The Evolutionary History of *Pleurothallis* Section *Macrophyllae-Fasciculatae* (*Orchidaceae*)

Kevin W. Holcomb

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Cover Photo: *Pleurothallis tremens*

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I. Introduction

The species within *Pleurothallis* Section *Macrophyllae-Fasciculatae* form one of the largest and most morphologically hyperdiverse groups within the *Pleurothallidinae*. Unfortunately, this hyperdiversity has commonly been treated as trivial intraspecific variation, and many distinct species have been repeatedly misidentified, treated as subspecies, lumped into unofficial species complexes, or incorrectly reduced to synonymy.

Although multiple phylogenetic studies have included these species, none has produced a well-supported phylogeny that resolves internal lineages for the group. That's because sampling has been too limited, and the underlying framework has been treated as strictly bifurcating, without testing other modes of speciation that may better account for the patterns we see in nature.

Under current sampling constraints, DNA alone cannot reliably support species- or genus-level boundaries in this group. Even so, limited DNA placement has been used to overturn older, morphology-based classifications, effectively pushing morphology out of the process.

A persistent limitation in *Pleurothallis* systematics is that the evidence base has historically been limited to herbarium material, protologues, and illustrations, none of which are inherently reliable descriptions of living habit or function. A protologue is only as accurate as the observations recorded in it, and an illustration is ultimately an interpretive rendering that may not reflect how the plant actually presents in the field.

Where protologues and illustrations often stop at a static description, field observations capture posture, presentation, and functional characters as they actually occur, repeatedly, across populations. For much of the last century, however, there simply have not been enough repeated field observations available across hundreds of *Macrophyllae-Fasciculatae* species to evaluate consistent morphological characters in a comparative way.

That constraint has changed. iNaturalist, a social network of naturalists, citizen scientists, and biologists built on the shared interest of mapping biodiversity, now contains millions of observations of plants, animals, and fungi from around the world. Instead of relying on a single pressed specimen, a single protologue, or a single plate, we can now see the same named species photographed repeatedly across its range, across seasons, and across microhabitats, often by many independent observers. Those observations are tied to dates, locations, and elevations, and they frequently include photo series that document the whole plant, not just a single flower.

Equally important, iNaturalist creates a comparative framework that traditional collections cannot provide: dozens or hundreds of images for a single species, and thousands across the group, taken under natural light, at natural angles, and in real weather. That makes it possible to evaluate whether a character is repeatable, stable, and geographically structured, or whether it is truly labile. It provides what has been missing for this group, a living, field-based evidentiary record that can be revisited as identifications improve and as additional observations accumulate.

Presented here is an interpretive model of the evolutionary history of *Pleurothallis* section *Macrophyllae-Fasciculatae*. This study is the first large-scale analysis of any group in subtribe *Pleurothallidinae* based primarily on field observations. A total of 2,908 iNaturalist observations were compiled and reviewed, and approximately 6,936 associated photographs were assessed with emphasis on lip position, lip architecture, and hinge functionality. The results have implications not just for the species within *Macrophyllae-Fasciculatae*, but for subtribe as a whole.

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II. Hyperdiversity Through Budding Speciation

The species in section *Macrophyllae-Fasciculatae* are generally described using the morphological species concept, which defines species by shared, repeatable, and distinctive morphological traits. The hyperdiverse morphological features of the lip are the primary diagnostic characteristics used to define species within this section.

Lindley (1859) was the first to recognize this group formally, establishing *Macrophyllae-Fasciculatae* as an infrageneric "section". Luer (1986) carried Lindley's concept forward by retaining *Macrophyllae-Fasciculatae* as a section within *Pleurothallis* (subgenus *Pleurothallis*). He then revised the internal structure of the group (1988) by splitting the section into two subsections, *Macrophyllae-Fasciculatae* and *Cardiostolae*.

A decade later, Luer (1998) shifted the rank again, reducing *Macrophyllae-Fasciculatae* from section to subsection and placing it in synonymy under *Acronia* section *Macrophyllae-Fasciculatae*. In that same treatment, he also established *Acronia* section *Abortivae* and series *Amphygiae*.

Subgenus *Acronia* was segregated from *Pleurothallis* and resurrected as the genus *Acronia* by Luer (2005) to unite subsection *Acroniae* and subsection *Macrophyllae-Fasciculatae*. Subsequent phylogenetic studies by Pridgeon et al. (2001), and later works by Karremans et al. in the 2010s, formalized the consolidation of these groups back into the genus *Pleurothallis*. However, these studies were based on extremely limited sampling and did not take morphology into consideration.

Luer published a rebuttal to Pridgeon's studies in 2002, criticizing both the limited sampling and the disregard for morphology. Yet Luer himself was quick to dismiss discrete, repeatable morphological structure as trivial variation. As a result, many distinct species have been treated as subspecies, lumped into unofficial species complexes, or incorrectly reduced to synonymy.

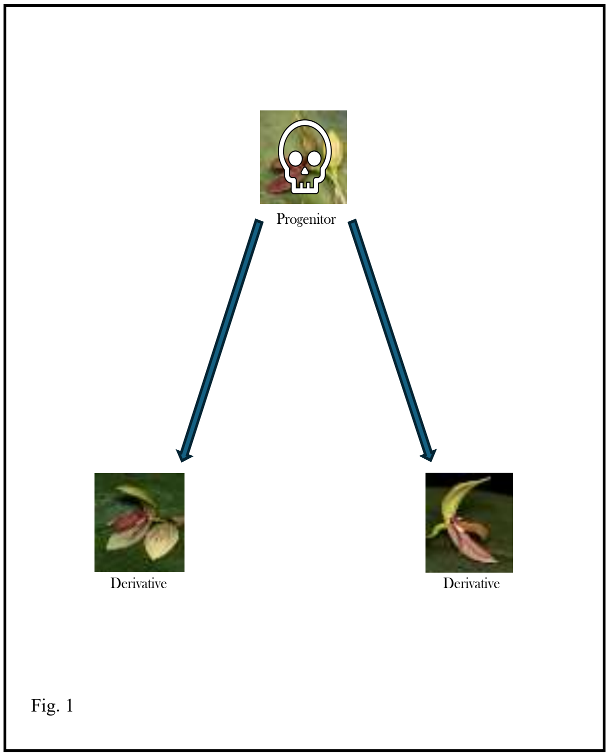


Fig. 1

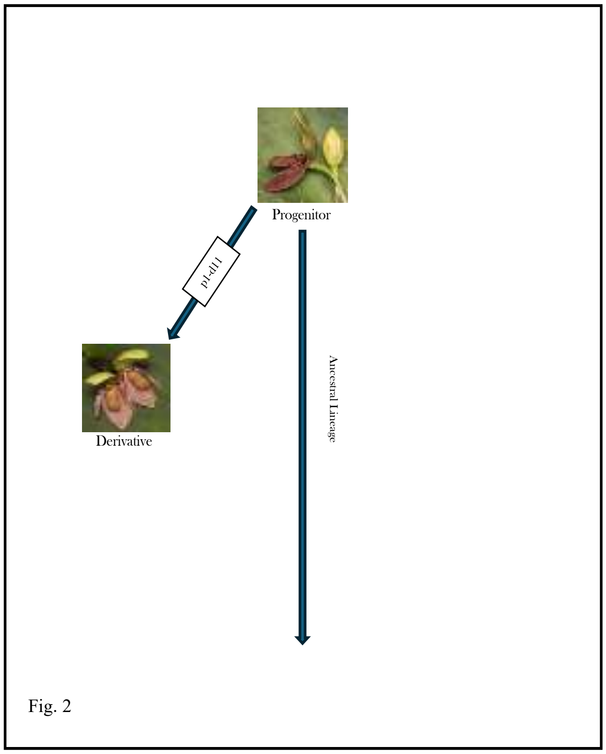
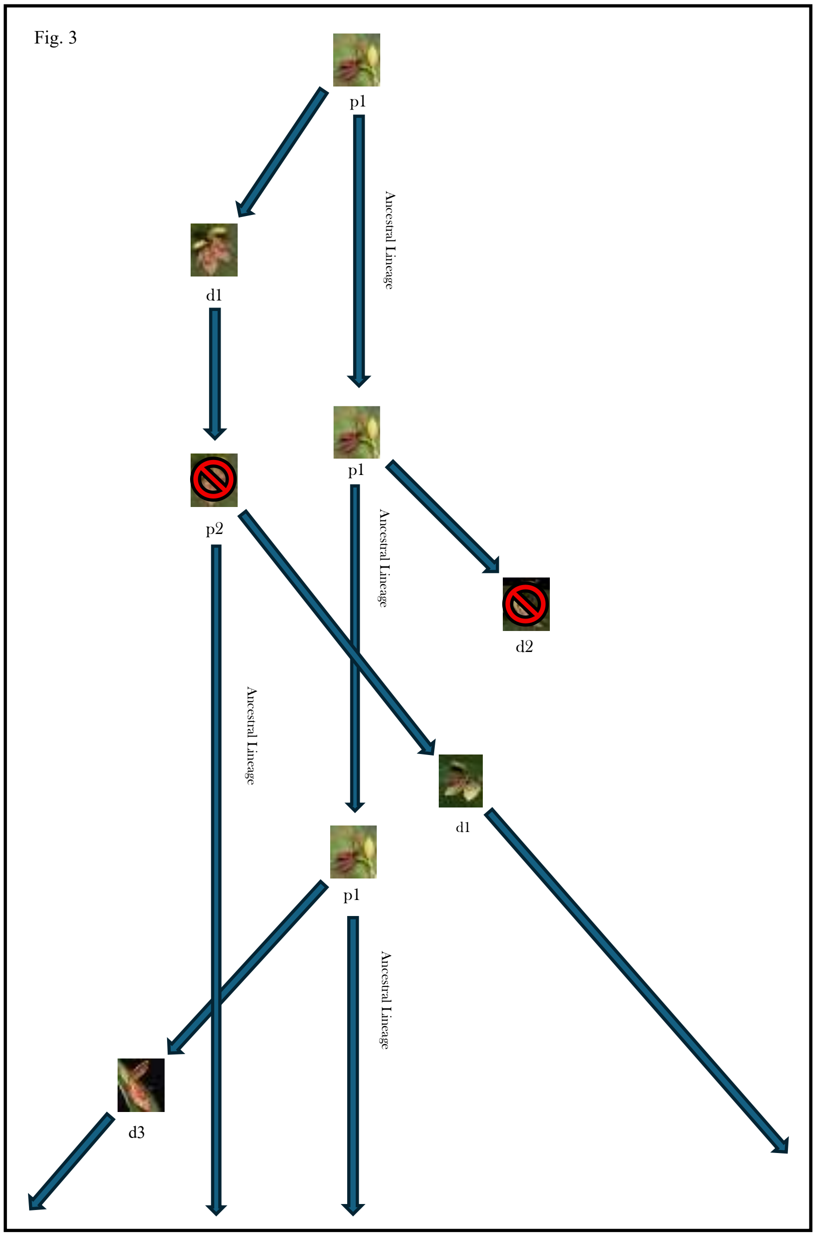


Fig. 2

(Fig. 1) In most evolutionary stories, speciation is a clean split. An ancestral species reaches a turning point, then branches into two new species, and the original form fades away. This is the classic bifurcating model, sometimes framed as "ancestral extinction," because the ancestor is assumed to go extinct as the descendants take its place. Both Luer's treatment and the later phylogenetic studies approached this group through that familiar lens, treating diversification as a series of tidy branch points, without testing other modes of speciation.

(Fig. 2) In section *Macrophyllae-Fasciculatae*, however, the pattern is noticeably different because these species evolved through budding speciation. Budding speciation occurs through the creation of progenitor-derivative (p-d) pairs. Instead of going extinct, an ancestral lineage, the progenitor, coexists with the newly formed species, the derivative.



(Fig. 3) Because the ancestral species does not go extinct when a new form appears, it can continue to bud off lineages over time, producing multiple progenitor–derivative pairs that coexist. In turn, a derivative lineage can itself become a new progenitor, budding off its own derivatives. The result is not a neat sequence of splits, but a layered pattern of overlap that creates an asymmetric ancestor–descendant pattern.

A reliable phylogeny would require nearly all of the descendant lineages, so that budding order, meaning which forms appeared first and which came later, can be inferred with confidence. Unfortunately, that evidence base has been irretrievably thinned. With only about 25% of Northern Andean forests remaining, many lineages were likely destroyed before they could ever be documented, let alone sequenced.

Those missing lineages leave gaps in an already overlapping pattern. When bifurcating methods are applied, they interpret the gaps as separate origins, manufacture artificial clades, and inflate separations that look genus-level on a tree but do not reflect the true structure in nature. Under current sampling constraints, DNA cannot reliably support species or genus boundaries in this group, because broad, representative sampling is not possible.

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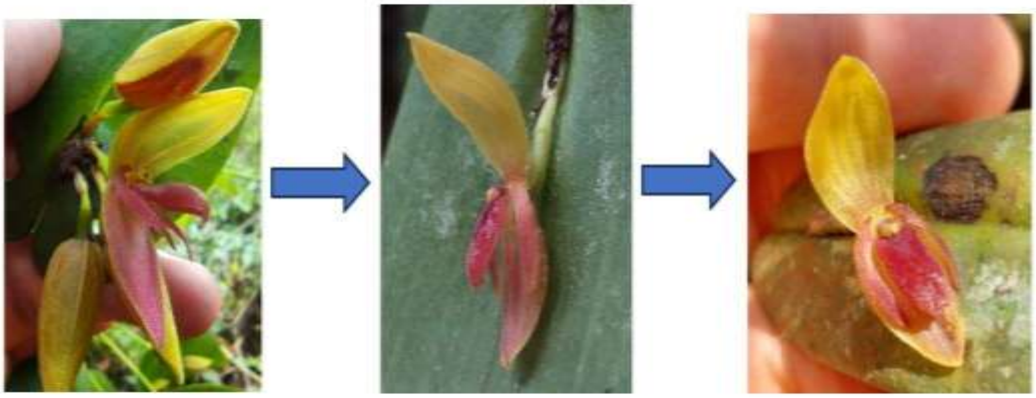

As a lineage buds off from its progenitor, it typically retains the same basic floral structure and then diverges through small, incremental morphological changes. Over time, that process produces morphotypes that can still resemble the original progenitor, even when they are not closely related sister lineages.

Pleurothallis appears to have accelerated in diversification around 10 million years ago and to have peaked around 6 million years ago. Because this happened so recently in evolutionary time, many morphotypes still exist today creating the hyperdiversity we see now.

Many of these morphotypes are, in fact, distinct species. However, when viewed individually, if the differences are subtle, they are often dismissed as “variation.” Even when the differences are quite obvious, they are still frequently minimized as “forms” or “subspecies.”

The morphological hyperdiversity observed in section *Macrophyllae-Fasciculatae* is not random intraspecific variation. It is a visible, living record of evolutionary history. These morphotypes each represent a lineage captured at a different stage of the evolutionary process like individual frames in a time-lapse sequence.

Since broad, representative DNA sampling is not possible, we have to rely on morphology to infer evolutionary relationships. The discovery of a new species within section *Macrophyllae-Fasciculatae* with a unique pollination mechanism like those of the Neotropical *Bulbophyllums* provides a concrete functional reference point for interpreting this evolutionary record.

Within *Macrophyllae-Fasciculatae*, evolution revolves around the lip. It begins erect, then becomes suberect, then settles into a prostrate position. From there, the pattern continues in the same direction. The lip is reduced, the hinge is progressively eliminated, and in the most extreme cases the lip dwindles into vestigialness.

A second theme emerges in the cloud forests, where constant moisture and heavy weather reshape both flower and plant, and where vegetative form and labellar architecture shift together as part of the same response. Across repeated observations, these mechanical and postural character states remain stable and diagnostically informative, while differences in size and color are comparatively labile and secondary.

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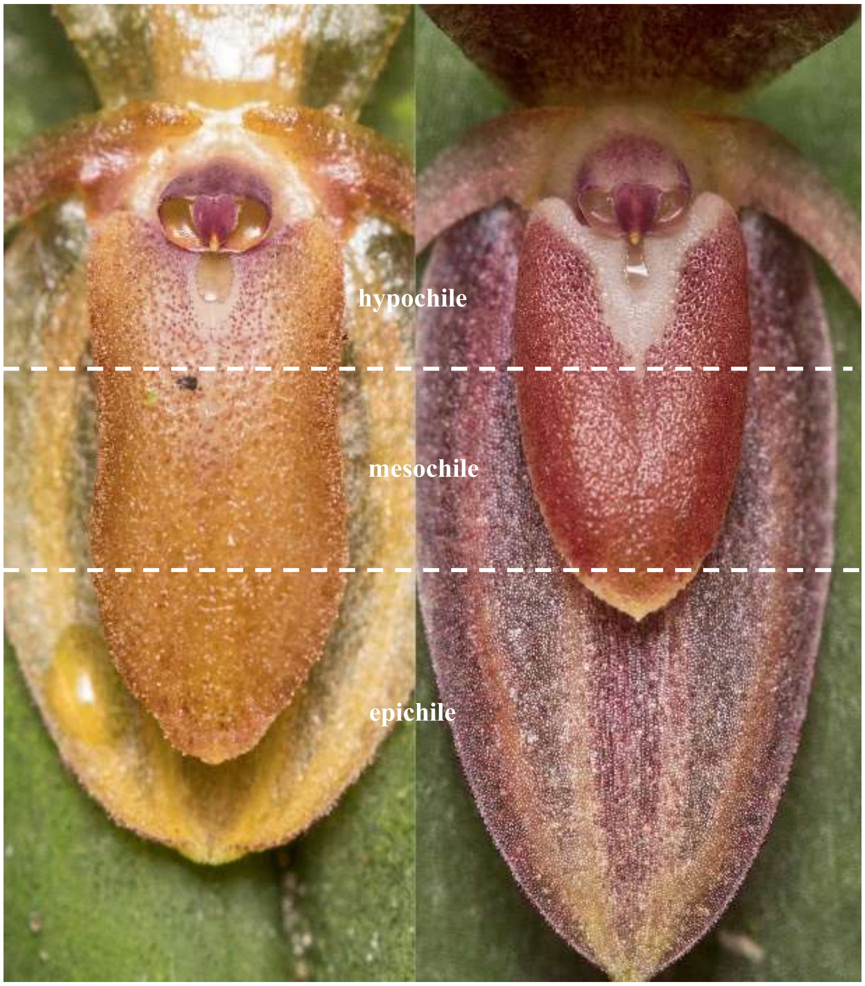
III. *Pleurothallis tremems*, A Relict Species Within Section *Macrophyllae-Fasciculatae*



Orchids are defined, in part, by a flower built on a simple plan: three sepals and three petals. During floral development, protein complexes transform the middle petal into something entirely different, the labellum, or lip.

