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Evolutionary diversification and historical biogeography of orchidaceae in Central America with emphasis on Costa Rica and Panama

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Chapter 3

Genus-level taxonomical changes in the *Lepanthes* affinity (Orchidaceae: Pleurothallidinae)

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Phytotaxa 340, 128–136. 2018.

Abstract. We propose a new classification of the *Lepanthes* affinity based on phylogenetic re-evaluation of the Pleurothallidinae. Fourteen genera are recognized as belonging to the affinity. They are found highly supported in a DNA-based phylogenetic inference of combined plastid (*matK*) and nuclear (nrITS) datasets. The necessary changes, including four novel generic concepts, needed to reorganize the *Lepanthes* affinity, are proposed here to insure monophyly. The integral discussion on the phylogenetics and biogeography of the group, together with morphological characterization of each clade is presented in Chapter 2.

3.1 Introduction

With about 5,200 known species, Pleurothallidinae is currently the most species-rich subtribe in the Neotropics, and one of the richest in the Orchidaceae. After the first phylogenetic study of the subtribe by (Pridgeon et al., 2001), and the subsequent proposal to recircumscribe most of its genera (Pridgeon and Chase, 2001), numerous studies aimed to refine or redefine generic concepts in the different clades of Pleurothallidinae have been published. Among the nine greater clades within the subtribe, the *Lepanthes* Sw. affinity (Karremans, 2016) is one of the most species-rich, encompassing more than 1,400 species. The currently recognized genera that are members of this clade are *Anathallis* Barbosa Rodrigues [116], *Draconanthes* (Luer) Luer [2], *Fronitaria* Luer [1], *Lankesteriana* Karremans [21], *Lepanthes* [1122], *Lepanthopsis* (Cogn.) Ames [45], *Trichosalpinx* Luer [124] and *Zootrophion* Luer [26] (Chase et al., 2015; Karremans, 2016). The polyphyletic nature of some of these genera, especially *Anathallis* and *Trichosalpinx*, was suggested by several independent DNA-based phylogenetic analyses and supported by morphological observations (Chiron et al., 2012; Karremans, 2014; Luer, 1997; Luer, 2006; Pérez-Escobar et al., 2017a; Pridgeon and Chase, 2001; Rykaczewski et al., 2017). Nevertheless, no integrate, corrective, classification system was proposed, most likely due to the difficulty of adequately inferring relatedness on the basis of morphology on its own, the availability of DNA data from far too few members of the affinity and the difficulties in sampling poorly known species of restricted distribution. We propose a new classification of the *Lepanthes* affinity based on our previous studies (Karremans, 2016, 2014; Pérez-Escobar et al., 2017a) and a phylogenetic re-evaluation of the Pleurothallidinae from a broad set of species belonging to the majority of the genera and subgenera proposed within the group (Bogarín et al. in review). To avoid dealing with nomenclatural issues in the cited study, the necessary changes needed to reorganize the *Lepanthes* affinity are proposed here to assure that its genera are monophyletic and reflect the nature of its relationships (Fig. 3.1). Within the *Lepanthes* affinity fourteen genera can be recognized with high support in maximum likelihood (ML) and Bayesian inference (BI) analyses (Fig. 3.1). This study supports the more generally accepted genera such as *Anathallis*, *Draconanthes*, *Fronitaria*, *Lankesteriana*, *Lepanthes*, *Lepanthopsis*, *Trichosalpinx* and *Zootrophion*. Also, highly supported as distinct clades are the less widely accepted genera *Pseudolepanthes* (Luer) Archila and *Tubella* (Luer) Archila. In addition to these, four novel generic concepts are required. They are *Gravendeelia*, *Opilionanthe*, *Pendusalpinx* and *Stellamaris*. In order to attain monophyly, and insure the least nomenclatural instability within this affinity, the following changes were proposed (Bogarín et al., 2017c):

3.2 Taxonomical treatment

3.2.1 *Anathallis* Barb.Rodr., Gen. Sp. Orchid. 1: 23. 1877.

Type: *Anathallis fasciculata* Barb.Rodr., Gen. Sp. Orchid. 1: 23–24. 1877.

