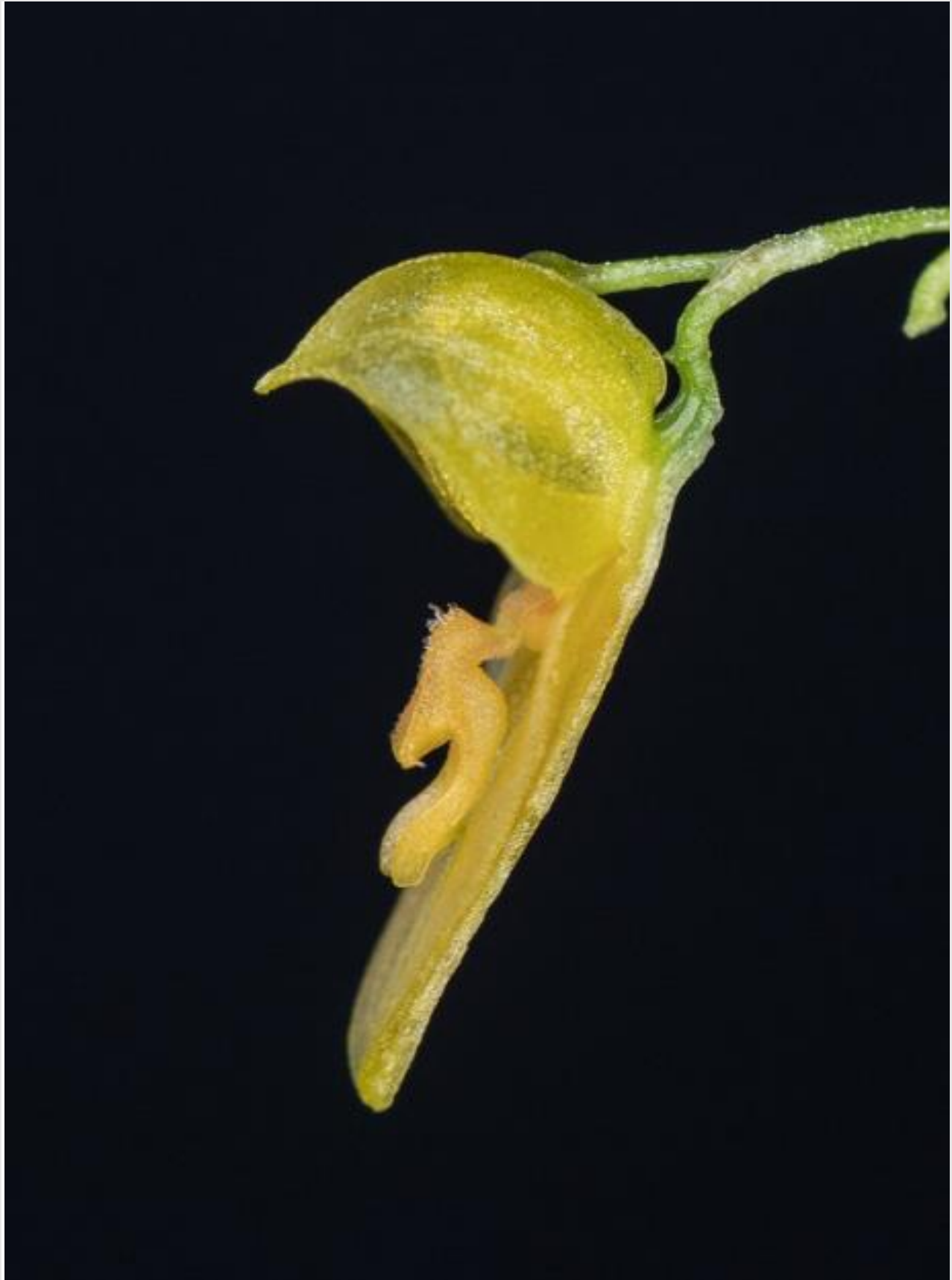


Biomechanical Evolution in the *Pleurothallidinae* (Orchidaceae)

Kevin W. Holcomb



PLEUROTHALLIDINAE

Volume 4.3
March 5, 2026
ISSN #2834-1783

Biomechanical Evolution in the *Pleurothallidinae* (Orchidaceae)

Kevin W. Holcomb

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

It is available to download at no charge and is licensed under the Creative Commons Attribution (Non-Commercial) 4.0 International License. To view a copy of this license, visit: [Creative Commons CC BY-NC-SA 4.0](https://creativecommons.org/licenses/by-nc-sa/4.0/)

Notice of Fair Use:

This research is intended for non-commercial educational and informational purposes only. It contains material which may be copyrighted, the use of which has not been specifically authorized by the copyright owner. However, the copyright owner has been credited for their work.

Under Section 107 of the Copyright Act of 1976, allowance is made for 'fair use' for purposes such as criticism, comment, news reporting, teaching, scholarship and research. Fair use is a use permitted by copyright statute that might otherwise be infringing.

PLEUROTHALLIDINAE

Copyright © 2022-2026
Kevin W. Holcomb
All rights reserved
ISSN #2834-1783
ORCID #0000-0002-0571-4462

Cover Photo: *Acostaea costaricensis*

Table of Contents

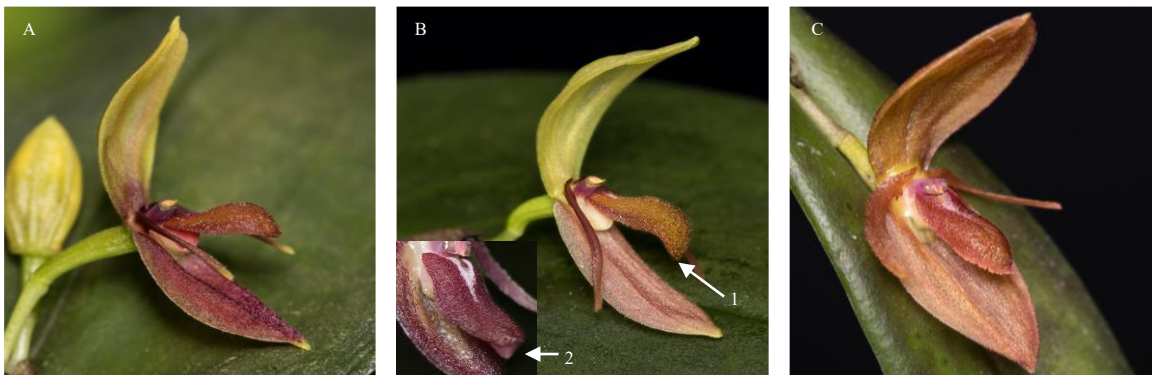
I.	Introduction	1
II.	Evaluation of Evolution in the <i>Pleurothallidinae</i>	4
III.	Interpretation Must Be Applied Consistently	6
IV.	Conclusion	11
V.	Reinstatement of the Genus <i>Acostaea</i> Luer (<i>Pleurothallidinae</i>)	12
VI.	Reinstatement of the Genus <i>Muscarella</i> Luer (<i>Pleurothallidinae</i>)	13
VII.	Reinstatement of the Genus <i>Salpistele</i> Dressler (<i>Pleurothallidinae</i>)	14
VIII.	References (Literary)	15

Note: This is presented as an interpretive model of evolutionary structure, not as a formal, rank-level revision at this time.

