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A taxonomic revision of *Encyclia* (Orchidaceae: Laeliinae) in Costa Rica

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A taxonomic revision of *Encyclia* (Orchidaceae) in Costa Rica is presented. The taxonomic history of the genus and its phylogenetic position are discussed. Characters of vegetative and floral morphology are described and their taxonomic significance is discussed. The genus is treated as comprising nine species in the country and a key to species is provided. Each taxon is described on the basis of Costa Rican material, illustrated in a composite plate, and its distribution within the country is assessed. Distribution maps for all the taxa are given. Overall distribution, derivation of name, synonymy, notes on species ecology and diagnostic features are presented for each taxon. The names *Encyclia tonduziana* and *Epidendrum mooreanum* are typified. *Botanical Journal of the Linnean Society*, 2012, **168**, 395–448.

ADDITIONAL KEYWORDS: Costa Rica – *Encyclia* – Laeliinae – Orchidaceae – taxonomy.

INTRODUCTION

William J. Hooker validated *Encyclia* in 1828 for a species native to Rio de Janeiro, Brazil, and to separate it from 'the splendid species of *Cattleya*', at that time only including three species (Hooker, 1828). Hooker's *Encyclia viridiflora*, the type species for the genus, is a rather peculiar and poorly known plant, with several unusual characteristics when compared with its close relatives, such as non-resupinate flowers, a short column, the lateral lobes of the lip almost completely fused with the midlobe and a non-forcipate basal callus (Hooker, 1828; Schlechter, 1914; Withner, 1980; 1996) (Fig. 1). By the middle of the 19th century, under the authority of Lindley, the genus was merged with *Epidendrum* L., and the type species was assigned to subgenus *Encyclium* Lindl. section *Hymenochyla* Lindl. (Lindley, 1831, 1842, 1853). In the *Botanical Register* for 1842, he arranged his division *Encyclium* of *Epidendrum* L. into three sections based upon the shape of the lip: *E. viridiflora* fell into section II, characterized by a slightly three-lobed lip, whereas most of the 'true' *Encyclia* taxa were included in section III, with the lip split into three deep divisions. By 1853, Lindley's views on the divisions of *Epidendrum* were organized into a formal system, with 12 subgenera. Subgenus *Encyclium*, including plants with the lip nearly free from the column, flowers without a spathe and pseudobulbous stems, was further subdivided into four sections, and section *Hymenochila* Lindl. (including *E. viridiflora*) into four informal subsections (Lindley, 1853).

In 1914, Schlechter thought it appropriate to restore the well-circumscribed genus *Encyclia* for those species that have a lip free from the column, or fused with it only at the base, and he transferred 28 species from *Epidendrum* to *Encyclia* (Schlechter, 1914). After his original proposal, and despite his many attempts to revive *Encyclia* (Schlechter, 1914, 1918, 1922, 1923), only Hoehne (1952) followed Schlechter and made additional transfers to the

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Figure 1. *Encyclia viridiflora* Hooker, the type species of the genus. From *Curtis's Botanical Magazine* 55 (n.s. 2): pl. 2831. 1828.

genus created by Hooker. From 1920 to 1970, most authors decided to treat members of this group as part of *Epidendrum* (e.g. Ames, Hubbard & Schweinfurth, 1936; Ames & Correll, 1953; Dunsterville & Garay, 1959, 1961, 1976, 1979; Foldats, 1970).

It was not until 1961 that Dressler offered conclusive evidence for recognizing the distinctness of *Encyclia* and the need to segregate it from *Epidendrum* (Dressler, 1961). Some years later, while studying the species of *Encyclia* of Mexico, Dressler and Pollard offered the first modern revision of the genus, encompassing a large group of species that included the cockleshell species of section *Osmophytum* Lindl. and their relatives and the large-lipped species of section *Euchile* Dressler & G.E. Pollard (1974). Dungs & Pabst (1967) also followed this idea. Brieger (1960) recognized many of the cockleshell species in *Hormidium* (Lindl.) Heynh., but Pabst, Moutinho & Pinto (1981) kept these species separate from *Encyclia*, transferring the larger ones to *Anacheilium* Rchb. ex Hoffmanns. and the smaller ones to *Hormidium*.

In 1966 Withner began his long-term revision of 'bulbous *Epidendrum*', working on the species of the Bahamas, Hispaniola and Cuba (Withner, 1966, 1969), before undertaking his detailed series devoted to the difficult taxonomy of the Central American species (Withner, 1970a, b, c, d, e, f, g, h, i, l, 1971). He recognized 32 species for Mexico and Central America, providing for the first time a key for their identification (Withner, 1970a), proposing informal grouping of species on the basis of their supposed affinities and suggesting patterns of evolution based on the distribution of species groups (Withner, 1970i).

Thirty years later, in 1996, in his series of monographs on subtribe Laeliinae, Withner eventually proposed the adoption of a narrower circumscription of *Encyclia*, closer to the original concept of Hooker (Withner, 1996). The generic limits of *Encyclia* as defined by Withner, i.e. plants with pyriform pseudobulbs, a terminal inflorescence not produced from a spathe, coriaceous to fleshy leaves, a membranous lip usually provided with well-developed lateral lobes that enclose the column (hence the name, from the Greek *enkyklein*, to encircle) and a forcipate callus on the disk of the lip, are today widely accepted. Because of the peculiar features of *E. viridiflora*, Withner (1996) also proposed dividing the genus into subgenera *Encyclia* (only including the type species) and *Hymenochila* (Lindl.) Withner, encompassing all the other species of 'true' *Encyclia*.

Early molecular studies by Higgins (1998) provided support for the idea that the cockleshell *Encyclia* species should be treated as *Prosthechea* Knowl. & Westc., and Withner's narrow circumscription of *Encyclia* was lately confirmed by phylogenetic analyses of Laeliinae based on DNA sequence data (Higgins, van den Berg & Whitten, 2003; van den Berg *et al*., 2000). Although many groups in the subtribe show low levels of genetic divergence, *Encyclia s.s.* forms a well-defined subclade, with *Euchile* Withner and *Meiracyllium* Rchb.f. as consecutive sister taxa, whereas *Prosthechea* is placed in a second subclade with *Alamania* Lex., *Artorima* Dressler & G.E.Pollard, *Hagsatera* R.González, *Dimerandra* Schltr., *Dinema* Lindl. and *Nidema* Britton & Millsp. (van den Berg *et al*., 2000).

The genus *Encyclia* in Costa Rica

From the perspective of the scientific study of plants belonging to *Encyclia*, the early steps of the history of the genus in Costa Rica coincide with the first botanical exploration of the country around the mid 19th

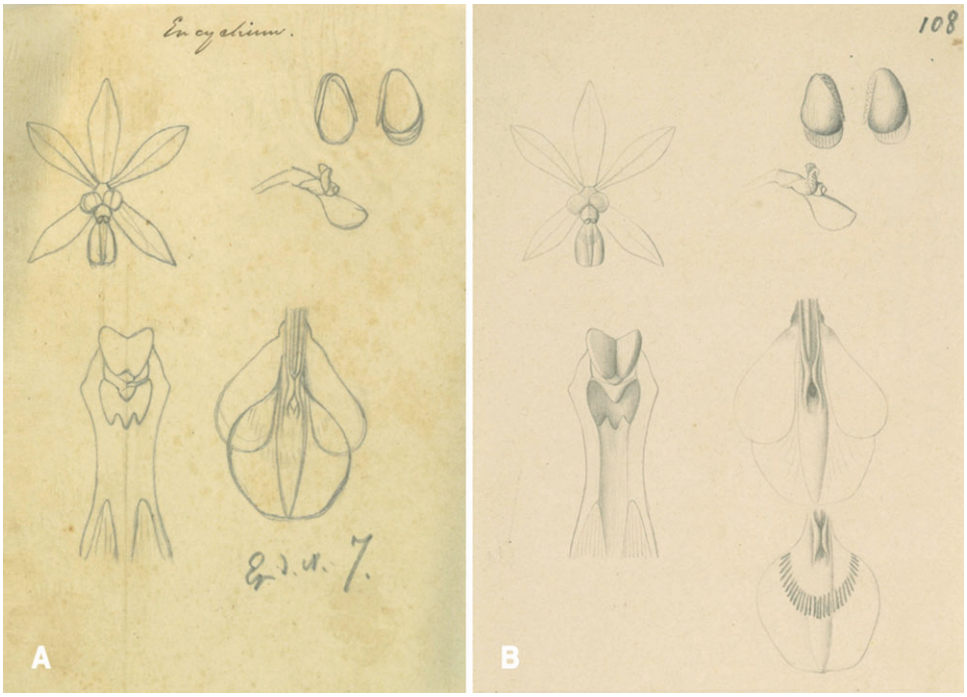


Figure 2. Endrés' illustrations of *Encyclia mooreana*. A, preparatory sketch (W 244475). B, final pencil drawing (W 24424). Reproduced with permission of the Director of the Herbarium, Natural History Museum, Vienna.

century. The first *Encyclia* specimen documented in the country was probably collected in 1847 by the Danish naturalist Oersted (1816–1872) in 'Santa Rosa en Guanacasto [Guanacaste]' (no. *115*), on his way to Nicaragua to explore the route of the San Juan River (Pupulin & Ossenbach, 2005). Reichenbach recorded it in his *Orchideae Oerstedianae* as *Epidendrum atropurpureum* Willd. Ten years later, Wendland (1825–1903), the second great botanical explorer of Costa Rica, collected another specimen of *Encyclia* at San Ramón de Alajuela in the Tilarán range, in June 1857 (no. *1009*), described by Reichenbach as *Epidendrum ramonense* (Reichenbach, 1866). Ten more years elapsed before Endrés (1838–1875), one of the greatest orchidologists to visit the country during the 19th century, collected further specimens of *Encyclia* in Costa Rica. Among his collections and drawings kept in Reichnebach's herbarium at the Natural History Museum in Vienna, five species are represented: *Encyclia cordigera* (Kunth) Dressler, *E. ceratistes* (Lindl.) Schltr., *E. chloroleuca* (Hook.) Neumann, *E. mooreana* (Rolfe) Schltr. (Fig. 2) and *E. peraltensis* (Ames) Dressler. When Rolfe eventually described *Epidendrum mooreanum* in 1891, he based the new species on a series of cultivated specimens received at Kew since 1889 from F.W. Moore, Mr W. Bull, Messrs Hugh Low and Co. and Sir Trevor Lawrence. Although most of these specimens bear no locality data, the specimen sent by Low was stated to be native to Costa Rica (Rolfe, 1891), where it was actually collected by Endrés around the mid 19th century.

Hemsley (1882–1886) in his *Biologia Centrali-Americana* and Alfaro (1888) recorded the same two species previously noticed by Reichenbach (1866), *E. atropurpureum* based on Oersted's collection and *Epidendrum ramonense* collected by Wendland. There is no mention of Endrés's gatherings by Hemsley (1884). By 1918, Schlechter was able to record four species for the flora of Costa Rica, i.e. *E. alata* (Batem.) Schltr., *E. atropurpurea* (Willd.) Schltr. (= *E. cordigera*), *E. mooreana* and *E. ramonensis* (Rchb.) Schltr. (= *E. ceratistes*) (Schlechter, 1918).

The beginnings of the 1920s marked a period of intensive botanical exploration in southern Central America, thanks to the newly established cooperation between European and North American scientists and resident naturalists in Costa Rica and Panama. Most outstanding in Costa Rica were the scientific links between Lankester and Oakes Ames at Harvard University and between the brothers A. & C. Brade, Brenes and Tonduz of the National Herbarium and Schlechter at Berlin-Dahlem. Both renowned orchid scientists also corresponded with Powell in Panama. As a result of increasing exploration, seven species currently referable to *Encyclia* were described from Costa Rica and Panama in just 2 years (Ames, 1922, 1923; Schlechter, 1922; Schlechter, 1923) (Figs 3, 4). These contributions, however, were largely floristic,

Figure 3. Holotype of *Epidendrum peraltense* Ames (= *Encyclia peraltensis* (Ames) Dressler), originally collected in Costa Rica. Reproduced with permission of the Director of the Herbarium, Harvard University Herbaria.

and the authors made no attempts to assess relationships within the genus (or sections) and to discuss affinities of the newly described taxa.

The National Museum of Costa Rica hosts several unpublished checklists authored between 1921 and 1934 by Brenes, then head of the Section of Botany of the Museum, which were transcribed from a series of his original manuscripts titled *Orchidaceae of Costa Rica*. Here, Brenes listed three species of *Encyclia*, namely *E. atropurpurea* (Willd.) Schltr. (*E. cordigera*), *E. meliosma* (Rchb.f.) Schltr. and *E. tonduziana* Schltr. (as a synonym of *Epidendrum oncidioides* var. *mooreanum* (Rolfe) Ames & C.Schweinf.), but he also listed *E. meliosma* under *Epidendrum*, in this case considering it a synonym of *Epidendrum oncidioides* Lindl. var. *mooreanum* (Rolfe) Ames, F.T.Hubb. & C.Schweinf. (Salazar Rodríguez, 2009). He did not included in the list *Encyclia brenesii* Schltr., based on a plant he collected at San José de San Ramón, which Schlechter had described in 1923 to honour its collector.

In 1936, Oakes Ames and his colleagues at the Cambridge Botanical Museum published the first modern synopsis and a general key to North and Central American species of *Epidendrum*, as the result of a study started by Ames and Hubbard in 1921 (Ames *et al*., 1936). Although essentially intended as a herbarium manual with bibliographical references, geographical ranges and type citations, the work set the basis for an overall appreciation of

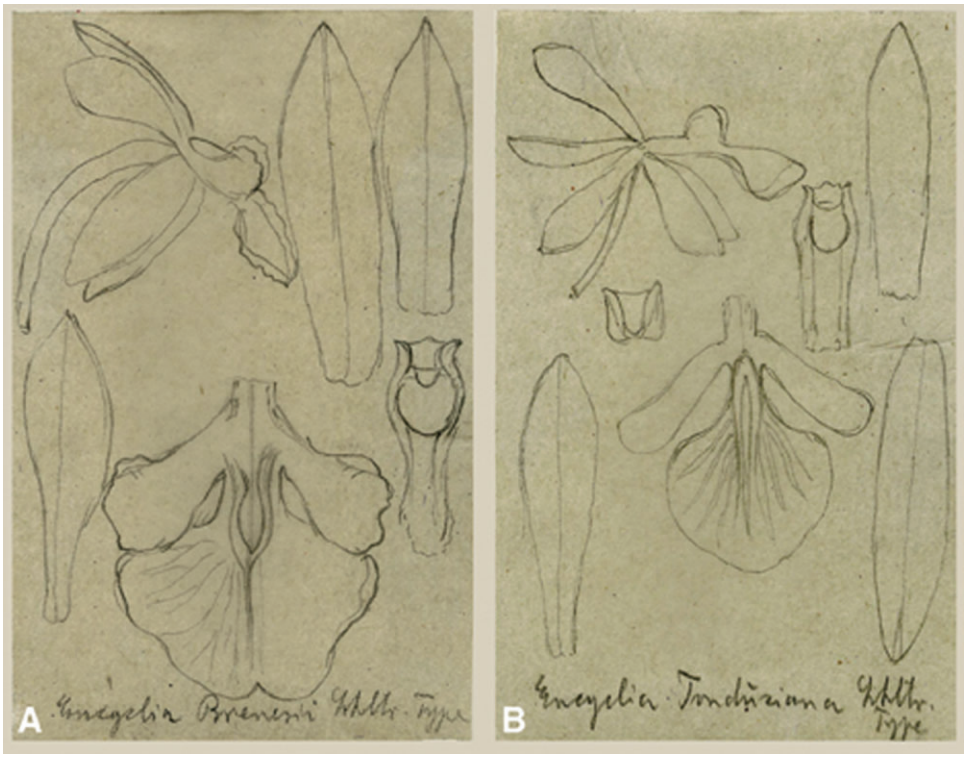


Figure 4. Illustrations of Costa Rican types of *Encyclia* species. A, *Encyclia brenesii*, from San José de San Ramón (Alajuela). B, *Encyclia tonduziana*, from San Jerónimo de Grecia. Reproduced with permission of the Director of the Herbarium, Harvard University Herbaria.

relationships among species groups of this polymorphic genus. The authors favoured a broad circumscription of *Epidendrum* in the traditional sense, established by Lindley in his *Folia Orchidacea* (Lindley, 1853). They recognized only two sections, *Encyclium* (including *Aulizeum* Lindl. ex Stein, *Hormidium*, *Osmophytum* Lindl. and *Psilanthemum* Klotsch ex Stein) and *Euepidendrum* (= *Epidendrum*), mainly separated by an admittedly artificial character, i.e. the presence or absence of pseudobulbs. At the specific level, Ames and collaborators adopted broad species concepts, with the resulting lumping of many closely related Central American taxa as varietal forms under older and not well-understood *Epidendrum* names. In this way, several recently described *Epidendrum* and *Encyclia* spp. from Mesoamerica were considered as a 'polymorphic alliance' (Ames *et al*., 1936) and treated as varieties of a single variable species, *Epidendrum oncidioides*. The latter species, originally described from South America (Lindley, 1833), was discussed by Dressler (1962) and shown to be an endemic from Brazil to Guyana, and substantially different from any other related taxa in Central America (Fig. 5).

Eventually, the lumping approach favoured by Harvard botanists was substantially adopted by Ames (1937) in his treatment of Orchidaceae for Standley's *Flora of Costa Rica*. Notwithstanding the flow of new *Encyclia* spp. described from Costa Rica and the closely allied flora of Panama during the first decades of the 20th century, the total number of species accepted by Ames for Costa Rican flora is the same of Schlechter's account in 1918. However, Ames excluded *E. alata* and recorded *Epidendrum oncidioides* var. *gravidum* (Lindl.) Ames, F.T.Hubb. & C.Schweinf., a concept based on *Epidendrum gravidum* Lindl. from Mexico, which he considered conspecific with his *E. peraltense*. 'Rare in Costa Rica,' *E. peraltense* was known at the time from only three specimens: the type collection by Lankester and Sancho and two more specimens collected by A. Alfaro from La Fuente, near Turrialba. Ames also recorded *E. atropurpurea*, 'frequently cultivated in San José,' *E. oncidioides* var. *mooreanum*, now known from many collections (including those by the Brade brothers (type of *Encyclia tonduziana* Schltr.) and by Brenes from the vicinity of San Ramón (type of *Encyclia brenesii* Schltr.)), and *E. oncidioides* var. *ramonense* (Rchb.f.) Hoehne, 'frequent in Costa Rica' (Ames, 1937).

In his series on the Central American bulbous species of *Epidendrum*, Withner accepted five species

Figure 5. *Epidendrum oncidioides* Lindl. (= *Encyclia oncidioides* (Lindl.) Schltr.), from *Edwards's Botanical Register* 19: pl. 1623. 1833.

for the flora of Costa Rica, namely *Epidendrum alatum*, *E. cordigerum*, *E. peraltense, E. mooreanum* Rolfe and *E. ramonense* (considered the Central American counterpart of the Venezuelan *E. ceratistes*) (Withner, 1970b, d). He also suggested that *Epidendrum gravidum* may be nothing more than a regularly flowering specimen with a group of fruits in formation, and that *E. peraltense* should be reduced into synonymy (Withner, 1970a, d) because of the similiariries among the two concepts in lip morphology.

In their list of the orchids of Costa Rica, Mora-Retana & García (1992) reported eight species: *E. alata* (Bateman) Schltr., *E. amanda* (Ames) Dressler, *E. ceratistes*, *E. cordigera, E. gravida* (Lindl.) Schltr., *E. mooreana, E. selligera* (Bateman ex Lindl.) Schltr. and *E. tuerckheimii* Schltr. A year later, Dressler (1993) in his *Field Guide of the Orchids of Costa Rica and Panama* recorded the same species, but added *E. guatemalensis* (Klotzsch) Dressler & G.E.Pollard.

In 1998, Withner reshaped his early contributions to the taxonomy of *Encyclia* and made the first attempt to arrange systematically the species native to Mesoamerica after the monumental work by Ames, Hubbard & Schweinfurth on Central American '*Epidendrum*', dated 1936. Withner assigned ten species to Costa Rica: *E. alata*, *E. amanda*, *E. ceratistes*, *E. cordigera*, *E. gravida, E. mooreana*, *E. peraltensis, E. selligera, E. stellata* and *E. tuerckheimii*. Then, he added two more unvouchered taxa: *E. davidhuntii* Withner & M.Fuente and *E. alanjensis* (Ames) Carnevali & G.A.Romero (Withner, 2001).

Pupulin (2002) recorded a total of ten species, presenting a list of synonyms for all the accepted taxa, based on vouchered specimens: *E. alanjensis*, *E. amanda*, *E. ceratistes*, *E. chloroleuca*, *E. cordigera*, *E. davidhuntii*, *E. mooreana*, *E. peraltensis* and *E. stellata*. Later, Dressler (2003) recognized six species, excluding *E. alanjensis, E. amanda, E. chloroleuca* and *E. davidhuntii*. Both authors also excluded three species ranging mainly from Mexico

and Guatemala to northern Nicaragua: *E. guatemalensis, E. selligera* and *E. tuerckheimii*.

In 2005, in his treatment of the genus for *Vanishing Beauty – Native Costa Rican Orchids*, the senior author discussed the status of eight previously known species (Pupulin, 2005). That treatment offered short ecological and geographical notes for most of the species and illustrates seven of the taxa in colour. The author also presented the photograph of one still-unpublished taxon, described later as *E. ossenbachiana* Pupulin (Pupulin, 2006), the newest addition to the genus in Costa Rica.

Notwithstanding the removal of the large group of species now included in *Prosthechea*, the taxonomy of Mesoamerican *Encyclia* spp. is still somewhat confusing. Most of the taxa from Central America show a remarkable similarity in vegetative and floral morphology, and the plethora of published names are often based on inadequate study of the type specimens and limited availability of plant material for comparison. The present work aims to clarify the status of *Encyclia* in Costa Rica, based on extensive survey of living material, morphological variation and ecological evidence.

MATERIAL AND METHODS

This revision was conducted mainly at the Lankester Botanical Garden (JBL), University of Costa Rica, where living specimens were cultivated and documented between 2003 and 2011. We relied mainly upon live collections made during fieldwork activities of JBL staff. Field research was conducted throughout the country and type localities were visited. Documented collections of living plants were also examined for rare taxa and to score for unusual forms. Data from all specimens cited have been recorded in a computerized database at JBL. All the pictures, documents, protologues and images of the type specimens analysed are available online at www. epidendra.org (Pupulin, 2007; Pupulin, 2009). Distribution maps were made using the geographic information system software ArcView GIS 3.3 (ESRI, Redlands, CA, USA). Georeferences for specimens were obtained by using a Garmin eTrex Vista GPS, maps, online gazetteers and Google Earth. Ecological zones were estimated using the Holdridge Life Zone System (Holdridge, 1967; Holdridge, 1987) and the *Mapa ecológico de Costa Rica* by Tosi (1969). Phenology data were recorded both in the field and in cultivated specimens or herbarium labels. Individual plants were photographed, illustrated and preserved as exsiccata and spirit-preserved specimens (including flowers, portions of the stems or entire plants) for future reference. Newly collected herbarium specimens were deposited at CR and USJ herbaria. Whenever possible, the herbarium specimens were complemented with sketches, photographs and formalin–acetic acid–alcohol (FAA) material. The material preserved in FAA is deposited at JBL and indicated in the treatment as 'JBL-spirit'. Herbarium and spirit material may consist of wild collected specimens or material collected entirely from cultivated plants. Flower comparisons were scanned at 1200 and 2400 dpi resolution with an Epson Perfection 2400 photo scanner. Sketches of specimens were drawn with Leica M3Z, M8, MZ7.5 and MZ9.5 stereomicroscopes provided with drawing tubes and conserved in the reference collections of JBL. All the taxa were illustrated by composite line drawings from living specimens. Illustrations included a typical plant habit, inflorescences or part of the inflorescences, three quarters view of the flower and a dissection of the perianth, anther cap and pollinarium or other taxonomically informative characters, depending on the taxa illustrated. Plate composition was as consistent as possible to facilitate species comparison. Descriptions were prepared from both living specimens and herbarium material. Visits to the following herbaria were made: AMES, BM, CR, INB, K, SEL, USJ and W. Type specimens from AMES, K and W were digitalized at 300 dpi and the resulting images were included in the reference collections. When necessary, flowers of herbarium material were rehydrated using boiling water and specimens drawn with the aid of a camera lucida.

SYSTEMATIC TREATMENT

ENCYCLIA HOOK., Bot. Mag. 55: pl. 2831. 1828.

Type species: Encyclia viridiflora Hook. Bot. Mag. 55: 2831. 1828. *Epidendrum viridiflorum* (Hook.) Lindl., Edwards's Bot. Reg. 28(Misc.): 30. 1842. *non Epidendrum viridiflorum* Sessé & Moç., Fl. Mexic., ed. 2: 203 1894., *nom. illeg.*

Doxosma Raf., Fl. Tellur. 4: 9 (1838).

Type species: Doxosma gracilis (Lindl.) Raf., Fl. Tellur. 4: 9 (1838). Bas. *Epidendrum gracile* Lindl.

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

Type species: Sulpitia odoratissima (Lindl.) Raf., Fl. Tellur. 4: 37 (1838) [as *S. odorata*]. Bas. *Epidendrum odoratissimum* Lindl.

PLANTS epiphytic or lithophytic, rarely terrestrial, caespitose, to 110 cm tall. RHIZOME inconspicuous or elongate. ROOTS fleshy, cylindrical, 1–4 mm in diameter, with green, reddish or yellowish tips.

KEY TO THE COSTA RICAN SPECIES OF *ENCYCLIA*

1. Flowers large, < 4 cm in diameter; the midlobe of the lip > 2 cm wide.....2
1 Flowers smaller, < 3 cm in diameter; the midlobe of the lip < 1 cm wide.....3
2 The sepals strongly incurved at apex; petals not unguiculate; lip with plain margins, white (or purple), the lateral lobes oblong–lanceolate, narrower at apex; column straight, wingless; pedicellate ovary smooth.....*E. cordigera*
2 The sepals straight at apex; petals distinctly unguiculate; lip with ruffled margins, yellow, the lateral lobes obovate, broader at apex; column arched, winged; pedicellate ovary verruculose–papillose.....*E. alata*
3 Flowers cleistogamous; column without a rostellum.....*E. gravida*
3 Flowers spreading at anthesis; column with a distinct, transversal rostellum.....4
4 Lateral lobes of the lip obovate, distinctly wider at apex.....5
4 Lateral lobes of the lip ligulate–oblong, the apex as wide as the base or narrower.....6
5 The midlobe of the lip blotched with purple, provided with a keel running from the callus to the apex; the anther cap with two apical horns.....*E. mooreana*
5 The midlobe of the lip concolorous cream, without central keel; the anther cap without horns.....*Encyclia* sp.
6 Column wings prominent, subquadrate, incurved under the isthmus of the lip.....7
6 Column wings small, subtriangular, straight, or absent.....8
7 Inflorescence dense; lateral branches of the inflorescences short, < 3 cm long; midlobe of the lip with three inconspicuous, low keels, the central one reaching about the half of the lip blade.....*E. peraltensis*
7 Inflorescence loose, lateral branches of the inflorescences long, 5–8 cm long; midlobe of the lip with three distinct keels, the central one running to the lip apex.....*E. chloroleuca*
8 The lateral lobes of the lip oblong or lanceolate, narrow.....9
8 The lateral lobes of the lip subrectangular, broad.....*E. ceratistes*
9 Lip with several, raised, verrucose keels; the lateral lobes of the lip longer than the midlobe; the midlobe concolorous cream.....*E. stellata*
9 Lip with a single, low, glabrous keel; the lateral lobes of the lip shorter than the midlobe; the midlobe of the lip blotched with purple.....*E. ossenbachiana*

PSEUDOBULBS spherical, subovoid, ovoid, conic–ovoid, fusiform, pyriform or subpyiriform, heteroblastic, subtended by scarious bracts shredded with age, one- to three- (rarely several-) foliate at apex. LEAVES generally two, rarely one, three or four, on short tubular petioles at apex of pseudobulbs, ligulate, oblong, linear or elliptic, acute or subacute, conduplicate, dorsally keeled, the apex somewhat irregularly bilobed, coriaceous, curving with age. INFLORESCENCE apical, erect or arching, stout, smooth or warty, racemose or paniculate to 150 cm long, spathe lacking; peduncle terete, to 45 cm long, covered by tightly sheathing bracts. FLOWERS showy, rarely autogamous, resupinate, rarely non-resupinate, sometimes scented, greenish, white or brownish, pink or purple–maroon, inconspicuous to showy, blotched or striped with magenta. SEPALS brownish, yellowish, green, pink or maroon, elliptic, ovate, obovate or spathulate, simple, free, sometimes with linear or reticulate veins, membranaceous to fleshy. PETALS of the same colour as sepals, simple, free, subequal to the sepals, the apex inflexed. LABELLUM three-lobed, narrowing to the middle forming an isthmus, free or basally adnate to the column, the lateral lobes arching and clasping the column, midlobe sessile or separated by a clear isthmus, generally white with a combination of brownish, pink or magenta with a central keeled callous, often two-ridged and radiating into several conspicuous smooth or warty keels entering the midlobe. COLUMN straight, semiterete, truncate, lateral wings or teeth present or absent, white or pinkish, with incumbent anther, the stigma dorsal, the rostellum entire. POLLINIA four, of equal size, ovate or obovate, yellow, with caudicles, without viscidium. ANTHER CAP cucullate, four-celled. CAPSULE pyriform to fusiform, smooth or warty.

