Speciation In Real-Time: An Evolutionary Analysis and Comparative Study on the Rapid Speciation and Hyperdiversity in *Pleurothallis (Orchidaceae)* Species within Section *Macrophyllae-Fasciculatae*

With Notes on Subgenus *Ancipitia* and Subgenus *Scopula*

Kevin W. Holcomb

PLEUROTHALLIDINAE
Volume 4.1
May 2025

The research presented here meets all the requirements for valid publication of new species as defined by the International Association for Plant Taxonomy (IAPT) and the *International Code of Nomenclature for algae, fungi, and plants.*

PLEUROTHALLIDINAE

ISSN #2834-1783
ORCID #0000-0002-0571-4462

Cover Photo: *Pleurothallis tremens*

Volume 4.1
ISSN #2834-1783

Contents

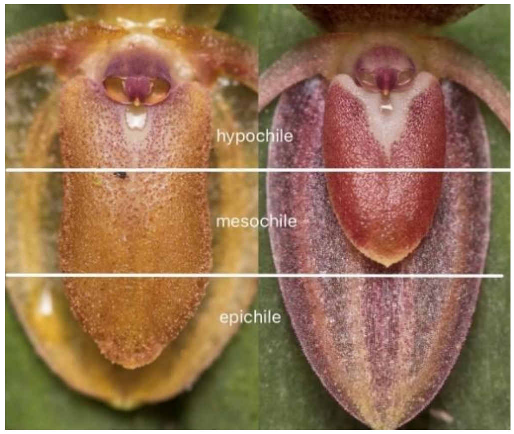
ISSN #2834-1783

Introduction

The species within *Pleurothallis* Section *Macrophyllae-Fasciculatae*, or PMF species as they will be called for the remainder of this article, constitute one of the largest and most hyperdiverse groups within the *Pleurothallidinae*. However, the high amount of diversity within this group has been largely dismissed as trivial variation.

PMF species are generally described using the morphological species concept, which characterizes species by distinctive morphological features. Most species in this group are identified primarily by the characteristics of the labellum (lip).

Volume 4.1
ISSN #2834-1783



It was long assumed that the gradual reduction in lip size among PMF species represented typical intraspecific variation. However, PMF species originated from ancestors with lips as long as the synsepal. Today, all PMF species exhibit some degree of lip degeneration, with six species having lips that are nearly or completely vestigial.

Advances in technology, such as digital cameras and now camera phones, have made it much easier to document observations of species in the field, and websites like iNaturalist allow these observations to be shared instantly. By providing a platform for anyone to record and share observations of species in the field, iNaturalist has created a massive dataset based primarily on data provided by citizen scientists. This dataset consists of over 6,000 photos associated with over 4,000 field observations of PMF species.

This is the first large-scale analysis of PMF species based on field observations, and it turns out, the diversity in this group is far from trivial. In fact, this might be the most important group of all in regard to understanding evolution within the *Pleurothallidinae*.

Materials and Methods

Step 1. All validly published species were classified into four groups based on lip shape, lip position (erect, suberect, or prostrate), and the functionality of the hinge connecting the lip to the foot of the spine.

Step 2. All species that are currently considered synonyms were excluded. However, synonymy is addressed in the nomenclature notes.

Step 3. The distribution maps were created from the collection data of the holotypes of all validly published species. Species without collection data were plotted using country of origin.

Step 4. Country-specific checklists and online databases were cross-referenced that all species groups were represented.

Step 5. Field observations were checked in iNaturalist to ensure that no records were added to date.

Step 6. An analysis of 8,788 photos associated with 4,070 field observations and any additional records was analyzed

Scan, tap, or click the QR code to see an interactive Distribution Map on Google Earth

Plant Material:

Live plant material from the author's personal collection,

as well as from Andy's Orchids, Encinitas, California, and

the permanent and living collection of the Fuqua Orchid Center at the Atlanta Botanical Garden was used to compile horticultural notes and diagnostic photos.

Format:

While this analysis and its results are presented in taxonomical format, it is not intended to revise *Pleurothallis*
Section *Macrophyllae*
-Fasciculatae
.

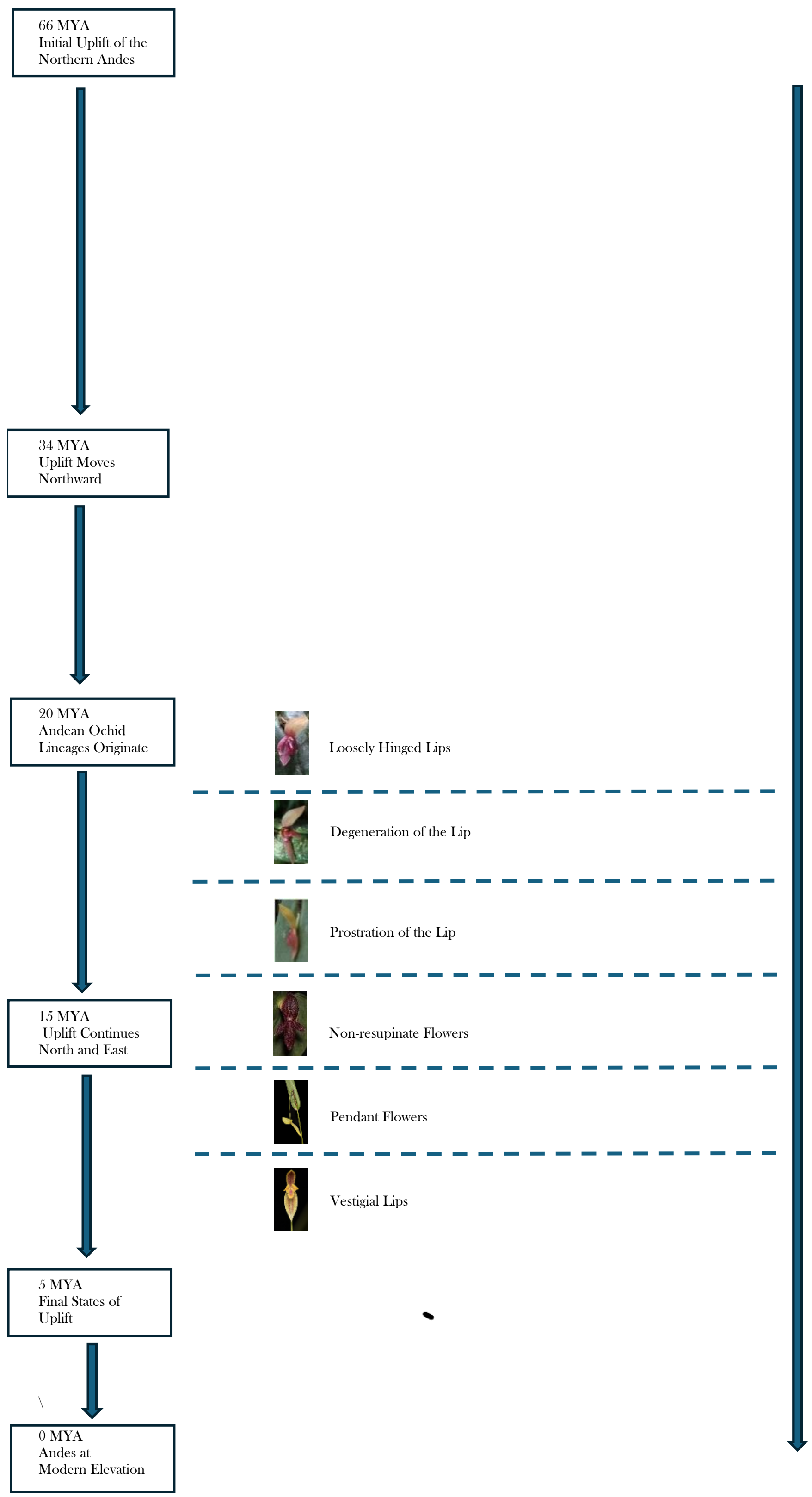
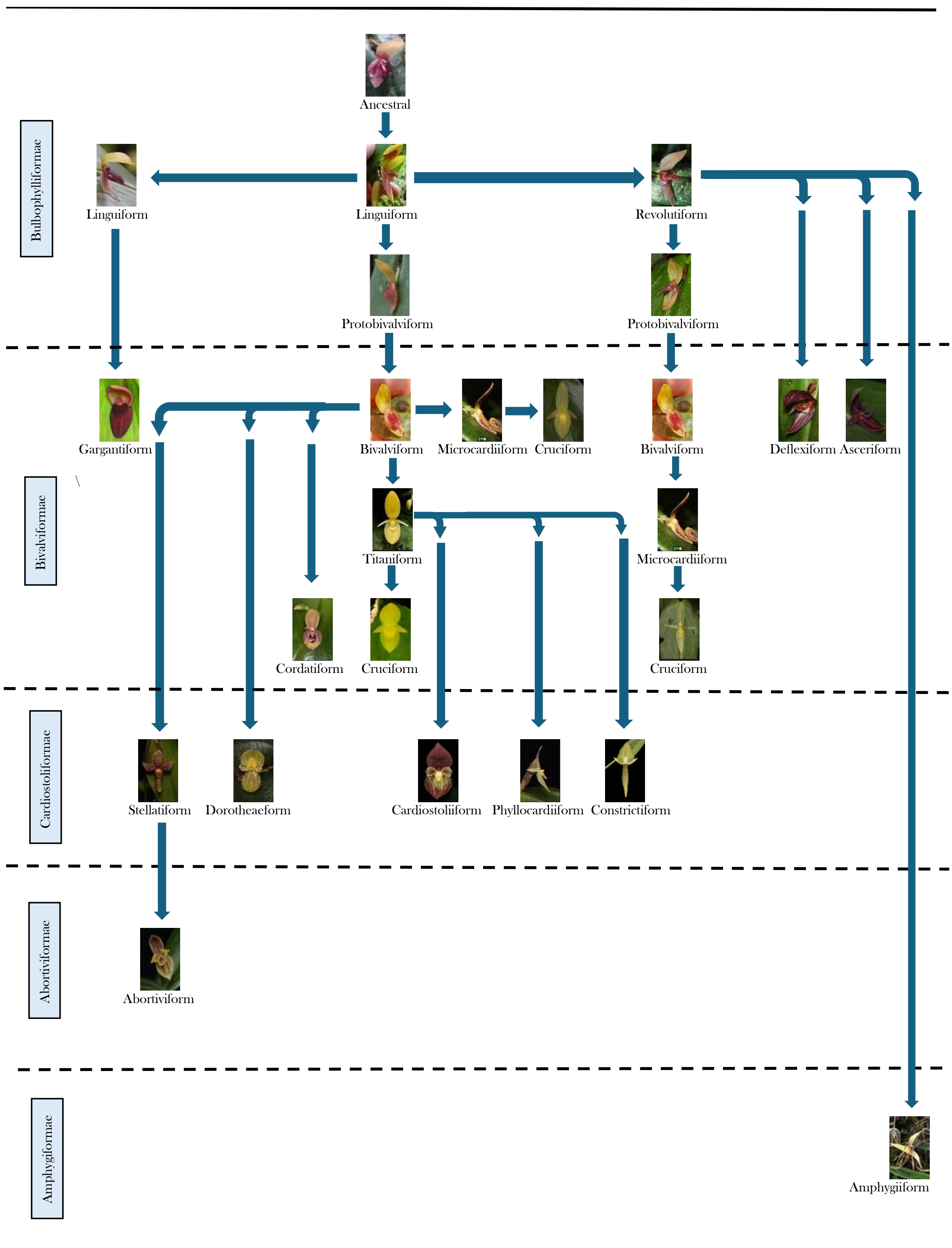

66 MYA
Initial Uplift of the
Northern Andes
34 MYA
Uplift Moves
Northward
20 MYA
Andean Ochid
Lineages Originate
Loosely Hinged Lips
Degeneration of the Lip
Prostration of the Lip
15 MYA
Uplift Continues
North and East
Non-resupinate Flowers
Pendant Flowers
Vestigial Lips
5 MYA
Final States of
Uplift
0 MYA
Andes at
Modern Elevation

Fig. 1.

