

FLORAE COSTARICENSIS SUBTRIBUI PLEUROTHALLIDINIS
PRODROMUS—SYSTEMATICS OF *ECHINOSEPALA* (ORCHIDACEAE)

FRANCO PUPULIN,¹⁻⁴ NOELIA BELFORT-OCONITRILLO,^{1,5} ADAM P. KARREMANS,^{1,6} AND DIEGO BOGARÍN^{1,7}

Abstract. We provide a general introduction to the *prodromi* to *Flora Costaricensis*, and an introduction to the precursors of subtribe Pleurothallidinae. We present a systematic revision of the genus *Echinosepala* for the flora of Costa Rica and a detailed discussion of molecular evidence with regard to most Costa Rican taxa, aimed at phylogenetically framing *Echinosepala* within the subtribe Pleurothallidinae, recognizing internal relationships among the species in the genus, and proposing evolutionary hypotheses. We recognize 10 species of *Echinosepala* in Costa Rica. Each species is described and illustrated with one or more botanical drawings and photographs, all based on Costa Rican material. Etymology, distribution, ecology, distinguishing features, and affinities with other taxa in the genus are discussed, taxonomic notes are provided, and a list of selected material examined for this study is included for each taxon. Two new species of *Echinosepala*, *E. glenioides* and *E. isthmica*, are described and illustrated, and their relationships are discussed. New combinations are proposed in *Echinosepala* for *Pleurothallis alexandrae* and *P. pastacensis*, and the former species is neotypified.

Keywords: flora of Costa Rica, new species, new combination, *Pleurothallis alexandrae*, *Pleurothallis pastacensis*, Pleurothallidinae

With this work, a first *prodromus* (Latin for “precursor”) to *Flora Costaricensis*, we are starting a series of papers that aim to present partial but coherent results obtained by our group of researchers in the study and critical appreciation of the orchid flora of Costa Rica. These *prodromi* will discuss the systematics of selected genera or phylogenetically related groups of species in larger genera, which will be included in forthcoming volumes of *Flora Costaricensis*. This *magnus opus* devoted to the rich flora of Costa Rica started in 1965 with the visionary effort of William Burger and has since been led by the Field Museum of Natural History in Chicago. Thirteen volumes of *Flora Costaricensis* have been published to date over a period of almost 40 years, covering entire plant families or parts thereof (Burger, 1971; Burger et al., 1977, 1983, 1991, 2000; Pohl, 1980; Durkee and Burger, 1986; Burger and van der Werff, 1990; Burger and Taylor, 1993; Burger

and Huft, 1995; Atwood and Mora de Retana, 1999; Luteyn and Wilbur, 2005; Pupulin, 2010).

As the general structure of *Flora Costaricensis* was conceived as individual volumes embracing complete families or at least vast taxonomic groups (to the ranks of subfamilies, tribes, and subtribes), the completion of Orchidaceae, with its high internal diversity and the rarity of certain taxa, proves to be an overwhelming challenge. A more convenient approach is the publication of individual papers dealing with the systematics of genera and/or groups already understood at the specific and intraspecific level, in anticipation of the final, comprehensive treatment (see, e.g., Pupulin and Bogarín, 2010, 2014b; Pupulin et al., 2010a; Bogarín, Serracín, and Samudio, 2014; Karremans et al., 2020). The present *prodromus* offers the first systematic insight into a complete group of Pleurothallidinae orchids for *Flora Costaricensis*.

FLORA COSTARICENSIS: PLEUROTHALLIDINAE

When, in 2009, we inscribed a project devoted to the systematic treatment of the subtribe Pleurothallidinae Lindl. ex G. Don (Orchidaceae: Epidendreae) for *Flora Costaricensis* at the University of Costa Rica (UCR), we knew that a work of such magnitude had never been attempted before in a country as highly biodiverse as Costa Rica. Modern orchid treatments intended for *Flora Costaricensis* (see Atwood and Mora de Retana, 1999;

Pupulin, 2010) are aimed at critically discussing the typification and identity of each taxon to the specific rank, including subspecific taxa and morphs when required, and to illustrate from living material all the taxa of a given group. Subtribe Pleurothallidinae encompasses in Costa Rica one-third of the total number of orchid species (Pupulin et al., 2019), making this vast assemblage of taxa one of the taxonomically more challenging in the country’s flora.

We would like to thank the staff and curators at AMES, CR, JBL, K, SEL, USJ, and W for their help in retrieving the *Echinosepala* specimens kept there and their supportive cooperation. We acknowledge our colleagues at the research department of Lankester Botanical Garden for the unselfish support they gave throughout the stages of the present work, sharing with us most of the fieldwork and providing stimulating ideas, discussion, and materials. Darha Solano Ulate splendidly rendered most of the illustrations for this paper, proving to be one of the most gifted botanical illustrators active today. The horticulture staff at Lankester Botanical Garden is thanked for their help in cultivating the living plants documented here. Acknowledgments are extended to the Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC) for issuing the scientific collection permits under which all the wild specimens for this study were collected. The present paper is part of Project 814-B0-052, “Flora Costaricensis: taxonomía y filogenia de la subtribu Pleurothallidinae, Orchidaceae,” supported by the Vice-Presidency of Research, University of Costa Rica.

¹ Lankester Botanical Garden, University of Costa Rica, P.O. Box 302-7050 Cartago, Costa Rica

² Harvard University Herbaria, Cambridge, Massachusetts, U.S.A.

³ The Marie Selby Botanical Gardens, Sarasota, Florida, U.S.A.

⁴ Corresponding author: franco.pupulin@ucr.ac.cr

⁵ Orchid Conservation Project, Bosque de Paz Biological Reserve, Bajos del Toro, Costa Rica

⁶ Naturalis Biodiversity Center, Endless Forms group, Leiden, The Netherlands

⁷ Herbario UCH, Universidad Autónoma de Chiriquí, David, Panamá

In the 15 years elapsed since the publication of the senior author's checklist of Costa Rican Orchidaceae (Pupulin, 2002), which recorded 427 species of Pleurothallidinae, and up to the last catalog of pleurothallid orchids given by Pupulin and coworkers (2019), 134 new species and new records for the flora of Costa Rica have been added by our group (Pupulin and Bogarín, 2004, 2007, 2010, 2011a,b, 2012, 2014a,b; Pupulin et al., 2007, 2009, 2010a,b, 2011, 2012; Bogarín et al., 2008, 2013, 2015; Bogarín and Fernández, 2010; Bogarín and Karremans, 2010, 2016; Pupulin, Bogarín, and Smith, 2010; Pupulin, Medina, et al., 2010; Bogarín and Pupulin, 2011; Fernández, 2011; Fernández and Bogarín, 2011, 2013; Karremans and Bogarín, 2011, 2013; Karremans and Muñoz García, 2011; Bogarín, Karremans, et al., 2012; Bogarín, Smith, et al., 2012; Karremans, 2012, 2014; Karremans and Smith, 2012; Karremans et al., 2012; Smith and Pupulin, 2012; Fernández, 2013; Smith et al., 2013, 2015; Bogarín and Kisel, 2014; Bogarín, Serracín, and Samudio, 2014; Fernández et al., 2014; Bogarín and Jiménez, 2015; Karremans, Bogarín, et al., 2015; Karremans, Pupulin, et al., 2015; Oses Salas and Karremans, 2016; Karremans and Díaz-Morales, 2017; Pupulin, Díaz-Morales, Aguilar, et al., 2017; Pupulin, Díaz-Morales, Fernández, et al., 2017; Pupulin, Karremans, et al., 2017). The last available enumeration of Pleurothallidinae in Costa Rica (Pupulin et al., 2019), which includes data published until 2017, accounts for 561 species in 30 genera. After that list, another 20 species were published as new for science or new records for the flora of the country (Bogarín et al., 2017, 2020; Karremans and Bogarín, 2017; Rojas-Alvarado and Karremans, 2017; Bogarín, Fernández, et al., 2018; Bogarín, Karremans, et al., 2018; Bogarín, Pérez-Escobar, et al., 2018; Karremans and Jiménez, 2018; Karremans, 2019; Karremans et al., 2019; Pridgeon, 2020; Pupulin, 2020; Pupulin and Bogarín, 2020; Pupulin and Oses, 2020). Several additional species, patiently awaiting their turn within the drawers of the research department at Lankester Botanical Garden, shall be published in the coming years.

Species richness is not evenly distributed among Costa Rican Pleurothallids. Traditionally smaller genera (but please remember that generic definitions and circumscriptions in the subtribe are still problematic, and that alternative systems of classification have been proposed and are sometimes in parallel use) have shown reduced growth in terms of diversity and number of species, with increments in overall diversity probably proportional to the total number of taxa for each genus in the concerned region. Nonetheless, it is noteworthy that also in most of the groups that are not centered in Mesoamerica in terms

of species diversity, like *Acianthera* Scheidw., *Anathallis* Barb. Rodr., *Dracula* Luer, *Dresslerella* Luer, *Myoxanthus* Poepp. & Endl., *Octomeria* R. Br., *Pabstiella* Brieger & Senghas, *Restrepiella* Garay & Dunst., and *Trichosalpinx* Luer, new taxa and new records are continually added to the checklist of the country's Pleurothallidinae. The case is different for the more speciose genera like *Lepanthes* Sw., *Pleurothallis* R. Br., and *Stelis* Sw., each of which already accounts for around 100–150 species in Costa Rica, and which together represent more than half of the known species of Pleurothallidinae in the country. Each of these genera will include, once their monographic treatments have been concluded, no less than 150 species.

With the advent of new techniques for the analysis of molecular data, the supraspecific systematics of the Pleurothallidinae have been discussed extensively (see, at least, Pridgeon et al., 2001; Luer, 2002; Karremans, 2016). However, less emphasis has been put into the effort of clarifying the internal relationships within the major groups, which would have greatly contributed to a better understanding not only of the phylogeographic and phylogenetic patterns of dispersion and speciation of the largest genera in the different regions of the American tropics, but also of their true diversity. For almost two centuries, pleurothallid orchids have been mainly described within the limits of a strictly floristic approach, with little or no consideration of either the relationships between species within any given genus or the delineation of groups of close relative taxa that could reflect the natural history of the largest genera. Molecular taxonomy mainly focuses on distinguishing and circumscribing monophyletic genera, rejecting artificial or erroneous systematic frameworks, but the difficulty of obtaining enough samples and molecular markers for analyses (Bogarín, Pérez-Escobar, et al., 2018) has in part obscured the true relationships among the species of the concerned groups. As a result, those genera whose monophyly received strongest molecular support were poorly investigated as to their internal relationships, irrespective of their size.

The five-year term sponsored by the University of Costa Rica for our study of the Subtribe Pleurothallidinae (the maximum period of funding for research projects by UCR) was highly productive, but it is obvious that the effort made by the team of Lankester Botanical Garden botanists to complete the chapter on Pleurothallidinae for *Flora Costaricensis* still has to offer novel results. To organize and present these results, we split Pleurothallidinae into blocks of genera, and the largest genera into smaller complexes of related species. Here we introduce the results of our systematic studies on *Echinosepala*.

MATERIALS AND METHODS

The general methods adopted for this study follow that presented in Pupulin, Karremans, et al. (2017). Plants of *Echinosepala* were collected around the country, from type localities and other critical areas, and brought to Lankester Botanical Garden (LBG) for cultivation and subsequent documentation. At least five specimens per morphospecies

were collected at any given locality whenever possible. Field notes were taken during fieldwork, including GPS and political data, elevation, ecological zones, and main types of vegetation. Plants were cultivated at JBL, and phenological data recorded.

Morphological Analysis

Over 180 individuals of *Echinosepala*, belonging to most of the morphospecies known for the country, were studied and documented. High-resolution macro- and microphotographs were taken according to the methods and with the camera and microscopic equipments detailed in Pupulin, Karremans, et al. (2017). Drawings of flowers and floral dissection were prepared according to the methods described therein. Vouchers were conserved in the liquid collection of JBL and/or in the herbaria of the National Museum of Costa Rica (CR) and the University of Costa Rica (USJ). Measurements were mostly taken under a dissecting stereoscope, or with the aid of the electronic scale bars inserted in the high-definition images of the floral details. Collections of the country, as well as relevant herbaria that allow digital access to their collections, were revised to study specimens of the taxa in this study, and specimens annotated when required.

Floral Ecology

Notes on floral ecology were taken from direct observation of the plants under the semiartificial conditions of the LBG open greenhouses. Photographs were taken of individual flowers over a lapse of two to three days to document temporal activity of the perianth.

DNA Extraction and Sequencing

The selection of the material was based on availability and interspecific variability. Vouchers of the specimens are kept in the liquid collections at JBL or L, unless specified otherwise. The list of the vouchers used in the phylogenetic analyses and their NCBI GenBank accession numbers are provided in Pupulin, Karremans, et al. (2017: Tab.

1). Methodology for DNA extraction, amplification, and sequencing of the material followed the steps given therein under the same heading.

Building the Data Sets

The STADEN (Staden et al., 2003) package was used for editing the sequences, and the Unicode nomenclature (IUPAC) was adopted where more than one base pair was equally probable. In the few cases when Pregap was unable to build a contig, sequences were merged by filling in missing positions with N's. Sequences were aligned manually in Mesquite v2.72 (Maddison and Maddison, 2007). After the alignments had been edited, additional sequences were obtained from GenBank, the latter using nBLAST. *Arpophyllum giganteum* AF266742 (ITS) was used as outgroup in all cases, as it is suggested to be the furthest related of all included species (Pridgeon et al., 2001; Pupulin, Karremans, et al., 2017).

Phylogenetic Analysis

The Bayesian Evolutionary Analysis Sampling Trees (BEAST; Drummond and Rambaut, 2007) was used to analyze the ITS matrix. Substitution and clock models were unlinked. GTR + Γ model, estimated frequencies, and eight categories were used. The Lognormal relaxed clock model was used. The tree prior was speciation-yule birth, and the number of generations was set to 30,000,000. The first 20% of the resulting trees were used as burnin. Trees were visualized in FigTree v1.3.1 (Rambaut, 2009). Posterior probability (PP) values were added to the branches of the trees using the labeling option, and branches were reordered for better visualization as discussed in Pupulin, Karremans, et al. (2017).

SYSTEMATICS OF *ECHINOSEPALA*

Echinosepala Pridgeon & M.W. Chase, Lindleyana 17(2): 100–101. 2002.

Synonyms: *Echinella* Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg. homonym, non* Ach. (1810, Closteriaceae). Type species: *Pleurothallis aspasicensis* Rchb.f. = *Echinosepala aspasicensis* (Rchb. f.) Pridgeon & M.W. Chase.

Myoxanthus subgen. *Satyria* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 44: 5. 1992. *Pleurothallis* subgen. *Acianthera* sect. *Satyria* (Luer) Luer, Lindleyana 11: 118. 1996. Type species: *Pleurothallis pan* Luer = *Echinosepala pan* (Luer) Pridgeon & M.W. Chase.

Myoxanthus subgen. *Silenia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 44: 6. 1992. *Pleurothallis* subgen. *Acianthera* sect. *Silenia* (Luer) Luer, Lindleyana 11: 118. 1996. Type species: *Pleurothallis aspasicensis* Rchb. f. = *Echinosepala aspasicensis* (Rchb. f.) Pridgeon & M.W. Chase.

Epiphytic, lithophytic or terrestrial, caespitose to repent, small to large *herbs*. *Stems* erect to curved, terete to slightly complanate, homoblastic, composed of 2 or more nodes,

enclosed by ancipitous, loose, rarely pubescent sheaths, commonly disintegrating with age. *Leaf* coriaceous, narrowly ovate to linear-elliptic, subacute to acuminate, cuneate below into a conduplicate, sessile base, with the veins typically very apparent. *Inflorescence* a fascicle of single, successive flowers from the base or the apex of the stem, or both; the peduncle terete. *Floral bract* loose, usually pubescent. *Ovary* minutely scaberulous to tomentose or long-haired. *Flowers* bilabiate, fleshy, with temporal activity, usually with putrid, reddish-purple colors, with sepals externally glabrous, scabrous or pubescent. *Dorsal sepal* free, subtriangular to lanceolate-elliptic to oblanceolate, obtuse to acuminate, abaxially glabrous to verruculose. *Lateral sepals* connate into an elliptic to obovate synsepal, subacute-rounded to broadly obtuse, the apices sometimes free, glabrous to verruculose within. *Petals* fleshy, lanceolate to obovate, asymmetric, rounded to acute or truncate. *Lip* 3-lobed, elliptic from a small claw, the apical lobe rounded to subtruncate, thickened at apex into a cushion-like pad, with a pair of intramarginal thin keels, lateral lobes erect, uncinat; the disc with an erect callus arising above the base, the lip sometimes with a horseshoe-

shaped pseudoglenion. *Column* semiterete, footed, with narrow wings above the middle. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, on a short, bilobed caudicle.

Before molecular systematics, *Echinosepala* species had been difficult to adequately place into a phylogenetic context, and only in the present century has its position in the groups of basal Pleurothallidinae (sensu Karremans, 2016) been fully understood. Of the 14 species currently recognized as belonging to the genus (Epidendra, 2019; IPNI, 2020), only 2 were originally described under the name *Echinosepala* (Pupulin, Karremans, et al., 2017); all others have been classified as species of *Acianthera*, *Myoxanthus*, and *Pleurothallis*.

Carlyle Luer (1992) first recognized that most species of the group were closely related and gathered them into *Myoxanthus* subgen. *Silenia* Luer and *Satyria* Luer. The two subgenera were mainly distinguished from other groups of *Myoxanthus* by the non-scurfy sheaths (except *Myoxanthus pan* [Luer] Luer = *Echinosepala pan* [Luer] Pridgeon & M.W. Chase) and the flowers produced from low on the ramicaul or terminally at the base of the leaf (instead of from near the apex of the stem). The long verrucose-ciliate upper margin of the anther cap is a common synapomorphy of the two subgenera.

Because of the strong morphological affinities of *Myoxanthus* subgen. *Satyria* and *Silenia* with *Pleurothallis* subgen. *Acianthera* (Scheidw.) Luer—a relationship also recovered by molecular analyses (see particularly Karremans et al., 2016)—Luer moved most species to *Pleurothallis* subgen. *Acianthera*, creating two new sections (Luer, 1995; validated in Luer, 1996).

The analyses of DNA data (Pridgeon and Chase, 2001; Pridgeon et al., 2001) confirmed that the species of *Myoxanthus* subgen. *Silenia* and subgen. *Satyria* formed a monophyletic group deserving generic recognition, and Pridgeon and Chase (2001) gave it formal status by creating *Echinella* Pridgeon & M.W. Chase (later corrected to *Echinosepala* Pridgeon & M.W. Chase [Pridgeon and Chase, 2002]). The phylogenetic analyses also confirmed a close relationship between *Echinosepala* and *Myoxanthus*, as noted by Luer. Together with *Barbosella* Schltr., *Dresslerella* Luer, *Pleurothallopsis* Porto & Brade, *Restrepia* Kunth, and *Restrepiella* Garay & Dunst., *Echinosepala* forms one of the nine major clades within the Pleurothallidinae, sister to the basal clade of *Octomeria*, and consecutively sister to the *Acianthera* clade (Karremans, 2016).

Morphologically, species of *Echinosepala* are characterized by caespitose to repent plants with monophyllous stems covered by tubular-ancipitous, minutely warty to (rarely) pubescent sheaths; the leaf coriaceous; the inflorescence solitary-flowered, produced from the apical or lower nodes of the stem; the flower fleshy, with the sepals frequently hirsute abaxially and variously verrucose adaxially, the lateral sepals connate into a concave

to cymbiform synsepal; the lip 3-lobed, with the erect lateral lobes oblong to unciniate, provided with a tall basal callus; the anther apical incumbent, the anther cap papillose to ciliate at apex; the 2 pollinia provided with whale-tail-shaped caudiculae (Luer, 1992; Pridgeon, 2005a).

The point of insertion of the inflorescence along the stem has been used as the main character to distinguish the two assemblages of species within the group. Luer (1992) created *Myoxanthus* subgen. *Silenia* to separate those species with a basal inflorescence (erroneously reported to be produced from the rhizome; e.g., Luer, 1992, 2003; Dressler, 1993; Pridgeon, 2005a) from the rest of the group, which supposedly have a terminal inflorescence. Pupulin, Karremans, et al. (2017) showed that the inflorescences of *Echinosepala* species are never rhizomic but are rather produced along the stem, where it is exerted from the apex of the second to third internode (see fig. 1 in Pupulin, Karremans, et al., 2017), and they expressed doubts that flowering from the nodes of the rhizome occurs at all in the Pleurothallidinae. Producing inflorescences from the lower nodes of the secondary stem is apparently an obligate feature in *E. lappiformis* (A.H. Heller & L.O. Williams) Pridgeon & M.W. Chase, *E. pan*, and *E. stonei* (Luer) Pridgeon & M.W. Chase, but it is facultative in *E. expolita* Pupulin & Belfort, where both apical and basal inflorescences are sometimes produced simultaneously. This condition has evolved in other groups of Pleurothallids, especially in *Acianthera*, and according to our molecular analyses even in *Echinosepala* it could have arisen independently in two different groups of species.

