

# CONTRIBUTIONS TOWARD A REASSESSMENT OF COSTA RICAN ZYGOPETALINAE (ORCHIDACEAE). 3. A SYSTEMATIC REVISION OF *DICHAEA* IN COSTA RICA

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**Abstract.** A systematic revision of the genus *Dichaea* (Orchidaceae) in Costa Rica is presented. The taxonomic history of the genus and its phylogenetic position are discussed, with emphasis on infrageneric grouping. Characters of vegetative and floral morphology are treated, and their taxonomic significance is discussed. Twenty-nine *Dichaea* taxa are recognized for the flora of Costa Rica, and a key to species is provided. Each taxon is described on the basis of Costa Rican material, illustrated in a composite plate, and its distribution in the country is assessed. Distribution maps for all the taxa are given. Overall distribution, derivation of name, notes on species ecology, and diagnostic features are presented for each taxon. Lectotypes are selected for *D. acostae* Schltr., *D. acrolephara* Schltr., *D. amparoana* Schltr., *D. costaricensis* Schltr., *D. dammeriana* Kraenzl., *D. lycopodioides* Rchb.f. ex Kraenzl., *D. poicillantha* Schltr., *D. selaginella* Schltr., *D. tuerckheimii* Schltr., *Epidendrum echinocarpon* Sw., and *E. trichocarpon* Sw. A new species, *D. gomez-lauritoi*, is described and illustrated from the wet Caribbean plains of central Costa Rica.

**Keywords:** Orchidaceae, Zygopetalinae, *Dichaea*, *Epidendrum*, Costa Rica

As understood today, the orchid genus *Dichaea* Lindl. includes some 110 species distributed from Mexico to Bolivia and Argentina, and the West Indies. The genus shows its greatest diversity in South America, the probable center of dispersion, with a high number of species representative of less derived groups and likely close to the genus's primitive lineages. Species diversity is particularly noteworthy along the Andes, in Ecuador, with 40 recorded taxa (Dodson, 2004), being the single country with the highest number of species. A second dispersal center is to be found in Costa Rica with 29 recorded species, roughly corresponding

to 30% of the whole genus, making this small region one of the countries with the highest diversity in *Dichaea* when compared with the adjacent regions.

In Costa Rica, plants of the genus *Dichaea* constitute a rather common element of the understory epiphytic vegetation, occupying a broad spectrum of different habitats ranging from the tropical wet forests near sea level to the montane cloud forests up to almost 2500 m elevation. Although the frequency of individuals is higher in pristine vegetation, probably because of the evenly shaded conditions preferred by most of the taxa, *Dichaea* plants are

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also commonly found as epiphytes in severely altered vegetation and on scattered trees. Only the driest regions of northern Pacific Costa Rica, with a dry season exceeding four months, can be considered inhospitable for the species of this otherwise ubiquitous genus.

Altitudinal distribution of *Dichaea* in Costa Rica, calculated from 785 herbarium specimens and living plants grown at Lankester Botanical Garden, University of Costa Rica, shows that frequency of individuals is reduced in lowland areas (less than 7% of the total gatherings from sea level to 300 m), rapidly increasing above 300 m elevation. Greatest frequency was recorded at altitudes ranging from 400 to 1500 meters, with a maximum peak around 1100 m (74 individuals = 9.5% of the total plants). Frequency drastically diminishes at higher altitudes, and *Dichaea* is scarcely represented above 2000 m (Fig. 1). Most of the Costa Rican species seem to be tolerant of quite varied climatic requirements, showing a rather wide range of altitudinal distribution, often spanning over a gradient of more than 1000 m. *Dichaea hystricina* Rchb.f. has been recorded from 400 to 1500 m, *D. costaricensis* Schltr. from 300 to 1400 m, *D. cryptarrhena* Rchb.f. ex Kraenzl. from 800 to almost 2000 m, *D. panamensis* Lindl. from near sea level up to 1400 m, and the widespread *D. poicillantha* Schltr. from 200 to almost 2500 m. However, some of the species

exhibit a narrower altitudinal range, and the available records correlate their distribution with more specific environmental conditions. *Dichaea squarrosa* Lindl. is restricted to the cool environment of submontane and montane wet forests at altitudes over 2000 m, whereas the few Costa Rican records of *D. glauca* (Sw.) Lindl. are from the premontane cloud forests at 1000–1600 m, and *D. eligulata* Folsom is exclusively known from the warm central and southern Pacific regions, where it is restricted to elevations between 400 and 800 m.

Dominant winds and waterfall regimes, mostly influenced by the continental divide, also affect species distribution. As a consequence, many of the species are restricted in Costa Rica to the evenly wet forests of the Caribbean watershed, which experience no definite dry season. They include *Dichaea acrolephara* Schltr., *D. costaricensis*, *D. fragrantissima* ssp. *eburnea* Dressler and Pupulin, *D. lankesteri* Ames, *D. obovatipetala* Folsom, *D. pendula* (Aubl.) Cogn., *D. sarapiquinsis* Folsom, *D. similis* Schltr., *D. tuerckheimii* Schltr., and *D. viridula* Pupulin. On the contrary, other species, like *D. acostae* Schltr., *D. eligulata*, *D. globosa* Dressler and Pupulin, and *D. gracillima* C. Schweinf., are seemingly restricted to the drier, Pacific slopes of Costa Rican mountain ranges.

Because of the broad overlapping in altitudinal distribution of many *Dichaea* species, up to

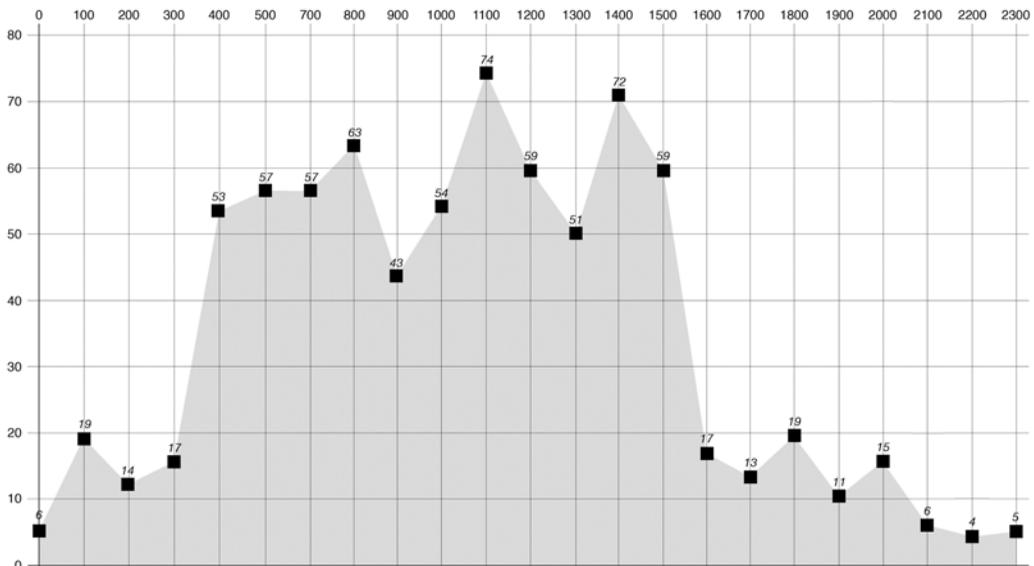


FIGURE 1. Altitudinal distribution of the genus *Dichaea* in Costa Rica calculated on 785 individuals. Vertical axis = number of individuals; horizontal axis = altitude in meters above sea level.

eight different taxa may be found in a single locality, often with three or four different species sharing the same phorophyte. A special "hotspot" in *Dichaea* diversity is to be found close to the continental divide in the Tilarán mountain range. Here, on the Caribbean slopes of Cerro de La Palma, *D. cryptarrhena*, *D. dammeriana* Kraenzl., *D. fragrantissima* ssp. *eburnea*, *D. hystricina*, *D. lankesteri*, *D. aff. poicillantha*, and *D. trulla* Rchb. f. grow sympatrically at 1200 m elevation. From the same general area is also recorded the elusive *D. gracillima*, so far documented by a single collection. Another locality particularly rich in *Dichaea* taxa is the area around the village of San Miguel, in the lower Sarapiquí valley, Central Volcanic range, where *D. costaricensis*, *D. elliptica* Dressler and Folsom, *D. fragrantissima* ssp. *eburnea*, *D. hystricina*, *D. oxyglossa*, *D. panamensis*, *D. sarapiquinsis*, and *D. trulla* were recorded growing together at about 400 m.

Plants of *Dichaea* often occur in rather large populations, sometimes with tens of individuals on the same phorophyte, but population density greatly differs among species. Almost 50 individuals of *D. cryptarrhena* were observed growing on two closely spaced trees in forest remnants near San Ramón, Costa Rica (ca. 1300 m), and 29 individuals of *D. obovatipetala* were scored on a 7-m-tall tree along the Río Pejivalle (720 m), on the Caribbean slopes of the Talamanca mountain range. On the other side, plants of *D. dammeriana* Kraenzl. are usually found as scattered individuals and rarely form small populations. The distinctive *D. gracillima* is known exclusively from three individuals collected in a well-sampled area (Schweinfurth, 1938), and the elusive *D. acostae* was never collected again after the original, independent findings by G. Acosta and A. M. Brenes in 1921 (Schlechter, 1923d).

The life cycle of *Dichaea* is probably long, and the longevity of some specimens can span over decades. Individual plants of *Dichaea* are usually composed of a relatively small number of annual stems, mostly varying from three to five, but much larger plants can be found growing on shady, old trunks of trees in pristine habitats, in some cases occupying an area close to a square meter, with individuals stems more than a meter long. We have no sufficient data to assess the actual age of such specimens, but an estimate of about 50 years is likely conserva-

tive. Plants of *Dichaea* usually produce three to six new apical leaves a year on mature stems (pers. obs.), and we can confidently estimate that specimens with over 100 leaves, like a plant of *D. trulla* collected in the Caribbean lowlands close to Guápiles (*Pupulin et al.* 6000, CR), are 25 to 35 years old, whereas individual stems with more than 250 leaves (e.g., *D. oxyglossa*, *Pupulin* 2619) are probably over 50 years old.

The characteristic vegetative architecture of the genus, with relatively long and mostly pendent stems covered by small leaves arranged in two ranks (from which the generic name, derived from the Greek *di-*, two, and *chaio*, to divide), and the single-flowered inflorescences, make the plants of this genus easy to recognize even when they are not in flower. However, similarities in floral morphology, as well as a noteworthy plasticity in vegetative characters, make this group taxonomically problematic. The delicate, ephemeral flowers usually do not conserve well in dried specimens, and the flowers of many species present temporal activity, opening just a few hours in the morning, so that most of the genus's material kept in herbaria is made up of sterile or only fruiting plants. The often inadequate descriptions and typification of the earlier taxa, together with the destruction of a large amount of critical specimens originally kept in the Berlin-Dahlem herbarium, largely contributed to the complicated taxonomic history of the genus. Because of the difficulty in understanding critical characters at the specific level on the sole basis of original protologues, traditional taxonomic treatments of the genus commonly accepted a few, poorly defined species, resulting in the application of a reduced number of all-purpose *Dichaea* names to a wide range of different taxa. Alternatively, workers on Neotropical floras preferred in many cases to simply ignore old taxonomic literature and previously published names based on poorly conserved types, favoring the creation of new taxa with little discussion, if any, of their phylogenetic affinities. In the case of the generic taxonomy relative to Costa Rica, it is perhaps relevant that most of the species, including many of those recently described, were never illustrated before, favoring the lumping of rather distinct taxa into broad synonymies on the sole basis of similarities in the original protologues.

Also at the infrageneric level, the establishment of groups' affinities and the delimitation of species within *Dichaea* proved to be rather controversial. The use of a limited number of morphological characters to assess phylogenetic affinities (in the case of *Dichaea* essentially restricted to characteristics of leaf articulation and ovary vestiture) has been a common approach to the generic taxonomy, often result-

ing in an artificial infrageneric classification. Traditionally overlooked characters, like root and stem anatomy, vegetative organization, inflorescence features, flower presentation, and floral morphology (including characteristics of the gynostemium and the pollinarium) proved to be amply informative for the systematics of the genus, and in many cases not supportive of traditional views on *Dichaea* phylogeny.

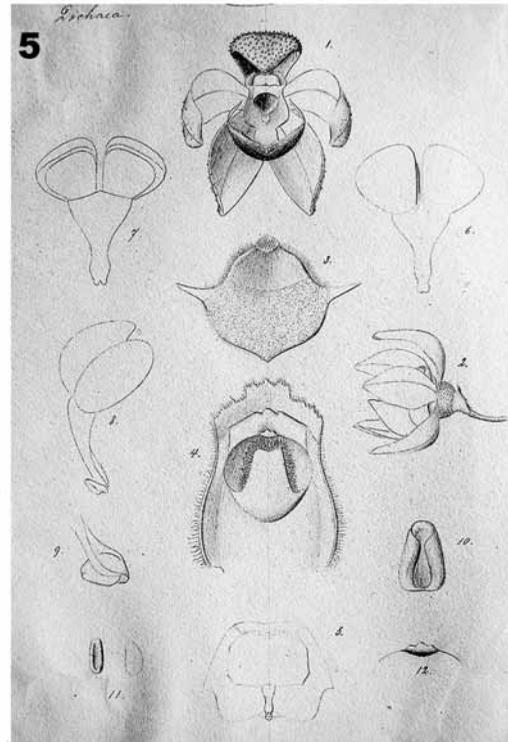
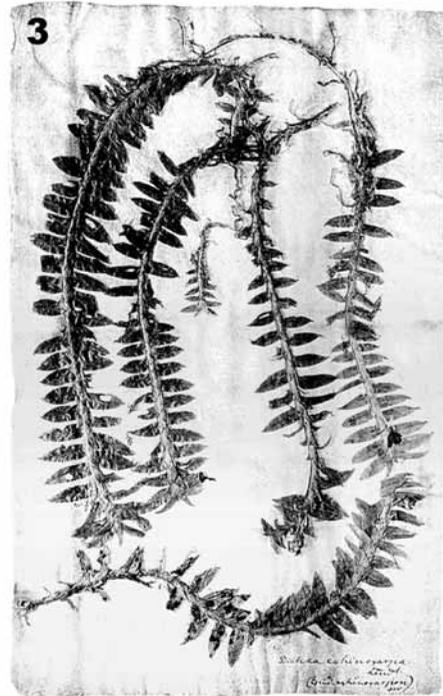
#### TAXONOMIC HISTORY

The French apothecary Jean-Baptiste Christian Fusée Aublet (Salon 1720–Paris 1778), who collected new medicinal plants in French Guyana for the Royal Apothecary between 1762 and 1764, was the first botanist to describe and illustrate a plant belonging to the genus *Dichaea*. In 1775, Aublet published in London his *Histoire des Plantes de la Guiane Française*, where he summarizes the results of his botanical work in South America, accounting for over 400 new species and 208 genera of plants arranged according to Linnaeus's recently established binomial system (Aublet, 1775). In the second volume of his *Histoire*, Aublet described *Limodorum pendulum*, based on a plant collected in the forests of the "Comitatus de Gêne" and flowering in May. His description, as well as the accompanying botanical illustration (Plate 322; Fig. 2 herein), leaves no doubts about the generic placement of the new species, but its interpretation at specific level is doubtful. Aublet's collections were divided at his death between Britain and France. The primary set of specimens and the original artworks for the book were acquired by Joseph Banks and eventually became part of the collections at the Natural History Museum in London. Among these materials, no *Dichaea* specimens are found, so our understanding of Aublet's concept relies entirely on the protologue and the illustration. Unfortunately, parts 3 and 4 of the original plate (and the corresponding description) likely represent a flower of another genus, or a mixed collection of parts from different flowers (Ames and Correll, 1943). It should be noted, however, that the illustration of the plant habit shows the fruiting flowers produced below the foliage, a character rather atypical of *Dichaea* species with non-articulate leaves and almost exclusively restricted, among members of *Dichaea* sect. *Dichaea*, to the species treated hereafter as *D. pendula* (Aubl.) Cogn.

The next four species of *Dichaea* to be formally described were found in the West Indies by the Swedish botanist Olof Swartz (Nordköping 1760–Uppsala 1818), who proposed them as members of the genus *Epidendrum* in his *Prodromus Descriptionem Vegetabilium in Indiam Occidentalem*, published in Uppsala in 1788 (Swartz, 1788). Swartz himself transferred these species to the genus *Cymbidium* in 1799, describing another new species of *Dichaea* with the name of *Cymbidium muricatum* (Swartz, 1799a,b), and in 1806 he published expanded descriptions of the same taxa together with further details on their ecology (Swartz, 1806). Among the species referable to the genus *Dichaea*, he considered his *Epidendrum echinocarpon* conspecific with the *Limodorum pendulum* of Aublet (Swartz, 1788, 1799a,b, 1806). The final destiny of the collections by Swartz remains uncertain, but Swartz's specimens of *Dichaea* from the "Herbarium Holmianum" (Stockholm) were recently found by the author among the material kept in Reichenbach Herbarium in Vienna, and his specimen of *Epidendrum echinocarpon* (*Rchb. Orch.* 25294!, W) surely corresponds to the modern concept of *D. pendula* (Fig. 3).

Prior to the formal description of *Dichaea*, two other species of the genus were added by Hipólito Ruiz and José Pavón, who described *Fernandezia laxa* from Peru in 1794 (Ruiz and Pavón, 1794), and by William Jackson Hooker, who proposed *Isochilus graminoides* (non *Epidendrum graminoides* Sw.) from Trinidad (Hooker, 1827).

In 1832, discussing the natural groups of *Cymbidium*, John Lindley recognized that the species allied to Swartz's *Cymbidium echinocarpon* were better referable to a distinct genus he called, for the first time, *Dichaea* (Lindley, 1832). The following year, he formally described *Dichaea* in his *Genera and*



FIGURES 2–5. 2, *Limodorum pendulum* Aubl. Plate 322 from *Histoire des Plantes de la Guiane Française*, 1775. Courtesy of G. A. Romero, Oakes Ames Orchid Herbarium, Harvard University Herbaria. 3, Type of *Epidendrum echinocarpon* Sw. (*Rchb. Orch.* 25294, W). Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna. 4, Type of *Cymbidium muricatum* Sw. (*Rchb. Orch.* 25291, W). Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna. 5, Drawing of *Dichaea poicillantha* by A. R. Endrés (*Rchb. Orch.* 38503, W). Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

*Species of Orchidaceous Plants*, characterizing the new genus by the caulescent plants provided with small, distichously arranged leaves; the solitary, "axillary" flowers; the unguiculate, deltoid lip articulate with the column foot; and the pollinarium with four superposed pollinia, a cuneate stipe, and a small viscidium (Lindley, 1833). He grouped in the genus the five West Indian species of Swartz and described two new taxa, among which *D. panamensis*, the first species of the genus (and likely the first orchid) to be described on the basis of Central American material (Cuming 1292 from Panama, K-L, photo!). Lindley did not explicitly indicate a *typus generis*, and Folsom (1987) concluded that the reference made by Lindley in 1832 to Swartz's *Cymbidium echinocarpon* should be considered as an implicit designation of the type. Nevertheless, being based on the superfluous and illegitimate name *Epidendrum echinocarpon* Sw. (which the author considered a synonym of the *Limodorum* described by Aublet from the French Guyana), *D. echinocarpa* (Sw.) Lindl. is a *nomen illegitimum*, and the genus is typified by *Limodorum pendulum* Aubl. [= *Dichaea pendula* (Aubl.) Cogn.].

The early list of *Dichaea* was further augmented by Poeppig and Endlicher (*D. calyculata* and *D. maculata*, 1838), Lindley (*D. ochracea*, 1839; *D. squarrosa*, 1840), Reichenbach filius (*D. oerstedii*, 1855; *D. brachyphylla*, *D. histrio*, *D. moritzii*, and *D. splitgerberi*, 1859; *D. hystricina*, 1865; *D. brachypoda* and *D. trulla*, 1866; *D. picta*, 1869; *D. lagotis*, 1877c; *D. kegelii*, 1877b; *D. gorgonensis*, 1877d; *D. diandra*, 1877a; *D. bryophila* and *D. mosenii*, 1881; *D. tigrina*, in Schiller, 1868), and Barbosa Rodrigues (*D. pumila* and *D. latifolia*, 1877; *D. coriacea*, 1882). By the end of the 19th century, almost 30 species of *Dichaea* were known.

In 1887, Pfitzer recognized in his ser. Dichaeinae only those species of *Dichaea* provided with muricate fruit and lacking a leaf abscission layer, two features he considered sufficient to separate them from the ser. Sarcanthinae (Pfitzer, 1887). Among the genera that present monopodial habit, or the *Pleurantheae duplicatae*, Pfitzer considered that *D. glauca*, *D. graminoides*, and their relatives were "much less" monopodial, and on the basis

of their characteristic glabrous capsules and articulate leaves, he proposed to group them in the new genus *Dichaeopsis* (Pfitzer, 1887). In 1888, in his treatment of the Monandrae-Dichaeinae orchids, Pfitzer characterized the genus *Dichaea* by the presence of non-articulate leaves and verrucose to muricate fruits, maintaining the segregation of the species with articulate leaves and glabrous fruits into the distinct genus *Dichaeopsis* (Pfitzer, 1888). At that time, some 10 species of *Dichaea* with smooth ovaries and eventually deciduous leaves had been described, but Pfitzer (1888) only mentioned the existence of five taxa in the genus *Dichaeopsis*, without expressly designating a *typus generis*. Although not discussing taxa at species level, he also recorded five species in the genus *Dichaea*, among which he only cited the still-unpublished *D. vaginata* Rchb.f. (sic). Kuntze eventually reduced the genus *Dichaeopsis* to sectional rank in 1903.

The next systematic treatment of the genus dealing with interspecific relationships was proposed by Cogniaux in his treatment of *Dichaea* for Martius's *Flora Brasiliensis* (Cogniaux, 1906). The treatment is limited to the Brazilian taxa, but his subgeneric grouping established the systematic basis followed by most of the subsequent authors for the next 80 years. Cogniaux retained the single genus *Dichaea*, dividing it into four sections on the basis of leaf articulation and fruit vestiture characteristics. Among the species with persistent leaves, he adopted a narrow circumscription of *Eudichaea* (including the type species) for the taxa provided with muricate fruits, creating sect. *Dichaeastrum* for the species with glabrous fruits. He followed Kuntze in treating *Dichaeopsis* at sectional rank but considered it in the strict sense proposed by Pfitzer, encompassing only those species provided with articulate leaves and glabrous ovary, and grouped the taxa with deciduous leaves and muricate ovary in sect. *Pseudodichaea*. Following Kuntze (1903), Cogniaux included in the taxonomy of the genus the name *Epithecia* Knowl. & Westc. as a synonym of *Dichaea*, in the erroneous belief that *Epithecia glauca* (Knowl. & Westc.) Knowl. & Westc. [= *Prosthechea glauca* Knowl. & Westc.] was conspecific with *Epidendrum glaucum* Sw., the basionym of *Dichaea glauca* (Sw.) Lindl.

From the beginning of the 20th century, the botanist most active in contributing descriptions of new species of *Dichaea* was Rudolf Schlechter. Between 1916 and 1929 he published 24 new species (Schlechter, 1916b, 1918a, 1920, 1921a,b, 1922a,b, 1923a–d, 1924a,b, 1929) from Mexico, Guatemala, Costa Rica, Panama, Colombia, Ecuador, Bolivia, and Brazil. By 1918, he recorded 12 species from Central America alone (Schlechter, 1918a). In 1914, Schlechter offered the first synopsis of the Dichaeinae, enlisting 15 species and 1 variety, and accepting Pfitzer's view about the existence of two separate genera within Dichaeinae (Schlechter, 1914). Here, he included in the genus *Dichaea* all the species with persistent leaf blades, maintaining Cogniaux's sections *Eudichaea* for the species with muricate fruit and *Dichaeastrum* for those with smooth capsules, and organizing sect. *Dichaea* into two series on the basis of the sessile or widely cuneiform versus narrowly unguiculate base of the lip. For the species with non-articulate leaves, Schlechter adopted the generic name *Epithecia* Knowl. & Westc. over *Dichaeopsis*. Nevertheless, his concept of *Epithecia* is more comprehensive than the genus *Dichaeopsis* as proposed by Pfitzer and adopted by Cogniaux for a section of *Dichaea*, comprising sects. *Dichaeopsis* and *Pseudodichaea*, that is, all the species with deciduous leaves, independently of the characteristic *indumentum* of the ovary and the resulting fruit. Section *Dichaeopsis* is further subdivided into two series, according to the proximal shape of the lip. After having direct access to the original publication by Knowles and Westcott in the *Floral-Cabinet* (1838), Schlechter corrected his mistake, adopting the genus *Dichaeopsis* (Schlechter, 1918b: 519). Nevertheless, in subsequent publications, he recognized the sole genus *Dichaea* (Schlechter, 1921b,c, 1922a,b, 1923a–d, 1924a,b, 1929). However, despite his monumental work in documenting species diversity in *Dichaea* all over the American tropics, Schlechter never organized his ideas about species relationships into a systematic framework, and the loss of his herbarium during 2nd world war (Ames, 1944) contributed to the difficulty in assessing species delimitations and clarifying nomenclatural problems affecting the genus.

In 1923, Fritz Kränzlin published the first systematic monograph on *Dichaea* in his treatment of the pseudomonopodial, monandrous orchids for Engler's *Pflanzenreich* (Kränzlin, 1923). Here he recognized 39 species and described 15 new taxa, some of which are now regarded as members of distinct orchid genera. Kränzlin accepted sects. *Eudichaea* Cogn. (including sect. *Dichaeastrum*) and *Dichaeopsis* (Pfitz.) Cogn., creating sect. *Maxillariopsis* for a group of species provided with a mentum, formed through the basal adnation of column and lateral sepals tissue. All of the species included by Kränzlin in his sect. *Maxillariopsis* are actually bulbous members of the genus *Maxillaria* or of some closely related genus with distichous leaves.

Kränzlin's revision was the last attempt to monograph the genus for over 60 years, and subsequent treatments of *Dichaea* were largely floristic. Probably because of the somewhat confusing grouping of species proposed by Kränzlin, and, as mentioned above, the difficulty of understanding critical characters at the specific level on the sole basis of original diagnoses (many of them excessively synthetic), a common view prevailed that accepted a few, poorly defined specific concepts, mostly based on inadequate knowledge of type materials. Louis O. Williams (1941) contributed to elucidate the *D. trichocarpa* complex in the Mexican region, and O. Ames and D. S. Correll (1943) produced a series of studies on *Dichaea*, mostly dealing with the status of *D. pendula*, the complex of species around *D. echinocarpa*, and *D. morrisii* and its allies. However, their conclusions contributed to the consolidation of a generalized taxonomic system founded on broadly defined specific concepts, which, as mentioned before, resulted in the application of a few all-purpose *Dichaea* names to a wide range of different taxa. Such a view was generally followed by most subsequent workers in Neotropical floras, who in many cases preferred to ignore old taxonomic literature favoring the adoption of well established—albeit incorrect—names for various complexes of species difficult to characterize. This approach was particularly evident in the name *Dichaea muricata* (see discussion hereafter under the treatment of *D. morrisii*), which was widely applied to a complex of very different species

in the West Indies and in Central and South America, none of which are referable to the type (Dressler et al., 2006).

It was not until 1987 that the first modern taxonomic revision of *Dichaea* was produced by James P. Folsom for his doctoral dissertation (Folsom, 1987). Although the monograph was limited to the members of *Dichaea* sect. *Dichaea*, the study set a sound basis for our actual understanding of the genus's taxonomy. Among the species with persistent leaves, Folsom limited the sect. *Dichaea* to the taxa provided with muricate ovaries, implicitly accepting the segregation of the species with smooth ovaries (namely *D. tenuifolia* Schltr. and *D. tuerckheimii* Schltr.) in sect. *Dichaeastrum*. He also excluded from his study the species allied to *D. hystricina*, for which he suggested the need of a recognition at sectional level. On the other hand, he retained *D. camaridioides* Schltr. within the studied group but suggested the convenience of creating a monotypic section for this atypical species. Within his narrow grouping of species assigned to sect. *Dichaea*, Folsom informally proposed a framework of putative specific affinities, envisioning the existence of different species complexes based on morphological similarities and geographic distribution. These include the large *D. oxyglossa* and *D. cryptharrhena* complexes (both centered in Costa Rica and western Panama), the South American *D. lagotis* complex (mainly defined by characteristics of leaf venation), and smaller complexes like the *D. squarrosa* complex (centered in northern Mesoamerica), *D. pendula*, and the Amazonian complex of *D. histrio*. Folsom's ideas about relationships within the sections were mainly aimed to show the highly reticulate nature of

the ancestral history of the group; nevertheless, even in a broader circumscription of sect. *Dichaea* as proposed in the present paper, many of his informal groups are largely supported as good indicators of the evolution patterns in the genus.

In the generic treatment of Dichaeinae for the revised edition of Schlechter's *Die Orchideen*, Senghas accepted *Dichaea* with two subgenera, formally validating subgen. *Epithecia* (Senghas, 1995: 1856) for the group of species with articulate, eventually deciduous leaf blades. However, basing his subgenus on *Epithecia* Knowles and Westcott (1838), Senghas perpetuates a misconception that plagued the taxonomy of *Dichaea* for almost a century. He also suggested *D. muricata* as the type species of the genus *Dichaea*, a lectotypification precluded by the type material of this taxon recently brought to light by Pupulin (in Dressler, 2005) (Fig. 4).

Recent studies by Kurt M. Neubig and collaborators at the University of Florida, based on sequence data of ITS nrDNA as well as matK, trnL-trnF spacer, and atpB-rbcL spacer plastid DNA (unpubl. data), and aimed at estimating the phylogeny of the sections of *Dichaea*, support *Dichaea* as a monophyletic genus. According to molecular data, sect. *Pseudodichaea* is a monophyletic group, which should include a few species that are traditionally placed in sect. *Dichaeopsis* on the basis of their smooth ovaries. Section *Dichaeopsis* is highly polyphyletic. Sections *Dichaeastrum* and *Dichaea* together form a monophyletic group; however, sect. *Dichaeastrum*, differentiated from sect. *Dichaea* primarily by a glabrous ovary, is potentially polyphyletic within sect. *Dichaea* (Neubig, 2005; Neubig et al., 2005).

#### PHYLOGENETIC PLACEMENT OF *DICHAEA*

Although he did not expressly discuss the generic relationships of his new genus, Lindley (1833) placed *Dichaea* in the Vandaeae, probably on the basis of the pollinarium provided with a caudicle united to a distinct viscidium. Later, he listed *Dichaea* within the Brassidaeae, close to *Fernandezia* Ruiz & Pav. (Lindley, 1853), with which the genus shares the presence of elongated stems covered with numerous 2 two-ranked, conduplicate, small leaves. All the other members of the Neotropical

Vandaeae provided with four superposed pollinia [i.e., *Batemanina* Lindl., *Colax* Lindl. (= *Pabstia*), *Galeottia* A. Rich., *Grobya* Lindl., *Huntleya* Lindl., *Promenaea* Lindl., *Stenia* Lindl., *Warrea* Lindl. (including *Warscewiczella* Rchb. f.), and *Zygopetalum* Hook.] were, however, grouped into the Maxillaridae (Lindley, 1853).

Bentham (1881) included the genus *Dichaea* in the tribe Vandaeae, subtribe Maxillarieae, a group of strictly American epiphytes character-

ized by the leaves lacking prominent ribs and the almost-always single-flowered inflorescences. Other genera in the subtribe were *Camaridium*, *Clowesia* (although considered doubtful in affinities), *Maxillaria*, *Mormolyca*, *Ornithidium*, *Schlimmia*, *Scuticaria*, and *Stenia*. He considered *Dichaea* to be closely allied to *Camaridium* and *Ornithidium*, mainly on the basis of vegetative architecture, that is, the stems provided with distichous leaf-sheaths, mostly bearing leaf blades, and the axillary, single-flowered peduncles. However, most of the genera of subtribe Zygopetalinae, including *Zygopetalum* and the genera of the *Huntleya* grade, were placed by Bentham in subtribe Cyrtopodieae, suggested as a connecting link among the Maxillarieae, characterized by taxa provided with a prominent mentum and the vegetative habit typical of Cymbidieae.

In 1887, Pfitzer created the series Dichaeinae to group species of Neotropical, ebulbose plants with two-ranked, duplicate leaves, single-flowered inflorescences, and four pollinia, including in the series the genus *Dichaea* and creating *Dichaeopsis* for a distinct subset of species, characterized by articulated leaves and glabrous ovaries. The phylogenetic placement of the genus *Dichaeopsis* is uncertain, but Pfitzer suggests it may be closer to the pseudobulbless Oncidiinae than to *Dichaea*, treating it as a sort of link between the sympodial and monopodial Pleuranthae duplicatae (Pfitzer, 1887). In his *System der Orchidaceen*, Schlechter (1916a) included *Dichaea* in the monotypic subtribe Dichaeae, grouped with Pachyphyllae, Pterostemmaeae, and Sarcanthae in the subseries Monopodiales of his Pleuranthae. Among the genera of the subseries (i.e., plants with apical development usually indeterminate), *Dichaea* is characterized by the presence of an infrastigmatic ligule; the single-flowered, lateral inflorescences; and the small-sized flowers.

In 1923, Kränzlin included *Dichaea* among the pseudomonopodial, monandrous orchids. This informal alliance embraced parts of Bentham's Sarcantae and Maxillarieae, Pfitzer's subtribes Dichaeinae and Pachyphyllinae and part of his Oncidiinae-Odontoglosseae, and Lockhartiinae Schltr. On the basis of vegetative architecture (i.e., the pseudobulbless, simple or few-branched stems;

the distichously arranged leaves; and the mainly single-flowered inflorescences), Kränzlin grouped here *Dichaea* with the genera *Centropetalum* Lindl., *Lockhartia* Hook., *Orchidotypus* Kraenzl., *Pachyphyllum* Kunth, and *Pterostemma* Lehm. & Kraenzl. Among the genera of the group, he distinguished *Dichaea* by the lateral sepals connate to the column forming a mentum (or chin), the leaves dorsoventrally flattened (not "equitant") and persistent, the anchoriform-to-rhombic lip, and the commonly muricate fruits.

Dressler and Dodson (1960) assigned *Dichaea* to the monotypic Dichaea alliance, one of the three alliances of the Oncidiinae (together with the *Oncidium* and the *Ornithocephalus* alliances), distinguishing it within the subtribe by the four pollinia, the column with a short rostellum, and the usually anchor-shaped lip. In his fundamental work on orchid systematics, Dressler (1981) included *Dichaea* in the monotypic subtribe Dichaeinae Schltr. (tribe Maxillarieae), characterizing the genus by its anomalous habit, interpreted as an extreme sympodial branching, with each inflorescence terminal on a stem of one internode. However, he noted a strong similarity between *Dichaea* and the *Chondrorhyncha* complex and suggested its possible derivation from Zygopetalinae-like ancestors. Although they placed tribe Maxillarieae in subfamily Epidendroideae instead of Dressler's Vandoideae, Burns-Balogh and Funk (1986) basically followed Dressler (1981) in the treatment of tribe Maxillarieae. It is characterized by the incumbent anther, four superposed pollinia in unequal sets, sterile caudicles and tegular stipe, and a solid viscidium. They included in Maxillarieae 10 subtribes, including the monotypic Dichaeinae, with an estimated 45 species in the genus *Dichaea*. The phylogenetic analysis carried out by the authors included *D. morrisii* Fawc. & Rendl. (*vel affinis*) and *D. panamensis* Lindl., two species of *Dichaea* with articulate leaves (Burns-Balogh and Funk, 1986: 65) differing in ovary vestiture. In his revision of the phylogenetic relationships and classification of the Orchidaceae, Dressler (1993b) definitively placed *Dichaea* in subtribe Zygopetalinae, a large assemblage of some 30 genera here tentatively divided into three alliances and four distinctive genera.

Among the genera with apparently no close relatives within the subtribe is *Dichaea*, defined by the monopodial plants and the single-flowered inflorescences. Other anomalous genera include *Cheiradenia*, *Scuticaria*, and *Vargasiella*; however, Dressler considered the latter genus sufficiently distinct from the rest of the Zygopetalinae to deserve its own monotypic subtribe (eventually formally validated by Romero and Carnevali, 1993).

Szlachetko (1995) considered *Dichaea* as the only member of a monotypic subtribe Dichaeinae, one of three subtribes of “monopodial orchids” included in tribe Dichaeae Pfitz. (together with Vargasiellinae Romero and Carnevali and Pachyphyllinae Pfitz.), interpreted as an early and blind evolutive offshoot of the oncidoid line. Within the tribe, Dichaeinae are here characterized by the duplicate leaves, the single-flowered inflorescence, the well-developed clinandrium, and the single stipe, dilated at apex. Szlachetko (1995) argued that the greatly reduced, oncidoid rostellum and viscidium of *Dichaea* would preclude the inclusion of the genus in the Zygopetalinae. Nevertheless, he noted that velamen and seed morphology indicate that the probable ancestor of *Dichaea* should be found among the maxillarioid genera.

In the same year, Senghas published the first part of his systematic revision of the tribe Oncidieae for the third, revised edition of Schlechter’s *Die Orchideen* (Senghas, 1995). Here he accepted *Dichaea* as the monotypic member of Dichaeinae, one of the four subtribes included in an informal *Subtribusgruppe* (or *tribella*) Tetrapolliniata. Dichaeinae is mainly distinguished from the other subtribes of the group (i.e., Ornithocephalinae Schltr.,

Telipogoninae Schltr., and Vargasiellinae) by the vegetative, “pseudomonopodial” habit and the single-flowered inflorescence. Subtribe Pachyphyllinae is excluded from the alliance on the basis of the number of pollinia.

Although primarily focused on generic relationships of Stanhopeinae, the combined *matK*, *trnL-F*, and ITS molecular analysis of the Maxillarieae carried out by W. M. Whitten and collaborators indicated high bootstrap support for the monophyly of Zygopetalinae and confirmed Dressler’s view about the inclusion in the subtribe of the morphologically anomalous genus *Dichaea*, together with a unexpected position of *Cryptarrhena* R. Br. embedded within the Zygopetalinae. These preliminary findings based on molecular evidence were recently confirmed by work aimed at clarifying generic relationships of Zygopetalinae through the analysis of combined nuclear and plastid DNA sequence data (Whitten et al., 2005). Here several grades are recognizable within the subtribe: a *Huntleya* grade (including *Dichaea*), with pseudobulbs mainly absent and conduplicate leaves; a *Zygopetalum* grade, with conspicuous pseudobulbs and usually convolute leaves; and a *Warrea* grade, with homoblastic pseudobulbs and plicate leaves. In the combined analysis, *Cryptarrhena* is strongly supported on a long branch basal to *Dichaea* and the *Huntleya* clade. *Dichaea* is supported as a monophyletic group, sister to *Huntleya* and to the rest of the so-called *Chondrorhyncha* complex (Garay, 1969), and the representative species are remarkable for the high levels of sequence divergence, showing a great potential of ITS and plastid regions sequencing for resolving species relationships within the genus.

#### THE GENUS *DICHAEA* IN COSTA RICA

The first species of *Dichaea* to be revealed to science from Costa Rica were collected by Hermann Wendland (1825–1903) during his visit to the country in 1856–1857. In 1866, on the basis of these collections, Reichenbach described *D. brachypoda* from San Miguel de Sarapiquí and recorded *D. trichocarpa* from the vicinity of Cartago (Reichenbach, 1866).

Around 1865–1866, A. R. Endrés moved to Costa Rica from Guatemala, and for the next 10 years he played a leading role in the botanical exploration of the country and the discovery of

hundreds of new orchid species (Ossenbach, 2003). He traveled extensively throughout the country, making collections along the Pejivalle and Pacuare rivers along the Caribbean drainage, visiting the Sarapiquí valley and the northern plains of San Carlos, as well as the region of Dota on the Pacific slopes of the Talamanca chain (Pupulin and Ossenbach, 2005). He sent his specimens, notes, and fine botanical sketches to Prof. Heinrich Gustav Reichenbach at Hamburg. Among these materials, analytical drawings of at least 11 different

species of *Dichaea* are conserved (Fig. 5–6), including *D. amparoana* (Endrés *Dichaea* No 4, W-R 38607!), *D. costaricensis* (Endrés *Dichaea* No 29, W-R 36740!), *D. hystricina* (Endrés *Dichaea* No 31, W-R 33347!), *D. lankesteri* (Endrés *Dichaea* No 32, W-R 18040!), *D. panamensis* (Endrés *Dichaea* No 28, W-R 36719!), *D. pendula* (Endrés *Dichaea* No 29, W-R!), *D. poicillantha* (Endrés *Dichaea* No 8, W-R 38602! & 38603!; Endrés *s.n.*, W-R 18035!), *D. trulla* (Endrés *Dichaea* No 26, W-R 38509!), *D. tuerckheimii* (Endrés *Dichaea* No 12, W-R 38527!; Endrés *s.n.*, W-R 38598!), *D. viridula* (Endrés *Dichaea* No 11, W-R 38598!; Endrés *Dichaea* No 26, W-R 36722!), and *D. fragrantissima* ssp. *eburnea* (Endrés *Dichaea* No 1, W-R 38612!; Endrés *s.n.*, W-R 10592!; Endrés *s.n.*, W-R 10597!;

18375!, later determined by Kränzlin as *D. morrisii*). Endrés's drawings offer precise views of the plants' habits, flowers, and floral dissections, including enlarged details of small and characteristic structures, such as columns, pollinaria, and microscopic sections of the fruits (e.g., W-R 38631!). Unfortunately, during the life of Reichenbach *f.* and after his death in 1889, the fundamental legacy by Endrés was left in oblivion in Reichenbach's herbarium.

The checklist of the orchids of Central America by Hemsley, originally published in a condensed version in the *Gardener's Chronicle* for 1879 (Hemsley, 1879) and later expanded in volume 3 of the botany series of Godman and Salvin's *Biologia Centrali-Americana* (Hemsley, 1883), is the first catalog of the genus *Dichaea* in Mesoamerica. Here Hemsley

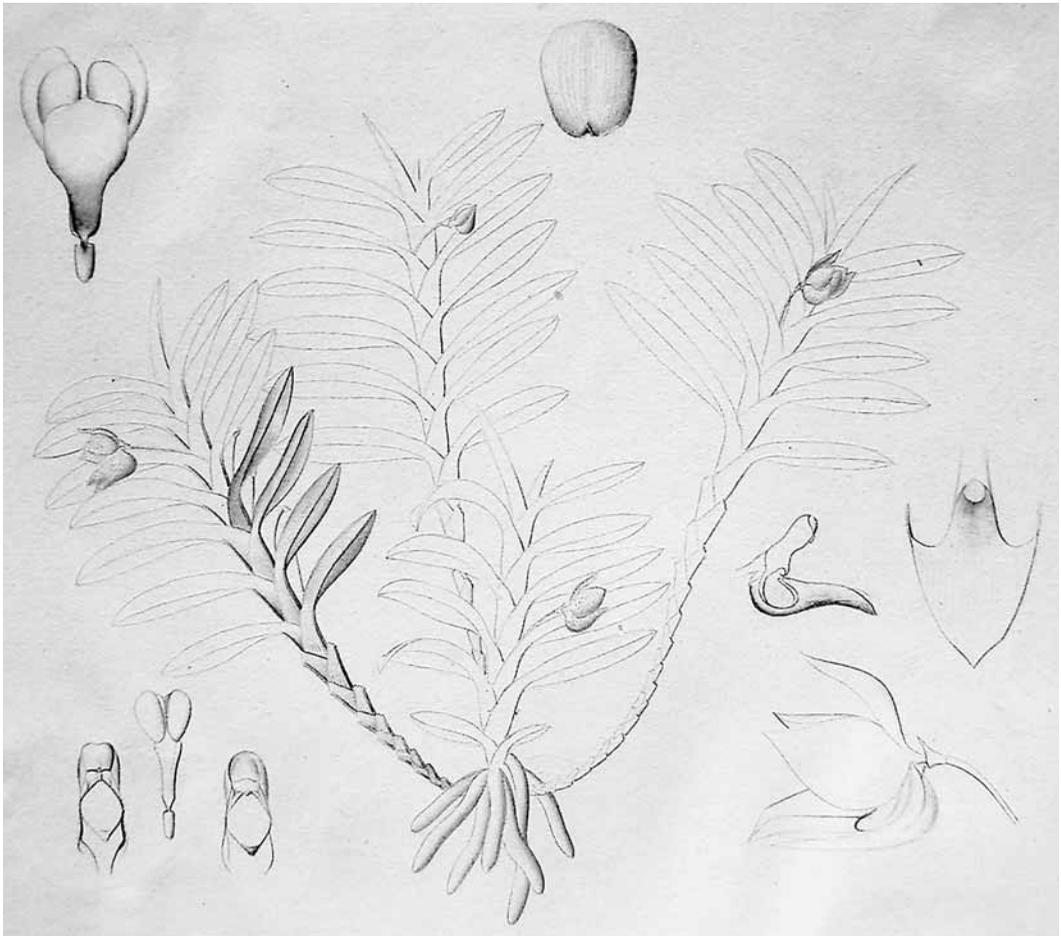


FIGURE 6. Drawing of *Dichaea panamensis* by A. R. Endrés (*Rchb. Orch.* 36719, W). Reproduced with the kind permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

reported nine known species and two unidentified taxa for the region. *Dichaea brachypoda* and *D. trichocarpa* are the only two species recorded from Costa Rica on the basis of Wendland's findings published by Reichenbach in his *Orchideae Wendlandianae* (1866). In 1915, in the treatment of Dichaeinae for his book on orchids, Schlechter did not refer explicitly to any of the species of Costa Rica, just mentioning *D. muricata* and *D. pendula* as native to Central America (Schlechter, 1915). However, in his catalog of Central American orchids, published just three years later, these two species are recorded as endemic to Mexico and Nicaragua, and to Mexico and Guatemala, respectively (Schlechter, 1918b). By the end of the second decade of the past century, the list of *Dichaea* Schlechter could record from Costa Rica was still based on the collections made by Wendland more than 60 years earlier.

The beginnings of the next decade, the 1920s, mark a period of great botanical activity in Costa Rica, thanks to the efforts by the botanists and collectors of the newly founded Instituto Físico-Geográfico and Museo Nacional (who included Guillermo Acosta, Anastasio Alfaro, Alfred and Curt Brade, Alberto M. Brenes, Henry Pittier, Adolf Tonduz, and Carl Wercklé) and their close relationship with Rudolf Schlechter at the Botanical Museum of Berlin-Dahlem. During this same period, and for the following 20 years, there was also a flourishing of field activity by the resident English naturalist Charles H. Lankester, who established fruitful scientific cooperation with Robert A. Rolfe at Kew and, most notably, with Oakes Ames at the Botanical Museum of Harvard University (Fig. 7). Most of the species of *Dichaea* from Costa Rica were described in those years: *D. ciliolata* (Rolfe, 1917), *D. acostae*, *D. acrolephara*, *D. amparoana*, *D. brenesii*, *D. bradeorum*, *D. costaricensis*, *D. oxyglossa* and *D. poicillantha* (Schlechter, 1923a–d), *D. cryptarrhena* and *D. dammeriana* (Kränzlin, 1923), *D. lankesteri* (Ames, 1923), and *D. standleyi* (Ames, 1925).

By 1937, in his treatment of the Orchidaceae for Standley's *Flora of Costa Rica*, Ames (1937) recorded 28 species, 15 of which were considered endemic at that time. Among his records, Ames included sterile collections tentatively identified as *Dichaea vaginata* Rehb. f. ex Kraenzl., as well as *D. graminoides* (Sw.)

Lindl. and *D. morrisii* Fawc. & Rendl., known only on the basis of "referred collections," and *D. echinocarpa* (Sw.) Lindl., here considered as closely allied but hardly reducible to *D. pendula* (Aubl.) Cogn. He also noted that, despite the citations by Reichenbach (1866) and Schlechter (1915), no Costa Rican specimens of *D. brachypoda* Rehb. f. (supposedly ranging to Colombia and Surinam) were seen.

Another distinctive species of *Dichaea* from Costa Rica, *D. gracillima*, was described the next year by C. Schweinfurth on the basis of a collection by A. M. Brenes from the vicinity of San Ramón (Schweinfurth, 1938); no subsequent collections of this rare species are known.

In 1984, during the preparatory work for his Ph.D. thesis, James B. Folsom of the University of Texas at Austin made extensive collections of *Dichaea* in Costa Rica. Among his Costa Rican findings, *D. sarapiquinsis*, *D. schlechteri*, and *D. eligulata* (the last one from material of unknown origin cultivated in Costa Rica) were proposed as new to science in his doctoral dissertation (1987) and were formally published in 1994 (Folsom, 1994).

In 1992, Mora-Retana and García offered the next catalog of *Dichaea* in Costa Rica in their updated checklist of Costa Rican Orchidaceae (Mora-Retana and García, 1992), where 27 species are recorded. Although the total number of taxa is very close to that recorded by Ames more than 50 years before, the opinions of the authors only coincide with Ames on 15 taxa (some of which, in the present treatment, are considered synonyms or not occurring in the study area). Mora-Retana and García first record for the country *D. cryptarrhena*, *D. diandra*, *D. glauca*, *D. neglecta*, *D. squarrosa*, *D. swartzii*, and *D. trulla*, in addition to *D. eligulata*, *D. obovatipetala*, *D. retroflexiligula*, *D. sarapiquinsis*, and *D. schlechteri*, still unpublished at that time. Contrary to the opinion of Ames, they excluded *D. acrolephara*, *D. bradeorum*, *D. brenesii*, *D. echinocarpa*, *D. muricata*, *D. obovatipetala*, *D. pendula*, *D. similis*, *D. suaveolens*, *D. tuerckheimii*, *D. vaginata*, *D. verrucosa*, and *D. wercklei*. A more-conservative view was adopted by Dressler (1993a) in his field guide to the orchids of Costa Rica and Panama, where he only accepted 20 species, among which *D. tenuifolia* is recorded for the first time. The treatment also offers the first comprehensive

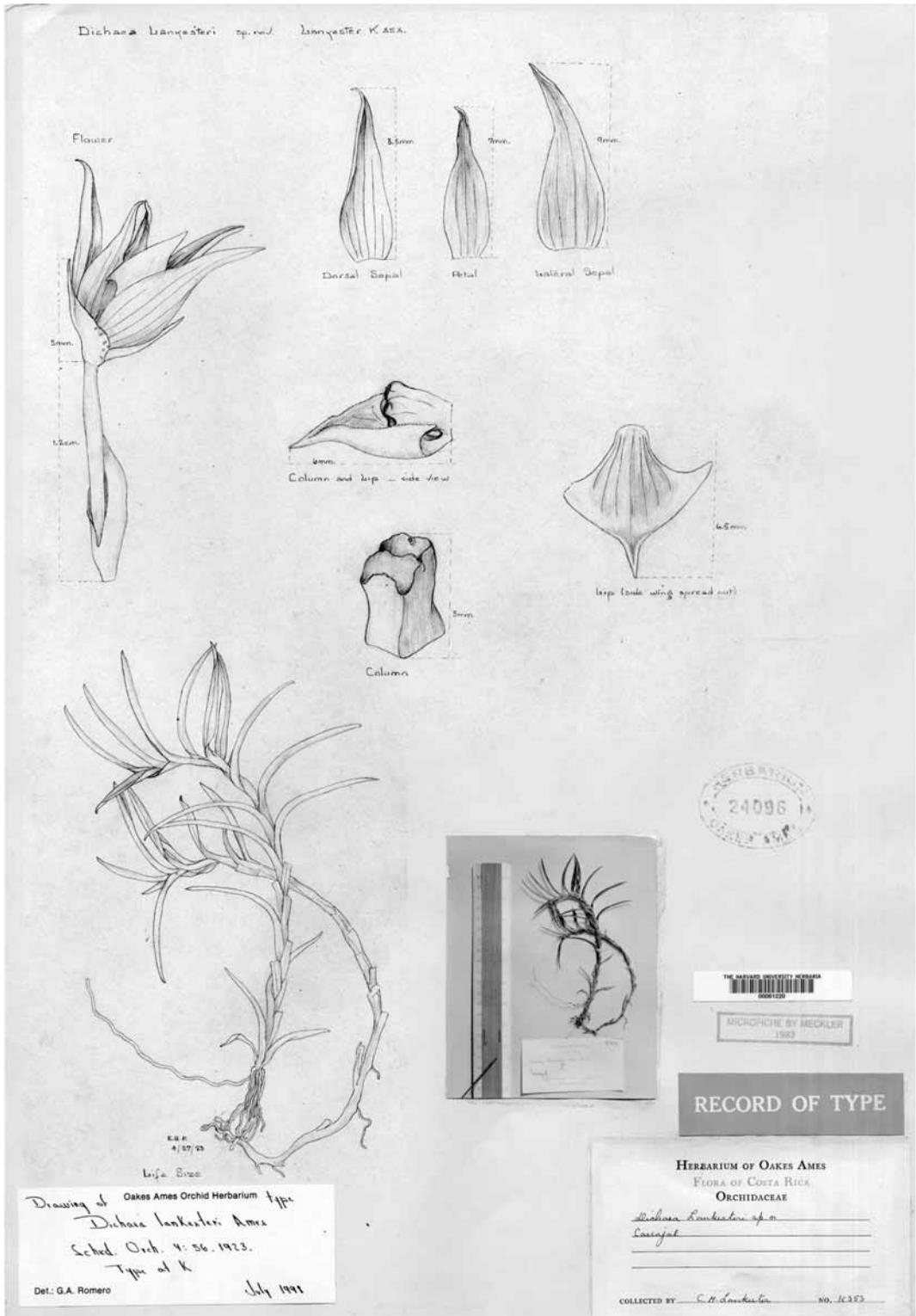


FIGURE 7. Tracing of the holotype of *Dichaea lankesteri* (AMES 24096), reproduced with the kind permission of the Director, Harvard University Herbaria.

key to the genus in Costa Rica, mostly based on characters of leaf articulation, size, and ornamentation; ovary vestiture; tepals morphology; and characteristics of the columnar ligule (Dressler, 1993a). Pupulin (2002) recorded a total number of 26 species, presenting a list of synonyms for all the accepted taxa, based on vouchered specimens, and including for the first time *D. gracillima* and *D. robusta*, together with the recently described *D. elliptica*, published by Dressler and Folsom that same year (Dressler, 2002). This figure was raised to 29 species in Dressler's treatment for the *Manual de plantas de Costa Rica* (Dressler, 2003), where he added *D. acostae* (known only from the type), *D. muricatoides* (hereafter considered conspecific with *D. poicillantha*), and *D. neglecta*, likely based on a misinterpreted

specimen from the Pacific region of Tarrazú. In 2005, in his treatment of the genus for *Vanishing Beauty—Native Costa Rican Orchids*, the author included 25 previously known species of *Dichaea*, describing a new species (*D. filiarum*) and presenting photographs of two still-unpublished taxa (*D. fragrantissima* ssp. *eburnea* and *D. globosa*) for a total of 28 taxa (Pupulin, 2005b). The treatment offers short ecological and geographical notes for most of the species and illustrates in color 20 of the taxa. The same author recognized the distinctness of Costa Rican populations of undulate-leaved *Dichaea*, publishing *D. viridula* in 2005 (Pupulin, 2005c), and eventually Dressler and co-authors (2006) elucidated the complex of species around *D. morrisii*, describing two new taxa from Costa Rica.

#### MATERIALS AND METHODS

Plants of *Dichaea* were collected all over Costa Rica during 2000–2006, with particular emphasis on the search at type localities and other previously less-sampled areas. Selected species intended for morphological comparison, representative of groups scarcely represented in Costa Rica, were also obtained from northern Mesoamerica (Guatemala, Nicaragua) and from South America (Ecuador). The specimens were grown until flowering in the greenhouses of Jardín Botánico Lankester (JBL), Universidad de Costa Rica, located at around 1300 m above sea level. Specimens collected prior to the beginning of the fieldwork intended for the present study, and accessed to the living plant collections of JBL, were also studied and determined; when associated to significant field data, they were included in the treatment. Other specimens from the concerned area were studied and annotated at AMES, CR, INB, K, SEL, USJ, and W. Phenology and floral activity were recorded both in the field and in cultivated specimens. Individual plants were photographed, illustrated, and conserved as *exsiccata* and spirit-preserved specimens (including flowers and representative portions of the stem) for future reference. Herbarium specimens were deposited at CR and USJ. FAA material was included in the reference collections of JBL, and indicated in the treatment as “JBL-Spirit.” Stem structure and vegetative organization of representative species were studied in living specimens, and vouchers were preserved in FAA (JBL-Spirit). Leaf venation was observed in transmitted light, and individ-

ual leafy stems were scanned in transmitted light at 2400 dpi resolution with an Epson Film Adapter B81317 on a flatbed scanner Epson Perfection 2400 Photo; reference vouchers were conserved in FAA. Pollinaria were scanned at 2400 dpi resolution, drawn with a Leica Wild M8 stereomicroscope provided with drawing tube, and conserved in the reference collections of JBL. All measurements were taken, when possible, from living specimens. Type specimens were photographed and/or scanned at high resolution (300 ppi), and the resulting digital images were included in the reference collections of JBL. Whenever possible, all the taxa included in the present study were illustrated in composite plates from living specimens; in the case of highly variable morphological species, plates were prepared from representative individuals of the different morphs. Illustrations included a typical plant habit, the flower and dissection of the perianth, lateral view of the column and lip, a ventral view of the column, and the pollinarium and anther cap. Plate composition was as consistent as possible to facilitate taxa comparison. Sixty-two morphological and anatomical equally weighted characters were scored for 28 Costa Rican species, plus two *Dichaea* species from outside the study area and three Zygopetalinae species as outgroups, and incorporated into a matrix (missing data coded as “?”). Maximum parsimony analysis was performed with PAUP\*4.0b10 (Swofford, 1999). Genetic distance trees were generated and manually compared for congruence.

## MORPHOLOGY

*Roots*

Roots of *Dichaea* are of two types: basal, anchoring the plant and growing on the substrate, and adventitious-aerial, sometimes becoming prostrate epiphytic. Functional distinction between the two types is less obvious in species with prostrate, creeping habit (e.g., *D. tuerckheimii* and *D. squarrosa*), but also in this case the lower nodes of the stem usually do not produce adventitious roots, and aerial roots are always associated with mature stems, being chronologically secondary. Independently of the type, *Dichaea* roots are typically cylindrical and never branched, unless the vegetative apex has suffered physical damage, but also in this case branching is occasional and seemingly restricted to some of the taxa (e.g., *D. obovatipetala* and *D. sarapiquinsis*). No root branching occurs in species provided with thick roots, that is, >2.5 mm in diam., like *D. glauca* and *D. panamensis*. Substrate and secondary epiphytic roots are usually wider in diameter than exclusively aerial roots, and in some species the side appressed to the host stem is somewhat flattened. At early developing stages, secondary roots are often covered with dense and low trichomes that likely correspond to modified epidermal cells, although no attempt has been made to survey the occurrence of this character throughout the genus. Analyses of root anatomy carried out for this study were scattered, and mostly aimed at testing structural analogies among *Dichaea* species pertaining to different groups. In tested samples, the roots vary in diameter between 0.3 and 5.5 mm. Differences in root diameter are mainly due to the variable thickness of the cortex (0.1–2.4 mm) rather than to variations in velamina organization and number of velamen layers. Stele diameter is rather constant within the sampled species, around 0.2 mm. Velamen in the examined taxa is mono- to bi-seriate, with the epivelamen cells smaller than the elongate cells of the endovelamen, roughly corresponding to the *Cymbidium* type according to Porembski and Barthlott (1988). In some cases (e.g., *D. trichocarpa*), the outer velamen layer is composed of irregularly shaped cells, some of which strongly elongate, giving the root a distinct tuberculate appearance. Along the outer velamen layer of *D. panamensis*, sparse unicellular trichomes are also present. Root thickness is mostly not taxonomically informa-

tive within species complexes but may be useful for recognition of selected taxa. When associated with other characters of gross vegetative morphology, root thickness allows the identification of some species (e.g., *D. glauca*, *D. panamensis*, and *D. squarrosa*) both in the field and in herbaria. In living specimens of *Dichaea glauca*, root diameter varies in section between 2.7 and 4.0 mm, but average diameter taken at five different points in individual plants is always greater than 3 mm and has diagnostic value. Roots of *D. panamensis* attain the greatest diameter in the genus, with individual sections up to 5.5 mm wide. However, a survey made on 10 individuals, each with five root measurements, shows that root diameter is highly variable in this species, with single values included between 1.8 and 5.5 mm, and individual plant averages varying from 2.02 to 3.98 mm. Apart from the features inherent to root anatomy, the relative position of the roots with respect to the stem proved to be informative at the sectional level. Together with the primary, basal roots anchoring the plant to the substrate, in most *Dichaea* species (both in the primitive and the advanced taxa) adventitious roots are produced all along the stem. Secondary roots are usually produced opposite to the inflorescence bractlet, immediately outside and apically proximate to the node. Frequency of production of caulinar roots varies according to the species. The most common types include the production of a new root proximally to each node (e.g., the *D. lankesteri* and *D. morrisii* groups, *D. cryptarrhena*, *D. squarrosa*, and *D. trulla*), and the exertion of secondary roots every two to three nodes (e.g., *D. hystricina*, *D. oxyglossa*, *D. obovatipetala*, *D. pendula*, and *D. viridula*). Greater interspacing between adventitious roots also exists, with new roots produced each 4 to 5 nodes (e.g., *D. tuerckheimii*) (Fig. 8–9). Because the leaf sheaths encircling the stem are closed only basally, the secondary roots usually do not pierce the sheath but emerge from the space left among the lateral margins of the subtending sheath (Fig. 10). In a relatively few cases, caulinar roots attain considerable length, being visible once emerged from the leaf sheaths and appearing axillary to the subtending leaf. In most cases, however, these roots are very short and remain completely enclosed and hidden within the sheaths, giving the plant the appearance of rooting only

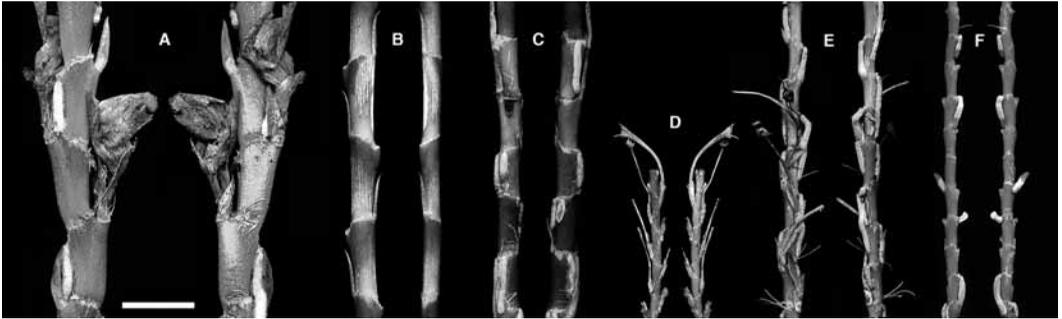


FIGURE 8. Stems of *Dichaea* species. **A**, *D. fragrantissima* ssp. *eburnea* (Blanco & al. 2706); **B**, *D. glauca* (JBL-01259); **C**, *D. trulla* (Whitten 2096); **D**, *D. panamensis* (Karremans 621); **E**, *D. lankesteri* (Bogarín 863); **F**, *D. pendula* (Pupulin 5512). Scale bar = 1 cm.

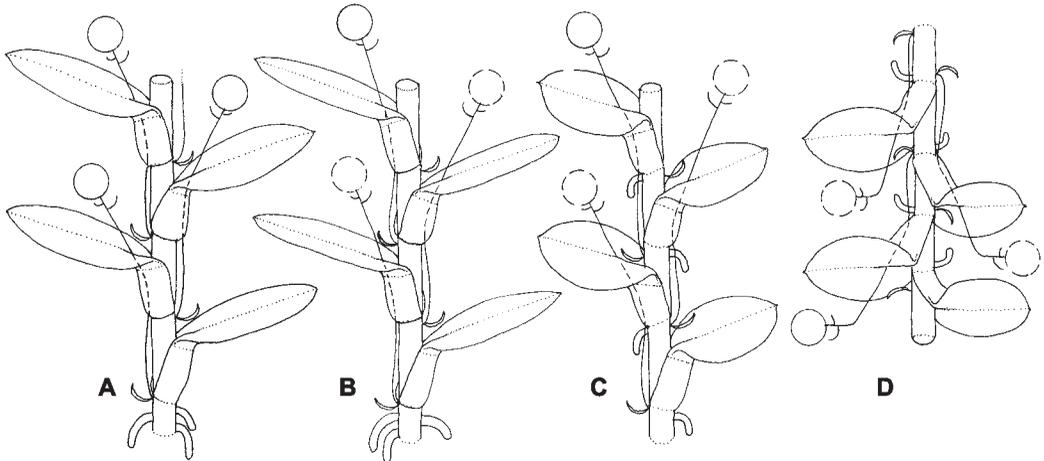


FIGURE 9. A schematic representation of the basic types of stem organization in *Dichaea*. **A**, Stem with roots restricted to the base and simultaneous inflorescences (*D. glauca*); **B**, stem with roots restricted to the base and successive inflorescences (*D. panamensis*); **C**, stem with basal and caulinar roots and successive inflorescences (*D. fragrantissima*); **D**, pendent stem with caulinar roots and successive inflorescences, showing the geniculate peduncles (*D. poicillantha*). Leaves are articulated in A, B, and C, but not D.

at the base. *Dichaea glauca* and *D. panamensis* are noteworthy in having only primary roots at the base of the stem. No adventitious roots are produced along the stem also in old plants of considerable length, although in *D. panamensis* new plantlets and associate roots may occasionally be produced at the nodes of older stems. The absence of secondary roots is usually positively associated with root diameter, and could be explained as a defense against tissue damage provoked by the lateral exertion of a thick root; however, roots of considerable diameter are also found in *D. squarrosa*, which regularly produces adventitious roots all along the stem.

#### Stem

As noted by Folsom (1987), the proper interpretation of nodal stem structure, and the consequent growth form of *Dichaea*, is at the heart of a minor controversy. Plants of *Dichaea* have been interpreted as monopodial (e.g., Dressler and Dodson, 1960: 51; Garay and Sweet, 1974), sympodial (e.g., Withner et al., 1974), and pseudomonopodial (Kränzlin, 1923; Withner et al., 1974). Withner et al. (1974: 322) noted that individual stems may continue to produce leaves for a long period of time, but when new stems finally develop, they are formed in sympodial fashion from the base of the previously formed growth. On the basis of

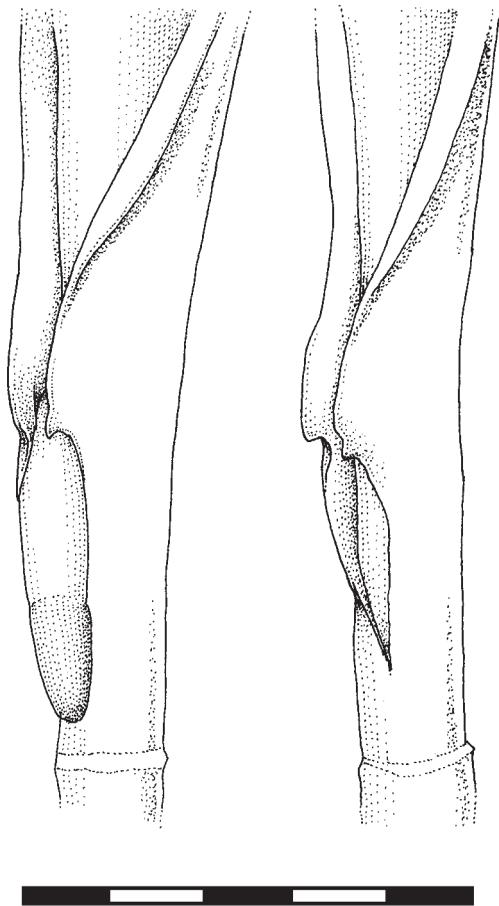
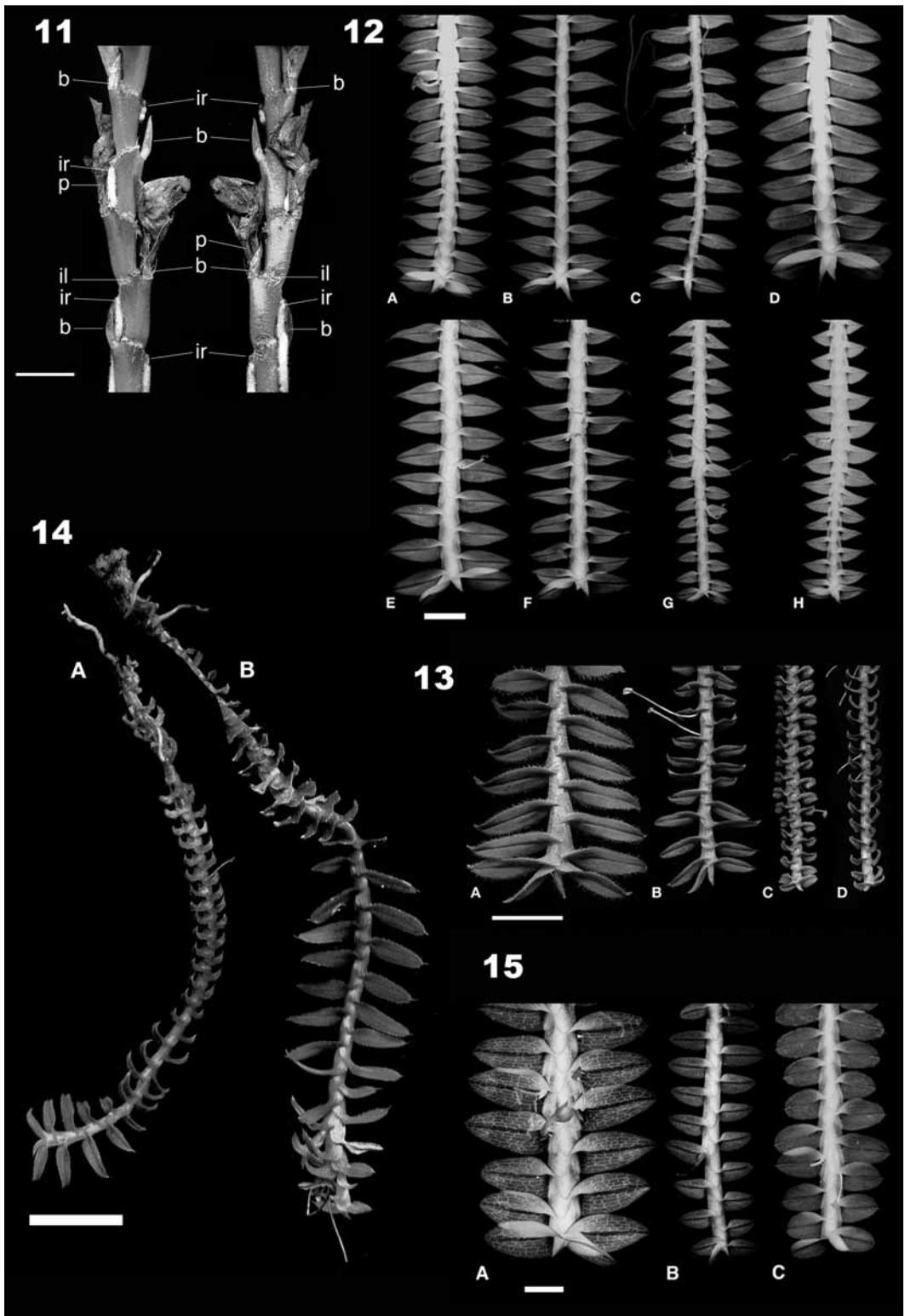


FIGURE 10. Caulinar root emerging from stem, without piercing the leaf sheath (*D. pendula*, Pupulin 5512). The root is removed in the right drawing. Scale bar = 5 mm.

data by Wirth (1964), Dressler (1981) considered the inflorescence of *Dichaea* as produced directly opposite to the base of a leaf, offering two alternative interpretations for this inflorescence type. In the first explanation, the growth habit of *Dichaea* would represent an extreme case of sympodial growth, with each flower terminal and the next internode of the stem produced from the axil of the subtending leaf. The alternative interpretation is that the axillary bud arises together with the tissues of the elongating internode, thus becoming opposite the leaf at the next node, above the leaf to which it is axillary (Dressler, 1981: 39–40), resulting in a modified scheme of the monopodial habit. Because of the proximity of the lateral structures (buds and adventitious roots) to

the node, intended as the horizontal zone along the axis at which a leaf is formed, their interpretation as axillary (hence a monopodial growth form of *Dichaea*) or terminal (sympodial habit) is doubtful (Fig. 11). However, lateral buds arise outside the leaf sheath, and previous analyses reveal that the vascular tissue supporting the lateral buds is at least partially arising from the previous node (Folsom, 1987). On the other side, the leaf sheath begins to differentiate from the parenchymatous cortex of the stem in internodal regions (opposite to the bud), until it becomes separated from the stem at the succeeding node. The anatomical work done by Folsom was unfortunately restricted to derived members of sect. *Dichaea*, but further analyses of species characterized by sets of plesiomorphic characters are currently under way to clarify the origin and interpretation of the unusual growth habit of *Dichaea* (F. Pupulin and J. Marín, in prep.).

The mature (reproductive) stems of *Dichaea* vary greatly in length (4–110 cm), arrangement, and spatial organization. Most of the Costa Rican species have pendent stems, somewhat varying from scandent to laxly pendent, whereas some taxa have distinctly suberect to erect habit and others are distinctly creeping. The stems in *Dichaea* are typically borne at right angles to vertical host stems, becoming shortly arching-pendent with age. However, in some species the stems are distinctly and laxly pendent also in early developing stages; truly pendent taxa usually have longer stems. In species with creeping habit or freely branching stems, stem orientation is various, although in mature specimens most of the stems of a single plant are pendent. In species with erect or semi-erect habit, the stems usually have greater diameter (e.g., the complex of *D. morrisii*), or they are rounded in section (e.g., *D. trulla*) or provided with distinctly ancipitous margins (e.g., *D. glauca*). Also when the stems are borne erect-spreading, they usually curl with age, often becoming arched and ultimately pendent. Characteristics of gross vegetative architecture are often diagnostic in the absence of fertile material. Stems are usually few-branched, but some species can be recognized in Costa Rica by their freely branching stems, forming large and intricate mats (e.g., *D. costaricensis*, *D. obovatipetala*, and *D. trichocarpa*), whereas others are characteristically simple, or branch



FIGURES 11–15. **11**, Stem structure in species of *Dichaea* sect. *Pseudodichaea* (*D. fragrantissima* ssp. *eburnea*, Blanco & al. 2706). *b* = bractlet; *il* = leaf insertion point; *ir* = root insertion point; *p* = peduncle. Scale bar = 1 cm.

only after the destruction of the stem apex (e.g., *D. filiarum* and *D. viridula*). In cross section, the stems of *Dichaea* vary from rounded (with rounded leaf sheaths) to compressed (with dorsoventrally flattened sheaths) to slightly winged laterally (ancipitous). Although they are not of diagnostic value within complexes of closely related species, characteristics of the stem show taxonomically important variation useful at the sectional level and for the identification of some taxa.

### Leaves

The sheaths and the foliar blades of *Dichaea* differ in structure and orientation. The leaf sheaths completely cover the stem and run parallel to the plant main axis, whereas the blades twist to lie on the same vertical plane. Plants of *Dichaea* present, consequently, a frontal and a "rear" side, the former defined by the orientation of the adaxial blade of leaves. Leaf blades arrange to face the light, and when the stem is twisted in the opposite direction, the new leaves emerge facing the light "front." No reorientation, however, occurs in older leaves. Apart from axial twist, the leaves of *Dichaea* also show various degrees of spreading with respect to stem. In some species (e.g., *D. glauca*) the leaves are oriented in the same direction as the stem axis, whereas in most of the taxa they are arranged perpendicularly to the stem, and in some cases they are strongly reflexed. However, the angle of insertion of the leaf is highly variable within species, often also on single specimens and individual stems, making this character unreliable for taxonomic purposes.

With the exception of the species of the *D. trichocarpa* complex, *D. acostae*, and *D. trulla*, which have rounded stems and consequently rounded, clasping sheaths, the leaf sheaths of the remaining taxa are dorsoventrally flattened, somewhat loose, and in some cases characteristically inflated toward the base. Apart from the above-mentioned features, characteristics of the leaf sheaths convey little taxonomic information. Aside from the study area, plants of *D. neglecta* present conspicuously green veins

against the paler intercostal areas of the sheaths, which are provided with distinct green dotting, but chlorenchyma clusters are also present in variable concentrations in other species like *D. costaricensis* and *D. sara-piquinsis*, among others.

The presence of an articulation between the leaf sheath and the blade, or a special layer of cells capable of breaking away near the base of the leaf, is a common character in most members of the advanced Epidendroideae, but it is seemingly lost in some highly evolved orchids such as some species of the genera *Dichaea*, *Epidendrum* L., and *Macroclinium* Barb. Rodr. (Dressler, 1981). The presence or absence of an abscission layer has been widely used in the past to assess relationships within *Dichaea*, and the present study confirms it as a taxonomically informative character at the sectional level. Species of sect. *Pseudodichaea* and taxa previously treated as the sect. *Dichaeopsis* present an abscission layer at the base of the blade, so that the leaves are eventually deciduous. Leaf articulation is lost in species of the derived sect. *Dichaea*, and the leaves consequently rot in place.

Spatial separation of the leaves has been suggested as a taxonomically informative character in *Dichaea* (Folsom, 1987), and vegetative features proved to be useful in delimiting group of species. However, phenotypic variability largely prevents their use at the specific level, and gross vegetative architecture is often variable within a single taxon (Fig. 12). Internode length and blade width, which together define spatial leaf separation along the stem, present great plasticity in some species (e.g., *D. hystericina* and *D. poicillantha*), and different vegetative "morphs" previously interpreted as expressions of specific variations were found intermixed on single vegetative shoots (Pupulin, 2005a), making leaf spacing a scarcely useful character to identify species (Fig. 13–14). Nevertheless, in the study area, plants of *D. cryptarrhena* can be usually recognized even when sterile by the closely spaced leaves with overlapping margins; seemingly,

FIGURES 11–15. CONT. **12**, Intraspecific variations in spatial organization, shape, and venation of leaves in *D. poicillantha*. **A**, Bogarín 712; **B**, Bogarín 189; **C**, Bogarín 708; **D**, Pupulin 4137; **E**, Pupulin 3420; **F**, Pupulin 4662; **G**, Whitten 2030; **H**, Pupulin 5113. Scale bar = 1 cm. **13**, Intraspecific variations in leaf size and shape in *D. hystericina*. **A**, Bogarín 1464; **B**, Pupulin 4320; **C**, Bogarín 4085; **D**, Pupulin 3925. Scale bar = 1 cm. **14**, Habit transformation on single stems of *D. hystericina*. **A**, Pupulin 3925; **B**, Pupulin 3466. Scale bar = 1 cm (from Pupulin, 2005a). **15**, Interspecific variations in leaf venation. **A**, Strongly evident cross-veins in *D. filiarum*; **B**, reduced cross-veining in *D. costaricensis*; **C**, absence of cross-veins in *D. cryptarrhena*. Scale bar = 1 cm.

the narrow leaves well separated along the stem can distinguish plants of *D. oxyglossa*.