I. Introduction

As discussed in Volume 4.1, the morphological hyperdiversity observed in *Pleurothallis* section *Macrophyllae-Fasciculatae* is not random intraspecific variation. It is a visible, living record of evolutionary history, the product of budding speciation.

Through budding speciation, ancestral lineages (progenitors) persist, and derivatives arise alongside them. Derivatives may themselves become progenitors. This creates morphotypes that can still resemble the original progenitor, even when they are not closely related sister lineages. Each morphotype represents a lineage captured at a different stage of the evolutionary process like individual frames in a time-lapse sequence.



Across the section, the lip changes in posture, hinge mobility, mass distribution, curvature, and contact geometry. These are not decorative differences. They are shifts in how force is transferred, how gravity acts on the flower, how wind is resisted, and how a pollinator interacts with the structure.

In some species the hinge remains freely articulated (A & B). In others the lip presses into the synsepal and becomes restricted, stabilized, and neutralized (C). Through this process, some species form an apical crusulum (1 & 2) which acts like a doorstop before the lip is fully appressed against the synsepal.

Section *Macrophyllae-Fasciculatae* is therefore not simply morphologically hyperdiverse. It is biomechanically layered. The hyperdiversity we see is a directional continuum of structural and mechanical solutions preserved in parallel.

This is not limited to *Pleurothallis* section *Macrophyllae-Fasciculatae*. Transitional traits were identified across other genera within the *Pleurothallidinae*. Convex lips flatten incrementally. Hinges restrict progressively. Columns shorten in sequence. Structural reduction follows direction.

These transitions were not hypothetical. They were observable in sequence, and their conclusions rested not on shape alone, but on how those shapes function.

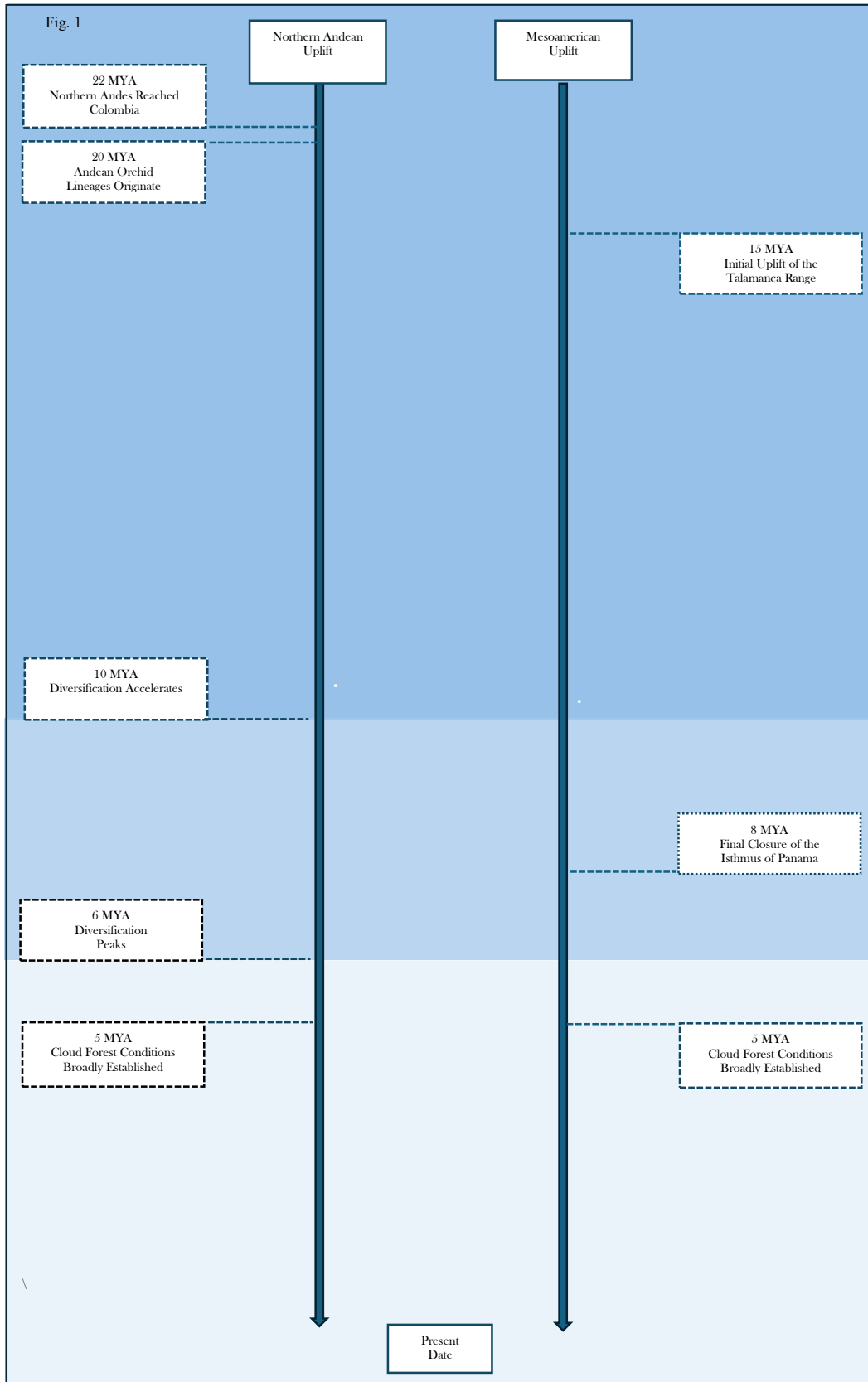
In recent decades, molecular phylogenetics has reshaped orchid classification. That shift has illuminated relationships that morphology alone could not resolve.

At the same time, the increasing reliance on abstract branching diagrams has often removed morphology, natural history, and to a great extent, logic, from the equation of taxonomic decision-making. The result is that the practice of classification has sometimes advanced without fully reintegrating functional structure into the interpretive process. That is the case within the *Pleurothallidinae*.

Andean orchid lineages began to appear approximately 20 million years ago, as mountain uplift reshaped wind exposure, precipitation patterns, drainage systems, and elevational gradients. The initial radiation of *Pleurothallis* occurred approximately 10 million years ago and diversification proceeded through three distinct environmental phases peaking approximately 6 million years ago. (Fig. 1)

In evolutionary terms, this is recent. Biomechanical evolution not just within *Pleurothallis*, but across the *Pleurothallidinae* subtribe, occurred within this same narrow geological window.

Lowland ancestors bearing loosely hinged, convex, bulbophylliform lips encountered increasing elevation and intensified wind exposure. Hinge restriction and lip stabilization followed. As uplift intensified, structural reinforcement and resupination emerged as mechanical responses to persistent directional stress. With the establishment of cloud forest conditions, pendant orientation and architectural sheltering evolved under constant moisture.



