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REVISIÓN TAXONÓMICA DEL GÉNERO *CAMPYLOCENTRUM* (ORCHIDACEAE: ANGRAECINAE) EN COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado de *Magister Scientiae* en Biología

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Dedicatoria

Esta tesis está dedicada a mi familia, especialmente a mis padres Inés y Gerardo, a mis hermanos Marielos y Sergio, a mi abuela Susana y a mis sobrinos Matías y Sofía por todo el apoyo durante mi carrera universitaria.

In memoriam Israel Bogarín Arguedas "Abuelo Chalo".

Labor omnia vincit.

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Prefacio

Se presenta una revisión taxonómica de *Campylocentrum* (Orchidaceae) en Costa Rica. *Campylocentrum* se caracteriza por las plantas epífitas, monopodiales con crecimiento terminal indefinido. Ambos, tallos elongados con hojas dísticas o acaulescentes, sin hojas están presentes en el género. Las hojas son conduplicadas, raramente teretes, articuladas con la vaina que rodea el tallo, a veces ausente o reducida a una hoja en forma de escama a lo largo de un tallo elongado. Las inflorescencias son racemosas, laterales, las flores con espolones en posición dística sobre el raquis. Se discuten la historia taxonómica del género y su posición filogenética. Se tratan los caracteres morfológicos florales y vegetativos, y se discute su significado taxonómico. El género comprende nueve especies en el país, y se proporciona una clave artificial de especies. Cada taxon es descrito con base en material costarricense, ilustrado en una lámina, y se evalua su distribución en el país. Se presentan mapas de distribución para todos los taxa. La distribución, la derivación del nombre, notas sobre ecología de especies, y rasgos diagnósticos se presentan para cada taxon. Dos especies necesitan ser lectotipificadas: *C. parvulum* y *C. multiflorum*. Se documenta e ilustra una nueva especie de Costa Rica. Es similar a *C. pachyrrhizum* pero difiere en las inflorescencias congestionadas, el espolón curvo hacia arriba, con la base angosta ensanchándose en el ápice y oscuramente trilobulado.

Abstract

A taxonomic revision of *Campylocentrum* (Orchidaceae) in Costa Rica is presented. *Campylocentrum* is characterized by epiphytic, monopodial plants with indefinite terminal growth. Either elongated, distichously leafy or acaulescent, leafless stems are present. The leaves are conduplicate, rarely terete, articulate with the sheath surrounding the stem, sometimes absent or reduced to scale-like leaves along an elongated stem. The inflorescences are lateral racemes with distichously arranged spurred-lip flowers on the rachis. The taxonomic history of the genus and its phylogenetic position are discussed. Characters of vegetative and floral morphology are treated, and their taxonomic significance is discussed. The genus is treated as comprising nine species in the country, and a key to species is provided. Each taxon is described on the basis of Costa Rican material, illustrated in a composite plate, and its distribution 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. Two species need to be lectotipifyed: *C. parvulum* and *C. multiflorum*. A new species from Costa Rica has been documented and is here illustrated. It is similar to *Campylocentrum pachyrrhizum* but differs in having a congested inflorescence, the spur of the lip curved upward, narrow at base and wider at apex, and obscurely three lobed.

Capítulo 1

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The genus *Campylocentrum* (Orchidaceae: Angraecinae) in Costa Rica: a review.

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ABSTRACT: A taxonomic revision of *Campylocentrum* (Orchidaceae) in Costa Rica is presented. *Campylocentrum* is characterized by epiphytic, monopodial plants with indefinite terminal growth. Either elongated, distichously leafy or acaulescent, leafless stems are present. The leaves are conduplicate, rarely terete, articulate with the sheath surrounding the stem, sometimes absent or reduced to scale-like leaves along an elongated stem. The inflorescences are lateral racemes with distichously arranged spurred-lip flowers on the rachis. The taxonomic history of the genus and its phylogenetic position are discussed. Characters of vegetative and floral morphology are treated, and their taxonomic significance is discussed. The genus is treated as comprising nine species in the country, and a key to species is

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RESUMEN: Se presenta una revisión taxonómica de *Campylocentrum* (Orchidaceae) en Costa Rica. *Campylocentrum* se caracteriza por las plantas epífitas, monopodiales con crecimiento terminal indefinido. Ambos, tallos elongados con hojas dísticas o acaulescentes, sin hojas están presentes en el género. Las hojas son conduplicadas, raramente teretes, articuladas con la vaina que rodea el tallo, a veces ausente o reducida a una hoja en forma de escama a lo largo de un tallo elongado. Las inflorescencias son racemosas, laterales, las flores con espolones en posición dística sobre el raquis. Se discuten la historia taxonómica del género y su posición filogenética. Se tratan los caracteres morfológicos florales y vegetativos, y se discute su significado taxonómico. El género comprende nueve especies en el país, y se proporciona una clave artificial de especies. Cada taxon es descrito con base en material costarricense, ilustrado en una lámina, y se evalua su distribución en el país. Se presentan mapas de distribución para todos los taxa. La distribución, la derivación del nombre, notas sobre ecología de especies, y

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Palabras clave/Key words: Angraecinae, *Campylocentrum*, *C. generalense*, Orchidaceae, taxonomy, Costa Rica.

