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TO BE, OR NOT TO BE A *STELIS*

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Abstract. Despite the availability of multiple sources of evidence and consistency in the support for a broadly circumscribed *Stelis* Sw. (Orchidaceae: Pleurothallidinae), some authors continue to be hesitant in its use. It is certain that the more typical species of *Stelis*, with their triangular, flattish flowers with very short fleshy petals and lip, form a monophyletic group that is easily recognized. However, it is likewise undisputed that they are not an isolated lineage in the subtribe and that several groups of species with a similar vegetative habit but lacking the typical *Stelis* flower are in fact very close relatives, sharing a relatively recent common ancestor. Those species groups need to be classified in a way that also reflects their own evolutionary history; alternatives to a broadly circumscribed *Stelis* are possible yet neither straightforward or practical at this time. An infrageneric classification for the whole group is provided here in an attempt to clarify which species belong where in this highly complex affinity. Emphasis is made on the difficulty of diagnosing the less typical members of each proposed subgenus or section, and on the importance of floral convergence and divergence as a result of pollinator adaptation. As here defined, *Stelis* is the largest genus in the Pleurothallidinae, with 1243 species.

Key words: convergence; evolutionary history; floral morphology; generic circumscription; Pleurothallidinae; pollinator adaptation

Introduction. What is a *Stelis*? Or better yet, what isn't a *Stelis*? Some authors may think this is the question we are still asking ourselves today, but in fact the matter has been settled for years. We have an indisputable answer. Rather, what we are still actually asking ourselves is how can we classify the different groups of species within the *Stelis* affinity in a way that both reflects their evolutionary history and satisfies most users of such a classification system. That is the only question that still remains, and for that we may never have an answer that pleases everyone.

Species of *Stelis* Sw. (Orchidaceae: Pleurothallidinae) in the tradicional, strict, sense are characterized by a more or less flat, triangular flower, bearing three subequal, larger, spreading sepals, compact petals and lip, and a short column, with an apical anther and stigma. It was one of the first genera to be recognized in subtribe Pleurothallidinae, and has been used relatively consistently for around two centuries. With few exceptions, members of *Stelis s.s.* have an easily recognizable standard flower morphology. DNA data proves they form a monophyletic group, and there is no dispute as to which species belong to it, and which do not. Let's be clear, there is no doubt that all 1,030 currently accepted species bearing flowers with the classic *Stelis* morphology are more closely related to each other than they are to any other species of Pleurothallidinae. In every sense, *Stelis* in its traditional circumscription is a well supported group. Why, then, don't we simply recognize them as a genus on their own and get on with it? Well, because the species of *Stelis s.s.* are not an island within the subtribe. They have many close relatives that need to be classified in a way that reflects their own evolutionary history as well. After all, there is undisputed evidence that species of *Stelis* in the strict sense share an ancestor with many species that lack the typical *Stelis*-like flowers.

Historically, recognition of genera in Pleurothallidinae has been done by segregating groups of species that could be easily set aside from all others through key morphological features (Karremans 2016). Most other species simply remained in a broadly defined *Pleurothallis* R.Br., not for being related to each other or sharing particular characteristics, but for the lack of the highly distinctive features of the segregated genera. *Pleurothallis sensu lato* had always been expected to

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be polyphyletic (Lindley 1859, Luer 1986, Neyland *et al.* 1995, Stenzel 2000). DNA based phylogenetic reconstructions essentially came to demonstrate how polyphyletic it actually was and to stress the necessity for a new circumscription of genus *Pleurothallis*, whose members were found to be diversely related to most of the other genera in Pleurothallidinae. What is relevant to this discussion is that several groups of species previously assigned to *Pleurothallis* were proven to be more closely related to *Stelis* in the strict sense than anything else, despite their floral morphology. These species can no longer be treated as *Pleurothallis* because we know for a fact that their ancestors took a different evolutionary path, which ultimately gave origin to *Stelis* in the strict sense.

It is undeniable that the generic circumscription of *Stelis*, as defined by Pridgeon (2005) and modified by Karremans *et al.* (2013), has not been broadly accepted. That is most likely due to the ease of florally recognizing a member of *Stelis sensu scrito* and the lack of obvious floral features uniting species of *Stelis sensu lato* (Solano-Gómez & Salazar 2013). It is desirable that genera are diagnosable using morphological features, and not only through DNA analyses. However, it is also very important to be accurate about the phylogenetic relationships among species, establishing groups that reflect the evolutionary histories of its members. If one were to look past the obvious differences in floral morphology, which undoubtedly respond to pollinator pressure, all members of *Stelis s.l.* are vegetatively very similar to each other. So much so that without flowers it is difficult to tell them apart.

A partitioning of *Stelis s.l.* into several smaller, discrete, morphologically better-defined genera is possible. It was in fact advocated by Karremans (2010) and Karremans & Bogarín (2013), and could be desirable. Nevertheless, to do so one needs to have a clear evolutionary picture of the whole group. It is not as easy as separating the most obvious close relatives into genera, or simply separating *Stelis s.s.* from everything else. The whole picture is much more complex and the reality is that although some relationships within *Stelis s.l.* are easily diagnosable, the placement of many species continues to be a challenge, even with DNA data. Anyone can diagnose a species as belonging to either *Salpistele* Dressler, *Stelis s.s.*, or *Physosiphon* Lindl., for example. However, not even the most adamant expert could've predicted that species of *Pleurothallis* sect. *Petiolatae* Luer were sister to those of *Salpistele*, or that the *Stelis imraei* (Lindl.) Pridgeon & M.W.Chase group belonged in a completely isolated lineage. It is this lack of predictability that makes classifying these groups challenging. Unfortunately, there is no easy way out. The recognition of any segregate genus from *Stelis s.l.* requires the recognition of several additional new genera and the recircumscription of most of the existing ones (Karremans 2016). The resulting classification would be neither intuitive or very useful. At this time, it is preferable to maintain *Stelis s.l.* rather than to promote the use of *Stelis s.s.* together with a series of ill-defined, non-monophyletic satellite genera.

Some authors may believe that solving the "*Stelis* issue" is merely a matter of segregating the members of *Stelis s.s.* from the remaining *Stelis s.l.*, but this is not a viable solution. Several groups within *Stelis s.l.* are more closely related to *Stelis s.s.* than to other members of *Stelis s.l.* It is also not a matter of simply recognizing the more apparent genera like *Crocodeilanthe* Rchb.f., *Dracontia* (Luer) Luer and *Salpistele*, as advocated by several authors (Karremans 2010; Karremans & Bogarín 2013; Toscano de Brito 2018a; Damián 2019). Most *Crocodeilanthe* species are indeed easily distinguished from other members of *Stelis s.l.*, but certainly not all of them have those very evident morphological features of their most distinctive members. They are closely related to the species previously assigned to *Pleurothallis* sect. *Acuminatae* Lindl. and those placed in genus *Physothallis* Garay, which look nothing like the *Crocodeilanthe* morphologically and should be either included or segregated as a genus as well. *Dracontia* may also seem straightforward, but it is not. At least one species placed in *Elongatia* (Luer) Luer, another from *Pseudostelis* Schltr., a few placed in *Effusiella* Luer, and the type of *Mystacorchis* Szlach. & Marg. are all intermingled with species of *Dracontia*. Species of *Salpistele*, which have the most divergent floral morphology among the *Stelis s.l.* are not only closely related to species of *Dracontia*, but they are sister to two species previously assigned to genus *Elongatia* and which are florally completely different. What do these species groups have in common? Most are vegetatively similar to each other, but again, this is true for all members of *Stelis s.l.*

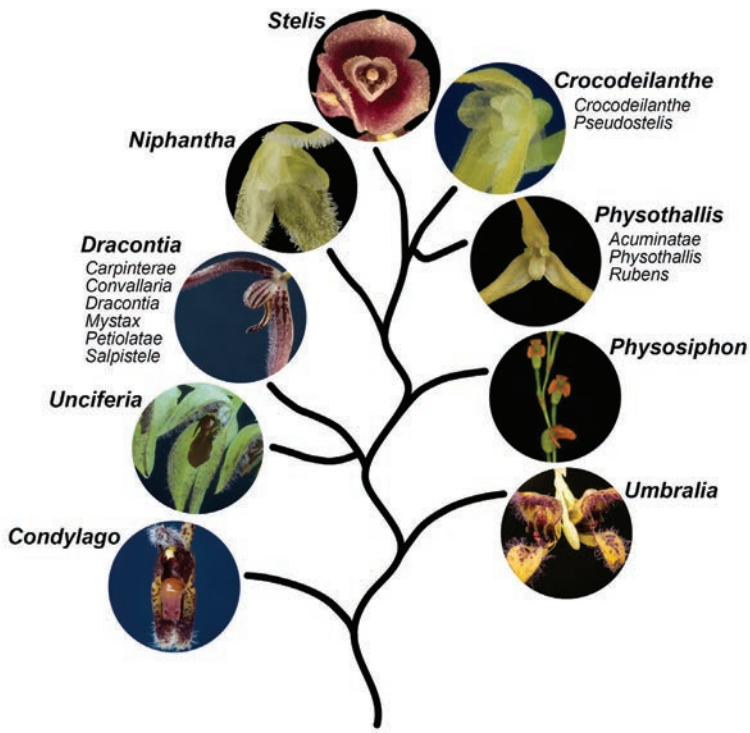


FIGURE 1. Relationships among the subgenera of *Stelis sensu lato* based on diverse phylogenetic reconstructions (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Chiron *et al.* 2012, Ramos-Castro *et al.* 2012; Karremans *et al.* 2013, Wilson *et al.* 2017, Pérez-Escobar *et al.* 2017, Chumová *et al.* 2018, Ponert *et al.* 2019), showing the proposed subgenera and sections.

Every single phylogenetic study including members *Stelis s.l.*, as proposed by Pridgeon (2005) and modified by Karremans *et al.* (2013), finds the genus to be monophyletic (Karremans 2010, Chiron *et al.* 2012, Ramos-Castro *et al.* 2012, Karremans *et al.* 2013, Wilson *et al.* 2013, 2017, Pérez-Escobar *et al.* 2017), and this continues to be the case in multi-gene genomic studies (Chumová *et al.* 2018, Ponert *et al.* 2019). Accepting *Stelis s.s.* as a genus on its own necessarily entails the recognition of many ill-defined genera that no user would be happy to adopt. The alternatives to *Stelis s.l.* are even less appealing than it itself. Does a broader concept of *Salpistele*, which as the oldest name in the group has priority over all others, be a more acceptable circumscription for the species of the *Dracontia* clade? Perhaps a more inclusive concept of *Physothallis*, harboring the species of *Pleurothallis* sect. *Acuminatae*? Or the recognition of monotypic genera for *Stelis carpinterae* (Schltr.) Pridgeon & M.W.Chase, *Stelis convallaria* (Schltr.) Pridgeon & M.W.Chase, and *Stelis mystax* (Luer) Pridgeon & M.W.Chase? Perhaps. Nevertheless, the fact remains that it is difficult to assign species to discrete groups in *Stelis s.l.*, any grouping being more or less artificial, and any alternative classification of this group results in genera that will not be more accepted and better defined or recognizable than *Stelis s.l.* Even though members of *Stelis s.s.* are florally very easily diagnosable for anyone, and, evidently, the flowers of other members of *Stelis s.l.* are very different, a broader circumscription of *Stelis*, with all its defects, still seems preferable over its alternatives. After all, we need to remember that although flowers are easily comparable with each other, they are under high selective pressure of pollinators, and may be more or less similar independently of relatedness (Karremans & Díaz-Morales 2019).

For the sake of consistency with previous works in related genera, including *Acianthera* Scheidw. (Karremans *et al.* 2016), *Andinia* (Luer) Luer (Wilson *et al.* 2017) and *Specklinia* Lindl. (Karremans *et al.* 2016), and in the interest of aiding the reader, an infrageneric classification of *Stelis s.l.* is provided (Fig. 1).

Taxonomic Treatment

Stelis Sw., J. Bot. (Schrader) 1799(2): 239. 1800, *nom. cons.*

Syn. *Humboltia* Ruiz & Pav., Fl. Peruv. Prodr.: 121. 1794, *nom. rej.*

Syn. *Physosiphon* Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835.

Syn. *Dialissa* Lindl., Ann. Mag. Nat. Hist. 15: 107. 1845.

Syn. *Crocodeilanthe* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 113. 1854.

Syn. *Pseudostelis* Schltr., Anexos Mem. Inst. Butantan, Secç. Bot. 1(4): 36. 1922.

Syn. *Physothallis* Garay, Svensk Bot. Tidskr. 47: 199. 1953.

Syn. *Steliopsis* Brieger in F.R.R.Schlechter, Orchideen Beschreib. Kult. Zücht., ed. 3, 8(29–32): 457. 1976, *nom. nud.*

Syn. *Apatostelis* Garay, Bot. Mus. Leafl. 27: 185. 1979, *nom. illeg.*

Syn. *Salpistele* Dressler, Orquideologia 14: 6. 1979.

Syn. *Condylago* Luer, Orquideologia 15: 118. 1982.

Syn. *Mystacorchis* Szlach. & Marg., Polish Bot. J. 46: 117. 2001.

Syn. *Dracontia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Syn. *Unciferia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004, *nom. illeg.* Non *Uncifera* Lindl., J. Proc. Linn. Soc., Bot. 3: 39. 1859.

Syn. *Lomax* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 88. 2006.

Syn. *Effusiella* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Syn. *Niphantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 120: 154. 2010.

Stelis* subgen. *Stelis (Figs. 2–4)

Syn. *Humboltia* Ruiz & Pav., Fl. Peruv. Prodr.: 121. 1794, *nom. rej.*

Syn. *Dialissa* Lindl., Ann. Mag. Nat. Hist. 15(96): 107. 1845. Type: *Dialissa pulchella* Lindl. Ann. Mag. Nat. Hist. 15(96): 107. 1845.

Syn. *Steliopsis* Brieger, Orchideen (Schlechter) 8(29-32): 457. 1976, *nom. nud.* Type: *Steliopsis anneliesae* Brieger, Orchideen (Schlechter) 8(29-32): 457. 1976, *nom. nud.*

Syn. *Apatostelis* Garay, Bot. Mus. Leafl. 27: 185. 1979, *nom. illeg.* Type: *Stelis hylophila* Rchb.f., Bonplandia (Hannover) 3: 241. 1855.

Stelis cochabambensis Karremans, *nom. nov.*

Repl. syn.: *Stelis dasysepala* Luer & R.Vásquez, Selbyana 32(1,2): 37. 2018, *nom. illeg.* Non *Stelis dasysepala* Luer & R.Escobar, Harvard Pap. Bot. 21(2): 198. 2016.

Stelis luerii Karremans, *nom. nov.*

Repl. syn.: *Stelis marginata* Luer & R.Vásquez, Selbyana 32(1,2): 71. 2018, *nom. illeg.* Non *Stelis marginata* Luer & R.Escobar, Harvard Pap. Bot. 21: 205. 2016.

Stelis peculiaris Karremans, *nom. nov.*

Repl. syn.: *Stelis praecipua* Luer & R.Vásquez, Selbyana 32(1,2): 87. 2018, *nom. illeg.* Non *Stelis praecipua* Luer, Harvard Pap. Bot. 22: 101. 2017.

Stelis subgen. *Stelis* is synonymous to *Stelis s.s.* as defined by Luer (2009). In other words, it includes all the classical species of *Stelis* with triangular, flattish flowers with very short petals and lip, the very short column has an apical anther and stigma, and the pollinaria have a drop-like viscidium attached to the short caudicles. Many species of *Stelis* subgen *Stelis* have been analyzed genetically and they always group together into a highly supported clade with low genetic variation. There is a single exception, and that is an accession labeled *Stelis nexipous* Garay in Karremans *et al.* (2013) that appeared associated with members of *Stelis* subgen. *Niphantha*. It is surely either a lab mixup or sequencing mistake.

A comprehensive species list is not yet presented here. However, of the 1243 species currently accepted in genus *Stelis s.l.* (Karremans, in prep.), 1030 belong to *Stelis s.s.* The remaining 213 species are listed under one of the other subgenera hereafter.

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

Bas. *Crocodeilanthe* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 113. 1854. *Pleurothallis* subgen. *Crocodeilanthe* (Rchb.f. & Warsz.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 34. 1986. Type: *Crocodeilanthe xiphizusa* Rchb.f., Bonplandia (Hannover) 2(9): 114. 1854.

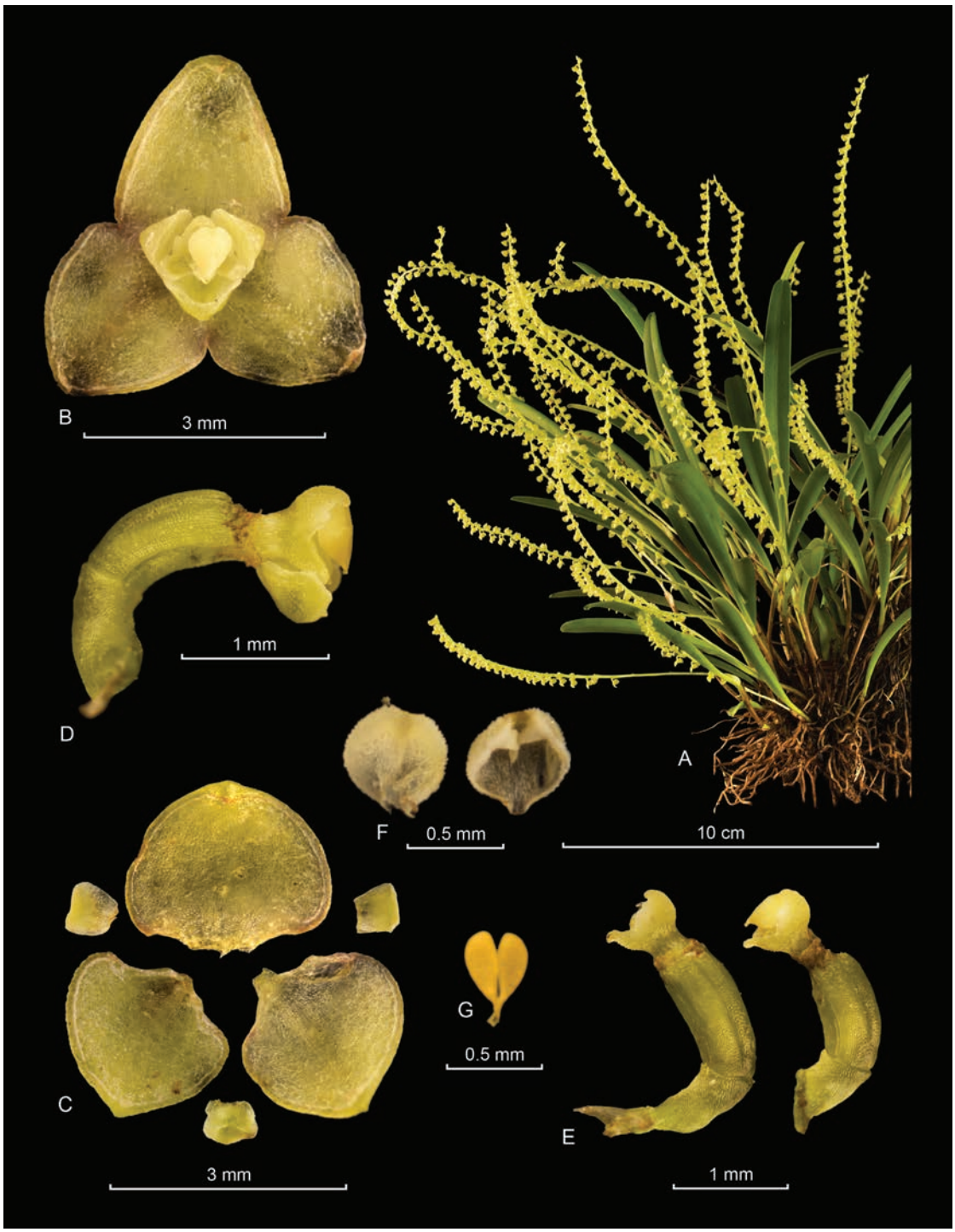


FIGURE 2. Lankester Composite Digital Plate (LCDP) of *Stelis sp*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral view. **F**. Anther cap. **G**. Pollinarium. Photographs by AK and I. Chinchilla based on *Karremans 7293* (JBL-spirit).