Encyclia includes some 160 species distributed from Mexico (Sonora State) and Florida through Central America, the Bahamas and the Caribbean islands, to Peru, Argentina and Brazil (Rio Grande do Sul State) in South America. In terms of number of species and endemism, three main distribution centres exist in Mexico, the Antilles (especially Cuba) and the Atlantic coast of Venezuela to Brazil, whereas Costa Rica, Panama and lowland Colombia and northern Andes are relatively poor in species diversity (van den Berg *et al.*, 2005) (Map 1).

SPECIES DESCRIPTIONS

1. *ENCYCLIA ALATA* (BATEM.) SCHLTR., Orchideen 207. 1914. *Epidendrum alatum* Batem., *Orchid. Mexico & Guatemala*, t. 18. 1840. *Type: Habitat in Honduras*

Map 1. Distribution of the genus Encyclia (modified from van den Berg & Carnevali, 2005).

prope Isabal, 1837, *G.U. Skinner s.n.* (K, not located; illustration of type in Bateman, 1840). (Figs 6, 7A, Map 2).

Description: PLANT epiphytic, caespitose, with a short rhizome, to 90 cm tall. ROOTS white, produced from the base of the pseudobulb and the rhizome, 1.5–3.0 mm in diameter. PSEUDOBULBS conic–ovoid to pyriform, subtended by papery sheaths, shredded with age, 3–11 × 1.5–6.0 cm, two (rarely three) leaves at apex. LEAVES two, rarely three on short tubular petioles at apex of pseudobulbs, ensate, linear–lanceolate, ligulate or elliptic, dorsally keeled, acute or subacute, conduplicate, coriaceous, the apex irregularly bilobed, 20–55 × 1.3–5.0 cm. INFLORESCENCE apical, racemose, rarely branching and forming a compound raceme or paniculate, exceeding the leaves, purplish, verruculose, peduncle cylindric, to 35–40 cm, scape bracts 5–3 mm, acute, scarious, surrounding scape; panicle 30–60 cm. FLORAL BRACTS 2–3 × 2.0–2.5 mm, triangular, basally clasping rachis, spreading. OVARY AND PEDICEL terete, warty, 3.0–3.5 mm. FLOWERS showy, resupinate, spreading, scented, sepals and petals basally olive or pale green, distally dark red-brown; lip yellow or green, cream with yellow margins, veins dark red; the lateral lobes basally stripped with dark red, callus reddish spotted. SEPALS subsimilar, oblanceolate–oblong to subspathulate, acute to

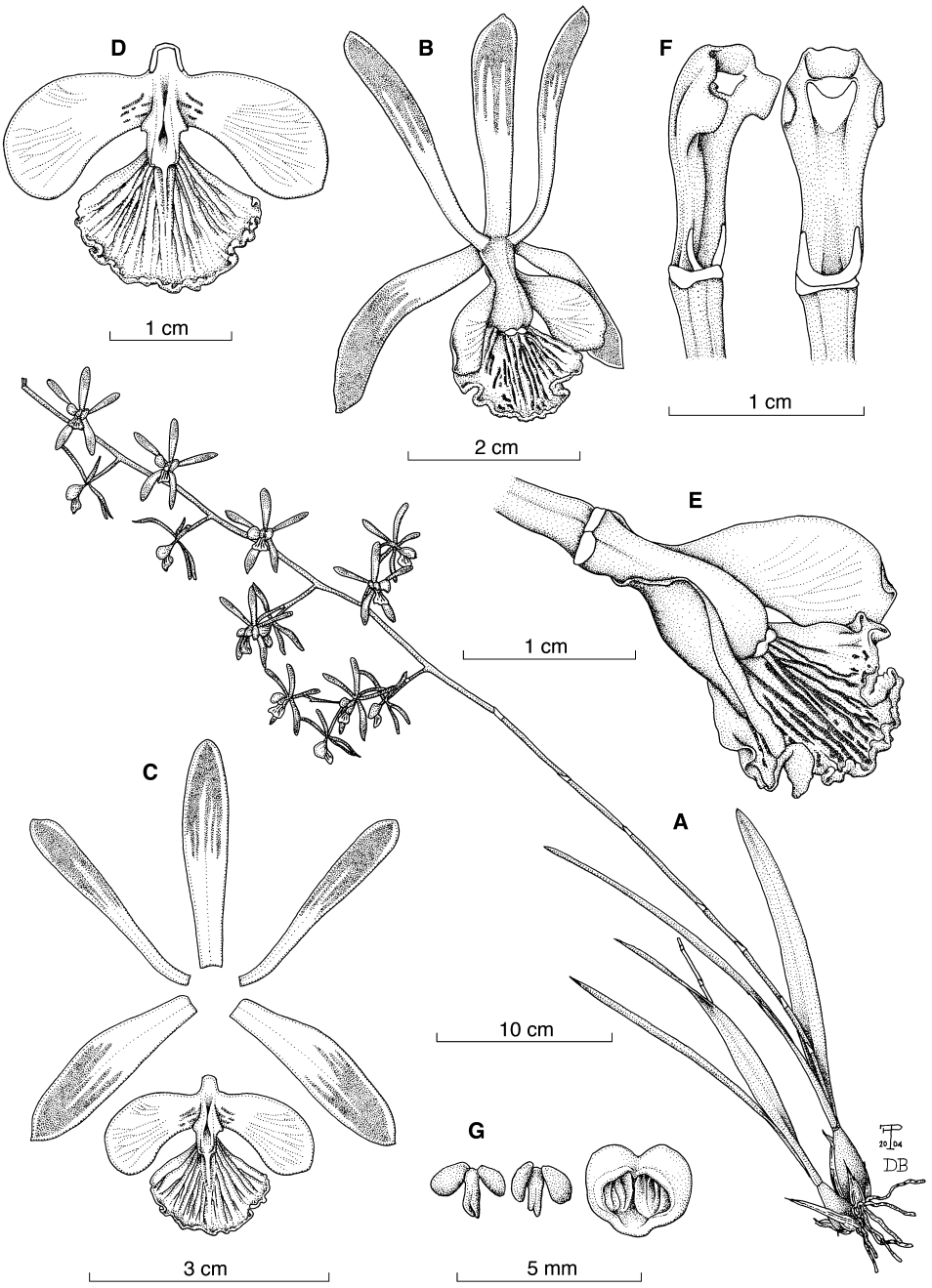


Figure 6. *Encyclia alata* (Batem.) Schltr. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, lateral view. F, column, lateral and front views. G, pollinarium and anther cap. Drawn by the authors from *Pupulin 4369* (USJ).

subacute, slightly revolute, dorsally weakly carinate. DORSAL SEPAL oblanceolate, acute or subobtuse, the margins revolute, 2.1–3.0 × 0.6–0.7 cm. LATERAL SEPALS, elliptic–oblanceolate, acute or subobtuse, 2–3 × 0.4–0.7 mm. PETALS spatulate–oblanceolate, acute or apiculate, unguiculate, revolute, 2.0–2.9 × 0.5–0.7 cm. LIP basally adnate to the column for 1.5 mm, deeply three-lobed, unguiculate, 1.8–2.3 × 2.3–2.6 cm across the lateral lobes; lateral lobes unguiculate, obovate, obtuse, subfalcate, wider and broadly rounded toward the apex, erect, hiding and flanking the column in natural position, 1.3 × 0.8 cm; isthmus about 6.0 × 2.5 mm, subquadrate, minutely papillose on the lateral margins; midlobe suborbicular,

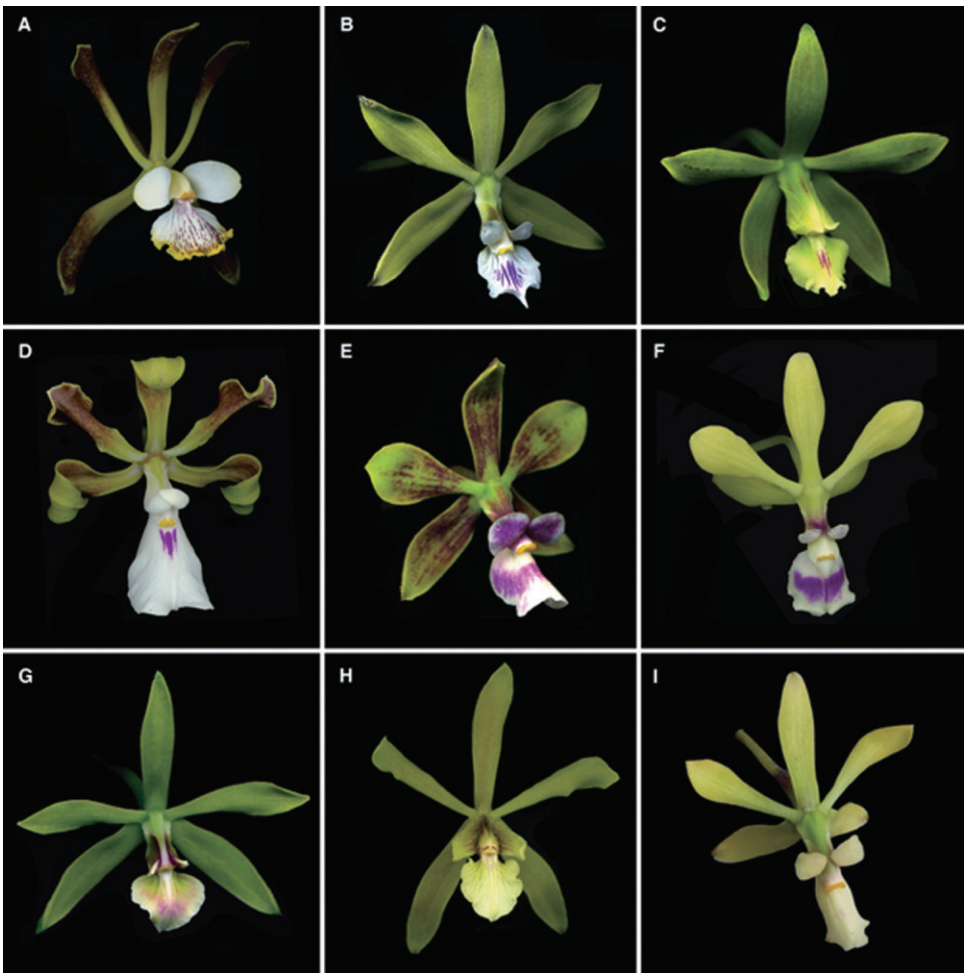
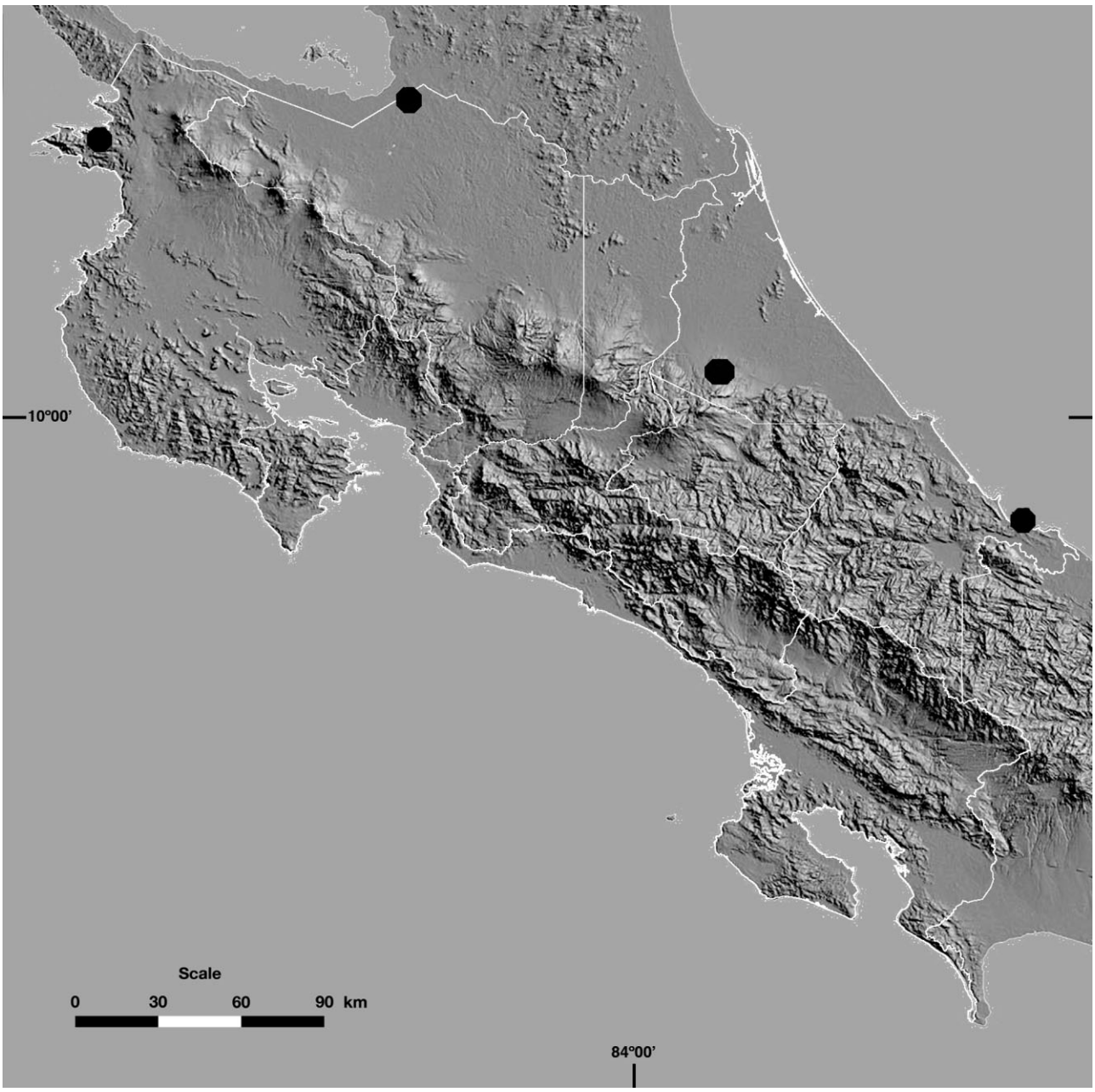


Figure 7. Flowers of *Encyclia* species from Costa Rica. A, *E. alata* (JBL-11938). B, *E. ceratistes* (*Bogarín 3797*). C, *E. chloroleuca* (*Pupulin 3043*). D, *E. cordigera* (*Pupulin 5996*). E, *E. mooreana* (*Bogarín 3787*). F. *E. ossenbachiana* (*Pupulin 5237*). G, *E. peraltensis* (*Bogarín 2632*). H, *E. stellata* (*Pupulin 5622*). I, *Encyclia* sp. (*Ossenbach S-005*). All the vouchers at JBL.

flabellate or transversely oblong, the margin undulate–crisped, apically truncate or obtuse, blade with purple raised nerves that pass into broken verrucose terminations, 1.1 × 1.2 mm, the callus composed by three longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, sulcate, joining at the base and extending onto the midlobe as thickened nerves, apically tridentate. COLUMN straight, stout, obovate, semiterete, slightly arcuate at apex, truncate, 1.0 × 0.5 cm, winged, wings 2.5 × 2.0 mm, transversely subquadrate–oblong, basally provided with a nectary, apically with two lateral teeth. ANTHER CAP widely ovate, cucullate, four-celled. POLLINIA four in two pairs, obovate, strongly flattened, on narrowly linear, basally bifid caudicles. CAPSULE fusiform, warty.

Other specimens examined: COSTA RICA. Alajuela. Vicinity of Los Chiles, Río Frío, 11°02′N, 84°44′W, 30–40 m, low tropical rainforest, with palms prominent, 1 August 1949, *R. W. Holm 821 & H.H. Iltis* (USJ). Guanacaste: La Cruz, Santa Elena, Cerros Santa Elena, 10°52′N 85°50′W, 500 a 600 m, 31 agosto 2003, *J.F. Morales 9643* (INB). Limón: Tortuguero, bosques primarios y tacotales en el camino a San Valentín, 10°09′;N 83°43′W, 400 m, 9 mayo 1995, *J.F. Morales 4063* (INB). Limón. Talamanca, Sixaola, R.V.S. Gandoca-Manzanillo, Puerto Viejo, Refugio Gandoca Manzanillo, Humedal de Punta Manzanillo, bordeado de *Raphia*, más adentro dominado por *Campnosperma*, *Ilex*, *Cassipourea* y *Chrysobalanus*, 9°37′30″N 82°38′38″W, 0–100 m, epífita en pantano, en la base de troncos, estéril, 19 Julio 2008, *B.*



Map 2. Distribution of *Encyclia alata* in Costa Rica.

Hammel, I. Perez 24855 (INB). Without locality data, *F. Pupulin 4369* (USJ).

Distribution: From Mexico to western Panama.

Etymology: From the Latin *alatus*, 'winged', in allusion to the remarkable lateral lobes of the lip.

Phenology: February to August.

Habitat and ecology: Epiphytic in tropical wet forest, tropical moist forest and tropical wet forest basal belt transition, where populations are mostly found along the Caribbean watershed from sea level to 600 m of elevation. Although this species is usually restricted to the Caribbean plains, a population has been recorded in premontane moist forest, basal belt transition on the Pacific watershed, in the Cerros de Santa Elena in northern Guanacaste. Plants can be found growing in secondary vegetation and primary forest.

Discussion: Encyclia alata is one of the showiest species of the genus in Costa Rica. It was described as *Epidendrum alatum* by J. Bateman in 1840 based on a collection of G. Skinner in Honduras (Bateman, 1840). As suggested by Withner (1970b) on the basis of morphological features of the flowers, *E. alata* has no close relatives in the flora of Costa Rica, and its affinities are likely with northern species centred in Mexico and Guatemala, such as *E. ambigua* (Lindl.) Schltr., *E. dickinsoniana* (Withner) Hamer and *E. guatemalensis* (Klotzsch) Dressler & G.E.Pollard. It is easily distinguished by the racemose inflorescences, rarely paniculate, the large, showy flowers with oblanceolate–oblong to subspathulate revolute sepals and petals that are basally olive or pale green and distally dark red–brown, the lip with conspicuous lateral lobes that are widely rounded apically, hiding and flanking the column in natural position. The midlobe has raised purple nerves that pass into broken verrucose terminations with a remarkable undulate–crisped band of intense orange which skirts the front part of the lip.

2. *ENCYCLIA CERATISTES* (LINDL.) SCHLTR., Repert. Spec. Nov. Regni Veg. Beih. 6: 74. 1919. *Epidendrum ceratistes* Lindl., Bot. Reg. 30(Misc.): 92.1844. *Type:* A native of the 'Spanish Main', whence it was brought by Mr Hartweg to the Horticultural Society, with whom it flowered in October last, *Hartweg s.n.* (holotype: K). (Fig. 7B, 8, 9, Map 3).

Synonyms: Epidendrum ramonense Rchb.f., Beitr. Orchid.-K. C. Amer. 81. 1866. *Encyclia ramonensis* (Rchb.f.) Schltr., Beih. Bot. Centralbl. 36(2): 473. 1918. *Epidendrum oncidioides* var. *ramonense* (Rchb.f.) Ames, F.T.Hubb. & C.Schweinf., Bot. Mus. Leafl. 3: 103.1935. *Encyclia oncidioides* var. *ramonensis* (Rchb.f.) Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 2(6): 153. 1952. *Type:* COSTA RICA. [ALAJUELA]: San Ramón in Costa Rica, *H. Wendland s.n.* (holotype: W).

Encyclia powellii Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 46. 1922. *Type:* PANAMA. CHIRIQUI-BEZIRK, 4000–5000 fuss, *C.W. Powell 83* (holotype: B, destroyed; lectotype designated by Christenson, (1991), AMES (but see Discussion); isolectotypes: AMES, K, MO).

Description: PLANT epiphytic, caespitose, to 90 cm tall. ROOTS white, produced from the base of the pseudobulb and the rhizome, 1.5–4.0 mm in diameter. PSEUDOBULBS subglobose, or subpyiriform, 2.5–6.0 × 1.8–2.5 cm, subtended by papery sheaths, shredded with age, 2.3–6.2 × 1.3–6.1 cm, two- to four-foliate at apex. LEAVES on short tubular petioles at apex of pseudobulbs, ligulate to narrowly lanceolate, ensate, acute or obtuse, the apex irregularly bilobed, coriaceous, curving with age, 12–45 × 0.8–2.5 cm. INFLORESCENCE apical, arching, stout, a simple, rarely paniculate raceme, to 95 cm long, green to reddish brown, sometimes becoming vivid purple with age, glabrous to scabriosusculous; peduncle cylindrical, to 45 cm long; lateral branches three- to five-flowered, to 5–9 cm long; scape bracts acute, scarious, surrounding scape, 1.2–2.0 cm; panicle 15–65 cm. FLORAL BRACTS 1.0–1.5 × 2.0–2.5 mm, triangular acute, adpressed to the rachis. PEDICEL 1 cm, verrucose. OVARY verrucose, 1.0–1.5 cm long. FLOWERS resupinate, spreading, scented, sepals and petals apple green or brownish green, midlobe white or cream with magenta stripes, lateral lobes basally tinged with brown. SEPALS subsimilar, elliptic, slightly conduplicate, acute or apiculate, carinate at apex. DORSAL SEPAL elliptic, subacute or apiculate, 1.4–1.8 × 0.3–0.4 cm. LATERAL SEPALS, elliptic, acute or apiculate, 1.5–1.8 × 0.3–0.4 cm. PETALS spatulate–elliptic or spatulate–obovate, acute, 1.3–1.7 × 0.3–0.5 cm. LIP basally adnate to the column for 2 mm, deeply three-lobed, unguiculate, 1.3–1.5 × 1.1–1.2 cm across the lateral lobes; lateral lobes unguiculate, oblong or lance–oblong, obtuse, reflexed apically, flanking the column in natural position, 0.4–0.5 × 0.27–0.33 cm; isthmus about 7.0 × 2.5 mm, subquadrate; midlobe ovate or deltoid–ovate, acute or apiculate, the margin entire to crenulate, blade with magenta nerves, 6–9 × 5–9 mm, the callus composed of two longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, sulcate, joining at the base and extending onto the base of the midlobe. COLUMN straight, stout, pandurate, semiterete, truncate, 6–8 × 2–3 mm, winged, wings 0.2–0.6 × 0.3–0.5 mm triangular, tooth-like, transversely subquadrate–oblong, basally provided with a nectary, apically with two lateral teeth. ANTHER CAP widely ovate, cucullate, four-celled. *Pollinia* four in two pairs, obovate, strongly flattened, on narrowly linear, basally bifid caudicles. CAPSULE fusiform, warty.

Distribution: From Mexico to Colombia and Venezuela.

Other specimens examined: COSTA RICA. Alajuela: Alfaro Ruiz, Palmira, Zona Protectora El Chayote, 2100 m, epiphytic on large trees along the continental divide, montane forest with *Quercus*, 8 March 2001, *F. Pupulin & G. Barboza s.n.* (USJ). San Ramón, Berlín, near the turning of the unpaved road to San Mateo, Cerro Pelón, 10°00′52″N, 84°23′55″W, 1200 m, Pacific watershed of the Cordillera de Tilarán, lower montane rainforest, scrub vegetation with scattered trees on exposed, windy crests, 21 November 2004, *F. Pupulin 5200 & E. Salas* (JBL-

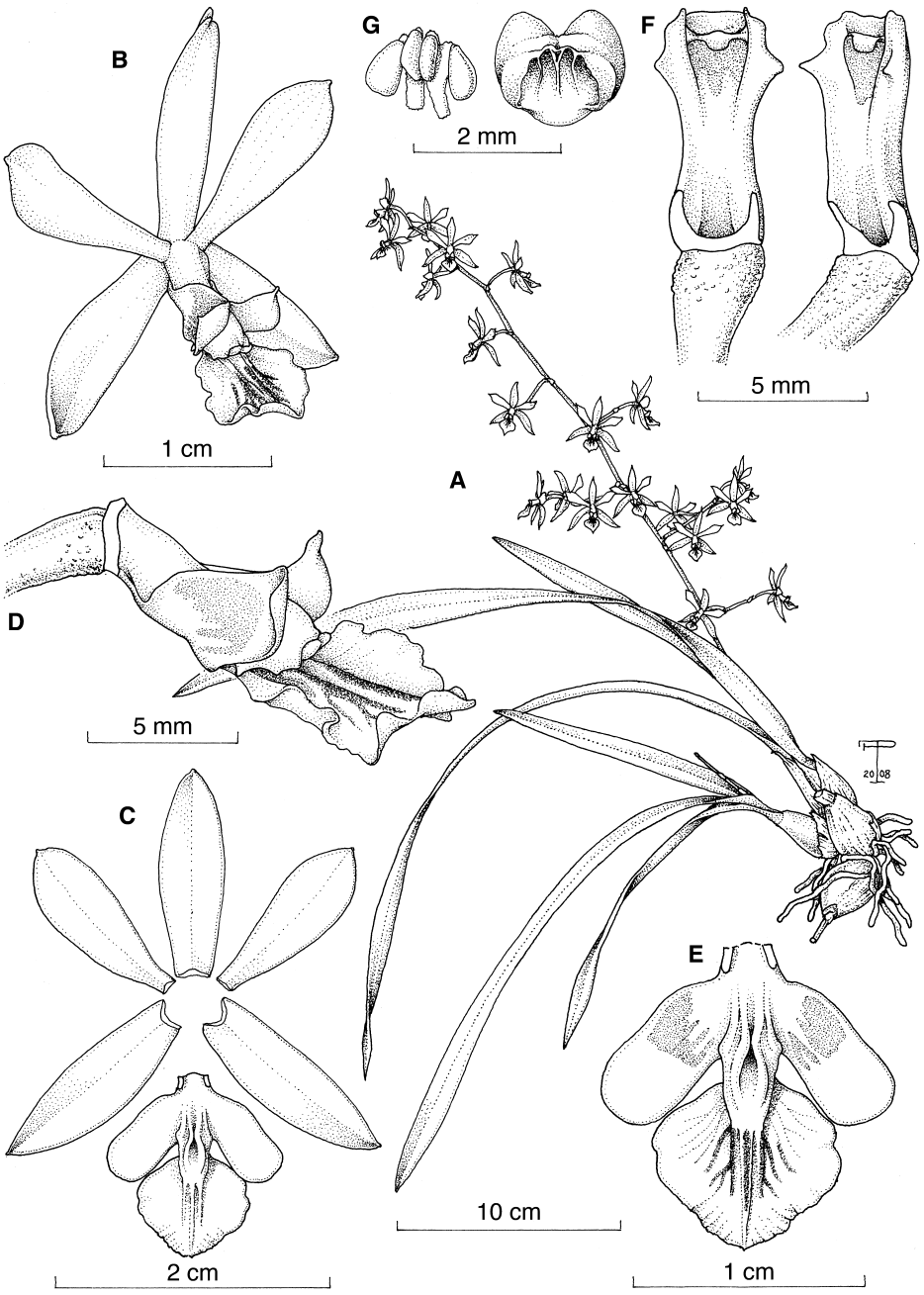


Figure 8. *Encyclia ceratistes* (Lindl.) Schltr. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, three quarters view. F, column, lateral and front views. G, pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 5520* (JBL-Spirit).

spirit). San Ramón, Berlín, near the turning of the unpaved road to San Mateo, Cerro Pelón, 10°00′52″N, 84°23′55″W, 1200 m, Pacific watershed of the Cordillera de Tilarán, lower montane rainforest, scrub vegetation with scattered trees on exposed, windy crests, 21 November 2004, *F. Pupulin 5303 & E. Salas-Pupulin* (JBL-spirit). San Ramón, Santiago, road to Berlín, *c.* km 4, 10°02′32″N, 84°29′31″W, 1225 m, premontane moist forest, epiphytic in secondary vegetation along the roadside, 7 March 2004, *F. Pupulin 5200 & E. Salas* (JBL-spirit). San Ramón, Piedades Sur, San Miguel (La Palma), camino a San Bosco, a orillas y dentro de un pequeño bosque secundario, 10°07′18.8″N 84°31′13.1″W, 1062 m, 21

