A NOTE ON *PROSTHECHEA* (ORCHIDACEAE: LAELIINAE), WITH A NEW SPECIES

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ABSTRACT. Current views about the phylogeny of Laeliinae (Orchidaceae) and the systematic position of *Prosthechea* and related genera are discussed. Morphologic characters used to circumscribe genera in the *Prosthechea* clade are reviewed. A new species from Costa Rica, *P. barbozaei*, is described and illustrated. *Prosthechea barbozaei* is closely related to *P. glauca* and *P. ortizii*, from which it may be distinguished by the ligulate sepals and oblong petals, the elliptic-oblong lateral lobes and the suborbicular, retuse midlobe of the lip, the shape of the callus and the androclinium, and the vegetative habit, with suborbicular, strongly ancipituous pseudobulbs, respectively.

Key words: Orchidaceae, Laeliinae, Prosthechea, Prosthechea barbozaei, Pseudoencyclia, Anacheilium, Hormidium, Panarica, Pollardia, morphology, systematics, Costa Rica

Introduction

It seems that new species of *Prosthechea* Knowles & Westc. closely related to the type species of the genus, *P. glauca*, appear periodically to allow botanists to discuss and review their concepts about the generic circumscription of this group of neotropical orchids (Dressler 1980). The taxonomic history of *Prosthechea* was enlightened by Higgins (1998), when he resurrected the genus to accommodate more than 60 species previously treated under *Amblostoma* Scheidw., *Anacheilium* Rchb.f. ex Hoffmanns., *Coelogyne* Lindl., *Encyclia* Hook., *Epicladium* Small, *Epidendrum* L., *Epithecia* Knowles & Westc., *Hormidium* Lindl. ex Heynh, and *Microstylis* Nutt.

Knowles and Westcott (1838) proposed the genus Prosthechea for a plant closely allied to Epidendrum, imported from Mexico and cultivated in England by George Barker of Springfield. Among the generic characters used to distinguish the new taxon from Epidendrum, the authors indicated differences in the structure of the lip and the gynostemium, as well as the subdorsal position of the anther (Knowles & Westcott 1838). The generic name was derived from the Greek prostheke, appendage, in allusion to the dorsal appendage of tissue at the apex of the column of the type species. The following year. in the same Volume 2 of the Floral Cabinet for 1838 (effectively published in 1839), the authors felt the need of a correction to the generic name Prosthechea, which was supposedly predated by a name "very similar in sound," and they proposed the homotypic Epithecia (Knowles & Westcott 1839). Among the generic names published in Index Kewensis, only Prosthesia Blume

(1826), in the Violaceae, actually presents some similarity in sound with Prosthechea, but it cannot be considered a homonym of the latter, which was validly published and has priority (Higgins 1998, 1999; Higgins et al. 2003). In 1840 John Lindley had the opportunity to study living specimens of the Mexican plant from Barker's collection and reduced the illegitimate Epithecia into synonymy under Epidendrum (Lindley 1840). Lindley's new combination, Epidendrum glaucum [1840] is another illegitimate name, a later homonym predated by Epidendrum glaucum Sw. [1788], a species that Lindley himself had previously transferred to his genus Dichaea (Lindley 1833). In 1842, in his treatment of the Encyclium subgenus of Epidendrum, Lindley grouped E. glaucum with another nine species on the basis of its 3-lobed lip provided with very reduced lateral lobes, shorter than the midlobe (Lindley 1842). As a consequence of Lindley's statements, the genus Prosthechea (together with its synonym Epithecia) fell into botanical oblivion for more than 150 years.