INTRODUCTION

The subtribe Angraecinae Summerh. encompasses a large group of highly derived Epidendroid orchids including about 18 genera and approximately 408 species of epiphytic, monopodial plants. The group is eminently Madagascan (where the largest number of genera and species occur), with members in mainland Africa, Sri Lanka and Ceylon, Mascarene and Comoros Islands and outliers in the tropical regions of the New World. Angraecinae has been formally assigned to the mainly Paleotropical tribe Vandeae Lindl. by Chase *et al.* (2003). Complementing the traditional classification of taxa within Vandeae (Dressler 1981, 1993a), which has been based previously on floral morphology, recent molecular studies support Vandeae as a monophyletic group. Formerly, Vandeae included the subtribes Aeridinae Pfitz. (formerly Sarcanthinae Benth.), Angraecinae and Aerangidinae Summerh. (Dressler 1993a). However, according to Carlsward et al. (2006a,

2006b), it consists of only two subtribes: Aeridinae and a broadly defined Angraecinae. Summerhayes (1966) circumscribed the two African and Malagasy subtribes, Angraecinae and Aerangidinae, based on rostellum shape and chromosome number. In this circumscription, the exclusively African Aerangidinae differs from Angraecinae in the beaklike rostellum, compared with the slit rostellum forming a short apron at the apex of the column in Angraecinae (Dressler 1981), but molecular evidence indicates that the Aerangidinae has to be reduced under a broad concept of Angraecinae. Individually, Aerangidinae and Angraecinae are polyphyletic, but together form a monophyletic group (Carlsward *et al.* 2006a). Members of this group have been known as the angraecoid orchids.

Angraecinae is characterized by plants with mostly reduced to elongated stems and distichous, conduplicate leaves (that have been lost in some species); the lateral inflorescences bear one to many, tiny to relatively large flowers, provided with a well-developed nectariferous spur formed of labellar tissues. The anther is incumbent, terminal, operculate, with reduced partitions, and the two pollinia have one or two well defined stipes and viscidia. The rostellum is deeply divided and the stigma is entire (Dressler 1981).

Recent molecular studies in American Angraecinae (Carlsward *et al.* 2003) show that *Campylocentrum* Benth. is sister to a broadly defined concept of *Dendrophylax* Rchb.f., which includes *Harrisella* Fawc. & Rendle, *Polyradicion* Garay and *Polyrrhiza* Pfitzer. *Campylocentrum* is characterized by epiphytic, monopodial plants with indefinite terminal growth. Either elongated, distichously

leafy or acaulescent, leafless stems are present. The roots are cylindrical or flattened. The leaves are conduplicate, rarely terete, articulate with the sheath surrounding the stem, sometimes absent or reduced into scale-like leaves along an elongated stem. The inflorescences are lateral racemes with distichously arranged spurred-lip flowers on the rachis. Vegetatively, *Dendrophylax* can be recognized by the plants always leafless with lax, sometimes branching, inflorescences bearing few flowers (one to six), and one or few flowers open at once (Carlsward *et al.* 2003).

The aphyllous condition, otherwise well represented in other groups of the Vandeae (in Aeridinae: *Taeniophyllum* Blume, *Chiloschista* Lindl., and some species of *Phalaenopsis* Blume), is restricted in the subtribe Angraecinae to members native to the American tropics and the African *Microcoelia* Lindl. (including the leafless *Solenangis* Schltr.), part of a broadly defined Angraecinae. Dressler (1981) suggested that the Angraecinae ancestor invader from Africa was probably a leafy, small flowered plant. The different evolutionary opportunities could perhaps explain the distribution pattern of large-flowered American Angraecinae, restricted to the northern Mesoamerica (Mexico to El Salvador), West Indies and southern Florida. There is evidence to consider that the evolution of leaflessness has arisen at least twice in the New World with *Dendrophylax* and *Campylocentrum* (Carlsward *et al.* 2006a). *Campylocentrum* is unique among Neotropical Angraecinae in including both leafy and leafless species, while *Dendrophylax* only includes leafless species.

Almost 100 names have been published in *Campylocentrum,* but the genus likely includes only about 60 species distributed from Mexico to Brazil, Bolivia and the West Indies, with a main centre of distribution in southern coastal Brazil (Todzia 1980, Carlsward *et al.* 2003) (Figure 1). This is the only genus of the Angraecinae present in Costa Rica. Species of *Campylocentrum* grow in wet forests from close to sea level to about 2000 m in elevation. Species of the genus are widespread in Costa Rica, and they may be rather common (or locally very common) in secondary forests without a marked dry season. Leafless species are seemingly restricted in distribution to tropical, lowland wet forest on both the Pacific and Caribbean slopes, up to elevations of 600 m (Todzia 1980; Pupulin & Bogarín 2005) (Figure 2). In the vicinity of Santa Rosa de Pocosol in San Carlos plain of Alajuela province, *C. fasciola*, *C. micranthum* and *C. poeppigii* grow sympatrically. In the area of La Esperanza de Atirro of Jiménez in Cartago province, *C. brenesii*, *C. panamense* and *C. tenellum* have been found growing together. In addition, *C. micranthum*, *C. multiflorum* and *C. panamense* grow sympatrically in the area of Quepos. Species of higher elevations like *C. schiedei*, which is restricted to elevations from 1000 to 1670 m, have been recorded growing with *C. brenesii* at La Carpintera, in the province of Cartago. No collections of *Campylocentrum* are known from the tropical dry forest of northern Pacific Guanacaste, but plants can be found in seasonal humid areas of Nicoya Peninsula (Figure 2). Some trees or shrubs such as *Citrus* spp. (Rutaceae), *Crescentia* spp. (Bignoniaceae), *Codiaeum variegatum* (Euphorbiaceae), *Coffea arabica* (Rubiaceae), *Hibiscus* sp. (Malvaceae), *Murraya paniculata* (Rutaceae), *Psidium guajava* (Myrtaceae), *Theobroma cacao*