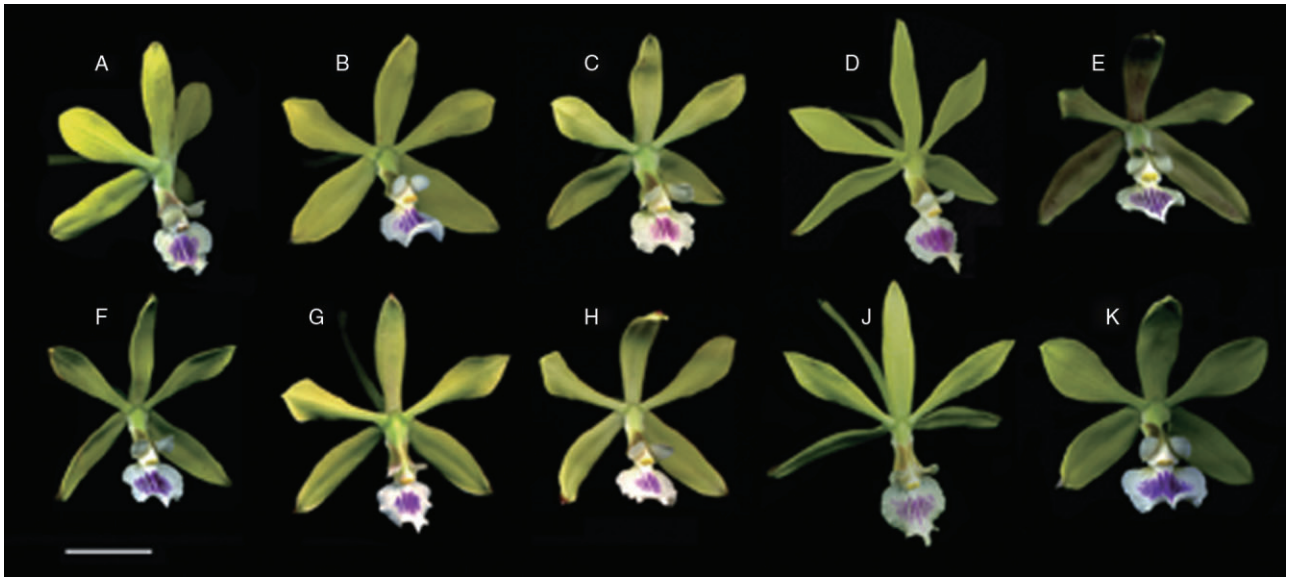
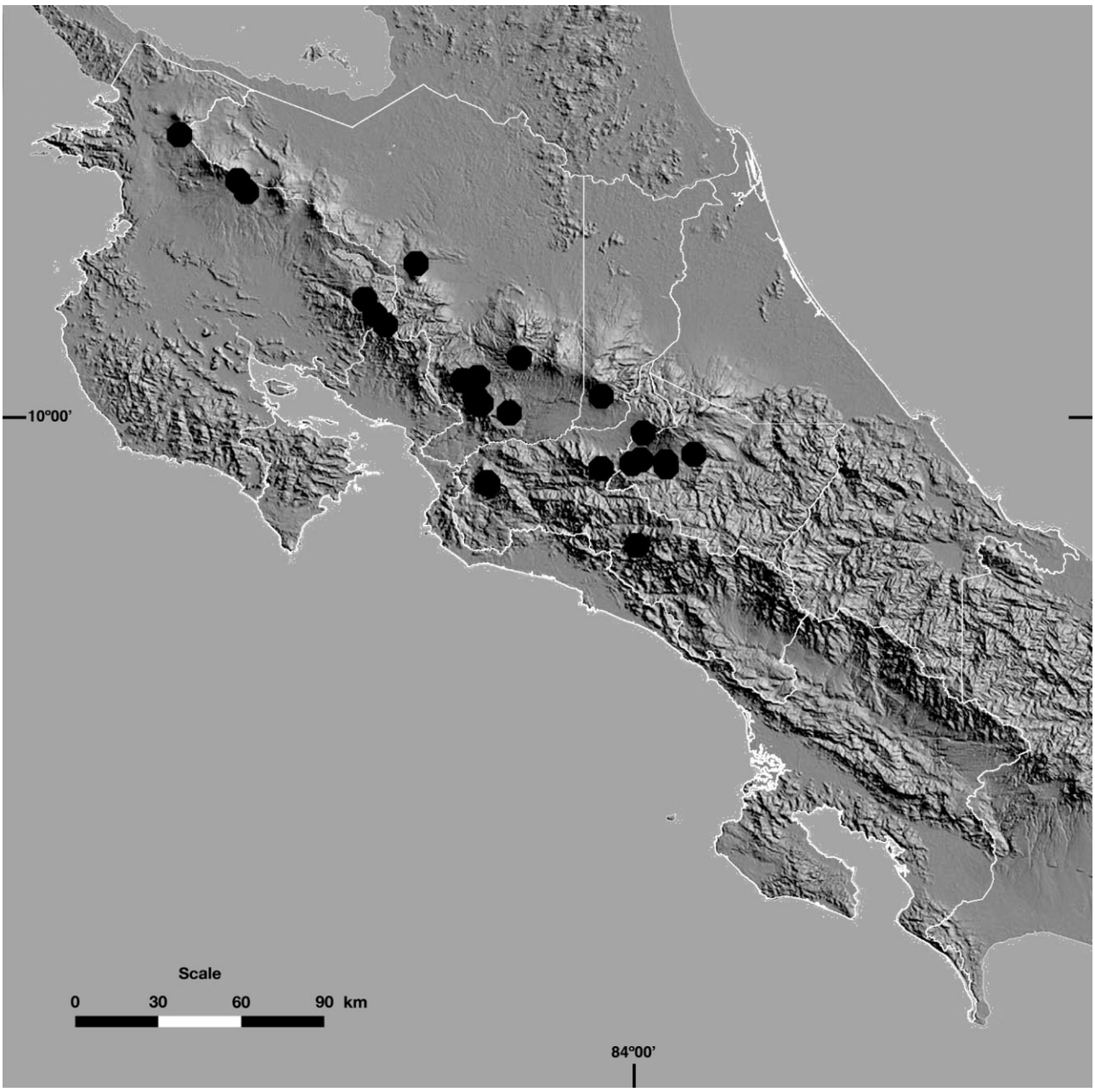


Figure 9. Floral variation in *Encyclia ceratistes*. A, *Bogarín 3796*. B, *Pupulin 5641*. C, *Pupulin 5520*. D, *Pupulin 5200*. E, *Bogarín 3804*. F, *Bogarín 3799*. G, *Pupulin 5641*. H, *Pupulin 6117*. J, *Pupulin 5303*. K, *Bogarín 3806*. Scale bar, 1 cm. All the vouchers preserved at JBL.

diciembre 2010, *A. Karremans 3250, J.A.J. Karremans & M. Contreras Fernández* (JBL-spirit). San Ramón, Santiago, Balboa, unpaved road to Río Jesús, Pacific watershed of the Cordillera de Tilarán, near the continental divide, about 1200 m, epiphytic on scattered trees in pastures, 17 April 2005, *F. Pupulin 5641* (JBL-spirit). Same locality, *F. Pupulin 5640* (JBL-spirit). Remnant forest, La Palma de San Ramón, 1240 m, 20 May 1969, *R. Lent 1687* (CR). Cartago: Cartago, Quebradilla, Z.P. Cerros de La Carpintera, 9°51′47″N, 83°58′18″W, 1450 m, 6 mayo 2003, *A. Quesada 1121, J.E. Sánchez, E. Serrano & E. Carman* (CR). Cerro Blanco, Quebradilla de Cartago, junio 1986, *D.E. Mora s.n.* (USJ). Cartago, Dulce Nombre, Jardín Botánico Lankester, 1500 m, bosque húmedo premontano, epífitas creciendo naturalmente en el bosque secundario, 14 abril 2004, *D. Bogarín 801* (JBL-spirit). Same locality, *D. Bogarín 802* (JBL-spirit). Same locality, 7 febrero 2005, *D. Bogarín 1387* (JBL-spirit). Cartago: Dulce Nombre, Jardín Botánico Lankester, *c*. 9°51′20″N 83°53′25″W, 1350 m, epiphytic on *Cupressus* trees within the botanical garden, plants forming natural populations, 6 February 2005, *F. Pupulin 5520* (JBL-spirit). Paraíso, alrededores de la Reserva Tapantí, 6 junio 1987, *G. Núñez Rivas 6* (USJ). Paraíso, Palomo de Cachí, colectada por Levinia Vargas, *C. Ossenbach 501* (JBL-spirit). El Pizote, San Ramón de Tres Ríos, 1500 m, 26 June 1984, *G. Herrera & L.D. Gómez 22860* (CR). [La Unión], all over the country at 3–5000' San Ramón, Cartago, June. May, *A.R. Endrés 110* (W). Guanacaste: Bagaces, Mogote, 10°44′N, 85°15′W, 500–600 m, sector sureste, camino a Don Lalo, alrededores del Cerro Mogote, 11 julio 1991. *G. Rivera 1433* (INB). Liberia, Mayorga, southwest slope of Cerro Cacao, along trail ascending from Estación La Tortuga, 10°56′N, 85°28′W, 1200 a 1300 m, 17 agosto 2007, *M. H. Grayum 12786* (INB). Liberia, Mayorga, Cerro Pedregal, 10°55′N 85°28′W en el sendero de la casa de Cacao al Mirador, 800 a 900 m, 13 julio 1996, *J. F. Morales 5491* (INB). Tilarán, Quebrada Grande, 10°23′N 84°52′W, Río Chiquito de Tilaran. 2 km Noreste de Río Chiquito. 1000 a 1100 m, Vertiente Norte, 1 diciembre 1987, *W. Haber 7852* (INB). Border between Guanacaste and Alajuela: Bagaces, Mogote, road from San Jorge de Liberia to Colonia Blanca, south-east slopes of Rincón de la Vieja volcano, 10°46′05.1″N, 85°16′45.3″W, 820 m, premontane dry, transition to premontane rainforest, 1 May 2006, *F. Pupulin 6117, D. Bogarín, A. Rambelli & G. Rambelli* (JBL-spirit). Guanacaste: Tilarán, Tierras Morenas, *c*. 500 m después de Sabalito camino a Naranjos Agrios, 10°34′24.7″N, 85°00′43.1″W, 650–700 m, bosque húmedo tropical transición a premontano, epífitas en borde de potrero y bosque secundario, 2 febrero 2006, *D. Bogarín 2452, con R.L. Dressler, R. Gómez & A. Rojas* (JBL-spirit). Puntarenas: Cañitas, Santa Elena, cabeceras del Río Lagarto, Zona Monteverde, 10°20′N, 84°50′W, 1350 m, epífita en árbol de potrero, *E. Bello 10* (CR). Puntarenas, Monteverde, 10°18′N, 84°48′W, 1500 a 1600 m, 13 junio 1987, *W. Haber 7220* (INB). San José: Acosta, montaña La Monja, floreció en mayo del 2002 en el jardín de la familia



Map 3. Distribution of *Encyclia ceratistes* in Costa Rica.

Valverde Arias, 1600 m, abril 1998, *R. Valverde 27* (JBL-spirit). Aserrí, Tarbaca, carretera al Cedral, 9°50′N 84°06′W, potreros arbolados y bosque remanente cruce a Saurez,1 km antes, cabeceras Río Tarbaca, 1800 a 1900 m, 28 febrero 1994, *J. F. Morales 4045* (INB). Desamparados, San Rafael, San Rafael Arriba, casa de Ana Morales, 9°53′N, 84°04′W, 1100 a 1200 m, 11 julio 2004, *J. F. Morales 10889* (INB). Puriscal, Chires, Vara Blanca de Puriscal, bosque secundario en la falda norte del Cerro La Cangreja, 9°43′N 84°22′W, 1200 a 1300 m, 3 marzo 2001, *J. F. Morales 7661* (INB). Turrubares, San Juan de Mata, 9°47′N, 84°28′W, sector faldas del Cerro Bares, 1500 a 1600 m, 31 marzo 1990, *R. Zúñiga 173* (INB).

Etymology: From the word *ceratos*, derived from Greek *keras* 'horn', in allusion to the horns of the column present in this species.

Phenology: February to July.

Habitat and ecology: Epiphytic in tropical moist forest, premontane belt transition, premontane moist forest, premontane wet forest and lower montane rainforest along the Cordilleras of Guanacaste, Tilarán, Central and Talamanca, from 700 to 2100 m of elevation. Plants can be found growing in secondary vegetation and primary forest. They have been seen on top of *Cupressus* L. trees in gardens where they form large populations.

Discussion: Encyclia ceratistes was described by Lindley in 1844 as *Epidendrum ceratistes*, based on a collection by Hartweg from the 'Spanish Main' (Lindley, 1844). It is easily distinguished by its long paniculate inflorescences with fragrant flowers, the sepals and petals spread, greenish to yellowish, the lip with the bases of the lateral lobes brown, the midlobe of the lip ovate, acute, with the sides of the apex folded and appearing pointed, white or cream with smooth, magenta veins along the callus and the column has tiny, tooth-like wings. *Encyclia ceratistes* resembles *E. mooreana* and *E. ossenbachiana*, all occurring sympatrically in Costa Rica and having long paniculate inflorescences with fragrant flowers similar in size. The shape of the lateral lobes of the lip has been widely used to separate species groups in Central American *Encyclia*, and it is a useful character in distinguishing the species of the *E. ceratistes* group (Ames *et al*., 1936; Williams, 1946, 1951; Hamer, 1974; Mora-Retana & Atwood, 1992; Dressler, 1993, 2004; Dressler, 2003). In *E. ceratistes*, the lateral lobes are oblong, rounded, white with brown at base, in *E. mooreana* they are notably narrowed at the base and widely expanded at apex, completely stained in purple, and in *E. ossenbachiana* they are linear–oblong, acute and marked with a round purple blotch at apex. *Enclyclia ceratistes* also differs in the spread sepals and petals, which are reflexed in *E. mooreana* and *E. ossenbachiana*, the ovate, acute midlobe of the lip with smooth purple veins vs. suborbicular, rounded or retuse with a purple blotch in the centre. *Epidendrum ramonense* described by Reichenbach f. in 1866, based on a collection by Wendland in San Ramón de Alajuela, Costa Rica, is here considered a synonym of *E. ceratistes*. Material examined from the type locality in San Ramón match with the variation of *E. ceratistes*. The drawing by Lindley kept at K has a lip with the midlobe ovate and folded apically appearing apiculate with purple veins in the centre. The column has two prominent arms. In the original protologue, Lindley (1844) stated that the column of *Epidendrum ceratistes* is 'bicornuta' (with two horn-like arms), whereas in Costa Rican populations the column only has two reduced teeth. Besides that, we see little basis to tell Costa Rican populations apart from their South American counterparts, but further studies taking in account the variation in Venezuelan populations may change this view in the future. In this case, the name *Encyclia ramonensis* (Rchb.f.) Schltr. (based on *Epidendrum ramonense* Rchb.f., type *H. Wendland s.n.*, W) could apply to Costa Rican populations. *Encyclia powellii* described from Panama by Schlechter (1922), based on a collection by Powell in Chiriquí, is considered here conspecific with *E. ceratistes*. The paniculate inflorescences, the brown blotch at the base of the lateral lobes and the acute midlobe of the lip with magenta veins agree with *E. ceratistes*. Powell was known to assign the same number to specimens/plants he believed to be belonging to the same species, even when collected in different places and at different times. As a result, his collection numbers were actually 'species numbers', not collection numbers in the conventional fashion. Thus, according to Carnevali (to F. Pupulin and D. Bogarín, pers. comm., 2011), the specimen selected by Christenson for lectotypification of *E. powellii*, should better be selected as a neotype.

3. *ENCYCLIA CHLOROLEUCA* (HOOK.) NEUMANN, Rev. Hort., II, 4: 138. 1846. *Epidendrum chloroleucum* Hook., Bot. Mag. 64: t. 3557 (1837). *Type:* [GUYANA]. Imported from Demerara by John Allcard, Esq. who kindly communicated the flowering specimen here represented in September, 1836, *John. Allcard s.n.* (K). Figures 7C and 10–13. Map 4.

Synonyms: Epidendrum amandum Ames, Schedul. Orchid. 4: 36 (1923). *Encyclia amanda* (Ames) Dressler, Phytologia 21: 440. 1971. *Type:* PANAMA. foothills east of Panama, flowers in January and February, sea level, *C.W. Powell 271* (holotype: AMES; isotype: MO).

Description: PLANT epiphytic, caespitose, to 23–30 cm tall. ROOTS produced from the base of the pseudobulb and the rhizome, flexuous, 2–3 mm in diameter, whitish with green or reddish tips. PSEUDOBULBS conic–ovoid, 1–4 × 0.8–3.5 cm, subtended by papery sheaths, shredded with age, 5.5–3.0 cm, two- to three-foliate at apex. LEAVES on short tubular petioles at apex of pseudobulbs, oblong, ligulate, ensate, acute or obtuse, the apex irregularly bilobed, coriaceous, curving with age, 10–30 × 0.7–2.2 cm. INFLORESCENCE apical, arching stout, a paniculate raceme 15–65 cm, green to reddish–brown, becoming purple with age, glabrous to slightly warty; peduncle cylindric to 30 cm long, lateral branches two- to seven-flowered, to 4–8 cm long; scape bracts acute, surrounding scape 5–8 mm; panicle 35 cm; floral bracts 2–3 mm, triangular, acute, basally clasping rachis. PEDICEL 1.5 cm long, glabrous to slightly pap-

Figure 10. The type specimen of *Epidendrum chloroleucum* (= *Encylia chloroleuca*) at Kew (K 000079542). Reproduced with the kind permission of the Board of Trustees, Royal Botanic Gardens, Kew.

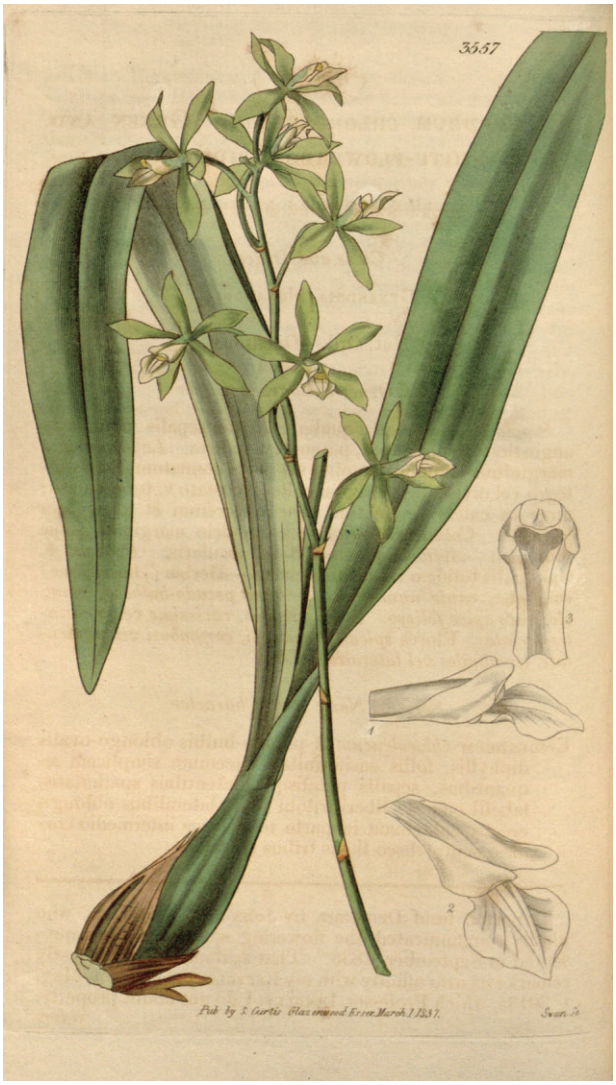


Figure 11. Original illustration of *Epidendrum chloroleucum* (= *Encylia chloroleuca*), from *Curtis's Botanical Magazine* 64 (n.s. 11): pl. 3557. 1837, probably drawn by William Jackson Hooker.

illose. OVARY cylindric, 1.2 cm long. FLOWERS sepals and petals greenish or yellowish, sometimes flushed with brown, lip white–cream marked with three to several magenta streaks on midlobe. DORSAL SEPAL elliptic, acute, 1.2–1.4 × 0.3–0.5 cm. LATERAL SEPALS elliptic, acute, 1.1–1.6 × 0.4–0.5 cm. PETALS spatulate–oblanceolate to spatulate–obovate, acute, 1.1–1.5 × 0.3–0.6 cm. LIP basally adnate to the column for 1.5 mm, deeply three-lobed, short–unguiculate, 1.0–1.4 × 1.1–1.6 cm across lateral lobes, lateral lobes unguiculate, oblong or ovate–oblong, obtuse, parallel to the column or reflexed apically and flanking the column in natural position, 4–6 × 0.2–0.4 mm; isthmus subquadrate, about 1.5 mm, midlobe

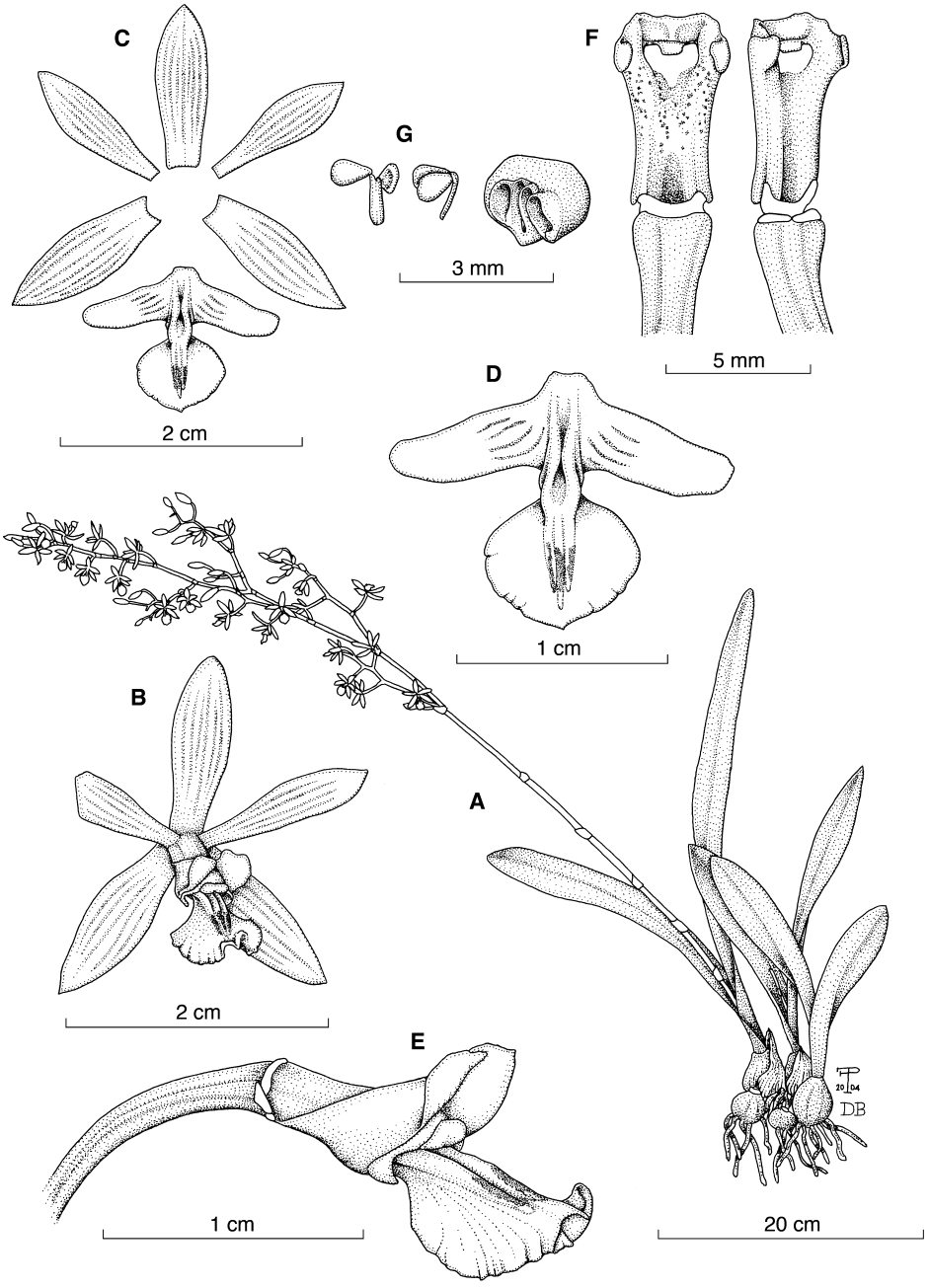


Figure 12. *Encyclia chloroleuca* (Hook.) Neumann. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, lateral view. F, column, lateral and front views. G, pollinarium anther cap. Drawn by the authors from *Pupulin 4305* (JBL-Spirit).

rhombic–obovate, acute or apiculate 6–8 × 6–7 mm, the callus composed of two longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, sulcate, joining at the base and passing into three thickened magenta veins extending nearly onto the apex of the ovate, acute midlobe 3 × 1.5 mm. COLUMN 0.7 cm, midtooth subequal to lateral teeth, column wings up to 1–2 × 0.7–0.8 mm, oblong. POLLINIA four in two pairs, obovate, on narrowly linear, basally bifid caudicles. CAPSULE fusiform, glabrous to slightly warty, 3.5 cm long.

Other specimens examined: COSTA RICA: Alajuela: San Carlos, Boca Tapada, alrededores del Hotel Laguna del Río Lagarto, 100 m, 10 octubre 2004, *C. Ossenbach 365* (JBL-Sirit). Upala, Aguas Claras,

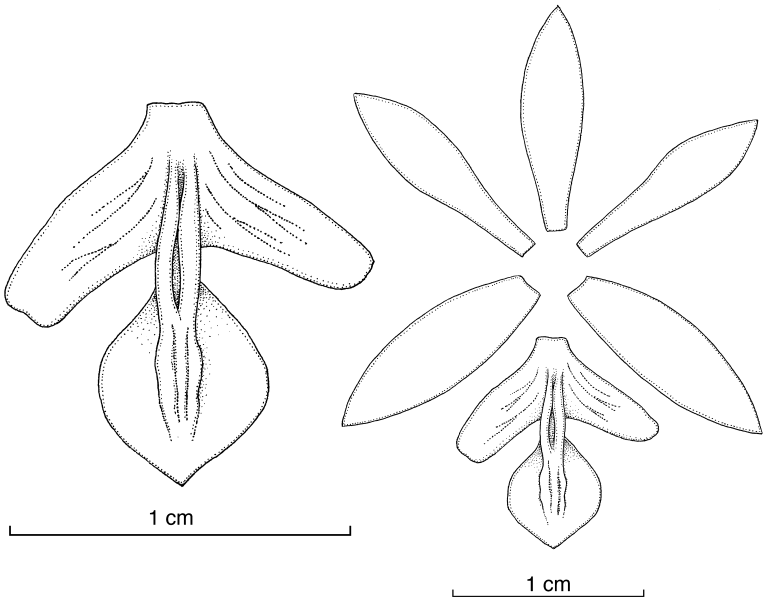


Figure 13. Floral analysis of a flower from the type of *Epidendrum chloroleucum* at K. Drawn by D. Bogarín from a rehydrated flower with the aid of a camera lucida.

Colonia Blanca, camino entre Colonia Verde y Colonia Libertad hacia Birmania, faldas al noreste del Volcán Rincón de La Vieja, 10°52′26.2″N, 85°14′51.3″W, 550–600 m, bosque muy húmedo tropical, epífitas en potreros y árboles aislados, 4 febrero 2006, *D. Bogarín 2438, J. Barrantes, R.L. Dressler, R. Gómez & A. Rojas* (JBL-spirit). Upala, Dos Ríos, camino de Dos Ríos a Brasilia, 10°59′58.2″N, 85°21′03.2″W, 360 m, bosque muy húmedo tropical transición a basal, epífitas en plantaciones de naranja (*Citrus sinensis*), 27 marzo 2007, *D. Bogarín 3111, S. Dalström, G. Gigot, M.P. Powell & F. Pupulin* (JBL-spirit). Upala, road from Potrerillos de Liberia to Brasilia, Caribbean watershed of northern volcanic chain, 10°59′58.2″N, 85°21′03.2″W, 360 m, tropical moist forest, 27 March 2007, *F. Pupulin 6536, D. Bogarín, S. Dalström, G. Gigot & M. Powell* (JBL-spirit). Cartago: Turrialba, Chirripó, Grano de Oro, *c*. 1000 m, premontane wet forest, without collector's data, flowered in cultivation in the collection of C. A. Bonilla at La Garita de Alajuela, 26 Jan. 2003, *F. Pupulin 4306*. Same locality, *F. Pupulin 4305*; Turrialba, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), sobre un *Cupressus* sp., en el jardín del Director General del CATIE, 600 m, 15 de Noviembre 2004, *A. Karremans 463* (JBL-spirit). Heredia: La Virgen de Sarapiquí, about 1 km east of the village, 120 m, epiphytic in abandoned *Citrus* orchard, 6 March 2001, *F. Pupulin 3043 & G. Barboza* (JBL-spirit). Guanacaste: La Cruz, Santa Cecilia, P. N. Santa Rosa, Estación Pinilla, falda noreste del Volcán Orosi, 10°59′21.0″N, 85°25′33.4″W, 696 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque alrededor de la estación, 29 enero 2009, *D. Bogarín 6167* & *F. Pupulin* (JBL-spirit). Without locality data, *A.R. Endrés s.n.* (W).

