An Evolutionary Analysis of *Pleurothallis (Orchidaceae)* Species in Subsection *Macrophyllae-Fasciculatae*

Kevin W. Holcomb

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Introduction

Pleurothallis Subsection *Macrophyllae-Fasciculatae* is the most species-rich infrageneric grouping with ca. 247–317 described species,

Presented here are 240 species as within MF and recommend 55 species be transferred to Cardiostolae.

Materials and Methods

This is the first large-scale analysis of PMF

Together with contemporary field observations, such as those recorded in iNaturalist, these data would then allow accurate distributions for the species to be developed .

depending on synonymy, and many more yet to be described. Despite the large number of species, to date no phylogenetic lineages within the group have been defined.

Step 1, holotypes and some isotypes from Icones Pleurothallidinarium were plotted using Google's My Maps.

Step 2, any new species recorded on POWO through current date were plotted using Google's My Maps.

Step 3, In addition, the author analyzed 2908 Observations (6,936 photos) Pleurothallis Subsection Macrophyllae-Fasciculatae on iNaturalist

2755 observations macrophyllae-fasciculatae 6,566 photos
91 observations P. adonis 227 photos
31 observations P. linguifera 77 photos
5 observations P. baezensis 5 photos
5 P. serricardia 10 photos
21 observations P. macrocardia 51 photos

These photos were compared to other observations of other species and a logical, deductive conclusion was made.

Compared against Lankester Catalogues.

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Living plant material are from the author's personal collection, Andy's Orchids, Encinitas, California, and the permanent, living collection of the Fuqua Orchid Center at the Atlanta Botanical Garden.

Analysis is based on Bulbophylliform and Steliform flowers.

Mapped out using herbarium specimens

Excluded: P. equipedites, P. crateriformis, P. ambyx, P. aurita, P. bitumida

P. bivalvis

P. bovilingua – Only known from a photograph

P. braidiana – country unknown

P. bulbosa - ?

P. cardiochila – flower missing

P. cassidata – no locality

P. cedrinorum - confusion

P. acutilabia moved to series amphygiae

For an interactive map:

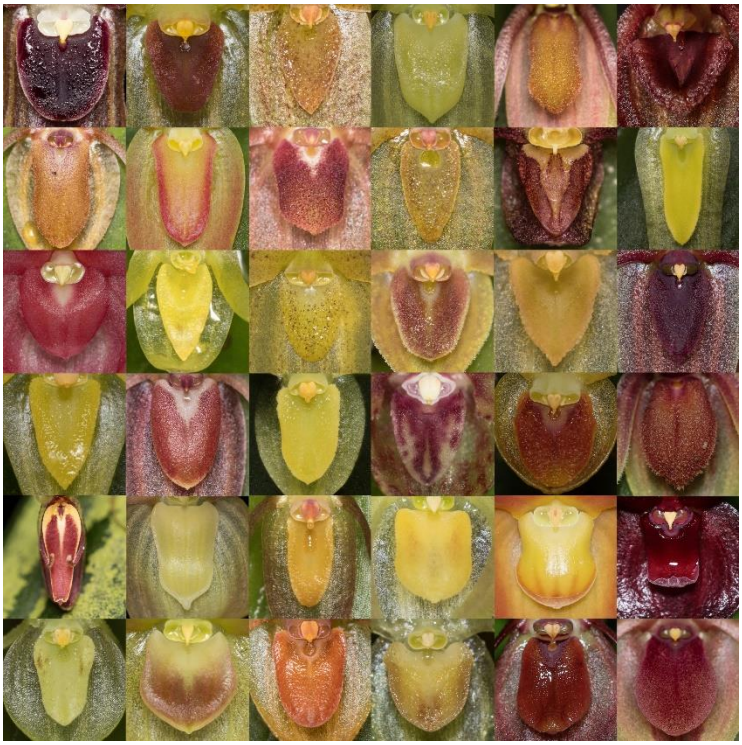
Macrophyllae-Fasciculatae

Not a hypothesis based paper, but a Qualitative analysis presented in a slide format.
Compared against Lankester's Catalogs and Icones

Results

Lip Reading: Labellar Morphology Defines Species in Subsection *Macrophyllae-Fasciculatae*

Pleurothallis species in Subsection Macrophyllae-Fasciculatae are generally described using the morphological species concept, which characterizes species by distinctive morphological features. Most species of *Pleurothallis* in this group are identified primarily by the characteristics of the labellum (lip).