The “basal” position of the inflorescence in species of *Echinosepala* convinced Luer (2004) to revive the genus *Brenesia* Schltr. (1923), created to accommodate the anomalous *Brenesia costaricensis* Schltr., a species with pendent inflorescences produced from the lower nodes of the stem and hirsute flowers. He transferred eight species previously treated under *Echinosepala* (Luer, 2004) to *Brenesia*, under the belief that they were related to each other. However, the relationship between species of *Brenesia sensu stricto* (i.e., *B. costaricensis*, *B. herrerae* [Luer] Luer, and *B. johnsonii* [Ames] Luer, plus *Acianthera sotoana* Solano) and species of *Echinosepala* is not supported by DNA studies. The broad phylogenetic analysis of *Acianthera* carried out by Karremans et al. (2016) retrieved that the clade including the type species of *Brenesia* is sister to a clade that includes *Antilla* and *Kraenzlinella*, which all together are highly supported as sisters to the rest of *Acianthera*.

Florally, species of *Echinosepala* are mostly characterized by the putrid, reddish-purple color of the bilabiate perianth, often spreading only partially, and the complicate abaxial indumentum of the sepals, which vary from almost glabrous (*E. isthmica*, described below), to sparsely warty-verruculose (*E. alexandrae* [Schltr.] Pupulin & Bogarín, *E. aspasicensis*, *E. glenioides* [hereafter], *E. uncinata* [Fawc.] Pridgeon & M.W. Chase), the warts sometimes grouped

into small tufts (*E. longipedunculata* Pupulin & Karremans and *E. vittata* [Pupulin & M.A. Blanco] C.O. Morales & N. Villalobos), to sparsely spiny (*E. expolita* Pupulin & Belfort), densely tomentose (*E. tomentosa* [Luer] Pridgeon & M.W. Chase), hirsute with soft trichomes (*E. lappiformis* [A.H. Heller & L.O. Williams] Pridgeon & M.W. Chase, *E. stonei* [Luer] Pridgeon & M.W. Chase), or echinate with stiff hairs (*E. pan*). Adaxially, the sepals are almost glabrous (*E. alexandrae*, *E. aspasicensis*, *E. uncinata*, *E. vittata*), sparsely warty (*E. tomentosa*), to covered with irregular, low (*E. lappiformis*) or tall (*E. stonei*) warts, or stiff, short, rounded (*E. longipedunculata*) or pointed (*E. expolita*, *E. pan*) warts. In some species, the base of the dorsal sepal is semitransparent (e.g. *E. aspasicensis*, *E. expolita*, *E. glenioides*), forming a window under the dark purple blotches (Pupulin, Karremans, et al., 2017: fig. 3). The petals are mostly glabrous to sparsely verruculose, but they may be distinctly warty toward the apex (*E. expolita*, *E. lappiformis*, *E. pan*, *E. stonei*). The lip is glabrous in most species, but it is warty at apex in *E. alexandrae* and *E. shuarii* (Luer) Luer (= *Pupulinia shuarii* [Luer] Karremans & Bogarín). It always presents a tall callus at the base, which can be rounded and broad, massive, slightly concave, smooth or transversely rugose, occupying all the lip base (*E. alexandrae*, *E. isthmica*, *E. lappiformis*, *E. stonei*, *E. uncinata*), or provided with a horseshoe-shaped, concave pseudoglenion (*E. aspasicensis*, *E. expolita*, *E. glenioides*, *E. longipedunculata*, *E. pan*, *E. tomentosa*, *E. vittata*). This produces a gelatinous, non-viscous, shiny exudate, which is spread through a longitudinal groove to the apex of the lip, where it apparently dries, becoming matte in two to three days. In most species, the midline of the lip presents

a pair of intramarginal low lamellae, typically undulate on the upper margin.

According to our analyses, species of *Echinosepala* form a highly supported clade, consecutively sister to *Myoxanthus*, *Dresslerella*, and a clade grouping species of *Pleurothallopsis* and *Restrepia*, and species of *Restrepiella* and *Barbosella*, on two branches (Fig. 1). Within *Echinosepala*, *E. glenioides* (as *E. aspasicensis*) and *E. longipedunculata* are highly supported as sister species, and in turn they are well supported as sister of *E. pan* and *E. expolita*, which cannot be differentiated by their ITS sequences. *Echinosepala alexandrae* (as *E. sempergemmata*) and *E. isthmica* (as *E. uncinata*) form a well-supported group, which in turn is sister (with low support) to *E. stonei*. In our analysis, the phylogenetic position of *E. stonei* is not resolved, but the species is surely not closely related to the group of *E. expolita/E.pan*. *Echinosepala tomentosa* and *E. vittata*, both characterized by miniature plant habits and flowers, are sister to all the other species in a highly supported group.

The actual diversity of this group has still to be fully understood. Pridgeon (2005a) reported only 8 species for the genus, but we have recorded 10 species in Costa Rica alone (Pupulin, Karremans, et al., 2017; herein) (Fig. 2–3). Including the new taxa described and resurrected in the present paper, at least 17 species are recognized today in the genus, distributed from Belize to the West Indies (Jamaica), to the Guyanas and Brazil, and down to Bolivia, including Peru (Zelenko and Bermudez, 2009), along the Andes, but the diversity of *Echinosepala* is likely much higher.

References: Pridgeon et al. (2001, 2005a,b), Karremans (2016), Pupulin, Karremans, et al. (2017).

GENUS DISCUSSION FOR *FLORA COSTARICENSIS*

Echinosepala is a genus of 17 or more species, distributed from Belize to the West Indies (Jamaica), the Guyanas and Brazil, and down to Bolivia along the Andes. According to the number of species recorded in Costa Rica alone, the diversity of *Echinosepala* is likely higher. Species of *Echinosepala* occur mostly epiphytically (rarely as lithophytic or terrestrial herbs) in warm tropical, premontane or cloud, evergreen, wet forests at elevations of 300–2000 m. Flowering has been mostly recorded from June to December. Morphologically, species of *Echinosepala* are characterized by caespitose to repent plants with monophyllous stems covered by tubular-ancipitous, minutely warty to (rarely) pubescent sheaths and coriaceous leaves; the inflorescence solitary-flowered, produced from the apical or lower nodes of the stem; the bilabiate flower fleshy, with putrid colors and complicate indumenta of the sepals, frequently hirsute abaxially and variously warty adaxially, the lateral sepals connate into a synsepal; the lip 3-lobed, with the erect lateral lobes oblong to uncinata, provided with a tall basal callus occupying all the disc, which can be rounded and broad, massive, smooth, or provided with a horseshoe-shaped,

concave pseudoglenion, producing a shiny, gelatinous exudate, and a pair of intramarginal, low keels; the apical anther incumbent, papillose to ciliate at apex; the 2 pollinia provided with whale-tail-shaped caudiculae. *Echinosepala* is likely to be pollinated by flies that hook the pollinarium to the rear portion of the scutellum. No pollination studies have been published to date, but flies of the Drosophilidae family were recorded visiting the flowers. Molecular analyses carried out by Pridgeon and collaborators (2001) and by our group (Pupulin, Karremans, et al., 2017) support the monophyly of *Echinosepala*, whose species form a highly supported clade, sister to *Myoxanthus*, *Dresslerella*, and a clade grouping species of *Pleurothallopsis* and *Restrepia*, and species of *Restrepiella* and *Barbosella*, on two branches. Within *Echinosepala*, the species with a pseudoglenion are highly supported as sister species, whereas those with a plate-like, bare callus form another well-supported group, which in turn is sister to *E. stonei* (Fig. 4). The species with miniature plant habits and flowers are sister to all the other species in a highly supported group.

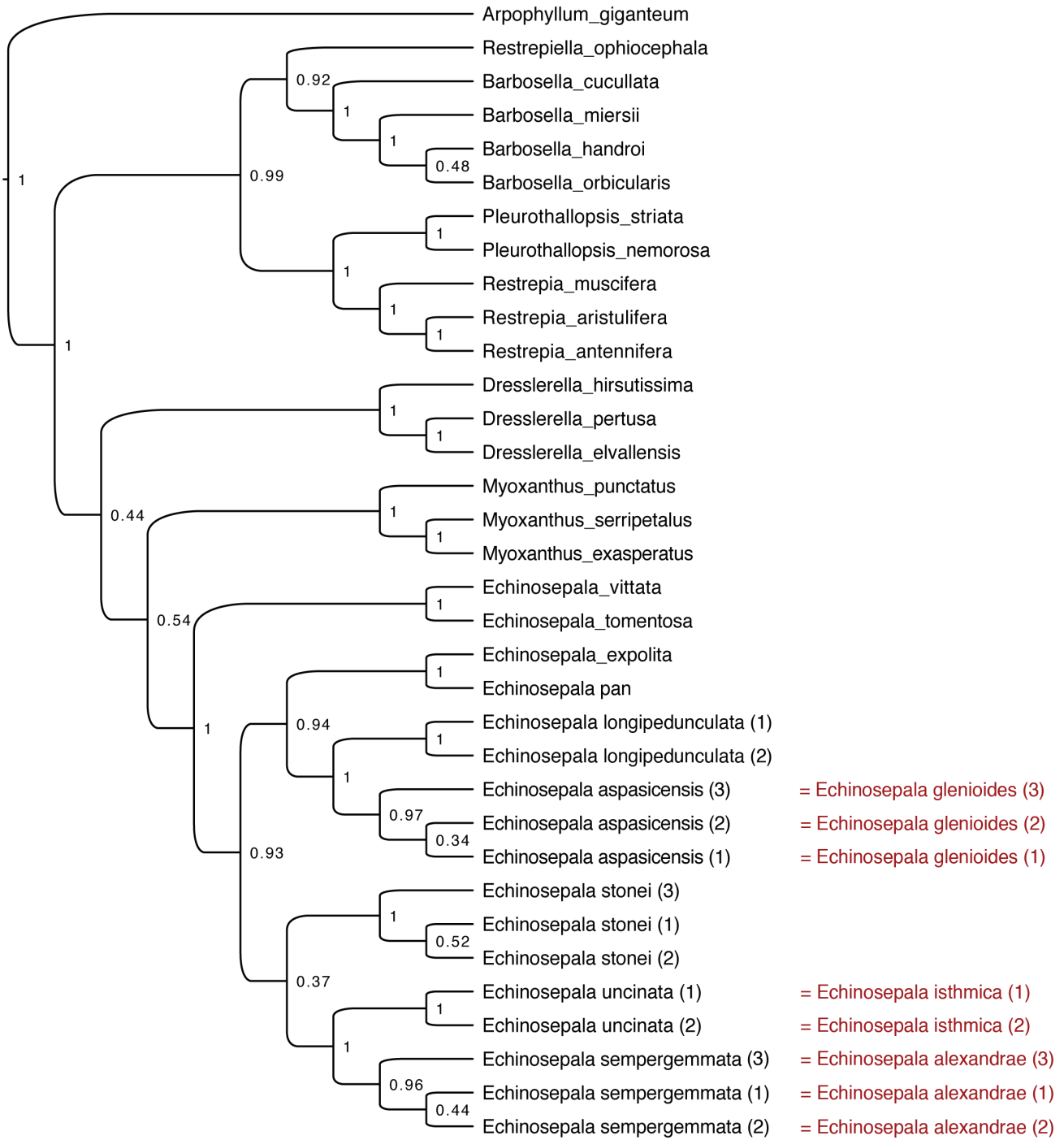


FIGURE 1. Phylogenetic relationship among the species of *Echinosepala* (modified from Pupulin, Karremans, et al., 2017). Species names in red are updated to the nomenclature proposed in the present paper.



FIGURE 2. Flowers of *Echinosepala* species from Costa Rica. A–B, *E. alexandrae* (Bogarín 7137); C–D, *E. expolita* (Bogarín 1871; Pupulin 7030); E–F, *E. glenioides* (Bogarín 3063; Bogarín 8211); G–H, *E. isthmica* (Bogarín 5855; Bogarín 5871); I, *E. lappiformis* (Bogarín 9554). All the vouchers at JBL. Photographs by F. Pupulin.



FIGURE 3. Flowers of *Echinosepala* species from Costa Rica. A–B, *E. longipedunculata* (Bogarín 5449; Karremans 4994); C, *E. pan* (Bogarín 10270); D, *E. stonoi* (Bogarín 5713); E, *E. tomentosa* (Bogarín 5622); F, *E. vittata* (Blanco 1324). All the vouchers at JBL. Photographs by F. Pupulin.

KEY TO THE SPECIES OF *ECHINOSEPALA* IN COSTA RICA

- 1a. Callus of the lip with an inverted U-shaped callus (pseudoglenion) at the base. 2
- 1b. Callus of the lip with the basal callus smooth to rugulose 8
- 2a. Inflorescences produced from the lower nodes of the stem 3
- 2b. Inflorescences produced from the apex of the stem 4
- 3a. Sheaths of the radicauls hirsute; leaves narrowly linear-lanceolate, >2.5 cm wide; sepals long-echinate abaxially *E. pan*
- 3b. Sheaths of the radical glabrous; leaves ligulate, <3 cm wide; sepals shortly tomentose abaxially *E. expolita*
- 4a. Mature plants <20 cm tall; flowers small, synsepal >1 mm long, lip >4 mm long. 5
- 4b. Mature plants >30 cm tall; flowers large, synsepal < 15 mm long, lip <7 mm long. 6
- 5a. The dorsal sepal yellow, the synsepal deep purple, adaxially densely tomentose *E. tomentosa*
- 5b. Sepals whitish, striped with red, abaxially with stiff hairs along the veins *E. vittata*
- 6a. Ovary and abaxial surface of the sepals tomentose; adaxial surface spiny. *E. expolita*
- 6b. Ovary and abaxial surface of the flowers warty; adaxial surface verruculose 7
- 7a. Pedicel <3 cm long; flowers purple-maroon; lip elliptic, acute, purple-red *E. glenioides*
- 7b. Pedicel >6 cm long; flowers yellow-orange; lip sub rectangular, truncate, yellow *E. longipedunculata*
- 8a. Inflorescences produced from the lower nodes of the stem 9
- 8b. Inflorescences produced from the apex of the stem 10
- 9a. Dorsal sepal narrowly triangular-lanceolate *E. lappiformis*
- 9b. Dorsal sepal broadly oblong *E. stonoi*
- 10a. Leaves ligulate; flowers autogamous, mostly cleistogamous, adaxially warty, midlobe of lip ovate, narrower than the lip base. *E. alexandrae*
- 10b. Leaves lanceolate; flowers not autogamous, adaxially subglabrous, midlobe of lip transversely rectangular, as wide as the lip base. *E. isthmica*

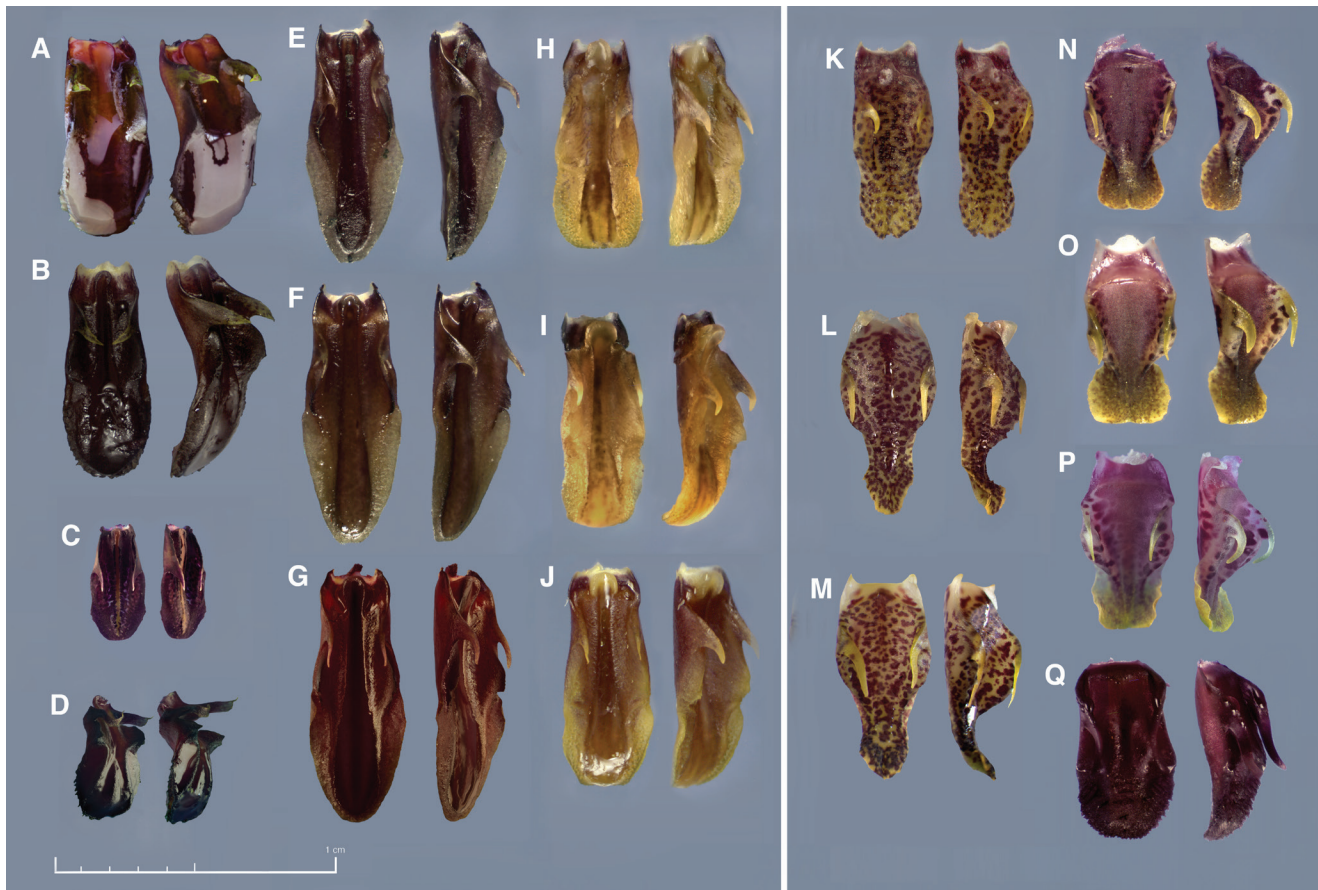


FIGURE 4. Labella of *Echinosepala* species. **A–J** (left of the bar), species provided with a pseudoglenion; **K–Q** (right of the bar), species without pseudoglenion. **A–B**, *Echinosepala expolita*; **C**, *E. tomentosa*; **D**, *E. pan*; **E–G**, *E. glenioides*; **H–J**, *E. longipedunculata*; **K–M**, *E. alexandrae*; **N–P**, *E. isthmica*; **Q**, *E. stonei*. Vouchers (all at JBL): Pupulin 7030 (A); Bogarín 1871 (B); Bogarín 5822 (C); Bogarín 10274 (D); Bogarín 1945 (E); JBL-20660 (F); JBL-27660 (G); Bogarín 3863 (H); Bogarín 5449 (I); Karremans 4994 (J); Bogarín 4601 (K); Bogarín 4678 (L–M); Bogarín 5855 (N); Bogarín 5871 (O); Bogarín 5855 (P); Bogarín 7190 (Q). Photographs by F. Pupulin.

TAXONOMIC TREATMENT

1. *Echinosepala alexandrae* (Schltr.) Pupulin & Bogarín, *comb. nov.*

Basionym: *Pleurothallis alexandrae* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 103. 1923. TYPE: COSTA RICA. [San José: Cerro el] Tablazo, 1900 m, blühend im Juli 1909, A. Brade & C. Brade 1159 (Holotype: B, destroyed; Neotype: designated here, tracings of Schlechter's drawings of the habit and floral analysis, mounted on the same sheet, AMES 00074034, Fig. 5A–B). Fig. 6–7 (Vouchers: Bogarín 5755, JBL, and Bogarín 4678, JBL).