PLEUROTHALLIDINAE

In several molecular reorganizations within the *Pleurothallidinae*, species shifted between genera do not simply differ in superficial morphology from their new allies. They exhibit mechanical systems that move in opposite functional directions from the defining architecture of the group in which they are placed while other treatments have layered architecturally distinct lineages together under a single generic name. At the same time, lineages sharing identical pollination mechanics with genera maintained as distinct under molecular analysis have been reduced to synonymy within broader circumscriptions.

Because progenitors persist under budding speciation, the outcome is an overlapping ancestor–descendant pattern, or lineage layering. 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, Northern Andean forest has been reduced to roughly 25 percent of its historical range. The Andean record, where much of this radiation originated, has been disproportionately reduced. 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.

Molecular placements must remain coherent when tested against functional architecture observable in living plants and against the geographic and temporal conditions under which those lineages diversified. Classification cannot be evaluated apart from uplift history, environmental pressure, and the uneven survival of intermediate forms.

DNA reveals patterns of relatedness. Biomechanics reveal how those lineages operate in wind, rain, and gravity within a defined geological timeframe. When they conflict sharply, especially across multiple species exhibiting inverted mechanics within a thinned and unevenly preserved lineage record, the conflict itself becomes evidence.

II. Evaluation of Evolution in the *Pleurothallidinae***Biomechanical Evolution in the *Pleurothallidinae* is Directional**

Loosely hinged, convex, bulbophylliform lips represent an ancestral condition. Therefore, directional modification should follow predictable trajectories as lineages encounter new environmental pressures.

Hinges do not move from freely mobile to neutralized in a single step. Lips do not shift from convex landing platforms to structurally flattened or concave forms without passing through gradations. Column posture does not shorten or reorient without detectable sequence.

Even in a strictly bifurcating model there should be intermediates. Major structural transitions do not occur without transitional states. Whether evolution proceeds through budding speciation or through clean bifurcation, directional change in a mechanical system requires intermediate architecture.

Hinges restrict incrementally under wind exposure. Lips stabilize against structural supports. Resupination appears as a mechanical shortcut. Pendant orientation emerges under persistent moisture. Structural reinforcement increases where pollinator mass or environmental load demands it.

These transitions should leave traces. They should produce transitional forms. They should generate gradients of hinge tension, lip mass, column curvature, and orientation relative to gravity. Convex lips flatten gradually. Column posture shortens in sequence. Mechanical systems do not reverse direction without intermediates.

Even under a bifurcating interpretation, abrupt inversion of mechanical systems without transitional structure would be unexpected. Under a budding model, where progenitors persist alongside derivatives, transitional states should be even more visible.

When mechanical systems move in opposite functional directions from the defining architecture of the group in which they are placed, and no intermediates connect them, the placement requires re-examination. The absence of intermediates is not trivial. It is structurally significant. The absence of transitional structure is itself evidence.

Molecular evidence alone does not replace functional architecture. DNA reveals relatedness. Biomechanics reveal how those lineages operate in wind, rain, gravity, and persistent moisture. Interpretation must consider both.

PLEUROTHALLIDINAE

Time Constrains Possibility

The principal radiation of *Pleurothallis*, for example, occurred between approximately 10 and 6 million years ago. In evolutionary terms, this is recent. Lineage layering persists. Morphotypes coexist. Structural history remains exposed in living form.

Six million years is sufficient for diversification within a mechanical system. It is not sufficient for wholesale reversal of complex hinge architecture or column orientation without leaving intermediates, particularly when parallel lineages within the same timeframe exhibit orderly directional change under identical uplift pressures.

Mechanical Systems Are Constrained by Both Function and Time

When genera are reorganized in ways that place freely mobile hinges within groups defined by neutralized lips, or pendulous, moisture-adapted architecture within erect, wind-sensitive groups, mechanical direction appears inverted relative to uplift-driven expectation.

This is not an argument against DNA. It is a boundary condition on interpretation. Molecular data reveal patterns of relatedness. Biomechanics reveals how those lineages function within a defined geological interval. When molecular results and mechanics converge, confidence increases. When mechanical systems invert without transitional structure within a compressed timeframe, the burden of proof shifts.

Geographic Distribution Within a Shared Andean Framework

Central America is not an evolutionary reboot. Central American *Pleurothallidinae* are not independent radiations detached from Andean history. They are descendants of Andean lineages dispersing northward as uplift progressed and as the Isthmus of Panama altered connectivity. Their mechanical architecture developed within the same timeframe and under the same environmental pressures. They cannot be treated as structurally isolated systems simply because they now occupy different geography.

The closure of dispersal corridors did not reset mechanical evolution. It redistributed lineages already shaped by uplift. When Central American species exhibit hinge architecture, lip mass, column curvature, and floral orientation consistent with Andean directional patterns, they must be interpreted within that shared framework. Geographic separation does not create a new origin; it carries an existing lineage into new terrain.

To treat Central American *Pleurothallidinae* as separate evolutionary starting points ignores both time and continuity. Their placement must remain consistent with Andean origin, budding speciation, and layered mechanical diversification.

III. Interpretation Must Be Applied Consistently

“What is a *Stelis*?” This question has been framed as settled, yet the resolution depends on how floral structure is interpreted within the evolutionary history of the *Pleurothallidinae* and on whether those interpretive criteria are applied consistently.

The principal radiation of the subtribe occurred within a narrow geological interval shaped by Andean uplift. Diversification proceeded through directional biomechanical modification under sustained environmental pressure. Any circumscription of *Stelis* must be evaluated within that layered history.

Within that continuum, the flat, stabilized flowers of *Stelis* represent an endpoint, a terminal expression of a broader directional trend: progressive hinge restriction, lip stabilization, column shortening, and planar presentation.

As one of the most recent major radiations within the subtribe, *Stelis* occupies a late position within that sequence. In a temporally compressed radiation, mechanically differentiated morphotypes may remain genetically shallow while expressing distinct structural states. Apparent molecular cohesion may therefore reflect recency rather than architectural centrality.

The interpretive question is not whether molecular data recover a broadly circumscribed *Stelis*, but whether that circumscription preserves directional biomechanical continuity or compresses layered, sequentially ordered lineages into a single terminal condition.

The circumscription of *Stelis* must therefore be evaluated in light of directional mechanical evolution within a compressed Andean timeframe. Classification must distinguish between shared ancestry and shared structural state. In a radiation shaped by budding speciation and lineage layering, recent descent does not necessarily equate to mechanical equivalence.

Volume 4.1 demonstrated that diversification within section *Macrophyllae-Fasciculatae* followed a consistent directional sequence. Lip posture shifted incrementally. Hinge mobility restricted progressively. Structural stabilization and reduction occurred in ordered phases tied to uplift, wind exposure, and moisture regime.

Volume 4.3 extends that framework beyond a single section. The same directional, biomechanical pattern is observable across the *Pleurothallidinae*. Convex, freely articulated lips give way to restricted hinges. Three-dimensional enclosure flattens or stabilizes. Resupination appears as a mechanical shortcut. Pendant orientation emerges under persistent cloud-forest moisture.

