ISSN 1409-3871

LANKESTERIANA

VOL. 13, No. 3 JANUARY 2014

INVITED PAPERS

continues

40TH ANNIVERSARY CELEBRATIVE ISSUE

REGULAR PAPERS

LANKESTERIANA
International Journal on Orchidology

Effective publication date: January 30, 2014

Layout: Jardín Botánico Lankester.
Cover: Lankester Botanical Garden's 40th Anniversary celebrating medal.
Printer: MasterLitho.
Printed copies: 500

Printed in Costa Rica / Impreso en Costa Rica

R Lankesteriana / International Journal on Orchidology
No. 1 (2001)-- . -- San José, Costa Rica: Editorial Universidad de Costa Rica, 2001--
v.
ISSN-1409-3871

1. Botánica - Publicaciones periódicas, 2. Publicaciones periódicas costarricenses

LANKESTERIANA 13(3): 155—156. 2014.

INTRODUCTORY PAPER*

INSTALACIÓN DE LA PRIMERA JUNTA ASESORA DEL JARDÍN CHARLES H. LANKESTER

RAFAEL LUCAS RODRÍGUEZ CABALLERO †

Escuela de Biología, Universidad de Costa Rica

Se necesitó 40,000,000 de años de la accidentada trayectoria geológica de esta región para formar el istmo centroamericano que conocemos y la ación del tibio, violento y húmedo clima del caribe para dar forma en él al paisaje natural, asombrosamente rico en especies y en números.

Se necesitó el alma de un hombre como Charles H. Lankester, que al tiempo que contribuía a la destrucción inexorable de este paraíso natural, precio obligado del avance de la agricultura y del "progreso", fue por 3 generaciones amigo y compañero de los exploradores de la flora costarricense, supo disfrutar de su belleza y llegó a apasionarse per ella en todas sus formas, que viendo 30 años antes de la oleada de preocupación que hoy corre por el mundo, la destrucción inminente de tantas especies y de tantos paisajes, supo soñar en un abrigo, un refugio para el bosque que veía desaparecer y dedicarse a realizar ese sueño en este rincón que hoy recibe su nombre… esfuerzo que mantuvo hasta los últimos instantes de su vida.

Se necesitó la mirada sensitiva de varias personas, entre las que destacaron la Dra. Mildred E. Mathias, la Sra. Betty Marshall y muy conspicuamente, la orquideóloga Rebecca Tyson Northen, quien afortunadamente nos acompaña hoy, para empe˜ãr en un llamado para buscar el modo de conservar este jardín y continuar la labor que quedaba inconclusa al extinguirse aquella chispa de entusiasmo que alentaba en Don Carlos…

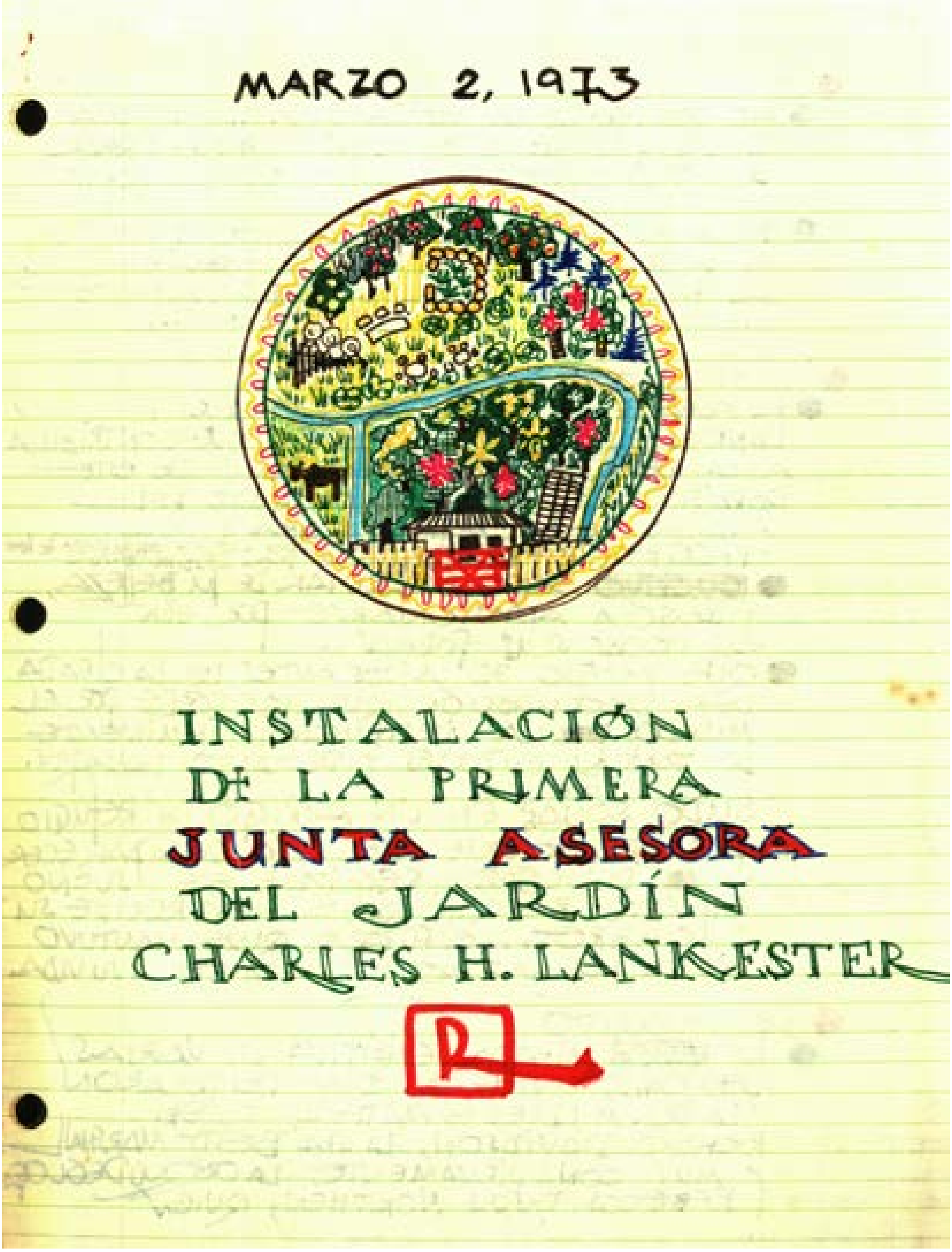
Se necesitó la devoción por todo lo que puede crecer y florecer y dar fruto, que alentaba en el corazón de otro inglés, Stanley Smith, manifestándose después de su deceso en un Fondo establecido para fomentar la horticultura dondequiera fuese posible, aún en tierras nunca visitadas por el, y cuyo director también nos acompaña… y las características generosidad y tendencia a la acción cooperativa del pueblo norteamericano, manifestándose en un llameo hecho por la Asociación Norteamericana de Orquideología por medio de su Fondo para Investigación y Educación, algunos de cuyos dirigentes hoy nos honran con su compañía… para reunir la suma necesaria y entregar este jardín a la Universidad de Costa Rica, la cual la aceptó comprometiéndose a mantener en él el ideal, la visión y el esfuerzo de Don Carlos Lankester.

Al reunirnos aquí para instalar la primera Junta Asesora del Jardín Carlos H. Lankester, rindamos homenaje a la belleza natural de nuestra tierra, que merece muchos esfuerzos más para su protección, a aquel individuo notable, Charles H. Lankester, quien mereció del pueblo que lo contara como uno de los suyos ["Don Carlos"], al amor por la horticultura de Stanley Smith, que desboradaba los bordes de su mundo para envolver la tierra entera en su entusiasmo y a esa fraternal generosidad de los orquideólogos norteamericanos, muchos de los cuales ni habían visitado Costa Rica ni pensaban llegar nunca a visitarla, pero supieron ayudar a lo que consideraban una causa digna de esfuerzo.

Que este homenaje de admiración, de recuerdo y gratitud nos guíe en el desarrollo futuro de este jardín.

---

* El manuscrito autógrafo de este discurso, pronunciado por el Dr. Rafael Lucas Rodríguez Caballero durante la ceremonia de inauguración del Jardín Botánico Lankester el 2 de marzo de 1973, ha sido amablemente proporcionado por sus herederos como contribución para las celebraciones del 40 Aniversario de la institución.



MARZO 2, 1973

INSTALACIÓN
DE LA PRIMERA
JUNTA ASESORA
DEL JARDÍN
CHARLES H. LANKESTER

R

FIGURE 1. Primera página del manuscrito autógrafo de Rafael Lucas Rodríguez Caballero, con el discurso pronunciado en ocasión de la inauguración del Jardín Botánico Lankester. En la parte superior se aprecia un mapa estilizado del Jardín Botánico Lankester en el año 1973. Cortesía de los herederos de R. L. Rodríguez Caballero.

LANKESTERIANA 13(3): 157—164. 2014.

INVITED PAPER*

RAPID TRANSFORMATION OF ORCHID FLORAS

JAMES D. ACKERMAN

Department of Biology and Center for Applied Tropical Ecology and Conservation,
University of Puerto Rico, PO Box 23360, San Juan, PR 00931-3360, U.S.A.
ackerman.upr@gmail.com

ABSTRACT. What does the future hold for the Orchidaceae? Historically the family has been quite plastic and responsive to large-scale habitat transformations, perhaps none so dramatic as the changes experienced during the formation of the cordilleras of the Northern Andes and lower Central America. Coupled with the backdrop of global fluctuations in climate, the rapid rise of these mountains over the last 0.5-2 M years have fragmented habitats and changed climate locally. These mountains are one of the most biologically diverse regions of the planet and may have served as a species pump for the Caribbean and other regions of Central and South America. The development of such diversity occurred over a scale of tens of millions of years to perhaps just a few thousand. While the same processes of the past are likely operational now, the current rate of habitat change may be unprecedented outside asteroid or major meteor impacts as global climate change accelerates, human-altered landscapes spread, and shifts occur in land use. We expect the structure and composition of orchid floras to change as populations respond evolutionarily through adaptation, extinctions and immigrations. Certainly the total destruction of a habitat, whether caused by volcanic eruptions or strip mining, is sure to have dire consequences but resiliency may occur if refugia serve as seed sources for colonization in the event of habitat recovery. As most orchids occupy ephemeral habitats or at least substrates, their natural population behavior likely entails cycles of local colonization and extinction as metapopulations. Another component of change is the increasing number of orchids that have become naturalized after human assisted dispersal (intentional or not). These alien orchids have overcome constraints imposed by pollination and mycorrhizal requirements. Will natural or human-assisted range expansions overcome extinction losses? Will they be among those that become the genetic material for a new wave of adaptive radiations? Much depends on population variation, patterns of gene flow, and rates of change. The Orchidaceae have had a history of ecological resiliency and evolutionary flexibility, which provides some degree of assurance. But this is no excuse for complacency since without some form of intervention the pace of change underway may be more than what orchid populations can overcome.

KEY WORDS: Orchidaceae, conservation, resiliency, floristic change, forest recovery

The orchid mystique is alive and well. The bizarre flowers, weird pollination mechanisms, and rarity of many species have captured the attention of enthusiasts and academics for nearly two centuries. Population declines of marquee species have been obvious due to over-collecting and habitat degradation (e.g., Miranda 1990, Cribb 1998, Soto Arenas *et al*. 2007). Consequently, orchids are frequent if not prominent occupants of endangered species lists and all 28,000-plus species of the family (Govaerts *et al.* 2010) have been placed on either appendix I or II of the Convention on International Trade in Endangered Species (CITES). Moreover, several books have focused on orchid conservation (e.g., IUCN/SSC Orchid Specialist Group 1996, Koopowitz 2001, Dixon et al. 2003). Are these symptoms of a dire outlook for the family? Will orchids survive rapid climate and land use changes?

To address these questions, I look at how the family has responded to disturbances through history. I emphasize processes related to diversification and population biology of the family in the northern Andes

---

* This contribution was prepared as part of the special edition of LANKESTERIANA that is dedicated to the commemoration of Lankester Botanical Garden´s 40th anniversary.

and the cordilleras of Panama and Costa Rica, two regions of extraordinary species diversity (Dressler 1981, Myers *et al.* 2000, Bogarín *et al.* 2013).

Early patterns of diversification. — Variance in age estimates for the Orchidaceae has been rather substantial (Arditti 1992, Gustafsson *et al.* 2010), but our current data indicate that the family is rather old. Initial age estimates of Ramírez *et al.* (2007) and Gustafsson *et al.* (2010) based on molecular clock calculations have been further refined by Guo *et al.* (2012) who have found that the most recent common ancestor of the Orchidaceae existed roughly 80-90 Ma, in the Late Cretaceous. From their analyses, most, if not all of the five current subfamilies diverged prior to the global disturbance and mass extinctions associated with the Cretaceous/Paleogene (K-Pg) boundary. This boundary, likely instigated by an asteroid impact at the edge of the present day Yucatan Peninsula (Morgan *et al.* 2008), not only caused extinctions of many forms of life, most famously the non-avian dinosaurs, but also opened doors to the evolutionary theater for diversification of other forms, including mammals and flowering plants. Beyond the K-Pg boundary, two clades represented by subfamilies Orchidoideae and Epidendroideae underwent evolutionary diversification that accounts for most of the species diversity of the orchid family as it is known today. Many clades from those subfamilies diverged just 15-20 Ma BP in the early Miocene (Ramírez *et al.* 2007, Guo *et al.* 2012). Of course, not all species that evolved during these years of diversification have survived. Extinction is a natural process and does not need the helping hand of humans. Nevertheless, we may assume that there has been an overall net gain in species. So, although the family's origins are rather old and some clades are relatively species-poor, the Orchidaceae as a whole is hardly relictual or static.

Recent evolutionary diversification. — While broad-scale orchid diversification events cannot be easily linked to large-scale disturbances, tectonic dynamics most assuredly fostered the diversification of orchids and other families (Hughes & Eastwood 2006). A good example is the recent rise of lower Central America and northern Andean cordilleras over the last 0.5-10 Ma (Dodson 2003, Kirby 2007, Karremans *et al.* 2013, Cascante-Marín & Nivia-Ruíz 2013). The result has been rapid diversification and fragmentation of habitats, which become isolated not only by valleys and ridges within mountain ranges, but also by intervening hotter and drier lowlands between them (Kirby 2011). Not surprisingly, topographic diversity is strongly associated with orchid diversity, even exceeding area as a factor linked to species richness (Dodson 2003, Ackerman *et al.* 2007). This relationship is well illustrated by the Maxillariinae of Panama and Costa Rica. Kirby (2011) found that widespread species of the subtribe tend to occupy lowlands whereas the narrow endemics and more derived species are those occupying the cooler, wetter montane slopes and valleys. While we expect such barriers to substantially limit gene flow, we still need to reconcile meta-analysis of F_{st} (or G_{st}) statistics that indicate high levels of gene flow among orchid populations (Phillips *et al.* 2012). But if natural selection is intense enough and sustained, then selection could overcome any homogenizing effect of occasional input from long-distance dispersal, allowing for local adaptation and diversification. Of course such population genetic data are only consistent with high levels of gene flow. Alternatively, it may also reflect only a relatively recent colonization event with little or no subsequent gene flow (Tremblay *et al.* 2005). Changes in neutral alleles would be mutation-dependent and divergence from parental populations may take a long time to occur. On the other hand, frequencies of alleles under selection may change rapidly as has been observed in other organisms (Losos 2014) and such differences would be missed by population genetic data based on assessment of neutral alleles.

While rapid rise of mountain ranges are clearly associated with the evolution of biological diversity, it is not a prerequisite for rapid orchid speciation. Gustafsson *et al.* (2010) found that much of the extant diversity of the orchid genus *Hoffmannseggella* in the geologically ancient eastern mountains of Brazil diverged since the Pliocene (< 2.5 Ma). During this same period significant fluctuations in moisture availability occurred (Auler & Smart 2001, Ledru *et al.* 2005), perhaps climatically fragmenting the landscape and affecting gene flow among populations with consequences akin to abrupt mountain building.

The driver for the remarkable evolutionary diversification of this family is likely tied to the process of pollination (van der Pijl & Dodson 1966, Stebbins 1984, Nilsson 1992, Chase 2001, Papadopulos *et al.* 2013), though the family also shows a broad range of physiological and vegetative adaptations (Dressler 1981, Benzing 1986, Arditti 1992), and we are only just beginning to understand the role of mycorrhizal associations in orchid evolution (e.g., Otero & Flanagan 2006; Motomura *et al.* 2010, Martos *et al.* 2012). The plethora of pollination mechanisms, some rather fantastic, and the exploitation of a broad spectrum of pollinators suggest that the post K-Pg diversification of insects, particularly Diptera, Lepidoptera and Hymenoptera, is closely tied to the evolutionary potential of the Orchidaceae, although not necessarily in a co-evolutionary dance (Ackerman 1983a, Ramírez *et al.* 2011, see also Schiestl & Dötterl 2012). Species with little sequence divergence may have arisen rapidly via exploitation of existing pollinator diversity. This is perhaps best exemplified by genera that employ sexual deception (e.g., *Lepanthes* R.Br., *Ophrys* L., *Telipogon* Kunth, *Chiloglottis* R.Br.; Blanco & Barboza 2007, Bateman *et al.* 2003, Neubig *et al.* 2012, Peakall *et al.* 2010).

Thus, the family is rather old, but much diversification is recent, geologically speaking. It appears that orchids are adept at responding evolutionarily to change occurring over millions of years to perhaps just a few thousand. Gentry and Dodson (1987) even suggested that speciation may occur over just a few decades, an idea with virtually no support, but it had planted the seed for breaking the shackles of gradualism in orchids (Tremblay *et al.* 2005).

Habitat changes over ecological time. — Change is ubiquitous and has always been that way, but the current rate of habitat change may be unprecedented outside asteroid or major meteor impacts as global climate change accelerates, human-altered landscapes spread, and shifts occur in land use. Habitat destruction is the foremost threat to orchids (IUCN/SSC Orchid Specialist Group 1996), so the question is whether the family as a whole has the resiliency to withstand the onslaught of change.

One obvious way in which orchids may respond to change is extinction. But considering the size of the family and the presumably high frequency of rare species, the number of known extinctions is quite low (IUCN/SSC Orchid Specialist Group 1996). This is counter-intuitive since rare species should be more vulnerable to habitat destruction. One explanation may be a function of the lack of human effort to document extinctions and the other may be a function of the biology of orchids. The former is difficult to verify so I will explore the latter.

Rapid changes in habitats have occurred throughout history and some dramatic events that have occurred recently will serve as examples. Disturbances that have caused population extinctions may occur at every scale. When a host tree sheds twigs and branches or dies entirely, so do its epiphytes. In 1989, a strong hurricane passed over Puerto Rico and through a relatively mature forest for the first time in many decades. Nearly half the trees fell or snapped off and those that withstood the winds had all their orchid epiphytes stripped away (Migenis & Ackerman 1993). Volcanic eruptions can be even more destructive than hurricanes. Krakatau is the best known example of nearly instant devastation when it exploded in 1883, destroying itself and nearby islands, covering extensive areas with debris, generating severe earthquakes and tsunamis, and by the infusion of sulfur dioxide in the stratosphere, cooling the planet for years afterwards (Thornton 1997). In a somewhat older violent eruption, Tungurahua II of the Ecuadorian Andes literally blew its top approximately 3000 years ago devastating the landscape with massive amounts of rubble and thick layers of ash (Hall *et al.* 1999), presumably creating lifeless moonscapes as were observed in the Krakatau explosion. Despite such ever-present yet rare natural threats to habitat stability, the most pressing issues for orchid conservation are the devastating consequences of human activities.

Like natural disturbances, those caused by man can be at every scale up to regional or even global. At very local levels human activities such as trampling can have both indirect and direct effects on orchids (Light & MacConaill 2007; Ballantyne & Pickering 2013). In the orchid-rich tropics, slash and burn agriculture created forest gaps, but much of that has been replaced by increasingly larger scale agriculture to the point of having farms measured in square kilometers rather than in hectares where topography and environmental conditions permit it. Perhaps the greatest changes will come from accelerating (anthropogenic or not) climate changes whose effects may be seen even within a span of a few years to decades (Allen & Breshears 1998, Kelly & Goulden 2008). Whether it is the warming trend with accompanying drier or wetter conditions (depending on region), or the increasing severity of weather, we have already begun to see changes and developing consequences, and cloud forests, where orchids thrive, seem to be highly susceptible (Pounds *et al*. 1999, Parmesan 2006, Gradstein 2008).

Recovery. — I expect that natural disturbances beget natural recoveries. Small-scale disturbances are common and most orchids likely have the capacity for recovery. After all, epiphytic orchids must constantly be on the move as bark and branches are shed and trees die, so orchid population dynamics may resemble metapopulation behavior (Ackerman 1983b, Tremblay *et al*. 2006). Certainly one expects that after a hurricane, orchids should be resilient since they have been for millions of years (Ackerman & Moya 1996, Mújica *et al*. 2013). Recovery can be relatively rapid, even after volcanic eruptions. Among the first vascular plants to colonize the remnants of Krakatau were orchids, and now the number of species continues to accumulate (63 species after 115 years) as the vegetation structure becomes more complex and more hospitable for epiphytes (Partomihardjo 2003). As for the Tungurahua II eruption in the Ecuadorian Andes, the mountain has rebuilt to 50% of its former size (Tungurahua III, Hall et al. 1999). The slopes have become re-vegetated, the orchid flora changes during this process, and colonizing species gradually disappear as others replace them. The overall effect is the mountain becomes orchid-rich once again, which includes a number of species that presumably occur nowhere else, with the implication that they may have evolved in just a few thousand years (Dodson 2003). The case of this volcano is not likely unusual. Ecuador has over 200 volcanoes and according to naturalist Alex Hirtz, approximately 20% of the orchid flora on each is endemic to that volcano (http://alexanderhirtz.com/orchid).

Recovery of orchid floras from anthropogenic disturbances is currently not well characterized, but will soon be with us on a grand scale. While deforestation still continues in some regions of the world at an alarming rate, there has been a reversal in the trend, mostly in shrubby arid zones and mountainous regions where modern large scale, mechanized agriculture has not been practical (Aide *et al*. 2012). A general reforestation trend has been occurring in both temperate and tropical regions such as Europe, USA, Puerto Rico, Dominican Republic, Costa Rica, Ecuador and Colombia, a phenomenon often associated with abandonment of small rural farms as a consequence of industrialization, economic growth, and sometimes armed conflicts (Sánchez-Cuervo *et al*. 2012). I expect that orchid population recovery should follow provided the existence of nearby refugia that may serve as propagule sources.

Once forests are restored or recover from human disturbances, will orchid floristic composition return to past conditions? Considering the forests themselves may not return to past structure and composition (e.g., Thompson *et al*. 2002, Lugo 2004), we may assume the same for orchid floras as change occurs for both ecological and evolutionary reasons. The extensive forested regions of Mexico, Guatemala, and Belize were once thought to be pristine, but we know now that they were deforested and extensively cultivated by Mayans, which was severe enough to create several episodes of significant erosion (Beach *et al*. 2006). The forests are now orchid-rich, but we will never know whether they have lost or even gained species from pre-Maya times. In a relatively well-documented case, approximately 95% of the island of Puerto Rico was deforested and converted to farmlands by the 1940s (Roberts 1942, Wadsworth 1950). This was followed by a change from an agrarian to an industrial-based society accompanied by human migration from rural areas to cities. The abandoned farmland formed secondary forests composed of a mix between native and non-native trees. Despite high human population densities, over 40% of the island now has forest cover (Grau *et al*. 2003). How did the orchid flora fair? Very few of the reported species for the island have been lost, and most of those that have not been seen for decades were known from only a single specimen, if any at all (Ackerman 1996). Small refugia were likely critical for floristic recovery as has been proposed for vegetation transition on other islands (de Boer *et al*. 2013). But where disturbance had been severely habitat altering, recovery for some orchid species has yet to occur, even after ecosystem recovery (Bergman *et al*. 2006). Shifts in the orchid flora over the last few decades have been dramatic. Large populations of twig epiphytes were once commonly encountered but now have become uncommon as forest recovery has progressed, shading out both the orchids and their hosts. Moreover, non-native orchids have taken hold in many parts of the island, currently making up about 7% of the orchid flora (Ackerman 2007).

Conclusions.— Orchids throughout their history seem to have done well in face of climatic change caused by shifting continents, mountain building, fluctuating sea levels and temperatures. All these phenomena occur today but the rate of change seems to be occurring faster than the detectable past. Nature reserves are of course as susceptible to climate change as anywhere else. Liu *et al*. (2010) estimate that populations of at least 15% of the orchid species in a diverse region of southwestern China will be threatened with extinction over the next two centuries given projected climate changes. We already see a drying trend in some cloud forests of the world, including Costa Rica, raising real concerns for those species such as the hundreds of Neotropical *Lepanthes* that depend on cool, wet conditions (Nadkarni & Solano 2002; Olaya-Arenas *et al*. 2011). How orchids respond remains to be seen but it seems certain that the floras at any given site will not be the same as before.

Orchids as a group show evolutionary flexibility whereby diversification in the family is often related to habitat complexity and fragmentation. Orchids also show ecological resiliency with the capacity for recolonization after habitat destruction and recovery. For particular orchid species, the realization of these capacities likely depends upon dispersal from refugia (large or small), the severity of disturbance, effects of invasive species, and the natural history of the individual orchid species. Should refugia cease to exist, or habitat restoration becomes constrained, then recovery of orchid floras will not only be lethargic, but the floristic outcome may only superficially resemble the species composition and relative abundance patterns of the past. And whether changes are local or global, we can only hope that the ability of orchids to adapt or migrate will keep pace.

Coda. — There are few botanical institutions in tropical regions of high orchid diversity. Over a relatively short period of time, Lankester Botanical Garden has become one of those that have had a significant role in tropical orchid systematics and conservation, effectively promoting in-house research; facilitating studies at other institutions through collaborations and the development of the online resource, Epidendra; and fostering communication among botanists by publishing *Lankesteriana* and sponsoring scientific meetings. Indeed, I have had many influences in the development of the ideas contained herein, but articles in *Lankesteriana* did as much as any to help coalesce them.

Acknowledgements. I thank Stephen Kirby and Raymond Tremblay for fruitful discussions over the years that helped solidify some ideas contained here, though any blame falls squarely on my shoulders. I delivered a version of this essay at IV Andean Orchid Conservation Conference (Guayaquil, Ecuador, 2012), and I thank the organizers, especially Alec Pridgeon and José Portilla Andrade, for facilitating my participation. Further financial support was provided by CREST-CATEC (Elvira Cuevas, project director, National Science Foundation, USA, HRD-0734826) for which I am grateful.

Literature Cited

Ackerman, J.D. 1983a. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biol. J. Linn. Soc. 20: 301-314.

Ackerman, J.D. 1983b. On the evidence for a primitively epiphytic habit in orchids. Syst. Bot. 8: 474-477.

Ackerman, J.D. 1996. Caribbean Islands. Pages 59-61 in IUCN/SSC Orchid Specialist Group. Orchids – status survey and conservation action plan. IUCN, Gland Switzerland and Cambridge, UK

Ackerman, J.D. 2007. Invasive orchids: weeds we hate to love? Lankesteriana 7: 19-21.

Ackerman, J.D. & E.J. Meléndez-Ackerman. 2008. Orquídeas. Pages 189-246 in R. L. Joglar, ed. Biodiversidad de Puerto Rico: Agustín Stahl, Flora, Hongos. Serie de Historia Natural de Puerto Rico. La Editorial Universidad de Puerto Rico, San Juan.

Ackerman, J.D. & S. Moya. 1996. Hurricane aftermath: resiliency of an orchid-pollinator interaction in Puerto Rico. Carib. J. Sci. 32: 369-374.

Ackerman, J.D., J.C. Trejo Torres & Y. Crespo Chuy. 2007.

Orchids of the West Indies: predictability of diversity and endemism. J. Biogeogr. 34: 779-786.

Aide, T.M., M.L. Clark, H.R. Grau, D. López-Carr, M.A. Levy, D. Redo, M. Bonilla-Moheno, G. Riner, M.J. Andrade-Nuñez & M. Muñiz. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001-2010). Biotropica 45: 262-271.

Allen, C.D. & D.D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc. Nat. Acad. Sci. (USA) 95: 14839-14842.

Arditti, J. 1992. Fundamentals of orchid biology. John Wiley & Sons, New York.

Auler, A.S. & P.L. Smart. 2001. Late quaternary paleoclimate in semiarid northeastern Brazil from U-series dating of travertine and water-table speleothems. Quatern. Res. 55: 159-167.

Ballantyne, M. & C. Pickering. 2012. Ecotourism as a threatening process for wild orchids. J. Ecotourism 11: 34-47.

Bateman, R.M., P.M. Hollingsworth, J. Preston, Y.-B. Luo, A.M. Pridgeon & M.W. Chase. 2003. Molecular phylogenetics and evolution of Orchidinae and selected Habenariinae (Orchidaceae). Bot. J. Linn. Soc. 142: 1-40.

Beach, T., N. Dunning, S. Luzzadder-Bech, D.E. Cook & J. Lohse. 2006. Impacts of the ancient Maya on soils and soil erosion in the central Maya Lowlands. Catena 65: 166-178.

Benzing, D.H. 1986. The genesis of orchid diversity: emphasis on floral biology leads to misconceptions. Lindleyana 1: 73-89.

Bergman, E., J.D. Ackerman, J. Thompson & J.K. Zimmerman. 2006. Land use history affects the distribution of the saprophytic orchid *Wullschlaegelia* calcarata in Puerto Rico. Biotropica 38: 492-499.

Blanco, M.A. & G. Barboza. 2007. Pseudocopulation pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae). Ann. Bot. 95: 763-772.

Bogarín, D., F. Pupulin, C. Arrocha & J. Warner. 2013. Orchids without borders: studying the hotspot of Costa Rica and Panama. Lankesteriana 13: 13-26.

Cascante-Marín, A. & A. Nivia-Ruíz. 2013. Neotropical flowering epiphyte diversity: local composition and geographic affinities. Biodivers. Conserv. 22: 113-125.

Chase, M.W. 2001. Origin and biogeography of Orchidaceae. Pages 1-5. In A. Pridgeon, P. Cribb & F. Rasmussen, eds. Genera Orchidacearum. Vol. 2. Oxford University Press, Oxford.

Cribb, P. 1998. The genus *Paphiopedilum*. 2nd edition. Natural History Publications (Borneo), Kota Kinabalu, Malaysia.

De Boer, E.J., H. Hooghiemstra, F.B. Vincent Florens, C. Baider, S. Engels, V. Dakos, M. Blaauw & K.D. Bennett. 2013. Rapid succession of plant associations on the small oceanic island of Mauritius at the onset of the Holocene. Quatern. Sci. Rev. 68: 114-125.

Dixon, K.W., S.P. Kell, R.L. Barrett & P.J. Cribb, eds. 2003. Orchid conservation. Natural History Publications (Borneo), Kota Kinabalu, Malaysia.

Dodson, C.H. 2003. Why are there so many orchid species? Lankesteriana “No. 7” 3(2): 99-103.

Dressler, R.L. 1981. The orchids: natural history and classification. Harvard University Press, Cambridge, MA.

Gentry, A.H. & C.H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Gard.74: 205-233.

Govaerts, R., K. Kratochvil, G. Gerlach, G. Carr, P. Alrich, A.M. Pridgeon, J. Pfahl, M.A. Campacci, D. Holland Baptista, H. Tigges, J. Shaw, P. Cribb, A. George, K. Kreuz & J. Wood. 2010. World Checklist of Orchidaceae. Facilitated by the Royal Botanic Gardens, Kew. http://www.kew.org/wcsp/monocots/ accessed 24 June 2010.

Gradstein, S.R. 2008. Epiphytes of tropical montane forests – impact of deforestation and climate change. Pages 51-65. *In* S.R. Gradstein, J. Homeier & D. Gansert, eds. The tropical mountain forest – patterns and processes in a biodiversity hotspot. Universitätverlag Göttingen.

Grau, H.R., T.M. Aide, J.K. Zimmerman, J.R. Thomlinson, E. Helmer and X. Zou. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. Bioscience 53: 1159-1168.

Guo, Y.-Y., Y.-B. Luo, Z.-J. Liu & X.-Q. Wang. 2012. Evolution and biogeography of the slipper orchids: Eocene vicariance of the conduplicate genera in the Old and New World tropics. PLoS ONE 7: e38788. doi:10.1371/journal.pone.0038788

Gustafsson, A.L., C.F. Verola & A. Antonelli. 2010. Reassessing the temporal evolution of orchids with new fossils and a Bayesian relaxed clock, with implications for the diversification of the rare South American genus Hoffmannseggella (Orchidaceae:Epidendroideae). BMC Evol. Biol. 10: 177. doi10.1186/1471-2148-10-177

Hall, M.L., C. Robin, B. Beate, P. Mothes & M. Monzier. 1999. Tungurahua Volcano, Ecuador: structure, eruptive history and hazards. J. Volcanology Geothermal Res. 91: 1-21.

Hughes, C. & R. Eastwood. 2006. Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. Proc. Nat. Acad. Sci. USA 103: 10334–10339.

IUCN/SSC Orchid Specialist Group. 1996. Orchids – status survey and conservation action plan. IUCN, Gland Switzerland and Cambridge, UK

Karremans, A.P., F.T. Bakker, F. Pupulin, R. Solano-Gómez & M.J.M. Smulders. 2013. Phylogenetics of *Stelis* and closely related genera (Orchidaceae: Pleurothallidinae). Pl. Syst. Evol. 299: 151-176. DOI 10.1007/s00606-012-0712-7

Kelly, A.E. & M.L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proc. Nat. Acad. Sci. USA 105:11823-11826.

Kirby, S.H. 2007. Geological processes and orchid biogeography with applications to southeast Central America. Lankesteriana 7: 53-55.

Kirby, S.H. 2011. Active mountain building and the distribution of "core" Maxillariinae species in tropical Mexico and Central America. Lankesteriana 11: 275-291.

Koopowitz, H. 2001. Orchids and their conservation. Timber, Press, Portland, Oregon.

Ledru, M.-P., F.W. Cruz Jr., C. Riccomini, I. Karmann & L. Martin. 2005. Paleoclimate changes during the last 100,000 yr from a record in the Brazilian Atlantic rainforest region and interhemispheric comparison. Quatern. Res. 64: 444-450.

Light, M.H.S. & M. MacConaill. 2007. Effect of trampling on a terrestrial orchid environment. Lankesteriana 7: 294-298.

Liu, H., C.-L. Feng, Y.-B. Luo, B.-S. Chen, Z.-S. Wang & H.-Y. Gu. 2010. Potential challenges of climate change to orchid conservation in a wild orchid hotspot in Southwestern China. Bot. Rev.76: 174-192.

Losos, J.B. 2014. What Darwin got wrong. Chron. Higher Ed. http://chronicle.com/article/What-Darwin-Got-Wrong/144021/?key=TGxzdFc9YXRHZH8yYTtHYW4DO3I5ZRh1NX8ZYn9wbl9QFw%3D%3D

Lugo, A.E. 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers Ecol. Environ. 2: 265-273.

Martos, F., F. Munoz, T. Pailler, I. Kottke, C. Gonneau & M.-A. Selosse. 2012. The role of epiphytism in architecture and evolutionary constraint within mycorrhizal networks of tropical orchids. Mol. Ecol. 21: 5098-5109.

Migenis, L.E. & J.D. Ackerman. 1993. Orchid-phorophyte relationships in a forest watershed in Puerto Rico. J. Trop. Ecol. 9: 231-240.

Miranda, F.E. 1990. Brazilian Laelias – part III: section Parviflorae. Amer. Orchid Soc. Bull. 59: 462-472.

Morgan, J., C. Lana, A. Kearsley, B. Coles, C. Belcher, S. Montanari, E. Díaz-Martínez, A. Barbosa & V. Neumann. 2006. Analyses of shocked quartz at the global K-P boundary indicate an origin from a single, high-angle, oblique impact at Chicxulub. Earth and Planetary Sci. Lett. 251: 264-279.

Motomura, H., M.-A. Selosse, F. Martos A. Kagawa & T. Yukawa. 2010. Mycoheterotrophy evolved from mixotrophic ancestors: evidence in *Cymbidium* (Orchidaceae). Ann. Bot. 106: 573-581.

Mújica, E., J. Raventos, E. González & A. Bonet. 2013. Long-term hurricane effects on populations of two epiphytic orchid species from Guanahacabibes Peninsula, Cuba. Lankesteriana 13: 47-55.

Myers, N., R.A. Mittermeter, C.G. Mittermeter, G.A.B. da Fonseca & J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Nadkarni, N.M. & R. Solano. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia 131: 580-586.

Neubig, K.M., W.M. Whitten, N.H. Williams, M.A. Blanco, L. Endara, J.G. Burleigh, K. Silvera, J.C. Cushman & M.W. Chase. 2012. Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. Bot. J. Linn. Soc. 168: 117-146.

Nilsson, L.A. 1992. Orchid pollination biology. Trends Ecol. Evol. 7: 255-259.

Olaya-Arenas, P., E.J. Meléndez-Ackerman, M.E. Pérez & R. Tremblay. 2011. Demographic response by a small epiphytic orchid. Amer. J. Bot. 98: 2040-2048.

Otero, J.T. & N.S. Flanagan. 2006. Orchid diversity – beyond deception. Trends Ecol. Evol. 21: 64-65.

Papadopulos, A.S.T., M.P. Powell, F. Pupulin, J. Warner, J.A. Hawkins, N. Salamin, L. Chittka, N.H. Williams, W.M. Whitten, D. Loader, L.M. Valente, M.W. Chase & V. Savolainen. 2013. Convergent evolution of floral signals underlies the success of Neotropical orchids. Proc. Roy. Soc. B 280: 20130960. http://dx.doi.org/10.1098/rspb.2013.0960

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Ann. Rev. Ecol. Evol. Syst. 37: 637-669.

Partomihardjo, T. 2003. Colonisation of orchids on the Krakatau Islands. Teleopea 10:299-310.

Peakall, R., D. Ebert, J. Poldy, R.A. Barrow, W. Francke, C.C. Bower & F.P. Schiestl. 2010. Pollinator specificity, floral odour chemistry and phylogeny of Australian sexually deceptive orchids: implications for pollinator-driven speciation. New Phytol. 188: 437-450.

Phillips, R.D., K.W. Dixon & R. Peakall. 2012. Low population genetic differentiation in the Orchidaceae: implications for the diversification of the family. Mol. Ecol. 21: 5208-5220.

Pounds, J.A., M.P L. Fogden & J H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611-614.

Ramírez, S.R., B. Gravendeel, R.B. Singer, C.R. Marshall & N.E. Pierce. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature 448:

1042-1045. Doi10.1038/nature06039

Ramírez, S.R., T. Else, M.K. Fujiwara, G. Gerlach, B. Goldman-Huertas, N.D. Tsutsui & N.E. Pierce. 2011. Asynchronous diversification in a specialized plant-pollinator mutualism. Science 333: 1742-1746. doi: 10.1126/science.1209175

Roberts, R.C. 1942. Soil survey of Puerto Rico. Washington DC: U.S. Printing Office. USDA Series 1936., No. 8.

Sánchez-Cuervo, A.M., T.M. Aide, M.L. Clark & A. Etter. 2012. Land cover change in Colombia: surprising forest recovery trends between 2001 and 2010. PLoS One 8: e43943. doi:10.1371/journal.pone.0043943

Schiestl, F.P. & S. Dötterl. 2012. The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre-existing bias? Evolution 66: 2042-2055.

Soto Arenas, M.A., R. Solano Gómez & E. Hágsater. 2007. Risk of extinction and patterns of diversity loss in Mexican orchids. Lankesteriana 7: 114-121.

Stebbins, G.L. 1984. Mosaic evolution, mosaic selection and angiosperm phylogeny. Bot. J. Linn. Soc. 88: 159-164.

Thompson, J., N. Brokaw, J.K. Zimmerman, R.B. Waide, E.M. III, Everham, D.J. Lodge, C.M. Taylor, D. García-Montiel & M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. Ecol. Appl. 12: 1344-1363.

Thornton, I.W.B. 1997. Krakatau: the destruction and reassembly of an island ecosystem. Harvard University Press, Cambridge, Massachusetts.

Tremblay, R.L., J.D. Ackerman, J.K. Zimmerman & R.N. Calvo. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biol. J. Linn. Soc. 84: 1-54.

Tremblay, R.L., E. Meléndez-Ackerman & D. Kapan. 2006. Do epiphytic orchids behave as metapopulations? Evidence from colonization, extinction rates and asynchronous population dynamics. Biol. Conserv. 129: 70-81.

van der Pijl, L. & C.H. Dodson. 1966. Orchid flowers: their pollination and evolution. University of Miami Press, Coral Gables.

Wadsworth, F.H. 1950. Notes on the climax forest of Puerto Rico and their destruction and conservation prior to 1900. Caribb. Forester 11: 48-47.

LANKESTERIANA 13(3): 165—184. 2014.

INVITED PAPER*

FROM CUBA TO MOST OF THE NEOTROPIC: *HABENARIA BICORNIS* (ORCHIDACEAE) IS WIDESPREAD FROM MEXICO TO SOUTHEASTERN BRAZIL

João A. N. Batista[1,3], Karina Proite[1], Bruno M. Carvalho[1], Aline A. Vale[1]
& Leonardo P. Felix[2]

[1]Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, Pampulha, Belo Horizonte, Minas Gerais 31270-910, Brazil

[2]Departamento de Ciências Biológicas, Centro de Ciências Agrárias, Universidade Federal da Paraíba, Campus II, Areia, Paraíba 58397-000, Brazil

[5]Author for correspondence: janb@icb.ufmg.br

ABSTRACT. *Habenaria bicornis* was first described in 1835 from Cuba and has only been known from that country and from a few records in Panama from the 1920s. Here we show that *H. bicornis* and *H. goyazensis*, known from Brazil and Guyana, are conspecific and that the species is distributed from Mexico to southeastern Brazil. Niche modeling and collection data indicate that this species has a preference for wet lowland savannas and its distribution is predicted to include most of the Neotropics with suitable habitats. The molecular phylogenetic analyses based on DNA sequences from the nuclear internal transcribed spacer (ITS) region and part of the plastid *matK* gene placed *H. bicornis* in an isolated position near the base of the Neotropical clade, although with low support. In terms of its morphology, its relationships are likewise not clear as there are no evident similarities between *H. bicornis* and the basal subclades or any other Neotropical subclade. Cytogenetic analysis indicated a basic chromosome number of x=21, similar to other basal Neotropical species.

RESUMEN: *Habenaria bicornis* fue descrita por primera vez en 1835, para Cuba, y era conocida apenas para este país y unos pocos registros de Panamá, de 1920. En el presente estudio, demostramos que *H. bicornis* y *H. goyazensis*, esta última conocida para Brasil y Guiana, son específicas y la especie se distribuye desde México hasta el sudeste de Brasil. El modelado de nicho y la recolección de datos indican que esta especie posee una preferencia por sabanas húmedas de tierras bajas y es predicho que su distribución incluye gran parte del Neotrópico con hábitats favorables. Los análisis filogenéticos moleculares con secuencias del ADN nuclear (ITS) y plastidial (*matK*) ubicaron *H. bicornis* en una posición aislada próximo a la base del clado Neotropical, aunque con bajo soporte. En términos de su morfología, sus relaciones no están aclaradas, ya que no hay similitudes evidentes entre *H. bicornis* y los subclados básales o cualquier otro subclado Neotropical. Los análisis citogenéticos indican un número cromosómico básico de x=21, similar a las otras especies basales del Neotrópico.

KEY WORDS: Biogeography, cytogenetics, molecular phylogenetics, Orchidinae, taxonomy

Habenaria Willd. (Orchidinae, Orchideae, Orchidaceae) is a large genus of terrestrial orchids comprising approximately 881 species (Govaerts *et al.* 2013) distributed throughout tropical and subtropical regions of the Old and New Worlds (Pridgeon *et al.* 2001). In a synopsis of the New World species of the genus, Batista *et al.* (2011a) listed 298 taxa for the Neotropics. Brazil, with 163 taxa, and Mexico, with 79 species, are the major centers of diversity of this genus in the New World. Although some species are

---

* This contribution was prepared as part of the special edition of LANKESTERIANA that is dedicated to the commemoration of Lankester Botanical Garden´s 40th anniversary.

widely distributed throughout the American tropics and subtropics, most (69%) are restricted to a single country. Narrow endemics are few, however, and in many cases endemic taxa can represent obscure taxa or species known from a few collections or just the type material, so that their exact identity often remains unclear.

Studies of New World *Habenaria* and New World Orchidaceae have generally been undertaken on a piecemeal basis, and limited by geographic and political subdivisions. Floras have been published for several countries, but revisions on continental scales are few and have largely been limited to groups with small numbers of species. As a consequence, several species (especially those with broad distributions) have been described several times from different countries. An example of this situation is *H. trifida* Kunth, which is currently known from Mexico to northern Argentina but first described from Colombia and only later from Brazil, Venezuela, Mexico, Paraguay, and Costa Rica – and now comprises 21 synonyms (Batista *et al*. 2011b).

Habenaria bicornis Lindl. was described by Lindley (1835) based on a collection of Poeppig from Cuba. Several authors subsequently confirmed the record for Cuba (Richard 1850, Grisebach 1866, 1873, Kränzlin 1892, Cogniaux 1909, Ames 1910, Galé 1938, León & Schweinfurth 1946) and the several collections known from that country suggest that the species is relatively common there. In the 1920s, Ames (1922) recorded *H. bicornis* in Panama based on a single collection from the Canal Zone (*Pittier 6792*). Several other authors subsequently reported the species from Panama (Ames 1928, Williams 1946, 1956, Dressler 1980, 1993, D'Arcy 1987, Correa *et al*. 2004), but only one additional collection was made (*Powell 315*), with most workers simply quoting the original record without critical re-examinations of the identity of the specimen. Presence in Panama of a species previously known only from Cuba seemed curious, but no one investigated further the subject or revised the identity of the Panamanian specimens. In a synopsis of New World *Habenaria*, Batista *et al*. (2011a) noted that *H. bicornis* is similar to *H. goyazensis* Cogn. and that the identities of the two species should be assessed in more detail. *Habenaria goyazensis* was described by Cogniaux (1893) based on a collection from central Brazil (*Gardner 3995*) and is currently known there from the Brazilian states of Goiás, Minas Gerais, Mato Grosso, Pará, Pernambuco, Sergipe, and Tocantins, as well as from Guyana (Batista *et al*. 2008, 2011a).

Here we investigated here the morphological and taxonomic relationships between *H. bicornis* and *H. goyazensis* based on examinations of the respective type material and additional herbarium collections. Based on a previous molecular phylogenetic analysis of New World *Habenaria* (Batista *et al*. 2013), we also assessed the phylogenetic relationships of *H. bicornis*, performed niche modeling analyses to infer the potential distribution of the species, and performed cytogenetic analyses to determine its chromosome number and CMA/DAPI banding patterns. This paper was prepared as part of the commemorations for the 40th anniversary of the Lankester Botanical Garden.

Material and Methods

Taxonomic analyses. – Descriptions were based on examination of pickled and herbarium material. Floral details were examined under a stereoscopic microscope and measured using a digital caliper. Gynostemium images of *H. bicornis* were done with a digital camera DFC295 coupled to a stereoscopic microscope (Leica M205C) and assembled using Leica Application Suite v. 3.8.0 software. Data relating to flowering times, habitat, and distribution were obtained from the labels of herbarium specimens. A total of 48 specimens and digital images (photographs) of *H. bicornis* were examined from the following herbaria: A, AMES, BHCB, BM, BR, CEN, EAN, EAP, G, GH, HB, IPA, K, MO, NY, OXF, P, RENZ, S, SP, US, and W. In addition to these herbaria, material of morphologically similar species were examined from: ALCB, B, CEPEC, CESJ, CTES,ESA, HBG, HRB, HRCB, HUEFS, IBGE, ICN, L, LP, M, MBM, MBML, OUPR, PMSP, R, RB, SI, SPF, UB, U, and UEC. Descriptive terminology is based on Stearn (1992) and Simpson (2006).

Taxon sampling for phylogenetic analyses. – The datasets for the phylogenetic analyses consisted of the combined ITS and partial *matK* DNA sequences of 208 terminals of 157 Neotropical *Habenaria* species, corresponding to 52% of the total number

Table 1. Voucher information and GenBank accessions for the new sequences produced for this work.

Taxon	**Voucher**	**Origin**	**ITS**	***matK***
Habenaria bicornis Lindl.	L.P. Felix 10803 (EAN)	Brazil: Paraíba	KF998087	KF998088

of species known from the Neotropics (Batista *et al.* 2011a, 2011b); four African *Habenaria* species and *Gennaria diphylla* Parl. were was used as the functional outgroup. This dataset is basically the same used to infer phylogenetic relationships of New World *Habenaria* by Batista *et al.* (2013), but including *Habenaria bicornis* and excluding most of the Old World taxa. Voucher information, geographic origins, and GenBank accession numbers can be found in Batista *et al.* (2013); information concerning the newly sequenced accessions is provided in Table 1.

Molecular markers. – Nucleotide sequences from one nuclear (ITS) and one plastid (*matK*) genome regions were analyzed. The ITS region consisted of the 3' and 5' ends of the 18S and 26S ribosomal RNA genes, respectively, the internal transcribed spacers (ITS1 and ITS2), and the intervening 5.8S gene of the nuclear ribosomal multigene family. Amplifications of this region were performed using primers 17SE and 26SE (Sun *et al.* 1994). We used an internal fragment of approximately 630 bp of the *matK* gene, amplified with primers matK-F2 and matK-R2 (Batista *et al.* 2013), which approximately corresponds to the region widely used for barcoding land plants (Chase *et al*. 2007). This fragment is the most variable region of the gene in several orchid groups (e.g., Whitten *et al*. 2000). DNA extraction, amplification, and sequencing were carried out following standard protocols, as described by Batista *et al.* (2013). Bidirectional sequence reads were obtained for all of the DNA regions, and the resulting sequences were edited and assembled using the Staden Package software (Bonfield *et al.* 1995). The edited sequences were aligned with MUSCLE (Edgar 2004), and the resulting alignments were manually adjusted using MEGA4 software (Tamura *et al.* 2007).

Phylogenetic analyses. – The data were analyzed by means of parsimony and Bayesian inference. Searches were performed only with a combined matrix, because no cases of strongly supported incongruence were detected in our previous analyses with the same datasets (Batista *et al.* 2013). Phylogenetic analyses using maximum parsimony (MP) were performed using PAUP* version 4 (Swofford 2002) with Fitch parsimony (equal weights, unordered characters; Fitch 1971) as the optimality criterion. Each search consisted of 1,000 replicates of random taxon additions, with branch swapping using the tree-bisection and reconnection (TBR) algorithm, saving ≤10 trees per replicate to avoid extensive swapping on suboptimal islands. Internal support was evaluated by character bootstrapping (Felsenstein 1985) using 1,000 replicates, simple addition, and TBR branch swapping, saving ≤10 trees per replicate. For bootstrap support levels, we considered bootstrap percentages (BPs) of 50–70% as weak, 71–85% as moderate, and >85% as strong (Kress *et al*. 2002).

Bayesian analysis was conducted using MrBayes v. 3.1.2 (Ronquist *et al*. 2005), treating each DNA region as a separate partition. An evolutionary model for each DNA region was selected using the Akaike Information Criterion (AIC) in MrModeltest 2 (Nylander 2004). Each analysis consisted of two independent runs, each with four chains, for 5,000,000 generations, sampling one tree every 1000 generations. To improve chain swapping, the temperature parameter for heating the chains was lowered to 0.01 in the combined analysis. Convergence between the runs was evaluated using the average standard deviation of split frequencies (<0.01). After discarding the first 50% of the trees as the burn-in, the remaining trees were used to assess topology and posterior probabilities (PPs) in a majority-rule consensus. PPs in Bayesian analysis are not directly comparable to BPs, being generally much higher (Erixon *et al.* 2003). Therefore, we used criteria similar to a standard statistical test, considering groups with PPs >0.95 as strongly supported, groups with PPs ranging from 0.90–0.95 as moderately supported, and groups with PPs <0.90 as weakly supported.

Niche modeling. – We assembled a database of 40 taxonomically depurated, georeferenced unique occurrence records, based on revision of specimens from 22 herbaria (see Taxonomic analyses, earlier). The geographic coordinates were plotted using ESRI ArcGIS 9 software. The extent of occurrence (EOO) was calculated by tracing a minimum polygon, with angles exceeding 180° and containing all points of occurrence (IUCN 2010). The environmental variables were extracted from the database in Worldclim (Hijmans *et al.* 2005) at a spatial resolution of 0.98 km. Niche model was generated using Maxent version 3.3.2 (Phillips *et al*. 2006, Sérgio *et al*. 2007) under the default values. The threshold was determined to turn the probability model into a model of presence and absence designed to distinguish appropriate and inappropriate areas for *H. bicornis*. We adopted the Lowest Presence Threshold (LPT) method, which is suitable for guiding field studies whose main purpose is to identify unknown distribution areas and to find new populations (Pearson *et al*. 2007). GIS techniques were applied (ESRI ArcGIS 9.2) for the visualization of modeling results and a presence and absence value of 0.15 was adopted (LPT) to view the predicted area. The model was evaluated based on the jackknife method developed by Pearson *et al*. (2007).

CMA/DAPI banding and FISH (fluorescent in situ hybridization). – Root tips from specimen L.P Felix 10803 were pretreated with 0.002 M of 8-hydroxyquinoline for 24 h at 10 ºC and fixed in Carnoy's solution. CMA/DAPI banding and FISH procedures were performed according to Souza *et al.* (2012). Fixed root tips were washed in distilled water and digested in a 2% (w/v) cellulase (Onozuka)/20% (v/v) pectinase (Sigma) solution at 37 ºC for 120 min and macerated in a drop of 45% acetic acid; the coverslip was later removed in liquid nitrogen. The CMA/DAPI double-staining technique was used for fluorochrome banding. Slides were aged for 3 days, stained with CMA (0.1 mg mL^{-1}) for 60 min, re-stained with DAPI (1 µg mL^{-1}) for 30 min, mounted in glycerol:McIlvaine buffer pH 7.0 (1:1), and subsequently aged for 3 days before analysis in an epifluorescence Leica DMLB microscope. Images were captured with a Cohu CCD video camera using Leica QFISH software, and were subsequently edited in Adobe Photoshop CS3 version 10.0. The rDNA sites were localized using 5S rDNA from *Lotus japonicus* (Regel) K.Larsen labeled with Cy3–dUTP (Amersham) and 45S rDNA from *Arabidopsis thaliana* (L.) Heynh. labeled with digoxigenin–11–dUTP as probes. Labeling was performed by nick translation. The 45S rDNA probe was detected with sheep anti-digoxigenin FITC conjugate (Roche) and amplified with rabbit anti-sheep FITC conjugate (Dako). The hybridization mixture contained 50% formamide (v/v), 10% dextran sulfate (w/v), 2× SSC, and 5 ng/µL of each probe. The slides were denatured at 75 oC for 3 min. Stringent washes were performed, reaching a final stringency of approximately 76%. Images of the best cells were captured as previously described.

Results and discussion

Taxonomic and morphological analyses. – Examination and comparison of the type specimens and several other collections of *H. bicornis* and *H. goyazensis* (see list of the materials examined) revealed that the two concepts are conspecific, sharing the following distinctive characters: well-developed, patent, lanceolate leaves up to 28 cm long and 2.5 cm wide; medium-sized flowers (dorsal sepal 4–8 mm long), anterior petal segment longer than the posterior segment; and spur 2.5–4.6 cm long, being about 1.3–2.1 times as long as the pedicellate ovary (Fig. 1 and Table 2). In terms of the overall morphology of the flowers, *Habenaria bicornis* shares some similar characters with, and has been mistaken for, other species such as *H. caldensis* Kraenzl. and *H. exaltata* Barb.Rodr. (Fig. 2) that also have a spur approximately twice the size of the pedicellate ovary

Right, FIGURE 1. Floral and vegetative morphology of *Habenaria bicornis* and similar species. From left to righ on each row: lateral view of ovary, spur and gynostemium, dissected perianth, and habit. *Habenaria bicornis*. A — *Batista 683*, CEN. B — *Santos et al. 2422*, CEN. C — *Pastore 1452*, BHCB. *Habenaria caldensis*. D — *Batista et al. 1382*, CEN. E — *Batista 2415*, BHCB. F — *Borba 102*, BHCB. G — *Munhoz & Martins 94*, BHCB. *Habenaria exaltata*. H, I — *Batista 2798*, BHCB. J — *Batista 2520*, BHCB. *Habenaria rodeiensis*. K, M — *Batista & Peixoto 3273*, BHCB. L — *Mota 2824*, BHCB. Scales = 1 cm, for ovary, spur, gynostemium, and dissected perianth; 5 cm for habit.

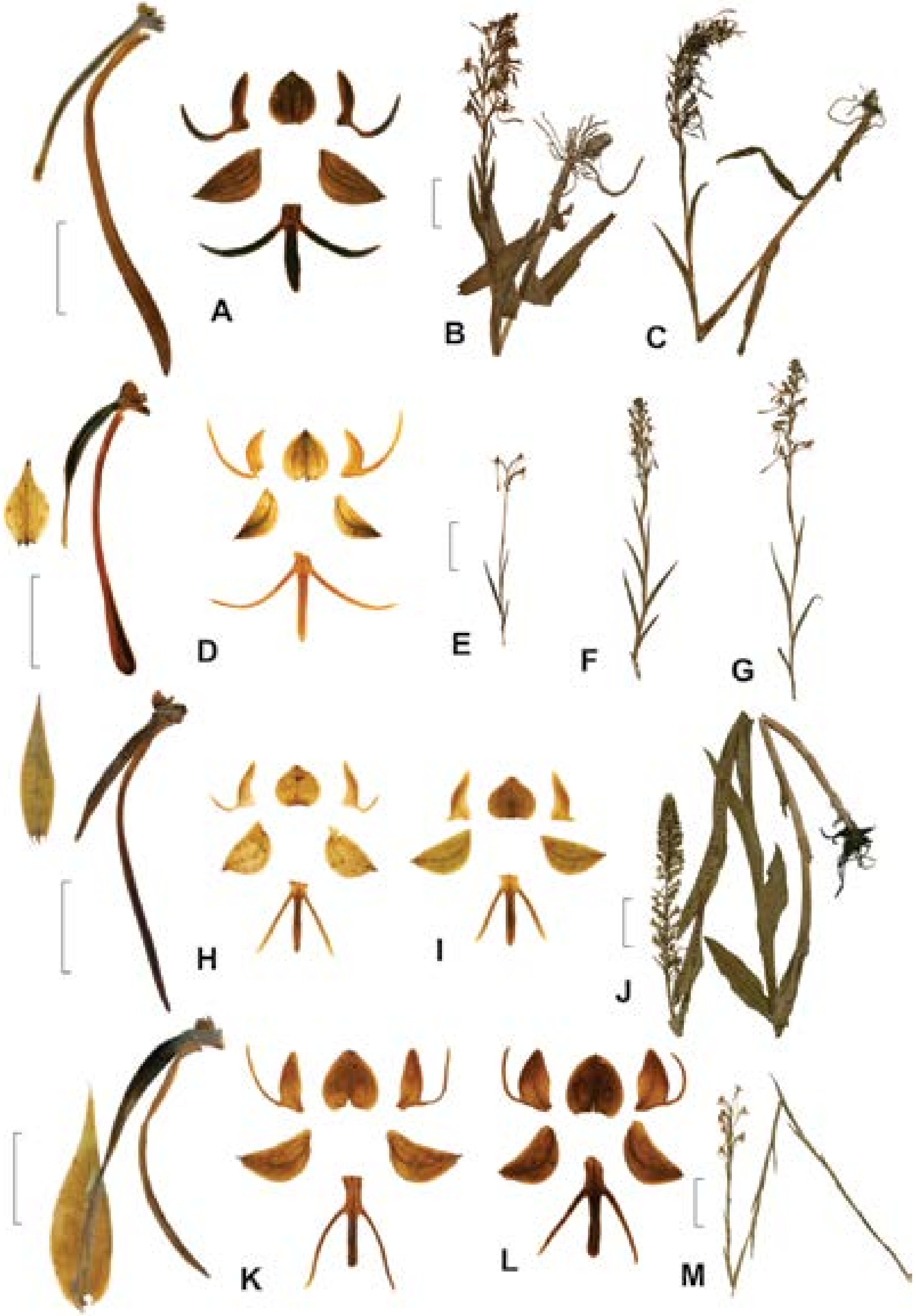

A
B
C
D
E
F
G
H
I
J
K
L
M

TABLE 2. Diagnostic characters comparing *H. bicornis* and morphologically similar species. Abbreviations for the Brazilian states are: BA, Bahia; DF, Distrito Federal; ES, Espirito Santo; GO, Goiás; MG, Minas Gerais; MT, Mato Grosso; PA, Pará; PB, Paraíba; PE, Pernambuco; PR, Paraná; RJ, Rio de Janeiro; RS, Rio Grande do Sul, SE, Sergipe; SP, São Paulo; TO, Tocantins.

	H. bicornis	***H. caldensis***	***H. exaltata***	***H. rodeiensis***
Leaves length × width (cm)	13–24(28) × (0.8)1.1–2(2.5)	5–12(16) × 0.3–0.9(1.4)	8.5–28 × 1.5–3.5	5–12 × 0.6–1.6
Dorsal sepal length × width (mm)	4–8 × 4.5–6(8)	5–7× 4.5–6	3.7–5.3 × 3.8–5.8	4.5–7× 4–6
Lateral sepals length × width (mm)	6.5–9.5 × 3–5	6.2–8.8 × 2.6–3.8	4.7–7.8 × 2.3–4.4	5.5–8 × 2.5–3
Corola color	base white, segments green	white throughout	base whitish, segments green	base white, segments light green to whitish
Posterior petal segment length × width (mm)	4.6–7.1 × 1.7–1.85	4.8–6 × 1.3–1.8	3.7–5.7 × 1–1.8	4.5–7.5 × 2–3.5
Anterior petal segment length (mm)	6.8–8.8	8–13	1.2–4.4	4.5–6(7)
Anterior petal segment length relative to posterior segment	1.3–1.5 times as long	1.6–2.2 times as long	0.2–1 times as long	1–1.2 times as long
Ovary length (mm)	13–28	10–14	11–15	12–16
Pedicel length (mm)	2.3–6	5–8	1.5–4.4	18–28
Spur length (mm)	25–46	32–41	28–35	28–36
Spur size relative to the pedicelate ovary	1.3–2.1 times as long	1.6–2.3 times as long	1.5–1.8 times as long	0.9–1.2 times as long
Spur position relative to floral bracts	free from the bracts	free from the bracts	free from the bracts	placed between the bracts
Spur	clavate	clavate	linear	linear
Spur apex	subacute to acute	rounded	acute	acute
Hemipollinaria	separated	united	separated	united
Rostellum midlobe apex	obtuse, placed between the anther loci	acute, projected beyond the anther loci	obtuse, placed between the anther loci	subacute, projected beyond the anther loci
Distribution	Mexico, Guatemala, Honduras, Panama, Cuba, Venezuela, Guyana and Brazil (PA, PB, PE, SE, GO, MT, TO, MG)	Brazil (BA, GO, MG)	Brazil (MG, PR, RS, SP) and Paraguay	Brazil (BA, DF, ES, GO, MG, MT, PR, RJ, SP), Paraguay and Peru*

*The records of *H. rodeiensis* from northern South America and Central America in Belize, Costa Rica and French Guiana need confirmation because this species is remarkably similar to *H. longipedicellata*, *H. lehmanniana* Kraenzl., and *H. ernestii* Schltr. That are known from northern Brazil or northern South America, and the separations between them are not clear.

(Fig. 1, and Table 2). However, *H. caldensis* differs in the smaller plants with smaller leaves, a completely white corolla, anterior petal segment 1.6–2.2 times as long as the posterior segment, and rounded spur apex. On the other hand, *H. exaltata* is distinguished from *H. bicornis* by its shorter anterior petal segment (1.2–4.4 mm long), which is about 0.2–1 times as long as the posterior segment, and the spur linear throughout (Figs. 1, 2; Table 2). Other differences are found in the morphology of the gynostemium: in *H. bicornis* the midlobe apex of the rostellum is obtuse, placed between the anther loci and the hemipollinaria

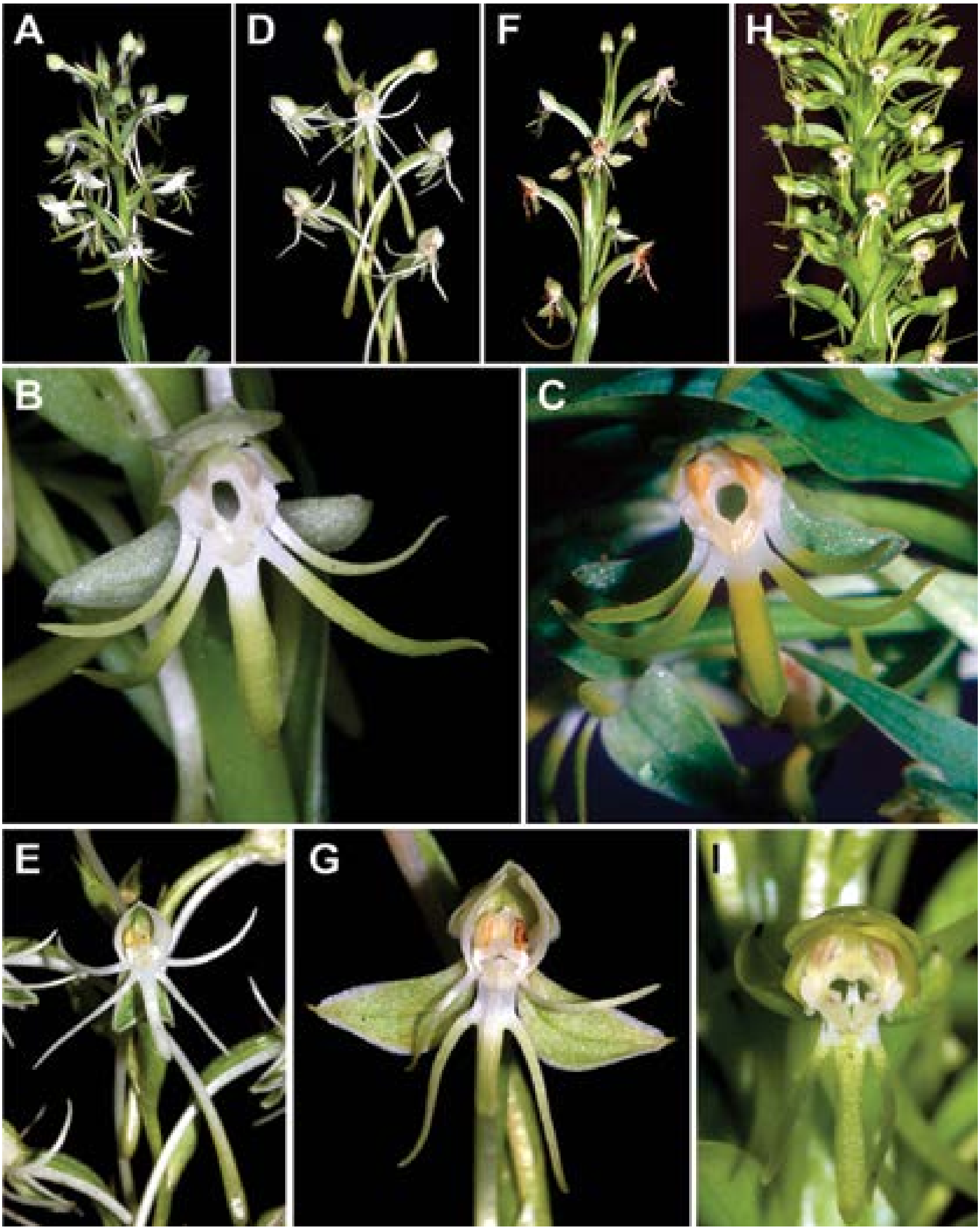


Figure 2. Inflorescences and flower morphology of *Habenaria bicornis* and similar species. *Habenaria bicornis*. A — Inflorescence. B — Flower, both from *Felix 10803*, EAN. C — Flower, from *Batista 683*, CEN. *Habenaria caldensis*. D — Inflorescence, from *Batista 2633*, BHCB. E — Flower, from *Batista 2621*, BHCB. *Habenaria rodeiensis*. F — Inflorescence. G — Flower, both from *Batista & Peixoto 3273*, BHCB. *Habenaria exaltata*. H — Inflorescence. I — Flower, both from *Batista et al. 2520*, BHCB.

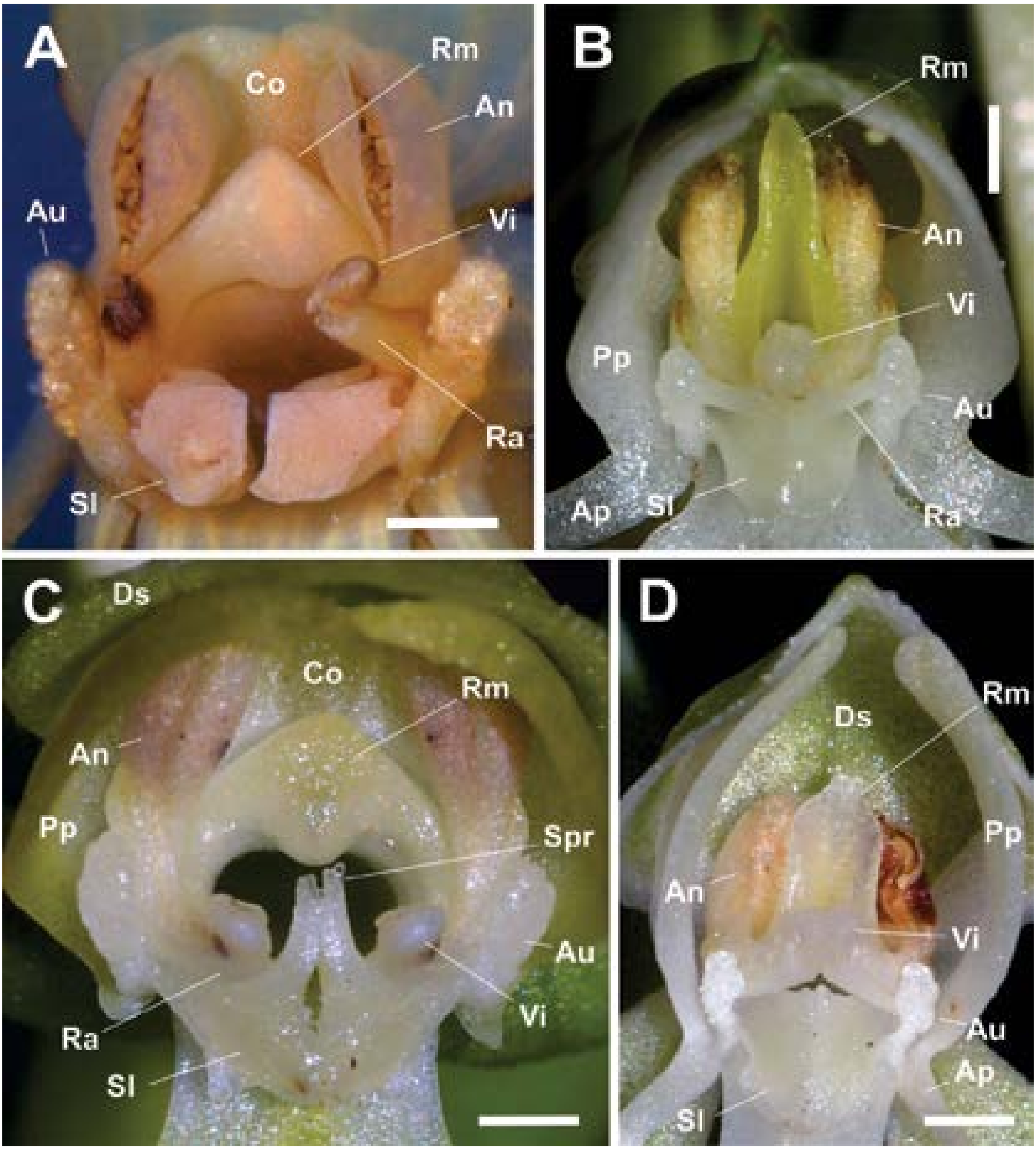


FIGURE 3. Gynostemium morphology. A — *Habenaria bicornis*, from *Batista et al. 683*, CEN. B — *Habenaria caldensis*, from *Batista 2621*, BHCB. C — *Habenaria exaltata*, from *Batista et al. 2520*, BHCB. D — *Habenaria rodeiensis*, from *Batista & Peixoto 3273*, BHCB. Scale bars A = 2 mm; B-D = 1 mm. Ac = anther canals; An = anther; Ap = anterior petal lobe; Au = auricules; Co = connective; Ds = dorsal sepal; Pe = petal; Pg = pollen grains; Pp = posterior petal lobe; Ra = rostellum arms; Rm = rostellum midlobe; Sp = stigmatic lobes; Spr = stigmatic projections; Vi = viscidium.

are separated, whereas in *H. caldensis* the rostellum midlobe apex is acute, projected beyond the anther loci, and the hemipollinaria are united (Fig. 3). In *H. exaltata* the stigma lobes have a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures (Fig. 3), which is a very distinctive character not found in any of the other species mentioned above. *Habenaria bicornis* has also been confused with *H. rodeiensis* Barb. Rodr. However, the leaves of the latter are smaller and more appressed to the stem, the pedicel is about the same size or longer than the ovary, the spur is linear throughout and usually covered by the bracts, the posterior segment of the petals is wider (Fig. 1; Table 2), and the hemipollinaria are united by the viscidia (Fig. 3). Further differences between *H. bicornis* and the species mentioned above are outlined in the key below and in Table 2.

With few exceptions, the identification of specimens of *H. bicornis* has been straightforward. This species was previously only known from Cuba, and is very distinct from other Cuban species of *Habenaria*. The identity of *H. goyazensis* and its taxonomic history, on the other hand, has been confusing because each taxonomist who examined material of the species (Cogniaux 1893, Kränzlin 1911, Hoehne 1940, Pabst & Dungs 1975, Snuverink & Westra 1983, Renz 1992) misidentified it or applied that name to other species. Lindley was apparently the first to examine collections of *H. goyazensis* because there is a sheet in his herbarium (K-L) with drawings of a plant and a flower (Fig. 4) of the type collection (*Gardner 3995*), but he apparently never assigned a name to this material. There is also a duplicate of the type collection (W-R 51336) at the Reichenbach herbarium (W-R) and another sheet in the same herbarium (W-R 54022) bearing a sketch of a flower from the type made by Reichenbach (Fig. 4), as well as a reproduction of Lindley's drawings at K-L. Curiously, the two major orchid taxonomists of the 19th century examined collection *Gardner 3995* in detail (judging from the illustrations they drew; Fig. 4), but neither reached a conclusion about its identity.

For his description of *H. goyazensis*, Cogniaux (1893) apparently did not examine duplicates of the type material nor the illustrations located at K-L and W-R, as his protologue only mentions material from B and G. Cogniaux's herbarium, now in BR, holds a fragment of the type collection of *H. goyazensis* as well as a complete specimen of the species (*Pohl s.n.*), although the latter is misidentified as *H. sartor* Lindl. Kränzlin (1911) examined two collections of *H. goyazensis* from Mato Grosso, Brazil, but identified one as *H. exaltata* (*Lindman 2765*) and the other as *H. caldensis* (*Lindman 2791½*). Hoehne (1940) examined and correctly identified the collection *Pickel 3615*, which is *H. goyazensis*, but his concept of the species was equivocal, as he used the same name for another species, currently known as *H. tamanduensis* Schltr. Pabst (Pabst & Dungs 1975) apparently only examined one collection of the species (*Macedo 1695*), which he identified as *H. caldensis*, using the name *H. goyazensis* for several other species (including *H. caldensis*, *H. dusenii* Schltr., *H. glaucophylla* Barb. Rodr., *H. longipedicellata* Hoehne, *H. macilenta* [Lindl.] Rchb.f., and *H. rodeiensis*). Other extra-Brazilian South American collections of *H. goyazensis* remained indeterminate or were more recently identified as *H. caldensis* by Snuverink & Westra (1983) and Renz (1992).

Excluding the material from Panama, other Central American and Mexican specimens of *H. bicornis* remained indeterminate or received disparate identifications (such as *H. bractescens* Lindl. or *H. jaliscana* S. Watson). Ames (1922, 1928) was the only taxonomist able to correctly identify extra-Cuban specimens of *H. bicornis*; probably because he had personally examined and correctly identified several specimens from Cuba.

Phylogenetic analyses. – The matrix with the combined ITS and partial *matK* gene consisted of 1372 aligned characters, of which 304 (22%) were parsimony-informative. The parsimony analysis retained a total of 5150 most parsimonious trees with a tree length of 935 steps, a consistency index (CI) of 0.65, and a retention index (RI) of 0.85. The strict consensus of 5150 trees was for the most congruent with the Bayesian majority-rule consensus tree, but because the latter was more fully resolved and had stronger overall support it was chosen for presentation here (Fig. 5). The relationships recovered were similar to those of our previous molecular phylogenetic study (Batista *et al.* 2013), with the New World *Habenaria* species forming a well-supported monophyletic group (1.00 PP, 87% BS, Fig. 5) that was sister to the African species *H. tridens* Lindl. (1.00 PP, 100% BS). Within the New World clade, several well-supported subclades were recovered (Fig. 5) that corresponded to the same subclades identified in our previous analyses (Batista *et al.* 2013). *Habenaria bicornis* formed a polytomy (0.75 PP) with a clade formed by subclades 2 and 3 and another formed by subclades 4

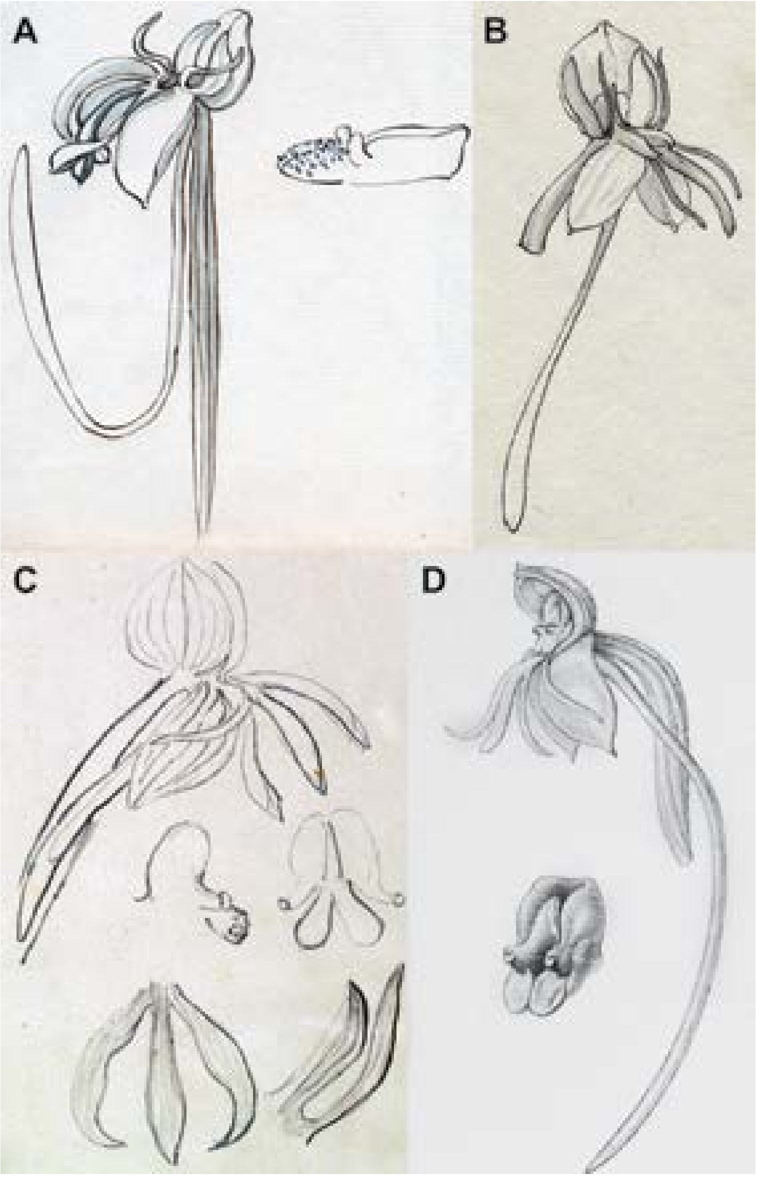
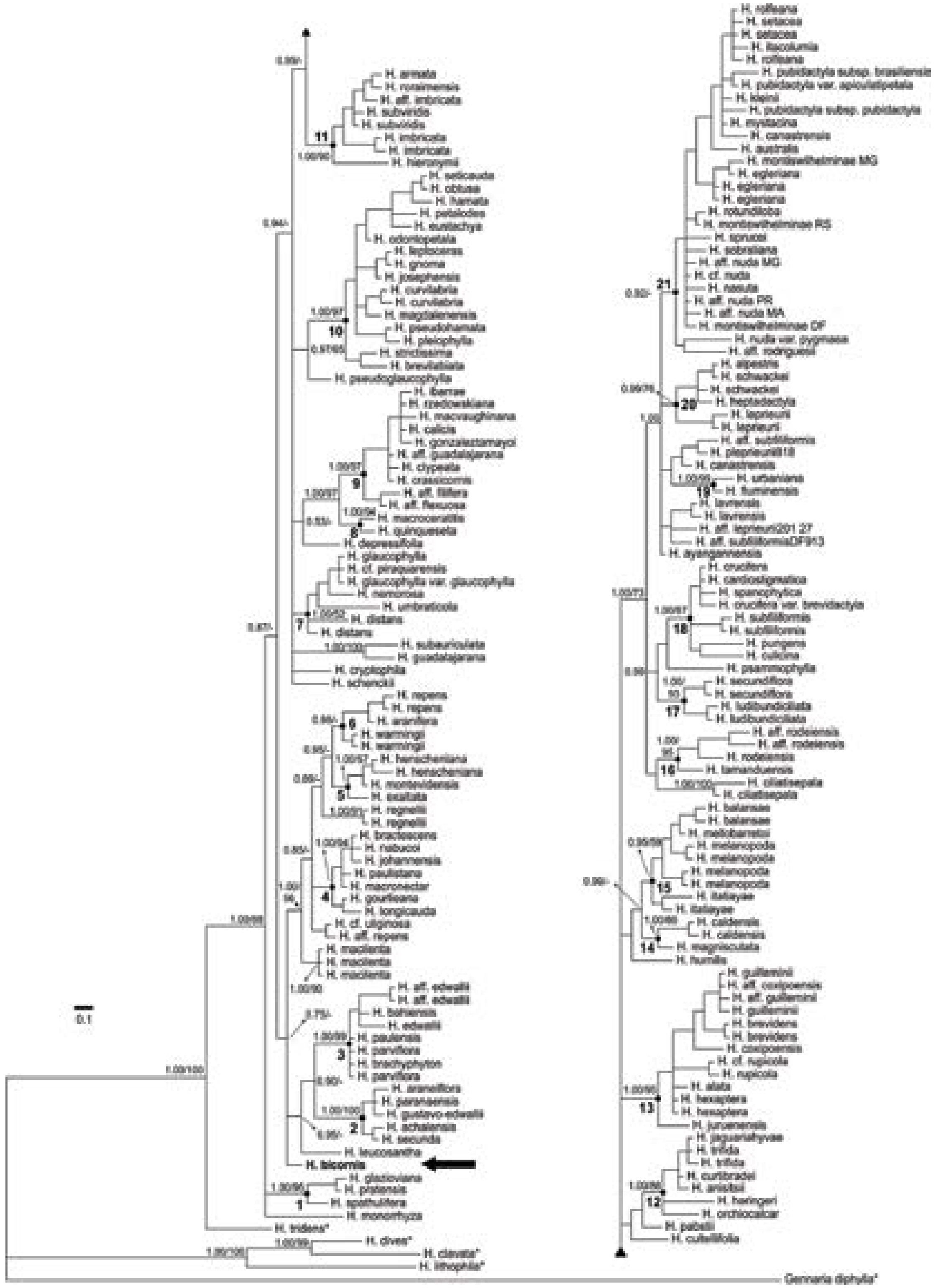


FIGURE 4. Historical illustrations of *Habenaria bicornis* and *H. goyazensis*. A — *Habenaria bicornis*. Lindley's original drawing of the species based on the holotype: *E.F. Poeppig s.n.* (K-L 000463128). B — *Habenaria goyazensis*. Lindley's drawing of the type material based on *G. Gardner 3995*(K-L 000363784). C — *Habenaria goyazensis*. Reichenbach's drawing of the type material (*Gardner 3995*), probably from W-R 51336. D — *Habenaria goyazensis*. Drawing published by Kränzlin (1911) based on *Lindman 2791 ½* (S 06-6545). A and B reproduced with the permission of the Royal Botanic Gardens, Kew. C provided by the National History Museum, Vienna.

Right, FIGURE 5. Bayesian majority-rule consensus tree of the combined ITS and *matK* (partial) datasets. Numbers next to the nodes represent the posterior probabilities from the Bayesian analysis (PPs) and bootstrap values from the parsimony analysis (PP/MP). Bootstrap values ≤50% are shown by a dash (-). Only values of the major clades are shown. Neotropical subgroups are numbered according to Batista et al. (2013). Old World taxa are indicated by an asterisk (*). The generic name for all *Habenaria* species is abbreviated. *Habenaria bicornis* is highlighted in bold and indicated by an arrow.


0.99/-
H. armata
H. roraimensis
H. aff. imbricata
H. subviridis
H. subviridis
11
H. imbricata
H. imbricata
1.00/90
H. hieronymi
0.94/-
H. seticauda
H. obtusa
H. hamata
H. petalodes
H. eustachya
H. odontopetala
H. leptoceras
H. gnoma
H. josephensis
H. curvilabria
H. curvilabria
H. magdalenensis
1.00/97
10
H. pseudohamata
H. pleiophylla
0.97/65
H. strictissima
H. brevilabiata
H. pseudoglaucophylla
H. ibarrae
H. rzedowskiana
H. macvaughiana
H. calicis
H. gonzaleztamayoi
H. aff. guadalajarana
H. clypeata
H. crassicornis
1.00/97
9
1.00/97
H. aff. filifera
H. aff. flexuosa
0.53/-
1.00/94
H. macroceratitis
8
H. quinquiseta
H. depressifolia
H. glaucophylla
H. cf. piraquarensis
H. glaucophylla var. glaucophylla
H. nemorosa
H. umbraticola
1.00/52
H. distans
7
H. distans
0.87/-
1.00/100
H. subauriculata
H. guadalajarana
H. cryptophila
H. schenckii
H. repens
H. repens
0.99/-
6
H. araneiflora
H. warmingii
H. warmingii
0.95/-
1.00/97
H. henscheniana
H. henscheniana
0.99/-
H. montevidensis
5
H. exaltata
1.00/91
H. regnellii
H. regnellii
0.95/-
1.00/94
H. bractescens
H. nabucoi
H. johannensis
H. paulistana
1.00/96
H. macronectar
4
H. gourlieana
H. longicauda
1.00/98
H. cf. uliginosa
H. aff. repens
H. macilenta
H. macilenta
H. macilenta
1.00/90
0.1
H. aff. edwallii
H. aff. edwallii
0.75/-
H. bahiensis
H. edwallii
1.00/99
H. paulensis
3
H. parviflora
H. trachyphyton
H. parviflora
1.00/100
0.90/-
H. araneiflora
H. paranaensis
1.00/100
H. gustavo-edwallii
2
H. achalensis
0.95/-
H. secunda
H. leucosantha
H. bicornis
1.00/95
H. glazioviana
H. pratensis
1
H. spathulifera
H. monorrhyza
H. tridens*
1.00/100
1.00/99
H. dives*
H. clavata*
H. lithophila*
Gennaria diphylla*
H. rolfeana
H. setacea
H. setacea
H. itacolumia
H. rolfeana
H. pubidactyla subsp. brasiliensis
H. pubidactyla var. apiculatipetala
H. kleinii
H. pubidactyla subsp. pubidactyla
H. mystacina
H. canastrensis
H. australis
H. montiswilhelminae MG
H. egleriana
H. egleriana
H. egleriana
H. rotundiloba
H. montiswilhelminae RS
H. sprucei
H. sobraliana
H. aff. nuda MG
H. cf. nuda
0.92/-
21
H. nasuta
H. aff. nuda PR
H. aff. nuda MA
H. montiswilhelminae DF
H. nuda var. pygmaea
H. aff. rodriguesii
H. alpestris
H. schwackei
H. schwackei
0.99/76
20
H. heptadactyla
1.00/-
H. leprieurii
H. leprieurii
H. aff. subfiliformis
H. pleprieurii818
H. canastrensis
1.00/99
H. urbaniana
19
H. fluminensis
H. lavrensis
H. lavrensis
H. aff. leprieurii201 27
H. aff. subfiliformisDF913
H. ayangannensis
H. crucifera
H. cantiostigmatica
H. spanophytica
1.00/72
H. crucifera var. brevidactyla
1.00/87
H. subfiliformis
18
H. subfiliformis
H. pungens
H. culicina
H. psammophylla
0.90/-
1.00/93
H. secundiflora
H. secundiflora
17
H. ludibundiciliata
H. ludibundiciliata
1.00/95
H. aff. rodeiensis
H. aff. rodeiensis
H. rodeiensis
16
H. tamanduensis
1.00/100
H. ciliatisepala
H. ciliatisepala
H. balansae
H. balansae
H. mellobarretoi
0.95/59
H. melanopoda
H. melanopoda
H. melanopoda
0.99/-
H. melanopoda
15
H. itatiayae
H. itatiayae
1.00/80
H. caldensis
H. caldensis
14
H. magniscutata
H. humilis
H. guilleminii
H. aff. coxipoensis
H. aff. guilleminii
H. guilleminii
H. brevidens
H. brevidens
H. coxipoensis
H. cf. rupicola
H. rupicola
1.00/90
H. alata
H. hexaptera
13
H. hexaptera
H. juruenensis
H. jaguariahyvae
H. trifida
H. trifida
H. curtibradei
H. arisitoi
1.00/86
H. haringeri
12
H. orchiocalcar
H. pabstii
H. cultellifolia

to 6. In the strict consensus of the parsimony analysis this node collapsed and *H. bicornis* was placed in a polytomy near the base of the Neotropical clade.

In terms of infrageneric classifications, Kränzlin (1892, 1901) placed *H. bicornis* in sect. *Macroceratitae* Kraenzl., while Cogniaux (1893) and Kränzlin (1901) placed *H. goyazensis* in sect. *Pentadactylae* Kraenzl. These classifications are clearly equivocal because *H. bicornis* and *H. goyazensis* do not match the morphological characters of the corresponding sections, and also because all Neotropical sections of the genus are polyphyletic or paraphyletic (Batista *et al*. 2013).

The morphological relationships of *H. bicornis* with other Neotropical species or subclades are likewise unclear because *Habenaria bicornis* is morphologically distinct from any of the basal subclades (Fig. 5, subclades 2 to 6) and any other Neotropical subclade.

Niche modeling. – The potential distribution of *H. bicornis* as modeled with Maxent using the threshold (LPT) value of 0.151 as the upper limit is shown in figure 6. The hit ratio generated by this model was 93%. The potential geographic distribution of the species extends from the Atlantic coast of the state of VeraCruz in Mexico, southwards to the coast of Santa Catarina State in southern Brazil, and eastwards to the Bahamas, northeastern Brazil, and the Guyanas. The bioclimatic variables that contributed most to the model were mean monthly diurnal temperature ranges (maximum temperature minus minimum temperature), precipitation seasonality, and annual temperature range (maximum temperature of warmest month minus minimum temperature of coldest month). Distribution modeling predicted a larger area of occurrence than that currently known for the species, which includes the Yucatan Peninsula in Mexico, Guatemala, Honduras, Panama, Cuba, Venezuela, Guyana, and Brazil. According to our results, however, *H. bicornis* should also be expected to occur in Belize, Nicaragua, Costa Rica, all the major islands of the Antilles, as well as Colombia, Suriname, Ecuador, Peru, Bolivia and Paraguay. Many of the predicted areas of occurrence should be expected based on the current known distribution of the species, such as other Mesoamerican countries and some areas of northeastern Brazil. However, some high probability areas of occurrence were unexpected, such as the coastline of Ecuador and parts of the states of Rio de Janeiro and Espirito Santo in southeastern Brazil (Fig. 6).

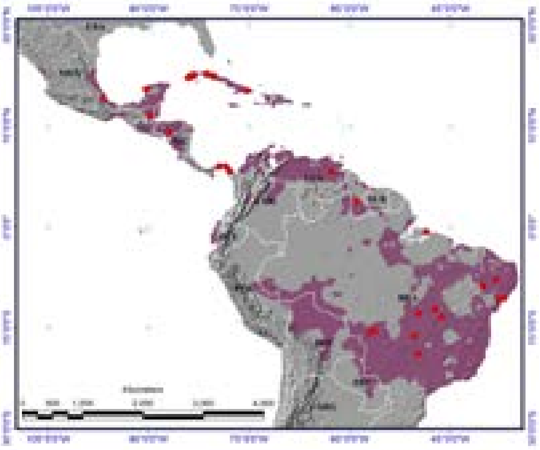


FIGURE 6. Occurrence records and potential distribution of *Habenaria bicornis* inferred with Maxent. Political divisions are highlighted in white. Country abbreviations are as follows: Arg, Argentina; Bol, Bolivia; Bra, Brazil; Col, Colombia; Ecu, Ecuador; Mex, Mexico; Nic, Nicaragua; Per, Peru; Pry, Paraguay; Sur, Suriname; Ven, Venezuela.

Cytogenetics. – *Habenaria bicornis* has $2n = 42$ (Fig. 7A-C, G) and a symmetrical karyotype, with chromosomes ranging in size from 2.9 to 9.8 µm and being mainly metacentric to submetacentric, except for two small acrocentric pairs (Fig. 7C, arrows). Regular meiosis was observed, with 21 chromosomes in each cell of the dyad in meiosis II (Fig. 7D-F). Although the species did not show clearly differentiated CMA/DAPI bands in meiosis, CMA−/DAPI+ pericentromeric regions (Fig. 7A, B) were observed in mitosis. Terminal chromosome regions staining slightly more intensely with CMA than with DAPI were observed only in mitotic prometaphases (Fig.7C). Two 45S rDNA sites were observed on the terminal chromosome regions of a large metacentric pair (Fig. 7G) that did not co-occur with CMA bands. Two 5S rDNA sites were observed in the interstitial and subterminal regions of a long arm on two chromosome pairs per monoploid complement (Fig. 7G). The basic number $x = 21$ is the most frequent among Neotropical and Old World

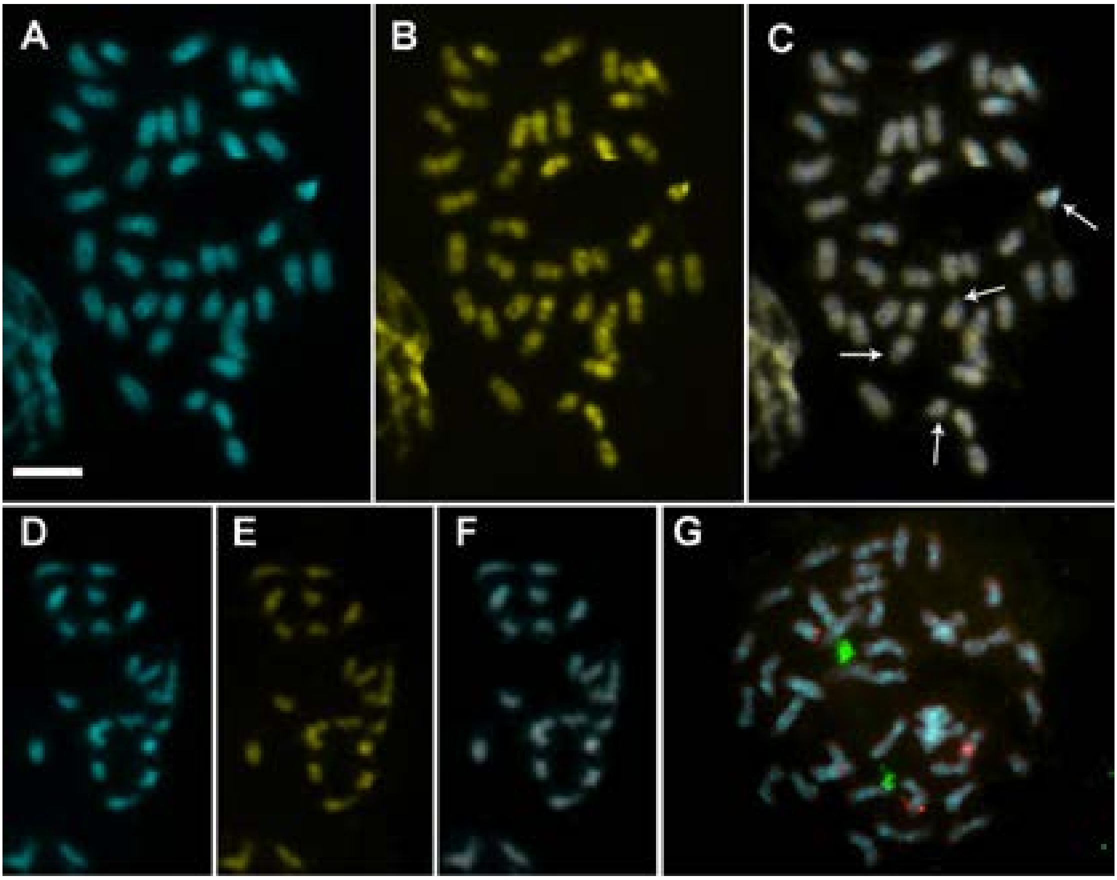


Figure 7. *Habenaria bicornis.* A-C, G. Mitotic metaphases. D-F. Meiotic metaphase II. A, D. Stained with DAPI. B, E. Stained with CMA. C, F. CMA/DAPI overlap showing CMA terminal bands and DAPI pericentromeric bands. G. FISH with 45S (green) and 5S rDNA sites (red). Arrows in C indicate acrocentric chromosomes; scale bar in A corresponds to 10 µm.

species of *Habenaria* (Felix & Guerra 1998, 2005). This number was previously reported for *H. pratensis* (Salzm. ex Lindl.) Rchb.f. and *H. repens* Nutt. (Felix & Guerra 1998), both of which are "basal" species in our previous molecular phylogenetic analysis of Neotropical *Habenaria* (Batista *et al*. 2013), suggesting that $x = 21$ maybe the ancestral basic number for Neotropical *Habenaria*.

The banding patterns observed in *H. bicornis* stand out because of the presence of pericentromeric and terminal heterochromatin. Pericentromeric heterochromatin has been observed in unrelated groups of orchids, such as *Psygmorchis pusilla* (L.) Dodson & Dressler (Felix & Guerra 1999; Epidendroideae, Oncidiinae), several species of *Ophrys* L. (D'Emerico *et al*. 2005; Orchidoideae, Orchidiinae), and *Heterotaxis discolor* (Lodd. ex Lindl.) Ojeda & Carnevali (Cabral *et al*. 2006; Epidendroideae, Maxillariinae), suggesting that the loss or acquisitions of this heterochromatin may be recurrent events in orchids. However, the occurrence of GC-rich heterochromatin on the terminal regions of all chromosomes in *H .bicornis* has not been reported for any other orchid species. The evolution of CMA/DAPI band patterns in subtribe Maxillariinae is highly variable within and between different monophyletic lineages and has been important for the cytotaxonomic characterization of several species (Moraes *et al*. 2012). If this is also true for *Habenaria*, CMA/DAPI band patterns may provide an additional tool for characterization of lineages and species and for testing phylogenetic hypothesis in the genus.

Taxonomic treatment

KEY TO *HABENARIA BICORNIS* AND MORPHOLOGICALLY SIMILAR SPECIES

1. Petal posterior segment 2.0–3.5 mm wide; spur about the same length as the pedicellate ovary, usually hidden between the bracts .... *H. rodeiensis*
1. Petal posterior segment 1.0–1.85 mm wide; spur 1.3–2.3 times as long as the pedicellate ovary, free from the bracts 2
   2. Petal anterior segment 0.2–1.0 times as long as posterior segment; spur linear throughout .... *H. exaltata*
   2. Petal anterior segment 1.3–2.2 times as long as posterior segment; spur clavate to subclavate 3
      3. Plants 19–44 cm tall including inflorescence; leaves 5–12(–16) × 0.3–0.9(–1.4) cm; petals and lip completely white; anterior petal segment 1.6–2.2 times as long as posterior segment; spur apex rounded; hemipollinaria united; rostellum midlobe apex acute, projected beyond the anther locules .... *H. caldensis*
      3. Plants (25–)37–90(–107) cm tall including the inflorescence; leaves 13–24(–28) × (0.8–)1.1–2.0(–2.5) cm; petals and lip with base white and green segments; anterior petal segment 1.3–1.5 times as long as posterior segment; spur apex subacute to acute; hemipollinaria separated; rostellum midlobe apex obtuse, situated between the anther locules .... *H. bicornis*

Habenaria bicornis Lindl., Gen. Sp. Orchid. Pl. 309. 1835. Type: CUBA. 1822, *E.F. Poeppig s.n.* (Holotype: K [s.n.]; isotype: K-L [000463128, drawings of holotype by Lindley]).

Synonyms: *Habenaria tricuspis* A. Rich., Hist. Fis. Cuba, Bot. 11: 249. 1850. Type: CUBA. 1836, *R. de La Sagra s.n*. (Holotype: P [00408997]; isotype: W-R [43232]).

Habenaria goyazensis Cogn., Fl. Bras. (Martius) 3(4): 77. 1893. Type: BRAZIL. Goyaz [Tocantins], campos (marsh) near Conceição [Conceição do Tocantins], fls. greenish-white, February 1840 (fl), *G. Gardner 3995* (Holotype: not indicated; Lectotype, designated by Batista *et al*. 2011a: K [000363814]; Isotypes: B [destroyed], BR [642571; fragment from B or G], BM [000032714], F [24791; negative from the specimen from G], G [00169025], K [000363815], K-L [000363784], OXF, W-R [51336, 54022], RENZ [1446; photo, drawing and fragment from W-R 51336]).

Terrestrial *herb*. *Roots* few, short, at the base of the stem. *Tuberoid* fusiform, 2.2–3.0 × 1.0–1.8 cm. *Stem* erect, (25–)37–90(–107) cm long, including the inflorescence, 3.0–7.7 mm wide. *Leaves* 6–10(–17), spreading, largest at the center of the stem, lanceolate, 13–24(–28) × (0.8–)1.1–2.0(–2.5) cm. *Inflorescence* 6–20 cm long, many-flowered, spiral; *floral bracts* lanceolate, acuminate, (1.3–)1.5–2.8(–3.2) cm long, shorter than or about the same size as the pedicellate ovary. *Flowers* 19–28(–33), resupinate, greenish-white; *pedicellate ovary* parallel to or spreading from the rachis, (13–)21–26(–32) mm long; ovary slightly arched, 13–28 mm; pedicel shorter than the ovary, 2.3–4.2 mm. *Sepals* green, aristate, smooth; dorsal sepal concave, when flattened ovate, 4–8 × 4.5–6.0(–8.0) mm; lateral sepals obliquely lanceolate, acute or subacute, reflexed, 6.5–9.5 × 3–5 mm. *Petals* bipartite; posterior segment falcate, 4.6–7.1 × 1.7–1.9 mm, subacute, lying beside or free from the dorsal sepal, base, middle part and inner margin white, outer margin from the middle to the apex light green; anterior segment divergent, linear, inserted at the base of the posterior segment, 6.8–8.8 × 0.4–0.8 mm, 1.3–1.5 times as long as the posterior segment, base whitish, towards the segments apex light green. *Lip* tripartite, light green, base white, towards the segments apex light green; undivided basal part prominent, 1–2.8 × 1.7–2.5 mm; side segments linear, 7.8–8.8(–11.0) × 0.6–0.9(–1.0) mm, 1.3–1.5 times as long as the median segment; median segment linear-ligulate, straight, 5.5–7.0 × 0.9–1.9 mm; *spur* slightly sinuous to hooked, sometimes projected frontwards, free from the bracts, subclavate, 1.3–2.1 times as long as the pedicellate ovary, 2.5–4.6 cm long, base 0.6–1.4 mm wide, whitish, apex 1.4–2.4 mm wide, green. *Gynostemium* erect, 2.6–2.9 mm high; connective emarginate, light green; auricles fleshy, verrucose, whitish, 0.6 × 0.7 mm, apex rounded. *Anther locules* 1.8–2.3 mm high, canals short, 1.0–1.1 mm long, hemipollinaria separated, 3.7 mm long, viscidium 0.75 × 0.6 mm, spaced 1.4–1.6 mm apart, caudicles 1.3 mm long, pollinia 1.6 × 1.1 mm. *Stigma lobes* 2, mostly separate, in contact only at the apex, oblong, light green, flat, receptive surface turned upwards, 2.1–2.3 mm long, apex 1.2 mm wide, obtuse, margins not involute, space between the stigma lobes oblong to elliptic. *Rostellum* 3.4 mm long, white; mid-lobe triangular, fleshy, erect, obtuse, completely placed between the anther loci, 1.8 mm high; side-lobes parallel throughout, 1.9 mm long.

Distribution and conservation status: *Habenaria bicornis* is distributed from southern Mexico (Campeche and Veracruz), Central America (Guatemala, Honduras, and Panama), the Caribbean (Cuba), northern South America (Venezuela and Guyana), to northern (Pará), northeastern (Paraíba, Pernambuco, and Sergipe), central (Goiás, Mato Grosso, and Tocantins) and southeastern (Minas Gerais) Brazil. Although the species is widespread throughout most of the Neotropics, it is uncommon and locally known from few collections (except from Cuba, where several collections are known, particularly from the province of Pinar del Rio). Despite its low frequency, but because of its broad distribution, *H. bicornis* can be classified as Least Concern (LC) according to the World Conservation Union Red List Categories and Criteria (IUCN, 2001).

Habitat, ecology and phenology: *Habenaria bicornis* is commonly found in lowland, permanently wet savannas (chagüite, matorral, selva baja caducifolia inundable, acuática, wet grassland, wet boggy meadow, sandy wet banks, moist grassy places, wet fields, campo alagado, campo úmido, pântano, brejo). The species also occasionally occurs at the interface between wet grassland and gallery forests. Elevations range from near the sea level to 800 m, but most records (90%) are from below 400 m. Flowering occurs from the peak of the rainy season to its end: from February to March in central and southeastern Brazil; and from June to October in northeastern Brazil and in the northern hemisphere (Table 3). As in most species of the genus, *H. bicornis* begins a new growth cycle during the rainy season. A new vegetative shoot grows from the tuber formed during the previous season and produces a new stem, which forms a new tuber and a terminal inflorescence. After maturation of the capsules as the dry season approaches, the stem and leaves wither and are lost, and the new tuberoid becomes dormant. Because of its habitat preferences, *Habenaria bicornis* seems to be less affected by fire regimens than other Neotropical species of the genus from seasonal humid grasslands (Batista *et al*. 2003, 2010, Batista & Bianchetti 2010), which usually depend upon fire for large-scale flowering.

Illustrations: Kränzlin (1911, table 2, fig. 2, as *H. caldensis*, based on *Lindman 2791 ½*), Hoehne (1940, plate 67; figure I, as *H. goyazensis*, based on *Pickel 3615*), Snuverink & Westra (1983: 572, fig. 3, as *H. caldensis*, based on *Wilson-Browne 2*), Batista *et al*. (2008, fig. 2K-L, as *H. goyazensis*, based on *Batista et al. 683*).

The illustration of *H. exaltata* in Flora Brasilica (Hoehne 1940, plate 68) is most probably based on *Lindman 2765* (S) and referable to *H. bicornis*. The material illustrated in Pabst & Dungs (1975: 250, fig. 97), and identified as *H. goyazensis*, is based in on *Chagas s.n.* – INPA 826, and is referable to *H. longipedicellata*.

Additional specimens examined: MEXICO. **Campeche:** Carretera Kalkiní-El Remate, 2 km antes de llegar a El

Table 3. Number of flowering specimens of *H. bicornis* for each of its main geographic distribution areas. The total includes all collected specimens from each region, including materials with fruits, and with or without collection dates.

Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mexico and Central America								2	2	1			8
Cuba								8	4	2			25
Northeastern Brazil and northern South America						1	1	2	2				8
Central and southeastern Brazil		4	1										7

Remate, selva baja caducifolia inundable, acuática, comum, flor verde-amarillenta, con el centro blanquecino, 11 October 1999 (fl), *M. Pena-Chocarro, J. Tun, L. Salinas & J. Hinojosa 599* (BM); **Veracruz:** Totutla, Mata Obscura, matorral en terreno plano, flores verdes tierno con el centro blanquecino, 30 September 1972 (fl), *A.F. Ventura 7072* (EAP). CUBA. *Herb. Estac. Centr. Agron. 753* (BR). **Cienfuegos:** Cieneguita, in wet grassy lands, not uncommon, 7 or 8 August 1895 (fl), *R. Combs 440* (AMES, GH, MO); Cieneguita, in wet grassland and open wood land, 3 September 1895 (fl), *R. Combs 755* (GH). **Guantánamo:** Oriente, in savanna, 2 August 1914 (fl), *E.L. Ekman 2375* (NY); Bayate, Sabana Miranda, 15 September 1915 (fl), *E.L. Ekman 6449* (US). **Matanzas:** San Miguel de los Baños, on slope of Jacán hill, Grassy place, 6 August 1919 (fl), *B. León & M. Roca 8898* (NY). **Pinar del Rio:** vicinity of Herradura, Royal Palm savanna, flowers greenish-yellow, 26-30 August 1910 (fl), *N.L. Britton, E.G. Britton, F.S. Earle & C.S. Gager 6337* (AMES, K, NY, US); Laguna Santa María, sandy pinelands, 8 September 1910 (fl), *N.L. Britton, E.G. Britton & C.S. Gager 7153* (AMES, NY); Vicinity of Pinar del Río, sandy wet bank, in pinelands, sepals green, 5-12 September 1910 (fr), *N.L. Britton, E.G. Britton & C.S. Gager 7247* (AMES, NY); Pinar del Río to Viñales, grassy bank, flowers greenish, 12 September 1910 (fl), *N.L. Britton, E.G. Britton & C.S. Gager 7302* (NY); north of La Guira, San Diego de los Baños, 26 August 1914 (fl), *B. León 4585* (NY); Pinar del Río, Sabana de Bacunagua, October 1931 (fl, fr), *B. León 15061* (US); Sumidero, Savanna del Sumidero, in campis graminosis, October 1823 (fl), *Poeppig 1845* (G, W, W-R 20324); 1824 (fl), *Poeppig s.n.* (W); *Poeppig s.n.* (W-R 20323); in savannarum regionis humiden locis uliginosis,flor albo, *Poeppig s.n.* (W-R 20322); campi inundati, *Poeppig s.n.* (P 386869); North of [Consolacion] del Sur, savana, 23 August 1924 (fl), *J.T. Roíg y Mesa & M.A. Chrysler 3263* (NY); west of Guane along the Mantua road, palm barren, moist grassy places, 25 November 1911 (fr), *J.A. Shafer 10480* (A, NY); Cuchillas de San Sebastian, vicinity of Sumidero, siliceous formation, grassy hillside, fls. greenish-white, 9 August 1912 (fl), *J.A. Shaffer & B. León 13714* (A, BM, NY); Cuchillas de San Sebastian, vicinity of Sumidero, top of Cuchillas, flower greenish-white, 9 August 1912 (fl), *J.A. Shaffer & B. León 13718* (NY). **Villa Clara:** Santa Clara, Banks of Lagoon Haití, Mordazo, 29 December 1915 (fr), *B. León & F.R. Cazanás 5924* (NY); Santa Clara, near Manacas, 27 December 1915 (fr), *B. León & F.R. Cazanás 5966* (NY). GUATEMALA. graminosis uliginosis, August 1870 (fl), *G. Bernoulli 922* (W-R). HONDURAS. **Francisco Morazán:** Near Las Mesas, in chagüite, common, 2 December 1950 (fr), *P.C. Standley 27834* (EAP); near Las Mesas, wet boggy meadow, petals greenish-white, 30 August 1948 (fl), *L.O. Williams & A. Molina 14712* (EAP). PANAMA. **Panamá:** Canal Zone, Las sabanas, fl. greenish, 10 September 1914 (fl), *H.F. Pittier 6792* (US); Panama City, near Matías Hernández, wet field, common but plants all dried, 30 December 1923 (fr), *P.C. Standley 28982* (US); Panama City, between Matías Hernández and Juan Diaz, 21 January 1924 (fr), *P.C. Standley 32032* (US). VENEZUELA. **Bolivar:** Cuidad Guayana, Mission deu Caroni, Canton de Upata (?), dan les savannes humiden, 1864 (fl), *Grosourdy s.n.* (P 00386911); **Portuguesa:** Guanare, Mesa Alta (Mesa del Indio), 10 km al N-W de Guanare, en chaparrales associados com sabanas, flores blanco-verdosas, 9º4’N, 69º44’W, 300 m, 19 September 1988 (fl), *G. Aymard & C. Ramirez 7067* (MO). GUYANA. **Upper Takutu-Upper Esequibo:** Rupununi River, savanna, August 1948 (fl), *G. Wilson-Browne 2* (K, NY, RENZ). BRAZIL. **Goiás:** Mossâmedes, Serra Dourada, Fazenda Agua Fria, *Pohl 1645* (BR, W); São Domingos, Fazenda Craibinha, cerrado, campo úmido, 16 March 2004 (fl), *A.A. Santos et al. 2422* (BHCB, CEN). **Minas Gerais:** Ituiutaba, margens do Rio Paranaíba, Fazenda Santa Terezinha, varjão (campo alagado), fl. verde-amareladas, 18 February 1949 (fl), *A. Macedo 1695* (HB). **Mato Grosso:** Serra das Araras, in campis, perianthum viride, 15 February 1894 (fl), *C.A.M. Lindman 2765* (S); prope rivum Esmeril, in campo uliginoso graminoso, *C.A.M. Lindman 2791 ½* (S, spirit). **Pará:** Marajó, 1877-1878 (fl), *Jobert 141* (P, RENZ). **Paraíba:** Remígio, terrenos alagados e encapoeirados, flores branco-creme, segmentos vegetativos verdes, 13 September 2005 (fl), *L.P. Felix 10803* (EAN). **Pernambuco:** Tapera (S. Bento), no pântano (lagoa do cercado), flores branco-amarellas, 26 June 1934 (fl), *B. Pickel 3615* (IPA, NY, SP); Lagoa do Ouro, 9º08’60”S, 35º28’60”W, 24 August 2013 (fl), *L.P Felix & E.M Almeida 14643* (EAN). **Sergipe:** Japaratuba, beira de rodovia pavimentada, campo limpo encharcado (brejo), ao lado de um filete d água, relevo plano, conspícuas, se destacando no campo, flores alvo-esverdeadas, 23 July 2005 (fl), *J.F.B. Pastore 1452* (BHCB). **Tocantins:** Araguaçu, 18-20 km após Araguaçu, na estrada para Alvorada, nas bordas de mata ciliar úmida com campo úmido adjacente, 16 February 1997 (fl), *J.A.N. Batista et al. 683* (CEN).