Heterotypic synonyms: *Pleurothallis sempergemmata* Luer, Selbyana 3(3–4): 386. 1977. TYPE: PANAMA. Chiriquí: epiphytic in forested valley above Guadalupe, alt. 2200 m, 17 Dec 1976, C. Luer 1360, A. Luer, R. Dressler, N. Williams & F. L. Stevenson (Holotype: SEL).

Myoxanthus sempergemmatum (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 38. 1986.

Echinella sempergemmata (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg.*

Echinosepala sempergemmata (Luer) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Brenesia sempergemmata (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, caespitose, erect *herb* up to 30 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, thicker in the distal portion, 5–13 cm long, homoblastic, composed by 5–8 internodes different in length, completely enclosed by 6–8 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the apex, 1.8–5.2 × 0.8–1.5 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, narrowly elliptic to lanceolate-elliptic, subacute to acute, minutely emarginate at apex, 12–20 × 2.6–5.0 cm, the midvein distinctly protruding abaxially. *Inflorescence* a fascicle of single, successive (or few simultaneous) flowers produced from a quickly degrading spathe at the apex of the ramicaul; the peduncle terete, suberect to prostrate, glabrous to minutely puberulous, 2.0–3.2 mm long. *Floral bract* papyraceous, inflated, lanceolate, acute, ca. 1.0–1.8 cm long.

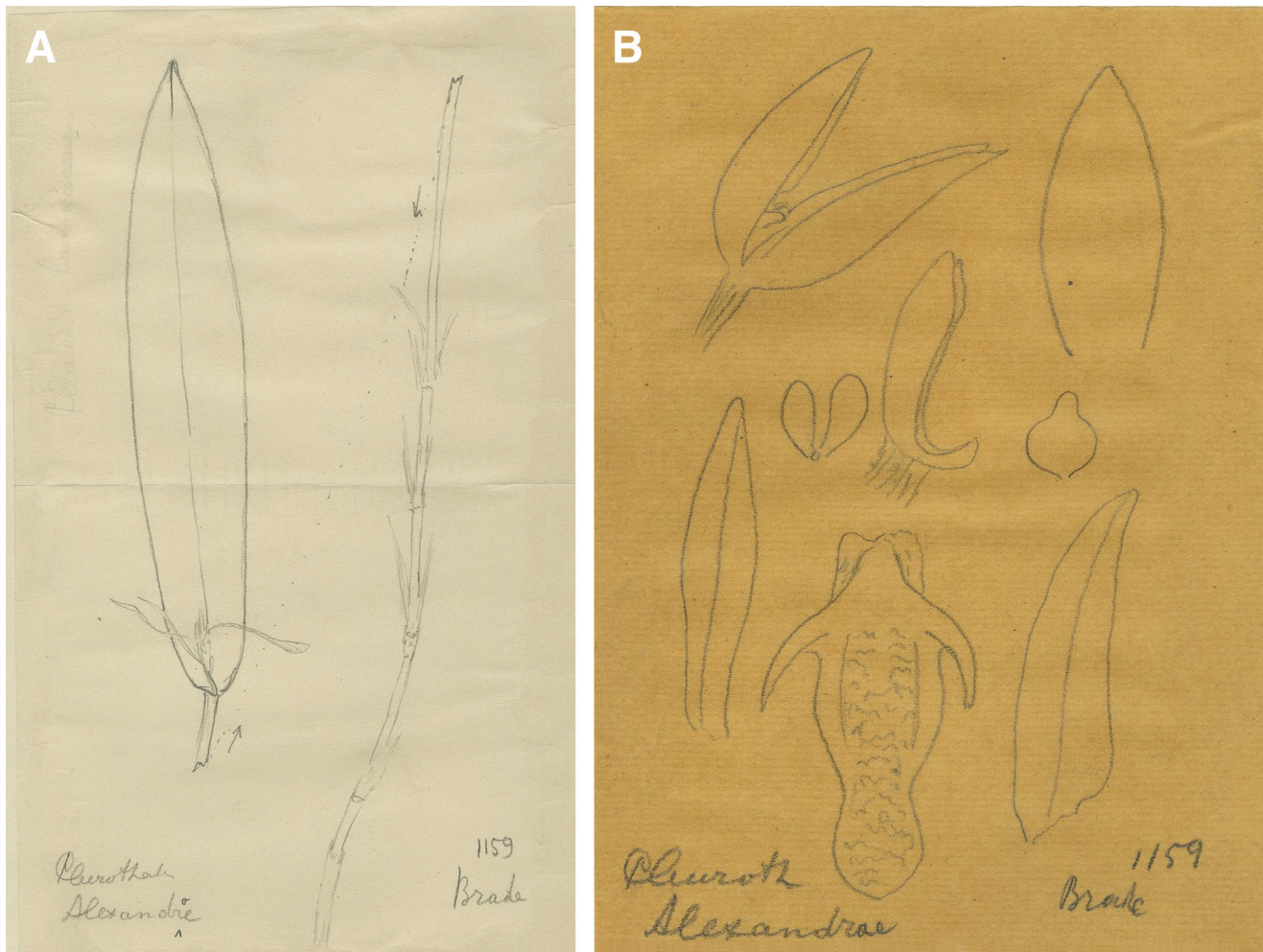


FIGURE 5. Neotype of *Pleurothallis alexandrae*. **A**, habit; **B**, flower analysis. Tracings of Schlechter's original illustrations based on the original collection A. Brade & C. Brade 1159 (AMES 00074034). Reproduced with the kind permission of the Curator, Oakes Ames Orchid Herbarium, Harvard University Herbaria.

Pedicel terete, 0.8–1.0 cm long; *ovary* linear-subclavate, to 7 mm long, papillous-puberulous, the short warts apically provided with a tuft of stiff, somewhat stellate bristles. *Flowers* bilabiate, autogamous, mostly cleistogamous and quickly developing into a fruit before reaching anthesis; when opening, the flowers self-pollinating during the first or second day of anthesis, if flowering more than one day, without temporal activity of the perianth; the sepals light to dull green, the adaxial basal half blotched and spotted purple-brown, abaxially striped with pale purple; the petals yellow, blotched with purple-red, sparsely verrucose; the lip purple-red. *Sepals* fleshy, densely and shortly stellate-puberulous on the abaxial side; *dorsal sepal* lanceolate-oblong, concave, narrowly obtuse, 14–18 × 6–8 mm, 5-veined, the inner surface glabrous, abaxially densely warty-pubescent, the warts apically provided with a stellate tuft of short hairs; *lateral sepals* connate into an ovate, obtuse to shortly bifid, abaxially warty-pubescent synsepal, the warts terminating with a stellate tuft of short hairs, 15–19 × 10–12 mm, each half 3-veined, the apices sometimes free to about 1 mm. *Petals* fleshy, elliptic-lanceolate to oblong-

lanceolate, obliquely asymmetric, narrowly obtuse to acute, 7–10 × 2.5–3.0 mm, 3-veined. *Lip* 3-lobed, ovate-elliptic, pandurate, from a small, thin, rectangular, white-hyaline claw, 7.2–8.0 × 2.8–3.1 mm (5.5 mm across the lateral lobes), the base subtruncate; the apical lobe elliptic to ovate-elliptic, obtuse, the margins more or less incurved, provided at the base with a pair of intramarginal, thin, crenulate keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly triangular-uncinate, antrorse; the disc with an erect, tall, broad, glabrous laminar callus. *Column* subarcuate, semiterete, ca. 8 mm long, provided with thickened, small, elliptic wings above the middle, the foot ca. 1 mm long. *Anther cap* ovate, cucullate, with long, stiff apical hairs, 2-celled. *Pollinia* 2, ovoid, flattened, on a short bifid caudicle. Fig. 2A–B.

Eponymy: named in honor of Rudolf Schlechter's wife, Alexandra, née Sobenikoff.

Distribution: Costa Rica to central Panama (Cerro Campana).

Ecology: in Costa Rica, *Echinosepala alexandrae* is an uncommon epiphyte, seemingly restricted to the Caribbean,

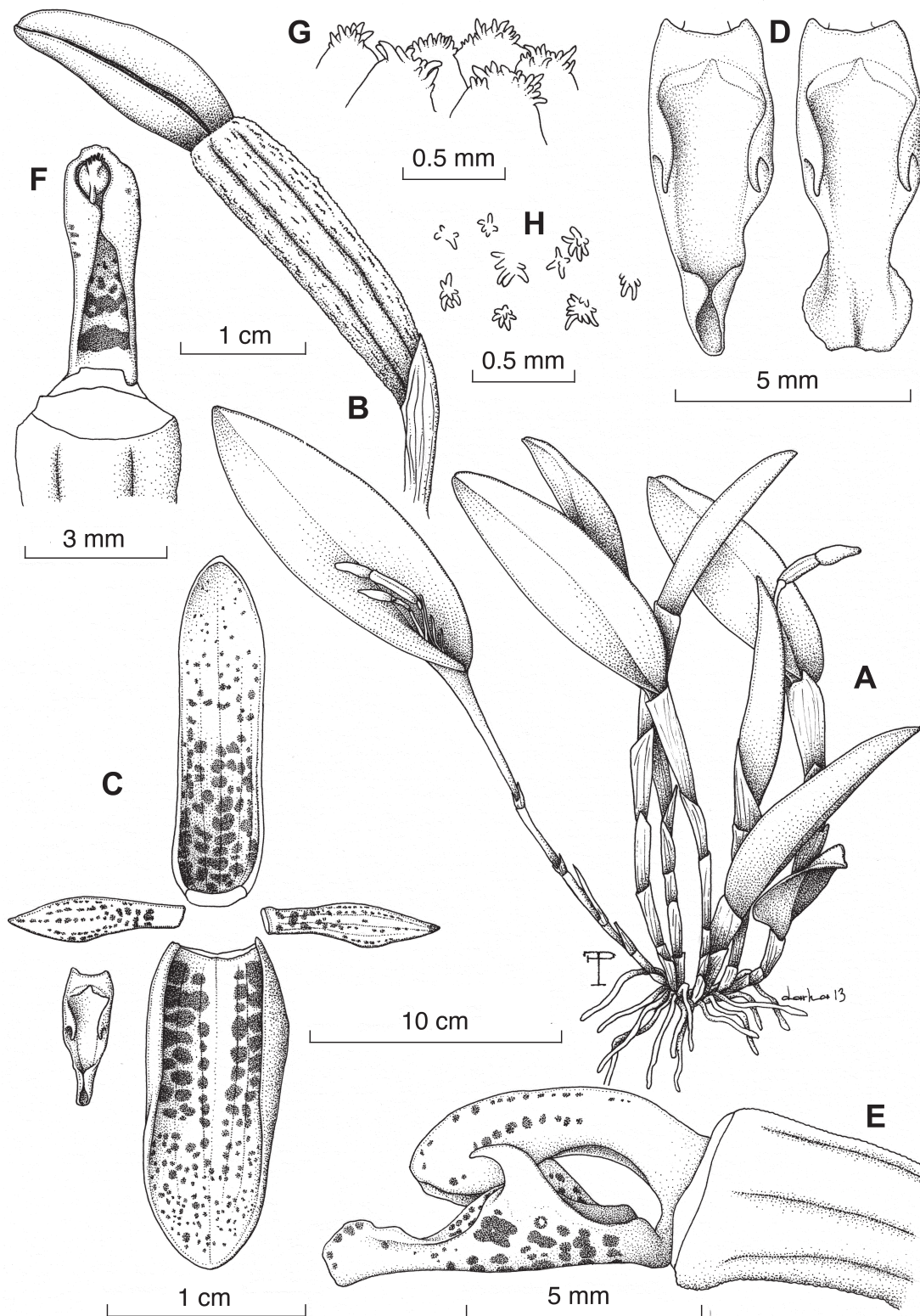


FIGURE 6. *Echinosepala alexandrae* (Schltr.) Pupulin & Bogarín. **A**, habit; **B**, developing ovary and flower remnants; **C**, dissected perianth; **D**, lip, ventral view (the apical lobe in natural position and spread); **E**, column and lip, lateral view; **F**, column of self-pollinated flower, ventral view; **G–H**, details of the ovary indumentum. Drawn from *Bogarín 5775* by F. Pupulin and D. Solano Ulate.

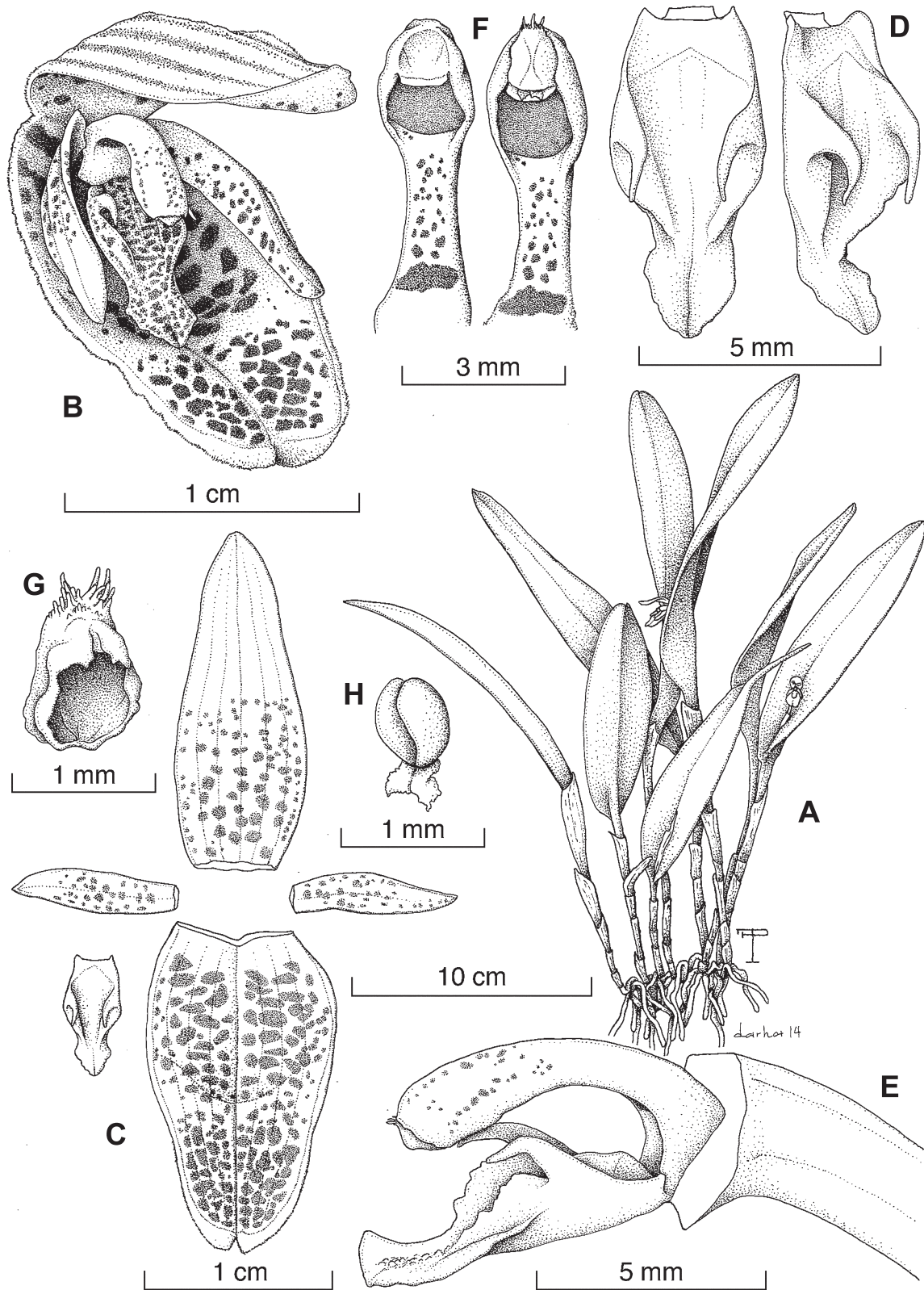


FIGURE 7. *Echinosepala alexandrae* (Schltr.) Pupulin & Bogarín. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip in ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column in ventral view (emasculate on the left); **G**, anther cap; **H**, pollinarium. Drawn from Bogarín 4678 by F. Pupulin and D. Solano Ulate.

submontane wet forests of the Tilarán, Central Volcanic, and Talamanca mountain ranges, at elevations between 1400 and 2600 m. The species mostly flower during the months of July–August, but sporadic flowering has been recorded from November to February.

Distinguishing features: the large plants with large, coriaceous leaves, the flowers buds quickly developing into fruits before or immediately after anthesis, the stellate appearance of the bristles covering the ovary and the abaxial surface of the sepals, and the elliptic-pandurate lip with the apical lobe narrow and with incurved margins distinguish this species.

The specific epithet *alexandrae*, created by Schlechter to honor his wife and conferred to a species of “*Pleurothallis*” collected in Costa Rica by the Brade brothers, is the first available name for the species that Carl Luer described in 1977 as *Pleurothallis sempergemmata* on the basis of a collection from Chiriquí, Panama (Luer, 1977). The type of *P. alexandrae* was lost during the bombing of the Berlin Herbarium in 1943, but fortunately Oakes Ames at Harvard University had Schlechter’s drawings traced for his own files before they were destroyed. The two sketches that Luer (1995) selected as the species lectotype show the large habit typical of the species, and the pandurate lip with a tall basal callus—with no pseudoglenion—and a small apical lobe, which are characteristic of *Echinosepala alexandrae* and its synonym *P. sempergemmata*. Even though Luer (1992) thought that *P. alexandrae* was a name for one of Endrés’s detailed illustrations of *Echinosepala* (W0021295) on the basis of material collected in Costa Rica (*Endrés s.n.*, *Restrepia* 156, W0021295, W18890142222), which he treated as *Myoxanthus aspicensis*, the two species are only superficially similar. Endrés’s illustration in Vienna (reproduced in Ossenbach et al., 2013: 173, fig. 171) depicts a species hereafter treated as *E. glenioides*, which has a horseshoe-shaped structure on the top of the basal callus (pseudoglenion), whereas *E. alexandrae* has a massive, tall plate-like callus without a pseudoglenion, similar to that of *E. isthmica*, to which it is phylogenetically related.

In his treatment of the Orchidaceae for the *Flora of Panama*, Williams (1946) dubitatively included *Pleurothallis alexandrae* in synonymy with *P. uncinata*, and this induced Dressler (1981) to retain this name, based on Costa Rican populations, for a Panamanian species distinct from *P. uncinata*. However, what Williams considers as possibly different from *Echinosepala uncinata* sensu lato—a collection by Cope from el Valle de Antón (Coclé)—cannot be *E. alexandrae*, because Williams describes the callus of this specimen as “prominent retrorse [...] and membranaceous at the base of the side lobes” (Williams, 1946), that is, provided with a pseudoglenion, a feature that is lacking in the true *E. alexandrae*. Bogarín, Serracín, Samudio, Rincón, et al. (2014) correctly recognize the affinity of this species, treating it as *E. aspicensis* (or *E. glenioides*, according to the present treatment). Also, Luer (1976) interpreted as *P. alexandrae* a species locally common in Panama, ranging south to Venezuela and possibly Colombia. He correctly stated that *P. alexandrae* is closely allied to *P. uncinata*, but

the specimen he illustrated (Luer, 1976: fig. 125, likely from Veraguas), does not match Schlechter’s concept however, as it clearly presents a lip with a basal pseudoglenion, and we interpret it as the species described hereafter as *E. glenioides*. Luer (1976) also compared the supposed *P. alexandrae* with his *P. pastacensis*, described from an Ecuadorean collection (Luer, 1976: 156, fig. 181), which in fact also belongs to the group of species provided with a pseudoglenion and has been treated as conspecific with *E. aspicensis* (e.g., Luer, 1986; Renner et al., 1990; Vásquez and Ibsch, 2000; Luer, 1992, 1995; Jørgensen and León-Yáñez, 1999; Pupulin, 2002; Bogarín, Serracín, Samudio, Rincón, et al., 2014; Jørgensen et al., 2014; Kolanowska, 2014). Even though it has been treated under several names, for example, *P. pastacensis* (Luer 1976) and *Myoxanthus pastacensis* (Luer) Luer (Luer, 1986), and as a synonym of *Brenesia aspicensis* (Jørgensen et al., 2014), *Echinella aspicensis* (Pupulin, 2002), *Echinosepala aspicensis* (Bogarín, Serracín, Samudio, Rincón, et al., 2014), *M. aspicensis* (Luer, 1992; Renner et al., 1990), and *P. aspicensis* (Luer, 1995; Jørgensen et al., 1999; Vásquez and Ibsch, 2000), we consider it a distinct and good species. As it lacks specific recognition as a member of *Echinosepala*, we propose it here:

Echinosepala pastacensis* (Luer) Pupulin, *comb. nov.