Leaf size is amply variable within the genus and it provides taxonomically useful information. Species of the *Dichaea morrisii* complex and *D. trulla* are easy to recognize also even when sterile by the large size of the leaves, usually longer than 5 cm, and this character has been used in separating species groups (e.g., Dressler, 1993a, 2003). On the other extreme, plants of *D. tuerckheimii* are unmistakable by their small leaves, barely reaching 4 mm in length. Within the larger complexes, however, phenotypic variability prevents the use of leaf size in species identification, with the possible exceptions of *D. dammeriana* and *D. pendula*, which consistently have leaves longer than 2 cm (Folsom, 1987).

In most of the species of *Dichaea*, leaf shape is grossly lanceolate-elliptic, with minor and often subtle variations toward more ovate-lanceolate or obovate-oblong outlines. Apically, leaves vary from rounded (e.g., *D. cryptarrhena*) to acuminate (e.g., *D. poicillantha*), but they are always provided with an abaxial, more-or-less elongate apicule. In *D. dammeriana*, the margins of the leaves tend to curl when the tissue dries, and old specimens as well as *exsiccata* of this species are usually recognizable by the apparent linear shape of the leaves. The succulent leaves of *D. squarrosa* also tend to assume a linear outline in dried material, but apart from these few cases, leaf shape is not a reliable taxonomic character to identify *Dichaea*. Some emphasis has been put in the past on characters and ornamentation of the leaf margins, which were variously described as minutely serrate, fimbriate, or ciliate. Apart from the distinctive *D. hystricina*, which presents cilia along all the leaf margins, in most of the species of *Dichaea* the apical portion of the leaf shows some degree of micro-ciliation, often variable among leaves of individual plants, offering no useful information as to species identity. Undulate margins of the leaves are diagnostic, in the study area, for *D. viridula*. Although difficult to describe by means of unequivocal terminology, leaf texture offers taxonomic information for some of the species in the concerned area. *Dichaea squarrosa* and, to a minor extent, *D. trichocarpa*, have thick to succulent leaves, a character often recognizable also in dried material. The leaves of *D. pendula*

are thin-textured, with the parallel veins somewhat visible in living plants, and the thin leaves of *D. viridula* have distinctly undulate margins. The leaves of *D. globosa*, which inhabits drier areas on the Pacific watershed, are usually thicker than those of related species in the *D. morrisii* complex.

Venation pattern, which has been considered to have diagnostic value in the past (Folsom, 1987), is generally of limited use in the taxonomy of *Dichaea* in Costa Rica and is not a reliable character to identify closely related species. In particular, the number of secondary veins (parallel to the midvein) proved to be highly variable within a single taxon, with a range of variation of 6–12 veins in *D. poicillantha*, including individual variation of 8–11 veins in leaves of a single stem (Fig. 12). The presence or absence, and the relative frequency, of cross-veins between the longitudinal veins of the leaf blades provide, in the geographic area of the present study, a diagnostic tool for some of the species. Whereas in most taxa no cross-veins are present, these veins are scattered in leaves of *D. costaricensis*, where they can be barely observed in live material, and they form an intricate net in the recently described *D. filiarum*, where they are evident also in the field just observing the leaves in transmitted light (Fig. 15).

The color of leaf blades in living specimens of *Dichaea* shows diagnostic variations, varying from grass green to dark green, olive green, or brownish, sometimes with a distinctly glaucous overcasting. This character is of limited utility in dried material, in which information on leaf pigmentation is lost. Unlike most of the species in sect. *Dichaea*, which present green leaves, some taxa have distinctly olive-green to brownish leaves and can usually be recognized also even when not in flower. In *D. dammeriana* and *D. filiarum* the upper surface of the leaves is somewhat prismatic, and in the latter species the adaxial pigmentation is often very dark brown. The apparently lepidote leaf surface in dried specimens of *D. dammeriana* is produced by the presence of over-sized raphide bundles in subepidermal cells, which become raised as the tissues dry (Folsom, 1987). The olive-green leaves of *D. viridula* are particularly thin, and the distinctly undulate leaf margins allow field recognition of this species even when sterile. Studies on leaf anatomy and epidermal cells

transformations, and their significance to improve photosynthetic response to suboptimal light exposition, are actually under way (F. Pupulin et al., in prep.), and at this stage we can only note that similar adaptations occur in other shade-tolerant taxa in the Zygotelinae, like species of *Benzingia* Dodson ex Dodson and *Chaubardiella* Garay. Cuticular deposits of wax can be observed in the leaves and sheaths of *D. glauca* and *D. panamensis*, giving these organs a glaucous appearance. Probably an adaptation to xeric conditions, the presence of a waxy cuticle that covers the epidermis is variable within species. In *D. glauca*, waxy deposits are always observed on both the adaxial and abaxial leaf surfaces, whereas in *D. panamensis* they may be present on both the surfaces or limited to the upper side of the blade, or completely absent. In cultivated specimens of *D. panamensis*, cuticular deposits are often lost, and the new leaves and sheaths are borne without protective layers.

#### *Inflorescence*

The inflorescences of *Dichaea* have been interpreted as borne opposite to the leaf and terminal (e.g., Withner et al., 1974). However, the inflorescence does not arise nodally but originates from the stem outside the leaf sheath and basal to the succeeding node (therefore appearing subopposite the next leaf). With the notable exception of *D. glauca*, which presents simultaneous inflorescences, all the other taxa from Costa Rica have successive inflorescences and the flowers are borne singly on the stem, or only occasionally in pairs. The structure of the inflorescence is remarkably similar throughout the examined species; it is composed of a terete peduncle, covered at the base by 2–3 bracts, bearing a single flower subtended by a double floral bract. Nevertheless, the relative position of the inflorescence (presenting the flower above or under the foliage) and the shape of the peduncle (straight vs. geniculate), determining flower orientation at anthesis, are taxonomically informative at the sectional level and, in rare instances, also can segregate species.

In the more primitive groups of species with articulate leaves (sect. *Pseudodichaea* + *D. glauca* + *D. trulla* + *D. panamensis*), the peduncle is straight and the flower is presented under the foliage, in a pendent-to-patent position according to stem orientation (flowers are patent to erect on suberect stems, almost pen-

dent in arcuate-pendent stems). In species of sect. *Dichaea*, which almost invariably present truly pendent stems, the peduncle is geniculate at the exertion point from the leaf sheath to become perpendicular to the stem. The flowers are accordingly presented above foliage and erect, parallel to the stem axis. Among species of sect. *Dichaea*, the straight inflorescence of *D. pendula*, bearing the flower under the foliage, is diagnostic; it is noteworthy that the pendent stems of *D. pendula* are arching apically, with the terminal portion almost horizontal, allowing a nearly erect orientation of the flower.

At the base of the inflorescence there are two or, more commonly, three tubular, overlapping bracts, which clasp the peduncle and are usually completely hidden by the leaf sheath. The apical bract is somewhat campanulate-inflated and partially exposed outside the sheath in *D. dammeriana*, *D. hystericina*, *D. pendula*, *D. trichocarpa*, *D. tuerckheimii*, and *D. viridula*. The bracts of the inflorescence are hyaline-membranaceous, becoming brown-papyraceous with age.

The membranaceous floral bracts of *Dichaea* are always in pairs. They include an apical bractlet (referred to as inner bract in the species description) extending abaxially to the lip, and a proximal, adaxial bract (outer bract), which envelopes the base of the apical bract, concealing the pedicel and the base or the whole of the ovary. The two flower bracts greatly differ among themselves: the outer bract is usually much larger, cucullate-funnelform, whereas the inner bract is commonly narrower and ligulate. The shape of the floral bracts and their length relative to the pedicel and the ovary are often species-specific, but individual variations largely prevent their taxonomic use.

#### *Ovary and Fruit*

The ovary of *Dichaea* is inferior and made up of three carpels, with parietal placentation. Although it is continuous with the flower pedicel, in species with elaborate ovary vestiture it is usually possible to distinguish the pedicel without ornamentations from the ovary, provided with various kinds of indument. In these cases, separate measurements are given in taxa descriptions for the pedicel and the ovary. Ovary vestiture has been traditionally used as an important character to group species in the genus *Dichaea*, and it is useful to separate

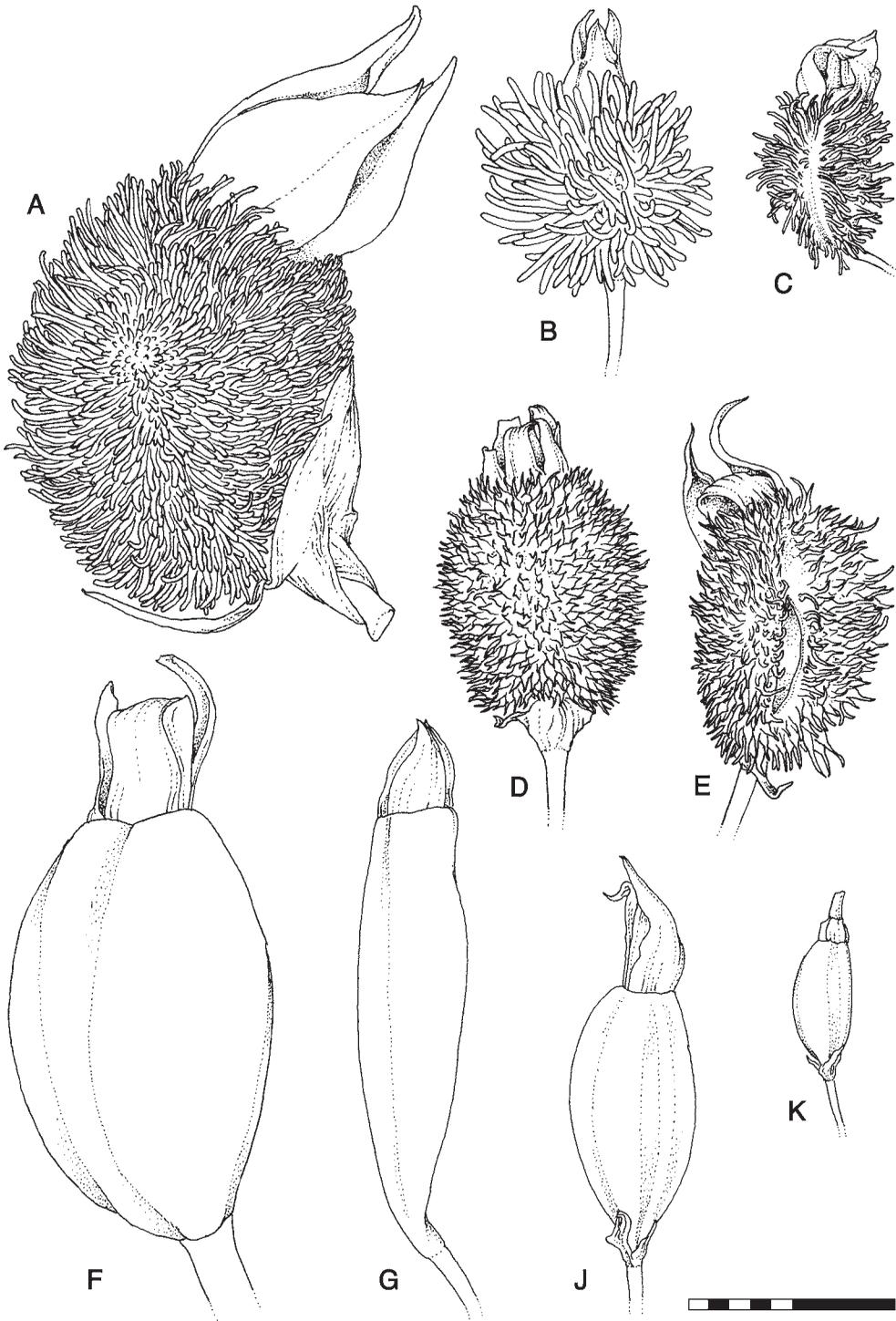


FIGURE 16. *Dichaea* fruits. **A**, *D. fragrantissima* ssp. *eburnea* (Pupulin 5149); **B**, *D. trichocarpa* (Gómez s.n.); **C**, *D. hystricina* (Bogarín 1085); **D**, *D. filiarum* (Pupulin 5254); **E**, *D. lankesteri* (Pupulin 5492); **F**, *D. trulla* (Bogarín 206); **G**, *D. glauca* (Pupulin 4734). **J**, *D. viridula* (Pupulin 5509); **K**, *D. tuerckheimii* (Pupulin 5456). Scale bar = 1 cm.

species in herbarium material when no flowers are conserved. The present analysis, as well as preliminary results of DNA data sets comparison (Neubig, 2005: 50 and fig. 4.2), shows that the presence of trichomes on the ovary evolved independently at least twice in sect. *Dichaea* and sect. *Pseudodichaea*. The glabrous condition of the ovary is plesiomorphic within Zygopetalinae, and species with nonornamented ovaries (previously treated as sect. *Dichaeastrum*, in part) are scattered among all the major clades of *Dichaea*.

Apart from the alternative condition glabrous/muricate, researchers have mostly neglected fruit characteristics of *Dichaea*, which may be useful in species classification

also even from specimens without flowers. In Costa Rican *Dichaea* species, the fruits vary in length from 6 mm (*D. tuerckheimii*) to 22 mm (*D. glauca* and *D. fragrantissima* ssp. *eburnea*), and from 3 mm (*D. tuerckheimii*) to 13–14 mm (*D. fragrantissima* ssp. *eburnea*, and *D. trulla*) in width (Fig. 16). Most of the fruits are elliptic at maturity, but the subglobose fruits of *D. trichocarpa* (ca. 8 × 7 mm) are diagnostic. When a muricate *indumentum* is present, the trichomes vary greatly in density, size, and shape. Trichomes' length varies from 0.8 mm (*D. filiarum*) to 6 mm (*D. morrisii*), with most of the species in the range of 1.5–3.0 mm (Fig. 17). The trichomes of species of sect. *Pseudodichaea* are usually closely spaced, soft,

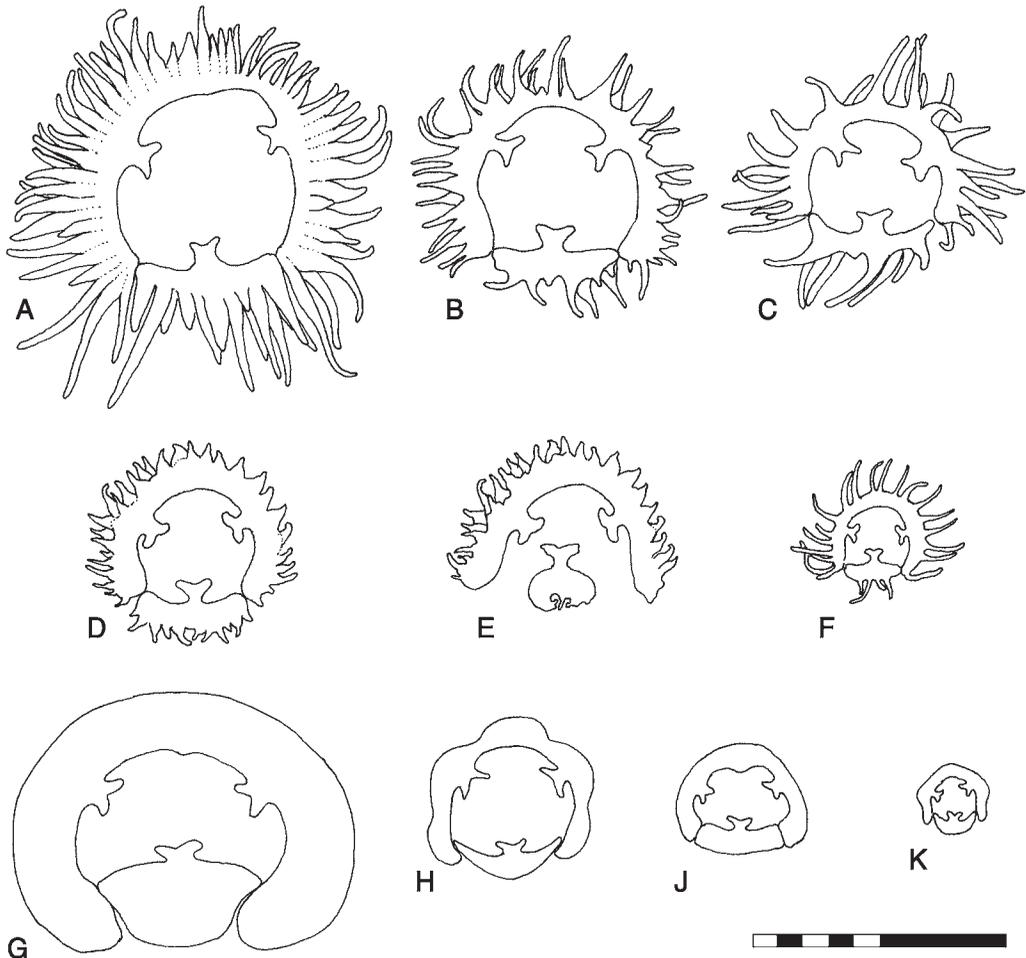


FIGURE 17. Transversal sections of *Dichaea* fruits. **A**, *D. fragrantissima* ssp. *eburnea* (Pupulin 5149); **B**, *D. lankesteri* (Pupulin 5492); **C**, *D. trichocarpa* (Gómez s.n.); **D–E**, *D. filiarum* (Pupulin 5254), the fruit split in E; **F**, *D. hystricina* (Bogarín 1085); **G**, *D. trulla* (Bogarín 206); **H**, *D. glauca* (Pupulin 4734); **J**, *D. viridula* (Pupulin 5509); **K**, *D. tuerckheimii* (Pupulin 5456). Scale bar = 1 cm.

flexuous, somewhat laterally flattened, and narrowly conic or rarely subcuspidate at the base. In *D. filiarum* the trichomes are characteristically scattered, soft, shortly triangular, and laterally flattened. The trichomes are distinctly inflated at the base in *D. lankesteri* and the closely related species of small-sized taxa of sect. *Pseudodichaea*. Comparatively long, digitate, cylindrical trichomes are found in *D. hystricina* (1.6–1.7 mm) and *D. trichocarpa* (2.7–3.0 mm); in the latter species, they are distinctly stiff (Fig. 16–17).

Although the ovary of *Dichaea* is tri-carpellate, the fruits do not split between the carpels but separate into two unequal valves. The lateral margins of the carpel abaxial to the lip present an increasing cell organization, ending in a layer of smaller cells acting as an articulation, whereas the uppermost carpels are fused on the adaxial margins. In this way *Dichaea* fruits split in two lines between the midveins of the abaxial and the lateral carpels, the two halves remaining attached apically (Fig. 17K).

#### Seeds

Seed analysis for the present study was sparse, but apparently seed morphology in *Dichaea* is quite uniform and not informative at the sub-generic and specific levels. Measurements were taken of seeds from mature fruits of *D. filiarum*, *D. hystricina*, *D. trichocarpa*, *D. tuerckheimii* and *D. viridula* (sect. *Dichaea*, including taxa with muricate and glabrous ovaries), *D. lankesteri* (sect. *Pseudodichaea*), and *D. glauca* (Table 1). Seeds of *Dichaea* are oblong and asymmetrical, with the base wider than the apex, yellowish to nearly white, varying in length from 120–140  $\mu\text{m}$  (*D. trichocarpa*) to 200–260  $\mu\text{m}$  (*D. viridula*) in the sampled species. No correlation exists between

the size of the flower and the resulting fruit and seed length. The medial testa cells are strongly elongate, with marginal ridge weakly to strongly developed, whereas the basal cells are nearly isodiametric. On the basis of their general morphology, *Dichaea* seeds correspond to the *Maxillaria* type (Barthlott and Ziegler, 1981; Ziegler, 1981), but with their reduced size they better fit the *Chondrorhyncha* variant *sensu* Dressler (1993b).

#### Flower

Floral features that are taxonomically useful, both at the sectional and specific levels, include flower color, shape, *indumentum* and characters of the margins (entire vs. ciliate) of sepals and petals, outline of the lip, presence versus absence of lip callosities, column orientation and shape, presence and shape of the infrastigmatic ligule, and pollinarium features (Fig. 18–21). Temporal activity of the flowers, often associated with the production of moderate to strong fragrances, has taxonomic significance at the sectional level.

The flowers of *Dichaea* are trimerous, zygomorphic, resupinate, and perfect. The single flowers are usually ephemeral, lasting in good condition for two to four days. Exceptions are the flowers of the tall-habit species of sect. *Pseudodichaea* and *D. trulla*, which can last for over a week. However, during the life span of a flower, attractiveness is often limited to the morning or the first hours of the afternoon, when the perianth is open (and the fragrance produced in scented species); afterward the flower closes. On overcast days, flower activity may be limited to a few hours early in the morning. Temporal activity of the flowers is scarce or totally absent in species of sect. *Pseudodichaea*, as well as in *D. panamensis*, *D. glauca*, and *D. trulla*, and it is likely a derived condition within the genus.

Three sepals, usually similar in size and shape, compose the calyx. The texture of sepals is amply variable. Species of the sect. *Dichaea* mostly have membranous, thin-textured sepals, but they are thick and somewhat waxy in *D. trichocarpa* and *D. squarrosa*. In sect. *Pseudodichaea*, subcoriaceous, waxy sepals are characteristic of the group of species with the tallest habit (*D. fragrantissima* ssp. *eburnea*, *D. globosa*, and *D. morrisii*). Among plesiomorphic taxa with doubtful affinities,

TABLE 1. Seed length (in  $\mu\text{m}$ ) of *Dichaea* species.

SPECIES	SEED LENGTH
<i>Dichaea filiarum</i>	160 – 190
<i>Dichaea glauca</i>	140 – 190
<i>Dichaea hystricina</i>	190 – 220
<i>Dichaea lankesteri</i>	190 – 230
<i>Dichaea trichocarpa</i>	120 – 140
<i>Dichaea tuerckheimii</i>	180 – 250
<i>Dichaea viridula</i>	200 – 260

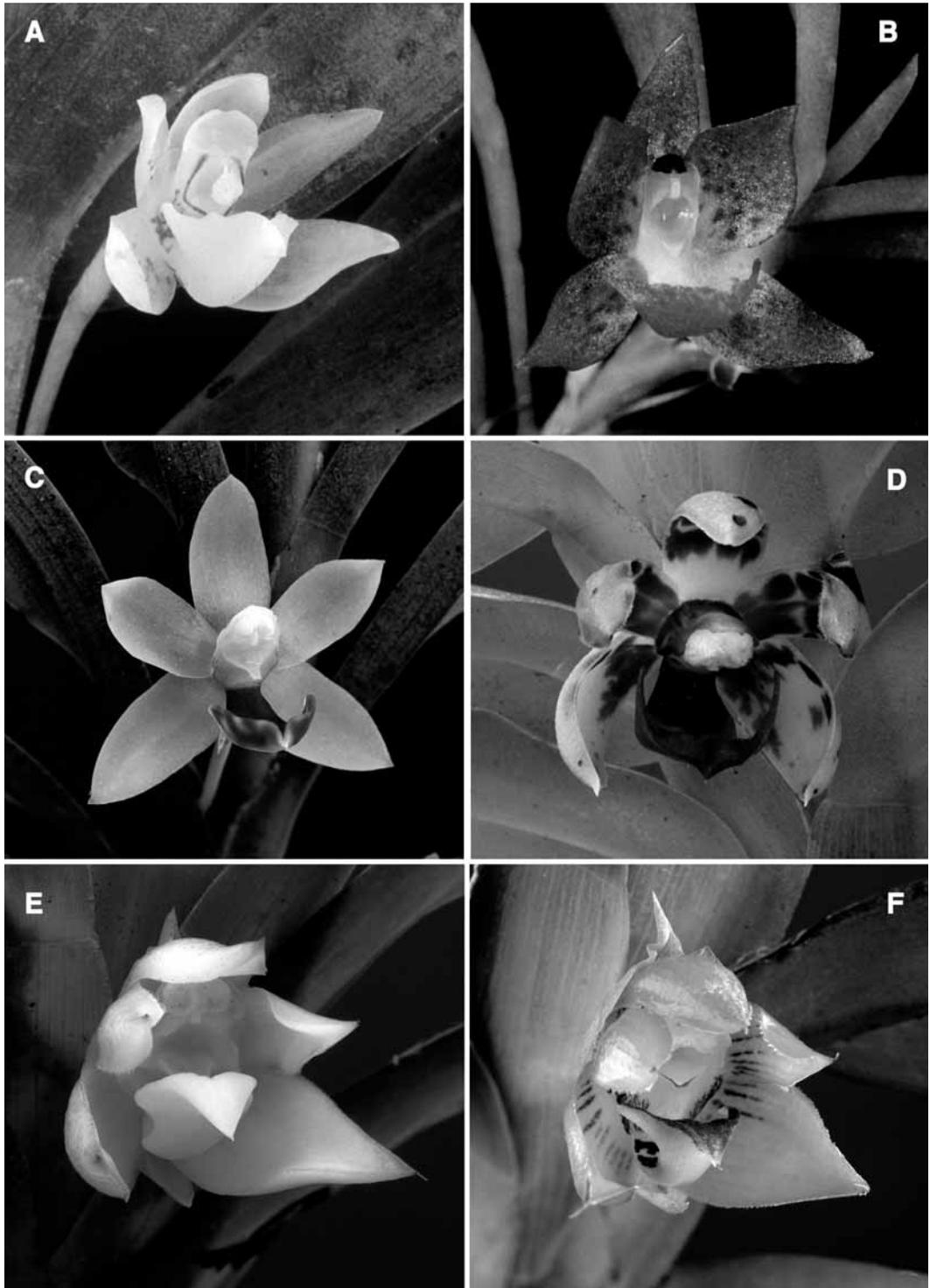


FIGURE 18. Flower morphology in Costa Rican *Dichaea* species. **A**, *D. glauca* (Pupulin 2051); **B**, *D. panamensis* (Pupulin 1079); **C**, *D. trulla* (Pupulin 751); **D**, *D. globosa* (Pupulin 1367); **E**, *D. fragrantissima* ssp. *eburnea* (Blanco 513); **F**, *D. morrisii* (Whitten 2171).

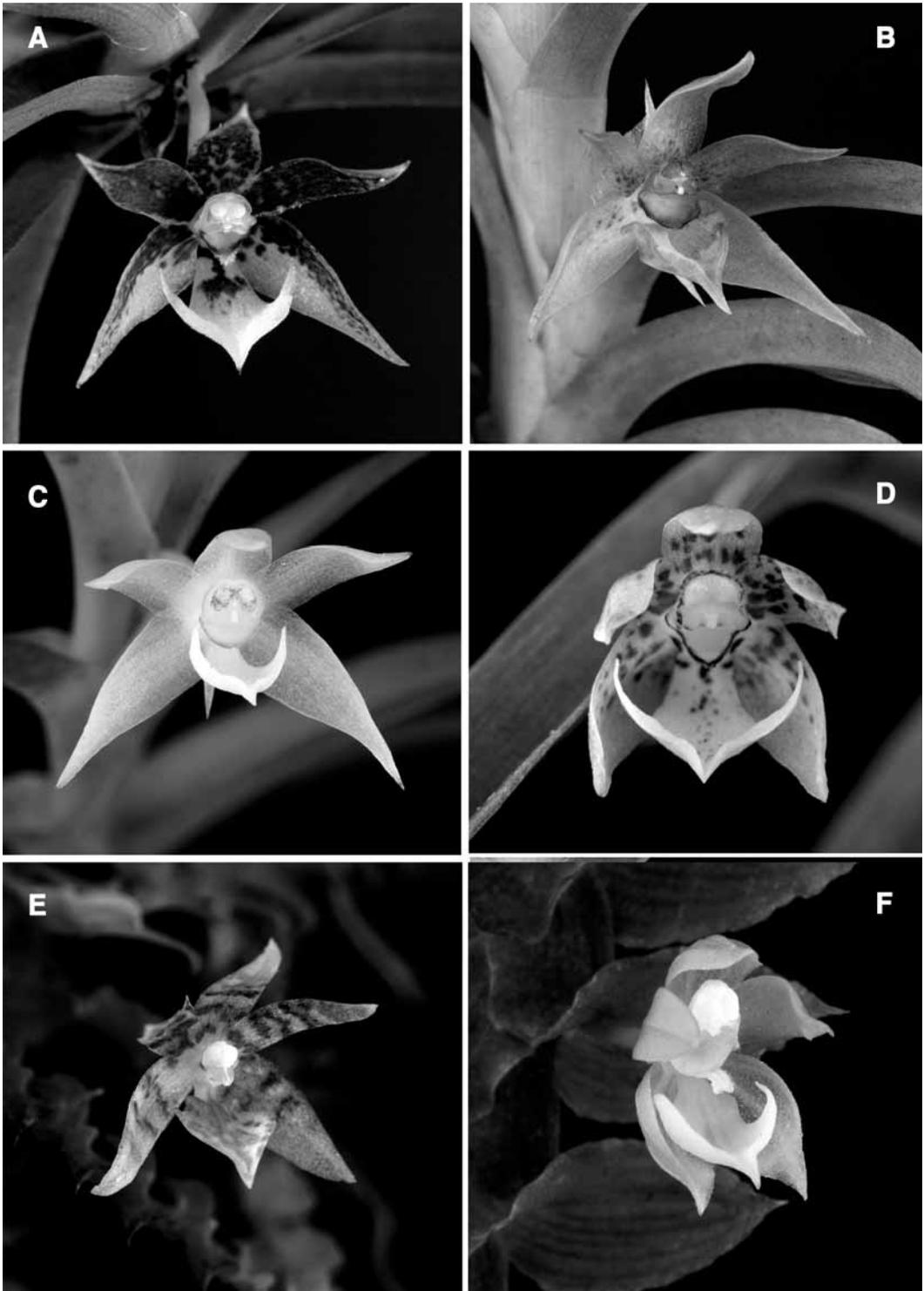


FIGURE 19. Flower morphology in Costa Rican *Dichaea* species. **A**, *D. acrolephara* (Pupulin 4851); **B**, *D. amparoana* (Bogarín 679); **C**, *D. lankesteri* (Pupulin 3030); **D**, *D. elliptica* (Pupulin 4945); **E**, *D. tuerckheimii* (Pupulin 4718); **F**, *D. viridula* (Pupuin 5509).

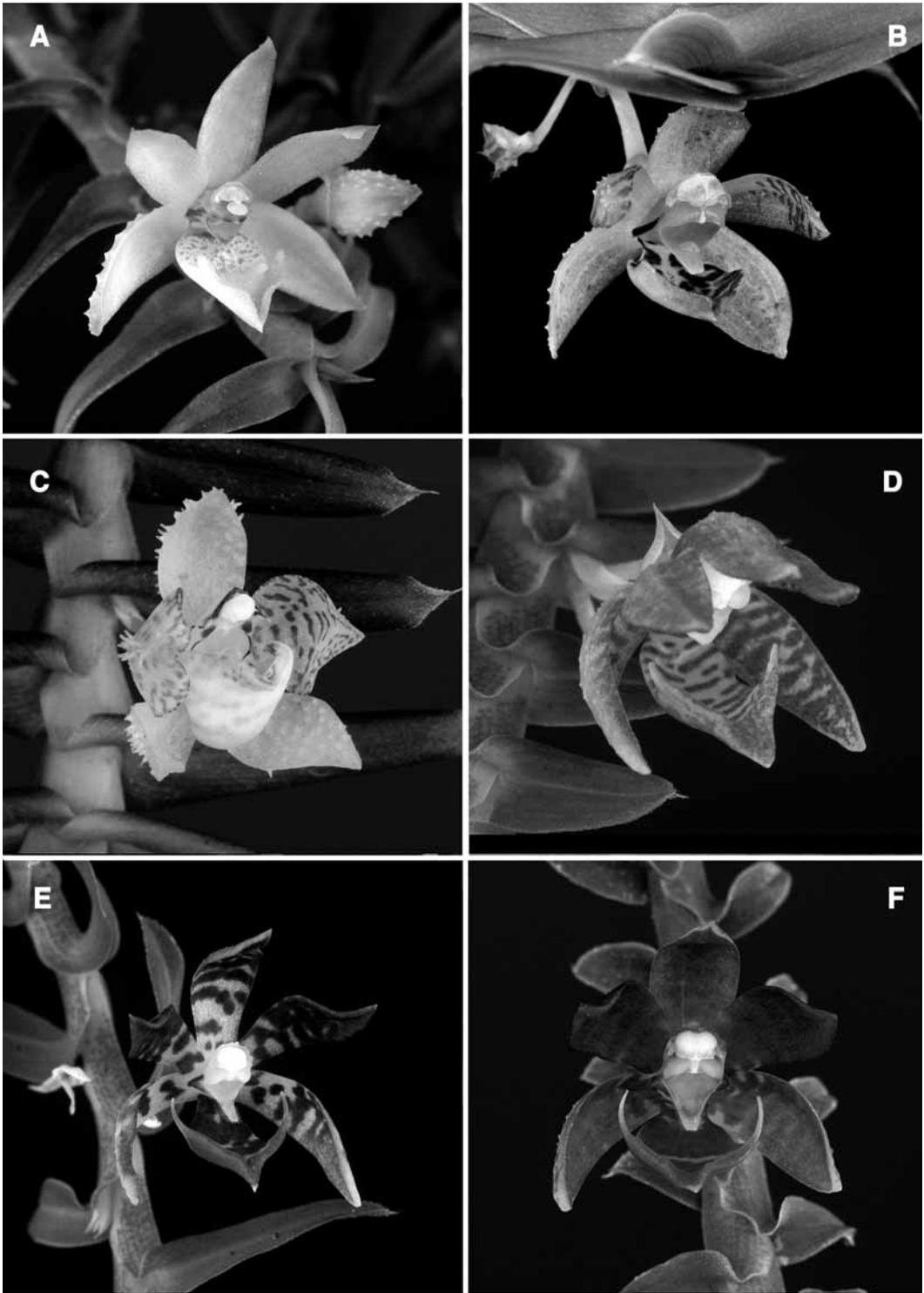


FIGURE 20. Flower morphology in Costa Rican *Dichaëa* species. **A**, *D. trichocarpa* (Bogarín 173); **B**, *D. pendula* (Pupulin 3024); **C**, *D. dammeriana* (Pupulin 3732); **D**, *D. costaricensis* (Pupulin 4797); **E**, *D. sara-piquinsis* (Pupulin 5013); **F**, *D. obovatipetala* (Pupulin 5066).

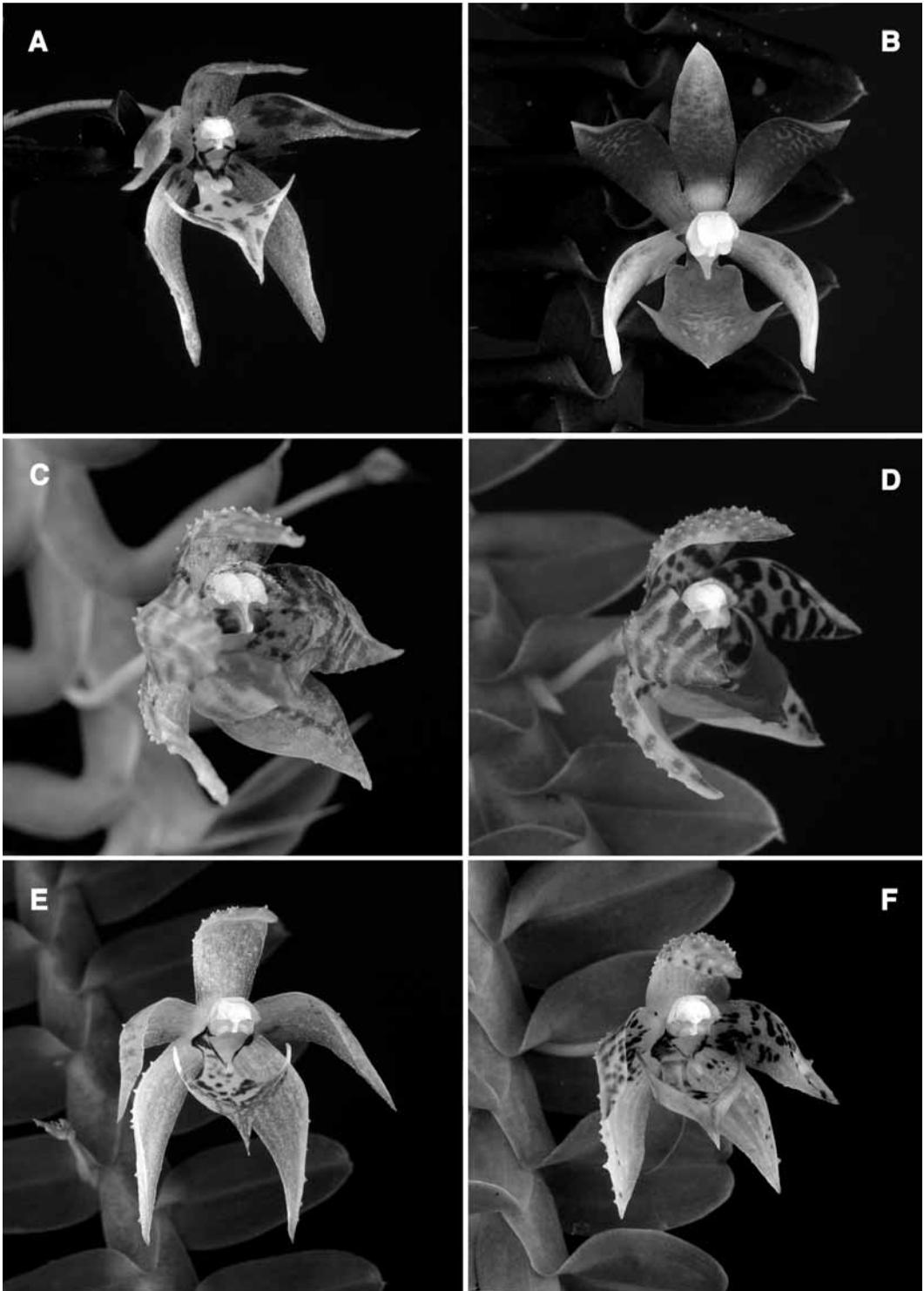


FIGURE 21. Flower morphology in Costa Rican *Dichaea* species. **A**, *D. oxyglossa* (Pupulin 2119); **B**, *D. filiarum* (Pupulin 5482); **C**, *D. eligulata* (Pupulin 1094); **D**, *D. poicillantha* (Bogarín 712); **E**, *D. similis* (Bogarín 329); **F**, *D. cryptarrhena* (Pupulin 5210).

succulent sepals are found in *D. glauca* and *D. trulla*. Most species of *Dichaea* possess lanceolate-elliptic, acute sepals, but taxa of sect. *Pseudodichaea* commonly have distinctly acuminate sepals, which become long-acuminate in *D. acrolephara*, *D. amparoana*, *D. lankesteri*, and *D. fragrantissima* ssp. *eburnea*. In the latter species, the sepals are almost triangular, whereas *D. morrisii* presents broadly ovate sepals. In sect. *Dichaea*, long-acuminate sepals are diagnostic for *D. oxyglossa* and *D. similis*. The oblique lateral sepals are often slightly larger than the dorsal sepal (e.g., *D. acrolephara*, *D. elliptica*, *D. filiarum*, *D. fragrantissima* ssp. *eburnea*, *D. morrisii*, *D. panamensis*, *D. trichocarpa*, and *D. squarrosa*). The lateral sepals are smaller than the dorsal sepal in *D. dammeriana* and in some of the morphs of the variable *D. poicillantha*. Whereas the dorsal sepal is always bilaterally symmetrical, in some species of *Dichaea* the lateral sepals are slightly to distinctly asymmetrical, the inner half being usually larger and more rounded. The number of veins in the two halves of the sepals is the same, but lateral veins may be observed branching from the lateral ones in the portion of the sepal adjacent to the lip. Species with strongly asymmetrical lateral sepals include *D. acrolephara* and *D. fragrantissima* ssp. *eburnea* in sect. *Pseudodichaea*, and *D. costaricensis* and *D. squarrosa* in sect. *Dichaea*. In *D. oxyglossa*, the lateral sepals are distinctly falcate, whereas subfalcate sepals may be observed in *D. filiarum* and *D. similis*. In *D. obovatipetala* and *D. sarapiquinsis*, the slightly protruded median keel produces a small, rounded abaxial apicule. With the notable exception of the tallest species of sect. *Pseudodichaea*, in all the taxa of the genus the lateral margins of the sepals are smooth. *Dichaea fragrantissima* ssp. *eburnea*, *D. globosa*, and *D. morrisii* have microciliate sepals, a character that is diagnostic for this species subset in sect. *Pseudodichaea*. The adaxial surface of the sepals is glabrous in all the examined species. On the contrary, the abaxial surface often presents various kinds of ornamentation. These vary from low, rounded, sparse tubercles to stiff clumps of spines, and depending on the nature of the superficial processes the sepals' surface may be characterized as tuberculate-verrucose, muricate, echinate, or aculeate. Ornaments are often scattered

with no definite pattern, but in some cases they show a tendency to group along the median keel (e.g., *D. costaricensis*, *D. eligulata*, and *D. pendula*). *Dichaea dammeriana* is distinctive in the strongly muricate-aculeate sepals, with the prickles mostly arranged in clumps and densely packed along the protruding midrib. The presence of abaxial superficial processes on the sepals should be interpreted as a synapomorphy in the genus, as no ornamentation at all occurs in less-advanced species of sect. *Pseudodichaea* nor in the seemingly plesiomorphic *D. glauca*, *D. panamensis*, or *D. trulla*. When the perianth presents some color pattern, the color is often restricted to the basal part of the sepals. The dorsal sepal is often more heavily colored than the lateral sepals, and in the latter the pigmented area is frequently restricted to the longitudinal half opposed to the lip.

The second whorl consists of three petals, one of which is clearly distinct in shape, size, and color. The lateral petals are usually smaller than the sepals, varying in shape from elliptic to lanceolate, and ending in acute to distinctly acuminate apices. Their texture is usually similar to that of the sepals, and species of sect. *Pseudodichaea* with tallest habit are characteristic for the waxy, succulent petals, often replicate toward the apex (*D. fragrantissima* ssp. *eburnea* and *D. morrisii*). In sect. *Pseudodichaea*, the presence of obovate sepals is diagnostic for *D. globosa*, whereas the petals of *D. fragrantissima* ssp. *eburnea* and *D. morrisii* are almost triangular. Together with other vegetative and floral features, obovate sepals allow recognition of *D. obovatipetala*, *D. sarapiquinsis*, and *D. viridula* in sect. *Dichaea*. *Dichaea panamensis* is unique, among the taxa of the concerned area, in having the petals distinctly broader than the sepals. Although in some species the lateral petals are spreading (e.g., *D. acrolephara*, *D. elliptica*, *D. lankesteri*, *D. trulla*, and *D. tuerckheimii*), usually they are somewhat porrect or curving at the apex, reducing the angle of flower entrance. Features of the petal margins have taxonomic significance at the sectional level. The petals are entire in all the examined taxa, with the exception of the larger species of sect. *Pseudodichaea*, which present microciliate margins. In most of the species in the study area, the petals are smooth adaxially, and usually also in the abaxial

surface. Exceptions are made by *D. trichocarpa*, *D. squarrosa*, and *D. dammeriana*, which regularly present abaxial tubercles or prickles. They are particularly noteworthy in *D. dammeriana*, in which the stiff tubercles are almost restricted to the central vein and the closely adjacent regions of the petals. Low abaxial tubercles are sometimes present also on the petals of *D. cryptarrhena*. In species with colored flowers, the petals are more definitely patterned than the sepals. The color spots, varying from dark purple to purple-violet, are confined to the adaxial surface, and in some species they tend to fuse together to form large blotches (e.g., *D. acrolephara*, *D. globosa*, and *D. poicillantha*), transverse bars (e.g., *D. costaricensis* and *D. filiarum*) or longitudinal stripes (outside the study area, *D. fragrantissima* ssp. *fragrantissima*). Among Costa Rican *Dichaea*, *D. obovatipetala* and (to a lesser extent) *D. sarapiquinsis* are unique in the very large violet blotches that almost completely cover the petal surface.

Opposed to the dorsal sepal, the median petal, the labellum or lip, is the landing platform for visiting insects and the source of floral fragrances in scented species (Folsom, 1987). It is structurally more complex and colorful than the other segment of the perianth, and its morphological features offer useful information for the taxonomy of the genus. In most cases, the lip of *Dichaea* is anchor-shaped and 3-lobed, with well-developed lateral lobes. In the study area, exceptions are the labellum of *D. tuerckheimii*, which is entire, and *D. pendula*, in which the presence of lateral lobes is facultative. In the species descriptions, the lip of *Dichaea* is divided into three main parts: a claw, which may be absent in taxa having sessile lips, a basal hypochile extending from the claw (or from the apex of the column foot in species with sessile lips) to the insertion of the lateral lobes, and a distal epichile, which is mostly provided with distinct lateral lobes. In most species, the lip blade is connected to the apex of the column foot by a distinctly thicker and linear portion of tissues, oval-shaped in section, from which the laminar portion of the lip expands. Although the claw is generally somewhat linear in lateral view, in some of the species it presents a distinct basal thickening (e.g. *D. costaricensis*, *D. eligulata*, *D. obovatipetala*, *D. oxyglossa*, and *D.*

*trulla*). In *D. filiarum*, *D. hystricina*, *D. morrisii*, and *D. sarapiquinsis*, the thickened area is so obvious that it can be described as a distinct callus. The transition between the claw and the base of the hypochile is not always obvious, and the claw apex merges into the lamina as a more or less definite rounded keel. In *D. glauca*, the flattened lamina flanks the claw from the base, and the hypochile may be characterized as sessile and carinate. However, in the species with clawed lips, an expansion point of the lamina, where it becomes flattened, may usually be observed. The expansion may be abrupt or somewhat continuous; when it is abrupt, the area with more pronounced expansion is defined as a shoulder. Consequently, shoulders are not distinct in all the species, and they are absent when the hypochile is simply obtuse. The shoulder area is often characterized by the presence of soft marginal hairs. As noted by Folsom (1987), the structure of the shoulders is associated with the positioning of visiting insects on the lip, and their characters are involved in the flower's pollination mechanisms. It is noteworthy that the shoulder area is commonly distinct in color from the rest of the lip blade. The hypochile is basally bituberculate in *D. hystricina* and *D. tuerckheimii*; as noted before, the lip of the latter species lacks a clear distinction between hypochile and epichile. *Dichaea trichocarpa* is unique in the concerned area in having a sessile, lenticular-concave, evenly thickened hypochile. A distinct median keel running along a hypochile with slightly thickened margins is diagnostic of *D. viridula*. At the apex of the hypochile, the epichile expands mostly abruptly, and the lateral lobes of the epichile are formed. In the species descriptions, the width of the hypochile is given at this point. The epichile outline (excluding the lateral lobes) varies from triangular (in most Costa Rican *Dichaea* species) to broadly triangular (e.g., *D. dammeriana*) to ovate or obovate, transversely elliptic, subreniform (e.g., *D. squarrosa*), or subquadrate (*D. trulla*). In its natural position, the epichile of most of the species is slightly to deeply concave. The leading edge is mostly acute or subacute, but features of the epichile apex are in many cases taxonomically useful at the specific level. The epichile of *D. amparoana* (in sect. *Pseudodichaea*) is distinctly acuminate, and

acuminate lips are diagnostic of *D. oxyglossa*, *D. viridula*, and *D. similis* in sect. *Dichaea*. In the latter species the lateral margins tend to enfold in the apical portion, creating a subulate apex. The leading edges of *D. dammeriana*, *D. eligulata*, *D. globosa*, and *D. poicillantha* are broadly obtuse (although usually provided with a small apicule), whereas the lips of *D. elliptica*, *D. trichocarpa*, and *D. trulla* are distinctly truncate to slightly retuse. In most of the species in the concerned area the epichile is smooth, but *D. sarapiquinsis* is distinctive in having low adaxial tubercles between veins in the apical portion, whereas the margins of the lip of *D. globosa* are distinctly thickened toward the apex, forming two cushion-like calli above the small abaxial apicule. At the base of the epichile, two lateral projections or lobes are produced. These are rather variable among species, and in some of the taxa it is difficult to discern a precise point where the lateral projection is formed, the lateral lobes being actually decurrent on the lip lamina. Distinct, usually narrowly linear, acuminate lobes are found in *D. amparoana*, *D. cryptarrhena*, *D. eligulata*, *D. filiarum*, *D. globosa*, *D. hystricina*, *D. morrisii*, *D. obovatipetala*, *D. oxyglossa*, *D. poicillantha*, *D. sarapiquinsis*, *D. similis*, and *D. viridula*. These vary from straight to (more commonly) subfalcate to distinctly falcate (e.g., *D. amparoana*, *D. cryptarrhena*, *D. globosa*, *D. hystricina*, and *D. viridula*); they may be spreading or retrorse. In their natural position the lateral lobes of the epichile are mostly erect, forming a rounded entrance that likely helps to orient the position of the pollinator during its access to the flower chamber and reduces the possibility that it will leave the flower from a side. In other species the lateral projections are triangular and somewhat continuous with the blade of the epichile. In *D. costaricensis*, *D. dammeriana*, *D. elliptica*, and *D. glauca*, no precise distinction exists between the lamina of the epichile and the short lateral lobes. The lateral lobes of *D. squarrosa* and *D. trichocarpa* are apically rounded to subquadrate, and *D. tuerckheimii* has no lateral projections at all. In Costa Rican populations of the widespread *D. pendula*, the presence of lateral lobes is facultative.

Opposite of the labellum is the adaxial, zygomorphic column. In comparison with the usu-

ally diminutive size of the flower, the column of *Dichaea* is stout and grossly cylindrical in general shape. In a few species (e.g., *D. glauca*, *D. trichocarpa*, and *D. tuerckheimii*), the column is more or less continuous with the longitudinal axis of the pedicel, but in the remaining taxa the column is suberect to erect, so that the rostellar area and the viscidium of the pollinarium are placed frontally. The base of the column is roughly cylindrical in section and extends to the rear into an obtuse, thick, and usually short foot. The foot area normally presents large pigmented blotches. Along the basal margins of the column there are more or less pronounced tissue extensions, which are termed "wings" in the species descriptions. The wings are usually flattened and decurrent along the flanks of the column up to the stigmatic area, and they are mostly provided with soft cilia of variable length along the margin. The presence of such columnar trichomes is likely a derived character within the genus, as most of the plesiomorphic species in sect. *Pseudodichaea* (with the exceptions of *D. acrolephara* and *D. morrisii*), as well as *D. glauca* and *D. panamensis*, present glabrous wings. Within sect. *Dichaea*, the only species with eciliate basal margins of the column is *D. tuerckheimii*, but the gynostemium of this species is anomalous in many respects when compared with the other members of the genus in Costa Rica. The shape of the wings, varying from narrowly elliptic to semi-rounded, triangular, or subquadrate, is usually species-specific, but this character can usually be appreciated only in living or liquid-preserved material, because the delicate tissues of the wings are strongly deformed in dried specimens and do not reconstruct properly when rehydrated. The basal wings are very reduced in *D. elliptica* and *D. panamensis*, and they are absent in *D. tuerckheimii*.

Above the base, the column of *Dichaea* usually widens and becomes ventrally flattened to host the stigmatic cavity. The stigma is normally transversely widely elliptic-subreniform, occasionally rounded or trapezoidal, shallow, and provided with rounded and mostly colored rims. In most of the species, the stigma lies frontal, or in a plane more or less perpendicular to the ovary axis; in *D. trichocarpa* and *D. trulla* the stigma is ventral, and in the former

species the anther is somewhat dorsal. The rostellar and supra-stigmatic area is completely reflexed in *D. tuerckheimii*, which also presents a projecting column and a dorsal anther, but in this case the ventral surface of the column forms an abrupt angle to present the stigma frontally. Other than these atypical cases, the shape of the stigma offers little taxonomic information. However, it should be noted that the rounded-elliptic stigma of *Dichaea* is anomalous within the Zygopetalinae, which normally present a very narrow, slit-like, transverse stigma flanked by more or less pronounced wings. At the base of the stigma there is a sterile tissue projection termed the ligule. In some cases (mostly in sect. *Pseudodichaea*), the ligule is barely a thickening of the stigmatic basal rim, but in most of the species it is long and conspicuous, varying from lanceolate to triangular or narrowly ligulate. The absence of a ligule is diagnostic, in the study area, for *D. eligulata*. The shape, orientation, and ornamentation of the ligule is species-specific and of great taxonomic utility. The ligule is usually pubescent at the apex, but it is glabrous in *D. amparoana*, *D. lankesteri*, and *D. morrisii* within sect. *Pseudodichaea*, and in *D. costaricensis*, *D. dammeriana*, *D. filiarum*, *D. trichocarpa*, and *D. tuerckheimii* within sect. *Dichaea*. Glabrous ligules are also present in *D. panamensis*, *D. gracillima*, and *D. glauca*, but in the latter case the infra-stigmatic ventral surface of the column is velutine-subpubescent. The ligule of most species projects forward (lying on a more or less horizontal plane), but in the group of tall species of sect. *Pseudodichaea*, as well as in *D. dammeriana*, *D. squarrosa*, and *D. panamensis*, it points downward. As a post-pollination phenomenon, the ligule usually collapses toward the column, closing the stigma cavity.

Above the stigmatic area and before the clinandrium, the column of *Dichaea* presents a large, normally bulgy-protruding rostellar and supra-rostellar area, longitudinally crossed by the stipe and the connected viscidium. Apart from the anomalous, almost horizontal supra-rostellar areas of *D. trichocarpa* and *D. tuerckheimii*, this region of the column is difficult to characterize for taxonomic purposes. The supra-rostellar area of *D. glauca*, a frequently cleistogamous or autogamous species, is not

continuous but presents two distinct and short lateral lobes.

Apically to the column (or rarely dorsally) is the clinandrium, which is rather variable in shape and structure. In *Dichaea panamensis* and the species of sect. *Pseudodichaea*, the clinandrium is usually very shallow, provided with marginally thickened, entire to slightly erose rims, and the anther cap is consequently protruding. In sect. *Dichaea* the clinandrium varies from shallow (*D. hystricina*, *D. pendula*, *D. squarrosa*, and *D. viridula*) to concave (*D. costaricensis*, *D. obovatipetala*, *D. sarapiquensis*, and *D. similis*) to petaloid, with well-developed and mostly dentate-lacerate margins (*D. cryptarrhena*, *D. eligulata*, *D. filiarum*, *D. oxyglossa*, and *D. poicillantha*). The clinandrium shape may be sometimes useful to separate closely related species.

#### Pollinarium

As most of the genera of the advanced Epidendroideae, *Dichaea* has a pollinarium composed of (2–)4 pollinia, caudicles, a stipe, and a viscidium (Fig. 22). The 4 pollinia (rarely fused into 2) of *Dichaea* are flattened parallel to the surface of the androclinium and superposed in 2 pairs of subsimilar to (mostly) distinctly different size, a character that constitutes one of the few synapomorphies of the subtribe Zygopetalinae. Although easily distorted in

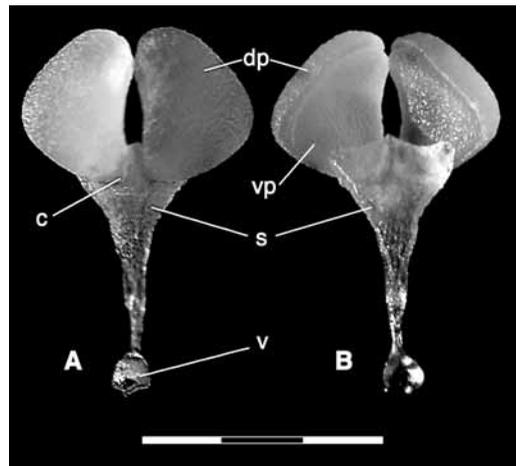


FIGURE 22. Pollinarium of *D. cryptarrhena* (*Pupulin* 5662). **A**, Dorsal view; **B**, ventral view. c = caudicle, dp = dorsal pollinium, s = stipe, v = viscidium, vp = ventral pollinium. Scale bar = 3 mm.

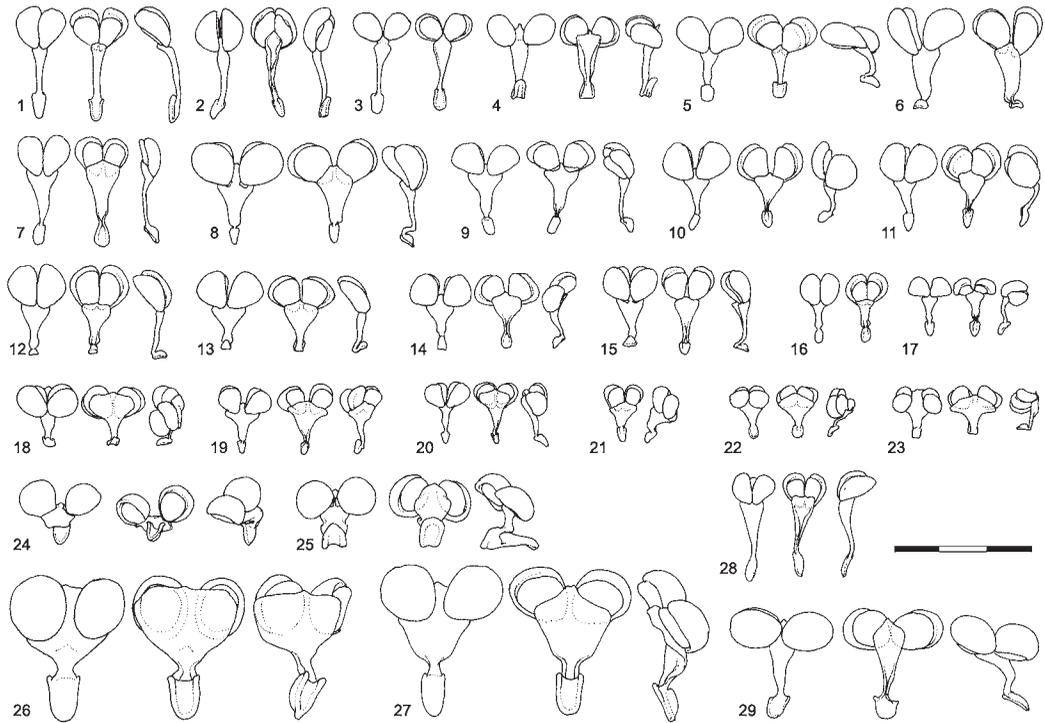


FIGURE 23. Pollinaria of *Dichaea* species. **1**, *D. dammeriana* (Bogarín 969); **2**, *D. filiarum* (Pupulin 4944); **3**, *D. squarrosa* (Pupulin 5127); **4**, *D. filiarum* (Bogarín 1117); **5**, *D. trichocarpa* (Karremans 573); **6**, *D. squarrosa* (Pupulin 5665); **7**, *D. neglecta* (Karremans s.n.); **8**, *D. glauca*. (Pupulin 4734); **9**, *D. sarapiquinsis* (Pupulin 5333); **10**, *D. cryptarrhena* (Pupulin 4436); **11**, *D. viridula* (Pupulin 5509); **12**, *D. poicillantha* (Bogarín 189); **13**, *D. poicillantha* (Pupulin 4662); **14**, *D. similis* (Pupulin 4089); **15**, *D. graminoides* (without data); **16**, *D. oxyglossa* (Pupulin 5141); **17**, *D. similis* (Surroca s.n.); **18**, *D. lankesteri* (Pupulin 5501); **19**, *D. elliptica* (Bogarín 1061); **20**, *D. amparoana* (Bogarín 679); **21**, *D. elliptica*; **22**, *D. elliptica* (Pupulin 4945); **23**, *D. acrolephara* (Bogarín 1009); **24**, *D. fragrantissima* subsp. *eburnea* (Pupulin 5138); **25**, *D. morrisii* (Whitten 2151); **26**, *D. globosa* (JBL-05319); **27**, *D. globosa* (Klark 856); **28**, *D. panamensis* (Bogarín 1075); **29**, *D. trulla* (Blanco 2812). 3, 6, 16, 21: dorsal and ventral view; all the others in dorsal, ventral, and lateral view. All drawn at the same scale several minutes after removal. Scale bar = 3 mm.

pressed specimens, the shape and orientation of the pollinia, and the size and shape of the stipe, are strongly informative about the phylogenetic relationships of Costa Rican *Dichaea* at the sectional level (Fig. 23). In species of sect. *Dichaea*, as well as in *D. acrolephara* and the closely related taxa of sect. *Pseudodichaea*, and in the distantly related *D. panamensis*, *D. glauca*, and *D. trulla*, the pollinia are obpyriform, the dorsal and greater pollinia slightly concave and superposed to the abaxial, smaller pair. *Dichaea trulla* (Fig. 24) and *D. tuerckheimii* are distinctive in having the pollinia arranged perpendicularly to the axis of the stipe, whereas in the other species the pollinia are oriented more or less parallel to

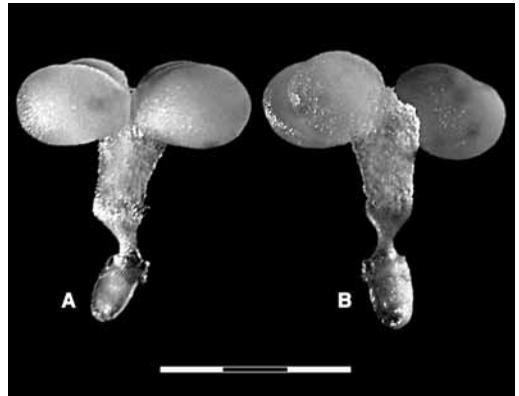


FIGURE 24. Pollinarium of *D. trulla* (Blanco 2812). **A**, Dorsal view; **B**, ventral view. Scale bar = 3 mm.

the longitudinal axis. In *D. morrisii* and the closely related species (*D. fragrantissima* ssp. *eburnea* and *D. globosa*), the pollinia are orbicular-lenticular and the inner pair is almost completely enclosed within the thick margins of the two abaxial pollinia. In species of sect. *Dichaea*, the stipe is more or less obtriangular, more rarely narrowly ligulate, with the apex rounded or, more commonly, obtuse and somewhat apiculate. In sect. *Pseudodichaea*, the stipe is broadly flabellate, often apically wider than the subtended pollinia (Fig. 23). Before removal, the stipe is basally recurved and the sticky surface of the viscidium lies in a frontal position, where it can be easily contacted by the clypeus of visiting bees (Dressler, 1981). Some minutes after removal, the base of the stipe straightens with a movement of 180° and the pollinia are positioned in the proper way to contact the stigmatic cavity (Fig. 25).

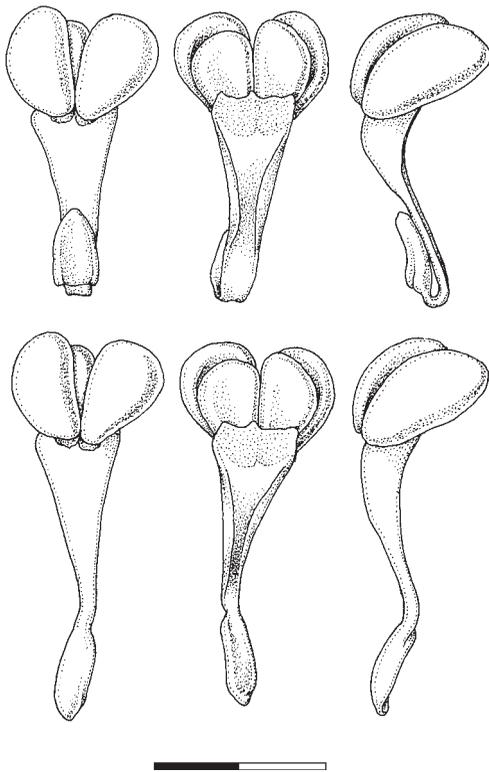


FIGURE 25. Pollinarium of *D. panamensis* (Bogarín 1075). Upper row (left to right: dorsal, ventral, and lateral views) immediately after removal; lower row 10 minutes after removal. Scale bar = 1 mm.

#### Subgeneric Grouping: Phylogeny and Biogeography

Data from morphological and anatomical features, recorded from 28 out of the 29 Costa Rican *Dichaea* species included in the present study plus 2 species from Nicaragua and Panama and 3 species of the subtribe Zygopetalinae (*Cryptarrhena guatemalensis* Schltr., *Galeottia grandiflora* A. Rich., and *Warrea costaricensis* Schltr.) selected as outgroups on the basis of previous molecular analyses (Whitten et al., 2000, 2005; Chase et al., 2003), were used to estimate phylogenetic relationships within the genus. Data were incorporated into a matrix (Table 2), and maximum parsimony analysis performed with PAUP\* 4.0b10 (Swofford, 1999).

On the basis of the data matrix analysis (Fig. 26–27), *Dichaea* is a monophyletic genus. *Dichaea glauca* and *D. gracillima* are the most basal species, consecutively sister to *D. panamensis* (the only Costa Rican representative of a group mainly Antillean and South American in distribution), and to the species of sects. *Pseudodichaea* and *Dichaea*. In some of the trees, *D. glauca* and *D. panamensis* form a basal, and in this study unresolved, polytomy. It is interesting to note that, despite their different vegetative habit and floral morphology, the leaves of both *D. glauca* and *D. panamensis* present thick and waxy cuticular layers. Furthermore, both species have unbranched stems and thick roots restricted to the basal portion of the stem, features that should be considered plesiomorphic for the genus. According to the analysis of morphological and anatomical data, species with articulate leaf blades (usually grouped in sect. *Dichaeopsis* and sect. *Pseudodichaea* on the basis of characteristics of ovary vestiture) pertain to several different lineages.

Section *Dichaeopsis sensu* Cogniaux (i.e., species with articulate leaves and glabrous ovaries) is largely polyphyletic. Although the present analysis could not satisfactorily resolve the polytomy of the basal taxa of *Dichaea*, the species included in the study pertain to three or four different lineages. The affinities of the anomalous *Dichaea glauca* (probably a monotypic group) are uncertain, but it is characterized by the ancipitous, erect stems, the thick roots produced only at the base of the stems, the glaucous leaves, the geniculate peduncles (borne erect), the inflorescences produced simultaneously, and the usual cleistogamous condition of the fleshy flowers. *Dichaea trulla* is very different from the other taxa of the genus in many

TABLE 2. Data matrix based on 62 morphological and anatomical data points.

<i>Galeottia grandiflora</i>	000000?000	0100001000	1010001010	0010000001	1110100001	0010000000	10
<i>Warrea costaricensis</i>	000000?000	0100000000	1010001000	0001000000	0100000001	0000000000	00
<i>Cryptarrhena guatemalensis</i>	010000?000	0100001000	1010000000	0111000011	1110000011	1010010000	10
<i>Dichaea acostae</i>	1111?11001	1000001001	0111111100	0100100001	1000000010	11110010?0	1?
<i>D. acroblephara</i>	1111011000	1000001001	0001111000	0110000010	1000000110	1000011000	00
<i>D. amparoana</i>	1111011000	1000000001	0001111000	0110000010	1000010010	1000011000	00
<i>D. costaricensis</i>	1111111001	1101001001	0111111010	0100100000	1000000010	1100011000	10
<i>D. cryptarrhena</i>	1111111001	1000001001	0111111100	0110100011	1011110110	1111111000	10
<i>D. dammeriana</i>	1111111001	1110001011	0111111100	0100111000	0000000010	1101011000	10
<i>D. eligulata</i>	1111111001	1000001001	0110111000	0100100001	1011100010	1000011000	10
<i>D. elliptica</i>	1111011000	1000001001	0001111000	0100000000	1000000010	1000011000	00
<i>D. filiarum</i>	1111011101	1101001011	0110111000	0100101000	1001000110	1111011000	10
<i>D. fragrantissima</i>	1111001000	0100000001	0001101010	1110000110	1100010010	1001011000	01
<i>D. fragrantissima</i> subsp. <i>eburnea</i>	1111001000	0100000001	0001100010	1110000110	1100010010	1001011000	01
<i>D. glauca</i>	0011001000	0100000101	1000000010	0100100000	1111000011	1001101000	11
<i>D. globosa</i>	1111001000	0100000001	0001101010	1100001100	1010000010	1001111000	01
<i>D. gracillima</i>	0111010000	0100001001	00010?0000	0100000011	100100001?	1000001000	??
<i>D. hystricina</i>	1111111011	1000101001	0010111000	0100101001	1101000010	1101101000	10
<i>D. lankesteri</i>	1111011000	1000000001	0001110000	0110000010	1000000010	1000011000	00
<i>D. morrisii</i>	1111001000	0100000001	0001101010	1100000110	1100000010	1000011000	01
<i>D. neglecta</i>	1111111011	1000001001	0111111100	0101100001	1010100010	1101111000	10
<i>D. obovatipetala</i>	1111111011	1000001011	0111011000	0100101000	1000000010	1101101000	10
<i>D. oxyglossa</i>	1111111111	1000001001	0110111000	0110100011	1001010010	1111101000	10
<i>D. panamensis</i>	0011001000	1100000101	0000001000	0100100000	1000000010	1101011000	10
<i>D. pendula</i>	1111011001	1000001001	0000111100	0101100001	0000000000	1101111000	10
<i>D. poicillantha</i>	1111111011	1000001001	0111111100	0101100001	1011110110	1111111000	10
<i>D. sarapiquinsis</i>	1111111011	1000001011	0111111000	0100101000	1000001010	1111111000	10
<i>D. similis</i>	1111111001	1000001001	0110111100	0110100011	1011110110	1111111000	10
<i>D. squarrosa</i>	1011110001	1100001001	0110111110	0101100000	1010000010	1000111000	10
<i>D. trichocarpa</i>	1111110001	1100001001	0111111100	0100110000	1010000010	1000011110	11
<i>D. trulla</i>	1011010000	0100000001	0001001011	0100101000	1000000010	1001111011	11
<i>D. tuerckheimii</i>	1111111001	1000001001	0011011000	0100100011	0111000000	1000001100	10
<i>D. viridula</i>	1111011101	1000011001	0110010000	0100001010	1111010011	1001111000	10

1. Roots: Basal = 0; Basal and caular = 1. 2. Roots: Thick = 0; Slender = 1. 3. Plant: Acaulescent = 0; Caulous = 1. 4. Pseudobulbs: Present = 0; Absent = 1. 5. Stem: Simple = 0; Branching = 1. 6. Stem: Erect = 0; Pendulous = 1. 7. Stem: Rounded = 0; Anceps = 1. 8. Stem: Short = 0; Long = 1. 9. Leaf sheaths: Green = 0; Spotted = 1. 10. Leaf articulation: Yes = 0; No = 1. 11. Leaf size: Large ( $\geq 5$  cm) = 0; Small ( $< 5$  cm) = 1. 12. Leaf texture: Herbaceous = 0; Thick = 1. 13. Raphids in leaves: Absent = 0; Present = 1. 14. Leaf venation: Parallel = 0; Reticulate = 1. 15. Leaf margin: Entire = 0; Ciliate = 1. 16. Leaf margin: Smooth = 0; Undulate = 1. 17. Leaf surface: Shiny = 0; Matte = 1. 18. Leaves glaucous: No = 0 >Yes = 1. 19. Leaf color: Green = 0; Bronze = 1. 20. Inflorescence: Many-flowered = 0; Single-flowered = 1. 21. Inflorescence: Successive = 0; Simultaneous = 1. 22. Pedicel: Straight = 0; Genuate = 1. 23. Flower position: Below foliage = 0; Above foliage = 1. 24. Floral bract: Smaller than ovary = 0; Larger than ovary = 1. 25. Ovary: Glabrous = 0; Muricate = 1. 26. Floral activity: No = 0; Yes = 1. 27. Flower color: Concolorous = 0; Blotched = 1. 28. Sepals: Glabrous = 0; Verrucose = 1. 29. Sepals texture: Papyraceous = 0; Fleshy = 1. 30. Sepals position: Spreading = 0; Reflexed = 1. 31. Sepals margin: Entire = 0; Ciliate = 1. 32. Lateral sepals: Convolute at the base = 0; Flat at the base = 1. 33. Sepals apex: Obtuse to acute = 0; Acuminate = 1. 34. Sepals color: Greenish white = 0; Orange = 1. 35. Petals size: Smaller than sepals = 0; Subequal to sepals = 1. 36. Petals: Glabrous = 0; Verrucose = 1. 37. Petal shape: Lance-elliptic = 0; Obovate = 1. 38. Petals margin: Entire = 0; Ciliate = 1. 39. Petals apex: Obtuse to acute = 0; Acuminate = 1. 40. Lip: Sessile = 0; Clawed = 1. 41. Lip shape: Subentire = 0; 3-lobed = 1. 42. Lip base: Smooth = 0; Callous = 1. 43. Hypochile shape: Cuneate = 0; Discoid = 1. 44. Hypochile shoulders: Absent = 0; Present = 1. 45. Hypochile margins: Glabrous = 0; Ciliate = 1. 46. Lip apex: Obtuse to acute = 0; Acuminate = 1. 47. Epichile vestiture: Smooth = 0; Verrucose = 1. 48. Apex of epichile: Entire = 0; Ciliate = 1. 49. Lateral lobes of the epichile: Indistinct = 0; Acuminate = 1. 50. Callus on the disc: Absent = 0; Present = 1. 51. Callus: Many-lobed = 0; Simple or absent = 1. 52. Column position: Suberect = 0; Erect = 1. 53. Clinandrium: Small = 0; Petaloid = 1. 54. Ligule: Absent = 0; Present = 1. 55. Ligule vestiture: Glabrous = 0; Ciliate = 1. 56. Basal wings: Absent = 0; Present = 1. 57. Rostellum: Acuminate = 0; Rounded = 1. 58. Anther position: Apical = 0; Dorsal = 1. 59. Pollinia: Ovoid = 0; Suborbicular = 1. 60. Pollinia: Parallel to stipe = 0; Transversal to stipe = 1. 61. Stipe: Narrowly triangular = 0; Trapezoid = 1. 62. Self-pollination: No = 0; Yes = 1.

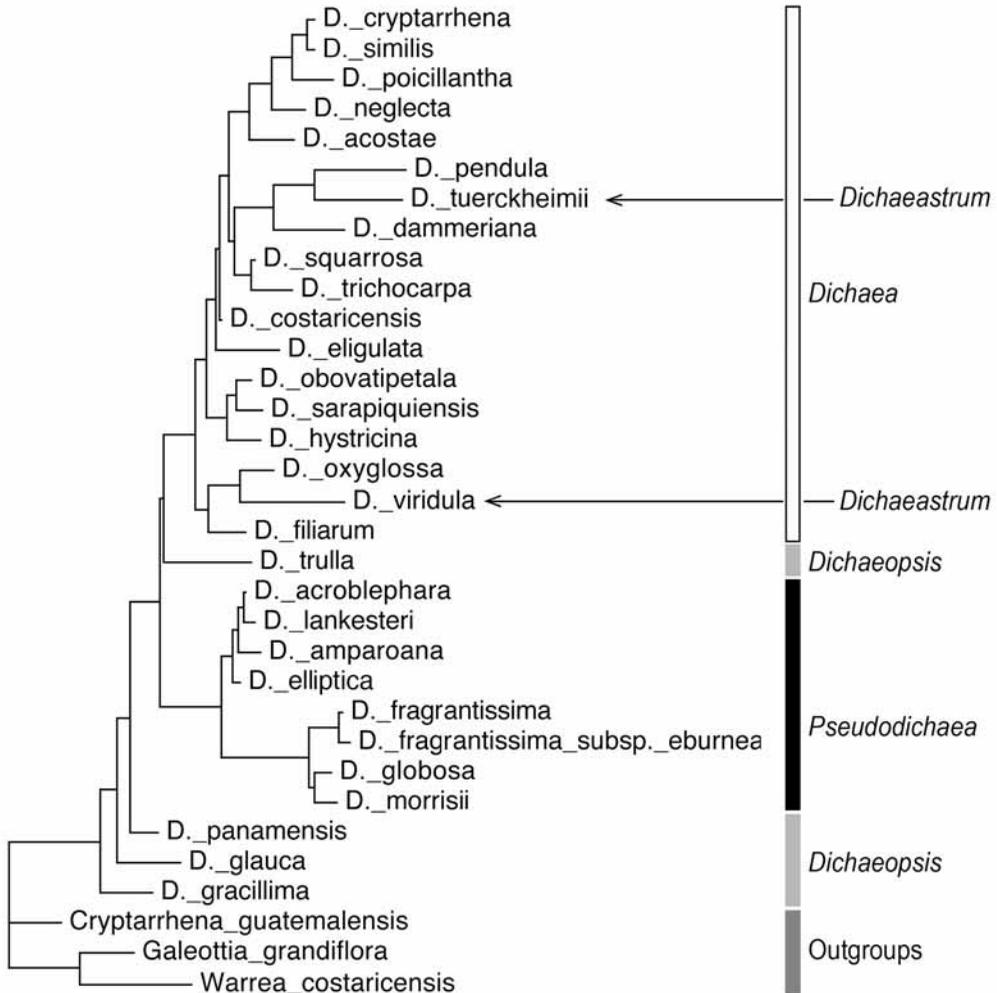


FIGURE 26. One of the >8000 equally parsimonious morphologic trees.

aspects. Apomorphies of this group (probably including *D. caveroi* D. E. Benn. & Christenson and *D. coriacea* Barb. Rodr. outside the study area) include large plants, rounded stems, very long and narrow leaves, fleshy perianth becoming reflexed with age, and pollinia borne transversely on the narrow stipe.

Species with articulate leaves and muricate ovary are on a distinct branch, sister to *Dichaea trulla* and to the clade of the taxa with persistent leaves. The group (treated here as sect. *Pseudodichaea*) is supported as monophyletic and can be characterized by the presence of caulinar roots, flattened stems, articulate leaves, straight peduncle, flowers produced

below foliage, and muricate ovaries, and by the absence of temporal activity of the flowers. However, on the basis of vegetative architecture and floral morphology, two main groups can be distinguished within the section. The group of *D. lankesteri* (four species) has small plants, and comparatively small, thin-textured flowers provided with entire sepals and petals. The group of *D. morrisii*, perhaps deserving sectional status, includes three species in the country, and it is characterized by large plants, ancipitous stems, and large, fleshy, mostly ringent flowers provided with finely ciliate tepals.