TAXONOMIC NOTES: Poeppig collected several specimens of *H. bicornis* in Cuba. The holotype in K is labeled just ‘Cuba, 1822’. The collection data of the other specimens varies from ‘Cuba, Savana del sumidoro, October 1823, *E.F. Poeppig 1845*’ (G 169029, W-R 20324, W s.n.), to ‘Cuba, 1824’ (W s.n.) or just ‘Cuba’ without any date or collection number (P 386869, W-R 20322, W-R 20323). In a synopsis of New World *Habenaria*, Batista *et al*. (2011a) incorrectly cited the most complete collection data as the type data and interpreted the specimens in G and P as isotypes.

Some authors have considered *H. bidentata* Poepp. ex Steud., a *nomen nudum*, a synonym of *H. bicornis* (Cogniaux 1909, Galé 1938). However, the name was first published by Sprengel (1826) as a synonym of *H. alata* Hook. Accordingly, there are several collections from Poeppig at W (W s.n., W-R 43241, W-R 20301, W-R 20302) originally identified as *H. bidentata* and which are all referable to *H. alata*. Some authors have considered *H. tricuspis* a synonym of *H. repens* (Cogniaux 1909, Ames 1910, Galé 1938, León & Schweinfurth 1946), but examinations of the type materials in P and W confirmed it as a synonym of *H. bicornis*. *Habenaria radicans* Griseb., from Cuba, was published as a synonym of *H. tricuspis* (Grisebach 1866), but the name is based on the specimen *C. Wright 3309* (AMES 70164, BM 32525, K), which is *H. repens*.

Acknowledgments. The authors thank the curators and staff of the following herbaria for providing digital images or access to their collections and support during our visits: A, ALCB, AMES, B, BHCB, BM, BR, CEN, CEPEC, CESJ, CTES, EAN, EAP, ESA, G, GH, HB, HBG, HRB, HRCB, HUEFS, IBGE, ICN, IPA, K, L, LP, M, MBM, MBML, MO, NY, OUPR, OXF, P, PMSP, R, RB, RENZ, S, SI, SP, SPF, U, UB, UEC, US, W; Gustavo Romero for scanning the image of *H. goyazensis* published by Kränzlin, Adalberto José dos Santos for permission and assistance in the use of Leica M205C stereoscopic microscope, Ana Cláudia Fernandes for translation of the abstract to Spanish, and two anonymous reviewers for improvements on the manuscript. JANB acknowledges financial support from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Amparo a Pesquisa do Estado de Minas Gerais (FAPEMIG) and a scholarship (Pq-2) from CNPq.

Literature cited

Ames, O. 1910. The genus *Habenaria* in North America. Orchidaceae 4: 1–288.

Ames, O. 1922. New or noteworthy orchids from different parts of the world. Orchidaceae 7: 83–140.

Ames, O. 1928. Orchidaceae. *In*: P.C. Standley (ed.), Flora of the Panama Canal Zone. Contributions from the United States national Herbarium. Vol. 27.

Batista, J.A.N., L.B. Bianchetti & E.G. Gonçalves. 2003. An overlooked new species of *Habenaria* (Orchidaceae) from Central Brazil. Novon 13: 397–402.

Batista, J.A.N., J.B.F. Silva & L.B. Bianchetti. 2008. The genus *Habenaria* (Orchidaceae) in the Brazilian Amazon. Rev. Bras. Bot. 31: 105–134.

Batista, J.A.N. & L.B. Bianchetti. 2010. Taxonomy, distribution and new taxa from the *Habenaria crucifera* (section Nudae, Orchidaceae) aggregate from Brazil and the Guianas. Brittonia 62: 57–79.

Batista, J.A.N., B.M. Carvalho, A.J. Ramalho & L.B. Bianchetti. 2010. Three new species of *Habenaria* (Orchidaceae) from Serra da Canastra, Minas Gerais. Phytotaxa 13: 27–39.

Batista, J.A.N., L.B. Bianchetti, R. González-Tamayo, X.M.C. Figueroa & P.J. Cribb. 2011a. A synopsis of new world *Habenaria* (Orchidaceae) I. Harvard Pap. Bot.16: 1–47.

Batista, J.A.N., L.B. Bianchetti, R. González-Tamayo, X.M.C. Figueroa & P.J. Cribb. 2011b. A synopsis of new world *Habenaria* (Orchidaceae) II. Harvard Pap. Bot. 16: 233–273.

Batista, J.A.N., K.S. Borges, M.W. Faria, K. Proite, A.J. Ramalho, G.A. Salazar & C. van den Berg. 2013. Molecular phylogenetics of the species-rich genus *Habenaria* (Orchidaceae) in the New World based on nuclear and plastid DNA sequences. Mol. Phylogenet. Evol. 67: 95–109.

Bonfield, J.K., K.F. Smith & R. Staden. 1995. A new DNA sequence assembly program. Nucleic Acids Res. 24: 4992–4999.

Cabral, J.S., L.P. Felix & M. Guerra. 2006. Heterochromatin diversity and its co-localization with 5S and 45S rDNA sites in chromosomes of four *Maxillaria* species (Orchidaceae). Genet. Mol. Biol. 29: 659–664.

Chase, M.W., R.S. Cowan, P.M. Hollingsworth, C. van den Berg, S. Madriñán, G. Petersen, O. Seberg, T. Jørgsensen, K.M. Cameron, M. Carine, N. Pedersen, T.A.J. Hedderson, F. Conrad, G.A. Salazar, J.E. Richardson, M.L. Hollingsworth, T.G. Barraclough, L. Kelly & M. Wilkinson. 2007. A proposal for a standardised protocol to barcode all land plants. Taxon 56: 295–299.

Cogniaux, A. 1893. Orchidaceae. *Habenaria*. Pp. 18–102 *in*: C.F.P. Martius, A.G. Eichler & I. Urban (eds.) Flora Brasiliensis 3(4). München, F. Fleischer.

Cogniaux, A. 1909. Orchidaceae VII. *Habenaria*. Pp. 297–309 *in*: I. Urban (ed.), Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis. Vol. 6. Leipzig, F. Borntraeger.

Correa, A., D. Mireya, C. Galdames & M.N.S. Stapf. 2004. Catálogo de las Plantas Vasculares de Panamá. Smithsonian Tropical Research Institute, Panama.

D'Arcy, W.G. 1987. Flora of Panama. Check list and index. Part I: The introduction and checklist. Missouri Botanical Garden. St. Louis, Missouri.

D'Emerico, S., D. Pignone, G. Bartolo, S. Pulvirenti, C.

Terrasi, S. Stuto & A. Scrugli. 2005. Karyomorphology, heterochromatin patterns and evolution in the genus *Ophrys* (Orchidaceae). Bot. J. Linn. Soc. 148: 87–99.

Dressler, R.L. 1980. Checklist of the orchids of Panama. Monographs in Systematic Botany from the Missouri Botanical Gardens 4: 1–26.

Dressler, R.L. 1993. Field guide to the orchids of Costa Rica and Panama. New York, Cornell University Press.

Edgar R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res*. 32: 1792–1797.

Erixon P., B. Svennblad, T. Britton & B. Oxelman. 2003. Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. Systematic Biol. 52: 665–673.

Felix L.P. & M. Guerra 1998. Cytological studies on species of *Habenaria* Willd. (Orchidaceae-Orchidoideae) occurring in the Northeast of Brazil. Lindleyana 13: 224–230.

Felix, L.P. & L.P. Guerra. 1999. Chromosome analysis in *Psygmorchis pusilla* (L.) Dodson & Dressler: the smallest chromosome number know in Orchidaceae. Caryologia 52: 165–168.

Felix, L.P. & L.P. Guerra. 2005. Basic chromosome numbers of terrestrial orchids. Pl. Syst. Evol. 254: 131–148.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Fitch W.M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. Syst. Zool. 20: 406–416.

Galé, J.A. 1938. Catálogo descriptivo de las orquideas cubanas. Bol. Estac. Exp. Agron. Santiago de las Vegas. Vol. 60

Govaerts, R., P. Bernet, K. Kratochvil, G. Gerlach, G. Carr, P. Alrich, A.M. Pridgeon, J. Pfahl, M.A. Campacci, D. Holland Baptista, H. Tigges, J. Shaw, P. Cribb, A. George, K. Kreuz & J. Wood. 2013. World Checklist of Orchidaceae. Royal Botanic Gardens, Kew. Available from: http://apps.kew.org/wcsp/ (accessed: 11 July 2013).

Grisebach, A. 1866. Catalogus plantarum cubensium. G. Engelmann, Leipzig.

Grisebach, A. 1873. *Habenaria*. Pp. 233 *in*: F.A. Sauvalle (ed.), Flora Cubana: enumeration nova plantarum cubensium. Havana, La Antilla.

Hoehne, F.C. 1940. Orchidaceas. *Habenaria*. Pp 52–254 *in*: F.C. Hoehne (ed.) Flora Brasilica 12(1). São Paulo, Secretaria da Agricultura, Indústria e Comércio de São Paulo.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. IUCN Species Survival Commission, Gland.

IUCN Standards and Petitions Subcommittee. 2010. Guidelines for Using the IUCN Red List Categories and Criteria. Version 8.1. Prepared by Standards and Petitions Subcommittee in March 2010.

Kränzlin F. 1892. Beitrage zu einer monographie der gattung *Habenaria* Willd. Engl. Bot. Jahrb. 16: 52–223.

Kränzlin, F. 1901 Orchidacearum genera et species. Vol. I. *Habenaria.* Mayer & Müller, Berlin.

Kränzlin, F. 1911. Beiträge zur orchideenflora Südamerikas. Kongl. Svenska Vetenskapsakad. Handl. 46: 1–105.

Kress W.J., L.M. Prince & K.J. Williams. 2002. The phylogeny and a new classification of the gingers (Zingiberaceae): evidence from molecular data. Amer. J. Bot. 89: 1682–1696.

León, H. & C. Schweinfurth. 1946. Familia 2. Orquideas. *In*: H. León (ed.) Flora de Cuba. Vol. 1. Contribuciones ocasionales del Museo de Historia Natural del Colegio de La Salle, 8. Habana, Cultural S.A.

Lindley, J. 1830–1840. The genera and species of orchidaceous plants. J. Ridgways, London.

Moraes, A.P., I.J. Leitch & A.R. Leitch. 2012. Chromosome studies in Orchidaceae: karyotype divergence in Neotropical genera in subtribe Maxillariinae. Bot. J. Linn. Soc. 170: 29–39.

Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Pabst, G.F.J. & F. Dungs. 1975. Orchidaceae Brasilienses. Vol. 1. Brucke-Verlag Kurt Schmersow, Hildesheim.

Pearson, R.G., C.J. Raxworthy, M. Nakamura & A.T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeog. 34: 102–117.

Phillips, S.J., R.P. Anderson & R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190: 231–259.

Pridgeon A.M., P.J. Cribb, M.W. Chase & F.N. Rasmussen .2001. Genera orchidacearum, Vol. 2. Orchidoideae, part 1. Oxford University Press Inc, New York.

Renz, J. 1992. The genus *Habenaria* (Orchidaceae) in the Guianas. Candollea 47: 483–512.

Richard, A. 1850. Ophrydeae. *Habenaria*. Pp. 249–250 *in*: D. Ramon de La Sagra (ed.), Historia fisica, politica y natural de la isla de Cuba. Segunda parte. Historia Natural. Tomo XI. Botanica. Paris, A. Bertrand.

Ronquist, F., J.P. Huelsenbeck & P. van der Mark. 2005. MrBayes: Bayesian Inference of Phylogeny. Program distributed by the authors. Available from: http://mrbayes.sourceforge.net/index.php.

Sérgio, C., R. Figueira, D. Draper, R. Menezes & A.J. Sousa. 2007. Modelling bryophyte distribution based on ecological information for extent of occurrence assessment. Biol. Conserv. 135: 341–351.

Simpson, M.G. 2006. Plant systematics. Elsevier Academic Press, Burlington, San Diego and London.

Snuverink, J.H & L.Y. Th. Westra. 1983. Studies on the flora of the Guianas. 3. A survey of *Habenaria* Willd. in Suriname (Orchidaceae). Proc. Kon. Nederl. Akad. Wetensch., C, 86(4): 567–594.

Souza, L.G.R., O. Crosa, P. Speranza & M. Guerra. 2012. Cytogenetic and molecular evidence suggest multiple origins and geographical parthenogenesis in *Nothoscordum gracile* (Alliaceae). Ann. Bot. 109: 987–999.

Sprengel, C.P.J. 1826. Systema vegetabilium. Editio decima sexta, vol. 3. Sumtibus Librariae Dieterichianae, Göttingae.

Stearn, W.T. 1992. Botanical Latin. 4o ed. Timber Press, Portland.

Swofford, D.L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Inc., Sunderland.

Sun, Y., D.Z. Skinner, G.H. Liang & S.H. Hulbert. 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. Theor. Appl. Genet. 89: 26–32.

Tamura, K., J. Dudley, M. Nei & S. Kumar. 2007. MEGA4: Molecular evolutionary genetics analysis (MEGA) software version 4.0. Mol. Biol. Evol. 24: 1596–1599.

Whitten, W.M., N.H. Williams & M.W. Chase. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: Combined molecular evidence. Amer. J. Bot. 87: 1842–1856.

Williams, L.O. 1946. Orchidaceae. *Habenaria*. Pp. 11–16 *in*: R.E. Wood & R.W. Schery (eds.), Flora of Panana. Part. 3. fas. 2. Annals of the Missouri Botanical Garden. Vol. 33(1). Facsimile reprint (1980).

Williams, L.O. 1956. An enumeration of the Orchidaceae of Central America, British Honduras and Panama. Ceiba 5(1): 1–256.

Appendix. Additional specimens examined of morphological similar species.

Habenaria caldensis. BRAZIL. *A. Ghillany s.n.* (HB 57918), *A. Glaziou 16372* (BR, P, RENZ), *A. Macedo 2964* (NY, RB, US), *5206* (HB), *A.C.D. Munhoz & C.A.N. Martins 91* (BHCB), *94* (BHCB), *A.C.D. Munhoz et al. 69* (BHCB), *84* (BHCB), *157* (BHCB), *165* (BHCB), *A. Salino et al. 10863* (BHCB), *A.B. Joly et al. 1246* (SP), *1366* (SP), *A.F. Regnell III 1181* (P, S, US, W), *A.J. Sampaio 6706* (BHCB, R), *6888* (SP, R), *A.P. Duarte 7835* (NY, RB), *B. Orssich s.n.* (HB 66528), *C.M. Sakuragui et al. in CFCR 15109* (SPF), *D. Zappi et al. 9568* (SPF), *E.N. Lughadha & J.R. Pirani H51022* (K), *E. Pereira 8903* (AMES, HB, RB), *E. Simonis & I. Cordeiro in CFCR 4098* (SPF), *E.L. Borba 102* (BHCB), *107* (BHCB), *E.P. Heringer & A. Castellanos 6014* (AMES, HB), *6074* (UB), *6219* (UB), *6219-A* (HB), *6228* (UB), *22243* (R), *E.P. Heringer 6229* (UB), *E.R. Pansarin & A.O. Simões 786* (CEN, UEC), *803* (CEN, UEC), *F.C. Hoehne s.n.* (SP 4945, SPF 65025), *G. Hatschbach & Z. Ahumada 31572* (MBM), *G. Hatschbach & J. Cordeiro 51837b* (MBM), *G. Hatschbach et al. 28748* (HB, MBM, NY, UEC, US), *36315* (HB, MBM, NY, RENZ), *40828* (MBM), *64355* (HBG, MBM), *64355* (BHCB, MBM), *G. Martinelli et al. 11343* (RB), *G. Windisch 2582* (HB), *G.W.A. Fernandes s.n.* (BHCB 27951), *H.S Irwin et al. 12406* (HB, NY), *18782* (HB, NY, UB), *19899* (AMES, HB, RB, UB), *19993* (AMES, HB, M, NY, RB,UB, US), *20869* (AMES, HB, NY, RB, UB, US), *22045* (UB), *22391* (HB, NY, UB), *22556* (HB, NY, UB), *22701* (UB), *23431* (AMES, HB, NY, RB, UB, US), *28037* (HB, UB), *32177* (NY, UB), *34025* (HB, HBG, NY, UEC), *34025a* (UB), *35417* (NY), *Jobert 87* (P), *J. Badini s.n.* (OUPR 9712, 9721, 9726), *J. Semir & A.B. Joly 3811* (SP), *3814* (SP), *J. Semir & M. Sazima 4941* (SP, UEC), *J.A. Lombardi 4615* (BHCB), *J.A.N. Batista 154* (CEN), *250* (CEN), *1828* (BHCB), *2621* (BHCB), *2633* (BHCB), *J.A.N. Batista & A.R.C. Lemos 1061* (CEN, UEC), *J.A.N. Batista & E.R. Pansarin 1139* (CEN), *1156* (CEN, UEC), *J.A.N. Batista & K. Proite 987* (CEN), *1021* (CEN), *J.A.N. Batista & L.B. Bianchetti 396* (CEN), *895* (CEN), *919* (CEN), *J.A.N. Batista et al. 714* (CEN, MBM, SP), *1359* (CEN, SP), *1382* (CEN), *1389* (CEN), *1798* (BHCB), *1818* (BHCB), *1900* (BHCB), *1950* (BHCB), *2405* (BHCB), *2413* (BHCB), *2415* (BHCB), *2458* (BHCB), *2737* (BHCB), *2794* (BHCB), *2820* (BHCB), *2856* (BHCB), *2877* (BHCB), *2955* (BHCB), *3120* (BHCB), *3147* (BHCB), *J.R. Pirani et al. 2212* (SPF), *2296* (SPF), *3963* (SPF), *in CFCR 9144* (SPF), *L. Damasio s.n.* (OUPR 9707, 9708), *L.B. Smith et al. 15958* (HB, US), *L. Mickeliunas & E.R. Pansarin 03* (CEN, UEC), *15* (CEN, UEC), *34* (CEN, UEC), *L. Th. Dombrowski 7000* (MBM), *L.A. Martens 255* (SPF), *M. Barreto 4870* (BHCB), *4871* (BHCB, SP), *8929* (BHCB, R, SP), *M. Magalhães 1100* (BHCB, SP), *1126* (BHCB), *M.F.A. Calió et al. 29* (SPF), *M.G.L. Wanderley et al. 577-A* (SP), *M.M. Arbo et al. 4629* (AMES, K), *5215* (AMES, SPF), *M.S. Werneck 66* (BHCB), *M. Sazima 13400* (UEC), *N.L. Menezes et al. 7099* (SP), *N.S. Bittencourt Jr. 00/42* (UEC), *P.L. Viana s.n.* (BHCB 69740), *P.L. Vianna 577* (BHCB), *Piliackas et al. 10907* (SPF), *R. Mello-Silva et al. in CFCR 8862* (SPF), *9040* (SPF), *R.C. Mota & P.L.*

Viana 1704 (BHCB, CEN), *1711* (BHCB), *R.C. Mota 1698* (BHCB, CEN), *1720* (BHCB), *1729* (CEN, BHCB), *2733* (BHCB), *R.S. Oliveira 276* (CEN, UB), *R.S. Oliveira et al. s.n.* (UB), *R.W. Windisch 2596* (HB), *R.W. Windisch 491 & A. de Ghillany* (HB), *S. Mayo et al. 7010-A* (SP), *S. Mayo et al. 7013* (SP), *T.F. Daniel & N. Hensold 2298* (SPF) *2298A* (SPF), *2315* (BHCB), *2369* (BHCB), *V.C. Souza et al. 8226* (ESA), *W.A. Teixeira s.n.* (BHCB 26081), *W.R. Anderson et al. 35415* (HB), *35417* (HB, MBM, NY, UB, US), *36098* (HB, NY, UB, US).

Habenaria exaltata. BRAZIL. *Amadeu 37* (HB, ICN), *E. Hassler 8721* (BM), *G. Hatschbach 10946* (HB, L, MBM, U), *13773* (MBM), *15962* (HB, MBM), *18323* (MBM), *G.F.J. Pabst 1318* (B, HB, HBG, K, RB, S), *J. Dutra 1074* (ICN, SI, SP), *J. Klein 149* (BHCB), *J.A.N. Batista et al. 2771* (BHCB), *2520* (BHCB), *2798* (BHCB), *J.L. Waechter 1976* (ICN), *L. Arzivenco 521* (ICN), *M. Emmerich 3174* (HB, R), *M. Pedron 6* (ICN), *P. Jorgensen 4646* (US), *4648* (S, SI), *P.K.H. Dusen 3272* (R, SP, SPF), *Z.A. Trinta 1204* (HB, HBG, K, L, LP, M).

Habenaria rodeiensis. BRAZIL. *A.A. Vale et al. 133* (BHCB), *A. de Saint-Hilaire B1 854* (P), *B2 2201* (P), *A. Krapovickas & C. L. Cristóbal 33555* (CTES), *A. Ruschi 52* (SP), *A.C. Brade 10657* (SP), *11367* (R), *12541* (RB), *s.n.* (R 28922, RB 53103), *C. Spannagel 228* (SP), *C.M. Izumisawa et al. 167* (PMSP), *C.N. de Fraga 609* (MBML), *D. Sucre 2522 & Braga 363* (RB), *D. Sucre 2292* (NY, RB, US), *E.P. Heringer et al. 6332* (IBGE, K), *11078* (HB), *16824* (HB), *18146-A* (IBGE), *18201* (IBGE), *E.R. Pansarin & L. Mickeliunas 1015* (BHCB, UEC), *E. Ule 4006* (HBG), *F.C. Hoehne 241* (SP), *F.H. Caetano s.n.* (HRCB), *F.R. Nonato 994* (HUEFS), *G. Edwall in CGGSP 367*0 (SP), *G. Hatschbach 1211* (MBM), *G. Hatschbach et al. 13451* (MBM), *G.F.J. Pabst 690* (HB), *928* (HB, NY), *937* (HB, NY), *938* (HB, K), *947* (HB), *964* (HB), *6822* (HB), *7323* (HB), *G.J. Shepherd et al. 7451* (UEC), *H. Schenck 2346* (BR), *J. Vidal 89* (R), *J.A.N. Batista 1419* (CEN), *J.A.N. Batista et al. 77* (CEN), *1471* (CEN), *1472* (CEN), *J.A.N. Batista & T.R. Peixoto 3273* (BHCB), *J.A. Jesus & T.S. Santos 404* (CEPEC), *Kuhlmann 6010* (RB), *L. Kollmann 86* (MBML), *2732* (MBML), *2733* (MBML), *L. Kollmann & R.R. Veruloet 2826* (MBML), *L. Kollmann et al. 2526* (MBML), *L.H. Bailey & E.Z. Bailey 1110* (AMES), *M. Mattos s.n.* (R 28932, 28954), *N.L. Abreu et al. 143* (CESJ), *O. Handro 2033* (SPF), *2085* (SPF), *P. Martuscelli 101* (SP), *R. Kautsky 88* (HB), *591* (HB), *R.C. Mota 2824* (BHCB), *R.F. Campos s.n.* (SP 28922), *R.M. Valadão et al. 67* (ALCB), *S.A. Mori et al. 10045* (CEPEC), *S. Lima & A.C. Brade 14322* (RB), *T. Konno et al. 763* (SP), *T. Jost et al. 364* (HRB), *V.C. Souza et al. 3651* (ESA), *W. Boone 366* (MBML), *533* (MBML).

LANKESTERIANA 13(3): 185—206. 2014.

INVITED PAPER*

ILLUSTRATIONS AND STUDIES IN NEOTROPICAL ORCHIDACEAE. THE *SPECKLINIA CONDYLATA* GROUP (PLEUROTHALLIDINAE) IN COSTA RICA AND PANAMA

Diego Bogarín[1,2,3], Zuleika Serracín[2] & Zabdy Samudio[2]

[1]Jardín Botánico Lankester, Universidad de Costa Rica. P.O. Box 302-7050 Cartago, Costa Rica, A.C.
[2]Herbario UCH, Universidad Autónoma de Chiriquí, 0427, David, Chiriquí, Panama
[3]Author for correspondence: diego.bogarin@ucr.ac.cr

Abstract. Taxonomy of discrete groups of taxa within Pleurothallidinae is critical for a better understanding of species diversity, evolution and phylogenetics. This paper focuses on the taxonomy and systematics of the species related to *Specklinia condylata* in Costa Rica and Panama. The taxonomic history and its phylogenetic position are discussed. The group is treated as comprising five species, three of them proposed as new to science. Each taxon is described on the basis of living material and illustrated in a composite plate. Overall distribution, maps, derivation of name, notes on species ecology, natural variation and diagnostic features are presented for each taxon. A key to the species and a comparative table is given to aid species identification.

Resumen: La taxonomía de grupos discretos de taxones dentro Pleurothallidinae es fundamental para una mejor comprensión de la diversidad de especies, evolución y filogenética. Este documento se centra en la taxonomía y sistemática de las especies relacionadas a *Specklinia condylata* en Costa Rica y Panamá. Se discute su historia taxonómica y posición filogenética. El grupo comprende cinco especies, tres de ellas se proponen como nuevas para la ciencia. Cada taxón se describe con base en material vivo y se ilustra en una lámina compuesta. Para cada taxón se presenta la distribución general, mapas, derivación del nombre, notas sobre ecología, variación natural y características diagnósticas. Se proporciona una clave para las especies y un cuadro comparativo para ayudar a la identificación de especies.

Key words / Palabras clave: new species, *Platystele, Sarcinula, Scaphosepalum,* taxonomy

Lindley (1830) established *Specklinia* Lindl. to include five species close to *Pleurothallis* R. Br. Lindley did not choose a type for the genus. In *Folia Orchidacea*, Lindley (1859) himself decided to merge the poorly defined group of about a dozen species contained in *Specklinia* into a broad concept of *Pleurothallis*. More than a century later, Garay & Sweet (1972) designated the orange-flowered *S. lanceola* (Sw.) Lindl. (=*Epidendrum lanceola* Sw.) as the lectotype of *Specklinia*. Then, Garay (1974) determined to treat *Specklinia* under *Pleurothallis s.l.* and proposed to classify the group under *Pleurothallis* subgenus *Specklinia* (Lindl.) Garay. Luer (1986) followed Garay in considering those species under a broad concept of *Pleurothallis* and created in addition two new subgenera: *Empusella* Luer and *Pseudoctomeria* Kraenzl. (Luer) and sections *Muscariae* Luer and *Tribuloides* Luer.

Species of *Specklinia* remained in *Pleurothallis* until Pridgeon & Chase (2001) assessed the monophyly of Pleurothallidinae. In one of the most parsimonious trees of the complete ITS nrDNA matrix, they found that *S. lanceola* belongs to a clade (treated as *Scaphosepalum clade or Clade F*) encompassing the species of subgenera *Specklinia* (sect. *Hymenodanthe* Barb.Rodr., *Muscariae* and

---

* This contribution was prepared as part of the special edition of Lankesteriana aimed to celebrate Lankester Botanical Garden´s (JBL) 40th anniversary.

Tribuloides), *Empusella* and *Pseudoctomeria*, together with the traditionally accepted genera *Acostaea* Schltr., *Dryadella* Luer, *Platystele* Schltr. and *Scaphosepalum* Pfitzer. Pridgeon & Chase (2001) and Luer (2006) published numerous transfers to *Specklinia*, making the genus large and difficult to define morphologically. Luer (2006) regarded the new circumscription of Pridgeon & Chase (2001) as a polyphyletic aggregation of many taxa. Instead, he proposed to split *Specklinia* into 13 genera: the five major groups of *Muscarella* Luer, *Pabstiella* Brieger & Senghas, *Panmorphia* Luer, *Sarcinula* Luer and *Specklinia*; the smaller groups of *Phloeophila* Hoehne & Schltr., *Ronaldella* Luer, *Sylphia* Luer and *Tribulago* Luer; and four other monospecific genera created for the rest of the morphologically “aberrant” species Luer (2006).

Different interpretations of the morphologic and phylogenetic evidence make *Specklinia* difficult to define. Almost 500 binomials attributed to the genus have been published but the exact number of species is still hard to calculate and it depends on the acceptance and definition of the groups within the clades (Pupulin *et al.* 2012). When Pridgeon & Chase (2001) redefined the genus, they recognized 86 species. In Pridgeon (2005), *Specklinia* was treated as comprising some 200 species, ranging from Mexico and the West Indies to Brazil and Bolivia.

Specklinia is still variable in terms of vegetative and floral morphology, however the genus can be recognized by the caespitose small plants with ramicauls shorter than the leaves, an abbreviated stem with an annulus, the leaves erect, elliptic, obovate or orbicular, coriaceous, the sepals and petals mostly acute or obtuse, membranous, the lateral sepals variously connate, the petals oblong-spatulate, acute or obtuse and the lip is hinged to the column foot. The column is winged, terete or clavate, with an erose or toothed clinandrium. The anther and stigma are ventral. The pollinarium is made up by two pollinia, free or lightly adherent to minute viscidia (Bogarín *et al.* 2013, Luer 2006, Pupulin *et al.* 2012, Pridgeon *et al.* 2005).

This paper is focused on a group of *Specklinia* that comprises the species close to *S. condylata* (Luer) Pridgeon & M.W.Chase. Here, it is informally treated as *S. condylata* group.

The *Specklinia condylata* Group. The first plant to be known of this group was collected by Augustus R. Endrés in the Pacific watershed of Cordillera de Talamanca in the locality of “Boca de Dota, towards Cerro Pito” in Costa Rica. He depicted the plant in a fine drawing accompanied with a detailed description, however the species was never published (W-0020241). Luer (1976) described the same species as *Pleurothallis condylata* based on a plant collected in western Panama around San Vicente de La Concepción, Chiriquí at 500 m of elevation. Luer (1976) compared the plant with *P. brighamii* S. Watson and its allies however the flower was described as comparatively larger, with yellow sepals and petals and dispersed purple-red dots or speckles. The purple, cuneate lip had the apex folded or decurved, appearing truncate. Luer (2006) also suggested a close relationship with *S. areldii* (Luer) Pridgeon & M.W.Chase from western Panama, a species with obovate, wider leaves, which we exclude from the *S. condylata* group because the acuminate sepals and the oblong lip, features that resemble more the flowers of S. *acrisepala* (Ames & C. Schweinf.) Pridgeon & M.W. Chase.

In general, plant morphology is fairly uniform and it is almost imposible to identify a specimen without flowers [even other closely allied species are quite similar when they are not in bloom i.e: *S. acrisepala* and *S. brighamii* (S.Watson) Pridgeon & M.W.Chase]. The separation among species is largely based on floral characters and/or the sum of a set of differences. Although, the group can be characterized mainly by the caespitose plants to 5.0-8.5 cm tall, with ramicauls enclosed by two tubular sheaths at base, the elliptic, oblong or obovate, coriaceous, conduplicate leaves, narrowing into a short petiole, the racemose inflorescences developed into a filiform peduncle with the rachis congested appearing fasciculate and the imbricate floral bracts covering the persistent pedicels forming like a mass of old bracts and pedicels. The flowers are produced successively and singly; the sepals and petals are entire, smooth, acute or obtuse, tailless, frequently speckled, maculate or stained; the lateral sepals are connate at the base, sometimes shallowly so, often forming a synsepal; and the petals widen towards the middle. The lip is oblong, spatulate or pandurate, always mostly purple, arcuate, entire, denticulate or erose, sulcate with a pair of longitudinal, parallel, apically convergent keels running up to the apex, basally glandular-trichomate, glutinose from the base towards the apex and between the calli on the median groove, hinged to the column foot. The apex is acute or obtuse but can be often curved downward so appearing retuse or emarginate. The column is arcuate, toothed and erose at apex. The anther and stigma are ventral and the pollinarium is made up by a pair of free, ovoid pollinia ending in a small hook at the base. The plants treated in this study are restricted to the tropical moist and wet forest from the central Pacific in Costa Rica towards western Panama at elevations between 300-1640 m (mostly between 300-600 m). They are somewhat common and can be found along streams and rivers in warm, humid areas in gallery forest, edges of primary forest or disturbed vegetation (Luer 2003). They mostly flower through the year. Potential pollinators have not been observed. The flowers produce a foetid, carrion-like smell in *S. berolinensis*, perhaps attracting flies.

Pridgeon *et al.* (2001) evaluated the phylogenetic position of *S. brighamii* and *S. condylata*. In one of the most parsimonious trees of the ITS nrDNA, both species were grouped into a subclade sister to *Platystele* and *Scaphosepalum*. The previous subclade is sister to another subclade comprising the species allied to *S. lanceola*, the type of *Specklinia.* However, the position of *S. brighamii-condylata* as sister to *Platystele* and *Scaphosepalum* is weakly supported (equally weighted bootstrap percentages < %50) in the ITS nrDNA analysis. Thus, the subclade *S. brighamii-condylata* is absent in the strict consensus tree from the combined matK/trnL-F/ITS nrDNA data set. In that combined analysis, the type clade of *Specklinia is sister to the Scaphosepalum-Platystele clade with 95% support*. Although the position of *S. brighamii-condylata* is not clear in Pridgeon & Chase (2001), they decided to transfer both species and their allies into *Specklinia*.

Luer (2002) considered that *Specklinia* as proposed by Pridgeon & Chase (2001) is still polyphyletic and suggested retaining the species in *Pleurothallis*. Later, Luer (2006) proposed to classify *S. condylata*, along with 24 other species, in *Sarcinula*, a genus characterized by the caespitose plants (similar to many others), elongated peduncles with a succession of overlapping floral bracts and a "fascicle" of pedicels forming a extremely congested raceme. The sepals are tailless and variously connate and the petals are acute or obtuse, widened towards the middle and always entire. Some species of *Muscarella* and *Panmorphia* also share the "fasciculate" congested raceme however the acuminate or tailed, fringed, denticulate or fimbriate sepals and shape of the lip distinguish them from *Sarcinula* (Luer 2006). Nevertheless, as proposed by Luer (2006), *Sarcinula* is polyphyletic and certainly includes several species embedded within the type clade of *Specklinia*, as found by Pupulin *et al.* (2012). Among them are the "orange-flowered" *Specklinia barbae* (Schltr.) Luer, *S. chontalensis* (A.H.Heller & A.D.Hawkes) Luer, *S. corniculata* (Sw.) Steud., *S. fulgens* (Rchb.f.) Pridgeon & M.W.Chase, *S. guanacastensis* (Ames & C.Schweinf.) Pridgeon & M.W.Chase and *S. psichion* (Luer) Luer. The type clade also encompasses: *S. lentiginosa* (F. Lehm. & Kraenzl.) Pridgeon & M.W. Chase, *S. tribuloides* (Sw.) Pridgeon & M.W.Chase and *S. endotrachys* (Rchb.f.) Pridgeon & M.W.Chase and its allies (Pupulin *et al.* 2012). The type of *Sarcinula*, *Specklinia acicularis* (Ames & C. Schweinf.) Pridgeon & M.W. Chase, has not been yet evaluated phylogenetically, however it is morphologically different from the species allied to *S. brighamii-condylata* as it has thick, acicular leaves (vs. oblong-elliptic, conduplicate) and the sepals are cellular-glandular, spiculate within (vs. glabrous).

The phylogenetic position of *S. brighamii-condylata* group is still subject of evaluation. Preliminary evidence presented in Bogarín *et al.* (2013) showed both species in a subclade basal to *Specklinia s.s.* The *Specklinia* clade which includes *S. lanceola* and its allies, *S. absurda* Bogarín, Karremans & R.Rincón, *S. fuegii* (Rchb.f.) Solano & Soto Arenas, [=*Sylphia fuegii* (Rchb.f.) Luer], *S. grobyi* (Bateman ex Lindl.) F. Barros, *S. picta* (Lindl.) Pridgeon & M.W. Chase and *S. costaricensis* (Rolfe) Pridgeon & M.W. Chase is again sister to the *Scaphosepalum-Platystele* clade (Bogarín *et al.* 2013, Pupulin *et al.* 2012, Pridgeon *et al.* 2001). Species closely allied to the *S. condylata* group include at least: *Specklinia acrisepala*, *S. alexii* (A.H. Heller) Pridgeon & M.W. Chase, *S. areldii, S. brighamii, S. calderae* (Luer) Luer, *S. scolopax* (Luer & R. Escobar) Pridgeon & M.W. Chase and *S. simmleriana* (Rendle) Luer.

A solid taxonomic basis is critical for phylogenetic evaluations. This paper is part of a series of contributions on the taxonomy of discrete groups of taxa within *Specklinia s.l.,* and other allied genera, intended for a better understanding of species diversity within clades and future phylogenetic evaluations. Here, we clarify the taxonomy of the *S. condylata* group. Fieldwork activities in Costa Rica and Panama led to the discovery of three new species allied to *S. condylata* that are here described and illustrated. Additional data related to *S. vierlingii* Baumbach are provided and discussed. Data on distribution, habitat and ecology, etymology, phenology and variation among populations are given for each species. A key to the species and a comparative table is given to aid species identification.

Materials and Methods. This study was performed at Jardín Botánico Lankester (JBL) and the Herbario UCH of the Universidad Autónoma de Chiriquí, Panamá. Sketches and images were prepared from living specimens with a Leica® MZ 9.5 stereomicroscope with drawing tube, Nikon® D5100 digital camera with a AF-S VR Micro-NIKKOR 105mm f/2.8G IF-ED lens and Epson Perfection Photo Scanner V600. Composite plates were diagrammed as consistently as possible to facilitate species comparison by using Adobe Photoshop®. Ink drawings were prepared in smooth Fabriano® paper of 240 g/m2 with a Rotring® Rapidograph 0.1mm using black capillary cartridges and traced in Artograph LightPad® A920. Specimens at JBL (from living and spirit collections), and dried and spirit material available at CR, INB, JBL, L, UCH and USJ were reviewed. The new species were illustrated from living specimens. Phenological data were recorded in the field, herbarium labels and from cultivated specimens. Ecological zones were estimated by using the Holdridge Life Zone System (Holdridge 1987) and the Mapa Ecológico de Costa Rica by Bolaños *et al. (2005). The map and georeferences for specimens were obtained by using a Garmin eTrex Vista GPS, Google Earth 6.1.0* © and the Epidendra (www.epidendra.org) database. The identity of *S. condylata* was studied by interpreting electronic images of the holotype of *S. condylata* available at SEL and Epidendra together with the protologue (Luer 1976). A visit to the type locality was organized in order to complement the interpretation of the type specimen with living material and to assess its natural variation. The plants gathered were documented by pictures and ink drawings following the procedures already described and deposited at UCH.

Taxonomic treatment

Specklinia acoana Bogarín, *sp. nov.*

TYPE: Costa Rica. San José: Pérez Zeledón, Platanares, near Villa Argentina, ca. 9°10’47”N 83°38’57”W, 950 m, recolectada por Jeremy Quesada, floreció en cultivo en el vivero de orquídeas de Gerson Villalobos en San Miguel de Santo Domino de Heredia, 27 octubre 2011, *D. Bogarín 9352* (holotype, JBL). Figs. 1, 2A, 2B, 3, 4A.

The combination of whitish flowers with dispersed stains and blotches on the sepals and petals; the spatulate, minutely denticulate lip, less than 5 mm long; and the connate sepals to 5 mm forming a concave synsepal to 12.0 x 7.0 mm distinguish S. acoana from its close allies.

Epiphytic, caespitose *herb*, up to 8.5 cm tall. Roots slender, flexuous, to 0.5 mm in diameter. *Ramicauls* slender, erect, 5-6 mm long, enclosed by 2 tubular sheaths up to 1 cm long. *Leaves* narrowly elliptic to obovate thick, coriaceous, acute, conduplicate, emarginate, with a short apiculus, 2.7-7.5 × 0.8-1.2 cm, cuneate, the base narrowing into an indistinct petiole less than 1 cm long. *Inflorescence* racemose, distichous, glabrous, patent, erect or suberect, successively single-flowered, born by a slender filiform peduncle, the rachis congested, appearing fasciculate, shorter than the leaves, up to 3.7 cm long, peduncle up to 3.3 cm long, rachis up to 0.4 cm long. *Floral bracts* ovate, acute, conduplicate, membranaceous, tubular, imbricating, up to 3 mm long. *Pedicel* 5 mm long, persistent. Ovary to 2 mm long, glabrous, green. *Flowers* the sepals and petals whitish-yellowish with purple-red stains, the lip purple, the column greenish with purple stains, anther cap reddish. *Dorsal sepal* ovate-elliptic, acute, entire, concave, 3-veined, dorsally keeled, connate to the lateral sepals for about 2 mm, 11 × 5 mm. *Lateral sepals* oblong, acute, connate for 5 mm, forming a mentum at base, 3-veined, dorsally keeled, 12 × 7 mm. *Petals* oblique, ovate-lanceolate, cuneate, acute, 3-veined, 4.1 × 2.6 mm. *Lip* spatulate, obovate, basally unguiculate,

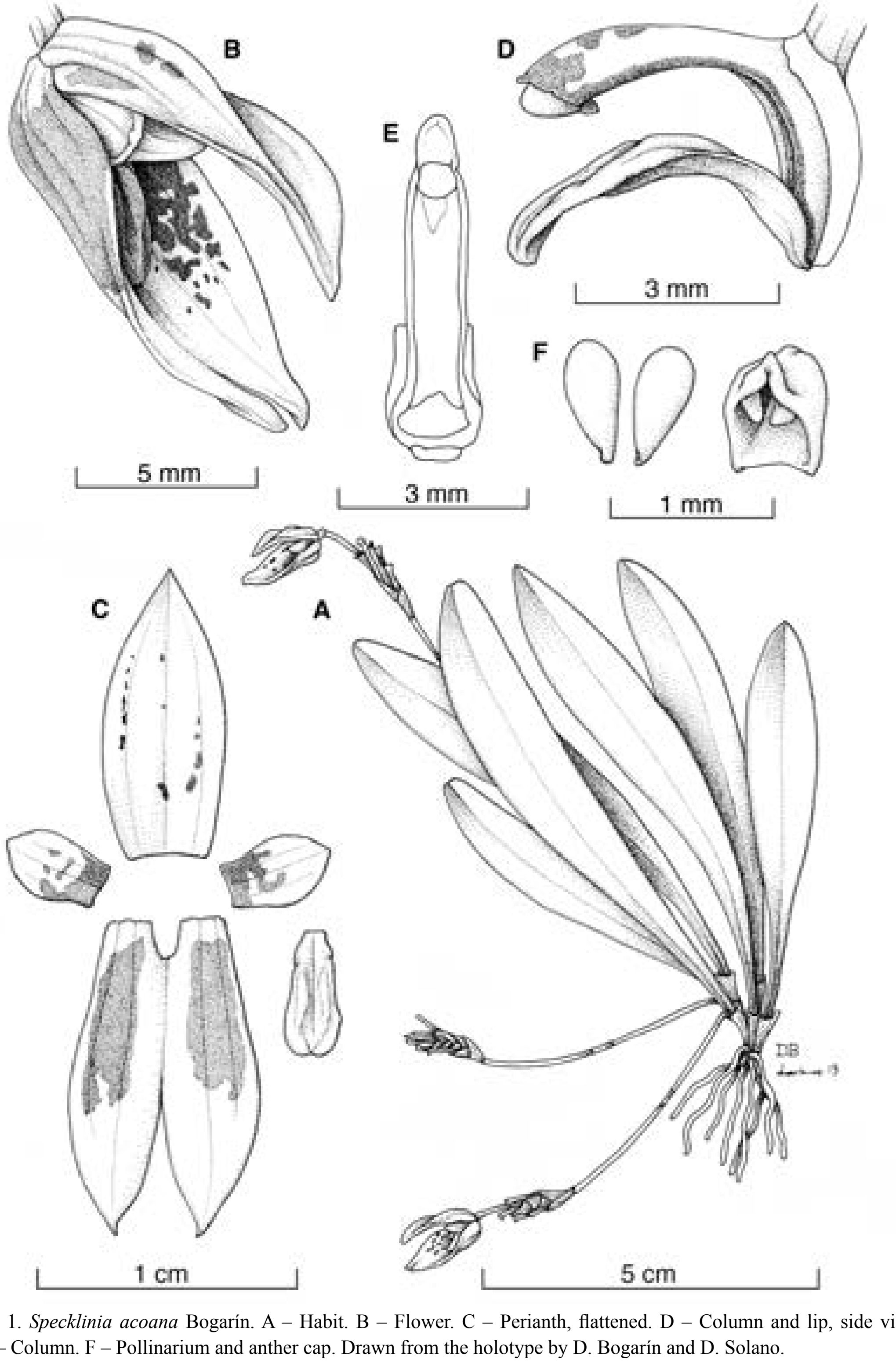


Figure 1. *Specklinia acoana* Bogarín. A – Habit. B – Flower. C – Perianth, flattened. D – Column and lip, side view. E – Column. F – Pollinarium and anther cap. Drawn from the holotype by D. Bogarín and D. Solano.

Figure 2. Flower morphology of: A. *Specklinia acoana* (*D. Bogarín 9352*). B. *Specklinia acoana* (*JBL-11957*). C. *Specklinia berolinensis* (F. Pupulin 2325). D. *Specklinia berolinensis* (*A. Karremans 5807*). E. *Specklinia condylata* (*D. Bogarín 10364*). F. *Specklinia condylata* (*D. Bogarín 7855*). G. *Specklinia icterina* (*D. Bogarín 8767*). H. *Specklinia vierlingii* (*F. Pupulin 2894*). I. *Specklinia vierlingii* (*D. Bogarín 7350*).

with a pair of small lobules at the middle, adnate to the column foot, slightly erose, arcuate, obtuse, with two longitudinal, parallel, apically convergent keels running up to the apex, sulcate, basally glutinose from the base towards the apex between the calli, 5.0 × 2.2 mm, the apex obtuse but often curved downward so appearing retuse. *Column* cylindric, footed, to 5.2 mm long, erose, the anther and stigma ventral, greenish stained with purple. *Pollinia* two, ovoid, without viscidium, ending in a hook. *Anther cap* cucullate, white, stained with purple.

Distribution: endemic to the southern Pacific of Costa Rica (Fig. 3).

Habitat and ecology: epiphytic in tropical moist forest, tropical moist forest premontane belt transition in secondary and primary vegetation at around 500-800 m of elevation.

Etymology: named after Asociación Costarricense de Orquideología (A.C.O) founded in 1970 by a group of orchid enthusiasts led by Miguel Angel Ramírez, Dorothy Lankester, Rafael Lucas Rodríguez Caballero, Roy Lent and Margarita de Lent among others with the support of the Latin-American Committee of Orchidology and Helena Baraya de Ospina, former President of the Sociedad Colombiana de Orquideología. A.C.O's efforts through Rafael Lucas Rodríguez were crucial to save the orchid garden of Charles H. Lankester at "El Silvestre" that was later transferred to the University of Costa Rica on March 2, 1973.

Phenology: plants flower through the year but mostly from October to November.

The combination of whitish flowers with dispersed stains and blotches on the sepals and petals; the spatulate, minutely denticulate lip, 5 mm long; and the sepals connate to 5 mm forming a concave synsepal to 12.0 x 7.0 mm distinguish *S. acoana* from other members of the group. It is most similar to *S. condylata*, however the latter has yellowish flowers with dispersed speckles on the sepals and petals (vs. whitish with blotches and stains) and the lip is longer, >7.5 mm long and wider > 3.0 mm (vs. ~5.0 mm long, <2.2 mm wide), pandurate (vs. spatulate to oblong) and the callus is made up by two prominent whitish-yellowish cushions at the middle (vs. two purple low keels) (Fig. 4A). For a detailed comparison among its allies see Table 1.

Additional material examined: Costa Rica. San José: Pérez Zeledón, Rivas, brought to Jardín Botánico Lankester by *D. Jiménez s.n.*, June 26, 2012 (JBL-spirit). Without locality data, flowered in cultivation at Jardín Botánico Lankester, Universidad de Costa Rica, October 31, 2009, *JBL-11957* (JBL-spirit) (Fig. 2B).

Specklinia berolinensis Bogarín, *sp. nov.*

TYPE: Costa Rica. San José: Pérez Zeledón, San Ramón Norte, trail to the summit of Cerro Pelón, 1420-1640 m, secondary mature and primary lower montane moist forest, 3 May 2000, *F. Pupulin 2325,*

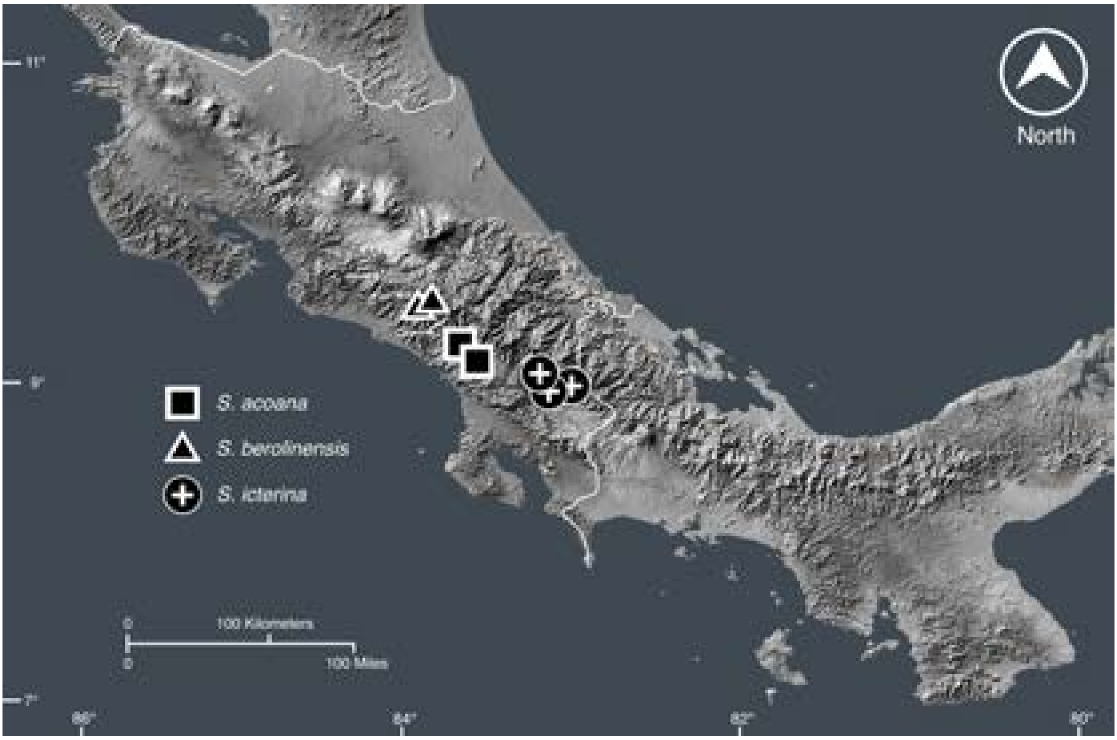


Figure 3. Geographic distribution of *Specklinia acoana*, *Specklinia berolinensis* and *Specklinia icterina*.

Table 1. Comparison of the main differences among the species of *S. condylata* group.

Character	***S. acoana***	***S. berolinensis***	***S. condylata***	***S. icterina***	***S. vierlingii***
Ovary	green	spotted with red	spotted with red	green	spotted with red
Dorsal sepal	ovate-elliptic, 11 x 5 mm	ovate, 8.0 x 4.5 mm	oblong-elliptic, 12.0-16.0 x 3.3-6.0 mm	ovate, 13.5 x 4.5 mm	oblong, 12.0-14.0 x 5.0-5.5 mm
Lateral sepals	12 x 7 mm, oblong, connate to 5 mm	oblong, 9.4 x 6.3 mm, connate 1.5 mm	oblong-ovate, 12-17 x 4-8 mm, connate 5-9 mm or sometimes almost free	ovate, 14.5 x 8.5 mm, connate to 5 mm	oblong-ovate, 12-14 x 6-7 mm, connate to 6.5 mm
Petals	ovate-lanceolate, 4.1 x 2.6 mm	oblong-obovate, 3.5 x 1.7 mm	obovate-lanceolate, 4.5-5.0 x 2.0-3.0 mm	obovate, 4.5 x 2.0 mm	narrowly oblong, 4.0-5.0 x 1.0-1.5 mm
Lip	spatulate to oblong, minutely denticulate, 5.0 x 2.2 mm	spatulate, entire, 4.5-5.0 x 1.7-2.0 mm	pandurate, denticulate, 7.5-8.0 x 3.0-3.5 cm	oblong, minutely denticulate, 5.0 x 2.5 mm	pandurate, erose, 8.0-10.0 x 3.5-4.0 mm
Lip apex	often with the apex folded	the apex never folding	often with the apex folded	often with the apex folded	rarely with the apex folded
Lip color	purple	purple	purple	basally yellowish, apically purple	purple
Column	greenish-yellowish, maculate, 5.2 mm	greenish-yellowish, 6.0 mm	greenish-yellowish, 9 mm	greenish, immaculate 5.4 mm	greenish-yellowish, 12 mm
Flower color	whitish with dispersed blotches and stains along sepals and petals	yellowish with blotches and stains along the veins of sepals and petals	yellowish with many dispersed red-purple speckles along sepals and petals	yellow, immaculate	yellowish-cream with purple speckles and blotches and sometimes with the veins purple
Habitat					
Elevation (m)	500-800	1420 to 1640	200 to 600 see Habitat and ecology for S. condylata	500 to 920	300 to 650
Life Zone	tropical moist forest, tropical moist forest premontane belt transition	premontane wet forest	tropical wet forest	premontane wet forest, rain forest transition and tropical wet forest premontane belt transition	tropical wet forest, tropical moist forest premontane belt transition and tropical moist forest

Figure 4. Comparison of lips (front view): A. *Specklinia acoana* (*D. Bogarín 9352*). B. *Specklinia berolinensis* (*F. Pupulin 2325*). C. *Specklinia icterina* (*D. Bogarín 8767*). D. *Specklinia condylata* (*D. Bogarín 10364*). E. *Specklinia condylata* (*D. Bogarín 7855*). F. *Specklinia vierlingii* (*F. Pupulin 2894*). Scale bar = 5 mm.

L. Spadari, J. Cambronero, V. Juárez-Pérez & K. Granado (holotype, JBL). Figs. 2c, 2d, 3, 4b, 5.

Specklinia berolinensis is distinguished by the yellowish flowers with purple blotches, stains and stripes along the veins of the sepals and petals, the smaller sepals < 3.5 mm long, the dorsal sepal < 8 mm long and lateral sepals < 9.5 mm long, the lateral sepals almost free and not developing an evident synsepal and the entire lip with rounded apex, never folding or curved down apically.

Epiphytic, caespitose, pendent or suberect *herb,* up to 8 cm tall. Roots slender, flexuous, to 0.5 mm in diameter. *Ramicauls s*lender, erect, terete, to 7 mm long, enclosed by 2 tubular sheaths up to 1 cm long. *Leaves* narrowly obovate thick, coriaceous, acute, conduplicate, emarginate, with a short apiculus, 3.5-8.0 × 0.6-0.9 cm, cuneate, the base narrowing into a indistinct petiole less than 4 mm long. *Inflorescence* racemose, distichous, glabrous, patent or creeping down, successively single-flowered, producing one flower at once, born by a slender filiform peduncle; peduncle bracts tubular to 3 mm long, the rachis congested appearing fasciculate, up to 6.5 cm long, peduncle 3-4 cm long, rachis up to 1.5 cm long. *Floral bracts* tubular, apiculate, conduplicate, membranaceous, imbricating, up to 4 mm long. *Pedicel* 5 mm long, persistent. *Ovary* to 2 mm long, glabrous, green spotted with red. *Flowers* hyaline, whitish or greenish, the sepals stained with purple red along the veins with few dispersed purple dots in between, the dorsal sepal adaxially striped with purple, the petals yellowish with purple stripes and purple apex, the lip purple, the column greenish-yellow with purple red stripes along the margin. *Dorsal sepal* ovate, acute, entire, reflexed, concave, 3-veined, dorsally keeled, connate to the lateral sepals for about 1.5 mm, 8.0 × 4.5 mm. *Lateral sepals* oblong, acute, connate for 1.5 mm, forming a mentum at base, 3-veined, dorsally keeled, 9.4 × 6.3 mm. *Petals o*blique, oblong-obovate, cuneate, acute, 3-veined, 3.5 × 1.7 mm. *Lip* spatulate, oblong-obovate, basally unguiculate, with a pair of small lobules at the middle, adnate to the column foot, entire, arcuate, rounded, with two longitudinal, parallel, apically convergent keels running up to the apex, sulcate, basally glutinose from the base towards the apex between the keels, 4.5-5.0 × 1.7-2.0 mm. *Column* cylindrical, footed, to 6 mm long, with a pair of apical arms, erose, the anther and the stigma ventral, greenish stained with purple. *Pollinia* two, ovoid, without viscidium, ending in a hook. *Anther cap* cucullate, white, stained with purple.

Distribution: restricted to the type locality at Berlín de Páramo de Pérez Zeledón, San José in the neighbouring areas of Fila Temblor, Fila Zapotales, Cerro Pelón and

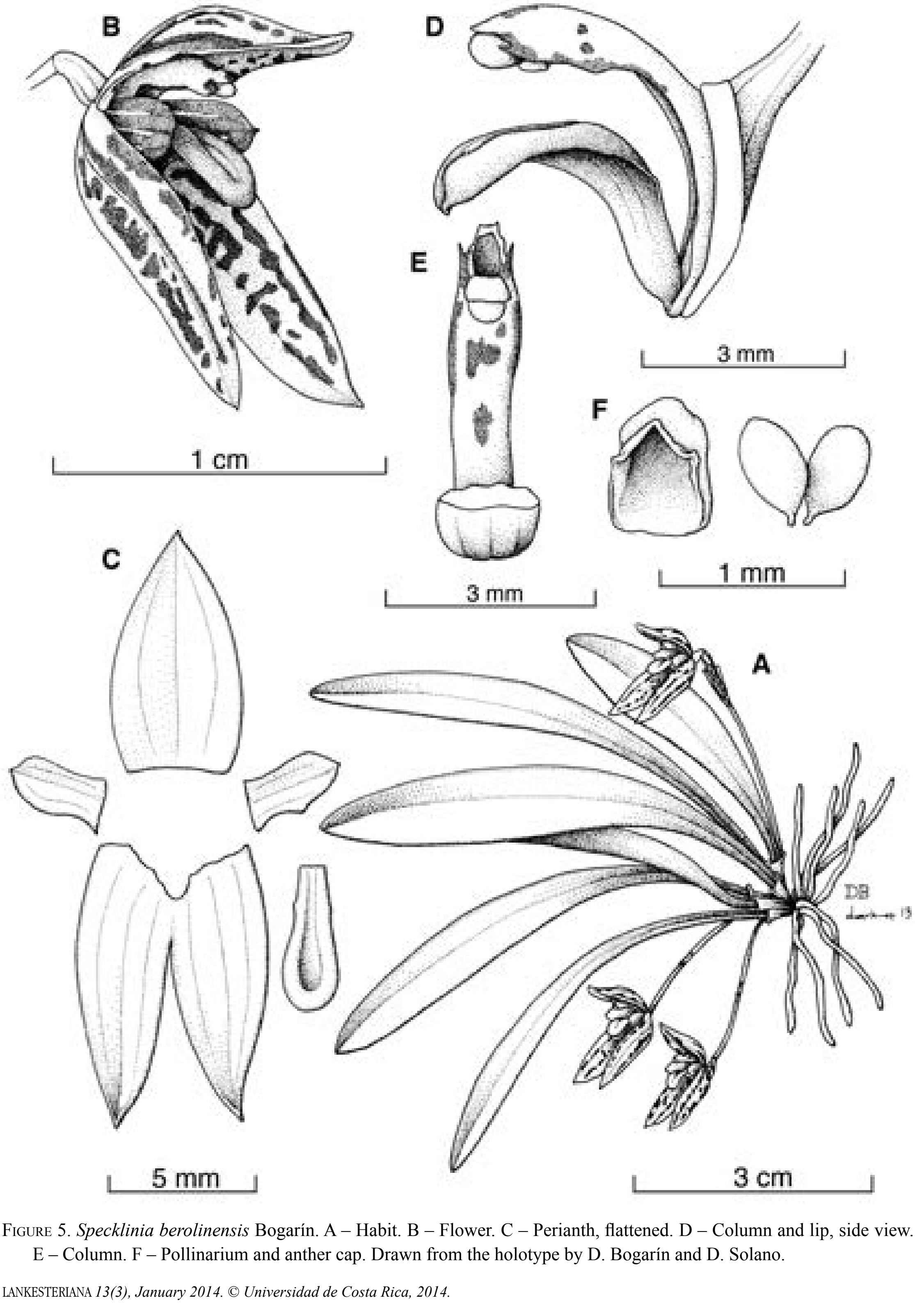


FIGURE 5. *Specklinia berolinensis* Bogarín. A – Habit. B – Flower. C – Perianth, flattened. D – Column and lip, side view. E – Column. F – Pollinarium and anther cap. Drawn from the holotype by D. Bogarín and D. Solano.

the headwaters of río División in the Pacific watershed of Cordillera de Talamanca in Costa Rica. (Fig. 3).

Habitat and ecology: epiphytic in premontane wet forest along the edge of primary forest in trunks with mosses from 1420 to 1640 m of elevation.

Etymology: named after the locality of Berlín de Pérez Zeledón, San José where this species is restricted.

Phenology: plants flower through the year but mostly from August to November.

Compared to its allies, *S. berolinensis* is distinguished by the yellowish flowers with purple blotches, stains and stripes along the veins of the sepals and petals (vs. dispersed speckles or blotches); the smaller sepals < 3.5 mm long (vs. > 4 mm) (see Table 1); the dorsal sepal < 8 mm long (vs. > 11 mm) and lateral sepals < 9.5 mm long (vs. > 12 mm); the lateral sepals almost free (connate for about 1.5 mm) and not developing an evident synsepal (vs. connate > 5 mm, developing an evident synsepal) and the entire lip, with rounded apex, never folding or curved down apically (vs. denticulate or erose, acute or obtuse and folding apically) (Fig. 4B). The inflorescences are patent but sometimes they are creeping down, prostrate on the substrate, just curving up when the first bud is mature. *Specklinia berolinensis* is found at higher elevations (between 1420 to 1640 m) in comparison to its allies that have been recorded from lower elevations (< 920 m, mainly between 300-600 m).

Specklinia berolinensis and *S. condylata* are quite different species separated mainly by the size and color of the flowers which are yellowish with blotches and stains along the veins of sepals and petals (vs. yellowish with many dispersed red-purple speckles along sepals and petals), the spatulate, entire, shorter lip to 4.5-5.0 × 1.7-2.0 mm (vs. pandurate, denticulate, larger to 7.5-8.0 × 3.0-3.5 cm) which never folds apically (vs. folding apically) and without two prominent cushions at the middle (vs. with prominent whitish-yellowish cushions at the middle). Flowers of *S. berolinensis* produce a strong carrion-like smell in the afternoon and evening similar to that of *S. vierlingii* but no smell has been perceived for *S. condylata*. Plants of both species are vegetatively similar but *S. berolinensis* has narrower leaves < 0.9 cm long whereas *S. condylata* has wider leaves > 0.9 cm long and up to 1.2 cm. Here, we accept *S. condylata* as a species ranging from the central Pacific of Costa Rica towards western Panama. This species shows variation in size of the flowers, the lip apex and coloration (see Table 1 and discussion of *S. condylata*). However this variation does not overlap with the features observed in *S. berolinensis*. The color and size of the flowers of *S. berolinensis* are consistent among the populations studied. Those features were not observed in the variation range of any of the populations of *S. condylata*.

Additional material examined: Costa Rica. San José: Pérez Zeledón, San Ramón Norte, trail to the summit of Cerro Pelón, 1420-1640 m, secondary mature and primary lower montane moist forest, 3 May 2000, *F. Pupulin 2326, L. Spadari, J. Cambronero, V. Juárez-Pérez & K. Granado* (JBL-spirit). San José: Pérez Zeledón, Berlín, A. Quesada-Chanto s.n. (JBL-spirit). Pérez Zeledón, Páramo, Berlín, Purruja, Fila Temblor, ca. 2 km al noroeste de Berlín, 9°26'13.22"N 83°46'41.97"W, 1429 m, bosque pluvial premontano, en bosque secundario, 21 marzo 2013, *A.Karremans 5807 & D. Bogarín* (JBL-spirit) (Fig. 2D).

Specklinia condylata (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 257. 2001. *Pleurothallis condylata* Luer, Selbyana 3(1-2): 80-81, f. 143. 1976. *Sarcinula condylata* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard 105: 208. 2006.

TYPE: Panama. Chiriqui: epiphytic in trees along the stream near San Vicente, alt. 500 m., between Concepción and Volcán, 11 Sept 1976, *C. Luer & H. Butcher 1198* (holotype, SEL). Figs. 2E, 2F, 4D, 4E, 6, 7, 8, 9, 10.

Epiphytic, caespitose, pendent or suberect, *herb*, up to 8 cm tall. *Roots* slender, flexuous, to 0.5 mm in diameter. *Ramicauls* slender, erect, 5-8 mm long, enclosed by 2 tubular sheaths up to 1 cm long. *Leaves* narrowly obovate, thick, coriaceous, acute, conduplicate, emarginate, with a short apiculus, 3.5-8.0 × 0.9-1.2 cm, cuneate, the base narrowing into a indistinct petiole less than 4 mm long. *Inflorescence r*acemose, distichous, glabrous, pendent or suberect, successively single-flowered, producing one flower at once, born by a slender filiform peduncle; peduncle bracts tubular to 3 mm long, the rachis congested, appearing fasciculate, 3.5-6.0 cm long, peduncle 3.5-

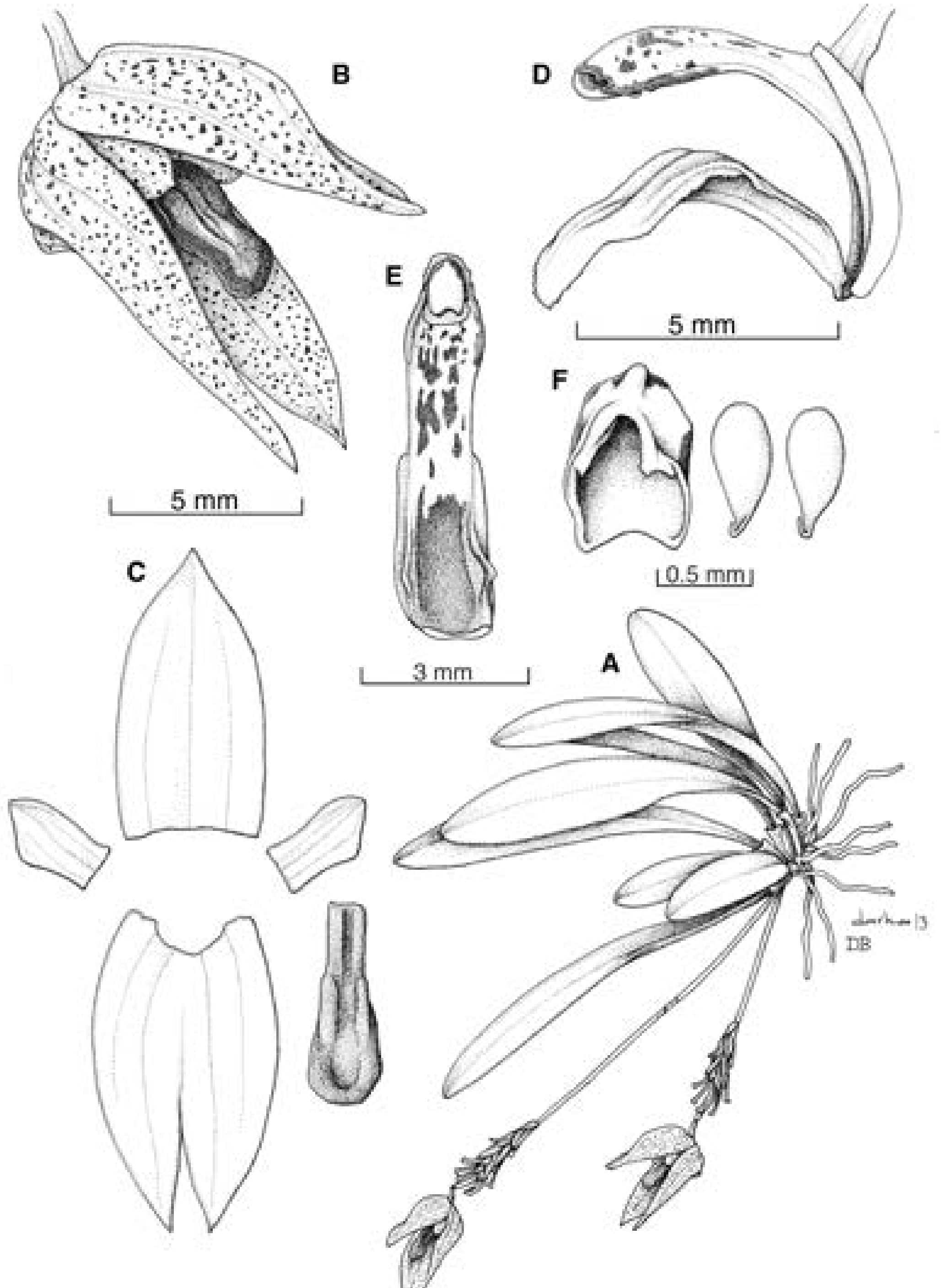


FIGURE 6. *Specklinia condylata* (Luer) Pridgeon & M.W.Chase. A – Habit. B – Flower. C – Perianth, flatten. D – Column and lip, side view. E – Column. F. Pollinarium and anther cap. Drawn by D. Bogarín and D. Solano based on *D. Bogarín et al. 10364* (UCH).

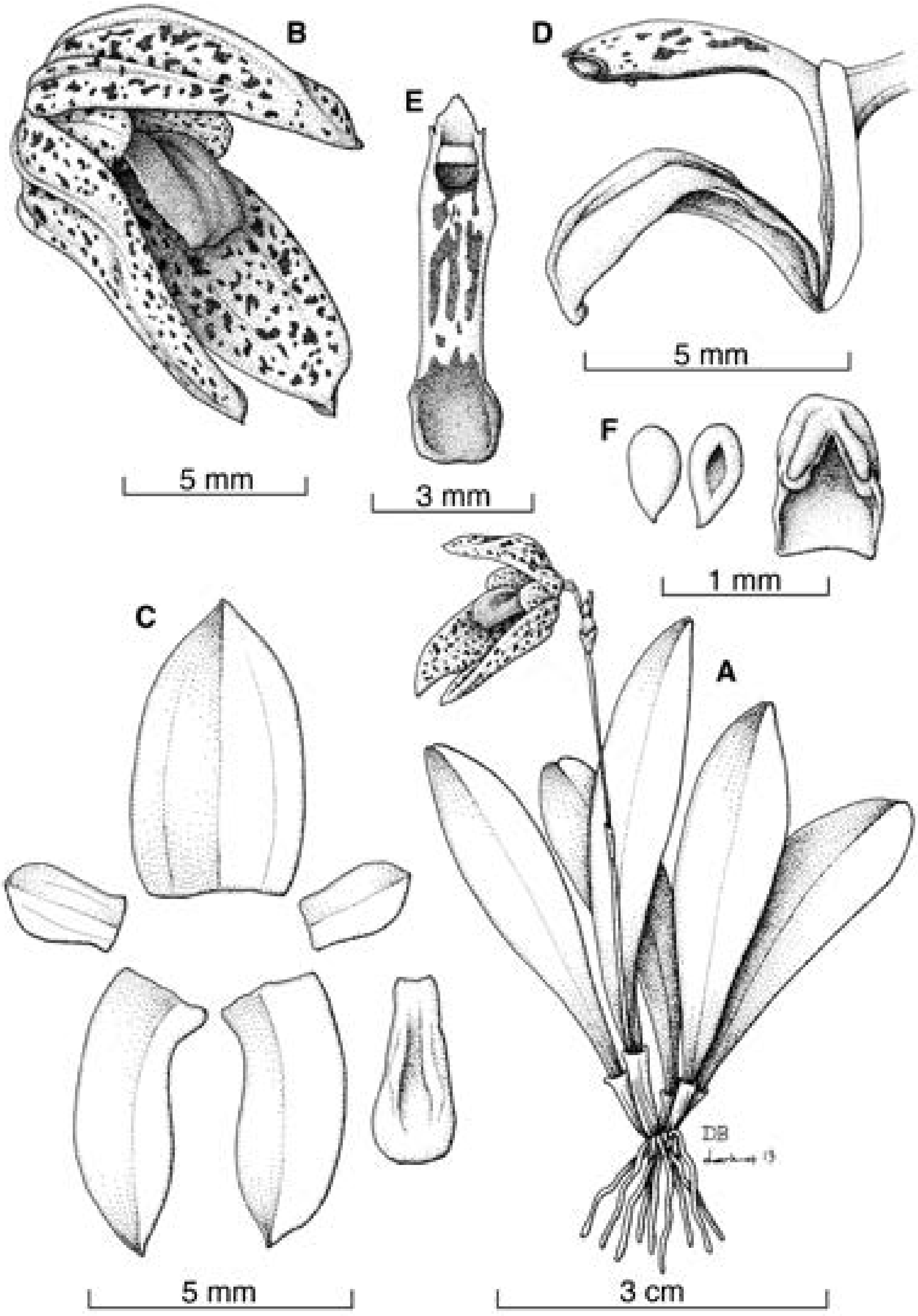


Figure 7. *Specklinia condylata* (Luer) Pridgeon & M.W.Chase. A – Habit. B – Flower. C – Perianth flattened. D – Column and lip, side view. E – Column. F – Pollinarium and anther cap. Drawn by D. Bogarín and D. Solano based on *D. Bogarín 7859* (JBL-spirit).

Figure 8. Comparison of the flower morphology of individuals of *Specklinia condylata:* A. (*D. Bogarín 7855*, Costa Rica). B. (*M. Fernández 173*, Costa Rica). C. (*M. Fernández 171*, Costa Rica). D. (*D. Bogarín 7859*, Costa Rica). E. (*Z. Samudio s.n.*, Panamá). F. (*D. Bogarín 10364*, Panamá). G. (*D. Bogarín 7855*, Costa Rica). H. (*D. Bogarín 7859*, Costa Rica). I. (*M. Fernández 168*, Costa Rica).

6.0 cm long, rachis up to 1 cm long. *Floral bracts* tubular, apiculate, conduplicate, membranaceous, imbricating, up to 2-4 mm long. *Pedicel* 4-7 mm long, persistent. *Ovary* to 3 mm long, glabrous, green or with purple spots. *Flowers* showy, hyaline, yellowish, sepals and petals densely speckled with purple-brown, the lip purple red, the column greenish stained with maroon. *Dorsal sepal* oblong-elliptic, acute, entire, reflexed, concave, 3-veined, dorsally keeled, connate to the lateral sepals for about 2 mm, 12.0-16.0 × 3.3-6.0 mm. *Lateral sepals* oblong-ovate, acute, connate for 5-9 mm, forming a mentum at base, 3-veined, dorsally keeled, 12-17 × 4-8 mm. *Petals* oblique, obovate-lanceolate, cuneate, acute, 3-veined, 4.5-5.0 × 2.0-3.0 mm. *Lip* spatulate, obovate, basally unguiculate, with a pair of small lobules at the middle, adnate to the column foot, minutely erose to fimbriate, arcuate, obtuse, with two longitudinal, parallel, apically

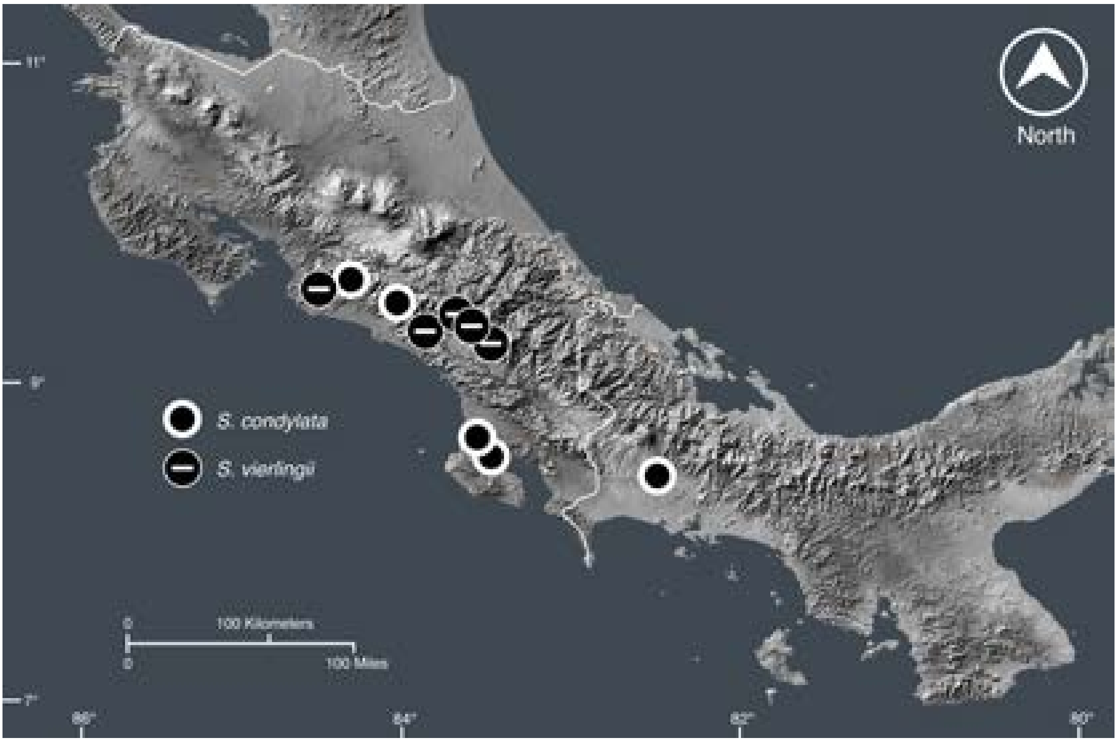


Figure 9. Geographic distribution of *Specklinia condylata* and *Specklinia vierlingii*.

convergent keels running up to the apex, forming two prominent cushions (whitish-yellowish) at the middle, sulcate, basally glutinose from the base towards the apex between the calli, 7.5-8.0 × 3.0-3.5 cm, the apex often curved downward so appearing retuse. *Column* cylindrical, footed, to 9 mm long, with a pair of apical arms, erose, the anther and stigma ventral, greenish stained with purple. *Pollinia* two, ovoid, without viscidium, ending in a hook. *Anther cap* cucullate, white, stained with purple.

Distribution: endemic to the Pacific lowlands of Costa Rica and Panama.

Habitat and ecology: epiphytic in tropical wet forest on trees along streams and rivers, gallery forests and edge of mature vegetation in humid areas of the Pacific coast from central Costa Rica towards western Panama, from 200 to 600 m of elevation Luer (2006) cited two records of *S. condylata* from cultivated plants obtained from L. Acosta allegedly from 1500 and 1800 m (one in a quite odd location above San Cristóbal where no plants of this group have been seen in the field or in any herbaria). The other comes from above San Vito the type locality of *S. icterina however it was not possible to check both specimens at MO. Although those records* seem to considerably extend the elevation range of *S. condylata*, no other records of this species are known from 600 to 1800 m. It seems that the locality given in the specimens of L. Acosta are erroneous or may correspond to a different species. Plants were observed growing on *Zygia longifolia* (Fabaceae) in Panama.

Etymology: from the Latin *condylatus*, “with knuckles, or knuckled” and Greek *kondylos* “knuckle, fist”, in allusion to the appearance of the lip of the type specimen.

Phenology: plants flower through the year but mostly from April to November.

Luer (1976) described this species from a collection in western Panama. He stated that the species is vegetatively similar to *P. brighamii* and its allies, although the flower is considerably larger and heavier. Luer (1976) characterized the species by the golden sepals and petals which are diffusely dotted with brownish-purple. The lip is deep purple, broadly dilated towards the deflexed apex, appearing truncate

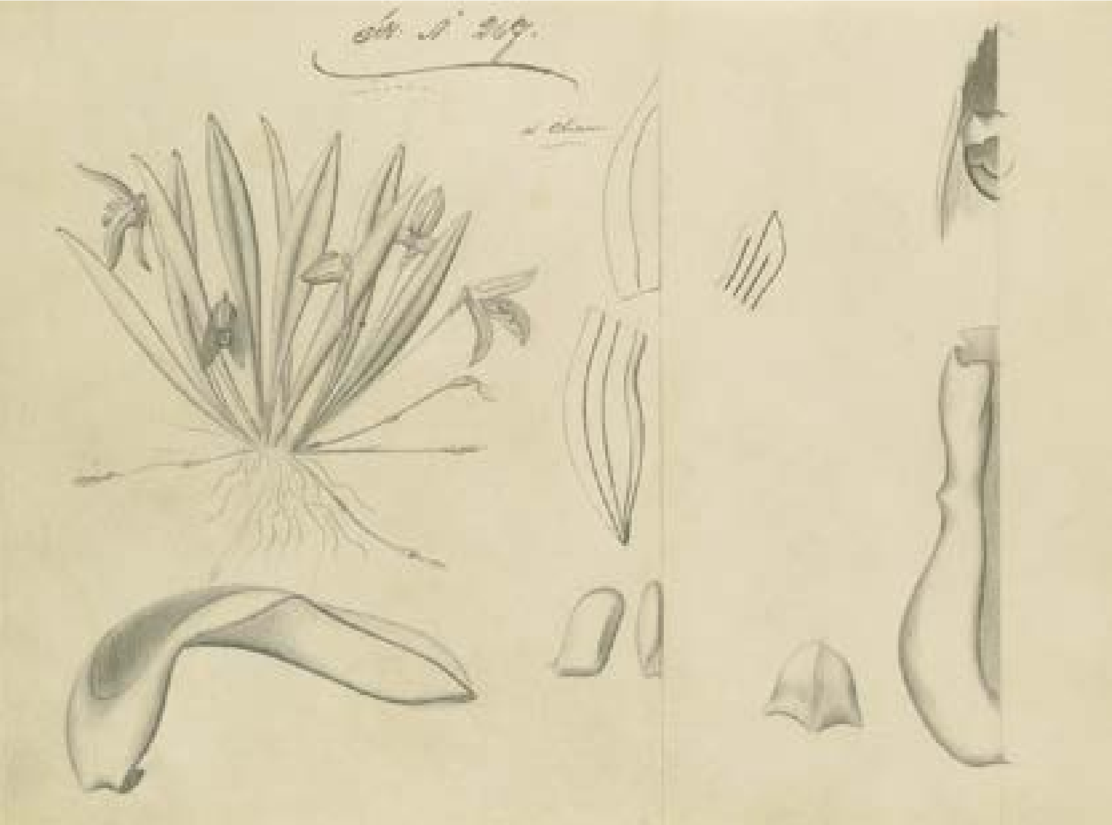


FIGURE 10. Drawing of *Specklinia condylata by A.R. Endrés (*W-0020241). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

or retuse, giving the appearance of two-knuckled fist in a gauntlet (Luer 2003). Luer (2006) also suggested a close relationship with *S. areldii* (Luer) Pridgeon & M.W.Chase (see introduction).

Augustus R. Endrés collected and illustrated the first specimen attributed to this species in Costa Rica, however it was never published (W-0020241) (Fig. 10). *Specklinia condylata* is easily distinguished by the yellowish sepals densely speckled with purple-brown, and the pandurate lip, deep purple or reddish with yellowish calli at the middle. It is most similar to S. vierlingii however the latter species has yellowish-cream flowers with purple speckles and blotches, sometimes with the veins purple (vs. yellowish, densely speckled with purple-brown) and the petals are narrowly oblong, < 1.5 mm wide (vs. obovate-lanceolate, > 2 mm wide). Specklinia acoana is also similar but the latter species has white flowers with purple stains and the lip is shorter, < 5 mm long (rather than > 7.5 mm long). Lip size is similar between S. condylata and S. vierlingii. Both species present a larger lip (> 7.5 mm long, > 3.0 mm wide) when compared to their allies (vs. < 5.0 mm long, < 2.5 mm wide). Other differences among its closest relatives are summarized in Table 1.

Plants gathered from the type locality in Panama show variation in the lip apex and coloration (Figs. 8E, 8F). The lip is often deflexed apically but not always and some flowers have a deep purple lip whereas others are reddish with yellowish calli (Fig. 4D, 4E). However, the characters cited by Luer (1976) in the protologue were also observed in the plants studied from the type locality. In Costa Rica, this species is also variable in the colour of flowers varying from yellowish to densely speckled with purple-brown and red to purple lip (Fig. 8). The lateral sepals are connate for 9 mm but sometimes they are almost free, connate to 5 mm (A.R. Endrés 267, W; M. Fernández 171, JBL). (Figs. 8H, 8E, 8C, 10).

Additional material examined: Costa Rica. San José: Puriscal, Chires, Santa Rosa, Parque Nacional La Cangreja, orillas del Río Negro y Quebrada La Cangreja, 9°42’02.5” N 84°23’29.9” W, 383 m, bosque muy húmedo tropical, epífitas en árboles caídos, 27 julio 2010, *D. Bogarín 7859, R.L. Dressler, M. Fernández & C. Smith* (JBL) (Figs. 7, 8H). Same locality, *D. Bogarín 7855* (JBL-spirit) (Fig. 8A, 8G), *M. Fernández 168* (Fig. 8I), *M. Fernández 171* (Fig. 8C), *M. Fernández 173* (JBL-spirit) (Fig. 8B) and *M. Fernández 175* (JBL-spirit). Tarrazú: Boca de Dota [Santa Marta de San Lorenzo de Tarrazú], towards Cerro Pito, Nov-Dec, A.R. Endrés 267 (W) (Fig. 10). Puntarenas: Osa, Sierpe, El Campo, subiendo por la fila entre Aguabuena y Baneguitas, cuenca superior de Quebrada Banegas, bajando hasta la Quebrada Digo digo, 8°42’00”N 83°31’00”W, 350 m, 13 enero 1991, *G. Herrera 4818* (INB). Osa, Sierpe, San Juan, cuenca superior de Río San Juan, 8°43’50”N 83°33’10”W, 600 m, epífita, 25 enero 1991, *G. Herrera 4871 (INB)*. Panama. Chiriquí: Bugaba, La Estrella, orillas del río Escárrea, cerca de San Vicente, 8°32’01.96”N 82°39’54.4”W, 253 m, epífitas en *Zygia longifolia*, 25 julio 2013, *D. Bogarín 10364, Z. Samudio & Z. Serracín* (UCH) (Fig. 6, 8F). Same locality, *Z. Samudio s.n., D. Bogarín & Z. Serracín* (UCH) (Fig. 8E). Chiriquí: sin más datos, obtenida de Finca Drácula, cultivada por Gerson Villalobos en Santo Domingo de Heredia, Costa Rica, 23 enero 2012, *D. Bogarín 9452* (JBL-spirit).

Specklinia icterina Bogarín*, sp. nov.*

TYPE: Costa Rica. Puntarenas: Coto Brus, Limoncito, Jabillo, orillas del Río Cotón, ca. 500 m, invenit William Chacón, floreció en cultivo en el Orquidario Happy Garden, 20 abril 2011, *D. Bogarín 8767* (holotype, JBL; isotype CR). Figs. 2G, 3, 4C, 11.

Specklinia icterina is readily distinguished by the immaculate yellow, ovate, acute sepals and petals, the oblong lip with the apex obtuse but often curved downward so appearing retuse or emarginate, basally yellowish with purple from the middle towards the apex, the green immaculate ovary and column and the white anther cap.

Epiphytic, caespitose *herb,* up to 7.5 cm tall. *Roots* slender, flexuous, to 0.5 mm in diameter. *Ramicauls* slender, erect, 5-6 mm long, enclosed by 2 tubular sheaths up to 1 cm long. *Leaves* narrowly elliptic to obovate thick, coriaceous, acute, conduplicate, emarginate, with a short apiculus, 6.0-7.0 × 1.0-0.8 cm, cuneate, the base narrowing into a indistinct petiole less than 1 cm long. *Inflorescence* racemose, distichous, glabrous, patent, erect or suberect, successively single-flowered, born by a slender filiform peduncle, the rachis congested, appearing fasciculate, up to 7.5 cm long, usually longer than the leaves, peduncle up to 5.7 cm long, rachis up to 1.8 cm long. *Floral bracts* ovate, acute, conduplicate, membranaceous, tubular, imbricating, up to 5 mm long. *Pedicels* to 1 cm long, persistent. *Ovary* to 2 mm long, glabrous, green. *Flowers* the sepals and petals yellow, immaculate, the lip yellowish-cream basally, purple red apically, with the callus yellowish, the column green, the anther cap white. *Dorsal sepal* ovate, acute, entire, concave, 3-veined, dorsally keeled, connate to the lateral sepals for about 1.5 mm, 13.5 × 4.5 mm. *Lateral sepals* ovate, acute, connate for 5 mm, forming a mentum at base, 3-veined, dorsally keeled, 14.5 × 8.5 mm. *Petals* oblique, obovate, cuneate, acute, 3-veined, 4.5 × 2.0 mm. *Lip* oblong, basally unguiculate, adnate to the column foot, minutely denticulate, arcuate, obtuse, with two longitudinal, parallel, apically convergent keels running up to the apex, sulcate, basally glutinose from the base towards the apex between the calli, 5.0 × 2.5 mm, the apex obtuse but often curved downward so appearing retuse or emarginate. *Column* cylindrical, footed, to 5.4 mm long, erose, arcuate, the anther and stigma ventral, greenish stained with purple. *Pollinia* two, ovoid, without viscidium, ending in a hook. *Anther cap* cucullate, white.

Distribution: only known from the southern Pacific in Costa Rica. It is likely found in Panama as one of the localities is about 3 km far away from the frontier. (Fig. 3).

Habitat and ecology: plants were found growing epiphytically in premontane wet forest, rain forest transition and tropical wet forest premontane belt transition in secondary and primary vegetation, from 500 to 920 m of elevation.

Etymology: from the Latin *icterinus* or *ictericus* and from the Greek *ikterikos, ἰκτερικός*, “jaundice or jaundiced” in allusion to the yellow coloured flowers.

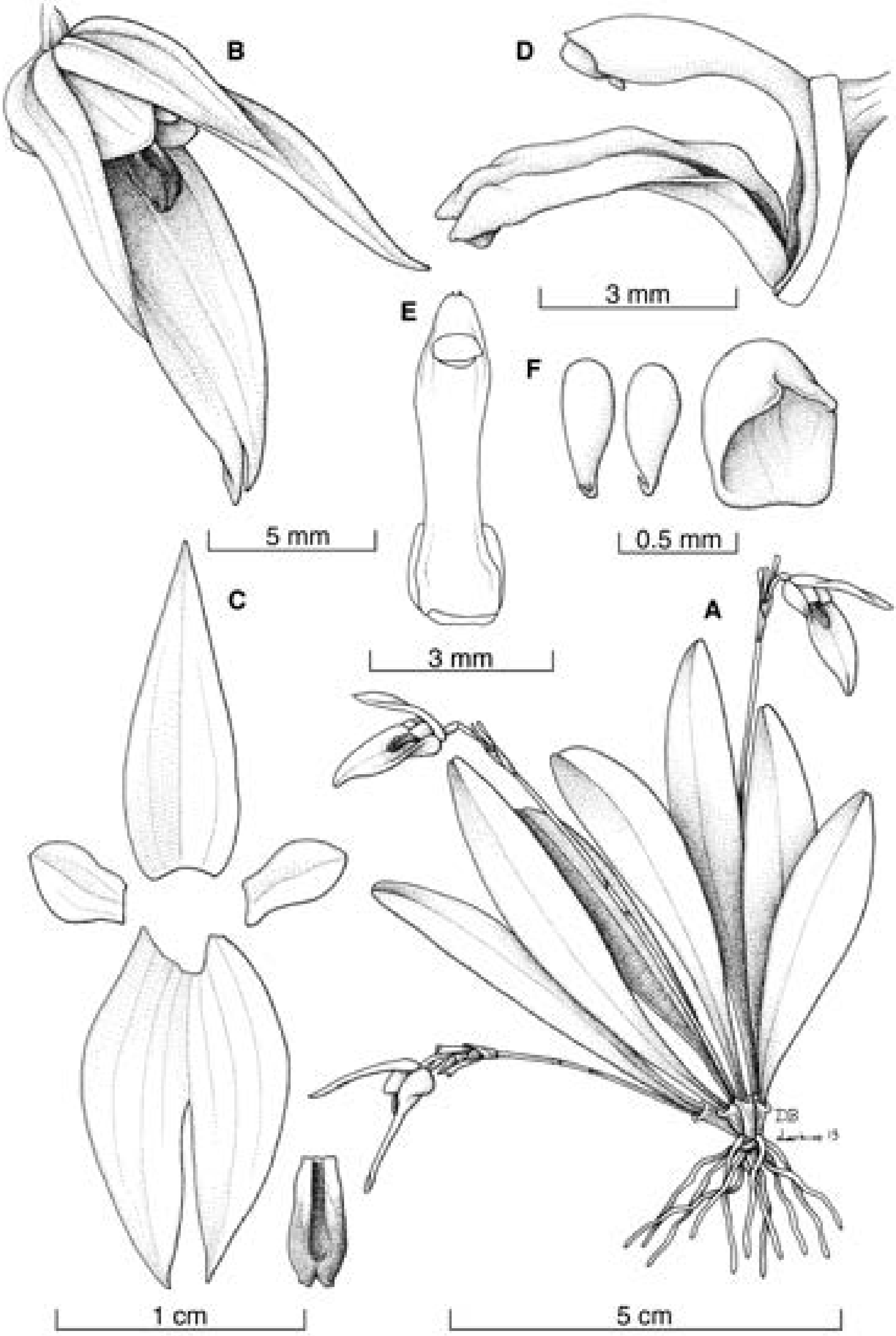


Figure 11. *Specklinia icterina* Bogarín. A – Habit. B – Flower. C – Perianth, flattened. D – Column and lip, side view. E – Column. F. –Pollinarium and anther cap. Drawn from the holotype by D. Bogarín and D. Solano.

Phenology: plants flower through the year but mostly from May to October.

Specklinia icterina is restricted to the premontane forest of San Vito, Sabalito and neighbouring areas in southern Pacific of Costa Rica close to the boundary with Panama. The plant is vegetatively similar to its allies however the species is readily distinguished by the immaculate yellow, ovate, acute sepals and petals; the oblong lip basally yellowish and purple from the middle towards the apex; the green immaculate ovary and column; and the white anther cap (Figs. 2g, 11). Frequently the lip apex is curved or folded apically so appearing retuse (Fig. 4c). It also happens in *S. acoana* and *S. condylata*, its close relatives. However, those species have purple or red brown maculate, speckled sepals, petals and column. From *S. condylata*, it also differs in the oblong, shorter lip up to 5 mm long, tinged basally with yellow (vs. pandurate, 7.5-8.0 mm long, purple). Other differences among its closest relatives are summarized in Table 1.

Additional material examined: Costa Rica. Puntarenas: Coto Brus, Sabalito, Miraflores, 8°49'20" N 82°54'42" W, 923 m, *F. Oviedo-Brenes 2537* (HLDG). Coto Brus, San Vito, sin más datos, cultivada por Gerson Villalobos en Santo Domingo de Heredia, Costa Rica, 23 enero 2012, *D. Bogarín 9453* (JBL-spirit).

Specklinia vierlingii Baumbach, Orchideen (Hamburg) 63(5): 405–406. 2012.

TYPE: Costa Rica. s.l.; ex cult. hort. Gerhard Vierling; leg. Norbert Baumbach et Jurgen Roth, 7 August 2012 (holotype, HAL). Figs. 2h, 2i, 9, 12.

Epiphytic, caespitose, pendent or suberect, *herb*, up to 6.5 cm tall. *Roots* slender, flexuous, to 0.5 mm in diameter. *Ramicauls* slender, erect, terete, to 5 mm long, enclosed by 2 tubular sheaths up to 1 cm long. *Leaves* narrowly obovate, thick, coriaceous, acute, conduplicate, emarginate, with a short apiculus, 2.5-6.5 × 0.6-1.0 cm, cuneate, the base narrowing into a indistinct petiole less than 4 mm long. *Inflorescence* racemose, distichous, glabrous, pendent or suberect, successively single-flowered, born by a slender filiform peduncle; peduncle bracts tubular to 3 mm long, the rachis congested appearing fasciculate, up to 6 cm long, peduncle 4.2-5.2 cm long, rachis up to 1.1 cm long. *Floral bracts* tubular, apiculate, conduplicate, membranaceous, imbricating, up to 4 mm long. *Pedicels 6 mm long, persistent. Ovary* to 3 mm long, glabrous, green spotted with red. *Flowers* showy, yellowish, the sepals stained or speckled with purple red from the centre towards the apex, the dorsal sepal adaxially striped with purple, the petals yellow with red purple stripes and purple apex, the lip purple red, the column greenish-yellow with purple red stripes. *Dorsal sepal* oblong, acute, entire, reflexed, slightly arcuate, 3-veined, dorsally keeled, connate to the lateral sepals for about 2 mm, 12.0-14.0 × 5.0-5.5 mm. *Lateral sepals* oblong-ovate, acute, connate for 6.5 mm into a ovate, acute, basally concave, entire, bifid synsepal, forming a mentum at base, 3-veined, dorsally keeled, 12-14 × 6-7 mm. *Petals* narrowly oblong, acute, 4.0-5.0 × 1.0-1.5 mm, subfalcate, 2-veined, with reflexed apex. *Lip* spatulate, obovate, basally unguiculate, with a pair of small lobules at the middle, adnate to the column foot, erose or fimbriate, arcuate, obtuse, with two longitudinal, parallel, apically convergent keels running up to the apex, sulcate, basally papillose and glutinose from the base towards the apex between the calli, with the apex rarely folded, 8.0-10.0 × 3.5-4.0 mm. *Column* cylindrical, footed, to 1.2 cm long, with a pair of apical arms, erose, the anther and stigma ventral, with purple dots and stripes along the margin. *Pollinia t*wo, ovoid, without a viscidium, ending in a hook. *Anther cap* cucullate, white, stained with purple.

Distribution: only known from central and southern Pacific lowlands in Costa Rica. (Fig. 9)

Habitat and ecology: epiphytic in tropical wet forest, tropical moist forest premontane belt transition and tropical moist forest in secondary and primary forest along humid patches of forest and river banks in the Pacific watershed of Cordillera de Talamanca from the central Pacific through Valle de El General and Fila Costeña in Costa Rica between 300 to 650 m of elevation.

Eponymy: named after Gerhard Vierling, who cultivates this species in Germany.

Phenology: plants flower through the year but mostly from May to November.

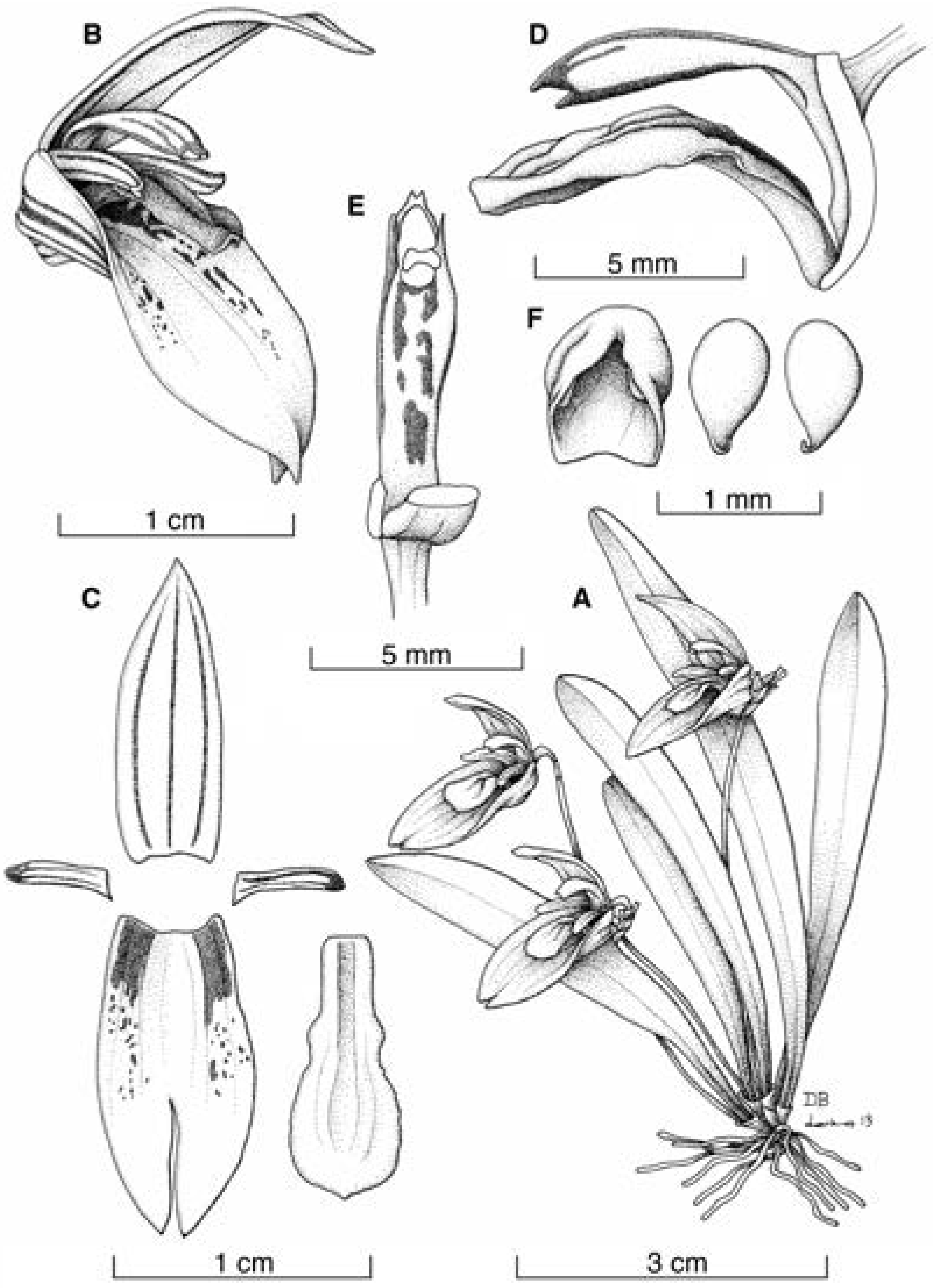


Figure 12. *Specklinia vierlingii* Baumbach. A – Habit. B – Flower. C – Perianth, flattened. D – Column and lip, side view. E – Column. F – Pollinarium and anther cap. Drawn by D. Bogarín and D. Solano based on *F. Pupulin 2894* (JBL-spirit).

This species was published by Baumbach (2012) based on a plant collected in Costa Rica and imported to Germany. According to the protologue, the plant comes from the Botanischer Garten Heidelberg and has been in culture by Gerhard Vierling. The holotype was deposited outside of the country of origin (HAL). During the preparation of this research, this species was well known by the authors for several localities in central and southern Pacific in Costa Rica, where it is endemic. It is clearly characterized by the yellowish-cream flowers with purple speckles or blotches, sometimes with purple veins. The most important feature to recognize this species is the narrowly oblong petals to 4.0-5.0 × 1.0-1.5 mm, unique among its relatives. Baumbach (2012) differentiated *S. vierlingii* from *S. condylata* by the much bigger flower size and the fimbriate lip. However, we found that floral measurements overlap between *S. condylata* and *S. vierlingii* (Table 1) and the lip is also fimbriate in both species (see the discussion of *S. condylata* and Table 1) (Fig. 4D-4F).

The illustration provided in the protologue by Baumbach (2012) is confusing and it mixes features of *S. condylata.* At least, he copied exactly the plant habit from the original drawing of *P. condylata* by Luer (1976). The drawing shows the same four leaves, roots and inflorescence that C. Luer drew for *P. condylata*. The flower dissection and the lateral view of the column and lip were also copied with a little modification of the lip apex and petals and they do not represent its real morphology. The drawing by Baumbach (2012) does not agree with the morphology of *S. vierlingii* as it was exactly copied from the drawing of the type of *S. condylata (*Luer 1976).

This species was intended to be published in this paper therefore, we provide the data we had prepared for its description such as full locality data, distribution map, illustrations and pictures of several individuals, a composite plate based on a living plant and a comparison among its closest relatives (Table 1) to aid with a proper identification of this species.

Additional material examined: Costa Rica. San José: Pérez Zeledón, El Brujo, road to El Llano, along the boarder of Río División, 320 m, 9°25’40”N 83°54’58”W, epiphytic on tall trees along the river shore, 21 January 2001, *F. Pupulin 2823, D. Castelfranco & L. Elizondo* (JBL-spirit). Same locality, *F. Pupulin et al 2894* (JBL-spirit) (Fig. 2H, 12). Pérez Zeledón, Viento Fresco de El Brujo, along the Quebrada del Camarón, about 450 m, 9°25’13”N 83°56’27”W, epiphytic in disturbed primary forest, wet premontane forest, 20 January 2001, *F. Pupulin 2817, D. Castelfranco & L. Elizondo* (JBL-spirit). Same locality, *F. Pupulin et al 2816* (JBL-spirit). San Isidro de General, barrio El Hoyón, márgenes del Río Pedregoso, 650 m, epífita en troncos musgosos de Ficus sp., floreció en setiembre del 2002 en cultivo de la familia Valverde Arias, Desamparados, San José, *R. Valverde 160* (JBL-spirit). Pérez Zeledón, General, Peñas Blancas, orillas del Río Caliente, 9°19’33.0” N 83°37’10.6” W, 629 m, bosque húmedo tropical, transición a premontano, en bosque secundario remanente a orillas del río, 28 julio 2009, *D. Bogarín 7350, J. Cambronero & F. Pupulin* (JBL-spirit) (Fig. 2I). Pérez Zeledón, R.F. Los Santos, Savegre Abajo, Finca de Neftalí Cordero, Fila el Zoncho, 9°27’18.0” N 83°51’09.7” W, 900 m, 11 mayo 1999, *A. Estrada 2185* (CR). Turrubares, Parque Nacional Carara, Valle del Tárcoles, Estación Bijagual, 9°45’30” N 84°33’10” W, 600 m, 26 julio 1995, *M. M. Chavarría 895* (INB-spirit).

Key to the species of *Specklinia condylata* group

1. Sepals and petals yellow, immaculate; base of the lip yellowish .... *S. icterina*
1. Sepals and petals maculate, stained or speckled; base of the lip purple 2
    2. Lip > 7.5 mm long, > 3.0 mm wide, column > 9 mm in length 3
    2. Lip < 5.0 mm long, < 2.5 mm wide, column < 6.5 mm in length 4
        3. Petals narrowly oblong, < 1.5 mm wide .... *S. vierlingii*
        3. Petals obovate-lanceolate, > 2 mm wide .... *S. condylata*
            4. Flowers whitish with stains and blotches dispersed on the sepals, sepals connate to 5 mm, 12.0 x 7.0 mm .... *S. acoana*
            4. Flowers yellowish with stains and blotches along the veins of the sepals, sepals connate to 1.5 mm, 9.4 x 6.3 mm .... *S. berolinensis*

ACKNOWLEDGMENTS. The scientific services of Ministerio del Ambiente, Energía (MINAE) and Sistema Nacional de Áreas de Conservación (SINAC) of Costa Rica and Autoridad Nacional del Ambiente (ANAM) of Panama for issuing the scientific permits, under which wild specimens were managed. We are indebted to Clotilde Arrocha, Ivonne Oviedo, Franco Pupulin, Rafael Rincón and Jorge Warner for their continuous support on the study of orchids in Panama. Darha Solano for finely inking the illustrations. Daniel Jiménez, Daniel Matamoros, Federico Oviedo-Brenes (HLDG), Jeremy Quesada and Gerson Rodríguez kindly provided data and plant material. Two anonymous reviewers greatly improved the manuscript. This research was enabled by the Project 814-B2-161 "Hacia una moderna flora de orquídeas de Panamá" by JBL and Herbario UCH, supported by the Vice-Presidency of Research, Universidad de Costa Rica and Universidad Autónoma de Chiriquí and "Flora Costaricensis: Taxonomía y Filogenia de la subtribu Pleurothallidinae (Orchidaceae) en Costa Rica" (814-BO-052).

LITERATURE CITED

Baumbach, N. 2012. Eine neue *Specklinia*-Art a us Costa Rica. Orchideen (Hamburg) 63(5): 404–406.

Bogarín, D., A.P. Karremans, R. Rincón & B. Gravendeel. 2013. A new *Specklinia* (Orchidaceae: Pleurothallidinae) from Costa Rica and Panama. Phytotaxa 115(2): 31-41.

Bolaños, R., V. Watson & J. Tosi. 2005. Mapa ecológico de Costa Rica (Zonas de Vida), según el sistema de clasificación de zonas de vida del mundo de L.R. Holdridge. Scale 1:750 000. Centro Científico Tropical, San José, Costa Rica, 1 p.

Garay, L.A. 1974. *Acostaea* y los géneros del complejo *Pleurothallis*. Orquideología 9: 103-124.

Garay, L.A. & H.R. Sweet. 1972. Notes on West Indian orchids. J. Arnold Arbor. 53: 515–530.

Holdridge, L. R. 1987. Ecología basada en zonas de vida, 3ª reimpresión. Instituto Interamericano de Cooperación para la Agricultura (IICA), San José, Costa Rica, 216 pp.

Lindley, J. 1830. The genera and species of orchidaceous plants 8. Asher, London. xvii, 554 pp.

Lindley, J. 1859. Folia Orchidacea, an enumeration of the known species of Orchids, 43: Pleurothallis part 2. 1–46.

Luer C.A. 1976. Miscellaneous species of *Pleurothallis*. Selbyana 3(1-2): 38-201.

Luer, C.A. 1986. Systematics of *Pleurothallis* (Orchidaceae). Icones Pleurothallidinarum III. Monogr. Syst. Bot. Missouri Bot. Gard. 20.

Luer, C. A. 2002. A systematic method of classification of the Pleurothallidinae versus a strictly phylogenetic method. Selbyana 23(1): 57–110.

Luer, C.A. 2003. *Pleurothallis*. Pp. 386-452 *in*: B.E. Hammel, M.H, Grayum, C. Herrera & N. Zamora (eds.), Manual de Plantas de Costa Rica. Volumen III: Monocotiledóneas (Orchidaceae-Zingiberaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 93.

Luer, C.A. 2006. A reconsideration of *Masdevallia*. Systematics of *Specklinia* and vegetatively similar taxa (Orchidaceae). Icones pleurothallidinarum XXVIII. Monogr. Syst. Bot. Missouri Bot. Gard. 105.

Pridgeon, A.M. 2005. 355. *Specklinia*. Pp. 402–405 *in*: A. M. Pridgeon, P.J. Cribb, M.W. Chase & F.N. Rasmussen (eds.), Genera orchidacearum Vol. IV. Oxford University Press, Oxford, UK.

Pridgeon, A.M. & M.W. Chase. 2001. A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). Lindleyana 16: 235-271.

Pridgeon, A.M., R. Solano & M.W. Chase. 2001. Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid DNA sequences. Amer. J. Bot. 88: 2286-2308.

Pupulin, F., A.P. Karremans & B. Gravendeel. 2012. A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica. Phytotaxa 63: 1-20.

LANKESTERIANA 13(3): 207—214. 2014.

INVITED PAPER*

A NEW SPECIES IN THE *COHNIELLA ASCENDENS* COMPLEX FROM AMAZONIAN VENEZUELA (ORCHIDACEAE, ONCIDIINAE)

WILLIAM CETZAL-IX[1,2,5], GERMÁN CARNEVALI[2,3] & ELIANA NOGUERA-SAVELLI[4]

[1]El Colegio de la Frontera Sur (ECOSUR), Unidad Chetumal, Av. del Centenario km 5.5,
Chetumal 77014, Quintana Roo, México

[2]Current address: Herbarium CICY, Centro de Investigación Científica de Yucatán, A.C. (CICY), Calle
43. No. 130. Col. Chuburná de Hidalgo, Mérida 97200, Yucatán, México

[3]Orchid Herbarium of Oakes Ames, Harvard University Herbaria. 22 Divinity Avenue,
Cambridge, Massachusetts 02138. U.S.A.

[4]Francisco de Montejo, Mérida 97203, Yucatán, México

[5]Author for correspondence: rolito22@hotmail.com

ABSTRACT. *Cohniella amazonica* (Orchidaceae, Oncidiinae, *Trichocentrum*-clade) a species in the *Cohniella ascendens* complex, from Amazonas, Venezuela, is herein newly described, illustrated, and characterized based on morphological characters. The new taxon is similar to *C. nuda*, from which it differs in the subquadrate-oblong lateral lobes of the labellum that are in the same plane as the central lobe, the 5-partite callus, the bipartite column wings, and the distribution range restricted to the northeastern portion of Amazonas, Venezuela. The conservation status of the new taxon is assessed as Data Deficient (DD) according to the IUCN (International Union for Conservation of Nature) criteria. We provide a key and table of characters to diagnose the *Cohniella ascendens* species complex, a comparative figure, and a map showing the geographical distributions of the species in this group.

RESUMEN: *Cohniella amazonica* (Orchidaceae, Oncidiinae, clado-*Trichocentrum*), una especie en el complejo *Cohniella ascendens* de Amazonas, Venezuela, es aquí descrito, ilustrado y caracterizado con base en caracteres morfológicos. El nuevo taxón es similar a *C. nuda*, de la cual se distingue por los lóbulos laterales del labelo subcuadrado-oblongos que se encuentran en el mismo plano que el lóbulo central, el callo 5-partito, las alas de columna bipartitas y la distribución restringida a la porción noreste de Amazonas, Venezuela. El estado de conservación del nuevo taxón es evaluado como Datos Deficientes (DD) de acuerdo a los criterios de la UICN (Unión Internacional para la Conservación de la Naturaleza). Proporcionamos una clave y una tabla de caracteres para diagnosticar las especies del complejo *Cohniella ascendens*, una figura comparativa y un mapa que muestra sus distribuciones geográficas de las especies de este grupo.