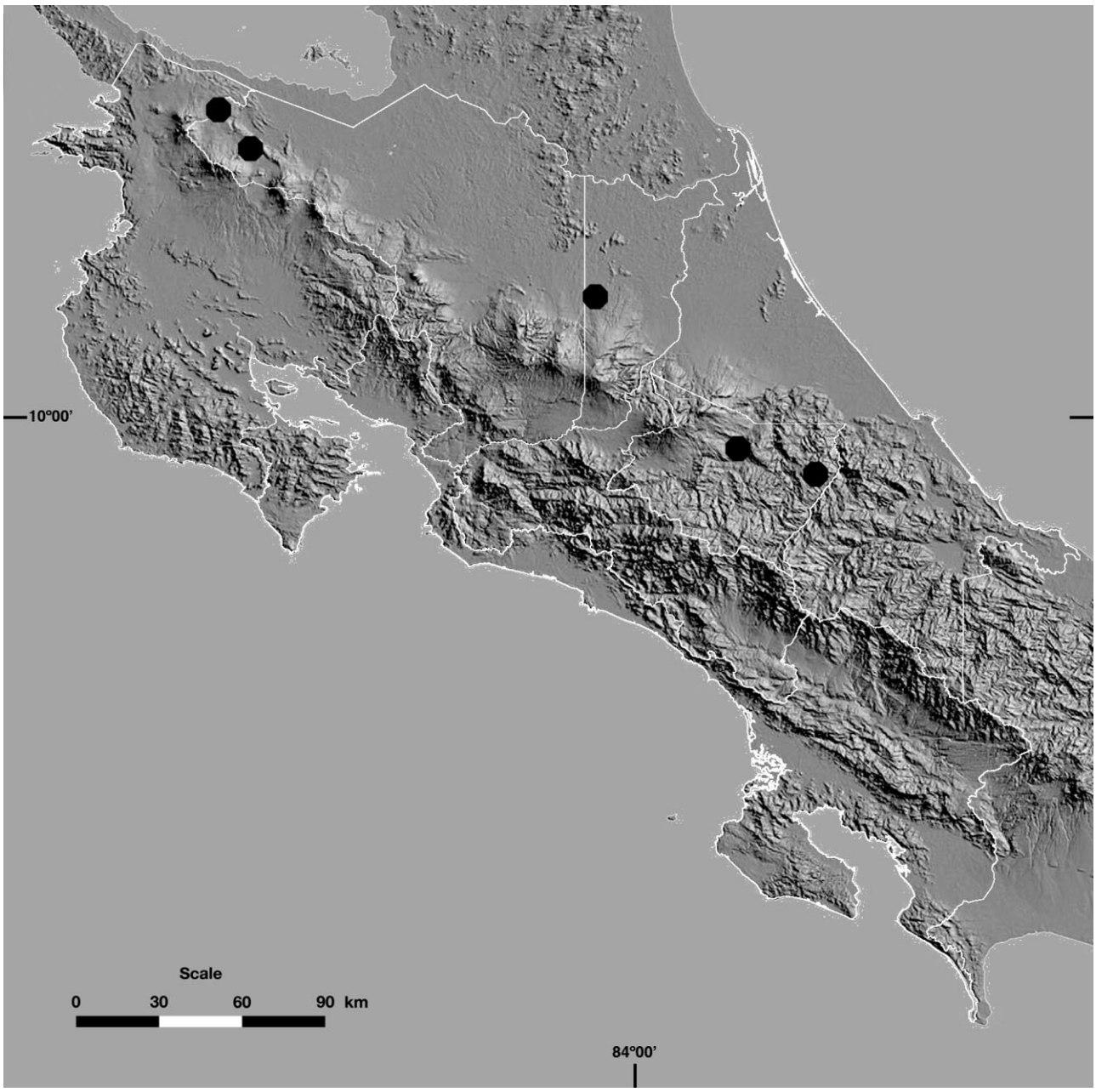
Distribution: At least from Belize to northern Brazil and Ecuador.

Etymology: From the Latin *chloroleucus*, 'greenish–white', in reference to the colour of the flowers.

Phenology: December to May.

Habitat and ecology: Epiphytic in tropical wet forest, premontane belt transition, premontane wet forest and tropical wet forest along the Cordilleras of Guanacaste, Tilarán, Central and Talamanca, from 100 to 1000 m of elevation. Plants can be found growing in secondary vegetation and primary forest. They have been collected in *Citrus* L. plantations and *Cupressus* trees in gardens.

Discussion: This species was described by W. Hooker as *Epidendrum chloroleucum* in 1837, based on a plant collected by J. Allcard in Demerara, Guyana (Hooker, 1837) (Figs 10, 11). Among the small-flowered species of *Encyclia* with green perianth and white, glabrous lip, the names *E. amanda*, *E. chloroleuca*, *E. davidhuntii* Withner, *E. gravida*, and *E. peraltensis* have been variously applied to plants from Costa Rica. Species concepts within this group are not sharply defined and the number of names probably



Map 4. Distribution of *Encyclia chloroleuca* in Costa Rica.

exceeds the actual number of taxa. Interpretation of gross plant morphology is made somewhat difficult by the tendency of some of the taxa to became reproductive at early developing stages. Plants of *E. chloroleuca* can flower as juvenile specimens when the total size of the plant do not exceed 15 cm, producing short and two- or three-flowered racemes barely exceeding the length of the leaves, often bearing imperfect flowers (i.e. with reduced petals and strongly conduplicate lip). In Costa Rica, *E. chloroleuca* is most similar to *Encyclia peraltensis* from which it differs in the lax inflorescences (vs. congested), the wider lateral lobes of the lip which are basally striped in brown (vs. having a dark purple stain in the inner side), the veins on the suborbicular, white, midlobe run towards the acute apex and are stained with magenta (vs. white veins running up to the half and the midlobe basally greenish with pink stains in the centre and the margin white). Both species range at similar elevations in Atlantic Costa Rica and could occur sympatrically. A drawing of the lip of a flower removed from the type specimen of *E. chloroleuca*

Figure 14. Holotype of *Epidendrum amandum* at the Oakes Ames Orchid Herbarium (AMES 00070063). Reproduced with the kind permission of the Director, Harvard University Herbaria.

shows a lip with oblong, obtuse lateral lobes and the midlobe ovate, acute with keels running towards the apex (Fig. 13). The shape of the lip of *E. chloroleuca* match well with the plants studied from the Atlantic lowlands of Costa Rica and clearly differs from those of *E. peraltensis*.

Encyclia amanda, originally described from Panama (Fig. 14) has flowers similar to those of *E. chloroleuca*, often flushed with brown toward the apex of sepals and petals and the lateral lobes of the lip are wide and the veins on the suborbicular midlobe run to the acute apex. Before the intensive field activity aimed at obtaining specimens for this study, *E. amanda* was known only from a limited number of specimens. Withner (1998) mentioned no more than eight collections in herbaria worldwide and included Costa Rica in the species distribution with no specimen citation (Withner, 2001). On the basis of the studied records, he characterized the species by the few-flowered (four or five), inflorescences that barely surpass the length of the leaves. Our collections revealed that this taxon is common in Costa Rica but extremely variable both in plant architecture and floral morphology (Fig. 15). Well-developed inflo-

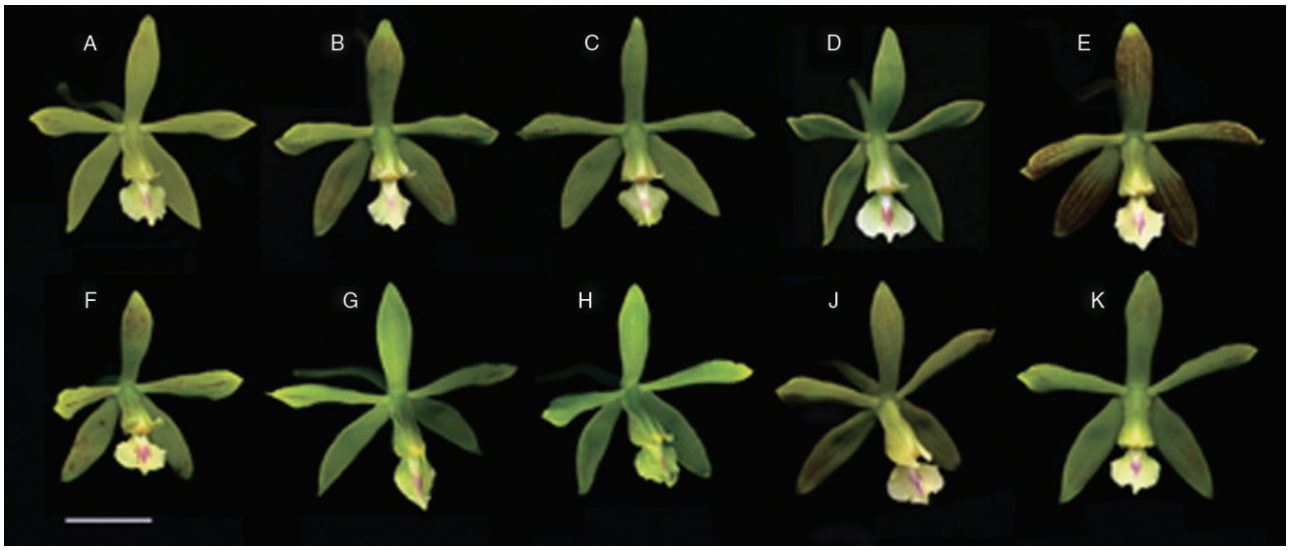


Figure 15. Floral variation in *Encylia chloroleuca*. A, *Pupulin 3043*. B, *Bogarín 2532*. C, *Bogarín 2544*. D, *Ossenbach 365*. E-F, *Pupulin 4305*. G, *Bogarín 3111*. H, *Pupulin 6536*. J-K, *Bogarín 2537*. Scale bar, 1 cm. All the vouchers preserved at JBL.

rescences are commonly paniculate, many-flowered (12–30) and 60–70 cm long, but juvenile specimens may flower with short, simple, few-flowered racemes to only 15 cm long. Flowers vary greatly both within and among populations, and cultivated specimens show that floral variation may be notorious even on the same specimen at different flowering times. When this range of variation is taken into account, the common Costa Rican taxon is not distinguishable from South American specimens of *E. chloroleuca* (which has nomenclatural priority), and the study of the type specimen of *E. chloroleucum* at Kew confirmed our suspicions.

Populations of greenish *Encyclia* spp. from central and eastern Panama and from northern Colombia, provided with distinctly unguiculate–spathulate petals, and variously identified as *E. amanda*, may perhaps correspond to a different and still-undescribed taxon. The taxonomy of the Andean and Brazilian taxa in the group is still in urgent need of revision and we cannot judge at this point how many specific epithets from these regions should be reduced to synonymy with *E. chloroleuca*.

4. *ENCYCLIA CORDIGERA* (KUNTH) DRESSLER, Taxon 13: 147 1964. *Cymbidium cordigerum* Kunth in F.W.H.von Humboldt, A.J.A.Bonpland & C.S.Kunth, Nov. Gen. Sp. 1: 341 1816. *Epidendrum cordigerum* (Kunth) Foldats. Bol. Soc. Venez. Ci. Nat. 28 (115–116): 234. 1969. *Type:* [VENEZUELA.] *Crescit regione ferventissima Provinciae Venezuelae inter Santa Barbara et Porto Cabello, alt. 85 hex. Floret Februario*, *Humboldt & Bonpland s.n.* (holotype: P). Figures 8D and 16–18, Map 5.

Synonyms: Epidendrum macrochilum Hook., Bot. Mag. 63: t. 3534 (1836). *Encyclia macrochila* (Hook.) Neumann, Rev. Hort., II, 4: 137. 1846. *Type:* [MEXICO.] 'A charming epiphyte, introduced from Mexico, by Charles Horsfall, Esq., in whose fine collection at Everton it flowered in June, 1836, when a drawing and specimen of the handsome flowers were kindly communicated by Mrs Horsfall', *C. Horsfall s.n.* (K).

Epidendrum macrochilum var. *roseum* Bateman, Orchid. Mexico Guatemala: t. 17. 1839. *Epidendrum atropurpureum* var. *roseum* (Bateman) Rchb.f., Bonplandia 2: 19. 1854. *Encyclia atropurpurea* var. *rosea* (Bateman) Summerh., Bot. Mag. 171: t. 290. 1957. *Encyclia cordigera* var. *rosea* (Bateman) H.G.Jones, Darwiniana 15: 23. 1969. *Type:* Guatemala, *J. Skinner s.n.* (K).

Epidendrum macrochilum var. *albopurpurea* C.Morren, Ann. Soc. Roy. Agric. Gand 2: 365, t. 86. 1846. *Type:* not indicated.

Epidendrum longipetalum God.-Leb., Orchidophile (Argenteuil) 12: 257 (1892), *nom. illeg.*

Encyclia atropurpurea var. *leucantha* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 45 .1922. *Encyclia cordigera* f. *leucantha* (Schltr.) Withner, Cattleyas & Relatives 5: 104. 1998. *Type:* Panama (lectotype, designated by Christenson, 1991: Panama. Sehr selten auf Hügeln bei Panama City, *C.W. Powell 149*, AMES; isolectotype, MO).

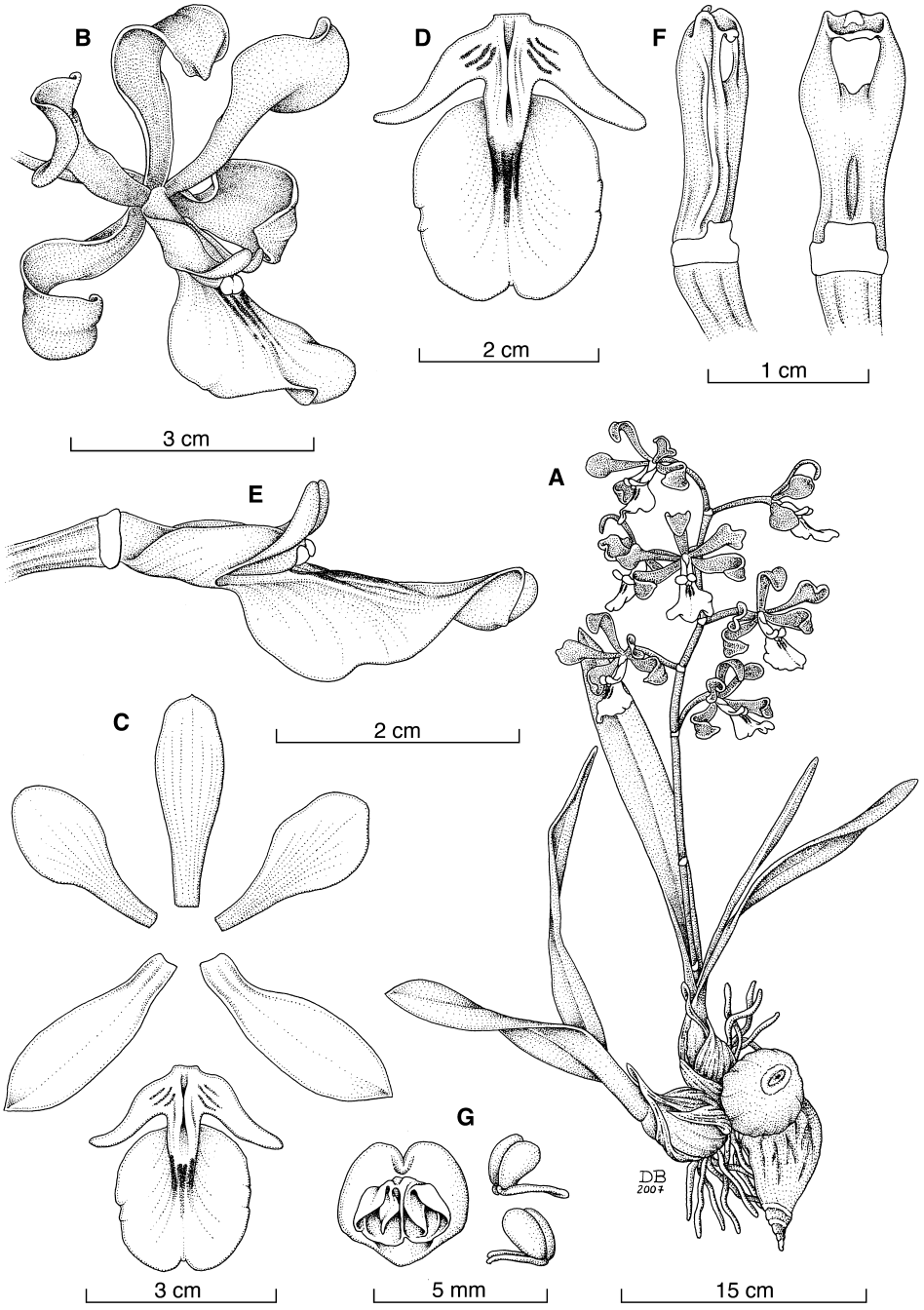


Figure 16. *Encyclia cordigera* (Kunth) Dressler. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, lateral view. F, column, lateral and front views. G, pollinarium anther cap. Drawn by D. Bogarín from *Bogarín 13* (JBL-Spirit).

Encyclia atropurpurea var. *rhodoglossa* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 45.1922. *Type:* Panama (lectotype, designated by Christenson, 1991: Panama. Sehr häufig auf Hügeln bei Panama City, *C.W. Powell 80*, AMES).

Epidendrum atropurpureum auct., *non Epidendrum atropurpureum* Willd., Sp. Pl. 4: 115. 1806.

Description: PLANT epiphytic, caespitose, to 80 cm tall. ROOTS produced from the base of the pseudobulb and the rhizome, flexuous, 2–3 mm in diameter, whitish with green tips. PEUDOBULBS ovoid to pyriform, 8–11 × 3–6 cm, subtended by ovate, acute papery sheaths, shredded with the age, two (rarely three-) foliate at apex. LEAVES on short tubular peti-

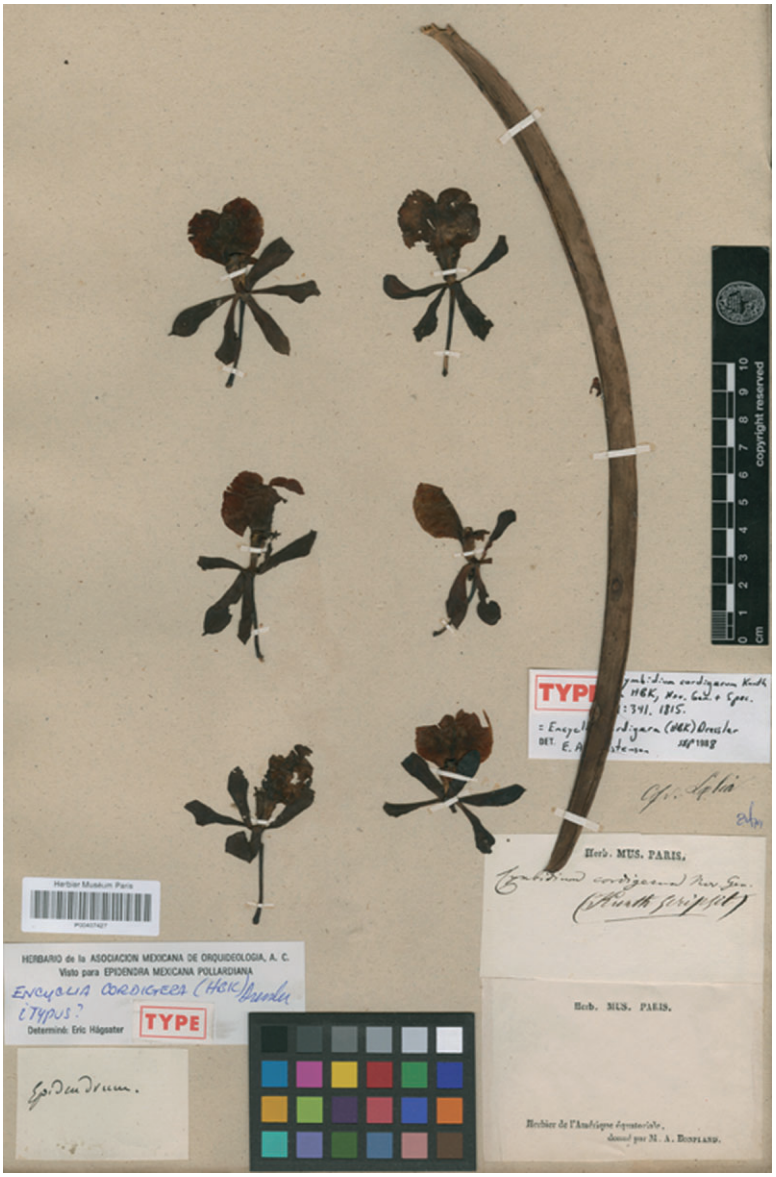
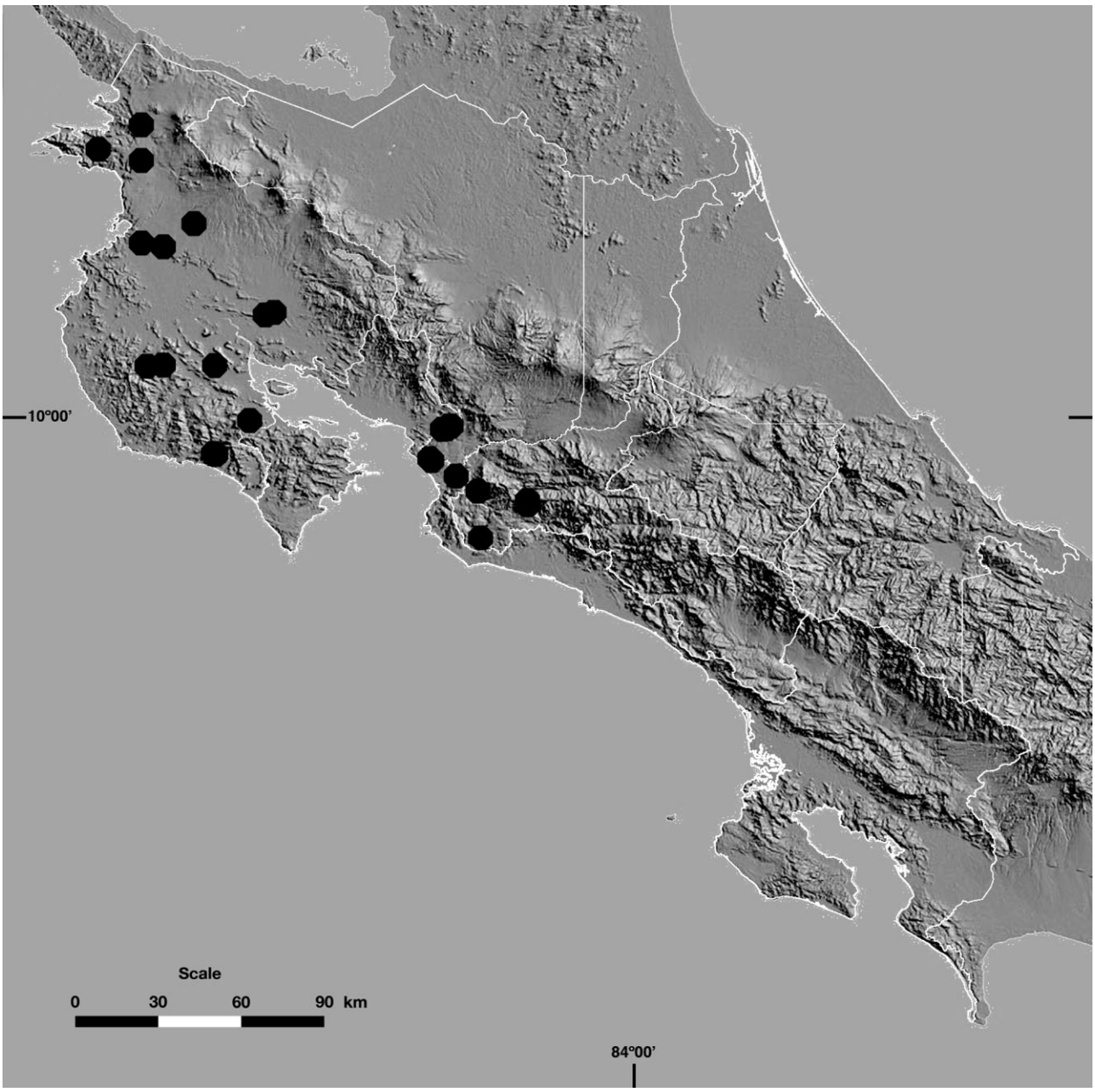


Figure 17. The holotype of *Cymbidium cordigerum* (= *Encyclia cordigera*) at Paris (P 00407427). Reproduced with the kind permission of the Director, Muséum National d'Histoire Naturelle, Herbier National de Paris.

Figure 18. Different forms of *Encyclia cordigera*. A, Costa Rica (*Pupulin 5996*). B, Costa Rica (*Araya s.n.*). C, Panama (*JBL-09971*). All vouchers at JBL-Spirit.



Map 5. Distribution of *Encyclia cordigera* in Costa Rica.

oles at apex of pseudobulbs, oblong or elliptic–oblong, ensate, coriaceous, conduplicate, dorsally keeled, acute to subacute, the apex irregularly bilobed, curving with age, 10–50 × 2–4 cm. INFLORESCENCE apical, racemose (sometimes branched from Panama through Venezuela), distichous, peduncle 13–35 cm, bracts 6–8 mm, acute, adpressed, infundibuliform, raceme 6–25 cm, rarely with one basal branch. FLORAL BRACTS triangular, acute, adpressed, scarious, 1–3 × 3–4 mm. OVARY and pedicel 2.5–3.3 cm, smooth, with minute lenticels. FLOWERS showy, resupinate, scented, the sepals and petals greenish to brownish, lip white, striped with magenta at base of lateral lobes and along the callus, strongly suffused with pink or magenta at the middle toward the apex (rarely pure white). DORSAL SEPAL spatulate, elliptic–oblanceolate, acute to subacute, dorsally carinate, apically curved, 2.6–3.6 × 0.5–1.1 cm. LATERAL SEPALS spatulate, cuneate–oblanceolate, acute, slightly apiculate, strongly curved toward the apex, dorsally carinate, 2.4–3.5 × 0.8–1.2 cm. PETALS unguiculate, spatulate–ovate or cuneate–ovate, acute

or apiculate, dorsally carinate, 2.3–3.5 × 1.0–1.8 cm. LIP basally adnate to the column for 3 mm, deeply three-lobed, shortly unguiculate, 2.9–3.1 × 2.8–3.1 cm across lateral lobes, lateral lobes oblong–lanceolate, falcate, obtuse, suberect and flanking the column in natural position, slightly stripped with magenta, 0.7–1.5 × 0.5–0.8 cm, isthmus about 1 mm long, subquadrate; midlobe 2.0–3.6 × 1.3–3.0 cm, suborbicular, obovate or oblong, retuse or obtuse, callus with two longitudinal fleshy keels which made up a fovea on the isthmus, 0.8–1.1 × 0.3–0.6 cm, sulcate, with a second callous composed with three magenta veins running and reducing slighltly toward the apex. COLUMN subterete, truncate, cuneate–obovate, subpandurate, basally sulcate, 1.0–1.8 cm, midtooth triangular, subequal to lateral teeth, without wings; anther apical; stigma dorsal. ANTHER CAP four celled, cucullate, ovate to orbicular. POLLINIA four, in two pairs with caudicles, without viscidium. CAPSULE 4.0 × 2.3 cm, fusiform to obovoid–ellipsoid.

Other specimens examined: COSTA RICA. Guanacaste: Cañas, Hacienda Taboga, epífita en *Guazuma ulmifolia* (Sterculiaceae), 13 febrero 1967, *C. Valerio s.n.* (USJ). Vicinity of Cañas, Finca Taboga uplands, 26 March 1970, *R. Daubenmine 664* (USJ). Liberia, La Guardia, Ex-Hort Gaia Botanical Garden, flowered in cultivation, February 2001 (JBL-spirit). Nicoya, 360 m, April 1997, *G. Agüero s.n.* (USJ). Nicoya, cerca de playa Tamarindo, 12 de abril del 2006, Hacienda Pinilla, 0–100 m, *A. Karremans 1273* (JBL-spirit); Península de Nicoya, 60–200 m, 09°52′48″N, 085°21′36″W, 11 August 1994, *Armando Estrada & A. Rodríguez 152* (CR). Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, Bosque de Cactus, 10°10′32.1″N 85°21′13.3″W, 639 m, bosque húmedo premontano transición a basal, epífitas en lomas rocosas, 28 enero 2009, *D. Bogarín 6148 & F. Pupulin* (JBL-Spirit). La Cruz, Santa Elena, Parque Nacional Santa Rosa, bosques entre la Casona y el puesto de entrada, 10°50′N 85°36′W, 200–300 m, 27 febrero 1996, *J. F. Morales 5313* (INB). Nandayure, Bejuco, Corozalito, Finca de Eduardo Quirós, 9°53′N, 85°22′W, 200–300 m, 11 agosto 1994, *A. Estrada 152* (INB). Santa Cruz, Santa Cruz, 10°10′N, 85°35′W, 100–200 m, siguiendo de la Quebrada Brasil hasta el Salto, 24 setiembre 1996, *U. Chavarría 1585* (INB). "Santa Rosa en Guanacasto [Guanacaste]", *A. Oersted 115* (W). Puntarenas: Garabito, Tárcoles, Along road to Bajamar, *c*. 3 km west of Río Cuarros bridge, 9°52′N, 84°40′W, 0–100 m, 26 March 1993, *M.H. Grayum 10395* (INB). Puntarenas, Lepanto, Reserva Karen Mogensen, Sendero Perez, 9°53′N, 85°03′W 300–400 m, 23 junio 2001, *U. Chavarría 2159* (INB). Esparza, Pacific coast, San Mateo, banks of Río Grande, February, *A.R. Endrés s.n.* (W). Esparza, San Rafael, El Barón, cerca de 400 m río abajo del puente sobre la Quebrada El Barón, 160 m, bosque húmedo tropical a orilla de la quebrada, epífita en *Annacardium excelsum* (Anacardiaceae), 16 febrero 2000, *D. Bogarín 13, A. Prendas & P. Rodríguez* (JBL-spirit). Esparza, San Rafael, Río Jesús María, cerca de 500 m río arriba a partir del Puente de Las Damas, 170 m, bosque húmedo tropical, en troncos caídos de *Anacardium excelsum* (Anacardiaceae), 29 diciembre 2000, *D. Bogarín 21, A. Prendas & P. Rodríguez* (JBL-spirit). Miramar: Sin más datos, febrero 1985, *O. Rodríguez s.n.* (USJ). San José: Puriscal, Mercedes Sur, Cerros de Puriscal, Cerro La Cangreja, Falda NE Alto Limón, camino Alto Concepción, entre Quebrada Estrella y Quebrada Guatuso, 9°43′N, 84°21′W, 500–600 m, 8 marzo 1997, *J. F. Morales 6100* (INB).