Basionym: *Pleurothallis pastacensis* Luer, *Selbyana* 3(1/2): 156. 1976. TYPE: ECUADOR. Pastaza: epiphytic in felled tree 20 km east of Puyo, 1000 m, 19 Mar 1976, C. Luer 949, J. Luer & P. Taylor (Holotype: SEL).

To prevent possible claims of confusion between *Pleurothallis alexandrae* Schltr. (1923) and *P. alexandri* Schltr. (1922), we would like to emphasize that the names are different, were created to honor different people, and refer to different species. Both are therefore legitimate as they are not likely to be confused under Article 53 of the International Code of Nomenclature (Turland et al., 2018).

Costa Rican material examined: Cartago: Alvarado, Cervantes, Parque Nacional Tapantí-Macizo Cerro de la Muerte, Sendero Arboles Caidos, 9.9016667, -83.7908333, 20 Aug 1992, J. F. Morales 415, V. Nilsson & R. Chacón Coto (CR). Macizo de la Muerte, southern Panamerican Highway, km 47, Palo Verde, epiphytic on large trees, remnants of primary and secondary vegetation, lower montane wet forest, 2000 m, Nov 2011, F. Pupulin 4284, E. Salas, H. León-Páez & A. C. Rodríguez (JBL). El Guarco, San Isidro, Casa Mata, Carretera Panamericana Sur, km 47, Palo Verde, 2000 m, 16 Nov 2002, F. Pupulin 4284, E. Salas, H. Montealegre & E. Salas (JBL). El Guarco, San Isidro, Casa Mata, Carretera Interamericana, km 40, desvío a San Cristóbal Norte, epífitas en árboles a orillas de la calle, bosque muy húmedo montano bajo, 9°46'32.21"N 83°56'34.40"W, 1869 m, 24 Apr 2008, D. Bogarín 4601, A. Karremans, Y. Kisel & R. Phillips (JBL). El Guarco, San Isidro, Madreselva, Tres de Junio, Carretera Interamericana Sur, km 66, entrada a la finca El Jaular, 9°40'11.7"N 83°51'55.9"W, 2609 m, bosque pluvial montano, en bosque secundario a la entrada de la finca, 24 Apr 2008, D. Bogarín

4678, *A. Karremans, Y. Kisel & R. Phillips* (JBL). El Guarco, El Empalme, Carretera Interamericana, Cartago to Cerro de La Muerte, km 66, epiphytic in roadside trees, 9°42'N 83°56'W, 2545 m, 23 Jul 2003, *M. Whitten 2153, M.A. Blanco & D. Bogarín* (JBL). Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque, 9°48'36.7"N 83°45'16.2"W, 1396 m, 24 Nov 2008, *D. Bogarín 5775, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Turrialba, Santa Cruz–Santa Teresita, Guayabo Arriba, Torito, 50 m después del Caño Seco, en árboles solitarios del potrero de los Mesén, 10°00'06.23"N 83°41'47.85"W, 1470 m, 18 Dec. 2010, *A. P. Karremans 3499 & M. Contreras Fernandez* (JBL). **Guanacaste:** Monteverde Reserve, 1500 m, 13 Jul 1992, *S. Ingram 1515, K. Ferrell & N. Edmondson* (SEL). **Heredia:** Cerro Chompipe, 2300 m, 27 Aug 1997, *R. L. Dressler s.n. & D. E. Mora* (JBL). San Rafael, Reserva Biológica “El Chompipe,” 2000–2050 m, 9 Aug 1991, *S. Ingram 843 & K. Ferrell* (SEL). **San José:** Cerro El Tablazo, 1900 m, fl. Jul 1909, *A. Brade & C. Brade 1159* (drawings, AMES).

2. *Echinosepala expolita* Pupulin & Belfort, *Lankesteriana* 17(2): 294. 2017. TYPE: Costa Rica. Alajuela: San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10°08'58.7"N 84°34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, 19 February 2008 *F. Pupulin 7030, R. L. Dressler & A. P. Karremans* (Holotype: JBL; Isotype: JBL). Fig. 8 (Voucher: *Pupulin 7030*, JBL).

Epiphytic, caespitose, erect herb up to 35 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, thicker in the distal portion, 6.0–12.5 cm long, homoblastic, composed of 5 internodes different in length, completely enclosed by 3–5 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.4–7.7 × 0.20–0.85 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, coriaceous, linear-elliptic, subacute, minutely emarginate at apex, 16.2–27.0 × 1.8–2.4 cm, with the midvein strongly protruding abaxially. *Inflorescence* a fascicle of single, successive flowers produced facultatively at the apex and the base of the ramicaul at once; the peduncle terete-subclavate, erect, glabrous, 1.8–2.5 cm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 1.8–2.4 cm long. *Pedicele* terete-subclavate, 1.8–2.5 mm long; *ovary* lanate-hirsute, completely covered by the bract, linear-subclavate, 3 mm long. *Flowers* bilabiate, with temporal activity, fully opening during the morning and closing in late afternoon; the sepals light greenish-yellow, with the adaxial basal half mottled purple-red and the distal half with pointed warts becoming denser toward the apex, abaxially flushed purple and densely warty-pubescent; the petals yellow, blotched with purple-red, sparsely verrucose; the lip dark purple, apically covered with a translucent wax in fresh flowers. *Dorsal sepal* elliptic-oblong, 0.4–0.9 × 1.9–2.0 cm, 7- to 9-veined, showing a semitransparent base, forming a window under the dark purple-red blotches, tomentose abaxially, adaxially

provided with spiny warts in the apical half. *Lateral sepals* connate into an elliptic, abaxially tomentose synsepal, 0.6–1.7 × 0.4–1.0 cm, each half 5-veined, the apices free about 6 mm, subacute-rounded, with pointed-spiny warts in the distal half. *Petals* fleshy, rhombic, obliquely asymmetric, acute, 6–7 × 1–3 mm, 3-veined, apically provided with spiny warts. *Lip* 3-lobed, narrowly elliptic from a small, rounded, thin, dark purple claw, 7.5 × 2.2 mm (5.0 mm across the lateral lobes), the base subtruncate; the apical lobe rounded-truncate, thickened at apex into a cushion-like, elliptic, low pad, provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc, more prominent to the base of the disk; lateral lobes erect, narrowly lanceolate, antrorse; the disc with an erect, narrow callus arising above the base the lip, covered on top by a horseshoe-shaped, channeled pseudoglenion extending in front into a low keel flushing into the apical pad. *Column* straight to subarcuate, semiterete, 4.4–5.5 mm long, provided with narrow, uncinat wings above the middle, the foot ca. 2.3 mm long. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bifid caudicle. Fig. 2C–D.

Etymology: from the Latin *expolitus*, shining, glossy, in allusion to the glossy apex of the lip in the fresh flowers.

Distribution: known only from the Caribbean watershed of the Cordillera de Tilarán in central Costa Rica.

Ecology: epiphytic in tropical, transition to premontane, and premontane wet forests along the Caribbean watershed of the Cordillera de Tilarán, at 800–1300 m elevation. Flowering has been recorded at least from March to June, and in November, but probably plants may flower at any time of the year. Flowers show temporal activity, fully opening during the morning and closing in late afternoon; usually they are almost to completely closed in the evening. During anthesis they emit a subtle but pungent smell, reminiscent of urea. The breakdown of urea to ammonia and carbon dioxide is known to lure insects, particularly certain flies.

Distinguishing features: the species may be distinguished by the large plants with narrowly lanceolate leaves longer than the subtending ramicauls, the inflorescences produced both at the apex and from one of the lower nodes of the stem, the lanate-hirsute ovary, and the large flower with the abaxial side of the sepals tomentose.

Florally, *Echinosepala expolita* is similar to *E. pan*, to which it appears related in the phylogenetic reconstruction, and from which it can be distinguished by the glabrous, inflated sheaths that cover the stem (vs. hirsute, tight), the distinctly broader ligulate-lanceolate leaves (vs. narrowly lanceolate), the lanate-hirsute ovary (vs. echinate), the much larger flower (sepals >15 mm vs. <10 mm long), and the tomentose abaxial indumentum of the sepals (vs. hirsute-echinate). At anthesis and in fresh flowers, the adaxial surface of the lip is covered with a translucent wax exudate, apparently produced within the basal pseudoglenion, which becomes progressively matte until the lip appears dry during the last days of anthesis.

The plant architecture of *Echinosepala expolita* is similar to *E. aspasicensis*, but the basal inflorescences distinguish the two species, also in sterile material. The inflorescences

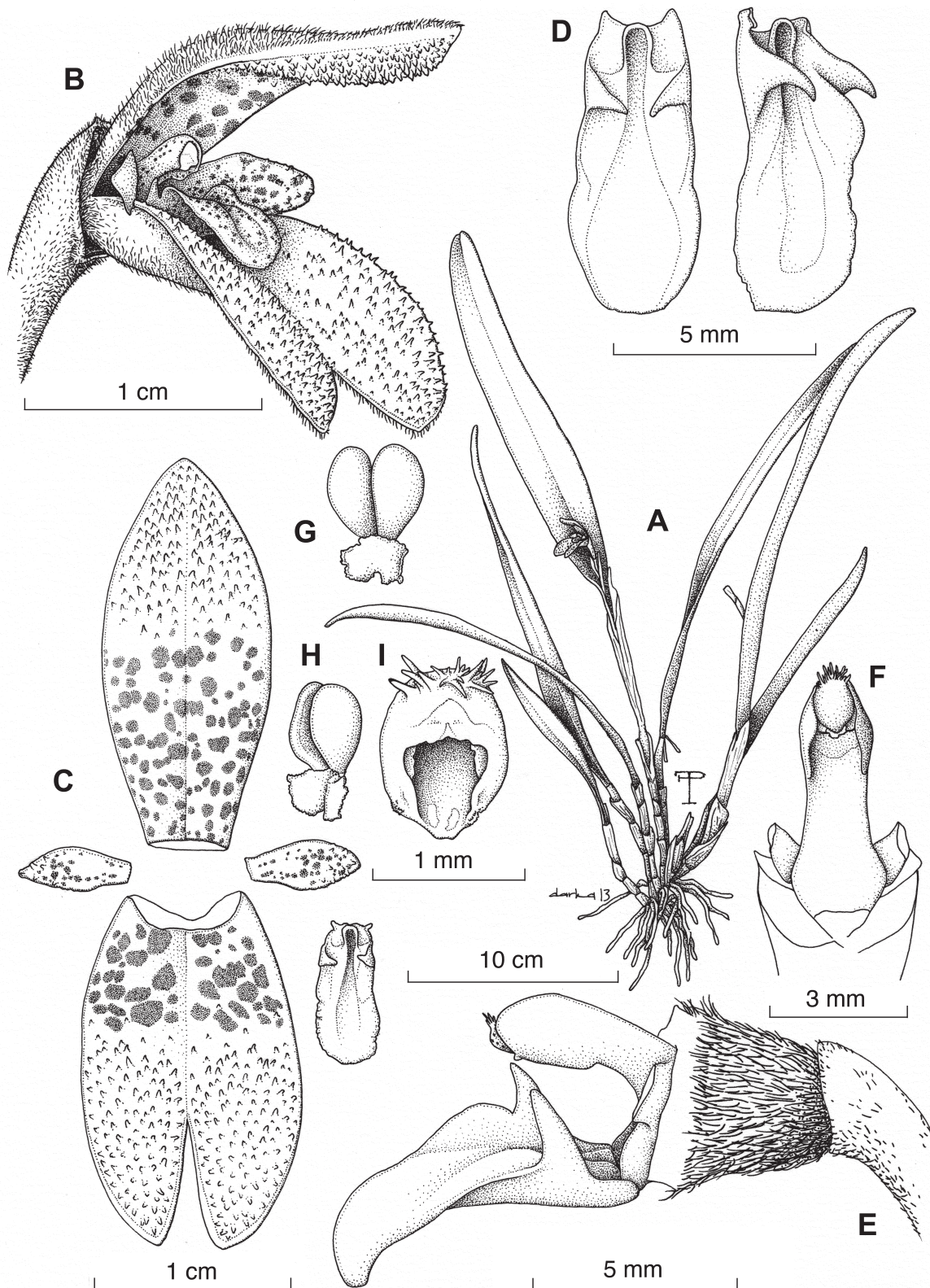


FIGURE 8. *Echinosepala expolita* Pupulin & Belfort. A, habit; B, flower; C, dissected perianth; D, lip in ventral and three-quarters views; E, column and lip, lateral view; F, column in ventral view; G–H, pollinarium (two views); I, anther cap. Drawn from *Pupulin 7030* by F. Pupulin and D. Solano Ulate.

produced from a lower node of the stem may have originated twice independently (in the *E. expolita* + *E. pan* clade and the clade of *E. stonei*). Alternatively, it may have evolved only once, with one or two reversals to the ancestral state (apical inflorescence). Either scenario indicates that species with basal inflorescence do not form a monophyletic group in *Echinosepala*.

Costa Rican material examined: **Alajuela:** San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10°08'58.7"N 84°34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, 19 February 2008 *F. Pupulin 7030*, *R. L. Dressler & A. P. Karremans* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06"N 84°36'11"W, 850 m, bosque muy húmedo tropical transición a premontano, sobre el Sendero La Catarata, epífitas en borde de bosque secundario a orillas del Río San Lorencito, 24 setiembre 2005, *D. Bogarín 1871* (JBL). San Ramón, Piedades S[ur] de San Ramón, Cerros de Laguna, 1190 m, 7 Nov 1922, *A. M. Brenes 26219* (*425 Herb. Brenes*) (CR). San Ramón, Cordillera de Tilarán, cerca a Balsa, ca. 12 km NE de San Ramón, 10°10'30"N 80°30'30"W, 1100 m, 18 June 1995. Epífita a 2 m. Flores grises con manchas moradas y rayos blanco-hueso, suculentas, *B. Hammel 19870* (CR).

3. *Echinosepala glenioides* Pupulin, *sp. nov.*

TYPE: Costa Rica. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, camino entre el portón del Mirador hacia el Río Humo, Proyecto Hidroeléctrico Tapantí, 9°41'32.9"N 83°47'03.2"W, 1650 m, bosque pluvial premontano "*supra arbores et ad truncos prostratos vetustos ad sylvarum versuras ad viam flumen Humo in Tapantí,*" 18 Nov 2010, *D. Bogarín 8211*, *R. Gómez*, *A. Karremans*, *B. Klein*, *G. Meza & F. Pupulin* (Holotype: JBL). Fig. 9 (Voucher: *Bogarín 8211*, JBL).

Species Echinosepala aspasicensis (Rchb.f.) Pridgeon & M.W. Chase *similis sed ovario glabro versus pubescentem, sepalo postico anguste obovato versus oblongo-lanceum, petalis obrullatis versus falcata, labello obrullato rotundato versus ligulatum attenuatum retusum, columna dimidio longa quam labello versus aequilongam recedit.*

Epiphytic, caespitose, erect herb up to 50 cm tall. *Roots* coarse, flexuous, 1.3–2.0 mm in diam. *Ramicauls* stout, erect, rarely subpendent, terete, thicker in the distal portion, 10.0–22.5 cm long, homoblastic, composed of 4–6 internodes different in length, completely enclosed by 4–6 papyraceous, tubular, ancipitous, loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.5–9.0 × 0.3–1.0 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, ligulate to oblong-elliptic, subacute, minutely emarginate at apex, 16–29 × 1.9–3.3 cm, with the midvein strongly protruding abaxially and the lateral veins also faintly visible on both sides. *Inflorescence* a fascicle of single, successive flowers produced at the apex of the ramicaul; the peduncle terete-subclavate, erect, microscopically pubescent, 1.0–2.2 mm long. *Floral bract* papyraceous, loose, obliquely obtuse, longer than the pedicel, 2.2–3.2 cm long. *Pedicel* terete-subclavate, ca. 5 mm long; *ovary* terete, linear-subclavate, glabrous, ca. 5 mm long. *Flowers* bilabiate, mostly ringent,

with temporal activity, fully opening during the morning and closing in late afternoon; the sepals light greenish-yellow, the dorsal semitransparent-fenestrate at the base, mottled purple-maroon particularly on the basal half, the dots and blotches more or less aligned with the veins, abaxially flushed purple and densely warty-pubescent; the petals dull yellow, heavily blotched or boldly striped with purple-maroon; the lip purple-red, apically covered with a translucent wax in fresh flowers; the column yellow, flecked with purple. *Dorsal sepal* oblanceolate to narrowly obovate, subobtusate, reclinate, rarely erect, 2.1–2.6 × 0.7–0.9 cm, 5-veined, with a semitransparent base, forming a window under the dark purple-red blotches, shortly and sparsely pubescent abaxially, adaxially provided with low warts in the apical half. *Lateral sepals* connate into an elliptic, obtuse, shortly bifid, abaxially shortly and sparsely pubescent synsepal, 1.80–2.20 × 0.9–1.1 cm, each half 4-veined, the apices free about 1 mm, with low rounded warts in the distal half. *Petals* fleshy, obrullate, acute, 6–7 × 1.6–2.0 mm, 3-veined. *Lip* 3-lobed, elliptic-subrhombic from a small, rectangular, thin, hyaline claw, 7.0–8.0 × 2.3–2.6 mm (ca. 5 mm across the lateral lobes), the base truncate with two short, digitate-conical, retrorse auricles; the apical lobe ovate, acute, minutely rounded, the apex with sparse warts, provided with a pair of intramarginal, thin, rounded keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinat-acuminate, antrorse; the disc with an erect, narrow callus arising above the base the lip, covered on the top by a horseshoe-shaped pseudoglenion, channeled in front up to the apical lobe. *Column* subarcuate, terete, 5 mm long, provided with narrow, elliptic, stigmatic wings above the middle, the foot ca. 1 mm long. *Anther cap* globose, subspherical, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, pyriform, on a broad, obreniform, bifid caudicle. Fig. 2E–F.

Etymology: from the words *glene*, the Greek for “socket or eyeball,” and the suffix *-oides*, from the Greek εἶδος (*éidos*, “likeness”), to suggest the imperfect resemblance of the ornamentation at the base of the callus with the glenion of other groups of Pleurothallidinae. The pseudoglenion is apparently an ancestral character in *Echinosepala*, as it has been recorded in both the basal *E. vittata* + *E. tomentosa* clade and in the clade including *E. glenioides* + *E. longipedunculata* and *E. expolita* + *E. pan*, whereas it is absent in the derived clades of *E. lappiformis* + *E. stonei* and *E. alexandrae* + *E. uncinata*.

Distribution: known at least from central Costa Rica to the Chiriquí province in western Panama, perhaps ranging to central Panama.

Ecology: an epiphyte of the large branches and trunks of trees in pristine and mature vegetation, *Echinosepala glenioides* is apparently restricted to the premontane and lower montane wet forests along the Caribbean watershed of the Costa Rican cordilleras, ranging from the Tilarán mountain chain southward to the cordillera of Talamanca, at elevations between 850 and 2000 m. Flowering mostly occurs from July to September, but sporadic flowering has been recorded as early as May.