KEY WORDS: *Cohniella*, *Trichocentrum*, Oncidiinae, Orchidaceae, Venezuela

The genus *Cohniella* Pfitzer includes 22 species, two natural hybrids, and five informal species complexes (Cetzal-Ix *et al*. 2013a). The genus is distinguished from others members of the Oncidiinae by the relatively small (<13 mm) and subspherical, 1-leaved pseudobulbs whose sheaths lack foliar blades, succulent, medium sized to large terete leaves, and *Oncidium*-like flowers (Carnevali *et al.* 2010); furthermore, anatomical characters such as unifacial leaves and the presence raphides in the epidermis (Cetzal-Ix *et al*. 2013b) also help distinguish the genus. Characters used to recognize species are primarily

---

* This contribution was prepared as part of the special edition of LANKESTERIANA that is dedicated to the commemoration of Lankester Botanical Garden´s (JBL) 40th anniversary. Botanical collections of the JBL have been relevant to understand the identity and distribution of *Cohniella* species in our previous studies, cited in this paper.

floral, such as the shape and position of the lateral lobes of the labellum, shape, position, and number of teeth of the callus of the labellum, shape and size of the column base, and shape and position of the column wings (Cetzal-Ix *et al.* 2013a). Regarding the species complexes, they are recognized by combinations of vegetative and floral characters. The vegetative characters include the size and thickness of the leaves, the length of the inflorescence relative to subtending leaf, the position, number, and the arrangement of flowers in the inflorescence. Floral characters useful in species diagnoses include size and color of the flowers, the shape of the platform of the labellum callus, and the shape and presence or absence of the base of the column.

Furthermore, species or species complexes can be easily identified using these characters in combination with discrete patterns of ecological and geographical distribution. The five species complexes in *Cohniella* are morphologically, ecologically, and geographically discrete; moreover, they are recovered as monophyletic in morphological and molecular phylogenetic analyses (Cetzal-Ix 2012a).

The *Cohniella ascendens* complex includes *C. aguirrei* (Königer) Königer, *C. ascendens* (Lindl.) Christenson, *C. helicantha* (Kraenzl.) Cetzal & Carnevali, *C. lacera* (Lindl.) Cetzal, and *C. nuda* (Bateman ex Lindl.) Christenson (Table 1). Its species occur in humid to subhumid habitats, from low-statured inundated, semi-evergreen to evergreen forests and, more rarely, in semideciduous forest at elevations of 0-800 meters. Members of the *Cohniella ascendens* complex share a habit featuring the semi-pendulous or semi-erect leaves with rarely racemose or paniculate inflorescences that usually do not exceed the length of the leaf, more infrequently exceeding it; furthermore, the sepals are rounded whereas the petals are subquadrate with subtruncate apex; the callus of the labellum presents a hemispherical platform. Species are distributed from northern Tamaulipas and the central portion of Mexico to the northern and northwestern Colombia and the northern half of Venezuela. *Cohniella ascendens* and *C. nuda* present the widest distributions within the complex (and the genus); other species, such as *C. aguirrei* and *C. lacera*, are much more geographically restricted (Figure 1).

n 1995 a plant collected by Carlos García Esquivel in an area of tropical humid forests with a strong dry season in northwestern Amazonas state, Venezuela was identified as *Oncidium cebolleta* (Jacq.) Sw. by one of us (GC). However, despite this plant has morphological features characteristic of the *Cohniella ascendens* complex. We here interpret the combination of morphological characters and distribution as evidence of species status for this plant, which is herein proposed as the new species

Material and methods. The description of the new species was prepared from herbarium material preserved in a 70:25:5 ethanol:water:glycerine solution. Additional material of related species used for this study has been previously cited in Cetzal-Ix & Carnevali (2010) and Cetzal-Ix (2012b) where flowers from herbarium material were soaked in concentrated ammonium hydroxide for about one minute for rehydration, then rinsed in water until soft and ready for study under a dissecting microscope. Flowers thus pretreated were temporarily preserved as above for further study and eventually returned to herbarium sheets. Pictures of live and herbarium flowers were taken with a SONY Cybershot DSC-W120; others were digitalized under an Epson Expression 1640 XL scanner. Digital images of flowers were captured at several resolutions, ranging from 600 to 1200 dpi. Digital line drawings were produced with Canvas X, using the digital images previously captured to provide outlines. Cartography was produced by plotting the locality data cited here and previous studies of Cetzal-Ix & Carnevali (2010) and Cetzal-Ix (2012b) on an image data "shaded and colored SRTM elevation model" (NASA/JPL/NIMA 2002) using ArcView 3.2 (ESRI 1999).

Taxonomic treatment

Cohniella amazonica Cetzal & Carnevali, *sp. nov.* (Figs. 1–4)

Type: VENEZUELA. Amazonas: Puerto Ayacucho, flowered in cultivation in the collection of Carlos García Esquivel in Caracas, Venezuela; leaf terete; flowers yellow, Dec. 1991, *C. García Esquivel s.n.* sub. *G. Carnevali 3080* (holotype: CICY; isotypes, AMES, VEN). .

TABLE 1. Morphological comparison of the *Cohniella ascendens* species complex.

Characters	***C. aguirrei***	***C. amazonica***	***C. ascendens***	***C. helicantha***	***C. lacera***	***C. nuda***
Leaf length (cm)	30-67	–	(13-)15-86	35-62	24-70	27-69
Inflorescence length (cm)	14-50	25	(11-)14-65(-80)	25-48	(7-)13-63	60-165
Flower position	Resupinate	Resupinate	Resupinate	Non-resupinate	Resupinate	Resupinate
Flower size (mm)	16-18	15-18	15-22	10-15	18-25	13-16
Central lobe of the labellum (mm)	4.0-4.2 × 7-8	3-5 × 5-6	5-7 × 8.5-13.0	3-5 × 7-9	7-10 × (12-)14-16	3-5 × 6-10
Central lobe of the labellum (proportions not counting the isthmus)	Wider than long	About as long as wide or longer than wide	Wider than long	Wider than long	Wider than long	Wider than long
Lateral lobes of the labellum (position)	Parallel to the central lobe	Parallel to the central lobe	Perpendicular to the central lobe	Parallel to the central lobe	Parallel to the central lobe	Parallel to the central lobe
Lateral lobes of the labellum (mm)	3-5 × 2-3	4-6 × 3.5-4.0	4-8 × 2-4	2-3 × 0.7-1.0	3-4 × 1.1-2.0	2.0-3.5(-5.0) × 0.8-2.0
Lateral lobes of the labellum shape	Triangular	Oblong	Oblong	Triangular	Linear	Linear
Isthmus (mm)	0.8-2.5 × 0.5-3.0	2.0-2.2 × 2.5-3.0	0.5-4.0 × 1.3-3.0	1.2-3.0 × 2.7-3.0	4-6 × 1.5-1.8	2-4 × 0.5-1.4
Labellar callus	5-partite	5-partite	5-partite	5-partite	1-partite	3-partite
Proximal teeth of the callus (shape)	Cylindrical	Conical	Cylindrical	Cylindrical	Absent	Absent
Distal teeth of the callus (shape)	Conical	Cylindrical	Conical	Conical	Absent	Conical
Lateral margins of labellum disc	Rugose	Smooth	Rugose	Rugose	Rugose	Smooth
Column wings (shape)	Terete	Bilobed	Terete	Terete	Triangular	Triangular

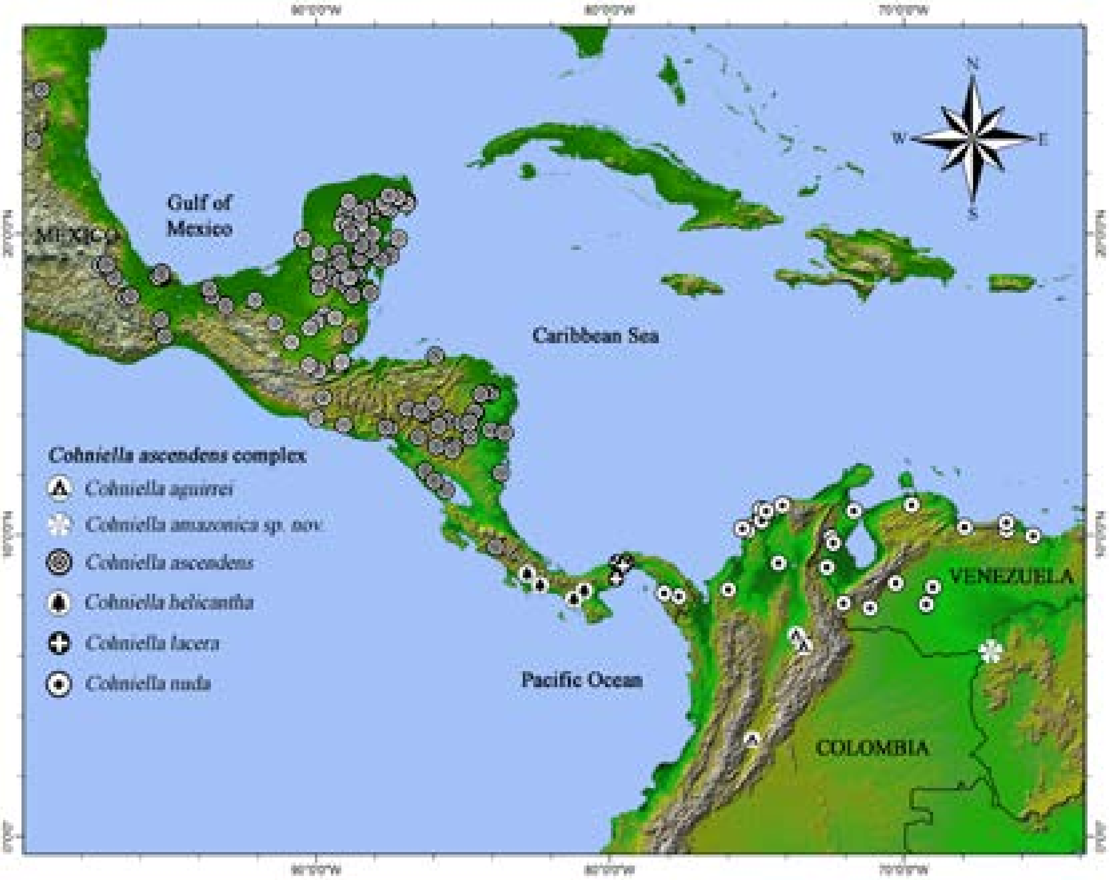


FIGURE 1. Distribution of the *Cohniella ascendens* species complex.

A *Cohniella* species belonging to the *Cohniella ascendens* complex and related to *C. nuda* from which it is different by the subquadrate-oblong lateral lobes of the labellum that are in the same plane as the central lobe, the 5-partite callus, the bipartite column wings, and distribution restricted to the northeastern portion of Amazonas, Venezuela.

Plant epiphytic. *Leaf* terete, missing from the only specimen available. *Inflorescences presumably* solitary and borne from the base of the pseudobulbs, to 25 cm long, a 9-flowered raceme; peduncle erect, 1.5 mm thick, terete, with 7 bracted internodes, peduncle bracts 6.0–8.0 × 2.5–3.0 mm, the basal-most longest, acuminate, tubular; floral bracts 2.0–2.5 × 0.5–1.0 mm, narrowly elliptic, acuminate. *Flowers* resupinate, 15–18 mm diameter, ovary with pedicel 13–17 mm long, of which 3–4 mm corresponds to the ovary, 0.8–1.0 mm thick. *Sepals* basally clawed, spreading or somewhat reflexed. *Dorsal sepal* 6–7 × 5.5–6.5 mm, obovate, apically obtuse and minutely apiculate, concave in the upper half, the claw 1.0–1.2 × 1.0–1.1 mm. *Lateral sepals* partially fused at the very base, then free, similar to dorsal, 6.0–7.0 × 5.5–6.5 mm. *Petals* 6–7 × 3–5 mm, oblong to oblanceolate, somewhat oblique, the apex rounded. *Labellum* 3-lobed, 10–11 mm long from the base to the apex of the central lobe, 8–11 mm wide across the apices of the lateral lobes, the lateral lobes in the same plane as the central lobe and more or less perpendicular to it. *Central lobe* 3–5 × 5–6 mm, oblong-spathulate in outline, apically rounded, basally produced into a long isthmus, 2.0–2.2 × 2.5–3.0 mm. *Lateral lobes* 4.0–6.0 × 3.5–4.0 mm, patent, somewhat reflexed in natural position, subquadrate to oblong, apically truncate-rounded, the upper and lower margins of the lateral lobes entire. *Disc* 3.5–4.0 × 3.5–4.0 mm,

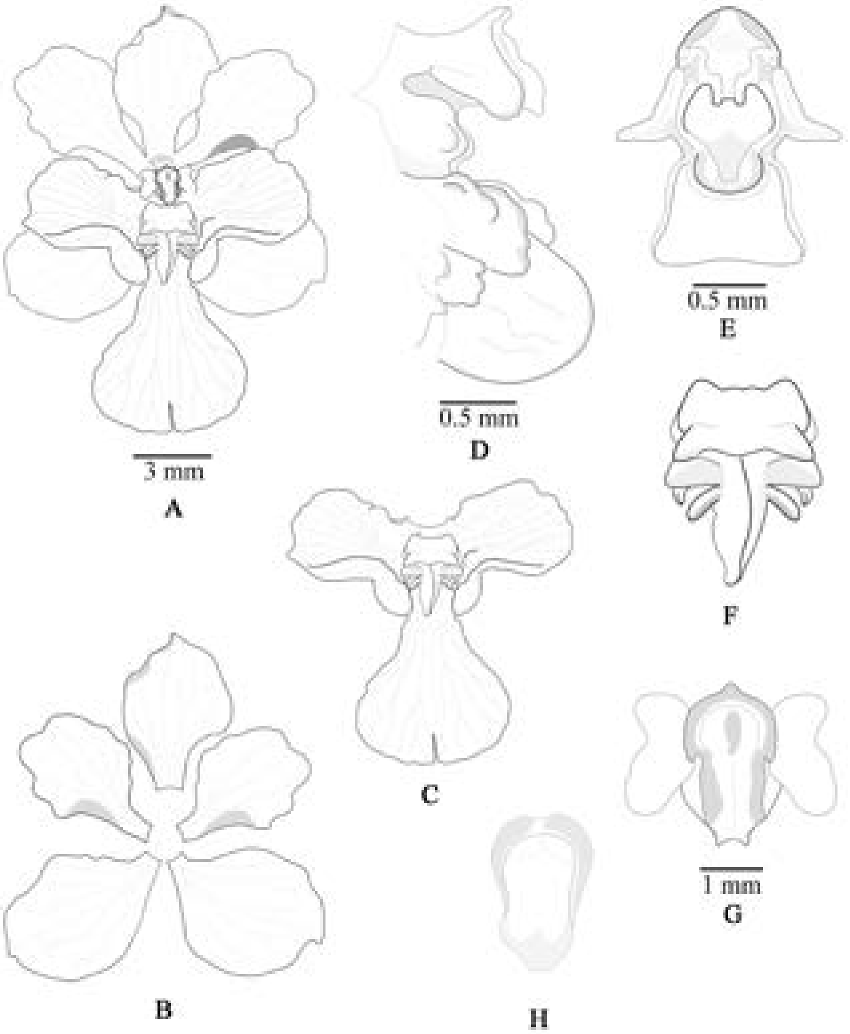


Figure 2. *Cohniella amazonica*. A — Flower. B, C — Labellum front view. D — Labellum back view. E — Sepals and petals. F — Disc and callus. G — Flower, lateral view. H — Column, front view. I — clinandrium, front view. Scale: A = 2 cm. B–E. = 6 mm. F = 2 mm. G = 3 mm. H–I = 1 mm. Drawn by W. Cetzal-Ix.

in general outline oblong, with a well-developed callus, ca. 2.2–2.5 × 2.5–2.8 mm, consisting of a large, more or less elevated and flat, hemispherical platform *ca.* 1.0–1.2 × 2.5–2.6 mm, basally with two lateral smaller, divergent, teeth that are conical and point upward, 1.0–1.2 mm long, distally with two divergent, cylindrical lateral teeth, these 0.4–05 × 0.2–0.3 mm; the central tooth 1.8 mm tall, laterally compressed, the lateral sides of the callus with two small, conical teeth, 0.5 mm tall. *Column* 2.5–3.0 × 1.0–1.2 mm, the ventral face perpendicular to the plane of the labellum lobes, ovate, subcylindric, tabula infrastigmatica subquadrate, stigmatic surface obovate, ca. 0.8 × 0.6 mm. *Column wings* 1.0–1.2 × 0.7–0.8 mm, bilobed, oblate. *Anther cap* 1.5–1.6 × 1.2–1.3 mm, apically operculate, obovate. *Pollinarium* and *capsule* not seen.

Etymology: The specific epithet refers to the Amazonas state of Venezuela where the only known specimen was collected.

Distribution and ecology. *Cohniella amazonica* is only known from the vicinity of Puerto Ayacucho in Amazonas State, Venezuela (Fig. 1). It grows in tropical humid forests, possibly in sympatry or parapatry with

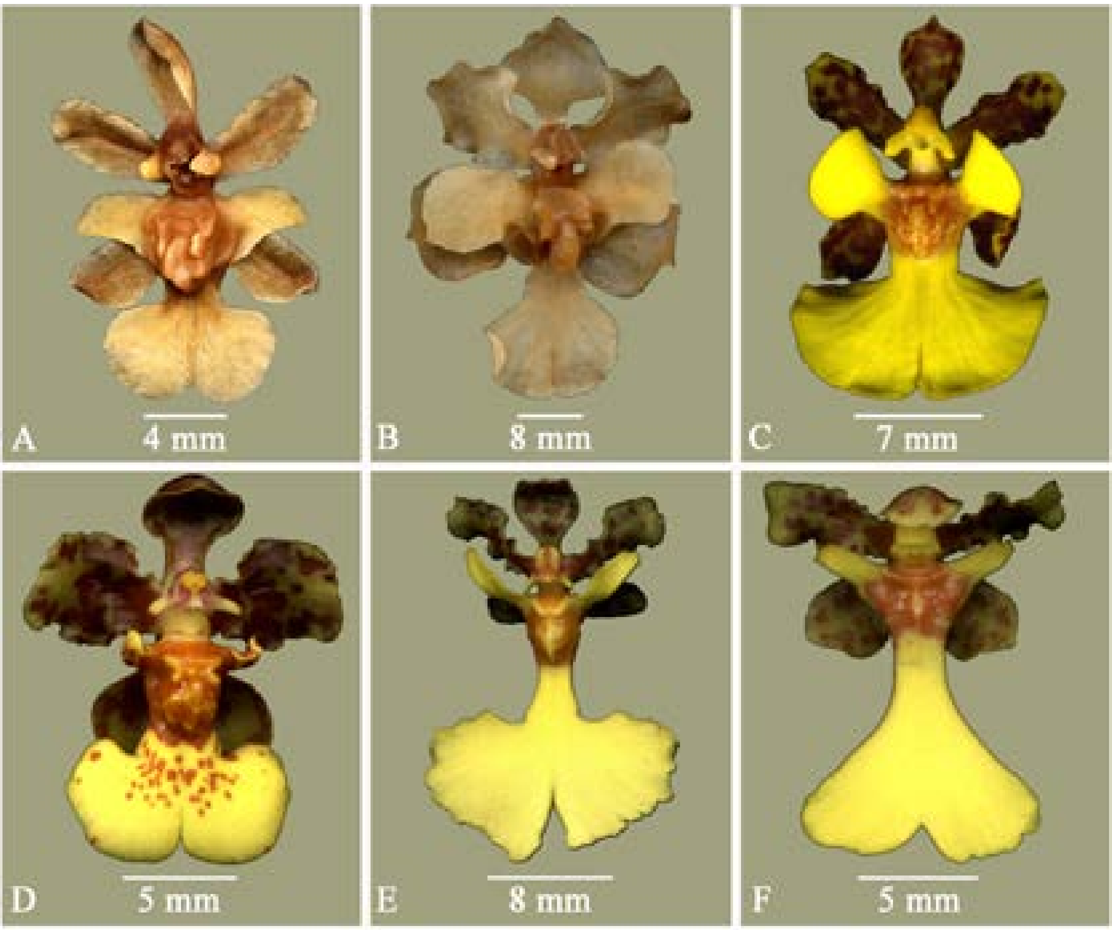


FIGURE 3. Morphological comparison of the *Cohniella ascendens* species complex. A — *Cohniella aguirrei* [based on *Königer 95*, M]. B — *Cohniella amazonica* [*Carnevali 3080*, CICY]. C — *Cohniella ascendens* [*Cetzal 17*, CICY]. D — *Cohniella helicantha* [*Carnevali 7027*, CICY]. E — *Cohniella lacera* [*Carnevali 7311*, CICY]. F — *Cohniella nuda* [*Carnevali 7283*, CICY].

C. cebolleta (Jacq.) Christenson, *C. croizatii* Cetzal & Carnevali, and *C. ultrajectina* Cetzal & Carnevali. However, these last three species are part of the *Cohniella cebolleta* complex which is characterized by the lateral margins of the disc convex with conical teeth, the column base conspicuous, 5-partite callus (3-partite in *C. croizatii*), the disc covered by brown or reddish spots only at base, and the platform of the callus rectangular (absent in *C. croizatii*) (Cetzal-Ix *et al*. 2013a). The hemispherical platform of the callus (Figs. 2F-4B) and relatively narrow central lobe, oblong-spathulate in outline and narrower than long renders this new species unmistakable among other *Cohniella* species of the area (Fig. 2A-C).

Cohniella amazonica, it is easy to distinguish from related species in the *Cohniella ascendens* complex such as *C. aguirrei*, *C. ascendens*, and *C. helicantha* by the narrow central lobe to the labellum (Fig. 3). Furthermore, the callus features conical lateral teeth at the base whereas distal calli are cylindrical; this pattern is reversed in the related taxa (Figs. 3-4).

IUCN Red List category. According to IUCN (2004), *Cohniella amazonica* would be considered as Data Deficient (DD). The species in known a single collection from the Puerto Ayacucho area, it is therefore suspected to be under no special threat, as this area is largely uninhabited except for a few indigenous tribes, primarily Yekuana. However, albeit the region around

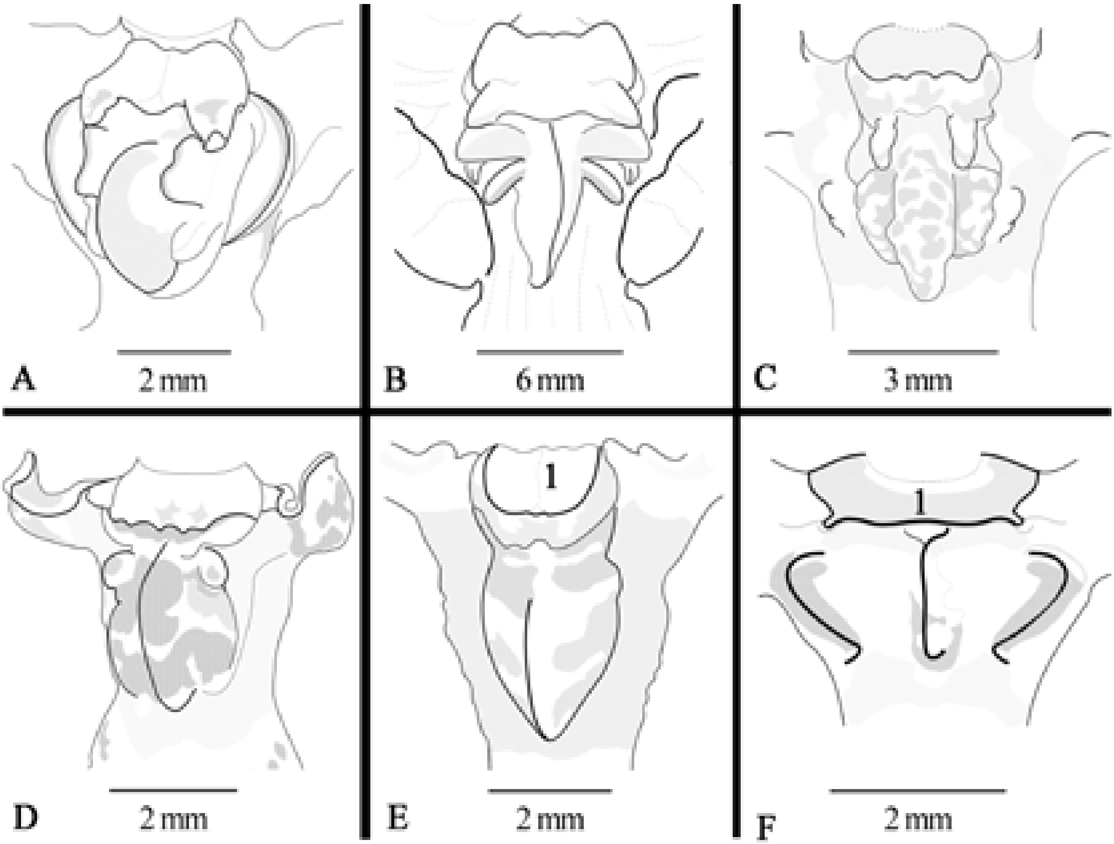


Figure 4. Comparison of the labellum callus of the *Cohniella ascendens* species complex. A — *Cohniella aguirrei* (based on material type). B — *Cohniella amazonica.* C — *Cohniella ascendens*. D — *Cohniella helicantha*. E — *Cohniella lacera*. F — *Cohniella nuda*. Drawn by W. Cetzal-Ix.

Puerto Ayacucho has been severely altered during the past few decades, there are still abundant forested patches in this area (Cetzal-Ix & Carnevali 2011).

Key to the species of the *Cohniella ascendens* complex

1. Isthmus of the labellum much longer than broad (2-4 × 0.5-2.0 mm); callus consisting of 1 to 3 teeth or keels 2
1. Isthmus of the labellum approximately as long as broad (0.5-4.0 × 0.5-3.0 mm); callus consisting of 5 teeth or keels 3
    2. Flowers 18-25 mm diameter; labellum with the lacerated margin; column wings conspicuous; callus of the labellum 1-partite; plants endemic to the central portion of Panama .... *C. lacera*
    2. Flowers 13-16 mm diameter; labellum with the entire or slightly lacerated; column wings reduced or absent; callus of the labellum 3-partite; plants from the eastern portion of Panama and northern Colombia and Venezuela .... *C. nuda*
3. Central lobe of the labellum 5-6 mm wide; lateral margins of the labellum smooth; column wings bipartite; plants from Venezuela .... *C. amazonica*
3. Central lobe of the labellum 7-13 mm wide; lateral margins of the labellum rugose; column wings terete; plants from Mexico to Colombia 4
    4. Flowers non resupinate; lateral lobes of the labellum triangular, short and thin (2-3 × 0.7-1.0 mm); plants from Panama and Colombia .... *C. helicantha*
    4. Flowers resupinate; lateral lobes of the labellum various (obovate, oblong or triangular), lengths and widths (3-8 × 2-4 mm); plants from Mexico to Colombia 5

5. Lateral lobes of the labellum erect, usually spathulate, broadly obovate; column wings terete; plants of northwestern Mexico to the southeast of Costa Rica .... *C. ascendens*

5. Lateral lobes of the labellum patent, not spathulate, oblong-triangular; column wings subtriangular; plants from the valleys between the central and eastern Andean Cordilleras from Colombia .... *C. aguirrei*

ACKNOWLEDGEMENTS. We thank Franco Pupulin (JBL) for inviting us to participate in this special issue of Lankesteriana. Gustavo A. Romero-González (AMES) and Rodrigo Duno (CICY) commented on earlier drafts of this article. Silvia Hernández Aguilar (CICY) helped us with the management of herbarium loans.

LITERATURE CITED

Carnevali, G., W. Cetzal-Ix, R. Balam-Narváez & G.A. Romero-González. 2010. A synopsis of *Cohniella* (Orchidaceae, Oncidiinae). Brittonia 62(2): 153–177.

Cetzal-Ix, W. 2012a. Sistemática, Filogenia y Biogeografía de *Cohniella* Pfitzer (Orchidaceae: Cymbidieae, Oncidiinae). El Colegio de la Frontera Sur, Chetumal, Quintana Roo, 276 pp.

Cetzal-Ix, W. 2012b. *Oncidium lacerum*, an older and ignored name for *Cohniella stipitata* (Orchidaceae, Cymbideae, Oncidiinae). Ann. Bot. Fenn. 49(1–2): 137–143.

Cetzal-Ix, W. & G. Carnevali. 2010. A revision of *Cohniella* Pfitzer (Orchidaceae) in Mexico. J. Torrey Bot. Soc. 137(2–3): 180–213.

Cetzal-Ix, W. & G. Carnevali. 2011. A new *Cohniella* Pftizer (Orchidaceae, Cymbidieae, Oncidiinae) from Amazonian Venezuela. Novon 21(2): 178–181.

Cetzal-Ix, W., G. Carnevali, E. Noguera-Savelli & G.A. Romero-González. 2013a. Really, what is *Cohniella cebolleta*? A recircumscription plus new and resurrected species and combinations. Syst. Bot. 38(3): 1–18.

Cetzal-Ix, W., E. Noguera-Savelli, D. Jauregui & G. Carnevali. 2013b. Anatomía foliar comparada y sistemática del clado-*Trichocentrum* con énfasis en *Cohniella* (Asparagales: Orchidaceae). Rev. Biol. Trop. 61(4): 1–20.

ESRI. 1999. *ArcView gis* 3.2, Environmental Systems Research Institute, Inc. New York.

IUCN. 2004. Guidelines for using the IUCN red list categories and criteria. Rapport IUCN. Gland, Switzerland and Cambridge, UK, 50 pp.

NASA/JPL/NIMA. 2002. NASA, Jet Propulsion Laboratory. NASA Earth Science Enterprise, Washington, D.C. Available from http://photojournal.jpl.nasa.gov/catalog/PIA03364 (accessed: 20 July 2013).

LANKESTERIANA 13(3): 215—227. 2014.

INVITED PAPER*

THE REVEREND CHARLES SAMUEL POLLOCK PARISH - PLANT COLLECTOR & BOTANICAL ILLUSTRATOR OF THE ORCHIDS FROM TENASSERIM PROVINCE, BURMA

DUDLEY CLAYTON

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, United Kingdom
dudley.clayton@btinternet.com

ABSTRACT. Charles Parish collected plants in Burma (now *Myanmar*) between 1852 and 1878. His orchid collections, both preserved and living plants, were extensive. He sent plant material and watercolour sketches to Sir William Hooker at Kew and living plants to the British orchid nursery of Messrs Hugh Low & Co. of Upper Clapton. H.G. Reichenbach obtained examples of the Parish plant material from Hugh Low and he visited Kew where he studied the Parish orchid specimens and illustrations and many of them were subsequently described by Reichenbach. His beautiful and accurate watercolour paintings of orchids were bound in two volumes and eventually came to Kew following his death. They have been extensively used by botanists such as Robert Rolfe, Victor Summerhayes, Gunnar Seidenfaden and Jeffery Wood when working on the orchid floras of the region. Parish's life, collecting activities and collections are discussed here.

The name Parish as a collector of orchids in Burma (Myanmar) will be familiar to those who study orchids but it is unlikely that many people will know very much about him. Charles Samuel Pollock Parish (1822-1897) (Fig. 1), like many of his contemporary clergymen in the 19th century, pursued his calling and combined this with the benefits of his classical education. His abiding interest was in natural philosophy, which he pursued with considerable vigour and specifically, botany and geology. He was born, the second son of the Reverend Henry Parish (1791-1873), on the 26th January 1822 at Dum Dum, a town about 4 miles northeast of Calcutta (*Kolkata*) in India and the primary artillery cantonment for the Bengal Army of the Honourable East India Company (HEIC). Henry Parish was appointed Chaplain in the HEIC in 1820 and shortly after Charles was born, he became Senior Chaplain, with the Garrison of Fort William in Calcutta. This was followed by service at Agra from November 1826 and this is where he remained until he retired in 1839 after completing eighteen years' service (McNally, 1976). A few months after their arrival at Agra, Henry Thomas, the eldest of three sons died, aged seven years.

No record has yet been found, but it is most likely that Charles Parish returned to England for his formal education in 1832 or thereabouts, aged ten. On 12th December 1837, aged fifteen, he was admitted to St Edmund Hall, Oxford where he was awarded a Bachelor of Arts degree on 2nd December 1841. Shortly after leaving Oxford, he moved to Somerset and at the general ordination held by the Lord Bishop of Bath and Wells on 7th June 1846 (*Bath Chronicle and Weekly Gazette*, 1846), he was ordained into Holy Orders as a deacon and then as a priest on 30th May 1847 (*Sherborne Mercury*, 1847). On 15th August 1846 he was appointed curate at West Hatch, Somerset (*Exeter and Plymouth Gazette*, 1846) but he moved during December 1849 to his second curacy at Bickenhall and Orchard Portman (*Sherborne Mercury*, 1849).

Parish started collecting plants in 1844 in the neighbourhood of Esher, Surrey, where he resided with his parents who had, following their return from India, based themselves to be near Epsom, the Parish family home. Charles Parish widened his search for plants to other parts of Surrey, Sussex and the London area and by 1845 he extended his collecting to Kent, where the Parish family had connections. In 1845 he

---

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

FIGURE 1. Reverend Charles Samuel Pollock Parish (1822-1897). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

visited Ayrshire, the Isle of Arran and Loch Lomond in the west of Scotland. Specimens were collected in Somerset from 1845 and in 1846 he visited Ireland. During the period 1846-1849, he collected more than 100 specimens each year, mainly from Somerset, neighbouring Wiltshire and Devon. He also made an extensive collection in Wales; in Snowdonia, along the west coast and in the north. His specimens were named and preserved to form a herbarium that includes a range of temperate terrestrial orchids (now deposited with the Somerset Heritage Centre).

To complement his botanical interest, he developed an understanding of geology and the *Blue Lias* formations at Lyme Regis with their rich source of fossils. With his keen scientific intellect, he explored the geology of Somerset and assembled a large collection of fossils. Sadly, this no longer exists and it was possibly dispersed and absorbed into other collections. To gain a better understanding of geology, he purchased Lyell's *Elements of Geology* and *Principles of Geology* and, as a result, he was fascinated with the description of a volcanic island in the Bay of Bengal (Parish, 1861):

> "I was particularly taken by the description of a certain volcanic island still active and standing up, far from land, like a solitary sentinel, in the Bay of Bengal, called 'Barren Island'. Besides its isolated position (for volcanoes are generally in groups) the remarkable feature of it, as described, was that the sea, entering by a gap in the outer crater, completely surrounded the inner or secondary crater, so that a boat could enter and be rowed round between the two.
>
> I thought, as I read the account, how much I should like to see this strange island, not thinking at the time that there was the remotest likelihood of my ever doing so, situated as the place was on the other side of the world and, moreover, very much out of the ordinary trade vessels. But as it is 'the unexpected that always happens' so this extremely improbable thing, in course of time, actually came about."

In 1852, following in his father's footsteps, he obtained an appointment with the HEIC and he was placed under the authority of the Bengal Presidency, effective from 19th May 1852. He arrived in Calcutta to be immediately dispatched to Burma, embarking on another vessel bound for Rangoon (*Yangoon*) where he arrived in late May or early June 1852 at the height of the 2nd Anglo-Burmese War (1852). Rangoon had just been captured after a sea assault by the forces of the HEIC.

Charles Parish was to remain at Moulmein (*Mawlamyaing*) for the next 25 years, apart from a period of leave in England during 1872-73. He served initially as Assistant Chaplain, then as Chaplain from 1863 and finally, in 1873, after his return from leave, as a Senior Chaplain. His duties were to look after the European officers and men of the growing Company garrison and their dependents at Moulmein and the other smaller garrisons, with their dependents, in Tenasserim Province. Following the Indian Mutiny, the HEIC ceased to exist with the transfer of its responsibilities to the Crown from 1st November 1858, but life for the servants of the old Company did not change. As part of his duties, Parish was responsible for the governance of the European School in Moulmein and he also had to make periodic visits to the outlying stations at Tavoy (*Dawei*) and Mergui (*Myeik*), coastal stations to the south, some 200 miles (320 km) and 300 miles (480 km) from Moulmein and he had to travel by boat. After 1858, a prison was opened at Port Blair on the Andaman Islands and Parish had to make regular visit to the islands as part of his duties.

In 1854, two years after he arrived in Moulmein, Charles Parish married Eleanor Isabella Sarah Johnson, the daughter of an officer of the 18th Regiment Native Infantry, Madras Army serving at Moulmein. They had seven children, four daughters and three sons, all born in Moulmein, but their second daughter only survived for one year. We know that Eleanor shared Charles' interest in botanical illustrating and a number of her illustrations form part of the collection in the two volumes donated to the Royal Botanic Gardens, Kew in 1898 by Eleanor, after the death of Charles Parish.

Parish now had the opportunity in Tenasserim to explore its forests and find a wide variety of plants, not just orchids. He was particularly impressed with the remarkable limestone rocks which stood perpendicularly out of a flat alluvial plain rising to 1000-2500 ft (305-762 m), generally straight and inaccessible. The pinnacles were worn by the rains into needle like points and they were wonderfully rich in plants, but only one in twenty could be climbed. His obvious desire to expand his botanical knowledge had to take second place to his duties and it meant he was unable to explore the region on a regular basis and make a systematic appraisal of the region. At best, he could venture some 20 miles (32 km) from Moulmein. The administration of the province was in the hands of the district officers and they were required to tour their districts on a regular basis, including the exploration of the unknown areas, surveying, recording the geographic features, agricultural practices, crops, indigenous plants and wildlife. Parish's botanical knowledge made him a valuable companion to take on some of these expeditions. Even if he was unable to make a particular journey, the district officers would gather botanical material and Parish thus increased his overall knowledge. He initially collected mosses and ferns, and some flowering, non-orchid, species, but from 1859, orchids became a major interest and it is mainly through the collecting and study of ferns and orchids that we know him.

The earliest preserved letter from Parish is in the Director's Correspondence at the Royal Botanic Gardens, Kew and is dated 31st July 1855. This letter and another from 31st August 1855 were written to Dr Thomas Thompson in response to enquiries made by Thompson when he was the Director at the Calcutta Botanic Gardens. Parish's letters were forwarded to Sir William Jackson Hooker (1785-1865), Director at the Royal Gardens Kew, because of the information they contained. Thompson identified Parish as a good contact for plant material from Tenasserim. Parish then began a regular correspondence with Sir William until just two months before the latter's death in August 1865. In addition to the letters, he sent regular consignments of plant material, mainly mosses, ferns and orchids, to Kew and orchids to Messrs Hugh Low & Co. of Clapton. The first consignments sent in the summer of 1859 to Hugh Low included *Cymbidium parishii* Rchb.f. and *Vanda gigantea* Lindl. (= *Vandopsis gigantea* (Lindl.) Pfitzer), both discovered by Parish during the expedition he made in February 1859 with Major (later Colonel) Samuel Tickell (1811-1875). *Vanda gigantea* was growing high up on a tree and he never found it again, and the one plant he had brought down was so large it scarcely fitted on to his elephant. The specimen could be placed across a man's shoulders but one man could not lift it! The first consignment of plants sent to Messrs Low & Co. was lost when the steamer *Cape of Good Hope* was cut in half by the P & O steamer *Nemesis*, and sank in the Hooghly River. Various other trials and tribulations were suffered with plant material sent to England, with ships foundering and packages delayed en-route by the shipping companies. Eventually, he used with success the Wardian case, a small sealed glasshouse.

Colonel (later General) Robson Benson, who was based at Rangoon and collected for James Veitch & Sons of Chelsea, was a friend of Parish. They met regularly and material was often exchanged. The annual visits to the outstations at Tavoy and Mergui were a highlight in Parish's year and as the European populations at these stations were small, Parish found he had sufficient spare time to explore the forests of Tavoy, Mergui and the Mergui Archipelago (*Myeik Kyunzu*). His comments on these visits were a regular feature of his letters to Sir William. Letters to Sir William's son, Joseph Dalton Hooker (1817-1911), who became Director at Kew after his father's death, were sporadic from 1862, but became regular again from 1865 until Parish retired in 1878. The memorable

FIGURE 2. *Cleisostoma parishii* (Hook.f.) Garay in *Bot. Mus. Leafl.* 23: 173. 1972. *Sarcanthus parishii* Hook.f., *Bot. Mag.* 86: t. 5217. 1860. Type: Burma, cult. Low, *Parish s.n.* (holo. K). Parish illustration vol. 2, p. 56, dated 1860. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

record left by Parish concerning his visit to Barren Island, already alluded to, and now lodged with the British Library (Parish, 1861), occurred during one of the routine visits he made to the Andaman Islands. In mid-October 1861, the local steamer made a straight course from the mouth of the Tavoy River to Port Blair and Barren Island lay in almost a direct line between the two places. As the island came into view and as Parish and a few others were anxious to land, the master of the steamer agreed. Initially, the steamer was sailed around the island and then 'hove to' at a convenient distance from the shore. Parish records his disappointment at finding no intervening and surrounding water, as described by Lyell. He may not have known that there had been an eruption in 1852 and this coupled with earlier eruptions in the century, changed the character of the island. Two or three officers and Parish were rowed ashore and they explored the island. The only orchid referred to in the article was encountered on their descent from the summit of the volcano, when Parish caught sight of a pure white speck in strong contrast with the background of black ashes, near the bottom of the opposite slope, and he wanted to see what it was. It turned out to be a fine healthy plant of *Dendrobium formosum*, a common but extremely beautiful orchid and known to the Burmese as the 'Silver Flower'. It was in full bloom and Parish thought it must have fallen off some overhanging tree on the ridge and slid or been washed down by the rain to its singular position.

Figure 3. *Coelogyne parishii* Hook.f. in *Bot. Mag*. 88: t. 5323. 1862. Type: Burma, Tenasserim, Moulmein, cult. Low, *Parish s.n.* (holo. K). Parish Illustration vol. 1, p. 84, dated 1860. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 4. *Cymbidium parishii* Rchb.f. in *Trans. Linn. Soc. London* 30: 144. 1874. Type: Burma, *Parish s.n.* (holo. W). Parish illustration vol. 2, p. 19, dated 1867. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

From 1859 Parish was writing articles and his discoveries were being discussed, in botanical journals. He identified some 350 indigenous orchids, and grew about 150 species in his garden. Parish used local knowledge as a means of obtaining material around Moulmein. A regular supply of plants arrived which he would plant in his garden and watch them grow, and as he remarked 'hardly a day passed on which I did not either draw or examine microscopically one orchid or another'. Finding suitable individuals to collect for him was not easy. In 1864 he lamented the loss of his regular Burmese collector who set a fire to drive a wild pig out of its lair, but died when the flames engulfed the tree that he had climbed to get out of the way.

Parish's 300 illustrations are bound in two volumes, each comprising about 80 pages. The pages are often annotated with more than one name and *Dendrobium* is the most abundant species in the record. Many are drawings of type material, including *Cleisostoma parishii* (Fig. 2), *Coelogyne parishii* (Fig. 3), *Cymbidium parishii* (Fig. 4), *Dendrobium parishii* (Fig. 5), *Hygrochilus parishii* (Fig. 6), *Paphiopedilum parishii* (Fig. 7), *Peristylus parishii* (Fig. 8), *Porpax parishii* (Fig. 9) and *Phalaenopsis parishii* (Fig. 10), were named in his honour by Reichenbach and Joseph Hooker. Reichenbach (1874) listed most of the more than 200 orchid species collected by Parish around Moulmein and described many novelties based on Parish's collections. Other Parish species were described by him in a variety of German and British journals.

Following his retirement, Parish made a substantial contribution on *Orchidaceae* in the third edition (1883) of Francis Mason's *Burma, its people and productions; Notes on the fauna, flora and minerals of Tenasserim, Pegu and Burma. Vol. II, Botany*, rewritten and enlarged by W. Theobald, who had just retired from his post as Deputy-Superintendent Geological Survey of India. A typical Parish entry concerns *Vanda*:

> "I come now to a very puzzling group of orchids. I have lying on the table before me as I write, figures and illustrations of *Vanda roxburghii*, of *V. roxburghii* var. *unicolor*, *V. bensonii*, *V. denisoniana*, and of a *Vanda* of my own finding, which I have marked doubtfully, as *V. bensonii*. Size and colour apart, I look in vain for anything among all these which, in any other order of plants, would be reckoned sufficient for a specific distinction. …."

Parish retired after more than 25 years in Burma, on 20th June 1878 but he remained an active clergyman in the Taunton area. His wife Eleanor and their children had remained at Taunton when Parish returned to Moulmein after his period of leave in 1872-73. On the 8th July 1885, it was reported that at the Orchid Congress held in London he was awarded a gold medal from the Royal Horticultural Society, in recognition of his exertions in connection with the importation of Burmese orchids, of which he was an extensive and enthusiastic collector when resident in the colony (*Taunton Courier, and Western Advertiser*, 1885). He died quietly in his sleep, on the 18th October 1897, aged 75, at Roughmoor House, his home in Bishop's Hull on the outskirts of Taunton.

ACKNOWLEDGMENTS. I am grateful to the Director of the Royal Botanic Gardens, Kew for enabling me to use the facilities at Kew as an honorary research associate. I particular wish to thank the staff of the Herbarium, Library and Archives for their valuable assistance with accessing Parish's illustrations and the Kew Director's Correspondence in relation to my on-going research of Charles Parish and his contribution to *Orchidaceae*. I also thank Dr Leonie Ryder of Brisbane, Queensland for providing me with her transcription of *A Little Known Volcano*. I also appreciated the opportunity to exchange information with her on the genealogical aspects of the Parish family, to which she has a maternal link back to a brother of Henry Parish. All images reproduced by kind permission of the Director and Trustees of the Royal Botanic Gardens, Kew.

LITERATURE CITED

British Newspaper Archive, British Library, London; accessed via a personal subscription:

Bath Chronicle and Weekly Gazette 1749-1950; 11th June 1846.

Exeter and Plymouth Gazette 1827-1950; 15th August 1846.

Sherborne Mercury 1789-1867; 12th June 1847 and 29th December 1849.

Taunton Courier, and Western Advertiser 1833-1963; 8th July 1885.

Kew Director's Correspondence (KDCAS651-657; KDCAS1812; KDCAS2090-2112; KDCAS2114-2138; KDCAS2155; KDCAS2809-2812; KDCAS2814-2826). Letters from CSP (Charles Samuel Pollock) Parish to

FIGURE 5. *Dendrobium parishii* Rchb.f. in *Bot. Zeitung* (*Berlin*) 21: 237 .1863. Type: Burma, *Parish s.n.* (holo. W). Parish illustration vol. 1, p. 49, dated 11 March 1882. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 6. *Hygrochilus parishii* (Veitch & Rchb.f.) Pfitzer in *Engler & Prantl (eds.), Nat. Pflanzenfam., Nachtr*. 1: 112. 1897) *Vanda parishii* Rchb.f., *Xenia Orchid*. 2: 138. 1868. Type: Burma, Moulmein, *Parish s.n.* (holo. W). Parish illustration vol. 2, p. 29, dated 5 April 1870. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 7. *Paphiopedilum parishii* (Rchb.f.) Stein, *Orchideen-Buch*: 479. 1892. *Cypripedium parishii* Rchb.f., *Flora* 52: 322. 1869. Type: Burma, *Parish s.n.* (holo. W-RCHB; iso. K). Parish illustration vol. 2, p. 88, dated 1867. Charles and Eleanor Parish are both identified as the artists. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 8. *Peristylus parishii* Rchb.f. in *Trans. Linn. Soc. London* 30: 139. 1874. Type: Burma, Tenasserim, Moulmein, cult. Dawson, *Parish s.n.* (holo. W-RCHB; iso. K). Parish illustration vol. 2, p. 81, dated 15 June 1868. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 9. *Porpax parishii* (Lindl. & Rchb.f.) Rolfe in *Orchid Rev.* 16: 8. 1908. *Eria parishii* Lindl. & Rchb.f., *Trans. Linn. Soc. London* 30: 147. 1874. Type: Burma, *Parish s.n.* (holo. W). Parish illustration vol. 1, p. 55, dated 1856. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

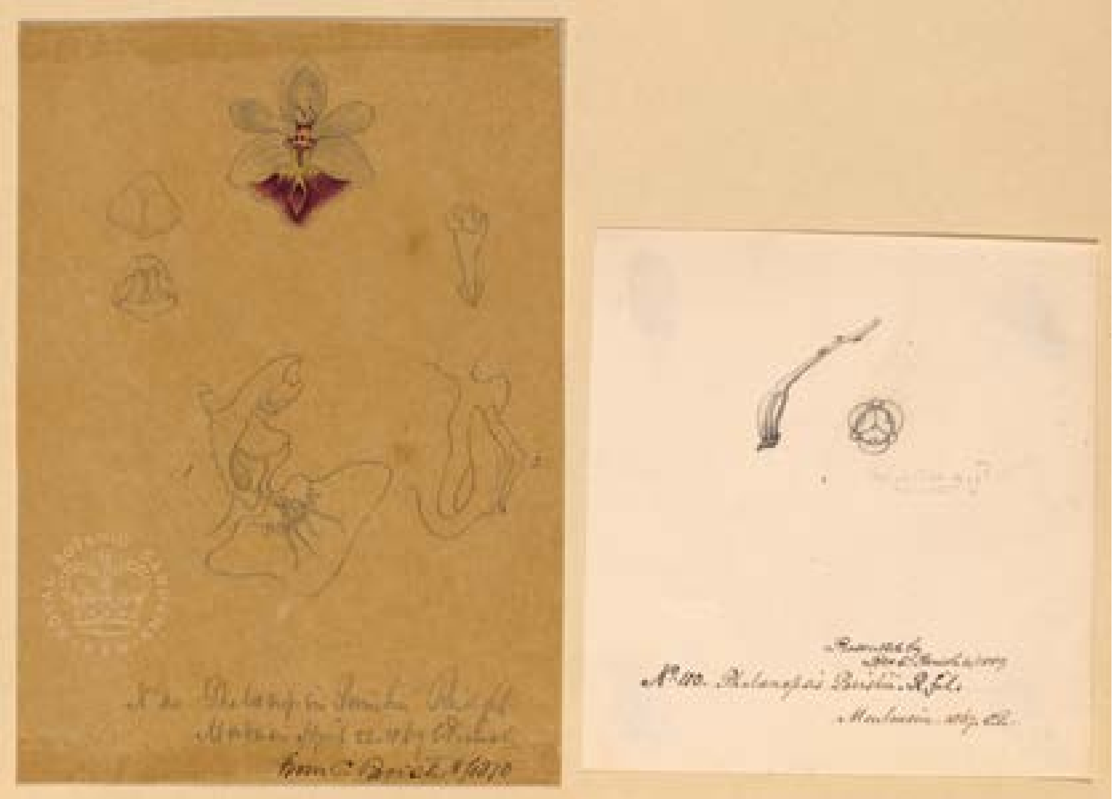


FIGURE 10. *Phalaenopsis parishii* Rchb.f. in *Bot. Zeitung* (*Berlin*) 23: 146. 1865. Type: Burma, Tenasserim, Moulmein, *Parish s.n.* (holo. W-RCHB). Parish illustration vol. 2, p. 70, dated 20 April 1869. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Sir William Jackson Hooker (1855-1865).

Kew Director's Correspondence (KDCAS5360-5363; KDCAS5365-5371; KDCAS5373-5380; KDCAS5382-5410; KDCAS5412-5413). Letters from CSP (Charles Samuel Pollock) Parish to Sir Joseph Dalton Hooker (1862-1882).

Mason, F. 1883. *Burma, its people and productions; Notes on the fauna, flora and minerals of Tenasserim, Pegu and Burma. Vol. II, Botany*, rewritten and enlarged by W. Theobald, Late Deputy-Superintendent Geological Survey of India. Published by Order of the Chief Commissioner of British Burma. Stephen Austin & Sons, Hertford.

McNally, S.J. 1976. *The Chaplains of the East India Company*. List of all Chaplains appointed to the service of the East India Company 1601-1861 (transcript) with biographical details, compiled 1935-1976 by Sidney James McNally, India Office clerk, 1922-1947. British Library, London, Oriental and India Office Collection.

Parish, C.S.P. 1856-1874. *Drawings* (*coloured*) *of Orchidaceae* (*executed chiefly at Moulmein*) in 2 volumes. Royal Botanic Gardens, Kew Catalogue No. 114242.

Parish, C.S.P. 1861. *A Little Known Volcano*, visited 19th October 1861 (a copy donated to the British Library by G.M. Parish, Broadstone, 1953. British Library, London, Oriental and India Office Collection, European Manuscripts, MSS. Eur. D674 (transcription by Dr L.A. Ryder (2012), Brisbane, Queensland, Australia).

Reichenbach, H.G. 1874. Enumeration of the orchids collected by the Rev. (E.C.) C.S.P. Parish in the neighbourhood of Moulmein, with descriptions of the new species in *Transactions of the Linnean Society of London*, 30: 133-155. London.

LANKESTERIANA 13(3): 229—250. 2014.

INVITED PAPER*

SLIPPER ORCHIDS IN ART AND SCIENCE

PHILLIP CRIBB

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, United Kingdom
P.Cribb@kew.org

ABSTRACT. The lady's slippers, orchids with showy and unusual flowers with considerable diversity in shape, size and colour, are amongst the most popular of all orchids in science and horticulture. Consequently, the botanical and horticultural literature on them is extensive. Artists and designers have also been intrigued by them and they feature in many illustrated botanical and horticultural books and decorative items, from tapestries to porcelain and stamps. In this article, the history of slipper orchids is illustrated by reference to illustrations of them, mostly in the collections of the Royal Botanic Gardens. Kew.

KEY WORDS: Orchidaceae, Cypripedioideae, botanical illustration, Kew

> "Be guided by nature". "Do not depart from it, thinking that you can do better yourself"
> Albrecht Dürer (1471-1528)

> "Modern botanical drawing may … be said to date from the publication in 1530 of Brunfels' *Herbarum Vivae Eicones"*
> Wilfred Blunt & William Stearn
> *The Art of Botanical Illustration* (1994)

Introduction. Modern botany has its origins in Ancient Greece (Arber, 1986; Pavord, 2005). The first herbal, describing and naming plants of use to physicians was prepared in the eastern Mediterranean by a student of Plato, the Greek physician Theophrastus of Lesbos (371-287 BC) (Arber, 1986). Much of the knowledge in his *Enquiry into Plants* and *On the causes of Plants* was distilled by Dioscorides (40-90 AD) in his *De Materia Medica*, a text that was copied and widely used by physicians for the following 1500 years. The earliest surviving copy is the *Codex Julian Anicia* of 512 AD, prepared for Juliana Anicia, the daughter of the Emperor Anicius Olybrius in Constantinople and preserved in the Austrian National Library in Vienna. Amazingly, this copy of Dioscorides' herbal is illustrated in colour with life-like and recognisable images of plants from the region. The significance of illustrations can be traced to the ease with which they can be used for identification purposes when compared with the written word. In essence, they make the process of identification and naming much quicker and easier. Images of orchids do not appear in the *Codex*, but first appeared in the new herbals that began to be published in the Renaissance.

Botanical art made its greatest impact with the publication of the first printed herbals. According to Wilfred Blunt and William Stearn (1994), "Modern botanical drawing may … be said to date from the publication in 1530 of Brunfels' *Herbarum Vivae Eicones"*. Otto Brunfels' herbal was illustrated with fine woodcuts based on original drawings by Hans Weiditz, a pupil of Albrecht Durer. Weiditz's originals survive in the herbarium of Felix Platter (Figs 1, 2), preserved in the City Library in Bern. Brunfels' herbal

---

* This paper was prepared in the framework of the celebration of Lankester Botanical Garden's 40th anniversary. Charles Lankester formed a close association with Victor Summerhayes, Kew's orchid specialist from 1928 until his retirement in 1964. They he corresponded frequently and Lankester sent many living and preserved plants to Kew that he could not identify. This relationship contributed many rarities to the Kew orchid herbarium and living collections over the years and enabled Lankester to provide identities and names for his many discoveries which he grew on in his private garden which is now the Jardin Botanico Lankester. The relationship between the botanists there and at Kew continues fruitfully to the present day. It is a pleasure to contribute this article to the celebration of Charles Lankester's legacy which is now a thriving source of expertise on Costa Rica's rich native flora

FIGURE 1. Felix Platter herbarium volume. Courtesy of the Historical Museum of Bern.

FIGURE 2. Orchids in the Felix Platter herbarium. Courtesy of the Historical Museum of Bern.

included orchids, although no lady's slipper, a surprise because it is native and not uncommon in Germany. We have to wait until later in the 16th century for slipper orchids or lady's slippers to make their first appearance in literature and illustration. Let us, first of all, consider what distinguishes the lady's slipper orchids.

Slipper orchids. Lady's slippers, comprising about 160 species (Pridgeon *et al.*, 1999), are found throughout Asia, Europe and the Americas as far south as Bolivia and Brazil, but are absent from Africa, Madagascar and Australia. They are among the most popular of orchids. The earliest record we have of their cultivation is that by Philip Miller in 1731. He grew the native Lady's slipper orchid (*Cypripedium calceolus*) at the Chelsea Physic Garden. Nowadays, no collection is complete without its selection of slipper orchids.

Lady's slippers have features that set them apart from other orchids, and form a distinct well-defined group within the family, distinguished by the flowers which have lateral sepals joined to form a synsepal, a slipper-shaped lip termed, two fertile lateral anthers of the inner whorl, a sterile more or less shield-shaped staminode at the apex of the column, and a stalked trilobed stigma that lies ventrally on the column behind the staminode. Consequently, they have been considered to be "primitive" orchids. They represent as small percentage of the family Orchidaceae, certainly less than 1% in terms of numbers of species and genera. Furthermore, many are rare and threatened with extinction in their native habitats.

Slipper orchids are now recognised as a distinct subfamily, the Cypripedioideae, within the Orchidaceae (Dressler 1981, 1993, Chase et al., 2003), comprising five genera. All slipper orchids were included in the genus *Cypripedium* for almost a century after the name was established by Linnaeus (1737). Constantine Samuel Rafinesque (1819, 1838), who knew the hardy American species at first hand, was the first to recognise the diversity within the slipper orchids, establishing the genera *Sacodon*, *Stimegas*, *Cordula*, *Menophora* and *Criosanthes* but his work was largely ignored by his contemporaries because it was published in obscure and little circulated works and he was less than clear himself about the status of his taxa.. Of these names *Sacodon* and *Criosanthes* refer to species now included in *Cypripedium*, while the rest refer to species now included in *Paphiopedilum* which has been conserved over *Cordula* and *Stimegas* (Farr *et al.* 1979).

H. G. Reichenbach (1854) established the genus *Selenipedium* for the tropical American species which have a trilocular ovary. Blume (1858) discounted this character because he found unilocular ovaries of some species were trilocular towards each end. However, George Bentham and Joseph Hooker (1883) followed Reichenbach in dividing the slipper orchids into two genera.

Ernst Pfitzer (1886, 1889, 1894) prepared the ground for the modern generic treatment of the slipper orchids by recognising the correlation of leaf type with perianth persistence. He established the genus *Paphiopedilum* for the tropical Asiatic and American species with hard leaves and a deciduous perianth, leaving the plicate-leaved northern temperate species with a persistent perianth in *Cypripedium* and the tropical American ones in *Selenipedium*.

Robert Rolfe (1896) revised the slipper orchids. He

Figure 3a. The Bischofzell tapestry, Basel City Museum, showing *Cypripedium calceolus* in the lower part. Courtesy of the Basel City Museum.

restricted the genus *Paphiopedilum* (now c. 70 species) to the Old World hard-leaved species with imbricate imbrications, but placed the New World hard-leaved species in a new genus *Phragmipedium* (now ca. 21 species) based on their leaf type and valvate imbrication of the sepals. The use of *Cypripedium* (now 47 species) and *Selenipedium* (now 5 species) followed that of Pfitzer.

The monotypic *Mexipedium*, the fifth slipper orchid genus, was established by Albert and Chase (1992) to accommodate a dwarf Mexican slipper orchid which had morphological features intermediate between those of the tropical American *Phragmipedium* and the tropical Asiatic *Paphiopedilum*. It was originally included by Soto *et al.* (1990) in *Phragmipedium* on account of its possession of the valvate aestivation of its sepals, the absence of sinuous epidermal cells in the perianth, the fusion of the side lobes of its lip and the ventral synsepal being larger than the dorsal sepal. Albert and Chase added a further character of branched inflorescences in *Phragmipedium* but absent from *Paphiopedilum*. Two years later, with the benefit of data from DNA analysis, Albert (1994) found that *Mexipedium* was basal in the *Phragmipedium* clade.

Slipper orchids have also fascinated generations of botanists. Notably, their pollination biology was first studied by Charles Darwin, the pre-eminent biologist. They have consequently featured prominently in botanical art. Here, the history of slipper orchids in art is considered and illustrated by some of the fine illustrations and representations that are in the collections of the Royal Botanic Gardens, Kew

Illustrations of slipper orchids

Cypripedium —. “Cypripediums - The grandest and most august of the Orchidaceae, one great race which is supreme alike in the open and under cover, deserves full treatment by itself.”

Reginald Farrer (1919) in *The English Rock Garden*

In the subdued light in the basement of the Historisches Museum Basel hangs a remarkable tapestry which depicts a summer scene of the small walled town of Bischofszell in north-eastern Switzerland just south of the Bodensee (Lake Constance) (Fig. 3a). The tapestry dates from 1510 and, for the botanist,

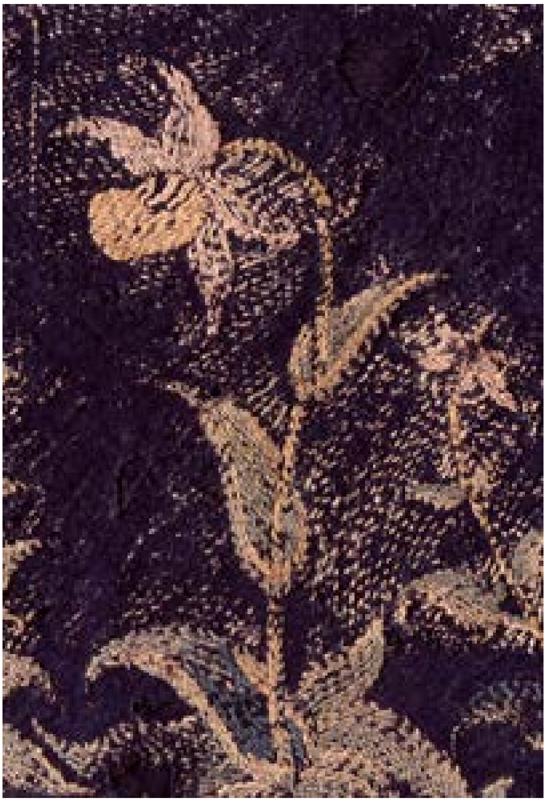


Figure 3b The Bischofzell tapestry, Basel City Museum. Detail od *Cypripedium calceolus*. Courtesy of the Basel City Museum.

Figure 4. Rembert Dodoens' illustration of *Cypripedium calceolus* in his *Florum, et coronarium odoratarumque nonnullarum herbarium historia* (1568). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

its beauty is enhanced by the accurate depiction of a number of native plants, including oxlip, columbine, wild strawberry and a lady's slipper orchid (Fig. 3b). This may well be its first depiction. The slipper orchid image is situated on the lower border slightly to the right of centre and shows a yellow-flowered plant, not the normal form which has a yellow pouch and maroon sepals and petals. However, plants with pure yellow of almost yellow flowers do occasionally occur in populations of more typical plants in Switzerland.

Linnaeus first used the name *Cypripedium* in 1737 in his *Flora Lapponica* in describing the European species as "*Cypripedium foliis ovato-lanceolatis*", the name *Cypripedium* alluding to Cyprus, the island that was the mythological birthplace of Aphrodite (Venus), and "*pedilum*" a shoe or slipper, in allusion to the popular name of "Lady's slipper". In 1753 he named and described two species *C. calceolus* and *C. bulbosum*. The former concept included the well-known European *C. calceolus* and the North American species now treated as *C. parviflorum* (var.b), *C. acaule* (var.g), and *C. guttatum* (var.d). The last is now considered to belong to the distinct and unrelated genus *Calypso*.

Linnaeus was by no means the first to describe slipper orchids. The earliest description and published illustration of a slipper orchid can be traced to the herbal of Rembert Dodoens (1568) entitled *Florum, et coronarium odoratarumque nonnullarum herbarium historia*. His wood-cut illustration of "*Damasonium nothum*" or "Papen schoen", a one-flowered plant of *C. calceolus* complete with rhizome and roots (Fig. 4), is simple but accurate and clearly identifiable. The drawing was sent to him by Joannes Vreccomtus of Brussels who had flowered the illustrated plant in his garden, the earliest record of its cultivation.

Mathias de L'Obel (1576) reproduced Dodoens' illustration in his *Plantarum seu stirpium historia* while Dodoens (1583) used it again in his *Stirpium historiae*

Figure 5. *Cypripedium calceolus* from Dodoens' herbal *Stirpium historiae pemptades* (1583). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

pemptades... together with a more refined illustration of a plant with a branched rhizome with several shoots, one of which bears two flowers and the other two seed pods (Fig. 5). The latter originated in the contemporary herbal *Rariorum aliquot stirpium...* of Charles de L'Ecluse (1583), also known as Clusius. Dodoens used the name "*Calceolus Marianus*", "Pfaffen schuh", "Papen schoen" and "*Calceolus Sacerdotis*", while Clusius, "referring to it as "Marienschuh", placed it next to the helleborines, "Elleborine ". Dodoens stated that it was found in "*Helvetiorum, & Norici, ac Pannoniae superioris sive Austriae montibus*". Clusius had seen the plant in the wild in Austria and Hungary and it seems likely that his illustration was based on a wild plant seen on his travels. The wood-cut would then have been produced for his own work but shared with Dodoens who was a good friend (Arber,1986).

Dodoens' plate reappears in several later herbals, notably those of John Gerard (1597) in his *Herball* and John Parkinson (1629) in his *Paradisi in sole paradisus terrestris....* Large chunks of Dodoens' work appear in Gerard's *Herbal* in translation. However, this was an accepted methodology of the day and Gerard did add notes on plants with which he was familiar. He calls *Cypripedium calceolus* "Our Ladies shooe or slipper" and notes that it "groweth upon the mountains of Germanie, Hungarie, and Poland". He grew a plant given to him by his friend the Apothecary Master Garret and this is the earliest reference I can trace of the cultivation of the species in the British Isles. It is interesting that Gerard was unaware that it was a native British species. Its recognition as such was left to John Parkinson (1629) who called it "*Helleborine vel Elleborine maior, sive Calceolus Mariae*".

Parkinson recorded it as growing in "Lancashire, neare the border of Yorkshire, in a wood or place called the Helkes, which is three miles from Inglborough, the higest Hill in England, and not farre from Ingleton, as I am informed by a courteous Gentlewoman, called Mistris Thomasin Turnstall, who dwelleth at Bull-banke, near Hornby Castle...(she) hathe often sent mee up the rootes to London which have faire flowers in my Garden". The Lady's Slipper survived in that area until into the present century and Parkinson's only mistake is his suggestion that Ingleborough is the highest hill in England. Parkinson was indeed an astute observer and noted that the seed of *C. calceolus* "is very small, very like unto the seede of the Orchides or Satyrions, and contained in such like long pods, but bigger." As far as I can determine he was the first to connect *Cypripedium* with the orchids and to note their tiny seeds. Michel Adanson (1763) was the first botanist to formally include slipper orchids in the orchid family.

The earliest known colour illustration of *C. calceolus* is that by Conrad Gesner (or Gessner) dating from 1541, a watercolour of a plant from Mt. Saleu in the Swiss Jura near Geneva (Fig. 6). It is an accomplished likeness, far superior to the later woodcuts in the L'Obel, Dodoens and Clusius herbals, while in botanical accuracy and detail of the rhizome, fruit and column it was not matched for another two hundred or more years. Gesner died from plague before he was able to publish his botanical illustrations. Schmiedel (1754-1759) published part of Gesner's botanical work for the first time as *Opera Botanica* and included the coloured illustration and account of *C. calceolus* as "*Calceolus Mariae*". They

Figure 6. Conrad Gesner's illustration of *Cypripedium calceolus*, ca. 1540. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 7. Leonard Plukenet's plate of *C. acaule* and *C. parviflorum* var. *parviflorum* and var. *pubescens* from his *Amaltheum Botanicum* (1700). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

have recently been reproduced in facsimile by Zoller, Steinmann & Schmidt (1973-1980). A useful list of early descriptions and illustrations of slipper orchids is included.

Another early colour illustration of *C. calceolus* is that by Daniel Rabel (1578-1638), recently reproduced in the second edition of Blunt & Stearn (1994). The original is in the Bibliotheque Nationale in Paris and it was probably painted in 1631 or 1632.

Parkinson (1640) returned to the theme of "Our Ladyes Slipper or the great wilde Helleborine" in his *Theatrum botanicum*. There he recorded a North American species, undoubtedly *C. reginae*, as a "sort thereof.......brought from the North parts of America, differing onely in being greater both in stalkes, leaves and flowers, which are not yellow but white, with reddish strakes through the bellies of them". An earlier reference to a North American species, however, is that of J.P. Cornut (1635) in his *Canadensium Plantarum Historia* where he listed "*Calceolus marianus canadensis*", a reference to *C. acaule,* the Moccasin flower.

Cypripedium reginae and three other North American taxa, *C. acaule* and *C. parviflorum* var. *parviflorum* ("*Calceolus...flore luteo minore*") and var.*pubescens*, were described by Leonard Plukenet (1700) in his *Mantissa*, the first two and the last being illustrated by him in 1705 in his *Amaltheum Botanicum* (Fig. 7). These line illustrations are the earliest representations of North American slipper orchids. The earliest coloured illustration of a North American species is that of "*Calceolus flore maximo rubente*" (=*C. acaule*) (Fig. 8) by Mark Catesby (1754) in *The Natural History of Carolina, Florida and the Bahama Islands*.

The first edition of Philip Miller's *Gardeners Dictionary*, published in 1731, included three species of hardy slipper orchid: the European species as "*Helleborine; flore rotundo, sive Calceolus*";

Figure 8. Mark Catesby's illustration of *Cypripedium acaule* from *The Natural History of Carolina, Florida and the Bahama Islands* (1754). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 9. *Cypripedium parviflorum* var. *pubescens* by Georg Dionysius Ehret, ca. 1758. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 10. Plate of *Cypripedium calceolus*, *C. macranthos* and *C.* x *ventricosum* from Gmelin's *Flora Sibirica* (1747-1749). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

and two North American species "*Helleborine; Virginiana, flore rotundo luteo*", one of the varieties of *C. parviflorum*, and "*Helleborine; Canadensis, sive calceolus mariae*", probably *C. reginae*. He commented that "all (are) Natives of Woody and shady Places". He provided a coloured illustration in his *Figures of the most beautiful, useful and uncommon plants figured in the Gardeners Dictionary* published in 1758. This illustration may, indeed, be the first of a British plant as Miller reiterates that it was "found in some Parts of England" and also mentions flowering it at Chelsea where, no doubt, the coloured illustration by R. Lancake was made. The German artist Georg Dionysius Ehret who worked at the Chelsea Physic Garden for Miller also illustrated a plant of the North American *C. parviflorum* var. *pubescens* (Fig. 9) which Miller probably grew at Chelsea.

Linnaeus (1753) apparently overlooked Parkinson's and Miller's references to North American species but including Cornut and Morison's names within *C. calceolus*, the European species which must have been familiar to him in his native Sweden.

William Aiton (1789) listed three species in his *Hortus Kewensis*: the European *C. calceolus*, and the North American *C. reginae* (as *C. album*) and *C. acaule* as being grown at Kew. *C. reginae* had been introduced by William Hamilton in 1786 and *C. acaule* by William Young in 1770.

Johann Amman (1741) and Johann Georg Gmelin (1747-1749) published the first descriptions and illustrations of Asian slipper orchids (Fig. 10). The former illustrated Siberian *C. macranthos* as "*Calceolus purpureus speciosus*"and *C. guttatum* as "*Calceolus minor flore vario*" . The latter figured *C. calceolus*, *C. ventricosum* and *C. macranthos*, the last as "*Calceolus purpureis speciosus*". Swartz (1800) based the names *C. ventricosum* and *C. macranthos* on Gmelin's collections.

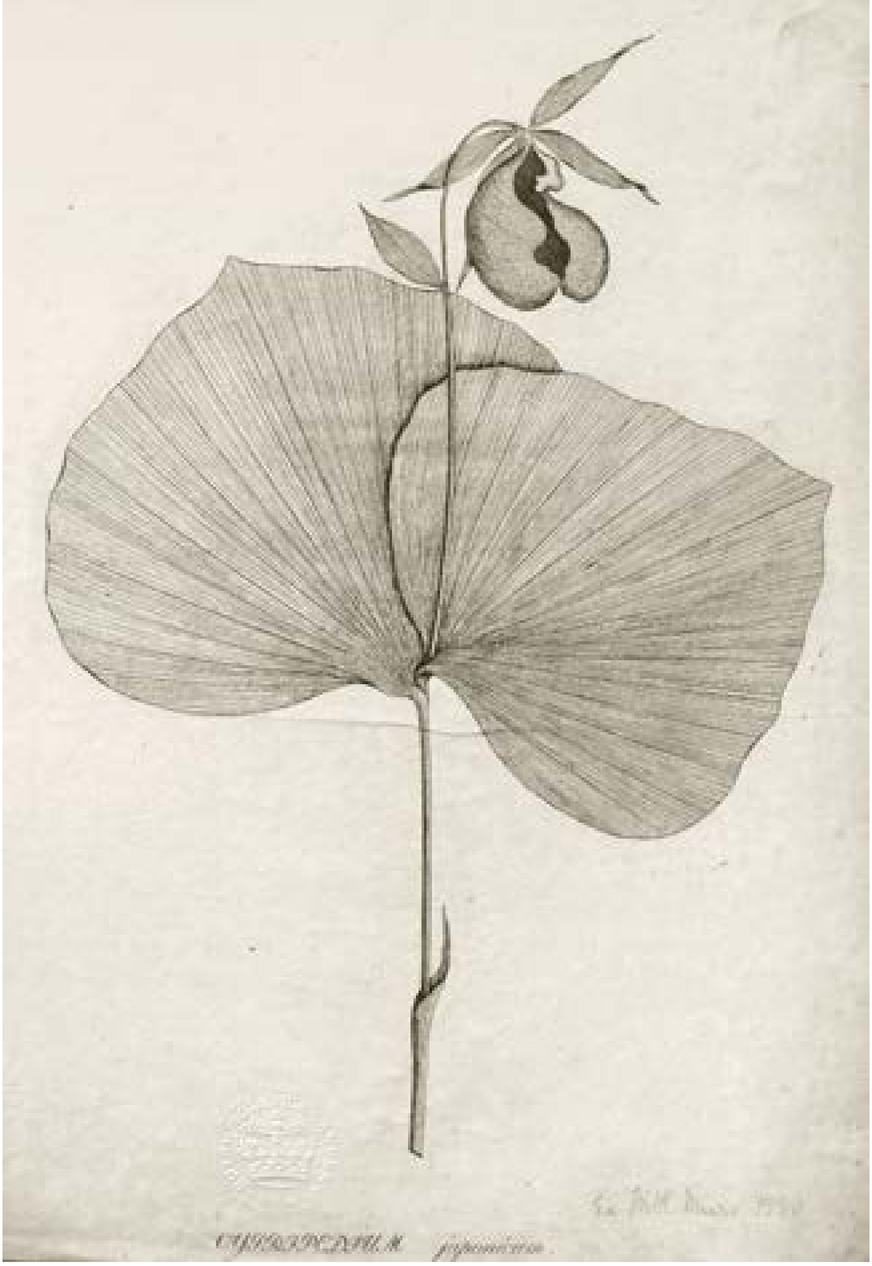


Figure 11. Carl Peter Thunberg's illustration of *Cypripedium japonicum* from his *Flora Japonica* (1784). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Linnaeus's pupil Carl Peter Thunberg was the first western botanist to visit Japan. *Cypripedium japonicum* and *C. macranthos* (as *C. calceolus*) were described in his *Flora Japonica* (1784), the former also being illustrated there (Fig. 11). The Japanese slipper orchids *C. japonicum*, *C. debile* and *C. macranthos* figured in Yokusai Iinuma's *Somoku Zusetsu* of 1874. However, Ludovic Savatier's watercolours of *C. japonicum* and *C. macranthos* made between 1856 and 1866 survive in the Kew collection. Most of the species in the Far East remained unknown for nearly a century more until botanists began to penetrate into the mountainous west of China.

Figure 12. *Paphiopedilum insigne* by an unknown Indian artist for the Calcutta Botanic Garden, ca. 1820. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 13. Samuel Curtis's *Paphiopedilum insigne* drawn for John Lindley's *Collectanea Botanica* (1821). Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

The first hint of the rich array of western Chinese *Cypripedium* species was the collection in 1864 by Père Armand David of the yellow-flowered *C. luteum* (now *C. flavum*) at Moupin in what is now western Sichuan. However, the diversity of the Chinese cypripediums was not apparent until the last few years of the 19th century. From 1894 onwards, the indefatigable French missionaries, Delavay, Soulie, Maire, Monbeig and Farges, based in Yunnan and Sichuan, began to send back large numbers of collections to Paris, many to be described as new to science by the French botanist Franchet. By the turn of the century the British collectors Augustine Henry in Hubei, Sichuan and Yunnan and Ernest Wilson in Sichuan and Hubei had added further species. New Chinese species have continued to be discovered and described this century (Tang & Wang, 1951; Cribb, 1992; Cribb & Chen, 1994; Chen *et al.*, 2013) and many have been illustrated in *Curtis's Botanical Magazine*, founded in 1878 and the oldest surviving journal illustrated in colour.

Paphiopedilum —. The increasing influence of the British in India opened up its rich tropical flora to botanists and horticulturists. The establishment of botanic gardens, initially to introduce crops for plantation culture, led to the flora being explored by a number of intrepid collectors and botanists, particularly those associated with the Calcutta Botanic Garden which had been established in 1787. William Roxburgh collected orchids and employed Indian artists to draw them. Nathaniel Wallich, his successor, developed the garden and started the herbarium of the East India Company, the latter being the basis of our current knowledge of the flora of India and neighbouring countries. He also employed native artists to illustrate novelties and these watercolour paintings are now held at Kew. Among these are some fine illustration of both cypripediums and paphiopedilums. Two from 1826 are reproduced here, namely *Paphiopedilum insigne* (Fig. 12) from the Khasia Hills and the Himalayan *P. venustum*. The former had earlier been sent by Wallich to London where Samuel Curtis illustrated it for John

Figure 14. Hugh Low's painting of his collection of *Paphiopedilum lowii,* drawn in Sarawak, Borneo, ca. 1847. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 15. Lilian Snelling's *Paphiopedilum callosum*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Lindley's *Collectanea Botanica* (1821) (Fig. 13).

Plant collectors occasionally illustrated the plants that they discovered. Several of these original paintings survive at Kew. Hugh Low's original watercolour of *Paphiopedilum lowii* (Fig. 14) also survives at Kew. The beautiful watercolours of Charles Parish, including his watercolour of the eponymous *Paphiopedilum parishii*, are dealt with in an accompanying article (Clayton, 2013). Many of their collections and those of other plant hunters ended up being sold by European nurseries, particularly those in England, and were illustrated when they first flowered in cultivation.

Over the past 226 years, many novelties have been first figured in the pages of *Curtis's Botanical Magazine*. Walter Hood Fitch, Matilda Smith, Lilian Snelling, Stella Ross-Craig, Margaret Stones, Pandora Sellars, Cristabel King and Carol Woodin have all produced outstanding illustrations of slipper orchids for the journal (Figs. 15-18). Some of Fitch's finest slipper orchid paintings were prepared for Robert Warner's *Select Orchidaceous Plants* (Lovell Reeve, London: 1862-1878) (Figs. 19, 20).

Kew possesses many remarkable illustrations in its archives, none more so that John Day's 53 scrapbooks, comprising over 2800 watercolour paintings of orchids (Cribb & Tibbs, 2004). Day cultivated and illustrated 44 species and 46 hybrid slipper orchids in three genera, *Cypripedium*, *Paphiopedilum* and *Phragmipedium*, in his scrapbooks. His illustrations labelled as *Selenipedium* and *Uropedium* are now considered to belong to the genus *Phragmipedium*, while the South-east Asian and Indian species of *Cypripedium* belong to *Paphiopedilum*.

During Day's lifetime many species new to science were discovered and described, including thirty species of *Paphiopedilum*, almost half of the genus. When he successfully flowered novelties he sent them to Professor H.G. Reichenbach for identification and naming. Hence many of Reichenbach's orchid names were based on Day's plants and his specimens and drawings form part of the type materials of many species.

FIGURE 16. Stella Ross-Craig's *Paphiopedilum tonsum*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Some of John Day's most prized orchids were slipper orchids. *Paphiopedilum dayanum* (Fig. 21) was named in his honour and *P. stonei* (Fig. 22) after John Stone, his gardener. He was amongst the first to illustrate *Paphiopedilum sanderianum* (Fig. 23), one of the world's most desirable orchids. The most famous slipper orchid in his collection was *Paphiopedilum stonei* var. *platytaenium* (Fig. 24) which was also probably the most valuable plant of the day and much sought after by other growers who were willing to pay high prices for rarities and spectacular orchids. His illustration of it is one of his finest watercolours.

Figure 17. Pandora Sellars' *Paphiopedilum superbiens*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 18. Carol Woodin's *Paphiopedilum vietnamense*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 19. Walter Hood Fitch's *Paphiopedilum hirsutissimum* for Robert Warner's *Select Orchidaceous Plants*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 20. Walter Hood Fitch's *Paphiopedilum callosum* for Robert Warner's *Select Orchidaceous Plants*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 21. John Day's *Paphiopedilum dayanum*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

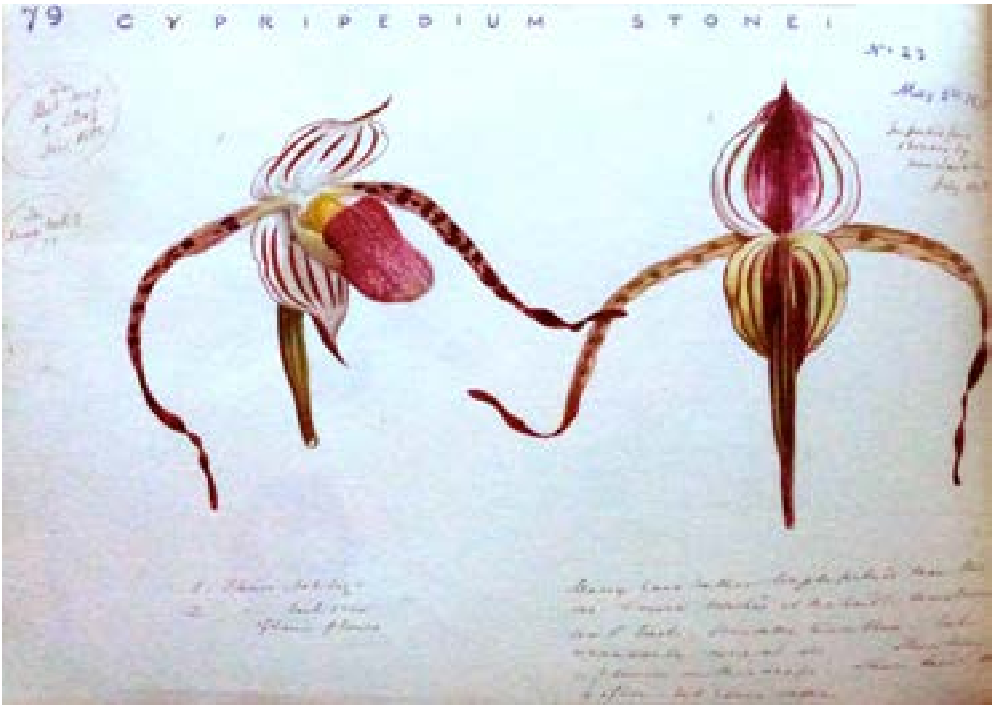


FIGURE 22. John Day's *Paphiopedilum stonei*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 23. John Day's *Paphiopedilum sanderianum*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 24. John Day's *Paphiopedilum stonei* var. *platytaenium*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Selenipedium* and *Phragmipedium —. The Spanish botanists Hippolito Ruiz López (1754-1816) and José Pavón Jiménez (1754-1840) were the first to discover and collect tropical American slipper orchids. Between 1777 and 1788, on behalf of the Spanish King Carlos III, they undertook a botanical exploration of Peru and Chile. The results of their expeditions, over 3000 collections of herbarium specimens and 2500 watercolour illustrations, formed the basis of their proposed ten-volume *Florae Peruviana et Chilensis* (1798-1802) of which only the first four appeared in their life-times. The illustrations, made by the artists Joseph Brunete and Isidro Gálvez, were deposited in the collections of the Royal Botanical Garden in Madrid. Amongst them are watercolours of *Phragmipedium caudatum* and *P. boissierianum*. Unfortunately, neither was described at the time by Ruiz and Pavón. John Lindley saw a flower of each that had been brought from the Ruiz and Pavón collection, still in Lima, by Matthews for Sir William Hooker. He described one as *Cypripedium caudatum*, but the second flower proved to be too badly preserved for description (Lindley, 1840).

Figure 25. Robert Schomburgk's *Phragmipedium lindleyanum*, drawn on Mt Roraima, Guyana. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 26. Everard Im Thurn's illustration of *Selenipedium palmifolium*, ca. 1884. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Sesse and Mociño collected the first Central American *Cypripedium* species in Mexico between 1787 and 1803. Their collections are in the herbarium of the Royal Botanic Garden, Madrid. They collected two species to which they gave the manuscript names "*C. turgidum*" and "*C. acuminatum*". The former name was eventually published posthumously in 1890 (by which time it had already been described by La Llave & Lexarza as *C. irapeanum*). The latter name, referable to Lindley's *C. molle*, has never been published. Contemporary coloured illustrations of the two Sesse & Moçino species are preserved in the Hunt Institute collection in Pittsburg (Cribb & Soto, 1993).

Lindley described *Cypripedium lindleyanum* based on a specimen collected and named by Robert Schomburgk (1804-1865) that had been collected by him near Mt Roraima in Guyana. Lindley commented at the time "I unwillingly consent, at the particular instance of Mr Schomburgk, to allow this plant to bear my name, who have no title to the compliment". Schomburgk's original watercolour illustration (Fig. 25) remains in Lindley's herbarium at Kew. Schomburgk's adventures on Roraima were probably the inspiration for Sir Arthur Conan Doyle's *Lost World* (1912). A watercolour of *Selenipedium palmifolium*, also drawn *in situ* by Everard Im Thurn (1852-1932) who scaled the mountain some years later, also survives at Kew (Fig. 26).

Friedrich Lehmann (1850-1893), the prolific orchid collector in Colombia and Ecuador also painted his discoveries, probably to show European nurseries what he had to offer when he occasionally visited Europe to solicit business. His paintings of phragmipediums were published recently in this journal (Cribb, 2010).

John Day' watercolours of *Phragmipedium* species include early depictions of *P. boissierianum*, *P. caudatum*, *P. schlimii* (Fig. 27), and *P. wallisii*.

Figure 27. John Day's *Phragmipedium schlimii*. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Artificial Hybrids —. John Day had access to, and illustrated in his scrapbooks, nearly all of the early slipper orchid hybrids raised by John Dominy and his successor John Seden for Messrs James Veitch & Sons of Exeter and Chelsea. The significance of these is considerable because systematic collections of illustrations of hybrids, for example that of the Royal Horticultural Society, did not start until the end of the 19th century when many of the early hybrids had already disappeared. Although enthusiastic about some, Day prophetically commented in his appraisal of *Cypripedium* (*Paphiopedilum*) Apiculatum, a hybrid between *P. barbatum* and *P.villosum* var. *boxallii*, that "I am afraid we shall be overcome with hybrids soon and orchids will gradually descend to the level of florist's flowers and lose their interest" (Scrap Book 51, p. 95). He also depicted all of the early *Paphiopedilum* hybrids, including *P.* Harrisianum (Fig. 28) and *P.* Morganiae (Fig. 29) and *Phragmipedium* hybrids, including *P.* Dominii (Fig. 30), *P.* Sedenii (Fig. 31), *P.* Cardinale and others in their first flowering at the Veitch nursery in Chelsea.

Thus, Day's paintings of the early hybrids are an invaluable record of English nurseries early ventures in orchid breeding. His pioneering work on illustrating hybrids was taken up by the Royal Horticultural Society which has employed a series of artists to paint awarded orchids for over a century, a collection that now includes many images of slipper and other orchids and a tradition that endures to the present day (Figs. 32). It seems likely that the idea for the RHS illustrations came from the common practice of orchid nurseries equipping their salesmen who sold orchids around the country with sets of watercolour paintings of their best clones so that growers could order plants based on the paintings. Some of these samples survive at Kew, such as that of *Paphiopedilum* W.R. Lee and *P.* Morganiae (Fig. 33).

Conclusion. Slipper orchids have been a popular subject for botanical artists for over four centuries and remain so today. Their unusual and often showy three-dimensional flowers are an artistic challenge, but the resulting images are often striking and far easier to interpret than descriptions, thereby facilitating

FIGURE 28. John Day's *Paphiopedilum* Harrisianum. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 29. John Day's *Paphiopedilum* Morganiae. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

FIGURE 30. John Day's *Phragmipedium* Dominianum. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 31. John Day's *Phragmipedium* Sedenii. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 32. *Paphiopedilum lawrenceanum* var. *hyeanum* by Nellie Roberts for the Royal Horticultural Society. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 33. Trade painting of *Phragmipedium* Morganiae from the late Victorian period. Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

Figure 34. Mary Grierson's *Cypripedium calceolus* for P. Francis Hunt's *Orchidaceae* (Bourton Press, Bourton. 1973).

identification and naming. Nowadays, most species have been illustrated many times, occasionally inaccurately as in Mary Grierson's painting of *Cypripedium calceolus* (Fig. 34) for Peter Hunt's *Orchidaceae* which endows it with tubers!

The history of their discovery and introduction into cultivation can be traced through the chronology of their depiction. The archives also can be used to trace the development of artificial breeding of slipper orchids for the horticultural trade, through collections of paintings by enthusiasts, for example, John Day and by the artists employed to illustrate awarded plants by the Royal Horticultural Society in London.

In recent years the popularity of botanical art has reached a level not previously seen since Victorian times. Watercolour paintings of slipper orchids are popular and fetch significant prices at art shows.

Slipper orchids have also been used to illustrate the cover of foodstuffs, such as ice cream and chocolates. However, it is probable that the most lucrative line for slipper orchid illustration is for postage stamp issues. *Cypripedium calceolus*, the Eurasian lady's slipper, has appeared on the stamps of numerous countries, including most European countries, the United Nations and, surprisingly the Grenadines of St Vincent in the Caribbean. Tropical slipper orchid species and hybrids are also popular subject for stamp issues. The small island of Jersey, for example, has produced stamps featuring both *Paphiopedilum* hybrids and the Peruvian *Phragmipedium besseae*.

Acknowledgements. I would like to thank Marilyn Ward and Julia Buckley for their help in sourcing illustrations at Kew; Dr. Margret Ribbert, Curator of the Historisches Museum Basel; and Samuel Sprunger and Werner Lehmann of the Swiss Orchid Foundation for alerting me to the image on the tapestry.

Literature cited

Aiton, W. 1789. *Hortus Kewensis*. G. Nicol, London.

Albert, V. A. 1994. Cladistic relationships of the slipper orchids (Cypripedioideae: Orchidaceae) from congruent morphological and molecular data. Lindleyana 9(2): 115-132.

Albert, V. A. & M. W. Chase. 1992. *Mexipedium*: a new genus of slipper orchids (Cypripedioideae: Orchidaceae). Lindleyana 7: 172–176.

Amman, J. 1741. *Quinque nova plantarum genera*. Science Academy, St Petersburg.

Arber, A. 1986. Herbals and their origin and evolution. 3rd ed. Cambridge University Press.

Blunt, W. & W. Stearn. 1994. *The Art of Botanical Illustration*. Antique Collectors Club, Woodbridge, Suffolk.

Blume, C. L. 1858. Collection des orchidées les plus remarquable de l'Archipel Indien et du Japon. G.C. Sulpke, Amsterdam.

Catesby, M. 1754. *The Natural History of Carolina, Florida and the Bahama Islands*.

Chase, M. W., K. M. Cameron, R. L. Barrett & J. V. Freudenstein. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. In Dixon, K.W., S. P. Kell, R. L. Barrett & P. J. Cribb (eds.), *Orchid Conservation*: 69-89. Natural History Publications, Kota Kinabalu, Sabah.

Chen, S.C., Z. H. Liu, L. J. Chen & L. Q. Li. 2013. *The genus* Cypripedium *in China*. Science Press, Beijing.

Cornut, J. P. 1635. *Canadensium Plantarum Historia*. S. le Moyne, Paris.

Cribb, P. J. 1992. The Chinese spotted-leaved cypripediums. Bull. Alp. Gard. Soc. 60, 2: 165-177.

Cribb, P. J. 2010. The life and travels of Friedrich Carl Lehmann. Lankesteriana 10, 2-3: 9-30.

Cribb, P.J. & S. C. Chen. 1994. Further thoughts on the Chinese spotted-leaved cypripediums. Orchid Rev. 102: 321-323.

Cribb, P.J. & M. A. Soto. 1993. The genus *Cypripedium* in Mexico and Central America. Orquidea (Mexico) 13, 1-2: 205-214.

Cribb P.J. & M. Tibbs. 2004) *A very Victorian passion. The orchid paintings of John Day*. Thomas Nelson, London.

Dodoens, R. 1568 *Florum, et coronarium odoratarumque nonnullarum herbarium historia*.

Dressler, R.L. 1981. *The Orchids. Natural History and Classification*. Harvard University press.

Dressler, R.L. 1993. *Phylogeny and classification of the orchid family*. Cambridge University Press.

Farr, E. R., J. A. Leussink, & F. A. Stafleu. 1979. *Index nominum genericorum*. Bohn, Scheltema & Holkema, Utrecht; Junk, The Hague.

Gmelin, J. G. 1747-1749. *Flora Sibirica, sive Historiae plantarum Sibiriae*. Science Academy, St Petersburg.

Iinuma, Y. 1874. *Somoku Dzusetsu*, ed. 2. Mino, Ogakai.

Linnaeus, C. 1737. *Flora Lapponica*. Amsterdam.

Linnaeus, C. 1753. *Species Plantarum*. L. Salvius, Stockholm.

Miller, P. 1731. *Gardeners Dictionary*. C. Rivington, London.

Parkinson, J. (1640). *Theatrum botanicum*. T. Cotes, Parkinson, J. 1640. *Theatrum botanicum*. T. Cotes, London.

Pavord, A. (2005). *The naming of names, the search for order in the world of plants*. Bloomsbury, London.

Pfitzer, E. (1886). Morphologische studien über die Orchideenblüthe. C. Winter, Heidelberg.

Pfitzer, E. (1889). Orchidaceae. In Engler, A., & Prantl, C. eds. Die natürlichen Pflanzenfamilien 2, 6. W. Engelmann, Leipzig.

Pfitzer, E. (1894). Übersicht des natürlichen systems der Pflanzen. C. Winter, Heidelberg.

Pridgeon, A., P. J. Cribb, M. W. Chase & F. Rasmussen (eds.). 1999. *Genera orchidacearum* vol. 1. Oxford University Press.

Rafinesque, C. S. 1819. Prodrome des nouveaux genre des plantes. J. Phys. Chim. Hist. Nat., 89: 96-107.

Rafinesque, C. S. 1838. *Flora telluriana*. C. Rafinesque, Philadelphia.

Reichenbach, H. G. 1854. *Xenia orchidacea*, vol. 1. Brockhaus, Leipzig.

Rolfe, R. A. 1896. The *Cypripedium* group. *Orchid Rev.* 4: 327-334, 363-367.

Schmiedel, D. C. C. (ed.) 1754-1759. *Conradi Gesneri... Opera Botanica*. J.M. Seligmann, Norimberg.

Soto, M. A., G. A. Salazar & E. Hagsater. 1990. *Phragmipedium xerophyticum*, a new species from south-east Mexico. *Orquidea* (Mexico) 12, 1: 1-10.

Zoller, H., M. Steinmann & K. Schmidt. 1972-1980. *Conradi Gesneri Historia plantarum*. Urs Graf, Dietikon, Zürich.

LANKESTERIANA 13(3): 251—258. 2014.

INVITED PAPER*

THREE NEW *MASDEVALLIA* SPECIES (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM PERU

STIG DALSTRÖM[1,3] & SAUL RUÍZ PÉREZ[2]

[1]2304 Ringling Boulevard, unit 119, Sarasota FL 34237, U.S.A.
Lankester Botanical Garden, University of Costa Rica, Cartago, Costa Rica
and National Biodiversity Centre, Serbithang, Bhutan
[2]Allamanda 142, Surco, Lima 33, Peru
[3]Corresponding author: stigdalstrom@juno.com

ABSTRACT. Three new *Masdevallia* species are described, illustrated and compared with similar species. A brief taxonomic discussion is held about the justification for describing the new taxa as *Masdevallia* and not as belonging to any of the recently proposed segregated genera. The first species is most similar to *M. rimarima-alba* but differs in having a more tubular flower and a narrower lip, the second species is similar to *M. dudleyi* and *M. nunezii* but differs in the richly pubescent sepals, and the third species is distinguished from other similar and multiflowered *Masdevallia* species by the rugose lip.

KEY WORDS: Orchidaceae, *Masdevallia*, Pleurothallidiinae, Epidendreae, new species, Peru, taxonomy

In the most traditional circumscription, genus *Masdevallia* Ruíz & Pav., is a large genus in the Pleurothallidiinae, distributed throughout the New World tropics from Mexico in the north to southern Bolivia, primarily along the Andes, but with a few species occurring in Brazil as well. The systematic classification of *Masdevallia* has changed considerably over the years, however, and many groups of species have been transferred to new genera, such as, *Dracula* Luer, *Dryadella* Luer, *Porroglossum* Schltr., *Scaphosepalum* Pfitzer and *Trisetella* Luer.

These transfers were to a considerable extent based on vegetative features in addition to flower morphology, which is user-friendly and makes the genera relatively easy to identify, even without the presence of flowers. A modern classification of the remaining about 350 species of *Masdevallia* (Luer 1986) included vegetatively rather similar plants, which made it easy to spot a *Masdevallia* even without flowers and from several meters distance. Recently, however, molecular work with DNA sequencing has complicated the picture (Abele *et al.* 2005, Pridgeon & Chase 2001), which led Luer to propose a division of the genus, by then about 500 species rich, into 16 new genera, in addition to three already described segregates and the original *Masdevallia* (Luer 2006).

Many growers and scientists have not accepted this proposition and maintain the genus more or less as it was circumscribed by Luer in 1986. For practical reasons, in addition to strict taxonomic reasons, we chose to follow a broader concept of the genus and therefore describe the species treated here as members of *Masdevallia sensu* Luer 1986, but at this time without placing them in any particular subgenus or section.

Masdevallia hortilankesteriani Dalström & Ruíz-Pérez, *sp. nov.*

TYPE: Peru. Junín. Terrestrial along road Comas–Cochas, S11°41.008’, W075° 04.22’, 2800 m. 13 Nov. 2011, *S. Dalström 3510* (holotype, USM). FIGS. 1–4.

Diagnosis: *Masdevallia hortilankesteriani* is similar to the sympatric *M. rimarima-alba* Luer (Fig. 5.) but differs by a more compact vegetative habit, a more campanulate flower with longer and thicker sepaline tails and a narrower lip.

Geophytic or lithophytic *herb*. *Plant* medium in size, caespitose, root-thickness medium for the

---

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

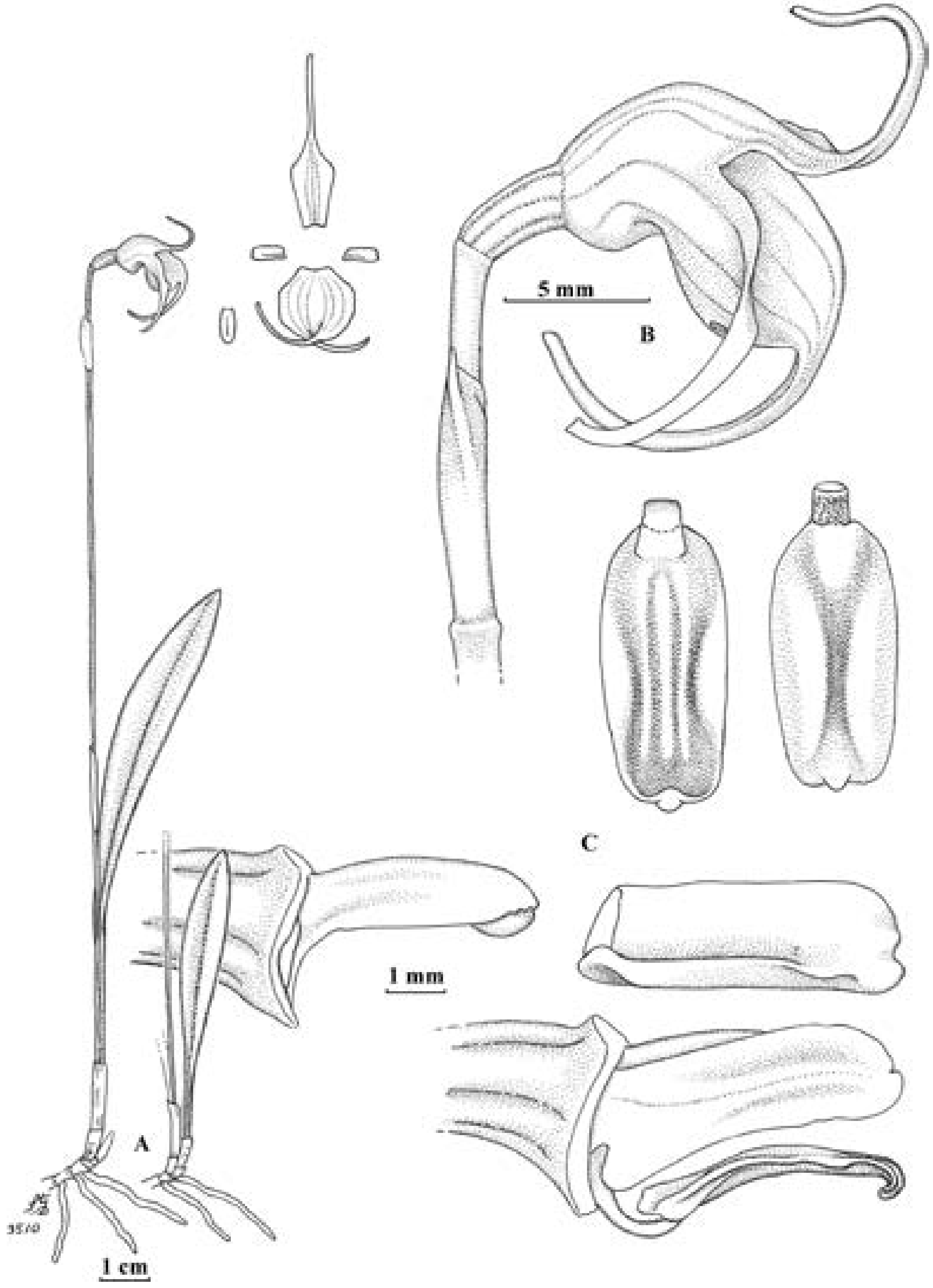


Figure 1. *Masdevallia hortilankesteriani*. A — Plant habit, with a dissected flower. B — Flower lateral view. C — Column, lip and petal views. Drawn from the holotype by Stig Dalström.

Figure 2. *Masdevallia hortilankesteriani* in natural habitat. Photo by Stig Dalström.

genus. *Ramicauls* erect, slender, 1.0–2.5 cm long, enclosed basally by 3 to 4 tubular sheaths. *Leaf* erect, coriaceous, petiolate, blade basally conduplicate and cuneate, elliptic, obtuse to acute, 6–10 × 0.8–1.1 cm, including the 1.5–3.0 cm long petiole. *Inflorescence* erect, terete, single-flowered, with a to *ca*. 15 cm long peduncle; *peduncular bract* 1, tubular, below the middle of the peduncle, *ca*. 1.7–1.8 cm long; *floral bract* appressed, tubular, *ca*. 1 cm long; *pedicel ca*. 2.0–2.2 cm long; *ovary* smooth, *ca*. 0.4 cm long. *Flower* attractive, campanulate; *dorsal sepal* white to pale rose, with purple longitudinal stripes along the 3 veins, glabrous and carinate externally, glabrous to microscopically pubescent internally, slightly concave, cuneate, angulate-obovate and connate to the lateral sepals for *ca*. 13 mm, acuminate into a dorsally rather thick, frontally dull greenish yellow, ventrally purplish tail, *ca*. 36 × 10 mm, including the *ca*. 16– 17 mm long tail; *lateral sepals* similar in texture and coloration, 3-veined, connate for *ca*. 13 mm, angulate-ovate, acuminate with apical, rather thick, slightly recurved tails, *ca*. 30 × 16 mm, including the *ca*. 13–15 mm long tails; *petals* white, cartilaginous, obliquely oblong and apically truncate and obliquely bilobed, with a ventral fleshy ridge, extending from a lobed, or "toothed", base, continuing along the lower edge and diminishing near the apex, *ca*. 6 × 2 mm; *lip* whitish, heavily flushed with brownish purple, with darker longitudinal ventral stripes and a dark purple-brown apex, hinged on the column foot, with a basal swelling and shallowly notched, cuneate, oblong-elliptic, apically truncate, recurved and bluntly apiculate, dorsally slightly canaliculate between low fleshy ridges, 5.0 × 2.5 mm; *column* white with brown-purple ventral stripes, semi-terete, straight, *ca*. 4 mm long, with an equally long, curved foot that is slightly pubescent dorsally near the apex; *anther cap* white and campanulate; *pollinia* not seen.

Figure 3. *Masdevallia hortilankesteriani* in natural habitat. Photo by Stig Dalström.

Figure 4. *Masdevallia hortilankesteriani* flower. Photo by Stig Dalström.

Paratypes: Peru. Junín. Terrestrial along road Comas—

FIGURE 5. *Masdevallia rimarima-alba*, Huasahuasi. Photo by Stig Dalström.

Cochas, S11°41.008’, W075° 04.22’, alt. 2800 m. 13 Nov. 2011, *S. Dalström 3508* (USM).

DISTRIBUTION: *Masdevallia hortilankesteriani* is only reported from steep grassy and rocky slopes of the Andes near the town of Comas, in the region of Junín, where it often grows in full sun along the road.

ETYMOLOGY: Named in honor of Lankester Botanical Garden and its staff, in recognition of their support for orchid research in general and in the New World tropics in particular.

Masdevallia karelii Dalström & Ruíz-Pérez, *sp. nov.*

TYPE: Peru. Puno, Sandia, along Rio Chullo in dense, mossy cloud forest, S14°20.769’, W69°26.836’, alt. ca. 2700 – 2800 m, 25 Nov. 2010, *S. Dalström 3533* (holotype, USM). FIGS. 6–8.

Diagnosis: *Masdevallia karelii* is most similar to species such as *Masdevallia dudleyii* Luer, *M. nunezii* Luer & Dalström, *M. juan-albertoi* Luer & M.Arias, and *M. terborchii* Luer, all occurring in the highlands of central Peru, but our new species is distinguished from them all by the rich magenta sepaline pubescence.

Epiphytic *herb*. *Plant* medium to tall in size, caespitose, root-thickness medium for the genus. *Ramicauls* stout and erect, blackish in the wild, (presumably from a benign fungus) 3.5–3.8 cm long, basally enclosed by 3 to 4 tubular sheaths. *Leaf* erect, coriaceous, petiolate, blade basally conduplicate and cuneate, elliptic to ovate, obtuse, 10–16 × 1.8–2.3 cm, including the to *ca*. 5 cm long blackish-flushed petiole. *Inflorescence* erect, slender, single-flowered, with a to *ca*. 13 cm long peduncle; *peduncular bract* above the middle of the peduncle, tubular *ca*. 0.9 cm long; *floral bract* tubular, to *ca*. 1.3 cm long; *pedicel ca*. 2 cm long; *ovary* smooth, *ca*. 0.8 cm long, densely covered by blackish dots in the wild. *Flower* campanulate, attractive; *dorsal sepal* basally dark yellow, then rich magenta purple, and apically white with 3 greenish veins and tail, minutely and scatteredly pubescent externally, and richly covered internally above the middle by long purple-magenta hairs, concave, cuneate, angulate-obovate, connate with the lateral sepals for *ca*. 1.2 cm, then obtuse to acute with a slender, gently curved tail, *ca*. 5.5 × 1.5 cm, including the 3.5 cm long tail; *lateral sepals* similar in color and texture, connate for *ca*. 1.4 cm, angulate-ovate, acute with a slender, recurved apical tail, *ca*. 5.0 × 2.7 cm, including the *ca*. 3 cm long tail; *petals* white, shortly unguiculate, cartilaginous, oblong, truncate and obliquely bilobed apically, and with a large, incurved basal lobe, or tooth, continuing as a fleshy keel along the lower edge, diminishing towards the apex, *ca*. 6 × 2 mm; *lip* whitish with magenta flush and specks, and a brownish apex, hinged on the column foot, with a basal swelling, the hypochile cordate to truncate, ovate to pandurate, the epichile with down-folded edges, acute, dorsally shallowly canaliculate between swollen longitudinal ridges, *ca*. 5.0 × 2.7 mm; *column* white with brown-purple ventral stripes, semiterete, straight, *ca*. 4.5 mm long, with an equally long, curved foot; *anther cap* white, campanulate; *pollinia* not seen.

DISTRIBUTION: *Masdevallia karelii* is only reported from a limited area near Sandia, Puno, Peru, where it grows epiphytically on mossy trunks and branches, commonly near and sometimes on the ground among mossy debris, at 2600 – 2800 m.

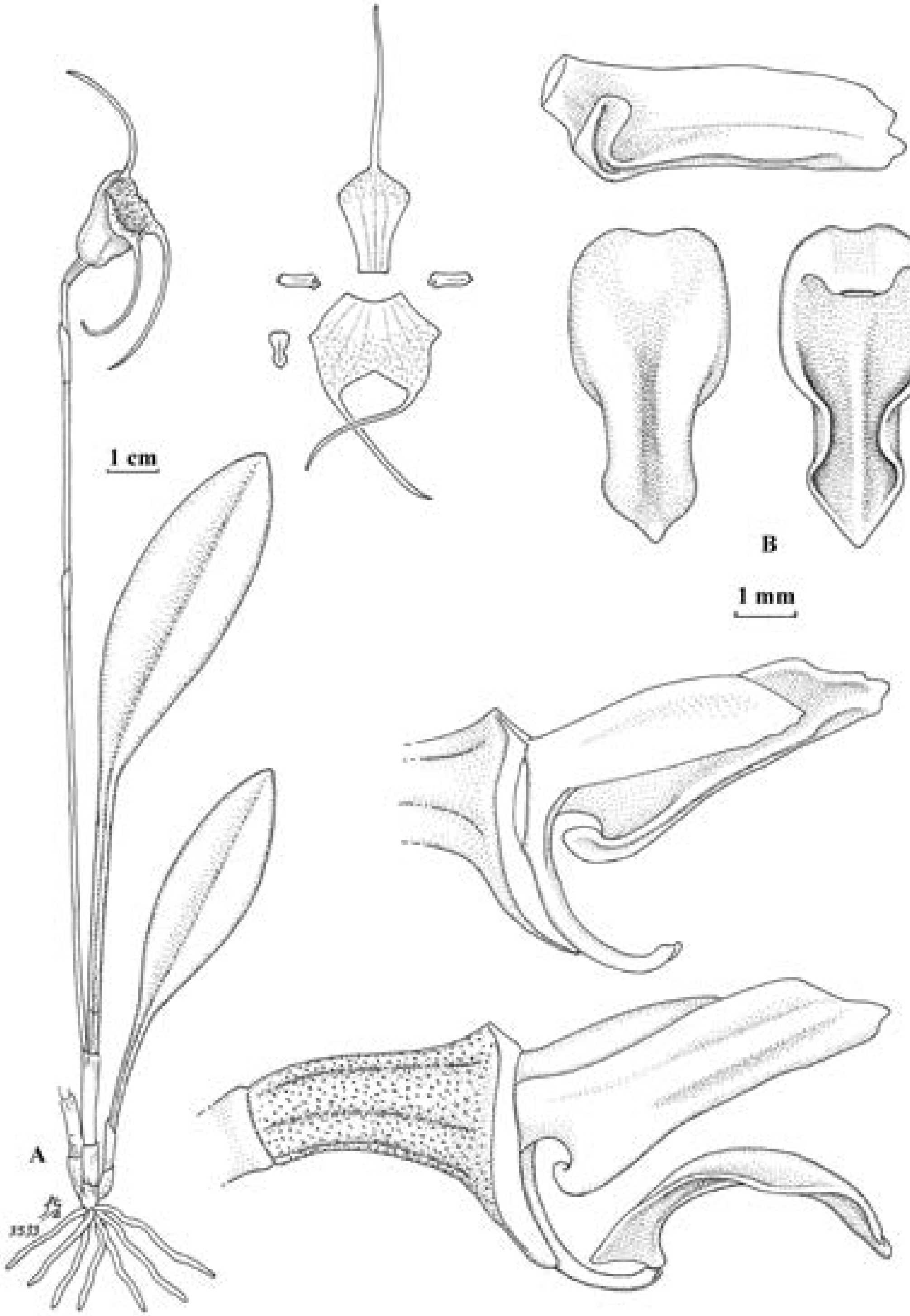


Figure 6. *Masdevallia karelii*. A — Plant habit with a dissected flower. B — Column, lip and petal views. Drawn from the holotype by Stig Dalström.

Figure 7. *Masdevallia karelii* in natural habitat (*S. Dalström 3533*). Photo by Karel Deburghgraeve.

Figure 8. *Masdevallia karelii* flower (*S. Dalström 3533*). Photo by Stig Dalström.

Eponymy: Named in honor of Karel Deburghgraeve who participated in the discovery of this colorful species.

Masdevallia rugosilabia Dalström & Ruíz-Pérez, *sp. nov.*

TYPE: Peru. Huancavelica, Salcabamba, Tayacaja, Huanca, alt. 2000 m, 8 June 2011, field-collected and flowered in cultivation by Perúflora 7 Dec. 2011, *S. Dalström 3491* (holotype, USM). Figs. 9, 10.