The majority of Andean orchid lineages, which include PMF species, appeared around 20 to 15 MYA.
This coincides with the Andes migration north after the initial uplift off the coast of what is modern day Quito, Ecuador.

PMF species evolved from a common ancestor with a Bulbophylliform pollination mechanism.
Bulbophylliform pollination mechanisms are inefficient in areas with high wind speeds.

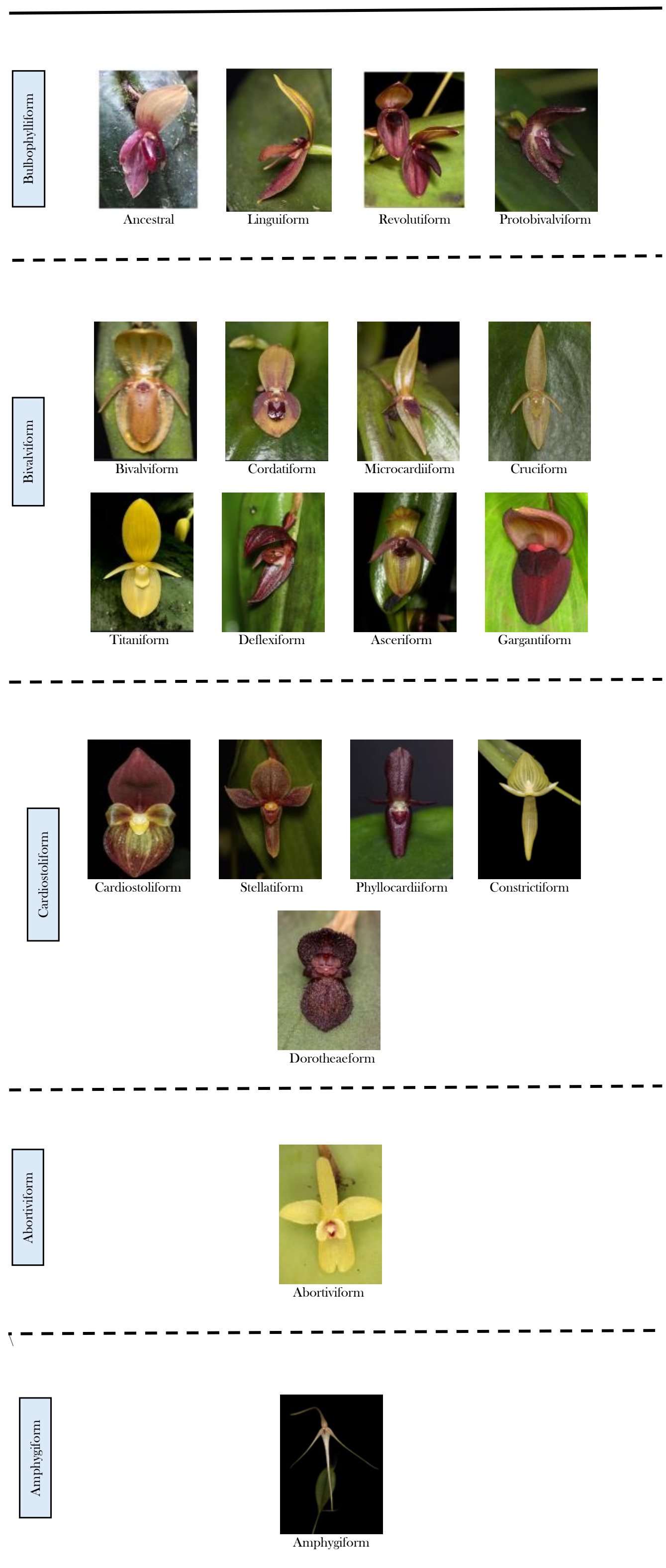


ISSN #2834-1783

Fig 2.

through budding speciation - a process where the ancestral species persists alongside its descendants. This mode of evolution allows us to directly observe how diversification unfolded rapidly over time.

As the Andes advanced northward and reached greater elevations, wind speeds intensified and weather patterns shifted dramatically. In response, PMF species evolved degenerated lips, minimizing hinge movement between the lip and the column foot. Additionally, PMF species adapted by producing flowers that were oriented against the force of gravity, further stabilizing the pollination mechanism.



ISSN #2834-1783

Fig 3.

There are 332 species which can be divided into five species groups and further divided into sixteen species complexes based on the most common floral shapes and/or flower orientation.

ISSN #2834-1783

<u>*Pleurothallis tremens*, a Relict Species Within Section *Macrophyllae-Fasciculatae*</u>

Once a year, I visit Andy's Orchids in Encinitas, California. I spend at least three days roaming through Andy's greenhouses, photographing plants, and taking notes.

While visiting in February 2023, every time I reached over one plant in particular, I thought I noticed some movement out of the corner of my eye. However, I assumed I was just imagining it, and didn't think twice about it. After a couple days, I went back to this plant and shook its pot. I was shocked to see that the lip jiggled. I leaned over and blew on one of the flowers and the lip trembled like the lip of many Bulbophyllum species.

Scan, tap, or click the QR code to see how the lip works

Andy is very frugal, so the majority of the plants in his collection were purchased from South American vendors on the last day of an orchid show. Andy bought this plant from an Ecuadoran vendor on the last day of an orchid show for $2 US.

Pleurothallis tremens is the only PMF species with a loosely hinged lip. It's also the last of its kind, and it changes everything we thought we knew about PMF species.

Pollinator Sharing with the Neotropical Bulbophyllums

The genus Bulbophyllum, with more than 2,000 described species, is the largest in the family *Orchidaceae*. There are approximately 60 species of neotropical Bulbophyllum distributed throughout South America, Central America, and the West Indies.

Loosely Hinged Lips

Pleurothallids are not related to the Neotropical Bulbophyllums. However, they share many similarities, particularly in their pollination mechanisms. Many genera of *Pleurothallidinae* have loosely hinged lips. Insect assisted pollination mechanisms. This is most likely due to pollinator sharing among the two sympatric genera. Both genera are pollinated by flies and many species share pollination with Family Sciaridae.

Scan the QR code to see the Insect Assisted Pollination Mechanism in *Trichosalpinx ciliaris*

ISSN #2834-1783

<u>Nectar Production</u>

PMF Species share many similar characteristics with the species in Section Napellii. Both have large, concave lips that are attached to the column foot by a hinge.

A 2003 study found that Bulbophylliform pollination mechanisms are not efficient in areas with high wind speeds. Not only does the pollinator have a difficult time landing on the lip, but it's also frequently thrown off the lip. The Neotropical Bulbophyllums produce nectar in order to get the pollinator to stay on the lip longer which increases the chances of pollination. PMF species also produce nectar. It's likely PMF evolved this trait for the same reason.

Scan the QR code to see a pollinator feeding on the lip of *Pleurothallis warrenprescottii*.

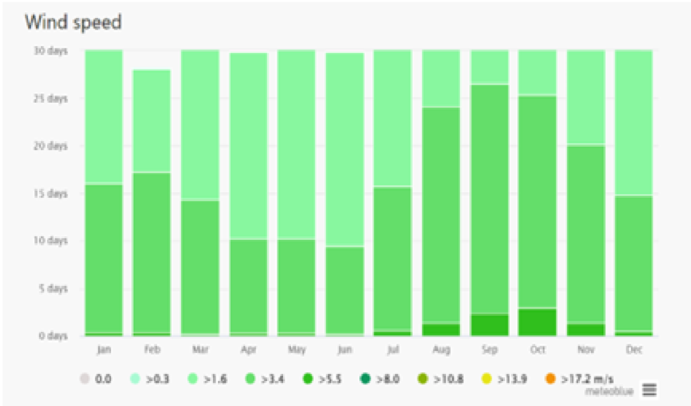
ISSN #2834-1783

More than 80% of the recognized species, representing five of the six currently accepted sections, are found in southeastern Brazil. It is currently accepted that the Neotropical Bulbophyllums are the result of a one-time colonization event from tropical Africa to South America. Although it is still uncertain when the event occurred, it is possible that southeastern Brazil is the origination point for the species within this clade.

The genus Bulbophyllum is the most successful genera within the *Orchidaceae*, yet there are only six species found in the Andes? PMF species outnumber Bulbophyllum species 49 to 1. Why is this?

Rapid Speciation and Hyperdiversity Driven by Andean Uplift

PMF species outnumber Bulbophyllum species. However, if you compare PMF species with Bulbophylliform pollination mechanisms, they are 1:1.



According to a 2003 study, Neotropical Bulbophyllum pollination mechanisms are only successful in wind speeds of 1.0-1.5 meters per second or less, what is typically referred to as light wind.

However, for most of the year, the Andes experience wind speeds in excess of 3.4 meters per second for at least 15 days a month. Not only does the pollinator have difficulty landing on the lip, the pollinator is thrown off the lip.

The Andes began their uprising near what is now Quito, Ecuador. The rise of the Andes created extreme weather patterns, and as wind speeds began to increase, the Neotropical Bulbophyllums and the ancestors of PMF species responded in a variety of ways.

Ancestral PMF species responded first through gravitropism. They developed suberect ramicauls that position the flower's lip against the force of gravity. This neutralizes the hinge. We can see this trait in all modern PMF species.

Ancestral PMF species also began to tighten the hinge that connects the lip to the column foot.

Scan the QR codes to see how the hinges work differently.

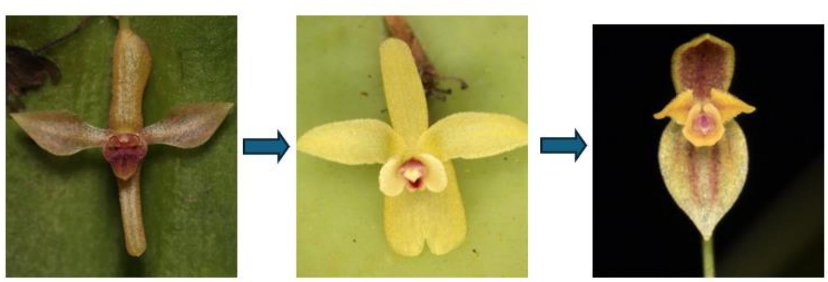
ISSN #2834-1783

When the Andes began to move north, we can see how a species with an erect lip evolved a suberect lip.

Then as the Andes moved farther north, and the elevations increased, species with suberect lips evolved into species with fully prostrate lips.

As the Andes continued to climb, we can see how species with significantly degenerated lips evolved by reflexing the synsepal which exposes the lip to the pollinator.

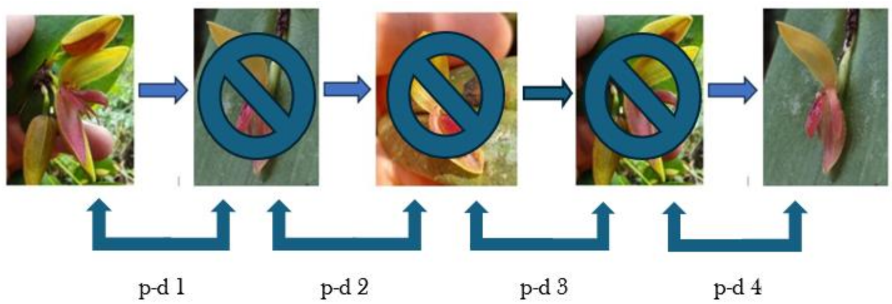
As the lip continued to degenerate, the basal lobes wrapped around the column.