In their treatment of Encyclia glauca (Knowles & Westc.) Dressler & Pollard (=Prosthechea glauca) for the revision of the genus Encyclia in Mexico, Dressler and Pollard (1976) noted that Prosthechea was the earliest generic name applied to a species of Encyclia section Osmophytum and probably the valid name for this group of orchids, if treated as a distinct genus. Describing Encyclia fortunae [=Prosthechea fortunae (Dressler) W.E. Higgins], Dressler made a second case for the adoption of the generic name Prosthechea, although he preferred at the time to formally include the new species, as well as the taxa close to P. glauca, into a subgenus of Encyclia (Dressler 1980). After resurrection of

the old Knowles and Westcott name (Higgins 1998), botanists working with neotropical floras largely agreed with the generic circumscription of Prosthechea, as proposed by Higgins, to embrace the species included by Dressler and Pollard (1971) in their Encyclia sect. Osmophytum (van der Berg et al. 2000, 2001; Mújica Benítez et al. 2000; Nir 2000, Hamer 2001, Pupulin 2002a, 2002b, Chiron 2003; Dressler 2003; Hágsater & Soto 2003; Higgins et al. 2003). Studies of phylogenetic relationships of the Laeliinae based on molecular data sets (van der Berg et al. 2000, 2001; Higgins et al. 2003) supported the view of Encyclia as a polyphyletic genus and the need to recognize *Prosthechea* as a distinct genus (Higgins 2003). Euchile (as proposed by Withner 1998) is sister to Prosthechea and could be recognized as a distinct genus based on morphology (Higgins 2003).

Recently, some different ideas, however, have been brought to light about Prosthechea. Withner (2001) proposed a very narrow delimitation of Prosthechea, which in his view should be circumscribed to a few species characterized by a long-clawed lip, without a forcipate callus, and a fleshy tooth at the apex of column, i.e., P. christyana (Rchb.f.) Garay & Withner, P. fortunae, P. glauca, P. serpentilingua Withner & Hunt, and P. squamata (Porto & Brade) W.E. Higgins [=P. megahybos (Schltr.) Dodson & Hágsater]. Although Withner did not take it in account, P. ortizii (Dressler) W.E. Higgins obviously pertains to the same group (Dressler 1995). Chiron (2003) recognized within Prosthechea sensu Higgins the existence of six different "informal groups" based on lip shape. Finally, on the basis of a cladistic study carried out utilizing morphological and ecological characters, Chiron and Castro Neto (2003) formally proposed to subdivide Prosthechea into four subgenera and to separate the new genus Pseudoencyclia Chiron & V.P. Castro, the latter characterized by laterally compressed pseudobulbs, thin leaves, resupinate flowers, a three-lobed lip with small lateral lobes, the vein of the callus extending to the lip apex, and the column provided with a large median tooth with two deep sinuses separating it from the lateral teeth. Within Pseudoencyclia, the authors claimed the existence of a well-defined complex "brassavolae," for which a formal taxonomic rank may be perhaps designated.

Withner and Harding (2004) have proposed dividing *Prosthechea* sensu lato into five genera: *Anacheilium, Hormidium, Panarica, Pollardia*, and *Prosthechea*. According to their key, *Anacheilium* is separated from *Pollardia* ("livida" complex) based on resupination; *Hormidium* ("pygmaea" complex) is separated from *Pros-*

thechea based on column mid-tooth shape; and Panarica ("brassavolae" complex) is separated from Prosthechea based on lip length. The authors admit that the placement of some species is problematic in their classification. The cockleshell anachelilums are not a cohesive group, when Prosthechea vespa is included in the genus Anachelilum.

Although phylogenetic studies began with morphology, the role of comparative morphology in plant systematics changed drastically after the advent of molecular methods in the late 1980s, shifting to evolutionary reconstruction and the study of structural similarities at levels where DNA analyses are for some reason difficult. Before the rbcL analyses started by Chase et al. (1993), relatively few large morphological cladistic studies were carried out, mainly because of the difficulty in building a sensible morphological data matrix (Stevens 1991). As Endress recently acknowledged, however, the results advanced by molecular studies, have opened new opportunities for morphology in plant evolutionary biology (Endress 2003). These may be synthesized in the refined analysis of characters induced by inconsistencies of molecular phylogenetic analyses and a better understanding of morphological features in a wider biological context. Moreover, comparative morphology is still helpful in selecting the appropriate taxa to be included in molecular phylogenetic reconstructions, mainly when molecular studies reveal some puzzling relationships. Nevertheless, the value of morphology as an evolutionary tool largely depends on the degree of knowledge of character distribution outside the group under study, which improves character selection and character-state scoring, and the accurateness of observations.

