

A NEW SPECIES OF *PLEUROTHALLIS*
(ORCHIDACEAE: PLEUROTHALLIDINAE)
IN SUBSECTION *MACROPHYLLAE-FASCICULATAE* WITH A UNIQUE,
HIGHLY REDUCED, MORPHOLOGICALLY DISTINCT LABELLUM

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ABSTRACT. *Pleurothallis minutilabia*, a species unique in subsection *Macrophyllae-Fasciculatae* because of the minute, highly reduced lip, is described and compared to the most similar species in the subsection. It is also compared morphologically to *Pleurothallis kaynagata* from section *Abortivae*, to which *P. minutilabia* is not related, but which also possesses a highly reduced lip. The morphology of the flower of *P. minutilabia* is discussed briefly in relation to possible pollination mechanisms. The distribution, restricted to Zamora Chinchipe, southern Ecuador, and the conservation status are addressed.

KEY WORDS: cloud forest, Ecuador, labellar morphology, *Pleurothallis*, pollination

Introduction. Within *Pleurothallis* R.Br. as circumscribed by Pridgeon *et al.* (2005), subsection *Macrophyllae-Fasciculatae* Luer represents the largest taxonomic group with between 236 and 305 described species, depending on synonymy (Wilson, unpubl.). A consistent characteristic among all the species of *Pleurothallis* subsection *Macrophyllae-Fasciculatae* described to date, without exception, is a prominent and conspicuous labellum or “lip” laying flat upon the synsepal or elevated slightly above it (Fig. 1), which was illustrated in detail for *Pleurothallis castanea* Mark Wilson, G.Merino & J.D.Werner, *Pleurothallis nangaritzae* M.M.Jiménez, Tobar & Mark Wilson and *Pleurothallis rubrifolia* Mark Wilson, Tobar & Salas Guerr. by Wilson *et al.* (2016). While the dimensions, morphology, texture and positioning of this lip vary among the species, the presence of such a visible lip is constant (Fig. 1). There are currently no described species of *Pleurothallis* in

subsection *Macrophyllae-Fasciculatae* with a highly reduced or apparently “vestigial” lip.

The first species of *Pleurothallis* to be described with a minute and apparently vestigial lip was *Pleurothallis abortiva* Luer (Fig. 2a; Luer 1980). Not fitting well morphologically within any other section or subsection within subgenus *Pleurothallis*, Luer (1986) created section *Abortivae* to include *P. abortiva* and a few other species. Subsequently, Luer (1988) removed all but *P. abortiva* from the section, rendering it monotypic. Luer (1998) retained the monotypic section and stated that *P. abortiva* “is distinguished from all other species of the subgenus by the small, vestigial lip”. The section remained monotypic until Doucette *et al.* (2016) described *Pleurothallis kaynagata* A.Doucette, Mark Wilson & J.Portilla which has a similar lip (Fig. 2b, 3, 4).

Until recently, *P. abortiva* (Fig. 2a) and *P. kaynagata* (Fig. 2b, 3, 4) of section *Abortivae*

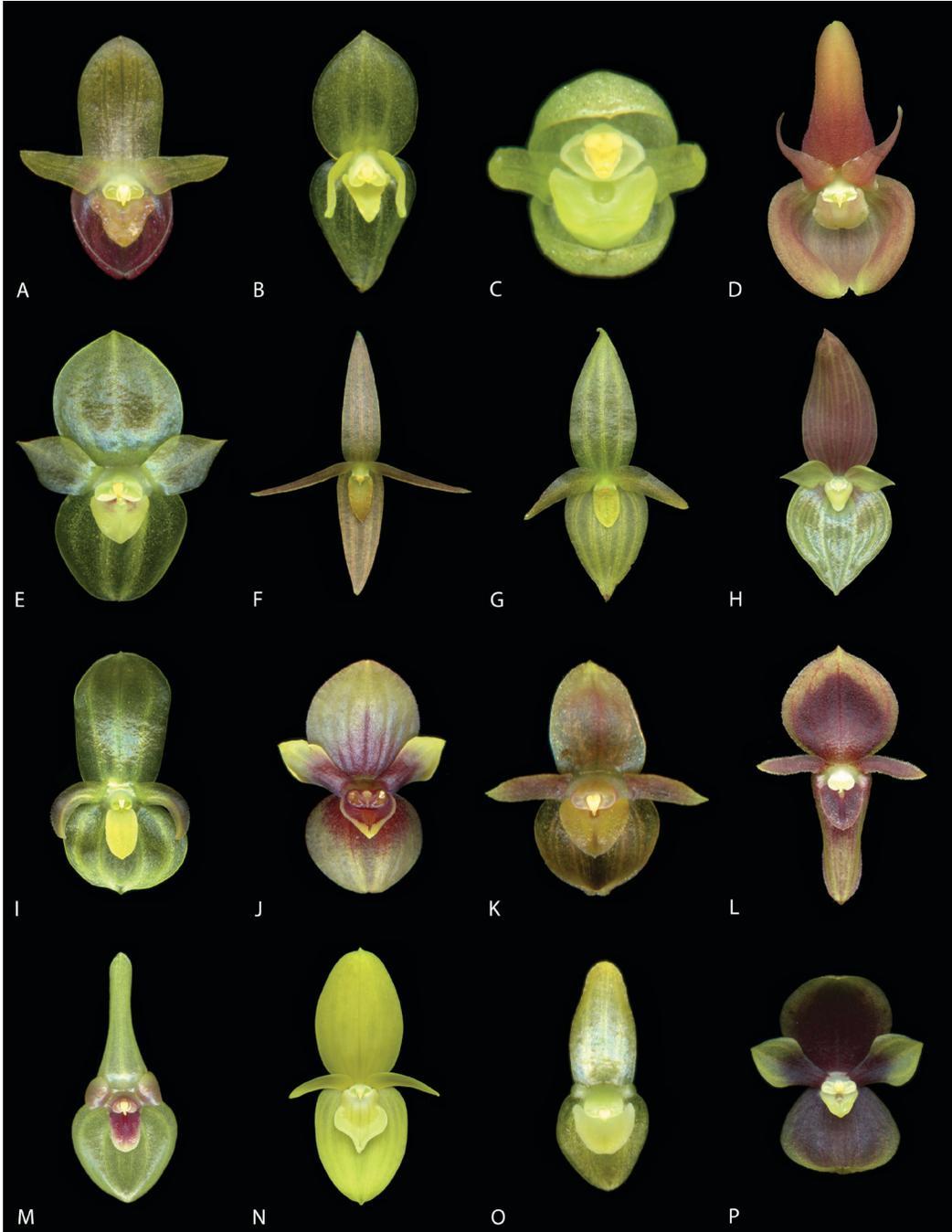


FIGURE 1. Flowers of various species of *Pleurothallis* subsection *Macrophyllae-Fasciculatae* demonstrating the prominent, clearly visible lip of the group. A. *P. arctata*. B. *P. baudoensis*. C. *P. calamifolia*. D. *P. calceolaris*. E. *P. conicostigma*. F. *P. crucifera*. G. *P. depressa*. H. *P. latipetala*. I. *P. octavioi*. J. *P. ortegae*. K. *P. pansamalae*. L. *P. platysepala*. M. *P. scurrula*. N. *P. titan*. O. *P. tridentata*. P. *P. volans*. Prepared from floral scans of plants in the Living Collection at Colorado College by M. Wilson. (Lips presented at the bottom, although some of these species are non-resupinate. Flowers not to the same scale.)