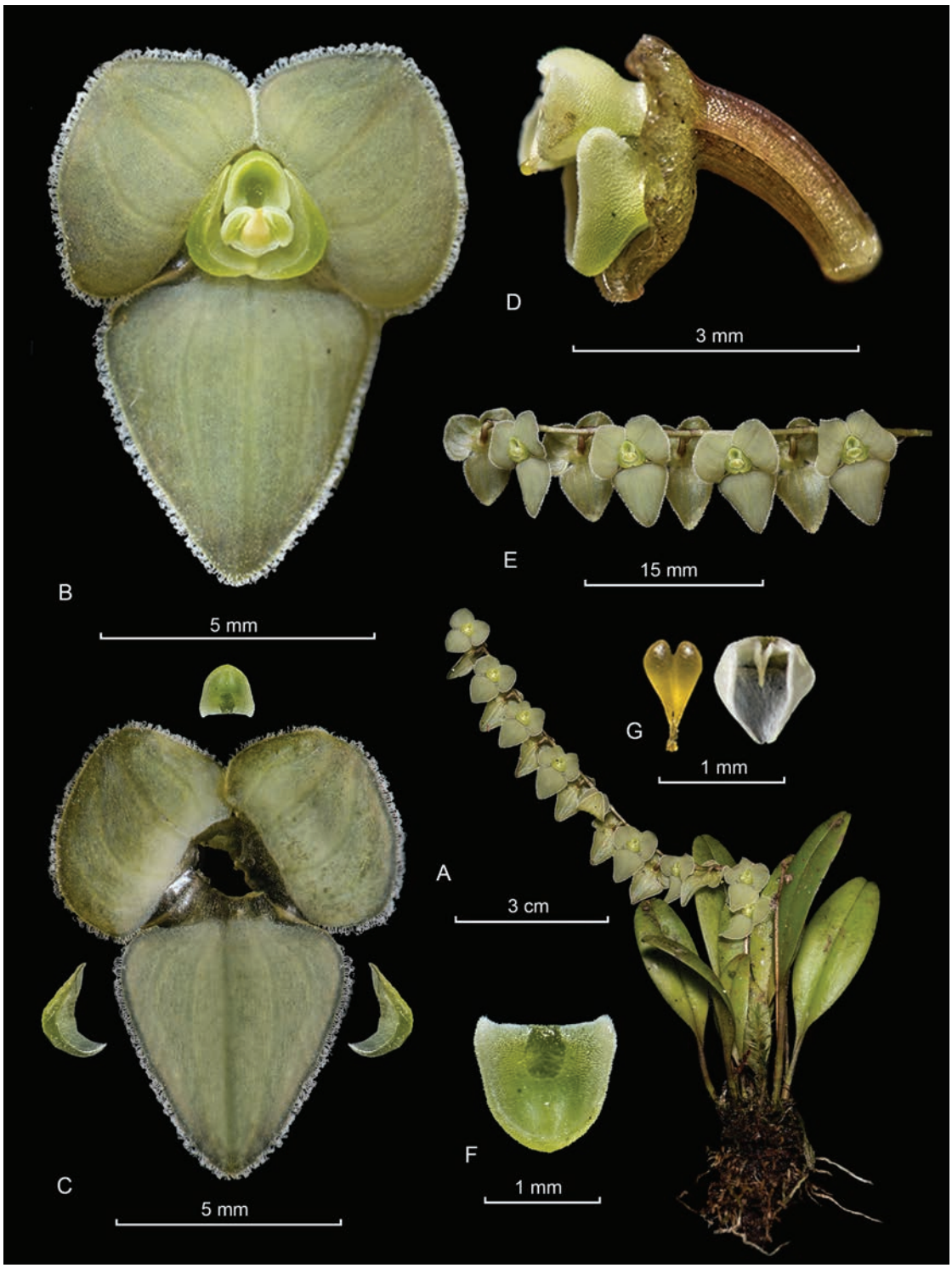


FIGURE 3. LCDP of a typical *Stelis s.s.* species. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Inflorescence. **F**. Lip. **G**. Anther cap and pollinarium. Photographs by J.S. Moreno based on *Moreno* 519 (CAUP).

Syn. *Pseudostelis* Schltr., Anexos Mem. Inst. Butantan, Secç. Bot. 1(4): 36. 1922. *Pleurothallis* subgen. *Pseudostelis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 87. 1999. Lectotype: *Physosiphon spiralis* Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835 (Garay 1974).

Stelis subgen. *Crocodeilanthe* includes 85 species, divided in two sections. *Stelis* sect. *Crocodeilanthe* is composed of 84 species of which 90% are found at high elevations in the Andes of Bolivia, Colombia, Ecuador, Peru and Venezuela. Many are local endemics. A few species are known from Costa Rica and Panama, and a single species is reported from the Greater Antilles, another from the Lesser Antilles and yet another from Brazil. Sect. *Pseudostelis* includes only one species, the common and widespread *Stelis deregularis* Barb. Rodr. which is found at mid elevations from Mexico to Brazil, through Central America.

Toscano de Brito (2018a) recognizes *Crocodeilanthe* at the generic level suggesting it may be easily defined by merging Luer's *Pleurothallis* subgen. *Crocodeilanthe* and *Pleurothallis* subgen *Pseudostelis*. The species of *Pseudostelis*, excluding *P. rufobrunnea* "which is clearly a member of the genus *Stelis*", are said to "share the same habit and floral morphology with *Crocodeilanthe*". Nevertheless, the placement of *Stelis magdalenae* (Rchb.f.) Pridgeon & M.W.Chase in *Crocodeilanthe* is not straight forward at all, and *Stelis simplex* (Ames & C.Schweinf.) Pridgeon & M.W.Chase certainly belongs to the *Dracontia* clade rather than *Crocodeilanthe*. Also, even though it may now seem obvious that *Stelis rufobrunnea* is in fact a member of *Stelis s.s.* and that *Stelis deregularis* belongs to *Crocodeilanthe*, both species were only faithfully placed on the basis of DNA data.

Furthermore, the suggestion that *Stelis gelida* (Lindl.) Pridgeon & M.W.Chase (type species of *Niphantha*) belongs to *Crocodeilanthe* is not supported genetically or morphologically. The subpandurate, arcuate lip, elongate column, incumbent anther and stigma, and whale-tail pollinaria clearly separate it from other *Crocodeilanthe* species. Multiple *Stelis gelida* accessions analyzed by Karremans *et al.* (2013) and again by Pérez-Escobar *et al.* (2017), were consistently found only distantly related to *Crocodeilanthe*. An accession labeled *Stelis antillensis* in Karremans *et al.* (2013), which was retrieved among those of *S. gelida*, is likely misidentified by the original sequence author (Stenzel) as was stated therein.

Figure 4. *Stelis hualluapampensis* Collantes & Karremans, a non-typical species of *Stelis s.s.* with subglobose flowers, fused lateral sepals and a lip-like dorsal sepal that sticks out of the flower. Photograph by B. Collantes.

The unresolved relationships between *Crocodeilanthe* species and those of the non-monophyletic *Pseudostelis*, in addition to the misplacement of the unrelated *Stelis gelida*, are evidence that the definition of this genus is not as straightforward as suggested. Even though it is possible to recognize most *Crocodeilanthe* species morphologically, the short lip and petals, the stout column with an apical anther, and pollina with a drop-like viscidium are a step prior to the typical *Stelis s.s.* floral morphology. As closest relative to *Stelis* in the strict sense, its recognition at generic level entails the recognition of several other splinter genera, which is not advised at the time.

Stelis* subgen. *Crocodeilanthe* sect. *Crocodeilanthe

Syn.: *Crocodeilanthe* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 113. 1854. *Pleurothallis* subgen. *Crocodeilanthe* (Rchb.f. & Warsz.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 34. 1986. Type: *Crocodeilanthe xiphizusa* Rchb.f., Bonplandia (Hannover) 2(9): 114. 1854.

Stelis aligera (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis aligera* Luer & R.Vásquez,

FIGURE 5. *Stelis atwoodii* (Luer) Pridgeon & M.W.Chase, an untypical member of *Stelis* subgen. *Crocodeilanthe*. Photograph by AK.

Revista Soc. Boliv. Bot. 1(2): 9. 1997. Syn.: *Crocodeilanthe aligera* (Luer & R.Vásquez) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis aloisii (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis aloisii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 8: 57. 1921. Syn.: *Crocodeilanthe aloisii* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis antillensis Pridgeon & M.W.Chase, Lindleyana 17(2): 98. 2002.

Repl. syn.: *Pleurothallis domingensis* Cogn., Symb. Antill. 6: 402. 1909. Syn.: *Crocodeilanthe domingensis* (Cogn.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis domingensis* (Cogn.) Pridgeon & M.W.Chase, Lindleyana 16: 262. 2001, *nom. illeg*. Non *Stelis domingensis* Cogn. in I.Urban, Symb. Antill. 6: 692. 1910.

Stelis apposita (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis apposita* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 12. 1998. Syn.: *Crocodeilanthe apposita* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis atwoodii (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001. (Fig. 5)

Bas.: *Pleurothallis atwoodii* Luer, Lindleyana 11(2): 67. 1996. Syn.: *Crocodeilanthe atwoodii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis avirostris (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis avirostris* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 13. 1998. Syn.: *Crocodeilanthe avirostris* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis batillacea (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis batillacea* Luer, Selbyana 3(1-2): 58. 1976. Syn.: *Crocodeilanthe batillacea* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis bracteosa (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis bracteosa* C.Schweinf., Fieldiana, Bot. 33: 20. 1970. Syn.: *Crocodeilanthe bracteosa* (C.Schweinf.) Luer, Harvard Pap. Bot. 16(2): 358. 2011.

Stelis bucaramangae (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis bucaramangae* Luer & R.Escobar, Orquideología 20: 38. 1996. Syn.: *Crocodeilanthe bucaramangae* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis cassidis (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis cassidis* Lindl., Ann. Mag. Nat. Hist. 15: 384. 1845. Syn.: *Crocodeilanthe cassidis* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis cauliflora (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis cauliflora* Lindl., Companion Bot. Mag. 2: 355. 1836. Syn.: *Crocodeilanthe cauliflora* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis choerorhyncha (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261-262. 2001.

Bas.: *Pleurothallis choerorhyncha* Luer, Orquideología 20: 204. 1996. Syn.: *Crocodeilanthe choerorhyncha* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis cosangae (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cosangae* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 18. 1998. Syn.: *Crocodeilanthe cosangae* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis cuatrecasasii (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cuatrecasasii* Luer, Orquideología 20: 208. 1996. Syn.: *Crocodeilanthe cuatrecasasii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis cyathiflora (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cyathiflora* C.Schweinf., Bot. Mus. Leafl. 15: 90, t. 27. 1951. *Crocodeilanthe cyathiflora* (C.Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis damianii Karremans, *nom. nov.*

Repl. syn.: *Crocodeilanthe chachapoyensis* Damian, Ann. Bot. Fenn. 56: 302. 2019. Non *Stelis chachapoyensis* Rchb.f., Bonplandia (Hannover) 3: 225. 1855.

Stelis dapsilis Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis maxima* Luer, Selbyana 3(1-2): 140. 1976. Syn.: *Crocodeilanthe maxima* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis maxima* (Luer) Pridgeon & M.W.Chase, Lindleyana 16: 264. 2001, *nom. illeg.* Non *Stelis maxima* Lindl., Ann. Mag. Nat. Hist. 15: 106. 1845.

Stelis decurrens Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis croatii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 18-19. 1998. Syn.: *Crocodeilanthe croatii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis croatii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16: 262. 2001, *nom. illeg*. Non *Stelis croatii* Luer, Lindleyana 11: 97. 1996.

Stelis toscanoi Karremans, *nom. nov.*

Repl. syn.: *Crocodeilanthe dewildei* Luer & Toscano (2018: 47). *Stelis dewildei* (Luer & Toscano) Karremans, Phytotaxa 406(5): 265. 2019, *nom. illeg*. Non *Stelis dewildei* Luer & R.Escobar, Harvard Pap. Bot. 22(1): 34. 2017.

Stelis duckei E.M.Pessoa & M.Alves, Brittonia 66(2): 156-157. 2014.

Syn.: *Crocodeilanthe duckei* (E.M.Pessoa & M.Alves) Toscano, Harvard Pap. Bot. 23(1): 54. 2018.

Stelis erectiflora (Luer) J.M.H.Shaw, Orchid Rev. 122(1308): 77. 2014.

Bas.: *Crocodeilanthe erectiflora* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 311. 2005.

Stelis expansa (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis expansa* Lindl., Fol. Orchid. ~Pleurothallis~ 4. 1859. Syn.: *Crocodeilanthe expansa* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis fons-florum (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis fons-florum* Lindl., Fol. Orchid. ~Pleurothallis~ 5, no. 15. 1859. Syn.: *Crocodeilanthe fons-florum* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis galeata (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis galeata* Lindl., Ann. Mag. Nat. Hist. 15: 107. 1845. Syn.: *Crocodeilanthe galeata* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis galerasensis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis galerasensis* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 28. 1998. Syn.: *Crocodeilanthe galerasensis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis gargantua Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis gigas* Luer & R.Escobar, Orquideología 20(1): 52. 1996. *Crocodeilanthe gigas* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis gigas* (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16: 263 (2001), *nom. illeg.* Non *Stelis gigas* Barb. Rodr., Gen. Spec. Orchid. 2: 89. 1881.

Stelis globosa Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis popayanensis* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 438. 1898. *Crocodeilanthe popayanensis* (F.Lehm. & Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis popayanensis* (F.Lehm. & Kraenzl.) Pridgeon & M.W.Chase, Lindleyana 16: 265. 2001, *nom. illeg.* Non *Stelis popayanensis* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26(3-4): 448. 1899.

Stelis heros Karremans, *nom. nov.*

Repl. syn.: *Crocodeilanthe steinbachii* Luer & Toscano, Harvard Pap. Bot. 23: 48. 2018. *Stelis steinbachii* (Luer & Toscano) Karremans, Phytotaxa 406(5): 267. 2019, *nom. illeg.* Non *Stelis steinbachii* Luer, Selbyana 32(1,2): 110. 2018.

Etymology: The name honors the three larger-than-life orchidologists that sadly passed away in 2019, Carl A. Luer, Robert L. Dressler and W. Mark Whitten.

Stelis infundibulosa (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis infundibulosa* Luer, Orquideología 20: 210. 1996. Syn.: *Crocodeilanthe infundibulosa* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis jurisdixii (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis jurisdixii* Luer & R.Escobar, Orquideología 20: 64. 1996. Syn.: *Crocodeilanthe jurisdixii* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis juxta (Luer, Thoerle & F.A.Werner) J.M.H.Shaw, Orchid Rev. 122(1308): 77. 2014.

Bas.: *Crocodeilanthe juxta* Luer, Thoerle & F.A.Werner, Harvard Pap. Bot. 16(2): 320. 2011.

Stelis laevigata (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis laevigata* Lindl., Ann. Mag. Nat. Hist. 15: 106. 1845. *Crocodeilanthe laevigata* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis laevis (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis laevis* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 33. 1998. Syn.: *Crocodeilanthe laevis* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis laminata (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis laminata* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 33-34. 1998. Syn.: *Crocodeilanthe laminata* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis lehmanniana (Schltr.) Karremans, Phytotaxa 203(3): 293. 2015.

Bas.: *Pleurothallis lehmanniana* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 235. 1920. *Crocodeilanthe lehmanniana* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis ligulata (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis ligulata* Lindl., Fol. Orchid. ~Pleurothallis~ 29. 1859. Syn.: *Crocodeilanthe ligulata* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis magdalenae (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis magdalenae* Rchb.f., Bonplandia (Hannover) 3: 72. 1855. *Crocodeilanthe magdalenae* (Rchb.f.) Toscano, Harvard Pap. Bot. 23(1): 54. 2018.

Stelis mandonii (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis mandonii* Rchb.f., Xenia Orchid. 3: 24. 1878. Syn.: *Crocodeilanthe mandonii* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis melanostele (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis melanostele* Luer & R.Vásquez, Phytologia 49(3): 210. 1981. Syn.: *Crocodeilanthe melanostele* (Luer & R.Vásquez) Toscano, Harvard Pap. Bot. 23(1): 54. 2018.

Stelis mendietae (Luer, Thoerle & F.A.Werner) J.M.H.Shaw, Orchid Rev. 122(1308): 77. 2014.

Bas.: *Crocodeilanthe mendietae* Luer, Thoerle & F.A.Werner, Harvard Pap. Bot. 16(2): 321. 2011.

Stelis molleturoi (Luer & Dodson) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis molleturoi* Luer & Dodson, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 38. 1998. *Crocodeilanthe molleturoi* (Luer & Dodson) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis moritzii (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis moritzii* Rchb.f., Linnaea 22: 824. 1849. Syn.: *Crocodeilanthe moritzii* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis neowerneri J.M.H.Shaw, Orchid Rev. 122(1308): 78. 2014.

Bas.: *Crocodeilanthe werneri* Luer & Thoerle, Harvard Pap. Bot. 16(2): 323. 2011. Non *Stelis werneri* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 42. 1924.

Stelis nivalis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 264-265. 2001.

Bas.: *Pleurothallis nivalis* Luer, Selbyana 1(4): 420. 1976. Syn.: *Crocodeilanthe nivalis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis orectopus (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis orectopus* Luer, Selbyana 3(3-4): 356. 1977. Syn.: *Crocodeilanthe orectopus* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pachypus F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 447. 1899.

Bas.: *Pleurothallis pachypus* (F.Lehm. & Kraenzl.) Garay, Canad. J. Bot. 34: 254. 1956. Syn.: *Crocodeilanthe pachypus* (F.Lehm. & Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis patateënsis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis patateënsis* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 42. 1998. Syn.: *Crocodeilanthe patateënsis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pellucida (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pellucida* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 42-43. 1998. Syn.: *Crocodeilanthe pellucida* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pennelliana (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pennelliana* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 43. 1998. Syn.: *Crocodeilanthe pennelliana* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pilifera (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pilifera* Lindl., Fol. Orchid. ~Pleurothallis~ 9. 1859. Syn.: *Crocodeilanthe pilifera* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pittieri (Schltr.) Rojas-Alv. & Karremans, Phytotaxa 406(5): 266. 2019.

Bas.: *Pleurothallis pittieri* Schltr., Repert. Spec. Nov. Regni Veg. 3(42-43): 247. 1907.

Syn.: *Crocodeilanthe floribunda* (Poepp. & Endl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Pleurothallis floribunda* Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 48-49, t. 84. 1835 [1836]. Non *Stelis floribunda* Kunth, Nov. Gen. Sp. (folio ed.) 1: 362. 1815 [1816].

Stelis possoae (Luer) Karremans, Phytotaxa 203(3): 293. 2015.

Bas.: *Pleurothallis possoae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 129-130. 2000. *Crocodeilanthe possoae* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis praealta (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis praealta* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 45. 1998. *Crocodeilanthe praealta* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis prolificans (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis prolificans* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 45. 1998. Syn.: *Crocodeilanthe prolificans* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis pulchella Kunth, Nov. Gen. Sp. (quarto ed.) 1(4): 364, t. 90. 1816. (Fig. 6)

Syn.: *Pleurothallis pulchella* (Kunth) Lindl., Exot. Fl. 2(14): sub t. 123. 1825 [1824]. *Crocodeilanthe pulchella* (Kunth) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis reptans Pridgeon & M.W.Chase, Lindleyana 17(2): 100. 2002.

Bas.: *Pleurothallis scansor* Luer, Phytologia 49(3): 216. 1981. Syn.: *Crocodeilanthe scansor* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. Non *Stelis scansor* Rchb.f., Bonplandia (Hannover) 3(17): 241. 1855.

Stelis retusiloba (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis retusiloba* C.Schweinf., Bot. Mus. Leafl. 15: 100. 1951. Syn.: *Crocodeilanthe retusiloba* (C.Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004.

Stelis rhodotantha (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis rhodotantha* Rchb.f., Linnaea 22: 825. 1849. Syn.: *Crocodeilanthe rhodotantha* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis rictoria (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis rictoria* Rchb.f., Linnaea 41: 14. 1877. *Crocodeilanthe rictoria* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis roseopunctata (Lindl.) R. Bernal, Phytoneuron 22: 5. 2015.

Bas.: *Pleurothallis roseopunctata* Lindl., Orchid. Linden. 2. 1846.

Syn.: *Dendrobium elegans* Kunth, Nov. Gen. Sp. 1: 358. 1816. *Pleurothallis elegans* (Kunth) Lindl., Edwards's Bot. Reg. 28(Misc): 70. 1842. *Crocodeilanthe elegans* (Kunth) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. Non *Stelis elegans* Luer & R.Vásquez, Phytologia 49(3): 228. 1981.

Stelis rostriformis Zambrano & Solano, Phytotaxa 376(4): 181. 2018.

Stelis sagittata Zambrano & Solano, Phytotaxa 376(4): 183. 2018.

Repl. syn.: *Pleurothallis jamiesonii* Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835. Syn.: *Crocodeilanthe jamiesonii* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 256. 2004. *Stelis jamiesonii* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 264. 2001, *nom. illeg.* Non *Stelis jamesonii* Lindl., J. Bot. (Hooker) 1: 11. 1834.

Stelis salpingantha (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis salpingantha* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 50-51. 1998. Syn.: *Crocodeilanthe salpingantha* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis simplicilabia (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis simplicilabia* C.Schweinf., Revista Acad. Colomb. Ci. Exact. 5(19): 350. 1943. Syn.: *Crocodeilanthe simplicilabia* (C.Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis siphonantha (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

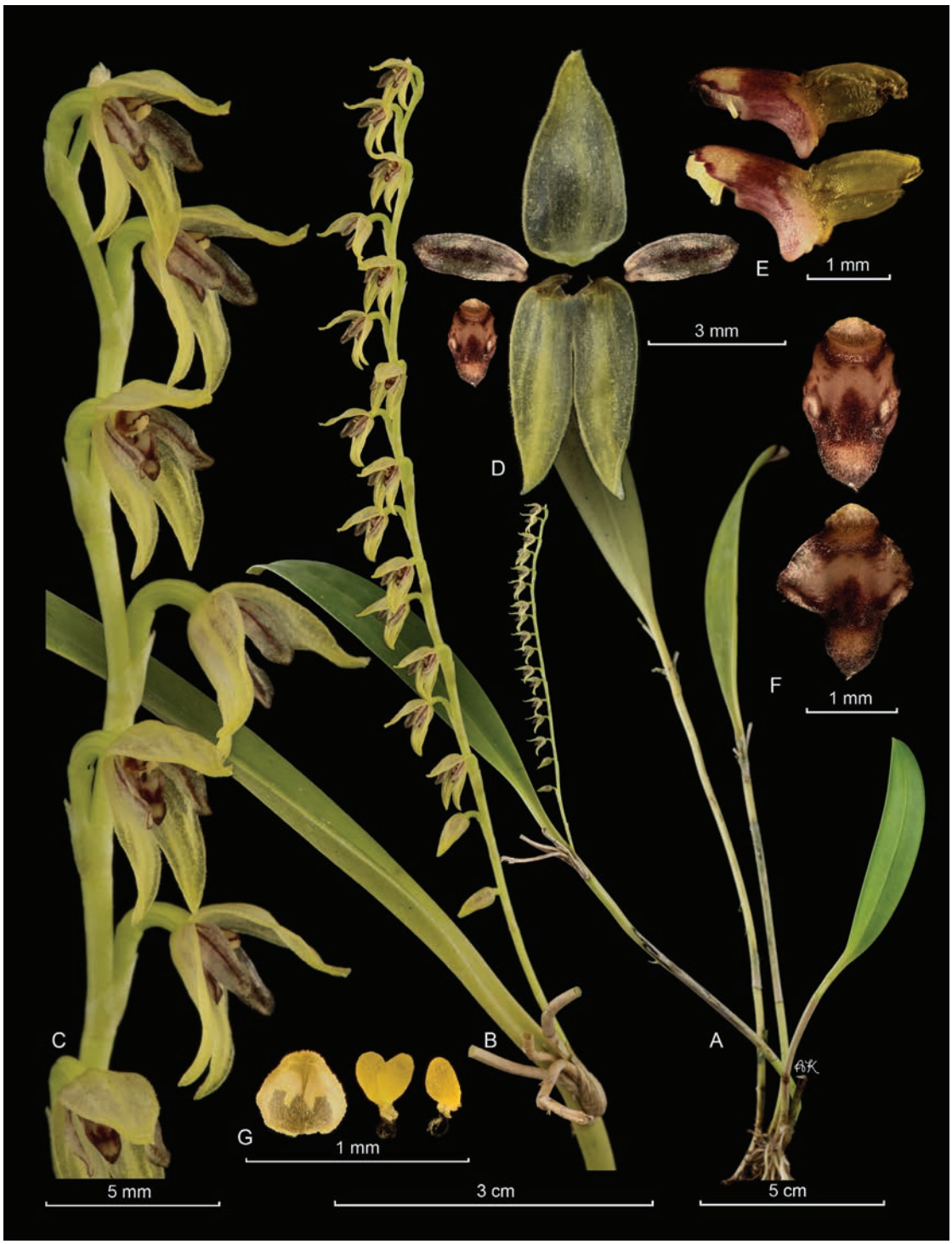


FIGURE 6. LCDP of *Stelis pulchella* a typical representative of *Stelis* sect. *Crocodeilanthe*. **A**. Habit. **B**. Inflorescence. **C**. Flowers. **D**. Dissected perianth. **E**. Column ventral and lateral view. **F**. Lip naturally and expanded. **G.** Anther cap and pollinarium. Photographs by AK based on *JBL-28245* (JBL-spirit).

