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A new natural hybrid between *Prosthechea cochleata* and *P. radiata* (Orchidaceae) from Alta Verapaz, Guatemala

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Abstract: A new natural hybrid between *Prosthechea cochleata* and *P. radiata* (Orchidaceae, Laeliinae) from the central part of Guatemala, *P.* × *chixoyensis* Mó & Cetzal, is herein described, illustrated, and characterized based on the morphological characters. The new nothospecies is most similar to *P. cochleata* but the petals are proportionally broader and the mucro of the labellum is subapical, as observed in *P. radiata*. Additionally, the perianth segments are neither as strongly reflexed as they are in *P. cochleata* nor patent as in *P. radiata*. A table of diagnostic characters for the new hybrid and its putative parents, a comparative figure, and a map showing their geographical distributions are also provided. Furthermore, a key to diagnose the hybrid from parental taxa and related species is also featured.

Key words: *Prosthechea* × *chixoyensis*, San Cristóbal Verapaz, subtropical moist forest, Guatemala

1. Introduction

The genus *Prosthechea* Knowles & Westc. includes between 100 and 114 species; the exact number depends on the accepted generic and specific synonymies, or unresolved names (Higgins, 2003; The Plant List, 2010). The genus is characterized by the fusiform, often flattened, pseudobulbs and scapose or sessile inflorescence (often with a prominent spathe). Depending on the clades, the flowers can be either resupinate or not. *Prosthechea* is further characterized, among genera related to *Encyclia* Hook., by the following combination of characters: the pseudobulbous plants; a labellum that is fully adnate to the basal half of the column; the thickened, often pubescent callus present in most species; and the column lacking wings but with a clinandrium bearing 3 conspicuous teeth. The genus is further characterized by the large druse-type glycoside crystals that are usually present throughout the plant in most of the reported species, exceptions being *P. pygmaea* (Hook.) W.E.Higgins and relatives, as well as the species sometimes included in the genus *Euchile* (Dressler & G.E.Pollard) Withner. For the purpose of this article, we followed Higgins (2005) in not recognizing the segregates proposed by Withner and Harding (2004), such as *Anacheilium* Hoffmanns., *Euchile*, *Hormidium* (Lindl.) Heynh., *Panarica* Withner & P.A.Harding, and *Pollardia* Withner & P.A.Harding. A comprehensive phylogenetic analysis of this complex of taxa is required to evaluate the merits of Withner and Harding's proposals.

As conceived here, *Prosthechea* species are distributed from Florida (USA) and Mexico southward to southern South America (Higgins, 2005). Species under this genus are either epiphytic or lithophytic herbs and prefer humid or wet habitats from sea level to an altitude of around 2600 m (Higgins, 2003). In Guatemala, 26 species of *Prosthechea* have been registered, 22 of which occur in the Alta Verapaz department (Dix and Dix, 2000; Ossenbach et al., 2007). *Prosthechea stenvensii* Archila, a taxon that is closely related to, if not conspecific with, *P. baculus* (Rchb.f.) W.E.Higgins, is reported to be an endemic species. In San Cristóbal Verapaz (one of the municipalities of Alta Verapaz), 13 species have been recorded, namely *Prosthechea baculus*, *P. brassavolae* (Rchb.f.) W.E.Higgins, *P. chondylobulbon* (A.Rich. & Galeotti) W.E.Higgins, *P. cochleata* (L.) W.E.Higgins, *P. glauca* Knowles & Westc., *P. livida* (Lindl.)

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W.E.Higgins, *P. michuacana* (Lex.) W.E.Higgins, *P. neurosa* (Ames) W.E.Higgins, *P. ochracea* (Lindl.) W.E.Higgins, *P. pseudopygmaea* (Finet) W.E.Higgins, *P. pygmaea*, *P. radiata* (Lindl.) W.E.Higgins, and *P. varicosa* (Bateman ex Lindl.) W.E.Higgins. These species predominantly grow in different ecosystems ranging from lowland moist forests to the dry or humid oak and pine-oak forests at higher elevations of up to 2100 m, often occurring in cloud forests.

Despite the fact that several species of *Prosthechea* can grow sympatrically (or parapatrically) in different areas of the Neotropics, no natural hybrids have ever been reported in the past. The plausible factors behind this are at present not known, but may include phenological factors, as well as the usage of different pollinators, or even incompatibility between species due to various degrees of relatedness. However, the existence of a variety of man-made hybrids involving *Prosthechea* species belonging to widely different sections of the genus (e.g., between members of the *Prosthechea s.s.*, *Panarica*, *Anacheilium*, and *Euchile* alliances; RHS, 2011) provides strong proof against the argument for widespread intrageneric incompatibility.

During a recent floristic inventory in the basin of the Chixoy River, in the southeastern portion of Alta Verapaz, Guatemala, plants with intermediate characteristics between *Prosthechea cochleata* and *P. radiata* were collected. We thereby interpret this combination of morphological characters as evidence of the hybrid status for these plants. We thus propose the new nothospecies *Prosthechea* × *chixoyensis* Mó & Cetzal.

