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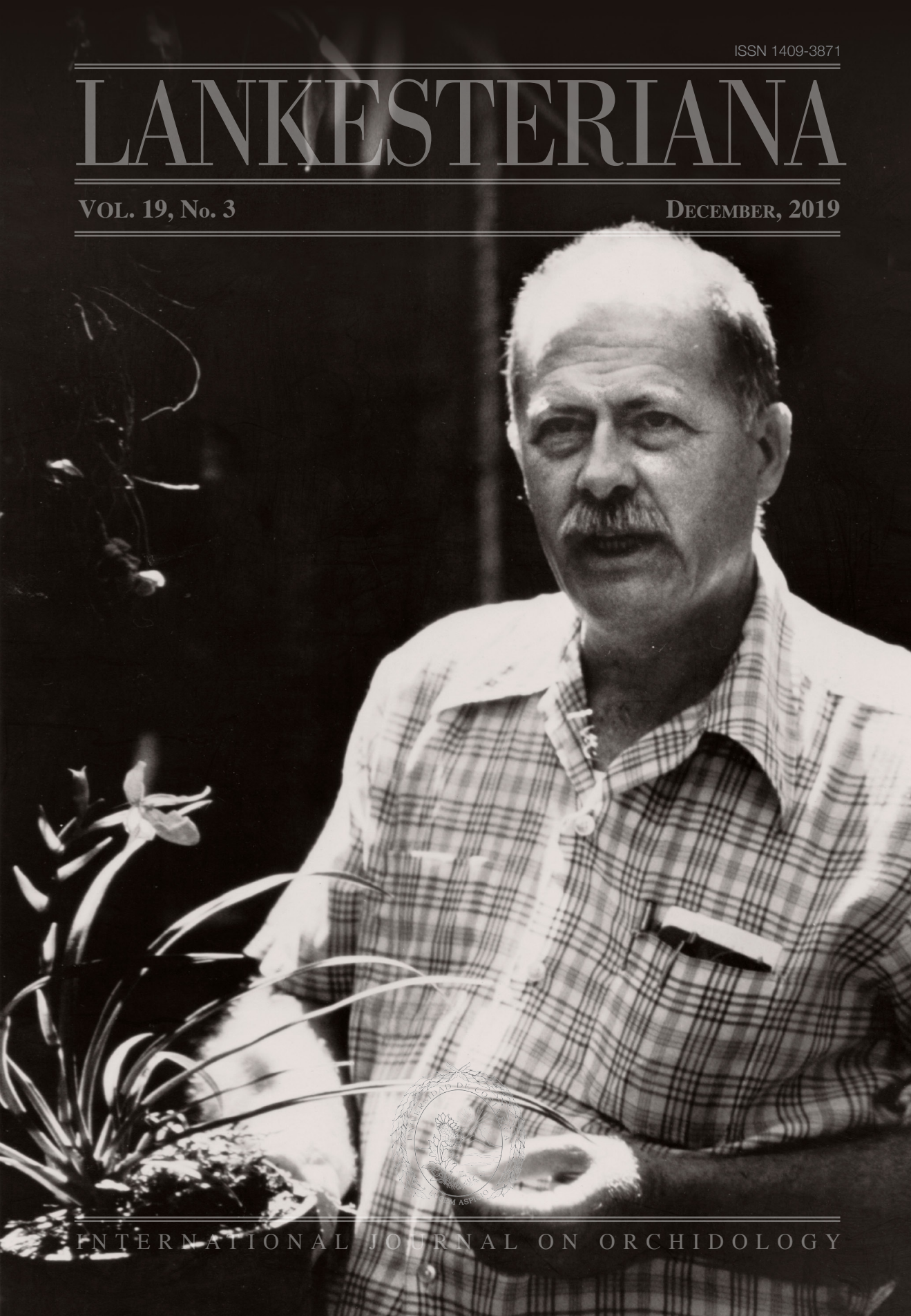

INTERNATIONAL JOURNAL ON ORCHIDOLOGY

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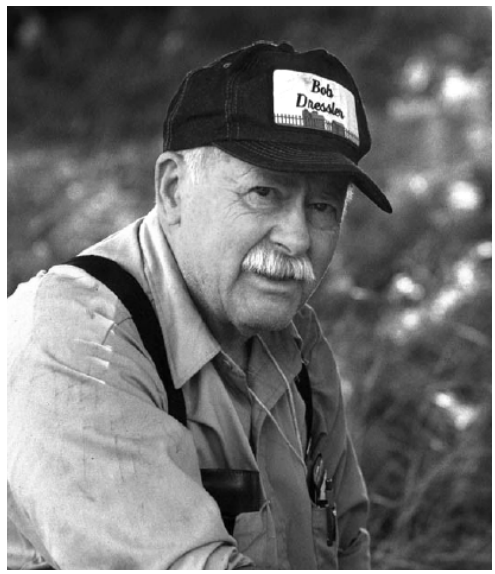

To the memory of our friend

Robert Louis Dressler

a giant in science
and a humble, perfect man

SAVE THE DATE

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LANKESTERIANA

INTERNATIONAL JOURNAL ON ORCHIDOLOGY

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LANKESTERIANA is worldwide distributed in over 350 national, university, and specialized libraries, and its webpage is visited by thousands of scientists and orchidologists yearly. References to the journal are found in virtually any scientific paper in orchidology published in the last decade, making the journal widely known.

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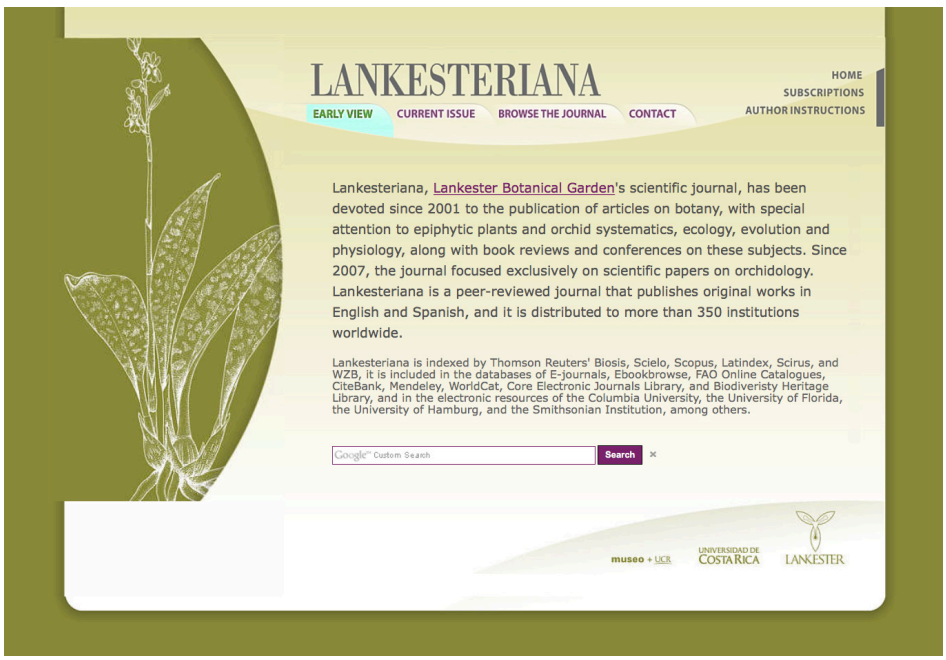

Originally devoted to the publication of articles on general botany, with special attention to epiphytic plants and orchid systematics, ecology, evolution and physiology, along with book reviews and conferences on these subjects, since 2007 LANKESTERIANA focuses exclusively on scientific orchidology.

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Through its Early view page, LANKESTERIANA is now committed to considerably shorten the times requested for effective publication of scientific, peer-reviewed papers. Papers in this section of LANKESTERIANA are published online as soon as the editorial process is concluded, and their effective date of publication is established by the date of the first publication online, recorded on the front page of each individual paper. They represent early views of the final papers exactly as they will be included in the hard-printed, complete issue of the journal.

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OBITUARY

ROBERT DRESSLER (1927–2019) – A BOTANIST FOR ALL SEASONS

In Monteverde, Costa Rica, ca. 1995. Photo by Kerry Dressler

In April of 2005, in the journal *Epidendrum* (one of the journals of Lankester Botanical Garden at that time), a small article was published, which I co-authored with Jorge Warner, then Director of the garden, under the title "*Bienvenidos, Dresslers*". Dr. Robert Louis Dressler (1927-2019), who is at this moment waiting peacefully for us on the other side of the river, had arrived in Costa Rica on March 11 of that year, to take over the position of Scientific Coordinator of the research staff of the garden. Ten years later, in 2015, Franco Pupulin, who was instrumental in bringing Dr. Dressler to the University of Costa Rica, called this *perhaps the most transcendental moment in the life of our botanical garden*.

And Franco continued: *from the point of view of our institution, the name of Dressler as a faculty member simply put us into the game. But from the point of view of the people who, like me, had the luck to learn, day by day, Bob's ideas and hypotheses, who had the fortune to go with him to the field as the best of the mates, to share with him endless talks and discussions about orchids and science, and men and life, to see him beginning his work early in the morning with willfulness, the inevitable cup of coffee and a smile, taking notes by hand of his daily observations in the little space left amid books and journals and notes in the middle of the less than perfect order of his office, to appreciate his simple and humble attitude in science and in friendship, it was an immense fortune to have him as the greatest of all possible companions*.

With Dressler on its staff, Lankester Botanical Garden became not only one of the most important centers on orchid research in our continente, but also a point of attraction to foreign botanists who would not miss the opportunity to discuss their projects with Dressler, and to accompany him on one of his numerous field trips. It is for me difficult to avoid the comparison and not to remember the words of Louis O. Williams, in his obituary for Charles H. Lankester in 1972: *Generous to a fault, hospitable to all, he was counselor to all scientists who came to Costa Rica*.

I am fortunate to have experienced his generosity from the first day I made contact with him. It must have been around 1997 -Dressler was living at that time in Florida- when I wrote to him asking for permission to use an illustration published in one of his articles. His reply came immediately: *You don't need my permission,*

feel free to use anything that I have ever published. Later, when I finally met him in person, he opened to me the few boxes with books and papers that he had brought with him from Florida, and let me make copies of documents which I will always cherish as witnesses of Dressler's long engagement with orchids, among them his correspondence with Ruth Oberg and Ed Greenwood in Mexico, and with Rafael Lucas Rodriguez in Costa Rica.

Robert Louis Dressler was born on June 2, 1927, and raised during the Great Depression in rural Taney County, Missouri. Taney County is in the Ozark Mountains, a fiercely independent but poor people. His father, Mryl, was an electrician who farmed 30 acres of rocky ground to put food on the table. While cutting wood in 1937, Myrl's electric saw kicked back and cut his arm, and he died four days later of a pulmonary embolism. So at the age of ten Bob (as he liked to be called) became the man of the family and helped to take care of his two younger sisters and mother. The family later moved to Inglewood, California, where his mother worked as a stenographer for an insurance company.

Bob developed a love of nature at an early age, handling snakes, asses, and old goats, which would give him valuable experience later in his professional life. He graduated from Gardena High School in Los Angeles, California, in 1945 and the following year served as a finance clerk in the U.S. Army. After that he attended the University of Southern California, where he was a member of Phi Beta Kappa Honor Society. He received his Bachelor of Arts degree in botany (*cum laude*) in 1951. Following that he went east to Harvard and received his Ph.D. in biology in 1957 with a dissertation on the genus *Pedilanthus* (Euphorbiaceae). His major professor was Reed Rollins, who co-founded the International Association of Plant Taxonomy and also the Organization for Tropical Studies.

From 1958 to 1963 he returned to his Missouri roots and used his systematics skills as editor of the *Annals of the Missouri Botanical Garden* while he was also Assistant Professor at Washington University (1961-1963) in St. Louis. His first taste of the Neotropics began in 1961 when he was hired on the staff of the Smithsonian Tropical Research Institute (STRI) in Panama, a position he held until 1990.

Robert Dressler in Harvard, 1957. Photographer unknown.

One of Bob's frequent companions in the field was Calaway Dodson, then professor at the University of Miami. Bob and Cal collaborated on numerous projects over the years. On a collecting trip to Panama in 1963, they met Martin Moynihan, who was a primate specialist and resident naturalist for the Smithsonian Institution's Tropical Field Station there. Moynihan mentioned he was looking for staff scientists, so Bob rushed to apply and was hired that same year at what would become known as the Smithsonian Tropical Research Institute.

Norris Williams first met Bob in Panama in 1965 while taking Owen Sexton's course in tropical ecology from Washington University. He became interested in the euglossine bees visiting orchid flowers and asked where he could learn more about them. Bob recommended Cal Dodson, but Cal was in Peru that year on a Fulbright scholarship, so Norris finished a master's degree at the University of Alabama, then applied for a predoctoral internship with Bob at STRI in Panama. He was the first of a host of students who moved into Bob's office, left for their doctorates and then returned with their own students. After completing his PhD, Norris would bring groups of students on

At Cerro Arizona, Panama. 1976.

field trips, and Bob would take them all over Panama. Among them were Jim Ackerman, John Atwood, Jim Folsom, Mark Whitten and Alec Pridgeon, all of whom went on to develop their own academic careers in orchids.

His wife Kerry aptly characterized Bob as like a spider at the center of his web while he worked at STRI. Sooner or later field biologists of all specialities and many nations would visit Panama to work with him, and they would all benefit from his field trips and knowledge.

Alec Pridgeon recalls: *I was one of those biologists, working on my Master of Science degree at Louisiana State University. Searching for a suitable topic for a master's thesis on orchids, I wrote to Bob at STRI in 1976 for ideas. He quickly responded that he suspected that the four species of Bothriochilus Lem. were closely related to the monospecific Coelia Lindl., separated only by the length of the spur, and perhaps ought to be combined. With specimens of the two genera supplied by Eric Hágsater of the Asociacion Mexicana de Orquideología, I then used chromosome counts, flavonoid chemistry analyses, scanning electron microscopy of pollinia, and studies in leaf anatomy to determine relationships. Three species of the two genera are virtually identical in all these aspects. On that basis Bothriochilus was moved to synonymy of Coelia, the earlier name. Nuclear and plastid DNA analyses by Cassio van den Berg 23 years later supported the monophyly of Coelia sensu lato. Bob had a gift for looking past phenotypic plasticity resulting from pollinator pressures and visualizing true genetic relationships. And he was happy to share that knowledge with a lowly master's student*.

During all these years Robert Dressler travelled incesantly through South and Central America, as well as to Mexico, where he enjoyed the hospitality of Eric Hágsater, whom he had met in Medellín, Colombia, in 1972. Eric recalls: *In the following 30 years or so, I would have the opportunity to travel with Bob into the field not only to many corners of Mexico, but also to Guatemala, to Panama, where Bob and Kerry lived, as well as to Costa Rica and Colombia on several occasions, often taking advantage of invitations to national orchid expositions and conferences*.

Bob was present at the inauguration of the new home of the Herbario AMO in Mexico City in January, 2002, where all Mexican orchid students gathered, both professionals and amateurs alike. It was Bob's style of guidance and open mind to share his knowledge and work with younger generations, with care in studying and annotating as much material as possible, and his extensive field experience set the basis for the style of the team work at the AMO herbarium that has subsisted until today.

With Kerry at Cerro Colorado, Panama, 1976.

In 2015, the Instituto de Biología of the Universidad Nacional Autónoma de México, the Asociación Mexicana de Orquideología, and the AMO Herbarium, joined to present a certificate of recognition to Robert Dressler for over four decades of support and sharing of his knowledge and friendship with the Mexican and world orchid community.

Kerry Radcliffe had worked as assistant to Dressler in the early 1970s, specializing in photography, and beginning a collection wich amounts presently around 25,000 pictures. In those years, Bob and Kerry spent a good deal of time in the field. One thing led inevitably to the other, and in 1977, they were married on his 50 birthday, June 2, 1977, at Marie Selby Botanical Gardens with Carl and Jane Luer as Best Man and Matron of Honor.

In 1984 Dora Emilia Mora de Retana, the Director of the Lankester Botanical Gardens in Cartago, Costa Rica, asked Bob to come up from Panamá and present a short course on classification of the orchids at the

Universidad de Costa Rica in San Jose. Bob and Kerry had been regular visitors to Costa Rica, collecting and collaborating with Costa Rican botanists like Rafael Lucas Rodriguez since Bob began working there in the early 1960s. He often attended local orchid shows as a guest judge and Dora Emilia had heard a presentation he had given and was excited at the prospect of him teaching a full semester in Costa Rica.

Bob spent one half of a sabbatical year in Costa Rica with his family and collected and photographed many Costa Rican species. The local orchid societies were always ready for a field trip and between those and his official course trips he covered much of the country. The idea of a field guide to the two countries he knew so well was already taking form and after retiring from STRI would lead to his book: *Field Guide to the Orchids of Costa Rica and Panama*, published by Cornell University Press in 1993.

Everywhere Dressler went he incorporated his findings into what became his first major book on the classification of the orchids. Many of the photographs taken on these trips were used in the volume which was printed and released by Harvard University Press in 1981, *The Orchids, Natural History and Classification* which has become a classic in orchid literature. Pridgeon commented on Dressler's work: *Today, after 20 years of extensive DNA sequencing around the world and discovery of a handful of true orchid fossils, we have a much firmer grasp of orchid relationships and evolution and now classify Orchidaceae into five subfamilies: Apostasioideae, Vanilloideae, Cypripedioideae, Orchidoideae and Epidendroideae. But it was Dressler's work in laying the foundation that now allows us to revel in all that we have learned in the last two decades*.

In his later years Bob was Courtesy Curator of the Florida Museum of Natural History, Associate of the Harvard University Herbaria, Senior Scientist at the Marie Selby Botanical Gardens, and Curator of the Missouri Botanical Garden, until he finally moved to Costa Rica in 2005.

Many other well-known botanists and orchid experts have expressed their opinión about Robert Dressler. At this point, let us have them come to word.

Norris Williams (Florida Museum of Natural History): *Bob Dressler is the best field botanist and field companion I have ever met. I have known him since 1965 when he inspired me to work with orchids, and I have never regretted it. He is generous with his time and knowledge, has a great sense of humor and is a true orchidophile. His books are great. I think the most important thing I can say about him is he is receptive to all new ideas, even if they contradict some of his earlier ideas. A truly inspiring botanist, a great friend and a wonderful person*.

Jim Ackermann (University of Puerto Rico): *I try to emulate Bob's approach to science with, I admit, varied success. Knowledge is fluid, fed by ideas, data and interpretation. All these change with time, and it is our task to evaluate new information on its merits and incorporate them in one's own world. And when new knowledge contradicts our own ideas, then we need to drop the ego, evaluate and incorporate when appropriate. Bob's classification systems were the best available for their times, and as new techniques and philosophical approaches suggested some alternative interpretations, Bob could have taken a defensive stance but instead embraced the brave new world*.

Raymond Tremblay (University of Puerto Rico): *Dr. Dressler's The Orchids: Natural History and Classification was a career inspiring book that guided my interest in biology and ultimately in trying to understand evolutionary processes in plants. I'm also grateful for his kind words and comments as a reviewer of my first submitted manuscript; his recommendations and encouragement increased my enthusiasm to continue publishing*.

Ken Cameron (University of Wisconsin, Madison): *It is fair to say that two books changed my life and pushed me forward into orchidology. the first was the Golden Guide to Orchids that I discovered around age eight. The second was Bob Dressler's The Orchids: Natural History and Classification, which I discovered a decade later in college as I considered a major in biology. His humility, scientific curiosity and encouragement of students was evident to me back in the 1990s when Mark Chase and I started using DNA data to understand evolutionary relationships among orchids. Bob's classification system was the hypothesis we were testing, and when patterns of relationships began showing up that challenged the Dressler system he was not defensive or ofended by these. Quite the contrary — he was excited by our results and encouraged us to keep going*.

With Kerry, Carl Luer and Jim Ackerman in the field. Panama, 1976.

With Franco and Elvira Salas at Tapantí. Costa Rica, 2003.

At Lankester Garden, ca. 2006.

With Friends in Colombia, 2015. Front row: Alec Pridgeon, Eric Hagsater, Franco Pupulin, Bob, Norris Williams. Back row: Ken Cameron, Raymond Tremblay, James Ackerman.

To continue and finish with Pupulin's memories of Dressler: *In the last ten years, we had in him a model of honesty, of happiness and unselfish generosity. We learned from him that study is a matter of love. Dr. Robert Louis Dressler taught us how to become better observers, better botanists, better scientists and professors. And he showed us, in his characteristic and straight way, how to be better people*.

Today, six academic generations of orchid researchers owe their careers in large part to Bob Dressler's imposing productivity and willingness to collaborate and share his vast knowledge. His hearty chuckle and modest demeanor invited approach by anyone who might otherwise be reticent to ask a question of such an extraordinarily brilliant scientist. Bob showed mastery of the Neotropical flora and fauna, but he has also shown all of us that nature and its preservation should be our highest priorities. As those who knew him will attest, he was clearly a biologist for all seasons, one who will live on in his respected publications and in our hearts.

A word of thanks:

To Franco Pupulin and Eric Hágsater for the fine words with which they described a truly fine man, and to Dr. Alec Pridgeon for his tribute to Robert Dressler, as published by the American Orchid Society in 2016. To all those others who shared with us their memories of Robert Dressler.

But above all to Kerry, for all the photographic material included in this text and for her loving remembrance of Bob Dressler, recently published in *Icones Orchidacearum*, from which the title of this epitaph has been borrowed. As the saying goes, behind every great man there is a great woman! Kerry, Bob was a fortunate man to have you on his side for so many years!

Carlos Ossenbach

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OBITUARY

CARLYLE A. LUER (1922–2019) - IN MEMORY OF A LEGEND, A TEACHER AND A FRIEND

Photo from Sarasota Scene Magazine

The first time I met Dr. Luer, as he was generally known in the orchid world, was on a dark and balmy night, November 6, 1981, at the Trailways bus station in Sarasota, Florida. He had invited me as a potential botanical illustrator to come by and visit the Marie Selby Botanical Gardens the next time I was heading towards South America. So here I was in a foreign country I had never visited before, dressed all wrong for the subtropical heat, dragging along too much luggage, which included a type writer, a fiddle and a black suit. I was on my way to spend a year in Ecuador after all and had no idea what to expect. When Dr. Luer saw all this he cracked up and laughed heartily. He then introduced himself as "Carl", grasped my hand in an iron grip and welcomed me to Florida. And "Carl" it was from there on. He had invited me to stay at his place during the visit, which I gladly accepted. But I almost had second thoughts when we arrived at his home. The dark wooden building was located in a dense patch of original forest and made me think of the residence of the Addams Family (a popular horror comedy TV series). But once inside, the warm welcome by Carl's wife and tireless travel companion Jane quickly changed my impression and I felt at home right away. There was "something" in the house that did not welcome me as warmly as the Luers though, and that was their hair-lipped and cock-eyed pet that Carl insisted was a "dog". This "dog" was a snarling and completely untrustworthy little creature named "Palenque", named after a river in Ecuador. The animal had some canine-looking features for sure but I had some serious doubts about the true identification. Carl loved Palenque though and the feelings were mutual.

The following day Carl introduced me to Selby Gardens and it was love at first sight, much thanks to Carl's efforts to introduce me to Calaway Dodson, the current Director of Research, and everybody else on the staff. Selby Gardens would not have existed as we know it today, if at all, without Carl's influence and he was very proud of what had become of the young institution, which opened its gates in 1975. This introduction was the beginning of a 38 year long friendship and professional collaboration. Carl had already established himself as a reputed orchid taxonomist, primarily based on his superb publications about the North American orchid flora. But his reputation as a Pleurothallid taxonomist was

also growing. The reason why he was focusing on this overwhelmingly large and confusing group of orchids was pure coincidental. Carl was a member of the Board of Trustees of Selby Gardens, but also a very active volunteer and generous donor. At one point Carl wanted to entertain his never resting mind and asked Dodson what he could do. Dodson might have felt slightly uneasy by having such a formidable work force, and a member of the Board of Trustees trotting around the premises without knowing what to do. He therefore suggested that Carl should work with pleurothallids. That ought to keep him busy, Dodson thought. Working with pleurothallids was not something that Dodson himself was particularly amused by so he could solve two issues with one suggestion that way. Little did he know what would happen next, and the rest is scientific history.

Carl was not the easiest individual to work with for several reasons. I suspect that the word "workaholic" may have originated from somebody who had worked for Carl. An unrelenting stubbornness and an almost inhuman determination to finish what he set out to do made him the perfect candidate to approach the intimidating task of pleurothallid taxonomy. Carl was also incredibly picky with getting the details just right, which meant his way. I had numerous experiences with running into this wall of rigidness over the years as my illustrations improved under the ever critical eyes of Carl. Every now and then I left his house muttering under my breath, having to re-draw certain details that had ended up a couple of millimeters towards the wrong side. But this also sharpened my focus and I could not have had a better teacher. The quest to please Carl drove me forward and when he nodded his approval without saying anything, I knew I had managed to please him. The greatest challenge came when he asked me if I wanted to do the watercolor illustrations for *Thesaurus Dracularum*, a monographic treatment of the genus with all species illustrated in actual size. I accepted of course, but with some trepidation. I had never done anything like that before and knowing how picky Carl was tied a considerable knot in my stomach. Traditionally, these types of illustrations are made without much "decorations", such as branches with moss etc. So the first volume of 16 species consisted of strictly clean illustrations, some of them rather stiff and inelegant in my retrospective opinion. But my

Carlyle Luer tending to orchid business at his beloved Selby Gardens in 1981. Photograph by Stig Dalström

artistic mind got bored pretty quickly so I decided to challenge Carl and added a few strains of moss on one of the roots just to see his reaction. When he spotted this "rebellious outbreak" of the traditional way of doing things he did not say a word. But after mulling things over for a while, his nose began to twitch and he eventually looked up and said that he liked it. From there on I always added something to the illustrations of both *Dracula* and later on *Masdevallia*, which made them a lot more fun to do.

I had the great fortune to spend some time with Carl in the field as well, both locally in the Everglades and in South America looking for new *Dracula* and *Masdevallia* species. My first field adventure together with Carl took place in Ecuador in 1982. It was a great but also rather scary experience because we joined forces with Father Angel Andreetta, the Salesian Missionary Priest who later developed the world-renown orchid nursery Ecuagenera together with the Portilla family. Though the company was impressive and perhaps a bit intimidating, both Carl's and Andreetta's driving skills were definitely hair-rising. But at least Carl did not try to hit the stray dogs, which were in deep jeopardy when Andreetta

Inspecting some of his pleurothallid collection, cultivated at Selby Gardens, 1981–1982. Photograph by Stig Dalström.

Carl and Stig Dasltröm in the field in Fakahatchee Strand State Preserve, *ca.* 1985. Photograph by Phillip Cribb.

Left, after a hair-rising journey through Ecuador, finally a couple of days resting at Rio Palenque Science Center, hosted by Calaway and Piedad Dodson, 1982. Right, Carl happily returning to the car with some Ecuadorean discoveries, 1984. Photographs by Stig Dalström.

Left, Carl and Jane Luer risking their lives pressing orchids on a busy Colombian highway, 1989. Right, Alan Guttridge of Coastal Printing (left), Carl Luer and Phillip Cribb analyzing some discarded sheets from *Thesaurus Dracularum*, 1989. Photographs by Stig Dalström.

Carl was like a schoolboy at summer camp when searching for orchids. Here with a *Dracula chimaera* in Colombia 1989. Photo by Stig Dalström.

was at the steering wheel. We survived though and eventually managed to find a few new *Masdevallia* species so the trip was quite successful in the end. The trip to Ecuador in 1984 was tough for different reasons. Carl got up before daylight every day and insisted that we should spend as much time in the field as possible, come rain (most of the time) or sunshine. In the late afternoons his "crew", consisting of Job Kuijt, a Canadian mistletoe expert, my Swedish travel companion Thomas Höijer and me were slumped in the car, exhausted, hungry and soaking wet. Carl on the other hand was standing outside pressing *Stelis* and other insignificant little orchids. He really enjoyed this, both because the "weaklings" were more tired than he was, but also because he usually had a number of unknown plants to work with. The rain did not bother him at all it seemed. All the collection information then went into a flimsy little notebook, which had the irreplaceable data from a number of previous field trips. One day disaster struck as he was fiddling with the ever growing herbarium press. He suddenly began looking stressed, frantically patted his pockets and started to look around. Obviously something was wrong so we had to ask what was happening. His note book was gone! With years of unique data! We all scrambled out of the car and into the twilight of the early evening. Then followed a thorough search where we had to take everything out of the car in a desperate search for this infinitesimal little note book. The panic was not far away from Carl's eyes when we finally located it under one of the seats. When I asked him why he brought the same little notebook to every trip instead of getting a separate one for each, he said that it would be a shame not to use every page.

Carl was an excellent illustrator himself and only reluctantly handed this task over to me. And the only reason to do so was because he could accomplish a lot more that way. But it bothered him to accept help from others and that created a conflict in him. He simply wanted to do everything himself and in his way. I believe that was one of the sources for his criticism and pickiness. But gradually he developed more confidence in my illustration skill and as long as he could cut them apart and re-arrange them anyway he wanted, he eventually (but grudgingly) accepted the situation. But I am sure he enjoyed this process as well, being a retired surgeon! I occasionally asked him how many drawings I had made over the years, but he had no idea. Thousands! The amazing thing is that I never got bored of doing them. The challenge of meeting Carl's expectations and critical scrutiny never ceased. The last delivery of finished *Stelis* drawings to be published in Harvard Papers in Botany was made just shortly before the tragic fall in the kitchen on October 8 when he injured his spine. Carl never recovered from this and his body gave up a month later after years of heroic battle against various physical health issues.

My last image of the great orchid legend, my teacher and friend, was Carl and Jane sitting in the living room sofa together, holding hands, with Carl watching a baseball game and Jane peacefully snoozing next to him.

Stig Dasltröm
Jardín Botánico Lankester, Universidad de Costa Rica and National Biodiversity Centre, Serbithang, Buthan
stigdalstrom@gmail.com

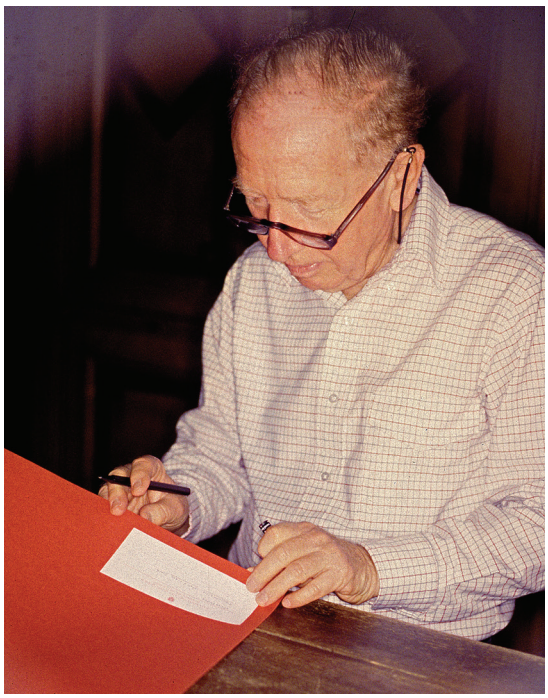
Carl and Thomas Höijer sorting the day's harvest of botanical treasures, 1984. Photo by Stig Dalström.

Some people are born to be legends, and there is no doubt that Carl Luer was one of those people. He ventured almost accidentally into the world of pleurothallids at a very late stage in his life, and, in what must be the worst case of a dare-gone-wrong in botanical history, at the time of his passing he had become the most prolific plant taxonomist of modern times.

Even though mostly known for his work on Neotropical epiphytes, Carl's interest in orchids began with terrestrials in his native North America. A surgeon by profession, Luer retired in the mid nineteen-seventies, and published around that same period his first two books on orchids; *The Native Orchids of Florida* (1972) and *The Native Orchids of the United States and Canada Excluding Florida* (1975). By that time he was already an active taxonomist. The first taxa that Carl Luer described were *Triphora craigheadii* Luer and *Triphora rickettii* Luer, both in 1966. He continued working on North American orchids for several years, publishing mostly new combinations, varieties and hybrids. It is not until 1975 that Luer publishes his first pleurothallids by the name of *Pleurothallis cypripedioides* Luer and *Pleurothallis quadriserrata* Luer, featured in his earliest Icones Pleurothallidinarum under the title "*Pleurothallis* of Ecuador (Orchidaceae)", in the inaugural issue of journal Selbyana. The rest, as they say, is history. Carl Luer's taxonomical career lasted over half a century, beginning with the publication of two *Triphora* Nutt. species in 1966, and ending with the description of *Stelis minima* Luer & Toscano on the 30th of June 2019. During those 53 years, this larger-than-life self-taught botanist published the astonishing amount of **5604 taxa** in the orchid family[1].

Luer is regarded by most of us as the father of the pleurothallids, the largest and most diverse group of orchids in the world. Despite initially publishing about three dozen North American terrestrial orchids, a species of *Epidendrum* L., an *Oncidium* Sw. and a

[1] The complete list of taxa can be sent upon request to the author.



Carl did not quit his taxonomic work until his body finally deserted him on November 9, 2019, at age 97. Photo by Stig Dalström

variety of *Encyclia* Hook., by the end of his career more than 99% of his proposed taxa belonged to subtribe Pleurothallidinae. When Carl arrived on the scene in 1975 there were only about 1650 accepted species in the subtribe, today well above five thousand three hundred species are recognized and the vast majority of this staggering increase results from his work. During the 44 years of what we believe is most appropriately termed the Luerian Era, pleurothallid research was completely revolutionized as interest in the group grew exponentially and novelties soared. Luer published dozens of skillfully crafted monographic treatments of the diverse genera, sections and subsections of the subtribe. It was Carl's surgical precision and methodological patience that resulted so fruitful. By systematically illustrating the details of every individual, carefully inspecting the type material, critically interpreting the protologues, scrutinizing the available literature and synthesizing his ideas, he was able to almost completely resolve the taxonomy of the most challenging group of orchids there is. His opera magna, a series by the name *Icones Pleurothallidinarum,* included 10 articles and 32 monographs. The "green books", as his monographs are popularly referred to, set the basis for every single

Carl with Adam Karremans at his home in Sarasota, Florida, February 2017. Photograph by Miriam Contreras.

The Luers together with Phillip Cribb. Photographer unknown.

study in the subtribe since their publication. Only in the Pleurothallidinae, Carl published 5568 taxa. Luer's greatest contribution to orchid science has most likely been the recognition of species diversity in this mammoth group, he single-handedly proposed **3271 new pleurothallid species**. He also published many new combinations (1968), subspecies (35), hybrids (11), and a form (1). Likewise, Carl set the foundations for systematic classification in the subtribe by describing dozens of new genera (74 in total), as well as subgenera (66), sections (57), subsections (20), and series (8). The remaining (57 names) were published invalidly or illegitimaly and were later republished by Luer..

Immortalized in his body of work, the name of Carlyle Luer will not be soon forgotten. He stands alone on the pinnacle of pleurothallid research, an exceptional position no one has nor will come close to in the near future. Unsurprisingly, many authors have acknowledged his impact on orchid science. Already in 1983, Dodson and Determann considered that his "contributions to the knowledge of the orchids have been outstanding", and that was before published his first monograph! To all of us fanatics of the Pleurothallidinae, his passing is a terrible and unsurmountable loss.

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Taxa Honoring Carlyle A. Luer

Acronia culpameae Luer
Andinia lueri S. Vieira-Uribe & Karremans
Brevilongium luerorum (Dodson) Christenson
Caluera Dodson & Determann
Caluera napoensis Szlach., Kolan. & Mystkowska
Caluera surinamensis Dodson & Determann
Caluera tavaresii Campacci & J.B.F.Silva
Caluera vulpina Dodson & Determann
Chondrorhyncha lueri Dodson & R. Vásquez
Chondrorhyncha luerorum R. Vásquez & Dodson
Comparettia luerae (Dodson) M.W. Chase & N.H. Williams
Cyclopogon luerorum Dodson
Cyrtochilum luerorum Dalström
Dendrophthora lueri Kuijt (Santalaceae)
Dichaea luerorum Dodson
Dipterostele lueri (Dodson & R. Vásquez) Garay & G.A. Romero
Dracontia lueriana Karremans
Dracula carlueri Hermans & P.J. Cribb
Dryadella lueriana Carnevali & G.A. Romero
Epidendrum lueri Dodson & Hágsater
Epidendrum luerorum Hágsater
Fernandezia luerorum Ormerod
Ixyophora luerorum (R. Vásquez & Dodson) P.A.Harding
Lepanthes luerorum B.T. Larsen
Liparis lueri Dodson
Lueranthos Szlach. & Marg.
Lueranthos vestigipetalus (Luer) Szlach. & Marg.
Luerella Braas
Luerella pelecaniceps (Luer) Braas
Macroclinium lueri Dodson & R. Vásquez
Masdevallia luerorum Bogarín, Oses & C.M. Sm.
Maxillaria lueri Dodson
Odontoglossum × luerorum Dalström & W.E. Higgins
Oncidium × lueroroides M.W. Chase & N.H. Williams
Oncidium lueri Dodson
Oncidium luerorum Dodson
Otoglossum luerorum (Dodson) M.W. Chase & N.H. Williams
Pabstiella lueriana Fraga & L. Kollmann
Platanthera × lueri P.M. Br.
Platystele carl-lueriana Karremans & Bogarín
Pleurothallis lueriana Karremans & Rodr.-Mart.
Pseudocymbidium lueri (Dodson) Szlach. & Sitko
Restrepiella lueri Pupulin & Bogarín
Rhinorchis luerorum Szlach. & Kolan.
Scelochilus luerae Dodson
Sigmatostalix × luerorum Nees
Sobralia luerorum Dodson
Solenocentrum lueri Dodson & R. Vásquez
Stelis dies-natalis Karremans & M. Díaz
Stelis heros Karremans
Stelis lueriana (Karremans) J.M.H.Shaw
Stelis luerii Karremans
Stellilabium lueri Dodson & R. Vásquez
Stenia lueriorum D.E. Benn. & Christenson
Telipogon lueri Dodson & D.E. Benn.
Zygostates luerorum Toscano & R. Vásquez

Luerela pelecaniceps, from the Lankester Botanical Garden living collection. Photograph by Lizbeth Oses.

Taxa honoring his wife Jane

Comparettia janeae (Dodson & R. Vásquez) M.W. Chase & N.H. Williams

Platystele jane-lueriana Karremans & Bogarín

Scelochilus janeae Dodson & R. Vásquez

Taxa honoring their son George

Myoxanthus georgei (Luer) Luer

Octomeria georgei Luer

Pleurothallis georgei Luer

[**APK**]

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RUDOLF SCHLECHTER'S SOUTH-AMERICAN ORCHIDS II. SCHLECHTER'S "NETWORK": BRAZIL (LA PLATA RIVER BASIN)*

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Abstract. As the second chapter of the series about Rudolf Schlechter's South-American Orchids, a background of the orchidological work by foreign and Brazilian orchidologists in southern Brazil is outlined, as well as the history of the most important botanical institutions in this region. In order to establish coherent geographical units, the institutions, botanists and collectors mentioned in this chapter are those whose main activity concentrated in the Brazilian part of the La Plata River Basin, or in other words, the Brazilian states including and southwards of Matto Grosso, Minas Gerais and Espirito Santo. The most important figures in Schlechter's Brazilian "network" are presented, with short biographical notes and description of their most important botanical exploits.

Key words: biography, history of botany, Orchidaceae, Brazil

Botany in Brazil at the turn of the 20th century. The development of a national botanical science in Brazil began with the foundation of the Rio de Janeiro Botanical Garden (JBRJ), created after the Portuguese Royal Family established itself in Brazil. It opened its doors to the public in 1808..

After periods of growth and others of complete neglect, botanical science in Brazil was given a renewed impulse by the new government after the military coup of 1889 overthrew the Empire of Brazil and established the first Brazilian Republic. Fundamental to this development was João Barbosa Rodrigues (1842–1909), who took over as Director of the Garden in 1890, a position he held until his death (Fig. 1).

During his term of almost 20 years, Barbosa Rodrigues propelled scientific research of the institution and he created the herbarium and the library, while also reorganizing the greenhouse, the nurseries and the Botanical Museum. Special attention was paid to the study of the Brazilian flora in its natural habitat. To this end, he created the position of *naturalista viajante* ('travelling naturalist') and improved the exchange with other scientific institutions. At the same time, and because of Barbosa Rodrigues' predilection for the Orchidaceae, the Botanical Garden of Rio de Janeiro became the most important orchid research center in tropical America. The main avenue of the garden, lined with rows of royal palms that in some cases date back to King *Dom João* in 1808, was restored under Barbosa Rodrigues' direction and is today one of the garden's main attractions (Fig. 2).