Diagnosis: *Masdevallia rugosilabia* is distinguished from all other species in the genus by the combination of a tall, slender, distantly successive- or bi-flowered, terete peduncle bearing carnose, nodding flowers with a concave and rugose epichile of the lip.

Epiphytic *herb*. *Plant* slender but tall for the genus, caespitose, root-thickness medium sized. *Ramicauls* erect 9.0–9.5 cm long, enclosed basally by 3 to 4 tubular sheaths. *Leaf* erect, coriaceous, slender, petiolate, the blade basally conduplicate and cuneate, ovate to elliptic, acute to obtuse, *ca*. 15.0 × 2.2 cm, including the 3.0 cm long petiole. *Inflorescence* dark purple, erect and slightly curved, successive flowered and producing (at least) 2 nodding flowers, rather thin, with a to *ca*. 16 cm long peduncle and a to *ca.* 4 cm long rachis; *peduncular bracts* 3, below the middle, *ca*. 5–10 mm long; *floral bracts* tubular, *ca.* 1.5 cm long; peduncle *ca*. 1.6 – 2.0 cm long; *ovary ca.* 0.4 cm long, weakly carinate. *Flower* nodding, campanulate; *dorsal sepal* dark brownish purple externally, dark yellowish brown covered by darker spots internally and with a dull, dark yellowish tail, slightly concave, glabrous externally and verrucose to rugose internally, connate with the lateral sepals for *ca*. 6–7 mm, oblong and weakly angulate-ovate, with a fleshy acuminate sepaline tail, *ca*. 20 × 4–5 mm, including the *ca*. 10 mm long tail; *lateral sepals* similar in color and texture, connate for *ca.* 10 mm, angulate-ovate, with a fleshy, slightly curved, short sepaline tail, *ca*. 15 × 10 mm, including the 5 mm long tail; *petals* white, thickly cartilaginous, truncate oblong, apically weakly constricted, then truncate and weakly trilobed, with a low, fleshy ridge emerging near the base and diminishing near the middle, and with an additional

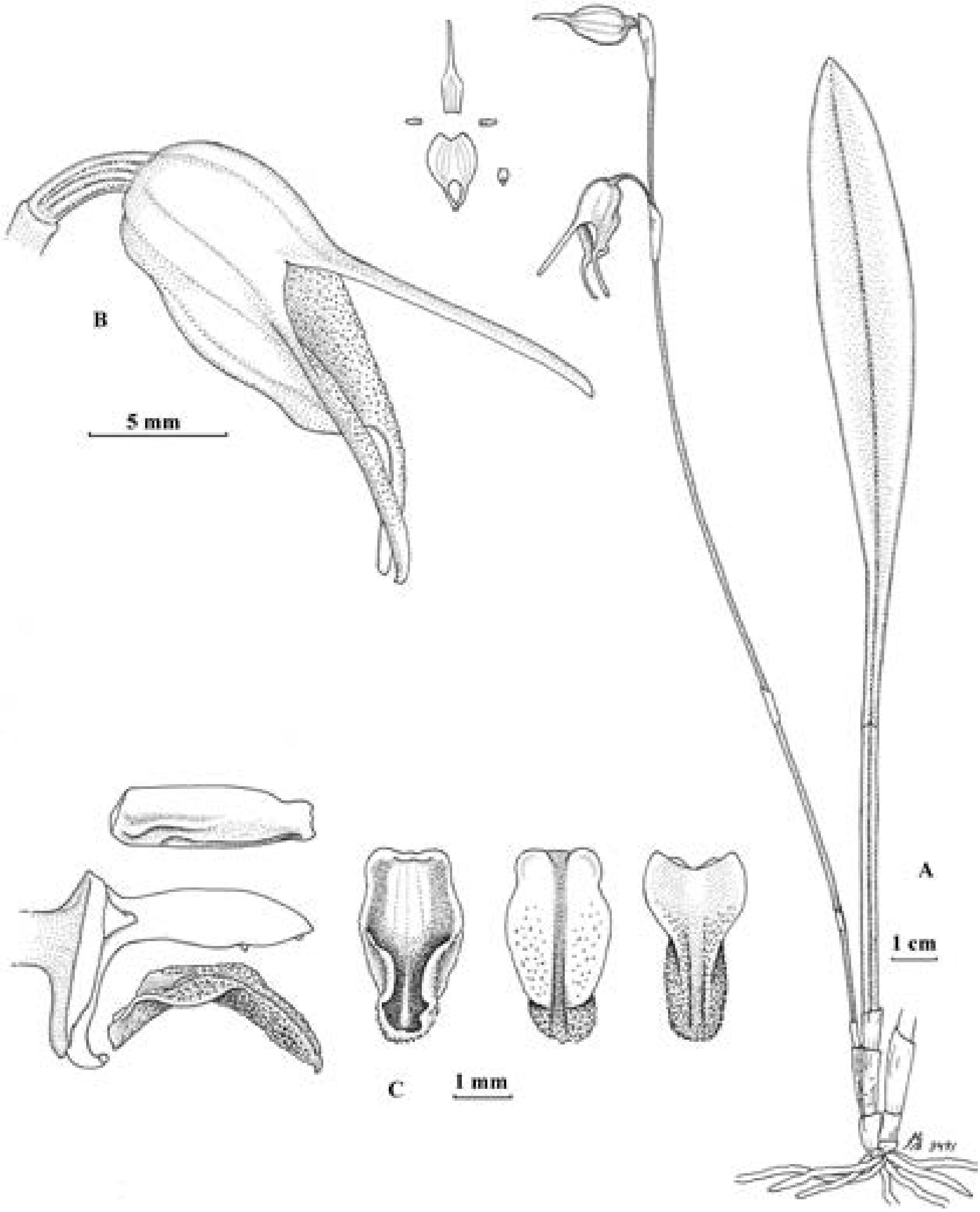


Figure 9. *Masdevallia rugosilabia*. A — Plant habit with a dissected flower. B — Column, lip and petal views. Drawn from the holotype by Stig Dalström.

Figure 10. *Masdevallia rugosilabia* flower (*S. Dalström 3491*). Photo by Stig Dalström.

fleshy ridge along the lower edge, emerging from near the middle up to the apex, *ca*. 3.5 × 1.2 mm; *lip* pale purple, hinged on the column foot, with a basal swelling, truncate to cordate, the hypochile flattened ovate and weakly rugose, the epichile down-folded and convex from above, rounded, rugose, dorsally canaliculate from near the base to the apex, *ca*. 3.5 × 2.0 mm; *column* white, semiterete straight, *ca*. 4 mm long, with an equally long, curved foot; *anther cap* white, campanulate; *pollinia* 2, flattened pyriform.

Distribution: Known only from the type locality in central Peru.

Etymology: The name refers to the rugose lip of the flower.

Acknowledgement. The authors thank the staff at the Instituto Recursos Naturales (INRENA), and Betty Millán at the Universidad de San Marcos, Museo de Historia Natural, Lima, for aiding in providing the necessary collecting permits. We also thank Wesley Higgins for commenting on the manuscript, Steve Beckendorf, Guido and Karel Deburghgraeve for stimulating company in the field, and Manolo Arias together with his staff and family in Lima for gracious logistic support.

Literature cited

Abele, C., B. Rudolph, J. Thiede & J. G. Rohwer. 2005. Phylogeny of the genus *Masdevallia* Ruíz & Pav., based on morphological an molecular data. Proceedings of the 18th World Orchid Conference, Dijon, France, 111-115.

Luer, C. A. 1986. Icones Pleurothallidinarum 2, Systematics of *Masdevallia* (Orchidaceae). Monographs in systematic botany from the Missouri Botanical Garden, vol. 16.

Luer, C. A. 2006. Icones Pleurothallidinarum 28, A reconsideration of *Masdevallia*, Systematics of *Specklinia* and vegetatively similar taxa (Orchidaceae). Monographs in systematic botany from the Missouri Botanical Garden, vol. 105.

Pridgeon, A. M. & M. W. Chase. 2001. A phylogenetic reclassification of Pleurothallidinae. Lindleyana 16(4): 235-271.

LANKESTERIANA 13(3): 259—282. 2014.

INVITED PAPER*

NEW SPECIES AND RECORDS OF ORCHIDACEAE FROM COSTA RICA. III

MELANIA FERNÁNDEZ[1,2,4], DIEGO BOGARÍN[1,2], ADAM P. KARREMANS[1,3] & DANIEL JIMÉNEZ[1]

[1]Jardín Botánico Lankester, Universidad de Costa Rica, P. O. Box 302-7050 Cartago, Costa Rica.
[2]Herbario UCH, Universidad Autónoma de Chiriquí, 0427, David, Chiriquí, Panama.
[3]Naturalis Biodiversity Center - NHN Universiteit Leiden, The Netherlands.
[4]Corresponding author: melania.fernandez@ucr.ac.cr

ABSTRACT. The establishment in Costa Rica of the great naturalist Charles H. Lankester in the 19th century brought a tremendous increase in the knowledge of Costa Rican Orchidaceae. His desire to leave the collections kept at his farm for a scientific and educational purpose was finally accomplished in 1973 with the foundation of Lankester Botanical Garden (JBL). Since then, JBL has followed Lankester's legacy with its consolidation as a leading center for the study of Neotropical orchids, resulting among others in more than 180 new Costa Rican species and records in the last 12 years. This manuscript includes the description of four new species and seven new records, as part of JBL's contribution to the completion of the Costa Rican orchid inventory.

KEY WORDS: *Epidendrum jorge-warneri*, *Platystele tica*, *Platystele catiensis, Platystele sylvestrei*, new species, new records, Orchidaceae, Costa Rica

Costa Rica has witnessed the emergence and consolidation of some of the finest botanists and naturalists of the Americas at the beginning of the last century. Names like Alberto Manuel Brenes, Charles H. Lankester, Henri Pittier,Adolphe Tonduz, Karl Wercklé, can be found among those who made significant contributions to the knowledge of Costa Rican flora. All but one of them shared a common scientific background. Charles H. Lankester (1879-1969) first arrived in Costa Rica at the end of the 19th Century, hired for three years by the Sarapiqui Estates Ltd. coffee company. Captivated by the natural richness of the country, he came back from England a few years later to build a life in Costa Rica His inclination and acute observation of natural creatures and phenomena in general, and of epiphytes in particular, soon brought the attention of some of the greatest orchidologists and botanists of the time: Dr. Oakes Ames (University of Harvard Herbarium), Paul C. Standley (Director of the United States National Museum) and Robert Allen Rolfe (curator of the orchid herbarium at the Royal Botanical Gardens, Kew), with whom he shared his many findings, product of his trips to botanically-rich areas in the region of the Cartago province. Lankester's tremendous passion for plants, great capacity to recognize details, and extraordinary horticultural skills made a significant contribution to the foundation of Costa Rican orchid studies. His last dream to preserve the botanical collections held in his farm and to make a contribution to conservation came true in 1973 with the foundation of the Lankester Botanical Garden.

This paper is the third part of a series aimed towards the completion of the Costa Rican Flora Orchidaceae. In the last few years knowledge on the Costa Rican orchid flora has grown substantially (Bogarín *et al.* 2008; Karremans *et al.* 2012). Bogarín (2011) reported 1519 species for the country, which meant up to 20 additions per year in the last decade. That trend was expected to be maintained by Karremans *et al.* (2012), but even though the country already hit the 1600 species mark (Karremans & Bogarín 2013), the novelties might increase rather than decrease in the

---

* This contribution was prepared as part of the special edition of LANKESTERIANA dedicated Lankester Botanical Garden´s 40th anniversary.

coming years. Here, we describe four new species and report the presence of six new records, illustrated with both photographs and detailed line drawings. Although *Sobralia bletiae* Rchb.f. was previously known to occur in Costa Rica, an illustration and photograph based on a Costa Rican specimen is also included.

1. ***Epidendrum jorge-warneri*** Karremans & Hágsater, *sp. nov*.

TYPE: Costa Rica. Puntarenas: Buenos Aires, Buenos Aires, Olán, cumbre del Cerro Tinuk, 9°17'29.1" N 83°10'11.2" W, 2417 m, bosque pluvial premontano, epífitas en bosque de páramo, 25 julio 2012, *A.P. Karremans 5545, D. Bogarín, D. Jiménez & V.H. Zúñiga* (holotype, CR!; isotype, JBL-Spirit!; figs. 1, 14A).

Epidendro anoglossoido Ames & C.Schweinf. *simile sed planta minore, caulis complanatis, folia breviore, floribus majoribus, sepalis et petalis longiores, labello lanceolato longiore differt.*

Epiphytic, sympodial, caespitose, erect *herb*, up to 20 cm tall. *Roots* from the base up to above half the length of the stems, fleshy, filiform. *Stem* 15-20 cm tall, branching conspicuously, cane-like, laterally flattened, erect. *Leaves* up to 5, distributed along the stem, mostly close to the apex as the basal ones fall off with time; leaf sheath tubular, rugose, 1.5 cm long; blades 2.8-3.6 × 0.8-1.3 cm, elliptic to narrowly-ovate, obtuse bilobed, articulate. *Spathaceous bracts* lacking. *Inflorescence* apical, mostly from lateral branches, distichous, flowering only once; peduncle up to 2 cm long; rachis curved, laterally flattened. *Floral bracts* equal to longer than the ovary, acute, flattened, 1 cm long. *Flowers* 2-4, simultaneous, resupinate, brownish-yellow; fragrance sweet during the day. *Ovary* 8.0-8.5 mm, laterally compressed, prominently inflated throughout. *Sepals* free, spreading, the dorsal prominently bent inwards, narrowly-ovate to elliptic, acute, 9-veined, margin entire; the *dorsal sepal* 15 × 3.5 mm; the *lateral sepals* 15 × 4.0-4.5 mm, oblique. *Petals* 13.0-13.5 × 1.5-2.0 mm, spreading, strongly bent backwards, ligulate to narrowly-elliptic, obtuse, 3-veined, margin entire. *Lip* 12.5 × 5.5-6.0 mm, united to the column, ovate-lanceolate, slightly 3-lobed, margin wavy, embracing the column, completely covering it; callus Y-shaped, prolonged into a central rib extending to the apex of the lip; lateral lobes hemi-rhomboid; mid-lobe triangular, acute, apiculate. *Column* 3.5 mm long, straight, with two apical somewhat rounded wings. *Clinandrium-hood* short. *Anther* narrowly ovate with a prominent central rib, 4-celled. *Pollinia* 4, obovoid, laterally compressed, caudicles granulose. *Rostellum* apical, slit. *Nectary* penetrating the ovary up to near the base. *Capsule* not seen. NOTE: Description based only on *Karremans 5545*.

DISTRIBUTION: known only from Costa Rica.

EPONYMY: The name honors Jorge Warner, current Director of the Lankester Botanical Garden of the University of Costa Rica. With more than a decade in his position he has been paramount in the development of the research center at the garden, and in the creation and execution of the research projects, which allows for this and most other findings.

HABITAT IN COSTA RICA: Known only from the plants found on the summit of Cerro Tinuk, Costa Rica. It grows epiphytically and lithophytically in a small area of isolated "paramo", at around 2400 m elevation.

PHENOLOGY: flowering recorded at least in July.

Epidendrum jorge-warneri belongs to the Ramosum Group which is characterized by the monopodial, branching stems, the spike-like, distichous inflorescence, and the single callus, and the Rugosum Subgroup which has a branching habit with few-flowered inflorescences from short, secondary stems, the leaf-sheaths rugose. The species can be recognized by the laterally compressed stems, the laterally compressed rachis and ovary, the 2-4, large, brownish-yellow flowers and the lip which embraces the column completely and the "Y" shapped callus of the lip.. *Epidendrum anoglossoides* Ames & C.Schweinf. is the most similar species, but it has much smaller, up to 9, greenish-yellow flowers, sepals and petals 7.5-9.5 mm long, lip 6 mm long, and callus of the lip tri-dentate.

2. ***Lepanthes ankistra*** Luer, Orquideología 16(3): 12. 1986.

TYPE: Panama. Prov. of Chiriquí: epiphytic in cloud forest on Cerro Colorado, alt. 1500 m, 15 February 1985, *C. Luer, J. Luer, R.L. Dressler & K. Dressler 10534* (holotype, MO).

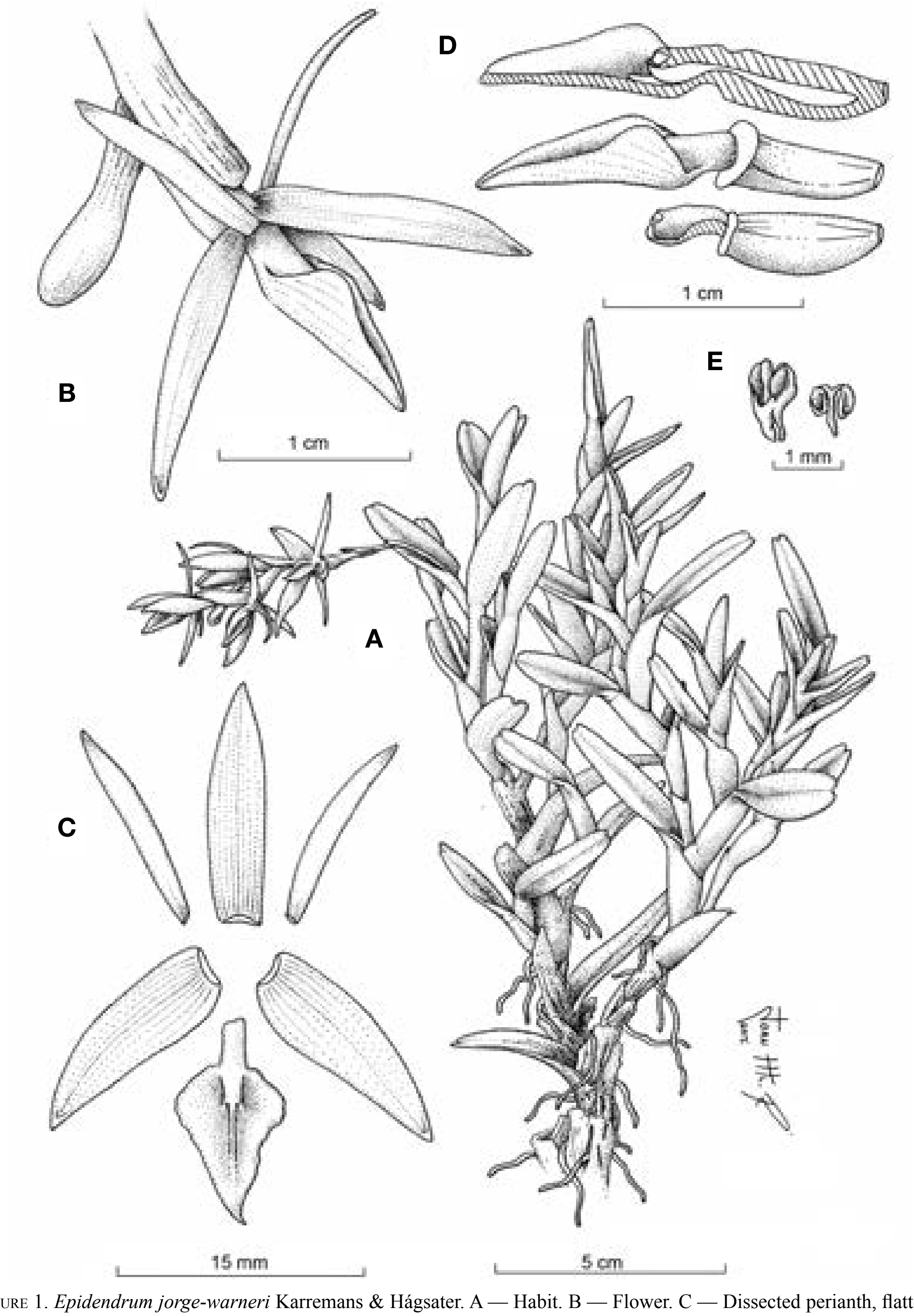


Figure 1. *Epidendrum jorge-warneri* Karremans & Hágsater. A — Habit. B — Flower. C — Dissected perianth, flattened. D — Column and lip, lateral view. E — Anther and pollinaria. Drawn by A.P. Karremans and J.M. Ramírez based on *A.P. Karremans 5545* (JBL-Spirit).

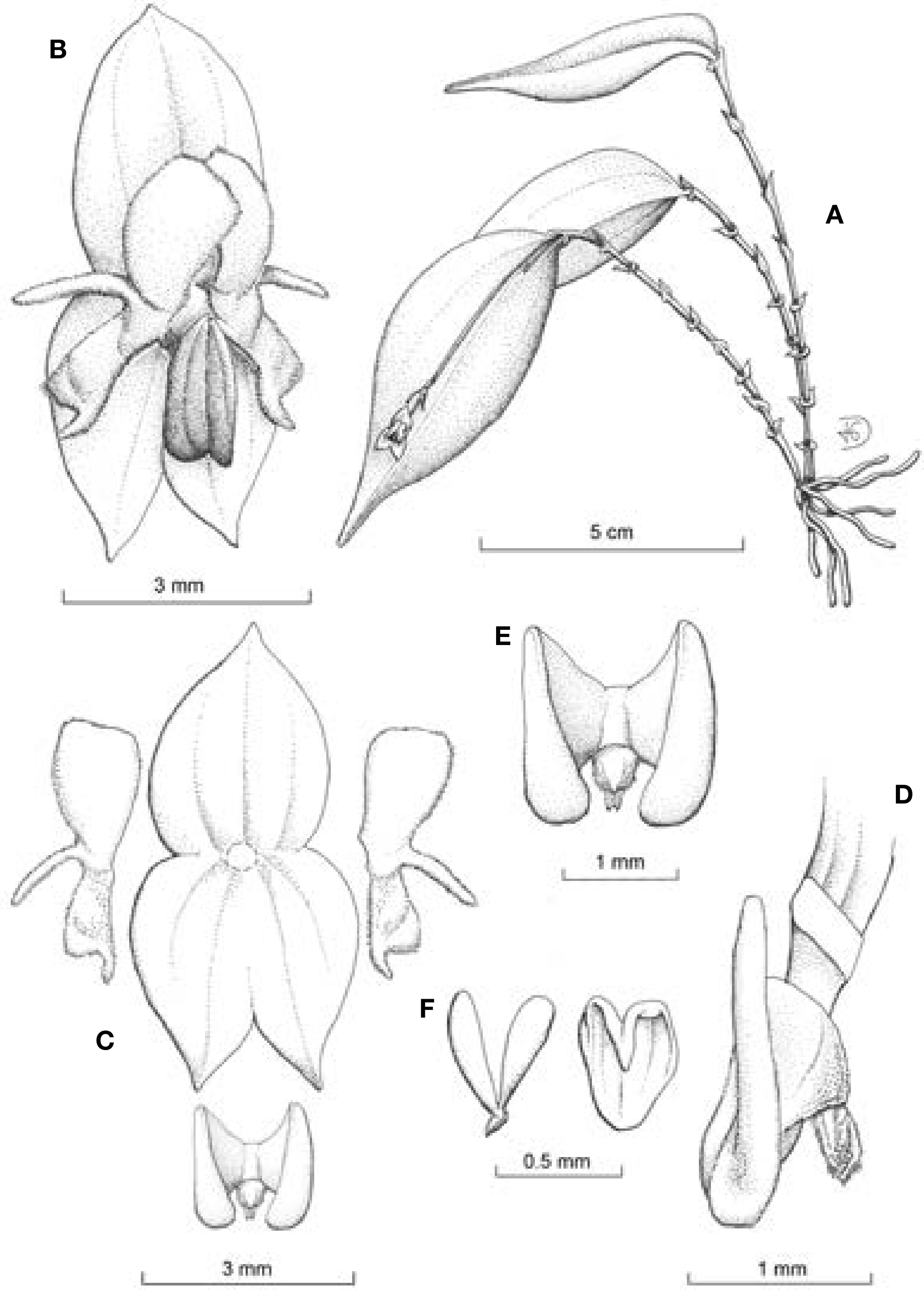


FIGURE 2. *Lepanthes ankistra* Luer & Dressler. A — Habit. B — Flower. C — Dissected perianth, flat. D — Column and lip, lateral view. E — Lip, spread. F — Pollinarium and anther cap. Drawing by D. Bogarín and D. Jiménez based on *D. Bogarín 9698*.

Distribution: endemic to the Cordillera de Talamanca in southern Costa Rica and western Panama.

Etymology: from the Greek *ankistra*, "fish-hooks" in allusion to the shape of the lower lobes of the petals.

Habitat in Costa Rica: epiphytic in premontane wet forest, on the Pacific watershed of the Cordillera de Talamanca from 1500 to 2147 m of elevation. Plants were found growing in primary oak forest.

Phenology: Plants were recorded in flower in June and July.

Costa Rican material studied: Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, Finca de la familia Sandí-Hartmann, camino hacia la fontera Costa Rica Panamá, 8°57'15.5" N 82°43'50.6" W, 2147 m, floreció en cultivo de Daniel Jiménez, 12 julio 2012, *D. Bogarín 9698* (JBL-Spirit!; figs. 2, 14b). COSTA RICA-PANAMÁ. Puntarenas-Bocas del Toro: Coto Brus-Valle del Risco, línea fronteriza sobre la divisoria de ıas ingresando por el camino de la Finca Sandí-Hartmann "El Capricho", 8°57'12.34"N 82°43'32.69"W, 2154 m, bosque pluvial montano bajo, 11 Diciembre 2013, *D.Bogarín 10741, A. Karremans, M. Fernández & L. Sandoval* (JBL-spirit!).

Among the Costa Rican *Lepanthes*, *L. ankistra* is recognized by the hanging, dark green-purple leaves with mucronate apices. The inflorescences lie upon the surface of the leaves, within the central groove. The flowers have pubescent petals with transverse setiform lobes at the base of the upper and lower lobes with sharply uncinate lower lobes. The lip lobes are hiding the column and the appendix is oblong, pubescent, scaphoid and conspicuous. This species is closely related to *L. brunnescens* Luer, an endemic to Cerro Jefe in central Panama, but the latter species lacks the uncinate lobes of the lower lobes of the petals. These *Lepanthes* species are unusual in Costa Rica. They are indeed closely allied to the South American *L. mucronata* Lindl., one of the most frequent species of the genus in the Andes (Luer 1996). Besides *L. mucronata*, there are at least 17 species from South America that may be related to *L. ankistra* and *L. brunnescens* (Luer 1996). The transverse setiform lobes at the base of the upper and lower lobes, the lip lobes united and hiding the column and the variously pubescent, scaphoid appendices may group all those species.

3. ***Lepanthes otopetala*** Luer, Lindleyana 6: 76. 1991.

TYPE: Panama. Chiriquí, collected by A. Maduro, without locality, flowered in cultivation by J & L Orchids, Easton, CT, May 1990, *C. Luer 14741* (holotype, MO).

Distribution: endemic to the Cordillera de Talamanca in southern Costa Rica and western Panama.

Etymology: from the Greek *otopetalon*, "an ear-like petal" in allusion to the ear-like upper lobes of the petals.

Habitat in Costa Rica: epiphytic in lower montane wet forest, on the Pacific watershed of the Cordillera de Talamanca at around 2400 m of elevation. Plants were found growing on primary oak forest.

Phenology: Plants were recorded in flower in April and May.

Costa Rican material studied: Puntarenas-Chiriquí: Coto Brus-Renacimiento, línea fronteriza hacia el Cerro Pando, después del mojón N.338, 8°55'11.22"N 82°43'18.18"W, 2446 m, bosque muy húmedo montano bajo, epífitas en bosque primario, 19 abril 2011, *D. Bogarín 8715, D. Jiménez & A.P. Karremans* (JBL-Spirit!; figs. 3, 14c).

This species shares features with the members of the *Lepanthes disticha* Garay & R.E. Schult. complex such as the erect plants, blackish amplectent lepanthiform bracts, the convex, elliptic leaves and inflorescences developed beneath the leaf. However, the matt dark purple leaves, the whitish flowers, denticulate sepals, ciliate lip blades and the conspicuous ear-like upper lobe of the petals, which is longer and wider than the lower lobe easily distinguish this species (Luer 1991). The voucher cited here was collected along the border of Costa Rica and Panama.

4. ***Lepanthes truncata*** Luer & Dressler, Orquideología 16(3): 9. 1986.

TYPE: Panama. Prov. of Bocas del Toro: epiphytic in wet forest between Fortuna and Chiriquí Grande,

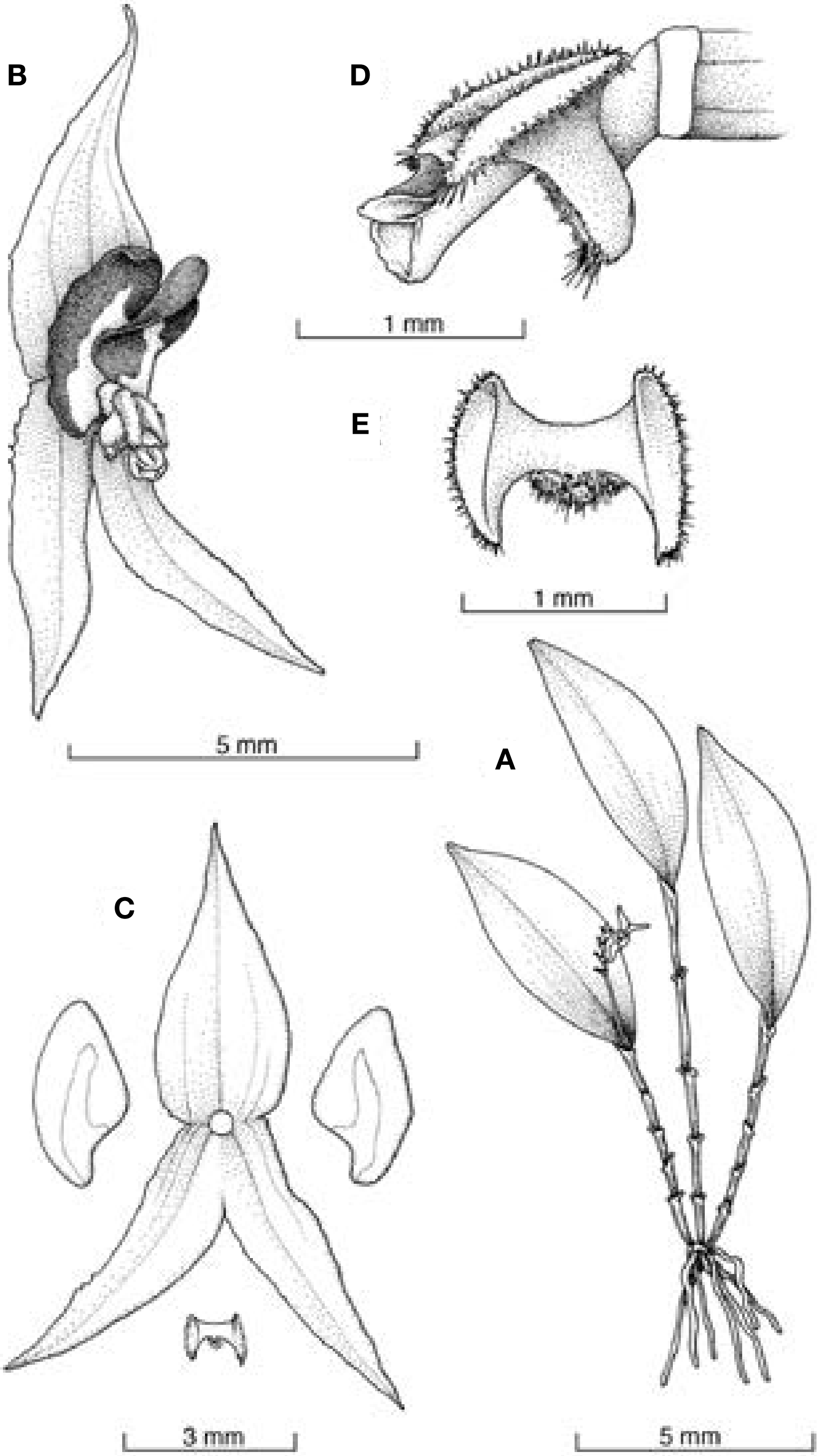


FIGURE 3. *Lepanthes otopetala* Luer. A — Habit. B — Flower. C — Dissected perianth, flat. D — Column and lip, lateral view. E — Lip, spread. Drawing by D. Bogarín and D. Solano based on *D. Bogarín 8715*.

alt. 350 m, 17 February 1985, *C. Luer, J. Luer, R.L. Dressler & K. Dressler 10618* (holotype, MO).

DISTRIBUTION: endemic to the Caribbean lowlands of Costa Rica and Panama.

ETYMOLOGY: from the Latin *truncatus*, "truncate" in allusion to the truncate apex of the upper lobes of the petals.

HABITAT IN COSTA RICA: epiphytic in premontane rain forest, on the Caribbean watershed of the Cordillera de Talamanca below 400 m of elevation.

PHENOLOGY: Plants were recorded in flower from May to October.

COSTA RICAN MATERIAL STUDIED: Cartago-Limón: Turrialba y Siquirres, Pacuarito-Tayutic, Parque Nacional Barbilla, sendero hacia el Río Dantas (Venado), 9°58'27.35"N 83°27'00.33"W, 382 m, bosque pluvial premontano, epífitas en bosque primario y secundario, 25 mayo 2012, *D. Bogarín 9652, A.P. Karremans & J. Sharma* (JBL-Spirit!; figs. 4, 14D–E).

This species is recognized by the pendent plants with satiny leaves, the inflorescence is developed above the leaf, the flowers have entire, yellowish sepals and petals and the lip is reddish-pink with the blades separated, not hiding the column, and the appendix is minute, pubescent. As noted by Luer & Dressler (1986), the most distinctive character of *L. truncata* is the broadly truncate apex of the upper lobe of the petals.

5. ***Platystele catiensis*** Karremans & Bogarín, *sp. nov.*

TYPE: Cartago: Turrialba, Turrialba, Campus del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), orillas del Río Reventazón, 9°53'38"N 83°38'55.5"W, 639 m, bosque muy húmedo premontano, epífitas bosque secundario detrás del edificio principal, 24 Mayo 2012, *A. P. Karremans 5442, D. Bogarín & J. Sharma* (holotype, JBL-Spirit!; isotype, JBL-Spirit!; figs. 5, 14F).

Species haec P. oxyglossa (Schltr.) Garay similis, sed floribus minoribus, petalis et labello quam sepalis aequilonguis, minutissime glandulosis, acutis, labello ovato-elliptico glanduloso differt.

Plant minuscule, epiphytic, caespitose, erect, up to 2.0 cm tall, including the inflorescence. *Roots* basal, flexuous, filiform. *Ramicauls* erect, slender, 1-2 mm long, enclosed by tubular, imbricating, slightly compressed, membranous sheaths, becoming brownish and papery with age. *Leaf* elliptic, erect, conduplicate, subacute, emarginate, abaxially keeled and terminating in a short apiculus, 5-8 × 2-3 mm, narrowed at the base into a conduplicate petiole. *Inflorescence* racemose, distichous, successively flowered, with one flower open at a time, up to 1.2-1.3 cm long, peduncle to 6-8 mm long, pedicels 1.0-2.0 mm long. *Floral bracts* acute, conduplicate, to 0.5 mm long. *Ovary* terete, smooth, to 0.4 mm long. *Flowers* sepals and petals transparent yellowish-green, lip and column reddish-orange, about 4.5 mm in diameter. *Dorsal sepal* narrowly lanceolate-elliptic, spreading widely, acute to shortly acuminate, marginally glandulose, 2.2-2.3 × 0.7 mm. *Lateral sepals* subequal to the dorsal sepal, lanceolate-elliptic, spreading widely, acute to shortly acuminate, marginally glandulose, 2.0-2.1 × 1.0 mm. *Petals* spreading widely, narrowly elliptic-lanceolate, acute to shortly acuminate, margins glandulose, 1-veined, 2.1 × 0.4 mm. *Lip* ovate-elliptic, shortly acuminate, glandular-hirsute, especially at the apex, with a small glenion at the base, 1.5 mm x 0.7 mm. *Column* short, sub-cylindrical, 0.4 mm long. *Anther* apical, *stigma* subapical, transversely bilobed at each side of the anther. *Pollinia* 2, ovoid. NOTE: Description based on *Karremans 30, 5442, 5443* and *Bogarín 9661*.

PARATYPES: Costa Rica. Cartago: Turrialba, Turrialba, CATIE, río Reventazón, tramo Bajo del Chino–Espaveles. 9°53'44" N 83°39'27" W, 600 m, 30 de enero del 2004, *A.P. Karremans 30 & J. Velásquez* (JBL-Spirit!). Turrialba, Turrialba, Campus del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), orillas del Río Reventazón, 9°53'38"N 83°38'55.5"W, 639 m, bosque muy húmedo premontano, epífitas bosque secundario detrás del edificio principal, 24 mayo 2012, *A. P. Karremans 5443, D. Bogarín & J. Sharma* (JBL-Spirit!). Cartago-Limón: Turrialba y Siquirres, Pacuarito-Tayutic, Parque Nacional Barbilla, sendero hacia el Río Dantas (Venado), 9°58'27.35"N 83°27'00.33"W, 382 m, bosque pluvial premontano, epífitas en bosque primario y secundario, *D. Bogarín 9661, A.P. Karremans & J. Sharma*, 25 Mayo 2012

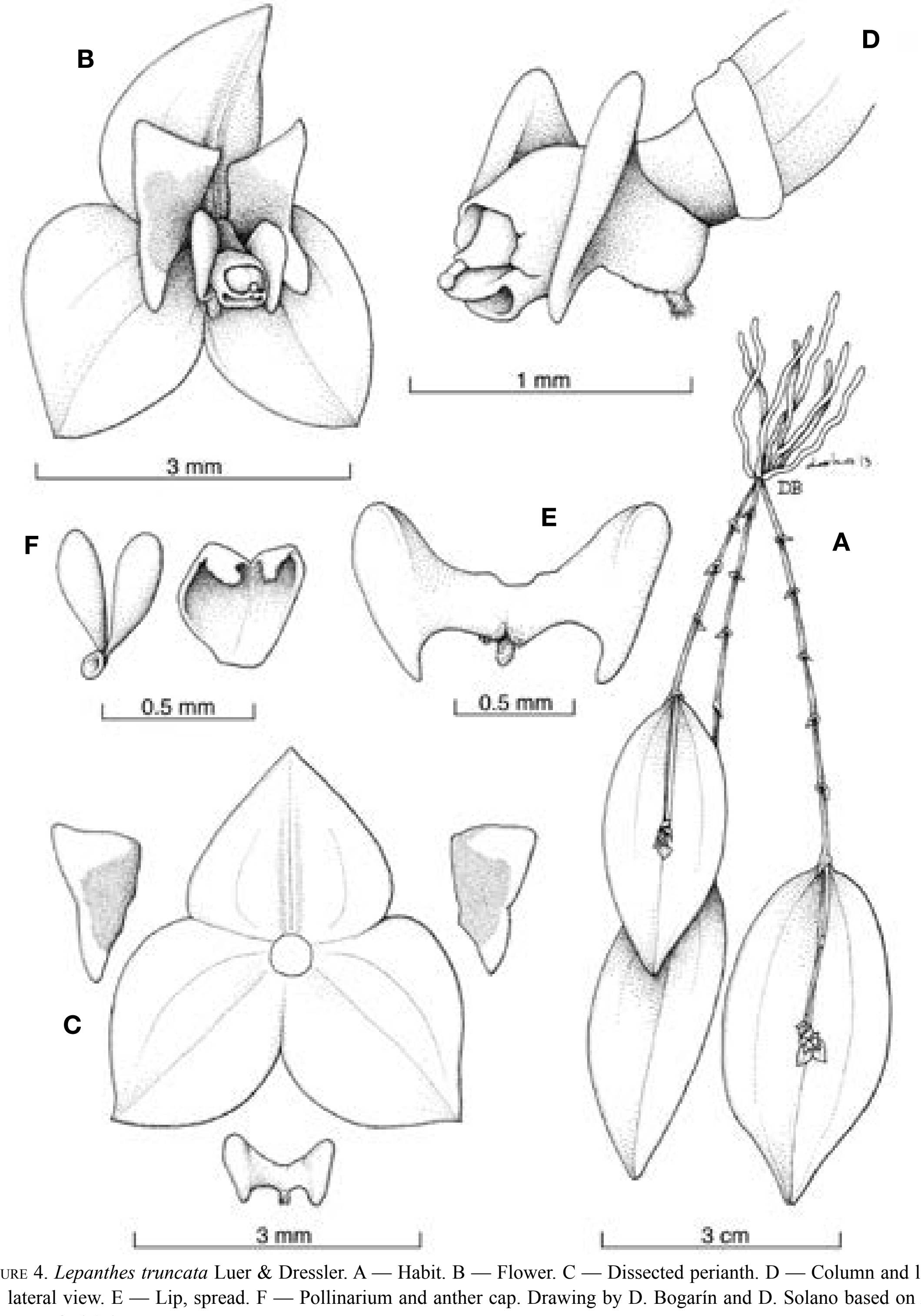


FIGURE 4. *Lepanthes truncata* Luer & Dressler. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip, spread. F — Pollinarium and anther cap. Drawing by D. Bogarín and D. Solano based on *D. Bogarín 9652*.

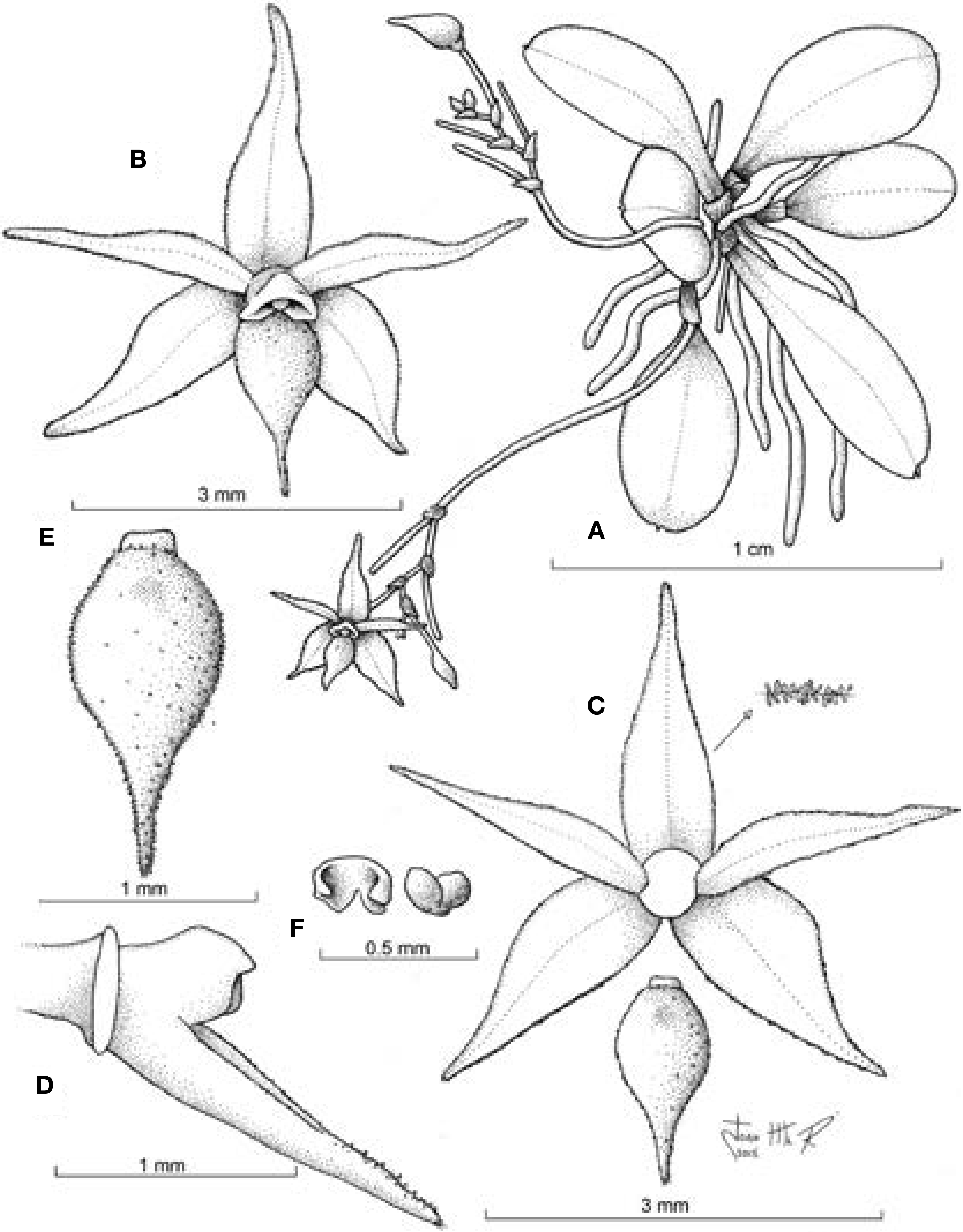


FIGURE 5. *Platystele catiensis* Karremans & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip, spread. F — Pollinarium and anther cap. G — Sepal margin. Drawing by D. Bogarín and J.M. Ramírez based on *A.P. Karremans 5442* (JBL-Spirit).

(JBL-Spirit!). Heredia: Sarapiquí, Puerto Viejo, Finca La Selva, 3 km SE of Puerto Viejo de Sarapiquí, 50-150 m, 22 Nov. 1979, *C. Todzia 1035* (CR!). Sarapiquí, Puerto Viejo, Estación Biológica La Selva, OTS field station near junction of Puerto Viejo and Sarapiquí rivers. Elevation 40-100 m. Camino Circular Lejano (CCL) 950. 11 Mar. 1991, *K. Richardson* (CR!). Sarapiquí, Puerto Viejo, Estación Biológica La Selva, at the confluence of Río Sarapiquí and Río Puerto Viejo, Atlantic slope. 10°26'00"N 84°01'00"W, 50-100 m, growing on twigs near major treefall along Camino Circular Lejano, 12 Oct. 1990, *M. Grayum 9994* (INB!). Limón: shores of Caño Perreira; periodically inundated swamp forest, Priora dominant. 20 Mar. 1897, *W.D. Stevens, G. Herrera & O.M. Montiel 25151* (INB!; MO).

Other Records: Costa Rica. Heredia: Sarapiquí, Puerto Viejo, Estación Biológica La Selva, *O. Vargas 2148* (Digital Photograph!).

Distribution: known only from Costa Rica.

Etymology: the name honors the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), where this species was first observed by the authors. CATIE is, like Lankester Botanical Garden, celebrating its 40th Anniversary in 2013.

Habitat in Costa Rica: epiphytic in primary and and mature secondary humid premontane forest, at around 300-650 m elevation. It is known from the Caribbean lowlands, especially the Sarapiquí, Siquirres and Turrialba areas. The species grows on the protected dense mature vegetation right behind the main building of CATIE, where it is found on small branches that fall from the large trees in the "Espaveles" path, which descends to the Turrialba-Reventazón river. Likewise on the path that descends to Dantas river in the Barbilla National Park.

Phenology: flowering recorded from January to October, however it is likely it flowers all year round.

Platystele catiensis has been confused in Costa Rica with the apparently widely distributed and variable *P. oxyglossa*. The latter is also found in the country (Luer 1990), but *P. catiensis* is typically found growing below elevations of 650 m in the Caribbean lowlands (vs. growing at an elevation of 1000-2500 m in the Central and Talamanca Cordillera), it has a much smaller plant that grows up to 2 cm including the inflorescence (vs. 6 cm tall), a denser and shorter inflorescence which is up to 1.3 cm long (vs. a stingy inflorescence up to 5 cm long), with 1.0-2.0 mm long pedicels (pedicels 2.5-7.0 mm long), with less than 5 mm between each one (distance between pedicels 2.0-5.0 mm long), and smaller flowers with sepals and petals up to 2.3 mm long (vs. up to 3.5 mm long), and the lip up to about 1.5 mm long (vs. 2.5 mm long). From the Guatemalan type material of *P. oxyglossa*, *P. catiensis* can be distinguished by the shorter (2.2-2.3 mm), shortly acuminate and marginally glandular sepals (vs. sepals 2.5 mm, long acuminate, glabrous), the petals and lip are longer, subequal to the sepals, the petal margin is glandular, while the lip is elliptic, and completely glandular-hirsute, especially near the apex (vs. sepals and lip 1.5 mm, much shorter than the sepals, and are glabrous, the lip is ovate-lanceolate). It might well turn out that none of the Costa Rican material can be referred to *P. oxyglossa*. In that case the larger species found in the Central Cordillera should be referred to as *Platystele schulzeana* (Schltr.) Garay, described from La Carpintera. For the time being we only segregate the easily distinguished and morphologically constant *P. catiensis*, and point out that the name *P. oxyglossa* has been applied to two different species in Costa Rica. A few Brazilian species have been placed under synonymy of *P. oxyglossa*, but from what we have seen they are most likely not the same species, and certainly are not the same as those found in Costa Rica. The recently described *Platystele paraensis* Campacci & da Silva has the typical general flower morphology of the *P. oxyglossa* complex, and is as tiny as *P. catiensis*. It can be distinguished by the single flowered inflorescence, the sepals that are long caudate, that have an orange mid-vein and are much longer than the lip, which is apically yellow-orange. Flower morphology and size is similar to *Platystele psix* Luer & Hirtz, however the Ecuadorian species has cellular-pubescent sepals and petals. Another similar species occurs in Panama and Ecuador, *Platystele taylorii* Luer can be however recognized by the lip that is long acuminate and exceeds the glabrous sepals.

6. *Platystele sylvestrei* Karremans & Bogarín, *sp. nov.*

TYPE: Costa Rica. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, camino entre el portón del Mirador hacia el Río Humo, Proyecto

Hidroeléctrico Tapantí, 9°41'32.9"N 83°47'03.2" W, 1650 m, bosque pluvial premontano "*supra arbores et ad truncos prostratos vetustos ad sylvarum versuras ad viam flumen Humo in Tapanti*", 18 Noviembre 2010, *D. Bogarín 8240, R. Gómez, A.P. Karremans, B. Klein, G. Meza & F. Pupulin* (holotype, JBL-Spirit!; fig. 6, 7).

Species haec P. oxyglossa (Schltr.) Garay similis, sed planta majore, floribus autogamus albus, sepalis petalisque angustissimis, labello angusto-ovato lanceolato differt.

Plant medium for the genus, epiphytic, caespitose, erect, up to 12-13 cm tall, including the inflorescence. *Roots* basal, flexuous, filiform. *Ramicauls* erect, slender, 5-8 mm long, enclosed by tubular, imbricating, slightly compressed, membranous sheaths, becoming brownish and papery with age. *Leaf* narrowly obovate-elliptic, erect, conduplicate, obtuse, emarginate, 20-35 × 5-7 mm, narrowed at the base into a conduplicate petiole. *Inflorescence* racemose, distichous, successively flowered, with one flower mature (not necessarily open) at a time, up to 12 cm long, peduncle to 7 cm long, pedicels 1.0-1.5 cm long. *Floral bracts* acute, conduplicate, to 1 mm long. *Ovary* terete to suborbicular, smooth, to 2 mm long (fertilized). *Flowers* cleistogamous or autogamous (at least in the material at hand), sepals and petals transparent whitish, with a violet blotch on the base of the lip and violet markings on the column, about 4 mm in diameter. *Dorsal sepal* narrowly ovate, spreading widely, acute, glabrous, 2.3-2.4 × 0.5 mm. *Lateral sepals* subequal to the dorsal sepal, narrowly ovate, spreading widely, acute, glabrous, 2.3 × 0.6-0.7 mm. *Petals* spreading widely, linear to narrowly lanceolate, acute, margin somewhat irregular, 1-veined, 2.0 × 0.2-0.3 mm. *Lip* very narrowly ovate-lanceolate, shortly acuminate, glabrous, without an evident glenion at the base, 1.6-1.7 × 0.5 mm. *Column* short, thick due to autogamy, sub-cylindrical, 0.5 mm long. *Anther* not noted, *stigma* deformed, apical. *Pollinia* not observed. Note: Description based only on *Bogarín 8240*.

Paratypes: Costa Rica. Alajuela: San Ramón, Piedades, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'51.9"N 84°35'36.5"W, 1410 m, Caribbean watershed of the Continental Divide, premontane cloud forest, 24 March 2005, *F. Pupulin 5595, E. Salas-Pupulin, D. Bogarín & A.C. Rodríguez* (JBL-Spirit!). Puntarenas: Reserva Biológica Monteverde, Ojo de Agua, Finca de Leonel Hernández. Bosque pantanoso semiachaparrado. Lado Pacífico de la reserva. 10°15'N 84°46'W, 1600 m. 14 nov. 1987. *W. Haber & E. Bello 7808* (INB!; Illustration-INB!). Puntarenas: Puntarenas. Monteverde Cloud Forest Reserve. Pacific slope and continental divide, road to divide, swamp along Sendero Pantanoso and Sendero Chomogo. 10°18'N 84°47'W, 1550-1600 m. Epiphyte. 14 Mar. 1990. *W. Haber & W. Zuchowski 9798* (INB!). Costa Rica - Panama: Puntarenas-Bocas del Toro: Coto Brus-Valle del Risco, línea fronteriza sobre la divisoria de aguas ingresando por el camino de la Finca Sandí-Hartmann "El Capricho", 8°57'12.34"N 82°43'32.69"W, 2154 m, bosque pluvial montano bajo, 11 diciembre 2013, *A.P. Karremans 6130, D. Bogarín, M. Fernández & L. Sandoval* (JBL-Spirit!; fig. 7A). Same locality and date, *D. Bogarín 10744, A.P. Karremans, M. Fernández & L. Sandoval* (JBL-Spirit!; fig. 7B).

Distribution: known only from Costa Rica and Panama.

Etymology: El Silvestre (the uncultivated) was the name of Charles H. Lankester's farm before becoming Lankester Botanical Garden in the hands of the University of Costa Rica. This species honors the garden's 40th anniversary.

Habitat in Costa Rica: epiphytic in mature humid premontane forest, between 1410 and 1650 m elevation. It is known from a few but distant localities, Tapantí National Park in Cartago, close to San Ramón in Alajuela, the Monteverde area in Puntarenas, and on both sides of the continental divide close to the Costa Rica - Panama border.

Phenology: flowering recorded at least in March and November and December, considering the successiveness of the inflorescence it is likely found flowering-fruiting all year round.

Platystele sylvestrei probably belongs to the *P. oxyglossa* species complex, however, it has a relatively large habit, reaching above 10 cm when including the inflorescence. The species can be easily recognized by

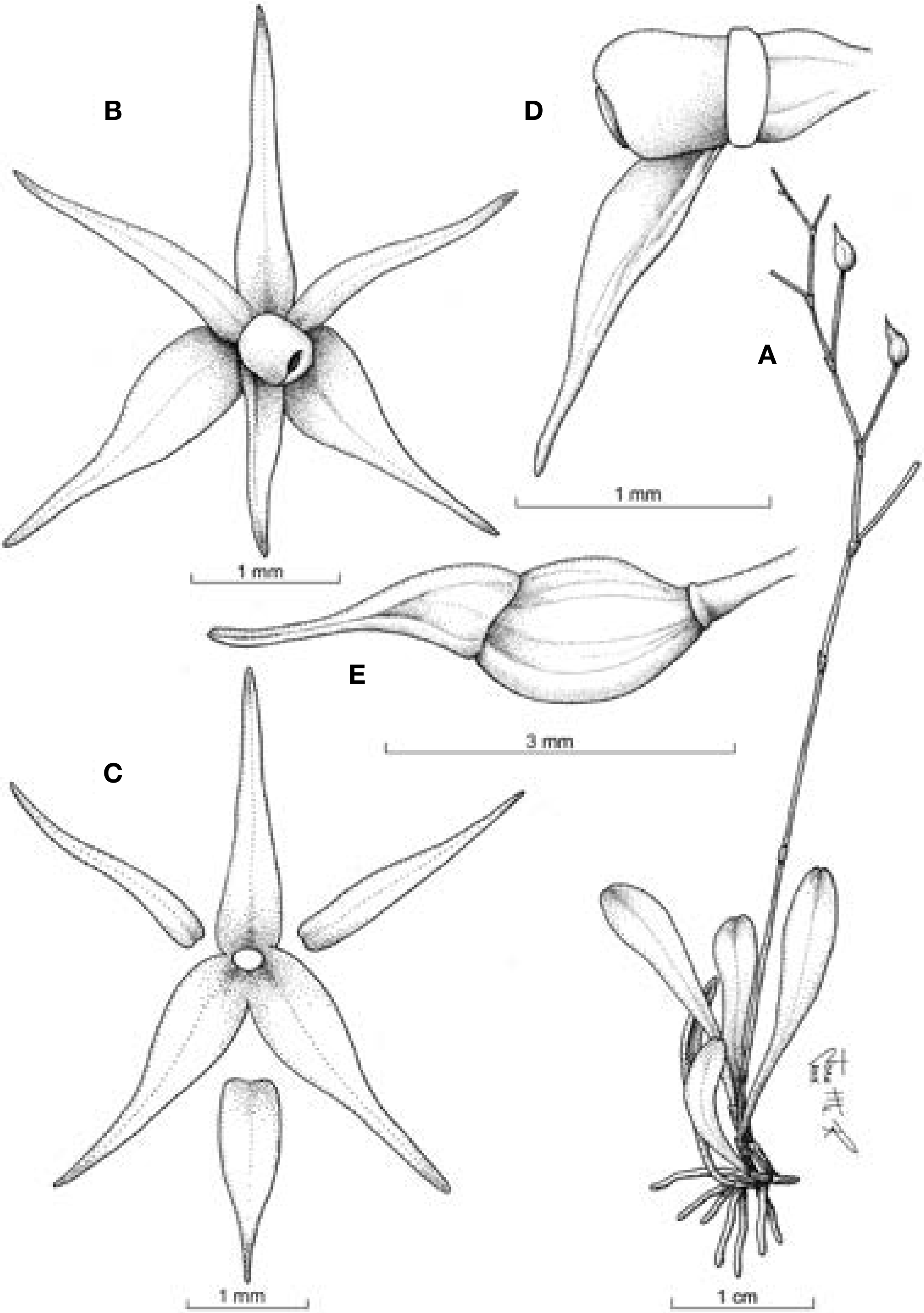


FIGURE 6. *Platystele sylvestrei* Karremans & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Fruit with persistent perianth, lateral view. Drawing by D. Bogarín and J.M. Ramírez from *D. Bogarín 8240* (JBL-Spirit).

Figure 7. *Platystele sylvestrei* Karremans & Bogarín. A — A rare case of a fully opening flower, already pollinated (*Karremans 6130*) . B — Plant habit showing the long lax inflorescences with the characteristic fruiting (*Bogarín 10744*). Photographs by A.P. Karremans (A) and D. Bogarín (B).

the lax inflorescence, the long pedicels, the whitish-transparent, autogamous/cleistogamous flowers and the narrow, glabrous flower segments, with a narrowly ovate-lanceolate lip.

7. ***Platystele tica*** Karremans & Bogarín, *sp. nov*.

TYPE: Costa Rica. Puntarenas: Buenos Aires, Volcán, 09°13'N, 83°26'W, *ca.* 450 m, bosque muy húmedo premontano transición a basal en bosque secundario muy alterado a orillas de un riachuelo, 17 de abril 2012, *A.P. Karremans 5315, J. Cambronero* & *J. Geml* (holotype, JBL-Spirit!; isotype, JBL-Spirit!; figs. 8, 9, 14G–H).

Species haec P. oxyglossa (Schltr.) Garay similis, sed planta minutissima, floribus minutissimis flavis, sepalis petalisque acutis latiores, labello ovato acuto differt.

Plant minuscule, epiphytic, caespitose, erect, up to 2.0 cm tall, including the inflorescence. *Roots* basal, flexuous, filiform. *Ramicauls* erect, slender, 1-2 mm long, enclosed by 2-3 tubular, imbricating, slightly compressed, membranous sheaths, becoming brownish and papery with age. *Leaf* elliptic, erect, fleshy, coriaceous, conduplicate, subacute, emarginate, abaxially keeled and terminating in a short apiculus, 5-7 × 1.5-2.5 mm, narrowed at the base into a conduplicate petiole. *Inflorescence* racemose, distichous, successively flowered, with one flower open at a time, up to 1.5 cm long, peduncle to 1.2 cm long, pedicels 1.5-2.0 mm long. *Floral bracts* acute, conduplicate, to 0.5-0.8 mm long. *Ovary* terete, smooth, to 0.3 mm long. *Flowers* monochrome yellow, about 1.8 mm in diameter. *Dorsal sepal* narrowly ovate-elliptic, spreading widely, acute, glabrous, 0.9 × 0.5 mm. *Lateral sepals* subequal to the dorsal sepal, broadly elliptic, spreading widely, acute, glabrous, 0.9 × 0.7 mm. *Petals* spreading widely, narrowly elliptic-lanceolate, acute, margins irregular, 1-veined, 0.9 × 0.3 mm. *Lip* ovate, shortly acuminate, glandular, especially at the apex, margin irregular, with a small glenion at the base, 0.8-0.9 × 0.4-0.5 mm. *Column* short, sub-cylindrical, 0.3-0.4 mm long. *Anther* apical, *stigma* subapical, transversely bilobed at each

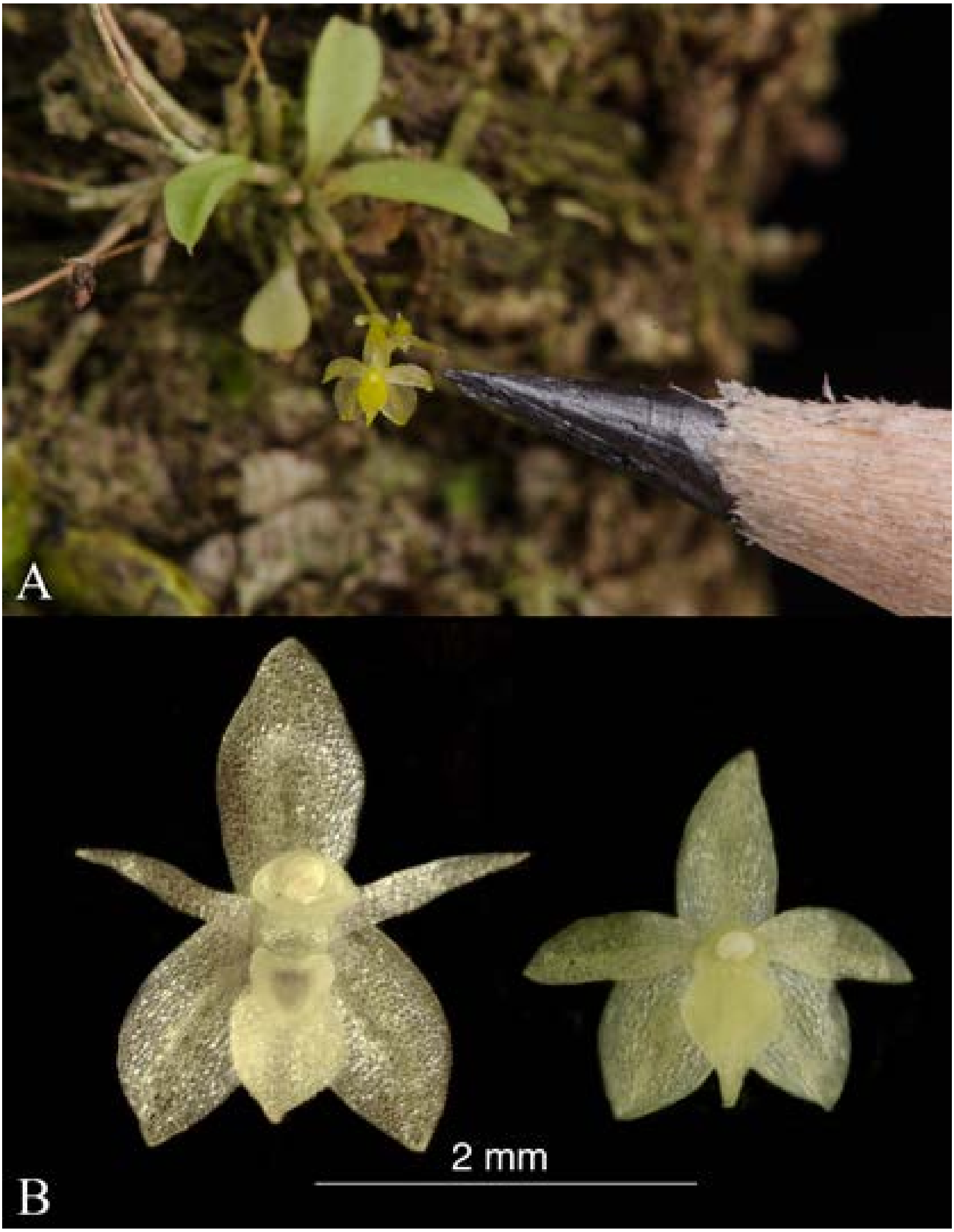


FIGURE 8. Size comparison of *Platystele tica* Karremans & Bogarín: A — The specimen that served as type material, *in situ*, compared with a pencil. B — On the left *Platystele microtatantha* (Schltr.) Garay (*Bogarín 10241*), on the right *Platystele tica* (*Karremans 5929A*). Photographs by A.P. Karremans.

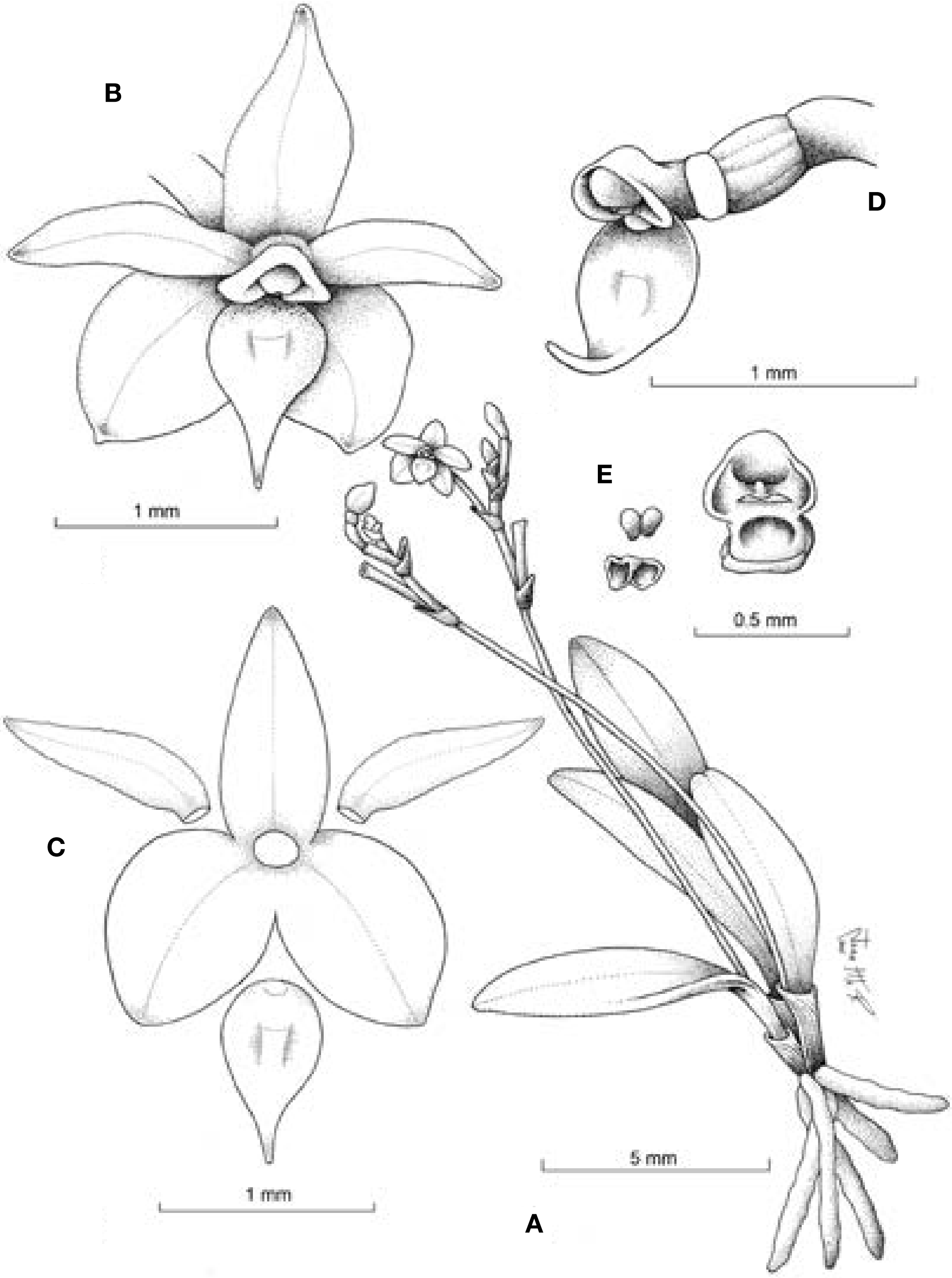


FIGURE 9. *Platystele tica* Karremans & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, front view. F —Pollinarium and anther cap. G — Sepal margin. Drawing by D. Bogarín and J.M. Ramírez based on *A.P. Karremans 5315* (JBL-Spirit).

side of the anther. *Pollinia* 2, ovoid. Note: Description based on *Karremans 5315*, *5829A* and *Pupulin 2928*.

Paratypes: Costa Rica. Puntarenas: Buenos Aires, Volcán, Cacao, orillas del Río Cacao en bosque secundario bajo el puente de la Carretera Interamericana, 9°13'10.441"N 83°28'19.002"W, 449 m, bosque muy húmedo premontano transición a basal, 20 marzo 2013, *A.P. Karremans 5829A*, *D. Bogarín, J. Cambronero & F. Pupulin* (JBL-Spirit!; figures 8 & 9). San José: Pérez Zeledón, El Brujo, road to El Llano, along the boarder of río División, 320 m, 9°25'40"N 83°54'58"W, epiphytic on tall trees along the river shore, 21 Jan. 2001, *F. Pupulin 2928, D. Castelfranco & L. Elizondo* (JBL-Spirit!).

Other records: Costa Rica. San José: Tarrazú. No protegida. Cuenca del Naranjo y Paquita. Valle del General, Longo May. Río Sonador, 1400-1800 m, 9°36'30"N 84°06'00"W, epífita, 16 may 2006, *J. F. Morales 13937* (INB!; INB-Spirit). Geographical distribution, plant habit and size, and flower coloration suggests that this specimen is *P. tica*, however, the flowers on the dried specimen are too damaged to tell with certainty and we were not able to locate the spirit specimen.

A text and its accompanying photographs by Pontus Aratoun featuring a *Platystele* species from Mecana beach, Choco, Colombia (available through http://miniorchids.wordpress.com), possibly represents the same species.

Distribution: known only from Costa Rica. It may also be present southwards into Colombia.

Eponymy: the name honors Costa Rica, country where this minuscule species was found, and the people of which are known as *tico* and *tica*. The nickname *tico* or *tica* comes from the Costa Rican linguistic custom of using it as a diminutive suffix, alluding thus as well to the small size of this *Platystele*.

Habitat: epiphytic in secondary forest in premontane wet forest, between about 300 and 450 m (1400-1800 m?) elevation. It is known only from the Costa Rican south-Pacific, in the Valle de El General area.

Phenology: flowering recorded at least from April to June, however considering the slowly successive inflorescences, each is likely to flower continuously for months at a time.

Platystele tica is without obvious close relatives in Costa Rica. General plant morphology would suggest affinity with the *P. oxyglossa* group, as does the lip shape. The new species, however, lacks the typical caudate sepals and the reddish-purplish coloring of the lip. Flower coloration and size are somewhat reminiscent of *Platystele minimiflora* (Schltr.) Garay, however that species has a creeping habit. *P. tica* has one of the smallest flowers in the genus rivaled only by that of *P. enervis* Luer, *P. ornata* Garay and *P. umbellata* P.Ortiz. It makes the previous Costa Rican famous dwarfs, *P. jungermannioides* (Schltr.) Garay and *P. microtatantha* (Schltr.) Garay, look large. This species might not necessarily be rare, we have observed at least a couple of specimens more in the field and photographed by enthusiasts, but considering the minuscule size of the plant and flower, the lack of herbarium collections and habitat loss in the area it grows, it is not unsurprising that it had escaped description.

8. ***Ponthieva villosa*** Lindl., Pl. Hartw. 155. 1845.

TYPE: Ecuador. *In montibus Paccha rarissima*, *T. Hartweg s.n.* (holotype: K). Syn. *Ponthieva crinita* Garay, Fl. Ecuador 9: 214. 1978 (AMES!).

Distribution: Costa Rica, Colombia, Ecuador and Peru.

Etymology: from the Greek κυστις, "bladder", "cyst" in reference to the prominent ventral vesicle behind the perianth.

Habitat in Costa Rica: the only known specimen was found growing as an epiphyte on a roadside close to Tapantí National Park, in sub montane wet forest, at about 1500 m.

Costa Rican material studied: Cartago: Paraíso, Orosi, Tapantí, sobre el camino a Tausito, unos 4 km del cruce al Parque Nacional Tapantí, 9°46'27.82"N 83°46'54.57" W, 1513 m, epífitas sobre árboles al lado de la calle, bosque pluvial premontano, 12 de febrero 2012, *A.P. Karremans 5040* (CR!; figs. 10, 14I).

The specimen here cited was collected singly, in bloom, on a roadside of a frequented collecting site, and was initially thought to be a novelty. However, the illustrations of *Ponthieva villosa* from Ecuador

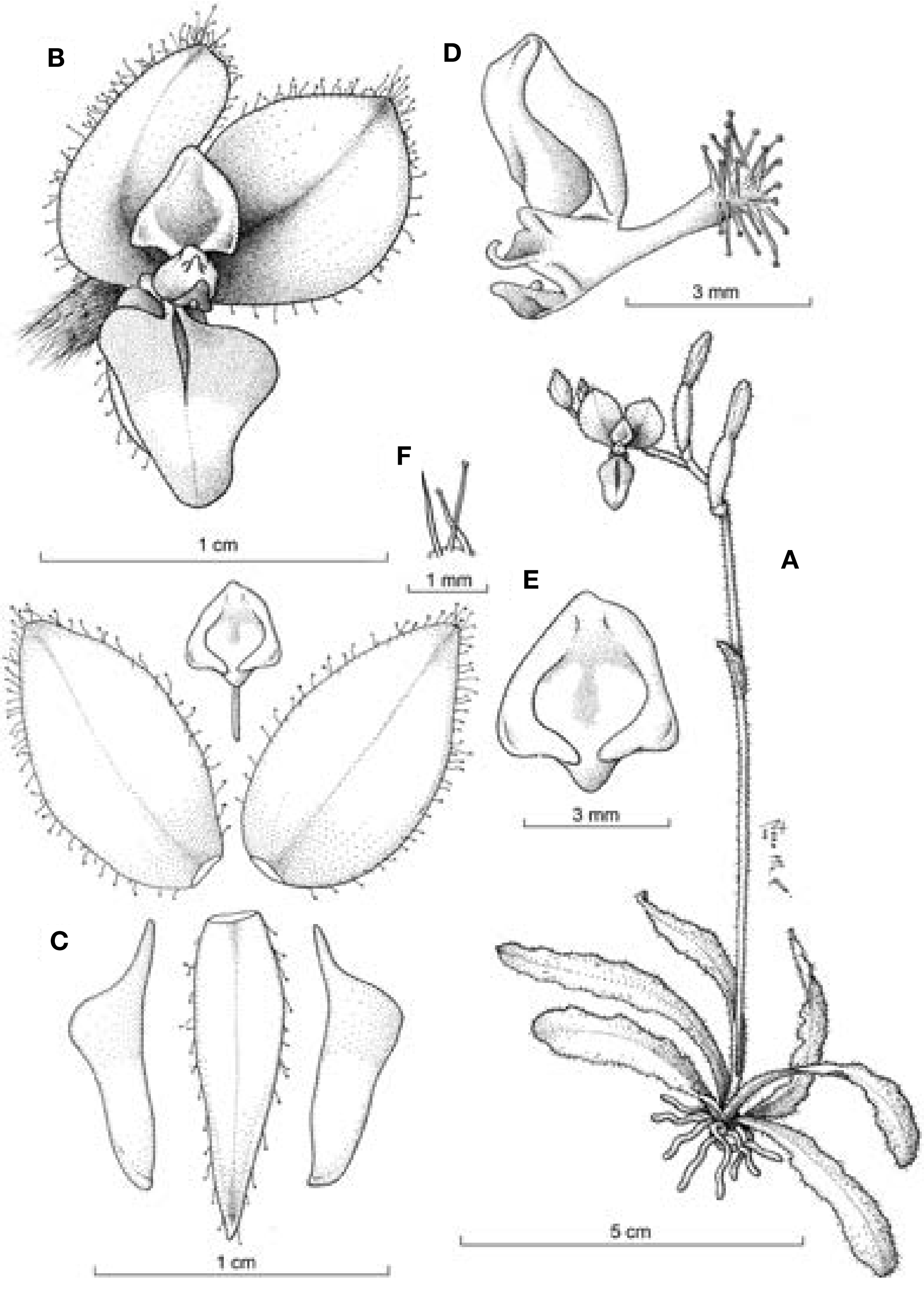


Figure 10. *Ponthieva villosa* Lindl. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip. F — Capitate hairs of the sepal margins. Drawn by A. P. Karremans and J. M. Ramírez from *A.P. Karremans 5040* (JBL-Spirit).

in Dodson and Dodson (1989) and from Colombia in Ortiz (1991), and the type specimen of *P. crinita* (which has been considered a synonym of *P. villosa*), are so similar to the Costa Rican plant that we are unable to distinguish them with the material and information at hand. Unfortunately not much is known about *P. villosa* in general, the original description is quite superficial and we have not been able to see the holotype. The specimen collected close to Tapantí is in any case a species morphologically quite distinct to any previously reported species of *Ponthieva* from Costa Rica, and for now will bear the name *P. villosa*. It can be recognized by the epiphytic plants that are completely hirsute, from the leaves to the back of the sepals. The leaves are quite narrow, with the margins undulate. The sepals are greenish, while the petals are yellowish-green with a large white spot above the middle. The lateral sepals are almost entirely free. The lip is prominently concave and glossy.

9. ***Restrepia aberrans*** Luer, Orquideología 20(2): 117. 1996.

TYPE: Panama. Bocas del Toro, epiphytic in forest above Chiriquí Grande, alt. 350 m, 17 Feb 1985, collected by C. Luer, J. Luer, R. Dressler & K. Dressler, flowered in cultivation by A. & P. Jesup in Bristol, CT., 26 Apr 1987, *C. Luer 10612* (holotype, MO).

DISTRIBUTION: Costa Rica and Panama.

ETYMOLOGY: from the Latin *aberrans*, “aberrant”, referring to unusual floral features that occur in no other species of the genus (Luer 1996).

HABITAT IN COSTA RICA: Known only from the premontane wet forests of Costa Rican Atlantic watershed between 350 m to 790 m of elevation, growing on branches of *Ficus* sp.

COSTA RICAN MATERIAL STUDIED: Cartago: Jiménez, Pejibaye, La Marta, laderas del río Gato. Reserva Biológica La Marta, sendero Tepemechines, creciendo en ramas de *Ficus sp.* 9º46’52”N 83º41’15”W, 790 m, colectada por Daniel Jiménez en mayo del 2012, *A.P. Karremans 5069* (JBL-Spirit!; figs. 11, 14J).

Restrepia aberrans can be recognized by the narrowly triangular dorsal sepal, concave at the base, the lateral sepals partially connate with erect sides towards the base, the parallel petals slightly widened at the apex, the trilobed lip with the lateral lobes erect, oblique, and two inner, erect blades; the column is half the length of the lip, widened towards the apex.

The specimen here cited was found growing in the premontane wet forest of La Marta Wildlife Refuge, located in the Costa Rican Atlantic lowlands. Based on the available literature, the only specimen known before this record was that of the type specimen, which was coincidentally found in the Atlantic lowlands of western Panama, near the border with Costa Rica. Opposed to the type specimen, no evidence of cleistogamy was observed in the Costa Rican plant. Likewise, the lateral sepals of the latter remained almost entirely connate until the flower decayed.

10. ***Sobralia bletiae*** Rchb.f., Bot. Zeitung (Berlin) 10: 713. 1852.

TYPE: : “Chiriqui” Panama, *Warszewicz s.n.* (holotype, W).

DISTRIBUTION: Venezuela, Ecuador, Panama, Costa Rica and Nicaragua.

ETYMOLOGY: most probably refers to the similarity of the flower with those of *Bletia*.

HABITAT IN COSTA RICA: Known from the tropical wet forests of the Osa peninsula in southern Costa Rica, growing at low elevations in secondary forests.

COSTA RICAN MATERIAL STUDIED: Puntarenas: Osa, Sierpe, camino a Bahía Drake, entre Rincón y Rancho Quemado, 8°40’52.3”N 83°32’57.5”W, 214 m, en bosque secundario y cercas a orillas del camino, bosque muy húmedo tropical “*sylvas ad peninsula Osa regione sinus Dulce versus Drake prope Rancho Quemado*”, 13 marzo 2011, *D. Bogarín 8497, A.P. Karremans & J. Sharma* (JBL-Spirit!; figs. 12, 14K); Puntarenas: Osa, P.N. Piedras Blancas, 8.69 -83.23, Estacion Rio Bonito, 100 m, *E. Fletes 424* (INB, MO); Puntarenas: Osa, Rincón de Osa. Streams and slopes adjacent to airfield, 08°42’N 083°31’W, 20 - 300 m, epiphytic in disturbed primary forest, 6-7 Feb. 1974, *R. L. Liesner 1817* (MO).

The habit of *S. bletiae* is similar to that of several other *Sobralia*, such as *S. decora* Bateman and *S. mucronata* Ames & C.Schweinf. It can be recognized

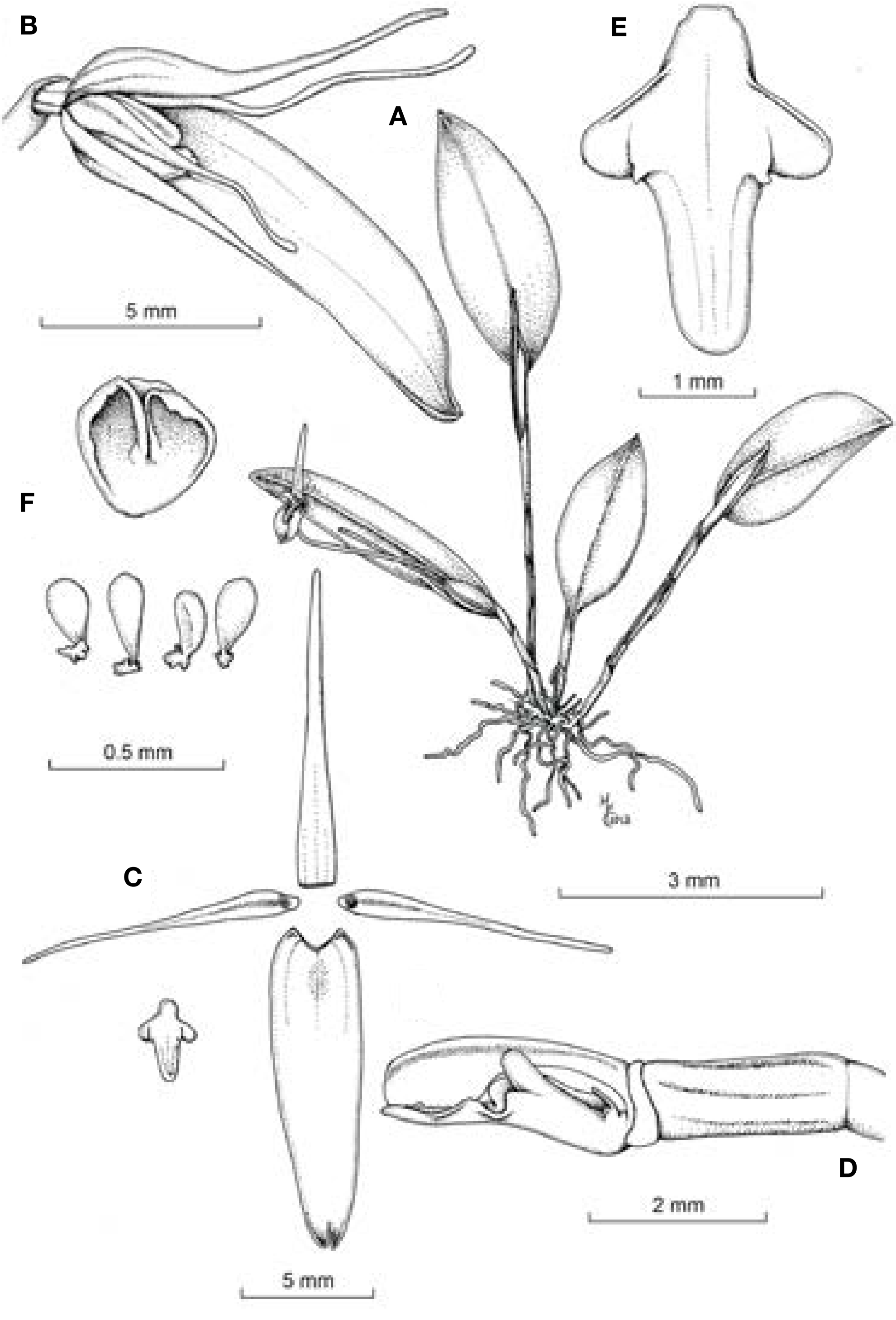


FIGURE 11. *Restrepia aberrans* Luer. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, front view. F — Lip, spread. G —Pollinarium and anther cap. Drawing by D. Bogarín & M. Fernández based on *A.P. Karremans 5069* (JBL-Spirit).

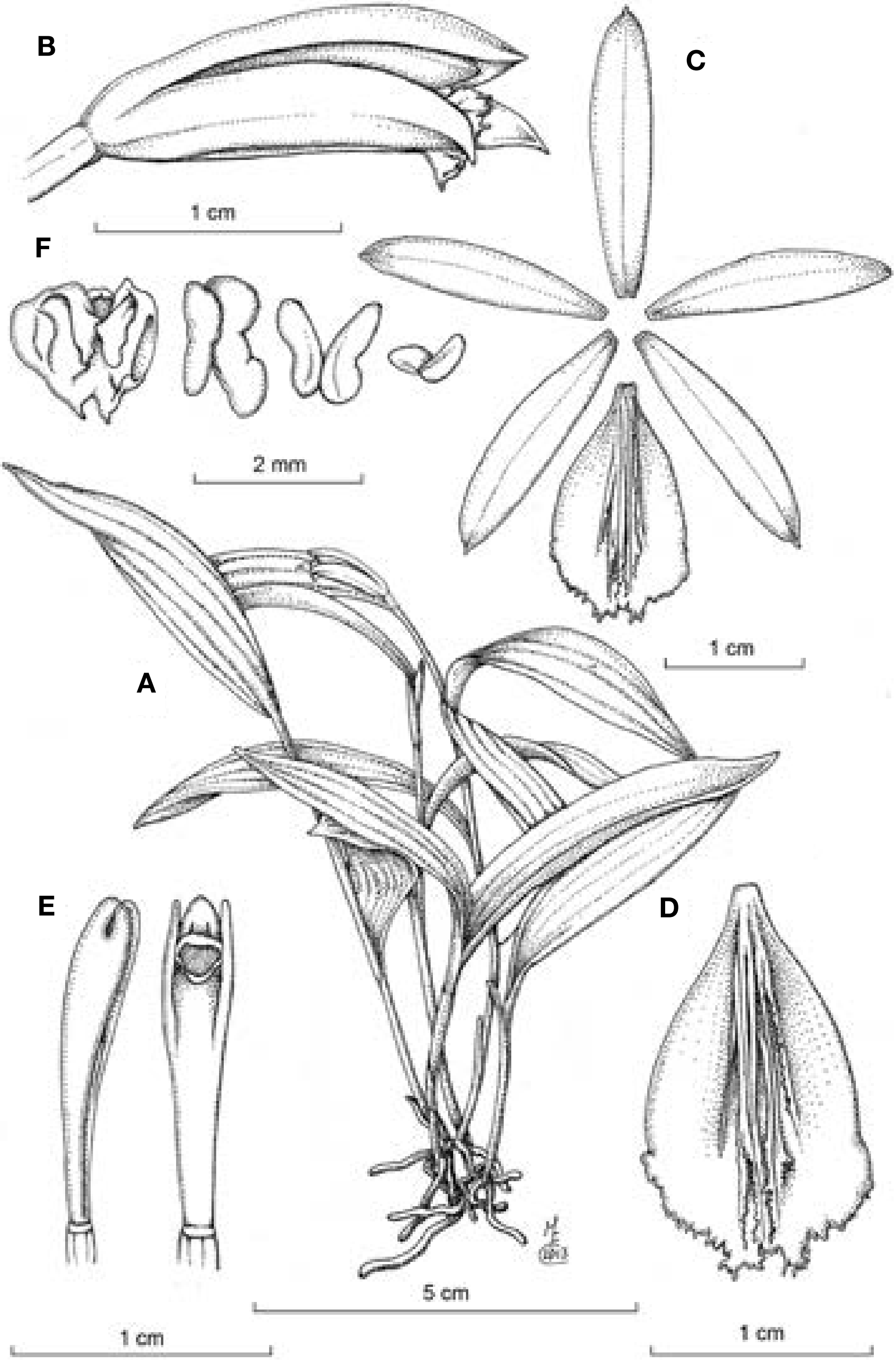


FIGURE 12. *Sobralia bletiae* Rchb.f. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, front view. F — Lip, spread. G —Pollinarium and anther cap. Drawing by D. Bogarín and M. Fernández based on *D. Bogarín 8497* (JBL-Spirit).

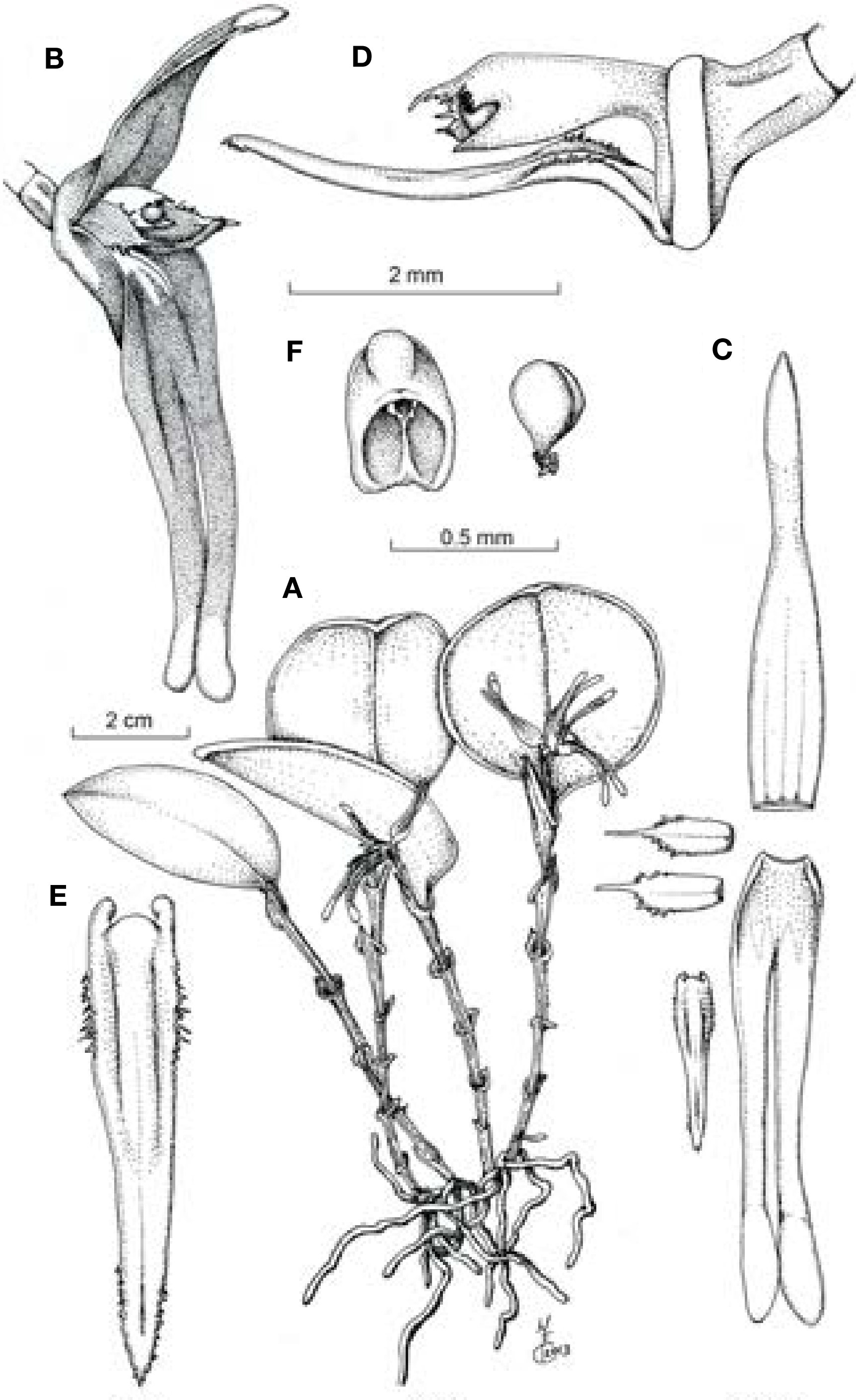
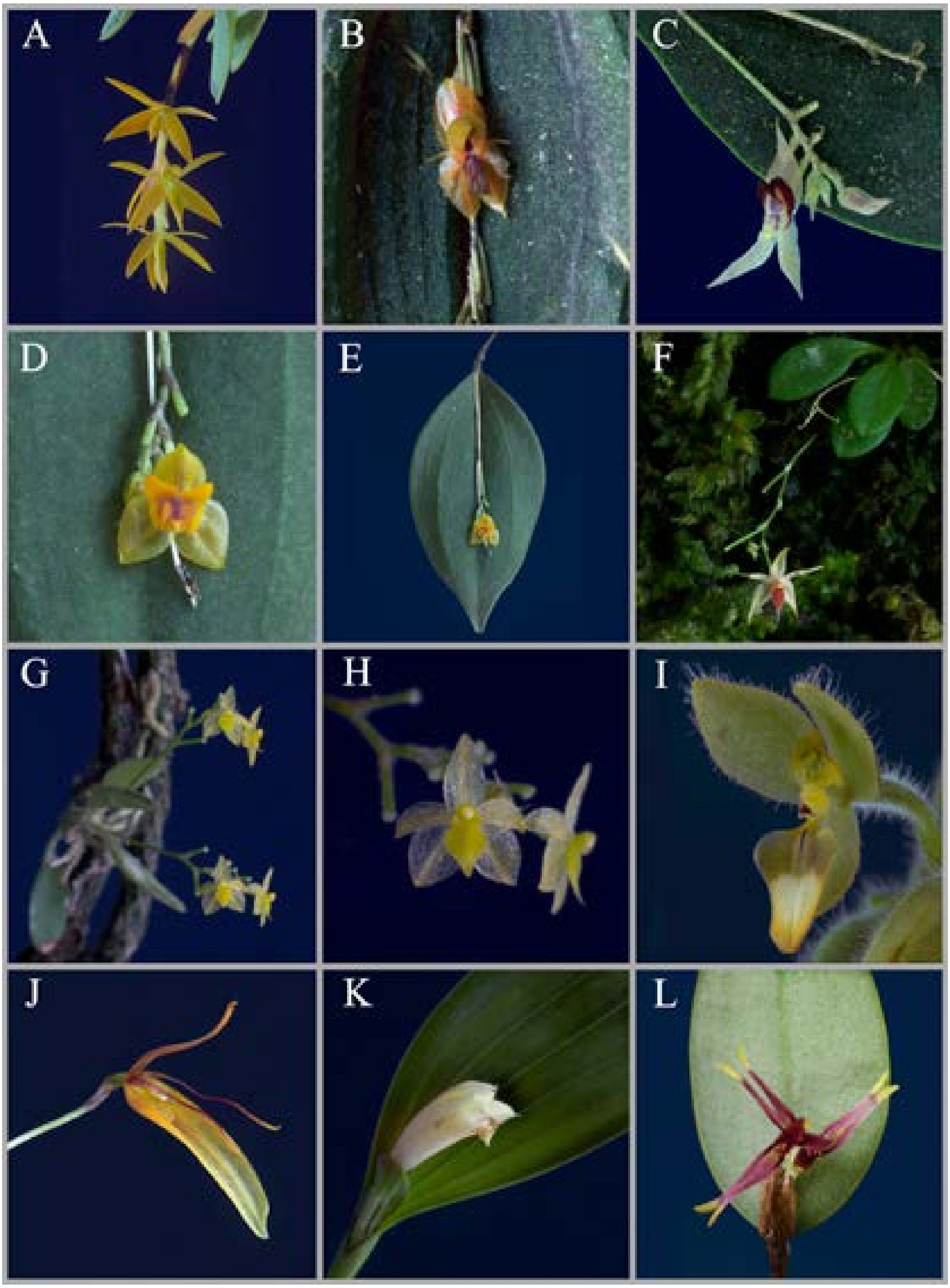


Figure 13. *Trichosalpinx caudata* Luer. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, front view. F — Lip, spread. G —Pollinarium and anther cap. Drawing by M. Fernández based on *M. Fernández 546* (JBL-Spirit).


A
B
C
D
E
F
G
H
I
J
K
L

by the small, tubular flower with creamy, parallel sepals and petals, the trilobed lip with five to seven, red-to-brown keels, and a mucronate apex. The column narrows towards the base, and the pollinia are dorsally flattened.

Although several authors had reported this species as present in Costa Rica (Ames 1937, Williams 1956, Mora & García 1992, Dressler 1993, García *et al.* 1993), the existence of two Costa Rican herbarium specimens was unknown until relatively recently (Pupulin 2002, Dressler 2003): *R. L. Liesner 1817* (MO), and *E. Fletes 424* (INB, MO), both from the lowlands of the Península de Osa. This species is illustrated for the first time based on Costa Rican material.

11. ***Trichosalpinx caudata*** Luer & R.Escobar, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 20. 1997.

TYPE: Colombia. Antioquia: La Tebaida, collected by E. Valencia, July 1988, flowered in cultivation at Colomborquídeas, 16 May 1993, *C. Luer 16907* (MO).

Distribution: Costa Rica, Panama and Colombia.

Etymology: from the Latin *caudatus*, "caudate", referring to the tails of the lateral sepals (Luer 1997).

Habitat in Costa Rica: *T. caudata* has been found growing epiphytically at low elevations in disturbed areas close to water bodies along the northern Atlantic plains and in open areas of the Osa Peninsula, mostly at 100–250 m [to 1200-1400 m] .

Costa Rican material studied: Alajuela: San Carlos, Boca Tapada, alrededores del Hotel Laguna de río Lagarto, en jardín del hotel Arenal Paraíso, 100 m, 10 oct 2004, *C. Ossenbach 368 & P. Casasa* (JBL-Spirit!). Puntarenas: Osa, Cortés, fila Dominicalito, 250 m, D. Jiménez invenit, *M. Fernández 546* (JBL-Spirit!; figs. 13, 14L). Puntarenas: Osa, San Juan, cuenca media del río San Juan, siguiendo el curso aguas arriba, 200 m, flor morada de ápice anaranjado, conspicuo, 5 noviembre 1990, *G. Herrera 4568* (CR!). San José: Pérez Zeledón, Carretera Interamericana, La Ese, km 114-122, orilla de la carretera, 9°26'N 83°35'W, 1200-1400 m, 12 julio 2005, *A. Rojas 6474 & H. Kennedy* (JBL-Spirit!).

Trichosalpinx caudata and *T. orbicularis* (Lindl.) Luer are vegetatively almost indistinguishable. Nevertheless, the long, caudate sepals of the first are the most conspicuous differentiating character. The sepals can reach up to 8.5 mm long (vs. 3.5-6.5 mm), the dorsal sepal is narrowly triangular (vs ovate), while the lateral sepals are connate only at the base, long-attenuate, and have a widened and fleshy apex. The petals are narrowly acute to acuminate (vs. acute to obtuse), densely fimbriate. The lip is usually twice longer than the column (vs. one-third longer than column).

Acknowledgements. We are thankful for the scientific services of Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC) for issuing the Scientific Passports under which wild species treated in this study were collected. To the Vice-Presidency of research of the University of Costa Rica for providing support under the projects "Inventario y taxonomía de la flora epífita de la región Mesoamericana" (814-A7-015), "Flora Costaricensis: Taxonomía y Filogenia de la subtribu Pleurothallidinae (Orchidaceae) en Costa Rica" (814-BO-052), "Filogenia molecular de las especies de Orchidaceae endémicas de Costa Rica" (814-B1-239) and "Hacia una moderna flora de orquídeas de Panamá" (814-B2-161). We are also grateful to the personnel at CR, INB, JBL and USJ for granting full access to their collections. Finally, we are grateful to Joan M. Ramírez and Darha Solano, illustrators at JBL, who prepared some of the plates included in the article.

Literature Cited

Ames, O. 1937. Orchidaceae. Orchid Family. *In* P. C. Standley (ed.) Flora of Costa Rica. Vol. 18. Field Museum of Natural History – Botany, p. 292.

Bogarín, D. 2011. How many orchid species in Costa Rica? A review of the latest discoveries. *In*: A. M. Pridgeon & H. G. Navarrete Zambrano (eds.). Proceedings of the Third Scientific Conference on Andean Orchids, Quito. Lankesteriana 11(3): 185—205.

Left, Figure 14. A — *Epidendrum jorge-warneri*, (A.P. Karremans 5545). B — *Lepanthes ankistra* (D. Bogarín 9698). C — *Lepanthes otopetala* (D. Bogarín 8715). D & E — *Lepanthes truncata* (D. Bogarín 9652). F — *Platystele catiensis* (A.P. Karremans 5442). G & H — *Platystele tica* (A.P. Karremans 5315). I — *Ponthieva villosa* (A.P. Karremans 5040). J — *Restrepia aberrans* (A.P. Karremans 5069). K — *Sobralia bletiae* (D. Bogarín 8497). L — *Trichosalpinx caudata* (M. Fernández 546). Photographs by D. Bogarín (B, C, D, E), M. Fernández (J, K), D. Jiménez (L), A. Karremans (A, F, G, I) and F. Pupulin (H).

Bogarín, D. & A. P. Karremans. 2010. Un nuevo *Platystele* (Orchidaceae: Pleurothallidinae) de la región central de Costa Rica/A new *Platystele* (Orchidaceae: Pleutothallidinae) from central Costa Rica. Orquideología 27: 208—220.

Bogarín, D., A. P. Karremans & F. Pupulin. 2008. New records and species of Orchidaceae from Costa Rica. Lankesteriana 8(2): 53—74.

Dodson, C.H. & P.M. de Dodson. 1989. Icones Plantarum Tropicarum 2(6): Orchids of Ecuador. Missouri Botanical Garden.

Dressler, R. L. 1993. Field Guide to the Orchids of Costa Rica and Panama. Cornell University Press, p. 319.

Dressler, R. L. 2003. *Sobralia*. Pp. 506—516 in: B. E. Hammel, M. H. Grayum, C. Herrera & N. Zamora (eds.). Manual de plantas de Costa Rica – Volumen III, monocotiledóneas (Orchidaceae-Zingiberaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 93.

García Castro, J. B., D. E. Mora de Retana & M. E. Rivas Rossi. 1993. Lista de Orquídeas Comunes a Costa Rica y Panamá. Brenesia 39—40: 106.

Karremans, A.P. & D. Bogarín. 2013. Costa Rica, land of endless orchids. Orchids (West Palm Beach) 82(7): 408—411.

Karremans, A.P., D. Bogarín, M. Fernández, C.M. Smith & M. Blanco. 2012. New species and records of Orchidaceae from Costa Rica. II. Lankesteriana 12(1): 19-51.

Luer, C.A. 1990. Icones Pleurothallidinarum VII: Systematics of *Platystele* (Orchidaceae) Monogr. Syst. Bot. Missouri Bot. Gard. 38: 1—115.

Luer, C.A. 1991. New species of *Lepanthes* (Orchidaceae). Lindleyana 6(2): 64—83.

Luer, C.A. 1996a. Icones Pleurothallidinarum XIV. Systematics of *Draconanthes*, *Lepanthes* subgenus *Marsipanthes*, and subgenus *Lepanthes* of Ecuador (Orchidaceae). Part Three: The genus Lepanthes subgenus *Lepanthes* in Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 61:1—255.

Luer, C.A. 1996b. Nuevas especies de *Restrepia* – New species of *Restrepia*. Orquideología 20(2): 117—120.

Luer, C.A. 1997. Systematics of *Trichosalpinx*. Monogr. Syst. Bot. Missouri Bot. Gard. 64: 20.

Luer, C. A. 2003. *Platystele*. Pp. 216—255 in: B. E. Hammel, M. H. Grayum, C. Herrera & N. Zamora (eds.). Manual de plantas de Costa Rica – Volumen III, monocotiledóneas (Orchidaceae-Zingiberaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 93.

Luer, C.A. & R.L. Dressler. 1986. Nuevas especies de *Lepanthes* de Panamá. Orquideologia 16(3): 3—26.

Mora-Retana, D.E. & J.B. García. 1992. Lista actualizada de las Orquídeas de Costa Rica. Brenesia 37: 79—124.

Ortiz, P. 1991. *Ponthieva* R.Br. Pp. 444—447 in: R. Escobar (ed.). Orquideas Nativas de Colombia – Volumen 3: *Maxillaria-Ponthieva*. Compañía Litográfica Nacional S.A. Medellín.

Pupulin, F. 2002. Catálogo revisado y anotado de las Orchidaceae de Costa Rica. Lankesteriana 4: 1—88.

Sánchez, S. L. & E. Hágsater. 2007. *Epidendrum anoglossoides* Ames & C.Schweinf. In Hágsater. E. & L. Sánchez S. (eds.) Icon. Orchid. 9. pl. 907.

Williams, L.O. 1956. An enumeration of the Orchidaceae of Central America, British Honduras and Panama. Ceiba 5(1): 25.

LANKESTERIANA 13(3): 283—290. 2014.

INVITED PAPER*

EL GRUPO EPIDANTHUS, SUBGRUPO SELAGINELLA DE *EPIDENDRUM*

ERIC HÁGSATER & ELIZABETH SANTIAGO AYALA

Herbario AMO, Montañas Calizas 490, México, D.F. 11000, México
herbamo@prodigy.net.mx, www.herbarioamo.org

RESUMEN. La revisión de una gran cantidad de ejemplares de herbario determinados como *Epidendrum selaginella* Schltr. que mostraban diferencias foliares evidentes comparadas con el ejemplar tipo que sirvió para describir esta especie ampliamente distribuida en Costa Rica y Panamá así como el análisis de los segmentos florales de los mismos permitieron reconocen 2 nuevas especies muy cercanas a *Epidendrum selaginella* y por mucho tiempo confundidas con esa especie centroamericana: *Epidendrum astroselaginella* y *Epidendrum stenoselaginella*. Se presenta una clave ilustrada.

ABSTRACT. The revision of a large number of herbarium specimens determined as *Epidendrum selaginella* Schltr. and which had evident foliar differences compared to the type served to prepare a detailed description of this widely distributed species in Costa Rica and Panama, and an analysis of the floral segments led to the recognition of two new species closely allied to *Epidendrum selaginella,* and confused with that Central American species: *Epidendrum astroselaginella*, and *Epidendrum stenoselaginella*. An illustrated key is provided.

KEY WORDS: *Epidendrum selaginella*, *astroselaginella*, *stenoselaginella*, *Epidanthus,* Costa Rica

Epidendrum, es considerado uno de los géneros más grandes de orquídeas neotropicales. Está constituido por unas 1500 especies distribuidas desde el sur de los Estados Unidos hasta el norte de Argentina (Hágsater 1985). En el transcurso de los años, muchos autores han intentado dividirlo en subgéneros (Barringer 1991), los cuales han llegado a reconocerse, en varios casos, como géneros (Williams 1940), basándose en características como el número de polinios, la presencia de tallos engrosados y/o la posición en la que se produce la inflorescencia. Con cerca de 300 especies secuenciadas en su ADN, hemos llegado a la conclusión de que se trata de un género monofilético en donde se pueden reconocer diversos grupos y sub grupos con características vegetativas similares (Hágsater & Soto 2005).

En 1940, Williams, tomando en cuenta básicamente en el número de polinios, propuso al grupo Epidanthus como un género: *Epidanthus* L.O. Williams y transfirió a este género 3 especies de *Epidendrum*: *E. paranthicum* Rchb.f., *E. muscicolum* Schltr. y *E. goniorhachis* Schltr. Garay (1977) y Barringer (1991) también evaluaron este grupo, el primero opinando que efectivamente debía tratarse como género separado, y el segundo estableciéndolo como un subgénero de *Epidendrum*, y agregando una especie nueva. Con el estudio de las numerosas especies que integran el género *Epidendrum,* se ha demostrado que el número de polinios no representa una característica exclusiva del grupo *Epidanthus*. En el género *Epidendrum,* existen especies que tienen 2, 4 y hasta 8 polinios (Hágsater & Santiago 2010).

El grupo Epidanthus, es de pocas especies y se caracteriza por tener plantas pequeñas, escandentes con tallos muy delgados, hojas cortas y angostas, algo carnosas con una lígula diminuta opuesta a la lámina foliar, inflorescencia apical, usualmente secundiflora con flores pequeñas. Está ampliamente distribuido desde el sur de México hasta Ecuador, con particular diversidad en Centro América. Actualmente, consideramos que está formado por 11 especies divididas en dos subgrupos: el subgrupo Epidanthus (que incluye a las especies que tienen hojas semiteretes, 2 polinios y el labelo generalmente 3-lobado, (con excepción de *Epidendrum*

---

* Este artículo fue preparado en el marco de las celebraciones del 40 Aniversario del Jardín Botánico Lankester.

Figura 1. *Epidendrum selaginella* Schltr. basado en *E.Hágsater 6537*, Panamá: Cerro Horqueta, testigo: AMO A-589. Foto E. Hágsater.

goniorhachis que tiene el labelo entero), y el subgrupo Selaginella, que incluye a las especies con hojas planas, 4 polinios y de labelo entero, en el cual ésta incluido *Epidendrum selaginella* Schltr.

Revisando detenidamente una gran cantidad del material de herbario determinado bajo el nombre de *Epidendrum selaginella* (Fig. 1 y 4), encontramos 2 nuevas especies relacionadas, y por mucho tiempo confundidas con ésta especie bastante común y ampliamente distribuida en Costa Rica y Panamá.

Epidendrum selaginella fue descrita por Rudolf Schlechter en 1906 a partir de un ejemplar colectado por J. Cooper en Costa Rica: Se reconoce fácilmente por sus plantas pequeñas (de no más de 12 cm de alto, incluyendo la inflorescencia) con tallos tipo caña, hojas cortas y planas, generalmente ovadas con el ápice bilobado, con inflorescencias secundifloras de 5 a 7 pequeñas flores verdes o amarillo verdosas. Uno de los detalles que llamó nuestra atención cuando revisamos el material herborizado fue precisamente la forma de las hojas en algunos ejemplares determinados bajo el nombre de ésta especie, los cuales tenían hojas de forma distinta. La lámina foliar de estas plantas era claramente linear lanceolada y de una anchura menor a las hojas de *E. selaginella* (Santiago y Hágsater 2007; Fig. 4). Estudiando detenidamente éstos ejemplares, rehidratando flores e ilustrando los segmentos florales de varias de éstas plantas, encontramos además, que había diferencias también con respecto a las flores. En algunos ejemplares, las flores estaban laxamente distribuidas a lo largo del raquis y la mecánica de la antesis de los segmentos florales también era notoriamente distinta (la posición de los mismos era casi totalmente extendida). Notando que éstas características se mantenían de forma constante entre éstas plantas, en el año de 2007 procedimos a describir dos especies nuevas. Una bajo el nombre de *Epidendrum astroselaginella* Hágsater & E.Santiago (Hágsater y Santiago 2007a; Fig. 2 y 5); la etimología del epíteto de ésta especie, hace referencia a la posición extendida de los segmentos florales y que recuerda a una estrella. Había otro pequeño grupo de ejemplares, de hojas angostas también, con la inflorescencia similar a *Epidendrum selaginella*, pero con diferencias

Figura 2. *Epidendrum astroselaginella* Hágsater & E.Santiago basado en *E.Hágsater s.n.*, Jardín Botánico Lankester, Costa Rica. Foto E. Hágsater.

a nivel floral. A éste segundo grupo de colectas, de una distribución más amplia que va desde Nicaragua hasta Panamá (Fig. 7), lo describimos como *Epidendrum stenoselaginella* Hágsater & E. Santiago (Hágsater y Santiago. 2007b; Fig. 3 y 6); el epíteto hace referencia a las hojas más angostas, comparada con *E. selaginella*.

Clave de identificación de las especies del grupo Epidanthus, subgrupo Selaginella

El subgrupo Selaginella se caracteriza por sus hojas aplanadas, semejantes en tamaño y forma, generalmente cortas (2.7-10.5 mm de largo), el labelo entero y la antera con 4 polinios.

1 Hojas ovadas a oblongo ovadas, hasta 3.4 mm de ancho, flores distribuidas densamente hacia el ápice de la inflorescencia, ovario y dorso de los sépalos densamente papilosos; Costa Rica y Panamá .... ***E. selaginella*** Schltr.

1’ Hojas linear lanceoladas, hasta 1.9 mm de ancho, flores distribuidas laxamente en la inflorescencia, ovario y sépalos glabros 2

Figura 3. *Epidendrum stenoselaginella* Hágsater & E.Santiago basado en *E.Hágsater 11115*; Costa Rica: Volcán Poás-San José, testigo: AMO 15886, holotipo. Foto: E. Hágsater.