This is not random diversification. It is layered, directional change produced through budding speciation. Progenitors persist. Derivatives arise alongside them. Mechanical solutions accumulate without erasing earlier forms.

The result is a biomechanically stratified subtribe, in which structural history remains visible in living architecture.

PLEUROTHALLIDINAE



Species historically described under *Acostaea* and now currently placed in *Specklinia* possess a lip that is sculpted, thickened, and architecturally complex (A–C). The deeply concave dorsal sepal (1) arches forward over the column, functioning as a protective roof that shields the column and anther from direct rainfall.



All *Acostaea* species have a sensitive, articulated, actively motile lip connected by a hinge to the column-foot (D). Upon stimulation of the callus, the lip flips upward (E), and together with the petals, forms a temporary chamber beneath the column (F). The pollinator is not trapped, but it is forced to exit upward in a single direction passing the stigma, rostellum, and pollinia. The upward-flipping lip therefore alters not only floral morphology but contact geometry and pollination sequence.



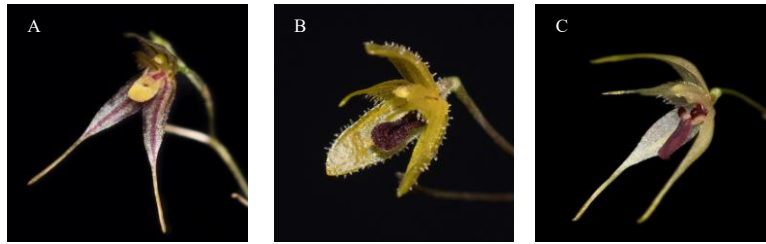
All *Porroglossum* species also have a sensitive, actively motile lip connected by a hinge to the column-foot (G). The lip is concave and the sepaline tube, a trait carried forward from its *Masdevallia* ancestors (H), arches over the column, functioning as a protective roof that shields the column and anther from direct rainfall.

Upon stimulation of the callus, the lip flips upward (I) and, together with the petals, forms a temporary chamber beneath the column. Unlike *Acostaea*, the petals don't form part of the chamber, they form an archway (2). The pollinator is not trapped, but it is forced to exit upward through the archway passing the stigma, rostellum, and pollinia. Just as in *Acostaea*, the upward-flipping lip alters not only floral morphology but contact geometry and pollination sequence.

Pollination mechanics are evolutionarily informative. If *Porroglossum* is maintained as distinct from *Masdevallia* while expressing the same snap-action, chamber-forming pollination mechanism, then pollination mechanics are being treated as subordinate to phylogenetic tree reconstruction by placing *Acostaea* within *Specklinia*.

Mechanical systems cannot be excluded from generic interpretation. If two genera exhibit the same or closely similar mechanical systems, that structural continuity must be addressed, even when molecular analyses suggest a different placement. The criteria applied in one case cannot be suspended in another.

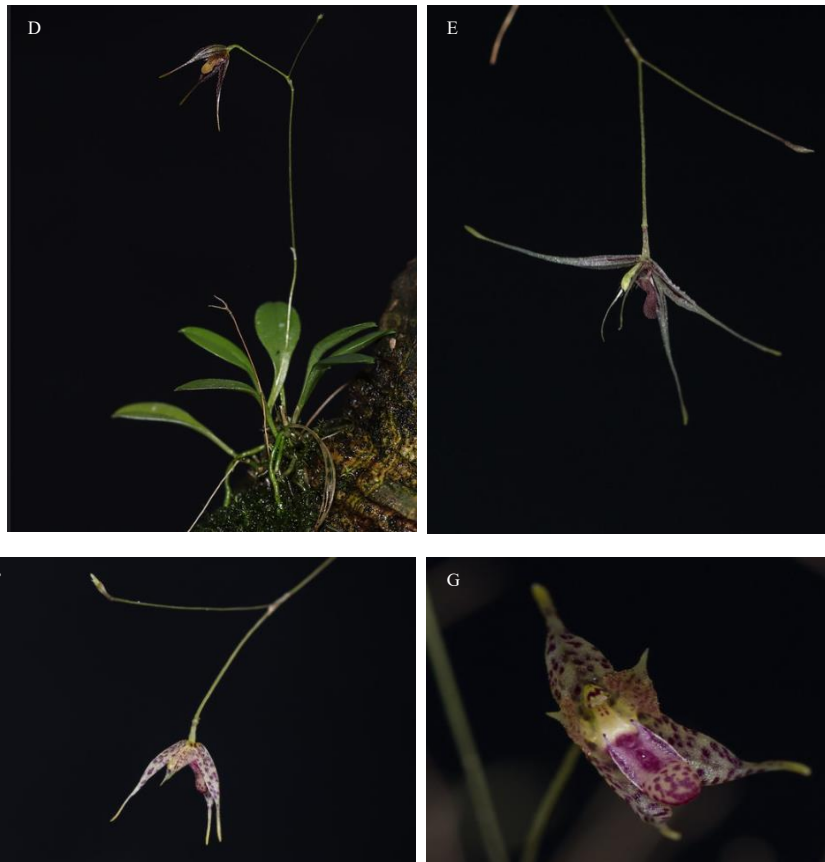
PLEUROTHALLIDINAE



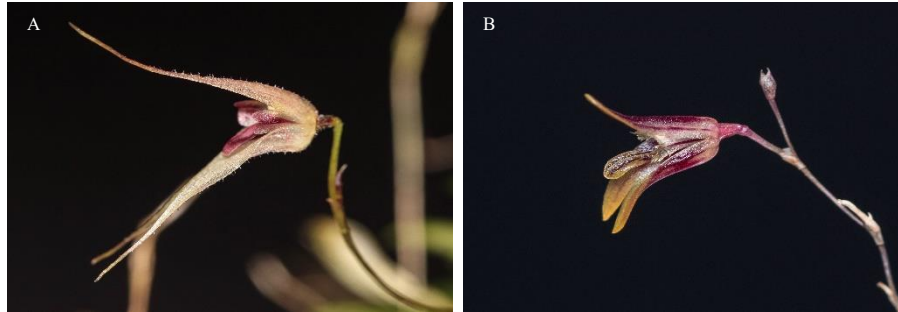
Species historically described as *Muscarella* and now placed in *Andreettaea* bear resupinate flowers with convex lips delicately hinged at the column foot. This hinge is functional. The lip shifts under weight and wind. The architecture expresses the bulbophylliform condition: a resupinate flower, a convex gravity-oriented lip, and a functional articulation at the column foot.



Scan, tap, or click the QR code below to view a live recording demonstrating labellar hinge articulation in *Muscarella*.



In most species of *Muscarella*, the lip remains mobile and responsive to weight and wind. Where mobility is reduced, it occurs within a different structural trajectory: either the lip is held obliquely against gravity (D & E) or it becomes fully appressed (F) with the flower held pendant as part of a distinct stabilization series. In these cases, orientation, hinge expression, and lip posture shift together as coordinated modifications.