2. Materials and methods

The specimens studied were prepared from plants collected in the field. Representative samples of the new natural hybrid and putative parents were deposited at BIGU and CICY (see additional specimens examined and Appendix). Morphological characters were revised under a dissecting microscope. Pictures of live flowers were digitalized under an Epson Expression 1640 XL scanner. Digital images of flowers were captured at several resolutions, ranging from 600 to 1200 dpi. A distribution map was produced by plotting the locality data cited in the Appendix on a DIVA-GIS base map (Hijmans et al., 2004) using ArcView 3.2 (ESRI, 1999); the map used to locate the study area was downloaded from Free Relief Layers for Google Maps (2013) and edited with Adobe Photoshop 6.0.1. (Adobe Systems Inc., USA).

3. Results

3.1. Taxonomic treatment

Prosthechea × ***chixoyensis*** Mó & Cetzal, **nothosp. nov.** (Figures 1 and 2).

Type: Guatemala, Alta Verapaz: San Cristóbal Verapaz, Ruta 7 w, entre Santa Elena y Baleu, camino a Chicaman El Quiche, Cuenca Chixoy, 15°22′00.14″N, 90°35′35.56″W, 1115 m, 21 June 2007, cultivada y florecida en el Orquideario de Agronomía CUNOR-USAC, *E.A. Mó & J.A. Mó 56* (holotype: BIGU, isotype: CICY).

Diagnosis: A *Prosthechea* nothospecies product of the cross between *P. cochleata* and *P. radiata*. It resembles *P. cochleata* but has proportionally shorter (2.5–3.6 vs. 4.0–4.5 cm) and broader (0.6–0.7 vs. 0.5–0.6 cm) perianth segments, featuring a subapical mucro, such as found in *P. radiata*. It differs in its features when compared with *P. radiata* in having a long spathaceous bract (2.2–3.0 vs. 1.9–2.0 cm), proportionally narrower perianth segments (2.5–4.0 × 0.5–0.7 vs. 2.3 × 0.8–1.1 cm), and labellum displaying a distinctive band of dark purple/black coloration as observed in *P. cochleata*.

Description: Plant epiphytic, pseudobulbous, erect, with a short, creeping rhizome. Roots flexuous. Pseudobulbs 10.0 × 1.5–3.5 cm, ovoid-elliptic, apically 2–(3)-leaved, flattened to flattened-subquadrate (thus intermediate between putative parental species) in cross-section. Leaf 10.0–13.0 × 1.5–3.5 cm, coriaceous, sessile, elliptic to elliptic-oblong, acute. Inflorescence terminal, a dense to laxly flowered raceme to 20–21 cm long, 3–6-flowered, produced from a long, spathaceous, conduplicate bract 2.2–3.0 cm long, the flowers appearing in slow succession with 2–6 open simultaneously; the peduncle 15–17 cm long, terete; bracts of the peduncle 1–4, triangular, acute, 7–6 mm long, floral bracts 5–6 mm long, narrowly triangular, acute. Ovary and pedicel 2.0–2.3 cm long, triquetrous in the upper half, cylindrical in the lower half. Flowers spreading widely with perianth segments somewhat retrorse, with sepals and petals cream or clear green, creamy white externally, the labellum cream or pale yellow with 13–19 purple nerves and a broad distal, transversal band of dark purple or dark violet-purple which may or may not be broken in the midsection, some bright yellow-green overlay in the distal half, particularly toward the center of the labellum; the nerves are continuous to the labellar margin in one of the morphs, whereas they are purple-colored on the proximal half and pale yellow green on the distal half in the other morph; the column greenish yellow or greenish yellow with reddish spots at base. Dorsal sepal 2.5–5.0 × 0.5–0.7 cm, elliptic-lanceolate, spreading, acute. Lateral sepals 2.5–4.0 × 0.6–0.7 cm, obliquely elliptic, acute. Petals 2.5–3.6 × 0.6–0.7 cm, obliquely elliptic, acute. Labellum 1.2–1.6 × 2.0–2.2 mm, adnate to the basal third of the column, widely ovate, acute, with a terminal or subapical mucro, the base cordate with the basal lobes embracing or not the column, deeply concave, margins slightly undulate or entire, slightly reflexed above the middle, callus 5–6 mm long and 2.0–2.5 mm wide, papillate. Column 0.9–1.2 cm long, stout, 3-toothed, with the midtooth subquadrate truncate or linear acute, half the