Dr. Antonio Pacheco Leâo (1872–1931) (Fig. 3) succeded Barbosa Rodriguez and directed the Botanical Garden of Rio from 1912 until his death in 1931: this was during the better part of Rudolf Schlechter's involvement with Brazilian orchids (Alves Machado 1964: 133).

Paulo Campos Porto and Rudolf Schlechter named the new orchid genus *Leaoa* in his honor, transferring *Hexadesmia monophylla* Rodr. and proposing the new combination *Leaoa monophylla* (Rodr.) Schlechter & Campos Porto [= *Scaphyglottis livida* (Lindl.) Schltr.] (Fig. 4).

Other botanists who would play an important role in the history of Brazilian orchidology began their careers through a direct or indirect relationship with the Garden. Paulo Campos Porto (1889–1961), grandson of Barbosa Rodrigues, and one of the main actors in our story, became a traveler naturalist of the Garden in 1914.

* Errata corrige. In the first chapter of this series: *I. Historical and bibliographical background* (Ossenbach & Jenny 2019), in page 129, an involuntary mistake was made. It was not Friedrich Kränzlin who worked in Heidelberg, but Ernst Hugo Heinrich Pfitzer (as correctly mentioned in page 125 of the same article). Thanks go to Bärbel Roth for calling this to our attention.

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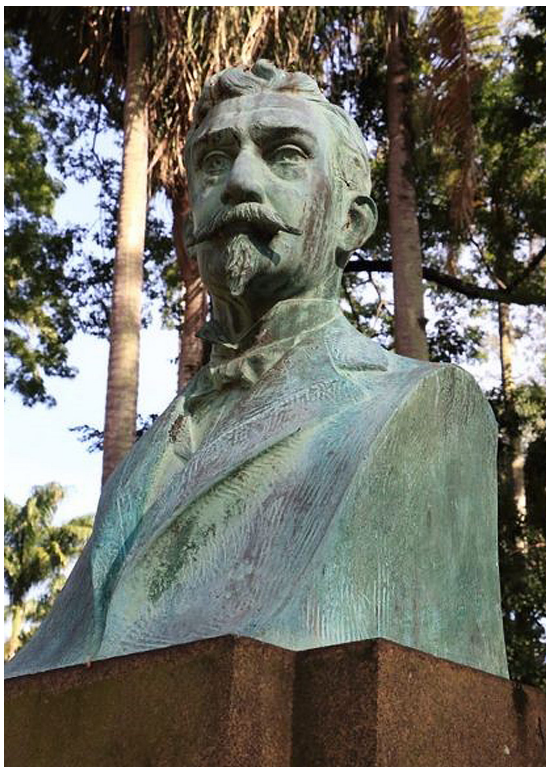


FIGURE 1. Bust of João Barbosa Rodrigues by Halley Pacheco de Oliveira, at the Botanical Garden in Rio de Janeiro.

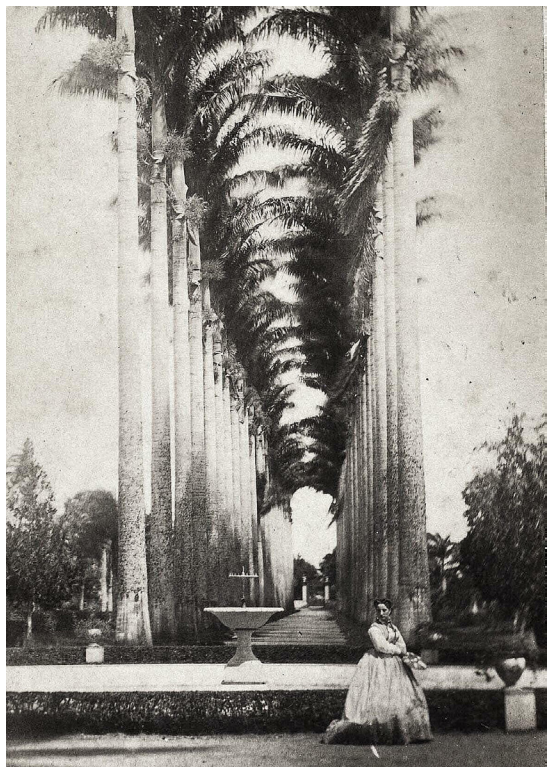


FIGURE 2. Avenue of Royal Palms at the Botanical Garden of Rio de Janeiro in 1860. Unknown photographer.

FIGURE 3. Antonio Pacheco Leâo. Unknown photographer.

FIGURE 4. *Leaoa monophylla* (as *Scaphyglottis livida*). Photograph by Eric Hunt.

Figure 5. Instituto Butantan, ca. 1903. Photograph by Werner Haberkorn.

Years later, in the periods between 1933 and 1938, and 1951 to 1958, he would occupy the same position as his grandfather: Director of the Botanical Garden.

Frederico Carlos Hoehne (1882–1959), a Brazilian botanist and ecologist of German origin, dedicated his life to the protection of nature in his country. In 1907 he became head gardener of the National Museum of Rio de Janeiro and from 1908 took part in several botanical expeditions through the interior of Brazil. Hoehne moved to São Paulo in 1917, where he became director of the Botanical Section of the Instituto Butantan. Established in 1901 in the district of Butantã, the Institute soon became one of the main scientific centers in Brazil (Fig. 5).

Although perhaps better known for its fundamental contributions to the development of antivenoms and medicines against many diseases, the botanical section of the Institute published a large number of new Brazilian orchid species in the *Anexos das Memórias do Instituto de Butantan*. Hoehne and Schlechter named *Habenaria butantanensis* (=*Habenaria balansae* Cogn.) (Fig. 6) and *Pleurothallis butantanensis* [=*Acianthera saundersiana* (Rchb.f.) Pridgeon & M.W. Chase] (Fig. 7) in honor of the Institute.

Finally, Alexander Curt Brade (1881–1971) moved from Costa Rica to Brazil in 1910. Because of his great interest in Brazilian orchids, he moved to Rio de Janeiro after World War I, where he worked at the Botanical Garden. He was appointed Acting Superintendent in 1934 and ultimately became Head of the Systemic Botany Department.

At the same time a number of private and public initiatives resulted in botanical expeditions to explore Brazil's immense territory. Knowledge about the flora of Brazil, including the Orchidaceae, grew rapidly. Worthy of note are the ethnographic expedition of Dr. Hermann Meyer to Mattogrosso, with the participation of Robert Pilger (1876–1953) as leading botanist, and the collecting journeys of the Swede Per Karl Haljmar Dusén (1855–1926) in Rio de Janeiro and its environs (1901–1904) and in the province of Paraná (1908–1916). Other contributors to Brazilian orchidology were private collectors and European nurseries who imported plants from Brazil. Many of these palnts were sent to the Botanical Garden and Museum in Berlin for determination.

When Schlechter was engaged by Robert Pilger to

FIGURE 6. *Habenaria butantanensis*. *Anexos das Memorias do Instituto Butantan*, Seccao de Botanica 1(2): pl. II.

determine his first Brazilian orchids, collected during the Meyer expedition to Mattogrosso, he probably was already aware of the immense richness of the Brazilian orchid flora. But even in his most optimistic moments he could not have dreamed that he would – over the next 25 years – describe a total of 13 new genera and over 350 new species.

In the following pages, as well as in future chapters referring to other South American countries, we will present short biographical notes of the most important botanists, plant collectors and orchid growers, a 'network' that over the years supplied Rudolf Schlechter with the material from which he made his most important discoveries. Some plant collectors have been left out, either because their contributions were of minor importance or because there is little information about their lives and work. Among the orchid growers,

FIGURE 7. *Pleurothallis butantanensis* (as *Acianthera saundersiana*). Photograph by Luis Filipe Varella.

only those will be presented who not only imported plants from Brazil but actually visited the country.

It should not surprise us that the majority of these botanists and collectors were German or of German origin. After the foundation of the Second German Reich in 1861 under Emperor Wilhelm I and his Chancellor Otto von Bismarck, imperial ambitions arose in Germany. The Reich acquired a group of colonies in Africa and the Pacific. The new colonies in Africa were German South West Africa (Namibia and parts of Botswana), German West Africa (Kamerun and Togo) and German East Africa (Tanganyika, Ruanda-Urundi and parts of Kenya and Mozambique). In Asia the Empire acquired the colonies that received the names of German New Guinea and German Samoa. German botanists – among them Rudolf Schlechter – took advantage of this situation and took part in scientific expeditions that were organized to explore the richness of the new lands.

On the other side of the Atlantic, a number of German colonies had been founded in Brazil in the second half of the 19th century. Worthy of mention are,Nova Friburgo, the earliest (established in 1824 in the state of Rio de Janeiro) (Fig 8A), Blumenau (establ. 1850 on the River Atajaí-Açu, state of Sta. Catharina) (Fig. 8B), Doña Franzisca (establ. 1851, state of Sta. Catharina), and Brusque (establ. in 1867 as Colônia Itajahy, state of Sta. Catharina). *Lepanthes blumenavii* Barb.Rodr. (Fig. 9A) and *Stenorrhynchos*

Figure 8. The German colonies of Novo Friburgo, ca. 1900 (A), and of Blumenau, ca. 1900. Unknown photographers.

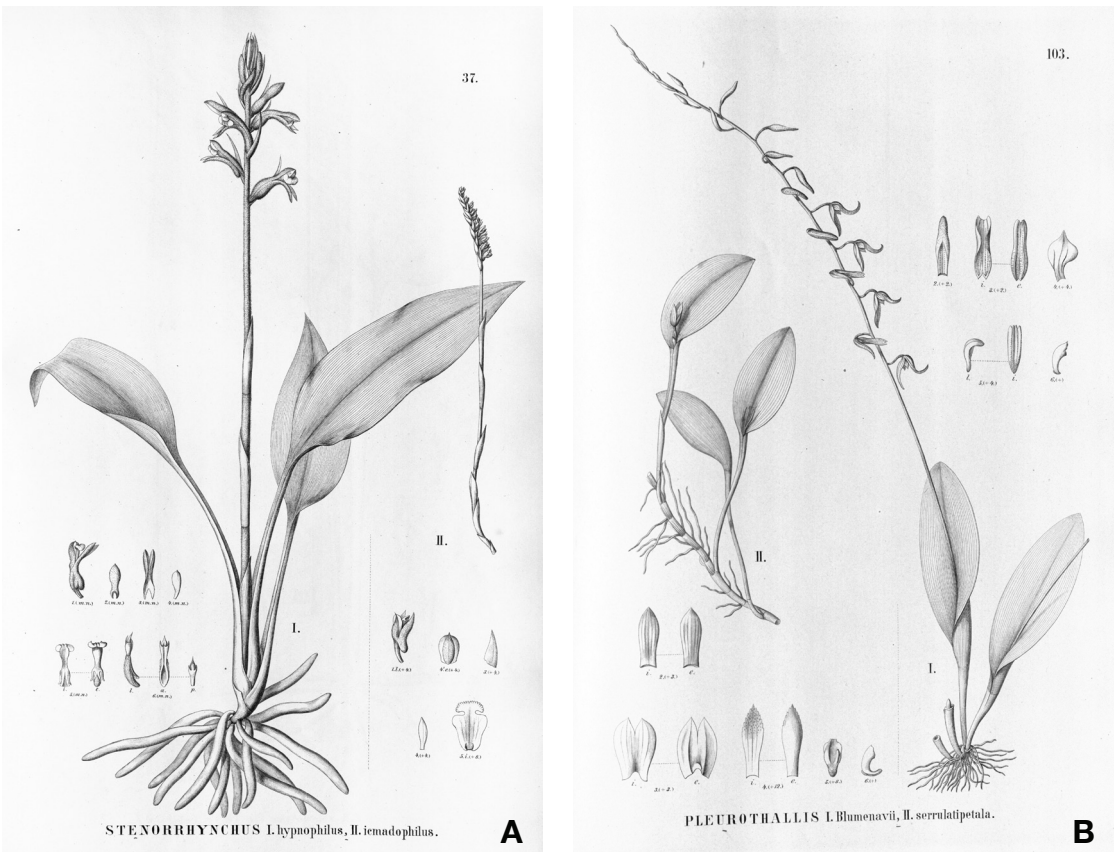


FIGURE 9. A. *Stenorrhynchos novofriburgensis* Rchb.f. (as *S. hypnophylum*). B. *Lepanthes blumenavii* In Martius, Eichler & Urban, *Flora brasiliensis*, 1896, 3(4), plates 37 and 103, respectively

FIGURE 10. German colony of Neu-Württemberg in 1903. Photograph by W. Schaefer. *In* Neumann, 2018.

novofriburgensis (Barb.Rodr.) Barb.Rodr. (Fig. 9B) were dedicated to the two former colonies. Neu-Württemberg (Fig. 10) was founded in 1899 by the German Hermann Meyer in the state of Rio Grande do Sul and directed between 1903 and 1907 by his cousin Alfred Julius Bornmüller.

These colonies often became the destination of German botanists and plant collectors and are frequently named as localities of collection for numerous orchid species. It is therefore easy to understand –if for no other reason than national affinity- that during the first decades of the 20th century, Rudolf Schlechter received from German botanists visiting Brazil or residents of the country of German origin the largest collections of specimens of Orchidaceae to be determined. In addition, it must be repeated that after Schlechter's return from his long expeditions to Africa and South East Asia he had already earned a reputation as one of the world's leading orchidologists.

For the purposes of this chapter, we have divided the immense Brazilian territory into three large regions, corresponding approximately to the basin of the Rio de la Plata, the Amazon River basin, and the so-called Northeast region (territories along the Atlantic coast, between the state of Espirito Santo and the mouth of the Amazon). The first two of these were explored by an important number of naturalists; the third, however, was largely neglected.

The La Plata River basin. Draining approximately 17 percent of the surface area of the South American continent,-comprising almost all the southern part of Brazil, the south-eastern part of Bolivia, a large part of Uruguay, the whole of Paraguay and an extensive part of northern Argentina- into the South-western Atlantic Ocean, the la Plata River system (Fig. 11) is one of the most important river basins of the world.

The La Plata basin rivals the better-known Amazon River system in terms of its biological and habitat diversity and is formed by three large river systems: the Paraná, the Paraguay and the Uruguay.

In its Brazilian portion, the La Plata Basin extends through the states of Rio Grande do Sul, Santa Catharina, Parana, Sâo Paulo, Rio de Janeiro, Espirito Santo, the southern regions of Minas Gerais, Goias and Matto Grosso, and Matto Grosso do Sul.

A dozen – mostly German, or German-Brazilian –

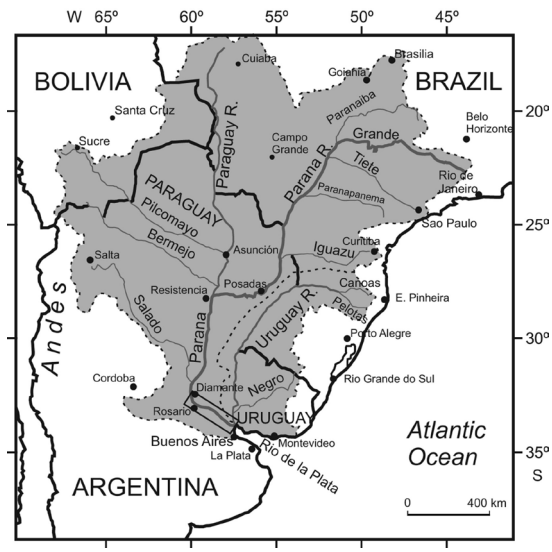


Figure 11. The La Plata River Basin.

explorers began arriving in the southern states of Brazil in the 1880s. They would become the most important source of new orchids that would be described some years later by R. Schlechter. The Swede Per Karl Halmar Dusen and the Brazilians Paulo Campos Porto and João Dutra would be the only non-Germans (from origin or language) in Schlechter's Brazilian network.

Johann Heinrich Rudolf Schenck (1860–1927; collected 1886–1887)

A German botanist, native of the city of Siegen, Johann Heinrich Rudolf Schenck (Fig. 12) was a brother of the well-known geographer Adolf Schenck. He began studying natural sciences at the University of Bonn and then continued his studies in Berlin under August Wilhelm Eichler and Simon Schwendener. He would later return to Bonn as a student of Eduard Strasburger, receiving his doctorate in 1884. In 1886–87 he accompanied Andreas Franz Wilhelm Schimper (1856–1901) on a scientific expedition to Brazil. After his return to Germany, he became a lecturer in Bonn, before being appointed director of the botanical garden at the Polytechnic Institute of Darmstadt in 1896. A few years later, between 1908 and 1909, he traveled to Mexico making important botanical collections. With George Karsten (1863–1937), he was co-author of the botanical journal *Vegetationsbilder* (Images of nature) (Karsten & Schenck 1904).

FIGURE 12. Johann Heinrich Rudolf Schenck. Unknown photographer. Library of the Botanical Garden of the University of Padua, Italy.

Figure 13. *Habenaria schenckii*. In Hoehne, *Flora Brasilica*, Fig. 1, 1940 (first from the left).

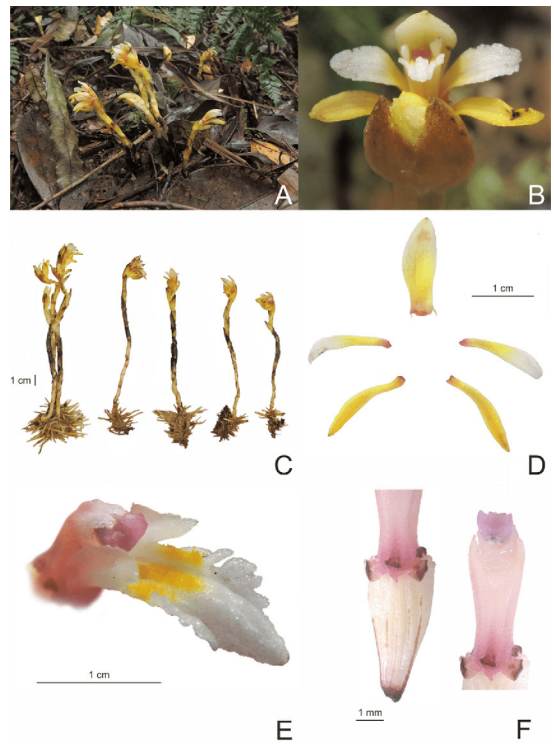


Figure 14. *Pogoniopsis schenckii.* Photographs and composite illustration by Felipe Brittencourt.

On their excursion to the tropics, Schimper and Schenck could not at first decide wether to go to Brazil or Cameroon. Considering the dangers of the expedition, Schimper – citing Grisebach – wrote to Schenck in 1885: "How general the perniciousness of climate may be follows from the fact that by far most scientific travellers in the most diverse landscapes become carried away with the experience, but in the tropical lands, almost without exception, well-known scientists are happy to return home. To die for science is, to be sure, no less 'dulce et decorum' than 'pro patria mori', but I wish not merely by my death, but also by my work, to earn a name for myself in the history of science*"* (Cittadino 1990: 104). One understands that a decision was made to travel to Brazil.

The day before their departure, Schimper wrote to Daniel Coit Gilman, President of Johns Hopkins University: "I shall leave Bonn tomorrow for a short trip to Brazil. My leave of absence being a short one, I shall not be able to spent more than three or four months in the great South American Empire, the richest country in the world for a botanist" (Cittadino 1990: 105).

Schimper and Schenck left for Brazil in August 1886, arriving in September at the house of Fritz Müller in the German colony of Blumenau in the state of Santa Catharina, on Brazil's southeastern coast. Müller, an expatriate naturalist, had been living in Brazil since 1852 and was one of the earliest German proponents of Darwinism. Schimper returned to Germany in mid-December, but Schenck stayed behind and visited a number of sites in Brazil before he too returned in July of 1887. It was Schenck's first and only excursion to the humid tropics.

In the *Flora Brasiliensis* of Martius, Engler and Urban (1896), Cogniaux mentions dozens of specimens of Orchidaceae collected by Schenck during his excursions with Schimper.From Schenck's collections in Brazil, Cogniaux described and named in his honor *Habenaria schenckii* (Fig. 13), *Pogoniopsis schenckii* (Fig. 14) and *Cryptophoranthus schenckii* Cogn. [= *Zootrophion atropurpureum* (Lindl.) Luer]. In addition, Schlechter described and dedicated to him *Stelis schenckii* Schltr. (Fig. 15).

Schenck was known for his co-authorship, together

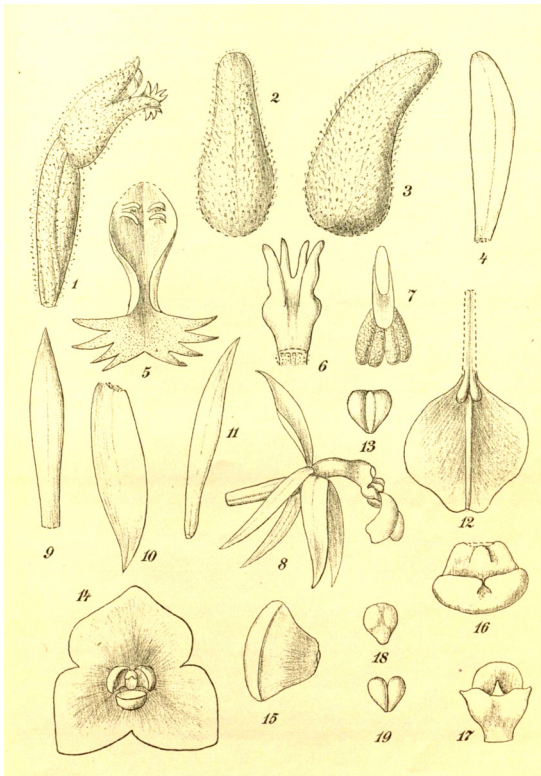


FIGURE 15. *Stelis schenckii* (14 through 19) and *Epidendrum goebeli* (6 through 13). In *Orchis* 9(6): plate 1.

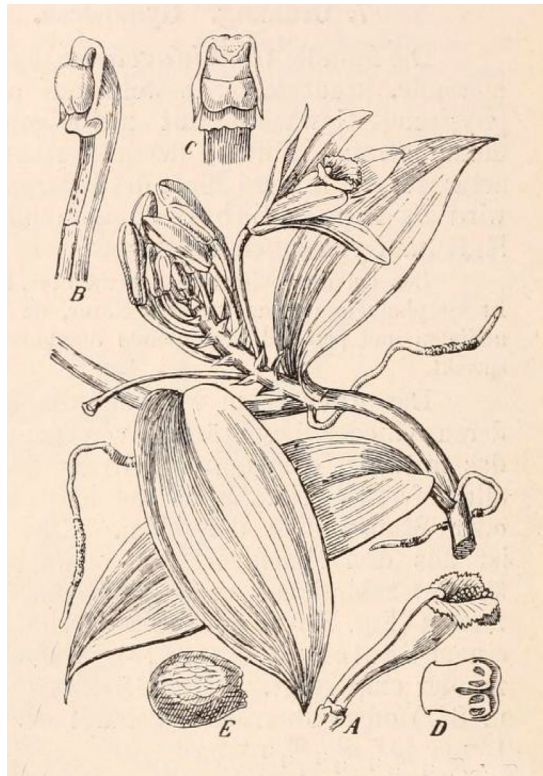


FIGURE 16. *Vanilla planifolia*. Fig. 843 *in* Strasburger, Schenck, Jost & Karsten, 1934.

with Ludwig Jost and Georg Karsten, of Eduard Strasbruger's *Lehrbuch der Botanik für Hochschulen* (*Text Book of Botany for High Schools*), published in1894, that was used until the second half of the 20th century. When Schenck died in 1927 the book was in its 16th edition. One of its illustrations was of *Vanilla planifolia* (Fig. 16).

KARL IMMANUEL EBERHARD RITTER VOON GOEBEL (1855–1932; collected 1890–91, 1913)

A German botanist whose main fields of study were comparative functional anatomy, morphology, and the developmental physiology of plants, Karl Immanuel Eberhard Ritter von Goebel (Fig. 17) began in 1873 studies of theology and philosophy at the University of Tübingen. It was the start of a brilliant career, which brought him to Strasbourg in 1876 to work with Anton de Bary. He took his Ph.D. from the university there in 1877. After three years of lecturing at the University of Würzburg, Goebel returned to Strasbourg in 1881 and went to Rostock in 1882, where he founded the botanical garden and a botanical institute. He moved again, this time to the University of Marburg as professor (1887–1891). He finally settled in Munich, where he would spend the rest of his life (Bower 1933).

While at the University of Munich, Goebel founded the Botanical Garden in Münich-Nymphenburg and served as its first director (Fig. 18).

Goebel was editor of *Flora* – the scientific botanical journal with the longest uninterrupted publication sequence (since 1818) – from 1889 onwards. In 1892 he became a member, and was later elected President, of the Bavarian Academy of Sciences; he was also elected a member of the Royal Society of Edinburgh, the Royal Society of London and the Accademia Nazional dei Lincei in Rome. In 1931 he was awarded the Linnean Medal of the Linnean Society of London.

Karl von Goebel undertook his first research trip to Ceylon and Java in 1885-1886, before going to South America for the first time in 1890-1891, where he explored Venezuela and then British Guiana. Years later, in 1913, he went on a holiday to Brazil in the company

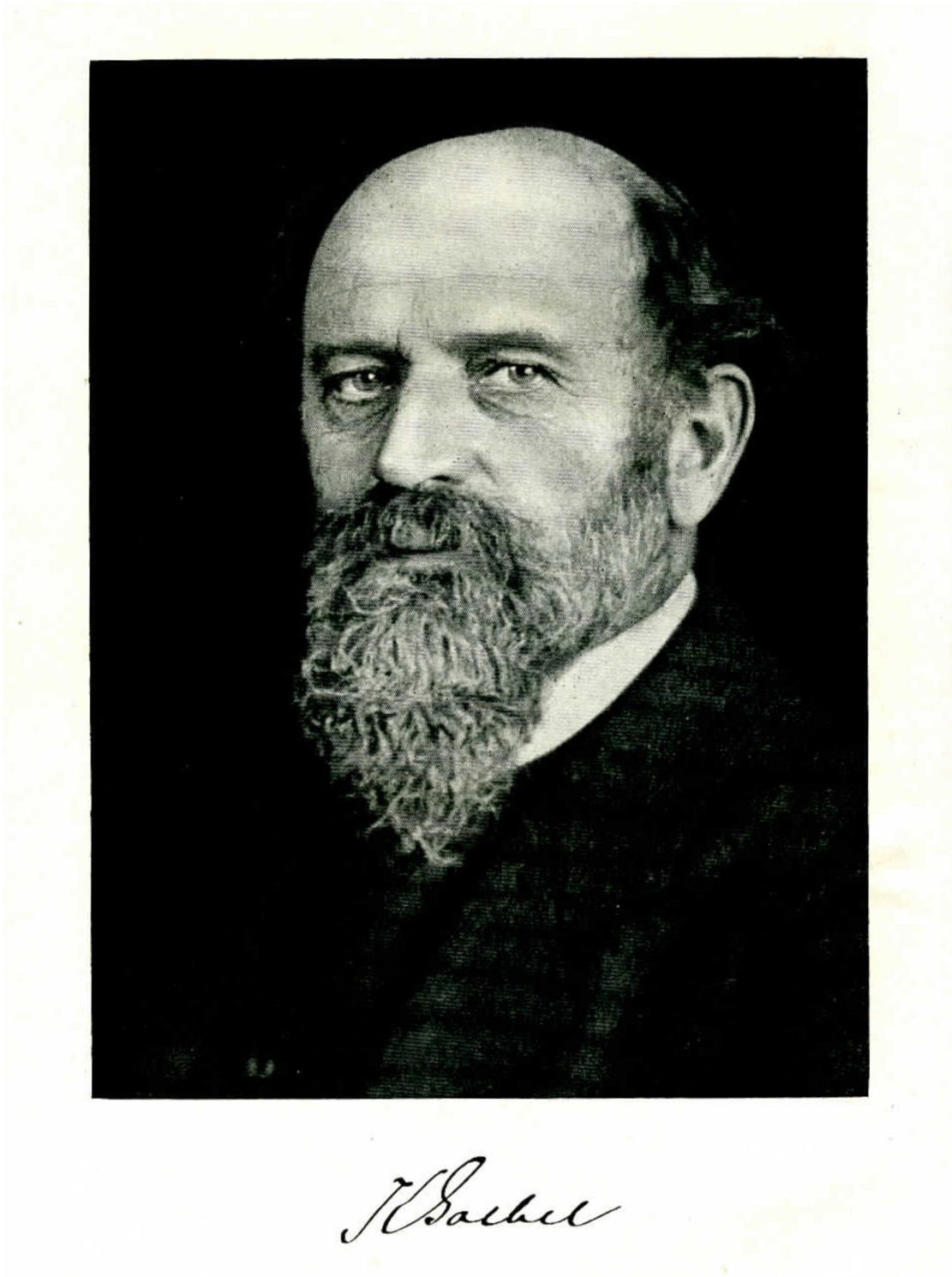


Figure 17. Karl Immanuel Eberhard Ritter von Goebel. Unknown photographer

FIGURE 18. Memorial to Karl von Goebel. Munich Botanical Garden

FIGURE 19. *Laelia goebeliana* (as *L. virens* Lindl.). Photograph by Mauro Rosim.

of his fellow botanist Wilhelm Benecke. There, over several months, he explored the surroundings of Rio de Janeiro and the Organ Mountains. The orchids collected during these excursions were sent for determination to Schlechter, who described amongst them a new species, *Epidendrum goebeli* Schltr. (Fig. 15). Another specimen of Orchidaceae collected by Goebel was described by Kupper and Kraenzlin as *Laelia goebeliana* (Renner 1955) (Fig. 19).

The plant family, Goebeliellaceae Verd., and the genus *Goebeliella* Steph. were named in Goebel's honor.

Karl Ritter von Goebel was a determined follower of the principles of organography, a scientific study that considered the parts of plants as "organs" and began to consider the relationship between different organs and different functions. His major work was published between 1898 and 1901 under the title of *Organographie der Pflanzen* (*Organography of plants*); it became an important reference work during the following decades. In it Goebel took some distance from the Darwinian theory of evolution. In a supplement to his work he wrote: "Two extreme aspects of biological science may be distinguished, and they are often pursued with but slight relation one to the other, viz., the morphological which concentrates upon the form of the object studied, and the physiological which concentrates on function. Neither of these can attain full success without the other. The best results follow from some middle position" (Goebel 1924: 35–35).

In relation to orchids, and in the same work, he stated: "[…] all the wonderful adaptations of orchid flowers are no more effective than countless much simpler devices. We find the intricate facilities of many orchid flowers, e. g. *Catasetum* with its technique for the ejection of the pollinia, Coryanthes with its lip bath for the flower visitors, as a work of art wonderful. But from a flat usefulness point of view, all this is "luxury adaptation", which is understandable to us if, for the forms they exhibit, it was one that was determined and given throughout their entire organization. Then it is not a [superfluos] luxury but a purposeful one for an o r c h i d (i.e. taking into account only what has been a c h i e v e d). Selection theory rejects such a design, which takes place through internal causes in a definite direction, but it is neither sufficient to explain the "origin of the species" nor to convey to us an understanding of the diversity of adaptations: just because it removes the "logos" from morphology and wants to dissolve them into a mixture of directionless variations" (letter spacing by von Goebel) (Goebel 1924: 35).

Francis E. Lloyd, who was well acquainted with Goebel's work, described the latter's point of view as follows: "Though he was little given to speculation, his wide and intimate knowledge of plant form led him to a modification of the Darwinian selection theory. He was convinced that the variety of plant form was much greater than the variety of the conditions under which they grow and saw in these various products many structures which could not be regarded as directly adaptive, but rather indifferent, being neither harmful nor useful. They can arise or disappear without being subject to selection, or they can group themselves and combine to produce members which may enable the plant to become adapted to quite other conditions than the primary ones, and the principle here implied was one of his chief guides in reflecting on the form relations of the plant" (Lloyd 1935: 206).

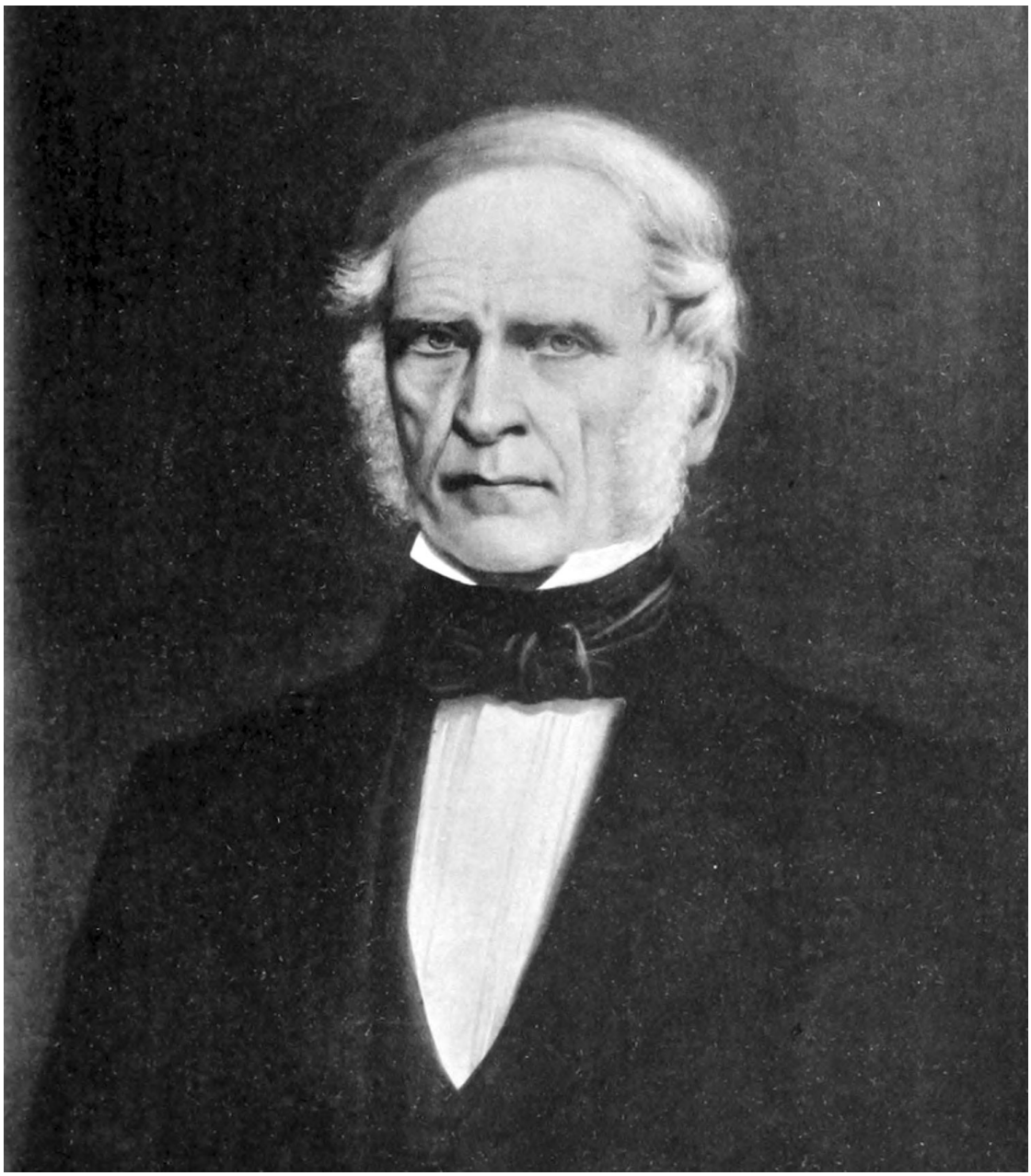


Figure 20. Anders Fredrik Regnell. Painting by Carl Gustav Holmgren..

The Regnellian Herbarium

A Swedish physician and botanist, Anders Fredrik Regnell (1807–1884) (Fig. 20) studied in Uppsala and received his medical doctorate in 1837. He served for several years at the Serafimer Hospital in Stockholm and took part in an expedition to the Mediterranean Sea during 1839–1840 on board of *HMS Jarramas*.

Regnell was of poor health and suffered from a serious lung disease. Thus, looking for a warmer climate, he left Sweden for Brazil in 1840 and settled in Caldas in the province of Minas Gerais, where he spent the rest of his life. During his years in Brazil Regnell acquired a substantial fortune earned through his successful practice as a physician.

FIGURE 21. *Regnellia purpurea*. In Barbosa Rodrigues, *Iconographie des Orchidees du Brésil*, vol. 5: plate 204.

FIGURE 22. Carl Axel Magnus Lindman. Courtesy of Johannes Lundberg, Swedish Natural History Museum, Stockholm.

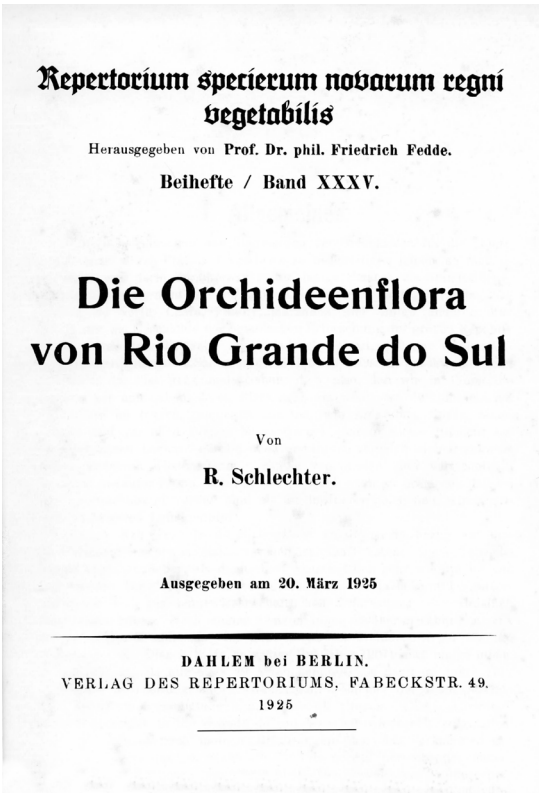
Regnell made substantial collections of plants, which he supplemented with those of G.A. Lindberg, S.E. Henschen, H. Mosén and J.F. Widgren. His collection was later bought by the Swedish government, to be divided between the Natural History Museum in Stockholm (NRM) and other institutions. The Regnellian Herbarium at NRM is today one of the largest collections of South American plants. In the last years of his life, Regnell endowed the Stockholm herbarium, established the Regnell Trust for the Medical Faculty in Uppsala, donated large sums to various Swedish scientific institutions and supported financially several European botanists. A travel grant he established in 1872 stated under its conditions that the chosen scholar was to collect plants in "*Brazil, or another inter-tropical country*" during a period of two years. The first of the so-called "Regnellian Expeditions", financed through Regnell's legacy, was in 1892–1894 to Brazil, Paraguay and Argentina, led by C. A. M. Lindman and G. A. Malme. Over 20 other expeditions have taken place since then.

The orchid genus *Regnellia*, typified by *Regnellia purpurea* (=*Bletia catenulata* Ruiz & Pav.) (Fig. 21) was named in his honor by João Barbosa Rodrigues.

Carl Axel Magnus Lindman (1856–1928; collected 1892–1894)

Born in Halmstadt (southern Sweden), Carl Axel Magnus Lindman (Fig. 22) studied Botany and Zoology from 1874 at the University of Uppsala, where he was appointed Professor of Botany, receiving his Ph.D. in 1886. His early inclination for an artistic career became evident when he began producing magnificent botanical illustrations. He came as amanuensis to the Swedish Natural History Museum in Stockholm in 1887, and in 1892 received the first Regnellian grant. This financed a botanical expedition to South America in the company of Oskar Andersson Gustav Malme.

In July of 1892 the two botanists arrived in Rio de Janeiro and until September they explored the surroundings of the city and undertook excursions as far as Minas Gerais and San João d'el Rey. In September they embarked for Rio Grande do Sul and



Repertorium specierum novarum regni vegetabilis

Herausgegeben von Prof. Dr. phil. Friedrich Fedde.

Beihefte / Band XXXV.

Die Orchideenflora von Rio Grande do Sul

Von

R. Schlechter.

Ausgegeben am 20. März 1925

DAHLEM bei BERLIN.
VERLAG DES REPERTORIUMS. FABECKSTR. 49.
1925

Figure 23. Title of Schlechter's *Die Orchideenflora von Rio Grande do Sul*, 1925.

botanized near Porto Alegre, the German colony of Santo Angelo, the Italian colony of Silveira Martins and the colony of Ijuhy. After nine months in southern Brazil, Lindman and Malme embarked for Montevideo and Buenos Aires. From there they went by paddle steamer along the Parana River to Asuncion, the capital of Paraguay, and thence to the Gran Chaco region along the Pilcomayo and Apa rivers, until in November 1893 they again reached the province of Matto Grosso in Brazil. After nine months in the Matto Grosso, Lindman and Malme sailed to Argentina in August of 1894 and from there, via Santos and Bahia, to Europe, where they arrived at the end of October 1894.