Distribution: From Mexico to Colombia and Venezuela.

Etymology: From the Latin *cordigerum* 'wearing a heart'.

Phenology: November to April.

Habitat and ecology: Epiphytic in tropical moist forest, premontane moist forest, basal belt transition and tropical dry forest, moist province transition. Plants are restricted to the northern and central Pacific lowlands of Puntarenas and Guanacaste from 0 to 700 m of elevation. Plants are common in sunny areas and disturbed lands such as pastures, river edges, tree fences and primary and secondary forest. Common hosts are *Annacardium excelsum* (Anacardiaceae), *Cedrela* spp. (Meliaceae), *Guazuma ulmifolia* (Malvaceae), *Tabebuia* spp. and *Crescentia alata* (Bignoniaceae) and *Samanea saman* (Fabaceae) among others.

Discussion: Encyclia cordigera is the most obvious and showiest species of the genus in Costa Rica and its flowers are among the largest in the genus. The name was based on *Cymbidium cordigerum* described by Kunth (1815) (Fig. 17). This species was long confused because of the misapplication of the name *Epidendrum atropurpureum* Willd., now included in *Psychilis* Raf., a genus of nearly 15 species endemic to the Caribbean Archipielago (Sauleda, 1988). Dressler (1964) concluded that the Plumier plate upon which the name *E. atropurpureum* was based does not correspond to the concept of *E. cordigerum*, thus combining the name *E. cordigerum* in *Encyclia*.

Plants of *E. cordigera* are easily distinguished by the racemose inflorescences (never branched) with showy, scented, large flowers. The pseudobulbs are ovoid to pyriform, conspicuous in healthy and well-

developed specimens. The brown spatulate sepals are strongly curved at apex, the suborbicular, obovate or oblong midlobe of the lip is white with three magenta stripes at base. It is larger (2.4–3.5 × 0.8–1.2 cm) in comparison with other species of the genus, being the most conspicuous structure of the flower. The column is not winged or toothed, apically with a conspicuous yellow anther cap.

Encyclia cordigera is reported to be pollinated by medium-sized, black female carpenter bees (*Xylocopa* sp., Hymenoptera: Anthophoridae) (Janzen *et al*., 1980; van der Cingel, 2001), and another species of *Xylocopa*, the Cuban endemic *X. cubaecola*, has been recorded as the effective pollinators of *Encyclia phoenicea* (Lindl.) Neumann (Diaz, 2001). Janzen *et al*. (1980) suggested that the shape and colour of the flower of *E. cordigera* are similar to the common legume tree, *Gliricidia sepium* (Jacq.) Kunth ex Walp (Fabaceae), which is heavily visited by the same bees searching for nectar. *Encyclia phoenicea* shows the same floral syndrome, with a large purple, saddle-shaped lip, and scented flowers with a fragrance of chocolate. *Encyclia cordigera* is also described as producing a strong honey and vanilla scent (Frowine, 2005), and the chemical analysis of the fragrances carried out by Del Mazo Cancino & Damon (2006) showed that the major components for *E. cordigera* were cis-geraniol (49.76%), followed by benzyl benzoate, indole and e-ocimene.

Through most of its range, *E. cordigera* exhibits a broad array of variation in flower colour (Fig. 18). The sepals and petals vary from apple green to yellow with brown apices to dark purple, whereas the lip may be pure white or more commonly marked on the disc with three purple stripes or a large rose blotch with darker stripes, but also entirely pale rose with purple base or completely deep purple, a colour that Withner (1998: 104) described as 'almost fluorescent, concolor rosy magenta'. Traditionally, the type has been associated with the white-lipped phase, and the purple form received varietal recognition as var. *rosea* and var. *rhodoglossa*. This interpretation, however, is not warranted. The type specimen (Fig. 17) was collected somewhere in the state of Carabobo, Venezuela, between the village of Santa Barbara and Puerto Cabello on the coast. Although the white-lipped phase is apparently more common in this region, Dunsterville & Garay (1961) also recorded populations with purple lips in the area of Maracaibo. Kunth based his description of *E. cordigera* on a dry specimen, noting that the petals and sepals were probably purple, but brown when dry ('*purpurea*?, *exsiccata fusca*'), whereas the midlobe of the lip was orange once dry ('*exsiccato aurantiaco*'). Both the lips of the white and the purple phases may dry to the same orange colour. In the actual type specimen at P, the lip is dark brown, and in our opinion it looks closer to the rose or purple form than to the white-lipped phase. However, according to G. Carnevali (to F. Pupulin & D. Bogarín, pers. comm., 2011), the white-lipped form from Venezuela can have dark petals and sepals and it is indistinguishable from the pink-rose form upon drying. Populations of *E. cordigera* in Costa Rica have a distinctly elliptic midlobe of the lip (Fig. 16), but Kunth (1815) described the lip of the type specimen as obcordate, a feature that agrees well with Panamanian populations of the purple–magenta phase of the species. We do not know, however, if this character is constantly associated with the two-colour phases throughout the entire distributional range of the species.

The pink form of *E. cordigera*, referred to as var. *rosea*, is widely cultivated in Costa Rica by orchid growers. However, although the form with white lip is relatively common in the northern, dry lowlands of the Guanacaste province, where it forms large populations, we have never seen a place in Costa Rica where plants of the pink form naturally occur. Nevertheless, purple-lipped populations in southern Costa Rica, close to the Panamanian border in the region of San Vito, have been reported and may well occur there (Pupulin, 2005). Some forms without any purple are also known (forma *leucantha* (Schltr.) Withner); they have solid green sepals and petals and pure white lip.

5. *ENCYCLIA GRAVIDA* (LINDL.) SCHLTR., Beih. Bot. Centralbl. 36(2): 472. 1918. *Epidendrum gravidum* Lindl. J. Hort. Soc. London 4: 114. 1849. *Epidendrum oncidioides* var. *gravidum* (Lindl.) Ames, F.T.Hubb. & C.Schweinf., Bot. Mus. Leafl. 3: 104. 1935. *Encyclia oncidioides* var. *gravida* (Lindl.) Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 2(6): 153. 1952. *Type:* MEXICO. Received from Mr Hartweg, in February, 1837, and said to be collected at Xapatam, in Mexico, *Hartweg s.n.* (holotype, K). (Figs 19–21).

Description: PLANT epiphytic, caespitose, to 30 cm tall. ROOTS produced from the base of the pseudobulb and the rhizome, flexuous, 2–3 mm in diameter, whitish with green tips. PSEUDOBULBS conic–ovoid, 2.7–4.0 × 1.8–2.3 cm, subtended by papery sheaths, shredded with age, 3.4–4.0 cm long, two-foliate at apex. LEAVES on short tubular petioles at apex of pseudobulbs, ligulate, acute, the apex irregularly bilobed, coriaceous, curving with age, 18–26 × 0.7–1.5 cm. INFLORESCENCE apical, suberect–arching, a paniculate raceme 15–50 cm, green, warty; peduncle cylindric to 24 cm long, lateral branches two- to five-flowered, to 4 cm long; bracts of the inflorescence narrowly ovate, acute, 7–9 mm long; rachis slightly fractiflex. FLORAL BRACTS triangular, acute, basally clasping rachis, 2–3 mm long. PEDICEL *c*. 1 cm long,

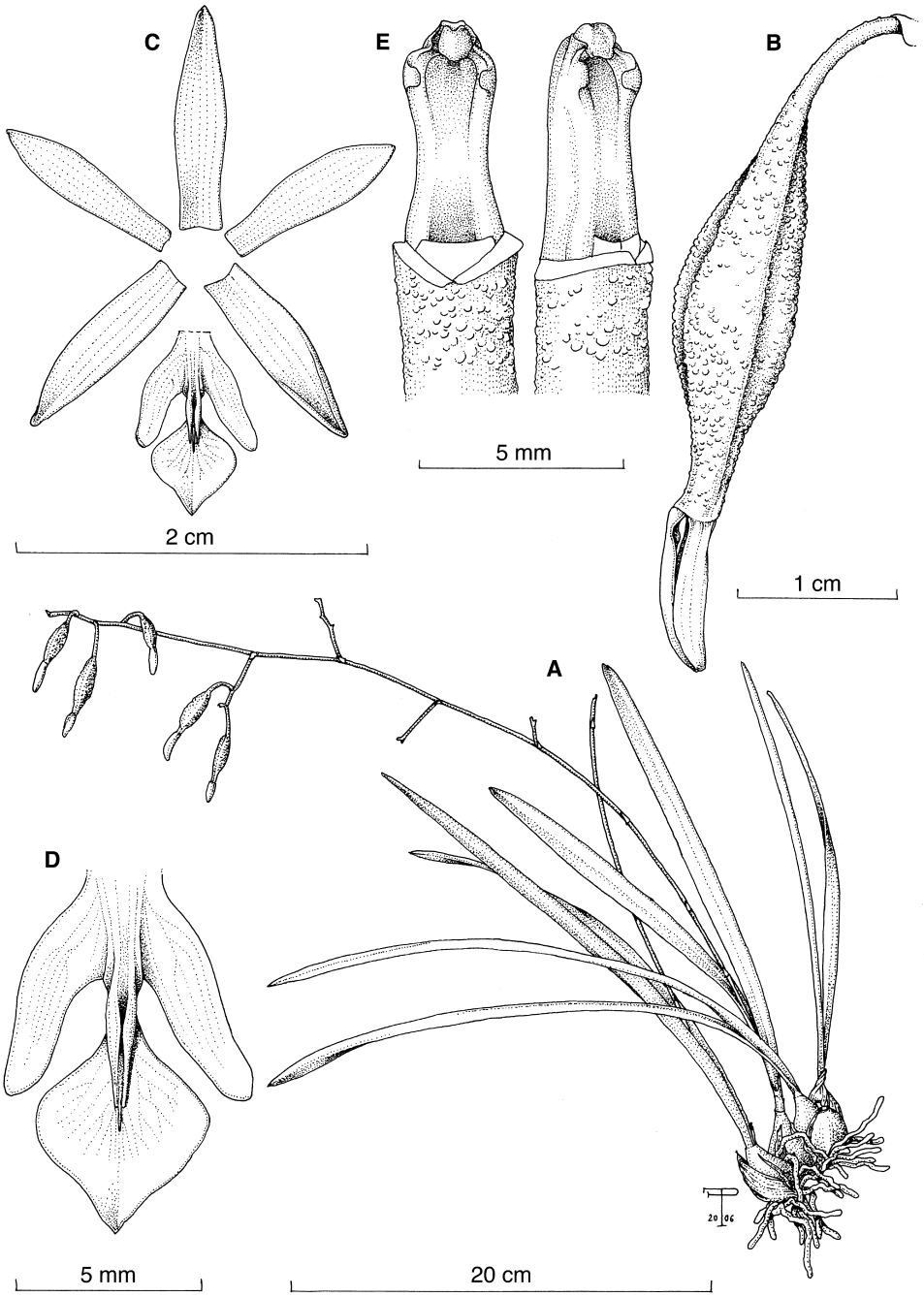


Figure 19. *Encyclia gravida* (Lindl.) Schltr. A, habit. B, fruit with perianth remains at apex. C, dissected perianth. D, lip, front view. E. column, lateral and front views. Drawn by F. Pupulin from *F. Pupulin 5377*.

slightly papillose. OVARY (fruiting) elliptic, 2.7 cm long, strongly verruculose. FLOWERS cleistogamous, greenish yellow, the abaxial apex of sepals flushed with brown, the lip white–cream. DORSAL SEPAL narrowly lanceolate, acute, conduplicate at apex, 12–13 × 3 mm. LATERAL SEPALS lanceolate–elliptic, acute, the apical margins thickened, involute, 12.0 × 3.0–3.5 mm. PETALS narrowly lanceolate, acute, 11.0 × 3.5 mm. LIP basally adnate to the column for *c*. 1 mm, deeply three-lobed, subsessile, 1.0 × 6.5 mm across lateral lobes, lateral lobes oblong, obtuse, 6.5 × 1.7 mm; isthmus narrowly rectangular–subpandurate, about 1.5 mm long, midlobe rhombic, acute, 5.0 × 4.5 mm, the callus composed of two

Figure 20. The type specimen of *Epidendrum gravidum* (= *Encylia gravida*) at Kew (K 000079647). Reproduced with the kind permission of the Board of Trustees, Royal Botanic Gardens, Kew.

longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, passing at apex into three slightly thickened keels, the central one smaller and lower, extending to the middle of the midlobe. COLUMN 6 mm long, the clinandrium shallowly cucullate, the wings subquadrate, incurved under the isthmus, up to 0.7 × 0.7 mm, the stigma shallow, subrounded, the rostellum absent. POLLINIA four in two pairs, on narrow, bifid caudicles. IMMATURE CAPSULE fusiform, densely warty, 3.8 cm long.

Other specimens examined: COSTA RICA. Without specific locality, cultivated at Jardín Botánico Lankester, Universidad de Costa Rica, accession no. JBL-04676, 7 December 2004, *F. Pupulin 5377* (JBL-spirit). Cartago: Paraíso, Dulce Nombre, road to Las Cóncavas, 9°50′08.7″N 83°53′12.8″W, *c.* 1250 m, epiphytic on short tree along the roadside, premontane wet forest, secondary vegetation, *F. Pupulin 6670, M. Pupulin & C. Pupulin* (USJ).

Distribution: From Mexico to Costa Rica and the Antilles.

Etymology: From the Latin *gravidus*, 'filled, pregnant or weighted down with', in reference to the autogamous condition of the flowers always producing fruits.

Phenology: Flowering has been recorded in December and February.

Habitat and ecology: An uncommon epiphyte, mostly occurring on large trunks in wet premontane forest.

Discussion: The flowers of *E. gravida* are cleistogamous and a rounded fruit is produced at each flower node before anthesis occurs. It is likely that references to Central American populations with flowers that open (e.g. Ackerman, 1995) are based on misidentifications of *E. stellata* specimens. Living specimens with fruits of *E. gravida* can be distinguished from other similar species, because the tissues of the perianth segments in fruiting flowers are still turgid and the sepals are more similar in appearance to fresh buds than to withered flowers. Of course, this distinction is much less obvious in dried specimens. However, the opened buds show a rhomboid midlobe of the lip, a distinctively long isthmus and linear lateral lobes that are diagnostic for the species. As noted by Ackerman (1995), the petals are often irregularly shaped along the margins as a consequence of cleistogamy, as it is most likely the perianth parts of cleistogamous taxa accumulate random mutations once their role as pollinator attractants has ceased.

We accept the concept of *E. gravida* with some reservation concerning the application of the name and the real identity of this taxon (Pupulin & Bogarín, 2011). Lindley (1849) originally described *Epidendrum gravidum* on the basis of a Mexican collection by Hartweg (Hartweg *s.n.*, the type, K!). The type specimen at Kew (Fig. 20) consists only of a single inflorescence originally bearing four fruits (one of which was removed in 1923 and sent to Oakes Ames for study); the remaining sepals measure 10–11 mm in length and *c.* 3 mm in width (Lindley, 1849; see also Carnevali, Ramírez & Romero, 1994). Lindley (1849) considered it a 'mere botanical curiosity,' and in the protologue he gave no information about the vegetative characters of the new taxon. Florally, it was characterized by the linear lateral lobes of the lip, the ovate, acute midlobe provided with thickened veins, and the column with stigmatic, inflexed wings. After the original description, the name has been mostly adopted to identify populations of *E. stellata*, which shares with *E. gravida* a distinctly papillate ovary and the presence of prominent veins on the lip, but in a few cases the material referred to seems to match the original concept of Lindley. Cleistogamy is a breeding system defined as

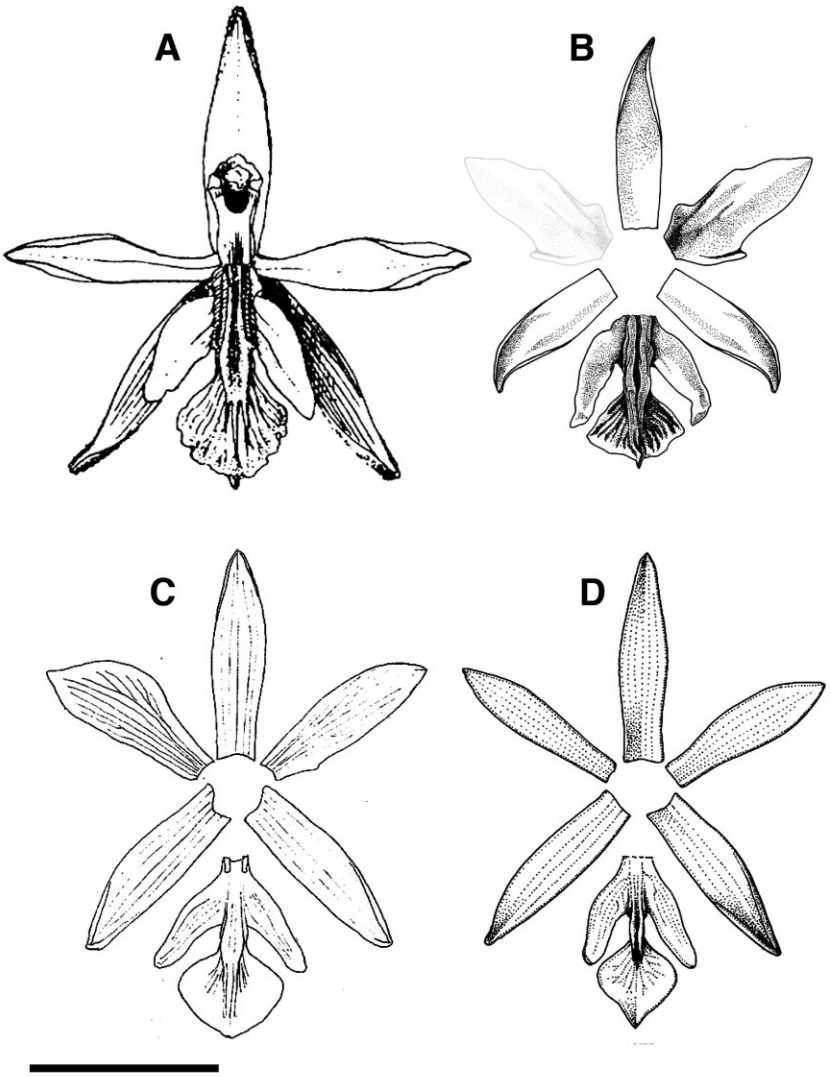


Figure 21. Comparison of the documented collections of *Encyclia gravida*. A, Mexico, *Purpus s.n.* B, Puerto Rico. C, Costa Rica, *Pupulin 6670*. D, Costa Rica, *Pupulin 5377*. A, drawn by Blanche Ames, from Ames 1923. B, drawn by M. Enríquez, from Ackerman 1995. C–D, drawn by F. Pupulin. Scale bar, 1 cm.

the production of permanently closed, self-pollinated flowers, and it is now recognized as an important system found in a variety of plant taxa (Culley & Klooster, 2007). Fertilization within cleistogamous flowers occurs without the intervention of pollinators, and in the Orchidaceae this is usually accomplished by direct transfer of pollen grains from anther to stigma. In cleistogamous species, self-pollinating flowers may be the only type produced, but they may also appear together on the same plant along with typically insect-pollinated flowers. Complete cleistogamy, defined as the production of only cleistogamous flowers on an individual, has been especially reported in orchid species, but most indications are based on observations of only a few individuals. There are obvious difficulties in documenting 'true' cleistogamous *Encyclia* individuals. Plants of other species related to '*E. gravida*' are frequently pollinated in the wild, and the pollination rate is high for several taxa. In Costa Rica, where large populations of *E. ceratistes* are found in pristine and altered habitats, it is not uncommon to observe inflorescences bearing tens of fruits. As these individuals are vegetatively indistinguishable from cleistogamous forms, the only way to tell the two entities apart is a careful observation of the perianth parts. In true cleistogamous specimens, the ovary begins to swell and elongate while the buds are in their early stage of development and the sepals are still turgid when the fruit approaches maturity, whereas in allogamous, post-anthesis fecund flowers

the perianth remains in place but begins to dry out a few days after pollination and becomes papyraceous with age. We found that there is no way to distinguish between the fruit of a cleistogamous plant and the developing fruit of a recently pollinated flower, the perianth of which is still turgid, without opening the perianth and looking at the remnant of the rostellum, which is completely absent in cleistogamous forms. This may perhaps explain why the number of documented specimens of 'gravid' *Encyclia* is small. Before World War II, Ames (Ames, 1923) illustrated the flower of another Mexican specimen collected by Purpus in Zacualpan, Veracruz, at that time kept in Schlechter's herbarium in Berlin but later destroyed (Fig. 21A), which may correspond morphologically to the species originally described by Lindley. A Puerto Rican cleistogamous specimen was documented by Ackerman (1995), who noted that the perianth parts of the opened flower are not exactly zygomorphic, probably because of some constraint during development (Fig. 21B). It is probably that another collection recorded by Schweinfurth (1940) from Maricao in Puerto Rico (Kevorkian 6177, AMES) belongs to this concept, because, according to the collector, the 'flowers [. . .] does not open.' We have documented two cleistogamous specimens from plants growing in the living collections of Lankester Botanical Garden, University of Costa Rica. We had the plants growing under controlled conditions for a while, and cleistogamy in this case appears to be genetically controlled. Even although the two individuals share some of the morphological features expected for this taxon, they also differ in a number of characters, in particular the shape of the petals, the length of the labellar isthmus, the relative thickening of the veins on the midlobe and the shape of the midlobe, which is almost rhombic in one specimen and transversely ovate in the other (Fig. 21C, D). Whereas one of the specimens lacks locality data, the other was collected in a region where only one other species of *Encyclia*, *E. ceratistes*, occurs naturally. During fieldwork for the present treatment, we made extensive collections of *Encyclia* specimens in this region, and to date we have observed only a single cleistogamous specimen. This may perhaps indicate that 'gravid' *Encyclia* plants do not form populations, one of the essential requirements to be considered a good species, and are nothing more than occasional mutants. When we compare the few documented specimens of cleistogamous *Encyclia*, it is evident that their similarity is superficial (Fig. 21), even when we could attribute these differences to some degree of deformity of the perianth parts, which do not spread out at the end of development. Apart from the vegetative architecture, which is largely uniform in *Encyclia* spp., and the features of the floral parts, which in turn vary considerably among individuals, the only shared character we observed in cleistogamous flowers is the absence of a definite rostellum, which would prevent the displacement of the pollen toward the stigmatic cavity. However, because of the paucity of available records of fecund plants of *Encyclia* to compare, this key feature alone is insufficient to assign cleistogamous individuals to a well-characterized species, and the possibility that the records simply represent self-pollinating forms belonging to different taxa cannot be discarded on the basis of floral morphology. The comparison of genetic sequences of individuals tentatively assigned to *E. gravida* with those of other sympatric *Encyclia* spp. could represent an important step toward a better circumscription of the taxa in this group and the appreciation of the evolutionary significance of different pollination strategies.

6. *ENCYCLIA MOOREANA* (ROLFE) SCHLTR., *Orchideen* 210 1914. *Epidendrum mooreanum* Rolfe, Bull. Misc. Inform. Kew 1891: 199. 1891. *Epidendrum oncidioides* var. *mooreanum* (Rolfe) Ames, Hubbard y C. Schweinf. Bot. Mus. Leafl. 3: 106. 1935. *Encyclia oncidioides* var. *mooreana* (Rolfe) Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 2(6): 154. 1952. *Types:* 'It was first sent to Kew by Mr F. W. Moore, Curator of the Royal Botanic Garden, Glasnevin (after whom it is named), in May 1889 (*F.W. Moore s.n.*, K 00079604, selected here as the lectotype), and afterwards by Mr W. Bull, of Chelsea (*W. Bull s.n.*, not found), Messrs Hugh Low & Co., of Clapton (*H. Low s.n.*, K 00079605), and by Sir Trevor Lawrence, Bart, M.P., of Burford Lodge, Dorking' (*T. Lawrence s.n.*, K 00079603). Figures 8E and 22–24, Map 6.

Synonyms: Encyclia brenesii Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 221. 1923. *Type:* COSTA RICA. ALAJUELA: San José de San Ramón, 1025 m, feb. 1922, *A.M. Brenes 253* (holotype: B, destroyed; neotype selected by Barringer (1986), drawings of the holotype, AMES).

Encyclia tonduziana Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 132. 1923.

SYNTYPES: COSTA RICA. [ALAJUELA]. Cismo bei San Jeronimo de Grecia, um 2100 m, blühend im April 1910, *A. Brade & C. Brade 1274* (syntype: B, destroyed; neotype, choosen here, tracing of Schlechter's sketch of the holotype, AMES 00099108; Fig. 25). COSTA RICA. [ALAJUELA]. Forêts de San Ramon, 1500–1600 m, May 1913, *A. Tonduz s.n.* [17649 Herb. Costaric.] (syntype: B, destroyed).

