INVITED PAPER*

# *LANKESTERIANA*, A NEW GENUS IN THE PLEUROTHALLIDINAE (ORCHIDACEAE)

Adam P. Karremans

Lankester Botanical Garden, University of Costa Rica, P.O. Box 302-7050 Cartago, Costa Rica.
Naturalis Biodiversity Center - NHN Universiteit Leiden, The Netherlands
adam.karremans@ucr.ac.cr

Abstract. We estimated phylogenetic relationships within *Anathallis* and related genera using Bayesian analyses of nrITS sequence data. The genus is biphyletic in the molecular trees. A novel generic concept, *Lankesteriana*, is proposed for the species *Anathallis barbulata* and 19 close relatives. The genus is more closely related to some species of *Trichosalpinx* and *Zootrophion* than to *Anathallis s.s*. Species previously transferred from *Pleurothallis* subgen. *Acuminatia* sect. *Acuminatae* to *Anathallis*, are here transferred to *Stelis*, to which they are related phylogenetically. A few additional transfers to *Anathallis* are made. *Lankesteriana* is described and characterized, and the necessary taxonomic transfers are made.

Key words: *Anathallis*, *Lankesteriana*, *Specklinia*, *Stelis*, phylogenetics, systematics

**Introduction**. The most recent reorganization of the generic classification of the Pleurothallidinae proposed by Pridgeon and Chase (2001) was largely based on the results of the molecular phylogenetic studies of the subtribe (Pridgeon *et al.* 2001). The initial analyses were made on a representative set of species and their results were extrapolated to the whole subtribe by correlation with the classification previously proposed by Luer (1986), based on morphological similarities. The circumscription of each genus was discussed and refined by Pridgeon (2005).

Subsequent molecular studies have shown that several of the genera of Pleurothallidinae still require a modified circumscription in order to comply with the monophyly criterion. *Anathallis* Barb.Rodr. is no exception. In the phylogenetic trees of Pridgeon *et al.* (2001), species of *Pleurothallis* R.Br. subgen. *Acuminatia* Luer (Luer 1999), including the type species of genus *Anathallis*, formed a clade together with species of *Pleurothallis* subgen. *Specklinia* sect. *Muscosae* Lindl. The clade was found sister to a clade which includes *Trichosalpinx* Luer and *Lepanthes* Sw., among others, and a broad concept of genus *Anathallis* was re-established (Prodgeon & Chase 2001; Pridgeon 2005).

However, Pridgeon's data set included only species of *Pleurothallis* subgen. *Acuminatia* sect. *Alatae* Luer and did not include representatives of sect. *Acuminatae* Lindl. had been initially analyzed. Karremans (2010) noted that species belonging to sect. *Acuminatae* were not related to those of sect. *Alatae*, but instead were found embedded within *Stelis* Sw. (*sensu* Pridgeon 2005), and suggested that, based on morphology, the same would be true for all other species in the section. The studies by Chiron *et al.* (2012) and Karremans *et al.* (2013a) confirmed that additional species of the sect. *Acuminatae* belonged in *Stelis*. The first set of authors even proposed a new combination for *Anathallis rubens* (Lindl.) Pridgeon & M.W.Chase in *Stelis*, but neglected to transfer all other species of the section.

Luer (2006) later segregated species of *Pleurothallis* subgen. *Specklinia* (Lindl.) Garay sect. *Muscosae* Lindl. into *Panmorphia* Luer resulting in a genus of 73 highly heterogeneous species with "*Specklinia*-like habit and *Anathallis*-like flowers". Luer later decided that the variation within *Panmophia* graded into the concept of *Anathallis*, and he reduced his *Panmophia* as a synonym of the latter (Luer 2009). Analyses of molecular data by Stenzel (2004) demonstrated that species of *Panmorphia* (including the type) were embedded within *Anathallis*.

* This paper was prepared in the framework of the celebration of Lankester Botanical Garden's 40th anniversary.

This conclusion was confirmed by Chiron *et al.* (2012), who included a broad representation of *Anathallis* species in their analyses.

One *Anathallis* species, the broadly distributed and highly variable *Anathallis barbulata* (Lindl.) Pridgeon & Chase, was shown to be distinct from all the other species (Chiron *et al.* 2012). It is probably the most well known species of the group here discussed. In Luer's subgeneric classification of genus *Pleurothallis* R.Br., *A. barbulata* and a few close relatives were placed in *Pleurothallis* subgen. *Specklinia* sect. *Muscosae* Lindl. (Luer 1986). Later on, they were transferred to *Anathallis* by Pridgeon and Chase (2001) and *Panmorphia* by Luer (2006). We present nrITS analyses showing that most species of *Panmorphia*, including the type species, *Anathallis sertularioides* (Sw.) Pridgeon & Chase, are embedded within *Anathallis*. Our data also show that *Anathallis barbulata* and a few sister species are not closely related to other *Anathallis* and require generic recognition to maintain monophyly.

Most of these *Specklinia*-like species of *Anathallis* have also been treated as species of *Specklinia* Lindl. at some point or another. A more extensive molecular phylogenetic analysis of *Specklinia* (Karremans *et al.* unpublished), excludes the species here treated as *Anathallis* (Pupulin *et al.* 2012, Bogarín *et al.* 2013, Karremans *et al.* 2013b), requiring the circumscription of those genera in the present manuscript. It becomes necessary as well to propose the systematic modifications required in order to attain monophyly within *Anathallis, Specklinia*, and *Stelis* and to propose a segregated generic concept for the *A. barbulata* and its close relatives.

**Material and Methods**. This study was conducted at Jardín Botánico Lankester (JBL) of the Universidad de Costa Rica and Naturalis Biodiversity Center - Leiden University, between October 2011 and October 2013. Living material was studied at Lankester Botanical Garden and the Hortus Botanicus in Leiden, while dried and spirit material was deposited at CR, JBL-spirit and L-spirit. Taxon names mostly follow Pridgeon (2005).

*Photography* —. Color illustrations of complete flowers were made using a Nikon D5100 digital camera, while photographs of the columns and pollinaria were taken using a DFC295 Leica digital microscope color camera with Leica FireCam version 3.4.1 software. Scanning electron microscope (SEM) micrographs were taken from flowers fixed in FAA (formalin 10%, glacial acetic acid 5%, water 35%, ethanol 50%). The floral samples were then dehydrated through a series of ethanol steps and subjected to critical-point-drying using liquid $CO_2$. Dried samples were mounted and sputter-coated with gold and observed with a JEOL JSM-5300 scanning electron microscope at an accelerating voltage of 10kV.

*Phylogenetic analysis* —. The data matrix included 56 individuals (Table 1), 18 of which were produced in this study. The remaining data were obtained from GenBank (Pridgeon *et al*. 2001, Chiron *et al*. 2012, Karremans *et al.* 2013a). Plants were obtained from living collections at Lankester Botanical Garden in Costa Rica, the Hortus Botanicus in Leiden, and private collections. Vouchers were deposited in spirit collections at JBL and L. Fresh leaf and flower cuttings of approximately 1 $cm^2$ were dried with silica gel. Samples (20 mg) were pulverized and extraction performed following the DNEasy procedure (Qiagen). The nuclear ribosomal internal transcribed spacer (nrITS) region was amplified using the methods and primers for sequencing and amplification described by Sun *et al*. (1994), and Sanger sequencing was done commercially by Macrogen on a 96-capillary 3730xl DNA Analyzer automated sequencer (Applied Biosystems, Inc.) using standard dye-terminator chemistry (Macrogen, Inc.).