In the case of Prosthechea s.l., dealing with a heterogeneous group of some 90 species that range from Florida to Argentina and the West Indies (Govaerts 2002), character selection and delimitation are critical. If one attempts to state the diagnostic features that should define Prosthechea s.s., as intended by Withner (2001), problems become easily apparent. Vegetative architecture is highly variable in the group: P. christyana and P. megahybos have conical-fusiform pseudobulbs, rounded in section, apically provided with two narrowly elliptic leaves [similar to those of P. ochracea. (Lindl.) W.E.Higgins]. Prosthechea ortizii has narrowly pyriform-ovate, slightly flattened, monophyllous pseudobulbs. Prosthechea serpentilingua presents narrowly ovate, ridged, 2-leaved pseudobulbs, with linear-elliptic leaves. Both P. glauca and P. fortunae have ovate-suborbicular, strongly flattened pseudobulbs, provided with 1 or 2

elliptic-lanceolate, glaucous leaves. The new species described hereafter has widely ovatesuborbicular, ancipitous, monophyllous pseudobulbs; the elliptic leaf is abaxially glaucous. When not in flower, the last three taxa are practically indistinguishable from plants of P. campylostalix (Rchb.f.) W.E.Higgins. Inflorescences. produced from a spathaceous bract, are simple (P. christyana, P. fortunae, P. megahybos, P. ortizii, P. serpentilingua) or paniculate racemes (P. glauca and the new species), erect (P. glauca, P. ortizii, P. serpentilingua) to arching (P. glauca, P. megahybos) or pendent (P. christyana), few-flowered (P. christyana, P. fortunae, P. megahybos, P. ortizii, P. serpentilingua) to many-flowered (P. glauca). The ovary is triquetrous in P. christyana, P. fortunae, and P. megahybos; it is rounded in P. glauca and P. serpentilingua, and slightly triquetrous at apex in P. ortizii and the new species. Also flower morphology is variable within the group. Sepals are distinctly larger than petals in all the taxa, with the notable exception of P. serpentilingua. which presents Encyclia-like petals, provided with a narrow claw and a widely elliptic lamina. The lip is clawed and usually three-lobed, with the lateral lobes smaller than mid-lobe, but it is simple in P. serpentilingua. A lip provided with small lateral lobes is also a common feature in the P. vespa complex. The midlobe is abruptly recurved in P. glauca, P. ortizii, and the new species; it is straight in P. christyana and P. fortunae, and slightly up-curved in P. megahybos. The basal callus is fleshy, trullate (P. christyana and P. megahybos), subrectangular and apically 3-toothed (P. fortunae), quadrate-oblong (P. glauca and P. ortizii), or rounded (the new species); it is absent in P. serpentilingua. The column of P. serpentilingua is straight and apically provided with a flap-like, petaloid appendage; whereas in the other species, it is more or less curved toward the lip and provided with a fleshy