Bas.: *Pleurothallis siphonantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 52-53. 1998. *Crocodeilanthe siphonantha* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis spathosa (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis spathosa* Luer & R.Escobar, Orquideología 20: 86. 1996. Syn.: *Crocodeilanthe spathosa* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis speciosa (Luer, Thoerle & F.A.Werner) E.M.Pessoa & M. Alves, Brittonia 66(2): 157. 2013.

Bas.: *Crocodeilanthe speciosa* Luer, Thoerle & F.A. Werner, Harvard Pap. Bot. 16(2): 321. 2011. Syn.: *Stelis speciosa* (Luer, Thoerle & F.A.Werner) J.M.H.Shaw, Orchid Rev. 122(1308): 78. 2014, *nom. illeg.*

Stelis stelidiopsis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 266-267. 2001.

Bas.: *Pleurothallis stelidiopsis* Luer, Phytologia 49(3): 218. 1981. Syn.: *Crocodeilanthe stelidiopsis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis stergiosii (Carnevali & I.Ramírez) Karremans, Phytotaxa 203(3): 293. 2015.

Bas.: *Pleurothallis stergiosii* Carnevali & I.Ramírez, Harvard Pap. Bot. 3: 247. 1998. Syn.: *Crocodeilanthe stergiosii* (Carnevali & I.Ramírez) Carnevali & I.Ramírez, Nuevo Cat. Fl. Vasc. Venezuela 578. 2008.

Stelis suinii (Luer) J.M.H.Shaw, Orchid Rev. 122(1308): 78. 2014.

Bas.: *Crocodeilanthe suinii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 249. 2006. Syn.: *Pleurothallis suinii* (Luer) Pfahl, Internet Orchid Sp. Photo Encycl. Nomencl. Notes 2. 2013. 2013.

Stelis taxis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis taxis* Luer, Selbyana 5(2): 184. 1979. *Crocodeilanthe taxis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis tepuiensis (Carnevali & I.Ramírez) Karremans, Phytotaxa 203(3): 294. 2015.

Bas.: *Pleurothallis tepuiensis* Carnevali & I.Ramírez, Novon 3(2): 121. 1993. Syn.: *Crocodeilanthe tepuiensis* (Carnevali & I.Ramírez) Carnevali & I.Ramírez, Nuevo Cat. Fl. Vasc. Venezuela 758. 2008.

Stelis tunguraguae (F.Lehm. & Kraenzl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis tunguraguae* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 439. 1899. Syn.: *Crocodeilanthe tunguraguae* (F.Lehm. & Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis uvaegelata Doucette ex L.E.Matthews, OrchideenJ. 6(3): 13. 2018.

Stelis vargasii (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis vargasii* C.Schweinf., Bot. Mus. Leafl. 10: 192. 1942. Syn.: *Crocodeilanthe vargasii* (C.Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis vasqueziana Karremans, Phytotaxa 203(3): 294. 2015.

Bas.: *Crocodeilanthe vasquezii* Luer, Harvard Pap. Bot. 17(2): 340. 2012.

Stelis vegrandis (Luer & Dodson) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis vegrandis* Luer & Dodson, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 56. 1998. Syn.: *Crocodeilanthe vegrandis* (Luer & Dodson) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis velaticaulis (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis velaticaulis* Rchb.f., Linnaea 22: 824. 1849. Syn.: *Crocodeilanthe velaticaulis* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis velatipes (Rchb.f.) Karremans, Phytotaxa 406(5): 267. 2019.

Bas.: *Pleurothallis velatipes* Rchb.f., Linnaea 22: 828. 1849. Syn.: *Crocodeilanthe velatipes* (Rchb.f.) Carnevali & G.A.Romero, Nuevo Cat. Fl. Vasc. Venezuela 758. 2008.

Stelis verbiformis (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis verbiformis* Luer, Selbyana 2: 389. 1978. *Crocodeilanthe verbiformis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis virgata (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis virgata* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 59. 1998. *Crocodeilanthe virgata* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis weddelliana (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis weddelliana* Rchb.f., Xenia Orchid. 3: 24. 1878. *Crocodeilanthe weddelliana* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 309. 2005.

Stelis xiphizusa (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16: 268. 2001.

Bas.: *Crocodeilanthe xiphizusa* Rchb.f., Bonplandia (Hannover) 2(9): 114. 1854. Syn.: *Pleurothallis xiphizusa* (Rchb.f.) Rchb.f., Ann. Bot. Syst. 6(2): 172-173. 1861.

Stelis zunagensis (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 268. 2001.

Bas.: *Pleurothallis zunagensis* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 65: 61. 1998. Syn.: *Crocodeilanthe zunagensis* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

DNA data is available for *Stelis atwoodi*, *S. galeata*, *S. pulchella*, *S. velaticaulis;* the latter species are morphologically highly similar to *Stelis xiphizusa*, type species of *Crocodeilanthe*, of which no DNA data is currently available. There is no doubt that all typical species of *Crocodeilanthe* belong here. They consistently group together into a well supported clade that is very closely related to *Stelis* in the strict sense (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Wilson *et al.* 2017, Ponert *et al.* 2019). This is consistent with the *Stelis*-like morphology of their flower, especially in an overall reduction in the column and lip, and pollinaria with a viscidium.

Stelis subgen. Crocodeilanthe sect. Pseudostelis (Schltr.) Karremans, *comb. et stat. nov.*

Bas.: *Pseudostelis* Schltr., Anexos Mem. Inst. Butantan, Secç. Bot. 1(4): 36. 1922. Syn. *Pleurothallis* subgen. *Pseudostelis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 87. 1999. Lectotype: *Physosiphon spiralis* Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835 (Garay 1974).

Stelis deregularis Barb.Rodr., Gen. Sp. Orchid. 2: 94. 1882. (Fig. 7)

Syn.: *Physosiphon deregularis* (Barb.Rodr.) Cogn., Fl. Bras. 3(4): 341-342. 1896. *Pseudostelis deregularis* (Barb.Rodr.) Schltr., Anexos Mem. Inst. Butantan, Secc. Bot. 1(4): 38. 1922. *Pleurothallis deregularis* (Barb.Rodr.) Luer, Selbyana 2(4): 385-386. 1978.

Syn.: *Physosiphon spiralis* Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835. *Crocodeilanthe spiralis* (Lindl.) Toscano, Harvard Pap. Bot. 23(1): 54. 2018. *Pseudostelis spiralis* (Lindl.) Schltr., Anexos Mem. Inst. Butantan, Secc. Bot. 1(4): 38. 1922. Non *Stelis spiralis* (Ruiz & Pav.) Pers., Syn. Pl. 2: 524. 1807.

DNA studies consistently find the accessions of *Stelis deregularis* as sister to the remaining species of *Stelis* subgen. *Crocodeilanthe* (Karremans *et al.* 2013, Pérez-Escobar *et al*. 2017). No DNA data is available for *Stelis bracteosa*, *S. magdalenae* and *S. melanostele* which have been suggested to be close relatives of *S. deregularis* (Luer 1999, Toscano de Brito 2018a). Based on morphology *Stelis bracteosa* and *S. melanostele* are consistent with *Stelis* subgen. *Crocodeilanthe* but their affinity with *S. deregularis* is not as clear. They, together with the unresolved *Stelis magdalenae*, are excluded from this section until proven to belong here.

Stelis* subgen. *Physothallis (Garay) Karremans, *comb. nov.*

Bas. *Physothallis* Garay, Svensk Bot. Tidskr. 47: 199. 1953. *Pleurothallis* subgen. *Physothallis* (Garay) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 53. 1986. Type: *Physothallis harlingii* Garay, Svensk Bot. Tidskr. 47(2): 199. 1953.

Syn. *Pleurothallis* subgen. *Acuminatia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 98.

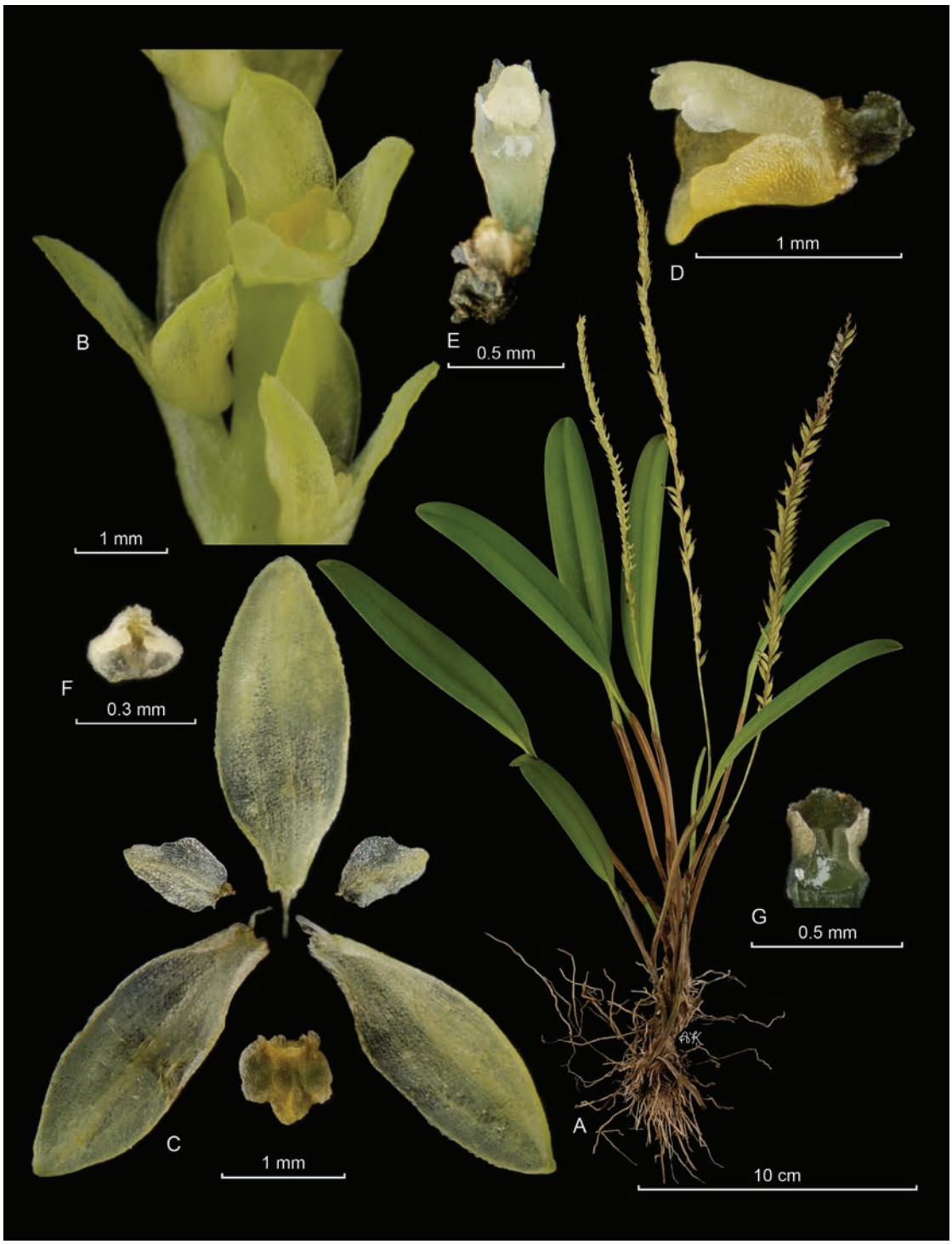


FIGURE 7. LCDP of *Stelis deregularis*, type species of *Stelis* sect. *Pseudostelis*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral view. **F**. Anther cap. **G.** Pollinarium on the stigma. Photographs by AK based on *Karremans 7303* (JBL-spirit).

1999. Type: *Dendrobium acuminatum* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 357. 1816.

The 31 species that belong to *Stelis* subgen. *Physothallis* are mostly found at high elevations in the Andes of Bolivia, Colombia, Ecuador, Peru and Venezuela. They are divided in three sections. *Stelis* sect. *Acuminatae* includes 27 species that generally have rather narrow distributions in the Andean countries, especially Bolivia and Peru, a single species from Central America, and a couple are reported from Mexico, Guyana and Brazil. The three members of *Stelis* sect. *Physothallis* are endemic to Ecuador. The sole member of *Stelis* sect. *Rubens* is widely distributed from Colombia to Bolivia and Brazil.

Despite being consistently found to be closely related to *Stelis s.s.* and *Crocodeilanthe* in every single phylogenetic study of the group (Karremans 2010, Chiron *et al.* 2012, Ramos-Castro *et al.* 2012, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Wilson *et al.* 2017), the inclusion of the members of Luer's *Pleurothallis* sect. *Acuminatae* in *Stelis s.l.* is still met with inexplicable resistance (e.g. Santos *et al.* 2018, 2019, Toscano de Brito 2018b, Govaerts *et al.* 2019). The exclusion of these species from genus *Anathallis* is not only evident morphologically (Karremans 2014), but is highly supported even in multi-gene genomic studies (Ponert *et al.* 2019). That they belong within a broadly defined *Stelis* is indisputable. What remains to be proven at this time is how these species interrelate as the analyses are inconclusive and the groupings proposed may be artificial. Three different clades are brought together: a) composed of the two species previously placed in genus *Physothallis*, plus *Stelis lennartii* (= *Pleurothallis anderssonii* Luer); b) the controversial *Stelis montserratii* (= *Pleurothallis rubens* Lindl.); and c) the remaining members of *Pleurothallis* sect. *Acuminatae*, including the type species *Stelis aurea* [= *Pleurothallis acuminata* (Kunth) Lindl.]. Each one is given sectional status.

The recognition of *Stelis s.s.* and *Crocodeilanthe* at generic level necessarily entails the recognition of *Physothallis* and probably of *Pleurothallis* sect. *Acuminatae* at generic level as well. This can only be done after resolving how the members of these two groups interrelate. .

Stelis* subgen. *Physothallis sect. Acuminatae (Lindl.) Karremans, comb. nov.

Bas. *Pleurothallis* sect. *Acuminatae* Lindl. Fol. Orchid. Pleurothallis 32. 1859. Type: *Dendrobium acuminatum* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 357. 1816.

Stelis ariasii (Luer & Hirtz) Karremans, Lankesteriana 13(3): 328. 2014.

Bas.: *Pleurothallis ariasii* Luer & Hirtz, Lindleyana 12(1): 42. 1997. Syn.: *Anathallis ariasii* (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 247. 2001.

Stelis asperilinguis (Rchb.f. & Warsz.) Karremans, Lankesteriana 13(3): 328. 2014.

Bas.: *Pleurothallis asperilinguis* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 114. 1854. Syn.: *Anathallis asperilinguis* (Rchb.f. & Warsz.) Pridgeon & M.W.Chase, Lindleyana 16(4): 247. 2001.

Stelis aurea (Lindl.) Karremans, Lankesteriana 13(3): 328. 2014. (Fig. 8)

Bas.: *Pleurothallis aurea* Lindl., Ann. Mag. Nat. Hist. 12(79): 397. 1843.

Syn.: *Anathallis racemosa* Barb.Rodr., Gen. Sp. Orchid. 1: 24. 1877. Syn.: *Pleurothallis racemosa* (Barb.Rodr.) Cogn., Fl. Bras. 3(4): 554. 1896.

Syn.: *Dendrobium acuminatum* Kunth, Nov. Gen. Sp. 1: 357. 1816. *Anathallis acuminata* (Kunth) Pridgeon & M.W.Chase, Lindleyana 16(4): 247. 2001. *Pleurothallis acuminata* (Kunth) Lindl., Edwards's Bot. Reg. 28(Misc.): 70, no. 13. 1842. Non *Stelis acuminata* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 141. 2004.

Stelis bevilacquana (Carnevali & I.Ramírez) Karremans, Phytotaxa 406(5): 265. 2019.

Bas.: *Pleurothallis bevilacquana* Carnevali & I.Ramírez, Orchids Venez. (ed. 2) 1141. 2000.

Stelis candida (Luer & Hirtz) Karremans, Lankesteriana 13(3): 328. 2014.

Bas.: *Pleurothallis candida* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 107. 1999. *Anathallis candida* (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 248. 2001.

Stelis catenata Karremans, Lankesteriana 13(3): 328. 2014.

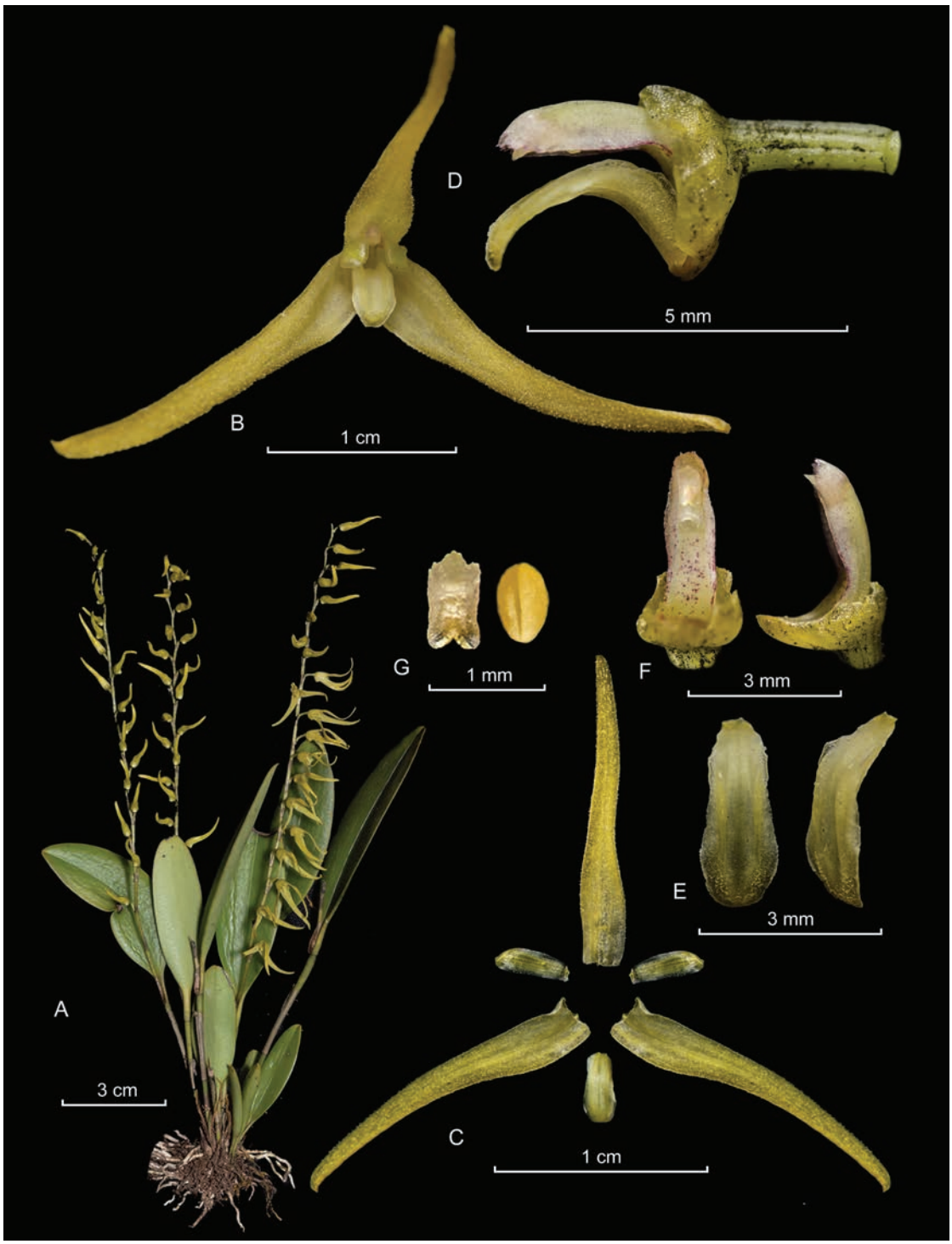


FIGURE 8. LCDP of *Stelis aurea*, type species of *Stelis* sect. *Acuminatae*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral view. **F**. Lip. **G**. Anther cap and pollinarium. Photographs by J.S. Moreno based on *Moreno* 520 (CAUP).

Repl. syn.: *Pleurothallis ramulosa* Lindl., Fol. Orchid. ~Pleurothallis~ 33. 1859. Syn.: *Anathallis ramulosa* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001. *Non Stelis ramulosa* Luer & Dalström, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 169. 2004.

