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NEW SPECIES OF *AA* AND NEW COMBINATIONS IN *MYROSMODES* (ORCHIDACEAE: CRANICHIDINAE) FROM BOLIVIA AND PERU

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Abstract. A new species of *Aa* from northern Peru is described: *Aa aurantiaca,* which has highly atypical orange flowers for the genus. Furthermore, two new combinations of *Myrosmodes* are proposed: *M. inaequalis* and *M. gymnandra*, with illustrations and diagnostic features of the new species.

Resumen. Se describe una nueva especie de *Aa* del norte del Perú: *Aa aurantiaca*; la cual tiene las flores de color naranja, siendo éste un color inusual para el género. Se proponen además dos nuevas combinaciones de *Myrosmodes*: *M. inaequalis* y *M. gymnandra*; se presentan ilustraciones y se discuten rasgos diagnósticos de las nuevas especies.

Key words. : Orchidaceae, Cranichideae, Peru, Bolivia, *Aa*, *Myrosmodes*

The genera *Aa* Rchb.f. and *Myrosmodes* Rchb.f. consist of terrestrial orchids possessing tiny, white to greenish-white, non-resupinate flowers. Although there are some records of *Aa paleacea* (Kunth) Rchb.f. in the mountains of Costa Rica (Dressler 1993), the species of *Aa* and *Myrosmodes* are mostly restricted to the South American Andean mountain range at high elevations.

The taxonomic status of the representatives of these genera has remained unclear for many years. The genera *Aa* and *Myrosmodes* were first described by Reichenbach *filius* in 1854. He distinguished *Aa* from *Altensteinia* Kunth and transferred *Altensteinia paleacea* (Kunth) Kunth to *Aa* [*Aa paleacea* (Kunth) Rchb.f.]. However, in a subsequent work Reichenbach (1878) reassessed his criteria and placed both *Aa* and *Myrosmodes* as synonyms of *Altensteinia*, and described nine new species, among them *Altensteinia gymnandra* Rchb.f. and *Altensteinia inaequalis* Rchb.f.. Later, Schlechter (1912, 1920a, 1920b) distinguished *Aa* from *Altensteinia* again but considered *Myrosmodes* as a synonym of *Aa* and combined it with that genus (e.g., *Aa gymnandra* (Rchb.f.) Schltr., *Aa inaequalis* (Rchb.f.) Schltr.). Subsequent taxonomists, for instance Schweinfurth (1958), recognized only *Altensteinia* as a valid genus and considered the other two genera as synonyms.

Garay (1978), as part of his work in *Flora of Ecuador*, revalidated the genera *Aa* and *Myrosmodes* and transferred some species of *Aa* and *Altensteinia* to *Myrosmodes*. Since then, the three genera have been widely accepted as distinct taxa. Further revision of *Myrosmodes* in Peru and Colombia led to the transfer of more species to this genus (Vargas 1995, Ortiz 1995, respectively). Up to the point of this publication, *Myrosmodes* comprised about 10 species.

Morphologically, *Altensteinia* is distinguished from *Aa* and *Myrosmodes* by having a terminal inflorescence, pubescent column, lobulate clinandrium, small stigma and anthesis occurring after the full development of leaves (Garay 1978). Conversely, *Aa* and *Myrosmodes* possess a lateral inflorescence and glabrous column, and anthesis occurs before the full development of leaves. *Aa* has an elongate peduncle enveloped by tubular hyaline-diaphanous sheaths, with dorsal sepal and petals free from the column, lip calceolate with involute and lacerate margins, and in many species, a pilose ovary. *Myrosmodes* has at least 6 morphological and ecological characters that distinguish this genus from *Aa* and *Altensteinia* and the rest of Prescottiinae: (1) a short peduncle with infundibuliform, scarious sheaths, (2) a cucullate lip that is tubular or flared, with fimbriolate margins with moniliforms hairs (Garay 1978, Vargas 1997), (3) an accrescent peduncle (after
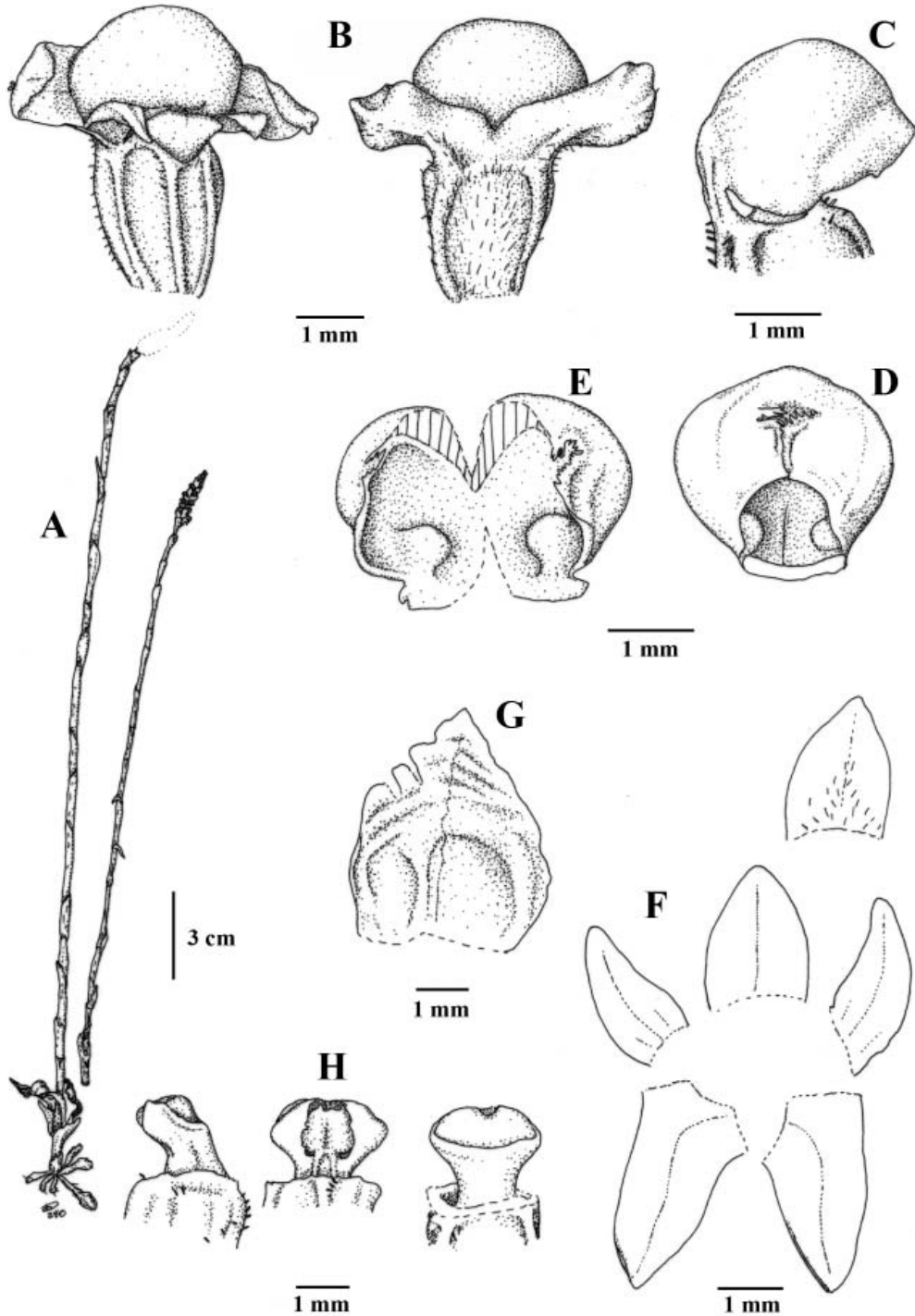
Figure 1. *Aa aurantiaca* D. Trujillo. A — Habit, plant without spike (left) and inflorescence (right). B — Flower, ventral and dorsal view. C — Lip, lateral view. D — Lip, ventral view. E — Lip, split. F — Dissected perianth. G — Floral bract. H — Column, lateral, dorsal and ventral view. Drawing by D. Trujillo based on *Trujillo 212*.

anthesis, the inflorescence peduncle elongates twice or more its original size, evident even in herbarium specimens), (4) basipetal floral development (with flowers growing from the inflorescence apex to its base), (5) andromonoecious inflorescence (with male flowers distinctly smaller (up to 300%) than hermaphrodite flower (Berry & Calvo 1991, Vargas 1997, and Trujillo pers. obs.), and (6) growing between 3300 to almost 5000 m.a.s.l and mostly in wet puna/paramo high-andean bogs from Venezuela to Argentina/Chile (world's record by *Myrosmodes pumilio* (Schltr.) C. Vargas, observed in Peruvian Andes and in bogs from Chile, Novoa, Vargas & Cisternas, in prep.).

Although a recent DNA study indicates that *Myrosmodes* may be embedded within *Aa* and that the recognition of the genus *Myrosmodes* is tenuous (Álvarez-Molina & Cameron 2009), the morphological and ecological evidence still supports its separation from *Aa*.

Still, we are a long way from knowing all the species that constitutes the genera *Aa* and *Myrosmodes*. A careful examination of the floral features is necessary for the proper identification of the specimens, and this is only possible by dissecting the flowers under a stereomicroscope. For example, in most of the original descriptions and illustrations of *Myrosmodes* (as *Aa* or *Altensteinia*) the authors did not indicate or show the features of the column, mainly the anther (Reichenbach 1854, 1878, Schlechter 1912, 1920a, 1920b, Mansfeld 1929). The knowledge of these features in the other *Myrosmodes* species is required in order to have a clearer delimitation of the species that compose this genus.

Based on revisions of the type material from the Reichenbach Herbarium (W) as part of the identification of a new species of *Aa* from northern Peru, it has become evident that the following new combinations in *Myrosmodes* are necessary. They were also mentioned by Vargas in his work in Cranichideae and Prescottiinae (unpublished thesis 1997).

Aa aurantiaca D. Trujillo, *sp. nov.*

TYPE: Peru. Dept. La Libertad: Prov. Santiago de Chuco, Quirovilca, Yanivilca, 3509 m, 22 May 2005, *D. Trujillo 212* (holotype, HURP; isotypes, HAO, SEL, M) (Fig. 1, 2).

Figure 2. Inflorescence of *Aa aurantiaca*. Photograph by D. Trujillo.

Differt ab simili Aa rosea Ames *flore aurantiaco, sepalis dorsaliter pilosis, petalis trinervatis ovato-lanceolatis et foramine labelli angustiore.*

Plant small, terrestrial. *Roots* fleshy, fasciculate, pubescent. *Leaves* withered at flowering time. *Inflorescence* slender, erect, up 30 cm long, enclosed by up to 23 diaphanous sheaths, terminated in a densely many flowered cylindrical spike 2.2-5.0 cm long, rachis of the spike sparsely pilose. *Floral bracts* ovate, acute to obtuse, margins slightly erose, reflexed, 4-5 x 4 mm, somewhat surpassing the flowers. *Flowers* non-resupinate, orange to reddish orange. *Dorsal sepal* oblong to ovate, obtuse, dorsally hairy, 1-nerved, reflexed, 2.0 x 1.3-1.5 mm. *Lateral sepals* shortly connate at the base, obliquely oblong-lanceolate, obtuse, dorsally hairy, somewhat carinate, 1-nerved, 3.0 x 1.5 mm. *Petals* obliquely ovate lanceolate, obtuse, 3-nerved, reflexed, up to 2.3 x 1.1 mm. *Lip*
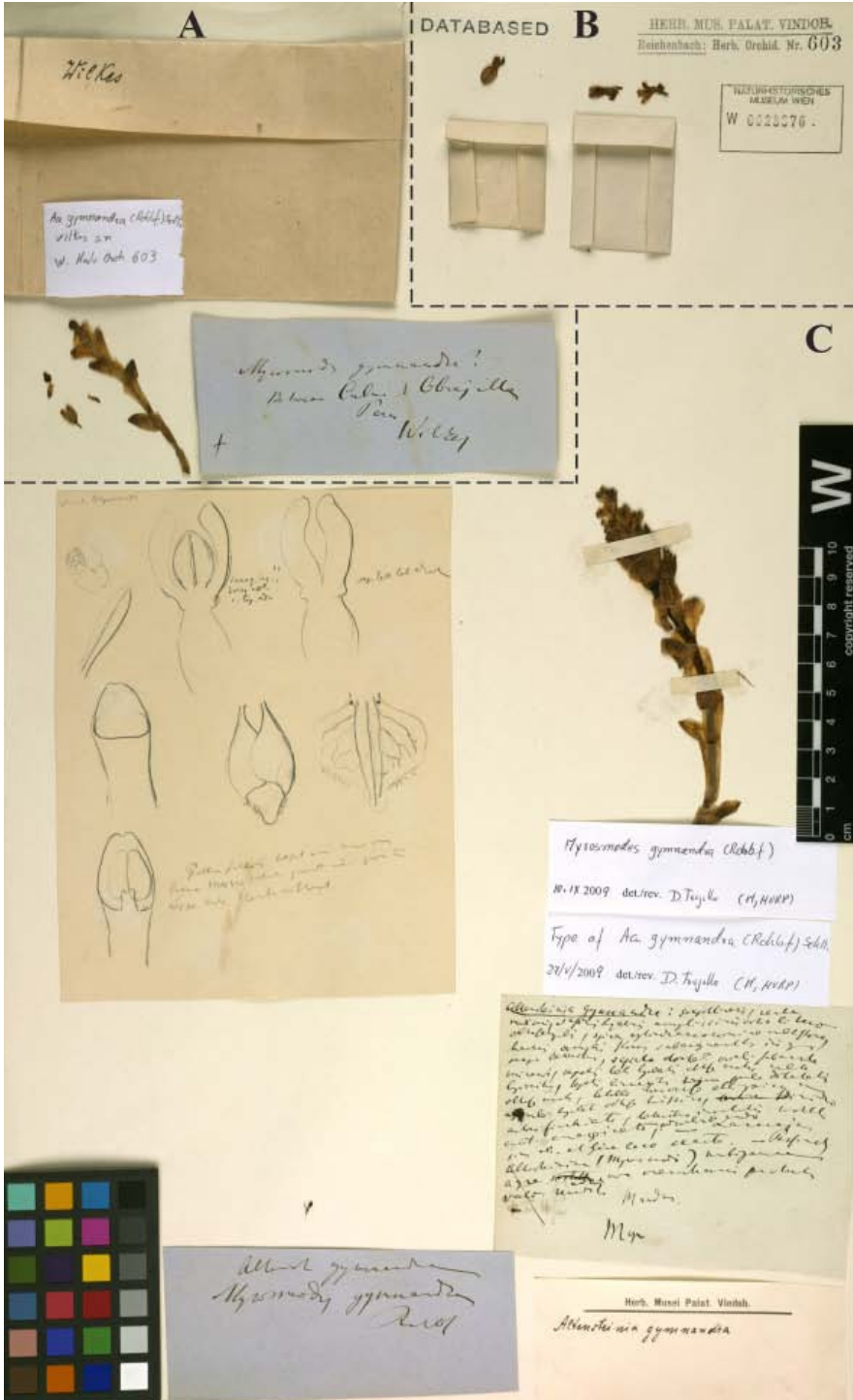
FIGURE 3. Single herbarium sheet at W-R bearing specimens of *Myrosmodes gymnandra* (Rchb.f.) C. Vargas composed of a mixed collection. A — Specimen *Wilkes s.n.* B — Specimens without collector information. C — Specimen *Mandon s.n.* (holotype).

calceolate (semiglobose), transversely elliptic, fleshy (except the margins), obscurely 3-lobed, with a narrow opening, the involute margins lacerate, base with two spherical calli, 2.0 x 2.5 mm (natural position). *Column* short, with an emarginate transverse rostellum, dilated above, 1.5 mm long, straight in young flowers and bent in old flowers. *Anther* erect, lateral margins lightly covered by the clinandrium. *Stigma* quadrate in young flowers and transversely elongate in old flowers. *Ovary* sessile, subcylindric, hairy, 2 mm long.

ETYMOLOGY: From Latin *aurantiacus*, referring to the orange color of the flowers.

DISTRIBUTION: Known only from the Department of La Libertad, Peru, between 3500 and 4000 m elevation.

PHENOLOGY: Flowering plants have been recorded between May and August.

HABITAT AND ECOLOGY: Plants of this species grow on grassy hillsides. Some populations grow sympatrically with other *Aa* species with white flowers; whose sepals and petals have light-green tones when young turning into light-cream to cream-brown when older (but never orange). Besides flower color, this *Aa* species can be distinguished from *Aa aurantiaca* by its wide opening lip, glabrous sepals and ovary, and acuminate floral bracts which notoriously surpass the flower (50% larger).

Aa aurantiaca is similar to *Aa rosei* Ames, but it can be distinguished by the orange flowers, dorsally hairy sepals, ovate-lanceolate, 3-nerved petals, and narrower opening of the lip.

Myrosmodes gymnandra (Rchb.f.) C. Vargas, *comb. nov.*

Basionym: *Altensteinia gymnandra* Rchb.f., Xenia Orch. 3: 18. 1878. TYPE: Bolivia. Prov. Larecaja, *Mandon s.n.* (holotype: W) (Fig. 3, 4).
Aa gymnandra (Rchb.f.) Schltr., Rep. Spec. Nov. Regni Veg.11: 150. 1912.

Myrosmodes gymnandra belongs to the subgenus *Myrosmodes*, i.e. it does not have a rostrate ovary (Vargas 1995). The inflorescence is 13 cm long. The dorsal sepal is oblong, obtuse, 4.4 x 2.0 mm. The lateral sepals are oblong, concave, obtuse, somewhat carinate, 6.0 x 2.6 mm. The petals are linear, subacute, with upper margin erose, 4.5 x 0.6 mm. The lip is obovate, subquadrate,

involute, trilobate, middle lobe subquadrate, margin apical with moniliform hairs, two calli at the base, 4.5 x 3.6 mm. The column is erect, and 3 mm long. The anther exceeds the apex of the stigma, with a free filament, 1.1 mm long. The rostellum is triangular and obtuse. The ovary is ellipsoid, 3.5 mm long. The floral bracts are subcircular to obovate, 11.0 x 10.2 mm.

In the protologue of the description of *A. gymnandra*, Reichenbach indicates that the specimen used to describe the species was *Mandon s.n.* Bolivia, Provincia Larecaja, without referring to a specific locality. However, in the Reichenbach Herbarium in Vienna (W), there was no specimen of *A. gymnandra* bearing the characteristic printed label of G. Mandon (as most of Mandon´s herbarium specimens). There is a herbarium sheet that contains the flower illustration as well as notes from Reichenbach with the description of *A. gymnandra* and a mix of two specimens (Fig. 3). One specimen is mounted on the herbarium sheet, which could be Mandon´s specimen (holotype) and the other is in an envelope (top left of the herbarium sheet), that corresponds to *Wilkes s.n.*, collected in Peru between Culnai and Obrajillo. The illustration showed here is based on the flower from the smallest envelope (middle) of the herbarium sheet (Fig. 3B), but it is not possible to precisely identify the specimen to which it belongs.

In the original description of *A. gymnandra*, Reichenbach (1878) did not mention two important features: the anther exceeds the apex of the stigma and the anther's filament is free (Fig. 4D). In Reichenbach's illustrations the free filament is also evident but the anther appears smaller (Fig. 3C). The free filament has been described as a distinct feature for *Myrosmodes filamentosum* (Mansf.) Garay. Even though *M. gymnandra* has some floral features similar to *M. filamentosum*, they can be distinguished because the latter has larger flowers, a short ovary neck and a slightly trilobate lip (Garay 1978).

Myrosmodes inaequalis (Rchb.f.) C. Vargas, *comb. nov.*

Basionym: *Altensteinia inaequalis* Rchb.f., Xenia Orch. 3: 19. 1878. TYPE: Peru. Dept. Puno: Macusani in puna brava, June 1854, *Lechler 1950* (holotype: W, isotype: W, G, AMES, K.). (Fig. 5)
Aa inaequalis (Rchb.f.) Schltr., Rep. Spec. Nov. Regni Veg. 11: 150. 1912.

FIGURE 4. *Myrosmodes gymnandra* (Rchb.f.) C. Vargas. A — Flower. B — Dissected perianth. C — Lip, left natural, right expanded out. D — Column, dorsal and ventral view. E — Floral bract. Drawing by D. Trujillo based on a specimen from Reichenbach Herbarium (W).

Myromodes inaequalis belongs to subgenus *Myrosmodes* (Vargas 1995). The inflorescence is up to 7 cm long. The dorsal sepal is oblong to oblong-obovate, obtuse to rounded, concave, 2.3 x 1.2 mm. The lateral sepals are oblong, obtuse, concave,

carinate, 2.6 x 1.1 mm. The petals are linear-ligulate, falcate, subacute, with upper margin erose, 2.0 x 0.4 mm. The lip is cucullate, cuneate at base, obovate to elliptic when expanded, entire, margin of upper half with moniliform hairs, two calli at the base, 2.4 x 2.1

Figure 5. *Myrosmodes inaequalis* (Rchb.f.) C. Vargas. A — Flower. B — Dissected perianth. C — Column and lip. D — Lip. E — Column, dorsal and ventral view. F — Floral bract. Drawing by D. Trujillo based on *Lechler 1950* (W).

mm. The column is erect, 1.6 mm long. The anther is subcircular and 0.7 mm long. The rostellum is truncate, emarginate, not triangular (as stated by Reichenbach). The ovary is elliptic, cylindrical, 3.5 mm long. The floral bracts are obovate to elliptic, 5 mm long.

Myrosmodes inaequalis resembles *Myrosmodes paludosa* (Rchb.f.) P. Ortiz.; however, they can be distinguished because the latter has a shorter anther, column dilated above, longer spike with more flowers and thicker peduncle which is twice as long as the

spike (while in *M. inaequalis* the peduncle is up to three times longer than the spike).

Literature Cited

Álvarez-Molina, A. & K.M. Cameron. 2009. Molecular phylogenetics of Prescottiinae s.l. and their close allies (Orchidaceae, Cranichideae) inferred from plastid and nuclear ribosomal DNA sequences. Amer. J. Bot. 96: 1020–1040.

Ames, O. 1922. *Aa rosei* Ames. Proc. Biol. Soc. Wash. 35: 81.

Berry, P.E. & R.N. Calvo. 1991. Pollinator limitation and position dependent fruit set in the high Andean orchid *Myrosmodes cochleare* (Orchidaceae). Pl. Syst. Evol. 174: 93-101.

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

Garay, L.A. 1978. Orchidaceae. Cypripedioideae Orchidoideae Neottioideae. In: G. Harling & B. Sparre (eds.), Flora of Ecuador, 225(1). University of Goteborg, Stockholm, Sweden.

Mansfeld, R. (ed.). 1929. Figuren-Atlas zu den Orchideenfloren der südamerikanischen Kordilleren-staaten. Repert. Sp. Nov. Regni Veg. Beih 57.

Ortiz, P. 1995. Orquídeas de Colombia. Corporación Capitalina de Orquideologia, Bogota. 2da. Ed.

Reichenbach, H.G. 1854. *Altensteinia, Aa* and *Myrosmodes*. Xenia Orchid. 1: 17-19.

Reichenbach, H.G. 1878. Orchideae Mandonianae. Xenia Orchid. 3: 17-19.

Schlechter, R. 1912. Die Orchideen Gattungen *Altensteinia* HBK, *Aa* Rchb.f. und *Myrosmodes* Rchb.f.. Repert Spec. Nov. Regni Veg. 11: 147-150.

Schlechter, R. 1920a. Orchidaceae novae et criticae. Repert. Sp. Nov. Regni Veg. 16: 353-358.

Schlechter, R. 1920b. Orchidaceae novae et criticae. Repert. Sp. Nov. Regni Veg. 16: 437-450.

Schweinfurth, C. 1958. Orchids of Peru. Fieldiana Bot.. 30(1): 1-260.

Vargas, C. 1995. New combinations in *Myrosmodes* Rchb.f. (Orchidaceae) Lindleyana 10: 5-6.

Vargas, C. 1997. Phylogenetic analysis of Cranichideae and Prescottiinae (Orchidaceae) with some taxonomic changes in Prescottiinae. M.S. thesis, University of Missouri-St. Luis, St. Louis Missouri, USA.

TWO NEW SPECIES OF *TEAGUEIA* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM EAST-CENTRAL ECUADOR

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Abstract. Abstract: Two new species of *Teagueia*, *T. barbeliana* and *T. puroana*, are described and illustrated. Their relationship to other *Teagueia*, their scientific importance, and their conservation is discussed. Closest relatives are *T. alyssana*, *T. sancheziae*, *T. cymbisepala*, and *T. jostii*, and like them, the new species are high-elevation (>3100m) endemics of the upper Río Pastaza watershed in the eastern Andes of Ecuador. *Teagueia barbeliana* differs from its relatives by broad rounded flower parts, lateral sepals connate for half their length, column apex winged. *Teagueia puroana* differs from relatives by its long-acuminate petals and sepals.

Resumen. Se describen e ilustran dos nuevas especies del género *Teagueia*, *T. barbeliana* y *T. puroana*. Se discuten sus afinidades, su importancia para la ciencia, y su conservación. Las especies más cercanamente emparentadas con las nuevas son *T. alyssana*, *T. sancheziae*, *T. cymbisepala*, y *T. jostii*, que al igual que las nuevas, son endémicas a las alturas (>3100m) de la cuenca alta del Río Pastaza en los Andes Orientales del Ecuador. *Teagueia barbeliana* se distingue por sus sépalos y pétalos redondos, sus sépalos laterales unidos hasta la mitad de su longitud, y las alas en el ápice de la columna. *Teagueia puroana* se distingue por sus pétalos y sépalos con colas largas..

Key words: *Teagueia puroana*, *Teagueia barbeliana*, Ecuador, orchid, new species

Prior to the year 2000, *Teagueia* Luer was known from only three Colombian and three Ecuadorian species, each apparently endemic to very small areas (Luer 1991). In the year 2000, LJ discovered four new species of *Teagueia* in one square meter of moss at 3100m on a remote mountain in the upper Río Pastaza watershed in the province of Tungurahua in Ecuador, on the rim of the Amazonian basin of South America. Those species were described as *T. alyssana* Luer & L. Jost, *T. sancheziae* Luer & L. Jost, *T. cymbisepala* Luer & L. Jost, and *T. jostii* Luer (Luer 2000). Further investigation led to the discovery of many more new species on that same mountain and neighboring mountains, all in cloud forest or páramo (alpine grassland) above 2800m (Jost 2004). The total number of new high-elevation morphospecies now known from the upper Río Pastaza watershed is about 28 (including the four formally described species just mentioned, and the two new ones described here).

Characteristics of the new species and their relatives. All of the 28 locally endemic high-elevation

morphospecies are slender, long-repent plants with loose, successive-flowering inflorescences. The long-repent habit easily distinguishes them from all other *Teagueia* species. The flowers also differ slightly from the previously-known Ecuadorian species of the genus. *Teagueia zeus* (Luer & Hirtz) Luer, *T. teagueii (*Luer) Luer, and *T. tentaculata* Luer & Hirtz all have a raised callus on the lip just below the column. In addition, the orifice in the center of their lip, which is characteristic of the genus, is long and narrow, extending almost from the callus to the apex of the lip. In the 28 long-repent species, on the other hand, there is no raised callus, and the orifice occupies less than half the midlobe of the lip.

Both of the new species described here are easily distinguished from all other described *Teagueia* species. *Teagueia barbeliana* is most like *T. cymbisepala*, but has more rounded flower parts than that species; the lateral sepals in particular are very broad and connate for half their length, each with four veins as opposed to the three or fewer veins of other known species. The lateral lobes of the lip clasp the column just behind the

stigma. The three-veined petals and winged column tip are also unusual. *Teagueia puroana* is most like *T. alyssana*, but it is immediately distinguished by the long tails on all sepals and petals exclusive of the lip, combined with lateral sepals that are only connate for 1/5 of their length, and lateral lobes of the lip which clasp the column just behind the stigma.

Evolution of the *Teagueia* species of the upper Río Pastaza watershed. The similarity of the 28 upper Río Pastaza watershed long-repent morphospecies of *Teagueia* strongly suggests that they form a monophyletic group. Preliminary results of molecular work on nearly all morphospecies by Mark Whitten, Kurt Neubig, and Lorena Endara (University of Florida- Gainesville), and previous unpublished work on a subset of species by Alec Pridgeon (Kew) and by Erik Rothacker (Ohio State University), confirm this. These morphospecies thus constitute one of the earth's most remarkable local plant evolutionary radiations, with more species in a much smaller area than better-known recently-evolved plant radiations such as Darwin's *Scalesia* Arn. (Asteraceae) on the Galapagos Islands (Tye 2000). The only comparable orchid radiation is the *Dendrochilum* Blume radiation on Mount Kinabalu, Borneo (Barkman & Simpson 2001). Molecular work by Mark Whitten's group at UF Gainesville may soon be able to assign a time scale on this *Teagueia* radiation, which appears to be very young, like many other Andean plant radiations (Hughes & Eastwood 2006, Scherson et al. 2008).

Distribution patterns of the *Teagueia* species in the upper Río Pastaza watershed. Almost all of these 28 *Teagueia* morphospecies appear to be restricted to a 30km x 20km block of forest bisected by the steep valley of the Río Pastaza, an important tributary of the Amazon. Extensive botanizing in the páramos and high cloud forests along the Quito-Baeza road and the páramos of Pisayambo (Parque Nacional Los Llanganates) north of the Río Pastaza failed to turn up any of these species. South of the Río Pastaza, we have found only two species on the Guamote-Macas road (70-90 km south of the Río Pastaza) and no species farther south. There are however many unexplored high mountains in the Llanganates range and between the Río Pastaza and the Guamote-Macas

road, where additional as-yet-unknown species may be found.

The distributions of the 28 morphospecies show strong geographic structure within the upper Río Pastaza watershed. The morphospecies found north of the Río Pastaza are not found south of it, and vice-versa, with one possible exception. These patterns are probably not sampling artifacts, as we have intensively examined each of the mountains where these long-repent *Teagueia* are known to occur. Such strong local distribution patterns are remarkable in light of the dispersal characteristics of orchid seeds. Other orchid genera in the same area show north-south distribution bands which cross the Río Pastaza (LJ pers. obs.)

The previously-described members of this group of 28 morphospecies, *T. alyssana*, *T. sancheziae*, *T. cymbisepala*, and *T. jostii*, were all from a mountain north of the Río Pastaza. The two species described in the present paper are the first species described from south of the Río Pastaza. They are among the most distinctive of the southern species.

Habitat and conservation status. Both species described here were discovered at very high elevations on Cerro Candelaria, Tungurahua province, Ecuador. Fourteen other morphospecies of *Teagueia* were also found on Cerro Candelaria. The two species described here are among the rarest of the Cerro Candelaria *Teagueia* species; only a few plants of each were found during extensive fieldwork on Cerro Candelaria. *Teagueia puroana* grows as an epiphyte on low branches and trunks of isolated stunted treelets in the páramo. *Teagueia barbeliana* grows in moss in open páramo at 3400-3800m. Both species experience hard freezes on most nights.

Teagueia barbeliana was later found on a second mountaintop about 18 km west of Cerro Candelaria. *Teagueia puroana* remains known only from Cerro Candelaria. The extraordinary scientific importance of this unique evolutionary radiation makes these mountains a global conservation priority. Shortly after their discovery, the first author and his associates in Ecuador and abroad started a conservation foundation, Fundación EcoMinga, to protect the endemic plants and animals of the upper Río Pastaza watershed. In partnership with the World Land Trust, Fundación EcoMinga has now purchased much of

Cerro Candelaria, including habitat for *T. puroana* and *T. barbeliana* and the fourteen other *Teagueia* morphospecies which grow there. These purchases were made possible by donations to the World Land Trust by Puro Coffee, Albertino Abela, and PricewaterhouseCoopers.

Species descriptions

Teagueia barbeliana L. Jost & A. Shepard, *sp. nov.*

Teagueiae cymbisepalae Luer et Jost similis, sed sepalis petalisque rotundioribus, sepalis lateralibus connatis per 1/2 marginem suas, lobis lateralibus labelli circum columnam.

TYPE: Ecuador. Tungurahua: Cerro Candelaria, 1°28'46"S, 78º17'51"W, 3400 m, Nov. 2002, *L. Jost 5132* (holotype: QCA!; isotype: QCNE!). Fig. 1.

Plant medium in size for the genus, lithophytic or terrestrial, long-repent, the rhizome exceeding 20 cm in length, producing a ramicaul and leaf at every third joint, 7-8 mm between joints; one coarse root emerging at each ramicaul-bearing joint. *Ramicauls* ascending, stout, 3 mm long, enclosed by 1 or 2 imbricating sheaths. *Leaf* erect, thickly coriaceous, reticulate-veined, petiolate, elliptical, obtuse, 10-15 mm long, 8-9 mm wide, the base cuneate into the petiole. which is 15-20 mm long. *Inflorescence* from near the apex of the ramicaul; an erect, successive, distantly several-flowered raceme, 4-6 cm to first flower, flowers spaced 12 mm apart, up to 7 flowers; one to three flowers open at once; *floral bracts* oblique, acute, thin, 4 mm long; pedicels 4.4 mm long; ovary 1.8 mm long. *Flowers* golden yellow suffused orange, with red on veins, the lip with a red stripe down its center; *dorsal sepal* ovate, 6.4 mm long, 4.2 mm wide, 3-veined; *lateral sepals* broadly ovate, acuminate, 5.3 mm long, 3.9 mm wide, 3-veined, rudimentary fourth vein, connate for 2.3 mm. *Petals* ovate, acuminate, 4.1 mm long, 2.8 mm wide, 3-veined. *Lip* ovate, 3.1 mm long, 2.3 mm wide, the apex truncate, the disc longitudinally cleft, spreading into a deep orifice above the middle, the base with angles embracing the column, curving outward to match the plane of the midlobe of the lip, the base fixed to the column-foot. *Column* terete, recurved at anther, 1.8 mm long, 1

mm wide at stigma, laterally winged at anther, wings confluent with stigma, stigma entire.

Etymology: Albertino Abela of London contributed significantly to the conservation of this orchid's habitat; this species is named in honor of his mother Barbel, at his request.

Paratypes: Ecuador. Tungurahua: Cerro Candelaria, 1°28'46"S, 78°17'51"W, Nov. 2003, *L. Jost, A. Shepard, S. Grossman, A. Araujo 6197* (QCA!), *6219* (QCA!), *6225* (QCA!), *6227* (QCA!); Cerro Chamana, 1°26'7"S, 78°23'1"W, 3500 m, Dec. 2003, *L. Jost et al. 6580* (QCA!).

Distribution: Rare and local from 3400-3800 m on two mountaintops just south of the Río Pastaza near the town of Baños, Tungurahua, Ecuador.

Teagueia puroana L. Jost & A. Shepard, *sp. nov.*

Teagueiae alyssanae Luer et Jost similis, sed sepalis petalisque longi-acuminatis, sepalis lateralibus connatis per 1/5 marginem suas, lobis lateralibus labelli circum columnam.

Type: Ecuador. Tungurahua: Cerro Candelaria, 1°28'46"S, 78°17'51"W, 3400 m, Nov. 2002, *L. Jost 5149* (holotype: QCA!). Fig. 2.

Plant small-medium in size for the genus, epiphytic, long-repent, the rhizome exceeding 13 cm long, producing a ramicaul and leaf at every third joint, 0.8-1.4 cm between joints; one coarse root emerging at each ramicaul-bearing joint. *Ramicauls* ascending, stout, 4 mm long, enclosed by 1 or 2 imbricating sheaths. *Leaf* erect, thickly coriaceous, reticulate-veined, petiolate, elliptical, obtuse, 15-20 mm long, 8-9 mm wide, the base cuneate into the petiole 15 mm long. *Inflorescence* from near the apex of the ramicaul; an erect, successive, distantly several-flowered raceme, 2-4.5 cm to first flower, the flowers spaced 5-7 mm apart, up to 11 flowers, with only one or two flowers open at once; *floral bracts* oblique, acute, thin, 4 mm long; pedicels 3.8-4.5 mm long; ovary 1.5 mm long. *Flowers* dark orange suffused dark reddish apically on all parts; *dorsal sepal* elliptical-ovate, long-acuminate, 7.1 mm long, 3.4 mm wide, 3-veined; *lateral sepals* obovate, long-acuminate, 7.6 mm long, 2.6 mm wide, 3-veined, connate for 1.4 mm;

FIGURE 1. *Teagueia barbeliana* L.Jost & A.Shepard. A — Plant. B — Flower. C — Lateral flower. D — Dissected flower. E — Oblique lip and column detail. F — Top view, column and lip collar. Scale bars: A, 5 cm; B-D, 2 mm; E-F, 1 mm. ILLUSTRATION VOUCHER: *L. Jost 5132* (QCA). Illustration by Lou Jost.
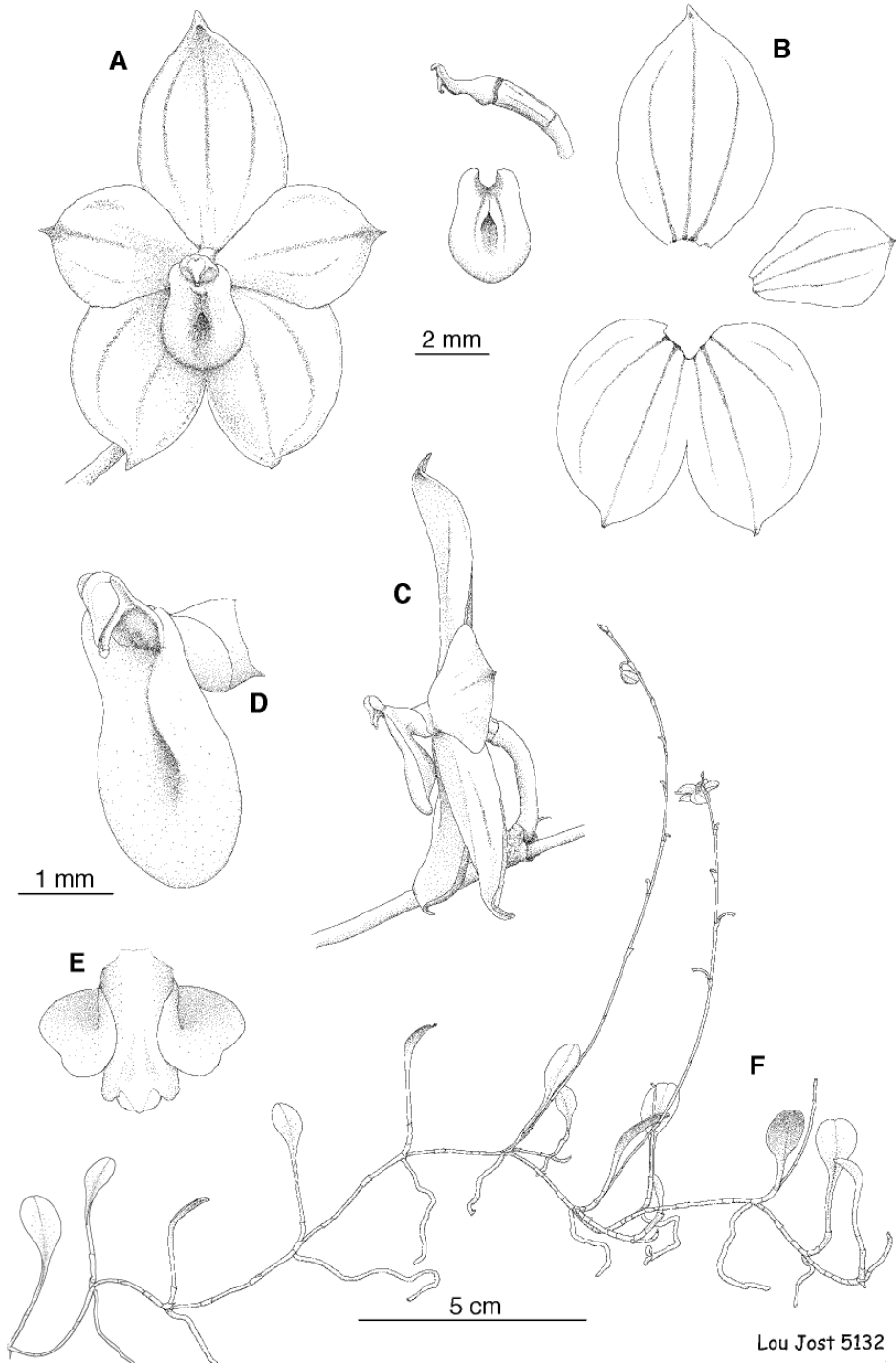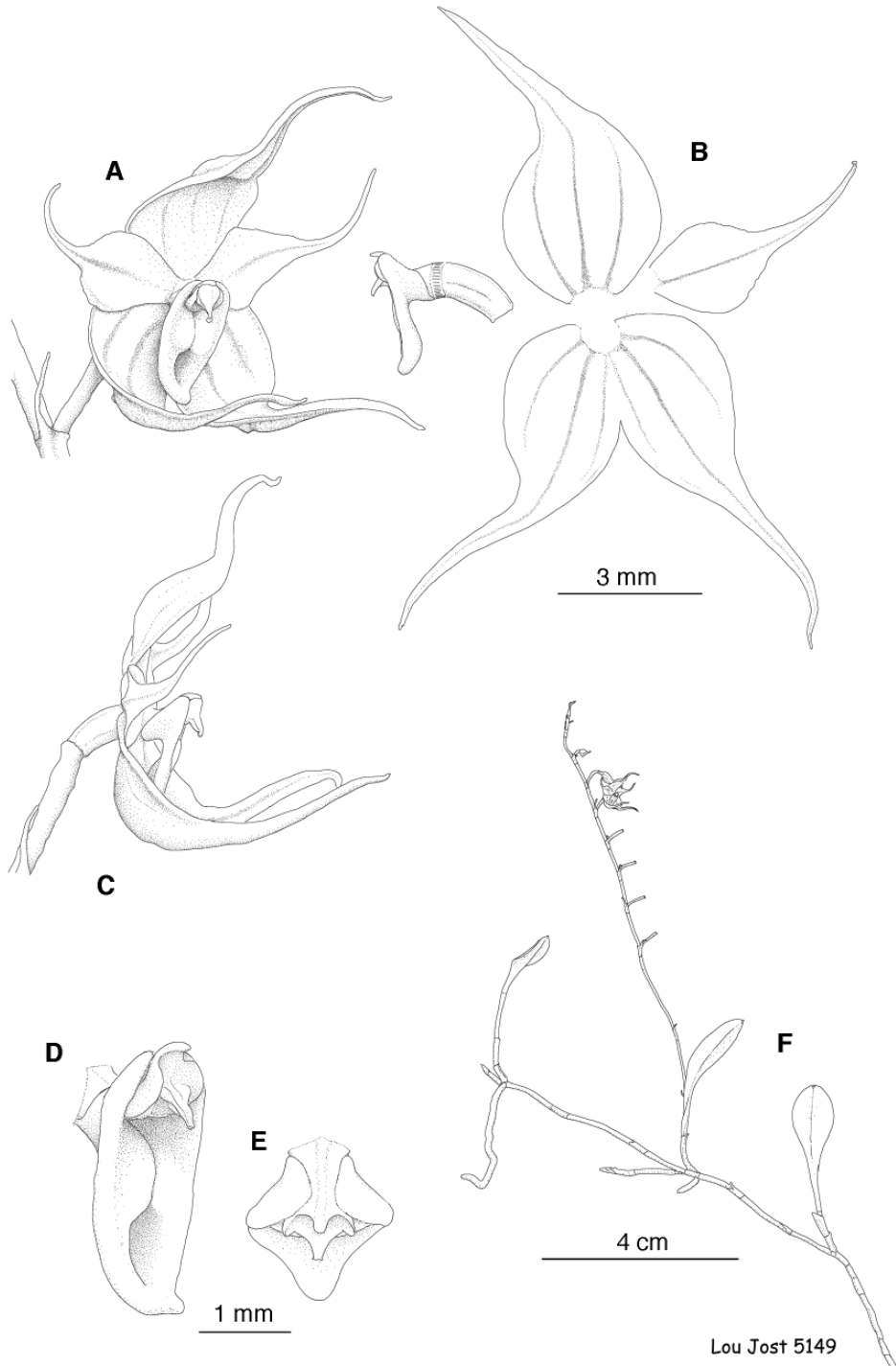
Figure 2. *Teagueia puroana* L.Jost & A.Shepard. A — Plant. B — Flower. C — Lateral flower. D — Dissected flower. E — Oblique lip and column detail. F — Top view, column and lip collar. Scale bars: A, 4 cm; B-D, 3 mm; E-F, 1 mm. Illustration voucher: *L. Jost 5149* (QCA). Illustration by Lou Jost.

petals ovate, long-acuminate, 5.1 mm long, 2 mm wide, 1-veined; *lip* oblong-ovate, 2.4 mm long, 1.4 mm wide, the apex rounded, the disc longitudinally cleft, spreading into a deep orifice above the middle, the base with rounded microscopically ciliate angles embracing the column, the angles nearly or actually in contact with each other above the column, the base fixed to the column-foot. *C*olumn terete, recurved at anther, 1.4 mm long, 0.8 mm wide at stigma; stigma entire.