In most orchids, the lip is large and can be divided into three equal regions, the hypochile at the base, the mesochile in the middle, and the epichile at the apex (Left). In *Macrophyllae-Fasciculatae*, however, the story is strikingly different. In nearly 97% of species, the lip is in some state of degeneration, and almost 5% have lips that are nearly or fully vestigial (Right).

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Pleurothallis tremens is what some might call a "missing link" However, this term is misleading since it implies this one species solves all the mysteries of evolution. More recently, the term "living fossil" would likely be applied, but this term is also misleading since the discovery of this species provides information that could not be interpreted from a fossil.

There are around 60 species of Neotropical *Bulbophyllums*. The species in section *Napellii* have large, convex lips connected by a hinge (A). These species produce nectar at the base of the lip to keep the pollinator on the lip longer, thereby increasing the chances of pollination.

Pleurothallis tremens is one of fourteen species in section *Macrophyllae-Fasciculatae* that still retain a large, erect or suberect, convex lip, held in place by a true hinge (B). In *P. tremens*, nectar is produced in the glenion at the base of the lip, a small reward that likely keeps a visitor on the lip long enough for pollination to occur (C).

In form and function, these flowers echo the lowland, *Bulbophyllum*-like condition, and they most plausibly represent ancestral traits retained through pollinator sharing with the Neotropical *Bulbophyllums*. For that reason, these fourteen species are treated here as the bulbophylliform members of *Macrophyllae-Fasciculatae*.

Bulbophyllum is considered the most successful genus in the *Orchidaceae*. Yet in the Northern Andes, only six Neotropical *Bulbophyllum* species are recorded. In the same landscape, *Pleurothallis* section *Macrophyllae-Fasciculatae* outnumbers them by roughly 57 to 1. If the flowers can look so similar at a glance, the question becomes unavoidable: what made *Macrophyllae-Fasciculatae* so much more successful here?

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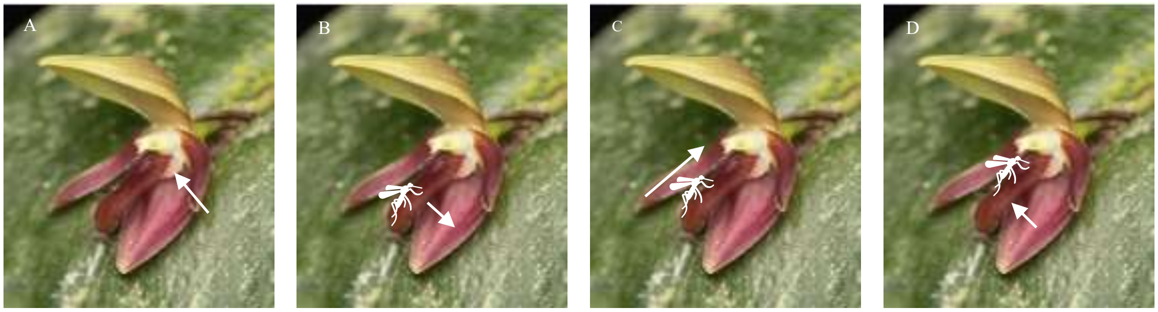

P. tremens is a relict species. It is the only known surviving ancestral species because it is the only species in section *Macrophyllae-Fasciculatae* with a bulbophylliform pollination mechanism.

In bulbophylliform pollination mechanisms, the lip is very loosely connected to the column foot by a hinge (A). The weight of the pollinator causes the lip to drop toward the synsepal (B). As the pollinator crawls up the lip toward the nectar-filled glenion (C), the lip snaps back into position, forcing the pollinator up against the column (D).

Bulbophylliform pollination mechanisms work best where the air is calm, with wind speeds of 1.0–1.5 m/s or less. The reason is simple. The lip is freely hinged, so it responds to the slightest breeze. In gusty conditions, a pollinator may struggle to land, and even when it does, it can be thrown off just as easily.

The Northern Andes did not rise overnight. Uplift began around 66 million years ago off the coast of Ecuador. By 22 million years ago, the Andes had already shifted northward and reached what is now Medellín, Colombia. Today, at modern elevations, the Northern Andes experience wind speeds in excess of 3.4 m/s for at least 15 days per month.

As bulbophylliform species migrated westward out of lowland habitats, they collided with a mountain barrier defined not only by topography, but by wind and weather regimes they were not evolved to withstand. The outcome is still visible. Bulbophylliform species are confined to the eastern side of the Andes, and they remain confined to the eastern side today.

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

The labellar degeneration observed in section *Macrophyllae-Fasciculatae* resulted from a series of adaptations to shifting wind and weather regimes across three intervals:

First, as bulbophylliform species moved out of lowland forests and into a highland barrier they were not built for; next, as Northern Andean uplift intensified and new mountain systems rose to the north in Mesoamerica, compounding exposure and selection from two directions; and finally, as cloud-forest conditions became widespread across the Andes and Central America.

Out of that long sequence of pressure and response came an extraordinary result: one of the most morphologically hyperdiverse assemblages in the *Orchidaceae*.

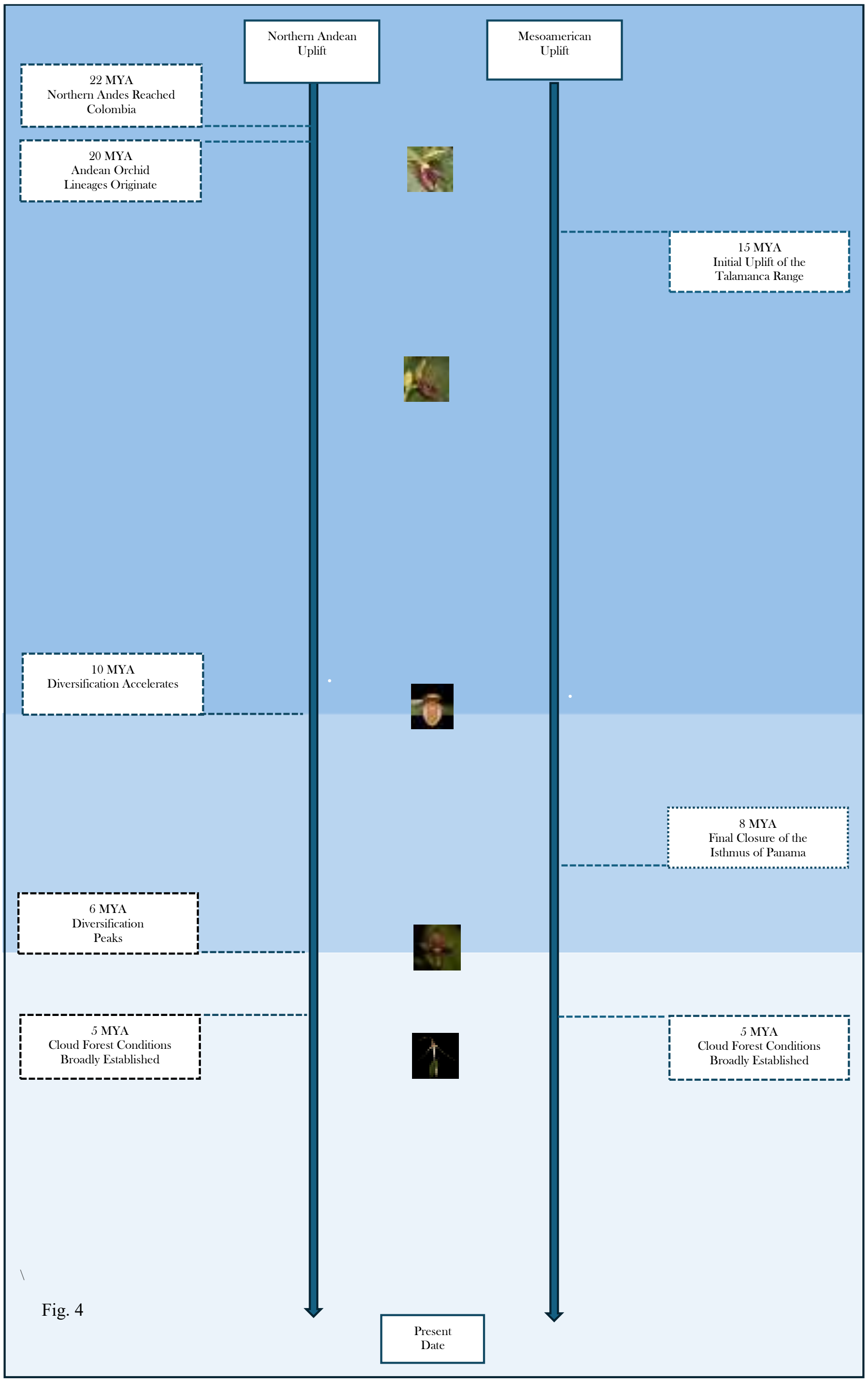

Fig. 4

IV. Rapid Speciation (Early Phase): Lowland-to-Highland Transition

Upon reaching the Andes, bulbophylliform species began to solve a single problem in different ways, by restricting the motion of the hinge that connects the lip to the column foot.

(A) In species with erect lips, the hinge still has full range of motion, but it has become constricted. The lip does not drop easily, and it now requires more weight before it will move.

(B) Over time, the lip declined into a suberect position, which further limits hinge motion by narrowing the space between the lip and the synsepal. Once the lip sat below a 45-degree angle, some species developed an acute apex (1) and others folded the apical lip margins under (2) to form a crusulum, or “little leg”. Both act like a doorstop to reduce the gap even further.

(C) Ultimately, the lip pressed fully against the synsepal. At that point the hinge was effectively neutralized because there was no longer room for the lip to move. These became the bivalviform species so commonly seen today.

(D) By holding the lip firmly against the synsepal and eliminating hinge movement, these species overcame the limitations of the bulbophylliform pollination mechanism. Pollination could remain reliable despite stronger, more variable winds beyond the eastern slopes, which likely triggered an acceleration of diversification as bivalviform species were able to expand onto the western side of the Northern Andes.

V. Rapid Speciation (Middle Phase): Intensification of Mountain Uplift

After bivalviform species spread onto the western side of the Northern Andes, they entered a landscape still being lifted, broken, and reshaped by ongoing uplift. Even with hinge movement already neutralized, these exposed slopes favored flowers that could hold a pollinator steady under turbulence.

Over time, the lip follows a clear, directional sequence, shifting from convex to planar (A), and then into a concave form (B). With the hinge increasingly stabilized by this posture, the flower becomes mechanically steadier, and that stability opens the door to expansion. Planar forms (C) push into southern Mexico, while the concave forms range farther still, reaching as far north as modern-day Mexico City and extending into the Caribbean islands (D).

D

Not all bivalviform species arrived at the same solution or arrived there at the same time. When bulbophylliform species first met the Andes, they spread along the eastern slope, eventually reaching northward as far as western Venezuela. The mountains themselves rose in pulses, and as wind and weather intensified, natural selection favored quicker, more reliable ways to steady the lip.

In some species, the petals curved upward against gravity and helped hold the lip in place as the lip gradually became smaller (A & B). In others, the lip itself changed shape. Its margins folded into a tight tube, and at the base those revolute edges formed a wedge that limited how far the hinge could move. In some species the petals reinforced the mechanism by curling tightly around the base of the lip, creating a second wedge that locks the first in place (C). Over time, those petals likely became the large, convex structures seen in species such as *Pleurothallis gargantua* (D).

In the bulbophylliform species, *P. mastodon* (E), the petals cradle the lip almost as if in prayer. Its bivalviform descendant, *P. dubbeldamii* (F), decided to let go of the lip, and let it settle onto the synsepal.

In other bulbophylliform species (A), the flower lies flat against the leaf, while the lip stands perpendicular to the ground against the force of gravity. The margins of the leaf fold under at the apex and also at the base where they act as a wedge, neutralizing the hinge as the lip continued to shrink over time, ultimately evolving into species such as *Pleurothallis deflexa* (B), *P. ascera* (C), and *P. tonduzii* (D).

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As the Northern Andes continued their climb toward modern elevations, the mountains of Mesoamerica were also rising to the north. That meant pressure arriving from two directions. Uplift in the south and east reshaped wind, moisture, and exposure, while new highlands in Central America altered the climate and the pathways by which populations could spread.

The shift from an erect to a prostrate lip position occurs incrementally across generations, until the lip consistently presses against the synsepal and the hinge becomes functionally neutralized. Cardiostoliform species appear to have diverged by taking a faster, two-pronged approach through resupination. Resupination lets the plant reposition the lip relative to gravity without reinventing the whole flower.

Instead of reshaping the lip first, the flower can change its function simply by twisting as it develops. A torsion in the bud, guided by gravitropic control, reorients the lip relative to gravity. Once the lip is repositioned, hinge action can be neutralized by posture alone, even before the lip is structurally reduced.

In these species, the bud rotates 180-degrees during floral development and then the pedicle constricts as the bud matures. When the flower finally opens, that constriction holds the lip pointing upward against the pull of gravity, as the lip shrinks over time.

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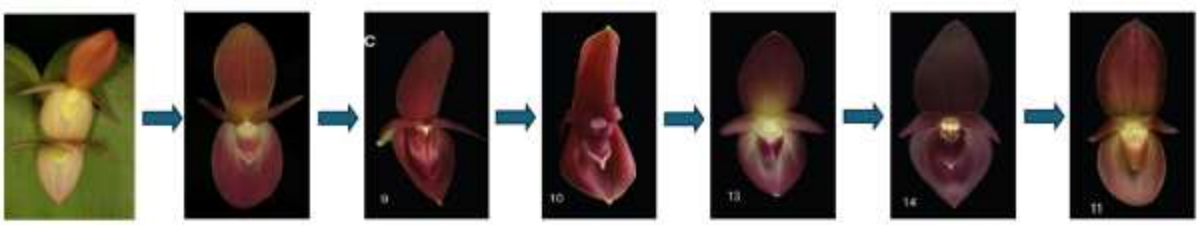
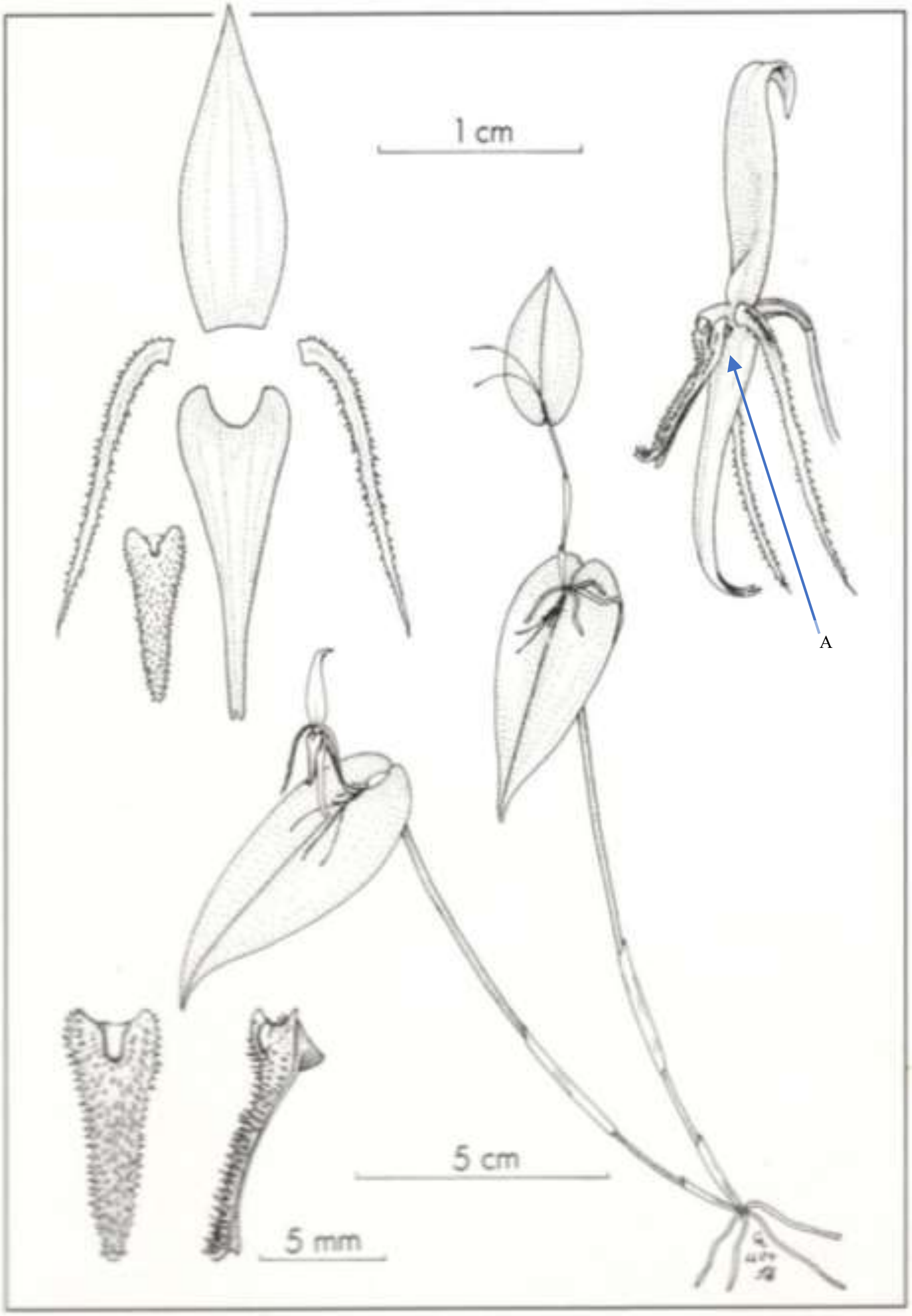


P. titan *P. titan fma. ascendipetala* *P. callosa* *P . cardiothallis* *P. scotinantha* *P. oncoglossa* *P. gonzaleziorium*

By the end of the middle phase of diversification all species in *Macrophyllae-Fasciculatae* had evolved lips that were securely pressed against the synsepal and neutralized the hinge completely. Winds were no longer a threat and diversification peaked. The pattern shifts from reshaping the lip to shrinking it.