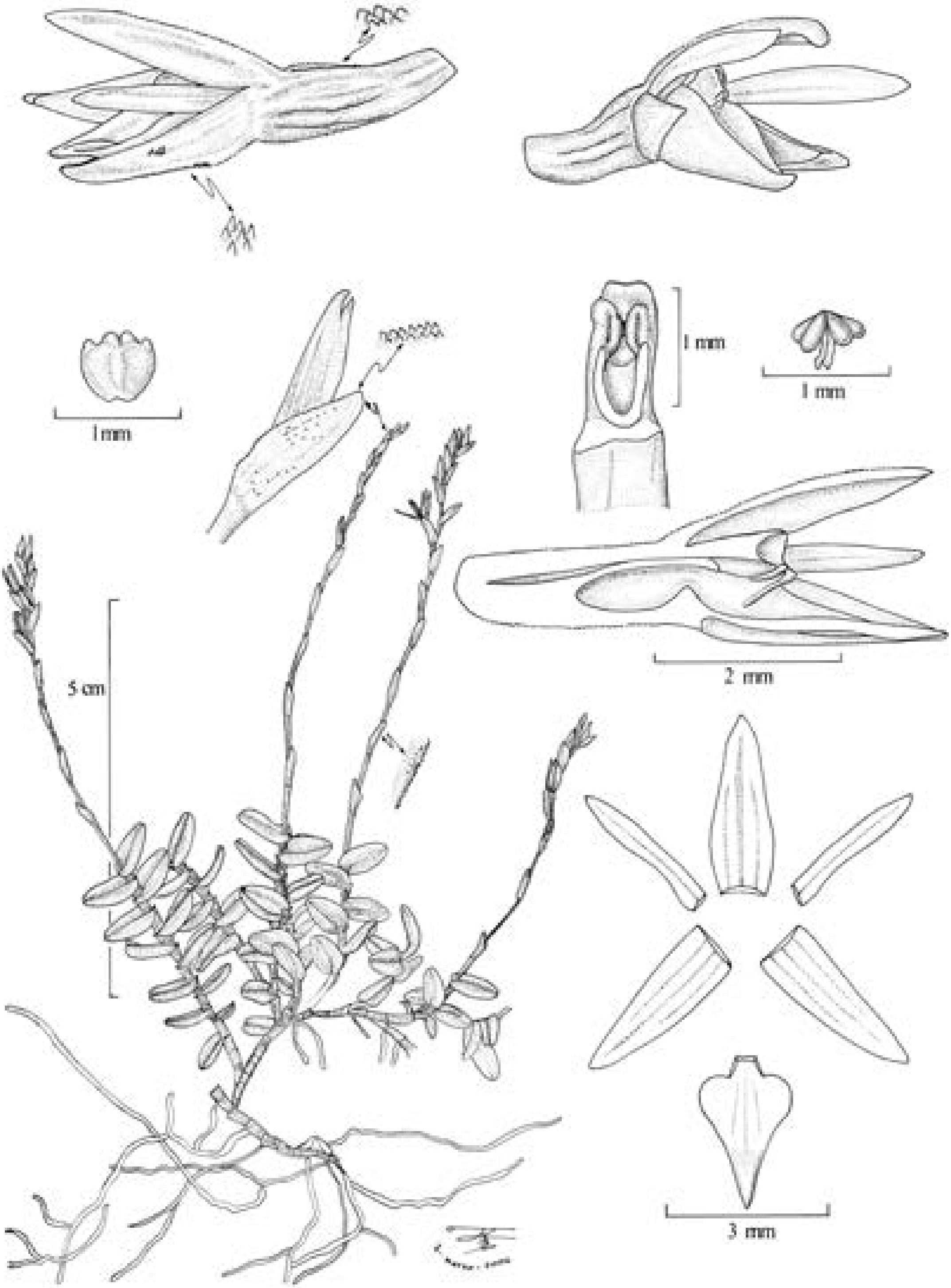


FIGURA 4. *Epidendrum selaginella* Schltr. basado en *R.L.Dressler 5730*; Panamá, Coclé, 8 km N of El Copé; testigo: AMO 2329. Dibujo de R. Jiménez Machorro.

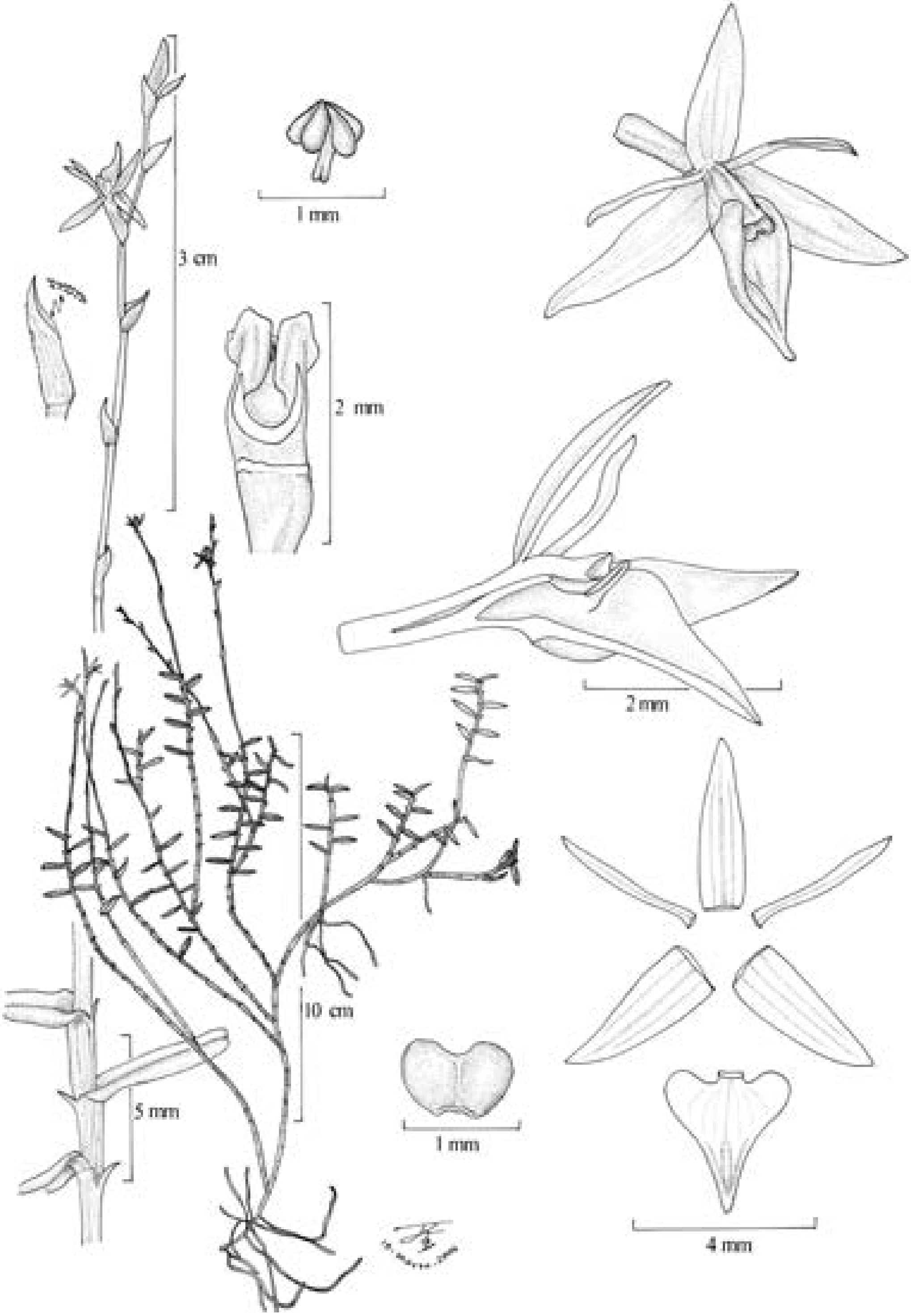


Figura 5. *Epidendrum astroselaginella* Hágsater & E.Santiago basado en *L.D.Gómez P. 23814*, Costa Rica, Cordillera de Talamanca; testigo: MO 3586978, holotipo. Dibujo de R. Jiménez Machorro.

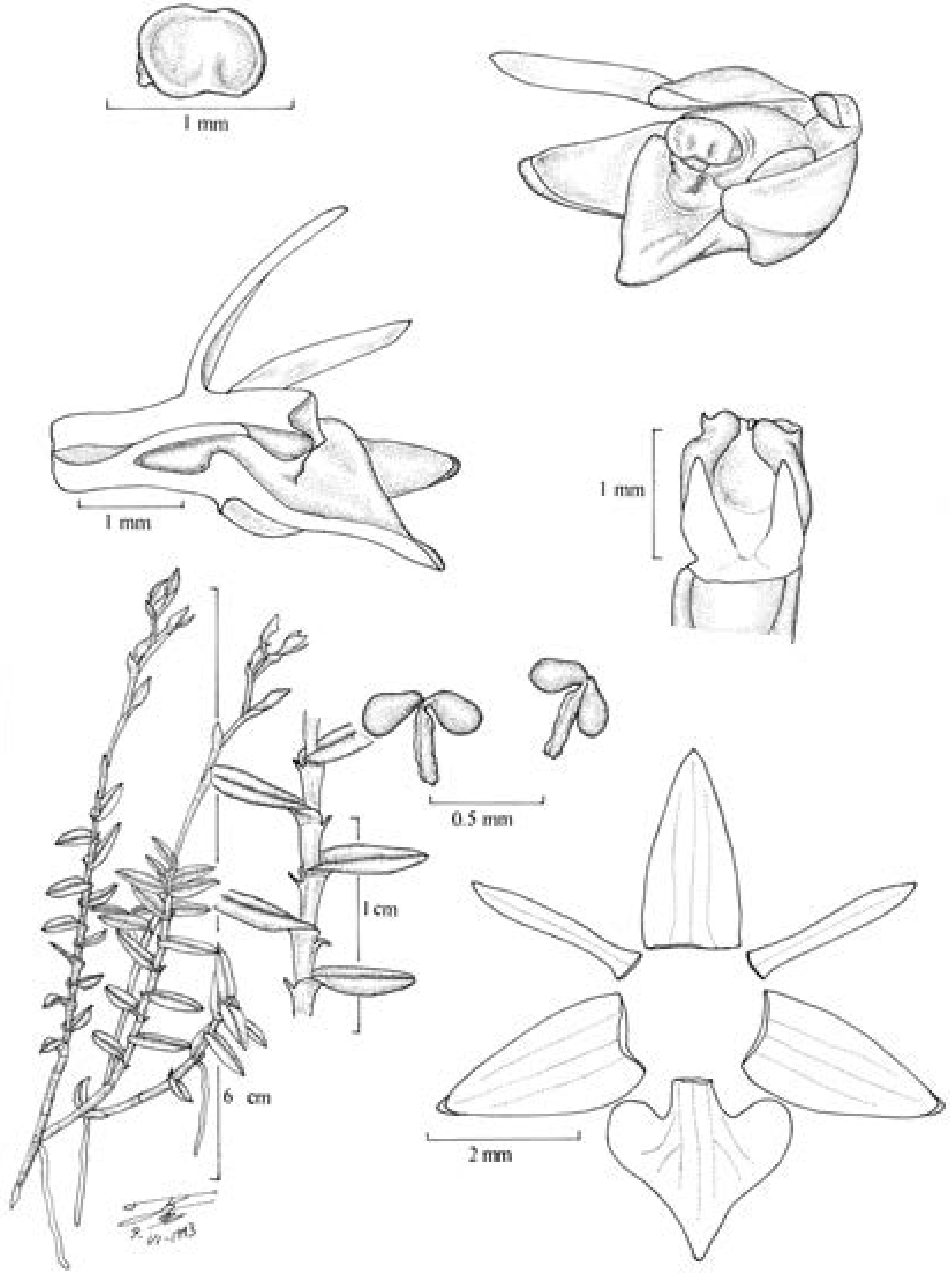


Figura 6. *Epidendrum stenoselaginella* Hágsater & E.Santiago basado en *E.Hágsater 11115*, Costa Rica, Volcán Poás-San José; testigo: AMO 15886, holotipo. Dibujo de R. Jiménez Machorro.

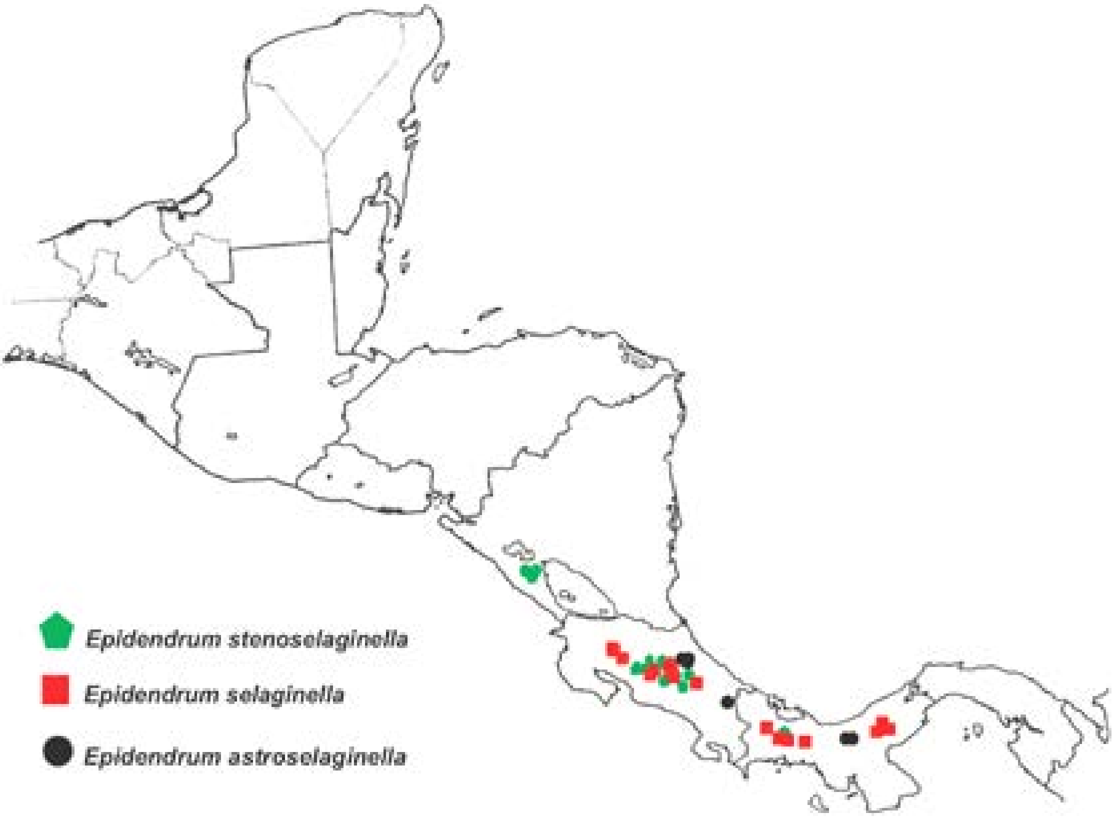


Figura 7. Mapa de distribución de *Epidendrum selaginella, E. stenoselaginella* y *E. astroselaginella*.

2 Segmentos florales extendidos, sépalos 3.5-4.2 mm de largo, labelo proporcionalmente más largo que ancho, columna con un par de dientes laterales prominentes; Costa Rica y Panamá .... **E. astroselaginella** Hágsater & E.Santiago

2’ Segmentos florales entreabiertos, sépalos 2.5-3 mm de largo, labelo proporcionalmente tan largo como ancho, columna con un par de dientes laterales incipientes; Nicaragua, Costa Rica y Panamá .... **E. stenoselaginella** Hágsater & E.Santiago

Literatura citada

Barringer, K. 1991. A revision of *Epidendrum* subgenus *Epidanthus* (Orchidaceae). Brittonia 43(4): 240-252.

Garay, L.A. 1977. *The Subtribe Epidanthinae* L. O. Wms. The Orchid Digest, 41(1): 19-22.

Hágsater, E. 1985. Towards an understanding of the genus *Epidendrum*. *En* K.W. Tan, (ed.), Proceedings of the 11th World Orchid Congress: 195-199. Miami, U.S.A.

Hágsater, E. y M.A. Soto. 2005. *Epidendrum*. *En* A.M. Pridgeon, P.J. Cribb, M.W. Chase y F.N. Rasmussen (eds.). *Genera Orchidacearum* 4: Epidendroideae, part one: 236-251. Oxford University Press, Cambridge, U.K.

Hágsater, E. y E. Santiago. 2007a. *Epidendrum astroselaginella. En* Hágsater, E. & L. Sánchez Saldaña (eds.), The Genus *Epidendrum*, Part 6, Species New and Old in *Epidendrum*. Icon. Orchid. 9: t. 917.

Hágsater, E. y E. Santiago. 2007b. *Epidendrum stenoselaginella. En* Hágsater, E. & L. Sánchez Saldaña (eds.), The Genus *Epidendrum*, Part 6, Species New and Old in *Epidendrum*. Icon. Orchid. 9: t. 991.

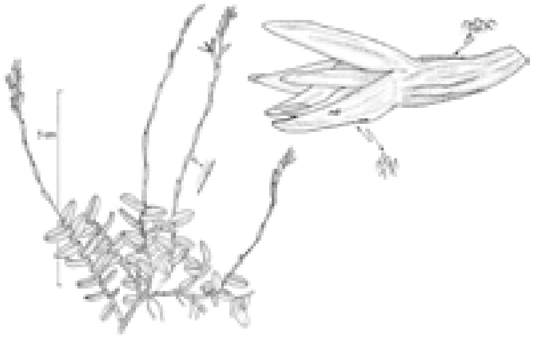
Hágsater, E. y E. Santiago. 2010. *Epidendrum peristerium. En* Hágsater, E. & L. Sánchez Saldaña (eds.), The Genus *Epidendrum*, Part 9, Species New and Old in *Epidendrum*. Icon. Orchid. 13: t. 1370.

Santiago, E. y E. Hágsater. 2007. *Epidendrum selaginella. En* Hágsater, E. & L. Sánchez Saldaña (eds.), The Genus *Epidendrum*, Part 6, Species New and Old in *Epidendrum*. Icon. Orchid. 9: t. 984.

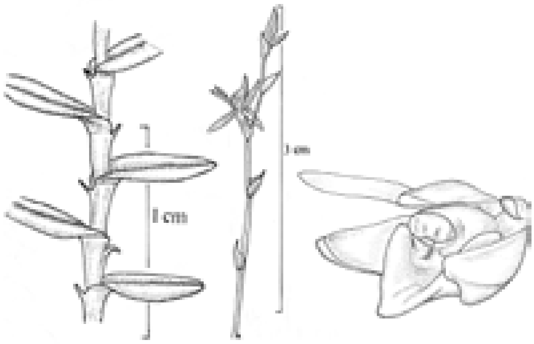
Williams, L.O. 1940. A new genus of the Orchidaceae from Central America. Bot. Mus. Leafl. 8: 148-151.

APÉNDICE. Clave ilustrada de identificación de las especies del grupo Epidanthus, subgrupo Selaginella.

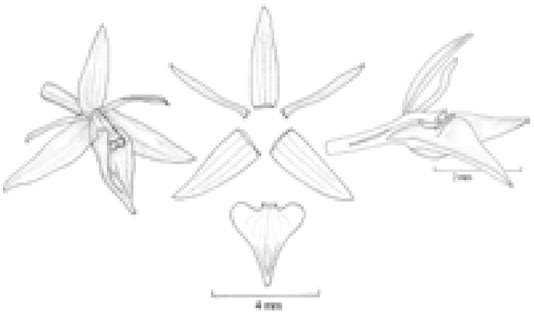
1 Hojas ovadas a oblongo ovadas, hasta 3.4 mm de ancho, flores distribuidas densamente hacia el ápice de la inflorescencia, ovario y dorso de los sépalos densamente papilosos; Costa Rica y Panamá .... ***E. selaginella*** Schltr.



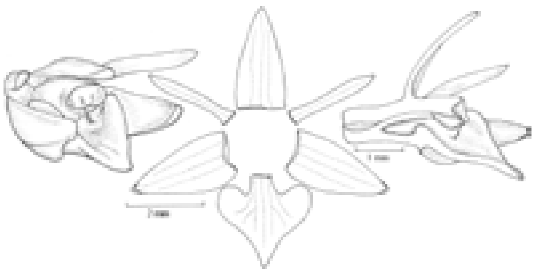
1’ Hojas linear lanceoladas, hasta 1.9 mm de ancho, flores distribuidas laxamente en la inflorescencia, ovario y sépalos glabros 2



2 Segmentos florales extendidos, sépalos 3.5-4.2 mm de largo, labelo proporcionalmente más largo que ancho, columna con un par de dientes laterales prominentes; Costa Rica y Panamá .... ***E. astroselaginella*** Hágsater & E.Santiago



2’ Segmentos florales entreabiertos, sépalos 2.5-3 mm de largo, labelo proporcionalmente tan largo como ancho, columna con un par de dientes laterales incipientes; Nicaragua, Costa Rica y Panamá .... ***E. stenoselaginella*** Hágsater & E.Santiago



LANKESTERIANA 13(3): 291—317. 2014.

INVITED PAPER*

WHAT IS IN AN ORCHID NAME: A TRIBUTE TO THE EARLY NATURALISTS IN COSTA RICA

RUDOLF JENNY

Moosweg 9, 3112 Allmendingen, Switzerland
rjorchid@gmx.ch

ABSTRACT. The early history of Costa Rican orchidology was deeply influenced by a number of naturalists, mainly European by birth, who dedicated themselves to explore a still virgin country, bringing back from their trips a treasure of species to be apprehended by science. While some of them where just occasional voyagers and explorers, other establish themselves in Costa Rica in a long and fecund relationship, that raised to the birth of a new generation of national naturalists in the first decades of the nineteenth century. Even if their faces are sometimes unknown, their names are linked forever to the orchid that helped to reveal to science and to humanity. What follows, and using as an excuse the name of some orchids, is a brief overview of the life and deeds of some of these early naturalists, as a tribute to their contribution to the development of Costa Rican orchidology.

KEY WORDS: History of botany, Costa Rica, Orchidaceae

Pablo Biolley and *Telipogon Biolleyi*

Paul (Pablo) Auguste Biolley (Fig. 1A) was born as son of a teacher on 16th of February 1862 in Neuenburg, Switzerland. He studied in Neuenburg and became member of the Société des Sciences Naturelles de Neuchatel and the Société Neuchatelois de Géographie. After graduating, he went as teacher for 2 years to the Netherlands. In 1885 Biolley was invited as teacher and scientist by the Costa Rican government of Bernardo SOTO, he arrived in San Jose in 1886. Together with Henri Francois Pittier, Biolley undertook a number of expeditions through Costa Rica, in 1902 he joined the expedition to the Coco-island and in 1907 he published results of this trip in the book "*Mollusques de la Isla del Coco*". His main interest was entomology, but beside insects he also collected plants and made important contributions to the knowledge of the flora of Costa Rica. Biolley was a quiet man, beside his duties as teacher he spent all his free time collecting animals and plants. He married a Costa Rican and got the Costa Rican nationality, for a short period in 1904 he became director of the Instituto Fisico-Geografico. Biolley was not very well accepted as teacher and was a victim of criticism from colleagues and staff; this was certainly one of the reasons why he started to drink. Alcohol finally was the reason of his early death on 16th of January 1908 at the age of only 46. Only a few publications by Biolley are known, beside the one about the molluscs mentioned above, his main works are "Elementos de Historia Natural" from 1887 and "Costa Rica et son avenir" (Costa Rica and its future), published in 1889 in Paris (Fig. 1B).

Telipogon bolleyi (Fig. 1C) was described in 1910 by Rudolf Schlechter in "Feddes Repertorium", the plant was collected in August 1889 in flower by Biolley in forests on the slope of the volcano Barba (no.*1340*) (Schlechter 1910). Schlechter's drawing of the flower was published by Mansfeld in "Feddes Repertorium" in 1931, the type of the species was lost in the fire of the herbarium in Berlin in 1943 (Mansfeld 1931) (Fig. 1D). From the same collection of Biolley a second, unnamed specimen with the same number 1340 is in the United States National Herbarium (Fig. 2A), originally from the herbarium of the Instituto Fisico-Geografico National Costaricensis, selected first by Calaway H. Dodson in 1983 as neotype and again by Robert L. Dressler in 1999 as the lectotype of *Telipogon biolleyi*.

---

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

COSTA RICA

SON AVENIR

Paul BIOLLEY

PARIS

A. GIARD, LIBRAIRE-ÉDITEUR

FIGURE 1. A — Portrait of Pablo Biolley. B — Frontispiece of Biolley's "Costa Rica and son venir", Paris 1889. C — *Telipogon biolleyi*, illustrated by Lothar Braas. D — *Telipogon biolleyi*, from the original sketch by R. Schlechter.

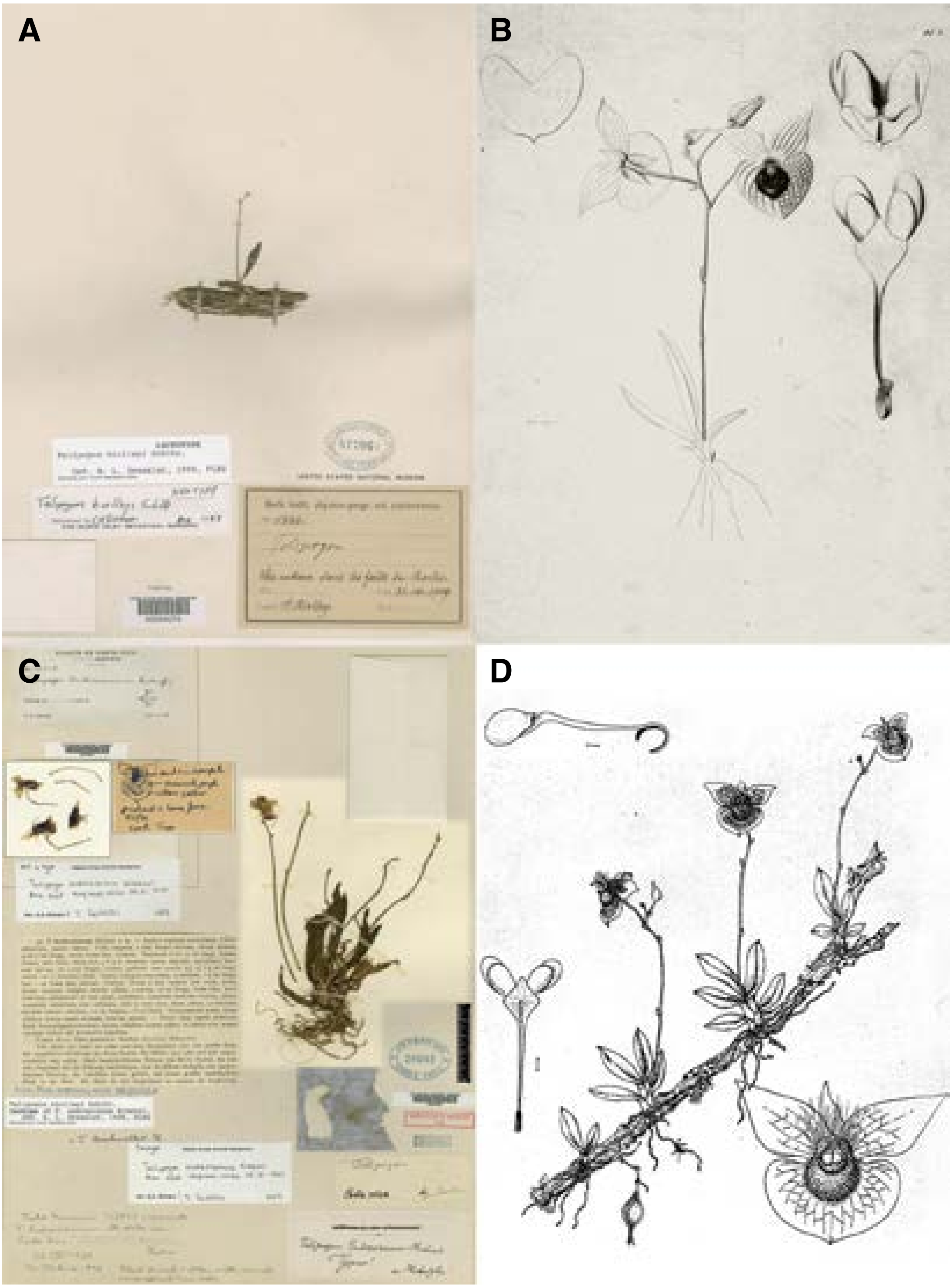


Figure 2. A — Lectotype of *Telipogon biolleyi* (US). B — Drawing of *T. biolleyi* by A. R. Endrés (W-R). C — Isotype of *T. endresianum* (AMES). D — *Telipogon endresianum*, from the Orchid Journal, 1953.

FIGURE 3. *Telipogon biolleyi*. A — habit. B — flower. Photographs by D. Bogarín.

Telipogon endresianum was described by Friedrich Wilhelm Ludwig Kränzlin in 1919 in "Annalen des Naturhistorischen Hofmuseums Wien", Kränzlin dedicated the species to August R. Endrés, his description was based on a perfect drawing and material collected by Endrés (Kränzlin 1919) (Fig. 2B). The type and the drawing are in the herbarium of Reichenbach in Vienna. Kränzlin also mentioned a specimen collected by Huebsch, this specimen is also in Vienna. Another Endrés' specimen, determined as an isotype of *Telipogon endresianum* is in the AMES herbarium at Harvard (Fig. 2C). A detailed drawing of Kränzlin's species was published by Paul H. Allen 1952 in Alex D. Hawkes' "*Orchid Journal*" (Allen 1952) (Fig. 2D). It was Dodson who first stated that *Telipogon endresianum* would be a synonym of the older *Telipogon biolleyi*.

Telipogon biolleyi (Fig. 3A—3B) is one of the most common species of the genus in Central-America. Like most other species it is a fast growing twig-epiphyte. Most species of *Telipogon* are very difficult to keep alive in cultivation for more than 2 or 3 years, this problem is known from many small twig-epiphytes. These plants are producing seeds in their second or third year, the generation-succession is fast and due to the fact that their typical habitat is changing fast, they do not survive long in nature. The only way to keep them for a longer time in culture is artificial pollination and propagation from seed. In nature, species of *Telipogon* are apparently pollinated by pseudocopulation of male Tachinid-flies. The males are attracted by the hairs and bristles around the column of the flowers, perhaps imitating a female fly.

Alberto Manuel Brenes and *Campylocentrum brenesii*

When Rudolf Schlechter published 1923 his "*Beiträge zur Orchideenkunde von Zentralamerika*" in "Feddes Repertorium Beihefte", more than half of the new species he described have been collected by Alberto Manuel Brenes in Costa Rica. Schlechter (1923) dedicated a series of orchid species to Brenes: *Barbosella brenesii, Campylocentrum brenesii,* *Catasetum brenesii, Dichaea brenesii, Elleanthus brenesii, Encyclia brenesii, Epidendrum brenesii, Habenaria brenesii, Lepanthes brenesii, Maxillaria brenesii, Microstylis brenesii, Notylia brenesii, Oncidium brenesii, Pleurothallis brenesii, Ponthieva brenesii, Spiranthes brenesii, Stelis brenesii, and Trichocentrum brenesii.*

At least in part Alberto Manuel Brenes (Fig. 4a—3b) also belongs to the Swiss connection like J.F. Adolphe Tonduz and Henry François Pittier. Brenes was born in San Ramon in Costa Rica on September 2th, 1870. He studied in Costa Rica until 1890, when he left Central America for Europe. He stayed in Paris for a short time and then went to Lausanne in Switzerland where he studied at the university for one year, followed by a time in Geneva where he stayed until 1898, taking botany and natural history courses with Professors Renvier, Dufour, Chodat and Briquet.

During the time when Brenes was in Europe, Henry François Pittier founded the Instituto Fisico-Geografico Costarricense, a government department devoted to the natural sciences, a part of this institute was the Herbario Nacional de Costa Rica and grew under the strong influence of Pittier. When Pittier left Costa Rica in 1903, the herbarium was taken over by the Museo Nacional. Brenes returned to Costa Rica in 1898 and started teaching at the Escuela de Farmacia (School of Pharmacy) in San Jose. In his spare time he collected plants together with Henry François Pittier, Pablo Biolley and J.F.Adolphe Tonduz. For health reasons Brenes left this appointment in 1903 and returned to San Ramon. In this time he worked for a few years at the Colegio de San Luis Gonzaga and changed to the Escuela Normal in 1911. In 1920 he became the head of the section of botany at the Museo Nacional, a position he held until 1935. In 1921 Brenes began a series of collections that would eventually total more than 23'000 numbers of plant specimens. He usually collected in the very rich forests around San Ramon. The vegetation in this area is extremely rich not only in orchid species but also in other plants because it forms a gap between the Cordillera Central and the Cordillera de Tilaran. Moisture-laden winds from the Caribbean plain are forced up to the eastern slope and across this gap, creating areas of cloud forest at unusually low elevations. Before 1924 the primary set of Brenes‘ collections was deposited in Costa Rica, although the unicates of many groups were sent to specialists. Rudolf Schlechter in Berlin received most of Brenes‘ orchid collections during this period. After Schlechter's time most of the orchids have been sent to Oakes Ames at Harvard and to the Field Museum in Chicago. Brenes also made a number of pencil-drawings of the plants he collected, these drawings are kept at the Departemento de Proteccion del Patrimonio Historico, Museo Nacional de Cost Rica. We don't know how many drawings Brenes made, the drawing of *Gongora armeniaca* is carrying the number *115* (Fig. 6d) the one of *Catasetum macrocarpum* the number *272*. Seven of them have been printed in the biography of Brenes by Alberto H. Salazar Rodríguez in 2009.

Rudolf Schlechter received trough Tonduz several collections of orchids from Costa Rica, including some specimens collected originally by Brenes. It was Tonduz who told Schlechter to get in direct contact with Brenes. Schlechter wrote 1919 to Brenes, asking him about the possibility to collect orchids for the planned orchid flora of Costa Rica. 1922 Schlechter received a very large collection of specimens from Brenes, the collection was extremely rich in small species from the subtribe Pleurothallidinae and Schlechter decided to publish 1923 the results in an own treatment under the title "*Orchidaceae Brenesianae*". All species named after Brenes and also the genus *Brenesia* have been published in this article in "Feddes Repertorium Beihefte". Schlechter's herbarium in Berlin was destroyed during the war in 1943 and all the specimens collected by Brenes were lost. Fortunately Oakes Ames was interested in Schlechter's Central American Orchidaceae and so he paid first an artist and later on Schlechter's wife Alexandra to make drawings of this material for his own herbarium So at least a larger part of Schlechter's collection from Costa Rica survived in form of drawings.

Brenes died in San Ramon in 18. May 1948. Still his name is present in Costa Rica, the journal "Brenesia", published by the Departemento de Historia Natural, Museo Nacional de Costa Rica is named after him, the first number was published in 1972. In the seventies a stamp with *Brenesia costaricensis* was issued by Costa Rica, in the same series with some other Orchids also a

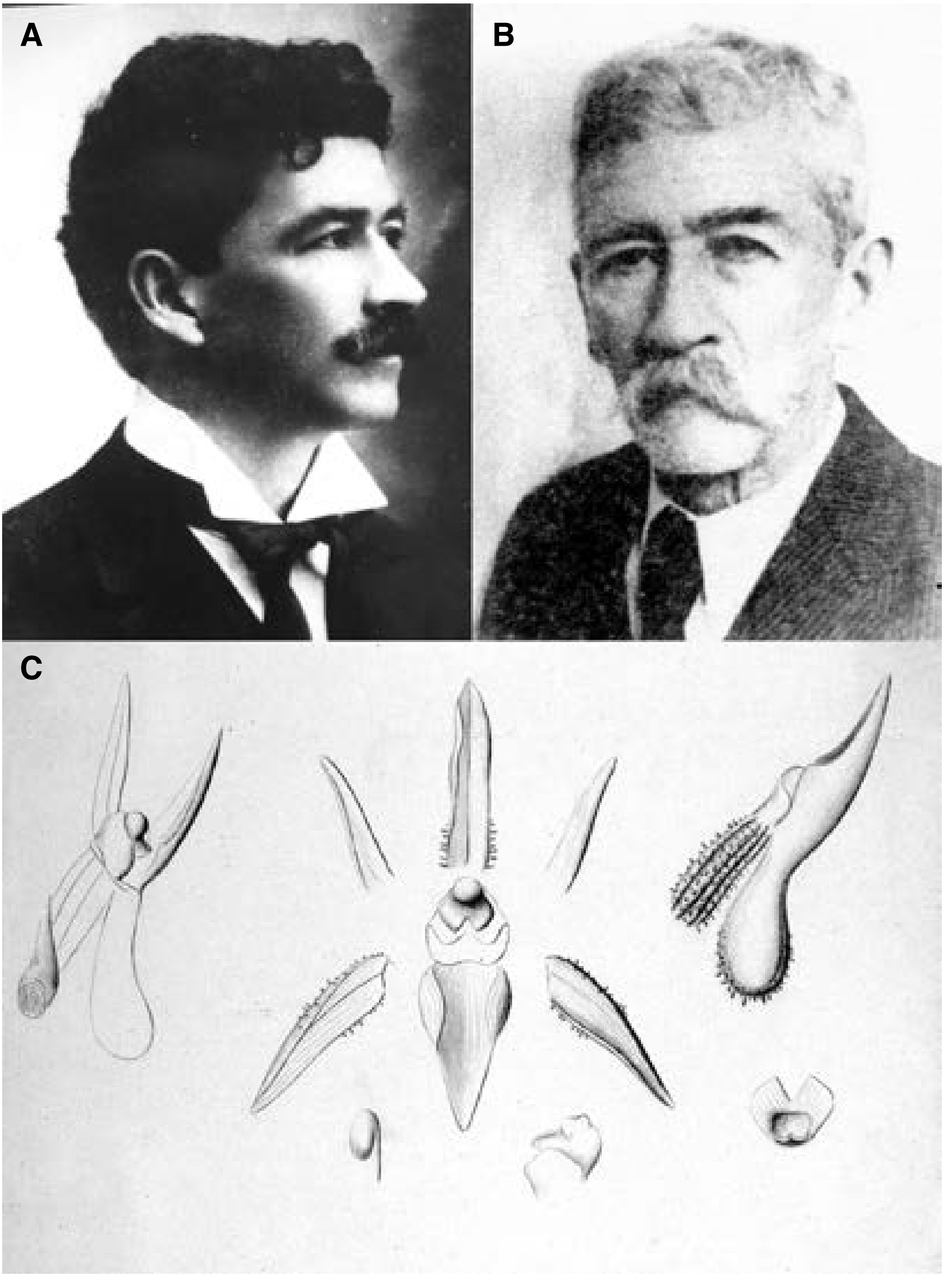


Figure 4. A, B — Two portraits of Alberto Manuel Brenes. C — Drawing of *Campylocentrum brenesii* by A. R. Endrés (W-R), from Bogarín & Pupulin 2010.

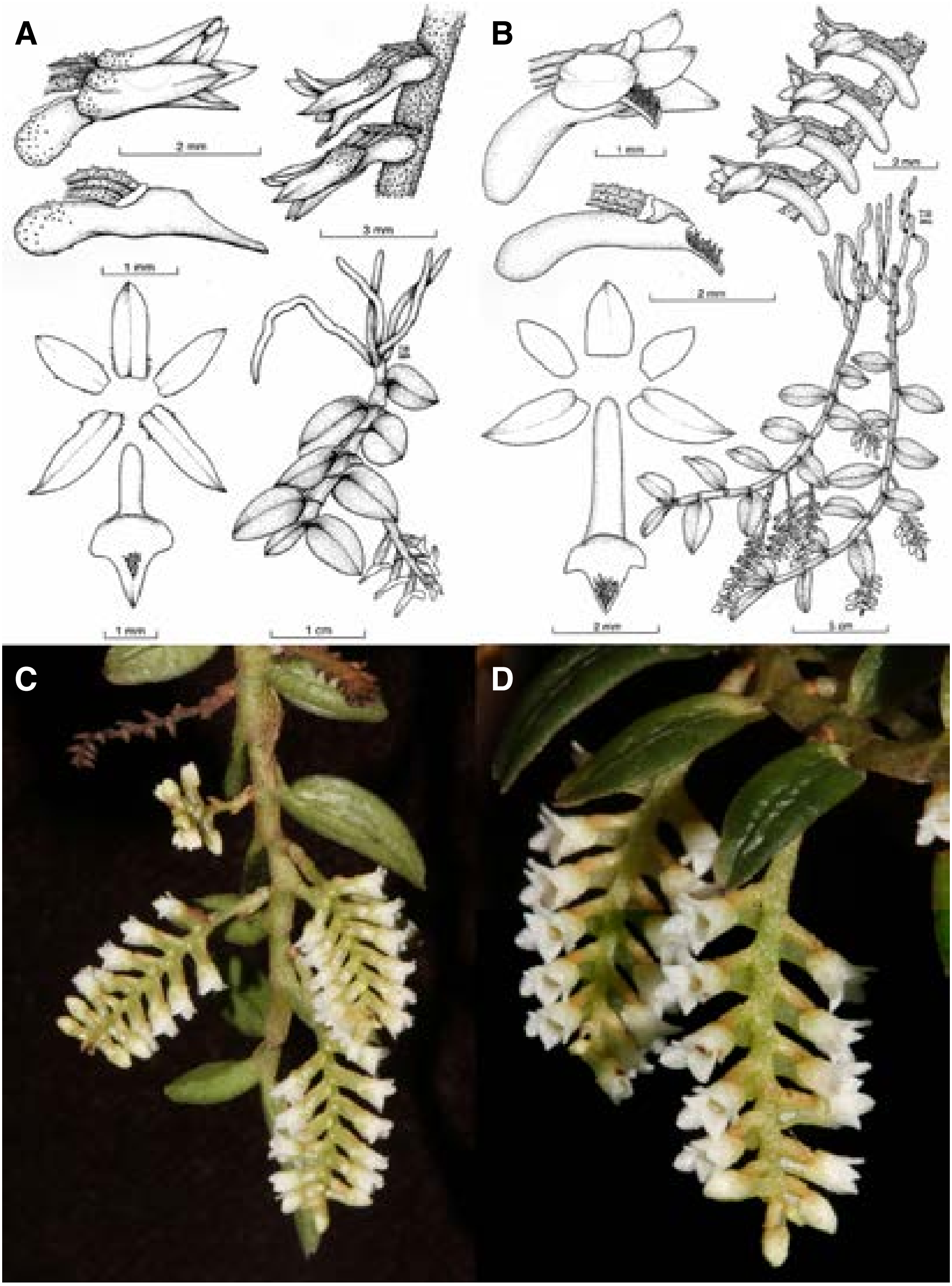


FIGURE 5. A, B — Two modern illustrations of *Campylocentrum brenesii* by D. Bogarín (from Bogarín & Pupulin 2010). C, D — Inflorescences of *Campylocentrum brenesii*.

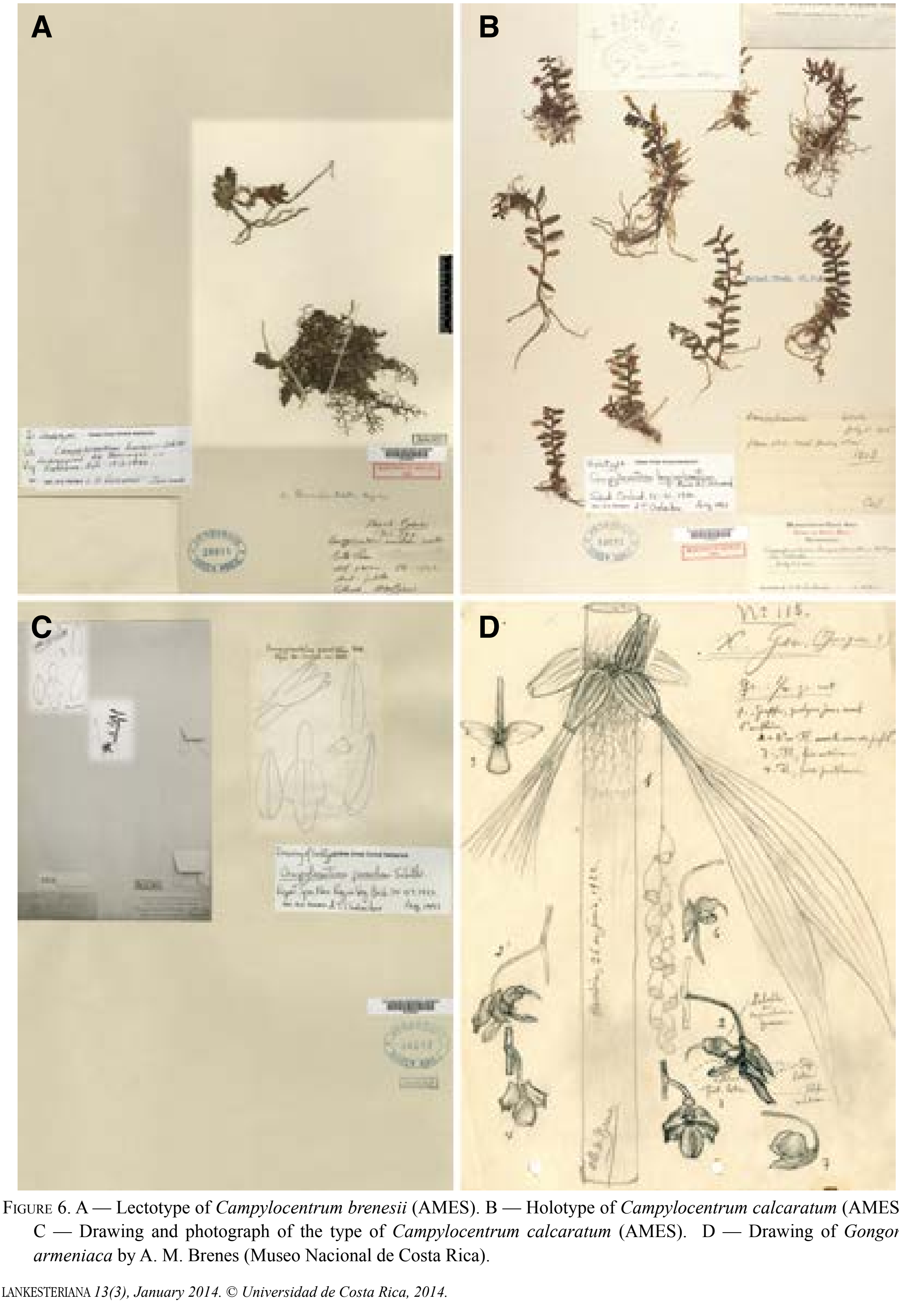


FIGURE 6. A — Lectotype of *Campylocentrum brenesii* (AMES). B — Holotype of *Campylocentrum calcaratum* (AMES). C — Drawing and photograph of the type of *Campylocentrum calcaratum* (AMES). D — Drawing of *Gongora armeniaca* by A. M. Brenes (Museo Nacional de Costa Rica).

stamp with a portrait of Brenes was included.

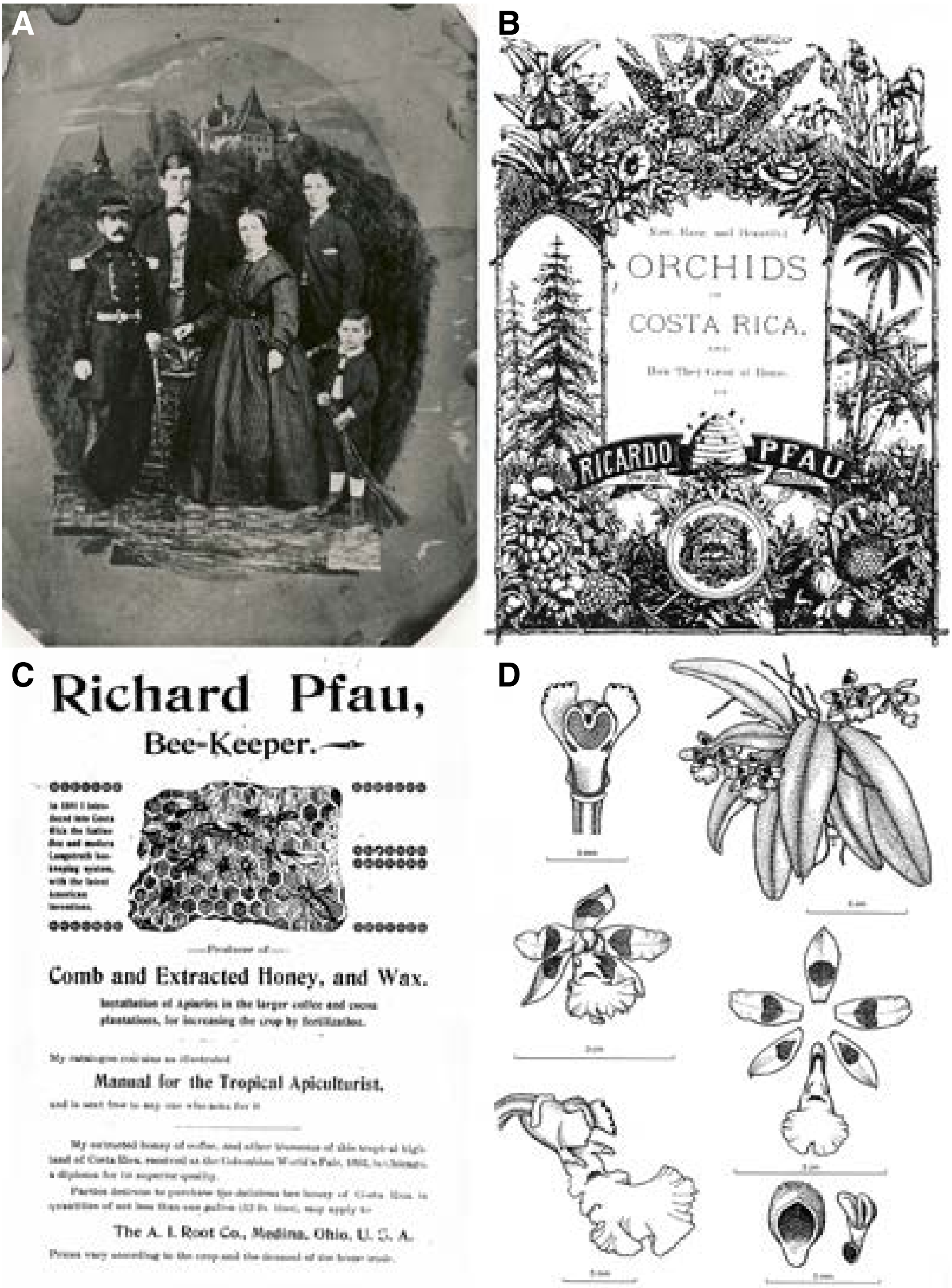
The genus *Campylocentrum* was mentioned the first time by George Bentham in 1881 in “Journal of the Linnean Society”. The genus belongs in fact to the Angraecinae and includes about 60 species distributed from Mexico to Brazil and Bolivia and in the West Indies. *Campylocentrum* is a sister genus of *Dendrophylax* and includes both leafy and leafless species. The genus *Todaroa*, described in 1844 in “Comptes Rendus Hebdomadaires des Seances de l’Academie des Sciences” by Achille Richard and Henri Galeotti[1], is today considered as synonym of *Campylocentrum*. Richard and Galeotti were not aware that the generic name *Todaroa* was already used for a genus of the Umbelliferae by Parlatore in 1844. Although Bentham agreed with the concept of *Todaroa* he could not use this name and proposed instead *Campylocentrum* as generic name (Bentham 1881). *Campylocentrum brenesii* was described by Rudolf Schlechter in 1923 in “Beiträge zur Orchideenkunde von Zentralamerika” in “Feddes Repertorium Beihefte” (Schlechter 1923). The plant Schlechter used as type was collected in 1921 by Brenes at San Pedro de San Ramon, Alajuela, Costa Rica. Schlechter’s herbarium in Berlin was destroyed in 1943 and the type-specimen of *Campylocentrum brenesii* was lost (Fig. 6c). Another specimen of the species, also collected by Brenes in September 1921 in Costa Rica was selected by Barringer in 1984 in “Fieldiana Botany” as the lectotype (Barringer 1984) (Fig. 6a). Another specimen of the species was collected by A.R. Endrés in the second half of the 19th century. The specimen remained undescribed in the herbarium of Heinrich Gustav Reichenbach in Vienna, together with two very accurate pencil-drawings by Endrés (Fig. 4c). Brenes collected the species again between 1925 and 1927 in the area of La Palma de San Ramón and at La Paz de San Ramón. Following the most recent revision of the genus *Campylocentrum* in Costa Rica, published by Diego Bogarín and Franco Pupulin in “Harvard Papers in Botany” from 2010, *Campylocentrum longicalcaratum* Ames & Ch.Schweinfurth (Fig. 6b) is a synonym of *Campylocentrum brenesii* (Fig. 5a–5d). The plant was collected in July 1925 by Charles H. Lankester near La Estrella, Costa Rica, and was described by Oakes Ames and Charles Schweinfurth in 1930 in “Schedulae Orchidianae”. Also *Campylocentrum parvulum* is defined as synonym of *Campylocentrum brenesii*., the species was described by Schlechter 1923 in “Feddes Repertorium Beihefte” after a collection by the brothers Alexander Curt Brade and Alfred Brade near La Palma, Costa Rica, in 1400 m altitude.

Richard (Ricardo) Pfau and *Trichocentrum pfavii*

We have only little information and details about the life of Richard (Ricardo) Pfau. The family Pfau (Fig. 7a) was very famous in Winterthur near Zurich in Switzerland, 5 generations of Pfau’s lived there, they where stove setters and stoves from their business where distributed all over Switzerland and southern Germany. Some members of the family where also active in politics and became members of the town council. Ricardo’s father Matthäus Pfau (13.1.1820 – 27.7.1877) was merchant, officer, banker and politician in Winterthur, and was in 1862 one of the 13 founding members of the precursor of the bank which should become 150 years later the largest bank in Switzerland. In 1865 Matthäus had to retire for health reasons. He bought the Kyburg-Castle and used his fortune to open 1866 the first museum in a historical castle in Switzerland. He moved with family and his art-collection to the Kyburg. Ricardo was the youngest of the three sons of Matthäus Pfau, born in 1856 and grown up at least in part in the Kyburg. The elder brothers where Jakob Pfau (born 1846) who became architect and later Professor at the Technikum in Winterthur, and Eduard (born 1851) who became merchant in Milan, Italy. Ricardo seems to have been the “black sheep of the family”. In 1887 he tried to publish a novel and asked Gottfried Keller, famous author in Zurich, for an expertise. However, the result was not as good as expected, the novel was never published. When Robert Keller, botanist and high school teacher in Winterthur, published in

---

[1] Index Kewensis is defining Richard and Galeotti’s publication in “Annales des Sciences Naturelles (ser.3,3:28.1845)” as the valid first description of *Todaroa*, but the publication in “Comptes Rendus Hebdomadaires des Seances de l’Academie desSciences” is one year older. If the first description of the genus *Clynhymenia* in the same publication of 1844 is accepted as valid, the same must be true for *Todaroa*.



Richard Pfau,

Bee-Keeper.

Comb and Extracted Honey, and Wax.

Manual for the Tropical Apiculturist.

The A. I. Root Co., Medina, Ohio, U. S. A.

FIGURE 7. A — The family Pfau; Richard is the boy with a gunon the right. B — Catalogue of Pfau's nursery in Costa Rica, *ca*. 1895. C — Pfau's illustrated manual for the tropical apiculturist (1895). D — Modern illustration of *Trichocentrum pfavii*, from Pupulin 1997.

1891 his “*Flora von Winterthur*” he mentioned in the introduction also a small collection of plants given to him by his friend Richard Pfau. Obviously Richard had collected plants around the Kyburg.

We don’t know when Richard left Europe for Costa Rica the first time but it seems to be around the year 1880. Following some of the articles he published in 1883 and 1884 in “Gardeners’ Chronicle” he already had been in Costa Rica but not permanently, he also cultivated Orchids and lived in Chiswick, England. Remarks in the publications like: “…but on experience in my own culture of Orchids in Chiswick, which I began only a few months ago” (Pfau 1883a), “….I discovered this species last year in a locality difficult to get at” (Pfau 1883b) and “….in my houses at Chiswick they seemed to do best in baskets” (Pfau 1883c). In Kew there is a business-card from Pfau, written in 1895 or 1896 with the following note: “Richard Pfau who thanks to the presentation of the Consul General of Switzerland has had the honor of paying Sir Joseph Hooker a visit 2 years ago before starting for Central-America, begs the favour an interview to show him some new plants he has found”. Obviously Richard made several trips to Costa Rica when he lived in England and sometime around 1885 he settled in San Jose, Costa Rica. He returned for a visit in 1893 and again 1896. In “Gardeners’ Chronicle” we find a note that Richard succeeded to bring in 1896 a small number of *Epidendrum endresii* and *Miltonia endresii* alive to England. Richard founded a nursery in San Jose in Costa Rica, he published – most probably in 1895 – a catalogue of Orchids he had for sale and export (Fig. 7B). In the catalogue he also gave advice about the cultivation and exportation of Orchids and he made comments like: “*Cattleya skinneri*, some ten years ago, was a common orchid all over Central America; but in the last few years it has been exported by shiploads; and today – at least in Costa Rica – it has almost become rare”. He sent plants to Europe and sold them like other collectors – e.g. Benedict Roezl and Gustav Wallis – through Eduard Ortgies from the Botanical Garden in Zurich. Richard also had an apiary in his nursery, he wrote: “In 1893 I introduced into Costa Rica the Italian Bee and modern Langstroth bee-keeping system, with the latest American inventions”, he sold the honey via a company in Medina, Ohio, USA and offered on demand “an illustrated manual for the tropical apiculturist” (Fig. 7C). Although Richard was as collector mainly active in Costa Rica it is – based on the plants he sent to Europe – probable that he also collected in Colombia, Panama and even Mexico. Richard Pfau died with 41 years on 14th of March 1897.

A few orchids carry his name as epithet (species name), but interestingly all are written as *pfavii* and not as *pfauii*. In the Latin alphabet the letter U is written as V, most probably this was the reason for Rolfe, Reichenbach and Schlechter to write *pfavii*.

Trichocentrum pfavii (Fig. 7D, 8C) was described by Reichenbach in “Gardeners’ Chronicle” in 1881 based on material collected 1880 by Pfau in Chiriqui, Costa Rica. Reichenbach got living material, dried specimens and a sketch, the type specimen in the herbarium of Reichenbach (no. 42179) includes two drawings of the species by Reichenbach himself and a few dried flowers (Fig. 7A).

Trichocentrum pfavii var. *zonale* (Fig. 8D), described in 1883 by Reichenbach in “Gardeners’ Chronicle” is a synonym of *Trichocentrum pfavii* (Reichenbach 1883). The commentary of Reichenbach is interesting: “Mr. Pfau appears to be an excellent correspondent and collector, but his *Trichocentrum* is an abdominable plant, quite a *crux Orchidologorum*. It defies all laws, and is polymorphous in the shape of the flowers and nature of the lip.” He had got a fresh inflorescence from Veitch and continued: “A fresh inflorescence just sent by Mr. Harry Veitch proves this once more. An unpublished species with much larger flowers and tomentose teeth at the base of the lip, turns out as belonging to this species, though it looked widely distinct. I would not quote this name, *Trichocentrum zonale*, were it not engraved on an unpublished lithographic plate belonging to one of my unpublished pamphlets. I can only regard it now as a variety”.

Trichocentrum pfavii subsp. *dotae* (Fig. 9A, 9B, 9D) was described by Franco Pupulin in 2001 in “Selbyana” (Pupulin, 2001). The plant was collected in April 1999 by A. Flores (San José, Dota, Santa María, road to San Joaquín) and flowered at Gaia Botanical Garden in 1999, the type specimen is at the herbarium of the Escuela de Biologia, Universidad de Costa Rica (USJ) (Fig. 9B). In the same publication Pupulin

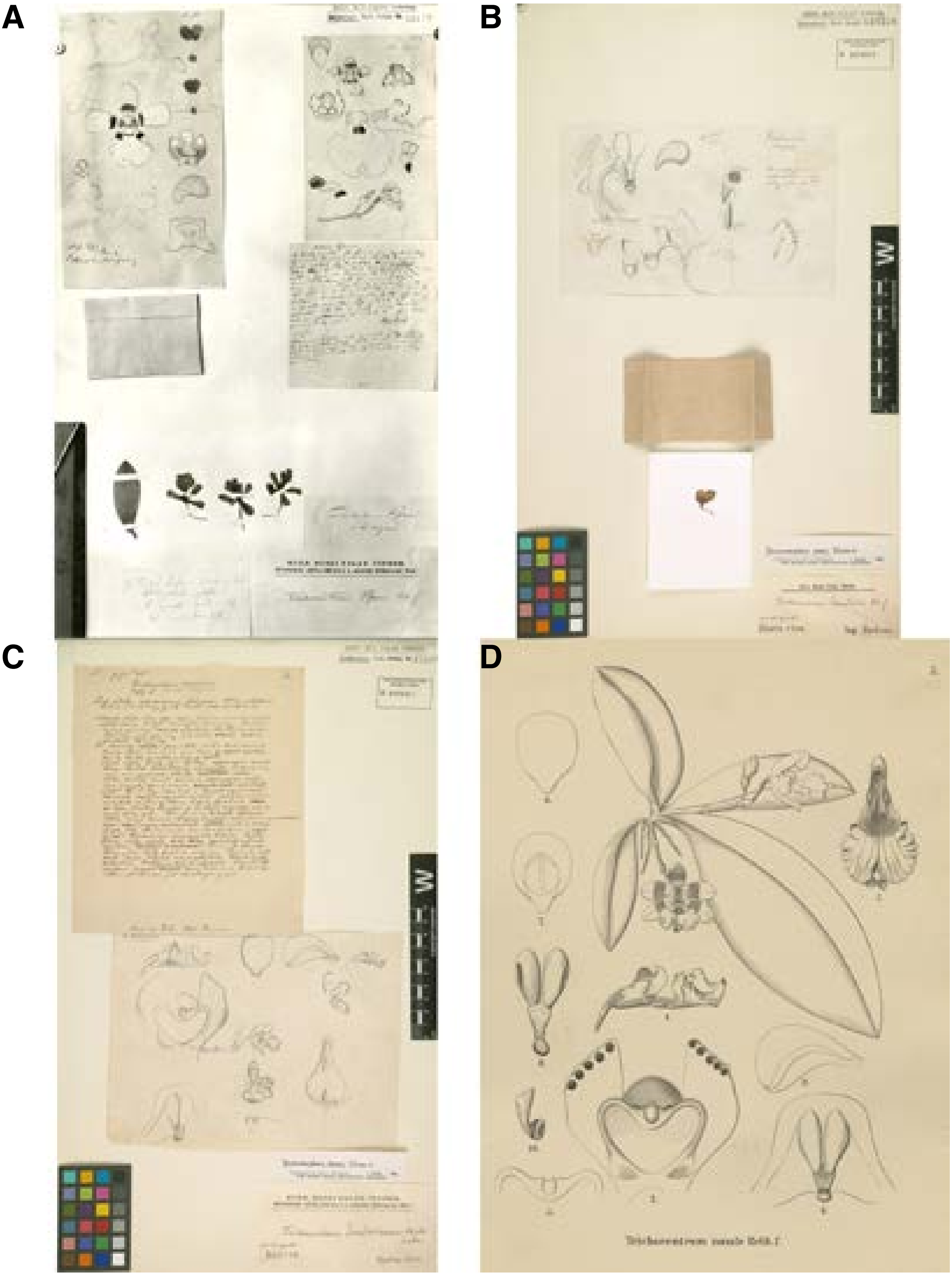


FIGURE 8. A — The holotype of *Trichocentrum pfavii* at W–R. B, C — Endrés sketches of the species he intended to describe as *Trichocentrum saundersii* (W-R). D — Unpublished plate of *Trichocentrum zonale*, from Reichenbach's *Xenia Orchidacea.*

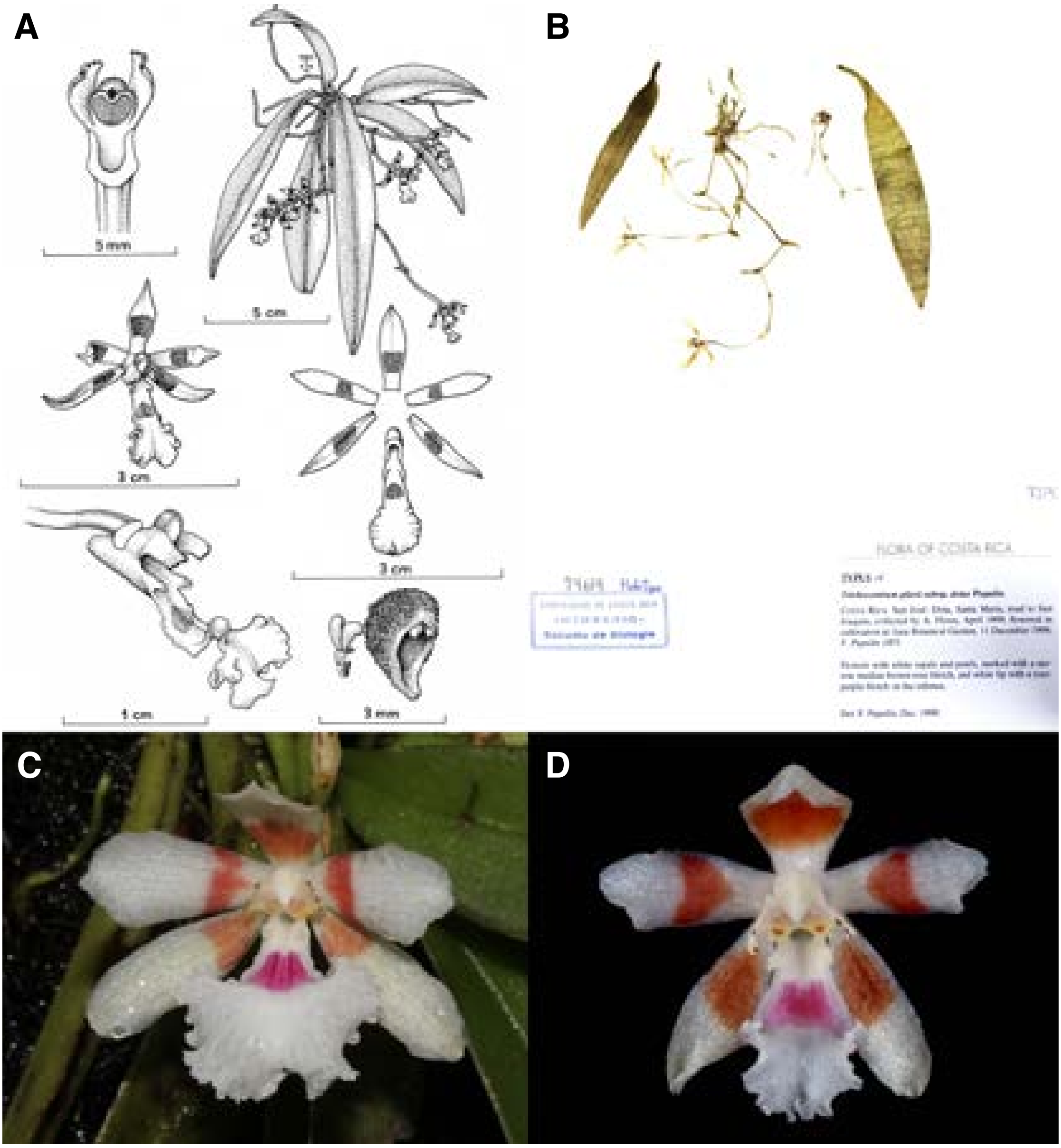


Figure 9. A, B — *Trichocentrum pfavii* subsp. *dotae*. Original illustration by F. Pupulin (2000), and the holotype in the Herbarium of the University of Costa Rica (USJ). C — *Trichocentrum pfavii*. D — *Trichocentrum pfavii* subsp. *dotae* (photographs by F. Pupulin).

created a section *Lobulatae* for the group of species around *Trichocentrum pfavii*.

Trichocentrum saundersianum and *Trichocentrum saundersii* are names on several sheets in the Reichenbach herbarium, the material was collected and illustrated by Endrés (Fig. 8B, 8C), but never validly published; it belongs to *Trichocentrum pfavii*.

Henry François Pittier and *Oncidium pittieri*

Henry François Pittier (Fig. 10A-10D) also came from Switzerland. He was born in Bex, Canton Waadt, on 13th of August 1857. He graduated as a civil engineer from the University of Lausanne. After the years at the university he started a map survey of the alpine flora of Switzerland. An accident ended with a broken leg and in the following period, immobilized by the accident, Pittier started to read intensively about natural sciences. He got into contact with the work of Haeckel and was so fascinated by Haeckel's ideas that he decided to go to Jena,and a short time later started doctoral studies at the University of Jena in Germany. The information about the academic titles of Pittier are not consistent; following Tobias Lasser, Pittier had a doctorate in philosophy from Jena and from Lausanne a doctorate of science. Following John D. Dwyer, he never finished his studies and remained a bachelor. Following his interests in the tropics, Pittier immigrated in October 1887 to Costa Rica[2], and never should come back to Switzerland. From 1887 to 1903 he organized and directed the Physico-Geographical Institute of Costa Rica, one of the objectives was to make a map survey of the republic of Costa Rica. It was there that Pittier met Adolphe Tonduz for the first time. Pittier was also involved in the organisation of a National Herbarium in San Jose. Between 1887 and 1904 Pittier collected in Costa Rica, often together with Adolphe Tonduz. One result of those collections was the "*Primitiae Florae Costaricensis*", which he published in three volumes between 1891 and 1901 in collaboration with Theodore Durand from the Botanical Garden in Brussels.

In 1904 Pittier went to Washington D.C. to work for the United States Department of Agriculture under the very promising title "Special agent in botanical investigation in tropical agriculture in the Bureau of plant industry". The title was changed to Botanist in 1912. Between 1905 and 1919 he worked in Washington in his office and travelled extensively in Central and South America, he collected in Panama, Mexico, Guatemala, El Salvador, Colombia and in Venezuela. Pittier's collections in Panama have been very important for the Flora of Panama.

At the age of 62 he left Washington and went to Venezuela as director of the Commercial Museum in Caracas. Again and in spite of his age he travelled extensively in Venezuela and published the famous "Manual de las Plantas usuales de Venezuela" in 1926 and its first supplement in 1939. Pittier also founded the National Herbarium in Caracas and published some 300 books and articles in different journals. He died in Venezuela at the age of 93 in 1950.[3] There are still discussions about the final number of plants collected by Pittier, but without any doubt he made a very important contribution to the knowledge of the floras especially of Panama, Costa Rica and Venezuela. Several orchids are dedicated to this important botanist, mainly by Rudolf Schlechter in Berlin, who got Pittier's orchids for identification. Some of them are *Oncidium pittieri* Schltr., *Maxillaria pittieri* Schltr., *Scaphosepalum pittieri* Schltr., *Pleurothallis pittieri* Schltr., *Lockhartia pittieri* Schltr., *Vanilla pittieri* Schltr., and *Epidendrum pittieri* Ames

Unfortunately most of Pittier's orchids have been destroyed during the second world war in Berlin, together with almost the entire herbarium of Schlechter. Some of the species have been illustrated in 1931 in "Feddes Repertorium", based on the original drawings of Schlechter and published by Rudolf Mansfeld.

Oncidium pittieri was described by Rudolf Schlechter in 1910 in "Feddes Repertorium" (Schlechter 1910). The plant was collected by Pittier near La Palma in Costa Rica in September 1896. The type specimen was destroyed in 1943 but a copy of it is still in the AMES herbarium (Fig. 10A). The flower

---

[2] Pittier come to Costa Rica hired by the government. See Ossenbach 2009: "However, the last two decades of the century showed for the first time the development of a 'national science' in Central America. In Costa Rica, "as part of an educational reform aimed at secularizing public education, the government of president Bernardo Soto (1885-1889) hired a group of European academics to staff the two new public high schools in the capital, San José (The 'Liceo de Costa Rica' for boys and the 'Colegio Superior de Señoritas' for girls, both founded under Soto's administration). The arrival of these academics marks the beginning of a small scientific renaissance in Costa Rica. Two institutions symbolize this renaissance: the Instituto Físico-Geográfico (IFG) (= *'Physical-Geographical Institute'*) and the National Museum, founded in 1887 and 1889, respectively." Among the hired teachers were Pablo Biolley (1861-1908) and Henri Francois Pittier (1857-1950), who arrived in 1886 and 1887.

[3] Henri Pittier National Park is the oldest national park in Venezuela, originally created in 1937 under the name of *Rancho Grande* by decree of President Eleazar López Contreras. The park was renamed in 1953 with the name of Henri Pittier, who arrived in Venezuela in 1917, classified more than 30,000 plants in the country and devoted many years studying the flora and fauna in the park.

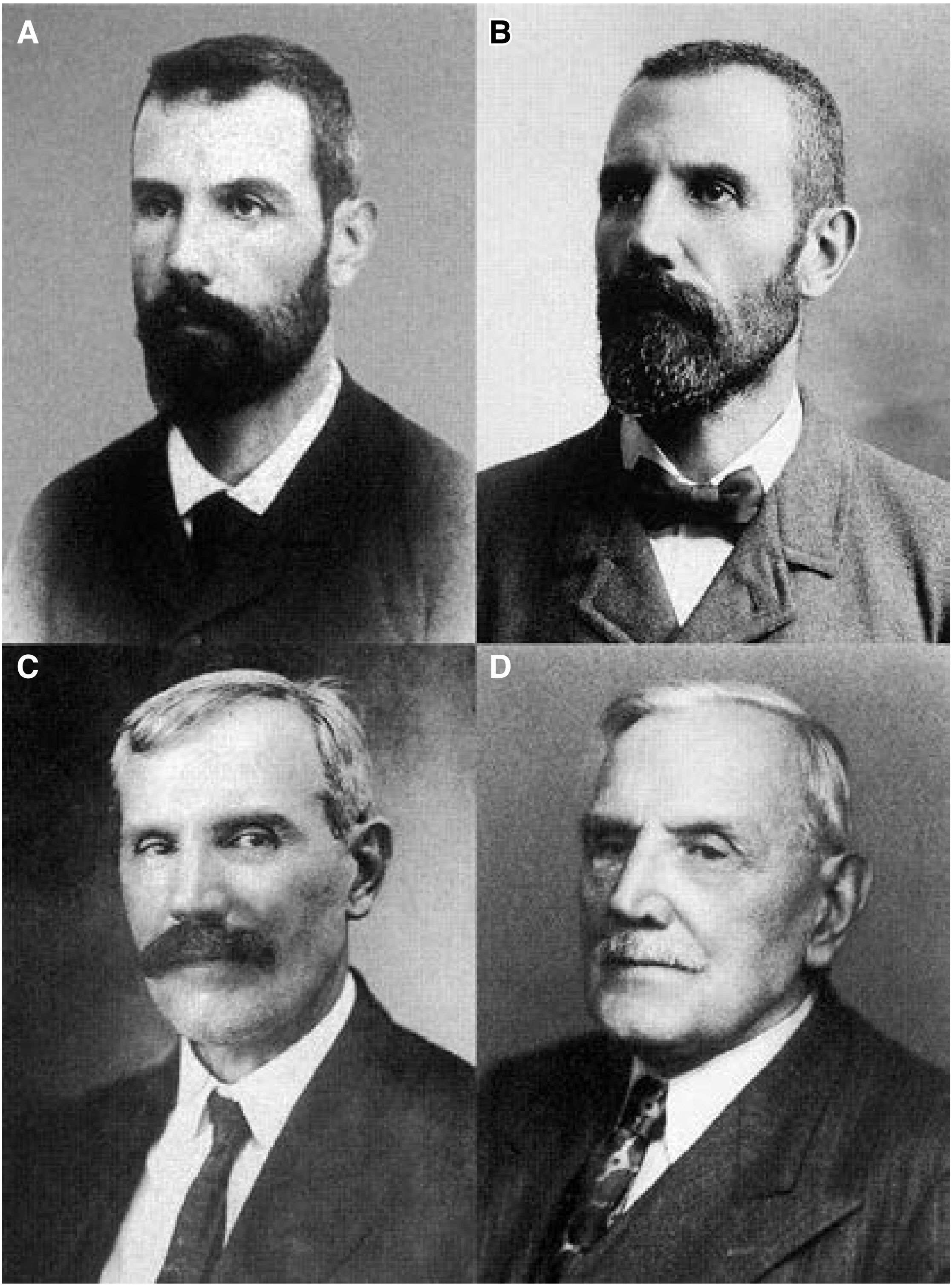


Figure 10. Portraits of Henry Francois Pittier. A — In 1880. B — In 1903. C — In 1914. D — In 1946.

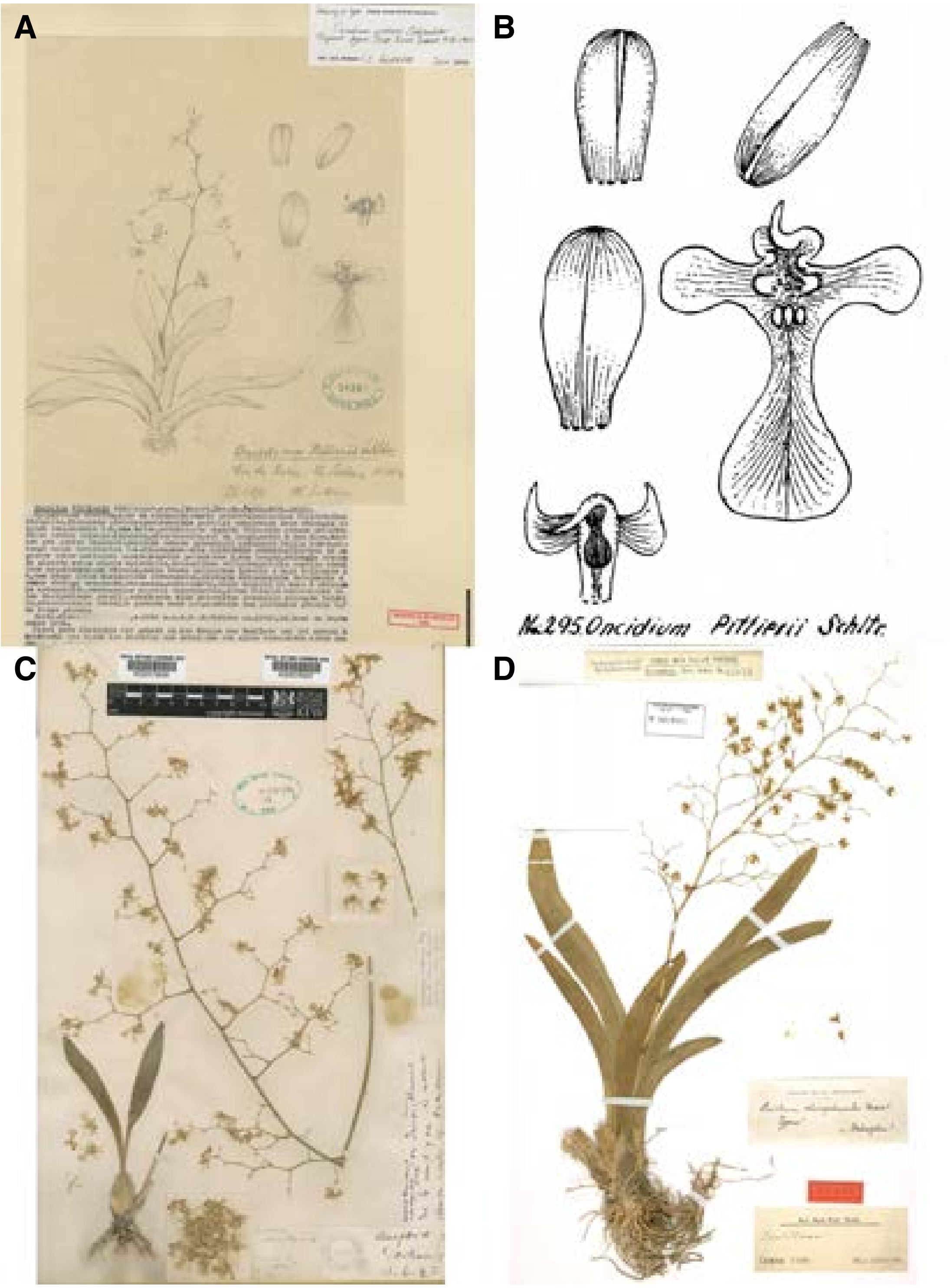


Figure 11. A — *Oncidium pittieri*, copy of Schlechter's drawing of the holotype. B — *O. pittieri*, Schlechter's sketch of the flower, published by Mansfeld (1931). C — Type of *Oncidium luteum* (K). D — Type of *Oncidium cheirophoroides* (W).

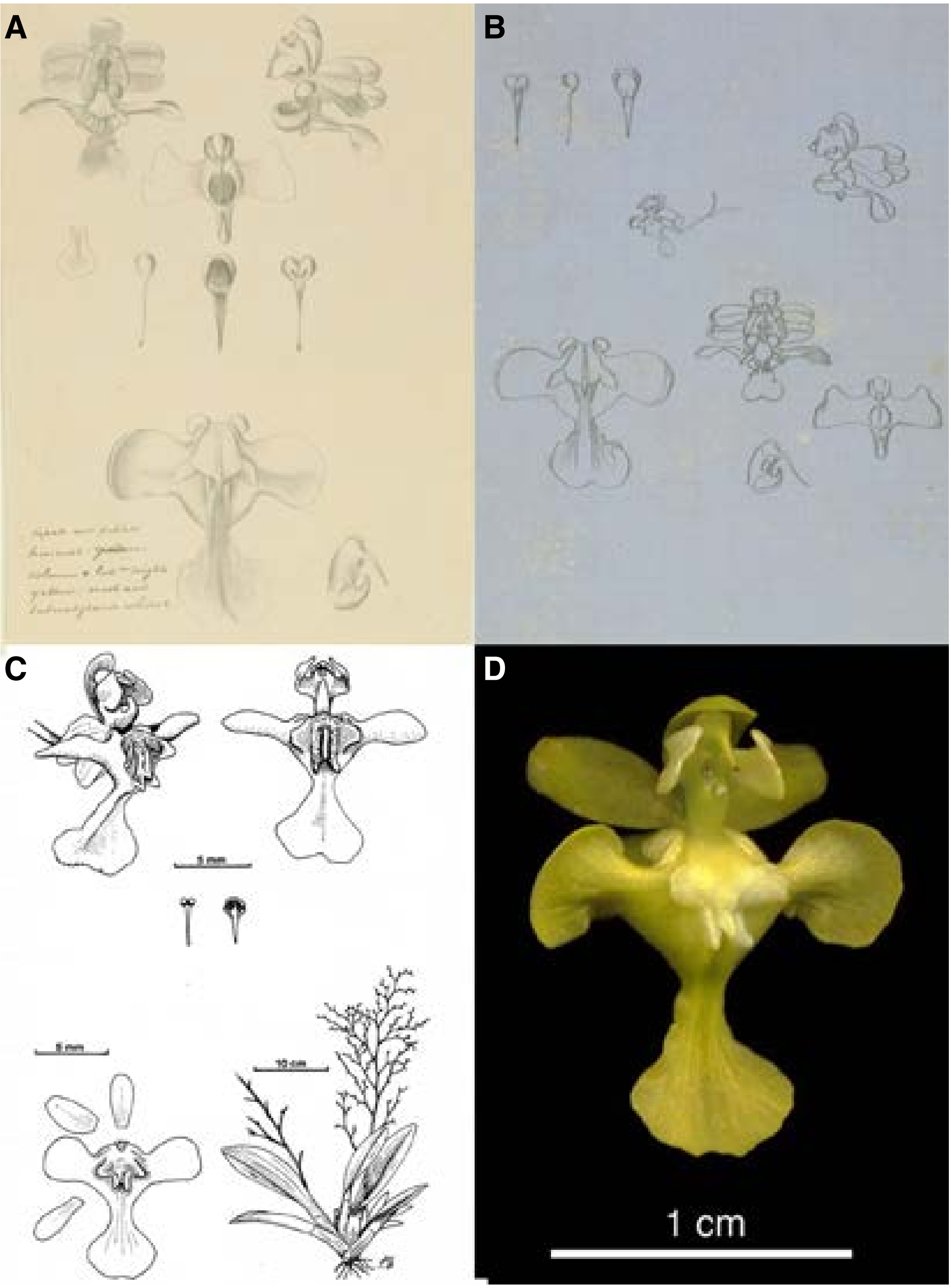


FIGURE 12. *Oncidium luteum.* A, B — Sketches by A. R. Endrés (W–R). C — Illustration from Icones Plantarum Tropicarum (pl. 1572). D — Photograh of the flower, by D. Bogarín..

dissection on this drawing is exactly the same as published by Mansfeld in 1931 (Fig. 11b) in "Feddes Repertorium Beihefte" (Mansfeld 1931). Obviously Schlechter was not aware of the existence of *Oncidium luteum*, described by Robert Allen Rolfe in 1893 in "Bulletin of Miscellaneous Information" (Rolfe 1893a). Rolfe's description was based on a plant cultivated in the collection of Trevor Lawrence in Burford Lodge and sent in summer 1892 to Kew for determination (Fig. 11c). It is not known from where Lawrence had the plant. Following descriptions, drawings and type-material, it is clear that – unfortunately – *Oncidium pittieri* has to be declared as synonym of the older *Oncidium luteum* (Fig. 12d, 12d).

Oncidium cheirophoroides is another synonym of *Oncidium luteum*, it was described by Friedrich Kränzlin in "Das Pflanzenreich" in 1922 (Kränzlin 1922). The material Kränzlin used was collected in Costa Rica by Endrés, the type specimen is in the herbarium of Reichenbach in Vienna (no.45055) (Fig. 11d). Two drawings by Endrés of an un-named *Oncidium* in the Reichenbach herbarium (no.33448 and 33732) (Fig. 12a, 12b) are showing also *Oncidium luteum* (determinated by Dressler in 2001).

Jean François Adolphe (Adolfo) Tonduz and *Masdevallia tonduzii*

Jean François Adolphe Tonduz (Fig. 13a, 13b) was born as the youngest of 7 children of Paul Gustave Tonduz on 18 September 1862 in Pully, Canton of Waadt, Switzerland. Between 1876 and 1881 he studied at the Technical School in Lausanne, after this he started to study medicine at the University of Lausanne from 1881 to 1885. During this time he got into contact with botany, and influenced by two of his teachers, J.B. Schnetzler and L. Favrat, he got more and more interested in natural history and especially botany. This was the reason why in 1885 he moved as Conservator to the Botanical Museum of the Botanical Institute of the same University in Lausanne. In 1889 William Barbey offered him to become Conservator at the Herbarium Boissier in Geneva, and it was Boissier himself who helped Tonduz in the same year to get an employment from the government of Costa Rica to study coffee-diseases. In May 1889 Tonduz left Geneva and arrived in Costa Rica on June 17th. A short time after his arrival he got into contact with Henry Francois Pittier de Fabrega, another Swiss active as botanist in Costa Rica. Soon they became good friends and together they travelled between 1889 and 1903 through Costa Rica. In 1889 Tonduz became collector for the Instituto Fisico-Geografica Nacional, founded by Pittier. Both collected some 20'000 specimens. Most of the herbarium specimens have been distributed by T. Durand, director of the Botanical Garden in Brussels, to different institutes. Almost complete sets are kept at the Conservatoire Jardin Botanique in Geneva and at the Smithsonian Institution in Washington. Between 1903 and 1920 Tonduz was employed at the Costa Rican Museo Nacional. In 1920 he went to Guatemala and worked there as plant pathologist for the Agricultural Service. He died in Guatemala on 20th of December 1921 at the age of 60. In one of his biographies his life is described as very eventful, changing from poorness to times of no financial problems, he himself is described as cultivated, generous and friendly. When Tonduz was not travelling he lived in San Francisco de Guadalupe,[4] where a road is named after him.

The last orchid collection from Tonduz reached Rudolf Schlechter in Berlin in 1921. After the war Rudolf Schlechter tried to find contact to collectors in Central America in order to finish his orchid flora of Central America. He got positive answers from several people, among them Don José C. Zeledón and his wife Doña Amparo de Zeledón in Costa Rica. Doña Amparo owned a large collection of orchids, mainly from Costa Rica and she allowed Tonduz and also Wercklé to select interesting material from her collection, she herself also paid Wercklé for his work. The genus *Amparoa*, *Habenaria amparoana, Sobralia amparoana* and *Gongora amparoana* are dedicated to her. Most of the species described by Schlechter in his article *Orchidaceae Amparoanae* in "Feddes Repertorium Beihefte" (Schlechter 1923) had been sent to him by Tonduz and were from plants from Doña Amparo's collection. Together with his own material, Tonduz sent a few plants collected by Alberto M. Brenes and helped Schlechter to get into direct contact with Brenes. During his time in Costa Rica, Tonduz kept the contact to the Botanical Garden

---

[5] Popular name in Costa Rica for a small grocery store.

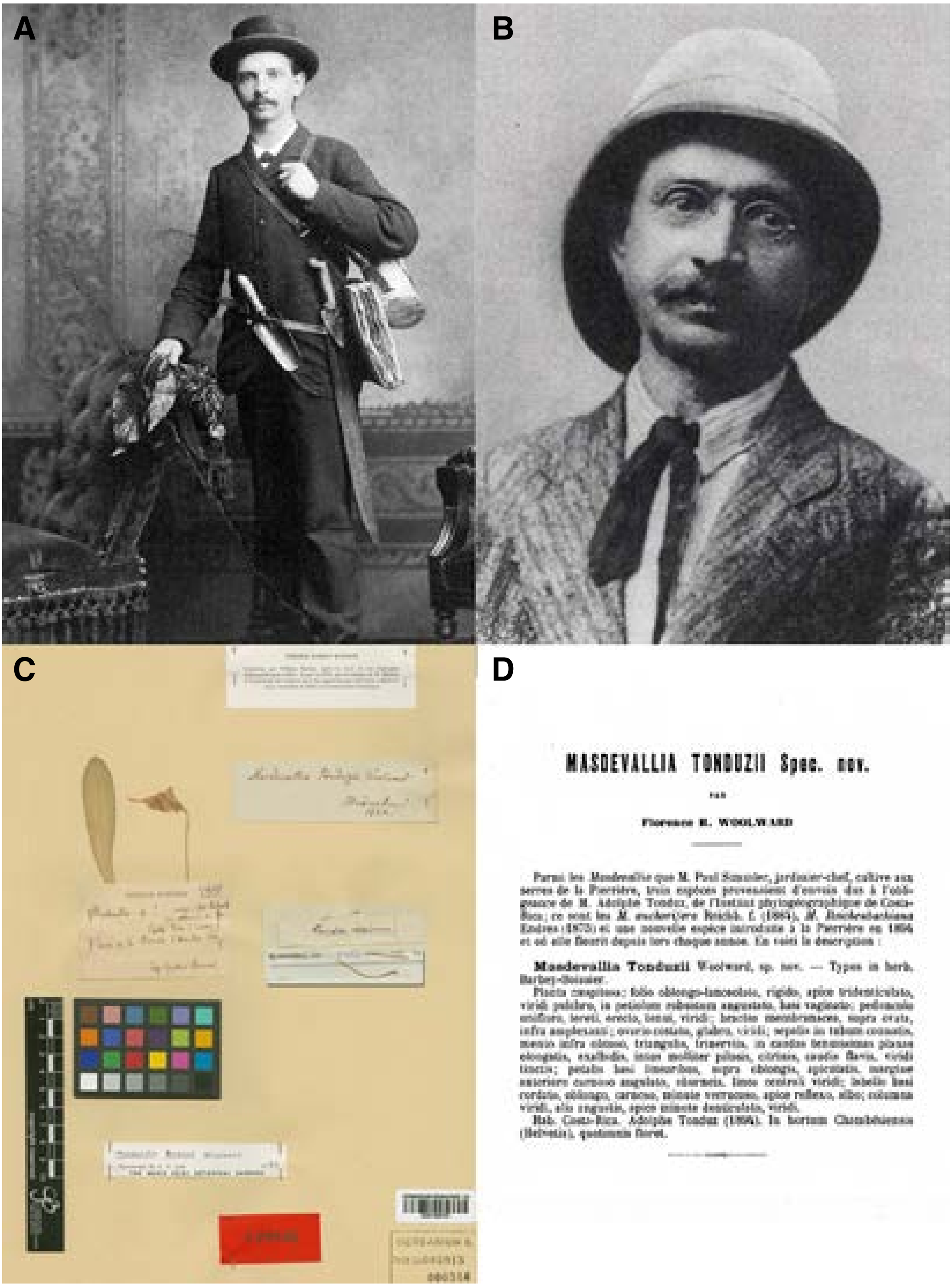
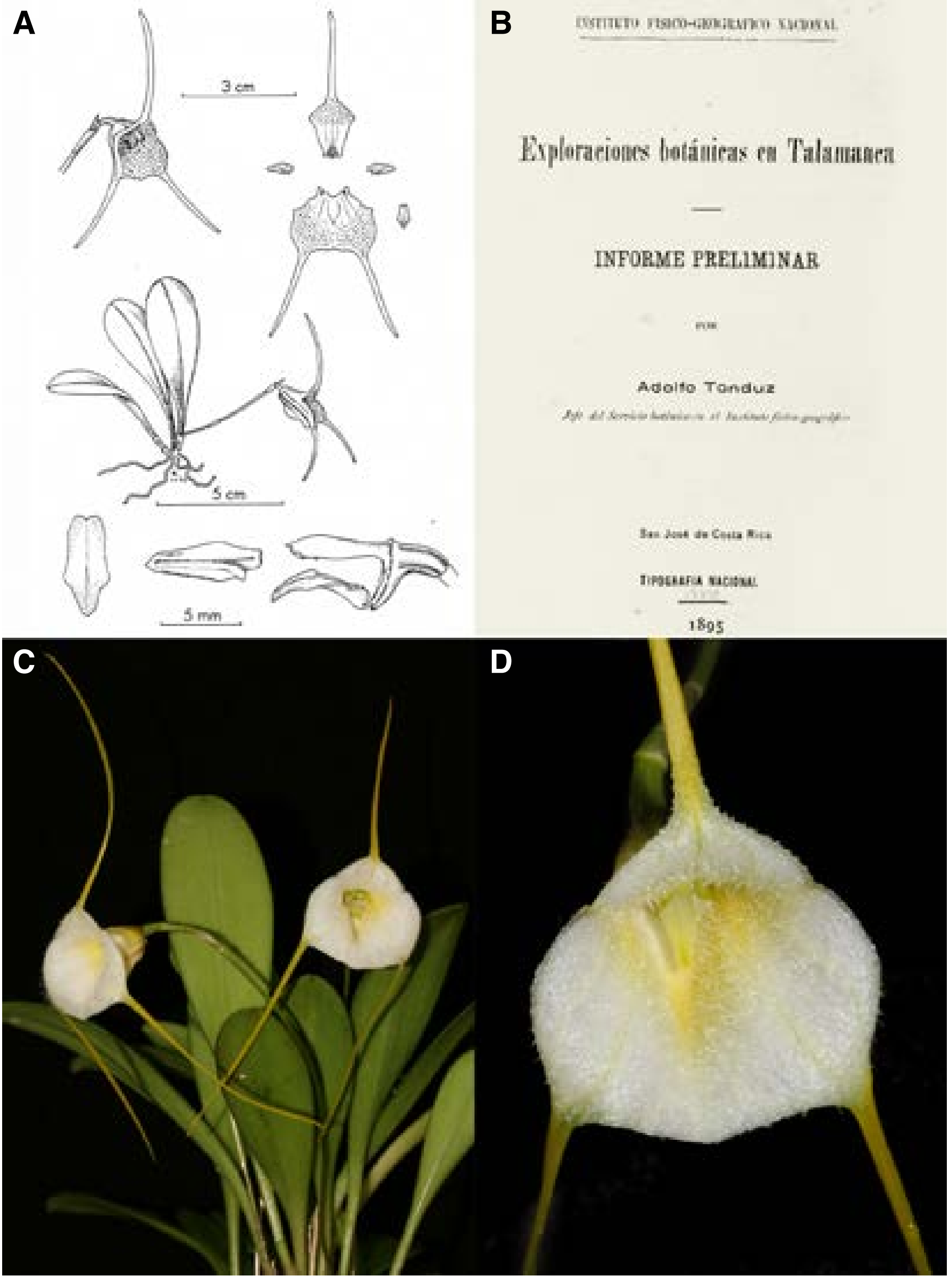


Figure 13. A, B — Portraits of Adolphe Tonduz when in Costa Rica. C — The holotype of *Masdevallia tonduzii* at G. D — Protologue of *Masdevallia tonduzii,* from Bulletin de l'Herbier Boissier (1906).



INSTITUTO FISICO-GEOGRAFICO NACIONAL

Exploraciones botánicas en Talamanca

INFORME PRELIMINAR

POR

Adolfo Tonduz

San José de Costa Rica

TIPOGRAFIA NACIONAL

1895

FIGURE 14. A — *Masdevallia tonduzii,* illustration from Icones Pleurothallidinarum 22 (2001). B — Frontispiece of Tonduz' "Exploraciones botánicas en Talamanca" (1895). C, D — *Masdevallia tonduzii*, habit and flower. Photographs by R. Jenny.

in Geneva and sent from time to time living material to Geneva. There are only a few known publications by Tonduz, one is “Exploraciones botanicas efectuadas en la parte meridional de Costa Rica” in 1893, two others are “Exploraciones botanicas en Talamanca” in 1895 (Fig. 14B) and “Herborisations au Costa Rica” in 1895 – 1897. The latter was published in several parts in the “Bulletin de l’Herbier Boissier”, it is a very detailed diary of some of his travels in Costa Rica.

Three genera are dedicated to Tonduz, *Tonduzia* Pittier (1908, Apocynaceae), *Tonduzia* F.L.Stevens (1927, invalid) and *Tonduzia* Boeck. ex Tonduz (Cyperaceae, 1895). Several orchid species are dedicated to Tonduz (Schlechter 1923), unfortunately only a few of them have been illustrated: *Elleanthus tonduzii, Stelis tonduziana, Camaridium tonduzii, Restrepia tonduzii, Cycnoches tonduzii,* and *Masdevallia tonduzii* (Woolward 1906).

Masdevallia tonduzii (Fig. 14A, 14C, 14D) was described by Florence Woolward in “Bulletin de l’Herbier Boissier” (Woolward 1906) (Fig. 13D), the plants had been collected by Tonduz and were incorporated in 1894 in the orchid collection of the Conservatoire Jardin Botanique in Geneva. Under cultivation of Paul Simmler *Masdevallia tonduzii* flowered every year, but only in 1900 Florence Woolward realized that it was a new species when she got some plants in her hands. Unfortunately it was too late to include the species in her famous book *The Genus Masdevallia* and she did not publish an illustration together with the first description. The plants remained in cultivation in Geneva at least until 1910, the type specimen is in the herbarium Boissier in Geneva (Fig. 13C).

Karl (Carlos) Wercklé and *Kefersteinia wercklei*

Karl (Carl, Carlos) Wercklé (Fig. 15A) was born on 18th of July 1860 in the village Wiebersweiler (Vivverville) in the department Alsace-Lorraine in France as son of Carl Wercklé and Christine Deher. We don’t know much about his early years, but obviously he visited the secondary school in Nancy. It is said that Wercklé was a man of extraordinary education, he was fluent in Spanish, German, French and English and it is also said that he understood enough of Latin, Greek and even Hebrew to read books in those languages. Beside this he had also skills as cartographer and as philosopher. We don’t know whether the story about his German manuscript “The Philosophy of the Absolute” which he planned to publish and which was stolen from his home and used in a local *pulperia*[5] to wrap soap and candles, is entirely true. Although French by birth Carlos always insisted to be German.

Sometime around 1892 Wercklé – most probably with his oldest sister Julia – left Europe for the USA and worked for the company of John Lewis Childs (Fig. 15B) of Long Island, New York. Childs (1856 – 1921) was selling seeds and bulbs and was founder of Floral Park (Fig. 15C). The only photograph of Wercklé we know shows him together with his boss John Lewis Childs and Anastasio Alfaro visiting an exhibition in 1893 in Chicago (Fig. 15A). Wercklé was sent to Costa Rica to collect plants and seeds for Childs, he arrived for the first time in Costa Rica in 1897; following some sources he had his sister Julie with him. He had Theophile Brune, another plant collector, with him or he met him for the first time in Costa Rica. We know that because some of Wercklé’s collections of orchids were dated November 1897, and there are specimens of the fern *Loxomopsis costaricensis* in the herbarium of Hermann Christ, described in 1904 and collected by Wercklé and Brune. Carlos’ sister got pneumonia and went back to the USA where she died a short time later. Carlos went with her and was 1898 employed by the Rose Hill Nursery of Henry A. Siebrecht and Albert Wadley of New Rochelle, a company specialized in tropical plants, ferns, palms and orchids. The company published catalogues in regular intervals and set up own orchid shows in New York. Obviously Wercklé also had relations to the New York Botanical Garden, he tried to find help to finance another trip to Costa Rica from the company and from Nathaniel Lord Britton, at this time director of the New York Botanical Garden. He had no success and so he returned on his own resources to Costa Rica, he reached Puerto Limon on 7th July 1902.

Rudolf Schlechter, orchidologist in Berlin, was trying to get contact to collectors in Central America in order to complete his planned orchid flora of Central America. He got positive answers from several people, among them also Don José Castulo Zeledón and Doña Amparo de Zeledón (Fig. 15D). Doña Amparo owned a large collection of orchids, mainly

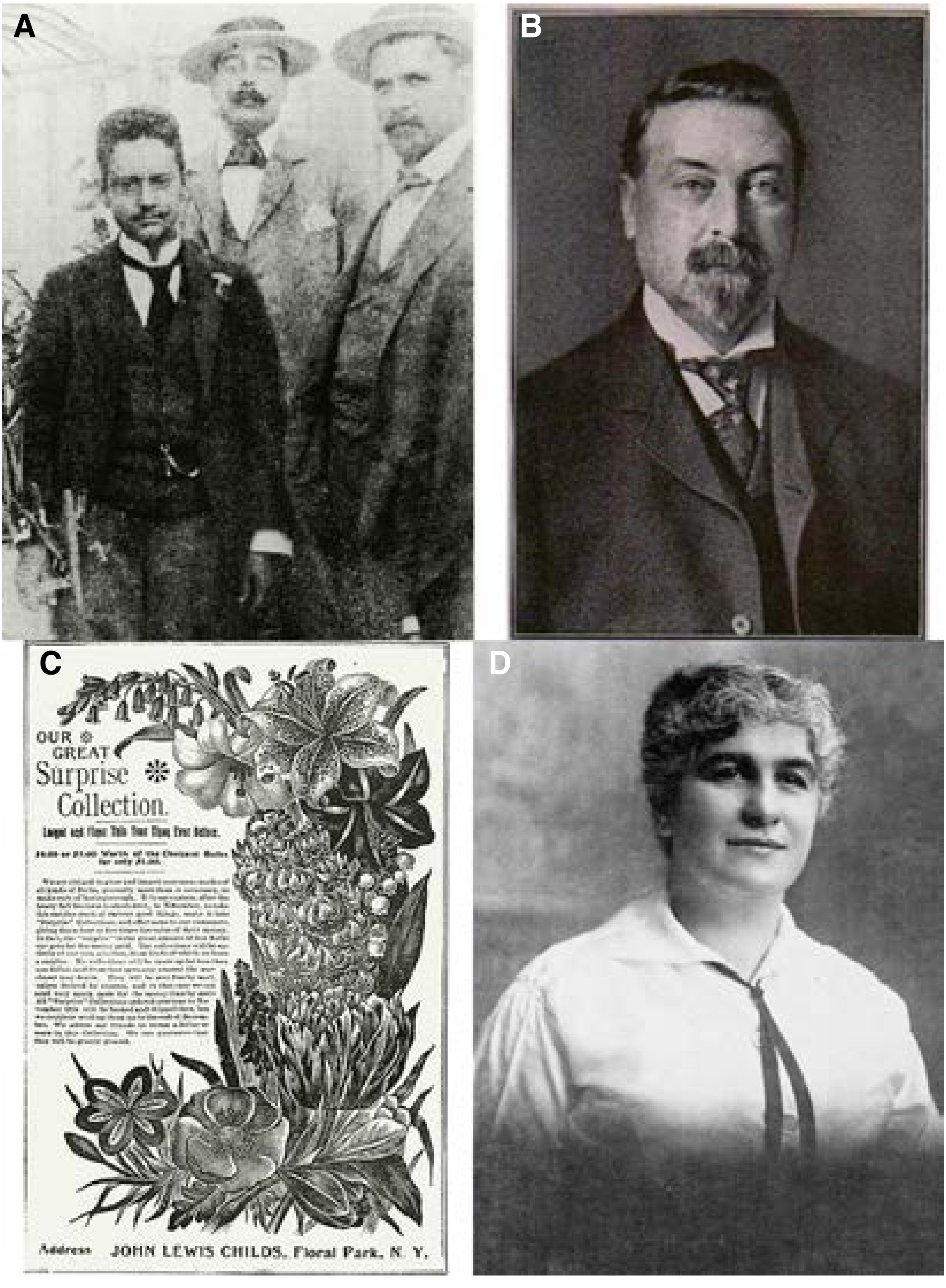


FIGURE 15. A — Carlos (Karl) Werckle (on the right) with Anastasio Alfaro (on the left) and John Lewis Child (center) in 1893. B — John Lewis Childs. C — Advertisement of Floral Park. D — Doña Amparo de Zeledón.

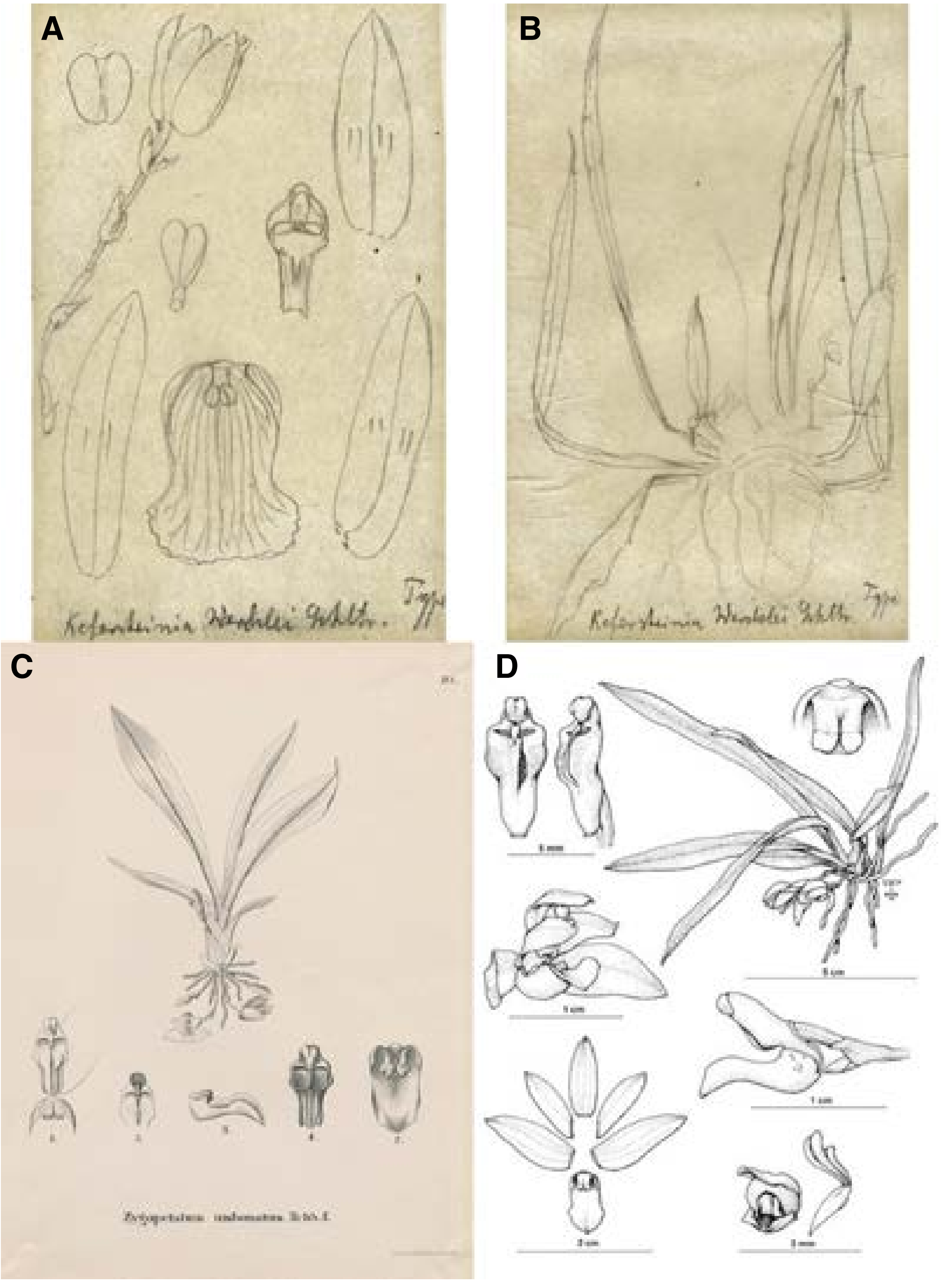


Figure 16. A, B — Copies of Schlechter's original sketches of the type of *Kefersteinia warcklei*. B — An unpublished plate from Reichenbach's Xenia Orchidacea, illustrating *K. wercklei* (as *Zygopetalum umbonatum*). C — A modern illustration of *K. wercklei*, from Pupulin 2001.

FIGURE 17. *Kefersteinia wercklei*, habit and flower.

from Costa Rica and based on recommendation of Alfred Brade, head-gardener of the town San Jose, she allowed Wercklé and Adolfo Tonduz to select interesting material for Schlechter. She herself also paid Wercklé for his work and sent him on collecting trips. Wercklé and Tonduz together collected almost 15'000 specimens for the herbarium of the Museo Nacional, although Wercklé's way to collect plant material was not state of the art: "…..his favourite way of preserving an interesting plant was to roll it into a bundle and stuff it in a pocket, where it remained indefinitely, it is thus only too easy sometimes to recognize in the herbarium his specimens, without even looking at the label" (Standley 1926). The plants they collected alive went first to the garden of Doña Amparo and where subsequently prepared by Tonduz for the herbarium. Based on Wercklé's collections, Schlechter described later 4 new orchid genera and more than 80 new species. Besides orchids, Wercklé was also very interested in ferns and bromeliads, he had an extremely good trained eye for them, and collected hundreds of species studied and described later by Hermann Christ in Basel, Switzerland. In 1906 the National Society for Agriculture sent Wercklé to southern Colombia, obviously he collected several Cacti and Bromeliads and took them home to Costa Rica. In 1911, Wercklé was employed for a few months by the herbarium of the Museo Nacional. Beside all those activities, Wercklé seems to have had his own "jardineria" first in Cartago and later in San Jose. He published a series of articles, the first one in 1901 in "Torreya", and in 1913 "the first scientific article ever written in Costa Rica about the orchids of this country" (Ossenbach 2003) in "Boletin do Fomento". His main work was "*La Subregion Fitogeografica Costarricense*" in 1909. Some of his articles were published in German periodicals like "Monatsschrift für Kakteenkunde" and "Der Tropenpflanzer".

From a letter of Henry Nehrling to Theodor Luqueer Mead from December 1918 we learn that Wercklé was also collecting and selling Bromeliads. Nehrling (1853–1929) started "Nehrling's Tropical Garden and Arboretum" in 1917 in Naples, Florida and was in close contact with Mead (1852–1936) who had a collection of tropical plants – including orchids – in Oviedo, Florida. Nehrling wrote to Mead: "Do you know a good book on the flora of Costa Rica? Carlos Werckle wrote me some time ago that he has discovered a number of new Bromeliads rivalling in beauty with *Caraguata zahnii, Massangea musaica* and others and still very distinct. He intends to send me a fine collection of the Costa Rican species, about 300 distinct kinds. He says that the center of distribution of Bromeliads in Costa Rica is found in the mountains around Cartago. Says that his wife "is in many respects an ideal, but she is extremely nervous, and not at all healthy". In another letter from November 1925 we read: "Carlos Werckle, an old friend of mine and now dead, discovered some most beautiful new species in the mountains of Costa Rica. They all have been described by Dr. Mez (Professor at the University of Königsberg). He sent me a consignment about 6 years ago – 50 species, mostly new. They came as far as Jacksonville but were returned by the man who acted for the Federal Plant Board and Werckle never could be induced to send me another lot, even after I had sent him special permits". Wercklé was not married, the remark about "his wife" is wrong, most probably he talked about his sister.

In 1922 Oakes Ames was looking for a collector in Central America and contacted Charles Lankester in Costa Rica in order to get his opinion about Wercklé, Lankester's answer from 11th of October 1922 was very clear: "Wercklé is a dipsomaniac, an appalling wreck of a fine intelligence, but has still some good local knowledge and might be of use yet" (Ossenbach 2003). In his later years Wercklé started to develop a passion for alcohol, he drank and this was most probably the reason for his early death on 24th of November 1924.

Kefersteinia wercklei (Fig. 16d, 17) was described in 1923 by Rudolf Schlechter in "Feddes Repertorium, Beihefte" based on a plant collected by Wercklé in June 1921 near La Palma. The article was dedicated to Doña Amparo de Zeledón as "*Orchidaceae Amparoanae*" (Schlechter 1923), the specimens were collected by Tonduz and Wercklé, cultivated first in the garden of Doña Amparo, dried by Tonduz and sent in several consignments to Schlechter. Again, the type specimen of *Kefersteinia wercklei* was lost in 1943, but a copy of Schlechter's drawing and the type specimen is in the AMES herbarium in Harvard (Fig. 16a, 16b). In 1944 Charles Schweinfurth described in "American Orchid Society Bulletin" *Chondrorhyncha pusilla* from Peru and recombined in a footnote the "allied" species *Kefersteinia wercklei* Schltr. to *Chondrorhyncha wercklei* (Schltr.) C. Schweinfurth (Schweinfurth 1944). The part about the subtribe Huntleyinae for the 3rd edition of Schlechters "*Die Orchideen*" was written by Karlheinz Senghas, Helga Dietrich and Günter Gerlach. The authors defined the new section Umbonata for the species-group around Kefersteinia costaricensis and included also *Kefersteinia wercklei*. They also mentioned the unpublished taxon *Kefersteinia umbonata* as synonym of *Kefersteinia wercklei* (Senghas *et al*. 1992). *Kefersteinia umbonata* is based on a drawing by Endrés named *Zygopetalum umbonatum* in Reichenbach;s herbarium in Vienna (W-R no.336). Of the same drawing a lithograph was made, planned to be published in "Xenia Orchidacea" and named *Zygopetalum umbonatum* (Fig. 16c). On a second sheet (W-R no.34708) we find the handwritten description as "*Zygopetalum* (near *Kefersteinia*)" and a drawing of the flower parts by Endrés. The binomial *Kefersteinia umbonata* is not mentioned on any of the sheets of the Endrés-material in Vienna. In the German journal "Journal für den Orchideenfreund" of 2003 Dariusz Szlachetko described the new genus *Senghasia* based on the section *Umbonata* of *Kefersteinia* with 12 species (Szlachetko 2003). He recombined *Kefersteinia wercklei* to *Senghasia wercklei*. The genus is named after Karlheinz Senghas, orchidologist, longtime-director at the Botanical Garden Heidelberg and co-author of the third edition of Rudolf Schlechters "*Die Orchideen*".