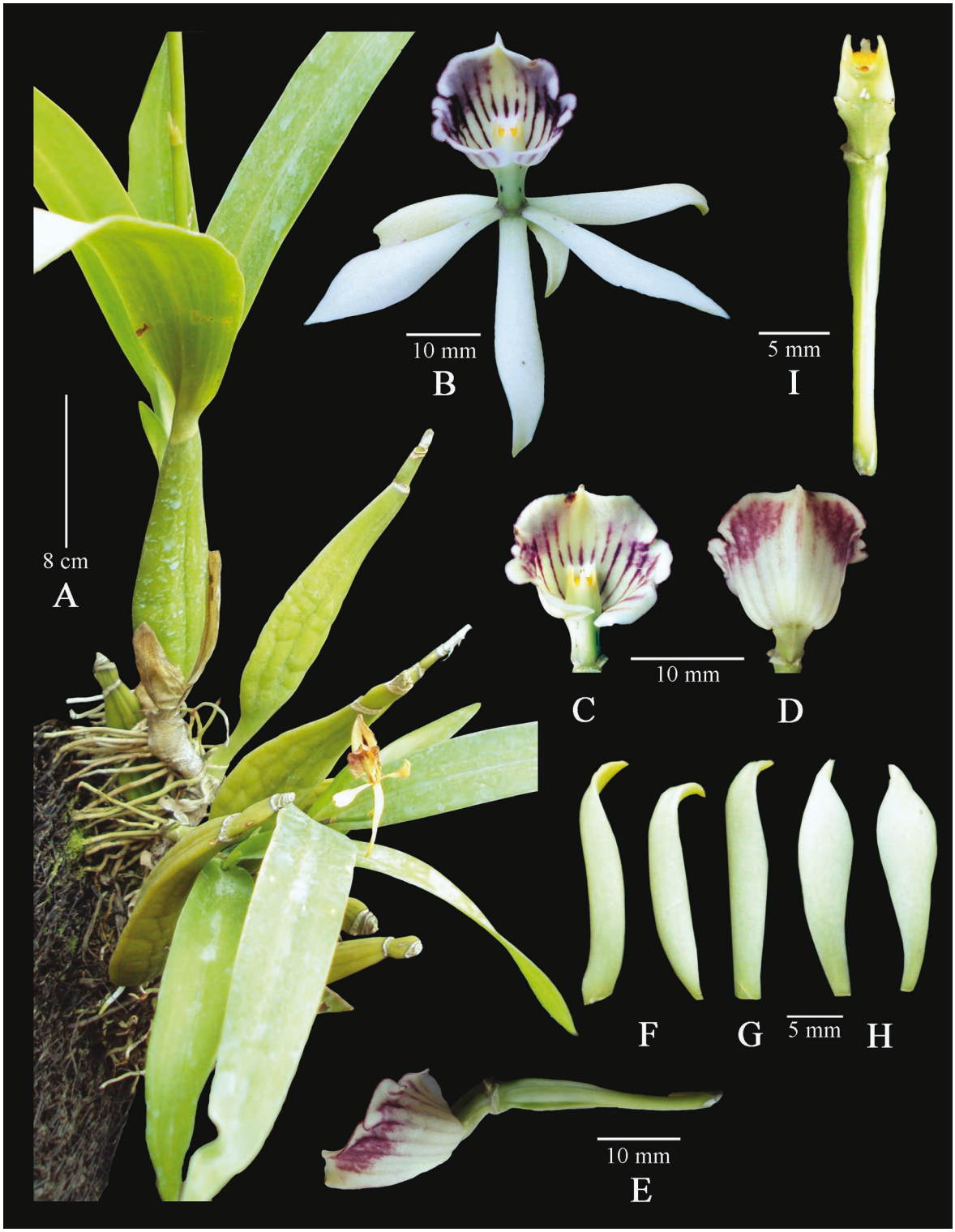

Figure 1. *Prosthechea* × *chixoyensis* (morph 1). A. Habit with inflorescence. B. Whole flower, front view. C. Labellum, front view. D. Labellum, back view. E. Lateral view of the ovary-pedicel and labellum. F. Petals. G. Dorsal sepal. H. Sepals. I. Column with ovary-pedicel, front view. Based on *Mó 56*, BIGU.