The sect. *Dichaea*, including plants with non-articulate leaves (so withering in place) and

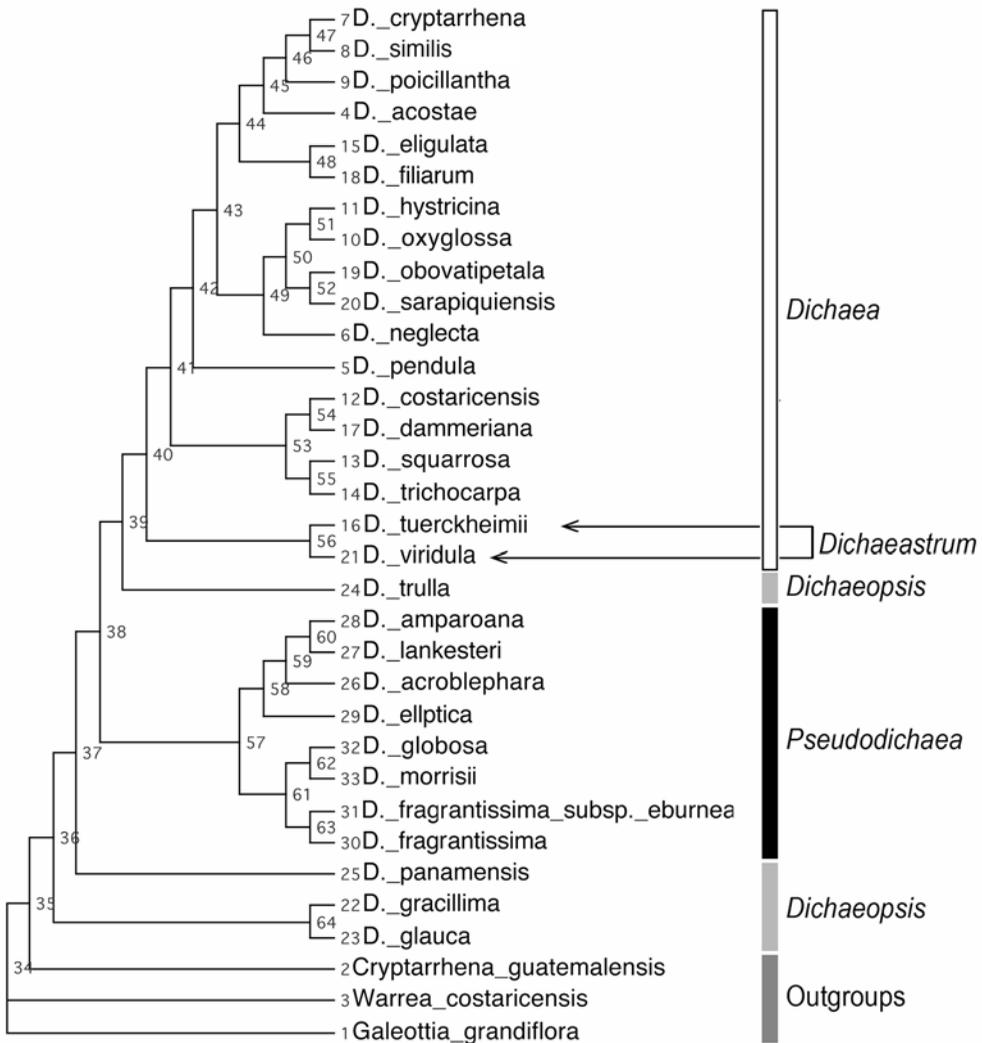


FIGURE 27. One of the 100 equally parsimonious trees from analysis of genetic distance.

muricate ovaries, is the largest group in the country with 17 species. The species pertaining to this section form a well-defined clade, but on the basis of plant and flower morphology, the circumscription of the group should be broadened to include species with glabrous ovaries. The two Costa Rican species with non-articulate leaves and glabrous ovary, *D. tuerckheimii* and *D. viridula*, traditionally treated as sect. *Dichaeastrum*, are embedded within sect. *Dichaea* in most of the trees, and the recognition of a separate section for them is not reasonable. However, in some trees (e.g., Fig. 27), *D. viridula* and *D. tuerckheimii* form together a group basal to the rest of sect. *Dichaea*, and the

inclusion in the analysis of other taxa with glabrous fruits from other regions may perhaps change their phylogenetic placement. On the basis of data from our analysis, sect. *Dichaea* can be characterized by mostly pendent plants with roots produced all along the stem, non-articulate leaves, usually geniculate peduncles, flowers produced above foliage (with the only exception of *D. pendula*), mostly ciliate shoulders of the lip, and temporal activity of the flowers. Species relationships within the section are not well resolved in the data analysis. However, in most of the trees, *D. acostae*, *D. cryptarrhena*, *D. similis*, and *D. poicillantha* form the most derived clade, characterized by

medium to very large, mostly pendent plants with flattened and usually branching stems, comparatively large flowers, ciliate shoulders of the lip, and distinct floral activity. Another recognizable subset is composed by *D. filiarum*, *D. obovatipetala*, *D. oxyglossa*, and *D. sarapiquinsis*, mostly characterized by the distinctive bronze-olive color of the foliage and mainly native from southern Mesoamerica and South America. *Dichaea squarrosa* + *trichocarpa*, *D. dammeriana*, *D. costaricensis*, and *D. pendula* form another subset in many of the trees, but the group is difficult to define on the basis of a unique set of characters.

Species groups with plesiomorphic characters within *Dichaea* (i.e., articulate leaves, straight pedicels, and reduced floral activity) are better represented in South America, and the high number of taxa recorded along the Ecuadorian Andes points toward a South American origin of the genus. Members of sect. *Pseudodichaea* are scarcely represented north of Costa Rica, and the distribution of the group is seemingly restricted to the South American continent and the southern portion of the Central American isthmus, excluding nuclear Mesoamerica and the Mexican region. However, also in the primitive groups, southern Mesoamerica (including the southern portion of Nicaragua) hosts a high percentage of endemic taxa. Six of the eight Costa Rican species of sect. *Pseudodichaea* are geographically restricted to this region, and only *D. elliptica* and *D. morrisii* span over Andean South America, and to South America and the West Indies, respectively. In general terms, species

diversity along the isthmus rapidly diminishes toward the North, with only 13 and 7 species recorded in Guatemala and Mexico, respectively (Dix and Dix, 2000; Espejo-Serna and López-Ferrari, 1997).

The floristic relationships of *Dichaea* species native to Costa Rica and southern Central America (including western Panama) are closer to the contingent found in nuclear Mesoamerica and the Mexican region than to the South American taxa (Fig. 28). The Antilles host a comparatively high number of species, with eight recorded taxa (Nir, 2000), many of which with few or no relationships with taxa of the continental floras and only a few species shared with the Central American isthmus. The hypothesis of an early migration from South America via the isthmian route (over the West Indian route) of the ancestors of today's Mesoamerican *Dichaea*, and a particularly high level of speciation occurring in the southern region of the isthmus, may perhaps explain the pattern of their geographic relationships, that is, the high number of taxa shared by southern Mesoamerica with nuclear Mesoamerica and the Mexican region as compared with their counterpart in South America. Assuming a South American origin of the genus, the distribution range of the plesiomorphic *D. glauca*, restricted to Mesoamerica and the West Indies, is noteworthy, and the species may perhaps be considered a relict. The wide geographical distribution of the other species basal to the genus, *D. panamensis*, also points toward an early dispersion of *Dichaea* from South American ancestors.

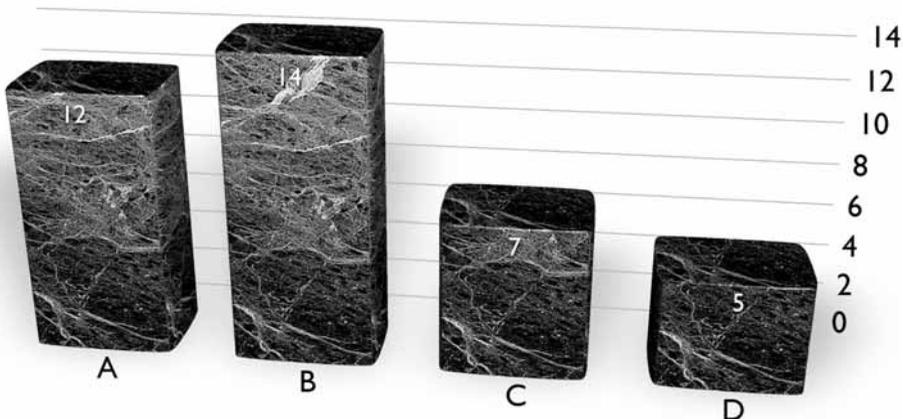


FIGURE 28. Floristic relationships of Costa Rican *Dichaea*. **A**, Species shared with nuclear Mesoamerica and the Mexican region; **B**, species restricted to Costa Rica and western Panama (southern Mesoamerica); **C**, species shared with South America; **D**, species shared with the West Indies.

SYSTEMATIC TREATMENT

*Dichaea* Lindl., Gen. Sp. Orch. Pl. 208: 1833. Type species: *Dichaea echinocarpa* (Sw.) Lindl., *nom. illeg.* = *Dichaea pendula* (Aubl.) Cogn. (Basionym: *Limodorum pendulum* Aubl.). *Dichaeopsis* Pfitz., Entw. Natürl. Anord. Orch. 107. 1887.

*Epithecia sensu* O. Kuntze, in T. von Post, Lex. Gen. Phan. 171. 1903; *sensu* Schlechter, Orchis 8: 5. 1914; *non* Knowl. & West. 1838 (= *Prosthechea* Knowl. & West.).

Epiphytic, caespitose, or scandent *herbs* without pseudobulbs. *Roots* terete, filiform to fleshy, rarely produced only at the base of the stem, commonly also caulinar, rarely branching. *Stems* 1 to several, elongate, erect to arching or laxly pendent, terete or dorsiventrally flattened, often freely branching, completely enclosed by persistent imbricating leaf-sheaths. *Leaves* distichous, articulate or not, simple, conduplicate, ovate to elliptic or lanceolate, rounded to acute, usually apiculate, abaxially carinate, the margins entire or variously microciliate toward the apex, rarely evenly ciliate, medium to dark green or grey-green to brownish, sometimes glaucous on one or both the surfaces. *Inflorescences* lateral, single-flowered, supra-axillary, produced sequentially or rarely simultaneously, emerging from the axils of the upper leaf-sheaths; the peduncle terete, straight or geniculate, basally provided with 2–3 conduplicate bractlets; floral bract double, conduplicate, shorter or longer than pedicellate ovary, the external one larger, widely ovate, cucullate-funneliform, the subopposite internal bractlet narrowly lanceolate to ligulate. *Ovary* pedicellate, short, glabrous or variously muricate. *Flowers*

resupinate, small, ringent to spreading, the sepals and petals ivory-white to greenish white or orange-grey, the sepals mostly flecked with purple-violet toward the base, the petals commonly heavily spotted or blotched with purple-violet, the lip white or spotted and blotched with violet, rarely solid purple, the column greenish white, commonly tinged violet on the foot and the lateral wings. *Dorsal sepal* ovate to elliptic-lanceolate, acute to subacuminate, concave toward the base, abaxially smooth or variously tuberculate, erect above the column. *Lateral sepals* obliquely ovate to elliptic-lanceolate, sometimes falcate, acute to subacuminate, concave toward the base, smooth or tuberculate. *Petals* ovate to elliptic or obovate, acute to abruptly acuminate, frequently concave. *Lip* distally 3-lobed to anchor-shaped, rarely subentire, variously clawed or infrequently sessile, usually conduplicate toward the apex, acute to rounded or truncate, often apiculate, the basal margins frequently ciliate, the distal margins irregularly microserrate; disc mostly ecallose or with a central ridge or 2 basal knobs. *Column* erect or straight, subterete, provided with a short foot, commonly with basal, ciliate wings, the anther terminal, the clinandrium shallow or hooded-petaloid; the stigma rounded, the lower rim commonly projecting into a variously shaped, frequently papillose-hirsute ligule. *Anther cap* widely elliptic to ovate-rhombic, cucullate, flattened, 2-celled. *Pollinia* 4, in 2 subequal pairs, rarely united in 2 heart-shaped pollinia, on a laminar, apically expanding stipe, continuous with the elliptic, sulcate, hyaline viscidium.

ARTIFICIAL KEY TO THE COSTA RICAN SPECIES OF *DICHAEA*

- 1a. Plants with articulate leaves, eventually deciduous; the peduncle usually straight; the hypochile of the lip glabrous ..... 2
- 1b. Plants with persistent leaves, rotting in place; the peduncle usually geniculate; the hypochile of the lip frequently ciliate along the margins ..... (sect. *Dichaea*) 13
- 2a. Ovary glabrous ..... 3
- 2b. Ovary muricate ..... (sect. *Pseudodichaea*) 6
- 3a. Stems flattened; roots produced only at the base of the stem; leaves ovate-elliptic, >7 mm wide; plants often glabrous ..... 4
- 3b. Stems terete; roots basal and caulinar (the latter often cryptic within the leaf sheaths); leaves narrowly ligulate, <5 mm wide; plants never glabrous ..... 5
- 4a. Plants spreading to pendent; mature leaves <25 mm long; inflorescences produced in succession; flowers greenish white, variously spotted/blotched with purple-red; petals much wider than sepals ..... *D. panamensis*
- 4b. Plants erect; mature leaves >40 mm long; inflorescences produced simultaneously; flowers ivory white; petals smaller than sepals ..... *D. glauca*
- 5a. Leaves <5 cm long; lateral sepals widely ovate-lanceolate, asymmetrical; lip to 4 mm long, clawed, the hypochile subquadrate from an abruptly rounded base; column 1.5 mm long ..... *D. gracillima*
- 5b. Leaves >7 cm long; lateral sepals elliptic, symmetrical; lip >7 mm long, sessile, the hypochile gradually obtusate; column 4–5 mm long ..... *D. trulla*

ARTIFICIAL KEY TO THE COSTA RICAN SPECIES OF *DICHAEA* CONT.

- 6a. Plants small, with leaves <40 mm long and 7 mm wide; flowers membranaceous, spreading; margins of sepals and petals glabrous ..... 7
- 6b. Plants large, with leaves >50 mm long and 10 mm wide; flowers fleshy, not completely spreading; margins of sepals and petals ciliate ..... 11
- 7a. Stems borne suberect to erect, becoming arcuate with age; flowers very fragrant; sepals long-acuminate; epichile as wide as long; infrastigmatic ligule glabrous ..... 8
- 7b. Stems borne pendent; flowers faintly fragrant or scentless; sepals acute to shortly acuminate; epichile much wider than long; infrastigmatic ligule apically pubescent ..... 9
- 8a. Flowers ivory white, the stigmatic rim pale rose; flowers boldly blotched with purple; lateral lobes of the epichile triangular ..... *D. lankesteri*
- 8b. Flowers pale pink, spotted purple at the base of sepals and petals, the lip apically rose, the stigmatic rim purple; lateral lobes of the epichile falcate ..... *D. amparoana*
- 9a. Leaves >4 (to 7) mm wide; flowers sparsely and finely spotted with pink; epichile truncate, the lateral lobes to 1.5 mm long ..... *D. elliptica*
- 9b. Leaves <3 mm wide; flowers concolorous white or boldly blotched with purple; the epichile obtuse to acute, the lateral lobes 2–3 mm long ..... 10
- 10a. Flowers white; sepals <6 mm long; lip with a short claw, 4.5 × 6 mm when spread, the lateral lobes rounded ..... *D. gomez-lauritoides*
- 10b. Sepals and petals greenish white blotched with purple, sometimes solidly purple; sepals >6.5 mm long; lip sessile, 6.5 × 7–8 mm when spread, the lateral lobes acuminate ..... *D. acroblyptaria*
- 11a. Lateral lobes of lip <2.5 mm long, oblong from obtuse angles; ligule of column subquadrate, truncate or bifid; petals sublanceolate, narrowly acute, widest basally; flowers ivory white with greenish apices ..... *D. fragrantissima* ssp. *eburnea*
- 11b. Lateral lobes of lip >2.5 (to 6.0) mm long, reflexed, acuminate; ligule of column triangular; petals ovate to obovate, widest distally; flowers green marked with red-purple ..... 12
- 12a. Petals oblong-ovate, widest near middle, acute; claw of lip ligulate, 1–3 mm wide distally, with a distinct callus at base; ligule of column porrect; sepals and petals marked with lines basally ..... *D. morrisii*
- 12b. Petals distinctly obovate, widest above middle, apiculate; claw of lip broadly obovate, 6–8 mm wide distally, without basal callus; ligule of column deflexed; sepals and petals usually blotched, rarely solid green ..... *D. globosa*
- 13a. Ovary glabrous ..... 14
- 13b. Ovary provided with distinct, variously shaped trichomes ..... 15
- 14a. Plant laxly pendent, the stems rarely branching, the leaves brownish green, undulate along the margins; flowers campanulate, pale green, unspotted; the lip anchor-shaped, with a central, low keel at the base ..... *D. viridula*
- 14b. Plant creeping, the stems freely branching, the leaves medium green, with flat margins; flowers spreading, greenish white, spotted violet; the lip ovate, with two lateral, basal calli ..... *D. tuerckheimii*
- 15a. Mature plants small, < 20 cm long; margins of the leaves entirely ciliate; the hypochile provided with two lateral, rounded knobs ..... *D. hystricina*
- 15b. Mature plants medium to large, 20 cm long; margins of the leaves glabrous, or minutely ciliate only in the apical portion; the hypochile variously shaped, but never with lateral knobs at the base ..... 16
- 16a. Stems terete, the sheaths tightly clasping ..... 17
- 16b. Plants usually distinctly pendent, the stems mostly oriented downward, blanketing tree trunk; stems flattened, the sheaths more or less loose; leaves thin to subcoriaceous ..... 19
- 17a. Plants pendent, the stems pointing downward; leaves thin-textured; petals obovate ..... *D. acostae*
- 17b. Plants often creeping, the stems developing in all directions along tree trunk; leaves coriaceous to succulent; petals ovate to broadly ligulate ..... 18
- 18a. Roots slender, < 0.5 mm in diam.; leaves coriaceous; base of the hypochile rounded, disk-shaped ..... *D. trichocarpa*
- 18b. Roots thick 1 mm in diam.; leaves succulent; base of the lip cuneate ..... *D. squarrosa*
- 19a. Apex of the pendent stem upcurving; leaves very thin-textured; flowers mostly produced below foliage; peduncle straight; lip subentire ..... *D. pendula*
- 19b. Apex of the pendent stem not upcurving; leaves subcoriaceous; flowers always produced above foliage; peduncle geniculate; lip with distinct lateral lobes ..... 20
- 20a. Petals obovate ..... 21
- 20b. Petals ovate to lanceolate-elliptic ..... 23
- 21a. Leaves >2 cm long; sepals abaxially aculeate; lip upcurved toward the column; ligule retrorse ..... *D. dammeriana*
- 21b. Leaves <1 cm long; sepals abaxially glabrous; lip straight; ligule pointing forward ..... 22

ARTIFICIAL KEY TO THE COSTA RICAN SPECIES OF *DICHAEA* CONT.

- 22a. Mature plants forming intricate mats, the stems highly branching; hypochile subacute, adaxially plain . *D. obovatipetala*
- 22b. Mature plants long, pendent, the stems rarely branching; hipochile subtruncate, minutely apiculate, adaxially provided with low tubercles among the main veins toward the apex . . . . . *D. sarapiquinsis*
- 23a. Column without infrastigmatic ligule . . . . . *D. eligulata*
- 23b. Column with a ligule projecting from the lower lobe of the stigma . . . . . 24
- 24a. Leaves with cross veining between main longitudinal veins . . . . . 25
- 24b. Leaves without cross veining . . . . . 26
- 25a. Leaves medium green with 2–3 cross veins; stems freely branching, plants forming mats; hypochile obtuse . . . . . *D. costaricensis*
- 25b. Leaves dark olive-brown with many cross veins; stems not branching; hypochile with distinct shoulders . . . . . *D. filiarum*
- 26a. Leaves olive brown, mostly retrorse; pedicel to 20 mm long; ligule bifid at apex. . . . . *D. oxyglossa*
- 26b. Leaves medium green, spreading; pedicel to 14 mm long; ligule entire, acute to truncate. . . . . 27
- 27a. Flowers with sepals and petals grey-orange, marked purple; lateral lobes of the epichile spreading; ligule truncate . . . . . *D. poicillantha*
- 27b. Flowers with sepals and petals greenish white, often marked violet; lateral lobes of the epichile retrorse; ligule acute . . . . . 28
- 28a. Leaves widely elliptic, usually overlapping; sepals spotted violet; hypochile with distinct shoulders . . . . . *D. cryptarrhena*
- 28b. Leaves lanceolate elliptic, not overlapping; sepals mostly concolorous, or with a few spots near the base; hypochile obtuse . . . . . *D. similis*

1. *Dichaea acostae* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 306. 1923. TYPE: COSTA RICA. [Alajuela:] Umgebung von San Ramón, im Jahre 1921, *G. Acosta s.n.* (Holotype: B, destroyed; Isotype, designated here as the lectotype, AMES 40542; tracings of Schlechter’s drawings of the Holotype: AMES 40542). Fig. 29, Map 1.

*Plant* epiphytic, caespitose, to 30 cm long. *Roots* basal, filiform, flexuous, glabrous. *Stems* terete, decumbent to pendent, rarely branching, 6–30 cm long, 0.2–0.3 cm wide across conduplicate sheaths. *Leaves* spaced along stem, spreading to retrorse, 8–10 × 3.2–4.0 mm, narrowly elliptic-oblong, apiculate; sheaths clasping, 5–6 × 4–5 mm. *Inflorescence* solitary, 1-flowered, subpatent, 10 mm long, provided with basal bracts. *Floral bract* double, the outer bract ovate-cucullate, ca. 2 mm long, the inner bract linear, ca. 2 mm long. *Ovary* 1.75 mm long, densely muricate. *Flower* small for the genus, not completely spreading, glabrous, blotched with violet. *Dorsal sepal* narrowly lanceolate, acute, 3-nerved, 5 × 1 mm. *Lateral sepals* obliquely narrowly lanceolate, acute to subacuminate, 3-nerved, 5 × 1.2 mm. *Petals* narrowly oblong, shortly acuminate, 4.7 × 1.5 mm. *Lip* 3-lobed, anchoriform, clawed, 4.0 × 5.5–6.0 mm when spread, the claw hemielliptic-obcuneate, 2.0 mm long, 2.5 mm wide api-

cally, the epichile transversely elliptic, rounded, shortly subapiculate, 2.0 × 3.5 mm, the lateral lobes linear-ligulate, rounded, spreading, 1 mm long, 0.4 mm wide at the base. *Column* 2 mm long; the clinandrium irregularly crenulate; ligule linear, minutely ciliate, 0.5 × 0.3 mm. *Pollinia* unknown. *Fruit* unknown.

The above description was prepared from the original protologue, the drawings of the holotype, and an isotype fragment.

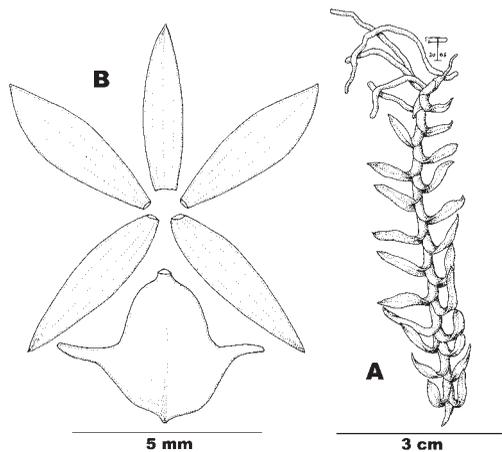
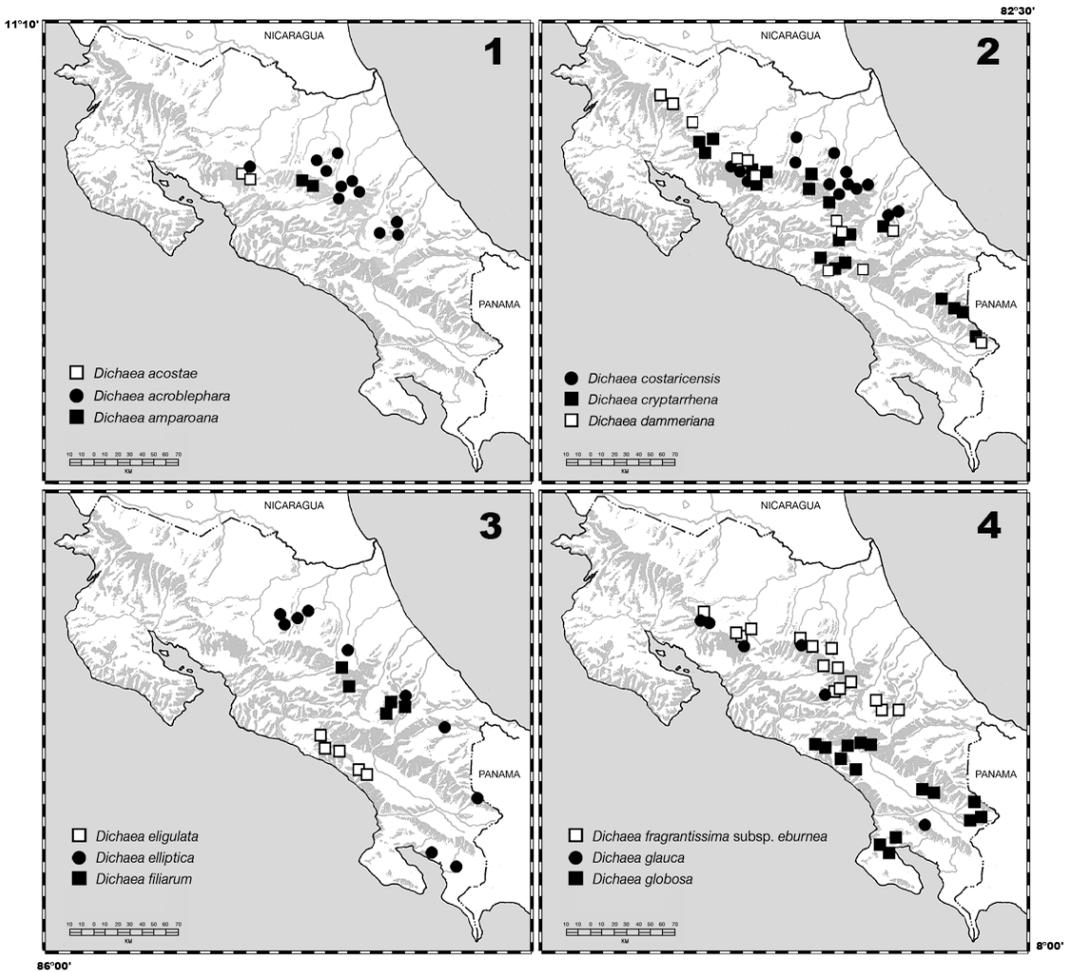


FIGURE 29. *Dichaea acostae* Schltr. A, Modified from the tracing of the holotype (AMES); B, drawn from the isotype (AMES).



MAPS 1–4. Distribution of *Dichaea* in Costa Rica. 1, *D. acostae*, *D. acrolephara*, and *D. amparoana*; 2, *D. costaricensis*, *D. cryptarrhena*, and *D. dammeriana*; 3, *D. eligulata*, *D. elliptica*, and *D. filiarum*; 4, *D. fragrantissima* ssp. *eburnea*, *D. glauca*, and *D. globosa*.

**Distribution:** known only from Costa Rica.

**Additional material examined or previously cited:** COSTA RICA. Alajuela: Bois secs, Santiago de San Ramón, 1075–1100 m, XI. 1921, A. M. Brenes 146, “Feuilles étroites. Fleurs mouchetées de violet” (B, destroyed).

**Eponymy:** named in honor of Guillermo Acosta, who collected the type specimen.

**Ecology:** a probably uncommon epiphyte in premontane rain forests, ostensibly on the Pacific watershed of the Cordillera de Tilarán in Costa Rica, at 1000–1100 m elevation. Flowering occurs at least from November to January.

Since the time of its description in 1923, *Dichaea acostae* was lost in botanical nomen-

clature, and the destruction of the holotype in Berlin contributed to its oblivion. Apparently the species was never collected again after 1921, when Guillermo Acosta and Manuel Alberto Brenes found it independently in the area of San Ramón. Nevertheless, the original protologue, the diagnostic sketches prepared by Schlechter, and the isotype fragment at AMES, selected here as the lectotype, account for a rather distinctive species. Schlechter compared the plant habit, provided with terete stems, to that of *D. squarrosa* Lindl., and the small flower to *D. costaricensis* and *D. vaginata* (the latter a synonym of *D. cryptarrhena*). The leaves are small, with only 3 longitudinal veins on each side of the midvein, and the flowers are among

the smallest of Costa Rican *Dichaeas*. Also the oblong petals, wider in the distal portion, are rather uncommon and diagnostic of the species. Schlechter (1923d) published the specific epithet as *acostaei*, but it must be corrected according to Article 60.11 and Recommendation 60C.1 of the International Code of Botanical Nomenclature (Greuter, 2000).

2. *Dichaea acrolephara* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 71. 1923. TYPE: COSTA RICA. [San José: Moravia,] San Jerónimo, blühend im Mai 1921, *C. Wercklé* 22 (Syntype: B, destroyed). Carillo [Carrillo], c. 400 m, blühend im Juni 1909, *A. Brade & C. Brade* 1173 (Syntype: B, destroyed; Lectotype, designated here, tracing of Schlechter's drawing of syntype, AMES 31565). Fig. 30, Map 1. Synonym: *Dichaea standleyi* Ames, Schedul. Orchid. 9: 57. 1925. TYPE: COSTA RICA. Limón: vicinity of Guápiles, 300–500 meters, March 12, 13, 1924. On tree; flowers white and purple red. *P.C. Standley* 37440 (Holotype: AMES 29640), *syn. nov.*

*Plant* epiphytic, caespitose, to 25 cm long. *Roots* filiform, exposed at the base, hidden by the leaf sheaths along the stem, 0.5–0.6 mm in diam. *Stems* compressed, suberect, becoming pendent with age, 10–25 cm long, 0.2–0.3 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, widely spaced along stem, spreading, subcoriaceous, green, 18–30(35) × 2–3 mm, ligulate to narrowly elliptic, acute to acuminate, the apical margins minutely pectinate-ciliate; sheaths clasping, 8–10 × 5–6 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent to pendent, to 18 mm long, provided with a basal, cylindrical bract, 3 mm long. *Floral bract* double, the outer *bract* widely ovate, 5 × 4 mm, the inner bract linear, acute, 4 mm long. *Pedicel* cylindrical, less than 1 mm long. *Ovary* 1.3–1.5 mm long, densely muricate. *Flower* spreading, the sepals and petals greenish white blotched with purple, sometimes solidly purple, the blotches restricted to the external half of the lateral sepals, the lip white, sparsely spotted with violet at the base, the column white, marked with violet along the basal wings and the margins of the stigma; no fragrance detected. *Dorsal sepal* erect, slightly concave, lanceolate-elliptic, subacuminate, 6.5–8.0 ×

2.5–2.8 mm. *Lateral sepals* obliquely ovate-lanceolate, concave, subacuminate, 7–9 × 3.2–3.5 mm. *Petals* elliptic-lanceolate, acute to subacuminate, 7.0–7.5 × 2.3–2.5 mm. *Lip* 3-lobed, anchoriform, sessile, 5.5–6.5 × 7–8 mm when spread, the hypochile obcuneate, 2.7–3.8 mm long, 2.5 mm wide apically, the epichile widely triangular, shortly apiculate, sometimes microscopically ciliate toward apex, 3.2 × 4.0 mm, the lateral lobes narrowly triangular, acuminate, spreading to reflexed, 1.8–2.5 × 0.8–1.0 mm. *Column* erect, 3 mm long, with distinct foot, provided at the base with elliptic, rounded, ciliate wings; the clinandrium shortly cucullate, irregularly erose; ligule oblong, thickened toward the papillose-hirsute apex, 1.2 × 0.8 mm. *Anther cap* subrhynchiform, emarginate, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a broadly obtriangular, rounded stipe; viscidium elliptic-peltate. *Fruit* an elliptic, densely muricate capsule.

**Distribution:** known only from Costa Rica.

**Additional material examined:** COSTA RICA. [Alajuela: San Ramón,] La Palma de San Ramón, 5–8.VIII. 1935, *A. M. Brenes* (72) 20638 Herb. Brenes (CR 18428, sterile). Cartago: [Turrialba,] vicinity of Pejivalle, about 900 m, February 7, 8, 1926, *P. C. Standley & J. Valerio* 47104 (AMES); Turrialba, Tuis, Cien Manzanas, 09°59'25"N, 83°33'47"W, ca. 950 m, along a minor tributary of Río Pacuare, 26 May 2003, *F. Pupulin et al.* 4795 (JBL-Spirit); Turrialba y Jiménez, La Suiza-Pejivalle, camino a Esperanza, 9°48'21"N, 83°39'10"W, 726 m, 28.8.2004, *D. Bogarín* 956 & *J. Carmona* (JBL-Spirit). Heredia: Sarapiquí, Horquetas, Refugio Caray, collected by Diego Bogarín, flowered in cultivation at Jardín Botánico Lankester, 29 June 2002, *F. Pupulin* 4025 (JBL-Spirit); [Sarapiquí, Puerto Viejo,] Finca La Selva, OTS field station near junction of Puerto Viejo and Sarapiquí rivers, 40–100 m, Circular Lejano, 500 m just across the bridge (growing with *Dichaea trulla*), 19 Mar. 1991, *K. Richardson* K-109 (CR); Sarapiquí, Puerto Viejo, Estación Biológica La Selva, a orillas del Río Sarapiquí, 40 m, bosque muy húmedo tropical, epífitas sobre troncos y ramas caídas en bosque secundario, 7 Junio 2003, *D. Bogarín* 207 (JBL-Spirit); Sarapiquí, Horquetas, road to Rara Avis, ca. km 4, farm La Selva, 10°20'24"N 83°59'30"W, 115 m, 26 July 2003, *F. Pupulin* 4850, *C. Pupulin*, *M. Pupulin*, *C. Ossensbach* &

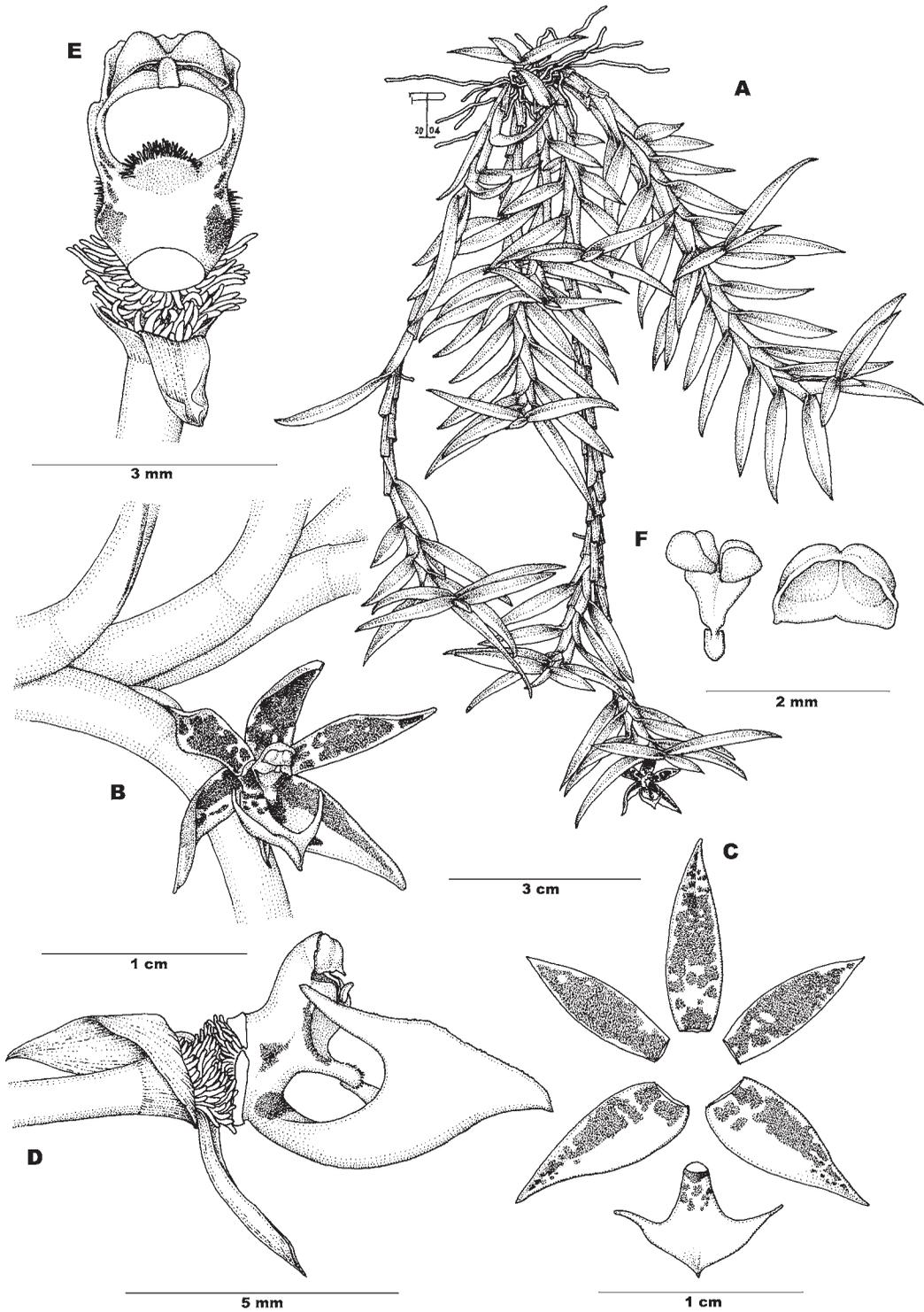


FIGURE 30. *Dichaea acrolephara* Schltr. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from Pupulin et al. 4851 (JBL-Spirit).

*B. Arias* (JBL-Spirit); same locality, *F. Pupulin* 4851, *C. Pupulin*, *M. Pupulin*, *C. Ossensbach* & *B. Arias* (JBL-Spirit); Sarapiquí, San Miguel, road to La Virgen, along the banks of Río Sarapiquí, 30.1.2000, 360 m, 21.9.2002, *F. Pupulin* 1955 (JBL-Spirit). Limón: vicinity of Guápiles, 300–500 m, March 12, 13, 1924, *P.C. Standley* 37405 (AMES); Pococi, Horquetas, Refugio Silvestre Privado Caray, 500 m, bosque húmedo montano bajo, epífita a la orilla del sendero, 12 Febrero 2001, *D. Bogarín* 42 (JBL-Spirit); Flores, Río Costa Rica, about 7 km upwater from the cross point with the way San José-Guápiles, 10°10'N, 83°51'W, ca. 400 m, collected by M. J. Moya & O. Rodríguez, 27 Apr. 2002, flowered in cultivation at Jardín Botánico Lankester, 14 June 2002, *F. Pupulin* 3863 (JBL-Spirit); Guápiles, Flores, along the Río Costa Rica, 10°10'N, 83°51'W, 500 m, 29.4.2001, *O. Rodríguez* 7 (JBL-Spirit); Guápiles, road from the San José-Limón highway to Reserva Forestal las Tintoreras, km 2, shores of Río Blanco, 10°12'05.2"N, 83°50'10.1"W, 200 m, epiphytic on large trees overhanging the river, wet tropical forest, 15 June 2006, *F. Pupulin* 6228, *D. Bogarín*, *R. L. Dressler* & *J. Gómez-Laurito* (CR); Pococi, Guápiles, Reserva Forestal las Tintoreras (ca. 5 km from the San José-Limón highway), shores of Río Blanco, secondary woods across the bridge on the river at the end of the road, 10°08'58.7"N, 83°49'37.4"W, 210 m, wet tropical forest, 15 June 2006, *F. Pupulin* 6231, *D. Bogarín*, *R. L. Dressler* & *J. Gómez-Laurito* (CR); Guápiles, carretera a Guápiles, orillas del Río Costa Rica, 10°12'37"N, 83°51'39"W, 260 m, 3.10.2004, *D. Bogarín* 1009 & *Botánica Forestal* (JBL-Spirit). San José: Braulio Carrillo Nat. Park, along Sendero La Botella, 10°10'00"N, 83°57'15"W, 700 m, 2 Sept. 1990, *S. Ingram* 564 & *K. Ferrell* (SEL, USJ).

**Etymology:** from the Greek *acros*, summit, and *blepharo*, ciliate, in reference to the marginally pectinate apex of the lip.

**Ecology:** a rather frequent epiphytic plant, growing in shade in tropical to premontane wet forests on the Caribbean watershed of the Cordillera Central and the Cordillera de Talamanca in Costa Rica, at 100–1300 m elevation. Flowering occurs from February to September.

In the protologue, Schlechter cited both *Wercklé* 22 and *Brade & Brade* 1173, without designating the type. The tracings of Schlechter's drawings of the plant and dissection of the flower of

a syntype at AMES (Fig. 31) bear no collecting data and cannot be assigned with certainty to any of the syntypes. Nevertheless, the shape of the lip and the thick infrastigmatic ligule shown in the analytical drawings agree with the character stated in the protologue. The type sheet at AMES also has a copy of a small watercolor prepared by one of the Brade brothers from a flower of their collection n. 1173 (Schlechter, 1923b: 154), showing the sepals and petals strongly blotched with violet, the blotches being restricted to the external half of the lateral sepals, and the white lip characteristic of the species. As noted by Dressler (2003), the lateral lobes of the lip of *D. acrolephara* contrast with those of *D. standleyi* in being minutely ciliate on the margins, but this character is variable in the species, and a collection made near the type locality of *D. standleyi* (*Bogarín et al.* 1009, USJ-Spirit, USJ, drawing) also shows small cilia along the margin of the reflexed lateral lobes.

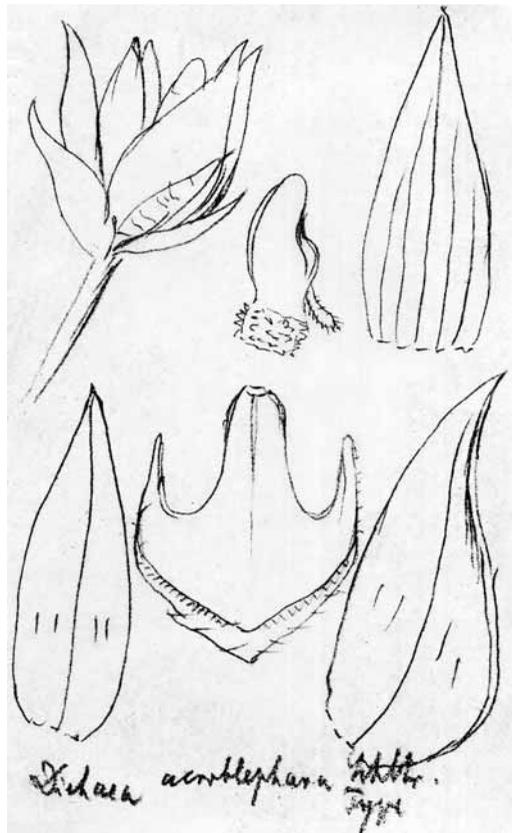


FIGURE 31. Copy of Schlechter's sketch of *Dichaea acrolephara* Schltr. (AMES). Reproduced with the kind permission of the Director, Harvard University Herbaria.

3. *Dichaea amparoana* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 71. 1923. TYPE: COSTA RICA. [San José: Moravia,] San Jerónimo, 1400 m, im Jahre 1922, *C. Wercklé 103* (Holotype: B, destroyed; Lectotype, designated here, tracings of Schlechter's drawings of the Holotype: AMES). Fig. 32, Map 1.

*Plant* epiphytic, caespitose, to 20 cm long. *Roots* filiform, exposed at the base, hidden by the leaf sheaths along the stem, ca. 0.5 mm in diam. *Stems* compressed, suberect to erect, 10–20 cm long, 0.35–0.55 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, densely spaced along stem, suberect to spreading, rather thin-textured herbaceous, green, 20–35(50) × 1.5–5.0(7.0) mm, linear-lanceolate, acute, the apical margins sometimes minutely serrulate-ciliate; sheaths clasping to slightly inflated, to 8.0 × 3.5 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, patent to suberect, to 14 mm long, provided with 2 basal, cucullate bracts 3 mm long. *Floral bract* double, the outer bract widely ovate, cucullate 5.5 × 4.0 mm, the inner bract narrowly linear-elliptic, acute, 4 mm long. *Pedicel* cylindrical, less than 1 mm long. *Ovary* 1.0–1.2 mm long, densely muricate. *Flower* spreading, the sepals and petals glabrous, pale rose, minutely spotted with purple at the base, the lip rose-purple, fading white at the base, the column rose-purple, marked with purple along margins of the stigma; no fragrance detected. *Dorsal sepal* erect, slightly concave, lanceolate, subacuminate, 7–9 × 2.5–3.0 mm. *Lateral sepals* obliquely ovate-lanceolate, concave, acuminate, 7–10 × 3.5–4.0 mm. *Petals* narrowly lanceolate, acuminate, 6–8 × 2.0–2.5 mm. *Lip* 3-lobed, anchoriform, clawed, 6.0–7.5 × 5.0–6.5 mm when spread, the claw obtuse, 2.5–3.0 mm long, 3.5–4.0 mm wide apically, the epichile widely triangular, acuminate, 4.5 × 4.0 mm, the lateral lobes narrowly falcate-triangular, acute, retrorse, 2 × 1 mm. *Column* suberect, 2.5 mm long, with distinct foot, provided at the base with elliptic, rounded, glabrous wings; the clinandrium subcucullate, entire; ligule widely transversely elliptic, glabrous, oblong, thickened toward the papillose-hirsute apex, 0.8 × 1.8 mm. *Anther cap* subrhynchiform, the margins sparsely ciliate, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a very broadly obtriangular, rounded stipe; viscidium elliptic-peltate. *Fruit* an elliptic, densely muricate capsule.

**Distribution:** known only from Costa Rica.

**Additional material examined:** COSTA RICA. Alajuela: San Ramón, Piedades, Piedades Norte, road to Bajo de La Paz, km 2.6, along the Río San Pedro, 10°08'59.9"N, 84°33'53.3" W, 1307 m, premontane wet forest, epiphytic along the shores of the river, 30 January 2005, flowered in cultivation at Jardín Botánico Lankester, 6 February 2006, *F. Pupulin 5501*, *D. Bogarín*, *M. Salas* & *P. Seaton* (CR). Heredia: Barva, San José de La Montaña, Calle Higuierón, 10°03'43"N, 84°6'6"W, 1800 m, bosque húmedo montano bajo, sobre paredón a orilla de la calle, 30 enero 2004, floreció en cultivo en el Jardín Botánico Lankester, mayo 2004, *D. Bogarín* & *A. Prendas 679* (CR, USJ, JBL-Spirit). Without locality, *A.R. Endres Dichaea* No. 4 (*Rchb. Orch.* 38607, W, drawings).

**Eponymy:** named in honor of Mrs. Amparo López Calleja de Zeledón, who strongly encouraged and sponsored orchid exploration in Costa Rica.

**Ecology:** an uncommon plant growing epiphytically or semi-terrestrially in humus in premontane to submontane wet forests on the Caribbean watershed of the Cordillera Central in Costa Rica, at 1300–1800 m elevation. Flowering occurs at least from January to March.

*Dichaea amparoana* has been known for a long time only from the type collection by C. Wercklé. No isotypes or paratypes of this species are known to exist, so the tracings of Schlechter's drawings of the plant and dissection of the flower are chosen as the lectotype (Fig. 33). The drawings at AMES clearly show the erect habit, the stem provided with rather short leaves, the lip with falcate-retrorse apical lobes, and the column with a glabrous, obtuse ligule, which distinguish this species and are consistent with the protologue. *Dichaea amparoana* fell into botanical oblivion after its description, and it has been considered conspecific with *D. lankesteri* Ames (Pupulin, 2002; Dressler, 2003). Nevertheless, the suberect habit, the densely foliated stems, the flowers tinged by pale rose and spotted with purple, the longer infrastigmatic ligule, and the retrorse, falcate lateral lobes of the lip distinguish it from other relatives. Wercklé's specimens bear no indication of flower color, but a plant of *Dichaea* recently collected not far from the type locality of *D. amparoana* (*D. Bogarín 679*, JBL-Spirit), probably corresponding to this

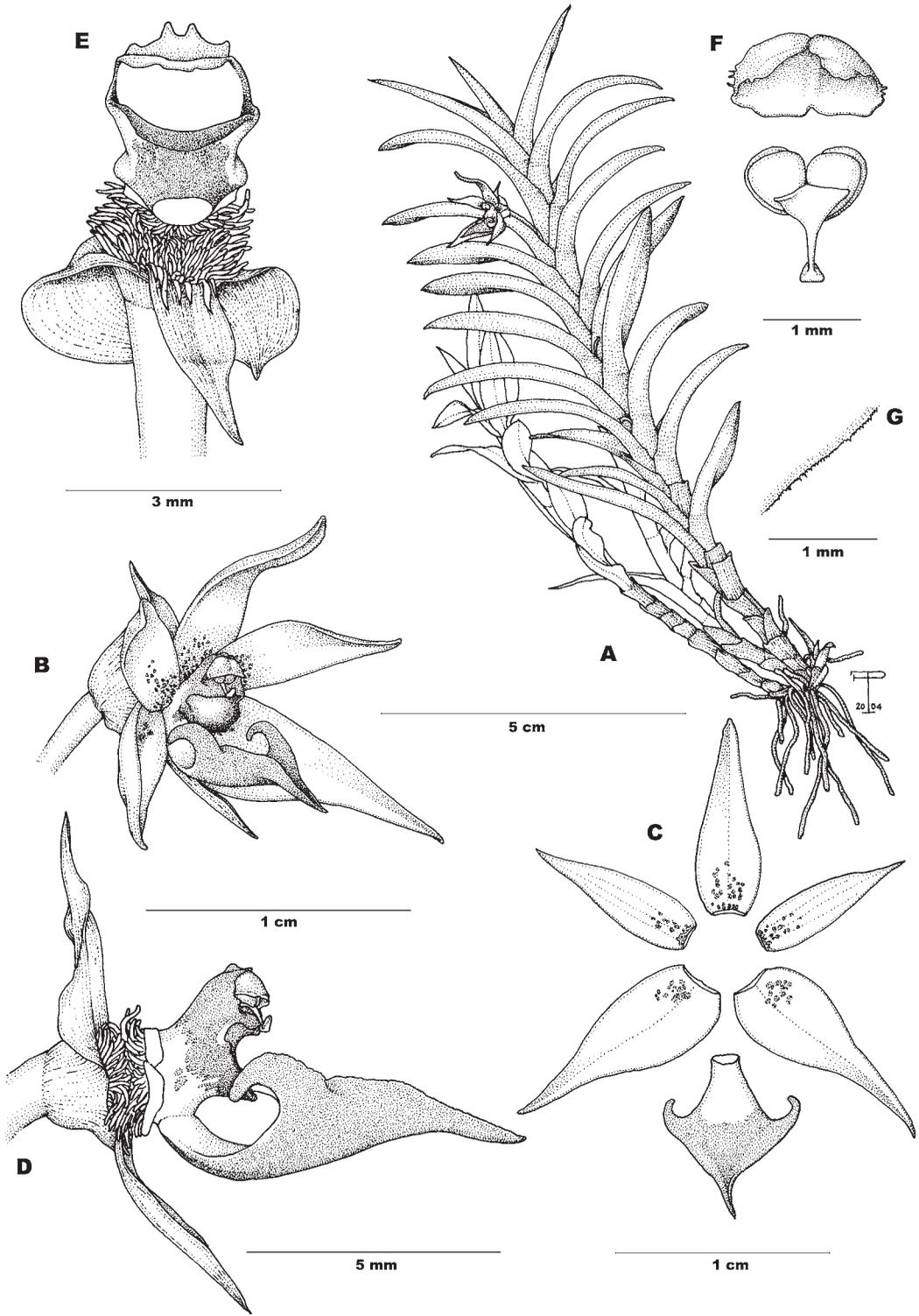


FIGURE 32. *Dichaea amparoana* Schltr. A, Habit. B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium; G, margin of leaf. Drawn from Bogarin & Prendas 679 (JBL-Spirit).

species, has pale rose flowers, the base of sepals and petals spotted with purple, the lip pink, and a dark violet rim around the stigmatic cavity.

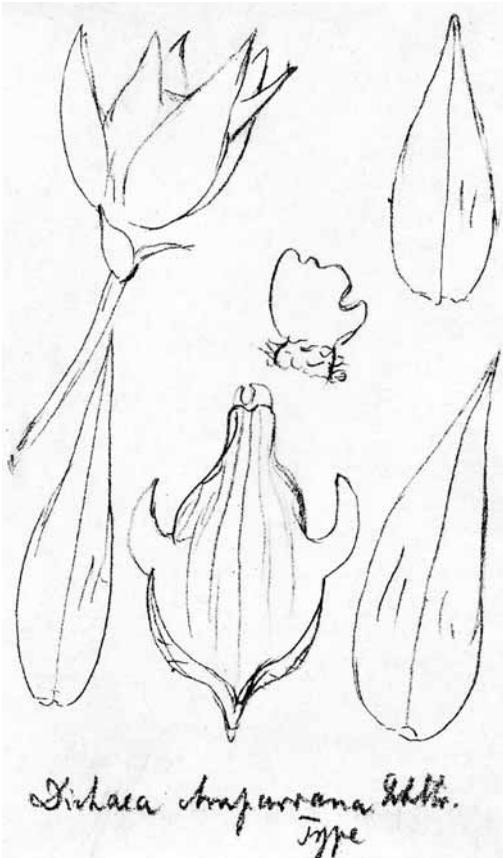


FIGURE 33. Copy of Schlechter's sketch of *Dichaea amparoana* Schltr., Wercklé 103 (AMES). Reproduced with the kind permission of the Director, Harvard University Herbaria.

4. *Dichaea costaricensis* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 73. 1923. Syntypes: Costa Rica. [San José: Carrillo,] La Palma (?), blühend im September 1921, *C. Wercklé* 77 (B, destroyed); Carrillo, blühend im Juni 1921, *C. Wercklé* 39 (B, destroyed); [Moravia,] San Jerónimo, 14,000 [1400] m, auf der pazifischen Seite, im Jahre 1920, *C. Wercklé* s.n. (B, destroyed). (Lectotype, proposed by Folsom (1987) and designated here, tracing of Schlechter's drawing of a syntype, collection data not noted: AMES 31569). Fig. 34, Map 2.

*Plant* epiphytic, caespitose, to 20 cm long. *Roots* exposed basally, hidden by leaf sheaths along the stem, flexuous, glabrous, ca. 1 mm in

diam. *Stems* subterete, scandent to pendent, freely branching, 6–20 cm long, 0.3–0.5 cm wide across conduplicate sheaths. *Leaves* closely spaced along stem, spreading, green, thick-herbaceous, sparsely cross-veined, 4–10 × 2–5 mm, elliptic-lanceolate, obtuse to rounded, minutely apiculate, the apical margins microscopically fimbriate; sheaths tightly clasping the stem, to 4 × 3 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent to subpendent, 0.4–0.7 cm long, provided at the base with 2–3, tubular, hyaline bracts, about 0.5 cm long. *Floral bract* double, the outer bract triangular ovate, acuminate, 3.0 × 3.5 mm, the inner bract narrowly lanceolate-oblong, 3.5 mm long. *Pedicel* cylindrical, less than 1 mm long. *Ovary* long muricate, 1 mm long. *Flower* ringent, with sepals and petals rather thick, grayish-cream to pale green-yellow, blotched and spotted with red-purple, the sepals externally minutely tuberculate, the lip white, barred and blotched red-purple, the column white, marked with purple on the margins of wings. *Dorsal sepal* elliptic-lanceolate, acute, with a rounded apicule, 7.5–8.5 × 3.0–3.8 mm. *Lateral sepals* obliquely narrowly elliptic-lanceolate, asymmetrical, rounded-acute, 8.7–9.5 × 3.2–4.0 mm. *Petals* elliptic-oblong to oblanceolate, subacute to obtuse, 7.0–7.8 × 3.2–3.6 mm. *Lip* 3-lobed, subsessile, 8.5 × 7 mm when spread, the hypochile widely obcuneate-elliptic, 4.5 mm wide apically, the epichile triangular, acute, spreading, decurrent on the lamina, 1.5 × 0.9 mm. *Column* erect, 4.5 mm long, provided with widely elliptic, flattened, ciliate wings, the clinandrium minutely erose; ligule widely triangular, acute or subobtusate, glabrous, 0.7 × 1.1 mm. *Anther cap* transversely ovate, 2-celled. *Pollinia* 4 in two superposed pairs of slightly different size, on a narrowly obtriangular, rounded stipe; viscidium elliptic. *Fruit* an elliptic capsule, muricate.

**Distribution:** Costa Rica and western Panama.

**Additional material examined:** COSTA RICA. Alajuela: Alajuela, Sarapiquí, Cinchona, bosque húmedo a la orilla de la calle, 600 m, 15 May 2005, flowered in cultivation at Jardín Botánico Lankester, 4 Aug. 2006, *E. Serrano* 229 & grupo de Asociación de Aves (CR); San Ramón, Cerros del Pezón, *A. R. Endres* 29 (W, drawings); Sarapiquí, San

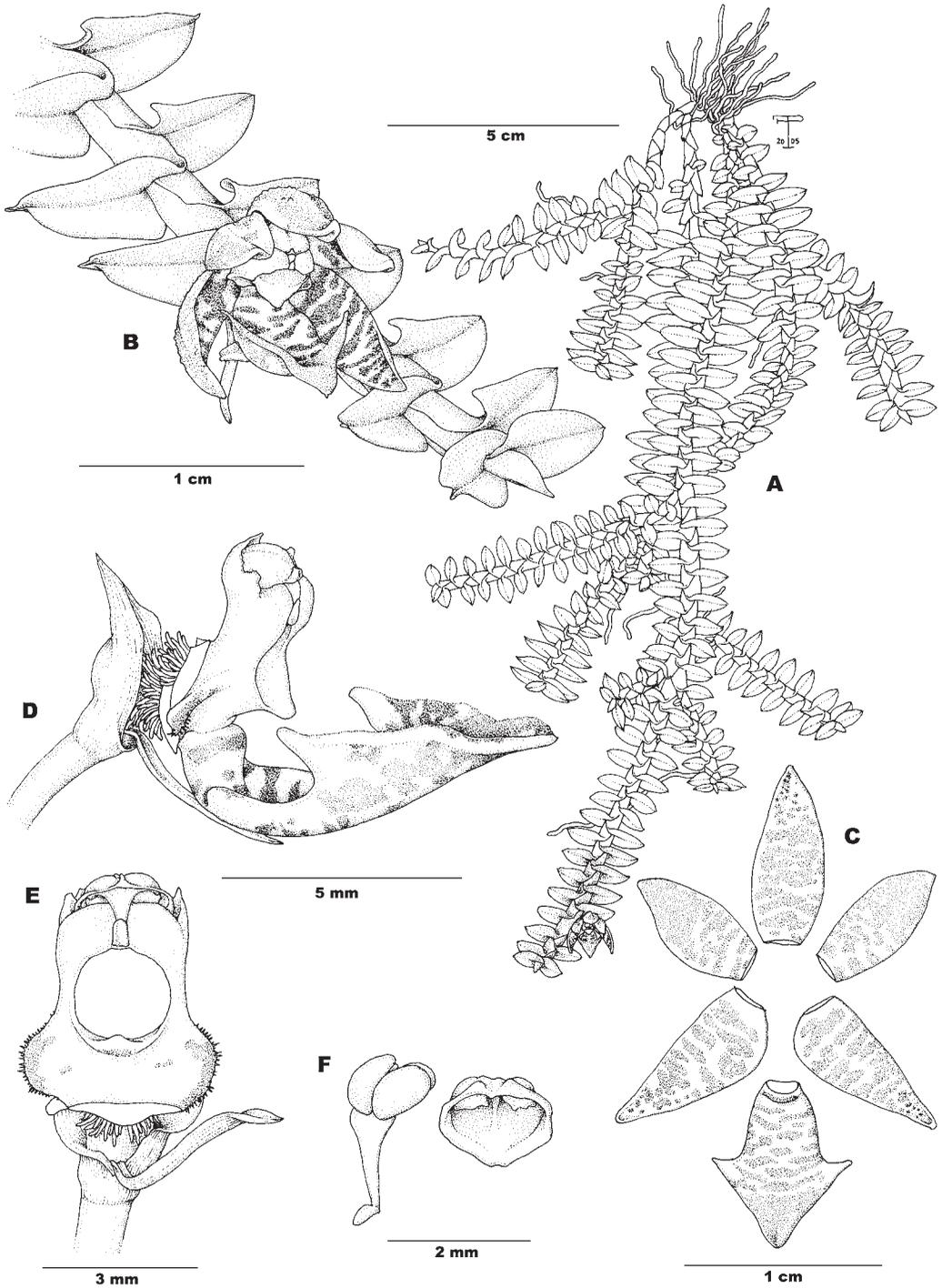


FIGURE 34. *Dichaea costaricensis* Schltr. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from Pupulin et al. 4797 (JBL-Spirit).

Miguel, unpaved road to the west of the village, 10°16'04.7"N, 84°11'01.4"W, ca. 500 m, on short trees along the roadside, tropical wet, transition to premontane wet forest, 16 June 2005, flowered in cultivation at Jardín Botánico Lankester, 14 Aug. 2006, *F. Pupulin 5700*, *D. Bogarín* & *A. C. Rodríguez* (CR); same locality, *F. Pupulin 5702*, *D. Bogarín* & *A. C. Rodríguez* (CR); Cerros del Pezón, *A. R. Endres* [*Dichaea* No. 13] (W, drawings); San Pedro de San Ramón, collines, 1050–1075 m, Dec. 1922, *A. M. Brenes* (222) 1412 (AMES 45068); San Ramón, La Palma, 1190 m, 30 Oct. 1922, *A. M. Brenes* (40) 370 (AMES); 1200 m, 18 Dec. 1922, *A. M. Brenes* (237)2961 (CR); Dec. 1922, *A. M. Brenes* 532 (AMES). Border between Alajuela and Heredia: Grecia, Sarapiquí, Colonia Virgen del Socorro camino a Cariblanco, bridge on Río San Fernando, 10°16'32"N, 84°10'16"W, 750 m, 13.2.2004, *F. Pupulin 5171*, *H. Leon-Paez*, *E. Salas* & *D. Bogarín* (JBL-Spirit). Cartago: Juan Viñas, Pejivalle, La Marta, shore of Rio Pejivalle, 09°47'47"N, 83°42'55"W, 690 m, 10.1.2004, flowered in cultivation at Jardín Botánico Lankester, 28 Jan. 2005, *F. Pupulin 5052*, *S. Dälstrom*, *H. Leon-Paez* (JBL-Spirit); Turrialba, Cien Manzanas, along a minor tributary of Río Pacuare 9°59'25"N, 83°33'47"W, 950 m, 26.5.2003, *F. Pupulin 4797*, *R.L. Dressler*, *K. Dressler*, *G. Gerlach*, *P. Kindlmann*, *E. Serrano*, *H. León-Páez* & *S. Pugh-Jones* (JBL-Spirit); Turrialba, Platanillo, 600 m, Río Platanillo, Tayutic, 20.2.2004, flowered in cultivation at Turrialba, Nov. 2004, *A. Karremans 111* (JBL-Spirit); same locality, *A. Karremans 114* (JBL-Spirit); same locality, 30.4.2005, *A. Karremans 799* (JBL-Spirit). Guanacaste: El Arenal, 485–600 m, 18–19 Jan. 1926, *P. C. Standley* & *J. valerio 45134* (US). Heredia: Sarapiquí, on road between Cariblanco and San Miguel, 10°16'N, 84°10'W, 12 July 1983, *K. Barringer 3737*, *E. Christenson* & *B. Pérez* (SEL); Colonia del Socorro, cerca del Río San Fernando, 10°16'30"N, 84°10'05"W, 700–900 m, 5 Aug. 1995, *J. F. Morales 4719* (INB); Horquetas, Sarapiquí, Finca Terrafolia, contiguo a Rara Avis, 10°18'14"N, 84°01'36"W, 500 m, 21.7.2003, flowered in cultivation at Jardín Botánico Lankester, 17 Sept. 2004, *W. M. Whitten 2095* & *M. Blanco* (JBL-Spirit); Horquetas de Sarapiquí, Reserva Rara Avis,

Sendero Tigre entre Catarata y Plástico, 10°17'03"N, 84°02'47"W, 540 m, 19 Jun. 1995, *S. Martén 891* (CR); Sarapiquí, Reserva Rara Avis, límite sur del Parque Nacional Braulio Carrillo, 10°16'8.97"N, 84°03'7.10"W, 705 m, 9 Aug. 2005, flowered in cultivation at Jardín Botánico Lankester, 16 Aug. 2006, *J. Warner 50*, *R. L. Dressler*, *A. Rojas*, *M. Muñoz* & *P. Protti* (CR). Limón: Vicinity of Guápiles, 300 to 500 m, March 12, 13 March 1924, *P. C. Standley 37417* (AMES); *P. C. Standley 37441* (AMES); *P. C. Standley 37536* (AMES); *P. C. Standley 37547* (AMES); Pococí, Guápiles, carretera Braulio Carrillo, ca. 2 km hacia abajo de la entrada del Teleférico del Bosque Lluvioso, en lomas a orilla de la carretera, 520 m, 10°11'33"N, 84°54'27"W, bosque muy húmedo tropical transición a premontano, 9 Julio 2004, *D. Bogarín 894* & *F. Pupulin* (JBL-Spirit); Pococí, Guápiles, San José-Limón Highway, ca. km 49, 10°11'38"N, 84°54'27"W, 450–520 m, 9.7.2004, flowered in cultivation at Jardín Botánico Lankester, 28 Sept. 2004, *F. Pupulin 5262* & *D. Bogarín* (JBL-Spirit); Guápiles, Parque Nacional Braulio Carrillo, Sector Quebrada González, Sendero Botarrama hacia orillas del Río Sucio, 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, 12 Jun. 2005, floreció en cultivo en el Jardín Botánico Lankester, 14 Aug. 2006, *D. Bogarín 1570* (CR). San José: Carillo, 500–700 m, Braulio Carrillo Park, 16 Sept. 1984, *J. P. Folsom 11,001B* (CR); Moravia, San Jerónimo, carretera a Braulio Carrillo, calle Yerbabuena, márgenes del Río Pará Blanco, 10°01'07"N, 84°00'17"W, 1400 m, 1.6.2002, *V. Blanco s.n.* (JBL-Spirit).

Without locality, *A. M. Brenes* (204) 1396 (AMES); *A. M. Brenes* (277) 1462 (CR, AMES); *Endres 517* (W); sin recolector, una planta decomisada en el Aeropuerto Juan Santamaría, 24 Febrero 2003, floreció en cultivo en el Jardín Botánico Lankester, 14 Apr. 2005 (JBL-Spirit).

**Etymology:** named from the country of origin.

**Ecology:** a rather frequent epiphyte in tropical wet, premontane wet, and cloud forest on the Caribbean drainage of the Guanacaste, Tilarán, and Central Volcanic chains in Costa

Rica, at 100–1200 m elevations. Flowering occurs year-round.

*Dichaea costaricensis* may be recognized by the relatively small, scandent plants, highly branching and often forming compact mats, the thick-herbaceous leaves with scattered cross-venation (a character shared, in Costa Rica, only with *D. filiarum*), and the flowers with grayish-cream base and red-purple pigmentation and the segments of the perianth subcoriaceous. In the protologue, Schlechter (1923a) cited Wercklé 77 and 39 and a Wercklé's collection without number from a different locality, without designating the type. No isosyntypes for this species or any material annotated by Schlechter are known to exist. The drawing at AMES (35169) shows the short, subquadrate ligule and the characteristic outline of the lip cited in the protologue, and they are chosen as the lectotype (Fig. 35).

5. *Dichaea cryptarrhena* Rchb.f. ex Kraenzl., Pflanzenr. 4(50): 36. [March] 1923. TYPE: COSTA RICA. Without collecting data, A. R. Endres 28 (Holotype: W-Reichenbach Orchid Herbarium Nr. 18372). Fig. 36, Map 2.

Synonyms: *Dichaea verrucosa* Ames & C. Schweinf., Schedul. Orchid. 8: 83. 1925. TYPE: COSTA RICA. [Cartago: Turrialba,] La Fuente, Peralta, Sept. 1923, C.H. Lankester 918 (Holotype: AMES 28692).

*Dichaea ovatipetala* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 266. [November] 1923. TYPE: COSTA RICA. [Alajuela:] Bois humides à San Pedro de San Ramón, 1150 m, Nov. 1921, A. M. Brenes 196 (Holotype: B, destroyed; Lectotype, designated by Barringer, 1984: AMES 31570).

*Plant* epiphytic, caespitose, to 80 cm long. *Roots* exposed basally, hidden by leaf sheaths along the stem, flexuous, glabrous, ca. 0.4 mm in diam. *Stems* flattened, pendent, occasionally growing upside appressed to the bark, rarely branching, 15–80 cm long, 0.4–0.7 cm wide across conduplicate sheaths. *Leaves* closely spaced along stem, mostly overlapping, spreading, green, thick-herbaceous, 10–15 × 4–8 mm, elliptic to elliptic-ovate, widely obtuse to rounded, minutely apiculate, the apical margins microscopically fimbriate; sheaths tightly

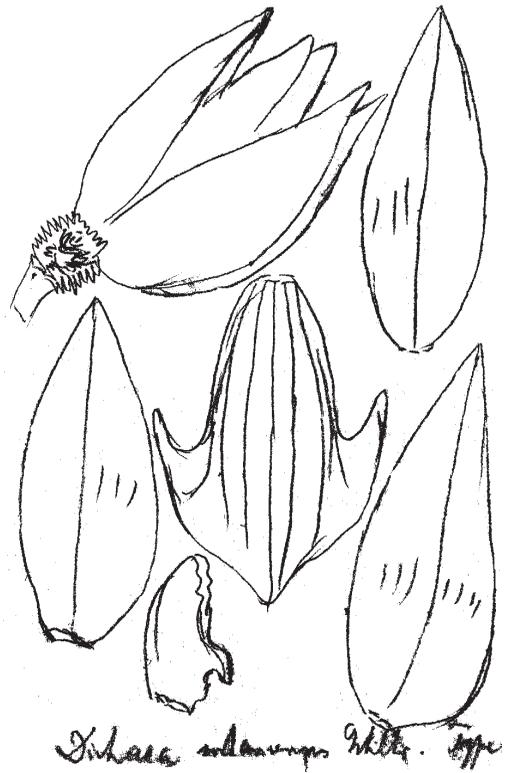


FIGURE 35. Copy of Schlechter's sketch of *Dichaea costaricensis* Schltr. (AMES). Reproduced with the kind permission of the Director, Harvard University Herbaria.

clasping the stem, to 10 × 6 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent, the peduncle geniculate, 0.8–1.4 cm long, provided at the base with tubular, papyraceous bracts, 0.3 cm long. *Floral bract* double, the outer bract infundibuliform, ovate, acute, 3.0 × 3.2 mm, the inner bract narrowly lanceolate, acute, 2.5 mm long. *Pedicel* cylindrical, to 3 mm long. *Ovary* long mucronate, 2 mm long. *Flower* spreading, with sepals and petals greenish white, finely spotted with violet, the sepals externally tuberculate, the lip white, spotted with violet at the base, the apex evenly violet, the column white, marked with purple on the wings and finely spotted with violet along the sides. *Dorsal sepal* elliptic-lanceolate, acute, 8.5–11.0 × 3.8–4.0 mm. *Lateral sepals* obliquely elliptic-lanceolate, acute to shortly acuminate, 8.3–10.0 × 3.5–3.7 mm. *Petals* subfalcate, elliptic-lanceolate, somewhat asymmetrical, shortly acuminate, 8.0–9.5 × 3.6–3.8

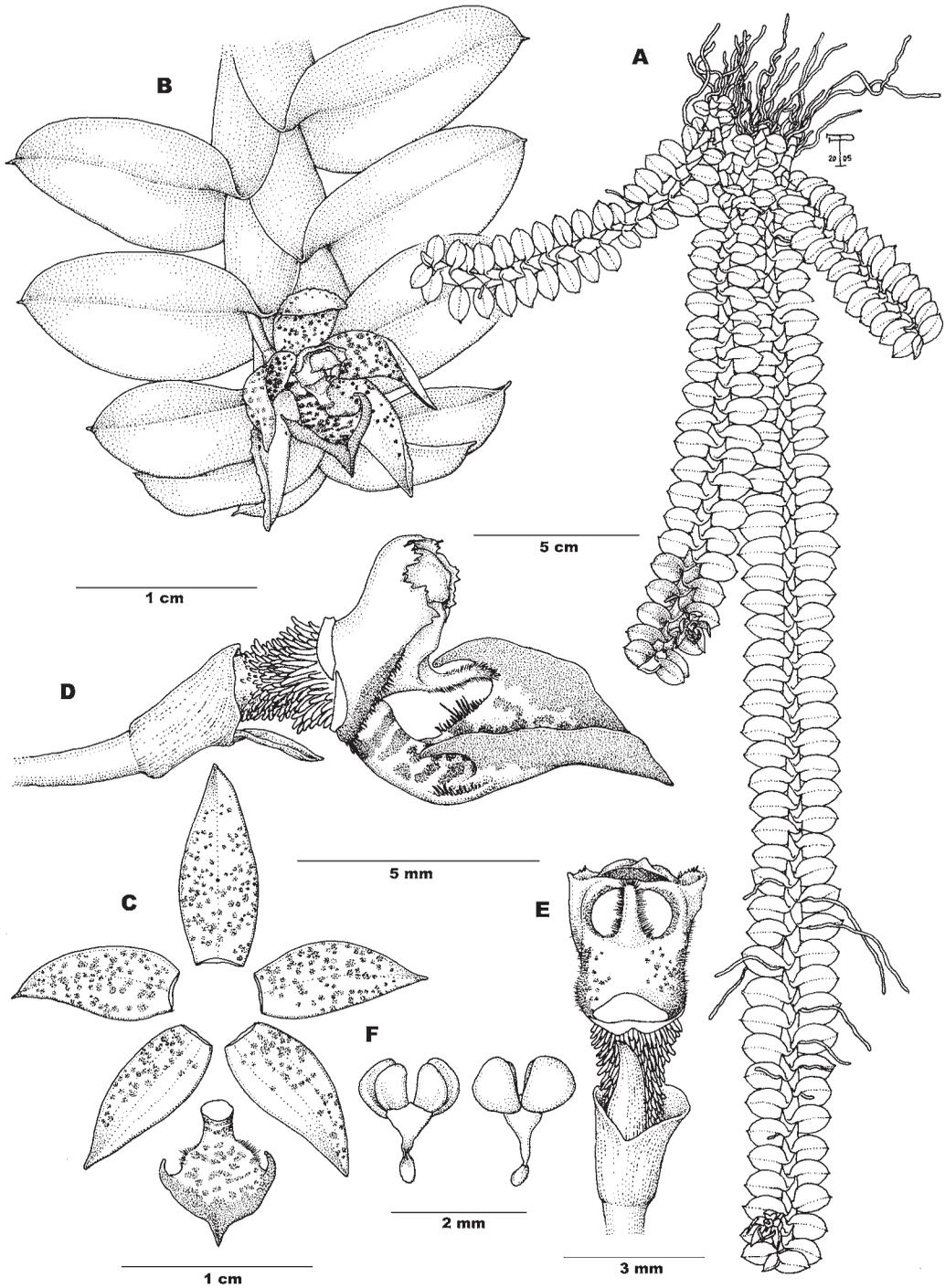


FIGURE 36. *Dichaea cryptarrhena* Rchb.f. ex Kraenzl. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium, ventral and dorsal views. Drawn from *Pupulin et al.* 3595 (JBL-Spirit).

mm. *Lip* 3-lobed, clawed,  $7 \times 6$  mm when spread, the claw linear, basally thickened-subterete, the hypochile subquadrate, producing distinct, ciliate shoulders, 4 mm wide apically, the epichile widely ovate-elliptic, acuminate, the lateral lobes narrowly triangular-acuminate, retrorse,  $1.3 \times 0.6$  mm. *Column* suberect, 3.5 mm long, provided with narrowly elliptic, ciliate wings, the clinandrium subpetaloid, irregularly erose; ligule narrowly triangular, acute, tomentose,  $2 \times 1$  mm. *Anther cap* transversely subrectangular, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a obtriangular, obtuse stipe; viscidium elliptic. *Fruit* an elliptic capsule, muricate.