Literature cited

Allen, P. H. 1952. *Telipogon endresianum* Kraenzlin. Orchid Journal (A.D.Hawkes) 1: 292–293

Ames, O. & C. Schweinfurth. 1930. New or noteworthy Orchids. Schedul. Orch. 10: 1–112.

Anonymous. 1897a. Gardeners' Chronicle ser.3,21: 241.

Anonymous. 1897b. Orchid Review 5:109

Anonymous. 1923. Berichte der Schweizerischen Botanischen Gesellschaft 32: ix–x.

Barringer, K. 1984. Typification of Schlechter's Costa Rican Orchidaceae, types collected by A. Brenes. Fieldiana Bot. new series 17: 1–24.

Beauverd, G. 1922. M. Adolphe Tonduz. Bulletin de la Societe Botanique de Geneve, ser.2, 14: 12–13.

Bentham, G. 1881. Notes on Orchideae. Journal of the Linnean Society 18(110): 337.

Bogarín, D & F. Pupulin. 2007. El genero *Campylocentrum* en Costa Rica: algunas preguntas criticas y unas pocas respuestas. The genus *Campylocentrum* in Costa Rica: some critical questions and a few answers. Proc. of the Second Scientific Conference on Andean Orchids: 12.

Bogarín, D. 2010. Revisión taxonómica del género *Campylocentrum* (Orchidaceae: Angraecinae) en Costa Rica. Dissertation. Universidad de Costa Rica. Pp. 39–122.

Bogarín, D. & F. Pupulin. 2010. The genus *Campylocentrum*

(Angraecinae) in Costa Rica: a revision. Harvard Papers in Botany 15(2): 353–414.

Cogniaux, A. C. 1897. Orchidees nouvelles ou recement introduites. Chronique Orchidéenne 1(4): 32.

Dressler, R. L. 1993. Field Guide to the Orchids of Costa Rica and Panama. Comstock Publishing.

Gómez, L. D. 1977. Contribuciones a la pteridologia Costarricense XII: Hermann Christ, su vida, obra e influencia en la botanica nacional. Brenesia 12–13: 57–59.

Gómez, L. D. 1978. Contribuciones a la pteridologia Costarricense XII: Carlos Wercklé. Brenesia 14–15: 361–393.

Häsler, B. & T. W. Baumann. 2000. Henri Pittier, 1857–1950, Leben und Werk eines Schweizer Naturforschers in den Neotropen. Reinhardt Verlag Basel.

Harding, P. 2008. Huntleyas and related orchids. Timber Press, Oregon.

Jiménez, J. A. 1945. Un Costarricense ilustre. Revista del Instituto de defensa del Café de Costa Rica 15(131): 523–525.

Königer, W. 2007. *Oncidium*, eine Monographie, 3. Verlag Helga Königer. Pp. 89–92.

Kränzlin, F. 1919. Beiträge zur Kenntnis der Gattung Telipogon H.B.K. Annalen des Naturhistorischen Hofmuseums Wien 33: 29–31.

Kränzlin, F. 1922. Orchidaceae-Monandrae, Tribus Oncidiinae - Odontoglosseae Pars II. Das Pflanzenreich IV.50(2): 199.

León, J. 1945. Notas sobre la labor botanica de don Alberto M. Brenes. Revista del Instituto de defensa del Café de Costa Rica 15(131): 526–527.

Lobo, S. 2004. Tipos de Orquidaceas Brenesianas, descritas por R.Schlechter, en el herbario nacional de Costa Rica. Lankesteriana 4(1): 37–45.

López, G.D. 2009. La Nación (Costa Rica). 8 March 2009.

Luer, C. A. 1986. Thesaurus Masdevalliarum 7: sub. t.13.

Luer, C. A. 2001. Icones Pleurothallidinarum 22. Monographs in Systematic Botany from the Missouri Botanical Garden, 86 :769–770.

Mansfeld, R. 1931. Bluetenanalysen neuer Orchideen, II. Mittelamerikanische Orchideen. Repertorium Specierum Novarum Regni Vegetabilis Beihefte 59(2): t.74; 78, fig. 295; 309.

Mirenda, T. 2010. Telipogons, the ultimate orchids. Orchids (West Palm Beach) 79: 552–554

Mora de Retana, D. E. & J. T. Atwood. 1993a. *Masdevallia tonduzii* Woolward. Sub. pl. 1558 in: Orchids of Costa Rica, part 3. Icones Plantarum Tropicarum 16.

Mora de Retana, D. E. & J. T. Atwood. 1993b. *Oncidium luteum* Rolfe. Sub. pl. 1572 in: Orchids of Costa Rica, part 3. Icones Plantarum Tropicarum 16.

Ortiz, F. 2002. Perfil de Don Alberto Brenes Mora. Brenesia 57-58: 19–24.

Ossenbach, C. 2003. History of Orchids in Central America, from prehispanic times to the new millennium 2: 131–132, 135. Unpublished manuscript.

Ossenbach, C. 2006. Orchids in Costa Rica, part I : The era of Rudolf Schlechter. Orchids (West Palm Beach) 75: 38–47.

Ossenbach, C. 2008. Adolphe Tonduz (1862–1921). Revista Biocenosis 21(1-2): 13–19.

Ossenbach, C. 2009. Orchids and Orchidology in Central America: 500 years of history. Lankesteriana 9(1–2): 149–157.

Pfau, R. 1883a. The climate of Central America, orchid culture. Gardeners' Chronicle, new ser. 20: 558–560.

Pfau, R. 1883b. Hints on the culture of some rare Central American orchids. Gardeners' Chronicle, new ser 20: 658.

Pfau, R. 1883c. *Cypripedium caudatum*. Gardeners' Chronicle, new ser. 20: 722.

Pfau, R. 1884a. *Cypripedium roebbeleni*. Gardeners' Chronicle, new ser. 21: 16.

Pfau, R. 1884b. *Trichocentrum pfavii*. Gardeners' Chronicle, new ser. 21: 50.

Pfau, R. 1894. Notes on the fertilisation of orchids in the tropics. Orchid Review 2: 295–296.

Pfau, R. 1895. New, rare, and beautiful orchids of Costa Rica and how they grow at home. San José, Costa Rica. Pp. 1–12.

Pfau, R. 1896. Costa Rica and its Orchids. Gardeners' Chronicle, ser.3, 19: 548–549.

Pittier, H. 1922. Gazette de Lausanne 154(55): 2 (24.2.1922).

Pupulin, F. 1995. A revision of the genus *Trichocentrum* (Oncidiinae). Lindleyana 10(3): 183–210.

Pupulin, F. 1997. The *Trichocentrum pfavii* group. Caesiana 8: 1–14.

Pupulin, F. 2001. Miscellaneous new taxa in neotropical Orchidaceae. Selbyana 22(1): 14–26.

Pupulin, F. 2005. Vanishing Beauty. Native Costa Rican Orchids. Vol. 1: Acianthera–Kegeliella. Editorial de la Universidad de Costa Rica, San José. P. XXI.

Pupulin, F. 2010. Orchidaceae werckleanae: typification of Costa Rican orchid species described from collections by K.Wercklé. Botanical Journal of the Linnean Society 163: 111–154.

Pupulin, F. & D. E. Mora de Retana.1994. A revision of the Costa Rican species of *Trichocentrum*. Selbyana 15(2): 87–103.

Reichenbach, H.G. 1881. New garden plants: *Trichocentrum pfavii, Cirrhopetalum abbreviatum, Cirrhopetalum trigonopus*. Gardeners' Chronicle, new ser. 16: 70.

Reichenbach, H.G. 1883. New garden plants: *Calanthe Lentiginosa, Trichocentrum pfavii, Trichocentrum pfavii zonale, Odontoglossum hebraicum lineoligerum,* *Dendrobium chrysanthum anophthalmum*. Gardeners' Chronicle, new ser. 19: 44.

Rolfe, R. A. 1893. New Orchids: Decade 6. Bulletin of Miscellaneous Information (Kew) 1893: 172.

Salazar Rodríguez, A.H. 2009. Alberto Manuel Brenes, el naturalista. Editorial de la Universidad de Costa Rica, San José.

Sánchez Porras, R. 2002. Pionero de la biologia en Costa Rica, Manuel Alberto Brenes. Brenesia 57-58: 7–18.

Schlechter, R. 1910. Orchidaceae novae et criticae, Decas XI. Repertorium Specierum Novarum Regni Vegetabilis 9: 30, 293.

Schlechter, R. 1923. Beiträge zur Orchideenkunde von Zentralamerika. Repertorium Specierum Novarum Regni Vegetabilis Beihefte 19: 1–75; 157; 268–269.

Schweinfurth, C. 1944. A genus and species unrecorded for Peru. American Orchid Society Bulletin 12(11): 384–385.

Senghas, K., H. Dietrich & G. Gerlach. 1992. 689. Chaubardiella. In: R.Schlechter, Die Orchideen Ed.3, 1B(26): 1646–1647.

Standley, P. C. 1926. Carlos Wercklé. Science 63(1626): 221–223.

Stevens, F. B. 1977. *Epidendrum pfavii* (Rolfe). Orchid Review 85(1008): 176–177.

Szlachetko, D. L. 2003. *Senghasia*, eine neue Gattung der Zygopetaleae. Journal für den Orchideenfreund 10(4): 332–344.

Todzia, C. A. 1980. Revision of the Costa Rican species of *Campylocentrum*. Brenesia 18: 117–136.

Wercklé, C. 1903. Gemüsepflanzen von Costarica. Der Tropenpflanzer 7: 425–439.

Wercklé, C. 1904. Heteromorphismus epiphytischer Cereen. Monatsschrift für Kakteenkunde 14: 62–63.

Wercklé, C. 1905. Cactaceae in Costa Rica. Monatsschrift für Kakteenkunde 15: 3–4, 165–168, 179–181.

Wercklé, C. 1907. Cacteen in Zentral-Columbien. Monatsschrift für Kakteenkunde 17: 18–20.

Williams, L. 1956. Enumeration of Orchidaceae of Central America, British Honduras and Panama. Ceiba 5(1): 195.

Woolward, F. H. 1906. *Masdevallia tonduzii* spec. nov. Bulletin de l'Herbier Boissier ser.2,6:82.

LANKESTERIANA 13(3): 319—332. 2014.

INVITED PAPER*

LANKESTERIANA, A NEW GENUS IN THE PLEUROTHALLIDINAE (ORCHIDACEAE)

ADAM P. KARREMANS

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

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

KEY WORDS: *Anathallis*, *Lankesteriana*, *Specklinia*, *Stelis*, phylogenetics, systematics

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

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

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

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

---

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Lankesteriana Karremans, Gen. Nov.

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

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

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

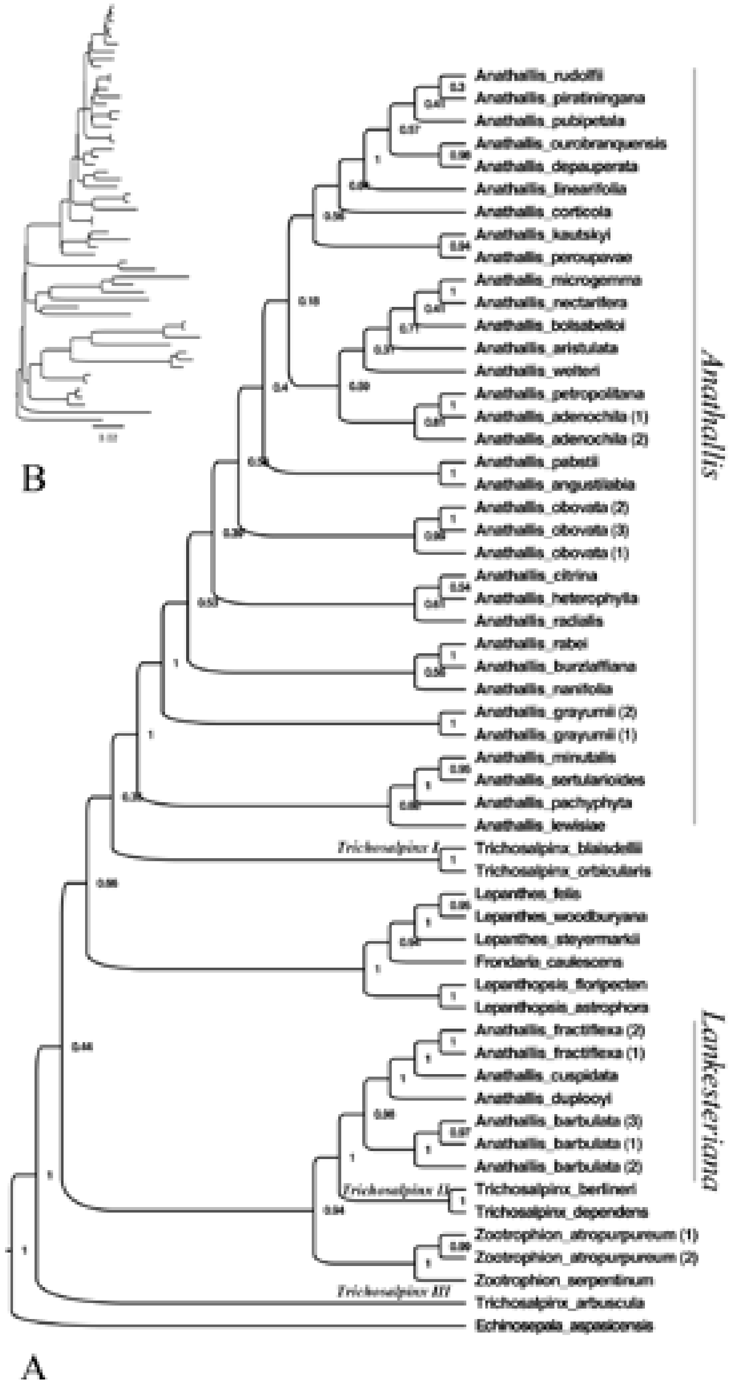


FIGURE 1. Consensus tree from a BEAST analysis of a matrix of 56 ITS sequences. The analysis ran for 20,000,000 generations. A — Branch length transformed to be equal for each species. Values on the nodes are Posterior Probabilities. Species names for each terminal is included. B —Relative branch lengths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

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

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

TABLE 1. Continues.

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

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

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

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

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

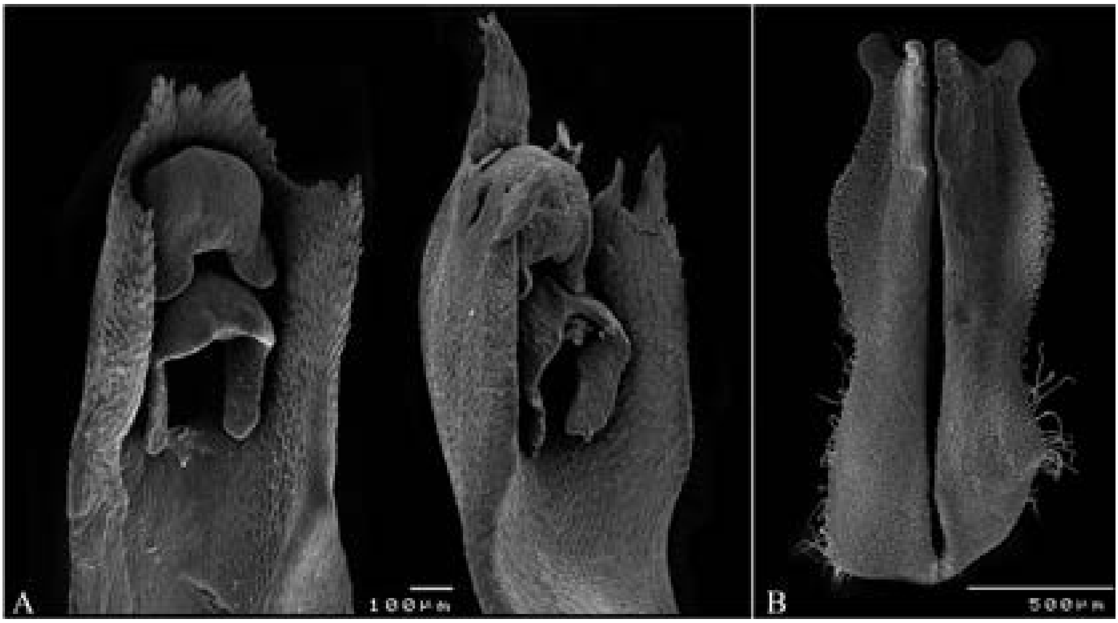
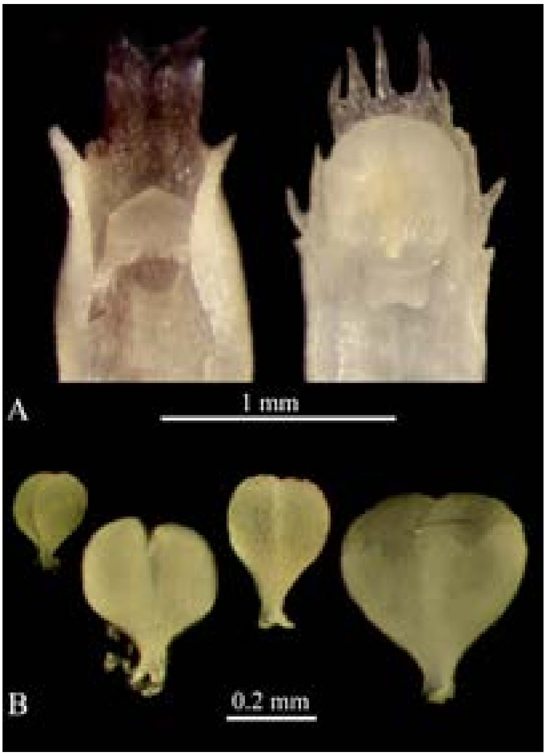


FIGURE 2. SEM images of micromorphology of *Lankesteriana* species. A — Column ventral view showing the androclinium, anther cap, helmet-like rostellum and stigma. B — The flattened lip, showing the midline depression, the basal sub-orbicular lobes and the glandular hairs near the apex. Specimens are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

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

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



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

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

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

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

KEY TO THE GENERA WITH *SPECKLINIA*-LIKE HABIT

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Species of *Anathallis* are distributed from southern Mexico through Central America, the Antilles and all South America down to Argentina. They are most diverse in Brazil at low to mid elevations. They are easily recognized by the more or less star-shaped flower, with linear to lanceolate, acute to acuminate petals that are similar to the sepals. The lip is horizontally placed and very sensitive, its general shape is linear-ligulate but frequently it has small lobes at the base and/or middle. The column is sharply winged and prominently fimbriate. The pollinaria come in pairs and have reduced whale-tail shaped caudicles.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Bas. *Pleurothallis jesupiorum* Luer & Hirtz, Lindleyana 11: 164. 1996.

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

Bas. *Pleurothallis lagarophyta* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 112. 1999.

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

Bas. *Pleurothallis lamprophylla* Schltr., Repert. Spec. Nov. Regni Veg. 15: 205. 1918.

Replaced synonym: *Pleurothallis dolichopus* Schltr., Repert. Spec. Nov. Regni Veg. 10: 394. 1912 = *Anathallis dolichopus* (Schltr.) Pridgeon & M.W. Chase.

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

Stelis lauta Karremans, ***nom. nov.***

Replaced Synonym: *Pleurothallis concinna* Luer & R.Vásquez, Revista Soc. Boliv. Bot. 2: 133. 1999.

Etymology: From the Latin *lautus*, elegant, fine, as a replacement for the also Latin adjective *concinnatus* used in the original description of this species.

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

Stelis lennartii Karremans, ***nom. nov.***

Replaced Synonym: *Pleurothallis anderssonii* Luer, Lindleyana 11: 145. 1996.

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

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

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

Bas. *Pleurothallis maguirei* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 113. 1999.

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

Bas. *Pleurothallis mediocarinata* C.Schweinf., Fieldiana, Bot. 33: 26. 1970.

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

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

Replaced synonym: *Pleurothallis stenophylla* Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 442. 1899 = *Anathallis stenophylla* (Lehm. & Kraenzl.) Pridgeon & M.W. Chase.

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

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

Bas. *Pleurothallis meridana* Rchb.f., Linnaea 22: 826. 1850.

Stelis montserratii (Porsch) Karremans, ***comb. nov.***

Bas. *Pleurothallis montserratii* Porsch, Oesterr. Bot. Zeitsch. 158. 1905.

Replaced synonym: *Pleurothallis rubens* Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835.

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

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

Bas. *Pleurothallis papuligera* Schltr., Repert. Spec. Nov. Regni Veg. 10: 453. 1912.

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

Bas. *Pleurothallis regalis* Luer, Selbyana 5: 178. 1979.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

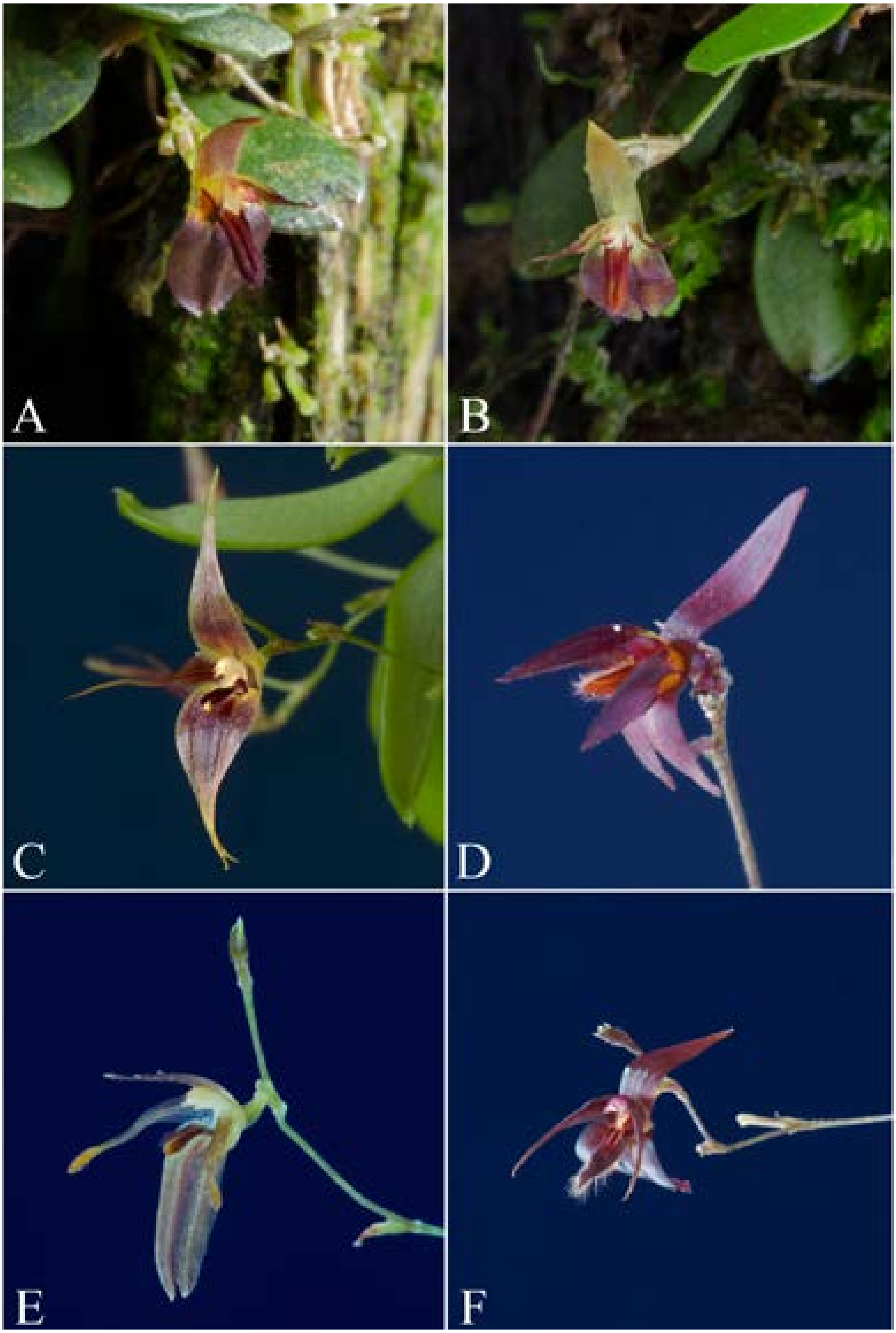
Conclusions. High species diversity and the many cases of convergence and parallelism make the systematics of the Pleurothallidinae quite hazardous. Morphological features are often congruent with phylogenetic hypotheses based on DNA data, but homoplasy can occur in morphological traits; similar morphological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

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

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

ACKNOWLEDGMENTS. I am thankful to the Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC) for issuing the Scientific Passports under which wild species treated in this study were collected. My colleagues Franco, Diego and Melania at Lankester Botanical Garden have been most insightful, and have helped with the collecting and documenting the studied material. Some of data was produced as part of the research projects under supervision of Barbara Gravendeel in diverse

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


A
B
C
D
E
F

labs at Leiden University and the Naturalis Biodiversity Center. In general I wish to thank all the staff of JBL and L for the unrestricted access and help. I am most thankful to Lio and Ibra for the delight they have been during this period. Lisa Thoerle and two other anonymous reviewers made a series of improvements to the manuscript, and I am very thankful to them. I am also in debt to the Vice-Presidency of Research of the University of Costa Rica for providing support through the projects "Inventario y taxonomía de la flora epífita de la región Mesoamericana" (814-A7-015), "Flora Costaricensis: Taxonomía y Filogenia de la subtribu Pleurothallidinae (Orchidaceae) en Costa Rica" (814-BO-052), "Filogenia molecular de las especies de Orchidaceae endémicas de Costa Rica" (814-B1-239) and "Taxonomía, filogenia molecular, aislamiento reproductivo y diferenciación de nichos de *Specklinia endotrachys*" (814-B3-075).

LITERATURE CITED

Bogarín, D., A.P. Karremans, R. Rincón & B. Gravendeel. 2013. A new *Specklinia* (Orchidaceae: Pleurothallidinae) from Costa Rica and Panama. Phytotaxa 115(2): 31-41.

Chiron, G.R., J. Guiard & C. van den Berg. 2012. Phylogenetic relationships in Brazilian *Pleurothallis* sensu lato (Pleurothallidinae, Orchidaceae): evidence from nuclear ITS rDNA sequences. Phytotaxa 46: 34–58.

Drummond, A.J. & A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7: 214.

Heneghan C, M. Thompson, M. Billingsley & D. Cohen. 2011. Data from: Medical-device recalls in the UK and the device-regulation process: retrospective review of safety notices and alerts. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.585t4.

Karremans, A.P. 2010. Phylogenetics of *Stelis* (Orchidaceae: Pleurothallidinae) and closely related genera, based on molecular data, morphological characteristics and geographical distribution in the Central American and Andean Cordilleras. MSc Thesis, Plant Sciences Group and Biosystematics Group, Wageningen University.

Karremans, A.P., F.T. Bakker, F. Pupulin, R. Solano-Gomez & M.J.M. Smulders. 2013a. Phylogenetics of *Stelis* and closely related genera (Orchidaceae: Pleurothallidinae). Plant Syst. Evol. 29(1): 69-86.

Karremans, A.P., F. Pupulin & B. Gravendeel. 2013b. Taxonomy, molecular phylogenetics, reproductive isolation, and niche differentiation of the *Specklinia endotrachys* species complex (Orchidaceae: Pleurothallidinae). Lankesteriana 13(1-2): 132-133.

Luer, C.A. 1986. Systematics of the genus *Pleurothallis* (Orchidaceae). Mongr. Syst. Bot. Missouri Bot. Gard. 20.

Luer, C.A. 1997. Systematics of *Trichosalpinx*. Monogr. Syst. Bot. Missouri Bot. Gard. 64.

Luer, C.A. 1999. lcones Pleurothallidinarum XVIII. Systematics of *Pleurothallis* Subgen. *Pleurothallis* Sect. *Pleurothallis* Subsect. *Antenniferae*, Subsect. *Longiracemosae*, Subsect. *Macrophyllae-Racemosae*, Subsect. *Perplexae*, Subgen. *Pseudostelis*, Subgen. *Acuminatia*. Mongr. Syst. Bot. Missouri Bot. Gard. 76.

Luer, C.A. 2002. A systematic method of classification of the Pleurothallidinae versus a strictly phylogenetic method. Selbyana 23(1): 57-110.

Luer, C.A. 2006. Icones Pleurothallidinarum XXVIII. Reconsideration of *Masdevallia*, and the Systematics of *Specklinia* and vegetatively similar genera (Orchidaceae). Mongr. Syst. Bot. Missouri Bot. Gard. 105.

Luer, C.A. 2009. Icones Pleurothallidinarum XXX. *Lepanthes* of Jamaica and Systematics of *Stelis*, *Stelis* of Ecuador, part four and addenda: systematic of *Masdevallia*, new species of *Lepanthes* from Ecuador, and miscellaneous new combinations. Mongr. Syst. Bot. Missouri Bot. Gard. 115.

Maddison, W.P. & D.R. Maddison. 2007. Mesquite: a modular system for evolutionary analysis. Mesquite v. 2.72. Available at http://mesquiteproject.org

Pridgeon, A.M. & M.W. Chase. 2001. A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). Lindleyana 16(4): 235-271.

Pridgeon, A.M., R. Solano, M.W. Chase. 2001. Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid DNA sequences. Am. J. Bot. 88(12): 2286-2308.

Pridgeon, A.M. 2005. Subtribe Pleurothallidinae. In: A.M. Prigeon, P.J. Cribb, M.W. Chase & F.N. Rasmussen (Eds.), Genera Orchidacearum. Volume 4 Epidendroideae (Part One). Pp. 319-422.

Pupulin, F., A.P. Karremans & B. Gravendeel. A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica. Phytotaxa 63: 1-20.

Rambaut, A. 2009. FigTree v1.3.1. Available at http://tree.bio.ed.ac.uk/software/

Staden, R., D.P. Judge & J.K. Bonfield. 2003. Analysing Sequences Using the Staden Package and EMBOSS. In: S. A. Krawetz and D. D. Womble (Eds.), Introduction to Bioinformatics. A Theoretical and Practical Approach. Human Press Inc., Totawa, NJ 07512.

Stenzel, H. 2004. Systematics and evolution of the genus *Pleurothallis* R. Br. (Orchidaceae) in the Greater Antilles. Dissertation Thesis. Mathematisch-Naturwissenschaftlichen Fakultät I der Humboldt-Universität zu Berlin.

Sun, Y., D.Z. Skinner, G.H. Liang & H. Hulbert. 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. Theor. Appl. Genet. 89: 26-32.

LANKESTERIANA 13(3): 333—335. 2014.

INVITED PAPER*

THE FIRST TEN YEARS OF SELBY GARDENS

Carlyle A. Luer

3222 Old Oak Drive, Sarasota, FL, 34239-5019, U.S.A.
cluer@juno.com

Abstract. In her will, Marie Selby left her home and grounds to be used as a “botanical garden” at the discretion of the directors of Palmer Bank. The property was zoned for high-rises, but opposition to a botanical garden was overcome. Cal Dodson, Professor of Botany at the University of Miami, was a chosen as a director. The Gardens soon acquired more grounds and staff. A volunteer program was begun, and volunteers contributed vastly to our rapid growth. Our many accomplishments include the quarterly *Bulletin*, first appearing in spring 1974, and the scientific journal, *Selbyana*, first published in January 1975. The growth of the Gardens would inevitably accelerate with the great infrastructure put in place during our first ten years.

Key words: William Selby, Marie Selby, Sarasota, botanical garden, Calaway H. Dodson

Bill and Marie Selby built their retirement home in Sarasota on the bay front in the early 1920s. Bill had amassed a fortune with Texaco Oil Company. Without heirs, they created the charitable William G. and Marie Selby Foundation with Palmer Bank as trustee. I knew Mr. Selby, only in consultation in his terminal illness in 1956. I cared for Mrs. Selby’s surgical problems, but I knew nothing about her intention of leaving her home for a “botanical garden.” Only in June 1972, one year after her death, were conditions of her will announced at a meeting of the board of Palmer Bank. By coincidence, I was in attendance. I had been a director for six or seven years, not because I knew anything about banking, but because of my surgical practice.

In her will, Mrs. Selby left her home and grounds with the adjacent vacant lot to the north, to be used as a “botanical garden” at the discretion of the directors of Palmer Bank. She had purchased the lot to the north, also on the bay, where the home of Russian Prince Michael Cantacuzene once stood, to prevent the construction of a high-rise. Her idea of a botanical garden had been a pretty garden where she could hold garden club meetings and social events. For maintenance, she designated a small endowment, all the rest of her estate reverting to the Selby Foundation. The endowment with the proceeds from the sale of her property would also revert to the Foundation, at the discretion of Palmer Bank.

Bill Coleman, the chairman of the board of Palmer Bank, was a friend of ours. We shared an interest in nature, and had made field trips into the Fakahatchee Swamp. I explained to the board the possibility of creating a true botanical garden, but there was no enthusiasm. Zoned for high-rises, her seven-acre property must have been worth a fortune. Privately, I described the potentialities to Coleman, and he was receptive. He was a forceful chairman, so during the summer of 1972, it was decided that there would indeed be a Marie Selby Botanical Gardens.

Consultants from the New York Botanical Garden and the University of Florida agreed that specializing in one small group of plants such as orchids would be feasible. Several alternative, larger sites east and south of Sarasota were investigated, but her home with seven acres of land near downtown Sarasota was finally decided upon, but not without considerable reservations. The property was zoned for high-rises, not a botanical garden. There was considerable opposition to a botanical garden from more than one source. All kinds of questions were raised by the city commission, and the city building, planning, and zoning boards. It seemed like one roadblock after another was being thrown in our path. Were we to become an amusement

---

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

park? Where would cars park? How about traffic? How about your neighbors? How about pollution? Would anything be sold? Could we be taxed? By the end of 1972, a special exemption for a botanical garden was granted reluctantly by the city. We applied for and received tax-exempt status from the IRS to become a charitable institution.

Next, a director had to be found. Cal Dodson, Professor of Botany at the University of Miami, at that time on a year sabbatical in Ecuador, was a candidate. In January 1973, Bill Coleman, his wife and their daughter, and Jane and I flew down to Ecuador to discuss the situation with him. Dodson thought that the proposition seemed too good to be true, that new botanical gardens were not being made any more. He was not aware of the impending Lankester Garden. He reasoned that if the scope of the garden were restricted to one small group of plants, such as epiphytes, it might fit on the small piece of land allotted. He accepted the offer. Abandoning his tenure with the University of Miami and his sabbatical, he and his family arrived in Sarasota the following month.

In February 1973, the Dodson family moved into the moldy Selby house that had been closed for over 18 months with a leaking roof before they found a place to live. Mrs. Selby's yard had become a massive jungle of weeds and Brazilian pepper trees during the last 20 years of her life. Months were spent clearing the invasive plants. Where to place what kinds of greenhouses and where to place the walkways had to be decided.

Among the first employees were two gardeners who had worked for Mrs. Selby. In April 1973, Dodson hired Ruby Hollis, who became a masterful secretary and backbone of administrative duties for the next generation. Hans Wiehler and Kiat Tan, doctoral candidates in botany from the University of Miami, were brought to the Gardens as staff members.

Soon after our beginning in 1973, one of our most important acquisitions with Selby Foundation funds was the botanical library of William Cole of Winter Park. From him and Weldon and Wesley, rare book dealers in England, we obtained famed treasures such as Bateman's *Orchidaceae of Mexico and Guatemala* as well as his *Monograph of Odontoglossum*, Lindley's *Sertum Orchidaceum*, Linden's *Pescatoria*, Warner's *Select Orchidaceous Plants*, Warner and Williams' *The Orchid Album*, a complete run of *Curtis' Botanical Magazine*, and Woolward's *Monograph of Masdevallia*.

An attractive, substantial "gate house," with a front reception desk, restrooms, and plant shop, was built in 1973 and opened to the public with a dedication ceremony in January 1974. The property across the street from the gate house, and the adjacent lot and house to the north, were acquired for parking, and the corner house by highway 41 was acquired for "administration," all with grants from The Selby Foundation in 1973. Across the street from the newly acquired administration building was the Payne mansion (also on the bay and zoned for a high rise) that belonged to Dr. Paulk, an orthodontist and friend of ours. After negotiations, the price agreed upon for the Payne house was paid by the Selby Foundation and a donor, so by the summer of 1973 we had considerably expanded the physical scope of the Gardens.

During the summer of 1973, the Gardens hosted its first visiting botanical scientist, Dr. Richard Keating of Southern Illinois University. He and his family lived on the grounds. Also that summer, the Gardens' official seal with four epiphytic species (an orchid, a bromeliad, a gesneriad, and a *Peperomia*) and the date 1973 was designed on our kitchen table.

Greenhouses were completed in the summer of 1974. In the largest one close to the gate house, we built a meandering trellis-covered walkway beside a massive, rugged, cliff-like wall of "lava rock" boulders, dripping wet and festooned with lush vegetation. It became the display house. Workers, volunteers, and many visitors came and went.

Paid memberships in the Gardens were begun. A volunteer program was started without which we could not have existed. Volunteers contributed vastly to our rapid growth. One of their many accomplishments was the quarterly *Bulletin*, the first number appearing in spring 1974. The first issue of *Selbyana*, the scientific journal, was published in January 1975.

Our small endowment was dwindling. Our new Selby Gardens Board of Directors of only five members eliminated the expensive services of an outside accounting firm, and gained complete independence from Palmer Bank, under which we had been a dependent and charged a fee. Even after elimination of the above losses of revenue, our income from the endowment was so meager, we could scarcely survive. On at least one occasion, a donor made the payroll.

In July 1975, we decided that we would start charging visitors a fee of one dollar. Already open a year and a half, none of us thought that this date would be cited incorrectly, some 30 years later, as the "beginning" of Selby Gardens.

Meanwhile, Dodson initiated a student internship program, and an orchid identification service. Harry Luther in bromeliads, John Atwood in orchids, and Mike Madison in aeroids joined us. Dr. Raven, director of the Missouri Botanical Garden, came down for the formal dedication of the Gardens, a gala reception held 3 April 1976. The Selby Foundation promised a certain amount of financial aid for each of our first five years to help with capital improvements, but that ceased after four.

The next acquisition of land, purchased by a donor, was the frame house on Orange Avenue with an existing driveway, next door to the building that presently houses the library. This would give us a second access to the Gardens, but the city said 'no,' because it would be 'too dangerous' near the busy intersection of 41 and Orange. After arguing our case before a hostile city commission, Ken Thompson, the city manager, said, 'let them try it.' Begrudgingly, Ken's suggestion was allowed. Of course, it worked, but we agreed that the exit would be limited by a 'no left turn.' Nothing more was ever heard.

The next acquisition was the two-story, frame house east of the administration building, purchased mostly from donated funds. It was used as student quarters until it was demolished for more parking. The corner building, previously a dental office, then insurance office, but now the library, was acquired next with funds from the Selby Foundation, Eric Young, an English philanthropist, and donors. It became known as the EYMC, the Eric Young Micropropagation Centre, which eventually failed and was abandoned.

Volunteers worked tirelessly on exhibits, luaus, plant sales, auctions, and all kinds of social events to raise money. Money was always a problem. We spent money we did not have, but we had tremendous assets, so there was never a possibility of our facing bankruptcy. Had we always waited until we could afford something, we would have been still sitting in Mrs. Selby's house. We were in debt, but by the end of eight years, our financial picture was looking better. Income from sales, special events, and donations was increasing, and the debt was decreasing.

The board had been expanded to include bankers who thought a new director was necessary. A retired Air Force General was hired to replace Dodson who was made Director of Research. Camaraderie and enthusiasm vanished. Volunteers were alienated. A promised research building with endowment from Jesse Cox failed to materialize. With fancy charts, the new director general "proved" how much the greenhouses with extensive collections, such as aeroids and gesneriads, were wasting money. He decided to convert a large, valuable greenhouse into a room for meetings and social events. After the slow years that followed, the growth of the Gardens would inevitably accelerate with the great infrastructure already in place. It could not fail, and it did not fail. The momentum regained in the last 30 years has been phenomenal.

LANKESTERIANA 13(3): 337—351. 2014.

ARTÍCULO INVITADO*

CONSIDERACIONES SOBRE LA HISTORIA DE LA PRIORIDAD TAXONÓMICA DE *ONCIDIUM ORNITHORHYNCHUM*

LAURA C. MAZO[1], ALBERTO GÓMEZ-GUTIÉRREZ[1,2,5], SONIA R. QUINTANILLA[1, 2],
JAIME E. BERNAL[1, 2] & PEDRO ORTIZ-VALDIVIESO, S.J.†[2,3]

[1]Instituto de Genética Humana, Facultad de Medicina, Pontificia Universidad Javeriana,
Cra 7 # 40-62, edificio 32, Bogotá D.C., 110231, Colombia
[2]Iniciativa Genómica Javeriana, Pontificia Universidad Javeriana, Cra 7 # 40-62, edificio 32,
Bogotá D. C., 110231, Colombia
[3]Asociación Bogotana de Orquideología, Avenida calle 63 # 68G-14, Bogotá D. C., Colombia
[5]Autor para correspondencia: agomez@javeriana.edu.co
† Pedro Ortiz-Valdivieso, S.J. (1926-2012)

RESUMEN: La historia de la prioridad taxonómica de la orquídea *Oncidium ornithorhynchum* está aún por aclarar si se consideran las diferentes descripciones y publicaciones de esta especie propuestas en los siglos XVIII y XIX por botánicos como José Celestino Mutis, John Lindley, Alexander von Humboldt, Aimé Bonpland y Carl S. Kunth, entre otros. Con el fin de resolver las inconsistencias en los reportes taxonómicos de esta especie en el transcurso del tiempo, y teniendo como base la reciente aclaración realizada por Jiménez y Hágsater sobre la identidad del ejemplar tipo conservado en París, hemos procedido a ordenar las fuentes primarias asociadas con su descripción y nomenclatura botánica.

ABSTRACT. The history of the nomenclatural taxonomic priority of the orchid *Oncidium ornithorhynchum* is yet to be clarified, as successive descriptions and publications of this species were proposed in the eighteenth and nineteenth centuries by botanists such as José Celestino Mutis, John Lindley, Alexander von Humboldt, Aimé Bonpland and Carl S. Kunth, among others. In order to resolve the inconsistencies in taxonomic reports of this species in the course of time, and based on the recent clarification by Jiménez and Hágsater on the type specimen conserved in Paris, we proceeded to review the primary sources associated with its description and botanical nomenclature.

PALABRAS CLAVES: Orquídeas, *Oncidium ornithorhynchum*, *O. pyramidale*, exsicados, herbario

Introducción. La familia de las orquídeas cuenta con el mayor número de especies de todo el reino vegetal aproximadamente 30000 (Montes y Eguiluz 1996). Ellas se encuentran en todos los continentes y en todos los climas, con excepción de las zonas polares. Colombia puede considerarse como una zona privilegiada para las orquídeas por la variedad de climas y zonas ecológicas de su territorio. Se han registrado hasta hoy más de 3000 especies de orquídeas en el territorio colombiano (Asociación Bogotana de Orquideología 2013).

Oncidium ornithorhynchum Kunth es una especie de orquídea perteneciente al género *Oncidium* Swartz (subtribu Oncidiinae) cuyo nombre deriva de la raíz griega *onkos*, tumor, refiriéndose al callo tuberculado del labelo. El nombre específico *ornithorhynchum* procede de las palabras griegas *ornitho*, relativo a las aves, y *rhynchos* que significa pico. Son plantas epífitas de los páramos, ubicadas entre 2850 y 3340 metros sobre el nivel del mar (msnm) y se reconocen por la inflorescencia erecta, en forma "piramidal" (Jiménez & Hágsater 2010, Pridgeon *et al.* 2009).

La descripción taxonómica de *Oncidium ornithorhynchum* ha variado con el tiempo y los círculos de investigadores involucrados, hasta presentarse confusiones fenotípicas y biogeográficas como la

---

* Este artículo fue preparado en el marco de la celebración del 40 aniversario del Jardín Botánico Lankester.

que reportaron recientemente Jiménez y Hágsater (2010). Este no es un caso único en el trabajo combinado del trío científico conformado por Humboldt, Bonpland y Kunth (H.B.K.), pues se conocen al menos 2 ejemplos más de inconsistencias biogeográficas en las colecciones H.B.K. La primera, en la que la localidad de la colección "Santa Fe" fue interpretada como "Santa Fe, México" (hoy en día parte del estado de Nuevo México, USA), lo cual no sólo le sucedió a Kunth, sino también a Linneo (Oscar Vargas, com. pers. 2012), como fue publicado respectivamente para dos especies de la familia Asteraceae, *Diplostephium phylicoides* (Kunth) Wedd. (Vargas 2011) y *Lycoseris mexicana* (L.) Cass (Díaz-Piedrahita *et al.* 1997)

La primera de estas inconsistencias en la colección H.B.K., fue reportada por Vargas (2011) en los siguientes términos:

"*Diplostephium phylicoides* (Kunth) Wedd., Chlor. And. 1: 205. 1856. Distribution: col. series: Phylicoidea. *Aster phylicoides* Kunth, Nov. Gen. Sp. Pl. 4:93. 1820. TYPE: COLOMBIA [erroneously cited as Mexico], [without date], *Humboldt & Bonpland s.n.* (P "Herb. Bonpland", holotype; P "Herb. Bonpland", isotype; F, fragment). The type specimen was supposed to be collected in Mexico, it is known that some of the Humboldt & Bonpland collections were wrongly labeled as collected in Santa Fe, Mexico (now USA), while they [were collected near] Bogotá (before: Santa Fe de Bogotá), Colombia".

La segunda inconsistencia biogeográfica en la colección H.B.K., correspondiente a la orquídea *Telipogon nervosus* Druce, fue reportada por el padre Pedro Ortiz-Valdivieso, en los siguientes términos:

"Una de las primeras plantas que envió Mutis a Linneo fue recolectada en las minas de oro de Suratá (Santander) que Linneo interpretó de manera equivocada y publicó como *Tradescantia nervosa* Linn. en 1771. Mutis, en cambio, sí se dio cuenta de que se trataba de lo que Linneo llamaba una ginandra (hoy orquídea) y pensó en darle el nombre de Mormolycanthus tradescantioides pero nunca la publicó el gaditano y esto lo conocemos solo por una carta de Mutis al botánico sueco Peter Jonas Bergius (1730-1790) con fecha de enero de 1786 (Archivo epistolar del sabio naturalista Don José Celestino Mutis 1968, pp. 277-292). Humboldt y Bonpland encontraron la misma planta, probablemente en los alrededores de Bogotá (donde todavía es frecuente), y no, como se afirma en *Nova genera*, donde se anota que crece "sobre los árboles en la regiones templadas del Reino neogranadino, junto a Santa Ana y Mariquita, alt. 400 toesas" (lámina LXXV del *Nova genera et species plantarum*). Esta especie nunca ha sido encontrada de nuevo en esa región y a alturas tan bajas (600 m sobre el nivel del mar), y de ordinario se ha encontrado entre los matorrales en el suelo. Probablemente hubo alguna confusión en las fichas. Pero lo que sí estuvo correcto fue el publicarla como un nuevo género *Telipogon angustifolius* Kunth solo que, como ya había sido publicada por Linneo con un epíteto específico propio, era necesario conservarlo, y así, en 1917, el botánico británico George Claridge Druce (1850-1932) hizo la nueva combinación a *Telipogon nervosus*, nombre que es actualmente aceptado". (Ortiz-Valdivieso & Gómez, en imprenta).

Con base en estos antecedentes, y en las consideraciones particulares expuestas en lo que concierne a la orquídea *Oncidium ornithorhynchum*, es conveniente ordenar la cronología de las diferentes descripciones taxonómicas de esta especie para resolver adecuadamente su identidad.

Cronología de la descripción de *Oncidium ornithorhynchum*. Esta especie fue colectada y registrada por primera vez por José Celestino Mutis (1732-1808) en la Real Expedición Botánica del Nuevo Reino de Granada que funcionó formalmente entre los años 1783 y 1816. En su descripción, Mutis no registró su nombre taxonómico en la lámina correspondiente, y ésta sería denominada posteriormente por los estudiosos del Real Jardín Botánico de Madrid, como *Oncidium pyramidale* Lindl refiriendo que el epíteto específico proviene del término latino *pyramis, -idis* = pirámide, en clara alusión a la forma de la inflorescencia de esta especie (Traducido del latín por Pedro Ortiz Valdivieso, S.J., 2000, p. 51).

En medio de los reportes botánicos de la Real Expedición Botánica del Nuevo Reino de Granada, y considerando que José Celestino Mutis llegó a este virreinato español en 1760, se puede considerar que

Figura 1. A — Lámina original a color de la orquídea *Oncidium pyramidale* en la colección de la Flora de la Real Expedición Botánica del Nuevo Reino de Granada. Esta aparece sin descriptor taxonómico. B — En el verso de la lámina original aparece efectivamente la inscripción "Oncidium pyramidale Lindl." manuscrita a lápiz en la parte inferior izquierda, y esta descripción fue atribuida a Charles Schweinfurth (1890-1970). Otras inscripciones reportadas sobre esta lámina original son: "537" [tachado]. Inscripción manuscrita a lápiz [s. XX], en la parte inferior derecha y "8.200" en el verso, inscripción manuscrita a lápiz, en la parte superior derecha. DIV. III A-486, en el Real Jardín Botánico de Madrid (http://www.rjb.csic.es/icones/mutis/paginas/laminadibujo.php?lamina=837).

el reporte no fechado de esta orquídea habría tenido lugar entre 1760 y 1808, año de su fallecimiento. Esta especie, dibujada por uno de los pintores de la Expedición Botánica en aquella época (Fig.1), fue descrita en el siglo XX por el Padre Pedro Ortiz Valdivieso, S.J. (1926-2012) como:

"Planta epifita de tamaño mediano, con pseudobulbos agregados ovoides, 2.5-7 cm de alto, cubiertos en la base por 2 o 3 pares de vainas conduplicadas, escamosas, con ápice agudo, bi-trifoliadas; tiene hojas elíptica-oblongas hasta oblanceoladas, agudas o corto-acuminadas, de 14-20 cm de largo y 3,38 cm de ancho. Se caracteriza por presentar una inflorescencia que nace de la axila de una vaina basal y es paniculada, multiflora, suberecta, de forma generalmente piramidal, de hasta 70 cm de largo, incluyendo el escapo, flores pequeñas, amarillas con manchas pardas, fragantes, con segmentos extendidos; sépalo dorsal oblongo-lanceolado, ca. 7.5 mm de ancho, laterales libres, linear-lanceolados, oblicuos ligeramente más largos que el dorsal, pétalos aovado-oblongos, abruptamente agudos, apiculados, de igual longitud sépalo dorsal pero el doble de ancho; labelo más largo que los otros segmentos, pandurado-trilobado, sésil, con base abrupto-auriculada, bilobado en el ápice, 10-12 mm de largo y 9.8–11.3 mm de ancho a través de los lóbulos laterales; los lóbulos laterales suborbiculares, lóbulo medio oborado, emarginado o bilobado; disco en la base, con un callo plurituberculado, blanco, columna pequeña, fuertemente signoidea en vista lateral *ca.* 3 mm de alto, con un par de aletas erectas en la pared apical, profundamente bilobuladas, tabla infra estigmática prominente; róstelo linear, antera

Figura 2. Lámina 39 que acompaña la publicación impresa de la orquídea *Oncidium pyramidale* en la obra *Flora de la Real Expedición Botánica del Nuevo Reino de Granada. Vol. XI, Orchideaceae, Vol XI. Tomo 5*.

Figura 3. Lámina no. 486a que acompaña la publicación original de *Oncidium pyramidale* en la obra *Flora de la Real Expedición Botánica del Nuevo Reino de Granada. Vol. XI, Orchideaceae, Vol XI. Tomo 5*.

alargada, polinios en número de 2 con estípite largo y viscidio pequeño (Figs. 2–3). Su hábitat y distribución es en diversas zonas montañosas de Colombia, en clima frio; aunque también ha sido herborizada en Ecuador y Perú" (Traducido del latín por Pedro Ortiz Valdivieso, S.J. 2000)

Por otro lado, a comienzos del siglo XIX, Alexander von Humboldt (1769-1859) y Aimé Bonpland (1773-1858) viajaron a América y colectaron varias especies de orquídeas, que fueron enviadas al herbario del Museo Nacional de Historia Natural de París (Fig. 4). Posteriormente, en el año 1815, basándose en el ejemplar tipo colectado por Humboldt y Bonpland, Carl Sigismund Kunth (1788-1855) publica la descripción de *Oncidium ornithorhynchum* (Fig. 5) en el tomo I de la obra *Nova Genera et Species Plantarum* (Fig. 6), sin referirse al color de la especie colectada. Esta especie habría sido publicada coloreada en amarillo sin autorización de los colectores en una de las ediciones de lujo del *Nova Genera et Species Plantarum*. En efecto, Jiménez y Hágsater (2010) refieren que más adelante, en el curso del siglo XIX, George Ure Skinner (1804-1867) habría enviado a James Bateman (1811-1897) una orquídea colectada en Guatemala, quien la publicó erróneamente en 1837 como *Oncidium ornithorhynchum* (Fig. 7) en su obra *The Orchidaceae of México and Guatemala* (Jiménez & Hágsater 2010) (Fig. 8). En esta publicación centroamericana solo se hace referencia a Humboldt y Kunth (sic), excluyendo al botánico Aimé Bonpland, colector y coautor del *Nova Genera et Species Plantarum*. También mencionan Jiménez y Hágsater (2010) que hay copias coloreadas a mano donde las flores de esta especie se representaban de color amarillo; afirmando que seguramente se debía a que el dibujo se hizo a partir de un espécimen seco, dando prioridad a la referencia sobre el lugar en donde habría sido colectada la planta.

Luego, en 1840, John Lindley (1799-1865) publica incorrectamente a esta misma especie como *Oncidium ornithorhynchum* (Fig. 9) en el *Botanical Register* (Fig. 10) y la describe, haciendo en primer lugar referencia a la descripción previa de Humboldt, Bonpland y Kunth y, en segundo lugar, a la descripción de Bateman.

En el año 1845, Sir William Jardine (1800-1874) y colaboradores describen esta orquídea por primera vez con el nombre de *Oncidium pyramidale* en *The Annals and Magazine of Natural History* (Fig. 11). Este nuevo nombre, cuya prioridad se atribuye a Lindley, obedece a que sería una especie intermedia entre *Oncidium excavatum* Lindl y *Oncidium ornithorhynchum*, y hace referencia a una colecta de Theodor Hartweg en la región de Pasto, en el sur de Colombia, sin especificar su color ni publicar la lámina correspondiente.

A mediados del siglo XIX y a comienzos del siglo XX, se propondrían como sinónimos de esta especie a *Oncidium chrysopyramis* Rchb.f. & Warsz (Fig. 12), publicada en el año 1854 por Berthold Seemann (1825-1871) y Wilhelm Seemann (c1820-1868) en *Bonplandia*, y a *Oncidium maderoi* Schltr (Fig. 13), publicada en el año 1920 por Friedrich Fedde (1873-1942) en *Repertorium Specierum Novarum Regni Vegetabilis*.

En el año 1922 Fritz Krænzlin (1847-1934) ilustró esta especie con el nombre *Oncidium pyramidale* Lindl. en su obra *Orchidaceae-Monandrae, Tribus Oncidiinae-Odontoglosseae pars II* (Fig. 14), especificando que se distribuye en Colombia y Ecuador, sin ninguna referencia a Centroamérica, ni a *Oncidium ornithorhynchum*.

Recientemente, en 1996, María Dolores Montes y Pedro Eguiluz, en su publicación *El cerro, frontera abierta recorrido ecológico por el cerro de Usaquén* reportan – con el nombre que les fue indicado por Pedro Ortiz Valdivieso – la presencia de *Oncidium*

Figura 4. Foto del ejemplar tipo de *Oncidium ornithorhynchum* en el herbario de París. Tomada por Alberto Gómez Gutiérrez.

Figura 5. Lámina no. 80 que acompaña la publicación original de *Oncidium ornithorhynchum* en la obra *Nova Genera et Species Plantarum*, basada en el ejemplar colectado por Humboldt y Bonpland en América y conservado en el herbario de París.

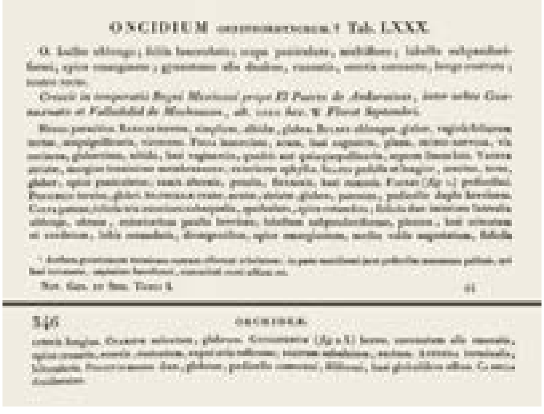


Figura 6. Descripción taxonómica original de Humboldt, Bonpland & Kunth, 1815, pp. 345-346.

Figura 7. Lámina que acompaña la publicación original de *Oncidium ornithorhynchum* en la obra *Orchidaceae of Mexico and Guatemala*.

ornithorhynchum en el norte de Bogotá y la describen como un género con flores (18 × 12 mm) y hojas (30 × 5 cm), “plantas medianas o pequeñas con o sin seudobulbos. Inflorescencia basal en racimo de pocas hasta muchas flores y variados tamaños, muchas veces vistosas. Se encuentra desde México hasta Chile, en todos los climas”. Estos autores dan una distribución claramente equivocada, siguiendo lo reportado por Kunth en cuanto a la localidad del tipo de *O. ornithorhynchum* como: “El Puerto Andaracuas, entre Guanajuato y Valladolid, Michoacán” (Jiménez & Hágsater 2010). Esa localidad corresponde a la provincia fisiográfica conocida como la Altiplanicie mexicana meridional y El Bajío, una zona muy seca, donde abundan los encinares secos, muy pobres en orquídeas epífitas, siendo la más frecuente *Laelia speciosa* Kunth (Hágsater *et al*. 2005).

De acuerdo con el reporte del GBIF (Global Biodiversity Information Facility) habría 131 ocurrencias de *Oncidium ornithorhynchum* en América incluyendo, de norte a sur, los siguientes países: Estados Unidos (1), México (88), Guatemala (6), Nicaragua (2), El Salvador (3), Panamá (1),

ONCIDIUM ORNITHORHYNCHUM.

FIGURA 8. Descripción taxonómica original de James Bateman, 1837, pp. 34-35.

Colombia (27) y Ecuador (3) (GBIF, consultado en noviembre 6 de 2013), sin reportarse hasta la fecha en esta base de datos ocurrencias de esta especie en otros países (Ortiz-Valdivieso S.J 2000). Sin embargo, al revisar el detalle de las plantas centroamericanas incluidas en este reporte, la imagen asociada es una orquídea violeta que, de acuerdo con el reporte de Jiménez y Hágsater (2010), correspondería mejor a *Oncidium sotoanum*.

Las últimas descripciones científicas de esta orquídea al iniciarse el siglo XXI incluyen las publicaciones enfocadas a la vez al ámbito botánico como al ámbito filogenético. Dentro de estas se encuentran "Comparative histology of floral elaiophores in the orchids *Rudolfiella picta* (Schltr.) Hoehne (Maxillariinae *sensu lato*) and *Oncidium ornithorhynchum* H.B.K (Oncidiinae *sensu lato*)" realizada por Kevin L. Davies y Malgorzata Stpiczynska en el año 2009. También, el artículo de Rolando Jiménez Machorro y Eric Hágsater del año 2010 que hemos venido citando, titulado "*Oncidium ornithorhynchum*, una especie mal interpretada y un nombre para una vieja especie: *Oncidium sotoanum* (Orchidacee)", en el que corrigen definitivamente el nombre de esta planta mexicana. Por otra parte, nuestro grupo publicó en 2012 el artículo "Extraction and amplification of DNA from orchid exsiccates conserved for more than half a century in a herbarium

FIGURA 9. Lámina que acompaña la publicación original realizada por John Lindley en *Edwards's Botanical Register*.

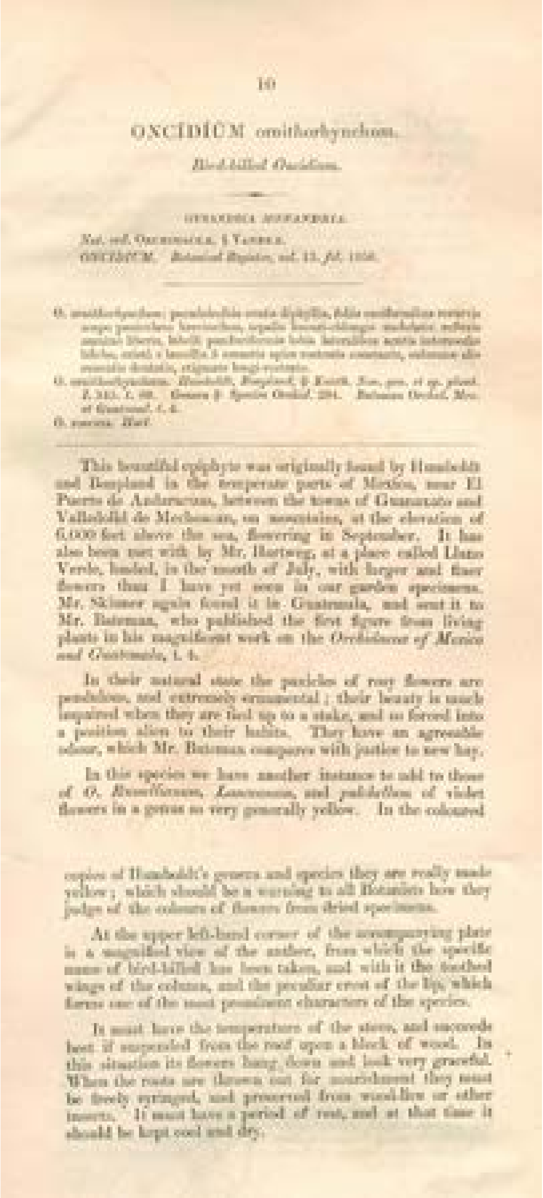
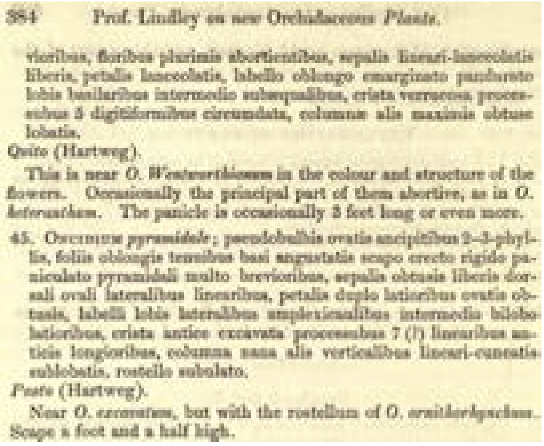


Figura 10. Descripción taxonómica original de John Lindley, 1840, pp. 30-31.

in Bogotá, Colombia", reportando la presencia de *Oncidium ornithorhynchum* en Duitama (Boyacá) a 2870 metros de altura y también en Santandercito (Cundinamarca) a 2000 metros de altura, de acuerdo con los registros del herbario "Lorenzo Uribe Uribe S. J." de la Pontificia Universidad Javeriana (Mazo *et al.* 2012).



384 Prof. Lindley on new Orchidaceous *Plants.*

vioribus, floribus plurimis abortientibus, sepalis lineari-lanceolatis liberis, petalis lanceolatis, labello oblongo emarginato pandurato lobis basilaribus intermedio subaequalibus, crista verrucosa processibus 5 digitiformibus circumdata, columnae alis maximis obtuse lobatis.

Quito (Hartweg).

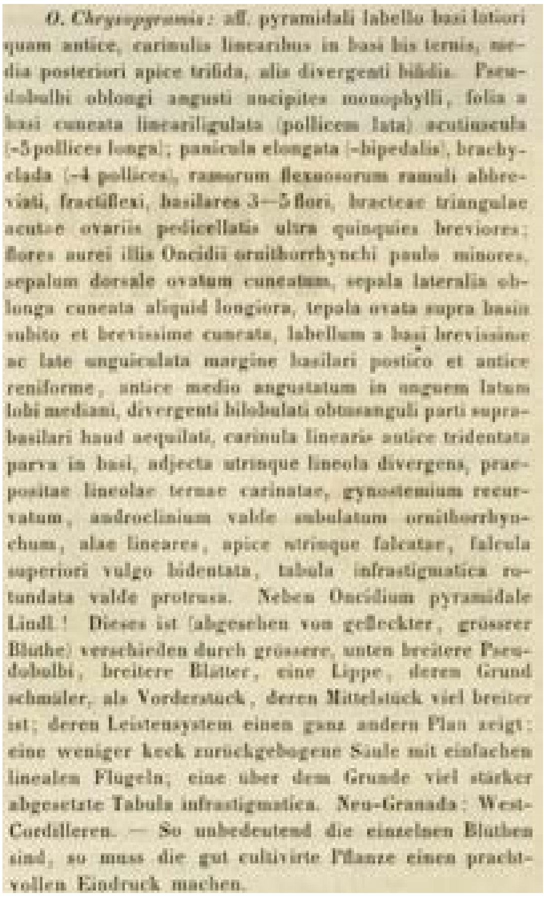
This is near *O. Wentworthianum* in the colour and structure of the flowers. Occasionally the principal part of them abortive, as in *O. heteranthum.* The panicle is occasionally 3 feet long or even more.

45. Oncidium *pyramidale*; pseudobulbis ovatis ancipitibus 2–3-phyllis, foliis oblongis tenuibus basi angustatis scapo erecto rigido paniculato pyramidali multo brevioribus, sepalis obtusis liberis dorsali ovali lateralibus linearibus, petalis duplo latioribus ovatis obtusis, labelli lobis lateralibus amplexicaulibus intermedio bilobo latioribus, crista antice excavata processibus 7 (?) linearibus anticis longioribus, columna nana alis verticalibus lineari-cuneatis sublobatis, rostello subulato.

Pasto (Hartweg).

Near *O. excavatum*, but with the rostellum of *O. ornithorhynchum.* Scape a foot and a half high.

Figura 11. Descripción taxonómica original de William Jardine *et al.* 1845, p. 384.



O. Chrysopyramis: aff. pyramidali labello basi latiori quam antice, carinulis linearibus in basi bis ternis, media posteriori apice trifida, aliis divergenti bifidis. Pseudobulbi oblongi angusti ancipites monophylli, folia a basi cuneata lineariligulata (pollicem lata) acutiuscula (-5 pollices longa); panicula elongata (-bipedalis), brachyclada (-4 pollices), ramorum flexuosorum ramuli abbreviati, fractiflexi, basilares 3—5 flori, bracteae triangulae acutae ovariis pedicellatis ultra quinquies breviores; flores aurei illis Oncidii ornithorrhynchi paulo minores, sepalum dorsale ovatum cuneatum, sepala lateralia oblonga cuneata aliquid longiora, tepala ovata supra basin subito et brevissime cuneata, labellum a basi brevissime ac late unguiculata margine basilari postico et antice reniforme, antice medio angustatum in unguem latum lobi mediani, divergenti bilobulati obtusanguli parti suprabasilari haud aequilati, carinula linearis antice tridentata parva in basi, adjecta utrinque lineola divergens, praepositae lineolae ternae carinatae, gynostemium recurvatum, androclinium valde subulatum ornithorrhynchum, alae lineares, apice utrinque falcatae, falcula superiori vulgo bidentata, tabula infrastigmatica rotundata valde protrusa. Neben Oncidium pyramidale Lindl.! Dieses ist (abgesehen von gefleckter, grösserer Bluthe) verschieden durch grössere, unten breitere Pseudobulbi, breitere Blätter, eine Lippe, deren Grund schmäler, als Vorderstuck, deren Mittelstuck viel breiter ist; deren Leistensystem einen ganz andern Plan zeigt; eine weniger keck zuruckgebogene Saule mit einfachen linealen Flugeln; eine uber dem Grunde viel stärker abgesetzte Tabula infrastigmatica. Neu-Granada: West-Cordilleren. — So unbedeutend die einzelnen Bluthen sind, so muss die gut cultivirte Pflanze einen prachtvollen Eindruck machen.

Figura 12. Descripción taxonómica original de Berthold Seemann y Wilhelm Seemann. 1854, p. 108

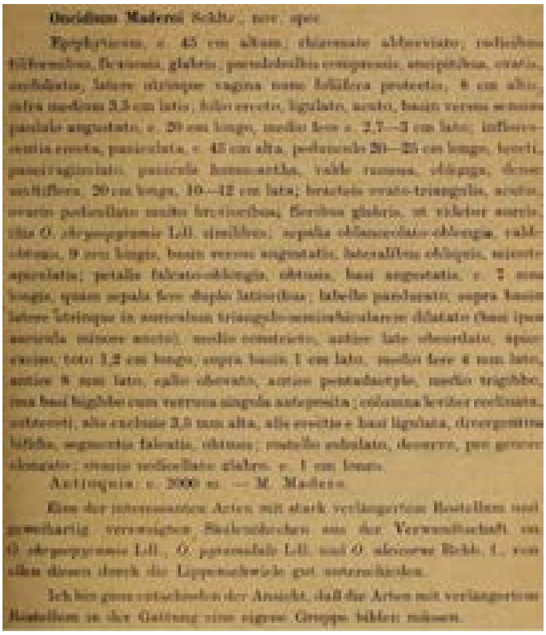


Figura 13. Descripción taxonómica original de Friedrich Fedde, 1920, p. 191.

Discusión. Al comparar cada una de estas publicaciones se observan varias inconsistencias en el epíteto específico, en el color de la flor y en el hábitat de la orquídea *Oncidium ornithorhynchum* (Tabla 1). En cuanto al color de la flor, tanto Lindley como Bateman hacen referencia en sus publicaciones a la obra de Humboldt (*Nova Genera et Species Plantarum*), el primero citando como colaboradores a Bonpland y a Kunth, como debe ser, y el segundo solamente a Kunth, excluyendo inexplicablemente a Bonpland. Mencionan que hay dos copias de esta obra coloreadas a mano donde las flores de esta especie se representan de color amarillo, afirmando que seguramente se debía a que el dibujo se hizo a partir de un espécimen seco (Jiménez & Hágsater 2010), sin considerar que el error podría corresponder, alternativamente, a un error de transcripción del lugar de colección de la planta llevada a Europa por Humboldt y Bonpland.

En 1990, Miguel Ángel Soto tuvo la oportunidad de ver en el herbario de París el ejemplar tipo de *Oncidium ornithorhynchum* (Fig. 4), y allí constató que la especie que se encontraba distribuida en México no correspondía con dicho ejemplar. Posteriormente, en 1997, Adolfo Espejo viajó al herbario de París y tuvo la posibilidad de tomarle una foto al ejemplar tipo de *O. ornithorhynchum* (Jiménez & Hágsater 2010). Con la ayuda de esta imagen, al examinar y comparar los ejemplares tipo de *Oncidium*, Rolando Jiménez confirmó en el año 2008 que la especie encontrada en el herbario de París, no concordaba con la especie que se distribuye en México y Centroamérica, en razón a las marcadas diferencias físicas que hay entre los dos ejemplares (Jiménez & Hágsater 2010). La especie que se encuentra en el herbario de París, presenta un margen membranoso en las vainas foliosas de la base del pseudobulbo; hay una sola inflorescencia

Figura 14. Descripción taxonómica original de Fritz Krænzlin, 1922, pp. 195-196.

Figura 15. Foto de *Oncidium ornithorhynchum*. Tomada por Pedro Ortiz-Valdivieso, S.J.† Colombia.

Figura 16. *Oncidium sotoanum* R. Jiménez & Hágsater. Basado en *R. Jiménez 626*, Orizaba Veracruz, Mexico, AMO [ilustración tomada de Icon. Orchid. (Mexico)1: pl.77].

Figura 17. Foto de *Oncidium sotoanum* R. Jiménez & Hágsater; M. A. Soto 4900, Chiapas. Tomada por de R. Jiménez M.

por pseudobulbo, erecta, con las ramas de la base alargadas, acortándose gradualmente hacia el ápice (inflorescencia piramidal), el pedúnculo y raquis son casi erectos, ligeramente sinuosos, el callo del labelo se compone de dos quillas cortas hacia los lados y otras tres hacia el ápice, las alas de la columna son erectas y cuneadas. En contraste, la especie mexicana tiene flores violetas con callo amarillo, el margen de las vainas foliosas es membranáceo pero este es inconspicuo, midiendo 1 mm de ancho; cada pseudobulbo produce simultáneamente 2-4 inflorescencias arqueadocolgantes, con las ramas de la base del raquis cortas, las de la mitad largas y las del ápice cortas; el raquis es en zigzag, el callo es distinto y las alas son oblicuamente dolabriformes y paralelas al cuerpo de la columna (Jiménez & Hágsater 2010).

Debido a la confusión en la descripción de esta especie, Rolando Jiménez y Eric Hágsater, en su artículo de 2010, postularon que debe haber un error en la indicación de la localidad del *Oncidium ornithorhynchum*, colectada por Humboldt y Bonpland, como si fuera de México. El ejemplar tipo, que se conserva en París, tanto como el dibujo correspondiente, muestran que este espécimen no es lo que a partir de Lindley se ha considerado como "*Oncidium ornithorhynchum* de México y Centroamérica" (y no de Suramérica), sino que corresponde a lo que se ha llamado *Oncidium pyramidale* de Colombia, Ecuador y Perú, siendo este *O. pyramidale* sinónimo de *O. ornithorhynchum* (Fig. 15). Por otra parte, la especie mexicana con flores violetas, se conoce ahora, con razones bien fundamentadas, como *Oncidium sotoanum* (Fig. 16-17). A pesar que se ha propuesto a *Oncidium chrysopyramis* Rchb.f. como sinónimo de *O. ornothorhynchum*, Rolando Jiménez y Eric Hágsater establecen que al presentar esta especie una

TABLA 1. Datos importantes de cada una de las publicaciones realizadas por 7 botánicos.

Titulo publicación	**Autor**	**Año**	**Epíteto específico**	**Nombre correcto**	**Color de la flor**	**Hábitat**
Real Expedición Botánica del Nuevo Reino de Granada	José Celestino Mutis [Pedro Ortiz Valdivieso]	1760- 1808 [2000]	[*Onc. pyramidale*]	*Onc. ornithorhynchum*	Amarilla	Colombia, [Ecuador y Perú]
Nova Genera et Species Plantarum	Alexander von Humboldt, Aimé Bonpland y Carl S. Kunth	1815	*Onc. ornithorhynchum*	*Onc. sotoanum*	Amarilla	México-Puerto de Andaracuas, entre Guanaxuato y Valladolid de Michoacán
Orchidaceae of Mexico and Guatemala	James Bateman	1837	*Onc. ornithorhynchum*	*Onc. sotoanum*	Violeta	Michoacán, Oaxaca y Guatemala
Edwards´s Botanical Register	John Lindley	1840	*Onc. ornithorhynchum*	*Onc. sotoanum*	Violeta	México y Guatemala
The Annals and Magazine of Natural History	William Jardine et al	1845	*Onc. pyramidale*	*Onc. ornithorhynchum*	-	Pasto
Orchidaceae-Monandrae, Tribus Oncidiinae-Odontoglosseae, pars II	Fritz Kranzlin	1922	*Onc. pyramidale*	*Onc. ornithorhynchum*	-	Colombia y Ecuador
El cerro, frontera abierta recorrido ecológico por el cerro de Usaquén	María Dolores Montes y Pedro Eguiluz	1996	*Onc. ornithorhynchum*	*Onc. ornithorhynchum*	-	Desde México hasta Chile

Tabla 2. Resumen de las publicaciones mencionadas a lo largo del escrito.

Año	Autor
1760-1808	José Celestino Mutis, quien colecta en el Nuevo Reino de Granada a partir de 1760 y fallece en 1808, dirige la Real Expedición Botánica del Nuevo Reino de Granada y describe *Oncidium ornithorhynchum* denominada posteriormente como *Oncidium pyramidale* en la *Flora de la Real Expedición Botánica del Nuevo Reino de Granada* (Real Expedición Botánica del Nuevo Reino de Granada, 1783-1816).
1801	Alexander von Humboldt y Aimé Bonpland viajan a Sudamérica y colectan la orquídea que bautizan *Oncidium ornithorhynchum*. La depositan en el herbario de París. (Jiménez & Hágsater 2010).
1815	Carl S. Kunth, con base en el tipo colectado por Humboldt y Bonpland, publica la especie *Oncidium ornithorhynchum* en su obra *Nova Genera et Species Plantarum* (Humboldt, Bonpland & Kunth 1815).
1836	Theodor Hartweg le envía a Loddiges una orquídea con el nombre *Oncidium ornithorhynchum* colectada en Oaxaca, México, de tal forma que la introdujo al cultivo en Europa; también este año George Skinner le envía una James Bateman. Flores violetas. (Jiménez & Hágsater 2010).
1837	James Bateman publica una orquídea con el nombre *Oncidium ornithorhynchum* en su obra *Orchidaceae of México and Guatemala*. Flores violetas (Bateman 1837).
1840	John Lindley publica esta orquídea en *Edwards's Botanical Register* con el nombre de *Oncidium ornithorhynchum* (Lindley 1840).
1845	William Jardine *et al.* la publican como *Oncidium pyramidale* en *The Annals and Magazine of Natural History* (Jardine *et al.* 1845).
1854	Berthold Seemann y Wilhelm Seemann reportan *Oncidium chrysopyramis* Rchb. f & Warsz como sinónimo de *Oncidium pyramidale* en *Bonplandia* 2: 108 (Seemann & Seemann 1854).
1920	Fedde publica *Oncidium maderoi* como sinónimo de *Oncidium pyramidale* en *Repertorium Specierum Novarum Regni Vegetabilis* (Fedde 1920).
1922	Fritz Kranzlin publica esta especie como *Oncidium pyramidale* en la obra *Orchidaceae-Monandrae, Tribus Oncidiinae-Odontoglosseae pars II* (Kranzlin 1922).
1968	Pedro Ortiz Valdivieso, S.J., reporta *Oncidium ornithorhynchum* en Colombia, y en el año 1975 la deposita en el herbario de la Pontificia Universidad Javeriana. Esta concuerda con la planta denominada *Oncidium pyramidale* de la Real Expedición Botánica y con la planta denominada *Oncidium ornithorhynchum* de la colección de Humboldt y Bonpland depositada en el Herbario de París
1990	Miguel Ángel Soto viaja a París y ve que la *Oncidium ornithorhynchum* que está en el herbario no concuerda con orquídeas mexicanas de la misma región (Jiménez & Hágsater 2010).
1996	María Dolores Montes y Pedro Eguiluz publican una *Oncidium ornithorhynchum* en su libro *El cerro, frontera abierta recorrido ecológico por el cerro de Usaquén* especificando que esta especie de encuentra desde México hasta Chile (Montes & Eguiluz 1996).
1997	Adolfo Espejo viaja al herbario de París y le toma una foto al tipo de *Oncidium ornithorhynchum* (Jiménez & Hágsater 2010).
2008	Rolando Jiménez, con base en la foto tomada por Adolfo Espejo, compara *O. ornithorhynchum* de París con la especie de México (Jiménez & Hágsater 2010).
2010	Rolando Jiménez y Eric Hágsater, publican que el tipo de *Oncidium ornithorhynchum* conservado en París coincide con la *Oncidium pyramidale* que se distribuye en Colombia, Ecuador y Perú de tal forma que el nombre *Oncidium pyramidale* queda como sinónimo del primero. En cuanto a la *Oncidium ornithorhynchum* que se distribuye en México, fue renombrada con el nombre de *Oncidium sotoanum* (Jiménez & Hágsater 2010).
2011	Laura Mazo *et al.* establecen la secuencia de los genes *matK* de tres (3) especímenes de *Oncidium ornithorhynchum* colectados en Colombia (Madrid-Cundinamarca y Duitama-Boyacá) de los cuales el primero correspondía a una planta fresca y los dos restantes se encontraron conservados en el "Herbario Julián Uribe Uribe S. J." de la Pontificia Universidad Javeriana, con 36 y 43 años de antigüedad, respectivamente (Mazo et al. 2012).

inflorescencia más laxa, no en forma “piramidal”, flores de menor tamaño y alas más angostas, es definitivamente diferente a la morfología de *Oncidium pyramidale* (Jiménez & Hágsater 2010).

En conclusión, tanto John Lindley como James Bateman, ilustraron una especie con flores rosadas o violetas, hábitat en México y con el nombre erróneo de *Oncidium ornithorhynchum*, diferenciándose un poco de Kunth quien la publicó con este mismo nombre y hábitat, aunque, a diferencia de los dos botánicos anteriores, la describió de manera explícita como una orquídea con flores amarillas. En contraste, tanto José Celestino Mutis, como Fritz Kranzlin y William Jardine la clasificaron con el nombre de *Oncidium pyramidal*e, flores amarillas (únicamente en la descripción de Mutis) y como hábitat: Colombia, Perú y Ecuador. Es importante recalcar que estos últimos 3 botánicos concuerdan con Kunth en el color amarillo de la flor, y se diferencian principalmente en su localización biogeográfica.

Lo anterior se explica gracias a la aclaración realizada por Jiménez y Hágsater, en donde se deduce que las descripciones de John Lindley y James Bateman corresponden ciertamente con la orquídea presente en México pero se equivocaron al nombrarla (siguiendo a Kunth) como *Oncidium ornithorhynchum*. Jiménez y Hágsater aclaran así, finalmente, la identidad de la planta centroamericana, distribuida en el sur de México y Centroamérica, como una nueva especie llamada *Oncidium sotoanum* y, a su vez, describen una nueva subespecie *O. sotoanum* ssp. *papalosmum* Jiménez, conocida únicamente de los estados de Oaxaca y Chiapas, México.

En el presente artículo nosotros postulamos que:

1. La orquídea descrita en Bogotá antes de 1808 por José Celestino Mutis, y luego en el curso del siglo XIX por Fritz Kranzlin y por William Jardine, con flores amarillas, distribución en Colombia, Perú, Ecuador, y denominada *Oncidium pyramidale*, es la que correspondería al mismo ejemplar publicado por Kunth con el nombre de *Oncidium ornithorhynchum*, en consonancia con que el epíteto especifico *Oncidium pyramidale* haya pasado a ser sinónimo del primero.
2. El ejemplar tipo de *Oncidium ornithorhynchum* que se encuentra hoy en el Herbario Histórico del Musée National d´Histoire Naturelle de Paris, y que tuvimos la ocasión de volver a examinar en el mes de marzo del presente año, correspondería mejor a una orquídea colectada en el territorio que se llamaba en aquella época “Virreinato de la Nueva Granada”, y que comprende hoy territorios de Colombia y Ecuador.
3. El registro manuscrito de esta orquídea en el Diario botánico o “Journal botanique” de Aimé Bonpland, podrá aclarar el origen biogeográfico del ejemplar tipo conservado en París, puesto que en general cada uno de los registros de este libro de campo fueron inscritos en orden consecutivo y cronológico, y podemos deducir, con base en las consideraciones del presente artículo, que el registro de esta especie se hallará en el tramo correspondiente a la zona sur de la actual Colombia, o bien a la zona Norte del actual Ecuador con fechas entre septiembre de 1801 y mayo de 1802.
4. Finalmente, nos proponemos intentar la comparación molecular del exsicado tipo conservado en París con ADN extraído de ejemplares de *Oncidium ornithorhynchum* colectados en Colombia o Ecuador.

AGRADECIMIENTOS. Los autores agradecen al personal del Herbario “Lorenzo Uribe, S.J.” (Facultad de Ciencias, Pontificia Universidad Javeriana), a los miembros del Instituto de Genética Humana (Facultad de Medicina, Pontificia Universidad Javeriana), particularmente a los colegas del grupo de investigación en ADN antiguo, así como a las doctoras Marpha Telepova, Cécile Aupic y Myriam Gaudeul, del Musée National d´Histoire Naturelle de Paris, y a la museógrafa Claudia Navas-Courbon, en la misma ciudad. Dedicamos este artículo a la memoria del Padre Pedro Ortiz Valdivieso, S.J. †

LITERATURA CITADA

Asociación Bogotana de Orquideología. http://www.orquideasbogotaabo.com/index.php?option=com_content&view=article&id=72&Itemid=30. Consultado: 17-01-2013.

Bateman, J. 1837-1843. *Oncidium ornithorhynchum*. Pp 34-35 *in*: The Orchidaceae of Mexico and Guatemala. London, Ridgway.

Davies, K. L & M. Stpiczynska. 2009. Comparative histology of floral elaiophores in the orchids *Rudolfiella picta* (Schltr.) Hoehne (Maxillariinae *sensu lato*) and

Oncidium ornithorhynchum H.B.K. (Oncidiinae *sensu lato*). Ann. Bot. 104: 221-234.

Díaz-Piedrahita, S. & C. Vélez-Nauer. 1997. Revisión de las tribus Barnadesiae y Mutisieae (Asteraceae) para la Flora de Colombia. *In*: Monografías del Jardín Botánico José Celestino Mutis, Vol. 1. Bogotá: Jardín Botánico "José Celestino Mutis".

Fedde, F. 1920. *Oncidium maderoi* Schltr. *In*: Repertorium specierum novarum regni vegetabilis. Dahlem bei Berlin: Verlag des repertoriums, Fabeckstr. 191 p.

Global Biodiversity Information Facility (GBIF) http://data.gbif.org/occurrences/searchCountries.htm?c[0].s=20&c[0].p=0&c[0].o=5322086 (consultado en: noviembre 6 de 2013)

Hágsater, E., M.A. Soto Arenas, G.A. Salazar Chávez, R. Jiménez Machorro, M.A. López Rosas & R.L. Dressler. 2005. Las Orquídeas de México. Instituto Chinoín, México, 304 p.

Hernández, G., 1968. Archivo epistolar del sabio naturalista José Celestino Mutis. Instituto Colombiano de Cultura Hispanica. Editorial Kelly. Bogotá, D.C. Vol 3, Tomo 1, pp. 277-292.

Humboldt, A., A. Bonpland & C. S. Kunth. 1815. "Oncidium ornithorhynchum". *In*: Nova Genera et Species Plantarum. París: Schoell. 1: 345-346.

Jardine, W., P. J. Selby, G. Johnson, C. Babington, J.H. Balfour & R. Taylor. 1845. *Oncidium pyramidale*. *In*: The Annals and Magazine of Natural History, including Zoology, Botany and Geology, Londres: R. and J. E. Taylor. 15: 384.

Jiménez, R. & E. Hágsater. 2010. *Oncidium ornithorhynchum*, una especie mal interpretada y un nombre para una vieja especie: *Oncidium sotoanum* (Orchidaceae). Lankesteriana 9(3): 411- 422.

Kranzlin, F. 1922. *Oncidium pyramidale* Lindl. Pp. 195-196 *in*: Orchidaceae-Monandrae: Tribus Oncidiinae-Odontoglosseae pars II.

Lindley, J. 1840. *Oncidium ornithorhynchum*. Pp. 30-31 *in*: Edward's Botanical Register, Vol. III. Londres: James Ridgway and Sonos, Piccadilly.

Mazo, L., A. Gómez, S. Quintanilla, J. Bernal & P. Ortiz-Valdivieso S.J. 2012. Extraction and amplification of DNA from orchid exsiccates conserved for more than half a century in a herbarium in Bogotá, Colombia. Lankesteriana 12(2): 121-129.

Montes, M.D. & P. Eguiluz. 1996. El cerro, frontera abierta. Recorrido ecológico por el cerro de Usaquén. Bogotá: Santillana. 110 p.

Ortiz-Valdivieso S.J, P. 2000. *Oncidium pyramidale* Lindl. *In*: Flora de la Real Expedición Botánica del Nuevo Reino de Granada (1783 – 1816). Vol. XI, Orchideaceae, Vol XI. Tomo 5. Madrid, España. Ediciones de Cultura Hispánica. 51 p.

Ortiz-Valdivieso, P. & A. Gómez. En imprenta. Las orquídeas de Colombia en la obra de Humboldt, Bonpland y Kunth. *In*: Los hermanos Alexander y Wilhelm von Humboldt en Colombia. Huellas históricas de la cooperación científica entre dos continentes.

Pridgeon, A. M., P. J. Cribb & M. W. Chase. 2009. Genera Orchidacearum, Vol. 5. Oxford University Press, Oxford New York.

Proyecto de digitalización de los dibujos de la Real Expedición Botánica del Nuevo Reino de Granada (1783-1816), dirigida por José Celestino Mutis: www.rjb.csic.es/icones/mutis. Real Jardín Botánico-CSIC. Consultado: 14-03-2013

Seemann, B. & W. Seemann. 1854. *Oncidium chrypsopyramis*. *In*: Bonplandia. Vol II. Londres: Williams y Norgate. París: Fr. Klincksieck. 158 p.

Vargas, O.M. 2011. A nomenclator of *Diplostephium* (Asteraceae: Astereae): a list of species with their synonyms and distributions by country. Lundellia 14: 32–51.

LANKESTERIANA 13(3): 353—357. 2014.

INVITED PAPER*

VANILLA RIVASII (ORCHIDACEAE), A NEW SPECIES FROM THE COLOMBIAN PACIFIC REGION

Francisco Molineros-Hurtado[1, 2], Robert Tulio González Mina[1, 2],
Nicola S. Flanagan[1, 3] & J. Tupac Otero[1,4,5]

[1]Grupo de Investigación en Orquídeas, y Ecología y Sistemática Vegetal
[2]Programa de Agronomía, Universidad del Pacifico, Avenida Simón Bolívar 54ª-10,
Buenaventura, Colombia
[3]Programa de Biología, Pontificia Universidad Javeriana, Cali, Colombia
[4]Departamento de Ciencias Biológicas, Universidad Nacional de Colombia,
Sede Palmira, Palmira, Colombia
[5]Instituto de Estudios Ambientales IDEA, Palmira. Universidad Nacional de Colombia,
Sede Palmira, Palmira, Colombia

Abstract. We describe a new species of fragrant *Vanilla* from the Chocó biogeographic region of Western Colombia, named *Vanilla rivasii* sp. nov. in honor of the local farmer who drew it to our attention. This species is related to the *Vanilla hostmannii* group, also containing *V. dressleri*, *V. ruiziana* and *V. cribbiana*, with which it shares flower traits such as the showy, yellowish flower with thickened longitudinal venation in the lip apex. *Vanilla rivasii* is characterised by possessing: a long racemose inflorescence up to 60 cm in length, carrying up to 150 yellow flowers, with two to four open simultaneously; a trilobed labellum with a conspicuously bi-lobulated central lobe; and basally fused lateral sepals. *Vanilla rivasii* can be distinguished from the most morphologically-similar species, *V. cribbiana* and *V. hostmannii*, by the number of veins in the cushion-like structure of the lip and the larger size and higher number of flowers per inflorescence. This discovery highlights northern South America as a centre of diversity for this economically-important genus, and underlines the need for further botanical exploration in the highly biodiverse region of the Chocó.

Key words: Orchidaceae, *Vanilla*, fragrant clade, *V. rivasii*, Buenaventura, Chocó, Colombia

Vanilla Plumier ex Miller, a pan-tropical genus within the Orchidaceae, contains over 100 species, with several species, principally *Vanilla planifolia* Andr., being of economic importance in the food and cosmetics industries. These commercially-valuable species form part of the so-called fragrant clade: *Vanilla* subgenus *Xanata* Soto Arenas & Cribb, comprising species producing fragrant fruits, and which are naturally distributed exclusively within the neo-tropics (Soto-Arenas & Cribb 2010). While *V. planifolia* is the predominant commercial species, other fragrant *Vanilla* species are of interest for their potential in vanilla breeding programmes. However, the diversity and biology of this clade has been poorly studied.

In a recent generic review, the existence of undescribed neotropical species became evident (Soto-Arenas & Dressler 2010), with a new species, *Vanilla espondae* Soto Arenas, described from the Magdalena river valley of Colombia (Soto-Arenas 2010). *Vanilla* is a taxonomically-challenging genus, with our understanding of the diversity and biology of these species hindered by plants being rare and hyper-dispersed in their native forest habitat. Furthermore, flowering is infrequent, and a large proportion of herbaria material is sterile.

In Colombia, 11 *Vanilla* species have been reported to date (Table 1). The genus *Vanilla* reaches its greatest diversity in South America, and, given the rare distributions of these plants, the inadequate nature

---

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

TABLE 1. List of *Vanilla* species reported for Colombia (Soto Arenas & Cribb 2010).

Species	Reference	Year
Vanilla calyculata Schltr	Repert. Spec. Nov. Regni Veg. Beih. 7: 42–43	1920
Vanilla columbiana Rolfe	J. Linn. Soc., Bot. 32: 468	1896
Vanilla dressleri Soto-Arenas	Lankesteriana 9(3): 303–305, f. 5	2010
Vanilla espondae Soto-Arenas	Lankesteriana 9(3): 281–284, f. 1–2	2010
Vanilla hostmannii Rolfe	J. Linn. Soc., Bot. 32: 462	1896
Vanilla odorata C. Presl	Reliq. Haenk. 1(2): 101	1827
Vanilla palmarum (Salzm. ex Lindl.) Lindl.	Gen. Sp. Orchid. Pl. 436	1840
Vanilla pompona Schiede	Linnaea 4: 573–574	1829
Vanilla ribeiroi Hoehne	Comm. Lin. Telegr., Bot. 1: 28	1910
Vanilla sprucei Rolfe	J. Linn. Soc., Bot. 32: 461	1896
Vanilla trigonocarpa Hoehne	Arq. Bot. Estado São Paulo 1(6): 126–127, t. 139	1944

of most herbarium specimens and the poor botanical records of lowland areas, it is likely more species will be reported for the country, both described and undescribed.

Here we describe a new *Vanilla* species native to the Chocó biogeographic region of the Pacific Coast of Colombia. This region has the highest documented plant diversity (Faber-Langendoen & Gentry 1991), and is still relatively under-explored botanically. The region retains more than 50% of its original vegetation cover, and continued taxonomic description of the diversity of the region is essential in order to establish conservation priorities.

Vanilla rivasii Molineros, Rob.González, Flanagan & J.T.Otero, *sp. nov.*

TYPE: Colombia, Valle del Cauca, Buenaventura, Sendero El Paraíso, cultivated by A. Rivas, *R. T. Gonzalez 1118* (holotype, CUVC). FIGURES 1–2.

Hemi-epiphytic *herb*. *Stems* dark green, 6.8-8.0 mm thick, terete, smooth, the internodes 8.0-9.3 cm long. Young aerial *roots* greenish to greyish, subterete to flattened, 4.2 mm thick. *Leaf* shortly petiolate, the petiole *ca*. 10 mm long, blade oblanceolate, acuminate, the apex incurved, base subobtuse, the basal margin revolute, subcoriaceous, pale green with a central concavity, 16.5-24.6 × 4.0-5.5 cm. Inflorescence terminal, sometimes lateral with pale green rachis of 12-40 cm in length and 0.7 cm in thickness with white dots in the epidermis, a shortly pedunculate raceme, the rachis congested, with up to 150 flowers, with bracts distant up to 6 mm. *Bracts* pale green, basal ones alternate distichal. *Distal bracts* ovate and concave, 3-4 × 5 mm. *Ovary* subterete to sub-trigonous, curved, pale green with white base and white dots in the epidemis, 45-55 mm length and 4.5 mm in diameter, white in the base and pale green in the rest. *Flowers* ephemeral with 2-4 open simultaneously, conspicuous with buds pale yellow at base, apex green, 10-12 cm diameter when spread out, aroma of rose and clover flowers; sepals yellowish green outer, whitish yellow inside, basal surface of the lip yellow, mid lobe and throat yellow lined dark yellow-ochre; the segments spreading, strong rose fragrance. *Dorsal sepal* yellowish green, deeply recurved, long-lanceolate, narrow at the base, apex sub-acute and sub-calyptrate, with 13 veins, of equal length to lateral sepals, 68 × 8-10 mm. *Lateral sepals* directed downwards, long-lanceolate, subacute, base long attenuate, lateral sepals fused in the proximal third of the length; with 13-14 veins, very smooth, 67 × 8-11 mm. *Petals* pale yellow to cream, slightly recurved at the apex, narrowly elliptic-oblanceolate, obtuse, concave, narrower than the sepals, longitudinally keeled on the abaxial surface, the keel broad and conspicuous, 7-8 veins, 68 × 9 mm. *Lip* showy, 66 × 35 mm forming a long

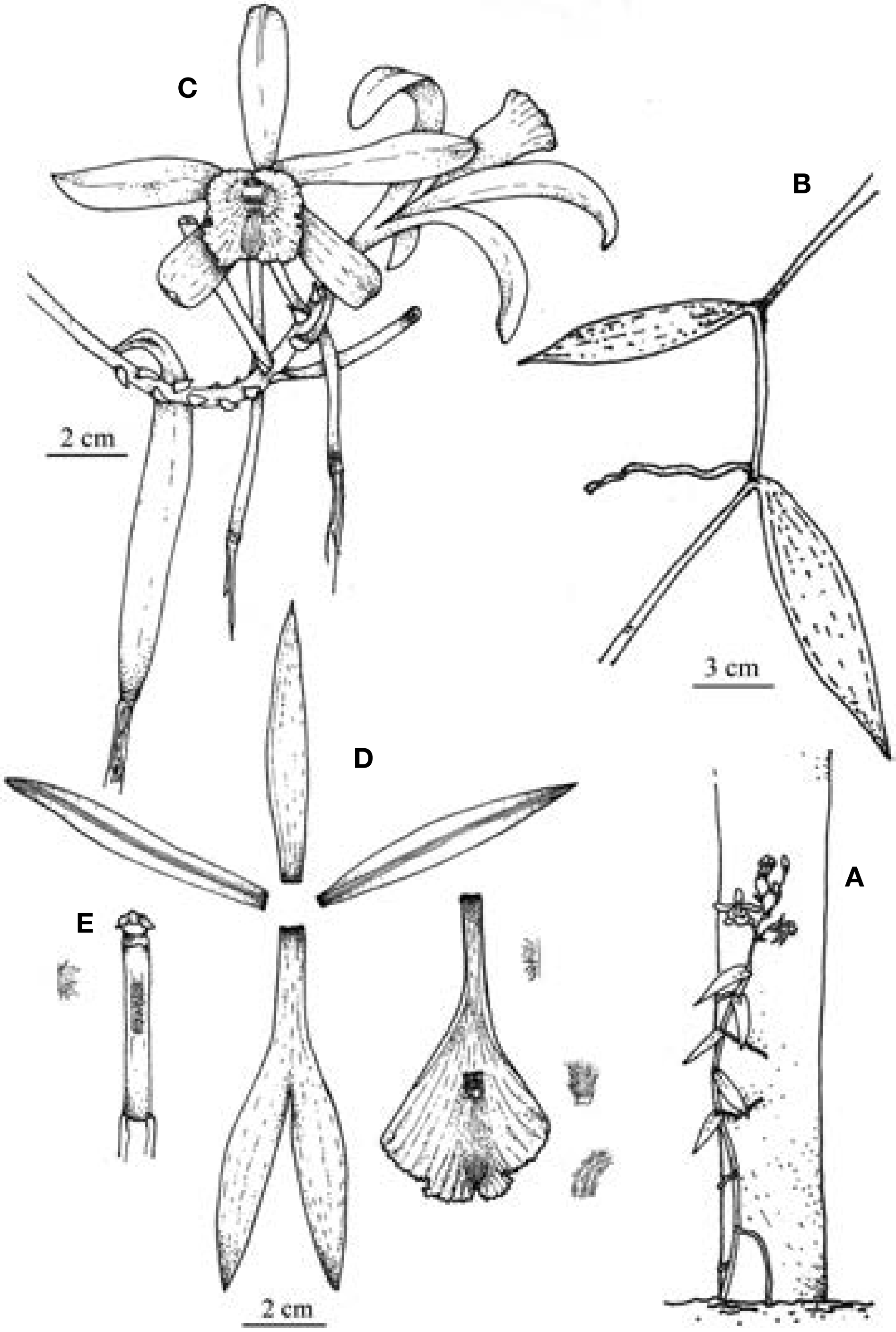


Figure 1. *Vanilla rivasii* Molineros-Hurtado, González, Flanagan & Otero. A — Habit. B — Portion of the stem with leaves and root. C — Inflorescence with flowers and fruits. D — Dissected perianth, with details of the indumenta. E — Column, ventral view, with detail of the ventarl indumentum. Prepared from the holotype by Robert Tulio Gonzalez. Drawing by Nhora Helena Ospina Calderón.

Figure 2. *Vanilla rivasii*, photograph of the flower *in situ*. Photo by F. Molineros-Hurtado.

tube, marginally fused to the column at least 40-42 mm, with 30 veins; when spread out trilobed with the midlobe oblong, bilobulated, the lateral lobes well defined with rounded shoulders, overlapping above the column, oblong-triangular to sub-square, tapering at apex, with thickened axial cushion near the lip apex *ca.* 6 × 23 mm with 7-8 thickened keels with papilose texture extended to the lateral lobes. The margin of the lip is sub-entire and flabellate; slightly verrucose at the base with brownish papillae, the apex somewhat narrowed and forming a cushion, the penicillate callus 4.5 × 6.0 mm covered by 4 yellow showy lacerate structures of scales thickened in the distal portion, separated 44 mm from the lip base. *Column* subterete, elongated 45.0-49.0 × 2.6 mm, yellow whitish, with brownish tricomes in the distal ventral part; membranous wings 5.3 mm; bilobed stigma with rectangular emergent lobes, 1.2 × 1.1 mm. *Anther* versatile, ovate, 3 × 2.6 mm. *Fruits* elongated, pale green, subtriangular with white dots in the epidermis. 130-180 × 11 mm, dehiscent when mature into two valves, with a strong vanilla aroma detectable over more than 200 m.

Paratype: Colombia, Valle del Cauca, Buenaventura, Bahía Málaga. *N. H. Ospina 466* (CUVC).

Other records: Colombia, Buenaventura, *F. G. Lehmann H.K.1185* (K, fruit!).

Distribution: Known only from the Pacific coastal region in the Valle del Cauca, and Chocó Departments, Colombia. The species has been observed occurring naturally in the wild in small isolated populations, mainly in regenerating secondary growth forest. Known populations comprise between one and twelve apparently separate plants. The largest population of twelve plants occurs over an area of 25 Ha. Localities have been identified up to 300 km apart. The association with secondary forest may be a consequence of sampling bias, as most exploration has been conducted close to populated regions. It is likely that, with further exploration of the Colombia Pacific region, particularly away from settlements along the coast, more populations will be found. The known localities will not be mentioned explicitly so as to protect the small populations of this species from the threat of collection from the wild.

Phenology: No clear seasonality has been observed. Initiation of flowering has been observed in the month of January, corresponding with a dryer climatic period in the region. However flowering has continued until April, June, July and September, resulting in inflorescences of up to 150 flowers. Natural fertilization has been observed of 6-18 % of flowers in an inflorescence.

Eponymy: This species is dedicated to Luis Álvaro Rivas, a local farmer committed to sustainable agricultural practices and biodiversity preservation.

The type specimen consists of the collection *R. T. Gonzalez 1118* from Buenaventura, and *N. H. Ospina 466* from Bahia Malaga, with pictures taken by F. Molineros-Hurtado.

Vanilla rivasii Molineros-Hurtado, González, Flanagan & Otero belongs within *Vanilla* subgenus *Xanata*. *Vanilla rivasii* has affinity to the *V. hostmannii* group, possessing the thickened veins in the lip apex and the distichous arrangement of the basal bracts of the inflorescence characteristic of this group. *Vanilla rivasii* may be distinguished from the other *Vanilla* species in the group by the frequent terminal position of the inflorescence, although occasionally this can be lateral. The bracts of the inflorescence are smaller than those of related species such as *V. cribbiana* Soto-Arenas, *V. ruiziana* Klotzsch, and the sympatric *V. dressleri* Soto-Arenas. Flowers are larger, with deeply recurved sepals. The lateral sepals are fused in the basal third. The mid-lobe of the labellum is conspicuously bilobulated with a thickened axial cushion near the apex bearing 7-8 thickened veins with papilose texture extending into the lateral lobes. *Vanilla rivasii* is morphologically most similar to *V. cribbiana* but differs from this species in the fused lateral sepals in the basal third, the bi-lobed shape of the central lobe of the labellum and the greater number of thickened veins. *Vanilla rivasii* differs from the sympatric species *V. dressleri* in the tri-lobed labellum and non-granulose sepals. Additionally, the living flower of *V. rivasii* has much less conspicuous orange longitudinal stripes on the labellum than those of *V. dressleri*. *Vanilla rivasii* is more heliophytic than *V. dressleri*, with subcoriaceous, deep green, smooth leaves. It differs from *V. ruiziana* from Peru and Bolivia which has an ovate mid lobe of the lip, and 1-3 thickened veins on the lip apex. *Vanilla rivasii* plants have been documented with terminal inflorescences producing up to 150 flowers (less in lateral inflorescences), compared with a maximum recorded for *V. hostmannii* of 60, and for *V. cribbiana*, and *V. dressleri* of ca. 10, and rarely up to 30 flowers. Mature fruits are dehiscent.

ACKNOWLEDGMENTS. We thank Nhora Helena Ospina Calderon for the line drawings; Álvaro Rivas for kindly sharing his knowledge and experience regarding vanillas; and the ´Semillero de Investigacion en Recursos Fitogeneticos´ at the Universidad del Pacifico. Support for field trips was obtained from the research offices of the Pontificia Universidad Javeriana, Cali, the Universidad Nacional de Colombia, sede Palmira, (DIPAL), and the Vicerectoría de Investigación of Universidad Nacional de Colombia.

LITERATURE CITED

Faber-Langendoen, D., & A.H. Gentry. 1991. The structure and diversity of rain forests at Bajo Calima, Choco Region, Western Colombia. Biotropica 23(1): 2-11.

Soto-Arenas, M.A. & R.L. Dressler. 2010. A revision of the Mexican and Central American species of *Vanilla* Plumier ex Miller with a characterization of their ITS region of the nuclear ribosomal DNA. Lankesteriana 9(3): 285-354.

Soto-Arenas, M.A. 2010. A new species of *Vanilla* from South America. Lankesteriana 9(3): 281-284.

Soto-Arenas, M.A. & P. Cribb. 2010. A new infrageneric classification and synopsis of the genus *Vanilla* Plum. ex Mill. (Orchidaceae: Vanillinae). Lankesteriana 9(3):355-398.

LANKESTERIANA 13(3): 359—374. 2013.

INVITED PAPER*

CHARLES H. LANKESTER (1879-1969): HIS LIFE AND LEGACY

Carlos Ossenbach

Orquideario 25 de mayo

Abstract. Charles Herbert Lankester (1879-1969) was without a doubt the most dominant figure of Central American orchidology during his time. Better known as 'Don Carlos', Lankester was born in Southampton, England, on June 14 1879. It was in London that he read an announcement offering a position to work as an assistant to the recently founded Sarapiquí Coffee Estates Company in Costa Rica, he applied and was hired. Surely influenced by his uncle's zoological background, Lankester was at first interested in birds and butterflies. However, living in Cachí, at that time one of the regions with the greatest botanical diversity, he must have fallen under the spell of the plant world as he soon began collecting orchids in the nearby woods. Many of the plants he collected at this time proved to be new species. With no literature at his hand to determine the plants he collected, Lankester started corresponding with the assistant director of the Royal Botanic Gardens at Kew, Arthur Hill in 1910, and somewhat later with Robert Allen Rolfe, Kew's most eminent authority on orchids. At the same time, Lankester began his collection of living plants that would become so famous years later. He returned to England in 1920 to enroll his five children in English schools. Lankester traveled to Africa from 1920 to 1922, hired by the British Government to do research on coffee plantations in Uganda. When returning to England, he found that Rolfe had died the year before. Many orchids that he had brought to Kew were left without identification. Lankester was back in Costa Rica in 1922, the year that was a turning point in his career as an orchidologist: it brought the first correspondence with Oakes Ames. Over the next fifteen years, Ames would discover more than 100 new species among the specimens he received from Costa Rica. In 1922, Ames began a series of publications on orchids, which he named Schedulae Orchidianae. In its third fascicle, in January 1923, Ames started to describe many of the Lankester orchids, which were deposited at Kew and had been left unidentified. Ames kept asking Lankester to send more and more specimens. After 1930, Lankester and Ames seem to drift slowly apart. Ames was taken in more by administrative work at Harvard, and Lankester traveled abroad more frequently. In 1955, after his wife's death and already 76 years old, Lankester decided to sell his farm but retained the small part which contained his garden, a piece of land called "El Silvestre". Lankester moved to a house he had bought in Moravia, one of the suburbs of the capital, San José. On a section of this farm called "El Silvestre", Lankester began his wonderful collections of orchids and plants of other families, which formed the basis of the Charles H. Lankester Botanical Garden of the University of Costa Rica.

Key words: Charles H. Lankester, Costa Rica, botany, history

> *"Twenty three years ago today, the good ship 'Atrato' (now alas asleep in the depths off the N. Irish coast) left Southampton with myself on board en route for Costa Rica, and here I am still ..."*
>
> Charles Lankester, letter to Oakes Ames,
> December 1923

Three famous names form the most illustrious trio of collectors in Costa Rica's history of orchidology: Auguste R. Endrés (1838-1874), Alberto Manuel Brenes (1870-1948) and Charles Herbert Lankester (1879-1969). Undoubtedly the most important of the three was Auguste R. Endrés, who prepared the country's first monographical treatment of a plant family. His orchid collections, with over 3,500 numbers, form an important part of the Reichenbach orchid herbarium at the Vienna Natural History Museum. In the first decades of the twentieth century, Alberto Manuel Brenes, born in San Ramón when Endrés was living in this small city of the northwestern

---

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

FIGURE 1. Charles H. Lankester (1879-1969), photographed *ca*. 1925.

Central Valley, did little botanical work but made extraordinary collections of orchids in the surrounding mountains. These include dozens of new species, described by Rudolf Schlechter in his *Additamenta ad Orchideologiam Costaricensem* (1923) in a chapter entitled *Orchidaceae Brenesianae.*

But it would be **Charles Herbert Lankester** (1879-1969) (Fig. 1), without doubt the dominant figure of Central American orchidology during his time, who should rightly bear the soubriquet of *lynx-eyed investigator*, given by Reichenbach some 50 years earlier to Auguste R. Endrés.

The early years (1900-1908). Better known as 'Don Carlos', Lankester was born in Southampton, England, on June 14 1879, the son of Charles Lankester and Helen West. He lost both parents when only three years old and was raised, together with his sister, by two aunts. After finishing school he started work at a photographic studio and later went to London, where he specialized in color photography at the Polytechnic Institute. It was in London that he read an announcement in the Daily Telegraph, offering a position in Costa Rica to a young Englishman willing to work as an assistant to the recently founded Sarapiquí Coffee Estates Company. Lankester applied and was hired, landing a few months later in Puerto Limón, then going on by train to the capital of Costa Rica, where he arrived just in time to take part in the "Ball of the New Century", given by the president of Costa Rica, Rafael Yglesias, in the National Theater, San José.

FIGURE 2. Ray Lankester by Leslie Ward, *Vanity Fair*, 1905.

Sarapiquí, in the Atlantic region, proved too humid for the commercial production of coffee and the plantations had to be abandoned three years after Don Carlos' arrival. It was here, surrounded by the most exuberant tropical vegetation, that his interests in plants, insects and birds began. As Dr. Louis Williams wrote in his obituary, *"Don Carlos Lankester arrived at the right place at the right time to join into the active biological exploration of Costa Rica, perhaps the most exciting place biologically on our continent."*

Lankester was not the first talented natural historian in his family; his father's cousin, Sir Edwin Ray Lankester (1847-1929) (Fig. 2), had been the third

Director of the Natural History Museum in London.

The arrival of Lankester in Costa Rica marked the end of a period - the last two decades of the nineteenth century - which had shown for the first time the development of a 'national science' in Central America. In Costa Rica, as part of an educational reform aimed at secularizing public education, the government of president Bernardo Soto (1885-1889) hired a group of European academics to staff the two new public high schools in the capital, San José;The 'Liceo de Costa Rica' for boys and the 'Colegio Superior de Señoritas' for girls, both founded under Soto's administration. The arrival of these academics marks the beginning of a small scientific awakening in Costa Rica. Two institutions symbolize this: the Instituto Físico-Geográfico (IFG) (=*'Physical-Geographical Institute'*) and the National Museum, founded in 1889 and 1887, respectively.

Among the teachers hired were Pablo Biolley (1861-1908) and Henri Francois Pittier (1857-1950) (Fig. 3), who arrived in 1886 and 1887. Pittier lived in Costa Rica until 1905 and spent some of this time conducting a systematic exploration of the Costa Rican flora; a study that had no equal in any country of tropical America at that time. According to Paul C. Standley, in his introduction to the *Flora of Costa Rica*: "Henri Pittier […] undoubtedly gained a more intimate knowledge of the natural history and especially the botany of Central America and northwestern South America than has ever been possessed by any single person (Standley, 1937:49)."

The combined labors of Pittier and Biolley, and, somewhat later, of Anastasio Alfaro, Adolph Tonduz, Carl Wercklé, and Brenes as well as the Brade brothers (Alfredo and Alexander Curt) resulted in the formation of the National Herbarium, which initially comprised more than 5,000 species. Again citing Standley, in 1903 the National Herbarium "was unequaled below the Río Grande del Norte (Standley, 1937:50)."

Lankester and Pittier began a lifelong friendship when the latter visited Sarapiquí. The other players in this scientific awakening, Alfaro, Biolley, Tonduz, Wercklé, the Brades, and, years later, Otón Jiménez would also be important to Lankester, as they often accompanied him on his collecting excursions and were frequent visitors to his farm in Cartago.

When his contract expired, Lankester went back to England. He returned to Costa Rica a few months later, summoned by Pittier to take over the experimental station, which the United Fruit Company planned to establish in Zent, near the Caribbean port of Limón. This project, however, never came to fruition. Lankester was thus forced to work with different companies until 1908, when he left for England to marry Dorothea Mary Hawker.

Figure 3. Henri Francois Pittier (1857-1950). Portrait by Sava Botzaris (Caracas, 1942).