ETYMOLOGY: Named in honor of Puro Coffee, UK, which contributed significantly to the conservation of this species.

PARATYPES: Ecuador. Tungurahua: Cerro Candelaria, 3600 m, 1°28'46"S, 78°17'51"W, Nov. 2002*, L. Jost 5140* (QCA!)*, 5141* (QCA!)*, 5209* (QCA!)*, 5210* (QCA!)*, L. Jost, A. Shepard, S. Grossman, A. Araujo 6213* (QCNE!)*, 6218* (QCA!)*, 6223* (QCA!)*.

DISTRIBUTION: Known only from 3600 m on Cerro Candelaria, just south of the Río Pastaza, near the town of Baños, Tungurahua, Ecuador.

LITERATURE CITED

Barkman, T.J., & B.B. Simpson. 2001. Origin of High-Elevation *Dendrochilum* Species (Orchidaceae) Endemic to Mount Kinabalu, Sabah, Malaysia. Syst. Bot. 26: 658-669.

Hughes, C., & Eastwood, R. 2006. Island Radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. PNAS, 103:10334-10339.

Jost, L. 2004. Explosive Local Radiation of the Genus *Teagueia* (Orchidaceae) in the Upper Pastaza Watershed of Ecuador. Lyonia 7: 41-47.

Luer, C.A. 1991. Icones Pleurothallidinarum VIII, Systematics of *Lepanthopsis*, *Restrepiella*, *Restrepiopsis*, *Salpistele* & *Teagueia*. Monogr. Syst. Bot. Missouri Bot. Gard. 64: 105-114.

Luer, C.A. 2000. Icones Pleurothallidinarum XX. Systematics of *Jostia, Andinia, Barbosella*,

Barbodria, and *Pleurothallis* Subgenus Antilla, Subgenus Effusia, Subgenus Restrepioidia

(Orchidaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 79:105-114.

Scherson, R., Vidal, R., & Sanderson, M. 2008. Phylogeny, biogeography, and rates of diversification of New World *Astragalus* (Leguminosae) with an emphasis on South American radiations. Am. J. Bot. 95: 1030-1039.

Tye, A. 2000. Las plantas vasculares endemicas de Galapagos. Pages 24-28 in Valencia, R., Pitman, N., Leon-Yanez, S., Jorgensen, P. (Eds.) Libro Rojo de las Plantas endemicas del Ecuador 2000. Herbarium of the Pontificia Universidad Catolica del Ecuador. Quito.

THE ROOT COLONIZING FUNGI OF THE TERRESTRIAL ORCHID
CYPRIPEDIUM IRAPEANUM

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Abstract. This study investigated the mycorrhizal status and the identification of the fungi colonizing the roots of the terrestrial orchid *Cypripedium irapeanu* by restriction fragment length polymorphisms and by rDNA internal transcribed spacer sequencing. The orchid is endemic of differents regions in Mexico, Guatemala and Honduras; usually at 1400-2250 m. It grows mainly in the remaining oak forests of the highlands and it is in the Mexican red list of plants in danger. The oak forests in Mexico are threatened constantly. The microscopic examination of stained root segments of the orchid revealed the presence of fungal structures of both orchidioid fungi (pelotons and coyled hyphae) and dark septate endophytes (DSE) (mielinized hyphae and microsclerotia). Analysis of ITS1-5.8-ITS2 region sequences suggested that mycorrhizal tissue was dominated by Tulasnaceae: *Sistotrema* sp*., Rhizoctonia solani,* and *Epulorhiza* sp. Among the DSE one isolate revealed 100% similarity to *Phomopsis* sp XJ-05, and another one 99% to the fungal endophyte MUT 885 which are both reported as dark septate endophytes. The putative dark septate endophyte *Phomopsis* sp XJ-05 was isolated not only from the roots but also from the germinated seeds of *C. irapeanum*.

Resumen. Este estudio investigó el status micorrízico y la identificación de los hongos que colonizan la raíz de la orquídea terrestre *Cypripedium irapeanum* por medio de los polimorfismos de los fragmentos de la restricción y la secuenciación del espacio tránscrito interno del rDNA. Esta orquídea es endémica de diferentes regiones de México, Guatemala y Honduras localizándose entre los 1400 y 2250 m de altitud. Crece principalmente en los remanentes de los bosques de encino del altiplano y está en la lista roja de México de las plantas amenazadas. Los bosques de encino en este país están constantemente amenazados. El examen al microscopio de los segmentos de raíces teñidas de las orquídeas nos mostró la presencia de estructuras fúngicas tanto de hongos de micorriza orquidoide (pelotones e hifas enrrolladas) como de los llamados endófitos obscuros septados (DSE) (hifas mielinizadas y microesclerosios). El análisis de la secuenciación de la región ITS1-5.6-ITS2 sugiere que el tejido micorrizado está dominado por Tulasneaceae: *Sistotrema* sp*., Rhizoctonia solani,* and *Epulorhiza* sp. Entre los DSE, uno de los 10 aislados mostró 100% de similaridad con *Phomopsis* sp XJ-05, y otro 99% con el endófito MUT 885, ambos reportados como endófitos obscuros septados. El hipotético endófito septado obscuro *Phomopsis* sp XJ-05 fue aislado tanto de las raíces como de las semillas que germinaron de *C. irapeanum* restriction fragment length polymorphisms and by rDNA internal transcribed spacer sequencing.

Key words: terrestrial orchid, orchidoide mycorrhiza, dark septate endophytes, microsclerotia

Introduction. Symbiosis are particularly important for plants resulting in significant nutritional advantage. Among these are the mycorrhizae from which most plants obtain the majority of their nutrients, including those limiting their growth. In general for the terrestrial orchids the mycorrhizal association is fundamental for the plant during germination and throughout all its life (Smith & Read 1997).

Of all orchids that have been studied, few have been the object of mycorrhizal studies. Among the Mexican terrestrial orchids just 3% of the orchids have been studied (Ortega-Larrocea & Rangel-Villafranco 2007).

Many species of terrestrial orchids are threatened or in danger due to the habitat loss by anthropogenic activities and the attractive beauty of its flowers (Dearnaley 2007). *Cypripedium irapeanum* (Fig. 1) grows mainly in the remaining oak forests of the Mexican highlands. The oak forests in Mexico are

Figure 1. *Cypripedium irapeanum* flower from Puebla State, Mexico.

threatened constantely by the urban activities and by the development of recreational sites. The change of soil use of the oak forests has conducted to the degradation by soil erosion and loss of these forests and have allow not only to the soil loss, and coquently to the loss of the symbiotic fungi, but also to the decrease of the number of pollinators and to the increase of pathogens, specially the attack of the capsules by screw warms; other problems that this plant has to face in the degraded habitat are cattle, and weed invasion (Valdés *et al.* 2005).

Cypripedium irapeanum was orginally described based on a collection from the mountains of Irapeo near the present city of Morelia in Michoacan, Mexico (Cribb & Soto Arenas 1993). In this country it is known as *pichohuastle*, a native name for the plant. The orchid is endemic of differents regions in Mexico (Chiapas, Durango, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Querétaro, Puebla, Veracruz), Guatemala and Honduras; usually at 1400-2250 m of altitud. The orchid is in the red list of plants in danger of the Mexican Department of Natural Resources (Semarnat 1995).

In relation to the temperate lady's slipper orchids, *Cypripedium*, there are few studies on its associated fungi. According to Shefferson *et al*. (2005), the genus *Cypripedium* is characterized by high specificity mycorrhizal association, then the lack of these fungi

may limit their establishment and distribution. Upon infection of this orchid by a compatible mycorrhizal fungus the seed ("dust seed") germinates into a seedling that consumes the fungal sugars, processus known as myco-heterotrophy. The plants may retain the myco-heterotrophy into adulthood (Gill 1989).

The internal transcribed spacer (ITS) regions of ribosomal DNA, including both ITS1 and ITS2, have been used extensively used for environmental sampling as a target because several taxonomic group-specific primer sets exist for this gene region (Gardes & Bruns 1993). The ITS has been the region of choice for molecular analysis of fungal communities of this region has been useful since Gardes & Bruns (1996) used its restriction digests (RFLP) to differenciate species of mycorrhizal fungi colonizing individual roots. Furthermore, the DNA sequences of the ITS1 and ITS2 are highly variable being a good marker to identify fungi to the genera and/or species level (Gardes & Bruns 1993, Gardes & Bruns 1996, Henrion *et al.* 1992, Smith *et al.* 2007).

Objective of this paper was the isolation and identification of the fungal root and seed endophytes as well as mycorrhyzal fungi of *C. irapeanum* by restriction fragment length polymorphisms and by rDNA internal transcribed spacer sequencing. The term "endophyte" refers to those fungi that can be detected at a particular moment within the tissues of apparentky healthy plant hosts (Schultz & Boyle 2005).

Materials and methods. Collected *C. irapeanum* is surviving in a remaining patch of an oak forest which is located out of Puebla city in the State of Puebla, at 1840 m. We collected *C. irapeanum* growing close to an oak tree.

Due to the scarcity of the orchids we obtained a collect autorization (No. D00.02-3478) from Semarnat. *Cypripedium irapeanum* plants were collected including the rhizome and the surrounded soil to ensure that the root system was kept intact. We also sampled seeds. The soil core with the alive whole plants were maintained in the greenhouse before to be processed.

In order to observe the root fungal colonization *in situ* the roots were hydrolyzed and stain by the Philips and Hayman procedures (1970) resulting in 20 to 30 root samples per plant. Inter and intracellular

melanized hyphae with microslclerotia were recorded as Dark Septate Endophytes (DSE).

The isolation of the seed and root endophytes of *C. irapeanum* was done after a surface sterilization with a 5% sodium hipochlorite solution for 10 min, followed by a 0.1 % mercuric chloride solution for 2 min, and several washings with sterile distilled water. This drastic sterilization was done to prevent growth of root external microorganisms. Seeds were sowed in flasks containing Knudson (1946) culture medium, and the root fragments (1 cm long) in Petri plates containing Melin-Norkrans (Molina & Palmer, 1982) culture medium. After 4 days of incubation, plates with the root fragments having superficial contaminants were eliminated and those with no contaminants were incubated at 24°C for 3 months. Pure fungal isolates were propagated in Melin-Norkrans agar medium. Colonial and microscopic morphology was photographically documented (data not shown).

Genetic characterization of *C. irapeanum* endophytes involved 1) extraction of fungal DNA from isolated and purified fungi, 2) amplification of fungal genome region useful in determining fungal identity (ITS1-5.8S-ITS2), 3) restriction and RFLP analysis of the region, 4) DNA sequencing of the region, and 5) BLAST analysis for identification of endophytes.

DNA extraction of isolates was done utilizing the CTAB method (Gardes & Bruns 1993). Obtained DNA was purified with the Concert Nucleic Acid Purification (Gibco), according to the manufacturer instructions. Concentration and purity of the DNA was evaluated with a GeneQuant spectrophotometer. The ITS region of the rRNA operon was amplified according to Gardes & Bruns (1993) using the primers ITS1 (TCCGTAGGTGAACCTGCGC), ITS-1F (CTTGGTCATTTAGAGGAAGTAA), ITS 4 (TCCTCCGCTTATTGATATGC) and ITS4-B (CAGGAGACTTGTACACGGTCCAG). PCR was carried out in a Biometra-T personal termocycler under 94°C for 85 s for the denaturation followed by 25 cycles of amplification and extension for 13 cycles at 95°C for 35s, 55°C for 55s and 72°C for 45s. This was followed by an incubation at 72°C for 10 more minutes. Obtained bands were visualized in an EtBr stained agarose gel.

PCR products were purified (Concert Nucleic Acid, Gibco) and restricted with enzymes *Hinf*1 (at 37°C for 5 hours), *Alu*1 (at 37°C for 1 hour), and *Taq*1 (at 65°C for 3 hours). Fragments were analiysed with the Kodak ID 3.6.1 program.

The amplicons were cloned and ligated using the TOPO XL PCR cloning (Qiagen) according to the manufacturer's instructions. The recombinant vector was used for transforming cells of *E. coli* DH5α. Screening for recombinant cells was carried out by blue/white selection. Sequencing reactions were done in a Li-Cor 4202 G sequencer. Before sequencing, the amplicons were purified with the Pure Link Quick Gel Extraction kit (Invitrogen) following the manufacturer's instructions.

Sequences were subjected to BLAST analysis to determine their homology with other sequences available in the Gene Bank for the ITS1-5.8S-ITS2 region. The CLUSTAL package (Thompson *et al*. 1994) was used to align the sequences with the corresponding fungal ITS rDNA sequences.

Results and discussion. The microscopic examination of stained root segments of the orchid revealed the presence of fungal structures of both orchidioid fungi, pelotons and coyled hyphae (Fig. 2) and DSE, mielinized hyphae and microsclerotia (Fig. 3). In 40% of the cortical cells pelotons were seen, and 30% of the cortical cells revealed the presence of microsclerotia inside the cells. We found partially digested pelotons in all *C. irapeanum* plants, suggesting that *C. irapeanum* may have mycoheterotrophic stages.

Table 1 shows the list of the endophytic fungi recovered from roots and germinated seeds of orchid *Cypripedium irapeanum.*

Dark Septate Endophytes were also observed in the germinated seeds. Two distinct types of microsclerotia were seen in the roots, one was of round shape and the other had irregular shapes (Fig. 3). A total of 10 different fungi were isolated, one from a germinated seed and 9 from the roots. Isolates 7, 9 and 10 were identified as DSE; Isolate 7 and 9 from the plants, and isolate 10 from the seeds. To our knowledge, this is the first report of the colonization of *Cypripedium irapeanum* by DSE fungi and the first report of the colonization and identification of both types of fungi in *C. irapeanum.*

As expected the amplified ITS1-5.8-ITS2 rDNA region resulted in a 650 bp product. Negative controls
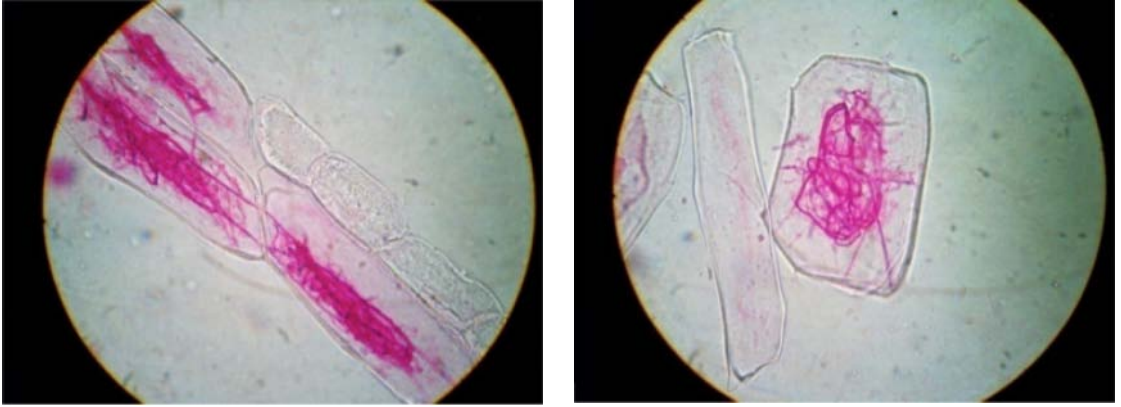
Figure 2. Squash preparation of a *C. irapeanum* stained root showing infection of cells, coiled hyphae and development of pelotons.

in PCRs (sterile milliporized water) consistently yielded no PCR product. The ITS 1F-ITS 4 combination yielded most of the PCR products except for the isolates 8, 9, and 10 which were amplified with the ITS 1-ITS 4B combination.

Restriction of the region yielded RFLPs different for all the analyzed fungi, except fot the isolates 9 and 10 that were identical. Nine RFLP patterns were yielded with *Alu*I and *TaqI* restriction enzymes and 7 patterns with *Hind*I (Fig. 4), suggesting the diversity of the endophytes.

Analysis of ITS1-5.8-ITS2 region sequences suggested that mycorrhizal tissue was dominated by Tulasnaceae: isolate 2 (GeneBank Accesion No. JF313323) revealed 98% identity to S*istotrema sp.*, isolate 3 (GeneBank Accesion No. JF313324) 99% to *Rhizoctonia solani*, and isolate 6 (GeneBank Accesion No. JF313322) *97% to Epulorhiza sp.,* confirming Shefferson *et al.* (2005) and Shimura *et al.* (2009) results for the genus *Cypripedium*. Diverse Tulasnaceae form mycorrhiza also with epiphytic orchids (Suárez *et al*. 2006). Figure 5 shows a phylogenetic tree indicating the placement of the mycorrhizal fungi recovered from the roots of *C. irapeanum*.

Table 1. Endophytic fungi recovered from roots and germinated seeds of orchid *Cypripedium irapeanum*

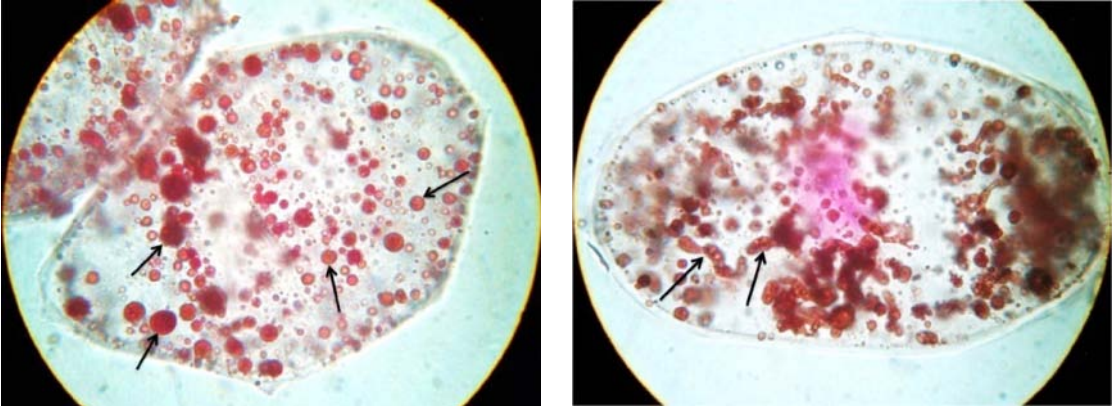| Isolate	Molecular identification	Type of root colonizing fungus
C1	Fusarium	Fungal endophyte (Bayman & Otero, 2006)
C2	Sistotrema	Mycorrhizal (Currah et al, 1990)
C3	Rhizoctonia solani	Mycorrhizal (Warcup, 1971)
C4	Fusarium	Fungal endophyte (Bayman & Otero, 2006)
C5	Cylindrocarpon	Fungal endophyte (Fisher & Petrini, 1989)
C6	Epulorhiza	Mycorrhizal (Shan et al, 2002)
C7	MUT 885	Dark Septate Endophyte (Girlanda et al, 2002)
C8	Gliocladium catenulatum	Biological control fungus (Paavanen-Huhtala et al, 2004)
C9	Phomopsis	Dark Septate Endophyte (from plant) (Jumpponen, 2001)
C10	Phomopsis	Dark Septate Endophyte (from germinated seeds)

FIGURE 3. Two distinct microsclerotia (arrowheads) within the roots of *C. irapeanum*, round shape and irregular shape.

Isolates 9 and 10 revealed 100% identity to *Phomopsis* sp XJ-05, and isolate 7 revealed 99% identity to the fungal endophyte MUT 885 (a DSE fungus according to Girlanda *et al*., 2002), corroborating the results of the RFLP analysis. *Phomopsis* sp XJ-05 was isolated not only from the roots of *C. irapeanum* plants but also from the germinated seeds, indicating a possible role of stimulation of germination.

Other endophytic fungi belonging to the Deuteromycetes were also isolated: isolate 1, identified as *Fusarium* sp 440 (99% identity); isolate 4 identified as *Fusarium* sp (97% identity); isolate 5 as *Cylindrocarpon* sp 4/97.1 (100% identity); and isolate 8 as *Gliocladium catenulatum* (99% identity).

The genus *Sistotrema* is defined by Currah *et al*. (1990) as a mycorrhizal fungi of boreal species. Moncalvo *et al*., (2006) states that this fungus as a highly phylogenetic. However, analysis of ITS1-5.8-ITS2 region sequences of our isolate C2 showed a high identity to this fungus.

Rhizoctonia is known for its association with most other orchids (Rasmussen, 1995). This fungus is a genus based on asexual stages, is a polyphyletic fungus which includes fungi from the families Tulasnellaceae, Sebacinaceae and Ceratobasidiaceae. *Rhizoctonia solani* is a known anamorph of *Thanatephorus cucumeris*, has been isolated from absorbent tissues of orchids and confirmed as mycorrhizal endophytes because are able to stimulate the seed germination and development of the plant *in vitro* assays (Warcup, 1971).

The *Epulorrhiza* species are known as anamorphs of the genus *Rhizoctonia*. Shan *et al.*, 2002 mention

that certain species of this genus have been continually isolated of terrestrial orchids; by means of the RFLP and CAPS analysis of *Rhizoctonia* they were able to classify the genus and its anamorps in 4 groups. Group II formed by *Epulorrhiza* showed a high ability to stimulate the germination and growth of several orchids. In contrast Group I stimulate a specific orchid. Other authors (Sharma *et al*. 2003) found that in advanced development of the plant the number of species of *Epulorrhiza* is low suggesting that the occurrence of the fungus may be less critical in this growth stage.

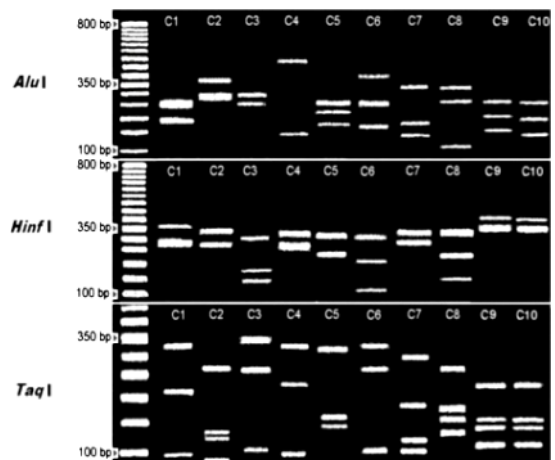DSE have been reported for nearly 600 plants host

FIGURE 4. Restriction fragmen tlength polymorphisms obtained by endonucleases of the internal transcribed spacer (ITS1-5.8S-ITS2) region of the different fungi isolated from *C. irapeanum*. Digestions were performed with Alu 1, Hinf 1, and Taq 1. M=molecular weight marker.
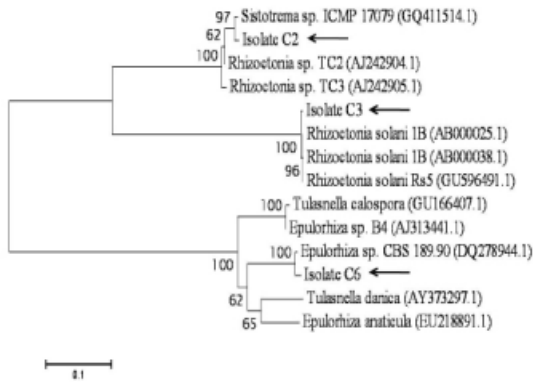
Figure 5. Neighbor-joining tree obtained from the internal
transcribed spacer (ITS1-5.8S–ITS2) sequence align-
ment of isolates C2, C3 and C6 with sequences of Tu-
lasnaceae. The Kimura two-parameter model was used
for pairwise distance measurement. Bootstrap values
above 50% are indicated (1000 replicates). Black ar-
rows indicate the mycorrhizal fungal isolates recovered
from the orchid *C. irapeanum*. Bar = Kimura distance.

species, including plants known to bear different types
of mycorrhizae occurring in highly diverse habitats.

Their widespread occurrence and high abundance
suggests lack of host specificity and an important role in
the different ecosystems (Jumpponen & Trappe, 1988;
Jumpponen, 1999). Jumpponen (2001) regards the DSE
as nonconventional mycorrhizal symbiosis because some
of them have found to enhance host mineral nutrition
and growth (Fernando & Currah, 1996). The presence of
DSE in the germinated seeds of *C. irapeanum* and their
lack in the ungerminated seeds suggests its possible role
for the germination of the orchid seed.

In relation of the occurrence of *Fusarium* as an
endophyte of *Cypripedium*, Bayman & Otero (2006)
have defined this genus and its telomorphs as a most
interesting group of the orchids endophytes due to
its hability to stimulate the seed germination of *C.
reginae.*

Other found endophytes in *C. irapeanum* were
Cylindrocarpum and *Gliocladium. Cylindrocarpon*
sp. 4/97.1 was reported as an endophyte of roots of
terrestrial orchids and mycoheterotrophic orchids
(Bayman & Otero, 2006). *Gliocladium catenulatum* is
well known as a biological control agent (Paavanen-
Huhtala *et al*., 2004) and parasite of other fungi (Tu &
Vaartaja, 1980) suggesting an important role against
pathogens in the orchid root.

Literature cited

Bayman, P. & J. Tupac Otero. 2006. *In*: Microbial Root
Endophytes. B. Shultz, C. Boyle and T. Sieber, Eds.
Springer, Heildeberg, New York. Pp 153-173.
Cribb, P. & M. A. Soto-Arenas. 1993. The genus
Cypripedium in Mexico and Central America. Orquídea
(Mex.) 13:205-214.
Dearnaley, J. D. W. 2007. Further advances in orchid
mycorrhizal research. Mycorrhiza 17: 475-486.
Currah, R. S., A. Smreciu, & S. Hambleton. 1990.
Mycorrhizae and mycorrhizal fungi of boreal species of
Plantanthera and *Coeloglossum* (Orchidaceae). Canad.
J. Bot. 68: 1171-1181.
Fernando, A. A. & R. S. Currah. 1996. A comparative study
of the effects of the root endophytes *Leptodontidium
orchidicola* and *Phaliocephala fortinii* (Fungi
Imperfecti) on the growth of some subalpine plants in
culture. Canad. J. Bot. 74: 1071-1078.
Gardes, M. & T. D. Bruns. 1993. ITS primers with
enhanced specificity for basidiomycetes-Aplication
to the identification of mycorrhizae and rusts. Molec.
Ecol. 2:113-118.
Gardes, M. & T. D. Bruns. 1996. Community structure of
ectomycorrhizal fungi in *Pinus muricata* forest: above-
and below-ground views. Canad. J. Bot. 74: 1572-1573.
Gill, D. E. 1989. Fruiting failure, pollinator inefficiency, and
speciation in orchids. *In*: D. Otte & J. A. Endler (eds.),
Speciation and its consequences. Sinauer Associates
Sunderland, Massachusetts. Pp. 458-481.
Girlanda, M., S. Ghignone, & A. M. Luppi. 2002. Diversity
of sterile root-associated fungi of two mediterranean
plants. New Phytol. 155: 481-498.
Hadley, G. 1970. Non-specificity of symbiotic infection in
orchid mycorrhiza. New Phytol. 69: 1015-1023.
Henrion, B. F., F. Le-Tacon & F. Martin. 1992. Rapid
identification of genetic variation of ectomycorrhizal
fungi by amplification of ribosomal RNA genes. New
Phytol. 122: 289-298.
Jumpponen, A. 1999. Spatial distribution of discrete RAPD
phenotypes of a root endophytic fungus, *Phialocephala
fortinii,* at a primary successional site on a glacier
forefront. New Phytol. 141: 333-344.

Jumpponen, A. 2001. Dark septate endophytes – are they mycorrhizal? Mycorrhiza 11: 207-211.

Jumpponen, A. & J. M. Trappe. 1998. Dark Septate Endophytes: A review of facultative biotrophic root-colonizing fungi. New Phytol. 140: 295-310.

Knudson, L. 1946. A new nutrient solution for the germination of orchid seed. Amer. Orch. Soc. Bull. 214-217.

Molina, R. & J. G. Palmer. 1982. Isolation, maintenance and pure culture manipulation of ectomycorrhizal fungi. *In*: Schenck N.C. (ed.), Methods and principles of mycorrhizal research. Amer. Phytopathol. Soc., St. Paul Minnesota. Pp. 115-129.

Moncalvo, J-M., R. H. Nilsson, B. Koster, S. M. Dunham, T. Bernauer, P. B. Matheny, T. M. Torner, S. Margaritescu, M. Weiß, E. Danell, G. Langer, E. Langer & K-H. Larsson. 2006. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. Mycologia 98:937-948.

Ortega-Larrocea, M. P. & M. Rangel-Villafranco. 2007. Fungus assisted reintroduction and longtem survival of two Mexican terrestrial orchids in the natural hábitat. Lankesteriana 7: 317-321.

Paavanen-Huhtala, S., H. Avikainen& T. Yli-Mattil. 2004. Development of strain-specific primers for a strain of *Gliocadium catenulatum* used in biological control. Eur. J. Pl. Pathol. 105: 187-198.

Phillips, J. M. & D. S. Hayman. 1970. Improvement procedures for clearing and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Brit. Mycol. Soc. 55: 158-161.

Rasmussen, H. N. 1995. Terrestrial Orchids: From Seed to Mycotrophic Plant. Cambridge University Press, Cambridge, UK.

Semarnat. 1995. Gaceta Ecológica 7: 1-72.

Shan, X. C., E. C. Y. Liew, M. A. Weatherhead & I. J. Hodgkiss. 2002. Characterization and taxonomic placement of *Rhizoctonia*-like endophytes from orchid roots. Mycol. 94:230-239.

Sharma, J., L. W. Zettler & J. W. van Sambeek. 2003.

A survey of mycobionts of federally threatened *Platanthera praeclara* (Orchidaceae). Symbiosis 34: 145-155.

Shefferson, R. P., M. Weiß, T.I.I.U. Kull & D. Lee Taylor. 2005. High specificity generally characterizes mycorrhizal association in rare lady's slipper orchids, genus *Cypripedium.* Molecul. Ecol. 14: 613-626.

Shimura, H., M. Sadamoto, M. Matsuura, T. Kawahara, S. Naito & Y. Koda. 2009. Characterization of mycorrhizal fungi isolated from the threatened *Cypripedium macranthos* in a northen island of Japan: two phylogenetically distinct fungi associated with the orchid. Mycorrhiza 19:525-534.

Smith, S. E. & D. J. Read. 1997. Mycorrhizal Symbiosis. Academic Press. Pp. 347-357.

Smith, M. E., G. W. Douhan & D. M. Rizzo. 2007. Intra-specific and intra-sporocarp ITS variation of ectomycorrhizal fungi as assessed by rDNA sequencing of sporocarps and pooled ectomycorrhizal roots from *Quercus* woodland. Mycorrhiza 18:15-22.

Suárez, J. P., M. Weiss, A. Abele, S. Garnica, F. Oberwinkler, & I. Kottke. 2006. Diverse tullasnelloid fungi form mycorrhizas with epiphytic orchids in an Andean cloud forest. Mycol. Res. 110: 1257-1270.

Schulz, B. & C. Boyle. 2005. The endophytic continuum. Mycol. Res. 109:661-687.

Thompson, J. D., D. G. Higgins & T. J. Gibson. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. Nucleic Acids Res 22: 4673-4680 doi:10.1093/NAR/22.22.4673.

Tu, J. C. & O. Vaartaja. 1980. The effect of the hyperparasite *Gliocadium virens* on a *Rhizoctonia* root rot of white beans. Canad. J. Bot. 59: 22-27.

Valdés, M., A. Espinosa & C. Trejo. 2005. *Pichohuastle*: orquídea nativa mexicana en peligro de extinción. Conversus (Instituto Politécnico Nacional) 38: 30-33.

Warcup, J. H. 1971. Specificity of mycorrhizal association in some Australian terrestrial orchids. New Phytol. 70: 41-46.

POPULATION STRUCTURE OF *ONCIDIUM POIKILOSTALIX* (ORCHIDACEAE), IN COFFEE PLANTATIONS IN SOCONUSCO, CHIAPAS, MÉXICO

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Abstract. We studied the population structure of *Oncidium poikilostalix* (Kraenzl.) M.W. Chase & N.H. Williams (Orchidaceae) newly reported for México in 2008 in the region of Soconusco (Chiapas state) in southeast Mexico, growing in shaded coffee plantations in two rural communities, Fracción Montecristo (FM) and Benito Juárez El Plan (BJ). In 2008-2009, we determined the characteristics of these coffee plantations, and the distribution of the various life stages (seedling, juvenile, adult) on the two phorophytes: coffee bushes (*Coffea arabica* L.) and shade trees (*Inga micheliana* Harms.). Principal Component Analysis and Discrimination Analysis were used to compare all the variables evaluated. There were 1123 individuals (82.63%) in FM and 236 (17.37%) in BJ. Of those, in FM 1060 individuals (94.4%) were epiphytic upon coffee bushes and 214 (91.06%) in BJ, the rest were epiphytic upon the shade trees (*I. micheliana*). Despite displaying the characteristics of a twig epiphyte, the preferred microsites of *O. poikilostalix* were the branches of the coffee bushes, with 703 individuals (55.18%) and the trunk of the shade trees, with 78 individuals (91.76%). More than a third of the population was juvenile stage (37.09%; 504 individuals). *Oncidium poikilostalix* probably entered México from Guatemala and appears to be a vigorous plant that is successfully adapting to its new sites of occupancy

Resumen. Se estudió la estructura poblacional de la orquídea epífita *Oncidium poikilostalix* (Kraenzl.) M.W. Chase & N.H. Williams (Orchidaceae), nuevo reporte para México en 2008, en la región del Soconusco, Estado de Chiapas, al sureste del país. Crece en plantaciones de café de sombra en dos comunidades rurales, Fracción Montecristo (FM) y Benito Juárez El Plan (BJ). En 2008-2009, se determinaron las características de estas plantaciones de café, y la distribución de los distintos estadíos de vida (plántulas, juveniles, adultos) de esta orquídea, en los dos forofitos encontrados: plantas de café (*Coffea arabica* L.) y árboles de sombra (*Inga micheliana* Harms.). Se utilizó Análisis de Componentes Principales y Análisis Discriminante, para comparar todas las variables evaluadas. Hubo 1.123 individuos (82,63%) de *O. poikilostalix* en FM y 236 (17,37%) en BJ. De ellos, creciendo sobre cafetos, 1.060 individuos (94,4%) en FM y 214 (91,06%) en BJ, el resto ocupando árboles de sombra (*I. micheliana*). A pesar de mostrar las características de una epífita de ramilla, el mayor número de ejemplares de *O. poikilostalix* se contabilizó en los cafetos, en el micrositio ramas, con 703 individuos (55,18%) y en el tronco, en los árboles de sombra, con 78 individuos (91,76%). Más de un tercio de la población fueron individuos juveniles (504 individuos, 37,09%). *Oncidium poikilostalix* probablemente entró a México desde Guatemala y parece ser una planta vigorosa, que se está adaptando con éxito a sus nuevos sitios de ocupación.

Keywords / Palabras clave: *Oncidium poikilostalix*, micrositio, estadíos de vida, forofito, árbol de sombra, cafeto.

Introduction. Mexico, with its diversity of ecosystems, is an orchid rich country with 1150 species currently registered (Espejo *et al.* 2004), expected to rise to 1300 - 1400 species (Hágsater *et al.* 2005). Many orchid species are confined to rather precise habitat and climatic parameters, their reproduction is notoriously slow and scarce (Ávila & Oyama 2002; Hágsater *et al.* 2005), and very little is known about most species.

The Soconusco region in the state of Chiapas, in south-east Mexico bordering with Guatemala, covers an area of 5475 km² which includes coastal plains and part of the Sierra Madre mountain range with tropical and temperate forest ecosystems (Sánchez & Jarquín 2004). Within that scenario a relatively high number of more than 280 orchid species have been reported for the region (Damon, 2011), including various endemic species.

An expanding human population, extending subsistence and commercial agriculture, forest fires and severe tropical storms have contributed to the destruction and fragmentation of natural forests (INEGI 1999; CNA & CMDI 2000; Tovilla 2004), and combined with the unsustainable and illegal exploitation of orchids have led to the rapid decline of orchid numbers and biodiversity, and the near extinction of the most vulnerable species, as has happened in many other parts of the world.

In Soconusco, most of the cloud forest, which is the most orchid rich ecosystem on the planet (60% of Mexico's orchid flora. Hágsater *et al.* 2005), has been transformed into coffee plantations. At first coffee was planted under the shade of original forest trees heavily populated by epiphytes, thus maintaining a high proportion of the original biodiversity (Hágsater *et al.* 2005). Today, many of those traditional plantations have been converted to improved varieties of coffee with monospecific shade, and some to full sun coffee. At least 213 orchid species (18.52% of Mexican total) can be found growing within coffee plantations (Espejo *et al.* 2004).

Oncidium poikilostalix (Kraenzl.) M.W. Chase & N.H. Williams was reported in 2008 as a new species for Mexico, with small populations in coffee plantations in two localities in Soconusco, Fracción Montecristo (FM) (latitude 15° 5' 31.5"; longitude 92° 9' 57.9") and Benito Juárez El Plan (BJ) (latitude 15° 5' 15.4"; longitude 92° 8' 54.7")), both within the municipality of Cacahoatán (Solano *et al*. in press), having been previously reported in Guatemala and Costa Rica as *Sigmatostalix costaricensis* Rolfe (Behar & Tinschert 1998) and as *Sigmatostalix picta* Lindl. for Nicaragua and South America (Atwood & Mora de Retana 1999). The colonization of new areas by O. *poikilostalix* demonstrates the importance of the Biological Corridor Boquerón-Tacaná, which connects both nations and forms part of the Mesoamerican

Biological Corridor (CCAD-PNUD/GEF 2002).

In this study we describe the population structure of *O. poikilostalix*, comment upon its reproductive behaviour as observed in 2008-9, and analyse the relationship with the phorophytes and microsites available in two shaded coffee plantations in Soconusco, Chiapas, as an exceptional opportunity to study the characteristics of an orchid extending its distribution in these times of climate change and biodiversity loss.

Materials and Methods

Characterization of the sites — We studied the coffee plantations where *O. poikilostalix* grows to describe the density of the coffee bushes, diversity and density of the shade trees and the management regimes applied to the coffee.

Sampling unit — Having analysed the distribution of *O. poikilostalix* in FM and BJ we set up three plots, or sampling units, measuring 625 m² (25 x 25 m; 0.0625 ha) in each coffee plantation, FM (plots 1, 2 and 3) and BJ (plots 4, 5 and 6). These plots are highly representative of the populations as a whole and contained the majority of individuals of the orchid present in these sites at the time of the study.

Determination and characterization of the phorophytes, Density, Height Above Ground (HAG) and Diameter at Breast Height (DBH) — In this study, the term phorophyte is only used for coffee bushes and shade trees that had one or more individuals of *O. poikilostalix* growing on them at the time of the study. We determined which species were used as phorophytes by *O. poikilostalix* within the study sites, counted the numbers of individuals and determined the density of each phorophyte.

The HAG of the phorophytes (coffee bushes and shade trees) was measured with a 4m straight ruler graduated with 50cm intervals and the DBH was determined using a metric tape.

Microsites — Guided by the vertical zonation proposed by Johansson (1974), we developed a version specifically for the coffee bushes and shade trees in this study, to describe the different microsites, or ecological units, available for colonization by epiphytes, as follows:
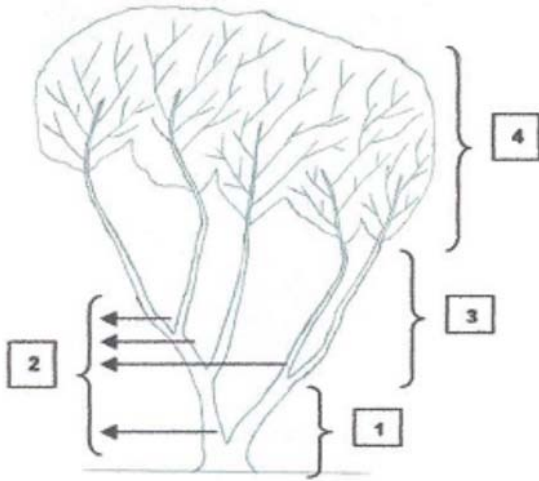
Figure 1. Microsites and vertical zonation of the coffee plants: 1) Trunk, 2) Fork, 3) Branches, 4) Twigs.

Microsites for coffee bushes (Fig. 1):
   Zone 1 – Trunk (Tr): From the base of the bush to the first primary branches.
   Zone 2 – Fork (F): Intersection between branches at various heights.
   Zone 3 – Branches (B): Thick branches with diameter > 3 cm.
   Zona 4 – Twigs (Tw): Thinner, outer branches, with a diameter < 3 cm.

Microsites for shade trees (Fig. 2):
   Zone 1 – Trunk (Tr): From the base of the tree to the first primary branches.
   Zone 2 – Fork (F): Intersection between branches at various heights.
   Zone 3 – Branches (B): Thick branches with diameter > 3 cm.

Due to pruning there was no zone 4 for trees. For each coffee bush and tree the length of Zone 1 and total length of Zone 3 were measured and numbers of Zone 2 were counted. It was not possible to quantify Zone 4 for the coffee bushes.

Life stages of O. poikilostalix — The plants of *O. poikilostalix* were classified using the following categories:
   Seedling (S): Earliest stage after the protocorm in which the young plant first acquires differentiated structures (2 mm to 2 cm).
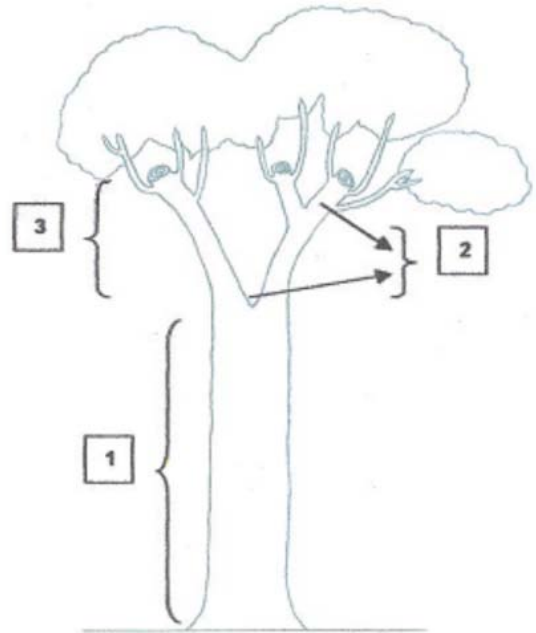

Figure 2. Microsites and vertical zonation of the shade trees (*Inga micheliana*): 1) Trunk, 2) Fork, 3) Branches.

   Juvenile (J): Sexually immature but well developed plant (> 2 cm).
   Adult (A): Sexually mature plants that have flowered at least once.

Sampling — We counted all the individuals of each life stage on each of the microsites of every phorophyte within the study sites.

Statistical Analysis — We used the programmes SAS (Version 5.1.2600) and Minitab (Version 15.1.30.0) to analyse the data, which included Analysis of Variance (ANOVA), the Kruskal-Wallis test and the Goodness of Fit of Chi-squared test. Combining all the variables measured (plot, phorophyte, HAG, DBH, microsite, life stage, number of microsites available) we carried out a Principal Component Analysis and Discrimination Analysis, corroborated by Pillai's Trace test and the Mahalanobis test, to derive the population structure and preferences of the orchid *O. poikilostalix*.

