *P. trimeroglossa* (Fig. 14) represent merely geographic variation in the species or whether there are in fact cryptic species within the concept of *P. trimeroglossa* presented here. Studies to resolve these questions are ongoing and this article represents just the first in a series on the *P. talpinaria*-*P. trimeroglossa* group.

While an accurate determination of the elevational range of these two species will require additional study, *P. talpinaria* appears to grow at a higher mean elevation than *P. trimeroglossa*. In Cundinamarca, Colombia, *P. talpinaria* occurs over an elevational range of approximately 2600–3200 m above sea level.

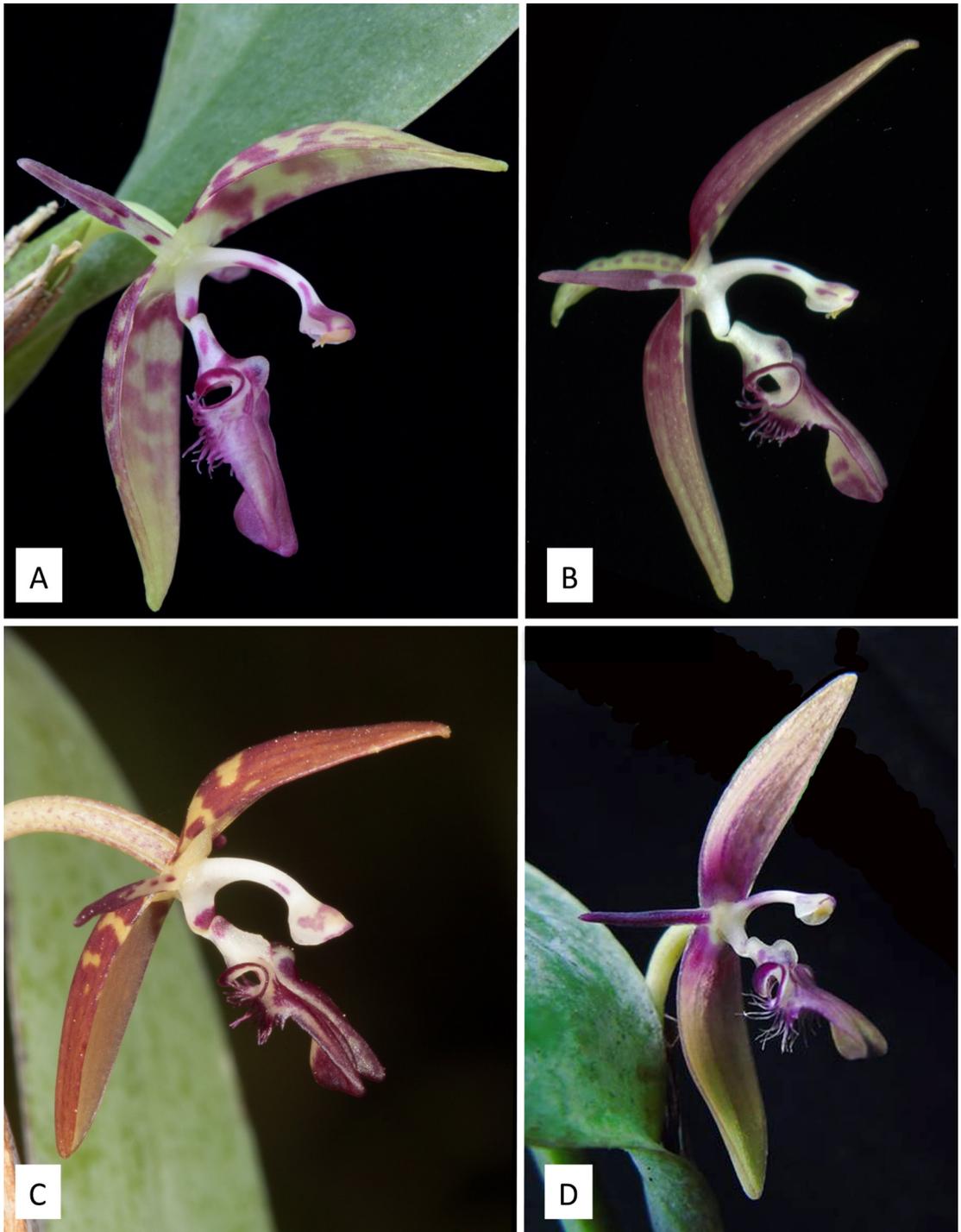


FIGURE 14. Color variation in *Pleurothallis trimeroglossa*. A. Ecuadorian specimen (*ex situ* photo by Wiel Driessen); B. Ecuadorian specimen from Ecuagenera (*ex situ* photo by Mark Wilson); C. Ecuadorian specimen from Mundiflora (photo by Mark Wilson); D. Peruvian specimen from Chachapoyas, Amazonas, Peru (*in situ* photograph by Marcos Salas Guerrero).