Comments: *Anathallis* species are easily recognized by the non-lepanthiform sheaths of the ramicaul, and the starshaped flower, with free perianth parts. The linear to lanceolate, acute to acuminate petals are similar to the sepals in size and shape. The sensitive lip is perpendicularly

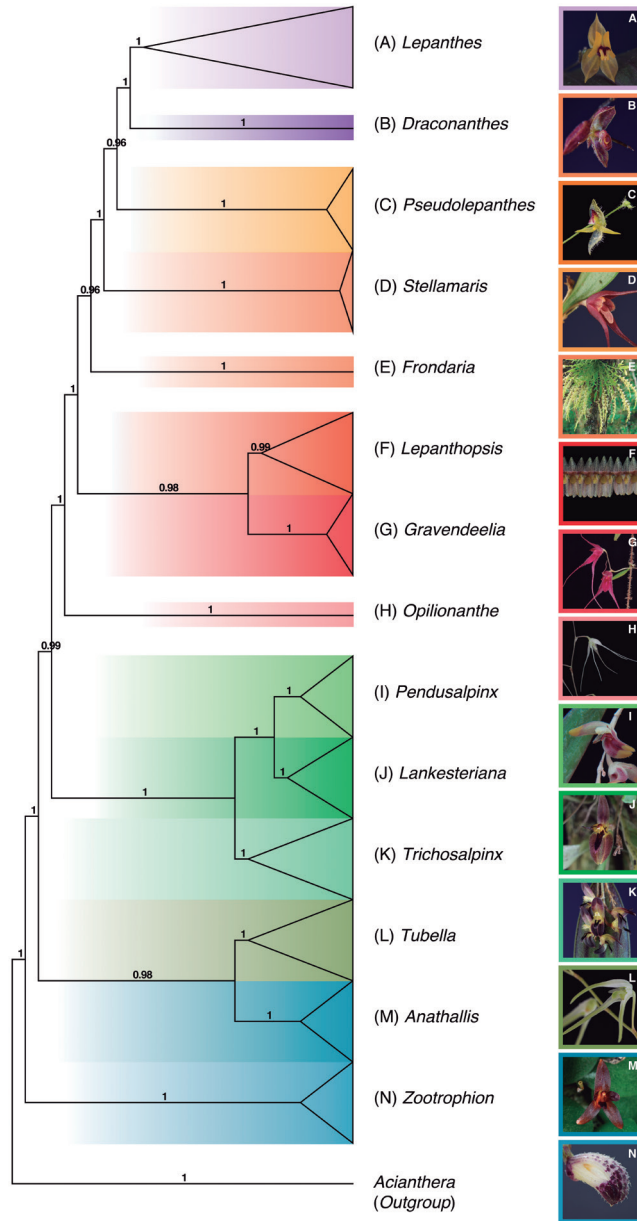


Figure 3.1. Phylogenetic analysis based on Bayesian inference of the *Lepanthes* affinity (nrITS and plastid matK sequences) from more than one-hundred different species. Terminals ending in triangles represent genera with multiple species and single terminals are monospecific genera (*Draconanthes*, *Frondaria*, *Gravendeelia*, *Opilionanthe* and *Stellamaris*). Photographs: A, B, D, F, J–K, L–N by D. Bogarín; C by S. Vieira-Uribe; E by Ecuagenera; G, H, I by W. Driessen.

hinged to the column foot, and its general shape is linear-ligulate but frequently it has small lobes at the base and/or middle. The column is sharply winged and prominently fimbriate. The pollinaria come in pairs and have reduced flat caudicles. There are currently 118 accepted species of *Anathallis*, including the one added hereafter. They are distributed from western Mexico through Central America, the Antilles and down to Argentina. They are most diverse in Brazil at low to mid elevations. *Anathallis*, as defined by Karremans (2014), is highly supported in our analyses and is modified only by the inclusion of the following species:

Anathallis convallium (Kraenzl.) Karremans & Mel.Fernández, *Phytotaxa* 340(2): 130. 2018. Basionym: *Pleurothallis convallium* Kränzlin, *Ark. Bot.* 16(8): 12. 1921.

This name has been placed under *A. linearifolia* (Cogn.) Pridgeon & Chase, a species from which it differs significantly.

3.2.2 *Gravendeelia* Bogarín & Karremans, *Phytotaxa* 340(2): 130. 2018.

Type: *Pleurothallis chamaelepanthes* Rchb.f., *Bonplandia* 3: 240. 1855.