Specklinia cactantha (A) exhibits floral architecture already highly modified for persistent cloud-forest conditions. Although the lip retains the outward appearance of a landing platform, it is nearly fully appressed to the synsepal. Hinge mobility is markedly reduced. The dorsal sepal arches forward, forming a roof over the column, and the flower presents a partially enclosed interior space. The system is stabilized. Movement is constrained.

The architecture in *Specklinia cactantha* does not resemble an ancestral precursor to *Acostaea*. It reflects a lineage already deeply engaged in structural stabilization and enclosure under cloud-forest pressures. The hinge is not incipient; it is diminished. The lip is not freely expressive; it is constrained. The chamber is not a transitional form toward mobility; it is a functional endpoint within its own trajectory.

In *Muscarella delicatula* (B), formerly placed in *Specklinia*, the same condition is observed: the lip appears platform-like but lies closely appressed, with severely hindered hinge expression. The dorsal sepal similarly forms a protective roof, producing an enclosed chamber rather than an exposed landing surface.

Taken together, these observations suggest that *Specklinia*, as represented by species such as *S. cactantha*, is not structurally positioned as a progenitor to *Acostaea* or a transitional form of *Muscarella*. Its mechanical system represents a separate adaptive pathway rather than an ancestral or transitional stage in the series.

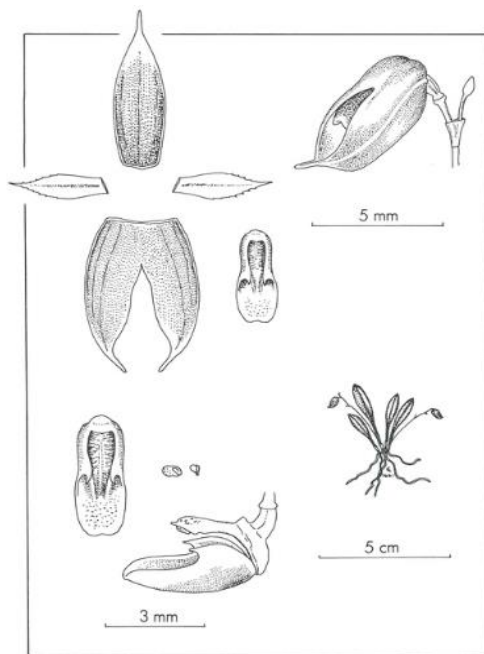


Plate 11. *Pleurothallis ocellus* (Luer) Luer

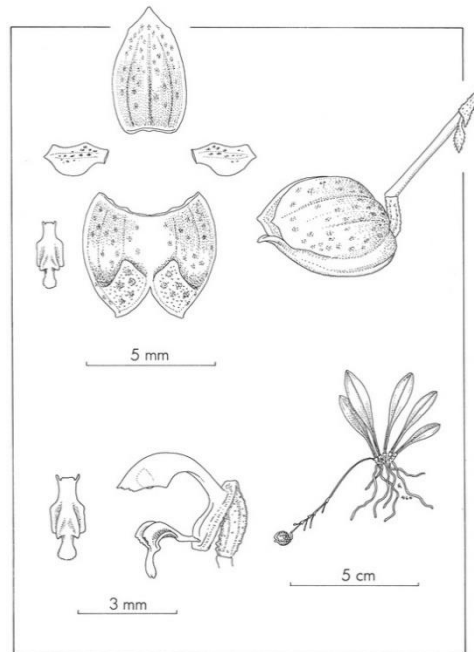
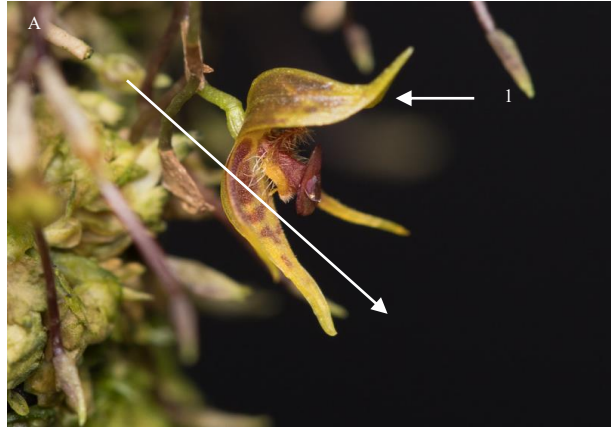


Plate 32. *Scaphosepalum ovulare* Luer

Andreettaea ocellus represents a fundamentally different floral architecture. Rather than a transitional condition, it reflects a resolved structural state within its own trajectory.

Comparison with *Scaphosepalum ovulare* reveals strong similarities in overall floral presentation. The resemblance is structural rather than superficial. *Andreettaea* is unlikely to remain a stable monospecific genus once fully evaluated within the broader *Scaphosepalum*.



The redistribution of *Salpistele* (A) between *Stelis* and *Andinia* was made on the basis of phylogenetic reconstructions. The architecture itself, however, was not thoroughly evaluated.

Geographically, all species of *Salpistele* occur in Central America, while much of the Northern Andean forest, where many related lineages originated, has been reduced to a fraction of its former range.

Central American taxa are descendants of Andean ancestors within the same uplift-driven radiation. They cannot be treated as independent developments detached from that history. The absence of transitional forms linking *Salpistele* to the reduced architecture of *Stelis* is therefore not a sampling artifact within the genus. It reflects structural continuity.

All species of *Salpistele* (A) bear elongate pedicels and present their flowers at a slight downward angle rather than in a freely pendulous position. The flowers hang obliquely beneath the inflorescence. The deeply concave dorsal sepal (l) arches forward and over the column, functioning as a protective roof, which shields the column and anther from direct rainfall.

In this orientation, a pollinator does not land upon an exposed platform. It enters a partially enclosed space. The column is not reduced or compressed. It remains elongate within this chamber. The entire floral architecture is aligned with gravity. It is angled, roofed, and enclosed.

Across all species of *Salpistele*, the lip remains three-lobed, u-shaped, and with the basal lobes flanking the column. The column remains elongate, and the dorsal sepal consistently forms a protective cover. The structural pattern is coherent across the group.



The same directional architecture appears in *Pleurothallis* section *Macrophyllae-Fasciculatae*, *Lepanthes*, and *Lepanthopsis* (A – E). In this light, the floral configuration of *Salpistele* does not represent a stage on the way to the flattened flowers of *Stelis*. It represents an endpoint, a terminal expression of a different adaptive solution.

IV. Conclusion

When Carl Luer began his extensive work on the *Pleurothallidinae*, it contained only 1,650 species and very little was known about them. Luer's *Icones Pleurothallidarum* remains a monumental effort, and it is hard to overstate how much structure it gave to the *Pleurothallidinae* when so little living context was available. There were no digital herbaria to search from a desk, no global image archives, and no quick way to test an idea against hundreds of comparable records. It is worth pausing to acknowledge what he accomplished in an analog world.

The species within the *Pleurothallidinae* are generally described using the morphological species concept, which defines species by shared, repeatable, and diagnostically consistent morphological traits. Working within that framework, Luer organized the subtribe's extraordinary hyperdiversity into a coherent morphological system, and over nearly half a century, he described 3,271 new species and established 74 new genera, giving formal structure to a group that had previously been poorly defined.