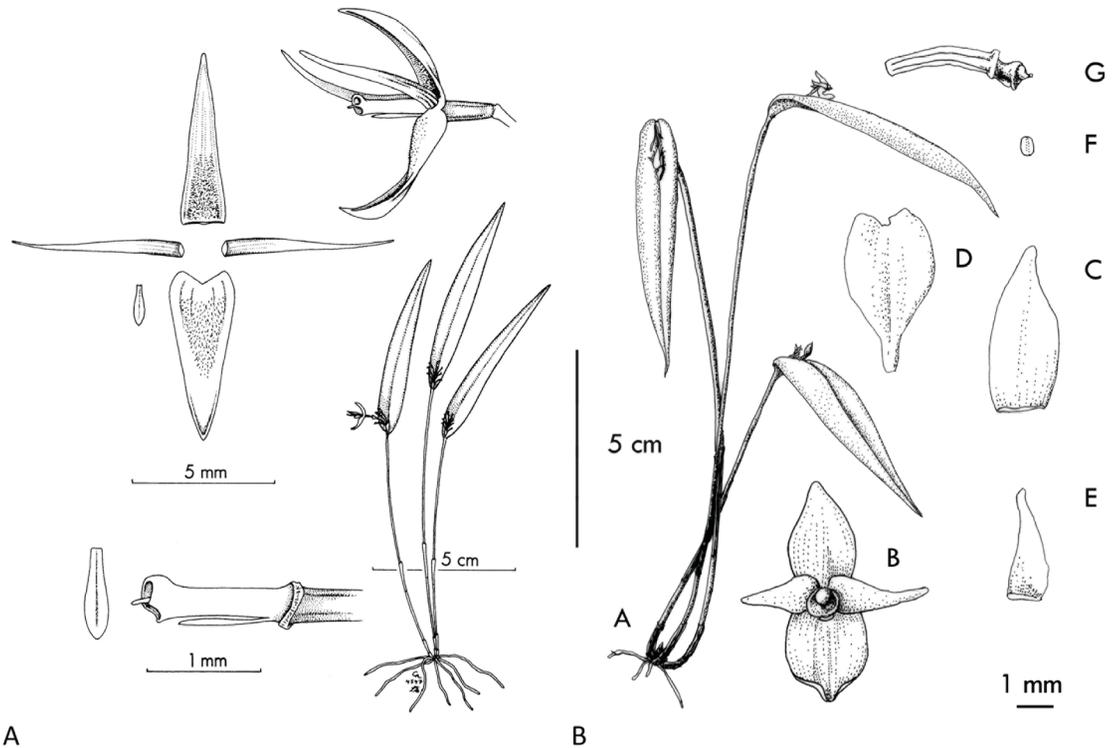


FIGURE 2. Drawings of A. *Pleurothallis abortiva* (drawing reproduced from Luer 1980, courtesy of Missouri Botanical Garden Press); and B. *Pleurothallis kaynagata* (drawing reproduced from Doucette *et al.* 2016, courtesy of Sociedad Colombiana de Orquideología and the journal *Orquideología*).

remained the only known *Pleurothallis* species with a minute, highly reduced and apparently vestigial lip, none existing in any of the other taxonomic groups within *Pleurothallis sensu* Pridgeon *et al.* (2005). The only thing remotely comparable being the very small, highly modified lips of the *P. crocodileiceps* species complex of subgenus *Ancipitia* (Wilson *et al.* 2017a, 2017b, 2018). However, in 2015 an undescribed species of *Pleurothallis* was collected from Podocarpus National Park during an intensive survey of poorly collected areas of Ecuador (Muchhala & Pérez 2015, Pérez *et al.* 2016, Orozco *et al.* 2017). The species was brought to the attention of Wilson because of the minute lip and the remarkable, though superficial, resemblance to *P. kaynagata*; the difference being that, based on the cordate leaves and bilobed stigma, the new species was most likely attributable to subsection *Macrophyllae-Fasciculatae*, not section *Abortivae*.

As stated above, all species of subsection

Macrophyllae-Fasciculatae described to date possess a prominent lip. The vast majority of these exhibit a “glenion” on the hypochile below and slightly in front of the anther/rostellum, which is hypothesized to provide a reward, though this has yet to be conclusively demonstrated. Further, many species in the subsection have been observed *in vivo* with a liquid substance on the lip (Wilson, unpubl.). These observations suggest the probable importance of the glenion and the nectar-like liquid in pollinator attraction and positioning during pollination (Luer 1986, Wilson *et al.* 2016). Therefore, any species with a highly reduced and apparently vestigial lip are of interest because they may exhibit a very different pollination syndrome from other members of the subsection. In this paper, the new species is described and illustrated and we present an hypothesis regarding the possible role of the unique labellar morphology in the reproductive ecology of the species.



FIGURE 3. *Pleurothallis kaynagata*. A. Whole flower – lateral view. B. Column and lip – lateral view. C. Column and lip – ventral view. Prepared by M. Wilson from material in Ecuagenera collection.

Materials and Methods

Plant material. — Living material of the putative new species was examined *in situ* in Ecuador by Tobar, Pérez, Romoleroux and Jiménez and in a private collection in The Netherlands by Wilson.

Morphological and taxonomic comparisons. — Since the new species was believed to be a member of subsection *Macrophyllae-Fasciculatae*, in order to determine taxonomic novelty the material was compared with all described species in that subsection. The new species was also compared in detail with *Pleurothallis kaynagata* from section *Abortivae* using material from the living collection at Colorado College (Wilson PL0734 and PL0735) and *Pleurothallis abortiva* from the type, drawings and description since no living material or photographs are known. Finally, the new species was compared with those described in subsection *Acroniae*, in case the species had mistakenly been published in that group.

Scanning electron microscopy. — For scanning electron microscopy (SEM) fresh-harvested flowers were preserved in Kew Mix (5% formalin [37.6% formaldehyde], 53% methanol, 5% glycerol, 37% deionized water). Flowers were dehydrated in successively higher concentrations of ethanol (80%, 95%, 100%, 100%) for 15 min each before being placed in freshly-opened 100% ethanol. Specimens were dried in a critical point dryer (model EMS 850, Electron Microscopy Sciences, Hatfield, PA, USA) prior to mounting on aluminum stubs and sputter coating (model Pelco SC-6, Ted Pella, Redding, CA, USA). Specimens were imaged using a scanning electron microscope (model JSM-6390LV, Jeol, Peabody, MA, USA) with an accelerating voltage of 10-15 kV.