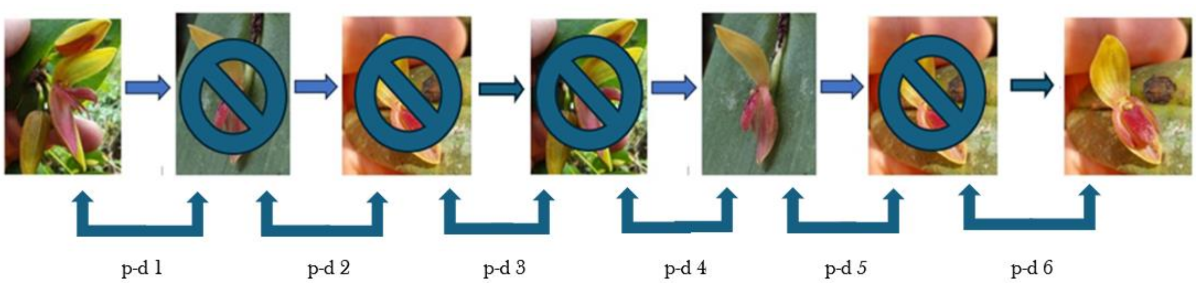
As the Andes reached their modern elevations, PMF species ultimately evolved nearly vestigial lips.

Budding Speciation

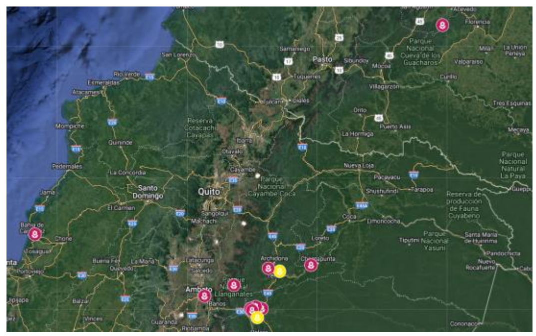
PMF species evolved through budding speciation. Budding Speciation is an evolutionary process in which the ancestor species exists alongside the new species through budding events. Budding speciation also results in asymmetrical ranges. As the derivative species replace the progenitor species, the derivative species' range is larger than the progenitor's.



A budding event produces progenitor-derivative (p-d) pairs. However, the lip doesn't go from erect to suberect in just one generation. It takes multiple generations to see a significant change.



Since PMF species evolved so recently, any "missing links "are dismissed as "trivial". They are anything but. Conversely, species that aren't related at all are dismissed as variants of another species.



P. pseudosphaerantha (red) is observed 5 times more often than P. spaerantha (yellow). In fact, it has been observed only once since 1975. This asymmetrical range shows how the flattened lip makes the species more successful and the new species eventually replaces the progen

ISSN #2834-1783

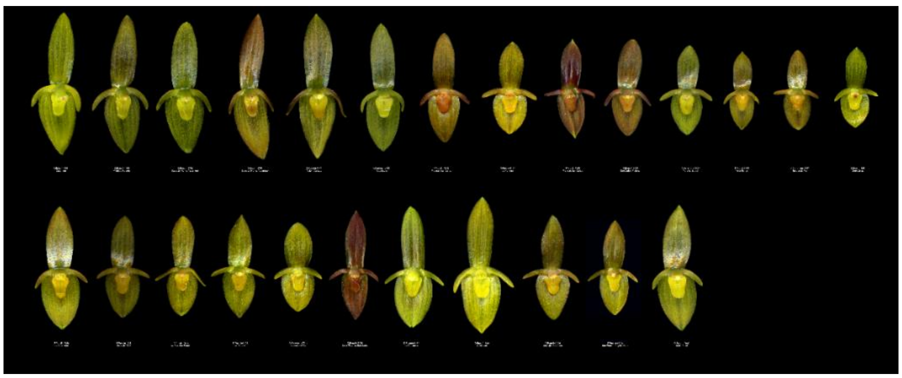
Variation

Isn't it just variation? Well, good question…

There is no consensus among taxonomists regarding a standard definition of variation within a species, particularly species within PMFs. In fact, the definition of the word is different in each dictionary.

We can use music as a guide. In classical music, there is a form called theme and variations. A main melody is played followed by variations on that theme. After the main theme is played, it is presented in multiple variations. In each variation, the theme may be slightly different, but it remains unmistakably recognizable.

In PMF species, the shape and position of the lip are the "theme" of a species. The size and color of the lip, petals, and sepals are the "variations" of the species. To put it in simple terms, variation is subtle. Common flower shapes are mistaken for variation in a species.



In 2011, Bogarin et. al. sampled 23 populations of P. homalantha in Costa Rica. Within the samples collected, the petals and sepals varied significantly in size, shape, and color. The lip also varied in size and color. However, in all populations, the shape and position of the lip are the same. This is an example of typical variation within a species.

Two forms of P. coriacardia, we will go into the details later, but they are the same species.

Here are three variations of P. titan. The first image is a brown species as described in the prologue of this species. The second image is the most familiar Canarian yellow form of the species, which was discovered after P. titan was described. The third image is a purple-yellow shape from Colombia that has rising petals compared to the descending petals of the type. In all three species, the lip has the same shape and is in the same position. None of them would be considered a different species. However, the third could be considered a distinct form of the species, P. titan f. ascendipetala.

Forms are important because they make biologists aware that such characteristics exist. The longer petals are probably a precursor to P. callosa.

Pleurothallis forceps-cancri fma. rectipetala is a distinct form of *Pleurothallis* forceps-cancri. The flowers are significantly larger than the type species, but the most significant difference is the shape of the petals. In reality, they are the opposite of falcated petals.

Subspecies

A subspecies is typically a geographically isolated variant. However, this is not only the most commonly observed form of this species, it is the most observed in iNaturalist. It appears that the only species affected by geographical barriers are species with bulbophylliform pollination mechanisms, which are ancestral species. There are no subspecies within PMF.

Hybridization

Natural hybridization has long been suspected and, in fact, likely has some part to play in the hyperdiversity of PMF species. Natural hybridization is suspected to be common in species that evolved through budding speciation. However, it is impossible to prove.

In April 2016, what appeared to be an aberrant form of Pleurothallis sphaerantha (Luer 1975) was documented on flickr by Andreas Kay. However, it is highly likely that the specimen observed was a natural hybrid.

Photos of this putative hybrid were studied in order to determine if it was a form of P. sphaerantha. Upon studying the flower closely, however, it was determined that the floral morphology of the putative hybrid was entirely different from that species.

It appears to be a natural hybrid of Pleurothallis pseudosphaerantha and another Pleurothallis species with an affinity to Pleurothallis erythrium. This assumption is based on observations of the two species within the vicinity where the putative hybrid was found. It exhibits characteristics in both its floral and vegetative morphology that are intermediate between the two species.

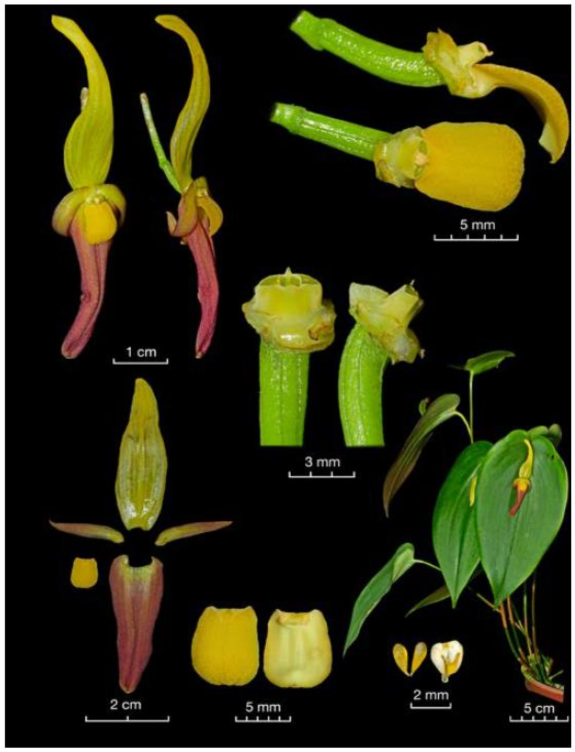


Figure 2. Plate of *Pleurothallis marioportillae* material used to prepare the type specimen. Clockwise: Intact flowers, quarter profile and profile, to 1 cm scale. Lip, profile attached to the column and ovary with petals and sepals removed, profile and upper surface, to 5 mm scale. Plant, to 5 cm scale. Pollinia and anther cap, to 2 mm scale. Lip, upper and lower surface, to 5 mm scale. Sepals, petals, and lip, to 2 cm scale. Column and ovary, to 3 mm scale (center). (photos by Hugo Medina).

While performing research for this article, the author was able to confirm several "nursery hybrids" which were circulating in the orchid trade as species. One of them was recently described as, *Pleurothallis* marioportillae, unfortunately.

A specimen at the Atlanta Botanical Garden had been studied, and in 2024, the author was able to confirm this plant was a spontaneous hybrid found at a local "grower's" property in Ecuador. It does not match any observation of a gargantiform species.

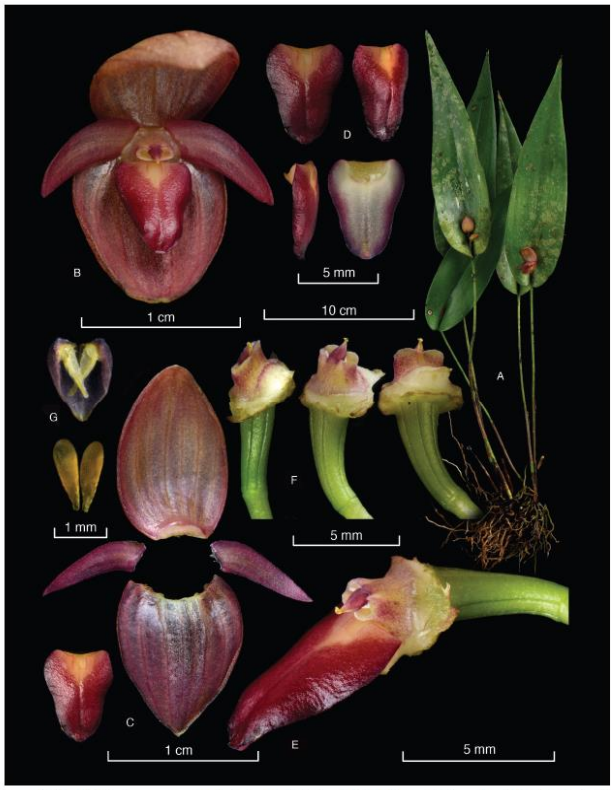
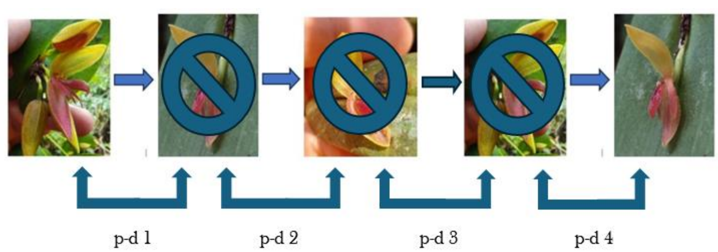


FIGURE 13. *Pleurothallis* ×*karremansiana* Pupulin, J. Aguilar & M. Díaz. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, in adaxial, three-quarter, lateral, and abaxial views; **E**, apex of ovary, column, and lip in lateral view; **F**, column in lateral, dorsal, and ventral views; **G**, anther cap and pollinarium (two views). Lankester Composite Dissection Plate prepared by M. Díaz from *Díaz 270* (JBL).