Diagnosis: *Gravendeelia* is most closely related to *Lepanthopsis*. It can be easily distinguished from that genus by the long-prolific, pendent habit (vs. caespitose, rarely prolific, erect), the few-flowered inflorescence (vs. generally multi-flowered), the cupped flower with extremely long sepals (flowers flat, sepals and petals similar), the elongate lip with two central keels (vs. lip compact, with a basal glenion), the elongate column with a distinct foot (vs. column short, stout, footless), the incumbent anther and ventral, entire stigma (vs. apical anther and bilobed stigma). Morphologically, *Gravendeelia* is reminiscent of *Tubella*, however it can be distinguished by the pendulous plants, the hirsute ovary (vs. glabrous), the hirsute sepals (vs. glabrous), and the short column foot (vs. prominent).

Comments: The only species currently known to belong to this genus is relatively common in Colombia and Ecuador, and is likely to represent a species complex in need of revision (the name bears two heterotypic synonyms at this time). The recognition of the novel genus *Gravendeelia* is highly supported in our analyses, the accessions of its only species formed a highly supported clade (Fig. 3.1) (PP=1.0), sister to *Lepanthopsis* (Fig. 3.1; P.P.: 0.98), and not closely related to any of the other species previously placed in *Trichosalpinx*. Treating *Gravendeelia* as part of a broadly defined *Lepanthopsis* is undesirable as it would result in an undiagnosable genus, whilst when kept separate they are easily recognizable.

Eponymy: The name honors orchid evolutionary biologist Dr. Barbara Gravendeel, Leiden University and Naturalis Biodiversity Center, The Netherlands, who has continuously supported these phylogenetic studies in the Pleurothallidinae.

Gravendeelia chamaelepanthes (Rchb.f.) Bogarín & Karremans, *Phytotaxa* 340(2): 130. 2018. Bas. *Pleurothallis chamaelepanthes* Rchb.f., *Bonplandia* 3: 240. 1855.

3.2.3 *Stellamaris* Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 131. 2018.

Type: *Pleurothallis pergrata* Ames, *Schedul. Orch.* 4: 24–25. 1923.

Diagnosis: *Stellamaris* is phylogenetically allied to *Draconanthes*, *Lepanthes* and *Pseudolep-*

anthes. From *Pseudolepanthes* it can be easily distinguished by the very short, few-flowered inflorescence (vs. elongate, multiflowered inflorescence), the long-caudate sepals (vs. shortly acuminate, similar to the petals), the ecallose lip (vs. lip with a prominent verrucose callus), the elongate column, with a prominent column foot (vs. column short, reflexed, footless), and the pollinia with a pair of flattened caudicles, lacking a viscidium (vs. pollinia with obsolete caudicles, with viscidium). From *Lepanthes*, *Stellamaris* can be recognized by the laminated petals (vs. transversally bilobed), the un-lobed lip (vs. lip bilobed, with a basal appendix), the incumbent anther and ventral stigma (vs. anther and stigma apical), and the pollinia without viscidium (vs. pollinia with a viscidium). From *Draconanthes*, *Stellamaris* can be distinguished by the very short, few-flowered inflorescence (vs. elongate, multi-flowered inflorescence), the laminate, un-lobed, elongate lip (vs. bilobed, with a rudimentary appendix, embracing the column). *Stellamaris* is florally most similar to the unrelated genus *Tubella*, however, it can be immediately set aside by the non-prolific habit, the hirsute lepanthiform sheaths, the inflorescence shorter than the leaf bearing one or two flowers, and an extremely reduced pedicel.

Comments: The only species currently known to belong to this genus is variable across its distribution, from Costa Rica to Colombia, and is likely to represent more than a single species. The recognition of the novel genus *Stellamaris* is highly supported in our analyses, the accessions of its only species formed a highly supported clade (Fig. 3.1) (PP=1.0), sister to a clade including *Lepanthes*, *Draconanthes* and *Pseudolepanthes* (Fig. 3.1) (PP=1.0), which are all morphologically distinct. Even though *Stellamaris*, *Gravendeelia* and *Tubella* show superficially similar flowers, they are not closely related phylogenetically.

Etymology: Derived from the Latin *Stellamaris* “starfish”, in allusion to the red or crimson starfish-like flowers with long-tailed sepals.

Stellamaris pergrata (Ames) Mel.Fernández & Bogarín, Phytotaxa 340(2): 131. 2018. Bas. *Pleurothallis pergrata* Ames, Schedul. Orch. 4: 24–25. 1923.

3.2.4 *Opilionanthe* Karremans & Bogarín, Phytotaxa 340(2): 131. 2018.

Type: *Trichosalpinx manningii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 113, f. 28. 2002.