Results

Morphological and taxonomic comparisons. — Exhaustive examination of all the published taxonomic literature for subsection *Macrophyllae-Fasciculatae*, section *Abortivae* and subsection *Acroniae* confirmed the novelty of the species. While attributable to subsection *Macrophyllae-Fasciculatae* based upon the cordate leaves spreading horizontally from the ramicaul and the bilobed stigma, the floral morphology

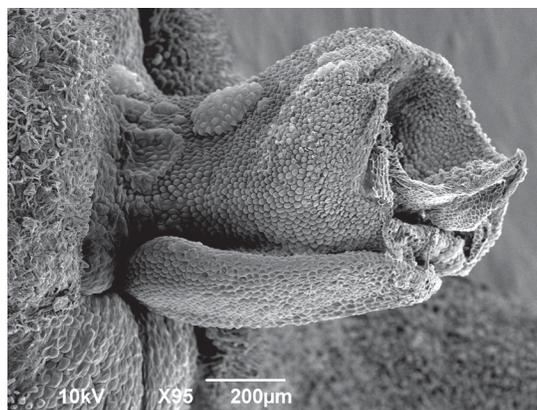


FIGURE 4. Scanning electron micrograph of *Pleurothallis kaynagata* column and lip. Prepared by G. Frank and M. Wilson from *P. kaynagata* PL0734 from living collection at Colorado College.

with the highly reduced and apparently vestigial lip indicates that the new species, to date, is unique in the subsection. The lip initially appears to be absent when the flower is viewed from the dorsal surface. Indeed, at first glance it resembles a flower in which the lip has been removed by a slug or snail, as occurs somewhat frequently. The lip becomes visible beneath the column only when the flower is tilted backwards (Fig. 5) or the flower is viewed from the side. Interestingly, the lip was observed to be loosely hinged and partially motile, though the point of articulation on the column was not visible. A flat, triangular flange projecting from the base of the lip appeared to limit the range of motility by resting against the synsepal.

Scanning electron microscopy. — Considering the uniqueness of the floral morphology, a detailed SEM examination was warranted (Figs. 6–9). When imaged from above, the lip is completely obscured by the column and projecting anther (Fig. 6a), but is exposed, nestled beneath the column, when the flower is tilted (Fig. 6b). The lip approximates an equilateral triangle, ~538 μm wide at the base and ~520 μm long, and is ~285 μm deep at the base, assuming minimal shrinkage during critical point drying (Figs. 7 and 8). The lip is subtended at its base by a downward projecting triangular extension, or flange, ~436 μm long (from point of attachment to the tip) or ~560 μm (from dorsal surface of lip to tip of flange) (Figs. 7 and 8). The most prominent feature is a papilla-lined cavity at the apex of the lip, ~78 μm

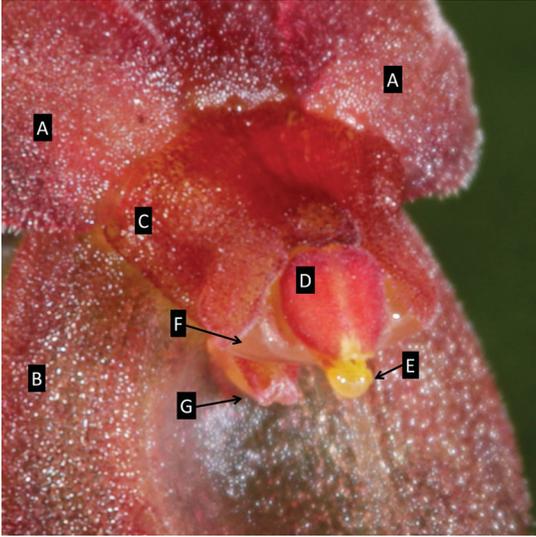


FIGURE 5. *Pleurothallis minutilabia* column and lip. A. Petals. B. Synsepal. C. Column. D. Anther cap. E. Viscidium. F. Stigma. G. Lip. Photograph by M. Wilson from *Wilson PL0996*.

wide, which appears to project backwards into the lip, creating a ridge along the dorsal surface (Figs. 7 and 8). While the dorsal surface was not completely visible, no glenion or other morphologically-distinct possibly secretory tissue was visible.

The pollinarium is typical for subsection *Macrophyllae-Fasciculatae*, consisting of two clavate pollinia, $522 \times 264 \mu\text{m}$, subtended by caudicles, with a spherical viscidium at the apex (Fig. 9).

TAXONOMY

Pleurothallis minutilabia Mark Wilson, F.Tobar, A.J.Pérez, *sp. nov.* (Figs. 5–11).

TYPE: Ecuador. Zamora-Chinchipe. Podocarpus National Park, Bombuscaro River sector, collected on the trail to the outlook, 1000–1400 m, $04^{\circ}06'38.9''\text{S}$, $78^{\circ}58'11.9''\text{W}$, 31 Mar 2015 (fl, flower in alcohol), A. J. Pérez, F. Tobar, N. Zapata, W. Santillán, H. Namcela 8539 (holotype QCA - 237066).

In subsection *Macrophyllae-Fasciculatae*, the most morphologically similar species is *Pleurothallis erythrium* Luer. The new species is easily distinguished from *P. erythrium* by the lip (ovate-triangular, approximately 50% the length of the synsepal, with

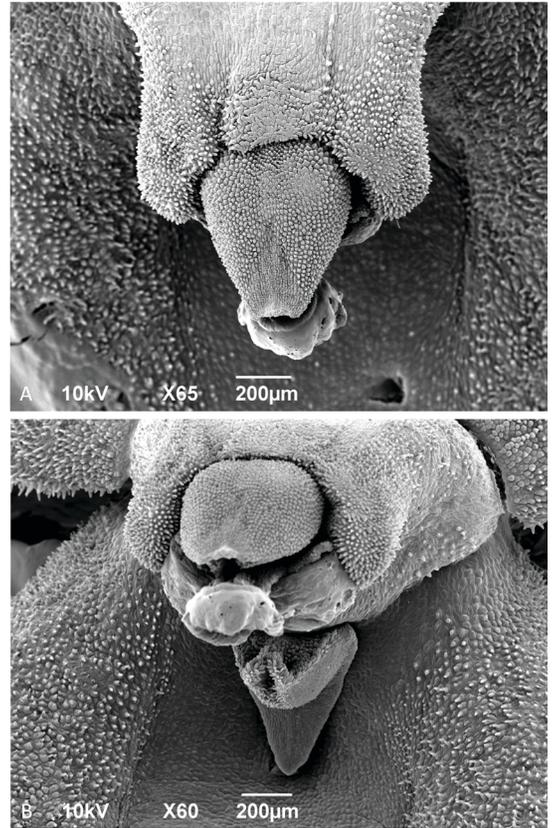


FIGURE 6. *Pleurothallis minutilabia* scanning electron micrographs. A. Column, anther cap, viscidium and synsepal (dorsal view). B. Column, lip and synsepal (tilted front view). Micrographs by M. Wilson from *Wilson PL0996*.

distinct glenion in *P. erythrium* versus highly reduced, not projecting beyond the column, glenion apparently absent and apical, papilla-lined cavity in *P. minutilabia*) and the surface of the petals and sepals (hirsute in *P. minutilabia* versus glabrous in *P. erythrium*).