**Distribution:** from Guatemala to Panama and Venezuela.

**Additional material examined:** COSTA RICA. Alajuela: Bajos del Toro, northern slopes of Volcán Poás, 1430 m, 30.8.2001, *F. Pupulin* 3304, *D. Castelfranco*, *M. Pupulin* & *C. Pupulin* (JBL-Spirit); Bajos del Toro, northern slopes of Volcán Poas, 1450 m, 5.3.2001, *F. Pupulin* 3037 (JBL-Spirit); Naranjo, Cirrí, LLano Bonito, Zona Protectora El Chayote, Fila La Picada, Cerro Chayote,  $10^{\circ}11'N$ ,  $84^{\circ}21'W$ , 1950 m, 6.4.2002, flowered in cultivation at Jardín Botánico Lankester, 24.6.2002, *F. Pupulin* 3595, *V. Blanco*, *H. Montealegre* & *A. C. Rodríguez* (JBL-Spirit); [San Ramón,] Colinas de Santiago près de San Ramón, 2 juin 1901, *A. M. Brenes* 14285 (AMES); [San Ramón,] Colinas de Piedades cerca de San Ramón, 1025 m, 2.VII.1924, *A. M. Brenes* (15) 873 Herb. Brenes (CR 30813, sterile); Colinas de Piedades cerca de San Ramón, 5.XI.1926, *A. M. Brenes* (60) 1541 (CR 30820, AMES); Piedades de San Ramón, 21 Jun. 1925, *A. M. Brenes* (77)1284 (AMES); Piedades Norte, La Paz, desviación a la izquierda, hacia el Cerro Azahar, km 2.6, orillas del Río San Pedro,  $10^{\circ}08'59.4''N$ ,  $84^{\circ}34'00.8''W$ , 1312 m, bosque pluvial premontano, en cercas y árboles en potreros y bosque secundario, 30.1.2005, floreció en cultivo en el Jardín Botánico Lankester, 16 Aug. 2006, *D. Bogarín* 1298, *F. Pupulin*, *M. Salas* & *P. Seaton* (CR); Piedades Norte,  $10^{\circ}08'42.3''N$ ,  $84^{\circ}32'02.3''W$ , 1180 m, crest of Continental Divide, premontane moist forest, 24 March 2005; flowered in cultivation at Jardín Botánico Lankester, 16 Aug. 2006, *F. Pupulin* 5616, *E. Salas-Pupulin*, *D. Bogarín* & *A.C. Rodríguez* (CR); San Pedro de San Ramón, 19 Jul. 1925, *A. M. Brenes* (144)1346

(AMES); 20 Oct. 1927, *A. M. Brenes* (71)1645 (AMES); San Ramón, La Palma, 30.X.1922, *A. M. Brenes* (47)377 (AMES); 11 Aug. 1925, *A. M. Brenes* (191)1386 (AMES); 5 Aug. 1935, *A. M. Brenes* 20639 (AMES); 2 Aug. 1925, *A. M. Brenes* (192)1387 (AMES); 30 Oct. 1922, *A. M. Brenes* (56)386 (AMES); San Ramón, La Palma, 3–10 Aug. 1935, *M. Quirós* (260)240 (AMES); [San Ramón,] between Ángeles Norte and ca. 7 km N of Balsa de San Ramón, 550–1150 m, 8 Aug. 1975, *J. Utley* & *K. Utley* 2807 (CR); Reserva Alberto Brenes, 910 m, 11 Sept. 1984, *J. B. Folsom* 10993 (CR, sterile); Santiago, road to Balboa, ca. km 4,  $10^{\circ}02'32''N$ ,  $84^{\circ}29'31''W$ , 1250 m, epiphytic on scattered trees along the road, 13 April 2006, flowered in cultivation at Jardín Botánico Lankester, 4 Aug. 2006, *F. Pupulin* 6063, *R. L. Dressler* & *E. Salas-Pupulin* (CR). Cartago: Estrella, Apr. 1887, *J. C. Cooper* 5969 (AMES); *J. C. Cooper s.n.* (AMES); Turrialba, Tayutic, Vereh, siguiendo la Fila entre Río Vereh y Río Jicotea,  $09^{\circ}46'30''N$ ,  $83^{\circ}32'40''W$ , 1500 m, 26 Jul. 1995, *G. Herrera* 8141 & *A. Cascante* (CR, sterile); Turrialba, Tayutic, Vereh, Grano de Oro,  $09^{\circ}48'50''N$ ,  $83^{\circ}22'40''W$ , 1200 m, 286 Jul. 1995, *G. Herrera* 8159 & *A. Cascante* (CR); Tayutic, Moravia, 5 km Oeste[?] del centro de Moravia, 1100–1200 m, 22.1.2005, *A. Karremans* 626, *D. Karremans* & *R. Ferreira* (JBL-Spirit); same locality, *A. Karremans*, 627, *D. Karremans* & *R. Ferreira* (JBL-Spirit). Guanacaste: forest remnants 5 km north of Sta. Elena on road to Las Nubes, 5 July 1989, *J. T. Atwood* 89–273 (SEL); on road to Las Nubes in remnant cloud forest near continental divide, 8 July 1989, *J. T. Atwood* 89–286 (SEL). Limón: Limón, Almirante, cuenca superior del Río Hicahry,  $9^{\circ}45'50''N$ ,  $83^{\circ}20'00''W$ , 1200 m, 11 Ag. 1995, *G. Herrera* 8403 (CR); N flank of Fila de Matama in headwaters of Río Boyei,  $09^{\circ}45'00''N$ ,  $83^{\circ}19'00''W$ , 1200–1300 m, 17 Aug. 1995, *M. Grayum* 11032 (INB). Puntarenas: 2 km east of Santa Elena de Monteverde on continental divide,  $10^{\circ}21'N$ ,  $84^{\circ}48'W$ , 6 Aug. 1988, *J. T. Atwood* 88–43 & *W. Haber* (SEL); *J. T. Atwood* 88–69 & *W. Haber* (SEL); Cordillera de Talamanca, area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier,  $9^{\circ}02'N$ ,  $82^{\circ}59'W$ , 6 Sept. 1984, *G. Davidse* 28407, *G. Herrera* & *M. H. Grayum* (SEL); Foothills of the Cordillera de

Talamanca, between Agua Caliente and the Río Canasta, 8°57'–9°02" N, 82°56'–82°59' W, 5 Sept. 1984, *G. Davidse 28354*, *G. Herrera & M. H. Grayum* (CR, SEL); Monteverde Cloud Forest Reserve, Dec. 1987, specimen made 12 Feb. 1988, *N. Nadkarni s.n.* (SEL); Monteverde, in Research Forest, epiphytic on *Ocotea tonduzii*, 10°20' N, 84°50' W, 23 Sept. 1988, *S. Ingram 304* (SEL); Monteverde Reserve; 2 km SW Station, 10°18' N, 84°48' W, 13 July 1992, *S. Ingram 1499*, *K. Ferrell Ingram & N. Edmondson* (SEL); Monteverde Reserve; 2 km SW Station, 10°18' N, 84°48' W, 6 Nov. 1992, *S. Ingram 1675 & K. Ferrell-Ingram* (SEL); [Coto Brus], Las Cruces, Jardín Botánico Wilson, OET, sendero este a Río Java 08°47'30" N, 82°58'00" W, 1100 m, 4 Set. 1993, *G. Vargas 1308*, *G. Herrera, G. Rivera & L. D. Gómez* (CR); same locality and date, *G. Vargas 1347*, *G. Herrera, G. Rivera & L. D. Gómez* (CR); P.I. la Amistad, Est. Pittier, Sendero Río Gemelo, 09°01'30" N, 82°57'40" W, 1680 m, 13 June 1995, *A. Picado 219 & E. Fletes* (INB); Coto Brus, Las Alturas de Cotón, Fila Cedro, unpaved road to Fila Cedro, 08°58'20" N, 82°52'40" W, 1670–1240 m, 20.3.2003, flowered in cultivation at Jardín Botánico Lankester, 8 Aug. 2003, *F. Pupulin 4436*, *H. León-Páez & A. C. Rodríguez* (JBL-Spirit). San José: [Desamparados,] Tablazo, 30 Oct. 1947, *J. A. Echeverría s.n.*, 1230 in Herb. Hecheverría (CR 30756, sterile); La Palma, February 3, 1924, *P. C. Standley 32977* (AMES); *P. C. Standley 32990* (AMES); March 17, 1924, *P. C. Standley 38264* (AMES); La Palma, 1400–1500 m, 12 Aug. 1979, *C. Todzia 679* (CR); La Palma, pressed Jul. 24, 1959, *C. K. Horich s.n.* (AMES); Alto de La Palma, along old road above Bajo La Honduras, 15 June 1983, *K. Barringer 3162* (CR, sterile); Km 119.2 south of Cartago on Rt. 2, 7 March 1988, *J. T. Atwood 86–46* (SEL); Braulio Carrillo Park, near La Montura, 1100–1200 m, 17 Sept. 1984, *J. P. Folsom 11005B* (CR, sterile); Dota, Santa María, unpaved road to San Joaquín, about km 6, 1825 m, 23 March 2004, flowered in cultivation at Jardín Botánico Lankester, 4 July 2004, *F. Pupulin 5210 & H. León-Páez* (JBL-Spirit); same locality, *F. Pupulin 5211 & H. León-Páez* (JBL-Spirit); Dota, Santa María, Cerro Tijerilla, 9°28'50" N, 83°57'40" W, 950 m, 21 Oct. 1998, *A. Estrada 1822 & J. Solano* (CR); Escazú, Bebedero, Cerros de Escazú, camino

hacia el Cerro Pico Blanco, 09°52'34" N, 84°08'05" W, 2271 m, 5.7.2003, *D. Bogarín 243 & A. Granados* (JBL-Spirit); Pérez Zeledón, Páramo, R. F. Los Santos, camino entre la Lira y San Gerardo de Dota, 9°30'14" N, 83°49'10" W, 1617 m, 8 Mar. 2001, *A. Quesada 552, R. Chacón, A. Estrada & Otros* (CR); Pérez Zeledón, Savegre, Peor es nada, margen izquierda de Quebrada Misteriosa, 09°31'10" N, 83°51'30" W, 1700 m, 4 Ago. 1994, *G. Herrera 7274, J. Sánchez & F. Durán* (CR). Without locality, flowered in cultivation at Jardín Botánico Lankester, 14 June 2006, accession No. *JBL-04905* (CR).

**Etymology:** from the Greek *crypto-*, hidden, and *harren*, male reproductive organ, stamen, likely in allusion to the prominent, hooded clinandrium that covers the anther.

**Ecology:** a common and widespread epiphyte, in Costa Rica it is found in premontane wet to montane cloud forest on the Caribbean drainage of the Cordilleras of Tilarán and Central Volcanic, and on the watersheds of both the Guanacaste and Talamanca chains, at 750–2000 m elevation. Flowering mostly occurs from April to June.

The simple stems, branching at the apex only after destruction of the stem, and the widely elliptic, usually overlapping, rounded, grass-green leaves, are useful diagnostic characters to distinguish *Dichaea cryptarrhena* even in sterile specimens. It can be distinguished from the closely related *D. poicillantha* Schltr. by the white to greenish-white flowers (vs. grayed orange), and from *D. similis* Schltr. by the much larger leaves and the density of violet markings on sepals and petals (reduced or absent in *D. similis*). Although many names have been applied to this species, it is rather uniform and unmistakable in both vegetative architecture and flower morphology.

6. *Dichaea dammeriana* Kraenzl., Pflanzn. 4(50): 41. 1923. TYPE: Syntypes: Colombia. Sierra Nevada de Santa Marta, *H. Smith 2773* (AMES, US [not seen], NY [not seen], photograph); Costa Rica. Without specific locality, 1868, *A. R. Endres 66* (Lectotype, designated here: AMES 26090; Isolectotypes: *W-Reichenbach Orchid Herbarium Nr.* 18036, 18747 [both sterile]; drawing of the syntype by Endres, *W-Reichenbach Orchid Herbarium Nr.* 18036, 30738; AMES 24898 [copy]). Fig. 37, Map 2.

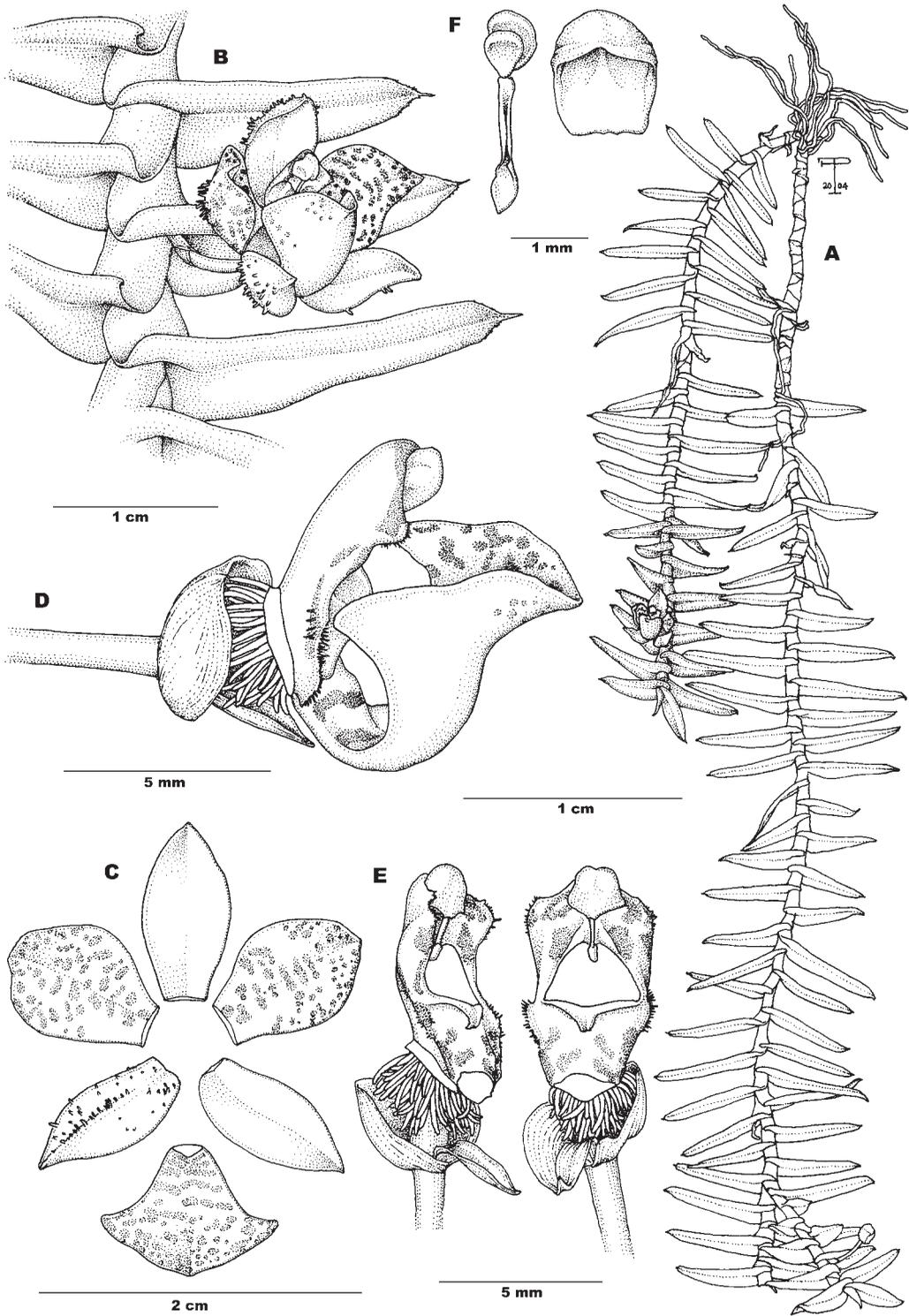


FIGURE 37. *Dichaea dammeriana* Kraenzl. A, Habit; B, flower; C, dissected perianth, the right lateral sepal in abaxial view; D, column and lip, lateral view; E, column, three quarters and ventral views; F, pollinarium and anther cap. Drawn from *Pupulin et al.* 3732 (JBL-Spirit).

*Plant* epiphytic, caespitose, to 40 cm long. *Roots* exposed basally, hidden by leaf sheaths along the stem, flexuous, glabrous, ca. 0.4 mm in diam. *Stems* slightly flattened, pendent, usually branching only after destruction of the stem apex, 12–40 cm long, 0.3–0.4 cm wide across conduplicate sheaths. *Leaves* widely spaced along stem, spreading, perpendicular to the stem, olive-green to medium brown, thick-herbaceous, 20–27 × 3–6 mm, lanceolate, becoming ligulate through the reflexion of lateral margins, acute, narrowly mucronate, the lateral margins recurved, the apical margins hispid-ciliate; sheaths loosely clasping the stem, to 8 × 7 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent to suberect, 0.8–1.2 cm long, the peduncle geniculate, provided at the base with two tubular, acute, papyraceous bracts, 0.2 cm long. *Floral bract* double, the outer bract suborbicular, obtuse, 4.0 × 3.7 mm, the inner bract narrowly lanceolate, acute, 3.5 × 0.8 mm. *Pedice*l cylindrical, ca. 1 mm long. *Ovary* long muriculate, 1 mm long. *Flower* ringent to spreading, with sepals and petals externally echinate-tuberculate, greenish yellow, immaculate, the petals paler and spotted with violet, the lip greenish white to white, spotted with violet-purple, the column white, blotched with purple along the wings, the foot and the apex of stigma. *Dorsal sepal* elliptic-oblancheolate, acute, 9.5–10.5 × 4.5–5.2 mm. *Lateral sepals* obliquely elliptic-oblancheolate, slightly asymmetrical, acute to shortly acuminate, 9–10 × 4.0–4.5 mm. *Petals* obovate, obtuse to subrounded, 8.0–9.5 × 6.5–7.0 mm. *Lip* 3-lobed, clawed, 6.5–7.5 × 8–11 mm when spread, the claw widely obcuneate, to 7 mm wide at apex, basally thickened-subtriangular, the epichile widely triangular, obtuse, the lateral lobes triangular, subacute, 2 × 2 mm. *Column* erect, dorsoventrally compressed, 5.5 mm long, provided with small, narrowly elliptic, ciliate wings, the clinandrium entire to minutely erose; ligule triangular, obscurely retuse, reflexed, glabrous, 1.0 × 2.5 mm. *Anther cap* ovate, cucullate, 2-celled. *Pollinia* 2 or 4 in superposed pairs of different size, on a narrow, sublinear-clavate, truncate stipe; viscidium narrowly ovate. *Fruit* an elliptic capsule, long echinate-muriculate.

**Distribution:** from Nicaragua to Venezuela and Ecuador.

**Additional material examined:** COSTA RICA. Alajuela: [San Ramón], La Palma de San

Ramón, 10.XI.1927, *A. M. Brenes* (90) 1650 Herb. Brenes (CR 18430, fruiting). San Pedro de San Ramón, 7.VII.1921, *A. M. Brenes* 80 (AMES); 1075–1250 m, VII.1921, *A. M. Brenes* 80(1763) (CR); 1125 m, 18.VII.1924, *A. M. Brenes* 909 (CR); 1150 m, 30.X.1922, *A. M. Brenes* 91(2901) (CR); San Ramón, Los Ángeles, road to La Fortuna, 10°09'43"N, 84°29'24"W, 1130 m, 27 February 2003, *F. Pupulin* 4360, *D. Bogarín*, *H. León-Páez* & *A. C. Rodríguez* (JBL-Spirit); Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06"N, 84°36'11"W, 800–900 m, orillas del Río San Lorencito, cerca del Sendero Terciopelo, 22 Mayo 2004, *D. Bogarín* 815 (CR, JBL-Spirit); Reserva Biológica Alberto M. Brenes, 10°13'08.5"N, 84°35'48.4"W, 965 m, orillas del Río San Lorencito, cerca de la Estación, 3 Setiembre 2004, *D. Bogarín* 969, *M. G. Gei* & *J. D. Zúñiga* (JBL-Spirit); Reserva Biológica Alberto M. Brenes, 10°13'37.2"N, 84°34'35.8"W, 732 m, camino al puente del Río San Lorenzo, 5 Setiembre 2004, *D. Bogarín* 1002 & *D. Salazar* (CR, JBL-Spirit); La Balsa, road from San Ramón to La Fortuna, proximity of Río La Balsa, 10°11'52.2"N, 84°30'54.4"W, 990 m, premontane wet forest, 26 December 2004 *F. Pupulin* 5442, *E. Salas-Pupulin*, *S. Dalström* & *C. Lewis* (JBL-Spirit); Piedades, Piedades Norte, road to Bajo de La Paz, km 2.6, along the Río San Pedro, 10°08'59.9"N, 84°33'53.3"W, 1307 m, premontane wet forest, epiphytic along the shores of the river, 30 January 2005, *F. Pupulin* 5508, *D. Bogarín*, *M. Salas* & *P. Seaton* (CR, USJ, fruiting, JBL-Spirit); unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'51.9"N, 84°35'36.5"W, 1410 m, Caribbean watershed of the Continental Divide, premontane cloud forest, 24 March 2005, *F. Pupulin* 5587, *E. Salas-Pupulin*, *D. Bogarín* & *A. C. Rodríguez* (JBL-Spirit); Santiago, mountains towards San Rafael, ca. 10°01'N, 84°30'W, 1300 m, 1 Feb. 2004, *F. Pupulin* 5097 & *E. Salas* (JBL-Spirit); Santiago, road to Balboa, calle Quirós, Alto Chavarría, Finca Salas, along a small creek, 10°02'55.7"N, 84°29'41.8"W, 1180 m, epiphytic on remnant trees, secondary vegetation, 14 April 2006, flowered in cultivation at Jardín Botánico Lankester, 12 June 2006, *F. Pupulin* 6075, *R. L. Dressler* & *E. Salas* (CR); Upala, Bijagua, NE slopes of Miravalles volcano, shores of Río Zapote, 10°44'37.4"N,

85°05'14.9" W, 700 m, premontane wet forest, 30 April 2006, flowered in cultivation at Jardín Botánico Lankester, 14 July 2006, *F. Pupulin* 6088, *D. Bogarín*, *A. Rambelli* & *G. Rambelli* (CR). Cartago: El Muñeco, south of Navarro, February 8–9, 1924, *P.C. Standley* & *J. Valerio* 33725 (AMES); Paraíso, Orosi, Purisil, Parque Purisil, 1400–1500 m, orilla de los senderos, 10 Mayo 2003, *D. Bogarín* 197 & *H. León-Páez* (JBL-Spirit); Turrialba, Moravia de Chirripó, Tsipirí, 9°48'N, 83°23'W, 1050 m, along a small creek and in disturbed primary forest, 3 May 2002, flowered in cultivation at Jardín Botánico Lankester, 14 May 2002, *F. Pupulin* 3732, *J. Warner* & *R. Gómez* (JBL-Spirit). Guanacaste: El Arenal, Jan. 18–19, 1926, *P. C. Standley* & *J. Valerio* 45315 (AMES). Border between Guanacaste and Alajuela: Upala, road from San Joge de Liberia to Colonia Blanca, SE slopes of Rincón de la Vieja volcano, 10°46'05.1"N, 85°16'45.3"W, 820 m, premontane dry, transition to premontane rain forest, 1 May 2006, *F. Pupulin* 6126, *D. Bogarín*, *A. Rambelli* & *G. Rambelli* (CR). Puntarenas: Coto Brus, San Vito de Java, Las Cruces, Wilson Botanical Garden, trail to Río Java, ca. 300 m after Quebrada Wilson, 8°47'08"N, 82°57'35"W, 1030 m, 14 November 2002, *F. Pupulin* 4253, *E. Salas*, *H. León-Páez* & *A. C. Rodríguez* (JBL-Spirit). San José: Dota, crest of Cerro Nara, 910–1000 m, submontane rain forest, 20 Feb. 2000, *F. Pupulin* 2100, *D. Castelfranco*, *M. L. Spadari* & *K. McFarland* (JBL-Spirit); Pérez Zeledón, Las Nubes de Quizarrá, 1250 m, collected by *R. L. Dressler* & *D. E. Mora*, 22 March 1995, flowered in cultivation at Jardín Botánico Lankester, 13 May 1998, *F. Pupulin* 702 (JBL-Spirit); Pérez Zeledón, San Ramón, unpaved road to Las Pegas, Páramo, Los Ángeles, 9°29'01"N, 83°45'16"W, 1480 m, 20.4.2003, *F. Pupulin* 4647, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (JBL-Spirit); Carrillo, Jahre 1922, *C. Wercklé* 124 (B, destroyed). Without definite locality, 1868, *A. R. Endres* 66 (W-R 18036, 14747, 10517, 14778, 14751).

**Eponymy:** named after Dr. Udo Dammer, who first noted this species in specimens distributed under the name of *D. graminoides*.

**Ecology:** a widespread but uncommon epiphyte, in Costa Rica it is mostly restricted to shaded spots in pristine vegetation in premontane wet to submontane cloud forest on the

Caribbean drainage of the Tilarán and Central Volcanic chains, and on both watersheds of the Cordillera of Talamanca, at 700–1400 m elevation. Flowering occurs year round.

*Dichaea dammeriana* is unmistakable in both vegetative and floral characters. The truly pendulous, rarely branching plants have well-spaced, long, and narrow leaves, perpendicular to the axis of the stem and characteristically olive-green to medium brown, a color shared in Costa Rica only with *D. filiarum* Pupulin. Folsom (1987) noted that the upper surface of the leaves of *D. dammeriana* bears numerous silver-white raised flecks, which correspond to sub-epidermal idioblasts containing oversized raphid bundles, which become protrusive in dried specimens. Dried leaves also become lepidote, and this induced Kränzlin to describe them as glaucous, which is not true in living plants. The flowers of *D. dammeriana* are distinctive in having long and numerous acicles on the abaxial surface of both the sepals and petals, particularly along the midrib, and for the up-curved, concave lip, which is held against the erect column. Although the pollinia of *D. dammeriana* have been reported as fused into two heart-shaped masses (Folsom, 1987), this condition is not consistent in Costa Rican material, which presents both 4 normal, obovate pollinia, and 2 fused pollinia.

Folsom (1987) proposed to lectotypify *D. dammeriana* with the folder No. 18036 in Reichenbach Herbarium at Vienna, including two specimens, as well as drawings by Endrés and Reichenbach. Both the specimens, however, are sterile. The best choice for typification is *Endrés* 66 at AMES (No. 26090) which is fertile and in excellent condition (Fig. 38), and it is designated here as the lectotype.

**7. *Dichaea eligulata*** Folsom, *Orch. Digest* 58: 185–186. 1994. TYPE: COSTA RICA. Locality of original collection unknown—growing on trees at Las Cruces [Wilson] Botanical Garden, probably collected in Costa Rica or adjacent Panama, 8 Jul 1981, *J. P. Folsom* 10261 (Holotype: CR; Isotype: TEX [not seen]). Fig. 39, Map 3.

*Plant* epiphytic, caespitose, to 20 cm long. *Roots* exposed basally, mostly hidden by leaf sheaths along the stem, flexuous, glabrous, ca. 0.4 mm in diam. *Stems* flattened, scandent to pendent, rarely branching, 8–20 cm long, 0.2–0.3 cm wide across conduplicate sheaths.



FIGURE 38. Lectotype of *Dichaea dammeriana* Kraenzl., *Endrés 66* (AMES). Reproduced with the kind permission of the Director, Harvard University Herbaria.

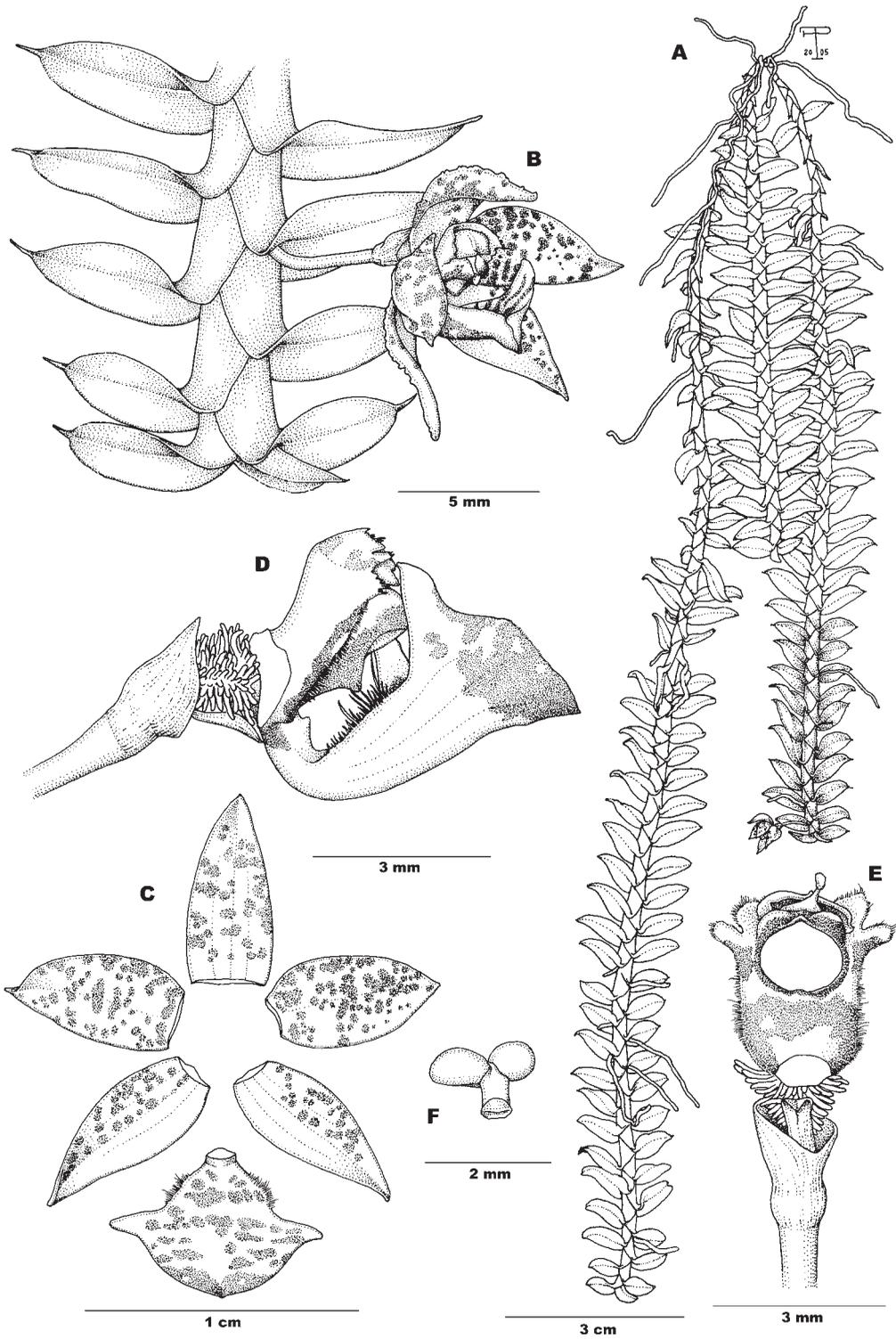


FIGURE 39. *Dichaea eligulata* Folsom. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, pollinarium. Drawn from: **A**, Pupulin et al. 2718 (JBL-Spirit!); **B-F**, Pupulin et al. 1094 (JBL-Spirit).

*Leaves* closely spaced along stem, not overlapping, reflexed, green, thick-herbaceous, 6–8 × 3–4 mm, lanceolate-elliptic, obtuse to subacute, long-apiculate, the apical margins minutely crenulate; sheaths clasping the stem, to 7 × 4 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent, the peduncle geniculate, 1.2–1.5 cm long, provided at the base with 2–3 tubular, acuminate bracts, ca. 0.4 cm long. *Floral bract* double, the outer bract widely ovate, shortly acuminate, 2.3 × 2 mm, the inner bract narrowly elliptic-lanceolate, acute, 2.2 mm long. *Pedicel* cylindrical, to 1.5 mm long. *Ovary* muricate, 1.5 mm long. *Flower* spreading, with sepals and petals greenish-white, spotted and blotched with violet, the spots restricted to the external half of lateral sepals, the sepals externally sparsely tuberculate, the lip white, spotted with violet, the apex violet, the column greenish white, ventrally marked with purple at the base, on the margins and along the rim of the stigma. *Dorsal sepal* elliptic-lanceolate, acute, 7–9 × 3.0–3.5 mm. *Lateral sepals* obliquely elliptic-lanceolate, acute to shortly acuminate, 7–8 × 3.0–3.5 mm. *Petals* elliptic to elliptic-lanceolate, obtuse to subacute, shortly acuminate, 6.0–7.5 × 3.0–3.5 mm. *Lip* 3-lobed, shortly clawed, cupped, up curving, 5 × 8 mm when spread, the claw basally thickened-subterete, the hypochile obcuneate-elliptic with indistinct, ciliate shoulders, 4 mm wide apically, the epichile widely ovate-elliptic, obtuse, the lateral lobes triangular, acute, spreading, 2 × 1 mm. *Column* erect, 3.5 mm long, provided with narrow, not protruding, straight, ciliate, ridge-like wings, the clinandrium strongly erose-lacerate; ligule almost absent, reduced to a rounded, glabrous extension of the basal stigma rim. *Anther cap* transversely subrectangular-obovate, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a ligulate, short, acute stipe; viscidium elliptic. *Fruit* not seen.

**Distribution:** Costa Rica and possibly western Panama.

**Additional material examined:** COSTA RICA. Puntarenas: Fila Costeña, Zapote de Pejivalle 9°48'N, 83°23'W, 1150 m, 3.05.2003, *F. Pupulin* 2647, *J. Warner* & *R. Gómez* (JBL-Spirit); Fila Costeña, Zapote de Pejivalle, 740–810 m, 10.12.2000, *F. Pupulin* 2637, *D. Castelfranco* & *E. Elizondo* (JBL-Spirit); same locality, *F. Pupulin* 2718, *D. Castelfranco* & *E.*

*Elizondo* (JBL-Spirit). San José: Acosta, Bijagual, 7 Oct. 1984, *R. L. Dressler* 62 & *Biología* 350 (USJ); Dota, eastern slopes of Cerro Nara, in premontane rain forest, disturbed primary forest, 9°29'01"N, 84°00'25"W, 740–840 m, 14 Jan. 1999, flowered in cultivation at Gaia Botanical Garden, 18 Oct. 2002, *F. Pupulin* 1094, *D. Castelfranco* & *M. L. Spadari* (JBL-Spirit); same locality, *F. Pupulin* 1089, *D. Castelfranco* & *M. L. Spadari* (JBL-Spirit); Pérez Zeledón, Fila Tinamastes, Finca Tinamastes, 650 m, 31.1.2000, floreció en cultivo en el Jardín Botánico Lankester, 8 Nov. 2002, *M. A. Blanco* 1374 (USJ). Pérez Zeledón, San Isidro de El General, carretera a Dominical, Fila Tinamastes, La Alfombra, 9°19'19.0"N, 83°45'58.1"W, 1000 m, bosque húmedo premontano, bosque secundario alterado y árboles a orillas de la carretera, 23 Oct. 2005, floreció en cultivo en el Jardín Botánico Lankester, 14 Aug. 2006, *D. Bogarín* 2015, *J. Cambroner*, *R. L. Dressler*, *R. Gómez*, *A. Karremans*, *F. Pupulin*, *A. Rambelli* & *S. Rambelli* (JBL-Spirit); Tarrazú, San Carlos, Bajos de la Virgen, confluencia Río Negro y Blanco, albergue Ríos Paraíso, 9°33'54"N, 84°07'28"W, 400 m, 29 Jul. 2003, *A. Quesada* 1147, *A. Estrada*, *A. Rodríguez* & *Otros* (CR); same locality, 30 Jul. 2003, *A. Quesada* 1180, *A. Estrada*, *A. Rodríguez* & *Otros* (CR); Tarrazú, San Marcos, R. B. Ríos Paraíso, 9°33'49"N, 84°07'26"W, 400 m, 17 May. 2004, *A. Ruiz* 805 & *A. Rojas* (CR). Without locality, flowered in cultivation at Jardín Botánico Lankester, *A. Quesada* s.n. (JBL-Spirit).

**Etymology:** from the Latin prefix *e-*, lacking, destitute, and the adjective *ligulata-*, ligulate, in allusion to the lack of a distinct infrastigmatic ligule on the column, characteristic of this species.

**Ecology:** an apparently rare epiphyte, in Costa Rica *D. eligulata* is known only from the premontane wet forests of the southeastern mountain chains facing the Pacific, at 400–800 m elevation. Flowering occurs from July to October.

*Dichaea eligulata* was described from a single, cultivated specimen, apparently collected in the neighborhood of Wilson Botanical Garden, not far from the border with Panama. The type locality of the species was tentatively assigned to Costa Rica (Folsom, 1994), but the adjacent region of western Panama was hypo-

thetically included in its distribution range. The specimens cited here confirm the presence of *D. eligulata* in Costa Rica and represent the first material of this species associated with field data. Among species of sect. *Dichaea*, *D. eligulata* may be easily recognized for the deeply erose-lacerate clinandrium and the infrastigmatic ligule reduced to the basal, rounded, glabrous portion of the protruding rim of the stigma. The lip of *D. eligulata* is characteristically concave and up-curved, a feature found in Costa Rica only in *D. dammeriana*, a distantly related species.

8. *Dichaea elliptica* Dressler & Folsom, *Lankesteriana* 3: 25. 2002. TYPE: PANAMA. Coclé: Aserradero El Copé, ca. 8 km N of El Copé, 800–900 m, 10 April 1977, R. L. Dressler 5641 (Holotype: MO; Isotype: PMA [not seen]). Fig. 40, Map 3.

*Plant* epiphytic, cespitose, to 22 cm long. *Roots* filiform, sometimes puberulent, exposed at the base, the caulinar roots hidden by the leaf sheaths, 0.5–0.8 mm in diam. *Stems* compressed, suberect, becoming spreading-pendent with age, 9–22 cm long, 0.2–0.3 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, widely spaced along stem, subspreading, thinly coriaceous, medium green, 13–28 × 3–7 mm, elliptic to lanceolate elliptic, acute to acuminate, the apical margins minutely pectinate-ciliate; sheaths clasping, 10–15 × 4–5 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent to pendent, to 14 mm long, provided with a basal, cylindrical, apically slightly dilated bract, 3.5 mm long. *Floral bract* double, the outer bract broadly ovate, acuminate, 4.0 × 3.5 mm, the inner bract linear, acute, 3 mm long. *Pedicel* cylindrical, ca. 2 mm long. *Ovary* 1.0–1.3 mm long, densely muricate, the trichomes long, flexuous. *Flower* spreading, the sepals and petals white to cream, finely speckled with purple-red, on the lateral sepals the spots mostly restricted to the external half, the lip white, sparsely flecked with purple-red, the column white, marked with violet-purple along the stigmatic margins and on ligule; no fragrance detected. *Dorsal sepal* erect, slightly concave, elliptic to lanceolate-elliptic, subacuminate, 6–8 × 2.3–2.8 mm. *Lateral sepals* obliquely ovate-elliptic, concave, subacuminate, dorsally subcarinate, 6–8 × 2.5–3.5 mm. *Petals* elliptic-

lanceolate to (rarely) elliptic-obovate, acute, 5.0–6.5 × 2.1–2.5 mm. *Lip* 3-lobed, anchoriform, sessile, 4.0–5.5 × 6.5–7.0 mm when spread, the hypochile broadly obtuse, 2.0–2.6 mm long, 1.7–2.0 mm wide apically, the epichyle transversely subtriangular-lunate, broadly obtuse to truncate, shortly apiculate, 2.0–2.3 × 6.5–7.0 mm, the distal margins sometimes microciliate, the lateral lobes narrowly triangular, subacuminate, spreading to reflexed, 0.6–0.8 × 0.4–0.5 mm. *Column* erect, 2.5–3.0 mm long, with a short foot; the clinandrium shallow, entire; ligule triangular, acute-rounded, papillose at apex, 0.77 × 0.90 mm. *Anther cap* subrhynchiform-cucullate, flattened, 2-celled. *Pollinia* 4 in two superposed pairs subequal in size, on a broadly obtriangular, rounded stipe; viscidium elliptic-peltate. *Fruit* an elliptic, densely muricate capsule.

**Distribution:** Nicaragua, Costa Rica, Panama, and Ecuador.

**Additional material examined:** COSTA RICA. Alajuela: Grecia, Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 380–400 m, epiphytic along the shores of Río Sarapiquí, 13 Feb. 2004, F. Pupulin 5133, D. Bogarín, H. León-Páez & E. Salas (CR, JBL-Spirit); same locality, 29.11.2004, F. Pupulin 5342, R. L. Dressler, K. Dressler & J. Warner (JBL-Spirit). Cartago: Juan Viñas, Pejivalle, La Marta, shore of Río Pejivalle, 9°47'47"N, 83°42'55"W, 690 m, 10.1.2004, F. Pupulin 5049. S. Dälstrom & H. Leon-Paez (JBL-Spirit); Turrialba, Peralta, 800 m, ca. 9°56'N, 83°41'W, 9 Aug. 2003, F. Pupulin 4945, C. Pupulin, M. Pupulin & H. León-Páez (CR; JBL-Spirit). Heredia: San Miguel de Sarapiquí, road to La Virgen, 360 m, 30.1.2000, F. Pupulin 1955 (JBL-Spirit); Sarapiquí, Horquetas road to Rara Avis, ca Km 4, granja La Selva, 10°20'24"N, 83°59'30"W, 115 m, 26.7.2003, F. Pupulin 4850, M. Pupulin, C. Pupulin, C. Ossenbach & B. Arias (JBL-Spirit). Limón: Talamanca, Bratsi, Bribrí, Uatsi (Volio), cerca de Lomas Mreduk, 9°32'02.2"N, 82°54'47.7"W, 260 m, 3 Octubre 2004, D. Bogarín 1017 & Botánica Forestal-UCR (CR). Puntarenas: Golfito, Golfito, Cerro Adams, camino a las Torres, ca. 1 km antes de la entrada a las instalaciones, 8°39'14.7"N, 83°09'55.8"W, 440 m, sobre una liana de *Doliocarpus* sp. (Dilleniaceae), 26 Octubre

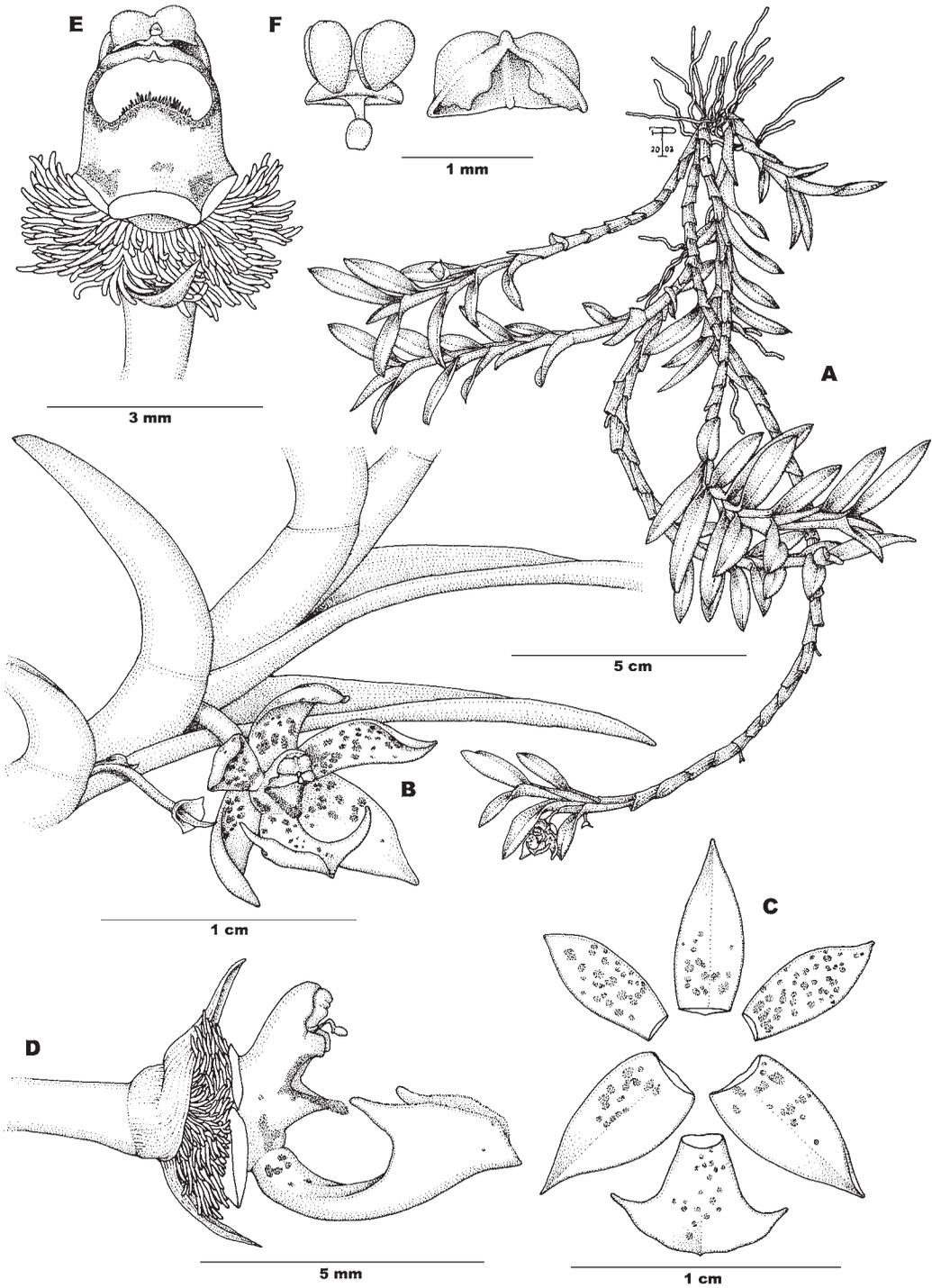


FIGURE 40. *Dichaea elliptica* Dressler & Folsom. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, pollinarium and anther cap. Drawn from *Pupulin et al.* 4945 (CR).

2004, *D. Bogarín 1061 & Botánica Forestal-UCR* (CR); Golfito, R. F. Golfito, Est. Agujas, Río Agujas, Sendero Sapó, 8°32'11"N, 83°25'31"W, 300 m, 14 Junio 1995, *A. Azofeifa 195* (INB); Las Alturas, above Las Cruces, flowered in cultivation 11 Sept. 1995, *J. Luer s.n.* (MO).

**Etymology:** from the Latin *ellipticus*, elliptic, in allusion to the shape of the leaves in the type specimen.

**Ecology:** epiphytic in shade in tropical to premontane wet forests on both watersheds of the main Costa Rican mountain chains, the species has been recorded at elevations from 100 to 1300 m. Flowering mostly occurs during the rainy season, from July to September, but sporadic flowering has been recorded also in February and May.

*Dichaea elliptica* pertains to the group of small-habit taxa of the sect. *Pseudodichaea*. The species is widely distributed, ranging at least from Nicaragua (Hamer, 1982a: pl. 650; 2001: 1656) to Ecuador (Dodson and Dodson, 1989: pl. 0434), but it spent most of its published history masquerading under the name of *D. brachypoda*, an unrelated species with glabrous ovaries and petals much larger than the sepals, treated here as a synonym of *D. panamensis*. It is likely that the specimen of *D. brachypoda* cited from Belize by McLeish and co-authors and characterized by a muricate ovary is also referable to sect. *Pseudodichaea*, but the sagittate, acute outline of the lip (McLeish et al., 1995: fig. 33L) suggests it is a taxon different from that treated here as *D. elliptica*. Specimens of *D. brachypoda* recorded from Venezuela (Dunsterville and Garay, 1965; Foldats, 1970: 447–448), Suriname (Werkhoven, 1986), and Brazil (Pabst and Dungs, 1977: 298 and fig. 1912), all of them bearing muricate fruits, correspond to distinct taxa and even to different sections of *Dichaea* (e.g., according to Pabst and Dungs, 1977: 188–189, *D. brachypoda* in Brazil has non-articulate leaves). The immature flower of *Freiberg 51* from central French Guyana (B) was compared with *D. brachypoda*, but on the basis of its glabrous ovary, Christenson (1997) considered it closest to *D. cogniauxiana* Schltr., in the erroneous belief that the ovary of *D. brachypoda* should be muricate. Unfortunately, the specific epithet *elliptica*, referring to the elliptic leaves, only matches in Costa Rica a minor number of specimens, and most of the examined plants

have lanceolate to narrowly lanceolate leaves. Among the species of its section, *D. elliptica* is characterized by the small flowers finely spotted with red and the subtruncate to truncate lip, the epichile being much wider than long. Although it was known from a single Costa Rican collection close to the border with Panama at the time of its description (Dressler and Folsom in Dressler, 2002), the distributional range of *D. elliptica* is now known to extend on both the watersheds of the Talamanca mountain range, as well as to the Caribbean slopes of the Tilarán and Central Volcanic ranges in northern Costa Rica.

9. *Dichaea filiarum* Pupulin, Vanishing Beauty 1: 206–207. 2005. TYPE: COSTA RICA. Cartago: Turrialba, Monumento Nacional Guayabo, 09°56'N, 83°43'W, ca. 800 m, premontane wet forest, epiphytic in the understory forest, 9 Aug. 2003, flowered in cultivation at Jardín Botánico Lankester, 8 October 2003, *F. Pupulin 4944*, *M. Pupulin*, *C. Pupulin* & *H. León-Páez* (Holotype: USJ). Fig. 41, Map 3.

*Plant* epiphytic, caespitose, to 60 cm long. *Roots* filiform, basal, 0.5–0.7 mm in diam. *Stems* compressed, pendent, few from base, 20–60 cm long, 0.5–0.8 cm wide across conduplicate sheaths, rarely branching toward the apex. *Leaves* closely spaced along stem, spreading, thick-coriaceous, dark olive green, 12–18 × 6–8 mm, broadly lanceolate, the apex shortly acuminate, abaxially apiculate, the apical margins raggedly serrulate, somewhat curled backwards, with conspicuous cross-veining; sheaths clasping, 6–8 × 5–8 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, perpendicular to stem, to 13 mm long, provided with a basal, cylindrical bract, 4 mm long. *Floral bract* double, the outer bract widely ovate, 5.0 × 3.5 mm, the inner bract narrowly oblong, 7 mm long. *Pedicel* cylindrical, 2 mm long. *Ovary* 2 mm long, muricate. *Flower* large for the section, usually not completely spreading, the sepals creamish white, slightly tinged with pale pink, abaxially cream, the dorsal sepal flecked pale purple-violet, the petals pale cream, flecked violet, the lip white, heavily barred pale violet, the column white with violet wings; no fragrance detected. *Dorsal sepal* erect, concave, narrowly elliptic-lanceolate, acute, 12 × 4 mm. *Lateral sepals* obliquely lanceolate, concave, acute, 11 × 4 mm. *Petals* oblanceolate, incurved toward apex, subacute,

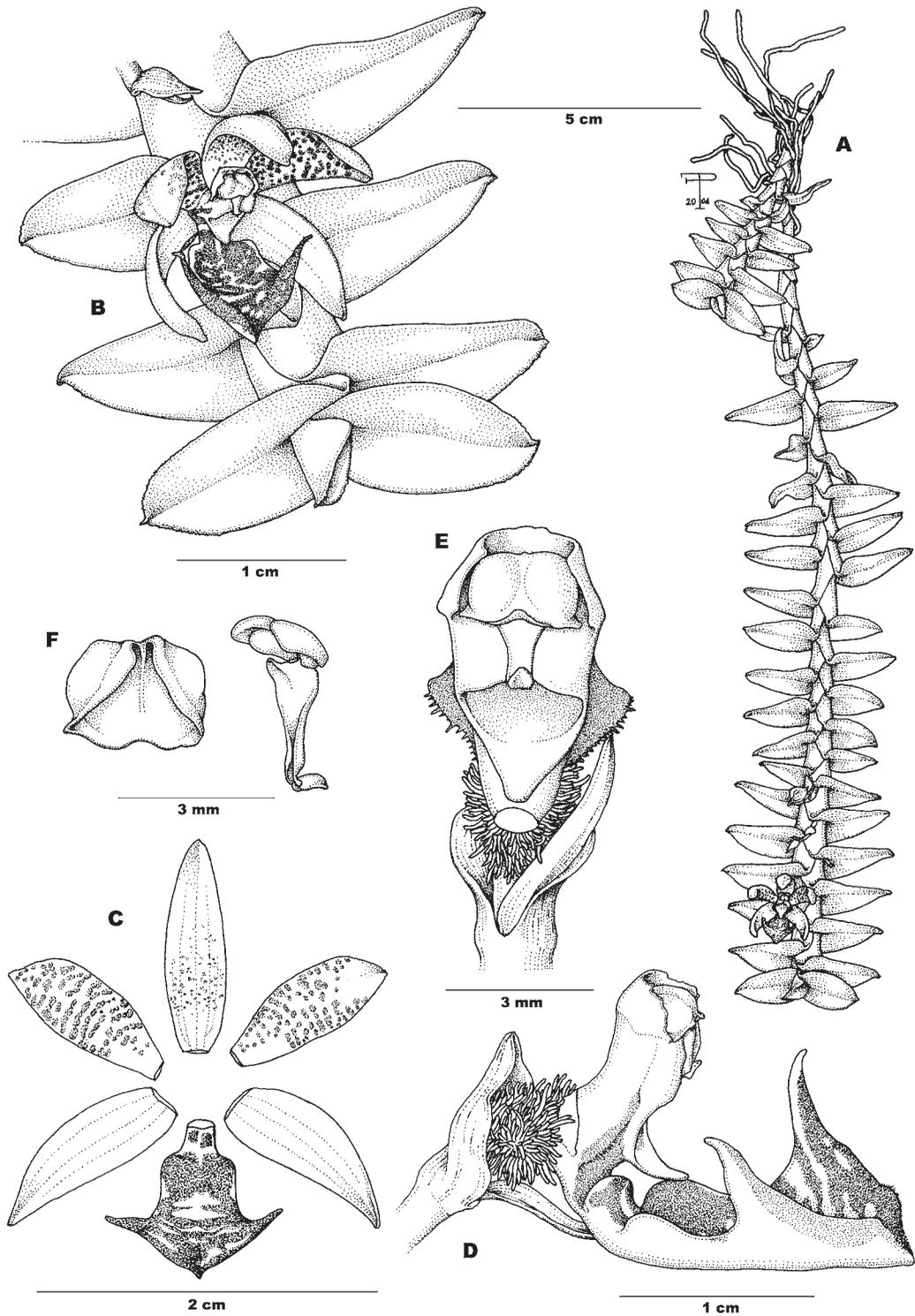


FIGURE 41. *Dichaea filiarum* Pupulin. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium. Drawn from Pupulin et al. 4944 (USJ).

10 × 4 mm. *Lip* 3-lobed, anchoriform, clawed, 8.5 × 10.0 mm when spread, the claw 1.5 × 1.5 mm, the hypochyle subquadrate, forming distinct shoulders, 4.0 × 4.5 mm, the epichyle shortly acuminate, microscopically ciliate toward apex, 3.5 × 6.0 mm, laterally producing spreading to recurved, triangular-acuminate lobes, 2.5 × 0.8 mm. *Column* erect, 5 mm long, with distinct foot, the clinandrium cucullate, irregularly crenulate, provided with widely triangular, ciliate wings; ligule oblong, glabrous, 1.5 × 0.8 mm. *Anther cap* subquadrate, retuse, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a obtriangular, apiculate stipe with the margins incurved; viscidium elliptic. *Fruit* an elliptic capsule, densely muricate, 13 × 10 mm.

**Distribution:** known only from Costa Rica.

**Additional material examined:** COSTA RICA. Cartago: Paraiso, Orosí, Tapantí National Park, Oropendola trail, close to the banks of Río Grande de Orosí, 1150 m, premontane wet forest, epiphytic in secondary, mature vegetation, 28 December 2004, *F. Pupulin* 5482, *M. Blanco*, *D. Bogarín*, *S. Dalström* & *C. Lewis* (JBL-Spirit); Turrialba, Tres Equis, Finca Tres Equis, 9°58'19.6"N, 83°34'14.3"W, 900 m, premontane wet forest, 14 March 2006, flowered in cultivation at Jardín Botánico Lankester, 4 Apr. 2006, *F. Pupulin* 5970, *D. Bogarín*, *R. L. Dressler* & *A. Karremans* (CR); Turrialba, Campus del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 9°54'03"N, 83°40'04"W, 643 m, bosque muy húmedo premontano, epífitas en zonas verdes y jardines, 20 Diciembre 2004, floreció en cultivo en el Jardín Botánico Lankester el 14 de Julio 2006, *D. Bogarín* 1117, *A. Karremans* & *A. Prendas* (CR). Limón: Pococí, Guápiles, San José-Limón highway, km 47, Quebrada Molinete, 10°10'43"N, 83°54'57"W, 470 m, tropical wet, transition to premontane wet forest, epiphytic in primary forest along the river banks, 9 July 2004, *F. Pupulin* 5250 & *D. Bogarín* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 28 July 2004, *F. Pupulin* 5253 & *D. Bogarín* (JBL-Spirit); *F. Pupulin* 5254 & *D. Bogarín* (JBL-Spirit); *F. Pupulin* 5263 & *D. Bogarín* (JBL-Spirit); Pococí, Guápiles, San José-Limón Highway, ca. km 49, ca. 500 m after the entrance to the Rain Forest Aerial Tram, Quebrada El Molinete, 10°10'43"N, 84°54'57"W, 470–500

m, 9.7.2004, *F. Pupulin* 5270 & *D. Bogarín* (JBL-Spirit). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, 29 June 2006, *W. Schug* s.n. (CR).

**Etymology:** from the Latin *filia*, daughter, and its genitive plural *filiarum*, "of the daughters," in honor of Margherita Pupulin and Carlotta Pupulin, who participated in the collection of the type specimen.

**Ecology:** epiphytic in shade in tropical to premontane wet forests on the Caribbean side of the Cordillera de Talamanca and Cordillera Central in Costa Rica, at 500–1200 m elevation. Flowering occurs during the rainy season, from April to October.

*Dichaea filiarum* pertains to a group of truly pendent species of sect. *Dichaea* native to northern and western South America, among which are *D. histrio* Rchb. f., *D. laxa* (Ruiz. & Pav.) Poepp. & Endl., *D. lagotis* Rchb. f., *D. potamophila* Folsom, *D. muyuyacensis* Dodson, and *D. violacea* Folsom. It is most similar to *D. muyuyacensis* from Peru (syn. *D. tuberculilabris* Folsom, from Panama) and to *D. laxa* from Bolivia and Peru, from which it differs in the non-tuberculate lip and the longer plants, and the non-tuberculate sepals, lanceolate lateral sepals, glabrous shoulders of the hypochile, and ligule, respectively. *Dichaea lagotis* has a bifid ligule very unlike that of *D. filiarum*, whereas the hypochiles of *D. histrio* and *D. potamophila* have no shoulders. The Panamanian *D. violacea* differs from *D. filiarum* in the strong violet coloration of the floral segments, its very wide hypochile, and the retrorse lobes of the epichile. Apart from *D. costaricensis*, which presents a few cross-veins between the parallel longitudinal veins of the leaves, *D. filiarum* is the only Costa Rican species having conspicuous cross-veining in its leaf blades (Fig. 15), a character otherwise mainly restricted to species native to South America.

10. *Dichaea fragrantissima* ssp. *eburnea* Dressler & Pupulin, *Novon* 16: 340. 2006. TYPE: COSTA RICA. Alajuela: San Ramón, Reserva Biológica A. M. Brenes, flowered in cultivation at Jardín Botánico Lankester, 7 July 2003, *M. Blanco* 513 (Holotype: USJ). Fig. 42, Map 4.

*Plant* epiphytic, caespitose, to 30 cm long. *Roots* filiform, 0.7–1.0 mm in diam., exposed at the base of the stem, the caulinar roots completely hidden by the leaf sheaths. *Stems* com-

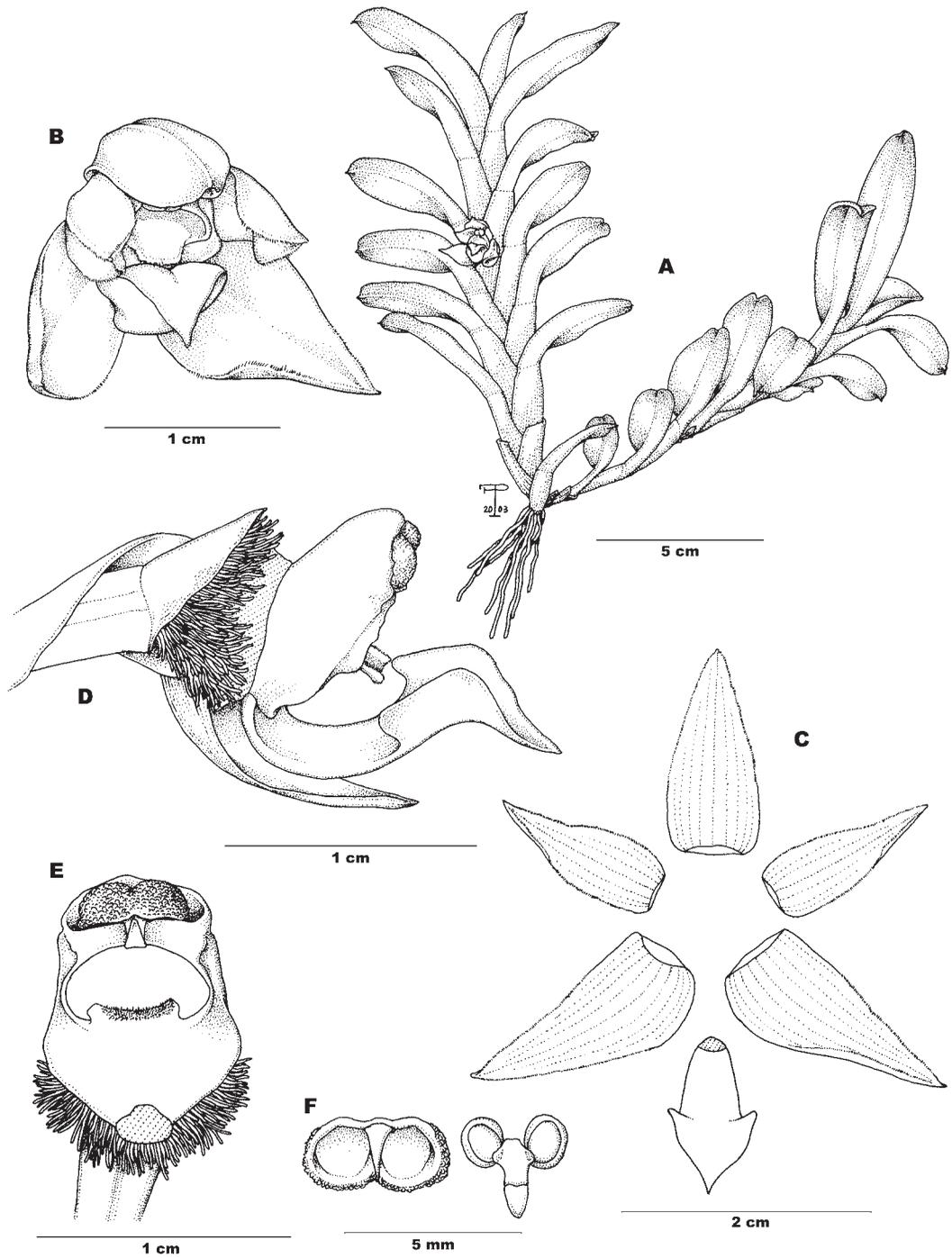


FIGURE 42. *Dichaea fragrantissima* ssp. *eburnea* Dressler & Pupulin. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium. Drawn from Blanco 513 (CR).

pressed, simple, suberect, becoming pendent with age, 16–30 cm long, 1.3–1.9 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, closely spaced along stem, spreading, thinly coriaceous, oblong, obtuse, retuse or apiculate, medium green, 3.5–7.3 × 0.6–1.6 cm; sheaths loose, strongly complanate, ancipitous, 10–15 × 4–5 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent to pendent, 15–20 mm long, provided with 2 basal, cylindrical, clasping bracts, to 5 mm long. *Floral bract* double, the outer bract ovate-orbicular, acuminate 11–14 × 8–14 mm, the inner bract lanceolate, ca. 11 × 2 mm. *Pedicel* cylindrical, 1.5 mm long. *Ovary* 1.5–1.8 mm long, densely muriccate. *Flower* ringent, ivory, with greenish apices, strongly scented. *Dorsal sepal* ovate-lanceolate, narrowly acute-acuminate, concave, dorsally subcarinate, the margins hispid-ciliate, 14–16 × 4.0–6.5 mm. *Lateral sepals* obliquely ovate-lanceolate, asymmetrical, concave, acute-acuminate, dorsally subcarinate, the margins hispid-ciliate, 14–15 × 5.5–7.0 mm. *Petals* ovate-lanceolate, narrowly acute-acuminate, the margins hispid-ciliate, 12–14 × 4–5 mm. *Lip* 3-lobed, sagittate, sessile, 10–14 × 5–6 mm when spread, the hypochile obtuse, ca. 5.5 mm long, 4 mm wide apically, dorsally keeled or not; the epichile triangular, acute to subacuminate, 5–6 × 5–6 mm, the lateral lobes from rounded angles triangular-oblong, to 1.2 × 1.0 mm. *Column* erect, 3.5–4.0 mm long, with distinct foot, sometimes with a rounded callus between column foot and lip; the clinandrium shallow, irregularly erose; ligule subquadrate, shallowly emarginate, minutely papillose at apex, 1.5–2.0 × 1.5–2.0 mm. *Anther cap* subrhynchiform-cucullate, flattened, 2-celled. *Pollinia* 4, rounded, in two superposed pairs of different size, on a broadly obtriangular, truncate stipe; viscidium peltate. *Fruit* an oblong-globose, muriccate capsule ca. 18 × 15 mm.

**Distribution:** Guatemala (?), Nicaragua, Costa Rica, and Panama.

**Additional material examined:** COSTA RICA. Alajuela: Alajuela, Reserva Forestal adjacent to Parque Nac. Braulio Carrillo, SE of Cariblanco, on NW slope of Río Sarapiquí canyon, 10°15'50"N, 84°10'20"W, 780 m, 19 Nov. 1990, *S. Ingram 682* & *K. Ferrell* (INB); Grecia, Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 380–400 m, 13.2.2004, *F.*

*Pupulin 5138*, *D. Bogarín*, *H. Leon-Páez* & *E. Salas* (JBL-Spirit); Monteverde, Reserva Biológica Monteverde, Río Peñas Blancas, 10°18'N, 84°54'W, 900 m, 11 Dec. 1987, *W. Haber 7867* & *E. Bello* (INB); Naranjo, Palmira, Bajos del Toro, road to Catarata del Río Toro, ca. km. 2.5, 10°15'00"N, 84°16'23"W, 1230 m, premontane wet forest, 13 Apr. 2003, *F. Pupulin 4600*, *E. Salas* & *H. León-Páez* (USJ-spirit); same locality, *F. Pupulin 4601*, *E. Salas* & *H. León-Páez* (JBL-Spirit); San Ramón: Reserva Forestal, 1350–1500 m, 18 Feb. 1983, *A. Carvajal 347* (MO); Reserva A. M. Brenes, cuenca del Río Lorencito, 850–1000 m, agosto 1991, floreció en cultivo, Jardín Botánico Lankester, 1 dic. 1994, *M. Germani 131* (USJ); R. F. San Ramón, Fila Volcán Muerto. Sendero El Sahíno, 10°12'55"N, 84°35'25"W, 1000–1100 m, 26 Apr. 1993, *E. López 39*, *Q. Jiménez* & *Curso de Botánica* (INB); Bajo la Balsa, 1100 m, 4 mar. 1983, *A. Carvajal 479* (MO); Road from San Ramón through Balsa, Río Balsa at bridge, ca. 10°10'–15'N, 84°30'–35'W, 700–800 m, 29 Aug. 1979, *W. D. Stevens 13802* (MO); Monteverde Reserve, S. side Río Peñas Blancas Valley, near Refugio Alemán, 10°18'N, 84°45'W, 880–950 m, 13 Dec. 1989, *W. Morris* & *L. Obando 4042* (CR, MO [not seen], SEL). Cartago: Paraíso. Orosi, Reserva Tapantí, vertiente arriba de Quebrada Seca, 26 nov. 1984, *R. L. Dressler y Biología 350*, No. 195 (USJ); Paraíso, Orosi, Tapantí, camino entre Tapantí y Tausito, ca. 3 km después del Restaurante Tejos, 9°46'27.9"N, 83°46'55.6"W, 1471 m, bosque pluvial premontano, epífitas en bosque a orillas del camino, 23.12.2005, floreció en cultivo en el Jardín Botánico Lankester el 22 de Junio 2006, *D. Bogarín 2274*, *M. A. Blanco* & *R. Dressler* (CR); Tapantí, road NE of restaurant Kirí, ca. Km 3, 9°45'43.8"N, 83°48'04.7"W, 1520 m, epiphytic along the roadside, premontane wet forest, 5 May 2006, flowered in cultivation at Jardín Botánico Lankester, 14 Aug. 2006, *F. Pupulin 6213*, *D. Bogarín* & *A. Rambelli* (CR); Taus, 6 June 1978, *C. Todzia 304* (CR); Turrialba, Santa Cruz, San Antonio, shores of Río Guayabito, Quebrada Loca, 9°57'56"N, 83°42'32"W, 1400–1450 m, premontane rain forest, 10 Feb. 2004, *F. Pupulin 5114*, *D. Bogarín*, *A. Karremans* & *H. León-Páez* (USJ-spirit); Turrialba, Grano de Oro, El Seis, Moravia de Chirripó, 09°49'50"N, 83°26'40"W, 1100 m, 10 Sept. 1993, *P. Campos*

193 & A. Campos (INB); Turrialba, Platanillo, Tayutic, laderas del Río Platanillo, 600 m, 20.2.2004, A. Karremans 135 (JBL-Spirit); Santa Cruz, San Antonio, 9°57'56"N, 83°42'32"W, 1400–1450 m, 10.2.2004, F. Pupulin 2944, D. Bogarín, A. Karremans & H. León-Páez (JBL-Spirit). Heredia: Sarapiquí, along Río San Fernando between Cariblanco and Colonia del Socorro, 900–1000 m, 10°15'N, 84°10'W, 12 July 1983, K. Barringer, E. Christenson, B. Pérez 3672 (MO). Border between Heredia and Alajuela: Grecia, Sarapiquí, Colonia Virgen del Socorro, road to Cariblanco, bridge on Río San Fernando, 10°16'32"N, 84°10'16"W, 750 m, shores of Río San Fernando, tropical wet, belt transition to premontane wet forest, 13 Feb. 2004, F. Pupulin 5164, D. Bogarín, H. León-Páez & E. Salas (USJ-spirit). Puntarenas: Monteverde Reserve, Peñas Blancas Valley, 1200 m, 22 Jul. 1989, J. T. Atwood 89–314 (SEL). San José: P. N. Braulio Carrillo, trail from highway to Río Hondura/Bajo La Hondura, about 5 km. after tunnel, 10°14'10"N, 83°59'20"W, 1250 m, 18 Dec. 1990, S. Ingram & K. Ferrell 812 (CR); Braulio Carrillo N.P., 500–700 m, 16 Sept. 1984, J. Folsom 11,010 (CR). Without specific locality, 1867, A. R. Endrés 161 (W).

**Etymology:** from the Latin words *fragrantissimus*, very scented, and *eburneus*, ivory white, in allusion to the scent and the color of the flower. The name *eburnea* was first suggested by A. R. Endrés in his correspondence with H. G. Reichenbach for a plant he collected in Costa Rica around 1867 (W-R 18375).

**Ecology:** plants of this species are usually found in mature vegetation, as epiphytes of shaded spots in tropical to premontane wet forests at elevations ranging from 400 to 1500 m. In Costa Rica, *D. fragrantissima* ssp. *eburnea* is apparently restricted to the Caribbean watershed of the Tilarán, Central Volcanic, and Talamanca mountain chains. Flowering mostly occurs during the dry season, from December through February, but a second flowering peak has been recorded in June–July.

This is the most-common large *Dichaea* in Costa Rica, especially in wet forests on the Caribbean slope. The subspecies is characterized by the ivory flowers with greenish apices of the sepals, occasionally provided (outside the study area) with short reddish streaks at the bases of the sepals and petals. The ssp. *eburnea*

is much more widespread than ssp. *fragrantissima*, and Dressler et al. (2006) suggested that ssp. *fragrantissima* is closer to the ancestral form of the species, the ivory coloring of the flowers in ssp. *eburnea* representing floral albinism and some degree of autogamy. The plants of ssp. *eburnea* are commonly self-pollinated. The voucher of *D. morrisii* reported from Guatemala (Dix and Dix, 2000) might be *D. fragrantissima*, significantly extending toward the north the distributional range of the species, and this view is supported by other Guatemalan orchid students (F. Archila, pers. comm., 2006).

11. *Dichaea glauca* (Sw.) Lindl., Gen. Sp. Orchid. Pl.: 209. 1833. *Epidendrum glaucum* Sw., Prodr.: 124. 1788. TYPE: JAMAICA. "Lectum in arboribus versus summum jugum Montium caeruleorum Jamaicae australis," O. Swartz s.n. (Holotype: W-Reichenbach Herbarium Nr. 25295). *Cymbidium glaucum* (Sw.) Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 71. 1799. *Dichaeopsis glauca* (Sw.) Schltr., Beih. Bot. Centralbl. 36(2): 519. 1918. *Epithecia glauca* Schltr., Orchis 9: 26. 1915, non Knowles & Westc., 1838. Fig. 43, Map 4. Synonyms: *Dichaea oerstedii* Rchb. f., Bonplandia 3: 219. 1855, *syn. nov.* TYPE: NICARAGUA. Am Vulcan El Viejo, A. S. *Oersted s.n.* (Holotype: W-Reichenbach Herbarium Nr. 19392). *Epithecia oerstedii* (Rchb. f.) Schltr., Orchis 8: 101. 1914, *syn. nov.* *Dichaeopsis oerstedii* (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 519. 1918, *syn. nov.*

*Dichaea willdenowiana* Kraenzl., Engl. Pflanzenr. Orchid.-Monandr.-Pseudomonopod. IV, 50(83): 46. 1923. Syntypes: Mexico: Villa Alta de Bataza, K. T. Hartweg 516 (W-Rchb Herb 19394); Oaxaca, Jalapa, H. C. Galeotti 5078 (W-Rchb Herb 19396); without locality, C. J. W. Schiede 45 (W-Rchb Herb 19393); K. T. Hartweg 46 (W-Rchb Herb 19397).

Plant terrestrial or epiphytic, cespitose, to 55 cm long. Roots thick, produced only at the base of the stem, to 3.5 mm in diam. Stems compressed-ancipitous, erect, rarely becoming arcuate-pendent with age, 12–55 cm long, 0.3–0.4 cm wide across conduplicate sheaths.

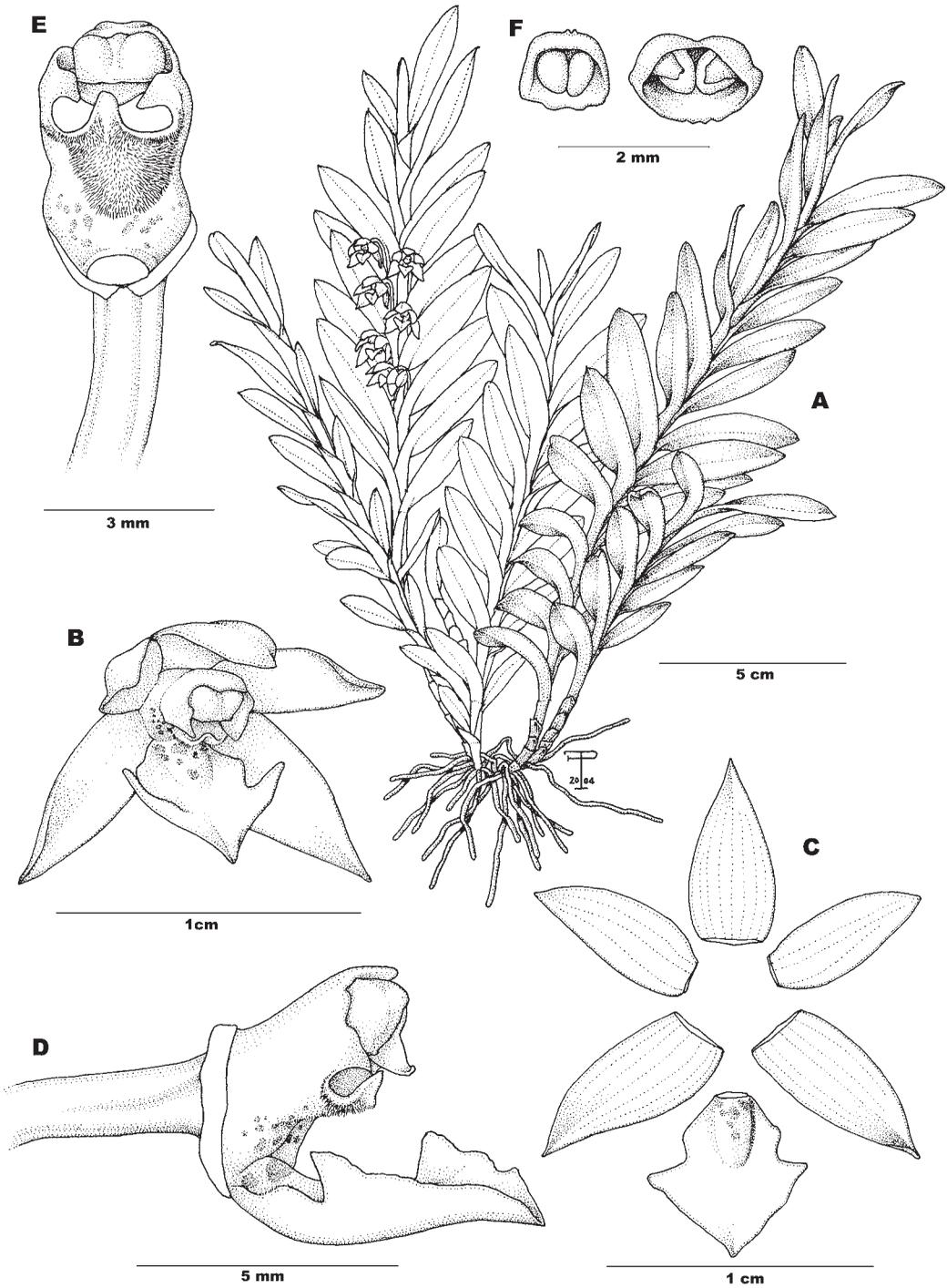


FIGURE 43. *Dichaea glauca* (Sw.) Lindl. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from Pupulin & Barboza 2226 (CR).

*Leaves* articulate with the sheaths, widely to closely spaced along stem, subspreading, thin-herbaceous, glaucous green, 25–48(60) × 7–13 mm, oblong-elliptic, acute, shortly mucronate; sheaths clasping, 13–22 × 5–6 mm. *Inflorescence* simultaneous (to 11), 1-flowered, emerging below foliage, erect, to 25 mm long, provided with 2 basal, tubular, clasping bracts, 2.5 mm long. *Floral bract* widely ovate, acute to acuminate, amplexicaul 2.5 × 2.0 mm. *Pedicellate ovary* subcylindric, glabrous, 10 mm long including the pedicel. *Flower* often cleistogamous, otherwise spreading and very scented, ivory white to grey-white, the base of the lateral sepals sometimes blotched with pale ochre, rarely spotted with red-brown at the base of all the tepals. *Dorsal sepal* erect to slightly curved, concave, lanceolate-elliptic, subacuminate, 6.2–9.0 × 3.5–4.2 mm. *Lateral sepals* obliquely lanceolate-elliptic, concave, acute, shortly subacuminate, 6.5–9.0 × 3.2–4.0 mm. *Petals* elliptic-lanceolate, acute, smaller than sepals, 6.3–8.5 × 2.8–3.3 mm. *Lip* 3-lobed, sagittate, sessile, fleshy, 6.0–8.2 × 6–8 mm when spread, the hypochile obtusely to transversely rectangular from a obtusely base, 3–4 mm long, ca. 4 mm wide apically, the epichile triangular, acute, concave, sometimes microscopically papillose, 3.2–4.0 × 3–4 mm, the lateral lobes triangular, acute, spreading to slightly reflexed, sometimes indistinct, 1.0 × 0.8–1.0 mm. *Column* straight, 4–5 mm long, with a short foot, minutely papillose under the stigma; the clinandrium prominent, cucullate, irregularly erose, with 2 lateral lobes projecting toward stigma; ligule triangular, acute, glabrous, apically somewhat reflexed toward the column, 1.3 × 1.0 mm. *Anther cap* subrhombiform, flattened, 2-celled. *Pollinia* 4 in two superposed, subequal pairs, on a narrowly obtruncate stipe; viscidium elliptic-peltate. *Fruit* an elliptic-fusiform, glabrous capsule, to 2.5 × 0.8 cm.