The Staden *et al*. (2003) package was used for editing of the sequences. Contigs were exported as .fas files and opened in Mesquite v2.72 (Maddison & Maddison 2007), where they were checked for base calling errors, the matrix was aligned manually. The ends of each data set were trimmed to eliminate possible erroneous data, and gaps were regarded as missing data (filled with Ns). The data matrix is deposited in the Dryad Digital Repository (Heneghan *et al.* 2011). *Echinosepala aspasicensis* was used as the outgroup, as it was found to be one of the most distantly related of all included species (Pridgeon *et al*. 2001). The trees were produced with an analysis of the nrITS dataset of 43 sequences using BEAST v1.6.0. (Drummond & Rambaut 2007). Parameters were set to preset, except for substitution model GTR with 10 categories, clock model uncorrelated lognormal, tree prior Yule process, and number of generations 20,000,000. The resulting trees were combined using TreeAnnotator v1.6.0., where the first 2000 trees were used as burn-in. FigTree v1.3.1. (Rambaut 2009) was used to edit the resulting tree. Posterior probabilities are given for each node in decimal form.

**Results**. The consensus gene tree (Fig. 1) was obtained from a BEAST analysis of a matrix of 56 ITS sequences (Table 1), including 41 individuals belonging to 34 different species of genus *Anathallis*. The resulting tree includes two highly supported clades of *Anathallis* species; the first is coded clade *Anathallis* and the second clade has been coded *Lankesteriana*.

Clade *Lankesteriana* (P.P. = 0.98) includes the accessions of the species *Anathallis barbulata*, *A. cuspidata*, *A. duplooyi* and *A. fractiflexa*. A clade including *Trichosalpinx berlineri* and *T. dependens* (*Trichosalpinx* II) is highly supported (P.P. = 1) as sister to the *Lankesteriana* clade. Sister to both is a clade including species of *Zootrophion* with high support (P.P. = 0.94).

Clade *Anathallis* is highly supported (P.P. = 1) and includes all accessions of genus *Anathallis* with the exception of those found in clade *Lankesteriana*. Clade *Anathallis* includes *A. obovata*, type species of the genus, and *A. sertularioides*, type species of genus *Panmorphia*. A clade including *Trichosalpinx blaisdellii* and *T. orbicularis* (*Trichosalpinx* I) is found with low support (P.P. = 0.35) sister to the *Anathallis*. Altogether they are sister, with medium support (P.P.=0.66), to a highly supported (P.P. = 1) clade which includes the accessions of *Frondaria* Luer, *Lepanthes* Sw. and *Lepanthopsis* (Cogn.) Ames.

Both mentioned clades are sister to each other, and in turn to an accession of *Trichosalpinx arbuscula* (*Trichosalpinx* III), with low support (P.P. = 0.44). High support (P.P. = 1) is found for a clade which includes all the accessions of *Anathallis*, *Frondaria*, *Lepanthes*, *Lepanthopsis*, *Trichosalpinx* and *Zootrophion* Luer.

Branch length varies greatly within the whole group. The length of accessions of clade *Lankesteriana* double or triple those of *Anathallis*, the latter having accumulated many more nucleotide changes.

**Discussion** . The DNA based evidence obtained here supports the results of Chiron *et al.* (2012), showing that *Anathallis* is non-monophyletic. The addition of other accessions of the variable *A. barbulata*, and of its close relatives *A. duplooyi*, *A. cuspidata* and *A. fractiflexa* confirms that this species group as a whole should be excluded from *Anathallis*. The two highly supported clades of *Anathallis* are not sister to each other. Most of these species had already been segregated from *Anathallis* into *Panmorphia* by Luer, together with several others. However, *Panmorphia* is not monophyletic. The type species of *Panmorphia* is a member if *Anathallis s.s.*, necessitating a novel generic concept for the remaining species of the former *Panmorphia*. When describing *Panmorphia*, Luer (2006) suggested that he could find a "continuum of variations among them", however, he did mention that "several affinities among the species can be recognized". One of those affinities was likely this little group. In fact, this species group can also be easily distinguished from other species of the genus on morphological grounds, and they are therefore recognized as a segregate genus here forth.

***Lankesteriana*** Karremans, Gen. Nov.

Type: *Pleurothallis barbulata* Lindl. Folia Orch. Pleurothallis 40. 1859. Replaced name for *Pleurothallis barbata* H.Focke, Bot. Zeitung (Berlin) 11(13): 227. 1853 (non *Pleurothallis barbata* Westc., Phytologist 1: 54. 1841).

*Species of Lankesteriana are somewhat similar to Anathallis but can be distinguished by the tri-alate ovary (vs. cylindrical), the bilabiate flowers with lateral sepals convergent and usually fused to above the middle (vs. sepals free and spreading), the deeply depressed midline of the lip (vs. not or superficially depressed), the bilobed, helmet-shaped rostellum (vs. ligulate, not bilobed). Additionally, none of the known species of Lankesteriana have: 1) a habit that exceeds 3 cm tall (excluding the inflorescence), 2) ramicauls longer than the leaf, 3) multiple flowers open simultaneously on an inflorescence; 4) whitish to greenish flowers; all of which are commonly found in Anathallis.*

Description: *Plants* very small, 0.5-3 cm tall (excluding the inflorescence), epiphytic, caespitose.