In the *Pleurothallis titan* group, the large, concave lip of the progenitor (*P. titan*) is followed by derivatives with progressively reduced lips, culminating in *P. gonzaleziorum*, which retains only the hypochile. This group also includes species like *P. calceolaris* and *P. cyanea*, both of which evolved from a morphotype with a deeply concave sysepal

VI. Rapid Speciation (Late Phase): Arrival of Cloud Forests Conditions



Pleurothallis killipii, with its large flowers atop an erect pedicel has always been an outlier in *Macrophyllae-Fasciculatae*. However, that isn't the only thing that makes it stand out.

In bivalviform species, the lip slowly dropped from erect to suberect until it finally settled against the synsepal neutralizing the hinge. Cardiostoliform species employed resupination to neutralize the hinge while the lip shrunk over time.

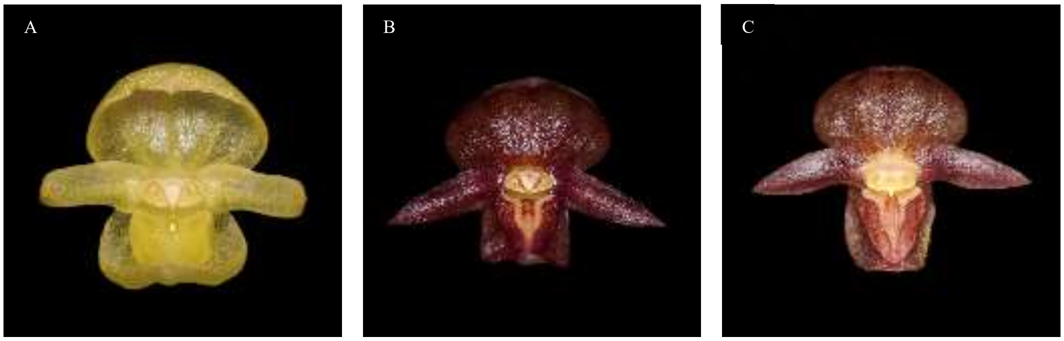
P.killipii appears to have taken an even quicker route. Instead of "dropping" into place, the lip seems to mesh into the synsepal from the base downward, like a zipper being closed. The first contact is made at the base (A), where the hinge would normally pivot.

Once the base is pressed into position, the hinge is fully neutralized. The lip becomes anchored, then progressively seated more completely, until it lies firmly against the synsepal.

Once the lip became fully pressed against the synsepal, it continued to degenerate and at the same time the pedicel began to elongate.

As cloud forests became more widespread in both the Northern Andes and Mesoamerica, a new pressure took over. Water. In these forests, plants stay constantly wet due to fog, drizzle, and cloud drip, not just by rainstorms.

In *Pleurothallis killipii*, the shift toward the amphygiiform condition reads like a direct response to that wet world. The once-erect pedicel becomes arching, and the bloom turns downward. The pendant flower becomes a roof giving pollinators a sheltered space, protected from runoff and splashing, and keeps the reproductive parts functional when everything else is dripping wet.



A deeply concave synsepal can quickly turn into a little reservoir. In response, cardiostoliform species began to open the flower, flattening the architecture so rain and cloud drip cannot sit and linger.

You can see the sequence in the *Pleurothallis sphaerantha* group. In *P. sphaerantha*, the orbicular flower still has deep, concave sepals (A). In *P. pseudosphaerantha*, the dorsal sepal becomes shallowly concave, and the synsepal reflexes, exposing the lip while also shedding water before it can pool (B). In an undescribed *P. pseudosphaerantha* morphotype, the trend continues. The dorsal sepal approaches a nearly convex shape, and the petals and synsepal begin to echo the flatter, more open look seen in species allied to *P. lilijae*.

At the same time, the reward system shifts. Many pollinators are not graceful hoverers. They crawl and probe. The glenion enlarges and gives way to a broad, nectar-filled labellar sulcus, an adaptation that likely keeps the pollinator in place longer and increases the odds that a visit ends in pollination.

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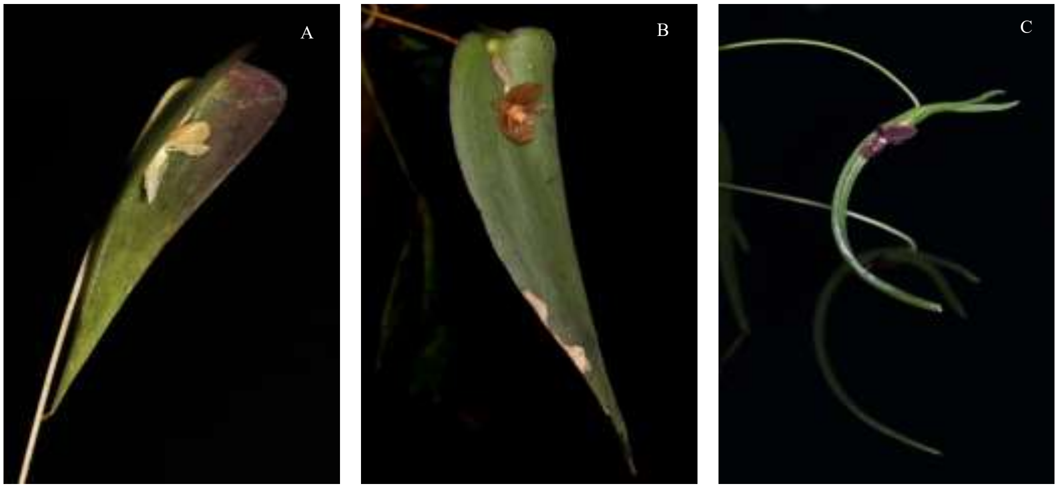

In addition, the leaf becomes architecture. In *Pleurothallis andreaskayi*, (A) the ramicaul leans forward, the leaf forms a shallow concavity, and the flower faces the ground, tucked beneath its own canopy. In species like *P. equipedites* (B), the leaves became pendant, and a flower held close against the surface sheds water cleanly instead of allowing it to pool in the lip. In *P. dilemma* (C) arching ramicauls again turn the flower downward. As the leaves reduce in size, they begin to serve two advantages at once: they retain moisture in colder conditions, and they offer less resistance to the wind, so the plant moves less, and the flower stays steadier when rainy weather closes in.

Cardiostoliform species evolved three additional kinds of resupination. In one pattern, the bud makes a full 360-degree rotation during development and ends exactly where it began (A). Functionally, that detail matters, because it helps keep water from pooling in the lip.

In other species, the pedicel constricts and pulls the developing flower forward (B). In another, the bud rotates 180 degrees, the pedicel extends, and then the bud rotates another 180 degrees so the flower ends up facing backward (C). The effect is the same each time: the lip is positioned beneath the flower, creating a sheltered space for the pollinator and reducing the impact of persistent moisture.

Some bivalviform species seem to borrow from their amphygiiform relatives. As the pedicel lengthens (Top), the flower tips over the edge of the leaf and hangs downward (Bottom). The pendant flower faces the ground and becomes a sheltered space where pollinators can land and feed away from the worst of the wind and rain.

Resupination appears again in some bivalviform species. The small glenion gives way to a broader, nectar-filled labellar sulcus, and the bud turns through a full circle, ending where it began, a simple maneuver that helps keep water from lingering on the lip.

Other bivalviform species evolved cruciform flowers that lie flat against the leaf, with the lip pressed tightly to the synsepal and a flattened, simplified column. When the column is flush and exposed cavities are reduced, there is less opportunity for droplets to sit on the reproductive parts and interfere with pollinia transfer.

In around 5% of *Macrophyllae-Fasciculatae* species, diversification reaches its most extreme endpoint in its war with water. The lip, once a gigantic landing platform, continues to shrink until it is scarcely there at all.

In some cardiostoliform species (A & B), as the lip diminishes, the basal lobes (1) rise up, flanking the column and curve inward, eventually wrapping around the column, until the lip is reduced to a vestige. In some bivalviform species (C), the lip shrinks, the hinge degenerates, and the structure eventually fuses to the column foot. Finally, in some amphygiiform species, the final step is taken. The lip is eliminated entirely.

VII. Subspecies

A subspecies, in the usual sense, is a regional expression, a population set apart by geography and shaped by isolation. That is not what the living record shows here.

These are not rare edge forms tucked behind a barrier. In several cases, the “subspecies” is the common face of the plant, and it is also the form most frequently documented in the field, including on iNaturalist. The clearest, barrier-bound pattern belongs to the ancestral bulbophylliform group, the only set that remains predictably confined by geography. Across *Macrophyllae-Fasciculatae*, “subspecies” fails to describe what is actually happening in nature.

In the *Pleurothallis microcardia* complex, Luer treats *P. microcardia* as a frequent, wide-ranging Andean entity with a broad morphological envelope, then holds several geographically patterned extremes inside that same concept as subspecies or “mere variations.” He emphasizes that the core flower plan remains recognizable even as leaf shape shifts and the proportions and placement of the flower change. He also points to outlying expressions that look distinct, including forms with threadlike petals whose tips curl around the leaf margins, flowers positioned higher on the leaf surface rather than centered at the base, and dorsal sepals that become exceptionally long.

Under a strictly bifurcating lens, that combination, a persistent “common” center plus multiple local extremes that still intergrade with, or “approach,” the core, is treated as an overgrown cloud of variation within one species. Under the framework advanced here, it reads differently.

It looks like layered lineages, a long-lived progenitor spread across a broad range, with localized derivatives repeatedly appearing while still retaining the same basic floral theme. Luer’s decision to park these derivatives as subspecies or extremes is not evidence that the group is merely “highly variable.” It is evidence that multiple lineages are being compressed into a single, overly broad *microcardia* concept.

The same tension appears in *Pleurothallis cordata* sensu lato. Luer acknowledges that multiple recognizable entities are mixed together, and he treats them as subspecies because intermediate flowers are not uncommon. In the interpretation used here, that mixture is not just a classificatory inconvenience. It is what you expect when a persistent ancestral form continues to coexist alongside close derivatives, similar enough in overall architecture to be dismissed as “variations,” even when they represent distinct lineages.

For that reason, subspecies is a poor fit for what Luer describes. A subspecies label typically implies one species expressed differently in different places, with a geographic gradient and without stable functional separation. The pattern here is not a single species grading smoothly across a landscape.

It is a set of coexisting lineages clustered under one name because the general flower plan is familiar and intermediates exist. In this framework, intermediates do not force a subspecies interpretation. They are expected where a persisting progenitor repeatedly produces derivatives that retain the same theme while diverging in a small number of mechanically meaningful characters.

Species relegated to subspecies, and later to synonymy, are not “lesser names.” In many cases, they represent valid, distinct species that have been repeatedly misidentified, lumped, or minimized by an overly broad species concept.

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VIII. Hybridization

Natural hybridization has long been suspected among species in section *Macrophyllae-Fasciculatae*. Interbreeding between two distinct species can produce hybrid offspring and, in some cases, hybrid species. Hybridization is often suggested as one mechanism that can accompany, or even accelerate, the production of closely related derivatives through budding speciation. In a group this diverse, however, these evolutionary processes can blur into the same visible outcome.

This is also where DNA is often raised as the solution. However, without broad sampling, including the intermediate forms that would connect one morphotype to the next, DNA can sometimes tell you that something is mixed, but it cannot reliably reconstruct the full history that produced the mixture, or separate hybrid signal from the layered overlap produced by budding.

In April 2016, an aberrant form of *Pleurothallis sphaerantha* was documented on flickr by Andreas Kay. Given the pattern seen elsewhere in this group, it is highly likely that the plant photographed was not simply an odd “variant,” but a natural hybrid.

The photographs of this suspected hybrid were examined to see whether it could be an unusual form of *Pleurothallis sphaerantha*. But when the flower was studied closely, the story changed. Its floral structure did not match *P. sphaerantha* at all, and the differences were not minor, they were fundamental.

All signs suggest this plant is a natural hybrid between *Pleurothallis pseudosphaerantha* and a second species closely allied to *Pleurothallis erythrium*. That interpretation is grounded in field context, because both candidate parents occur in the same area where the putative hybrid was photographed. The plant itself also tells the story, showing a blend of traits in both flower and vegetative habit that fall neatly between the two.

One specimen at the Atlanta Botanical Garden does not resemble any described species in *Macrophyllae-Fasciculatae*, and it does not settle into any of the morphotypes seen elsewhere in this study. Instead, it carries a mixed set of characters that never resolves into a coherent pattern.

The plant was confirmed to be a spontaneous hybrid that had been found growing on the site of an orchid nursery in Ecuador. Shortly after that confirmation, it was described as *Pleurothallis marioportillae*. It is unfortunate that hybrid material was treated as a distinct species, but in a strange way it provides something useful: a living reference point for what hybridization looks like in this group when it is caught in the act.

A morphotype, once established, repeats. It has an internal consistency. Across multiple plants and across geography, the same character package shows up again and again, especially in the lip, where the diagnostic architecture is concentrated.

When a specimen does not fall easily into any of the morphotypes, the simplest and most logical explanation is that it is the product of hybridization. It remains a hypothesis, but it is a useful one, especially in nursery settings where many closely related species flower in close proximity to each other and natural populations may occur nearby.

What is striking is how rarely this turns into accidental seed set under ex situ cultivation. Over a fifteen-year interval in enclosed growing conditions, where fungus gnats are commonly present on flowering plants, only a single capsule formed spontaneously. The same pattern is echoed under institutional care. At the Atlanta Botanical Garden, capsules are removed unless they result from hand pollination, yet spontaneous capsule formation is described as uncommon, and removals are rarely required.

It would be easy to assume that some species in *Macrophyllae-Fasciculatae* are cryptic. Cryptic species are distinct species that are difficult or impossible to separate by morphology alone and are often revealed through molecular work. However, in a system shaped by budding speciation, a genetic split does not automatically mean two species, and a lack of genetic separation does not automatically mean one species, especially when lineages overlap, persist, and bud repeatedly.

Many species in *Macrophyllae-Fasciculatae*, and in *Pleurothallidinae* more broadly, appear to reproduce primarily by outcrossing. In practical terms, successful capsule set often depends on pollen from another unrelated individual.

In addition, it appears that many species in *Macrophyllae-Fasciculatae* may rely on selectivity to prevent hybridization. Timing, scent, and the precise moment a reward is offered can act like a gate, drawing in the right visitor while neighboring flowers, sometimes only inches away, are effectively ignored.

Nectar is not simply a reward. It can be a retention mechanism, keeping the insect on the lip long enough for pollen transfer under shifting environmental constraints. Some species in *Macrophyllae-Fasciculatae* have lips with a nectar-secreting epithelium, a feature also present in Neotropical *Bulbophyllums*. Some species begin producing nectar as soon as the flower opens.

Scan, tap, or click the QR code to see a pollinator on the species in the image above.

However, *Pleurothallis perfusa* does not produce a significant amount of nectar until the third day of anthesis, while the flower remains viable for only about five days, suggesting that reward presentation can be delayed and tightly timed.

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Detectable fragrance is uncommon in this section, but at least one undescribed Colombian species observed in cultivation produces a light rose fragrance. Scent may be especially important when the goal is to recruit a very specific kind of small fly.

Some orchids, such as *Dracula*, are known to lure fungus-visiting flies by mimicking mushroom cues, including odor. If similar scent targeting occurs here, it would help explain why similar flowers can remain reproductively separate even when they grow side by side.