Results

Characterization of the sites — The coffee plantations FM and BJ consist of arabica coffee bushes (*Coffea arabica* L. Rubiaceae) and monospecific shade trees

TABLE 1. Colonization of phorophytes, coffee, and shade trees (*Inga micheliana*) per year of study, in Fracción Montecristo (FM) and Benito Juárez (BJ).

2008		
	FM	**BJ**
Coffee bushes	109	37
Shade trees	6	2
Total phorophytes	115	39
General % ocupation	23.27	8.72

2009		
	FM	**BJ**
Coffee bushes	108	37
Shade trees	6	0
Total phorophytes	114	37
General % ocupation	23.07	8.25

("Chalum"; *Inga micheliana* Harms.: Mimosaceae) as well as occasional species of native, fruit or timber trees which also serve to shade the coffee bushes, such as *Cedrela mexicana* Roem. (Meliaceae), *Citrus* sp. (Rutaceae) and *Nectandra* sp. (Lauraceae) in FM and *Inga lauriana* (Sw.) Willd. (Fabaceae), *Citrus* sp., *Trema micrantha* (L.) Blume (Ulmaceae) and *Vernonia deppeana* Less. (Asteraceae), in BJ. Both plantations can be considered as simple polycultures (*sensu* Williams-Linera & López-Gómez, 2008, for coffee plantations in the Mexican state of Veracruz). The plantations of FM and BJ are approximately 15 and 20 years old and are situated at an average altitude of 1410 m and 1440 m, respectively.

In both FM and BJ no agrochemicals are applied, and management is limited to manually eliminating weeds with a machete twice a year, and the pruning of shade trees and coffee bushes once a year. Most importantly, unlike in most plantations in the region, these farmers do not eliminate the moss, and with it the epiphytes, that grow on the branches and trunks of the coffee bushes.

Determination of the phorophytes — Most of the trees were *I. micheliana* and this was the only tree

species that acted as a phorophyte. The coffee bushes themselves were also phorophytes.

As shown in Table 1, not all the coffee bushes and shade trees were colonized by *O. poikilostalix*. The Chi-squared test showed a significant difference between the colonization of the two phorophytes, with an apparent preference for coffee bushes in 2008 (χ^2= 123.662; d.f.= 1; P= 9.98887e-29), which was maintained in 2009 (χ^2= 127.954; d.f.= 1; P= 1.14875e-29). In 2009, 23 *O. poikilostalix* were lost due to maintenance activities, thus reducing also the number of trees determined as phorophytes. "Chalum" (*I. micheliana*) was the only tree species to act as a phorophyte (58 individuals, 79.45% of all trees. 27 FM; 31 BJ) and population sizes of *O. poikilostalix* were notably different between sites and phorophytes (Table 7).

Density of coffee bushes and shade trees — Within the experimental plots, in FM there were 459 coffee bushes and 35 shade trees, whereas in BJ there were 410 coffee bushes and 38 shade trees. The density of coffee bushes was 2448 and 2187 coffee bushes/ha in FM and BJ, respectively, whereas shade tree density was more variable, at 187 and 203 trees/ha for FM and BJ, respectively.

Height Above Ground (HAG) and Diameter at Breast Height (DBH)of the phorophytes — There were significant differences between the heights of the coffee bushes in the three plots of FM (Fc= 5.51; d.f.= 5; P= 5.3e-05), but not for the shade trees (Fc= 1.21; d.f. = 5; P= 0.315) (Table 2). For DBH (Table 2), the Kruskal-Wallis test showed significant differences between coffee bushes (χ^2= 13.73; d.f.= 5; P= 0.017), but not for shade trees (Fc= 2.04; d.f. = 5; P= 0.084), evaluating with ANOVA. Some coffee bushes were not included due to measuring less than 1.30 m in height.

TABLE 2. Height Above Ground (HAG) (m) and Diameter at Breast Height (DBH) (cm) averages for the phorophytes, coffee bushes and shade trees, in Fracción Montecristo (FM) and Benito Juárez (BJ).

	Coffee		Trees	
	FM	**BJ**	**FM**	**BJ**
Average HAG	3.93	3.03	6.08	6.23
Average DBH	9.58	9.37	76.08	62.84

Table 3. General average dimensions (m) of the trunk microsites (Zone 1) and branches (Zone 3) and average number of forks (Zone 2) for the phorophytes, coffee bushes and shade trees, in Fracción Montecristo (FM) and Benito Juárez (BJ).

	Coffee		Trees	
	FM	BJ	FM	BJ
Trunk (Zone 1)	1.53	1.17	3.39	2.96
Branches (Zone 3)	2.15	1.62	2.7	3.24
Fork (Zone 2)	1.25	1.5	1.11	0.97

Availability of Microsites — As was expected, the total length of the branches (Zone 2) of the coffee bushes and the length of the trunks (Zone 1) of the trees were greater than the other microsites of these phorophytes (Table 3). The forks between branches could be found at different heights above the ground.

Number of orchids per microsite — The majority of individuals of *O. poikilostalix* occupied Zone 3, the branches, in the case of the coffee bushes (703 individuals) and Zone 1, the trunk, of the shade trees (78 individuals). Plot 1 (FM) had the greatest population (762 individuals), with the highest numbers of individuals in each microsite [Zone 1, 148; Zone 2 (coffee bushes only), 2; Zone 3, 383; Zone 4 (coffee bushes only) 229] and there was a significant difference between Plot 1 as compared to Plots 2 and 3 (χ^2= 44.23; d.f.= 2; P= 2.48644e-10) (Fig. 3). For BJ, the number of orchid individuals on the coffee plants differed significantly between all three plots (χ^2= 7.43; d.f.= 2; P= 0.024) (Fig. 4).

Shade trees were less favoured as phorophytes than coffee bushes, and no orchids were found growing in Zone 2, the forks of the trees. However, one specimen of *I. micheliana* had 52 individuals, 46 on Zone 1, and 6 on Zone 3.

Principal Component Analysis — Comparing all the variables for both types of phorophyte (plot, height above ground, DBH, number of orchid individuals on each microsite, number available of each microsite) we determined whether there were differences between the experimental plots.

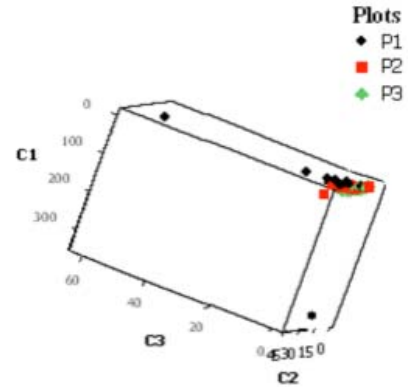For coffee bushes in FM, there was a significant

Figure 3. Scatter Plot produced by Principal Component Analysis, for coffee bushes in Fracción Montecristo (FM). Variables included: Height Above Ground (HAG), Diameter at Breast Height (DBH), number of orchid individuals on each microsite, number available of each microsite.

Figure 4. Scatter Plot produced by Principal Component Analysis, for coffee bushes in Benito Juárez El Plan (BJ). Variables included: Height Above Ground (HAG), Diameter at Breast Height (DBH), number of orchid individuals on each microsite, number available of each microsite.

difference between Plot 1 and Plots 2 and 3, (Table 3) corroborated by the Mahalanobis test (Table 4). In BJ, there were significant differences between all the plots (Fig. 4), confirmed by the Mahalanobis test (Table 5).

In the case of the shade trees in FM, Plot 2 was significantly different to Plots 1 and 3 (Fig. 5) corroborated by the Mahalanobis test (Table 6). In BJ, the apparent significant difference between Plot 3

TABLE 4. Mahalanobis test in Discriminant Analysis for shade tree phorophytes in Fracción Montecristo.

Prob > Mahalanobis Distance for Squared Distance to Plot			
Plot	P1	P2	P3
P1	1.0000	0.0003	<.0001
P2	0.0003	1.0000	0.7010
P3	<.0001	0.7010	1.0000

TABLE 5. Mahalanobis test in Discriminant Analysis for coffee plant phorophytes in Benito Juárez.

Prob > Mahalanobis Distance for Squared Distance to Plot			
Plot	P4	P5	P6
P4	1.0000	<.0001	0.0003
P5	<.0001	1.0000	<.0001
P6	0.0003	<.0001	1.0000

and Plots 1 and 2 was shown to be non-existent by the application of Pillai's Trace test (Fig. 6).

Number of individuals of life stages — For the shade trees, in FM, the distribution of the three life stages was: S - 35, J - 7, A - 21. In BJ there were no seedlings observed on the shade trees, J - 10, A - 12. For coffee bushes in FM: S - 344, J - 399, A - 317; BJ: S - 63, J - 88, A - 63. The majority of individuals of all life stages were found growing on Zone 3 (703 individuals) and

Pillai's Trace: P=0.0123; F=2.36

FIGURE 5. Scatter Plot produced by Principal Component Analysis, for shade trees in Fracción Montecristo (FM). Variables included: Height Above Ground (HAG), Diameter at Breast Height (DBH), number of orchid individuals on each microsite, number available of each microsite.

TABLE 6. Mahalanobis test in Discriminant Analysis for shade tree phorophytes, Fracción Montecristo.

Prob > Mahalanobis Distance for Squared Distance to Plot			
Plot	P1	P2	P3
P1	1.0000	0.0154	0.1967
P2	0.0154	1.0000	0.0360
P3	0.1967	0.0360	1.0000

very few were found on Zone 2 (4). Plot 1 had the most individuals and the greatest number of all life stages growing on all the microsites.

Discussion

Height, DBH y density of present and potential phorophytes. Its influence on the ecosystem — The density and architecture of present and potential phorophytes, linked to the HAG and DBH of the trees and coffee bushes, create variations in the conditions of temperature and humidity which in turn affect the germination and establishment of epiphytes (Benzing 1990). In the case of the forks between branches, the levels of humidity and amount of humus accumulated, which are favourable for the establishment of many epiphytes, depend upon the size and position of the fork in relation to sources of organic matter and moisture. The combination of these aspects can have a substantial effect upon the penetration of light, air
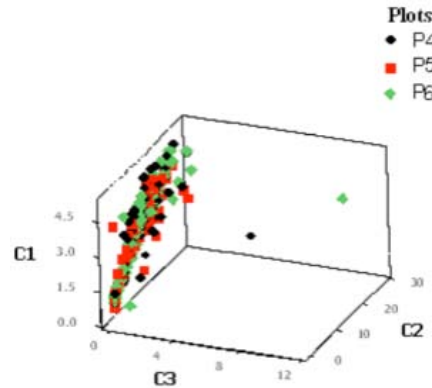

Pillai's Trace: P= 0.1510; F= 1.53

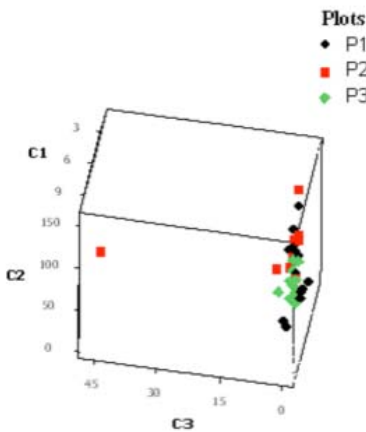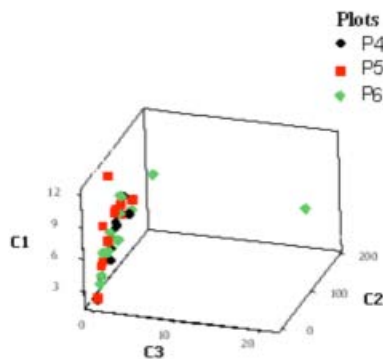FIGURE 6. Scatter Plot of Principal Component Analysis, for shade trees in Benito Juárez El Plan (BJ). Variables included: Height Above Ground (HAG), Diameter at Breast Height (DBH), number of orchid individuals on each microsite, number available of each microsite.

Table 7. *Oncidium poikilostalix*: number of individuals per microsite, life stage and type of phorophyte in 2008, for Fracción Montecristo (FM) and Benito Juárez (BJ).

	Coffee					Trees			
FM No. individuals	Zone 1	Zone 2	Zone 3	Zone 4	Total	Zone 1	Zone 2	Zone 3	Total
Seedlings	78	1	146	119	**344**	35	0	0	**35**
Juvenile	52	1	225	121	**399**	5	0	2	**7**
Adults	42	0	218	57	**317**	16	0	5	**21**
Total	172	2	589	297	1060	56	0	7	63
BJ									
Seedlings	14	0	23	26	**63**	0	0	0	**0**
Juvenile	11	1	49	27	**88**	10	0	0	**10**
Adults	13	1	42	7	**63**	12	0	0	**12**
Total	38	2	114	60	214	22	0	0	22

circulation and the surface available for establishment of epiphytes. Those same variables will also affect the abundance and diversity of bacteria and mycorrhizal fungi, the availability of pollinators and the abundance of herbivores and their natural enemies.

The density of coffee bushes was 2448 and 2187 coffee bushes/ha in FM and BJ, respectively, which compares to a density of approximately 2000 bushes/ha in traditional coffee plantations in Colombia, contrasting with intensive plantations in that country which may have up to 10,000 bushes/ha of dwarf, high yielding varieties (Gallego 2005). Shade tree density was more variable, at 187 and 203 trees/ha for FM and BJ, respectively. These densities are similar to the density of shade trees in coffee plantations in Veracruz, which range from 193 - 220 trees/ha, but which are taller than the trees in our study, possibly due to less aggressive pruning. However, the density of trees in the original cloud forest is approximately 638 trees/ha, with a maximum height of approximately 22m (Williams-Linera & López-Gómez 2008), and *O. poikilostalix* may be better adapted to the environmental conditions, and for attracting pollinators and dispersing seeds within this denser vegetation of the original cloud forest.

Number of orchids per type of phorophyte and per microsite — Vascular epiphytes tend to display patterns of vertical distribution on their phorophytes that reflect their range of tolerance for light and humidity and other ecophysiological adaptions (Johansson 1974; Krömer *et al.* 2007). A study carried out in humid tropical forests in Alto Orinoco in Venezuela suggests that forks represent an extremely important microsite for many epiphytic species of plants, whereas other species clearly favour vertical substrates (Hernández-Rosas 2000). In forks, retention of both humidity and organic matter are greater than for vertical substrates, as water drains away very quickly on vertical substrates, carrying with it organic matter and dissolved nutrients.

In this study, the percentage colonization of both phorophytes was similar, 13.79% of shade trees and 16.8% of coffee bushes, and the higher numbers of *O. poikilostalix* on coffee bushes could simply be due to the presence of more than 10 times more coffee bushes (869) than shade trees (73) in the experimental plots. *Oncidium poikilostalix* has a relatively high pollination rate and each capsule contains thousands of seeds (García-González 2009, unpublished data) which are carried by multidirectional breeze and thermal currents, the similarity of the percent colonization, despite the great difference in the quantities of potential phorophytes in the experimental plots, suggest that only this small, and constant fraction of phorophyte populations have the necessary microorganisms and /or environmental conditions to permit the establishment of colonies of *O. poikilostalix* and that it is a minority case.

From a numerical point of view 1273 out of a total of 1358 (93.74%) individuals of *O. poikilostalix* were found growing on coffee bushes indicating that they offer adequate conditions for germination and development, and conditions that are probably similar to the original substrate preferences of this orchid. This is interesting as *Coffea arabica* is an introduced species, with just over one century in the Soconusco region (Baxter 1997; ICO 2009) and has effectively creating a new habitat or opportunity. In tropical forests the canopy is closed, there is little vegetation on the forest floor and even twig epiphytes growing on the outer extremes of the branches are not exposed to full sun or extreme dryness. In coffee plantations the canopy is more open, shade trees are widely spaced and light penetrates down to the coffee bushes. We have no information concerning the type of phorophytes and microsites colonized by *O. poikilostalix* in natural habitats, but obviously the branches of coffee bushes, followed by the trunks of coffee bushes and shade trees are the conditions that most clearly fulfil the requirements and mimic the natural habit of *O. poikilostalix*. In the case of shade trees, the trunk is maybe too thick, too dark, and maybe even too constantly damp, whereas the pruned branches are maybe too exposed in this more open type of vegetation cover. The trees are regularly pruned, to increase the light reaching the coffee plants, and the profusion of thinner branches is eliminated and with it any orchids attached to them.

The long fibrous roots capable of wrapping round thin branches and the size of *O. poikilostalix* indicate twig epifitism but in this study this species was shown to prefer thicker branches and to be able to establish on trunks, but this may be an artefact of management practices carried out within coffee plantations wherein thinner branch growth is annually pruned out, both in shade trees and coffee bushes. The branches represent an intermediate microsite, in terms of light intensity, air currents, bark texture, available surface area, thickness, and in the absence of stable twig microsites, may offer the next best option and fall within the natural range of tolerance of this orchid. Twig epiphytes tend to mature relatively rapidly but have shorter lifecycles than most orchid species that may be a reflection of their risky and ephemeral

habitat (Gravendeel *et al.* 2004; Hágsater *et al.* 2005; Mondragón *et al.* 2007). Various species of small twig epiphytes colonize the thinnest branches of coffee bushes in Soconusco region, especially *Erycina crista galli* (Rchb.f.) N.H.Williams & M.W.Chase, *Leochilus labiatus* (Sw.) Kuntze, *L. oncidioides* Knowles & Westc., *L. scriptus* (Sw.) Rchb.f., *Notylia barkeri* Lindl., and *Ornithocephalus tripterus* Schltr. (Damon 2009, unpublished data), and all are even smaller than *O. pokilostalix*, which may explain why this orchid appears to fall outside of the twig epiphyte category.

Differences between Plots and number of individuals of life stages — We found significant differences between the coffee bushes and the shade trees, affecting all the variables monitored, but mainly due to the great difference in the number of plants of each category. All life stages of *O. poikilostalix* were found on the trunk of the shade trees (Table 7). In FM, with the largest and most established population of *O. poikilostalix*, our data for the number of seedlings and numbers of adult plants indicate low survival rates on Zone 1, the trunk (Table 7). The trunks of the trees will receive orchid seeds falling from above and the high humidity possible favours the presence of mycorrhizal fungi which facilitate the germination of the seeds. However, later on, development of the young plant may be hindered by low light levels, reduced air circulation and, during the rainy season, humidity may reach intolerable levels complicated by mud splashed from the ground. In BJ the behaviour of the orchid appeared to be different, with far greater levels of survival on the trunks, but the population is still too small to draw conclusions.

On the branch microsite, in both FM and BJ, where a greater number of individuals were found from all three life stages, recruitment of seedlings was relatively lower, although survival rates were higher in most of the Plots (Table 7). After Zone 3, the next most occupied microsite was the twigs, Zone 4 (Table 7), although in Plots 3 and 5 no individual were observed on this microsite. Plot 3 had a slightly greater density of coffee bushes implying less light reaching the coffee twigs, but Plot 5 was no different, making it difficult to explain this difference. The

relative abundance on this microsite agrees with the size and physical characteristics of *O. poikilostalix*, but levels of survival were not high, as few adult plants were observed in comparison with the numbers of seedlings and juveniles, although this could simply be due to the rough handling and breakage of twigs during the harvest, and partial removal of twigs during annual pruning.

In the case of shade trees the low numbers of individuals of *O. poikilostalix* (Table 7) prevented an adequate analysis of the distribution of individuals of the three life stages.

Oncidium poikilostalix is an orchid that appears to be well adapted to the conditions in the coffee agroecosytems of southeast Mexico, colonizing most of the available microsites on both shade trees and coffee bushes, although we have no means of comparing our data with populations inhabiting the original, natural habitat of this plant. Despite our observation that a small proportion of individuals of *O. poikilostalix* were lost due to management practices in 2009, the majority of the coffee plantations in Soconusco region are administered by small producers, which for cultural and economic reasons carry out the bare minimum of maintenance procedures, which favours stability and the persistence of epiphytes. Under these conditions, *O. poikilostalix* is slowly expanding its distribution and may threaten the smaller populations of the similar *Sigmatostalix guatemalensis* (awaiting verification of its new name within *Oncidium*. Rodolfo Solano-Gómez, personal communication), which is a protected plant in Mexico and established in small numbers within the coffee plantations FM and BJ.

LITERATURE CITED

Atwood, J.T. & D.E. Mora de Retana. 1999. Family # 39 Orchidaceae: Tribe Maxillarieae: subtribes Maxillariinae and Oncidiinae. Fieldiana, Bot. 40 (1-4): 1-82.

Ávila, I. & K. Oyama. 2002. Manejo sustentable de *Laelia speciosa* (Orchidaceae). Biodiversitas (Boletín Bimestral de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) 7 (43): 9-12.

Baxter, J. 1997. El libro del café. Susaeta Ediciones, Madrid.

Behar, M. & O. Tinschert. 1998. Guatemala y sus orquídeas. Bancafé, Guatemala.

Benzing, D.H. 1990. Vascular Epiphytes. Cambridge University Press, New York.

CCAD-PNUD/GEF. 2002. El Corredor Biológico Mesoamericano, México. Proyecto Para la Consolidación del Corredor Biológico Mesoamericano. Serie Técnica 05. [Internet page] [cited on 20 december 2009]. Available at URL: http:www.ccad.ws/pccbm/docs/cbmmexico.pdf

CNA & CMDI (Comisión Nacional del Agua y Centro para la Migración y el Desarrollo Internacional). 2000. Plan de conservación de suelos y agua para la costa de Chiapas, México.

Damon, A. 2011. Diversidad y conservación de las orquídeas del corredor biológico Tacaná-Boquerón. Final report of project. FONDOS MIXTOS-CHIAPAS: CHIS-2006-C06-45802. 2007-2010.

Espejo, A., A.R. López-Ferrari; R. Jiménez & L. Sánchez. 2004. Las orquídeas de los cafetales en México: una opción para el uso sostenible de ecosistemas tropicales. Rev. Biol. Trop. 53 (1-2): 73-84.

Gallego, M.C. 2005. Intensidad de manejo del agroecositema del café (*Coffea arabica* L.) (monocultivo y policultivo) y riqueza de especies de hormigas generalistas. Boletín del Museo de Entomología de la Universidad del Valle 6 (2): 16-29.

Gravendeel, B., A. Smithson, F.J.W. Slik & A. Schuiteman. 2004. Epiphytism and pollinator specialization: drivers for orchid diversity?. Phil. Trans. R. Soc. Lond. B. 359: 1523-1535.

Hágsater, E.; M. Soto; G. Salazar; R. Jiménez; M. López & R. Dressler. 2005. Las Orquídeas de México. Productos Farmacéuticos, S.A. of C.V, México.

Hernández-Rosas, J.I. 2000. Patrones de distribución de las epífitas vasculares y arquitectura de los forofitos de un bosque húmedo tropical del Alto Orinoco, Estado de Amazonas, Venezuela. Acta Biológica Venezuelica 20 (3): 43-60.

ICO (International Coffee Organization). 2009. Historical data. [Internet page] [cited on 22 october 2009]. Available at URL: http:www.ico.org/historical.asp

INEGI (Instituto Nacional de Estadística, Geografía e Informática). 1999. El crecimiento de la población y sus repercusiones sobre el medio ambiente de México. Anuario Estadístico, México.

Johansson, D. 1974. Ecology of vascular epiphytes in West African Rain Forest. Acta Phytogeogr. Suecica 59:1-129.

Krömer, T.; M. Kessler & S.R. Gradstein. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol. 189: 261-278.

Mondragón, D.; C. Maldonado & R. Aguilar-Santelises. 2007. Life history and demography of a twig epiphyte: a case study of *Erycina crista-galli* (Orchidaceae). Selbyana 28 (2): 137-144.

Sánchez, J.E. & R. Jarquín (ed.). 2004. La Frontera Sur. Reflexiones sobre el Soconusco, Chiapas, y sus problemas ambientales, poblacionales y productivos.

CD. ECOSUR.

Solano, R., Jiménez-Machorro, R. & Damon, A. (in press). Two new records and one rediscovery for Orchidaceae of Mexico. Acta Botánica Mexicana.

Tovilla, C. 2004. La dimensión de la crisis ambiental en la costa de Chiapas y la necesidad de un programa de ordenamiento de las actividades. *In*: Sánchez, J.E. & R. Jarquín (ed.). 2004. La Frontera Sur. Reflexiones sobre el Soconusco, Chiapas, y sus problemas ambientales, poblacionales y productivos. CD. ECOSUR.

Williams-Linera, G. & A. López-Gómez. 2008. Estructura y diversidad de la vegetación leñosa. *In*: Manson, R.H.; V. Hernández-Ortiz; S. Gallina & K. Mehltreter (ed.). 2008. Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación. Instituto de Ecología A.C. (INECOL) e Instituto Nacional de Ecología (INE-SEMARNAT), México, pp. 55-68.

AA FROM LOMAS FORMATIONS. A NEW ORCHIDACEAE RECORD FROM THE DESERT COAST OF PERU

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ABSTRACT. Orchid species of the genus *Aa* have been described as mostly restricted to high elevations zones in the Andes and mountains of Costa Rica. Here, we record populations of *Aa weddelliana* at lower elevations in lomas formations from the desert coast of Peru; this is the fourth species of Orchidaceae registered in Peruvian lomas. Furthermore, we illustrate and discuss some floral features of *Aa weddelliana*.

RESUMEN. Las especies del género *Aa* han sido descritas como orquídeas restringidas generalmente a zonas altas de los Andes y montañas de Costa Rica. Se presenta el registro de poblaciones de *Aa weddelliana* a elevaciones más bajas, en formaciones de lomas en la costa desértica del Perú, siendo ésta la cuarta especie de Orchidaceae registrada para las formaciones de lomas. Asimismo, ilustramos y discutimos algunos aspectos florísticos de *Aa weddelliana*.

KEYWORDS / PALABRAS CLAVE: Orchidaceae, Peru, Lomas formations, Desert, *Aa*

The western coast of South America between Peru and Chile (5º-30ºS latitude) is occupied by a continuous belt of desert of 3500 km long and a surface area of about 2900 km². Its aridity is mainly due to the Humboldt Current and the South Pacific anticyclone (Rundell *et al*. 1991). A combination of climate factors on the coast during winter (June-September) allows the formation of thick fog masses in the ocean. Fog comes into the continent and is intercepted by foothills near the sea, creating ample water for vegetation to flourish for a period of months. This peculiar habitat is called *lomas* formations and is unique in its plant community (Weberbauer 1945, Oka & Ogawa 1984, Ferreyra 1993, Dillon *et al.* 2003). Lomas formations occur in the desert as "fog oases" or "islands of vegetation" in disconnected localities along the coast of Peru and Chile, at elevations that generally do not exceed the 1000 m. In Peru, it has been identified in over 70 localities ranging from Trujillo (8° S latitude) to Tacna (18º S latitude). These localities are composed of a variable mixture of annuals, short-lived perennials and in some cases even woody vegetation (Dillon *et al.* 2003). Some years are affected by ENSO (El Niño

Southern Oscillation) events, where the occurrence of unusual precipitations during summer (December-March) alters the normal cycle of vegetation, allowing for the development of vegetation during this period.

The genus *Aa* Rchb.f. includes terrestrial orchids with tiny and non-resupinate flowers distributed from Venezuela to the north of Chile and Argentina with a disjunct population in Costa Rica. Although some authors have claimed the distribution of *Aa* in South America is restricted to the highest zone of the Andes (i.e. above 3100 m.a.s.l.; Wood 2003, Álvarez-Molina & Cameron 2009), there are some populations of *Aa* at lower elevations. For instance, *Aa achalensis* Schltr. reaches 700 m of elevation in north-central Argentina (Cucucci 1964).

The revision of the orchid collection at USM and recent field work in the Southern Peruvian lomas reveal the presence of populations of *Aa* at elevations between 300 to 1000 m in four lomas formations from 11°21' S to 15º 46'S latitude: Lomas de Lachay National Reserve, Department of Lima; a locality at south of Nazca, Department of Ica (the exact locality was not recorded by the collector); and Los Cerrillos

and Lomas de Atiquipa, Department of Arequipa (Fig 1,2). Except for the different size of the flowers – the larger flowers are from the more southerly lomas specimens– all the specimens studied correspond to *Aa weddelliana* (Rchb.f.) Schltr. (Fig 3,4). Previously, this species has only been recorded at elevations between 2700-3800 m in Peru, Bolivia and Argentina (Schweinfurth 1958, Tropicos.org 2010).

To the best of our knowledge, there are no previous records of Orchidaceae from the Departments of Ica and Arequipa. Therefore, *A. weddelliana* is the first record from these departments. Nevertheless, it is not the only orchid recorded from the Peruvian lomas formations (Fig 1). Previous authors have identified plants of *Chloraea pavonii* Lindl. in Lomas de Chancay and Amancaes; and *Malaxis andicola* (Ridl.) O. Ktze. in Cerro Cabras (Schweinfurth 1958, 1959, Correa 1969, Garay & Romero-González 1998). The revision of herbaria collections also shows the presence of *Pelexia matucanensis* (Kraenzl.) Schltr. in Cerro Campana, Cerro Cabras and Casma (*A.Lopez 710*, HUT; N. *Angulo 765*, HUT and *Ferreyra 8049*, MOL respectively). Like *A. weddelliana*, most of the records of *C. pavonii*, *M. andicola* and *P. matucanensis* came from the localities of middle to high elevation of the Andean Cordillera (Bennett & Christenson 1998, Schweinfurth 1958).

The origin of vascular plant species within lomas formations have been grouped into 4 categories: (1) pan-tropical or weedy species, (2) long-distance disjunctions from the Northern Hemisphere desert, (3) species disjunct from the adjacent Andean Cordillera, and (4) plants restricted to the coastal desert (Dillon *et al.* 2003, 2009). The origin of orchid species in lomas formations likely belongs to the third category.

Álvarez-Molina and Cameron (2009) point out several morphological traits found in plants of *Aa* as *Myrosmodes* Rchb.f. (*Aa*'s closely related genus and also considered a high elevation specialist of the Andes) that allow them to cope with the moist, freezing, and windy environments of the paramos and the arid conditions of the puna. Probably, equivalent traits will also allow *A. weddelliana* to develop in the harsh conditions of lomas, especially the fluctuations between arid and humid conditions and strong winds that come from the sea.

FIGURE 1. Map including Peruvian lomas formations localities where Orchidaceae species have been recorded. *Aa weddelliana* (triangle), *Chloraea pavonii* (circle), *Malaxis andicola* (asterisk), *Pelexia matucanensis* (square).

FIGURE 2. *Aa weddelliana* in the Lomas de Atiquipa, Department of Arequipa. A. Panoramic view of Lomas de Atiquipa during winter. B. Plant of *Aa weddelliana*. C. Habitat of *Aa weddelliana* in Lomas de Atiquipa. D. Inflorescence of *Aa weddelliana*. Photographs by Amalia Delgado.

FIGURE 3. *Aa weddelliana*. A. Habit. B. Flower, three views. C. Lip in natural position. D. Dissected perianth. E. Floral bract. F. Column, three views. Drawing by D. Trujillo based on *K. Rahn 198*, USM.

FIGURE 4. Comparison of the flowers of *Aa weddelliana*. A. Flower from the holotype (*G. Mandon 1167*, W). B. Flower of a plant from Lomas de Lachay (*A. Cano 710*, USM-161164). C. Flower of a plant from Lomas de Atiquipa (*R. Ferreyra 14034,* USM). a– Flower. b– Floral bract. c– Dissected perianth. d– Column, ventral and dorsal view. Drawing by D. Trujillo.

Regardless, more field work and a careful examination of *Aa* material from the herbarium collection are necessary in order to document the real distribution of *A. weddelliana*, its ecology, morphological diversity and adaptations to different environments.

The following description of *A. weddelliana* was based on the type material and specimens from the lomas formations studied in the present work.

***Aa weddelliana* (Rchb.f.) Schltr.,** Repert. Spec. Nov. Regni Veg. 11: 150. 1912. *Altensteinia weddelliana* Rchb. f.. Xenia Orchidacea 3: 19. 1878.

TYPE: Bolivia, Vicinity Soratta. Paracollo, in Scritosis. 3400 m. December 1856-January 1857. *Mandon 1167* (holotype: W; isotype: G,K). Fig. 4A.

Plant small, terrestrial herb. *Roots* fasciculate, fleshy. *Leaves* (present before flowering) forming a basal rosette, narrowly oblong, acute to acuminate, up to 11.0 x 1.7 cm. *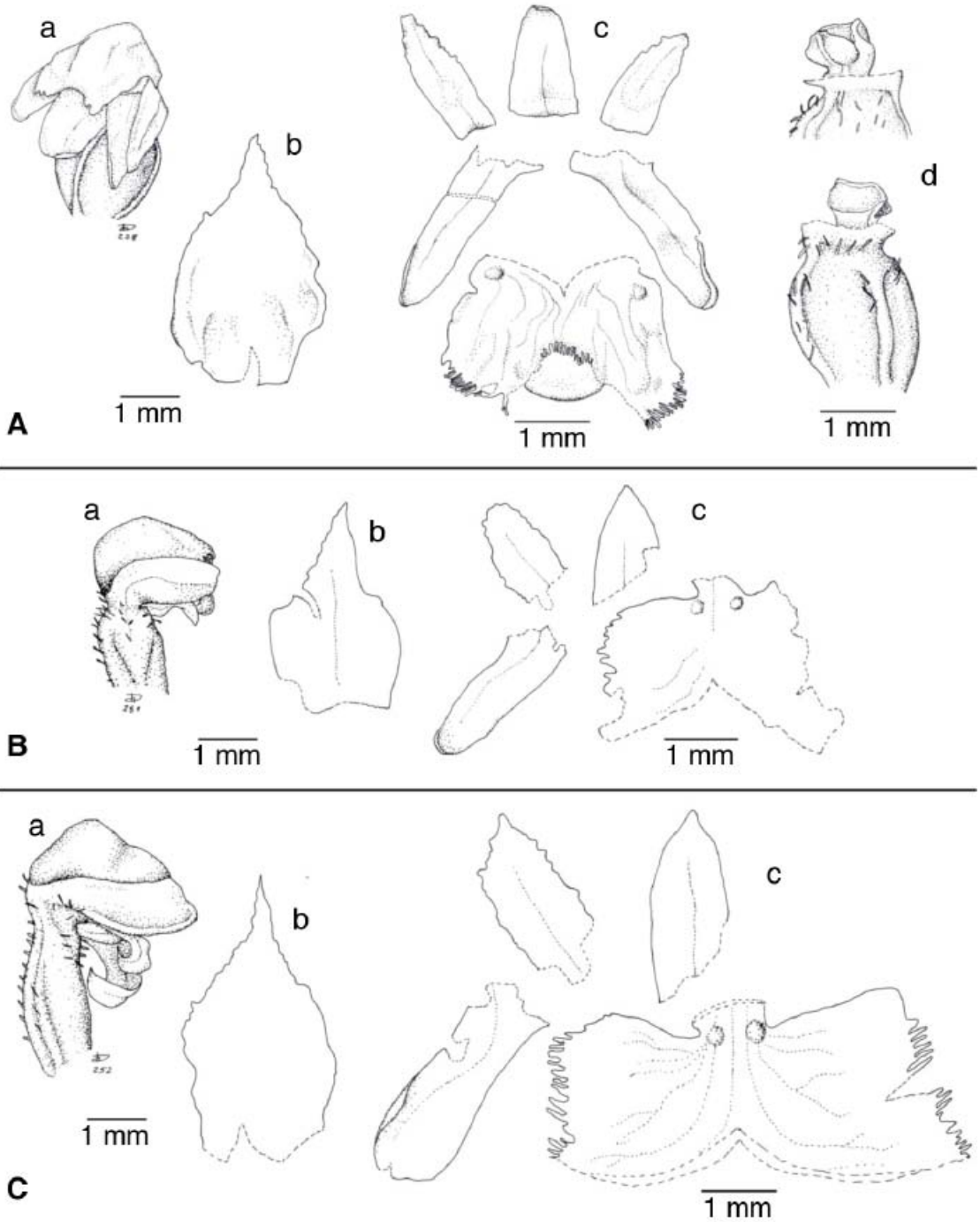Inflorescence* slender, erect, up 50 cm long, enclosed by 10 to 13 diaphanous sheaths, terminated in a densely many flowered cylindrical spike of 4-12 cm long, rachis of the spike sparsely pilose. *Floral bracts* ovate, acute to acuminate, margins slightly erose, reflexed, 4-6 x 2.5- 3.0 mm, somewhat surpassing the flowers. *Flowers* non-resupinate, white with pink-brown tones. *Dorsal sepal* oblong-ovate, acute, 1-nerved, 1.5-2.5 x 0.8-1.0 mm. *Lateral sepals* shortly connate at the base, obliquely oblong, obtuse, dorsally hairy at the base, apex slightly erose, 1-nerved, 2.5-3.0 x 0.7-1.0 mm. *Petals* falcate-ligulate, obtuse to acute, margin variable erose (mostly the distal half), 1-nerved, 1.6-2.7 x 0.7-1.0 mm. *Lip* calceolate, the opening slightly projected toward, transverse, entire to obscurely 3-lobed, margins lacerate, base with two calli, 4 mm wide when expand. *Column* short, retuse rostelum, 0.7-1.5 mm long, straight in young flowers and bent in old flowers. *Stigma* quadrate in young flowers and transversely elongate in old flowers.. *Ovary* subcylindric, hairy, 2.0-2.5 mm long.

Material studied: PERU. **Arequipa:** Caravelí, Arajaipampa, Lomas de Atiquipa, 980 m en suelo franco arcilloso, creciendo bajo el refugio de *Cytharexylum flexuosum*, flores blancas, 16 febrero 2008, *A. Delgado 4021*. Caravelí, lomas de Los Cerrillos, entre Nazca y Chala, 700 m, habitat rocoso, sépalos y pétalos rosado-parduzcos, labelo blanquecino, 23 setiembre 1958, *R. Ferreyra 13455*, USM. Caravelí, encima de Atiquipa, sobre rocas, 600-700 m, flores blancas, 20 diciembre 1959, *R. Ferreyra 14034*, USM (illustration voucher, Fig. 4C). **Ica:** Nazca, km 52.4 al sur de Nazca, entre rocas, 18 octubre 1957, *K. Rahn 198*, USM (illustration voucher, Fig. 3). **Lima:** Huaura, Lomas de Lachay, suelo arenoso, con zonas pedregoso-rocoso, 300-700 m, hierba epífita, escasa, sólo frutos secos, 23 febrero 1996, *A. Cano et al. 7101*, USM-166101. Chancay, Lomas de Lachay, Km 105 carretera Panamericana Norte, suelos arenosos, arenoso-arcillosos, con partes pedregosas y rocosas, 300-700 m, hierba epífita, escasa, solo frutos secos, 24 febrero 1996, *A. Cano et al. 7101*, USM-161164 (illustration voucher, Fig. 4B).

Other records: PERU. **Ica:** Ica, Santiago, Lomas de Amara - Ullujalla, loma con gran captación de humedad de neblina y vientos fuertes, 834 m, suelo arenoso semidescubierto con parches dispersos, 7 diciembre 2007, *A. Orellana & O. Whaley 353* (digital photo).

Distribution: Central and southern coast of Peru, Bolivia and North Argentina, between 300 and 3800 m of elevation.

Habitat and ecology: In sandy, sandy-clay, stony and rocky soils of lomas formations, paramos and puna. Occasionally plants of *A. weddelliana* can grow on decaying tree trunks in the lomas formations and is recorded as epiphyte (personal communication with the collector of *A. Cano* 7101). Flowering from September to February.

In the original description of *A. weddelliana*, Reichenbach (1878) indicated that the floral bracts are shorter than the flower and 5-lobed rostellum. However, after examination of the type material in W (Fig 4A.), it was found that when the floral bracts –reflexed in natural position– are expanded and measured, they are longer than the flower. The rostellum is without lobes; the appearance of lobes must be a deformation created during the preparation of the herbarium material or the rehydration of the flower for study. Two floral features were also noticed during the present study that were neither mentioned in the original description of Reichenbach, nor in the work of Schweinfurth (1958): petals with erose margin and ovary hairy.

Literature Cited

Álvarez-Molina, A. & K.M. Cameron. 2009. Molecular phylogenetics of Prescottiinae s.l. and their close allies (Orchidaceae, Cranichideae) inferred from plastid and nuclear ribosomal DNA sequences. Amer. J. Bot. 96: 1020–1040.

Bennett, D.E. & E.A.Christenson 1998. *Chloraea pavoni* Lindl. Icones Orchid. Peruv. pl. 425.

Cocucci, A.E. 1964. The life-history of *Aa achalensis* Schlechter (Orchidaceae) Phytomorphology 14: 588-597.

Correa, M.N. 1969. "*Chloraea*" género sudamericano de Orchidaceae. Darwiniana 15:374-500.

Dillon, M.O., M. Nakazawa & S. Leiva. 2003. The lomas formations of coastal Peru: composition and biogeographic history. Pp. 1-9 *in*: J. Haas & M.O. Dillon (eds.), El Niño in Peru: biology and culture over 10,000 years. Fieldiana Bot. 43.

Dillon, M.O., T. Tu, L. Xie, V. Quipuscoa & J. Wen. 2009. Biogeographic diversification in *Nolana* (Solanaceae), a ubiquitous member of the Atacama and Peruvian deserts along the western coast of South America. J. Syst. Evol. 47: 457–476.

Ferreyra, R. 1993. Registros de la vegetación en la costa peruana en relación con el Fenómeno El Niño. Bull. Inst. fr. etudes andines. 22: 259-266.

Garay, L.A. & G. Romero-González. 1998. Schedulae Orchidum. Harvard Pap. Bot. 3: 53-62.

Oka, S. & H. Ogawa. 1984. The distribution of lomas vegetation and its climatic environments along the Pacific Coast of Peru. Geogr. Rep. Tokyo metrop. Univ. 19:113-125.

Reichenbach, H.G. 1878. Orchideae Mandonianae. Xenia Orchid. 3: 17-19.

Rundell, P.W., M.O. Dillon, B. Palma, H.A. Mooney, S.L. Gulmon & J.R. Erlenberg. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. Aliso 13: 1-49.

Schlechter, R. 1912. Die Orchideen Gattungen *Altensteinia* HBK, *Aa* Rchb.f. und *Myrosmodes* Rchb.f.. Repert Spec. Nov. Regni Veg. 11: 147-150.

Schweinfurth, C. 1958. Orchids of Peru. Fieldiana Bot. 30: 1-260.

Schweinfurth, C. 1959. Orchids of Peru. Fieldiana Bot. 30: 261-531.

Tropicos.org. 2010. Missouri Botanical Garden. http://www.tropicos.org/Name/23505925. Accessed 08 Nov 2010.

Weberbauer, A. 1945. El mundo vegetal de los Andes peruanos. Estudio fitogeográfico. Lima. Ministerio de Agricultura.

Wood, J. 2003. *Aa*. Pp. 24-26 *in*: A.M. Pridgeon, P.J. Cribb, N.W. Chase & F.N. Rasmussen (eds.), Genera Orchidacearum, 3: Orchidoideae part 2, Vanilloideae. Oxford University Press, Oxford.

ANATOMÍA FOLIAR DE OCHO ESPECIES DE ORQUÍDEAS EPÍFITAS

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Resumen. Para contribuir con el conocimiento de las bases vegetativas del epifitismo en Orchidaceae, se desarrolló un estudio de las variaciones anatómicas foliares que pueden presentarse en diferentes tipos de plantas epifitas. Se escogieron cuatro especies que representaran las diferentes categorías de epífitas—epífita de humus (*Oncidium abortivum* Rchb.f.), epífita de corteza (*Epidendrum excisum* Lindl.) y epifitas de ramita (*Rodriguezia lehmannii* Rchb.f. e *Hirtzia escobarii* Dodson) —, y cuatro especies que crecieran como epífitas y como plantas terrestres—*Elleanthus oliganthus* (Poepp. & Endl.) Rchb.f., *Elleanthus purpureus* (Rchb.f.) Rchb.f., *Pleurothallis cordifolia* Rchb.f. & H.Wagener, y *Stelis* sp. Distintas combinaciones de caracteres xerofíticos propios de plantas adaptadas a crecer en ambientes con baja disponibilidad de recursos hídricos se evidenciaron en todas las especies: mayor desarrollo de células de la epidermis adaxial, engrosamientos de las paredes periclinales de la epidermis, tricomas glandulares, estomas con poro protegido, ocurrencia de hipodermis, haces de células esclerenquimáticas, presencia de diferentes tipos de idioblastos y células esclerenquimáticas rodeando los haces vasculares. Las epífitas de ramita, restringidas a los ejes más pequeños y expuestos de sus hospederos, presentaron varios de estos caracteres.