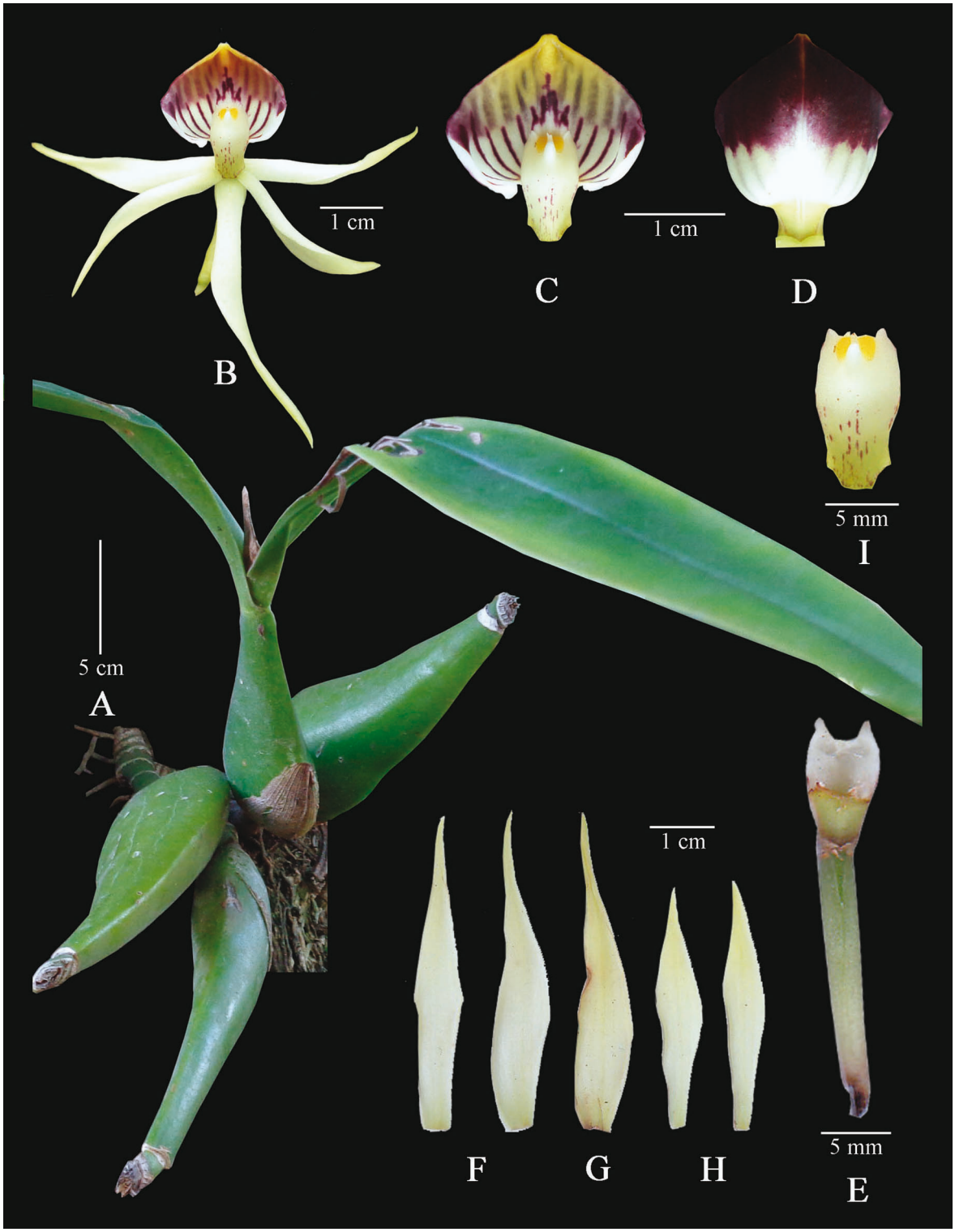

Figure 2. *Prosthechea* × *chixoyensis* (morph 2). A. Habit. B. Whole flower, front view. C. Labellum, front view. D. Labellum, back view. E. Column with ovary-pedicel, front view. F. Petals. G. Dorsal sepal. H. Sepals. I. Column, back view. Based on *Mó & Mó 60*, BIGU.

length of the lateral teeth, with a triangular ligula under the midtooth and shorter than it. Anther cap oblong, yellow, 4-celled. Pollinia 4, pyriform, complanate. Fruit a triquetrous capsule.

Distribution and ecology: *Prosthechea* × *chixoyensis* is known only from 2 specimens from the surroundings of the Chixoy River or Río Negro in the municipality of San Cristóbal Alta Verapaz, Alta Verapaz, Guatemala. The localities of the 2 specimens are near the hydroelectric dam between the Alta Verapaz and Quiché departments. The putative parents of *P.* × *chixoyensis* have also been recorded in the same area (Figure 3; Appendix), as well as *P. baculus*, *P. chondylobulbon*, *P. glauca*, *P. livida*, *P. michuacana*, *P. ochracea*, and *P. pygmaea*. This area is part of a transitional life zone between subtropical wet forest (cold; bmh-S(f)) and tropical moist forest (temperate; bh-S(t)) (Figure 4)