Stelis coripatae (Luer & R.Vásquez) Karremans, Lankesteriana 13(3): 328. 2014.

Bas.: *Pleurothallis coripatae* Luer & R.Vásquez, Phytologia 46(6): 362. 1980. Syn.: *Anathallis coripatae* (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 248. 2001.

Stelis dimidia (Luer) Karremans, Lankesteriana 13(3): 328. 2014.

Bas.: *Pleurothallis dimidia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 109. 1999. Syn.: *Anathallis dimidia* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 248. 2001.

Stelis jesupiorum (Luer & Hirtz) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis jesupiorum* Luer & Hirtz, Lindleyana 11(3): 164. 1996. Syn.: *Anathallis jesupiorum* (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 249. 2001.

Stelis lagarophyta (Luer) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis lagarophyta* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 112-113. 1999. Syn.: *Anathallis lagarophyta* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 249. 2001.

Stelis lauta Karremans, Lankesteriana 13(3): 329. 2014.

Repl. syn.: *Pleurothallis concinna* Luer & R.Vásquez, Revista Soc. Boliv. Bot. 2(2): 133. 1999. Syn.: *Anathallis concinna* (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 248. 2001. Non *Stelis concinna* Lindl., J. Bot. (Hooker) 1: 11. 1834.

Stelis maguirei (Luer) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis maguirei* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 113. 1999. *Anathallis maguirei* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 249. 2001.

Stelis mediocarinata (C.Schweinf.) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis mediocarinata* C.Schweinf., Fieldiana, Bot. 33: 26. 1970. Syn.: *Anathallis mediocarinata* (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 249. 2001.

Stelis melanopus (F.Lehm. & Kraenzl.) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis melanopus* F.Lehm. & Kraenzl., Bot. Jaarb. 26: 443. 1899.

Syn.: *Pleurothallis stenophylla* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 442. 1899. *Anathallis stenophylla* (F.Lehm. & Kraenzl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001. Non *Stelis stenophylla* Rchb.f., Bonplandia (Hannover) 3: 70. 1855.

Stelis meridana (Rchb.f.) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis meridana* Rchb.f., Linnaea 22: 826. 1849. Syn.: *Anathallis meridana* (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 249. 2001.

Stelis papuligera (Schltr.) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis papuligera* Schltr., Repert. Spec. Nov. Regni Veg. 10: 453. 1912. Syn.: *Anathallis papuligera* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis peruviana Damián & Karremans, Systematic Botany 41(2): 293. 2016.

Stelis poasensis (Ames) Chinchilla & Karremans, Phytotaxa 406(5): 266. 2019. (Fig. 9)

Bas.: *Pleurothallis poasensis* Ames, Sched. Orch. 1: 10-11. 1922.

Syn.: *Pleurothallis dolichopus* Schltr., Repert. Spec. Nov. Regni Veg. 10(257-259): 394. 1912. *Anathallis dolichopus* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 248. 2001. Non *Stelis dolichopus* Schltr., Orchis 6: 63. 1912.

Syn.: *Pleurothallis lamprophylla* Schltr., Repert. Spec. Nov. Regni Veg. 15(427-433): 205-206. 1918, *nom. illeg. Stelis lamprophylla* Karremans, Lankesteriana 13(3): 329. 2014, *nom. nov*. Non *Pleurothallis lamprophyllum* G.Nicholson, Ill. Dict. Gard., Cent. Suppl. 608. 1901.

FIGURE 9. *Stelis poasensis* (Ames) Chinchilla & Karremans, a typical species of *Stelis* sect. *Acuminatae.* Photograph by AK.

Syn.: *Pleurothallis peregrina* Ames, Sched. Orch. 6: 67-68. 1923.

Stelis regalis (Luer) Karremans, Lankesteriana 13(3): 329. 2014.

Bas.: *Pleurothallis regalis* Luer, Selbyana 5(2): 178. 1979. Syn.: *Anathallis regalis* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis scariosa (Lex.) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Dendrobium scariosum* Lex., Nov. Veg. Descr. 2(Orchid. Opusc.): 39-40. 1825. Syn.: *Pleurothallis scariosa* (Lex.) Lindl., Edwards's Bot. Reg. 28: Misc. 71. 1842. *Anathallis scariosa* (Lex.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis schlimii (Luer) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis schlimii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 120. 1999. Syn.: *Anathallis schlimii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis sclerophylla (Lindl.) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis sclerophylla* Lindl., Edwards's Bot. Reg. 21, sub. t. 1797 no. 31. 1835. *Anathallis sclerophylla* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis soratana (Rchb.f.) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis soratana* Rchb.f., Xenia Orchid. 3: 25. 1878. Syn.: *Anathallis soratana* (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis spathilabia (Schltr.) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis spathilabia* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 56. 1924. Syn.: *Anathallis spathilabia* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Stelis spathuliformis (Luer & R.Vásquez) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis spathuliformis* Luer & R.Vásquez, Revista Soc. Boliv. Bot. 2(2): 137. 1999. Syn.: *Anathallis spathuliformis* (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Stelis unduavica (Luer & R.Vásquez) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis unduavica* Luer & R.Vásquez, Phytologia 46(6): 372. 1980. Syn.: *Anathallis unduavica* (Luer & R.Vásquez) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Stelis vasquezii (Luer) Karremans, Lankesteriana 13(3): 330. 2014.

Bas.: *Pleurothallis vasquezii* Luer, Phytologia 49(3): 220. 1981. *Anathallis vasquezii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

DNA data is available for several species belonging to this group, including the type of the section *Stelis aurea* (as *Anathallis angustipetala*), as well as *S. dimidia*, *S. jesupiorum*, *S. poasensis* (as *Anathallis dolichopus* and *S. lamprophylla*), *S. sclerophylla* (as *Anathallis sclerophylla*). They consistently group together into a

Figure 10. *Stelis montserratii* (Porsch) Karremans, type species of *Stelis* sect. *Rubens*. Photograph by J. Meijvogel.

well supported clade that is closely related to *Stelis* in the strict sense (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Wilson *et al.* 2017, Ponert *et al.* 2019).

Stelis* subgen. *Physothallis* sect. *Rubens Karremans, *sect. nov.*

Type: *Pleurothallis rubens* Lindl., Edwards's Bot. Reg. 21: pl. 1797, no. 32. 1836.

Distinguished from sect. *Acuminatae* by the subpandurate lip, the long-cucullate, pointed apex of the column.

Stelis montserratii (Porsch) Karremans, Lankesteriana 13(3): 329. 2014. (Fig. 10)

Bas.: *Pleurothallis montserratii* Porsch, Oesterr. Bot. Z. 158. 1905.

Syn.: *Pleurothallis rubens* Lindl., Edwards's Bot. Reg. 21: pl. 1797, no. 32. 1836. *Specklinia rubens* (Lindl.) F.Barros, Hoehnea 10: 110. 1984. *Anathallis rubens* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001. *Specklinia rubens* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 263. 2004. *Stelis neorubens* Chiron, Phytotaxa 46: 55. 2012. Non *Stelis rubens* Schltr., Repert. Spec. Nov. Regni Veg. 8(191-195): 564. 1910.

Syn.: *Anathallis amblyopetala* (Schltr.) Pridgeon & M.W. Chase, Lindleyana 16(4): 247. 2001. *Pleurothallis amblyopetala* Schltr., Repert. Spec. Nov. Regni Veg. 12: 486. 1913.

Syn.: *Pleurothallis excisa* C.Schweinf., Bot. Mus. Leafl. 16: 48. 1953.

DNA studies confirm that the species previously known as *Pleurothallis rubens* is closely related to *Stelis*

Figure 11. *Stelis harlingii* (Garay) Pridgeon & M.W.Chase, type species of *Stelis* subgen. *Physothallis*. Photograph by E. Hunt.

in the strict sense (Chiron *et al.* 2012, Ramos-Castro *et al.* 2012, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). It is yet unclear how it relates to other members of *Stelis* subgen. *Physothallis* and until that is resolved it is recognized as a distinct lineage within the group.

Stelis* subgen. *Physothallis* sect. *Physothallis

Stelis cylindrica (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Physothallis cylindrica* Luer, Selbyana 3(3-4): 224. 1977. *Pleurothallis cylindrica* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 53. 1986.

Stelis harlingii (Garay) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001. (Fig. 11)

Bas.: *Physothallis harlingii* Garay, Svensk Bot. Tidskr. 47(2): 199-202. 1953. *Pleurothallis neoharlingii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 53. 1986.

Stelis lennartii Karremans, Lankesteriana 13(3): 329. 2014.

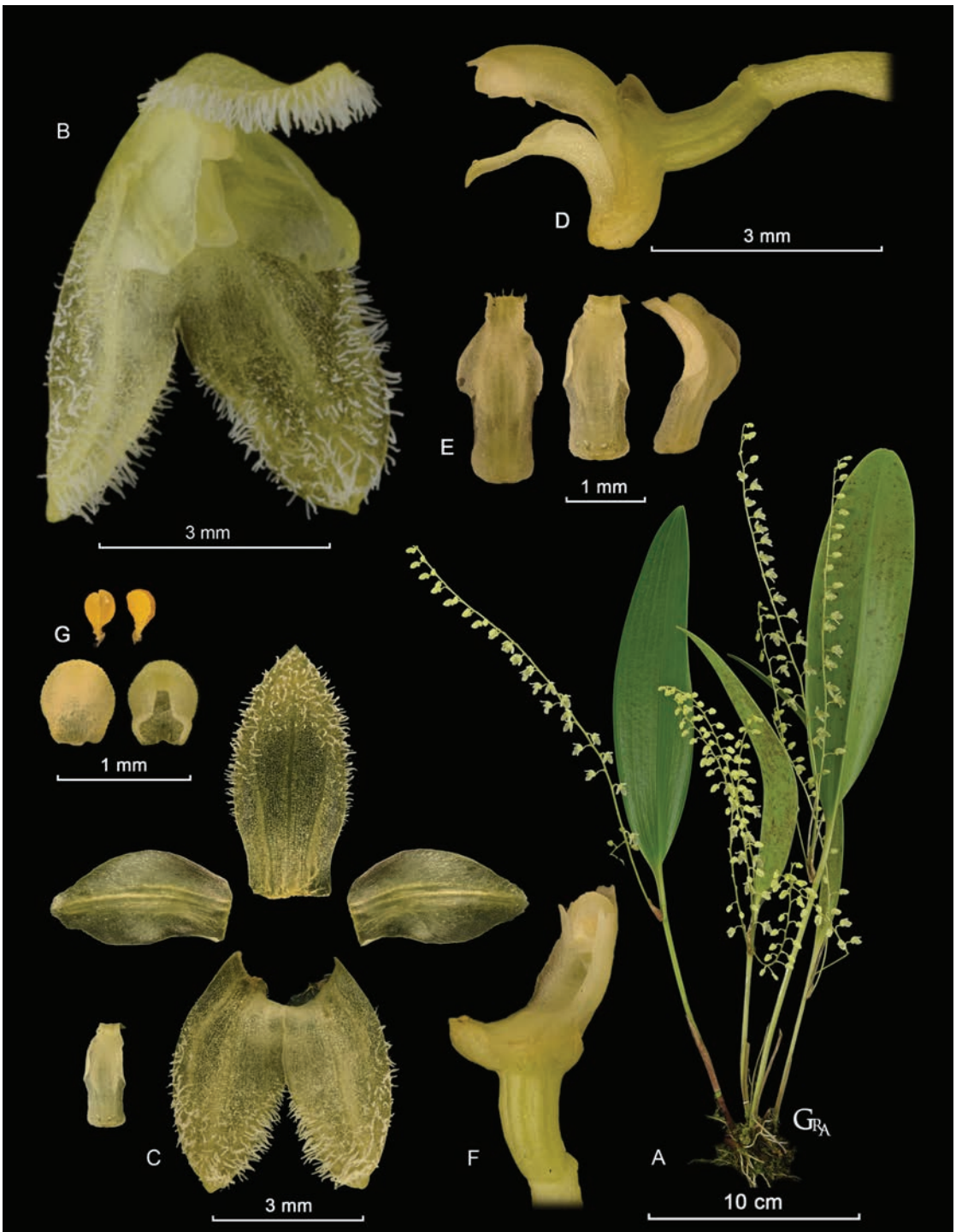


FIGURE 12. LCDP of *Stelis gelida*, type species of *Stelis* subgen. *Niphantha*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Lip, three views. **F**. Column, three quarters view. **G**. Pollinarium and anther cap, two views. Photographs by G. Rojas-Alvarado based on *Díaz-Morales 216* (JBL-spirit).

Repl. syn.: *Pleurothallis anderssonii* Luer, Lindleyana 11(3): 145. 1996. *Anathallis anderssonii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 247. 2001. Non *Stelis anderssonii* Luer & Endara, Monogr. Syst. Bot. Missouri Bot. Gard. 112. 2007.

Despite their morphological appearances, accessions of *Stelis harlingii* and *Stelis lennartii* form a well supported clade that appears to be somehow related to the other members of *Stelis* subgen. *Physothallis* (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). Altogether they are sisters of *Stelis* subgen. *Stelis* and *Stelis* subgen. *Crocodeilanthe* (Ramos-Castro *et al.* 2012, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Ponert *et al.* 2019)

Stelis* subgen. *Niphantha (Luer) Karremans, *comb. nov.*

Bas.: *Niphantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 120: 154. 2010. Type: *Pleurothallis gelida* Lindl., Edwards's Bot. Reg. 27: Misc. 91. 1841.

Stelis gelida (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001. (Fig. 12)

Bas.: *Pleurothallis gelida* Lindl., Edwards's Bot. Reg. 27: Misc. 91. 1841. Syn.: *Specklinia gelida* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 260. 2004. *Niphantha gelida* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 120: 154. 2010. *Crocodeilanthe gelida* (Lindl.) Carnevali & I.Ramírez, Smithsonian Contr. Bot. 100: 133. 2014.

Stelis pidax (Luer) Karremans, Phytotaxa 203(3): 293. 2015.

Bas.: *Pleurothallis pidax* Luer, Selbyana 5(2): 174-175. 1979. Syn.: *Anathallis pidax* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001. *Specklinia pidax* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 263. 2004. *Niphantha pidax* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 120: 154. 2010.

Stelis subgen. *Niphantha* currently includes two species of whitish, hirsute flowers. *Stelis gelida* is a common species with the widest distribution in the genus, it is found from Florida and Mexico, through Central America and the Antilles, down to Peru, Bolivia and Brazil. *Stelis pidax* is only known from Ecuador.

Accessions of both *Stelis gelida* and *S. pidax* where consistently found to form a clade sister to *Stelis s.s.*, *Crocodeilanthe* and *Physothallis* (Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). This is consistent with the highly unusual morphology of these two species. Some authors have suggested that *Stelis gelida* is morphologically similar to species of *Crocodeilanthe*, and may be belong there (Carnevali & Dorr 2014; Toscano de Brito 2018a). However, the similarities are at best superficial. The reddish, tightly clasping ramicaul bracts, pandurate lip, elongate and curved column, with conspicuous apical teeth, the incumbent anther, and lack of viscidium, among many other features, are unlike any *Crocodeilanthe* species.

Stelis* subgen. *Physosiphon (Lindl.) Karremans, *comb. nov.*

Bas.: *Physosiphon* Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835. *Pleurothallis* subgen. *Physosiphon* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 50. 1986. Lectotype: *Stelis tubata* G.Lodd., Bot. Cab. 17: t. 1601. 1830, *selected here*. (Fig. 13)

Syn. *Lomax* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 88. 2006. Type: *Physosiphon punctulatus* Rchb.f., Botanische Zeitung (Berlin) 24(49): 385. 1866.

Stelis asperrima (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis asperrima* Luer, Phytologia 49(3): 201. 1981. Syn.: *Physosiphon asperrimus* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 252. 2006.

Stelis emarginata (Lindl.) Soto Arenas & Solano, Icon. Orchid. (Mexico) 5-6: t. 681. 2002 [2003].

Bas.: *Pleurothallis emarginata* Lindl., Gen. Sp. Orchid. Pl. 6. 1830. *Physosiphon emarginatus* (Lindl.) Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835.

Syn.: *Stelis tubata* G.Lodd., Bot. Cab. 17(161): t. 1601. 1830. *Physosiphon loddigesii* Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1836, *nom. inval. Physosiphon loddigesii* Lindl. ex Hook. Icon. Pl. 6: t. 508. 1843, *nom. inval*. *Pleurothallis tubata* (G.Lodd.) Steud., Nomencl. Bot. (ed. 2) 2: 356. 1841. *Physosiphon tubatus* (G.Lodd.) Rchb.f., Ann. Bot. Syst. 6(2): 188. 1861.

FIGURE 13. *Stelis tubata* G.Lodd., selected as lectotype of genus *Physosiphon* Lindl., illustration of type reproduced in the Botanical Cabinet 17: t. 1601. 1830.

Stelis greenwoodii Soto Arenas & Solano, Icon. Orchid. (Mexico) 5-6: , t. 682. 2002 [2003].

Syn.: *Physosiphon greenwoodii* (Soto Arenas & Solano) Pfahl, Internet Orchid Sp. Photo Encycl. Nomencl. Notes 1. 2014. 2014.

Stelis pertusa I.Jiménez, Lankesteriana 15(3): 192. 2015.

Stelis punctulata (Rchb.f.) Soto Arenas, Icon. Orchid. (Mexico) 5-6: t. 690. 2002 [2003]. (Fig. 14)

Bas.: *Physosiphon punctulatus* Rchb.f., Bot. Zeitung (Berlin) 24(49): 385. 1866. Syn.: *Lomax punctulata* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 88-89. 2006.

Stelis tacanensis Solano & Soto Arenas, Icon. Orchid. (Mexico) 5-6: t. 693. 2002 [2003].

Syn.: *Physosiphon tacanensis* (Solano & Soto Arenas) Archila & Szlach., Orchid Gen. Sp. Guatemala 643. 2018.

The six species that belong to *Stelis* subgen. *Physosiphon* are distributed from Mexico and Guatemala, where the highest diversity is found, through Central America, and down to Bolivia.

DNA data is available for *Stelis emarginata*, *S. punctulata* and *S. tacanensis*, they consistently group together in a clade that is sister to a clade that includes *Stelis* subgen. *Niphantha*, *Stelis* subgen. *Physothallis*, *Stelis* subgen. *Crocodeilanthe* and *Stelis* subgen. *Stelis* (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017).

Alrich and Higgins (2011) mistakenly indicate that *Physosiphon spiralis* Lindl. (= *Stelis deregularis*) was selected as lectotype for genus *Physosiphon* by Garay (1974). The author selects *P. spiralis* as lectotype for *Pseudostelis*, not *Physosiphon*. Here *Stelis tubata* (= *S. emarginata*), which had already been mentioned by Pfeiffer (1873) as type, is selected as lectotype for this species as it is clearly what Lindley based his concept of *Physosiphon* on.

Stelis* subgen. *Dracontia (Luer) Karremans, *comb. nov.*

Bas. *Pleurothallis* subgen. *Dracontia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 38. 1986. *Dracontia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. Type: *Pleurothallis tuerckheimii* Schltr., Repert. Spec. Nov. Regni Veg. 10(251-253): 292. 1912.

Figure 14. *Stelis punctulata* (Rchb.f.) Soto Arenas, type species of genus *Lomax* (= *Stelis* subgen. *Physosiphon*). Photograph by AK.

Syn. *Salpistele* Dressler, Orquideologia 14: 6. 1979. Type: *Salpistele brunnea* Dressler, Orquideología 14(1): 6-8. 1979.

Syn. *Mystacorchis* Szlach. & Marg., Polish Bot. J. 46: 117. 2001. Type: *Pleurothallis mystax* Luer, Selbyana 3: 146. 1976.

About three fourths of the 40 species that belong to *Stelis* subgen. *Dracontia* are endemic to Costa Rica and Panama. A few species extend northwards into Mexico and Guatemala, a couple are known from the Antilles, and three make it downwards into the Andes.

The floral morphology of this group is highly variable, lacking apparent diagnostic features. It is made up of a clade with the species of Luer's *Pleurothallis* subgen. *Dracontia,* together with *Pleurothallis* subgen. *Mystax*, intermingled with several species placed in *Pleurothallis* subgen. *Effusia* Lindl. and one of *Pleurothallis* sect. *Elongatae* Lindl. It includes a clade composed of the species of *Salpistele* and *Pleurothallis* sect. *Petiolatae*. Despite the discrepancy in floral morphology, there is no doubt that species of *Dracontia*, *Mystax*, *Petiolatae* and *Salpistele* are closely related as suspected from vegetative features and consistently demonstrated by DNA studies (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Wilson *et al.*

2017). Future genetic studies are necessary to confirm the placement of some species listed here that have not been previously analyzed, especially those placed by Luer in *Pleurothallis* subgen. *Effusia*.

Despite its distinctive floral morphology, the recognition of genus *Salpistele* as originally circumscribed necessarily entails the recognition of *Dracontia*, *Mystacorchis* and several other small genera. The more distinctive groups are here given sectional status.

Stelis* subgen. *Dracontia* sect. *Dracontia

Syn. *Pleurothallis* sect. *Brobdingnagia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 66. 1998. Type: *Pleurothallis grandis* Rolfe, Bull. Misc. Inform. Kew 1918(7): 234. 1918.

Syn. *Pleurothallis* sect. *Cylindria* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 66. 1998. Type: *Pleurothallis macrantha* L.O.Williams, Ann. Missouri Bot. Gard. 28(4): 417. 1941.

Stelis aenigma Karremans & M.Díaz, Lankesteriana 17(2): 197. 2017.

Stelis alajuelensis Pridgeon & M.W.Chase, Lindleyana 17(2): 98. 2002.

Repl. syn.: *Pleurothallis ramonensis* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 193-194. 1923. *Dracontia ramonensis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Stelis ramonensis* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16: 266. 2001, *nom. illeg.* Non *Stelis ramonensis* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 176. 1923.