In 1925, Schlechter published his magnificent *Die Orchideenflora von Rio Grande do Sul* (Fig. 23). He described in this work some 30 orchid species collected by Lindmann, and an additional 9 collected by Malme. In the foreword, Schlechter wrote: *The collections by Prof. Lindman and Dr, Malme will undoubtedly remain as fundamental for our knowledge of the flora of Rio Grande do Sul*.

Schlechter named after him *Lepanthes lindmaniana* Schltr., while Kraenzlin named for Lindman the following orchids: *Bifrenaria lindmanniana* Kraenzl., *Dipteranthus lindmanii* Kraenzl. (Fig. 24A), *Habenaria lindmaniana* Kraenzl., *Pelexia lindmanii* Kraenzl.,

Figure 24. A. *Dipteranthus lindmanii* (=*Zygostates alleniana* Kraenzl.). B. *Stenorrhynchos lindmanianum* [=*Pelexia laxa* (Poepp. & Endl.) Lindl. Photographs by R. Jenny (A) and Andreas Kay† (B).

FIGURE 25. *Ophrys muscifera* Huds. Carl M. Lindman, *Bilder ur nordens flora*, plate 408.

FIGURE 26. Gustav Oskar Andersson Malme. Archives of R. Jenny.

Rodriguezia lindmanii Kraenzl., *Spiranthes lindmaniana* Kraenzl. *Stenorrhynchos lindmanianum* Kraenzl. (Fig. 24B), and *Vanilla lindmaniana* Kraenzl.

In 1896 Carl M. Lindman became the tutor of the Swedish Crown Princes (among them the later King Gustav V), a position he held until 1900. He was elected to the Swedish Academy of Sciences in 1905 (Anonymous 1949). When a position for a Professor of Botany opened at the Swedish Natural History Museum, both Malme and Lindman applied. The position was given to Lindman, who held it until his retirement in 1923.

In 1900 Lindman published an interesting work entitled *Vegetationen i Rio Grande do Sul (Sydbrasilien)* [*The vegetation of Rio Grande do Sul (Southern Brazil)*]. However, the work for which he is best remembered is *Bilder ur nordens flora* (*Illustrations of the flora of the North*) One of its illustrations was the terrestrial *Ophrys muscifera* Hook. (Fig. 25).

The genus *Lindmania* Mez (Bromeliaceae) was named in Carl M. Lindman's honor.

GUSTAV OSKAR ANDERSSON MALME (1864–1937; collected 1892–1894, 1901–1903)

Lindman's travel companion, Gustav Oskar Andersson Malme (Fig. 26) was born in Soedermanland. He began bis studies in Stockholm before moving to Uppsala, where he received his Ph. D. in Botany and Zoology in 1892.

Gustav Malme's itinerary during the 1892–1894 expedition has already been described since Lindman and Malme travelled always together. However, Malme's harvest of Orchidaceae was much smaller than Lindman's, at least according to Schlechter in his *Orchideenflora von Rio Grande do Sul*. This becomes evident if we examine the holdings of the herbarium of the Swedish Natural History Museum in Stockholm: a total of 333 orchid specimens collected by Lindman against 45 collected by Malme.

In 1901 Malme went on a new expedition to South America, on a second Regnellian grant. He arrived in Buenos Aires in October 1901 and travelled

Figure 27. Train station, village of Cruz Alta, Rio Grande do Sul, ca 1915. One of Malme's collecting localities in 1902.

immediately to Porto Alegre, the capital of Rio Grande do Sul. There he had to stay for almost six months, and had to postpone his planned expedition to Aconcagua, on the border between Argentina and Chile, because war was threatening following several years of territorial disputes between the two countries. Matto Grosso was also out of the question, because of the civil war that was raging in the region. The unexpected stay was used to make botanical excursions to Cachoeira and Cruz Alta (Fig. 27). The latter became one of his favorite collection areas.

Finally, in March 1902, Malme decided to travel to Matto Grosso, intending to sail to Buenos Aires and from there take the steamboat along the Parana and Paraguay rivers to the village of Cuíaba. But because of an outbreak of plague he was held in quarantine for five days on the island of Flores, in Uruguay and arrived in Buenos Aires after the boat had already sailed. Malme then decided to take a freight boat to Corumbá (near the borders of Brazil, Bolivia and Paraguay), where he arrived in June. He went further on to Cuíaba and Santa Anna da Chapada (July through August). In his travel log Malme described Santa Anna as an "*inexhaustible field for a botanist*". His plant collections grew so rapidly that he had to return to Cuíaba to sort and pack his specimens.

Finally, in January of 1903 Gustav Malme was able to begin his long-planned journey to Aconcagua, where he made further botanical collections at 3,000 meters above sea level. After another short visit to Matto Grosso, Gustav Malme finally embarked in Buenos Aires for his return to Europe in September 1903. Over the previous two years he had made a collection of over 2,600 plant specimens.

Kraenzlin described *Physurus malmei* Kraenzl. (Fig. 28) in Malme's honor, while João Dutra named *Pleurothallis malmeana* after him.

A total of six plant genera have been named in honor of Gustav Malme, among them: *Malmella* and *Malmia* (lichens), *Malmeomyces* (fungi), *Malmea* (Annonaceae), and *Malmeanthus* (Asteraceae).

Eduard Martin Reineck (1869–1931; collected 1896–1899)

A German gardener from the city of Arnstadt, Eduard Martin Reineck (1869–1931) went to Brazil in 1896 accompanied by his assistant, Joseph Czermak, a merchant from Kassel. Together they botanized in

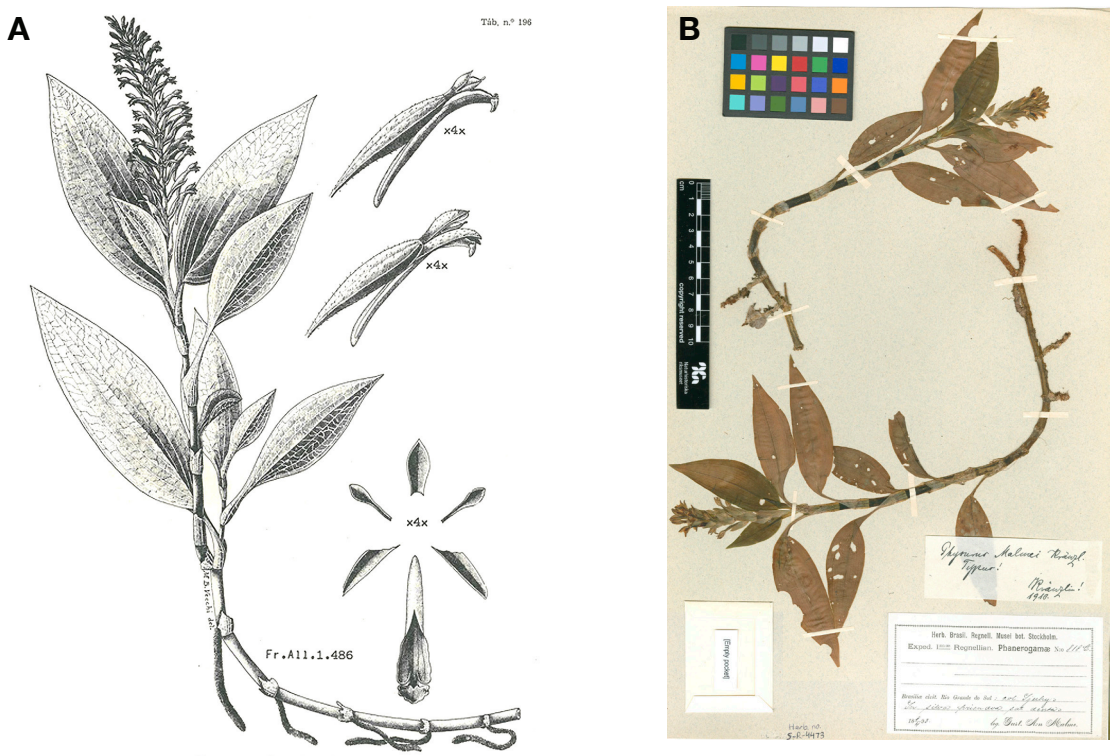


FIGURE 28. *Physurus malmei.* A. As *P. anatanhensis* Barb. Rodr., in Hoehne 1945. *Flora Brasilica*, plate 196. B. Type specimen at the Swedish Museum of Natural History (SR-4473).

FIGURE 29. Porto Alegre, *ca.* 1895. Unknown photographer.

the surroundings of Porto Alegre (Fig. 29), in the state of Rio Grande do Sul, until 1899. Their collections amounted to over 8,000 specimens, among them over 800 Phanerogamae which went for determination to John Isaac Bricquet, director of the *Conservatoire Botanique* at Geneva.

In a number of articles published in German botanical journals, Reineck described his excursions around Porto Alegre and to the Mountains around Belem Vélho. Orchids are frequently mentioned in his narrations. In his *Riograndenser Orchideen, Cacteen und Baumbewohner* (*Orchids, Cacti and inhabitants of trees from Rio Grande do Sul*), published in 1903, Reineck mentions a number of orchids, which he calls "flowers of fairy tales", among them *Oncidium barbatum* Lindl., *Oncidium* sp., *Spiranthes bracteosa* Lindl., *Epidendrum variegatum* Jacq., *Isochilus linearis* (Jacq.) R. Br., *Habenaria sartor* Lindl., *Cattleya guttata* Lindl., *Octomeria pusilla* Lindl. *Octomeria* sp., *Brassavola cordata* Lindl., *Cattleya intermedia* Graham, *Epidendrum elongatum* Jacq., *Habenaria parviflora* Lindl., and *Miltonia flavescens* Lindl. Reineck mentioned that when he wrote this article (February 1899), his orchid collection comprised 25 different species (Reineck 1899, 2003).

Most of these species are listed by Schlechter in his *Die Orchideenflora von Rio Grande do Sul* (1925). In this work Schlechter alss mentions, amongst Reineck and Czermak's collections, specimens of *Stenorhynchus paraguayensis* (Rchb.f.) Cogn., *Pleurothallis ruscifolia* R. Br., *Epidendrum mosenii* Rchb.f., and *Brassavola perrinii Lindl.*

However, many of Reineck's specimens of Orchidaceae could not be studied in detail since he split his collections and sold them to different herbaria. According to Schlechter, a complete collection of Reineck and Czermak's specimens cannot be found.

The herbarium of the Natural History Museum in Paris holds several specimens of Orchidaceae collected by Reineck in Brazil: *Cyclopogon apricus* (Lindl.) Schltr., *Oncidium flexuosum* Sims (Fig. 30), and *Miltonia flavescens* Lindl. Another specimen, this of *Brachystele bracteosa* (Lindl.) Schltr., is kept at the Botanical Garden in Meise (Belgium).

Reineck paid a short visit to the area around Bahia Blanca, Argentina, in October 1899. However, he does not mention any orchids in his account of this excursion.

Figure 30. *Oncidium flexuosum*. Specimen collected by Reineck & Czermak, Herbarium Paris MNHN-P-P00437231.

Eduard Reineck returned to Germany with his plant collections in 1899. These constituted the core of his commercial activities, which he began in 1901 and continued over the next 25 years. The years spent in Brazil gave Reineck a leading position among his contemporaries and in 1902 he was named editor of the *Deutsche Botanische Monatsschrift*, a position he kept until 1912. Reineck used this journal, as well as the *Allgemeine Botanische Monatsschrift* to advertise his collections of herbarium specimens (Fig. 31). The sale of these specimens would be Reineck's main source of income for the rest of his life.

Also It is also worth mentioning that – as a supplement to his commercial activities – Reineck took active part in the *Internationaler Botanischer Tauschverein* (International Botanical Exchange

FIGURE 31. Reineck's advertisement for his Herbarium specimens, among them "South-European and foreign Orchids". In *Allgemeine Botanische Zeitschrift*, vol. 21: 96, 1903.

Association), established in 1907, of which he was one of the founding members. Reineck's activity becomes evident if we consider the number of public and private institutions with which he traded. We can find his plants in differrent European herbaria (BC, BM, BP, DBN, E, G, GH, GOET, HBG, K, L, M, MANCH, O, P, SAM, W), in America (AMES, MVM, SI, US), Asia (CAL) and even in South Africa (NH, SAM) (Benedí & Sáez, 1996:571). In total, over 8,000 specimens, proceeding from all continents, were offered and sold by Reineck.

Unfortunately, Reineck will not be remembered for his contributions to botany in general and orchidology (which in Schlechter´s words were unsatisfactory) in particular, but for his dubious business practices. It has been determined without doubt that Reineck, at least in the last 20 years of his commercial activity, falsified specimens, exchanged labels and disguised localities, all to add value to plants he was selling commercially.

We will not extend ourselves on this subject; enough has been written about Reineck's *false plants*, as Benedí called them. Standley (1927), Benedí (1987) and Benedí & Sáez (1996) went into detailed research work and demonstrated that Reineck, when it came to selling herbarium specimens, was capable of anything. Paul C. Standley, in his article of 1927, shows how far Reineck could go in order to sell his *false plants*. Regarding Reineck's falsification of Brother G. Arsène's Mexican collections, Standley wrote: "The distributor of these plants was not content with ascribing specimens wrongly to Brother Arsène, but his ingenuity was equal to the creation of a new and fictitious collector, Herrera. This is a common Spanish family name, but I have no hesitation in asserting that this particular Herrera never existed. The name selected is not above criticism; Munchausen would have been a better choice. "Herrera's" collections were manufactured from those of Pringle. In many instances the type collections of Pringle's new species were thus divided. Here, too, only the name of the species was invariably retained. The date of collection is sometimes earlier and sometimes later than Pringle's. The locality is usually the same, but often the altitude (given in feet on Pringle's labels and in meters on those of "Herrera") has been altered" (Standley 1927: 132).

PER KARL HALJMAR DUSÉN (1855–1926; collected 1901–1916)

"Southern Brazil especially ranks amongst the better explored floristic regions, and Swedish botanists have contributed more than all others to the richness of our collections and our knowledge". With these words Friedrich Kraenzlin introduced his *Orchidaceae Dusenianae novae* (1921), in which he described the orchid collections of Per Karl Haljmar Dusén (Fig. 32) in the Brazilian states of Paraná and Santa Catharina. A few years earlier, Kraenzlin had already described new orchid species based on collections by Dusén in his *Beiträge zur Orchideenflora Südamerikas* (1911). Rudolf Schlechter would follow with the publication of new species by Dusén in his *Beiträge zur Kenntnis der Orchidaceenflora von Paraná* (only terrestrial orchids), and in 1925 with *Die Orchideenflora von Rio Grande do Sul*.

Per Karl Haljmar Dusén (1855–1926) was born in Vimmerby (province of Småland) in Sweden, where his father was director of a primary school. After studying at the Superior Technical High School of Stockholm, he graduated as a mechanical engineer. However, he only worked in this profession until 1880, when he accepted a position as professor at the Popular School

Figure 32. Per Karl Haljmar Dusén. Oil on canvas by Alfred Andersen.

for Natural Sciences and Mathematics, a post he held until 1898, when he was employed as an assistant at the Swedish Museum of Natural History. In his interest for Botany he was strongly influenced by his cousin, K. F. Dusén, of Kalmar, who was a renowned bryologist. Mosses were Dusén's main interest during these initial years and he would dedícate considerable efforts to their study during the rest of his life. His first publication was about the flora and geology of the región of Omberg, in Oestergoetland.

Dusén travelled extensively and went on botanical expeditions to a large number of foreign countries: Tropical Africa (Cameroon, Equatorial Guinea, Liberia); North America (Greenland and Mexico): West Indies (Haiti); and South America (Argentina, Chile, Paraguay, Brazil). But Brazil would be his favorite collecting ground. The expeditions there began in 1903–1904 -during which Dusén dedicated himself extensively to the study of the flora of the state of Paraná- and continued from 1908 to 1912 and from 1913 to 1916 (Hoehne 1930).

Dusén's first encounter with the South American flora took place in 1895, when he participated in the expedition commanded by Otto Nordenskjoeld to study the natural history of Patagonia and Tierra del Fuego. Dusen collected three species of the terrestrial genus Chloraea during the expediton. We will come back to this part of Dusen's life in future chapters concerning Chile and Argentina. Dusén returned to Sweden, but very soon, in September 1901, he was back in America, this time in Brazil. From 1901 to 1904 he held the position of assistant to the Botanical Section of the Natural History Museum in Rio de Janeiro, with a brief interlude in the city of Curitiba (state of Parana), his first Brazilian expedition, from November 1903 to May 1904.

Per Dusén's life was adventurous. In 1905, in recognition of his knowledge of southern South America, he went again to Patagonia with a new expedition, this time led by Arthur Thessler, which started from Buenos Aires to study the possibilities of establishing a Finnish colony in Patagonia. During a severe snow storm, he almost lost his life. He extended his stay and in 1906 was contracted by the Chilean government as part of another expedition, this time for the exploration of the Aysén River and the topographical delimitation of the border between Chile and Argentina.

In 1908 Dusén was surprised by an invitation from the State Government of Paraná, to undertake the botanical exploration of the state. Dusén spent four years in Paraná, during which time he collected over 40,000 specimens of phanerogams and 800 specimens of mosses. After his return to Sweden, he received the third invitation from Paraná and spent the next three years (1913–1916) in the country.

It was not by chance that Dusén collected the vast majority of his plants in Paraná. Besides the exuberant flora of Paraná and the great number of undescribed plants in the region, an important factor was his friendship with C. J. F. Westerman, the railways director of Paraná state. Westerman provided him with a specially modified railway wagon, furnished as a dormitory and working place, with room enough for a laboratory for collections and research. Dusén thus travelled the region in his own railway carriage. After collecting in a particular area, his living quarters were coupled to a locomotive and taken to a new unexplored place. The researcher remained there during a further period, moving along once again when he finished his exploration. This is why most of the new species discovered by Dusén were collected along the route of the railways, ranging from São Paulo to Paraná and the borders of the state of Santa Catarina (Fig. 33).

The outbreak of WWI left Dusén in difficult financial circumstances and he was forced to return to Sweden again. In precarious conditions, he subsisted for a time on the income from the sale of his herbarium specimens. However, friends and relatives obtained a pension for him from the Swedish government in the amount of 3,000 crowns. On this modest sum he lived the remaining years of his life, dedicating himself to the study of his botanical material.

His legacy as a plant collector amounts to more than 70,000 vascular plants and 1,000 mosses (Fig. 34). Most of his collections are kept at the Swedish Museum of Natural History in Stockholm, but a large number can also be found in Brazilian herbaria in Rio de Janeiro and Curitiba. The Swedish Natural History Museum keeps a total of 1,593 orchid specimens collected by Per Karl Dusén, among them 64 types of plants new to science (Raulino Reitz 1949) (Fig. 35).

Rudolf Schlechter described a large number of new orchid species from Dusen's excursions in Parana in his *Beiträge zur Orchidaceenflora von*

Figure 33. One of Duséns many collection areas: the railway station of Morretes, province of Paraná, *ca*. 1884. Photograph by Marc Ferrez.

Figure 33. Dusén's specimens, field books and plant press. *In* Dos Santos 2016: 885..

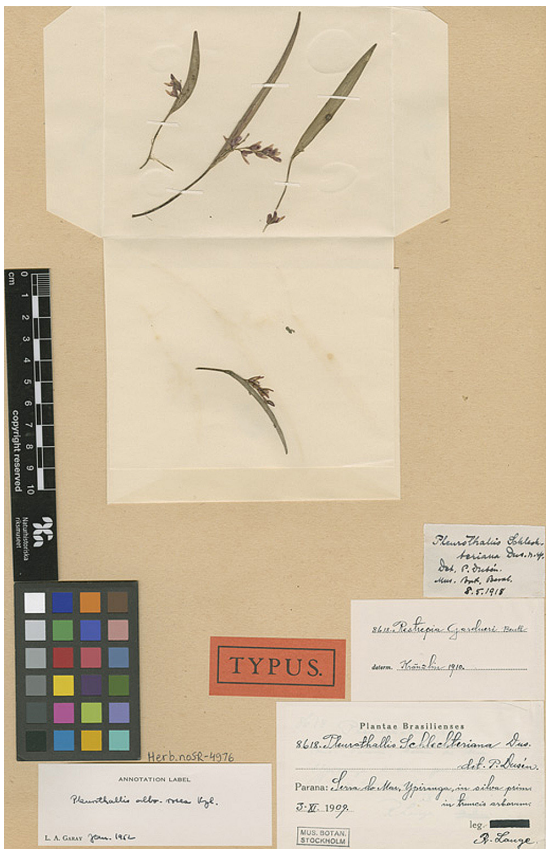


FIGURE 35. *Pleurothallis schlechteriana* Dusén (ined.). Intended type specimen at theSwedish Museum of Natural History (S-R-4976).

FIGURE 36. *Pleurothallis per-dusenii*. Photograph by Ron Parson.

Paraná (1920). He wrote in the foreword: "Dr. Dusén gave me in the year 1918 the terrestrial orchids collected by him in the years of 1913-1916, for their determination. He also requested to review the determinations made by Prof. Kraenzlin from his earlier excursions. The collection has showed that we have to expect a large number of new species, even from regions in Brazil that were considered as well explored. The epiphytic orchids will be determined by Dr. Dusén himself" (Schlechter 1920).

Kraenzlin, on his side, published a number of new orchid species collected by Dusén in his *Orchidaceae Dusenianae novae* (1921).

Among the new orchid species collected by Dusén, 17 were dedicated to him by his contemporaries: 6 by Rudolf Schlechter (*Cryptophoranthus dusenii*, *Cyclopogon dusenii*, *Cyrtopodium dusenii*, *Habenaria dusenii*, *Octomeria dusenii*, *Promenaea dusenii*), one by Frederico C. Hoehne [*Pleurothallis per-dusenii* (Fig. 36)], 10 by Friedrich Kränzlin [*Amblostoma dusenii*, *Bulbophyllum dusenii, Eulophia dusenii*, *Gomesa duseniana*, *Ornithocephalus dusenianus* (Fig. 37), *Polystachya dusenii*, *Psilochilus dusenianus* Kraenzl. ex Garay & Dunst., *Quekettia duseniana*, *Stenorrhynchos dusenianum*, and *Xylobium dusenii*], and one by Alberto José de Sampaio [*Restrepia dusenii* (Fig. 38)].

Dusén was honored in the name of over 160 plants through epithets such as "dusenii", "duseniella", "dusenianus", etc. In addition, a new genus, *Dusenia* O.Hoffm. in the Asteraceae, was dedicated to him. was dedicated to him. On his part, Dusen dedicated a new orchid species to Rudolf Schlechter: *Pleurothallis schlechteriana* Dusén (ined.) (Fig. 35).

The herbarium Per Karl Dusén in Curitiba (PKDC) was named in his honor.

Figure 37. *Ornithocephalus dusenianus* [as *Zygostates pustulata* (Kraenzl.] Schltr. Photograph by Lourens Grobler.

Figure 38. *Restrepia dusenii.* Photograph by Eric Hunt.

Frederico Carlos Hoehne (1882–1959; collected 1908–1959)

As one of the eight children of German immigrants, who had arrived (themselves children) in Brazil in 1858, Frederico Carlos Hoehne (Fig. 39) was born in Juiz de Fora, Minas Gerais. Hoehne's father, a farmer, had a small orchid collection that became an attraction for visitors, and many of the plants were sold to contribute to the family's economy. At just eight years of age, Hoehne started his own *orquidário* and he later wrote that his interest in botany had begun at that time.

Having finished his high school studies in 1899, and without the means to finance an academic career, Hoehne had to educate himself while he continued with the observation of plants, living in part from the sale of orchids.

Specialized books were brought from Rio de Janeiro and the orchid collection, which he learned to determine and classify, was expanded, now also from exchange with other growers. His ambition was now to discover new species. Young Hoehne's orchid collection soon replaced that of his father and became locally famous. By 1907, at the age of 25, Hoehne had turned into an expert, consulted by orchidophiles and orchidologists. It was in that year that his career

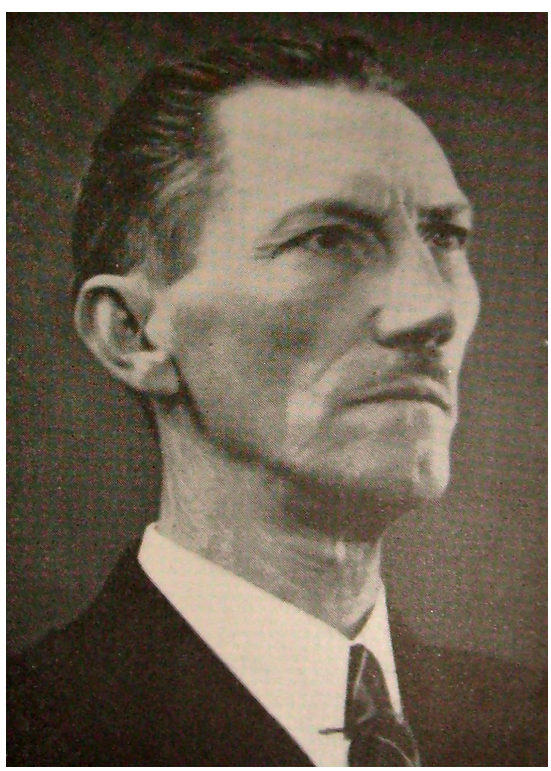


Figure 39. Frederico Carlos Hoehne. Unknown photographer.

FIGURE 40. National Museum of Brazil, ca 1900. National Archives of Brazil.

FIGURE 41. Cândido Mariano da Silva Rondon. Unknown photographer.

Figure 42. Roosevelt (right) and Rondon (center) in the forest of Matto Grosso in 1914. Unknown photographer. Library of Congress.

took a dramatic turn: with the help of the President of the Municipal Council of Juiz de Fora, Hoehne – without a formal scientific education – was appointed chief-gardener of the National Museum of Rio de Janeiro, at that time the largest scientific institution in the country. The museum, founded in 1818, was moved, in May of 1900, from its original location to the former Palácio Imperial de São Cristóvão, also known as Quinta da Boa Vista (Fig. 40).

One year later, in 1908, Frederico C. Hoehne was called to form part of the first of the famous expeditions led by Colonel Cândido Mariano da Silva Rondon (1865–1958) (Fig. 41). Rondon was well known for his lifelong support of the indigenous Brazilian tribes. He became later the first director of the Indian Protection Service and supported the creation of the Xingu National Park. The Brazilian state of Rondônia is named after him.

Rondon led three major expeditions into the Matto Grosso, surveying the lands between Matto Grosso and the Amazon (1908–1909), laying telegraph lines between Brazil and Bolivia in 1910 and finally, in 1913–1914, leading the Roosevelt-Rondon Scientific expedition to the *Rio da Dúvida* ("River of Doubt"), afterwards named Rio Roosevelt or sometimes Rio Teodoro.

The expedition, led by former U.S. President Theodore Roosevelt and Cândido Rondon (Fig. 42), sought to determine where and by which course the river flowed into the Amazon. Roosevelt, together with his son Kermit, undertook this adventure after failing to retain his office in the elections of 1912. A fervent lover of nature, Roosevelt had used his authority to protect wildlife and public lands by creating the United States Forest Service and establishing 150 national forests, 51 federal bird reserves, 4 national game preserves, 5 national parks, and 18 national monuments.

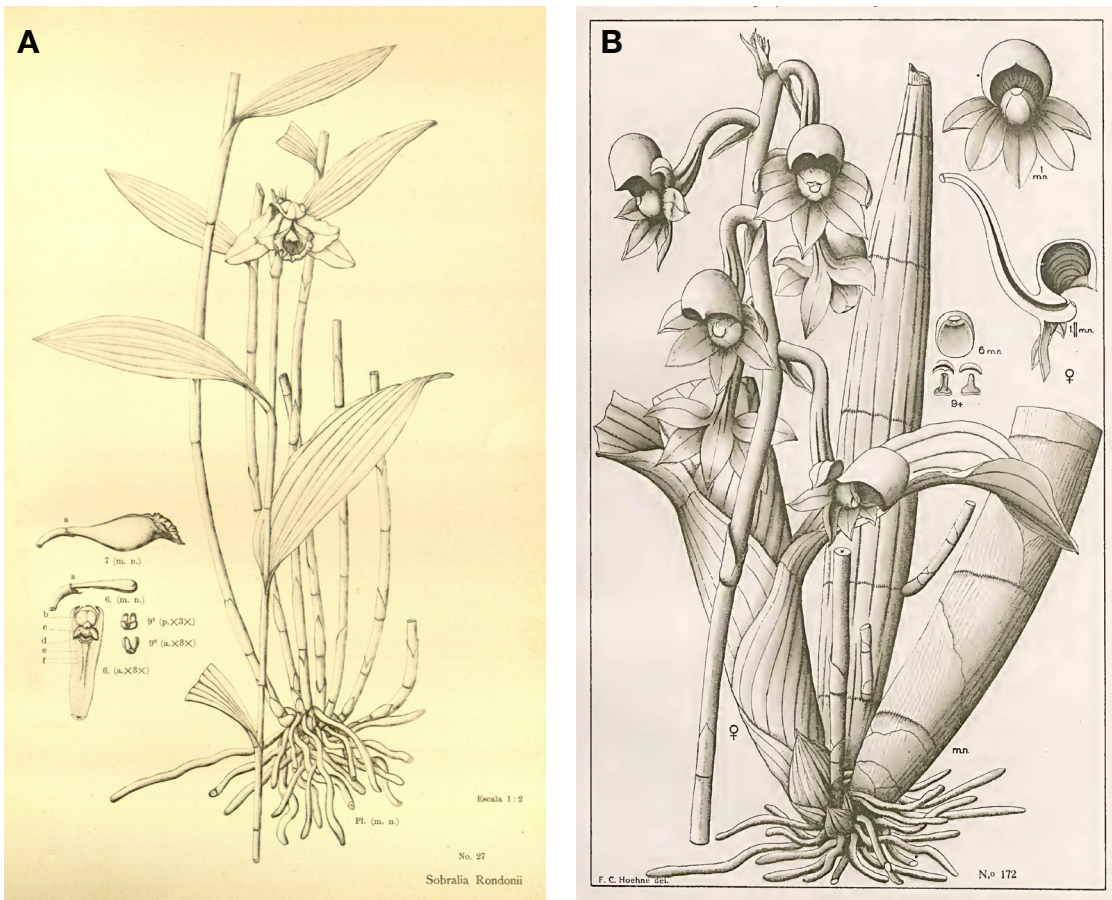


FIGURE 43. A. *Sobralia rondonii*. B. *Catasetum rooseveltianum*. Drawings by Hoehne (1910) in his Report on the Botany of the Telegraphic Lines Commission, part I (plate 27 and 172 respectively).

Hoehne was chosen as the botanist of these expeditions (during the second he had the company of his brothers-in-law Hermano and Geraldo Kuhlman) and later made significant contributions to the expeditions' reports (published between 1910 and 1923), detailing their botanical findings. In some of these reports (Hoehne 1914, 1916, 1916a) he described and illustrated a large number of orchid species. Among them, he dedicated to Rondon and Roosevelt *Sobralia rondonii* and *Catasetum rooseveltianum* respectively (Fig. 43).

In the course of Rondon's expeditions, Hoehne and his collaborators collected over 10,000 plant specimens, corresponding to at least 4,000 different species, of which 200 had not previously been described. Thus, Hoehne finally realized the dream of his youth of discovering plants new to science. In addition, dozens of plants of the native Brazilian flora where named in his honor, as homage from his colleagues, assistants and admirers. Frederico C. Hoehne was honored by numerous institutions, among them the American Orchid Society made him an honorary member and the University of Göttingen, Germany conferred the title of *Doctor Honoris Causa*, on him in 1929.

It was in the city of São Paulo (where he moved in 1917) that Hoehne reached the high point of his scientific career and followed a systematic pursuit both in the study and the protection of nature. His career was intimately related to the foundation of the Instituto de Botânica do Estado de São Paulo, where in 1917 he was given the task of organizing a botanical garden for the cultivation and acclimation of medicinal plants. At the same time, he dedicated

Figure 44. Fernando Costa (left) and Frederico Hoehne with the first orchids that arrived at the Botanical Garden of São Paulo in 1928. Unknown photographer.

himself to a larger project, the establishment of a Botanical Section at the Instituto Butantã, on the outskirts of São Paulo.

Hoehne's research related to the Brazilian orchid flora had the support of Rudolf Schlechter, botanist from the Botanical Museum of Berlin-Dahlem. The scientific exchange of knowledge and natural history material proved to be, throughout the 19th century, the most efficient form of gathering collections of universal character. This idea has persisted until the present. Hoehne and Schlechter corresponded from 1919; the latter became an avid collaborator of those studying the orchid flora of Brazil and was, among German botanists, the first to recognize the scientific merits of Barbosa Rodrigues.

In 1928 Hoehne was called by Fernando Costa, Secretary of Agriculture of the state of São Paulo to *make plans form the organization of a botanical garden, that would grow and exhibit the most interesting ornamental plants of the indigenous flora* (Hoehne 1941:14). The Botanical Garden of São Paulo was established in an area that had been preserved since 1893 because of the natural springs that existed in the area which provided water to the eastern suburbs of São Paulo. The springs were abandoned in 1928 due to falling water levels and the land was assigned to the new botanical garden. Roadsand two hothouses were built. The *Orquidário* was formally inaugurated in 1930 although the first orchids had already arrived at the garden in 1928 (Fig. 44).

The garden gained more autonomy when it was subordinated to the Secretary of Agriculture, Industry and Commerce and in 1942 became the Department of Botany, a status it holds until the present day. Hoehne worked in the garden until 1952, when he had to go into compulsory retirement because of his age.

Frederico C. Hoehne published his *Contribuções ao Conhecimento das Orchidáceas do Brasil* in 1922. Part I was published in collaboration with

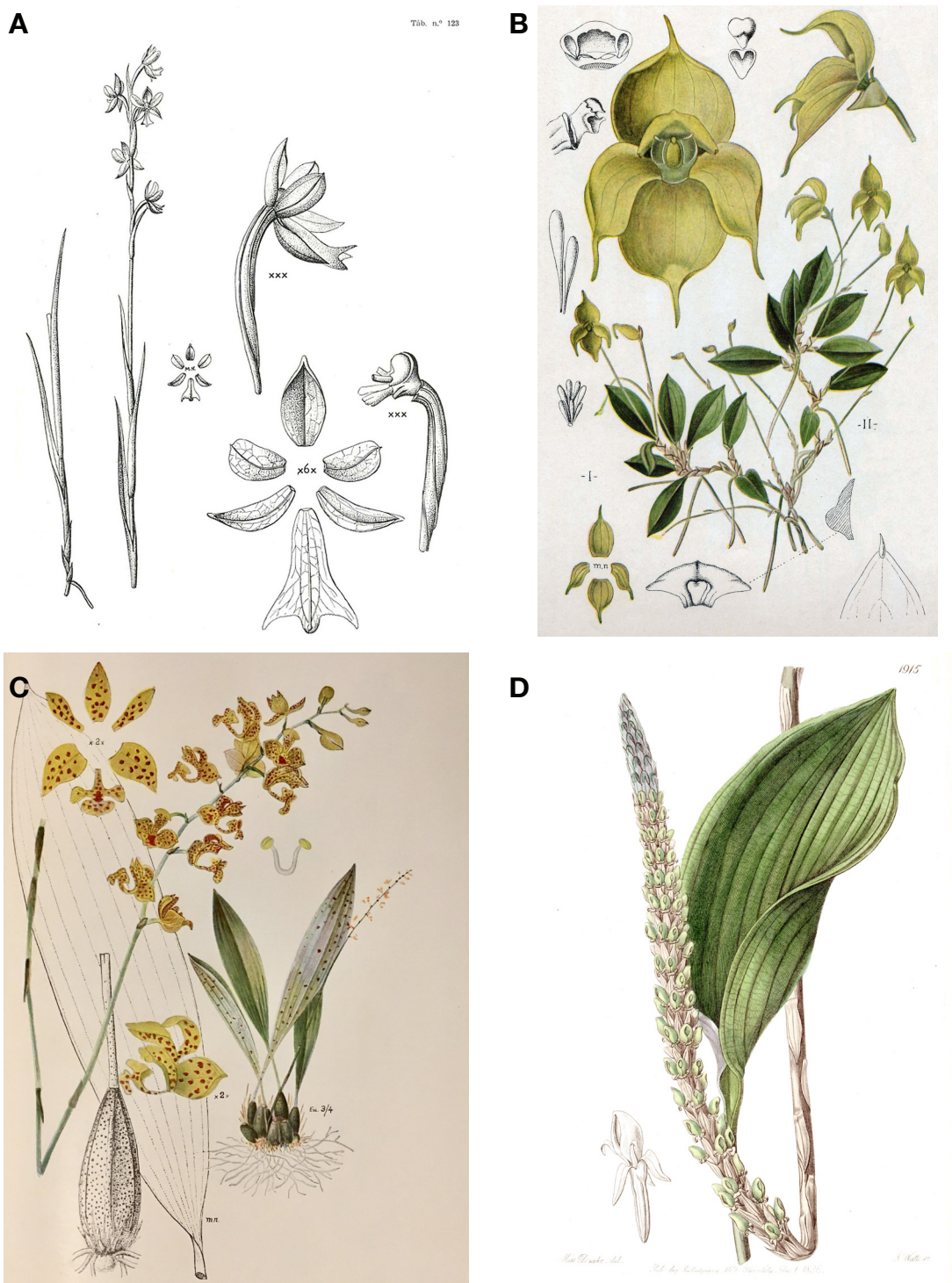


FIGURE 45. A. *Itaculumia ulaei*. B. *Yolanda restrepioides* (left). C. *Rudolfiella auantiaca*. D. *Prescottia schlechteri* (as *P. colorans* Lindl.). A, C, drawingd by Hoehne in his *Flora Brasilica* (pl. 122, 28). B, in Hoehne, *Iconografia de Orchidaceas do Brasil*, pl. 89. D, from *Edwards's Botanical Register*, 1836, pl. 1915.

Figure 46. *Maxillaria hoehnei* Schltr. (as *M. picta* Hook). Photograph by Eric Hunt.

Figure 47. *Cattleya hoehnei*. Photograph by C. van den Berg.

Rudolf Schlechter; parts II and III in co-authorship with the German botanist Kurt Krause, a former collaborator of Schlechter's. But Hoehne's major work was the *Flora Brasilica*, begun in 1940 and carried on after his death by Acides Ribeiro Texeira. Twelve fascicles were issued up to 1968. His last major publication was *Iconografia de Orchidaceas do Brasil* (1949) (Silva 2013).

The São Paulo journal *Hoehnea* (1971–) is named after him, as are the genera *Hoehnea* Epling (Lamiaceae), *Hoehnella* A.Ruschi (Orchidaceae) and *Hoehnephytum* A.L.Cabrera (Asteraceae).

Between 1908 and 1948 Frederico C. Hoehne described over 1,000 new species of plants of which some 450 were orchids. Among his discoveries, he published four new orchid genera: *Itaculumia* (Fig. 45A), *Loefgrenianthus*, *Yolanda* (Fig. 45B) and *Rudolfiella* (Fig. 45C). A total of seven orchids named by Hoehne after Rudolf Schlechter are proof of the life-long friendship and collaboration between the two botanists: *Epidendrum rudolfianum, Habenaria rudolfi-schlechteri, Maxillaria rudolfii, Habenaria rudolfi-schlechteri, Physurus schlechterianus, Prescottia schlechteri* (Fig. 45D), and *Theodorea schlechteri*.

A large number of species of Orchidaceae were named after Hoehne by different authors. Rudolf Schlechter dedicated to Hoehne *Acacallis hoehnei, Cryptophoranthus hoehnei, Habenaria hoehnei, Maxillaria hoehnei* (Fig. 46), *Octomeria hoehnei, Pleurothallis hoehnei,* and additionally *Cleistes hoehneana* Schltr. ex Mansf. and *Oncidium hoehneanum* Schltr. ex Mansf. In a similar way, Kraenzlin described *Polystachya hoehneana*. Guido Pabst followed with *Brachystele hoehnei* and *Camaridium hoehnei*. And finally, a number of authors dedicated orchids to him, so *Bulbophyllum hoehnei* E.C.Smidt & Borba, *Catasetum hoehnei* Mansf., *Cattleya hoehnei* Van den Berg (Fig. 47), *Epidendrum hoehnei* A.D.Hawkes, *Eurystyles hoehnei* Szlach., *Lankesterella hoehnei* Leite, *Maxillaria hoehneana* P.F.Hunt, and *Mormodes hoehnei* F.E.L.Miranda & K.G.Lacerda.