P. trimeroglossa on the other hand has been recorded over the range 1780–2842 m. *P. trimeroglossa* has been photographed as low as 1780 m Rioja, San Martín, Peru (José Dilmer Edquen Oblitas, pers. comm.); the type material was collected in Huancayo, Junín, Peru at an elevation of 2400 m; and it has been collected in Amazonas, Peru from 2680 m to 2842 m (*M. Salas Guerrero 129*).

Undoubtedly, the most distinctive floral feature of all three species is the highly modified, tri-lobed labellum. The auriculate, highly fimbriate basal lobes are unique in *Pleurothallis*, and even in *Pleurothallidinae*, as far as we are aware. We might assume that such a lip has evolved to attract a very specific type of pollinator. As mentioned earlier, the few field observations that have been made suggest that species in *Pleurothallis sensu* Pridgeon (2005) are pollinated predominantly by Diptera and secondarily by Coleoptera and Hymenoptera. In none of the observations of living plant material or numerous photographs of the three species have we ever seen any evidence of a liquid nectar-like reward. Nor did SEM indicate the presence of even a vestigial nectary or “glenion” as occurs in *Pleurothallis* subsections *Macrophyllae-Fasciculatae* (Wilson *et al.* 2016) and *Acroniae* (Wilson unpubl. data), or any other possible secretory tissue (Fig. 11). This suggests that these are rewardless flowers and that pollination involves some form of deception. The flowers seem inordinately complex for a mimic of another rewarding species, both in the extensive fimbriation and the presence of an articulation allowing free labellar motility. We hypothesize therefore that these flowers are pollinated by sexual deceit and that pollination involves pseudocopulation with a relatively large dipteran or hymenopteran pollinator. We further hypothesize that the large callus near the base of the lip in *P. trimeroglossa*, that is absent in *P. talpinaria*, serves to position a somewhat smaller pollinator against the anther. Of course, such speculation will have to be confirmed by *in situ* observation in the future.

Taxonomic treatment

Pleurothallis talpinaria Rehb.f., *Flora* 69: 554. 1886. Bas. *Talpinaria bivalvis* H.Karst. *Fl. Columb.* (H. Karst.) i. 153. t. 76 (1859).

TYPE: Colombia. Cundinamarca: Bogotá. *H. Karsten 6* (holotype: W! [0075479]).

ADDITIONAL MATERIAL STUDIED: Colombia. Cundinamarca: Bogotá. *H. Karsten 6* (isotype: AMES! [00287011]). Ecuador. Purchased from Ecuagenera without collection data and flowered in cultivation at Colorado College, *M. Wilson & J. Portilla PL0946* (COCO!).

Pleurothallis trimeroglossa Schltr. *Repert. Spec. Nov. Regni Veg. Beih.* 9: 78. 1921.

TYPE: Peru. Junín: Huancayo, collected 31 March, 1913, *A. Weberbauer 6541* (lectotype: USM!).

ADDITIONAL MATERIAL STUDIED: Peru. Junín: Huancayo. *A. Weberbauer 6541* (isotype: AMES! [00074792]). Drawing of type (AMES! [00074793]). Peru. Chachapoyas, Amazonas. *M. Salas Guerrero 129* (USM!). Ecuador. Purchased from Ecuagenera without collection data as *P. talpinaria* and flowered in cultivation at Colorado College and identified as *P. trimeroglossa*, *M. Wilson & J. Portilla PL0600* and *PL0947* (COCO!).

Pleurothallis jostii Mark Wilson & J. Portilla, *sp. nov.* (Figs. 15–17).

TYPE: Ecuador. Flowered in cultivation at Ecuagenera Orchid Nursery, Gualaceo, Ecuador as *Pleurothallis talpinaria* “purple”, without collection data, November 2015, *M. Wilson & J. Portilla PL0974* (holotype: HA!).