The abaxial surface of the lip of *Pleurothallis* species can easily be compared to the face of a human being. Like a human's face, the dorsal surface exhibits the majority of defining characteristics, such as shape, size, and any special features, which include dimples, warts, lines, wrinkles, and even freckles (spots) that can distinguish one species from another.

The profile (side) of the lip may reveal additional characteristics that help distinguish species from one another. For example, *P. giraffa's* (above) elongated, "giraffe-like" column, for which it gets its name, isn't obvious until it's viewed from the side.

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When viewed from above, the species within the P. adonis/linguifera complex look like species within the very broad P. bivalvis complex. However, when the flowers are viewed from the side, one can see they all have large, convex lips. Why does the hinge still work? Gnats aren't heavy enough. This isn't an evolutionary trait, it's an ancestral trait.

Pleurothallis tremens, a Relict Species of *Pleurothallis* in Subsection *Macrophyllae-Fasciculatae*

While visiting Andy's

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Pleurothallis tremens
Wind-assisted Pollination Mechanism

Bulbophylliform Flowers

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 Antilles. Over 80% of the recognized species representing five of the six currently accepted sections can be 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 flowers of Bulbophyllum species have lips which are connected to the column foot by a hinge. Of the six sections of Bulbophyllum, species in Section Napellii (C & D) have large, convex lips similar to Pleurothallis species in the P. adonis complex.

Only 7 species in the Andes

Bulbophyllum flowers exhibit two types of pollination mechanisms: Wind-assisted fly pollination and Insect-weight assisted mechanism. Both of these pollination mechanisms are found in the Bulbophylliform flowers of the P. adonis complex. This suggests a common ancestor branched off and evolved into the Pleurothallis adonis complex, the only species with Bulbophylliform flowers. The species within the Pleurothallis adonis complex are the ancestors of all species within Macrophyllae-Fasciculatae.

Until recently, only one of the two Bulbophyllum pollination mechanisms, insect weight-assisted pollination, was observed in the species within the Pleurothallis adonis complex. However, Pleurothallis tremens from Ecuador is the only species of Pleurothallis that exhibits the wind-assisted

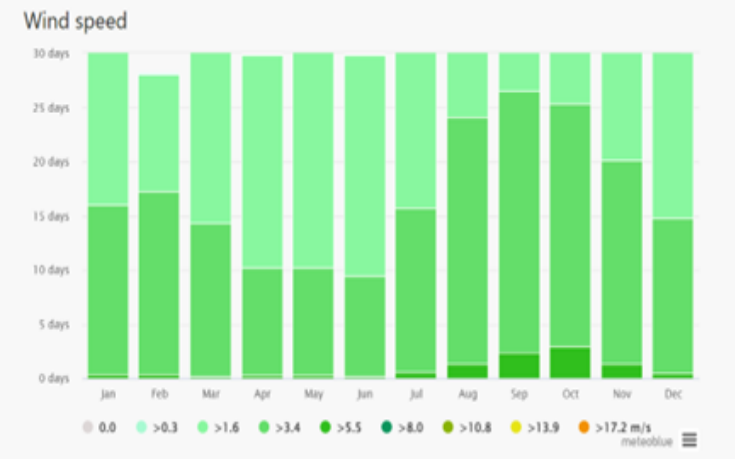
pollination mechanism. The Bulbophylliform flowers of the Pleurothallis adonis complex exhibit both pollination mechanisms that are found in Bulbophyllum

Speciation In Real Time: The Complex Diversity of *Pleurothallis* Species in Subsection *Macrophyllae-Fasciculatae*

Around 80 MYA, the Andes emerged along the western coast of South America and continued eastward. Possibly multiple events. The northern Andes uplifted rapidly creating montane forests with heavy winds.