João Gerlado Kuhlmann (1882–1958; collected 1910–1943)

In December of 1910 Frederico C. Hoehne returned to the Matto Grosso on his second expedition led by Cándido Rondon again in charge of the botanical work. Unable to find skilled assistants in the region, Hoehne was permitted to bring this brothers-in-law Hermano and João Geraldo Kuhlmann (Fig. 48) from Rio (Hoehne had married Clara Eduarda Frieda Kuhlmann in 1907).

Over the next 19 months, Hoehne and the

FIGURE 48. João Geraldo Kuhlmann. Fundação Cultural de Blumenau/ Arquivo Histórico José Ferreira da Silva.

Figure 49. Boy's school in Blumenau, in the 1880s. Brasiliana Fotográfica Digital.

Figure 50. *Casa dos Pilões,* now Museu Kuhlmann. Unknown photographer.

Kuhlmann brothers explored the forests and fields, collecting botanical specimens along the Juruena and the Tapajós rivers. They finally reached Santarém and continued from there to Belém, repeating – 83 years later – the route of Baron von Langsdorff's expedition in 1828 (after Sá *et al.* 2008).

Born from German parents in the German colony of Blumenau, in the southern state of Sta. Catharina, Kuhlmann was a largely self-taught botanist (as was his brother-in-law F.C. Hoehne). His formal education never went further than Blumenau´s primary school (Fig. 49)], but over the years he would become one of Brazil's leading botanists..

Invited by director Antonio Pacheco Leão, Kuhlmann joined the Botanical Garden of Rio in 1919, where he was put in charge of the Botanical Section and at the same time taught at the Superior School of Agriculture and Veterinary Science of Viçosa. Finally, in 1944 he was named by the Secretary of Agriculture Director of the Botanical Garden in Rio de Janeiro, a post he held until 1951. Under his administration, scientific research flourished at the garden, especially since Kuhlmann could count on brilliant collaborators, such as Adolpho Ducke and Alexander Curt Brade.

Kuhlmann and his family lived on the garden premises, in a house called *Casa dos Pilões* (Fig. 50), the Pestle House, built as a production unit of the Royal Gunpowder Factory at Rodrigo de Freitas Lagoon, where the Botanical Garden of Rio had been founded by King João VI in 1808. In 1960, after Kuhlmann's death, the Federal Government established the "Museu Botânico Kuhlmann" in this house (Reitz 1972).

João Geraldo Kuhlmann was Honorary President of the International Botanical Congresses at Tucumán, Argentina (1940), Stockholm (1955) and Paris (1954). The *Herbário Rondoniense João Geraldo Kuhlmann* was established in 2009 at the Federal University of the state of Rondônia.

During his early expeditions with Hoehne and later, until his nomination as Director of the Botanical Garden in Rio, Kuhlmann was an avid collector. Among his specimens we find a small group af orchids at the Oakes Ames Orchid Herbarium of Harvard University: *Epistephium parviflorum* Lindl., *Epistephium subrepens* Hoehne, *Habenaria amazonica* Schltr., *Habenaria depressiflora* Hoehne, *Habenaria duckeana* Schltr., *Habenaria leaoana* Schltr., *Habenaria marupaana* Schltr., *Habenaria platydactyla* Kraenzl., and *Habenaria trifida* Kunth. Many of them were described by Schlechter in his *Orchidaceae kuhlmannianae* (1926).

The following orchid species were named in Kuhlmann's honor: *Campylocentrum kuhlmannii* Brade, *Centrogenium kuhlmannianum* Hoehne (Fig. 51A), *Epidendrum kuhlmannii* Hoehne, *Neobartlettia kuhlmannii* Schltr.(Fig. 51B), *Habenaria kuhlmannii* Schltr. (Fig. 51C), *Epidendrum geraldoi* Porto & Brade, and *Zygostates kuhlmannii* Brade.

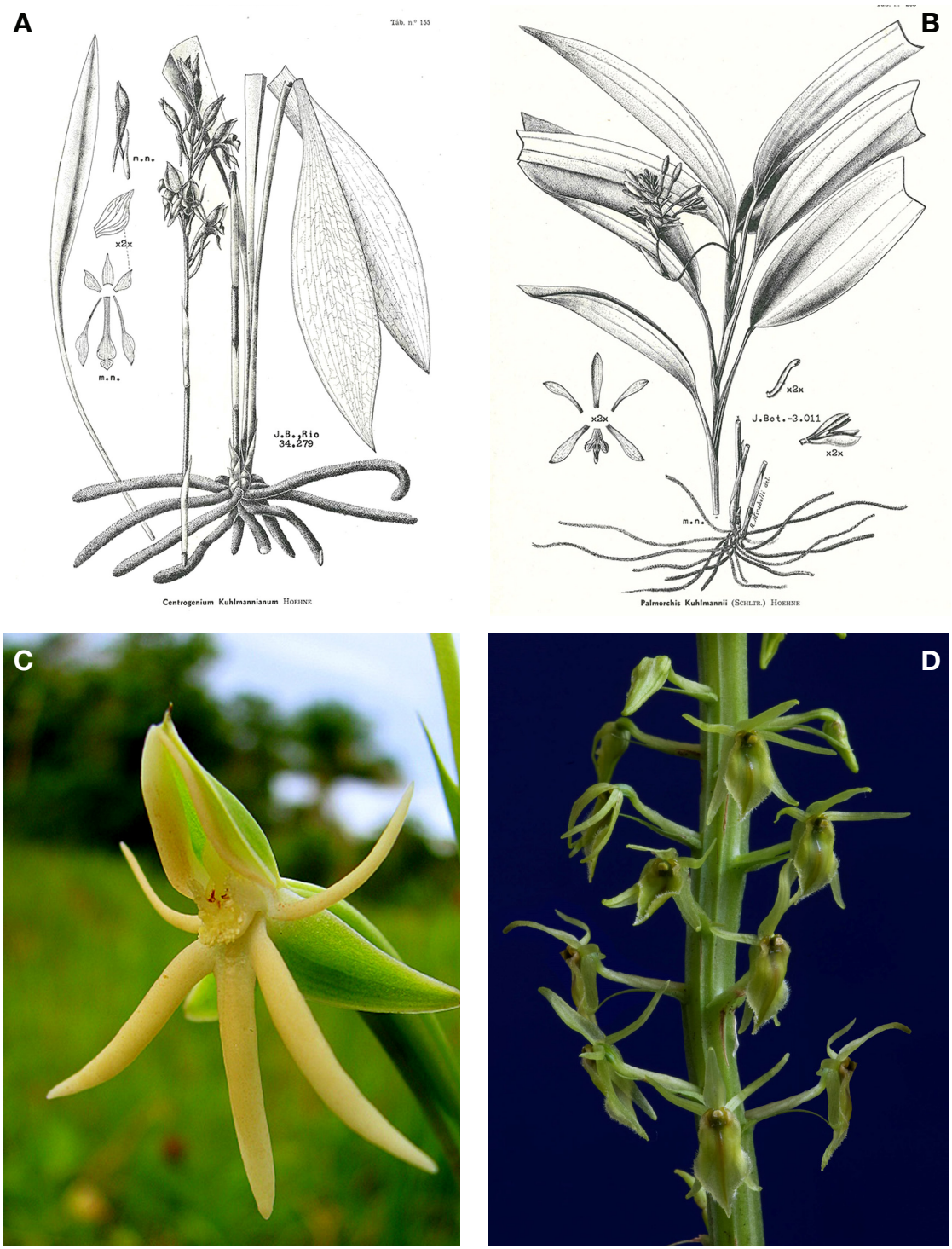


Figure 51. A. *Centrogenium kuhlmannianum*. B. *Neobartlettia kuhlmannii*. C. *Habenaria kuhlmannii* (as *Habenaria trifida* Kunth). D. *Liparis fratrum Schltr.* [as *Crossoglosa fratrum* (Schltr.) Dressler ex Dodson]. A, B, drawings by Hoehne in his *Flora Brasilica* (pl. 155 and 203, respectively). C, photograph by A.V. Popovkin. D, photograph by F. Pupulin.

Alexander Curt Brade (1881–1971; collected 1910–1971)

In 1923 Rudolf Schlechter described a new orchid species collected in Costa Rica, which he named *Liparis fratrum* (Fig. 51D). Few know that *fratrum* is a Latin genitive that translates literally as "belonging to the brothers". Schlechter had chosen this name in honor of two German brothers who had made important orchid collections in Costa Rica: Alfred Brade and his younger brother Alexander Curt Brade (Fig. 52).

Alfred Brade (1867–1955) had arrived at Puerto Limón in 1893 and after two years of work in the banana plantations of the Atlantic region found a position in the nurseries of Julian Carmiol in San José. With Carmiol he shared his enthusiasm for Botany and he dedicated himself for years to explore all accessible regions in the country. After several years he made himself independent from Carmiol and founded the Brade Nurseries. With the years he dedicated himself more and more to horticulture and finally abandoned botanical exploration completely (Ossenbach 2009: 151). Alexander Curt Brade, by profession a civil engineer, was the driving force behind those collections. Alexander Curt came to Costa Rica in 1908 invited by his brother but stayed only for a short time, traveling in August of 1910 to Brazil, where he reached glory as one of South America's greatest orchidologists. Rudolf Schlechter, in his *Additamenta ad Orchideologiam Costaricensem* (1923) dedicated an entire chapter to the collections that he had received from the Brade brothers: *Orchidaceae Bradeanae Costaricensis*. He was very specific to use this title because he later published *Orchidaceae Bradeanae Paulensis* to distinguish the Brazilian from the Costa Rican Brade collections (Ossenbach, 2009: 151).

Schlechter praised the great quality and excellent preparation of the Brade's herbarium specimens and called the collection "a milestone in the botanical exploration of the country"(Markgraf 1973: 4).

Alexander's intention to return to Germany was postponed after receiving an invitation from his nephew, the surveyor Walter Petry, to visit him in southern Brazil. He sailed via New York to Santos. A few days were spent in Rio de Janeiro, where Brade climbed Corcovado and Tijuca Peak, without guessing that years later he would develop his most important scientific activity here. The journey went on to Santos and then Iguapé along the Pariquera Mirim River (Fig. 53). Here again Brade found a neo-tropical flora, which was, however, quite different from the Central American flora he had studied in Costa Rica.

Alexander Brade worked in São Paulo as engineer in charge of a new building for the local brewery and at the same time as a surveyor with his nephew. He spent his free time exploring the dry vegetation of the 'Campos' and in the luxuriant forests of the Serra do Mar. His living seemed secured and in 1916 he found in Hanna Kähler a companion for his life. World War I had begun in Europe but Brazil seemed far away and Brade felt no danger. It was not until 1917, when Brazil declared war on Germany, that Brade -like all other German employees- lost his job at the brewery. He had to find a new way of earning a living and -again with his nephew- bought a neglected 'Fazenda', *Morro de San Pedro*, on the banks of the Peroupava River. Slowly he brought the farm into the production of rice and sugar cane. After 10 years he was again in a comfortable position only to lose, in 1928, all his possessions to a terrible flood. Brade and his family barely escaped with their lives.

It was destiny that showed Brade a way out of this desperate situation. During his years as *fazendero* he had not wasted time but kept collecting plants. His herbarium had already over 10,000 specimens and he sent most of them for determination to the National Museum in Rio de Janeiro. The Director of the Botany Department, Professor Sampaio, offered him a position as free-lance botanist (*botanico contratado*). Brade would live the rest of his life on Botany.

He gave up the idea of returning to Germany. Later, after 1945, a return to his homeland became totally impossible: the family possessions were destroyed, and most of his relatives had died during the war. In 1933 Brade adopted Brazilian citizenship and could thereafter take a full-time position as botanist at the Botanical Garden in Rio – at the time under the directorship of Paulo Campos Porto – until he was named Director of the Section of Systematic Botany (*Chefe da Seccão de Botanica Sistemática*).

FIGURE 52. Alexander Curt Brade. In Pabst 1967: 163.

Figure 53. Steamship Izabel arriving at Iguapé, *ca.* 1915. Unknown photographer.

In this position he travelled extensively in the states of Rio de Janeiro, Espirito Santo and Minas Gerais until in 1952 he was forced to retire, having reached the mandatory retirement age of 70. His passion for botany continued however to his last days.

Alexander Curt Brade published a large number of articles on the flora of Brazil. Two among them – which he published in co-authorship with Campos Porto – are of special importance for us: *Index Orchidacearum in Brasília inter mdccccvi et mdcccxxxii explorata sunt* (1935) and *Orchidaceæ Novæ Brasilienses I-VIII* (1935-1958).

Brade's botanical work was enormous. Orchidaceae was one of his favorite plant families, and he established close relationships with all the important orchidologists of his time: Paulo Campos Porto, Rudolf Schlechter, Frederico C. Hoehne, Guido Pabst, and Friedrich Kraenzlin. He described a number of new orchid genera and dozens of new orchid species.

Among the orchid genera described by Brade or by Brade & Campos Porto, we find: *Pygmaeorchis* Brade, *Duckeella* Porto & Brade (Fig. 54), *Eunannos* Porto & Brade, *Pleurothallopsis* Porto & Brade, and *Pseudolaelia* Porto & Brade.

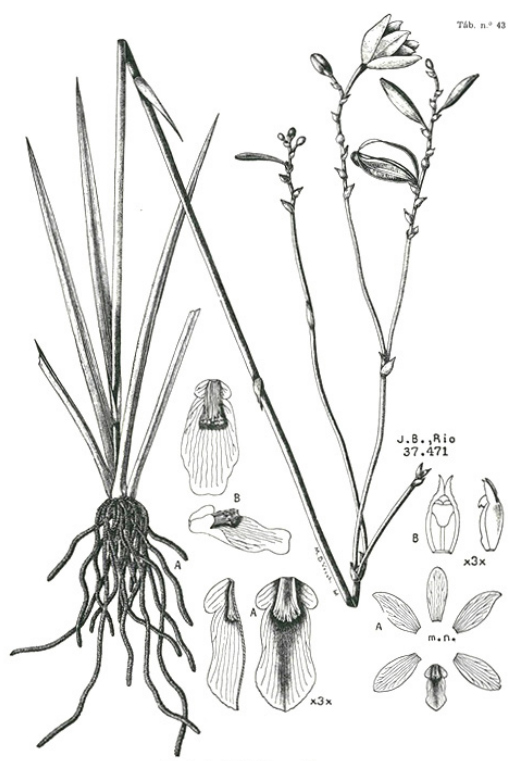


Figure 54. *Duckeella adolphii*. Drawing by Hoehne in his *Flora Brasilica*, plate 43.

Table 1. Orchid species described by Alexander Curt Brade.

Bifrenaria caparaoensis Brade	*Encyclia gallopavina* Brade	*Pleurothallis adirii* Brade
Bifrenaria villosula Brade	*Encyclia jenischiana* Brade	*Pleurothallis bocainensis* Porto & Brade
Bulbophyllum adiamantinum Brade	*Encyclia megalantha* Brade	*Pleurothallis caparaoensis* Brade
Bulbophyllum campos-portoi Brade	*Encyclia pauciflora* Brade	*Pleurothallis carrisii* Brade
Bulbophyllum vaughanii Brade	*Encyclia purpurachyla* Brade	*Pleurothallis castellensis* Brade
Campylocentrum iglesiasii Brade	*Encyclia randii* Brade	*Pleurothallis gracilisepala* Brade
Campylocentrum kuhlmannii Brade	*Encyclia xipheroides* Brade	*Pleurothallis guimaraensii* Brade
Capanemia duseniana Brade	*Encyclia yauaperyensis* Brade	*Pleurothallis imbeana* Brade
Centroglossa castellensis Brade	*Epidendrum geraldii* Brade	*Pleurothallis mathildae* Brade
Cirrhaea nasuta Brade	*Epidendrum geraldoi* Brade	*Polystachya rupicola* Brade
Cryptarrhena brasiliensis Brade	*Epithecia mattogrossensis* Brade	*Pygmaeorchis brasiliensis* Brade
Cryptophoranthus jordanensis Brade	*Lepanthopsis congestiflora* Brade	*Saundersia paniculata* Brade
Cycnoches espiritosantense Brade	*Lepanthopsis unilateralis* Brade	*Scaphyglottis matogrossensis* Brade
Cyrtopodium intermedium Brade	*Maxillaria caparaoensis* Brade	*Stenocoryne caparaoensis* Brade
Dichaea mattogrossensis Brade	*Maxillaria matogrossensis* Brade	*Stenocoryne villosula* Brade
Dipteranthus ovatipetalus Brade	*Maxillaria modesta* Brade	*Theodorea paniculata* Brade
Encyclia advena Brade	*Mormodes amazonica* Brade	*Theodorea paniculata* Brade
Encyclia albopurpurea Brade	*Mormodes amazonica* Brade	*Thysanoglossa organensis* Brade
Encyclia bicornuta Brade	*Notylia trullulifera* Brade	*Trichopilia santos-limae* Brade
Encyclia conspicua Brade	*Platystele brasiliensis* Brade	*Trichopilia santoslimae* Brade
Encyclia euosma Brade	*Pleurothallis adamantinensis* Brade	*Zygostates kuhlmannii* Brade

The list of new orchids described by Brade finds no end (Table 1). A great part of these species was described in Schlechter's *Orchidaceae Bradeanae Paulensis* (1925a).

Campos Porto and Brade described an important number of new orchid species: *Capanemia adelaidae, Centrogenium janeirense, Centrogenium schlechterianum, Centroglossa nunes-limae, Constantia cipoensis, Duckeella adolphii* (Fig. 54), *Encyclia squamata, Epidendrum duckei, Epidendrum janeirense, Epidendrum magdalenense, Epidendrum mantiqueranum, Hapalorchis pauciflora, Octomeria anceps, Octomeria cucullata, Phymatidium limae, Pleurothallis bocainensis, Pleurothallis lichenophila, Pleurothallis limae, Pleurothallis radialis, Pseudolaelia corcovadensis, Thysanoglossa jordanensis,* and *Zygostates octavioreisii*.

Aditionally, a number of new orchids was described by Hoehne & Brade: *Cladobium spannagelianum* and *Pleurothallis peroupavae*; and by Brade & Pabst: *Erythrodes fissirostris*, *Erythrodes mendoncae, Habenaria mello-barretoi, Octomeria itatiaiae*, and *Pelexia magdalenensist*.

Before Brade's botanical knowledge had grown to the point of allowing him to make his own determinations, his orchid specimens were determined by others. The largest number were described by Rudolf Schlechter: *Cranichis bradei, Cyclopogon bradei, Cyrtopodium bradei* Schltr. ex Hoehne, *Dipteranthus bradei, Habenaria bradei, Maxillaria bradei, Pelexia bradei* Schltr. & Mansf., *Physosiphon bradei, Pleurothallis bradei, Polystachya bradei* Schltr. ex Mansf., *Pseudostelis bradei, Spiranthes bradei, Stenorrhynchos bradei*, and *Vanilla bradei* Schltr. ex Mansf.

Hoehne described from Brade's collections *Habenaria curti-bradei* Hoehne, *Cyrtopodium bradei* Schltr. ex Hoehne, and *Masdevallia bradei* Schltr. ex Hoehne. Finally, Kraenzlin described *Epidendrum bradeanum*, *Habenaria bradeana* and *Pogonia bradeana,* and Guido Pabst *Laelia bradei* (Fig. 55), and *Pleurothallis curti-bradei*.

The herbarium of the Botanical Garden in Rio de Janeiro and its scientific journal were named in Brade's honor *Herbarium Bradeanum* and *Bradea*, respectively (Scheliga 2003) (Fig. 56).

Paulo Campos Porto (1889–1968; collected 1917–1936)

As the grandson of Brazil's greatest orchidologists of the 19th century, João Barbosa Rodrigues, it can be said that Paulo Campos Porto (Fig. 57) was born with orchids in his blood.

Campos Porto occupied important positions in botanical institutions during his life, and together with Hoehne, Brade, Pabst, Kuhlmann and a few others formed the nucleus of Brazilian orchidology during the first seven decades of the 20th century. In 1914, with a position as naturalista viajante, he became part of the staff of the Botanical Garden of Rio de Janeiro, an institution he would serve as Director during the periods of 1933–1938 and 1951–1958. He was also Director of the Institute of Plant Biology and Director of the Audit Council for the Brazilian Scientific and Artistic Expeditions. He occupied the position of Secretary of State for Agriculture of Bahia, where he was involved in the creation of the Monte Pascoal National Park (1951).

An important milestone in Campos Porto's life was his participation in the Federal Forest Council and in the Organizatory Committee for the creation of the Itatiaia National Park (Fig. 58). His activity in this Committee was fundamental to the constitution of the Itatiaia Forest Reserve. It had been already decided that the reserve would be managed as a dependency of the garden in Rio (1914). The first land had been bought in 1908, and the first steps leading to the constitution of the reserve were undertaken after Antônio Pacheco Leão took over as Director of the Botanical Garden in Rio, in 1915. The creation of the Itatiaia Biological Station (1929) led to the subsequent formal creation of the Itatiaia National Park, the first national park in Brazil (1937) (Fonseca Casazza 2014).

Aside from his involvement in the purchase of the land where the Biological Station was later established under his direction, Campos Porto began a systematic exploration of the region in 1915, organizing constant botanical excursions to the Serra de Itatiaia. In several of these excursions he was accompanied by Maria do Carmo Vaughan Bandeira (1902–1992), a young botanist who was the first woman to hold a position as researcher at the Botanical Garden in Rio (Fig. 59). Maria Bandeira, for reasons still unknown, abandoned her promising career in 1931 and went

Figure 55. *Laelia bradei*. Photograph by Mauro Rosim.

Figure 56. *Bradea* logotype.

Figure 57. Paulo Campos Porto. Archives of Rudolf Jenny.

FIGURE 58. Pico Agulhas Negras, Itatiaia National Park. Photograph by Gabriel Vallim.

FIGURE 59. Maria Bandeira and Campos Porto in front of the Biological Station of the Itatiaia Forest Reserve (now Itatiaia National Park). Unknown photographer.

Figure 60. *Bulbophyllum campos-portoi*. Photograph by Sandro Lucas Xavier Tobias.

Figure 61. *Stelis campos-portoi* (as *Stelis pauciflora* Lindl.). Photograph by Luis Filipe Varella..

into a convent in Rio where she lived for the rest of her life as a cloistered nun (Bediaga *et al*. 2016).

The activities of Campos Porto in the study and protection of Brazil's natural heritage was, however, not limited to Itatiaia. The 1930s were marked by the revolution of 1930, which brought to power Getúlio Dornelles Vargas, who in November of that year was named President of the Provisional Government. Among other aspects of the Vargas Government (who remained in power until 1945) was the idea of establishing measures for the protection of natural areas. In this process, botany played an important role. A series of protectionist laws were approved during this period, among them the National Codes for Forestry, Hunting and Fishing, Water and Mines, and the establishment of the Audit Council for the Brazilian Scientific and Artistic Expeditions, of which Paulo Campos Porto became Director. This council was created in 1932, with the purpose of establishing rules and codes for private national and foreign expeditions across the country.

In addition to these official duties, Campos Porto took part in other scientific and environmentalist activities. He was member of the Technical Council in the First Brazilian Conference for the Protection of Nature in 1934 and in 1938 organized the First South American Botanical Conference. All this, together with the positions of Director of the Institute of Plant Biology and the Botanical Garden of Rio de Janeiro, converted Campos Porto into a cornerstone of nature conservation policies during the first years of the Vargas government.

The conservation of Brazil's natural heritage in the light of science, the appreciation of its beauty and the research into its economic possibilities is not a novel ideal but already a deep concern of a group of scientists in the first decades of the 20th century.

Campos Porto described only one orchid by himself: *Cattleya itatiayae* Porto. Many others were described by him in co-authorship with Alexander Curt Brade (see previous chapter). Together with Schlechter he described the genus *Leaoa* Schltr. & Porto with its type species *Leaoa monophylla* Schltr. & Porto (Fig. 4). Finally, based on collections by Loefgren he described *Maxillaria barbosae* Loefgr. ex Porto and *Pleurothallis glandulifera* Loefgr. ex Porto.

The following species of Orchidaceae were named in his honor: *Bulbophyllum campos-portoi* Brade (Fig. 60), *Encyclia campos-porto*i Pabst, *Epidendrum campos-portoi* Barberena, *Habenaria campos-portoi* Schltr., *Octomeria campos-portoi* Schltr., and *Stelis campos-portoi* Garay (Fig. 61).

Albino Hatschbach Sobrinho (1874–1973; collected 1915–1925)

In his *Orchidaceae Hatschbachianae* Schlechter (1926a) wrote: "I received since the years of 1920 in regular intervals from Mr. Albino Hatschbach in Curytiba, Parana, small packets of orchids for determination […] Our knowledge about the orchid

FIGURE 62. Albino Hatschbach Sobrinho (1890-1973). Archives of Rudolf Jenny.

flora of Parana and the distributuion of the species is, after receiving this collection, now much more complete. It is, after the collections of Dr. Peter Dusen, undoubtedly the most important ever gathered in Parana" (Schlechter 1926a: 32). With these words, Schlechter introduced one of the most important and successfull plant collectors who worked in Paraná, Brazil's southernmost state, during the first decades of the 20th century, Albino Hatschbach Sobrinho (Fig. 62), the son of an Austrian father and a Brazilian mother.

The orchid colllection described by Schlechter in his above quoted work comprised a total of over 140 specimens, mostly epiphytes; for Schlechter a welcome supplement to the orchids of Per Dusen, who had sent to Berlin mostly terrestrial plants.

At the age of nine Hatschbach was sent to Germany to complete his studies. He spent a total of nine years there, during which time he became familiar with the work of Rudolf Schlechter; this awoke in him the passion for orchids. Albino Hatschbach returned to Curitiba in 1908 to work in his grandfather's shoe factory.

His love for orchids received a new impulse from one of his neighbors, Bruno Rudolf Lange (see below), one of the first orchid collectors in Paraná. Together with Lange, Hatschbach made long excursions to the Atlantic forests and collected large numbers of orchids, which he sent occasionally to Schlechter in Berlin for determination. Schlechter published Hatschbach's specimens in his *Beitraege zur Kenntnis der Orchidaceenflora von Parana II, Orchidaceae Hatschbachianae* (1926a). He described them as so extraordinarily well prepared that in most cases a determination could be easily made.

Hatschbach established also a working relationship with Per H. Dusén, who collected in Parana during his time.

Orchids became his main pastime and Albino Hatschbach became a pioneer or orchid culture in Curitiba. He was one of the founders of the *Sociedade Paranaense de Orquidófilos* and its president for several periods.

In 1925 he returned to Germany; he had been invited by Schlechter to visit him in Berlin. However, on his arrival in Lisbon he received from Dr. Mansfeld the sad news that Schechter had passed away just a few weeks before. Nevertheless, he continued his journey and soon arrived in Dahlem, the suburb of Berlin where the Botanical Museum had been established. He wanted to revere *in loco* the memory of the great botanist. After wandering through the workrooms and admiring the collection of over 5,000 drawings of orchid species, all made by Schlechter himself, he met Dr. Mansfeld, who at that time was already an authority on orchids. Several years later, in an interview with Edmundo Gardolinski, Hatschbach remembered Mansfeld's words: "Schlechter's knowledge of orchids was at a level that nobody would reach without working at least 10 years at it". Hatschbach left Berlin, "this paradise of the world of orchidology", as he said, "with deep sadness and much sorrow" (Gardolinski 1960: 141).

Hatschbach then began corresponding with Frederico Carlos Hoehne, who already had a excellent reputation in the orchid world. Years later he corresponded also with Guido Pabst, a rising star in Brazilian orchidology. Pabst asked him in one of his letters to collect for him specimens of *Oncidium albinoi* (Fig. 63A), which he had never seen.

Figure 63. A. *Oncidium albinoi* [as *Baptistonia albinoi* (Schltr.) Chiron & V.P. Castro]. B. *Pleurothallis hatschbachii* [as *Pleurobohryum hatschbachii* (Schltr.) Hoehne]. C. *Maxillaria hatschbachii* (as *M. madida* Lindl.). D. *Octomeria hatschbachii*. Photographs by Luis Filipe Varella (A, D), Jan Meijvogel (B), Edison da Silva Bezerra (C).

Hatschbach regretted to answer: "in the place where I found these plants there are today only houses" (Anonymous 1974: 258).

It was with good reason that Schlechter wrote, after the end of World War I: "Since in today's Germany no one is in the condition to pay for these [Hatschbach´s] collections, we do but only one thing, to erect a symbolic monument by giving his name to the new species" (Gardolinski 1960: 140). Thus, Schlechter dedicated to Hatschbach the following new orchid species: *Capanemia hatschbachii*, *Cyclopogon hatschbachii, Oncidium albinoi* (Fig. 63B), *Pleurothallis hatschbachii* (Fig. 63A), *Maxillaria hatschbachii* (Fig. 63C), *Epidendrum hatschbachi, Octomeria hatschbachii* (Fig. 63D), and *Oncidium hatschbachii*.

Albino Hatschbach died in 1973. He left two sons, Erin Hatschbach and Gert Hatschbach (1923–2013) The latter, Gert, following in his father's footsteps, studied botany; in 1966 he founded the Botanical Museum of the city of Curitiba.

The orchids collected by Gert Hatschbach were described mainly by Frederico Carlos Hoehne. The Orchid Herbarium of Oakes Ames, at Harvard University, holds the following specimens collected by G. Hatschbach: *Brachystele hatschbachii* Pabst, *Epidendrum avicula* Lindl., *Pleurothallis bacillaris* Pabst, *Pleurothallis bleyensis* Pabst, *Pleurothallis gonzalezii* Pabst, and *Pleurothallis piraquarensis* Hoehne.

Dedicated to Gert Hatschbach were: *Pleurothallis gert-hatschbachii* Hoehne (Fig. 64), *Cleistes gert-*

FIGURE 64. Holotype of *Pleurothallis gert-hatchbachii.* Specimen at Instituto de Botânica, São Paulo, #55315.

Figure 65. Parana Railway under construction, early 1880s. Photographs by Marc Ferrez.

hatschbachiana Hoehne, *Brachystele hatschbachii* Pabst, *Cyrtopodium hatschbachii* Pabst, *Psilochilus hatschbachii* Kolan., *Habenaria hatschbachii* Pabst, and *Bulbophyllum hatschbachianum* E.C.Smidt & Borba.

A word must be said about the fundamental role that the Parana Railway played in the botanical exploration of the state. Roads were limited to urban areas and their surroundings, and only the railway was able to transport botanists and plant collectors into promising plant collection areas. This was the case – as we have seen – for Per Dusén, but it was no different for Hatschbach, nor – as we will see – for Bruno Rudolf Lange.

The main part of this railway network was the line from the Atlantic port of Paranaguá to Curitiba, which was constructed between 1880 and 1884 (Fig. 65). The work was divided into three parts: Paranaguá−Morretes, Morretes−Roça Nova, and Roça Nova−Curitiba. If we look at the collecting localities mentioned by Schlechter in his works about the orchid flora of Parana, we will find that over half of them, are close to the train stations on this route.

Bruno Rudolf Lange (1860–1922; collectd 1890–1935)

Born in Leipzig, Germany, Bruno Rudolf Lange (Fig. 66) arrived in Curitiba, the capital of the state of Parana, in 1883 as a result of the Brazilian Government's program of recruiting European engineers for the construction of the southern railroads.

As already mentioned, Lange was the first to induce Hatschbach into collecting orchids. Additionally, as engineer in charge of the railway, he was instrumental in securing both Dusén and Hatschbach safe, fast transportation to the most remote collecting areas along the Paranaguá-Curitiba line. Along this line, one of the stations was built at a point named Volta Grande and inaugurated around 1904. In 1925 this station was renamed in Lange's honor as *Estaçao Engenheiro Lange*, and still exists (Fig. 67). Bruno R. Lange was also responsible for other important projects, such as the reform of the Curitiba Train Station, and those of Paranaguá and Antonina.

Lange's descendants played important roles in the artistic and scientific life of Parana. His son Frederico Augusto Lange was a famous painter and a researcher in

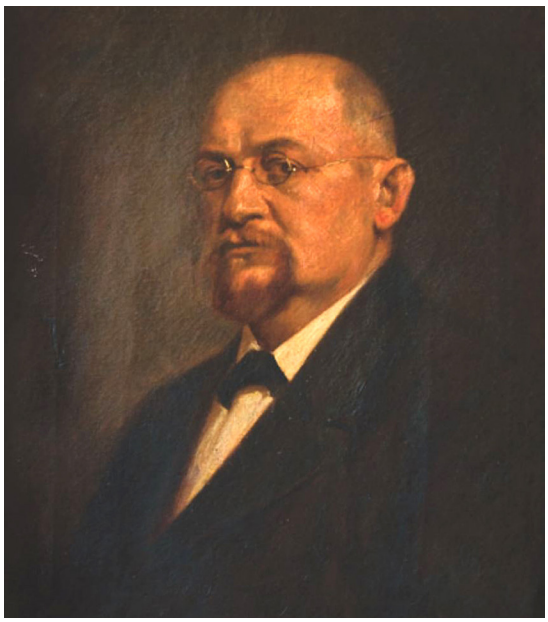


Figure 66. Bruno Rudolf Lange. Oil on canvas by Alfredo Andersen, 1903.

Figure 67. *Estaçao Engenheiro Lange*, 1940s.

Figure 68. *Cyclopogon langei* [as *C. congestus* (Vell.) Hoehne]. Photograph by Luis Filipe Varella.

malacology; his grandson Rudolf Bruno Lange became one of the most famous naturalists of Parana, a specialist in entomology, matozoology and orniothology, and Director of the Paraná Museum in Curitiba while teaching at the Catholic University of the state.

Lange made a small collection of orchids, among which we find *Pelexia hysterantha* (Rodr.) Schltr. and *Cyclopogon chloroleucus* (Rodr.) Schltr., as well as two new species that were dedicated to him: *Cyclopogon langei* Schltr. (Fig. 68) and *Pleurothallis langeana* Kraenzl.

At the end of this chapter we want to mention a few collectors who made smaller, albeit important contributions to the knowledge of the orchid flora of Rio Grande do Sul. Little is known about their lives, the biographical information publicly available is too scarce. However, their orchid collections brought to light a number of new orchid species, all of them described by Schlechter in 1925 in his *Orchideenflora von Rio Grande do Sul*.

Francisco D'Aquino (?–?) and **L. Burger** (?–?); both collected 1910–1925

In 1942, Urbano Kley published an article in *Orquidea*, under the title *Cattleya aquinii* Barb. Rodr. In a free translation, here is what he had to say about the history of this plant: "as a friend and disciple of the late Francisco d'Aquino, and knowing the history of this plant, I have dared to write this brief historical sketch, wishing to contribute to the knowledge of the circumstances leading to the discovery of this botanical treasure. Around the years 1874 to 1875, Mr. Antonio J. da Silva Valadares, from the capital of Rio Grande do Sul, received from different locations a great number of tree trunks covered with *Cattleya intermedia*, among which a plant stood out, different from the others because of its color and form of the flowers. This *Cattleya* called the attention of Francisco d'Aquino, a good friend of Mr. Valadares and one of the most important orchidophils of his time. Seeing Aquino's interest in this plant, Valadares presented it to him. Aquino cultivated it for eight years and some time later made several divisions of it, distributing them among his fellow orchid collectors. As can be seen, the few existing specimens are descendants of this first plant. Being Aquino a collaborator of the great Brazilian scientist, Dr. Barbosa Rodrigues, at the time Director of the Botanical Garden in Rio de Janeiro,

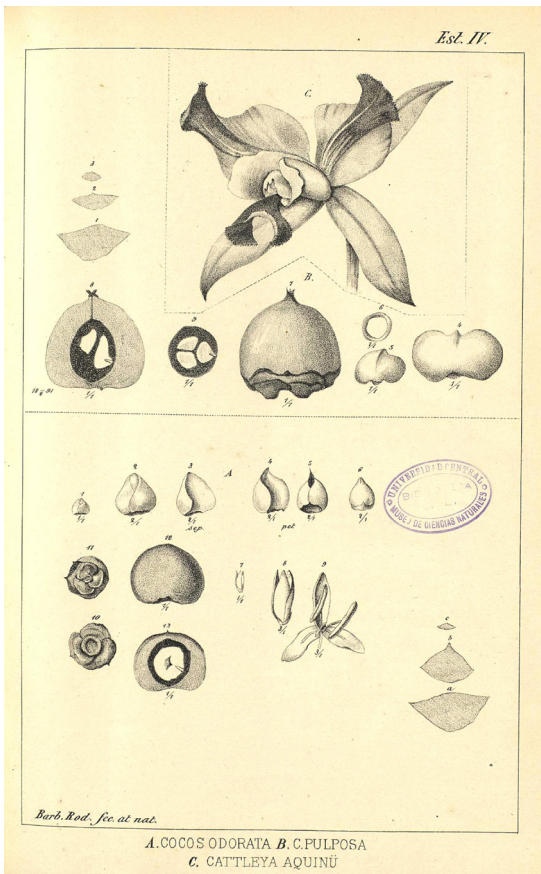


Figure 69. *Cattleya aquinii* Barb. Rodr. (above). Drawing by Barbosa Rodrigues in *Plantas novas cultivadas no Jardim Botanico do Rio de Janeiro*, vol. 1: plate IV, 1891.

he gave him one of the divisions, which was recognized by Barbosa Rodrigues as a new species from the state of Rio Grande do Sul and described and illustrated by him in his work *Plantas novas cultivadas no Jardim Botanico do Rio de Janeiro*" (Kley 1942:120) (Fig. 69).

These lines were written in 1891. Some 30 years later, Schlechter began preparing his orchid flora of Rio Grande do Sul. He wrote then: "to achieve my goal, I made contact with various orchid lovers in Porto Alegre. Through their collaboration I was able to start corresponding with a few collectors. Above all, I must thank Mrs. L. Burger and Francisco Aquino, for the eagerness with which they promoted my interests".

Aquino sent an important number of orchid specimens to Schlechter, of which many were proven as new to science. With his own specimens, Aquino sent a number of orchids collected by Burger – of whom we could only retrieve the initial and family name – which are all labeled *Burger [xxx] in collectionis Aquino*. Curiously the specimens collected by Burger outnumber those of Aquino by at least 7:1. This means that the main collector was undoubtedly L. Burger.

Only 2 orchid specimens collected by Aquino and described by Schlechter were new to science: *Pleurothallis aquinoi* (Aquino iv) and *Polystachya micrantha* (Aquino xxii).

Burger's new orchids were much more numerous: *Cleistes australis* (Burger xxiv), *Pelexia burgeri* (Aquino xxx), *Pelexia gracilis* (Burger xiv), *Stelis aquinoana* (Burger xxxi), *Octomeria unguiculata* (Burger xxix), *Epidendrum burgeri* (Burger xvi, xvii), *Promenaea riograndensis* (Burger xxxii), *Phymatidium aquinoi* (Burger xix), *Ornithocephalus brachystachyus* (Burger xvi), and *Zygostates aquinoi* (Burger xx),

Additionally, Schlechter described together with Hoehne from Burger's collections *Epidendrum pseudodifforme* Hoehne & Schltr. (Burger xviii).

As in other cases, it is surprising to see how important plant collectors, such as Aquino and Burger, who made important contributions to the knowledge of the orchids of their homeland, remain largely unknown. It seems like an axiom that the closer in time a specific botanist or collector is, the harder it is to find biographical information about him, if not, with some probability, by means of an investigation on the spot and through family documents - an effort that goes beyond the intentions of this work and probably exceeds the value of the individual contributions. As we will see, the same can be said about the life of a few Brazilian orchid lovers, which we will try to describe next, and with whom we will end this chapter.

Urbano Kley (?–?; collected 1910–1925)

In the introduction to work on the orchids of Rio Grande do Sul, Schlechter wrote: "I must thank Mr. Urbano Kley for a collection of 18 numbers, among which I found various quite interesting species". Among these he described a new species, *Habenaria kleyi* (Fig. 70). A few other orchids were sent by Kley to Schlechter, but apparently he did not collect them himself: *Habenaria schmittmeyeri* was described by Schlechter from a specimen labeled: "M. Schnittmeyer in collectione Kley", meaning that it was a certain Max Schnittmeyer who made the original collection. A few

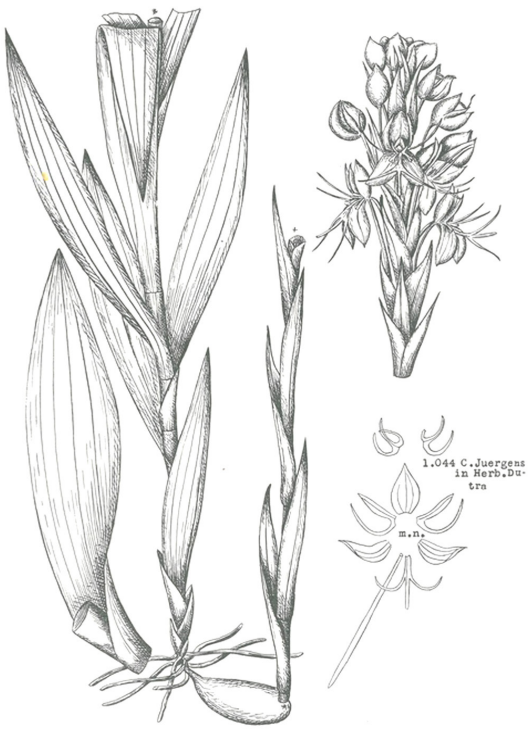


FIGURE 70. *Habenaria kleyi.* Drawing by Hoehne in his *Flora brasilica,* plate 13.