In the cladistic analysis based on morphological features by Chiron and Castro Neto (2003), *Prosthechea* is defined by usually fusiform pseudobulbs, non-resupinate flowers, and the column provided with a fleshy, apical tooth. Within Prosthechea, the authors proposed subgenera Prosthechea, Osmophytum, Hormidium, and Equiloba (with four sections), the former largely corresponding to Prosthechea sensu Withner (2001), with the exception of *P. serpentilingua*, which Chiron & Castro Neto argued was described on the basis of misshapen flowers of an Encyclia species close to E. osmantha. Because of the systematic relevance of flower position, authors, in their analysis, gave double weight to character 19 (flower resupinate or not). The type species of the genus, P. glauca, however, has resupinate flowers, as well as suborbicular, strongly ancipitous pseudobulbs. Also the flowers of P. megahybos (treated as P. squamata in the analysis) are resupinate, similar to most of the species included in Pseudoencyclia, and the same is true for all species close to P. glauca (or the genus Prosthechea in the sense of Withner, plus P. ortizii). The columns of the two species of Prosthechea subgen. Prosthechea included in the analysis and stated to be straight (character 50) are actually curved toward the lip. Taxonomic and nomenclatural consequences of the cladistic analysis formally recognize the existence of several, distinct subsets of species within Prosthechea as well as the compulsion to describe a new genus (Pseudoencyclia) for taxa excluded from the narrow definition of Prosthechea. The authors admit that subset Pseudoencyclia is difficult to characterize (Chiron & Castro Neto 2003: 24) for any specific synapomorphy. The generic characters of Pseudoencyclia defined in the protologue are pseudobulbs more or less laterally compressed, leaves usually thin, inflorescence produced from a spathe, flowers resupinate, petals never larger than sepals, lip 3lobed, without nectar guides, with the lateral lobes smaller than midlobe and usually upcurved toward the column, callus with the vein prolonging to the apex of lip, column without wings and provided with a fleshy apical tooth, separated from the lateral teeth by a deep sinus. Such characters are indistinguishable from the features of the type species of the genus Prosthechea, P. glauca, and species close to it.

Members of the genus Prosthechea s.l. show a wide and continuous variation in vegetative and floral characters throughout their distributional range. This continuum in overall morphology is perhaps more evident in northern Mesoamerica, which is probably the distribution center of many species complexes (Pupulin 2002), than in South American floras, where species subsets are someway more sharply defined. Characters that should define Pseudoencyclia are spread across Prosthechea s.l., and the recognition of Pseudoencyclia at the generic level is not predictive based on its morphological characteristics. Results of molecular analyses using nuclear and plastid sequence data (Higgins et al. 2003) reveal, among Laeliinae, that the clades Encyclia s.s., Prosthechea, Euchile, and Dinema have strong bootstrap support. They also reveal that the clade of *P. pygmaea* (Hook.) W.E. Higgins and P. pseudopygmaea (Finet) W.E. Higgins, as well as that of P. ionocentra (Rchb.f.) W.E. Higgins and P. prismatocarpa (Rchb.f.) W.E. Higgins [the latter treated by Chiron and Castro Neto (2003) as the genus Pseudoencyclia] are imbedded in *Prosthechea*. Waiting for the results of a larger, multi-gene analysis (C. van der Berg unpubl. data), and combined morphologic and DNA studies of the Laeliinae, it seems advisable to retain a wide concept of *Prosthechea*, which is a predictive group easy to define using morphological as well as molecular characters.

NEW SPECIES

As a result of the continuous work in inventorying the epiphytic flora of Costa Rica carried out by researchers at Jardín Botánico Lankester, Universidad de Costa Rica, and the associate staff, the following species is described as new to science.

Prosthechea barbozaei
Pupulin, sp. nov. TYPE:
COSTA RICA. Alajuela: Reserva Bosque Nuboso Monteverde, Peñas Blancas, 900 m, premontane wet forest, collected by G. Barboza, 6 June 2001, flowered in cultivation at the Orchid Garden in Monteverde, 27 December 2003, F. Pupulin 5011 (holotype, USJ; isotype, USJ-Spirit).

A *Prosthecheae glaucae* Knowles et Westc. similis, sepalis ligulatis petalisque oblongis, labelli lobulis lateralibus elliptico-oblongis, lobo intermedio suborbiculari retuso, callo tricostato, columna longiore dentibus lateralibus ellipticis, dente medio ovato subaequantibus recedit; a *P. ortizii* (Dressler) W.E. Higgins pseudobulbis late ovatis vel suborbicularis valde ancipitiis, foliis glaucis, labelli callo tricostato recedit.