There may be natural hybrids in this section. There may be cryptic species as well. The problem is not whether those things can happen. The problem is what the evidence can actually resolve.

In *Macrophyllae-Fasciculatae*, the structure is overlapping ancestor–descendant continuity, not a clean series of splits. With much of the Northern Andean forest gone, many of the intermediate forms that would connect one population to the next were likely lost before they could ever be collected or sequenced. Under those constraints, DNA cannot reliably sort hybrid signal from shared ancestry, and it cannot reliably distinguish cryptic species from incomplete sampling.

In this system, molecular data can add noise as easily as it adds clarity. For that reason, the working evidence must remain morphological, grounded in repeatable floral characters that can be observed, compared, and verified in living plants.

Direct pollination research in this group remains limited, but the existence of a documented nocturnal fungus-gnat pollination system involving fragrance and nectar rewards and prolonged insect visitation shows that time-structured attraction and retention are biologically plausible and should be taken seriously as a barrier to hybridization.

XI. Intraspecific Variation

There is no consensus among taxonomists regarding a standard definition of intraspecific variation in *Pleurothallidinae*. In botany, intraspecific variation generally refers to phenotypic or genetic differences among individuals of the same species, such as size, color, or minor proportional shifts.

The difficulty is that species in *Macrophyllae-Fasciculatae* often show differences that are not merely cosmetic but appear to track directional change across populations. At what point is a trait no longer just "variation," but evidence of a distinct, repeatable form with evolutionary significance?

P. titan

P. callosa

P. titan

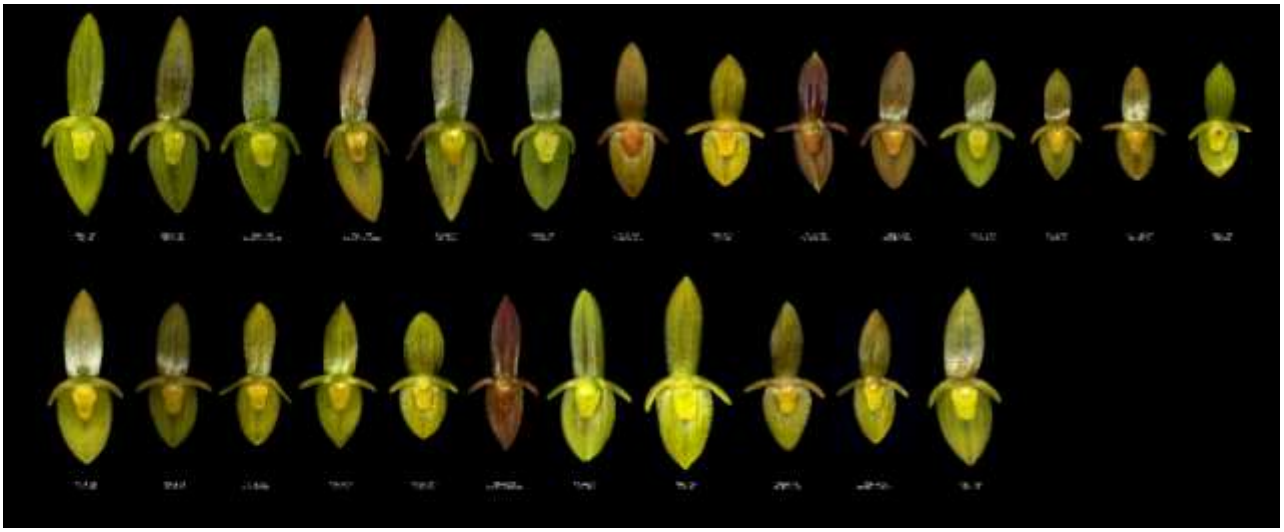
P. titan fma. ascendipetala

P. titan fma. ascendipetala

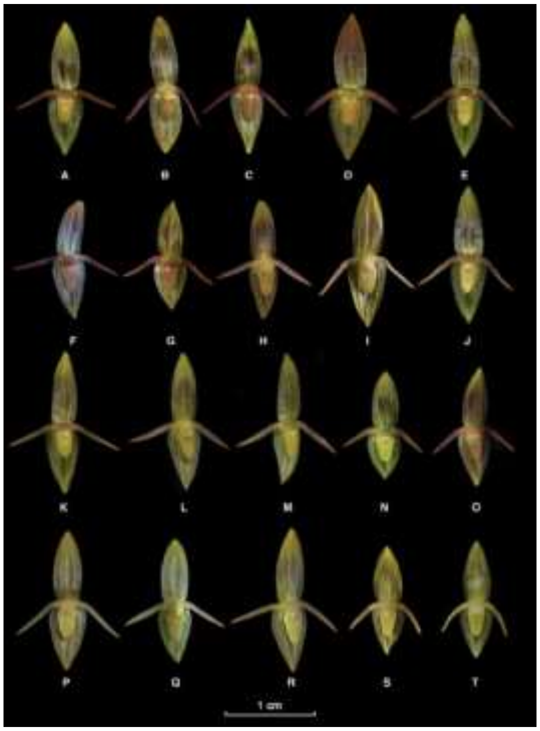
P. cardiothallis

For example, *P. titan* typically has descending (pointing down) petals. However, a form of *P.titan* was found in Colombia with the same basic flower shape but the petals are ascending (pointing up).

Not every derivative becomes a new species, but many become distinct forms, and those forms matter. They give biologists a character they can track, compare, and test across geography. In this case, the ascending petals look like an early step toward the fully reflexed petals seen in *P. cardiothallis*, a small change that hints at where the lineage is headed next.



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, or intraspecific variation.



They completed a similar sampling with *P. winkeliana* in 2025. In all 20 populations of *P. winkeliana*, the petals and sepals varied significantly in size, shape, and color. The lip also varied in size and color. Once again, in all populations, the shape and position of the lip are the same.

We can use music as a guide here. 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 *Macrophyllae-Fasciculatae*, 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, intraspecific variation in *Macrophyllae-Fasciculatae* is common, but subtle.

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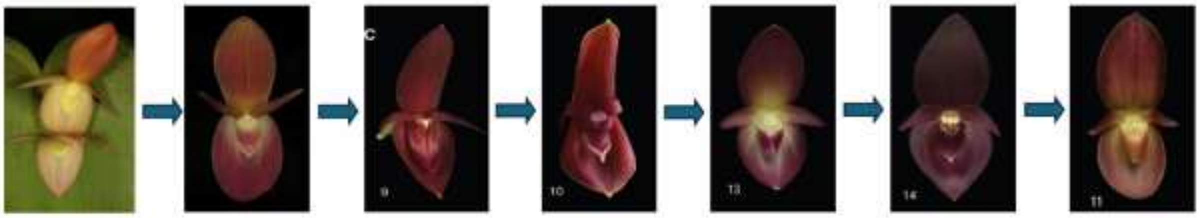
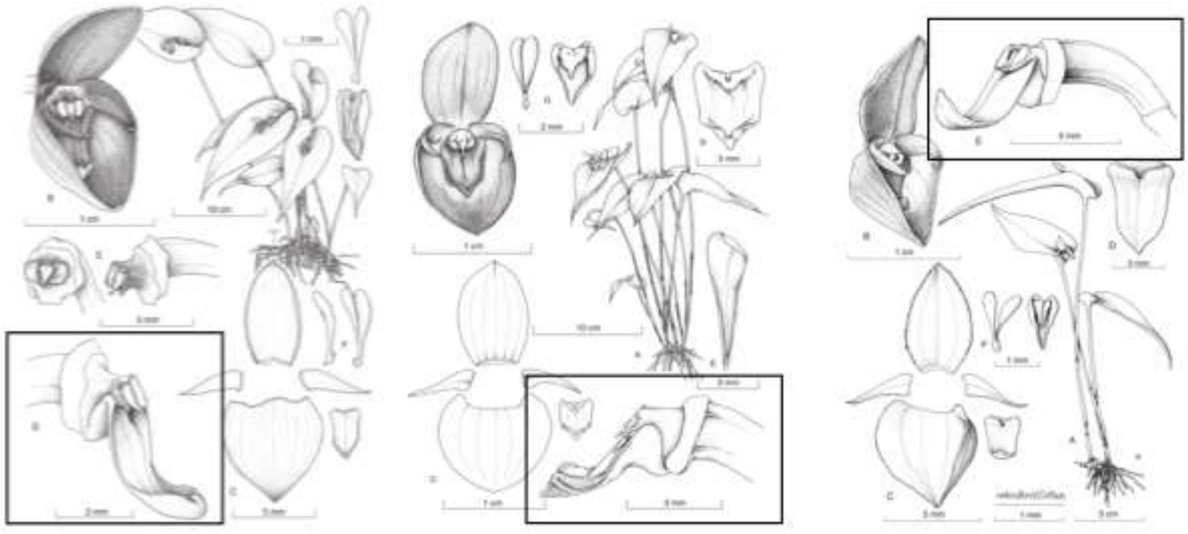
X. Costa Rica, A Hotspot of Budding Speciation

Costa Rica is a hot spot for evidence of budding speciation. In 2021, Pupulin et al. published a study on the Flora of Costa Rica focused on the *Pleurothallis cardiothallis* and *P. phyllocardia* groups. They examined diversity, general and floral ecology, color dimorphism, and natural hybridization to address systematic significance.

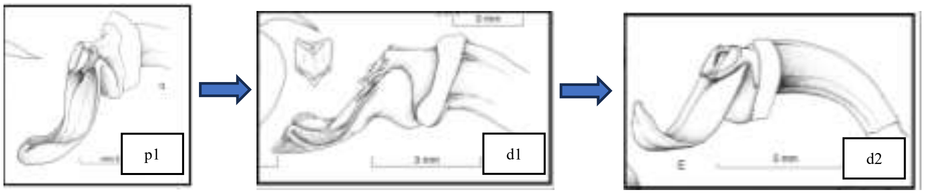


P. titan *P. titan fma. ascendipetala* *P. callosa* *P . cardiothallis* *P. scotinantha* *P. oncoglossa* *P. gonzaleziorium*

However, what stands out on the page is not random variation These photographs read like a sequence, with multiple distinct species separating from *Pleurothallis titan* while still retaining the same basic floral theme.



The three published illustrations of *Pleurothallis navisepala* capture the same kind of directional shift in the labellum that is easy to miss when a species is treated as a single “variable” concept.



In the Pupulin 8435 illustration (A), the lip is distinctly concave, with a clear, functional bowl-like profile. In the Zúñiga 174 illustration (B), that same profile appears shortened and less deeply concave, as if the original architecture is being reduced rather than replaced. In the Pupulin 8028 illustration (C), the lip is essentially planar, with any remaining curvature compressed along the midline instead of expressed as a deep concavity.

Read together, these drawings do not look like random variation. They read like a coherent sequence, concave to shallowly-concave to curved-planar, consistent with lineage layering, where a persisting, progenitor-like form coexists alongside one or more derivatives that retain the same basic design in progressively reduced, more degenerate states.

However, in Costa Rica, one species in particular, *Pleurothallis sanchoi* (A), is the face of budding speciation. You see, *P. sanchoi*, like a familiar 1960's American TV show about a witch (or genie, if you prefer), has a wacky, look-alike relative. This relative, *P. nitida* (B) with its flamboyant, fimbriated petals, is from Panama. There have been endless debates arguing whether these are two different species or one variable species.

They are, in fact, separate species, and there is a third species which was relegated to synonomy, *P. gonioglossa*. At this point, the story sounds more like a 1980's daytime talk show because *P. nitida* is the persistent progenitor of both *P. sanchoi* and *P. gonioglossa* as well as several more species. Unlike an 80's TV show, however, the DNA results cannot confirm parentage.

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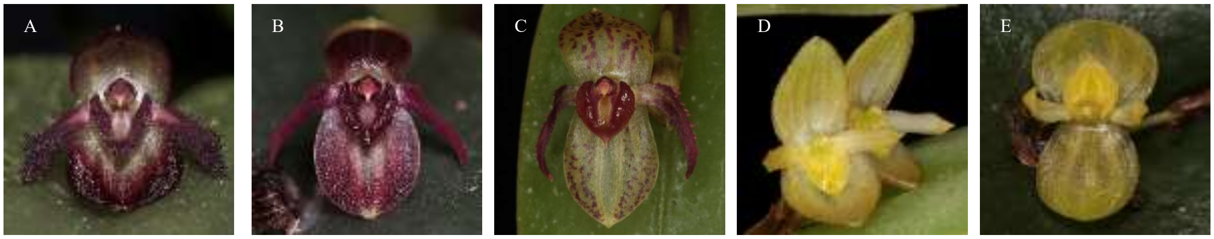

Pleurothallis nitida appears to be a persisting progenitor, with *P. sanchoi*, *P. gonioglossa*, and *P. dorotheae* representing successive derivatives.

When the flowers are viewed in sequence, the progression is unmistakable:

(A) *P. nitida* is, for the most part, a typical resupinate bivalviform species, except the lip has degenerated into a deep labellar sulcus.

(B) *P. sanchoi* abandons the more flamboyant look of its progenitor. The petal fimbriations are lost, and the flower opens wider.

(C) In *P. gonioglossa*, the lip becomes more rounded, and the flower is fully spreading, exposing the labellar sulcus.

(D) With further change, as seen in this undescribed morphotype, the petals shrink, and the labellar sulcus begins to produce nectar.

(E) In *P. dorotheae*, the flower completes a full 360-degree rotation. Under cloud-forest conditions, the synsepal and labellar sulcus would otherwise remain filled with water, interfering with pollination. A non-resupinate presentation solves that problem.

In 2013, Wilson et al. proposed placing these species in a distinct “Mesoamerican clade”. Although there are several morphologically similar South American species such as *P. phymatodea*, the molecular data concluded they were unrelated.

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However, as the preceding sequence shows, the non-resupinate dorotheaeform species did not appear out of nowhere. They evolved from resupinate bivalviform ancestors over many generations.

The South American bivalviform analogs that would complete that sequence are missing from the analysis, and the most likely reason has been stated before. Since only about 25% of Northern Andean forest remains, many of the intermediates were probably lost before they could be collected, photographed, or sequenced.

A second gap appears when the map is drawn from holotype collection data. Between Panama and Colombia, there is a broad corridor from which few, if any, species have been collected. By default, that means the Panama–Colombia corridor and the adjacent northern Andean interfaces were not sampled at all.

Under the speciation structure documented here, those missing intermediates are not incidental. They are the very species that would connect the story across geography. When they are absent, a strictly branching analysis can turn an incomplete chain into the illusion of separate origins.

There is also a practical problem because cultivated material was used in the analysis. When sequences come from cultivated, non-vouchered material, identity can be uncertain, and plants may express differently under greenhouse conditions.

For these reasons, DNA cannot reliably support a distinct Mesoamerican clade. Here, once again, relationships have to be inferred from morphology.

However, this study is valuable, because it captured something remarkable. In stark contrast to the Northern Andes, Costa Rican forest cover has increased substantially, recovering from roughly 25% to around 57%. Panama shows similarly high forest coverage.

Although the study did not sample broadly enough to confirm whether the South American species are closely related, it did show that the Mesoamerican species form a coherent group. Morphology supports the same conclusion. In fact, these species may provide the clearest window we have, a living sequence that helps us peel back the overlapping layers that now make DNA so hard to interpret.

Costa Rica is an example of what can be accomplished through conservation. Where habitat recovers and reconnects, closely related forms such as *P. nitida*, *P. sanchoi*, and *P. gonioglossa* can persist side by side. As their populations expand, intermediates are more likely to be encountered, photographed, and recognized. In practical terms, Costa Rica does not simply "host" diversity, it preserves the continuity that allows these relationships to be seen.

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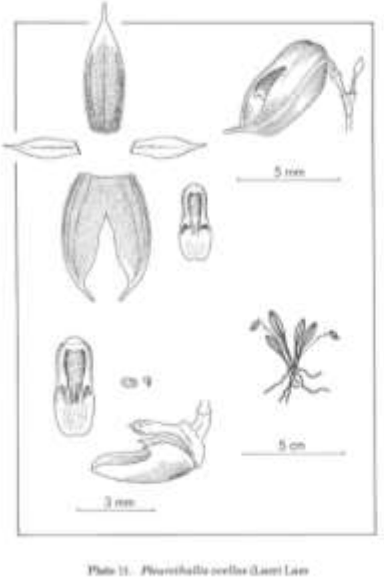
XI. Notes on Other Genera

Evidence of budding speciation is not confined to *Macrophyllae-Fasciculatae*. It shows up across the *Pleurothallidinae*, in genus after genus, when the flowers are compared in sequence rather than in isolation.

In *Pleurothallis anthrax* (subgenus *Ancipitia*), as the concave lip continues to degenerate, small basal lobes start to appear (A). In *P. odobeniceps*, the lip is reduced further, and those basal lobes are pushed upward into hook-like structures (B). In a similar, undescribed species, the lip is essentially vestigial, and the hook-like lobes fold over what remains (C).



In 2022, the genus *Muscarella* was merged into the previously monotypic genus *Andreettaea*. Although the study states that the decision was based on morphological and molecular data, the morphology of the flowers points in different evolutionary directions. The lone *Andreettaea* species has a non-resupinate flower with a concave lip.

However, all 56 *Muscarella* species, as seen in the above photos, have resupinate flowers with loosely hinged, convex lips. Convex, hinged lips came first. It is a different mechanical system altogether. It did not spontaneously appear and it cannot be dismissed as variation. Therefore, *Muscarella* could not have descended from *Andreettaea*, underscoring once again that DNA alone cannot reliably support genus or species boundaries in *Pleurothallidinae*.