Plant epiphytic, caespitose, to ~8–10 cm tall. *Roots* fibrous, slender. *Ramicauls* slender, terete, suberect-spreading, 5.4–11.6 cm long, enclosed by thin, papery, tubular sheaths, basal sheath 3.2–5.8 mm long, mid-ramicaul sheath 13–17 mm long. *Leaves* horizontal, ovate, acute, $2.0\text{--}3.8 \times 1.2\text{--}2.8$ cm, base sessile, shallowly cordate, coriaceous. *Inflorescence* fascicle of successive, single flowers, $6.0\text{--}7.8 \times 4.3\text{--}4.9$ mm, resupinate, borne from reclining spathaceous bract 3.8–6.0 mm long, pedicel 2.5–2.9 mm long, ovary 1.8–2.2 mm long. *Dorsal sepal* beige suffused with

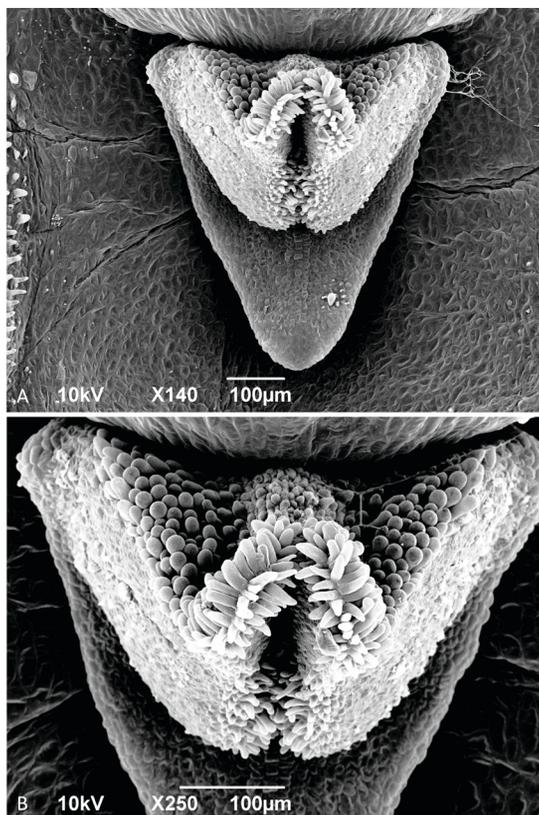


FIGURE 7. *Pleurothallis minutilabia* scanning electron micrographs. A. Lip with flange (front view). B. Lip (front view). Micrographs by K. Zhao and M. Wilson from *Wilson PL0996*.

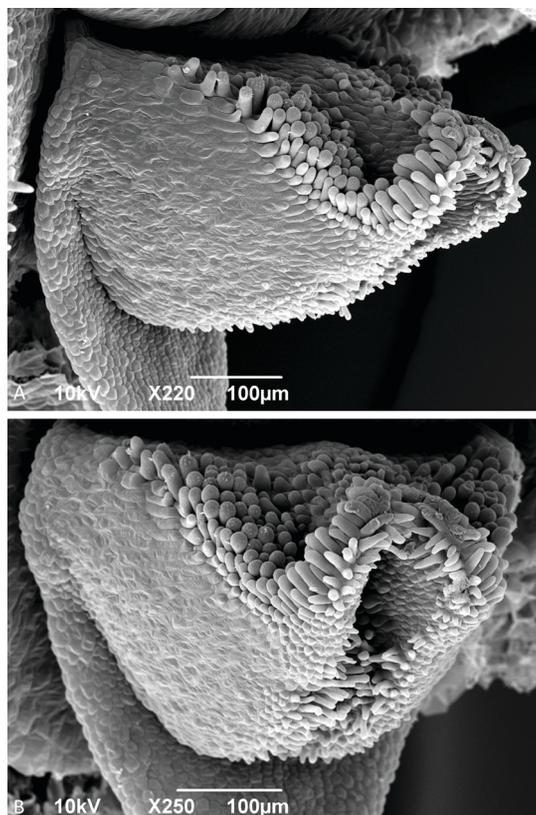


FIGURE 8. *Pleurothallis minutilabia* scanning electron micrographs. A. Lip (lateral 3/4 view). B. Lip (lateral 2/3 view). Micrographs by H. Hampson from *Wilson PL0996*.

red-purple, ovate, subacute, 3.4–4.0 × 2.2–2.9 mm, 3-veined, pubescent. *Synsepal* beige suffused with red-purple, ovate, subacute, 2.9–3.5 × 2.7–3.0 mm, concave centrally, 2-veined, pubescent. *Petals* beige suffused with red-purple, ovate-lanceolate, acute 3.1–3.3 × 1.0–1.1 mm, one-veined, pubescent. *Labellum* rufous, triangular, slightly wider than long, 520 × 538 µm, stout, 285 µm thick, concave dorsally, involute (“hooked”) apex, keeled ventrally, flat flange projecting downwards from underside of base, 436 µm (from point of attachment on underside to tip). *Column* rufous, stout, 1.0–2.0 × 1.2–1.4 mm, papillose, anther apical, stigma bilobed, ventral. *Pollinarium* two clavate pollinia 522 × 264 µm, short caudicle, spherical viscidium.

ADDITIONAL MATERIAL STUDIED: The Netherlands. Heijningen, flowered in cultivation without collection data, December 2017, *Wilson PL0996* (paratype: COCO).

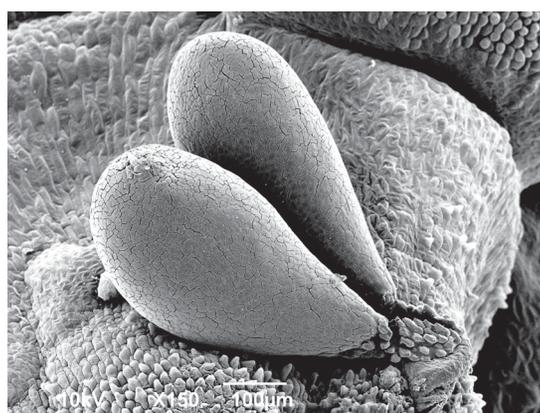


FIGURE 9. Scanning electron micrographs of *Pleurothallis minutilabia* pollinarium. Micrograph by K. Zhao and M. Wilson from *Wilson PL0996*.