Plant epiphytic, pseudobulbous, cespitose, small to ca. 11 cm high. Roots slender, flexuous, ca. 1.8 mm in diameter. Rhizome abbreviate. Pseudobulbs clustered, ovoid to suborbicular, strongly complanate, $2.1-3.0 \times 1.8-2.4$ cm, monophyllous, subtended at the base when young by 2 conduplicate, triangular, acute, papyraceous sheaths to 1.9×1.3 cm. *Leaf* elliptic, subacute, minutely apiculate, conduplicate at the base, 7×3 cm, abaxially glaucous. *Inflores*cence produced from a short, spathaceous, conduplicate bract ca. 1.1 cm long, a simple or paniculate raceme to 22 cm long, the lateral branches short, basal, to 3 cm long; the peduncle terete, to 15 cm long; bracts of the inflorescence 4, triangular-ovate, acute, 5×3 mm; floral bracts narrowly triangular, acute, 4.0×1.5 mm. Ovary pedicellate, glaucous, slightly triquetrous at apex, provided with a rounded nectary at the junction with the lip, to 1.4 cm long including the pedicel. Flowers spreading, with sepals and petals greenish-yellow blotched brown, glaucous externally, the lip greenish-yellow, the column greenish-yellow, suffused brown at the base, sparsely spotted purple at apex. Sepals subsi-

milar, ligulate-lanceolate, acute, conduplicate, rather fleshy toward the apex, 9×2.7 mm. **Pet**als somewhat porrect, oblanceolate-oblong, obtuse, 7.5×1.8 mm. *Lip* clawed, to 8.0×4.5 mm wide across lateral lobes; the claw linear, 4 mm long; the lamina 3-lobed, the lateral lobes subfalcate-elliptic, rounded, erect in natural position, 2×1 mm; midlobe ovate, retuse, strongly reflexed, 3×3 mm; callus a prominent, fleshy, rounded tooth, flanked by 2 low, conical, rounded knobs. Column subtriquetrous, 6 mm long, arched toward the lip, concave ventrally, 3-toothed at apex; midtooth rounded, 1 mm long, the lateral teeth shorter, rounded. Anther cap reniform, 4-celled. Pollinia 4, flattened, provided with caudicles.

Distribution. Known only from the type locality in Costa Rica.

Ecology. Epiphytic in dense woods, premontane wet forest, on the Caribbean slopes of Tilarán range in northern Costa Rica at 900 m elevation. Flowering at least in December and January.

Etymology. Named in honor of Gabriel Barboza, well-recognized orchidologist and owner of the Orchid Garden at Monteverde, who discovered the species during one of his field trips aimed to bring light to the rich orchid flora of the Monteverde region.

This species is closely related and vegetatively similar to *Prosthechea glauca* from southern Mexico [R.L. Dressler 1396 (AMES!); M.A. Soto 5478 (AMO, drawing!)], Guatemala [J.A. Steyermark 42371 (AMES!)], El Salvador [F. Hamer & O. Pank 47 (AMES!)], and Honduras [E.S. Siegerist 636 (SEL)]. It may be distinguished from P. glauca by the flowers with ligulate sepals and oblong petals, and the peculiar lip, provided with elliptic-oblong lateral lobes and a suborbicular, retuse midlobe. The callus has a central, rounded, prominent ridge, flanked by two lower knobs. The apex of the column presents an ovate, entire terminal tooth (subquadrate and crenulate in P. glauca), and lateral elliptic teeth slightly shorter than the central tooth (subquadrate and much shorter than apical tooth in P. glauca). Prosthechea barbozaei also is close to P. ortizii, from which it mainly differs in vegetative habit, the latter having narrowly pyriform-ovate pseudobulbs (length: width ratio > 3 in P. ortizii; = 1.2 in P. barbozaei). Pseudobulbs are only slightly flattened in P. ortizii, whereas they are strongly ancipitous in P. barbozaei. Moreover, the callus on the lip is simple in P. ortizii; but in P. barbozaei, it presents a central, higher keel, flanked by two small, conical knobs.