Diagnosis: *Opilionanthe* has apparently no close relatives, it is phylogenetically sister to a clade which includes *Lepanthes*, *Lepanthopsis* and all of their allies. The cupped flower with long-caudate sepals is somewhat reminiscent of species of *Gravendeelia*, *Stellamaris* and *Tubella*, however, it can be immediately distinguished from those by the long-caudate petals which are similar to the sepals (vs. acute to obtuse, conspicuously shorter than the sepals). From the first two genera it may also be distinguished by the long, multi-flowered inflorescence (vs. short, few-flowered). In species of *Anathallis*, the sepals and petals are frequently similar to each other, however, *Opilionanthe* can be distinguished from species of that genus by the lepanthiform-bracts and prolific habit.

Comments: The recognition of *Opilionanthe* is highly supported in our analyses, the accessions of its only species formed a highly supported clade (Fig. 3.1) (PP=1.0), sister to a clade that includes *Draconanthes*, *Fronitaria*, *Gravendeelia*, *Lepanthes*, *Lepanthopsis*, *Pseudolepanthes* and *Stellamaris* (Fig. 3.1) (PP=1.0). The single species known to belong this genus is endemic to Peru.

Etymology: From Opiliones, an order of arachnids known as harvestmen, harvesters or daddy longlegs, and the Greek anthos, “flower”, in allusion to the long, slender acuminate petals and sepals reminiscent to the long-legged opiliones, distinctive of this genus among its relatives.

Opilionanthe manningii (Luer) Karremans & Bogarín, *Phytotaxa* 340(2): 131. 2018. Basionym: *Trichosalpinx manningii* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 88: 113, f. 28. 2002.

3.2.5 *Pendusalpinx* Karremans & Mel.Fernández, *Phytotaxa* 340(2): 131–132. 2018.

Type: *Pleurothallis berlineri* Luer, *Selbyana* 3(1–2): 60. 1976. Synonym: *Trichosalpinx berlineri* (Luer) Luer, *Phytologia* 54(5): 394. 1983.

Diagnosis: *Pendusalpinx* is sister to genus *Lankesteriana*, but can be immediately distinguished by the large, up to 30 cm tall, pendulous plants (vs. short, less than 3 cm tall, erect), with ramicauls longer than or similar to the leaf (vs. much shorter than the leaf), covered by large, lepanthiform bracts (bract inconspicuous, not lepanthiform), the glaucous leaves twisted at the base (vs. green, straight), the pendent inflorescence, shorter than the leaf, with several flowers open at once (vs. erect to arching, longer than the leaf, with one flower open at a time), the petals are triangular to elliptic (vs. generally lanceolate), and the lip flat (vs. with a deep mid-line depression). Species of *Pendusalpinx* are superficially more similar to *Trichosalpinx*, but can be distinguished by the pendulous plants, the ramicauls covered by conspicuous, whitish bracts (vs. smaller, brown bracts), the glaucous leaves, pendent, basally twisted (vs. green, erect, straight) leaves, and a pair of broad angled wings above the middle of the column (vs. without broad angled wings above the middle).

Comments: The genus includes six species that are distributed from Colombia and Venezuela to Bolivia and Peru. They are not present in Central America, the Antilles and Brazil. The recognition of the novel genus *Pendusalpinx* is highly supported in our analyses, the accessions of several of its species consistently formed a highly supported clade (Fig. 3.1) (PP=1.0), sister to *Lankesteriana* (Fig. 3.1) (PP=1.0), as was previously found by Karremans (2014) and Pérez-Escobar *et al.* (2017). The two genera are highly supported, genetically well separated and morphologically distinct in virtually every aspect. *Pendusalpinx* species share several features with *Trichosalpinx*, nevertheless, they are consistently found sister to *Lankesteriana* instead. The two genera are here highly supported as sisters of *Trichosalpinx* in the strict sense, nevertheless, such a relationship has not been found in previous DNA based studies, and in the interest of stability and definability they are recognized as distinct.

Etymology: Derived from the Latin *pendulous* “pendent” and *salpinx* “funnel-shaped” (taken from *Trichosalpinx*); a pendent *Trichosalpinx*.

Pendusalpinx berlineri (Luer) Karremans & Mel.Fernández, *Phytotaxa* 340(2): 132. 2018. Basionym: *Pleurothallis berlineri* Luer, *Phytologia* 54(5): 394. 1983.

Pendusalpinx dependens (Luer) Karremans & Mel.Fernández, *Phytotaxa* 340(2): 132. 2018. Basionym: *Pleurothallis dependens* Luer, *Selbyana* 3(1–2): 94, f. 150. 1976.