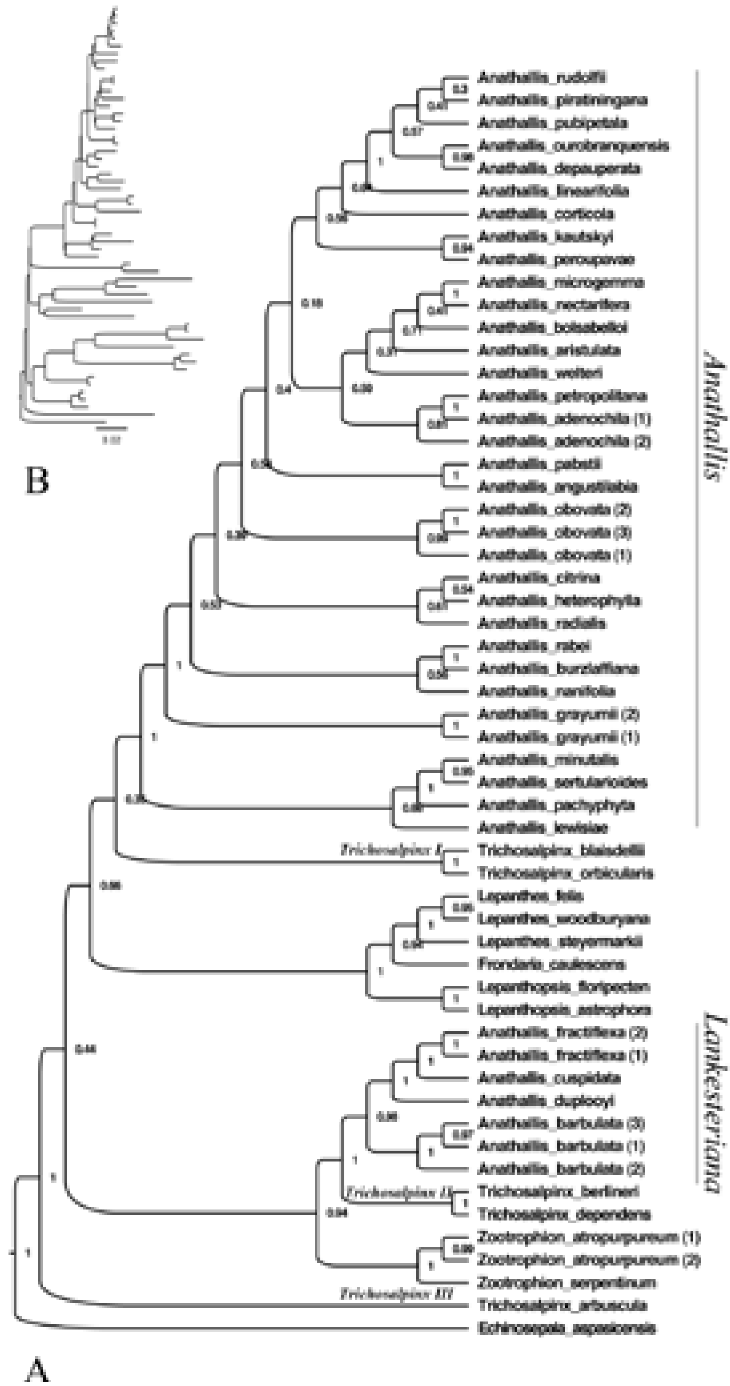



FIGURE 1. Consensus tree from a BEAST analysis of a matrix of 56 ITS sequences. The analysis ran for 20,000,000 generations. A — Branch length transformed to be equal for each species. Values on the nodes are Posterior Probabilities. Species names for each terminal is included. B —Relative branch lengths maintained, showing amount of evolutionary changes. Scale equals a 2% change. Posterior probability values and species names are excluded, but are equal to those of A. Trees edited by A.P. Karremans using FigTree.

TABLE 1. List of vouchers and GenBank number used in the phylogenetic analyses. Scientific names mostly follow Pridgeon 2005.

| Taxon | Voucher collector and number | GenBank number | Source |
|---|---|---|---|
| *Anathallis adenochila* (Loefgr.) F.Barros (1) | *van den Berg 2148* (HUEFS) | JQ306490 | Chiron *et al.* 2012 |
| *Anathallis adenochila* (Loefgr.) F.Barros (2) | *Karremans 4871* (L) | KC425725 | This study |
| *Anathallis angustilabia* (Schltr.) Pridgeon & M.W.Chase | *Manning 890604* (K) | AF262868 | Pridgeon *et al.* 2001 |
| *Anathallis aristulata* (Lindl.) Luer | *van den Berg 2042* (HUEFS) | JQ306338 | Chiron *et al.* 2012 |
| *Anathallis barbulata* (Lindl.) Pridgeon & M.W. Chase (1) | *Chiron 11071* (HUEFS) | JQ306457 | Chiron *et al.* 2012 |
| *Anathallis barbulata* (Lindl.) Pridgeon & M.W. Chase (2) | *Bogarín 8606* (JBL) | KC425726 | This study |
| *Anathallis barbulata* (Lindl.) Pridgeon & M.W. Chase (3) | *Karremans 5750* (L) | KF747834 | This study |
| *Anathallis bolsanelloi* Chiron & V.P.Castro | *van den Berg 2000* (HUEFS) | JQ306342 | Chiron *et al.* 2012 |
| *Anathallis burzlaffiana* (Luer & Sijm) Luer | *Karremans 4857* (L) | KC425727 | This study |
| *Anathallis citrina* (Schltr.) Pridgeon & M.W.Chase | *van den Berg 2086* (HUEFS) | JQ306498 | Chiron *et al.* 2012 |
| *Anathallis corticicola* (Schltr. ex Hoehne) Pridgeon & M.W.Chase | *Hermans 3685* (K) | AF262870 | Pridgeon *et al.* 2001 |
| *Anathallis cuspidata* (Luer) Pridgeon & M.W. Chase | *Bogarín 9619* (JBL) | KF747835 | This study |
| *Anathallis depauperata* (Cogn.) | *Karremans 4808* (L) | KC425735 | This study |
| *Anathallis duplooyi* (Luer & Sayers) Luer | *Karremnas 4888* (JBL) | KF747836 | This study |
| *Anathallis fractiflexa* (Ames & C. Schweinf.) Luer (1) | *Bogarín 8988* (JBL) | KC425728 | This study |
| *Anathallis fractiflexa* (Ames & C. Schweinf.) Luer (2) | *Bogarín 8988* (JBL) | KC425729 | This study |
| *Anathallis grayumii* (Luer) Luer (1) | *Karremans 2747* (JBL) | KC425730 | This study |
| *Anathallis grayumii* (Luer) Luer (2) | *Pupulin 3794* (JBL) | KC425731 | This study |
| *Anathallis heterophylla* Barb.Rodr. | *van den Berg 2031* (HUEFS) | JQ306339 | Chiron *et al.* 2012 |
| *Anathallis kautskyi* (Pabst) Pridgeon & M.W.Chase | *van den Berg 2051* (HUEFS) | JQ306340 | Chiron *et al.* 2012 |
| *Anathallis lewisiae* (Ames) Solano & Soto Arenas | *Bogarín 1056* (JBL) | KC425733 | This study |
| *Anathallis linearifolia* (Cogn.) Pridgeon & M.W.Chase | *Hrmans 2336* (K) | AF262869 | Pridgeon *et al.* 2001 |
| *Anathallis microgemma* (Schltr. ex Hoehne) Pridgeon & M.W.Chase | *Manning 940319* (K) | AF262894 | Pridgeon *et al.* 2001 |
| *Anathallis minutalis* (Lindl.) Pridgeon & M.W.Chase | *Jimenez-M. 1044* (UNAM) | AF262922 | Pridgeon *et al.* 2001 |
| *Anathallis nanifolia* (Foldats) Luer | *Karremans 4793* (L) | KC425736 | This study |
| *Anathallis nectarifera* Barb.Rodr. | *van den Berg 2078* (HUEFS) | JQ306458 | Chiron *et al.* 2012 |
| *Anathallis obovata* (Lindl.) Pridgeon & M.W.Chase (1) | *Kollmann 6092* (MBML) | JQ306497 | Chiron *et al.* 2012 |
| *Anathallis obovata* (Lindl.) Pridgeon & M.W.Chase (2) | *Stenzel 840* (CU) | JF934822 | Stenzel 2004 |
| *Anathallis obovata* (Lindl.) Pridgeon & M.W.Chase (3) | *Karremans 4796* (L) | KF747797 | This study |
| *Anathallis ourobranquensis* Campacci & Menini | *Chiron 11220* (HUEFS) | JQ306459 | Chiron *et al.* 2012 |
| *Anathallis pabstii* (Garay) Pridgeon & M.W.Chase | *Karremans 4821* (L) | KC425737 | This study |
| *Anathallis pachyphyta* (Luer) Pridgeon & M.W.Chase | *Karremans 4795* (L) | KC425734 | This study |
| *Anathallis peroupavae* (Hoehne & Brade) F. Barros | *Karremans 5759* (L) | KF747837 | This study |
| *Anathallis petropolitana* (Hoehne) Luer & Toscano | *van den Berg 2089* (HUEFS) | JQ306491 | Chiron *et al.* 2012 |
| *Anathallis piratiningana* (Hoehne) F.Barros | *van den Berg 2066* (HUEFS) | JQ306344 | Chiron *et al.* 2012 |
| *Anathallis pubipetala* (Hoehne) Pridgeon & M.W.Chase | *van den Berg 2106* (HUEFS) | JQ306460 | Chiron *et al.* 2012 |
| *Anathallis rabei* (Foldats) Luer | *Karremans 4794* (L) | KC425738 | This study |
| *Anathallis radialis* (Porto & Brade) Pridgeon & M.W.Chase | *Chiron 10144* (HUEFS) | JQ306345 | Chiron *et al.* 2012 |
| *Anathallis rudolfii* (Pabst) Pridgeon & M.W.Chase | *van den Berg 2127* (HUEFS) | JQ306461 | Chiron *et al.* 2012 |
| *Anathallis sertularioides* (Sw.) Pridgeon & M.W.Chase | *Solano 807* (UNAM) | AF262871 | Pridgeon *et al.* 2001 |