Abstract. Leafs of representative epiphytic orchids were examined for anatomical detail. Four species representing the different epiphyte categories were selected for the study: *Oncidium abortivum* Rchb.f. (humus epiphyte), *Epidendrum excisum* Lindl. (branch epiphyte), *Rodriguezia lehmannii* Rchb.f., and *Hirtzia escobarii* Dodson(twig epiphytes). Additionally, four orchid species capable of developing as terrestrial plants and as epiphytes were also examined: *Elleanthus oliganthus* (Poepp. & Endl.) Rchb.f., *Elleanthus purpureus* (Rchb.f.) Rchb.f. *Pleurothallis cordifolia* Rchb.f. & H.Wagener, and *Stelis* sp. Various xerophytic characters, that could be considered leaf adaptations to water shortage in the epiphytic habit, were common for most species: greater development of adaxial epidermal cells, stomata with protected pores, occurrence of hypodermis, presence of fiber bundles, different type of idioblasts, and sclerenchyma present adjacent to the xylem and phloem. Twig epiphytes, restricted to the outermost axes of their hosts, exhibit several of these modifications.

Palabras clave / Key words: Anatomía foliar, Orchidaceae, Epifitismo, Adaptación, Leaf anatomy, Epiphytism, Adaptation.

Introducción. La familia Orchidaceae es considerada una de las familias más grandes de plantas vasculares con más de 25,000 especies distribuidas por todo el planeta (Dressler 1981, 2005). Con el 70% de sus especies presentando una forma de vida epífita, constituyen más de dos tercios de todas las epífitas vasculares, siendo el grupo más diverso de este tipo de plantas (Atwood 1986, Kress 1986). Con el objeto de clasificar a las orquídeas epífitas, Dressler (1981) planteó tres categorías ecológicas generales: las epífitas de humus, que crecen solamente donde exista una capa de humus; las epífitas de corteza, que se adhieren con firmeza a troncos y ramas grandes; y las epífitas de ramita, plantas diminutas que se encuentran en los ejes más pequeños y expuestos de sus hospederos.

Varias modificaciones estructurales y adaptaciones fisiológicas están relacionadas con la expresión y surgimiento del epifitismo dentro de las Orchidaceae. Estas incluyen: la anatomía particular de sus raíces (presencia de exodermis y velamen); los pseudobulbos

o engrosamientos en el tallo; la disposición, morfología y anatomía de las hojas; los patrones de crecimiento; y la ruta metabólica fotosintética conocida como metabolismo ácido de las crasulaceas–CAM, por sus siglas en inglés (Dressler 1981, Benzing & Ott 1981, Benzing *et al*. 1983, Benzing & Atwood 1984, Benzing 1989, Benzing 1990, Sinclair 1990, Silvera *et al*. 2009). La interacción de estos caracteres y mecanismos, en combinación con las características reproductivas únicas que presentan—como la gran cantidad de semillas diminutas adaptadas a la dispersión por viento (microspermia), la relación simbiótica con micorrizas para la germinación (micotrofía), y la estructura floral modificada para polinizadores específicos (resupinación, labelo, columna y polinaria)—, han otorgado a las orquídeas grandes oportunidades evolutivas que han facilitado su expansión y la colonización del dosel en los bosques tropicales (Benzing & Atwood 1984, Benzing 1986, Goh & Kluge 1989).

Se ha argumentado que la limitante abiótica más relevante para el crecimiento y funcionamiento vegetativo de las epífitas vasculares es la escasez de agua (Zotz & Hietz 2001). La toma efectiva de agua, el almacenamiento dentro de la planta y el control de la pérdida de ésta, son factores determinantes en la expresión del epifitismo en las orquídeas (Sinclair 1990). Johansson (1975) sostuvo que el patrón de distribución espacial de las orquídeas epífitas parecía ser el resultado de la interacción entre la necesidad por captar altas intensidades lumínicas y la capacidad de tolerar la fuerza de evaporación del aire. Puesto que las hojas son el lugar principal en donde se lleva a cabo la fotosíntesis, estas deben mantener un intercambio de gases adecuado con el aire circundante, lo que conlleva una pérdida de agua inevitable. Cualquier planta sujeta a escasez de agua, debe poseer modificaciones en la morfología, anatomía y fisiología de sus hojas, y la estructura de estas, también debe reflejar la respuesta de la planta a los recursos que se encuentran a su disposición (Sinclair 1990, Garnier & Laurent 1994, Reich *et al*. 1999).

La reducción de la transpiración y el almacenamiento de agua, hacen parte de las estrategias que poseen las hojas para tolerar sequías. En las orquídeas, dentro los caracteres de las hojas que permiten reducir la pérdida de agua se encuentran: el grosor de la cutícula, la densidad y distribución de los estomas, la presencia de pelos superficiales y el hecho de ser deciduas (Sinclair 1990). Para el almacenamiento de agua, las hojas de algunas orquídeas poseen una hipodermis que funciona como tejido de acumulación de agua , que en algunos géneros puede llegar a ocupar hasta el 80% del volumen de la hoja (Pridgeon 1986). Dentro del tejido hipodérmico también se pueden encontrar idioblastos con paredes engrosadas que acumulan agua y evitan el colapso del tejido durante los periodos de desecación (Olatunji *et al*. 1980). En otros casos, las células del mesófilo se agrandan y pueden asumir una función de almacenamiento mientras retienen algunos cloroplastos (Sinclair 1990).

Con el presente trabajo se amplía el conocimiento sobre los caracteres foliares asociados con el hábito epífito, basándose en ocho especies de orquídeas que representan formas de crecimiento variado. A continuación, se describe la anatomía foliar de cuatro especies que representan a los distintos tipos ecológicos de epífitas propuestos por Dressler (1981), y cuatro especies que se encontraron creciendo como plantas terrestres y como epífitas.

Materiales y métodos. Se escogieron cuatro especies de orquídeas que representaran a cada una de las categorías de epífitas propuestas por Dressler (1981)—epífita de humus, epífita de corteza y epífita de ramita—y cuatro especies de orquídeas que crecían como plantas terrestres, enraizadas y expuestas en taludes de una carretera y como epífitas de corteza, sobre árboles dentro de un bosque húmedo de montaña (Tabla 1).

Las especies estudiadas fueron colectadas en su hábitat natural: *Elleanthus oliganthus*, *E. purpureus*, *Pleurothaillis cordifolia*, *Stelis* sp. y *Rodriguezia lehmannii*, en la vereda Monte Bello , municipio de Pueblo Rico, departamento de Risaralda (05º14'40" N, 76º06'15" W); *Oncidium abortivum* y *Epidendrum excisum*, en un bosque húmedo de montaña de la vereda Cedeño , municipio Támesis, departamento de Antioquia (05º34'53" N, 75º42'13" W); e *Hirtzia escobarii* en cultivos de guayaba en la vereda Toriba Bajo , Municipio San Francisco, departamento de Cundinamarca (04º37'0" N, 74º48'0" W).

Los individuos muestreados fueron plantas adultas, en estado de floración y que no presentaban síntomas

Tabla 1. Lista de especies de orquídeas estudiadas.

Especie	Categoría de epífita	Colector y No.	Herbario
Oncidium abortivum Rchb.f.	Epífia de humus	*J. Figueroa 36*	ANDES
Epidendrum excisum Lindl.	Epífita de corteza	*J. Figueroa 14*	ANDES
Hirtzia escobarii Dodson	Epífita de ramita	*J. Figueroa 7*	ANDES
Rodriguezia lehmannii Rchb.f.	Epífita de ramita	*R. Arévalo 684*	ANDES
Elleanthus oliganthus (Poepp. & Endl.) Rchb.f	Epífita de corteza / terrestre	*R. Arévalo 456*	ANDES
Elleanthus purpureus (Rchb.f) Rchb.f	Epífita de corteza / terrestre	*R. Arévalo 679*	ANDES
Pleurothallis cordifolia Rchb.f. & H.Wagener	Epífita de corteza / terrestre	*R. Arévalo 482*	ANDES
Stelis sp.	Epífita de corteza / terrestre	*R. Arévalo 504*	ANDES

de ataques por parte de patógenos o herbívoros. Hojas maduras y completamente expandidas (1 hoja por planta, 5 plantas por especie) fueron almacenadas en solución fijadora 1:1:18 de 40% formol, ácido acético y 70% alcohol (70%) (FAA) para ser llevadas al laboratorio donde se efectuaron los análisis anatómicos. A cada hoja se le hicieron cortes transversales a mano alzada y a nivel de la parte media. Se tomaron medidas del grosor de la hoja y de las cutículas (5 medidas por hoja, 25 por especie) usando un microscopio Nikon® Eclipse 4000 equipado con un micrómetro ocular. Los resultados fueron registrados a través de microfotografías. La presencia de elementos lignificados se detectó mediante el uso de azul de toluidina 0 (Herr 1993). Se describe la anatomía foliar de las distintas especies teniendo en cuenta múltiples observaciones (cortes) y con base en los siguientes caracteres: cutícula, células epidérmicas, estomas, haces fibrosos, hipodermis, mesófilo y haces vasculares.

Resultados

Epífita de humus

Oncidium abortivum: *hojas* coriáceas, duras, conduplicadas, lanceoladas, 332.4 ± 64.9 μm de grosor. *Cutícula* adaxial 2.7 ± 0.3 μm de grosor; abaxial 1.5 ± 0.2 μm de grosor. *Células epidérmicas* oblongas; las células adaxiales más grandes que las abaxiales. *Estomas* al mismo nivel de las células epidérmicas; cámara subestomática más grande que células del mesófilo adyacentes. *Haces fibrosos* abaxiales en dos series que se alternan (Fig. 1A). Hipodermis adaxial uniseriada, interrumpida por idioblastos angulares con paredes lignificadas gruesas (Fig. 1B); abaxial ausente. Mesófilo homogéneo, 10–12 células de grosor, redondas a oblongas, con paredes delgadas. Haces vasculares de diferentes tamaños, intercalados; xilema y floema rodeado por vaina vascular más gruesa hacia los polos.

Epífita de corteza

Epidendrum excisum: *hojas* coriáceas, carnosas, conduplicadas, ovadas, 1014.0 ± 161.62 μm de grosor. *Cutícula* 12.7 ± 1.68 μm de grosor; 8.7 ± 0.82 μm de grosor. *Células epidérmicas* rectangulares a cuadradas, paredes celulares periclinales engrosadas (Fig. 2A). *Estomas* ligeramente hundidos en relación a las células epidérmicas; cámara subestomática más pequeña que células adyacentes del mesófilo; con proyecciones cuticulares (Fig. 2B). *Haces fibrosos* ausentes. Hipodermis adaxial 3–4 células de grosor, presencia de idioblastos con leves engrosamientos parietales en bandas irregulares (Fig. 2A); abaxial uniseriada. paredes celulares engrosadas. Mesófilo homogéneo, 13–15 células de grosor, células con grandes vacuolas (Fig. 2C); idioblastos con rafidios de gran tamaño (Fig. 2D). Haces vasculares de diferentes tamaños, intercalados; xilema y floema rodeado por vaina vascular más gruesa hacia el polo del xilema en los haces más grandes (Fig. 2C).

Epifitas de ramita

Hirtzia escobarii: *hojas* coriáceas, carnosas, fuertemente conduplicadas, elípiticas, angostas, 2315.4 ± 196.9 μm de grosor. *Cutícula* adaxial 5.6 ± 0.2 μm
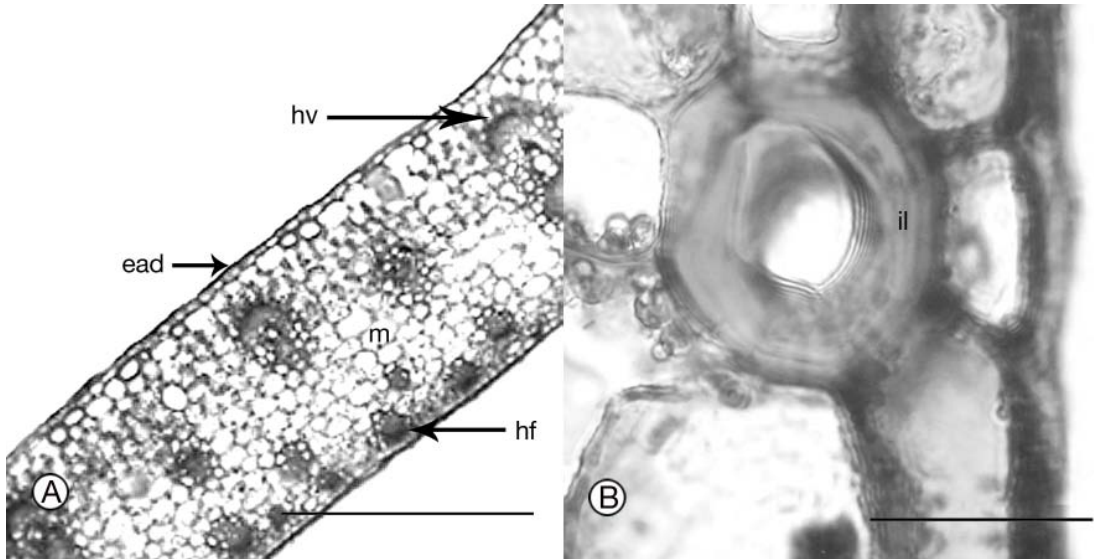
Figura 1. *Oncidium abortivum:* **A.** Aspecto general; células de la epidermis adaxial (ead) de mayor tamaño que las de la epidermis abaxial, células del mesófilo (m) redondas a oblongas, haces vasculares (hv) de varios tamaños, dos series de haces fibrosos en región abaxial (hf). **B**. Idioblasto angular con engrosamiento parietal lignificado (il). Escalas: A=300μm; B=40μm.

de grosor; abaxial 3.8 ± 0.82 μm de grosor. *Células epidérmicas* oblongas. *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática más pequeña que células adyacentes del mesófilo; proyecciones cuticulares externas presentes. *Haces fibrosos* compuestos por varias células con paredes lignificadas gruesas, dispuestos en una serie a nivel de la hipodermis abaxial (Fig. 3A: hf). Hipodermis adaxial uniseriada, células dipuestas anticlinalmente, de tamaño variado, con paredes lignificadas gruesas (Fig. 3B: hl); abaxial uniseriada, células isodiamétricas a oblongas, con paredes lignificadas gruesas, interrumpida por haces fibrosos (Fig. 3A). Mesófilo homogéneo, alrededor de 20 células de grosor, células isodiamétricas hacia la parte media, alargadas anticlinalmente hacia ambas superficies, células con grandes vacuolas que ocupan gran parte del volumen celular; idioblastos globosos con leves engrosamientos transversales en bandas irregulares (Fig. 3C). Haces vasculares de diferentes tamaños, intercalados; xilema y floema rodeado por vaina vascular cuyas células esclerenquimáticas presentan paredes más gruesas hacia los polos (Fig. 3D).

Rodriguezia lehmannii: *hojas* coriáceas, carnosas, conduplicadas y elípticas, 1570.4 ± 265.07

μm de grosor. *Cutícula* adaxial lisa, 12.3 ± 2.67 μm de grosor; abaxial ligeramente bulada, 6.0 ± 1.01 μm de grosor. *Células epidérmicas* oblongas, dispuestas periclinalmente, de mayor tamaño en la superficie adaxial (Fig. 4A). *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática de menor tamaño que células adyacentes del mesófilo; proyecciones cuticulares externas pronunciadas formando una cámara supraestomática (Fig. 4B). *Haces fibrosos* compuestos por grupos de células esclerenquimáticas, en una serie y al mismo nivel de la hipodermis abaxial (Fig. 4A y C). Hipodermis adaxial uniseriada interrumpida por idioblastos elipsoidales a cilíndricos y con engrosamientos parietales helicoidales (Fig. 4D); la abaxial uniseriada, con células de paredes lignificadas gruesas intercalándose con haces fibrosos (Fig. 4C). Mesófilo relativamente homogéneo, 9–10 células de grosor, las adaxiales con más cloroplastos y todas con vacuolas grandes que ocupan gran parte del volumen celular (Fig. 4D). Haces vasculares hacia la parte media de la hoja; xilema y floema rodeado por vaina vascular cuyas células esclerenquimáticas presentan paredes celulares más gruesas hacia el polo del floema (Fig.4E).
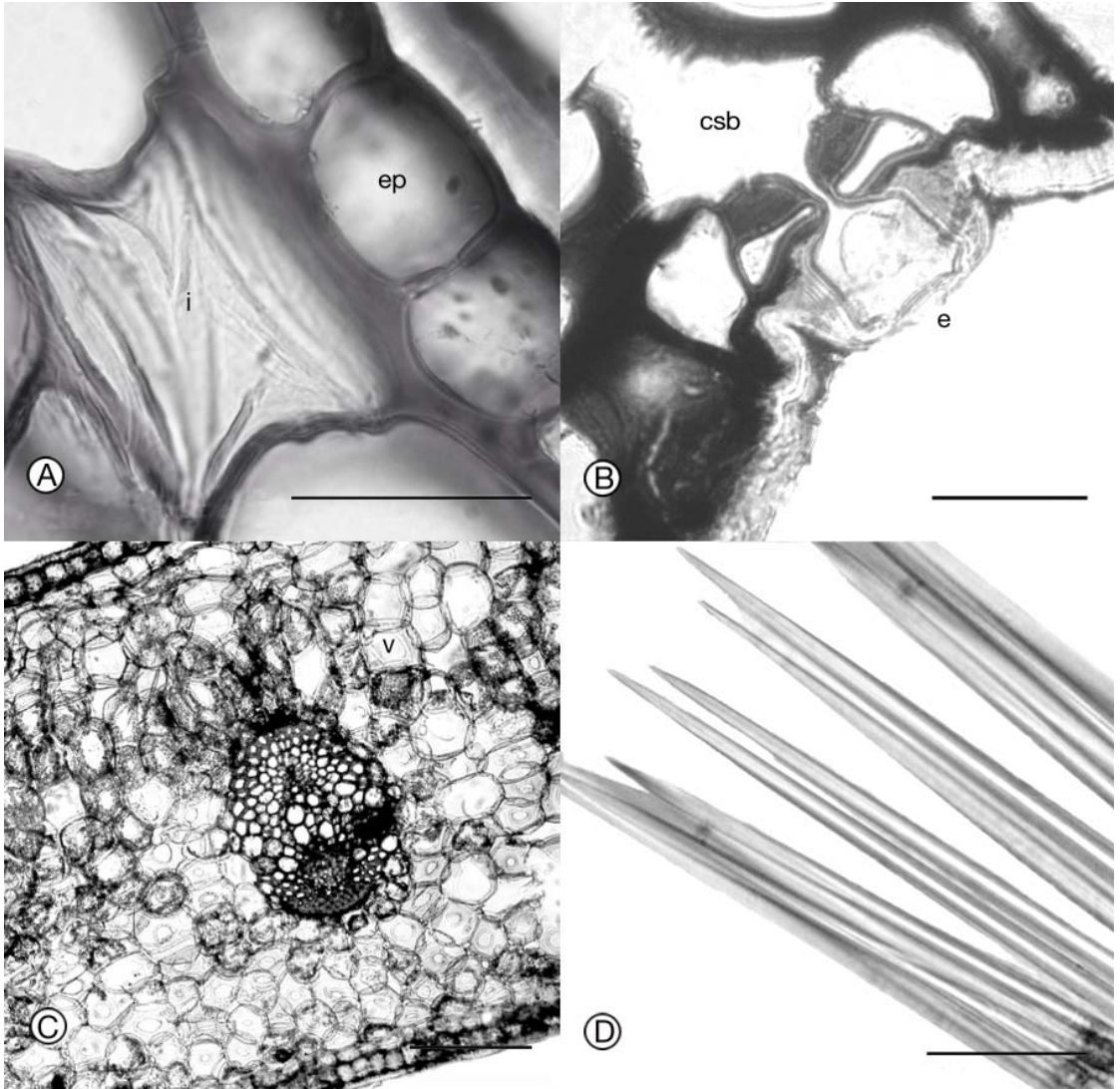
Figura 2*. Epidendrum* cf. *excisum.* **A.** Idioblasto (i) con engrosamiento parietal secundario en forma de bandas irregulares, paredes periclinales de la epidermis gruesas (ep). **B.** Estoma (e) con células guardia de lumen triangular y cámara subestomática (csb) de menor tamaño que células del mesófilo adyacentes. **C.** Aspecto general; vacuolas (v) que ocupan gran parte del volumen celular. **D.** Rafidios de gran tamaño. Escalas: A=10µm; B,D=30 µm; C=200 µm.

Epífitas y terrestres

Elleanthus oliganthus: hojas plicadas, ovadas, 217.0 ± 15.8 µm de grosor en epífitas y 228.8 ± 20.2 µm de grosor en terrestres. *Cutícula* adaxial levemente bulada, 4.6 ± 0.8 µm de grosor en epífitas y 4.2 ± 1.0 en terrestres; abaxial de textura algo verrugosa—con pequeñas proyecciones granulares (Fig. 5A), 2.3 ± 0.4 µm de grosor en epífitas y 2.4 ±

0.2 µm de grosor en terrestres. *Células epidérmicas* oblongas a isodiamétricas, las adaxiales más grandes e isodiamétricas; tricomas glandulares situados en superficie abaxial (Fig. B). *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática del mismo tamaño que células adyacentes del mesófilo; leves proyecciones cuticulares externas e internas (Fig. 5A, e). *Haces fibrosos* ausentes. *Hipodermis* ausente. *Mesófilo* relativamente homogéneo, 5–7 células de

Figura 3. *Hirtzia escobarii:* **A.** Hipodermis abaxial lignificada (hl) interrumpida por haces fibrosos (hf). **B.** Hipodermis adaxial de células con paredes lignificadas gruesas (hl), vacuolas (v) que ocupan gran parte del volumen celular. **C.** Idioblasto globoso con engrosamiento parietal secundario en forma de bandas irregulares (i). **D.** Disposición radiada de células que rodean haz vascular (hv), xilema y floema rodeado por vaina vascular (vv). Escalas: A,B=60μm , C=30 μm. D=10μm.

grosor, células oblongas; idioblastos con rafidios presentes (Fig. 5C). *Haces vasculares* de diferentes tamaños, haces grandes se alternan con dos tipos de haces mas pequeños; los haces grandes con el xilema y floema rodeado por vaina vascular más gruesa hacia los polos (Fig. 5D).

Elleanthus purpureus: *hojas* plicadas, ovadas, 175.4 ± 9.4 μm de grosor en epífitas y 255.3 ± 14.6 μm

de grosor. *Cutícula* adaxial lisa a ligeramente bulada a lo largo del contorno de las células epidérmicas, 4.5 ± 0.4 μm de grosor en epífitas y 7.0 ± 0.9 μm de grosor en terrestres; abaxial finamente bulada a lo largo del contorno de las células epidérmicas, 1.9 ± 0.3 μm de grosor en epífitas y 3.7 ± 0.5 μm de grosor en terrestres (Fig. 6A). *Células epidérmicas* isodiamétricas a oblongas; tricomas glandulares situados en depresiones epidérmicas presentes en

Figura 4. *Rodriguezia lehmannii:* **A.** Aspecto general; células de la epidermis adaxial (ead) de mayor tamaño que las de la epidermis abaxial, hipodermis adaxial (h) constituida por idioblastos (i) con engrosamientos parietales helicoidales, células del mesófilo con vacuolas que ocupan gran parte del volumen celular (v), haces vasculares (hv) grandes y pequeños. **B.** Estoma (e) con proyecciones cuticulares (pc) pronunciadas y cámara supraestomática (csp) alargada. **C.** Hipodermis abaxial lignificada (hl) interrumpida por haces fibrosos (hf). **D.** Idioblasto (i) elipsoidal con engrosamiento parietal secundario helicoidal. **E.** Haz vascular (x y f) rodeado por vaina vascular (vv), cuyas células esclerenquimáticas presentan paredes celulares más gruesas hacia el polo del floema (f). Escalas: A,B,C=30μm; D=400 μm; E=40μm.

ambas superficies (Fig. 6B). *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática de igual o mayor tamaño que células adyacentes del mesófilo; proyecciones cuticulares externas presentes (Fig. 6A). *Haces fibrosos* ausentes. *Hipodermis* ausente. *Mesófilo* heterogéneo, 7–10 células de grosor, 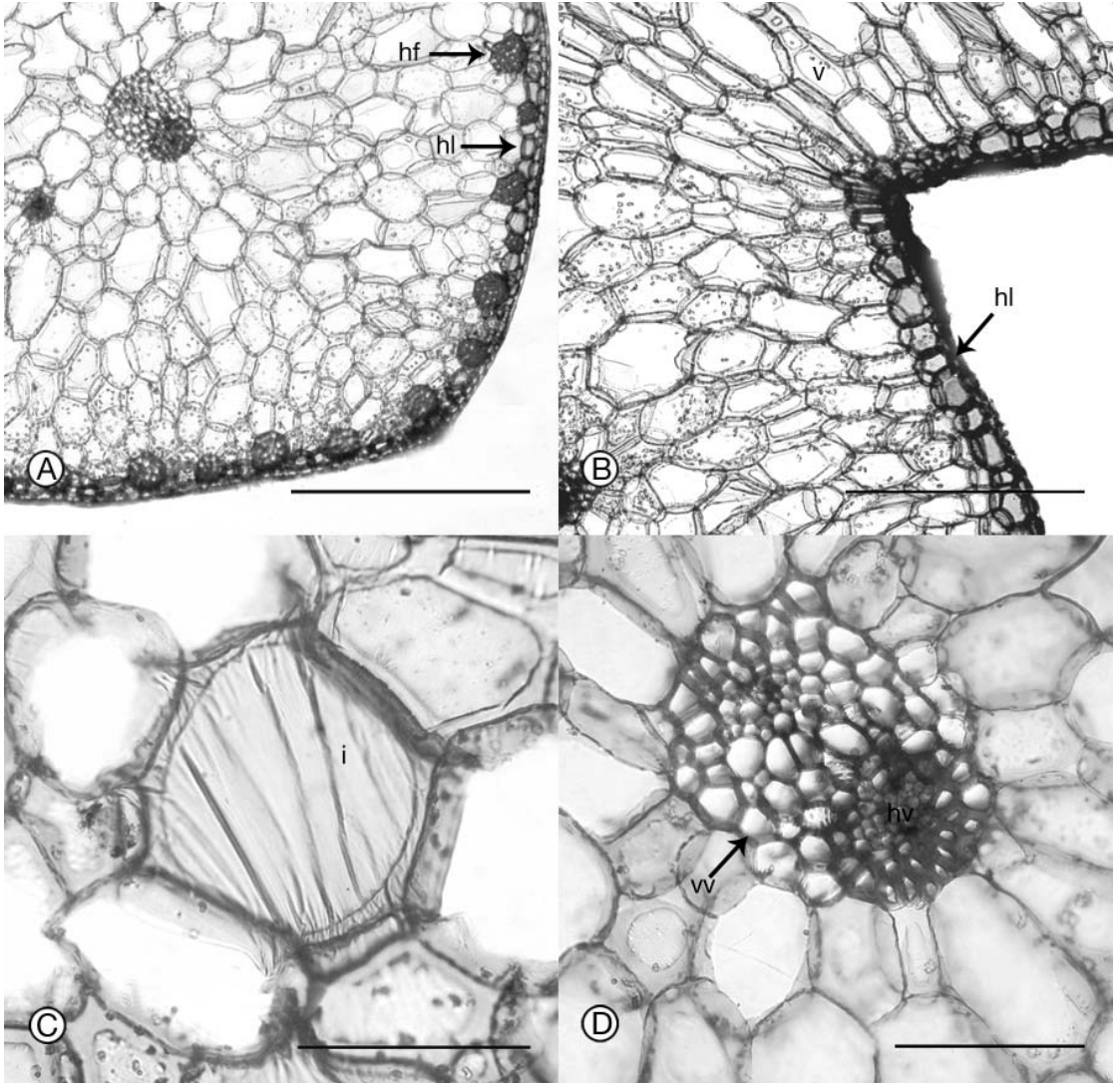las células abaxiales, dispuestas periclinalmente, oblongas a isodiamétricas, con espacios intercelulares conspicuos (parénquima esponjoso); las adaxiales en dos series de células isiodiamétricas (parénquima empalizada) (Fig. 6C); idioblastos con rafidios e idioblastos mucilaginosos presentes. *Haces vasculares* de diferentes tamaños, haces grandes se alternan con dos tipos de haces

Figura 5. *Elleanthus oliganthus.* **A.** Estoma (e) con células guardia de lumen triangular y cámara subestomática. (csb) de igual tamaño a células del mesófilo adyacentes, leves proyecciones cuticulares. internas (pc). **B.** Tricoma glandular de la superficial abaxial de la hoja. **C.** Aspecto general; cutícula adaxial levemente abollada (cad), cutícula abaxial abollada de textura verrugosa (cab), células del mesófilo oblongas dispuestas periclinalmente (m), idioblasto con rafidios (ir). **C.** Haz vascular central (hvc), células de esclerénquima (ce) concentradas hacia los polos del floema y del xilema. Escalas: A=30 µm; B=50µm; C=100 µm; D=200 µm.

más pequeños; xilema y floema rodeado por vaina vascular más gruesa hacía los polos.

Pleurothallis cordifolia: *hojas* coriáceas, algo carnosas, fuertemente cordadas, 838.7 ± 75.6 µm de grosor en epífitas y 942.1 ± 71.3 µm de grosor en terrestres. *Cutícula* adaxial lisa, 7.9 ± 0.7 µm de grosor en epífitas y 7.9 ± 1.4 µm de grosor en terrestres;

abaxial lisa, 2.1 ± 0.2 µm de grosor en epífitas y 2.6 ± 0.4 µm de grosor en terrestres. *Células epidérmicas* oblongas a rectangulares; tricomas 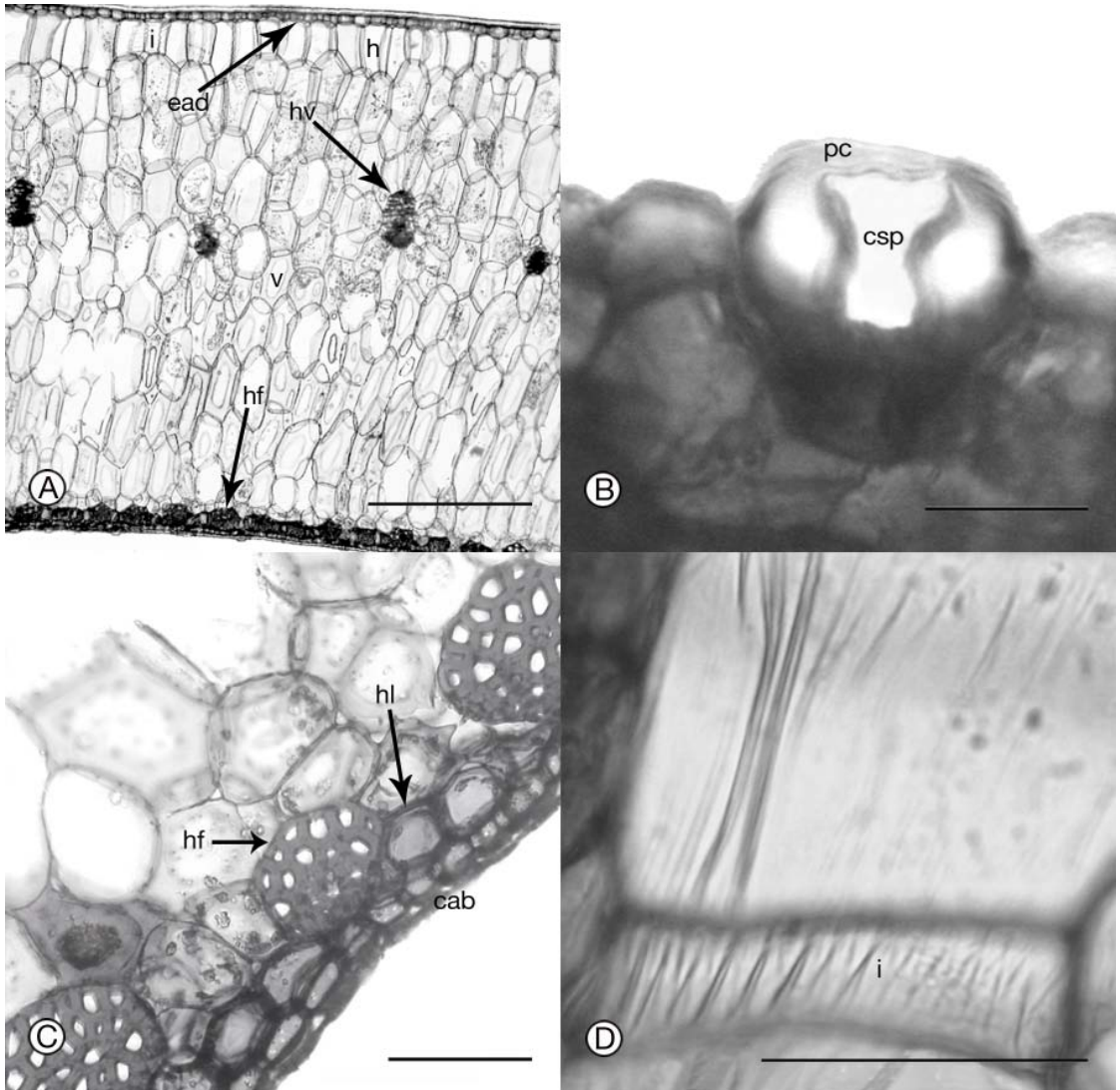glandulares situados en depresiones epidérmicas presentes en ambas superficies (Fig. 7A). *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática de mayor o igual tamaño que células adyacentes del mesófilo (Fig. 7B). *Haces fibrosos* ausentes.

Figura 6. *Elleanthus purpureus.* **A.** Cutícula abaxial finamente abollada (cab), estoma (e) con proyecciones cuticulares curvas y cámara subestomática (csb) de menor tamaño que células del mesófilo adyacentes. **B.** Tricoma glandular (tg). **C.** Aspecto general; cutícula adaxial lisa a ligeramente abollada (cad), células del mesófilo (m) oblongas a isodiamétricas con espacios intracelulares conspicuos (ei). Escalas: A=30 μm; B=50 μm; C=300 μm.

Hipodermis adaxial compuesta por dos series, células con engrosamientos parietales helicoidales; abaxial uniseriada, células con engrosamientos parietales helicoidales. *Mesófilo* heterogéneo, 8–10 células de grosor; el parénquima esponjoso compuesto por células oblongas a isodiamétricas; grandes idioblastos ovoides, con engrosamientos helicoidales e idioblastos con rafídios (Fig. 7C y D); el parénquima empalizada compuesto por dos series, una serie de células columnares, y otra de células oblongas a isodiamétricas (Fig. 7E); en algunas células del mesófilo se presentan pequeñas gotas amarillas de aceite. *Haces vasculares* de diferentes tamaños, distribuidos en una serie ubicada entre el mesófilo de empalizada y el esponjoso: xilema y floema rodeado por vaina vascular; una serie de células esclerenquimáticas separa el xilema del floema.

Stelis sp.: *hojas* coriáceas, carnosas, ovadas, 661.3 ± 60.5 μm de grosor en epífitas y 814.0 ± 121.7 μm de grosor en terrestres. *Cutícula* adaxial lisa, 4.6 ± 0.4 μm de grosor en epífitas y 7.2 ± 2.1 μm de grosor en terrestres; abaxial lisa 2.0 ± 0.1 μm de grosor en epífitas y 2.8 ± 0.9 μm de grosor en terrestres. *Células epidérmicas* dispuestas periclinalmente y oblongas a rectangulares, las adaxiales más grandes; tricomas glandulares en depresiones epidérmicas presentes en

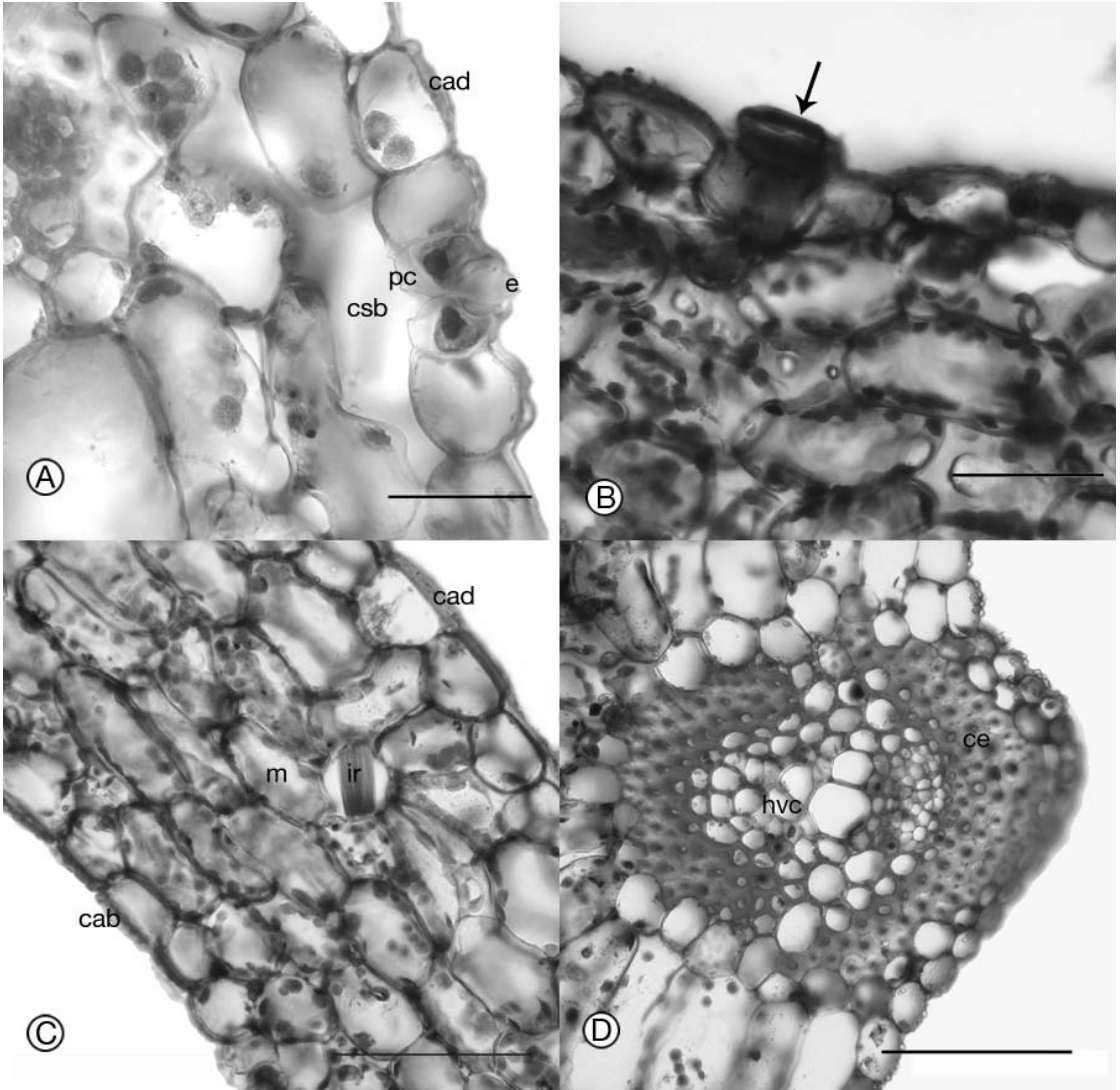Figura 7. *Pleurothallis cordifolia.* **A.** Tricoma glandular (tg). **B.** Estoma (e) con células guardia de lumen triangular y cámara subestomática (csb) de igual tamaño que células del mesófilo adyacentes. **C.** Idioblastos (i) ovoides con engrosamiento parietal secundario helicoidal. **D.** Idioblasto con rafidios (ir). **E.** Aspecto general; células de la epidermis adaxial (ead) de mayor tamaño que las de la epidermis abaxial, parénquima empalizada (pem) de células columnares y dispuestas anticlinalmente, parénquima esponjoso (pes) de células oblongas a isodiamétricas. Escalas: A=50μm; B=30μm; C=100μm; D=40μm; E=300μm.

Figura 8. *Stelis* sp. **A.** Cutícula abaxial lisa (cab), estoma (e) con células guardia de lumen triangular y cámara subestomática (csb) de mayor tamaño que células adyacentes del mesófilo. **B.** Aspecto general; células de la epidermis adaxial (ead) de mayor tamaño que las de la epidermis abaxial, parénquima empalizada (pem) de células columnares dispuestas anticlinalmente, parénquima esponjoso (pes) de células oblongas a isodiamétricas, hipodermis adaxial (had) de 2 a 3 capas de células, hipodermis abaxial (hab) uniseriada. **C.** Haz vascular con serie de células esclerenquimáticas (ce) separando el xilema del floema. Escalas: A=30μm, B=400 μm, C=10μm.

ambas caras y más abundantes en la superficie abaxial (no se muestran). *Estomas* al mismo nivel de las demás células epidérmicas; cámara subestomática de mayor tamaño que células adyacentes del mesófilo; pequeñas proyecciones cuticulares externas presentes (Fig. 8A). *Haces fibrosos* ausentes. *Hipodermis* adaxial 2–4 células de grosor, isodiamétricas; abaxial uniseriada. *Mesófilo* heterogéneo, 12–15 células de grosor; el parénquima esponjoso más grueso, compuesto por células oblongas a isiodiamértricas y dispuestas periclinalmente, espacios intercelulares conspicuos; el parénquima empalizada compuesto por 1–2 series adaxiales de células columnares y otra serie abaxial de

células oblongas a isodiámétricas (Fig. 8B); presencia de idioblastos elongados con engrosamientos parietales helicoidales (no mostrados). *Haces vasculares* de varios tamaños, distribuidos en una serie; los más grandes ubicados entre los dos tipos de mesófilo y los más pequeños abaxiales; esclerénquima ocurre en forma de vainas vasculares conspicuas y completas; una serie de células esclerenquimáticas separa el xilema del floema (Fig. 8C).

Resumen. En las especies estudiadas se presentaron los dos tipos de hojas que se pueden encontrar en las orquídeas (*sensu* Withner *et al*. 1974), plicadas y

coriáceas. Todas las especies se diferenciaron en cuanto al grosor de sus hojas y las más delgadas fueron las hojas plicadas de las dos especies de *Elleanthus*. Entre las especies con hojas coriáceas, las dos epífitas de ramita (*Hirtzia escobarii* y *Rodriguezia lehmannii*) presentaron las hojas más gruesas, mientras la epífita de humus (*Oncidium abortivum*) presentó las hojas más delgadas. En cuanto al grosor de la cutícula, en todas las especies se encontró que la cutícula adaxial era más gruesa que la cutícula abaxial. Al igual que en otros representantes de la familia (Ayensu & Williams 1972, Mohana-Rao & Khasim 1987, Stern *et al*. 1993, Kurzweil *et al*. 1995), las hojas de *O. abortivum*, *E. purpureus*, *R. lehmannii*, *Pleurothallis cordifolia* y *Stelis* sp., presentaron una epidermis adaxial con células más grandes que las de la epidermis abaxial (Tabla 2). Tricomas glandulares fueron evidenciados tanto en las hojas coriáceas de las especies de *Pleurothallis*, como en las hojas plicadas de ambas especies de *Elleanthus*, aunque en *E. oliganthus* se observaron únicamente a nivel de la superficie abaxial (Tabla 2). Todas las especies estudiadas presentaron hojas hipoestomáticas y con los estomas al mismo nivel de las demás células epidérmicas (o ligeramente hundidos como *Epidendrum excisum*). En algunas especies estudiadas se observaron pequeñas proyecciones cuticulares curvas sobre las células guardia, similares a las que ya han sido descritas en otras especies de orquídeas (Ferreira 1992, Leiria 1997). La epífita de ramita, *R. lehmannii*, presentó proyecciones cuticulares externas pronunciadas, formando una cámara externa bastante alargada (Fig. 4B).