Pendusalpinx echinata (Luer & Hirtz) Karremans & Mel.Fernández, *Phytotaxa* 340(2): 132. 2018. Basionym: *Trichosalpinx echinata* Luer & Hirtz in Luer, *Selbyana* 30: 24, f. 47. 2009.

Pendusalpinx glabra (D.E.Bennett & Christenson) Karremans & Mel.Fernández, Phytotaxa 340(2): 132. 2018. Basionym: *Trichosalpinx glabra* Bennett & Christenson, Brittonia 46(3): 256, 258–259, f. 18. 1994.

Pendusalpinx patula (Luer) Karremans & Mel.Fernández, Phytotaxa 340(2): 132. 2018. Basionym: *Trichosalpinx patula* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 82. 1998.

Pendusalpinx sijmii (Luer) Karremans & Mel.Fernández, Phytotaxa 340(2): 132. 2018. Basionym: *Trichosalpinx sijmii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 8: 113–114, f. 29. 2002.

Pendusalpinx vasquezii (Luer) Karremans & Mel.Fernández, Phytotaxa 340(2): 132. 2018. Basionym: *Trichosalpinx vasquezii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 35, f. 24. 1997.

3.2.6 *Pseudolepanthes* (Luer) Archila, Revista Guatemal. 3(1): 76. 2000.

Basionym: *Trichosalpinx* subgen. *Pseudolepanthes* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 5. 1997.

Type: *Trichosalpinx pseudolepanthes* Luer & Escobar, Orquideología 16(2): 183. 1984.

Comments: This genus has not received wide recognition as distinct among authors (Pridgeon, 2005). However, our initial phylogenetic sampling supports this group as sister to *Draconanthes* and *Lepanthes* and not particularly closely related to *Trichosalpinx* (Luer, 1997). From those genera, it is distinguished by the presence of a large, verrucose callus on the disc of the lip. It is distinguished from *Lepanthes* by the absence of a basal appendix and the unlobed petals (vs. transversally bilobed), the lip is not bilobed with the lobes embracing the column as in *Draconanthes* and most of the *Lepanthes* species. From *Trichosalpinx* it differs in the progressively elongated, successively flowered inflorescences longer than the leaves (vs. several flowered inflorescences, shorter or as long as the leaves) and the short, footless column (vs. elongated, footed).

Etymology: Derived from the Latin pseudo “false” and *Lepanthes*, a “false *Lepanthes*” referring to the morphological similarities with the genus *Lepanthes*.

3.2.7 *Tubella* (Luer) Archila, Revista Guatemal. 3(1): 46. 2000.

Basionym: *Trichosalpinx* subgen. *Tubella* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 66. 1986. Type: *Pleurothallis acremona* Luer, Selbyana 5(2): 157. 1979. Synonym.: *Trichosalpinx* subgen. *Tubella* sect. *Tubellae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 68. 1986.

Type: *Pleurothallis acremona* Luer, Selbyana 5(2): 157. 1979. Synonym.: *Pleurothallis* sect. *Acuminatae* subsect. *Lepanthiiformes* Lindley, Fol. Orchid. Pleurothallis 32. 1859, *nom. illeg.* Type. *Pleurothallis arbuscula* Lindley, Edwards’s Bot. Reg. 28: Misc. 72–73. 1842.

Comments: Species of *Tubella* have a slender habit, commonly with proliferating ramicauls covered by lepanthiform sheaths, the inflorescence is longer than the leaf, the ovary is glabrous, the sepals membranaceous, glabrous, shortly acuminate, concave, the petals much shorter, entire, elliptic, the lip simple, commonly three-lobed, the base unguiculate, lacking lobules, the column elongated, apically winged, with a prominent column foot (Fernández, 2014). Species of *Tubella* are phylogenetically related to *Anathallis* from which they are separated by the slender habit, proliferating ramicauls with lepanthiform sheaths (vs. creeping or caespitose without proliferat-

ing ramicauls, and lacking the lepanthiform sheaths), and inflorescences longer than the leaves bearing several flowers (vs. inflorescences frequently shorter than the leaf and few-flowered). The flowers of *Tubella* are superficially similar to *Gravendeelia*, *Stellamaris* and *Opilionanthe* in the cupped flower with long caudate sepals and elongate column, however, they are not related phylogenetically. *Tubella* is redefined from its previous circumscription by the exclusion of the species belonging to *Gravendeelia*, *Opilionanthe*, and *Stellamaris*, which are not closely related, and by the inclusion of the following six species:

Tubella adnata (I.Jiménez) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. 2018. Basionym: *Trichosalpinx adnata* Jiménez, *Lankesteriana* 15(3): 194. 2015.