**Distribution:** from central Mexico to Costa Rica and the West Indies (Cuba, Hispaniola [Dominican Republic and Haiti], Jamaica).

**Additional material examined:** COSTA RICA. Alajuela: Bajos del Toro, Bosque de Paz, Sendero Botánico, about 1490 m, on fallen tree, tropical lower montane rain forest, transition to montane, 13 Feb. 2000, flowered in cultivation at Jardín Botánico Lankester, 23 July 2006, *F. Pupulin* 2051 & *M. L. Spadari* (CR);

Valverde Vega, cuenca del Río Toro, Reserva Biológica Bosque de paz, 20 Dec. 2004, *M. Muñoz* 04–147 (USJ, sterile); Piedades de San Ramón, 21.VI.1925, *A. M. Brenes* (86) 1293 (AMES 45063). Cartago: El Muñeco, south of Navarro, February 8–9, 1924, *P. C. Standley* 33774 (AMES). Puntarenas: Monteverde, on old trees in pastures, 1520 m, premontane moist to wet forest, 25 March 2000, *F. Pupulin* 2226 & *G. Barboza* (CR); Monteverde, Bullpen, ca. 1550 m, 10°18'N, 84°47'W, epiphytic on remnants of primary forest, 1 June 2001, *F. Pupulin* 3197, *P. Cribb* & *G. Barboza* (CR); Santa Elena, Cerro Plano, finca Beeche, 10°19'13"N, 84°48'35"W, 1580 m, epiphytic on old trees in pastures, 30 April 2003, *F. Pupulin* 4734 & *G. Barboza* (JBL-Spirit); same locality, *F. Pupulin* 4734 & *G. Barboza* (CR); Puntarenas, Faja Costeña de Puntarenas, Río Cotón, Aguas Calientes, 08°59'20"N, 83°55'40"W, 950–1030 m, 20 June 1995, *J. F. Morales* 4455 (INB). Without definite locality, *Endrés* 11 (W-R 14750); *Endrés* 143 (W-R 14749, 14764, 14775, 18034); *Endrés* s.n. (W-R 10501); *Hübsch* s.n., 1882–85 (W-R 6143).

**Etymology:** from the Latin *glaucus*, glaucous, in reference to surface of the leaves, covered with a cuticular, waxy layer.

**Ecology:** a rather uncommon plant, rarely found as an epiphyte or as a terrestrial in mosses, *D. glauca* usually occupies more exposed places when compared to other typical, shade-loving species of *Dichaea*. In Costa Rica, it has been recorded from the moist regions of the Tilarán mountain range, at elevations around 1200–1600 m. Flowering occurs from February to September.

*Dichaea glauca* is quite unmistakable, both in plant and flower morphology. Plants of *D. glauca* are among the few taxa in Costa Rica to present erect stems, and they are sometimes found growing terrestrially in layers of mosses or other decaying substrates. The stems are always simple, strongly flattened (ancipitous), provided with distinctly thick roots (to 3.5 mm in diam.) only at the base and with glaucous sheaths and leaves. It is also the only species in Costa Rica to produce simultaneous inflorescences. The white and strongly scented flowers show no temporal activity. Cleistogamous flowers are often produced on individual plants otherwise able to develop flowers with fully spreading perianth; in such cleistogamous flow-

ers no stipe is produced, and the abaxial pair of pollinia is transformed into a unique structure.

The holotype of *D. oerstedii*, described by Reichenbach on a Nicaraguan collection by Oersted, is sterile, and the illustration of the flower by the collector is quite schematic. The only surviving stem is strongly flattened and completely covered by the leaf sheaths, the upper one still articulate with the corresponding, oblong leaves; the rather thick roots are apparently restricted to the base of the stem. The sizes of the leaves in the holotype (to 4 × 1 cm), as well as Oersted's original statement about their "subcoeruleo-pruinosis" appearance (glaucous, covered with a waxy layer), agree with characters of *D. glauca*.

12. *Dichaea globosa* Dressler & Pupulin, Novon 16: 340. 2006. TYPE: COSTA RICA. San José: Pérez Zeledón, El General Valley, vicinity of San Isidro del General, 730 m, 3 Mar. 1966, A. Molina R., W. C. Burger & B. Wallenta 18291 (Holotype: F [not seen]; Isotype: CR). Fig. 44, Map 4.

*Plant* epiphytic, caespitose, to 50 cm long. *Roots* slender, basal and caulinar, 0.5–1.0 mm in diam., the caulinar roots completely hidden by the leaf sheaths. *Stems* compressed, erect, becoming arcuate-pendent with age, 10–50 cm long, 16–20 mm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, closely spaced along stem, spreading, subcoriaceous, medium to dark green, often adaxially glossy, 38.0–6.3 × 10–21 mm, elliptic-oblong, obtuse, apiculate; sheaths loose, strongly ancipitous, 30–35 × 30–38 mm. *Inflorescence* successive, 1-flowered, emerging below foliage, the peduncle straight, slightly pendent to erect-spreading, 10–15 mm long, basally provided with two infundibuliform, acuminate, clasping bracts, 6–9 × 8 mm. *Floral bract* double, the outer bract broadly ovate, acuminate, 10 × 6–8 mm, the subopposite inner bractlet lanceolate, acuminate, ca. 9 × 2 mm. *Pedicellate ovary* subcylindric, muricate, 2.0–2.3 mm long including the pedicel. *Flower* large, coriaceous, subglobose, with sepals and petals green, blotched and spotted with purple, rarely solid green, the lip dark purple or pinkish purple. *Dorsal sepal* curved over the column, broadly ovate, acute, concave, the margins microscopically ciliate, 11.5–15.0 × 5–10 mm. *Lateral sepals* obliquely broadly ovate, abruptly acute,

apiculate, strongly concave, the margins microciliate, 12–14 × 6–9 mm. *Petals* obovate, obtuse, minutely apiculate, the margins microciliate, 10–12 × 5–7 mm. *Lip* sessile, obovate-anchoriform, conduplicate-concave, 10–13 × 10–12 mm when spread, the hypochile rounded-discoid, 7–8 mm long, 5–8 mm wide apically, the epichile transversally elliptic, rounded-subtruncate, apiculate, the distal margins thickened with a median groove, 2–4 × 12 mm, the lateral lobes narrowly triangular-falcate, acuminate, retrorse, 5–7 × 2 mm. *Column* short, stout, suberect, with prominent foot, 6–7 mm long; the clinandrium shallow, entire; the stigma transversely elliptic-subrectangular; infrastigmatic ligule triangular, rounded, apically pubescent, ca. 3 × 2 mm. *Pollinia* 4 in two superposed, subequal pairs, complanate-rounded, on a oblong, obtuse stipe and a peltate, hyaline viscidium. *Fruit* a subglobose-oblong, muricate capsule, ca. 21 × 17 mm.

**Distribution:** Costa Rica and Panama.

**Additional material examined:** COSTA RICA. Puntarenas: Aguirre, La Unión de Paso Real, Río El Chorro, 9°30'57"N, 84°05'08"W, 100 m, tropical wet forest, 27 May 1999, *F. Pupulin 1476* & *D. Castelfranco* (JBL-Spirit); Savegre, Quebrada Arroyo, 200–400 m, epiphytic in secondary and disturbed primary vegetation, tropical wet, transition to premontane wet forest, 30 May 2001, *F. Pupulin 3165*, *D. Castelfranco*, *P. Cribb* & *R. L. Dressler* (JBL-Spirit!); Buenos Aires, Cañas, Llano Bonito, tropical rain forest transition to premontane rain forest, 9°14'07.7"N, 83°24'06.6"W, 460–600 m, 23.10.2005, *F. Pupulin 5811*, *D. Bogarín*, *R. L. Dressler*, *R. Gómez*, *A. Karremans* & *A. Rambelli* & *S. Rambelli* (JBL-Spirit); Buenos Aires, Cordillera de Talamanca, Ujarrás, margen izquierda del Río Ceibo, 09°14'00"N, 83°18'00"W, 500 m, 9 March 1993, *G. Herrera 5829* (INB); Coto Brus, Zona Protectora Las Tablas, Finca Las Alturas, camino entre Las Alturas y Fila Tigre, 8°55'56"N, 82°50'44"W, 1540–1400 m, 22.3.2003, flowered in cultivation at Jardín Botánico Lankester, accession No. JBL-05319, 27.10.2004, *F. Pupulin 4517*, *H. Montealegre* & *A. C. Rodríguez* (USJ, JBL-Spirit); S.E. of San Vito, ca. 450 m, flowered in cult. 11 Mar. 2004, *R. L. Dressler 6408* (MO); Coto Brus, San Vito, ca. 1.5 km camino del Jardín Botánico Wilson hacia Copal, 8°46'52.3"N,

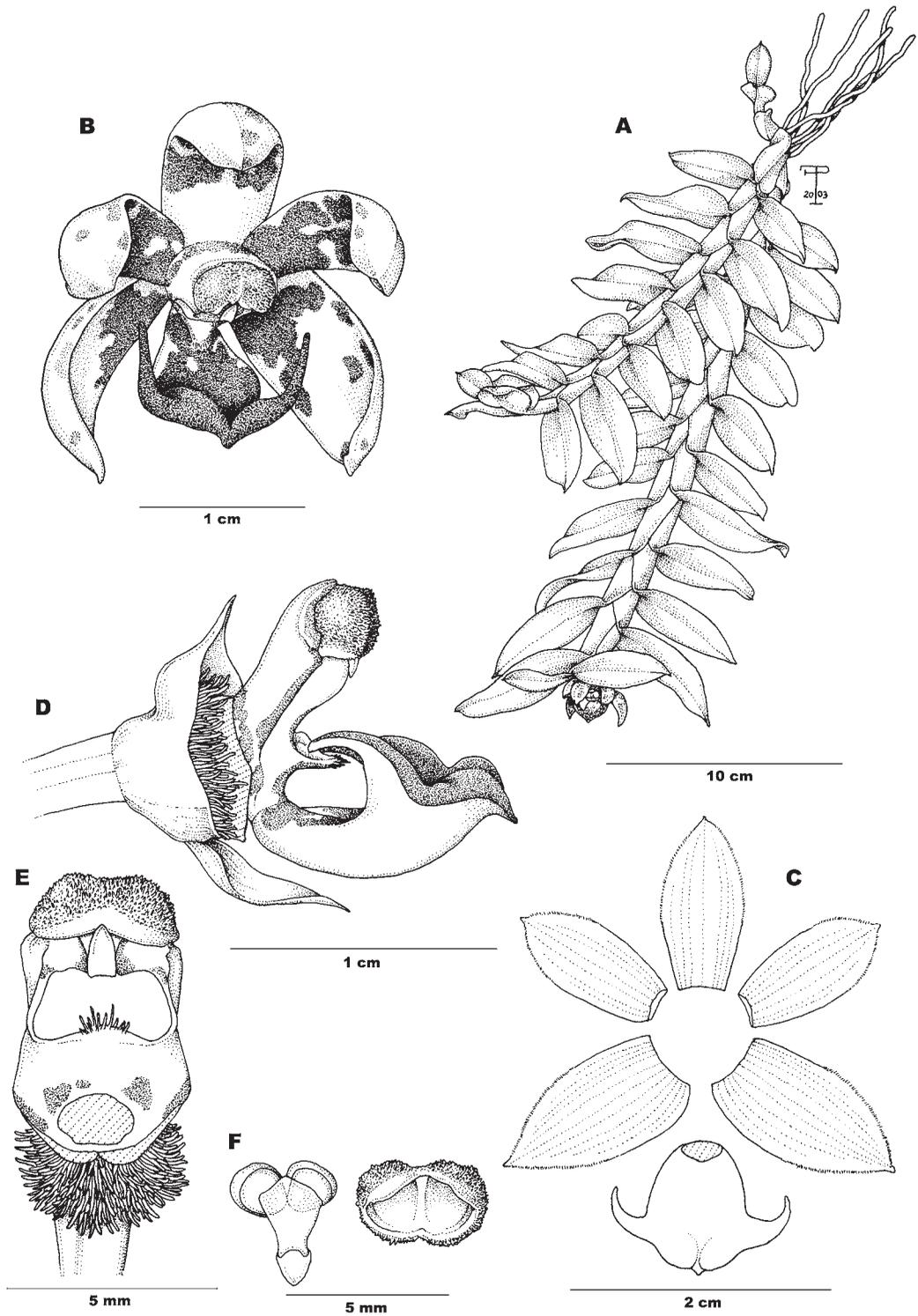


FIGURE 44. *Dichaea globosa* Dressler & Pupulin. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from *Pupulin et al.* 3165 (JBL-Spirit).

82°57'58.7" W, 1270 m, bosque muy húmedo premontano transición a basal, en bosque secundario y árboles en borde de potreros, 25 Octubre 2005, floreció en cultivo en el Jardín Botánico Lankester el 15 de Abril 2006, *D. Bogarín 2057*, *R. L. Dressler*, *R. Gómez*, *A. Karremans*, *F. Pupulin*, *A. Rambelli* & *S. Rambelli* (CR); Osa, Rancho Quemado, Sector este, Sierpe, cerca de una laguna, 8°42'20"N, 83°33'40"W, 200–230 m; 9 Nov. 1991, *J. Marín 273* & *F. Quesada* (MO); *J. Marín 272* & *F. Quesada* (CR); Osa, Golfito, Bosque de los Austriacos, Tropenstation La Gamba, 8°42'40"N, 83°37'00"W, 125–400 m, 3–4.7.2004, *E. Serrano 129* & *M. Blanco* (JBL-Spirit); Osa, Fila Estero Guerra, Sierpe, 8°34'30"N, 83°34'30"W, 300 m, 27 Sept. 1991, *J. Marín 206* (INB). San José: Dota, Crest of Cerro Nara, 1050–1140 m, pressed from cult. 25 June 1999, *F. Pupulin 1124*, *D. Castelfranco* & *M. L. Spadari* (MO); 15 Feb. 1999, *F. Pupulin 1123*, *M. L. Spadari* & *K. McFarland* (USJ); 20 Feb. 2000, *F. Pupulin 2080* (USJ); eastern slopes of Cerro Nara, 9°29'01"N, 84°00'25"W, 740–840 m, 14.1.1999, *F. Pupulin 1087*, *D. Castelfranco* & *M.L. Spadari* (JBL-Spirit); same locality, *F. Pupulin 1088*, *D. Castelfranco* & *M.L. Spadari* (JBL-Spirit); Pérez Zeledón, Fila Costeña, Zapote de Pejivalle, 740–810 m, 10 Dic. 2000, *F. Pupulin 2639*, *D. Castelfranco* & *J. Cambroner*, (JBL-Spirit); Las Nubes de Quizarrá, 9°23'31"N, 83°35'56"W, 1100 m, 23 enero 1999, *F. Pupulin 1189*, *D. Castelfranco* & *M. L. Spadari* (USJ); along the Río Quizarrá, 1080 m, epiphytic in remnants of primary vegetation, 9 November 2000, *F. Pupulin 2533*, *D. Castelfranco* & *J. Prada* (JBL-Photo); La Unión General, May 1935, *C. H. Lankester s.n.* (AMES); General Viejo, Finca Miraflores, along the banks of Quebrada Grande, 9°23'35"N, 83°39'52"W, ca. 780 m, epiphytic on large trees remnants of primary forest, gallery forest, 31 March 2002, *F. Pupulin 3574*, *V. Savolainen*, *M. Powell*, *V. Juárez-Pérez* & *C. Granados Herrera* (USJ-Spirit); : Pérez Zeledón, San Isidro de El General, carretera a Dominical, Fila Tinamastes, La Alfombra, 9°19'19.0"N, 83°45'58.1"W, 1000 m, bosque húmedo premontano, bosque secundario alterado y árboles a orillas de la carretera, 23 Octubre 2005, floreció en cultivo en el Jardín Botánico Lankester, 4.8.2006, *D. Bogarín 2010*, *J. Cambroner*, *R.L. Dressler*, *R. Gómez*, *A. Karremans*, *F. Pupulin*, *A. y S. Rambelli*

(JBL-Spirit); Refugio de Vida Silvestre Boracayán, in the Fila Costeña along the San José–Puntarenas Province border, ca. 10 km E of Dominical, just N of Fila Alivio in the upper Río Barucito basin, a southern tributary of Río Barú, 09°13.6'N, 83°45.9'W, 600 m, 29.05.2003, flowered in cultivation at Jardín Botánico Lankester, accession No. JBL-09172, June 2004, *J. R. Clark 256*, *B. K. Holst*, *M. Blanco*, *S. Dalström*, *N. Edmondson*, *W. Higgins*, *J. M. Heaney* & *J. Katzenstein* (JBL-Spirit).

**Etymology:** from the Latin *globosus*, round-shaped, in reference to the subglobose appearance of the flower.

**Ecology:** a rather infrequent plant, *D. globosa* is mostly found as an epiphyte on shady, mossy trunks and large branches in the understory of tropical and premontane rain to moist forests, at elevations of 100–1100 (1400) m. In Costa Rica, it is restricted to the Pacific slopes of the Cordillera de Talamanca in the central region and the General and Coto Brus valleys, as well as to the Cordillera Costeña (Brunqueña) and the Golfo Dulce areas in the southern Pacific region. Flowering mostly occurs from December to June.

*Dichaea globosa* is easily distinguished from *D. morrisii* by the fleshy, subtruncate lip, by the very broad claw of the lip, and by the distinctly obovate, apiculate petals. Among Costa Rican species with large plants, the subglobose flowers usually blotched with purple, the rounded hypochile and the narrow, falcate lateral lobes of the lip are diagnostic. The geographic distribution of the species in Costa Rica suggests that *Dichaea globosa* is probably a plant of drier forests than either *D. morrisii* or *D. fragrantissima* ssp. *eburnea*.

13. ***Dichaea gomez-lauritoides*** Pupulin, *sp. nov.* TYPE: COSTA RICA. Limón: Guápiles, camino a Río Frío, bosques remanentes entres los Ríos Blanco y Corinto, 200–250 m, 8–10 April 1982, “Epífita, flores blancas”, *J. Gómez-Laurito 8174* (Holotype: CR 89411). Fig. 45.

*Habitu Dichaeae graminoidi* (Sw.) Lindl. *similis, sed ovario muriculato* (vs. *glabro*) *labelloque base cuneata* (vs. *bilobata*) *ecallosa*; a *Dichaeae acrolepharae* Schltr. *foliis linearis angustioribus in caulibus late dispositis, floribus perpusillis albidis distincta*.

*Plant* epiphytic, caespitose, to 37 cm long. *Roots* filiform, exposed at the base and along the lower, naked portion of the stem, hidden by

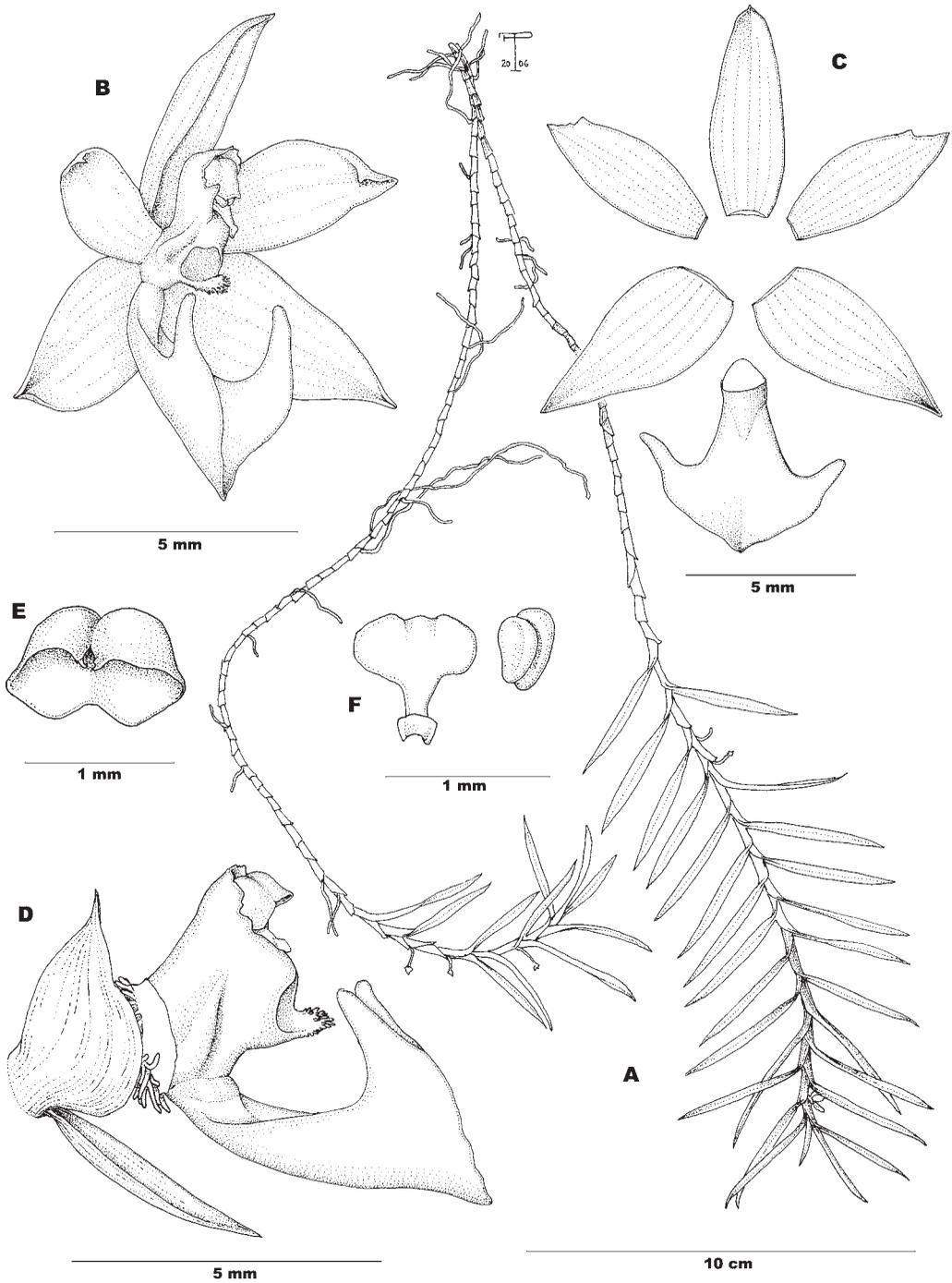


FIGURE 45. *Dichaea gómez-lauritoi* Pupulin. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, anther cap; F, stipe and pollinia. Drawn from the holotype (CR).

the leaf sheaths on upper stem, 0.3–0.5 mm in diam. *Stems* slightly compressed to subcylindric, pendent, 33–37 cm long, 0.13–0.18 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, widely spaced along stem, subspreading, membranaceous, green, 32–40 × 2.5–3.0 mm, narrowly linear-elliptic, acute, the apical margins microciliate; sheaths clasping, conduplicate-ancipitous, slightly dilated toward the apex, 11–13 × 4.0–4.8 mm, distinctly flushed with pale purple-brown in dried material. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent, 11–13 mm long, provided with a basal, lanceolate, clasping, membranaceous bract, 4.5 × 1.0 mm. *Floral bract* double, the outer bract widely triangular-ovate, cuspidate, 4.0 × 2.5 mm, the inner bract linear-lanceolate, acute, 4 mm long. *Pedicellate ovary* cylindrical-subclavate, 1.2 mm long, apically muricate. *Flower* spreading, white; no fragrance recorded. *Dorsal sepal* erect, concave, elliptic, obtuse, minutely apiculate, 5.5 × 2.1 mm. *Lateral sepals* obliquely ovate-elliptic, concave, subacuminate, 6.0 × 2.7 mm. *Petals* narrowly elliptic, acute, the superior margin provided with a short tooth toward the apex, 5 × 2 mm. *Lip* 3-lobed, anchoriform, with a short and stout claw ca. 0.5 mm long decurrent on the lamina, entire lip 4.5 × 6.0 mm when spread, the hypochile obcuneate, 2 mm long, 3 mm wide apically, the epichile widely triangular, obtuse, 3.8 × 2.5 mm, the lateral lobes triangular-ligulate, rounded, retrorse, 2.0 × 0.5 mm. *Column* suberect, 2.4 mm long, provided along the basal margins with subcarinate, thickened-linear, glabrous wings; the clinandrium shortly cucullate, irregularly erose; the stigma ovate, apically emarginate; ligule short-triangular, thickened toward the papillose-hirsute apex, 0.8 × 0.5 mm. *Anther cap* subrhreniform, emarginate, 2-celled. *Pollinia* 4 in two pairs of different size, on a obpyriform-spatulate, truncate stipe; viscidium elliptic. *Fruit* not seen.

**Distribution:** known only from Costa Rica.

**Eponymy:** named in honor of Jorge Gómez-Laurito, outstanding Professor of Botany at the University of Costa Rica and internationally renowned botanist, who discovered the species.

**Ecology:** an apparently rare plant, *D. gomez-lauritoi* was collected only once in the warm, extremely wet forest of the Caribbean plains lying at the base of the steep Central Volcanic

range. At the type locality, at an elevation of about 200 m, the climate is constantly rainy, and no definite dry season exists. From the same area, enclosed between the Blanco and Corinto rivers, *D. acrolephara*, *D. fragrantissima* ssp. *eburnea*, *D. panamensis*, *D. sara-piquinsis*, and *D. tuerckheimii* have also been recorded. Flowering occurs at least in April.

The features of the plant and the flower have no close affinities with any of the known *Dichaea* species. The vegetative habit is almost indistinguishable from that of *D. graminoides*, a species originally described from Jamaica (Swartz s.n., *Rchb. Orch.* 25413!, W, the type) and recorded from Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Panama, the West Indies, and northern South America (Soto Arenas, 2002), but so far never found in Costa Rica. The only specimen from Costa Rica annotated as *D. graminoides* is Gómez-Laurito 8174 at CR, and its narrow, linear-elliptic leaves, well spaced along the stems, and the leaf sheaths somewhat tinged with pale brown, are in fact very similar to those of *D. graminoides*. The floral features, however, prevent such a determination. The ovary of *D. gomez-lauritoi* is muricate (vs. glabrous in *D. graminoides*), and the lip is sagittate from a cuneate base (vs. panduriform, bilobed at the base), without the central linear, tabular callus characteristic of *D. graminoides*. Florally, *D. gomez-lauritoi* is closely related to *D. acrolephara*, from which is distinct by the plant habit, the much smaller flower (tepals <6 mm, vs. >7 mm) concolorous white (vs. boldly blotched with purple), and the distinctly thickened area at the base of the hypochile. When the type specimen of *D. gomez-lauritoi* was collected in 1982, the San José–Limón Highway was not yet under construction, and major habitat transformations may perhaps explain the difficulty in finding other plants in the same area, even with the help of the original collector.

14. *Dichaea gracillima* C. Schweinf., Bot. Mus. Leafl. 5(6): 98. 1938. TYPE: COSTA RICA. [Alajuela:] Piedades de San Ramón, “Bois, Alt. 1100 m. 26-X-1925,” A. M. Brenes (274) 1459 (Holotype: AMES 45278; Isotypes: CR 89411, NY [not seen]). Fig. 46.

*Plant* epiphytic, caespitose or branching near the base of the stems, to 30 cm long. *Roots* rather thick, basal and caulinar, to 1.2 mm in

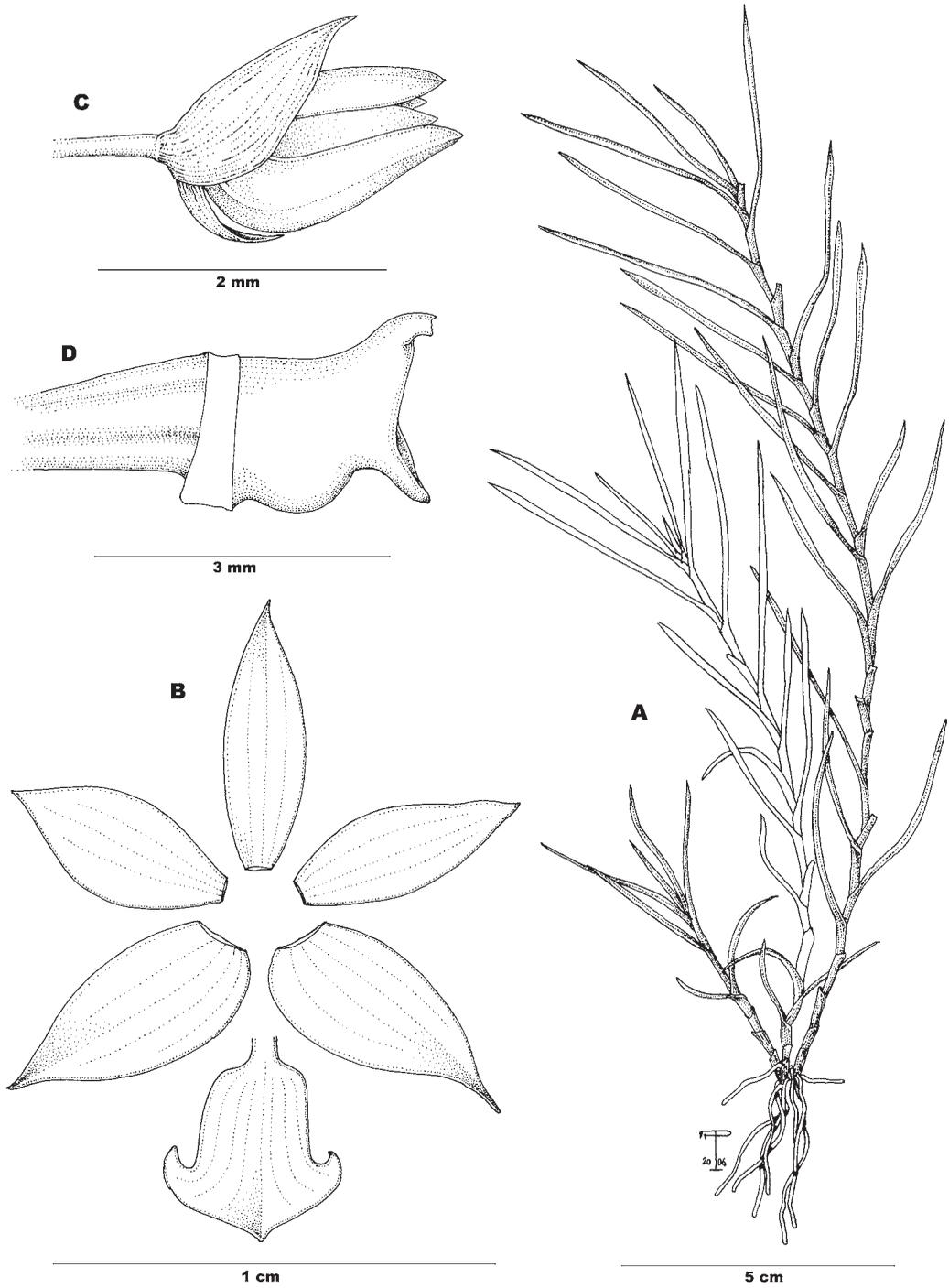


FIGURE 46. *Dichaeta gracillima* C. Schweinf. **A**, Habit; **B**, dissected perianth; **C**, floral bud, lateral view; **D**, column, lateral view. Drawn from *Brenes (274) 1459* (AMES).

diam. *Stems* slender, compressed, erect, becoming arcuate-pendent with age, 11–30 cm long, 0.1–0.2 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, widely spaced along stem, subspreading, subcoriaceous, dark green, 35–47 × 2 mm, narrowly linear, shortly acuminate, apiculate, basally strongly conduplicate; sheaths clasping, 13–18 × 5–6 mm. *Inflorescence* successive, 1-flowered, emerging below foliage, erect-spreading, 10–12 mm long, basally provided with two imbricating, tubular, clasping bracts, 2 mm long. *Floral bract* double, the outer bract infundibuliform, acute, 1.5 × 1.2 mm, the subopposite inner bract narrowly linear, 1.5 mm long. *Pedicellate ovary* subcylindric, glabrous, 3 mm long including the pedicel. *Flower* small, submembranaceous, no color recorded, apparently concolorous. *Dorsal sepal* erect, elliptic-lanceolate, strongly concave, subacuminate, abaxially carinate at apex, 5.0 × 2.2 mm. *Lateral sepals* obliquely ovate-lanceolate, asymmetrical, strongly concave, acuminate, dorsally carinate, 5.0 × 3.2 mm. *Petals* lanceolate-elliptic, acuminate, smaller than sepals, 4.2 × 2.1 mm. *Lip* shortly clawed, obovate-anchoriform, concave, 4.0 × 3.7 mm when spread, the hypochile subquadrate from a rounded base, 2.2 mm long, 2.2 mm wide apically, the epichile broadly triangular, abruptly acute, 1.5 × 4.0 mm, the lateral lobes triangular-lanceolate, acuminate, retrorse, 0.6 × 0.5 mm. *Column* short, stout, straight, apparently with a very short foot, ca. 2 mm long; the clinandrium entire; ligule triangular, shallowly rounded, glabrous, erect, 0.4 × 0.5 mm. *Pollinia* 4 in two superposed pairs of different size, complanate-subpyriform. *Fruit* not seen.

The above description was prepared from the holotype and an isotype, with information from the original protologue and Schweinfurth's drawings of the holotype.

**Distribution:** endemic to Costa Rica.

**Etymology:** from the Latin *gracillimum*, very slender, in reference to the slender stems and leaves of this distinctive species.

**Ecology:** a rare plant, found only once close to the continental divide in the Tilarán mountain range, at 1100 m elevation. Brenes's field notes were usually rather accurate, but in the case of *D. gracillima* he indicated the locality only as Piedades de San Ramón. Close to San Ramón, there existed at that time (and still exist) two localities named Piedades, Piedades

Norte and Piedades Sur, the first lying on the Caribbean watershed of the Cordillera de Tilarán, and the second on the upper Pacific slopes. The climate of the two localities is rather different, Piedades Norte being influenced by the moist winds from the Caribbean, and Piedades Sur being affected by the driest influence of the Pacific region. Many attempts were made to find plants of the elusive *D. gracillima* on both the Piedades, as well as along La Palma ridge that connect them, but they were unproductive. Flowering occurs at least in October.

*Dichaea gracillima* is vegetatively unmistakable, with its erect, slender, compressed stems and the widely spaced subcoriaceous, narrowly linear leaves almost reaching 5 cm in length. The flowers are among the smallest in the genus, with the tepals 4 to 5 mm long, and the subquadrate hypochile from a rounded base is diagnostic.

15. *Dichaea hystricina* Rchb. f., *Flora* 48: 279. 1865. TYPE: CUBA [Orientali:] prope villam Monte Verdi dicta, Aug. 13, 1859, C. Wright 1478 (Holotype: W-Reichenbach Orchid Herbarium Nr. 17196; Isotype: AMES 61211). Fig. 47, Map 5.

Synonyms: *Dichaea ciliolata* Rolfe, *Bull. Misc. Inform. Kew* 1917: 83. 1917. TYPE: COSTA RICA. [Cartago: Orosi.] near Cachí, C. H. Lankester 12 (Holotype: K, photograph).

*Dichaea selaginella* Schltr., *Repert. Sp. Nov. Regni Veg. Beih.* 7: 202. 1920. TYPE: COLOMBIA. Cauca, M. Madero s.n. (Holotype: B. destroyed; Lectotype, selected here: drawing of the holotype published by Mansfeld, 1931).

*Dichaea lycopodioides* Rchb. f. ex Kraenzl., *Engl. Pflanzenr. Orchid.-Monandr.-Pseudomonopod.* 35. 1923, *nom. nud.*

*Plant* epiphytic, caespitose, to 18 cm long. *Roots* produced all along the stem (the adventitious roots not exposed), glabrous, flexuous, slender, about 0.3 mm in diam. *Stems* flattened, suberect to pendent, simple to few-branched, 6–18 cm long, 0.2–0.3 cm wide across conduplicate sheaths. *Leaves* usually closely spaced along stem, spreading, sometimes not axially twisted (so the plant without a distinct “front”), medium green, the new leaves distinctly paler

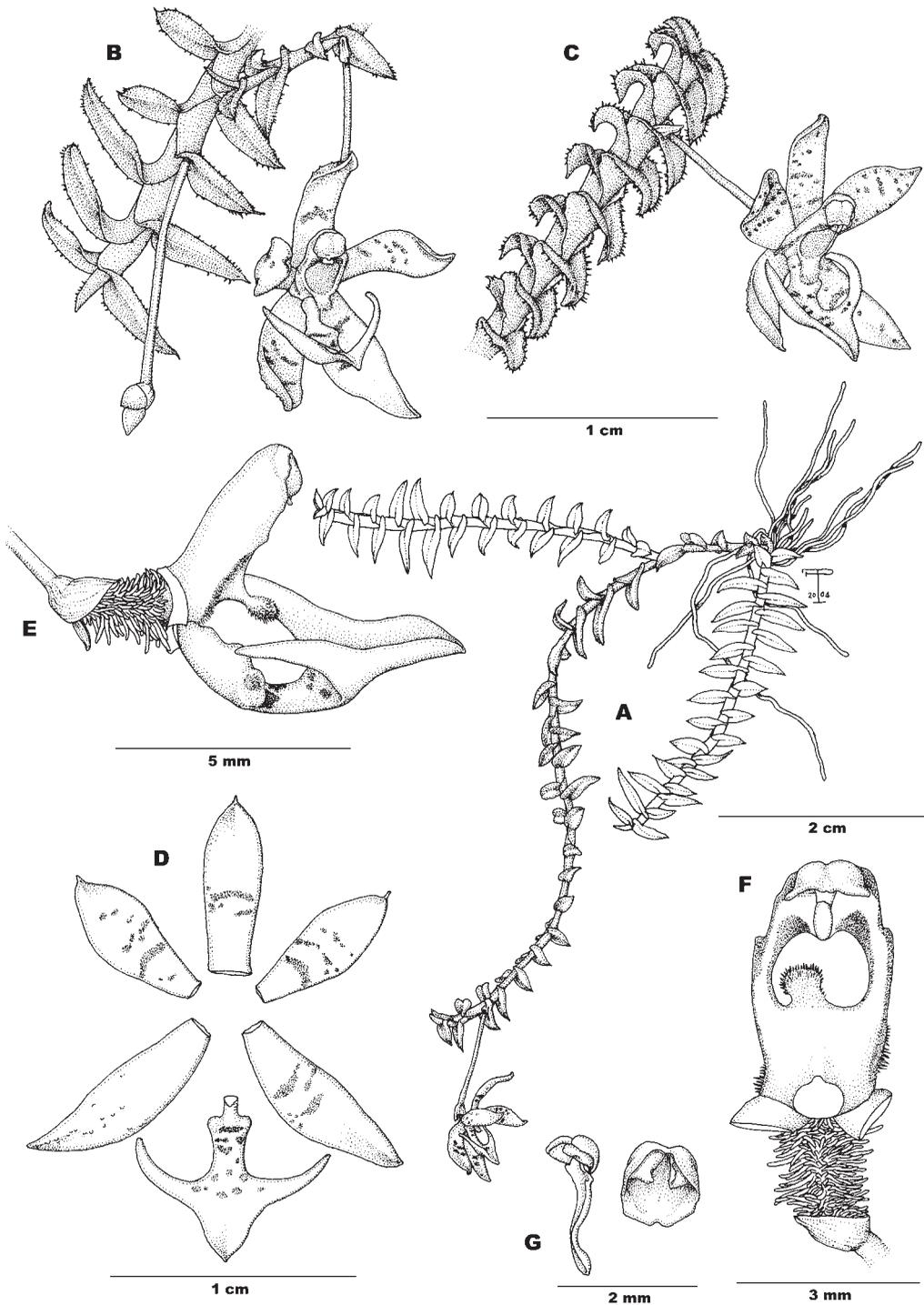
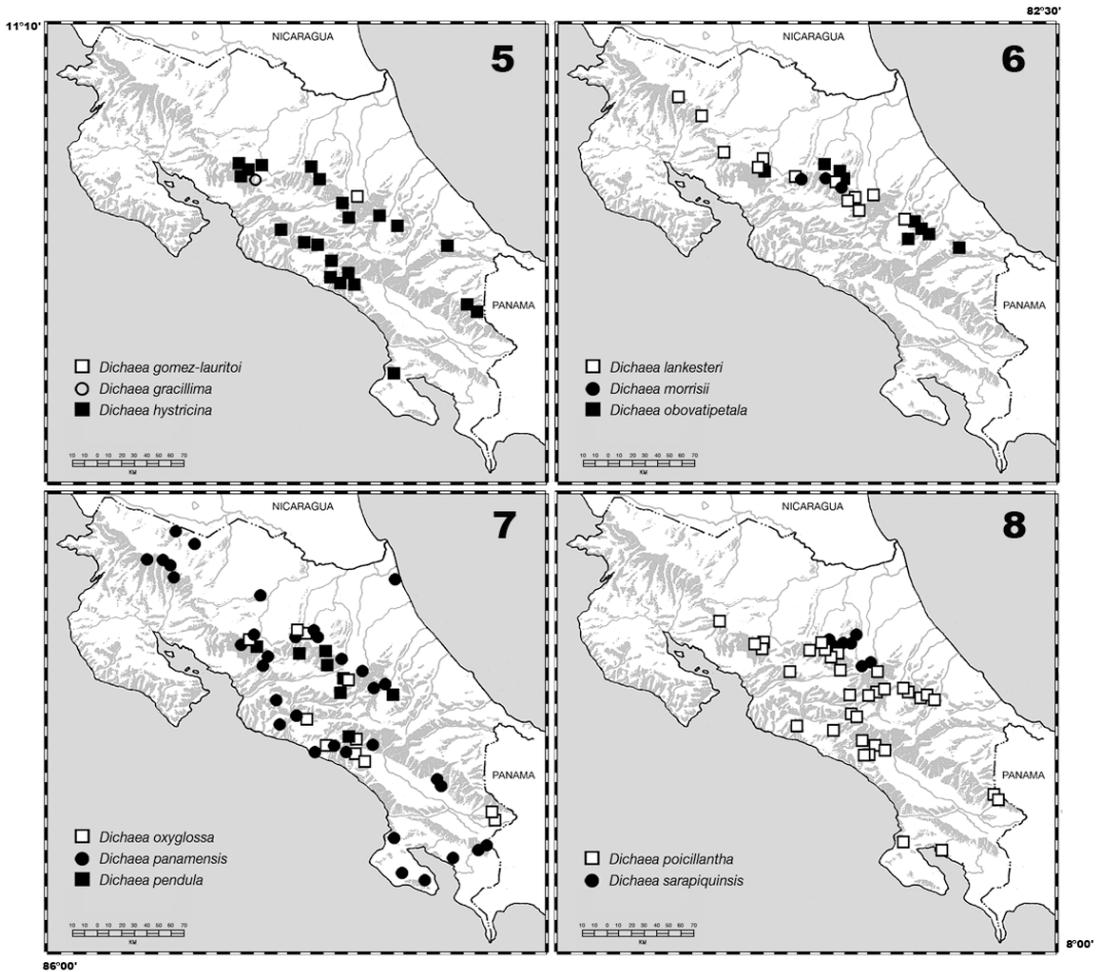


FIGURE 47. *Dichaea hystericina* Rchb.f. A, Habit; B–C, apex of stem and flower; D, dissected perianth; E, column and lip, lateral view; F, column, ventral view; G, pollinarium and anther cap. Drawn from: A, B, D–G, *Pupulin et al.* 1618 (JBL-Spirit); C, *Pupulin et al.* 3925 (JBL-Spirit).



MAPS 5–8. Distribution of *Dichaea* in Costa Rica. 5, *D. gomez-laurittoi*, *D. gracillima*, and *D. hystricina*; 6, *D. lankesteri*, *D. morrisii*, and *D. obovatipetala*; 7, *D. oxyglossa*, *D. panamensis*, and *D. pendula*; 8, *D. poicillantha* and *D. sarapiquinsis*.

and bright green, subcoriaceous, narrowly elliptic to lanceolate-elliptic, acute, apiculate-mucronate, 2–15 × 1.0–4.5 mm, often varying in length along the stem, the margins evenly ciliate; sheaths slightly loose, to 5 × 5 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, the peduncle straight, to 13 mm long, provided at the base with a triangular, acute bract, about 1.4 mm long. *Floral bract* double, the outer bract suborbicular-funneliform, acute, shorter than pedicellate ovary, 1.4 × 2.0 mm, the inner bractlet narrowly lanceolate, 1.3 mm long. *Pedicellate ovary* cylindrical-subclavate, densely echinate, ca. 2.3 mm long including the pedicel. *Flower* spreading, the sepals and petals greenish cream flecked or

finely spotted with purple, the lip white, variously suffused with pink (mostly toward the base and the lateral lobes), sparsely dotted with purple, the column greenish white, marked purple along the ribs of the stigma and the clinandrium, the ligule purple, the anther cap white; no fragrance detected. *Dorsal sepal* oblanceolate, acute, apiculate, 5.4–7.2 × 2.0–2.5 mm, abaxially provided with sparse, low warts. *Lateral sepals* obliquely elliptic to lanceolate-elliptic, asymmetrical, slightly falcate, acute to subacuminate, apiculate, concave, 7.3–8.7 × 2.3–2.8 mm, adaxially sparsely warty. *Petals* oblanceolate, acute, shortly acuminate, often slightly recurved, 6.2–6.9 × 2.5–3.0 mm. *Lip* 3-lobed, from a fleshy claw, 6–7 × 8–9 mm when

spread, the hypochile subrectangular, provided at the base with two lateral knobs, 2.5 mm wide apically, the epichile sagittate, acute, the lateral lobes narrowly triangular-filiform, acute, retrorse, 3.5 × 1.1 mm. *Column* suberect, to 7.5 mm long, with an indistinct foot about 0.5 mm long, provided with small, rectangular, ciliate wings to the 2/3 of column length; the clinandrium shallow; ligule elliptic from a linear base, apically thickened-globose, rounded, papillose, 2.7 × 0.8 mm. *Anther cap* widely ovate-subquadrate, flattened, 2-celled. *Pollinia* 4 in two superposed pairs of slightly different size, on a narrowly obtriangular-ligulate, subtruncate stipe with lightly inrolled margins; viscidium elliptic. *Fruit* an elliptic, densely muricate capsule, ca. 6 × 3 mm.

**Distribution:** from Mexico to Venezuela and Ecuador, and the West Indies (Cuba, Hispaniola [Dominican Republic], Guadeloupe, Puerto Rico, Trinidad).

**Additional material examined:** COSTA RICA. Alajuela: Alajuela, Reserva Forestal adjacent to Parque Nac. Braulio Carrillo, SE of Cariblanco, on NW slope of Río Sarapiquí canyon, 10°15'50"N, 84°10'20"W, 780 m, 19 Nov. 1990, *S. Ingram 739 & K. Ferrell* (INB); [San Ramón,] vieux troncs des bois á San Pedro de San Ramón, 950 m, VII-1921, *A. M. Brenes (21) 1721* (CR 33831); [San Ramón,] San Isidro, Río Grande, 900 m, 16-V-1923, *A. M. Brenes (267) 562* Herb. Brenes (CR 18447, sterile); [San Ramón,] San Pedro, 950 m, VI-1921, *A. M. Brenes (31) 1730* Herb. Brenes (CR 18459, sterile); [San Ramón,] La Palma (Piedades Sur), 1100 m, 22-X-1929, *A. M. Brenes (75) 11396* Herb. Brenes (CR 18429, fruiting); San Ramón, Los Ángeles, deviation point to Villa Blanca, 10°09'11"N, 84°28'28"W, 1120 m, 27.2.2003, *F. Pupulin 4320, D. Bogarín, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); Piedades Norte-Zapotal, camino entre el Cerro Azahar hacia Los Bajos y San Antonio de Zapotal, Finca de Don Guillermo, 10°10'07"N, 84°35'50"W, 1423 m, 24.3.2005, *D. Bogarín 1464, E. Salas, F. Pupulin & A. C. Rodríguez* (JBL-Spirit); Piedades, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'51.9"N, 84°35'36.5"W, 1410 m, Caribbean watershed of the Continental Divide, premontane cloud forest, 24 March

2005, flowered in cultivation at Jardín Botánico Lankester, 4 July 2006, *F. Pupulin 5594, E. Salas-Pupulin, D. Bogarín & A. C. Rodríguez* (CR); Santiago, mountains toward San Rafael, epiphytic in secondary vegetation and scattered trees in pastures 10°01'N, 84°30'W, 1300 m, 1.2.2004, *F. Pupulin, 5095 & E. Salas* (JBL-Spirit). Cartago: Jiménez, Taus, 10 Dec. 1984, *R. L. Dressler 164 & Biología 350* (USJ); Paraíso, Cachí, camino de Loaiza hacia el Alto Araya, 9°49'23"N, 83°49'58"W, 1000–1300 m, 12.7.2003, *D. Bogarín 303, D. Kikut & A. Prendas* (JBL-Spirit); Turrialba, Moravia de Chirripó, 9°50'18"N, 83°26'45"W, 1150–1250 m, 13.6.2002, *F. Pupulin 3925, M. Bonilla, R. Gómez, H. Montealegre & W. Schug* (JBL-Spirit); Turrialba, Tuís, Cien Manzanas, 9°51'25"N, 83°33'47"W, ca. 950 m, along a minor tributary of Río Pacuare, premontane wet forest, secondary vegetation and remnants of primary, 26 May 2003, flowered in cultivation at Jardín Botánico Lankester, 29 July 2006, *F. Pupulin 4804, R. L. Dressler, K. Dressler, J. Aguilar, G. Gerlach, P. Kindlmann, H. León-Paéz, S. Pugh-Jones & E. Serrano* (CR). Limón: Talamanca, Alto Urén, quebrada antes de la casa de Don Gabriel, 09°27'00"N, 82°59'30"W, 700–900 m, 24 Sept. 1994, *G. Gallardo 326 & E. Lépiz* (INB). Puntarenas: Aguirre, road between Quepos and San Marcos de Tarrazú, 9°33'01"N, 84°05'01"W, 750 m, wet premontane forest, secondary forest, at the edge of pasture transition to primary forest, 8 June 1999, flowered in cultivation at Gaia Botanical Garden, 23 Nov. 2002, *F. Pupulin 1618 & D. Castelfranco* (JBL-Spirit); Coto Brus, P. I. La Amistad, Pittier, Santamaría, camino a Hamaca, 9°00'25"N, 82°57'05"W, 1400 m, 15 June 1995, *A. Azofeifa 154* (INB); Z.P. las Tablas, Cuenca Térraba-Sierpe, Est. Biológica Las Alturas, juntas de Río Bella Vista y Cotón, 8°56'45"N, 82°51'29"W, 1320 m, 6 Sept. 1999, *E. Alfaro 2484* (INB) Osa, Rancho Quemado, Siepre, siguiendo el nuevo camino a Drake, 8°41'20"N, 83°35'40"W, 300 m, 17 June 1990, *G. Herrera 4195* (INB). San José: Acosta, Fila Bustamante, Fila San Jerónimo, camino al bajo del río Cabeceras, Quebrada San Jerónimo, 09°42'57"N, 84°17'02"W, 900–1000 m, 24 June 1995, *J. F. Morales 4488* (CR; INB); Estación Carrillo de 700 a 450 m de

la Fila al Cañón del Río Sucio, 12–11–83, *J. A. Chacón & G. Herrera 1640* (CR, fruiting); Braulio Carrillo Park, Carrillo 500–700 m, 16 Sept. 1984, *J. P. Folsom 11011* (CR); Dota, Z.P. Cerro Nara, Faja Costeña del Valle de Parrita, Cerro Chingo, 09°29'11"N, 84°02'02"W, 500 m, 18 July 1995, *J. F. Morales 4554 & J. González* (INB). Pérez Zeledón, Río Nuevo, Fila Jilguero, sendero a la derecha de Cuatro Cruces, 9°28'28"N, 83°51'49"W, 1700 m, 5 Nov. 2002, *A. Quesada 1059 & R. Chacón* (CR, sterile); Pérez Zeledón, Miraflores, road to Santa Cruz, 1350 m, 2.12.2001, *F. Pupulin 3466, D. Castelfranco & J. Cambroner* (JBL-Spirit); San Ramón Norte, trail to the summit of Cerro Pelón, 1420–1640 m, 3.5.2002, *F. Pupulin 2362, M. L. Spadari, J. Cambroner, V. Juárez-Pérez & K. Granado* (JBL-Spirit); road from San Isidro to Dominical, deviation to Pacuarillo, Bijagual, 9°17'35.5"N, 83°45'24.0"W, 1000 m, premontane wet forest, 23 October 2005, flowered in cultivation at Jardín Botánico Lankester, 25.4.2006, *F. Pupulin 5793, D. Bogarín, R. L. Dressler, R. Gómez, A. Karremans, A. Rambelli & S. Rambelli* (CR); Puriscal, Cerros de Puriscal, Cerros de Turrubares, Llano Caite, sendero a Carmona, 09°47'21"N, 84°27'42"W, 1250–1500 m, 5 Jan. 1996, *J. F. Morales 5049, B. Hammel & Q. Jiménez* (CR; INB); Tarrazú, cuenca del Naranjo y Paquita, Fila Chonetera, cabeceras Quebrada Azul, 3 km SW de San Joaquín, 9°34'25"N, 84°00'50"W, 900–1100 m, 25 Sept. 1998, *J. F. Morales 6651* (INB); Tarrazú, Nápoles, 09°35'40"N, 84°04'05"W, 1500 m, 5 Aug. 2001, *M. Blanco 1978, J. J. Morales, J. González, L. Cortés, P. Labiak & D. Tuberquia* (USJ). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, 22 June 2006, accession No. *JBL-11987* (CR).

**Etymology:** from the Latin *hystricinus*, porcupine-like, in reference to the “spiny” fruits of the species.

**Ecology:** a rather frequent, widespread and variable plant, *D. hystricina* is found as a shade-epiphyte on mossy trunks and rather large branches in the understory of premontane and submontane moist to wet forests, at elevations ranging from 400 to 1600 m. In Costa Rica, populations of *D. hystricina* are found all along the Caribbean slopes and close to the

continental divide on the Pacific watershed of the Cordillera de Tilarán, and on both the watersheds of the Central Volcanic and Talamanca mountain ranges to the border with Panama. Flowering occurs mostly from June to November, but sporadic flowering has been recorded year-round.

*Dichaea hystricina* was described by Reichenbach *filius* in 1865 based on a collection by C. Wright from Cuba. The linear-ligulate leaves provided with hairs along the margins, the muricate ovary, and the clawed lip, with small lobules at the base and expanded into a sagittate lamina, mentioned in the original protologue (Reichenbach, 1865) are diagnostic of the species. The type specimen, together with Reichenbach's sketches of the plant habit and details of the flower, is kept at the herbarium of the Natural History Museum in Vienna (*Rchb. Orch. 17196*, W), and an isotype also exists at the Oakes Ames Orchid Herbarium of Harvard University (AMES 61211). The presence of trichomes along the margins of the leaves is not uncommon in members of the genus *Dichaea*, but these are usually restricted to the apical portion of the leaf. The long hairs that cover the entire leaf margins, as well as its small habit, are useful characters for recognizing plants of *D. hystricina* in the field even when they are not in flower. Specimens of typical *D. hystricina* have freely branching, suberect to pendent stems to 15 cm long, and narrowly ovate leaves up to 1 cm long, mucronate at apex and hispid-ciliate on the margins (on the holotype specimen, Reichenbach had annotated for this species the intended name of *Dichaea ciliata*). In 1905, R. A. Rolfe described *D. ciliolata* on the basis of a collection by C. H. Lankester near Cachí, on the eastern side of the Costa Rican Central Valley. The main character he used to distinguish the new species from *D. hystricina* was the vegetative habit, characterized by erect, up-curving, rarely branching stems, with short leaves less than 5 mm long. Treating *D. ciliolata* for his monograph, Kränzlin stressed the distinctiveness of the plant habit, but he also distinguished it from *D. hystricina* by the smaller size of the flower and the presence of a thickening on the column foot (Kränzlin, 1923), two characters that cannot be reliably observed in fresh flowers. Around 1880

Reichenbach received at Hamburg some analogous plants, collected in Costa Rica by A. R. Endrés, and he annotated them as *D. lycopodioides*, an intended name he never published (*Rchb. Orch.* 14756, 14768, and 14769, W). Like Lankester's *Dichaea* "*ciliolata*," some of the plants collected by Endrés have long (to 25 cm), up-curved, mostly unbranched stems, with very short internodes and leaves less than 5 mm long. When preparing his revision of the genus *Dichaea* for Engler's *Pflanzenreich*, Kränzlin studied the plants collected by Endrés, and in the paragraph of observations about *D. ciliolata* for his 1923 treatment he validated the name suggested by Reichenbach. Both of the sheaths in Reichenbach's Herbarium in Vienna, annotated by Kränzlin as the type of *D. lycopodioides*, correspond to Endrés's collections from Costa Rica. However, only plate No. 14769, selected



FIGURE 48. Lectotype of *Dichaea lycopodioides* Rchb. f. ex Kraenzl., Endrés s.n. (*Rchb. Orch.* 14769, W). Reproduced with the permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

here as the lectotype, bears the indication "*Dichaea lycopodioides*" in Reichenbach's handwriting (Fig. 48). Meanwhile, in 1920, Rudolf Schlechter described *D. selaginella* from the department of Cauca in Colombia. The type specimen was destroyed by fire in 1943, but in 1929 R. Mansfeld published the tracing of the sketch prepared by Schlechter from a flower of the holotype (Fig. 49), and the floral characters of *D. selaginella* are indistinguishable from those of *D. hystricina* (Mansfeld, 1929). Also the vegetative features cited by Schlechter in the protologue, that is, the stems 1.5 mm in diam. and the oblong-lanceolate leaves 5–7 mm long, ciliate on the margins, agree with the habit of *D. hystricina*. A number of different specimens annotated by Kränzlin as type material of *D. selaginella* at W, all of them collected in Costa Rica by Endrés, have nothing to do with Schlechter's species but represent a name never published by Kränzlin to be reduced under *D. tuerckheimii*, the smallest of all *Dichaea* species.

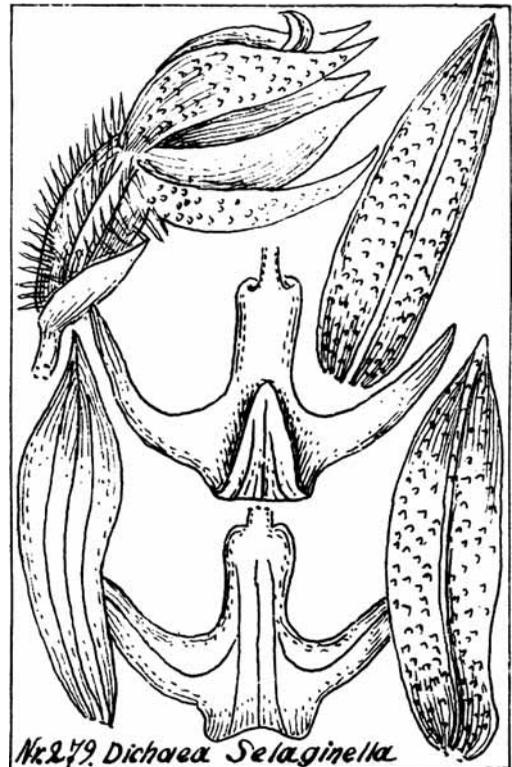


FIGURE 49. Copy of Schlechter's sketch of *Dichaea selaginella* Schltr., reproduced by Mansfeld (1931).

Although a single type of "ciliate" *Dichaea* is usually found at any specific locality, sometimes we observed both the "morphs" growing sympatrically, a point already noted by Dodson in Ecuador (in Mora-Retana and Atwood, 1993). As it is perhaps obvious to expect from a species with such a wide distribution range, *D. hystricina* shows in Costa Rica a great variation in the morphology of the plants, including length of the stems and the internodes, degree of branching, and leaf size (Pupulin, 2005a). However, no substantial difference can be observed among the flowers produced by plants of the *hystricina* type and the *ciliolata* type, and no correlation seems to exist between the shape of the plants and the morphology of flowers, which is largely uniform. Pupulin (2005a) noted that the plants are able to shift from one morph to the other, also along a single stem, producing longer internodes and progressively longer and broader leaves.

16. *Dichaea lankesteri* Ames, Sched. Orch. 4: 56. 1923. TYPE: COSTA RICA. [San José:] Cascajal, C. H. Lankester K353 (Holotype: K [Photo: AMES ex K]; drawings of the Holotype: AMES 24096). Fig. 50, Map 6.

*Plant* epiphytic, caespitose, to 40 cm long. *Roots* filiform, exposed at the base, hidden by the leaf sheaths along the stem, ca. 0.5 mm in diam. *Stems* compressed, suberect, becoming horizontal to pendent with age, frequently branching, 10–40 cm long, 0.35–0.50 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths and ultimately deciduous, densely spaced along stem, spreading-decurved, thin-textured, membranaceous, medium grass-green, adaxially somewhat shiny, 25–40(45) × 3.5–5.0(6.0) mm, linear-lanceolate, acute, the apical margins microscopically pectinate-ciliate; sheaths clasping, to 8.0 × 3.7 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, patent to suberect, to 17 mm long, provided with a basal, cylindrical, elongate bract 5 mm long. *Floral bract* double, the outer bract broadly ovate, cucullate-concave, 6 × 5 mm, the inner bract narrowly linear-lanceolate, acute, 5 mm long. *Pedicel* cylindrical, ca. 1 mm long. *Ovary* 1.0–1.3 mm long, densely hispid-muricate. *Flower* spreading, the sepals and petals glabrous, cream white, sometimes slightly

flushed with pale green toward the apex of sepals, the column white, with a narrow rose stain along the proximal margin of the stigma; flowers strongly scented, the scent vanilla-like. *Dorsal sepal* erect, slightly concave, triangular-lanceolate, acuminate, 8.5–10.0 × 2.5–3.5 mm. *Lateral sepals* obliquely triangular-lanceolate, concave, acuminate, 8.5–10.0 × 3.0–4.2 mm. *Petals* narrowly lanceolate, acuminate, concave toward the base, 7–8 × 2.0–2.3 mm. *Lip* 3-lobed, anchoriform, subsessile, 6–8 × 5–7 mm when spread, the hypochile broadly obtuse, 2 mm long, 3.5 mm wide apically, the epichile triangular, acute, 5–6 × 4.5–5.5 mm, the lateral lobes narrowly triangular-subfalcate, acute, retrorse, 2.0 × 1.5 mm. *Column* suberect, 2.3 mm long, with a short foot, provided at the base with small, semi-elliptic, rounded, glabrous wings; the clinandrium shallow, entire; ligule transversely broadly triangular, obtuse to rounded, glabrous, the apex sometimes slightly reflexed, 0.7 × 1.5 mm. *Anther cap* cucullate-rheniform, compressed, 2-celled. *Pollinia* 4 in two superposed, subequal pairs, on a broadly obtriangular-oblong, truncate stipe; viscidium elliptic, hyaline. *Fruit* an elliptic, densely muricate capsule.

**Distribution:** Costa Rica and western Panama.

**Additional material examined:** COSTA RICA. Alajuela. Bajos del Toro, northern slopes of Volcán Poas, 1450 m, 5.3.2001, *F. Pupulin 3030* (USJ, JBL-Spirit); [San Ramón.] entre Los Ángeles y Piedades Norte, 1050–1075 m, 30-I-1925, A. M. Brenes (527) 1386 Herb. Brenes (CR 18461); along road from San Ramón northward through Balsa, ca. 11 km N of bridge over Quebrada Volio and ca. 2.3 km N of bridge over (apparently) Río Balsa, at culvert of a small stream, ca. 10°11'N, 84°30'W, 10 Sept. 1979, *W. D. Stevens 14248* (SEL); Piedades, Piedades Norte, road to Bajo de La Paz, km 2.6, along the Río San Pedro, 10°08'59.9"N, 84°33'53.3"W, 1307 m, premontane wet forest, epiphytic along the shores of the river, 30 January 2005, flowered in cultivation at Jardín Botánico Lankester, 6 June 2006, *F. Pupulin 5492*, *D. Bogarín*, *M. Salas & P. Seaton* (CR); Piedades, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'51.9"N, 84°35'36.5"W, 1410 m, Caribbean watershed of the Continental

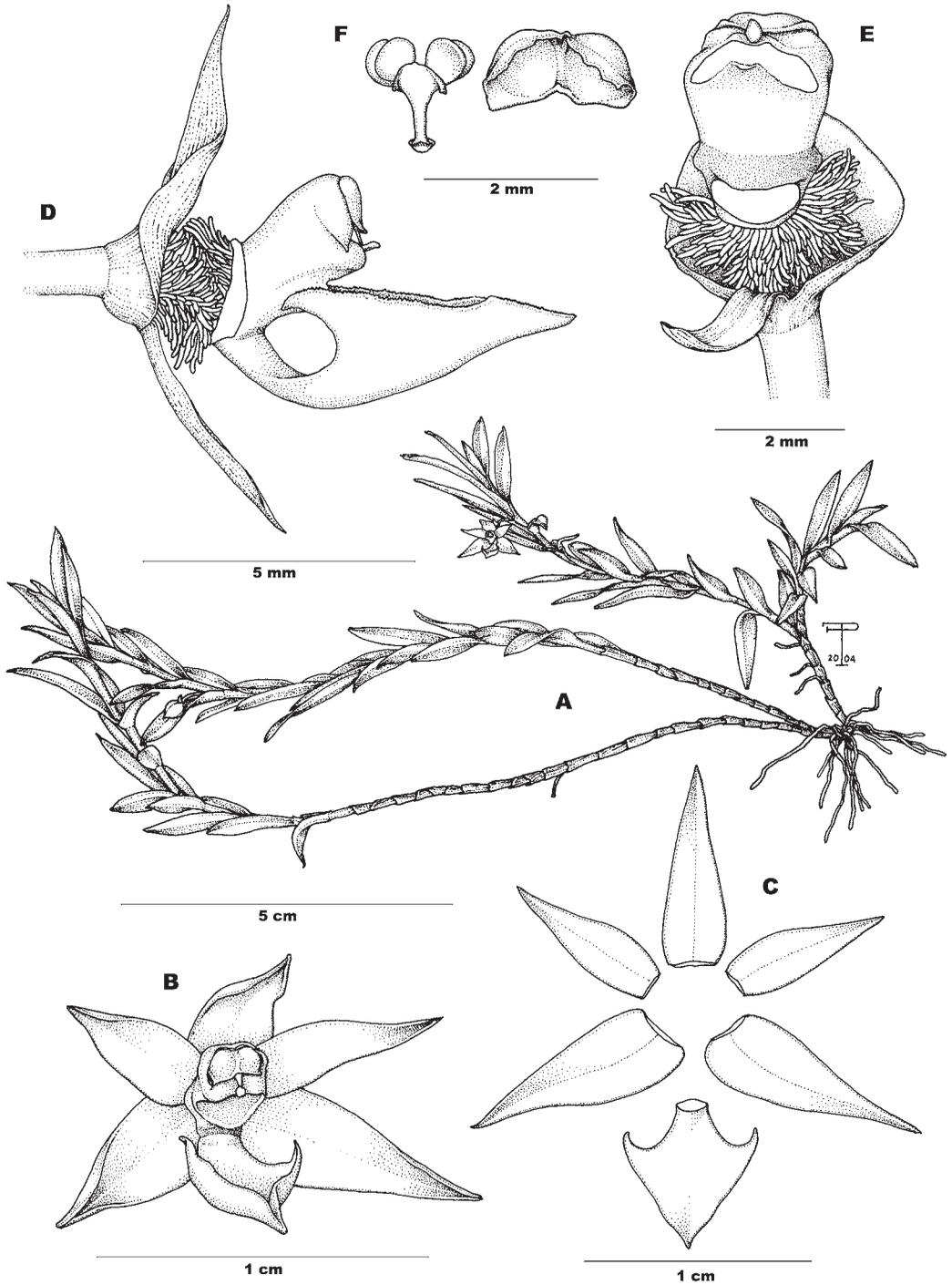


FIGURE 50. *Dichaea lankesteri* Ames. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from *Pupulin et al. 3030* (JBL-Spirit).

- Divide, premontane cloud forest, 24 March 2005, *F. Pupulin 5579*, *E. Salas-Pupulin*, *D. Bogarín* & *A. C. Rodríguez* (CR, JBL-Spirit); Piedades Norte-Zapotal, camino entre el Cerro Azahar hacia Los Bajos y San Antonio de Zapotal, Finca de Don Guillermo, 10°10'07.9"N, 84°35'50.3"W, 1423, bosque pluvial premontano, epífitas en bosque secundario, 24 Marzo 2005, floreció en cultivo en el Jardín Botánico Lankester el 19 de Mayo 2006, *D. Bogarín 1469*, *F. Pupulin*, *A. C. Rodríguez* & *E. Salas* (CR); Piedades Sur, Potrerillos, road to Socorro de Piedades Sur, slopes of Cerro La Palma, 10°08'09.9"N, 84°34'47.5"W—10°08'25.0" through N, 84°34'45.9"W, 1300–1450 m, 12 April 2006, premontane wet forest, *F. Pupulin 6023*, *R. L. Dressler* & *A. Carbajal* (CR); 15 km NNW of San Ramón by road, 2.5 km of Balsa on road to San Lorezo, 10°22'N 84°30'W, 1050–1100 m, 25 Apr. 1983, *R. Liesner 14863* & *E. Judziwicz* (INB); Upala, Bijagua, Zapote, Finca La Escondida, ca. 5 km de la entrada de la finca hacia la ladera noreste del Volcán Miravalles, 10°46'00.8"N, 85°05'35.7"W, 900–1000 m, bosque pluvial premontano, epífitas en bosque secundario, 3 Feb. 2006, floreció en cultivo en el Jardín Botánico Lankester, 14 Aug. 2006, *D. Bogarín 2486*, *J. Barrantes*, *R. L. Dressler*, *R. Gómez* & *A. Rojas* (CR). Cartago: Jiménez, Valle del Reventazón, Tausito y La Selva, 09°47'02"N, 83°46'01"W, 1300 m, 22 June 1995, *J.F. Morales 4954* (INB); Paraíso, Orosí Tapantí, Parque Nacional Tapantí, Sendero Árboles Caídos, 1400–1600 m, 18.7.2003, *D. Bogarín 346*, *J. Andrade*, *A. Granados*, *A. Jiménez* & *F. Villanea* (USJ, JBL-Spirit); [Jiménez], vicinity of Pejivalle, February 7–8, 1926, *P. C. Standley* & *J. Valerio 47138* (AMES); El Muñeco, on the Río Navarro, March 6–7, 1926, *P. C. Standley* & *Rubén Torres R. 51395* (AMES). Guanacaste: Tilarán, Tierras Morenas, desviación a la izquierda después del Río Cabuyo, entrada al Proyecto Geotérmico Tenorio y Cerro Jilguero, ca. 7 km al noreste de Tierras Morenas, ladera sureste del Volcán Tenorio, 10°36'55.7"N, 85°00'43.1"W, 900–1100 m, bosque pluvial premontano, epífitas a orillas del camino y bosque secundario, 2 Febrero 2006, floreció en cultivo en el Jardín Botánico Lankester el 22 de Junio 2006, *D. Bogarín 2422*, *R. L. Dressler*, *R. Gómez* & *A. Rojas* (CR). Heredia: San Rafael, Ángeles, 2.5 km norte del Monte de La Cruz, camino entre el Cerro Chompipe y Alto del Roble hacia Río Las Vueltas, 1990 m, 10°5'16"N, 84°04'15"W, bosque pluvial premontano, epífitas en ramas caídas en bosque secundario a orillas del camino, 7 Julio 2004, floreció en cultivo en el Jardín Botánico Lankester el 4 de Abril 2006, *D. Bogarín 864* & *A. Prendas* (CR, JBL-Spirit); same locality, *D. Bogarín 863* & *A. Prendas* (JBL-Spirit). Limón: Siquirres, Guayacán, Amphibian Research Center, márgenes del Río Siquirres, ca. 500 m, epífitas en troncos caídos, 13 Noviembre 2005, floreció en cultivo en el Jardín Botánico Lankester el 19 de Mayo 2006, *G. Rojas 95*, *R. Blanco* & *B. Kubicki* (CR). Puntarenas: Monteverde Cloud Forest Reserve, Pacific slope to continental divide, 5 Aug. 1988, *J. T. Atwood 88–7* & *W. Haber* (SEL); Monteverde Reserve; 2 km SW Station, 10°18'N, 84°48'W, 20 Apr. 1993, *S. Ingram 1846* & *K. Ferrell-Ingram* (SEL); Monteverde Cloud Forest Reserve along Sendero Valle, 18 June 1989, *J. T. Atwood 89–202* (SEL); Monteverde Cloud Forest Reserve on Sendero Brillante, Elfin forest, 10°17'N, 84°87'W, 8 Dec. 1989, *J. T. Atwood 4092* & *W. Morris* (AMES, SEL); Santa Elena, Reserva Biológica Bosque Nuboso Monteverde, the Triangle, S. Wilford Guindon trail, ca. 1600 m, 29 Apr. 2003, *F. Pupulin 4706*, *G. Barboza*, *M. Powell* & *V. Savolainen* (USJ). Puntarenas on border with Alajuela: Monteverde Cloud Forest Reserve, 13 June 1989, *J. T. Atwood 89–182* (SEL!, USJ!); Santa Elena, road to the Reserva Biológica Bosque Nuboso Monteverde, 1530 m, 29.4.2003, *F. Pupulin 4704* & *G. Barboza* (JBL-Spirit). San José: La Hondura, March 2–4, 1924, *P. C. Standley 33078* (AMES); *P. C. Standley 36182* (AMES); *P. C. Standley 36329* (AMES); Vásquez de Coronado, Parque Nac. Braulio Carrillo, Zurquí Station, about 0.5 km SE of Estación de Peaje, at Park border, 10°03'10"N, 84°00'20"W, epiphytic on tree trunk at pasture secondary forest edge, 26 Oct. 1990, *S. Ingram 630* & *K. Ferrell* (INB, SEL); Parque Nacional Braulio Carrillo, Zurquí Station, along Sendero Natural, 10°03'30"N, 84°00'40"W, 11 Dec. 1990, *S. Ingram* & *K. Ferrell 780* (AMES; INB); Braulio Carrillo Park, near Administration & tunnel, 1400–1550 m, 18 Sept. 1984, *J. B. Folsom 11028B* (CR, sterile); La Palma, March 17, 1924, *P. C. Standley 38324* (AMES).

**Eponymy:** named in honor of Charles Herbert Lankester, British naturalist who lived in Costa Rica and collected the type specimen.

**Ecology:** a relatively frequent epiphyte on shaded and mossy branches of the understory in very wet premontane forests on the Caribbean slopes and close to the continental divide along the Guanacaste, Tilarán, Central Volcanic, and northern Talamanca mountain ranges, at 1000–1800 m elevation. Flowering mostly occurs at the beginning of the rainy season, from April to July.

Among *Dichaea* species of the sect. *Pseudodichaea*, *D. lankesteri* is easily recognized by the horizontal to arching-pendent mature stems, the grass-green foliage, somewhat shiny on the upper surface, and the white to creamish white, immaculate, strongly fragrant flowers. It is closely related to *D. amparoana*, from which it can be distinguished by the suberect-arching (vs. erect) habit, the white flowers (vs. pale rose, spotted with pale purple), the stouter lateral lobes of the lip, and the shorter infrastigmatic ligule.

17. *Dichaea morrisii* Fawc. & Rendle, J. Bot. 48: 107. 1910; emend. in W. Fawcett & A.B. Rendle, Flora of Jamaica 1: 139, plate 30, Fig. 13–16. 1910. TYPE: JAMAICA. Mt. Moses, 3500 ft., *D. Morris* J.P. 2269 (Syntype: BM; Isosyntypes: NJ, K, W); Hardware Gap, *G. E. Nichols* s.n. (Syntype: BM, Isosyntypes: NJ, Yale). Fig. 51, Map 6.

*Plant* epiphytic, caespitose, to 60 cm long. *Roots* filiform, 0.7–1.0 mm in diam., exposed at the base of the stem, the caulinar roots completely hidden by the leaf sheaths. *Stems* compressed, simple, suberect, becoming pendent with age, 15–60 cm long, 0.4–0.7 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, closely spaced along stem, spreading, membranaceous, oblong-ligulate, rounded to subacute, abaxially minutely apiculate, medium green, 3.3–6.8 × 0.8–1.5 cm; sheaths loose, strongly complanate, ancipitous, 21–28 × 17–21 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent, 21–25 mm long, provided with a basal, cylindrical, clasping, scarious bract, to 7 mm long. *Floral bract* double, the outer bract broadly triangular-ovate, acuminate, 11–13 × 9–11 mm, the inner bract lanceolate, acuminate, 15 × 5 mm. *Pedicel* cylindrical, 2.5 mm long. *Ovary* 3.2–3.5 mm long, densely muricate. *Flower*

ringent, the sepals and petals green, flushed white toward the base, basally striped with purple; the lip white, the hypochile boldly blotched with purple, the epichile solid violet; column white, flecked with purple on basal wings; no odor detected in Costa Rican material. *Dorsal sepal* broadly ovate, acuminate, fleshy, concave, dorsally subcarinate, the margins ciliate, 12–13 × 7–8 mm. *Lateral sepals* obliquely broadly ovate, concave, acute, dorsally carinate, the margins hispid-ciliate, 12–13 × 8.5–9.0 mm. *Petals* ovate-lanceolate, abruptly subacuminate, the margins hispid-ciliate, 10 × 5 mm. *Lip* 3-lobed, sagittate, sessile, 12 × 7 mm when spread, the hypochile linear, ca. 8 mm long, 4 mm wide apically, provided at the base with a transversal, rounded-elliptic callus; the epichile triangular-sagittate, acute, 4 × 7 mm, the lateral lobes narrowly linear, acuminate, retrorse, to 4 × 1 mm. *Column* erect, 5.0 mm long, with distinct foot, the basal margins finely ciliate; the clinandrium shallowly subpetaloid, irregularly erose; ligule triangular, obtuse-subtruncate, minutely papillose at apex, 0.8 × 1.2 mm. *Anther cap* elliptic-subreniform, cucullate, flattened, 2-celled. *Pollinia* 4, rounded, in two superposed pairs of different size, on an oblong, subacute stipe; viscidium narrowly peltate, hyaline. *Fruit* an oblong-elliptic, muricate capsule, 15 × 11 mm.