Luer was not a botanist. He was a medical doctor. In relative terms, he was a citizen scientist, and many have argued that he was unqualified to make the determinations he did without formal training in botany. Whatever one thinks of that argument, it does not change the fact that his work still provides the structural foundation for all taxonomic treatments within the *Pleurothallidinae* to this day.

Subsequent phylogenetic studies dismantled much of his morphology-based framework. As this article makes abundantly clear, those phylogenetic studies were a solution to a problem that did not exist. For roughly twenty-five years, morphological and mechanical interpretation have been ignored in favor of trees built on incomplete sampling.

We are no longer constrained by the limitations of an analog world. Restoring logical morphological and mechanical boundaries will bring clarity and stability back to the *Pleurothallidinae*. If one man described over 3,000 species in an analog world, imagine what can be accomplished in the digital world we now live in today.

V. Reinstatement of the Genus *Acostaea* Luer (*Pleurothallidinae*)

Morphological and Mechanical Basis for Generic Recognition

Species historically described under *Acostaea* possess a sensitive, actively motile lip articulated to the column-foot. Upon stimulation of the callus, the lip flips upward, creating a temporary chamber beneath the column. The pollinator cannot withdraw laterally or retreat along the entry path. Escape is possible only upward, and that route compels passage past the stigma, rostellum, and pollinia. The upward displacement therefore alters orientation, contact geometry, and pollination sequence in a coordinated mechanical event.

In *Specklinia*, the prevailing architectural pattern is a convex, gravity-oriented lip functioning as a landing platform. Under a pollinator's weight, the lip descends or flexes downward. Even where articulation is present, the movement does not generate enclosure. The lip remains a platform rather than a directional mechanism, and stabilization or reduction represents the dominant structural trend.

Acostaea does not conform to that trajectory. The lip is not a simple convex surface. It is sculpted, thickened, and architecturally complex. Its hinge is not a modification of a downward-flexing system, nor a stage of restriction. It represents a distinct mechanical configuration in which upward displacement, lip mass, and sculptural definition combine to form a one-way pollination chamber. This is a fundamentally different functional architecture.

If *Acostaea* were derived from *Specklinia*, intermediate hinge orientations or partially enclosing geometries would be expected. Such intermediates are not observed. Across the species of *Acostaea*, hinge axis, lip thickness, sculptural pattern, and directional chamber formation remain internally consistent.

Classification must preserve coherent mechanical systems. When hinge orientation, lip architecture, and pollination mechanics diverge in this manner, architecture governs circumscription. *Acostaea* is therefore reinstated here as a morphologically and mechanically coherent genus.

Mechanical Parallels with *Porroglossum*

In *Porroglossum*, the petals form an arched corridor rather than rigid sidewalls. When the lip snaps inward, the pollinator is thrust into a narrowed passage beneath the column. The petals define a vaulted exit channel, not a sealed chamber. Escape is possible only upward through this archway, and that route forces contact with the stigma and pollinia.

In *Acostaea*, the spatial geometry differs in appearance but not in outcome. When the lip flips upward, the petals and lip define a chamber beneath the column. It is not a closed trap. It is a directional structure with a single functional exit, and that exit is likewise upward past the reproductive structures.

Mechanically, the systems are homologous in principle:

- A tensioned hinge attached to the column-foot.
- Stimulus-triggered loss of turgor.
- Rapid upward displacement of the lip.
- Temporary confinement within a defined chamber.
- A forced upward exit past stigma and pollinia.

The external architecture differs, vaulted corridor in *Porroglossum* chambered enclosure in *Acostaea*, but the underlying biomechanics are the same. Both are tension-loaded, snap-action systems that convert entry into guided egress.

Mechanical systems cannot be excluded from generic interpretation. When two genera exhibit the same or closely similar mechanical architectures, that structural continuity must be addressed directly, even when molecular analyses suggest a different placement. The criteria applied in one case cannot be suspended in another.

Structural coherence and biomechanical distinction are taxonomically significant. If those standards are acknowledged as relevant, they must be applied evenly across the subtribe.

If *Porroglossum* is maintained as distinct while expressing the same snap-action, chamber-forming pollination mechanism found in other lineages, then floral mechanics are being treated as subordinate to branching topology. That standard must remain consistent. A lineage defined by a tensioned hinge at the column-foot, stimulus-triggered lip displacement, and a chamber in which the only escape route carries the insect upward past the stigma and pollinia cannot be placed within a genus characterized by a different functional architecture without directly addressing that structural discontinuity. Either pollination mechanics are evolutionarily informative, or they are not. The criteria cannot shift from one lineage to another.

VI. Reinstatement of the Genus *Muscarella* Luer (*Pleurothallidinae*)

Morphological and Historical Basis for Generic Recognition

Muscarella is the most taxonomically unstable of the genera treated here, not because it lacks coherence, but because its circumscription has been historically conflated. When Luer established *Muscarella*, he included a heterogeneous assemblage of species. Some expressed the bulbophylliform architecture characteristic of *Pleurothallis* section *Macrophyllae-Fasciculatae*, resupinate flowers, convex lips, and functional articulation at the column foot. Others did not. Several species now demonstrably belong in *Specklinia*.

Doucette subsequently transferred the group to *Andreettaea*, treating it as congeneric with *Andreettaea ocellus*. That move merged mechanically distinct floral systems and compounded the instability.

Re-examination of the protologues, type material, and living plants resolves the confusion. The assemblage historically placed in *Muscarella* separates into two coherent lineages: one belonging in *Specklinia*, and the other representing *Muscarella sensu stricto*.

At the same time, *Andreettaea* itself proves unlikely to be monospecific and is structurally discordant from core *Muscarella*. Its morphology aligns more closely with *Scaphosepalum*, particularly with species such as *Scaphosepalum ovulare*, whose floral envelope and sepal configuration show overwhelming similarity.

Structural and Mechanical Distinction

The distinction between *Muscarella* and *Andreettaea* is architectural and functional. *Andreettaea ocellus* bears a non-resupinate flower with a concave lip. The lip does not function as a mobile landing platform.

Core *Muscarella* species bear resupinate flowers with convex lips delicately hinged at the column foot. This hinge is functional. The lip shifts under weight and returns. The architecture expresses the bulbophylliform condition: a resupinate flower, a convex gravity-oriented lip, and a functional articulation at the column foot.

Resupination determines orientation. Convexity determines landing. The hinge determines motion. A concave, non-resupinate flower invites contact differently from a convex, resupinate flower whose lip shifts under load. The difference alters approach vector, balance, and column contact geometry.

Internal Structural Continuity

Within *Muscarella sensu stricto*, the lips follow a clear directional series: erect convex lips; lips with shallow basal depressions; fully prostrate lips with developed sulci; and pendant floral orientation accompanying lip modification. In species such as *Muscarella gongyloides*, lip posture, sulcus formation, and floral orientation shift together as coordinated modifications within a continuous structural framework.

Removal of Misplaced Species to *Specklinia*

Luer noted that *Muscarella delicatula* and *M. longilabris* may align more closely with *Specklinia*. Re-analysis confirms that observation.