Tubella carmeniae (Luer) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. 2018. Basionym: *Trichosalpinx carmeniae* Luer, *Harvard Pap. Bot.* 17: 366, f. 42. 2012.

Tubella gabi-villegasiae (I.Jiménez) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. 2018. Basionym: *Trichosalpinx gabi-villegasiae* I.Jiménez, *Lankesteriana* 15(3): 196. 2015.

Tubella giovi-mendietae (I.Jiménez) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. Basionym: *Trichosalpinx giovi-mendietae* I.Jiménez, *Lankesteriana* 15(3): 199. 2015.

Tubella reticulata (Thoerle & C.Soto) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. Basionym: *Trichosalpinx reticulata* Thoerle & Soto, *Lankesteriana* 15(1): 95–96, f. 1A–F, 2. 2015.

Tubella wernerii (Luer) Mel.Fernández & Bogarín, *Phytotaxa* 340(2): 133. Basionym: *Trichosalpinx wernerii* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 88: 114, f. 30. 2002.

3.3 Additional Nomenclatural Changes

Platystele kayi (Thoerle & Cornejo) Bogarín & Karremans, *Phytotaxa* 340(2): 133. 2018. Basionym: *Lepanthopsis kayi* Thoerle & Cornejo *Harvard Pap. Bot.* 21: 247. 2016.

Comments: This recently described species was placed by the authors in *Lepanthopsis*. However, the ramicaul much shorter than the long petiolate leaf (vs. ramicaul normally longer than the non-petiolate leaf), bearing tubular sheaths (vs. sheaths lepanthiform), the lip that exceeds the length of sepals (vs. lip shorter than sepals), and the obsolete, truncate rostellum (vs. rostellum conspicuously triangular) are indicative of *Platystele* Schltr., not *Lepanthopsis*.

3.4 Conclusions

The polyphyletic nature of the genera *Anathallis* and *Trichosalpinx* has been previously recognized by several authors (Chiron et al., 2012; Karremans, 2014; Pridgeon et al., 2001). Nevertheless, no alternative classification proposal was published for the species belonging to the genera for lack of a clear overview of the relationships amongst their members, and other close relatives (Karremans, 2016; Pridgeon, 2005). Ongoing phylogenetic studies, including a broad set of species from this group, demonstrate the need of an integrate reclassification of the *Lepanthes* affinity (Bogarín et al., in review). Species previously assigned to genus *Trichosalpinx* (in the sense of

Luer (1997) and Pridgeon, (2005)) were found to belong to six unrelated clades, diversely allied to several other traditionally recognized genera. Species belonging to *Gravendeelia*, an ally of *Lepanthopsis*, *Tubella*, an ally of *Anathallis*, and *Stellamaris*, allied to *Lepanthes*, are not particularly closely related but have superficially similar flowers. In Pleurothallidinae, and orchids in general, similarity in floral morphology as a response to pollinator pressure is a well-known trend (Papadopoulos et al., 2013b), and it is not farfetched to suspect that such is the case here as well. Each of these clades is recognized as a distinct genus, rather than including them in broader circumscriptions of their respective sister genera. The plant and floral morphology of the species belonging to these clades are so different from that of their respective sister genera, and so similar amongst each other, that it would leave the resulting broader genera completely undiagnosable. Species of *Lankesteriana*, previously believed to be related to some *Anathallis*, are confirmed instead sister to *Pendusalpinx* with high support, and both in turn sister of *Trichosalpinx* in the strict sense. However apparently closely related, these three clades are recognized as distinct genera here. Species of *Lankesteriana* have accumulated many genetic and morphological differences, as evidenced by their unusually long branch lengths. Their plant morphology is distinct from that of *Pendusalpinx* and *Trichosalpinx* in almost every aspect (Karremans, 2014). Joining these two genera would result in a morphologically undiagnosable genus, and would suppress the diverging evolutionary path of these groups. *Gravendeelia* and *Stellamaris* are here proposed as monotypic genera, which is unfavored by some authors. Nevertheless, both are typified by a common, broadly distributed species, which is highly variable along its distribution. It is likely that these in fact represent species complexes rather than a single species, thus being currently monotypic is not a strong argument for their inclusion in broader concepts of their sister genera, especially when morphological discrepancies are evident. *Opilionanthe*, also monotypic, is sister to several well recognized genera, and clearly represents a unique lineage within the group.