Diagnosis. *Pleurothallis jostii* can be distinguished from *P. talpinaria* by the smaller flower; the color of the sepals, yellow brown heavily mottled with purple-brown *vs.* pale cream; the color of the petals, deep purple *vs.* pale cream; the color of the labellum, white mottled with purple *vs.* predominantly pale purple; the length of the column which is 4.6–4.8 mm in *P. jostii* *vs.* ~6.8 mm in *P. talpinaria*; the shorter labellum, 7.5–8.0 mm long *vs.* ~11 mm long; and the shorter hypochile at the articulation with the column foot in *P. jostii*. *Pleurothallis jostii* can be distinguished from *P. trimeroglossa* by the smaller flower; the petal width which is 1.0–1.4 mm in *P. jostii* *vs.* ~0.6 mm in *P. trimeroglossa*; the absence of a domed callus on the hypochile of *P. jostii* and the presence of a distinct,

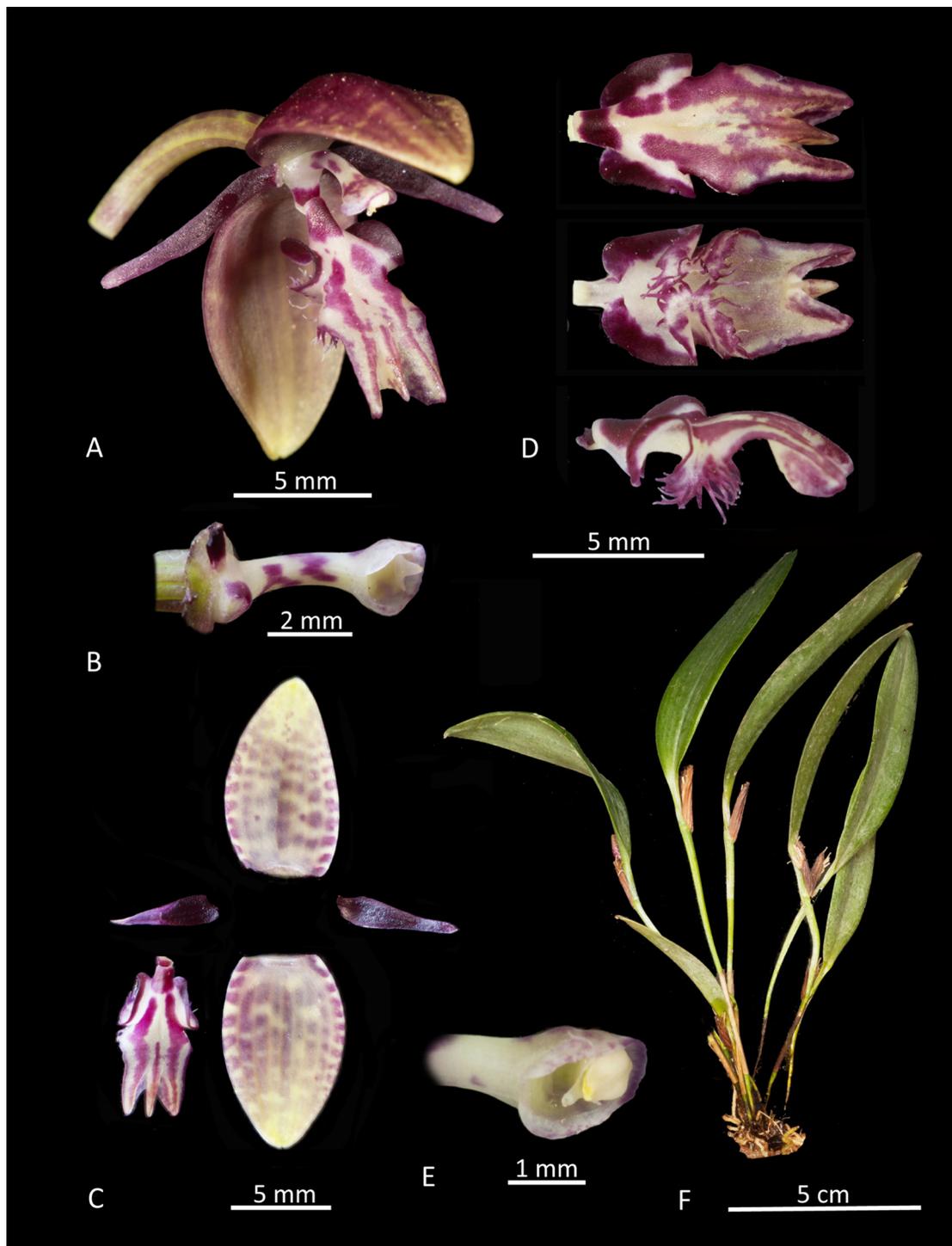


FIGURE 15. Lankester composite digital plate of *Pleurothallis justii*. A. Whole flower (3/4 view); B. Column (3/4, ventral view); C. Floral dissection; D. Labellum (dorsal, ventral and lateral views); E. Column tip and anther; F. Whole plant. LCDP prepared by Mark Wilson from the holotype *M. Wilson & J. Portilla PL0974*.

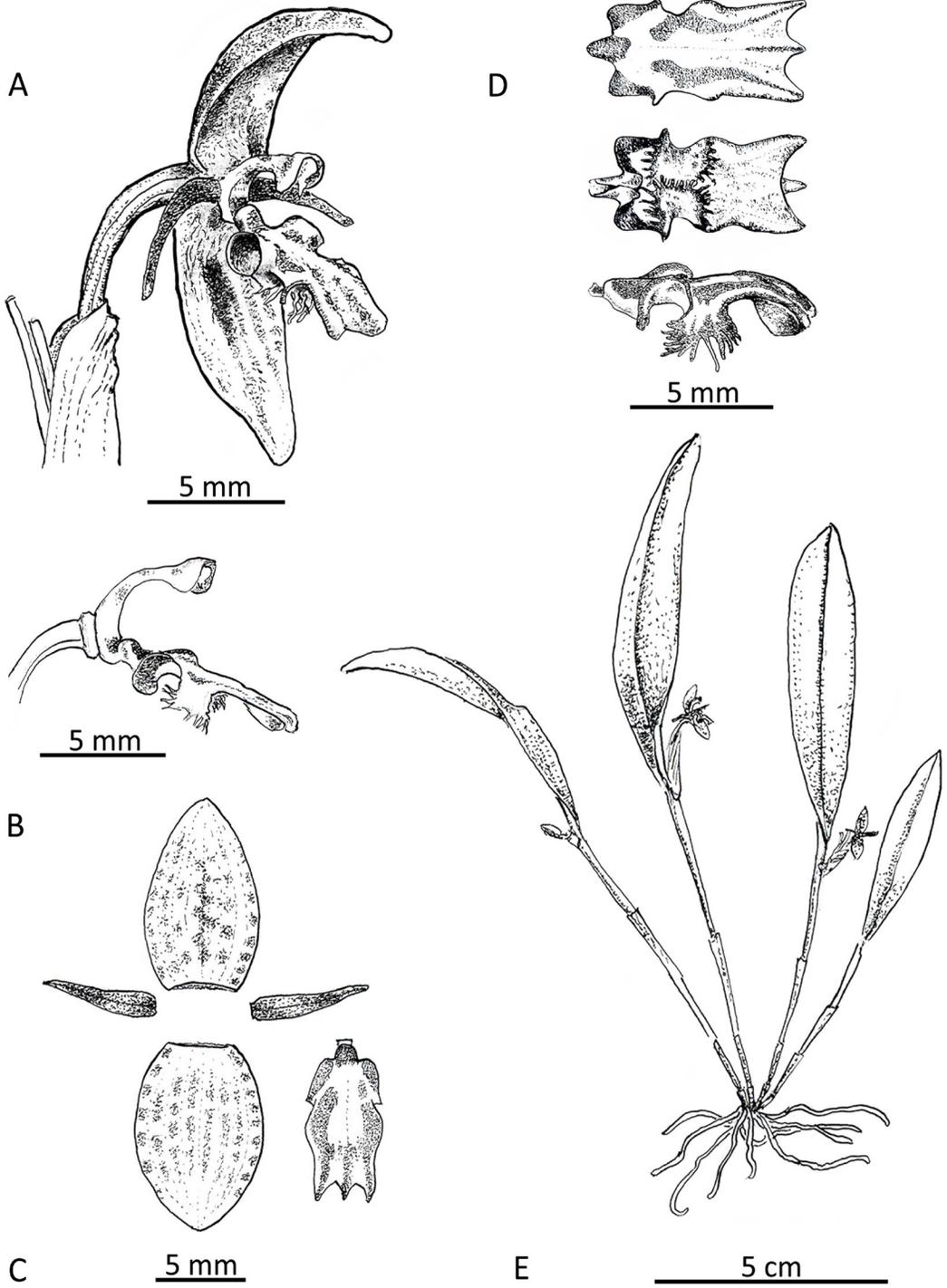


FIGURE 16. Drawing of *Pleurothallis jostii*. A. Whole flower (3/4 view). B. Column and labellum. C. Floral dissection. D. Labellum (dorsal, lateral and ventral views). E. Whole plant. Drawing by Luis Baquero from holotype *M. Wilson & J. Portilla PL0974*.