TABLE 1. Continues.

| Taxon | Voucher collector and number | GenBank number | Source |
|---|---|---|---|
| *Anathallis welteri* (Pabst) F.Barros | *van den Berg 2009* (HUEFS) | JQ306341 | Chiron *et al.* 2012 |
| *Echinosepala aspasicensis* (Rchb. f.) Pridgeon & M.W. Chase | *Hermans 2160* (K) | AF262905 | Pridgeon *et al.* 2001 |
| *Frondaria caulescens* (Lindl.) Luer | *Luer 18778* (K) | AF262914 | Pridgeon *et al.* 2001 |
| *Lepanthes felis* Luer & R. Escobar | *Hermans 2899* (K) | AF262891 | Pridgeon *et al.* 2001 |
| *Lepanthes steyermarkii* Foldats | *Hermans 2682* (K) | AF262889 | Pridgeon *et al.* 2001 |
| *Lepanthes woodburyana* Stimson | *Hermans 2931* (K) | AF262890 | Pridgeon *et al.* 2001 |
| *Lepanthopsis astrophora* Garay | *Manning 941040* (K) | AF262893 | Pridgeon *et al.* 2001 |
| *Lepanthopsis floripecten* (Rchb. f.) Ames | *van den Berg 2063* (HUEFS) | JQ306336 | Chiron *et al.* 2012 |
| *Trichosalpinx arbuscula* (Lindl.) Luer | *Hermans 1266* (K) | AF262888 | Pridgeon *et al.* 2001 |
| *Trichosalpinx berlineri* (Luer) Luer | *Hermans 1605* (K) | AF262900 | Pridgeon *et al.* 2001 |
| *Trichosalpinx blaisdellii* (S.Watson) Luer | *Kew 1997-7412* (K) | AF262887 | Pridgeon *et al.* 2001 |
| *Trichosalpinx dependens* (Luer) Luer | *van den Berg 2011* (HUEFS) | JQ306456 | Chiron *et al.* 2012 |
| *Trichosalpinx orbicularis* (Lindl.) Luer | *Hermans 1349* (K) | AF262886 | Pridgeon *et al.* 2001 |
| *Zootrophion atropurpureum* (Lindl.) Luer (1) | *Kew 1997-7414* (K) | AF262898 | Pridgeon *et al.* 2001 |
| *Zootrophion atropurpureum* (Lindl.) Luer (2) | *van den Berg 2056* (HUEFS) | JQ306415 | Chiron *et al.* 2012 |
| *Zootrophion serpentinum* Luer | *Manning 921030* (K) | AF262899 | Pridgeon *et al.* 2001 |

*Ramicauls* ascending, shorter than the leaf, never proliferating, with 1-3 imbricating, tubular, glandular to microscopically glandular sheaths. Leaf erect to prostrate. *Inflorescence* elongate, frequently exceeding the leaves, successive, with one flower open at a time. *Flowers* usually brownish-purple, sepals glabrous to ciliate. *Ovary* trialate. *Sepals* elliptic, acute, the lateral ones fused to above the middle or least convergent, forming a synsepal. *Petals* lanceolate to ovate-elliptic, widest near the middle, obtuse or acute, to acuminate, sometimes caudate. *Lip* oblong, to more or less pandurate, with a pair of basal sub-orbicular lobes, with a deep linear middle depression. *Column* winged, androclinium fimbriate-dentate, rostellum helmet-shaped, with prominent lateral lobes. *Anther* helmet-shaped. *Pollinia* in pairs, with reduced, granulose, whale-tail shaped caudicles (Fig. 2 & 3).

ETYMOLOGY: The name honors both the Lankester Botanical Garden of the University of Costa Rica, which is celebrating 40 years of existence, and also the homonymous scientific journal *Lankesteriana, International Journal on Orchidology*.

DISTRIBUTION AND ECOLOGY: Nineteen species of *Lankesteriana* Karremans are recognized here, however as is frequent with other tiny Pleurothallids, species of this genus tend to be overlooked in the field and lumped together into broad and variable species concepts. Species of *Lankesteriana* are distributed from southern Mexico, through Central America, the Andes, and all the way down to Bolivia and Brazil (Fig. 4). Costa Rica, Ecuador and Colombia contain the largest number of species, whereas Brazil, the center of diversity of sister genus *Anathallis*, has just a few *Lankesteriana*; they are notably absent from the Antilles. They occur between 280 and 2800 m in elevation, but most are found at mid elevations between 600 and 2000 m.

Luer (1986) had noted that flowers of species here treated as *Lankesteriana* were similar to some species of *Trichosalpinx* subgen. *Trichosalpinx* (*Trichosalpinx* I & II in Fig. 1). In fact, they resemble species of *Trichosalpinx* much more than *Anathallis*. *Trichosalpinx* was established by Luer for a group of species which shared the lepanthiform bracts of the stem and which did not fit well in either *Draconanthes* (Luer) Luer, *Lepanthes* or *Lepanthopsis* (Luer 1997), however that meant that they did not share a particular synapomorphy, and may not represent a natural grouping. The inclusion