In the field, *Lepanthes calodictyon* (Left) and *L. tentaculata* (Right) do not behave like two distinct species. They are reported growing together, sometimes side by side, in the same light, the same moisture, the same thin strip of habitat where differences, if they are real, should be easy to support.

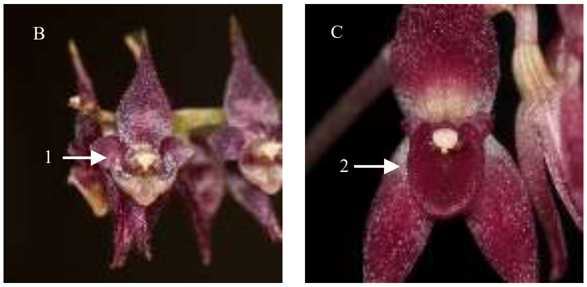
Even Luer's own account leans in that direction. He notes that *L. tentaculata* is often found in association with *L. calodictyon*, and he points to a short list of traits to justify keeping the names apart, including rounder, reticulated leaves, longer filiform petal processes, and a tiny, heart-shaped lip tucked beneath the column.

But those characters read less like a hard boundary and more like two faces of the same species. When two named species share the same ground, and the supposed diagnostics look like variations on a common design, the pattern is exactly what budding speciation tends to leave behind: a persisting progenitor accompanied by a derivative expression, close enough in overall architecture to be mistaken for "variation," yet distinct enough to be noticed, named, and argued over.

In that light, *L. calodictyon* and *L. tentaculata* look more like two morphotypes occupying the same forest, at the same time. They are, most likely, the same species.

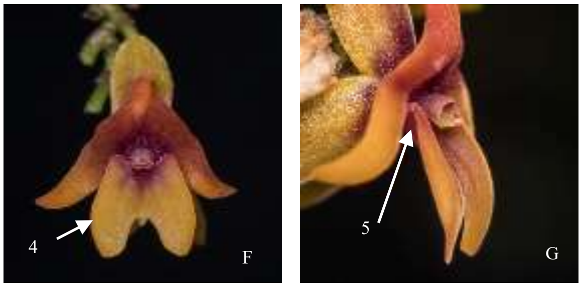
When most people see *Pleurothallis fantastica* (Left) or *P. neossa* (Right) for the first time, they usually remark on their resemblance to *Lepanthes*. That similarity is not coincidental. The simplest explanation is that *Lepanthes* followed much the same directional path of floral evolution seen in section *Macrophyllae-Fasciculatae*.

Trichosalpinx species with erect, convex lips (A) likely split into *Lepanthes* and *Lepanthopsis* through reduction of the lip We don't have to search hard for evidence of transitional traits.



Lepanthopsis species exhibit two primary lip shapes. In *Lepanthopsis prolifera* (B) we can see the basal lobes (1) of the reduced lip beginning to curve up and around the column. The second lip shape can be seen in the disc-shaped lip (2) of *L. melanantha* (C)

The basal lobes in species with lips like *L. prolifera* follow the same directional pattern seen in *P. fantastica*: over time they rise, curl inward, and eventually wrap around the column, forming the structures referred to as the lip blades (3) in most *Lepanthes*, such as *L. acutissima* (D). In other lines, as in *L. melanantha*, the disc-shaped lip continues to degenerate instead, ending in the flat, appressed lip (4) seen in species such as *L. floripecten* (E).



Transitional traits are even more obvious in *Lepanthes domingensis* (F). *L. domingensis* has a highly degeneraed, large, convex lip (4), and if you look closely, an appendage-like nub is already present, which will eventually become the appendix. For additional supporting evidence, look at the lip from the side (G) and the transition becomes even clearer: the basal lobes (5) are already beginning to rise and flank the column. Over time, those basal lobes become the lip blades

To understand how species such as *Lepanthes isosceles* (H) could lose the lip entirely, we only have to look at *Pleurothallis kaynagatae* (I), where reduction has been carried to the same endpoint.

This study demonstrates that these diagnostic characters are not confined to section *Macrophyllae-Fasciculatae*. They recur across the *Pleurothallidinae*, suggesting a broadly shared directional pattern of floral evolution within the subtribe. For that reason, these repeatable, field-verifiable floral mechanics are treated here as the primary evidence, ahead of DNA, for diagnosis and for interpreting evolutionary structure in the *Pleurothallidinae*.

XII. DNA Is Not Useless

DNA is not useless. However, future DNA work has to be designed and interpreted differently, with the right expectations, and with the flower kept in the foreground. This is where the framework presented here matters. It does not replace molecular work. It gives molecular work a map.

Instead of sampling a handful of names and hoping the tree will sort them out, future DNA studies can be structured around the repeatable mechanical states documented in living plants. In other words, morphology becomes the sampling design, not an afterthought.

A useful study in this system would be organized around three things:

Morphotypes - Sample across the full range of lip posture, hinge outcomes, and presentation states, not as a token checklist, but as the central design. If the hypothesis is directional evolution in mechanical states, then the sampling must cover those states deliberately.

Geographic Structure - Sampling has to follow the geography as faithfully as possible. A few sequences from Costa Rica and a few from Colombia are not enough if the corridor between them is missing. Where the geography is unsampled, conclusions about “separate origin” should be treated as provisional at best.

Multiple Specimens - A single sequence per named species is almost guaranteed to mislead in a system shaped by overlap, persistence, and potential mixing. Repeated sampling within a morphotype across localities is the only way to see whether a pattern is stable, localized, or an artifact.

Future DNA work in *Pleurothallidinae* will be most useful when it starts using the flower as the guide. The characters emphasized here, lip posture, hinge function, resupination, and presentation, are not cosmetic. They describe functional states at the pollination interface, and they recur with enough consistency across the subtribe, and across almost every genus, to be read directly in life.

In practical terms, that means the priority should remain morphological: field-verifiable mechanics first, molecular data second, interpreted through the framework rather than over it. DNA can still contribute, but only when it is sampled broadly, tied to real vouchers, and asks questions the system can actually answer.

This study offers a way forward. It provides a structured field language for recognizing the diversity that still survives, and it provides a sampling blueprint for any future molecular work that aims to test, rather than overwrite, the evolutionary pattern written into these flowers.

XIII. Materials and Methods

This study evaluated evolutionary patterns in *Pleurothallis* Section *Macrophyllae-Fasciculatae* using a combined approach: (1) morphology-first grouping grounded in lip architecture, (2) georeferenced distribution mapping constructed from holotype locality data and country-of-origin records, and (3) large-scale field-observation review using iNaturalist photographs and locality metadata. This design is intended to test whether hyperdiversity is structured by discrete, mechanically interpretable character states and geography, rather than reflecting unbounded within-species variability.

Morphological Grouping Framework

All validly published species were assigned to morphological groups using a standardized set of lip-based characters: (1) lip shape and degree of convexity or degeneration, (2) lip position relative to the synsepal (erect, suberect, or prostrate), and (3) hinge functionality (functional, constrained, or rendered non-functional by lip position and morphology). These characters were selected because the lip is the principal interface between flower and pollinator, and because lip position and hinge behavior represent discrete functional states.

Distribution Mapping and Validation

Distribution maps were constructed from holotype collection locality data for all validly published species. For species lacking usable collection locality data, provisional plotting was performed using country of origin. Country-specific checklists and online databases were cross-referenced to reconcile nomenclature and reported ranges. iNaturalist locality clusters were then compared against the holotype-based maps to identify range confirmation, plausible range extension, or potential misidentification requiring morphological re-check.

Field Observations and Photographic Dataset

A total of 2,908 iNaturalist observations of species in *Macrophyllae-Fasciculatae* were compiled and reviewed. The associated locality metadata were used to validate and refine distribution maps. Approximately 6,936 accompanying photographs were examined for morphology, with emphasis on lip position and lip shape. To supplement the field record, an additional 1,418 photographs from the author's photgraphic portfolio of living plants were reviewed to reinforce diagnostic characters and to evaluate whether key traits remain stable under cultivation.

Each photographic record was assessed for repeatable, mechanically interpretable characters. In this framework, the posture and architecture of the lip define the primary diagnostic "theme," while differences in size and color of the lip, petals, and sepals are treated as secondary variation. Observations were flagged for secondary review when lip position, lip architecture, or hinge behavior departed from the expected pattern for a named species or morphological group, allowing potential misidentifications, discontinuities, and candidate distinct forms to be screened consistently across the dataset.

Hybrid Screening Logic

Candidate hybrids were flagged when the locality context suggested that plausible parent species occur together, and when the flower showed mixed character combinations or exaggerated traits that did not fit the otherwise consistent lip theme observed for that group. Because hybrids in this section often present with amplified or unusual features, extreme forms were not treated as evidence of species-level divergence unless they recurred as a repeatable, geographically structured morphotype.

Synonymy Screening Logic

In this treatment, synonymy is applied only when a published name fails to add any stable, repeatable characters that separate it from an already described species. In other words, two names are treated as the same species when they share the same diagnostic floral architecture, and the supposed differences collapse into posture, size, or minor variation that does not hold consistently across plants. By contrast, plants that show transitional character states, especially along the lip's degeneration sequence, are not treated as synonyms, because transitional structure is evidence of an evolutionary sequence

Plant Material

Living plant material from the author's personal collection was examined. Plants were grown in a modified grow tent with a portable air conditioning unit and humidifier. Plants were cultivated in pots using live red sphagnum moss (*Sphagnum capillifolium*). Maximum daytime temperature was 70°F (21°C) and maximum nighttime temperature was 58°F (14°C). Average humidity was approximately 85%.

Living plant material from Andy's Orchids (Encinitas, California) was also studied and photographed on-site. Plants were grown in an enclosed greenhouse with a maximum daytime temperature of 65°F (15°C) and a maximum nighttime temperature of 50°F (10°C). Average humidity was approximately 85%.

Additional living material from the permanent collection at the Atlanta Botanical Garden was used to compile horticultural notes and diagnostic photographs. The Tropical High Elevation House (THEH) provides an ex-situ naturalistic environment cooled by a commercial air washer. Maximum daytime temperature was 75°F (24°C) and maximum nighttime temperature was 55°F (13°C). Average humidity was approximately 85%.

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XIV. *Pleurothallis* Section *Macrophyllae-Fasciculatae*

This subsection–morphotype structure is presented as an interpretive model of evolutionary structure, not as a formal, rank-level revision.

The morphology and biogeographic structure documented here support uniting *Pleurothallis* section *Macrophyllae-Fasciculatae* with series *Amphygiae* and section *Abortivae*, which should be subdivided into four subsections: *Bulbophylliformae*, *Bivalviformae*, *Cardiostoliformae*, and *Amphygiiformae*.

These subsections can be further divided into sixteen morphotypes listed here in progressive order: bulbophylliform, linguiform, revolutiform, protobivalviform, bivalviform, microcardiiform, cordatiform, cruciform, titaniform, grandifloriform, dorotheaeform, penduliform, cardiostoliform, phyllocardiiform, amphygiiform, and abortiviform

Most of these morphotypes are defined by a shared floral architecture, supported by repeatable suites of characters, including how the lip is presented and how the hinge functions (loose, constrained, or rendered non-functional), together with consistent geographic structure. A smaller number reflect later cloud-forest adaptations, where flower presentation and vegetative form shift together under constant moisture and heavy weather.

At a higher rank, the same pattern, meaning repeatable mechanical characters paired with coherent geographic structure, provides sufficient evidence to warrant resurrecting *Acronia* as a subgenus within *Pleurothallis*. However, that decision would not be confined to *Macrophyllae-Fasciculatae*.

It would reach into adjacent groups and require a broader systematic treatment to reassess boundaries across the genus. For that reason, the subgeneric resurrection is treated here as a supported direction indicated by the data, while the formal changes advanced in this study remain focused on the subsections and morphotypes that can be directly defended from the present evidence base.

Methodological Justification: Resupination and Labellum Mechanics as Systematic Characters

These systematic decisions are grounded in a standardized set of lip-based characters. These characters were selected because the lip is the principal interface between flower and pollinator, and because lip position and hinge behavior represent discrete functional states rather than continuous variation:

(1) lip shape and degree of convexity or degeneration,

(2) lip position relative to the synsepal (erect, suberect, or prostrate), and

(3) hinge functionality (functional, constrained, or rendered non-functional by posture and morphology).

The evidence base used to test repeatability is deliberately field-centered. Distribution maps were built from holotype locality data and then compared against iNaturalist locality clusters to identify confirmations, plausible range extensions, and candidate misidentifications requiring morphological re-check.

In parallel, thousands of photographic records were reviewed with emphasis on lip position, lip shape, and hinge behavior, and each record was assessed for mechanically interpretable characters.

Within this framework, the posture and mechanics of the lip define the primary diagnostic theme, while differences in the size and color of the lip, petals, and sepals are treated as secondary variation. Changes in lip posture and mechanics are diagnostic clues, not variation to be dismissed.

Resupination is a developmental reorientation that determines how the flower presents relative to gravity and to a pollinator, while lip architecture, including concavity versus convexity and the presence of a functional hinge, governs the mechanics of landing, retention, and release during a visit. These traits are not minor proportional shifts. They define different mechanical states, and therefore different pollination interfaces, that are coherent and diagnosable in the field.

This functional-morphological logic also supports higher-rank judgments when a lineage occupies a different mechanical design space. For example, a non-resupinate flower with a concave, non-hinged labellum is not interchangeable with a resupinate flower bearing a loosely hinged, convex labellum. Those architectures imply different gravity orientation, different landing mechanics, and different retention dynamics.

It is implausible to reduce such a shift to simple variation, and it is equally implausible to treat it as a spontaneous, character-level novelty that can be dismissed when molecular results imply otherwise. In *Macrophyllae-Fasciculatae*, where incomplete sampling and lineage persistence can decouple genetic structure from practical, diagnosable boundaries, mechanically grounded floral characters provide a necessary, field-verifiable check on rank decisions.

Taken together, the subsection–morphotype structure proposed here, and the methodological framework that supports it, represent a practical solution to a predictable problem in *Macrophyllae-Fasciculatae*: lineage persistence, repeated budding, and incomplete geographic sampling can produce molecular patterns that are insufficient for delimiting ranks that must remain diagnosable in nature.

Treating lip posture, hinge functionality, and resupination as discrete mechanical states, classification can be anchored to characters that are repeatable, field-verifiable, and directly tied to the pollination interface. On that basis, the changes advanced here remain appropriately confined to what the present evidence can defend, while still indicating the broader systematic directions implied by the same mechanical and biogeographic logic.

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Nomenclatural acts in this article are limited to the description of three new taxa and the resurrection of eight taxa previously relegated to synonomy:

New Taxa (3):

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

Diagnosis: *Pleurothallis elefa* is a revolutiform species. In these species, the revolute margins of the lip form a tight tube which in the case of this species makes the lip resemble an elephant's trunk. The descending, outward curved petals look like tusks.

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

Diagnosis: *Pleurothallis tremens*, is a relict species within section *Macrophyllae-Fasciculatae*, because it is the only surviving ancestral species within the section. *P. tremens* is one of 14 bulbophylliform species which are the ancestors of all *Pleurothallis* species in section *Macrophyllae-Fasciculatae*, and it is the only species in this section with a bulbophylliform pollination mechanism, a suberect, convex lip connected to the column foot by a true hinge.

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

Diagnosis: *Pleurothallis warrenprescottii* is very similar to *P. erythrium*. Both are protobivalviform species with suberect lips. However, *P. warreprescottii* is distinguished by the presence of a crusulum at the apex of the lip. This feature is absent in *P. erythrium*. *P. warrenprescottii's* most significant distinguishing feature is a lip which is covered in nectar droplets. In *P. erythrium*, nectar production is restricted to the glenion. Vegetatively, the two species can be distinguished by the thick, succulent leaves of *P.* warrenprescottii vs. the thin leave of *P. erythrium*

Reinstatement of Accepted Taxa (8):

Pleurothallis archidiaconi (Ames)

Taxonomic Treatment: Accepted species; status reinstated (treated as distinct from the broad *Acronia bivalvis* concept in Icones 27) as defined in sections VII, XIV, and XIV(d) of this publication.

Pleurothallis erymnochila (Luer)

Taxonomic Treatment: Accepted species; status reinstated (treated as distinct from the broad *Acronia bivalvis* concept in Icones 27) as defined in sections VII, XIV, and XIV(d) of this publication.

Pleurothallis exserta (Luer)

Taxonomic Treatment: Accepted species; synonymy reversed (error-correction). Icones 27 baseline being reversed: Luer treats *Pleurothallis exserta* as a synonym under *Acronia diabolica*. *P. exserta* can be distinguished from *P. diabolica* due to major differences in plant size and flower size. In addition, *P. exserta* uses retrotorsion during bud development; *P. diabolica* does not. These diagnostioc differences are based on the illustrations of both species and by verified photographs of both taxa.

Pleurothallis gonioglossa (Schltr)

Taxonomic Treatment: Accepted species; synonymy reversed (error-correction) as defined in section XII of this publication.

Pleurothallis ignivomi (Schltr)

Taxonomic Treatment: Accepted species; status reinstated (treated as distinct from the broad *Acronia bivalvis* concept in Icones 27) as defined in section XII of this publication.

Pleurothallis monocardia (Rchb.f.)