(Sterculiaceae) and *Terminalia catappa* (Combretaceae), often cultivated in gardens or commercial plantations in wet areas, are common hosts of *Campylocentrum* plants. However, some species, like *C. panamense*, are almost exclusively found in the understory of mature secondary forest.

Data on *Campylocentrum* pollination are scanty. The spurred, nectariferous, sweetly scented flowers, mostly white to pale greenish, suggest a pollination syndrome oriented toward microlepidoptera and possibly some bees. Field observations in Costa Rica were so far unsuccessful in recording actual pollinators, but fruiting rate is usually very high and most of the flowers produce seeds. In Brazil, *C. aromaticum* is mainly pollinated by halictid bees (Singer & Cocucci 1999, Singer 2003). According to Singer (2003), also flies and bugs are able to dislodge the pollinaria and perhaps can act as accessory pollinators. In addition, *C. burchellii* Cogn., a leafless species, was recorded as pollinated by meliponini bees (Singer 2003). Also, small butterflies have been observed visiting *Campylocentrum* flowers during the day (R.L. Dressler, pers. comm. 2008).

Although plants of *Campylocentrum* are rather common elements of disturbed vegetation, leafless species are difficult to detect in the field when not in flower, where it is almost impossible to observe the core of roots among the mosses, ferns, bromeliads and other plants growing epiphytically in secondary areas and abandoned plantations. *Campylocentrum* are not common plants in cultivation and many specimens are confused or wrongly identified in herbaria. The small flowers are characterized by a general shape with little variation in overall

morphological pattern, and the difficult to observe critical characters of the flowers in dried material has sometimes caused confusion in species identification. The present work aims to clarify the status of *Campylocentrum* in Costa Rica, based on an extensive survey of living material, morphological variation and ecological evidence.

Materials and methods

This revision was conducted mainly at the Lankester Botanical Garden (LBG), University of Costa Rica, where living specimens have been cultivated and documented between 2003 and 2009. In this study, we have relied mainly upon live collections and gatherings during fieldwork activities of LBG staff. Field research was conducted over the country and type localities were visited. Data from all specimens cited have been recorded in a computerized database at LBG. They are also available on www.epidendra.org website (Pupulin 2007, 2009). Distribution maps were made using the geographic information system software ArcView GIS 3.3 (ESRI, California, USA). Georeferenced specimens were obtained by using a Garmin eTrex Vista GPS, maps and online gazetteers. Ecological zones were estimated by using the Holdridge Life Zone System (Holdridge 1967, Holdridge 1987) and the Mapa ecológico de Costa Rica by Tosi (1969).

Phenology data were recorded both in the field and in cultivated specimens or herbarium labels. Individual plants were photographed, illustrated and preserved as *exsiccata* and spirit-preserved specimens (included flowers, portions of the stems or entire plants) for future reference. Herbarium specimens were deposited at

CR and USJ herbaria. Whenever possible, the herbarium specimens were complemented with sketches, photographs and FAA material. The material preserved in FAA is deposited at JBL, and indicated in the treatment as "JBL-spirit". Herbarium and spirit material may consist of wild collected specimens or material collected entirely from cultivated plants.

Anatomical and morphological data as well as root structure were obtained from living specimens cultivated at LBG. Transverse (TS) sections of roots were made by hand using a razor blade. They were fixed in FAA, stained with toluidine blue and mounted on slides following the procedures described in Sandoval (2005). All sections were observed using light microscopy.

Stem, flower and fruit comparisons were scanned at 1200 and 2400 dpi resolution with an Epson Perfection 2400 photo scanner. Sketches of specimens were drawn with a Leica MZ 7.5 stereomicroscope provided with drawing tube, and conserved in the reference collections of JBL. All the taxa were illustrated by composite line-drawings from living specimens. Two plates for each of the following species were prepared: *C. micranthum*, *C. multiflorum* and *C. panamense*. In the case of highly variable morphological species of the *C. brenesii* complex, plates were drawn from representative individuals of the different morphs. Illustrations included a typical plant habit, inflorescences or part of the inflorescences, the flower and dissection of perianth, anther cap and pollinarium or other taxonomically informative characters depending on the taxa illustrated. Plate composition was as consistent as possible to facilitate species comparison.