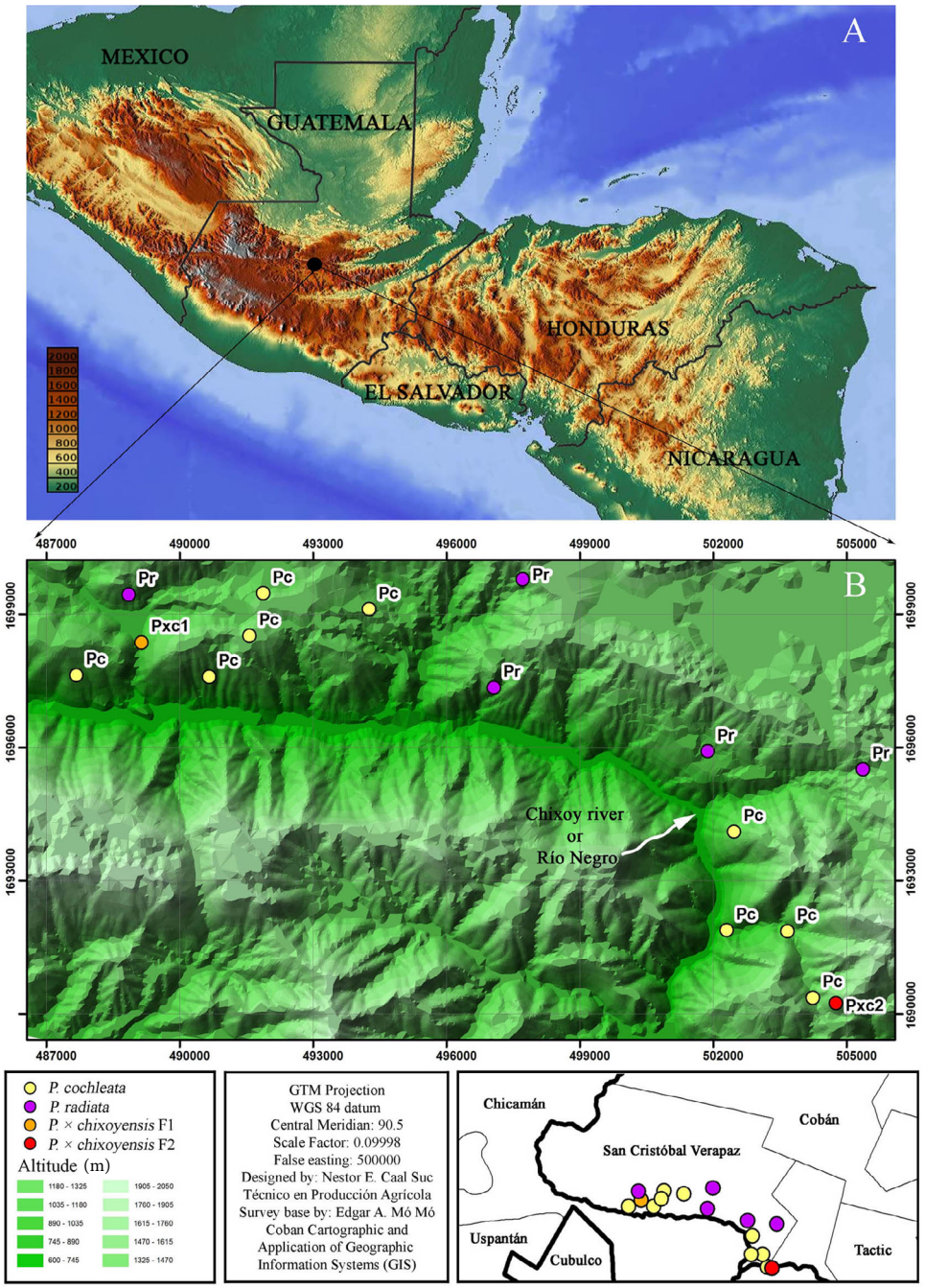

Figure 3. Distribution of *Prosthechea* × *chixoyensis* and its putative parental species.

Figure 4. Habitat of *Prosthechea* × *chixoyensis* and its putative parental species (A–C).

(Holdridge, 1987), with average annual temperatures between 17–21 °C, at elevations of 1000–2100 m. It is part of the high mountains and plateau system that originates in Chiapas and ranges into northern Honduras along a NW-SE general direction. The area is located within the physiographic province of the Central Cordillera, which is characterized by being within the Motagua and Chixoy-Polochic faults (Meza-Ligorria, 1997).

Additional specimen examined: Alta Verapaz: San Cristóbal Verapaz, Camino a la Presa Chixoy, Cuenca

Chixoy, 15°16′46.50″N, 90°27′29.05″W, 1400 m, 26 June 2011, cultivada y florecida en el Orquideario de Agronomía CUNOR-USAC, *E.A. Mó & J.A. Mó 60* (BIGU).

Etymology: The specific epithet has been derived from the type locality of the nothospecies, the Chixoy River or Río Negro close to the Chixoy basin in San Cristóbal Verapaz, Alta Verapaz, Guatemala. An artificial hybrid between the 2 parental species was registered in 1970 at the Royal Horticultural Society registry by Wallace H Otaguro of Honolulu, Hawaii, as *Prosthechea* × Radio-cochlea. However, the International Code of Botanical Nomenclature clearly states that the name of an artificial hybrid should comply with all the requirements of regular scientific name proposals, including type citation and a Latin diagnosis. *Prosthechea* × Radio-cochlea was described in 1970 and since it lacks these requirements, it is not validly published. We have opted for the proposal of a new specific, Latinized epithet that reflects the geographical origin of this nothospecies. We thereby comply with articles H.10.1 and 32.4 of the Melbourne code (McNeill et al., 2012).

4. Discussion

The proposed parental species, both members of the *Anacheilium* alliance within *Prosthechea*, are broadly sympatric over much of their geographical ranges, with all of the distribution of *Prosthechea radiata* nested within that of *P. cochleata*. *Prosthechea cochleata* is widely distributed from the United States (southern Florida) and the West Indies and northern Mexico to Colombia and Venezuela, whereas *P. radiata* ranges from central Mexico to northwestern Nicaragua (Karremans, 2009). Both parental taxa are sympatric or variously allo- or parapatric across portions of their diverse geographical ranges from southeastern Mexico to northwestern Nicaragua (Carnevali et al., 2001). However, there are no previous records of gene exchange between these 2 species.

The proposed nothospecies is intermediate between both parental species. It is currently known from 2 genotypes, each mostly resembling an alternative parent, hereafter referred to as morph 1 (Figure 1) and morph 2 (Figure 2). The type collection (*Mó & Mó 56*) belongs to morph 1. This morph features the round, blunt labellum and cream-white perianth segments of *P. radiata*. In common with *P. radiata* (Figure 5) it also displays a subapical mucro at the labellum morphological apex. However, the labellum features the broad distal, transversal band of dark purple or dark violet-purple typical of *P. cochleata* (Figure 6), albeit developed to a lesser degree (see detailed description above, the Table, and Figure 1).