In *M. longilabris*, the lip is firmly united to the column foot and lacks functional articulation. Without a hinge, the flower does not operate within the bulbophylliform mechanical regime.

In *M. delicatula*, articulation may be present, but the lip is laminar rather than convex and does not present a gravity-oriented landing surface. Vegetative habit closely resembles Antillean *Specklinia*.

Similarly, *M. segregatifolia* lacks the mechanical coherence of core *Muscarella* and is returned to *Specklinia*.

Reassessment of *Andreettaea*

Andreettaea ocellus represents a different floral architecture entirely. The non-resupinate orientation and concave lip depart from the bulbophylliform system.

Comparison with *Scaphosepalum ovulare* reveals strong similarities in sepal inflation, envelope formation, and overall floral presentation. The resemblance is structural rather than superficial.

Andreettaea is unlikely to remain a stable monospecific genus once fully evaluated within the broader *Scaphosepalum* clade.

Conclusion

The historical instability of *Muscarella* reflects taxonomic over-inclusion, not lack of coherence. Once species lacking hinge function and convex landing architecture are removed to *Specklinia*, *Muscarella* emerges as a morphologically and mechanically coherent genus.

VII. Reinstatement of the Genus *Salpistele* Dressler (Pleurothallidinae)

Morphological and Mechanical Basis for Generic Recognition

Within the *Pleurothallidinae*, floral architecture follows directional mechanical trends under uplift-driven environmental pressure. Lip posture, hinge expression, column length, and floral orientation change in ordered sequence. Generic recognition must reflect those structural trajectories.

The redistribution of *Salpistele* between *Stelis* and *Andinia* does not align with the architecture expressed in living plants.

The defining feature of *Salpistele* is a three-lobed, U-shaped lip forming a partial enclosure around an elongate column. The apical lobe reflexes beneath the column. The basal lobes rise along its sides and are frequently pubescent. The lip is neither reduced nor planar. It is thickened, curved, and structurally enveloping.

In *Stelis*, the prevailing trend is lip reduction and planar presentation. The lip is typically small and flattened, often forming little more than a plate beneath a shortened column. In *Andinia*, both lip and column are abbreviated, producing compact flowers with compressed proportions.

Salpistele follows a different architectural direction. The column remains elongate and spatially defined. The lip wraps and frames rather than flattens. The flower encloses rather than exposes.

All species of *Salpistele* bear elongate pedicels and present their flowers obliquely beneath the inflorescence. They are not freely pendulous. In this orientation, a pollinator does not land upon an exposed platform. It enters a partially enclosed chamber.

The dorsal sepal is deeply concave and arches forward over the column, forming a protective roof that shields the column and anther from direct rainfall. The column remains elongate within this sheltered space. The floral architecture is aligned with gravity but not flattened by it. It is angled, roofed, and enclosed.

This configuration does not represent a stage along the path toward lip reduction observed in *Stelis*. Where *Stelis* trends toward simplification and planar exposure, *Salpistele* develops curvature, enclosure, and elongation. Where *Andinia* shows column shortening and compact architecture, *Salpistele* retains extension and spatial depth.

Directional reduction does not reverse abruptly. Floral systems trending toward planar simplification do not generate elongate columns encircled by reflexed, channel-forming lips without intermediate structure. No such intermediates are observed.

Across all species of *Salpistele*, the same structural pattern recurs:

- Three-lobed, column-embracing lip
- Elongate column
- Concave, forward-arching dorsal sepal
- Oblique, roofed floral presentation

The architecture is internally coherent, and that coherence is taxonomically significant. Within a subtribe shaped by directional biomechanical change, generic limits must preserve consistent structural trajectories. *Salpistele* expresses a stable architectural solution distinct from the reductional pathway characteristic of *Stelis* and the abbreviated configuration of *Andinia*.

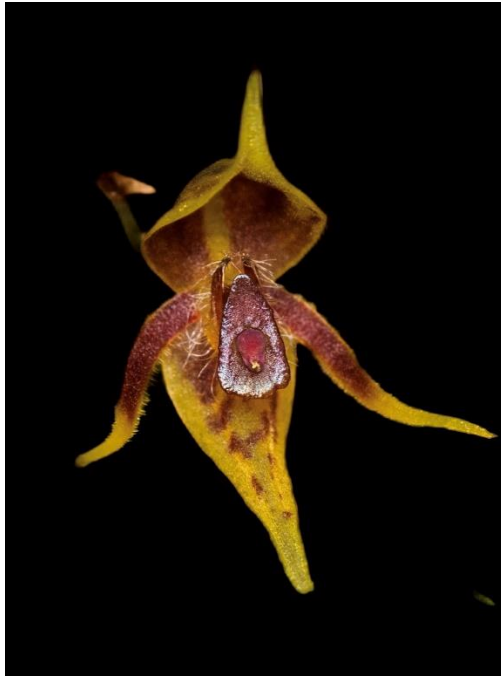
Geographically, all species of *Salpistele* occur in Central America within the same uplift-driven radiation that produced related Andean lineages. Central American taxa are descendants of that shared history, not independent structural origins. The absence of transitional forms linking *Salpistele* to the reduced architecture of *Stelis* reflects continuity within its own trajectory rather than deficiency of sampling.

Generic recognition should preserve coherent mechanical architecture where it is consistently expressed. The floral type represented by *Salpistele* is neither transitional nor ambiguous. It is a resolved structural state within a directional evolutionary framework.