ETYMOLOGY: Named for the minuscule size of the lip.

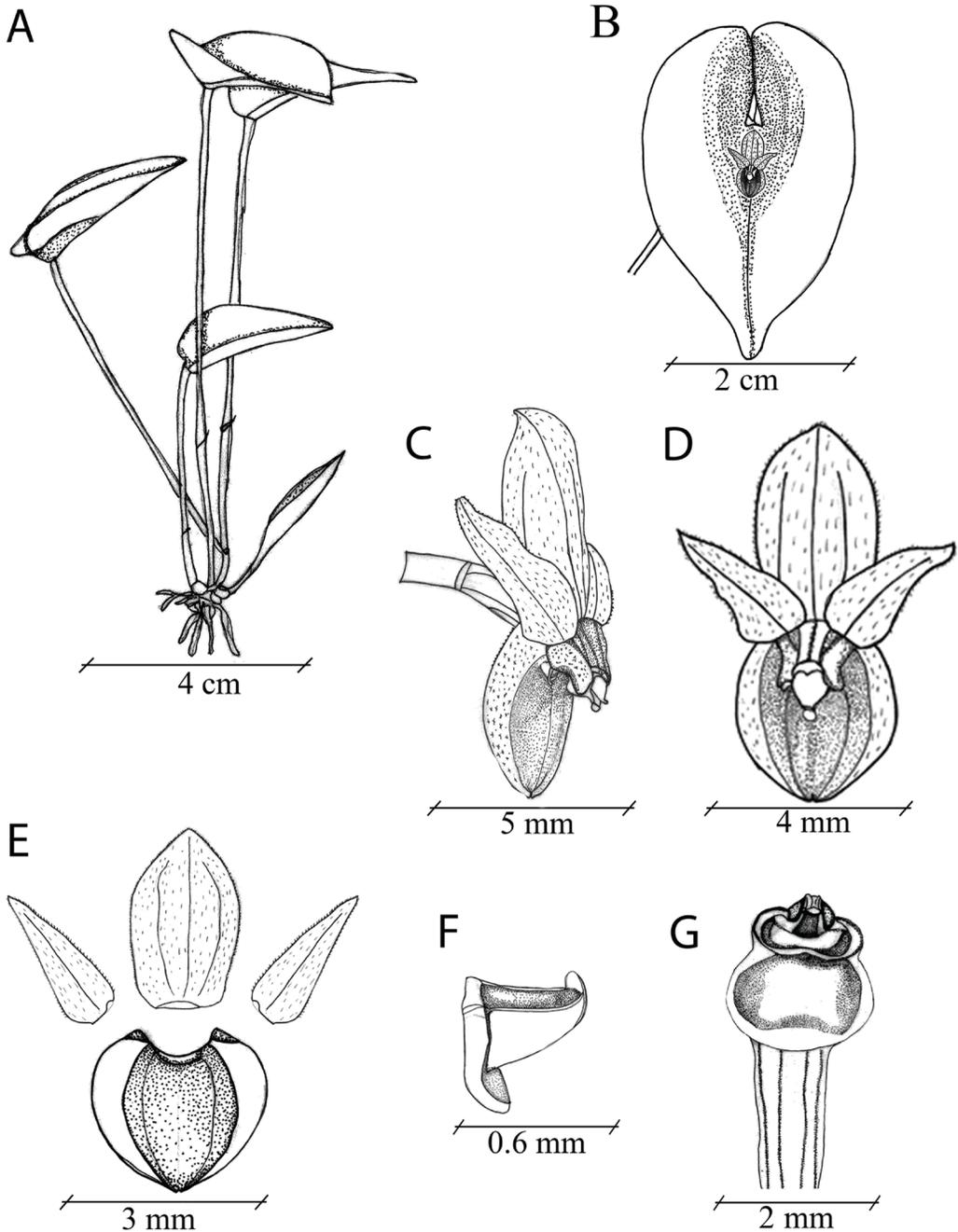


FIGURE 10. Drawing of *Pleurothallis minutilabia*: A. Whole plant. B. Leaf with flower. C. Flower (3/4 view). D. Flower (front view). E. Floral dissection. F. Labellum. G. Column and ovary (ventral surface). Illustration by F. Tobar and K. Romoleroux, from material used to prepare the type specimen.

Pleurothallis minutilabia is placed in the group *Macrophyllae-Fasciculatae* (Luer 1986, 1988, 2005) based on morphological attributes: spreading-to-erect,

well-developed ramicauls; sessile, cordate leaves, not in same plane as ramicaul; single-flowered inflorescence emerging from the apex of the ramicaul at the base