The paratype collection (*Mó & Mó 60*) represents morph 2 (Figure 2), where the labellum is more ovate and bears a well-developed band of dark color as in *Prosthechea cochleata* (Figure 6). It also features the narrow, reflexed perianth segments of that species. However, the proximal section of the underside of the labellum is white instead of yellow-green and its base is truncate or only shallowly cordate. In this morph, the labellum also lacks the subapical mucro found both in *P. radiata* and in morph 1. Morph 2 superficially resembles *P. trulla* (Rchb.f.) W.E.Higgins from the west and north of the Tehuantepec isthmus, but in this last species the inflorescences usually bears a higher number of flowers (3–9) open simultaneously, the perianth segments are proportionally shorter and wider, and the nerves of the labellum are only dark purple-colored on the proximal half. Comparisons between the 2 morphs of the hybrid and its putative parental species are featured in the Table and Figures 1, 2, 5, and 6.

One of the authors (EM) has made observations of *Danaus gilippus thersippus* (false monarch). Whether this species is a legitimate pollinator remains to be further investigated, but the floral syndrome strongly suggests pollinators other than butterflies, most likely wasps, as suggested by van der Pijl and Dodson (1966) for the closely related *Prosthechea baculus* (as *Encyclia pentotis* (Rchb.f.) Dressler). Recently, Damon and Salas-Robledo (2007) hypothesized a euglossine bee (*Euglossa atrovenata* Friese) as pollinator for the related species *Prosthechea chacaoensis* (Rchb.f.) W.E.Higgins and *Xylocopa nautlana* Cockerell and *X. fimbriata* Fabricius as putative pollinators of *P. chondylobulbon*. However, these reports were based upon pollinaria gathered on captured bees and there is no certainty that they actually belong to the *Prosthechea* species or to any other member of the *Encyclia* alliance.

Currently it is not known whether only one (and, if so, which) or both parental species are either the pod or pollen parents in the hybrid combination. The fact that the 2 known genotypes are so unlike each other, each one resembling an alternative parental species, strongly indicates that the species are serving as pollen or pod parents alternatively in each case.

The taxonomic status of the *Prosthechea cochleata* parent is open to question. This species appears to consist of at least 2 entities with strong geographical correlates. One, ranging from central Mexico into possibly northern Panama, and undoubtedly the parent of *Prosthechea* × *chixoyensis*, features large flowers with relatively long perianth segments (dorsal sepal to 3.5–5.5 cm long) and inflorescences. The other morph is characterized by smaller plants and flowers with shorter perianth segments (dorsal sepal 2.5–3.0 cm long) on inflorescences mostly not exceeding the length of the leaves. This morph ranges from northern South America to Florida (USA) through the West Indies and also features a proportionally broader band of dark purple on the distal half of the labellum. Whether these 2 sets of populations represent 2 different