La hipodermis, considerada una de las características más comunes en plantas de crecimiento epifito, se evidenció en todas las especies de hojas coriáceas, pero de manera distinta (Tabla 2). Constituida por células de mayor tamaño que las de la epidermis, se presentó adaxial y abaxialmente, exceptuando a la epífita de humus (*Oncidium abortivum*), donde solo ocurrió adaxialmente (Fig. 1A). En epífitas de corteza como *Epidendrum excisum* y *Stelis* sp. se observó una hipodermis adaxial de varias series, con algunas células de paredes gruesas en *E. excisum* (Fig. 2A) . En las epífitas de ramita (*Hirtzia escobarii* y *Rodriguezia lehmannii*), además de presentar hipodermis uniseriadas, gruesas y lignificadas, la hipodermis abaxial se ve interrumpida, en intervalos mas o menos regulares, por haces fibrosos (Fig. 4C). Estos haces

también fueron observados a nivel del mesófilo en la epífita de humus *O. abortivum* (Fig. 1A).

Se presentaron especies con hojas de mesófilo homogéneo y especies con hojas de mesófilo heterogéneo. En aquellas especies con mesófilo heterogéneo (*Pleurothallis cordifolia*, *Stelis* sp. y *Elleanthus purpureus*), el mesófilo se diferencia claramente en parénquima de empalizada y parénquima esponjoso. En las especies en las que el mesófilo es relativamente homogéneo (*E. oliganthus* y *Rodriguezia lehmannii*), se observan variaciones en el tamaño y forma de las células, así como en la cantidad de cloroplastos, sin embargo no existe una clara diferenciación en dos tipos de parénquima. En el mesófilo de la epífita de corteza *Epidendrum excisum*, y de las epífitas de ramita, *Hirtzia escobarii* y *Rodriguezia lehmannii*, predominan células con vacuolas bastante grandes que ocupan la mayor parte del volumen celular (Fig. 3A y 4D). Además, estas especies presentan espacios intercelulares reducidos, donde las cámaras subestomáticas son de menor tamaño que las células adyacentes del mesófilo (Fig. 2B).

Se encontraron diferentes tipos de idioblastos— globosos en *Hirtzia escobarii* , elipsoidales a cilíndricos en *Rodriguezia lehmannii*, angulares en *Oncidium abortivum*, elongados en *Stelis* sp. y ovoides en *Pleutothallis cordifolia*—, con distintos tipos de engrosamiento parietal—irregulares en *Epidendrum excisum* e *H. escobarii* y helicoidales en *R. lehmannii*, *P. cordifolia* y *Stelis* sp. En las epífitas de corteza, *E. excisum* , *Elleanthus oliganthus*, *E. purpureus* y *P. cordifolia*, se presentaron idioblastos con rafidios de oxalato de calcio (Fig. 2D, 5B, y 7D), corroborando descripciones anteriores sobre otros representantes de la familia (Metcalfe 1963; Wattendorff 1976; Franceschi & Horner; Kauschik 1982; Pridgeon 1982; Campos Leite & Oliveira 1987; Ferreira 1992; Widholzer 1993; Leiria 1997; Godoy & Costa 2003).

En todas las especies los haces vasculares son colaterales y presentan células esclerenquimáticas que los envuelven parcial o totalmente. De acuerdo a la especie, estas células esclerenquimáticas que conforman la vaina vascular pueden estar más concentradas hacia los polos y/o variar en el grosor de sus paredes. En las dos especies de *Elleanthus*, en *Oncidium abortivum* y en *Epidendrum excisum*, la vaina vascular es mucho más gruesa hacia los polos del xilema y el floema que hacia la parte media. En

Tabla 2. Caracteres morfológicos y anatómicos presentes en ocho especies de orquídeas epífitas. + = presente; – = ausente.

Especie	Pseudobulbos	Caracteres foliares relacionados con almacenamiento de agua y resistencia a desecación		
		Epidermis		Mesófilo
		Celulas epidérmicas	Tricomas glandulares	
Elleanthus oliganthus	–		+	
Elleanthus purpureus	–	adaxiales más desarrolladas	+ (abaxial)	
Epidendrum excisum	–		–	hipodermis, idioblastos
Hirtzia escobarii	+		–	hipodermis lignificada, idioblastos, haces fibrosos
Oncidium abortivum	+	adaxiales más desarrolladas	–	hipodermis, idioblastos, haces fibrosos
Pleurothallis cordifolia	–		+	hipodermis, idioblastos
Stelis sp.	–	adaxiales más desarrolladas	+	hipodermis, idioblastos
Rodriguezia lehmannii	+	adaxiales más desarrolladas	–	hipodermis lignificada, idioblastos, haces fibrosos

las epífitas de ramita *Hirtzia escobarii* y *Rodriguezia lehmannii*, las células esclerenquimáticas se encuentran mas concentradas hacia el polo del xilema y las células que se encuentran hacia el polo contrario del floema presentan paredes más gruesas (Fig 3D y 4E).

Cabe resaltar, que dentro de las especies estudiadas que no presentaron pseudobulbos se pueden evidenciar dos tendencias. En las especies de *Pleurothallis cordifolia*, *Stelis* sp. y *Epidendrum excisum*, la ausencia de engrosamientos a nivel del tallo se ve contrarrestada por el desarrollo de hojas suculentas con hipodermis adaxial y abaxial, además de la presencia de células con engrosamiento parietal secundario (Tabla 2). Por su parte, en las especies de *Elleanthus* la ausencia de pseudobulbos se ve acompañada por hojas delgadas que no presentan tejido de almacenamiento de agua, ni células esclerenquimáticas (Tabla 2).

Discusión. En este estudio se pudo evidenciar como especies más expuestas a los rayos solares presentan hojas y cutículas más gruesas, como el caso de la

epífitas de ramita (*Rodriguezia lehmannii* y *Hirtzia escobarii*). De la misma manera, individuos terrestres de las especies de *Elleanthus purpureus*, *Pleurothallis cordifoila* y *Stelis* sp., que se encontraban expuestos en los taludes de la carretera, presentaron hojas y cutículas significativamente más gruesas (R. Arévalo, unpubl. data). Según Kurzweil *et al.* (1995), las células epidérmicas de mayor tamaño pueden estar relacionadas con la función de reserva de agua (Oliveira & Sajo 1999), especialmente en aquellas hojas que no poseen tejidos de almacenamiento, como es el caso de *E. purpureus*. Se ha demostrado que los tricomas glandulares en especies de *Pleurothallis* no están involucrados en procesos de toma de agua y nutrientes por parte de la hoja (Benzing & Pridgeon 1983). Sin embargo, la función de estas estructuras podría consistir en la secreción de mucílago, que actuaría reduciendo la transpiración (Pridgeon 1982), o contribuyendo con la absorción de agua (Raciborski 1898), y de cierta manera compensando la ausencia de tallos engrosados/pseudobulbos.

Puesto que en Orchidaceae los estomas raramente ocurren hundidos (Rasmussen 1987), estos suelen exhibir otros caracteres xeromórficos. A menudo los estomas se encuentran rodeados por proyecciones cuticulares externas que forman una cámara supraestomática que protege contra la pérdida excesiva de agua y gases (Eames & MacDaniels 1925, Metcalfe 1963, Machado & Barros 1995). Estas cámaras supraestomáticas mantienen un compartimiento de aire húmedo que permite reducir la transpiración y son comunes en orquídeas epifitas que enfrentan altas temperaturas y poca disponibilidad de agua (Rosso 1966, Rasmussen 1987), como el caso de la epífita de ramita *Rodriguezia lehmannii*.

Los grupos de células esclerenquimáticas, o haces fibrosos, confieren resistencia mecánica a las hojas en casos de deshidratación y suelen presentarse en las hojas de orquídeas especializadas a sobrevivir en hábitats xerofíticos (Withner *et al*. 1974). Por consiguiente, era de esperarse la presencia de estos haces en las epífitas de ramita, aunque también fueron observados a nivel del mesófilo en la epífita de humus *Oncidium abortivum* (Tabla 2).

La abundancia de células del mesófilo con vacuolas bastante grandes que ocupan la mayor parte del volumen celular en la epífita de corteza *Epidendrum excisum* y en las de ramita (*Rodriguezia lehmannii* y *Hirtzia escobarii*), se presenta junto con espacios intercelulares reducidos, donde las cámaras subestomáticas son de menor tamaño que las células adyacentes del mesófilo. Éstas características foliares suelen estar asociadas a plantas con metabolismo CAM (Nelson *et al*. 2005). La presencia de idioblastos en el mesófilo estaría relacionada con la retención de agua y/o el soporte mecánico, evitando el colapso celular durante la desecación (Pridgeon 1982). Adicionalmente, se ha argumentado que los idioblastos con rafidios, que se hayaron en las epífitas de corteza (excepto *Stelis* sp.), pueden estar relacionados con el balance iónico y osmoregulación de la planta (Bonates 1993).

El engrosamiento en las paredes de las células esclerenquimáticas que conforman la vaina vascular podría conferirle mayor resistencia mecánica a las hojas en casos de deshidratación. La presencia de estos engrosamientos estaría relacionada entonces con la menor disponibilidad de agua que existe en un hábito

epífito extremo, como el que se presenta en los ejes más pequeños y expuestos de los árboles hospederos–las ramitas.

El análisis de las hojas estudiadas indica la presencia de caracteres que pueden ser interpretados como adaptaciones a la economía de agua. En cada una de las plantas estudiadas se presenta una particular combinación de estos, aunque no se evidencia una clara diferenciación en la anatomía de las plantas según la categoría ecológica a la que pertenecen. Sin embargo, las epifitas de ramita se diferencian de las demás al presentar una hipodermis lignificada y varios de los caracteres propios de plantas adaptadas a crecer en ambientes con baja disponibilidad de recursos hídricos: (1) hojas y cutículas bastante gruesas; (2) estomas con cámaras supraestomáticas (en el caso de *Rodriguezia lehmannii*); (3) haces fibrosos; (4) hipodermis abaxial y adaxial; (5) células con grandes vacuolas; (6) vainas vasculares gruesas; y (7) teniendo en cuenta las características celulares del mesófilo, muy probablemente metabolismo CAM. Estas características deben facilitarles la colonización de la zona más expuesta a alta luminosidad y con mayor fluctuación en la disponibilidad de agua que puede encontrarse en un árbol hospedero—las ramitas. Los resultados encontrados apoyan la idea que estas plantas constituyen un ejemplo de extrema modificación morfológica y fisiológica al epifitsimo.

Literatura citada

Atwood, J.T. 1986. The size of the Orchidaceae and the systematic distribution of epiphytic orchids. Selbyana 9: 171–186.

Ayensu, E.S. & N.H. Williams. 1972. Leaf anatomy of *Palumbina* and *Odontoglossum,* subgenus *Osmoglossum.* Amer. Orchid Soc. Bull. 41: 687–696.

Benzing, D.H. & A.M. Pridgeon. 1983. Foliar trichomes of Pleurothallidinae (Orchidaceae): Functional significance. Amer. J. Bot. 70(2): 173–180.

Benzing, D.H. & D.W. Ott. 1981. Vegetative reduction in epiphytic Bromeliaceae and Orchidaceae: Its Origin and significance. Biotropica 13: 131–140.

Benzing, D.H. & J.T. Atwood. 1984. Orchidaceae: ancestral habitats and current status in forest canopies. Syst. Bot. 9: 155–165.

Benzing, D.H. 1986. The genesis of orchid diversity: emphasis on floral biology leads to misconceptions. Lindleyana 1(2): 73–89.

Benzing, D.H. 1989. The evolution of epiphytism. Vol. 76, Pp. 15–40 en: U. Lüttge (ed.), Vascular plants as epiphytes: evolution and ecophysiology. Springer-Verlag, Berlin.

Benzing, D.H. 1990. Vascular epiphytes. Cambridge University Press, Cambridge.

Benzing, D.H., W.E. Friedman, G. Peterson & A. Renfrow. 1983. Shootlessness, velamentous roots, and the pre-eminence of Orchidaceae in the epiphytic biotope. Amer. J. Bot. 70(1): 121–133.

Bonates, L.C.M. 1993. Estudos ecofisiológicos de Orchidaceae da Amazonia II – Anatomia ecológica foliar de espécies com metabolismo CAM de uma campina da Amazônia Central. Acta Amazonica 23(4): 315–348.

Campos Leite, V.M. & P.L. Oliveira. 1987. Morfoanaomia foliar de *Cattleya intermedia* (Orchidaceae). Napaea 2: 1–10.

Dressler, R.L. 1981. The orchids: Natural History and Classification. Harvard University Press, Cambridge.

Dressler, R.L. 2005. How many orchid species? Selbyana 26(1): 155–158.

Eames, A.J. & L.H. MacDaniels. 1925. An introduction to plant anatomy. McGraw-Hill Book Company Inc, Nueva York.

Ferreira, J.L.B. 1992. Anatomia foliar de espécies da subtribo Pleurohallidinae (Orchidaceae). Tesis de Maestría. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Franceschi, V.R. & H.T. Horner Jr. 1980. Calcium oxalate crystals in plants. Bot. Rev. 46: 361–427.

Garnier E. & G. Laurent. 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. New Phytol. 128: 725–736.

Godoy, R. & C. Costa. 2003. Anatomia foliar de quarto espécies do gênero *Cattleya* Lindl. (Orchidaceae) do Planalto Central Brasileiro. Acta Bot. Brasil. 17(1): 101–118.

Goh C.J. & M. Kluge 1989. Gas exchange and water relations in epiphytic orchids. Cap. 6, Pp. 139–163 en: L. Ulrich (ed), *Vascular Plants as epiphytes, Evolution and ecophysiology*. Springer-Verlag, Berlin.

Herr, J.M. 1993. Clearing techniques for the study of vascular plant tissues in whole structures and thick sections. Vol. 5, Pp. 63–84 en: C.A. Goldman, P.L. Hauta, M.A. O'Donnell, S.E. Andrew and R. Vna der Heiden (eds), Tested studies for laboratory teaching. Proceedings of the 5th Workshop/Conference of the Association for Biology Laboratory Education (ABLE).

Johansson, D.A. 1975. Ecology of epiphytic orchids in west African rain forest. Amer. Orchid Soc. Bull. 44: 125–136.

Kauschik, P. 1982. Anatomy of *Aerides* (Orchidaceae) and its ecological and taxonomical bearing. Phytomorphology 40: 157–166.

Kress, W.J. 1986. The systematic distribution of vascular epiphytes: an update. Selbyana 9: 2–22.

Kurzweil, H., H.P. Linder, W.L. Stern & A.M. Pridgeon. 1995. Comparative vegetative anatomy and classification of Diseae (Orchidaceae). Bot. J. Linn. Soc. 117: 171–220.

Leiria, D.P.S. 1997. Anatomia foliar das especies nativas do gênero *Oncidium* Sw., Seção *Synsepala* (Orchidaceae) ocorrentes no morro Santana (POA) – RS. Tesis de Maestría. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Machado, R.D. & C.F. Barros. 1995. Epidermis and epicuticular waxes of *Syagrus coronata* leaflets. Canad. J. Bot. 73: 1947–1952.

Metcalfe, C. 1963. Comparative Anatomy as a Modern Botanical Discipline. Vol. 1. Advance in Botanical Research. Academic Press, Londres y Nueva York.

Mohana-Rao, P.R. & S.M. Khasim. 1987. Anatomy of three species of *Bulbophyllum* (Orchidaceae) with comments on their ecological adaptability and taxonomy. Proc. Indian Acad. of Sci. Pl. Sci. 97: 391–397.

Nelson, E.A., T.L. Sage & R.F. Sage. 2005. Functional leaf anatomy of plants with crassulacean acid metabolism. Funct. Plant Biol. 32: 409–419.

Olaunji, O.A. & R.O. Nengim. 1980. Ocurrence and distribution of tracheoidal elements in the Orchidaceae. Bot. J. Linn. Soc. 80: 357–370.

Oliveira, V.D.C & M.D.G. Sajo. 1999. Anatomia foliar de especies epifitas de Orchidaceae. Revista Brasil. Bot. 22(3): 365–374.

Pridgeon, A.M. 1981. Absorbing trichomes in the

Pleurothallidinae (Orchidaceae). Amer. J. Bot. 68(1): 64–71.

Pridgeon, A.M. 1982. Diagnostic anatomical characters in the Pleurothallidinae (Orchidaceae). Amer. J. Bot. 69(6): 921-938.

Pridgeon, A.M. 1986. Anatomical adaptations in Orchidaceae. Lindleyana 1: 90–101.

Raciborski, M. 1898. Biologische Mittheilungen aus Java. Flora 85: 325–361.

Rasmussen, H. 1987. Orchid stomata structure, differentiation, funtion, and phylogeny. Vol. IV, Pp. 105–138 en: J. Arditti (ed), Orchid biology: reviews and perspectives. Cornell Universiy Press, Nueva York,

Reich P.B., D.S. Ellsworth, M.B. Walters, J.M. Vose, C. Gresham, J.C. Volin & W.D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80(6): 1955–1969.

Rosso, S.W. 1966. The vegetative anatomy of the Cypripedioideae (Orchidaceae). Bot. J. Linn. Soc. 59: 309–341

Sinclair, R. 1990. Water relations in orchids. Vol. V, Pp. 63–120 en: J. Arditti (ed.), Orchid biology–reviews and perspectives. Timber Press, Portland, Oregon.

Stern, W.L., M.W. Morris, W.S. Judd, A.M. Pridgeon & R.L. Dressler. 1993. Comparative vegetative anatomy and systematics of Spiranthoideae (Orchidaceae). Bot. J. Linn. Soc. 113: 161–197.

Wattendof, J.A. 1976. Third type of raphide crystal in the plant kingdom: Six-sided raphides with laminated sheaths in *Agave americana* L. Planta 130: 303–311.

Widholzer, C.F. 1993. Morfo-anatomia foliar de espécies do gênero *Sophronites* Ldl. (Orchidaceae) ocorrentes o Rio Grande do Sul, Brasil. Dissertação de Mestrado. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Withner, C.L., P.K. Nelson, & P.J. Wejksnora. 1974. The anatomy of orchids. Pp. 267-334 en: C.L. Withner (ed), The Orchids: scientific studies. John Wiley, Nueva York,

Zotz G, V. Thomas & W. Hartung. 2001. Ecophysiological consequences of differences in plant size: abscisic acid relationships in the epiphytic orchid *Dimerandra emarginata.* Oecologia 129:179–185.

CONSERVATION OF MADAGASCAR'S GRANITE OUTCROP ORCHIDS: THE INFLUENCE OF FIRE AND MOISTURE[1]

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Abstract. Is there a difference in response to disturbance, or resource limitation, by similar taxa based on micro-site habitat heterogeneity? For this study we examined how fire and moisture availability influences the distribution of terrestrial and lithophytic orchids specific to Madagascar's granite outcrops (inselbergs). We compared orchid density in an area with a complex mosaic of burned and non-burned vegetation patches (three years after the event). Lithophytic species (subtribe Angraecinae) were sensitive to fire, but tolerant of limited moisture availability, and had a uniform distribution pattern associated with vegetation mat size. In contrast, most terrestrial species (subtribe Habenariinae) were not impacted by fire, but were limited to slopes with high water seepage, and had a clumped distribution pattern. The results suggest varying ecological niches between orchid subtribes, and among species, occurring on shared substrate. Within the larger area, we also compared three inselbergs with different fire disturbance history. One site with potential for lightning based fires, but absence of anthropogenic fires, had the greatest diversity (subtribes, genera, and species) of orchids and the highest occurrence of species restricted to a single site. For land management purposes it is inappropriate to assume that inselberg specific orchids will have the same response to environmental stressors. Angraecinae orchids are especially at risk from human associated fire disturbance and should be regarded as indicators for future conservation efforts.

Resumé. Quelle est la réponse aux perturbations, et la limitation de l'humidité, par des taxons similaires basés sur l'hétérogénéité des micro-site de l'habitat? Pour cette étude nous avons examiné comment la disponibilité de feu et de l'humidité influence la répartition des orchidées endémiques malgaches spécifique des affleurements de granit (inselbergs). Trois ans après le passage du feu, nous avons compare les modes de distribution et l'abondance d'orchidées dans un habitat d'une mosaïque complexe de brûlures, en tenant compte de la densité par rapport à l'intensité des dégâts d'incendie et de la disponibilité de l'humidité. Les espèces du sous-tribu Angraecinae ont été sensibles au feu, mais tolérant à une disponibilité limitée de l'humidité. orchidées Angraecinae avait un modèle uniforme de la distribution influencée par la taille du tapis de végétation. Les espèces de la sous-tribu Habenariae étaient tolérants de feu, mais limitée aux pentes rocheuses humides par des écoulements d'eau. Habenariae ont été randomizes regroupés en masses compactes, influencée par des facteurs non encore identifiés. Les résultats suggèrent l'existence de différentes stratégies de survie des espèces. Il serait inexact de penser que les orchidées voisins sur un substrat de granite aurait la même réponse à des facteurs environnementaux ou de perturbation. orchidées Angraecoid sur les inselbergs sont exposés à des menaces spécifiques et doivent être considérées comme des espèces indicatrices de la conservation est prioritaire à l'avenir.

Key Words / Mots-clés: conservation; inselberg de granit; Le Madagascar; Orchidaceae; Angraecinae; Habenariinae

Introduction. Madagascar is considered to be an international conservation priority area because of the high concentration of endemism and biodiversity threatened with extinction (Bosser *et al.* 1996, Barthlott & Porembski 1998, Du Puy & Moat 1998, Myers *et al.* 2000). The majority of conservation efforts to date have focused on evergreen humid forests, or deciduous, seasonally dry forests (Bosser *et al.* 1996, Du Puy & Moat 1998), rather than granite outcrops known as inselbergs - a habitat noted for unique flora that includes orchids, succulents, carnivorous, and desiccant tolerant species (Bosser *et al.* 1996, Barthlott & Porembski 1998, Fischer & Theisen 2000, Porembski & Barthlott 2000).The lack of inselberg protection is in part explained by the difficulty in identifying priority habitat at the landscape scale (based on vegetation type and subtle habitat characteristics) using satellite imagery (Du Puy & Moat 1998). There is also less social incentive to protect inselbergs because of the absence of charismatic species (such as lemurs) that appeal to ecotourism and environmental organizations (Leader-Williams & Dublin 2000), however recent multi-taxa analyses recognize the conservation importance of sites that were previously neglected such as habitat with sparse forest cover (ie central plateau massifs) or smaller sized forest remnants (Bosser *et al.* 1996, Kremen *et al.* 2008). A different challenge with managing, and maintaining, inselberg biodiversity is due to the limited number of ecological studies available (Barthlott & Porembski 1998, Fischer & Theisen 2000, Porembski & Barthlott 2000), especially those that investigate the role of disturbance on plant communities specific to this habitat type (Bosser *et al.* 1996, Porembski *et al.* 2000, Yates *et al.* 2003).

Fire is one of the most common forms of habitat disturbance within Madagascar and is primarily associated with human activities rather than lightning (Bloesch 1999, Kull 2000). Culturally, fire is used for agriculture, cattle grazing, deforestation, and even as form of political protest (Bloesch 1999, Kull 2000, Kull 2002, Klein 2004). Restriction of human based fires is often at odds with the interests of villagers, except in instances where the local belief systems (ie taboos against burning holy sites) either directly or indirectly benefits conservation efforts (Bloesch 1999, Klein 2004). Even though fire has been a part of the Malagasy landscape for many generations, there is still

much debate about the impact of fire disturbance on native habitat and the appropriate fire management approach for the future (Bloesch 1999, Kull 2000, Kull 2002, Klien 2004, Raxworthy & Nussbaum 2006). Some scientific studies estimate that deforestation accounts for the rapid loss of 40% to 80% of Madagascar's original forest cover (Du Puy & Moat 1998, Harper *et al.* 2007), while other studies indicate that habitat destruction has been grossly overestimated (Kull 2000, Kull 2002, Klein 2004).

The historic landscape of the highlands of Madagascar was most likely a non-continuous mix of schlerophyllous forest, shrubland, and montane heathland with seasonal fires associated with lightning (Raxworthy & Nussbaum 1996, Bloesch 2002, Burney *et al.* 2003). The introduction of human set fires, extinction of megafauna, and the spread of livestock grazing dramatically changed the fire regime; fire intensity and frequency increased and resulted in the emergence of homogenous prairie grasslands as the dominant vegetation type (Bosser *et al.* 1996, Raxworthy & Nussbaum 1996, Du Puy & Moat 1998, Bloesch 1999, Fischer & Theisen 2000, Bloesch 2002, Burney *et al.* 2003). The conversion of mountain forest to grassland is considered to be nearly irreversible (Bloesch 1999). Within Madagascar, inselbergs have been described as naturally protected against fire with the bare rock around their base that acts a barrier to inhibit the spread of fire from adjacent locations (Nilsson & Rabakonandrianina 1988). The assessment of inselbergs as refuge for fire sensitive species in a fire prone landscape is consistent with observations of rock outcrops in Australia (Hopper 2000, Clarke 2002). This observation does not exclude potential lightning based fires from occurring; other studies have noted extensive fires from this ignition source (Yates *et al.* 2003). However high elevation areas, or other habitat with sparse or stunted vegetation (ie inselbergs), have a reduced fuel capacity that tends to result in lower intensity fires restricted to patches (Bloesch 2002) in contrast to dynamics of fires in dense forests (Clarke 2002).

We addressed this ecological knowledge gap by examining the impact of fire disturbance, and moisture availability, on flora specific to inselbergs of Madagascar. Orchids were used as indicator species of this habitat type because of the complexity of their

ecological relationships and high levels of endemism (Nilsson & Rabakonandrianina 1988, Nilsson *et al.* 1992, Pettersson & Nilsson 1993, Jacquemyn *et al.* 2005, Linder *et al.* 2005). We also recognized the lack of ecological research on Malagasy orchids, aside from those related to evolution or pollination biology (Bosser *et al.* 1996). For the first portion of the study we included a general examination of orchid biodiversity and fire history of the Mt. Angavokely area, followed by a comparison of species occurrence and turnover within, and between, three inselbergs. We then performed a more in-depth analysis of orchid abundance on the inselberg that was most recently burned. Overall we determined that some endemic orchid species were highly sensitive to fire disturbance, while others were more influenced by moisture availability, in an area with high micro-site habitat heterogeneity.

Methods

Site Description – Our primary (in-depth) study took place on the Ambatolava inselberg of the Mt. Angavokely Forest Station located in the central highlands of Madagascar, 40 km SE of Antananarivo (18°55'4" S, 47°43'9" E). The site is managed by Direction Générale des Eaux et Forêts. Over the past twenty years, significant orchid related research has occurred at Mt. Angavokely (Nilsson & Rabakonandrianina 1988, Nilsson *et al.* 1992, Pettersson & Nilsson 1993, Kluge *et al.* 1998, Kluge & Brulfert 2000), in part because of the presence of high orchid diversity with 101 species and 22 genera identified (Ceplitis & Broström 1998). The property is 695 ha in size, of which inselbergs with rupicolous shrubland vegetation comprise 110 ha, plantations of non-native pine and eucalyptus comprise 435 ha, and a mix of moist sub-montane forest and schlerophyllous forests occur in the remaining area (estimate of 1949 aerial photograph, Ceplitis & Broström 1998). The elevation ranges from 1,365m to 1,770m. Annual precipitation ranges from 1,500mm to 2,000mm, occurring 180 days of the year (Ceplitis & Broström 1998), with fog as the primary source of moisture during the dry season that spans from April to October (Kluge & Brulfert 2000).

The inselbergs of Madagascar have granite substrate, high levels of UV radiation and wind, temperature fluctuations, and thin nutrient poor soils (Barthlott & Porembski 1998, Fischer & Theisen 2000, Porembski & Barthlott 2000, Porembski *et al.* 2000). Inselbergs are often describe as 'biological islands' because their habitat characteristics and vegetation is exceptionally distinct from the surrounding landscape matrix (Porembski *et al.* 2000). The vegetation is dominated by species such as *Helichrysum* spp. and *Senecio* spp. (Asteraceae); *Kalanchoe synsepala* Baker (Crassulaceae); *Coleochloa setifera* (Ridl.) Gilly (Cyperaceae); *Aloe capitata* Baker (Liliaceae); *Angraecum sororium* Schltr. (Orchidaceae)*; Nematostylis anthophylla* A. Rich. (Rubiaceae); *Xerophyta dasyliriodes* Baker (Velloziaceae); and various specis of moss, lichen, cyanobacteria, carnivorous plants, and ferns (Barthlott & Porembski 1998, Fischer & Theisen 2000, Kluge & Brulfert 2000) (Fig. 1).

Fire History – Our study took place in 2004, three years after a fire that burned an estimated third of the Mt. Angavokely area. The timing allowed us to assess signs of species recovery or colonization post fire disturbance. We assessed fire history using historical site descriptions and photographs (Nilsson & Rabakonandrianina 1988, Nilsson *et al.* 1992, Pettersson & Nilsson 1993), and by interviewing local residents and elders of the neighbouring villages of Ambohijafy and Ambohimiadona. Additional photographs, taken post-fire by J.J. Randriamanindry were also used as reference. Within the Mt. Angavokely forest area, we specifically researched the fire history of three of the largest inselbergs (Ambatolava, Ambatomisondrotra, Angavobe).

The first inselberg, Ambatolava, 1645m, had a fire that occurred in November 200l. The fire was believed to be human caused because it occurred during a period of political instability. Villagers may have used arson as a form of protest, or as an attempt to expand agropastoral fires during civil unrest (Bloesch 1999, Kull 2002). The intensity of the fire was also influenced by the surrounding plantations of pyrophytic *Eucalyptus robusta* Sm., *Pinus patula* Schltdl. and Cham., and *Pinus khasya* Royle ex Hook. f.. with a higher fuel load accumulation (dry needles, fallen leaves, and bark) than the neighboring sections of native forest. In addition, the fire was ignited towards the lower side of Ambatolava and resulted

Figure 1. **A.** The orchid *Angraecum sororium* on an unburned vegetation mat in the foreground. Severely burned vegetation mats are neighboring in the background. Whitman, 2003. **B.** The orchid *Cynorkis uniflora* on a wet slope amongst charred vegetation remains. Randriamanindry, 2003.

in an uphill burn pattern of higher intensity (Bloesch 1999) in contrast to lightning based fires (ignition at the highest point) that tend to have a downhill burn pattern of reduced destructive potential. Prior to the 2001 fire, Ambatolava was noted for its high density of *A. sororium* (Nilsson & Rabakonandrianina 1988).

The second inselberg, Ambatomisondrotra, 1650m, was the site of a high intensity fire that occurred in the early 1990's (also believed to be human caused). Prior reports noted that the area once had similar vegetation composition as the unburned regions of the Ambatolava inselberg (unpubl. data). The fire resulted in near complete removal of larger shrubs from the mid to upper portion of the inselberg. Ambatomisondrotra had a more uniform burn pattern than Ambatolava because of the steepness of the slope (Bloesch 1999) and from observations of the site shortly after the event (Randriamanindry, pers. comm. 2004).

The third inselberg Angavobe, 1755m, was a site with unique cultural significant that influenced the fire regime history. Local villagers described social *fady*, a taboo based belief system, that discouraged people from setting fire to the forest because of the presence of royal tombs (featuring pre and post Christianity stylization) and sacrificial stones (Randriamanindry, pers. comm. 2004). The oldest tomb was associated with Andrianajavonana, "the noble who disappeared" a Merina king of the Central Highlands estimated to be from the 14th century (Randriamanindry, pers. comm. 2004). Commoners were socially prohibited from harming the forest on Angavobe nearest the tombs because it was considered to be property of royalty even after death (Randriamanindry, pers. comm. 2004). A secondary social incentive was reinforced in the 1800's during the reign of Queen Ranavalona I when the Angavobe caves were used as refuge from slavery and religious prosecution (Randriamanindry, pers. comm. 2004). This social belief system created small protected areas of native vegetation where lightning, but not human based fires, have existed for generations.

General Orchid Survey – We conducted a rapid biodiversity assessment of orchid occurrence (presence or absence of species) at the Ambatolava, Angavobe, and Ambatomisondrotra inselbergs, and a more in-depth survey of orchid abundance specifically at Ambatolava. Plants were photographed and identified

to genus or species in the field. No plants were taken from the site or harmed due to the endangered status of many endemic orchids. Species lists and images were then compared to botanical inventories conducted by the University of Antananarivo, Madagascar; Uppsala University, Sweden (Ceplitis & Broström1998); the Missouri Botanical Gardens W³TROPICOS database; and species descriptions by Perrier (1939 & 1941), Du Puy *et al.* (1999), Hermans *et al.* (2007), and Cribb & Hermans (2010).

Patterns of Orchid Diversity. – For the larger-scale portion of this study we compared the species present on all the three inselbergs (γ-diversity), per inselberg (α-diversity), and between inselbergs (β-diversity), using data from the general orchid survey. We were especially interested in the beta-diversity measures of species turnover between sites (Ambatolava, Ambatomisondrotra, and Angavobe) that were similar in elevation range, climate, geological history, and that shared a regional species pool, yet possessed differing fire history. Our goal was to gain a preliminary understanding of how gradients of historical habitat disturbance, rather than elevation (Jacquemyn *et al.* 2005), might influence the distribution patterns of orchids. The inselbergs (going east to west) were arranged: Angavobe to Ambatomisondrotra to Ambatolava, and ran roughly in a line 5km in length and separated by a minimum of 2 km from each other. We used three equations (Jaccard distance, Sørensen distance, and Simple Matching Coefficent) based on the applied recommendations for presence/absence data noted by Anderson *et al.* (2011). All indices used emphasized distance or dissimilarity between sites (value of 0 meaning identical species composition). The beta-diversity was calculated as follows: Jaccard distance $d_J [1 - a/(a + b + c)]$; Sørensen distance $d_S = [1 - 2a/(2a + b + c)]$; and Simple Matching Coefficient, $d_{SM} = 1 - (a + e) / (a + b + c + e)$; where a is a species presence at both sites (11), b (10) or c (01) is a species present at only one of the two sites, and e (00) is a species missing from both sites but found within the greater area (Anderson *et al.* 2011).

In-depth Survey of Orchid Abundance. - For the site specific (more intensive) portion of this study we focused on the Ambatolava Inselberg, the only location with burn patterns that could be clearly evaluated in

relation to a fire with a known occurrence date (2001). At the Ambatolava site we surveyed seven 50m x 2m line transects located between 1460m to 1645m in elevation. We drew the transect lines across all accessible regions using a 50m survey tape, compass, and GPS (Garmin Geko 301). The line transects were a minimum distance of 75m apart and ran horizontally from south to north on the central ridge or eastern slope (the western side was inaccessible). Within 1m on either side of the transect line per vegetation mat we counted the number of orchids present based on distinct above ground growth, rather than the number of canes, stems, or underground growth. We defined a vegetation mat in a generalized manner that included monocotyledonous mats dominated by *C. setifera* or *X. dasyliriodes*, ephemeral flush vegetation, moss cushions, or charred humus or vegetation remains (Barthlott & Porembski 1998, Fischer & Theisen 2000, Kluge & Brulfert 2000, Porembski & Barthlott 2000, Porembski *et al.* 2000).

We identified flowering species along the transect lines and categorized all orchids as lithophytic (epilithic) or terrestrial. Lithophytic orchids are found primarily on granite (or occasionally as epiphytes), and are slow growing with drought tolerant waxy leaves and aerial roots. Many lithophytic species in Madagascar are associated with the subtribe Angraecinae (species such as *Angraecum sororium* or *Jumellea rigida* Schltr.*)* or from the subtribe Aerangidinae with species such as *Aerangis ellisii* (B.S. Williams) Schltr.. Terrestrial orchids are also found on inselbergs and occasionally grasslands, with tuberous roots and periods of underground dormancy during the dry season. Many terrestrial orchids are from the subtribe Habenariinae (such as *Cynorkis uniflora* Lindl.*)* or Brownleeinae (such as *Brownleea coerulea* Harv. ex Lindl.).

Environmental Factors – We surveyed environmental factors that were hypothesised to play a significant role in the micro-site distribution patterns of orchids. The first environmental factor we examined in the field was based on the impact of fire, categorized by severity and defined as:

- *Non-burned*: areas with no signs of fire or significant heat damage;
- *Minor to moderate*: areas with a mosaic of heat or fire damage to no more than two thirds of the

vegetation, upper branches of plants may have had some heat damage or fire effects but little to no signs of ground level fire;

- *Severe*: majority of the pre-fire vegetation charred or dead with signs of high heat intensity and fire effects at ground level.

The second factor examined was the influence of moisture availability (separate from water acquired directly from precipitation, fog, or dew accumulation on leaves) defined as:

- *Wet:* areas with continuous water seepage, dark granite slick from moisture saturation and cyanobacteria, with thick layers of moss or ephemeral flush vegetation (Barthlott & Porembski, 1998; Porembski *et al.* 2000; Fischer & Theisen, 2000).
- *Dry:* areas with no sign of water seepage, dry soil, and granite above and below the vegetation mat light in color.

Statistical Analyses – We analyzed the evenness of vegetation mat categories (combinations of fire severity and moisture availability) using a two by three contingency table. The relationship between orchid density per m² and fire severity (non-burned, minor-moderate, and severe) was analyzed using a non-parametric Kruskal-Wallis test; moisture availability (with or without presence of seasonal water seepage) was analyzed using a two-sample Wilcoxon test. We analyzed the number of orchids in relation to the size of non-burned vegetation mats with linear regression, if there was a significant positive relationship then a pre-fire population estimate would be made. Next, we analyzed the interspecies interaction for orchids in all areas using linear correlation. Lastly, we described the spatial distribution (random, even, or clumped) using the Index of Dispersion and Index of Clumping. All analyses were specific to species, genus, or subtribe depending on the sample size and evenness between groups. All statistical analyses had α=0.05 and were performed with R software version 2.3.1 (www.r-project.org).

Results

General Orchid Survey – A total of seventeen orchid species from seven genera and six subtribes (plus two unusual white morphs) were found on one or more of

TABLE 1. General survey of orchid presence and absence on three inselbergs at the Mt. Angavokely Forest Station.

		Angavobe	Ambatolava	Ambatomisodrotra
Aerangidinae	*Aerangis ellisii*	X	X	
Angraecinae	*Angraecum sororium*	X	X	X
Angraecinae	*Jumellea maxillarioides*	X		
Angraecinae	*Jumellea rigida*		X	X
Brownleeinae	*Brownlea coerulea*	X		
Bulbophyllinae	*Bulbophyllum* sp. 1	X		
Habenariinae	*Cynorkis angustipetala*		X	
Habenariinae	*Cynorkis baronii*			X
Habenariinae	*Cynorkis coccinelloides*			X
Habenariinae	*Cynorkis fastigiata*	X	X	X
Habenariinae	*Cynorkis gibbosa*	X		X
Habenariinae	*Cynorkis gibbosa**	X		
Habenariinae	*Cynorkis lilacina*		X	
Habenariinae	*Cynorkis perrieri*	X		
Habenariinae	*Cynorkis uniflora*	X	X	X
Habenariinae	*Cynorkis uniflora**	X		
Habenariinae	*Cynorkis* sp. 1	X		
Habenariinae	*Cynorkis* sp. 2			X
Polystachyeae	*Polystachya rosea*	X		

* Unusual white flower morph

the inselbergs surveyed (Table 1 & 2). The orchids present were estimated to represent 17% of the overall Orchidaceae diversity across all habitats of the greater Mt. Angavokely area (Ceplitis & Broström1998), and represented 17 out of 33 (51%) of the inselberg specific species found in Madagascar (Fischer & Theisen 2000). The most common orchids encountered at all three inselbergs included *Cynorkis fastigiata* Thouars, *Cynorkis uniflora*, and *Angraecum sororium*. Some species were found at two locations, such *Aerangis ellisii*, *Cynorkis gibbosa* Ridl., and *Jumellea rigida*. However, a total of eleven orchids (65%) were restricted to a single site (Table 1 & 2).

The Ambatolava inselberg was the only site with *Cynorkis angustipetala* Ridl., *Cynorkis lilacina* Ridl., and an unidentified *Cynorkis sp.* Thouars.. Ambatomisondrotra was the only site with *Cynorkis baronii* Rolfe, or *Cynorkis coccinelloides* Schltr., and was unique in that it was also the site of the largest colony of *C. uniflora* noted. We also observed a distinct absence of Angraecinae species (including seedlings) from the entire upper region of the inselberg that had been burned; the exception being a *J. rigida* near the unburned forest edge. Angavobe, the area

with lightning but not human associated fires, had the highest diversity of orchids unique to a single site, including *Brownleea coerulea*, unidentified *Bulbophyllum sp*. Thouars, *Cynorkis perrieri* Schltr., unidentified *Cynorkis sp*. Thouars, *Jumellea maxillarioides* (Ridl.) Schltr., *Polystachya rosea* Ridl. and unusual white morphs of *Cynorkis gibbosa* Ridl. and *Cynorkis uniflora* Lindl.. Angavobe was notable as the location with the most massive *A. sororium* surveyed with individual canes >4m in length (max. height of 1.5m noted elsewhere) and with >250 nodes present that typically mark annual growth (one pair of leaves per year). We estimated the largest *A. sororium* (individual or colony) at Angavobe to be hundreds of years old.

Patterns of Orchid Diversity - The transition of species diversity (β-diversity) using Jaccard distance (d_J), Sørensen distance (d_S), and Simple Matching Coefficient (d_{SM}) was estimated for paired site combinations. Each individual inselberg was represented by a single letter as follows: Ambatolava (L) – *burned 2001*, Ambatomisondrotra (M) – *burned 1990's*, and Angavobe (G) –*human fires absent*. The

Table 2. Patterns of orchid diversity on inselbergs.

			Unique occurrence count		
Total Diversity of Inselbergs Surveyed			SUBTRIBE	GENUS	SPECIES
Combined list of all species found on the three inselbergs, Angavobe, Ambatolava, and Ambatomisondrotra			6	7	17
Diversity per Inselberg	*Fire History*		SUBTRIBE	GENUS	SPECIES
Total for Angavobe	Absence of human associated fires		6	7	11
Total for Ambatomisondrotra	Human associated fire in 1990's		2	3	8
Total for Ambatolava	Human associated fire in 2001		3	4	7
Orchid Distribution, Patterns of Overlap or Isolation					
Description	*Distribution*	*Code*	SUBTRIBE	GENUS	SPECIES
Widespread	Angavobe, Ambatolava, & Ambatomisodrotra	GLM	2	3	3
Variable	Angavobe & Ambatolava	GL	1	1	1
Variable	Angavobe & Ambatomisodrotra	GM	0	0	1
Variable	Ambatolava & Ambatomisodrotra	LM	0	0	1
Site specific	Angavobe only	G	3	3	6
Site specific	Ambatolava only	L	0	0	2
Site specific	Ambatomisondrotra only	M	0	0	3

results are summarized as: L & M - ($d_J = 0.64$, $d_S = 0.47$, $d_{SM} = 0.41$), L & G ($d_J = 0.71$, $d_S = 0.56$, $d_{SM} = 0.59$), and M & G ($d_J = 0.73$, $d_S = 0.58$, $d_{SM} = 0.65$). All indices revealed a similar trend; paired burned sites (L & M) had a lower β-diversity distance score (reduced turnover and greater similarity of species present) than pairing of inselbergs with burned and non-burned fire history. The inclusion of information on species ***absence*** (relative to γ-diversity) resulted in the greatest dissimilarity between inselberg combinations as noted with the Matching Coefficient ($d_{SM\,max}$ - $d_{SM\,min} = 0.24$), compared to Jaccard distance ($d_{J\,max} - d_{J\,min} = 0.10$) and Sørensen distance ($d_{S\,max} - d_{S\,min} = 0.11$) that emphasized joint species presence. Joint absences also revealed that the combined species diversity for burned sites (Ambatolava and Ambatomisondrotra) was missing six out of the seventeen possible inselberg orchids surveyed from the larger area (30% of the γ-diversity).