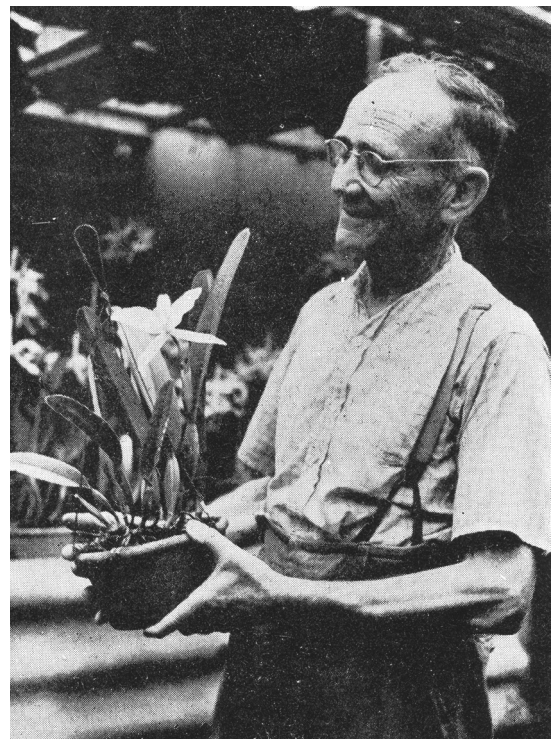


FIGURE 71. Urbano Kley showing one of his Laelias. Unknown photographer. Archives of Rudolf Jenny.

other specimens, among them *Neolauchea pulchella* Kraenzl., *Cirrhaea saccata* Lindl. and *Maxillaria plebeja* Rchb.f. were collected by a HEINRICH RENNER and labeled similarly: "H. Renner in collectione Kley".

Urbano Kley (Fig. 71), a merchant and orchid grower from Porto Alegre and son if German immigrants, liked to call himself a "disciple of Franzisco Aquino". In 1949 he was one of the founding members of the CGO, the *Circulo Gaucho de Orquidofilos*. This seems to be all we can access in relation to his life, according to public information sources, confirming the axiom we mentioned above. Even if he had devoted his entire life to orchids, the documents published on the biography of Urbano Kley do not allow us to elucidate his figure more, unless we undertake an exhaustive search starting from the family environment.

CARLOS JÜRGENS (?–?; collected 1921–1924)

Who was Carlos Jürgens? Schlechter (1925: 2) wrote: "the collection of Mr. Carlos Jürgens, who has so far sent me 103 numbers, has been a special contribution to the orchid flora of Rio Grande do Sul. His specimens are not only extremely well prepared, but also accompanied with important details about flower color and collecting localities […]. It cannot be denied that the orchid collection of Carlos Jürgens must be considered as the most important for the state of Rio Grande do Sul".

Before Schlechter published his orchid flora of Rio Grande do Sul, the name of Carlos Jürgens appeared as one of the settlers of the German colony of Nueva Germania, in northeastern Paraguay. Nueva Germania was founded in 1886 by Bernard Förster and Carlos Jürgens is named in 1901 as one of farmers who had developed new methods for the germination of the seeds of "yerba mate" (*Ilex paraguariensis* A.St.-Hil.).

A few years later, we find again a Carlos Jürgens, now in Argentina, in the German colony of San Carlos de Bariloche, where he is cited as the President of the German Church and School Association, a position he held from 1913–1917.

However, we have not found any other information, and it seems doubtful – Jürgens being a relatively common German family name – that the

Figure 72. *Capanemia juergensiana* [as *C. superflua* (Rchb.f.) Garay]. Photograph by Luis Filipe Varella.

Figure 73. *Octomeria fialhoensis* (as *O. diaphana* Lindl.). Photograph by Luis Filipe Varella.

C. Jürgenses named above are one and the same as Schlechter's outstanding orchid collector. Thus we are forced to concentrate on Jürgens' orchids and collecting localities, but cannot say anything else about Jürgens himself.

Schlechter described a total of 12 new orchid species from Jürgens' collections. Of these, 9 where dedicated to him: *Capanemia juergensiana* (Fig. 72)*, Platyrhiza juergensii, Habenaria juergensii, Sarcoglottis juergensii, Cryptophoranthus juergensii, Stelis juergensii, Pleurothallis juergensii, Octomeria juergensii*, and *Maxillaria juergensii*.

João Dutra (1862–1936; collected 1925)

When Schlechter was reviewing the final version of his orchid flora of Rio Grande do Sul, he unexpectedly received an additional collection. In his words: "After the work had been already finished, I received from Dr. Dutra, in São Leopoldo, a small important collection, containing a number of new species. Very valuable were also the accompanuing notes in which Dr. Dutra described many orchids from his region, which were so well characterized that I found some new species which were until then unknown to me" (Schlechter 1925:3).

As with others, Dutra's life remains a mystery. We only know that he lived and collected in and around São Leopoldo, then a small town, about 20 miles of Porto Alegre.

According to Pabst, for unknown reasons Dutra could not work on orchids during his life as much as he would have wished. Because of this he kept many new orchid species in his herbarium which he never published and so soon lost priority on them. In the foreword to volume II of his *Orchidaceae Novae Riograndenses a Cl. João Dutra descripta vel nominata sed nunquam luci editae* (=New Orchidaceae from Rio Grande, described and named in the collection of João Dutra, but never published), Pabst (1959: 125) wrote: "We want here to present a homage to Dr. João Dutra, who studied the Orchidaceae and the Phanerogams of Rio Grande. For certainly unwilling reasons he could not publish during his lifetime the new species which he recognized so that many of them lost their priority".

Pabst described a number of new species, for which Dutra had already chosen a name, so that they all appear as authored by "Dutra ex Pabst". Among them we find *Octomeria fialhoensis* (Fig. 73), *Barbosella riograndensis*, *Bipinnula canisii, Cryptophoranthus spicatus* Dutra, *Cyclopogon vittatus, Pleurothallis malmeana*, and *Sanderella leopoldinensis*.

A number of other species were dedicated to him by Schlechter, Pabst and Ruschi: *Campylocentrum dutraei* Schltr., *Cyclopogon dutraei* Schltr., *Habenaria dutraei* Schltr., *Pleurothallis dutrae* Pabst (Fig. 74), *Encyclia dutrae* Pabst (Fig. 75), and *Pseudolaelia dutraei* Ruschi.

Acknowledgements. Our warm thanks to Johannes Lundberg, Ph.D., Herbarium Manager, Swedish Natural History Museum, Stockholm, for the portrait of Carl M. Lindman. To Ron Parson for permission to use his photograph of *Pleurothallis per-dusenii* (*Acianthera crinita*). And, as always, to Mark Budworth for his outstanding philological revision.

FIGURE 74. *Pleurothallis dutrae* [as *Acianthera dutrae* (Pabst) C.N.Gonc. & Waechter]. Photograph by Dalton Holland Baptista.

FIGURE 75. *Encyclia dutraei* [as *E. pauciflora* (Barb. Rodr.) Porto & Brade]. Photograph by PeterB.

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NOTES ON THE GENUS *STICHORKIS* (ORCHIDACEAE, MALAXIDINAE) IN MALESIA: NEW COMBINATIONS, SYNONYMS AND LECTOTYPIFICATIONS

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Abstract. 41 new combinations, two synonyms and three lectotypifications from the genus *Stichorkis* are proposed. This work aimed to solve taxonomic ambiguity and nomenclatural crisis for Malesian *Stichorkis*.

Key words: Malaxideae, new combinations, Orchidaceae, Philippines, plant Taxonomy, tropical botany

Introduction. The orchid genus *Stichorkis* Thouars (nom. & typ. cons.) is represented by approximately 60 species distributed from the Comoro Islands, Mauritius, Reunion to Sri Lanka, India, through Malesia to Fiji with the centre of diversity in New Guinea where 23 species are recorded (Naive *et al.* 2019). In the process of examining all types of orchids in Malesia, in preparation for previous and ongoing revision, it became clear that more names than those published by Cootes (2011) need combination in Philippine *Stichorkis*. In this paper, we transfer five taxa from *Cestichis* Thouars ex Pfitzer and one from *Liparis* Rich., two of which had been overlooked. The other four had an incorrect basionym when previously transferred, therefore making the names either invalid or illegitimate (Article 41.6; Turland *et al.* 2018). Thus, the opportunity to emend the nomenclature is taken here. We also use the occasion to lectotypify these names, which is why type data are cited here. Furthermore, nine new combinations from West Malesia and 26 new combinations from East Malesia are proposed.

New combinations and a new synonym from the Philippines

Stichorkis elmeri (Ames) Naive & Ormerod, ***comb. nov.***

Basionym: *Cestichis elmeri* Ames, Orchidaceae 1: 10. 1905.

Synonym: *Liparis elmeri* (Ames) Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 210. 1911. *Disticholiparis elmeri* (Ames) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PHILIPPINES. Luzon: Mt. Santo Tomas, Prov. Benguet, "forming colonies on trees", 1 July 1904, *A.D.E. Elmer 6553* (holotype: AMES00106597!; isotypes: K, US, NY). FIG. 1B.

Distribution: This Philippine endemic species is only recorded and observed in the provinces of Benguet and Quezon of Luzon island (Pelser *et al*. 2011).

Among the Malaxidinae herbarium specimens, especially at AMES, we found plants preliminarily called *Cestichis elmeri*. The plants are without any doubt is representative of the genus *Stichorkis* and is therefore recognized here as a new combination. According to Ames (1905), this species is closely similar to *S. merrillii* (Ames) Naive & Ormerod by having an orbicular-apiculate labellum, non-emarginate anther, and laxer inflorescence. This taxon is not to be confused with *Liparis elmeri* Ames, described in 1912 and renamed *L. dumaguetensis* Ames. The latter is a terrestrial species with convolute leaves, unrelated to the genus *Stichorkis*.

Stichorkis gibbosa (Finet) J.J.Wood, Orchids Mount Kinabalu 2: 531. 2011.

Basionym: *Liparis gibbosa* Finet, Bull. Soc. Bot. France 342. 1908. *Disticholiparis gibbosa* (Finet) Marg. & Szlach., Orchidee (Hamburg) 55: 178, 2004.

TYPE: INDONESIA. Java, without locality, *Blume s.n.* (holotype: P-image!)

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Liparis quadribullata Schltr., Repert. Spec. Nov. Regni Veg. 10: 29. 1911. TYPE: INDONESIA. Sulawesi, Toli-Toli District, upper Lampasioe River, 150 m, January 1910, *Schlechter 20668* (holotype: B, destroyed; isotypes: AMES, K), ***syn. nov.***

Distribution: Myanmar, Vietnam, Cambodia, Laos, Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Indonesia, New Guinea, Pacific Islands, Philippines.

Stichorkis gracilis (Ames) Naive & Ormerod, ***comb. nov***.

Basionym: *Cestichis gracilis* Ames, Orchidaceae 2: 136. 1908.

Synonyms: *Liparis amesiana* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 210. 1911. *Disticholiparis gracilis* (Ames) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004. *Stichorkis amesiana* (Schltr.) Cootes, Philipp. Nat. Orch. Sp.: 245. 2011, *nom. illeg.*

TYPE: PHILIPPINES. Luzon, Bataan Prov., Mt. Mariveles, 31 January 1904, *E.B. Copeland 274* (lectotype, here designated: AMES8217!; isolectotypes: K, US); Rizal Prov., Mt. San Isidro, 10 January 1907, *M. Ramos 1782* (syntype: AMES-image!; isosyntype: K). FIG. 1C.

Distribution: Endemic to the Philippines. Recorded in the provinces of Bataan, Rizal, Mindoro, Bukidnon, and Davao.

Because of the earlier *Liparis gracilis* J.D. Hook. of 1890 (= *L. elegans* Lindl.) and *L. gracilis* Rolfe of 1891 (= *L. gracilenta* Dandy), Schlechter renamed *Cestichis gracilis* Ames as *Liparis amesiana* when he moved the plant to *Liparis*. Since the name *Cestichis gracilis* is the oldest and the epithet is still available, it is the one that must be used when treating the plant in *Stichorkis*. We have chosen *Copeland 274* as lectotype since this has a copy of the original illustration appended to it by Ames.

Stichorkis merrillii (Ames) Naive & Ormerod, ***comb. nov.***

Basionym: *Cestichis merrillii* Ames, Orchidaceae 1: 11. 1905.

Synonyms: *Liparis merrillii* (Ames) Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 210. 1911. *Disticholiparis merrillii* (Ames) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PHILIPPINES, Luzon, Bataan Prov., Mt. Mariveles, 1200 m, 1 January 1905, *E.D. Merrill 3736* (holotype: AMES00106604!; isotype: US 00093468). FIG, 1D.

Distribution: Endemic to the Philippines. Recorded in the provinces of Bataan, Ifugao, Mountain Province, Nueva Ecija, Nueva Vizcaya, Quezon, Rizal, Mindoro, Leyte, Misamis, Zamboanga.

Though Ames (1905) listed two collections when he published this species, he implied in his notes that Merrill 3736 was the type, and that H.N. Whitford 317 (AMES) was a second collection, i.e. a paratype. Jim Cootes transferred this taxon to *Stichorkis* in 2011, but unfortunately cited the incorrect basionym (*Liparis merrillii*), thus making the proposal invalid.

Stichorkis nutans (Ames) Naive & Ormerod, ***comb. nov.***

Basionym: *Cestichis nutans* Ames, Philipp. J. Sci., C 4: 597. 1909.

Synonym: *Liparis nutans* (Ames) Ames, Orchidaceae 5: 81. 1915.

TYPES: PHILIPPINES. Mindanao, Lake Lanao, Camp Keithley, May 1907, *M.S. Clemens s.n.* (lectotype, here designated: AMES00106605!); Surigao Prov., 6 April 1906, *P.H. Bolster 289* (syntype: AMES-image!); Palawan, Mt. Victoria, March 1906, *F.W. Foxworthy s.n.* (= BS 638) (syntype: AMES-image!). FIG. 1E.

Distribution: Endemic to the Philippines. Recorded in the provinces of Palawan, Agusan, Bukidnon, Lanao, Misamis Oriental, Surigao.

Like *S. merrillii* above this taxon had been transferred to *Stichorkis* but by incorrectly citing the later name in *Liparis*, making the proposal invalid. This species closely resembles *S. davidlohmanii* (Fig. 1A), however, it differs significantly in having a pyriform pseudobulb (vs. obovoid pseudobulb) and cuneate, non-canaliculate, conduplicate labellum (vs. obovate, canaliculate, non-conduplicate labellum).

Stichorkis philippinensis (Ames) Naive & Ormerod, ***comb. nov.***

Basionym: *Cestichis philippinensis* Ames, Orchidaceae 1: 7. 1905.

Synonym: *Liparis philippinensis* (Ames) Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 210. *Disticholiparis philippinensis* (Ames) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPES: PHILIPPINES, Luzon, Bataan Prov., Mt. Mariveles, 25 May 1904, *T.E. Borden 799* (lectotype, here designated: AMES5966!; isolectotype: US-image!); Mt. Mariveles, 8 August 1904, *E.D. Merrill 3856* (syntype: AMES!; isosyntypes: K-image!, NY-image!); Mt. Mariveles, 9 August 1904, *T.E. Borden 1597* (syntype: AMES-image!). FIG. 1F.

Distribution: Endemic to the Philippines. Recorded in the provinces of Abra, Bataan, Benguet, Cagayan, Laguna, Mountain Province, Nueva Vizcaya, Pampanga, Rizal, Mindoro, Panay, Leyte, Negros, Agusan, Bukidnon, Cotabato.

Again, as in some of the above names, the incorrect basionym was cited when transferring this taxon to *Stichorkis*, rendering the combination invalid.

Stichorkis propinqua (Ames) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis propinqua* Ames, Orchidaceae 7: 110. 1922

Synonym: *Disticholiparis propinqua* (Ames) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 179. 2004.

TYPE: PHILIPPINES, Bancalan Island, sea level, 14 October 1916, C.M. Weber 011 (holotype: AMES00100960!; isotypes: K, NY, S, SING!, US).

Distribution: Endemic to the Philippines. Recorded in the provinces of Bancalan Island, Davao, Laguna, Mindoro, Palawan, Quezon and Rizal.

New combinations and a new synonym from West Malesian taxa

Stichorkis anopheles (J.J.Wood) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis anopheles* J.J.Wood, Nord. J. Bot. 11, 1: 85. 1991.

Synonym: *Disticholiparis anopheles* (J.J.Wood) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: MALAYSIA. Sabah, Tambunan District, Mt. Trus Madi, above Kidukarok, 1560 m, 15 June 1988, *Surat in J.J. wood 871* (holotype: K).

Distribution: Malaysia (Sabah).

Stichorkis araneola (Ridl.) Naive & Ormerod, ***comb. nov***.

Basionym: *Liparis araneola* Ridl., J. Linn. Soc., Bot. 31: 265. 1896.

Synonym: *Disticholiparis araneola* (Ridl.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: INDONESIA. Kalimantan, Pontianak, *cult. Bot. Gard. Singapore s.n.* (holotype: SING!).

Distribution: Indonesia (Kalimantan).

Stichorkis bibullata (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis bibullata* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 9: 143. 1927.

Synonym: *Disticholiparis bibullata* (J.J.Sm.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: SUMATRA. Aceh, Gajo Loees, Leg. Van Daalen*, cult. Hort. Bogor. 200* (holotype: BO).

Distribution: Indonesia (Sumatra)

Stichorkis biglobulifera (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis biglobulifera* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 9: 143, 1927.

Synonym: *Disticholiparis biglobulifera* (J.J.Sm.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: SUMATRA. Gunung Singgalang, 1900 m, Leg. Groeneveldt, *cult. Hort. Jacobson 1322* (holotype: BO).

Distribution: Indonesia (Sumatra).

Stichorkis kemulensis (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis kemulensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 149. 1932.

Synonym: *Liparis amesiana* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 11: 124. 1931 nom. illeg. (non Schltr. 1911).

TYPE: INDONESIA. Kalimantan, West Koetai, Gunung Kemoel, 1500 m, 15 October 1925, *Endert 4167* (holotype: L).

Distribution: Indonesia (Kalimantan).

Stichorkis kerintjiensis (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis kerintjiensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 10: 50. 1928.

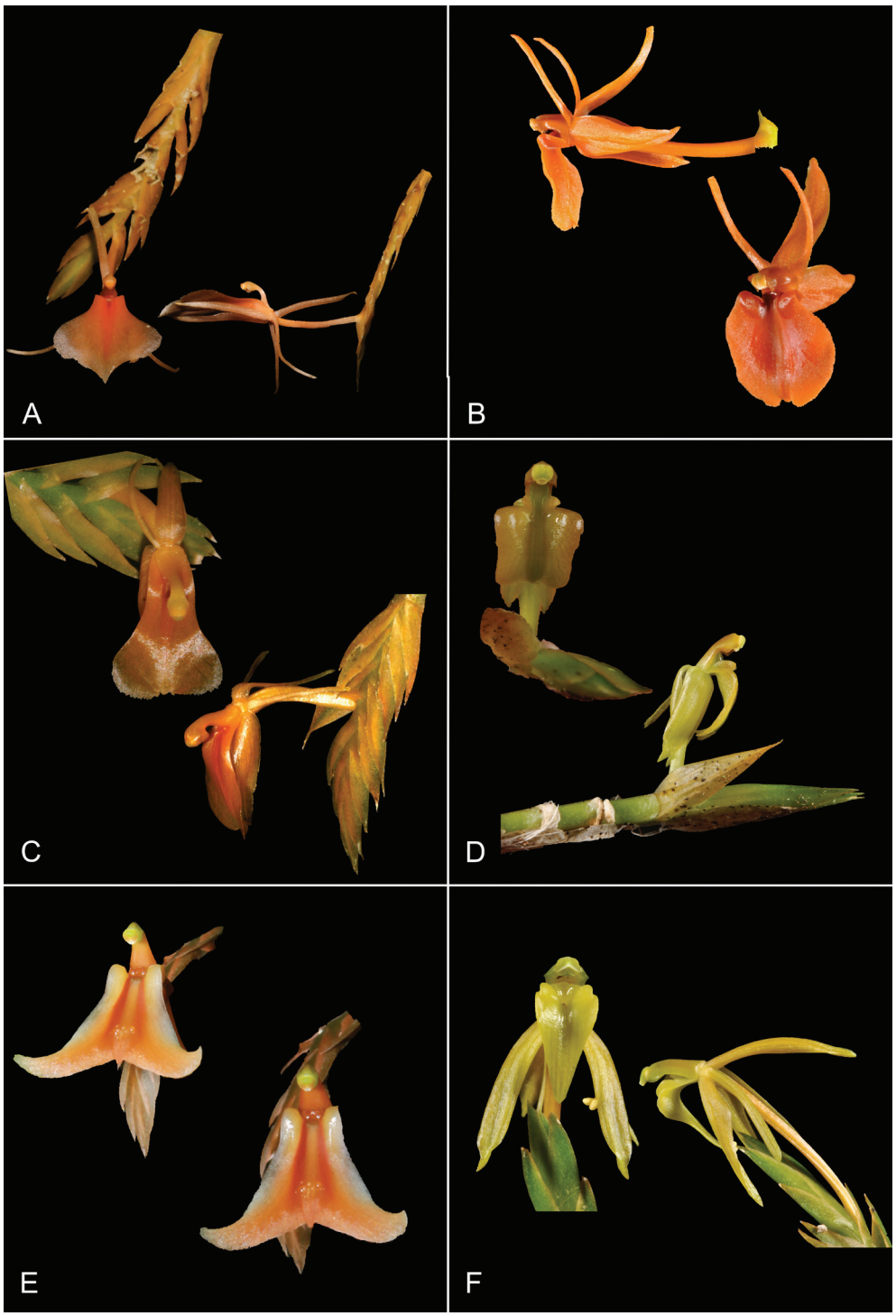

FIGURE 1. Selected Philippine *Stichorkis* species **A.** *S. davidlohmanii* **B.** *S. elmeri* **C.** *S. gracilis* **D.** *S. merrillii* **E.** *S. nutans* **F.** *S. philippinensis*. Photographs by: M. A. K. Naive (A, E), Ravan Schneider (C), Pieter Pelser & Julie Barcelona (B, D, F).

Synonym: *Disticholiparis kerintjiensis* (J.J.Sm.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPES: INDONESIA. Sumatra, Gunung Kerintji, 1200 m, 8 March 1920, *Bünnemeijer 8600* (syntype: BO); Gunung Kerintji, 1700 m, 16 March 1920, *Bünnemeijer 8911* (syntype: BO; isosyntypes: AMES!, K, L); Gunung Kerintji, 1200 m, 17 March 1920, *Bünnemeijer 8955* (syntype: BO; isosyntype: AMES!).

Distribution: Indonesia (Sumatra).

Stichorkis lycopodioides (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis lycopodioides* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 11: 121. 1931.

TYPE: INDONESIA. Kalimantan, West Koetai, Long Petak, 450 m, 20 September 1925, *Endert 3492* (holotype: L).

Distribution: Indonesia (Kalimantan).

Stichorkis mucronata (Blume) J.J.Wood, Orchids Mount Kinabalu 2: 532. 2011.

Basionym: *Malaxis mucronata* Blume, Bijdr. Fl. Ned. Ind.: 391. 1825. *Liparis mucronata* (Blume) Lindl., Gen. Sp. Orchid. Pl.: 32. 1830. TYPE: INDONESIA. Java, mountain of Bantam Province and Buitenzorg Province, *H. Kuhl & J.C. van Hasselt s.n.* (holotype: L-image!).

Liparis celebica Schltr., Repert. Sp. Nov. Regni Veg. 10: 28. 1911. TYPE: INDONESIA. Sulawesi, Minahassa Peninsula, Mt. Masarang, 1200 m, November 1909, *Schlechter 20668* (holotype: B, destroyed; isotypes: AMES!, G, K, L, NSW!, S), ***syn. nov.***

Distribution: Borneo, Jawa, Lesser Sunda Is., Sulawesi, and Sumatera.

Stichorkis togensis (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis togensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 9: 457. 1928.

TYPE: INDONESIA. Maluku Prov., Buru, Gunung Toga, 1900 m, February 1912, *Stresemann 572* (holotype: L).

Distribution: Indonesia (Maluku Prov., Buru Island).

Stichorkis trullifera (Ames & C.Schweinf.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis trullifera* Ames & C.Schweinf., Contr. Arn. Arb. 8: 26. 1934.

Synonym: *Disticholiparis trullifera* (Ames & C.Schweinf.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 179. 2004.

TYPE: INDONESIA. Sumatra, Kabajakan to Tretet trail, 1065-1525 m, 13 January 1932, *Bangham 867* (holotype: AMES!; isotype: AMES!).

Distribution: Indonesia (Sumatra).

New combinations for East Malesian taxa

Stichorkis anceps (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis anceps* Schltr., Bot. Jahrb. Syst. 58: 65. 1922.

TYPE: PAPUA NEW GUINEA. Sepik District, Hunstein Peak, 1300 m, March 1913, *Ledermann 11310* (holotype: B, destroyed).

Distribution: Papua New Guinea.

Stichorkis anemophila (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis anemophila* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 214. 1911.

Synonym: *Disticholiparis anemophila* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: PAPUA NEW GUINEA. Ibo Range, 110 m, December 1917, Schlechter 17100 (syntype: B, destroyed; isosyntypes: AMES!, BO, E, G 00354754, GH 00100778, K 000943205, L, MO, NSW!); Bismarck Range, 1400 m, November 1909, *Schlechter 18592* (syntype: B, destroyed; isosyntypes: G, L, S).

Distribution: Papua New Guinea.

Stichorkis apiculata (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis apiculata* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 216. 1911.

Synonym: *Disticholiparis apiculata* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: PAPUA NEW GUINEA. Kani Range, 1000 m, September 1909, *Schlechter 16552* (holotype: B, destroyed; isosyntypes: BM, BO, K, L, NSW!, S).

Distribution: Papua New Guinea.

Stichorkis arrigens (J.J.Sm.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis arrigens* J.J.Sm., Nova Guinea 18: 25. 1935.

TYPE: INDONESIA. Papua Prov., Nassau Mts., Exploration Bivouac, 700 m, October 1926, *Docters van Leeuwen 10524* (holotype: BO; isotypes: BO, L).

Distribution: Indonesia (Papua Prov.).

Stichorkis brunnescens (Schltr.) Ormerod & Naive, ***comb. nov***

Basionym: *Liparis brunnescens* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 213. 1911.

Synonym: *Disticholiparis brunnescens* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 176. 2004.

TYPE: PAPUA NEW GUINEA. Finisterre Range, 1300 m, January 1909, *Schlechter 19102* (holotype: B, destroyed).

Distribution: Papua New Guinea.

Stichorkis cyclostele (Schltr.) Ormerod & Naive, ***comb. nov***

Basionym: *Liparis cyclostele* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 212. 1911.

Synonym: *Disticholiparis cyclostele* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PAPUA NEW GUINEA. Waria River, near Jaduna, 300 m, April 1909, *Schlechter 19301* (syntype: B, destroyed; isosyntypes: AMES!, BO, G, L, NSW!, S); Waria River, near Pema, May 1909, *Schlechter s.n.* (syntype: B, destroyed)

Distribution: Papua New Guinea.

Stichorkis finetiana (Schltr.) Ormerod & Naive, ***comb. nov***

Basionym: *Liparis finetiana* Schltr., Repert. Sp. Nov. Regni Veg. 10: 29. 1911.

Synonym: *Liparis disticha auct. non* (Thouars) Lindl.: Schltr., Bot. Jahrb. Syst. 39: 60. 1906.

TYPE: NEW CALEDONIA. Near Paita, 200 m, October 1902, *Schlechter 14858* (syntype: B, destroyed; isosyntypes: AMES! 00600518, K! 000943536, P, PR, WRSL); Mt. Iguambi, near Oubatche, 800 m, December 1902, *Schlechter 15489* (syntype: B, destroyed; isosyntype: P).

Distribution: New Caledonia; Fiji.

Stichorkis gautierensis (J.J.Sm.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis gautierensis* J.J.Sm., Repert. Sp. Nov. Regni Veg. 11: 136. 1912.

TYPE: INDONESIA. Papua Prov., Gautier River, 700 m, November 1911, *Gjellerup 875* (holotype: BO; isotype: L).

Distribution: Indonesia (Papua Prov.).

Stichorkis geelvinkensis (J.J.Sm.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis geelvinkensis* J.J.Sm., Repert. Sp. Nov. Regni Veg. 12: 395. 1913.

Synonym: *Disticholiparis geelvinkensis* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: INDONESIA. Papua Prov., Geelvink Bay, Giriwo River, July 1912, *Janowsky 100* (holotype: BO; isotype: L).

Distribution: Indonesia (Papua Prov.).

Stichorkis gjellerupii (J.J.Sm.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis gjellerupii* J.J.Sm., Repert. Sp. Nov. Regni Veg. 11: 557. 1912.

TYPE: INDONESIA. Papua Prov., Gautier Range, 400 m, November 1911, *Gjellerup 881* (holotype: BO).

Distribution: Indonesia (Papua Prov.).

Stichorkis glumacea (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis glumacea* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 219. 1911.

Synonym: *Disticholiparis glumacea* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PAPUA NEW GUINEA. Maboro Range, Govidjoa Creek, 1200 m, June 1909, *Schlechter 19805* (holotype: B, destroyed).

Distribution: Papua New Guinea.

Stichorkis govidjoae (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis govidjoae* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 218. 1911.

Synonym: *Disticholiparis govidjoae* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PAPUA NEW GUINEA. Govidjoa Creek,

1200 m, June 1909, *Schlechter 19083* (holotype: B, destroyed).
Distribution: Papua New Guinea.

Stichorkis graciliscapa (Schltr.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis graciliscapa* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 211. 1911.
Synonym: *Disticholiparis graciliscapa* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.
TYPE: PAPUA NEW GUINEA. Djamu Gorge, 450 m, November 1907, Schlechter 16807 (holotype: B, destroyed; isotypes: L, NSW!, S).
Distribution: Papua New Guinea.

Stichorkis inamoena (Schltr.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis inamoena* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 216. 1911.
Synonym: *Disticholiparis inamoena* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.
TYPE: PAPUA NEW GUINEA. Bismarck Range, 1600 m, November 1908, *Schlechter 18784* (holotype: B, destroyed).
Distribution: Papua New Guinea.

Stichorkis janowskyi (J.J.Sm.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis janowskyi* J.J.Sm., Repert. Sp. Nov. Regni Veg. 12: 395. 1913 (as 'janowskii', corrected by Smith in Nova Guinea 12(3): 230. 1915).
TYPE: INDONESIA. Papua Prov., Giriwo River, July 1912, *Janowsky 210* (holotype: BO).
Distribution: Indonesia (Papua Prov.).

Stichorkis lamproglossa (Schltr.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis lamproglossa* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 220. 1911.
Synonym: *Disticholiparis lamproglossa* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.
TYPE: PAPUA NEW GUINEA. Finisterre Range, 1100 m, November 1908, *Schlechter 18625* (holotype: B, destroyed; isotypes: AMES!, BO, G, L, NSW!, S).
Distribution: Papua New Guinea.

Stichorkis loliacea (Ridl.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis loliacea* Ridl., Trans. Linn. Soc. s.2, Bot. 9: 164. 1916.
TYPE: INDONESIA. Papua Prov., W bank of Tsingarong River, Camp 6A, 945 m, January 1913, *Kloss s.n.* (holotype: BM).
Distribution: Indonesia (Papua Prov.).

Stichorkis miniata (Schltr.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis miniata* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 218. 1911.
Synonym: *Disticholiparis miniata* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.
TYPE: PAPUA NEW GUINEA. Govidjoa Creek, 1000 m, June 1909, *Schlechter 19838* (holotype: B, destroyed).
Distribution: Papua New Guinea.

Stichorkis murkelensis (J.J.Sm.) Naive & Ormerod, ***comb. nov.***
Basionym: *Liparis murkelensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 10: 127. 1928.
TYPE: INDONESIA. Maluku Prov., Seram, Gunung Moerkele, 2000-2500 m, 1 July 1918, *Rutten 1483* (syntype: L); Gunung Moerkele, 2000-2500m, 1 July 1918, *Rutten 1491* (syntype: L).
Distribution: Indonesia (Maluku Prov., Seram Island).

Stichorkis nebuligena (Schltr.) Ormerod & Naive, ***comb. nov.***
Basionym: *Liparis nebuligena* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 212. 1911.
Synonym: *Disticholiparis nebuligena* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.
TYPE: PAPUA NEW GUINEA. Torricelli Range, near Akur, 700 m, September 1909, *Schlechter 20112* (syntype: B!); Kani Range, 1000 m, December 1907, *Schlechter 16961* (syntype: B, destroyed; isosyntypes: AMES!, BO, E, G, GH, K, L, MO, NSW, S); Maboro Range, 1300 m, May 1909, *Schlechter 19514* (syntype: B, destroyed).
Distribution: Papua New Guinea.

Stichorkis ochrantha (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis ochrantha* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 214. 1911.

Synonym: *Disticholiparis ochrantha* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 178. 2004.

TYPE: PAPUA NEW GUINEA. Minjem Valley, Kelel, 400 m, July 1907, *Schlechter 16308* (syntype: B!; isosyntypes: AMES!, BM, G , K, L, NSW, S); near Ambo, 500 m, September 1908, *Schlechter 18260* (syntype: B, destroyed; isosyntypes: AMES!, BM, BO, E, GM, K, L, NSW!, S).

Distribution: Papua New Guinea.

Stichorkis pandaneti (J.J.Sm.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis pandaneti* J.J.Sm., Nova Guin. 12: 16. 1913.

TYPE: INDONESIA. Papua Prov., Noord River, September 1907, *Versteeg 1743* (syntype: BO); same area, September 1909, *von Roemer 156* (syntype: BO); same area, October 1911, *von Roemer 440* (syntype: BO).

Distribution: Indonesia (Papua Prov.).

Stichorkis pseudodisticha (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis pseudodisticha* Schltr., in Schum. & Laut., Fl. Deutsch. Schutzgeb. Südsee, Nachtr. 2: 106. 1905.

Synonym: *Disticholiparis pseudodisticha* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 179. 2004.

TYPE: PAPUA NEW GUINEA. Bismarck Range, 1200 m, January 1902, Schlechter 14064 (holotype: B, destroyed; istotypes: BM, BRI, K, P).

Distribution: Indonesia (Papua Prov.); Papua New Guinea.

Stichorkis trachyglossa (Schltr.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis trachyglossa* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 217. 1911.

Synonym: *Disticholiparis trachyglossa* (Schltr.) Marg. & Szlach., Orchidee (Hamburg) 55, 2: 179. 2004.

TYPE: PAPUA NEW GUINEA. Torricelli Range, 800 m, September 1909, *Schlechter 20338* (holotype: B, destroyed; isotypes: BM, BO, K, L, NSW!, S).

Distribution: Papua New Guinea.

Stichorkis triticea (Ridl.) Ormerod & Naive, ***comb. nov.***

Basionym: *Liparis triticea* Ridl., Trans. Linn. Soc. s.2, Bot. 9: 164. 1916.

TYPE: INDONESIA. Papua Prov., Camp 1, 215 m, November/December 1912, *Kloss s.n.* (syntype: BM); W bank of Tsingarong River, Camp 6A, 945 m, 15 January 1913, *Kloss s.n.* (syntype: BM).

Distribution: Indonesia (Papua Prov.).

Stichorkis togensis (J.J.Sm.) Naive & Ormerod, ***comb. nov.***

Basionym: *Liparis togensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg, sér. 3, 9: 457. 1928.

TYPE: INDONESIA. Maluku Prov., Buru, Gunung Toga, 1900 m, February 1912, *Stresemann 572* (holotype: L).

Distribution: Indonesia (Maluku Prov., Buru Island).

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TELIPOGON MAYOI (ORCHIDACEAE), A NEW SPECIES FROM WESTERN ANDES OF COLOMBIA

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Abstract. *Telipogon mayoi,* from the western Colombian Andes, is proposed as a new species. The species was found in "La Elvira" National Protective Forest in the Yumbo Municipality, one of the oldest protected areas in Colombia, close to the Farallones de Cali National Park, both localities in the Dapa Mountains. Specimens of *Telipogon mayoi* were previously misidentified as *Telipogon lankesteri* Ames and *T. williamsii* P.Ortiz, but detailed analysis of the floral morphology revealed that it is different. *Telipogon mayoi* is most similar to *T. lankesteri* but it is characterized by the crenulated margins of the leaves (*vs.* entire margins), the ovate oblong lip (*vs.* oblong lanceolate) and furcate setae on the column (*vs*. simple setae). We provide a description, illustrations, a plate, *in situ* photographs, a distribution map, and ecological notes.

Resumen. *Telipogon mayoi* proveniente de los Andes occidentales de Colombia, es propuesta como nueva especie. La especie fue hallada en la Municipalidad de Yumbo en la Reserva Forestal Protectora Nacional "La Elvira", una de las áreas protegidas más antiguas de Colombia, cercana al Parque Nacional Natural Farallones de Cali, ambas localidades en las montañas de Dapa. Especímenes de *Telipogon mayoi* fueron previamente identificados como *Telipogon lankesteri* Ames y *T. williamsii* P.Ortiz, pero un análisis minucioso de la morfología floral reveló que tiene una identidad distinta. *Telipogon mayoi* es más similar a *T. lankesteri* pero se caracteriza por presentar márgenes crenulados en las hojas (*vs*. márgenes enteros), un labelo ovado oblongo (*vs.* oblongo lanceolado), y setas furcadas en la columna (*vs*. setas simples). Se provee una descripción, ilustraciones, una lámina, fotografías *in situ*, un mapa de distribución y notas ecológicas.

Key Words: Andes, cloud forest, Colombia, miniature *Telipogon*, Oncidiinae

Introduction. *Telipogon* Kunth is a neotropical orchid genus, which currently contains around 260 accepted species (Martel unpublished data). Species of this genus can be found from southern Mexico to Central America, the Caribbean and in the Andes, from Venezuela to northern Bolivia between 500 and 3600 m (Martel & Nauray 2013, Collantes & Martel 2015). *Telipogon* species are usually associated as having colorful and showy flowers (see Dodson & Escobar 1987, Dodson 2004). However, some *Telipogon* species possess very small and non-showy flowers; those species were formerly included in the genus *Stellilabium*. The genus *Stellilabium* was transferred to *Telipogon* based on molecular data (Williams *et al.* 2005). Recently, Martel *et al.* (2017) proposed to use the term "miniature *Telipogon*" to distinguish the *Telipogon* species that fit with the characteristics of the former *Stellilabium*. Thus, miniature *Telipogon* are characterized as being small plants, usually less than 10 cm, and flowers of less than 2 cm diameter (Martel *et al*. 2017). Despite the difference in size, morphologically, miniature *Telipogon* are consistent with flower morphology of the genus (e.g. usually non-resupinate flowers, lip similar to the petals, a robust and short column, and a pollinarium with four pollinia) and especially they present an uncinate viscidium (Martel *et al*. 2017). Although miniature *Telipogon* present broader distribution ranges compared to other *Telipogon*, they are not well represented in herbaria, because their small size makes them easily overlooked (Martel 2016a, 2016b, Martel *et al*. 2017). In Colombia, due to the complexity and variety of ecosystems, rainfall, microclimate diversity and orographic factors, there is still great orchids gaps as many areas are waiting for botanical exploration (Reina-Rodríguez 2016, 2019). Around 70 species of *Telipogon* occur in the country (Govaerts *et al*. 2019);

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however, Betancur *et al.* (2015) recognized only 67 species, of which 38 are endemic. Nevertheless, this number would be surely increased as new *Telipogon* species are recently being described from there (e.g. Kolanowska *et al*. 2017, Perez-Escobar *et al*. 2017).

In 2018 as part of a study for evaluate the climate change on orchids, in western Colombian Andes, diverse orchid plants were marked and codded in the wild. In 2019, during the monitoring of those plants, one member of the team noticed that a specimen codded as *T. williamsii* P.Ortiz, which occurs in the area, was different from the other plants also codded as *T. williamsii*. Furthermore, a similar specimen was published as *T. lankesteri* in a nearby location (i.e. Yumbo Municipality) some years ago (see Pérez-Escobar *et al.* 2011). A detailed examination of these plants revealed that they do not belong with those afore mentioned species, but to an undescribed species of *Telipogon*. Therefore, we propose this as a new taxon and provide here a description, illustrations and a distributional map of the species.