Stelis alta Pridgeon & M.W.Chase, Lindleyana 17(2): 98. 2002. (Fig. 15)

Repl. syn.: *Pleurothallis grandis* Rolfe, Bull. Misc. Inform. Kew 1918(7): 234. 1918. *Dracontia grandis* (Rolfe) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Stelis grandis* (Rolfe) Pridgeon & M.W.Chase, Lindleyana 16: 263. 2001, *nom. illeg.* Non *Stelis grandis* Rchb.f., Bonplandia (Hannover) 3: 70. 1855.

Stelis carnosilabia (A.H.Heller & A.D.Hawkes) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis carnosilabia* A.H.Heller & A.D.Hawkes, Phytologia 14(1): 9-10. 1966. Syn.: *Dracontia carnosilabia* (A.H.Heller & A.D.Hawkes) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis cobanensis (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cobanensis* Schltr., Repert. Spec. Nov. Regni Veg. 11(271-273): 42. 1912. Syn.: *Dracontia cobanensis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Rhynchopera cobanensis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 121. 2007.

Stelis conochila (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis conochila* Luer, Lindleyana 11: 75. 1996. Syn.: *Dracontia cobanensis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis convoluta (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis convoluta* Lindl., Ann. Mag. Nat. Hist. 15: 107. 1845. Syn.: *Effusiella convoluta* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis cylindrata Pridgeon & M.W.Chase, Lindleyana 17(2): 98. 2002. (Fig. 16)

Repl. syn.: *Pleurothallis macrantha* L.O.Williams, Ann. Missouri Bot. Gard. 28(4): 417. 1941. *Dracontia macrantha* (L.O.Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Stelis macrantha* (L.O.Williams) Pridgeon & M.W.Chase, Lindleyana 16: 264. 2001, *nom. illeg.* Non *Stelis macrantha* Rolfe, Bull. New York Bot. Gard. 4: 450. 1907.

Stelis dies-natalis Karremans & M.Díaz, Lankesteriana 17(2): 194. 2017.

Stelis dilatata (C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis dilatata* C.Schweinf., Bot. Mus. Leafl. 10: 177. 1942. Syn.: *Effusiella dilatata* (C.Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis dracontea (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001. (Fig. 17)

Bas.: *Pleurothallis dracontea* Luer, Phytologia 49(3): 204-205. 1981. Syn.: *Dracontia dracontea*

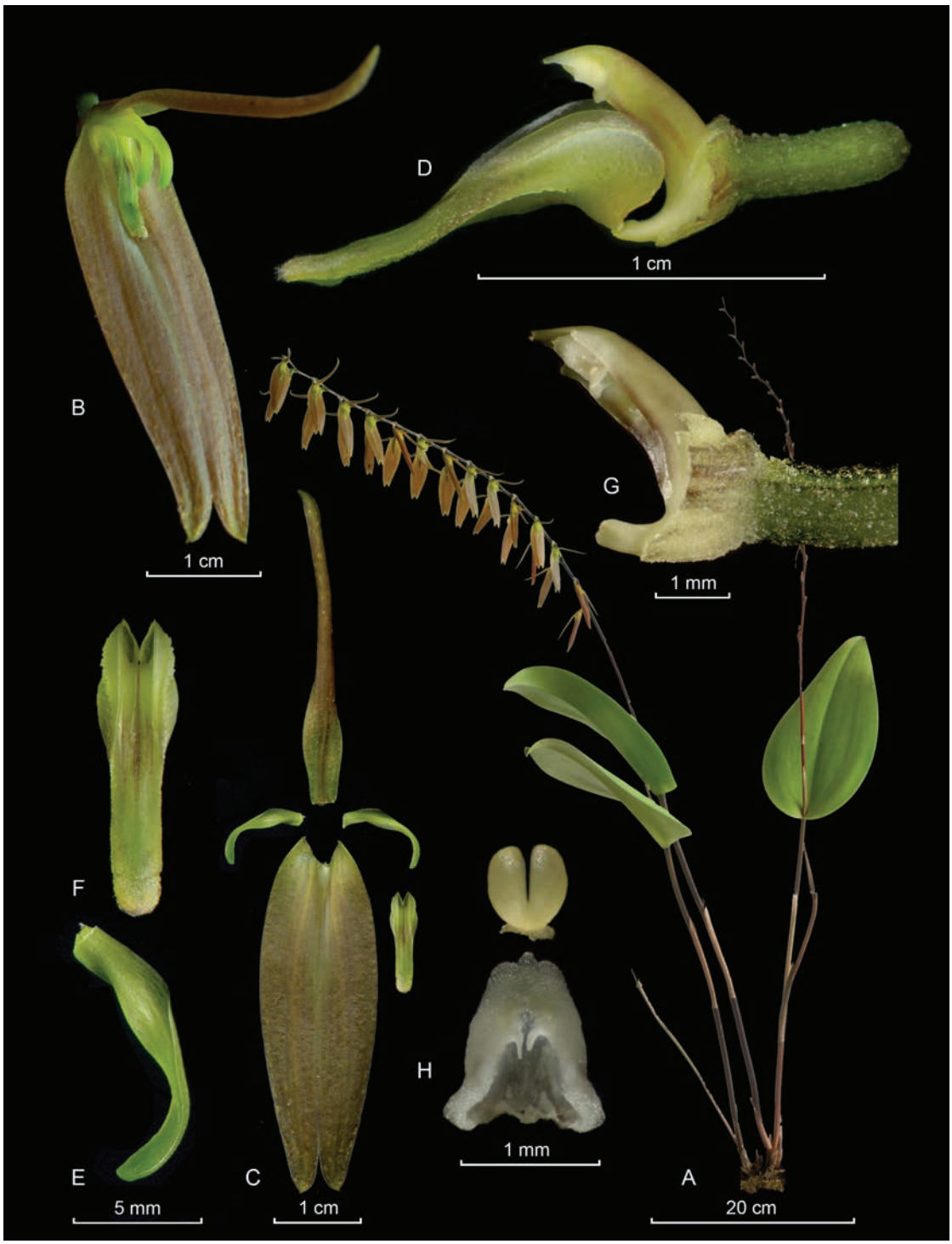


FIGURE 15. LCDP of *Stelis alta* Pridgeon & M.W.Chase, type species of *Pleurothallis* sect. *Brobdingnagia* Luer (= *Stelis* sect. *Dracontia*). **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Petal. **F**. Lip. **G**. Column side view. **H**. Anther cap and pollinarium. Photographs by F. Pupulin based on *Bogarín 4604* (JBL-spirit).

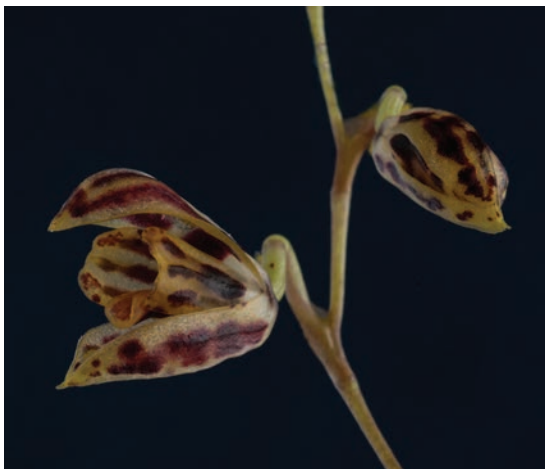
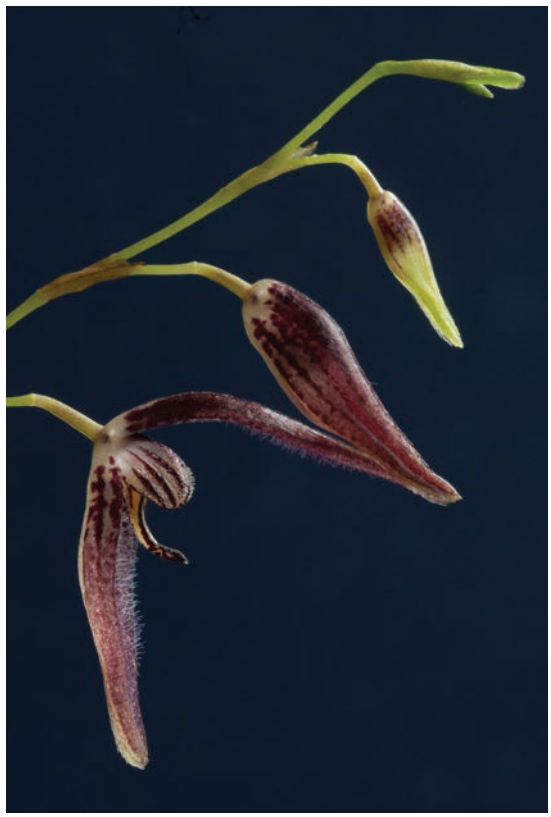


FIGURE 16. *Stelis cylindrata* Pridgeon & M.W.Chase, type species of *Pleurothallis* sect. *Cylindria* Luer (= *Stelis* sect. *Dracontia*). Photograph by AK.



Right, FIGURE 17. *Stelis dracontea*, a typical species of *Stelis* sect. *Dracontia.* Photograph by AK based on *Bogarín 616* (JBL-spirit).

(Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis ferrelliae Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis ingramii* Luer, Lindleyana 11(2): 81. 1996. *Dracontia ingramii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Stelis ingramii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16: 263. 2001, *nom. illeg.* Non *Stelis ingramii* Luer, Lindleyana 11: 100. 1996.

Stelis fortunae (Luer & Dressler) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis fortunae* Luer & Dressler, Lindleyana 6(2): 97, 100. 1991. Syn.: *Dracontia fortunae* (Luer & Dressler) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis gigantea Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis powellii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 22. 1922. *Dracontia powelli* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Stelis powellii* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16: 265. 2001, *nom. illeg.* Non *Stelis powellii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 16. 1922.

Stelis hydra (Karremans & C.M.Sm.) Karremans, Phytotaxa 203(3): 292. 2015.

Bas.: *Dracontia hydra* Karremans & C.M.Sm., Harvard Pap. Bot. 17(1): 13. 2012.

Stelis lueriana (Karremans) J.M.H.Shaw, Orchid Rev. 122(1308): 77. 2014.

Bas.: *Dracontia lueriana* Karremans, Ann. Naturhist. Mus. Wien, Ser. B, Bot. Zool. 113: 128. 2012.

Stelis megachlamys (Schltr.) Pupulin, Lankesteriana 4: 74. 2002. (Fig. 18)

Bas.: *Pleurothallis megachlamys* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 108. 1923.

Syn.: *Pleurothallis tuerckheimii* Schltr., Repert. Spec. Nov. Regni Veg. 10(251-253): 292. 1912. *Dracontia tuerckheimii* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. Non *Stelis tuerckheimii* Schltr., Repert. Spec. Nov. Regni Veg. 8(191-195): 564. 1910.

Stelis megachlamys f. ***viridiflavens*** (Roeth & Baumbach.) Karremans, *comb. nov.*

FIGURE 18. LCDP of *Stelis megachlamys* (Schltr.) Pupulin, type species of *Stelis* subgen. *Dracontia*. **A**. Habit. **B**. Inflorescence. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Petals. **F**. Lip. **G**. Column lateral view. **H**. Column ventral and side view. **I**. Anther cap and pollinarium. Photographs by AK based on *Bogarín 2161* (JBL-spirit).

Bas.: *Dracontia tuerckheimii* f. *viridiflavens* Roeth & Baumbach, Orchidee (Hamburg) 58: 98. 2007.

Syn.: *Pleurothallis kelloggii* Archila, Rev. Guatem. 15(1): 106. 2012.

Stelis montis-mortense (Karremans & Bogarín) Bogarín & Karremans, Lankesteriana 14(3): 270. 2014.

Bas.: *Dracontia montis-mortense* Karremans & Bogarín, Syst. Bot. 38(2): 307. 2013.

Stelis multirostris (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 17(2): 100. 2002.

Bas.: *Pleurothallis multirostris* Rchb.f., Linnaea 41: 49. 1877.

Syn.: *Epidendrum racemiflorum* Sw., Prodr. 125, 1788. *Dendrobium racemiflorum* (Sw.) Sw., Nov. Act. Upsal. 6: 83, 1799. *Pleurothallis racemiflora* (Sw.) Lindl. in Hook. Exot. Fl. 2: t. 123. 1825 [1824]. *Anathallis racemiflora* (Sw.) Pridgeon & M.W.Chase, Lindleyana 16: 250. 2001, *nom. inval*. *Stelis racemiflora* (Sw.) Pridgeon & M.W.Chase, Lindleyana 16: 266. 2001, *nom. inval*. Non *Stelis racemiflora* (Lindl. ex Lodd.) W.H.Baxter in J.C.Loudon, Hort. Brit., Suppl. 3: 643. 1850.

Syn.: *Pleurothallis oblongifolia* Lindl., Companion Bot. Mag. 2(24): 355. 1836. *Stelis oblongifolia* (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16: 265. 2001, *nom. illeg*. *Dracontia oblongifolia* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004. *Rhynchopera oblongifolia* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 121. 2007. Non *Stelis oblongifolia* Lindl., Fol. Orchid. 8: 12. 1859.

Syn.: *Pleurothallis tricostata* Cogn., Symb. Antill. 7: 175, 1912.

Even though *Epidendrum racemiflorum* Sw. has priority over *P. oblongifolia* and *P. multirostris*, the name is already occupied by *Stelis racemiflora* (Lindl. ex Lodd.) W.H.Baxter which is not based on the same taxon. The true identity of *Epidendrum racemiflorum* Sw. has been confused since the nineteen hundreds, and the taxonomy of this name continues to be highly confused today. The available type material shows a species belonging to *Stelis* sect. *Dracontia*, which has generally been known as *Pleurothallis oblongifolia*. However, when Lindley, in Hooker, transferred Swartz's name to *Pleurothallis*, he described and illustrated a different species. That other species is here treated under the name *Pleurothallis quadrifida* (Lex.) Lindl., and it is further discussed below.

Pridgeon and Chase (2001) proposed the names *Anathallis racemiflora* and *Stelis racemiflora* using the basionym "*Pleurothallis racemiflora* Lindl. ex Lodd. in Hook., Exot. Fl. 2: t. 123. 1825". Both names are invalid for two reasons, under article 36.3 (ICN; Turland *et al.* 2018) for being published simultaneously and under article 41.5 (ICN; Turland *et al.* 2018) for the erroneous citation and reference to the publication of the basionym. Although not the only interpretation, it is more parsimonious to assume that the authors referred to *Pleurothallis racemiflora* (Sw.) Lindl. in Hook., Exot. Fl. 2: t. 123. 1825 [1824], which is based on *Epidendrum racemiflorum* Sw., Prodr. 125, 1788. In Pridgeon and Chase (2002), the authors placed their *S. racemiflora* under the synonymy of *A. racemiflora*, but did not validate the name, for they failed to indicate this was intended, and again cited the wrong basionym.

Stelis pachyglossa (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pachyglossa* Lindl., Edwards's Bot. Reg. 26: Misc. 68. 1840. Syn.: *Dracontia pachyglossa* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis papillifera (Rolfe) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis papillifera* Rolfe, Bull. Misc. Inform. Kew 1916(3): 77. 1916. Bas.: *Dracontia papillifera* (Rolfe) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis pileata (Karremans & Bogarín) Karremans & Bogarín, Phytotaxa 203(3): 293. 2015.

Bas.: *Dracontia pileata* Karremans & Bogarín, Syst. Bot. 38(2): 308, 310-311. 2013.

Stelis platystylis (Schltr.) Solano & Soto Arenas, Icon. Orchid. (Mexico) 10: t. 1097. 2008.

Bas.: *Pleurothallis platystylis* Schltr., Repert. Spec. Nov. Regni Veg. 10(257-259): 395. 1912. Syn.: *Effusiella platystylis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007. *Anathallis platystylis* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 250. 2001.

Stelis prolixa (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis prolixa* Luer & Hirtz, Lindleyana 11(3): 179-180. 1996. Syn.: *Effusiella prolixa* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis simplex (Ames & C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis simplex* Ames & C.Schweinf., Sched. Orch. 10: 37-38. 1930. Syn.: *Crocodeilanthe simplex* (Ames & C.Schweinf.) Toscano, Harvard Pap. Bot. 23(1): 54. 2018.

Stelis tenebrosa (Archila, Szlach. & Chiron) Karremans, Phytotaxa 203: 293. 2015.

Bas.: *Dracontia tenebrosa* Archila, Szlach. & Chiron, Revista Guatemal. 16(1): 30. 2013.

Stelis thymochila (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis thymochila* Luer, Selbyana 3(3-4): 398-399, f. 299. 1977. Syn.: *Dracontia thymochila* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis tintinnabula (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis tintinnabula* Luer, Lindleyana 11(2): 94. 1996. Syn.: *Dracontia tintinnabula* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis tortilis (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis tortilis* Luer & R.Escobar, Orquideología 14(2): 180. 1981. Syn.: *Effusiella tortilis* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis viridiflava (Karremans & Bogarín) Karremans, Phytotaxa 203(3): 294. 2015.

Bas.: *Dracontia viridiflava* Karremans & Bogarín, Syst. Bot. 38(2): 311. 2013.

Thirty species belong to *Stelis* sect. *Dracontia*. DNA data is available for *Stelis alta, S. carnosilabia, S. cobanensis, S. conochila, S. cylindrata, S. hydra, S. ferrelliae, S. gigantea, S. hydra, S. lueriana, S. megachlamys, S. multirostris, S. pachyglossa, S. papillifera, S. pileata, S. platystylis, S. ramonensis* and *S. viridiflava*

Figure 19. *Stelis mystax*, type species of *Stelis* sect. *Mystax* (Luer) Karremans. Photograph by D. Bogarín based on *Bogarín 2988* (JBL-spirit).

(Pridgeon et al. 2001, Solano-Gómez 2005, Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Ponert *et al.* 2019). They have consistently been shown to belong to *Stelis sensu lato*, where, despite the floral appearances, they are most closely related to species of *Stelis* sect. *Mystax*, *Stelis* sect. *Petiolatae* and *Stelis* sect. *Salpistele*. Although the flowers are quite unique, the plants of species belonging to this group are virtually indistinguishable from many typical *Stelis* species (*Stelis s.s.*). So much so, that *Stelis simplex* has not been associated with this group given the simple, very *Stelis*-like, flowers. The same happens with *Stelis platystylis, S. prolixa* and *S. tortilis* which due to their rather undifferentiated flowers have not been placed here.

Stelis* subgen. *Dracontia* sect. *Mystax (Luer) Karremans, *comb. et stat. nov.*

Bas. *Pleurothallis* subgen. *Mystax* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 50. 1986. Type: *Pleurothallis mystax* Luer, Selbyana 3: 146. 1976.

Syn. *Mystacorchis* Szlach. & Marg., Polish Bot. J. 46: 117. 2001. Type: *Pleurothallis mystax* Luer, Selbyana 3: 146. 1976.

Stelis mystax (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001. (Fig. 19)

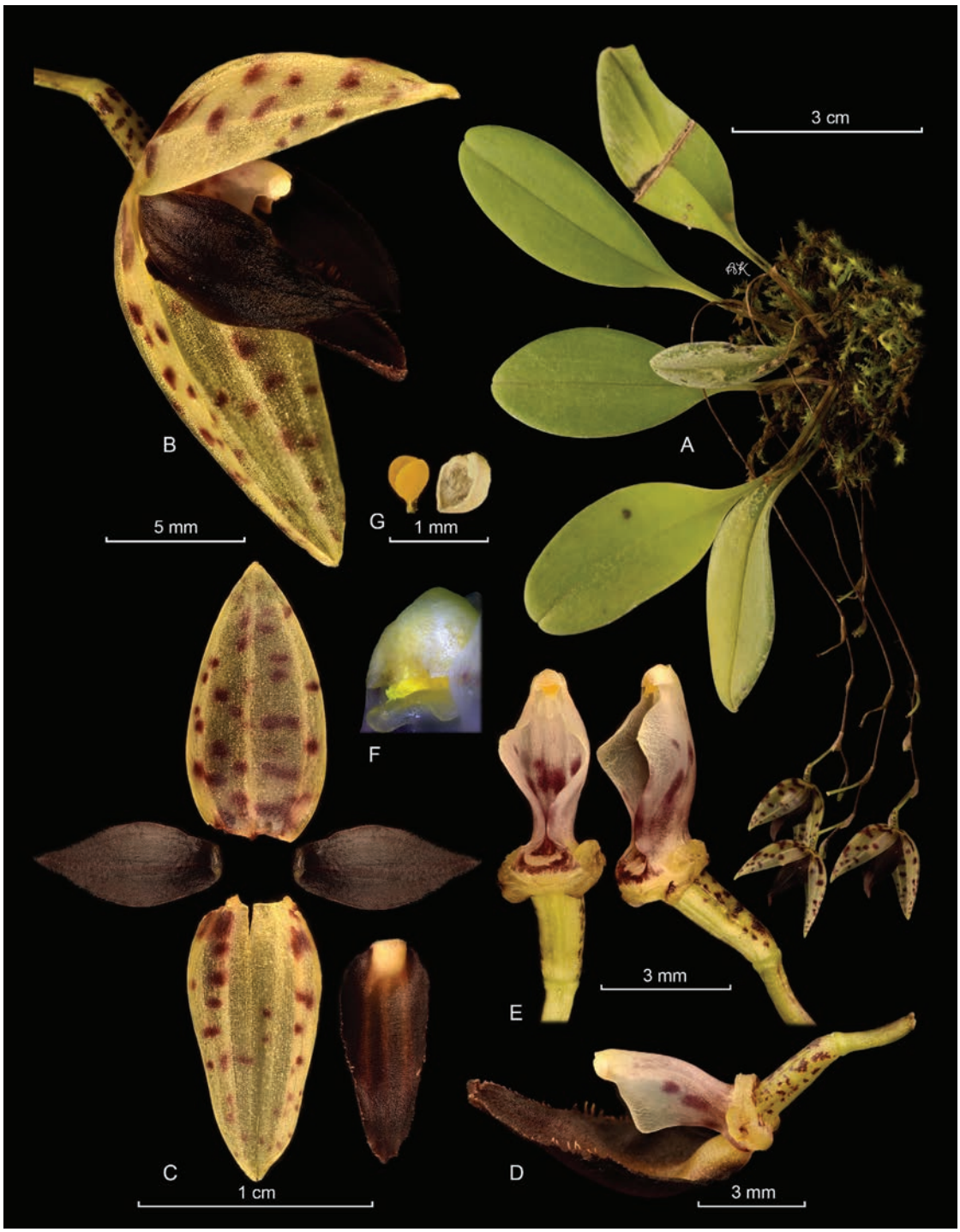


FIGURE 20. LCDP of *Stelis guttata* (Luer) Pridgeon & M.W.Chase, type species of *Stelis* sect. *Petiolatae* (Luer) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral views. **F**. Column apex. **G**. Anther cap and pollinarium, placed in the stigma. Photographs by AK based on *Karremans 7201* (JBL-spirit).