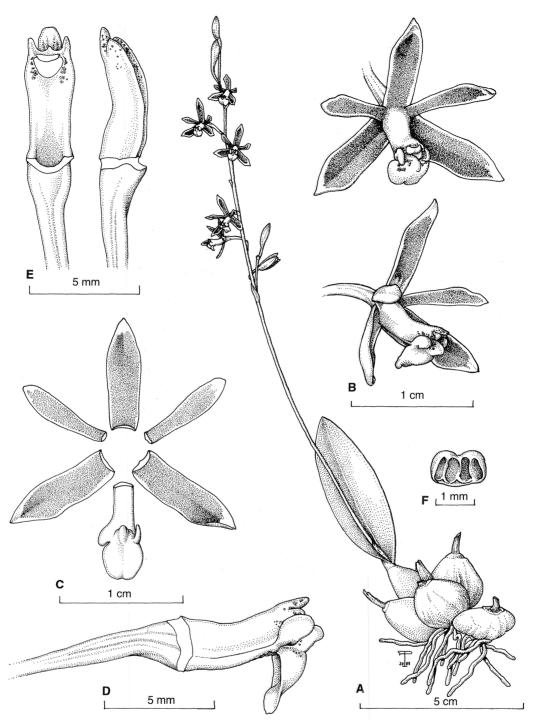


FIGURE 1. *Prosthechea barbozaei* Pupulin. **A.** Habit. **B.** Flower, frontal and lateral views. **C.** Dissected perianth. **D.** Column and lip, lateral view. **E.** Column, ventral and lateral views. **F.** Anther cap. Drawn by author from holotype.

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LITERATURE CITED

- Blume, K.L. 1826. *Prosthesia* (Violaceae). Bijdr. Fl. Ned. Ind. 15: 866.
- Chase, M.W., D.E. Soltis, R.G. Olmstead, D. Morgan, D.H. Les, B.D. Mishler, M.R. Duvall, R.A. Price, H.G. Hills, Y.-L. Qiu, K.A. Kron, J.H. Rettig, E. Conti, J.D. Palmer, J.R. Manhart, K.J. Sytsma, H.J. Michaels, W.J. Kress, K.G. Karol, W.D. Klark, M. Hedén, B.S. Gaut, R.K. Jansen, K.-J. Kim, C.F. Wimpee, J.F. Smith, G.R. Furnier, S.H.. Strauss, Q.-Y. Xiang, G.M. Plunkett, P.S. Soltis, S.M. Swensen, S.E. Williams, P.A. Gadek, C.J. Quinn, L.E. Eguiarte, E. Golenberg, G.H. Learn, Jr., S.W. Graham, S.C.H. Barrett, S. Dayanandan and V.A. Albert. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. Ann. Missouri Bot. Gard. 80: 528–580.
- Chiron, G.R. 2003. An introduction to the genus *Prosthechea*. Orch. Rev. 111: 93–97.
- Chiron, G.R. and V.P. Castro Neto. 2003. Révision du genre *Prosthechea* Knowles & Westcott et nouveau genre dans la tribu Laeliinae (Orchidaceae). Richardiana 4(1): 9–35.
- Dodson, P.M. and C.H. Dodson. 1989. *Encyclia squamata* (Barb. Rodr.) Porto & Brade. Icon. Pl. Trop., ser. 2: sub pl. 457.
- Dressler, R.L. 1980. Una *Encyclia* feita de Panamá occidental. *Encyclia fortunae* Dressler. Orquídea (Méx.) 7(4): 353–356.
- ——. 1995. New orchid species from Costa Rica. Novon 5: 140–145.
- ——. 2003. Orchidaceae. *In* B.E. Hammel, M.H. Grayum, C. Herrera and N. Zamora, eds. Manual de plantas de Costa Rica, Vol. 3. Monocotiledóneas (Orchidaceae-Zingiberaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 93: 1–595.
- Dressler, R.L. and G.E. Pollard. 1971. Nomenclatural notes on the Orchidaceae. IV. Phytologia 21(7): 433–439.
- ——. 1976. The genus *Encyclia* in Mexico. Asociación Mexicana de Orquideología, Mexico.
- Endress, P.K. 2003. Morphology and angiosperm systematics in the molecular era. Bot. Rev. 68(4): 545–570.
- Govaerts, R. 2002. Checklist of American Orchidaceae. Global Data Projects, Royal Botanic Gardens, Kew. Computer printout (12 December 2002).