Description: PLANT epiphytic, caespitose, to 80 cm tall. ROOTS white, produced from the base of the pseudobulb and the rhizome, 2–3 mm in diameter. PSEUDOBULBS conic–ovoid, subglobose, or subpyiri-

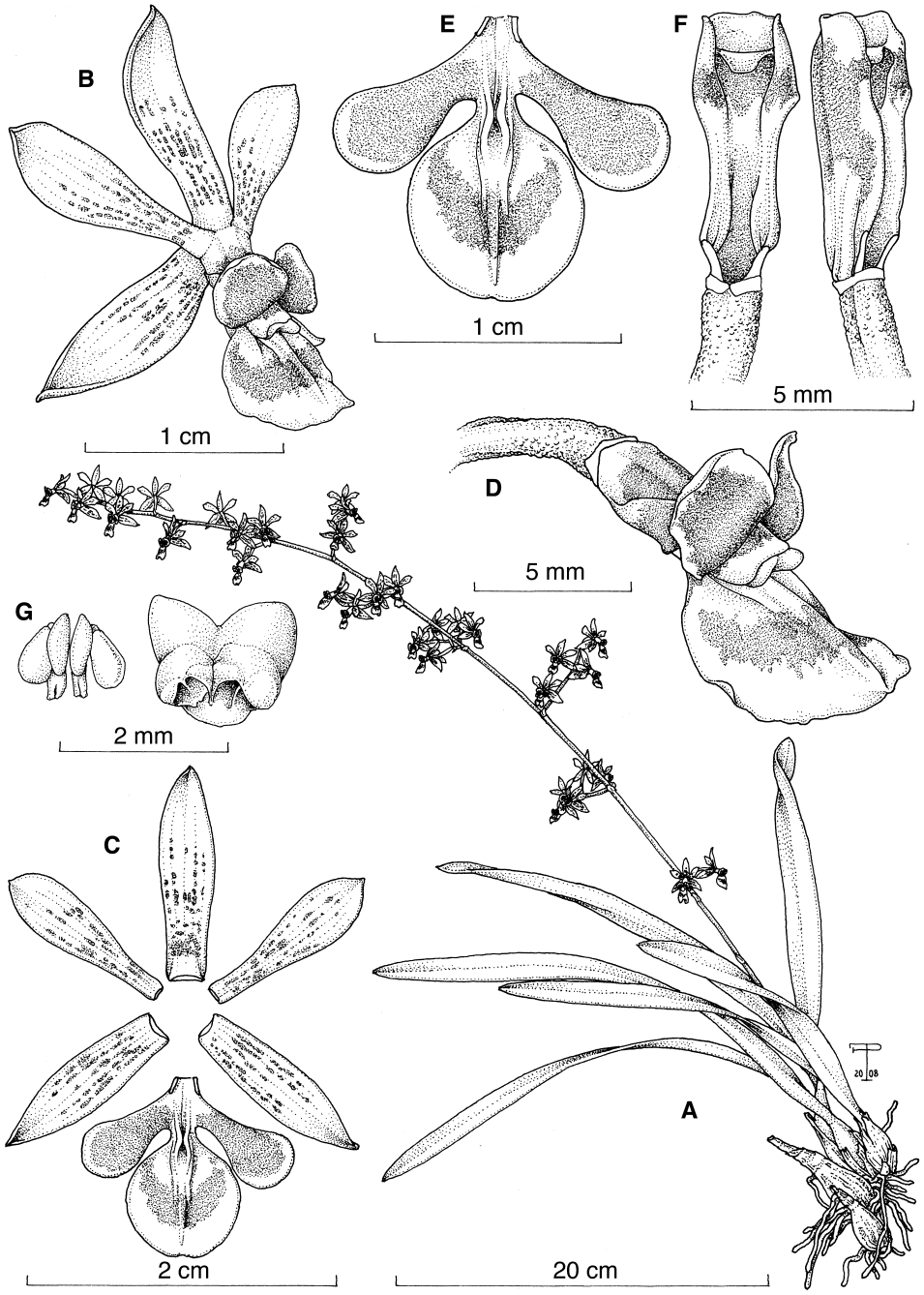


Figure 22. *Encyclia mooreana* (Rolfe) Schltr. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, three quarters view. F, column, lateral and front views. G, pollinarium anther cap. Drawn by F. Pupulin from *Pupulin 5521* (JBL-Spirit).

form, subtended by ovate, acute, papery sheaths, shredded with age, 2.3–6.0 × 1.2–6.0 cm, two- to three-foliate at apex. LEAVES ligulate to narrowly lanceolate, acute or obtuse, ensate, the apex irregularly bilobed, conduplicate, coriaceous, curving with age, 15–35 × 0.8–2.8 cm. INFLORESCENCE apical, arching, stout, a primarily paniculate raceme, to 120 cm long, purplish green to blackish purple, commonly verruculose, rarely subglabrous; peduncle cylindrical, to 55 cm long; lateral branches three- to 12-flowered, 6–24 cm long, rarely secondarily branching; scape bracts acute, 7–20 mm; panicle 10–80 cm. FLORAL BRACTS 1–3 × 3–4 mm, acute, adpressed. PEDICEL 1 cm, verrucose. OVARY verrucose, 1.0–

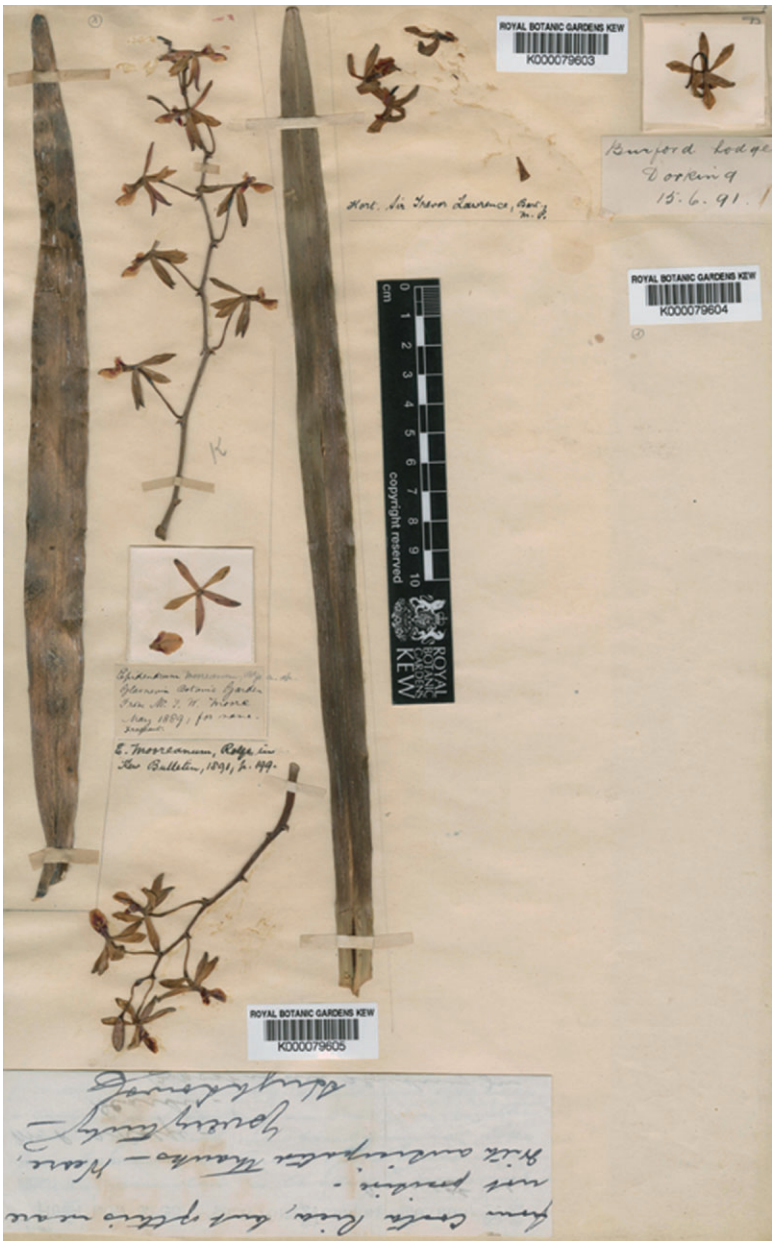


Figure 23. Type sheet of *Epidendrum mooreanum* (= *Encyclia mooreana*) at Kew (K 000079603-604-605). Reproduced with the kind permission of the Board of Trustees, Royal Botanic Gardens, Kew.

1.5 cm long. FLOWERS showy, resupinate, spreading, scented, sepals and petals basally olive or pale green or stained with dark red–brown; lateral lobes of lip basally purple, apically pink to purple or with white margins, midlobe white marked with pink to purple. SEPALS subsimilar, elliptic to elliptic–obovate, slightly conduplicate, acute or apiculate, carinate at apex. DORSAL SEPAL elliptic to obovate, acute, 1.2–1.3 × 0.3–0.4 cm. LATERAL SEPALS oblanceolate, elliptic or oblong–elliptic, apiculate, 1.2–1.4 × 0.3–0.4 cm. PETALS elliptic to obovate–spatulate, acute or apiculate, occasionally erose distally, 1.0–1.3 × 0.3–0.6 cm. LIP basally adnate to the column for 1 mm, deeply three-lobed, unguiculate, 1.0–1.2 × 1.0–1.2 cm, across the lateral lobes; lateral lobes unguiculate, obovate to spatulate, obtuse, reflexed apically, flanking the column in natural position, 0.4–0.6 × 0.3–0.4 cm; isthmus about 1.5 × 2.0 mm, subquadrate; midlobe ovate to suborbicular, obtuse to slightly emarginate, the margin entire to slightly crenulate, usually folding downward laterally, blade with many low, smooth veins 0.6–0.9 × 0.6–0.9 cm, the callus com-

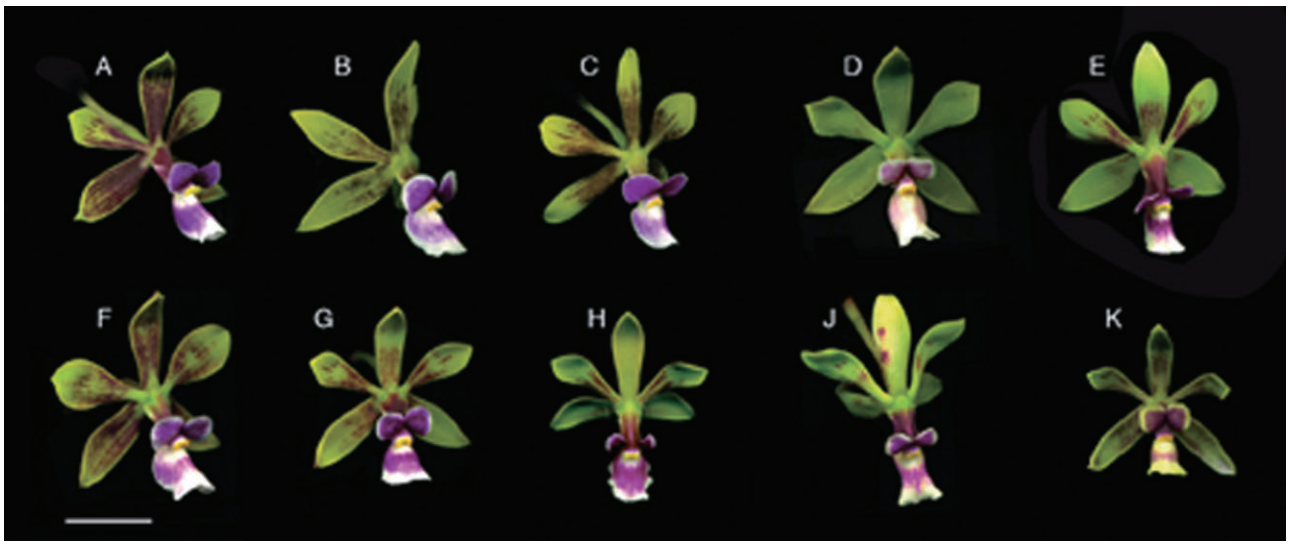
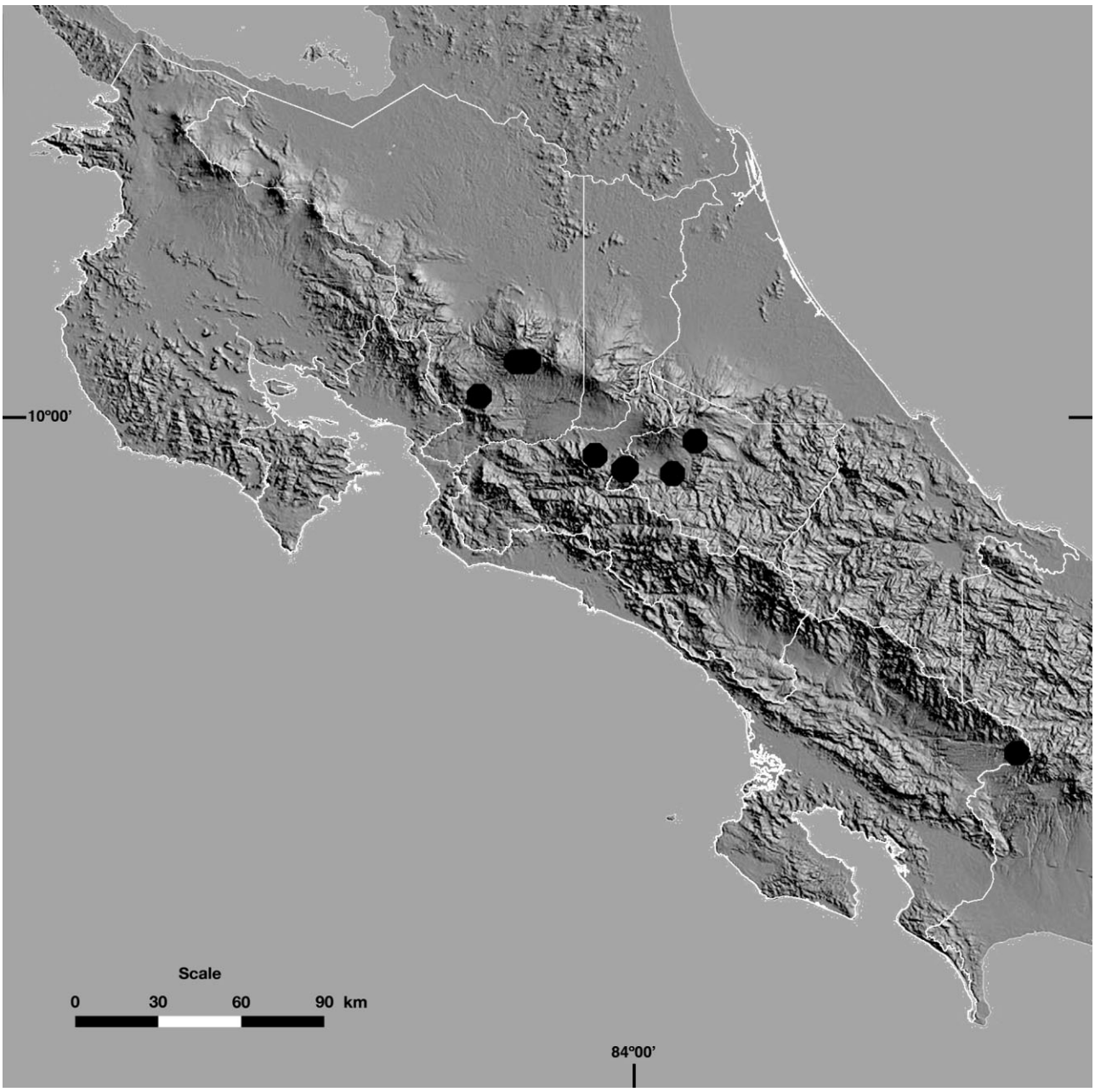


Figure 24. Floral variation in *Encyclia mooreana*. A, *Karremans 1356*. B, *Bogarín 5210*. C, *Gómez 3*. D, *JBL-08701*. E, *Bogarín 3789*. F, *Bogarín 3787*. G, *Bogarín 3791*. H, *JBL-08341*. J, *Bogarín 3792*. Scale bar, 1 cm. All the vouchers preserved at JBL.

posed by two longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, sulcate, joining at the base and extending onto the base of the midlobe. COLUMN straight, stout, pandurate, semiterete, truncate, dorsally dark purple, winged, the wings stigmatic, triangular, tooth-like, midtooth subequal to lateral teeth, transversely subquadrate–oblong, basally provided with a nectarium, apically with two lateral teeth, 0.5–0.7 × 0.3–0.5 cm. ANTHER CAP widely ovate, cucullate, four-celled. POLLINIA four in two pairs, obovate, strongly flattened, on narrowly linear, basally bifid caudicles. CAPSULE fusiform, verrucose.

Other specimens examined: COSTA RICA. Alajuela: Naranjo, Cirrí Sur, Cerro Palmira, bosque secundario y primario en la falda oeste, 10°11′N 84°21′W, 1900–2000 m, 27 noviembre 1993, *J. F. Morales 2123* (INB). From San Ramón and Zarcero, in the province of Alajuela, and the south-western slopes of Poás volcano, *A. R. Endrés 349* (W). Cartago: Alvarado, Pacayas, cuadrante de la ciudad, 9°55′24.1″N 84°48′33.3″ W, 1730 m, bosque muy húmedo montano bajo, epífita en *Thuja* sp. (Cupressaceae) en el jardín de la iglesia, 27 enero 2005, *D. Bogarín 1291, D. L. Kikut & A. Prendas* (JBL-spirit). El Guarco, entre Corralillo y Copalchí, sin más datos, planta colectada por Rafael A. González, 7 abril 2004, *D. Bogarín 800* (JBL-spirit). Paraíso, Navarro, Alto de Monestel, La Máquina, *c.* 1300 m, 8 abril 2004, *R. Gómez 3*, *M. Bonilla & J.C. Cervantes* (JBL-spirit). Same locality, *R. Gómez 3* (JBL-spirit). Turrialba, Santa Cruz, más o menos 4–5 km de la Iglesia de Santa Cruz, en el camino a Las Abras, despúes de Calle Vargas, cerca de Buenos Aires, en el punto del cruce entre Las Abras, Calle Vargas y Las Virtudes, al lado de la calle en un potrero pantanoso, 9°59′32‘N, 83°44′13’W, 1750–1850 m, 5 agosto 2006, *A. Karremans 1356 & D. Karremans* (JBL-spirit). En potreros al lado derecho del río Turrialba, desde la carretera Santa Cruz-Pacayas hacia las cataratas sobre el río, en árboles solitarios y de borde, 9°57′N 83°46′W, 1600–1700 m, 15 julio 2007, *A. Karremans 1849 & Consuelo Lok* (JBL-spirit). Costa Rica-Panamá: Puntarenas-Chiriquí: Coto Brus-Renacimiento, 4 km al noreste de Mellizas, Cerro Quijada del Diablo, sobre la línea fronteriza, 8°54′34.18″N 82°44′38.22″W, 2104 m, bosque muy húmedo premontano, epífitas en bosque secundario a orillas del camino, 19 Abril 2011, *D. Bogarín 8627, D. Jiménez & A. Karremans* (JBL-spirit). San José: Aserrí, Legua, La Legua, camino desde Fila El Alto hacia la cumbre del Cerro Caraigres (Cerro Dragón), 9°43′01.0″N 84°07′43.5″W, 2266 m, bosque pluvial montano bajo, epífita en bosque secundario sobre el borde de bosque y potrero, 23 Abril 2009, *D. Bogarín 6900, Y. Kisel, P. Renshaw, R. Trejos & M. Turjak* (JBL-spirit). San José: Desamparados, San Miguel, entre Tablón y Copalchí, 2 km oeste de Tablón, 9°50′07.10″N 84°01′37.20″W, 1854 m, epífitas en bosque secundario y árboles de potreros en bosque muy húmedo montano bajo, 2 octubre 2008, *D. Bogarín 5210, R.L. Dressler, R. Gómez, F. Pupulin, & R. Trejos* (JBL-spirit). San José: Desamparados, San Miguel, between Tablón and Copalchí, 2 km west of Tablón, 9°50′07.1″N 84°01′37.2″W, 1860 m, submontane moist forest, epiphytic in secondary vegetation



Map 6. Distribution of *Encyclia mooreana* in Costa Rica.

and scattered trees in pastures, 2 October 2008, *F. Pupulin 7188, D. Bogarín, R.L. Dressler & R. Gómez* (JBL-spirit). Escazú, camino de Bebedero hacia el Cerro Pico Blanco, 1850 m, bosque muy húmedo tropical montano bajo, epífitas en arbustos y árboles en potreros, 5 julio 2003, *D. Bogarín 223 & A. Granados* (JBL-spirit). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, 6 February 2005, *F. Pupulin 5521* (USJ, JBL-spirit).

Distribution: El Salvador to western Panama.

Eponymy: In honour of Frederick William Moore (1857–1949), Curator of the Royal Botanic Garden, Glasnevin of Dublin, Ireland, who first sent to Kew a plant of this species in May 1889.

Phenology: February to July.

Habitat and ecology: Epiphytic in tropical moist forest, premontane belt transition, premontane wet forest, premontane moist forest and lower montane wet forest along the Cordilleras of Guanacaste,

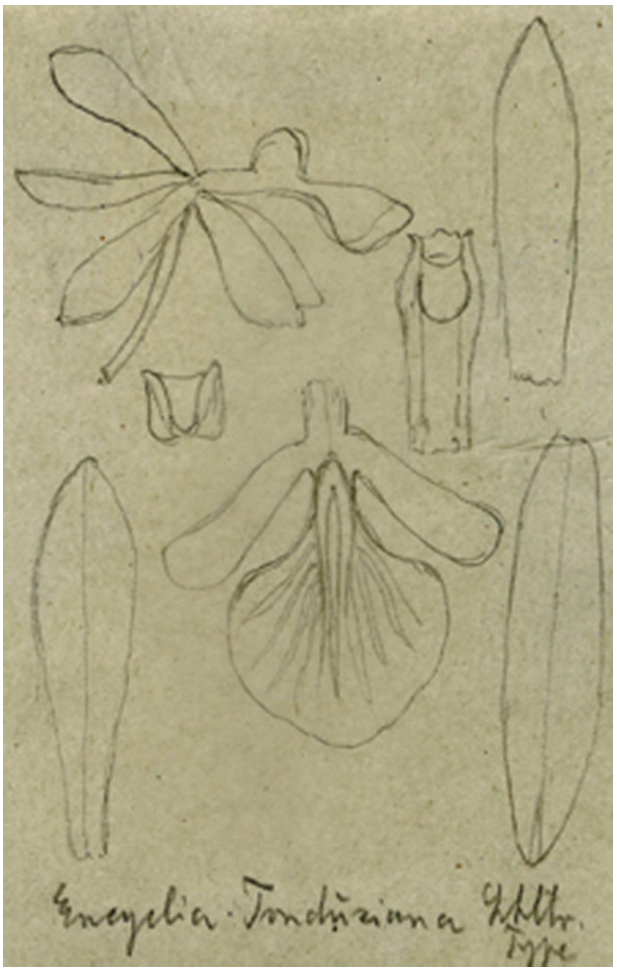


Figure 25. Neotype of *Encyclia tonduziana* Schltr. The drawing and the analysis of the flower are tracings of the original Schlechter's sketches from the holotype. Reproduced with the permission of the Director of the Herbarium, Harvard University Herbaria.

Tilarán, Central and Talamanca, from 1300 to 2100 m of elevation. Plants can be found growing in secondary vegetation and primary forest.

Discussion: Rolfe described *Epidendrum mooreanum* in 1891 based on three specimens without locality data and one specimen from Costa Rica. He placed the species in the section *Encyclium* of the Lindley's group *Hymenochila*. In 1914, Schlechter transferred it to *Encyclia.* The type sheet at K includes flowers of three of the four syntypes, but only two of them (*F. W. Moore s.n* and *H. Low s.n.*) include a portion of the inflorescence and of the vegetative parts (Fig. 23). They are also the only two type specimens associated with locality data. The material from the Royal Botanic Garden of Glasnevin was not only the first received by Rolfe (who dedicated the new species to its Curator), but it also has a dissected flower, which was probably that studied by Rolfe to describe *Epidendrum mooreanum*: for this reason we select it as the lectotype.

In 1923, Schlechter described *E. mooreana* twice with the names of *Encyclia brenesii* and *E. tonduziana*, both based on Costa Rican specimens collected by A. M. Brenes and the Brade brothers, respectively. Later, Ames *et al*. (1935) reduced Rolfe's *E. mooreanum* to a variety of *Epidendrum oncidioides,* a species otherwise known only from South America.

The species is recognized by the olive-green purple stained reflexed sepals and petals, the violet–purple lip, including the rounded and expanded tips of the lateral lobes which are basally narrow and wider at apex, the midlobe is suborbicular usually folding downward laterally. *Encyclia mooreana* is closest in appearance to *E. ceratistes* and *E. ossenbachiana*. With *E. ossenbachiana* they share the purple blotch on the blade of the midlobe and at the apex of the reflexed lateral lobes of the lip (however, in *E. ossenbachiana* the blotch is shortened into a dot at apex rather than the expanded blotch of *E. mooreana*) and the rounded, suborbicular midlobe. The sepals, petals and column of *E. ceratistes* and *E. ossenbachiana* are always pale green and not blotched (vs. purple blotched in *E. mooreana*). Other distinguishing features are discussed above for *E. ceratistes* and later for *E. ossenbachiana*.

7. *ENCYCLIA OSSENBACHIANA* PUPULIN, Selbyana 27: 4. 2006. *Type:* COSTA RICA. CARTAGO: Tierra Blanca, Río Reventado, along the river edge, *c*. 1900 m, a plant collected by Rafael A. González Rodríguez, July 2001, flowered in cultivation at Jardín Botánico Lankester, Dulce Nombre de Cartago, 8 July 2003, *D. Bogarín 357* (holotype: USJ). Figures 26–27, Map 7.

Description: PLANT epiphytic, caespitose, to 70 cm tall. *Roots* white, produced from the base of the pseudobulb and the rhizome, 0.9–1.1 mm in diameter. *PSEUDOBULBS* ovoid to subpyiriform, subtended by scarious bracts shredded with age, 3.5–5.5 × 2.3–3.0 cm, two- (rarely three-) foliate at apex. LEAVES ligulate–oblong, acute, the apex somewhat irregularly bilobed, conduplicate, coriaceous, curving with age, 24–55 × 1.9–2.3 cm. INFLORESCENCE apical, arching, stout, warty, a paniculate raceme to 150 cm long. PEDUNCLE terete, to 45 cm long, covered by six to eight scarious, tightly sheathing bracts 8–11 mm long; lateral branches perpendicular to the main rachis, densely warty, 7–14 cm long, two- to 11-flowered. FLORAL BRACTS triangular–ovate, acute, scarious, 3 mm long, 2.5–3.0 mm wide. OVARY pedicellate, terete, warty, arching, to 1.5 cm long includ-

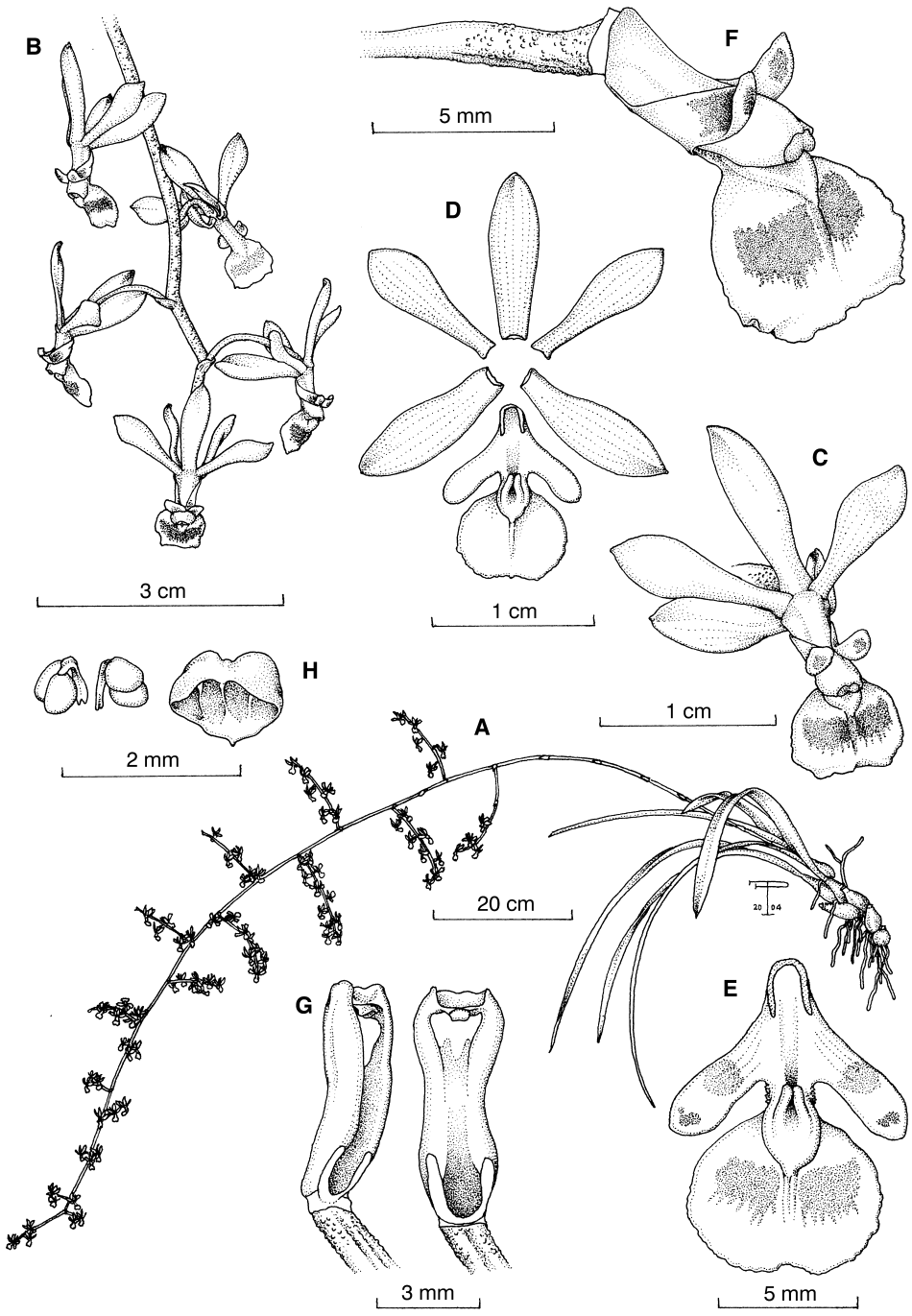


Figure 26. *Encyclia ossenbachiana* Pupulin. A, habit. B, detail of the rachis. C, flower. D, dissected perianth. E, lip, front view. F. ovary, column and lip, three quarters view. G, column, three quarters and ventral views. H, pollinaria and anther cap. Drawn by F. Pupulin from *Bogarín 357* (USJ).

ing the pedicel. FLOWERS resupinate, spreading–reflexed, scented, the sepals and petals pale apple green, the sepals dorsally blotched with brown at the apex, the lip white, blotched purple on the centre of midlobe, the lateral lobes abaxially provided with a large brown blotch and a purple blotch at the centre of the adaxial apex; the callus white; the column pale green at the base, white at apex, with a bright yellow anther. SEPALS subsimilar, oblanceolate–oblong, acute, reflexed, dorsally carinate and provided with a prominent, apical callus, slightly conduplicate towards the apex. DORSAL

Figure 27. Flowers of *Encylia ossenbachiana*, from *Bogarín 357* (JBL-spirit).