In-depth Survey of Orchid Abundance – At Ambatolava, we surveyed 700 m², and counted 45 vegetation mats totaling 450.7 m². The vegetation mats varied greatly in shape, size (5.35m²±SE0.83) and distance (2.65m²±SE0.74) from each other edge to edge. We counted a total of 45 lithophytic orchids

from the subtribe Angraecinae (36 *A. sororium* and nine *Jumellea rigida*) and 310 terrestrial orchids from the subtribe Habenariinae (one *Cynorkis angustipetala* Ridl., 52 *C. fastigiata* Thou., and 257 *C. uniflora*). All species were endemic to Madagascar, except for *C. fastigiata,* a species indigenous to Madagascar, Comoros, the Mascarenes, and Seychelles (Perrier 1939 & 1941). Both subtribes were present at an equal number of sites (fourteen out of forty five vegetation mats), but the distribution by individual species was unpredictable. Some orchids were relatively abundant, but restricted to a limited number of locations (such as *C. uniflora* with 257 individuals at eight sites). We then found it necessary to group the orchids together by subtribe for a more even comparison of the taxa.

Environmental Factors – We categorized 15 of the vegetation mats as non-burned (118m² = 26%), 11 with minor to moderate fire damage (113m² = 25%), and 19 (219.70² = 49%) as having severe fire damage. Non-burned and severely burned vegetation mats were observed directly neighboring each other. The moisture of the slopes also varied, 25 mats (285.8m² = 63%) ranged from being damp to having continuous water seepage, and the other 20 mats (164.90m² =36%) were extremely dry. The 2x3 contingency table analysis

showed a significant difference in the evenness of the fire/moisture combinations of vegetation mat categories (Pearson's Chi Square= 8.246, p=0.016), but there was no clear pattern to predict which areas would be burned (wet with severe fire damage was the most common combination). However, other factors might have influenced fire patterns such as wind exposure, steepness of slope, or distance to the plantation tree line. Vegetation mats that were the least impacted by fire were in depressions or fissures in the rock; sheltered from wind; or were isolated from each other.

Orchid Response to Environmental Factors – For the lithophytic Angraecinae orchids, fire severity was highly significant Fig 1. A. (all species, Kruskal-Wallace chi-squared 18.6445, df = 2, p-value = <0.001; *A. sororium*, Kruskal-Wallace chi-squared 19.025, df = 2, p-value = <0.001) There was no significant relationship between orchid density and moisture availability by subgroup or by species. The orchids had the highest density (0.32 per m², equal to 84% of those surveyed) in unburned areas, followed by (0.06 per m², equal to 16% of those surveyed) in minor to moderately burned areas, and no individuals in severely burned areas. The significant results for the terrestrial Habenariinae were opposite from that of the lithophytic Angraecineae. Fire was not significant, yet moisture availability was highly significant Fig 1. B. (all species, Wilcox rank sum, w= 149, p-value = 0.005; *C. uniflora,* Wilcox rank sum, w= 170, p-value = 0.006). The exception to the Habenariinae trend was *C. fastigata*, which was not sensitive to moisture availability, but was to fire (Kruskal-Wallis chi-squared = 8.210, df = 2, p-value = 0.016). Terrestrial Habenariinae orchids had the highest density average (1.1 per m², equal to 99% of those surveyed) in wet areas, including locations with severe fire damage. Species level analyses were non-significant for the least common of the orchids surveyed, *C. angustipetala* (Habenariinae) and *J. rigida* (Angraecinae).

Orchid Distribution - Angraecinae had a significant relationship between the number of orchids and the size of a non-burned vegetation mat (adjusted R² = 0.473, p-value = 0.003, n=15), but Habenariinae did not, even in wet non-burned areas. Prefire population estimates were made for Angraecinae (but could not be made for Habenariinae) based on the linear

equation (number of orchids= 0.251 * mat size + 0.562). We estimated that 67% of the lithophytic Angraecinae orchids at Ambatolava perished during the 2001 fire.

There was no significant interaction between the two orchid subtribes (Angraecinae and Habenariinae); including results from a post-hoc analysis of positive environmental factors (non-burned sites, wet sites, and non-burned wet sites). There was a positive association between *A. sororium* and *C. fastigata* (Kendall's Rank Correlation, tau = 0.590, p-value = <0.001) and to a lesser extent between *A. sororium* and *J. rigida* (Kendall's Rank Correlation, tau = 0.273 , p-value = 0.049). Angraecinae had a uniform pattern of distribution (Index of Dispersion = 0.436, Index of Clumping = -0.564) with the highest density in non-burned areas. Habenariinae had a clumped pattern of distribution (Index of Dispersion = 8.711, Index of Clumping = 7.711) with the highest density in wet areas.

Discussion

General Orchid Survey – The diversity of endemic orchids on inselbergs, and the vulnerability of some species to anthropogenic disturbance, reinforces the conservation importance of this unique habitat type. The most compelling observation from the general orchid survey was the higher biodiversity at Angavobe, a site with lightning based fires but absence of anthropogenic fires, compared to Ambatomisondrotra (fire in 1990's) or Ambatolava (fire in 2001). Angavobe was also the site with the highest number of species (six) and genera (three) restricted to a single site. One concern for the future is whether or not Angavobe will continue to be regarded as an important cultural site, or if the traditional knowledge of restricted burning near tombs and sacrificial stones will be lost with the passing of generations or the immigration of individuals from different regions who are unaware of this social *fady*. Additional conservation protection of the Angavobe inselberg, ideally in partnership with neighboring villagers, environmental organizations, and regional land managers, is highly recommended.

Spatial Patterns of Orchid Diversity – We found that sites with a shared history of fire disturbance (Ambatomisondrotra and Ambatolava) had species composition more similar to each other than

combinations with differing fire history regardless of spatial orientation; a pattern most noticeable when factoring in joint-absences of species (Matching Coefficet). Our average Sørensen distance (0.53) was more similar to the average value (0.5) noted on African (Cameroon, Gabon, Guinea) inselbergs across a range of plant formations (Parmentier *et al.* 2005), than the beta-diversity of orchids (0.25) observed across elevational gradients on the neighboring island of Réunion (Jacquemyn *et al.* 2005), suggesting that our results may be more of a reflection of inselberg plant communities than patterns specific to orchids. A larger scale analysis of Malagasy orchid beta-diversity, especially in relation to gradients of habitat disturbance, is recommended for the future.

Orchid Response to Environmental Factors – Lithophytic Angraecinae orchids were fire sensitive and were interpreted to rely on other adaptations to successfully tolerate temperature and moisture fluxuations and to compete against dominant inselberg vegetation such as *X. dasyliriodes* or *A. capitata*. Angraecinae survival adaptations include environmental stress tolerance (Kluge *et al.* 1998, Kluge & Brulfert 2000), year round photosynthesis, and the ability to grow taller than neighboring shrubs or forbs to compete for resources. Inter and intraspecific competition may explain the uniform distribution pattern noted.

We were surprised that Angraecinae orchids were so sensitive to heat damage given that Porembski & Barthlott (2000) noted that some drought tolerant monocots were protected from fire by the dense growth of leaves and roots covering the pseudostem. However we did observe that *A. sororium* had more signs of heat damage than fleshy succulents (ie *Aloe capitata)* of similar height in the same area. Post-fire regeneration by *A. sororium* in areas of moderate fire damage was only noted at the center of exceptionally large orchid patches. Angraecinae orchids may be more vulnerable to fire due to their year round foliage, aerial roots, and tolerance for the driest slopes. They also tend to acquire a thick cushion of moss, leaves, and organic material around their base (Kluge & Brulfert 2000) that helps to hold moisture, but may also increases the available fuel biomass (intensity of fire) per vegetation mat.

An important conservation question raised by this study is: "how long will it take for Angraecinae to recover from human associated fire damage?" Populations may be resilient against disturbance events by the longevity of reproductively successful individuals, but only if the habitat conditions remain suitable for their offspring and enough unique individuals remain to prevent a genetic bottleneck. The largest Angraecinae observed flowering (*A. sororium*) was interpreted to be very long lived (multi-decade, or even multi-century at Angavobe), an age span consistent with other inselberg species (Porembski & Barthlott 2000). However no Angraecinae seedlings were found repopulating burned mats three years or even >10 years post-fire despite the relatively high availability of seed sources from multiple individuals within the area (unpubl. data). Inhibited establishment of seedlings post-fire has also been described for other non mat-forming inselberg species (Porembski & Barthlott 2000) and is a threat to endemic flora as the rate of human caused fires increases. For future studies it would be useful to gain a more expansive and long-term (multi-generational) understanding of metapopulation dynamics of Angraecinae orchids, especially compared to Habenariinae, to establish a stronger estimate of recovery time post-disturbance.

The terrestrial Habenariinae orchids of our study were limited primarily by their micro-habitat preference for wet slopes rather than by fire. Prior studies of *C. uniflora* also noted the highest orchid abundance in locations with continuous or ephemeral water seepage (Nilsson *et al.* 1992, Fischer & Theisen 2000). The smaller size (10-30cm), lack of water storing fleshy leaves or pseudobulbs, and the rapid season-specific growth of these orchids may explain their moisture dependency. Future studies that include other environmental factors found to be significant for inselberg flora, such as soil pH, depth, or distance to native forest (Parmentier 2003), might explain why Habenariinae orchids displayed such clumped patterns of distribution and abundance independent from vegetation mat size or co-occurrence of Angraecinae species.

The enigmatic orchid of this study was *C. fastigiata,* with habitat preferences similar to *A. sororium*. One possible explanation is that both orchids share similar mycorrhizal fungi preferences

for germination; or that *C. fastigiata* fills a different habitat or successional niche than *C. uniflora* or *C. angustipetala*. This result raises the debate as to whether species should be grouped together based on phylogenetic similarity or by habitat needs.

Within Madagascar, it has been noted that Habenariinae orchids (genus *Cynorkis* and *Habenaria*) and similar terrestrial orchids of various other subtribes (genus *Liparis, Eulophia, Benthamia, Lissochilus, Disa, Satyrium*) benefit from occasional fires and sustainable disturbance that create "orchid meadows" with reduced interspecies competition (Rabetaliana *et al.* 1999, Bloesch *et al.* 2002). This trend has also been described globally for terrestrial orchids in locations such as Australia (Yates *et al.* 2003), and South Africa (Linder *et al.* 2005), with some pyrogenic orchids (such as *Cyanicula ashbyae* Hopper and A.P.Br.) only flowering within the first year post-fire (Yates *et al.* 2003). Fire may be less of a threat to Habenariinae orchids because of their tuberous roots, underground dormancy during the dry season, and tolerance of thinner topsoil that can occur after burning and erosion.

A different question raised by this study is: "why did the two orchid subtribes have different survival strategies, or ecological niches, within a shared habitat if their distribution was independent from each other?" One explanation is that when fire occurs, it creates an irregular mosaic-like pattern of fire disturbance, allowing for different stages of succession per vegetation mat with reduced competition for resources. Another perspective is that inselbergs might support both equilibrium and non-equilibrium based plant communities within a small spatial scale and that the differences between orchid subtribes are a reflection of larger species composition trends. Angraecinae might be considered to be a part of an equilibrium (or late-successional) based community, influenced by biotic competition year round; whereas Habenariinae might be within a non-equilibrium, ephemeral flush vegetation community heavily influenced by abiotic conditions or stochastic disturbances (Porembski *et al.* 2000).

Conclusion. From this study it can be concluded that it is inappropriate to assume that all species of inselberg Orchidaceae have the same response to

fire or habitat moisture requirements. Lithophytic Angraecinae were sensitive to fire, but tolerant of limited moisture availability, and had a uniform pattern of distribution. In contrast, terrestrial Habenariinae were not as affected by fire but were limited to slopes with high water seepage and had a clumped pattern of distribution. Lithophytic Angraecinae orchids are considered to be at risk and an increase in the frequency or severity of fire may negatively affect sustainable population sizes. Further conservation of inselberg habitat and its unique flora is strongly recommended.

Literature Cited

Anderson, M.J., T.O. Crist, J.M. Chase, M. Vellend, B.D. Inouye, A.L. Freestone, N.J. Sanders, H.V. Cornell, L.S. Comita, K.F. Davies, S.P. Harrison, N.J.B. Kraft, J.C. Stegen & N.G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14: 19-28.

Barthlott, W. & S. Porembski. 1998. Diversity and phytogeographical affinities of Inselberg vegetation in tropical Africa and Madagascar. Pp. 119-129 *in:* C.R. Huxley, J.M. Lock & D.F. Cutler (eds.), Chorology, taxonomy and ecology of the floras of Africa and Madagascar. Kew, Kew Publishing.

Bloesch 1999. Fire as a tool in the management of a savanna/dry forest reserve in Madagascar. Appl. Veg. Sci. 2: 117-124.

Bloesch, U., Bosshard, A.P. Shachenmann, H. Rabetaliana & F. Klötzli. 2002. Biodiversity of the subalpine forest-grassland ecotone of the Andringitra Massif,

Madagascar. Pp. 165-175 *in:* C. Körner & E.M. Spehn (eds.), Mountain biodiversity- a global assessment. London, Parthenon Publishing.

Bosser, J.M., Du Puy, D.J. & P. Phillipson. 1996. Madagascar and surrounding islands. Pp. 103-107 *in:* IUCN/SSC Orchid Specialist Group; Status Survey and Conservation Action Plan – Orchids. IUCN Switzerland and UK.

Burney, D.A., G.S. Robinson & L.P. Burney. 2003. Sporomiella and the late Holocene extinctions in Madagascar. P Natl. Acad. Sci. 100: 10800-10805.

Ceplitis, A. & A. Broström. 1998. Vascular plant diversity in a mountain rainforest at Station Forestière d'Angavokely, Madagascar. Minor field study report 039. Uppsalla, Committee for Tropical Ecology Uppsalla University.

Clarke, P.J. 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? J. Biogeogr. 29: 677-684.

Cribb, P.J. & J. Hermans. 2010. Field guide to the orchids of Madagascar. Kew, Kew Publishing.

De La Bathie, H.P. 1939, 1941. Flora of Madagascar, 49th Family - Orchids. Paris, France. Translated by S. Beckman. 1981. Volume I and II combined. Lodi, California.

Du Puy, D. & J.F. Moat. 1998. Vegetation mapping and classification in Madagascar (using GIS): implications and recommendations for the conservation of biodiversity. Pp 97 -117 *in:* C.R. Huxley, J.M. Lock, & D.F. Culter (eds.), Chronology, taxonomy and ecology of the floras of Africa and Madagascar. Kew, Kew Publishing.

Du Puy, D., P.J. Cribb, J. Bosser, J. Hermans & C. Hermans. 1999. The Orchids of Madagascar. First edition. Kew, Royal Botanical Gardens.

Fischer, E. & I. Theisen. 2000. Vegetation of Malagasy inselbergs. Pp. 259-276 *in*: S. Porembski & W. Barthlott (eds.), Inselbergs biotic diversity of isolated rock outcrops in tropical and temperate Regions. Berlin, Springer-Verlag.

Jacquemyn, H., C. Micheneau, D.L. Roberts & T. Pailler. 2005. Elevation gradients of species diversity, breeding system and floral traits of orchid species on Réunion Island. J. Biogeogr. 32: 1751-1761.

Klein, J. 2004. Fiddling while Madagascar burns. Deforestation discourses and highland history. Norw. J. Geog. 58: 11-22.

Kluge, M., B.Vinson & H. Ziegler. 1998. Ecophysiological studies on orchids of Madagascar: incidence and plasticity of crassulacean acid metabolism in species of the genus Angraecum Bory. Plant Ecol. 135: 43-57.

Kluge, M & J. Brulfert. 2000. Modes of photosynthesis in plants of Mt. Angavokely (Central High Plateau of Madagascar). Pp. 161-174 *in:* S. Porembski and W. Barthlott (eds.), Inselbergs biotic diversity of isolated rock outcrops in tropical and temperate regions. Berlin, Springer-Verlag.

Kull, C.A. 2000. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environ. Hist. 6: 423-450.

Kull, C.A. 2002. Madagascar aflame: landscape burning as peasant protest, resistance, or a resource management tool? Pol. Geogr. 21: 927-953.

Kremen, C., A. Cameron, A. Moilanen, S.J. Philips, C.D. Thomas, H. Beentje, J. Dransfield, B.L. Fischer, F. Glaw, T.C. Good, G.J. Harper, R.J. Hijams, D.C. Lees, E. Louis Jr., R.A. Nussbaum, C.J. Raxworthy, A. Razafimpahanana, G.E. Schatz, M. Vences, D.R. Vieties, P.C. Wright & M.L. Zjhra. 2008. Aligning conservation priorities across taxa in Madagscar with High-Resolution Planning Tools. Science 320: 222-226.

Harper, G.J., M.K. Steininger, C.J. Tucker, D. Juhn & F. Hawkins. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34: 325-333.

Hopper, S.D. 2000. Creation of conservation reserves and managing fire on granite outcrops – a case of study of Chiddarcooping Nature Reserve in Western Australian wheatbelt. J. Roy. Soc. W. Aust. 83: 173-186.

Hermans, J., C. Hermans, D. du Puy, P.J. Cribb & J. Bosser. 2007. Orchids of Madagascar. Second edition. Kew, Kew Publishing.

Leader-Williams, N & H.T. Dublin. 2000. Charismatic megafauna as 'flagship species'. Pp 53-81 *in:* A. Entwistle & N. Dunstone (eds.), Priorities for the Conservation of Mammalian Diversity: Has the Panda Had its Day? Cambridge, Cambridge University Press.

Linder, H.P., H. Kurzweil & S.D. Johnson. 2005. The Southern African orchid flora: composition, sources and endemism. J. Biogeogr. 32: 29-47.

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

Nilsson, L.A. & E. Rabakonandrianina. 1988. Hawk-moth scale analysis and pollination specialization in the epilithic Malagasy endemic *Aerangis ellisii* (Reichenb. fil.) Schltr. (Orchidaceae.) Bot. J. Linn. Soc. 97: 49-61.

Nilsson, L.A., E. Rabakonandrianina, R. Rotaharivelo & J.J. Randriamanindry. 1992. Long pollinia on eyes: hawk-moth pollination of *Cynorkis uniflora* Lindley (Orchidaceae) in Madagascar. Bot. J. Linn. Soc.109: 145-160.

Parmentier, I. 2003. Study of the vegetation composition in three inselbergs from continental equatorial Guinea (western central Africa): effects of site, soil factors, and position relative to forest fringe. Belg. J. Bot. 136: 63-72.

Pettersson, B. & L.A. Nilsson. 1993. Floral variation and deceit pollination in *Polystachya rosea* (Orchidaceae) on an inselberg in Madagascar. Opera Bot. 121: 237-245.

Porembski, S. & W. Barthlott. 2000. Granitic and gneissic outcrops (Inselbergs) as centers of diversity for desic-cation-tolerant vascular plants. Plant Ecol. 151: 19-28.

Porembski, S., R. Seine & W. Barthlott. 2000. Factors controlling species richness of Inselbergs. Pp. 451-481 *in:* S. Porembski and W. Barthlott (eds.), Inselbergs biotic diversity of isolated rock outcrops in tropical and temperate regions. Berlin, Springer-Verlag.

Rabetaliana, H., M. Randriambololona & P. Schachenmann. 1999. The Andringitra National Park in Madagascar. Unasylva 50: 25-30.

Raxworthy, C.J. & R.A. Nussbaum. 1996. Montane amphibian and reptile communities in Madagascar. Conserv. Biol. 10: 750-756.

Yates, C.J., S.D. Hopper, A. Brown & S. van Leeuwen. 2003. Impact of two wildfires on endemic granite outcrop vegetation in Western Australia. J. Veg. Sci. 14: 185-193.

ORCHID GENERA LECTOTYPES

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Abstract. The typification of Orchidaceae genera has been disorganized since currently there is not an up to date central database to track these nomenclatural publications. A listing of published generic typifications for Orchidaceae is provided.

Key words: Nomenclature, Typification, Orchidaceae

Introduction. When an orchid genus is described it in based on a specific species known as the type species. When that species is described the name is based on a specific specimen, the holotype. The International Code of Botanic Nomenclature (ICBN) states: The application of names of taxa of the rank of family or below is determined by means of nomenclatural types (types of names of taxa). The application of names of taxa in the higher ranks is also determined by means of types when the names are ultimately based on generic names (Article 7.1) and a nomenclatural type (typus) is that element to which the name of a taxon is permanently attached, whether as the correct name or as a synonym. The nomenclatural type is not necessarily the most typical or representative element of a taxon (Article 7.2).

There are many kinds of types defined in the ICBN. Loosely used the term type can have many meanings and should be clarified.

- **nomenclatural type.** The element to which the name of a taxon is permanently attached (Art. 7.2).
- **holotype.** The one specimen or illustration used by the author or designated by the author as the nomenclatural type (Art. 9.1).
- **isotype.** A duplicate specimen of the holotype (Art. 9.3).
- **syntype.** Any specimen cited in the protologue when there is no holotype, or any of two or more specimens simultaneously designated as types (Art. 9.4).
- **isosyntype.** A duplicate of a syntype (Art. 9.10).

- **paratype.** A specimen cited in the protologue that is neither the holotype nor an isotype, nor one of the syntypes if two or more specimens were simultaneously designated as types (Art. 9.5).
- **neotype.** A specimen or illustration selected to serve as nomenclatural type if no original material is extant or as long as it is missing (Art. 9.6).
- **lectotype.** A specimen or illustration designated from the original material as the nomenclatural type if no holotype was indicated at the time of publication, or if it is missing, or if it is found to belong to more than one taxon (Art. 9.2).
- **epitype.** A specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name cannot be identified for the purpose of precise application of the name of a taxon (Art.9.7).

Why is this important? Many genera were described before a type designation was required and a type species was not designated. Publication on or after 1 January 1958 of the name of a new taxon of the rank of genus or below is valid only when the type of the name is indicated (Art. 37.1). However the ICBN does provide that if the name of a new genus reference to one species name only, or the citation of the holotype or lectotype of one previously or simultaneously published species name only, even if that element is not explicitly designated as type, is acceptable as indication of the type (Art. 37.3). This leaves many genera without type species.

Recognizing that all taxa do not have a type the ICBN provides that one can be selected:

•   If no holotype was indicated by the author of a name of a species or infraspecific taxon, or when the holotype has been lost or destroyed, or when the material designated as type is found to belong to more than one taxon, a lectotype or, if permissible a neotype as a substitute for it may be designated (Art. 9.9).

There are additional rules for typification of taxa that require the proper use of terminology. Article 9.8. states that The use of a term defined in the ICBN as denoting a type, in a sense other than that in which it is so defined, is treated as an error to be corrected (for example, the use of the term lectotype to denote what is in fact a neotype).

The type of typification is dependent on availability of original material:

•   A **lectotype** is a specimen or illustration designated from the **original material** as the nomenclatural type, if no holotype was indicated at the time of publication, or if it is missing, or if it is found to belong to more than one taxon (Art. 9.2).
•   A **neotype** is a specimen or illustration selected to serve as nomenclatural type if **no original material is extant**, or as long as it is missing (see also Art. 9.6).

Further guidance is given by the ICBN for the selection of a new type

•   In lectotype designation, an isotype must be chosen if such exists, or otherwise a syntype if such exists. If no isotype, syntype or isosyntype (duplicate of syntype) is extant, the lectotype must be chosen from among the paratypes if such exist. If no cited specimens exist, the lectotype must be chosen from among the uncited specimens and cited and uncited illustrations which comprise the remaining original material, if such exist (Art. 9.10).
•   If no original material is extant or as long as it is missing, a neotype may be selected. A lectotype always takes precedence over a neotype (Art. 9.11), except when the holotype or a previously designated lectotype has been lost or destroyed

and it can be shown that all the other original material differs taxonomically from the destroyed type, a neotype may be selected to preserve the usage established by the previous typification (Art. 9.14).

Some authors in the past have listed a type species for a genus even when the original author did not designate a type. This had the inadvertent effect of lectotypification or neotypification of the genus. The ICBN how requires that the designation of a new type use of the term "lectotypus" or "neotypus" and location of the type.

•   On or after 1 January 1990, lectotypification or neotypification of a name of a species or infraspecific taxon by a specimen or unpublished illustration is not effected unless the herbarium or institution in which the type is conserved is specified (Art.9.20).
•   On or after 1 January 2001, lectotypification or neotypification of a name of a species or infraspecific taxon is not effected unless indicated by use of the term "lectotypus" or "neotypus", its abbreviation, or its equivalent in a modern language (Art.9.21).

Currently typification is not adequately tracked in the online taxonomic databases, such as, Index Nominum Genericorum (ING), International Plant Names Index (IPNI), Tropicos, World Checklist of Selected Plant Families. The authors encourage the database owners to add this valuable information since earlier type choices have priority. An excellent example of a database is the Linnaean Plant Name Typification Project, based at The Natural History Museum (London), that has been collating and cataloguing information on published type designations for Linnaean plant names and, where none exists, has been collaborating with specialists in designating appropriate types. For each species, the database provides the place of publication, stated provenance, the type specimen (or illustration) and a reference to where the type choice was published, and an indication of the current name of the taxon within which Linnaeus' original binomial is now placed.

The Typification of Orchidaceae Genera

Aa Rchb.f., Xenia Orchid., 1: 18 (1854).
TYPE SPECIES: *A. paleacea* (Kunth) Schltr. (*Ophrys paleacea* Kunth) selected by Schlechter, Repert. Spec. Nov. Regni Veg., 11: 147 (1912); Baillon, Dict. Bot., 4: 309 (1892); and Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 1 (1871).

Acampe Lindl., Fol. Orchid., 4: Acampe, 1 (1853).
TYPE SPECIES: *A. multiflora* (Lindl.) Lindl. (*Vanda multiflora* Lindl.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 9 (1871).
LECTOTYPE: *A. rigida* (Buch.-Ham. ex Sm.) P.F.Hunt (*Aerides rigida* Buch.-Ham. ex Sm.) designated by Seidenfaden, Bot. Mus. Leafl., 25(2): 54 (1977); and indirectly by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 890 (1991).

Aceras R.Br., Hortus Kew., ed. 2, 5: 191 (1813).
LECTOTYPE: *A. anthropophorum* (L.) R.Br. (*Ophrys anthropophora* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 437 (1989).

Achroanthes Raf., Med. Repos., ser. 2, 5: 352 (1808)
TYPE SPECIES: *A. unifolia* (Michx.) Raf. (*Malaxis unifolia* Michx.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 22 (1871).

Achroanthes Raf. Amer. Monthly Mag. & Crit. Rev., 2: 268 (1818) and 4: 195 (1819).
TYPE SPECIES: *Malaxis ophioglossoides* Muhl. ex Willd. (*Arethusa ophioglossoides* Muhl.) selected by Garay & H.R. Sweet, J. Arnold Arbor., 53(1): 515 (1972).

Acianthera Scheidw., Allg. Gartenzeitung, 10(37): 292 (1842).
NEOTYPE SPECIES: *A. punctata* Scheidw. designated by Luer, Monogr. Syst. Bot. Missouri Bot. Gard., 20: 12 (1986).

Acineta Lindl., Edwards's Bot. Reg., 29(Misc.): 67 (1843).
TYPE SPECIES: *A. superba* (Kunth) Rchb.f. (*Anguloa superba* Kunth) selected by G. Gerlach, Gen. Orch., 5: 399 (2009).

Acianthus R.Br., Prodr. Fl. Nov. Holland., 321 (1810).
TYPE SPECIES: *A. exsertus* R.Br. selected by N. Hallé, Fl.

Nouvelle Caledonie & Depend., 8: 418 (1977).
TYPE SPECIES: *A. fornicatus* R.Br. selected by M.A. Clements, Austral. Orchid Res., 1: 9 (1989) and Jones, D.L. & Clements, M.A., Lindleyana, 2: 157 (1987).

Acostaea Schltr., Repert Spec. Nov. Regni Veg. Beih, 19: 22, 283 (1923).
LECTOTYPE: *A. costaricensis* Schltr. designated by Summerhayes, Index Nom. Gen. (Pl.), 1: 16 (1967) card #64/24402 (1967); and Pupulin, Bot. J. Linn. Soc., 163: 116 (2010).

Aerides Lour., Fl. Cochinch., 2: 516 & 525 (1790).
LECTOTYPE: *A. maculosa* (Wight) Lindl. (*Saccolabium speciosum* Wight) designated by Christenson, Kew Bulletin, 41(4): 837 (1986).

Aeridium Salisb., Trans. Hort. Soc. London, 1: 295 (1812).
TYPE SPECIES: *A. odorum* Salisb. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 67 (1871).

Aerobion Kaempf. ex Spreng. Syst Veg. 3: 679 (1826).
LECTOTYPE: *A. superbum* (Thouars) Spreng. (*Angraecum superbum* Thouars) designated by Garay, Kew Bull., 28(3): 496 (1973).

Altensteinia Kunth, Nov. Gen. Sp. Pl., 1: 332 (1816).
TYPE SPECIES: *A. fimbriata* Kunth selected by Reichenbach f., Xenia Orchid., 1: 18 (1854).

Amalia Rchb.f., Herb. Nomen., 52 (1841).
LECTOTYPE: *Bletia grandiflora* La Llave designated by Garay & H.R. Sweet, J. Arnold Arb., 53: 515 (1972).

Amparoa Schltr., Repert. Spec. Nov. Regni Veg. Beih., 19: 64 (1923).
LECTOTYPE: *A. costaricensis* Schltr. designated by Pupulin, Bot. J. Linn. Soc., 163: 119 (2010).

Amphigena Rolfe, Fl. Cap. (Harvey), 5(3): 197 (1913).
TYPE SPECIES: *A. leptostachya* (Sond.) Rolfe (*Disa leptostachys* Sond.) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 236 (1951).

Amphorkis Thouars, Nouv. Bull. Sci. Soc. Philom. Paris, 1(19): 316 (1809).
LECTOTYPE: *A. inermis* Thouars designated by A. Richard, Mem. Soc. Hist. Nat., Paris, 4: 30 (1828).

Anacamptis Rich., De Orchid. Eur., 19, 25 (1817), and Mém. Mus. Hist. Nat., 4: 47, 55 (1818).

LECTOTYPE: *A. pyramidalis* (L.) Rich. (*Orchis pyramidalis* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 439 (1989).

Anathallis Barb.Rodr., Gen. Sp. Orchid, 1: 23, t. 470 (1877).

LECTOTYPE: *A. fasiculata* Barb.Rodr. designated by Garay, Orquideología, 9: 122 (1974).

Ancistrorhynchus Finet, Bull. Soc. Bot. France, 54(9): 44 (1907).

TYPE SPECIES: *A. recurvus* Finet selected by Summerhayes, Bot. Mus. Leafl., 11: 204, 213 (1944).

Anguloa Ruiz & Pavón, Fl. Peruv. Prodr., 118, t. 26 (1794).

TYPE SPECIES: *A. uniflora* Ruiz & Pavón selected by Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil., 1: 228 (1798) and Oakeley, Orchid Digest, 63(4 Suppl.): 3 (1999).

Ania Lindl., Gen. Sp. Orchid. Pl., 129 (1831).

TYPE SPECIES: *A. angustifolia* Lindl. selected by Senghas, Orchideen (Schlechter), ed. 3, 1: 863 (1984).
LECTOTYPE: *A. angustifolia* Lindl. designated by H. Turner, Orch. Monog., 6: 49 (1992) and P.J. Cribb, Gen. Orch., 4: 159 (2005).

Anochilus Schltr. ex Rolfe, Fl. Cap. (Harvey), 5:(3): 280 (1913).

TYPE SPECIES: *A. inversus* (Thunberg) Rolfe (*Ophrys inversa* Thunberg) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 238 (1951).

Appendicula Blume, Bijdr. Fl. Ned. Ind., 7: 297, t. 40 (1825).

TYPE SPECIES: *A. alba* Blume selected by N. Hallè, Fl. Nouvelle Caledonie & Depend., 8: 345 (1977).
LECTOTYPE: *A. alba* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 123 (1991).

Appendiculopsis Szlach., Fragm. Florist. Geobot., 3(Suppl.): 119 (1995).

LECTOTYPE: *A. stipulata* (Griffith) Szlach. (*Appendicula stipulata* Griffith) designated by Szlachetko, Fragm. Florist. Geobot., 3(Suppl.): 119 (1995).

Arachnis Blume, Bijdr. Fl. Ned. Ind., 8: 365, t. 26 (1825).

LECTOTYPE: *A. flos-aeris* (L.) Rchb.f. (*Epidendrum flos-aeris* L.) designated by J.J. Wood, Taxon, 48: 47 (1999).

Arethusa L., Sp. Pl. (Linnaeus), ed. 1, 2: 950 (1753).
TYPE SPECIES: *A. bulbosa* L. selected by Britton & Brown, Ill. Fl. N.U.S., ed 2, 1: 562 (1913).

Arundina Blume, Bijdr. Fl. Ned. Ind., 8: 401, t. 73 (1825).

LECTOTYPE: *A. speciosa* Blume designated by Garay & H.R. Sweet, Orchids S. Ryukyu Islands, 52 (1974).

Ascocentrum Schltr., Repert. Spec. Nov. Regni Veg. Beih., 1: 975 (1913).

LECTOTYPE: *A. miniatum* (Lindl.) Schltr. (*Saccolabium minitum* Lindl.) designated by Summerhayes, Index Nom. Gen. (Pl.), 1: 139 (1967) card #64/24468.
LECTOTYPE: *A. ampullaceum* (Roxburgh) Schltr. (*Aerides ampullacea* Roxburgh) designated by Christenson, Kew Bulletin, 41(4): 836 (1986).

Ascochilus Ridl., J. Linn. Soc., Bot., 32: 374 (1896).
LECTOTYPE: *A. siamensis* Ridl. designated by Garay, Bot. Mus. Leafl., 23(4): 161 (1972).

Auliza Salisb., Trans. Hort. Soc. London, 1: 294 (1812).

TYPE SPECIES: *A. ciliaris* (L.) Salisb. (*Epidendrum ciliaris* L.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 321 (1871).
TYPE SPECIES: *A. nocturna* (Jacq.) Small selected by Small, Fl. Miami, 56 (1913) and Garay & H.R. Sweet, J. Arnold Arbor., 53(4): 516 (1972).
LECTOTYPE: *A. nocturna* (Jacq.) Small (*Epidendrum nocturnum* Jacq.) **invalidly** designated by Hágsater & Soto Arenas, Gen. Orch., 4: 237 (2005).

Barbosella Schltr., Repert. Spec. Nov. Regni. Veg., 15: 259 (1918).

LECTOTYPE: *B. miersii* (Lindl.) Schltr. (*Pleurothallis miersii* Lindl.) designated by Angely, Fl. Analitica São Paulo, 6: 1282 (1973).
TYPE SPECIES: *B. gardneri* (Lindl.) Schltr. (*Pleurothallis gardneri* Lindl.) selected by Luer, Selbyana, 5: 386 (1981).

Bartholina, R.Br., Hortus Kew., ed. 2, 5: 194 (1813)
TYPE SPECIES: *B. pectinata* (Thunberg) R.Br. nom. illeg. (*Orchis pectinata* Thunberg nom. illeg.). This type

name is now considered a synonym of *Bartholina burmanniana* (L.) Ker-Gawler (*Orchis burmanniana* L.) which was lectotyped by H.P. Linder, Taxon, 48: 48 (1999).

Beloglottis Schltr., Beih. Bot. Centralbl., 37(2): 364 (1920).

TYPE *B. costaricensis* (Rchb.f.) Schltr. selected by Garay, Fl. Ecuador, 9: 253 (1978).

LECTOTYPE: *B. boliviensis* Schltr. designated superfluously by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982).

LECTOTYPE: *B. costaricensis* (Rchb.f.) Schltr. (*Spiranthes costaricensis* Rchb.f.) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 132 (2008).

Benthamia A.Rich., Mem. Soc. Hist. Nat. Paris, 4: 37 (1828).

LECTOTYPE: *B. latifolia* A.Rich. designated by P.J. Cribb, Gen. Orch., 2: 261 (2001).

Bifrenaria Lindl., Gen. Sp. Orchid. Pl., 152 (1832).

TYPE SPECIES: *B. atropurpurea* (Loddiges) Lindl. (*Maxillaria atropurpurea* Loddiges) selected by S. Koehler, Brittonia, 56(4): 318 (2004).

Bipinnula Comm. ex Juss., Gen. Pl., 65 (1789).

LECTOTYPE: *B. biplumata* (L.f.) Rchb.f. (*Arethusa biplumata* L.f.) designated by M.N. Correa, Gen. Orch., 3: 5 (2003).

Blephariglotis Raf., Fl. Tellur., 2: 38 (1837).

TYPE SPECIES: *B. albiflora* (Michx.) Raf. (*Orchis cilaris* var. *alba* Michx.) selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 556 (1913).

Bletia Ruiz & Pav., Fl. Peruv. Prodr., 119, t. 26 (1794).

TYPE SPECIES: *B. catenulata* Ruiz & Pav. selected by Britton & Millspaugh, Bahama Fl., 96 (1920).

Bletilla Rchb.f., Fl. Serres Jard. Eur., ser. 1, 8: 246 (1853).

TYPE SPECIES: *B. gebina* (Lindl.) Rchb.f. (*Bletia gebina* Lindl.) *typ. cons.*

TYPE SPECIES: *B. florida* (Salisb.) Rchb.f. (*Limodorum floridum* Salisb.) this name is currently considered a species of the genus *Bletia*, **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 423 (1871).

Bolusiella Schltr., Beih. Bot. Centralbl., 36(2): 105 (1918).

LECTOTYPE: *B. maudae* (Bolus) Schltr. (*Angraecum maudae* Bolus) designated by Butzin, Taxon, 32(4): 630 (1983).

Bontiana Petiver, Gaz., 1: 70, t. 44 (1704).

LECTOTYPE: *B. luzonica* Petiver designated by P.J. Cribb, Taxon, 48: 47 (1999).

Brachionidium Lindl., Fol. Orchid., 8: Brachionidium 8 (1859).

TTYPE SPECIES: *B. parvifolium* (Lindl.) Lindl. (*Restrepia parvifolia* Lindl.) selected by Garay, Canad. J. Bot., 34(4): 729 (1956).

Brachystele Schltr., Beih. Bot. Centralbl., 37(2): 370 (1920).

LECTOTYPE: *B. unilateralis* (Poiret) Schltr. (*Ophrys unilateralis* Poiret) designated by M.N. Corrêa, Fl. Patagónica, 8(2): 208 (1969) and Darwiniana, 11(1): 29 (1955); Cabrera, DAGI Publ. Técn., 1(6): 16 (1942); and Angely, Fl. Analitica São Paulo, 6: 1270 (1973)

LECTOTYPE: *B. guayanensis* (Lindl.) Schltr. (*Goodyera guayanensis* Lindl.) designated superfluously by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982).

Brasiliorchis R.B. Singer, S. Koehler & Carnevali, Novon, 17(1): 94 (2007).

LECTOTYPE: *B. picta* (Hook.) R.B. Singer, S. Koehler & Carnevali (*Maxillaria picta* Hook.) designated by R.B. Singer, Novon, 17: 97 (2007).

Brenesia Schltr., Repert. Spec. Nov. Regni Veg. Beih., 19: 200 (1923).

LECTOTYPE: *B. costaricensis* Schltr. designated by K. Barringer, Fieldiana, Bot., 17: 4 (1986).

Brownleea Harvey ex Lindl., J. Bot. (Hooker), 1: 16 (1842).

TYPE SPECIES: *B. parviflora* Harvey ex Lindl. selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 235 (1951).

Buchtienia Schltr., Repert. Spec. Nov. Regni Veg. Beih., 27: 33 (1929).

LECTOTYPE: *B. boliviensis* Schltr. designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 153 (2008).

Bulbophyllum Thouars, Hist. Orchid., Table 3, sub 3u, tt. 93-110 (1822).

LECTOTYPE: *C. subulata* Blume designated by Butzin, Taxon, 32(4): 630 (1983); and Royen, Orchid. High Mts. New Guinea, 455 (1979).

LECTOTYPE: *C. graminea* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 126 (1991); and P.J. Cribb, Gen. Orch., 4: 546 (2005).

Cestichis Thouars ex Pfitzer, Entwurf Anordn. Orch., 56, 101 (1887).

TYPE SPECIES: *C. caespitosa* (Lam.) Ames (*Epidendrum caespitosum* Lam.) selected by D.L. Jones & M.A. Clements, Orchidian, 15(1): 37 (2005).

Chaetocephala Barb.Rodr., Gen. Sp. Orchid., 2: 37, t. 802 (1881).

LECTOTYPE: *C. punctata* Barb.Rodr. designated by Summerhayes, Index Nom. Gen. (Pl.), 1 : 327 (1967) card #64/15508.

Chamaeangis Schltr., Beih. Bot. Centralbl., 36(2): 107 (1918).

LECTOTYPE: *C. gracilis* (Thouars) Schltr. (*Angraecum gracile* Thouars) designated by Garay, Bot. Mus. Leafl., 23(4): 165 (1972) and Butzin, Taxon, 32(4): 630 (1983).

Chamorchis Rich., De Orchid. Eur., 20, 27, 35 (1817), and Mém. Mus. Hist. Nat., 4: 49 (1818).

LECTOTYPE: *C. alpina* (L.) Rich. (*Ophrys alpina* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 445 (1989).

Cheirorchis Carrière, Gard. Bull. Straits Settlem., 7: 40 (1932).

TYPE SPECIES: *C. breviscapa* Carrière indirectly selected by Holttum, Kew Bull., 14: 272 (1960).

Chelonanthera Blume, Bijdr. Fl. Ned. Ind., 8: 382, t. 51 (1825).

TYPE SPECIES: *C. gibbosa* Blume NOTE: ING lists the name as lectotyped by Pfitzer, Pflanzenr., IV. 50 IIB (Heft 32): 141 (1907) but there is nothing listed in the article as a type.

Chitonanthera Schltr., Nachtr. Fl. Schutzgeb. Südsee, 193 (1905).

TYPE SPECIES: *C. angustifolia* Schltr. selected by Schuiteman & de Vogel, Blumea, 48: 511 (2003).

Chloidia Lindl., Gen. Sp. Orchid. Pl., 484 (1840).

TYPE SPECIES: *C. polystachya* (Sw.) Rchb.f. (*Serapias polystachya* Sw.) indirectly selected by Cogniaux, Fl. Bras. (Martius), 3(4): 276 (1895).

Chloraea Lindl., Quart. J. Sci. Lit. Arts, ser. 2, 1: 47 (1827).

LECTOTYPE: *C. virescens* (Willd.) Lindl. (*Cymbidium virescens* Willd.) designated by M.N. Correa, Fl. Patagonica, 7(2): 200 (1970) and Gen. Orch., 3: 7 (2003).

Christensonella Szlach., Mytnik, Górniak & Smiszek Polish Bot. J., 51(1): 57 (2006).

TYPE SPECIES: *C. paulistana* (Hoehne) Szlach., Mytnik, Górniak & Smiszek (*Maxillaria subulata* Hoehne) selected by M.W. Chase, Gen. Orchid., 5: 135 (2009).

Chrysoglossum Blume, Bijdr. Fl. Ned. Ind., 7: 337, t. 7 (1825).

TYPE SPECIES: *C. ornatum* Blume selected by J.J. Smith, Bull. Jard. Bot. Buitenzorg, ser. 2, 8: 3 (1912).

Chytroglossa Rchb.f., Hamburger Garten-Blumenzeitung, 19: 546 (1863).

LECTOTYPE: *C. aurata* Rchb.f. designated by Angely, Fl. Analítica São Paulo, 6: 1328 (1973).

LECTOTYPE: *C. marileoniae* Rchb.f. designated by Toscano, Lindleyana, 16(3): 189 (2001).

Cirrhaea Lindl., Edwards's Bot. Reg., 18: t. 1538 (1832).

TYPE SPECIES: *Cirrhaea dependens* (Loddiges) Loudon (*Cymbidium dependens* Loddiges) selected by G. Gerlach, Gen. Orch., 5: 404 (2009).