Materials and methods. Plant specimens were collected in "La Elvira" National Protective Forest Reserve in the Arroyohondo River Basin, Western Andes of Colombia. Plant material was preserved as voucher and in spirits in the herbarium (CUVC) at the Universidad del Valle in Cali. Photographs were taken *in situ* with a Cannon EOS 60D® using a 60 mm macro. Dissections of the plant and flower were arranged according to LCDP format and were edited with Adobe Photoshop® CS4. The spirit material was used to prepare the line drawing. Location map was prepared with ArcGIS 10, module ArcMap ESRI®. The conservation assessment complies with the criteria of the IUCN (2019). To determine the weather conditions in Colombia, Ecuador and Costa Rica, the website (http://es.climate-data.org) was visited. Authors and names of plants follow the databases The International Plant Name Index (http://www.ipni.org), Tropicos (http://www.tropicos.org) and Epidendra (http://www.epidendra.org).

Taxonomic treatment

Telipogon mayoi Reina-Rodr. & C.Martel, ***sp. nov.*** (Fig. 1–3).

TYPE: Colombia. Valle del Cauca: Municipio de Yumbo, Corregimiento Dapa, Parcelación Los Morales. Parcela Familia Rubiano-Hurtado. Microcuenca El Rincón, afluente del río Arroyohondo. Bosque subandino, 3°34′40.73″N 76°34′19.12″W, 2106 m, 16.VI.2019. *fl., G. Reina-Rodríguez et al. 2982*. (CUVC-in spirit!)

Diagnosis: *Telipogon mayoi* Reina-Rodr. & C.Martel is similar to *T. lankesteri*, but differs by the crenulate margins in the leaves (vs. entire margins), the ovate oblong lip (vs. oblong lanceolate), ciliate margins of the lip (vs. entire margins), furcate setae on the column (vs. simple setae).

Plant epiphytic, 4.0–4.5 cm long, erect. *Roots* 9–16 mm long, adventitious, sinuous. *Leaf* 4, blade 4.0–8.0 × 2.0–2.5 mm, elliptical, smooth, apex acuminate, margin crenulate. *Inflorescence* 4.0–8.3 cm long, 1–2 branched, erect, flattened, racemose. *Floral bracts* 0.8–1.0 mm long, light green, decurrent, triangular-ovate, slightly winged, apiculate. *Pedicels* 0.8–1.0 mm, erect, green. *Flowers* 6–8 mm in diameter, resupinate, one or two flowers open at a time, pedicelate; *floral pedicels* 0.8–1.0 mm, erect, green. *Ovary* 1.3 mm long, light green, straight, with ribs. *Sepals* basal red wine color at the base, greenish yellow distally; *dorsal sepal* 4.0–4.2 × 1.8–2.0 mm, ovate, 1-veined, apex sub-acute, mucronate; *Lateral petals* 4.0–4.1 × 1.8–2.0 mm, ovate, 1-veined, apex acute to sub-acute, mucronate, basally red wine color, distal half greenish yellow. *Lip* 4.0–4.1 × 1.7–1.8 mm, ecallose, ovate oblong, 3-veined, ciliate margins, the hairs retorse, surface hirsute, apex sub-acute, mucronate. *Column* 1.5–1.7 × 1.0–1.2 mm, height, basally ovate, ventrally unguiculate, dorsally densely setose; *stigmatic surface* concave, lustrous; *setae* furcated, 3 tuffs. *Anther cap* 1.1 × 1.3 mm, cordate, red. *Pollinarium* 0.5 × 0.3 mm; *pollinia* 4, yellow, obovate two pairs of different size; *caudicle* 0.5 mm diam., elastic, hyaline; *viscidium* orange, uncinate. *Seed pod* sub-spherical to ovoid.

Eponomy: The species is named after Mayo Rubiano, the youngest member of the team in Dapa, an orchid enthusiast and who first noticed that the plant designed as type here was different from *T. williamsii*.

Conservation status: An assessment of the conservation status of the new species cannot be made at this time due to only two locations (i.e. Yumbo Munici-

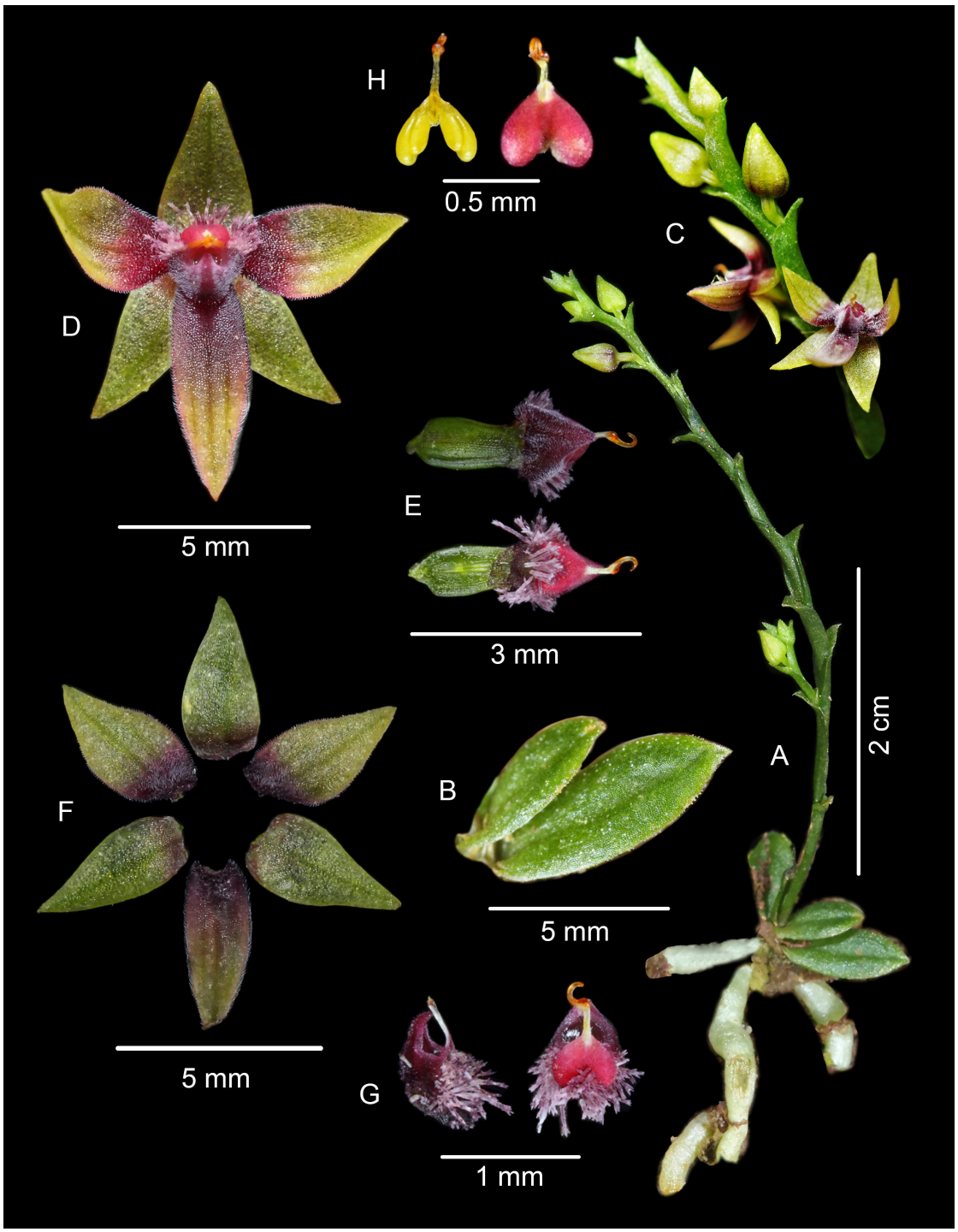

Figure 1. *Telipogon mayoi* Reina-Rodr. & C.Martel. **A**. Habit. **B**. Leaves, upper view. **C**. Inflorescence, detail of the apex. **D**. Flower, frontal view. **E**. Ovary and column, ventral and dorsal views. **F**. Perianth, dissected. **G**. Column, lateral and dorsal views. **H**. Pollinarium without and with the anther cap. Photographs by G. Reina-Rodríguez and F. López-Machado based on *Reina-Rodríguez et al. 2982* (CUVC-in spirit).

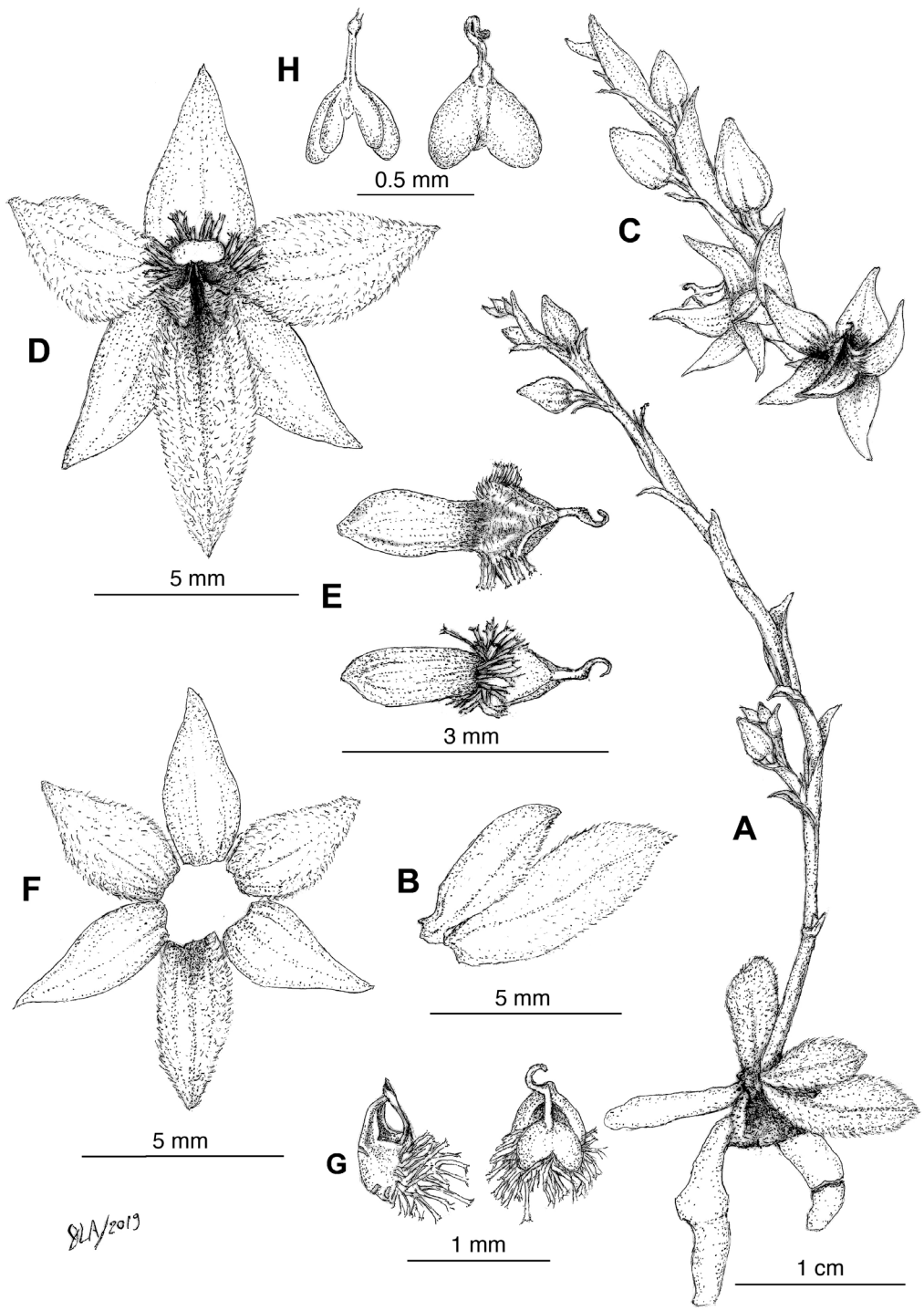

Figure 2. Line drawing of *Telipogon mayoi* Reina-Rodr. & C.Martel. **A**. Habit. **B**. Leaves. **C**. Flowers in the inflorescence. **D**. Frontal view of the flower. **E**. Column, anther cap and bristles, ventral and dorsal views. **F**. Dissected perianth. **G**. Ovary and column, lateral and dorsal views. **H**. Pollinia without and with the anther cap. Drawn by Jairo Larrahondo based on *Reina-Rodríguez et al. 2982* (CUVC-in spirit).

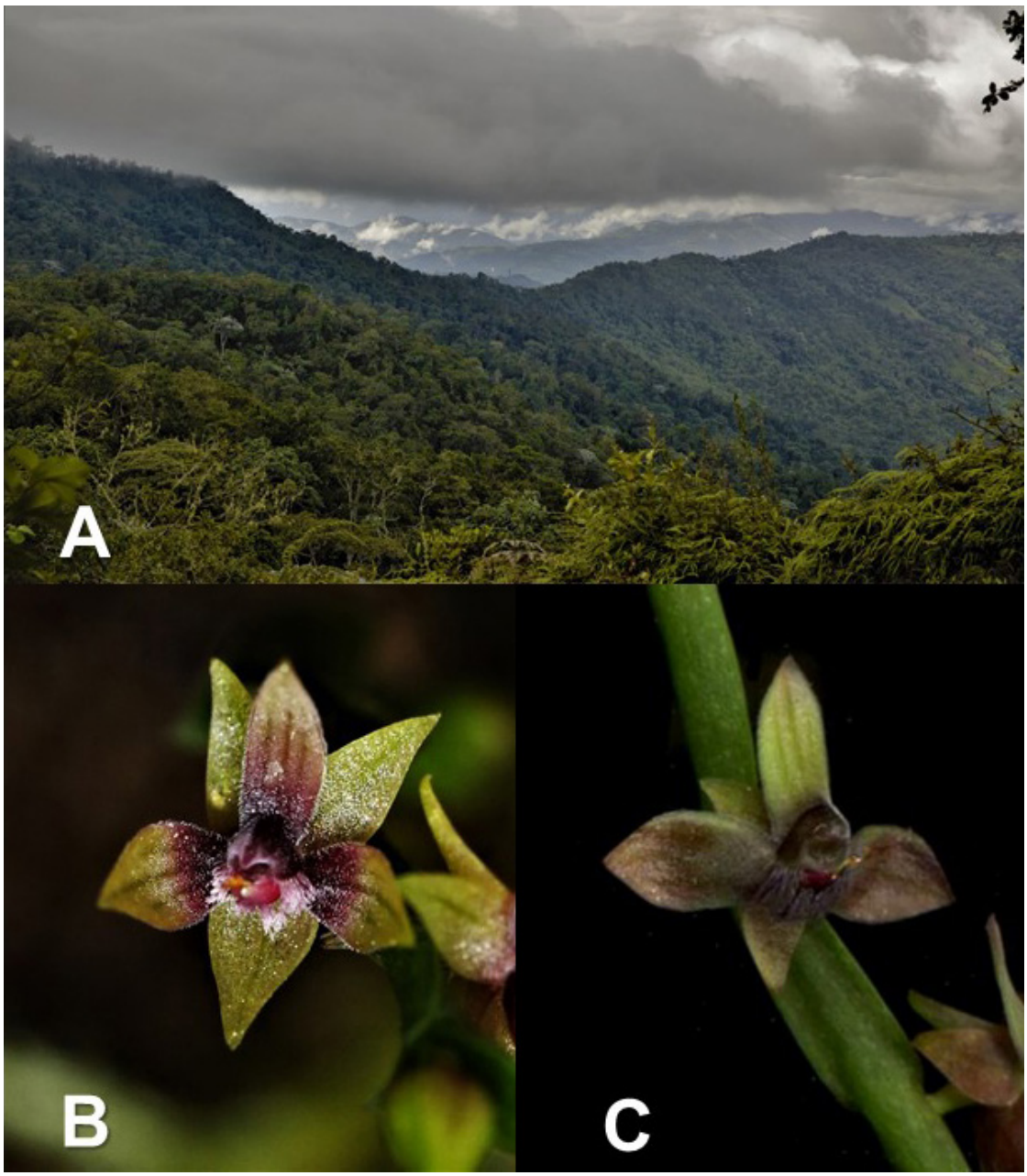

Figure 3. **A**. Dapa mountains, the type locality of *Telipogon mayoi*, in western Colombia Andes. **B**. Flower of *T. mayoi* (*Reina-Rodríguez et al*. *2982*, CUVC). **C**. Flower of *T. lankesteri* (*Bogarín 2317*, Jardín Botánico Lankester). Photographs from G. Reina-Rodríguez (A–B) and D. Bogarín (C).

pality and La Elvira Protected area) are known and there is no information available on the populations. Therefore, it must be classified as a data deficient (DD), following the IUCN Red List criteria (IUCN 2019).

Ecology and distribution: *Telipogon mayoi* is endemic to Colombia and it is known from two localities in the Corregimiento of Dapa and La Elvira protected area in the Yumbo Municipality, Valle del Cauca Department. Plants of *T. mayoi* grow in the montane for-

ests of western Colombian Andes between 2000–2100 m, which presents steep slopes and well drained soils of volcanic origin from the Cretaceous (CVC 2009). Weather conditions in the area were reported as presenting between 1900–2100 mm annual precipitation and between 15°C and 17°C annual temperature average (CVC 2009). According to Holdridge (1987), this area can be classified as Montane rain forest, more widely known as subandean forest.

The habitat, where *T. mayoi* is found, is dominated by *Brunellia comocladifolia* Bonpl., *Alchornea latifolia* Sw., *Hedyosmum bonplandianum* Kunth and *Billia rosea* (Planch. & Linden) C.Ulloa & P.Jørg. Plants of *T. mayoi* grow on shrubs of *Meriania* Sw., *Tibouchina* Aubl. and *Psidium* L. (Perez-Escobar *et al.* 2011) We observed it growing on shurbs of *Miconia cauda* DC. The community of epiphytes in Dapa is dominated by *Cyrtochilum* Kunth, *Oncidium* Sw., *Epidendrum* L., *Pleurothallis* R.Br., *Masdevallia* Ruiz & Pav. and *Lepanthes* Sw. (Baker 2019).

Additional material: Municipio de Yumbo, Corregimiento de Dapa, via Bitaco, cerca de la Hacienda "Los Españoles", 2039 m, *O. Perez & M. Kolanowska 872* (VALLE!).

Discussion. Plants of *T. mayoi* were first recorded some years ago as *T. lankesteri* by Pérez-Escobar *et al.* (2011), which came from a forest just 4.1 km far from the type locality (Fig. 4). This misidentification is understandable since *T. mayoi* and *T. lankesteri* belong to the miniature *Telipogon* group and some individuals, recorded by Pérez-Escobar *et al*. (2011), did also lose the leaves during blooming, as *T. lankesteri* does. However, there are clear morphological differences between *T. mayoi* and *T. lankesteri* (see Zambrano Romero *et al.* 2018; Table 1), and not all the plants of *T. mayoi* lose leaves during blooming. Thus, *T. mayoi* possesses leaves with crenulated margins (instead of entire margins in *T. lankesteri*), an ovate oblong lip (instead of an oblong lanceolate lip in *T. lankesteri*), with ciliate margins in the lip (instead of entire margins in *T. lankesteri*), furcate setae on the column (instead of simple setae on the column in *T. lankesteri*). To the best of our knowledge, there is no real material of *T. lankesteri* recorded from Colombia, so it seems it does not occur there. *Telipogon*

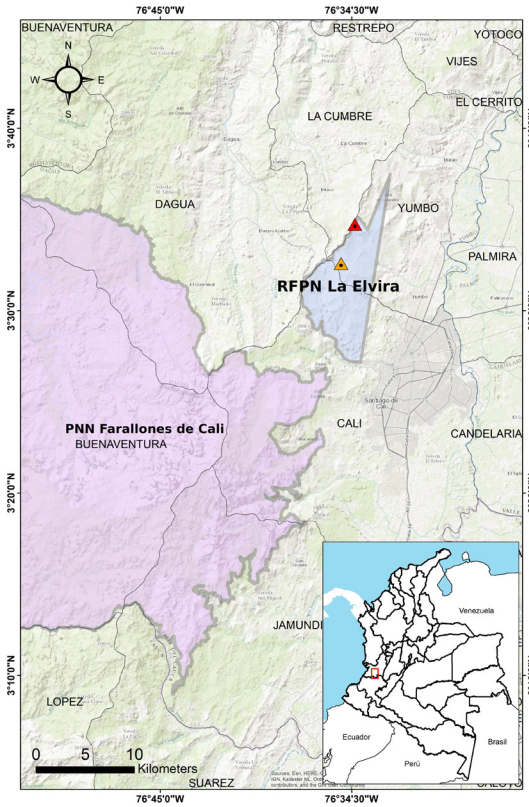

Figure 4. Distribution map of *Telipogon mayoi*. Red triangle indicates the type locality and orange triangle represents the record of Pérez-Escobar *et al.* (2011). PNN: National Natural Park Farallones de Cali (196350 ha); RFPN: National Protective Forest Reserve La Elvira (7064 ha). Base map ESRI. Map elaborated by Kevin Reyes.

mayoi is similar to *T. williamsii* in the habit; however, *T. mayoi* is easily differentiated by the simple lip (instead of the bilobed lip in *T. williamsii*) with absence of a callus (instead of a distinctive callus in *T. williamsii*) and the densely furcate setae (instead of few, simple setae in *T. williamsii*; see Table 1). Plants of *Telipogon mayoi* slightly resembles those of *T. sonia-juaniorum* Zambrano, Bogarín & Solano from Ecuador, as both species have small plants and their flowers present 3 tufts of setae on the column. However, *T. mayoi* can be recognized by the ovate oblong lip (instead of the elliptic lip in *T. sonia-juaniorum*), the half of the flower diameter in *T. sonia-juaniorum* than *T. mayoi* and the furcate setae (instead of mainly simple setae in *T. sonia-juaniorum*; Table 1).

Table 1. Differences in distributional range, abiotic and biotic characters between *Telipogon mayoi, T. lankesteri, T. sonia-juaniorum* and *Telipogon williamsii*.

	Telipogon mayoi	*Telipogon lankesteri*	*Telipogon williamsii*	*Telipogon sonia-juaniorum*
Distributional and abiotic conditions				
Distributional range	W. Colombian Andes, middle lands	Caribbean Costa Rican lowlands	Andes Colombia, Ecuador and Venezuela, middle lands	SW. Ecuadorian Andes, middle lands
Life zone (*sensu* Holdridge 1987)	Montane rain forest	Tropical moist forest	Montane rain forest	Premontane moist forest
Habitat	Secondary cloud forest	Secondary moist forest	Secondary cloud forest	Semi-deciduous montane forests
Elevation range (m)	2000–2100	800	1800–2550	1100–1300
Mean annual rainfall (mm)	1800	2800	1800–2272	1477
Annual mean temperature (°C)	14.2	22.8	17.4	22.4
Morphological and/ phenological conditions				
Habit	Epiphyte	Epiphyte	Epiphyte	Epiphyte
Flowering period	May-June	September	January, May, July	June and September
Leaf blade size (mm)	4–8 × 2–2.5	7–15 × 1–2	40 × 12	5–7 × 2.5–3.0
Leaf blade margin	serrulate	entire	entire	crenulate
Inflorescence length (cm)	ca. 4.0	ca. 20.0–23.0	ca. 4.0–8.0	ca. 5.5
Sepal size(mm)	4.0–4.1 × 1.8–2.0	2.8–3.0 × 0.8–1.0	5.0 × 2.0	2.2 × 1.5
Flower diameter (mm)	8.0	6.0	12.0	4.5
Column setae	branched	unbranched	unbranched	simple to rarely furcate

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SCAPHOSEPALUM LUANNAE, A NEW SPECIES, AND *SCAPHOSEPALUM ANCHORIFERUM* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM NORTH-WESTERN ECUADOR

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Abstract. A new species, *Scaphosepalum luannae,* is described, and new records for *Scaphosepalum anchoriferum* from Ecuador are presented. *Scaphosepalum luannae* is superficially similar *to S. swertiifolium* but its differs in the the dark green leaves, conspicuously nerved at the abaxial side and shiny at the adaxial side, the sub-quadrate petals with a basal lobe at the columnar margin and the lip with a truncate base without lobes with an oblong and flat hypochile. *Scaphosepalum luannae* and *S. anchoriferum* were discovered growing sympatrically in a poorly explored cloud forest from north-western Ecuador, near the border with Colombia.

Resumen. Una nueva especie, *Scaphosepalum luannae*, es descrita y se presenta el nuevo registro de *Scaphosepalum anchoriferum* en Ecuador. *Scaphosepalum luannae* es superficialmente similar a *S. swertiifolum* pero se diferencia en las hojas verdes, oscuras, conspicuamente nervadas en el lado abaxial y brillosas en el lado adaxial, los pétalos sub-quadratos con un lóbulo basal en el margen columnar y el labelo con su base truncada sin lóbulos y, un hipoquilo oblongo y plano. *Scaphosepalum luannae* y *S. anchoriferum* se descubrieron creciendo de manera simpátrica en un bosque nublado poco explorado del nor-oeste de Ecuador, muy cerca de la frontera con Colombia.

Key words / Palabras clave: Ecuador, nueva especie, new species, Reserva Dracula, *Scaphosepalum anchoriferum*

Introduction. The species of *Scaphosepalum* Pfitzer (Pleurothallidinae) are recognized by the non-resupinate flowers and the connated sepals with osmophores at the base forming a deep and rounded structure with conspicuous sepaline tails in most of the species (Luer 1988). More than 50 species have been described many of them discovered in the past three decades (Luer 1988, 1991, 1992, 1998a, 1998b, 2000, 2009, Endara *et al*. 2011, Chase *et al*. 2015, Karremans 2016, Karremans *et al*. 2016, Valenzuela 2015, Baquero 2017).

Luer (1988) recognized some species-complexes with extensive geographical distributions and populations with similar morphological traits across the geographical range, like *Scaphosepalum breve* (Rchb.f.) Rolfe, *Scaphosepalum odontochilum* Kraenzl. or *Scaphosepalum swertiifolium* (Rchb.f.) Rolfe. Nonetheless, some years after his monograph of the genus, Luer described more species as *Scaphosepalum martineae* Luer, *S. redderianum* Luer, *S. jostii* Luer or *S. globosum* Luer, segregated from the species-complexes where they would originally fit (Luer 1988a, 1998b, 2009). *Scaphosepalum. jostii* and *S. globosum*, two species related to *S. odontochilum*, were considered distinct species; as well as *S. martineae* and *S. redderianum* (Luer 1998b, 2009). A similar case happens with a recently discovered new species of *Scaphosepalum* which is described here.

Another species, *Scaphosepalum anchoriferum* (Rchb.f.) Rolfe, which has a wide phenotypic variation among several populations (Luer 1988b), is mostly known from Costa Rica and Panama, except for a mention of the species for Ecuador by Luer (2003) without voucher specimen. Nevertheless, in north-western Ecuador, several plants of *S. anchoriferum* have been recently found, corroborating Luer´s observation. The new species mentioned above and *S. anchoriferum* were found growing sympatrically in a forest in north-

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western Ecuador. Notes on the new species and *S. anchoriferum* from north-western Ecuador are given here.

Materials and methods. Plants of *Scaphosepalum luannae* and *S. anchoriferum* were discovered and collected by the team of the Botanical Garden of Quito. These plants were cultivated by the Botanical Garden of Quito, where they were used for morphological comparisons, together with specimens preserved in alcohol. The flowers of the plants cultivated for more than 15 months shown no appreciable differences in morphology compared to those observed in the field when the specimens were collected.

Due to the small size of the flowers, measurements were largely conducted on the basis of photos with a 10 mm ruler and the open-source, image-processing program ImageJ (National Institutes of Health) downloaded from https://imagej.nih.gov/ (Lind 2012). The material was photographed with a ruler at the same focal distance. The photos were opened in ImageJ and 10 mm of the ruler were set as a scale. The program calculates the number of pixels to the given unit, providing measurements for the photographed objects.

Taxonomic treatment

Scaphosepalum luannae Baquero, ***sp. nov.*** (Fig. 1–4).

TYPE: Ecuador. Carchi: between Chical y El Carmen, 0°54'42.5" N 78°12'48.7" W, 1750 m, collected by Luis Baquero on 8th of May 2016, *LB 3121* (holotype, QCNE).

Diagnosis. *Scaphosepalum luannae* is similar to *S. swertiifolium* but it differs in the smaller (7–10 vs. 8–21 cm long), dark green, reflective leaves (vs. light green, non-reflective) conspicuously nerved at the abaxial surface (vs. not conspicuously nerved); the shorter ramicauls (3.5–5.0 vs 4–10 cm long); the well-developed, subquadrate, reflexed osmophores of the lateral sepals (vs. transversely lunate, markedly divergent); the sub-quadrate petals with a callous lobe at the base of the columnar margin (vs. ovate, oblique, ecallose), the lip truncate at the base, elobulate (vs. provided wit minutely auricles); and the flat and oblong hipochile (vs. shallowly concave, more or less oblong in *S. swertiifolium*) (Fig. 3–4).

Plant epiphytic, densely caespitose, to 10 cm tall. *Roots* slender, 0.6 mm in diameter. *Ramicauls* erect, slender, 2.0–3.5 cm long, enclosed by 3 sheaths. *Leaf* elliptic, acute, sub-erect, thinly coriaceous, markedly veined at the abaxial side, 7–10 cm long including the petiole, 3.5–5.0 cm wide, cuneate below into a slender, channeled petiole 2 cm long, dark green adaxially, glaucous green abaxially, conspicuously shiny-reflective at both sides. *Inflorescence* a loose, flexuous, successively several to many-flowered raceme from low on the ramicaul, 5–7 cm long, each flower borne on a slender, glabrous, horizontal peduncle 2.5–4.0 cm long. *Floral bracts* thin, shorter than the pedicel, conduplicate, acuminate, bristle-pointed, 3 mm long. *Pedicel* 4 mm long. *Ovary* ribbed, 2.5 mm long. *Sepals* cream, suffused with pink spots which turn into pink stripes towards the junction of the lateral sepals, margins ciliate, with two carinae (a high and a low carina); *dorsal sepal* tricarinate, ovate, concave in the basal quarter, 12.0 × 2.5 mm in natural position, narrowly tubular with revolute margins, the apical three-fourths rose to pink; *lateral sepals* trapezoid, diverging, prickly, thick, reflexed, terminating in a straight, white tail 10–15 mm long, connate 8 mm, with an oblong, concave lamina 9 mm long unexpanded, the apical portion of each sepal suffused with pink and rose dots; cushion (osmophore) 4 × 3 mm (2 × 3 mm in the shorter sides of the trapezium), the total length of each lateral sepal including the tail 19–24 mm. *Petals* sub-quadrate, cream suffused with yellow, columnar margin with a round projection, labellar margin glandulose in texture, suffused with red stripes and blotches, 3.0 × 2.5 mm. *Lip* purple, oblong-subpandurate, reflexed near the middle, 2.2 × 1.0 mm; the epichile narrowly obovate, slightly ciliate at the edge; the disc with a pair of tall, erect, keeled lamellae above the middle; the hypochile rectangular, shallow, the base truncate. *Column* white suffused with rose at the apex, arcuate, semiterete, slender, 3.5 mm long, with two wings in the middle, with a short, 0.5 mm long foot. *Pollinia* 2, yellow. *Fruits* and seeds not observed.

Eponymy: This species is named in honor of Luanne Lemmer of Washington State, USA. Luanne, her husband Eric Veach, and their two sons, Malcolm and Nigel, are passionate supporters of conservation and have given important help to Rainforest Trust and EcoMinga for the establishment of the Dracula

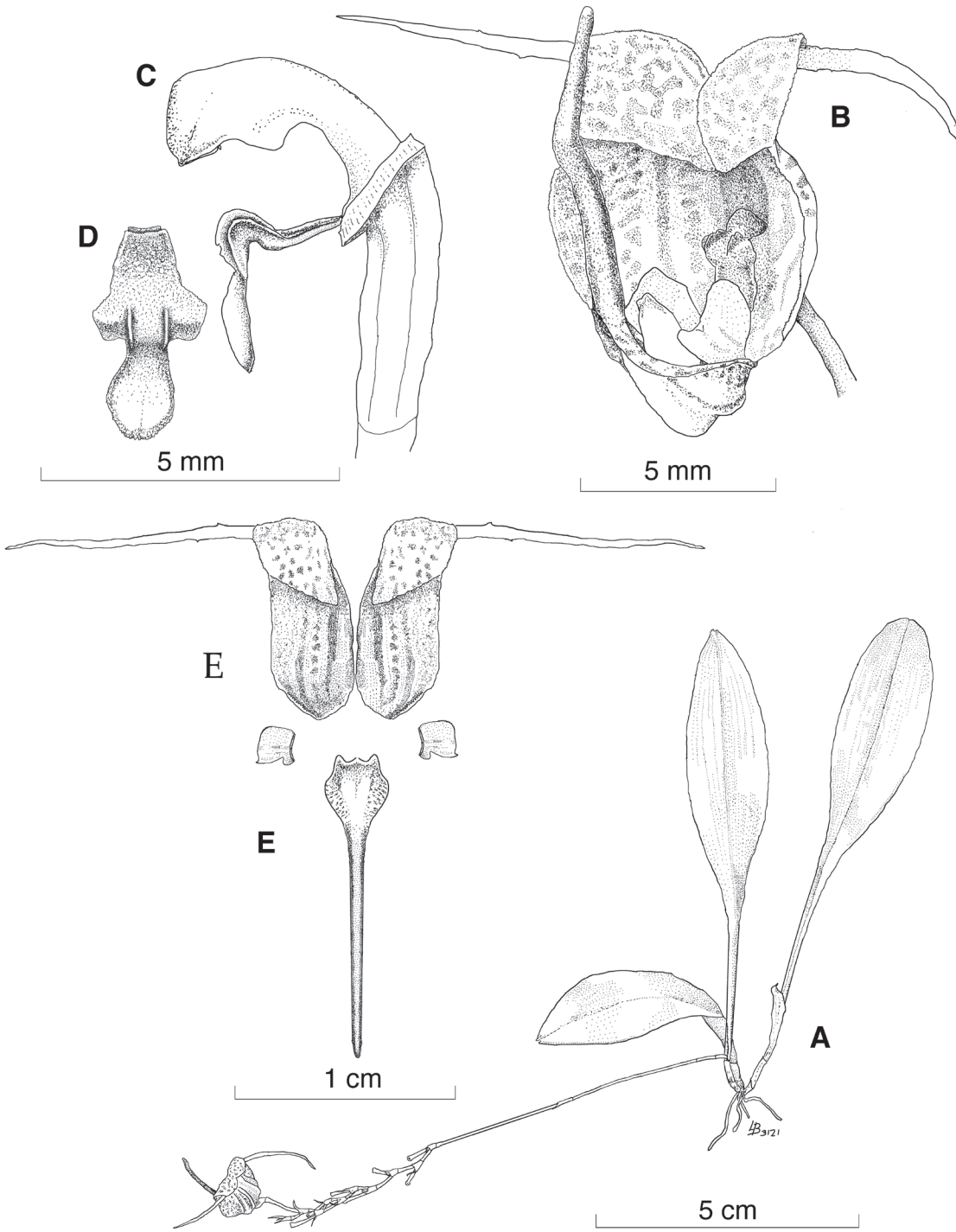

Figure 1. *Scaphosepalum luannae*. **A**. Habit. **B**. Flower in ¾ view. **C**. Column and lip. **D**. Lip, adaxial view. **E**. Dissected flower. Illustration by Luis Baquero based on the holotype.

FIGURE 2. *Scaphosepalum luannae* photographs. **A**. Flower of *S. luannae*: **A1**. Frontal view, **A2**. Lateral view B. Flower of *S. luannae in situ*. **C**. Lip and petal of *S. luannae*: **C1**. Lip, three quartres view. **C2**. Petal, adaxial view. Photos by Luis Baquero, based on the holotype.

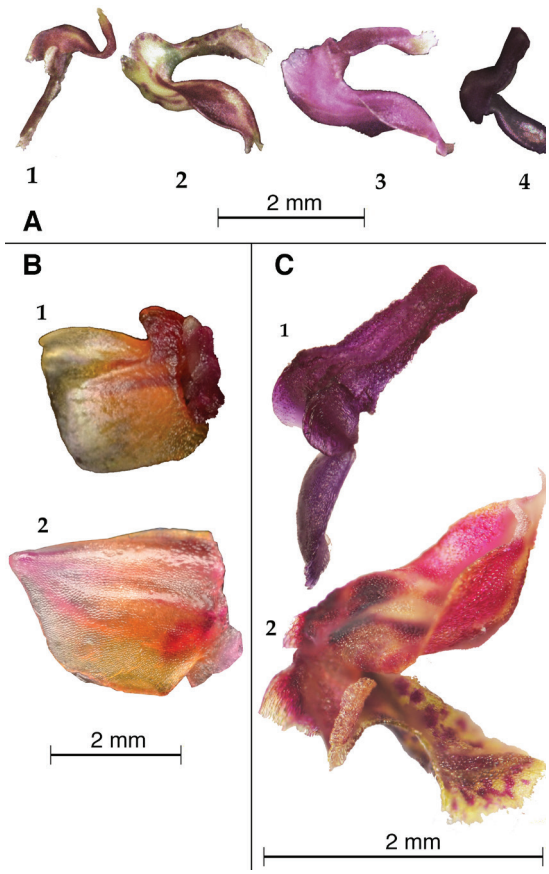

Figure 3. Comparison of the lips and petals of *Scaphosepalum luannae* and other similar species. **A**. Lips of three species of *Scaphosepalum*: *S. cimex* (**A1**), *S. swertiifolium* (**A2, A4**) and *S. luannae* (**A3**). **B**. Petals of *S. luannae* (**B1**) and *S. swertiifolium* (**B2**). **C**. Lips of *S. luannae* (**C1**) and *S. swertiifolium* (**C2**). Photos by Luis Baquero.

Orchid Reserve, which now protects this species.

Other studied material: Ecuador. Carchi, Cerro Oscuro, 0°54'42.5"N 78°12'48.7"W, 1818 m, cultivated at the Jardín Botánico de Quito, *LB 3132* (QCNE-spirit).

Distribution: This species is known from three areas close to Chical in north-western Ecuador. *Scaphosepalum luannae* was first found by the author in a remnant of cloud forest around km 9 of the Chical-El Carmen road. Eventually, more plants where found growing in Cerro Oscuro very close to Chical, and afterwards in the Peñas Blancas ridge, within sight of the mountains of Colombia. It would not be surprising if the species is eventually found growing in adjacent regions of Colombia.

Habitat and ecology: *Scaphosepalum luannae* grows as an epiphyte in moist cloud forest simpatrically with *S. decorum* Luer & Escobar, *S. cimex* Luer & Hirtz, *S. ophidion* Luer, *S. reptans* Luer & Hirtz, *S. swertiifolium* and the recently discovered *S. zieglerae* Baquero. No intermediates of *S. luannae* and *S. swertiifolium* have been found at the locality where they grow sympatrically, which might suggest both species have independent pollinators. In addition, the only known population of *S. zieglerae* was found very close to the type locality of *S. luannae* (Luer 1988, Luer 2009, Baquero 2017).

The most similar species to *Scaphosepalum luannae* is *S. swertiifolium* mainly due to the long sepaline tails. Although, there are some color variations in *S. swertiifolium* (even a big pink big flowered form from Colombia), in all the geographic variations and sub-species of this widely distributed species, the shape and structure of the lip and petals are always different from those of *S. luannae*. The sub-quadrate petals of *S. luannae* have a tooth-like, conspicuous, rounded and callous projection at the base of the columnar margin that is absent in any variation or subspecies of *S. swertiifolium*. The lip of *S. luannae* has an oblong and flat hypochile with a truncate, elobulate base, while in *S. swertiifolum* the hypochile of the lip is suborbicular and shallowly concave, always minutely bilobulate at the base (Fig. 3). Apart from the morphology of the lip, petals, and osmophores, *S. luannae* is also immediately distinguished from *S. swertiifolium* by the shiny surface and dark olive color of the leaves, which are always smaller in the former species. Another unique feature of *S. luannae* is the abaxial side of the leaves with strongly marked veins, which is not seen in any other species in the genus (Fig. 4).

***Scaphosepalum anchoriferum* in Ecuador**. *Scaphosepalum anchoriferum* was discovered in the area of Peñas Blancas, Carchi province of north-western Ecuador, close to the border with Colombia. It grows sympatrically with *S. luannae, S. cimex* and *S. swertiifolium*. The flowers are brightly colored and with a relatively shallow synsepal compared to forms found in Costa Rica and Panama (Luer 1998).