Descriptions were prepared from both living specimens and herbarium material. Visits to the following herbaria were made: AMES, BM, CR, INB, K, SEL, USJ and W. Type specimens from AMES, K and W were digitalised at 300 dpi and the resulting images were included in the reference collections. When necessary, flowers of herbarium material were rehydrated using boiling water and specimens drawn with the aid of a camera lucida.

PLANT MORPHOLOGY

Campylocentrum comprises monopodial, epiphytic plants with indefinite terminal growth ranging from elongated, distichously leafy, suberect to pendent, often branching stems to abbreviated, acaulescent, condensed stems bearing nonphotosynthetic scales (Figure 3—5). One species, *C. poeppigii* has elongate stems with minute, caducous leaves (Figure 4c, 5d). Among Neotropical Angraecinae, *Campylocentrum* includes both leafy and leafless species whereas *Dendrophylax* includes only leafless species.

Roots

Roots are cylindrical or flattened ranging from 1-4 mm in diameter with green or yellowish (rarely reddish-brown) tips, often clorophyllous inside developing along the stem opposite to the leaves. Roots can be basal and they usually anchor the plant to the substrate. Adventitious-aerial roots are commonly produced in leafy species as well as in *C. poeppigii,* which make up a mass together with the stems. In leafless species, the roots are produced from a very reduced stem. The root is

the main structural and functional organ of leafless plants. Roots are rarely branched and in *C. poeppigi,* plantlets developing directly from roots have been observed. Leafless species like *C. generalense* and *C. pachyrrhizum* are easily recognized by having thick, flat, roots whereas the other leafless species have cylindrical roots.

Roots play an important role in leafless species where photosynthesis is carried out in this organ due to the absence of leaves. The root must have developed an analogous system to substitute for the stomatal complex of leaves that regulates the water loss and the exchanging of CO_2 and O_2. The presence of aeration complexes in photosynthetic roots acting as cortical stomatal complexes as defined by Carlsward et al. (2006b) may be important in the evolution of the leafless habit. The hypothesis discussed by Carlsward et al. (2006b) for regulation of gas exchange is that in conjunction with pneumathodes within the velamen aeration units probably serve as the only means of gas exchange in roots of leafless Vandeae and are potentially analogous to the stomatal complex of leaves. As aeration units are present in many leafy vandaceous taxa, but they have not been observed in other groups of orchids, Carlsward et al. (2006b) suggested a preadaptive significance within Vandeae to the formation of aeration units in the process of becoming leafless.

In leafy species, there may be three velamen cell layers of angular, pentagonal or hexagonal shaped cells like in *C. schiedei* or two layers as in *C. panamense* (Figure 6, d, 6e, 6f). The exodermis is made up by ∩-thickened cell

walls or O-thickened as observed by Carslward et al. (2006b) in *C. micranthum*. In leafless species, velamen layers are reduced to one thin layer. The exodermis is made up by ∩-thickened cells. The thickened walls are thicker in leafless species (Figure 6a, 6b). Remarkably, in *C. generalense* those cell wall thickenings are conspicuous and angular shaped (Figure 6c). Starch grains were observed in the parenchyma cells of cortex. Hyphal infections have been observed in this tissue especially on the roots facing the substrate. The endodermis is made up by sclerenchyma walled cells that are conspicuous when stained with toluidine blue. In *C. schiedei*, endodermis cells have thin walled cells contrasting with those of leafless species that are thicker with a very reduced cytoplasm. Vascular tissue is embedded in sclerenchyma associated with both phloem and xylem poles. Unicellular root hairs were observed in *C. poeppigii and C. generalense*. The reduction of velamen layers and the thickenings of exodermis and endodermis showed in leafless species may be indicative of a mean to prevent water loss via transpiration but also a mean to protect the cortex and the vascular tissue from mechanical damage (Carlsward et al. 2006b).

Stems

The stems are elongated in leafy species or very reduced and inconspicuous in leafless species. They have distichous meristems producing leaves, roots and inflorescences. Elongated leafy stems are covered by amplectent, tubular, leaf sheaths subtending the leaves (Figure 5). The inflorescences and roots emerge laterally from the stems, breaking the leaf sheath tissue basally. They have

indefinite terminal growth. Often, the stem can produce secondary stems. In *C. brenesii*, *C. micranthum, C. poeppigii and C. schiedei* branching plants have been observed. The few specimens available of *C. panamense* and *C. tenellum* showed a single non-branching stem. In leafless species, we did not observe branching stems.

Leaf

Remarkable variations in leaf shape and size are present in the genus. In leafless species, the leaf underwent a notorious reduction during its evolution. Leafless species have a very reduced stem where a core of roots, small scales and inflorescences are developed (Figure 4, 5b). Leafy species have well developed conduplicate leaves (Figure 3, 5). They may be coriaceous as in *C. brenesii*, *C. micranthum* and *C. schiedei* or subcoriaceous as in *C. panamense*. Few studies have been focused on the anatomy of the genus but a good description of leaf anatomy in *C. micranthum* is presented by Carlsward et al. (2006b). A reduction of leaf size is diagnostic of *C. poeppigii,* which is the only species in having minute, scale-like conical caducous leaves developed on elongated stems (Figure 4c, 5d). Although the leaves are small and caducous, *C. poeppigii* should be regarded as a leafy *Campylocentrum*. In leafy species the blades are articulated with the leaf sheaths. In *C. tenellum*, leaf sheaths are diagnostic and they are easily recognized in having conspicuous lacerations along the margin (Figure 3f, 5f).