Taxonomic Treatment: Accepted species; status reinstated (treated as distinct from the broad *Acronia bivalvis* concept in Icones 27) as defined in sections VII, XIV, and XIV(d) of this publication.

Pleurothallis rhopalocarpa (Schltr.)

Taxonomic Treatment: Accepted species; status reinstated (treated as distinct from the broad *Acronia bivalvis* concept in Icones 27) as defined in sections VII, XIV, and XIV(d) of this publication.

Pleurothallis embreei (Luer & Hirtz)

Taxonomic Treatment: Accepted species; synonymy reversed (error-correction). Icones 27 baseline being reversed:

Luer's decision to treat *Pleurothallis embreei* as a synonym of *Acronia cedrinorum* was based on protologues and illustrations that erroneously contained mismatched information for three unrelated species. The Icones 27 composite illustration for *P. calogramma* uses the correct flower for *P. calogramma* but the habit drawing of *P. embreei*. Luer then uses the flower and habit of *P. embreei* as the representation for *P. cedrinorum* (habit drawings identical across plates). *P. cedrinorum* has a concave-lip versus the convex lip of *P. embreei*. The result is downstream misidentification consequences on iNaturalist (forced misapplication to *P. calogramma* due to non-acceptance).

The following taxonomic treatments are not nomenclatural acts, but were used for the purpose of the species total used in this paper only:

Putative Hybrids Elevated to Species Rank (2):

Pleurothallis ×subversa (Pupulin & Bogarín)

Taxonomic Treatment: the taxon is treated here at species rank as *Pleurothallis subversa*.

Pleurothallis ×subversa was published as a putative natural hybrid, named for its "subverted" floral orientation, a direct reference to its nonresupinate presentation. The protologue diagnoses it cleanly by a combination that does not read as "blurred intermediacy" in the field: relatively large plants with narrowly ovate-lanceolate leaves, cordate at the base; a truly pendent, partially reflexed, nonresupinate flower; bronze sepals and red petals; and a white lip flushed bright red toward the apex and margins. The authors further note that the overall stance and leaf texture strongly recall *P. compressa*, and they propose *P. compressa* as one parent, with the second parent likely being a large-flowered species close to *P. cardiothallis* (with *P. cardiothallis* and *P. oncoglossa* both discussed as plausible candidates in the region). For this treatment, the decisive point is practical and morphological: the diagnostic traits cited in the protologue are repeatable and separable, and they give the plant a stable identity that can be recognized without a genetic argument.

Pleurothallis ×karremansiana (Pupulin, J. Aguilar & M. Díaz)

Taxonomic Treatment: the taxon is treated here at species rank as *Pleurothallis karremansiana* .

Pleurothallis ×karremansiana was published as a putative natural hybrid, interpreted as the product of *P. tonduzii* and *P. gonzaleziorum* occurring together at Bosque de Paz. The protologue's "hybrid" diagnosis, however, is built on a tight, internally consistent character package that is both recognizable and usable: cordate, narrowly ovate, matte leaves; purple flowers with broadly ovate, arched, inflexed sepals; narrowly triangular-subfalcate petals; and a pandurate lip with a glenion deeply recessed between thickened basal lobes. In lip architecture specifically, the same coherence holds, the lip is described as conduplicate with a central depression, convex margins slightly folded under, and a subterminal constriction that ends in a terminal lobule. Most importantly, the authors report a second individual found growing in the wild at Bosque de Paz, allowing them to discard the idea that it represents a one-off garden hybrid. Because the diagnostic characters emphasized in the protologue form a repeatable, determinate morphology rather than a transient "mix,"

Excluded From the Species Count as Likely Nursery Hybrids (2):

Pleurothallis gigiportillae (Doucette & Portilla)

Taxonomic Treatment**:** *Excluded as a likely nursery hybrid (greenhouse-origin material), not accepted as a species here.*

This name enters the literature with a built-in problem: it is based on cultivated material without a specific wild locality. The type is explicitly reported as "without specific locality," and as having flowered in cultivation at the Ecuagenera Orchid Nursery. That is exactly the context where hybrid material is most likely to surface, circulate, and later be mistaken for a "unique" species.

The flower itself reads like a mismatch of signals. The plant presents large, strongly convex petals, a look that in a grandifloriform build would normally interfere with hinge mechanics and constrain lip function, yet here the petals remain free while the lip is described as strongly reduced (including a pubescent, detrorse apex) and the column-foot condition is unusual enough that the authors themselves note it as difficult to place. In other words, the character package does not settle into a coherent mechanical plan that repeats across a known lineage.

On the evidence standard used throughout this study, that combination is not something we can safely treat as "unique." In this group, a real morphotype repeats, it shows up again in other plants, and it carries a consistent lip state, hinge outcome, and sepal posture across geography. *P. gigiportillae* does not match any described species, does not fall into any established morphotype, and no comparable wild material has surfaced through field observation in a way that would demonstrate a repeating, geographically structured form.

For these reasons, Pleurothallis gigiportillae is treated here as likely nursery-origin hybrid material and is excluded from the species count, pending evidence of stable repetition in the wild.

Pleurothallis marioportillae (Doucette, Medina & Portilla)

Taxonomic Treatment**:** *Excluded as a likely nursery hybrid (greenhouse-origin material), not accepted as a species here.*

This specimen does not resemble any described species in section *Macrophyllae-Fasciculatae*, and it does not settle into any of the morphotypes documented across this study. Instead, the flower has a Frankenstein quality, a stitched-together look, as if different parts were borrowed from different templates. The character set is mixed, and it stays mixed. The published description frames the plant as wild-rescue material gathered under an Ecuadorian ex situ authorization, with the type said to have flowered in cultivation at Ecuagenera, and the species reported as known only from the type locality.

However, research concluded it originated on the site of an orchid nursery and was recognized as a spontaneous hybrid before the name was published. On the evidence standard used throughout this treatment, that matters. In this group, a morphotype, once real, repeats. It has internal consistency, and it shows up again across multiple plants, often across geography, in the same core character package. When a plant will not settle into any morphotype, and when its traits read as a mosaic rather than a coherent plan, the most conservative interpretation is hybrid origin.

That interpretation is also strengthened by absence. No comparable plant has surfaced in field photographs, in cultivation records with reliable locality context, or in the broader comparative record assembled for this work. In other words, *marioportillae* does not behave like a lineage with a stable, repeatable character set. It behaves like a one-off assembly.

For these reasons, *Pleurothallis marioportillae* is treated here as likely hybrid material of nursery origin, and it is excluded from the species count pending clear evidence of a repeating, geographically structured morphotype in the wild.

To Be Relegated to Synonymy (2):

Pleurothallis pudica (Karremans)

Taxonomic Treatment: *Pleurothallis pudica* is treated here as a synonym of *P. phyllocardia* because the distinguishing character emphasized in the original account is not diagnostic. The protologue frames *P. pudica* around a "shy" presentation, with the flower turning toward the leaf and "hiding," and it highlights the downward, reclining posture of the bloom. However, that posture is already part of the character set used to recognize *P. phyllocardia*, whose flowers are likewise described as reclining toward the leaves due to a downward-bent peduncle. A cluster of supporting characters (smaller habit, rounder and flatter flowers, shorter petals, and a more rectangular lip) do not establish a separate, repeatable diagnostic package, and they do not outweigh the underlying shared architecture; therefore *P. pudica* should be reduced to synonymy under *P. phyllocardia*.

Pleurothallis variabilis (Luer)

Taxonomic Treatment: *Pleurothallis ripleyi* and *P. variabilis* were published simultaneously, and the protologues separate them only on minor, non-diagnostic differences that do not hold as stable boundaries when the flowers are compared across material. In both, the defining architecture is the same: a thickened lip dominated by a prominent basal callus and glenion, expressed in a consistent floral plan rather than true "variability"; under the first-reviser rule, the author selects the name *P. ripleyi* for use here. The epithet variabilis is also misleading in this case, because the species is not meaningfully variable in the characters that matter, whereas *P. ripleyi* anchors the name to a person and a concrete historical reference.

To Be Removed from This Sectional Concept by Transfer to Other Subgenera (3):

Pleurothallis glochis (Luer & Escobar)

Taxonomic Treatment: *Pleurothallis glochis* was originally placed by Luer in series *Amphygiae* within subsection *Acroniae*, the "single-flowered" *Acroniae* concept defined largely by a long-pedunculate presentation and a particular floral gestalt (notably prominent petals and a terete column). However, field observations indicate that *P. glochis* does not meet the diagnostic characters of *Amphygiae*/*Amphygiiformae* and is instead more consistent in overall habit and floral structure with subgenus *Scopula*. For that reason, despite its historical placement in *Amphygiae*, it is treated here as transferred to subg. *Scopula* rather than retained in subsection *Amphygiiformae*.

Pleurothallis ankyloglossa (Luer & Hirtz)

Taxonomic Treatment: *Pleurothallis ankyloglossa* was included by Luer alongside the Amphygiae concept, effectively serving as a bridge between the long-pedicellate, amphygiiform assemblage and the multi-flowered taxa traditionally maintained in subgenus *Pleurothallis*. In this treatment, however, *P. ankyloglossa* is removed from the present sectional concept and treated in subgenus *Pleurothallis*. Its overall affinities are closer to the multi-flowered *Pleurothallis* set, including species such as *P. stricta* and *P. languida*, than to subsection Amphygiiformae as circumscribed here. Future work may support recognition of a distinct morphotype for these multi-flowered taxa, which would clarify whether *P. ankyloglossa* should ultimately be grouped more explicitly with that assemblage rather than cited only as a historical link.

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Pleurothallis knappii (Luer)

Taxonomic Treatment: *Pleurothallis knappii* was likewise positioned by Luer in proximity to Amphygiae, implying a connection between the amphygiiform assemblage and certain multi-flowered species of subgenus *Pleurothallis*. In this treatment, *P. knappii* is removed from the present sectional concept and treated in subgenus *Pleurothallis*. The species aligns more closely with the multi-flowered *Pleurothallis* group, including taxa such as *P. stricta* and *P. languida*, than with subsection Amphygiiformae as defined here. Its mention alongside Amphygiae is therefore retained only to document how the connection was framed historically. Additional research may support recognition of a distinct morphotype for the broader multi-flowered assemblage, which could warrant reevaluating how *P. knappii* is best grouped in a future nomenclatural supplement.

To Be Included in This Sectional Concept by Transfer from Other Subgenera (2):

***Pleurothallis tryssa**,* (Luer)

Taxonomic Treatment: *Pleurothallis tryssa* is transferred here from subgenus *Pleurothallis* into subsection Amphygiiformae. *Pleurothallis grobleri* (Luer 2014), treated as a single-flowered member of series Amphygiae, provides the missing anchor. Its flower structure and vegetative habit align closely with the *inaudita–tryssa–tomtroutmanii* set, supporting *P. grobleri* as a persisting progenitor and placing *P. tryssa* within the same amphygiiform sequence as a successive derivative. In *P. tryssa*, the trend advances toward smaller, more open flowers, with a further reduced ***convex*** lip and an inflorescence that may carry up to nine flowers and slightly exceed the leaf. On that character package and its placement within the stepwise progression from *P. grobleri* through *P. inaudita*, *P. tryssa* is treated here as part of subsection Amphygiiformae rather than retained in subg. *Pleurothallis*.

***Pleurothallis tomtroutmanii**,* (Holcomb)

Taxonomic Treatment: *Pleurothallis tomtroutmanii* is transferred here from subgenus *Pleurothallis* into subsection Amphygiiformae. The linkage is supported by *Pleurothallis grobleri* (Luer 2014), a single-flowered species treated in series Amphygiae whose floral structure and vegetative habit closely match the *inaudita–tryssa–tomtroutmanii* set, providing an anchor for interpreting the group as a coherent amphygiiform assemblage. Within that sequence, *P. tomtroutmanii* represents a further extension of the trend, with more elongated flowers, a concave lip, and a distinctly pendant inflorescence that is significantly longer than the leaf and may bear up to thirteen flowers. On that basis, and in keeping with the stepwise pattern inferred from the *grobleri* anchor, *P. tomtroutmanii* is treated here as belonging to subsection Amphygiiformae rather than retained in subg. *Pleurothallis*.

a. Species Attributed to *Pleurothallis* Section *Macrophyllae-Fasciculatae*

Within *Pleurothallis* section *Macrophyllae-Fasciculatae*, together with the allied lineages historically treated under *Abortivae* and *Amphygiae*, there are 342 validly published species.

Subsection *Bulbophylliformae*

adonis
baezensis
brinkmaniana
calogramma
elefa
erythrium
lemniscifolia
linguifera
mastodon
oxapampae
revolutiformis
serricardia
tremens
warrenprescottii

Subsection *Bivalviformae*

acestrophylla
adeleae
aguirrei
ambyx
andreettae
angusta
angustissima
applanata
archidiachoni
ariana-dayanae
ascera
asplundii
aurita
austinrumleyi
batrachus
belocardia
bitumida
bivalvis
blepharopetala
bogarinii
bothros
bovilingua
braidiana
bucculenta
bulbosa
calceolaris
callifera
callosa
calolalax
canaligera
canidentis
cardiochila
cardiophyllax
cardiothallis
carduela
carnosa
carrenoi
cassidata
cedrinorum
celsia
chama
chaparensis
chavezii
chicalensis
cobriformis
complanata
conformalis
constricta
convexa
cop-biodiversitatis
cordata
cordifolia
coriacardia
correllii
corysta
cottenii
crateriformis
crossota
crucifera
cubitoria
cutucuensis
cuzcoensis
cyanea
dariensis
deflexa
depressa
dewildei
dibolia
discoidea
dorotheae
dorothyfuqae
dracuncula
dubbeldamii
embreei
ensata
erymnochila
escobarii
excavata
folsomii
fonnegrae
fossulata
franciana
galerita
ganymedes
gargantua
geographica
giraffa
giraldoi
glabra
globosa
gonzaleziorum
grandiflora
grandilingua
hawkingii
hawkinsii
hemileuca
hispidula
hoeijeri
homalantha
homeroi
ignivomi
imperialis
isthmica
jennydandreae
josefinae
jupiter
karremansiana
kashi-menkakarai
lacera
lapoi
leucantha
llanganatensis
loreae
lunaris
lutheri
machupicchuensis
macra
macrocardia
maduroi
marioandresavilae
markgruinii
marthae
matrisilvae
matudana
megaglossa
megalorhina
microcardia
millei
miniatura
moniquirensis
monocardia
navisepala
neorinkei
nephroglossa
nitida
nossax
obpyriformis
octavioi
omoglossa
oncoglossa
oscarii
palliolata
pandurata
pansamalae
paquishae
paraniesseniae
perfusa
persimilis
petroana
phyllocardioides
phymatodea
pileata
platysepala
pridgeoniana
quitu-cara
recurvata
reginae
reptans
rhinocera
rhodoglossa
rhopalocarpa
robusta
ruberrima
rutrifolia
saccatilabia
sanchoi
sannio
sarcochila
scabrilinguis
scaphipetala
scotinantha
scurrula
sergioi
sigynes
simulans
siphoglossa
solaris
solomonii
sotarae
stenota
suiniana
tamaensis
tandapiensis
teaguei
tectosepala
telamon
tinajillensis
titan
tonduzii
trachysepala
tragulosa
transversilabia
tridentata
trigyna
tuberculosa
tyria
undulata
upanoeinsis
vide-vallis
villahermosae
vinealis
winkeliana
zarumae

Subsection *Cardiostoliformae*

adelphe
adventurae
alopex
altimonile
andreaskayi
anthurioides
apopsis
arctata
barrowii
baudoensis
bilobulata
calamifolia
cardiostola
carmensotoana
carpishensis
castanea
compressa
conicostigma
culpameae
dejavu
diabolica
diazii
dilemma
elliottii
epiglottis
equipedites
exserta
fantastica
gonzaloi
index
iris
jaramilloi
labajosii
lanigera
latipetala
lilijae
longipetala
luna-crescens
lynniana
magnipetala
mahechae
marioi
mesopotamica
minutilabia
muriculata
nangaritzae
neobarbosae
neossa
nipterophylla
ortegae
orygmoglossa
peculiaris
pelicophora
penelops
perijaensis
peroniocephala
perryi
phyllocardia
platypetala
portillae
prolaticollaris
pseudosphaerantha
puyoensis
pyelophera
radula
ramiromedinae
rectipetala
rikseniana
rubrifolia
rubroinversa
rugosa
sabanillae
semiscabra
sphaerantha
stelidilabia
stellata
subtilis
subversa
tapantiensis
tobarii
triangulabia
troglodytes
valladolidensis
volans
whitteniana

Subsection *Amphygiiformae*

abortiva
acutilabia
allenii
amphygia
annectens
archicolonae
asteria
bucranon
cauda-phocae
flavomarginata
forceps-cancri
fugax
gracilipedunculata
grobleri
gymnastica
habenula
imitor
inaudita
kaynagatae
killipii
lacrima
liripipia
lobata
mark-wilsonii
mundiflorae
orecta
pseudopogon
quadricaudata
quaternaria
ramosii
sagittilabia
sobrina
somnolenta
stevensonii
tetrachaeta
thoerleae
tipuloides
tomtroutmanii
tryssa
wigginsii

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b. Subsection *Bulbophylliformae*

The species within the *P. adonis-linguifera* complex serve as the baseline for this subsection. Although bulbophylliform species occur all along the eastern ridge of the Northern Andes from Ecuador to Venezuela, there are only 14 described species that fit into this subsection. However, many more likely exist.