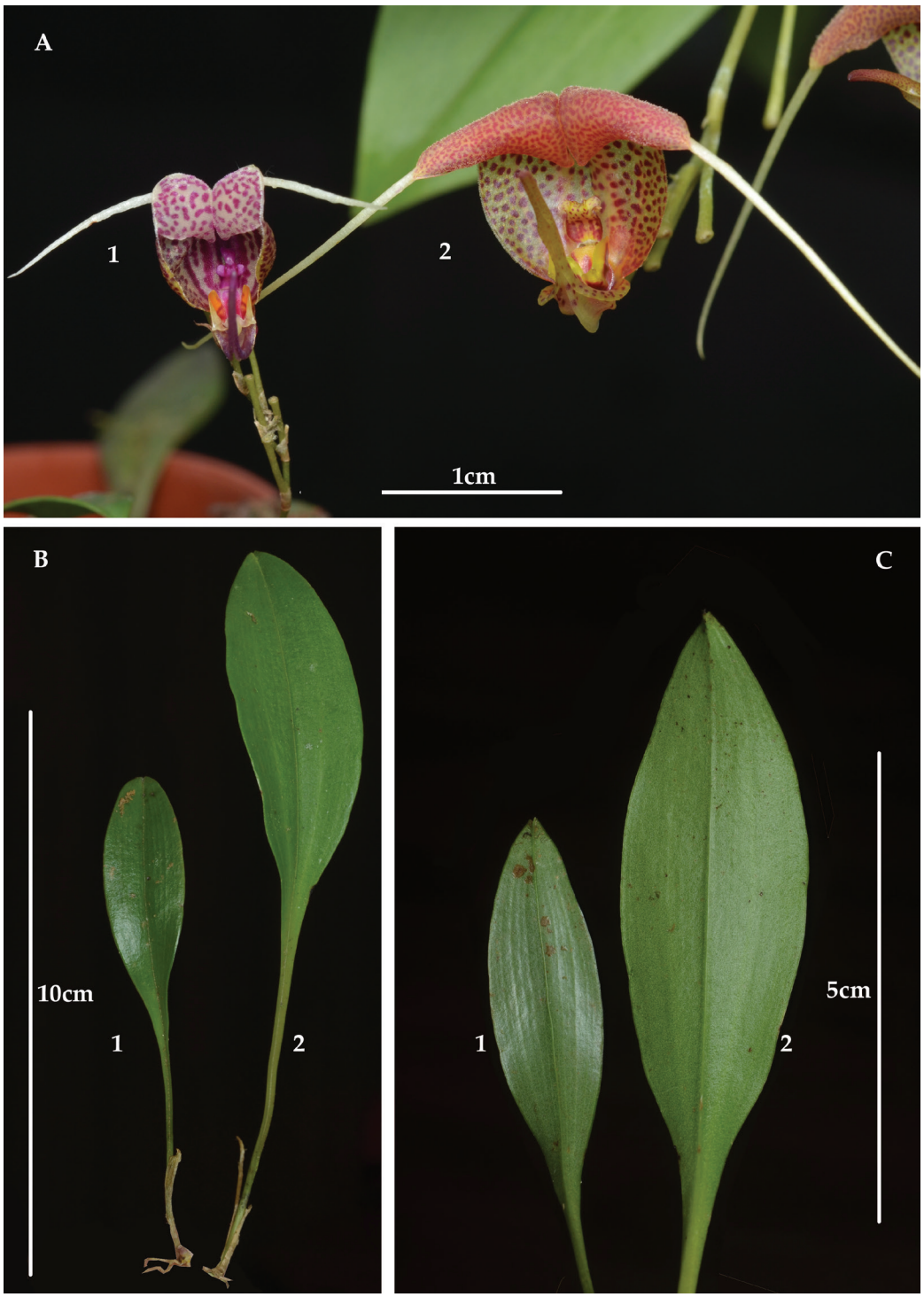

FIGURE 4. Comparison between *Scaphosepalum luannae* and *S. swertiifolium*. **A**. Flowers of *S. luannae* (**A1**) and *S. swertiifolum* (**A2**). **B**. Leaves of *S. luannae* (**B1**) and *S. swertiifolium* (**B2**) in adaxial view. **C**. Leaves of *S. luannae* (**C1**) and *S. swertiifolium* (**C2**) in abaxial view. Photos by Luis Baquero.

Considering that *Scaphosepalum bicolor* Luer is the most similar species to *S. anchoriferum* found in Colombia, it is most probable that *S. anchoriferum* will eventually be discovered in this country as well. The shape of the flower and the bright colored sepals of the Ecuadorian variety seems to differ from the typical *S. anchoriferum*. Nevertheless, the lips of plants from Panama and Ecuador are identical in structure and shape when compared. Both varieties have lips which are oblong-subpandurate, dilated in the middle third, with a pair of denticulate lamellae, the epichile orbicular, serrulate, the hypochile more or less oblong, truncate, minutely bilobulate (Fig. 5). Also, the habit of the plants and consistency of the leaves (coriaceous, "harder" than in other species like *S. swertiifollium*) are the same in the plants from Ecuador and Panama.

Scaphosepalum anchoriferum (Rchb.f.) Rolfe (Fig. 5). Ecuador. Carchi: between Chical y El Carmen, 0°59'24.0"N 78°13'14.9"W, 1636 m, collected by Luis Baquero *et al.* on February 26, 2017, *LB 3128* (holotype, QCNE).

Plant epiphytic, densely caespitose, to 10 cm tall. *Roots* slender, 0.5 mm in diameter. *Ramicauls* erect to sub-erect, slender, 1–4 cm long, enclosed by 3 sheaths. *Leaf* elliptic, subacute, erect to sub-erect, thinly coriaceous, markedly veined at the abaxial side, 7–15 cm long, 2.0–5.0 cm wide, gradually narrowed below in to a slender, channeled petiole 1–4 cm long. *Inflorescence* a congested, successively several-flowered raceme from low on the ramicaul, up to 8 cm long, born by a slender, smooth, horizontal to descending peduncle up to 10 cm long. *Floral bracts* thin, 3 mm long, 2–7 mm long. *Ovary* ribbed, 2 mm long. *Sepals* yellow-green, suffused with red-purplish spots, the margins ciliate. *Dorsal sepal* yellow-green, tri-carinate at the outer surface, ovate, acute, concave below the middle, narrowed and with revolute margins above the middle, 10 × 4 mm expanded. *Lateral sepals* yellow spotted with red dots, concave, the lamina elliptic, 10.2 × 6.1 mm, connate 10 mm, the apical half of each lateral sepal occupied by a thick, well-developed, triangular, microscopically densely pubescent cushion 4 × 6 mm, the obtuse, diverging apices contracted into a slender, decurved tail 5 mm long. *Petals* yellow, marked with red-purple, ovate, acute, more or less dilated on the labellar margin, 4.5 × 2.5 mm. *Lip* yellow spotted with red-purple, oblong-subpandurate, 3.5 × 2 mm, reflexed and dilated near the middle, with a pair of denticulate lamellae extending from the base to one third of its length, the epichile orbicular, serrulate, the hypochile more or less oblong, truncate, minutely bilobulate. *Column* yellow-green, suffused with red, semiterete, slender, 4 mm long, broadly winged above the middle, with a thick, 2 mm long foot. *Pollinia* 2, yellow. *Fruits* and seeds not observed.

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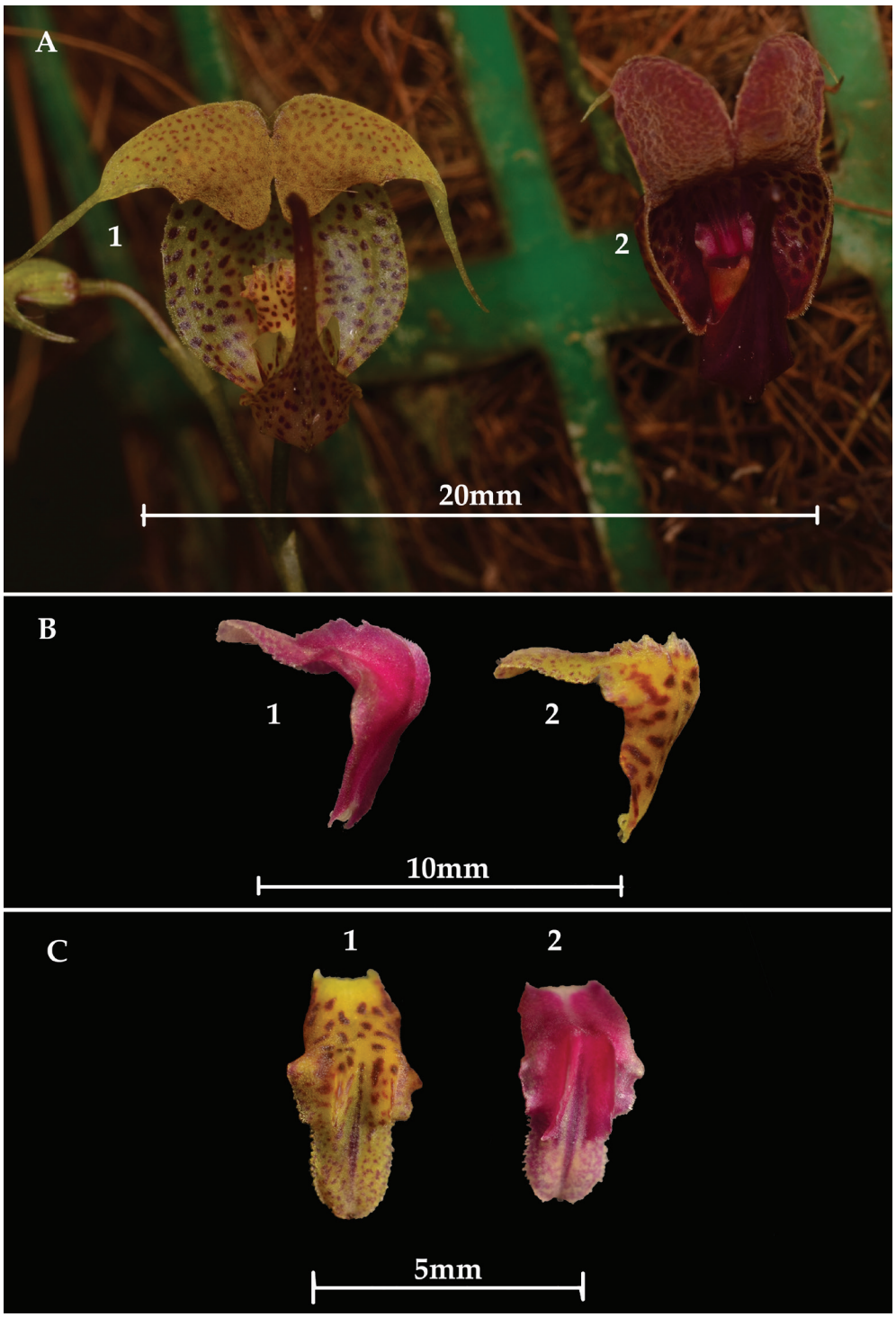

Figure 5. *Scaphosepalum anchoriferum*. **A**. Flowers from Ecuador (**A1**) and Panama (**A2**). **B**. Lateral view of the lips of *S. anchoriferum* from Panama (**B1**) and from Ecuador (**B2**). C. Dorsal view of the lips of *S. anchoriferum* from Ecuador (**C1**) and from Panama (**C2**). Photos by Luis Baquero.

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TO BE, OR NOT TO BE A *STELIS*

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

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

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

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

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

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

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

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

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

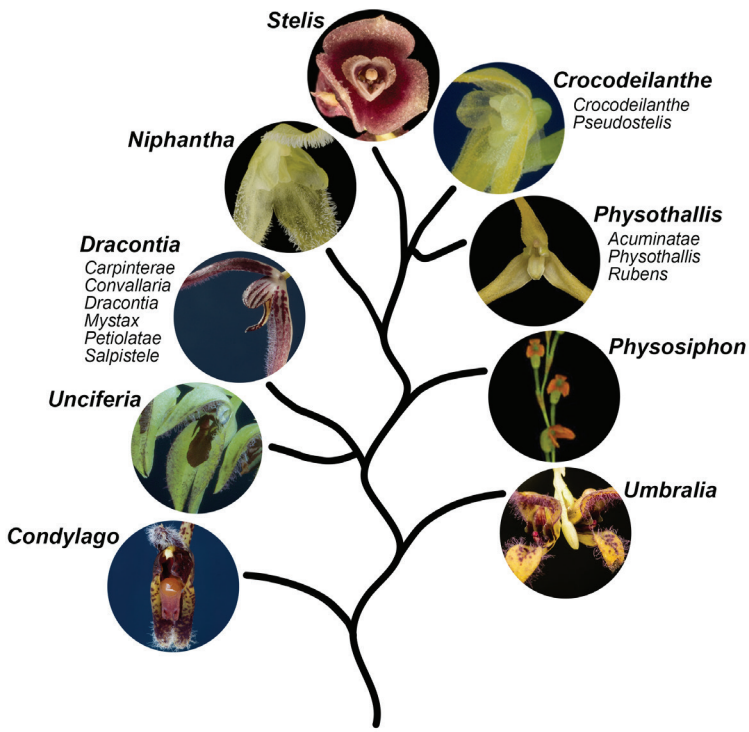

FIGURE 1. Relationships among the subgenera of *Stelis sensu lato* based on diverse phylogenetic reconstructions (Pridgeon *et al.* 2001, Solano-Gómez 2005, Karremans 2010, Chiron *et al.* 2012, Ramos-Castro *et al.* 2012; Karremans *et al.* 2013, Wilson *et al.* 2017, Pérez-Escobar *et al.* 2017, Chumová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

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

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

Taxonomic Treatment

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis* subgen. *Stelis (Figs. 2–4)

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

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

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

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

Stelis cochabambensis Karremans, *nom. nov.*

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

Stelis luerii Karremans, *nom. nov.*

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

Stelis peculiaris Karremans, *nom. nov.*

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

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

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

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

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

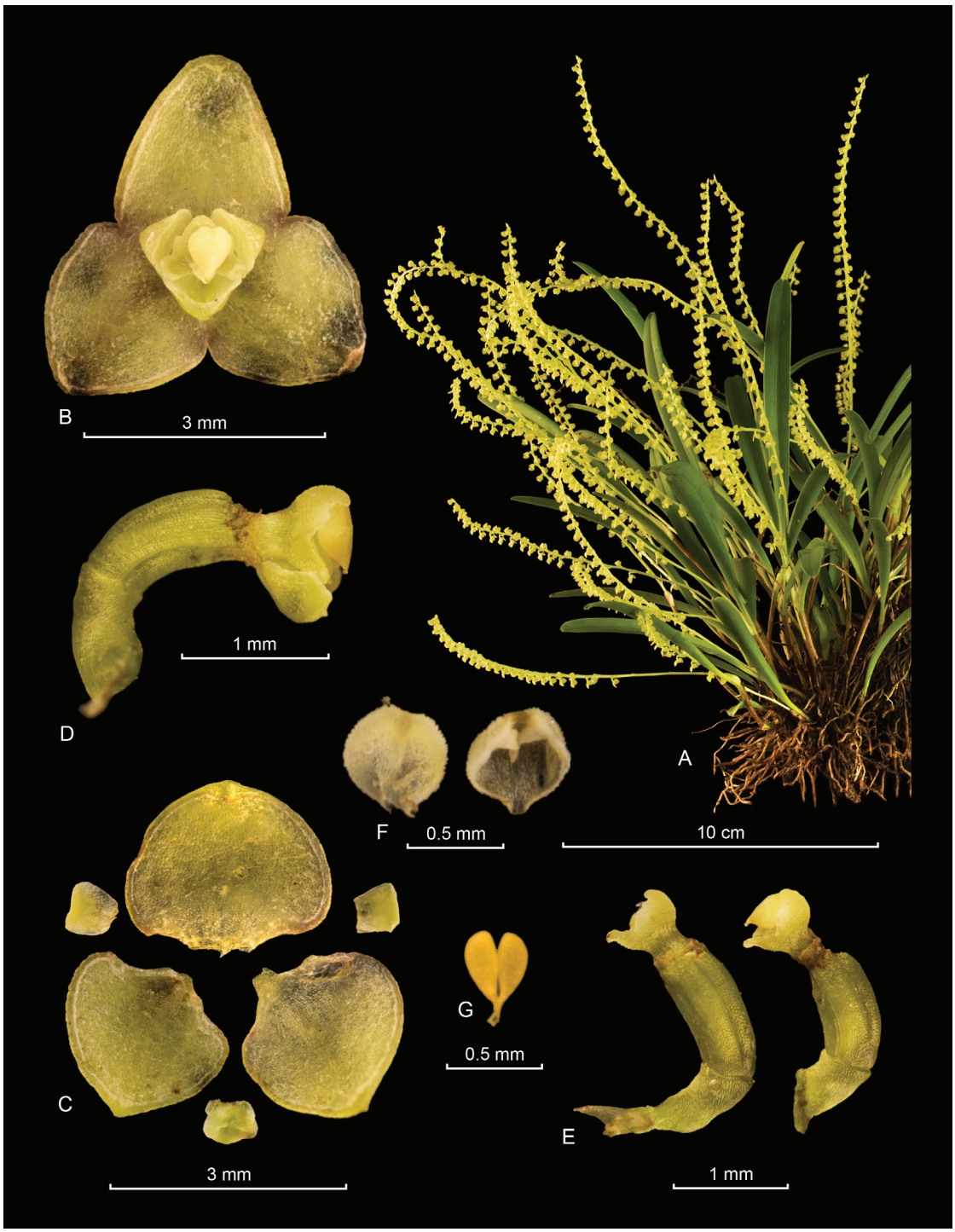

FIGURE 2. Lankester Composite Digital Plate (LCDP) of *Stelis sp*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral view. **F**. Anther cap. **G**. Pollinarium. Photographs by AK and I. Chinchilla based on *Karremans 7293*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

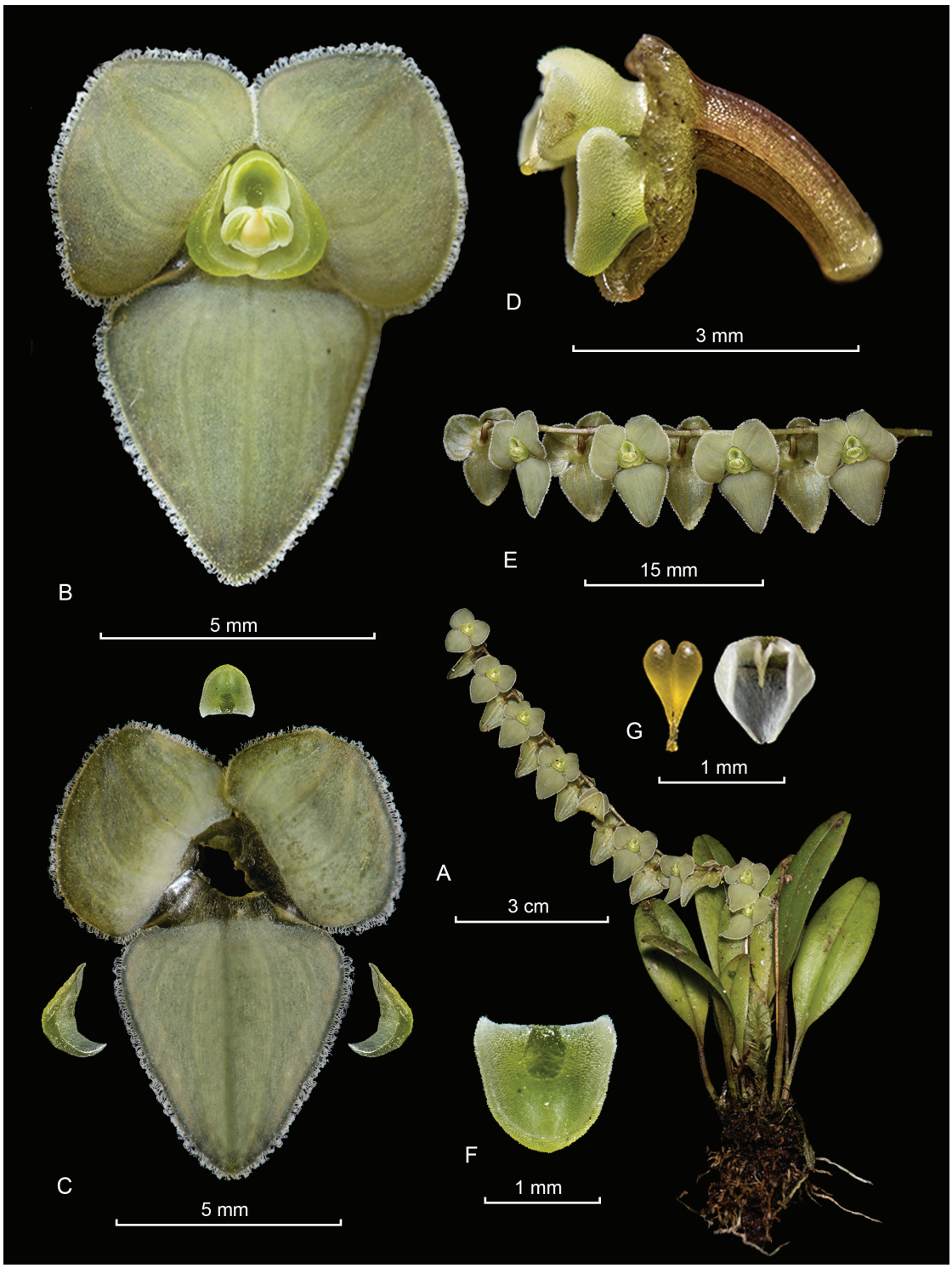

FIGURE 3. LCDP of a typical *Stelis s.s.* species. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Inflorescence. **F**. Lip. **G**. Anther cap and pollinarium. Photographs by J.S. Moreno based on *Moreno* 519 (CAUP).

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

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

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

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

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

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

Stelis* subgen. *Crocodeilanthe* sect. *Crocodeilanthe

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis damianii Karremans, *nom. nov.*

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

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

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

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

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

Stelis toscanoi Karremans, *nom. nov.*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis heros Karremans, *nom. nov.*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

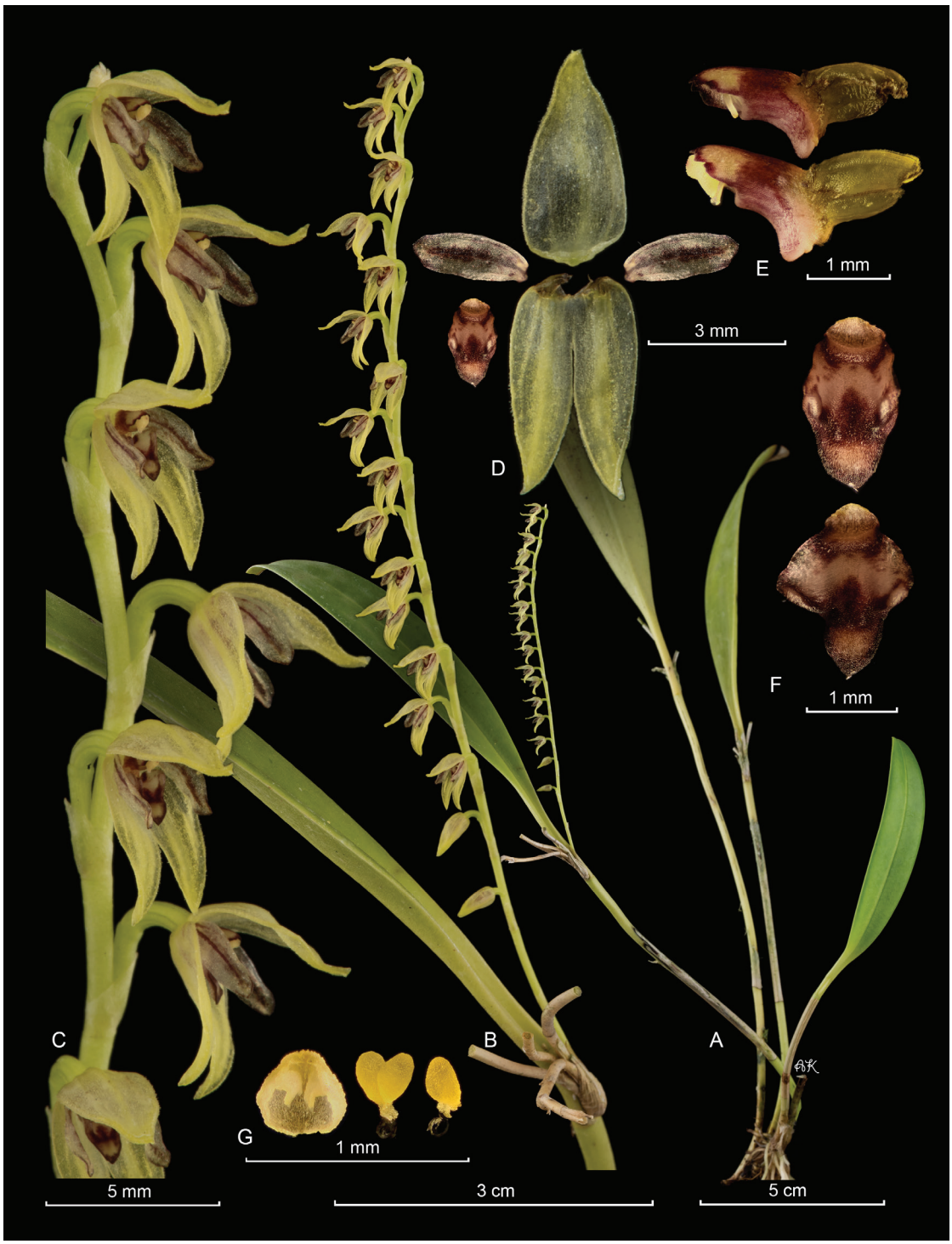

FIGURE 6. LCDP of *Stelis pulchella* a typical representative of *Stelis* sect. *Crocodeilanthe*. **A**. Habit. **B**. Inflorescence. **C**. Flowers. **D**. Dissected perianth. **E**. Column ventral and lateral view. **F**. Lip naturally and expanded. **G.** Anther cap and pollinarium. Photographs by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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

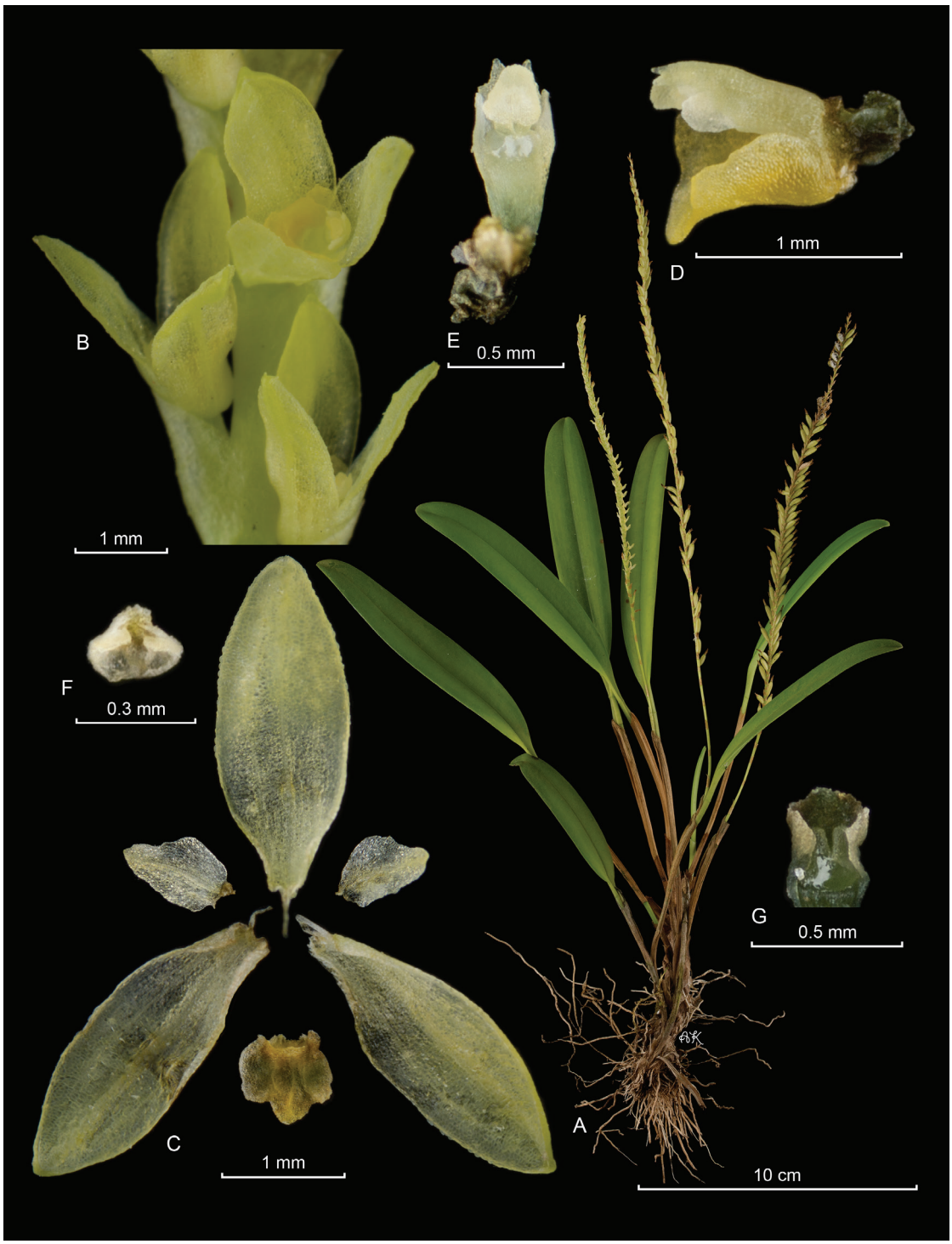

FIGURE 7. LCDP of *Stelis deregularis*, type species of *Stelis* sect. *Pseudostelis*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral view. **F**. Anther cap. **G.** Pollinarium on the stigma. Photographs by AK based on *Karremans 7303*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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

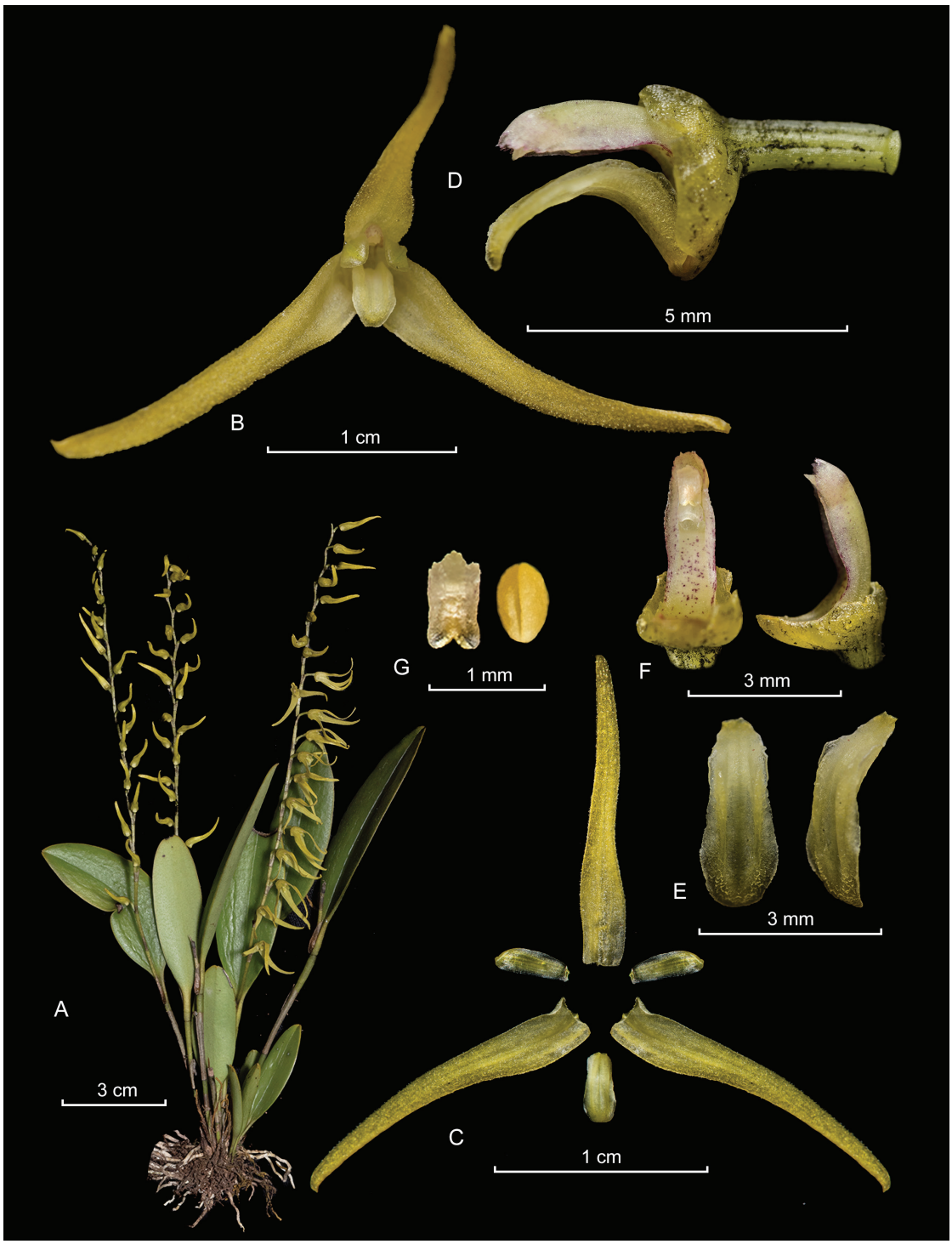

FIGURE 8. LCDP of *Stelis aurea*, type species of *Stelis* sect. *Acuminatae*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral view. **F**. Lip. **G**. Anther cap and pollinarium. Photographs by J.S. Moreno based on *Moreno*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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis* subgen. *Physothallis* sect. *Physothallis

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

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

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

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

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

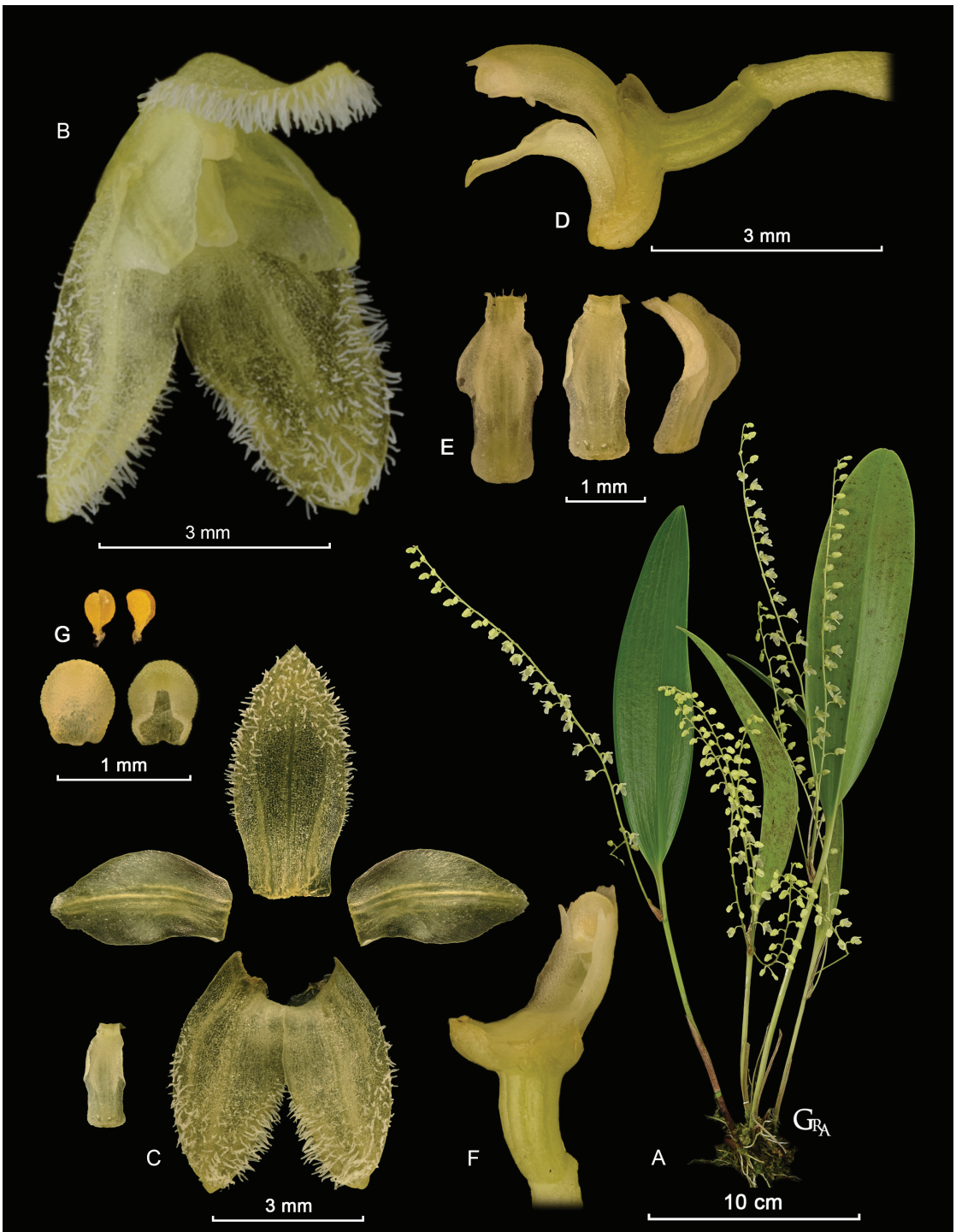

FIGURE 12. LCDP of *Stelis gelida*, type species of *Stelis* subgen. *Niphantha*. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Lip, three views. **F**. Column, three quarters view. **G**. Pollinarium and anther cap, two views. Photographs by G.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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis* subgen. *Dracontia* sect. *Dracontia

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

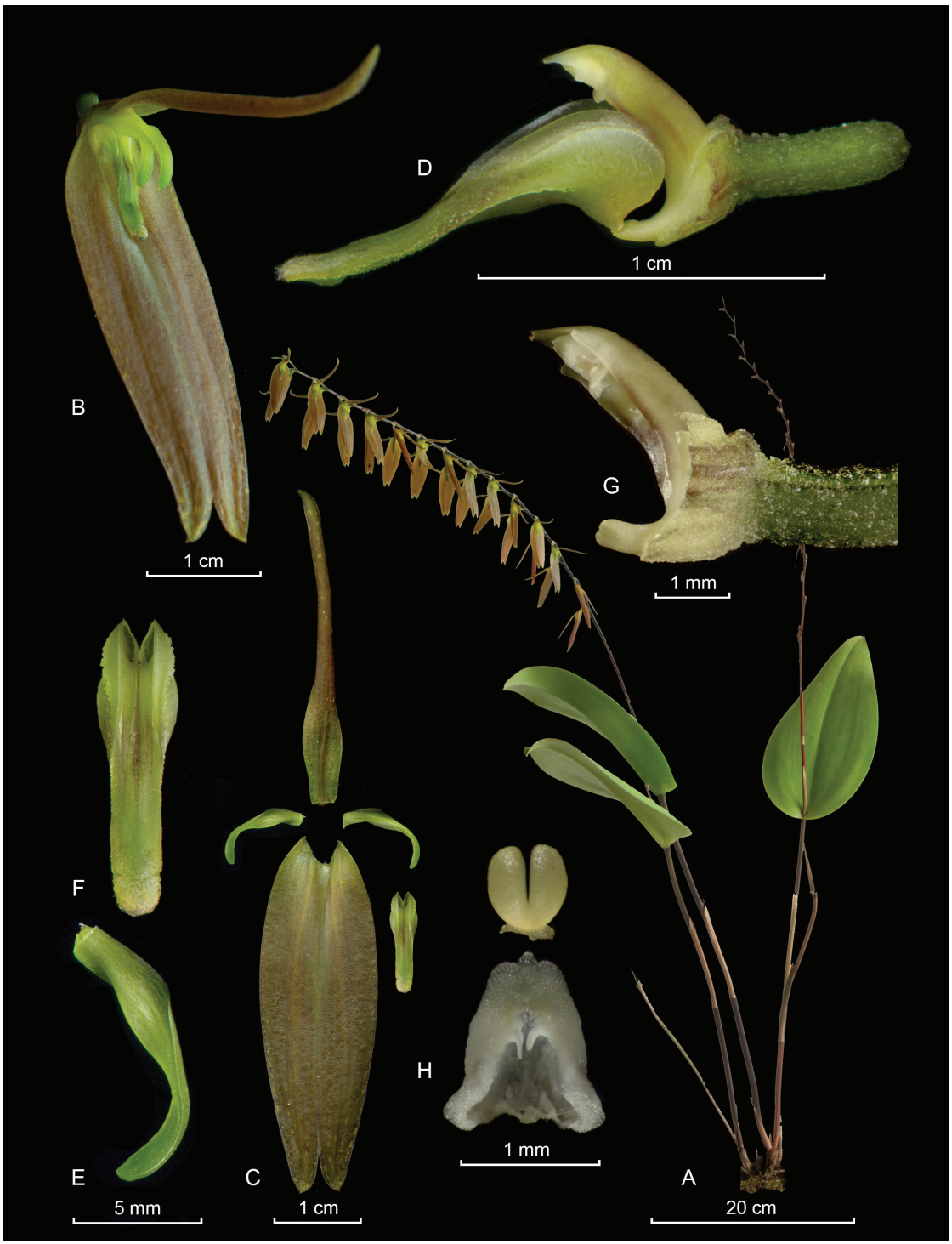

FIGURE 15. LCDP of *Stelis alta* Pridgeon & M.W.Chase, type species of *Pleurothallis* sect. *Brobdingnagia* Luer (= *Stelis* sect. *Dracontia*). **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Petal. **F**. Lip. **G**. Column side view. **H**. Anther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

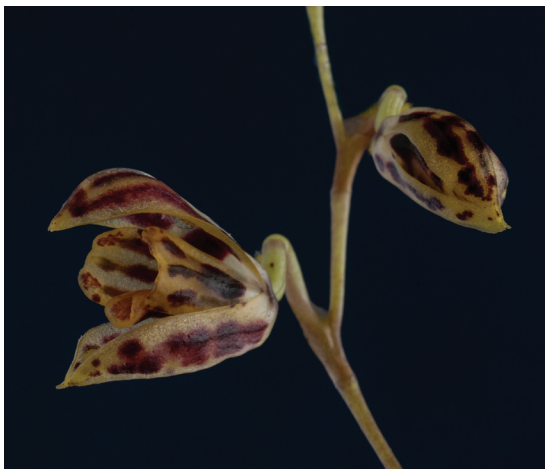

FIGURE 16. *Stelis cylindrata* Pridgeon & M.W.Chase, type species of *Pleurothallis* sect. *Cylindria* Luer (= *Stelis* sect. *Dracontia*). Photograph by AK.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

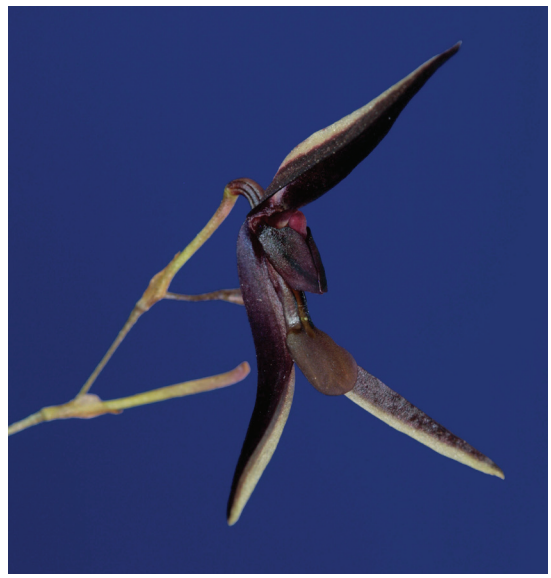

Figure 19. *Stelis mystax*, type species of *Stelis* sect. *Mystax* (Luer) Karremans. Photograph by D. Bogarín based on *Bogarín 2988* (JBL-spirit).