Cirrhopetalum Lindl., Gen. Sp. Orchid. Pl., 58 (1830), and Bot. Reg., 10: sub 832 (1824)

LECTOTYPE: *Bulbophyllum longiflorum* Thouars designated by Garay et al., Nord. J. Bot., 14(6): 614 (1994).

Cladobium Schltr., Beih. Bot. Centralbl., 37(2): 431 (1920).

LECTOTYPE: *C. ceracifolium* (Barb.Rodr.) Schltr. (*Spiranthes ceracifolia* Barb.Rodr.) designated by Burns-Balogh, Amer. J. Bot., 69: 1131 (1982).

TYPE SPECIES: *C. ceracifolium* (Barb.Rodr.) Schltr. indirectly selected by Garay, Bot. Mus. Leafl. 28: 330 (1982).

Cleisostoma Blume, Bijdr. Fl. Ned. Ind., 8: 362, t. 27 (1825).

TYPE SPECIES: *C. sagittatum* Blume selected by Garay, Bot. Mus. Leafl., 23(4): 168 (1972) and Christenson, Kew Bulletin, 41(4): 835 (1986).

LECTOTYPE: *C. sagittatum* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 893 (1991).

Cleistes Rich. ex Lindl., Gen. Sp. Orchid. Pl., 409 (1840).

TYPE SPECIES: *C. grandiflorum* (Aublet) Schltr. (*Limodorum grandiflorum* Aublet) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(1): 781 (1871).

Cnemidia Lindl., Edwards's Bot. Reg., 19: sub 1618 (1833).

TYPE SPECIES: *Cnemidia angulosa* Lindl. selected by Hooker f., Fl. Brit. Ind., 6: 92 (1890).

Coccineorchis Schltr., Beih. Bot. Centralbl., 37(2): 434 (1920).

LECTOTYPE: *C. corymbose* Kraenzl. designated by Burns-Balogh, Amer. J. Bot., 69: 1131 (1982).

LECTOTYPE: *C. cernua* (Lindl.) Garay (*Stenorrhynchos cernuum* Lindl.) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 158 (2008).

Codonorchis Lindl., Gen. Sp. Orch. Pl., 410 (1840).

LECTOTYPE: *C. lessonii* (d'Urville) Lindl. (*Epipactis lessonii* d'Urville) designated by M.N. Correa, Fl. Patagónica, 8(2): 191 (1969).

Coelia Lindl., Gen. Sp. Orchid. Pl., 36 (1830).

TYPE SPECIES: *C. bauerana* Lindl., nom. illeg.

TYPE SPECIES: *C. triptera* (Sm.) G. Don ex Steudel, (*Epidendrum tripterum* Sm.) selected by Steudel, Nomencl. Bot., 1: 394 (1841).

Coeloglossum Hartman, Handb. Skand. Fl., 323, 329 (1820).

TYPE SPECIES: *C. viride* (L.) Hartman (*Satyrium viride* L.) selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 552 (1913).

LECTOTYPE: *C. viride* (L.) Hartman designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 447 (1989).

Coelogyne Lindl., Collect. Bot., sub t. 33 (1821).

TYPE SPECIES: *C. cristata* Lindl. selected by C.H. Curtis, Orchids (Curtis), 82 (1950).

LECTOTYPE: *C. cristata* Lindl., designated by Butzin, Taxon, 32(4): 630 (1983); Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(12): 1767 (1990);

Cogniauxiocharis (Schltr.) Hoehne, Arq. Bot. Estado São Paulo, n.s., 1(6): 132 (1944).

LECTOTYPE: *C. glazioviana* (Cogn.) Hoehne (*Pelexia glazioviana* Cogn.) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 167 (2008).

Coilostylis Raf., Fl. Tellur., 4: 37 (1838).

LECTOTYPE: *C. emarginata* (L.) Raf. (*Epidendrum ciliare* L.) designated by Christenson, Richardiana, 3: 114 (2003).

Colax Lindl., Edwards's Bot. Reg., 29(Misc): 50 (1843).

TYPE SPECIES: *C. viridis* (Lindl.) Lindl. (*Maxillaria viridis* Lindl.) selected by Pupulin, Gen. Orchid., 5(2): 517 (2009).

Comparettia Poepp. & Endl., Nova Gen. Sp., 1: 42, t. 73 (1836).

TYPE SPECIES: *C. falcata* Poepp. & Endl. indirectly selected by Reichenbach f., Ann. Bot. Syst., 6: 688 (1863).

TYPE SPECIES: *C. saccata* Poepp. & Endl. selected by Britton & Wilson, Sci, Surv. Porto Rico, 5(2): 211 (1924).

LECTOTYPE: *C. falcata* Poepp. & Endl. designated by Angely, Fl. Analitica São Paulo, 6: 1321 (1973).

Comperia K. Koch, Linnaea, 22: 287 (1849).

TYPE SPECIES: *C. comperiana* (Steven) Asch. & Graebn. (*Orchis comperiana* Steven) selected by Ascherson & Graebner, Syn. Mitteleur. Fl., 3: 620 (1907); and Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 837 (1872) indirectly selected type species.

Corallorhiza Gagnebin, Acta Helv. Phys.-Math., 2: 61 (1755).

TYPE SPECIES: *C. innata* R.Br. indirectly selected by McVaugh, Fl. Novo-Galiciana, 16: 57 (1983).

LECTOTYPE: *C. trifida* (L.) Châtelain (*Ophrys corallorrhiza* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 449 (1989).

Corybas Salisb., Parad. Lond., 2: t. 83 (1807).

Type species: *Corysanthes bicalcarata* R.Br. This name is considered a synonym of *Corybas aconitiflorus* Salisb. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 883 (1872).

Corycium Sw., Kongl. Vetensk. Acad. Nya Handl., ser. 2, 21: 220, t. 3g (1800).
Type species: *C. crispum* (Thunberg) Sw. (*Arethusa crispa* Thunberg) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 883 (1872).
Type species: *C. orobanchoides* (L.f.) Sw. (*Satyrium orobanchoides* L.f.) selected by H. Kurzweil, Gen. Orch., 2: 23 (2001).

Corysanthes R.Br., Prodr. Fl. Nov. Holland., 328 (1810).
Type species: *C. fimbriata* R.Br. selected by Endlicher, Gen. Pl. (Endlicher), 218 (1837).

Costaricaea Schltr., Repert. Spec. Nov. Regni Veg. Beih., 19: 30 (1923).
Lectotype: *C. amparoana* Schltr. designated by Pupulin, Bot. J. Linn. Soc., 163: 122 (2010).

Cranichis Sw., Nov. Gen. Spec, Pl. Prodr., 8: 120 (1788).
Type species: *C. muscosa* Sw. selected by Acuña, Cat. Descr. Orquid. Cuba, 60: 48 (1939).

Cremastra Lindl., Gen. Sp. Orchid. Pl., 172 (1833).
Type species: *Cremastra wallichiana* Lindl. nom. illeg. This type name is now considered a synonym of *C. appendiculata* (D. Don) Makino (*Cymbidium appendiculatum* D. Don) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 908 (1872).

Crepidium Blume, Bijdr. Fl. Ned. Ind., 8: 387, t. 63 (1825).
Lectotype: *C. reedii* Blume designated by Seidenfaden, Dansk Bot. Arkiv, 33 (1): 43 (1978).
Type species: *C. reedii* Blume selected by Szlachetko, Fragm. Florist. Geobot. Suppl., 3: 123 (1995).

Cryptophoranthus Barb.Rodr., Gen. Sp. Orchid. Nov., 2: 79, t. 476 (1881).
Type species: *C. fenestratus* (Barb.Rodr.) Barb.Rodr. (*Pleurothallis fenestrata* Barb.Rodr.) selected by Acuña, Cat. Descr. Cuba, 60: 115 (1939).
Lectotype: *C. fenestratus* (Barb.Rodr.) Barb.Rodr. designated by Butzin, Taxon, 32(4): 631 (1983); and

Angely, Fl. Analitica São Paulo, 6: 1279 (1973).

Cryptostylis R.Br., Prodr. Fl. Nov. Holland., 317 (1810).
Type species: *C. erecta* R.Br. selected by N. Hallé, Fl. Nouvelle Caledonie & Depend., 8: 481 (1977).
Lectotype: *C. longifolia* R.Br., designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75: 1021 (1990).

Cybelion Spreng., Veg. (Sprengel), ed. 16, 3: 679, 721 (1826).
Type species: *C. pulchellum* (Kunth) Spreng. (*Ionopsis pulchella* Kunth) selected by Garay & H.R. Sweet, J. Arnold Arbor., 53(4) 518 (1972).

Cymbidiella Rolfe, Orchid Rev., 26: 58 (1918).
Lectotype: *C. flabellata* (Thouars) Rolfe (*Cymbidium flabellatum* Thouars) designated by Alrich & W.E. Higgins, Ill. Dict. Orchid Gen., 108 (2008).
Type species: *C. flabellata* (Thouars) Rolfe selected by M.W. Chase, Gen. Orchid., 5: 98 (2009).

Cymbidium Sw., Nova Acta Regiae Soc. Sci. Upsal., ser. 2, 6: 70 (1799).
Lectotype: *C. aloifolium* (L.) Sw. (*Epidendrum aloifolium* L.) designated by P.F. Hunt, Kew Bull., 24(1): 94 (1970) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 884 (1991).

Cymbiglossum Halbinger, Orquidea (Mexico City), n.s., 9(1): 1-2 (1983).
Type species: *C. cervantesii* (Lex.) Halbinger (*Odontoglossum cervantesii* Lex.) selected by M.W. Chase, Gen. Orchid., 5: 341 (2009).

Cynorkis Thouars, Nouv. Bull. Sci. Soc. Philom Paris, 1: 317 (1809).
Type species: *C. fastigiata* Thouars selected by P.J. Cribb, Man. Cult. Orch. Sp., 108 (1981).

Cypripedium L., Sp. Pl. (Linnaeus), ed. 1, 2: 951 (1753).
Lectotype: *C. calceolus* L. designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 452 (1989).

Cyperorchis Blume, Rumphia, 4: 47 (1849), and Mus. Bot., 1: 48 (1849).
Lectotype: *Cyperorchis elegans* (Lindl.) Blume

(*Cymbidium elegans* Lindl.) designated by P.F. Hunt, Kew Bull., 24(1): 94 (1970).

Cyrtidiorchis Rauschert, Taxon, 31(3): 560 (1982).
Type species: *C. rhomboglossum* (F. Lehmann & Kraenzl.) Schltr. (*Chrysocycnis rhomboglossa* F. Lehmann & Kraenzl.) selected by P. Ortiz, Orquid. Colombia, ed. 2, 70 (1995).

Cyrtidium Schltr., Repert. Spec. Nov. Regni Veg. Beih., 27: 178 (1924).
Type species: *C. rhomboglossum* (F. Lehmann & Kraenzl.) Schltr. (*Chrysocycnis rhomboglossa* F. Lehmann & Kraenzl.) selected by Garay, Orquideologia, 4: 8 (1969).

Cyrtochilum Kunth, Nov. Gen. Pl., 1: 349, t. 84 (1816).
Lectotype: *C. undulatum* Kunth designated by Garay, Bradea, 1(40): 398 (1974).

Cyrtopera Lindl., Gen. Sp. Orchid. Pl., 189 (1833).
Type species: *C. woodfordii* (Sims) Lindl. (*Cyrtopodium woodfordii* Sims) selected by A. Richard, Dict. Univ. Hist. Nat., 4: 561 (1844).

Cyrtorchis Schltr., Orchideen (Schlechter), ed. 1, 595 (1914).
Lectotype: C. arcuata (Lindl.) Schltr. (*Angraecum arcuatum* Lindl.) designated by Summerhayes, Kew Bull., 3: 278 (1948).

Cyrtosia Blume, Bijdr. Fl. Ned. Ind., 8: 396, t. 6 (1825).
Type species: *C. javanica* Blume selected by Blume, Rumphia, 1: 199 (1837).
Lectotype: *C. javanica* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(12): 1760 (1990).

Cystorchis Blume, Coll. Orch., 1: 87 (1855).
Type species: *C. variegata* Blume selected by Ridley, J. Linn. Soc. (Bot.), 32: 399 (1896).

Cytherea Salisb., Parad. Lond., 2(1): errata (1807), and Trans. Hort. Soc. London, 1: 301 (1812).
Type species: *C. bulbosa* (L.) Oakes (*Cypripedium bulbosum* L.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 994 (1872).

Dactylorhiza Necker ex Nevski, Trudy Bot. Inst. Akad. Nauk S.S.S.R., ser. 1, Fl. Sist. Vyssh. Rast., 4: 332 (1937).

Type species: *D. umbrosa* (Karelin & Kirilov) Nevski (*Orchis umbrosus* Karelin & Kirilov) selected by Soó, Jahresber. Naturwiss. Vereins Wuppertal, 21-22: 13 (1968).

Deiregyne Schltr., Beih. Bot. Centralbl., 37(2): 425 (1920).
Lectotype: *D. chloreaeformis* (A.Rich. & Galeotti) Schltr. (*Spiranthes chloreaeformis* A.Rich. & Galeotti) designated by Garay, Bot. Mus. Leafl., 28: 312 (1980). Note: The choice of *D. chloreaeformis* is against the protologue, see Szlachetko, Fragm. Florist. Geobot., 40: 794 (1995)
Lectotype: *D. hemichrea* (Lindl.) Schltr. (*Spiranthes hemichrea* Lindl.) designated by Burns-Balogh, Amer. J. Bot., 69: 1131 (1982).

Dendrobium Sw., Nova Acta Regiæ Soc. Sci. Upsal., ser. 2, 6: 82 (1799).
Type species: *D. moniliforme* (L.) Sw. (*Epidendrum moniliforme* L.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1030 (1872) and M.A. Clements, Austral. Orchid Res., 1: 57 (1989).
Lectotype: *D. moniliforme* (L.) Sw. designated by R.K. Brummitt, Taxon, 31: 542 (1982) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 125 (1991).

Dendrochilum Blume, Bijdr. Fl. Ned. Ind., 8: 398, t. 52 (1825).
Type species: *D. aurantiacum* Blume selected by Bechtel et al., Man. Cult. Orchid Sp., ed 1, 127 (1981).

Dendrocolla Blume, Bijdr. Fl. Ned. Ind., 7: 286, t. 67 (1825).
Type species: *D. hystrix* Blume designated by J.J. Smith, Bull. Jard. Bot. Buitenzorg, ser. 3, 3: 303 (1921).

Dendrolirium Blume, Bijdr. Fl. Ned. Ind., 7: 343, t. 69 (1825).
Type species: *D. ornatum* Blume selected by Breiger, Orchideen (Schlechter), ed. 3, 11/12: 717 (1981).

Desmotrichum Blume, Bijdr. Fl. Ned. Ind., 329 (1825).
Lectotype: *D. angulatum* Blume designated by P.F. Hunt & Summerhayes, Taxon, 10: 102 (1961).

Diaphananthe Schltr., Orchideen (Schlechter), ed. 1, 593 (1914).
Lectotype: *D. pellucida* (Lindl.) Schltr. (*Angraecum*

pellucidum Lindl.) designated by Schlechter, Beih. Bot. Centralbl., 36(2): 97 (1918).

Dichaea Lindl., Gen. Sp. Orchid. Pl., 208 (1833).
TYPE SPECIES: *D. echinocarpa* (Sw.) Lindl. (*Epidendrum echinocarpon* Sw.) selected by Lindley, Bot. Reg., 18: sub 1530 (1832); and Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 214 (1924).

Dichaeopsis Pfitzer, Entwurf Anordn, Orch., 107 (1887).
LECTOTYPE: *D. graminoides* (Sw.) Schltr. (*Epidendrum graminoides* Sw.) designated by Garay & H.R. Sweet, J. Arnold Arbor., 53(4): 519 (1972).

Dicrypta Lindl., Gen. Sp. Orchid. Pl., 44, 152 (1830).
TYPE SPECIES: *D. crassifolia* (Lindl.) Lindl. (*Heterotaxis crassifolia* Lindl.) selected by I. Ojeda, Gen. Orchid., 5(2): 147 (2009).

Didactyle Lindl., Fol. Orchid., 1: Didactyle, 1 (1852).
TYPE SPECIES: *Bulbophyllum gladiatum* Lindl. **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1070 (1872).

Dikylikostigma Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem., 7: 321 (1919).
LECTOTYPE: *D. preussii* Kraenzl. designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 153 (2008).

Dimerandra Schltr., Repert. Spec. Nov. Regni Veg. Beih., 17: 43 (1922).
TYPE SPECIES: *D. rimbachii* (Schltr.) Schltr. (*Epidendrum rimbachii* Schltr.) designated by Siegerist, Bot. Mus. Leafl., 30: 204 (1986).

Dinema Lindl., Orchid. Scelet., 16 (1826).
TYPE SPECIES: *D. polybulbon* (Sw.) Lindl. (*Epidendrum polybulbon* Sw.) selected by Lindley, Coll. Bot., Append.: no. 125 (1826).

Diphryllum Raf., Med. Repos., ser. 2, 5: 357 (1808).
TYPE SPECIES: *Diphryllum bifolium* Raf. designated by Rafinesque.
TYPE SPECIES: *Listera convallarioides* (Sw.) Nuttall (*Epipactis convallarioides* Sw.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1091 (1872).

Diplorrhiza Ehrhart, Beitr. Naturk. (Ehrhart), 4: 147 (1789).

TYPE SPECIES: *Satyrium viride* L. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1099 (1871).

Discyphus Schltr., Repert. Spec. Nov. Regni Veg. Beih., 15: 417 (1919).
LECTOTYPE: *D. scopulariae* (Rchb.f.) Schltr. (*Spiranthes scopulariae* Rchb.f.) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 153 (2008).

Disperis Sw., Kongl. Vetensk. Acad. Nya Handl., 21: 218, t. 3f (1800).
TYPE SPECIES: *D. circumflexa* (L.) T. Durand & Schinz (*Ophrys circumflexa* L.) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 237 (1951) and H.P. Linder et al., Orchid S. Afr., 299 (1999).
LECTOTYPE: *D. circumflexa* (L.) T. Durand & Schinz designated by J.C. Manning, Taxon, 48: 48 (1999).
LECTOTYPE: *D. capensis* (L.) Sw. (*Arethusa capensis* L.) designated by J.C. Manning, Taxon, 48: 46 (1999).

Diuris Sm., Trans. Linn. Soc. London, Bot., 4: 222 (1798).
TYPE SPECIES: *D. aurea* Sm., selected by Smith, Exot. Bot., 1: 15 (1805).

Domingoa Schltr., Symb. Antill., 7: 496 (1913).
TYPE SPECIES: *D. haematochila* (Rchb.f.) Carabia (*Epidendrum haematochilum* Rchb.f.) selected by Carabia, Mem. Soc. Cub. Hist. Nat., 17(2): 143 (1943) and Acuña, Cat. Descr. Orquid. Cuba, 60: 64 (1938).

Dorycheile Rchb., Deut. Bot. Herb.-Buch, 56 (1841).
TYPE SPECIES: *D. rubra* (L.) Fuss (*Serapias rubra* L.) selected by Fuss, Fl. Transsilv., 628 (1866) and Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1128 (1872).

Drakaea Lindl., Sketch Veg. Swan R., Appendix: 55 (1840).
TYPE SPECIES: *D. elastica* Lindley designated by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1134 (1872) and Clements, M.A. Aust. Orch. Res., 1: 72 (1989).

Dryadorchis Schltr., Repert. Spec. Nov. Regni Veg. Beih., 1: 976 (1913).
TYPE SPECIES: *D. barbellata* Schltr. selected by Senghas, Orchideen (Schlechter), ed. 3, 1(19-20): 1201 (1988).

Dryopeia Thouars, Hist. Orchid., tt. 1-3 (1822).
LECTOTYPE: *D. oppositifolia* Thouars designated by

Kurzweil & Manning, Adansonia, ser. 3, 27(2): 167 (2005).

Dryorkis Thouars, Nouv. Bull. Sci. Soc. Philom. Paris, 1: 316 (1809).
Lectotype: *D. tripetaloides* Thouars designated by Kurzweil & Manning, Adansonia, ser. 3, 27(2): 172 (2005).

Elleanthus C. Presl, Rel. Haenk., 1: 97 (1827).
Type species: *E. lancifolius* C. Presl. selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 203 (1924).

Eltroplectris Raf., Fl. Tellur., 2: 51 (1836).
Type species: *E. calcarata* (Sw.) Garay & H.R. Sweet (*Neottia calcarata* Sw.) selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 186 (1924) and Garay, Fl. Ecuador, 9: 239 (1978).

Ephemerantha P.F.Hunt & Summerhayes, Taxon, 10(4): 102 (1961).
Lectotype: *E. angulata* (Blume) P.F. Hunt & Summerhayes (*Desmotrichum angulatum* Blume) designated by P.F. Hunt & Summerhayes, Taxon, 10(4): 102 (1961).

Epiblastus Schltr., Nachtr. Fl. Deutsch. Schutzgeb. Südsee, 136 (1905).
Type species: *E. ornithidioides* Schltr. selected by van Royen, Alpine Fl. New Guinea, 2: 489 (1979).

Epidendrum L., Sp. Pl. (Linnaeus), ed. 1, 2: 952 (1753) (*nom. rej.*).
Type species: *E. nodosum* L. selected by Britton & Wilson, Sci. Surv. Puerto Rico, 5(2): 203 (1924).

Epidendrum L., Sp. Pl. (Linnaeus), ed. 2, 2: 1347 (1763) (*nom. cons.*).
Lectotype: *E. nocturnum* Jacq. designated by Sprague, Prop. Brit. Bot., 53 (1929) and Voss et al., Regnum Veg 111: 335 (1983).

Epilyna Schltr., Beih. Bot. Centralbl., 36(2): 374 (1918).
Lectotype: *E. jimenezii* Schltr. designated by Pupulin, Bot. J. Linn. Soc., 163: 132 (2010).

Epipactis Zinn, Cat. Pl. Hort. Gott., 85 (1757).
Lectotype: *E. helleborine* (L.) Crantz (*Serapias helleborine* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 470 (1989), P.J. Cribb & J.J. Wood, Taxon, 48: 49 (1999)

and Voss et al., Regnum Veg 111: 333 (1983).

Epipogium J.G. Gmelin ex Borkhausen, Tent. Disp. Pl. *German*., 139 (1792).
Lectotype: *E. aphyllum* Sw. (*Satyrium epipogium* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 477 (1989).

Eriochilus R.Br., Prodr. Fl. Nov. Holland., 323 (1810).
TYPE SPECIES: *E. cucullatus* (Labillardière) Rchb.f. (*Epipactis cucullata* Labillardière) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1240 (1872).
Type species: *E. autumnalis* R.Br. (nom. illeg.) selected by S.D. Hopper & A.P. Brown, Nuytsia 16(1): 30 (2006).

Erporkis Thouars, Nouv. Bull. Sci. Soc. Phil., Paris, 1: 317 (1809).
Lectotype: *Goodyera occulta* Thouars designated by Ormerod, Gen. Orch., 3: 136 (2003).

Eulophia R.Br. ex Lindl.. Bot. Reg., 7: sub 578 [573], as *Eulophus* (1821), and Bot. Reg., 8: t. 686 (1822).
Lectotype: *Eulophia guineensis* Lindl. designated by W. Greuter et al., Regnum Veg., 118: 186 (1988).

Eurycentrum Schltr., Nachtr. Fl. Deutsch Schutzgeb. Südsee, 89 (1905).
Lectotype: *E. obscurum* (Blume) Schltr. (*Cystorchis obscura* Blume) designated by Ormerod, Gen. Orch., 3: 90 (2003).

Eurystyles Wawra, Österr. Bot. Zeitschr., 13: 223 (1863).
Lectotype: *E. cotyledon* Wawra designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 149 (2008).

Evelyna Poepp. & Endl., Nova Gen. Sp., 1: 32 (1836).
Type species: *E. capitata* Poepp. & Endl. selected by Dressler, Gen. Orch., 4: 598 (2005) and Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1321 (1874).

Evota Rolfe, Fl. Cap. (Harvey), 5(3): 268 (1913).
Type species: *E. harveyana* (Lindl.) Rolfe (*Ceratandra harveyana* Lindl.) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 238 (1951).

Fernandezia Ruiz & Pavón, Fl. Peruv. Prodr., 123, t. 27 (1794).
Lectotype: *E. subbiflora* Ruiz & Pavón designated

by Dunsterville & Garay, Venez. Orchids Ill., 5: 124 (1972).

Flickingeria A.D. Hawkes, Orchid Weekly, 2(46): 451 (1961).

LECTOTYPE: *F. angulata* (Blume) A.D. Hawkes (*Desmotrichum angulatum* Blume) designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 125 (1991).

Fractiunguis Schltr., Anexos Mem. Inst. Butantan, Secç. Bot. 1(4): 56 (1922).

TYPE SPECIES: *F. reflexus* (Rchb.f.) Schltr. (*Hexisea reflexa* Rchb.f.) selected by Acuña, Cat. Descr. Orquid. Cuba, 60: 89. (1938).

LECTOTYPE: *F. reflexus* (Rchb.f.) Schltr. designated by Dressler, Gen. Orch., 4: 310 (2005).

Funkiella Schltr., Beih. Bot. Centralbl., 37(2): 430 (1920).

LECTOTYPE: *F. hyemalis* (A.Rich. & Galeotti) Schltr. (*Spiranthes hyemalis* A.Rich. & Galeotti) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 168 (2008) and Burns-Balogh, Amer. J. Bot., 69: 1131 (1982).

Galearis Raf., Herb. Raf., 71 (1833).

LECTOTYPE: *G. spectabilis* (L.) Raf. (*Orchis spectabilis* L.) designated by Sheviak, Taxon, 48: 49 (1999).

Galeoglossum A.Rich. & Galeotti, Ann. Sci. Nat., Bot., sér. 3, 3: 31 (1845).

TYPE SPECIES: *G. prescottioides* A.Rich. & Galeotti selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1401 (1872).

LECTOTYPE: *G. prescottioides* A.Rich. & Galeotti designated by Salazar, Proc. Second Sci. Conf. Andrean Orchids, 169 (2009).

Galeottiella Schltr., Beih. Bot. Centralbl., 37(2): 360 (1920).

LECTOTYPE: *G. sarcoglossa* (A.Rich. & Galeotti) Schltr. (*Spiranthes sarcoglossa* A.Rich. & Galeotti) designated by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982) and Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 146 (2008).

Gastrochilus D. Don, Prodr. Fl. Nepal., 32 (1825).

LECTOTYPE: *G. calceolaris* (Buch.-Ham. ex Sm.) D. Don (*Aerides calceolare* Buch.-Ham. ex Sm.)

designated by Christenson, Kew Bulletin, 41(4): 836 (1986).

Gavilea Poepp., Frag. Syn. Pl. Chil., 188 (1833).

LECTOTYPE: *G. leucantha* Poepp. designated by M.N. Corrêa, Fl. Patagónica, 8(2): 191 (1969) and Gen. Orch., 3: 10 (2003).

Gennaria Parlatore, Fl. Ital. (Parlatore), 3: 404 (1860).

TYPE SPECIES: *G. diphylla* (Link) Parlatore (*Satyrium diphyllum* Link) selected by Schlechter, Repert. Spec. Nov. Regni Veg., 15: 296 (1918).

Gigliolia Barb.Rodr., Gen. Sp. Orch. Nov., 1: 25 (1877).

LECTOTYPE: *G. geraensis* Barb.Rodr. indirectly designated by Garay, Orquideologia, 9: 117 (1974).

Glossochilopsis Szlach., Fragm. Florist. Geobot., 3(Suppl.): 122 (1995).

LECTOTYPE: *G. chamaeorchis* (Schltr.) Szlach. (*Microstylis chamaeorchis* Schltr.) designated by Margonska, Richardiana, 8(2): 75 (2008).

Glossodia R.Br., Prodr. Fl. Nov. Holland., 325 (1810).

TYPE SPECIES: *G. major* R.Br. selected by M.A. Clements, Austral. Orchid. Res., 1: 83 (1989).

Gonogona Link, Enum. Hort. Berol. Alt., 2: 369 (1822).

TYPE SPECIES: *Goodyera repens* (L.) R.Br. (*Satyrium repens* L.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1481 (1872).

Goodyera R.Br., Hortus Kew, ed. 2, 5: 197 (1813).

TYPE SPECIES: *G. repens* (L.) R.Br. (*Satyrium repens* L.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1485 (1872), Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 569 (1913) and Sprague, J. Bot., 64: 113 (1926).

LECTOTYPE: *G. repens* (L.) R.Br. designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 479 (1989).

Grastidium Blume, Bijdr. Fl. Ned. Ind., 7: 333, 433 (1825).

TYPE SPECIES: *G. salaccense* Blume selected by Breiger, Orchideen (Schlechter), ed. 3, 11/12: 653 (1981).

Gymnadenia R.Br., Hortus Kew., ed. 2, 5: 191 (1813).

LECTOTYPE: *G. conopsea* (L.) R.Br. (*Orchis conopsea* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr.

Heim. Orch. Baden-Württ., 21(3): 482 (1989).

Gymnadeniopsis Rydb., Man. Fl. N. States (Britton), 293 (1901).
Type species: *G. nivea* (Nuttall) Rydb. (*Orchis nivea* Nuttall) selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 552 (1913).

Gyrostachys Pers. ex Blume, Coll. Orch., 127 (1859).
Type species: *G. spiralis* (L.) Pers. ex Blume (*Ophrys spiralis* L.) selected by Kuntze, Rev. Gen. Pl., 2: 663 (1891).
Lectotype: *G. spiralis* (L.) Pers. ex Blume designated by Garay, Bot. Mus. Leafl., 28(4) 360 (1980)[1982].

Habenaria Willd., Sp. Pl., ed. 4, 44 (1805).
Type species: *H. macroceratitis* Willd. (*Orchis habenaria* L.) selected by Kraenzlin, Bot. Jahrb. Syst., 16: 58 (1892).
Type species: *H. monorrhiza* (Sw.) Rchb.f. (*Orchis monorrhiza* Sw.) **invalidly** selected by Lindley, Bot. Reg., 18: sub 1499 (1832). The above type name is now considered a synonym of the species *Habenaria quinqueseta* var. *macroceratitis* (Willd.) Luer (*Habenaria macroceratitis* Willd.) which was lectotyped by P.J. Cribb, Taxon, 48: 48 (1999).

Hammarbya Kuntze, Revis. Gen. Pl., 2: 665 (1891).
Lectotype: *H. paludosa* (L.) Kuntze (*Ophrys paludosa* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 487 (1989).

Hapalorchis Schltr., Beih. Bot. Centralbl., 37(2): 362 (1920).
Type species: *H. candidus* (Kraenzl.) Schltr. (*Sauroglossum candidum* Kraenzl.) selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 186 (1924).
Lectotype: *H. cheirostyloides* Schltr. designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 134 (2008).

Haraella Kudô, J. Soc. Trop. Agric., 2: 26 (1930).
Lectotype: *H. retrocalla* (Hayata) Kudô (*Saccolabium retrocallum* Hayata) designated by Butzin, Taxon, 32(4): 631 (1983).

Herminium L., Opera Var., 251 (1758), and Fl. Lapp. (Linnaeus), 247 (1737).
Lectotype: *H. monorchis* (L.) R.Br. (*Orchis monorchis* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr.

Heim. Orch. Baden-Württ., 21(3): 489 (1989); and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(7): 1027 (1990).

Hetaeria Blume, Bijdr. Fl. Ned. Ind., 8: 409, t. 14 (1930).
Lectotype: *H. oblongifolia* Blume designated by L.G. Adams, Taxon, 36(3): 651 (1987).

Himantoglossum Spreng., Syst. Veg. (Sprengel), ed. 16, 3: 675, 694 (1826).
Lectotype: *H. hircinum* (L.) Spreng. (*Satyrium hircinum* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 491 (1989).

Holothrix Rich. ex Lindl., Gen. Sp. Orchid. Pl., 257, 283 (1835).
Type species: *H. hispidula* (L.f.) T. Durand & Schinz (*Orchis hispidula* L.f.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1658 (1872).

Humboldtia Ruiz & Pavón, Fl. Peruv. Chil. Prodr., 121, t. 27 (1794).
Lectotype: *H. purpurea* Ruiz & Pavón designated by Garay & H.R. Sweet, J. Arnold Arbor., 53(4): 522 (1972).

Huntleya Bateman ex Lindl., Edwards's Bot. Reg., 23: sub 1991 (1837).
Type species: *H. sessiliflora* Bateman ex Lindl. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1680 (1872).

Ibidium Salisb., Trans. Hort. Soc. London, 1: 291 (1812).
Type species: *I. spirale* (L.) Salisb. (*Ophyrs spiralis* L.) selected by House, Bull. Torr. Club, 32: 380 (1905).

Ionopsis Kunth, Nov. Gen. Sp., 1: 348, t. 83 (1815).
Type species: *I. utricularioides* (Sw.) Lindl. (*Epidendrum utricularioides* Sw.) selected by M.W. Chase, Gen. Orchid., 5: 281 (2009).

Isochilus R.Br., Hortus Kew, ed. 2, 5: 209 (1813).
Lectotype: *I. linearis* (Jacq.) R.Br. (*Epidendrum lineare* Jacq.), designated by Angely, Fl. Analitica São Paulo, 6: 1303 (1973) and Summerhayes, Index Nom. Gen. (Pl.), 2: 880 (1979) card #64/23515.
Type species: *I. linearis* (Jacq.) R.Br. selected by

Pfeiffer, Nomencl. Bot. (Pfeiffer), 1(2): 1767 (1872); and type indirectly selected by Reichenbach f., Bonplandia (Hannover), 2: 22 (1854).

Jacquiniella Schltr., Repert. Spec. Nov. Regni Veg. Beih., 7: 123 (1920).
TYPE SPECIES: *J. globosa* (Jacq.) Schltr. (*Epidendrum globosum* Jacq.) selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 197 (1924).

Jensoa Raf., Fl. Tellur., 4: 38 (1836)[1837]
LECTOTYPE: *J. ensata* (Thunberg) Raf. nom. illeg. (*Limodorum ensatum* Thunberg) designated by P.F. Hunt, Kew Bull., 24(1): 94 (1970).

Jimensia Raf., Fl. Tellur., 4: 38 (1836)[1837].
TYPE SPECIES: *J. nervosa* Raf., nom. illeg., *Bletilla striata* (Thunberg) Rchb.f. (*Limodorum striatum* Thunberg), indirectly selected by Garay & R.E. Schultes, Bot. Mus. Leafl., 18(5): 184 (1958).

Jumellea Schltr., Orchideen (Schlechter), ed. 1, 609 (1914).
LECTOTYPE: *J. recurva* (Thouars) Schltr. (*Angraecum recurum* Thouars) designated by Garay, Bot. Mus. Leafl., 23(4): 182 (1972).

Kefersteinia Rchb.f., Bot. Zeitung (Berlin), 10: 633 (1852).
TYPE SPECIES: *K. graminea* (Lindl.) Rchb.f. (*Zygopetalon gramineum* Lindl.) designated by Garay, Orquideologia, 4: 150 (1969).

Kingidium P.F. Hunt, Kew Bull., 24(1): 97 (1970).
LECTOTYPE: *K. taeniale* (Lindl.) P.F.Hunt (*Aerides taenialis* Lindl.) designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 891 (1991).

Kingiella Rolfe, Orchid Rev., 25(297): 196 (1917).
LECTOTYPE: *K. taenialis* (Lindl.) Rolfe (*Aerides taenialis* Lindl.) designated by P.F. Hunt, Amer. Orchid Soc. Bull., 40(12): 1094 (1971).

Kraenzlinorchis Szlach., Orchidee (Hamburg), 55(1): 57 (2004).
LECTOTYPE: *K. mandersii* (Collett & Hemsl.) Szlach. (*Habenaria mandersii* Collett & Hemsl.) designated by H. Kurzweil, Thai For. Bull. (Bot.), 77 (2009).

Kuhlhasseltia J.J. Sm., Icon. Bogor., 4: 1, t. 301 (1910).

LECTOTYPE: *K. javanica* J.J.Sm. designated by Ormerod, Gen. Orch., 3: 110 (2003).

Laelia Lindl., Gen. Sp. Orch. Pl., 115 (1831).
TYPE SPECIES: *L. grandiflora* (Lex.) Lindl. (*Bletia grandiflora* Lex.) indirectly selected by Dandy, Kew Bull., 86. (1935).

Lanium Lindl. ex Benth., Hooker's Icon. Pl., 14: 24, t. 1334 (1881).
TYPE SPECIES: *L. avicula* (Lindl.) Benth. (*Epidendrum avicula* Lindl.) selected by Angely, Fl. Analitica São Paulo, 6: 1294 (1973).

Lecanorchis Blume, Mus. Bot., 2: 188 (1856).
LECTOTYPE: *L. javanica* Blume designated by Garay & H.R. Sweet, Orchids S. Ryukyu Islands, 49 (1974).

Leochilus Knowles & Westc., Fl. Cab., 2: 143 (1838).
TYPE SPECIES: *L. oncidioides* Knowles & Westc. designated by Knowles & Westcott.
TYPE SPECIES: *Oncidium macrantherum* Hook. **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 64 (1874).

Lepanthes Sw., Nova Acta Regiae Soc. Sci. Upsal., 6: 85 (1799).
TYPE SPECIES: *L. concinna* Sw. selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 206 (1924).

Lepanthopsis Ames, Bot. Mus. Leafl., 1(9): 3 (1933).
TYPE SPECIES: *L. floripecten* (Rchb.f.) Ames (*Pleurothallis floripecten* Rchb.f.)
selected by Garay, Orquideologia, 9: 116 (1974).

Leptoceras (R.Br.) Lindl., Sketch Veg. Swan River Colony, 53 (1840).
TYPE SPECIES: *L. menziesii* (R.Br.) Lindl. (*Caladenia menziesii* R.Br.) selected by A.S. George, Nuytsia, 1: 183 (1971).

Leucostachys Hoffmannsegg, Verz. Orchid., 26 (1842).
TYPE SPECIES: *L. procera* (Ker Gawler) Hoffmannsegg (*Neottia procera* Ker Gawler) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 102 (1874).

Limnorchis Rydb., Mem. New York Bot. Gard., 1: 104 (1900).
TYPE SPECIES: *L. hyperborea* (L.) Rydb. (*Orchis hyperborea* L.) selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 554 (1913).

Limodorum Boehm. (nom. cons.), Definitiones Generum Plantarum: 358 (1760).
LECTOTYPE: *L. abortivum* (L.) Sw. (*Orchis abortiva* L.) designated by Greuter et al., Regnum Veg. 118: 183 (1988) and H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., (3): 493 (1989).

Limodorum L., Sp. Pl., ed. 1, 2: 950 (1753).
TYPE SPECIES: *L. tuberosum* L. selected by & Brown, Ill. Fl. N.U.S., ed. 2, 1: 562 (1913).

Liparis Rich., De Orchid. Eur., 21, 30 & 38, f. 10 (1817).
LECTOTYPE: *L. loeselii* (L.) Rich. (*Ophrys loeselii* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 495 (1989).

Lissochilus R.Br. ex Lindl., Bot. Reg., 7: t. 573, sub 578 (1821), and Coll. Bot. (Lindley), t. 31 (1822).
TYPE SPECIES: *L. speciosus* R.Br. ex Lindl. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 135 (1874).

Listera R.Br., Hortus Kew., ed. 2, 5: 201 (1813).
LECTOTYPE: *L. ovata* (L.) R.Br. (*Ophrys ovata* L.) selected by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 499 (1989).

Listrostachys Rchb.f., Bot. Zeitung (Berlin), 10: 930 (1852).
TYPE SPECIES: *L. jenischiana* Rchb.f. designated by H.G. Reichenbach.
TYPE SPECIES: *L. pertusa* (Lindl.) Rchb.f. (*Angraecum pertusum* Lindl.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 136 (1874).

Ludisia A.Rich., Dict. Class. Hist. Nat., 7: 437 (1825).
LECTOTYPE: *L. discolor* (Ker Gawler) A.Rich. (*Goodyera discolor* Ker Gawler) designated by Ormerod, Lindleyana, 17(4): 211 (2002).

Luisia Gaudichaud-Beaupré, Voy. Uranie, Bot., 426, t. 37 (1826)[1829].
TYPE SPECIES: *L. tenuifolia* Blume not validly selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 168 (1874).

Lycaste Lindl., Edwards's Bot. Reg., 29(Misc): 14 (1843).
TYPE SPECIES: *L. macrophylla* (Poepp.) Lindl. (*Maxillaria macrophylla* Poepp.) selected by Acuña, Cat. Descr. Orquid. Cuba, 60: 165 (1938).
LECTOTYPE: *L. macrophylla* (Poepp.) Lindl. designated

by Bullock, Kew Bull., 13: 254 (1958).
LECTOTYPE: *L. plana* Lindl. designated by Oakeley, Lycaste, Ida and Anguloa, 22 (2008) and McVaugh, Fl. Novo-Galiciana, 16: 188 (1985).

Lyperanthus R.Br., Prodr. Rl. Nov. Holland., 325 (1810).
TYPE SPECIES: *L. suaveolens* R.Br. selected by M.A. Clements, Austral. Orchid. Res., 1: 90 (1989).

Lyroglossa Schltr., Beih. Bot. Centralbl., 37(2): 448 (1920).
LECTOTYPE: *L. bradei* Schltr. ex Mansf. designated by Burns-Balogh, Amer. J. Bot., 69(7): 1132 (1982).
TYPE SPECIES: *L. grisebachii* (Cogn.) Schltr. (*Spiranthes grisebachii* Cogn.) selected by Angely, Fl. Analitica São Paulo, 6: 1277 (1973).

Macdonaldia Gunn ex Lindl., Sketch Veg. Swan Riv., 50, t. 9 (1840).
TYPE SPECIES: *M. smithiana* Lindl. selected by M.A. Clements, Austral. Orchid Res., 1: 137 (1989).
LECTOTYPE: *M. antennifera* Lindl. designated by Szlachetko, Fragm. Florist. Geobot., 3(Suppl.): 112 (1995).

Malaxis Sw., Prodr. (Swartz), 8: 119 (1788).
TYPE SPECIES: *M. rheedii* Sw. **invalidly** selected by Ascherson, Fl. Prov. Brandenb., 1: 699 (1864).
TYPE SPECIES: *M. spicata* Sw. selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 570 (1913).

Malleola Schltr., Repert. Spec. Nov. Regni Veg. Beih., 1: 119 (1913).
LECTOTYPE: *M. sphingoides* J.J.Sm. designated by Garay, Bot. Mus. Leafl., 23(4): 184 (1972) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 894 (1991).
TYPE SPECIES: *M. undulata* J.J.Sm. & Schltr. selected by Christenson, Kew Bulletin, 41(4): 837 (1986).

Maxillaria Ruiz & Pavón, Fl. Peruv. Prodr., 116, t. 25 (1794).
TYPE SPECIES: *M. longipetala* Ruiz & Pavón **invalidly** selected by Acuña, Cat. Descr. Orquid. Cuba, 60: 171 (1938).
LECTOTYPE: *M. ramosa* Ruiz & Pavón designated by Garay & H.R. Sweet, J. Arnold Arbor., 53(4): 524 (1972).
TYPE SPECIES: *M. platypetala* Ruiz & Pavón selected

Brieger & P.F. Hunt, Taxon, 18: 602 (1969).

LECTOTYPE: *M. platypetala* Ruiz & Pavón designated by Garay, Harvard Pap. Bot., 2: 52 (1997).

Megastylis (Schltr.) Schltr., Bot. Jahrb. Syst., 45: 379, 384 (1911).

TYPE SPECIES: *M. gigas* (Rchb.f.) Schltr. (*Caladenia gigas* Rchb.f.) selected by N. Hallé, Fl. Nouvelle Caledonie & Depend., 8: 487 (1977).

Menadenium Raf. ex Cogn., Fl. Bras. (Martius), 3(5): 581 (1902).

TYPE SPECIES: *M. kegelii* (Rchb.f.) Cogn. (*Zygopetalum kegelii* Rchb.f.) selected by Pupulin, Gen. Orchid., 5: 544 (2009).

Mesadenella Pabst & Garay, Arquin. Jard. Bot. Rio, 12: 205 (1952).