FIGURE 17. Whole plant of *Pleurothallis jostii*. Photograph by Ronald Hanko.

domed callus on the hypochile of *P. trimeroglossa*; the shorter hypochile at the articulation with the column foot in *P. jostii*.

Plant small, to 15 cm tall, epiphytic, caespitose. *Roots* fibrous. *Ramicauls* slender, terete, 4.0–7.9 cm long. *Leaves* erect, slightly arching, elliptical, subacute to acute, 4.1–8.5 × 1.2–2.5 cm, cuneate at base, fleshy, highly coriaceous, older leaves glaucous and waxy, with some purple coloration, petiole 4–13 mm long. *Inflorescence* single-flowered peduncle, from erect spatheaceous bract, 0.9–1.7 cm long; *ovary* 7.0 mm long. *Flowers* 16–19 × 10–14 mm, resupinate. *Dorsal sepal* pale yellow-brown, heavily suffused with purple-brown, heaviest on outer surface, ovate, subacute, concave, 10.0–10.5 × 5.5–6.7 mm, glabrous, entire. *Synsepal* pale yellow-brown, heavily suffused with purple-brown, heaviest on outer surface, ovate-elliptic, subacute, concave, 10.0–10.5 × 6.0–6.8 mm, glabrous, entire. *Petals* deep purple, linear-lanceolate, somewhat oblique, acute 6–7 × 1.0–1.4 mm, glabrous, entire. *Labellum* white to pale cream mottled with purple, protruberant, five-lobed, 7.5–8.0 × 3.3–3.9 mm, apex divided into three acute lobes, shallowly sulcate below

middle lobe, basal lobes rounded, fimbriate, revolute along front and rear edge, base short, terete, articulated on column foot. *Column* white lightly mottled with purple, slender, terete, arching, broadened at apex, 4.6–4.8 mm long, gently curved, smooth, pronounced column foot, hooded clinandrium, anther sub-apical.

ADDITIONAL MATERIAL STUDIED: Ecuador. Purchased from Ecuagenera without collection data as *P. talpinaria* “purple”, flowered in cultivation at Colorado College and identified as an undescribed species, *M. Wilson & J. Portilla* PL0314, PL0517 and PL0782 (paratypes: COCO!).

ETYMOLOGY: In honor of Lou Jost for his ongoing efforts to conserve Ecuadorian flora and fauna through Fundación EcoMinga.

This species has only been observed in the collection of Ecuagenera, or in collections containing plants derived from that commercial grower. As always with species described from collections, there is the risk that the plant represents an unintentional greenhouse hybrid. We do not believe that to be likely in this case, because the morphology is sufficiently

distinct from *P. talpinaria* and *P. trimeroglossa* that it is almost certainly not a hybrid of those two species. And, since the floral morphology of these species is so unique, it is almost impossible to consider it a hybrid of *P. talpinaria* or *P. trimeroglossa* with a *Pleurothallis* species from any other subgenus.

While we assume that the species is from Ecuador, the global hobbyist and commercial exchange of species has completely obscured origins of *Pleurothallis* species in collections that are not associated with verified *in situ* occurrence data. Therefore, while the holotype of the species comes from an Ecuadorian collection and is deposited in an Ecuadorian herbarium, the species should not be added to the flora of Ecuador until the geographic origin of the species is located.

Conclusions. The three species, *P. talpinaria*, *P. trimeroglossa* and *P. jostii* are distinct in morphology, size and coloration. *P. talpinaria* and *P. trimeroglossa* probably occupy distinct, non-overlapping geographic ranges, *P. talpinaria* in Colombia (central and

northeastern) and Venezuela (southwestern) and *P. trimeroglossa* in Peru, Ecuador (southeastern) and possibly Bolivia. However, confirmation of these ranges requires additional study and the geographic occurrence of *P. jostii* remains to be determined. The unique and fascinating labella of these species has implications for pollination mechanisms and we speculate that this group is pollinated by pseudocopulation. Testing of this hypothesis will require *in situ* observation.