In 2021, Pupulin et. al. identified three putative hybrids in Costa Rica. However, it is more than likely that all three are distinct species. All three species exhibit characteristics that are typical for budding speciation, particularly the lip morphology.

<u>Phylogenetic Analysis</u>



Budding speciation complicates phylogenetic reconstruction as it requires the inclusion of all descendant lineages to produce a reliable phylogeny. Due to these challenges, we must rely primarily on morphological characteristics to infer evolutionary relationships.

Based on this analysis, PMF species should be expanded to include Section Amphygiae and Section Abortivae, and divided into five subsections:

__Bulbophylliform Species__

The 12 species in Subsection Bulbophylliformae constitute 3.35% of all species within Section *Macrophyllae-Fasciculatae*. The group consists of one relict species, five linguiform species, two revolutiform species, and four protobivalviform species. The species in this group are only found on the eastern side of the Andes.

<u>Linguiform Flowers</u>

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Revolutiform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Protobivalviform Flowers

Both linguiform and revolutiform species evolved into protobivalviform species.

They then adapted through lip prostration and the erect lip became suberect.

As the lip approached full prostration, the margins bent under the lip creating a small leg or *crusulum.* The cluster helps neutralize the hinge by acting as a door stop.

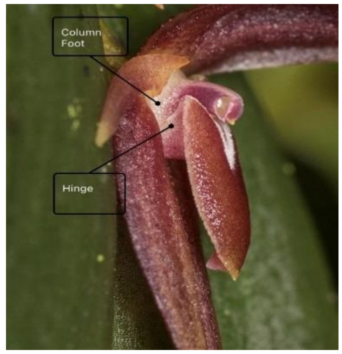
This is an adaptation also seen in the Neotropical Bulbophyllums.

Bivalviform Species

The morphology of the flower of A. bivalvis is considered the "'standard" from which all others deviate.

Bivalviform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.



Eventually, they developed prostrate, convex lips that neutralize the hinge. These species evolved into the P. bivalvis complex.

Microcardiiform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Species that had developed prostrate lips also began to evolve further through lip degeneration.

Left. P. bivalvis with a convex lip. Right. P. austinrumleyi with a degenerated, convex lip.

Cordatiform Flowers

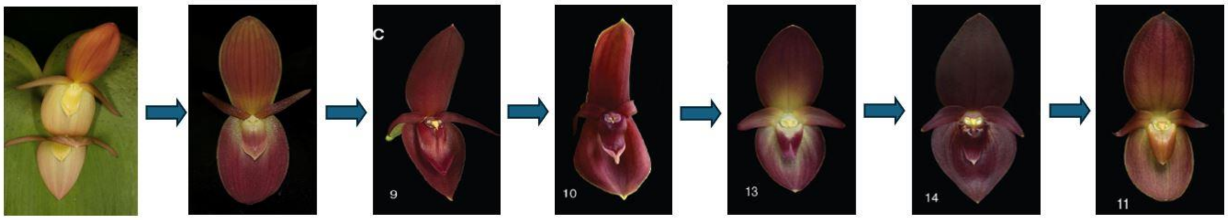
Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Cruciform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

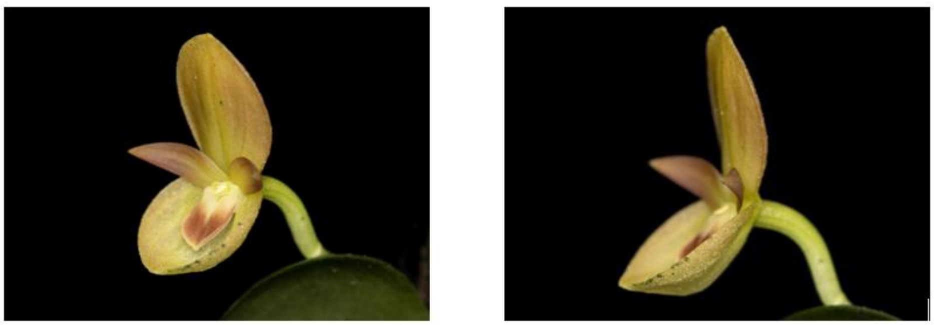
Titaniform Flowers

Pleurothallis titan is possibly one of the most well-known species of *Pleurothallis*. Just hearing the name of this species conjures up mental images of its large yellow flowers, but interestingly, when the species was originally described in 1977, a specimen of yellow flowers had not yet been seen. Although a yellow-flowered specimen was found only a few years later, it would take nearly three decades for the description to be revised to reference the species' familiar Canarian yellow flowers.



If you rearrange the photos and add P. titan, you can see that these species are descendants of P. titan and the lip has continued to degenerate with each successive descendant species.

Titaniform species evolved concave synsepals and evolved into the P. calceolaris complex.



Volume 4.1
ISSN #2834-1783

Deflexiform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Asceriform Flowers

The P. ascera complex probably evolved from an ancestral species similar to P. serricardia. P. serricardia has revolute margins, but the apex folded under.

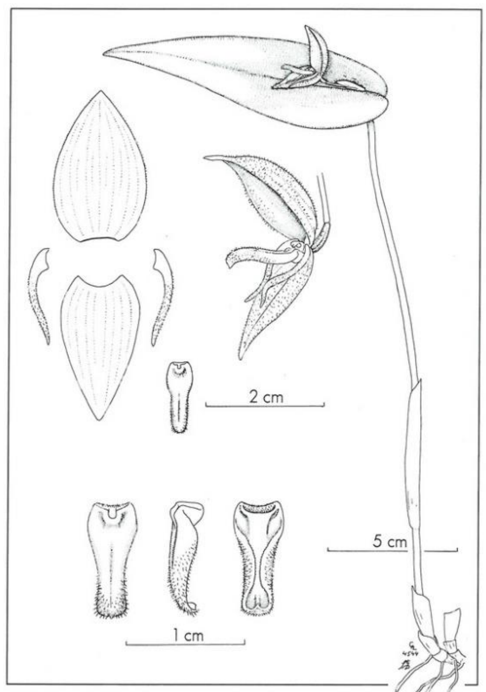


Fig. 185. Acronia serricardia

ISSN #2834-1783

Gargantiform Flowers

The P. gargantua complex evolved from a linguiform species which used its petals to prevent the hinge. The petals later evolved into wedges as seen in P. *llanganatensis* and P. teaguei, and later into large convex petals as seen in P. marthae and P. gargantua. Although it is severely degenerated in these species, the hinge is still fully functional if the petals are removed.

ISSN #2834-1783

<u>Cardiostoliform Species</u>

As the Andes continued northward and reached higher elevations, another group of ancestral species with degenerate lips adapted through gravitropism. We see the first flowers reupinated. Resupination positions the lip against the force of gravity and neutralizes the hinge.

Cardiostoliform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Scan the QR code to see how the hinge works.

ISSN #2834-1783

In addition to resupination, other species developed arching ramicauls, flowers that hold the lip upwards, and others produce downward-facing flowers.

Volume 4.1
ISSN #2834-1783

As species evolved significantly degenerated the lips, the glenion began to expand becoming wider and deeper.

The glenion was eventually replaced by a deep groove that is filled with nectar and keeps the pollinator on the lip longer.

<u>Stellatiform Flowers</u>

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Degenerated leaves bevame paedomorphic.

Phyllocardiiform Flowers

ISSN #2834-1783

Constrictiform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Ramicauls*: up* to 20 cm long, very thin, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

Mucilage similar to Elleanthus

The basal lobes eventually surrounded the column

Dorotheaeform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

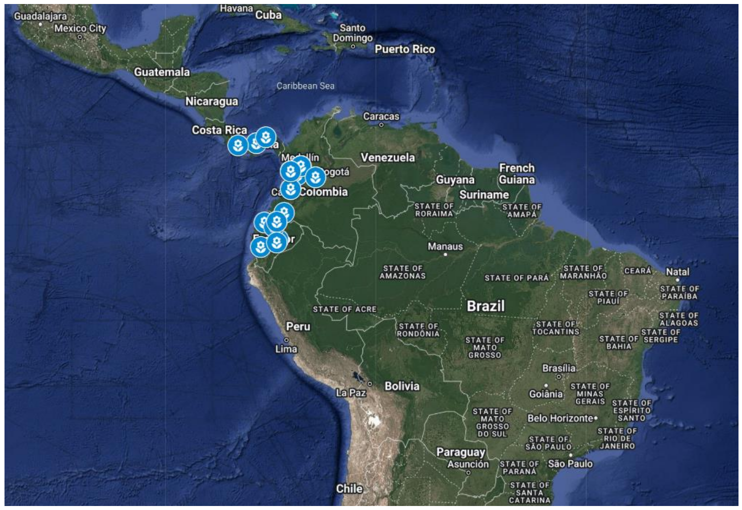
__Abortiviform Species__

.

Abortiviform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Amphygiform Species



Amphygiform Flowers

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Lip is prostrate from the base first.

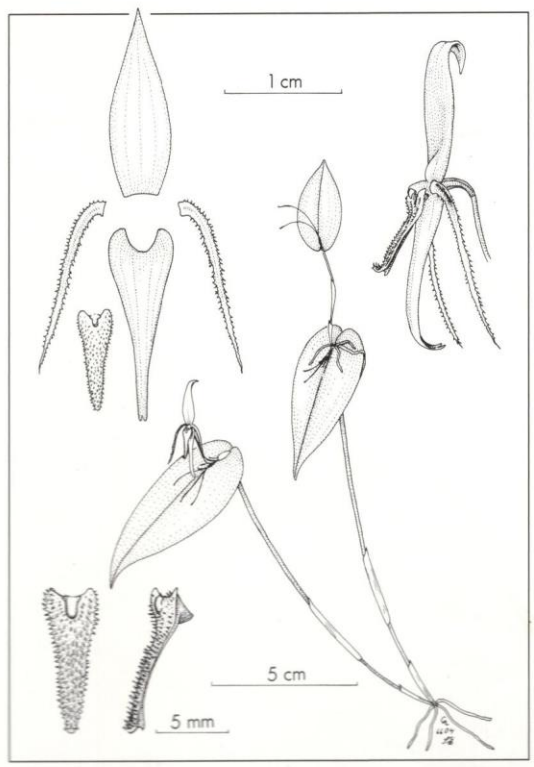


Fig. 110. Acronia killipii

ISSN #2834-1783

49 observations on iNaturalist. All had prostrate lips.

Notes on Subgenus Ancipitia and Subgenus Scopula

Three similar Ancipitia species.

P. anthrax is a possible progenitor to P. odobeniceps. From left to right: The lip of P. anthrax has rounded lateral lobes. As the lip degenerates futher, the lateral lobes in the lip of P. odobeniceps are forced up and a curved. In a similar, undescribed crocodiliceps-type species, the lip is nearly vestigial and the lateral lobes have folded over the lip.

The lip of P. gratiosa has forced the basal lobes up flanking the column, but they have not yet folded over the lip.

Subgenus Ancipitia and Subgenus Scopula should be combined and split into two subsections: Subsection Ancipitia and Subsection Scopula.