TYPE SPECIES: *M. esmeraldae* (Linden & Rchb.f.) Pabst & Garay (*Spiranthes esmeraldae* Linden & Rchb.f.) selected by M.N. Correa, Darwiniana, 11: 68 (1955).

LECTOTYPE: *M. esmeraldae* (Linden & Rchb.f.) Pabst & Garay designated by Burns-Balogh, Amer. J. Bot., 69: 1132 (1982).

Mesadenus Schltr., Beih. Bot. Centralbl., 37(2): 367 (1920).

TYPE SPECIES: *M. galeottianus* (A.Rich.) Schltr. (*Spiranthes galeottiana* A.Rich.) selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 186 (1924).

Microchilus C. Presl, Rel. Haenk., 1: 94 (1827).

LECTOTYPE: *M. minor* C. Presl designated by Ormerod, Gen. Orch., 3: 121 (2003).

Microtatorchis Schltr., Nachtr. Fl. Deutsch. Schutzgeb. Südsee, 234 (1905).

LECTOTYPE: *M. perpusilla* Schltr. designated by Bullock, Index Nom. Gen. (Pl.), 2: 1093 (1976) card #30/05211 (1958).

Microtis R.Br., Prodr. Fl. Nov. Holland., 320 (1810).

LECTOTYPE: *M. rara* R.Br. designated by Garay & H.R. Sweet, Orchids S. Ryukyu Islands, 42 (1974).

Mischobulbum Schltr., Repert. Spec. Nov. Regni Veg. Beih., 1: 98 (1911).

TYPE SPECIES: *M. scapigerum* (Hook.f.) Schltr. (*Nephelaphyllum scapigerum* Hook.f.) selected by Senghas, Orchideen (Schlechter), ed. 3, 1: 851 (1984).

LECTOTYPE: *M. scapigerum* (Hook.f.) Schltr. designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(12): 1765 (1990).

Monadenia Lindl., Gen. Sp. Orchid. Pl., 356 (1838).

LECTOTYPE: *M. brevicornis* Lindl. designated by H.P. Linder, Bothalia, 13(3-4): 342 (1981).

Monanthochilus R. Rice, Oasis (Dora Creek), 3(Suppl.): 2 (2004).

LECTOTYPE: *M. chrysanthus* (Schltr.) R. Rice (*Sarcochilus chrysanthus* Schltr.) designated by R. Rice, Oasis (Dora Creek), 3(Suppl.): 2 (2004).

Monixus Finet, Bull. Soc. Bot. France Mém., 54(9): 15 (1907).

LECTOTYPE: *M. striatus* (Thouars) Finet (*Angraecum striatum* Thouars) designated by Garay, Kew Bull., 28: 496 (1973).

Mycaranthes Blume, Bijdr. Fl. Ned. Ind., 7: 352, t. 57 (1825).

TYPE SPECIES: *M. lobata* Blume selected by P.J. Cribb, Gen. Orch., 4: 564 (2005).

Myrobroma Salisb., Parad. Lond., 2: t. 82 (1807).

TYPE SPECIES: *M. fragrans* Salisb. nom. illeg. This species is now considered a synonym of *Vanilla planifolia* Jacks. ex Andrews.

TYPE SPECIES: *Vanilla planifolia* Jacks. ex Andrews not validly selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 395 (1874).

LECTOTYPE: *Vanilla planifolia* Jacks. ex Andrews designated by Garay & H.R. Sweet, Fl. Lesser Antilles, 44 (1974).

Mystacidium Lindl., Compan. Bot. Mag., 2(19): 205 (1837).

TYPE SPECIES: *Limodorum longicornu* Sw. This name is now accepted as a synonym of *Mystacidium capense* (L.f.) Schltr. (*Epidendrum capense* L.f.) invalidly selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 401 (1874).

Nematoceras Hook.f., Fl. Nov.-Zel., 1(4): 249, t. 57 (1853).

TYPE SPECIES: *N. oblonga* Hook.f. **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 426 (1874).

TYPE SPECIES: *N. macranthum* Hook.f. selected by D.L. Jones & M.A. Clements, Orchadian, 13(10): 449 (2002).

Neokoehleria Schltr. Repert. Spec. Nov. Regni Veg., 10: 390 (1912).
Type species: *N. equitans* Schltr. selected by M.W. Chase, Gen. Orchid., 5: 248 (2009).

Neotinea Rchb.f., De Pollin. Orchid., 9, 18 & 29 (1852).
Type species: *Aceras intactum* (Link) Rchb.f. (*Orchis intacta* Link) **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 428 (1874).

Neottia Guettard (nom. cons.), Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris), 4: 374 (1754).
Lectotype: *N. nidus-avis* (L.) Rich. (*Ophrys nidus-avis* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 504 (1989) and Greuter et al., Regnum Vegetabile 118: 184 (1988).

Neottianthe Rchb., Icon. Bot. Pl. Crit., 6: 26 (1828).
Lectotype: *N. cucullata* (L.) Schltr. (*Orchis cucullata* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 506 (1989).

Nephelaphyllum Blume, Bijdr. Fl. Ned. Ind., 8: 372, t. 22 (1825).
Lectotype: *N. pulchrum* Blume designated by Averyanov, Bot. Zhurn.(Moscow & Leningrad), 75(12): 1765 (1990).

Nigritella Rich., De Orchid. Eur., 19, 26, 34 (1817).
Lectotype: *N. nigra* (L.) Rchb.f. (*Satyrium nigrum* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 507 (1989).

Notylia Lindl., Bot. Reg., 11: sub 930 (1825).
Lectotype: *N. punctata* (Ker-Gawler) Lindl. (*Pleurothallis punctata* Ker-Gawler) designated by Butzin, Taxon, 32(4): 631 (1983).

Odontochilus Blume, Coll. Orchid., 79 (1859).
Lectotype: *O. flavescens* (Blume) Blume (*Anoetochilus flavescens* Blume) designated by Averyanov, Turcazaninowia, 11(1): 136 (2008).

Oeceoclades Lindl., Edwards's Bot. Reg., 18: sub 1522 (1832).
Type species: *O. maculata* (Lindl.) Lindl. selected by Lindley, J. Proc. Linn. Soc., Bot., 3: 36 (1859).
Lectotype: *O. maculata* (Lindl.) Lindl. (*Angraecum maculatum* Lindl.) designated by Garay & P. Taylor,

Bot. Mus. Leafl., 24(9): 253 (1976).

Oeoniella Schltr., Beih. Bot. Centralbl., 33(2): 439 (1915).
Type species: *O. polystachys* (Thouars) Schltr. (*Epidendrum polystachys* Thouars) selected by Senghas, Orchidee (Hamburg), 14: 215 (1963).

Oncidium Sw., Vet. Akad. Handl. Stockholm, 21: 239 (1800).
Type species: *O. altissimum* (Jacq.) Sw. (*Epidendrum alissimum* Jacq.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 497 (1874) and M.W. Chase, Gen. Orch., 5: 308 (2009).
Lectotype: *O. variegatum* Sw. designated by Garay, Bradea, 1(40): 398 (1974).
Type species: *O. carthagenense* (Jacq.) Sw. (*Epidendrum carthagenense* Jacq.) **invalidly** selected by Britton & Wilson, Bahama Fl., 97 (1920).

Ophrys L., Sp. Pl. (Linnaeus), ed. 1, 2: 945 (1753).
Lectotype: *O. insectifera* L. designated by M.L. Green, Prop. Brit. Bot., 185 (1929) and H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 512 (1989).

Orchis L., Sp. Pl. (Linnaeus), ed. 1, 2: 939 (1753).
Type species: *O. militaris* L. selected by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 1: 551 (1913).
Lectotype: *O. militaris* L. designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 521 (1989).

Oreorchis Lindl., J. Proc. Linn. Soc., Bot., 3: 26 (1858).
Lectotype: *O. patens* (Lindl.) Lindl. (*Corallorhiza patens* Lindl.) designated by Pearce & P.J. Cribb, Edinb. J. Bot., 54: 292 (1997).

Orthoceras R.Br., Prodr. Fl. Nov. Holland., 316 (1810).
Type species: *O. strictum* R.Br. selected by M.A. Clements, Austral. Orchid. Res., 1: 100 (1989).

Orthopenthea Rolfe, Fl. Cap. (Harvey), 5(3): 179 (1912).
Type species: *O. bivalvata* (L.f.) Rolfe (*Ophrys bivalvata* L.f.) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 235 (1951).

Otochilus Lindl., Gen. Sp. Orchid. Pl., 53 (1830).
Lectotype: *O. porrectus* Lindl. designated by Butzin,

Taxon, 32(4): 631 (1983).

LECTOTYPE: *O. fuscus* Lindl. designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(12): 1767 (1990).

Otostylis Lindl., Gen. Sp. Orchid. Pl., 53 (1830).
TYPE SPECIES: *O. brachystalix* (Rchb.f.) Schltr. (*Zygopetalum brachystalix* Rchb.f.) selected by Pupulin, Gen. Orch., 5: 515 (2009).

Oxystophyllum Blume, Bijdr. Fl. Ned. Ind., 7: 335, t. 38 (1825).
TYPE SPECIES: *O. rigidum* Blume selected by Breiger, Orchideen (Schlechter), ed. 3, 11/12: 676 (1981).

Pachygenium Szlach., Tamayo & Rutk., Polish Bot. J., 46(1): 3 (2001).
LECTOTYPE: *P. albicans* Cogn. designated by Burns-Balogh, Amer. J. Bot., 69: 1131 (1982).
LECTOTYPE: *P. oestriferum* (Rchb.f. & Warm.) Szlach., Tamayo & Rutk. (*Spiranthes oestriferum* Rchb.f. & Warm.) designated by Szlachetko, Tamayo & Rutkowski, Polish Bot. J., 46(1): 3 (2001).

Pachyplectron Schltr., Bot. Jahrb. Syst., 39: 51 (1906).
TYPE SPECIES: *P. arifolium* Schltr. selected by N. Hallé, Fl. Nouvelle Caledonie & Depend., 8: 506 (1977) and P.J. Cribb, Gen. Orch., 3: 131 (1999).

Pachystelis Rauschert, Feddes Repert., 94: 456 (1983).
LECTOTYPE: *P. jimenezii* (Schltr.) Rauschert (*Scaphyglottis jimenezii* Schltr.) designated by Rauschert, Feddes Repert., 94: 456 (1983).

Palmorchis Barb.Rodr., Gen. Sp. Orch. Nov., 1: 169 (1877).
TYPE SPECIES: *P. pubescens* Barb.Rodr. selected by Schlechter, Repert. Spec. Nov. Regni Veg., 16: 442 (1920).

Pecteilis Raf., Fl. Tellur., 2: 37 (1837).
TYPE SPECIES: *P. susannae* (L.) Raf. selected by Schlechter, Repert. Spec. Nov. Regni Veg., 4: 120 (1919).
LECTOTYPE: *P. susannae* (L.) Raf. (*Orchis susannae* L.) designated by Butzin, Taxon, 32(4): 631 (1983), P.J. Cribb, Taxon, 48: 49 (1999).
TYPE SPECIES: *P. gigantea* (Sm.) Raf. (*Orchis gigantea* Sm.) **invalidly** selected by S. Misra, Orchids Orissa, 139 (2004).

Pelatantheria Ridl., J. Linn. Soc., Bot., 32: 371 (1896).
LECTOTYPE: *P. ctenoglossum* Ridl. designated by Butzin, Taxon, 32(4): 632 (1983) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 893 (1991).

Pelexia Poiteau ex Lindl., Bot. Reg., 12: sub 985 (1826).
TYPE SPECIES: *P. spiranthoides* Lindl. This name is now considered a synonym of
P. adnata (Sw.) Poiter ex Rich. (*Satyrium adnatum* Sw.) which was lectotyped by Garay, Fl. Less. Antill., Orchid., 68 (1974).

Pennilabium J.J.Sm., Bull. Jard. Bot. Buitenzorg, ser. 2, 13: 47 (1914).
LECTOTYPE: *P. angraecum* (Ridl.) J.J.Sm. (*Saccolabium angraecum* Ridl.) designated by Garay, Bot. Mus. Leafl., 23(4): 189 (1972) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 892 (1991).

Penthea Lindl., Gen. Sp. Orchid. Pl., 360 (1838) and Intr. Nat. Syst. Bot., ed. 2, 446 (1836).
TYPE SPECIES: *P. patens* (L.f.) Lindl. (*Ophrys patens* L.f.) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 236 (1951).
TYPE SPECIES: *P. melaleuca* (Thunberg) Lindl. (*Serapias melaleuca* Thunberg) **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 627 (1874).

Pentisea (Lindl.) Szlach., Polish Bot. J., 46(1): 19 (2001).
LECTOTYPE: *P. gemmata* (Lindl.) Szlach. (*Calaenia gemmata* Lindl.) designated by Szlachetko, Polish Bot. J., 46(1): 19 (2001).

Peristylus Blume, Bijdr. Fl. Ned. Ind., 8: 404 (1825).
gemmata: *P. grandis* Blume designated by Greuter et al., Regnum Veg., 118: 183 (1988) and Seidenfaden, Dansk Bot. Arkiv, 31(3): 27 (1977).

Petalochilus R.S.Rogers, J. Bot., 62: 65 (1924).
TYPE SPECIES: *P. calyciformis* R.S. Rogers selected by D.L. Jones & M.A. Clements, Orchadian, 13(9): 406 (2001).

Phloeophila Hoehne & Schltr., Arch. Bot. São Paulo, 1(3): 199 (1926).
LECTOTYPE: *P. paulensis* Hoehne & Schltr. designated by Garay, Orquideologia, 9: 117 (1974).

Pholidota Lindl. ex Hook., Exot. Fl., 2: t. 138 (1825).

TYPE SPECIES: *P. imbricata* Hook. selected by M.A. Clements, Austral. Orchid. Res., 1: 105 (1989). This selection was not needed as Hooker originally had just one species.)

Phragmipedium (Pfitzer) Rolfe, Orchid Rev., 4: 331 (1896).
TYPE SPECIES: *P. caudatum* (Lindl.) Rolfe (*Cypripedium caudatum* Lindl.) selected by Sprague & Summerhayes, Kew Bulletin, 309 (1927).

Phymatidium Lindl., Gen. Sp. Orchid. Pl., 209 (1833).
LECTOTYPE: *P. delicatum* Lindl. designated by Angely, Fl. Analitica São Paulo, 6: 1328 (1973) and Toscano, Lindleyana, 16(3): 209 (2001).

Physoceras Schltr., Repert. Spec. Nov. Regni Veg. Beih., 33: 78 (1924).
LECTOTYPE: *P. bellum* Schltr. designated by Summerhayes, Index Nom. Gen. (Pl.), 3: 1335 (1979) card #64/24066 and J. & C. Hermans et al., Orchids Madagascar, 249 (2007).

Physosiphon Lindl., Edwards's Bot. Reg., 21: sub 1797 (1835).
TYPE SPECIES: *P. loddigesii* Lindl., nom. illeg.
TYPE SPECIES: *P. tubatus* (Loddiges) Rchb.f. (*Stelis tubata* Loddiges) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(1): 705 (1873).
LECTOTYPE: *Pseudostelis spiralis* (Lindl.) Schltr. (*Physosiphon spiralis* Lindl.) designated by Garay, Orquideologia, 9: 118 (1974).

Physurus Rich. ex Lindl., Gen. Sp. Orchid. Pl., 501 (1840).
TYPE SPECIES: *P. plantagineus* (L.) Lindl. (*Satyrium plantagineum* L.) selected by Britton & Millspaugh, Bahama Fl., 87 (1920).

Pilophyllum Schltr., Orchideen (Schlechter), ed. 1, 131 (1914).
LECTOTYPE: *P. villosum* (Blume) Schltr. (*Chrysoglossum villosum* Blume) designated by van der Burgh & de Vogel, Orchid Monog., 8: 172 (1997).

Pilumna Lindl., Edwards's Bot. Reg., 30(Misc.): 73 (1844).
TYPE SPECIES: *P. laxa* Lindl. selected by M.W. Chase, Gen. Orch., 5: 380 (2009).

Piperia Rydb., Bull. Torrey Bot. Club, 28: 269, 632 (1901).

TYPE SPECIES: *P. elegans* (Lindl.) Rydb. (*Platanthera elegans* Lindl.) selected by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 1: 555 (1913).

Pityphyllum Schltr., Repert. Spec. Nov. Regni Veg. Beih., 7: 162 (1920).
LECTOTYPE: *P. antioquiense* Schltr. designated by H.R. Sweet, Orquideologia, 7: 205 (1973).

Platanthera Rich., De Orchid. Eur., 20, 26, 35 (1817).
LECTOTYPE: *P. bifolia* (L.) Rich. (*Orchis bifolia* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3):539 (1989).

Platyclinis Benth., J. Linn. Soc., Bot., 18: 295 (1881).
LECTOTYPE: *P. abbreviata* (Blume) Benth. ex Hemsl. (*Dendrochilum abbreviatum* Blume) designated by H.A. Pedersen, J.J. Wood & J.B. Comber, Opera Bot., 130: 29 (1997).

Pleione D. Don, Prodr. Fl. Nepal., 36 (1825).
LECTOTYPE: *P. praecox* (J.E. Sm.) D. Don (*Epidendrum praecox* J.E. Sm.) designated by Zhu and S. Chen, Novon, 8: 461 (1998).

Pleuranthium Benth., J. Linn. Soc., Bot., 18: 312 (1881).
TYPE SPECIES: *P. dendrobii* (Rchb.f.) Benth. (*Epidendrum dendrobii* Rchb.f.) selected by Pfitzer, Nat. Pflanzenfam., 2(6): 145 (1889).

Pogonia Juss., Gen. Pl. (Jussieu), 65 (1789).
TYPE SPECIES: *P. ophioglossoides* (L.) Ker-Gawler (*Arethusa ophioglossoides* L.) selected by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 1: 559 (1913).

Polycyncis Rchb.f., Bonplandia, 3(15-16): 218 (1855).
TYPE SPECIES: *P. muscifera* (Lindl. & Paxton) Rchb.f. (*Cycnoches musciferum* Lindl. & Paxton) selected by G. Gerlach, Gen. Orchid., 5: 434 (2009).

Ponera Lindl., Gen. Sp. Orchid. Pl., 113 (1831).
TYPE SPECIES: *P. juncifolia* Lindl. designated by Lindley.
TYPE SPECIES: *P. graminifolia* (Knowles & Westc.) Lindl. (*Nemaconia graminifolia* Knowles & Westc.) **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 812 (1874).

Prasophyllum R.Br., Prodr. Fl. Nov. Holland., 317 (1810).
TYPE SPECIES: *P. australe* R.Br. selected by M.A.

Clements, Austral. Orchid. Res., 1: 109 (1989).

Pristiglottis Cretz. & J.J.Sm., Acta Fauna Fl. Universali, ser. 2, 1: 4 (1934).
TYPE SPECIES: *P. uniflora* (Blume) Cretz. & J.J.Sm. (*Cystopus uniflorus* Blume) selected by Weatherby, Bull. Misc. Inform., 1935: 421 (1935).

Promenaea Lindl., Edwards's Bot. Reg., 29(Misc): 13 (1843).
LECTOTYPE: *P. lentiginosa* (Lindl.) Lindl. (*Maxillaria lentiginosa* Lindl.) designated by Butzin, Taxon, 32(4): 632 (1983).

Pseuderiopsis Rchb.f., Linnaea, 22: 852 (1850).
LECTOTYPE: *P. schomburgkii* Rchb.f. designated by Romero, Harvard Pap. Bot., 10(2): 245 (2005).

Pseudoeurystyles Hoehne, Arq. Bot. Ext. S. Paulo, 1: 129 (1943).
LECTOTYPE: *P. lorenzii* (Cogn.) Hoehne (*Stenoptera lorenzii* Cogn.) designated by Angely, Fl. Analitica São Paulo, 6: 1273 (1973).

Pseudogoodyera Schltr., Beih. Bot. Centralbl., 37(2): 369 (1920).
LECTOTYPE: *P. wrightii* (Rchb.f.) Schltr. (*Goodyera wrightii* Rchb.f.) designated by Swart, Index Nom. Gen. (Pl.), 3 : 1434 (1979) card #10/23843; Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 144 (2008); and Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982).

Pseudorchis Ség., Pl. Veron., 3: 254 (1754).
LECTOTYPE: *P. albidus* (L.) Á. Löve & D. Löve (*Satyrium albidum* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 544 (1989).

Pseudostelis Schltr., Anexos Mem. Inst. Butantan, 1: 36 (1922).
TYPE SPECIES: *P. spiralis* (Lindl.) Schltr. (*Physosiphon spiralis* Lindl.) selected by Garay, Orquideologia, 9: 118 (1974).
LECTOTYPE: *Stelis deregularis* Barb.Rodr., designated superflously Luer, Monogr. Syst. Bot. Missouri Bot. Gard., **2**0: 36 (1986).

Pteroglossa Schltr., Beih. Bot. Centralbl., 37(2): 450 (1920).
LECTOTYPE: *P. macrantha* (Rchb.f.) Schltr. (*Spiranthes macrantha* Rchb.f.) designated by Angely, Fl. Analitica São Paulo, 6: 1277 (1973), Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 168 (2008) and Burns-Balogh, Amer. J. Bot., 69: 1132 (1982).

Pterostylis R.Br., Prodr. Fl. Nov. Holland., 326 (1810).
TYPE SPECIES: *P. obtusa* R.Br. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 875 (1874).
LECTOTYPE: *P. curta* R.Br. designated by Greuter et al., Regnum Veg., 118: 183 (1988).

Pterygodium Sw., Kongl. Vetensk. Acad. Nya Handl., ser. 2, 21: 217, t. 3e (1800).
TYPE SPECIES: *P. alatum* (Thunberg) Sw. (*Ophrys alata* Thunberg) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 876 (1874).
TYPE SPECIES: *P. catholicum* (Thunberg) Sw. (*Ophrys alata* Thunberg) selected by E.P. Phillips, Gen. S. Afr. Fl. Pl., ed. 2, 237 (1951).
LECTOTYPE: *P. catholicum* (Thunberg) Sw. designated by K.E. Steiner, Taxon, 48: 48 (1999).

Rhipidoglossum Schltr., Beih. Bot. Centralbl., 36(2): 80 (1918).
LECTOTYPE: *R. xanthopollinium* (Rchb.f.) Schltr. (*Aeranthus xanthopollinius* Rchb.f.) designated by Summerhayes, Blumea, Suppl., 1: 80 (1937).

Rhynchopera Klotzsch, Icon. Pl. Rar. (Link), 2: 103, t. 41 (1844).
TYPE SPECIES: *R. pedunculata* Klotzsch designated by Klotzsch.
TYPE SPECIES: *R. punctata* H. Karsten not validly selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 962 (1874).

Rhynchophreatia Schltr., Bot. Jahrb. Syst., 56: 488 (1921)
LECTOTYPE: *Rhynchophreatia wariana* Schltr. designated by Fosberg & Sachet, Micronesica, 20: 151 (1987).

Rhynchostylis Blume, Bijdr. Fl. Ned. Ind., 7: 285, t. 49 (1825)
LECTOTYPE: *R. retusa* (L.) Blume (*Epidendrum retusum* L.) designated by Christenson, Kew Bulletin, 41(4): 836 (1986).

Robiquetia Gaudichaud-Beaupré, Freycinet's Voy. Uranie, Bot., 426, t. 34 (1826)[1829]

LECTOTYPE: *R. brevifolia* (Lindl.) Garay (*Saccolabium brevifolium* Lindl.) designated by Christenson, Kew Bulletin, 41(4): 835 (1986).

Rodriguezia Ruiz & Pavón, Fl. Peruv. Prodr., 115, t. 25 (1794).

LECTOTYPE: *R. lanceolata* Ruiz & Pavón designated by Garay & H.R. Sweet, J. Arnold Arbor., 53: 527 (1972).

Rodrigueziopsis Schltr., Repert. Spec. Nov. Regni Veg., 16: 427. (1920).

LECTOTYPE: *R. eleutherosepala* (Barb.Rodr.) Schltr. (*Rodriguezia eleutherosepala* Barb.Rodr.) designated by Angely, Fl. Analitica São Paulo, 6: 1322 (1973) and Garay & H.R. Sweet, J. Arnold Arbor., 53: 527 (1972). TYPE SPECIES: *Rodrigueziopsis microphyton* (Barb. Rodr.) Schltr. (*Rodriguezia microphyta* Barb.Rodr.) selected by M.W. Chase, Gen. Orchid., 5: 271 (2009).

Roeperocharis Rchb.f., Otia Bot. Hamburg., 104 (1881).

LECTOTYPE: *R. bennettiana* Rchb.f. designated by P.J. Cribb, Gen. Orch., 2: 359 (2001).

Roezliella Schltr., Repert. Spec. Nov. Regni Veg., 15: 146 (1918)

TYPE SPECIES: *R. dilatata* (Rchb.f.) Schltr. (*Sigmatostalix dilatata* Rchb.f.) selected by M.W. Chase, Gen. Orchid., 5: 308 (2009).

Saccolabium Blume, Bijdr., 292, t. 50 (1825).

LECTOTYPE: *S. pusillum* Blume designated by Christenson, Kew Bull., 41(4): 835 (1986).

Sanderella Kuntze, Revis. Gen. Pl., 2: 649 (1891).

TYPE SPECIES: *S. discolor* (Barb.Rodr.) Cogn. (*Parlatorea discolor* Barb.Rodr.) selected by Cogniaux, Fl. Bras., 3(6): 239 (1905).

Sarcopodium Lindl. & Paxton, Paxton's Fl. Gard., 1: 155 (1850).

TYPE SPECIES: *S. lobbii* (Lindl.) Lindl. & Paxton (*Bulbophyllum lobbii* Lindl.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 1051 (1874). TYPE SPECIES: *S. amplum* (Lindl.) Lindl. (*Dendrobium amplum* Lindl.) **invalidly** selected by Kraenzlin, Pflanzenr. IV. 50. II(B) 21 (Heft 45): 319 (1910).

Satyrium L., Sp. Pl. (Linnaeus), ed. 1, 2: 944 (1753).

LECTOTYPE: *S. viride* L. designated by M.L. Green, Prop. Brit. Bot., 185 (1929).

Sauroglossum Lindl., Edwards's Bot. Reg., 19: t. 1618 (1833).

LECTOTYPE: *S. elatum* Lindl. designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 144 (2008).

Scaphosepalum Pfitzer, Nat. Pflanzenfam., 2(6): 139 (1888).

LECTOTYPE: *S. ochthodes* (Rchb.f.) Pfitzer (*Masdevallia ochthodes* Rchb.f.) designated by Garay, Orquideologia, 9: 124 (1974).

Scaphyglottis Poepp. & Endl., Nov. Gen. Sp. Pl., 1: 58 (1836).

TYPE SPECIES: *S. parviflora* Poepp. & Endl. **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 1068 (1874). The accepted name for *S. parviflora* is *Camaridium vestitum* (Sw.) Lindl.

LECTOTYPE: *S. graminifolia* (Ruiz & Pavón) Poepp. & Endl. (*Fernandezia graminifolia* Ruiz & Pavón) designated by Dressler, Taxon, 9: 214 (1960) and Garay & H.R. Sweet, J. Arnold. Arbor., 53: 528 (1972).

Schiedeella Schltr., Beih. Bot. Centralbl., 37(2): 379 (1920).

LECTOTYPE: *S. saltensis* (Ames) Schltr. (*Spiranthes saltensis* Ames) designated by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982). TYPE SPECIES: *S. transversalis* (A.Rich. & Galeotti) Schltr. (*Spiranthes transversalis* A.Rich. & Galeotti) selected by Garay, Bot. Mus. Leafl., 28(4)**:** 357 (1982). LECTOTYPE: *S. llaveana* (Lindl.) Schltr. (*Spiranthes llaveana* Lindl.) designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 173 (2008).

Schoenorchis Blume, Bijdr. Fl. Ned. Ind., 8: 361 (1825).

TYPE SPECIES: *S. juncifolia* Blume selected by Garay, Bot. Mus. Leafl., 23(4): 202 (1972). LECTOTYPE: *Schoenorchis gemmata* (Lindl.) J.J.Sm. (*Saccolabium gemmatum* Lindl.) designated by Christenson, Kew Bulletin, 41(4): 836 (1986). LECTOTYPE: *S. juncifolia* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 894 (1991).

Selenipedium Rchb.f., Xenia Orch., 1: 3, t. 2 (1854).

TYPE SPECIES: *S. chica* Rchb.f. selected by Sprague &

Summerhayes, Bull. Misc. Inform., 308 (1927).

Sepalosaccus Schltr., Repert. Spec. Nov. Regni Veg. Beih., 19: 245 (1923).

LECTOTYPE: *S. humilis* Schltr. designated by K. Barringer, Fieldiana, Bot., 17: 18 (1986).

Serapias L., Sp. Pl. (Linnaeus), ed. 1, 2: 949 (1753).

TYPE SPECIES: *S. lingua* L. selected by Sw., Kongl. Vetensk. Acad. Nya Handl., 21: 224 (1800).

LECTOTYPE: *S. lingua* L. designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 558 (1989).

Smithsonia C.J.Saldanha, J. Bombay Nat. Hist. Soc., 71(1): 73 (1974).

LECTOTYPE: *S. viridiflora* (Dalzell) C.J. Saldanha (*Micropera viridiflora* Dalzell) designated by Christenson, Kew Bulletin, 41(4): 836 (1986).

Sobennikoffia Schltr., Repert. Spec. Nov. Regni Veg. Beih., 33: 361 (1925).

LECTOTYPE: *S. robusta* (Schltr.) Schltr. (*Oeonia robusta* Schltr.) designated by Butzin, Taxon, 32(4): 632 (1983).

Sobralia Ruiz & Pavón, Fl. Peruv. Prodr. 120, t. 26 (1794).

LECTOTYPE: *S. dichotoma* Ruiz & Pavón designated by Angely, Fl. Analítica São Paulo, 6: 1268 (1973).

Specklinia Lindl., Gen. Sp. Orchid. Pl., 8 (1830).

LECTOTYPE: *S. lanceola* (Sw.) Lindl. (*Epidendrum lanceola* Sw.) designated by Garay & H.R. Sweet, J. Arnold Arbor., 53: 528 (1972).

Spiranthes Rich., De Orchid. Eur., 20, 28 & 36 (1817).

LECTOTYPE: *S. spiralis* (L.) Chevallier (*Ophrys spiralis* L.) designated by M.L. Green, Prop. Brit. Bot., 100 (1929) and H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 562 (1989).

TYPE SPECIES: *S. aestivalis* (Poiret) Rich. (*Ophrys aestivalis* Poiret) **invalidly** selected by Correll, Fl. Texas, 3(3): 169 (1944).

Stauropsis Rchb.f., Hamburger Garten-Blumenzeitung, 16: 117 (1860).

TYPE SPECIES: *S. philippinensis* (Lindl.) Rchb.f. (*Trichoglottis philippinensis* Lindl.) selected by Reichenbach f., Ann. Bot. Syst., 6: 882, 932 (1864).

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

LECTOTYPE: *S. ophioglossoides* (Jacq.) Sw. (*Epidendrum ophioglossoides* Jacq.) designated by M.L. Green, Prop. Brit. Bot., 100 (1929) and Pridgeon, Gen. Orch., 4: 405 (2005).

LECTOTYPE: *S. purpurea* (Ruiz & Pav.) Willd. (*Humboldtia purpurea* Ruiz & Pavón) designated by Garay & H.R. Sweet, J. Arnold Arbor., 53: 528 (1972).

Stenorrhynchos Rich. ex Spreng., Syst. Veg. (Sprengel), ed. 16, 3: 677 (1826).

TYPE SPECIES: *S. speciosum* (Jacq.) Spreng. (*Neottia speciosa* Jacq.) selected by Britton & Millspaugh, Bahama Fl., 86 (1920).

LECTOTYPE: *S. speciosum* (Jacq.) Spreng. designated by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982).

LECTOTYPE: *S. orchioides* (Sw.) Rich. (*Satyrium orchioides* Sw.) **invalidly** designated by M.N. Corrêa, Darwiniana, 11: 70 (1955).

Stichorkis Thouars, Nouv. Bull. Soc. Philom., 19: 318 (1809).

LECTOTYPE: *S. disticha* (Thouars) Pfitzer (*Malaxis disticha* Thouars) designated by Rasmussen, Bot. Not., 132: 390 (1979).

Sullivania F.Muell., J. Proc. Roy. Soc. New South Wales, 15: 229 (1882).

TYPE SPECIES: *Caleya sullivanii* F.Muell. selected by D.L. Jones & M.A. Clements, Orchadian, 15(1): 36 (2005).

Synassa Lindl., Bot. Reg., 19: sub 1618 (1833).

LECTOTYPE: *S. corymbosa* Lindl. designated by Rutkowski et al., Phylogeny & Taxonomy Subtribes Spiranthinæ, 145 (2008).

Synoplectris Raf., Fl. Tellur., 2: 87 (1837).

LECTOTYPE: *S. grandiflora* (Hook.) Klotzsch (*Neottia grandiflora* Hook.) designated by Garay, Bot. Mus. Leafl., 28: 352 (1982).

Systeloglossum Schltr., Repert. Spec. Nov. Regni Veg. Beih., 19: 252 (1923).

LECTOTYPE: *S. costaricense* Schltr. designated by Barringer, Fieldiana, Bot., 17: 21 (1986).

Taeniophyllum Blume, Bijdr. Fl. Ned. Ind., 8: 355, t. 70 (1825).

LECTOTYPE: *T. obtusum* Blume designated by Garay, Bot. Mus. Leafl., 23(4): 205 (1972) and Averyanov,

Bot. Zhurn. (Moscow & Leningrad), 76(6): 892 (1991).

Telipogon Kunth, Nov. Gen. Sp., 1: 335, t. 75 (1815).
TYPE SPECIES: *T. nervosus* (L.) Druce (*Tradescantia nervosa* L.) selected by M.W. Chase, Gen. Orch., 5: 362 (2009).

Tetragamestus Rchb.f., Bonplandia, 2: 21 (1854).
TYPE SPECIES: *Scaphyglottis arundinacea* Regel **invalidly** selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 1373 (1874).
TYPE SPECIES: *T. aureus* Rchb.f. indirectly selected by Reichenbach f., Linnaea, 41: 85 (1876).

Thelasis Blume, Bijdr. Fl. Ned. Ind., 8: 385, t. 75 (1825).
TYPE SPECIES: *T. carinata* Blume selected by M.A. Clements, Austral. Orchid. Res., 1: 137 (1989).
LECTOTYPE: *T. obtusa* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 124 (1991).
TYPE SPECIES: *T. obtusa* Blume selected by J.J. Wood, Gen. Orch., 4: 593 (2005).

Thelychiton Endl., Prodr. Fl. Norfolk., 32 (1833).
TYPE SPECIES: *T. macropus* Endl. selected by M.A. Clements, Austral. Orchid Res., 1: 56 (1989).

Tomotris Raf., Fl. Tellur., 2: 89 (1837).
LECTOTYPE: *T. flava* (Sw.) Rchb.f. (*Serapias flava* Sw.) designated by Rasmussen, Bot. Tidssk., 71: 168 (1977).

Trachelosiphon Schltr., Beih. Bot. Centralbl., 37(2): 423 (1920).
LECTOTYPE: *Eurystyles actinosophylla* (Barb.Rodr.) Schltr. (*Spiranthes actinosophila* Barb.Rodr.) designated by Acuña, Cat. Descr. Orquid. Cuba., 60: 43 (1938).
LECTOTYPE: *T. ananassocomos* Rchb.f. designated by Burns-Balogh, Amer. J. Bot., 69(7): 1131 (1982).

Trachyrhizum (Schltr.) Brieger, Schlechter Orchideen (ed. 3), 1(11-12): 687 (1981).
TYPE SPECIES: *T. schlechteri* (Schltr.) Rauschert (*Dendrobium trachyrhizum* Schltr.) selected by Rauschert, Feddes Repert., 94(7-8): 469 (1983).
TYPE SPECIES: *Dendrobium chalmersii* F.Muell. invalidaly selected by M.A. Clements, Telopea., 10(1): 280 (2003).

Traunsteinera Rchb., Fl. Saxon., 87 (1842), and Deut. Bot. Herb.-Buch, 50 (1841).
LECTOTYPE: *T. globosa* (L.) Rchb. (*Orchis globosa* L.) designated by H. Baumann et al., Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ., 21(3): 564 (1989).

Trichoceros Kunth, Nov. Gen. Sp., 1: 337, t. 76 (1815).
TYPE SPECIES: *T. antennifer* (Humb. & Bonpl.) Kunth (*Epidendrum antenniferum* Humb. & Bonpl.) selected by M.W. Chase, Gen. Orch., 5: 378 (2009).

Trichoglottis Blume, Bijdr. Fl. Ned. Ind., 8: 359, t. 8 (1825).
TYPE SPECIES: *T. retusa* Blume selected by Garay, Bot. Mus. Leafl., 23(4): 208 (1972).
LECTOTYPE: *T. miserum* (Ridl.) Holttum (*Saccolabium miserum* Ridl.) designated by Christenson, Kew Bulletin, 41(4): 836 (1986).

Trichotosia Blume, Bijdr. Fl. Ned. Ind., 7: 342 (1825).
LECTOTYPE: *T. pauciflora* Blume designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(1): 126 (1991).
TYPE SPECIES: *T. pauciflora* Blume selected by P.J. Cribb, Gen. Orch., 4: 583 (2005).

Tridactyle Schltr., Orchideen (Schlechter), ed. 1, 602 (1914).
LECTOTYPE: *T. bicaudata* (Lindl.) Schltr. (*Angraecum bicaudatum* Lindl.) designated by Summerhayes, Kew Bull., 282 (1948).

Trigonanthe (Schltr.) Brieger, Schlechter's Orchideen, ed. 3, 7: 448 (1975).
TYPE SPECIES: Masdevallia simula Rchb.f. selected by Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 26 (1986).

Triphora Nuttall, Gen. N. Amer., Pl., 192 (1818).
TYPE SPECIES: *T. pendula* Nuttall, nom. illeg. (*Arethusa pendula* Willd., nom. illeg). This type name is now considered a synonym of *T. trianthophora* (Sw.) Rydb. (*Arethusa trianthophoros* Sw.) selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 1484 (1874).

Triphorhiza Ehrhart, Beitr. Naturk. (Ehrhart), 4: 149 (1789).
TYPE SPECIES: *Satyrium albidum* L. selected by Pfeiffer, Nomencl. Bot. (Pfeiffer), 2(2): 1486 (1874).

Tylostigma Schltr., Beih. Bot. Centralbl., 4: 298 (1916).
LECTOTYPE: *T. madagascariensis* Schltr. designated by P.J. Cribb, Gen. Orch., 2: 379 (2001).

Uncifera Lindl., J. Proc. Linn. Soc., Bot., 3: 39 (1859)
LECTOTYPE: *U. obtusifolia* Lindl. designated by Christenson, Kew Bulletin, 41(4): 837 (1986) and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 76(6): 893 (1991).

Vanilla Plum. ex Mil., Gard. Dict., abridged ed. 4, 3: without page number (1754).
TYPE SPECIES: *V. mexicana* Mil. designated by Mansfeld, Kulturpflanze, 2: 587 (1959); Angely, Fl. Analitica São Paulo, 6: 1267 (1973), and Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(12): 1760 (1990).
TYPE SPECIES: *V. mexicana* Mil. selected by Britton & Wilson, Bahama Fl., 83 (1920).
LECTOTYPE: *V. planifolia* Jacks. designated by Garay & H.R. Sweet, Fl. Lesser Antilles, 44 (1974).

Vrydagzynea Blume, Coll. Orchid., 71, tt. 17 (1858).
LECTOTYPE: *V. albida* (Blume) Blume (*Hetaeria albida* Blume) designated by Averyanov, Bot. Zhurn. (Moscow & Leningrad), 75(7): 1023 (1990).

Warczewiczella Rchb.f., Bot. Zeitung (Berlin), 10: 635 (1852).
TYPE SPECIES: *W. discolor* (Lindl.) Rchb.f. (*Warrea discolor* Lindl.) selected by Britton & Wilson, Sci. Surv. Porto Rico, 5(2): 214 (1924).

Zeuxine Lindl., Coll. Bot. (Lindl.), App. [n. 18] (1826).
TYPE SPECIES: *Z. stratematica* (L.) Schltr. (*Orchis stratematica* L.) designated by P.J. Cribb, Taxon, 48: 49 (1999).

Zygosepalum Rchb.f., Ned. Kruidk. Arch., 4: 330 (1859).
TYPE SPECIES: *Z. kegelii* (Rchb.f.) Rchb.f. (*Zygopetalum kegelii* Rchb.f.) selected by Pupulin, Gen. Orch., 5: 544 (2009).

Zygostates Lindl., Edwards's Bot. Reg., 23: 1927 (1837)
LECTOTYPE: *Z. lunata* Lindl. designated by Angely, Fl. Analítica São Paulo, 6: 1328 (1973).
LECTOTYPE: *Z. cornuta* Lindl. designated by Toscano, Lindleyana, 16(3): 193 (2001).

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[1] These lists are only current as of March 1 2010.

Commentary. When using various sources for basic lectotype research we have come across some listings that state the name as being lectotypified, but upon further investigation of the original cited literature find the statement to be untrue. All the taxonomic citations in this paper have been verified with original literature.

There are many names currently listed in *Index Nominum Genericorum* (ING) as being lectotypified. Many of the names are correctly listed, but there are also many names that are not true lectotypes but just various authors listing a name as a type species for a given genus (selected). There are others listed as having lectotypes but upon reading the literature cited find that the authors provided no types or lectotype names[1].

Genus names listed in ING that are just listings of type species for a genus and have NOT been lectotypified:

Aa, Amphigena, Ancistrorhynchus, Anochilus, Arethusa, Blephariglotis, Bletia, Brownleea, Centrostigma, Cephalanthera, Ceratandropsis, Chrysoglossum, Cladobium, Cleisostoma, Comparettia, Corysanthes, Crepidium, Cyrtopera, Cyrtosia, Cystorchis, Dryadorchis, Epiblastus, Evota, Gennaria, Gymnadeniopsis, Habenaria, Kefersteinia, Limnorchis, Malaxis, Oeceoclades, Orthopenthea, Palmorchis, Penthea, Physosiphon, Physurus, Piperia, Pleione, Pogonia, Pterygodium, Satyrium, Schoenorchis, Stauropsis, Stenorrhynchos, Trichoglottis, Triphora.

These names are listed in ING as lectotypified, which at the time they were not, but have since been lectotypified by various authors in other literature:

Ania, Barbosella, Coelogyne, Cypripedium, Cyrtochilum, Disperis, Goodyera, Ophrys, Orchis, Pecteilis, Schiedeella.

These are names listed in ING as lectotypified, but they are NOT:

Capanemia, Chelonanthera, Dendrochilum, Diaphananthe.

The names that Alrich previously published (Selbyana 29(2) 2008) as published by Pfeiffer, are just that a list of type names for various genera and are NOT true lectotypes.

Literature Cited

Farr, E. R. & G. Zijlstra (eds.). Index Nominum Genericorum (Plantarum). 1996+. Published on the Internet; http://botany.si.edu/ing/ (accessed 1 March 2010).

Govaerts, R., J. Pfahl (Florida, 2006), M.A. Campacci (Brazil, 2005), D. Holland Baptista (Brazil, 2005), H. Tigges (Germany, 2005), J.Shaw (RHS, 2005), P. Cribb (K, 2003), A. George (K, 2003), K. Kreuz (2004, Europe), J. Wood (K, 2003, Europe). 2010. World Checklist of Orchidaceae. The Board of Trustees of the Royal Botanic Gardens, Kew. Published on the Internet; http://www.kew.org/wcsp/ (accessed 1 March 2010).

McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema & N. J. Turland. 2006. International Code of Botanical Nomenclature (Vienna Code). Regnum Vegetabile 146. A.R.G. Gantner Verlag KG.

The International Plant Names Index., 2008. Published on the Internet; http://www.ipni.org (accessed 1 March 2010).

Tropicos, botanical information system at the Missouri Botanical Garden. Published on the Internet; http://www.tropicos.org (accessed 1 March 2010).