Bas.: *Pleurothallis mystax* Luer, Selbyana 3(1-2): 146-147, f. 176. 1976. Syn.: *Mystacorchis mystax* (Luer) Szlach. & Marg., Polish Bot. J. 46(2): 117. 2001.

A single, aberrant species belongs to *Stelis* sect. *Mystax*. It is endemic to Panama, and morphologically has no close relatives. The available accessions of this species have been consistently found to group with other members of *Stelis* subgen. *Dracontia*, namely the very distinct, and also unique, Central American species, *Stelis carpinterae* and *Stelis convallaria* (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). The plant and flower morphology are somewhat reminiscent of species belonging to *Stelis* sect. *Dracontia*, but the spathulate lip is quite unique.

Stelis* subgen. *Dracontia* sect. *Petiolatae (Luer) Karremans, *comb. nov.*

Bas. *Pleurothallis* sect. *Petiolatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 70. 1994. Type: *Pleurothallis guttata* Luer, Selbyana 3(1-2): 116-177. 1976.

Stelis guttata (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001. (Fig. 20)

Bas.: *Pleurothallis guttata* Luer, Selbyana 3(1-2): 116-177. 1976. Syn.: *Elongatia guttata* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Stelis janetiae (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis janetiae* Luer, Selbyana 5(2): 169-170. 1979. Syn.: *Elongatia janetiae* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

Only two species are known to belong to *Stelis* sect. *Petiolatae*, and DNA data is available for both. Luer (1994) placed them in *Elongatia* (= *Pleurothallis*), with which they indeed share a very similar floral morphology. However, these two species endemic to Costa Rica and Panama belong without a doubt in *Stelis sensu lato* (Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). They are the closest relatives of *Stelis* sect. *Salpistele*, and even though their flowers are very different, the plants are basically larger versions of those.

Stelis* subgen. *Dracontia* sect. *Salpistele (Dressler) Karremans, *comb. nov.*

Bas. *Salpistele* Dressler, Orquideologia 14: 6. 1979. Type: *Salpistele brunnea* Dressler, Orquideología 14(1): 6-8. 1979.

Stelis brunnea (Dressler) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001. (Fig. 21)

Bas.: *Salpistele brunnea* Dressler, Orquideología 14(1): 6-8. 1979.

Stelis cymbisepala Pridgeon & M.W.Chase, Lindleyana 17(2): 98-99. 2002.

Repl. syn.: *Salpistele dressleri* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 39: 128. 1991. Non *Stelis dressleri* Luer, Phytologia 49(3): 227-228. 1981.

Stelis deutroadrianae J.M.H.Shaw, Orchid Rev. 122(1308): 77. 2014.

Repl. syn.: *Salpistele adrianae* Luer & Sijm, Selbyana 30(1): 18. 2009. *Stelis adriananijhuisae* Bogarín & Serr., Lankesteriana 14(3): 265. 2014, *nom. superfl.* Non *Stelis adrianae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 36. 2002.

Stelis gnoma Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Salpistele parvula* Luer & Dressler, Monogr. Syst. Bot. Missouri Bot. Gard. 39: 132. 1991. Non *Stelis parvula* Lindl., Fol. Orchid. ~Stelis~ (8): 7. 1852–1855 [1859].

Stelis maculata Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Salpistele lutea* Dressler, Orquideología 14(1): 8-10. 1979. Non *Stelis lutea* Lindl., Fol. Orchid. ~Stelis~ 7. 1852–1855 [1859].

Five species are known to belong to *Stelis* sect. *Salpistele*, and DNA data is available for *Stelis brunnea*, *S. deutroadrianae* and *S. maculata*. Despite their *Lepanthes*-like flowers, species of this group have been consistently shown to belong to *Stelis sensu lato* based on DNA analyses (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017; Wilson *et al.* 2017). Although not evident from floral morphology, they are without a doubt sister to the members of *Stelis* sect. *Petiolatae*, with which they share the small plants with petiolate leaves and a creeping inflorescence with successive flowers.

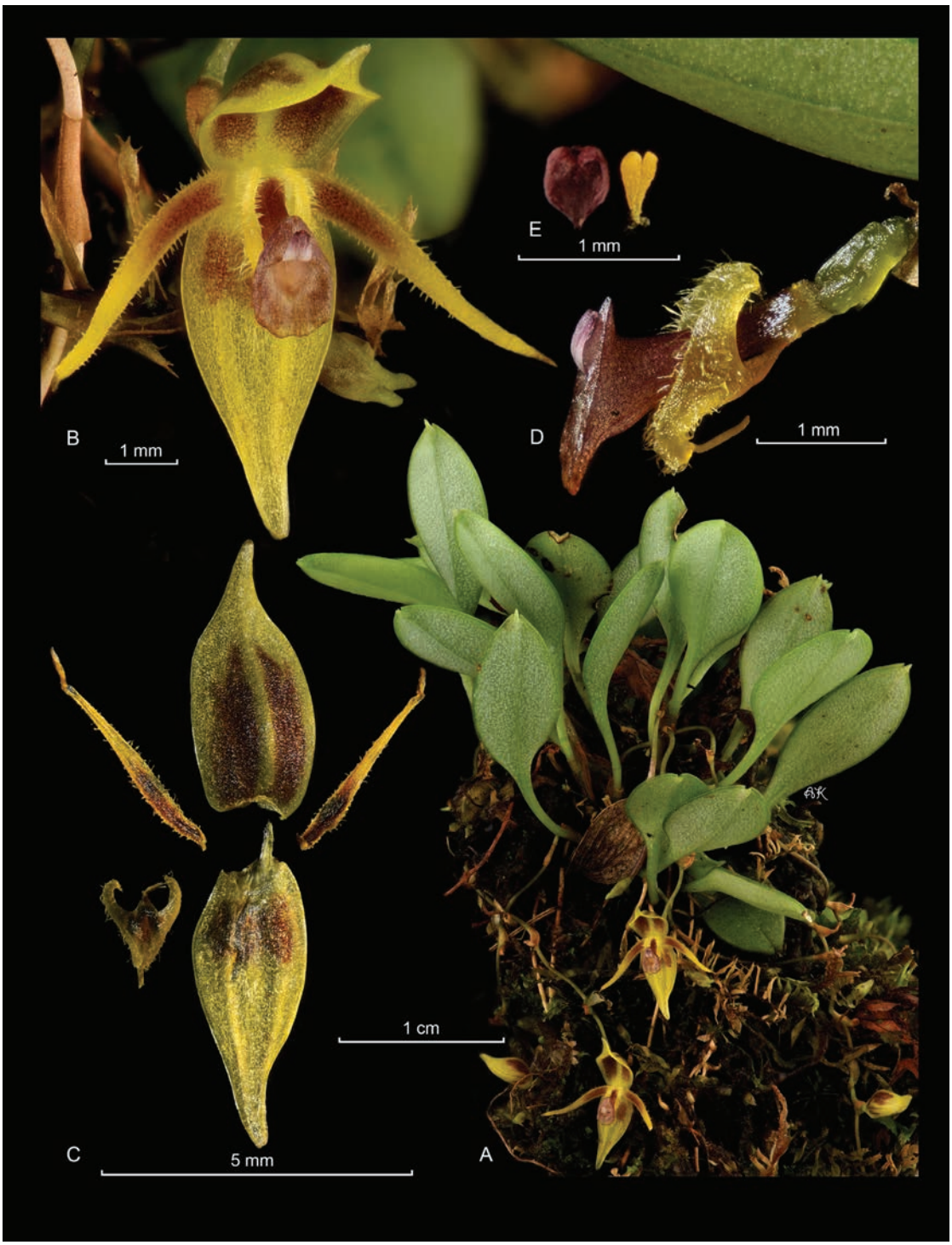


FIGURE 21. LCDP of *Stelis brunnea*, type species of Stelis sect. Salpistele (Dressler) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Anther cap and pollinarium. Photographs by AK based on *Karremans 8260* (JBL-spirit).

With them they also share the geographical area, both groups are restricted to Costa Rica and Panama.

Stelis* subgen. *Dracontia* sect. *Carpinterae Karremans, *sect. nov.*

ETYMOLOGY: The name honors Los Cerros de La Carpintera, in Cartago, Costa Rica, where the type material of its only species was collected.

Type: *Pleurothallis carpinterae* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 105. 1923.

This section can be easily recognized by the long, slender ramicauls that bear a significantly shorter, thin, ovate to sub-cordate, acute leaf. The successive, few-flowered inflorescence reclines on the leaf, the glabrous sepals are yellowish-cream spotted purple. The petals have more or less the same pattern but are darker, spathulate. The lip is as long as the sepals, orange, pandurate, unguiculate. The column slender, clavate, with a thick pedestal-like base.

Stelis carpinterae (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001. (Fig. 22)

Bas.: *Pleurothallis carpinterae* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 105. 1923. Syn.: *Elongatia carpinterae* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257. 2004.

The only species belonging to *Stelis* sect. *Carpinterae* is restricted to Costa Rica and western Panama. Even though Luer (1994) placed it among the species of *Elongatia* (= *Pleurothallis*), morphologically it has no close relatives. The accessions of this species were consistently found to group with other members of *Stelis* subgen. *Dracontia*, namely the very distinct, and also unique, Central American species, *Stelis mystax* and *Stelis convallaria* (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017).

Stelis* subgen. *Dracontia* sect. *Convallaria Karremans, *sect. nov.*

ETYMOLOGY: The name refers to the similarity of its bell-shaped flowers to those of genus *Convallaria* L. (Asparagaceae), a terrestrial herb from Europe and Asia that is known as Lilly of the valley.

Type: *Pleurothallis convallaria* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 185-186. 1923.

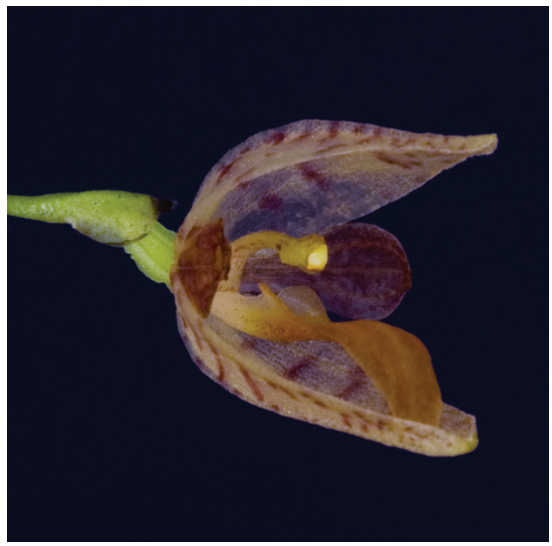


FIGURE 22. *Stelis carpinterae*, type species of *Stelis* sect. *Carpinterae* Karremans. Photograph by D. Bogarín based on *Bogarín 7159* (JBL-spirit).

The habit is similar to other species belonging to *Stelis* subgen. *Dracontia*, except that the multiple inflorescences are clasped basally by the leaf. The inflorescences are semi-erect and bear multiple drooping bell-shaped flowers. The dark purple sepals are covered in a striking white a pubescens that trembles in the wind. The dark purple petals are unusual in that they are widest apically, truncate and bilobed. The lip is transversally bilobed, long-unguiculate and tricarinate. The column is elongate, bent, with a broad clinandrium.

Stelis convallaria (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001. (Fig. 23)

Bas.: *Pleurothallis convallaria* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 185-186. 1923. *Effusiella convallaria* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

The single species belonging to *Stelis* sect. *Convallaria* is known from Guatemala, Nicaragua, Costa Rica and Panama. Although morphologically somewhat aberrant, the accessions of this species are consistently found to be related to other members of *Stelis* subgen. *Dracontia*, especially two other unique Central American species, *Stelis mystax* and *Stelis carpinterae* (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017).

FIGURE 23. LCDP of an autogamous specimen of *Stelis convallaria*, type species of *Stelis* sect. *Convallaria*. **A**. Habit. **B**. Inflorescence. **C**. Flower. **D.** Dissected perianth. **E**. Column with lip, lateral view. **F**. Column ventral and lateral views. **G**. Anther cap and pollinarium, placed in the stigma. Photographs by K based on *Karremans 7201* (JBL-spirit).

Stelis* subgen. *Unciferia (Luer) Karremans, *comb. nov.*

Bas. *Pleurothallis subgen. Unciferia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 89. 1998. *Pleurothallis sect. Unciferae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 94. 1986. *Unciferia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004, *nom. illeg.* Type: *Pleurothallis segoviensis* Rchb.f., Bonplandia (Hannover) 3(15-16): 223-224. Non *Uncifera* Lindl., J. Proc. Linn. Soc., Bot. 3: 39. 1859.

Syn. *Effusiella* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007. Type: *Pleurothallis amparoana* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 23, 104. 1923.

Stelis amaliae (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis amaliae* Luer & R.Escobar, Orquideología 14(2): 124. 1981. Syn.: *Unciferia amaliae* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis ancistra (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis ancistra* Luer & Hirtz, Lindleyana 11(3): 144-145. 1996. Syn.: *Unciferia ancistra* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis bifalcis (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis bifalcis* Schltr., Beih. Bot. Centralbl., Abt. 2 36(2): 395. 1918. *Unciferia bifalcis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis brenneri (Luer) Karremans, Phytotaxa 203(3): 292. 2015.

Bas.: *Pleurothallis brenneri* Luer, Selbyana 3(1-2): 64. 1976. Syn.: *Effusiella brenneri* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis canae (Ames) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis canae* Ames, Sched. Orch. 2: 18-19. 1923. Syn.: *Unciferia canae* (Ames) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis chlorina (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 261. 2001.

Bas.: *Pleurothallis chlorina* Luer, Phytologia 47(2): 75. 1980. Syn.: *Effusiella chlorina* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis crenata (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis crenata* Lindl., Gard. Chron. 6(13): 207. 1846. Syn.: *Pabstiella crenata* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 119. 2007.

Stelis cypripedoides (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cypripedioides* Luer, Selbyana 1(1): 70. 1975. Syn.: *Effusiella cypripedioides* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis diminuta (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis diminuta* Luer, Phytologia 49(3): 204. 1981. *Effusiella diminuta* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis fornicata (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis fornicata* Luer, Lindleyana 11(3): 160-161. 1996. Syn.: *Effusiella fornicata* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis immersa (Linden & Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Pleurothallis immersa* Linden & Rchb.f., Bonplandia (Hannover) 3(15-16): 224. 1855. Syn.: *Effusiella immersa* (Linden & Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis insectifera Karremans, *nom. nov.*

Repl. syn.: *Pleurothallis melicoides* Schltr., Repert. Spec. Nov. Regni Veg. 19: 24. 1923. Syn.: *Stelis melicoides* (Schltr.) Bogarín, Proc. 22nd World Orchid Conf. I. 354. 2019, *nom. illeg.* Non *Stelis melicoides* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 66. 1921.

Stelis jalapensis (Kraenzl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001.

Bas.: *Masdevallia jalapensis* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 117-118. 1925. Syn.: *Pleurothallis jalapensis* (Kraenzl.) Garay, Bot. Mus. Leafl. 30(3): (58)192. 1985 [1986]. *Pleurothallis jalapensis* (Kraenzl.) Luer, Lindleyana 6(2): 103, f.. 1991, *nom. illeg. Specklinia jalapensis* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 261. 2004. *Effusiella jalapensis* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007, *nom. inv. Effusiella jalapensis* (Kraenzl.) Archila, Revista Guatemal. 17(2): 76. 2014.

Stelis kefersteiniana (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Bas.: *Pleurothallis kefersteiniana* Rchb.f., Bot. Zeitung (Berlin) 10: 673. 1852.

Syn.: *Specklinia flexuosa* Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 52, t. 90. 1835. *Pleurothallis flexuosa* (Poepp. & Endl.) Lindl., Edwards's Bot. Reg. 28: Misc. 69, no. 7. 1842. Syn.: *Effusiella flexuosa* (Poepp. & Endl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007, *nom. inval. Stelis flexuosa* (Poepp. & Endl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001, *nom. illeg.* Non *Stelis flexuosa* Lindl., Ann. Mag. Nat. Hist. 12(79): 397. 1843.

Stelis lehmanneptis (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis lehmanneptis* Luer & R.Escobar, Orquideología 21: 100. 1998. *Effusiella lehmanneptis* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis lehmannii Pridgeon & M.W.Chase, Lindleyana 17(2): 99. 2002.

Repl. syn.: *Pleurothallis petiolaris* Luer, Orquideología 20: 220. 1996. *Effusiella petiolaris* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007. *Stelis petiolaris* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001, *nom. illeg.* Non *Stelis petiolaris* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 36. 1924.

Stelis listerophora (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis listerophora* Schltr., Repert. Spec. Nov. Regni Veg. 3(33-34): 107. 1906. Syn.: *Effusiella listerophora* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis niesseniae (Luer) Karremans, Phytotaxa 406(5): 265. 2019.

Bas.: *Pleurothallis niesseniae* Luer, Orquideología 22(1): 59-61. 2001. Syn.: *Effusiella niesseniae* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis nigriflora (L.O.Williams) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001.

Bas.: *Pleurothallis nigriflora* L.O.Williams, Amer. Orchid Soc. Bull. 11(5): 168. 1942. *Effusiella nigriflora* (L.O.Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis nonresupinata Solano & Soto Arenas, Icon. Orchid. (Mexico) 5-6: t. 688. 2002 [2003].

Stelis oestlundiana (L.O.Williams) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis oestlundiana* L.O.Williams, Bot. Mus. Leafl. 12(7): 243. 1946. Syn.: *Effusiella oestlundiana* (L.O.Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis ornata (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001. (Fig. 24)

Bas.: *Pleurothallis ornata* Rchb.f., Garten Zeitung 1: 106. 1882. *Effusiella ornata* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis oscargrouchii Karremans, Phytotaxa 203(3): 293. 2015.

Repl. syn.: *Specklinia ximenae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 311. 2005. Syn.: *Pleurothallis ximenae* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 238, 242. 2004, *nom. inval. Specklinia ximenae* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004, *nom. inval. Effusiella ximenae* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007, *nom. inval*. Non *Stelis ximenae* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 175. 2004.

Figure 24. *Stelis ornata* (Rchb.f.) Pridgeon & M.W.Chase, a species with striking appendages on the sepals, but otherwise a typical member of *Stelis subgen. Unciferia* (Luer) Karremans. Photograph by H. Oakeley.

Figure 25. *Stelis pilosa* Pridgeon & M.W.Chase, type species of genus *Effusiella* (Luer) Luer (= *Stelis* subgen. *Unciferia*). Photograph by AK.

Stelis pilosa Pridgeon & M.W.Chase, Lindleyana 17(2): 100. 2002. (Fig. 25)

Repl. syn.: *Pleurothallis amparoana* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 23, 104. 1923. *Effusiella amparoana* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007. *Stelis amparoana* (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16: 261. 2001, *nom. illeg.* Non *Stelis amparoana* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 16. 1923.

Stelis pilostoma (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pilostoma* Luer, Lindleyana 11(2): 89. 1996. *Unciferia pilostoma* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis pompalis (Ames) Pridgeon & M.W.Chase, Lindleyana 16(4): 265. 2001.

Bas.: *Pleurothallis pompalis* Ames, Sched. Orch. 7: 23-25. 1924. Syn.: *Unciferia pompalis* (Ames) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis pseudocheila (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis pseudocheila* Luer & R.Escobar, Orquideología 16(2): 173. 1984. Syn.: *Effusiella pseudocheila* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis psilantha (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis psilantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 95. 1998. Syn.: *Unciferia psilantha* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis resupinata (Ames) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Pleurothallis resupinata* Ames, Orchidaceae 2: 272. 1908. Syn.: *Effusiella resupinata* (Ames) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

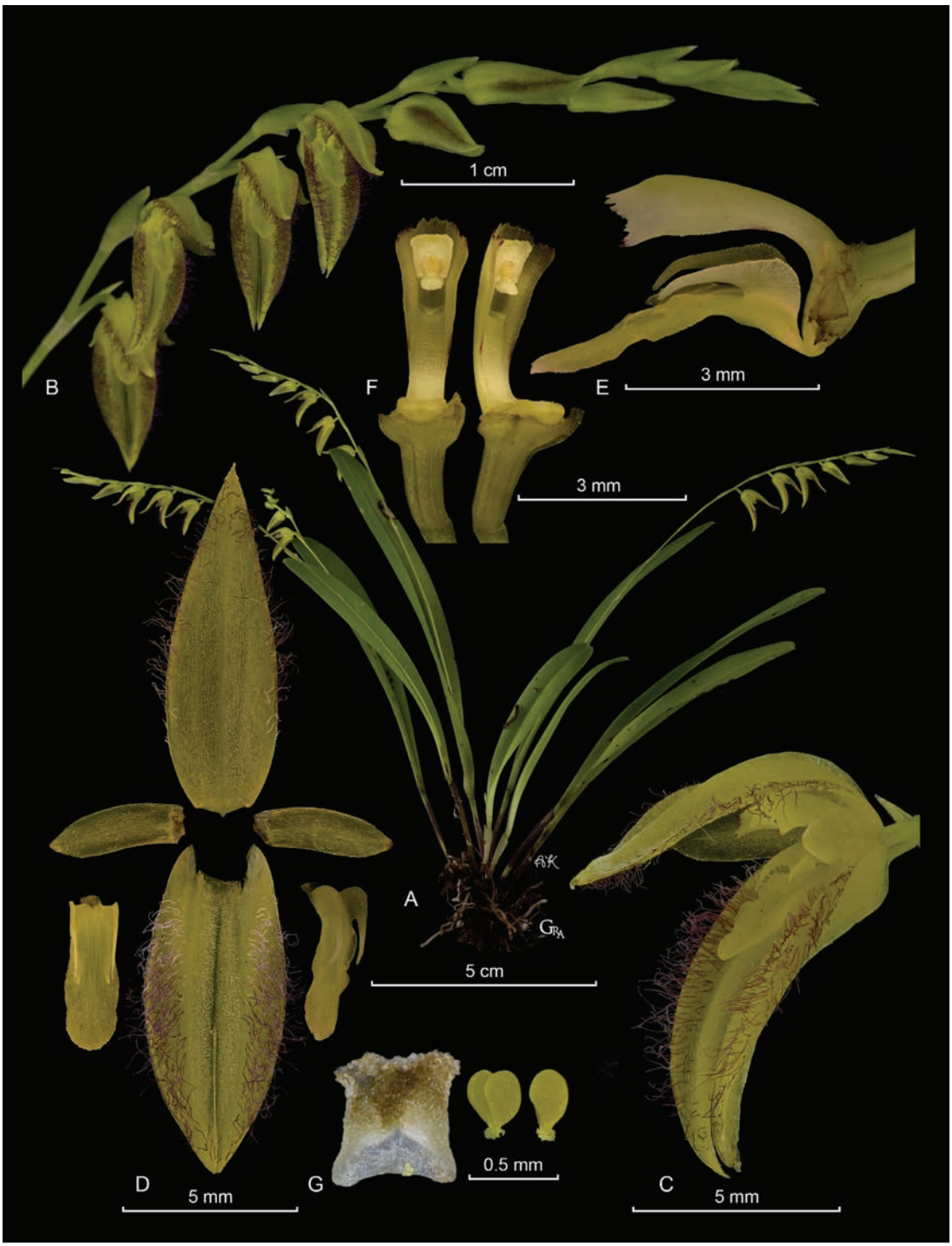


FIGURE 26. LCDP of *Stelis segoviensis*, type species of *Stelis* subgen. *Unciferia*. **A**. Habit. **B**. Inflorescence. **C**. Flower. **D**. Dissected perianth. **E**. Column with lip, lateral view. **F**. Column ventral and lateral view. **G**. Anther cap and pollinarium. Photographs by AK based on *Rojas-Alvarado 311* (JBL-spirit).