- Hágsater, E. and M.A. Soto, eds.. 2003. Orchids of Mexico. Parts 2 and 3. Icon. Orchid. 5, 6. Mexico, Instituto Chinoin.
- Hamer, F. 2001. Orchidaceae. *In* V.S. Hollowell, ed. Flora de Nicaragua. Monogr. Syst. Bot. Missouri Bot. Gard. 85: 1612–1860.
- Higgins, W.E. 1997 [1998]. A reconsideration of the genus *Prosthechea* (Orchidaceae). Phytologia 82(5): 370–383.
- ——. 2003. *Prosthechea*, a chemical discontinuity in the Laeliinae. Lankesteriana 7: 39–42.
- Higgins, W.E., C. van den Berg and W.M. Whitten. 2003. A combined molecular phylogeny of *Encyclia* (Orchidaceae) and relationships within Laeliinae. Selbyana 24(2): 165–179.
- Knowles, G.B. and F. Westcott. 1838. *Prosthechea glauca*. Fl. Cab. 2: 111–112.
- ——. 1839. Epithecia glauca. Fl. Cab. 2: 167–168. t. 187.
- Lindley, J. 1833. *Dichaea*. Gen. Sp. Orch. Pl.: 208– 209.
- _____. 1842. *Encyclium*. Edwards' Bot. Reg. 28: 28–36.
- Mújica Benítez, E., R. Pérez Márquez, J.L. Bocourt Vigil, P.J. López Trabanco and T.M. Ramos Calderón. 2000. Géneros de orquídeas cubanas. Editorial Félix Varela, La Habana.
- Nir, M. 2000. Orchidaceae Antillanae. DAG Media Publishing, New York.
- Pupulin, F. 2002a. The *Prosthechea prismatocarpa* complex (Orchidaceae: Laeliinae) in Costa Rica, with a new species, *P. tardiflora*. Lankesteriana 3: 19–24.
- 2002b. Catálago revisado y anotado de las Orchidaceae de Costa Rica. Lankesteriana 4: 1– 88.
- Stevens, P.F. 1991. Character states, morphological variation, and phylogenetic analysis: a review. Syst. Bot. 16: 553–583.
- van den Berg, C., W.E. Higgins, R.L. Dressler, W.M. Whitten, M.A. Soto Arenas, A. Culham and M.W. Chase. 2000. A phylogenetic analysis of Laeliinae (Orchidaceae) based on sequence data from Internal Transcribed Spacers (ITS) of nuclear ribosomal DNA. Lindleyana 15: 96–114.
- van den Berg, C., W.E. Higgins, R.L. Dressler, W.M. Whitten, A. Culham and M.W. Chase. (in press). Molecular systematics of the Laeliinae. *In* Proceeding of the 16th World Orchid Conference.
- Withner, C.L. 1998. The Cattleyas and Their Relatives, Vol. 5. Brassavola, Encyclia, and Other Genera of Mexico and Central America. Timber Press, Portland.
- ------. 2001. An overview of the genus *Prosthechea* sens. str. with a new species, *P. serpentilingua*, and the strange case of *Prosthechea squamata*. Orch. Dig. 65: 78–81.
- Withner, C.L. and P.A. Harding. 2004. The Cattleyas and Their Relatives: The Debatable Epidendrums. Timber Press, Portland.