In *Icones Pleurothallidinarum* XXVII, Luer acknowledges that many collections “defy the definitions,” with intermediates that blur identification. He frames the problem as a taxon with overlapping distributions and uncertain identifications across many specimens.

He states a primary distinction based on dorsal sepal venation, describing *Pleurothallis adonis* as three-veined and “typical” *Pleurothallis linguifera* as five-veined, while also noting five or seven veins for *P. linguifera* elsewhere. Luer also contrasts lip form, describing a more tubular or revolute condition versus a more oblong condition, but he concedes that some collections show the principal characters reversed.

That concession matters, because it supports an alternative interpretation: multiple distinct species have been repeatedly misidentified and then folded into *P. adonis* or *P. linguifera*, rather than one species that is simply “highly variable.” Field observations confirm that several species remain undescribed.

The discovery of *Pleurothallis tremens* would normally prompt a re-examination of non-type herbarium material assigned to *P. adonis*, *P. linguifera*, and related taxa. If additional ancestral or near-ancestral lineages exist, they may already be sitting in collections under incorrect names.

However, herbarium preservation places hard limits on what can be tested. Flowers are commonly dried, pressed, or dissected. That prevents functional assessment of the lip hinge and makes it impossible to determine whether a specimen once had a freely hinged, bulbophylliform mechanism.

For that reason, any re-examination has to focus on character combinations that remain readable after preservation, such as labellum shape and posture, column-foot and labellum attachment features, and consistent suites of floral proportions, interpreted alongside geographic structure.

Where living plants can be observed, lip motility should be tested directly in the field. A simple disturbance test, using air movement and light touch, is sufficient to determine whether a lip is freely hinged, constrained, or functionally fixed. That information cannot be recovered from preserved material, yet it is essential for interpreting bulbophylliform affinity.

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c. Species Attributed to Subsection *Bulbophylliformae*

There are 14 species within this subsection which can be divided into four distinct morphotypes:

Bulbophylliform: *Pleurothallis tremens* is the only species currently documented with a bulbophylliform pollination mechanism and is the only species within this morphotype grouping. Concave dorsal sepal, lip suberect, convex, very loosely hinged.

Linguiform: Concave dorsal sepal. Lip deeply convex, erect to suberect, species with suberect lips have an acute apex which is treated as an apical crusulum used to reduce the space between the lip and synsepal.

adonis *brinkmaniana* *calogramma* *lemniscifolia* *linguifera*

Revolutiform: Concave dorsal sepal. Lip deeply convex, margins revolute typically forming a tight tube. Basal margins sometimes block the hinge. Occasionally petals wrap tightly around the base of the lip reinforcing the basal margins.

baezensis *elefa* *revolutiformis* *serricardia*

Protobivalform: Evolved from both linguiform and revolutiform species. Concave dorsal sepal. Lip convex, suberect typically below a 45-degree angle. Flowers have more bivalviform characteristics. In some species the apical margins have folded into an apical crusulum that reduces the space between the lip and synsepal.

erythrium *mastodon* *oxapampae* *warrenprescottii*

d. Subsection *Bivalviformae*

Pleurothallis bivalvis has been treated as the yardstick, the “standard” flower from which everything else is measured. Plants that drift only slightly from that pattern get folded into a broad “complex,” while the most striking departures are allowed to stand as separate species.

The trouble is that the original name was built on a flower with a missing lip. A “standard” anchored to a type that cannot show the very structure everyone argues about is not a secure foundation. Based on the evidence, a neotype or epitype anchored to a plant with the expected prostrate, convex lip would be a more defensible way to stabilize what *P. bivalvis* actually represents.

In *Icones Pleurothallidinarum* XXVII, Luer treats P. *bivalvis* broadly, as P. *bivalvis* sensu lato, and frames it as a species complex rather than a narrowly delimited species. He ties the name to Lindley’s type from near Mérida, Venezuela, notes that the lip was detached from the type flower, and then describes a recurring “basic pattern” that, in his view, appears again and again across an enormous range. Describing a “basic pattern” from a type with no lip is inherently problematic, because the character that most often separates these plants in life is the one the holotype doesn’t define.

Luer’s core argument is scale. He points to innumerable collections, from Central America through the Andes, that fit this *bivalvis* pattern, and he treats most departures as minor variants. In his view, the variations occur in so many combinations that it becomes illogical to split off a few named segregates while leaving the rest unnamed. As a result, he gathers many regional concepts under the *bivalvis* umbrella, not because the differences are invisible, but because he does not see them forming clean, consistent breaks beyond size and small proportional shifts.

To keep the complex workable, he downplays vegetative traits, especially leaf form, which he regards as too variable to carry much taxonomic weight. He leans instead on floral characters, and he uses dorsal sepal venation as a practical boundary condition. He describes the type as three-veined, notes that most collections appear effectively three-veined, with accessory veins more apparent in larger flowers, and he explicitly excludes clearly five-veined collections from *P. bivalvis* sensu lato, because including them would only deepen the identification problem he is trying to contain.

This same pattern reappears in the *Pleurothallis microcardia* complex. Luer treats P. *microcardia* as frequent and wide-ranging, with a broad envelope of expression, then retains several geographically patterned outliers as subordinate ranks. He calls attention to forms with threadlike petals whose tips curl around the leaf margins, flowers that lie higher on the leaf surface rather than sitting near the base, and dorsal sepals that become exceptionally long.

In a strictly branching framework, that reads as a single, unusually variable species. In the speciation structure advanced here, it reads as something else: a persisting, common, progenitor-like flower plan, plus multiple daughter species that remain close enough to the shared architecture to be mistaken for “variation,” even when they repeat the same departures in the same places.

In *Pleurothallis cordata* sensu lato, Luer is even more direct. He acknowledges that multiple recognizable entities are mixed together, and he treats them as subspecies because intermediate flowers are not uncommon. A subspecies, in the ordinary sense, is a regional expression shaped by geographic separation. That is not what the evidence suggests here. These are not rare edge forms tucked behind a barrier.

In several cases the “subspecies” expression is common, repeatable, and widely encountered, including in modern photographic records. In this group, “subspecies” often becomes a catch-all for overlapping, coexisting species that share the same basic floral plan, and that is why so many names have been minimized, and so many distinct species have been repeatedly misidentified or reduced into synonymy.

Finally, Luer describes *Pleurothallis ruberrima* as frequent and “extremely variable” across a vast Andean range, from western Venezuela into Bolivia. He emphasizes long ramicauls with erect, narrow leaves, and large flowers produced on long, flexible, drooping peduncles that dangle over the leaf margins.

He also stresses inconsistency: the dorsal sepal is multiveined, but the vein count varies, the sepal margins are usually recurved, and the lip is proportionately small, with a disc that ranges from only slightly convex to thickly callous. He closes with a familiar conclusion, namely that proposed “variations” are inconstant and grade into one another.

The difficulty is that the published illustrations under the *P. ruberrima* name do not merely show a single flower plan with minor drift. They show incompatible lip shapes. The species depicted in Fig. 172a retains only the hypochile, similar to species like *P. calceolaris* and *P. cyanea*. In Fig. 172b, the flower has a clearly deflexed lip similar to *P. constricta*. The flower in Fig. 172c has a nearly vestigial lip.

Alongside those lip differences, there are conspicuous shifts in overall floral morphology. Read together, the set looks less like one species expressing variation, and more like multiple species being carried under one name.

Cultivated material acquired as *P. ruberrima* points the same way. Plants can produce flowers spanning roughly 2 to 8 cm, and some show lips reduced to only a few millimeters in width. That spread is not automatically “variation,” especially when the lip itself is changing from deflexed to vestigial.

It suggests that other species, particularly pendant-flowered species, have been mixed in due to an overly broad concept that treats any dangling flower as the same thing. There is an additional detail, however, that may matter even more.

In some of these pendant-flowered species that still retain a lip, nectar has been replaced by a thick, gelatinous secretion. In some *Elleanthus* species, mucilage-rich, sticky secretions produced by floral colleters are chemically complex and are discussed as functional exudates that can protect tissues and influence pollinators. If a comparable shift is occurring here, then at least part of what is being lumped under *P. ruberrima* may represent different pollinator systems, not just different "forms."

This is also where the pendant condition needs to be handled carefully. Pendant flowers show up repeatedly as cloud-forest weather becomes the dominant pressure, and they appear across multiple underlying flower architectures.

In that sense, "penduliform" is not a single ancestral design. It is a late-phase solution that can be layered onto bivalviform, microcardiiform, cordatiform, titaniform, and grandifloriform species.

Used as a morphotype label, it describes an evolutionary response, not a claim of close relationship. The practical implication is simple: pendant posture alone is not a safe container for species limits, and *P. ruberrima* as currently applied looks like a composite that needs to be re-sorted by lip architecture, column structure, secretion type, and the rest of the mechanical package, not by color and dangling habit.

In 2013, Wilson et al. proposed a distinct "Mesoamerican clade" and treated those Mesoamerican species as unrelated to morphologically similar South American species such as *P. phymatodea*. However, the non-resupinate dorotheaeform species did not appear out of nowhere. They evolved from resupinate bivalviform ancestors over many generations.

The South American bivalviform analogs that would complete that sequence are missing from the analysis. A second gap appears when the map is drawn from holotype collection data. Between Panama and Colombia there is a broad corridor from which few, if any, species have been collected. By default, that means the Panama–Colombia corridor and the adjacent northern Andean interfaces were not sampled at all.

Under the speciation structure documented here, those missing intermediates are not incidental. They are the very species that would connect the story across geography. When they are absent, a strictly branching analysis can turn an incomplete chain into the illusion of separate origins.

There is also a practical problem because cultivated material used in the analysis. When sequences come from cultivated, non-vouchered material, identity can be uncertain, and plants may express differently under greenhouse conditions. For these reasons, DNA cannot reliably support a distinct Mesoamerican clade.

Of the four proposed subsections, *Bivalviformae* has been the most neglected, and requires a lot of sorting and correcting. There are many names currently treated as synonyms that represent distinct species. Applying these logical boundaries and morphotypes will bring order and clarity to the subsection.

e. Species Attributed to Subsection *Bivalviformae*

There are 203 species within this subsection which can be divided into 8 distinct morphotypes.

Bivalviform: Sepals equal size. Deeply to shallowly concave dorsal sepal. Dorsal sepal and synsepal rounded or oblong. Lip convex, planar, or concave, prostrate against the synsepal. Some species have nearly vestigial lips.

acestrophylla
archidiachoni
asplundii
austinrumleyi
bivalvis
bothros
bucculenta
bulbosa
callifera
canaligera
canidentis
cardiophyllax
carduela
cedrinorum
celsia
chama
convexa
cop-biodiversitatis
cordifolia
correllii
cottenii
cutucuensis
dariensis
discoidea
dubbeldamii
embreei
folsomii
fonnegrae
geographica
giraffa
giraldoi
grandilingua
hawkingii
hemileuca
homalantha
homeroi
isthmica
karremansiana
kashi-menkakarai
lapoi
leucantha
macrocardia
matrisilvae
matudana
megaglossa
obpyriformis
omoglossa
recurvata
robusta
solomonii
sotarae
tandapiensis
telamon
trigyna
tyria
upanoeinsis
vide-vallis

Microcardiiform: Sepals equal size, elongated and narrower than bivalviform species. Deeply to shallowly concave dorsal sepal. Lip convex, planar, or concave, prostrate against the synsepal.

andreettae
angustissima
ariana-dayanae
chaparensis
coriacardia
cuzcoensis
fossulata
franciana
ignivomi
microcardia
millei
miniatura
moniquirensis
paquishae
persimilis
petroana
rhinocera
scabrilinguis
tamaensis
tectosepala
undulata
vinealis

Cordatiform: Sepals equal size. Dorsal sepal shallowly concave to convex. Lip is typically planar, although a few are slightly convex. Sepals are typically hyperextended.

angusta *applanata* *complanata* *cordata* *crossota* *dibolia* *erymnochila* *escobarii*
hawkinsii *hispidula* *marioandresavilae* *monocardia* *phyllocardioides* *rhodoglossa* *rhopalocarpa* *rutrifolia*
sergioi *trachysepala* *tuberculosa*

Titaniform: Typically, large to very large flowers. Sepals equal size. Dorsal sepal shallowly concave to convex. Synsepal shallowly concave to very deeply concave. Lip tightly appressed to the synsepal, concave in most but reduced to only the hypochile in some species.

bovilingua *calceolaris* *callosa* *calolalax* *cardiochila* *cardiothallis* *cyanea* *dewildei*
gonzaleziorum *lunaris* *navisepala* *oncoglossa* *oscarii* *perfusa* *scotinantha* *solaris*
titan *villahermosae*

Grandifloriform: Flowers small to very large. Dorsal sepal deeply concave. Synsepal flattened or slightly convex. Lip margins folded to block the hinge in some species. Petals descending in a few species. In the majority, the petals are used as a wedge between the lip and the synsepal. If the petals are removed, the hinge is fully functional. Petals also cradle the lip in some species.

aguirrei *chavezii* *galerita* *imperialis* *maduroi* *neorinkei* *pandurata* *sarcochila*
tonduzii *ascera* *corysta* *gargantua* *jupiter* *markgruinii* *nephroglossa* *pileata*
siphoglossa *blepharopetala* *deflexa* *grandiflora* *llanganatensis* *marthae* *nossax* *quitu-cara*
suiniana *cassidata* *dracuncula* *hoeijeri* *lutheri* *megalorhina* *palliolata* *reginae*
teaguei

<u>Cruciform</u>: Flowers typically fully appressed against the leaf. Some species have dorsal sepals hyperextended but not yet fully appressed. Column reduced and flush with the lip. Lip convex to concave, fully appressed to the synsepal.

braidiana *carnosa* *chicalensis* *crucifera* *cubitoria* *depressa* *glabra* *jennydandreae*
josefinae *pridgeoniana* *winkeliana*

<u>Dorotheaeform</u>: A few species appear typically bivalvilform except the lip is degenerated to form a deep, labellar sulcus. Most species are non-resupinate with a deep labellar sulcus.

ambyx *aurita* *bitumida* *bogarinii* *carrenoi* *cobriformis* *crateriformis* *dorotheae*
excavata *globosa* *lacera* *loreae* *nitida* *pansamalae* *paraniesseniae* *phymatodea*
reptans *saccatilabia* *sanchoi* *scaphipetala* *simulans* *transversilabia* *tridentata*

<u>Penduliform</u>: Pendant flowers show up repeatedly in bivalviform, microcardiiform, cordatiform, titaniform, and grandifloriform species. Lips of the species are the same as what is found within these morphotypes. However, the flowers are pendant, typically hanging over the edge of the leaf, or from the spathaceous bract at the base of an erect leaf.

adeleae *batrachus* *conformalis* *constricta* *ensata* *ganymedes* *machupicchuensis* *macra*
octavioi *platysepala* *ruberrima* *sannio* *scurrula* *sigynes* *stenota* *tinajillensis*
tragulosa *zarumae*

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f. Subsection *Cardiostoliformae*

Luer first recognized subsection *Cardiostolae* as a coherent unit by its overall habit and its build. These are plants with deflexed, heart-shaped leaves, with mature blades more or less conduplicate at the base, then bent almost 180 degrees away from the ramicaul. In the flower, the column is stripped of wings, the column-foot is rudimentary or absent, and the anther sits apical to subapical as part of the same diagnostic package.

From there, the story moves quickly, because many of these species do not rely on slow, incremental reshaping of the lip to change function. They use resupination as a shortcut. A twist in the developing bud, guided by gravitropic control, can reposition the labellum relative to gravity without rebuilding the entire flower. Once the lip is moved into a new orientation, hinge action can be neutralized by posture alone, even before the lip is structurally reduced.

Several resupination patterns recur. In one, the bud rotates 180 degrees during development, and as it matures the pedicel constricts, pulling the flower forward and holding the lip upward against gravity while the lip continues to shrink over time. In another, the bud makes a full 360-degree rotation and ends exactly where it began, a net-zero movement that still has functional consequences, especially for shedding water. In yet another, the bud rotates 180 degrees, the pedicel extends, and then the bud rotates another 180 degrees so the flower finishes facing backward. In each case, the outcome is consistent. The lip ends up placed where it is sheltered, and where persistent moisture has fewer chances to pool.

In cloud-forest weather, water becomes a constant pressure. The synsepal, so often a neat concave basin, can turn into a reservoir in fog, drizzle, and cloud drip. In response, these species began to open the flower, flattening the architecture so water cannot sit and linger. Across the sequence captured in the field and in plates, the same directional shift repeats. Deeply concave sepals give way to shallow concavity, then toward flatter, more open forms. The synsepal reflexes, exposure increases, and the flower sheds water before it can collect.

At the same time, the leaf becomes part of the engineering. Some species lean the ramicaul forward so the leaf rooflines the flower, and the bloom faces the ground beneath its own canopy. Others push the habit even farther, with pendant leaves and flowers held close against the surface, so water runs cleanly away instead of flooding the lip region. In colder, wetter, windier sites, leaf reduction serves two purposes at once. It helps retain moisture close to the plant, and it offers less resistance to the wind, so the flower stays steadier when weather closes in.

The reward system shifts as well. The glenion enlarges, and in many species it gives way to a broad, nectar-filled labellar sulcus, an arrangement that likely keeps the pollinator in place longer and raises the odds that a visit ends in pollination.