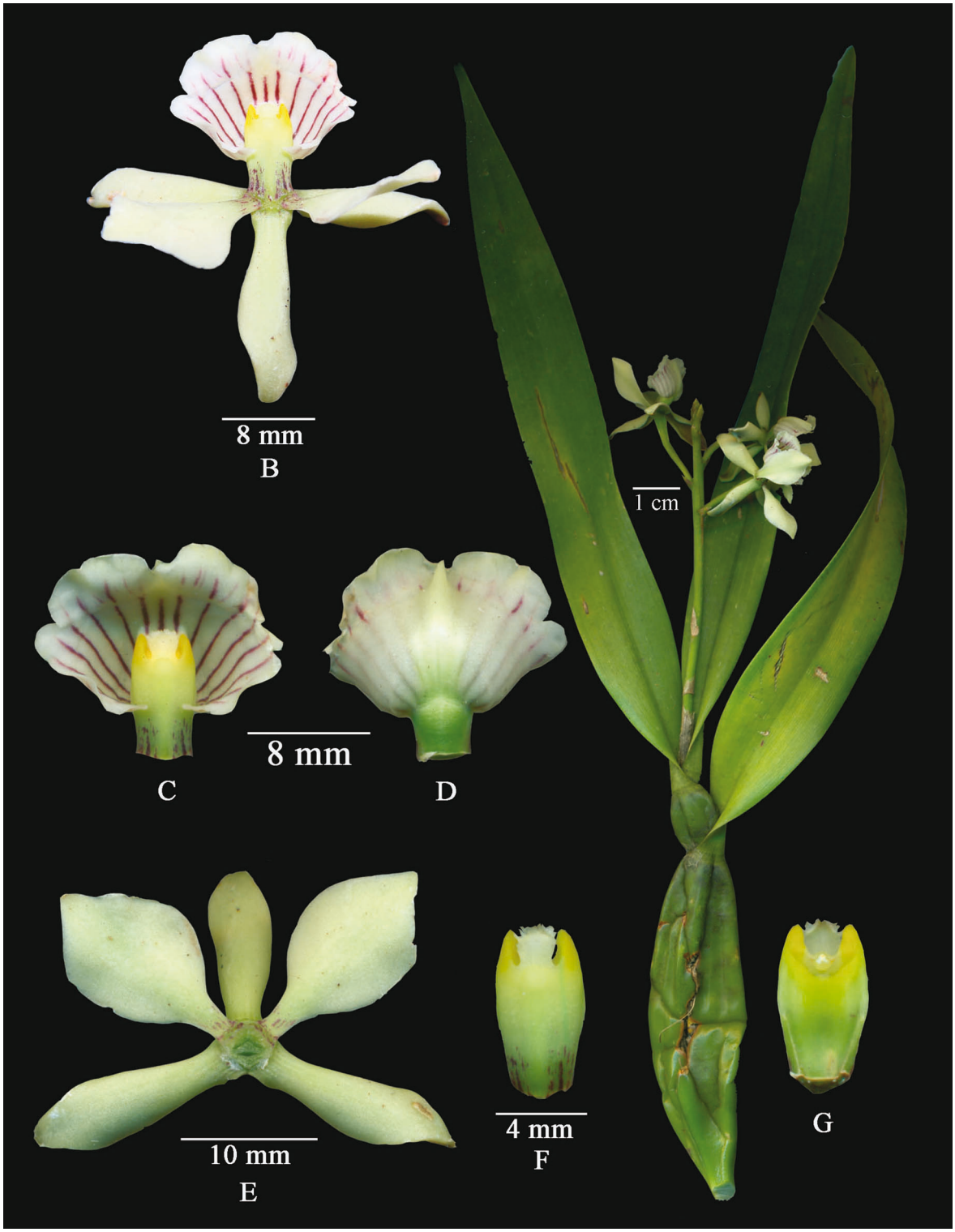

Figure 5. *Prosthechea radiata*. A. Habit with inflorescence. B. Whole flower, front view. C. Labellum and column, front view. D. Labellum, back view. E. Petals and sepals. F. Column, front view. F. Column, front view. G. Column, back view. Based on *Cetzal & Noguera 243*, CICY.

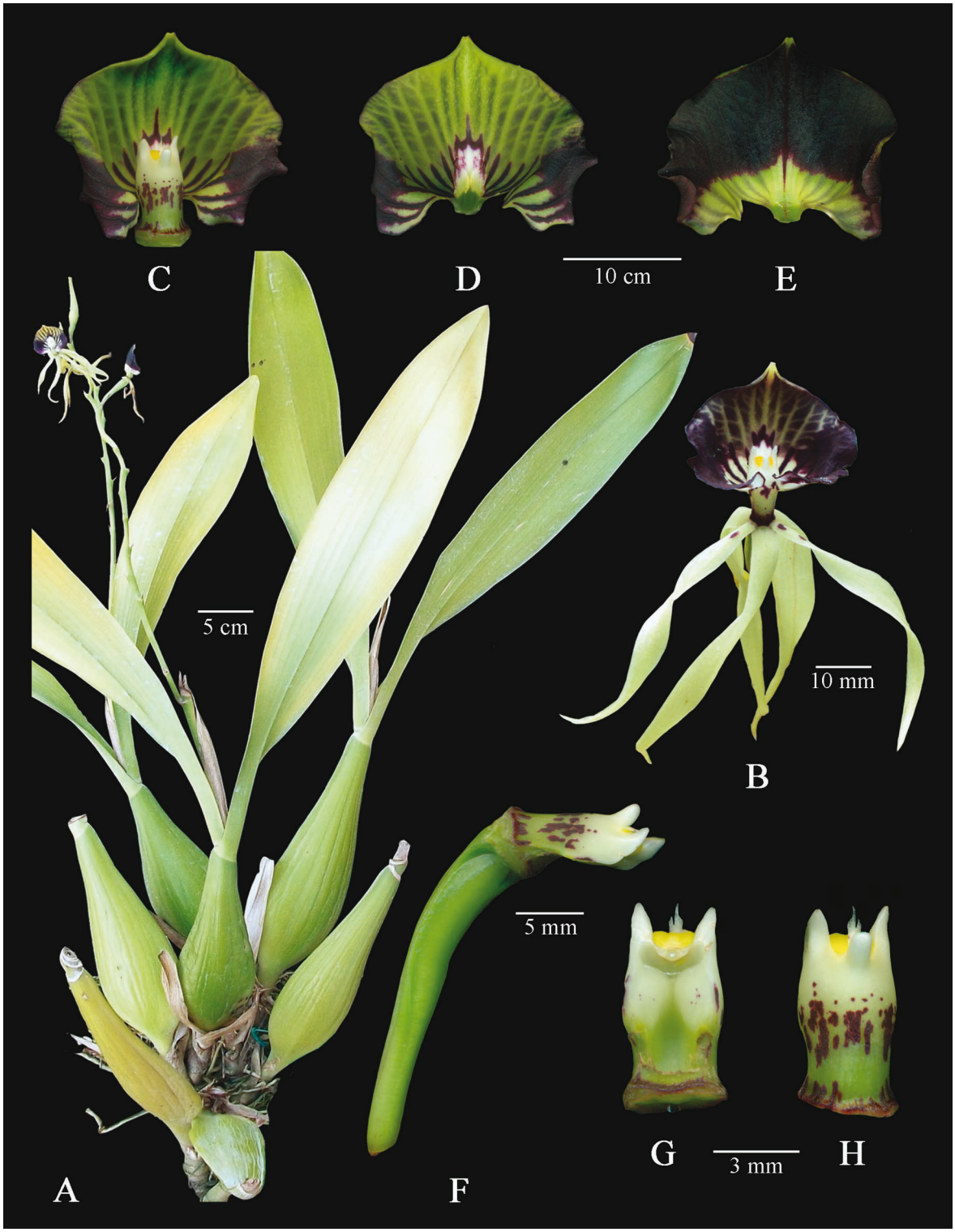

Figure 6. *Prosthechea cochleata*. A. Habit. B. Whole flower, front view. C. Labellum and column, front view. D. Labellum, front view. E. Labellum, back view. F. Column with ovary-pedicel, lateral view. G. Column, front view. H. Column, back view. A–B based on *Mó & Mó 58*, BIGU; C–H, *Cetzal & Noguera 370*, CICY.