Distinguishing features: the large plant (the largest of the genus in Costa Rica), with almost linear-ligulate leaves,

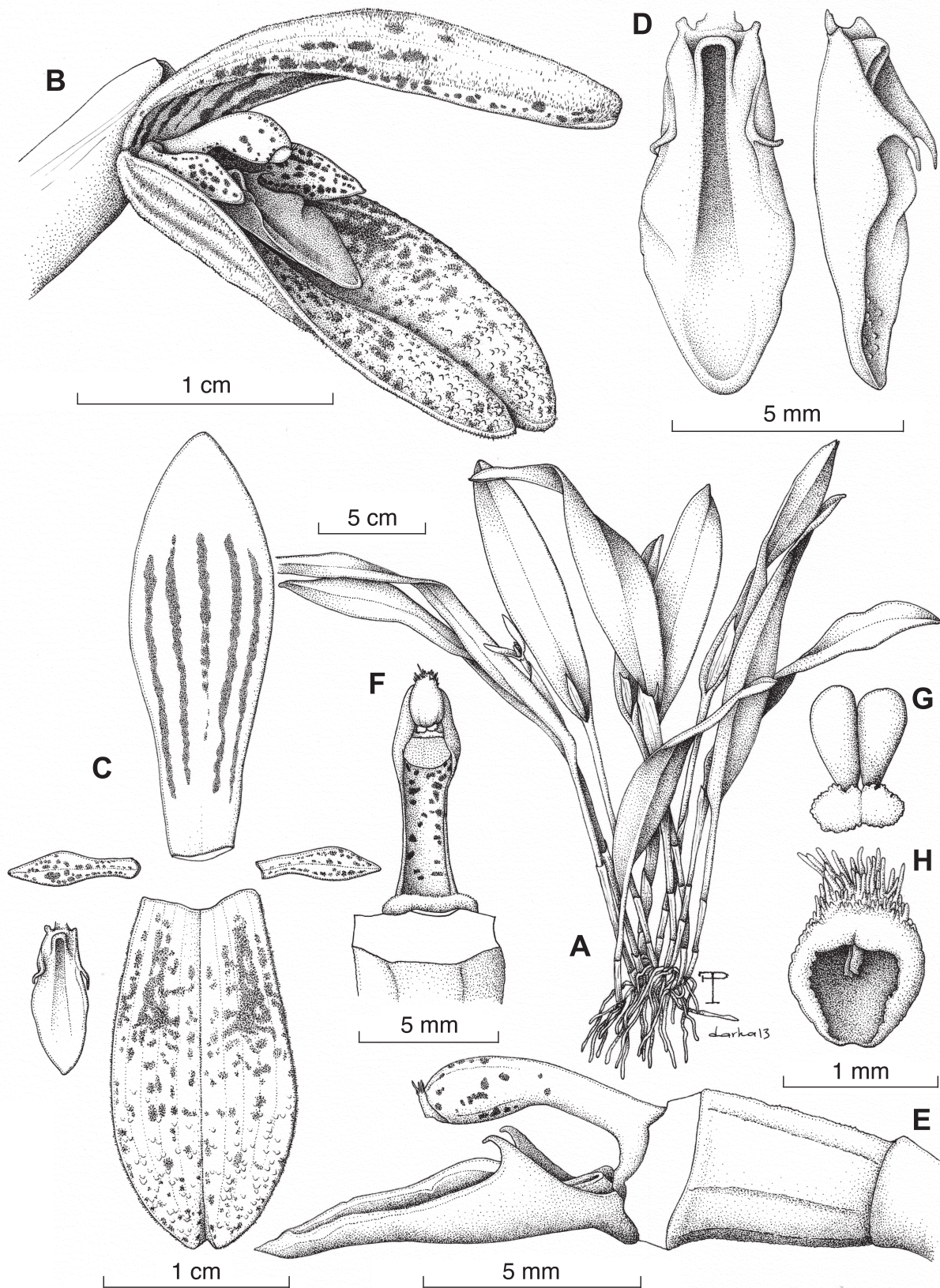


FIGURE 9. *Echinosepala glenioides* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip in ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column in ventral view; **G**, pollinarium; **H**, anther cap. Drawn from *Bogarin 8211* by F. Pupulin and D. Solano Ulate.

the glabrous ovary, the large flowers (with sepals over 2.5 cm long) mostly ringent, the dorsal sepal fenestrate at the base, the long, elliptic-subrhombic lip provided with narrow uncinately lateral lobes, and a basal pseudoglenion distinguish this species among other relatives in Costa Rica.

Populations of *Echinosepala glenioides* have been traditionally treated as the northernmost records of *E. aspasicensis*, originally described from the Colombian Andes (Dressler, 1981, 1993; Luer, 1992, 1995, 2003; Hamer, 2001; Pupulin, 2002; Ossenbach et al., 2010; Bogarín, Serracín, Samudio, Rincón, et al., 2014; Pupulin et al., 2019), a poorly known species allegedly distributed from Costa Rica to Guyana, Brazil, and down to Bolivia along the Andean chain (Luer, 1992). The plant material on which the description of *Pleurothallis aspasicensis* was based had been sent to Reichenbach by Hermann Wager from Caracas, where he was collecting orchids for the firm of Jean Linden (Reichenbach, 1855). The holotype specimen, supposedly among Reichenbach's materials in Vienna, has not been located. Nevertheless, during one of his visits to Lindley, Reichenbach gave him a piece of the original collection, today housed at Kew, which Luer (1992) selected as lectotype. No vegetative parts are included, and the crushed flower lacks the lip, so our understanding of Reichenbach's concept of *P. aspasicensis* is largely based on the original protologue. Several of the features described by Reichenbach prevent the application of this name to Costa Rica populations here described as *E. glenioides*. The leaves were described as lanceolate, versus oblong-ligulate in Costa Rican material; the sepals as "oblongo-lanceis," versus the dorsal sepal distinctly oblanceolate to obovate; the lip apically attenuate and retuse, versus acute in *E. glenioides*; and the column as long as the lip ("gynostemio labello aequilongo"), versus barely half the length of the lip in Costa Rican material.

Florally, *Echinosepala glenioides* is also similar to *Pleurothallis pastacensis* Luer (which has been generally treated as a synonym of *E. aspasicensis*), but it differs from the Ecuadorean taxon by the caespitose habit with narrow leaves (vs. distinctly repent with wider leaves), the 1-flowered inflorescence (vs. simultaneously many-flowered), the distinctly larger flowers, the sparse hairs of the sepals' indumentum (vs. arranged in tufts), and the glabrous midlobe of the lip (vs. verrucose).

Broadly distributed in Costa Rica, *Echinosepala glenioides* is florally variable among populations (Fig. 2E–F). One of the vouchers used for the molecular analyses does not group with the other two accessions of *E. glenioides* (Fig. 1), leaving an open question about the existence in Costa Rica on another, cryptic taxon closely related to *E. glenioides*. We were unable, however, to characterize this genetically distinct individual on the basis of distinguishing morphological features, so given the present status of our knowledge we favored including it within the variation of *E. glenioides*.

Costa Rican material examined: **Alajuela:** San Carlos, Fortuna, volcán Chato, sobre el sendero a la laguna de la cima de volcán, en bosque primario, muy húmedo premontano, 10.4427778 -84.6808333, 27 Jul 2011, A.

P. Karremans 4407 (CR, JBL). San Ramón, Candelaria, March–June 1867, *A. Endrés s.n.* [Restrepia 156] (W). San Ramón, Candelaria, 1867, *A. Endrés s.n.* [Restrepia 156] (W). San Ramón, Piedades, Potrerillos, road to Socorro de Piedades Sur, slopes of Cerro La Palma, premontane wet forest, 10°08'09.9"N 84°34'47.5"W, 1300–1450 m, 12 Apr 2006, *F. Pupulin 6045*, *R. L. Dressler & A. Carbajal* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto Brenes, ascenso por el sendero Saíno, bosque muy húmedo tropical transición a premontano, epífita en bosque secundario, 10°13'08"N 84°35'48"W, 900–1000 m, 25 Sept 2005, *D. Bogarín 1945* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto Brenes, sobre el sendero Pájaro Sombrilla, 10°13'N 84°37'W, 850 m, 3 Oct 2003, *D. Bogarín 436* (JBL). San Ramón, Ángeles, Reserva Río San Lorenzo de UCR, headwaters of the Río San Lorenzo below Fila Volcán Muerte. 10–23 N. 14 Jul 1983, *K. A. Barringer 3783 & B. Pérez* (CR). San Ramón, Ángeles, Balsa, road between San Ramón and La Fortuna de San Carlos, epiphytic on trees in pastures close to Río Balsa, premontane rain forest, 10°10'03.6"N 84°29'35.7"W, 1150 m, 29 May 2013, *F. Pupulin 1150*, *D. Bogarín, M. Díaz, & M. Fernández* (JBL). San Ramón, Ángeles, Ángeles Sur, road 141 to La Fortuna, deviation point on the left to Ángeles Sur, premontane rain forest, epiphytic on scattered trees in pastures along the border of a secondary, mature forest, 10°08'32.78"N 84°29'28.30"W, 1140 m, 22 Apr 2011, *F. Pupulin 8033 & M. Pupulin* (JBL). San Ramón, Santiago, finca of Jesús Salas Jiménez, mountains toward the towers of Berlín, lower montane rain forest, epiphytic in old trees along coffee plantations, 10°02'21"N 84°12'02"W, 1300 m, 30 May 2013, *F. Pupulin 8497*, *D. Bogarín, M. Díaz, & M. Fernández* (JBL). **Cartago:** Orosi, Purisil, Parque Purisil, 1400–1500 m, 15 Feb 2005, *H. León-Páez 92* (JBL). **Heredia:** Heredia–San Rafael, Vara Blanca, 2 km noreste de Alto del Roble, faldas al norte del Cerro Chompipe, Refugio de Vida Silvestre Cerro Dantas, márgenes de la Quebrada Grande, epífitas en bosque secundario, bosque pluvial premontano, 10°05'30.5"N 84°03'51.4"W, 1981 m, 14 Apr. 2005, *D. Bogarín 1521*, *M. G. Gei & A. Vaughan* (JBL). **Limón:** Matina, Batán, Parque Nacional Braulio Carrillo, Carrillo Station, along trail SE of Station, W of Quebrada González, 10.1625 -83.25, 19 Sept 1990, *S. Ingram 530 & K. Ferrell* (CR). **San José:** Vásquez de Coronado, Jesús, Bajo La Hondura, Parque Nacional Braulio Carrillo, camino de la ermita hacia Río Blanco, bosque pluvial premontano, epífitas en árboles a orillas del camino, 10°03'03"N 83°59'14"W, 900–1100 m, 21 Jan 2007, *D. Bogarín 3063*, *R. L. Dressler, F. Pupulin & W. Rossi* (JBL).

4. *Echinosepala isthmica* Pupulin, *sp. nov.*

TYPE: COSTA RICA. Limón: Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10°11'1.5"N 83°28'29.3"W, 627 m, 3 Dec 2008, flowered in cultivation at Lankester Botanical Garden, 29 Sept. 2102, *D. Bogarín 8571*, *R. L. Dressler, R. Gómez & R. Trejos* (Holotype: JBL). Fig. 10 (Voucher: *Bogarín 8571*, JBL).

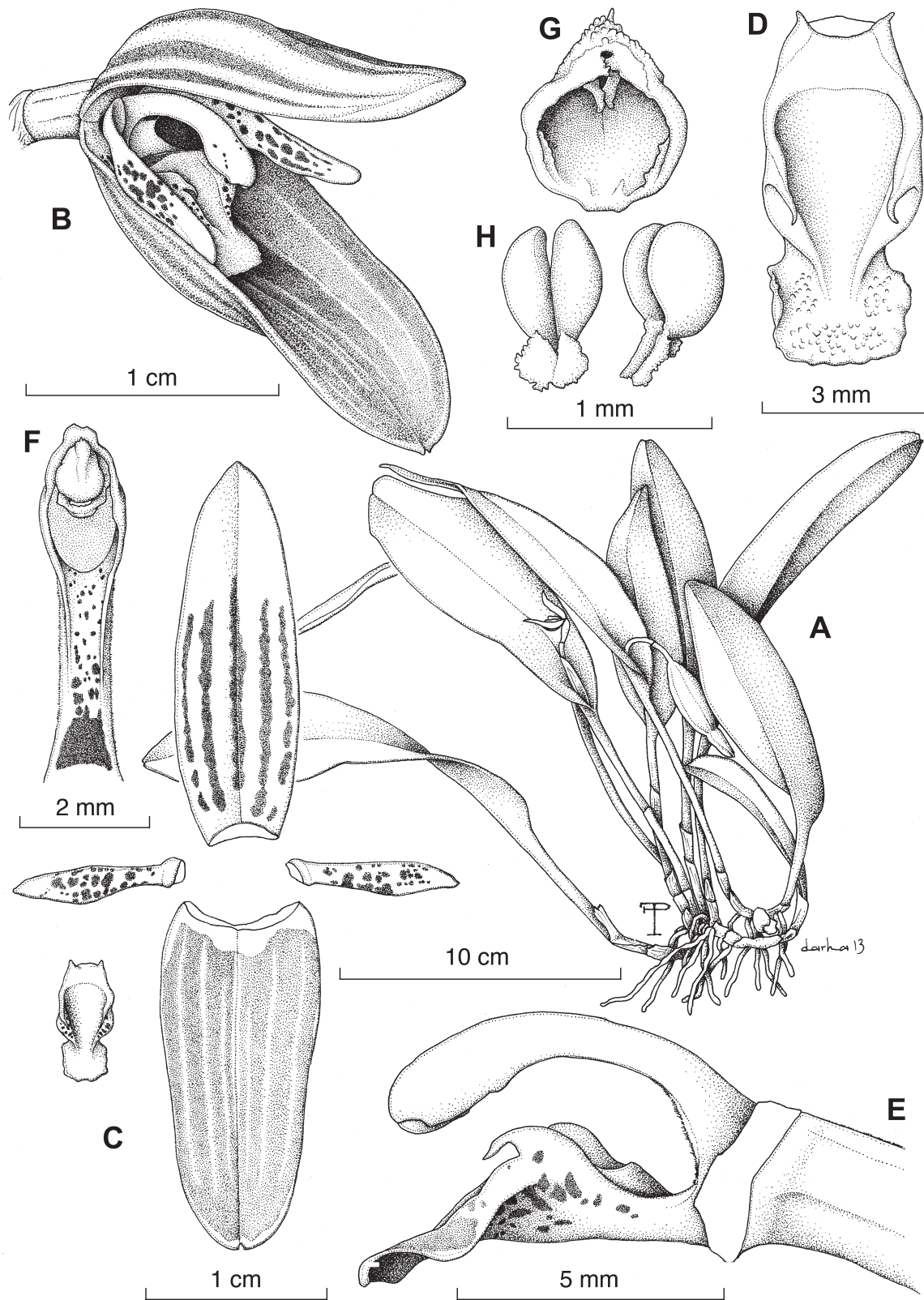


FIGURE 10. *Echinosepala isthmica* Pupulin. A, habit; B, flower; C, dissected perianth; D, lip, ventral view; E, column and lip, lateral view; F, column in ventral view; G, anther cap; H, pollinarium, two views. Drawn from *Bogarin 8571* by F. Pupulin and D. Solano Ulate.

A Echinosepala uncinata (Fawc.) Pridgeon et M.W. Chase *similis, sed caulibus dimidio brevioribus et foliis parvioribus, labello multo brevioribus et latiore, lobo apicali rectangulari vel late obovato integro vs. subrotundatum minute denticulatum, callo basali insignis massivo altoque vs. sublaevem, columna longiore distincte curvata plerumque recedit.*

Epiphytic, caespitose to shortly repent, erect herb up to 25 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, 6.0–13.5 cm long, homoblastic, composed of 5–7 internodes different in length, rarely producing secondary shoots from the apex, completely enclosed by 5–8 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.5–4.6 × 0.3–0.9 cm, eventually disintegrating with age. *Leaf* erect, coriaceous, narrowly ovate to lanceolate-elliptic, acute, minutely emarginate at apex, 13.2–16.0 × 2.2–4.2 cm, the midvein distinctly protruding abaxially. *Inflorescence* a fascicle of single, successive flowers produced at the apex of the ramicaul from a narrowly rectangular, papery, loose, obliquely truncate spathe to about 1.5 cm long; the peduncle terete, prostrate, furfuraceous to minutely and sparsely pubescent, 1.8–2.5 cm long. *Floral bract* papyraceous, loose, triangular, subacute, 1 cm long. *Pedicel* terete-subclavate, 1.8–2.3 mm long; *ovary* sparsely pubescent, completely covered by the bract, linear-subclavate, ca. 5 mm long. *Flowers* bilabiate, not completely spreading, remaining fully opening after anthesis with no temporal activity observed; the sepals greenish-cream, striped to almost solidly mottled purple, subglabrous to sparsely pubescent abaxially; the petals yellow, blotched with purple-red; the lip yellow, densely spotted brown apically, rose-purple, blotched purple at the base, the lateral lobes yellow; the column white, sparsely dotted purple at the apex, flushed yellow basally. *Dorsal sepal* elliptic-lanceolate, acute, 1.3–1.9 × 0.6–0.9 cm, 5-veined, translucent. *Lateral sepals* connate into a narrowly ovate, obtuse to subrounded, minutely excised synsepal, 0.4–1.7 × 1.6–1.7 cm, each half 3-veined, glabrous within. *Petals* fleshy, oblanceolate, obliquely asymmetric, acute, 7–12 × 2–3 mm, 3-veined. *Lip* 3-lobed, subrectangular-pandurate from a small, transversely rectangular, thin, hyaline claw, 6.2–7.3 × 2.5–3.0 mm (5.0 mm across the lateral lobes), the base subtruncate, provided with 2 small, acicular, retrose, pointed auricles; the apical lobe transversely rectangular to broadly obovate, truncate, the margins sometimes subundulate, provided with a pair of intramarginal, thick keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinata, antrorse; the disc with an erect, broad, massive plate-like callus arising above the base of the lip, flushing in front to the base of the midlobe. *Column* arcuate, semiterete, 6.3–7.0 mm long, provided with inconspicuous, elliptic wings above the middle, the foot ca. 1.5 mm long. *Anther cap* globose, cucullate, with short, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, ovoid, laterally flattened, on a short bifid caudicle. Fig. 2G–H.

Etymology: named in reference to the Central American isthmus, where the species ranges at least from Nicaragua southward to Panama.

Distribution: Nicaragua, Costa Rica, Panama, and Colombia.

Ecology: in Costa Rica, *Echinosepala isthmica* has the widest ecologic tolerance, spanning from the tropical forests close to sea level (50 m) to the premontane wet forest at about 1500 m of elevation. The species has been recorded from both the Caribbean watersheds of the continental divide. It mostly flowers from July to September, with sporadic, early flowerings recorded in June.

Distinguishing features: the distinctly lanceolate leaves on a medium-sized plant, the comparatively large, subglabrous to minutely and sparsely tomentose flowers, with the purple blotches of the dorsal sepal arranged in stripes and the synsepal almost solidly purple-maroon, and the rectangular-pandurate lip with the apical lobe broader than long and a massive callus but no pseudoglenion distinguish this species.

Echinosepala isthmica has been treated as conspecific with *E. uncinata* (Williams, 1946; Dressler, 1981, 1993; Luer, 1992, 1995, 2003; Hamer, 1984, 2001; Pupulin, 2002; Ossenbach et al., 2010; Bogarín, Serracín, Samudio, Rincón, et al., 2014), originally described from Jamaica by William Fawcett (1895). Plants of *E. uncinata* are however much larger, approaching in size and appearance those of *E. alexandrae*, with ramicauls reaching almost 25 cm in length (vs. up to 13.5 cm in *E. isthmica*). The flowers are also different. The lip of *E. uncinata* is comparatively longer, with minute denticulations on the margin (vs. rectangular to broadly obovate, entire, in *E. isthmica*), the basal callus is low and narrow (vs. massive, as wide as the hypochile and high), and the column is stout, straight (vs. slender, distinctly curved), more similar to that of *E. alexandrae*. The illustration of *Pleurothallis uncinata* in *Flora of Jamaica* (Fawcett and Rendle, 1910: pl. 10) shows a large plant with several fruits and, if not for the midlobe of the lip as wide as the hypochile, we would have been tempted to consider the native species of Jamaica as the first available name for the Costa Rican and Panamanian populations described later as *P. alexandrae* and *P. sempergemmata*.

Echinosepala isthmica may occasionally produce new vegetative shoots, made up of stem and leaf, and ultimately roots, at the apex of the pseudobulb (e.g., Bogarín 5855; Fig. 11). These adventitious plantlets could eventually detach from the main stem and, on finding the appropriate conditions, form new individuals independent of the mother plant. This form of vegetative reproduction is rare in *Echinosepala*, and up to now it has been observed only in *E. isthmica*, but it is not uncommon in other groups of Pleurothallidinae.

We are not including Belize at this time in the distribution of *E. isthmica*, as the species recorded there by McLeish and colleagues (1995) could well be conspecific with the true *E. uncinata* from the Antilles. Florally, the collection by Adams (no. 253, K) from the Mountain Pine Ridge in Cayo District, Belize, is very close to *E. isthmica*, but the plant is much larger, with ligulate-oblong leaves, quite distinct from populations from Nicaragua southward. The close relationships of the coastal flora of Belize with that of the West Indies are well known, even in the subtribe



FIGURE 11. Adventitious plantlets on the apex of the stem in *Echinosepala isthmica* (Bogarín 5855). Scale bar = 5 cm. Photograph by F. Pupulin.

Pleurothallidinae, and the species has not been recorded so far south of Belize. Populations of *E. uncinata* previously recorded from Nicaragua (Hamer, 1984, 2001; van den Berghe and van den Berghe, 2008) and Caribbean Costa Rica (Atwood, 1987) surely belongs to *E. isthmica*.