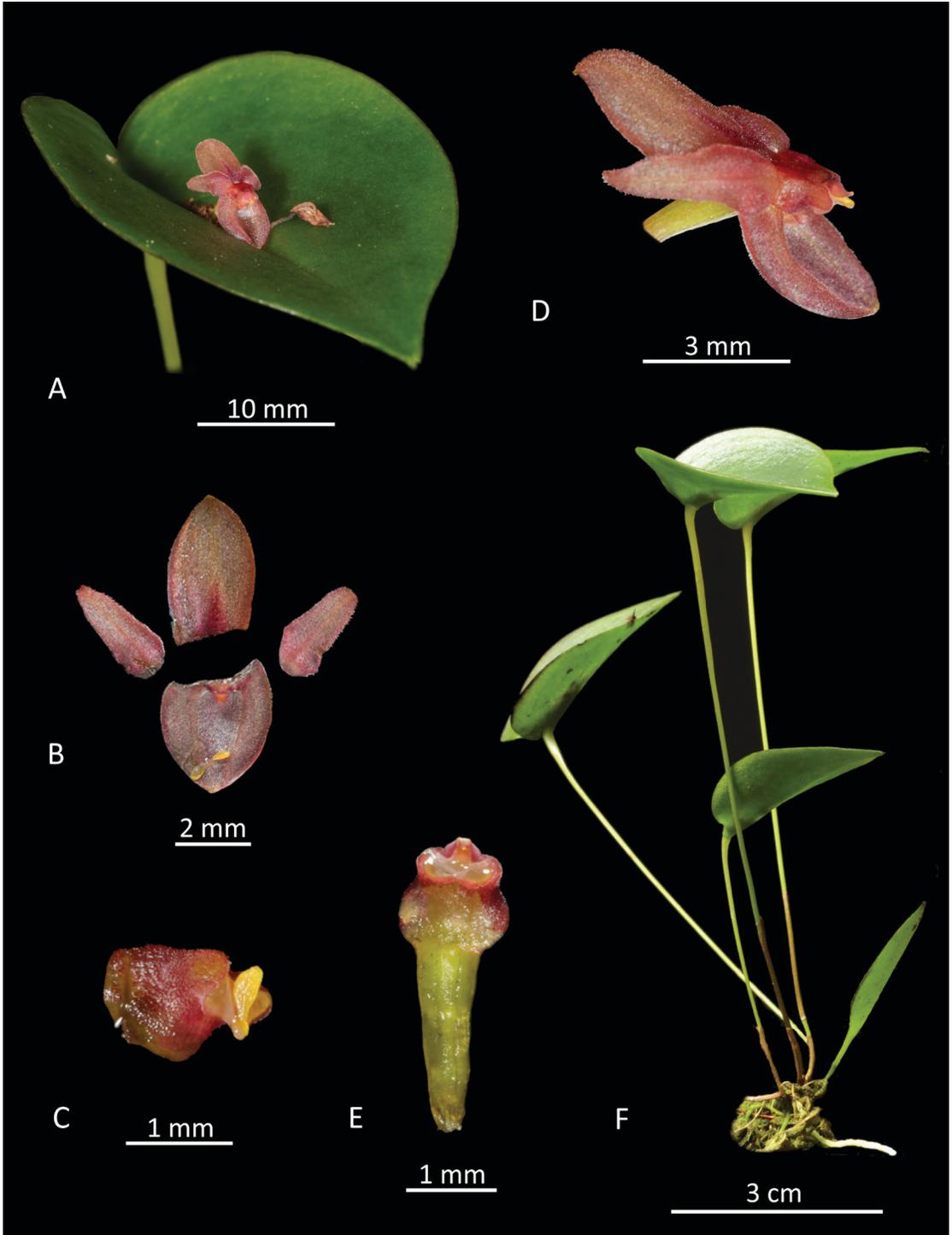


FIGURE 11. *Pleurothallis minutilabia* Lankester composite dissection plate. A. Leaf and flower. B. Floral dissection – sepals and petals. C. Column. D. Whole flower – lateral view. E. Column and ovary – ventral view. F. Whole plant. LCDP prepared by M. Wilson from *Wilson PL0996*.

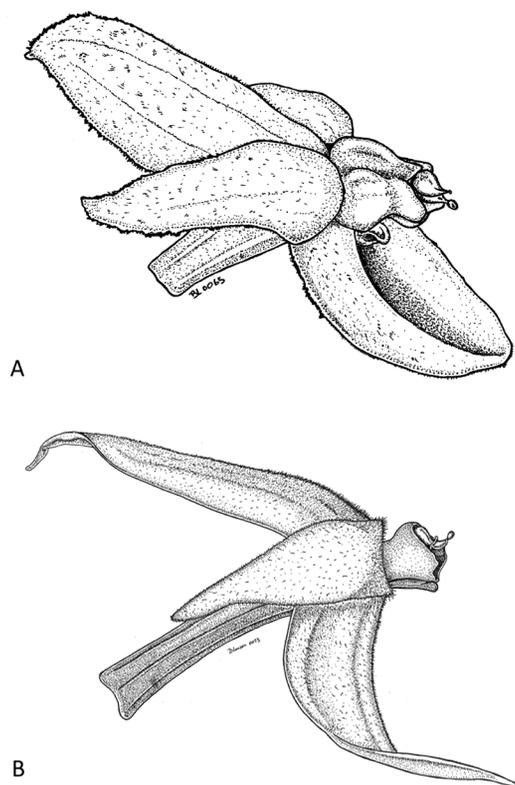


FIGURE 14. A. *Pleurothallis minutilabia* flower (lateral view). B. *Pleurothallis kaynagata* flower (lateral view). Illustrations by B. Larsen from Wilson PL0996 and Wilson PL0734, respectively.

series *Amphigyae* (Luer 1998), the only two other possible groups. The labellar morphology of *P. minutilabia* is completely unique within the subsection. Of the 236+ species described to date, all possess a small-to-large lip which projects beyond the column (Fig. 1); of those examined so far, the vast majority possess a glenion on the lip; and many have been observed with a liquid substance somewhere on the lip (Wilson *et al.*, unpubl.). In *P. minutilabia*, however, the lip is completely obscured until the flower is tilted backwards or sideways to reveal the minute, highly reduced structure beneath the column. The only parallel is in the apparently vestigial lips of *P. abortiva* and *P. kaynagata* (Figs. 2–4).

Following the taxonomy of Luer, *Pleurothallis kaynagata* would be attributable to section *Abortivae*. However, Doucette *et al.* (2016) hypothesized that the closest relative is *Pleurothallis neossa* (Luer & Hirtz) J.M.H.Shaw of subsection *Acroniae*, which

has been borne out by recent phylogenetic analysis (Wilson, unpubl.). Although Luer (2005) chose to combine subsections *Macrophyllae-Fasciculatae* and *Acroniae* under the resurrected name *Acronia* C.Presl., preliminary phylogenetic analyses indicate that the two groups are phylogenetically distinct (Wilson *et al.* 2011, 2013).

Although not closely related, flowers of *P. minutilabia* and *P. kaynagata* are morphologically similar (Fig. 14): both flowers are beige, lightly suffused with burgundy; both flowers are hirsute, uniformly covered in short hairs (a characteristic rare within *Macrophyllae-Fasciculatae*); both flowers are relatively open, with reflexed petals; and, both have a short column with a highly reduced lip. The lip of *P. minutilabia* at $\sim 520 \times 538 \mu\text{m}$ (or $\sim 0.5 \times 0.5 \text{ mm}$), however, is significantly smaller than that of *P. abortiva* $1.6 \times 0.5 \text{ mm}$ (Luer 1980) or that of *P. kaynagata* $1.0 \times 0.7 \text{ mm}$ (Doucette *et al.* 2016). And, the lip of *P. minutilabia* is very different in morphology from those of the other two species. While the lips of *P. abortiva* and *P. kaynagata* are ovate, membranous and adpressed to the ventral surface of the column (Luer 1980, Doucette *et al.* 2016) (Figs. 2–4), the lip of *P. minutilabia* is stout, triangular, concave dorsally, with a papilla-lined cavity at the apex (Figs. 6–8). Further, the lip has a flat, triangular flange at the base of the lip which lies against the synsepal and appears to maintain the position of the lip in the vertical plane.

Luer (1998) referred to the lip of *Pleurothallis abortiva* as “vestigial”. According to the Oxford Living Dictionary vestigial can be defined as: “*degenerate, rudimentary, or atrophied, having become functionless in the course of evolution*” and according to the Merriam-Webster dictionary the definition is: “*remaining in a form that is small or imperfectly developed and not able to function*”. In both definitions, loss of function is a central concept. We hypothesize that, at least in *Pleurothallis minutilabia*, the highly reduced, but morphologically unique and structurally complex lip is not vestigial according to these definitions. The micromorphology of the lip revealed by SEM, including the papilla-lined, apical labellar cavity and the supporting flange seem far too elaborate to comprise a vestigial structure. We hypothesize, therefore, that the lip of *P. minutilabia* performs a very specific function during the reproductive ecology of the species.