**Distribution:** the West Indies (Jamaica, the type, Hispaniola), Costa Rica, Panama, Colombia, and Ecuador.

**Additional material examined:** COSTA RICA. Alajuela: Grecia, Río Cuarto, Ángeles, Laguna Bosque Alegre, bosque muy húmedo tropical, transición a premontano, epífitas en bosque secundario a orillas de la laguna, 10°18'8.9"N, 84°12'22.2"W, 910 m, 09.12.2004, flowered in cultivation at Jardín Botánico Lankester, November 2005, *D. Bogarín* 1178, *L. Madrigal*, *M. Alfaro* & *E. Chacón* (USJ; JBL-spirit); Bajos del Toro, Río Segundo (a minor tributary of Río Toro), 1420 m, 12 Feb. 2000, *F. Pupulin* 2003 & *M.L. Spadari* (USJ). Heredia: San Rafael, Road to Cerro Chompipe, epiphytic on trees in pasture along the road, 10°04'56"N, 84°04'41"W, 1960 m, 25.7.2003, flowered in cultivation at Jardín Botánico Lankester, December 2003, *W. M. Whitten* 2171, *M. Blanco*, *D. Bogarín* & *H. León-Páez* (USJ; JBL-spirit).

**Eponymy:** named from Sir D. Morris, who first discovered the species.

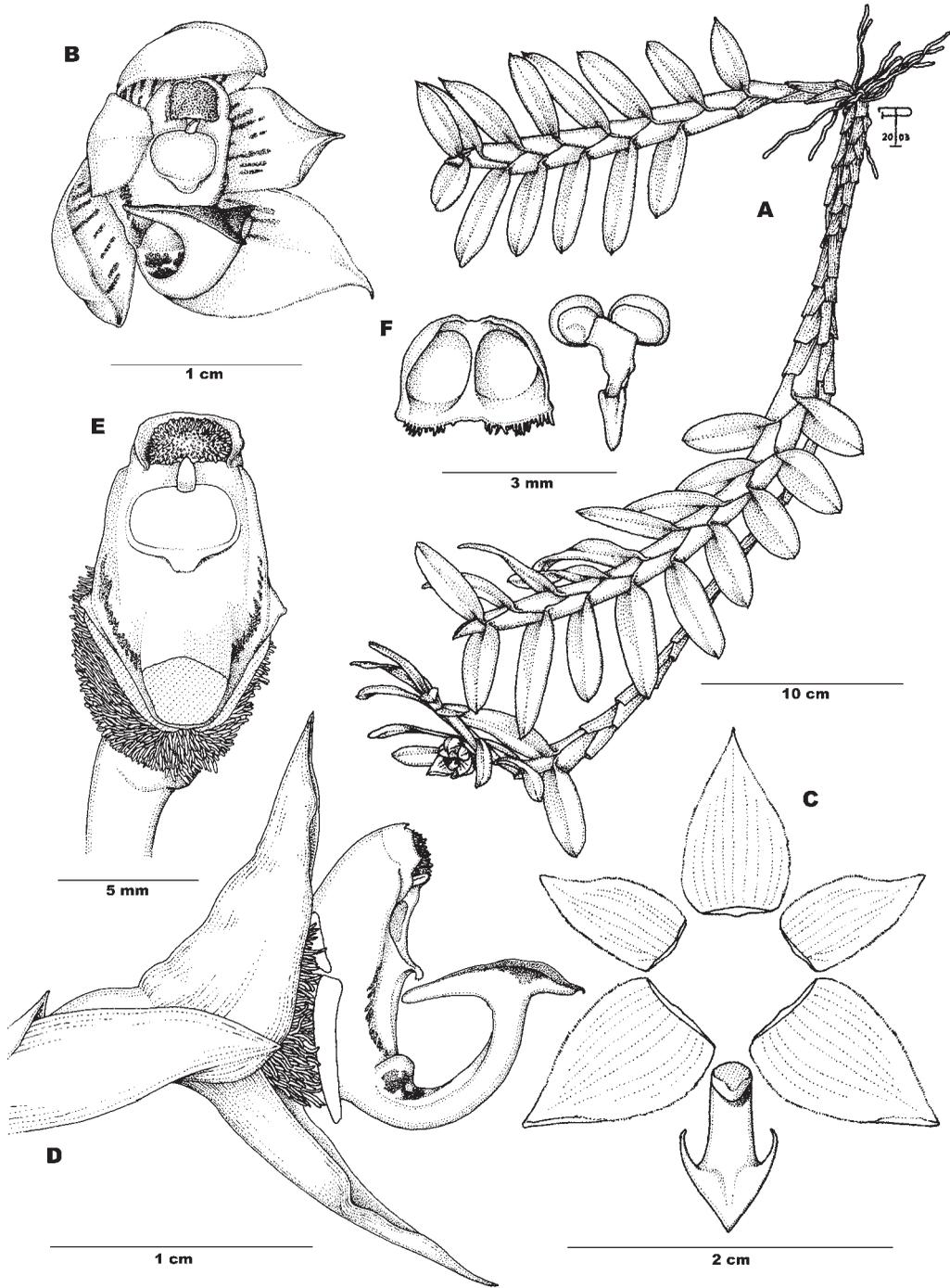


FIGURE 51. *Dichaea morrisii* Fawc. & Rendle. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium. Drawn from Whitten *et al.* 2171 (JBL-Spirit).

**Ecology:** epiphytic in premontane and submontane wet forests at 900–2000 m elevation. Flowering has been recorded in November and December, corresponding to the end of the rainy season.

Notwithstanding its wide geographic distribution, *D. morrisii* is apparently the rarest of the tall *Dichaea* species in Costa Rica, and its presence in the country may be confirmed only through three recent collections, all of them from the Central Volcanic chain. A photograph of the flower from a Costa Rican specimen is presented by Pupulin (2005b: 223).

The correct name to apply to this taxon is at the center of a minor taxonomic controversy. William Fawcett and Alfred Barton Rendle described *Dichaea morrisii* in 1910 on the basis of two specimens originally collected in the mountain regions of Jamaica (Fawcett and Rendle, 1910b). That same year, in their treatment of the genus *Dichaea* for the first volume of the *Flora of Jamaica*, the two authors made a few emendations to the original protologue (Fawcett and Rendle, 1910a). Here they also included among the Jamaican taxa *D. muricata* (Sw.) Lindl., applying this name to a species of sect. *Dichaea*, with persistent leaves. This interpretation of the old *Cymbidium muricatum*, originally published by Swartz in 1789 and later emended in 1806, was first suggested by Cogniaux (1906, 1910), and the name has been used rather consistently in the West Indies to identify plants of *D. latifolia* Lindl. (e.g., Schultes, 1960; Garay and Sweet, 1974). On the mainland, on the contrary, *D. muricata* has been applied to the commonest medium-sized member of Subgenus *Dichaea* in each area, including *D. costaricensis*, *D. cryptarrhena*, *D. laxa* (Ruiz and Pav.) Poepp. & Endl., *D. histrio* Rchb.f., *D. poicillantha* and *D. splitgerberi* Rchb.f., among others (e.g., Allen, 1949; Ames, 1937; Ames and Correll, 1953; Foldats, 1970; Schweinfurth, 1961; Williams, 1956). When Swartz first published *Cymbidium muricatum*, the description was brief and might have fit almost any member of *Dichaea*, but in 1806 he described the plant as somewhat erect with leaves 1.5 inches long, and stressed it was more erect, was much wider, and had larger flowers and fruits than *C. echinocarpon* [= *D. pendula* (Aubl.) Cogn.], clearly referring to a large *Dichaea* plant. The description of *Cymbidium muricatum* can be interpreted as representing

the species described as *Dichaea morrisii* by Fawcett and Rendle in 1910; this interpretation was first suggested by Folsom (1987) and supported by Nir (2000). The type specimens of Swartz are usually to be found in either Stockholm (S) or the British Museum (BM), but searches for the type of *Cymbidium muricatum* in these herbaria have been unsuccessful. There are two, similar, small, vegetative specimens at Copenhagen (C) that are labeled “missit Swartz, Herbarium Vahljanum,” and the specimen labeled as *Cymbidium muricatum* Sw. was taken as type by Nir (2000). While studying *Dichaea* material in the Reichenbach Herbarium, I found an excellent specimen labeled as “*Dichaea muricata* Lindl.” and “*muricatum* Fl. Ind. Occ.” (*Rchb. Orch.* 25291!, W). This specimen is clearly the species described as *D. morrisii* by Fawcett and Rendle (1910a) and has three leafy stems with two capsules (Fig. 4). It is clear that Reichenbach had on loan Swartz’s types from Stockholm, and in all probability, these specimens were never returned. In a note of his *Beiträge zu einer Orchideenkunde Central-Amerika’s* he expressly wrote: “Typi Swartziani herbarii Holmiani ac proprii praesto sunt” (Reichenbach, 1866: 79). A proposal to lectotypify *Cymbidium muricatum* with the specimen found at the Reichenbach Herbarium and to reject the name is pending (Dressler and Folsom, 2005). However, throughout its distribution range, the name *Dichaea muricata* has been widely and constantly applied to a number of species of a different group (subgenus or sect. *Dichaea*, lacking leaf abscission layers), and herbarium identifications as *D. muricata* may be found on almost any species of *Dichaea* with non-articulate leaves. Considering the long-standing confusion about the identity of *Cymbidium muricatum*, which has been “persistently used for [...] taxa not including its type” (Greuter et al., 2000), a proposal for rejection of the name *Dichaea muricata* was submitted by R. L. Dressler and J. Folsom (2005). Pending the decision of the Committee, the alternative and unequivocal name *D. morrisii* is adopted in the present treatment.

18. *Dichaea obovatipetala* Folsom, *Orch. Digest* 58: 186–187. 1994. TYPE. PANAMA. Bocas del Toro: 15 km N of border with Chiriquí, road from Fortuna to Chiriquí

Grande, 100 m, 10 Apr. 1985, *J.P. Folsom 11302M* (Holotype: PMA [drawings]; Isotypes: TEX, HNT [not seen]). Fig. 52, Map 6.

*Plant* epiphytic, caespitose, to 30 cm long. *Roots* exposed basally, the caulinar roots mostly hidden by leaf sheath, occasionally aerial, flexuous, glabrous, ca. 0.6 mm in diam. *Stems* flattened, scandent to pendent, freely branching, often forming intricate mats, 11–30 cm long, 1.5–2.0 mm wide across conduplicate sheaths. *Leaves* widely spaced along stem, spreading, olive green, thick-herbaceous, 6–7 × 4–5 mm, ovate-lanceolate, acute, abaxially provided with a distinct apicule, the apical margins microscopically and irregularly fringed-fimbriate; sheaths compressed, somewhat loose, often pustulate, to 7 × 4 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent, 0.6–0.8 cm long, the peduncle geniculate, provided at the base with 2–3, tubular-compressed, sheathing bracts, about 5 mm long. *Floral bract* double, the outer bract funnel-shaped, broadly ovate-suborbicular, acuminate, 1.7–3.0 × 1.5–3.0 mm, the inner bract narrowly lanceolate-oblong, to 4 mm long. *Pedicel* cylindrical, less than 1 mm long. *Ovary* long-muricate, 1 mm long. *Flower* spreading, with sepals and petals boldly blotched dark violet on a pale grayish-cream background, the sepals externally minutely tuberculate, the lip white, blotched dark violet, the column white, marked with violet at the base and on the margins of wings; flowers moderately scented, the scent vanilla-like. *Dorsal sepal* elliptic-oblong, acute, with a rounded apicule, somewhat bent over the column, 7.5–10.0 × 3.5–4.0 mm. *Lateral sepals* obliquely elliptic-oblong, slightly asymmetrical, acute to shortly acuminate, 7.5–10.0 × 3.5–4.5 mm. *Petals* obovate-elliptic, acute, slightly conduplicate, 6.5–8.5 × 3.5–4.0 mm. *Lip* 3-lobed, subsessile, 6.0–7.8 × 7–8 mm when spread, the hypochile obtusely rounded, sometimes with indistinct shoulders, 3–4 mm long, 5 mm wide apically, the epichile triangular-ovate, rounded, apically infolded, the lateral lobes narrowly triangular-linear, acute, spreading-retrorse, 0.8 × 2.0 mm. *Column* erect, 3.7–4.3 mm long, provided with narrowly elliptic-subrectangular, flattened, ciliate wings, the clinandrium shallow, irregularly erose; ligule lanceolate-oblong, rounded-truncate, the apex shortly hispid, 1.5 × 0.6 mm. *Anther cap* transversely subrectangular, flat-

tened, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a narrowly obtriangular, truncate stipe; viscidium elliptic, hyaline. *Fruit* an elliptic capsule, muricate.

**Distribution:** Costa Rica and Panama.

**Additional material examined:** COSTA RICA. Alajuela: Grecia, Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 380–400 m, epiphytic along the shores of Río Sarapiquí, tropical wet, transition to premontane wet forest, 13 Feb. 2004, *F. Pupulin 5141*, *D. Bogarín*, *H. León-Páez* & *E. Salas* (JBL-Spirit); San Ramón, Piedades, Potrerillos, road to Socorro de Piedades Sur, slopes of Cerro La Palma, 10°08'09.9"N, 84°34'47.5"W, 10°08'25.0"N, 84°34'45.9"W, 1300–1450 m, premontane wet forest, 12 April 2006, flowered in cultivation at Jardín Botánico Lankester, 4 Aug. 2006, *F. Pupulin 6051*, *R. L. Dressler* & *A. Carbajal* (CR). Cartago: Juan Viñas, Pejivalle, shore of Río Pejivalle, bridge point, down stream, 9°48'40"N, 83°42'06"W, 700 m, premontane wet forest, on tall trees overhanging the river, 10 Jan. 2004, *F. Pupulin 5013*, *S. Dalström* & *H. León-Páez* (CR); same locality, *F. Pupulin 5015*, *S. Dalström* & *H. León-Páez* (USJ; JBL-Spirit); same locality, *F. Pupulin 5019*, *S. Dalström* & *H. León-Páez* (USJ; JBL-Spirit); Pejivalle, shore of Río Pejivalle, 9°48'40"N, 83°42'06"W, 700 m, 10.1.2004, *F. Pupulin 5023*, *S. Dalström*, *H. León-Páez* (USJ, JBL-Spirit); Pejivalle, La Marta, shore of Río Pejivalle, 9°47'47"N, 83°42'55"W, 690 m, epiphytic in secondary vegetation along the river, premontane wet forest, 10 Jan. 2004, *F. Pupulin 5055*, *S. Dalström* & *H. León-Páez* (USJ, JBL-Spirit); *F. Pupulin 5058*, *S. Dalström* & *H. León-Páez* (USJ, JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 16 Aug. 2006, *F. Pupulin 5056*, *S. Dalström* & *H. León-Páez* (CR); Juan Viñas, entre Tucurrique y Pejivalle, borde del Río, 31 agosto 1984, *R.L. Dressler & Biología 350 No. 16* (USJ); same locality, *R.L. Dressler & Biología 350 No. 17* (USJ); Turrialba, CATIE, en el Jardín Botánico de Cabiria, 600 m, *A. Karremans 898* (JBL-Spirit); Turrialba, Peralta, 800 m, ca. 9°56'N, 83°41'W, premontane wet forest, 9 Aug. 2003, *F. Pupulin 4946*, *C. Pupulin*, *M. Pupulin* & *H. León-Páez* (JBL-Spirit). Heredia: Varablanca, San Rafael, km 1.7 after the village of San Rafael, along the

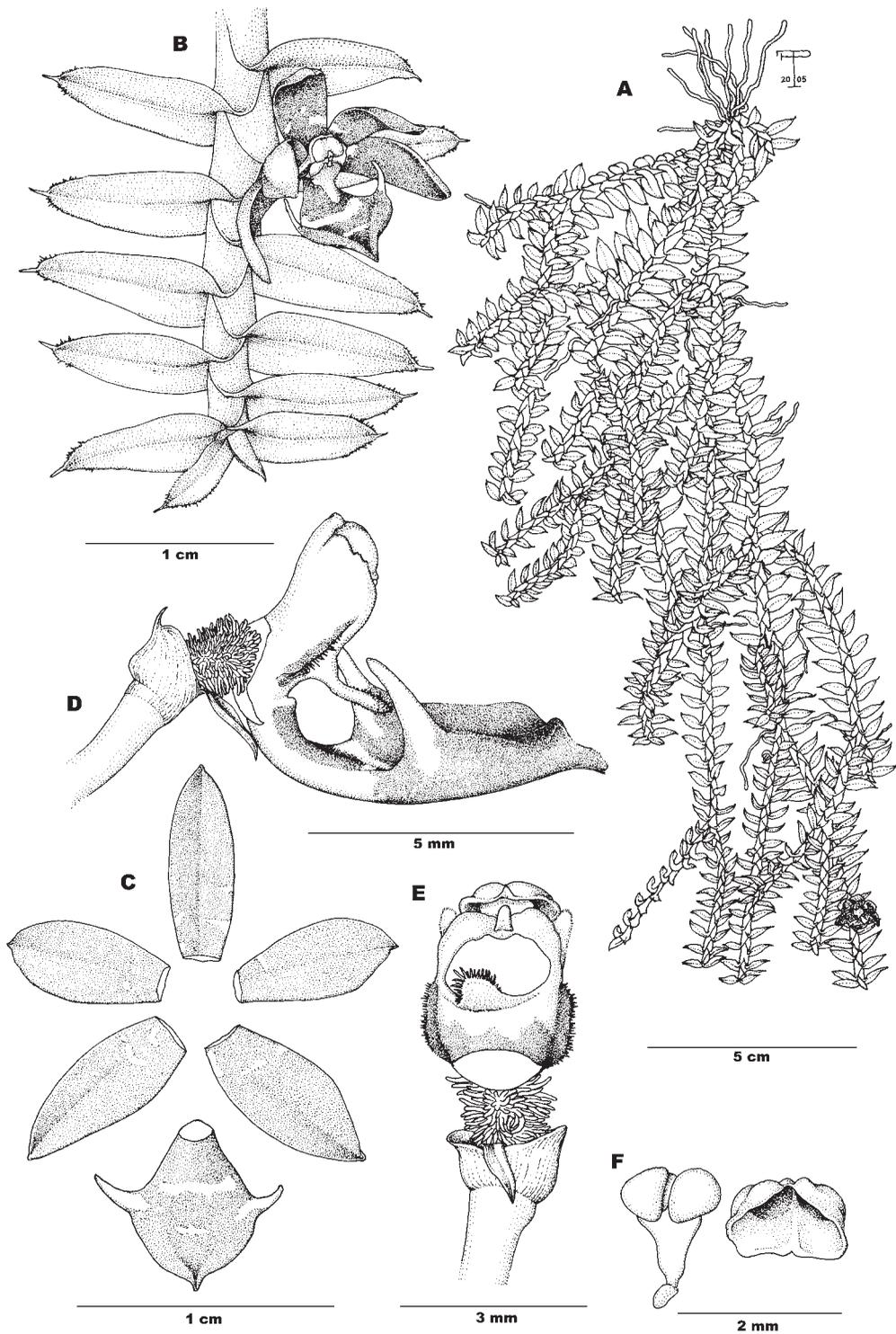


FIGURE 52. *Dichaea obovatipetala* Folsom. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from *Pupulin* 4202 (JBL-Spirit).

Río San Rafael, 10°10'N, 84°07'W, ca. 1750 m, lower montane wet forest, riparian gallery forest, collected by F. Pupulin, E. Salas & H. León-Páez, 6 July 2002, flowered in cultivation at Jardín Botánico Lankester, 18 October 2002, *F. Pupulin 4202* (JBL-Spirit); Sarapiquí, Horquetas, Finca Terrafolia, contiguo a Rara Avis, 10°18'14"N, 84°01'36"W, 500 m, 21.7.2003. *W. M. Whitten 2050* & *M. Blanco* (JBL-Spirit). Limón: Talamanca, Amubri, camino a Soki entre la quebrada Amubri, margen izquierda del Río Lari, 09°29'40"N, 82°49'40"W, 200 m, 30 June 1989, *A. Chacón 31* (INB).

**Etymology:** from the Latin *obovatus*, shaped like an inverted egg, and *petalum*, petal, in allusion to the characteristic shape of the petals, wider above the middle.

**Ecology:** epiphytic in tropical and premontane wet forests at 400–1800 m elevation, in Costa Rica the species is restricted to the Caribbean watershed of the Central Volcanic and Talamanca mountain ranges. Flowering has been recorded from October to February.

The olive green foliage, the freely branching stems, which often form intricate mats, and the scented, almost completely violet flowers with obovate petals distinguish *D. obovatipetala* among Costa Rican species of *Dichaea* of the sect. *Dichaea*. It is closely related to *D. sarapiquinsis* Folsom, which differs by the laxly pendent, rarely branching stems, the flowers not heavily blotched with violet, and the verrucose apex of the lip.

19. *Dichaea oxyglossa* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 267. 1923. TYPE. COSTA RICA. [Alajuela:] Santiago de San Ramón, 1075 m, Nov. 1921, *A. M. Brenes 144* (Holotype: B, destroyed; tracings of Schlechter's holotype, AMES; Lectotype, selected by Barringer, 1984: CR 18455). Fig. 53, Map 7.

*Plant* epiphytic, caespitose, to 70 cm long. *Roots* exposed basally, the caulinar roots hidden by leaf sheath, only occasionally aerial, flexuous, glabrous, ca. 0.5 mm in diam. *Stems* flattened, laxly pendent, rarely branching, 15–70 cm long (longer stems bearing up to 250 leaves), 0.7–1.0 mm wide across conduplicate sheaths. *Leaves* widely spaced along stem, spreading-retorse, olive green to brownish green, thin-herbaceous, 4–7 × 2.5–3.5 mm, lanceolate-elliptic, cuneate-rounded to suba-

cute, abaxially apiculate; sheaths compressed, apically slightly loose, to 5.5 × 2.5 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent, to 1.8 cm long, the peduncle geniculate, slender, provided at the base with 2 tubular, acute, sheathing bracts, 4 mm long. *Floral bract* double, the outer bract broadly ovate, rounded-apiculate, 1.8–2.2 × 1.4–1.8 mm, the inner bract narrowly lanceolate, 1.8 mm long. *Pedicel* cylindrical, ca. 1.5 mm long. *Ovary* papillate to sparsely short-muricate, 1.2 mm long. *Flower* spreading, with sepals and petals hyaline cream to greenish white, the sepals sparsely spotted with purple toward the base, the petals with large purple-violet blotches, the lip white, blotched dark violet, the column white, marked with violet on the margins of wings and on stigmatic rims; no odor detected. *Dorsal sepal* elliptic-lanceolate, acuminate, concave, slightly bent over the column, 8.5–11.0 × 2.5–3.2 mm. *Lateral sepals* obliquely lanceolate, subfalcate, acuminate, concave, 8–11 × 2.5–3.0 mm. *Petals* elliptic-lanceolate, subfalcate at apex, acuminate, slightly concave, 7.5–10.5 × 2.5–3.0 mm. *Lip* 3-lobed, shortly clawed, 6.0–6.5 × 7.5–9.0 mm when spread, the hypochile obtriangular, provided with indistinct, rounded shoulders, 2 mm long, 2.8 mm wide apically, the epichile broadly triangular, apically infolded, acuminate, the lateral lobes narrowly triangular-linear, acuminate, spreading, confluent on the blade, 2.3 × 1.0 mm. *Column* suberect, 2.2–2.8 mm long, provided with narrowly semi-elliptic, flattened-backswept, ciliate wings, the clinandrium shallow, irregularly erose; the stigma rounded obtrullate; the infrastigmatic ligule oblong, projecting slightly upward, apically dilated-inflated, retuse, pubescent, 1.7 × 1.1 mm. *Anther cap* transversely elliptic, flattened, 2-celled. *Pollinia* 4 in two superposed pairs of different size, on a narrowly obtriangular, apically dilated, rounded stipe; viscidium elliptic, hyaline. *Fruit* an elliptic, muricate capsule.

**Distribution:** Costa Rica and western Panama.

**Additional material examined:** COSTA RICA. Alajuela: Grecia, Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, shores of Río Sarapiquí, tropical wet, belt transition to premontane wet forest, 10°19'16"N, 84°10'34"W, 400 m, 29.11.2004, flowered in cultivation at Jardín Botánico Lankester, 20 September 2005, *F. Pupulin*

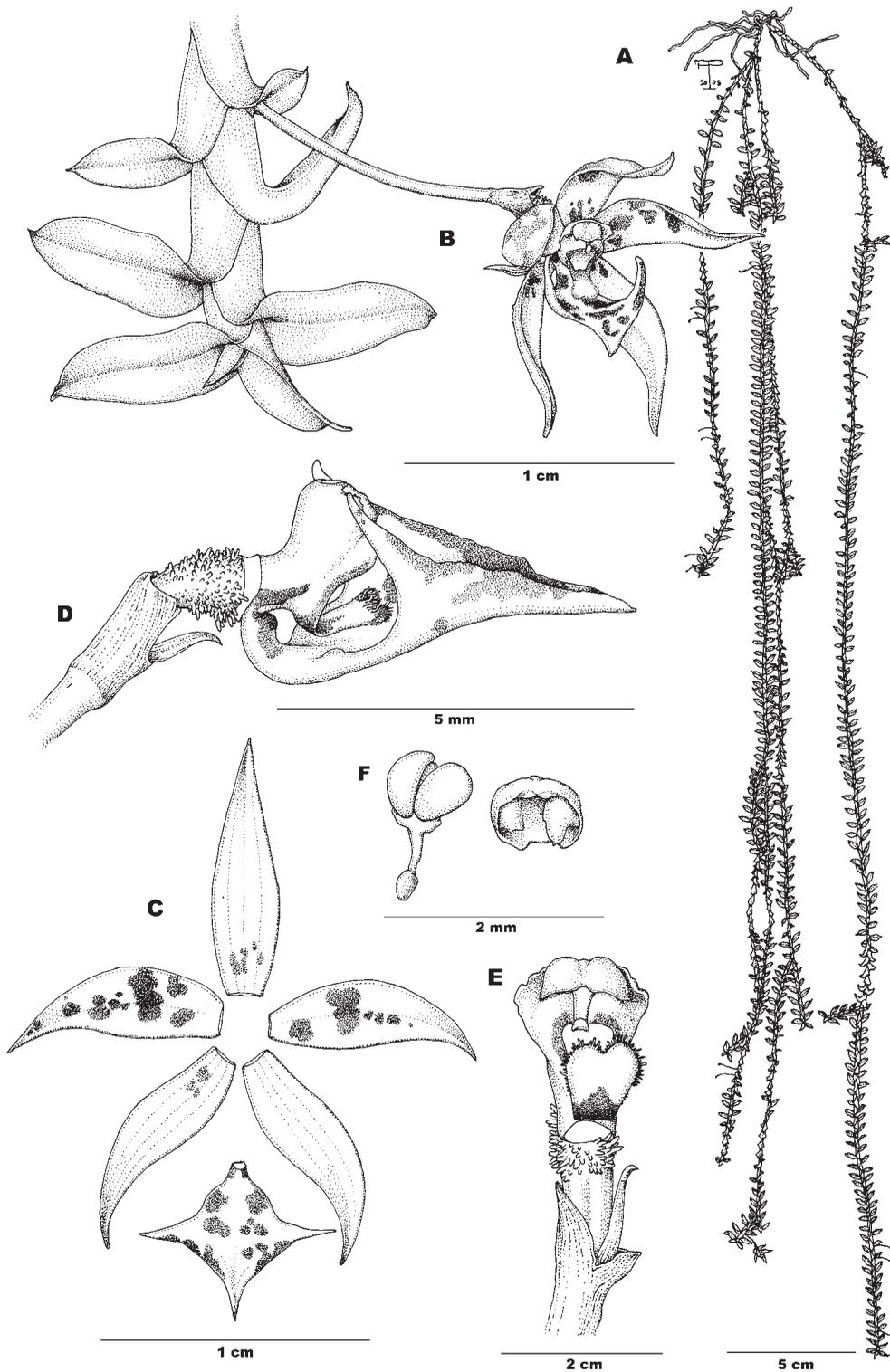


FIGURE 53. *Dichaea oxyglossa* Schltr. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from *Pupulin 4202* (JBL-Spirit).

5339, *R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit); San Ramón, Piedades, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, Caribbean watershed of the Continental Divide, premontane cloud forest, 10°09'51.9"N, 84°35'36.5"W, 1410 m, 24.03.2005, flowered in cultivation at Jardín Botánico Lankester, 20 September 2005, *F. Pupulin 5585, E. Salas-Pupulin, D. Bogarín & A. C. Rodríguez* (JBL-Spirit). Cartago: Paraíso, Orosi, Purisil, Parque Purisil, orilla de los senderos, bosque pluvial montano a montano bajo, bosque secundario y remanentes de primario, 1400–1500 m, 10.05.2003, *D. Bogarín 186 & H. León-Páez* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, August 2003, *D. Bogarín 190 & H. León-Páez* (USJ, JBL-Spirit); same locality, flowered 3 May 2006, *D. Bogarín 184 & H. León-Páez* (CR); Orosi, Parque Nacional Tapantí, sendero Oropendola, 09°44'13"N, 83°46'49"W, 1100–1300 m, 28.12.2004, *M. Blanco 2734, D. Bogarín, F. Pupulin & S. Dalstrom* (JBL-Spirit). Border between Heredia and Alajuela: Grecia, Sarapiquí, Colonia Virgen del Socorro, road to Cariblanco, bridge on Río San Fernando, 10°15'18"N, 84°10'20"W, 750 m, 29.11.2004, *F. Pupulin 5355, R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit). Puntarenas: Coto Brus, San Vito de Java, road from Las Cruces to Río Claro, Fila Cruces-Zapote, 8°47'04"N, 83°02'02"W, 1530 m, 13.11.2002, *F. Pupulin 4232, E. Salas, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); San Vito, Las Cruces, ca. 1.5 km camino del Jardín Botánico Wilson hacia Copal, 8°46'52.3"N, 82°57'58.7"W, 1270 m, bosque muy húmedo premontano transición a basal, 25 Oct. 2005, flowered in cultivation at Jardín Botánico Lankester, 16 May 2006, *D. Bogarín 2048, R. L. Dressler, R. Gómez, A. Karremans, F. Pupulin, A. Rambelli & S. Rambelli* (JBL-Spirit). Pérez Zeledón, San Isidro, road from Dominical to San Isidro del General, about 11 km, 9°18'31"N, 83°46'31"W, 950 m, 10.11.2001, flowered in cultivation at Jardín Botánico Lankester, April 2003, *F. Pupulin 3393, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); Pérez Zeledón, Miraflores, carretera a Santa Cruz, 1350 m, 2.12.2001, flowered in cultivation at Jardín Botánico Lankester, April 2003, *F. Pupulin 3444, D. Castelfranco & J. Cambroner* (USJ, JBL-Spirit). San José: Dota: Crest of Cerro

Nara, 910–1000 m, premontane rain forest, 20 Feb. 2000, flowered in cultivation at Gaia Botanical Garden, 16 Mar. 2000, *F. Pupulin 2119, D. Castelfranco, M. L. Spadari & K. McFarland* (JBL-Spirit); San Ramón, camino a Los Ángeles de Páramo, 9°28'14"N, 83°44'59"W 1800 m, 20.4.2003, flowered in cultivation at Jardín Botánico Lankester, 2 May 2005, *F. Pupulin 4691, J. Cambroner, H. León-Páez, M. Powell, E. Salas & V. Savolainen* (JBL-Spirit); Tarrazú, Fila Bustamante, Fila Costeña de Tarrazú, Cerro Toro, 1.5 km SW del basurero, camino a Esquipulas, 09°34'25"N, 84°03'58"W, 1200–1300 m, 5 September 1996, *J. F. Morales 5787, B. Hammel & T. Croat* (INB).

**Etymology:** from the Greek *oxys*, sharp, pointed, and *glossa*, tongue, in allusion to the acuminate epichile and its lateral lobes.

**Ecology:** epiphytic in shady, moist areas, in tropical and premontane wet forests at 400–1500 m elevation, mostly on the Caribbean slopes and close to the continental divide in the Tilarán and Central Volcanic mountain ranges, and on both watersheds of the Cordillera de Talamanca. Flowering has been recorded year-round, but the species flower most frequently from April to September.

The long, laxly pendent, rarely branching stems, the thin-textured, olive green leaves, the elongate peduncle, the translucent flowers with long-acuminate sepals and petals, and the apically inflated-dilated, emarginate infrastigmatic ligule are diagnostic, and make this species quite unmistakable among Costa Rican Dichaeas.

20. *Dichaea panamensis* Lindl., Gen. Sp. Orch. Pl. 209: 1833. *Epithecia panamensis* (Lindl.) Schltr., Orchis 9: 25. 1915. *Dichaeopsis panamensis* (Lindl.) Schltr., Beitr. Bot. Centralbl. 36, Abt. 2: 519. 1918. TYPE: PANAMA. In Panamá et Columbia occidentali [Taboga Island], 1831, *H. Cuming 1292* (Holotype: K). Fig. 54, Map 7.

Synonym: *Dichaea brachypoda* Rchb. f., Beitr. Orch. Centr.-Amer. 78: 1866, *syn. nov.* TYPE: COSTA RICA: [Heredia: Sarapiquí,] San Miguel, 14.5.1857, *H. Wendland s.n.* (Holotype: W, photograph seen). *Epithecia brachypoda* (Rchb.f.) Schltr., Orchis 9: 25. 115.

*Plant* epiphytic, caespitose, to 20 cm long. *Roots* basal, glabrous, flexuous, very thick,

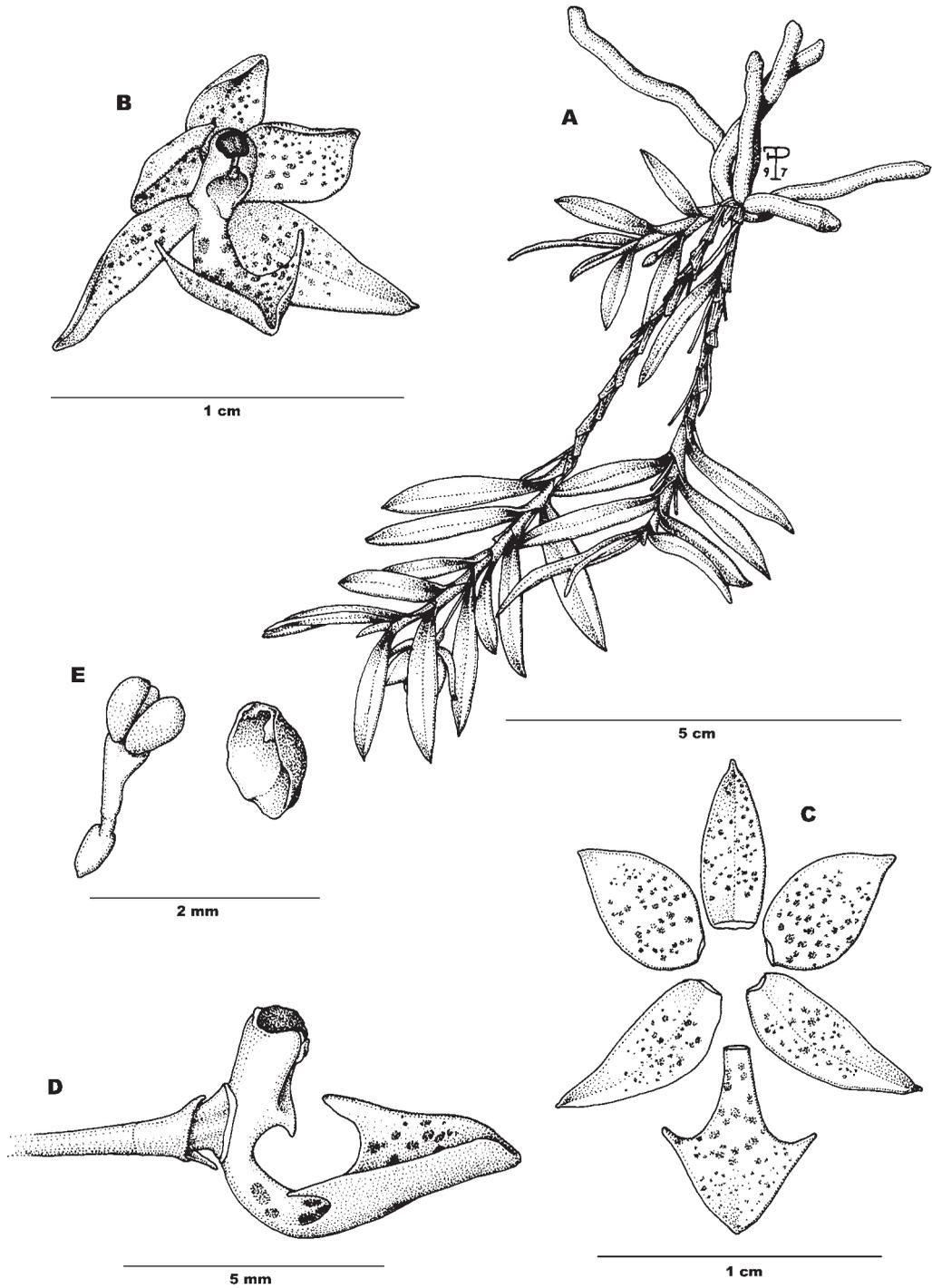


FIGURE 54. *Dichaea panamensis* Lindl. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, pollinarium and anther cap. Drawn from *Pupulin s.n.* (Puntarenas: Aguirre, Manuel Antonio).

wider than the stem, about 2 mm in diam. *Stems* flattened, suberect to spreading or pendent, simple, rarely producing new plantlets with roots at the nodes, 6–21 cm long, 0.15 cm wide across conduplicate sheaths. *Leaves* widely spaced along stem, oblique to spreading, medium to dark green, frequently glaucous on one or both surfaces, subcoriaceous, narrowly linear-elliptic to lanceolate, acute, apiculate, 12–20 × 3–4 mm, usually varying in length along the stem, the blade articulated to the sheath encircling the stem and ultimately deciduous; sheaths tightly clasping, to 4 × 3 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, the peduncle straight, to 15 mm long, provided at the base with 2 tubular, acute bracts, about 1.5 mm long. *Floral bract* double, the outer bract suborbicular-funneliform, obtuse, shorter than pedicel, 2 × 2 mm, the inner bract narrowly lanceolate, 2.5 mm long. *Pedicellate ovary* cylindrical-subclavate, glabrous, ca. 2.5 mm long including the pedicel. *Flower* ringent, rarely subspreading, the sepals and petals greenish cream spotted and/or blotched with purple, sometimes almost solidly purple, the lip creamish white, sparsely spotted with purple, mostly toward the apex, rarely solid purple, the column greenish white, flecked violet along the margins of the stigma, anther cap purple-red; no fragrance detected. *Dorsal sepal* elliptic-lanceolate, acute, dorsally carinate, 6–9 × 2.5–3.2 mm. *Lateral sepals* lanceolate-elliptic, asymmetrical, slightly falcate, acute, apiculate, usually upcurved in natural position, 7.5–12.0 × 3.0–4.1 mm. *Petals* obliquely ovate, shortly acute, much wider than sepals, 6.0–8.5 × 4–5 mm. *Lip* 3-lobed, from a fleshy claw, 7–10 × 6–9 mm when spread, the hypochile obtuse, sometimes provided at the base with a thickened area, 4–5 mm wide apically, the epichile broadly triangular-sagittate, obtuse to subrounded, minutely apiculate, adaxially carinate toward the apex, the lateral lobes narrowly triangular, acute, spreading-retrorse, decurring in the lamina, 1.5 × 1.0 mm. *Column* erect, 5–6 mm long, with a distinct foot about 2 mm long, the reclined clinandrium shallow; ligule small, widely triangular, projecting downward, subacute, glabrous, 0.6 × 1.5 mm. *Anther cap* transversely elliptic-suborbicular, flattened, 2-celled. *Pollinia* 4 in two superposed pairs of slightly different size, on a narrowly obtriangular-ligulate, subtruncate stipe with inrolled

margins; viscidium elliptic. *Fruit* an elliptic, glabrous capsule.

**Distribution:** Mexico to Venezuela, Ecuador, and Brazil.

**Additional material examined:** COSTA RICA. Alajuela: Atenas, Potrerillos, S. Pablo & Sa. Balsa, left bank of Rio Grande San Mateo, July, *Endres s.n.* (W-R 14787); Grecia, Río Cuarto, Ángeles, Laguna Bosque Alegre, 10°18'08.9"N, 84°12'22.2"W, 910 m, a orillas de la laguna, 9 Dic. 2004, *D. Bogarín 1075*, *L. Madrigal, M. Alfaro & E. Chacón* (JBL-Spirit); Guatuso, San Rafael, Puerto Nuevo, Santa Fé, shores of Río Caño Ciego, 10°42'59.6"N, 84°43'26.9"W, 100 m, epiphytic on *Zygia longifolia* along the river, 15 Dec. 2005, *D. Bogarín 2234 & F. Pupulin* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 25 May 2006, *F. Pupulin 5919 & D. Bogarín* (CR); same locality, flowered in cultivation at Jardín Botánico Lankester, 4 Apr. 2006, *F. Pupulin 5920 & D. Bogarín* (CR); [San Ramón,] bois humides á San Pedro de San Ramón, 800 m, VI.1922, *A. M. Brenes 280* (CR 18460); [San Ramón,] San Miguel de San Ramón, orillas del Río Barranca, 19-I-1937, *A. M. Brenes s.n., 21949* Herb. Brenes (CR 18463, sterile); San Ramón, Piedades, road from San Pedro to Piedades Sur, bridge on Río Barranca, 10°06'34.6"N, 84°30'20.3"W, 900 m, Pacific watershed of the Continental Divide, along the Río Barranca, 24 Mar. 2005, *F. Pupulin 5572*, *E. Salas-Pupulin, D. Bogarín & A. C. Rodríguez* (CR, JBL-Spirit); same locality, *F. Pupulin 5574*, *E. Salas-Pupulin, D. Bogarín & A.C. Rodríguez* (CR); Piedades, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'51.9"N, 84°35'36.5"W, 1410 m, Caribbean watershed of the Continental Divide, premontane cloud forest, 24 March 2005, flowered in cultivation at Jardín Botánico Lankester, 4 Apr. 2006, *F. Pupulin 5592*, *E. Salas-Pupulin, D. Bogarín & A. C. Rodríguez* (CR); Sarapiquí, San Miguel, road to Colonia Carvajal, ca. 400 m after the first bridge on Río Sarapiquí, 10°19'13.5"N, 84°10'27.2"W, 400 m, shores of Río Sarapiquí, tropical wet, transition belt to premontane wet forest, secondary vegetation, 16 June 2005, flowered in cultivation at Jardín Botánico Lankester, 10 March 2006, *F. Pupulin 5669*, *D. Bogarín & A. C. Rodríguez* (CR); Upala, Colonia Libertad 2 km al Noreste, cuenca del

- Río Caño Negro, 300–400 m, 3 May 1988, *G. Herrera 1969* (CR, sterile); Upala, bridge on Río Zapote, 10°53'49.2"N, 85°00'56.8"W, 80 m, tropical moist, transition to tropical wet forest, epiphytic along the river, 15 Dec. 2005, *F. Pupulin & D. Bogarín 5922* (JBL-Spirit); Upala, Aguas Claras, Buenos Aires, road toward Las Bromelias Lodge, Aguas Termales, N slopes of Rincón de la Vieja volcano, 10°46'58.9"N, 85°15'19.4"W, 720 m, premontane wet forest, primary and mature secondary vegetation, 2 May 2006, *F. Pupulin 6148*, *D. Bogarín*, *A. Rambelli & G. Rambelli* (CR); same locality, *F. Pupulin 6149*, *D. Bogarín*, *A. Rambelli & G. Rambelli* (CR); same locality, *F. Pupulin 6151*, *D. Bogarín*, *A. Rambelli & G. Rambelli* (CR); Aguas Claras, Colonia Blanca, camino entre Colonia Verde y Colonia Libertad hacia Buenos Aires, faldas al noreste del Volcán Rincón de La Vieja, 10°52'26.2"N, 85°14'51.3"W, 550–600 m, bosque muy húmedo tropical, epifitas en potreros y árboles aislados, 4 Febrero 2006, florecio en cultivo en el Jardín Botánico Lankester el 4 de Abril 2006, *D. Bogarín 2556*, *J. Barrantes*, *R. L. Dressler*, *R. Gómez & A. Rojas* (CR). Cartago: Turrialba, Moravia de Chirripó, Tsipirí, 9°48'N, 83°23'W, 1090 m, on steep slopes along a small creek, 26 Apr. 2002, *F. Pupulin 3667*, *M. Bonilla*, *R. Gómez*, *H. Montealegre & J. C. Cervantes* (JBL-Spirit); Turrialba, Tayutic, Chirripó Abajo, Bloriñak, 9°46'45"N, 83°22'40"W, 600 m, 7 Ago. 1995, *G. Herrera 8317* (CR); Turrialba, Tayutic, Platanillo, Laderas del Río Platanillo, 600 m, 20 Feb. 2004, *A. Karremans 110* (JBL-Spirit); Tayutic, laderas del Río Platanillo, 600 m, 20.2.2004, *A. Karremans 110* (JBL-Spirit); Tayutic, Moravia, 5 km oeste del centro de Moravia, 1100 m, 22.1.2005, *A. Karremans 621*, *D. Karremans & R. Ferreira* (JBL-Spirit). Guanacaste: La Cruz, P.N. Guancaste, Sendero a Estación Maritza, 10°57'40"N, 85°29'40"W, 800 m, 11 Feb. 1995, *M. Lobo 60* (INB); Liberia, Parque Rincón de la Vieja, de la planta hidroeléctrica 2 km agua arriba siguiendo el canal, 10°46'N, 85°17'W, 0 m, 7 Feb. 1988, *G. Herrera 1532* (CR; INB); Liberia, Cordillera de Guanacaste, P.N. Guanacaste, Sendero Pedregal, 10°55'43"N, 85°28'10"W, 1100 m, 10 feb. 1995, *A. Picado 95*, *E. Alfaro*, *R. Villalobos & J. F. Morales* (INB). Border between Guanacaste and Alajuela: Upala, road from San Jorge de Liberia to Colonia Blanca, SE slopes of Rincón de la Vieja volcano, 10°46'05.1"N, 85°16'45.3"W, 820 m, premontane dry, transition to premontane rain forest, 1 May 2006, *F. Pupulin 6116*, *D. Bogarín*, *A. Rambelli & G. Rambelli* (CR). Heredia: Sarapiquí, Parque Nac. Braulio Carrillo, Magsasay Station, along sendero Terciopelo, between border with La Selva and Magsasay, 10°24'30"N, 84°02'40"W, 150 m, 19 Oct. 1990, *S. Ingram 613 & K. Ferrell* (CR); Chilamate de Sarapiquí, finca El Bejuco, S. base of Cerro Sardinal, 10°27'N, 84°04'W, 70–100 m, 2 Jun. 1985, *M. Grayum & B. Jacobs 5323* (CR); Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 380–400 m, epiphytic along the shores of Río Sarapiquí, 13 Feb. 2004, *F. Pupulin 5140*, *D. Bogarín*, *H. León-Páez & E. Salas* (JBL-Spirit); San Miguel, unpaved road to the west of the village, 10°16'04.7"N, 84°11'01.4"W, ca. 500 m, on short trees along the roadside, 16 Jun. 2005, *F. Pupulin 5703*, *D. Bogarín & A.C. Rodríguez* (JBL-Spirit); Sarapiquí, Llanura de Santa Clara, Río Frío, quebradas tributarias del Río San José, cerca de la Finca La Ceiba, 10°14'08"N, 83°55'23"W, 200 m, 10 May 1995, *J. F. Morales 4070*, *E. Lépiz*, *V. H. Ramírez & A. Rojas* (INB; CR, sterile); Sarapiquí, camino de Horquetas a Rara Avis, km 4, 140 m, 3 enero 2003, floreció en cultivo en Horquetas de Sarapiquí, 9 abril 2006, *C. Ossensbach 282*, *M. Zamora & W. Salazar* (CR). Limón: Pococí, Guápiles, Hacienda La Cuenca, falda norte del Volcán Turrialba, 10°08'58"N, 83°46'46"W, 600–650 m, 1.1.2005, *M. Blanco 2765*, *A. Chávez*, *L. duToit & C. Ugalde* (JBL-Spirit); Cerro Coronel, E of Río Zapote, along and above near road, 10°40'N, 83°40'W, 10–100 m, 24 Jan 1986, *W. Douglas Stevens 23931* (CR); Tortuguero, R.B. Caño Palma, sendero Raphia, 10°35'00"N, 83°32'00"W, 10 m, 26 Abr. 1995, *G. Herrera 7769* (CR). Puntarenas: Aguirre, Savegre, Santo Domingo, on fallen tree along the bank of Río Savegre, 85 m, 27.11.1999, *F. Pupulin 1855*, *D. Castelfranco*, *M.L. Spadari & J. Matey* (JBL-Spirit); Buenos Aires, Cañas, Llano Bonito, 9°14'07.7"N, 83°24'06.6"W, 460–600 m, tropical rain, transition to premontane rain forest, 24 October 2005, flowered in cultivation at Jardín Botánico Lankester, 14 March 2006, *F. Pupulin 5820*, *D. Bogarín*, *R. L.*

*Dressler, R. Gómez, A. Karremans, A. Rambelli & S. Rambelli* (CR); Buenos Aires, Ujarrás, margen izquierda del Río Ceibo, 09°14'00"N, 83°18'00"W, 500 m, 9 March 1993, *G. Herrera* 5827 (CR, fruiting; INB); Golfito, near and along trail leading from kilometro 3/Torres rd. to Quebrada Culebra (tributary of Río Sorpresa), ca. 2.5 km (by air) NE of Golfito, 08°39'00"N, 83°09'00"W, 300–370 m, 1 Feb. 1992, *M. Grayum* 10084, *C. Formoso & N. Martín* (CR); Golfito, Puerto Jiménez, P.N. Esquinas, Fila way, 8°41'N, 83°13'W, 200 m, 17 Feb. 2000, *R. Wania* 100 (CR, fruiting); Golfito, epífitas en tronco caído en las alturas de la Fila la Gamba, 350 m, 29.8.2005, *G. Rojas* 69 (CR, JBL-Spirit); Osa, west end of main ridge of Fila Retinto, along trail from Palmar Norte to Jalisco, 08°59'30"N, 83°28'00"W, 700 m, 13 Dec. 1989, *M. Grayum* 9538 & *B. Hammel* (CR); Osa, lower slopes of Fila Huacas, ca. 4 km NE (by road) from Carretera Interamericana at Las Huacas (Venecia) along road to Sinaí, 08°52'00"N, 83°17'00"W, 400–500 m, 23 Feb. 1992, *M. Grayum* 10159 & *R. Evans* (CR); Osa, El Tigre, abecera de Río Agujas, Finca Azofeifa, 08°32'00"N, 83°28'00"W, 700 m, 19 Nov. 1993, *R. Aguilar* 2667 (INB); Osa, Sierpe, San Juan, Fila Casaloma, estribaciones Cerro Chocuaco, 8°43'20"N, 83°32'20"W, 500 m, 28 Jan, 1991, *G. Herrera* 4888 (INB); Osa, El Campo, subiendo la fila entre Aguabuena y Baneuitas, cuenca superior de Quebrada Banegas, 8°42'N, 83°32'W, 100–400 m, 14 Jan. 1991, *G. Herrera* 4821 (INB); Parque Nac. Corcovado, Ollas trail, 8°27–30'N, 83°33–38'W, 0–100 m, 10 Jan. 1989, *C. Kernan* 886 & *P. Phillips* (CR); Parque Nacional Corcovado, Dos Brazos de Río Tigre, Jiménez, cuenca superior del Río nadrigal, 8°29'50"N, 83°28'55"W, 600 m, 8 Dec. 1990, *G. Herrera* 4746 (INB). San José: Acosta, Bajos de Jorco, Bajos de Toledo, márgenes del río Grande, 800 m, 12.2001, *R. Valverde* 900 (JBL-Spirit); Braulio Carrillo Park, 500–700 m, 16 Sept. 1984, *J. B. Folsom* 11006 (CR); Parque Nac. Braulio Carrillo, Quebrada Sanguijuela, 10°09'N, 85°57'W, 500–700 m, 17 May 1988, *M. M. Chavarría* 159 & *G. Umaña* (CR); Pérez Zeledón, La Alfombra, Alto de San Juan, Agrícola ganadera El Sueño, 700 m, 30.3.2002, *A. Quesada-Chanto* 24, *A. Quesada* & *Y. Quesada* (JBL-Spirit); Pérez Zeledón, Las

Nubes de Quizarrá, 1080 m, epiphytic on trees in remnants of primary vegetation and secondary mature vegetation, along the Río Quizarrá, 9 November 2000, *F. Pupulin* 2576, *D. Castelfranco & J. Prada* (CR); Puriscal, Cerros de Puriscal, Cerro Pelón, 09°43'50"N, 84°23'59"W, 750 m, 21 Apr. 1995, *J. F. Morales* 3943 (CR, sterile; INB); Tarrazú, Valle del Candelaria, Had. Tiquires, sendero a Tiquiritos, en la cima de la Fila Zoncucano, 9°42'35"N, 84°13'35"W, 1000–1050 m, 20 July 1995, *J. F. Morales* 4580 & *J. González* (INB); Turrubares, Z. P. Turrubares, cuenca del Río Grande de Tárcoles, cabecera del Río Carara, 9°48'00"N, 84°29'00"W, 800–1000 m, 6 Apr. 1993, *B. Hammel* 18977, *M. Grayum* & *R. Zuñiga* (INB); Turrubares, cuenca del Tulín, sector Bijagual, 9°44'50"N, 84°33'50"W, 550 m, 16 May 1997, *A. Rodríguez* 2188, *V. H. Ramírez & A. Soto* (INB).

**Etymology:** named from the country where the type specimen was originally found.

**Ecology:** in Costa Rica, *D. panamensis* is a common species, recorded from warm tropical to premontane wet forests on both drainages, at 50–1350 m elevation, but is most commonly found in the range between 400 and 900 m. It is a shade-loving epiphyte, occupying many different niches, with preference for old, moist branches and trunks of the understory vegetation. Flowering occurs year-round, with a peak between April and June, corresponding to the beginning of the rainy season.

Although amply variable in flower size and color, *Dichaea panamensis* is vegetatively and florally unmistakable. The plants, rooting only at the base of the stems, have very thick roots, and the leaves are mostly of variable length along a single stem. The leaves of *D. panamensis* are usually recorded as glaucous, but in the study area this character is very variable; plants with glaucous leaves and with green leaves may be found at the same locality, and green and glaucous leaves are often present intermixed on different stems of individual specimens and sometimes also on a single stem. The waxy cuticular layer is often lost under the environmental conditions provided by Lankester Garden's greenhouses. The flowers of *D. panamensis* vary in color from pale greenish white to almost solid purple, with any combination of purple spotting, blotching, and flushing. However, their ringent shape (the

flowers never spread out completely), the arrow-shaped lip, and the glabrous ovary make them easy to recognize. On the basis of morphological features, *D. panamensis* is likely related to a complex of species mainly Antillean in distribution, including *D. picta* Rchb. f., *D. rendlei* H. A. Gleason, and *D. trinitensis* H. A. Gleason, characterized by articulate leaves, thick roots restricted to the base of the stem, and the anther cap tinged with purple-red.

*Dichaea brachypoda* is known only by the fragmentary holotype specimen, with the flower severely damaged. Another sterile specimen identified by Reichenbach as *D. brachypoda*, collected along the Río Chagres in central Panama by Augustus Fendler (at that time collecting plants for Asa Gray) is kept at AMES (Fendler 333, AMES 76347!). Since the time of its description in 1866, the species has been rather mysterious. Judging from the holotype in the Reichenbach Herbarium, the specimen was likely prepared from Wendland's material cultivated in the Costa-Rica Haus in Herrenhausen, and no other collections were subsequently recorded from Costa Rica. In the holotype specimen the flower has a glabrous ovary, and Kränzlin (1923), who had access to the type when it was likely in better condition, noted this useful diagnostic character. Nevertheless, the interpretation of *D. brachypoda* as having a muricate ovary prevailed in literature, resulting in the haphazard application of this name to a broad complex of unrelated species distributed from Nicaragua (Hamer, 1982a) to Ecuador (Dodson and Dodson, 1989), Venezuela (Dunsterville and Garay, 1965; Foldats, 1970: 447–448), Suriname (Werkhoven, 1986), and Brazil (Pabst and Dungs, 1977), only sharing the character of leaf articulation. One of the Mesoamerican species of this group, provided with muricate ovary and petals smaller than the sepals, recently received formal recognition as *D. elliptica* (Dressler, 2002; see treatment *supra*). When Reichenbach described *D. brachypoda*, he had already studied and annotated the type of *D. panamensis* in Lindley's herbarium; he also made a copy of Lindley's sketches of the flower, the column, and the lip, now included in the Reichenbach Herbarium in Vienna (Rchb. Orch. 19219!, W). Actually, the

holotype of *D. panamensis* consists of a plant with four stems, mostly without any leaves, one of which bears an immature fruit. No flowers are conserved, but the sketches by John Lindley show a campanulate flower with the petals similar to the sepals, a column that is globose at the base and narrowed toward the apex, and a lip provided with a narrow, linear claw and a triangular-sagittate blade. The type sheath also includes another specimen of *D. panamensis*, collected by W. Hinds in the "Island of Gorgona. S. America" (i.e., Colombia), which Reichenbach annotated as "totally different." It is not surprising that, on the basis of his knowledge of Lindley's drawings, he could not recognize Hinds's collection as a true *D. panamensis*, nor that he considered Wendland's collection from "San Miguel in Costa Rica" as a still-undescribed taxon. He compared his new species with Hooker's *Isochilus graminoides* (Hooker, 1826 = *Dichaea trinitensis* H. A. Gleason), but he noted that the petals are much wider than the sepals, and that the lip is cuneate at the base and triangular sagittate at the apex (Fig. 55), all characters that are undistinguishable from those of *D. panamensis*. Reichenbach also noted that the dried flower of *D. brachypoda* had a dark purple lip, and material of *D. panamensis* from the type locality at San Miguel (e.g., *Pupulin* 5681) pertains to the purple phase of this species. Fenzler's specimen from Panama, identified by Reichenbach as *D. brachypoda*, consists only of two sterile



FIGURE 55. *Dichaea brachypoda* Rchb.f. Lip of Wendland s.n. (Holotype: Rchb. Orch., W). Photo courtesy of J. Folsom.

stems, but the thick roots restricted to the base of the stem and the variable length of the leaves are unmistakably similar to those of *D. panamensis*. Kränzlin (1923) reduced *D. acuminata* Schltr., described from Colombia, in synonymy under *D. brachypoda*, but the muricate ovary of the former species prevents such a conclusion.

21. *Dichaea pendula* (Aubl.) Cogn. in Urb., Symb. Antill. 4: 182. 1903. *Limodorum pendulum* Aubl., Hist. Pl. Guyane Franc. 2: 819–821, pl. 322. TYPE: FRENCH GUIANA. “Habitat in sylvis Comitatus de Gêne,” *Aublet s.n.* (Holotype: no extant material has been located; the illustration of vegetative parts on plate 322 may be selected for lectotypification, but excluding flower details, which represent mixed collections). Fig. 56, Map 7.

Synonyms: *Epidendrum echinocarpon* Sw., Prodr. 124. 1788, *nom. illeg.* *Cymbidium echinocarpon* (Sw.) Sw., Nova Acta Reg. Soc. Sc. Upsal. 6: 71. 1799, *nom. illeg.* *Dichaea echinocarpa* (Sw.) Lindl., Gen. Sp. Orch. Pl. 208. 1833, *nom. illeg.* *Pachyphyllum echinocarpon* (Sw.) Spreng., Syst. Veg. 3: 731. 1826, *nom. illeg.* TYPE: JAMAICA. “Provenit ad latera saxorum arborumque inter muscos in umbrosis montium Jamaicae australis,” *O. Swartz s.n.* (Lectotype, selected here: *W-Reichenbach Herbarium Nr. 25294*).

*Dichaea trachysepala* Schltr., Repert. Sp. Nov. Regn. Veg. Beih. 27. 181. 1924. TYPE: COLOMBIA. Cundinamarca: southwest of Bogotá, 2000 m, 1922, *R. Schnitter s.n.* (Holotype: B, destroyed).

*Dichaea echinocarpa* var. *lobata* Ames & Correll, Bot. Mus. Leaflet. 11(3): 71, plate 4, Fig. 2. 1943. *Dichaea lobata* (Ames & Correll) L. O. Williams, Ceiba 1(3): 189. 1950. TYPE: COSTA RICA. San José: La Palma, about 1600 m, *P. C. Standley 33120* (Holotype: AMES 30208, in part).

*Dichaea pendula* var. *swartzii* C. Schweinf., Bot. Mus. Leaflet. 17(2): 161–162. 1955, *nom. illeg.* *Dichaea swartzii* (C. Schweinf.) Garay & Sweet, J. Arnold Arbor. 53: 397–398. 1972, *nom. illeg.*

*Plant* epiphytic, rarely terrestrial in humus embankments, caespitose, to 100 cm long. *Roots* filiform, basally exposed, glabrous, flexuous, about 0.4 mm in diam., the caulinar roots completely hidden by leaf sheaths. *Stems* flattened, pendent, apically arching to become patent-suberect, frequently branching, 15–100 cm long, 0.1 cm wide across conduplicate sheaths. *Leaves* closely spaced along stem, spreading, pale green, thin-herbaceous, the midvein neatly prominent abaxially, lanceolate, abruptly acuminate, dorsally apiculate, the apical margins irregularly and microscopically serrulate, 18–30 × 6–8 mm; sheaths loose, strongly compressed, to 7–8 × 3–4 mm. *Inflorescences* 1–2 per node, successive, 1-flowered, emerging below foliage (rarely above), the peduncle straight, to 16 mm long, provided at the base with 3 tubular, subacute bracts, the apical one subcampanulate and partially exposed, about 1.5 mm long. *Floral bract* double, the outer bract broadly ovate-funneliform, obtuse, shorter than pedicel plus ovary, 4.0 × 3.8 mm, the inner bract lanceolate-elliptic, 4.5 mm long. *Pedicel* cylindrical, ca. 2 mm long. *Ovary* densely muricate, 2.5–3.0 mm long. *Flower* subspreading, the sepals and petals pale orange, the petals pale orange, distally spotted with purple, the lip white, boldly blotched with violet, with white margins, the column white, blotched with violet along the margins of the foot and the wings; no fragrance detected. *Dorsal sepal* elliptic to oblong, acute, curved over the column, dorsally carinate and sparsely verruculose, 7–8 × 3.5–4.5 mm. *Lateral sepals* elliptic to elliptic-ovate, slightly asymmetrical, acute, apiculate, dorsally carinate and sparsely verruculose, 7.5–8.0 × 3.7–4.7 mm. *Petals* elliptic, acute, with a rounded apicule, smaller than sepals, 6.3–7.5 × 3.0–3.8 mm. *Lip* thick, concave, subentire to distinctly 3-lobed, from a fleshy claw, 7.0–7.5 × 6–8 mm when spread, the hypochile broadly obtuse, with distinct shoulders, the basal margins and shoulders microciliate, 6.5 mm wide apically, the epichile broadly triangular, obtuse, minutely apiculate, sometimes provided with short-triangular to linear-falcate, acute to long-acuminate, retrorse lateral lobes, 2–3 × 1 mm. *Column* suberect, 4.2–4.6 mm long, with a short foot about 0.6 mm long, basally subterete, apically dilated into a shallow, reclined clinandrium,

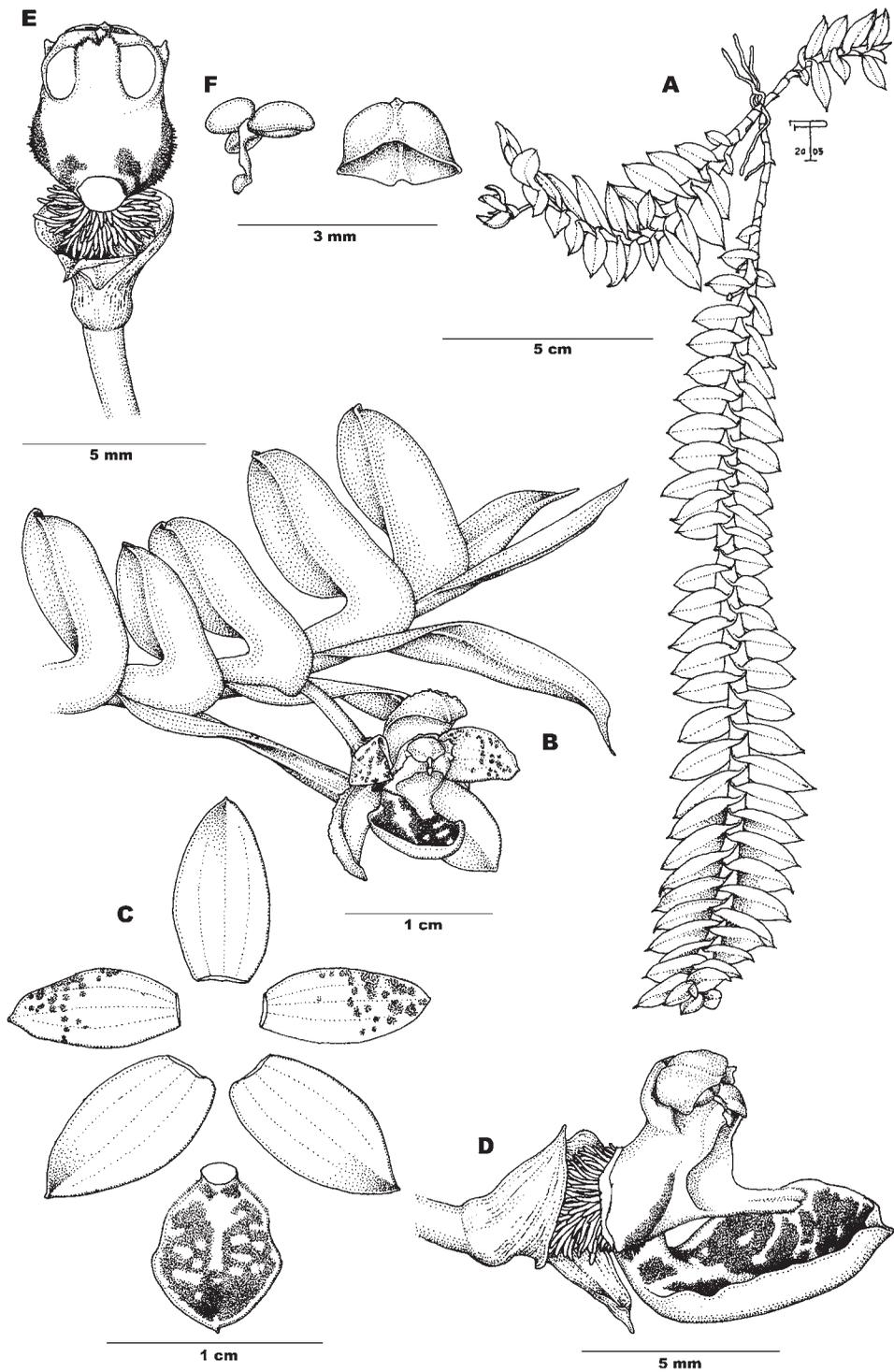


FIGURE 56. *Dichaea pendula* (Aubl.) Cogn. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from *Pupulin* 3024 (JBL-Spirit).

with entire margins, provided at the base with 2 semi-elliptic, narrow, flattened, ciliate wings; the stigma ovate-rounded, strongly depressed; ligule broadly linear to lanceolate, projecting forward, truncate, bifid, apically soft-hispid, 1.8 × 1.2 mm. *Anther cap* helmet-shaped, transversely elliptic, slightly flattened, 2-celled. *Pollinia* 4, suborbicular, in two superposed pairs of different size, on a narrowly obtriangular-ligulate, subtruncate stipe with inrolled margins; viscidium elliptic, hyaline. *Fruit* an elliptic, muricate capsule.

**Distribution:** from Costa Rica and Panama to most of South America (Colombia, Ecuador, Bolivia, Venezuela, French Guyana, and northern Brazil) and the West Indies (Cuba, Dominica, Hispaniola, Jamaica, Guadalupe, Martinique, and Puerto Rico).

**Additional material examined:** COSTA RICA. Alajuela: Bajos del Toro, northern slope of Volcán Poás, epiphytic in secondary forest along a small river, 1450 m, 5 March 2001, flowered in cultivation at Jardín Botánico Lankester, 22 Nov. 2002, *F. Pupulin 3024* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 1 July 2006, *F. Pupulin 3036* (JBL-Spirit); San Ramón, Alto de La Palma de San Ramón, 1250 m, 26-VII-1924, *A. M. Brenes (74) 686* (CR); same locality, 1295 m, 20-XI-1922, *A. M. Brenes 187* (NY); same locality, 1250 m, 6-XI-1923, *A. M. Brenes 2995* (NY); Piedades, Piedades Norte, road to Bajo de La Paz, km 4, summit of Cerro Azahar, 10°08'59.5"N, 84°35'00.3"W, 1563 m, crest of continental divide, premontane to lower montane cloud forest, 30 January 2005, flowered in cultivation at Jardín Botánico Lankester, May 2006, *F. Pupulin 5512*, *D. Bogarín, M. Salas & P. Seaton* (JBL-Spirit). Cartago: El Muñeco, on the Río Navarro, 1400–1500 m, 6–7 Mar. 1926, *P. C. Standley & J. Valerio 51703* (AMES); Orosi, Parque Nacional Tapantí, sendero Oropéndola, 10°07'48"N, 84°02'23"W, 1160 m, 25.5.2003, flowered in cultivation at Jardín Botánico Lankester, June 2004, *F. Pupulin 4750* (JBL-Spirit); Orosi, 09°44'13"N, 83°46'49"W, 1100–1300 m, 28.12.2004, *M. Blanco 2731, D. Bogarín, F. Pupulin & S. Dalstrom* (JBL-Spirit); Turrialba, Turrialba, Santa Cruz, después de La Pastora, desde el puente sobre el Río Turrialba hasta unas cataratas sobre el río, 1800–2000 m, 31.01.2005, flowered in cultiva-

tion at Jardín Botánico Lankester, 6 June 2005, *A. Karremans 737* (JBL-Spirit). Heredia: Cerro de Las Caricias, 2000–2400 m, *P. C. Standley & J. Valerio 52457* (AMES). San José: Pérez Zeledón, San Ramón, unpaved road to Las Pegas, Páramo, Los Ángeles, 9°29'01"N, 83°45'16"W, 1480 m, 20.4.2003, flowered in cultivation at Jardín Botánico Lankester, 25 May 2005, *F. Pupulin 4630, J. Cambroner, H. León-Páez, M. Powell, E. Salas & V. Savolainen* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 27 June 2006, *F. Pupulin 4629, J. Cambroner, H. León-Páez, M. Powell, E. Salas & V. Savolainen* (JBL-Spirit); Vásquez de Coronado, Alto la Palma, camino al bajo La Hondura, 10°02'47"N, 83°59'25"W, 1450–1500 m, 19 June 1995, *J. F. Morales 4717* (INB).

**Etymology:** from the Latin *pendulus*, pendant, in reference to the typical habit of the plant.

**Ecology:** in Costa Rica, *D. pendula* is apparently restricted to the very wet premontane and submontane forest of the Tilarán, Central Volcanic, and Talamanca mountain chains, at elevations between 1200 and 2400 m. Here the plants are usually found on the trunks of old trees in deep shade. Although most of the records are from the Caribbean slopes of the northern chains, the species has been also recorded from the Pacific watershed of the continental divide in southern Costa Rica. Flowering has been recorded from November to June, but likely the plants flower most of the year.

Among Costa Rican species of the sect. *Dichaea*, the soft herbaceous, thin-textured, large leaves distinctly keeled along the midvein and the flowers usually produced below the foliage (occasionally in pairs) are diagnostic of *D. pendula*. Although it is unmistakable in its vegetative and floral characters, the species has a rather chaotic taxonomic history. Aublet described it from French Guyana, but both the protologue and the original illustration are incongruous. The proportionally small lip illustrated by Aublet, less than one-third the size of sepals and petals, is completely atypical of any of the known species of *Dichaea*, and it is likely part of a different collection. On that basis, Ames and Correll (1943) proposed relegating the name by Aublet to the *nomina confusa*, accepting for this taxon the later epithet

*echinocarpa*, originally published by Swartz (1788) as a member of the genus *Epidendrum* and transferred to *Dichaea* by Lindley in 1833. Unfortunately, the name *Epidendrum echinocarpon* was illegitimate at the time of its publication, because Swartz expressly stated in the protologue it was synonymous with *Limodorum pendulum* (Swartz, 1788). Accordingly, all the subsequent combinations based on *Epidendrum echinocarpon* have to be considered as *nomina illegitima*.

When Ames and Correll (1943) described variety *lobata* of *Dichaea echinocarpa* from Costa Rica, they ostensibly considered that the *forma typica* should approach material from the West Indies, from where the type of *Epidendrum echinocarpon* was described (Jamaica, Swartz *s.n.*), which usually has no labellar lobing. I have no direct knowledge of any specimen from French Guyana to correctly interpret the morphology of the lip in the *forma typica* of *D. pendula*, and neither the description nor the illustration originally provided by Aublet help to clarify the concept, but in the published illustrations based on South American material (Dunsterville and Garay, 1959; Foldats, 1970), the lip of *D. pendula* is typically anchoriform, the epichile provided with distinct lateral lobes. Schweinfurth (1955) is to be credited for having first understood that the unlobed material from the Antillean islands should be considered a variation with respect to the typical form of South American *D. pendula* (with labellar lobing), but failing in the indication of a new type, his var. *swartzii* is typified by *E. echinocarpon* and therefore it should be considered a *nomen illegitimum*. The original material of *Epidendrum echinocarpon* by Swartz, kept at W and selected here as the lectotype, is composed by six leafy stems and is fertile (Fig. 3).

Most of the Costa Rican specimens I examined have a subentire lip, without any lobing of the epichile; however, transitional forms between this morph and the concept of *D. echinocarpa* var. *lobata* seemingly exist throughout the entire distributional range of *D. pendula*.

22. *Dichaea poicillantha* Schltr., Repert. Sp. Nov. Regni. Veg. Beih. 19: 73–74. 1923. TYPE: COSTA RICA. [San José: Moravia.] San Jerónimo, im Jahre 1921, C. Wercklé 32

(Holotype: B, destroyed; Lectotype, proposed by Folsom, 1987, and designated here: tracing of Schlechter's drawing of the type, AMES). Fig. 57–59, Map 8.

*Plant* epiphytic, caespitose, to 90 cm long. *Roots* filiform, basally exposed, glabrous, flexuous, about 0.4 mm in diam., the caulinar roots mostly hidden by leaf sheaths, rarely aerial. *Stems* flattened, stiffly pendent, frequently branching, 15–90 cm long, 0.1–0.15 cm wide across conduplicate sheaths. *Leaves* closely to widely spaced along stem, spreading, medium green to olive green or bronze green, soft-herbaceous to subcoriaceous, broadly ovate to elliptic-lanceolate, acute, dorsally apiculate, the margins smooth or microscopically serrulate toward the apex, 7–20 × 3–7 mm; sheaths clasping, loose at margin, compressed, to 4–10 × 2–5 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, the peduncle geniculate on emerging from sheath, 8–13 mm long, provided at the base with 3 sheathing, tubular, subacute bracts about 1.5 mm long. *Floral bract* double, the outer bract broadly ovate, clasping-funnelform, abruptly apiculate, shorter than pedicel plus ovary, 3.5–4.5 × 3–4 mm, the inner bract lanceolate, 2.5–3.0 mm long. *Pedicel* cylindrical, 1.5–2.0 mm long. *Ovary* densely soft-muricate, ca. 2 mm long. *Flower* bowl-shaped to spreading, the sepals and petals pale greyed-orange, sparsely spotted with violet, the lateral sepals mostly spotted in upper half, the petals pale orange, boldly blotched with violet-purple, the lip white with violet shoulders, the epichile solid violet; the column yellow-green with violet wings, marked violet along the margins of the stigma and on foot; no fragrance detected. *Dorsal sepal* oblong-elliptic to elliptic, acute to subacuminate, often curved over the column, dorsally low-tuberculate, 8.5–14.0 × 3.5–6.0 mm. *Lateral sepals* narrowly ovate to elliptic-oblong, acute to shortly acuminate, concave, dorsally low-tuberculate, 7.5–11.0 × 3.2–5.0 mm. *Petals* elliptic to oblong, bent, acute to subacuminate, with a rounded apicule, sometimes longer than sepals, 7.5–11.0 × 3.0–5.5 mm. *Lip* 3-lobed, anchoriform from a short, fleshy claw, 6.0–7.5 × 8.5–13.0 mm when spread, the hypochile squared-broadly obtuneate, with rounded, ciliate shoulders, 5.5 mm wide apically, the epichile transversely elliptic, broadly obtuse to rounded, minutely

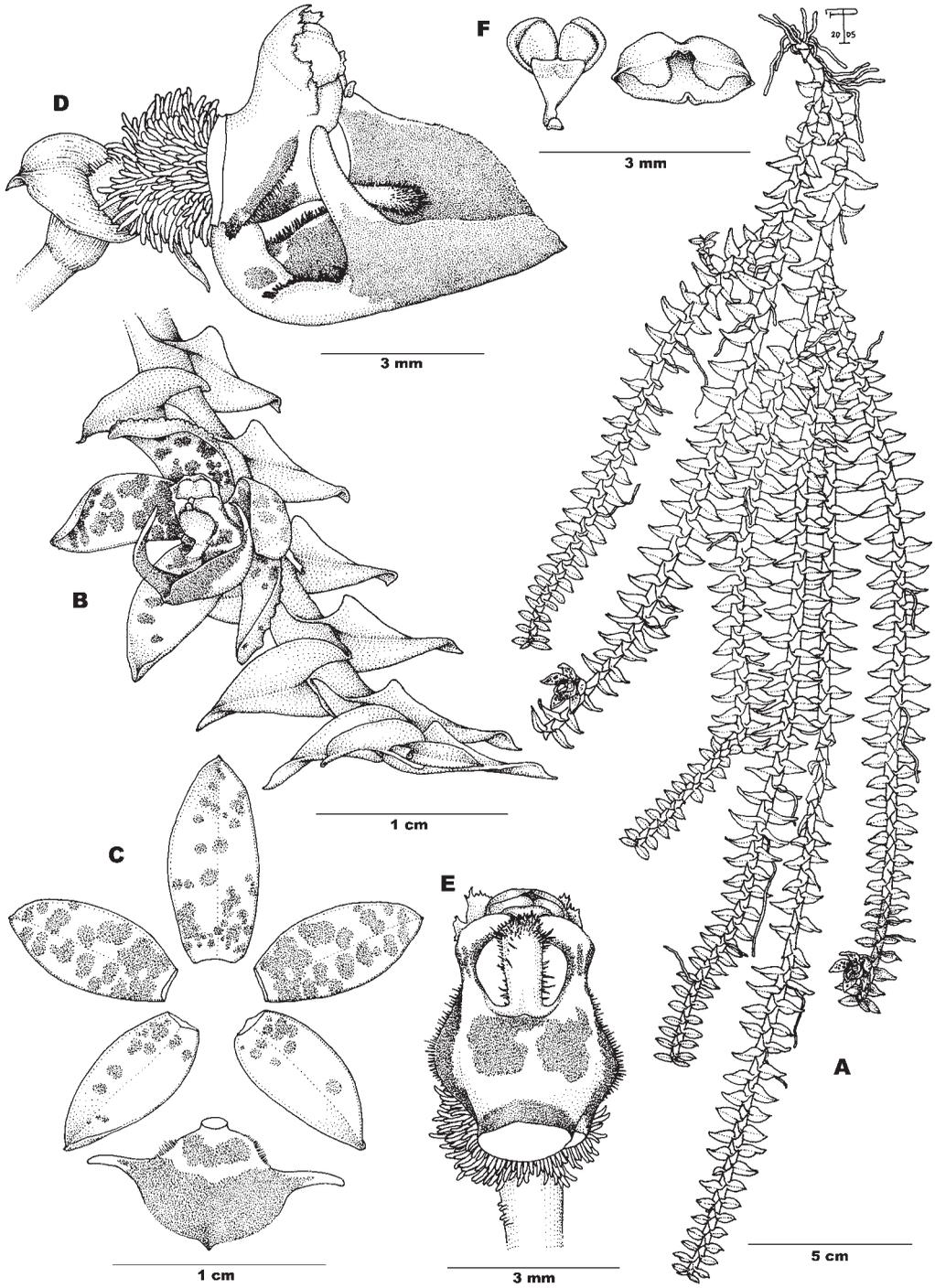


FIGURE 57. *Dichaea poicillantha* Schltr. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from Whitten 2030 (JBL-Spirit).