SEPAL 10 × 3 mm. LATERAL SEPALS slightly oblique, 10–11 × 3.5–4.0 mm. PETALS spatulate to unguiculate, obtuse, minutely apiculate, reflexed, 9 × 3.0–3.5 mm. LIP basally adnate to the column for 2 mm, deeply three-lobed, 10 mm long, 8 mm wide across the lateral lobes; lateral lobes linear–oblong, rounded, slightly wider toward the apex, erect and flanking the column in natural position, the apices neatly reflexed, 5 × 2 mm; isthmus about 1 mm long, subquadrate, minutely papillose on the lateral margins; midlobe suborbicular, retuse, 6 × 7 mm, provided at the base with an ovate–elliptic, laminar, flat callus, decurrent in front into a low keel running toward the lip apex, on which is a second callus composed by two retrorse rounded keels, highest in the rear portion, joining at the base to form a narrow cuniculus. COLUMN straight, subclavate, semiterete, truncate, 7 mm long. ANTHER CAP widely ovate, cucullate, four-celled. POLLINIA four in two pairs, obovate, strongly flattened, on narrowly linear, basally bifid caudicles.

Other specimens examined: COSTA RICA. Alajuela: Alfaro Ruiz, Palmira, Zona Protectora El Chayote, 2100 m, epiphytic on large trees along the continental divide, montane forest with *Quercus*, 8 March 2001, F. Pupulin & G. Barboza, flowered in cultivation at Jardín Botánico Lankester, 2 June 2004, *F. Pupulin 5237* (JBL-spirit). Cartago: Tierra Blanca, Río Reventado, along the river edge, *c*. 1900 m, a plant collected by Rafael A. González Rodríguez, July 2001, flowered in cultivation at Jardín Botánico Lankester, Dulce Nombre de Cartago, 8 July 2003, *D. Bogarín 357* (USJ, JBL-spirit). Alvarado, Pacayas, watercolour by Rafael Lucas Rodríguez Caballero (JBL). Cartago: Turrialba, Santa Cruz, Finca Blanco y Negro, en el bosque al lado del Río Jesus María, 9°57′53″N, 83°44′08″W, 1400 m, 7 de enero 2007, *A. Karremans 1584 & D. Karremans* (JBL-spirit).

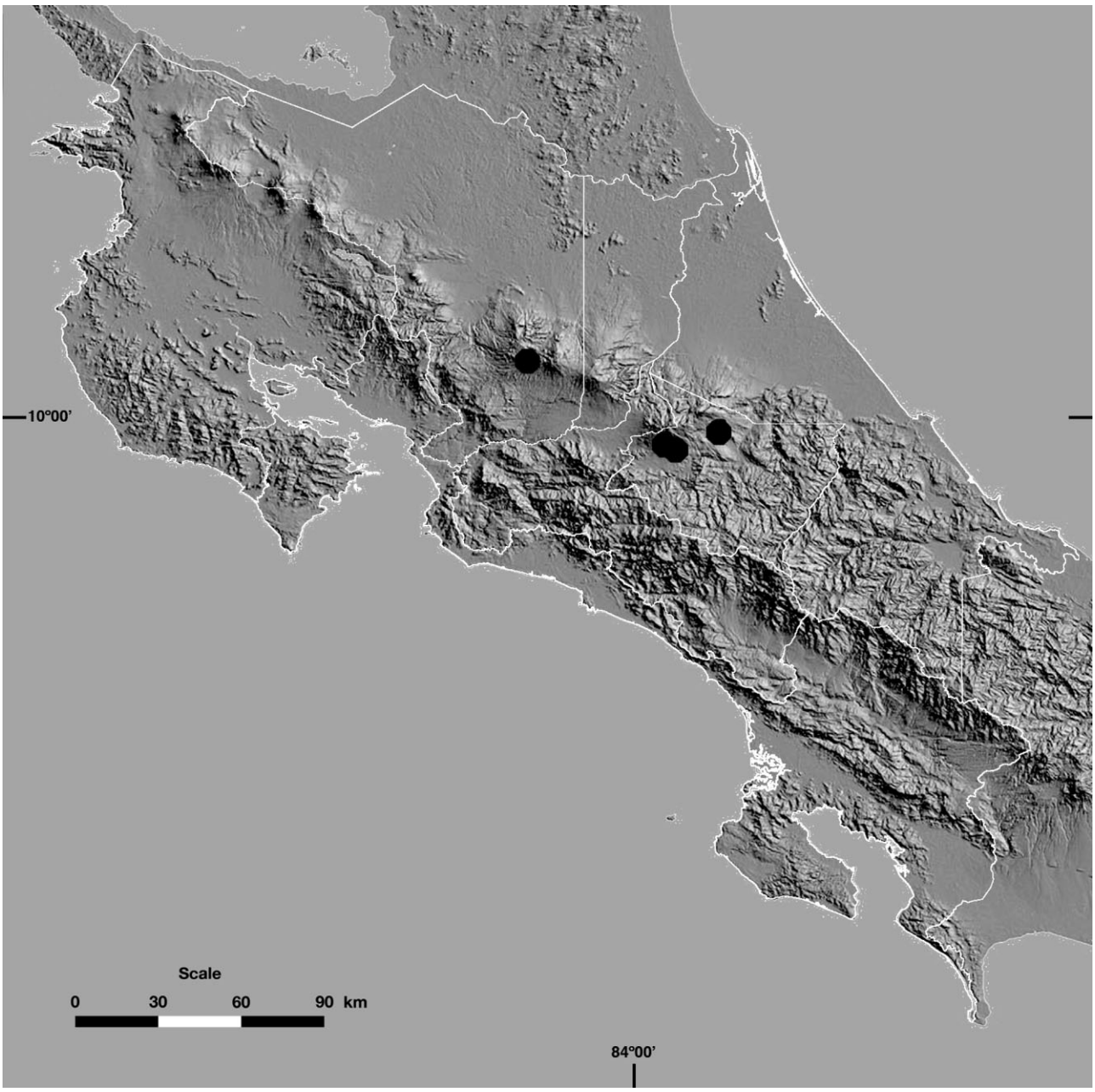
Distribution: Only known from Costa Rica.

Eponymy: Named in honour of Carlos Ossenbach Sauter, a well-recognized researcher of the history of botany, and particularly of the orchidology in the Neotropical region.

Phenology: June to July.

Habitat and ecology: Epiphytic in secondary vegetation in premontane rainforests at the Central Volcanic range from 1400 to 2100 m of elevation.

Discussion: Encyclia ossenbachiana is the most recently described species from Costa Rica, published by Pupulin (2006). In flower size, *E. ossenbachiana* approaches *E. mooreana*. It also resembles that species in the purple blotches at the apex of the reflexed lateral lobes of the lip and on the blade of the midlobe. The lateral lobes, however, are linear–oblong in *E. ossenbachiana*, whereas they are notably narrowed at the base and widely expanded at apex in *E. mooreana*, and the midlobe is subquadrate–truncate in *E. ossenbachiana* vs. rounded in *E. mooreana*. The two species also differ in the colour of sepals and petals, which are completely green in *E. ossenbachiana* and flecked with purple in *E. mooreana* and in the shape of the callus. On the top of the laminar callus that is typical of many *Encyclia* spp., *E. ossenbachiana* presents two retrorse, rounded keels that join at the base to form a narrow cuniculus. The oblong–ligulate lateral lobes of the lip of *E. ossenbachiana* are comparatively narrower and marked with a round purple blotch at apex, but they agree in shape to those of *E. ceratistes*. Nonetheless, the two species differ in many aspects. The inflorescence and the ovary of *E. ossenbachiana* are densely verruculose (vs. slightly warty to glabrous



Map 7. Distribution of *Encyclia ossenbachiana*.

in *E. ceratistes*), the perianth segments are smaller in *E. ossenbachiana* (10–11 vs. 13–16 mm long), the sepals and petals are strongly reflexed in *E. ossenbachiana* (spreading in *E. ceratistes*) and the column is not winged at all (vs. having two abbreviated teeth). A photograph of the flowers of *E. ossenbachiana* was published by Pupulin (2005: 261) without determination (Fig. 27). Rafael Lucas Rodríguez depicted this species in an unpublished watercolour kept at the University of Costa Rica based on a plant collected in Pacayas, near the type locality.

8. ENCYCLIA PERALTENSIS (AMES) DRESSLER, *Novon* 7: 124 1997. *Epidendrum peraltense* Ames, Schedul. Orch. 4: 46. 1923. *Type:* COSTA RICA. [CARTAGO: Turrialba] Peralta, alt. 1500 ft, *C.H. Lankester & A. Sancho 378* (holotype: AMES). Figures 28–29, Map 8.

Description: PLANT epiphytic, caespitose, to 60 cm tall. ROOTS white, produced from the base of the pseudobulb and the rhizome, 2.5–3 mm in diameter. PSEUDOBULBS globose, conic–ovoid or subpyriform,

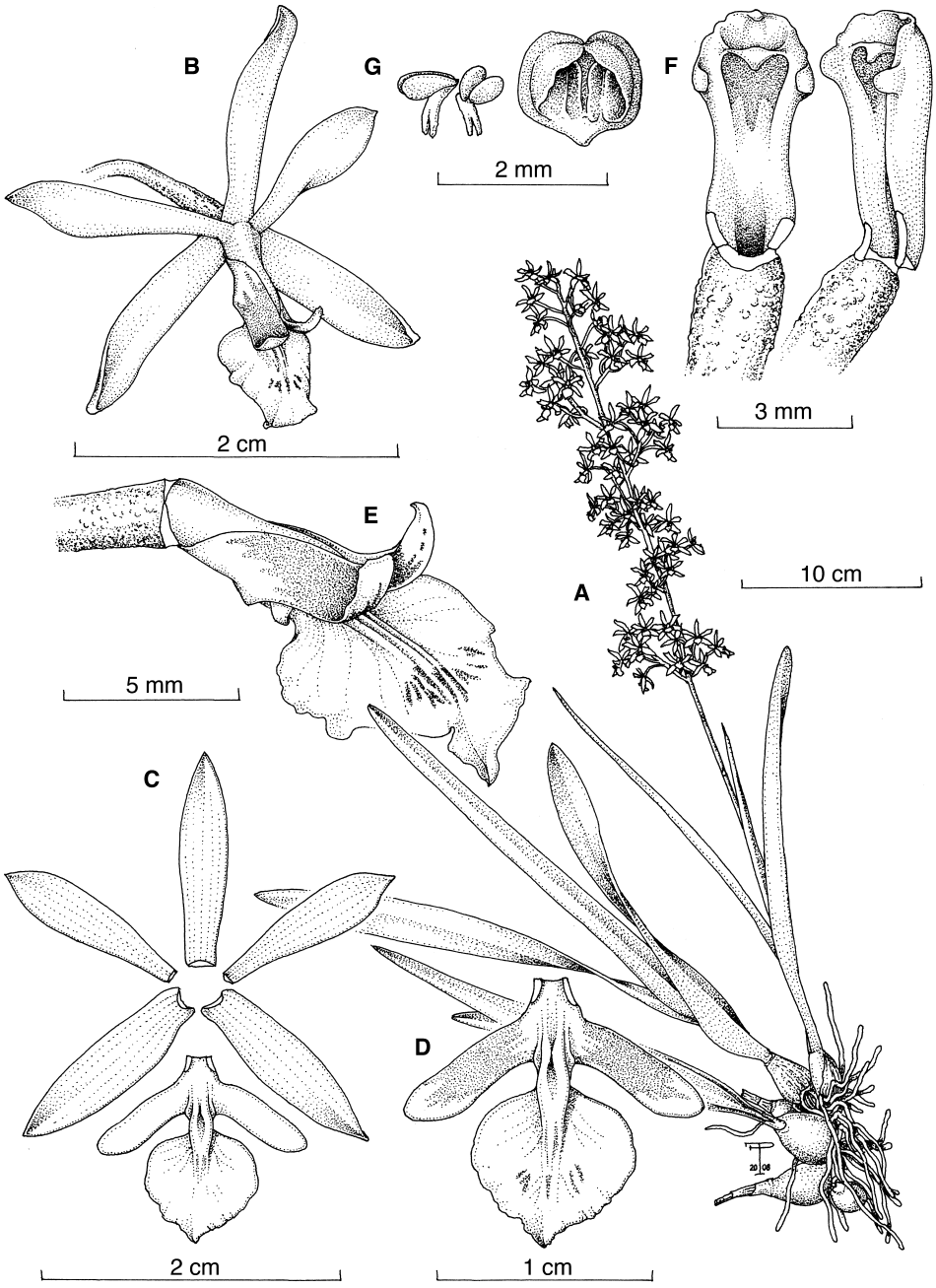


Figure 28. *Encyclia peraltensis* (Ames) Dressler. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, three quarters view. F, column, lateral and front views. G, pollinarium anther cap. Drawn by F. Pupulin from *Bogarín 2632* (JBL-Spirit).

2–6 × 1.5–5.0 cm, subtended by ovate, acute papery sheaths, shredded with age, 3.0–3.5 × 2–4 cm, two- to three-foliate at apex. LEAVES ligulate, acute or obtuse, the apex irregularly bilobed, conduplicate, coriaceous, 18–40 × 1.0–2.5 cm. INFLORESCENCE apical, erect, a paniculate raceme up to 40 cm long PEDUNCLE terete, to 20 cm long, covered by six to eight scarious, tightly sheathing bracts 8–15 mm long; lateral branches abbreviated, perpendicular to the main rachis, 1.5–3.0 cm long, three- to seven-flowered. FLORAL BRACTS about 1.5 mm long, triangular, basally clasping rachis, spreading. OVARY AND PEDICEL terete, smooth, 1.5 mm long. FLOWERS sepals and petals apple green, sometimes flushed with brown, lip white or cream marked with rose–purple, lateral lobes suffused with magenta. DORSAL

Figure 29. Inflorescence of *Encyclia peraltensis*, from *Bogarín 2632* (JBL-spirit).

SEPAL elliptic, acute, 1.2–1.4 × 0.3–0.5 cm. LATERAL SEPALS elliptic, acute, shortly carinate thickened beneath the apex, 1.2–1.4 × 0.3–0.5 cm. *Petals* spatulate–oblanceolate to spatulate–obovate, acute, 1.1–1.5 × 0.2–0.3 cm. LIP basally adnate to the column for 1 .5 mm, deeply three-lobed, short–unguiculate, 0.5–1.0 × 1.1–1.3 cm across lateral lobes, lateral lobes linear–oblong, obtuse, paralell to the column or reflexed apically and flanking the column in natural position, 4–7 × 0.2–0.4 mm; isthmus subquadrate, about 1.5 mm, midlobe orbicular to ovate, acute 6–8 × 5–6 mm, the callus composed by two longitudinal fleshy keels which made up a fovea on the isthmus, ellipsoid, sulcate, joining at the base and passing into three raised veins extending onto the midle of the midlobe 1.5 × 2.0 mm. COLUMN 6 mm, midtooth subequal to lateral teeth, column wings up to 0.5 × 0.7 mm, oblong. POLLINIA four in two pairs, obovate, on narrowly linear, basally bifid caudicles. CAPSULE fusiform, glabrous, 3 cm long.

Other vouchers examined: COSTA RICA. Cartago: Turrialba, La Suiza, camino entre Tres Equis y Pacayitas, 1 km sur de Buenos Aires, 9°54′13.5″N, 83°34′17.4″W, 904 m, bosque muy húmedo premontano, epífita en *Cupressus lusitanicus* (Cupressaceae), 8 marzo 2006, *D. Bogarín 2632, R.L. Dressler, A. Karremans & F. Pupulin* (JBL-spirit). Ujarráz [Ujarrás], Aug. et Sept., *A.R. Endrés s.n.* [Gen. Coll. Orch. N.°233] (W). Heredia: Sarapiquí, above Horquetas, Terra Folia Reserve, near Rara Avis, 10°18′ 14.6′N, 84°01′36.5′ W, 500 m, wet premontane forest, epiphytic, 21 July 2003, *M. Whitten 2091 & M. Blanco* (JBL-spirit).

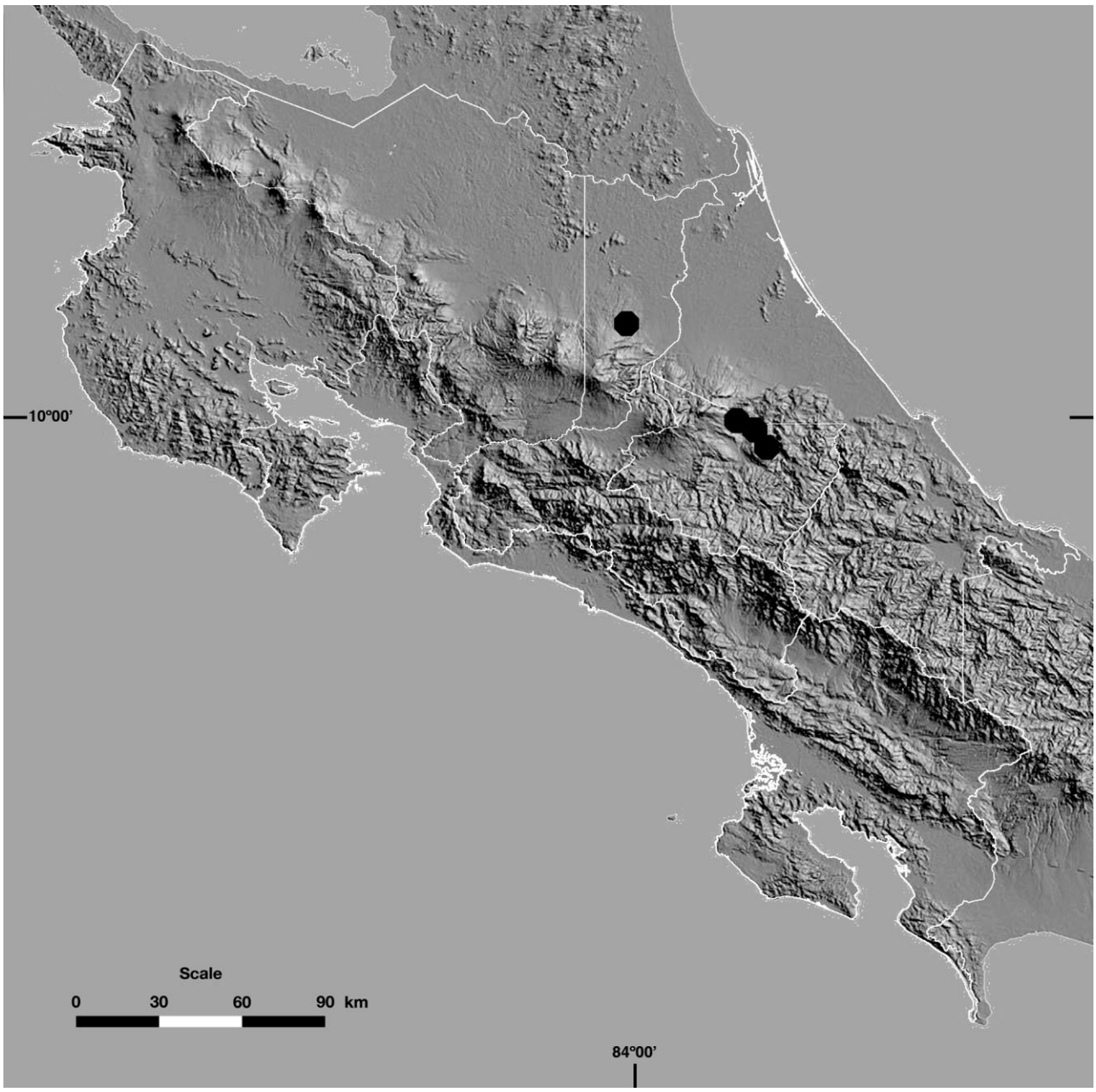
Distribution: Only known from Costa Rica.

Etymology: Named after the type locality of Peralta in Turrialba, Costa Rica.

Phenology: March to May.

Habitat and ecology: Epiphytic in secondary and primary vegetation in premontane moist forest and tropical wet forest premontane belt transition along the Caribbean watershed of the Central Volcanic range and Talamanca range from 500 to 900 m of elevation.

Discussion: Encyclia peraltensis was described by Ames in 1923 based on a collection of C. H. Lankester and A. Sancho in the Atlantic region of Costa Rica (Ames, 1923). The interpretation of this species has been difficult because of the few collections known in herbaria. Living plants cultivated at the Lankester Botanical Garden showed some critical characters not seen in other *Encyclia* spp. *Encyclia peraltensis* is characterized by the conspicuously dense inflorescences with the lateral branches clustered, abbreviated and perpendicular to the main rachis, the lateral lobes of the lip are oblong, narrowing towards the apex and boldly flushed with purple in the inner side, the midlobe of the lip is ovate, acute, basally greenish with pink stains in the centre and the margin white. *Encyclia peraltensis* might be confused with the high-elevation species, *E. ceratistes* but differs in having clustered inflorescences with abbreviated branches, the column with conspicuous arms (vs. abbreviated teeth in *E. ceratistes*), the lateral lobes of the lip are linear–oblong, having a dark purple stain (vs. brown blotch) midlobe of the lip lacks the smooth magenta veins and the three keels are running up to the half of the midlobe (vs. running up to the apex). *Encyclia chloroleuca* is also similar but differs in the wider lateral lobes of the lip which are basally striped in brown lacking the dark purple stain of *E. peraltensis*, the veins on the suborbicular midlobe run towards



Map 8. Distribution of *Encyclia peraltensis*.

the acute apex and are stained with magenta (vs. white veins running up to the half in *E. peraltensis*). Both species range at similar elevations in Atlantic of Costa Rica and could occur sympatrically. Dressler (1997) combined *E. peraltense* in *Encyclia* and suggested that the species could be a natural hybrid of uncertain parentage. The characters showed by the plants studied did not appear to be intermediate with other members of the genus. In his treatment of the Central American species of *Encyclia*, Withner (1998) proposed the same combination, but the photograph published with the name *E. peraltensis* is rather different from plants of Costa Rican populations, mainly in the large, suborbicular midlobe of the lip, finely striped with rose–purple. According to Dressler (to F. Pupulin, pers. comm., 2006), the photograph was probably taken outside Costa Rica, and the plant illustrated by Withner is probably native to the Bahamas archipelago. Judging from the published drawing and photographs of the holotype by Withner (2001), it is possible that the plants of *E. davidhuntii* Withner & de Fuente 'noted from [. . .] Costa Rica'

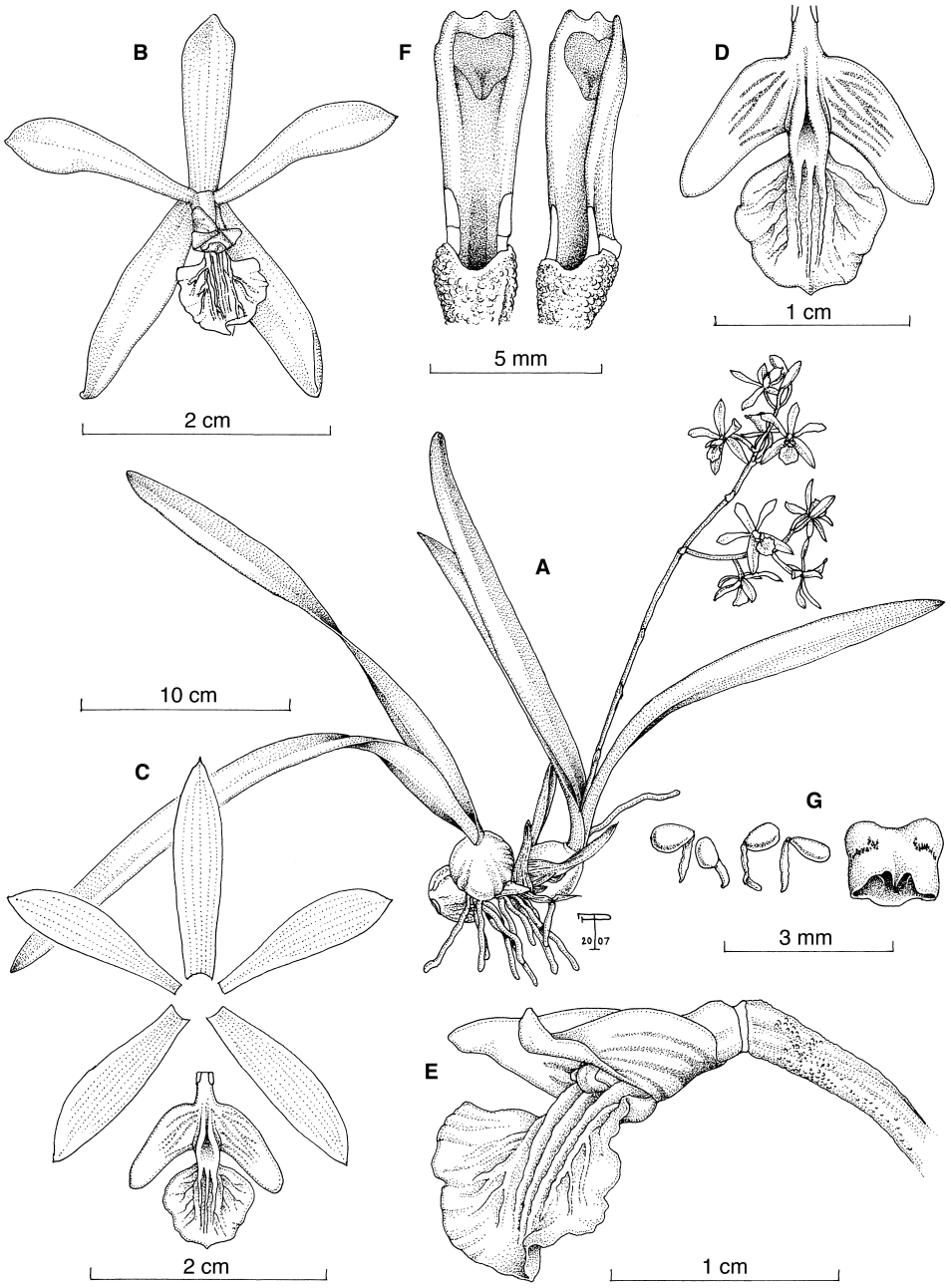


Figure 30. *Encyclia stellata* (Lindl.) Schltr. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, three quarters view. F, column, lateral and front views. G, pollinarium anther cap. Drawn by F. Pupulin from *Pupulin 4365* (USJ).

(Withner, 2001) were misidentified specimens of the similar *E. chloroleuca* or *E. peraltensis* (see discussion of *E. davidhuntii* under 'Excluded species').

9. *ENCYCLIA STELLATA* (LINDL.) SCHLTR., *Orchideen* 214 1914. *Epidendrum stellatum* Lindl., *Fol. Orchid. Epidendrum 21. 1853. Type:* [VENEZUELA.] Wild in Caracas, *Purdie s.n.* (holotype: K). Figures 30–31, Map 9.

Synonyms: Encyclia hunteriana Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 46. 1922. *Type:* PANAMA: BEI DAVID, im Chiriqui-Distrikt, etwa in

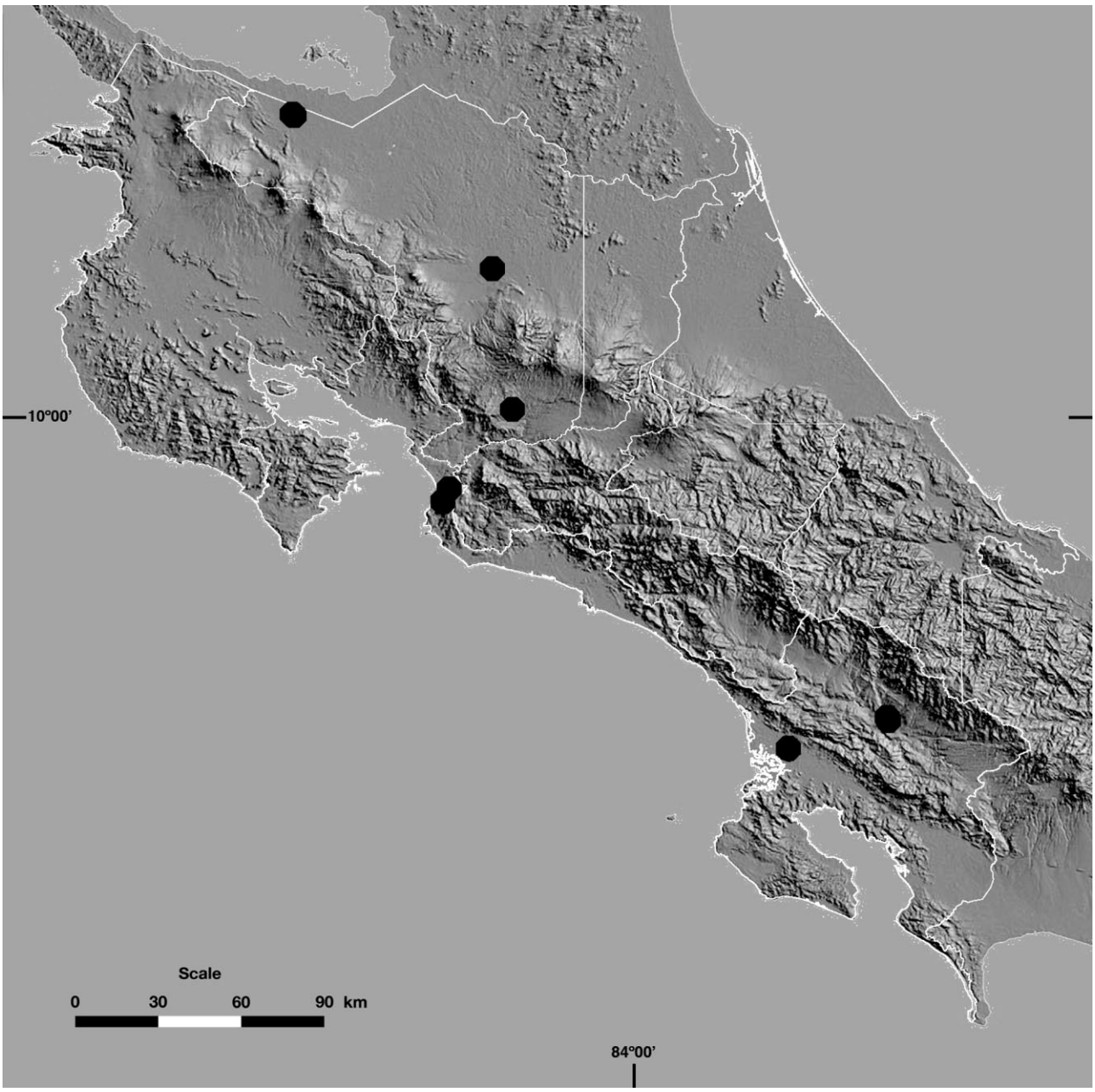
Figure 31. Flowers of *Encyclia stellata*, from *Pupulin 4365* (USJ).