Discussion

- Pleurothallis Section Macrophyllae-Fasciculatae is hyperdiverse.
- Study focuses on morphological evolution and real-time speciation.

Citizen science data reshaped taxonomy.

- Lip morphology is critical for species identification.

- Real-time speciation documented.
- Section Macrophyllae-Fasciculatae critical for studying evolution.
- Citizen science data reshaped taxonomy.

- Explains rapid, observable diversification.

Taxonomic Revision Proposal
- Expand PMF to include Sections Amphygiae and Abortivae.
- Five proposed subsections:

Genus *Pleurothallis*
Type: *Pleurothallis calceolaris* Rchb.f..

Subgenus *Pleurothallis*
Type: *Pleurothallis calceolaris* Rchb.f..

Section *Macrophyllae-Fasciculatae*
Type: *Pleurothallis grandiflora* Lindl.

Subsection *Bulbophylliformae*
Type: *Pleurothallis tremens* K.W. Holcomb 2025

Subsection *Bivalviformae*
Type: *Pleurothallis bivalvis* Lindl.

Subsection *Cardiostoliformae*
Type: *Pleurothallis cardiostola* Rchb.f.

Subsection *Abortiviformae*
Type: *Pleurothallis abortiva* Luer

Subsection *Amphygiformae*
Type: *Pleurothallis amphygia* Luer & R. Escobar

Nomenclatural Notes

Exceptions and Exclusions

P. belocardia was excluded from the comparative study because all illustrations have been destroyed.

P. braidiana and P. cassidata were not included in the distribution maps because there is no country of origin associated with either species.

P. marioportillae was excluded as a confirmed spontaneous nursery hybrid.

P. gigiportillae was excluded from both the distribution maps and the comparative study because it is likely to be a hybrid.

P. glochis was excluded because it belongs to Subgenus Scopula.

P. knappiae and P. ankyloglossa were excluded because they belong to the subgenus *Pleurothallis*.

PleuThere are 333 species withinPMF species can be divided into four groups, or subsections, based on morphological characteristics of the lip. These four series can be divided into 18 subgroups based floral morphology.
Based on this analysis:

There are four species that have been synonymized, which must be reincorporated as distinct species.

There are six distinct species that have been mistakenly dismissed as forms of other species.

There are six natural hybrids that must be elevated to the species level.

There are two species that are probably hybrids and that should be moved to a lower level.

Complejos de Pleurothallis linguifera y *Pleurothallis adonis*

There has been a significant amount of confusion regarding the species in this group, in particular, P. adonis and P. linguifera. When Luer published volume 27 of Icones Pleurothallidinarium, he stated that the only real difference between the two species is the shape of the lip, convex in P. linguifera versus tubular in P. adonis and the number of veins in the dorsal sepal, a 5-vein dorsal sepal in P. linguifera versus a multivene dorsal sepal in P. adonis. This is a confusing comparison, as a 5-vein dorsal sepal is also a multivene dorsal sepal. However, he was implying that P. linguifera always has only 5 veins, but P. adonis always has more than 5 veins. To add further confusion, he goes on to state that these traits can be reversed in some collections. Unfortunately, this contradiction, in addition to the many other significant differences that he overlooked, means that a real

Pleurothallis bivalvis Sensu Lato

Pleurothallis cordata Sensu Lato

Serie Amphygiae

Abortivae Section

Pleurothallis tremens, K.W. Holcomb, ***sp. nov.***

Plant: Medium-sized, epiphytic, cespitose plant, very thin roots.

Ramicauls: up to 20 cm long, very thin, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

Leaf: is 7.5 cm long, 2.25 cm wide, leathery, ovate, acute, the base cuneate, sessile.

Inflorescence: a single resupinate, successive flower, 6 cm long, born from a spataceous bract at the base of the leaf.

Labellum (Lip): 3 mm long, 2 mm wide, peach with yellow margins, triangular with a well-developed orbicularis glenion, trilobed, erect basal lobes flanking the spine, apex acute.

Dorsal Sepal: 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Synsepal: 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Petals: 27 mm long, 4 mm wide, 3-ribbed, peach-colored, descending, tiny ciliate, elliptical, subsigmoid, oblique, acute, acuminate.

Column: 2 mm long, 1 mm wide, semiterete, anther and apical transverse stigma.

Etymology: From the Latin *tremens* "trembling", in reference to the loosely hinged lip.

ECUADOR: Without collection data. *K.W. Holcomb 18318 (Holotype: GEO)*

Pleurothallis tremens is the only species within Section *Macrophyllae-Fasciculatae* that has a loosely hinged lip.

Volume 4.1
ISSN #2834-1783

Pleurothallis revolutiformis, K.W. Holcomb, ***sp. nov.***

Medium-sized, epiphytic, cespitose plant, very thin roots.

Ramicauls up to 20 cm long, very thin, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

The leaf is 7.5 cm long, 2.25 cm wide, leathery, ovate, acute, the base cuneate, sessile.

Inflorescence a single resupinate, successive flower, 6 cm long, born from a spataceous bract at the base of the leaf.

Labellum (lip) 3 mm long, 2 mm wide, peach with yellow margins, triangular with a well-developed orbicularis glenion, trilobed, erect basal lobes flanking the spine, apex acute.

Dorsal sepal 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Sinsepal 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Petals 27 mm long, 4 mm wide, 3-ribbed, peach-colored, descending, tiny ciliate, elliptical, subsigmoid, oblique, acute, acuminate.

Column 2 mm long, 1 mm wide, semiterete, anther and apical transverse stigma.

Etymology: From the Latin *tremens* "trembling", in reference to the hinged lip.

ECUADOR: Vallidolid: No collection data. *K.W. Holcomb 18318 (Holotype: GEO)*

Pleurothallis tremens es

Reinstatement of the Name, *Pleurothallis rhopalocarpa*

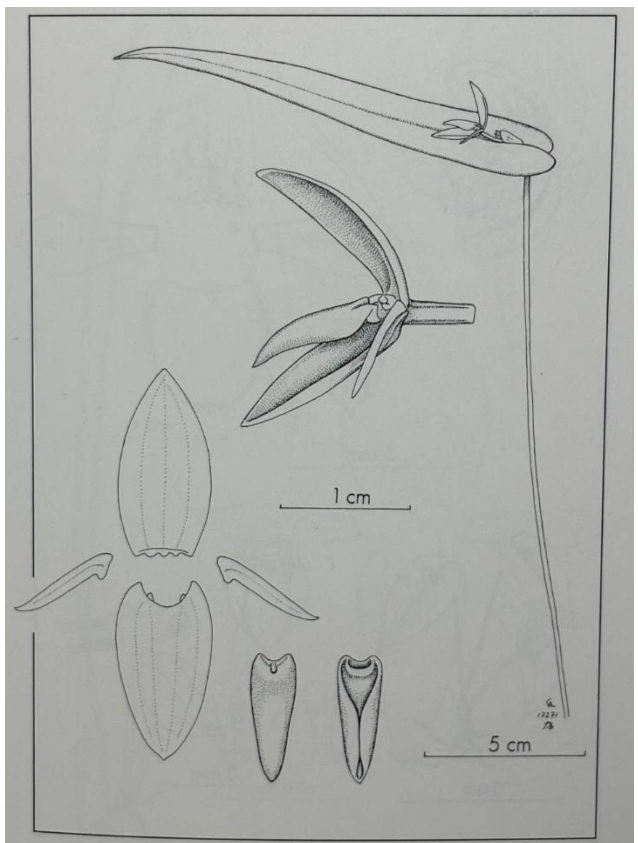


Fig. 5b. Acronia adonis

ISSN #2834-1783

Pleurothallis warrenprescottii, K.W. Holcomb, ***sp. nov.***

Medium-sized, epiphytic, cespitose plant, very thin roots.

Ramicauls up to 20 cm long, very thin, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

The leaf is 7.5 cm long, 2.25 cm wide, leathery, ovate, acute, the base cuneate, sessile.

Inflorescence a single resupinate, successive flower, 6 cm long, born from a spataceous bract at the base of the leaf.

Labellum (lip) 3 mm long, 2 mm wide, peach with yellow margins, triangular with a well-developed orbicularis glenion, trilobed, erect basal lobes flanking the spine, apex acute.

Dorsal sepal 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Sinsepal 30 mm long, 5 mm wide, with 3 veins, peach-colored, membranous, glabrous, ovate at the base, concave, acute, acuminate.

Petals 27 mm long, 4 mm wide, 3-ribbed, peach-colored, descending, tiny ciliate, elliptical, subsigmoid, oblique, acute, acuminate.

Column 2 mm long, 1 mm wide, semiterete, anther and apical transverse stigma.

Etymology: From the Latin *tremens* "trembling", in reference to the hinged lip.

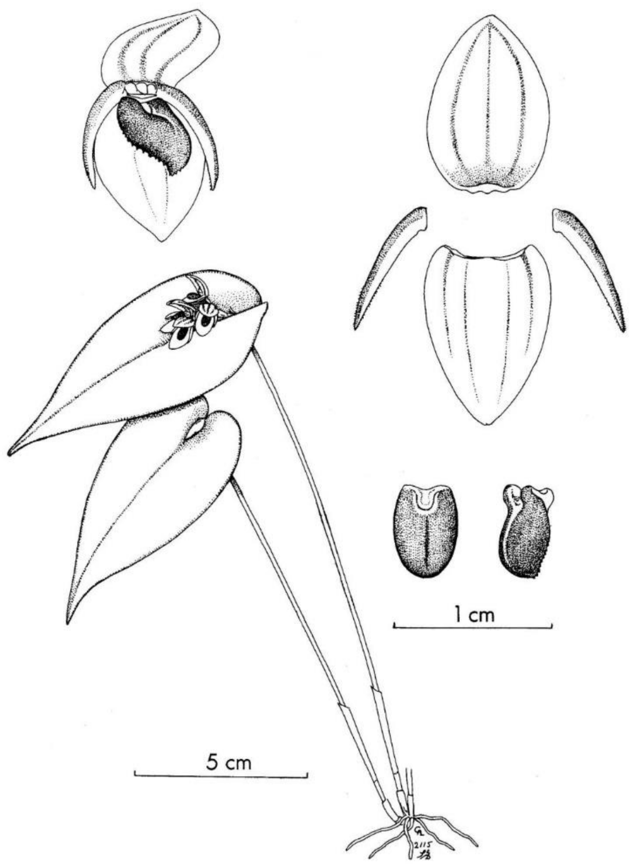
ECUADOR: Vallidolid: No collection data. *K.W. Holcomb 18318 (Holotype: GEO)*

Pleurothallis tremens es

Reinstatement of the Name, *Pleurothallis rhopalocarpa*

ISSN #2834-1783

Reinstatement of the Name *Pleurothallis embreei* and Clarification of *Pleurothallis calogramma*