VIII. References (Literary)

- Arias, T., Moreno, J. S., Reyes, S., et al. (2025). Plastome phylogenomics of the diverse Neotropical orchid genus *Lepanthes* with emphasis on subgenus *Marsiphanthes* (Pleurothallidinae: Orchidaceae). *BMC Ecology and Evolution*, 25, 79. <https://doi.org/10.1186/s12862-025-02396-6>
- Belfort Oconitrillo, N., Salguero Hernández, G., Oses, L., Gil-Amaya, K., Rojas-Alvarado, G., Chinchilla, I., Díaz-Morales, M., Pupulin, F., Bogarín, D., & Karremans, A. (2024). New species and records of Orchidaceae from Costa Rica IV. *Lankesteriana*, 24, 141–192. <https://doi.org/10.15517/lank.v24i2.60686>
- Bogarín, D., Hernández, Z., Samudio, Z., Rincón, R., & Pupulin, F. (2014). An updated checklist of the Orchidaceae of Panama. *Lankesteriana*, 14, 135–364. <https://doi.org/10.15517/lank.v14i3.17958>
- Bush, M. B., Rozas-Dávila, A., Raczka, M., Nascimento, M., Valencia, B., Sales, R. K., McMichael, C. N. H., & Gosling, W. D. (2022). A palaeoecological perspective on the transformation of the tropical Andes by early human activity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1849), 20200497. <https://doi.org/10.1098/rstb.2020.0497>
- Caetano, D., & Quental, T. (2023). How important is budding speciation for comparative studies? *Systematic Biology*, 72. <https://doi.org/10.1093/sysbio/syad050>
- Crawford, D. J. (2010). Progenitor-derived species pairs and plant speciation. *Taxon*, 59, 1413–1423. <https://doi.org/10.1002/tax.595008>
- Diaz Hernandez, A. G., Ocupa-Horna, L., Godo, L., & Wilson, M. (2018). A new species of *Andinia* (Orchidaceae, Pleurothallidinae) from Huánuco, Peru, and the first Peruvian locality for *Andinia* schizopogon. *Phytotaxa*, 361, 222. <https://doi.org/10.11646/phytotaxa.361.2.7>
- Doucette, A. (2022, September 16). New combinations in *Andreettaea* (Pleurothallidinae [Orchidaceae]). *Internet Orchid Species Photo Encyclopedia: Nomenclature Notes*, 8(1). <http://www.orchidspecies.com>
- Doucette, A. D., Medina, H., Portilla, J., & Cameron, K. M. (2022). The phylogenetic placement of *Andreettaea* ocellus has significant implications for generic circumscription of Pleurothallidinae (Orchidaceae). *Orchids*, 91, 768–779.
- Etter, A., & Wyngaarden, W. (2000). Patterns of landscape transformation in Colombia, with emphasis in the Andean region. *AMBIO*, 29, 432–439. <https://doi.org/10.1579/0044-7447-29.7.432>
- Fischer, G., Gravendeel, B., Sieder, A., Andriantiana, J., Heiselmayer, P., Cribb, P., Smidt, E., Samuel, R., & Kiehn, M. (2007). Evolution of resupination in Malagasy species of *Bulbophyllum* (Orchidaceae). *Molecular Phylogenetics and Evolution*, 45, 358–376. <https://doi.org/10.1016/j.ympev.2007.06.023>
- Gazel, E., Hayes, J., Ulloa, A., Alfaro, A., Coleman, D., Drew, C., & Carr, M. (2019). The record of the transition from an oceanic arc to a young continent in the Talamanca Cordillera. *Geochemistry, Geophysics, Geosystems*, 20. <https://doi.org/10.1029/2018gc008128>
- Holcomb, K. W. (2026). The Evolutionary History of Pleurothallis Section *Macrophyllae-Fasciculatae* (Orchidaceae). *Pleurothallidinae*, 4.1. ISSN 2834-1783.
- Karremans, A. (2016). Genera Pleurothallidarum: An updated phylogenetic overview of Pleurothallidinae. *Lankesteriana*, 16, 219–241. <https://doi.org/10.15517/lank.v16i2.26008>
- Karremans, A. (2019). To be, or not to be a *Stelis*. *Lankesteriana*, 19. <https://doi.org/10.15517/lank.v19i3.40082>
- Karremans, A., & Díaz-Morales, M. (2019). The Pleurothallidinae: Extremely high speciation driven by pollinator adaptation [Unpublished manuscript].
- Luer, C. A. (1975). *Icones Pleurothallidarum* (Orchidaceae) Pleurothallis of Ecuador III. *Selbyana*, 1, 303.
- Luer, C. A. (1977). *Icones Pleurothallidarum* (Orchidaceae): Various species in the Pleurothallidinae. *Selbyana*, 3, 400.
- Luer, C. A. (1986). *Icones Pleurothallidarum* IV. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 20.
- Luer, C. A. (1988). *Icones Pleurothallidarum* VIII. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 24.
- Luer, C. A. (2005). *Icones Pleurothallidarum* XXVII: *Dryadella* and *Acronia* section *Macrophyllae-Fasciculatae*. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 103, 1–311.
- Luer, C. A. (2006). *Icones Pleurothallidarum* XXVIII. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 105, 1–281.
- Marder, E., Smiley, T., Yanites, B., & Kravitz, K. (2025). Direct effects of mountain uplift and topography on biodiversity. *Science*, 387, 1287–1291. <https://doi.org/10.1126/science.adp7290>

- Pérez-Escobar, O. A., Zizka, A., Bermúdez, M. A., Meseguer, A. S., Condamine, F. L., Hoorn, C., Hooghiemstra, H., Pu, Y., Bogarín, D., Boschman, L. M., Pennington, R. T., Antonelli, A., & Chomicki, G. (2022). The Andes through time: Evolution and distribution of Andean floras. *Trends in Plant Science*, 27(4), 364–378. <https://doi.org/10.1016/j.tplants.2021.09.010>
- Pérez-Escobar, O., Bogarín, D., Przelomska, N., Ackerman, J., Balbuena, J. A., Bellot, S., Buehlmann, R., Cabrera, B., Cano, J., Charitonidou, M., Chomicki, G., Clements, M., Fernández, M., Flanagan, N., Gravendeel, B., Hágsater, E., Halley, J., Hu, A.-Q., ... Antonelli, A. (2023). The origin and speciation of orchids. *bioRxiv*. <https://doi.org/10.1101/2023.09.10.556973>
- Pérez-Escobar, O., Chomicki, G., Condamine, F., Karremans, A., Bogarín, D., Matzke, N., Silvestro, D., & Antonelli, A. (2017). Recent origin and rapid speciation of Neotropical orchids in the world's richest plant biodiversity hotspot. *New Phytologist*, 215, 891–905. <https://doi.org/10.1111/nph.14629>
- Pridgeon, A. M., & Chase, M. W. (2001). A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). *Lindleyana*, 16(4), 235–271.
- Pridgeon, A. M., & Chase, M. W. (2002). Nomenclatural notes on Pleurothallidinae (Orchidaceae). *Lindleyana*, 17(2), 98–101.
- Teixeira, S. de P., Borba, E. L., & Semir, J. (2004). Lip anatomy and its implications for the pollination mechanisms of *Bulbophyllum* (Orchidaceae) species. *Annals of Botany*, 93(5), 499–505. <https://doi.org/10.1093/aob/mch072>
- Trávníček, P., Ponert, J., Dantas-Queiroz, M. V., & Chumova, Z. (2025). Integrating genome-wide traits and multi-loci phylogeny to investigate orchid evolution: A case study on Pleurothallidinae. *The Plant Journal*, 122. <https://doi.org/10.1111/tj.70281>
- Turland, N. J., Wiersema, J. H., Barrie, F. R., et al. (2018). *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)*. Koeltz Botanical Books.
- Wilson, M., Pupulin, F., Archila, F., Damon, A., & Gómez, R. (2013). A newly recognized clade of Pleurothallis with Mesoamerican distribution. *Lankesteriana*. <https://doi.org/10.15517/lank.v0i0.11567>
- Wilson, M., Frank, G., Jost, L., Pridgeon, A., Vieira-Uribe, S., & Karremans, A. (2017). Phylogenetic analysis of *Andinia* (Pleurothallidinae; Orchidaceae) and a systematic re-circumscription of the genus. *Phytotaxa*, 295, 101. <https://doi.org/10.11646/phytotaxa.295.2.1>



Salpistele brunnea

PLEUROTHALLIDINAE

Copyright © 2022-2026
Kevin W. Holcomb
All rights reserved
ISSN #2834-1783
ORCID #0000-0002-0571-4462