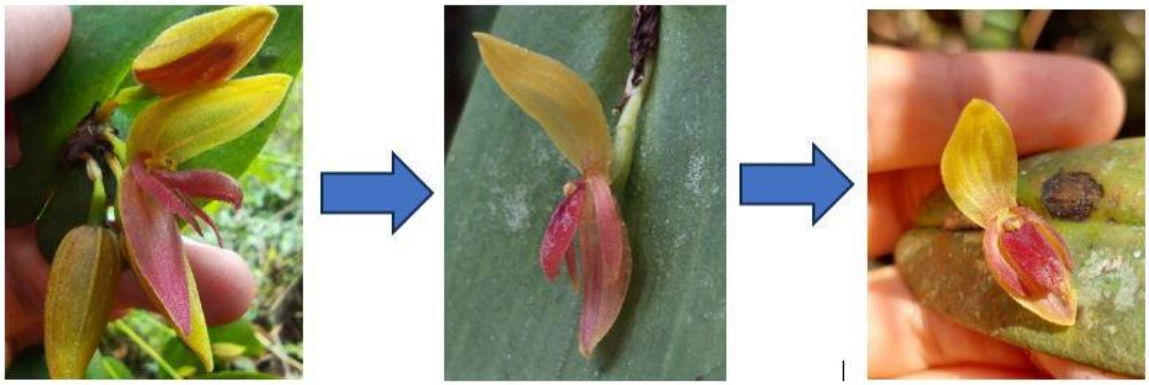
According to a 2003 study, Neotropical Bulbophyllum pollination mechanisms are only successful in wind speeds of 1.0-1.5 meters per second or less, what is typically referred to as light wind.

However, for most of the year, the Andes experience wind speeds greater than 3.4 meters per second for at least 15-days per month. Bucking Bronco. Gnats aren't heavy enough.



Budding Speciation

Budding speciation is defined as a speciation event in which the new species co-occurs with its direct ancestor. Therefore, we can see evolution occurring in real-time, similar to Darwin's finches.



Ancestral Species Transitional Species Derivative Species

Ancestral Species

Transitional Species

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You can see the adonis characteristics.

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Derivative Species

The lip is non-functional.

Revolute Lip Margins

- This is the only species with this adaptation.
- The margins of the lip have folded under so tightly that the hinge has been rendered non-functional.
- P. megalorhina might have this adaptation. However, this species is only known from the preserved holotype specimen. The flower was dissected. Therefore, the hinge cannot be tested.

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Folded or Deflexed Lips

Cradled Lip

Pleurothallis mastodon

- The elephant tusks actually cradle the lip preventing the hinge from moving.
- This is also seen in P. quitu-cara

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Wedged Petals

- Possibly the first adaptation
- The only study of Pleurothallis pollination
- A 2014 study (Alzate et. al.)
- Seasonality

Pleurothallis gargantua

Adnate Convex Lips

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Left: Pleurothallis austinrumleyi;
Right: Pleurothallis aff. bivalvis

Flat Lips

Concave Lips

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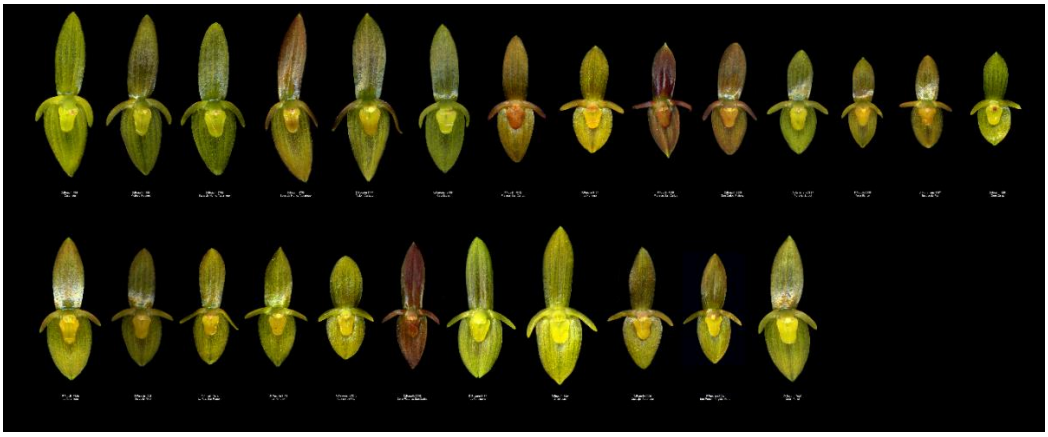
- Lip is inside-out

What Is Variation?