First botanical activities (1910-1922). In 1910, he returned to Costa Rica with his wife (Fig. 4), taking over the administration of a coffee farm in Cachí, on the eastern limits of Costa Rica's Central Valley, where he lived for the next nine year. As Amelia and Philip Calvert would write a few years later: "Mr. Lankester's house was beautifully situated half a mile from the Reventazón River and about a hundred and fifty feet above it. It was not a typical Costa Rica residence, for although built of adobe it was two-storied and had no patio. A wide veranda or "corridor" ran across the

Figure 4. Dorothea Mary Hawker, Lankester's wife.

entire front on the first and second floors, charming places, for they were set with plants and hung with baskets of orchids, some of which were in full flower when we were there (Calvert & Calvert, 1917: 160)" (Figs. 5–6).

Surely influenced by his uncle's zoological background, Lankester was at first interested in birds and butterflies. However, living in Cachí, at that time one of the regions with the greatest botanical diversity, he must have fallen under the spell of the plant world as he soon began collecting orchids in the nearby woods. Many of the plants he collected at this time proved to be new species. With no literature at his hand to determine the plants he collected, Lankester started corresponding with the assistant director of the Royal Botanic Gardens at Kew, Arthur Hill in 1910, and somewhat later with Robert Allen Rolfe, Kew's most eminent authority on orchids.

The first mention of orchids in his correspondence is in a letter to Hill of December 1910, where he wrote: *"I have a few orchids chiefly of botanical interest, which I will send when it gets warmer on your side"*. *Stelis barbata* Rolfe (Fig. 7), a plant collected near Cachí and sent to Kew, where it flowered in November 1912 and described by Rolfe in the Bulletin of Miscellaneous Information of Kew in 1913, was the first new orchid discovered by Lankester in Costa Rica. Others would follow: *Dichaea ciliolata* Rolfe, *Pleurothallis dentipetala* Rolfe and *Pleurothallis costaricensis* Rolfe.

Figure 5. Orchids in Lankester's house in Cachí, photographed by himself.

Figure 6. Orchids in Lankester's house in Cachí, photographed by himself.

At the same time, Lankester began his collection of living plants that would become so famous years later. Lankester returned to England in 1920 to enroll his five children (four daughters and one son) in English schools. Another daughter, his youngest, was born in England that same year. Lankester traveled to Africa

FIGURE 7. *Stelis barbata* Rolfe, Lankester's first collection of a new orchid species. Photograph by R. Parsons.

from 1920 to 1922, hired by the British Government to do research on coffee plantations in Uganda. When Lankester returned to England, he found that Rolfe had died the year before, just as he was preparing to travel to Costa Rica and Panama on his first field trip to tropical America. Many orchids that Lankester had brought to Kew were left without identification.

The relation with Oakes Ames. Lankester was back in Costa Rica in 1922, the year that was a turning point in his career as an orchidologist: it brought the first correspondence with Oakes Ames (1874-1950) -- the start of a deep and long-lasting friendship.

To understand what was happening in the world of orchidology, it must be remembered that up to the 1920s, the study and knowledge of orchids was strictly an European business. Orchidology in the nineteenth century had been dominated by an Englishman, the great John Lindley (1790-1865), followed by a German, Heinrich Reichenbach junior (or filius, as he liked to be called) (1824-1889). After Reichenbach's death in 1889, Robert Allen Rolfe (1855-1921) became the world's foremost orchidologist, soon challenged and replaced by the German Rudolf Schlechter (1872-1925). It was not until Rolfe's death in 1921, followed by Schlechter's in 1925, that the first American expert on orchids would arise in the figure of Oakes Ames (1874-1950) (Fig. 8), who took a dominant position in the orchid world that was never challenged until his death.

After returning from a trip to Europe, Ames wrote his first letter to Lankester (Sept. 17 1922): *"At Kew I saw many specimens collected by you in Costa Rica, the greater part unnamed. As it will take some time for Kew to recover from the loss of Rolfe and as the Germans are making great efforts to assemble Costa Rican material through Wercklé, Jimenez and Tonduz, it seemed to me that you might be willing to co-operate with me by stimulating orchidological interest among your neighbors."* And continued: *"It would surely be worthwhile if you can see your way clear to send me herbarium specimens and to send collectors into the orchid regions of Costa Rica. I have already identified and described as new, one of your species of Pleurothallis. I refer to P. palliolata (Lankester 192).*

Figure 8. Oakes Ames (1874-1950), American orchidologist and founder of the world's largest orchid herbarium.

Figure 9. *Pleurothallis palliolata* Ames, collected by Lankester near his house in Cachí. Photograph by E. Hunt.

The specimen was sent for determination by Hort. Kew" (Fig.9). Ames finished this famous first letter to Lankester by saying: *"We must work fast if we hope to keep abreast of the Germans. I was surprised to see how far reaching their efforts have been to secure a monopoly of tropical American species."*

We must keep in mind that, at that time, Rudolf Schlechter, the famous German orchidologist, was describing hundreds of new Central American orchid species, based on the collections by Powell in Panama and by Wercklé, Brenes, Tonduz and Jiménez in Costa Rica.

Ames' letter to Lankester was followed by one from Charles W. Powell, who had been collecting for years in Panama and who had met Don Carlos some years earlier. In a letter dated September 25 1922, Powell wrote to Ames: *"This will introduce to you (by letter) my good friend Mr. C.H. Lankester, of "Las Cóncavas", Cartago, Costa Rica. Mr. Lankester wishes to take up with you the subject of Costa Rican Orchids, with which he is well familiar. He has a number of specimens now at Kew unidentified or undetermined, which he would like you to have you procure and determine for him. Also he wishes to send to you anything new which he may discover for determination".*

In his answer to the letter from Powell, Ames showed his delight in learning that he could count on Lankester's help: "*Now that I know from your letter that he has contemplated sending his things to me, this day begins with plenty of sunshine even though heavy clouds obscure the sky* (Letter from Ames to Powell, October 6 1922)." Ames was undoubtedly playing a double game: while he could not sever his relations with Schlechter (the German had too much information that Ames needed desperately), he tried to block Schlechter's access to Powell's and Lankester's materials.

Lankester answered Ames' first letter immediately, and went on to become the expert's favorite collector. Over the next fifteen years, Ames would discover more than 100 new species among the specimens he received from Costa Rica. In his letter to Ames of October 11, 1922, Lankester wrote: *"I fear stimulation of orchidological interest is exceedingly improbable or likely to be successful in Costa Rica…. I think I alone have the necessary madness."* Orchids had become the center of Lankester's world, and would remain so until his very last day.

In 1922, Ames began a series of publications on orchids, which he named *Schedulae Orchidianae*. In its third fascicle, in January 1923, Ames started to describe many of the Lankester orchids, which were deposited at Kew and had been left unidentified because of Rolfe's death. Dozens of new species were discovered (see appendix). Ames described more and more new orchids from Costa Rica and kept asking Lankester to send more and more specimens. *"Your specimens have arrived... They made my day cheerful to the end. I wished they were more. But if you had sent ten times as many, I would still say that* (August, 1923)*."*

One of the specimens that Lankester sent to Ames was the reason for a famous anecdote: "*Your number*

Figure 10. *Lankesterella costaricensis* Ames, the type species of the genus that Ames dedicated to his favorite collector. Photograph by F. Pupulin.

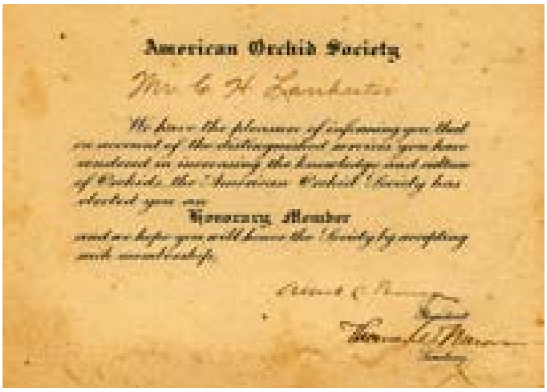
387 is not an orchid, it is a Bromeliad" wrote Ames in 1923. Lankester replied: "*Look again*". An unusual new orchid genus had been discovered. Ames admitted his error and a week later wrote to Lankester: "*There seems to be a new genus among your specimens, Lankesterella would be a good name"* (Fig. 10).

After World War I, prices for tropical commodities such as coffee and bananas rose quickly. The restrictions imposed on the import of such goods into Europe and the United States by four years of naval warfare were now replaced by an increasing demand. Owners of coffee plantations in Costa Rica had one of their most prosperous periods during the 1920s, and coffee production and exports increased constantly. Lankester was not the only one to take advantage of the situation. In 1924, he moved to "Las Cóncavas", a coffee farm that he had acquired in the vicinity of Cartago. Coffee had been the reason for his initial emigration from England to Costa Rica, and his livelihood would depend on coffee for the rest of his life.

His orchid collection was already enormous. In August 1924, he wrote to Ames: *"...we hope to move over to the 'finca' about the middle of November, this means among other things the translation of about 1,800 orchids over unimaginable roads."* It is therefore easy to understand why Lankester's farm would become, over the years, a Mecca for botanists and orchidologists from all over the world. With its beautiful collections of plants, "Las Cóncavas" could not go unnoticed by the world's naturalists. The gardens had important collections of cacti, palms and bromeliads although orchids were always Lankester's favorites. Among the visitors to "Las Cóncavas " were famous names such as Arthur Hill, director of Kew Gardens, Thomas Barbour of Harvard, Harvey Stork, William Maxon, Wilson Popenoe, Philip Calvert, James Rehn and Louis Otho Williams.

By December 1924, after only two years of corresponding with Lankester, Ames had already described 66 new species among his collections. A self-made man with no formal botanical training, Lankester had developed a sharp eye for novelties. The year of 1925 shows us Charles Lankester, who had just reached the age of 45, at what appears to be the peak of his success as a planter and as an orchidologist. He saw his children again during a

FIGURE 11. Lankester, wife and daughter, 1925.



American Orchid Society

Honorary Member

FIGURE 12. Lankester named honorary member of the American Orchid Society.

short trip to England (Fig. 11), his new coffee farm was in full production, and in July of that year he was elected an honorary member of the American Orchid Society (Fig. 12).

What was, however, the real condition of Lankester's business? There seem to have been problems which went largely untold. By 1924, he had already tried to convince Ames to invest in his coffee farm -- a proposal that Ames had politely declined. Then, in November 1925, he seemed to have decided to sell everything and to leave Costa Rica: *"It is just possible I may complete sale of this place during the coming week, if so Costa Rica will soon see me no more."* We will probably never know what really happened, but luckily Lankester did not sell and did not leave although it seems that he was never without financial problems until the end of his life. He continued collecting orchids to send to Ames, now often attaching to his herbarium specimens crude sketches or black and white photographs, all preserved today in Ames´ documents at the Oakes Ames Orchid Herbarium (Fig. 13).

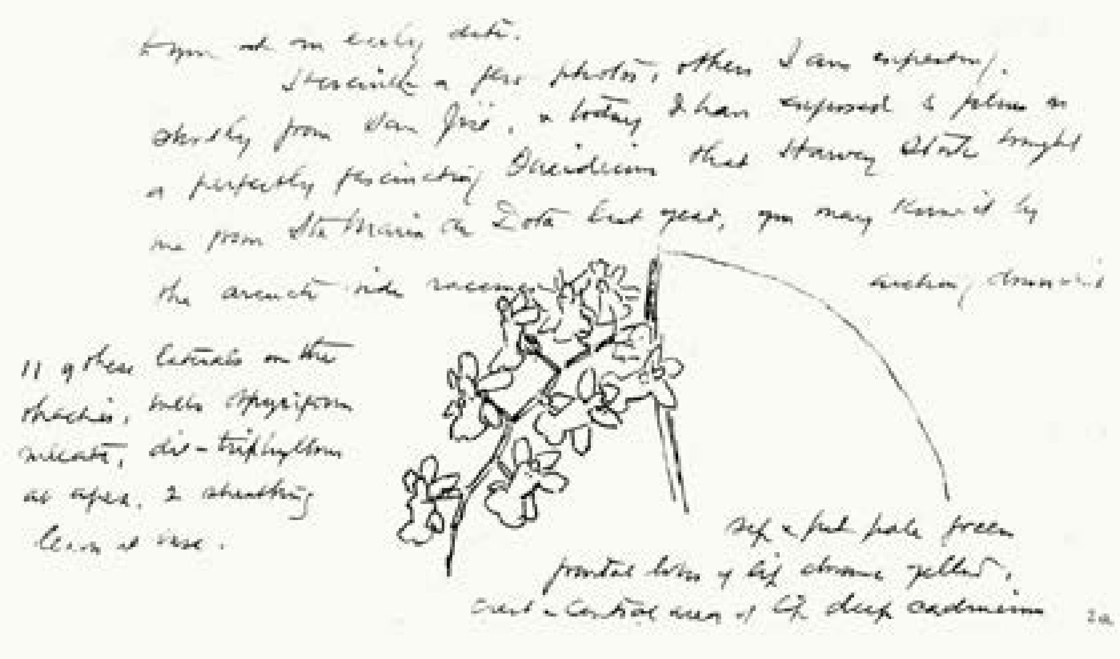


FIGURE 13. Letter from Lankester to Ames, with a sketch of a species of *Oncidium.*

Figure 14. Paul Carpenter Standley (1884-1963). Courtesy of Jorge Gómez Laurito.

Paul Standley in Central America (1921-1925). A very special visitor came to Costa Rica in January 1924 and again in December 1925: Paul Carpenter Standley (1884-1963) (Fig. 14). Three years earlier, on December 19, 1921, Standley, a botanist with the U. S. National Museum, had arrived at the port city of La Libertad, El Salvador , the first visit to Central America of the man who was probably the most important figure in the history of botanical exploration of the region during the first half of the 20th century.

In a conversation with Otón Jiménez, Pittier said: "*Much can be expected from such a young and capable element*" (Jiménez, 1963: 2). For over 40 years, Standley collected intensively in all of the countries of Central America and published a series of fundamental works about their floras. He acquired an intimate knowledge of the region, not only about its botanical aspects, but also its culture and traditions. He was a friend to all the Central American scientists of his time and contributed like no other to furthering the study and research of the local naturalists and collectors, as well as to the development of existing herbaria and the creation of many new ones. "*... Standley hoped that every Central American country would have a botanical library adequate for the study of its flora, and a comprehensive herbarium, formed by local collectors*" (McCook, 1999: 119).

Standley arrived in Panama in November 1923. Over the following five months, he collected 7,500 plant specimens in the Canal Zone. In December 1923, January 1924 and during a week in November 1925 (during his second stay in Panama), he collected 800 additional plants on the island of Barro Colorado, recently established as a protected area. As a result of these visits, he wrote his *Flora of Barro Colorado Island* and the *Flora of the Panama Canal Zone*, published in 1927 and 1928 respectively, by the Smithsonian Institution.

The two visits by Standley to Panama were followed by extensive collecting trips to Costa Rica, a country that Standley visited during the first months of 1924 and then again between December 1925 and March 1926. Standley collected an enormous amount of material in Costa Rica -- over 15,000 plant specimens, of which no less than 30 orchid species were new to science. "*Standley is in New York to-day. When he arrives in Costa Rica, shower orchids on him. Make it a rule that no orchid goes unpressed*" (Ames to Lankester, November 13, 1923). "*At this stage of the undertaking, quantity rather than quality is important*" (id., December 3, 1923). While Standley was working in Honduras, Lankester visited him, and the two became intimately acquainted; they continued to have frequent contact until their later years. Standley always remembered the gesture of the Lankesters in December 1925, while he was collecting in the region of Santa María de Dota: *"The writer has not forgotten that they sent a special messenger upon a two days' journey to bring a greeting at Christmas time* (Standley, 1937: 59)."

Years of indecision: between England and Costa Rica (1925-1939). Lankester was still far from finishing with his orchid collections. Ames continued the publication of his *Schedulae Orchidianae*, now with Charles C. Schweinfurth as co-author. With the publication of fascicle 9 in July 1925, the number of new species collected by Lankester and described by Ames reached 99. In 1927, Lankester visited Charles W. Powell, Panama's famous orchid collector, and wrote to Ames in one of his most famous passages: *"I have just spent a fortnight with my fellow sufferer from Orchiditis, CWP, and it was a very delightful time of talk and talk and then talk. I wish we could have had you there as High Priest of our cult. Possibly a few tangles might have been unraveled."*

After 1930, Lankester and Ames seem to drift slowly apart. Ames was taken in more and more by administrative work at Harvard, and Lankester traveled abroad more frequently. In a letter of April 1932, Ames complained about the separation. *"I have missed you. Those little crumbs from your orchidologist feasts always made me feel that you were near at hand. Since your return to England I have felt that you had departed almost to another planet!"*

Later in 1932, and back in Costa Rica, Lankester was named by the president of Costa Rica as a member of the board of the National Museum; a great honor that he shared with two other famous figures in the history of the orchids of Costa Rica: Anastasio Alfaro and the *grande dame* of Costa Rican orchid history, Amparo Zeledón. Abroad again, Lankester visited the Canary Islands in 1934, exploring Tenerife with Professor Balinaga, director of the Botanical Gardens there. The following year he went to Brazil and, after traversing the Continent, left through Bolivia.

In 1934, already 55 years old, Lankester was back in Costa Rica, where he collected the last three orchids that Ames described based on Lankester's collections. These were published between 1934 and 1935 in the Harvard University Botanical Museum leaflets. The orchids were three different species of *Stelis: Stelis crystallina*, *S. latipetala* and *S. transversalis* (Fig. 15).

The American naturalist Alexander F. Skutch (1904-2004), who lived in Costa Rica from 1935 until his death, soon became one of the country's most respected leaders in the study of natural sciences – especially ornithology-- and in the development of an original philosophical paradigm for understanding the relationship between mankind and its natural environment. Skutch collected orchids in Guatemala in 1933 and 1934, before moving to Costa Rica, so that it should come as no surprise that he soon met Lankester. In 1950, Skutch married Lankester's daughter Pamela; they spent the rest of their lives on a small farm on the River Peñas Blancas that Skutch named "Los Cusingos", after the local name for the orange beaked-toucanet (*Pteroglossus frantzii*).

At the end of a decade marked by enormous indecision about his future, torn between his love for his adopted country – despite difficulties - and missing both his homeland and his children, Lankester went to England again before the outbreak of World War II. He returned to Costa Rica with his wife at the end of 1939, very narrowly missing being torpedoed in the convoy in which they crossed the Atlantic; a small ship to the side of them was the unfortunate victim. Lankester's last package of plants was sent to Ames, according to our records, in March 1942 although their correspondence continued until Ames passed away in 1950.

The final years (1949-1969). In the early 1940's, Lankester began what he meant to be his final tribute to the orchids of his adopted country: a book that would be entitled *Costa Rican Orchids*. News of this work soon spread, and the orchid world wanted to see it. Paul H. Allen, the foremost expert on the orchids of Panama, wrote to Lankester in 1946: *"Through the grapevine, I have heard that you have done a manual on the Orchids of Costa Rica. It is most fortunate in my opinion that you have done so, since you have probably seen more species in the field than any living collector."*

Lankester did not only want to write a book, he also wanted to raise funds for the conservation of his farm as a paradise of Costa Rican orchids. He wrote to Rodney Wilcox Jones, president of the American Orchids Society from 1942 to 1948, who gave a polite but clearly negative response: *"... I would be inclined to believe there is not much that can be done... Of course, now with your book coming along, I can see where it could be a basis to start an interest in conserving your place as an orchid haven..."*. The years went by, and the manuscript was never published, although Lankester's dream of preserving his garden was fulfilled a few years after his death.

More and more, Lankester dedicated himself to building up his orchid and plant collections. In 1949, he sold his house in London, deciding to stay in Costa Rica although three of his daughters were married and living in England. As he wrote to Gordon Dillon in 1960: *"No idea of returning to live in England, I sold my house in London in 1949, but retain the link of 3 married daughters there, a summer like last years' is certainly inviting, but the winters ..."* (Fig. 16).

Figure 15. Lankester in his garden at "Las Cóncavas", 1936.

In 1955, after his wife's death and already 76 years old, Lankester decided to sell his farm but retained the small part which contained his garden, a piece of land called "El Silvestre". Lankester moved to a house he had bought in Moravia, one of the suburbs of the capital, San José. A few years later, on June 10, 1961, in a ceremony at the British Embassy in San José, Lankester was named an Officer of the Order of the British Empire by order of Queen Elizabeth II, an honor of which Lankester would be proud to the end of his days (Fig. 17). Gordon Dillon had especially gentle words about Lankester a few months before his death, and in one of his letters called him *plantsman extraordinaire.*

Charles Herbert Lankester passed away in 1969, alone but for the company of his daughter Dorothy, and having had financial problems during his last years. Shortly before his death, Lankester confessed to Dorothy: *"I am only sorry that, with all the opportunities I had, I never made enough money."* As one of his friends wrote in his guest book: *"Time is unfair to this place and these people"* (Fig. 18).

Louis Williams described Lankester in his obituary

Figure 16. Lankester with wife Dorothy in 1952.

Figure 17. Lankester receiving the Order of the British Empire from the British Embassador, San José, 1961.

with these words: *"Generous to a fault, hospitable to all, he was counselor to all scientists who came to Costa Rica. His interests were catholic - butterflies, birds, but most especially epiphytic plants, orchids, bromeliads and aroids."* And Paul Standley wrote: *"A naturalist in the best and widest sense of that word."*

Figure 18 . Charles H. Lankester shortly before his death, in his house in Moravia, 1968.

The Lankester Botanical Garden. "Cóncavas"(= concavities) is the local Spanish name for circular, clay-filled depressions, several hundred feet in diameter and three to four feet-deep. They are frequently found to the east of the Costa Rican city of Cartago. These depressions often fill with water and form large lagoons, a paradise for the migratory birds, which fly to Costa Rica during the last months of the year to escape the harshness of the North American winter.

A coffee farm with the name of "Las Cóncavas" featured one of these beautiful lagoons. Established in the second half of the 19th century by Francisco Quesada, it was bought in 1924 – as we have seen- by Charles H. Lankester (Fig. 19). On a section of this farm called "El Silvestre", Lankester began his wonderful collections of orchids and plants of other families, which formed the basis of the Charles H. Lankester Botanical Garden of the University of Costa Rica.

"El Silvestre", which Lankester kept when he sold the rest of his farm in 1955, was inherited by his daughter Dorothy (Fig. 20), but difficult financial circumstances made it seem impossible to fulfill Lankester's dream of

Figure 19. A “concava” at Lankester’s farm in Cartago. Photographed by C. Lankester.

Figure 20 . Dorothy Lankester.

conserving the place as an “orchid heaven”. Dorothy was forced to put the garden up for sale. However, through the efforts of the Costa Rican Orchid Society and Costa Rican biologist Rafael Lucas Rodríguez, a group of members of the American Orchid Society (led by Rebecca T. Northen), raised half of the purchase price: $25,000. The other half was donated by the Stanley Smith Horticultural Trust of Great Britain. An evaluation committee was formed, and the garden was inspected by Thomas A. Bartenfeld, president of the Conservation Committee of the AOS, Eric Young, president of the Orchid Society of Great Britain and Dr. Calaway H. Dodson, whose expertise on Costa Rica was of great value. Their decision was positive, and the funds were deposited. The University of Costa Rica purchased the property and began to operate it as a botanical garden. And so, on March 2 1973, the Charles H. Lankester Botanical Garden was formally inaugurated (Fig. 21).

Figure 21. Rafael Lucas Rodríguez during the opening address at the inauguration of the Lankester Botanical Garden. Next to him Gordon Dillon, Secretary of the American Orchid Society and to the right Rebecca Northen, who led the fundraising efforts in the United States to buy the gardens.

The first years were difficult. Without a proper budget, the garden could not be kept open to the public and could only be visited by special appointment with Rafael Lucas Rodríguez. It was not until 1979 that the University named Dora Emilia Mora de Retana (Fig. 22) as the first director of the Garden. Under her direction, the garden was slowly transformed from a small farm of 10,7 hectares (aprox. 25 acres) into a world-renowned botanical garden. In a very similar way to Charles Lankester, Dora Emilia turned the Garden into a meeting place for the world’s most prestigious orchidologists. Calaway H. Dodson, Norris H. Williams, Robert L. Dressler, John T. Atwood, Carlyle A. Luer, Rudolf Jenny, Eric Hágsater, Henry Oakeley, Günter Gerlach, Klaus C. Horich and many others were frequent guests at Charles Lankester’s old farm at “Las Cóncavas”. Her interaction with other botanists resulted in 300 Costa Rican orchids being illustrated in the series *Icones Plantarum Tropicarum*, mostly based on the living collections kept at the gardens. As Atwood remembers, Dora Emilia’s did not see Lankester Gardens as just a tourist garden for generating income, but as a garden dedicated to Costa Rican orchid research. In 1984, she organized the first formal course in orchidology in collaboration with Robert L. Dressler, who at the time was a visiting

FIGURE 22. Dora Emilia Mora (right) with Pamela Lankester (left), wife of Alexander Skutch.

FIGURE 23. Joaquín Bernardo García Castro (1944-2001). Photograph by Eduardo Bitter.

professor at the University of Costa Rica. Her main scientific legacy to the knowledge of Costa Rican orchid taxonomy was the treatment of the subtribes Maxillarinae and Oncidiniinae for the *Flora Costaricensis*, prepared in collaboration with John Atwood.

Many new orchid species were dedicated to Dora Emilia Mora de Retana. Hágsater named his *Epidendrum mora-retanae* in her honor, Gerlach his *Kefersteinia retanae*, Dressler his *Sobralia doremiliae*, Luer his *Stelis morae* and Dodson & Escobar their *Telipogon retanae*.

We leave Dora Emilia with Atwoods' final words in her obituary: *"...her greatest legacy is to rise above personal ambitions to foster efforts of those around her. Because of her, Lankester Gardens is blessed with a talented, imaginative, and altruistic staff..."*

Joaquín B. García Castro (1944-2001) (Fig. 23), called "Quincho" by his friends, was Dora Emilia's friend and main collaborator for over 25 years. Together, they published the first checklist of Costa Rican orchids after Paul Standley's *Flora of Costa Rica* (1937), to which Oakes Ames had contributed with the treatment of Orchidaceae. In this *Lista actualizada de las orquídeas de Costa Rica*, Dora Emilia and Joaquín García added 46 genera and 467 species to the previous catalogue.

A doctor of medicine and a university professor, Joaquín García was, for many years, the mentor of numerous Costa Rican orchid lovers. A brilliant scholar, Joaquín liked to lecture his friends on complicated themes, such as the biochemistry of colors in orchid flowers or the fundamentals in orchid hybrid genetics. As John Atwood liked to say: "I don't have the brains of Joaquín, therefore I need a well-organized library." Always generous with his knowledge and his time, Joaquín served several terms as president of the Costa Rican Orchid Society. Shortly after his death, Franco Pupulin named *Prosthechea joaquingarciana* in his honor.

The Lankester Botanical Garden has become the most important center for orchid research in Central America and the Caribbean. For this reason, in 2003 the University of Costa Rica changed its status and converted the garden into an 'experiment station'. In December 2005, the Ministry of the Environment declared the Lankester Botanical Garden "National Center for the Conservation of Flora" and "National Epiphyte Sanctuary". For its institutional merits, Luer named *Masdevallia lankesteriana*, and Pupulin named *Chondrorhyncha lankesteriana* (today *Stenotyla lankesteriana*) in honor of the gardens.

Literature cited

Atwood, J.T. 2001. Dora Emilia Mora de Retana, a remembrance. Lankesteriana 2: 9.

Jiménez, O. 1963. *Paul C. Standley*. Chicago Natural History Museum Press.

Jiménez, O. 1963. 1967. Charles Herbert Lankester. Revista de Agricultura, Oct. 1967: 248-264.

McCook, S. 1999. Creole Science: Botanical Surveys of Costa Rica, 1880-1940. Endeavour 23(3): 118-120.

Northen, R. 1964. Charles H. Lankester – Orchidologist of Costa Rica. Amer. Orchid Soc. Bull. January 1964: 43-50.

Ossenbach, C. 2003. *Breve Historia de la Orquideología en Costa Rica*. Editorial de la Universidad de Costa Rica.

Ossenbach, C. 2006. Orchids in Costa Rica - Part II: Charles H. Lankester and Oakes Ames. Orchids (West Palm Beach), February 2006: 120-127.

Ossenbach, C. 2006. Orchids in Costa Rica - Part IV: The Charles H. Lankester Botanical Garden. Orchids (West Palm Beach), April 2006: 284-291.

Ossenbach, C. 2009. Orchids and Orchidology in Central America: 500 years of history. Lankesteriana 9 (1-2): 1-268.

Schlechter, R. 1923. *Additamenta ad Orchideologiam Costaricensem*. Repert. Sp. Nov. Regni Veg. 19.

Standley, P.C. 1937. *Flora of Costa Rica,* Part I. Field Museum of Natural History, Botanical Series, Vol. 18, publication 391.

Williams, L.O. 1969. In Memoriam: Charles Herbert Lankester – 1879-1969. Amer. Orchid Soc. Bull. : 860-862.

Appendix

New orchid species collected by Charles Lankester

Campylocentrum lankesteri Ames
Campylocentrum longicalcaratum Ames & C.Schweinf.
Chondrorhyncha estrellensis Ames
Cranichis lankesteri Ames
Cranichis saccata Ames
Cryptocentrum gracillimum Ames & C.Schweinf.
Dichaea ciliolata Rolfe
Dichaea lankesteri Ames
Dichaea verrucosa Ames & C.Schweinf.
Elleanthus tricallosus Ames & C.Schweinf.
Epidendrum adnatum Ames & C.Schweinf.
Epidendrum bilobatum Ames
Epidendrum circinatum Ames
Epidendrum crescentilobium Ames
Epidendrum cristobalense Ames
Epidendrum dentiferum Ames & C.Schweinf.
Epidendrum dolabrilobum Ames & C.Schweinf.
Epidendrum equitantifolium Ames
Epidendrum estrellense Ames
Epidendrum exile Ames
Epidendrum intermixtum Ames & C.Schweinf.
Epidendrum lankesteri Ames
Epidendrum nervosiflorum Ames & C.Schweinf.
Epidendrum peraltense Ames
Epidendrum ramosissimum Ames & C.Schweinf.
Epidendrum rugosum Ames
Epidendrum santaclarense Ames
Epidendrum vagans Ames
Habenaria lankesteri Ames
Hexisea lankesteri Ames
Hexisea sigmoidea Ames & C.Schweinf.
Lankesterella Ames
Lankesterella costaricensis Ames
Lepanthes cascajalensis Ames
Lepanthes chameleon Ames
Lepanthes estrellensis Ames
Lepanthes exasperata Ames & C.Schweinf.
Lepanthes eximia Ames
Lepanthes grandiflora Ames & C.Schweinf.
Lepanthes micrantha Ames
Lepanthes rostrata Ames
Lepanthes sanchoi Ames
Lepanthes subdimidiata Ames & C.Schweinf.
Lepanthes tridens Ames
Limodorum lankesteri Ames & C.Schweinf.
Lockhartia lankesteri Ames
Malaxis lankesteri Ames
Malaxis uncinata Ames & C.Schweinf.
Masdevallia fimbriata Ames & C.Schweinf.
Maxillaria arachnitiflora Ames & C.Schweinf.
Maxillaria confusa Ames & C.Schweinf.
Maxillaria foliosa Ames & C.Schweinf.
Maxillaria lankesteri Ames
Notylia lankesteri Ames
Oncidium lankesteri Ames
Ornithidium lankesteri Ames
Ornithocephalus lankesteri Ames
Physosiphon obliquipetalus Ames & C.Schweinf.
Pleurothallis angusta Ames & C.Schweinf.
Pleurothallis arietina Ames
Pleurothallis cachensis Ames
Pleurothallis cerea Ames

Pleurothallis costaricensis Rolfe
Pleurothallis crassilabia Ames & C.Schweinf.
Pleurothallis crescentilabia Ames
Pleurothallis cucullata Ames
Pleurothallis dentipetala Rolfe ex Ames
* *Pleurothallis dichotoma* Ames (nom. ill.)
Pleurothallis geminicaulina Ames
Pleurothallis glomerata Ames
Pleurothallis longipedicellata Ames & C.Schweinf.
Pleurothallis nana Ames & C.Schweinf.
Pleurothallis palliolata Ames
*Pleurothallis papillifera*Rolfe
Pleurothallis peperomioides Ames
Pleurothallis peraltensis Ames
Pleurothallis peregrina Ames
Pleurothallis periodica Ames
Pleurothallis pompalis Ames
Pleurothallis rectipetala Ames & C.Schweinf.
Pleurothallis saccata Ames
Pleurothallis sanchoi Ames
Pleurothallis scandens Ames
Pleurothallis segregatifolia Ames & C.Schweinf.
Pleurothallis strumosa Ames
Pleurothallis vinacea Ames
Restrepia lankesteri Ames & C.Schweinf.
Scaphyglottis bicallosa Dressler
Sobralia atropubescens Ames & C.Schweinf.
Sobralia carazoi C.H. Lank. & Ames
Sobralia mucronata Ames & C.Schweinf.
Spiranthes lankesteri Standl. & L.O.Williams
Stelis barbata Rolfe
Stelis carnosiflora Ames & C.Schweinf.
Stelis cascajalensis Ames
Stelis crystallina Ames
Stelis cucullata Ames
Stelis cuspidata Ames
Stelis distantiflora Ames
Stelis elliptica Ames & C.Schweinf.
Stelis fractiflexa Ames & C.Schweinf.
Stelis glandulosa Ames
Stelis lankesteri Ames
Stelis latipetala Ames
Stelis minutiflora Ames & C. Schweinf. (*nom. ill.*)
Stelis propinqua Ames
Stelis sanchoi Ames
Stelis transversalis Ames
Stelis vestita Ames
Stellilabium distantiflorum Ames & C.Schweinf.
Stenorrhynchus bracteosus Ames & C.Schweinf.

New species collected by Lankester in other plant families

ASTERACEAE
Vernonia lankesteri S.F.Blake ex Standl.
BROMELIACEAE
Araeococcus pectinatus L.B.Smith
CACTACEAE
Discocactus lankesteri Kimnach
CAPPARACEAE
Capparis lankesteri Standl.
EUPHORBIACEAE
Croton triumfettoides Croizat
MALVACEAE
Wercklea lutea Rolfe
PIPERACEAE
Peperomia lankesteri Trel.
RANUNCULACEAE
Thalictrum lankesteri Standl.
SAPOTACEAE
Bumelia lankesteri Standl.
SOLANACEAE
Lycianthes lankesteri Standl.
VERBENACEAE
Citharexylum lankesteri Moldenke

LANKESTERIANA 13(3): 375—392. 2014.

INVITED PAPER*

GENERIC AND SUBTRIBAL RELATIONSHIPS IN NEOTROPICAL CYMBIDIEAE (ORCHIDACEAE) BASED ON *MATK/YCF1* PLASTID DATA

W. Mark Whitten[1,2], Kurt M. Neubig[1] & N. H. Williams[1]

[1]Florida Museum of Natural History, University of Florida
Gainesville, FL 32611-7800 USA
[2]Corresponding author: whitten@flmnh.ufl.edu

Abstract. Relationships among all subtribes of Neotropical Cymbidieae (Orchidaceae) were estimated using combined *matK/ycf1* plastid sequence data for 289 taxa. The matrix was analyzed using RAxML. Bootstrap (BS) analyses yield 100% BS support for all subtribes except Stanhopeinae (87%). Generic relationships within subtribes are highly resolved and are generally congruent with those presented in previous studies and as summarized in *Genera Orchidacearum*. Relationships among subtribes are largely unresolved. The Szlachetko generic classification of Maxillariinae is not supported. A new combination is made for *Maxillaria cacaoensis* J.T.Atwood in *Camaridium*.

Key words: Orchidaceae, Cymbidieae, Maxillariinae, *matK, ycf1*, phylogenetics, *Camaridium, Maxillaria cacaoensis, Vargasiella*

Cymbidieae include many of the showiest Neotropical epiphytic orchids and an unparalleled diversity in floral rewards and pollination systems. Many researchers have posed questions such as “How many times and when has male euglossine bee pollination evolved?”(Ramírez *et al.* 2011), or “How many times have oil-reward flowers evolved?” (Reis *et al.* 2000) within this clade, but answering such questions requires a densely sampled and well-supported phylogenetic hypothesis. Although the broad outlines of relationships within Cymbidieae were revealed by the *rbcL/matK* analyses of Freudenstein *et al.* (2004) and summaries of Chase *et al.* (2003), both of these studies were constrained by low taxon sampling and low bootstrap support for many clades. The most recent publication of the *Genera Orchidacearum* series (Pridgeon 2009) provided a concise and authoritative summary of knowledge of this clade that includes 11 subtribes. Phylogenetic trees for Neotropical Cymbidieae published in that volume were based upon our nrITS/*matK*/*ycf1* data sets that were unpublished and included many sequences not deposited in GenBank. In attempting to rework these data for publication, we decided that attempting to align nrITS sequences across the entire tribe was unrealistic due to high levels of sequence divergence, and instead to concentrate our efforts on assembling a larger plastid data set based on two regions (*matK* and *ycf1*) that are among the most variable plastid exon regions and can be aligned with minimal ambiguity across broad taxonomic spans. Although various plastid spacer regions such as *trnL-F* or *atpB-rbcL* are more rapidly evolving (Shaw *et al.* 2005), they (like nrITS) are difficult or impossible to align with confidence across Cymbidieae. In this paper, we present phylogenetic analyses of ca. 280 taxa of Cymbidieae including representatives of 10 subtribes and most genera (excluding many Oncidiinae) utilizing the majority of the *matK* exon and a ca. 1500 base pair (bp) portion of the 3’ end of *ycf1*. Phylogenetic relationships within Oncidiinae were addressed in detail by Neubig *et al.* (2012). Relationships within Maxillariinae were studied using nrITS/*matK*/*atpB-rbcL* spacer by Whitten *et al.*(2007), and the *Bifrenaria* clade was analyzed in more detail using nrITS/*trnL-F* by Koehler *et al.* (2002). Zygopetalinae relationships were previously studied using nrITS/*matK*/*trnL-F* (Neubig *et al.*, 2009b; Whitten *et al.*, 2005).

---

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

Methods

Most *matK* sequences were downloaded from GenBank from previous studies of Cymbidieae subtribes. Additional sequences were generated using primers *matK*-19F (CGTTCTGACCATATTGCACTATG) and *matK* 1520R (CGGATAATGTCCAAATACCAAATA) and the amplification and sequencing protocols of Whitten *et al.* (2007). A ca. 1500 bp portion of 3' portion of *ycf1* was amplified and sequenced using the primers and protocols in Neubig *et al.* (2009a). A list of taxa, vouchers, and GenBank numbers is presented in Table 1. Matrices were aligned using Muscle (Edgar, 2004)followed by manual adjustment of gaps to maintain reading frame using Se-Al (Rambaut 1996). The *matK* matrix was trimmed to eliminate a region of ambiguous alignment in the first 100 bp. *Polystachya* was chosen as the outgroup based upon broader sampling (Neubig *et al.* 2009a). Matrices and a list of vouchers are deposited in the Dryad Digital Repository (http://doi.org/10.5061/dryad.2rm60) or are available from the author. The resulting combined matrix consists of 288 ingroup taxa and 1 outgroup (*Polystachya*); the aligned matrix consists of 3618 characters (1605 for *matK*; 2013 for *ycf1*). Gaps are coded as missing data.

The aligned matrix was analyzed using maximum likelihood (ML) as implemented in RAxML-HPC Blackbox version 7.6.3 (Stamatakis, 2006) via the CIPRES Science Gateway computing facility (http://www.phylo.org/index.php/portal/). Analyses were run using default values with 200 fast bootstrap replicates. The resulting bootstrap trees were saved to a treefile, opened in PAUP* (Swofford 2003), and a majority-rule consensus tree was generated to display bootstrap support values. FigTree 1.4.0 (Rambaut 2013) was used to edit and print the best ML tree.

Results and Discussion

The resulting best ML tree is presented in Figures 1-5; bootstrap (BS) values above 75% are annotated on this tree. Overall, the tree agrees well with previous studies based on plastid and nuclear regions (Górniak *et al.* 2010). Subtribe Cymbidiinae is represented by only a single taxon (*Cymbidium*); it is sister to all remaining taxa. All subtribes (as delimited in *Genera Orchidacearum*) received 100% BS support (except for Stanhopeinae), but most relationships among subtribes lack BS support.

Eulophiinae — (Fig. 1). Out of the nine genera recognized in this subtribe, our sampling included the only two Neotropical genera; the majority of species are from the tropics of Africa, Madagascar, Asia, and Australia. Eulophiinae are weakly sister to Catasetinae in the single ML tree.

Catasetinae — (Fig. 1). Recent molecular phylogenetic studies (Batista et al., In press) place the three species of *Cyanaeorchis* Barb.Rodr. in Catasetinae; it is sister to *Grobya* Lindl., and they are sister to all remaining Catasetinae. Our sampling includes five of the seven genera, with *Grobya* and *Mormodes* absent; other phylogenetic studies confirm *Grobya* as monophyletic and a member of Catasetinae (Monteiro *et al.* 2010). Unpublished *ycf1* and *matK* sequences for *Cyanaeorchis arundinae* (Rchb.f.) Barb.Rodr. and unidentified *Grobya* species (Whitten and Batista, unpubl.) confirm these relationships. Oscar Peréz (pers. comm.) also reported finding plastid/nuclear incongruence among sections of *Cycnoches*.

Cyrtopodiinae — (Fig. 1). Our analyses confirm the distinctiveness of this monogeneric subtribe from the vegetatively similar Catasetinae; *Cyrtopodium* is weakly sister to all remaining Cymbidieae, and not to Catasetinae, confirming the relationships found by Pridgeon and Chase (Pridgeon & Chase 1998).

Oncidiinae — (Fig. 1). Our sampling of Oncidiinae was minimal, including placeholder representatives of the major clades within the subtribe; a much more extensive sampling based on *matK/ycf1* plus other regions was presented by Neubig *et al.* (2012). Oncidiinae are in a highly supported clade that includes subtribes Eriopsidinae, Zygopetalinae, Stanhopeinae, Coeliopsidinae, and Maxillariinae but relationships within this clade are poorly supported.

Eriopsidinae — (Fig. 2). Dressler (1981) included *Eriopsis* in Cyrtopodiinae on the basis of floral traits and pollinarium structure but later regarded it as *incertae sedis* (Dressler 1993). Szlachetko (1995) created a subtribe to accommodate this anomalous genus; our trees confirm its uniqueness relative to other subtribes.

Table 1. List of taxa sequenced with GenBank numbers and voucher information.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Acineta chrysantha (C. Morren) Lindl.	KF660253	KF660372	Whitten 91360 (FLAS)
Acineta superba (Kunth) Rchb.f.	KF660254	KF660523	Whitten 3378 (FLAS)
Aetheorhyncha andreettae (Jenny) Dressler	AY869932	KF660386	Dressler 6360 (FLAS)
Aganisia fimbriata Rchb.f.	AY870006	KF660404	Breuer s.n. (M)
Aganisia pulchella Lindl.	AY870007	KF660403	Breuer s.n. (M)
Anguloa hohenlohii C. Morren	AF239429	KF660512	Whitten 3023 (FLAS)
Anguloa uniflora Ruiz & Pav.	KF660255	KF660364	Whitten 3263 (FLAS)
Batemannia lepida Rchb.f.	AY869990	KF660323	Gerlach 92-3900 (M)
Benzingia cornuta (Garay) Dressler	AY869927	KF660450	Whitten 1818 (FLAS)
Benzingia estradae (Dodson) Dodson	AY869930	KF660398	Gerlach 96-4287 (M)
Benzingia hajekii (D.E.Benn. & Christenson) Dressler	AY869929	KF660377	Whitten 1751 (FLAS)
Benzingia reichenbachiana (Schltr.) Dressler	AF239421	KF660363	Whitten 1747 (FLAS)
Bifrenaria inodora Lindl.	DQ210744	KF660365	Whitten 0097 (FLAS)
Bifrenaria tetragona (Lindl.) Schltr.	DQ210751	KF660529	Whitten 0506 (FLAS)
Bifrenaria tyrianthina (Lodd. ex Loudon) Rchb.f.	DQ210752	KF660379	Whitten 0507 (FLAS)
Braemia vittata (Lindl.) Jenny	AF239476	KF660338	Chase 84748 (FLAS)
Brasiliorchis gracilis (Lodd.) R. B. Singer, S. Koehler & Carnevali	DQ210811	KF660426	Whitten 2303 (FLAS)
Brasiliorchis schunkeana (Campacci & Kautsky) R. B. Singer, S. Koehler & Carnevali	DQ210799	KF660421	Whitten 1992 (FLAS)
Brassia aurantiaca (Lindl.) M.W.Chase	AF239492	FJ563573	Williams s.n. (FLAS)
Brassia jipijapensis Dodson & N.H.Williams	FJ564762	FJ563258	Whitten 1829 (FLAS)
Camaridium bradeorum Schltr.	DQ210963	KF660468	Whitten 2639 (FLAS)
Camaridium carinatum (Barb.Rodr.) Hoehne	DQ210828	KF660431	Whitten 2337 (FLAS)
Camaridium ctenostachys (Rchb.f.) Schltr.	DQ210967	KF660471	Whitten 2647 (FLAS)
Camaridium cucullatum (Lindl.) M.A Blanco	DQ210753	KF660354	Whitten 2547 (FLAS)
Camaridium dendrobioides Schltr.	DQ210952	KF660463	Whitten 2627 (FLAS)
Camaridium horichii (Senghas) M.A. Blanco	DQ210937	KF660461	Whitten 2602 (FLAS)
Camaridium nutantiflorum Schltr.	DQ210964	KF660469	Whitten 2643 (FLAS)
Camaridium ochroleucum Lindl.	DQ210626	KF660312	Gerlach 2003-3648 (M)
Camaridium paleatum (Rchb.f.) M.A.Blanco	DQ210907	KF660458	Whitten 2561 (FLAS)
Camaridium scalariforme (J.T.Atwood) M.A.Blanco	DQ210957	KF660466	Whitten 2633 (FLAS)
Camaridium vestitum (Sw.) Lindl.	DQ209866	KF660304	Atwood & Whitten 5070 (SEL)
Catasetum expansum Rchb.f.	KF660256	KF660525	Whitten 3543 (FLAS)
Chaubardia klugii (C.Schweinf.) Garay	AY869973	KF660378	Whitten 1853 (FLAS)
Chaubardia surinamensis Rchb.f.	AY869974	KF660309	Gerlach 2001-2159 (M)
Chaubardiella pubescens Ackerman	AY869944	KF660416	Whitten 1620 (FLAS)
Chaubardiella subquadrata (Schltr.) Garay	AY869945	KF660407	Whitten s.n. (FLAS)
Chaubardiella tigrina (Garay & Dunst.) Garay	AY869946	KF660311	Gerlach 1651 (M)
Chondrorhyncha hirtzii Dodson	AY869916	KF660389	Whitten 1637 (FLAS)
Chondrorhyncha hirtzii Dodson	AY869913	KF660406	Maduro & Olmos 217 (FLAS)
Chondrorhyncha rosea Lindl.	AY869914	KF660385	Whitten 1760 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Chondroscaphe amabilis (Schltr.) Senghas & G.Gerlach	AY869966	KF660391	Whitten 1855 (FLAS)
Chondroscaphe bicolor (Rolfe) Dressler	AY869971	KF660390	Dressler ex Hoffman s.n. (FLAS)
Chondroscaphe eburnea (Dressler) Dressler	AY869915	KF660408	Dressler 6361 (FLAS)
Chondroscaphe flaveola (Linden & Rchb.f.) Senghas & G.Gerlach	AY869969	KF660320	Gerlach 93-3342 (M)
Christensonella ferdinandiana (Barb.Rodr.) Szlach., Mytnik, Górniak & Smiszek	DQ210670	KF660353	Koehler 109 (UEC)
Christensonella nardoides (Kraenzl.) Szlach., Mytnik, Górniak & Smiszek	DQ210890	KF660452	Whitten 2502 (FLAS)
Christensonella pacholskii (Christenson) S.Koehler	DQ210851	KF660437	Whitten 2393 (FLAS)
Cirrhaea fuscolutea Lindl.	KF660257	KF660508	Whitten 2976 (FLAS)
Cirrhaea seidelii Pabst	KF660258	KF660333	Gerlach s.n. (M)
Cischweinfia pusilla (C.Schweinf.) Dressler & N.H.Williams	FJ565130	FJ563799	Whitten 3300 FLAS
Clowesia dodsoniana E.Aguirre	KF660259	KF660524	Whitten 3542 (FLAS)
Cochleanthes flabelliformis (Sw.) R.E.Schult. & Garay	AY869965	KF660513	Whitten 99113 (FLAS)
Coeliopsis hyacinthosma Rchb.f.	AF239440	KF660337	Whitten 93153 (FLAS)
Comparettia falcata Poepp. & Endl.	FJ563869	FJ563283	Williams N084 (FLAS)
Comparettia macroplectron Rchb.f. & Triana	FJ565135	FJ563804	Whitten 3425 (FLAS)
Coryanthes elegantium Linden & Rchb.f.	KF660260	KF660318	Whitten 87267 (FLAS)
Coryanthes macrantha (Hook.) Hook.	KF660261	KF660319	Gerlach O-21458 (M)
Coryanthes verrucolineata G.Gerlach	KF660262	KF660317	Gerlach 96-4284 (M)
Cryptarrhena guatemalensis Schltr.	AY869983	KF660476	Pupulin & Campos 2957 (USJ)
Cryptarrhena lunata R.Br.	AY869982	KF660405	Whitten 98000 (FLAS)
Cryptocentrum beckendorfii Carnevali	KF660263	KF660307	Beckendorf s.n. (CICY)
Cryptocentrum peruvianum (Cogn.) C.Schweinf.	DQ210820	KF660430	Whitten 2322 (FLAS)
Cryptocentrum roseans (Schltr.) A.D.Hawkes	DQ210903	KF660457	Whitten 2554 (FLAS)
Cycnoches cooperi Rolfe	KF660264	KF660526	Whitten 3591 (FLAS)
Cycnoches lehmannii Rchb.f.	KF660265	KF660328	Whitten 87011 (FLAS)
Cycnoches manoelae P.Castro & Campacci	KF660266	KF660310	Gerlach 05-1231 (M)
Cycnoches pachydactylon Schltr.	KF660267	KF660316	Gerlach 00-3414 (M)
Cymbidium devonianum Paxton	KF660268	KF660325	Chase 87030 (K)
Cyrtidiorchis alata (Ruiz & Pav.) Rauschert	DQ210627	KF660321	Gerlach 94-4005 (M)
Cyrtidiorchis alata (Ruiz & Pav.) Rauschert	DQ211044	KF660505	Whitten 2932 (FLAS)
Cyrtochilum serratum (Lindl.) Kraenzl.	FJ563842	FJ562462	Chase O-032 (K)
Cyrtopodium andersonii (Lamb. ex Andrews) R.Br.	KF660269	KF660329	Kew no voucher
Cyrtopodium flavum (Nees) Link & Otto ex Rchb.	KF660270	KF660522	Whitten 3377 (FLAS)
Cyrtopodium longibulbosum Dodson & G.A.Romero	KF660271	KF660453	Whitten 2504 (QCA)
Daiotyla albicans (Rolfe) Dressler	AY869917	KF660396	Whitten 1932 (FLAS)
Dichaea eligulata Folsom	EU123625	EU123747	Pupulin 1094 (USJ-L)
Dichaea fragrantissima Folsom	EU123628	EU123750	Pupulin 4601 (USJ-L)
Dichaea panamensis Lindl.	EU123650	EU123772	Whitten 2556 (FLAS)
Dichaea trulla Rchb.f.	EU123671	EU123792	Whitten 2475 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Dipteranthus grandiflorus (Lindl.) Pabst	AF350587	FJ563191	Chase O-103 (K)
Dressleria dilecta (Rchb.f.) Dodson	AF239507	EU490731	Whitten F1046 (SEL)
Dressleria fragrans Dodson	KF660272	KF660327	Dodson 8855 (SEL)
Dressleria helleri Dodson	KF660273	KF660326	Hills 87145 (FLAS)
Embreea herrenhusana (Jenny) Jenny	KF660275	KF660314	Gerlach 04-2526 (M)
Embreea rodigasiana (Claes ex Cogn.) Dodson	KF660276	KF660313	Gerlach 05-2172 (M)
Eriopsis biloba Lindl.	DQ210866	EU490743	Whitten 3327 (FLAS)
Eriopsis biloba Lindl.	DQ210866	KF660441	Whitten 2439 (FLAS)
Eriopsis biloba Lindl.	DQ461806	KF660515	Whitten 3153 (QCA)
Erycina pusilla (L.) N.H.Williams & M.W.Chase	FJ565025.	FJ563690	Whitten 1771 FLAS
Eulophia guineensis Lindl.	AF239509	EU490745	Whitten 99029 (FLAS)
Eulophia petersii (Rchb.f.) Rchb.f.	KF660274	KF660332	Chase 22361 (K)
Fernandezia cuencae (Rchb.f.) M.W.Chase	FJ565079	KF660454	Whitten 2537 (FLAS)
Fernandezia sanguinea (Lindl.) Garay & Dunst.	FJ565009	FJ563674	Whitten 1700 FLAS
Fernandezia tica Mora-Ret. & García Castro	FJ564944	FJ563591	Dressler & Atwood s.n. FLAS
Galeandra devoniana M.R.Schomb. ex Lindl.	KF660278	KF660330	Pupulin 1133 (JBL)
Galeottia burkei (Rchb.f.) Dressler & Christenson	AY869987	KF660400	Maguire & Politi 28175 (AMES)
Galeottia ciliata (Morel) Dressler & Christenson	AY869989	KF660401	Breuer s.n. (M)
Galeottia colombiana (Garay) Dressler & Christenson	AY869986	KF660397	Gerlach 93-3396 (M)
Gongora amparoana Schltr.	AF239481	KF660367	Whitten 91036 (FLAS)
Gongora armeniaca (Lindl.) Rchb.f.	AF239482	KF660334	Hills 86143 (FLAS)
Gongora armeniaca (Lindl.) Rchb.f.	AF239482	KF660374	Whitten F1636 (FLAS)
Gongora escobariana Whitten	KF660279	KF660347	Whitten 95023 (FLAS)
Gongora hirtzii Dodson & N.H.Williams	KF660280	KF660349	Whitten 93109 (FLAS)
Gongora ilense Whitten & Jenny	AF239480	KF660509	Whitten 2982 (FLAS)
Gongora portentosa Linden & Rchb.f.	AF239485	KF660341	Bennett 5258 (FLAS)
Gongora portentosa Linden & Rchb.f.	KF660281	KF660350	Bennett 5279 (FLAS)
Gongora seideliana Rchb.f.	KF660282	KF660348	Whitten F-1635 (FLAS)
Gongora sphaerica Jenny	KF660283	KF660331	Whitten 2003 (FLAS)
Gongora tridentata Whitten	AF239483	KF660373	Whitten 1083 (FLAS)
Grandiphyllum robustissimum (Rchb.f.) Docha Neto	FJ563959	FJ563597	Whitten 1777 FLAS
Guanchezia maguirei (C.Schweinf.) G.A.Romero & G.Carnevali	KF660284	KF660410	Maguire & Politi 27931 (AMES)
Heterotaxis crassifolia Lindl.	DQ210897	KF660455	Whitten 2544 (FLAS)
Heterotaxis equitans (Schltr.) Ojeda & Carnevali	DQ210877	KF660448	Whitten 2483 (FLAS)
Heterotaxis maleolens (Schltr.) Ojeda & Carnevali	DQ209972	KF660486	Whitten 2764 (FLAS)
Heterotaxis santanae (Carnevali & I.Ramírez) Ojeda & Carnevali	DQ209973	KF660487	Whitten 2765 (FLAS)
Heterotaxis valenzuelana (A.Rich.) Ojeda & Carnevali	DQ210950	KF660510	Whitten 2620 (FLAS)
Heterotaxis violaceopunctata (Rchb.f.) F.Barros	DQ210807	KF660424	Whitten 2294 (FLAS)
Hintonella mexicana Ames	FJ564940	FJ562874	Whitten W513 (FLAS)
Horichia dressleri Jenny	AF239458	KF660340	Whitten 93151 (FLAS)

Table 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Houlletia brocklehurstiana Lindl.	KF660285	KF660335	Gerlach s.n. (M)
Houlletia odoratissima Linden ex Lindl. & Paxton	KF660286	KF660315	Gerlach 97-3285 (M)
Houlletia sanderi Rolfe	AF239467	KF660376	Whitten 93079 (FLAS)
Houlletia tigrina Linden ex Lindl.	AF239466	KF660375	Whitten 91354 (FLAS)
Huntleya wallisii (Rchb.f.) Rolfe	EU123674	EU123796	Whitten 88026 (FLAS)
Hylaeorchis petiolaris (Schltr.) Carnevali & G.A.Romero	DQ211020	KF660352	Whitten 2874 (FLAS)
Inti bicallosa (Rchb.f.) M.A.Blanco	DQ209946	KF660417	Whitten 1677 (FLAS)
Inti bicallosa (Rchb.f.) M.A.Blanco	DQ210960	KF660467	Whitten 2636 (FLAS)
Inti chartacifolia (Ames & C.Schweinf.) M.A.Blanco	DQ209942	EU490750	Whitten 1597 (FLAS)
Inti chartacifolia (Ames & C.Schweinf.) M.A.Blanco	DQ211000	KF660485	Whitten 2752 (FLAS)
Ixyophora viridisepala (Senghas) Dressler	AY869942	KF660418	Whitten 1749 (FLAS)
Kefersteinia excentrica Dressler & Mora-Ret.	AY869934	KF660507	Dressler 6236 (FLAS)
Kefersteinia maculosa Dressler	AY869938	KF660422	Whitten 1997 (FLAS)
Kefersteinia microcharis Schltr.	AY869937	KF660308	Pupulin 252 (USJ)
Kefersteinia trullata Dressler	AY869936	KF660423	Whitten 1998 (FLAS)
Kegeliella atropilosa L.O.Williams & A.H.Heller	AF239459	KF660342	Whitten 93101 (FLAS)
Kegeliella kupperi Mansf.	AF263666	KF660339	Whitten F167 (FLAS)
Koellensteinia graminea (Lindl.) Rchb.f.	AY870003	KF660429	Chase 159 (K)
Lacaena spectabilis (Klotzsch) Rchb.f.	KF660287	KF660346	Whitten F-184 (FLAS)
Lockhartia amoena Endres & Rchb.f.	FJ564686	FJ563116	Blanco 1803 (FLAS)
Lueckelia breviloba (Summerh.) Jenny	KF660288	KF660382	Gerlach 96-6072 (M)
Lueddemannia pescatorei (Lindl.) Linden & Rchb.f.	AF239472	KF660488	Gerlach 2003-1482(M)
Lycaste aromatica (Graham) Lindl.	AF263669	KF660322	Freudenstein s.n.
Lycomormium fiskei H.R.Sweet	AF239441	KF660528	Whitten 91340 (FLAS)
Mapinguari auyantepuiensis (Foldats) Carnevali & R.B.Singer	DQ210830	KF660432	Whitten 2347 (FLAS)
Mapinguari longipetiolatus (Ames & C.Schweinf.) Carnevali & R.B.Singer	DQ210747	KF660305	Atwood & Whitten 5075 (SEL)
Maxillaria acostae Schltr.	DQ210965	KF660470	Whitten 2644 (FLAS)
Maxillaria angustissima Ames, F.T.Hubb. & C.Schweinf.	DQ210993	KF660479	Whitten 2735 (FLAS)
Maxillaria augustae-victoriae F.Lehm.&Kraenzl.	DQ211026	KF660500	Whitten 2893 (FLAS)
Maxillaria brachybulbon Schltr.	DQ210773	KF660414	Whitten 1583 (FLAS)
Maxillaria buchtienii Schltr.	DQ211047	KF660506	Whitten 2940 (FLAS)
Maxillaria cacaoensis J.T.Atwood	KC747493	KC747494	Whitten 3362 (FLAS)
Maxillaria calantha Schltr.	DQ210900	KF660456	Whitten 2550 (FLAS)
Maxillaria canarina D.E.Benn. & Christenson	KF660289	KF660518	Whitten 3256 (FLAS)
Maxillaria chionantha J.T.Atwood	DQ210969	KF660472	Whitten 2649 (FLAS)
Maxillaria confusa Ames & C.Schweinf.	DQ210994	KF660480	Whitten 2736 (FLAS)
Maxillaria dalessandroi Dodson	DQ211024	KF660499	Whitten 2889 (FLAS)
Maxillaria dillonii D.E.Benn. & Christenson	KF660290	KF660496	Whitten 2878 (FLAS)
Maxillaria ecuadorensis Schltr.	DQ210989	KF660478	Whitten 2724 (FLAS)
Maxillaria elegantula Rolfe	DQ210921	KF660460	Whitten 2576 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Maxillaria exaltata (Kraenzl.) C.Schweinf.	DQ210818	KF660428	Whitten 2317 (FLAS)
Maxillaria gentryi Dodson	DQ210975	KF660475	Whitten 2656 (FLAS)
Maxillaria grayi Dodson	KF660291	KF660497	Whitten 2879 (FLAS)
Maxillaria guadalupensis Cogn.	DQ210775	KF660415	Whitten 1593 (FLAS)
Maxillaria guadalupensis Cogn.	KF660292	KF660445	Whitten 2468 (FLAS)
Maxillaria hennisiana Schltr.	DQ210918	KF660459	Whitten 2572 (FLAS)
Maxillaria litensis Dodson	KF660293	KF660498	Whitten 2888 (FLAS)
Maxillaria longipes Lindl.	DQ210999	KF660484	Whitten 2751 (FLAS)
Maxillaria longissima Lindl.	DQ210996	KF660482	Whitten 2745 (FLAS)
Maxillaria lueri Dodson	DQ210954	KF660464	Whitten 2629 (FLAS)
Maxillaria meridensis Lindl.	DQ210870	KF660443	Whitten 2451 (FLAS)
Maxillaria ochroleuca Lodd. ex Lindl.	DQ210844	KF660435	Whitten 2378 (FLAS)
Maxillaria platypetala Ruiz & Pav.	DQ211033	KF660502	Whitten 2909 (FLAS)
Maxillaria porrecta Lindl.	DQ210948	KF660462	Whitten 2617 (FLAS)
Maxillaria pulla Linden & Rchb.f.	DQ210872	KF660444	Whitten 2459 (FLAS)
Maxillaria silvana Campacci	DQ210997	KF660483	Whitten 2747 (FLAS)
Maxillaria sp. nov.	KF660294	KF660520	Whitten 3337 (FLAS)
Maxillaria splendens Poepp. & Endl.	FJ565112	FJ563781	Whitten 2949 FLAS
Maxillaria triloris E.Morren	DQ209887	KF660411	Blanco 1640 (USJ)
Maxillaria triloris E.Morren	DQ211038	KF660503	Whitten 2917 (FLAS)
Maxillariella arbuscula (Lindl.) M.A.Blanco & Carnevali	DQ211013	KF660491	Whitten 2810 (FLAS)
Maxillariella elatior (Rchb.f.) M.A.Blanco & Carnevali	DQ210797	KF660420	Whitten 1986 (FLAS)
Maxillariella oreocharis (Schltr.) M.A.Blanco & Carnevali	DQ210971	KF660473	Whitten 2652 (FLAS)
Maxillariella ponerantha (Rchb.f.) M.A.Blanco & Carnevali	DQ210973	KF660474	Whitten 2654 (FLAS)
Maxillariella procurrens (Lindl.) M.A.Blanco & Carnevali	DQ210854	KF660438	Whitten 2397 (FLAS)
Maxillariella variabilis (Bateman ex Lindl.) M.A.Blanco & Carnevali	DQ210995	KF660481	Whitten 2737 (FLAS)
Miltonia regnellii Rchb.f.	AF239491	FJ563571	Chase 86059 (K)
Mormolyca peruviana C.Schweinf.	DQ210885	KF660451	Whitten 2497 (FLAS)
Mormolyca polyphylla Garay & Wirth	DQ211009	KF660489	Whitten 2789 (FLAS)
Mormolyca richii (Dodson) M.A.Blanco	DQ210836	KF660434	Whitten 2362 (FLAS)
Mormolyca ringens (Lindl.) Gentil	DQ210680	KF660493	Whitten 2857 (FLAS)
Mormolyca schlimii (Linden & Rchb.f.) M.A.Blanco	DQ210847	KF660436	Whitten 2386 (FLAS)
Neogardneria murrayana (Gardner ex Hook.) Schltr. ex Garay	AY869997	KF660402	Gerlach s.n. (M)
Neomoorea wallisii (Rchb.f.) Schltr.	DQ210743	EU490754	Whitten 3010 (FLAS)
Nitidobulbon nasutum (Rchb. f.) I.Ojeda & Carnevali	DQ210756	KF660419	Whitten 1869 (FLAS)
Nitidobulbon proboscideum (Rchb. f.) I.Ojeda & Carnevali	DQ209857	KF660303	Atwood & Whitten 5056 (SEL)
Notyliopsis beatricis P.Ortiz	FJ565086	FJ563753	Whitten 2674 FLAS
Oeceoclades maculata (Lindl.) Lindl.	KF660295	KF660519	Whitten 3333 (FLAS)
Oncidium cirrhosum (Lindl.) Beer	FJ563845	FJ562480	Chase 86235 (K)
Oncidium sphacelatum Lindl.	FJ563863	FJ563267	Whitten 3467 (FLAS

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Oncidium weinmannianum (Königer) M.W. Chase & N.H. Williams	FJ565036	FJ563701	Whitten 2328 FLAS
Ornithidium aggregatum Rchb.f.	DQ210880	KF660449	Whitten 2488 (FLAS)
Ornithidium canarense (J.T.Atwood) M.A.Blanco & Ojeda	DQ209959	KF660440	Whitten 2437 (FLAS)
Ornithidium coccineum (Jacq.) Salisb. ex R.Br.	DQ209875	KF660494	Whitten 2860 (FLAS)
Ornithidium donaldeedodii Ackerman & Whitten	KF660296	KF660527	Forbes s.n. (UC)
Ornithidium fulgens Rchb.f.	DQ209968	KF660465	Whitten 2630 (FLAS)
Ornithidium giganteum Lindl.	DQ210817	KF660427	Whitten 2316 (FLAS)
Ornithidium multicaule (Poepp. & Endl.) Rchb.f.	DQ211032	KF660501	Whitten 2905 (FLAS)
Ornithidium serrulatum Lindl.	DQ211010	KF660490	Whitten 2800 (FLAS)
Ornithidium sophronitis Rchb.f.	DQ210809	KF660425	Whitten 2296 (FLAS)
Ornithocephalus dalstroemii (Dodson) Toscano & Dressler	FJ564705	FJ563134	Blanco 2980 FLAS
Ornithocephalus dalstroemii (Dodson) Toscano & Dressler	FJ564705	FJ563761	Blanco 2980 FLAS
Ornithocephalus inflexus Lindl.	DQ315891	FJ563120	Blanco 2545 (FLAS)
Otoglossum globuliferum (Kunth) N.H.Williams & M.W.Chase	FJ564700	FJ563129	Blanco 2856 (FLAS)
Otoglossum globuliferum (Kunth) N.H.Williams & M.W.Chase	FJ564700	FJ563129	Blanco 2856 FLAS
Otostylis lepida (Linden & Rchb.f.) Schltr.	AY870009	KF660399	Gerlach 94-968 (M)
Otostylis paludosa (Cogn.) Schltr.	KF660297	KF660517	Whitten 3250 (FLAS)
Paphinia clausula Dressler	KF660298	EU490758	Whitten 3600 (FLAS)
Paphinia neudeckeri Jenny	AF239471	KF660371	Whitten 88041 (FLAS)
Peristeria elata Hook.	AF239442	EU490761	Whitten 90158 (FLAS)
Pescatoria cerina (Lindl. & Paxton) Rchb.f.	AY869952	KF660384	Whitten s.n. (FLAS)
Pescatoria coronaria Rchb.f.	AY869954	KF660368	Whitten 1758 (FLAS)
Pescatoria lamellosa Rchb.f.	AY869953	KF660369	Whitten 1755 (FLAS)
Pescatoria lawrenceana (Rchb.f.) Dressler	AF350662	KF660393	Whitten 1636 (FLAS)
Pescatoria lehmannii Rchb.f.	AF239422	KF660492	Whitten 2848 (FLAS)
Pescatoria pulvinaris (Rchb.f.) Dressler	AY869950	KF660388	Whitten 1748 (FLAS)
Pityphyllum huancabambae (Kraenzl.) Whitten	DQ209957	KF660439	Whitten 2402 (FLAS)
Pityphyllum laricinum (Kraenzl.) Schltr.	DQ209961	KF660446	Whitten 2473 (FLAS)
Pityphyllum saragurense (Dodson) Whitten	DQ461805	KF660514	Whitten 3084 (QCA)
Polycycnis gratiosa Endres & Rchb.f.	AF239469	EU490769	Whitten 93178 (FLAS)
Polycycnis gratiosa Endres & Rchb.f.	AF239469	EU490769	Whitten 93178 (FLAS)
Polyotidium huebneri (Mansf.) Garay	FJ563960	FJ563598	Romero 3124 AMES
Polystachya cultriformis (Thouars) Lindl. ex Spreng.	DQ091312	KF660306	Carlsward 213 (SEL)
Promenaea stapelioides (Link & Otto) Lindl.	AY870002	EU123797	Whitten 94102 (FLAS)
Promenaea xanthina (Lindl.) Lindl.	AY870000	KF660366	Whitten 1860 (FLAS)
Psychopsiella limminghei (E.Morren ex Lindl.) Lückel & Braem	FJ565152	FJ563820	Whitten 3561 FLAS
Psychopsis sanderae (Rolfe) Lückel & Braem	FJ564712	FJ563158	Chase 86126 (K)
Rhetinantha acuminata (Lindl.) M.A.Blanco	DQ210981	KF660477	Whitten 2698 (FLAS)
Rhetinantha notylioglossa (Rchb.f.) M.A.Blanco	DQ210645	KF660351	Koehler 0033 (UEC)

Table 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Rossioglossum krameri (Rchb. f.) M.W. Chase & N.H. Williams	FJ563847	FJ562488	Chase 83166 (K)
Rudolfiella floribunda (Schltr.) Hoehne	AF239433	EU490776	Whitten 97020 (FLAS)
Rudolfiella sp.	FJ564977	FJ563642	Whitten 1618 FLAS
Sauvetrea chicana (Dodson) M.A.Blanco	DQ461813	KF660516	Whitten 3187 (QCA)
Sauvetrea chicana (Dodson) M.A.Blanco	KF660299	KF660521	Whitten 3338 (FLAS)
Sauvetrea laevilabris (Lindl.) M.A.Blanco	DQ210832	KF660433	Whitten 2358 (FLAS)
Schlimmia alpina Rchb.f. & Warsz.	KF660300	KF660345	Bennett 5130 (MOL)
Schlimmia stevensonii Dodson	AF239463	KF660343	Whitten 94107 (FLAS)
Scuticaria hadwenii (Lindl.) Planch.	AF239424	KF660370	Whitten 97109 (FLAS)
Scuticaria salesiana Dressler	DQ210875	KF660447	Whitten 2478 (FLAS)
Sievekingia herrenhusana Jenny	AF239453	KF660336	Whitten 93010 (FLAS)
Soterosanthus shepheardii (Rolfe) Jenny	AF239457	EU490784.	Dodson 18580-3 (FLAS)
Stanhopea anfracta Rolfe	AF239450	KF660511	Whitten 3022 (FLAS)
Stanhopea annulata Mansf.	AF239444	EU490786	Whitten 87242 (FLAS)
Stanhopea cirrhata Lindl.	AF239464	KF660360	Whitten F1296 (FLAS)
Stanhopea confusa G.Gerlach & Beeche	AF239449	KF660359	Whitten 94006 (FLAS)
Stanhopea ecornuta Lem.	AF239445	KF660362	Whitten 90026 (FLAS)
Stanhopea pulla Rchb.f.	AF239451	KF660361	Whitten 93117 (FLAS)
Stanhopea tigrina Bateman ex Lindl.	FJ564736	FJ563222	Whitten 3585 FLAS
Stenia bismarckii Dodson & D.E.Benn.	AY869920	KF660392	Whitten 1698 (FLAS)
Stenia calceolaris (Garay) Dodson & D.E.Benn.	AY869919	KF660394	Whitten 1699 (FLAS)
Stenotyla lankesteriana (Pupulin) Dressler	AY869962	KF660383	Dressler 6363 (FLAS)
Stenotyla lendyana (Rchb.f.) Dressler	AY869963	KF660381	Dressler 6228 (FLAS)
Stenotyla picta (Rchb.f.) Dressler	AY869961	KF660395	Dressler 6235 (FLAS)
Sudamerlycaste ciliata (Ruiz & Pav.) Archila	KF660301	KF660495	Whitten 2877 (FLAS)
Telipogon hystrix (Dodson) N.H.Williams & Dressler	DQ315899	FJ563601	Whitten 1824 (FLAS)
Telipogon parvulus C.Schweinf.	DQ315909	FJ563574	Whitten 99259 (FLAS)
Telipogon pogonostalix Rchb.f.	AF239488	FJ562506	Chase O-123 (K)
Tolumnia gundlachii (C.Wright ex Griseb.) N.H.Williams & Ackerman	FJ565132	FJ563801	Whitten 3358 FLAS
Tolumnia pulchella (Hook.) Raf.	FJ564820	FJ563411	Whitten 3499 (FLAS)
Trevoria zahlbruckneriana (Schltr.) Garay	KF660302	KF660324	Dodson 17309 (MO)
Trichocentrum jonesianum (Rchb.f.) M.W.Chase & N.H.Williams	AF350653	FJ562496	Chase 86118 (K)
Trichocentrum luridum (Lindl.) M.W.Chase & N.H.Williams	FJ564957	FJ563449	Carnevali 6243 (CICY)
Trichoceros antennifer (Humb. & Bonpl.) Kunth	FJ564953	FJ563612	Whitten 1803 (FLAS)
Trigonidium acuminatum Bateman ex Lindl.	DQ210640	KF660358	Koehler 363 (UEC)
Trigonidium acuminatum Bateman ex Lindl.	DQ210867	KF660442	Whitten 2442 (FLAS)
Trigonidium egertonianum Bateman ex Lindl.	DQ210714	KF660356	Koehler 317 (UEC)
Trigonidium egertonianum Bateman ex Lindl.	DQ210730	KF660357	Koehler 361 (UEC)
Trigonidium insigne Rchb.f. ex Benth. & Hook.f.	DQ211041	KF660504	Whitten 2926 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Trigonidium turbinatum Rchb.f.	DQ210713	KF660355	Koehler 315 (UEC)
Trizeuxis falcata Lindl.	FJ563850	FJ563198	Chase O-129 (K)
Vasqueziella boliviana Dodson	AF239473	KF660344	Vasquez s.n. (FLAS)
Warczewiczella discolor (Lindl.) Rchb.f.	AY869959	KF660412	Whitten 1859 (FLAS)
Warczewiczella marginata Rchb.f.	AY869958	EU490794	Whitten s.n. (FLAS)
Warczewiczella wailesiana (Lindl.) E.Morren	AY869960	KF660387	Gerlach 93-3314 (M)
Warrea warreana (Lodd. ex Lindl.) C.Schweinf.	AF239417	EU123798	Whitten 1752 (FLAS)
Xylobium leontoglossum (Rchb.f.) Benth. ex Rolfe	DQ209970	KF660413	Whitten 2683 (FLAS)
Xylobium pallidiflorum (Hook.) G.Nicholson	AF239434	EU490795	Whitten 1876 (FLAS)
Xylobium zarumense Dodson	AF239435	KF660380	Whitten 1881 (FLAS)
Zygopetalum maxillare Lodd.	AY869996	FJ562864	Whitten 94103 (FLAS)
Zygosepalum tatei (Ames & C.Schweinf.) Garay & Dunst.	AY869994	KF660409	Maguire & Politi 27494 (AMES)

Zygopetalinae — (Fig. 2). Our results are largely congruent with our previous study (Whitten *et al.* 2005) based on *matK*/*trnL-F*/ITS data, although there is less support for many genera. The non-monophyly of *Warczewiczella* is unusual, and might be due to mislabeled DNA samples; resampling with new collections is needed. Relationships within *Dichaea* were clarified by Neubig *et al.* (2009b). Subtribe Vargasiellinae consists of one genus with two poorly collected species, one from the tepuis of Venezuela and the other from eastern Peru. We were unable to obtain DNA of these taxa. Dressler (1993) included *Vargasiella* C.Schweinf. in Zygopetalinae but suggested it might warrant subtribal status. Romero-González and Carnevali (1993) validated the subtribal name and suggested that it should remain in its own subtribe pending better specimens and molecular data. Recent collections and DNA sequences of *Vargasiella peruviana* C.Schweinf. place it with high support in Zygopetalinae in an unresolved clade with *Warrea warreana* (Lodd. ex Lindl.) C.Schweinf. and *Warreopsis* spp. (Szlachetko *et al.*, in press; M. Kolanowska, pers. comm.). *Vargasiella* is sister to *Warrea* but with weak support. These data confirm Dressler's intuition (Dressler 1993) regarding its subtribal position; therefore, Vargasiellinae should not be recognized.

Coeliopsidinae — (Fig. 3). Our sampling included one species of each of the three genera comprising this small subtribe. The subtribe is highly supported but weakly sister to Stanhopeinae in agreement with Whitten *et al.* (2000).

Stanhopeinae — (Fig. 3). Although the circumscription of generic boundaries within this subtribe are highly congruent with morphology-based classifications, this subtribe has the lowest BS support (87%). The odd monotypic *Braemia vittata* (Lindl.) Jenny is sister to all other genera. These data are highly congruent with the trees of Whitten *et al.* (2000), but the placement of *Sievekingia* requires more study. In the Whitten *et al.* (2000) analyses based upon *matK/trnL-F*/nrITS, *Sievekingia* is strongly sister to *Coryanthes*. In the plastid *matK/ycf1* trees, the single sample of *Sievekingia* is sister to the multiflowered clade of *Stanhopea* (creating a paraphyletic *Stanhopea*). More extensive sampling with nuclear and plastid regions is needed to resolve this, because it appears to be one of the few instances of conflict between nrITS and plastid trees in Cymbidieae. One possible source of error within the *Stanhopea/Coryanthes/Sievekingia* clade is from missing data in *ycf1* for *Coryanthes*; the 3720F primer did not amplify for *Coryanthes*; consequently, about half of the *ycf1* sequence data are missing for *Coryanthes* species.

Maxillariinae — (Figs. 4, 5). Relationships within Maxillariinae were addressed in greater detail by Whitten *et al.* (2007), Blanco *et al.* (2007; 2008), and Blanco (2013) based upon a larger taxon sampling of *matK*/nrITS1&2/*atpB-rbcL* spacer. Our sampling with *matK/ycf1* was smaller (119 taxa vs. over 600),

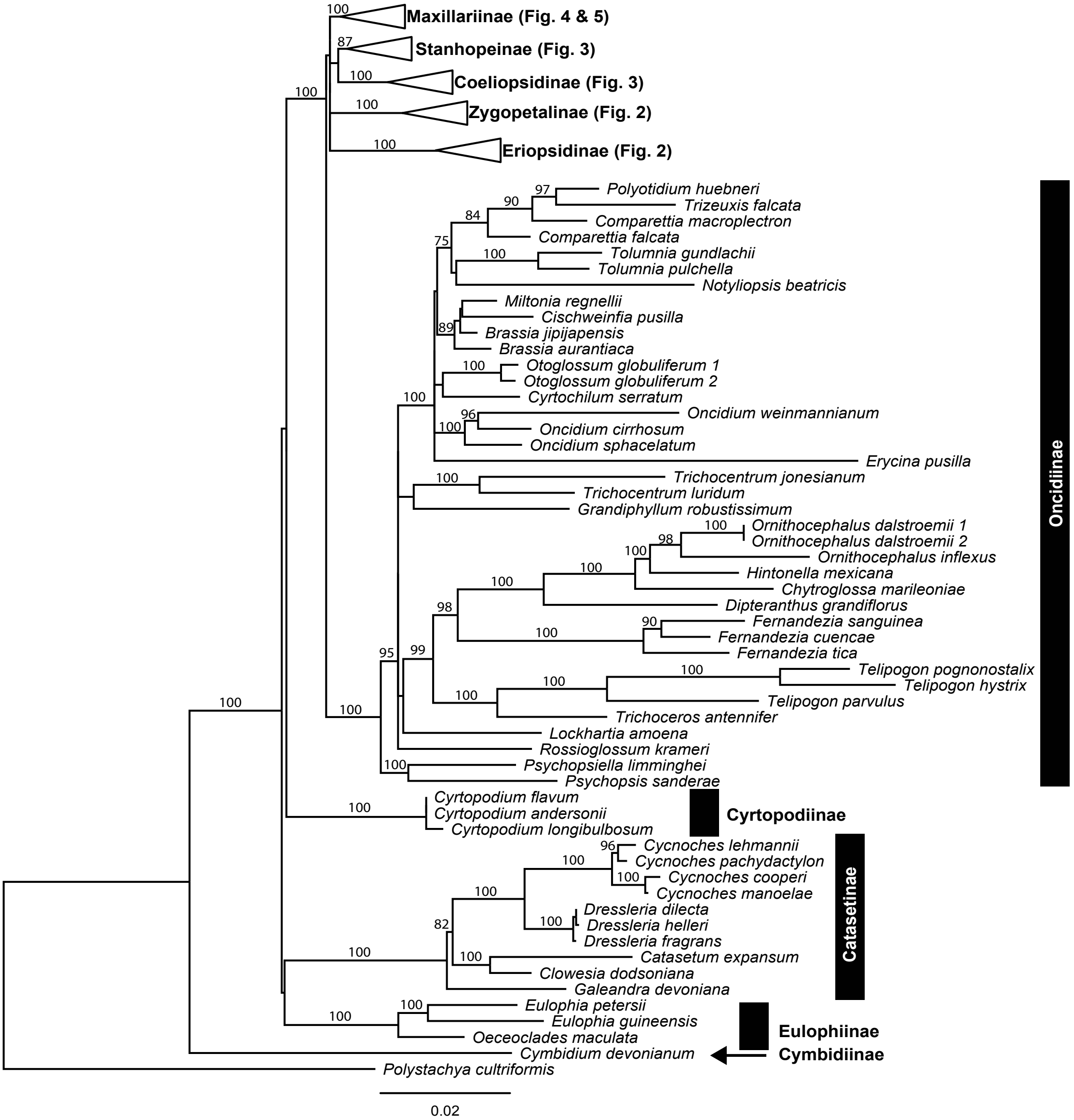


FIGURE 1. Best ML tree with bootstrap values added, showing Cymbidiinae, Eulophiinae, Catasetinae, Cyrtopodiinae, and Oncidiinae.

but the two data sets recovered the same major clades, supporting the generic concepts presented by Blanco *et al.* (2007). Our sampling included two individuals of several species; in each pair, there are nucleotide differences separating the two, indicating that *ycf1*/ *matK* is often capable of resolving not only closely related species but also intraspecific variation.

Several taxa not present in the 2007 sampling were added to this study. These include *Cryptocentrum beckendorfii* Carnevali *and Maxillaria cacaoensis* J.T.Atwood. *Cryptocentrum beckendorfii*, an anomalous species with large pseudobulbs, is placed within *Cryptocentrum* with 100% BS support (Fig. 5). *Maxillaria cacaoensis* was hypothesized by Atwood to be a member of the *Camaridium cucullatum* (Lindl.) M.A.Blanco clade (=*Psittacoglossum* La Llave & Lex., but DNA samples of this rare taxon became available only recently. *Maxillaria*

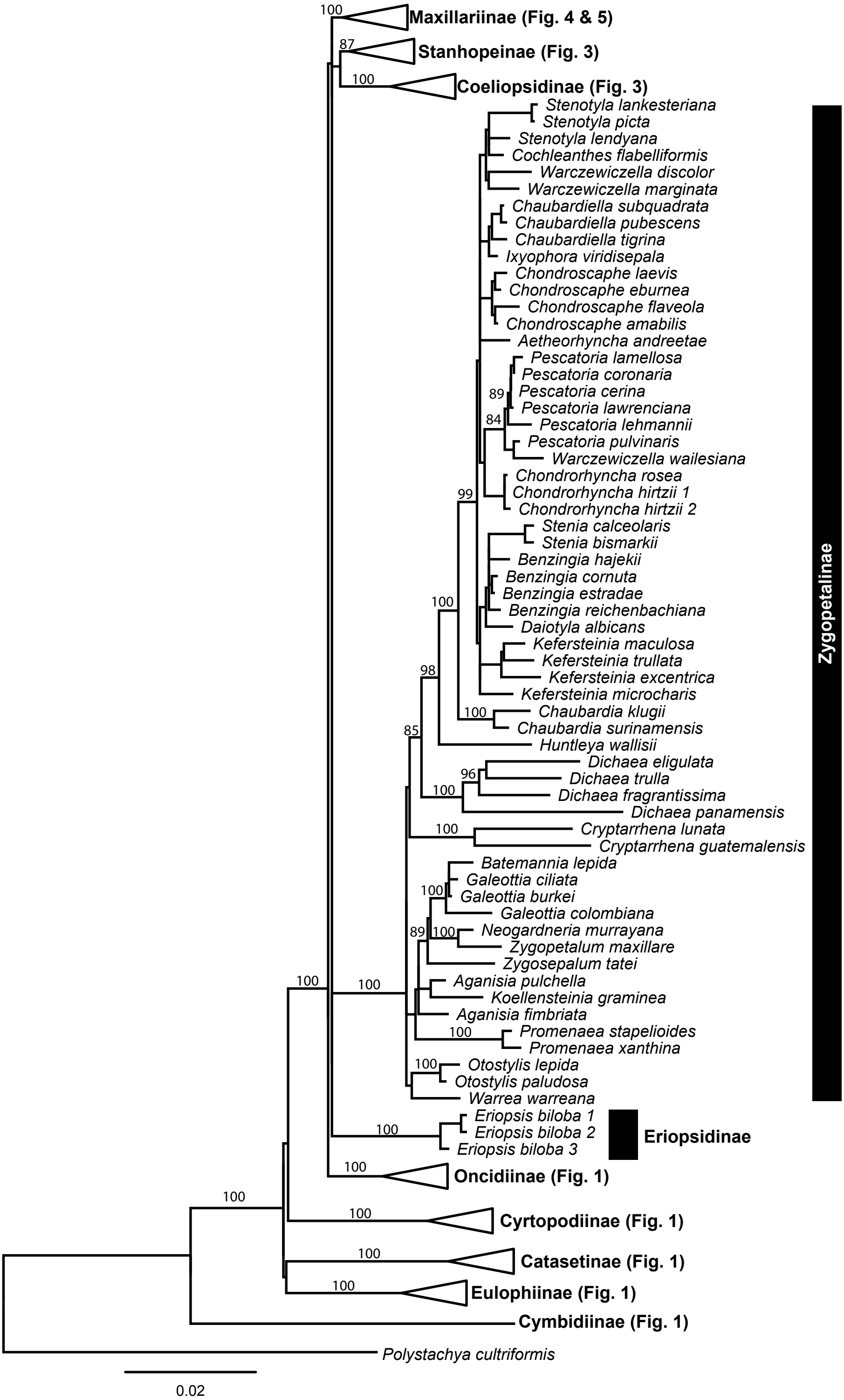


FIGURE 2. Best ML tree with bootstrap values added, showing Eriopsidinae and Zygopetalinae.

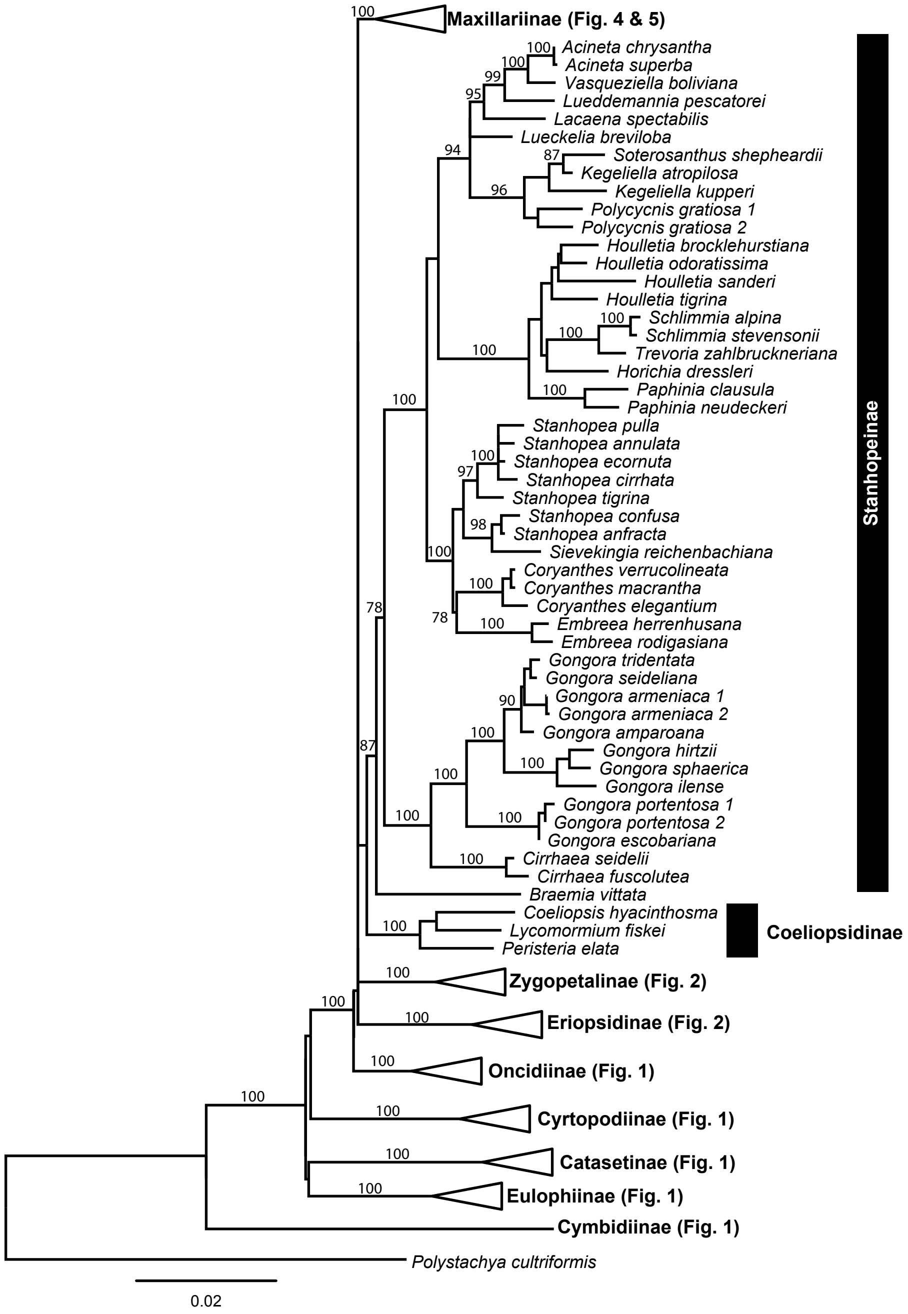


FIGURE 3. Best ML tree with bootstrap values added, showing Coeliopsidinae and Stanhopeinae.

cacaoensis is sister to *C. cucullatum* in our *ycf1/matK* trees (Fig. 5), and requires a new combination in *Camaridium*. It was erroneously transferred to *Mapinguari* Carnevali & R.B.Singer by Szlachetko *et al.* (2012). Morphologically, it resembles a dwarf *C. cucullatum*, and the capsule has apical dehiscence, a trait shared by all *Camaridium* species for which we have observed mature fruits. Based upon these molecular and morphological data, we transfer this species to *Camaridium*.

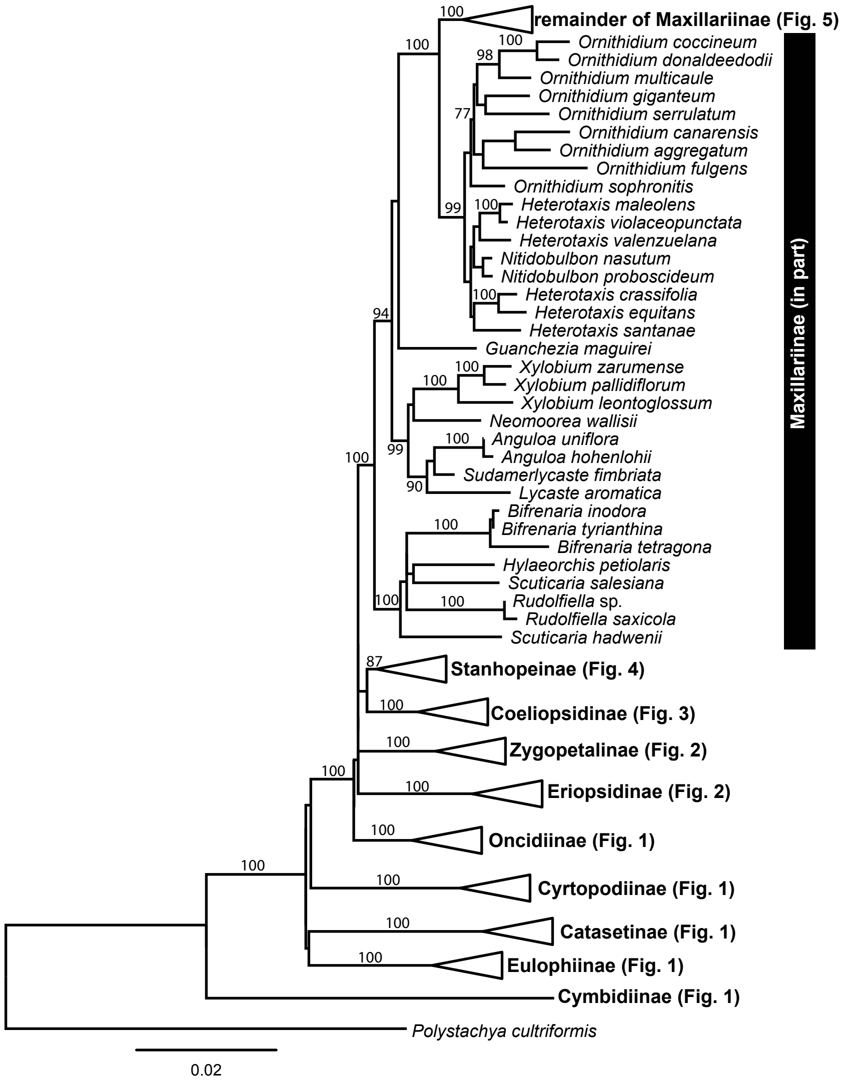


FIGURE 4. Best ML tree with bootstrap values added, showing basal portion of Maxillariinae.

Camaridium cacaoense (J.T.Atwood) Whitten, ***comb. nov.***

Basionym: *Maxillaria cacaoensis* J.T.Atwood, Selbyana 19(2):254. 1999 (1998, pub. 1999).

Mapinguari cacaoense (J.T.Atwood) Szlach. & Sitko, Biodiv. Res. Conservation 25:30. 2012, ***syn. nov.***

The Whitten *et al.* (2007) and Blanco *et al.* (2007) classifications of Maxillariinae were based upon analyses of nrITS/*matK*+*trnK*/*atpB-rbcL* spacer for over 600 individuals. An alternative classification was published by Szlachetko *et al.* (2012). The Szlachetko classification was based on analyses of a 249-taxon nrITS matrix that is largely congruent (though less resolved) than the Whitten *et al.* trees. The resulting Szlachetko classification accepts most of the genera proposed by Blanco *et al.* (2007) but splits many of them to increase the number of genera from 17 to 37.

A detailed, genus-by-genus critique of the Szlachetko *et al.* (2012) classification falls outside the scope of this paper, but we reject the generic concepts presented in their paper. Szlachetko and coworkers reject monophyly as a criterion for generic rank; therefore, many of their genera are paraphyletic

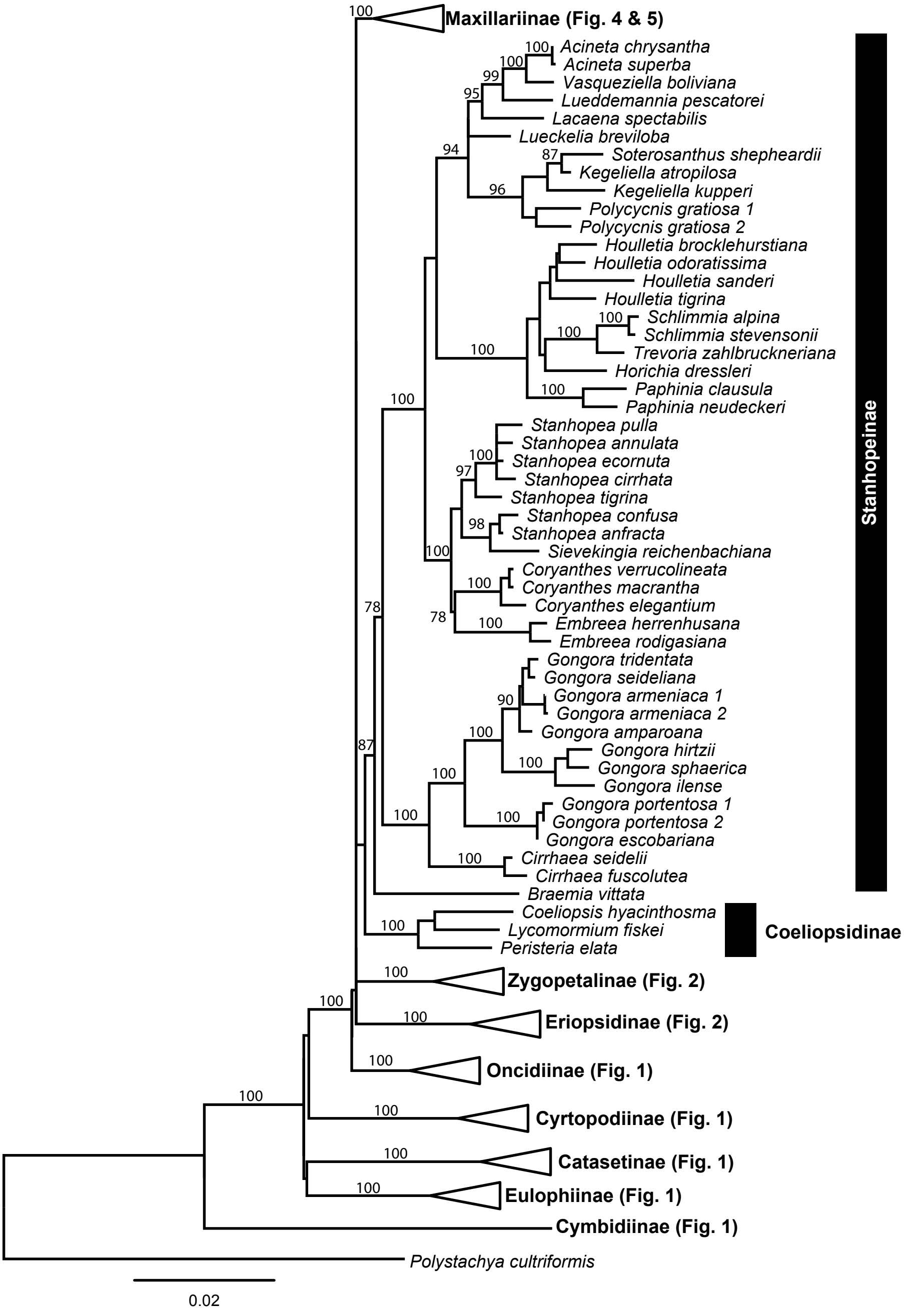


Figure 5. Best ML tree with bootstrap values added, showing remainder of Maxillariinae.

or polyphyletic as plotted onto any molecular or morphological tree and are based on idiosyncratically selected morphological characters (floral and/or vegetative), often without molecular data or with contradicting molecular evidence.

Many of their new genera consist of one or two morphologically odd species embedded within larger genera [e.g., *Marsupiaria* Hoehne = *Heterotaxis valenzuelana* (A.Rich.) Ojeda & Carnevali; *Vazquezella* Szlach. & Sitko = *Heterotaxis* *equitans* (Schltr.) Ojeda & Carnevali; *Chrysocycnis* Linden & Rchb.f., *Anthosiphon* Schltr., *Hoehnella* Szlach. & Sitko = *Rhetinantha witseniodes* (Schltr.) M.A.Blanco; *Pseudocymbidium* Szlach. & Sitko = *Maxillaria lueri* Dodson]. Other genera are composed of 15 or more species that are monophyletic but are embedded within other genera (e.g. *Calawaya* Szlach. & Sitko, embedded in *Maxillaria* Ruiz & Pav.). *Camaridium* Lindl. is split into at least eight genera. Some segregates (*e.g.*, *Chaseopsis* Szlach. & Sitko) are based solely upon morphological traits and include species that were not included in either molecular study [*e.g.*, *Camaridium burgeri* (J.T.Atwood) M.A.Blanco]. Their circumscription of *Chaseopsis* omits taxa that are sister to the generitype in the molecular trees but lack the defining essential "generic" characters (*e.g., Maxillaria flava* Ames, F.T.Hubb. & C.Schweinf. = *Camaridium ramonense* (Schltr.) M.A.Blanco; *Maxillaria lankesteri* Ames = *Camaridium aurantiacum* (Schltr.) M.A.Blanco). The Szlachetko *et al.* classification produces genera that are easily suited to production of dichotomous keys, because any morphologically anomalous species are automatically placed into another genus. Because there is no objective basis for selecting "critical" characters that define genera, their classification is without merit.

Conclusions

The *matK*/*ycf1* data produce trees that are highly congruent with the classification presented in volume 5 *Genera Orchidacearum*. Most subtribes have high bootstrap support, and generic relationships are congruent with previous molecular studies. In comparison to plastid intron/spacer regions (*e.g., trnL-F*, *atpB-rbcL*), these coding regions can be aligned with much more confidence across larger taxonomic groups (*e.g.*, tribes), especially if they are aligned using amino acid translations. This combination also appears capable of providing species-level discrimination in some genera, although more detailed sampling is needed to evaluate this fully. In terms of sequencing ease and cost effectiveness vs. phylogenetic resolution, the combination of *matK*/*ycf1*/nrITS may prove efficient within Orchidaceae. Nevertheless, these plastid trees fail to provide resolution and support of relationships among subtribes.

Givnish *et al.* (2013) recently utilized complete plastomes to estimate phylogenetic relationships among 39 orchid taxa. Although only a few subtribes of Cymbidieae were represented in their data set, subtribal relationships were still unresolved. Their results imply that the addition of more plastid genes with the objective of resolving these nodes may be futile and that these relationships will only be resolved by the addition of nuclear data sets. Clearly, much more data are needed before we fully understand the patterns of evolution within Cymbidieae.

We hope to add more representatives of Cymbidiinae, Eulophiinae, and Catasetinae. Catasetinae might provide an excellent system for study of the evolution of diverse floral reward systems; it includes five genera that are all androeuglossophilous fragrance-reward flowers (*Catasetum*, *Cycnoches*, *Clowesia*, *Dressleria*, *Mormodes*); these five genera are sister to *Galeandra*, with nectar deceit flowers, to *Grobya*, with oil-reward flowers (Pansarin et al., 2009), and to *Cyanaeorchis*, with unknown pollinators.

Previous attempts to utilize molecular clock methods to estimate the age of subtribes within Cymbidieae (Ramírez *et al.* 2011) utilized more limited taxon sampling that was biased towards androeuglossophilous taxa. Our more complete sampling of generic relationships based on more sequence data might warrant reexamination of these age estimates.

Acknowledgments. We thank Günter Gerlach (Munich Botanical Garden), Ron Determann, Becky Brinkman (Atlanta Botanical Garden), Gustavo Romero (AMES), Andy and Harry Phillips (Andy's Orchids) and the Portilla family (Ecuagenera) for generous access and help in obtaining specimens and vouchers. Lorena Endara provided valuable assistance in Ecuador, and Mario Blanco and Robert Dressler (Lankester Garden) provided specimens and valuable discussions. Kent Perkins was invaluable in accessioning and imaging specimens. Marta Kolanowska generously shared unpublished information on the placement of *Vargasiella*. Alec Pridgeon provided valuable criticisms and edits. We thank Savita Shanker and Patrick Thimote at the Interdisciplinary Center for Biotechnology Research at UF for DNA sequencing services.

LITERATURE CITED

Batista, J. A. N., A. C. M. Mota, K. Proite, L. de Bem Bianchetti, G. A. Romero-Gonzalez, H. Huerta, and G. Salazar. In press. Molecular phylogenetics of *Cyanaeorchis* (Cymbidieae, Epidendroideae,Orchidaceae) and a new species from the cerrado of central and southeastern Brazil. Phytotaxa.

Blanco, M., G. Carnevali, W. M. Whitten, R. B. Singer, S. Koehler, N. H. Williams, I. Ojeda, K. Neubig, and L. Endara. 2007. Generic realignments in Maxillariinae (Orchidaceae). Lankesteriana 7:515-537.

Blanco, M. A. 2013. New combinations and synonyms in the Maxillariiinae (Orchidaceae). Selbyana 31:52-59.

Blanco, M. A., G. Carnevali, W. M. Whitten, R. B. Singer, S. Koehler, N. H. Williams, I. Ojeda, K. M. Neubig, and L. Endara. 2008. Generic realignments in Maxillariinae (Orchidaceae): Corrigenda et addenda. Lankesteriana 8:15.

Chase, M. W., K. M. Cameron, R. L. Barrett, and J. V. Freudenstein. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. Pages 69–89 *in* Orchid Conservation (K. W. Dixon, S. P. Kell, R. L. Barrett, and P. J. Cribb, eds.). Natural History Publications, Kota Kinabalu, Sabah, Malaysia.

Dressler, R. L. 1981. The Orchids: Natural History and Classification. Harvard University Press, Cambridge, Massachusetts, USA.

Dressler, R. L. 1993. Phylogeny and Classification of the Orchid Family. Dioscorides Press, Portland, Oregon, USA.

Edgar, R. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. doi:10.1186/1471-2105-5-113. BMC Bioinformatics 5: 113.

Freudenstein, J. V., C. van den Berg, D. H. Goldman, P. J. Kores, M. Molvray, and M. W. Chase. 2004. An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. American Journal of Botany 91:149-157.

Givnish, T. J., M. Ames, S. P. Lyon, K. M. Cameron, K. M. Neubig, W. M. Whitten, M. K. Arroyo, J. Leebens-Mack, M. A. Clemets, and N. H. Williams. Year. The 39 Steps: A plastome phylogeny for orchid tribes, with implications for the evolution of epiphytism, CAM photosynthesis, and net rates of species diversification *in* Monocots V: 5th International Conference on Comparative Biology of Monocotyledons, New York Botanical Gardens:48-49.

Górniak, M., O. Paun, and M. W. Chase. 2010. Phylogenetic relationships within Orchidaceae based on a low-copy nuclear coding gene, *Xdh*: Congruence with organellar and nuclear ribosomal DNA results. Molecular Phylogenetics and Evolution 56:784-795.

Koehler, S., N. H. Williams, W. M. Whitten, and M. D. E. do Amaral. 2002. Phylogeny of the *Bifrenaria* (Orchidaceae) complex based on morphology and sequence data from nuclear rDNA internal transcribed spacers (ITS) and chloroplast *trnL-trnF* region. International Journal of Plant Sciences 163:1055-1066.

Monteiro, S. H. N., A. Selbach-Schnadelbach, R. P. d. Oliveira, and C. van den Berg. 2010. Molecular phylogenetics of *Galeandra* (Orchidaceae: Catasetinae) based on plastid and nuclear DNA Sequences. Systematic Botany 35:476-486.

Neubig, K. M., W. M. Whitten, B. S. Carlsward, M. A. Blanco, L. Endara, N. H. Williams, and M. Moore. 2009a. Phylogenetic utility of *ycf1* in orchids: a plastid gene more variable than *matK*. Plant Systematics and Evolution 277:75-84.

Neubig, K. M., W. M. Whitten, N. H. Williams, M. A. Blanco, L. Endara, J. G. Burleigh, K. Silvera, J. C. Cushman, and M. W. Chase. 2012. Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. Botanical Journal of the Linnean Society 168:117-146.

Neubig, K. M., N. H. Williams, W. M. Whitten, and F. Pupulin. 2009b. Molecular phylogenetics and the evolution of fruit and leaf morphology of Dichaea (Orchidaceae: Zygopetalinae). Annals of Botany 104:457-467.

Pansarin, L. M., M. D. Castro, and M. Sazima. 2009. Osmophore and elaiophores of *Grobya amherstiae* (Catasetinae, Orchidaceae) and their relation to pollination. Botanical Journal of the Linnean Society 159:408-415.

Pridgeon, A. M., and M. W. Chase. 1998. Phylogenetics of subtribe Catasetinae (Orchidaceae) from nuclear and chloroplast DNA sequences. Pages pp. 275-281 *in* Proceedings of the 15th World Orchid Conference (C. E. de Britto Pereira, ed.) Naturalia Publications, Turriers, France.

Pridgeon, A. M., P.J. Cribb, M. W. Chase, and F.N. Rasmussen. 2009. Genera Orchidacearum Volume 5 Epidendroideae (Part Two). Oxford University Press, Inc., New York.

Rambaut, A. 1996. Se-Al: Sequence Alignment Editor. Available at http://evolve.zoo.ox.ac.uk/.

Rambaut, A. 2013. FigTree, version 1.4.0.

Ramírez, S. R., T. Eltz, M. K. Fujiwara, G. Gerlach, B. Goldman-Huertas, N. D. Tsutsui, and N. E. Pierce. 2011. Asynchronous diversification in a specialized plant-pollinator mutualism. Science 333:1742-1746.

Reis, M. G., A. D. de Faria, V. Bittrich, M. D. E. Amaral, and A. J. Marsaioli. 2000. The chemistry of flower rewards - *Oncidium* (Orchidaceae). Journal Of The Brazilian Chemical Society 11:600-608.

Romero-Gonzalez, G. A., and G. Carnevali. 1993. Reappraisal of subtribe Vargasiellinae (Maxillarieae, Orchidaceae). Novon 3:79-80.

Shaw, J., E. B. Lickey, J. T. Beck, S. B. Farmer, W. Liu, J. Miller, K. C. Siripun, C. T. Winder, E. E. Schilling, and R. L. Small. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. Am. J. Bot. 92:142-166.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688-2690.

Swofford, D. L. 2003. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4.0b10. Sinauer.

Szlachetko, D., M. Sitko, PTukallo, and J. Mytnik-Ejsmont. 2012. Taxonomy of the subtribe Maxillariinae (Orchidaceae, Vandoideae) revised. Biodiversity Research and Conservation 25:13-38.

Szlachetko, D. L. 1995. Systema Orchidalium, Fragmenta Floristica et Geobotanica. Supplementum 3. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.

Szlachetko, D. L., M. Górniak, M. Kolanowska, J. Mytnik-Ejsmont, A. K. Kowalkowska, and T. Koliński. in press. Taxonomic position of the genus *Vargasiella* (Orchidaceae, Vandoideae) based on molecular and morphological evidence. Molecular Phylogenetics and Evolution.

Whitten, M. W., N. H. Williams, R. L. Dressler, G. Gerlach, and F. Pupulin. 2005. Generic relationships of Zygopetalinae (Orchidaceae: Cymbideae): Combined molecular evidence. Lankesteriana 5:87-107.

Whitten, W. M., M. A. Blanco, N. H. Williams, S. Koehler, G. Carnevali, R. B. Singer, L. Endara, and K. M. Neubig. 2007. Molecular phylogenetics of *Maxillaria* and related genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. American Journal of Botany 94:1860-1889.

Whitten, W. M., N. H. Williams, and M. W. Chase. 2000. Subtribal and generic relationship of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. American Journal of Botany 87:1842-1856.

LANKESTERIANA 13(3) — January 2014

REGULAR PAPERS

LANKESTERIANA 13(3): 395—399. 2014.

A NEW LARGE-FLOWERED *ODONTOGLOSSUM* (ORCHIDACEAE: ONCIDIINAE) FROM THE CUSCO REGION IN PERU

Stig Dalström[1,3] & Saul Ruíz Pérez[2]

[1] 2304 Ringling Boulevard, unit 119, Sarasota FL 34237, U.S.A.
Lankester Botanical Garden, University of Costa Rica, Cartago, Costa Rica
and National Biodiversity Centre, Serbithang, Bhutan
[2]Allamanda 142, Surco, Lima 33, Peru
[3]Corresponding author: stigdalstrom@juno.com

Abstract. Plants of a colorful *Odontoglossum* were recently found by separate parties in the Cusco region of central Peru. The species was incorrectly identified as *Odontoglossum epidendroides*, independently by both parties. Although similar in appearance, a closer examination of the flower reveals that it represents a new species, which is scientifically described here and compared with similar species. The new taxon is distinguished from the similar *O. cruentum* and *O. juninense* by morphological features of the column, such as the lateral curvature profile, with larger and more rectangular wings, and in combination with the well developed falcate callus structure on the lip. Our new species is also distinguished from the rather similar *O. epidendroides* by having flowers with a shorter column with shorter wings.

Key words: Orchidaceae, Oncidiinae, *Odontoglossum*, new species, Cusco, Peru, taxonomy

The genus *Odontoglossum* Kunth (treated by some authors as *Oncidium*), has revealed miscellaneous new species in recent time. Some are rather similar to closely related taxa while others show surprisingly distinct morphologic features, such as the floristically diminutive *Oncidium koechlinianum* Collantes & G.Gerlach (2011), which was transferred to *Odontoglossum* by Dalström (2012a, where valid reasons for maintaining the taxonomic status of the genus is argued and outlined). Recent fieldwork performed by the authors and others also show that some previously lumped or misidentified taxa deserve an elevated taxonomic status, such as *Odontoglossum furcatum* Dalström (2012b), and the species published here.

Odontoglossum auroincarum Dalström & Ruíz-Pérez, *sp. nov.*

TYPE: Peru. Cusco. Alfamayo, *ca.* 2600 m, S 13° 03.647'; W 72° 24.351', Dec. 3, 2011. *S. Dalström 3594* (holotype, USM). Figs. 1, 2A, 2A1, 2A2, 3, 4).

Diagnosis: *Odontoglossum auroincarum* is similar to *O. epidendroides* Kunth (Figs. 2E, 2E1, 2E2, 5), but differs from it by having flowers with a shorter (*ca.* 10–11 mm long versus 13– 14 mm), and differently curved column with shorter wings. It differs from *O. cruentum* Rchb.f., (Figs. 2B, 2B1, 2B2, 6), and *O. juninense* Schltr. (Figs. 2D, 2D1, 2D2, 7), by a different lateral curvature profile of the column, with broader and more rectangular column wings as well as a less lobulate anther-cap.