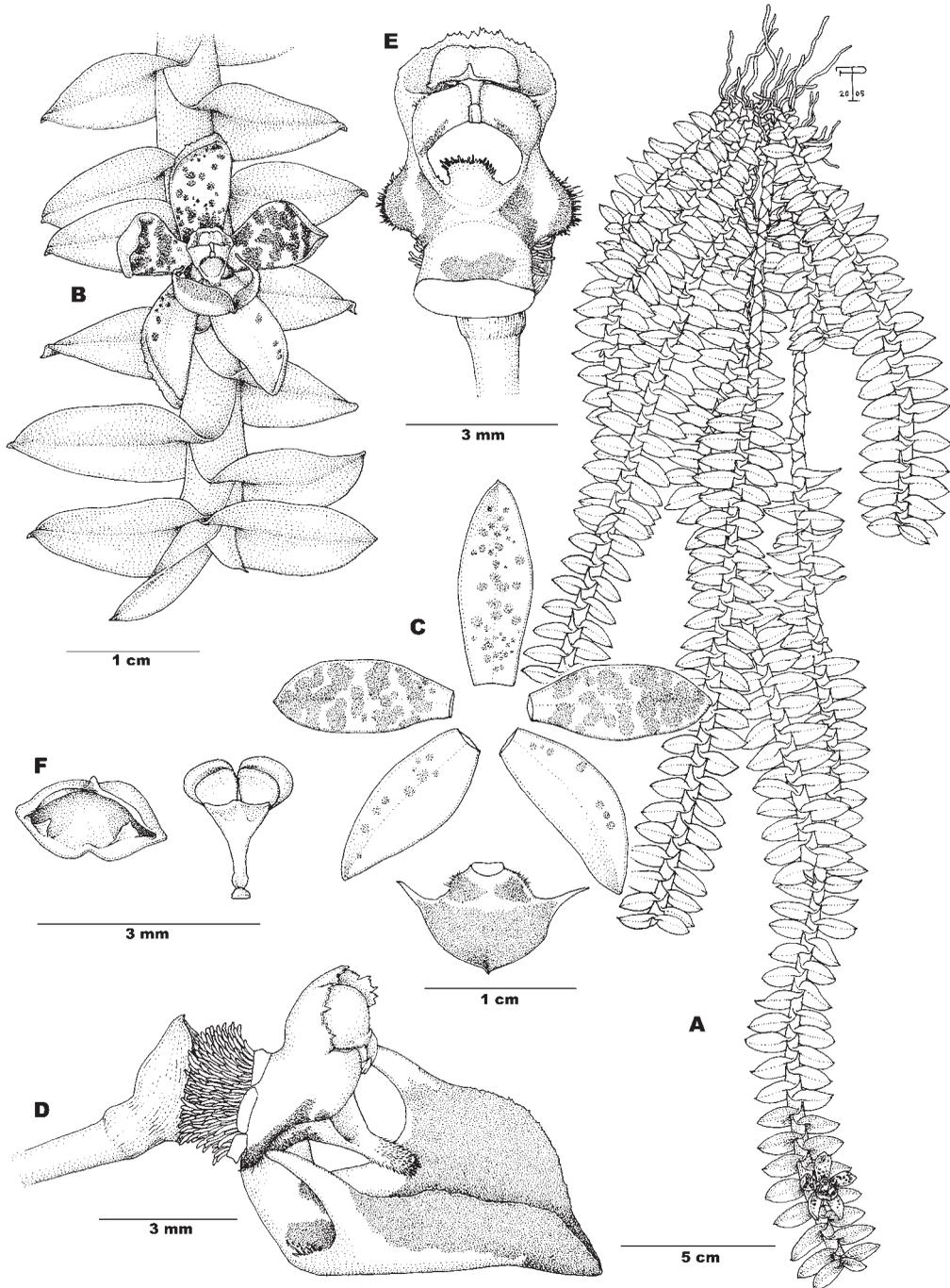


FIGURE 58. *Dichaea poicillantha* Schltr. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, anther cap and pollinarium. Drawn from Pupulin et al. 3420 (CR).

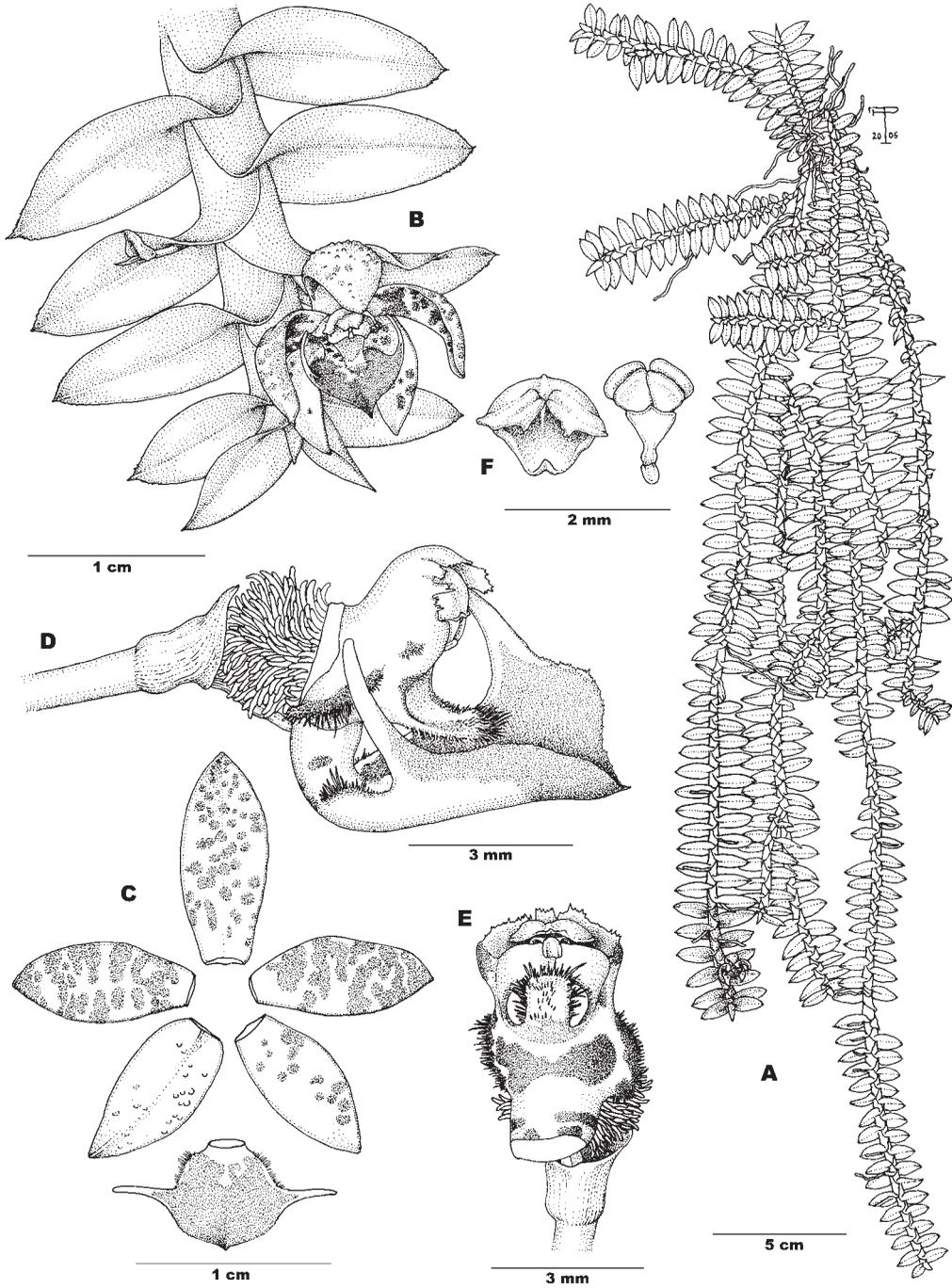


FIGURE 59. *Dichaea poicillantha* Schltr. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, anther cap and pollinarium. Drawn from Pupulin et al. 2397 (JBL-Spirit).

apiculate, sometimes funnelliform subapically, provided with long-attenuate, spreading to slightly retrorse lateral lobes, 2–3 × 0.5 mm. *Column* suberect to erect, 3.5–4.0 mm long, with a short foot about 0.7 mm long, basally subterete, apically dilated into a petaloid, erect clinandrium, with irregularly erose-denticulate margins, provided at the base with two semi-elliptic, basally subquadrate, flattened, densely ciliate wings; the stigma ovate-rounded to obtrullate, depressed; ligule broadly oblong, projecting forward, truncate, apically soft-hispid, 1.3–1.8 × 1.0–1.2 mm. *Anther* cap cucullate, transversely elliptic, flattened, 2-celled. *Pollinia* 4, obovate-complanate, in two superposed pairs of different size, on a narrowly obtriangular, truncate stipe; viscidium elliptic-peltate, hyaline. *Fruit* an elliptic, muricate capsule.

**Distribution:** Nicaragua to Panama, perhaps ranging north to Mexico.

**Additional material examined:** COSTA RICA. Alajuela: Bajos del Toro, 1450 m, 5.3.2001, flowered in cultivation at Jardín Botánico Lankester, July 2003, *F. Pupulin* 3032 (JBL-Spirit); Grecia, Sarapiquí, entre Cariblanco e Isla Bonita, Cuesta Ángel, bosque muy húmedo tropical, transición a premontano, epifitas a orillas de la carretera, 10°15'40"N, 84°10'26.4"W, 933 m, 09.12.2004, *D. Bogarín* 1084, *L. Madrigal*, *M. Alfaro* & *E. Chacón* (JBL-Spirit); same locality, *D. Bogarín* 1097, *L. Madrigal*, *M. Alfaro* & *E. Chacón* (CR, JBL-Spirit); Grecia, Piedades, Río Cuarto, Ángeles, Laguna Bosque Alegre, bosque muy húmedo tropical, transición a premontano, 10°18'8.9"N, 84°12'22.2"W, 910 m, 09.12.2004, flowered in cultivation at Jardín Botánico Lankester, 2 May 2005, *D. Bogarín* 1083, *L. Madrigal*, *M. Alfaro* & *E. Chacón* (JBL-Spirit); [San Lorenzo], Reserva Alberto Brenes, ridge top at 1140 m near camp, 11 Sept. 1984, *J. B. Folsom* 10990A (CR, sterile); San Ramón, Piedades Sur, Cerros de La Palma, 13–3–1982, *A. Carvajal* U. 3 (CR, sterile); [San Ramón,] Laguna cerca de La Palma de San Ramón, 1190 m, 26.VII.1924, *A. M. Brenes* (74) 932 Herb. Brenes (CR 30814, sterile); La Palma de San Ramón, 1175 m, 5.VIII.1924, *A. M. Brenes* (110) 968 Herb. Brenes (CR 30815, sterile); La Palma de San Ramón, 1175 m, 8.VIII.1924, *A. M. Brenes* (64) 1022 Herb. Brenes (CR 30816, sterile); La

Palma de San Ramón, 1175 m, 27.X.1924, *A. M. Brenes* (309) 1168 Herb. Brenes (CR 30817, sterile); Monteverde, Reserva Biológica Monteverde, Río Peñas Blancas, Laguna Pocosol, 10°21'N, 84°40'W, 700–800 m, 26 March 1990, *E. Bello* 2078 (INB); Reserva Biológica Monteverde, Río Peñas Blancas, Refugio Alemán, Quebrada Rojas, 10°18'20"N, 84°45'10"W, 850–900 m, 29 Feb. 1992, *E. Bello* 4448 (INB); San Ramón, Piedades Norte, road to Bajo de La Paz, km 4, summit of Cerro Azahar, 10°08'59"N, 84°35'00"W, 1563 m, 30.01.2005, *F. Pupulin* 5511. *D. Bogarín*, *M. Salas* & *P. Seaton* (JBL-Spirit); San Ramón, Santiago, mountains toward Las Torres de Berlín, 10°02'22"N, 84°29'01"W 1340 m, 2.8.2003, flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin* 4910, *M. Pupulin*, *C. Pupulin*, *H. León-Páez*, *E. Salas*, *D. Bogarín* & *E. Serrano* (CR, JBL-Spirit); San Ramón, Santiago, road to Berlín, ca. km 4, premontane moist forest, epiphytic in secondary vegetation along the roadside, 10°02'32"N, 84°29'31"W 1225 m, 7.3.2004, flowered in cultivation at Jardín Botánico Lankester, 25 May 2005, *F. Pupulin* 5197 & *E. Salas* (JBL-Spirit); Santiago, finca of Jesús Salas Jiménez, mountains toward the towers of Berlín, 10°02'22"N, 84°29'01"W, 1350 m, lower montane rain forest, epiphytic in primary vegetation, 25 December 2004, flowered in cultivation at Jardín Botánico Lankester, 25 May 2006, *F. Pupulin* 5434, *E. Salas-Pupulin*, *S. Dalström*, *C. Lewis* & *J. Salas* (CR); same locality, flowered in cultivation 22 June 2006, *F. Pupulin* 5433, *E. Salas-Pupulin*, *S. Dalström*, *C. Lewis* & *J. Salas* (CR). Cartago: El Guarco, El Empalme, Carretera Interamericana, Cartago to Cerro de La Muerte, 9°44'20"N, 83°57'13"W, 2030 m, 23.7.2003, *M. Whitten* 2126, *M. Blanco* & *D. Bogarín* (JBL-Spirit); Jiménez, Tucurrique, Sabanillas, camino hacia Cerros Duán, ascenso por el margen de la Quebrada Honda, 9°50'39.9"N, 83°45'19.2"W, 1145 m, bosque pluvial premontano, en bosque secundario a orillas de la quebrada, 6 Febrero 2005, floreció en cultivo en el Jardín Botánico Lankester el 27 de Abril 2006, *D. Bogarín* 1337 & *J. C. Cervantes* (CR); same locality, flowered at Jardín Botánico Lankester, 11 March 2006, *D. Bogarín* 1369 & *J. C. Cervantes* (CR);

- Jiménez, Pejivalle, Tausito, Reserva Biológica El Copal, Senderos Tigre, Mariposa y Gárvula, 9°47'02.7"N, 83°45'04.3"W, 1020 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del sendero, 18 Junio 2005, floreció en cultivo en el Jardín Botánico Lankester el 25 de Abril 2006. *D. Bogarín 1615*, *J. Carmona*, *M. G. Gei*, *J. Gómez-Laurito* & *D. Salazar* (CR); Orosi, Parque Nacional Tapantí, sendero Oropendola, 1100–1300 m, 28.12.2004, flowered in cultivation at Jardín Botánico Lankester, 21 Apr. 2005, *M. Blanco 2705*, *D. Bogarín*, *F. Pupulin* & *S. Dalstrom* (JBL-Spirit); Paraíso, Cachí, Peñas Blancas, 380–400 m, 30.1.2004, flowered in cultivation at Jardín Botánico Lankester, July 2005, *G. Chacón s.n.* (JBL-Spirit); Paraíso, Orosi, Purisil, Parque Purisil, orilla de los senderos, bosque pluvial montano a montano bajo, bosque secundario y remanentes de primario, 1400–1500 m, 10.05.2003, flowered in cultivation at Jardín Botánico Lankester, Sept. 2003, *D. Bogarín 187* & *H. León-Páez* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, Mar. 2003, *D. Bogarín 188* & *H. León-Páez* (JBL-Spirit); *D. Bogarín 189* & *H. León-Páez* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, May 2003, *D. Bogarín 198* & *H. León-Páez* (JBL-Spirit!); Turrialba, Jocotea, Finca la Pradera, Valle del Reventazón, 09°47'15"N, 83°32'35"W, 1000 m, 22 June 1995, *G. Rivera 2511* & *A. Rojas* (INB); Turrialba, Moravia de Chirripó, 9°50'18"N, 83°26'45"W, 1135 m, 12.6.2002, *F. Pupulin 3904*, *M. Bonilla*, *R. Gómez*, *H. León-Páez* & *W. Schug* (JBL-Spirit); Turrialba, Santa Cruz, San Antonio, 9°57'56"N, 83°42'32"W, 1400–1450 m, 10.2.2004, flowered in cultivation at Jardín Botánico Lankester, June 2004, *F. Pupulin 5113*, *D. Bogarín*, *A. Karremans* & *H. León-Páez* (CR, JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin 5119*, *D. Bogarín*, *A. Karremans* & *H. León-Páez* (JBL-Spirit!); flowered in cultivation at Jardín Botánico Lankester, 25 May 2006, *F. Pupulin 5112*, *D. Bogarín*, *A. Karremans* & *H. León-Páez* (CR); flowered in cultivation at Jardín Botánico Lankester, July 2004, *D. Bogarín 712*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (JBL-Spirit); same locality, *D. Bogarín 717*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (JBL-Spirit!); *D. Bogarín 720*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, June 2004, *D. Bogarín 706*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (JBL-Spirit); flowered 6 June 2006, *D. Bogarín 713*, *A. Karremans*, *H. León-Páez* & *F. Pupulin* (CR); Santa Cruz, San Antonio, shores of Río Guayabito, Quebrada Loca, premontane rain forest, 9°57'56"N, 83°42'32"W, 1400–1450 m, 10.02.2004, flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin 5118*, *D. Bogarín*, *A. Karremans* & *H. León-Páez* (JBL-Spirit); Santa Cruz, En la Finca Blanco y Negro, laderas del Río Jesús María, 1500 m, 20.02.2005, flowered in cultivation at Jardín Botánico Lankester, 15 July 2005, *A. Karremans 767* (CR!, JBL-Spirit); Santa Cruz, San Antonio, 9°57'56"N, 83°42'32"W, 1400–1500 m, 10.2.2004, flowered in cultivation at Jardín Botánico Lankester, July 2004, *D. Bogarín 719*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (CR, JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, 28 May 2005, *D. Bogarín 717*, *F. Pupulin*, *A. Karremans* & *H. León-Páez* (JBL-Spirit); Santa Cruz, San Antonio, orillas del Río Guayabito, Quebrada Loca 9°57'56"N, 83°42'32"W, 1400–1500 m, 26.9.2004, *A. Karremans 405* & *D. Karremans* (JBL-Spirit!); same locality, *A. Karremans 410* & *D. Karremans* (JBL-Spirit); Santa Cruz, al lado de la carretera, desde los materiales Chinchilla, hasta el centro de Santa Cruz, 1400 m, 19 de Diciembre 2004, floreció en cultivo en el Jardín Botánico Lankester el 16 de Mayo 2006, *A. Karremans 511* (CR); Tayutic, Moravia, 5 Kilometros al oeste del centro de Moravia, sobre sendero al lado de la calle que va a Platanillo, 1000–1200 m, 22.01.2005, flowered in cultivation at Jardín Botánico Lankester, 11 Oct. 2005, *A. Karremans 622*, *D. Karremans* & *P. Ferreira* (CR!, JBL-Spirit); límite entre Turrialba y Jiménez, La Suiza, Pejivalle, Fila Rincón de la Esperanza, entre Río Atirro y Río Nubes, 9°46'43.3"N, 83°37'36.0"W, 1150 m, bosque muy húmedo premontano, epífitas a orillas del camino en bosque secundario, 15 Setiembre 2005, floreció en cultivo en el Jardín Botánico Lankester el 25 de Abril 2006, *D. Bogarín 1823*, *R. L. Dressler*, *M. G. Gei*, *R. Gómez* & *G. Rojas* (CR). Guanacaste: Monteverde, 3.5 km N Santa Elena on road to

- San Gerardo, 0.5 km N of junction road and Río Negro, 10°21'N, 84°48'W, 1540 m, 20 Aug. 1988, *W. Haber 8620 & W. Zuchowski* (INB). Heredia: Barva, Barva, San José de La Montaña, Sacramento, Finca de Emilia Sánchez, cerca de Montaña La Isla, epífita en árboles aislados en potreros, 10°06'58.9"N, 84°07'12.3"W, 2466 m, 21.02.2005, flowered in cultivation at Jardín Botánico Lankester, 19 May 2005, *D. Bogarín 1435, I. Chaves, D. Bogarín & G. Bogarín* (JBL-Spirit); San Isidro-San Rafael, ca. 3 km al norte de Concepción sobre Calle Chilillal, bosque húmedo premontano, epífitas en paredón a orillas del camino, 10°03'44.3"N, 84°02'45"W, 1700 m, 05.06.2005, *D. Bogarín 1523, M. Espinoza & F. Villanea* (JBL-Spirit); Sarapiquí, Above Horquetas, Terra Folia Reserve, near Rara Avis, wet premontane forest, epiphytic, 10°18'14.6"N, 84°01'36.5"W 500 m, 21.07.2003, flowered in cultivation at Jardín Botánico Lankester, May 2004, *W.M. Whitten 2036 & M. Blanco* (JBL-Spirit); Vara Blanca, San Rafael, 1.7 Km después de San Rafael, 10°10'N, 84°07'W 1750 m, 6.7.2002, flowered in cultivation at Jardín Botánico Lankester, 5 Nov. 2002, *F. Pupulin 4081, E. Salas & H. Montealegre* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin 4091, E. Salas & H. Montealegre* (JBL-Spirit); road to Cerro Chompipe, trees in pastures along the road, wet montane forest patches, epiphytic in pastures trees, 10°04'56.6"N, 84°04'41.4"W, 1960 m, 25.07.2003, flowered in cultivation at Jardín Botánico Lankester, July 2004, *M. Whitten 2201, M. Blanco, D. Bogarín & H. León-Páez* (JBL-Spirit). Border between Heredia and Alajuela provinces: Grecia, Sarapiquí, Colonia Virgen del Socorro, road to Cariblanco, bridge on Río San Fernando, 10°15'18"N, 84°10'20"W, 750 m, 29.11.2004, flowered in cultivation at Jardín Botánico Lankester, 31 May 2005, *F. Pupulin 5365, R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit). Limón: Limón, Almirante, 2 km O de Fila Matama, 9°45'20"N, 83°17'20"W, 1350 m, 17 Ago. 1995, *G. Herrera 8541, W. Gamboa & A. Rojas* (CR). Puntarenas: Coto Brus, Las Alturas de Cotón, Fila Cedro, sendero a Río Cedro, 8°58'20"N, 82°52'40"W 1240–1670 m, 20.3.2003, *F. Pupulin 4393, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); Las Alturas de Cotón, Zona Protectora Las Tablas, Las Alturas Biological Station, southern slopes of Cerro Chai, 8°56'59"N, 82°50'01"W, 1500 m, lower montane wet forest, primary vegetation, 26 October 2005, *F. Pupulin 5842, D. Bogarín, R. L. Dressler, R. Gómez, A. Karremans, A. Rambelli & S. Rambelli* (JBL-Spirit); Zona Protectora Las Tablas, sendero El Tajo, 8°58'00"N, 82°54'45"W, 2000 m, 3 Sept. 1992, *A. Fernández 360* (INB); Coto Brus, P.I. La Amistad, Cordillera de Talamanca, Estación Pittier, sendero Río Gemelo, 09°01'30"N, 82°57'40"W, 1680 m, 29 Jan. 1995, *E. Alfaro 12* (CR 191646, sterile); P.I. La Amistad, Cordillera de Talamanca, Estación Pittier, sendero Pittier, 09°01'30"N, 82°57'40"W, 1680 m, 15 July 1995, *E. Navarro 164* (INB); Parque Nacional Amistad, Las Tablas, near the upper Río Cotón, 8°57'N, 82°47'W, 1400–1500 m, 16 Jul. 1982, *C. Todzia 1926, L. D. Gómez & R. W. Pohl* (CR 91668, sterile); San Vito de Java, Río Claro, Fila Cruces-Zapote, 8°47'04"N, 83°02'02"W, 1530 m, 13.11.2002, flowered in cultivation at Jardín Botánico Lankester, July 2003, *F. Pupulin 4244, E. Salas, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin 4242, E. Salas, H. Montealegre & A. C. Rodríguez* (JBL-Spirit); Golfito, Osa-Golfito, La Gamba, "Bosque de los Austriacos," bosques secundarios, 8°42'40"N, 83°13'0"W, 125–400 m, 03.07.2004, flowered in cultivation at Jardín Botánico Lankester, 19 May 2005, *E. Serrano 131 & M. Blanco* (JBL-Spirit); same locality, flowered 11 May 2006, *E. Serrano 133 & M. Blanco* (CR); Osa, Rancho Quemado, sector este, Sierpe, 8°42'20"N, 83°33'40"W, 200–230 m, 9 Nov. 1991, *J. Marín 284* (INB); Puntarenas: Cuencas del Lagarto y Guacimal, Monteverde, 10°15'42"N, 84°48'00"W, 1300 m, 13 Abr. 1994, *K. Martínez 340* (INB); Santa Elena, Monteverde, Bullpen, ca. 1500 m, 29.4.2003, flowered in cultivation at Jardín Botánico Lankester, July 2003, *F. Pupulin 4716 & G. Barboza* (JBL-Spirit). San José: Alajuelita, La Cruz de Alajuelita, epífita en árboles cerca de un Río, 09 de Mayo de 1999, floreció en cultivo el 25 de Abril 2006, *Chacón-Valverde, D. García, A. Viquez & G. Viquez s.n.* [JBL-09376] (CR); Braulio Carrillo

Park, near La Montura, 1100–1200 m, 17 Sept. 1984, *J. B. Folsom 11016* (CR 105569, sterile); *J. B. Folsom 11017A* (CR 105569, sterile); Dota, Copey, Providencia, Zapotal, Montaña fría en las márgenes del Río Savegre, 9°31'59"N, 83°50'12"W, 1630 m, 11 Jul. 2002, *J. Sánchez 1305* (CR 229957); Dota, Santa María, unpaved road to San Joaquín, 9°35'30"N, 84°58'26"W, 1620 m, 23.3.2004, flowered in cultivation at Jardín Botánico Lankester, June 2004, *F. Pupulin 5204* & *H. León-Páez* (JBL-Spirit); same locality, *F. Pupulin 5209* & *H. León-Páez* (JBL-Spirit); *F. Pupulin 5211* & *H. León-Páez* (JBL-Spirit); Pérez Zeledón, General Viejo, La Hermosa, 9°18'N, 83°46'W, 780 m, 10.11.2001, flowered in cultivation at Jardín Botánico Lankester, Nov. 2002, *F. Pupulin 3419*, *H. Montealegre* & *A. C. Rodríguez* (USJ); same locality, flowered in cultivation at Jardín Botánico Lankester, June 2002, *F. Pupulin 3420*, *H. Montealegre* & *A. C. Rodríguez* (CR, JBL-Spirit); Miraflores, road to Santa Cruz, 1350 m 2.12.2001. *F. Pupulin 3480*, *D. Castelfranco* & *J. Cambroner* (JBL-Spirit); Montecarlo, along the Río Peñas Blancas, 9°22'11"N, 83°35'04"W 1274 m, 6.7.2003, *F. Pupulin 4815*, *M. Pupulin*, *C. Pupulin*, *G. Castelfranco* & *H. León-Páez* (JBL-Spirit); same locality, *F. Pupulin 4824*, *M. Pupulin*, *C. Pupulin*, *D. Castelfranco* & *H. León-Páez* (JBL-Spirit); Peñas Blancas, along the Río Peñas Blancas, 9°19'20"N, 83°37'08"W ca. 800 m, 6.7.2003, flowered in cultivation at Jardín Botánico Lankester, June 2004, *F. Pupulin 4819*, *M. Pupulin*, *C. Pupulin*, *G. Castelfranco* & *H. León-Páez* (JBL-Spirit); road from San Isidro to Dominical, turning to Pacuarillo, Bijagual, 9°17'35.5"N, 83°45'24.0"W, 1000 m, premontane wet forest, 23 October 2005, flowered in cultivation at Jardín Botánico Lankester, 25.4.2006, *F. Pupulin 5770*, *D. Bogarín*, *R. L. Dressler*, *R. Gómez*, *A. Karremans*, *A. Rambelli* & *S. Rambelli* (CR); same locality, flowered in cultivation at Jardín Botánico Lankester, 14 June 2006, *F. Pupulin 5799*, *D. Bogarín*, *R. L. Dressler*, *R. Gómez*, *A. Karremans*, *A. Rambelli* & *S. Rambelli* (CR); San Ramón, camino lastreado a Las Pegas, Páramo, Los Ángeles, 9°29'01"N, 83°45'16"W 1480 m, 20.4.2003, flowered in cultivation at Jardín Botánico Lankester, July 2003, *F. Pupulin 4662*, *J.*

*Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (JBL-Spirit); same locality, *F. Pupulin 4680*, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (JBL-Spirit); *F. Pupulin 4684*, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, May 2004, *F. Pupulin 4639*, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (CR!, JBL-Spirit); flowered in cultivation at Jardín Botánico Lankester, 25 May 2006, *F. Pupulin 4644*, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (CR); San Ramón, camino a Los Ángeles de Páramo, 9°28'14"N, 83°44'59"W 1800 m, 20.4.2003, flowered in cultivation at Jardín Botánico Lankester, 6 May 2005, *F. Pupulin 4700*, *J. Cambroner*, *H. León-Páez*, *M. Powell*, *E. Salas* & *V. Savolainen* (JBL-Spirit); San Ramón Norte, Cerro Pelón, 1420–1640 m, 3.5.2000, flowered in cultivation at Jardín Botánico Lankester, July 2004, *F. Pupulin 2397*, *M. L. Spadari*, *J. Cambroner*, *V. Suárez-Pérez* & *K. Granados* (CR, JBL-Spirit); Tarrazú, San Marcos, Santa Marta, unpaved road to Nápoles, about km 4, 9°36'40"N, 83°00'51"W, 1412 m, 23.3.2004, *F. Pupulin 5222*, & *H. León-Páez* (JBL-Spirit); Turrubares, ca. 2 km N of Bijagual, near Bijagual guard station, Carara reserve, 9°45'N, 84°34'W, 430 m, 7 Aug. 1985, *M. H. Grayum 5886*, *R. Werner*, *J. C. French* & *P. Sleeper* (INB). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, 5.8.2004, *A. Karremans 332* & *333* (JBL-Spirit); 1.7.2004, JBL-04898 (JBL-Spirit).

**Etymology:** from the Greek *poikilos*, spotted, and *anthos*, flower, in reference to the heavily spotted sepals and petals of this species.

**Ecology:** a widespread species in tropical to submontane wet forests at 200–2500 m elevation, often forming large clumps. Large populations of *D. poicillantha* are commonly found in shady areas along the Caribbean slopes and close to the continental divide in the Tilarán and Central Volcanic ranges, as well as on both the watersheds of the Cordillera de Talamanca. No records are known from the northern volcanic chain of Guanacaste. Flowering has been recorded throughout the year, with a flowering

peak during the months between May and July, corresponding to the beginning of the rainy season in the country.

As the oldest name of a complex of Mesoamerican *Dichaea* that shows a vast array of variations both in vegetative and floral morphology, the *D. poicillantha* concept is the core of the greatest taxonomic problem in the concerned area. No isotypes, syntypes, or paratypes for this species exist. The drawing at AMES (31572!) designated as the type shows the broad ligule and the labellar outline that are diagnostic characters (Fig. 60). Nonetheless, material currently assigned to this taxon differs in many ways from the sketch prepared from the holotype, particularly in the shape of the hypochile and the lateral lobes of the lip, and the circumscription of specific boundaries for *D. poicillantha* is one of the mayor challenges to the student of *Dichaea* in Mesoamerica. During the preparatory work intended for the present study, hundreds of living specimens somewhat referable to the *D. poicillantha* concept were grown under similar conditions, studied, photographed, and drawn. Because of the exceeding variability in vegetative architecture, the field-collected specimens were grouped into three main morphs, according to leaf arrangement, size, shape, texture, and color. Morph 1 included plants with closely spaced, thick-herbaceous to subcoriaceous, short (<10 mm long), broadly ovate, bronze-green leaves. The leaves of plants of morph 2 were closely spaced, soft-herbaceous, comparatively short (<13 mm long), lanceolate and medium green. Within morph 3 were grouped plants with well-spaced, soft-herbaceous, comparatively large (to 25 mm), narrowly elliptic-lanceolate, medium green to pale olive green leaves (grossly corresponding to the *D. muricatoides* concept). Variations in flower morphology mainly lay in flower size, relative size of sepals and petals, and the size of the petaloid clinandrium. However, no correlation was observed between morphs on the basis of vegetative characters and the corresponding flower morphology.

Genetic samples of two of the extreme variations (*W. M. Whitten 2030* [morph 1], and *F. Pupulin 4662* [morph 3], both JBL-Spirit!) were analyzed by Kurt Neubig at the Florida Museum of Natural History using a combined three-gene matrix, and they were found to be

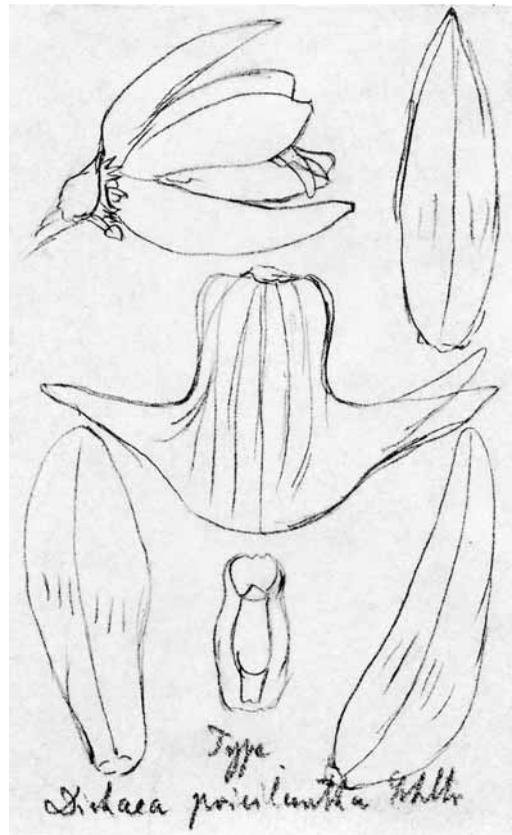


FIGURE 60. Copy of Schlechter's sketch of *Dichaea poicillantha* Schltr., *Wercklé 32* (AMES). Reproduced with the kind permission of the Director, Harvard University Herbaria.

conspecific (K. Neubig, pers. comm.). The inclusion of these variations results in a species difficult to define on the sole basis of morphological characters. Potential synapomorphies include the stiffly pendent, multi-branched habit; the greyed-orange background color of the sepals; the transversely elliptic, rounded-apiculate epichile provided with long, narrowly ligulate lateral lobes, almost transversal to the lip axis when spread; and the broad, truncate ligule of the column.

Folsom (1987: 158) noted that populations of *Dichaea muricatoides* collected near Costa Rica are difficult to distinguish if not inseparable from *D. poicillantha*. From the large samples of living specimens of the different morphs of *D. poicillantha* collected all over the country, and at least one specimen from Nicaragua (*A. Karremans 1140*, JBL-Spirit! and living collec-

tion), I find no way to recognize a distinct subset to which the name *D. muricatoides* could be applied. The aim of the present work is to resolve the taxonomic identity of Costa Rican populations of *Dichaea*, and on that basis I will simply exclude *D. muricatoides* from the flora of Costa Rica. However, it is my personal belief that *D. muricatoides* should be reduced in synonymy under the older name *D. poicillantha*, although my limited knowledge of material from the northern portion of the Central American isthmus and from Mexico precludes at the moment such a definitive conclusion. Folsom (1987) proposed to neotypify *D. tuerckheimii* Kraenzl. (the basionym of *D. muricatoides*) with material collected by H. von Tuerckheim in Alta Verapaz (US), but the recent finding by the author of the holotype in Reichenbach's Herbarium in Vienna (Guatemala. *H. von Tuerckheim s.n., Rchb. Orch. 12932!*, W) (Fig. 61) makes this decision superfluous.

23. *Dichaea sarapiquinsis* Folsom, Orch. Digest 58: 188–189. 1994. TYPE: COSTA RICA. Heredia: near Pto. Viejo, on trees along stream system in property adjacent to La Selva Biological Preserve, 22 May 1981, *J. P. Folsom* 9999 (Holotype: CR; Isotype: TEX [not seen]). Fig. 62, Map 8.

*Plant* epiphytic, caespitose, to 60 cm long. *Roots* filiform, exposed at the base, the caulinar roots mostly hidden by leaf sheaths, 0.4–0.6 mm in diam. *Stems* laxly pendent, flattened, 20–60 cm long, 0.8–1.2 mm wide across conduplicate sheaths, rarely branching. *Leaves* widely spaced along stem, spreading-retorse, thin-herbaceous, olive green, 7–9 × 3.0–3.8 mm, ovate-lanceolate, subacute, the apex shortly acuminate, abaxially apiculate, the apical margins irregularly and minutely serrulate, curled backwards, without conspicuous cross-veining; sheaths clasping, the margins free, undulate, 4.0–4.5 × 2.0–2.5 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage; pedicel terete, geniculate to become perpendicular to stem, 7–11 mm long, provided with 2–3 basal, tubular, short acuminate bracts, expanding apically, 4–5 mm long. *Floral bract* double, the outer bract widely ovate, acuminate, cucullate, 2.5–3.0 × 2.5 mm, the inner bract narrowly lanceolate, 2.5 mm long. *Pedicel* cylindric, ca. 1 mm long. *Ovary* 1 mm long, densely muricate. *Flower* small, sub-

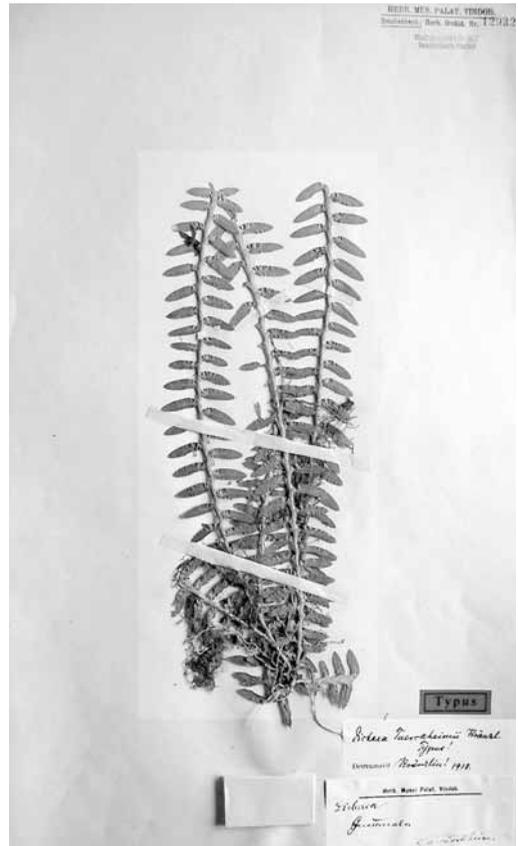


FIGURE 61. Holotype of *Dichaea tuerckheimii* Kraenzl., *Wercklé 32 (Rchb. Orch. 12932!*, W). Reproduced with the permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

spreading, the sepals cream-white, barred to boldly blotched with violet-purple, abaxially sparsely low-tuberculate, the lip almost completely violet, with a white band at the apex of the hypochile; the column white, marked with violet along wings and on the foot; no fragrance detected. *Dorsal sepal* somewhat curved over the column, concave, oblong, acute, 7–9 × 2.7–3.0 mm. *Lateral sepals* obliquely elliptic-lanceolate, concave, acute, 7–8 × 3 mm. *Petals* broadly oblanceolate, incurved toward apex, subacute, 6–7 × 3.5–4.0 mm. *Lip* 3-lobed, anchoriform, with an indistinct claw, 6 × 7.0–8.5 mm when spread, the claw 0.5 mm, the hypochile broadly cuneate, with indistinct, rounded shoulders, 3 mm long, 5 mm wide at apex, the epichile transversely ovate-elliptic, truncate, sometimes shortly apiculate, low tuberculate toward apex, 3 × 7 mm,

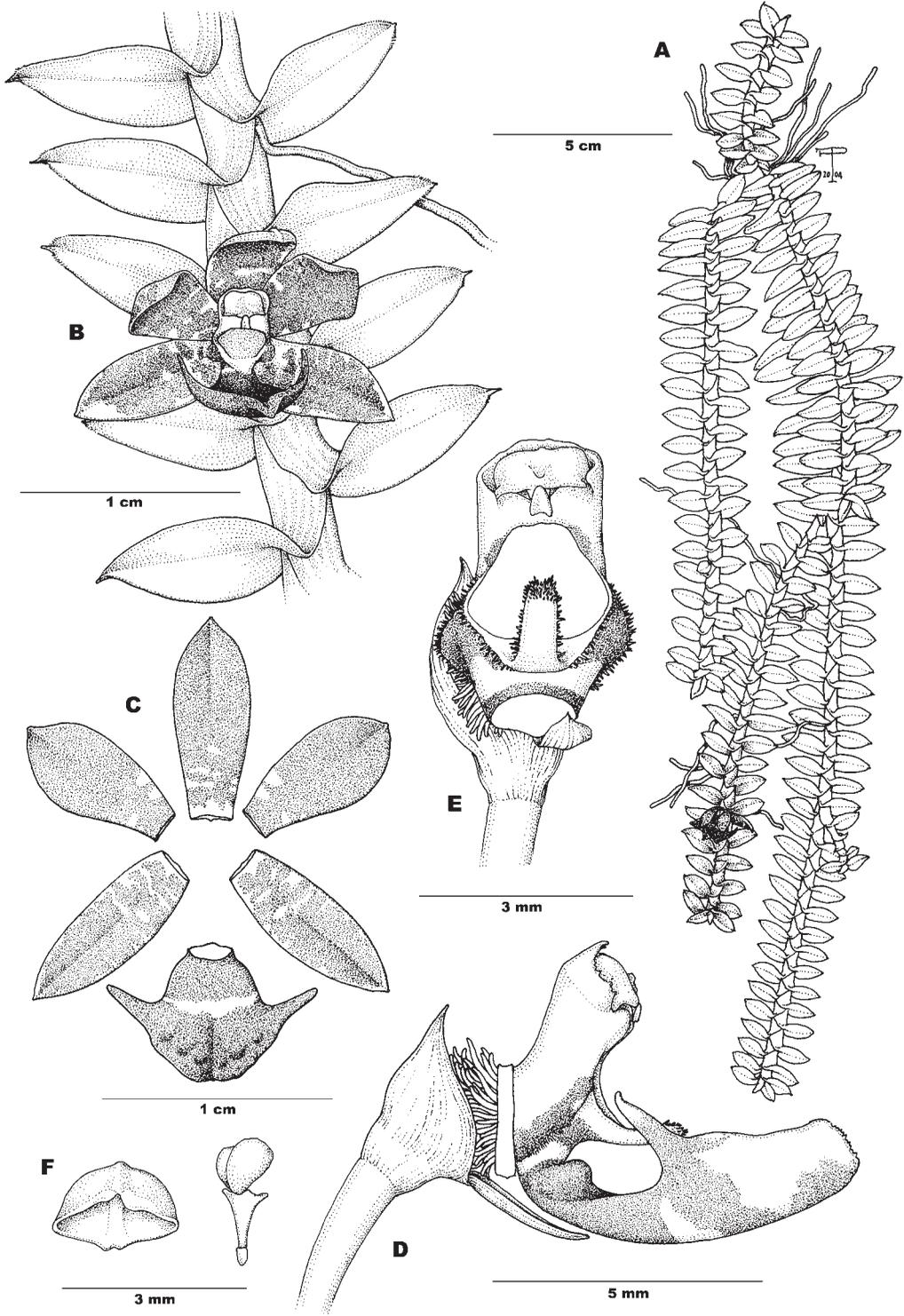


FIGURE 62. *Dichaea sarapiquinsis* Folsom. A, Habit; B, flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium (only two pollinia shown). Drawn from Pupulin et al. 4856 (JBL-Spirit).

laterally producing recurved, linear-subulate, acute lobes, 2.0–2.5 × 1.0–1.3 mm. *Column* erect, 5 mm long, with distinct foot, the clinandrium shallowly cucullate, irregularly erose-crenulate, provided with rounded, flattened, ciliate wings; the stigma transversely rhombic; ligule projecting to apically slightly curved upward, oblong, truncate, apically short hispid, 1.5 × 0.5 mm. *Anther cap* broadly ovate, cucullate, flattened, 2-celled. *Pollinia* 4, in two pairs of different size, on a narrowly obtriangular, apically dilated stipe; the viscidium elliptic-peltate, hyaline. *Fruit* an elliptic capsule, densely muricate.

**Distribution:** known only from Costa Rica.

**Additional material examined:** COSTA RICA: Alajuela: Grecia, Sarapiquí, San Miguel, unpaved road to the west of the village, 10°16'04.7"N, 84°11'01.4"W, ca. 500 m, on short trees along the roadside, tropical wet, transition to premontane wet forest, 16 June 2005, flowered in cultivation at Jardín Botánico Lankester, 14 Aug. 2006, *F. Pupulin 5694*, *D. Bogarín & A. C. Rodríguez* (CR); San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 400 m, shores of Río Sarapiquí, tropical wet, belt transition to premontane wet forest, 29 November 2004, *F. Pupulin 5330*, *R. L. Dressler, K. Dressler & J. Warner* (USJ); *F. Pupulin 5337*, *R. L. Dressler, K. Dressler & J. Warner* (USJ); same locality, flowered in cultivation at Jardín Botánico Lankester, 17 January 2005, *F. Pupulin 5333*, *R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit); 4 August 2006, *F. Pupulin 5341*, *R. L. Dressler, K. Dressler & J. Warner* (CR); Sarapiquí, San Miguel, road to Colonia Carvajal, right side of the road just before the first bridge on Río Sarapiquí, 10°18'58"N, 84°11'05"W, 450 m, 16.6.2005, *F. Pupulin 5692*, *D. Bogarín & A. C. Rodríguez* (JBL-Spirit). Heredia: Sarapiquí, Horquetas, road to Rara Avis, ca. 6 km, granja La Selva, 10°20'15"N, 84°00'15"W, 275 m, tropical rain forest, along the edge of pasture, 26 July 2003, *F. Pupulin 4856*, *M. Pupulin, C. Pupulin, C. Ossenbach & B. Arias* (JBL-Spirit); Sarapiquí, Llanura de Santa Clara, Río Puerto Viejo cerca de Horquetas, 10°21'39"N, 83°58'08"W, 150 m, 22 Sept. 1995, *J. F. Morales 4815* (INB). Border between Heredia and Alajuela provinces: Grecia, Sarapiquí, Colonia Virgen del Socorro, road to Cariblanco, bridge on Río San Fernando,

shores of Río San Fernando, 10°15'18"N, 84°10'20"W, 750 m, tropical wet, belt transition to premontane wet forest, 29 November 2004, flowered in cultivation at Jardín Botánico Lankester, 14 Aug. 2006, *F. Pupulin 5354*, *R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit); same locality, *F. Pupulin 5367*, *R. L. Dressler, K. Dressler & J. Warner* (JBL-Spirit). Limón: Pococí, Guápiles, Parque Nacional Braulio Carrillo, Sector Quebrada González, Sendero Botarrama hacia orillas del Río Sucio, 10°9'9.3"N, 83°56'43.5"W, 467 m, bosque muy húmedo tropical transición a premontano, epifitas en bosque secundario alrededor del sendero, 12 Junio 2005, *D. Bogarín 1559* (JBL-Spirit); Guápiles, carretera Braulio Carrillo, 500 m hacia abajo de la entrada del Teleférico del Bosque Lluvioso, orillas de la Quebrada El Molinete, 506 m, 10°11'34"N, 84°54'16"W, bosque muy húmedo tropical transición a premontano, epifitas a orillas del río, 9 Julio 2004, floreció en cultivo en el Jardín Botánico Lankester, 14 Aug. 2006, *D. Bogarín 877 & F. Pupulin* (JBL-Spirit).

**Etymology:** named from the Costa Rican region and river (Sarapiquí) where populations including the type specimen were originally found.

**Ecology:** epiphytic in wet and warm tropical forests, mostly along rivers, between 200 and 400 m elevation, along the Caribbean plains and the basal slopes of the Central Volcanic chain. Plants grow in medium shade, mostly along water streams, where they form large populations. Flowering has been recorded from November to May, but likely the plants flower most of the year.

*Dichaea sarapiquinsis*, so far exclusively known from Costa Rica, is closely related to *D. obovatipetala*, which ranges southward to Panama. The differences among the two taxa are subtle, mainly consisting of a different organization of the stems (laxly pendent, rarely branched in *D. sarapiquinsis* vs. scandent to stiffly pendent and many-branched in *D. obovatipetala*), the shape of the lip epichile (subtruncate in *D. sarapiquinsis* vs. rounded, apically infolded in *D. obovatipetala*), and the presence in *D. sarapiquinsis* of low but distinct tubercles along the veins toward the adaxial leading edge of the lip, which are absent in *D. obovatipetala*. Among Costa Rican species of the sect. *Dichaea*, this ridging is diagnostic of *D. sarapiquinsis*. As noted by Folsom (1987),

the flowers of *D. sarapiquinsis* also show a general tendency in having a less strongly violet color pattern when compared with *D. obovatipetala*, but this character is rather variable in the examined specimens.

24. *Dichaea similis* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 307. [November] 1923. TYPE: COSTA RICA. [Alajuela:] Umgebung von San Ramón, im Jahre 1921, *G. Acosta s.n.* (Holotype: B, destroyed; Isotype: AMES 40552 [a fragment of stem]; copy of Schlechter's drawings of the type, made under the supervision by Schlechter's, AMES 40552]. Fig. 63, Map 9.

Synonym: *Dichaea schlechteri* Folsom, Orch. Digest 58: 189–190. 1994, *syn. nov.* TYPE: COSTA RICA. San José: Braulio Carrillo Park, 500–700 m, 16 Sep. 1984, *J. P. Folsom 11005* (Holotype: CR; Isotype: TEX [not seen]).

*Plant* epiphytic, caespitose, to 60 cm long. *Roots* flexuous, glabrous, ca. 0.4 mm in diam., exposed at the base of the stem, the caulinar roots mostly hidden by leaf sheaths, rarely aerial. *Stems* flattened, patent (when young) to pendent, rarely branching, 15–60 cm long, 0.2–0.3 cm wide across conduplicate sheaths. *Leaves* closely spaced along stem, not overlapping, spreading, green, soft-herbaceous, broadly ovate, obtuse, minutely apiculate, 6–11 × 4–9 mm; sheaths tightly clasping the stem, to 6 × 7 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, patent, the peduncle geniculate, 1.2–1.5 cm long, provided at the base with 2 tubular, papyraceous bracts, 0.2 cm long. *Floral bract* double, the outer bract infundibuliform, ovate, shortly acuminate, shorter than pedicellate ovary, 2.5 × 3.5 mm, the inner bract narrowly lanceolate, acute, 2.5 mm long. *Pedicel* cylindrical, to 1.7 mm long. *Ovary* long muricate, 2 mm long. *Flower* ringent to subspreading, with sepals and petals greenish white, spotted with violet, the sepals externally sparsely tuberculate, the lip white, speckled with violet, the column white, marked with purple on the wings and along the margins of the stigma. *Dorsal sepal* narrowly elliptic-lanceolate, acute, 6–12 × 2.5–4.0 mm. *Lateral sepals* obliquely narrowly elliptic-lanceolate, subfalcate, acute to subacuminate, 6–10 × 2.5–3.5 mm. *Petals* lanceolate, shortly acuminate, 6–10 × 3–4 mm. *Lip* 3-lobed, clawed, 5–7 × 7–9 mm when spread, the claw linear, basally

thickened-subterete, the hypochile transversely elliptic-cuneate, without shoulders, the margins ciliate, 3.0–4.5 mm wide apically, the epichile triangular, apiculate, the apical margins introrse, the lateral lobes narrowly triangular-subulate, acuminate, spreading, to 3.0 × 0.8 mm. *Column* erect, 4 mm long, provided with small, narrowly elliptic, sparsely short-ciliate wings, the clinandrium petaloid, irregularly erose; ligule narrowly triangular-linear, truncate, tomentose, 2.5 × 0.8 mm. *Anther cap* broadly ovate, cucullate, flattened, 2-celled. *Pollinia* 4 in two superposed pairs subequal in size, on a obtriangular, obtuse-subtruncate stipe; viscidium elliptic. *Fruit* not seen.

**Distribution:** Costa Rica and Nicaragua.

**Additional material examined:** COSTA RICA. Alajuela: Alfaro Ruiz, Naranjo, Palmira, Bajos el Toro, camino a Catarata del Rio Toro, ca. Km 2.5, 10°15'00"N, 84°16'23"W, 1230 m, 13.4.2003, flowered in cultivation at Jardín Botánico Lankester, June 2004, *F. Pupulin 4594*, *E. Salas & H. León-Páez* (JBL-Spirit); same locality, *F. Pupulin 4598*, *E. Salas & H. León-Páez* (JBL-Spirit); Grecia, Sarapiquí, entre Cariblanco e Isla Bonita, Cuesta Angel, 10°15'40"N, 84°10'26"W, 933 m, 23.12.2004, *D. Bogarín 1157 & M. Blanco* (JBL-Spirit); Palmira, Pueblo Nuevo, camino a los Bajos del Toro, 2050 m, 30.8.2001, flowered in cultivation at Jardín Botánico Lankester, 31 May 2005, *F. Pupulin 3284*, *D. Castelfranco*, *M. Pupulin & C. Pupulin* (JBL-Spirit); San Carlos, Ciudad Quesada, plaza de la nueva terminal de buses, 10°19'56"N, 84°25'59"W, 590 m, 25.03.2001. *W. Schug 205 & M. E. Naranjo Vargas* (JBL-Spirit); San Ramón, Ángeles, Reserva Biológica Alberto Brenes, 10°13'08"N, 84°35'48"W, 900–1000 m, 25.9.2005, *D. Bogarín 1932* (JBL-Spirit); Santiago, mountains toward Las Torres de Berlín 10°02'22"N, 84°29'01"W, 1340 m, lower montane wet forest, epiphytic in primary forest and secondary vegetation along pastures and coffee plantations, 2 Aug. 2003, *F. Pupulin 4919*, *M. Pupulin*, *C. Pupulin*, *E. Salas*, *H. León-Páez*, *D. Bogarín & E. Serrano* (CR); Santiago, finca of Jesús Salas Jiménez, mountains toward the towers of Berlín, 10°02'22"N, 84°29'01"W, 1350 m, lower montane rain forest, epiphytic in primary vegetation, 25 Dec. 2004, flowered in cultivation at Jardín Botánico Lankester, 16 Aug. 2006, *F. Pupulin 5417*, *E. Salas-Pupulin*, *S. Dalström*, *C. Lewis & J. Salas* (CR). Heredia:

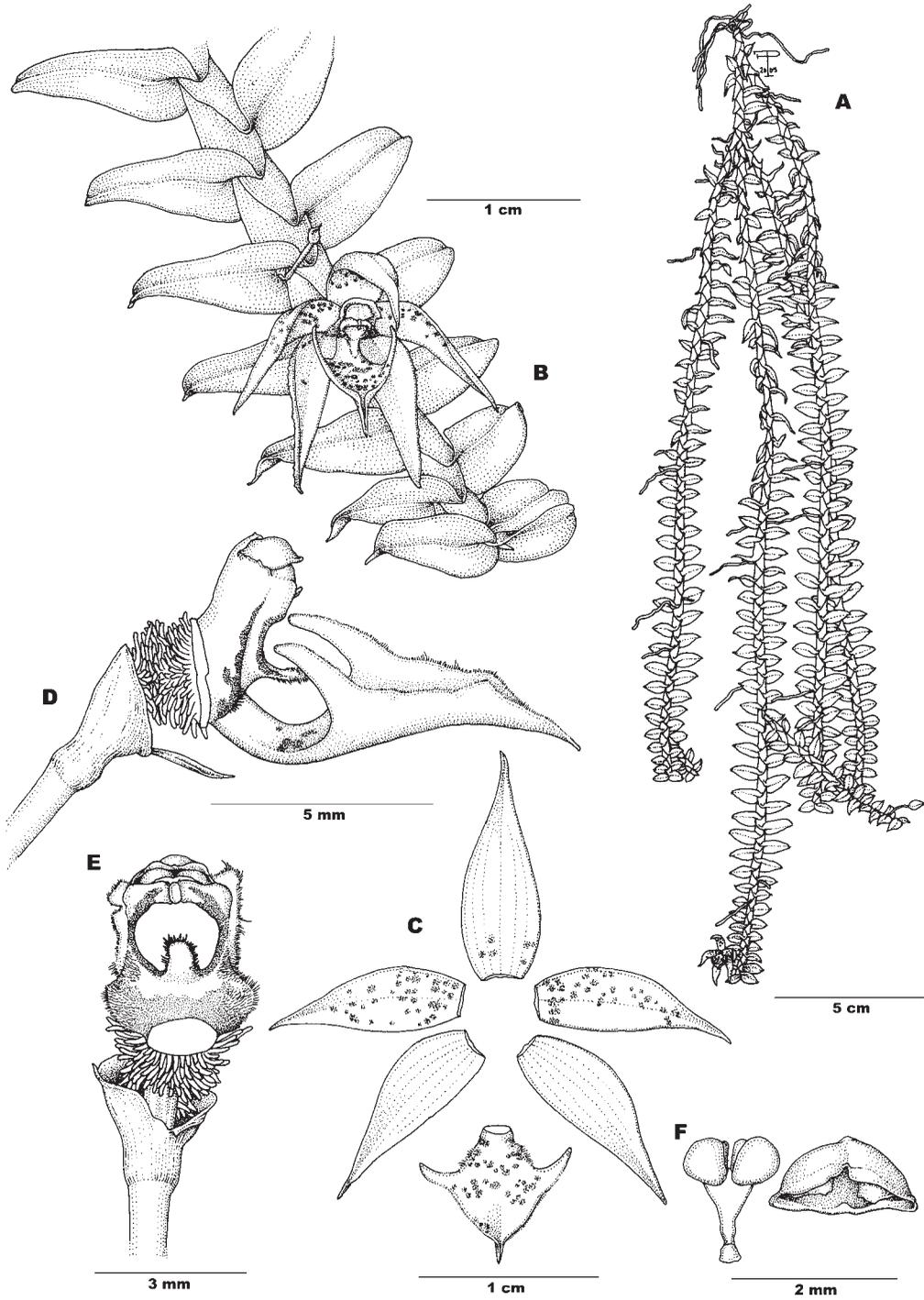
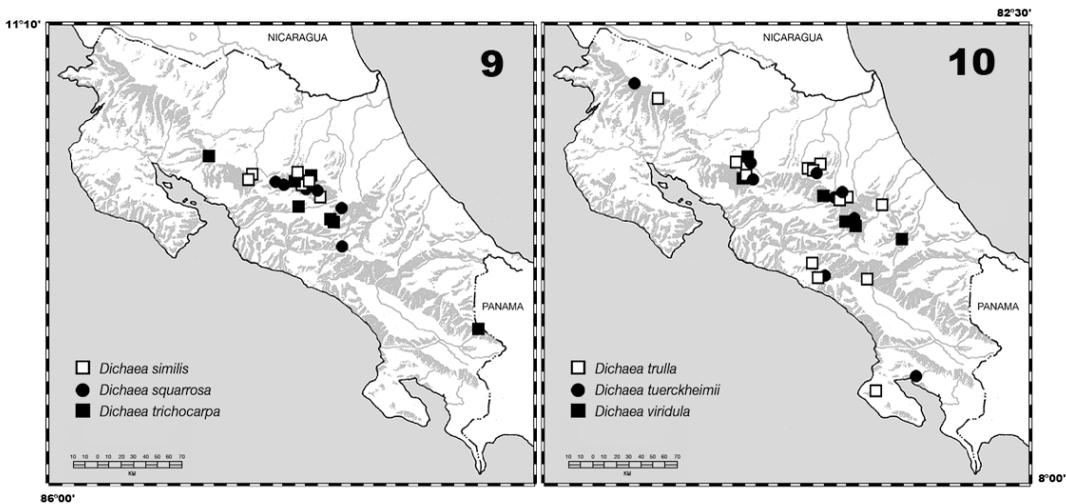


FIGURE 63. *Dichaea similis* Schltr. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, pollinarium and anther cap. Drawn from *Pupulin* 4808 (JBL-Spirit).



MAPS 9–10. Distribution of *Dichaea* in Costa Rica. 9, *D. similis*, *D. squarrosa*, and *D. trichocarpa*; 10, *D. trulla*, *D. tuerckheimii*, and *D. viridula*.

San Rafael camino hacia el Cerro Achiotillal, entre Río Nuevo y Quebrada Cabra, 10°07'48"N, 84°02'23"W, 1700 m, 15.7.2003, flowered in cultivation at Jardín Botánico Lankester, January 2003, *D. Bogarín* 328, *A. Prendas & L. Prendas* (USJ, JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, January 2003, *D. Bogarín* 329, *A. Prendas & L. Prendas* (USJ, JBL-Spirit); *D. Bogarín* 330, *A. Prendas & L. Prendas* (JBL-Spirit); Vara Blanca, San Rafael, 1.7 km después de San Rafael, a lo largo del Río San Rafael 10°10'N, 84°07'W, 1750 m, 6.7.2002, flowered in cultivation at Jardín Botánico Lankester, January 2004, *F. Pupulin* 4089, *E. Salas & H. León-Páez* (JBL-Spirit); Vara Blanca, San Rafael, puente sobre el Río San Rafael, 10°10'35"N, 84°07'57"W, 1811 m, 23.12.2004, *D. Bogarín* 1179 & *M. Blanco* (JBL-Spirit); Braulio Carrillo, San Jerónimo de Moravia, km 13, 30 may 1987, *E. Vargas* 23 (USJ) Without specific locality, 30.01.2005, flowered in cultivation at Jardín Botánico Lankester, 31 May 2005, *J. Warner s.n.* (JBL-Spirit); without specific locality, collected by C. Surroca, flowered in cultivation at Jardín Botánico Lankester, 30 April 2005, *F. Pupulin* 5644 (CR, JBL-Spirit); Without collecting locality, flowered in cultivation on a tree at Jardín Botánico Lankester in Dulce Nombre de Cartago, 18.6.2003, *F. Pupulin* 4808 (USJ, JBL-Spirit).

**Etymology:** from the Latin *similis*, similar, alike, originally used by Schlechter in reference to the similarity of this species to *D. ovatipetala*, here treated as a synonym of *D. cryptarrhena*.

**Ecology:** uncommon epiphyte in the submontane wet forests of the Tilarán and Central Volcanic ranges, at 500–1100 m elevation. Flowering occurs at least from January to September.

The adoption in this treatment of the name *Dichaea similis* is the most reasonable solution to accommodate a number of *Dichaea* specimens, mainly native from the Caribbean slopes of the Tilarán and Central Volcanic mountain ranges, which do not fit a strict concept of *D. cryptarrhena* as it is adopted here. Plants of *D. cryptarrhena* may show some variability in leaf size and shape, mainly in the juvenile phase, but mature, healthy specimens are usually recognized by their broad, thick-herbaceous, overlapping leaves. Floral morphology is remarkably consistent in this species. The problem of a satisfactory disposition for a number of *Dichaea* plants with more scandent habit, provided with smaller leaves of a thinner substance, closely spaced along the stem but usually not overlapping, was first addressed by Folsom in his monographic treatment of sect. *Dichaea* (Folsom, 1987: 222–226). In 1994 he formally proposed to group these plants under his *D. schlechteri*, typified by a specimen from the Braulio Carrillo National Park, along the basal slopes of the Cordillera Volcánica Central,

although he claimed for the difficulty of resolving the relationships in the complex of *D. cryptarrhena*/*D. poicillantha*/*D. oxyglossa* (Folsom, 1994: 189–190). In the present treatment I agree with Folsom in recognizing the separate nature of this taxon, but I find it inseparable from Schlechter's concept of *D. similis* (1923d), which Folsom included under the synonymy of *D. cryptarrhena*. As circumscribed here, *D. similis* encompasses plants with stiff-pendent to subscaudent habit and spreading, soft-herbaceous leaves closely spaced along stem, not overlapping and rarely longer than 10 mm. The flowers of *D. similis* have sepals and petals with few violet spots, frequently concolorous pale green, and the column has comparatively more prominent wings and a narrower ligule with respect to *D. cryptarrhena*. Furthermore, the lateral lobes of the epichile of *D. similis* are spreading to slightly retrorse, whereas the lip of *D. cryptarrhena* has strongly retrorse-falcate to uncinately lateral lobes. Hamer (1982b) illustrated a plant from Nicaragua referable to this concept. Genetic material from a single specimen of *D. similis* from Costa Rica (as *Dichaea schlechteri*, *D. Bogarín 329*, voucher in the Spirit collection of Lankester Botanical Garden) was analyzed by Kurt Neubig at the Florida Museum of Natural History, University of Florida. The plastid data gave a unique phylogenetic position, showing *D. similis* sister to *D. cryptarrhena*, but ITS gave a strongly polymorphic signal. Four clones of this PCR yielded two different copies when sequenced, three of which were congruent with the plastid data, and the fourth most closely related to *D. oxyglossa* (Neubig, 2005). These data seemingly point toward the two parental types expected in nuclear DNA from an interspecific hybrid, and Neubig (2005) suggests that the sequenced accession is probably a recent hybrid between the true *D. similis* and *D. oxyglossa*. The potential presence of hybrid swarms in the genus may perhaps explain the difficulty in establishing clear-cut circumscriptions between species of *Dichaea* of the *D. cryptarrhena*/*D. poicillantha*/*D. oxyglossa* complex.

25. *Dichaea squarrosa* Lindl., Ann. Nat. Hist. 4: 384. 1840. TYPE: MEXICO. Mountains of Tequila, Hartweg s.n. (Holotype: K; Isotype: K [drawing]). Fig. 64, Map 9.

*Plant* epiphytic, caespitose, to 20 cm long. *Roots* basal and caulinar, often exposed and

aerial or hidden by leaf sheaths, flexuous, minutely verrucose, to 2.2 mm in diam. *Stems* subterete, scandent to pendent (rarely suberect), freely branching, 6–20 cm long, 0.3–0.5 cm wide across conduplicate sheaths. *Leaves* widely spaced along stem, spreading-retrorse, grayed-green, thick-succulent, 4–14 × 2–4 mm, lanceolate, obtuse to rounded, minutely apiculate; sheaths tightly clasping the stem, to 8 × 3 mm. *Inflorescences* solitary, 1-flowered, emerging above foliage, the peduncle geniculate, 4–7 mm long, provided at the base with a tubular, acute bract, about 2 mm long. *Floral bract* double, the outer bract widely triangular-funnelform, acute, 2 × 2 mm, the inner bract narrowly lanceolate, 2 mm long. *Pedicel* cylindrical, ca. 1 mm long. *Ovary* short muriculate, 1 mm long. *Flower* commonly ringent, rarely spreading, strongly scented, with sepals and petals thick-succulent, cream-yellow to pale orange, the sepals externally tuberculate, the lip white, barred and blotched violet toward the base, apically solid violet, the column white to pale orange-yellow, marked with violet on the margins of wings and along the stigmatic rim. *Dorsal sepal* elliptic, obtuse to shortly acute, 6.7–8.0 × 3–4 mm. *Lateral sepals* obliquely broadly elliptic, asymmetrical, shortly acute, 6.8–8.0 × 4.0–4.5 mm. *Petals* elliptic-oblong, shortly subacute, 6.0–8.0 × 3.0–5.5 mm. *Lip* 3-lobed, subsessile, 5.0–5.8 × 5.7–7.1 mm when spread, the hypochile widely obtusely rounded, with scarcely pronounced, glabrous shoulders, 5 mm wide apically, the epichile triangular, obtuse, apiculate, the lateral lobes broadly triangular, rounded, spreading, decurrent on the lamina, 1.3 × 1.0 mm. *Column* suberect, 4.5 mm long, provided with rounded, flattened, ciliate wings, the apical reclined clinandrium small, continuous with the basal wings; ligule small, broadly triangular, projecting downward, truncate, pubescent, 0.7 × 1.7 mm. *Anther cap* broadly cordate, 2-celled. *Pollinia* 4 in two superposed pairs of slightly different size, on a narrowly obtriangular-ligulate, broadly obtuse stipe; viscidium elliptic, hyaline. *Fruit* a muriculate capsule.

**Distribution:** Mexico to western Panama.

**Additional material examined:** COSTA RICA. Alajuela: vicinity of Fraijanes, *P. C. Standley & R. Torres R. 47555, 47611* (AMES); Zarcero, *A. Smith H. 180* (AMES!). Cartago: Pacayas, Esperanza, Cabo de Acha, eastern

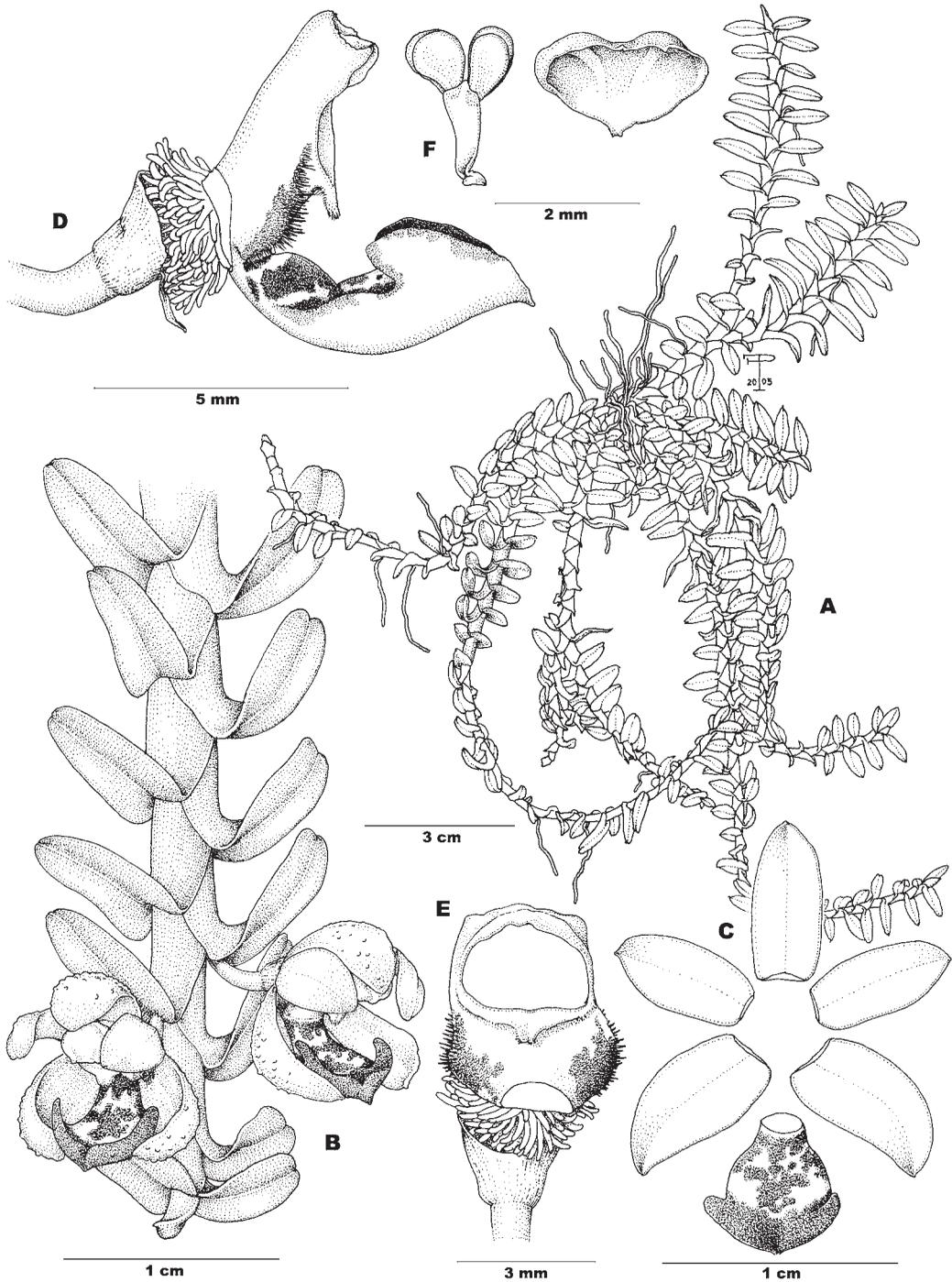


FIGURE 64. *Dichaea squarrosa* Lindl. **A**, Habit; **B**, apex of stem and flowers; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, pollinarium and anther cap. Drawn from Bogarín 254 (JBL-Spirit).

slopes of Irazú volcano, 10°01'N, 83°48'W, ca. 2350 m, 15 April 2006, *F. Pupulin 6060* & *E. Salas-Pupulin* (CR). Heredia: Cinco Esquinas, Los Cartagos, Cerro de la Giralda, 10°08'N, 84°10'W, ca. 2000 m, epiphytic on short trees along the roadside, lower montane wet forest, 13 Feb. 2004, *F. Pupulin 5127*, *D. Bogarín*, *H. León-Páez* & *E. Salas* (JBL-Spirit); Barva, San José de la Montaña, road to Sacramento, Finca Steinvoth, 10°05'46"N, 84°05'42"W, 2000 m, lower montane moist forest, collected by E. Biamonte, 23 June 2003, flowered in cultivation at Coronado, San José, 15 June 2005, *F. Pupulin 5665* (JBL-Spirit); Parque Nac. Braulio Carrillo, Estación Barva, 10°08'00"N, 84°08'15"W, 2500 m, 4 May 1990, *G. Rivera 257* (CR; INB); Sacramento, Finca de Emilia Sánchez, 2150 m, bosque pluvial montano bajo, epífita en árboles a orilla de potreros, 28 Febrero 2003, *D. Bogarín 126*, *G. Bogarín* & *I. Chaves* (JBL-Spirit). San José: Dota, southwest slope of cerro San Francisco, along the road from El Empalme to Santa María de Dota, 2150 m, 3 Jan. 1992, *J. R. Grant 92-01678* & *J. R. Rundell* (CR, sterile); Escazú, Z.P. Cerros de Escazú, cuenca del Río Tarbaca, 9°49'43"N, 84°07'03"W, 1700–1900 m, 20 Jul. 1992, *J. F. Morales 265* (CR); Bebedero, Cerros de Escazú, camino hacia el Cerro Pico Blanco, 9°52'34"N, 84°08'05"W, 2271 m, 5.7.2003, *D. Bogarín 254* & *A. Granados* (JBL-Spirit); Escazú, parte alta del Cerro Pico Blanco, 2100–2271 m, 9°52'34"N, 84°8'5"W, bosque muy húmedo tropical montano bajo, epífitas en bosque secundario joven con remanentes de primario, 5 Julio 2003, *D. Bogarín 241* & *A. Granados* (JBL-Spirit); same locality and date, *D. Bogarín 242* & *A. Granados* (JBL-Spirit); Goicochea, Rancho Redondo, boscecillo residual a la vera dl camino, 09°57'45"N, 83°57'05"W, 3000–2050 m, 23 Nov. 1993, *J. Gómez-Laurito 13496*, *J. A. López* & *A. Mora* (USJ); León Cortés, Frailes de Desamparados, a mitad del camino entre San Antonio y San Pablo, selva de *Quercus seemannii*, 1910 m, 11 Feb. 1986, *M. Kapelle 799* & *M. Gutiérrez U.* (CR, sterile).

**Etymology:** from the Latin *squarrosus*, squarrous, rough, in reference to the small verrucose excrescences that cover the abaxial surface of the sepals and petals.

**Ecology:** in Costa Rica, *D. squarrosa* is a rather uncommon epiphyte, seemingly restricted to the Caribbean, submontane wet

forests of the main mountain chains, at elevations between 2000 and 2500 m. Flowering occurs at least in June and July.

*Dichaea squarrosa* is one of the easiest species to identify in the study area. The rounded stems and the almost linear, leathery, thick, coriaceous leaves usually allow positive determination of this species even from sterile and dried material. The leaves of *D. trichocarpa*, which also presents rounded stems, are lanceolate and have a much thinner substance. Moreover, the lip of *D. squarrosa* is clawed, with an obtuse hypochile, whereas *D. trichocarpa* has a sessile lip and a rounded-discoid hypochile. The main differences between the two species were summarized by Williams (1941), who first removed *D. squarrosa* from the synonymy of *D. trichocarpa*, under which it had been placed by Kränzlin (1923).