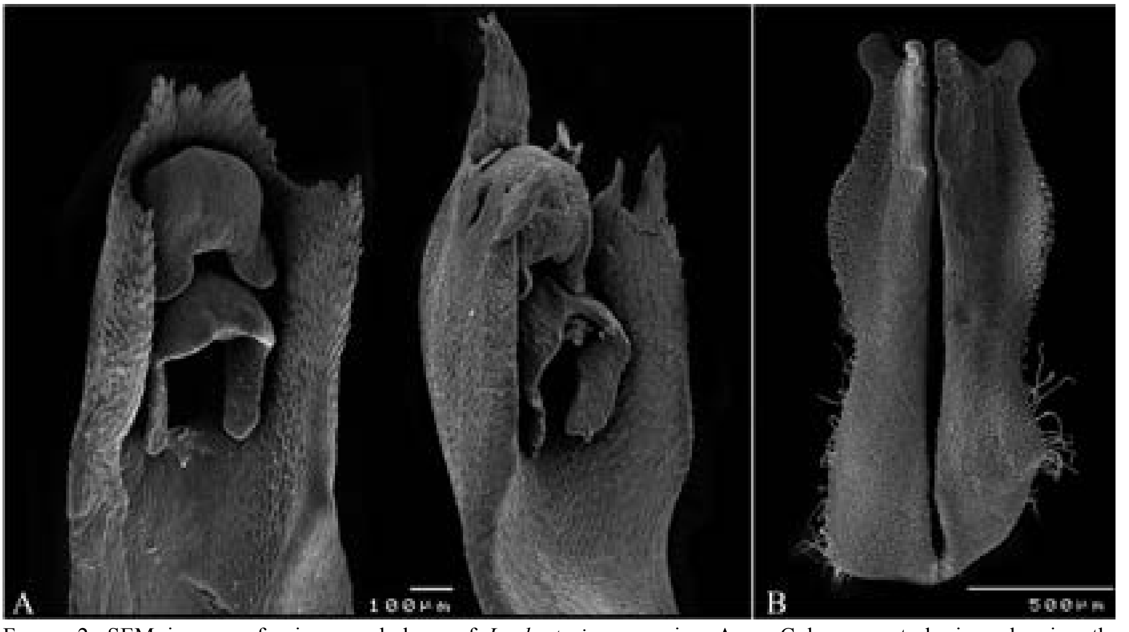
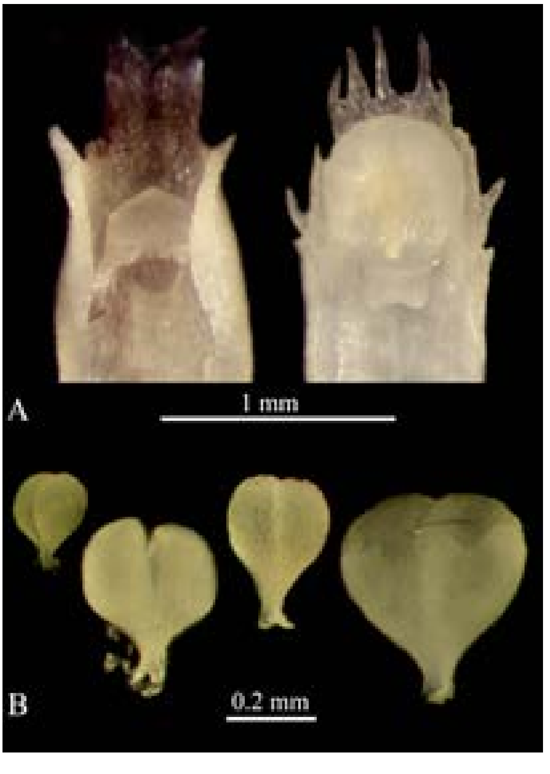



FIGURE 2. SEM images of micromorphology of *Lankesteriana* species. A — Column ventral view showing the androclinium, anther cap, helmet-like rostellum and stigma. B — The flattened lip, showing the midline depression, the basal sub-orbicular lobes and the glandular hairs near the apex. Specimens are *Lankesteriana cuspidata* (A-left & B; *Bogarín 9619*; JBL-spirit) and *Lankesteriana barbulata* (A-right; *Karremans 5444*; JBL-spirit). Photographs by A.P. Karremans




of a few species of *Trichosalpinx* in the DNA studies of Pridgeon *et al.* (2001) evidenced the polyphyly of the genus. A phylogenetic analysis of genus *Trichosalpinx*, including many more additional species, further evidences the need for a complete re-circumscription of this highly polyphyletic genus, which is diversely interrelated with all other genera in the clade (Fernández *et al.* unpublished).

Subgenus *Trichosalpinx* is biphyletic in the analysis presented here (Fig. 1), with a clade including the type of the genus (*Trichosalpinx* I), sister to *Anathallis*, and a second clade (*Trichosalpinx* II), sister to *Lankesteriana*. A reconsideration of *Trichosalpinx* will be a hazardous

Left, FIGURE 3. Micrographs taken with the Leica stereo microscope. A. Apex of the column in ventral view, from left to right, of *Lankesteriana cuspidata* (*Fernández 695*; JBL-spirit) and *Anathallis polygonoides* (*JBL-28237*; JBL-spirit). B. Pollinaria, from left to right, of *Lankesteriana cuspidata* (*Fernández 695*; JBL-spirit), *Anathallis polygonoides* (*JBL-28237*; JBL-spirit), *Anathallis lewisae* (*Bogarín 1056*; JBL-spirit) and *Trichosalpinx blaisdellii* (*Pupulin 1092*; JBL-spirit). Photographs by A.P. Karremans.

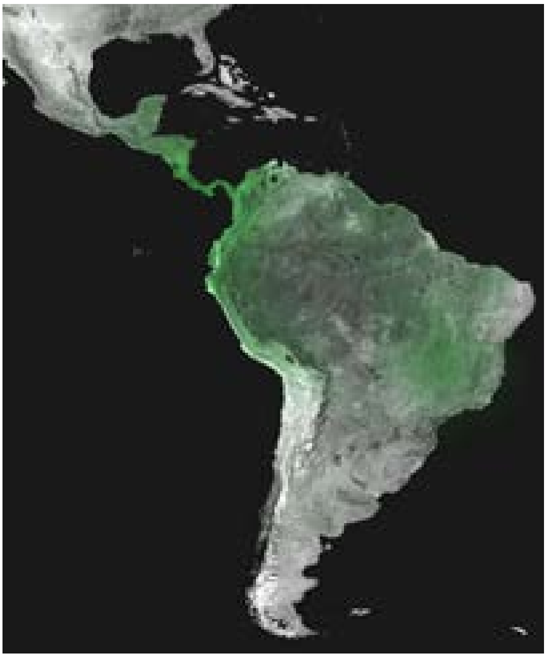


Figure 4. Distribution map (in green) of the 19 known species of *Lankesteriana* Karremans. The highest diversity of the genus in found from Costa Rica to Colombia and Ecuador.

task that falls outside of the scope of this study. It suffices to say that we consider sister genera *Anathallis* and *Trichosalpinx* (*Trichosalpinx* I) distinct enough to keep them as separate genera and that the clade which includes *Lankesteriana* and *Trichosalpinx* II was until now unnamed. When revising *Trichosalpinx* in the future it can be re-considered if it is advantageous to include the few species belonging to *Trichosalpinx* II in a broadened *Lankesteriana*, however, based on morphology and genetic distance, such a move is in our view unfavorable.

With species of subgen. *Trichosalpinx* they share the fused sepals (with a few exceptions), the usually purplish-brown flowers, the extremely sensitive linear lip, with a pair of rounded lobes at the base, and a midline depression and the helmet-shaped rostellum. These traits suggest that both groups share a similar pollinator group. Species of subgen. *Trichosalpinx* however can be easily distinguished from those of *Lankesteriana* by the much larger plants, with long ramicauls covered with lepanthiform bracts and the simultaneously multi-flowered inflorescences.