Inflorescences

Inflorescences are distichous and produced along the stem opposite to the leaves. They develop just below the emerging point of roots. Several inflorescences can develop simultaneously from the same individual. Up to three inflorescences can develop from the same point in *C. micranthum* and *C. schiedei*. At base, there are two or three tubular overlapping bracts. The peduncle and rachis are cylindrical, fleshy with hairy surface. Floral bracts are scarious, conduplicate and triangular shaped. Conspicuous floral bracts are present in the inflorescences of *C. generalense* and *C. pachyrrhizum*. After flowering, if no fruits are developed, sometimes they remain photosynthetic until dry. The position of flowers in the inflorescence is a good character in distinguishing *Campylocentrum* species. Lax inflorescences are diagnostic of *C. schiedei* whereas congested inflorescences are present in *C. brenesii*, *C. panamense*, *C. micranthum* (Figure 3). In leafless species, lax inflorescences are present *in C. fasciola* and *C. multiflorum* but in *C. generalense* they are congested (Figure 4).

Flowers

Flower morphology is taxonomically useful in distinguishing *Campylocentrum* species. Flowers are distichously arranged on the rachis. Often they can be distichous like *C. brenesii*, *C. fasciola* or secund like *C. micranthum*, *C. panamense*, *C. schiedei*. After flowering, they remain photosynthetic and are persistent until they become dry. They are unicolor, white, whitish or yellowish. *Campylocentrum* flowers are easily recognized by having a spur made up by labellar tissues. The most

important characters in distinguishing between the species are the flower size, the spur length compared with lip blade, the length of the lip midlobe and the lateral lobes, the shape, direction and ornamentation of the spur and the shape of the apex of sepals and petals.

The sepals are subequal often partially connate and usually spreading only at apex. Adaxially there may be pubescent as in *C. brenesii* and *C. tenellum* or scurfy as in some specimens of *C. micranthum*. Petals are subequal, smaller and wider to the sepals, spreading at apex. The saccate lip is always 3-lobed in Costa Rica material. The lip blade has a sparsely pubescent callous, which is conspicuous in *C. brenesii*, *C. micranthum* and *C. tenellum*. In *C. poeppigii* the lip blade is smooth. The spur is often curved downward but may be straight or slightly curved upward. Likewise, the spur can be lobed as in *C. micranthum*, *C. multiflorum, C. poeppigii* and *C. tenellum*, or ornamented with keels like that of *C. fasciola*. Although leaves and stems show a vast array of variation, flower morphology is characterized by a general shape with little variation in overall morphological pattern.

Pollinarium

The pollinarium consists in two globose or ovoid pollinia on short, ligulate, hyaline stipes. They are protected by a flat or subcucullate, operculate, 2-celled anther cap (Figure 7).

Fruits

Fruit capsules are ovoid to narrowly oblong, 6-valved with prominent dehiscence lines running along the carpel midribs (Figure 8). Often they are covered by sparse trichomes. Fruits are common seen in *Campylocentrum* populations (Figure 9). Dehiscence is lateral. The hygroscopic trichomes called elaters and its aggregation or capillitium have been observed in *Campylocentrum*. The capillitium is responsible in dispersing seeds when the elaters twist with changes of temperature and humidity (Blanco et al. 2006, Hallé 1986). Just few seconds after the fruit is opened the elaters start to shoot the seeds into the air. Remains of perianth remain at fruit apex. The seeds are filiform to fusiform.

TAXONOMIC HISTORY

John Lindley described and illustrated the first specimen belonging to *Campylocentrum* in 1835 as a member of *Angraecum* Bory (Lindley 1835). Lindley stated that this species is quite distinct from any other previously described *Angraecum*, but retains the peculiar characters of this genus without any deviation.

The type of Lindley's *Angraecum micranthum* was originally associated with a collection by Loddiges supposedly from Sierra Leone, Africa, which was flowered in England by Messrs Loddiges, of Hackney, London (Figure 10). He noted that, curiously, *Angraecum* should be exclusively African and no certain species has yet been found beyond America or adjacent islands (Lindley 1835). However, this locality data was soon found to be erroneous (Rolfe 1903). According to Rolfe

(1903), Lindley mounted the drawing with Surinam specimens, and corrected the record on the herbarium sheet (Loddiges s.n., K-L!). (see also Reichenbach 1849: 857, who refers to a Surinam's collection by Weigelt and Kappler s.n. K-L!; Nir 2000) (Figure 10).

Several hypotheses have been proposed to clarify the origin of this specimen, ostensibly belonging to Neotropical Angraecinae. Some authors favoured a Jamaican origin of *Angraecum micranthum* (Fawcett and Rendle 1982; Ackerman 1995; Espejo-Serna and López-Ferrari 1997), while others hypothesized that the type locality is Guatemala (Carnevali et al. 2001).