In a few members of this subsection, diversification reaches its most extreme endpoint. The lip, once a landing platform, continues to shrink until it is scarcely there at all. As that reduction progresses, the basal lobes rise, flank the column, then curl inward. Eventually they begin to wrap around the column itself, and the lip is reduced to a vestige.

Taken together, this is not a loose collection of “similar-looking” plants. It is a repeatable suite of vegetative posture, column simplification, resupination behavior, moisture-shedding flower architecture, and correlated changes in reward and lip reduction. That combination is sufficient evidence to justify treating these species as a distinct subsection.

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g. Species Attributed to Subsection *Cardiostoliformae*

There are 85 species within this subsection which can be divided into 2 distinct morphotypes. Many of these morphotypes can be placed into one of four categories of resupination.

Cardiostoliform: Dorsal sepal shallowly concave to convex. Synsepal shallowly concave, convex, revolute, or reflexed. Lips degenerated by 50% or more. Ramicauls erect,.suberect, pendant, or arching. The "lilijae" type flowers are the original template for the species in this group. Species with reflexed petals appeared later.

adelphe
adventurae
alopex
andreaskayi
apopsis
arctata
barrowii
baudoensis
calamifolia
cardiostola
carmensotoana
carpishensis
castanea
compressa
conicostigma
culpameae
diabolica
diazii
dilemma
elliottii
epiglottis
equipedites
exserta
fantastica
gonzaloi
iris
labajosii
lanigera
latipetala
lilijae
lynniana
magnipetala
mahechae
marioi
minutilabia
muriculata
nangaritzae
neobarbosae
neossa
nipterophylla
ortegae
orygmoglossa
peculiaris
pelicophora
penelops
perijaensis
peroniocephala
perryi
platypetala
portillae
pseudosphaerantha
puyoensis
pyelophera
ramiromedinae
rikseniana
rubrifolia
rubroinversa
sabanillae
semiscabra
sphaerantha
stelidilabia
stellata
subtilis
subversa
tobarii
troglodytes
valladolidensis
volans
whitteniana

Phyllocardiiform: Dorsal sepal shallowly concave to convex. Synsepal shallowly concave, convex, revolute, or reflexed. Lips rugose or verrucose, degenerated by 50% or more. Ramicauls erect,.suberect, pendant, or arching almost always with a suberect spathaceous bract.

altimonile
anthurioides
bilobulata
dejavu
index
jaramilloi
longipetala
luna-crescens
mesopotamica
phyllocardia
prolaticollaris
radula
rectipetala
rugosa
tapantiensis
triangulabia

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Types of Resupination

Geniculate Inversion: A normal 180° resupination occurs during development, then a late-stage geniculation and/or pedicel constriction changes the final presentation so the flower is held "inverted" relative to gravity, with the lip pointing upward (or at least held up against the pull of gravity) when the flower opens.

Net-zero Resupination: The bud rotates a full 360° during development and finishes where it began, so the open flower can look non-resupinate even though it did resupinate. Functionally, it is "rotation without a net change" in final orientation.

Geniculate Deflection: A normal 180° resupination occurs, then the pedicel kinks and/or constricts in a way that pushes the flower forward and down, so the lip ends up facing the ground or pressed toward the leaf surface. This is the "downward" counterpart to geniculate inversion.

Retrotorsion: The bud resupinates (180°), then continues with an additional backward twist (another 180°) so the flower ends up rotated back toward the leaf. The final effect is a flower that looks "turned around," with the lip repositioned into a more sheltered, backward-facing presentation.

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h. Subsection *Amphygiiformae*

In *Icones Pleurothallidinarum* XVII, Luer treats series *Amphygiae* as the single-flowered, long-pedicellate subset within subsection *Acroniae*. In his key, he characterizes these plants as usually resupinate, often long-pedicellate, with prominent petals that commonly descend and become sigmoid, and with a triangular, acute lip whose basal angles may appear lobe-like. He also notes a semiterete column in this set. In other words, *Amphygiae* is his "single-flowered *Acroniae*" concept, defined mainly by flower posture, pedicel length, petal shape, and a triangular acute lip, rather than by vegetative traits.

Pleurothallis killipii, with its large flowers presented on an erect pedicel, has always read as an outlier within *Macrophyllae-Fasciculatae*. In bivalviform species, the lip declines over many generations, from erect to suberect, until it finally settles against the synsepal and the hinge becomes functionally neutralized. Cardiostoliform species accelerate that transition by employing resupination, neutralizing hinge action through posture while the lip continues to shrink.

In *P. killipii*, the shift looks different. Instead of "dropping" into place, the lip appears to mesh into the synsepal from the base downward, like a zipper being closed. The first contact occurs at the base, exactly where a hinge would normally pivot.

Once that basal contact is made, the hinge is effectively neutralized. The lip becomes anchored, then progressively seated more completely, until it lies firmly against the synsepal. After the lip is fully pressed into position, it continues to degenerate, and at the same time the pedicel begins to elongate.

As cloud forests became more widespread in both the Northern Andes and Mesoamerica, a new pressure took over: water. In these forests, plants are kept constantly wet by fog, drizzle, and cloud drip, not just by rainstorms. For a flower that depends on a visitor staying put, that matters.

In *P. killipii*, the shift toward the amphygiiform condition reads like a direct response to that wet world. The once-erect pedicel becomes arching, and the bloom turns downward, tucking the column region beneath the leaf like a small roof.

Many pollinators are not elegant hoverers. They crawl and they probe. A pendant flower gives them a sheltered working space, protected from runoff and splashing, and it keeps the reproductive parts functional when everything else is dripping wet.

Luer explicitly treats *P. quadricaudata, P. tetrachaeta*, and *P. tipuloides* as "closely allied" and "superficially similar," noting that the long-attenuate sepals and petals are "inseparable," and even suggesting that lip morphology "may be found to merge" if enough specimens were available. That framing has encouraged decades of casual lumping and routine misidentification. In fact, the three are not "basically the same," and they do not behave like interchangeable local variants.

P. quadricaudata typically produces much larger flowers with markedly longer petals that usually descend, often held nearly parallel to the synsepal. The flower is held on an erect pedicel, commonly aligned parallel with the leaf, with the lip facing upward. Luer's own description emphasizes the scale and presence of the long-tailed perianth, and notes that the long-tailed flower rests on the dorsum of an ovate leaf.

P. tetrachaeta, by contrast, has a more delicate, pendant-leaning presentation: the pedicel arches, and the flower faces downward. Even where the long-attenuate sepals and petals resemble the others, Luer separates it by a much smaller lip, "only half the size," lacking basal lobes.

P. tipuloides is the most divergent of the three, and it aligns more naturally with *P. killipii* than with *P. tetrachaeta*. Its flowers are carried on an erect pedicel with stiff petals held in a neutral, extended position, and the lip is entirely different from the others. In Luer's key, *P. tipuloides* is separated immediately by a longer lip with erect, denticulate basal lobes. His species description repeats that diagnosis: an ovate-trilobed lip about 5 mm long, with erect, rounded, denticulate basal lobes embracing the column.

These differences matter because they are not cosmetic. They alter how the flower is presented to a pollinator, how water runs across the perianth, and how reliably the column region remains functional in persistently wet conditions. A pendant or downward-facing flower creates a sheltered working space beneath the leaf, protected from runoff and splash, and that shelter matters in cloud forests where fog, drizzle, and cloud drip keep flowers continuously wet.

Luer segregates section *Abortivae* for a single species, *Pleurothallis abortiva*. He explains the name as referring to an "abortive" condition, and he defines the section by a combination he treats as unique within the subgenus: a small, vestigial lip positioned beneath a much larger, terete, footless column, meaning it lacks a column-foot. He notes a superficial resemblance to the single-flowered members of series *Amphygiae* but separates *P. abortiva* immediately on the basis of that vestigial lip paired with a large, terete, footless column.

Field observations suggest that a small cluster of species repeatedly shares this same essential column and stigma architecture, even as the lip ranges from nearly vestigial to effectively absent. Vegetatively, these plants also resemble amphygiiform species, and they show the same range of presentation, from erect to suberect pedicels, to arching pedicels, to fully pendant flowers.

The field record further suggests *P. habenula* as a persisting progenitor to *P. kaynagatae*, and *P. fugax* (or similar species) as a potential progenitor to *P. neossa*. The remaining species cluster more closely with the *habenula-kaynagatae* set in overall build, and they share the same column structure whether the lip is reduced to a remnant or disappears entirely. For these reasons, section *Abortivae* is absorbed here into subsection *Amphygiiformae* as abortiviform morphotypes, rather than retained at a separate sectional rank.

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The publication of *Pleurothallis lacrima* in 2022, an amphygiiform species bearing multiple flowers, prompted a re-examination of taxa historically placed in subgenus *Pleurothallis*. *P. lacrima* produces flowers that fall unequivocally within the *P. quadricaudata* group, yet they are only a fraction of the size. It also breaks with the standard *Amphygiae* expectation of solitary blooms. Instead of being single-flowered, *P. lacrima* carries three to five flowers per inflorescence.

A similar mismatch appears in the 2023 publication of *P. inaudita*. There, *P. imitor* is used for comparison, but the two are not comparable in either presentation or structure. *P. inaudita* aligns far more closely with *P. tryssa*, differing mainly in having fewer flowers per inflorescence, each substantially larger.

Pleurothallis grobleri (Luer 2014) provides the missing anchor. It is a single-flowered species treated in series *Amphygiae*, yet its flowers closely match those of *P. inaudita*, *P. tryssa*, and *P. tomtroutmanii*, and the vegetative habit is similarly congruent. This combination supports *P. grobleri* as a persisting progenitor from which the *inaudita–tryssa–tomtroutmanii* set can be interpreted as successive derivatives. The inferred direction is consistent and stepwise:

(A) *P. grobleri* begins the series with larger, solitary flowers.

(B) *P. inaudita* follows with a more open flower, a reduced lip, and one to three flowers per inflorescence; the inflorescence sits on top of the leaf and is shorter than the leaf.

(C) *P. tryssa* advances the trend, producing much smaller, more open flowers, a further reduced convex lip, and an inflorescence of up to nine flowers that is just slightly longer than the leaf.

(D) *P. tomtroutmanii* extends the presentation further still, with more elongated flowers, a concave lip, and a pendant inflorescence that is significantly longer than the leaf and may carry up to thirteen flowers.

For these reasons, *P. inaudita*, *P. tryssa*, and *P. tomtroutmanii* are included in subsection *Amphygiiformae*. Additional research may support recognition of a distinct morphotype for other multi-flowered taxa historically maintained in subgenus *Pleurothallis*, including *P. languida*, *P. phalangifera*, *P. tenuisepala*, and *P. stricta*.

Luer had already implied this connection indirectly by including *P. knappii* and *P. ankyloglossa* alongside the *Amphygiae* concept, effectively bridging the multi-flowered taxa of subgenus *Pleurothallis* with the amphygiiform assemblage.

In this treatment, however, *P. knappii* and *P. ankyloglossa* are removed from this sectional concept and treated in subgenus *Pleurothallis*. Their placement is therefore cited only to show how the connection was framed historically, not as part of the circumscription adopted here.

i. Species Attributed to Subsection *Amphygiiformae*

There are 40 species within this subsection which can be divided into 2 distinct morphotypes:

Amphygiiform: Sepals concave, oblong, or attenuate, equal size. Lip convex to concave. Flowers are produced from an elongated erect, suberect, arching, or pendant pedicel.

acutilabia
allenii
amphygia
annectens
archicolonae
asteria
bucranon
cauda-phocae
flavomarginata
forceps-cancri
fugax
grobleri
gymnastica
imitor
inaudita
killipii
lacrima
liripipia
mark-wilsonii
mundiflorae
orecta
quadricaudata
quaternaria
ramosii
sagittilabia
sobrina
somnolenta
stevensonii
tetrachaeta
thoerleae
tipuloides
tomtroutmanii
tryssa

Abortiviform: Sepals concave, oblong, acute, equal size. The species in this morphotype share the same column structure whether the lip is reduced to a remnant or disappears entirely.

abortiva *gracilipedunculata* *habenula* *kaynagatae* *lobata* *pseudopogon* *wigginsii*

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j. New Taxa

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

Plant large in size, epiphytic, possibly terrestrial, caespitose, roots very slender.

Ramicauls up to 26 cm long, very slender, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

Leaf 14 cm long, 7.5 cm wide, coriaceous, ovate, acute, the base cuneate, sessile.

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

Labellum (Lip) 11 mm long, 4.5 mm wide, purple, convex, oblong with a well-developed orbicular glenion at the base and a longitudinal groove that starts at the glenion and runs the length of the lip to the apex, basal lobes rounded, apex subacute with a small crusulum on the abaxial side of the lip, very loosely connected to the column foot by a true hinge.

Dorsal Sepal 16 mm long, 11 mm wide, 3-veined, purple suffused with white at the apex, membranous, glabrous, ovate.

Synsepal 15 mm long, 11 mm wide, 3-veined, yellow suffused with purple at the base, glabrous, ovate, concave.

Petals 12 mm long, 2 mm wide, 1-veined, rose colored, descending, slightly incurved, narrowly oblong, acute.

Column 3 mm long, 2 mm wide, semiterete, bilobed, anther apical, stigma apical.

Etymology: From the Latin *tremens* “trembling”, a reference to the loosely-hinged lip that moves in the slightest breeze.

ECUADOR: Without collection data. *K.W. Holcomb 18031 (Holotype: GEO)*

Diagnosis: *Pleurothallis tremens*, is a relict species within Section *Macrophyllae-Fasciculatae*, because it is the only surviving ancestral species within the section. *P. tremens* is one of 14 bulbophylliform species which are the ancestors of all *Pleurothallis* species in Section *Macrophyllae-Fasciculatae*, and it is the only species in this section with a bulbophylliform pollination mechanism, a suberect, convex lip connected to the column foot by a true hinge.

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

Plant 21 cm tall, epiphytic, caespitose, roots very slender.

Ramicauls up to 27 cm long, very slender, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

Leaf 12 cm long, 6.75 cm wide, dark green with light green veins, coriaceous, cordate, acute, the base cuneate, sessile.

Inflorescence 1 to 3, simultaneous, resupinate flowers, borne from a reclining spathaceous bract at the base of the leaf.

Labellum (Lip) 18 mm long, 2 mm wide, bright orange suffused with red along the basal margins, erect, deeply convex, basal margins revolute forming a tight tube a quarter below the base to the apex, verrucose, with a well-developed glenion at the base, connected to the column foot by a constricted, weight-sensitive hinge.

Dorsal Sepal 17 mm long, 8 mm wide, 5-veined, shallowly concave, peach, membranous, glabrous, ovate, acuminate.

Synsepal 17 mm long, 8 mm wide, 5-veined, pink, membranous, glabrous, oblong-ovate, reflexed, acute.

Petals 11 mm long, 2 mm wide, 1-veined, red, erect, flaring at the lower third, acute.

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

Etymology: From the Latin *elefa* " the elephant", in reference to the revolute lip and elongated petals that look like an elephant’s trunk and tu.

ECUADOR: No collection data. *K.W. Holcomb 18033 (Holotype: GEO)*

Diagnosis: *Pleurothallis elefa* is a revolutiform species. In these species, the revolute margins of the lip form a tight tube which in the case of this species makes the lip resemble an elephant’s trunk. The descending, outward curved petals look like tusks.

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

<u>Plant</u>: Small, epiphytic, caespitose, very thin roots.

<u>Ramicauls</u>: to 11 cm long, very thin, suberect, enclosed by a thin tubular sheath below the middle and another at the base.

<u>Leaf</u>: is 7.5 cm long, 2.25 cm wide, cordate, coriaceous, ovate, acute, the base cuneate, sessile.

<u>Inflorescence</u>: a fascicle of successive, single yellow flowers, born from a spataceous bract at the base of the leaf.

<u>Labellum (Lip)</u>: 3.5 mm long, 2.5 mm wide, yellow, suberect, convex, glabrous with a nectar-secreting epithelium covered with droplets and a well-developed glenion at the base, trilobed, basal lobes rounded, apex round.

<u>Dorsal Sepal</u>: 6.5 mm long, 3 mm wide, with 3 veins, yellow, membranous, glabrous, ovate, shallowly concave, acute.

<u>Synsepal</u>: *6* mm long, 3.5 mm wide, with 3 veins, yellow, membranous, glabrous, ovate, shallowly concave, the sides slightly reflexed, acute.

<u>Petals</u>: 5 mm long, 1 mm wide, 1-veined, yellow, reflexed, acute.

<u>Column</u>: 1 mm long, 1 mm wide, bilobned, anther apical, stigma apical.

<u>Eponomy:</u> Named for Warren Prescott of Atlanta, Georgia. A dear friend of the author.

ECUADOR: No collection data. *K.W. Holcomb 18034 (Holotype: GEO)*

<u>Diagnosis</u>: *Pleurothallis warrenprescottii* is very similar to *P. erythrium*. Both are protobivalviform species with suberect lips. However, *P. warreprescottii* is distinguished by the presence of a crusulum at the apex of the lip. This feature is absent in *P. erythrium*. *P. warrenprescottii's* most significant distinguishing feature is a lip which is covered in nectar droplets. In *P. erythrium*, nectar production is restricted to the glenion. Vegetatively, the two species can be distinguished by the thick, succulent leaves of *P.* warrenprescottii vs. the thin leave of *P. erythrium*.

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