ISSN #2834-1783

Reinstatement of the Name, *Pleurothallis tamaensis*

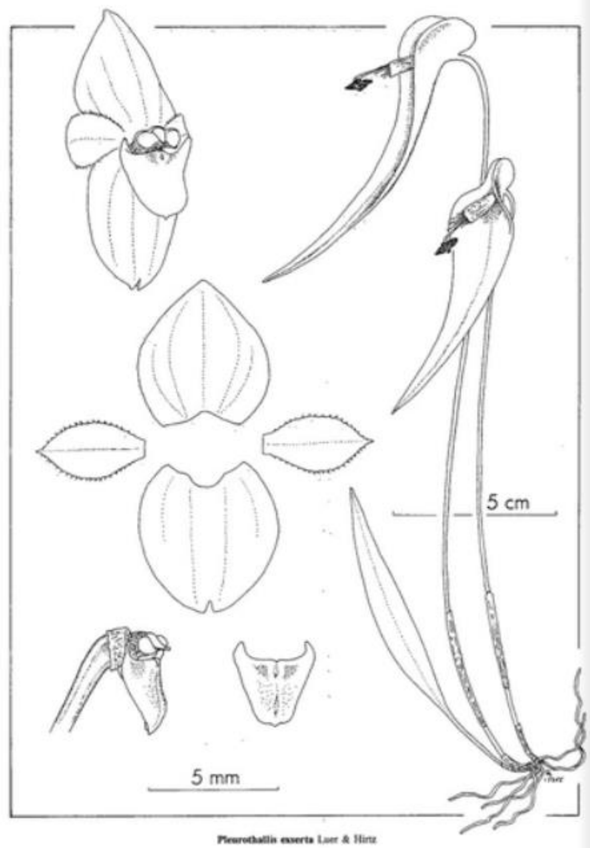
Reinstatement of the Name, *Pleurothallis erymnochila*

Reinstatement of the Name, *Pleurothallis monocardia*

Reinstatement of the Name, *Pleurothallis ignivomi*

Reinstatement of the Name, *Pleurothallis archidiaconi*

<u>Reinstatement of the Name, *Pleurothallis exserta*</u>



Pleurothallis exserta Luer & Hirtz

142

ISSN #2834-1783

alt. 2200 m, 8 Feb. 1987, *C. Luer, J. Luer, & A. Hirtz 12725* (Holotype: MO); epiphytic in cloud forest between Limón and Gualaceo, alt. 2200 m, 8 Feb. 1987, *C. Luer, J. Luer, & A. Hirtz 12722* (MO).

This species is difficult to assign to a subsection of section *Pleurothallis*. It is best placed in subsection *Macrophyllae-Racemosae*, but it straddles the line between the two series.

Pleurothallis eccentrica has been found colonizing a damp road embankment, as well as in trees in the same locality. It is most unusual in some morphological features. The base of the mature, narrowly ovate leaf varies from cuneate without a petiole to indistinctly or distinctly petiolate. Smaller leaves are more likely to be petiolate than larger leaves. Either may bear a long-pedunculate inflorescence. The inflorescence is either single-flowered or distantly and successively two-flowered.

Pleurothallis exserta Luer & Hirtz, sp. nov.

Species haec *Pleurothallis cardiostolae* Reichb. f. affinis, sed floribus multiminoribus ex spatha erecta exsertis cum pedunculis pedicellis ovariisque elongatis differt.

Plant medium in size to large, epiphytic, densely caespitose; roots slender, densely fasciculate. Mature ramicauls slender, erect, round in cross-section, with close, tubular sheaths above the base, 20-40 cm long, the immature ramicaul up to 5 cm long. Mature leaf deflexed, sessile, rigid, coriaceous, narrowly ovate, 11-13 cm long, 1.2-2 cm wide expanded, the apex acute, more or less curved upward above the middle, conduplicate below the middle, the base deeply cordate with the rounded basal lobes erect, sometimes touching, the immature leaf erect, narrowly ovate, up to 12 cm long, acute at the apex and base. Inflorescence a fascicle of solitary, successive flowers borne from an erect, foliaceous spathe 15-20 mm long, 7-9 mm broad, at the base of the leaf; peduncles slender, 10-12 mm long, confined within the spathe; floral bract 6 mm long; pedicel, 10-12 mm long; ovary 10 mm long; sepals and petals purple-brown with darker veins, to completely purple; dorsal sepal broadly ovate, obtuse, more or less convex, 5-6 mm long, 5-6 mm wide, 5-veined; lateral sepals connate into a broadly ovate, obtuse, more or less convex, minutely bifid synsepal, 5-6 mm long, 5-6 mm wide, 4-veined; petals more or less revolute above the middle, elliptical, subacute, 4 mm long, 2 mm wide, 1-veined, the margins minutely ciliate; lip dark purple or purple-brown, ovate-triangular, broadly obtuse, cellular-glandular, 3 mm long, 3 mm wide across the base, the basal lobes acute, incurved, to either side of the column, the disc lightly cleft toward the apex, and with a narrow, lightly channeled callus above the base, the base acutely reflexed, subtruncate, firmly hinged to the column-foot; column dark purple, stout, 0.5 mm long, 1 mm broad, the anther and bilobed stigma apical, the foot rudimentary.

ETYMOLOGY: From the Latin *exsertus*, "exserted, protruding beyond surrounding organs," referring to the flower exserted beyond the spathe.

TYPE: ECUADOR: Prov. of Esmeraldas: epiphytic in wet forest west of Lita, alt. 750 m, 18 Jan. 1987, *C. Luer, J. Luer, A. Hirtz, C. H. Dodson, D. Benzing & D. Bermudas 12355* (Holotype: MO); same area, 18 Jan. 1987, *C. Luer et al., 12395, 12401* (MO).

This species of section *Macrophyllae-Fasciculatae* subsection *Cardiostolae* is relatively frequent in the wet, forested lowland of northwestern Ecuador. Vegetatively it is similar to the widely distributed *Pleurothallis cardiostola* Reichb. f. with the acutely deflexed, narrowly but deeply cordate leaves. The rounded basal lobes are inflexed, sometimes meeting above the conspicuous, erect, sleeve-like spathe. The flower, also basically similar to that of *P. cardiostola*, is much smaller and it is exserted well beyond the end of the spathe by a proportionately longer peduncle, pedicel, and ovary.

Pleurothallis hoeijeri Luer & Hirtz, sp. nov.

Planta grandis caespitosa, foliis grandibus late ovatis profunde cordatis, floribus atropurpureis, sepalo dorsali cucullato, petalis ciliatis infra labellum convenientibus, labello crasso ovoideo breviter fimbriato, disco elevato cum marginibus altis, apice obtuso sparse breviterque spiculato, stigmata bilobato.

Plant large, epiphytic, caespitose; roots slender, fasciculate. Ramicauls stout, erect, round in cross-section, with a close, tubular sheaths near the middle and another at the base, 30-38 cm long. Leaf spreading, expanded, sessile, coriaceous, broadly ovate, 12-15 cm long, 10-12 cm wide, the apex acute, acuminate, the base deeply cordate, the lobes up to 3 cm deep. Inflorescence a fascicle of solitary, successive flowers, sometimes 3 or 4 borne simultaneously, from a reclining spathe 1.5-2 cm long, at the base of the leaf; peduncles 5-6 mm long, confined within the spathe; floral bracts 8 mm long; pedicel 8-10 cm long; ovary 8-10 mm long; flowers resupinate, deep purple; dorsal sepal white at the base, broadly ovate, subacute, deeply concave, glabrous, 14 mm long, 9 mm wide unexpanded, 7-(9-) veined; lateral sepals connate into an oblong-ovate, obtuse, synsepal 14 mm long, 5 mm wide, 6-veined; petals falcate, acute, minutely fimbriate, 5.5 mm long, 1.25 mm wide, 1-veined, curved to meet beneath the lip; lip thick, broadly ovate, minutely fringed, 3.5 mm long, 3 mm wide,

ISSN #2834-1783

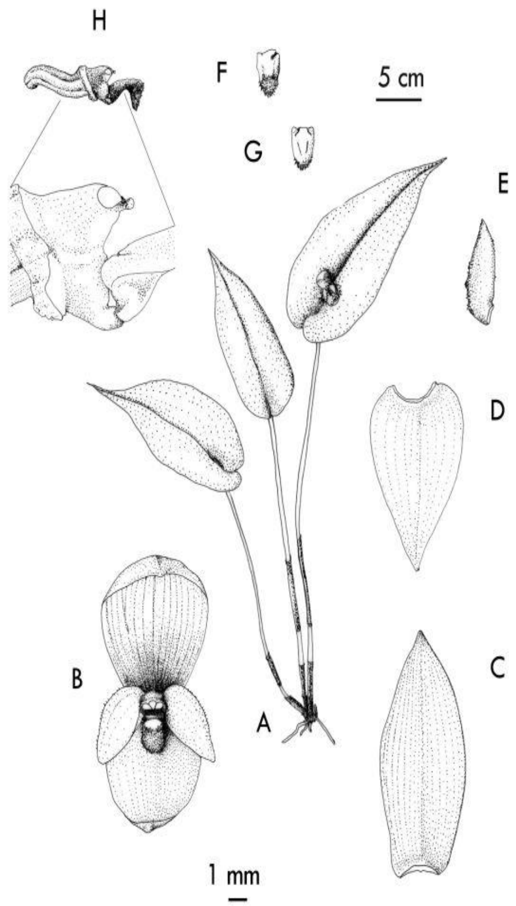


FIGURE 6. *Pleurothallis gigiportillae*. A. Habit, drawn to 5 cm scale. B. Flower. C. Dorsal sepal. D. Lateral sepals. E. Petal. F. Lower surface of lip. G. Upper surface of lip. H. Flower with petals and sepals removed. All drawn to 1 mm scale.

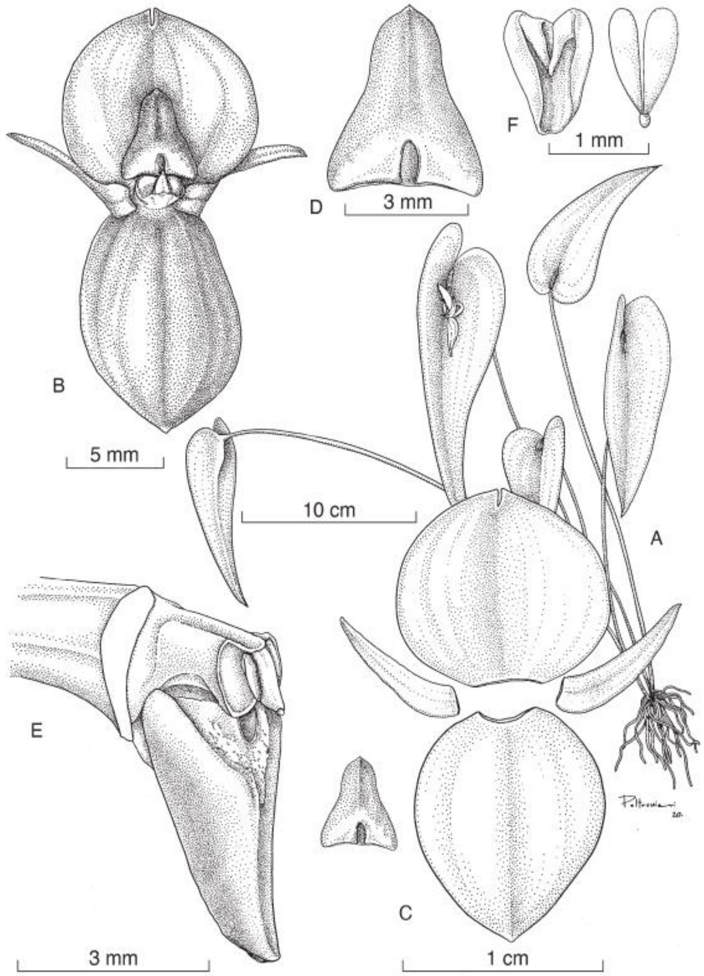


FIGURE 52. *Pleurothallis ×subversa* Pupulin & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** ovary, column, and lip in lateral view; **F,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Pupulin 8817* (JBL).