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

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

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

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

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

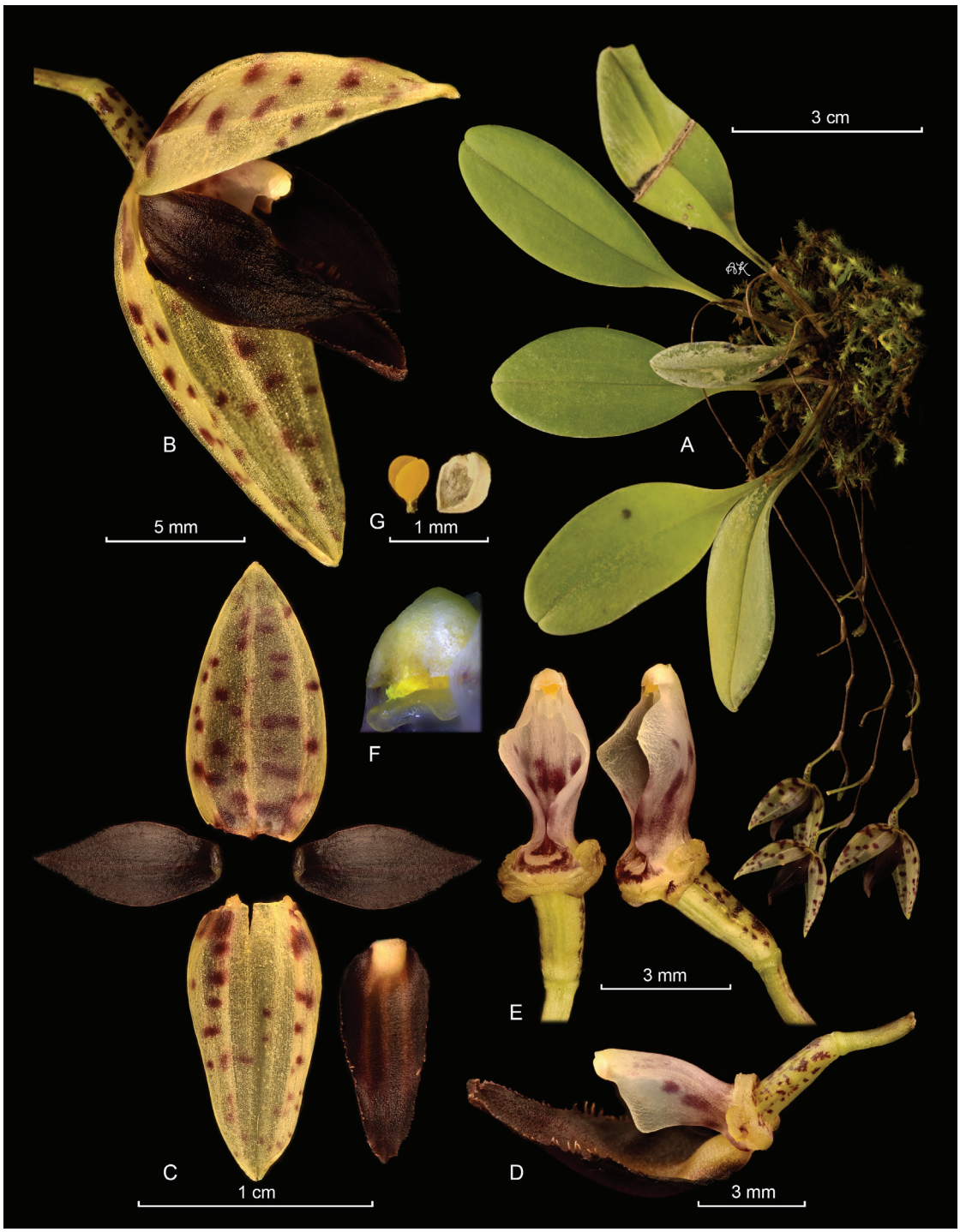

FIGURE 20. LCDP of *Stelis guttata* (Luer) Pridgeon & M.W.Chase, type species of *Stelis* sect. *Petiolatae* (Luer) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Column ventral and lateral views. **F**. Column apex. **G**. Anther cap and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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

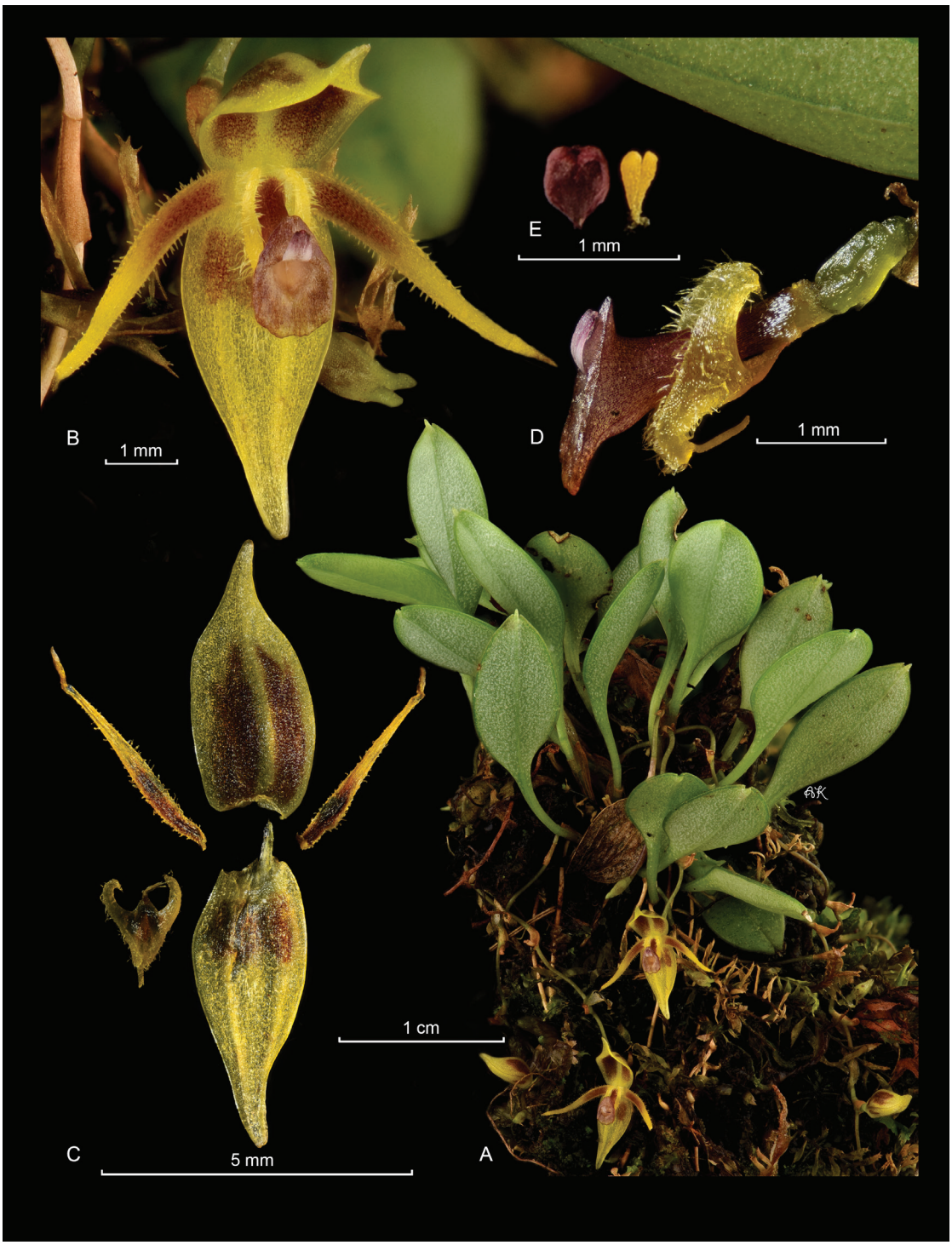

FIGURE 21. LCDP of *Stelis brunnea*, type species of Stelis sect. Salpistele (Dressler) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E**. Anther cap and pollinarium. Photographs by AK based on *Karremans 8260* (JBL-spirit).

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

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

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

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

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

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

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

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

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

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

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

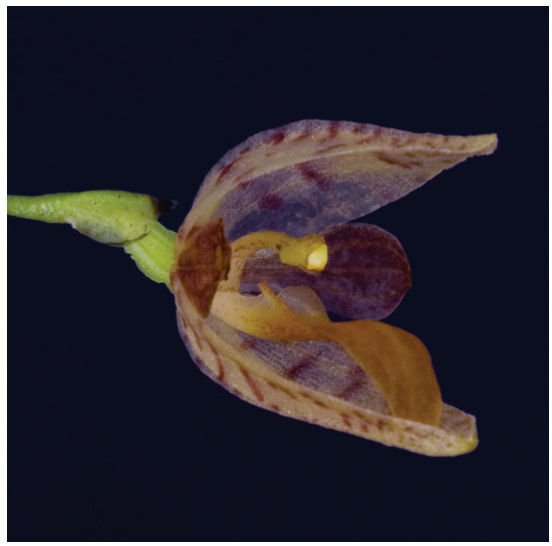

FIGURE 22. *Stelis carpinterae*, type species of *Stelis* sect. *Carpinterae* Karremans. Photograph by D. Bogarín based on *Bogarín 7159* (JBL-spirit).

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

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

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

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

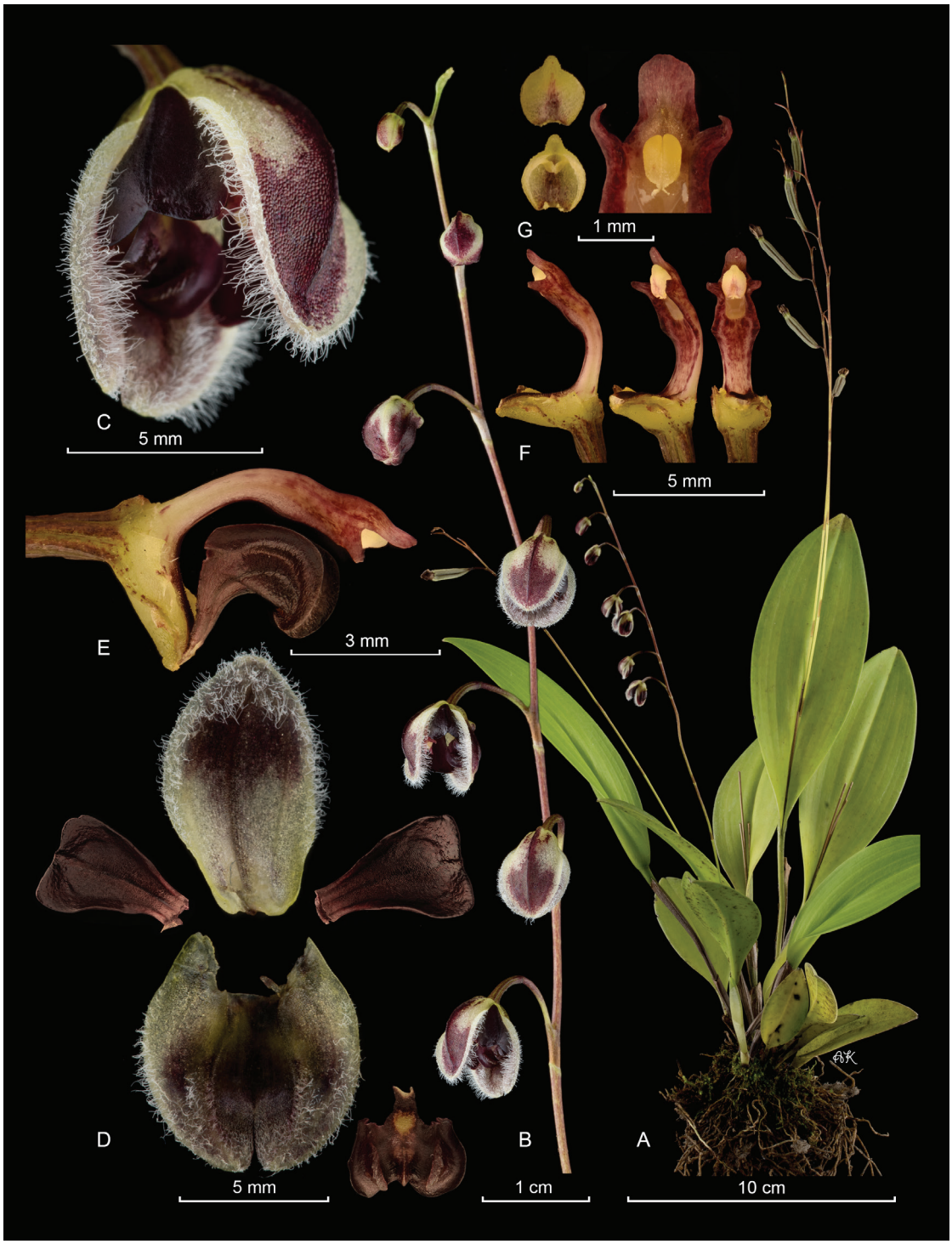

FIGURE 23. LCDP of an autogamous specimen of *Stelis convallaria*, type species of *Stelis* sect. *Convallaria*. **A**. Habit. **B**. Inflorescence. **C**. Flower. **D.** Dissected perianth. **E**. Column with lip, lateral view. **F**. Column ventral and lateral views. **G**. Anther cap and pollinarium,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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stelis insectifera Karremans, *nom. nov.*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

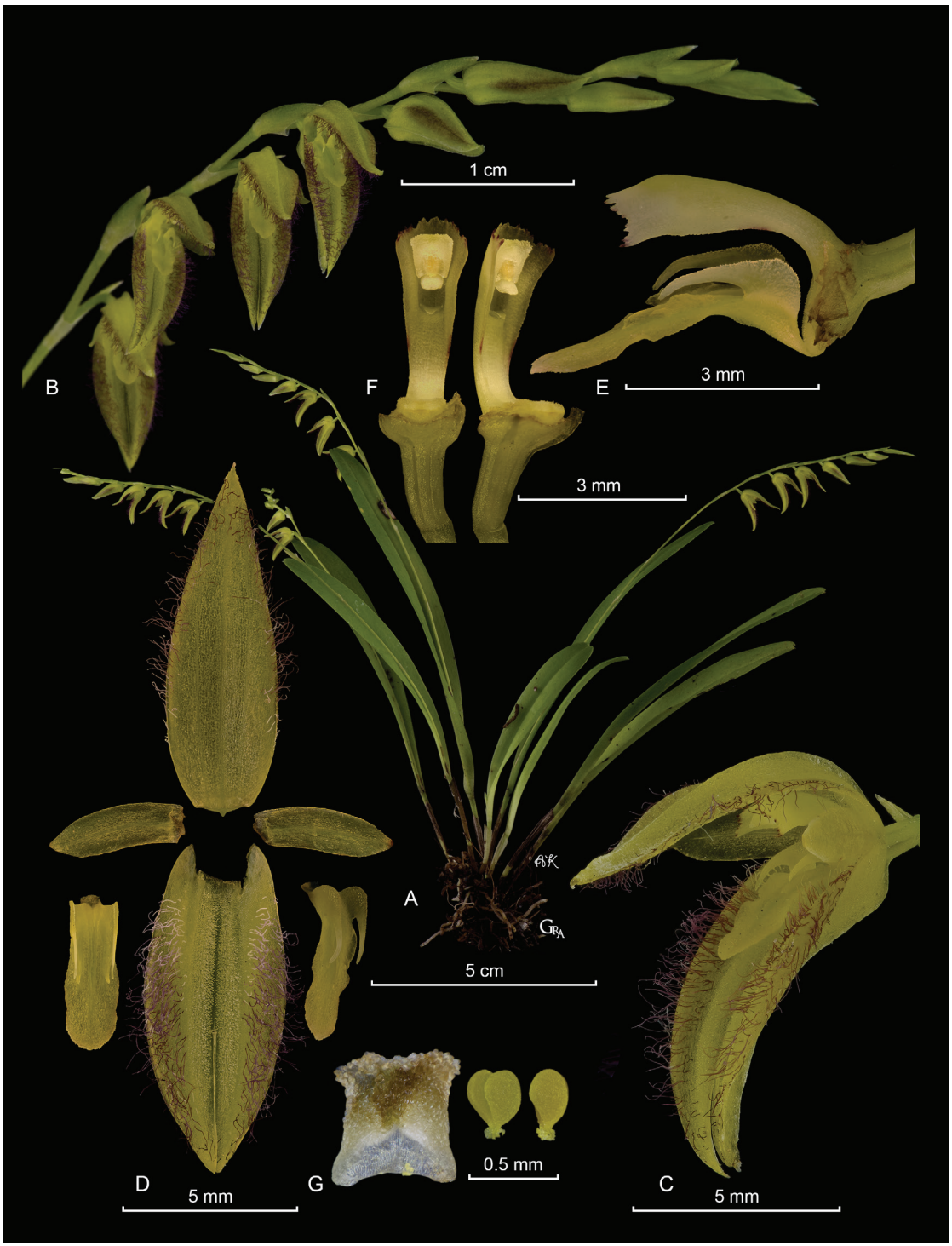

FIGURE 26. LCDP of *Stelis segoviensis*, type species of *Stelis* subgen. *Unciferia*. **A**. Habit. **B**. Inflorescence. **C**. Flower. **D**. Dissected perianth. **E**. Column with lip, lateral view. **F**. Column ventral and lateral view. **G**. Anther cap and pollinarium. Photographs by AK based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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

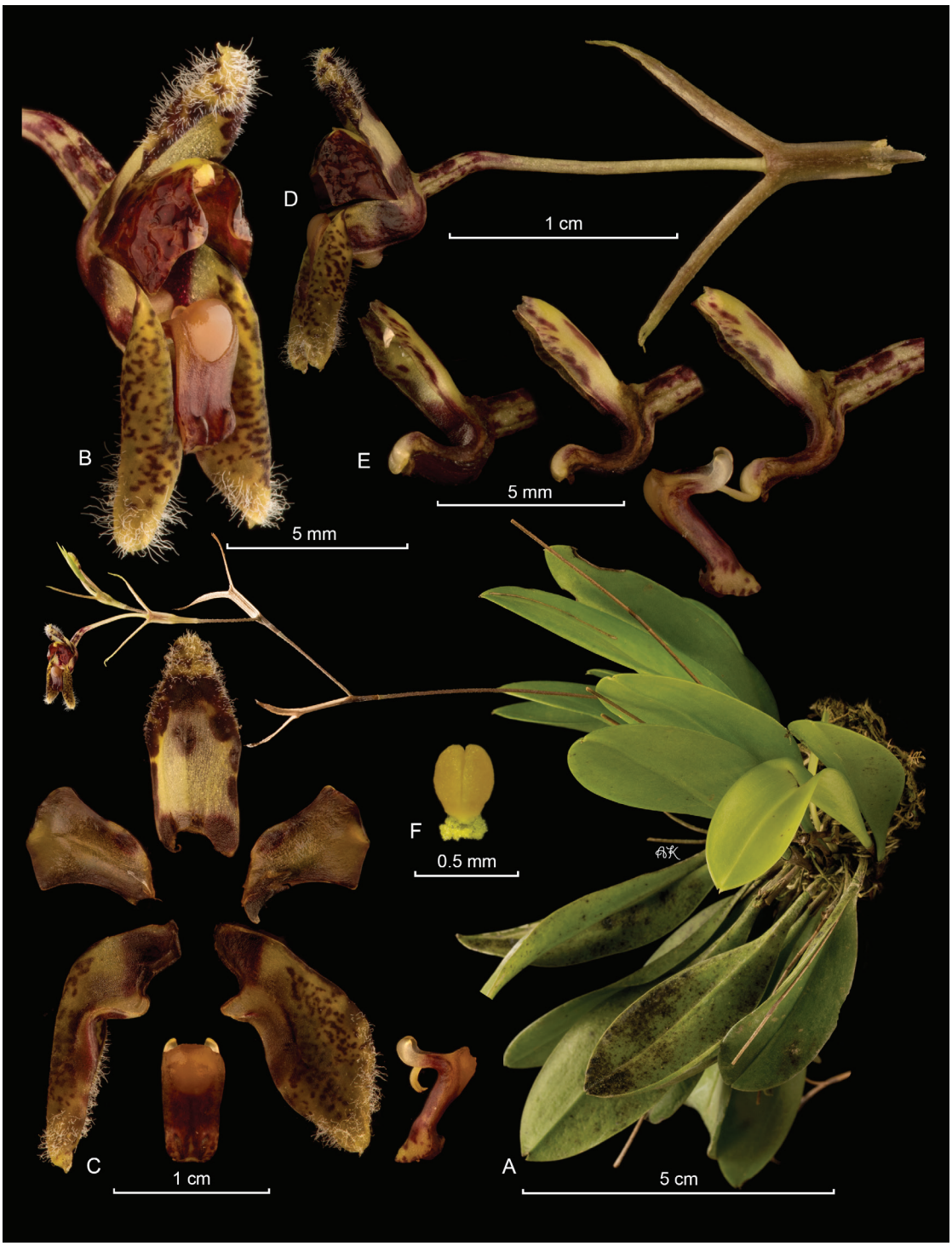

FIGURE 27. LCDP of Stelis furculifera, one of the two members of Stelis subgen. Condylago (Luer) Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Flower, floral bract, lateral view. **E**. Column semi-ventral, side view, with and without the lip attached. **F**. Pollinarium.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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

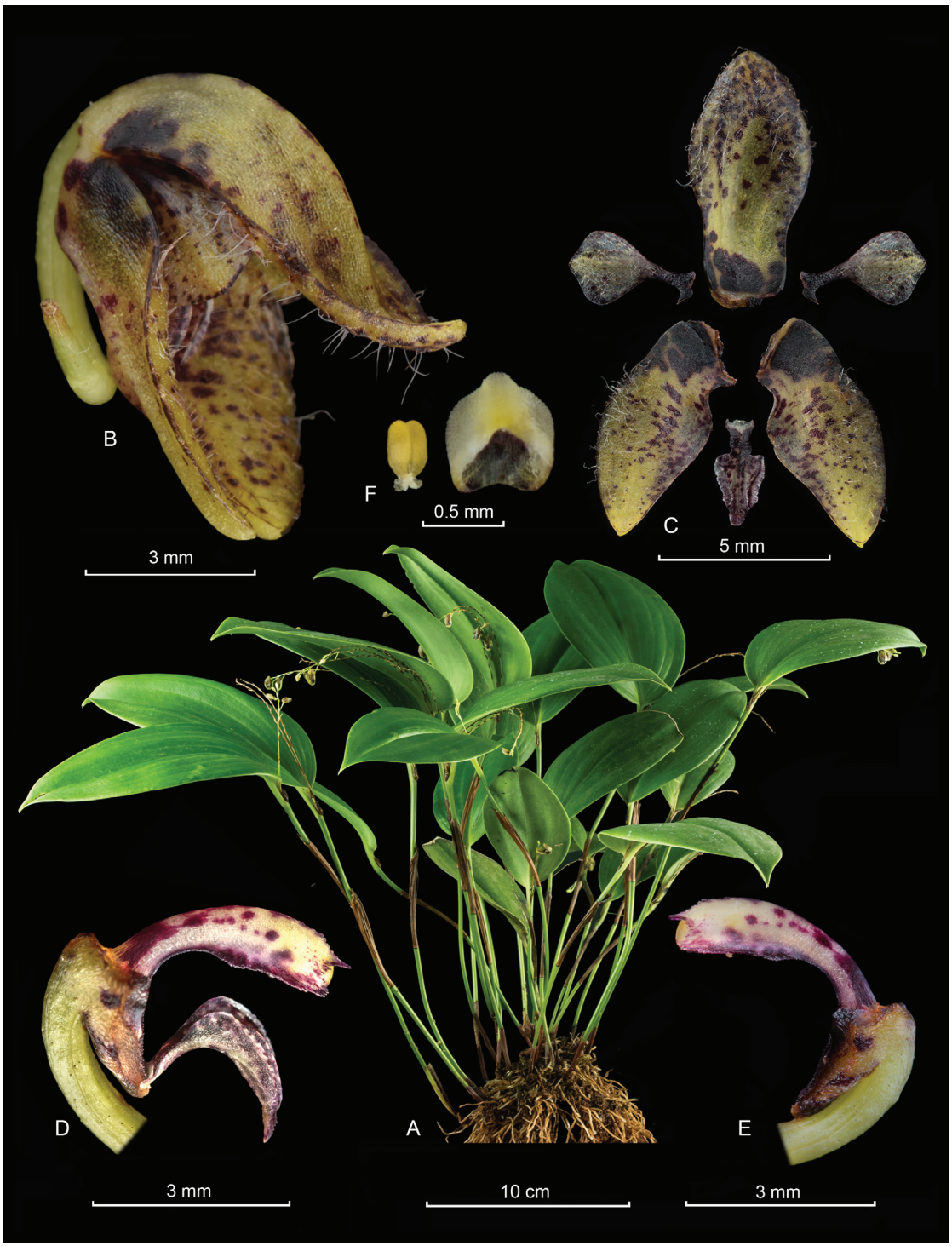

FIGURE 28. LCDP of *Stelis imraei*, type species of *Stelis* subgen. *Umbralia* Karremans. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **D.** Column lateral view. **E**. Anther cap and pollinarium. Photographs by I. Chinchilla based on *Bogarín 752* (JBL-spirit).

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

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

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

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

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

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

Excluded Taxa

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

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

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

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

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

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

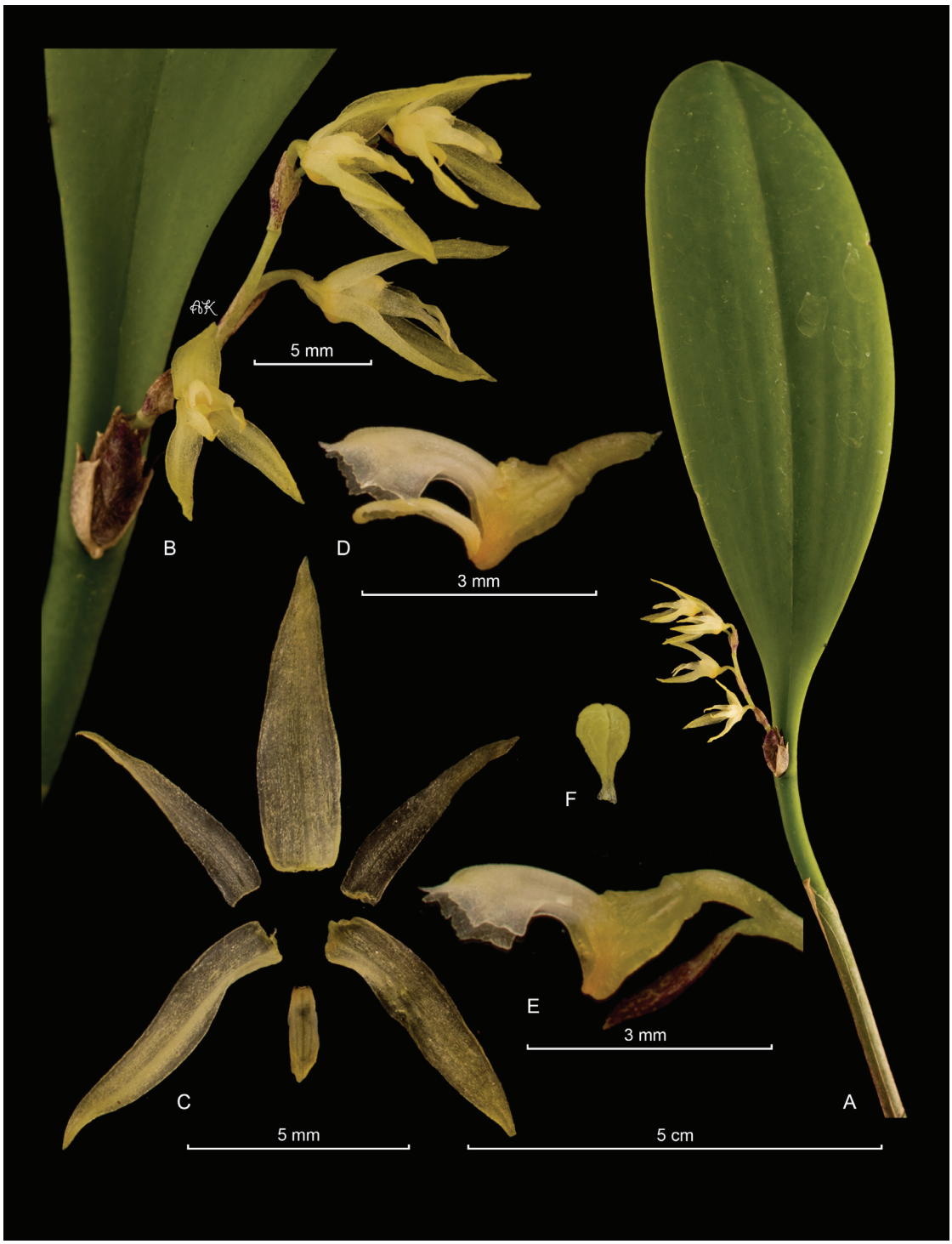

FIGURE 29. LCDP of *Anathallis obovata*, type species of *Anathallis*. **A**. Habit. **B**. Inflorescence. **C**. Dissected perianth. **D**. Column with lip, lateral view. **D.** Column ventral and lateral view. **E**. Pollinarium. Photographs by AK based on *JBL-28233* (JBL-spirit).

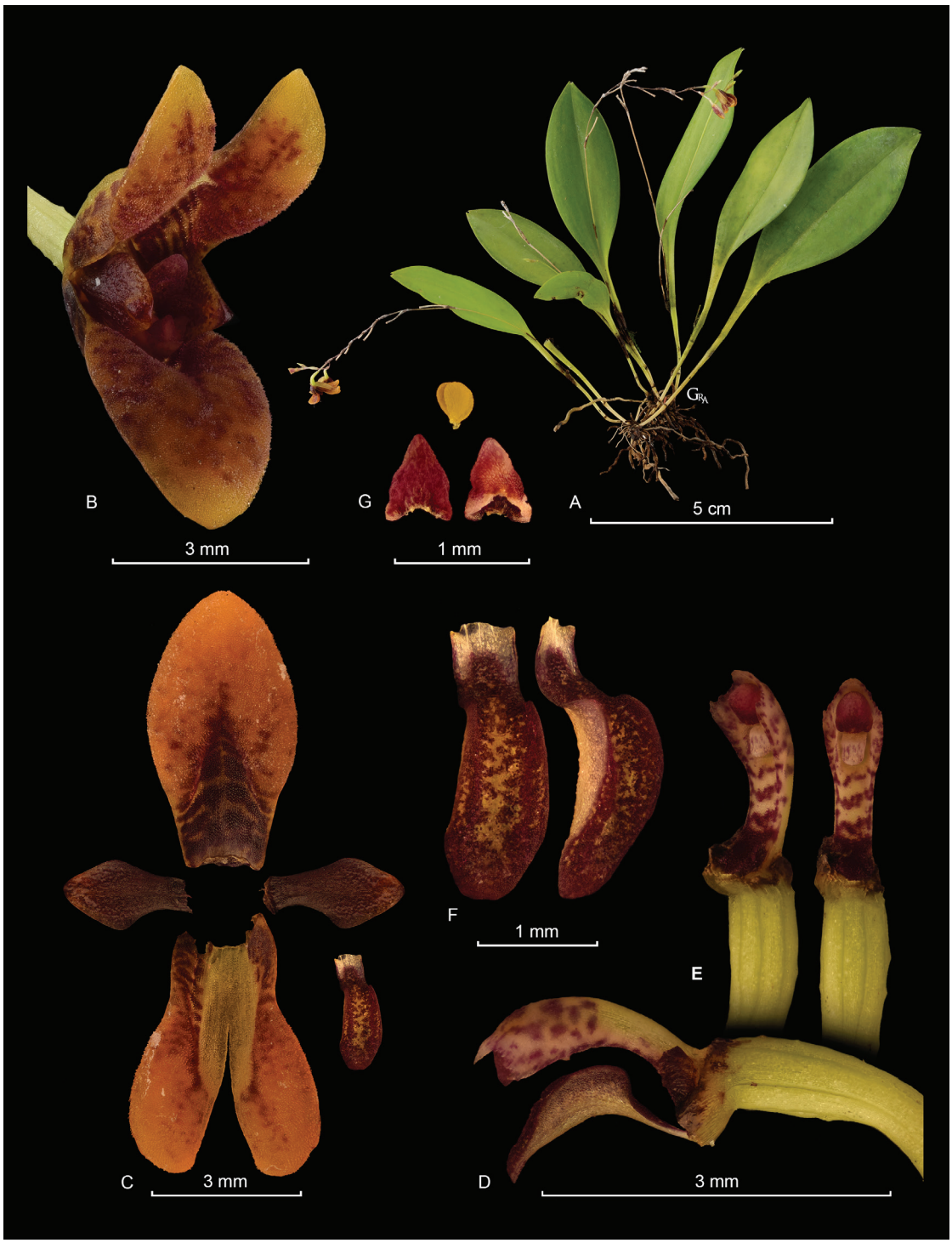

FIGURE 30. LCDP of *Pabstiella hypnicola*, type species of *Pleurothallis* subgen. *Effusia* (= *Pabstiella*). **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Column with lip, lateral view. **E.** Column ventral and lateral view. **F**. Lip. **G**. Anther cap and pollinarium. Photographs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

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

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

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

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

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

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

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

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

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

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

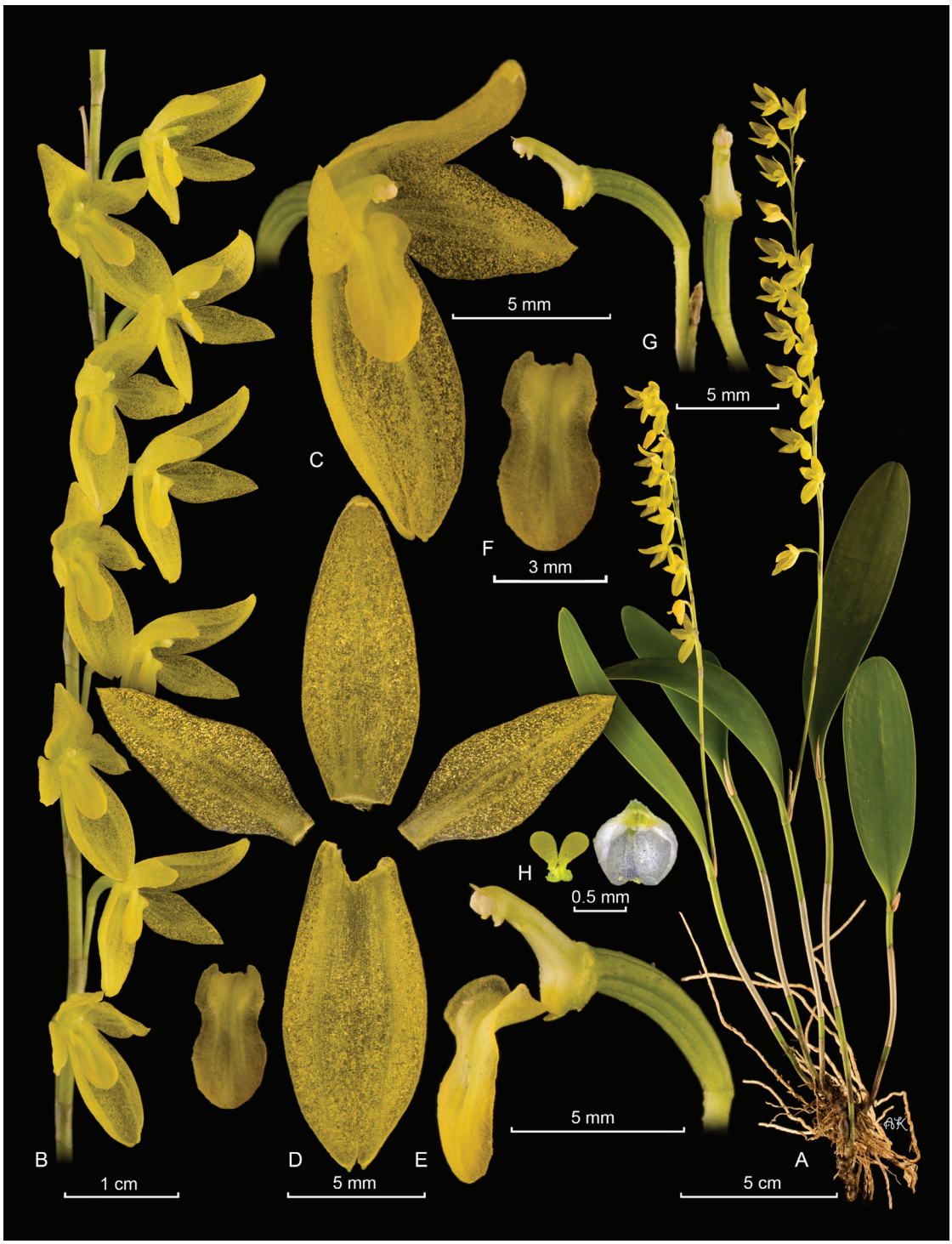

FIGURE 32. LCDP of *Pleurothallis quadrifida*, type species of *Lalexia* (= *Pleurothallis* subgen. *Lalexia*). **A**. Habit. **B**. Inflorescence. **C**. Flower. **D**. Dissected perianth. **E**. Column with lip, lateral view. **F**. Lip. **G.** Column ventral and lateral view. **H**. Anther cap and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

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

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

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

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

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

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

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

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