Costa Rican material examined: Alajuela: San Ramón: Camino a San Carlos, between Potrero Volio and Legua, July, A. *Endrés s.n.* [*Restrepia* 262] (W). Upala, Bijagua. Parque Nacional Volcán Tenorio, sobre los senderos principales del parque, bosque primario y secundario, 10°42'58.3"N 84°59'33.1"W, 1121 m, 28 Jul 2011, A. P. Karremans 4446 (JBL). Upala, Bijagua. Parque Nacional Volcán Tenorio, sobre los senderos principales del parque. Epífitas en bosque primario, bosque húmedo premontano, 10°42'54"N 84°59'14"W, 686 m, 19 May 2016, A. P. Karremans 7112, N. Davin & J. E. Jiménez (JBL). **Cartago:** Jiménez, Pejibaye, entre Taus y Tausito, Selva, orillas del Río Taus y Quebrada Selva, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 9°47'10.3"N 83°45'37.5"W, 1095 m, 24 Nov 2008, D. Bogarín 5853, R. L. Dressler, R. Gómez & R. Trejos (JBL). Paraíso, Orosi, Tapantí, sobre el camino a Tausito, unos 1.5 km del cruce al Parque Nacional Tapantí, epífitas y semi-terrestres sobre el acantilado al lado de la calle, bosque pluvial premontano, 9°46'18.48"N 83°47'34.36"W, 1412 m, A. P. Karremans 6678 & I. Chinchilla (JBL). Turrialba Santa Cruz–Santa Teresita, Guayabo Arriba, Torito, 50 m después del Caño Seco, en árboles solitarios del potrero de los Mesén, 10°00'06.23"N 83°41'47.85"W, 1470 m, 18 Dec 2010, A. P. Karremans 3199 & M. Contreras Fernandez (JBL). **Heredia:** Sarapiquí, Puerto Viejo, Estación Biológica La Selva, epífitas en ramas caídas, 50 m, 3 Nov 2006, G. Rojas 144 (JBL). **Limón:** Pococí, Guápiles, Hacienda La Cuenca, bosque pluvial premontano, falda norte del Volcán Turrialba, 10°8'7.81"N 83°46'46.2"W, 611 m, 1 Jan 2005, M. A. Blanco 2762, A. Chaves, L. duToit & C. Ugalde (JBL). Pococí, Guápiles, Guápiles, Pocora, La Argentina Sur, márgenes del río Dos Novillos, sendero Las Cataratas, bosque premontano muy húmedo, vegetación primaria madura, 500–700 m, 12 Sept 2004, R. Valverde 1303 (JBL). Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10°01'1.5"N 83°28'29.3"W, 627 m, 3 Dec 2008, D. Bogarín 5853, R. L. Dressler, R. Gómez & R. Trejos (JBL). Same collecting data, D. Bogarín 5871, R. L. Dressler, R. Gómez & R. Trejos (JBL). **Puntarenas:** Buenos Aires, Olán, ascenso por la falda sur del Cerro Tinuk, bosque pluvial premontano, epífita en bosque secundario y primario, 9°17'23.5"N 83°10'33.5"W, 2164 m, 5 Jul 2012, D. Bogarín 9716, E. Herrera, D. Jiménez, A. P. Karremans & V. H. Zúñiga (JBL). **San José:** Pérez Zeledón, Montecarlo, without collector, 20 Sept 1991, JBL-02659 (JBL).

5. *Echinosepala lappiformis* (A. Heller & L.O. Williams) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Basionym: *Pleurothallis lappiformis* A. Heller & L.O. Williams, Fieldiana, Botany 31(2): 42, f. 8. 1964.
TYPE: NICARAGUA. Chontales: epiphytic at

Pistacho Peak near Babilonia Mine, alt. 650 m, Jul 1962, A. Heller 6620 (Holotype: F). Fig. 12 (Voucher, Bogarín 9554, JBL).

Homotypic synonyms: *Myoxanthus lappiformis* (A. Heller & L.O. Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 38. 1986.

Echinella lappiformis (A. Heller & L.O. Williams) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg.*

Brenesia lappiformis (A. Heller & L.O. Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, shortly repent, erect to subprostrate herb up to 25 cm tall. *Roots* coarse, flexuous, ca. 2.0 mm in diam. *Ramicauls* stout, terete, 15–50 mm long, homoblastic, composed of 2–3 nodes, the lower one much shorter, completely enclosed by 3 papyraceous, fibrous, tubular, obtuse, whitish sheaths, increasing in size toward the upper one, to 3 cm long, fragmented with age. *Leaf* thickly coriaceous, elliptic, acute, minutely emarginate, 6–12 × 2–3 cm, cuneate below into a conduplicate, sessile base, the midvein strongly protruding abaxially. *Inflorescence* a single flower emerging from the lower nodes of ramicauls; the peduncle terete, suberect to erect, minutely pubescent, 3–4 mm long, subtended by a fibrous, brown, acute bract ca. 3 mm long. *Floral bract* fibrous-papyraceous, brownish, inflated, obliquely truncate, 7–8 mm long. *Pedicel* obconical, pubescent, 2–3 mm long; *ovary* clavate, purple, 3 mm long, densely long-pubescent to echinate. *Flowers* bilabiate, the dorsal sepals apically connate to the tip of the synsepal, fleshy, nonresupinate, held almost vertically, neither temporal activity of the perianth nor scent detected, bright red-purple, the petals basally white, densely long pubescent-echinate externally, rugose-verrucose within. *Dorsal sepal* narrowly triangular, acute, 17–20 × 4–5 mm, 3-veined. *Lateral sepals* connate to the apex into an obovate, obtuse, concave synsepal, the margins erect, adaxially transversely verruculose, 20–22 × 14–16 mm. *Petals* fleshy, linear-oblong, acute, fleshy, adaxially verrucose in the distal half, 11–12 × 3 mm, 3-veined. *Lip* 3-lobed, elliptic from a thin, rectangular, rose-hyaline claw, 7–8 × 3–4 mm (6 mm across the lateral lobes), the base truncate; the apical lobe ovate, minutely truncate, denticulate, verrucose, provided with a pair of intramarginal, thick, apically verruculose keels running inside the lateral lobes toward the disc; lateral lobes erect, elliptic-subuncinate, antrorse; the disc transversely rugose-sulcate. *Column* straight, semiterete, 6–7 mm long, provided with narrow, rectangular wings above the middle ending at apex into pointed teeth, the foot ca. 1 mm long. *Anther cap* globose, cucullate, with stiff hairs on the upper margin, 2-celled. *Pollinia* 2, ovoid, laterally compressed, on a short bilobed caudicle. Fig. 21.

Etymology: from the Latin *lappa*, “bur,” for the similarity of the flower to a spiny fruit.

Distribution: originally described from Nicaragua (Williams, 1964), the species is reported to range southward to northern South America, where it was recorded from Colombia (Misas Urreta, 2005), Ecuador, and Venezuela (Luer, 1992). We have examined specimens from Nicaragua,

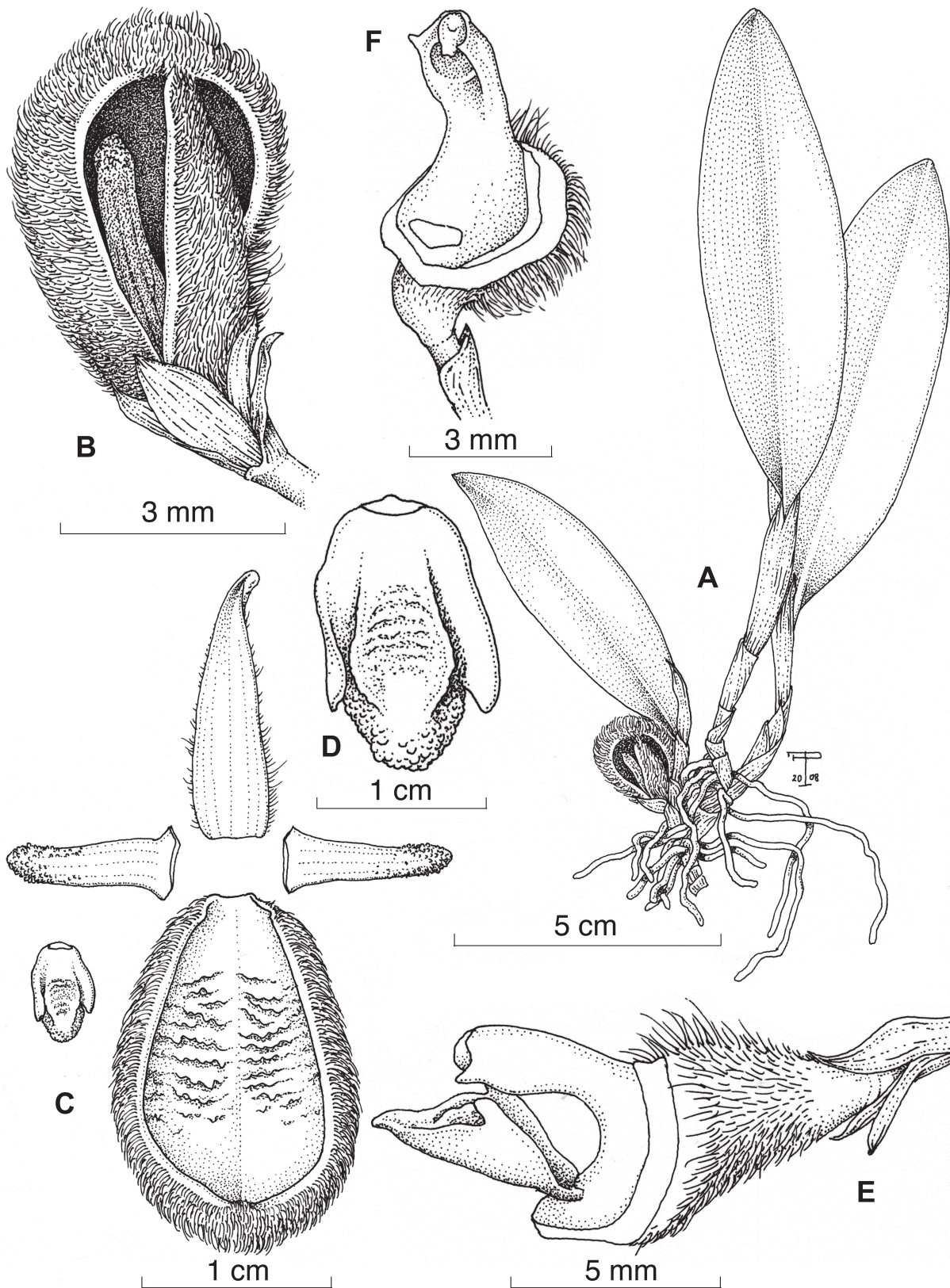


FIGURE 12. *Echinosepala lappiformis* (A. Heller & L.O. Williams) Pridgeon & M.W. Chase. A, habit; B, flower; C, dissected perianth; D, lip, ventral view; E, column and lip, lateral view; F, column, three-quarters view. Drawn from *Bogarin 95541* by F. Pupulin.

Panama, and Colombia, which surely correspond to this taxon, but we have not had access to materials from Ecuador and Venezuela to confirm their identities.

Ecology: epiphytic in partial to deep shade on large branches of trees, in primary and mature secondary vegetation, *Echinosepala lappiformis* has been recorded in Costa Rica exclusively from the warm, wet tropical forests of the Caribbean plains at elevations between 50 and 650 m. Flowering has been recorded in cultivation from March to June.

Distinguishing features: *Echinosepala lappiformis* is easily recognized by the red-purple, long pubescent-echinate flowers borne at the base of the stems, with the narrowly triangular dorsal sepal apically connate to the apex of the synsepal. *Echinosepala stonei*, superficially similar, has the dorsal sepal obtuse, free. The Panamanian *E. balaeniceps*, not recorded from Costa Rica, has a much larger flower with a tall, longitudinal callus on the disc.

Costa Rican material examined: **Heredia:** Sarapiquí, Horquetas, ca. 80 m, Feb 2005, *C. Ossenzbach s.n.* (JBL). **Limón.** Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10°11'1.5"N 83°28'29.3"W, 627 m, 3 Dec 2008, *D. Bogarín 5876*, *R. L. Dressler*, *R. Gómez* & *R. Trejos* (JBL). Pococí, Guápiles, Parque Nacional Braulio Carrillo, Sector Quebrada González, Sendero Las Palmas, detrás de las instalaciones, 10°9'9.3"N 83°56'43.5"W, 467 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario alrededor del sendero, 22 Mar 2012, *D. Bogarín 9554*, *M. Fernández*, *A. P. Karremans* & *C. Smith* (JBL). Pococí, Guápiles, 5 km al sur de la carretera, fin del camino paralelo con el Río Blanco, cerca de la Finca Tintoreras, bosque muy húmedo tropical, 10°2'16.2"N 83°53'2.1"W, 350–400 m, 15 Jun 2006, *R. L. Dressler 6768*, *D. Bogarín*, *J. Gómez-Laurito* & *F. Pupulin* (JBL). Guápiles, carretera Braulio Carrillo, ca. 2 km hacia abajo de la entrada del Teleférico del Bosque Lluvioso, en lomas a orilla de la carretera, bosque muy húmedo tropical transición a premontano, epífitas en árboles caídos en bosque secundario, 10°11'32"N 84°54'27"W, 520 m, 9 Jul 2004, *D. Bogarín 890* & *F. Pupulin* (JBL).

6. *Echinosepala longipedunculata* Pupulin & Karremans, *Lankesteriana* 17(2): 299. 2017. TYPE: COSTA RICA. Cartago: La Unión, San Rafael, Cerros de La Carpintera, Campamento Escuela Iztarú, 9°53'08.2"N 83°58'15.6"W, 1778 m, bosque húmedo premontano, epífitas en potreros arbolados, 30 octubre 2008, floreció en cultivo en el Jardín Botánico Lankester, 19 de junio 2012, *D. Bogarín 5449*, *R. L. Dressler*, *R. Gómez*, *F. Pupulin*, & *R. Trejos* (Holotype, JBL). Fig. 13 (Voucher: *Bogarín 5449*, JBL).

Epiphytic, caespitose, erect herb up to 30 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, slightly complanate, thicker in the distal portion, 5.5–10.0 cm long, homoblastic, composed of 2 nodes different in length, the lower one much shorter (to 1.5–2.2 cm long), completely enclosed by 3 papyraceous, tubular, ancipitous,

apically loose, obliquely truncate, whitish sheaths, increasing in size toward the upper one, 2.0–6.5 × 1.3–2.0 cm, the oldest ones breaking longitudinally into long fibers and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, linear-elliptic, subacute, minutely emarginate at apex, 14–18 × 2.3–3.0 cm, cuneate below into a conduplicate, sessile base, with the midvein strongly protruding abaxially and several lateral veins faintly visible on the adaxial blade. *Inflorescence* a fascicle of single, successive flowers at the apex of ramicaul; the peduncle terete, suberect to gently arching, sparsely and minutely pubescent, 3–8 cm long, subtended by a papyraceous, whitish, ancipitous, obliquely truncate spathe 2.7–4.2 cm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtusate, 7–10 mm long. *Pedicel* terete-subclavate, 4–5 mm long; *ovary* completely covered by the bract, linear-subclavate, 5 mm long, minutely scaberulous. *Flowers* bilabiate, with temporal activity, opening early in the morning and closing in the afternoon during three or four days; the sepals yellow, mottled dark purple in the inner side, flushed purple and densely scabrous to shortly pubescent externally, abaxially verrucose, the warts scattered at the base and becoming denser toward the apex, the petals yellow, heavily blotched with purple-red, the lip orange yellow. *Dorsal sepal* oblanceolate, obtuse, 19–21 × 6–7 mm, 7- to 9-veined. *Lateral sepals* connate into an elliptic synsepal, verruculose in the distal half, 17–19 × 9–10 mm, each sepal 5-veined, the free apices subacute-rounded. *Petals* fleshy, narrowly lanceolate, obliquely asymmetric, acute, 6–7 × 1.5–1.8 mm, 3-veined, the central vein raised into a rounded keel. *Lip* 3-lobed, narrowly elliptic from a small, rectangular, thin, hyaline claw, 7 × 2 mm (4.5 mm across the lateral lobes), the base subtruncate; the apical lobe rounded to subtruncate, thickened at apex into a cushion-like, elliptic, low pad, provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinately, antorse; the disc with an erect, narrow callus arising at the base of the lip, the highest part covered by a horseshoe-shaped, channeled pseudoglenion extending in front into a low keel flushing into the apical pad. *Column* straight to subarcuate, semiterete, 5.0–5.5 mm long, provided with narrow, elliptic wings above the middle, the foot ca. 1.5 mm long. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bilobed caudicle. Fig. 3A–B.

Etymology: from the Latin *longipedunculatus*, “with a long peduncle,” in reference to the unusually elongate peduncle of the flower, which can reach 8 cm in length.

Distribution: known only from Costa Rica, where it has been recorded from the Caribbean watershed of the Talamanca, Central Volcanic, and Guanacaste mountain chains.

Ecology: epiphytic in partial shade on large branches and trunks of trees, in primary and mature secondary vegetation, recorded in lower montane wet, premontane rain, and premontane wet forests at elevations of about 1300–1800 m. Flowering has been recorded under cultivation from March to June, September, and November.

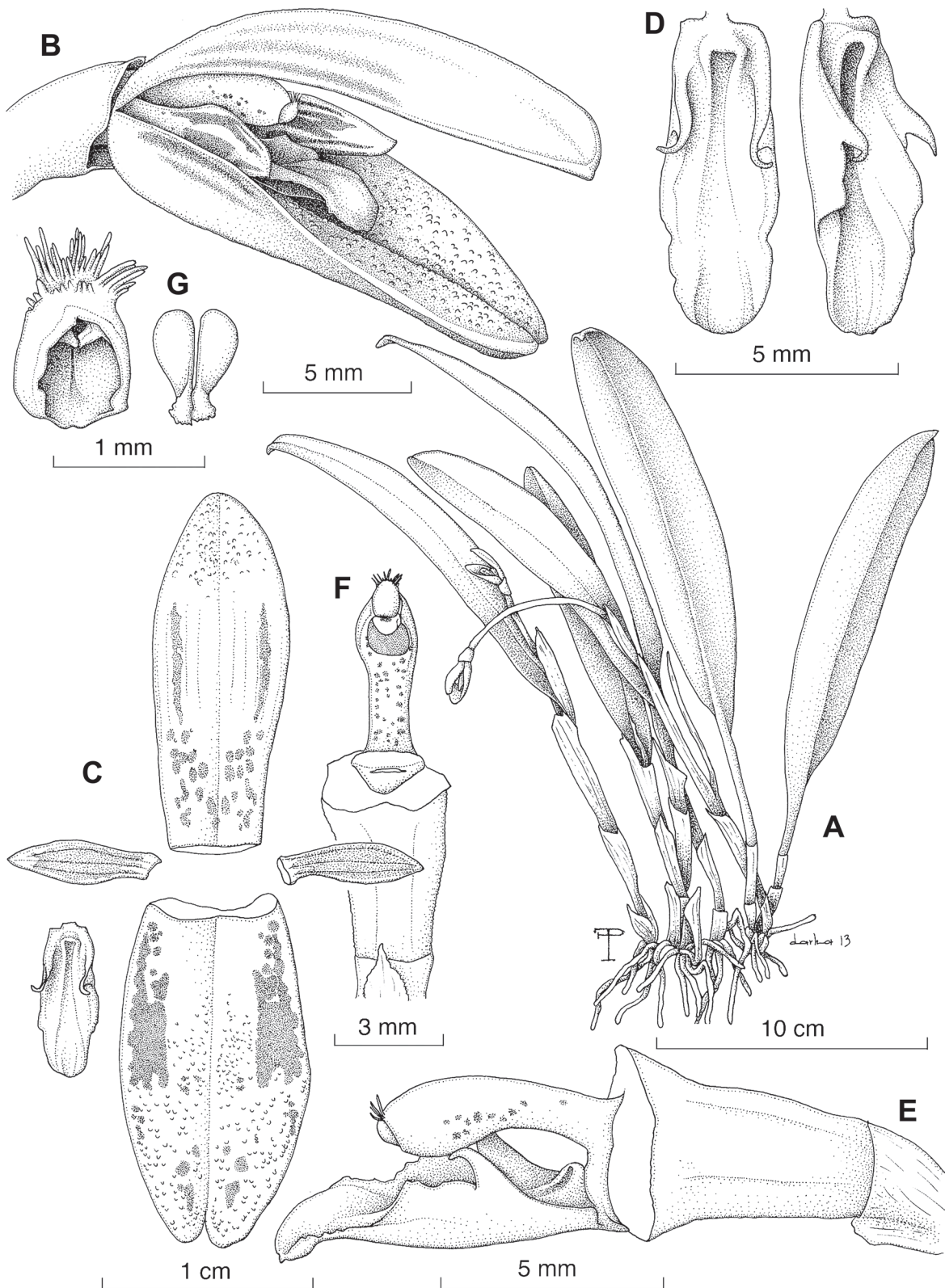


FIGURE 13. *Echinosepala longipedunculata* Pupulin & Karremans. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, column, ventral view; **G**, anther cap and pollinarium. Drawn from *Bogarin 5449* by F. Pupulin and D. Solano Ulate.

