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LANKESTERIANA, A NEW GENUS IN THE PLEUROTHALLIDINAE (ORCHIDACEAE)
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**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, the type species of genus *Anathallis*, formed a clade together with species of *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.

However, Pridgeon’s data set included only species of *Pleurothallis* subgen. *Acuminatia* sect. *Alatae* Luer and did not include representatives of sect. *Acuminatia* Lindl. had been initially analyzed. Karremans (2010) noted that species belonging to sect. *Acuminatia* were not related to those of sect. *Alatae*, but instead were found embedded within *Stelis* (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. *Acuminatia* 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. *Muscoseae* Lindl. into *Pannorphia* 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 *Pannorphia* graded into the concept of *Anathallis*, and he reduced his *Pannorphia* as a synonym of the latter (Luer 2009). Analyses of molecular data by Stenzel (2004) demonstrated that species of *Pannorphia* (including the type) were embedded within *Anathallis*.

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*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, Bogarin 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. Fresh leaf and flower cuttings of approximately 1 cm² 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 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 CO₂. 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 cm² 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.).

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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 *Lankesteriana* 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.


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) rami caulis 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 et al. 2012.

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<th>Taxon</th>
<th>Voucher collector and number</th>
<th>GenBank number</th>
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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 triolate. 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-ornicular 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...
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
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
purlish-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 denti-
culate, infrequently caudate, column ornate .... 2

2. Petals linear to lanceolate, acute to acuminate,
column wings quadrate to triangular, androcli-
nium conspicuously fimbriate .......................... 3

3. Inflorescence single or simultaneously multi-
flowered. Flowers star-shaped, 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 ..... 4

   .................................................... 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 ..... 5
   ................................................................ Pabstiella

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

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.*

Lankesteriana caudatipetala (C.Schweinf.) Karremans, *comb. nov.*

Lankesteriana comayaguensis (Ames) Karremans, *comb. nov.*

Lankesteriana cuspidata (Luer) Karremans, *comb. nov.*

Lankesteriana duplooyi (Luer & Sayers) Karremans, *comb. nov.*


Lankesteriana escalarensis (Carnevali & Luer) Karremans, *comb. nov.*


Lankesteriana haberii (Luer) Karremans, *comb. nov.*

Lankesteriana imberbis (Luer & Hirtz) Karremans, *comb. nov.*


Lankesteriana involuta (L.O.Williams) Karremans, *comb. nov.*

Lankesteriana muricaudata (Luer) Karremans, *comb. nov.*


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.*


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


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.*


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


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


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.*


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


*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.*


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

Stelis jesupiorum (Luer & Hirtz) Karremans, comb. nov.

Stelis lagarophyta (Luer) Karremans, comb. nov.

Stelis lamprophylla (Schltr.) Karremans, comb. nov.


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.

Etymology: From the Latin laetus, 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 (Luer & R.Vásquez) Pridgeon & M.W. Chase]. A new name for the species is proposed.

Stelis lennartii Karremans, nom. nov.

Etymology: The name honors Lennart Andersson, to whom the species was originally dedicated.

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

Stelis maguirei (Luer) Karremans, comb. nov.

Stelis mediocarinata (C.Schweinf.) Karremans, comb. nov.

Stelis melanopus (F.Lehm. & Kraenzl.) Karremans, comb. nov.


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.

Stelis montserratii (Porsch) Karremans, comb. nov.


Note: The name Pleurothallis rubens has priority over P. montserratii, however as Stelis rubens Schlr. (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.

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

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

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

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

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


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

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 may 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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