Meereshöhe, *C. W. Powell 84* (holotype: B, destroyed; lectotype designated by Christenson, (1991), AMES, isolectotypes: MO).

Epidendrum alanjense Ames, Schedul. Orchid. 1: 13. 1922. *Encyclia alanjensis* (Ames) Carnevali & G.A.Romero ex Pupulin, Lankesteriana 4: 18. 2002. *Encyclia alanjensis* (Ames) Carnevali & G.A. Romero, Lindleyana 9: 67. 1994 *nom. invalid. (pro syn.). Type:* PANAMA: CHIRIQUI: Alanje, *H. Pittier s.n.* (holotype: US).

Description: PLANT epiphytic, caespitose, to 50 cm tall. ROOTS, white, produced from the base of the pseudobulb and the rhizome, 2–3 mm in diameter. PSEUDOBULBS conic–ovoid, 1.8–6.0 × 2.0–3.5 cm, subtended by papery sheaths, shredded with age, 2.3–4.0 × 1–4 cm, two- (rarely three-) foliate at apex. LEAVES ligulate, acute or obtuse, ensate, the apex irregularly bilobed, coriaceous, curving with age, 14–35 × 0.6–2.2 cm. INFLORESCENCE apical, erect, a paniculate raceme up to 25 cm long. PEDUNCLE terete, to 10 cm long, covered by three- to five-scarious, tightly sheathing bracts 3–7 mm long; lateral branches abbreviated, perpendicular to the main rachis, verrucose, 2–5 cm long, two- to four-flowered. FLORAL BRACTS about 1.5 mm long, triangular, basally clasping rachis, spreading. OVARY AND PEDICEL terete, smooth, to 2.5 mm long. FLOWERS sepals and petals apple green or greenish–yellow, lip white or cream, becoming yellow, lateral lobes basally stripped with rose–purple. DORSAL SEPAL elliptic to oblanceolate, acute, 1.7–2.0 × 0.35–0.40 cm. LATERAL SEPALS 1.5–1.9 × 0.3–0.5 mm, elliptic to oblanceolate, acute; petals 15–17 × 3–4 mm, spatulate–elliptic, acute or obtuse. LIP basally adnate to the column for 1 mm, deeply three-lobed, short–unguiculate, 1.2–1.5 × 1.1–1.2 cm across lateral lobes, lateral lobes, lateral lobes ovate to oblong, obtuse, flanking the column in natural position 7–8 × 2.5–3.0 mm, 1.0–1.5 mm distally, isthmus subquadrate, about 2 mm, midlobe 6.5–9.0 × 6–8 mm, ovate or elliptic–ovate, obtuse to acute, callus ellipsoid, sulcate, joining at the base and passing into three thickened raised veins extending onto the midlobe blade with several raised, verrucose nerves, 4 × 2 mm. COLUMN 6–7 mm, mid-tooth subequal to lateral teeth, column wing to 0.3 × 0.3 mm, triangular. POLLINIA four in two pairs, obovate, basally with bifid caudicles. CAPSULE ellipsoid, verrucose, beaked, 3.0 × 1.2 cm.

Other specimens examined: COSTA RICA. Alajuela: [San Carlos], directly across the river west of Muelle de San Carlos, 22 km north-northeast of Quesada by air, *c*. 100 m alt., 10°29′N, 84°28′W, 8 April 1983, *R. Liesner 14083* (CR); Naranjo: San Miguel, Cerro Crisanto, 10°02′N 84°24′W, 1100–1200 m, 15 marzo 2003, *J. F. Morales 10166* (INB); Upala, San José (Pizote), 10°59′N 85°07′W, 0 a 100, Villa Nueva, 11 km al Noreste de San José, 18 abril 1988, *G. Herrera 1841* (INB). Puntarenas: Buenos Aires, Sabana Guril, 9°01′N, 83°11′W, 100–200 m, 4 marzo 2000, *E. Alfaro 2893* (INB). Puntarenas: Garabito, Jacó, frente a la entrada a Quebrada Ganado, 9°43′35.1″N, 84°37′35.1″W, 31 m, bosque muy húmedo tropical, epífita en *Ficus* y *Tabebuia* a orillas de la carretera en bosque alterado, 31 marzo 2005, *D. Bogarín 1483, F. Pupulin & A.C. Rodríguez* (JBL-spirit). Garabito, Quebrada Ganado, Costanera road, in front to the deviation point to Quebrada Ganado, 09°43′39.9″N, 84°37′34.2″W, 30 m, epiphytic on *Ficus* tree and other trees along the roadside, tropical moist forest, 31 March 2005, *F. Pupulin 5623, D. Bogarín & A.C. Rodríguez* (JBL-spirit). Same locality, *F. Pupulin 5622, D. Bogarín & A.C. Rodríguez* (JBL-spirit). Puntarenas: Garabito, Jacó, Río Tarcolitos, cruce entre la carretera costanera a Tárcoles, en potreros al límite suroeste del Parque Nacional Carara, 9°45′31.26″N, 84°36′58.12″W, 70 m, bosque húmedo tropical, epífita



Map 9. Distribution of *Encyclia stellata* in Costa Rica.

en *Samanea saman* (Cenízaro), 19 marzo 2008, *D. Bogarín 4098* (JBL-spirit). Garabito, Jacó, Playa Azul, en potreros 1.5 km después de Tárcoles, antes de llegar al cruce entre Playa Azul y el Río Grande de Tárcoles, 9°46′33.44″N, 84°37′37.15″W, 70 m, bosque húmedo tropical, epífitas en *Samanea saman* (Cenízaro), 19 marzo 2008, *D. Bogarín 4088* (JBL-spirit). Garabito, Quebrada Ganado (Pacífico), flores enviadas al Jardín Botánico Lankester para identificación, 10 abril 2003, *E. Pacheco s.n.* (JBL-spirit). Osa, Cortés, Puerto Cortés, Ojo de Agua, ruta 2, carretera Costanera Sur, frente al Hospital de Ciudad Cortés, 8°59′13.47″N 83°32′30.56″W, 33 m, bosque muy húmedo premontano transición a basal, epífitas en cercas de potreros a orillas de la carretera, 20 Abril 2011, *D. Bogarín 8765, D. Jiménez & A. Karremans* (JBL-spirit). Zona Sur, without specific locality, a plant flowered in cultivation at Palmares, 27 February 2003, *F. Pupulin 4365* (JBL-spirit).

Distribution: Costa Rica to Colombia and NW Venezuela.

Etymology: Derived from the Latin *stella*, 'star', in allusion to the stellate flowers and flat round lip which are striking peculiarities in the dried state seen by the author.

Phenology: January to April.

Habitat and ecology: Epiphytic in secondary tropical moist forest and tropical wet forest basal belt transition, from central Pacific to southern Pacific and along the Caribbean plains from 30 to 150 m of elevation. It has been recorded growing on *Tabebuia rosea* DC. (Bignoniaceae), *Samanea saman* (Fabaceae) and *Ficus* sp. (Moraceae).

Discussion: It was described under *Epidendrum stellatum* by Lindley in 1853, based on a plant collected by A. Purdie in Caracas, Venezuela (Lindley, 1853). The species is easily distinguished by the verrucose ovary, the midlobe of the lip with three narrow, conspicuous, warty keels running from the base toward the apex with several lower keels radiating from the centre to the sides and the lateral lobes of the lip narrowing toward the tips. The inflorescences are short and often branched basally in comparison with the long branched inflorescences of *E. ceratistes*, *E. mooreana* and *E. peraltensis*. The column lacks wings or teeth. The sepals and petals are green and the neatly veined, warty lip is white, turning yellowish–cream with age, often with magenta stripes at the base of the lateral lobes and midlobe of the lip. It has been previously recorded from Costa Rica under the name *E. gravida*, a different, cleistogamous plant originally described from Mexico (see Discussion). *Epidendrum alanjense* Ames and *Encyclia hunteriana* Schltr., both described in 1922 on the basis on Panamanian collections from the region of Chiriquí, by H. Pittier and C. Powell, respectively, are indistinguishable from *E. stellata*.

10. *ENCYCLIA* SP. Figures 32 and 33.

Description: PLANT epiphytic, cespitose, with a short rhizome, to 25 cm tall. ROOTS flexuous, produced from the base of the pseudobulb and the rhizome, 0.9–1.2 mm in diameter. PSEUDOBULBS ovoid, subtended by small, triangular, scarious bracts shredding with age, 1.8–3.1 × 1.3–1.8 cm, two-foliate at apex. LEAVES narrowly ligulate–elliptic, acute, coriaceous, straight to curved, 11–19 × 1.2–2.0 cm. INFLORESCENCE terminal, arching to pendent, minutely warty, a paniculate, many-flowered raceme to 150 cm long; peduncle terete, to 20 cm long, covered by five to seven triangular, acute, tightly sheathing bracts 6–8 mm long; lateral branches inserted at an acute angle on the main rachis, warty, strongly fractiflex, 6–11 cm long, four- or five-flowered. FLORAL BRACTS triangular–ovate, acute, scarious, 3.5 × 2.5 mm. OVARY pedicellate, terete, apically subclavate, warty, to 1.4 cm long including the pedicel. FLOWERS resupinate, spreading, the sepals and petals pale greenish yellow, the sepals dorsally blotched with purple–brown at the apex along the midvein, the lip cream white, the lateral lobes abaxially provided with a pale brown blotch in the middle; the callus white; the column pale green at the base, white at apex, with a bright yellow anther. *Sepals* subsimilar, narrowly elliptic–oblong, acute, dorsally carinate, the margins slightly reflexed. DORSAL SEPAL 12.0 × 3.2–3.5 mm. LATERAL SEPALS slightly oblique, 12.0 × 3.5 mm. PETALS unguiculate, oblong, spatulate to unguiculate, subacute, minutely apiculate, gently incurved toward the apex, 12 × 3 mm. LIP basally adnate to the column for 1 mm, deeply three-lobed, 12 × 12 mm across the lateral lobes; lateral lobes marrowly obovate–oblong, rounded, distinctly wider toward the apex, erect and flanking the column in natural position, the apices neatly upcurved–reflexed, 6.5 × 3.0 mm; isthmus *c*. 1 mm long, subquadrate, provided with a thick, bicarinate, raised callus, the keels joining at the middle to form a narrow cuniculus, decurrent in front into a low, somewhat flattened keel running toward the lip apex; midlobe ovate-suborbicular, minutely retuse, longitudinally strongly reflexed, 7 × 7 mm, the margins crenulate. COLUMN straight, semiterete, truncate, slightly narrowed in the middle portion, 6.5 mm long, provided with two short, sharply triangular teeth aside the stigma. ANTHER CAP transversely elliptic–subrectangular, cucullate, four-celled. POLLINIA four in two pairs, obovate, strongly flattened, on linear, basally retuse caudicles.

Specimens examined: COSTA RICA. Without locality data: flowered at Orquidario 25 de Mayo, property of Carlos Ossenbach at Sabanilla, San José, Costa Rica, August 2008, accession N°. S-005, *C. Ossenbach s.n.* (JBL-spirit).

Distribution: Costa Rica.

Phenology: The only plant known was recorded in flower in August.

Habitat and ecology: Unknown.

Discussion: During the survey of *Encyclia*, we visited as many collections as possible in Costa Rica, to better document and understand the possible variation we can expect in plant and flower morphology for each taxon. It was in the course of this survey that, in August of 2008, we found a plant grown by Carlos Ossenbach in his vast collection of Costa Rican native

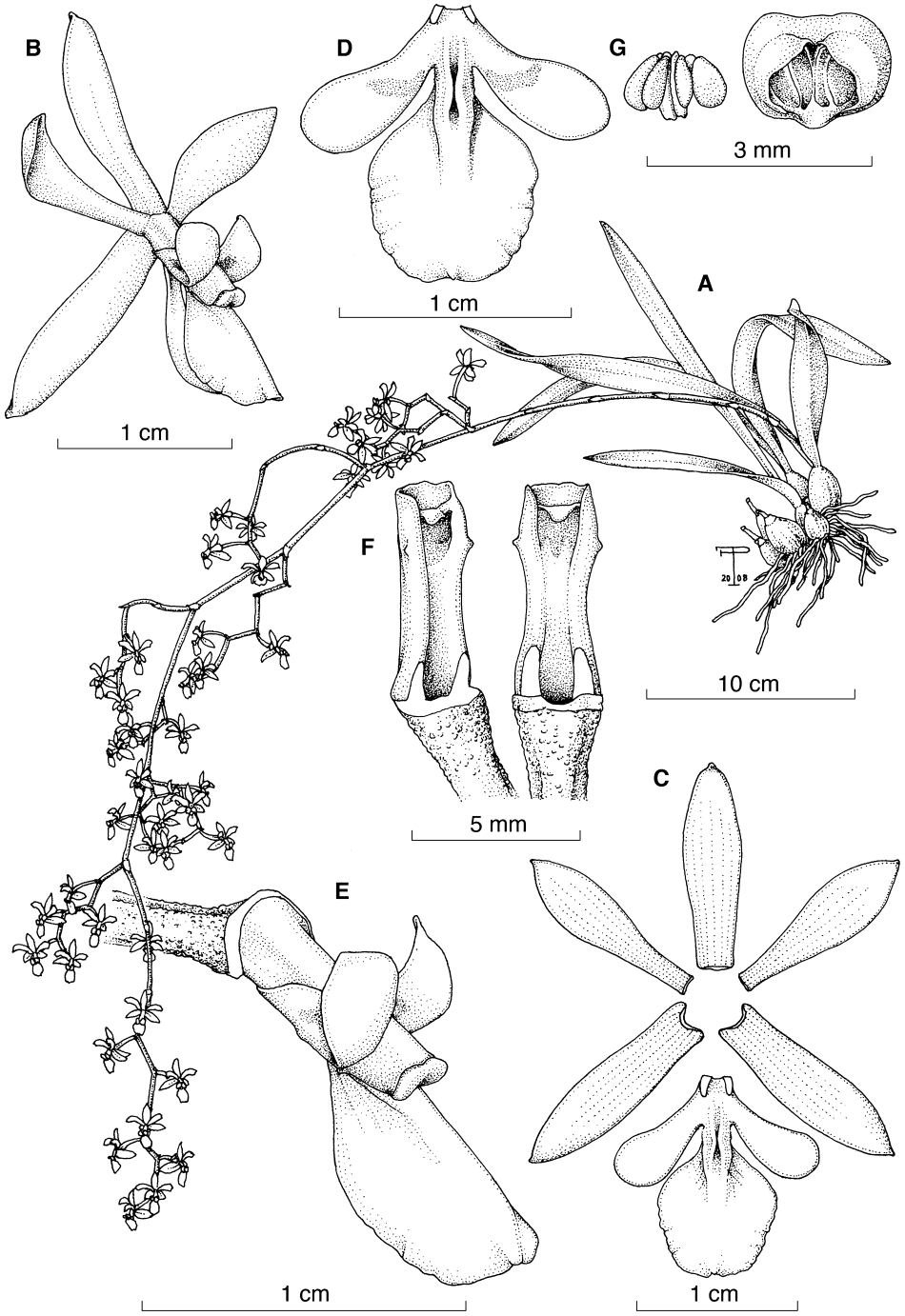


Figure 32. *Encyclia* sp. A, habit. B, flower. C, dissected perianth. D, lip, front view. E. column and lip, three quarters view. F, column, lateral and front views. G, pollinarium and anther cap. Drawn by F. Pupulin from *Ossenbach s.n.* (JBL-Spirit).

species, which does not fit any of the species previously described in *Encyclia*. We refrain from describing here it as new to science because, even although the plant was certainly collected in Costa Rica, we have no additional data to determine if this only known specimen is not a 'sport' mutant or hybrid. In the narrowly obovate lateral lobes of the lip, distinctly broader at apex, it resembles *E. mooreana*, but the flowers are uniformly greenish yellow with the lip cream (vs. green flecked with purple, the lip white,

Figure 33. Flowers of *Encylia sp.*, from *Ossenbach s.n.* (JBL-spirit).

boldly blotched with purple), the midlobe of the lip is ovate and smooth (vs. rounded, provided with three distinct keels), and the anther cap is transversely elliptic (vs. obcordate, two-horned), reminiscent of that of *E. ossenbachiana*. The column presents two lateral, abbreviated, triangular teeth, similar to those of *E. ceratistes*, but the latter also has a three-carinate, more or less flat midlobe of the lip (vs. strongly convex, smooth) with oblong lateral lobes (vs. obovate) and two-horned anther cap (vs. transversely elliptic). From the point of view of flower morphology, there is no way to reduce this specimen within the range of variation of other *Encyclia* spp. from Costa Rica, and we hope that our description and illustration will promote a more careful appreciation of other specimens both in the field and in cultivation, hopefully providing additional data that would eventually lead to its formal description.

Excluded species

Encyclia davidhuntii Withner & de Fuente, Orchidee (Hamburg) 52(4): 446. 2001. *Type:* BELIZE. Coll. ad Orange Walk, Mar. 2001, *M. de la Fuente s.n.* (holotype, AMES, not located).

Withner and M. de la Fuente (Withner, 2001) described *E. davidhuntii* from a cultivated specimen, originally collected somewhere in the district of Orange Walk, in north-western Belize. In the protologue, however, they also cited supposed specimens from Guatemala, Honduras and Costa Rica, without giving exact reference to any voucher from these countries. We were unable to locate the holotype at AMES, but judging from the illustration and the photograph of the type specimen (Withner, 2001), *E. davidhuntii* is scarcely distinct in our opinion from *E. chloroleuca*, which also occurs in Belize (McLeish, Pearce & Adams, 1995). Even though a discussion of the taxonomic status of *E. davidhunthii* is outside the scope of the present paper, this species is obviously a member of the 'greenish *Encyclia*' group, numerous species of which are still in need of a better circumscription based on appreciation of natural variation and geographic range. In the absence of precise records about the distribution of this taxon in Costa Rica, and considering the reduced number of available herbarium specimens of other *Encyclia* spp. with greenish flowers, the inclusion of Costa Rica as part of the natural distribution of *E. davidhuntii* is probably based on misinterpreted specimens of *E. chloroleuca* and/or *E. peraltensis*.

Encyclia guatemalensis (Klotzsch) Dressler & G.E.Pollard, Phytologia 21(7): 437. 1971 (Bas. *Epidendrum guatemalense* Klotzsch, Allg. Gartenzeitung 20(32): 250. 1852). *Type:* GUATEMALA. 'Dieses schöne *Epidendrum* blühte inde Juli im Orchideenhaufe des herrn Kunst und Handelsgärtner Allardt, und stammt nach dessen Aussage aus Guatemala', *J. F. Klotzsch s.n.* (holotype, B, destroyed; flower and photo, AMES).

Dressler (1993) recorded *E. guatemalensis* among Costa Rican *Encyclia* spp. in his field guide to the orchids of Costa Rica and Panama. No vouchers, however, were cited to support this inclusion, and *E. selligera* was not included in Dressler's treatment intended for the *Manual de plantas de Costa Rica* (Dressler, 2003). The species currently known only from Mexico (Carnevali *et al.*, 2001), Guatemala (Ames & Correll, 1953) and Belize (McLeish *et al.*, 1995).

Encyclia selligera (Bateman ex Lindl.) Schltr., Orchideen 211. 1914 (Basionym *Epidendrum selligerum* Bateman ex Lindl., Edwards's Bot. Reg. 24: misc. 40. 1838). *Type:* GUATEMALA. 'Native of Guatemala. Sent by Mr Skinner in 1836 to Mr Bateman', *G. Skinner s.n.* (holotype, K).

Mora-Retana & García (1992) and Dressler (1993) recorded *E. selligera*, without reference to any voucher. The species is actually known from Mexico (Breedlove, 1986; Hamer, 1988; Hágsater & Soto,

2003), Guatemala (Hamer, 1988; Hágsater & Soto, 2003), El Salvador (Hágsater & Soto, 2003), Honduras (Hamer, 1988; Hágsater & Soto, 2003) and Nicaragua (Hamer, 1988; Hágsater & Soto, 2003). Records from the Bahama Archipelago (Dodson, 1992; Hágsater & Soto, 2003) are probably based on misidentifications of another West Indian species (G. Carnevali, pers. comm.).

ENCYCLIA TUERCKHEIMII SCHLTR., Beih. Bot. Centralbl., Abt. 2, 36(2): 410. 1918. *Type:* GUATEMALA. Alta Verapaz: Cobán, 1350 m, Jul. 1912, *H. von Türckheim 2456* (holotype, B, destroyed; isotype, US; drawings of type, AMES).

The presence of *E. tuerckheimii* in Costa Rica was reported by Mora-Retana & García (1992), Dressler (1993), Dodson (1992) and Hágsater & Soto (2003), but their data are not supported by vouchered records. *Encyclia tuerckheimii* is probably endemic to Guatemala (the type) and Mexico (Hágsater & Soto, 2003).

List of species

[Names in bold refer to accepted species]

Cymbidium cordigerum = ***Encyclia cordigera***
Encyclia alanjensis = ***Encyclia stellata***
1. ***Encyclia alata***
Encyclia amanda = ***Encyclia chloroleuca***
Encyclia atropurpurea var. *leucantha* = ***Encyclia cordigera*** f. ***leucantha***
Encyclia atropurpurea var. *rosea* = ***Encyclia cordigera***
Encyclia atropurpurea var. *rhodoglossa* = ***Encyclia cordigera***
Encyclia brenesii = ***Encyclia mooreana***
2. ***Encyclia ceratistes***
3. ***Encyclia chloroleuca***
4. ***Encyclia cordigera***
Encyclia cordigera f. *leucantha* = ***Encyclia cordigera***
Encyclia cordigera var. *rosea* = ***Encyclia cordigera***
Encyclia doeringii = ***Encyclia cordigera***
5. ***Encyclia gravida***
Encyclia hunteriana = ***Encyclia stellata***
Encyclia macrochila = ***Encyclia cordigera***
6. ***Encyclia mooreana***
7. ***Encyclia ossenbachiana***
8. ***Encyclia peraltensis***
Encyclia powellii = ***Encyclia ceratistes***
Encyclia oncidioides var. *gravida* = ***Encyclia gravida***
Encyclia oncidioides var. *mooreana* = ***Encyclia mooreana***
Encyclia oncidioides var. *ramonensis* = ***Encyclia ceratistes***
Encyclia ramonensis = ***Encyclia ceratistes***
9. ***Encyclia stellata***
Encyclia tonduziana = ***Encyclia mooreana***
10. ***Encyclia*** sp.
Epidendrum alanjense = ***Encyclia stellata***
Epidendrum alatum = ***Encyclia alata***
Epidendrum amandum = ***Encyclia chloroleuca***
Epidendrum atropurpureum Auct., *non* Willd. = ***Encyclia cordigera***
Epidendrum chloroleucum = ***Encyclia chloroleuca***
Epidendrum cordigerum = ***Encyclia cordigera***
Epidendrum gravidum = ***Encyclia gravida***
Epidendrum longipetalum = ***Encyclia cordigera***
Epidendrum macrochilum = ***Encyclia cordigera***
Epidendrum macrochilum var. *albopurpurea* = ***Encyclia cordigera***
Epidendrum macrochilum var. *roseum* = ***Encyclia cordigera***
Epidendrum mooreanum = ***Encyclia mooreana***
Epidendrum oncidioides var. *gravidum* = ***Encyclia gravida***
Epidendrum oncidioides var. *mooreanum* = ***Encyclia mooreana***
Epidendrum oncidioides var. *ramonense* = ***Encyclia ceratistes***
Epidendrum peraltense = ***Encyclia peraltensis***
Epidendrum ramonense = ***Encyclia ceratistes***
Epidendrum stellatum = ***Encyclia stellata***

Index to numbered collections

Numbers in bold in parentheses refer to the species number in the treatment.
Agüero s.n. [April 1997] (**4**).
Alfaro 2893 (**9**).
Allcard s.n. [1837] (**3**).
Bogarín 357 (**7**); *800* (**6**); *801* (**2**); *802* (**2**); *1387* (**2**); *4088* (**9**); *4098* (**9**).
Bogarín, Barrantes, Dressler, Gómez and Rojas 2438 (**3**).
Bogarín, Dalström, Gigot, Powell and Pupulin 3111 (**3**).
Bogarín, Dressler, Gómez and Rojas 2452 (**2**).
Bogarín, Dressler, Karremans and Pupulin 2632 (**8**).
Bogarín and Granados 223 (**6**).
Bogarín, Jiménez and Karremans 8627 (**6**).
Bogarín, Jiménez and Karremans 8765 (**9**).
Bogarín, Kikut and Prendas1291 (**6**).
Bogarín, Kisel, Renshaw, Trejos & Turjak 6900 (**6**).
Bogarín, Prendas and Rodríguez 13 (**4**); *21* (**4**).
Bogarín and Pupulin 6148 (**4**); *6167* (**3**).
Bogarín, Pupulin and Rodríguez1483 (**9**).
Bogarín, Dressler, Gómez, Pupulin, and Trejos 5210 (**6**).
Brade and Brade 1274 (**6**).
Brenes 253 (**6**).

Chavarría 1585 (**4**); *2159* (**4**).
Endrés 110 (**2**); *349* (**6**); *s.n.* [W *Rchb-Orch* 1889–142116] (**3**); *s.n.* [Esparza] (**4**); *s.n.* [Ujarrás] (**8**).
Estrada 152 (**4**).
Estrada and Rodríguez 152 (**4**).
Gómez, *Bonilla and Cervantes 3* (**6**).
Grayum 10395 (**4**); *12786* (**2**).
Haber 7220 (**2**); *7852* (**2**).
Hammel and Perez 24855 (**1**).
Hartweg s.n. [1844] (**2**); *s.n.* [June 1849] (**5**).
Herrera 1841 (**9**).
Herrera and Gómez 22860 (**2**).
Holm and Iltis 821 (**1**).
Humboldt and Bonpland s.n. [1816] (**4**).
Karremans 463 (**3**).
Karremans and Karremans 1356 (**6**); *1584* (**7**).
Karremans, Karremans and Contreras Fernandez 3250 (**2**).
Karremans and Lok 1849 (**6**).
Lankester and Sancho 378 (**8**).
Lawrence s.n. (**6**).
Liesner 14083 (**9**).
Moore s.n. [May 1889] (**6**).
Mora s.n. [junio 1986] (**2**).
Morales 2123 (**6**); *4045* (**2**); *4063* (**1**); *5313* (**4**); *5491* (**2**); *6100* (**4**); *7661* (**2**); *9643* (**1**); *10166* (9); *10889* (**2**).
Núñez Rivas 6 (**2**).
Oersted 115 (**4**).
Ossenbach 365 (**3**); *501* (**2**); *S-005* (**10**).
Pacheco s.n. (**9**).
Pittier s.n. (**9**).
Powell 271 (**3**); *83* (**2**); *84* (**9**).
Pupulin 4305 (**3**); *4306* (**3**); *4365* (**9**); *4369* (**1**); *5520* (**2**); *5521* (**6**); *5237* (**7**); *5377* (**5**); *5640* (**2**); *6670* (**5**).
Pupulin and Barboza 3043 (**3**); *s.n.* [March 2001] (**2**).
Pupulin, Bogarín, Dalström, Gigot and Powell 6536 (**3**).
Pupulin, Bogarín, Dressler and Gómez 7188 (**6**).
Pupulin, Bogarín, Rambelli and Rambelli 6117 (**2**).
Pupulin, Bogarín and Rodríguez 5622 (**9**); *5623* (**9**).
Pupulin and Salas 5200 (**2**).
Pupulin and Salas-Pupulin 5303 (**2**).
Purdie s.n. (**9**).
Quesada, Sánchez, Serrano and Carman 1121 (**2**).
Rivera 1433 (**2**).
Rodríguez s.n. [febrero 1985] (**4**).
Rodríguez-Caballero s.n. (**7**).
Skinner s.n. [1837] (**1**).
Valerio s.n. [febrero 1967] (**4**).
Valverde 27 (**2**).
Wendland s.n. (**2**).
Whitten and Blanco 2091 (**8**).
Zúñiga 173 (**2**).

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