Key to the genera with *Specklinia*-like habit

1. Inflorescence frequently lax-flexuous, sepals usually caudate, petals fimbriate, acute to caudate, column inornate to narrowly winged ........................................................................ *Muscarella* (*Specklinia*)
1. Inflorescence mostly congested-straight, sepals usually not caudate, petals entire to minutely denticulate, infrequently caudate, column ornate ......... 2
   2. Petals linear to lanceolate, acute to acuminate, column wings quadrate to triangular, androclinium conspicuously fimbriate .......................... 3
      3. Inflorescence single or simultaneously multi-flowered. Flowers star-shapped, lateral sepals free, flowers mostly white, green or yellow, lip lacking a deep mid-line depression, rostellum ligulate ......................................... *Anathallis*
      3. Inflorescence successively single flowered. Flowers bilabiate, lateral sepals fused, flowers brownish-purple, lip with deep a midline depression, rostellum helmet-like bilobate ..... ................................................. *Lankesteriana*
   2. Petals elliptic to spathulate, obtuse, column wings rounded, androclinium erose or inornate ......... 4
      4. Lip mostly linear-ligulate, column wings prominent, pollinia without caudicles ............ ........................................................ *Specklinia*
      4. Lip trilobed, with a pair of suborbicular lobes close to the middle, columninconspicuously ornate or inornate, pollinia with caudicles ..... ........................................................ *Pabstiella*

***Lankesteriana abbreviata*** (Schltr.) Karremans, ***comb. nov.***

Bas. *Pleurothallis abbreviata* Schltr., Repert. Spec. Nov. Regni Veg. 10: 352. 1912.

***Lankesteriana barbulata*** (Lindl.) Karremans, ***comb. nov.***

Bas. *Pleurothallis barbulata* Lindl. Folia Orch. Pleurothallis 40. 1859. Replacement name for *P. barbata* H.Focke, 1853.

Note: *Specklinia pereziana* Kolan. published in 2011 from Colombia, is virtually indistinguishable from *Lankesteriana barbulata*, a common, widely distributed, variable species with several heterotypic synonyms. As *L. barbulata* was not even mentioned by the author there is no evidence to separate the two.

***Lankesteriana casualis*** (Ames) Karremans, ***comb. nov.***
Bas. *Pleurothallis casualis* Ames, Sched. Orch. 9: 30, 1925.

***Lankesteriana caudatipetala*** (C.Schweinf.) Karremans, ***comb. nov.***
Bas. *Pleurothallis caudatipetala* C.Schweinf. Bot. Mus. Leafl. 10: 175. 1942.

***Lankesteriana comayaguensis*** (Ames) Karremans, ***comb. nov.***
Bas. *Pleurothallis comayaguensis* Ames, Bot. Mus. Leafl. 4: 31, 1936.

***Lankesteriana cuspidata*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis cuspidata* Luer, Selbyana 3: 282, 1977.

***Lankesteriana duplooyi*** (Luer & Sayers) Karremans, ***comb. nov.***
Bas. *Pleurothallis duplooyi* Luer & Sayers. Rev. Soc. Bol. Bot. 3: 48, 2001.

***Lankesteriana edmeiae*** (F.J. de Jesus, Xim. Bols. & Chiron) Karremans, ***comb. nov.***
Bas. *Anathallis edmeiae* F.J. de Jesus, Xim. Bols. & Chiron, Richardiana 13: 296. 2013.

***Lankesteriana escalarensis*** (Carnevali & Luer) Karremans, ***comb. nov.***.
Bas. *Pleurothallis escalarensis* Carnevali & Luer, Novon 13: 414. 2003.

***Lankesteriana fractiflexa*** (Ames & C.Schweinf.) Karremans, ***comb. nov.***
Bas. *Pleurothallis fractiflexa* Ames & C.Schweinf., Sched. Orch. 10: 26, 1930.

***Lankesteriana haberi*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis haberi* Luer, Selbyana 23:36. 2002.

***Lankesteriana imberbis*** (Luer & Hirtz) Karremans, ***comb. nov.***
Bas. *Pleurothallis imberbis* Luer & Hirtz, Lindleyana 11: 163, 1996.

***Lankesteriana inversa*** (Luer & R.Vásquez) Karremans, ***comb. nov.***
Bas. *Pleurothallis inversa* Luer & R.Vásquez, Rev. Soc. Bol. Bot. 3: 50. 2001.

***Lankesteriana involuta*** (L.O.Williams) Karremans, ***comb. nov.***
Bas. *Pleurothallis involuta* L.O.Williams, Bot. Mus. Leafl. 12: 239. 1946.

***Lankesteriana millipeda*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis millipeda* Luer, Orquideología 20: 216. 1996.

***Lankesteriana minima*** (C.Schweinf.) Karremans, ***comb. nov.***
Bas. *Pleurothallis minima* C.Schweinf., Bot. Mus. Leafl. 3: 82. 1935.

***Lankesteriana muricaudata*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis muricaudata* Luer, Selbyana 7: 119. 1982.

***Lankesteriana rubidantha*** (Chiron & Xim.Bols.) Karremans, ***comb. nov.***
Bas. *Specklinia rubidantha* Chiron & Xim.Bols., Richardiana 9: 125. 2009.

***Lankesteriana steinbuchiae*** (Carnevali & G.A.Romero) Karremans, ***comb. nov.***
Bas. *Pleurothallis steinbuchiae* Carnevali & G.A.Romero, Novon 4: 90. 1994.

***Anathallis*** Barb.Rodr., Gen. Sp. Orch. Nov. 1: 23. 1877.
TYPE: *Anathallis fasciculata* Barb.Rodr., Gen. Sp. Orch. Nov. 1: 23. 1877.

This relatively old genus remained mostly unused until it was re-established by Pridgeon and Chase (2001), and re-defined by Pridgeon (2005). It was not clear how many and which species actually belonged to the concept, but initially about 90 species were transferred. About 90 more names were added by other authors since then (mostly transfers from other genera, but also new species). If we exclude the species that belong to *Lankesteriana* and *Stelis*, we end up just shy of 140 species, a number which seems reasonable.

Species of *Anathallis* are distributed from southern Mexico through Central America, the Antilles and all South America down to Argentina. They are most diverse in Brazil at low to mid elevations. They are easily recognized by the more or less star-shaped flower, with linear to lanceolate, acute to acuminate petals that are similar to the sepals. The lip is horizontally placed and very sensitive, 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 whale-tail shaped caudicles.

One species before treated as *Specklinia* is transferred here to *Anathallis* based on those morphological features.

***Anathallis napintzae*** (Luer & Hirtz) Karremans, ***comb. nov.***

Bas. *Pleurothallis napintzae* Luer & Hirtz, Lindleyana 11: 173. 1996.

***Stelis*** Sw., J. Bot. (Schrader) 2: 239. 1799.

Lectotype: *Epidendrum ophioglossoides* Jacq., Enum. Pl. Carib., 29. 1760.

Although this genus has been traditionally accepted (Karremans *et al.* 2013), it was greatly modified by Pridgeon and Chase (2001) and Pridgeon *et al.* (2005). As such the genus was broadened from its classic definition (Luer 2009) to include several species groups before placed in *Pleurothallis*. *Stelis* in its broad sense was phylogenetically analyzed and extensively discussed by Karremans (2010) and Karremans *et al.* (2013), and was proven largely monophyletic if the species of *Pleurothallis* subgen. *Acuminatia* sect. *Acuminatae* were transferred to it. That species group was found to be closely related to the species of *Stelis* in a strict sense (Luer 2009). It will suffice to say here that although smaller, better defined and informative generic concepts are preferred by the author, these species are transferred to a broad sense of *Stelis* where they are more accurately placed than previously.

In any other scenario this species group would require generic recognition, however, several other genera would have to be recognized and/or re-circumscribed as well. This might be possible at a later stage when the species belonging to each of those other groupings are well understood. The species transferred here were in any case already proven non-monophyletic as a group by Karremans *et al.* (2013), however, all still within the broad concept of *Stelis*.