The exact origin of Lindley's specimen, alternatively assigned to Surinam, the West Indies, and Guatemala, seems difficult to ascertain, because *C. micranthum* ranges from Mexico and the Antilles to South America, and it shows considerable morphological variation in the shape and size of leaves and flowers throughout its distribution. New useful evidence to clarify the real origin of *A. micranthum* emerged from the molecular work on Neotropical Angraecinae carried out by Carlsward and collaborators (2003). The study shows that plants of *C. micranthum* from the West Indies and continental Neotropical lands are different entities and should be considered as different species. In addition, the two entities show differences in their inflorescence structure: the Antillean specimens have distichous flowers rather than the secund flowers of the continental specimens (Carlsward *et al.* 2003; Ackerman 1995). The type specimen of *A. micranthum* and the illustration of the type plant (K-L!) show characteristic secund flowers (Figure

10). However, recent data from the orchid flora of the Antilles by Ackerman (pers. comm. 2007) reveal that both entities referred to as "*C. micranthum*" (i.e., with distichous and secund flowers) have been recorded in the West Indies. Thus, the entities with secund flowers might correctly be *C. micranthum*, whilst the other with distichous flowers should perhaps be *Campylocentrum jamaicense* (Rchb.f. ex Griseb.) Benth. ex Fawc. Other differences between these two species include bilobed leaves and smooth, fusiform fruits in *C. jamaicense* vs. entire or acute to asymmetrical leaf apices and ribbed capsules in *C. micranthum* (Ackerman 1995). Since *C. micranthum* has been recorded both in the Antilles and in American continental areas, it is difficult to test the different hypotheses about the origin of Lindley's specimen. However, the scanty evidences seemingly support a Surinamese origin, rather than Antillean or Guatemalan, for the type of *C. micranthum* (Reichenbach 1849; Rolfe 1903).

In 1840, Lindley described five additional species of vandoid orchids from the New Word, again under *Angraecum*. The leafless *Angraecum fasciola* was based on a collection by Robert H. Schomburgk in Demerara, Guyana (*Schomburgk s.n.*, K, Figure 11), and four other South American species were named as *Angraecum brevifolium*, *A. ornithorrhynchum*, *A. polystachyum* and *A. tenue*. In Lindley's words, all of them were minute and inconspicuous species (Lindley 1840).

Clearly this group of plants is entirely Neotropical and represents a New World disjunction of the predominantly African Angraecinae. The peculiarity of these Paleotropical elements in the American flora, whose occurrence is rather

uncommon particularly in the most advanced groups of the Epidendroideae, was first noted by the French botanists A. Richard and H. Galeotti (1845) in their publication of *Todaroa* (Richard and Galeotti 1845). It was the first attempt to segregate Neotropical members of Angraecinae from *Angraecum*. Unfortunately, however, they selected *Todaroa micrantha* as the *typus generis*, basing it on a species different from that previously described by Lindley as *A. micranthum,* and using the same specific epithet (Figure 12, 13). They overlooked *A. micranthum*, the leafless *A. fasciola* and the four South American "*Angraecum*" described in the *Botanical Register* (Lindley 1835, 1840).

New species of Neotropical "*Angraecum*" were described by Reichenbach (1849). He published *Angraecum poeppigii,* based on a plant collected by Eduard Friedrich Poeppig in Cuba. In the same work, he also described the leafy *Angraecum schiedei*, based on a collection by C. J. Schiede, C. Ehrenberg and F. E. Leibold (W) from Xalapa, Mexico (Figure 14). However, Reichenbach ignored Richard and Galeotti's publication on *Todaroa,* and described his species under the genus *Angraecum*, leaving the previous *T. micrantha* (a species conspecific with *A. schiedei*) in oblivion.

In 1864, Reichenbach transferred his Neotropical Angraecinae species together with Lindley's species to the genus *Aeranthes*, overlooking again *T. micrantha* (Reichenbach 1864a, 1864b). Also, he founded the genus *Dendrophylax* intended to classify other species of West Indies Angraecinae (Reichenbach 1864c). The next year, he described the aphyllous *Aeranthes pachyrrhizus* based

on a collection by C.H.Wright from Cuba (Reichenbach 1865). This species is recognized by its characteristically thick, flat roots and congested inflorescences with conspicuous floral bracts. In1866, he cited only *A. schiedei* for the Central American flora in his *Beiträge zu einer Orchideenkunde Central-Amerika's* (Reichenbach 1866).

Campylocentrum was established when George Bentham published *Notes on Orchidaceae* in 1881. He eventually proposed the genus to accommodate the Neotropical monopodial orchids treated by Lindley and Reichenbach.f. under *Angraecum* and *Aeranthes*, placing his new genus in the mainly Paleotropical Sarcanthinae (=Aeridinae). He stated that the New World taxa treated under *Dendrophylax* and *Todaroa* are sufficiently distinct from their African allies by the shape of the perianth and other minor characters (Bentham 1881). Bentham agreed with Richard and Galeotti's concept of *Todaroa*, but he noted that the name *Todaroa* had been previously established by Parlatore (1843), in the *Histoire Naturelle des Îles Canaries*, for a genus of Apiaceae (= Umbelliferae). Consequently, he proposed *Campylocentrum* as a substitute for the illegitimate *Todaroa*, stating that "I should propose to replace it by *Campylocentrum*". However, according to article *33.1*. of the Code of Botanical Nomenclature (see, in particular, *Ex. 2.*), Bentham's statement does not constitute a valid publication of the combination *C. micranthum,* since he did not specifically associate the epithet *micranthum* with the generic name *Campylocentrum* (McNeill *et al.* 2006).