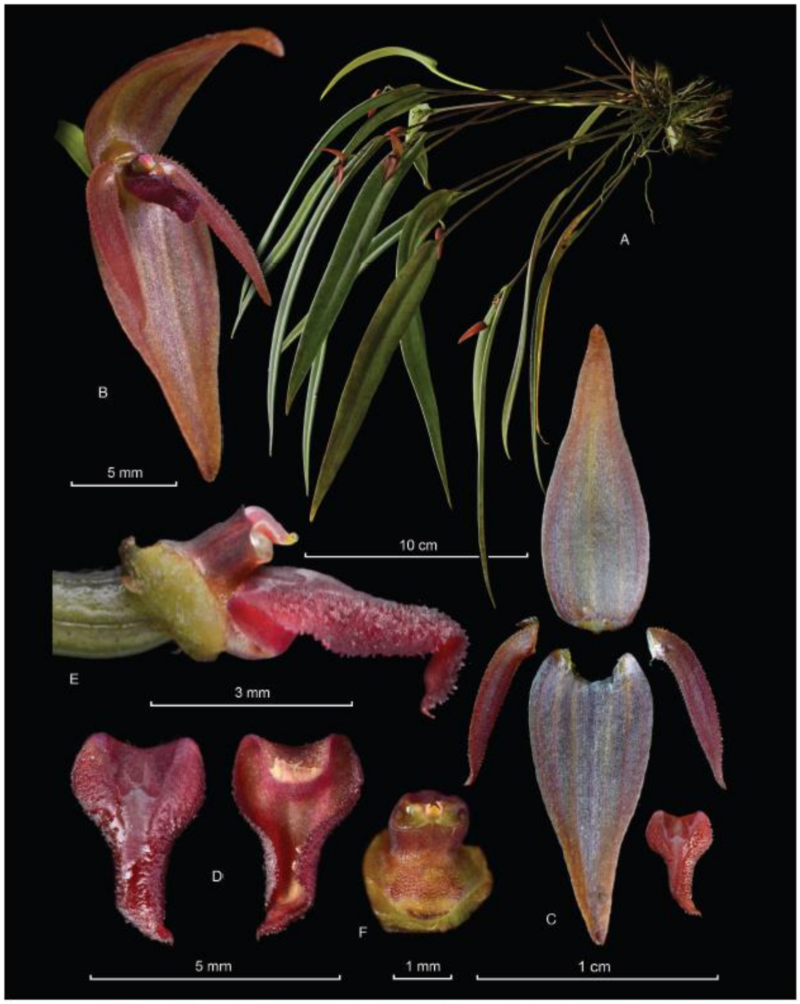


FIGURE 16. *Pleurothallis ×parentis-certa* Pupulin & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, in adaxial and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column, ventral view. Lankester Composite Dissection Plate prepared by D. Bogarín and F. Pupulin from *Bogarín 11802* (JBL).

ISSN #2834-1783

<u>Literature Cited</u>

Baquero, Luis & Monteros, Marco & Iturralde, Gabriel & Jiménez, Marco & Dueñas, R. (2024). Pleurothallis Markgruinii, A New Pleurothallidinae (Orchidaceae) From Northwestern Ecuador. 1-18. 10.24823/Ejb.2024.2032.

Belfort Oconitrillo, Noelia & Salguero Hernández, Grettel & Oses, Lizbeth & Gil-Amaya, Karen & Rojas-Alvarado, Gustavo & Chinchilla, Isler & Díaz-Morales, Melissa & Pupulin, Franco & Bogarín, Diego & Karremans, A.. (2024). New Species And Records Of Orchidaceae From Costa Rica. Iv.. Lankesteriana. 24. 141-192. 10.15517/Lank.V24I2.60686.

Bogarín, Diego & Hernández, Zuleika & Samudio, Zabdy & Rincón, Rafael & Pupulin, Franco. (2014). An Updated Checklist Of The Orchidaceae Of Panama. Lankesteriana. 14. 135-364. 10.15517/Lank.V14I3.17958.

Bogarín, Diego & Pupulin, Franco & Arrocha, Clotilde & Warner, Jorge. (2011). Orchids Without Borders: Studying The Hotspot Of Costa Rica And Panama. Lankesteriana. 10.15517/Lank.V0I0.11529.

Buitrago, Carol And Alzate, Néstor And Otero, Joel. (2014). Nocturnal Pollination By Flies Of The Fungus Of The Endemic Colombian Species, Pleurothallis Marthae (Orchidaceae: Pleurothallidinae). Lankesterian. 13. 10.15517/Lank.V13I3.14429.

Caetano, Daniel & Quental, Tiago. (2023). How Important Is Budding Speciation For Comparative Studies?. Systematic Biology. 72. 10.1093/Sysbio/Syad050.

Carlyle A. Luer & Lisa Thoerle 2013, Harvard Papers In Botany, Vol. 18, No. 2, Pp. 173 To 196 Miscellaneous New Species In The Pleurothallidinae (Orchidaceae)

Cassola, Fábio & Nunes, Carlos & Garibotti Lusa, Makeli & Garcia, Vera & Mayer, Juliana. (2019). Deep In The Jelly: Histochemical And Functional Aspects Of Mucilage-Secreting Floral Colleters In The Orchids Elleanthus Brasiliensis And E. Crinipes. Frontiers In Plant Science. 10. 10.3389/Fpls.2019.00518.

Chen, Rujin & Es, Rosen & Masson, Patrick. (1999). Gravitropism In Higher Plants. Plant Physiology. 120. 343-50. 10.1104/Pp.120.2.343.

Crawford, D.J. (2010), Progenitor-Derived Species Pairs And Plant Speciation. Taxon, 59: 1413-1423. 10.1002/Tax.595008

Damián-Parizaca, Alexander & Monteros, Marco & Rimachi, Daxs & Walston, Joseph & Mitidieri, Nicole. (2025). A New Species Of Pleurothallis (Pleurothallidinae, Orchidaceae) From The Historic Sanctuary Of Machupicchu, Perú. Phytokeys. 254. 29-40. 10.3897/Phytokeys.254.142116.

De-Kayne, Rishi & Schley, Rowan & Barth, Julia & Campillo, Luke & Chaparro Pedraza, Catalina & Joshi, Jahnavi & Salzburger, Walter & Van Bocxlaer, Bert & Cotoras, Darko & Fruciano, Carmelo & Geneva, Anthony & Gillespie, Rosemary & Heras, Joseph & Koblmüller, Stephan & Matthews, Blake & Onstein, Renske & Seehausen, Ole & Singh, Pooja & Svensson, Erik & Cerca, José. (2025). Why Do Some Lineages Radiate While Others Do Not? Perspectives For Future Research On Adaptive Radiations. Cold Spring Harbor Perspectives In Biology. 17. A041448. 10.1101/Cshperspect.A041448.

Doucette, Alfonso & Portilla, Jose & Cameron, Kenneth. (2016). Ten New Taxa In The Orchid Subtribe Pleurothallidinae (Epidendroideae, Epidendreae) From Ecuador. Phytotaxa. 257. 230. 10.11646/Phytotaxa.257.3.2.

Doucette, Alfonso & Wilson, Mark & Portilla, José & Kay, Andreas & Moreno, Juan & Cameron, Kenneth. (2016). Two New Species Of Pleurothallis And A New Name For Acronia Rinkei. Revista Colombiana De Orquideologia. 33. 123-139.

Fischer, Gunter & Gravendeel, Barbara & Sieder, Anton & Andriantiana, Jacky & Heiselmayer, Paul & Cribb, Phillip & Smidt, Eric & Samuel, Rosabelle & Kiehn, Michael. (2007). Evolution Of Resupination In Malagasy Species Of Bulbophyllum (Orchidaceae). Molecular Phylogenetics And Evolution. 45. 358-376. 10.1016/J.Ympev.2007.06.023.

Fischer, Gunter & Gravendeel, Barbara & Sieder, Anton & Andriantiana, Jacky & Heiselmayer, Paul & Cribb, Phillip & Smidt, Eric & Samuel, Rosabelle & Kiehn, Michael. (2007). Evolution Of Resupination In Malagasy Species Of Bulbophyllum (Orchidaceae).

Gervasi, Daniel & Schiestl, Florian. (2017). Real-Time Divergent Evolution In Plants Driven By Pollinators. Nature Communications. 8. 14691. 10.1038/Ncomms14691.

Grandcolas P, Nattier R, Trewick S. Relict Species: A Relict Concept? Tendencias Ecol Evol. December 2014; 29(12):655-63. Doi: 10.1016/J.Tree.2014.10.002. Epub Nov 4, 2014. Pmid: 25454211.

Gravendeel, Barbara & Dirks, Anita. (2015). Floral Development: Lip Formation In Orchids Unravelled. Nature Plants. 1. 15056. 10.1038/Nplants.2015.56.

Hsu, H. F. Et Al. Nature Plants 1, 15046 (2015).

Jiménez, Marco & Baquero, Luis & Wilson, Mark & Iturralde, Gabriel. (2018). Pleurothallis Chicalensis, A New Species In Subsection Macrophyllae-Fasciculatae (Orchidaceae: Pleurothallidinae) From Northwestern Ecuador. Lankesteriana. 18. 10.15517/Lank.V18I2.34050.

Jiménez, Marco & Vélez, Leisberth & Garzón-Suárez, Henry & Monteros, Marco & Wilson, Mark. (2023). Five New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) In Subsection Macrophyllae-Fasciculatae From Southeastern Ecuador. Phytotaxa. 607. 13. 10.11646/Phytotaxa.607.3.1.

Karremans, A. & Aguilar-Sandí, Diego & Artavia-Solìs, Miguel & Cedeño Fonseca, Marco & Chinchilla, Isler & Gil-Amaya, Karen & Rojas-Alvarado, Gustavo & Solano-Guindon, Naomi & Villegas-Murillo, Jordán. (2019). Nomenclatural Notes In The Pleurothallidinae (Orchidaceae): Miscellaneous. Phytotaxa. 406. 259-270. 10.11646/Phytotaxa.406.5.1.

Karremans, A. & Jiménez, José. (2018). Pleurothallis Hawkingii And Pleurothallis Vide-Vallis (Orchidaceae; Epidendroideae), Two New Species From Cordillera De Guanacaste In Costa Rica. Phytotaxa. 349. 185. 10.11646/Phytotaxa.349.2.10.

Karremans, A. & Moreno, Juan & Gil-Amaya, Karen & Gutiérrez Morales, Nicolás & Espinosa Moreno, Felipe & Mesa-Arango, Santiago & Restrepo, Eugenio & Rincón-González, Milton & Serna Sánchez, Alejandra & Sierra-Ariza, Mario Alexei & Vieira-Uribe, Sebastian. (2023). Colombian Orchidaceae: A Catalogue Of The Pleurothallidinae. Lankesteriana. 23. 10.15517/Lank.V23I2.56158.

Karremans, A. And Díaz-Morales, Melissa. (2019). The Pleurothallidinae: Extremely High Speciation Driven By Pollinator Adaptation.

Karremans, A.. (2016). Genera Pleurothallidinarum: An Updated Phylogenetic Overview Of Pleurothallidinae. Lankesteriana. 16. 219-241. 10.15517/Lank.V16I2.26008.

Karremans, A.. (2019). To Be, Or Not To Be A Stelis. Lankesteriana. 19. 10.15517/Lank.V19I3.40082.

Karremans, A.. (2023). Demystifying Orchid Pollination: Stories Of Sex, Lies, And Obsession.