***Stelis ariasii*** (Luer & Hirtz) Karremans, ***comb. nov.***

Bas. *Pleurothallis ariasii* Luer & Hirtz, Lindleyana 12: 42. 1997.

***Stelis asperilinguis*** (Rchb.f. & Warsz.) Karremans, ***comb. nov.***.

Bas. *Pleurothallis asperilinguis* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 114. 1854.

***Stelis aurea*** (Lindl.) Karremans, ***comb. nov.***

Bas. *Pleurothallis aurea* Lindl., Ann. Mag. Nat. Hist. 12: 397. 1843.

Replaced synonym: *Dendrobium acuminatum* Kunth in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. 1: 357. 1816 = *Anathallis acuminata* (Kunth) Pridgeon & M.W. Chase.

Note: The name *Dendrobium acuminatum* has priority over *P. aurea*, however *Stelis acuminata* Luer & Hirtz occupies the combination in *Stelis*. The heterotypic synonyms of this species, if not proven distinct and if not occupied in genus *Stelis*, have priority in the necessity of a new name. Therefore *Stelis aurea* is proposed for this species.

***Stelis candida*** (Luer & Hirtz) Karremans, ***comb. nov.***

Bas. *Pleurothallis candida* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 107. 1999.

***Stelis catenata*** Karremans, ***nom. nov.***

Replaced synonym: *Pleurothallis ramulosa* Lindl., Fol. Orchid. 9: 33. 1859.

Etymology: From the Latin *catenatus* referring to the chains of ramicauls formed.

Note: The name *Stelis ramulosa* Luer & Dalström (2004) occupies the combination in *Stelis* required for *Pleurothallis ramulosa* [=*Anathallis ramulosa* (Lindl.) Pridgeon & M.W. Chase]. Its heterotypic synonym *Pleurothallis superposita* Schltr. (1916) can't be combined in *Stelis* either as *Stelis superposita* Schltr. (1915) is also occupied. A new name for the species is therefore proposed.

***Stelis coripatae*** (Luer & R.Vásquez) Karremans, ***comb. nov.***

Bas. *Pleurothallis coripatae* Luer & R.Vásquez, Phytologia 46: 362. 1980.

***Stelis dimidia*** (Luer) Karremans, ***comb. nov.***

Bas. *Pleurothallis dimidia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 109. 1999.

***Stelis jesupiorum*** (Luer & Hirtz) Karremans, ***comb. nov.***
Bas. *Pleurothallis jesupiorum* Luer & Hirtz, Lindleyana 11: 164. 1996.

***Stelis lagarophyta*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis lagarophyta* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 112. 1999.

***Stelis lamprophylla*** (Schltr.) Karremans, ***comb. nov.***
Bas. *Pleurothallis lamprophylla* Schltr., Repert. Spec. Nov. Regni Veg. 15: 205. 1918.
Replaced synonym: *Pleurothallis dolichopus* Schltr., Repert. Spec. Nov. Regni Veg. 10: 394. 1912 = *Anathallis dolichopus* (Schltr.) Pridgeon & M.W. Chase.

Note: The name *Pleurothallis dolichopus* has priority over *P. lamprophylla*, however *Stelis dolichopus* Schltr. occupies the combination in *Stelis*. The heterotypic synonyms of this species, if not proven distinct and if not occupied in genus *Stelis*, have priority in the necessity of a new name. Therefore *Stelis lamprophylla* is proposed for this species.

***Stelis lauta*** Karremans, ***nom. nov.***
Replaced Synonym: *Pleurothallis concinna* Luer & R.Vásquez, Revista Soc. Boliv. Bot. 2: 133. 1999.
ETYMOLOGY: From the Latin *lautus*, elegant, fine, as a replacement for the also Latin adjective *concinnatus* used in the original description of this species.

Note: The name *Stelis concinna* Lindl. (1834) occupies the combination in *Stelis* required for *Pleurothallis concinna* [=*Anathallis concinna* (Leur & R.Vásquez) Pridgeon & M.W. Chase]. A new name for the species is proposed.

***Stelis lennartii*** Karremans, ***nom. nov.***
Replaced Synonym: *Pleurothallis anderssonii* Luer, Lindleyana 11: 145. 1996.
ETYMOLOGY: The name honors Lennart Andersson, to whom the species was originally dedicated.

Note: The name *Stelis anderssonii* Luer & Endara occupies the combination in *Stelis* required for *Pleurothallis anderssonii* [=*Anathallis anderssonii* (Luer) Pridgeon & M.W. Chase]. A new name for the species is proposed.

***Stelis maguirei*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis maguirei* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 113. 1999.

***Stelis mediocarinata*** (C.Schweinf.) Karremans, ***comb. nov.***
Bas. *Pleurothallis mediocarinata* C.Schweinf., Fieldiana, Bot. 33: 26. 1970.

***Stelis melanopus*** (F.Lehm. & Kraenzl.) Karremans, ***comb. nov.***
Bas. *Pleurothallis melanopus* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 443. 1899.
Replaced synonym: *Pleurothallis stenophylla* Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 442. 1899 = *Anathallis stenophylla* (Lehm. & Kraenzl.) Pridgeon & M.W. Chase.

Note: The name *Pleurothallis stenophylla* has priority over *P. melanopus*, however *Stelis stenophylla* Rchb.f. occupies the combination in *Stelis*. The heterotypic synonyms of this species, if not proven distinct and if not occupied in genus *Stelis*, have priority in the necessity of a new name. Therefore *Stelis melanopus* is proposed for this species.

***Stelis meridana*** (Rchb.f.) Karremans, ***comb. nov.***
Bas. *Pleurothallis meridana* Rchb.f., Linnaea 22: 826. 1850.

***Stelis montserratii*** (Porsch) Karremans, ***comb. nov.***
Bas. *Pleurothallis montserratii* Porsch, Oesterr. Bot. Zeitsch. 158. 1905.
Replaced synonym: *Pleurothallis rubens* Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835.

Note: The name *Pleurothallis rubens* has priority over *P. montserratii*, however as *Stelis rubens* Schltr. (1910) occupies the combination in *Stelis*, a new name has to be proposed in that genus. Chiron *et al.* (2012) proposed *Stelis neorubens* Chiron, however the heterotypic synonyms of this species, if not proven distinct and if not occupied in genus *Stelis*, have priority in the necessity of a new name. Therefore *Stelis montserratii* is proposed for this species and has priority over *S. neorubens*, unless it is proven a distinct species.

***Stelis papuligera*** (Schltr.) Karremans, ***comb. nov.***
Bas. *Pleurothallis papuligera* Schltr., Repert. Spec. Nov. Regni Veg. 10: 453. 1912.

***Stelis regalis*** (Luer) Karremans, ***comb. nov.***
Bas. *Pleurothallis regalis* Luer, Selbyana 5: 178. 1979.

***Stelis scariosa*** (Lex.) Karremans, ***comb. nov.***

Bas. *Dendrobium scariosum* Lex. in P.de La Llave & J.M.de Lexarza, Nov. Veg. Descr. 2(Orchid. Opusc.): 39. 1825.

***Stelis schlimii*** (Luer) Karremans, ***comb. nov.***

Bas. *Pleurothallis schlimii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 120. 1999.

***Stelis sclerophylla*** (Lindl.) Karremans, ***comb. nov.***

Bas. *Pleurothallis sclerophylla* Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835.