- For the purpose of this analysis, this study is being used to define "variation".
- Luer's P. adonis
- There is a need for a consensus on variation.

Variation vs. form

What about hybridization?

Derivative Variants

Pleurothallis titan is arguably 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 yellow-flowered specimen had not yet been seen. Although a yellow-flowered specimen was found just a few years later, it would take almost three-decades for the description to be revised to reference the familiar canary yellow flowers of the species.

Advances in technology, such as digital cameras and now camera phones, have made it much easier to document species observations in the field, and websites like flickr and iNaturalist allow these observations to be shared instantaneously. If *Pleurothallis titan* were being described today, in 2022, the description of the species would probably look very different from the original 1977 publication.

The following compilation of photographs represent observations by both citizen scientists and professional scientists. These observations illustrate the wide range of color variation exhibited in the flowers of *Pleurothallis titan*.
Evolution is an infinite process.

- May be different color, smaller or larger flowers, but the lip is the same.
- Left: A brown flower as described by Luer in 1977.
- Top right: The typical yellow flower that has become common in the horticultural trade.
- Bottom right: A purple form with ascending petals.
- Although the color is different in each form, and the last specimen has ascending petals, the lip is the same in all three. There is no debate that these are all P. titan.

Descendant Species

Titaniform Flowers

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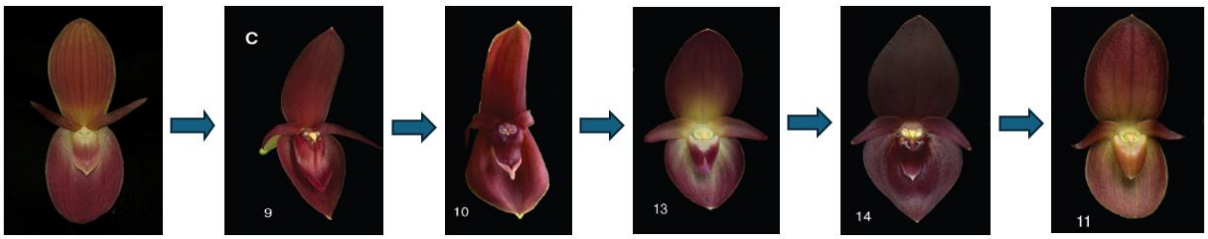
The Current State



Recommendation for the Resurrection of *Pleurothallis* Subsection *Cardiostolae*

Could evolve faster

Evolution is an infinite process.

Resupination in guat to mexico

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Summary

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New Species

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

Plant medium in size, epiphytic, caespitose, roots very slender.

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

Leaf 7.5 cm long, 2.25 cm wide, coriaceous, ovate, acute, the base cuneate, sessile.

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

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

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

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

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

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

Etymology: From the Latin *tremens* "trembling", a reference to the ;oosely-hinged lip.

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

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Pleurothallis tremens is

Pleurothallis tremens

Pleurothallis adonis

Scan the QR codes with your phone to see how each of the pollination mechanisms work.

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

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

Leaf 7.5 cm long, 2.25 cm wide, coriaceous, ovate, acute, the base cuneate, sessile.

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

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

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

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

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

Pleurothallis tremens is

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

Plant medium in size, epiphytic, caespitose, roots very slender.

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

Leaf 7.5 cm long, 2.25 cm wide, coriaceous, ovate, acute, the base cuneate, sessile.

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

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

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

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

Pleurothallis tremens is

New Combinations

Pleurothallis rhopalocarpa, K.W. Holcomb, comb. ***nov.***

Plant medium in size, epiphytic, caespitose, roots very slender.

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

Leaf 7.5 cm long, 2.25 cm wide, coriaceous, ovate, acute, the base cuneate, sessile.

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

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

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

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Pleurothallis tremens is

iNaturalist Observations and Photo Credits

Due to copyright restrictions, a complete list of links to the iNaturalist observations can be provided upon request.

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