Stelis retusa (Lex.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Dendrobium retusum* Lex., Nov. Veg. Descr. 2(Orchid. Opusc.): 40. 1825. *Specklinia retusa* (Lex.) Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835. *Pleurothallis retusa* (Lex.) Lindl., Edwards's Bot. Reg. 28: Misc. 81-82. 1842. Syn.: *Effusiella retusa* (Lex.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007, *nom. inval.*

Stelis rostratissima (Luer & J. Portilla) Karremans, Phytotaxa 203(3): 293. 2015.

Bas.: *Pleurothallis rostratissima* Luer & J. Portilla, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 108. 2002. Syn.: *Effusiella rostratissima* (Luer & J. Portilla) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis segoviensis (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001. (Fig. 26)

Bas.: *Pleurothallis segoviensis* Rchb.f., Bonplandia (Hannover) 3(15-16): 223-224. 1855. Syn.: *Unciferia segoviensis* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis thomasii (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis thomasii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 84, 130. 2000. *Effusiella thomasii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis trichostoma (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis trichostoma* Luer, Selbyana 5(2): 185. 1979. *Effusiella trichostoma* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis trulla (Rchb.f. & Warsz.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis trulla* Rchb.f. & Warsz., Bonplandia (Hannover) 2: 114. 1854. *Effusiella trulla* (Rchb.f. & Warsz.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis uncinata Pridgeon & M.W.Chase, Lindleyana 17(2): 100. 2002.

Repl. syn.: *Pleurothallis kareniae* Luer, Lindleyana 11(2): 83, f. 19. 1996. *Unciferia kareniae* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004. *Stelis kareniae* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 264. 2001, *nom. illeg.* Non *Stelis kareniae* Luer, Lindleyana 11(2): 100, f. 31. 1996.

Stelis villosa (Knowles & Westc.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis villosa* Knowles & Westc., Fl. Cab. 2: 78. 1838. Syn.: *Effusiella villosa* (Knowles & Westc.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis vinacea (Ames) Bogarín, Proc. 22nd World Orchid Conf. I. 358. 2019.

Bas.: *Pleurothallis vinacea* Ames, Schedul. Orchid. 6: 69. 1923.

Stelis wagneri (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis wagneri* Schltr., Repert. Spec. Nov. Regni Veg. 17(8-12): 141. 1921. *Unciferia wagneri* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis werckleana Bogarín & Pupulin, Proc. 22nd World Orchid Conf. I. 358. 2019.

Repl. syn.: *Pleurothallis wercklei* Schltr., Repert. Spec. Nov. Regni Veg. 17: 141. 1921. Non *Stelis wercklei* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 20. 1923.

Stelis xerophila (Schltr.) Soto Arenas, Icon. Orchid. (Mexico) 5-6: t. 695. 2002 [2003].

Bas.: *Pleurothallis xerophila* Schltr., Beih. Bot. Centralbl., Abt. 2 36(2): 398. 1918. Syn.: *Specklinia xerophila* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Stelis zootrophionoides Castañeda-Zárate & Ramos-Castro, PLoS ONE 7(11): 5. 2012.

Syn.: *Effusiella zootrophionoides* (Castañeda-Zárate & Ramos-Castro) Archila, Revista Guatemal. 17(2): 76. 2014.

The 42 species that belong to *Stelis* subgen. *Unciferia* are found only from Mexico to Bolivia and Peru, they are especially diverse in Middle America and no records exist for the Antilles or Brazil.

DNA data is available for *Stelis canae*, *S. immersa*, *S. jalapensis*, *S. kefersteiniana*, *S. listerophora*,

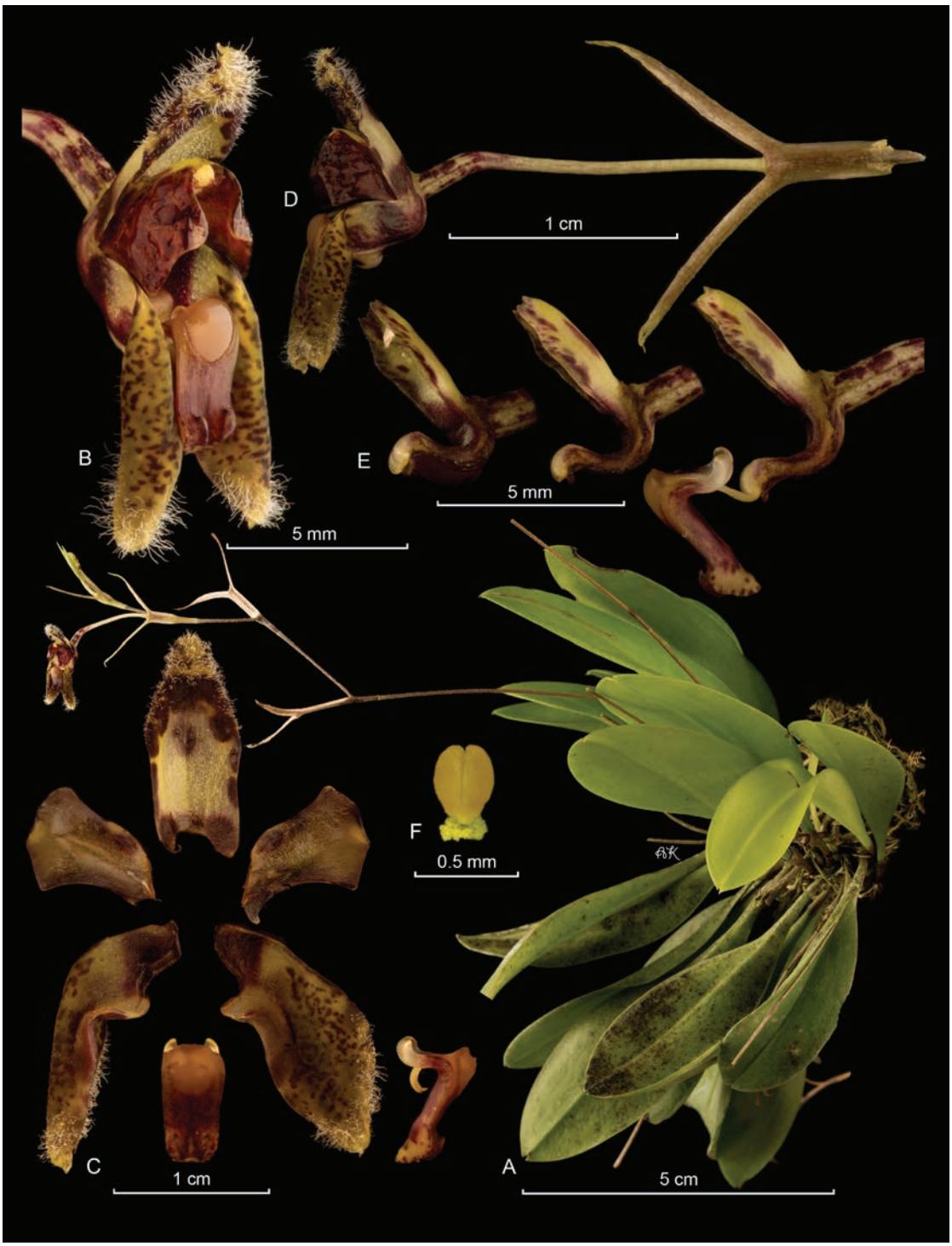


FIGURE 27. LCDP of Stelis furculifera, one of the two members of Stelis subgen. Condylago (Luer) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Flower, floral bract, lateral view. **E**. Column semi-ventral, side view, with and without the lip attached. **F**. Pollinarium. Photographs by AK based on *Bogarín 5901* (JBL-spirit)..

S. nigriflora, *S. ornata*, *S. pilosa*, *S. pompalis*, *S. resupinata*, *S. retusa*, *S. segoviensis*, *S. trichostoma*, *S. zootrophionoides* (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Ramos-Castro *et al.* 2012; Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017, Ponert *et al.* 2019). They all consistently appear within *Stelis* in the broad sense, and mostly as sisters to the members of *Stelis* subgen. *Dracontia*. However, diverse analyses (using different genes, methods or taxa) provide contradicting relationships among them. *Stelis pilosa*, type species of genus *Effusiella*, appears to be a close relative of *Stelis segoviensis*, type species of genus *Unciferia*, but there is also support for a relationship between some of the members of *Stelis* subgen. *Unciferia* and species of either *Stelis* subgen. *Condylago* and *Stelis* subgen. *Dracontia*. It may therefore not be a monophyletic group and requires further analysis.

Stelis* subgen. *Condylago (Luer) Karremans, *comb. nov.*

Bas. *Condylago* Luer, Orquideologia 15: 118. 1982. Type: *Condylago rodrigoi* Luer, Orquideología 15(2-3): 118-122. 1982.

Stelis furculifera (Dressler & Bogarín) Bogarín, Lankesteriana 14(3): 267. 2014. (Fig. 27)

Bas.: *Condylago furculifera* Dressler & Bogarín, Harvard Pap. Bot. 12(1): 2-5. 2007.

Stelis rodrigoi (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 266. 2001.

Bas.: *Condylago rodrigoi* Luer, Orquideología 15(2-3): 118-122. 1982.

The two species that belong to *Stelis* subgen. *Condylago* are restricted to Panama and Colombia respectively. DNA data is only available for *Stelis rodrigoi* and most analyses find it as a sister to the rest of *Stelis sensu lato* (Karremans 2010, Ramos-Castro *et al.* 2012; Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). However, a relationship with members of *Stelis* subgen. *Unciferia* was also found by authors (Pridgeon *et al.* 2001, Ponert *et al.* 2019).

Stelis* subgen. *Umbralia Karremans, *subgen. nov.*

ETYMOLOGY: From the Latin *umbra*, shade or shadow, in reference to the short twisted inflorescence hidden under the shade of the convex leaf.

Type: *Pleurothallis imraei* Lindl., Fol. Orchid. ~Pleurothallis~ 9. 1859.

Distinguished from all other subgenera by the large caespitose plants bearing ovate to suborbicular leaves that are typically convex. The inflorescence is significantly shorter than the leaf and twists in such a way that the flowers are frequently hidden behind the leaf blade. The ovary is strongly bent, causing the flowers to be oriented upwards. The sepals are internally pubescent, the lateral sepals forming a synsepal with a mentum at the base. The petals are conspicuously spathulate, obtuse. The lip is convex in natural position, unguiculate, delicately hinged to the column foot, lanceolate when extended, obtuse. The column is cylindrical, incurved, with a pair of small wings, apically denticulate. Pollinia two, forming a whale-tail type pollinarium with a pair of flattish caudicles.

Stelis cocornaënsis (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis cocornaënsis* Luer & R.Escobar, Orquideología 20: 45. 1996. Syn.: *Specklinia cocornaënsis* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 259. 2004. *Effusiella cocornaënsis* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis erucosa (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 262. 2001.

Bas.: *Pleurothallis erucosa* Luer & R.Escobar, Orquideología 21(1): 88. 1998. Syn.: *Specklinia erucosa* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 260. 2004. *Effusiella erucosa* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Stelis imraei (Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 263. 2001. (Fig. 28)

Bas.: *Pleurothallis imraei* Lindl., Fol. Orchid. ~Pleurothallis~ 9. 1859. Syn.: *Humboldtia imraei* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891. *Specklinia imraei* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 261. 2004. *Effusiella imraei* (Lindl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 106. 2007.

Syn.: *Pleurothallis umbraticola* Schltr., Repert. Spec. Nov. Regni Veg. 27(1-8): 56-57. 1929.

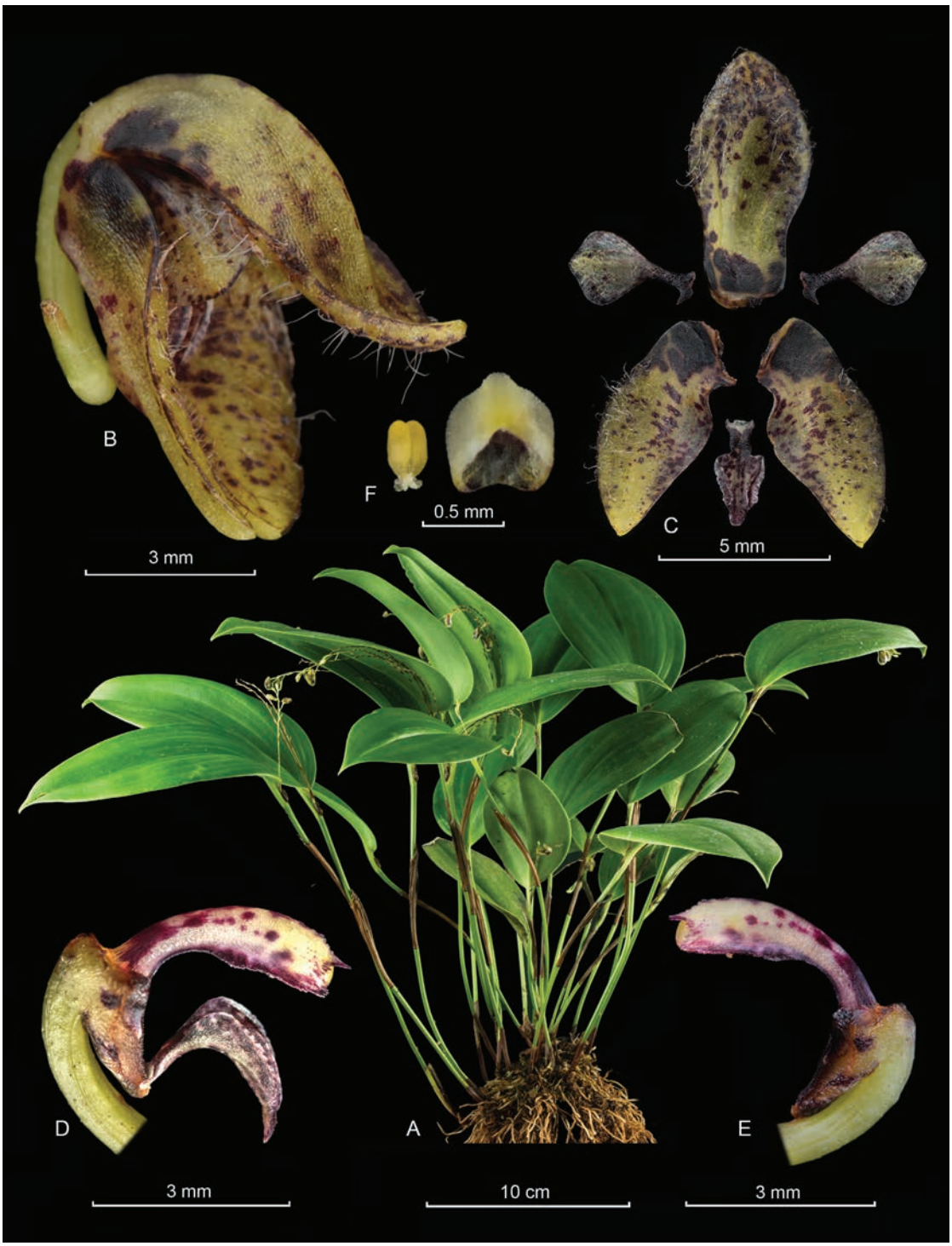


FIGURE 28. LCDP of *Stelis imraei*, type species of *Stelis* subgen. *Umbralia* Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **D.** Column lateral view. **E**. Anther cap and pollinarium. Photographs by I. Chinchilla based on *Bogarín 752* (JBL-spirit).

Stelis tarantula (Luer & Hirtz) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis tarantula* Luer & Hirtz, Lindleyana 11(3): 186-187. 1996. Syn.: *Specklinia tarantula* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 264. 2004. *Effusiella tarantula* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007.

Stelis vaginata (Schltr.) Pridgeon & M.W.Chase, Lindleyana 16(4): 267. 2001.

Bas.: *Pleurothallis vaginata* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 197. 1923. Syn.: *Specklinia vaginata* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 264. 2004. *Effusiella vaginata* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 107. 2007. *Pleurothallis imraei* var. *vaginata* (Schltr.) O. Gruss & M. Wolff, Orchid Atlas 359. 2007.

Five species are currently recognized as belonging to *Stelis* subgen. *Umbralia*. They are mostly found from Costa Rica to Ecuador, with the highest diversity in Colombia. This subgenus includes the very variable *Stelis imraei*, which is most like a species complex distributed from Costa Rica to Peru and Bolivia, the Guyanas, and the Lesser Antilles.

Although Luer (2000) placed these species among the *Effusiella*, and the flowers are indeed similar, vegetative morphology is quite unlike any other *Stelis*. Not surprisingly, the DNA data available for *Stels imraei* places it as sister to all other members of *Stelis* in the broad sense (Karremans 2010, Karremans *et al.* 2013). A multigene analysis of the Pleurothallidinae including an accession of *Stelis cocornaënsis* places it as sister to *Stelis* subgen. *Dracontia* (Ponert *et al.* 2019). It is certainly possible to segregate this group into a genus of its own, however, such a proposal would be inconsistent with the current interpretation that this group is best treated a single genus at this time.

Excluded Taxa

The following groups are still associated with *Stelis* in the broad sense, or with certain species groups therein, in literature. They are here explicitly stated with hopes that they can be definitively be excluded from *Stelis* and no longer be associated with any taxa belonging to it.

Pleurothallis sect. *Alatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 99. 1999. Type: *Specklinia obovata* Lindl. Edwards's Bot. Reg. 25: Misc. 75. 1842. (Fig. 29) = ***Anathallis*** **Barb.Rodr.**

DNA data has consistently shown that members of *Pleurothallis* subgen. *Acuminatia* sect. *Acuminatae* belong in *Stelis*, whilst those placed in *Acuminatia* sect. *Alatae* belong to *Anathallis* (Karremans *et al.* 2013; Karremans 2014, Pérez-Escobar *et al.* 2017). Morphologically this is easily diagnosable as species of sect. *Alatae*, like other species of *Anathallis*, have star-shaped flowers, with acuminate petals that are as long as the sepals, a flattened lip and the sharply winged, apically fringed column. Whereas species of sect. *Acuminatae*, like other species of *Stelis*, bear obtuse petals, that are significantly shorter than the sepals, have a non-flattened lip, and the column is not prominently winged or fringed (Karremans 2014; 2016).

Pleurothallis subgen. *Effusia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 54. 2000. Syn.: *Pleurothallis* sect. *Effusae* Lindl. Edwards's Bot. Reg. 28: Misc. 74. 1842. Type: *Pleurothallis hypnicola* Lindl. Edwards's Bot. Reg. 28: Misc. 75. 1842. (Fig. 30) = ***Pabstiella*** **Brieger & Senghas**

DNA data has consistently shown that *P. hypnicola* and its relatives belong in *Pabstiella* rather than *Stelis* (Karremans *et al.* 2013, Pérez-Escobar *et al.* 2017). Even though not closely related, there is a striking similarity between species of *Pabstiella* and some members of *Stelis* subgen. *Unciferia*, a convergence that most likely responds to a similar pollination syndrome. With few exceptions, species of *Pabstiella* are found in Brazil, where the members of *Stelis* subgen. *Unciferia* are absent. The latter instead are most diverse in Middle America, where very few *Pabstiella* species have been recorded.

Elongatia (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 257 (2004). Bas.: *Pleurothallis* subgen. *Elongatia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 41. 1986. Syn.: *Pleurothallis* sect. *Elongatae* Lindl. Edwards's Bot. Reg. 28: Misc. 68.