When Rolfe (1903) validly published the combination *Campylocentrum micranthum*, he ostensibly based it on Lindley's *Angraecum micranthum*. Although, Rolfe's new combination has been used by several authors (Todzia 1980, Pupulin (2002), Dressler 2003, Carlsward *et al.* 2003, Carlsward *et al.* 2006a, 2006b), Nir (2000) discovered an overlooked citation in which the French botanist Paul Jean Baptiste Maury (1889) published in his *Plantes du Haut-Orénoque* the first combination in *Campylocentrum* for Lindley's *Angraecum micranthum*. This name, having priority, definitively prevents the use of the specific epithet *micranthum* for Mexican populations of *Campylocentrum* originally described as *Todaroa micrantha*. Moreover, Rolfe's new combination should be regarded as a superfluous name (Maury 1889, Rolfe 1903).

As the type of the genus *Campylocentrum* is the same as the substitute name *Todaroa*, and the specific epithet *micranthum* is predated in *Campylocentrum* by *C. micranthum* (Lindley) Maury, the genus must be typified by the next available name for *Todaroa micrantha*, that is, *Campylocentrum schiedei* (Rchb.f.) Benth ex. Hemsl., based on *Angraecum schiedei* Rchb.f. (Figure 12—14).

The checklist of the orchids of Central America by William Botting Hemsley, later published in volume 3 of the botany series of Godman and Salvin's Biologia Centrali-Americana (Hemsley 1884), only reports *Campylocentrum schiedei* for Mexico and Guatemala. The transfer of *A. schiedei* to the genus *Campylocentrum* was made there by Hemsley (1884), who published the first combination in this

genus, *Campylocentrum schiedei* (Rchb.f.) Benth ex. Hemsley. Also, he reduced *Todaroa* Rich & Galeotti to synonymy with *Campylocentrum*.

The German botanist Otto Kuntze erroneously transferred *A. micranthum* to the Old World genus *Epidorchis* Thouars in his *Revisio Generum Plantarum* in 1891. It seems that Kuntze did not agree with the New World genus *Campylocentrum,* still believing in an African origin for this group of plants. The botanists Theophile Alexis Durand and Hans Schinz followed this idea, transferring *A. micranthum* to the African genus *Mystacidium* Lindl. in *Conspectus Florae Africae* (Durand & Schinz 1895). No subsequent authors accepted these two propositions (i.e., Rolfe 1903, Cogniaux 1906).

In 1903, R.A. Rolfe published a note on *Campylocentrum*, discussing the unclear history of the genus, transferring there seventeen species previously described in *Aeranthes*, *Angraecum* and *Epidendrum*, and including in *Campylocentrum* Reichenbach's *A. pachyrrhizum* and *A. poeppigii*. Rolfe recognized *C. pachyrrhizum* as a distinctive acaulescent species, remarkable for its thick fleshy roots, with short racemes and distichous bracts, considering *Angraecum spathaceus* Griseb. as a synonym of the former. Also, he reported *C. poeppigii* as the second caulescent leafless species in the genus (Rolfe 1903). After Rolfe's treatment, *Campylocentrum* was amply and generally accepted by subsequent authors. A. Cogniaux, with his orchid treatment for the *Flora Brasiliensis* (1906), greatly contributed to the consolidation of the genus, adding many collections to the list of *Campylocentrum* species.

PHYLOGENETIC PLACEMENT OF *CAMPYLOCENTRUM*

Before the establishment of *Campylocentrum* by Bentham (1881), Lindley described the first species referable to the genus under *Angraecum* (Lindley 1835). He placed *Angraecum* in the Vandeae in his *Genera and Species of Orchidaceous Plants* (Lindley 1833). Later, George Bentham (1881, 1883) created Vandeae Subtribe Sarcanthinae and placed *Campylocentrum* in the new subtribe . Although Bentham published the subtribal name as Sarcantheae, according to the Articles 19.3 and 19.6 of the International Code of Botanical Nomenclature it must be corrected as Sarcanthinae (McNeill et al. 2006). However, Lindley had applied the generic name *Sarcanthus* twice, applying it for two different species: *Sarcanthus* Lindl. (Bot. Reg. 9:pl. 875. 1824; type species: *Epidendrum praemorsum* Roxb. = *Acampe* Lindl., *nom. cons.*), and *Sarcanthus* Lindl. (Coll. Bot., pl. 39B 1826; type species: *Sarcanthus rostratus* Lindl.) the latter generic name a later homonym and a synonym of the earlier *Cleisostoma* Blume (Garay 1972). So, Sarcanthinae being an illegitimate subtribal name, it was replaced by Aeridinae (Dressler 1993a, Garay 1972).