Distinguishing features: *Echinosepala longipedunculata* is most similar to *E. aspasicensis*, with which it shares the large habit of the plant and the general morphology of the flower. Nevertheless, *E. longipedunculata* can be recognized by the unusually long floral pedicel, which can reach 8 cm in length (vs. 2.0–3.5 cm in *E. aspasicensis*), the greenish-yellow flowers (vs. purple-brown), the verrucose-tuberculate adaxial surface of the sepals (vs. glabrous), and the shorter, truncate, orange lip (vs. 1.5 × longer, obtuse to acute, purple).

Costa Rican material examined: **Cartago:** Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1430–1620 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 23 mayo 2007, floreció en cultivo en el Jardín Botánico Lankester, 30 marzo 2013, *D. Bogarín 3863*, *M. Bonilla*, *R. Gómez*, *R. Trejos* & *J. D. Zúñiga* (JBL). Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, unos 9 km después de la entrada principal del parque, 500 m después del puente superior sobre el río Grande de Orosi sobre la calle que va a la represa, 9°41'56.24"N 83°46'53.12"W, 1570 m, epífitas en árboles al lado de la calle principal, bosque pluvial premontano, 10 de febrero 2012, floreció en cultivo en el Jardín Botánico Lankester, 9 marzo 2013, *A. P. Karremans 4994* (JBL). **Guanacaste:** Liberia, Liberia. Parque Nacional Rincón de la Vieja, sendero que recorre el sector Volcán Santa María, 10°47'26.00"N, 85°19'16.00"O, 1304 m, bosque húmedo montano bajo, epífita, 24 Jan. 2015, flowered in cultivation at Lankester Botanical Garden, 29 nov 2016, *I. Chinchilla 2216*, *R. Espinoza*, *C. Moraga*, *A. Guadamuz* & *A. Rojas-Alvarado* (JBL).

7. *Echinosepala pan* (Luer) Pridgeon & M.W. Chase, *Lindleyana* 17(2): 101. 2002.

Basionym: *Pleurothallis pan* Luer, *Selbyana* 3(3–4): 360–362, f. 280. 1977. TYPE: PANAMA. Veraguas: epiphytic in cloud forest northwest of Santa Fé, alt. ca. 750 m, *R. L. Dressler s.n.* (Holotype: SEL). Fig. 14 (Voucher: *Bogarín 10274*, JBL).

Homotypic synonyms: *Myoxanthus pan* (Luer) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 15: 38. 1986.

Echinella pan (Luer) Pridgeon & M.W. Chase, *Lindleyana* 16(4): 253. 2001, *nom. illeg.*

Brenesia pan (Luer) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 95: 255. 2004.

Epiphytic, caespitose to shortly repent herb, up to 25 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, 4.5–5.7 cm long, homoblastic, composed of 2–3 nodes different in length (increasing from the basal to the apical internode), each completely enclosed by equally long, tubular, ancipitous, papyraceous, obliquely truncate, hirsute, tight, apically loose sheaths, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaves* erect, coriaceous, narrowly linear-lanceolate, acute, 1.4–1.8 × 10–22 cm, the base sessile. *Inflorescence* a fascicle of flowers produced singly from the lower nodes of the ramicauls; the peduncle terete-subclavate, short, 6–10 mm long, pubescent. *Floral bract* papyraceous, loose, obliquely truncate-subobtusate, 5–8 mm long, densely

pubescent. *Pedicel* 2 mm long, pubescent; *ovary* obconical, 2 mm long, densely long-echinate. *Flowers* bilabiate, fleshy, short pedunculate, no temporal activity detected, emitting an urine-like odor, the sepals dull greenish-yellow, spotted and blotched with dark purple, the petals yellow, dotted with purple, the lip dark purple-red, the column white to rose-purple, spotted dark purple. *Dorsal sepal* elliptical-obovate, obtuse, fleshy, concave, reclined over the column, 11–15 × 6–9 mm (ca. 4 mm wide at the base), 5-veined, adaxially provided with spiny warts becoming denser toward the apical portion, abaxially long-echinate. *Lateral sepals* connate into a broadly elliptic-obovate elliptic-ovate, apically excised for about half their length, 8.3–12.0 × 7.5–9.3 mm, each half 3-veined, adaxially provided with spiny warts from the distal half and becoming denser to the apical portion, abaxially long-echinate. *Petals* rhombic, fleshy, obliquely asymmetric, subacute, subacutely angled on both margins, 4.3–5.0 × 2.9–3.8 mm, 3-veined, adaxially verrucose in the thickened apical portion. *Lip* 3-lobed, narrowly elliptic-oblong from a small, truncate, dark purple claw, 5.3–6.0 × 2.1–3.6 mm (6.8 mm wide across the expanded lateral lobes), the base truncate, with two small, conical, retrorse auricles; the lateral lobes erect, narrowly uncinately; the apical lobe elliptic to broadly elliptic, rounded-truncate, thickened at apex into a cushion-like, low pad, covered with a translucent wax in fresh flowers and provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc; the disc with an erect, narrow callus arising above the base of the lip, covered on the top by an inverted U-shaped (horseshoe-shaped), channeled pseudoglenion flushing into the apical pad. *Column* stout, straight, semiterete, to 3.2 mm long, 1.5 mm wide, provided with narrow stigmatic wings, the foot ca. 2.5 mm long. *Anther cap* globose, cucullate, 2-celled, with long stiff hairs in the upper margin, red-colored abaxially. *Pollinia* 2, ovoid, laterally flattened, on a short bilobed caudicle. Fig. 3C.

Etymology: named after the Greek god of the forest and leader of the Satyrs, Pan, whose hair was short-horned and bristly, resembling the abaxial indumentum of the sepals.

Distribution: known exclusively from Costa Rica and Panama, ranging from the Tilarán mountain chain in northern Costa Rica, to the regions of El Valle de Antón and Santa Fé in central Panama.

Ecology: *Echinosepala pan* is apparently a rare species, growing epiphytically in primary and secondary forests, usually along streams. In Costa Rica it has been recorded in the premontane wet forests along the Caribbean watershed of the Cordillera de Tilarán, Cordillera Volcánica Central, and Cordillera de Talamanca, at elevations ranging between 550 and 1150 m. Flowering has been recorded from June to September.

Distinguishing features: *Echinosepala pan* is close to *E. expolita*, with which it shares the dark flowers and the lip provided with a narrow, horseshoe-shaped callus. It can be distinguished from the latter by the narrowly linear-lanceolate leaves (vs. broader ligulate-lanceolate), the smaller flowers (sepals <10 mm vs. >15 mm long), the hirsute and tight sheaths clasping the ramicauls (vs. glabrous and inflated), and the abaxial long-echinate indumentum of the sepals (vs. shortly tomentose).

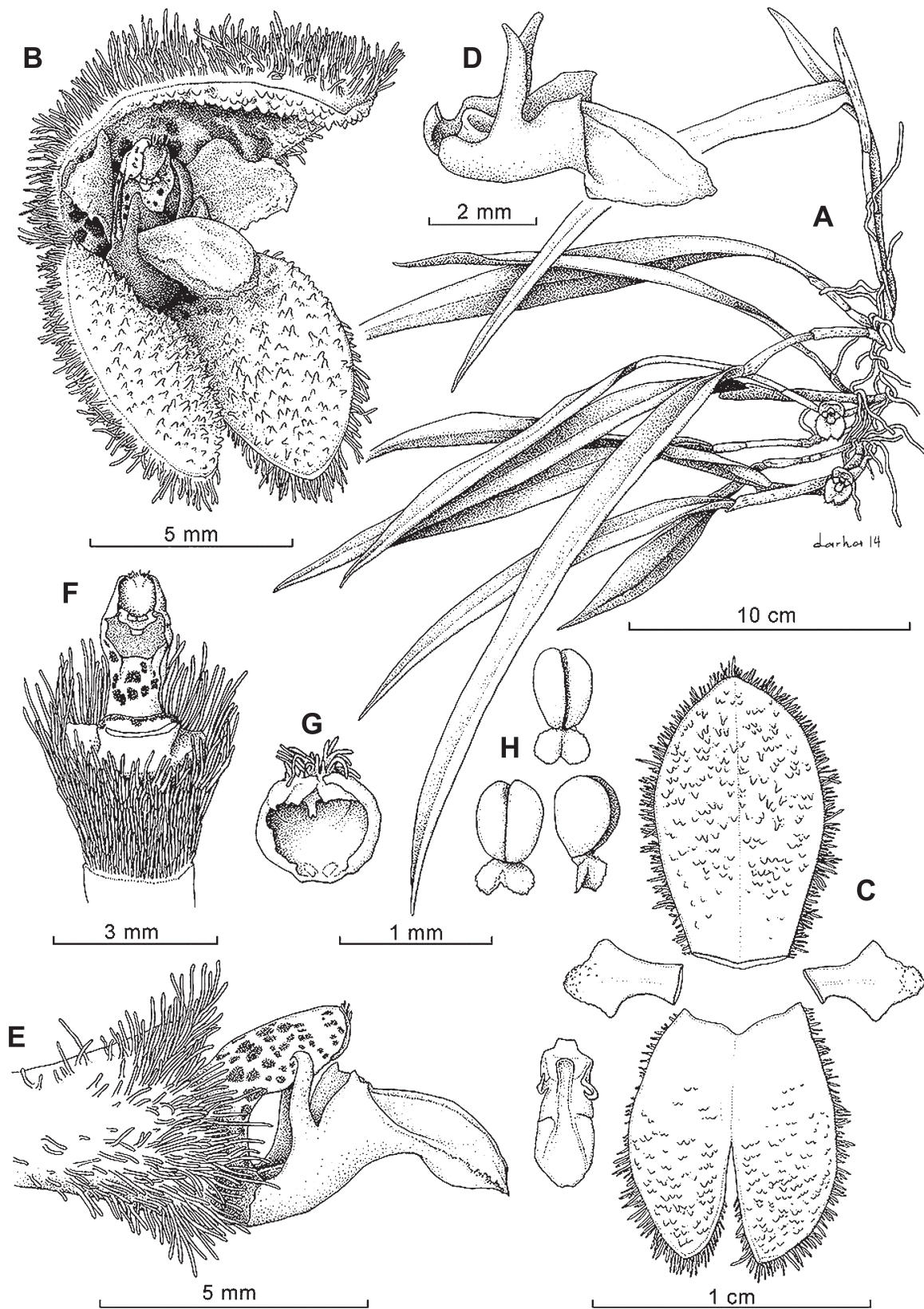


FIGURE 14. *Echinosepala pan* (Luer) Pridgeon & M.W. Chase. A, habit; B, flower; C, dissected perianth; D, lip, three-quarters view; E, column and lip, lateral view; F, column, ventral view; G, anther cap; H, pollinarium, three views. Drawn from *Bogarin 10274* by D. Solano Ulate.

Costa Rican material examined: Alajuela: San Ramón, 1867, *A. Endrés s.n.* [*Pleurothallis* No. 315] (W). San Ramón, Ángeles, Reserva Biológica A.M. Brenes, 30 Dec. 1990, *M. Freiberg s.n.* (JBL). Same collecting data, flowered in cultivation at Lankester Botanical Garden, Sept 2066, *M. Freiberg s.n.* (JBL). San Ramón, Ángeles, Reserva Forestal de San Ramón, 850–1000 m, Aug. 1991, *M. Germani 115* (JBL). San Ramón, Los Ángeles, deviation point to Villa Blanca, km 1.5, epiphytic in windward premontane forest, secondary vegetation, 10°19'11"N 84°28'28"W, 1120 m, 27 Feb 2003, *F. Pupulin 4327*, *D. Bogarín*, *H. Montealegre* & *A. C. Rodríguez* (JBL). **Limón:** Pococí, Guápiles, Bellavista 600 m oeste de la Escuela La Guaría de Bellavista, 10°8'35.111"N 83°48'43.052"W, 569 m, bosque muy húmedo tropical, epífitas en bosque secundario a orillas de una quebrada, 7 jun 2013, *D. Bogarín 10270* (JBL).

8. *Echinosepala stonei* (Luer) Pridgeon & M.W. Chase, *Lindleyana* 17(2): 101. 2002.

Basionym: *Pleurothallis stonei* Luer, *Phytologia* 44(3): 171. 1979. TYPE: COSTA RICA. San José: epiphytic in cloud forest southeast of San José, cultivated in California, flowered in cult. 3 Mar 1978, submitted to the OIC, no. 2022, *C. Luer 2781* (Holotype, SEL). Fig. 15 (Voucher, *Bogarín 5777*, JBL).

Homotypic synonyms: *Myoxanthus stonei* (Luer) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 15: 38. 1986. *Echinella stonei* (Luer) Pridgeon & M.W. Chase, *Lindleyana* 16(4): 253. 2001, *nom. illeg.*

Brenesia stonei (Luer) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 95: 255. 2004.

Epiphytic, shortly repent, erect herb up to 25 cm tall. *Roots* stout, flexuous, coarse, 1–2 mm in diam. *Ramicauls* erect, stout, terete, 6–8 cm long, homoblastic, composed of 2–4 internodes different in length (increasing from the basal to the apical internode), each completely enclosed by equally long, tubular, papyraceous, loose, obliquely truncate-subobtuse, glabrous sheath, the oldest breaking longitudinally and eventually disintegrating with age. *Leaves* sessile, erect, coriaceous, broadly elliptic, 9–13 × 2–4 cm, conduplicate, with a prominent midvein, the apex asymmetrically retuse, the base cuneate. *Inflorescence* a fascicle of flowers produced singly from the lower nodes of the ramicauls; the peduncle terete-subclavate, short, glabrous, ca. 1 cm long. *Floral bract* papyraceous, inflated, loose, obliquely truncate, acuminate, glabrous, 5–7 mm long. *Pedicel* terete, arcuate, glabrous, 5 mm long; *ovary* obovate, densely pubescent, not covered by the bract, ca. 4 mm long. *Flowers* held vertically, nonresupinate, deeply concave-cucullate, fleshy, short pedunculate, with a faint urine-like scent, the apex of the dorsal sepal not connate to the synsepal but accommodated inside forming two lateral entrances; the sepals dark red-purple colored with whitish hairs abaxially, petals and lip dark red-purple, column dark red. *Dorsal sepal* broadly elliptic-oblong, acute, fleshy, 14 × 7 mm, 5-veined, the free apex accommodated inside the synsepal, adaxially covered with irregular, tall warts; abaxial indumentum hirsute with soft trichomes. *Lateral*

sepals connate into a broadly oblong, concave, apiculate synsepal, fleshy, to 17 × 13 mm, each half 3-veined, adaxially covered with irregular, tall warts, abaxially hirsute with soft trichomes. *Petals* clavate, fleshy, narrowly rounded, obtuse, transversely rugose, 3 × 8 mm, warty from the middle portion toward the apex. *Lip* 3-lobed, fleshy, elliptic-ovate from a small, thin, rectangular, white-hyaline claw, 4 × 8 mm (ca. 6 mm across the lateral lobes), the base truncate; the apical lobe elliptic-ovate, obtuse, smooth becoming densely rugose in the distal portion; the lateral lobes suberect, narrowly uncinata, antrorse, acuminate; the disc provided with a massive, tall, rounded and broad, slightly concave callus, occupying all the lip base and extending to the disc; pseudoglenion absent. *Column* stout, straight, semiterete, 5–6 mm long, 1–2 mm wide, provided with narrow, uncinata wings above the middle, the foot ca. 3 mm long. *Anther cap* globose, 2-celled, cucullate, with stiff hairs in the upper margin. *Pollinia* 2, ovoid, on a granulose, short, bifid caudicle. Fig. 2I.

Eponymy: named for Richard L. Stone of Los Altos Hills, California, who discovered the species and flowered it in the United States.

Distribution: known only from Costa Rica.

Ecology: a rare epiphyte on trees, paddocks, and secondary forest edges. *Echinosepala stonei* is apparently restricted to the lower montane and premontane rain forests along the Caribbean watershed of the Talamanca mountain chain (and perhaps the Central Volcanic Cordillera), where it has been recorded from 800 to 1900 m in elevation. Flowering has been recorded from January to March.

Distinguishing features: the purple-red, hirsute flowers borne at the base of the ramicaul, with the dorsal sepal broad, elliptic, obtuse, apically free, and the clavate petals with tall warts distinguish *Echinosepala stonei* from the closely related *E. lappiformis*, which has a narrowly triangular, acute dorsal sepal apically connate to the apex of the synsepal, and narrowly lanceolate, low-tuberculate petals.

Echinosepala stonei is apparently a very rare species, for a long time exclusively known from the type collection, flowered in cultivation in California, and allegedly collected “southeast of San José” (Luer, 1979), an imprecise locality. Here we can substantiate the presence of *E. stonei* in Costa Rica, on the basis of three collections from the Caribbean slopes of Cerro Duán, in the northern region of the Talamanca cordillera.

Costa Rican material examined: Cartago: Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, 9°48'36.7"N 83°45'16.2"W, 1396 m, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque, 24 Nov 2008, *D. Bogarín 5714*, *R. L. Dressler*, *R. Gómez* & *R. Trejos* (CR). Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque. 9°48'36.7"N 83°45'16.2"W, 1396 m, 24 Sept 2008, *D. Bogarín 5740*, *R. L. Dressler*, *R. Gómez* & *R. Trejos* (JBL). Same locality data, *D. Bogarín 5777*, *R. L. Dressler*, *R. Gómez* & *R. Trejos* (JBL). Paraíso,

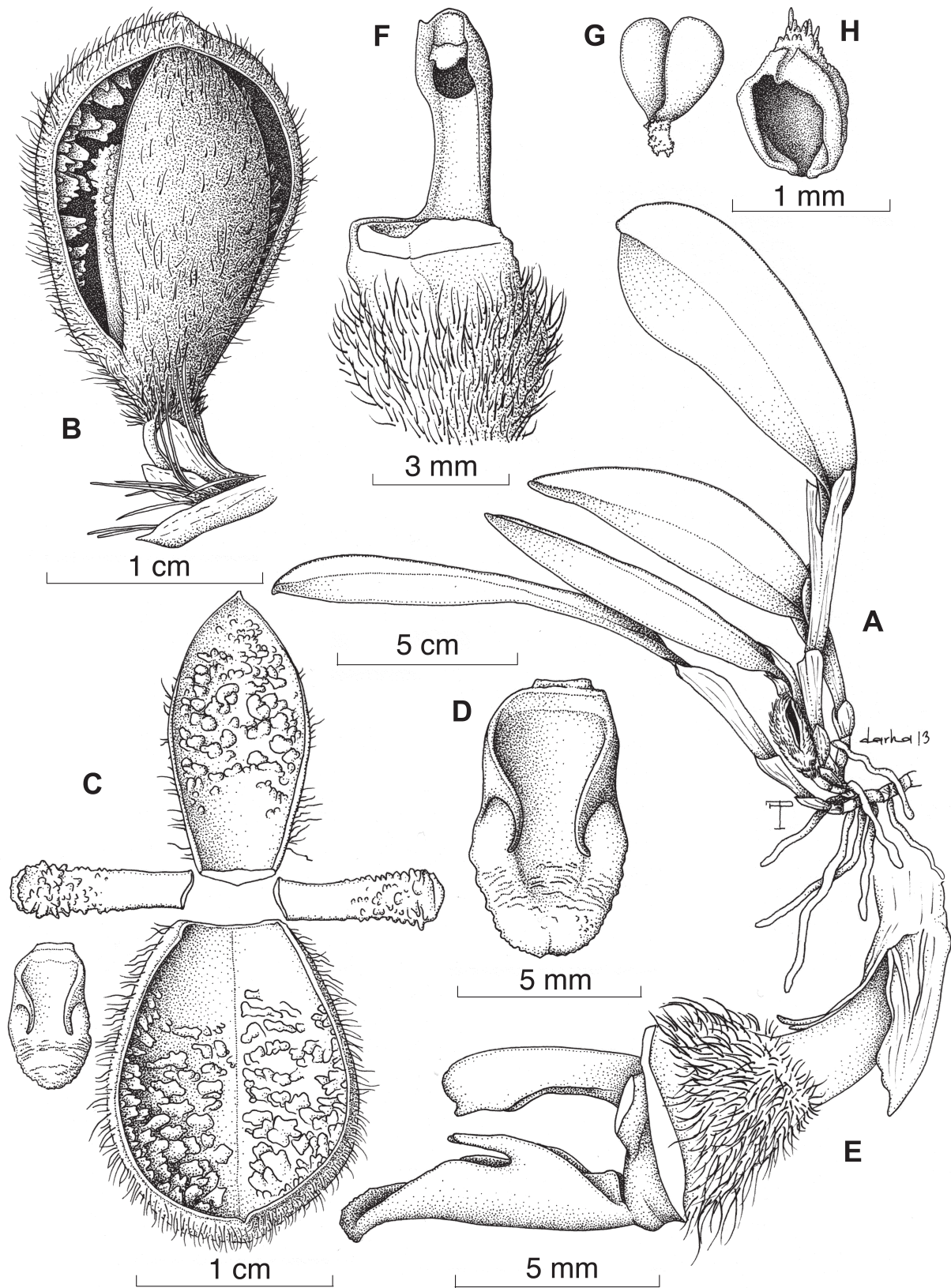


FIGURE 15. *Echinosepala stonei* (Luer) Pridgeon & M.W. Chase. A, habit; B, flower; C, dissected perianth; D, lip, ventral view; E, column and lip, lateral view; F, column, ventral view; G, anther cap; H, pollinarium. Drawn from *Bogarin 5777* by D. Solano Ulate.