Epiphytic *herb*. *Pseudobulbs* caespitose, ancipitous, ovoid to pyriform, glossy, bifoliate, 4–5 × 7–8 cm, surrounded basally by 5 to 7 distichous sheaths, the uppermost foliaceous. *Leaves* subpetiolate, conduplicate, elongate elliptic to slightly obovate, acuminate 27–31 × 2.5–3.0 cm. *Inflorescences* axillary from the uppermost sheaths, erect to arching, weakly fractiflex 12- to 15-flowered racemes, or up to 25-flowered widely branched panicles (old inflorescences on type specimen). *Pedicel* with *ovary* 2.0 – 2.5 cm long. *Floral bracts* appressed, scale-like to *ca.* 1 cm long. *Flower* relatively large and showy, stellate; *dorsal sepal* dark yellow with large irregular red-brown spotting, cuneate, ovate laminate, acuminate and slightly oblique, *ca.* 35 × 10–11 mm; *lateral sepals* similar in color, slightly unguiculate, ovate laminate, acuminate, slightly oblique, *ca.*

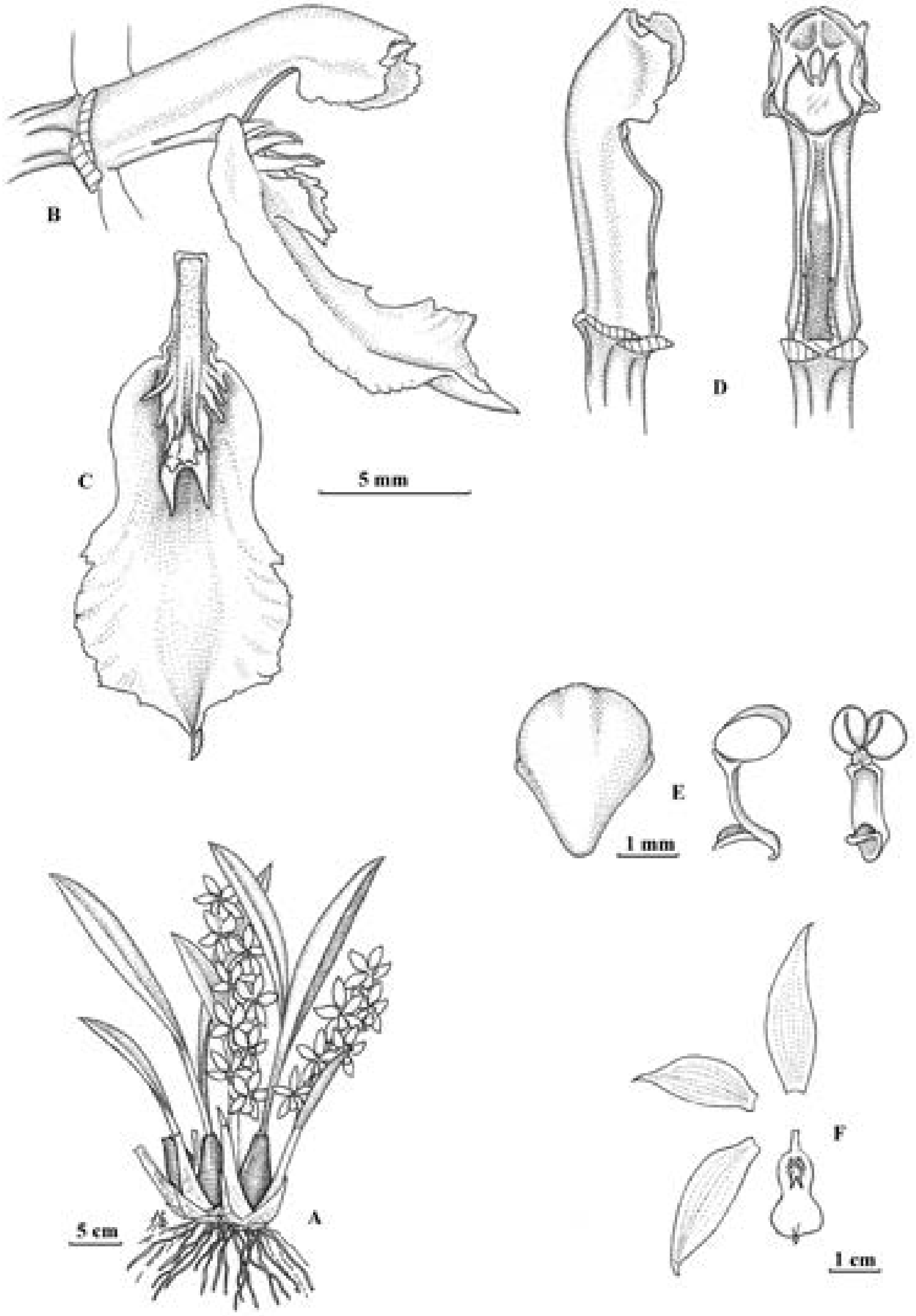


Figure 1. *Odontoglossum auroincarum*. A — Plant habit. B — Column and lip, lateral view. C — Lip, frontal view. D — Column, lateral and ventral views. E— Anther cap, dorsal view, and pollinarium, lateral and back views. F — Flower dissected. Drawn from holotype by Stig Dalström.

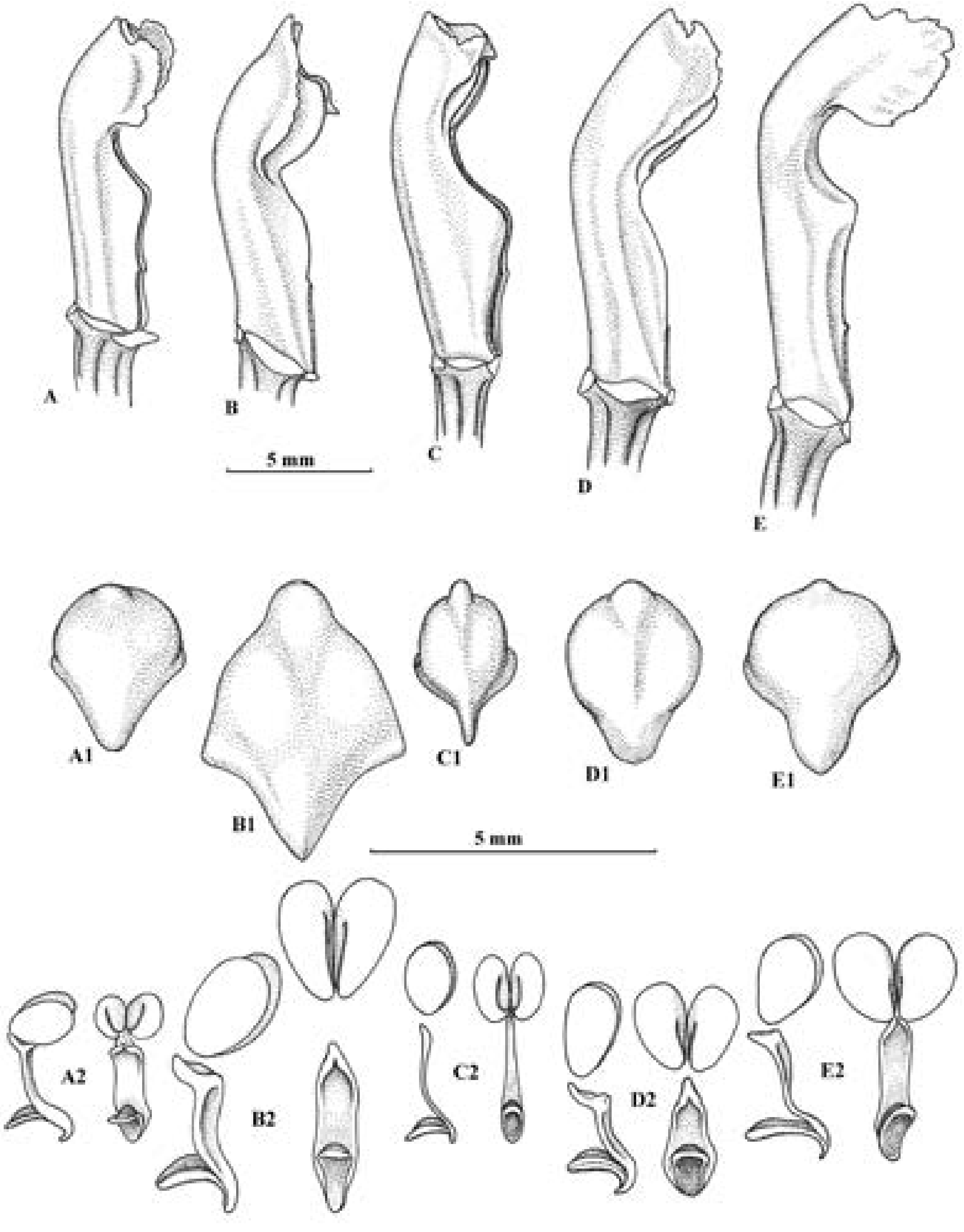


Figure 2. A. *Odontoglossum auroincarum,* (S. Dalström 3594, USM), *c*olumn lateral view. A1. Anther cap dorsal view. A2. Pollinarium lateral and back views. B. *Odontoglossum cruentum* (*S. Dalström 481*, SEL), column lateral view. B1. Anther cap dorsal view. B2 Pollinarium lateral and back views. C. *Odontoglossum subuligerum* (*S. Dalström 3611*, USM), column lateral view. C1. Anther cap dorsal view. C2. Pollinarium lateral and back views. D. *Odontoglossum juninense* (*S. Dalström 2378*, Dalström archives), column lateral view. D1. Anther cap dorsal view. D2. Pollinarium lateral and back views. E. *Odontoglossum epidendroides* (*S. Dalström 3282*, USM), column lateral view. E1. Anther cap dorsal view. E2. Pollinarium lateral and back views. Drawn by Stig Dalström.

FIGURE 3. *Odontoglossum auroincarum*, plant habit. Photo by Stig Dalström.

FIGURE 4. *Odontoglossum auroincarum*, flower in close-up. Photo by Stig Dalström.

33 × 10–11 mm; *petals* similar in color, broadly unguiculate, ovate laminate, acuminate, oblique, *ca.* 27 × 8–10 mm; *lip* similar in color, adnate to the basal and lateral flanks of the column for *ca.* 2.0–2.5 mm, then free and strap-like for *ca.* 1 mm, apical portion angled downwards into a large, pandurate lamina, with serrate to lacerate frontlobes, and a folded, canaliculate, apiculate apex, *ca.* 17–18 × 7–8 mm; *callus* white, of a fleshy, basally minutely pubescent, central, longitudinal, flattened keel, emerging from the base to *ca.* one third of the length of the lamina, terminating in a shallowly canaliculate, raised ridge, ending with several pairs of acute, projecting angles, with a larger, erect, irregular, denticulate knob, and 3 to 4 pairs of lateral, falcate, variously sized spreading keels; *column* pale greenish white with some minor brown ventral dots, erect and straight for *ca.* 2/3 of its length, then curved towards the lip, ventrally canaliculate, basally micro-pubescent, with distinct ventral angles below the stigma, which is covered laterally by a pair of almost rectangular, serrate wings, *ca.* 10–11 mm long; anther cap pale yellow, campanulate, rostrate, with a minute and low apical lobule; pollinarium of two pyriform, cleft/folded pollinia on a yellow colored, almost rectangular, *ca.* 1.8 mm long stipe, on a hooked and pulvinate viscidium.

OTHER MATERIAL STUDIED: Peru. Cusco, Urubamba, Machu Picchu, collected in the Machu Picchu Sanctuary and cultivated in the garden of the INKATERRA Machu Picchu Pueblo Hotel, photo by Benjamín Collantes in “Orquideas en INKATERRA Machu Picchu Pueblo Hotel” (Collantes *et al.* 2007).

DISTRIBUTION: Known only from the cloud forests of Alfamayo, and from the Machu Picchu sanctuary in the Urubamba region of Cusco, central Peru.

ETYMOLOGY: The name refers to the golden yellow color of the flowers of this species and is a tribute to ‘botanical Inca gold’, which comes from the area in Peru that once was the center of the powerful Inca culture.

The first plants of *Odontoglossum auroincarum* were collected within the borders of the Machu Picchu sanctuary by the staff of the INKATERRA hotel. Plants were replanted in the orchid garden of the hotel and flowered there. Photos of the flowers were then taken by Benjamín Collantes and published, labeled “*Odontoglossum epidendroides*” (Collantes *et al.* 2007). A few years later, plants were found in the Alfamayo region by the second author of this paper, and brought into cultivation for propagation. When the plants flowered they were still believed to be *O. epidendroides*, but with some question marks. Eventually a detailed drawing of the flower could be made, which was compared with drawings of similar species. The conclusion was that a new and attractive species had been discovered. Although superficially and rather confusingly similar to several other yellow flowered species, the morphological features of the column and lip structure as well as the anther and pollinarium are quite distinct and display

Figure 5. *Odontoglossum epidendroides*, flower in close-up. Photo by Stig Dalström.

Figure 6. *Odontoglossum cruentum*, flower in close-up. Photo by Stig Dalström.

Figure 7. *Odontoglossum juninense*, flower in close-up. Photo by Stig Dalström.

a combination of characteristics that create a unique species profile. The only sympatric *Odontoglossum* species of this particular complex with a flexible lip is *O. subuligerum* Rchb.f. (Figs. 2C, 2C1, 2C2, 8) which is easily distinguished by the large knob on the anther cap and by the extremely narrow pollinarium stipe.

Acknowledgements. The authors wish to thank the staff at the Instituto Recursos Naturales (INRENA), and Betty Millán at the Universidad de San Marcos, Museo de Historia Natural, Lima, for aiding in providing the necessary collecting permits. We also thank Wesley Higgins for commenting on the manuscript, Steve Beckendorf, Guido and Karel Deburghgraeve for stimulating company in the field, and Manolo Arias together with his staff and family in Lima for gracious logistic support.

Figure 8. *Odontoglossum subuligerum*, Chapare, Bolivia, flowers close-up. Photo by Jan Sönnemark.

Literature cited

Collantes, B., C. Soto & J. Koechlin. 2007. Orchids Orquídeas en Inkaterra Machu Picchu Pueblo Hotel. Inkaterra Asociación, Lima, Perú.

Collantes, B. & G. Gerlach. 2011. Über zwei neue Orchideen aus Machu Picchu (Peru) aus der Subtribus Oncidiinae. OrchideenJournal (2): 79-81.

Dalström, S. 2012a. New combinations in *Odontoglossum* (Orchidaceae: Oncidiinae) and a solution to a taxonomic conundrum. Lankesteriana 12(1): 53–60.

Dalström, S. 2012b. A well-known but previously misidentified *Odontoglossum* (Orchidaceae: Oncidiinae) from Ecuador. Lankesteriana 12(3): 155–160.

LANKESTERIANA 13(3): 401—405. 2014.

A NEW AND STRIKING *ODONTOGLOSSUM* (ORCHIDACEAE: ONCIDIINAE) FROM PERU

Stig Dalström[1,3] & Saul Ruíz Pérez[2]

[1] 2304 Ringling Boulevard, unit 119, Sarasota FL 34237, U.S.A.
Lankester Botanical Garden, University of Costa Rica, Cartago, Costa Rica
and National Biodiversity Centre, Serbithang, Bhutan
[2]Allamanda 142, Surco, Lima 33, Peru
[3]Corresponding author: stigdalstrom@juno.com

Abstract. A new species of *Odontoglossum* with an extraordinary long column and filamentose lip callus is described, illustrated with a photograph and a line drawing, and compared with similar and presumably closely related species, such as *O. epidendroides* and *O. juninense*. The new species belongs to the *Odontoglossum* complex with a flexible lip-base attachment, but differs from all other species in that complex primarily by the elongate base of the column, below the attachment of the strap-like lip-base.

Key words: Oncidiinae, *Odontoglossum*, new species, Pasco, Peru, taxonomy

In the accompanying text to the plate of *Odontoglossum wattianum* Rolfe, which was published in Reichenbachia (Sander 1892), we can read: "It is a great thing now-a-days to be able to introduce species of Odontoglossums absolutely new to science. Years ago, when the wilds of Columbia were more untrodden than they are now, we found less difficulty, but year by year such prizes get rarer. The time is not far distant when home skill in hybridization will have to supply novelties in Odontoglossums."

This quote illustrates an often heard opinion about the scarce possibilities of finding new species of *Odontoglossum* (treated as *Oncidium* by some authors, see below). Even today experienced "orchid hunters" seem to think that there is not much more to discover when it comes to this attractive genus. But this has been proven to be a hasty conclusion thanks to the discovery of several new species in later years (Dalström 1993, 1996, 1999, 2010, 2012b, 2013) although in honesty, it must be said that *Odontoglossum* taxonomy needs some special effort to be understood properly. This also appears to be one of the main reasons why genera *Cochlioda* Lindl., *Odontoglossum* Kunth, *Sigmatostalix* Rchb.f. and *Solenidiopsis* Senghas were transferred to *Oncidium* (Chase *et al.* 2008, 2009). This transfer may well have been allowed by molecular analysis but the argument that few people can separate an *Odontoglossum* from an *Oncidium* Sw., which has been heard in subsequent discussions, is not really true once you become more familiar with these plants.

The first author of the present paper has outlined an alternative taxonomic treatment (Dalström 2012a), which explains why keeping a slightly enlarged genus *Odontoglossum* is preferable, and also how to separate this genus from *Oncidium* based on a combination of morphological, ecological and geographical characteristics. This is supported by the same molecular evidence used by Chase *et al.* (2009) in their transfer of *Odontoglossum* species to *Oncidium*. Another argument that has been heard in the debate about how to best treat these orchids is that many new names have to be created for various smaller groups of plants if we want to keep *Odontoglossum* as a valid genus. However, the only new names that eventually may have to be created concern two smaller groups of species (here referred to as the '*boothianum* clade' and the '*chrysomorphum* clade' respectively) that for some intriguing reasons are placed near the base of the larger *Odontoglossum* clade. In contrast to using this as an argument for lumping all concerned taxa into a large 'waste basket' *Oncidium*, we believe that this is really a strong reason to do the opposite and further study these smaller clades in order to find out why they are placed where they are.

Morphological analysis of the species in the *O. boothianum* and *O. chrysomorphum* clades show

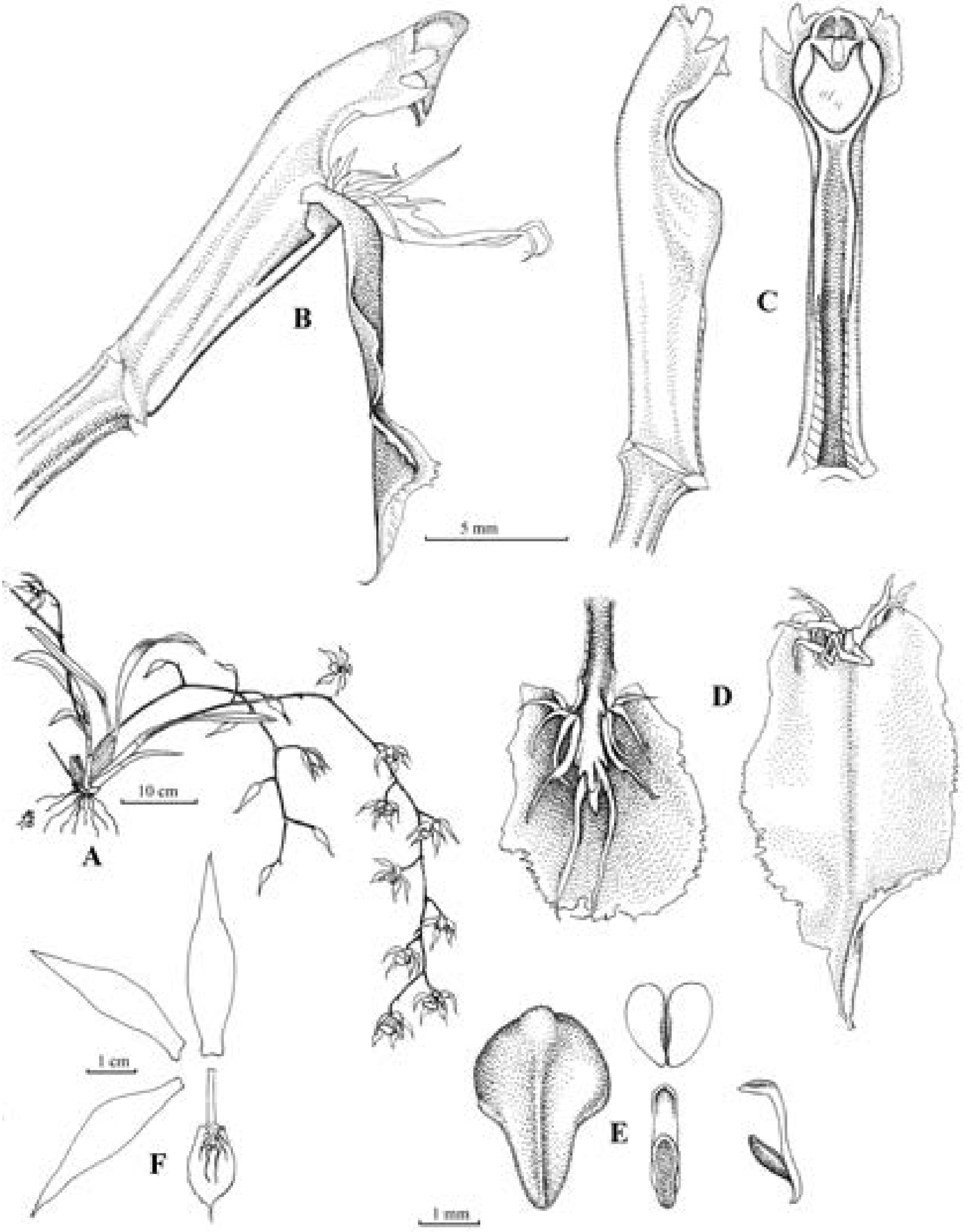


FIGURE 1. *Odontoglossum filamentosum*. A — Plant habit. B — Column and lip lateral view. C — Column lateral and ventral views. D — Lip dorsal and frontal views. E — Anther cap frontal view, and pollinarium ventral and lateral views. F — Flower dissected. Drawn from the plant that served as holotype by S. Dalström.

some interesting and distinctive features, such as the compressed, glossy and often purple-mottled, unifoliate pseudobulbs, that seem intermediate between some species of *Odontoglossum sensu strictu*, and species from some '*Oncidium sensu lato*' clades, particularly the clade that produce aborted flowers (here referred to as species of *Heteranthocidium* Szlach., Mytnik & Romowicz, also known as the '*Oncidium abortivum* group'). Some of the species in the *chrysomorphum* clade also produce aborted flowers occasionally, in addition to displaying morphological similarities in the pollination apparatus (column, rostellum and pollinarium shapes primarily) to species in the *Heteranthocidium* complex. Since many *Heteranthocidium* species grow together and flower simultaneously with many *Odontoglossum* species, while more 'typical' *Oncidium* species do not, the possibilities of ancient natural hybridization seem plausible, which may explain the origin and placement of this clade. Plants in the *boothianum* clade also show similar intermediate features and only marginally differ from the *chrysomorphum* clade. The fact that these two smaller groups occur one after the other near the base of the *Odontoglossum* clade may perhaps be the result from several occasions of ancient natural hybridization. These speculations, however, should not be taken for anything other than just that at this time, but rather than to close the door (and settle the debate) to a deeper understanding of the evolution of these orchids, they should be seen as encouragements to further studies.

Although many *Odontoglossum* species may appear superficially similar, the one described here does not need any particular effort to be recognized as new and different. It is characterized by a unique combination of morphologic features such as the elongated column together with the extremely long and irregularly filamentose callus teeth on the lip, which readily set it apart from its closest relatives; *O. epidendroides* Kunth (Fig. 3), and *O. juninense*. Schltr (Fig 4).

Odontoglossum filamentosum Dalström & Ruíz-Pérez, *sp. nov*. Figs. 1–3.

TYPE: Peru. Pasco: Exact locality unknown but recent observations suggest that the true origin is somewhere near the town of Oxapampa. The type plant flowered in cultivation 10 Feb. 2013, *G. Deburghgraeve 282* (holotype: W).

Diagnosis: *Odontoglossum filamentosum* differs from the similar *O. epidendroides* Kunth (Fig. 3), and *O. juninense* Schltr. (Fig. 4), by the unique combination of the elongated column, *ca.* 1.7 cm long versus *ca.* 1.0–1.1 cm (*O. epidendroides*), and *ca.* 1 cm (*O. juninense*) together with the extremely long and filament-shaped callus on the lip, versus much less devloped and shortly digitate to curved and spinose callus teeth for the others.

Epiphytic *herb*. *Pseudobulbs* caespitose, oblong ovoid, bifoliate, *ca*. 5– 8 × 2–3 cm, surrounded basally by 6 to 8 distichous sheaths, the uppermost foliaceous. *Leaves* subpetiolate, conduplicate, elongate elliptic to obovate, narrowly acute to shortly acuminate, 19–27 × 2.0–3.3 cm. *Inflorescences* 1 to 3, axillary from the base of the uppermost sheaths, arching to subpendent, loosely flowered, flexuous, few to many flowered racemes or loosely paniculate with few basal few-flowered side-branches, to *ca.* 60 cm long; *bracts* 0.5– 1.3 cm long. *Pedicel* with *ovary* 2.5–3.5 cm long. *Flower* stellate to slightly campanulate and rather arachnoid; *dorsal sepal* yellow almost covered with large brown spots, subunguiculate, elliptic to ovate, acuminate, *ca*. 4.4 × 1.0 cm; *lateral sepals* similar in color, slightly obliquely elliptic, narrowly acute, *ca*. 4.5 × 1.1 cm; *petals* similar in color but less brown, obliquely elliptic, acuminate, *ca*. 3.8–4.0 × 1.0 cm; *lip* basally pale yellow with a large brown spot covering most of the lamina, and with a pale yellow to white edge, unguiculate, adnate to the base and lateral flanks of the column by a linear *ca*. 8 mm long claw/unguis, then free, developing very short, erect sidelobes, abruptly plicate and laminate, indistinctively cordate, obovate to oblong pandurate, apical part of lamina more or less concave, erose to fimbriate, apically slightly canaliculate or convolute, acuminate, *ca*. 3.0 – 3.4 × 1.0 cm; *callus* white, of a low, median, longitudinal, fleshy, glabrous keel, emerging from the base and extending to the lamina where it develops into a series of spreading, more or less falcate, narrowly denticulate to spinose, or filamentose keels, with a larger, multi-lacerate and filamentose, laterally compressed projecting pair in the middle, with a small tooth in between; *column* basally pale green, then white with some brown marking near

Figure 2. *Odontoglossum filamentosum*, floral diagram (*G. Deburghgraeve 282*). Photo: G. Deburghgraeve.

Figure 3. *Odontoglossum filamentosum*, plant habit (*G. Deburghgraeve 282*). Photo: G. Deburghgraeve.

the apex, erect, clavate, straight for 3/4th of the length, then weakly curved towards the lip, canaliculate ventrally, the ventral flanks ending in distinct angles below the stigma, and with a pair of rather short, lacerate to palmate wings on each side of the stigma, *ca*. 1.7 cm long; *anther cap* white, more or less marked with brown, campanulate, rostrate, dorsally lobulate; *pollinarium* of two obovoid to pyriform, cleft/folded pollinia on an oblong-rectangular *ca.* 2.5 mm long stipe on a hooked, pulvinate viscidium.

The type plant was originally imported to Europe as "*Odontoglossum epidendroides*", or possibly "*O. juninense*" (the details were lost with time). The original identification was probably based on similarities to then known *Odontoglossum* species. Due to legislative complications it has not yet been possible to deposit a type specimen in a Peruvian herbarium (USM) at this time. When, and if, the government of Peru establish the first CITES registered institution in their' country, this issue may be solved in a favorable way.

Additional records: Peru. Pasco (?): Exact origin unknown but probably from the area near Oxapampa,

Figure 4. *Odontoglossum epidendroides*. Photo: S. Dalström.

Figure 5. *Odontoglossum juninense*. Photo: S. Dalström.

flowered in cultivation in Palca, Peru, by Manuel Arias, Dec. 2002, *S. Dalström 2765* (color transparency in Dalström Archives).

Distribution: Recent observations suggest that this species is limited to seasonally wet cloud forests near the town of Oxapampa, Pasco, Peru, at approximate elevations of 2400 – 2500 m.

Etymology: The name refers to the extraordinarily long and filament-shaped lip callus.

Acknowledgements. The authors thank Wesley Higgins for commenting on the manuscript, Guido Deburghgraeve for cultivating the type plant, and Manolo Arias together with his staff and family in Lima for gracious logistic support. The authors also thank the staff at the Instituto Recursos Naturales (INRENA) for aiding in providing necessary permits, and Betty Millán and Ricardo Fernández at the Universidad de San Marcos, Museo de Historia Natural, Lima, for supporting ongoing orchid research projects and making herbarium material available for studies.

Literature cited

Chase, M. W., N. H. Williams, K. M. Neubig & W. M. Whitten. 2008. Taxonomic transfers in Oncidiinae to accord with Genera Orchidacearum*,* vol. *5*. Lindleyana in Orchids (West Palm Beach) 77(12): 20-31.

Chase, M.W. 2009. Subtribe Oncidiinae. *In* Pridgeon, A.M., M.W. Chase, P.J. Cribb, & F.N. Rasmussen [eds]. Genera Orchidacearum, Vol. 5. Epidendroideae. Oxford University Press.

Dalström. S. 1993. A new species of *Odontoglossum* (Orchidaceae; Oncidiinae) from Bolivia. Lindleyana 8(1): 15-19.

Dalström. S. 1996. A New Small Flowered Species of *Odontoglossum* (Orchidaceae; Oncidiinae) of the *O. astranthum* complex from Bolivia. Lindleyana 11(2): 114-117.

Dalström. S. 1999. A new Bolivian species of *Odontoglossum* (Orchidaceae; Oncidiinae) in the *astranthum* complex. Lindleyana 14(2): 87-91.

Dalström. S. 2010. A new species of *Odontoglossum* (Orchidaceae: Oncidiinae) from Ecuador. Lankesteriana 9(3): 505-508.

Dalström. S. 2012a. New combinations in *Odontoglossum* (Orchidaceae: Oncidiinae) and a solution to a taxonomic conundrum. Lankesteriana 12(1): 53-60.

Dalström. S. 2012b. A well-known but previously misidentified *Odontoglossum* (Orchidaceae: Oncidiinae) from Ecuador. Lankesteriana 12(3): 155-160.

Dalström. S. 2013. Eine neues, seltsames *Odontoglossum* as dem Astranthum-Komplex (Orchidaceae: Oncidiinae) der Amazonas-Region in Peru. Orchideenjournal (2): 62-67

Sander, F. 1892. *Odontoglossum wattianum*. Reichenbachia 1(2), sub Pl. 9. H. Sotheran & Co., London.

LANKESTERIANA 13(3): 407—417. 2014.

NOCTURNAL POLLINATION BY FUNGUS GNATS OF THE COLOMBIAN ENDEMIC SPECIES, *PLEUROTHALLIS MARTHAE* (ORCHIDACEAE: PLEUROTHALLIDINAE)

Carol Andrea Duque-Buitrago[1], Néstor Fabio Alzate-Quintero[1] & J. Tupac Otero[2, 3, 4]

[1] Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Herbario FAUC, Universidad de Caldas, PO Box 275, Manizales, Colombia
[2] Departamento de Ciencias Biológicas, Facultad de Ciencias Agropecuarias, Universidad Nacional de Colombia, Sede Palmira
[3] Instituto de Estudios Ambientales IDEA, Universidad Nacional de Colombia, Sede Palmira
[4] Author for correspondence: jtoteroo@unal.edu.co

Abstract. Contemporary patterns of plant biodiversity result from the ecological and evolutionary processes generated by species interactions. Understanding these interactions is key for effective biodiversity conservation at the species and the ecosystem level. Orchid species often have highly specialised pollinator interactions, and the preservation of these is critical for in situ orchid conservation. The majority of orchid species occur in tropical regions, and information regarding their interactions is limited. We present data on pollinator identities, pollination mechanisms and flowering phenology of the Colombian endemic orchid, *Pleurothallis marthae*. We evaluated the mechanisms of attraction, the presence of osmophores, and the reproductive system of the species. *Pleurothallis marthae* is self-compatible with nocturnal anthesis pollinated by *Mycetophila* sp. (Mycetophilidae), probably attracted by a string fungus like smell liberated by the flower and *Bradysia* sp. (Sciaridae) that feed on nectar in the labellum. Osmophores and nectaries were detected in the epidermis of the sepals and petals. We present new evidence that the genus *Pleurothallis* is adapted to Diptera pollination. Our study indicates that the pollination mechanism of *P. marthae* is based on the nocturnal attraction of two species of fungus gnats, probably combining food attraction and brood place deception.

Resumen. Los patrones contemporáneos de biodiversidad vegetal son el resultado de procesos ecológicos y evolutivos generados por la interacción entre especies. El entendimiento de estas interacciones es clave para la conservación de la biodiversidad a nivel de especies y ecosistemas. A menudo las orquídeas tienen interacciones de polinización altamente especializadas, y su preservación es crucial para la conservación de orquídeas *in situ*. La mayoría de las especies de orquídeas ocurren en regiones tropicales, y la información sobre sus polinizadores es limitada. Aquí presentamos datos sobre la identidad de polinizadores, mecanismos de polinización y fenología floral de la orquídea *Pleurothallis marthae*, endémica de Colombia. Evaluamos los mecanismos de atracción, la presencia de osmóforos, y su sistema reproductivo. Encontramos que se trata de una especie auto-compatible con antesis nocturna polinizada por *Mycetophila* sp. (Mycetophilidae), especie atraída probablemente por el olor a hongo que libera la orquídea y *Bradysia* sp. (Sciaridae), la cual se alimenta de gotas de néctar en el labelo. Los osmóforos y nectarios fueron detectados en la epidermis de los sépalos y pétalos. El mecanismo de polinización de *P. marthae* se basa en la atracción nocturna de moscas especializadas en hongos, y combina atracción alimenticia y mimetismo de sitios de apareamiento.

Key words: *Bradysia*, orchid pollination, fungus gnats, pollinators, *Mycetophila*, olfactory mimicry

Introduction. As we are facing the sixth global biodiversity extinction (Canadell & Noble 2001), the ultimate goal of plant conservation biology is to preserve an adequate environment in which species can persist (Swarts & Dixon 2009), with continued evolutionary change. The effective conservation of individual species requires a deep taxonomic understanding (Flanagan *et al.* 2006), especially among those groups highly diversified such as Pleurothallidinae. It also demands the maintenance of species interactions in natural environments. One of the critical interactions for many plants is pollination by animals. It is also one of the interactions that have provided substantial evidence of evolutionary processes in the wild; revealing amazing adaptations associated with pollen transport (Darwin 1885). Nevertheless, pollination had been nominated as an endangered interaction due to losses of plant species and their pollinators as well as their natural habitats (Kearns *et al.* 1993). A flowering plant family that combines both, threat conservation in some species and interesting pollination interactions is the Orchidaceae.

Orchidaceae is the largest family of flowering plants with about 800 genera and more than 28,000 species (Govaerts *et al.* 2012); many species are endangered, and listed in biodiversity red lists; for example, in Colombia there is a partial list of 207 endangered orchids (Calderón 2007). There are several critical aspects of orchid biology that contribute to those threats. Orchid conservation requires the consideration of two bottlenecks in the orchid's life cycle: seed germination and pollination (Tremblay & Otero 2009). Orchids depend on specific fungi for seed germination (Otero *et al.* 2002; 2004; 2007) that may have had complex co-cladogenic processes (Otero *et al.* 2011); however, there is still much to learn about many orchid mycorrhizal interactions, especially in the tropics (Otero & Bayman 2007). In the Andes, the highest threat to orchid conservation is habitat loss; nevertheless, pollination is also crucial.

Orchids are renowned for the complex and intriguing pollination mechanisms adapted to pollination by animals (Darwin 1885, van der Pijl & Dodson 1966, Singer 2002, Borba & Braga 2003), especially insects (Dressler 1981). It is now well known that bees and wasps are responsible for about 60% of the pollination of the family (Williams 1982, Ackerman 1983; Whitten *et al.* 1993; Camargo *et al.* 2006), flies pollinate 15-25% of species (Borba & Semir 2001), and Lepidoptera, Coleoptera and birds pollinate about 15-25% remaining (van der Pijl & Dodson 1966; Singer *et al.* 2007; Cuartas-Domínguez & Medel 2010). Orchids may provide a variety of rewards to their pollinators, such as oils, floral fragrances and occasionally pollen-like substances (Neiland & Wilcock 1998; Pansarin 2008); however, nearly a third of orchid species provide no floral resources, and depend on various forms of deception for pollination (Ackerman 1986; Nilsson 1992; Cozzolino & Widmer 2005). One of the most common means of deception, sexual mimicry, is reported in about 20 genera of Orchidaceae with various pollinator types such as solitary and social bees, wasps, beetles and flies (Dafni 1984; Sasaki *et al.* 1991). This mechanism includes visual and/or olfactory features attracting insects. The best known cases of reproductive deception involve pseudo-copulation, a phenomenon unique to orchids (Nilsson 1992). Where, flowers mimic female structures and chemical pheromones of certain insects (Singer *et al.* 2004; Blanco & Barboza 2005), and are pollinated by male insects seeking a mate (Dressler 1981; Williams & Whitten 1983; Singer 2002). The emission of fragrances that resemble the insect sexual pheromones for reproduction is an important factor associated with the mimicry, including mating or oviposition sites (Albores-Ortiz & Sosa 2006; Barbosa *et al.* 2009; Barriault *et al.* 2010; Endara *et al.* 2010 Peakall *et al.* 2010).

Some studies suggest that the subtribe Pleurothallidinae (Orchidaceae: Epidendreae) is mainly adapted to pollination by Diptera species (van der Pijl & Dodson 1966; Chase 1985; Duque 1993; Borba & Semir 2001; Blanco & Barboza 2005; Pupulin *et al.* 2012), with several reports of deception by sexual mimicry (Christensen 1994; Blanco & Barboza 2005). Borba & Semir (2001) studied four Brazilian species and reported different fragrances and pollinator activities. *Acianthera johannensis* (Barb. Rodr.) Pridgeon & M.W. Chase (as *Pleurothallis johannensis* Barb. Rodr.) and *Acianthera fabiobarrosii* (Borba & Semir) F. Barros & F. Pinheiro (as *P. fabiobarrosii* Borba & Semir) are pollinated by females of the genera *Tricimba* (Chloropidae) and have a diurnal smell of fish and no nectar production, while *Acianthera teres* (Lindl.) Borba (as *P. teres* Lindl.) and *Acianthera* ochreata (Lindl.) Pridgeon & M.W. Chase (as *P. ochreata* Lindl.) have a diurnal smell of rancid cheese and produce nectar like liquid at the base of the labellum. The latter are pollinated by *Megaselia* spp. (Phoridae) (Borba & Semir 2001), *Acianthera adamantinensis* (Brade) F. Barros (as *Pleurothallis adamantinensis* Brade) has a dog feces odor and is pollinated by flies *Hippelate* ssp. (Chloropidae) (Borba & Semir 2001). Those five species had high genetic variability showing a high percentage of polymorphic loci ranged from 50 to 83%, with a mean number of alleles per locus between 2.1 and 3.8, and a mean heterozygosity (He) ranged from 0.25 to 0.43 (Borba *et al.* 2001). *Acianthera johannensis*, *A. fabiobarrosii*, and *A. adamantinensis* showed a low level of genetic structuring while *A. teres* and *A. ochreata* showed high genetic structuring (Borba *et al.* 2001). However, the actual evidence has not been applied for conservation purposes, but in recent years the genus had been subdivided in smaller groups.

Pleurothallis marthae (Luer & Escobar) Luer is an interesting research model because it has relatively large flowers of 2 cm that facilitate observation and is a frequent species in Yotoco Nature Reserve, Colombia. Little information is reported in the literature on this species. It is listed in the CITES Appendix II (W3Tropicos, accessed on Dec 2012) and is endemic to Colombia. Recently it was recorded from Yotoco Nature Reserve (Escobar 2001; Pérez-Escobar *et al.* 2009). The species grows as both an epiphyte near the ground (no more than one meter high) and a terrestrial plant, at 1400-1800 m elevation in mountain forest.

The objectives of this study are to describe the pollination system and mechanisms of pollinator attraction of *P. marthae*.

Material and Methods

Study species. — *Pleurothallis marthae* is a terrestrial species or rarely epiphytic, without pseudobulbs, leaves broad, deeply cordate (Luer & Escobar 1996), it has a little bundle of pink flowers on the base of the leaf. The flowers are relatively large for the genus. This species was described as *P. marthae* by Luer & Escobar from a collection by E. Valencia from Garrapatas (Valle del Cauca, Colombia) (Luer & Escobar 1996) and then transferred to *Acronia* Luer (2005). As *Acronia* is not broadly accepted we use *Pleurothallis*. *P. marthae* has flowers with two different coloration patterns and morphology (morphs). The first (yellow-morph) has yellowish dorsal sepal the broadly ovate, obtuse, concave, with translucent horizontal lines and dots, the lateral sepals completely connate (synsepal) is lilac, with glandular trichomes, petals rose, concave, with glandular trichomes too, lip light rose, thick, convex, transversely obovate. The second (pink-morph) has a pink dorsal sepal with translucent horizontal lines and dots, the synsepal is magenta with glandular trichomes, the petals are larger than the yellow-morph (Fig. 1) and the lip is similar to yellow-morph. In both morphs the column is short and cream-colored with an apical anther and a bilobed stigma (Fig. 1).

Study site. — We did this study at the Yotoco Forest Reserve (YFR), located on the eastern slope of the western Cordillera de Los Andes in Colombia, in the municipality of Yotoco. The site was situated in remnants of the subtropical wet-dry transition forest of Valle del Cauca (3°50'N, 76°20'W) at an elevation of 1400-1600 m. Average annual temperature is 20° C; average annual precipitation is 1500 mm; and relative humidity averages 85% (Escobar 2001).

Two populations were surveyed, accounting 250 individuals in total; each individual was marked with an aluminum tag with a previously assigned code. Individuals were considered genets if all shoots were attached to a single rhizome and were physically separate from other plants. Individuals were characterized by size class according to the length of the longest shoot. The classes are the following: SIZE I (6-20 cm), SIZE II (21-40 cm), SIZE III (41-60 cm), SIZE IV (> 61 cm).

Reproductive events. — The numbers of open flowers (OF), pollinaria removed (PR), closed stigmas (CS) and swollen ovaries (SO) were recorded weekly as indirect evidence of reproductive effort and pollination events. As the data were not normally distributed, the differences between size classes for each reproductive event were analyzed using a Kruskal-Wallis test. The correlation between pollinator activity and flowering anthesis was evaluated with a linear regression. All data were analyzed with Statgraphics ® Plus Version 5.1®.

Flower visits. — Observations were initially made between 0600 and 1800 h to identify periods of activity of flower visitors and pollinators. Very low activity was observed during the day, so the observation period were extended until 2000 h. Visitors were observed using red light located two meters from the plants to broaden the spectrum of light to avoid pollinator disturbance they were highly sensitive to direct illumination. With these additional hours we discovered visitation was nocturnal, so all further nocturnal observation periods were done between 1800 - 0600 h, for a total of 97 hours of observation (not including the diurnal times). For 30 individuals, the time of arrival of visitors was recorded, duration of visit, behavior within the flower, and number of visitors, and additionally video and

FIGURE 1. Flower of *Pleurothallis marthae*: a) lateral view, b) frontal view, c) two color morphs, d) Habit of *Pleurothallis marthae*.

photographic records. Flower visitors and pollinators were differentiated by behavior. Floral visitors were collected in plastic vials, transported to the zoology laboratory at Universidad of Caldas where high resolution macro photos were taken. As Colombian law prohibits exportation of wild biological material, Dr Sarah Siqueira de Oliveira, at the University of São Paulo identified the specimens from the photographs.

Osmophore detection.. — From each of the populations, we collected fresh flowers from 10 individuals and stained in a bath of neutral red 1:1000 for 20 minutes (Stern *et al.* 1986) to detect scent-secreting glands (osmophores) or nectaries as neutral red indicate sites that is metabolically active (Kearns & Inouye 1993).

Reproductive system. — We bagged 40 flower buds of 20 plants with net mesh to exclude insect visitors. Once the flowers were in anthesis and receptive, as indicated by a wet and sticky stigmatic surface, we performed the following hand-pollination treatments: autogamy (removal of pollinaria from a flower and pollen transfer to the same flower); geitonogamy (removal of pollinaria from one flower and pollen transfer to another flower of the same plant); xenogamy (removal of pollinaria from a flower and pollen transfer to a flower of another plant); and natural pollination. All treatments with the exception of the natural pollination treatment were bagged again to prevent insect visitors impacting the results. Pollinations were monitored until fruits matured or aborted. We analyzed differences among treatments with a non-parametric Kruskal-Wallis test.

Results. Flower buds develop in 10-15 days, and flowers remain open for 10-12 days, provided that pollination did not occur. The flowers produce fungus-like odor and lightly sweet nectar at night time. Anthesis of *P. marthae* began at 18:30 when flowers began to release a fungus-like odor (as detected by the human

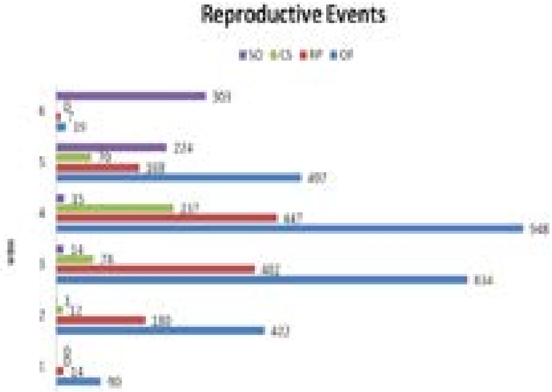


Figure 2. Linear regression of the number of flowers per reproductive season vs. number of fruits.

Figure 3. *Bradysia* sp. with *Pleurothallis marthae* pollinaria adhered to the dorsal side of the thorax.

nose) and nectar secreted by the lip. As time passed the smell gradually increased in intensity, and peaked at 23:30. There after the intensity decreased until approximately 05:00, when it became imperceptible. The fluid secreted from the lip remained in the flower from 19:00 until 09:00.

Reproductive events. — The species flowered from early May through mid June (six weeks), with a peak at the fourth week. There were significant differences in weekly flower abundances among size classes (H test, P-value = 0.03) with small individuals producing fewer flowers than the large ones. Nevertheless, the number of pollinia removed (H test, P-value = 0.14), stigmas closed (H test, P-value = 0.31) and ovaries swelled (H test, P-value = 0.19) did not differ significantly. There was a significant relationship between weekly abundance of flowers and abundance of pollinators visiting flowers during the anthesis period (H test, P-value = 0.02). There was a correlation between number of pollinator visit and the number of flowers in anthesis per reproductive season (Fig. 2). The time from pollination to fruit dehiscence was between 9 and 10 weeks. The reproductive events did not differ statistically between two different coloration patterns (morphs) observed (H test, P-value > 0.05).

Flower visitors. — The most common flower diurnal visitors were herbivorous caterpillars (Lepidoptera: Geometridae), which feed on buds, ovaries, and fruits in early developmental stages. We also observed adults of two Orthoptera species: Eumastacidae and Acrididae feeding on flowers and foliage. We also saw Heliconius cydno cydnides Staudinger (Lepidoptera: Heliconidae) visiting several flowers in a typical foraging behavior and two species of spiders, Araneidae and Thomisidae, families known to hunt pollinators. Occasionally, we observed ants eating the nectar from the lip.

We observed two pollinators species, *Bradysia* sp. (Diptera: Sciaridae) and *Mycetophila* sp. (Diptera: Mycetophilidae), both fungus gnats. The *Bradysia* sp. (Fig. 3) visited several flowers on the same plant (Fig. 4) by first landing on the synsepal, and then crossing the petals to consume the nectar on the labellum for a few seconds. Subsequently, the gnat contacted the apex of the column and probably causing the pollinarium to adhere to the ventral section of the thorax. Visits of *Bradysia* sp. were very brief (10 seconds) and were only observed on two occasions, in one of them, the individual had two pollinaria attached.

The *Mycetophila* sp. (Fig. 5) was presumably attracted by the fungus-like floral fragrance. The gnats landed on the flower (synsepal, lip, petals, or column) and began a series of wing and thorax movements while lifting the hind legs (Fig. 6), and sometimes moving the abdomen as if to oviposit. Probably pollinaria adhere to the ventral part of the thorax when individuals court and mate. Individuals stayed on the flower for a long time (sometimes overnight). We often observed many individuals of *Mycetophila* sp. visiting the flower at the same time (10 individuals), observed 47 individuals in total. On several occasions we observed mating among the *Mycetophila* sp. but we did not observe pollination events. Nevertheless, indirect evidence of their

FIGURE 4. Visit sequences of *Bradysia* sp. in *Pleurothallis marthae* flowers. a — *Bradysia* sp. arriving to the petals and facing to the labellum; b — *Bradysia* sp. consuming nectar from the labellum; c — *Bradysia* sp. crossing by the column and climbing by the lower part of the dorsal sepal; d — *Bradysia* sp. crossing by the lower part of the dorsal sepal to exit the flower.

FIGURE 5. *Mycetophila* sp. with pollinaria of *Pleurothallis marthae*. a — *Mycetophila* sp. in a flower of *Pleurothallis marthae* with a pollinarium in the ventral part of the thorax. b — Close up of *Mycetophila* sp. and pollinarium. The pollinarium was detached of the insect during the specimen manipulation.

pollination activity was obtained from the collection from the field of these diptera species with *P. marthae* pollinarium attached.

Osmophore detection. — Osmophores were detected in the epidermis of synsepals, dorsal sepal and petals, with an obvious presence in scattered spots located mainly at the edges of the structure (Fig. 7). The petal tips had glandular trichomes.

Reproductive system. — Our hand-pollination experiments indicated that *Pleurothallis marthae* is self-compatible. Self-pollination treatment within a flower produced 60% fruit set; pollination between flowers of the same clump produced 50% fruit set; cross-pollinations had 60% fruit set and natural pollination produced 40%. No significant differences were observed between the different treatments (H test, P value> 0,05).

Figure 6. Display of *Mycetophila* sp. in *Pleurothallis marthae* flowers.

Discussion. Base on the finding of *Pleurothallis marthae* is probably pollinated by two species of fungus gnats: *Mycetophila* sp. and *Bradysia* sp. Visitors can remove pollinia and not necessarily be pollinators, nevertheless, form in which deposited pollinia, court and mate in the flowers, fungus-like odor, absence of other species through visits and biology of fungus gnat, we believe that they are pollinators. This case is similar to that found by Endara *et al.* (2010), in this work on pollination of *Dracula lafleurii* Luer & Dalström and *Dracula felix* (Luer) Luer, authors argue that the pollination process occurs when individuals of *Zygothrica* perform court and mate in the flowers.

The effectiveness of fungus gnats orchid as pollinators had been briefly documented by van der Pijl and Dodson (1966) on the pollination of *Stelis aemula* Schltr. Most recently, other orchids had been reported as fungus gnats pollinated, for example *Lepanthes glicensteinii* is pollinated by *Bradysia floribunda* in Costa Rica (Blanco & Barboza 2005), *Octomeria crassifolia* is pollinated by *Bradysia* sp. in Brazil (Barbosa *et al.* 2009). In California, *Listera cordata* (= *Neottia cordata*; Orchidoideae) is pollinated by *Mycetophila* sp. and *Sciara* sp. (Ackerman & Mesler 1979).

Mycetophila forms distinct groups of closely related species, which are within the group usually separable only by the characters on the male terminalia. *Mycetophila* is one of the most abundant families of order Diptera encompassing more than 3000 described species, with a world-wide distribution (Gaston 1991). *Pleurothallis marthae* has flowers with two different coloration patterns (morphs). Pollination success was detected equally in both morphs, suggesting that color is not a key factor determining reproductive success, and supporting the hypothesis that both fragrances and nectar are key attracting factors. Nevertheless, we found a positive relationship between flower abundance and the number of pollinator visits. This may be because with a greater number of flowers there

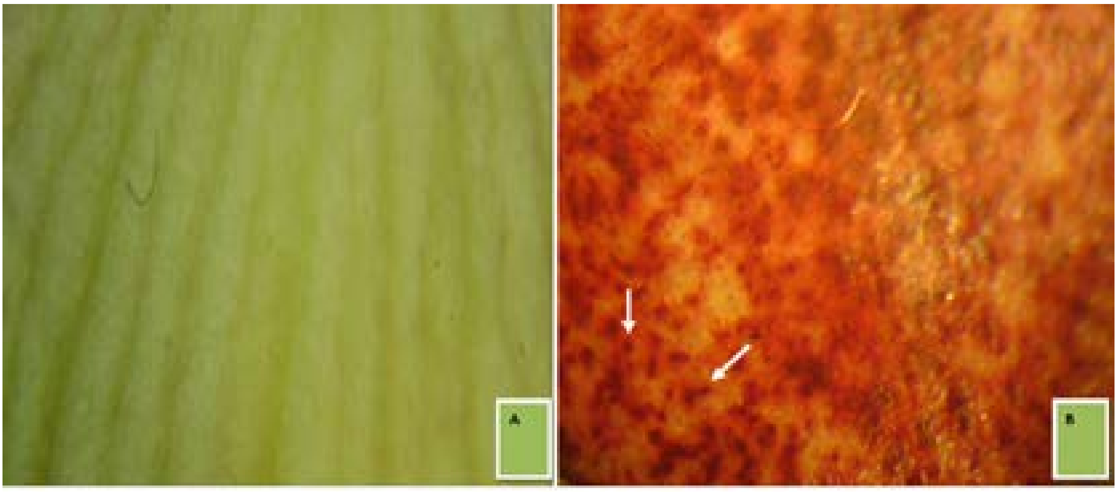


FIGURE 7. Portion of the dorsal sepal (a) before and (b) after staining with neutral red. Arrows shows the presence of osmophores and/or nectaries in the adaxial side of the sepal.

is likely to be an increase in the emission of aroma and possibly a greater supply of nectar, making these flowers more effective at attracting pollinators.

Pleurothallis marthae seems to mimic the smell of a fungus; this case had been reported in *Zootrophion* sp. (Orchidaceae) and coincides with the syndrome of sapromyophily (pollination syndrome of flowers producing smell of decaying flesh) proposed by Faegri & van der Pijl (1971).

Although oviposition behavior was observed by *Mycetophila* sp., we did not observe eggs or larvae under microscope, which suggests a mechanism in which the flowers attract female flies, and those females at the same time attract males (Ackerman & Mesler 1979). *Mycetophila* sp. was observed mating on the flowers on several occasions. Displaying *Mycetophila* sp. were most commonly observed on the specific parts of the flower in which we located the scent glands (osmophores), suggesting that the attraction of this species occurs by the emission of a fragrance. Additionally, floral display was also very important as plants with more open flowers had higher fitness that may be complementary.

Both pollinator species are commonly known as fungus gnats because they are almost always dependent upon fungal substrates for larval development. The *Bradysia* sp. may have been initially attracted by the smell and then by the presence of nectar, which may be a mechanism to keep the flies on flowers for longer periods of time to enhance the probability of pollination (de Melo *et al.* 2010).

Our results on the reproductive system suggest that *P. marthae* is self-compatible; this finding is compatible with the observed behavior of pollinators, whose continued presence at a single flower and at the flowers of a single plant is likely to promote *P. marthae* reproduction. This phenomenon has also been observed in other species (Mesler *et al.* 1980; Borba & Semir 2001; Singer 2001; Barbosa *et al.* 2009). While we did not conduct a pollination treatment to test for self-pollination, fruit and seed production in most self-compatible orchids are pollinator-dependent, and *P. marthae* is likely no exception (Rodríguez-Robles *et al.* 1992; Singer & Zasima 1999; Singer 2001; Singer *et al.* 2004).

The natural fruit set observed in this study was 60%. This value is higher than the ranges suggested by Neiland & Wilcock (1998) for tropical orchids, although those reported for *Listera cordata* 61-78% (Ackerman & Mesler 1979) and *Habenaria parviflora* 93.3-96.7% (Singer 2001), species pollinated by Diptera, are higher. Together, these findings suggest that Diptera pollination can be a very favorable strategy for orchids.

We present new evidence of fly pollination in the genus *Pleurothallis*. Fly pollination had already been reported for species *Lepanthes glicensteinii* Luer, *Listera cordata* (L.) R. Br., *Tolmiea menziesii* (Pursh) Torr. & A. Gray, *Asarum caudatum* Lindl., *Dracula lafleurii* Luer & Dalström and *Dracula felix* (Luer) Luer, *Specklinia pfavii* (Rchb.f.) Pupulin & Karremans and *Specklinia spectabilis* (Ames & C.Schweinf.) Pupulin & Karremans (Mesler *et al.* 1980; Lu 1982; Goldblatt *et al.* 2004; Okuyama *et al.* 2004; Endara *et al.* 2010, Pupulin *et al.* 2012), revealing them to be very important pollination vectors that have highly specialized relationships with the plants they pollinate. As far as we know, our study is the first case suggesting fungal-like odors may be involved in attracting pollinators in *Pleurothallis* and the second for the Subtribe Pleurothallidinae (Christensen 1994). It is the first report of nocturnal pollination of the genus and species pollinated by fungus gnats. *Lepanthes* may be nocturnally pollinated too (Tremblay & Ackerman 2007). Further studies in our research group are focused in the understanding of the fragrance composition of of *P. marthae* flowers. The knowledge of this obligatory interspecific interactions is critical for the conservation management of this Colombian endemic orchid, *P. marthae*; of course, we have to include the conservation of their nocturnal fungus gnat pollinators.

Acknowledgements. The authors are thankful for the Mobility grant awarded to the first author by Santander Universities. We thank Sarah Siqueira de Oliveira for the identification of Diptera; Carlos Alberto Jaramillo, Valentín Hidalgo and the staff of the Yotoco Forest Reserve of the Universidad Nacional de Colombia-Palmira for assistance in the development of this study; James D. Ackerman, Nicola S. Flanagan, Paul Bayman, Nhora Helena Ospina and Marcela Cuartas for their comments and contributions to the manuscript; and the Grupo de Investigación en Orquídeas, Ecología y Sistematica Vegetal (COL 0066015) of the Universidad Nacional de Colombia-Palmira for logistical support.

Literature cited

Ackerman, J.D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biological Journal of the Linnean Society 20: 301-314.

Ackerman, J.D. 1986. Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1: 108-13.

Ackerman, J.D. & M.R. Mesler. 1979. Pollination Biology of *Listera cordata* (Orchidaceae). American Journal of Botany 66: 820-824.

Albores-Ortiz, O. & V. Sosa. 2006. Polinización de dos especies simpátricas de *Stelis* (Pleurothallidinae, Orchidaceae). Acta Botánica Mexicana 74: 155-168.

Barbosa, A.R., M.C. de Melo & E.L. Borba. 2009. Self-incompatibility and myophily in *Octomeria* (Orchidaceae, Pleurothallidinae) species. Plant Systematics and Evolution 283: 1-8.

Barriault, I, D. Barabe, L. Cloutier & M. Gibernau. 2010. Pollination ecology and reproductive success in Jack-in-the-pulpit (*Arisaema triphyllum*) in Quebec (Canada). Plant Biology 12: 161-171.

Blanco, M.A. & G. Barboza. 2005. Pseudocopulatory Pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by Fungus Gnats. Annals of Botany 95: 763-772.

Borba, E.L. & P.I. Braga. 2003. Biologia reprodutiva de *Pseudolaelia corcovadensis* (Orchidaceae): melitofilia e autocompatibilidade em uma Laeliinae. Revista Brasileira de Botânica 26: 541-549.

Borba, E.L., J.M. Felix, V.N. Solferini & J. Semir. 2001. Fly-pollinated *Pleurothallis* (Orchidaceae) species have high genetic variability: evidence from isozyme markers. American Journal of Botany 88: 419-428.

Borba, E.L. & J. Semir. 2001. Pollinator Specificity and Convergence in Fly-pollinated *Pleurothallis* (Orchidaceae) Species: A Multiple Population Approach. Annals of Botany 88: 75-88.

Calderón-Saenz E. 2007. Libro rojo de plantas de Colombia. Volumen 6: Orquídeas, primera parte. Serie de Libros Rojos de Especies Amenazadas de Colombia. Bogotá, Colombia. Instituto Alexander von Humboldt-Ministerio de Ambiente, vivienda y desarrollo territorial. 828 p.

Camargo, E., V, Silva & E. Leit. 2006. Reproductive biology of two *Cattleya* (Orchidaceae) species endemic to north-eastern Brazil. Plant Species Biology 21: 85-91.

Canadell, J. & I. Noble. 2001. Challenges of a changing earth. Trends in Ecology and Evolution 16: 664-666.

Chase, M.W. 1985. Pollination of *Pleurothallis endotrachys*. American Orchid Society-Bulletin 54: 431-434.

Christensen, D.E. 1994. Fly pollination in the Orchidaceae. In J. Arditti [ed.], Orchid Biology: Reviews and perspectives, VI, 415-454. (John Wiley & Sons. New York, USA.

Cozzolino, S. & A. Widmer. 2005. Orchid diversity: an evolutionary consequence of deception? Trends in Ecology and Evolution 20: 487-494.

Cuartas-Domínguez, M. & R. Medel. 2010. Pollinator-mediated selection and experimental manipulation of the flower phenotype in *Chloraea bletioides*. Functional Ecology 24: 1219 -1227. http://dx.doi.org/10.1111/j.1365-2435.2010.01737.x

Dafni, A. 1984. Mimicry and Deception in Pollination. Annual Review of Ecology and Systematic 15: 259-278.

Darwin, C.D. 1885. The various contrivances by which orchids are fertilized by insects. John Murray, London, UK.

Dressler, R.L. 1981. The Orchids, natural history and classification. The Smithsonian Institution, Washintong DC, USA.

Duque, O. 1993. Polinización en *Pleurothallis*. Orquideología 19: 55-69.

Endara, L., Grimaldi, D. A., & Roy, B. A. 2010. Lord of the flies: pollination of *Dracula* orchids. Lankesteriana 10: 1-11.

Escobar, E. 2001. Presentación de Yotoco "Reserva Natural" Flora: Plantas Vasculares. Universidad Nacional de Colombia, Palmira, Colombia.

Faegri, K. & L. van der Pijl. 1979. The principles of pollination biology. Oxford: Pergamon Press.

Flanagan, N.S., R. Peakall, M.A. Clements & J.T. Otero. 2006. Conservation of taxonomically difficult species: the case of the Australian orchid, *Microtis angusii*. Conservation Genetics 7: 847-859.

Gaston, K.J. 1991. The magnitude of global insect species richness. Conservation Biology, 5: 283-296.

Goldblatt, P., P. Bernhardt, P. Vogan & J.C. Manning. 2004. Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). Plant Systematics and Evolution 244: 55-67.

Govaerts, R., J. Pfahl, M.A. Campacci, D. Holland-Baptista, H. Tigges, J. Shaw, P. Cribb, A. Geore, K. Kreuz & J. Wood. 2012. World checklist of Orchidaceae. The Board of Trustees of the Royal Botanic Gardens, Kew. http://www.kew.org/wcsp/monocots/ [accessed 24 June 2012].

Kearns, C.A. & D.W. Inouye. 1993. Techniques for Pollination Biologists. University Press of Colorado, Colorado, USA.

Kearns, C.A., D.W. Inouye & N.M. Waser. 1998. Endangered Mutualism: the conservation of plant-pollinators interactions. Annual Review of Ecology and Systematics 29: 83-112.

Lu, K.L. 1982. Pollination Biology of *Asarum caudatum* (Aristolochiaceae) in Northern California. Systematic Botany 7:150-157.

Luer, C.A. & R. Escobar. 1996. Nuevas especies de *Pleurothallis* de Colombia. Orquideología 20: 68-71.

Luer, C.A. 2005. Icones pleurothallidinarum XXVII. Dryadella and Acronia section *Macrophyllae-Fasciculatae*: addenda to *Acianthera*, *Andinia*, *Dracula*, *Dresslerella*, *Lepanthes* and *Masdevallia* new taxa, validation of taxa, errata. Missouri Botanical Garden, St. Louis.

de Melo, M.C., E.L. Borba & P.E. Sousa. 2010. Morphological and histological characterization of the osmophores and nectaries of four species of *Acianthera* (Orchidaceae: Pleurothallidinae). Plant Systematic Evolution 286: 141-151.

Mesler, M.R., J.D. Ackerman & K.L. Lu. 1980. The effectiveness of fungus gnats as pollinators. American Journal of Botany 67: 564-567.

Neiland, M.R. & C. Wilcock. 1998. Fruit Set, Nectar Reward, and Rarity in the Orchidaceae. American Journal of Botany 85: 1657-1671.

Nilsson, L.A. 1992. Orchid pollination biology. Trends in Ecology and Evolution 7: 255-259.

Okuyama, Y., M. Kato, N. Murakami. 2004. Pollination by fungus gnats in four species of the genus *Mitella* (Saxifragaceae). Botanical Journal of the Linnean Society 144: 449-460.

Otero, J.T., J.D. Ackerman & P. Bayman. 2002. Diversity and host specificity of endophytic Rhizoctonia-like fungi from tropical orchids. American Journal of Botany 89: 1852-1858.

Otero, J.T., J.D. Ackerman & P. Bayman. 2004. Differences in mycorrhizal preferences between two tropical orchids. Molecular Ecology 13: 2393-2404.

Otero, J.T. & P. Bayman. 2007. Mycorrhizae in orchid conservation. In: E Calderón-Sáens [ed.], The Red Book of Orchids of Colombia, V, 6: Orchids, First Part. Series The Red Book Species of endangered species of Colombia, 771-796. Instituto Alexander von Humboldt, Ministerio de Ambiente, Vienda y Desarrollo Territorial, Bogota, Colombia.

Otero, J.T., N.S. Flanagan, E.A. Herre, J.D. Ackerman, P. Bayman. 2007. Widespread mycorrhizal specificity correlates to mycorrhizal function in the neotropical, epiphytic orchid, *Ionopsis utricularioides* (Orchidaceae). American Journal of Botany 94: 1944-1950.

Otero, J.T., P.H. Thrall, M.A. Clements, J.T. Miller & J.J. Burdon. 2011. Co-diversification of Orchids (Pterostylidinae) and their Associated Mycorrhizal Fungi. Australian Journal of Botany 59: 480-497.

Pansarin, E.R. 2008. Reproductive biology and pollination of *Govenia utriculata*: A syrphid fly orchid pollinated through a pollen-deceptive mechanism. Plant Species Biology 23: 90-96.

Peakall, R., D. Ebert, J. Poldy, R.A. Barrow, W. Francke, C.C. Bower & F.P. Schiestl. 2010. Pollinator specificity, floral odour chemistry and the phylogeny of Australian sexually deceptive *Chiloglottis* orchids: implications for pollinator-driven speciation. New Phytologist 188: 437-450.

Pérez-Escobar, O.A., E. Parra-Sanchez & P. Ortiz-Vadivieso. 2009. Inventario orquideológico de la Reserva Bosque de Yotoco, Valle del Cauca. Acta Agronómica 58: 189-196.

Pupulin, F., A.P. Karremans & B. Gravendeel. 2012. A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica. Phytotaxa 63: 1–20.

Rodríguez-Robles, J.A., E.J. Meléndez & J.D. Ackerman. 1992. Effects of display size, flowering phenology, and nectar availability on effective visitation frequency in *Comparettia falcata* (Orchidaceae). American Journal of Botany 79: 1009-1017.

Sasaki, M., M. Ono, T. Asada & T. Yoshida. 1991. Oriental orchid (*Cymbidium pumilum*) attracts drones of the Japanese honeybee (*Apiscerana japonica*) as pollinators. Experientia 47: 1229-1225.

Singer, R.B. 2001. Pollination biology of *Habenaria parviflora* (Orchidaceae: Habenariinae) in Southeastern Brazil. Darwiniana 39: 201-207.

Singer, R.B. 2002. The pollination mechanism in *Trigonidium obtusum* Lindl. (Orchidaceae: Maxillariinae): Sexual mimicry and trap-flowers. Annals of Botany 89: 157-163.

Singer, R.B. & M. Sazima. 1999. The pollination mechanism in the '*Pelexia* alliance' (Orchidaceae:Spiranthinae). Botanical Journal of the Linnean Society 131: 249-262.

Singer, R.B., A. Flach, S. Koehler, A.J. Marsaioli & M.D.C.E. Amaral. 2004. Sexual mimicry in *Mormolyca ringens* (Lindl.) Schltr. (Orchidaceae:Maxillariinae). Annals of Botany 93: 755-762.

Singer, R. B., Breier, T. B., Flach, A., & Farias-Singer, R. 2007. The pollination mechanism of *Habenaria pleiophylla* Hoehne & Schlechter (Orchidaceae: Orchidinae). Functional Ecosystems and Communities, 1: 10-14.

Swarts, N.D. & W. Dixon. 2009. Terrestrial orchid conservation in the age of extinction. Annals of Botany 104: 543-556.

Tremblay, R. & J.D. Ackerman. 2007. Floral color patterns in a tropical orchid: are they associated with reproductive success? Plant Species Biology 22: 95-105.

Tremblay, R. & J.T. Otero. 2009. Orchid conservation biology: Predicting species dynamics and community interactions. In: A.M. Prigeon & J.P. Suárez [eds.], Proceedings of the Second Scientific Conference on Andean Orchids, 97-107. Universidad Técnica Particular de Loja, Loja, Ecuador.

van der Pijl, L. & C.H. Dodson. 1966. Orchid Flowers: their pollination and evolution. University of Miami Press, Miami, USA.

Whitten, W.M., A.M. Young & D.L. Stern. 1993. Non-floral sources of chemicals that attract male euglossine bees. Journal of Chemical Ecology. 19:3017-3027.

Williams, N.H. 1982. The biology of orchids and euglossine bees. In: J. Arditti [ed.], Orchidbiology II, 121-169. Cornell University Press, Ithaca, New York.

Williams N.H. & W.M. Whitten. 1983. Orchid floral fragrances and male euglossine bees. Methods and advances in the last sesquidecade. Biological Bulletin, 164: 355-395.

LANKESTERIANA 13(3): 419—427. 2014.

ORGANIZACIÓN ESPACIAL Y ESTRUCTURA DE UNA POBLACIÓN DE *IONOPSIS UTRICULARIOIDES* (ORCHIDACEAE) EN UN ÁREA SUBURBANA DE PINAR DEL RÍO, CUBA

Alfredo García-González* & Frander B. Riverón-Giró

El Colegio de la Frontera Sur (ECOSUR), Unidad Tapachula. Carretera Antiguo Aeropuerto, km 2.5,
Apartado Postal 36, Tapachula, Chiapas, México. C.P. 30700
*Autor para correspondencia: alfredmx22@gmail.com

Resumen. Se determinó la estructura poblacional y hábitos de crecimiento de una población de *Ionopsis utricularioides* (Orchidaceae), en un huerto de naranjos (*Citrus sinensis*; Rutaceae), localizado en la finca "La Juanita", Pinar del Río, Cuba. Se tuvieron en cuenta todos los árboles de naranjo del huerto y la población total de *I. utricularioides*. Se midieron las siguientes variables: altura y diámetro de los naranjos y ramas donde crecían las orquídeas, distribución de las orquídeas en los forófitos (tronco, ramas o ramillas), estadio de vida de las orquídeas (inmaduras o adultas), orientación de las orquídeas en el forófito, si las plantas estaban solitarias o agregadas y especie de los vecinos en el caso de las agregadas. Se estudiaron un total de 10 árboles de *C. sinensis*, ocho de ellos forófitos de la orquídea. Se contabilizaron 217 plantas de *I. utricularioides*. En el tronco de los árboles no se encontraron plantas de *I. utricularioides* y en las ramillas creciá 98.61% de la población. El número de plantas es relativamente abundante en los dos estadios de vida. Gran parte de las plantas de *I. utricularioides* se encontraron creciendo en agregación con otros individuos de su misma especie o con otras especies de epífitas vasculares. Esta es una población establecida y madura. Crecer en agregación le puede brindar ventajas competitivas a *I. utricularioides*.

Abstract. We determined the population structure and some habitat conditions of a *Ionopsis utricularioides* (Orchidaceae) population in an orange orchard (*Citrus sinensis*, Rutaceae), located in the "La Juanita" farm, Pinar del Río, Cuba. We took into account all the orange trees of the orchard, and located all the individuals of *I. utricularioides*. The following variables were analyzed: height and diameter of branches in growing orchids, orchid distribution on phorophytes (trunk, branches or twigs), life stage of the orchids (immature or adults), orientation of orchids in the phorophyte, if the plants were solitary or aggregated, and kind of neighbours in the case of the aggregate. Of the 10 trees of *C. sinensis*, eight trees had orchids of *I. utricularioides*, with 217 plants. Almost all orchids were observed on the twigs (98.61 %) and none were observed on the trunk of the tree. The number of plants is relatively high in the two stage of life. Most plants of *I. utricularioides* were found growing aggregate with individuals of the same species, or with other species of vascular epiphytes. This is a stable and mature population. Growing up in aggregation can give competitive advantages to *I. utricularioides*.

Palabras claves: micrositio, forófito, clases de vida, plantas agregadas, plantas solitarias**,** naranjo

Introducción. Las orquídeas son probablemente las más evolucionadas de todas las plantas vasculares y son un componente muy importante de la biodiversidad a consecuencia de su gran diversidad de especies (Mujica *et al*. 2000). No obstante, las orquídeas epífitas y terrestres difieren en un importante número de aspectos (Zotz & Schmidt 2006). Las orquídeas epífitas no tienen una fase bajo tierra y en ocasiones sus bajas densidades sugieren poca competencia intra o inter específica (Zotz & Hietz 2001). Además, los soportes (a nivel de corteza, ramas, troncos y especies de forófitos) ejercen una influencia muy fuerte en la dinámica de las poblaciones de epífitas (Zotz & Schmidt 2006).

En Cuba actualmente se reconocen aproximadamente 99 géneros y 308 especies de la familia Orchidaceae (Llamacho & Larramendi 2005), de las cuales 71 % son epífitas (Díaz 1999, Llamacho & Larramendi 2005).

Una de las especies de orquídeas epífitas que habitan en Cuba es *Ionopsis utricularioides* (Sw.) Lindl. (Ackerman 1995, Mujica *et al*. 2000, Llamacho & Larramendi 2005, Acevedo-Rodríguez & Strong 2012) (Figs. 1A–1B). Esta es una especie neotropical, con un amplio ámbito de distribución, que incluye Florida, México, Antillas Mayores y Menores, América Central, América del Sur e islas Galápagos (Ackerman 1995, Mujica *et al*. 2000, Llamacho & Larramendi 2005, FNA 2008). Es muy común encontrarla creciendo en zonas antropizadas (Ackerman 1995, Hágsater *et al*. 2005, Llamacho & Larramendi 2005), asociada a plantaciones de cítricos, café y cacao (Hágsater *et al*. 2005, Llamacho & Larramendi 2005).

Teniendo en cuenta que *I. utricularioides* es una especie que frecuentemente crece asociada a cultivos exóticos; se procedió a evaluar la organización espacial de esta orquídea sobre arboles de *Citrus sinensis* (L.) Osbeck (Rutaceae) y se estudiaron otras variables relacionadas con su ecología en un agroecosistema en Pinar del Río, Cuba, para analizar la preferencia que manifiesta por los espacios que ocupa sobre los forófitos y determinar las respuestas adaptativas y morfológicas que le permiten ser exitosa en estas condiciones antrópicas.

Materiales y Métodos

Caracterización del sitio —. El estudio se desarrolló durante los años 2010 y 2011, en un huerto de naranjos (*C. sinensis*), una especie frutal originaria de las regiones tropicales y subtropicales de Asia y el Archipiélago Malayo, introducida en el Nuevo Mundo en 1493 (ACTAF 2011). Este huerto, de aproximadamente 0.375 ha (375 m²), se localiza en los 22°28'599"N 083°37'678"W, en la finca "La Juanita", aproximadamente 10 km al noreste de la ciudad de Pinar del Río, Cuba. El promedio anual de precipitaciones en esta área es de 1600 mm, y las temperaturas promedio oscilan entre 23 y 25 °C (Díaz & Cádiz 2008). En este huerto de naranjos crecen naturalmente diferentes especies de epífitas vasculares, predominando *I. utricularioides*.

Unidad de muestreo —. Se identificaron todos los árboles de *C. sinensis* existentes en el huerto y se registró cuáles eran forófitos. En este estudio, el término forófito sólo se utiliza para los árboles de naranjo en los que crecía *I. utricularioides* (García-González & Pérez 2011). En cada forófitos se contaron todas las plantas de *I. utricularioides* y se anotaron las siguientes variables: altura y diámetro de la rama en la que crecían, micrositio que ocupaban (tronco, ramas o ramillas), clase de vida de las orquídeas (inmaduras o adultas), orientación cardinal de las plantas sobre el forófito y estado en el que crecían (solitarias o agregadas). En este estudio, el término forófito sólo se utiliza para los árboles de naranjo que tenían *I. utricularioides* (García-González & Pérez 2011).

Altura y DAP de los naranjos —. La altura (m) de todos los árboles de naranjo se estimó empleando una vara recta de madera, de 4 m de largo, graduada a intervalos de 50 cm (García-González *et al*. 2011). El DAP (diámetro a la altura del pecho, a 1.30 m de altura) (cm) se determinó midiendo la circunferencia (C) del tronco de todos los naranjos y luego aplicando a este valor la fórmula DAP= C / π. De forma similar se determinó la altura y diámetro de las ramas en las que crecían orquídeas.

Micrositios —. Se siguió la zonación vertical propuesta por García-González *et al*. (2011), para arbustos de café (*Coffea arabica* L.) y se elaboró un sistema propio para los árboles de naranjo (Fig. 1C), donde se eliminó el micrositio horquetas. Mediante observaciones previas al estudio se observó que en estos naranjos las horquetas eran pequeñas y estrechas, por lo que no presentaban características ecológicas (ej.: acumulación de materia orgánica, mayor presencia de musgos y líquenes) que las diferenciaran significativamente de las ramas.

- Tronco: de la base del árbol hasta el inicio de las ramas primarias.
- Ramas: ramas con circunferencia >3 cm.
- Ramillas: ramas delgadas con circunferencia <3 cm.

Clases de vida —. Siguiendo la clasificación de García-González *et al*. (2011), que reconocen tres estadios de vida (plántulas, juveniles, adultos), se desarrolló una versión propia para este estudio, donde las plantas de *I. utricularioides* se clasificaron solo en dos estadios de vida: inmaduras (I) y adultas (A). Todas las plantas de orquídea que presentaban indicios de floración actual o de años anteriores, fueron incluidas en A, las restantes en I.

Orientación en el forófito —. Mediante cuatro tramos de cuerda de 2 m, que fueron colocados en el suelo en forma de cruz, teniendo como punto central el tronco

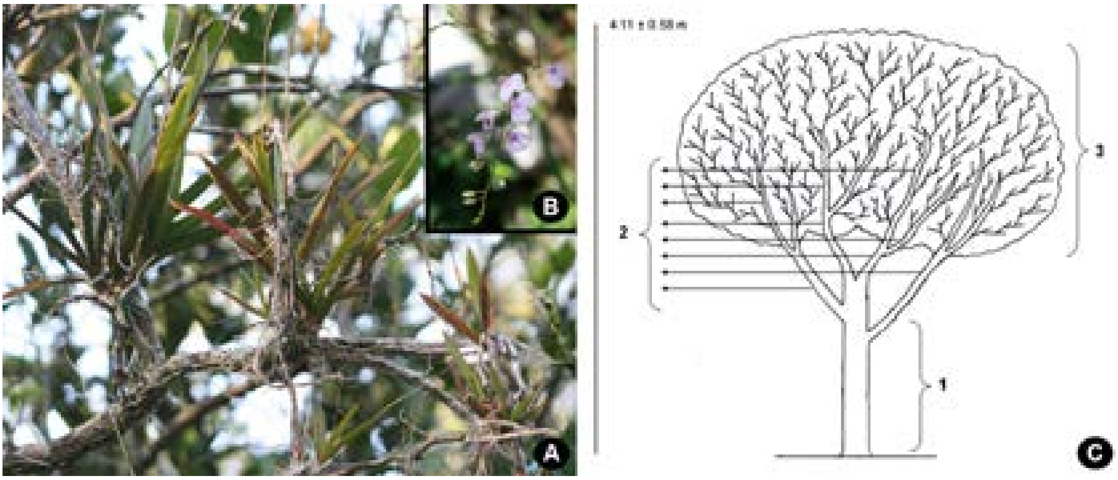


Figura 1. *Ionopsis utricularioides* (Sw.) Lindl.; A — plantas en árboles de naranjo; B — flores; C — zonación vertical de los árboles de naranjo: Micrositio 1: tronco; Micrositio 2: ramas; Micrositio 3: ramillas (ilustración: Alfredo García-González).

de los naranjos, y empleando una brújula, se determinó la posición en que se encontraba ubicada cada orquídea en el forófito: norte (N), sur (S), este (E), oeste (O), noroeste (NO), noreste (NE), sureste (SE) y suroeste (SO).

Estado de las orquídeas (solitarias o agregadas) —. Las plantas de *I. utricularioides* se dividieron en dos grupos, según lo planteado por Mujica (2007) y González *et al.* (2007) para *Broughtonia cubensis* (Lindl.) Cogn:

- Plantas agregadas: Aquéllas que están en un radio de 10 cm o menos de otro individuo de *I. utricularioides* o de otras especies de epífitas vasculares.
- Plantas solitarias: Aquéllas que están en un radio mayor de 10 cm de otro individuo de *I. utricularioides*, de otras especies de epífitas vasculares, o habitando en solitario en un forófito.

Análisis estadísticos —. Utilizando el programa StatXact-4 (Versión 4.0.1), se hizo una comparación entre las frecuencias de aparición por medio de una prueba de Montecarlo. Este algoritmo se empleó en el caso de las variables: número de orquídeas en cada micrositio, número de orquídeas creciendo agregadas y creciendo solitarias, y número de orquídeas que crecían agregadas con otras plantas de su misma especies y las agregadas con otras especies de epífitas vasculares. Se utilizaron los programas Oriana (Versión 1.01) para la prueba de Uniformidad Circular de Rayleigh, y SPSS 15.0 para hacer gráficos de frecuencias con las categorías de altura (Bajo: 1.28-2.28 m, Medio: 2.29-3.28 m, Alto: 3.29-4.16 m) y con las categorías de diámetro (Muy finas: 0.06-0.47 cm, Medianamente finas: 0.48-0.79 cm, Finas: 0.8-2.8 cm) en las que se encontraron las plantas de *I. utricularioides* en cada forófito. Los datos de altura y de diámetro se dividieron equitativamente en tres categorías, teniendo en cuenta los mínimos y máximos donde se localizaron orquídeas en cada forófito. Se aplicaron como estadísticos descriptivos la media y la desviación estándar.

Resultados

Organización espacial —. Se evaluaron un total de 10 árboles para detectar la presencia de la orquídea. Estos árboles tienen una altura promedio de 4.11 ± 0.58 m, y un DAP promedio de 10.92 ± 1.74 cm (Tabla 1). Se identificaron ocho forófitos en los que se contabilizaron 217 plantas de *I. utricularioides* (Tabla 1). La mayor parte de las orquídeas se encontraron en la categoría “Medio” de altura (2.29-3.28 m) (Fig. 2), y en la categoría “Muy finas” de diámetro (0.06-0.47 cm) (Fig. 3).

Micrositios, clases de vida, orientación y estado de las orquídeas—. En el tronco no se encontró creciendo ninguna planta de *I. utricularioides*. En las ramas se localizó 1.38 % de las orquídeas

Tabla 1. Árboles de naranjo estudiados, altura y diámetro a la altura del pecho (DAP) de cada uno, número de plantas de *Ionopsis utricularioides* en cada forófito, micrositio donde se encuentran creciendo las orquídeas en cada forófito (tronco, ramas o ramillas) y estadio de vida de cada planta de orquídea (I: inmaduras o A: adultas).

Árbol	Altura (m)	DAP (cm)	No. de orquídeas	Tronco	Ramas	Ramillas	Orquídeas por estadios de vida	
							I	A
1	3.7	8.59	15	0	0	15	2	13
2	4.2	10.82	2	0	0	2	0	2
3	4.15	10.03	2	0	0	2	0	2
4	4.4	10.82	9	0	0	9	0	9
5	4.35	12.1	13	0	0	13	2	11
6	4	12.1	102	0	3	99	55	47
7	4.2	12.42	33	0	0	33	10	23
8	4.6	11.46	0	0	0	0	0	0
9	4.8	13.21	41	0	0	41	22	19
10	2.7	7.64	0	0	0	0	0	0
Total	----	----	217	0	3	214	91	126
Promedio	4.11 ± 0.58	10.92 ± 1.74	----	----	----	----	----	----

contabilizadas y en las ramillas 98.61 % (Tabla 1), lo cual implica diferencias muy significativas entre ellos (Montecarlo, p< 0.001).

El número de plantas de *I. utricularioides* entre ambas clases de vida no presenta diferencias significativas (Montecarlo, p= 0.231), siendo relativamente abundante en las dos clases (I: 41.9 %; A: 58.1 %) (Tabla 1). No hay una marcada preferencia de *I. utricularioides* por ninguna orientación en particular (Uniformidad Circular de Rayleigh, p= 0.75), aunque

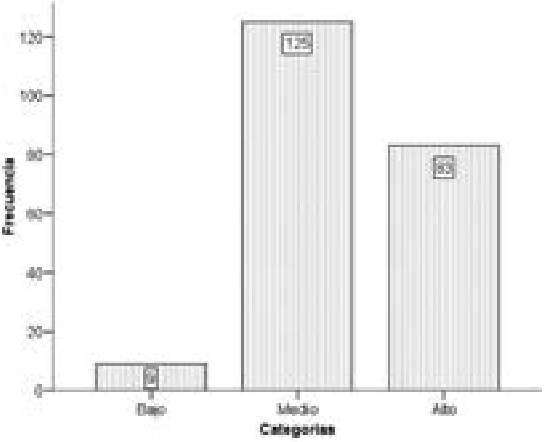


Figura 2. Categorías de altura en las que se encontraron las plantas de *Ionopsis utricularioides* en cada forófito (Bajo: 1.28-2.28 m, Medio: 2.29-3.28 m, Alto: 3.29-4.16 m) y número de plantas en cada categoría.

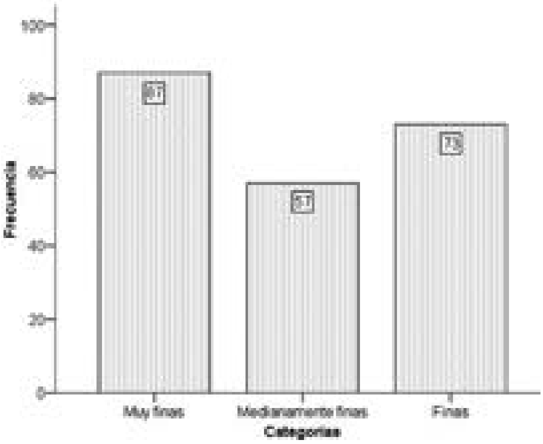


Figura 3. Categorías de diámetro en las que se encontraron las plantas de *Ionopsis utricularioides* en cada forófito (Muy finas: 0.06-0.47 cm, Medianamente finas: 0.48-0.79 cm, Finas: 0.8-2.8 cm) y número de plantas en cada categoría.

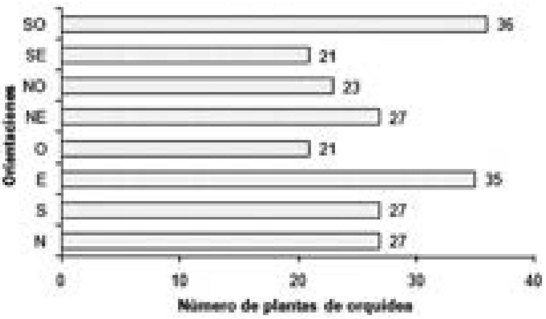


Figura 4. Orientación de *Ionopsis utricularioides* en los forófitos (N: norte, S: sur, E: este, O: oeste, NE: noreste, NO: noroeste, SE: sureste, SO: suroeste).

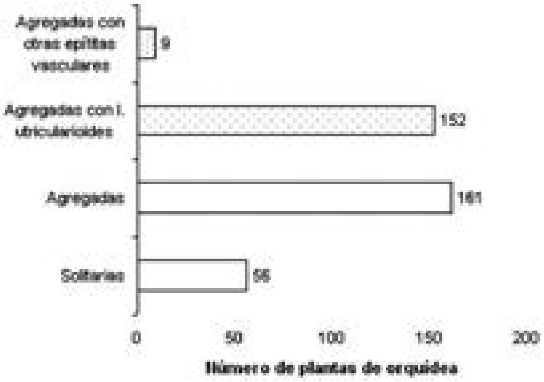


Figura 5. Estado en el que se encuentran creciendo las plantas de *Ionopsis utricularioides* (solitarias o agregadas) y especies con las que se encuentran agregadas (con otras *I. utricularioides* o con otras epífitas vasculares).

las orientaciones con mayor número de plantas fueron E (16.1 %) y SO (16.6 %) (Fig. 4).

Gran parte de las plantas de *I. utricularioides* se encontraron creciendo en agregación (74.2 %), con otras orquídeas de la misma especie o con otras especies de epífitas vasculares (Fig. 5), existiendo diferencias significativas entre el número de plantas creciendo agregadas y las que crecían solitarias (Montecarlo, $p < 0.001$). También existen diferencias significativas entre las plantas creciendo agregadas con *I. utricularioides* (94.4 %) y las agregadas con otras especies de epífitas vasculares (5.6 %) (Montecarlo, $p < 0.001$). Las orquídeas que crecen agregadas tienen como promedio 2.93 ± 1.87 plantas en un radio de 10 cm. Sólo se encontraron otras dos especies de epífitas vasculares en agregación con *I. utricularioides*, estas son: *Tillandsia flexuosa* Sw. (siete plantas) y *Tillandsia recurvata* (L.) L. (dos plantas).

Discusión. Se conoce poco acerca de la especificidad de hospederos en las orquídeas (Walter 1991. Tremblay *et al*. 1998. Llamacho & Larramendi 2005. Trapnell & Hamrick 2006. Mujica *et al*. 2010), aunque se sabe que algunas especies de árboles como *Citrus* spp., son especialmente buenos hospederos para determinadas especies de orquídeas (Walter 1991, Llamacho & Larramendi 2005).

Pese a ser *C. sinensis* una especie exótica en Cuba (ACTAF 2011), en este estudio es el único forófito en que se localizó *I. utricularioides*, aunque se hicieron varios recorridos exploratorios en los parches remanentes de bosque existentes en los alrededores de la población de orquídeas estudiada. No obstante, en este sitio *C. sinensis* es generalista, siendo capaz de albergar otras especies de epífitas vasculares, específicamente del género *Tillandsia*, aunque *I. utricularioides* es predominante. Solo se localizó otra población de *I. utricularioides* en cuatro árboles de naranjo (*C. sinensis*) en una huerta abandonada, aproximadamente a 3 km de la población analizada. Es muy probable que de estas orquídeas se haya originado la población estudiada, debido a que están relativamente cerca, estos árboles de naranjo (*C. sinensis*) eran antiguos y muchas de las *I. utricularioides* que los ocupaban eran de mayor tamaño y aparentemente de mayor edad que las de la población estudiada.

Luego de que las semillas de orquídea llegan a un sustrato, su germinación y posterior establecimiento depende de muchos factores bióticos y abióticos (Trapnell & Hamrick 2006). La preferencia de *I. utricularioides* por *C. sinensis* puede estar asociada a la arquitectura, porte y características de la corteza (Ter Steege & Cornelissen 1989; González *et al*. 2007), su composición química (González *et al*. 2007, Mujica *et al*. 2010) y la estructura de su cobertura de copa, ramificación, tamaño y disposición de las hojas (Benzing 1979). *Citrus sinensis* presenta una estructura de copa poco densa y con abundancia de ramas finas. Otro factor que probablemente tenga gran influencia en la selección de sustrato de *I. utricularioides* es la posible presencia del o los hongos micorrícicos con los que se asocia esta especie de orquídea para germinar y desarrollarse (Walter 1991, Otero *et al.* 2004, Trapnell & Hamrick 2006, Mujica 2007, Otero *et al.* 2007, Mujica *et al.* 2010, Raventós *et al.* 2011).

Esta última afirmación requiere estudios más enfocados para determinar la posible presencia de hongos micorrícicos en el caso específico *C. sinensis-I. utricularioides* y determinar con cuales se relaciona esta especie de orquídea en este forófito. Otero *et al*. (2004) y Otero *et al.* (2007), plantean que *I. utricularioides* generalmente se asocia y es más eficaz en la explotación de un efectivo clado de hongos filogenéticamente estrecho, pertenecientes a los *Ceratobasidium* D.P. Rogers. Estos hongos tienen una amplia distribución, y su asociación con *I. utricularioides* puede explicar en parte la amplia distribución geográfica y la abundancia de esta especie de orquídea (distribución geográfica y la abundancia de esta especie de orquídea (Otero *et al*. 2004, Otero *et al.* 2007).

De los 10 árboles de naranjo estudiados, dos de igual porte, edad y bajo las mismas condiciones que los ocho restantes, se encontraban totalmente desprovistos de orquídeas (Tabla 1). Esto puede estar ocasionado por circunstancias aleatorias en la dispersión de las semillas de *I. utricularioides* por el viento, pero es factible que en el futuro cercano estos naranjos también sean colonizados. Es muy probable que el primer forófito colonizado, a partir del cual comenzó la expansión, haya sido el árbol número 6, que es el que cuenta con el mayor número de orquídeas de forma general (Tabla 1) y el mayor número de orquídeas, tanto inmaduras como adultas (Tabla 1). Las orquídeas adultas de este forófito también son las más grandes y desarrolladas.

Se pueden encontrar plantas de *I. utricularioides* a lo largo y ancho de la copa de los naranjos, pero manteniéndose generalmente en las ramas finas y expuestas de los árboles (Fig. 2 y Fig. 3), con una marcada ausencia de orquídeas en el tronco, escases en las ramas y abundancia en las ramillas (Tabla 1). Esta distribución probablemente esté relacionada con lo planteado por Johansson (1974) y Krömer *et al*. (2007), cuando afirman que las epífitas vasculares tienden a mostrar patrones de distribución vertical en sus forófitos que reflejan su rango de tolerancia a la luz, la humedad y otras adaptaciones ecofisiológicas. La preferencia de *I. utricularioides* por las ramillas probablemente se encuentra estrechamente relacionado con la mayor intensidad luminosa en este micrositio.

En estudios análogos desarrollados en cafetales de sombra en el Soconusco, Chiapas, México, con *Oncidium poikilostalix* (Kraenzl.) M.W. Chase & N.H. Williams, una orquídea con porte y características ecológicas similares a *I. utricularioides*, el micrositio preferido por la especie fue las ramas (García-González et al. 2011). En este caso la preferencia puede ser consecuencia de las prácticas agroculturales que se le hacen a la plantación de café (*Coffea arabica* L.), donde el extremo de las ramas se poda periódicamente, perdiéndose gran parte de las ramillas, eliminando con ellas las plantas que las ocupaban y limitando la disponibilidad de este microhábitat (García-González *et al.* 2011).

Las preferencias de micrositio y las adaptaciones morfológicas que muestra *I. utricularioides*, como ser plantas de porte pequeño a mediano (Ackerman 1995, Mujica *et al.* 2000), tener hojas con cutículas muy gruesas para conservar el agua en los tejidos (Hágsater *et al.* 2005) y, en comparación con otras especies de orquídeas, tener raíces numerosas, delgadas, largas y morfológicamente adecuadas para curvarse y formar un entramado alrededor de los soportes finos (Ackerman 1995, Mujica *et al.* 2000), concuerdan con las características típicas de las llamadas orquídeas de ramilla (Hágsater *et al.* 2005), lo que coincide con lo planteado por Ackerman (1995). No está del todo claro como estas orquídeas obtienen los nutrientes que necesitan y algunos autores sugieren que pueden ser parcialmente parásitas de sus árboles hospederos (Ruinen 1953). Frecuentemente crecen en ramillas muertas o poco vigorosas, pero no existe evidencias de que obtengan nutrientes de sus hospederos (Hágsater *et al.* 2005). De la biología de este tipo de orquídeas aún se desconocen muchos aspectos, planteándose por ejemplo que florecen a muy temprana edad (unos meses o un año después de germinar) y que tienen tiempos generacionales muy cortos (de 1-5 años), siendo un fenómeno muy raro entre las plantas epífitas, que suelen ser muy longevas (Hágsater *et al.* 2005).

Dentro del microhábitat ramillas también se pueden apreciar pequeñas diferencias de ubicación entre las alturas a las que se encontraron las orquídeas y entre los diámetros donde crecen (Fig. 2 y Fig. 3). La categoría “Muy finas” de diámetro (0.06-0.47 cm) está acorde con las características de las orquídeas de ramilla, pero manteniendo esta preferencia, crecen más fácilmente en la categoría “Medio” de altura (2.29-3.28 m), donde cuentan con las condiciones para las que están adaptadas y al mismo tiempo están más protegidas que en la categoría "Alto" (3.29-4.16 m).

La relativa abundancia de *I. utricularioides* tanto adultas, como inmaduras (Tabla 1), indica una población equilibrada, con una saludable tasa de reclutamiento y recambio. Las plantas inmaduras garantizan el relevo de las posibles bajas que ocurren de forma natural (Mujica 2007). La predominancia de orquídeas adultas (Tabla 1) refleja una población establecida y madura, con abundancia de plantas reproductoras, que garantizan en gran medida el mantenimiento y la expansión de la especie hacia nuevos nichos no ocupados, siendo la etapa adulta la más importante de la vida de las orquídeas (Zotz 1998; Winkler & Hietz 2001; García-Soriano 2003; Mondragón 2009). No obstante, es conveniente profundizar en los estudios reproductivos de esta especie, para lograr obtener datos cuantitativos relativos a su tasa de floración, polinización, germinación y mortalidad en este sitio, que permitan apreciar exactamente el estado actual de la población y su posible comportamiento y permanencia en el futuro.

Ionopsis utricularioides no muestra ninguna preferencia de orientación cardinal en el forófito (Fig. 4). Probablemente en este caso las plantas germinen y se establezcan indistintamente en cualquiera de las orientaciones donde sean depositadas las semillas por el viento y encuentren las condiciones adecuadas, siendo más susceptible esta especie de orquídea a la influencia de factores como la luz y el grosor de la rama. El mayor número de plantas en las orientaciones E y SO (Fig. 4) puede ser completamente aleatorio, por lo que la diferencias no son significativas en comparación con el resto de las orientaciones (Fig. 4). No obstante, la ubicación de las orquídeas en una u otra orientación probablemente también pueda estar determinada por la dirección y velocidad predominante de los vientos del área (González *et al*. 2007), las necesidades particulares de luz y humedad de esta especie y la orientación de los sitios donde se encuentran las plantas en los forófitos, en relación con los demás árboles que los rodean (Mujica 2007). Por ejemplo, Tremblay y Velázquez (2009), en el Bosque Nacional El Yunque, en Puerto Rico, encontraron que la orquídea *Lepanthes eltoroensis* Stimson si manifiesta preferencia por crecer en el lado noroeste de los troncos de los árboles que ocupa, probablemente a consecuencia de los constantes vientos que suben del mar Caribe, con más frecuencia por barrancos ubicados al sudeste del área, principalmente vientos del este y del noreste.

Al igual que ocurre con *I. utricularioides*, González *et al.* (2007) y Raventós *et al.* (2011) reportan que en el Parque Nacional Guanahacabibes, Cuba, es más frecuente encontrar a *B. cubensis* creciendo en parches o en agregación, fenómeno habitual en muchas especies de orquídeas epífitas (Ackerman 1995; Tremblay 1997). También similar a *I. utricularioides*, *B. cubensis* se agrega más comúnmente con plantas de su misma especie, pero a continuación los vecinos más usuales fueron cuatro especies de orquídeas, aunque esta agregación interespecífica es rara (González *et al*. 2007).

El micrositio principal que ocupa *I. utricularioides* en los forófitos (Tabla 1), probablemente esté directamente relacionado con que la especie potencie el patrón agregado por encima del patrón solitario (Fig. 5). Aunque como plantea González *et al*. (2007), es posible que entre las *I. utricularioides* que crecen agregadas se establezcan relaciones de competencia intraespecífica o de competencia interespecífica con las especies de *Tillandsia*, y que esto sea una de las fuerzas que condicionan la estructura y dinámica de la población, es probable que luego de eliminar el exceso de competidores, se establezca un equilibrio beneficioso entre las plantas agregadas sobrevivientes. Generalmente las ramillas es el microhábitat con menor disponibilidad de recursos para la orquídea (Chase 1987. Brown 1990. Gravendeel *et al*. 2004. Hágsater *et al.* 2005, Mondragón *et al.* 2007), por lo que las plantas de *I. utricularioides* que crecen agregadas con otras de la misma especie o con otras especies de epífitas vasculares, forman entramados de raíces que pueden funcionar como cestas, brindándoles a estas orquídeas mayores ventajas competitivas y mayores posibilidades de supervivencia, al ser capaces de retener mejor la humedad y acumular mayor cantidad de materia orgánica y partículas de polvo.

Por otro lado, dado que las ramillas es la porción más delgada de los árboles, con altos niveles de perturbación e inestabilidad (Chase 1987, Brown 1990, Gravendeel *et al*. 2004, Hágsater *et al.* 2005, Mondragón *et al.* 2007), las acumulaciones de raíces también pueden ayudar a las plantas que crecen agregadas a permanecer ancladas al soporte y por tanto, a perdurar. En éste microhábitat, para *I.*

utricularioides, representa una ventaja tener el mayor número posible de raíces, extenderlas alrededor de la propia ramilla y de las ramillas vecinas, y formar entramados con las raíces de las epífitas con las que crece agregada, logrando un anclaje firme frente a tempestades, fuertes vientos o si se seca y quiebra su ramilla. Es muy frecuente observar *I. utricularioides* solitarias o grupos de éstas, que perdieron su ramilla y se sostienen colgando de sus entramados de raíces que se extienden a otras ramillas. Generalmente en estos casos los grupos de *I. utricularioides* se sostienen más firmemente, mientras las plantas solitarias se aprecian con un anclaje más endeble y más propensas a caer al suelo y morir.

Agradecimientos. Agradecemos a la familia García, propietarios de la finca “La Juanita”, por el apoyo brindado en la realización de este estudio. Al Lic. Yoeslandy García Marsilio por su importante colaboración en el trabajo de campo. Al Dr. Dennis Denis Ávila, por sus valiosos conocimientos, puestos en función de este estudio. A la organización IDEA WILD por el equipamiento proporcionado, fundamental para la realización de este trabajo. A los dos revisores anónimos que tuvieron a su cargo la corrección del manuscrito original, por su tiempo y dedicación.

Literatura Citada

Acevedo-Rodríguez, P. & M.T . Strong. 2012. Catalogue of seed plants of the West Indies. Smithsonian Contributions to Botany. Number 98. Smithsonian Institution Scholarly Press, Washington D.C.

Ackerman, J. D. 1995. An orchid flora of Puerto Rico and the Virgin Islands. The New York Botanical Garden, Memoirs 73. Nueva York, E.U.

ACTAF (Asociación Cubana de Técnicos Agrícolas y Forestales). 2011. Instructivo técnico para el cultivo de los cítricos. Biblioteca ACTAF. Instituto de Investigaciones en Fruticultura Tropical (IIFT), Cuba. Ministerio de la Agricultura (MINAGRI), Cuba.

Benzing, D. H. 1979. Alternative interpretations for the evidence that certain orchids and bromeliads act as shoot parasites. Selbyana 5: 135-144.

Brown, A. D. 1990. El epifitismo en las selvas montanas del Parque Nacional “El Rey”, Argentina: composición florística y patrón de distribución. Rev. Biol. Trop. 38: 155-166.

Chase, M. W. 1987. Obligate twig epiphytism in the Oncidiinae and other Neotropical orchids. Selbyana 10: 24-30.

Díaz, M. A. 1999. Orquídeas cubanas: Pasado, presente y futuro. Seminario Mesoamericano de Orquideología y Conservación. Universidad de Costa Rica, San José, Costa Rica.

Díaz, L. M. & A. Cádiz. 2008. Guía taxonómica de los anfibios de Cuba. Figura 3 (Regiones climáticas de Cuba). Volumen 4. Abc Taxa. Belgian Development Cooperation.

FNA (Flora of North America). 2008. *Ionopsis utricularioides* (Swartz) Lindley. Orchidaceae. Vol. 26: 646-647. (Consultado: 20 de julio de 2011, http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=116467).

García-González, A., A. Damon., L. G. Esparza & J. Valle-Mora. 2011. Population structure of *Oncidium poikilostalix* (Orchidaceae), in coffee plantations in Soconusco, Chiapas, México. Lankesteriana 11: 23-32.

García-González, A. & R. Pérez. 2011. La comunidad orquideológica en la Reserva de la Biosfera Sierra del Rosario, Cuba. Rev. Biol. Trop. 59: 1805-1812.

García-Soriano, R. 2003. Demografía, manejo y conservación de *Artorima erubescens* en Oaxaca, orquídea endémica del sur de México. Tesis en opción al grado científico de Master en Ciencias. Universidad Autónoma de Yucatán, Mérida, México.

González, E., J. Raventós, E. Mújica & A. Bonet. 2007. Estructura y ecología de la población del endemismo cubano *Broughtonia cubensis* (Orchidaceae), en Cabo San Antonio, Península de Guanahacabibes, provincia de Pinar del Río, Cuba. Lankesteriana 7: 469-478.

Gravendeel, B., A. Smithson, F. J. W. Slik & A. Schuiteman. 2004. Epiphytism and pollinator specialization: drivers for orchid diversity?. Phil. Trans. R. Soc. Lond. B.

Hágsater, E., M. Soto, G. Salazar, R. Jiménez, M. López & R. Dressler. 2005. Las orquídeas de México. Productos Farmacéuticos, S.A. de C.V. Instituto Chinoin. México D.F., México.

Johansson, D. 1974. Ecology of vascular epiphytes in West African Rain Forest. Acta Phytogeogr. Suecica 59:1-129.

Krömer, T., M. Kessler & S. R. Gradstein. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol. 189: 261-278.

Llamacho, J. A. & J. A. Larramendi. 2005. Las orquídeas de Cuba. Greta, Sevilla, España.

Mondragón D. 2009. Population viability analysis for *Guarianthe aurantiaca*, an ornamental epiphytic orchid harvested in Southeast México. 24: 35-41.

Mondragón, D., C. Maldonado & R. Aguilar-Santelises. 2007. Life history and demography of a twig epiphyte: A case study of *Erycina crista-galli* (Orchidaceae). Selbyana 28: 137-144.

Mujica, E. 2007. Ecología de las orquídeas epífitas *Broughtonia cubensis* (Lindley) Cogniaux, *Dendrophylax lindenii* (Lindley) Bentham et Rolfe y *Encyclia bocourtii* Mújica et Pupulin en el Cabo San Antonio, Península de Guanahacabibes, Cuba. Análisis espacio-temporal e implicaciones del impacto de un fenómeno atmosférico severo. Tesis en opción al grado científico de Doctor en Ciencias. Universidad de Alicante, España.

Mujica, E., J. Raventós & E. González. 2010. Análisis de la selección de sustrato por parte de *Dendrophylax lindenii* (Orchidaceae) en Cabo San Antonio, Península de Guanahacabibes, Pinar del Río, Cuba. Lankesteriana 9: 533-540.

Mujica, E., R. Pérez, J. L. Bocourt, P. J. López & T. M. Ramos. 2000. Géneros de orquídeas cubanas. Felix Varela, La Habana, Cuba.

Otero, J. T., J. D. Ackerman & P. Bayman. 2004. Differences in mycorrhizal preferences between two tropical orchids. Molecular Ecology 13: 2393-2404.

Otero, J. T., N. S. Flanagan, A. E. Herre, J. D. Ackerman & P. Bayman. 2007. Widespread mycorrhizal specificity correlates to mycorrhizal function in the neotropical, epiphytic orchid *Ionopsis utricularioides* (Orchidaceae). American Journal of Botany 94: 1944-1950.

Raventós, J., E. Mujica, T. Wiegand & A. Bonet. 2011. Analyzing the spatial structure of *Broughtonia cubensis* (Orchidaceae) populations in the dry forests of Guanahacabibes, Cuba. Biotropica 43: 173-182.

Ruinen, J. 1953. Epiphytosis. A second view on epiphytism. Annales Bogorienses 1: 101-157.

Ter Steege, H. & J. H. C. Cornelissen. 1989. Distribution and Ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21: 331-339.

Trapnell, D. W. & J. L. Hamrick. 2006. Variety of Phorophyte species colonized by the neotropical epiphyte, *Laelia rubescens* (Orchidaceae). Selbyana 27: 60-64.

Tremblay, R. L. 1997. Distribution and dispersion patterns of individuals of nine species of *Lepanthes* (Orchidaceae). Biotropica 29: 38-45.

Tremblay, R. L. & J. Velazquez. 2009. Circular distribution of an epiphytic herb on trees in subtropical rain forest. Tropical Ecology 50: 211-217.

Tremblay, R. L., J. K. Zimmerman, L. Lebrón, P. Bayman, I. Sastre, F. Axelrod & J. Alers-García. 1998. Host specificity and low reproductive success in the rare endemic Puerto Rico orchid *Lepanthes caritensis*. Biological Conservation 85: 297-304.

Walter, D. S. 1991. Orchidaceae. En: Janzen, D.H. (edit.). Historia natural de Costa Rica. Editorial de la Universidad de Costa Rica.

Winkler, E. & P. Hietz. 2001. Population of three epiphytic orchids (*Lycaste aromatica*, *Jacquiniella leucomelana*, and *J. teretifolia*) in a Mexican humid montane forest. Selbyana 22: 27-33.

Zotz, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata*. J. Trop. Ecol. 14: 725-741.

Zotz, G. & G. Schmidt. 2006. Population decline in the epiphytic orchid *Aspasia principissa*. Biol. Conserv. 129: 82-90.

Zotz, G. & P. Hietz. 2001. The ecophysiology of vascular epiphytes: current knowledge, open questions. J. Exper. Bot. 52: 2067-2078.

LANKESTERIANA 13(3): 429–430. 2014.

REVIEWERS OF THE MANUSCRIPTS SUBMITTED TO LANKESTERIANA, VOL. 13

The Editor-in-Chief, Managing Editor, Editorial Committee, Editorial Board and Editorial staff of LANKESTERIANA acknowledge the reviewers listed below for their willing cooperation. It is greatly appreciated that they have generously invested their time and competence in providing valuable comments and advice, for the benefits of the authors, the editorial staff, and the readers of LANKESTERIANA.

James D. ACKERMAN, Department of Biology and Center for Applied Tropical Ecology and Conservation, University of Puerto Rico, San Juan, PR, U.S.A.

Jesús AGUIRRE GUTIERREZ, Naturalis Biodiversity Center – NHN Leiden University, The Netherlands.

Rafael ARÉVALO BURBANO, University Of Wisconsin, Madison, U.S.A.

Cássio VAN DEN BERG, Univ. Estadual de Feira de Santana, Feira de Santana, Brazil.

Diego BOGARÍN, Lankester Botanical Garden, University of Costa Rica.

Ken CAMERON, University of Wisconsin, Madison, WI, U.S.A.

Germán CARNEVALI, Centro de Investigaciones Científicas de Yucatán, México.

Guy CHIRON, Herbiers, Claude Bernard University Lyon 1, France.

Benjamin COLLANTES MEZA, Inka Terra Association (ITA), Peru.

Phillip J. CRIBB, Royal Botanic Gardens, Kew, U.K.

Stig DALSTRÖM, Lankester Botanical Garden, University of Costa Rica, and National Biodiversity Centre, Serbithang, Bhutan.

Nicolas DAVIN, Naturalis Biodiversity Center – NHN Leiden University, The Netherlands.

Calaway DODSON, Missouri Botanical Garden, U.S.A.

Robert L. DRESSLER, Lankester Botanical Garden, University of Costa Rica.

Lorena ENDARA, Florida Museum of Natural History, University of Florida, U.S.A..

Melania FERNÁNDEZ, Lankester Botanical Garden, University of Costa Rica.

Günter GERLACH, Botanischer Garten München–Nymphenburg, Münich, Germany.

Barbara GRAVENDEEL, Naturalis Biodiversity Center – NHN Leiden University, The Netherlands.

Eric HÁGSATER, Herbario AMO, México D.F., México.

Wesley E. HIGGINS, The American Orchid Society, Coral Gables, U.S.A.

Luko HILJE, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Costa Rica.

Rudolf JENNY, Jany Renz Herbarium, University of Basel, Switzerland.

Rolando JIMÉNEZ, Herbario AMO, México D.F., México.

Carlyle A. LUER, Missouri Botanical Garden, U.S.A.

Ernesto MUJICA, Centro de Investigaciones y Servicios Ambientales ECOVIDA, Pinar del Rio, Cuba.

Carlos OSSENBACH, Orquideario 24 de mayo, Sabanillas de Montes de Oca, Costa Rica.

Joel Tupac OTERO OSPINA, Universidad Nacional de Colombia.

Alec M. PRIDGEON, Sainsbury Orchid Fellow, Royal Botanic Gardens, Kew, U.K.

Rafael RINCÓN, Herbario UCH, Universidad Autónoma de Chiriquí, Panama.

David A. ROBERTS, Durrell Institute of Conservation and Ecology, University of Kent, U.K.

Gustavo A. ROMERO–GONZÁLEZ, Harvard University Herbaria, Harvard University, Cambridge, Massachusetts, U.S.A.

Gerardo A. SALAZAR CHÁVEZ, Instituto de Biología, Universidad Nacional Autónoma de México.

Luis Sánchez Saldaña, Herbario AMO, México D.F., México.

Lisa Thoerle, The Orchid Digest, Laguna Niguel, CA, U.S.A.

Rodolfo Solano Gómez, Universidad Nacional Autónoma de México.

Raymond Tremblay, University of Puerto Rico – Río Piedras, PR, U.S.A.

Jorge Warner, Lankester Botanical Garden, University of Costa Rica.

W. Mark Whitten, Florida Museum of Natural History, University of Florida, U.S.A..