26. *Dichaea trichocarpa* (Sw.) Lindl., Gen. Sp. Orch. Pl. 202. 1833. *Epidendrum trichocarpon* Sw., Prodr. 124. 1788. *Cymbidium trichocarpon* Sw., Nova Acta Reg. Soc. Sc. Uppsal. 6: 71. 1799; Fl. Ind. Occ. 3: 1455, *emend.* TYPE: JAMAICA. "Parasiticum in truncis muscosis arborum, versus juga montium Jamaicae australis," *O. Swartz s.n.* (Lectotype, designated here: W-Reichenbach Orchid Herbarium Nr. 25293). Fig. 65, Map 9.

*Plant* epiphytic, caespitose, to 50 cm long. *Roots* basal and caulinar, often exposed and aerial or hidden by leaf sheaths, flexuous, to 0.8 mm in diam. *Stems* subterete, slightly compressed, scandent to pendent, freely branching, 10–50 cm long, 0.20–0.25 cm wide across conduplicate sheaths. *Leaves* widely spaced along stem, retrorse-spreading, medium green, thin leathery, 3–11 × 2–3 mm, lanceolate, acute to shortly acuminate; sheaths tightly clasping the stem, to 6 × 3 mm, often marked with darker green spots. *Inflorescences* solitary, 1-flowered, emerging above foliage, the peduncle gently geniculate, 4–12 mm long, provided at the base with a tubular, acute bract, about 3 mm long, slightly emerging from sheath. *Floral bract* double, the outer bract widely ovate-funneliform, subcuspidate, 2.5 × 2.5 mm, the inner bractlet narrowly lanceolate, 1.5–2.0 mm long. *Pedicellate ovary* ca. 2 mm long, the ovary densely long-muricate. *Flower* spreading, strongly scented, with sepals and petals thick-succulent, white to cream-white, the sepals

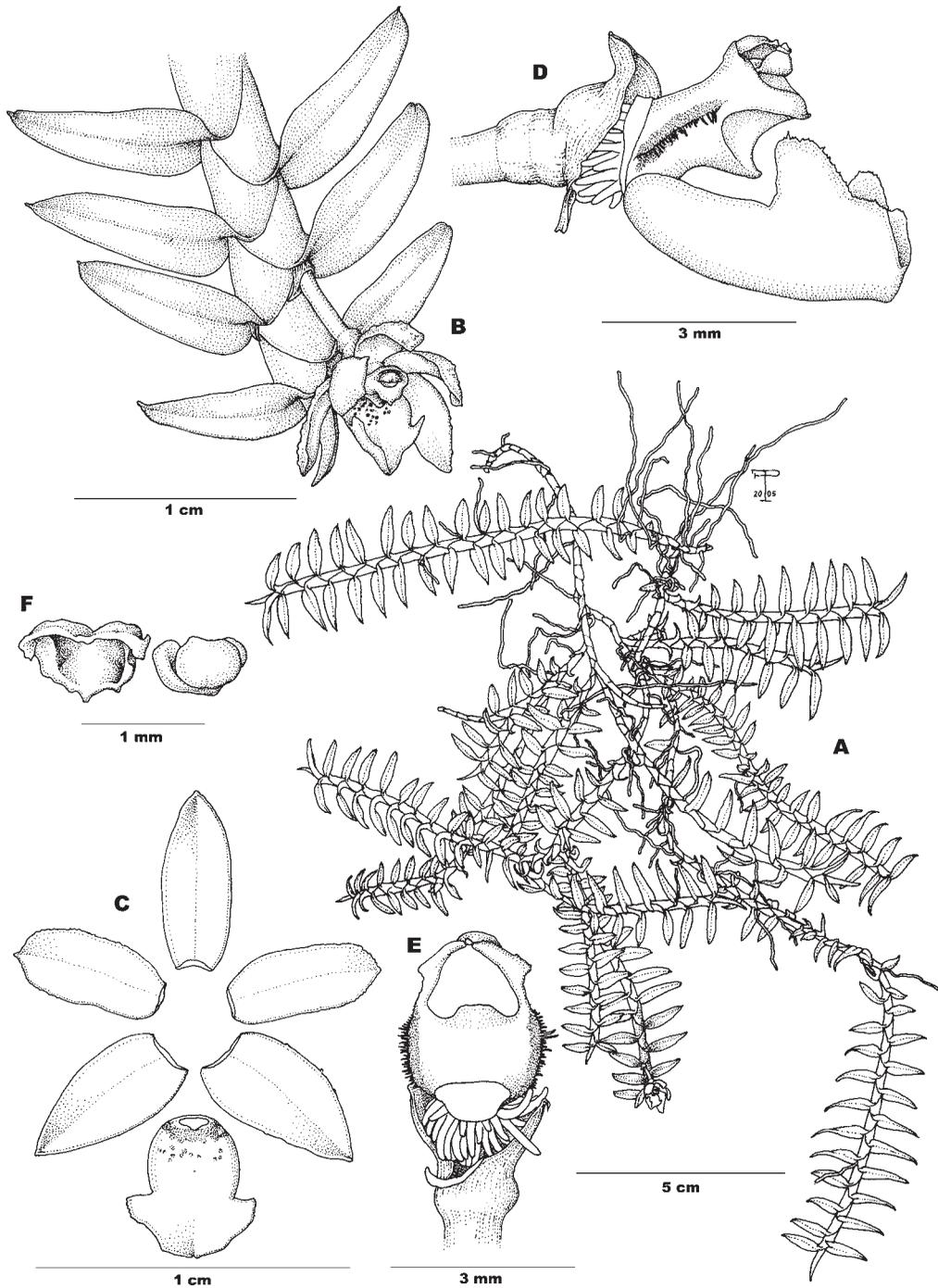


FIGURE 65. *Dichaea trichocarpa* (Sw.) Lindl. A, Habit; B, apex of stem and flower; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, anther cap and pollinarium. Drawn from *Pupulin et al.* 3207 (JBL-Spirit).

externally tuberculate, the lip yellowish white marked with violet or yellow at the base to almost solid violet, the column white to pale yellow, marked with violet on the margins of wings. *Dorsal sepal* lanceolate-elliptic, acute, abaxially carinate, 5–7 × 2–3 mm. *Lateral sepals* obliquely ovate-elliptic to oblong-lanceolate, acute, abaxially carinate, 5–7 × 2.5–4.0 mm. *Petals* elliptic-oblong, obtuse, shortly subapiculate, irregularly toothed toward the apex, 4.5–6.0 × 2.0–2.5 mm. *Lip* 3-lobed, sessile, 3–5 × 2.7–3.3 mm when spread, the hypochile suborbicular-discoid, concave in natural position, 2.5–3.0 mm wide apically, the epichile broadly triangular-subtrapezoidal, obtuse-subtruncate, strongly conduplicate, the lateral lobes not sharply distinct from epichile blade, broadly triangular, rounded-subtruncate, irregularly toothed toward the apex, spreading, 1.0 × 1.3 mm. *Column* continuous with the ovary axis, subterete, 3 mm long, provided with narrowly rectangular, flattened, ciliate wings, the supra-rostellar area and the clinandrium strongly reclined, shallow; ligule small, thickened at the base, broadly triangular, truncate to slightly bifid, glabrous to microscopically pubescent, 0.8 × 1.0 mm. *Anther cap* broadly obovate-subcordate, 2-celled. *Pollinia* 2, transversely elliptic-subcordate, complanate, different in size, superposed, without stipe and definite viscidium. *Fruit* a rounded, muricate capsule.

**Distribution:** from Guatemala to Panama, and the Greater Antilles.

**Additional material examined:** COSTA RICA. Alajuela: Valverde Vega, cuenca del Río Toro, Bajos del Toro, reserva Biológica Bozque de Paz, 1450 m, 20 July 2004, S. Kirby 04–75, M. Muñoz & P. Protti (USJ). Cartago: Cartago, Quebradilla, Z.P. Cerros de la Carpintera, 09°52'28"N, 83°58'07"W, 1745 m, 6 May 2003, A. Quesada 1124, J. E. Sánchez, E. Serrano & E. Carman (CR, sterile); 10 km S of Cartago by air, along confluence of Río Empalme and Río Estrella, 1 km S of Palo Verde, 9°46'N, 83°57'W, 1450 m, 21 Apr. 1983, R. Liesner 14525 & E. Judziewicz (INB); El Guarco, without specific locality, flowered in cultivation at el Jardín Botánico Lankester, 6 July 2006, R. Gómez s.n. (CR); La Unión, Tres Ríos, Finca Tinoco, Zona Protectora Cerros de la Carpintera, 1700–1800 m, 12.2.2005, E. Serrano 215 & W. Salazar (JBL-Spirit). Heredia: San Rafael, camino al Monte de La Cruz, desviación al Residencial El Tirol, orillas

del Río Segundo, 1800 m, 17.4.2003, D. Bogarín 173 (USJ, JBL-Spirit); San Rafael, entrada por el Residencial El Tirol, en potreros cercanos al Cerro Delicias y orilla del Río Segundo, 1800 m, bosque húmedo premontano, epífitas a orillas de quebrada y potreros arbolados, 6 Julio 2003, floreció en cultivo en el Jardín Botánico Lankester, 23.7.2006, D. Bogarín 300 (CR). Puntarenas: Coto Brus, Parque Nac. Amistad, Las Tablas, near the upper Río Cotón, 08°57'N, 82°47'W, 1400–1500 m, 14 Jul. 1982, C. Todzia 1912, L. D. Gómez & R. W. Pohl (CR); Monteverde community, on Lowther property, 1475 m, 25 July 1989, J. T. Atwood 89–327 (INB). San José: Desamparados, El Tablazo, 1500 m, 25 Jun. 1978, C. Todzia 346 (CR 66496, with other mixed collection).

**Etymology:** from the Greek *trichos*, hair, and *karpon*, fruit, in allusion to the strongly muricate capsules of this species.

**Ecology:** in Costa Rica, *D. trichocarpa* is a rather uncommon epiphyte, usually found in submontane wet forest and cloud forests close to the continental divide, at elevations between 1400 and 2000 m. Flowering mostly occurs in July and August, but the species also flowers irregularly during the year.

The subterete stems, the semi-succulent, usually strongly retrorse leaves, and the scented flowers provided with a discoid, concave hypochile easily distinguish *Dichaea trichocarpa* from the closely related *D. squarrosa* and other species in the genus.

Folsom (1987) proposed to lectotypify *Dichaea trichocarpa* with a specimen at S, but the primary set of Swartz's collections, originally kept at Stockholm, are to be found in the Reichenbach herbarium at W (see discussion under *D. morrisii*). Here two original Swartz's specimens of *Epidendrum trichocarpon*, on loan from S, are kept (W *Rchb-Orch* 25293! and 19304!), which annotated by Swartz as "trichocarpon" and "Epidendrum trichocarpon," respectively. The smaller, sterile specimen (*Rchb-Orch* 19304) also bears Swartz's signature. The lectotype, designated here, is composed of three branched stems, all of which bear fruits (Fig. 66).

27. *Dichaea trulla* Rchb. f., Beitr. Orch. Centr.-Amer. 104. 1886. *Epithecia trulla* Schltr., Orchis 9: 26. 1915. *Dichaeopsis trulla* Schltr. Bot. Zentralbl. Beih. 36(2): 519. 1918. TYPE:

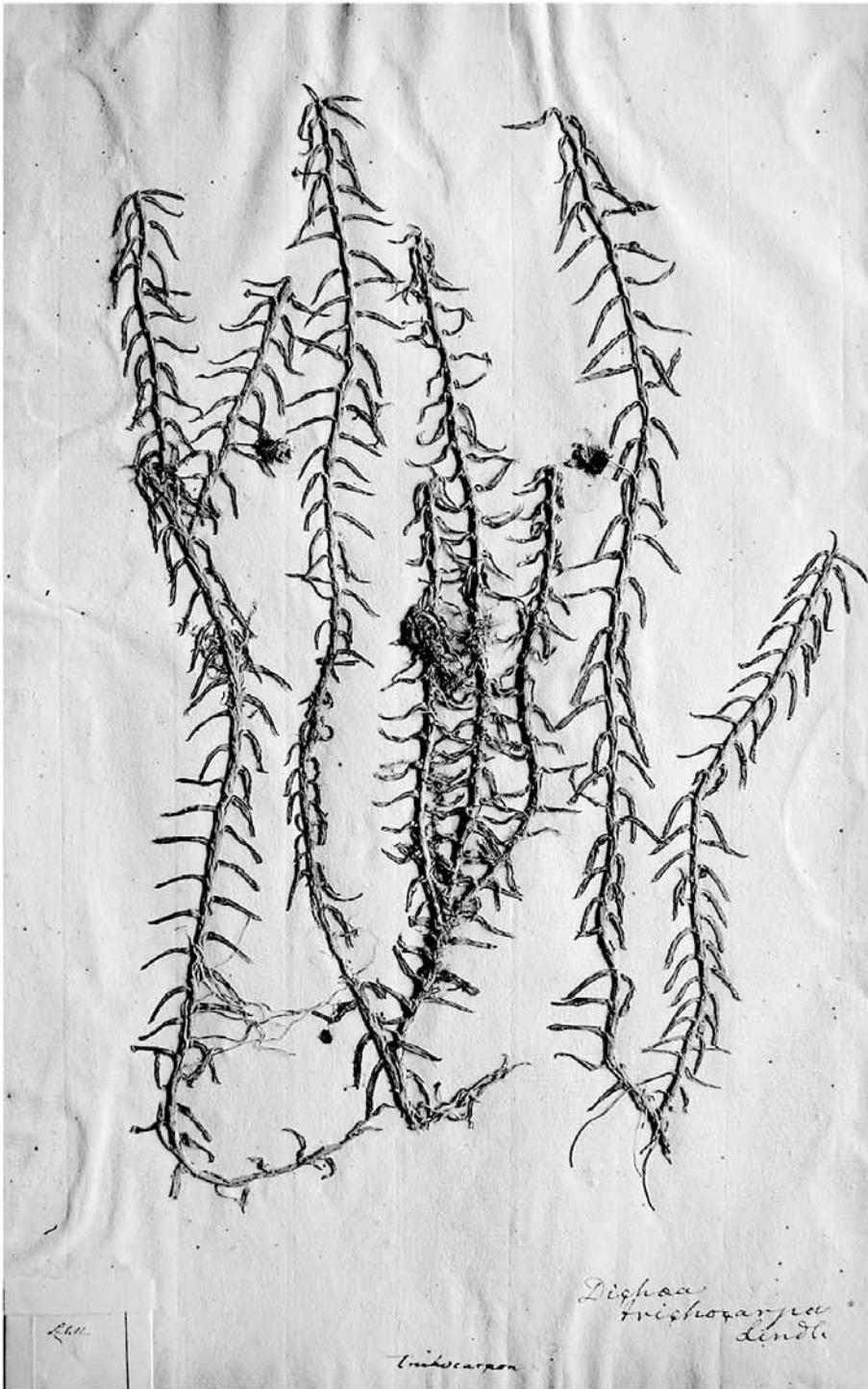


FIGURE 66. Holotype of *Epidendrum trichocarpon* Sw., Swartz *s.n.* (*Rchb. Orch.* 25293, W). Reproduced with the permission of the Director of the Herbarium, Naturhistorisches Museum, Vienna.

NICARAGUA. [Zelaya, Bluefields,] Pearley Lagoon auf Palmen, 5.1.1855, *H.R. Wulfschlägel s.n.* (Holotype: W-Reichenbach Orchid Herbarium). Fig. 67, Map 10.

Synonyms: *Dichaea powellii* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 17: 90. 1922. TYPE: PANAMA. Canal Zone, foothills east of Panama Cty, near Bohio, sea level, "Flowers sepals et al. petals a yellow greenish. The lip a deep blue," *C. W. Powell 23* (Holotype: B, destroyed, copy of Schlechter's drawing of type, AMES 26859; Isotype, selected as lectotype by Christenson, 1991: AMES 61229).

*Dichaea brenesii* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 264. 1922. TYPE: COSTA RICA. San Pedro de San Ramón, 1075 m, XI-1921, *A. M. Brenes 66* (Holotype: B, destroyed, copy of Schlechter's drawing of type, AMES 31568; Isotype, designed by Barringer, 1984, as lectotype: CR 18458).

*Plant* epiphytic, caespitose, to over 1 m long. *Roots* basal and caulinar, the caulinar ones short and completely hidden by leaf sheaths, flexuous, to 0.8 mm in diam. *Stems* subterete, erect when young, becoming archly pendent with age, the apex gently up-curved, 15–110 cm long, 0.3–0.5 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, widely spaced along stem, spreading, (medium to) dark green, shiny, subcoriaceous, abaxially subcarinate, 5–11 × 0.4–0.6 cm, narrowly lanceolate-ligulate, acute to acuminate; sheaths tightly clasping the stem, to 2.5 × 1.0 cm, often flushed with purple-brown. *Inflorescences* solitary, 1-flowered, emerging below foliage, the peduncle straight, 22–25 mm long, provided at the base with two imbricating, membranaceous, acute bracts, about 3 mm long. *Floral bract* double, the outer bract ovate-funnelform, subcuspidate, 4 × 4 mm, the inner bractlet narrowly lanceolate, 3.0–3.5 mm long. *Pedicellate ovary* 2.5 mm long, cylindric-subclavate, glabrous. *Flower* spreading, thick-succulent, microscopically pubescent, the sepals and petals becoming reflexed with age, yellowish green to pale green, the lip dark violet blue on a white background, the column white to pale yellowish green. *Dorsal sepal* oblong to narrowly obovate-elliptic, acute, abaxially carinate, 7–10 × 4–5 mm. *Lateral sepals* obliquely elliptic to elliptic-lanceolate, acute, abaxially carinate, 7–11 × 4–5 mm. *Petals* elliptic-lance-

olate, acute to shortly apiculate, slightly conduplicate-concave toward the apex, 1–10 × 3.5–4.5 mm. *Lip* 3-lobed, broadly trulliform, sessile, 8–9 × 6–7 mm when spread, the hypochile narrowly obtuse, thickened at the base into a transversely elliptic, rounded callus, 5–6 mm wide apically, the epichile semiorbicular-rheniform, obtuse to truncate, with a small abaxial apicule, deeply conduplicate-concave in natural position, the lateral lobes not sharply distinct, short, triangular, obtuse to acute, retrorse, 1.0 × 0.7 mm. *Column* continuous with the ovary axis, subterete, ventrally flattened, to 6.5 mm long, provided with linear, flattened, ciliate wings, the clinandrium shallow with shortly bidentate margins; ligule triangular, acute, apically pubescent, gently arching toward the column, 2 × 1 mm. *Anther cap* transversely elliptic, emarginate, 2-celled. *Pollinia* 4, broadly elliptic-suborbicular, complanate, in two superposed pairs of different size, transversely arranged on a narrow ligulate stipe; viscidium peltate. *Fruit* an elliptic capsule, 2.0 × 1.3 cm.

**Distribution:** from Honduras to Panama, Venezuela and Guyana, Colombia, Ecuador, Peru, and Bolivia.

**Additional material examined:** COSTA RICA. Alajuela: Ángeles, Reserva Forestal San Ramón, trail South of the Station, 10°12'40"N, 84°36'20"W, 1000 m, 5 Jun. 1993, *J. Bittner 2034* & *G. Herrera* (CR); Grecia, Sarapiquí, San Miguel, road to Colonia Carvajal, bridge on Río Sarapiquí, 10°19'16"N, 84°10'34"W, 400 m, shores of Río Sarapiquí, tropical wet, belt transition to premontane wet forest, 29.11.2004, flowered in cultivaton at Jardín Botánico Lankester, 10 May 2006, *F. Pupulin 5327*, *R. L. Dressler*, *K. Dressler* & *J. Warner* (CR); San Ramón, Piedades, Potrerillos, road to Socorro de Piedades Sur, slopes of Cerro La Palma, 10°08'09.9"N, 84°34'47.5"W–10°08'25.0"N, 84°34'45.9"W, 1300–1450 m, premontane wet forest, 12 April 2006, flowered in cultivation at Jardín Botánico Lankester, 27 June 2006, *F. Pupulin 6014*, *R. L. Dressler* & *A. Carbajal* (CR). Guanacaste: La Cruz, camino a Pitilla, 1300 m al Norte de la estación, 10°59'26"N, 85°25'40"W, 700 m, 16 Jan. 1993, *C. Moraga 532* (INB); Parque Nacional Guanacaste, Estación Pitilla, 9 km al S de Santa Cecilia, 10°59'25"N, 85°25'40"W, 700–1000 m, 6 march 1991, *C. Moraga 314* (INB). Heredia: Sarapiquí, cerca de la Estación

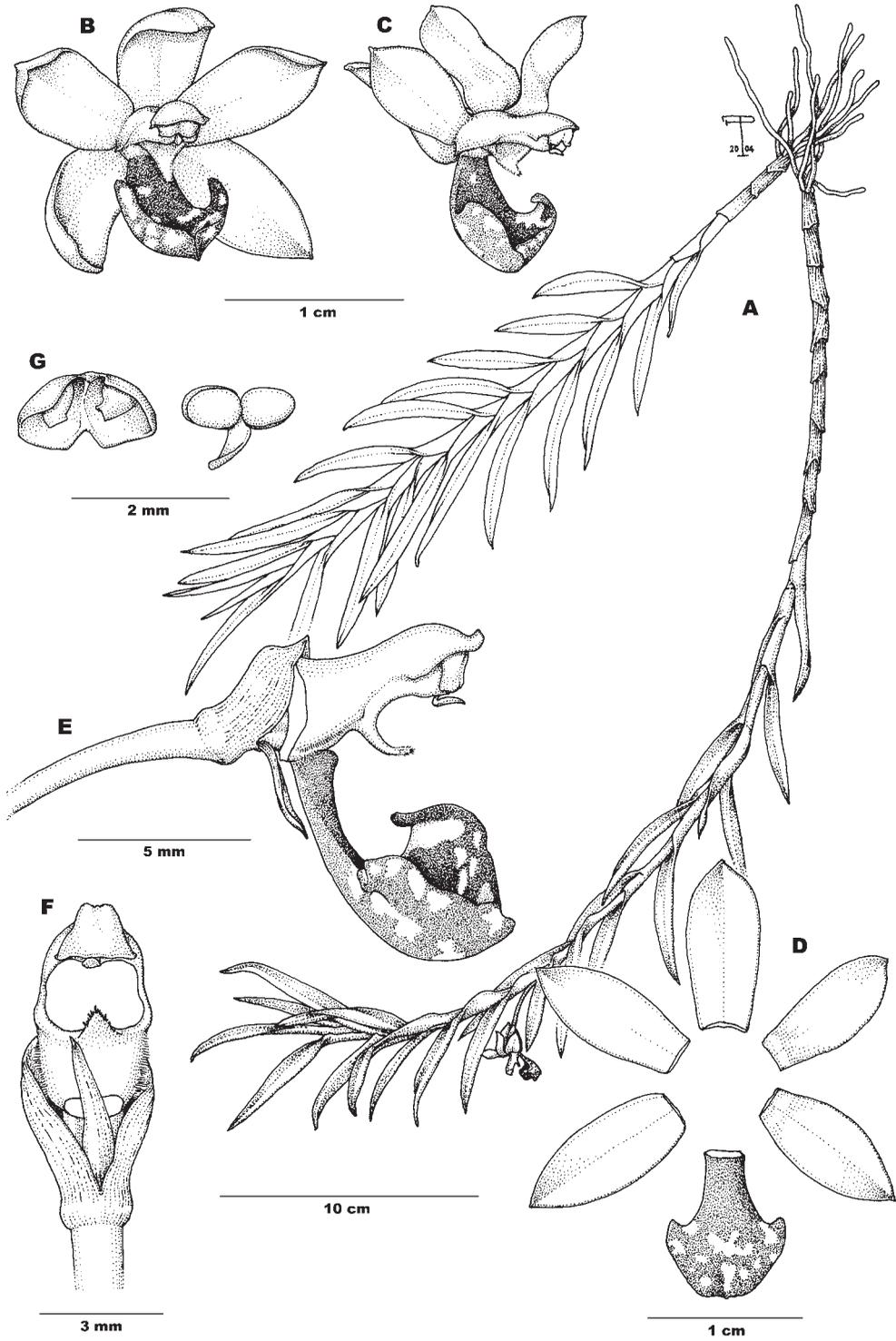


FIGURE 67. *Dichaea trulla* Rchb.f. **A**, Habit; **B**, flower at anthesis; **C**, flower, seven days old; **D**, dissected perianth; **E**, column and lip, lateral view; **F**, column, ventral view; **G**, anther cap and pollinarium. Drawn from *Castelfranco & Pupulin 136* (JBL-Spirit).

Biológica La Selva, orillas del Río Sarapiquí, 40 m, 7.6.2003, *D. Bogarín 206* (JBL-Spirit); Sarapiquí, Horquetas, Finca Terrafolia, contiguo a Rara Avis, 10°18'14"N, 84°01'36"W, 500 m, 21.7.2003, *W. M. Whitten 2096 & M. Blanco* (JBL-Spirit); Finca La Selva, OTS Field Station near junction of Puerto Viejo and Sarapiquí Rivers, Camino Circular Lejano 500 just across the bridge, occurring with *Dichaea standleyi*, 40–100 m, 19 Mar. 1991, *K. Richardson K-108* (CR, sterile); Sarapiquí, Rara Avis, 15 km Sur Oeste de Las Horquetas, 10°17'03"N, 84°02'47"W, 500–800 m, 20 Oct 1997, *G. Beckers 17* (CR, fruiting). Limón: Pococí, Guápiles, San José-Limón highway, km 47, ca. 500 m after the entrance of Rain Forest Aerial Tram, Quebrada Molinete, 10°10'43"N, 83°54'57"W [10°11'34"N, 84°54'16"W], 470–500 m, tropical wet, transition to premontane wet forest, epiphytic in primary forest along the river banks, 9 July 2004, *F. Pupulin 5245 & D. Bogarín* (JBL-Spirit); Llanura de Santa Clara, Río Corinto, en Finca Catie-Fundecor, 10°12'45"N, 83°53'15"W, 200–300 m, 11 Jan. 1996, *J. F. Morales 5078 & M. Saborío* (INB); Talamanca. R.I. Talamanca, Alto Urén, quebrada antes de la casa de Don Gabriel, 09°27'00"N, 82°59'30"W, 700–900 m, 24 Sept. 1994, *G. Gallardo 297 & E. Lépiz* (INB). Puntarenas: Aguirre, road to Quepos to San Marcos de Tarrazú, 27.5.1999, 9°33'01"N, 84°00'01"W, 750 m, flowered in cultivation at Gaia Botanical Garden, 18.12. 2000, *F. Pupulin 1518 & D. Castelfranco* (JBL-Spirit); Golfito, Península de Osa, Est. Agujas, Río Agujas, Sendero Sapo, 832'11"N, 83°25'31"W, 300 m, 14 June 1996, *A. Azofeifa 194* (INB). San José: Dota, eastern slopes of Cerro Nara, in premontane rain forest, disturbed primary forest, 9°29'01"N, 84°00'25"W, 840–740 m, 14 Jan. 1999, *F. Pupulin 1068, D. Castelfranco & M. L. Spadari* (JBL-Spirit); Pérez Zeledón, Las Nubes de Quizarrá, 1080 m, epiphytic on trees in remnants of primary vegetation and secondary mature vegetation, along the Río Quizarrá, 9 November 2000, *F. Pupulin 2575, D. Castelfranco & J. Prada* (JBL-Spirit), Tarrazú, Z.P. Cerro Nara, 9°29'40"N, 84°00'50"W, 900–1000 m, 21 Jul. 1998, *O. Valverde 1049* (CR, fruiting).

**Etymology:** from the Latin *trulla*, the popular term for an ancient Roman dipper in the form of a shallow bowl with a single horizontal handle, in allusion to stirring-spoon-shaped epichile of the lip with its long "claw."

**Ecology:** *Dichaea trulla* is a widespread and common epiphyte in tropical and premontane rain to wet forests, where it can be found between 50 and 1300 m. In northern Costa Rica, it seems restricted to the Caribbean watershed or occasionally on both the slopes close to the continental divide. Along the Talamanca chain, plants of this species have been collected at mid-elevations also on the Pacific watershed. Flowering occurs sporadically throughout the year.

*Dichaea trulla* is the tallest member of the genus, and its characteristic habit, provided with long, narrow and pointed leaves, makes it unmistakable even when it is not in flower. Flower shape and color are remarkably similar throughout the distributional range of the species in Costa Rica, where *D. trulla* has no closely allied species. Although some authors include under the synonymy of *D. trulla* also *D. coriacea* Barb. Rodr. (e.g., Dunsterville and Garay, 1961; Foldats, 1970; Dodson and Dodson, 1980; Sprunger, 1996), it is likely this species originally described from Brazil should be considered a different taxon. In the protologue (Barbosa Rodrigues, 1881), the flowers are stated to have pure white lips, and although no mention is made of the inflorescences, the drawing of the holotype prepared by Barbosa Rodrigues (reproduced in Sprunger et al., 1996: 393) shows a stem producing 8 simultaneous inflorescences, with 3–4 flowers at or near to anthesis. Simultaneous flowering is rare in the genus *Dichaea*, which mostly exhibits successive, 1-flowered inflorescences, and in the study area the only simultaneously many-flowered species is the distantly related *D. glauca*. However, it is interesting to note that *D. coriacea* shares with *D. trulla* the unusual shape of the pollinarium, with the pollinia arranged transversely on the stipe.

28. *Dichaea tuerckheimii* Schltr., Orchis 10: 188. 1916, non Kraenzl. (1923). *Dichaea guatemalensis* Schltr., Orchis 10: 190, *sphalm.* TYPE: GUATEMALA. "Wurde von Baron v. Tuerckheim im Jahre 1912 an Herrn Prof. Dr. Goldschmidt in Essen geschickt und blühte in dessen Sammlung im Juli 1916" (Holotype: B, destroyed; Lectotype, selected here, flower analysis published with the protologue (Schlechter, 1916a), reproduced in Mansfeld, 1931: pl. 80, No. 317]. Fig. 68, Map 10.

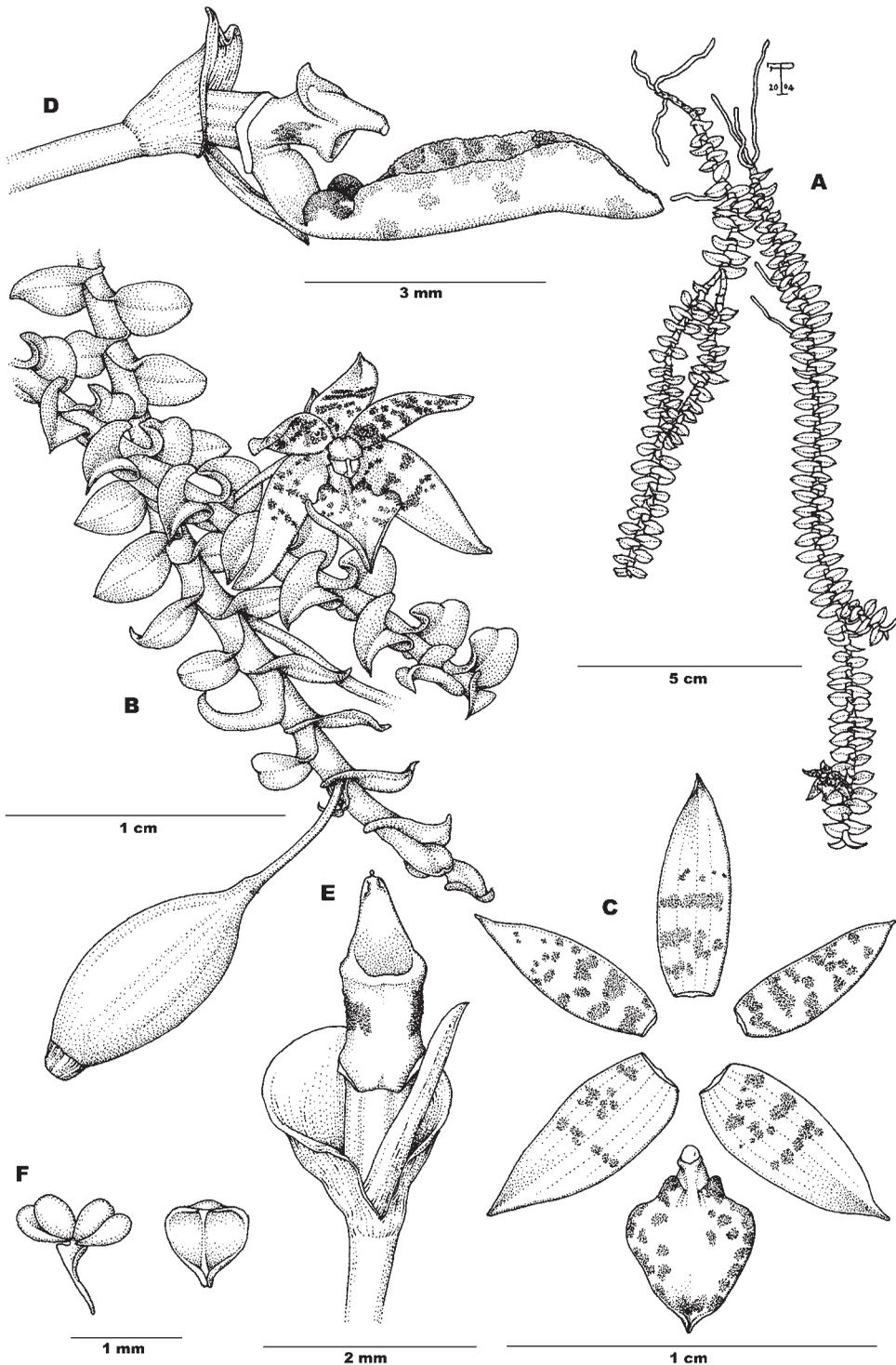


FIGURE 68. *Dichaea tuerckheimii* Schltr. A, Habit; B, apex of stems with flower and fruit; C, dissected perianth; D, column and lip, lateral view; E, column, ventral view; F, pollinarium and anther cap. Drawn from Whitten 2097 (JBL-Spirit).

Synonyms: *Dichaea glabrescens* Kraenzl., Pflanz. 4(50): 41. 1923. TYPE: COSTA RICA. [1867], A. R. Endrés 118 (Holotype: *Rchb. Orch.* 10508, W).

*Dichaea wercklei* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19: 74. 1923. TYPE: COSTA RICA. [San José: Carrillo,] La Palma, fruchtend im Juni 1921, C. Wercklé 79 (Syntype: B, destroyed; lectotype, selected here, tracing of Schlechter's drawing of the type, AMES 31573; flower analysis reproduced in Mansfeld, 1931); ebendort, 1400 m, ohne Blüten im März 1908, A. Brade & C. Brade 1300 (Syntype: B, destroyed).

*Plant* epiphytic, prostrate-scandent, forming large mats to 60 cm wide. *Roots* filiform, basal and caulinar, to 0.3 mm in diam, the upper roots mostly hidden by leaf sheaths, sometimes exposed and aerial. *Stem* subterete, slightly compressed, 5–14 cm long, 0.6–1.0 mm wide across conduplicate sheaths, covered by the leaf sheaths, freely branching. *Leaves* numerous, distichous, not articulated, delicately membranous, well spaced along the stem, smooth, spreading, medium green, 3–4 × 1.5–2.0 mm, ovate to ovate-oblong, acute to subacuminate, the apex shortly aristulate; sheaths 2.5–3.0 × 3 mm, clasping, the apical margins slightly inflated, often spotted darker green. *Inflorescence* axillary, 1-flowered, produced above the foliage; the peduncle terete, glabrous, green, suberect to gently geniculate, 7–8 mm long, provided at the base with a papyraceous, imbricating, acute bract, about 1 mm long. *Floral bracts* in pair, the outer one orbicular, cucullate, acute to apiculate, 2 × 2 mm, the inner one linear, acute, 2.3–3.0 mm long. *Ovary* pedicellate, terete, glabrous, to 1.5 mm long including the pedicel. *Flowers* small, spreading, membranous, glabrous, the sepals and petals cream to pale green, densely blotched with violet purple, the lip white to cream-white, spotted violet, the column white, marked violet along infrastigmatic margins. *Dorsal sepal* ovate-elliptic to lanceolate, acute-subacuminate, 4.0–4.5 × 1.3–1.5 mm. *Lateral sepals* obliquely elliptic-lanceolate, acute-subacuminate, slightly concave, 4.0–4.5 × 1.5–1.8 mm. *Petals* narrowly lanceolate-elliptic, narrower than sepals, shortly acuminate, 3.8–4.0 × 1.0–1.3 mm. *Lip* shortly unguiculate, the claw fleshy, linear-obcuneate, 0.5 mm long, with a

central, low ridge decurrent in the blade; the lamina ovate-triangular from a rounded base, subacute, shortly acuminate, slightly concave, 4.0–4.5 × 2.0–2.2 mm, provided at the base with 2 small, mammillate, rounded calli. *Column* straight, parallel to the ovary axis, terete, 1.8 mm long, the suprarostellar area and the shallow clinandrium strongly reflexed; stigma sub-orbicular, protruding at the base into a rounded, glabrous ligule. *Anther* dorsal, the anther cap ovate-cordate, membranous, 2-celled. *Pollinia* 4, obpyriform, slightly compressed, on a narrow obtriangular stipe; viscidium linear-oblong, white. *Fruit* an elliptic, glabrous capsule, 9 × 3 mm.

**Distribution:** from Guatemala to Colombia.

**Additional material examined:** COSTA RICA. Alajuela: San Ramón, La Balsa, road from San Ramón to La Fortuna, proximity of Río La Balsa, 10°11'52"N, 84°30'54"W, 990 m, 26.12.2004, F. Pupulin 5456, E. Salas-Pupulin, S. Dalstrom & C. Lewis (JBL-Spirit); San Pedro de San Ramón, 1075 m, 11-I-1924, A. M. Brenes (199) 811 Herb. Brenes (CR); Upala, Bijagua, NE slopes of Miravalles volcano, shores of Río Zapote, 10°44'37.4"N, 85°05'14.9"W, 700 m, premontane wet forest, 30 April 2006, F. Pupulin 6099, D. Bogarín, A. Rambelli & G. Rambelli (CR, sterile). Cartago: Pejibaye, unpaved road from Purisil to Tausito, Reserva Sura Mina Iriria Tsochok Doboni Meye (La Madre Tierra), 09°46'38"N, 83°46'30"W, 1295 m, premontane wet forest, secondary vegetation and remnants of primary, 25 July 2006, F. Pupulin 6270, D. Bogarín, M. Dix, R. L. Dressler & A. Karremans (CR). Heredia: Sarapiquí, Horquetas, ca. 2 km sobre camino al asentamiento El Manú, 200–250 m, C. Ossensbach 343, P. Casasa & B. Arias (JBL-Spirit); Horquetas, Finca Terrafolia, contiguo a Rara Avis, 10°18'14"N, 84°01'36"W, 500 m, 21.7.2003, M. Whitten 2097 & M. Blanco (JBL-Spirit). Limón: Parque Nacional Braulio Carrillo, Sector Quebrada González, ca. 700 m, 11.3.2003, D. Bogarín 136 & Grupo de Historia Natural UCR I-2003 (JBL-Spirit); Guápiles, Río Corinto, sendero paralelo al Río Corinto y sus riberas, 83°56'10"N, 10°19'09"W, 500 m, 7 Sept. 1990, C. Chávez 50 (INB). Puntarenas: Golfito, Puerto Jiménez, P.N. Esquinas, Cataratas way, 8°41'N, 83°13'W, 100 m, 15 Feb. 2000, P. Hietz 25 (CR). San José: Carrillo, Braulio Carrillo Park, 500–700 m, 16 Spet. 1984, J. P. Folsom

11002A (CR); Dota, eastern slopes of Cerro Nara, in premontane rain forest, disturbed primary forest, 9°29'01" N, 84°00'25" W, 840–740 m, 14 Jan. 1999, *F. Pupulin 1110*, *D. Castelfranco & M. L. Spadari* (CR).

**Eponymy:** named in honor of Baron Hans Freiherr von Türckheim (Karlsruhe, 1853–1920), who collected the type specimen.

**Ecology:** epiphytic in deep shade in wet tropical to premontane forests and cloud forests at 100–1300 m elevation. Populations of this species may be found on the Caribbean drainage of the Guanacaste, Tilarán, and Central Volcanic mountain ranges, and on both the watersheds of the continental divide along the Talamanca range. Flowering mostly occurs from May to August, but sporadic flowering has been observed throughout the year.

The fern-like, very small habit (the smallest in the genus), the scandent-prostrate, freely branching stems, and the persistent, delicately membranous, glabrous leaves easily distinguish *D. tuerckheimii* from any other *Dichaea* species. Flower morphology is also peculiar for the presence of two mammillate basal calli on the lip, the entire lamina, and the straight column with reflexed, dorsal anther.

The holotype of *Dichaea tuerckheimii*, ostensibly collected in the Cobán area by H. F. von Tuerckheim, was destroyed in the herbarium of Berlin, and no isotypes are known to exist. However, the description of the plant habit provided by Schlechter in the protologue, as well as the accompanying analysis of the flower

selected here as the lectotype (Schlechter, 1916b: pl. 44 and fig. 17–24), leaves no doubts about the identity of this species (Fig. 69).

In the protologue of *Dichaea wercklei*, Schlechter cited *Wercklé 79*, a plant with fruits, and a sterile collection *sine numero* from the same locality by the brothers Brade. No isotypes are known to exist. The tracings of Schlechter's sketches at AMES show a fruiting specimen and analytical drawings of the perianth, prepared from a faded flower (Schlechter, 1923a: 74). In selecting them as the lectotype (Fig. 70), I assume they were prepared from Wercklé's specimen, hence the specific epithet.

29. *Dichaea viridula* Pupulin, Harvard Pap. Bot. 10(1): 85. 2005. TYPE: COSTA RICA. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, El Mirador, 9°44'13.5" N, 83°46'49.6" W, 1376 m, epífita en sitio sombreado en ramitas jóvenes de *Oreomunnea* (Juglandaceae), 24 August 2004, *D. Bogarín 925*, *H. León-Páez & E. Hoppe* (Holotype: USJ-Spirit). Fig. 71, Map 10.

*Plant* epiphytic, caespitose, pendent, to 60 cm long. *Roots* filiform, ca. 1 mm in diam. *Stem* compressed, covered by the slightly inflated leaf sheaths, rarely branching toward the apex. *Leaves* numerous, distichous, closely spaced along the stem, not articulated, delicately membranous, smooth, deflexed, 7–12 × 3.5–6.5 mm, ovate-lanceolate to oblong, obtusely acute, the apex aristulate, dark green, the margins neatly undulated; sheaths 4–5 mm

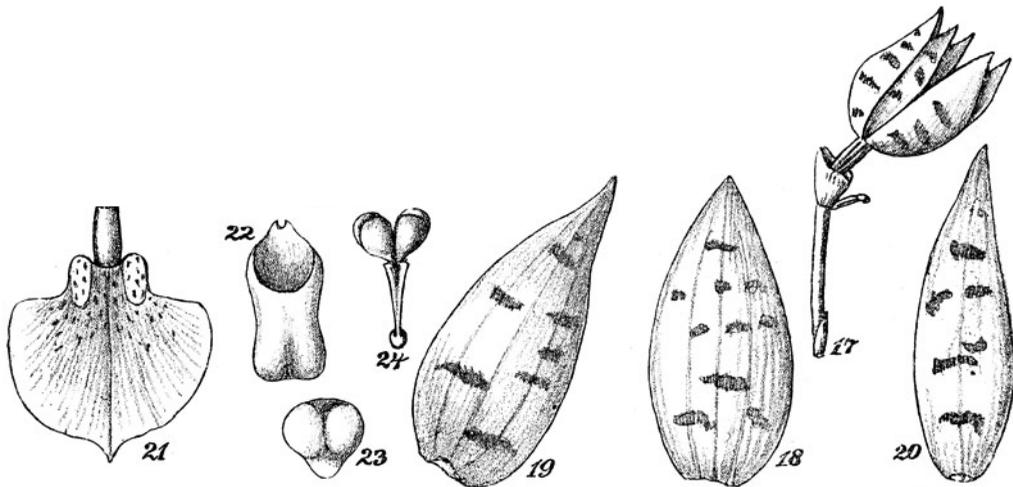


FIGURE 69. Lectotype of *Dichaea tuerckheimii* Schltr., *Türckheim s.n.* (Orchis 10: plate 44, fig. 17–24. 1916). Courtesy of G. A. Romero, Oakes Ames Orchid Herbarium, Harvard University Herbaria.

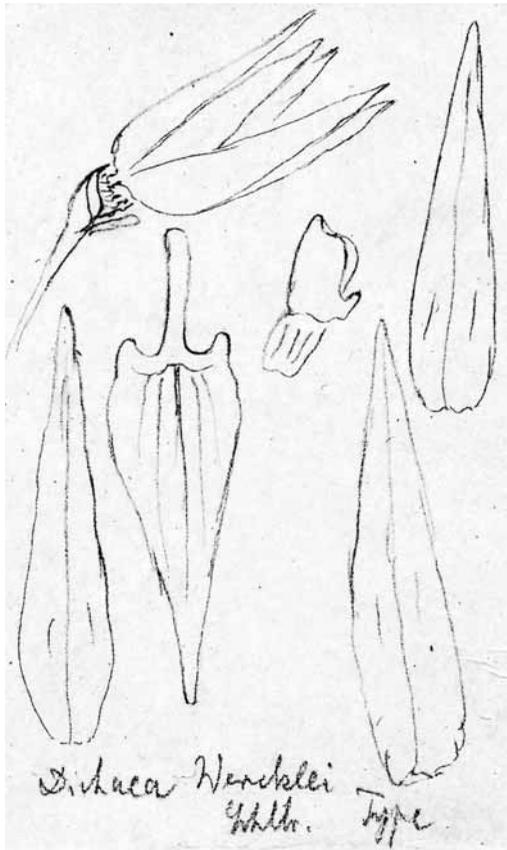


FIGURE 70. Copy of Schlechter's sketch of *Dichaea wercklei* Schltr., *Wercklé* 79 (AMES). Reproduced with the kind permission by the Director, Harvard University Herbaria.

long, somewhat inflated, margins slightly undulated. *Inflorescence* axillary, 1-flowered, produced above the foliage; the peduncle terete, glabrous, green, geniculate, 7–9 mm long. *Floral bracts* in pair, the outer one orbicular, cucullate, acute to apiculate, the inner one linear, acute, shorter than pedicellate ovary. *Ovary* pedicellate, terete, glabrous, to 3 mm long including the pedicel. *Flowers* small, subglobose, membranous, glabrous, the sepals and petals pale green, the lip and the column white. *Dorsal sepal* elliptic-lanceolate, acute-acuminate, cucullate, 6 × 2 mm. *Lateral sepals* obliquely elliptic, concave, 6.0 × 2.5 mm. *Petals* elliptic-lanceolate, narrower than sepals, abruptly acuminate, 3.0 × 1.5 mm, abaxially carinate along the mid-nerve. *Lip* cupped, the hypochile subrhomboid, from a cuneate base, provided with 2 small, rounded, tumid, lateral lobes and a low, smooth, rounded, ridge-like longitudinal callus; the epichile hastate 3-

lobed, with obtusely falcate, retrorse lateral lobes, the apical lobe triangular-cuspidate, the margins slightly incrassate; 5.5 × 2.0 mm wide across the hypochile, 5.5 mm wide across the spread lateral lobes. *Column* suberect, semiterete, 2.7 mm long, slightly recurved at the triangular apex, slightly dilated on each side of stigma, the margins of clinandrium incurved; stigma sub-orbicular, the lower margin provided with a subcuneate, up-curved, apically bilobed, puberulent ligule. *Anther* terminal to sub-ventral, the anther cap obovate-rhombiform, membranous, 2-celled. *Pollinia* 4, triangular-obovate, compressed, on a spatulate stipe; viscidium linear-oblong, white. *Fruit* an elliptic, glabrous capsule, 12 × 5 mm.

**Distribution:** endemic to Costa Rica.

**Additional material examined:** COSTA RICA. Alajuela: San Ramón, Camino a San Carlos, Quebrada Verde, [ca. 900 m], Fl. October-December. A. R. *Endrés Dichaea* No. 11 (*Rchb. Orch.* 38508, W, drawings); Piedades, Piedades Norte, road to Bajo de La Paz, km 4, summit of Cerro Azahar, 10°08'59.5"N, 84°35'00.3"W, 1563 m, crest of continental divide, premontane to lower montane cloud forest, 30 January 2005, *F. Pupulin* 5509, *D. Bogarín*, *M. Salas* & *P. Seaton* (USJ); Piedades Norte, unpaved road from Piedades Norte to Piedades Sur, San Antonio de Zapotal, 10°09'52"N, 84°35'37"W, 1410 m, Caribbean watershed of the Continental Divide, 24.3.2005, *F. Pupulin* 5589, *E. Salas*, *D. Bogarín* & *A.C. Rodríguez* (JBL-Spirit); same locality, *F. Pupulin* 5610, *E. Salas*, *D. Bogarín* & *A.C. Rodríguez* (JBL-Spirit); same locality, flowered in cultivation at Jardín Botánico Lankester, 14 Aug. 2006, *F. Pupulin* 5600, *E. Salas-Pupulin*, *D. Bogarín* & *A. C. Rodríguez* (JBL-Spirit). Cartago: Jiménez, road from La Selva to Purisil, 9°46'25.2"N, 83°47'09.3"W, 1650–1700 m, submontane wet forest, epiphytic along the roadside, 5 May 2006, flowered in cultivation at Jardín Botánico Lankester, 6 June 2006, *F. Pupulin* 6195 & *A. Rambelli* (CR); Orosi, Tapantí National Park, Oropendola trail, 1160 m, epiphytic on trunks in shade, lower montane wet forest, secondary vegetation, 25 May 2003, *F. Pupulin* 4752 (USJ, sterile!, drawings!); same locality, 29 December 2004, *M. Blanco et al.* 2637, fruiting (USJ-Spirit); Turrialba, Pacayitas, unpaved road to La Suiza, ca. Km 8, 9°52'29.9"N 83°35'03.6"W, 1150 m, premontane wet forest, 14 March 2006, flowered in cultivation at Jardín Botánico Lankester, 21 March 2006, *F. Pupulin*

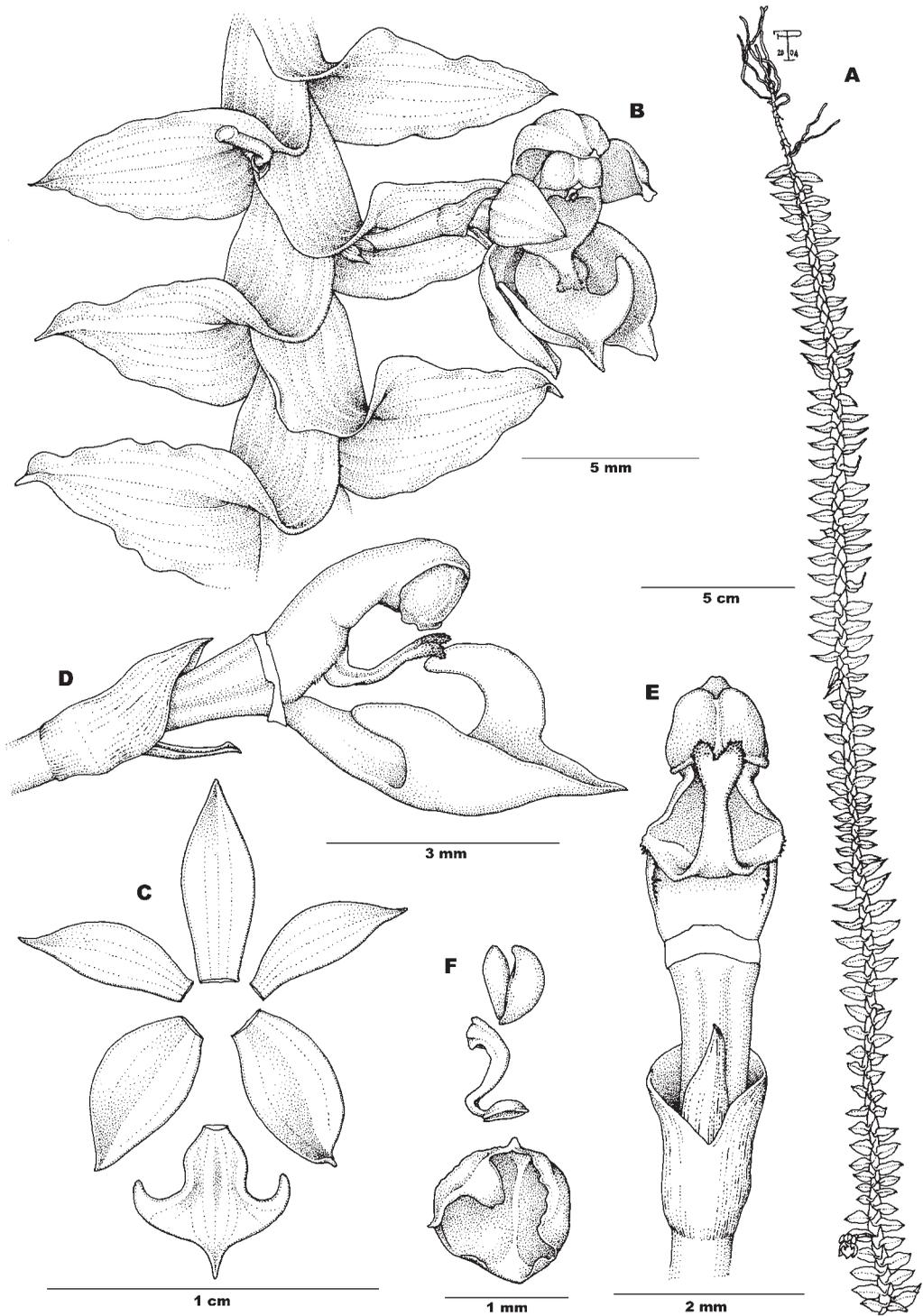


FIGURE 71. *Dichaea viridula* Pupulin. **A**, Habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, stipe and two pollinia, and anther cap. Drawn from: A–B, *Bogarin et al.* 925 (JBL-Spirit); C–G, *Pupulin 4652* (USJ).

5974, *D. Bogarín*, R. L. Dressler & A. Karremans (CR). San José: Bajo de la Hondura, 12 de marzo 1912, *H. Bertolini* 4 (sterile, CR). Without locality, A. R. Endrés *Dichaea* No. 26 (*Rchb. Orch.* 36722, W, drawings).

**Etymology:** from the Latin *viridulus*, greenish, in allusion to the color of the sepals and petals.

**Ecology:** epiphytic in deep shade in wet premontane forest at 700–1400 m elevation, restricted to the Caribbean drainage of Cordillera de Tilarán and Cordillera de Talamanca in central Costa Rica. Flowering

was recorded in May, August, October, and December, and probably the plants flower year-round. Plants in fruit were observed in December and January.

Among Costa Rican species of sect. *Dichaea*, *D. viridula* may be easily recognized by the plant habit, characterized by leaves very thin-textured, with the margins neatly undulate; leaf venation is strongly apparent also in the loose leaf sheaths. Another distinctive feature is the bilobed, barbate, up-curved infrastigmatic ligule, shared in the region only by the distantly related *D. oxyglossa* Schltr.

#### EXCLUDED SPECIES

*Dichaea diandra* Rchb. f., Bot. Zeit. 35: 41. 1877. TYPE. COSTA RICA. *Endrés s.n.* (Holotype: to be found in the Reichenbach Herbarium, W, not located; no isotypes known to exist).

Endrés's type collection is likely referable to a species of sect. *Dichaea*, the only group that present abaxially verrucose sepals ("*sepalis extus minute verrucosis*"; Reichenbach, 1877), and *D. diandra* may perhaps be considered a first name for *D. oxyglossa*. The ligulate leaves, the inflorescences distinctly longer than the leaves ("*racemis folia longe excedentibus*"), and the shortly unguiculate, rhombic lip provided with distinct shoulders ("*labello humerato rhombeo*") agree with the features of *D. oxyglossa*. However, Reichenbach's diagnosis is contradictory. He first assigns the species to a group provided with muricate fruits ("*Echinocarpae*"), but later on he describes the ovary as glabrous ("*ovario laeve*"). Naked pollinia, without any stipe or viscidium ("*caudicula glandulaque destitutis*") are otherwise known in *D. trichocarpa*, but the lip of this species with its characteristic discoid hypochile is hard to define as *humeratus*. The column of *D. diandra*, provided with two lateral anthers ("*in mediana oppositis*"), was likely a monster, and in the absence of a type specimen and any other material associated with the original protologue, Reichenbach's diandrous *Dichaea* cannot be assigned with certainty to any of the known taxon.

*Dichaea graminoides* (Sw) Lindl., Gen. Sp. Orch. Pl. 209. 1833.

Basionym: *Epidendrum graminoides* Sw., Prodr. 125. 1788. *Cymbidium graminoides* (Sw.) Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 71. 1799. *Isochilus graminoides*

(Sw.) Hook., Exot. Fl. 3: t. 196. 1826. *Epithecia graminoides* (Sw.) Schltr., Orchideen: 534. 1914. *Dichaeopsis graminoides* (Sw.) Schltr., Beih. Bot. Centralbl. 36(2): 519. 1918.

Although recorded by Mora-Retana and García (1992) and by Dressler (1993b), no voucher has so far confirmed the presence in Costa Rica of this widely distributed and distinctive species. *Dichaea graminoides* is known from the adjacent regions of Nicaragua and Panama, and its presence in Costa Rica is likely. Its basally biauriculate lip, provided with a high longitudinal callus, should be diagnostic.

*Dichaea muricatoides* Hamer & Garay, Orq. El Salv. 1: 148. 1974.

Basionym: *Dichaea tuerckheimii* Kraenzl., Pflanzenr. Pflanzenr. 4(50): 39. 1923, non Schltr. 1916. TYPE: GUATEMALA: *H. F. von Türckheim s.n.* (Holotype: W-Reichenbach Herbarium Nr. 12932).

In his recent treatment of Costa Rican Orchidaceae, Dressler (2003) included *Dichaea muricatoides* on the basis of *Solis R. 515* at CR. The cited collection was not located at the herbarium of the National Museum, but the description provided by Dressler did not differ from some of the morphs of the variable *D. poicillantha*. I have no direct knowledge of *Dichaea* specimens of the *D. poicillantha* complex from Mexico and the northern regions of Mesoamerica, and the elucidation of their correct taxonomy goes beyond the scope of the present treatment. However, on the basis of the high variability exhibited by populations of *D. poicillantha* in Costa Rica (see discussion *supra*), both vegetatively and florally, I strongly suspect that *D. muricatoides* should be considered a later name for the same species.

*Dichaea neglecta* Schltr., Beih. Bot. Centralbl. 36,2: 420. 1918. *Dichaea muricata* var. *neglecta* Kraenzl., Pflanzenr. 4(50): 38. 1923. Syntypes: Mexico. *Schiede 1053* (B, destroyed; drawing of the type, AMES 24900); Valle de Córdoba, Jan. 1866, *Bourgeau 1920* (B, destroyed; Isosyntype: AMES!); Xalapa, *Olson Seffer s.n.* (B, destroyed); Veracruz, Zacuapam, 900–1000 m, Febr. 1913, *C. A. Purpus 2154, pro parte* (B, destroyed).

Mora-Retana and García (1992) included the species in their checklist, but they provided no information about any voucher specimens. The only voucher of *Dichaea neglecta* so far known from Costa Rica, *J. F. Morales et al. 5787* (INB!), cited by Dressler (2003), is based on a misidentified specimen of *D. oxyglossa*. *Dichaea neglecta* may be recognized by the

freely branched stems, the boldly dark-green-spotted, unusually wide and strongly flattened leaf sheaths (the stem appearing very wide), and the obovate lip with the narrow lateral lobes inserted in the basal half. The species has been recorded from Mexico, Guatemala, Belize, El Salvador, Honduras, and Nicaragua, the latter country likely representing its southern distribution limit.

*Dichaea robusta* Schltr., Repert. Sp. Nov. Regni Veg. Beih. 27: 83. 1929.

Both Pupulin (2002) and Dressler (2003) cited *Dichaea robusta*, a species originally described from Bolivia, as a possible name for the species restricted in Costa Rica to the lowland and mid-altitude forests of the Pacific slopes, later described as *D. globosa*.

#### INDEX OF ACCEPTED SPECIES

*Dichaea acostae* Schltr.

*Dichaea acroblephara* Schltr.

*Dichaea amparoana* Schltr.

*Dichaea brachypoda* Rchb.f. = *Dichaea panamensis* Lindl.

*Dichaea brenesii* Schltr. = *Dichaea trulla* Rchb.f.

*Dichaea ciliolata* Rolfe = *Dichaea hystricina* Rchb.f.

*Dichaea costaricensis* Schltr.

*Dichaea cryptahrrhena* Rchb.f. ex Kraenzl.

*Dichaea dammeriana* Kraenzl.

*Dichaea echinocarpa* (Sw.) Lindl. = *Dichaea pendula* (Aubl.) Cogn.

*Dichaea echinocarpa* var. *lobata* Ames & Correll = *Dichaea pendula* (Aubl.) Cogn.

*Dichaea eligulata* Folsom

*Dichaea elliptica* Dressler & Folsom

*Dichaea filiarum* Pupulin

*Dichaea fragrantissima* ssp. *eburnea* Dressler & Pupulin

*Dichaea glabrescens* Kraenzl. = *Dichaea tuerckheimii* Schltr.

*Dichaea glauca* (Sw.) Lindl.

*Dichaea guatemalensis* Schltr. = *Dichaea tuerckheimii* Schltr.

*Dichaea globosa* Dressler & Pupulin

*Dichaea gomez-laurittoi* Pupulin

*Dichaea gracillima* C. Schweinf.

*Dichaea hystricina* Rchb.f.

*Dichaea lankesteri* Ames

*Dichaea lobata* (Ames & Correll) L. O. Williams = *Dichaea pendula* (Aubl.) Cogn.

*Dichaea lycopodioides* Rchb.f. ex Kraenzl. = *Dichaea hystricina* Rchb.f.

*Dichaea morrisii* Fawc. & Rendle

*Dichaea obovatipetala* Folsom

*Dichaea oerstedii* Rchb.f. = *Dichaea glauca* (Sw.) Lindl.

*Dichaea ovatifetala* Schltr. = *Dichaea cryptahrrhena* Rchb.f. ex Kraenzl.

*Dichaea oxyglossa* Schltr.

*Dichaea pendula* (Aubl.) Cogn.

- Dichaea pendula* var. *swartzii* C. Schweinf. = *Dichaea pendula* (Aubl.) Cogn.  
*Dichaea panamensis* Lindl.  
*Dichaea poicillantha* Schltr.  
*Dichaea powellii* Schltr. = *Dichaea trulla* Rchb.f.  
*Dichaea sarapiquinsis* Folsom  
*Dichaea schlechteri* Folsom = *Dichaea similis* Schltr.  
*Dichaea selaginella* Schltr. = *Dichaea hystericina* Rchb.f.  
*Dichaea similis* Schltr.  
*Dichaea squarrosa* Lindl.  
*Dichaea standleyi* Ames = *Dichaea acroblephara* Schltr.  
*Dichaea swartzii* (C. Schweinf.) Garay & Sweet = *Dichaea pendula* (Aubl.) Cogn.  
*Dichaea trachysepala* Schltr. = *Dichaea pendula* (Aubl.) Cogn.  
*Dichaea trichocarpa* (Sw.) Lindl.  
*Dichaea trulla* Rchb.f.  
*Dichaea tuerckheimii* Schltr.  
*Dichaea verrucosa* Ames & C. Schweinf. = *Dichaea cryptarrhena* Rchb.f. ex Kraenzl.  
*Dichaea viridula* Pupulin  
*Dichaea wercklei* Schltr. = *Dichaea tuerckheimii* Schltr.  
*Dichaea willdenowiana* Kraenzl. = *Dichaea glauca* (Sw.) Lindl.

## LIST OF EXSICCATA AND SPIRIT-PRESERVED SPECIMENS

Numbers in bold in parentheses refer to the species number in the treatment.

- Acosta s.n.* [AMES 40542] (1); *s.n.* [AMES 40552] (24).  
*Aguilar* 2667 (20).  
*Alfaro* 12 (22); 2484 (15).  
*Atwood* 86–46 (5); 89–182 (16); 89–202 (16); 89–273 (5); 89–286 (5); 89–314 (10); 89–327 (26).  
*Atwood & Haber* 88–7 (16); 88–69 (5).  
*Atwood & Morris* 4092 (16).  
*Aublet s.n.* (21).  
*Azofeifa* 154 (15); 194 (27); 195 (8); 195 (20).  
*Barringer* 3162 (5).  
*Barringer & al.* 3672 (10); 3737 (4).  
*Beckers* 17 (27).  
*Bello* 2078 (22); 4448 (22).  
*Bertolini* 4 (29).  
*Bittner & Herrera* 2034 (27).  
*Blanco (M.)* 1374 (7).  
*Blanco (M.) & al.* 1978 (15); 2637 (29); 2705 (22); 2731 (21); 2734 (19); 2765 (20).  
*Blanco (V.) s.n.* (4).  
*Bogarín* 42 (2); 173 (26); 206 (27); 207 (2); 300 (26); 815 (6); 1559 (23); 1570 (4); 1932 (24).  
*Bogarín & Blanco* 1157 (24); 1179 (24).  
*Bogarín & Botánica Forestal-UCR* 1009 (2); 1017 (8); 1061 (8).  
*Bogarín & Carmona* 956 (2).  
*Bogarín & Cervantes* 1337 (22); 1369 (22).  
*Bogarín & Granados* 241 (25); 242 (25); 243 (5); 254 (25).  
*Bogarín & Grupo de Historia Natural UCR* 136 (28).  
*Bogarín & León-Páez* 184 (22); 186 (19); 187 (22); 188 (22); 189 (22); 190 (19); 197 (6); 198 (22).  
*Bogarín & Prendas* 679 (3); 863 (16); 864 (16).  
*Bogarín & Pupulin* 877 (23); 894 (4); 2234 (20).  
*Bogarín & Salazar* 1002 (6).  
*Bogarín & al.* 126 (25); 303 (15); 346 (16); 328 (24); 329 (24); 330 (24); 706 (22); 712 (22); 713 (22); 717 (22); 719 (22); 720 (22); 925 (29); 969 (6); 1075 (20); 1083 (22); 1084 (22); 1097 (22); 1117 (9); 1178 (17); 1298 (5); 1435 (22); 1464 (15); 1469 (16); 1523 (22); 1615 (22); 1823 (22); 2010 (12); 2015 (7); 2048 (19); 2057 (12); 2274 (10); 2422 (16); 2486 (16); 2556 (20).  
*Brade & Brade* 1173 (2); 1306 (3).  
*Brenes* (15)873 (5); (21)1721 (15); (31)1730 (15); (40)370 (4); (47)377 (5); (56)386 (5); (60)1541 (5); (64)1022 (22); (71)1645 (5); (72)20638 (1); (74)686 (21); (74)932 (22); (75)11396 (15); (77)1284 (5); 80(1763) (6); 86(1293) (11); (90)1650 (6) (91)2901 (6); (110)968 (22); 144 (CR 18455) (19); (144)1346 (5); 146 (1); 187 (21); (191)1386 (5); (192)1387 (5); 196 (5); (199)811 (28);

- (204)1396 (4); (222)1412 (4); (237)2961 (4); (267)562 (15); (274) 1459 (14); (277)1462 (4); 280 (20); (309)1168 (22); (527) 1386 (16); 532 (4); 909 (6); 2995 (21); 14285 (5); 20639 (5); *s.n.* (CR 18463) (20).
- Campos & Campos* 193 (10).
- Carvajal* 3 (22); 347 (10); 479 (10).
- Chacón* 31 (18); *s.n.* (22).
- Chacón & Herrera* 1640 (15).
- Chacón-Valverde s.n.* [JBL-09376] (22).
- Chavarría & Umaña* 159 (20).
- Chávez* 50 (28).
- Clark & al.* 256 (12).
- Cooper* 5969 (5); *s.n.* [Apr. 1887] (5).
- Davidse & al.* 28407 (5); 28354 (5).
- Douglas Stevens* 23931 (20).
- Dressler* 6408 (12).
- Dressler & Biología* 350, No. 16 (18); No. 17 (18); No. 62 (7); No. 164 (15); No. 195 (10).
- Echeverría s.n.*, (CR 30756) (5).
- Endrés II* (11); 28 (5); 29 (4); [31?, W-R 14768] (15); 66 (6); 143 (11); 517 (4); 161 (10); [*Dichaea* No. 4] (3); [*Dichaea* No. 13] (4); [*Dichaea* No. 26] (29); *s.n.* (W-R 14787) (20); *s.n.* [W-R 10501] (11); *s.n.* [W-R 14768] (15).
- Estrada & Solano* 1822 (5).
- Fernández* 360 (22).
- Folsom* 9999 (23); 10993 (5); 10990A (22); 10994 (5); 11005 (24); 11002A (28); 11005B (5); 11006 (20); 11010 (10); 11011 (15); 11011B (4); 11016 (22); 11017A (22); 11028B (16).
- Galeotti* 5078 (11).
- Gallardo & Lépiz* 297 (27); 326 (15).
- Germani* 131 (10).
- Gómez s.n.* (26).
- Gómez-Laurito* 8174 (13).
- Gómez-Laurito & al.* 12496 (25).
- Grant & Rundell* 92–01678 (25).
- Grayum* 11032 (5).
- Grayum & Evans* 10159 (20).
- Grayum & Hammel* 9538 (20).
- Grayum & Jacobs* 5323 (20).
- Grayum & al.* 5886 (22); 10084 (20).
- Haber & Bello* 7867 (10).
- Haber & Zucowski* 8620 (22).
- Hammel & al.* 18977 (20).
- Hartweg* 46 (11); 516 (11).
- Herrera* 1532 (20); 1969 (20); 4195 (15); 4746 (20); 4821 (20); 4888 (20); 5827 (20); 5829 (12); 7769 (20); 8317 (20); 8403 (5).
- Herrera & Cascante* 8141 (5); 8159 (5).
- Herrera & al.* 7274 (5); 8541 (22).
- Hitetz* 25 (28).
- Horich s.n.* [Jul. 1959] (5).
- Hübsch s.n.* [1882–85] (11).
- Ingram* 304 (5).
- Ingram & Ferrell* 564 (2); 613 (20); 630 (16); 682 (10); 739 (15); 780 (16); 812 (10); 1675 (5); 1846 (16).
- Ingram & al.* 1499 (5).
- JBL-00495* (5); *JBL-04898* (22); *JBL-11987* (15).
- Kapelle & Gutiérrez U.* 799 (25).
- Karremans* 110 (20); 111 (4); 114 (4); 135 (10); 332 (22); 333 (22); 511 (22); 622 (22); 737 (21); 767 (22); 799 (4); 898 (18).
- Karremans & al.* 621 (20); 626 (5); 627 (5).
- Karremans & Karremans* 405 (22); 410 (22).
- Kernan & Phillips* 886 (20).
- Kirby* 04–75 (26).
- Lankester* 12 (1555); 918 (5); K353 (16); *s.n.* [AMES] (12).
- Liesner & Judziewicz* 14525 (16); 14863 (16).
- Lobo* 60 (20).
- López & al.* 39 (10).
- Luer s.n.* (8).
- Madero s.n.* (15).
- Marín* 206 (12); 284 (22).
- Marín & Quesada* 272 (12); 273 (12).
- Martén* 891 (4).
- Martínez* 340 (22).
- Moraga* 314 (27); 532 (27).
- Morales* 265 (25); 3943 (20); 4455 (11); 4488 (15); 4717 (21); 4719 (4); 4815 (23); 4954 (16); 6651 (15).
- Morales & González* 5078 (27).
- Morales & Saborío* 4554 (15); 4580 (20).
- Morales & al.* 4070 (20); 5049 (15); 5787 (19).
- Morris (D.)* 2269 (17).
- Morris & Obando* 4042 (10).
- Muñoz* 04–147 (11).
- Nadkarni s.n.* [Dec. 1987] (5).
- Navarro* 164 (22).
- Oersted s.n.* [W-R 19392] (11).
- Ossenbach & al.* 282 (20); 343 (28).
- Picado* 95 (20).
- Picado & Fletes* 219 (5).
- Pupulin* 702 (6); 1955 (2); 2080 (12); 3024 (21); 3030 (16); 3032 (22); 3036 (21); 3037 (5); 3863 (2); 4025 (2); 4662 (22); 4750 (21); 5644 (24); 5665 (25).
- Pupulin & Barboza* 2226 (11); 4704 (16); 4716 (22); 4734 (11); 4735 (11).
- Pupulin & Bogarín* 5245 (27); 5250 (9); 5253 (9); 5254 (9); 5262 (4); 5263 (9); 5264 (18); 5270 (9); 5922 (20).

- Pupulin & Castelfranco* 1476 (12); 1518 (27); 1618 (15).
- Pupulin & León-Páez* 5210 (5); 5211 (5).
- Pupulin & Rambelli* 6195 (29).
- Pupulin & Salas-Pupulin* 5095 (15); 5097 (6); 6080 (25).
- Pupulin & Spadari* 2003 (17); 2051 (11).
- Pupulin & al.* 1068 (27); 1087 (12); 1088 (12); 1089 (7); 1094 (7); 1110 (28); 1123 (12); 1124 (12); 1189 (12); 1855 (20); 2100 (6); 2119 (19); 2362 (15); 2397 (22); 2533 (12); 2575 (7); 2576 (20); 2637 (7); 2639 (12); 2647 (7); 2718 (7); 2944 (10); 3165 (12); 3197 (11); 3284 (24); 3304 (5); 3393 (19); 3419 (22); 3420 (22); 3444 (19); 3466 (15); 3480 (22); 3574 (12); 3595 (5); 3667 (20); 3732 (6); 3904 (22); 3925 (15); 4081 (22); 4089 (24); 4091 (22); 4202 (18); 4232 (19); 4242 (22); 4244 (22); 4253 (6); 4320 (15); 4360 (6); 4393 (22); 4436 (5); 4517 (12); 4594 (24); 4598 (24); 4600 (10); 4601 (10); 4629 (21); 4630 (21); 4639 (22); 4644 (22); 4647 (6); 4662 (22); 4680 (22); 4684 (22); 4691 (19); 4700 (22); 4706 (16); 4752 (29); 4797 (4); 4804 (15); 4808 (24); 4815 (22); 4819 (22); 4824 (22); 4850 (2); 4851 (2); 4856 (23); 4910 (22); 4919 (24); 4944 (9); 4945 (8); 4946 (18); 5013 (18); 5015 (18); 5019 (18); 5023 (18); 5052 (4); 5055 (18); 5056 (18); 5058 (18); 5112 (22); 5113 (22); 5114 (10); 5118 (22); 5119 (22); 5127 (25); 5138 (10); 5140 (20); 5141 (18); 5153 (8); 5164 (10); 5171 (4); 5197 (22); 5204 (22); 5209 (22); 5211 (22); 5222 (22); 5227 (27); 5327 (27); 5330 (23); 5333 (23); 5337 (23); 5339 (19); 5341 (23); 5354 (23); 5355 (19); 5365 (22); 5367 (23); 5417 (24); 5433 (22); 5434 (22); 5442 (6); 5456 (28); 5482 (9); 5492 (16); 5501 (3); 5508 (6); 5509 (29); 5511 (22); 5512 (21); 5572 (20); 5574 (20); 5579 (16); 5585 (19); 5587 (6); 5589 (29); 5592 (20); 5594 (15); 5600 (29); 5610 (29); 5616 (5); 5644 (24); 5669 (20); 5692 (23); 5694 (23); 5700 (4); 5702 (4); 5703 (20); 5770 (22); 5793 (15); 5799 (22); 5811 (12); 5820 (20); 5842 (22); 5919 (20); 5920 (20); 5970 (9); 5974 (29); 6014 (27); 6023 (16); 6051 (18); 6063 (5); 6075 (6); 6088 (6); 6099 (28); 6116 (20); 6126 (6); 6148 (20); 6149 (20); 6151 (20); 6213 (10); 6228 (2); 6231 (2); 6270 (28).
- Quirós* (260)240 (5).
- Quesada s.n.* (7).
- Quesada & Chacón* 1059 (15).
- Quesada & al.* 552 (5); 1147 (7); 1124 (26); 1180 (7).
- Quesada-Chanto & al.* 24 (20).
- Richardson K-108* (27); *K-109* (1).
- Rivera* 257 (25).
- Rivera & Rojas* 2511 (22).
- Rodríguez* 7 (2).
- Rodríguez & al.* 2188 (20).
- Rojas* 69 (20).
- Rojas & al.* 95 (16).
- Ruiz & al.* 805 (7).
- Sánchez* 1305 (22).
- Schiede* 45 (11).
- Schnitter s.n.* (21).
- Schug s.n.* (9).
- Schug & Naranjo V.* 205 (24).
- Serrano & Blanco* 129 (12); 131 (22); 133 (22).
- Serrano & Salazar* 215 (26).
- Serrano & al.* 229 (4).
- Smith H.* 180 (25).
- Standley* 32977 (5); 32990 (5); 33774 (11); 36182 (16); 33078 (16); 33120 (21); 33150 (21); 36329 (16); 37405 (2); 37440 (2); 37418 (4); 37441 (4); 37536 (4); 37547 (4); 38264 (5); 38324 (16).
- Standley & Torres* 47555 (25); 47611 (25); 51395 (16);
- Standley & Valerio* 33725 (6); 45134 (4); 45315 (6); 47104 (2); 47138 (16); 51703 (21); 52457 (21);
- Stevens* 13802 (10); 14248 (16).
- Swartz s.n.* [*Rchb. Orch.* 25294, W] (21); *s.n.* [*Rchb. Orch.* 25295, W] (11);;
- Todzia* 346 (26); 679 (5).
- Todzia & al.* 1912 (26); 1926 (22).
- Tuerckheim s.n.* [*Rchb. Orch.* 12932, W] (22).
- Utley & Utley* 2807 (5).
- Valverde* 900 (20); 1049 (27).
- Vargas* 23 (24).
- Vargas & al.* 1308 (5); 1347 (5).
- Wania* 100 (20).
- Warner s.n.* (24).
- Warner et al.* 50 (4).
- Wendland* 809 (20).
- Wercklé* 22 (2); 32 (22); 39 (4); 77 (4); 103 (3); 124 (6); *s.n.* [Jan. 1920](4).
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- Whitten & Blanco* 2036 (22); 2050 (18); 2095 (4); 2096 (27); 2097 (28).
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