Cachí, Peñas Blancas, entre Cerros Duán y Alto Velo de Novia, 9°48'43.76"N 83°46'36.61"W, 1829 m, bosque muy húmedo premontano, epífitas en árboles en potreros y borde de bosque, 11 Mayo 2009, *D. Bogarín 7190*, *R. Gómez*, *Y. Kisel*, *P. Renshaw* & *R. Trejos* (JBL).

9. *Echinosepala tomentosa* (Luer) Pridgeon & M.W. Chase, *Lindleyana* 17: 101. 2002.

Basionym: *Pleurothallis tomentosa* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 76: 177. 1999. TYPE: COSTA RICA. Without locality, [San José: Candelaria] ca. 1867, *A. R. Endres 630* (Holotype: W). Fig. 16 (Voucher: *Bogarín 5622*, JBL).

Homotypic synonyms: *Pleurothallis tomentosa* Luer, *Orquideología* 21: 337. 2000, *nom. illeg.*

Echinella tomentosa (Luer) Pridgeon & M.W. Chase, *Lindleyana* 16: 253. 2001.

Myoxanthus tomentosus (Luer) Pupulin & M.A. Blanco, *Lankesteriana* 2: 18. 2001.

Brenesia tomentosa (Luer) Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 95: 255. 2004.

Epiphytic, caespitose, erect *herb* up to 2 cm tall. *Roots* coarse, flexuous, 1 mm in diam. *Ramicauls* stout, erect, terete, slightly complanate, thicker in the distal portion, 2.5–12.5 long, homoblastic, composed of 2 internodes different in length, the lower one much shorter (to 1.0–1.5 cm long), completely enclosed by four papyraceous, tubular, ancipitous, apically loose, obliquely truncate, greenish sheaths, increasing in size toward the upper one, 1.5–5.0 × 0.5 cm, the youngest with purple spots, the oldest ones breaking longitudinally into long fibers and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, narrowly elliptic, subacute, minutely emarginate at apex, 8.2–11.2 × 1.5–2.4 cm, cuneate below into a conduplicate, sessile base, with the midvein strongly protruding abaxially and several lateral veins faintly visible on the adaxial blade. *Inflorescence* a fascicle of single, successive flowers at the apex of ramicaul; the peduncle terete, suberect, sparsely and minutely pubescent, 3 mm long, subtended by a papyraceous, whitish, ancipitous, obliquely truncate spathe 7 mm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 7 mm long. *Pedicel* terete-subclavate, 4 mm long, pubescent; *ovary* completely covered by the bract, linear-subclavate, 1.5 mm long, pubescent. *Flowers* bilabiate, no temporal activity of the perianth observed; the dorsal sepal yellow, blotched with dark purple in the inner side along the veins, the synsepal deep purple, adaxially densely tomentose, the lip dark purple, column yellow with purple blotches. *Dorsal sepal* linear-elliptic, obtuse, 11.5–13.0 × 3.3–4.0 mm, 5-veined, adaxially tomentose. *Lateral sepals* connate into an elliptic, synsepal, verruculose in the distal half, 11–13 × 5–6 mm, each half 8-veined, the free apices subacute-rounded, adaxially tomentose. *Petals* fleshy, narrowly lanceolate, obliquely asymmetric, acute, 4.5–5.0 × 1.3–2.0 mm, 3-veined, the central vein raised into a rounded keel. *Lip* 3-lobed, ovate to oblong from a small, rectangular, thin, hyaline claw, 6 × 2 mm (3.2 mm across the lateral lobes), the base subtruncate; the apical lobe obtuse,

narrowly uncinuate, antrorse; with a pair of intramarginal, thin keels running toward the apex and canaliculate along the middle; lateral lobes suberect, with a horseshoe-shaped, channeled pseudoglenion at the base. *Column* straight to subarcuate, semiterete, clavate, 4.3 × 1.2 mm long, the foot ca. 1.3 mm long. *Anther cap* globose, cucullate, with a fimbriate crest, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bilobed caudicle. Fig. 3E.

Etymology: from the Latin *tomentosus*, “covered by short, rigid hairs,” in reference to the adaxial surface of sepals.

Distribution: endemic to the central Pacific watershed of the Cordillera de Talamanca, Costa Rica.

Ecology: epiphytic in partial shade on large branches and trunks of trees, in primary and mature secondary vegetation, in premontane rain, and premontane wet forests at elevations of about 1200–1400 m. Flowering has been recorded in cultivation in April and March.

Distinguishing features: *Echinosepala tomentosa* is distinguished by the inflorescences developed at the apex of the stem, the leaves of fertile stems less than 12 cm long and the adaxially densely tomentose sepals, the yellow dorsal sepal and the purple synsepal. It is similar to *E. vittata*, but that species has sepals abaxially with stiff hairs along the veins and they are whitish, striped with red.

Luer (1999) described *Pleurothallis tomentosa* based on a collection by A. R. Endrés in 1867, apparently without locality data. However, the description made by A. R. Endrés (*Restrepia* 630, W0020266) states “Candelaria, March,” a place comprising the drainage basins of the Tarrazú, Alumbre, and Santa Elena rivers flowing into the Pacific watershed of Cordillera de Talamanca (Ossenbach et al., 2010). Luer suspected the species to be extinct, as no collections after 1867 were known. However, we found populations of this species in the Central Pacific region (Tarrazú) of Costa Rica, where the species is locally relatively frequent.

Additional Costa Rican material examined: Puntarenas: Parrita, Parrita, 9 km suroeste de San Carlos de Tarrazú, La Virgen, potreros hacia la cumbre de Fila Chonta, 9°34'33.92"N 84°9'24.49"W, 1240.2 m, bosque pluvial montano bajo, epífitas en bosque secundario remanente y potreros, 25 Febrero 2020, *D. Bogarín 12945*, *S. Abarca*, *I. Chinchilla*, *G. Parra* & *R. Parra* (JBL). **San José:** Tarrazú, San Lorenzo, ca. 4 km al sureste de Santa Marta, camino a Bajo Reyes, 9°36'38.2"N 84°00'52.1"W, 1475 m, bosque muy húmedo premontano, en parche de bosque secundario maduro, 20 Noviembre 2008, *D. Bogarín 5622*, *R. L. Dressler*, *M. Fernández*, *R. Gómez* & *R. Trejos* (JBL).

10. *Echinosepala vittata* (Pupulin & M.A. Blanco) C.O. Morales & N. Villalobos, *Lankesteriana* 4(3): 203. 2004.

Basionym: *Myoxanthus vittatus* Pupulin & M.A. Blanco, *Lankesteriana* 2: 16. 2001. TYPE: COSTA RICA. San José: Pérez Zeledón, El Brujo, near Río División, 450 m, 30 Jan. 2000, flowered in cultivation at Jardín Botánico Lankester, 3 June 2001, *M. A. Blanco 1324* (Holotype: USJ, Isotype: JBL). Fig. 17 (Voucher: *Blanco 1324*, USJ).

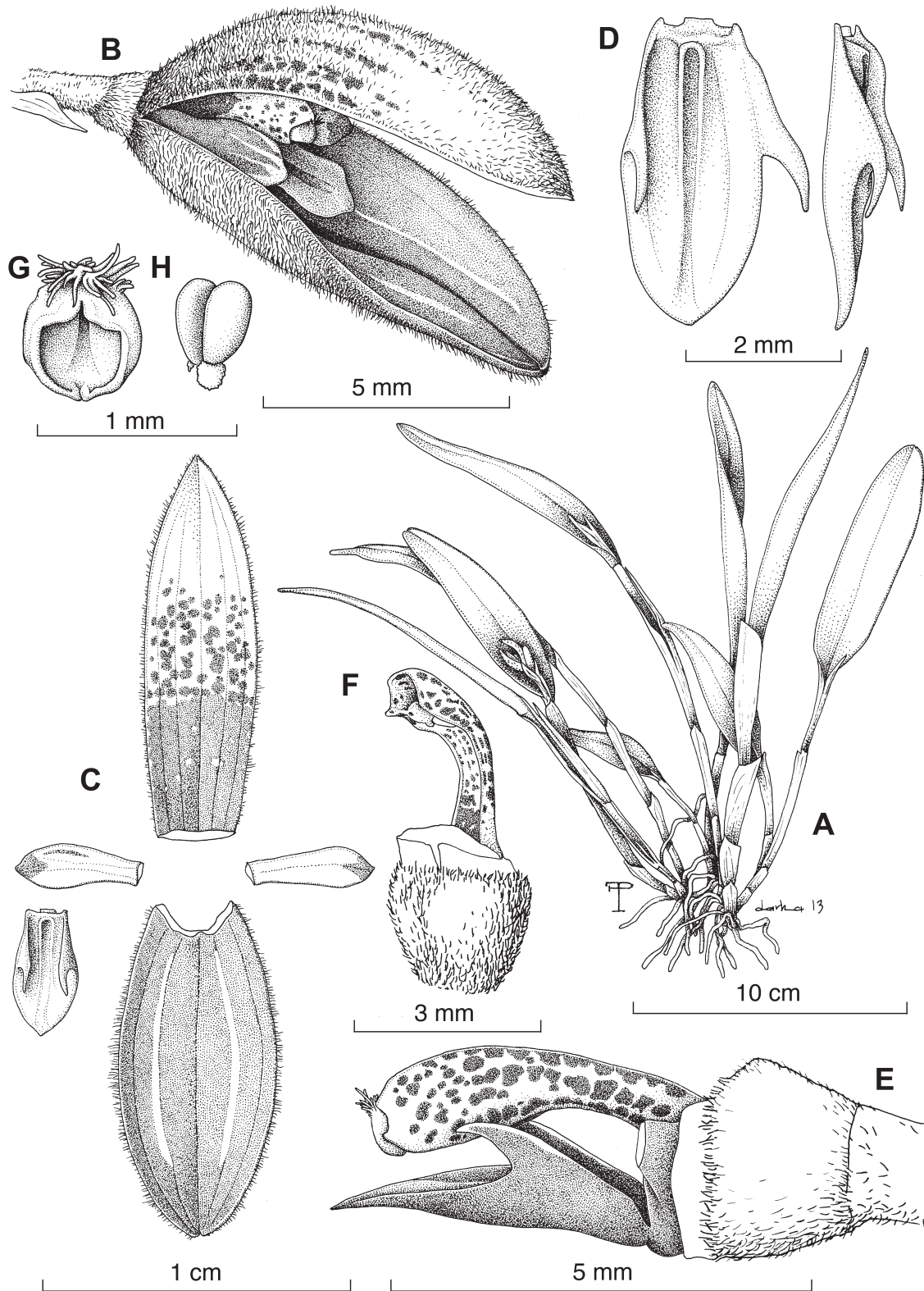


FIGURE 16. *Echinosepala tomentosa* (Luer) Pridgeon & M.W. Chase. A, habit; B, flower; C, dissected perianth; D, lip, ventral and three-quarters views; E, column and lip, lateral view; F, column, three-quarters view; G, anther cap; H, pollinarium. Drawn from *Pupulin* 5622 by F. Pupulin and D. Solano Ulate.

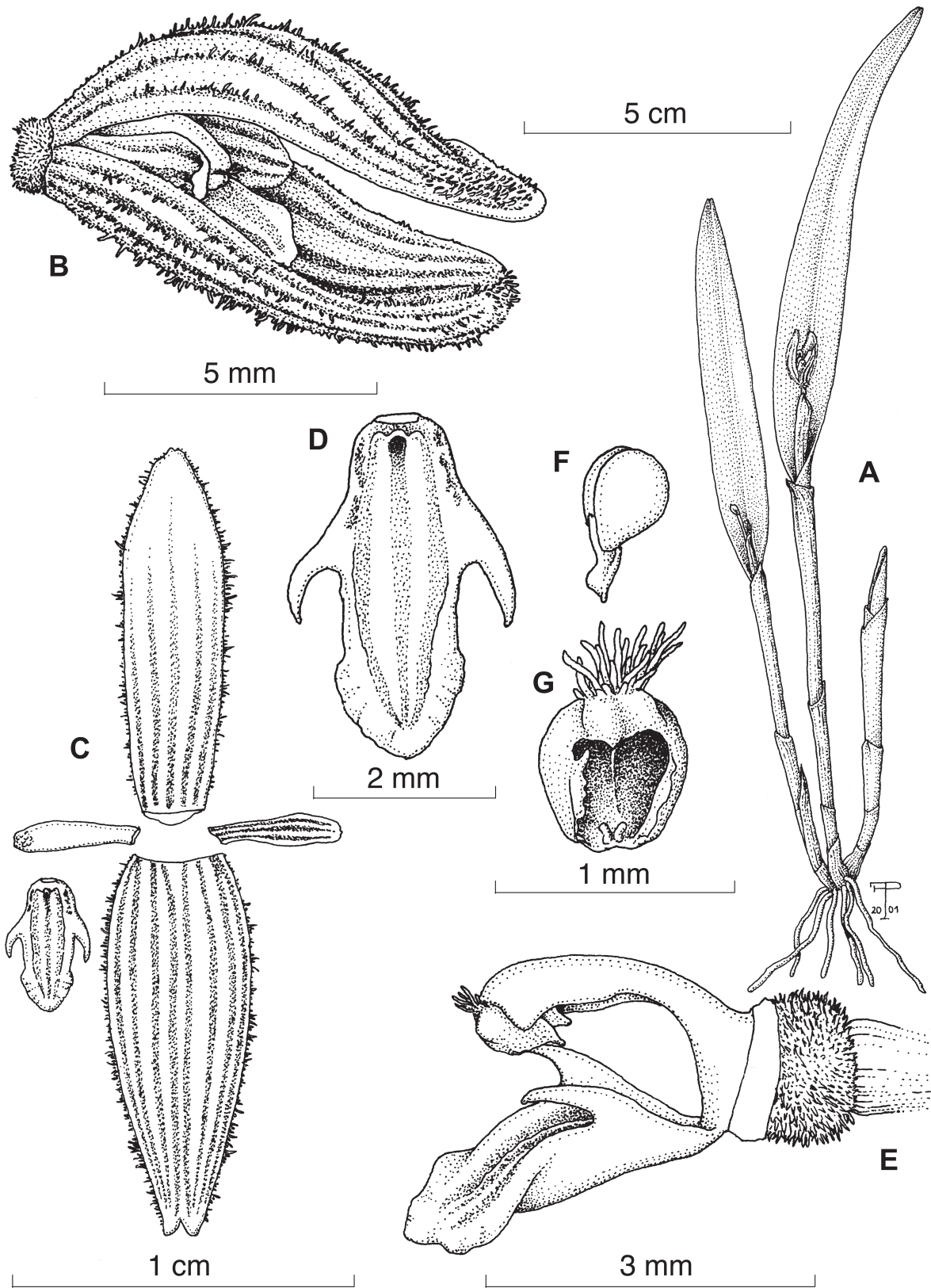


FIGURE 17. *Echinosepala vittata* (Pupulin & M.A. Blanco) C.O. Morales & N. Villalobos. A, habit; B, flower; C, dissected perianth; D, lip, ventral view; E, column and lip, lateral view; F, pollinarium; G, anther cap. Drawn from Blanco 1324 by F. Pupulin.

Homotypic synonyms: *Echinella vittata* (Pupulin & M.A. Blanco) Pupulin, Lankesteriana 4: 17. 2002, *nom. illeg.*

Pleurothallis grammata Dressler, Lankesteriana 3: 28. 2002, *nom. subst.*

Echinosepala vittata (Pupulin & M.A. Blanco) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 119. 2007, *nom. illeg.*, *nom. superfl.*

Epiphytic, caespitose *herb* up to 17 cm tall. *Roots* coarse, ca. 2 mm in diam. *Ramicauls* stout, erect, 4–7 cm long, enclosed by 3–4 loose, tubular sheaths, fragmented with age. *Leaf* erect, thickly coriaceous, narrowly lanceolate-elliptic, minutely emarginate, 7–10 × 1.3–1.5 cm, cuneate below into a conduplicate, sessile base. *Inflorescence* a fascicle of single, successive flowers, produced at the apex of ramicaul, the peduncle terete, sparsely pubescent, 0.8–1.3 cm long, subtended by a papyraceous, ancipitous spathe 1.4–1.6 cm long. *Pedicele* terete-subclavate, 2–3 mm long; *ovary* less than 1 mm long, densely pubescent. *Flowers* small, fleshy, whitish, longitudinally striped with purple, densely short-pubescent externally, glabrous within. *Dorsal sepal* linear-oblong, obtuse, 1.0–1.2 × 0.3 cm, 5-veined. *Lateral sepals* connate into a lanceolate, shortly emarginate, concave synsepal, 1.0–1.3 × 0.4–0.5 mm, each half 4-veined. *Petals* fleshy, linear-oblong, obtuse, minutely apiculate, adaxially provided with a tuft of short papillae near the apex, 4 × 1 mm, 3-veined. *Lip* 3-lobed, ligulate, subacute, 4 mm long, 2.5 mm wide between lateral lobes; the apical lobe smooth, slightly undulate along the margins; the lateral lobes erect, narrowly uncinately, antrorse; the disc with an erect, narrow, low, horseshoe-shaped, channeled callus above the base, extending in front into a low keel just to near the lip apex, laterally provided with a pair of low lamellae extending to the apex, hinged on the end. *Column* arcuate, semiterete, 1.6 mm long, provided with narrow wings above the middle, the foot less than 1 mm long. *Anther cap* globose, cucullate,

with long hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short, bifid caudicle. Fig. 3F.

Etymology: from the Latin *vittatus*, “longitudinally striped,” in reference to the stripes on sepals and petals.

Distribution: known only from northern and central Costa Rica, where it has been recorded on both watersheds of the continental divide.

Ecology: epiphytic in tropical wet forest, premontane belt transition, at 450–750 m in elevation. Flowering has been recorded from November to June.

Distinguishing features: *Echinosepala vittata* is closely related to *E. glenioides*, *E. longipedunculata*, and particularly to *E. tomentosa*, all provided with a pseudoglenion at the base of the lip, but it is distinguished by the small size, the densely pubescent ovary, the whitish flower striped with purple, the sepals adaxially smooth, and the ligulate, obtuse lip. *Echinosepala tomentosa* may be distinguished from *E. vittata* by the purple-black flowers with an oblong lip, rounded at apex.

Together with *Echinosepala tomentosa*, the other species with a short vegetative habit and small flower, *E. vittata* groups into the basal-most clade of *Echinosepala*, sister to all the other species in the genus.

Additional Costa Rican material examined: Alajuela: Upala, Bijagua. En la calle nueva desde el Celeste Mountain Lodge al parque Volcán Tenorio, orillas del bosque y potrero al lado del camino, 10°43'8.46"N 85°0'2.07"W, 729 m, 14 Dec 2016, A. P. Karremans 7524, M. Cedeño, I. Chinchilla, M. Díaz y G. Rojas-Alvarado (JBL). **San José:** León Cortés, San Pablo, R.F. Los Santos, El Abejónal, 7 Jan 1935, *E. Azofiefa* 286 (CR). Pérez Zeledón, El Brujo, near Río División, 450 m, 30 Jan. 2000, flowered in cultivation at Jardín Botánico Lankester, 3 June 2001, M. A. Blanco 1324 (JBL). Pérez Zeledón, Viento Fresco de El Brujo, 9°25'13"N 83°56'27"W, 450 m, 21 Jan 2001, F. Pupulin 2878, D. Castelfranco & E. Elizondo (JBL).

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