Table. Morphological comparison of *Prosthechea* × *chixoyensis* and its putative parental species.

Characters	*P. cochleata*	*P.* × *chixoyensis* Morph 1	*P.* × *chixoyensis* Morph 2	*P. radiata*
Pseudobulbs (cm)	14 × 4	10.0 × 1.5	10.0–13.0 × 3.5	8.0 × 3.5
Inflorescence bracts (spathe) (cm)	13–15	2.2–3.0	2.2–3.0	1.9–2.0
Ovary-pedicel length (cm)	2.6–2.7	2.0–2.3	2.0–2.3	2.5
Number of flowers	3–37	6	3	4–12
Petals (cm)	4.0–4.5 × 0.5–0.6	2.5–3.0 × 0.6–0.7	3.0–3.6 × 0.6–0.7	2.3 × 1.1
Dorsal sepal length (cm)	5.3–5.5	2.5–2.6	4.8–5.0	2.3
Lateral sepals length (cm)	4.5–5.2	2.5–2.6	3.0–4.0	2.2
Petals and sepals (color)	Clear green	Cream or clear green	Cream or clear green	White or cream
Subapical mucro at the labellum	Present	Present	Absent	Absent
Labellum (cm)	(13–)2.0–2.1 × (18–)3.0–3.1	1.2 × 2.2	1.6 × 2.0	1.2 × 1.4
Labellum color underside	Yellow green at base with a broad (3/4 of total width) very dark purple band, with the purple nerves only evident at the base	Cream with purple apex	Cream at the middle and purple from the middle to the apex	White or cream
Nectar guides on the labellum (stripes)	Purple from the base to near the middle and yellow green from the middle to the apex	Purple from the base to the apex of the labellum	Purple from the base to near the middle and yellow green from the middle to the apex	Purple from the base to the apex of the labellum
Column color	Light green at base and apex white with reddish spots in the middle	Greenish yellow	Greenish yellow with reddish spots at base	Greenish yellow

species or subspecific entities remains to be the analyzed in the future. The name *Prosthechea cochleata* var. *grandiflora* (Mutel) Christenson, of uncertain origin, may refer to the large-flowered entity from Megamexico and southern Central America, but little is known about this name at this time and further research is warranted.

This nothospecies is known from only 2 collections, separated by a distance of 13–14 km. Both localities are within the basin of the Chixoy River. Because of the paucity of records, it is difficult to properly evaluate the conservation status. However, it is interesting to note that despite the broadly overlapping distribution areas of both parental species, the natural hybrid seems to occur only here. Thus, it seems reasonable to assume that whatever factor(s) that disrupt the isolation barriers may be confined to this area only (e.g., Machaka-Houri et al., 2012). Thus, we could also assume that the nothospecies is most likely restricted to the aforementioned zone, an estimated area of 31 km^2. With this area in mind, the conservation status of *Prosthechea* × *chixoyensis* can be safely assessed as CR (Critically Endangered) according to the B set of criteria of the IUCN (2001). Besides the limited extent of its distributional area, the Chixoy Basin is severely threatened by rock extraction for construction, as well as gypsum mining (Oliva del Valle, 1994). Furthermore, the vegetation of the area is also threatened by indiscriminate timber harvest for charcoal production by local peasants. Further disturbing factors involve the clearing of the forest to grow several kinds of beans (*Phaseolus vulgaris* L., *P. lunatus* L., and *P. coccineus* L.) and corn (*Zea mays* L.).

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Appendix

Representative herbarium specimens of the distribution in the basin of the Chixoy River of *Prosthechea cochleata* and *P. radiata*.

Prosthechea cochleata. GUATEMALA. Alta Verapaz: San Cristóbal Verapaz, Ruta 7 w, Baleu, camino a Chicaman El Quiche, Cuenca Chixoy, 15°22′40″N, 90°34′53.02″W, 1370 m, 8 July 2011, cultivada y florecida en el Orquideario de Agronomía CUNOR-USAC, *E.A. Mó & J.A. Mó 57* (BIGU); San Cristóbal Verapaz, Camino a la Presa Chixoy, Cuenca Chixoy, 15°16′52.92″N, 90°27′44.31″W, 1418 m, 11 June 2007, cultivada y florecida en el Orquideario de Agronomía CUNOR-USAC, *E.A. Mó & J.A. Mó 58* (BIGU). ***Prosthechea radiata***: GUATEMALA. Alta Verapaz: San Cristóbal Verapaz, Camino a Pueblo Viejo y Agua Blanca, Cuenca Chixoy, 15°19′59.49″N, 90°27′14.42″W, 1350 m, 8 July 2011, cultivada y florecida en el Orquideario de Agronomía CUNOR-USAC, *E.A. Mó & E.R. Paredes 59* (BIGU).

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