ACKNOWLEDGEMENTS. The authors are grateful to Colorado College for research funding for Wilson and Dupree and provision of greenhouse and herbarium facilities; to Dr. Ron Hathaway of Colorado College for assistance with SEM; to Universidad de las Americas, Quito, Ecuador for support of Luis Baquero; to Ecuagenera and Mundiflora for access to plant collections; to members of the Portilla family for their warm hospitality; to Dale Borders, Ronald Hanco and Eric Hunt for the use of their photographs; to Adam Karremans and Diego Bogarin for instruction in preparation of LCDPs; and to the Editors of Lankesteriana and the anonymous reviewers for other suggestions to improve the manuscript.

LITERATURE CITED

- Archila, F. & Chiron, G. R. (2015). Elaiophores, a labellum anatomic structure important in the pollination syndrome in *Pleurothallis*. *Revista Guatemalensis*, 18(1), 15–23.
- Bennett, D. E. & Christenson, E. A. (1993). *Icones Orchidacearum Peruvianum*. St. Louis: Missouri Botanical Gardens Press.
- Calderón-Sáenz, E. (2011). *Pleurothallis colossus*: Pollination by Anthomyiid flies at El Refugio nature reservation. *Orchids*, 80(12), 740–743.
- Dodson, C. H. & Dodson, P. M. (1980). *Orchids of Ecuador, Series 1, Fascicles 1–4, Icones Plantarum Tropicarum*. Sarasota, FL, U.S.A.: The Marie Selby Botanical Gardens.
- Dodson, C. H. & Dodson, P. M. (1982). *Orchids of Ecuador, Series 1, Fascicle 5, Icones Plantarum Tropicarum*. Sarasota, FL, U.S.A.: The Marie Selby Botanical Gardens.
- Dunsterville, G. C. K. & Garay, L. A. (1961). *Venezuelan Orchids Illustrated. Volume II*. Amsterdam, The Netherlands: Andre Deutsch.
- Duque H., Ó. (1993). Polinización en *Pleurothallis*. *Orquideología*, 19(1), 55–69.
- Duque-Buitrago, C. A., Alzate-Quintero, N. F. & Tupac Otero, J. (2014). Nocturnal pollination by fungus gnats of the Colombian endemic species, *Pleurothallis marthae* (Orchidaceae: Pleurothallidinae). *Lankesteriana*, 13(3), 407–417.
- Foldats, E. T. L. (1970). *Flora de Venezuela: Orchidaceae. Volumen XI, Segunda parte*. Caracas, Venezuela: Instituto Botánico.
- Jiménez-Pérez, I. (2011). Nuevos registros de orquídeas de los bosques montanos de Bolivia. Parte I. *Ecología en Bolivia*, 46(1), 57–61.
- Karsten, G. K. W. H. (1859). *Florae Columbiae terrarumque adjacentium specimina selecta in peregrinatione duodecim annorum observata delineavit et descripsit* (pp. 153–155). Berolini: Typis fratrum unger. Recovered from <http://www.biodiversitylibrary.org/item/9238#page/1/mode/1up>
- Luer, C. A. (1975a). Icones Pleurothallidarum: *Pleurothallis* of Ecuador (Orchidaceae). *Selbyana*, 1(1), 56–100.
- Luer, C. A. (1975b). Icones Pleurothallidarum (Orchidaceae): *Pleurothallis* of Ecuador II. *Selbyana*, 1(2), 172–195.
- Luer, C. A. (1975c). Icones Pleurothallidarum (Orchidaceae): *Pleurothallis* of Ecuador III. *Selbyana*, 1(3), 220–303.
- Luer, C. A. (1976). Icones Pleurothallidarum: Miscellaneous species of *Pleurothallis*. *Selbyana*, 3(1–2), 38–201.
- Luer, C. A. (1986). Icones Pleurothallidarum III:

- Systematics of *Pleurothallis*. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 20, 1–109.
- Luer, C. A. (1998). Icones Pleurothallidarum XVI. Systematics of *Pleurothallis* subgenera *Crocodelanthe*, *Rhynchopera* and *Talpinaria*. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 65, 1–122.
- Luer, C. A. (2004). Icones Pleurothallidarum XXVI. *Pleurothallis* subgenus *Acianthera* and three allied subgenera. A second century of new species of *Stelis* of Ecuador. *Epibator*, *Ophidion*, *Zootrophion*. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 95, 1–265.
- Luer, C. A. (2009). Miscellaneous new species in the Pleurothallidinae (Orchidaceae). *Selbyana*, 30(1), 1–71.
- Luer, C. A. (2011). Miscellaneous new species in the Pleurothallidinae (Orchidaceae) excluding species from Brazil. *Harvard Papers in Botany*, 16(2), 311–360.
- Luer, C. A. & Thoerle, L. (2013). Miscellaneous new species in the Pleurothallidinae (Orchidaceae). *Harvard Papers in Botany*, 18(2), 173–196.
- Pridgeon, A. M., Cribb, P.J., Chase, M. W. & Rasmussen, F. N. (2005). *Genera Orchidacearum. Volume 4. Epidendroideae (Part one)*, (385–390). Oxford, U.K.: Oxford University Press.
- Pridgeon, A. M., Solano, R. & Chase, M. W. (2001). Phylogenetic relationships in Pleurothallidinae (Orchidaceae): Combined evidence from nuclear and plastid DNA sequences. *American Journal of Botany*, 88, 2286–2308.
- Reichenbach, H. G. (1886). Orchideae describuntur. *Flora*, 69(35), 547–562.
- Schlechter, F. R. R. (1921). Repertorium Specierum Novarum Regni Vegetabilis Beih, 9: 78.
- Schlechter, F. R. R. (1929). Figuren-Atlas zu den Orchideenfloren der südamerikanischen Kordillerenstaaten. In: Koeltz (Ed.), *Feddes repertorium specierum novarum regni vegetabilis, Volumen 57*. Berlin: Selbstverlag.
- Schneider, M. (1958). Algunas especies Colombianas de *Pleurothallis*. *Caldasia*, 8(37): 99–120.
- Schweinfurth, C. (1942). Orchidaceae Peruviana. *Botanical Museum Leaflets (Harvard University)*, 10, 173–216.
- Schweinfurth, C. (1959). Orchids of Peru. *Fieldiana – Botany*, 30(2), 261–531.
- Schweinfurth, C. (1970). First Supplement to the Orchids of Peru. *Fieldiana – Botany*, 33, 1–85.
- Tropicos. (2017). Missouri Botanical Garden, Missouri, USA. Available from <http://www.tropicos.org/Home.aspx> (Accessed on June 10 2017).
- Wilson, M., Baquero, L., Dupree, K., Jiménez, M. M., LeBlanc, C. M., Merino, G., Portilla, J., Salas Guerrero, M., Tobar Suárez, F. & Werner, J. D. (2016). Three new species of *Pleurothallis* (Pleurothallidinae; Orchidaceae) in subsection *Macrophyllae-Fasciculatae* from northern South America. *Lankesteriana*, 16(3), 349–366. Doi: <http://dx.doi.org/10.15517/lank.v16i3.27314>
- Wilson, M., Belle, C., Dang, A., Hannan, P., Kenyon, C., Low, H., Stayton, T. & Woolley, M. A. (2011). A phylogenetic analysis of the genus *Pleurothallis*, with emphasis on *Pleurothallis* subsection *Macrophyllae-Fasciculatae*, using nuclear ITS and chloroplast DNA sequencing. *Lankesteriana*, 11(3), 369. Doi: <http://dx.doi.org/10.15517/lank.v11i3.18304>
- Wilson, M., Belle, C., Dang, A., Hannan, P., Kellogg, L., Kenyon, C., Low, H., Mochizuki, A., Nguyen, A., Sheade, N., Shan, L., Shum, A., Stayton, T., Volz, C., Vosburgh, B., Wellman, H. & Woolley, M. A. (2013). A preliminary phylogenetic analysis of *Pleurothallis sensu lato* based upon nuclear and plastid sequences. *Lankesteriana*, 13(1–2), 139. Doi: <http://dx.doi.org/10.15517/lank.v0i0.11568>
- Wilson, M., Frank, G.S., Jost, L., Pridgeon, A., Vieira-Uribe, S. & Karremans, A. (2017). Phylogenetic analysis of *Andinia* (Orchidaceae: Pleurothallidinae) and a systematic re-circumscription of the genus. *Phytotaxa*, 295(2), 101–131. <https://doi.org/10.11646/phytotaxa.295.2.1>