Lindley, John, And Jean Jules Linden. Orchidaceae Lindenianae ; Or, Notes Upon A Collection Of Orchids Formed In Colombia And Cuba By J. Linden. Bradbury And Evans, 1846,

Lindley, John, Et Al. The Genera And Species Of Orchidaceous Plants. Ridgways, 1830,

Luer, C. A. (1975). Icones Pleurothallidinarum (Orchidaceae) Pleurothallisof Ecuador Iii. Selbyana 1: 303

Luer, C. A. (1980). Phytologia 47(2): 76-77

Luer, C. A. (1996). Icones Pleurothallidinarum (Orchidaceae) Miscellaneous Species In The Pleurothallidinae. Selbyana 3

Luer, C. A. (1998). Icones Pleurothallidinarum Xvii: Systematics Of Subgen. Pleurothallissect. 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. (1977). Icones Pleurothallidinarum (Orchidaceae) Various Species In The Pleurothallidinae. Selbyana 3:400.

Luer, C.A. (1977). New Species Of Pleurothallis (Orchidaceae) From Ecuador. Lindleyana 11, 141-197.

Luer, C.A. (2005). Icones Pleurothallidinarum Xxvii: Dryadella And Acronia Section Macrophyllae-Fasciculatae. Missouri Botanical Garden Systematic Botany Monographs, 103, 1–311.

Luer, C.A., A Revision Of Some Sections Of Subgenus Pleurothallis, Lindleyana 3: 143 (1988)

Marder, Eyal & Smiley, Tara & Yanites, Brian & Kravitz, Katherine. (2025). Direct effects of mountain uplift and topography on biodiversity. Science (New York, N.Y.). 387. 1287-1291. 10.1126/science.adp7290.

Mó, Edgar & Cetzal Ix, William & Basu, Saikat & Casanova Lugo, Fernando & Pallandre, Jean-Marc & Noguera-Savelli, Eliana & Vega, Hermes. (2017). Diversity Of Pleurothallidinae In Guatemala: An Endangered Orchid Subtribe With High Economic And Horticultural Potentials. International Journal On Environmental Sciences. 8. 64-86.

Mohl, Hugo Von, And D. F. L. Von Schlechtendal. Botanische Zeitung. A. Förstner, 1843,

Moreno, Juan & Galindo, Robinson & Alegría, Melisa & Wilson, Mark & Zuluaga, Alejandro. (2023). A New Species Of Pleurothallis (Pleurothallidinae) From The Southwestern Andes Of Colombia In The National Natural Park Farallones De Cali. Lankesteriana. 23. 401-407. 10.15517/Lank.V23I2.56290.

Nunes, Elaine & Smidt, Eric & Stützel, Thomas & Coan, Alessandra. (2014). What Do Floral Anatomy And Micromorphology Tell Us About Neotropical Bulbophyllum Sect. Didactyle (Orchidaceae: Bulbophyllinae)?. Botanical Journal Of The Linnean Society. 175. 438-452. 10.1111/Boj.12176.

Nunes, Elaine & Smidt, Eric & Stützel, Thomas & Coan, Alessandra. (2015). Comparative Floral Micromorphology And Anatomy Of Species Of Bulbophyllum Section Napelli (Orchidaceae), A Neotropical Section Widely Distributed In Forest Habitats. Botanical Journal Of The Linnean Society. 177. 378-394. 10.1111/Boj.12253.
Ocupa-Horna, Luis & Wilson, Mark & Jiménez, Marco. (2023). A New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) In Subsection Macrophyllae-Fasciculatae Found In Carpish Montane Forest Regional Conservation Area, Peru. Phytotaxa. 629. 163-175. 10.11646/Phytotaxa.629.2.6.

Parins-Fukuchi, Charles & Saulsbury, James. (2025). The Consequences Of Budding Speciation On Trees. Systematic Biology. 10.1093/Sysbio/Syaf012.

Pérez-Escobar Oa, Zizka A, Bermúdez Ma, Meseguer As, Condamine Fl, Hoorn C, Hooghiemstra H, Pu Y, Bogarín D, Boschman Lm, Pennington Rt, Antonelli A, Chomicki G. The Andes Through Time: Evolution And Distribution Of Andean Floras. Plant Sci. Trends 2022 Apr; 27(4):364-378. Doi: 10.1016/J.Tplants.2021.09.010. Epub January 6, 2022. Pmid: 35000859.

Pérez-Escobar, Oscar & Bogarín, Diego & Przelomska, Natalia & Ackerman, James & Balbuena, Juan Antonio & Bellot, Sidonie & Buehlmann, Roland & Cabrera, Betsaida & Cano, José & Charitonidou, Martha & Chomicki, Guillaume & Clements, Mark & Fernández, Melania & Flanagan, Nicola & Gravendeel, Barbara & Hágsater, Eric & Halley, John & Hu, Ai-Qun & Antonelli, Alexandre. (2023). The Origin And Speciation Of Orchids. 10.1101/2023.09.10.556973.

Pérez-Escobar, Oscar & Chomicki, Guillaume & Condamine, Fabien & Karremans, A. & Bogarín, Diego & Matzke, Nicholas & Silvestro, Daniele & Antonelli, Alexandre. (2017). Recent Origin And Rapid Speciation Of Neotropical Orchids In The World'S Richest Plant Biodiversity Hotspot. New Phytologist. 215. 891–905. 10.1111/Nph.14629.

Phillips, Ryan & Xu, Tingbao & Hutchinson, M.F. & Dixon, Kingsley & Peakall, Rod. (2013). Convergent Specialization – The Sharing Of Pollinators By Sympatric Genera Of Sexually Deceptive Orchids. Journal Of Ecology. 101. 10.1111/1365-2745.12068.

Pupulin, Franco & Aguilar, Jaime & Belfort Oconitrillo, Noelia & Díaz-Morales, Melissa & Bogarín, Diego. (2021). Florae Costaricensis Subtribui Pleurothallidinis (Orchidaceae) Prodromus Ii. Systematics Of The Pleurothallis Cardiothallis And P. Phyllocardia Groups, And Other Related Groups Of Pleurothallis With Large Vegetative Habit. Harvard Papers In Botany. 26. 10.3100/Hpib.V26Iss1.2021.N14.

Pupulin, Franco & Bogarín, Diego & Karremans, A.. (2023). Lankester Catalogue Of Costa Rican Orchidaceae. Lankesteriana. 10.15517/Lank.V23Isupplement.58145.

Pupulin, Franco & Díaz-Morales, Melissa & Fernández, Melania & Aguilar, Jaime. (2017). Two New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) From Costa Rica In The P. Phyllocardia Group. Lankesteriana. 17. 10.15517/Lank.V17I2.29850.

Schlechter, R. (1920). Repertorium Specierum Novarum Regni Vegetabilis, 7:112

Sierra-Ariza, Mario Alexei & Rincón-González, Milton & Wilson, Mark & Villanueva-Tamayo, Boris. (2022). Una Nueva Especie De Pleurothallis (Pleurothallidinae) Subsección Macrophyllae-Fasciculatae Para La Región Andina Colombiana. Lankesteriana. 22. 25-35. 10.15517/Lank.V22I1.50823.

Sierra-Ariza, Mario Alexei. (2023). Two New Species Of Pleurothallis (Pleurothallidinae) Subsection Macrophyllae-Fasciculatae From The Central Andes Of Colombia. Lankesteriana. 23. 10.15517/Lank.V23I1.54321.

Sierra-Ariza, Mario. (2024). Pleurothallis Cop-Biodiversitatis (Pleurothallidinae), A New Species From Colombia. Lankesteriana. 10.15517/Lank.V24I3.61038.

Teixeira Sde P, Borba El, Semir J. Lip Anatomy And Its Implications For The Pollination Mechanisms Of Bulbophyllum (Orchidaceae) Species. Ann Bot. May 2004; 93(5):499-505. Doi: 10.1093/Aob/Mch072. Epub Mar 5, 2004. Pmid: 15003955; Pmcid: Pmc4242314.

Unterfrauner, Elisabeth & Fabian, Claudia & Hemming, Gary & Garcia, Beatriz. (2025). What's in it for citizen scientists? An Analysis of Participant Inclusivity in Citizen Science Projects in Advanced Physics Research. Open Research Europe. 4. 124. 10.12688/openreseurope.17436.3.

Vega, Hermes & Cetzal Ix, William & Mó, Edgar & Romero-Soler, Katya. (2022). An Updated Checklist Of The Orchidaceae Of Honduras. Phytotaxa. 562. 1–80. 10.11646/Phytotaxa.562.1.1.

Vélez, Leisberth & Jiménez, Marco & Gutiérrez, Diego & Baquero, Luis. (2022). Pleurothallis Ariana-Dayanae, A New Species In Subsection Macrophyllae-Fasciculatae (Pleurothallidinae) From The Cordillera Del Cóndor, Ecuador. Lankesteriana. 22. 101-109. 10.15517/Lank.V22I2.51750.
Villaseñor, Jose. (2016). Checklist Of The Native Vascular Plants Of Mexico. Revista Mexicana De Biodiversidad. 87. 10.1016/J.Rmb.2016.06.017.
Williams, L. O. (1942), Ann. Missouri Bot. Gard. 29(4): 341-342.

Wilson, Mark & Baquero, Luis & Dupree, Katharine & Jiménez, Marco & Leblanc, Cheryl & Merino, Gilberto & Portilla, Jose & Guerrero, Marcos & Suárez, Francisco & Werner, Jon. (2016). Three New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) In Subsection Macrophyllae-Fasciculatae From Northern South America. Lankesteriana. 16. 349-366. 10.15517/Lank.V16I3.27314.

Wilson, Mark & Jiménez, Marco & Jost, Lou & Kay, Andreas & Frank, Graham & Baquero, Luis. (2018). A New Species Of Pleurothallis (Orchidaceae, Pleurothallidinae) From Northwestern Ecuador With Affinities To Both Subgenera Ancipitia And Scopula. Phytotaxa. 343. 249. 10.11646/Phytotaxa.343.3.5.

Wilson, Mark & Larsen, Bruno & Moreno, Juan & Ward, Raven & Riksen, Joost & Piña, Luis & Sierra-Ariza, Mario Alexei & Jiménez, Marco & Rincón, Milton & Galindo, Robinson & Garzón-Suárez, Henry & Haelterman, David. (2022). New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae), A New Record Of The Country And Labular Morphology In The P. Cardiostola-P. Lilijae Complex Of The Macrophyllae-Fasciculatae Subsection. Harvard Papers In Botany. 27. 187-220. 10.3100/Hpib.V27Iss2.2022.N10.

Wilson, Mark & Pupulin, Franco & Archila, Fredy & Damon, Anne & Gómez, Rodolfo. (2013). A Newly Recognized Clade Of Pleurothallis With Mesoamerican Distribution. Lankesteriana. 10.15517/Lank.V0I0.11567.

Wilson, Mark & Zhao, Kehan & Hampson, Haley & Romoleroux, Katya & Jiménez, Marco & Tobar-Suarez, Francisco & Larsen, Bruno. (2018). A New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) In Subsection Macrophyllae-Fasciculatae With A Unique, Highly Reduced, Morphologically Distinct Labellum. Lankesteriana. 18. 217-230. 10.15517/Lank.V18I3.35495.

Zambrano, Javier & Gómez, Rodolfo & Wilson, Mark. (2017). A New Species Of Pleurothallis (Orchidaceae: Pleurothallidinae) From Southwestern Ecuador: Pleurothallis Marioi. Phytotaxa. 308 (1). 080–088. 10.11646/Phytotaxa.308.1.6.

Acknowledgements