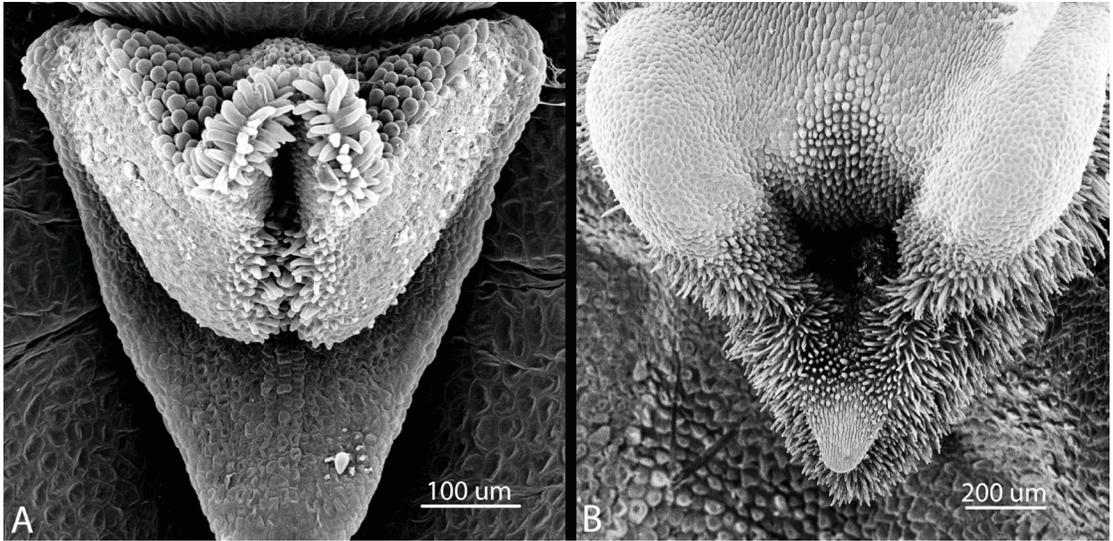


FIGURE 15. Papilla-lined, apical labellar cavities. A. *Pleurothallis minutilabia*. B. *Pleurothallis wielii*. Scanning electron micrographs by K. Zhao, K. Dupree and M. Wilson.

The last two decades have seen substantial progress in the study of pollination strategies in Pleurothallidinae, including in the genera *Acianthera* Scheidw. (Borba & Semir 2001); *Andinia* (Luer) Luer (Álvarez 2011); *Dracula* Luer (Endara *et al.* 2010, Policha *et al.* 2016); *Lepanthes* Sw. (Blanco & Barboza 2005, Blanco & Vieira 2011, Calderón-Sáenz 2012); *Restrepia* Kunth (Millner & Baldwin 2016); *Specklinia* Lindl. (Karremans *et al.* 2015); and *Trichosalpinx* Luer (Bogarín *et al.* 2018). In comparison to these other Pleurothallidinae much less is known about pollination strategies in *Pleurothallis*, with only a few careful studies having been published (Calderón-Sáenz 2011, Damon & Salas-Roblero 2007, Díaz-Morales & Karremans 2015, Duque-Buitrago *et al.* 2014) and only one of these being of a species in subsection *Macrophyllae-Fasciculatae* (Duque-Buitrago *et al.* 2014). Nevertheless, we can observe that in almost all species of *Pleurothallis* subsection *Macrophyllae-Fasciculatae*, there is a distinct lip projecting beyond the column; typically with a glenion on the hypochile; and a liquid substance, a probable pollinator reward, is often observed on the lip (Wilson *et al.* unpubl.). The lip of *P. minutilabia* is unique among the 236+ species of the subsection and, therefore, one might conclude, functions differently than the other lips.

We hypothesize that *Pleurothallis minutilabia* is deceit-pollinated through pseudocopulation by a

male insect and that the lip plays a specific, important role in the process. To date, among Pleurothallidinae, pseudocopulation has been observed only in *Andinia* (Álvarez 2011) and *Lepanthes* (Blanco & Barboza 2005, Blanco & Vieira 2011, Calderón-Sáenz 2012) and, admittedly, apart from reduced size, there are no morphological similarities between the lips of these species and that of *P. minutilabia* that would support this hypothesis. However, the extreme reduction in size despite morphological complexity; the apical papilla-lined cavity into which the abdomen of an insect could be inserted; and the labellar motility modulated by the subtending flange all suggest to us a possible pseudocopulatory role for the lip. Interestingly, the papilla-lined cavity of *P. minutilabia* strongly resembles the cavity in the lips of the *P. crocodiliceps* complex (Fig. 15) (Wilson *et al.* 2017a, 2017b, 2018), which are also hypothesized to involve deceit-pollination by pseudocopulation. Acknowledging that only *in situ* observations of the pollination process can conclusively demonstrate deceit-pollination by pseudocopulation in *P. minutilabia*, given the difficulty of performing such studies in a sparsely distributed, tropical montane species, in the meantime additional studies are planned to address the hypothesis. These include light microscopy of labellar sections with staining for possible reward chemicals; transmission electron microscopy of labellar sections

to further examine the apical labellar cavity; and gas chromatography-mass spectroscopy (GC-MS) to examine floral volatiles.

We further hypothesize that the phylogenetically unrelated *Pleurothallis kaynagata* is also deceit-pollinated through pseudocopulation and that floral morphological similarities between *P. kaynagata* and *P. minutilabia* represent convergent evolution due to similar pollination syndromes. The reproductive ecology of *P. minutilabia*, *P. kaynagata* and the *P. crocodileiceps* species complex and the hypothesized involvement of deceit pollination via pseudocopulation is one area of ongoing research in the Wilson lab.