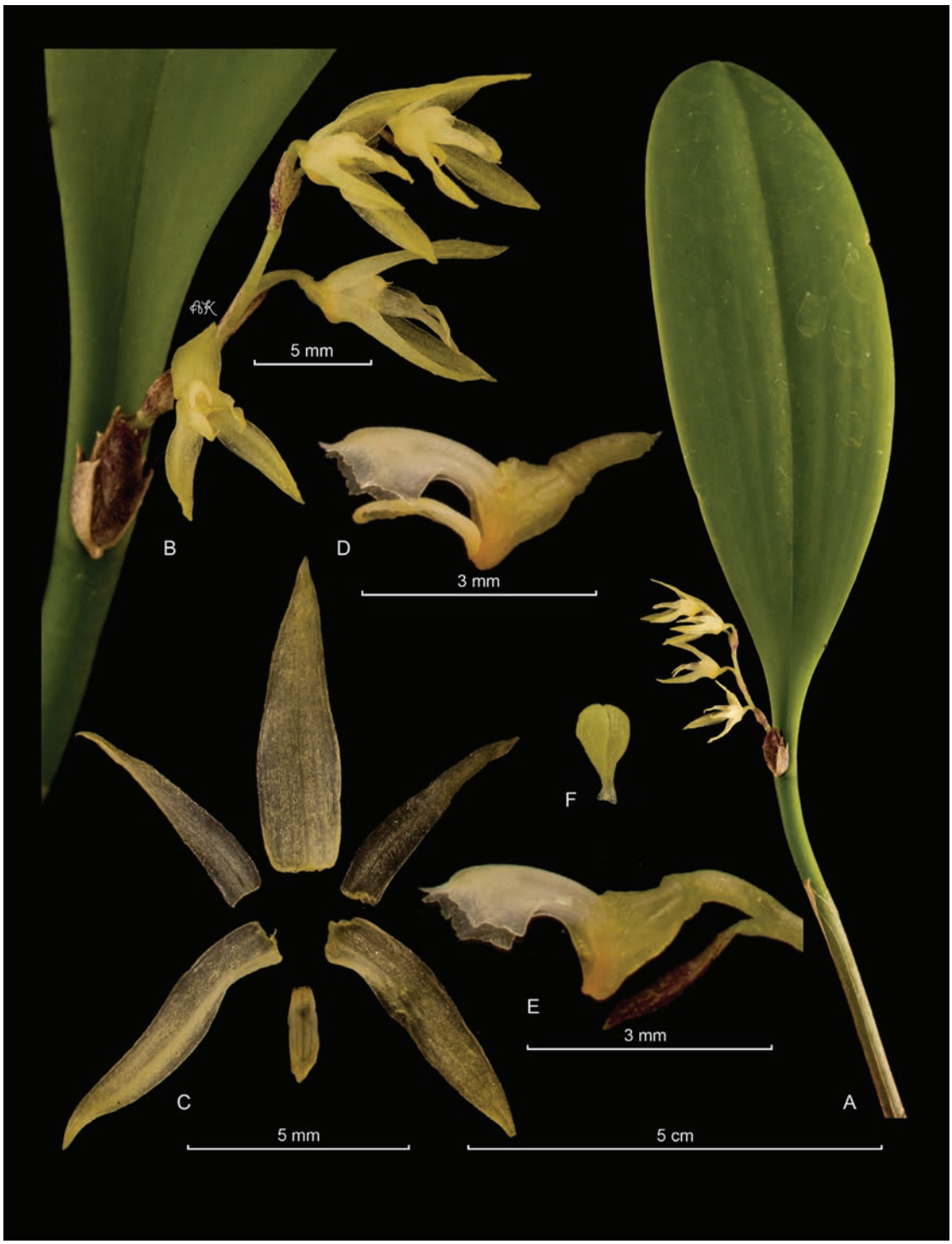


FIGURE 29. LCDP of *Anathallis obovata*, type species of *Anathallis*. **A**. Habit. **B**. Inflorescence. **C**. Dissected perianth. **D**. Column with lip, lateral view. **D.** Column ventral and lateral view. **E**. Pollinarium. Photographs by AK based on *JBL-28233* (JBL-spirit).

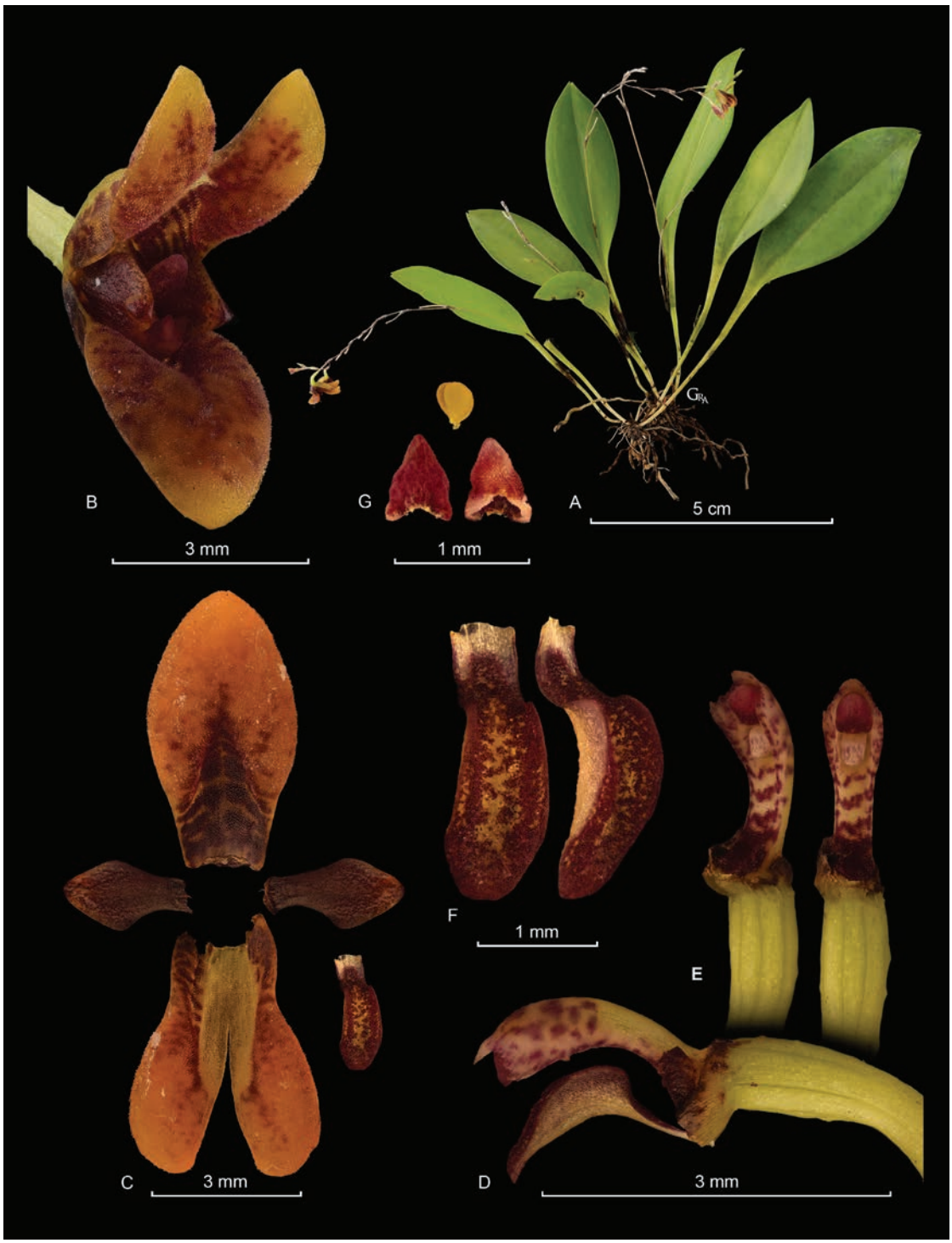


FIGURE 30. LCDP of *Pabstiella hypnicola*, type species of *Pleurothallis* subgen. *Effusia* (= *Pabstiella*). **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E.** Column ventral and lateral view. **F**. Lip. **G**. Anther cap and pollinarium. Photographs by G. Rojas-Alvarado based on *HBL960631* (JBL-spirit).

FIGURE 31. *Pleurothallis restrepioides* Lindl., type species of *Elongatia* (= *Pleurothallis*). Photograph by J. Varigos.

1842. Lectotype: *Pleurothallis restrepioides* Lindl. Companion Bot. Mag. 2: 356. 1836. (Fig. 31) = ***Pleurothallis* R.Br.**

DNA data has consistently shown that *P. restrepioides*, type species of *Elongatia*, and its closest relatives belong in *Pleurothallis* rather than *Stelis* (Karremans *et al.* 2013; Wilson *et al.* 2013, Pérez-Escobar *et al.* 2017). The flowers of *Elongatia* are superficially similar to the members of *Stelis* sect. *Carpinterae* and *Stelis* sect. *Petiolatae*. From the first they are distinguished by very large plants, with thick coriaceous leaves, from the second by the large plants with sessile leaves. From both, *Elongatia* species are distinguished by the erect, elongate inflorescence with multiple simultaneous flowers.

Pleurothallis* subgen. *Lalexia (Luer) Karremans, *comb. et stat. nov.*

Bas.: *Lalexia* Luer, Harvard Pap. Bot. 16: 358. 2011. Syn. *Loddigesia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 251. 2006, *nom. illeg.* Non *Loddigesia* Sims Bot. Mag. 24: pl. 965. 1806. Type: *Dendrobium quadrifidum* Nov. Veg. Descr, 2(Orch. Opusc.): 40-41. 1825. (Fig. 32)

Morphologically this taxon could be confused with a member of *Stelis* in the broad sense, and in fact many authors still place it in *Stelis* rather than *Pleurothallis*. Stenzel (2004) doubted the results of his own phylogenetic reconstruction in which two accessions of *Pleurothallis ghiesbreghtiana* A.Rich. & Galeotti (= *P. quadrifida*) were found sister to *Pleurothallis* rather than *Stelis*. However, except for the phylogenetic inference presented by Solano-Gómez (2005), all other DNA based studies consistently show that *P. quadrifida*, type species of *Lalexia*, is sister to the remaining species of *Pleurothallis* rather than *Stelis* (Stenzel 2004, Karremans *et al.* 2013, Wilson *et al.* 2013, 2017, Pérez-Escobar *et al.* 2017). The exclusion from *Stelis* is supported by multi-gene genomic studies (Ponert *et al.* 2019).

Its only member, *Pleurothallis quadrifida*, is a widely distributed and common species without any close relatives. It is easily recognized by the thick coriaceous leaves, erect, elongate, simultaneous inflorescences bearing large bright yellow flowers. It is unique in the glabrous flowers, with petals similar in size the sepals, the pandurate lip and the simple column with sub-apical anther. Unlike the majority of the members of the subtribe, the sweetly fragrant bright yellow flowers of this species may be adapted to pollination by Hymenoptera rather than Diptera, as a parasitoid wasp was documented removing pollinaria (Karremans & Díaz-Morales 2019).

Pleurothallis quadrifida (Lex.) Lindl., Edwards's Bot. Reg. 28(Misc.): 70. 1842.

Bas.: *Dendrobium quadrifidum* Lex. in P.de La Llave & J.M.de Lexarza, Nov. Veg. Descr. 2(Orchid. Opusc.): 40. 1825. *Humboltia quadrifida* (Lex.) Kuntze, Revis. Gen. Pl. 2: 668. 1891. *Stelis quadrifida* (Lex.) Solano & Soto Arenas, Icon. Orchid. 5-6: xi. 2002 [2003]. *Specklinia quadrifida* (Lex.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 263. 2004. *Loddigesia quadrifida* (Lex.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 251. 2006. *Lalexia quadrifida* (Lex.) Luer, Harvard Pap. Bot. 16: 358. 2011.

Syn.: *Pleurothallis racemiflora* Lindl. ex Lodd. Bot. Cab. 10: t. 949. 1824 [1825], *nom. illeg.* Non *Pleurothallis racemiflora* (Sw.) Lindl. in Hook. Exot. Fl. 2: t. 123. 1825 [1824]. *Stelis racemiflora* (Lindl. ex Lodd.) W.H.Baxter in J.C.Loudon, Hort. Brit., Suppl. 3: 643. 1850, *nom. illeg. Pleurothallis longissima* Lindl., Fol. Orchid. ~Pleurothallis~ 31. 1859.

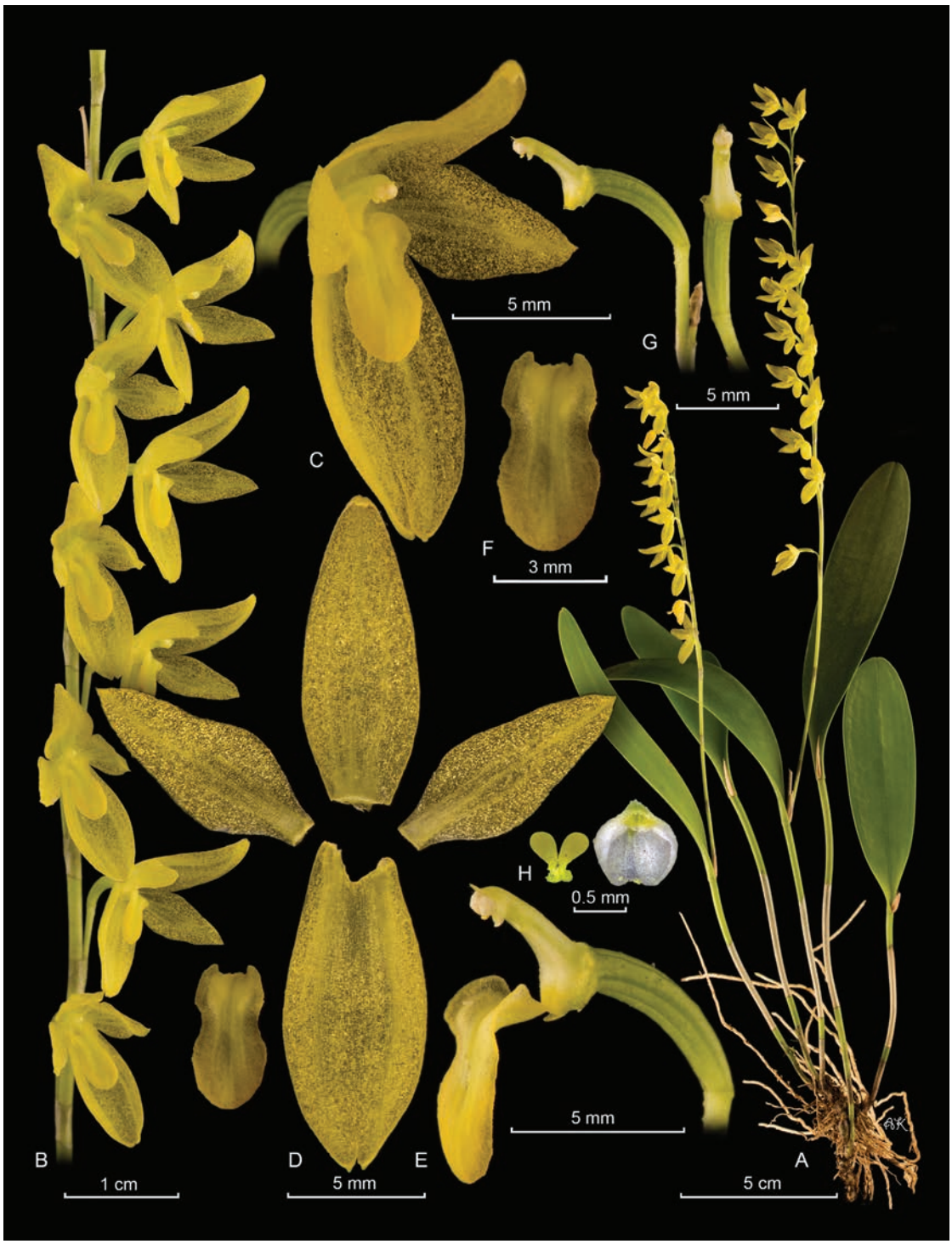


FIGURE 32. LCDP of *Pleurothallis quadrifida*, type species of *Lalexia* (= *Pleurothallis* subgen. *Lalexia*). **A**. Habit. **B**. Inflorescence. **C**. Flower. **D**. Dissected perianth. **E**. Column with lip, lateral view. **F**. Lip. **G.** Column ventral and lateral view. **H**. Anther cap and pollinarium. Photographs by AK based on *Karremans 6436* (JBL-spirit).

Great taxonomical confusion surrounds the name *Pleurothallis racemiflora* in commonly used databases and literature, warranting the current note. When Lindley, in Hooker (1824), transferred Swartz's *Epidendrum racemiflorum* to *Pleurothallis*, rather than describing and illustrating Swartz's species (treated above as *Stelis multirostris*) he presented another species, treated here as *Pleurothallis quadrifida.* Lindley later realized his initial mistake and rectified "*P. longissima* (*P. racemiflora*, Lindl. in Hook. Exot. Fl. t 123, nec Swartzii)... It is not the *Dendrobium racemiflorum* Sw. as I formerly supposed" and that "*P. racemiflora* (*Dendrobium racemiflorum* Swartz, Fl. Ind. Occ. 1543. *P. oblongifolia* Lindl. in Comp. Bot. Mag. 2. 355)... Original specimens from Swartz show that this is the plant meant by Swartz".

However, the damage was already done. In the Botanical Cabinet, Loddiges (1825) features the same *Pleurothallis racemiflora* that Lindley had misinterpreted (thus *Pleurothallis quadrifida*), and not that of Swartz (= *Stelis multirostris*). Loddiges' name has been regarded by various authors as a combination for the basionym *Epidendrum racemiflorum* Sw. or simply as a citation of *P. racemiflora* (Sw.) Lindl. Nevertheless, in the original publication there is no reference to either, and as both text and illustration are based on Loddiges' own material that actually represents a different species as that of Swartz, it must be interpreted that the author is publishing a new taxon. The name is therefore to be cited correctly as *P. racemiflora* Lindl. ex Lodd. and it is an heterotypic homonym of *P. racemiflora* (Sw.) Lindl.

As *P. racemiflora* (Sw.) Lindl. latter was published a few months prior to *P. racemiflora* Lindl. ex Lodd., it has priority. Therefore, *P. racemiflora* Lindl. ex Lodd. is valid, yet illegitimate under article 53.1 (Turland *et al.* 2018). The name *Stelis racemiflora* published by Baxter in the "Supplement to J.C. Loudon's Hortus Britannicus" clearly cites Loddiges as author, and thus should be correctly cited as *Stelis racemiflora* (Lindl. ex Lodd.) W.H.Baxter. Although most names from the Hortus Britannicus are considered invalid, this new combination is in accordance with articles 35.2, 38.1, 38.2 and 41.4 as it associates the genus and final epithet and associating the new combination with a basionym and earlier description (Turland *et al.* 2018). However, it is based on an illegitimate name, and thus illegitimate too. Both are here regarded as heterotypic synonyms of *P. quadrifida* as they are based on Loddiges' material rather than Swartz's. *Pleurothallis longissima* Lindl. is based on the same type as *P. racemiflora* Lindl. ex Lodd., and thus can be considered a replacement name.

Conclusions. To be, or not to be a *Stelis*, that is the question. For that we hope to have an answer. Recognizing a member of *Stelis* in the classic strict sense is certainly straightforward. Most species (not all) have a standard and distinctive floral morphology. If the group was an isolated lineage within the Pleurothallidinae there would be no need for the current discussion. However, that is not the case. We now know for a fact that many groups of species that lack the typical *Stelis*-flower are actually close relatives. An alternative would be not to add these groups to a broader *Stelis* but to recognize each of them as genera as well. But is that alternative more intuitive or informative? It doesn't seem to be that way at all.

Sadly, none of the possible ways in which we can translate the evolutionary history of this group of species into a stable classification system appears to be very appealing. *Stelis* in the broad sense defined here is made up of a series of strikingly different species groups that indisputably share a common ancestor and a common evolutionary history. In the past, flower morphology has been the main source for information regarding evolutionary history between taxa, however today we know that flower morphology in distant taxa may appear very similar due to convergence evolution. Why, despite their indistinguishable flowers, are we happy to accept that *Bulbophyllum careyanum* Spreng., *B. striatellum* Ridl., *B. laxiflorum* Lindl., *B. maxillare* Rchb.f. and *B. tremulum* Wight, are not actually species of Pleurothallidinae belonging to the genera *Acianthera* Scheidw., *Muscarella* Luer, *Myoxanthus* Poepp. & Endl., *Masdevallia* Ruiz & Pav. and *Trichosalpinx* Luer, respectively? Because it has been established beyond a doubt that these groups are unrelated and their floral similarity is merely a consequence of convergent evolution due to similar pollination syndromes.

Similarly, we should accept that convergent morphologies occur within the Pleurothallidinae, the group with highest diversification rates and species number in Orchidaceae. It is a fact that species of *Andinia* (Luer) Luer are not closely related to species of *Lepanthes* Sw., and that neither of them is a close relative of species of *Salpistele* Dressler (= *Stelis*), despite having almost identical flowers. In the same way, it has been proven that species of *Anathallis* Barb.Rodr. are not closely related to the florally similar of *Lankesteriana* Karremans. We know that those floral convergences result from adaptation to the same pollinators or pollination strategies (Wilson *et al*. 2017; Bogarín *et al*. 2018; Karremans & Díaz-Morales 2019). Specifically, in the case of *Stelis s.l.*, Karremans & Díaz-Morales (2019) stress the point that species of *Stelis* subgen. *Unciferia* have been reported to be pollinated by flies of the families Phoridae and Chloropidae which are exactly the same families of flies that pollinate species of *Acianthera*, an unrelated genus with flowers that are indeed much more similar than those of *Stelis s.s*. The authors also show that the transitional morphology of species belonging to *Stelis* subgen. *Crocodeilanthe* results in the placement of pollinaria on the top of the head of their pollinators, which is midway between the scutellum placement of members of *Stelis* subgen. *Unciferia* and the placement close to the mouthparts observed in *Stelis s.s*. (Karremans & Díaz-Morales 2019).

As circumscribed here, *Stelis* includes 1243 species, making it the most species rich genus in the Pleurothallidinae, and one of the largest in Orchidaceae. The most specious group in the genus is *Stelis* subgen. *Stelis*, which harbors some 1030 species with the more classical *Stelis* flower morphology. The other 213 species are divided into eight subgenera that although florally different are closely related and share the same common ancestor of *Stelis s.s.*

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