***Stelis soratana*** (Rchb.f.) Karremans, ***comb. nov.***

Bas. *Pleurothallis soratana* Rchb.f., Xenia Orchid. 3: 25. 1881.

***Stelis spathilabia*** (Schltr.) Karremans, ***comb. nov.***

Bas. *Pleurothallis spathilabia* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 56. 1924.

***Stelis spathuliformis*** (Luer & R.Vásquez) Karremans, ***comb. nov.***

Bas. *Pleurothallis spathuliformis* Luer & R.Vásquez, Revista Soc. Boliv. Bot. 2: 137. 1999.

***Stelis unduavica*** (Luer & R.Vásquez) Karremans, ***comb. nov.***

Bas. *Pleurothallis unduavica* Luer & R.Vásquez, Phytologia 46: 372. 1980.

***Stelis vasquezii*** (Luer) Karremans, ***comb. nov.***

Bas. *Pleurothallis vasquezii* Luer, Phytologia 49: 220. 1981.

**Conclusions**. High species diversity and the many cases of convergence and parallelism make the systematics of the Pleurothallidinae quite hazardous. Morphological features are often congruent with phylogenetic hypotheses based on DNA data, but homoplasy can occur in morphological traits; similar morphological features may not always reflect a similar evolutionary history. Molecular data provide an independent data set that can be used to evaluate morphological homoplasy. Several modifications to the genera *Anathallis*, *Specklinia* and *Stelis* have been proposed here in an effort to circumscribe genera that are both monophyletic and diagnosable using morphological characters. With the exclusion of the species belonging to *Lankesteriana* and *Stelis*, the recircumscribed *Anathallis* is monophyletic based on all available data.

It must be stressed that the present work does not intend to be a molecularly based phylogenetic study of *Anathallis* and *Lankesteriana*. Instead, a systematic re-circumscription of those genera is proposed using an all evidence approach in which clear morphological patterns are correlated with available DNA evidence. The analyses of additional genetic regions and of a broader species set might refine the phylogenetic relationships among these species, however, as already evidenced in several earlier studies the basic phylogenetic reconstruction produced using a representative number of nrITS sequences is mostly found unchanged (Pridgeon & Chase 2001; Karremans 2010; Karremans *et al.* 2013), especially when the found clades have been thoroughly characterized morphologically (Luer 2002; Karremans 2010).

*Lankesteriana* (Fig. 5) is a well supported and defined genus of some 19 species. They are widely distributed in the Neotropics with the noteworthy exception of the Antilles. The genus is phylogenetically closely related to some species of *Trichosalpinx* and *Zootrophion*, however, the tiny habit with an extremely reduced ramicaul with adpressed inconspicuous bracts, and the relatively long successively single flowered inflorescences resemble species of *Anathallis* and *Specklinia* much more closely. On the other hand, the frequently purplish flowers with usually fused lateral sepals and an extremely sensitive lip are once again reminiscent of some species of *Trichosalpinx* subgen. *Trichosalpinx*.

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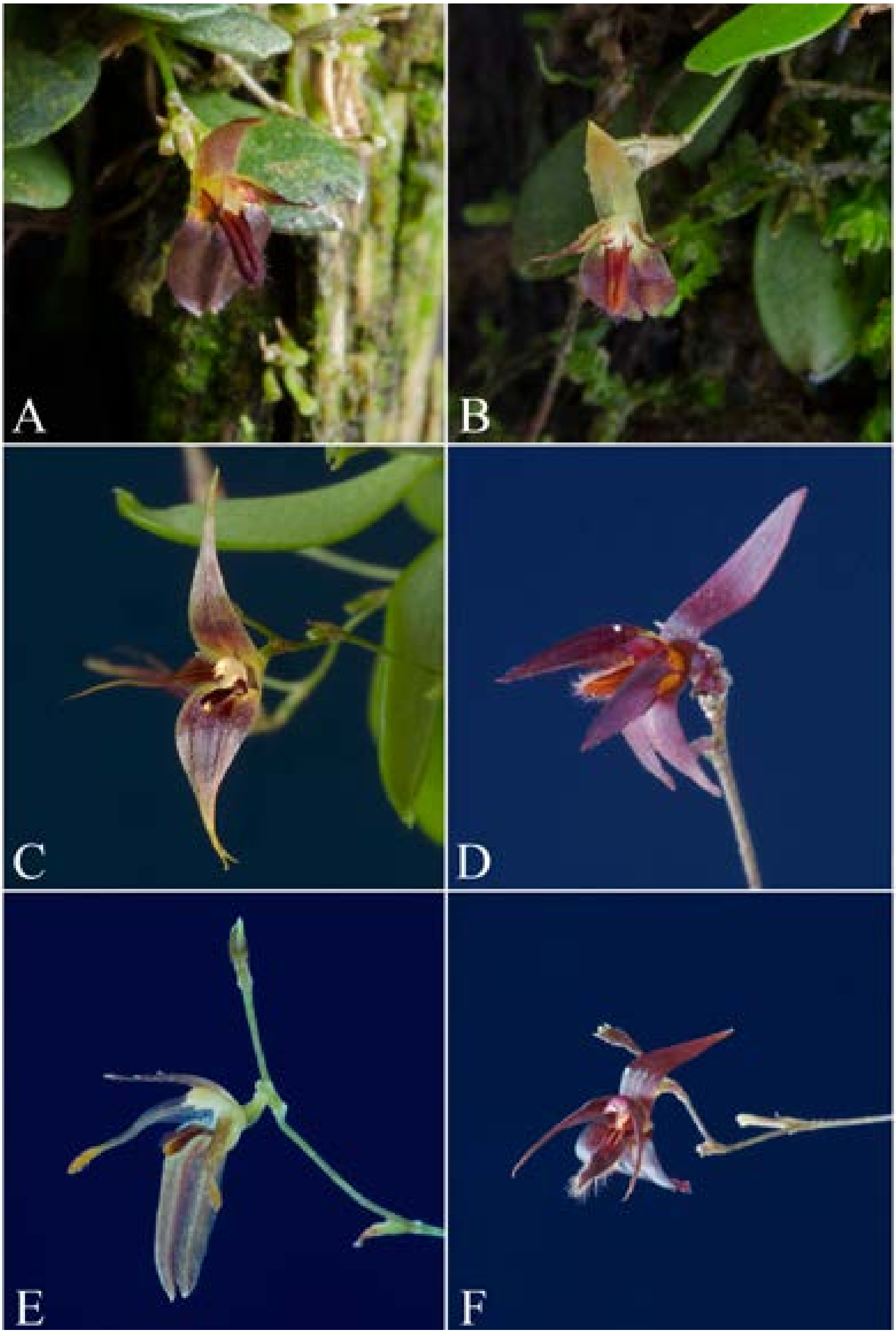
Right, figure 5. Representative species of genus *Lankesteriana*. A — *Lankesteriana barbulata* (*Karremans 5187*; JBL-spirit). B — *Lankesteriana barbulata* (*Karremans 5447*; JBL-spirit) C — *Lankesteriana cuspidata* (*Bogarín 9619*; JBL-spirit). D — *Lankesteriana duplooyi* (*Karremans 4888*; JBL-spirit). E — *Lankesteriana fractiflexa* (*Bogarín 8988*; JBL-spirit). F — *Lankesteriana sp.nov.* (*Karremans 4900*; JBL-spirit). Photographs by A.P. Karremans.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