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LITERATURE CITED

- Álvarez, L. E. (2011). Polinización *Lepanthes*. *El Orquideólogo: Boletín de la Asociación Bogotana de Orquideología*, 46, 15–16.
- Blanco, M. A. & Barboza, G. (2005). Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. *Annals of Botany*, 95, 763–772. doi: <https://doi.org/10.1093/aob/mci090>
- Blanco, M. A. & Vieira-Urbe, S. (2011). Pollination in *Lepanthes*. *Orchids*, 80(6), 356–357.
- Bogarín, D., Fernández, M., Borkent, A., Heemskerk, A., Pupulin, F., Ramírez, S., Smets, E. & Gravendeel, B. (2018). Pollination of *Trichosalpinx* (Orchidaceae: Pleurothallidinae) by biting midges (Diptera: Ceratopogonidae). *Botanical Journal of the Linnean Society*, 186(3), 510–543. doi: <https://doi.org/10.1093/botlinnean/box087>
- Borba, E. L. & Semir, J. (2001). Pollinator specificity and convergence in fly-pollinated *Pleurothallis* (Orchidaceae) species: A multi-population approach. *Annals of Botany*, 88, 75–88.
- Calderón-Sáenz, E. (2011). *Pleurothallis colossus*: Pollination by Anthomyiid flies at El Refugio Nature Reservation. *Orchids*, 80(12), 740–743.
- Calderón-Sáenz, E. (2012). Remoción de polinarios de *Lepanthes yubarta* por una mosca fungosa del género *Bradysia*, bajo condiciones seminaturales. *Orquideología*, 29(1), 31–34.
- Damon, A. & Salas-Roblero, P. (2007). A survey of pollination in remnant orchid populations in Soconusco, Chiapas, Mexico. *Tropical Ecology*, 48(1), 1–14.
- Díaz-Morales, M. & Karremans, A. (2015). Pollination biology of five species of Pleurothallidinae in a montane region in Costa Rica. Poster presented at the V Scientific Conference on Andean Orchids, Cali, Colombia, Nov 2015.
- Doucette, A., Wilson, M., Portilla, J., Kay, A., Moreno, J. S. & Cameron, K. M. (2016). Two new species of *Pleurothallis* and a new name for *Acronia rinkei*. *Orquideología*, 23(2), 123–139.
- 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.
- Endara, L., Grimaldi, D. A. & Roy, B. A. (2010). Lord of the flies: pollination of *Dracula* orchids. *Lankesteriana*, 10(1), 1–11. doi: 10.15517/LANK.V10I1.18318
- IUCN (2012). The IUCN red list of threatened species, version 2017-1. IUCN Red List Unit, Cambridge U.K. Retrieved from: <http://www.iucnredlist.org/> [Accessed 18 Jan 2018].
- Karremans, A. P., Pupulin, F., Grimaldi, D., Beentjes, K. K., Bütöt, R., Fazzi, G. E., Kaspers, K., Kruizinga, J., Roessingh, P., Smets, E. F. & Gravendeel, B. (2015). Pollination of *Specklinia* by nectar-feeding *Drosophila*: the first reported case of a deceptive syndrome employing aggregation pheromones in Orchidaceae. *Annals of Botany*, 116 (3), 437–445. doi: <https://doi.org/10.1093/aob/mcv086>
- Luer, C. A. (1980). Miscellaneous new species in the Pleurothallidinae (Orchidaceae). *Phytologia*, 47, 59–84.
- Luer, C. A. (1986). Icones Pleurothallidarum III: Systematics of *Pleurothallis*. *Monographs in Systematic Botany*, 20, 1–109.
- Luer, C. A. (1988). A revision of some subsections of genus *Pleurothallis*. *Lindleyana*, 3, 133–149.
- Luer, C. A. (1998). Icones Pleurothallidarum XVII: Systematics of subgen. *Pleurothallis* sect. *Abortivae*, sect. *Truncatae*,

- sect. *Pleurothallis*, subsect. *Acroniae*, subsect. *Pleurothallis*, subgen. *Dracontia*, subgen. *Unciferia*. *Monographs in Systematic Botany from Missouri Botanical Garden*, 72, 1–121.
- Luer, C. A. (2005). Icones Pleurothallidinarum XXVII: *Dryadella* and *Acronia* section *Macrophyllae-Fasciculatae*. *Monographs in Systematic Botany from Missouri Botanical Garden*, 103, 1–311.
- Millner, H. J. & Baldwin, T. C. (2016). Floral micromorphology of the genus *Restrepia* (Orchidaceae) and the potential consequences for pollination. *Flora*, 225, 10–19.
- Ministerio del Ambiente del Ecuador. (2013). *Sistema de Clasificación de los Ecosistemas del Ecuador Continental*. Subsecretaría de Patrimonio Natural, Quito, 232 pp.
- Muchhala, N. & Pérez, A. J. (2015). *Burmeistera zamorensis* (Campanulaceae, Lobelioideae), a new species from southern Ecuador. *Novon*, 24, 36–38.
- Orozco, C. I., Pérez, A. J., Romoleroux, K. & Murillo Aldana, J. (2017). The discovery of a new species of *Brunellia* (Brunelliaceae) with ephemeral petals from Llanganates National Park, Ecuador. *Phytotaxa*, 311(3), 263–269.
- Pérez, A. J., Arroyo, F., Neill, D. A. & Vázquez-García, J. A. (2016). *Magnolia chiguila* and *M. mashpi* (Magnoliaceae): two new species and a new subsection (*Chocotalauma*, sect. *Talauma*) from the Chocó biogeographic region of Colombia and Ecuador. *Phytotaxa*, 284, 267–276. doi: <https://doi.org/10.11646/phytotaxa.286.4.5>
- Policha, T., Davis A., Barnadas, M., Dentinger, B. T. M., Raguso, R. A. & Roy, B. (2016). Disentangling visual and olfactory signals in mushroom-mimicking *Dracula* orchids using realistic three-dimensional printed flowers. *New Phytologist*, 210(3), 1058–1071. doi: <https://doi.org/10.1111/nph.13855>
- Pridgeon, A. M., Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (2005). *Genera Orchidacearum. Vol. 4. Epidendroideae (Part one)*, (pp. 385–390). Oxford, U.K.: Oxford University Press.
- 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: 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: 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). Preliminary phylogenetic analysis of *Pleurothallis sensu lato* based upon nuclear and plastid sequences. *Lankesteriana*, 13(1–2), 139. doi: 10.15517/LANK.V0I0.11568
- Wilson, M., Dupree, K., Driessen, W., Larsen, B. T., Löckher, A., Niessen, A., Portilla, J., Salas Guerrero, M., Suarez, M. A. & Tobar Suárez, F. (2017a). A clarification of the taxonomy of *Pleurothallis crocodiliceps* Rehb.f. (Pleurothallidinae, Orchidaceae) and four new species of *Pleurothallis* in subgenus *Ancipitia*. *Lankesteriana*, 17(2), 165–191. doi: 10.15517/LANK.V17I2.29911
- Wilson, M., Vieira-Uribe, S., Aguirre, G., Posada, J. F. & Dupree, K. (2017b). Two new species of *Pleurothallis* (Pleurothallidinae, Orchidaceae) in subgenus *Ancipitia* from Colombia. *Orquideología*, 34, 34–51.
- Wilson, M., Jimenez, M. M., Jost, L., Kay, A., Frank, G. & Baquero, L. E. (2018). A new species of *Pleurothallis* (Orchidaceae, Pleurothallidinae) from northwestern Ecuador with affinities to both subgenera *Ancipitia* and *Scopula*. *Phytotaxa*, 343(3), 249–258. Doi: <http://dx.doi.org/10.11646/phytotaxa.343.3.5>