Bentham defined the subtribe as having "*caulis non pseudobulbosus, basi v. undique reptans radicans, folia disticha, coriacea v. carnosa, non plicata, rarious tenuia v. O. Pedunculi secus caulem laterales v. axillares*" ("Stems non pseudobulbous, prostrate and rooting on all sides, leaves distichous, coriaceous to

fleshy, non plicate, rarely thin, the peduncle along the stem, lateral or axillar"). Other genera placed in the subtribe were the Neotropical *Lockhartia* Hook., *Centropetalum* Lindl., *Pachyphyllum* Kunth and *Dendrophylax*, and the Old World genera *Luisia* Gaudich., *Cottonia* Wight, *Stauropsis* Rchb.f., *Arachnanthe* Blume, *Phalaenopsis*, *Doritis* Lindl., *Rhynchostylis* Blume, *Sarcochilus* R. Brown, *Trichoglottis* Blume, *Aeranthes*, *Aerides* Lour., *Renanthera* Lour., *Vanda* Jones, *Saccolabium* Blume, *Uncifera* Lindl., *Sarcanthus*, *Cleisostoma* Blume, *Schoenorchis* Blume, *Ornithochilus* Lindl., *Taeniophyllum*, *Microssacus* Blume, *Diplocentrum* Lindl., *Angraecum*, *Cryptopus* Lindl., *Oeonia* Lindl. and *Mystacidium*.

Later in 1887, Pfitzer created the tribe Sarcantheae placing it under Vandeae, and grouping *Campylocentrum* into that tribe. Following Pfitzer (1887), Cogniaux (1906) also treated the genus in Sarcantheae. At the same time, he established the first subgeneric classification of *Campylocentrum*, creating three sections. The section *Eucampylocentrum* includes the species with elongated leafy stems, the section *Dendrophylopsis* encompasses acaulescent leafless species, while *C. poeppigii,* the only species with elongated stems and scale-like leaves, is assigned to the section *Pseudocampylocentrum*.

Later, Schlechter (1915, 1916) included *Campylocentrum* in the subtribe Sarcanthinae (=Aeridinae), grouped with Pachyphyllinae, Pterostemmatinae and Dichaeinae in the subseries Monopodiales of his subgroup Pleuranthae. At the same time, he placed Pleuranthae under tribe Kerosphaerae, division Acrotonae of the subfamily Monandrae.

Other authors as Williams (1951, 1956), Williams and Allen (1980), Ames and Correll (1953) accepted including *Campylocentrum* under Sarcanthinae, mainly following Schlechter's classification system. Hawkes and Heller (1959) mentioned the subtribe Campylocentrinae, a name also used by Hoehne in Flora Brasilica (1943), but apparently the name was never formally proposed. Hawkes (1961) cited that "monopodial orchids comprise only two subtribes, the Sarcanthinae and Campylocentrinae". According to the author, the Campylocentrinae comprises derived epiphytic plants, often leafless. Under that subtribe he included *Campylocentrum*, *Dendrophylax* and *Polyrrhiza*.

Dressler & Dodson (1960) placed the genus in the subfamily Orchidoideae tribe Epidendreae Lind., subtribe Sarcanthinae and agreed that this group does not deserve a subtribal status, refusing Hawkes and Heller's suggestion about the subtribe Campylocentrinae. They noted that in floral specialization and complexity they parallel the Oncidiinae and are not easily separated in a key to the subtribes from the monopodial Oncidiinae, however there is no close relation between the two groups.

More recently, Dressler (1981, 1993a) placed *Campylocentrum* in the subfamily Vandoideae Endlicher, tribe Vandeae and subtribe Angraecinae. He characterized the group as eminently Madagascan with some representatives in mainland Africa and outliers in America. Burns-Balogh & Funk (1986) generally followed Dressler (1981) in the treatment of Vandae. Szlachetko (1995) used floral and rostellar morphology to propose a reorganization of Vandeae, but maintained

Campylocentrum under subtribe Angraecinae. Following Dressler (1993a) and Szlachetko (1995), Senghas (2002) also assigned *Campylocentrum* to the subtribe Angraecinae.

Cameron *et al.* (1999) supported Angraecinae under Vandeae but found no evidence to support the previously recognized subfamily Vandoideae. Recently, Carlsward and co-workers performed detailed studies of Vandeae (Carlsward *et al.* 2006a) and New World Angraecinae (Carlsward *et al.* 2003) from analyses incorporating *ITS*, *matK*, and *trnL-F* molecular data. They showed that Paleotropical Angraecinae form a basal grade within which the Neotropical Angraecinae constitute a derived, well-supported clade (99% BS). So, within the Neotropical Angraecinae, there is a strong support to place *Campylocentrum* and *Dendrophylax* (including *Harrisella, Polyradicion*, *Polyrrhiza*) under subtribe Angraecinae, as suggested by Dressler (1993a) (Carlsward *et al.* 2003, Chase *et al.* 2003, Carlsward *et al.* 2006a). The most parsimonious tree resulting from ITS matrix (Carlsward *et al.* 2006a) showed the Neotropical Angracecinae clade next to the Old World species of *Angraecum*, like *A. chevalieri* Summerh., *A. erectum* Summerh. and *A. cultriforme* Summerh., all of them from Continental Africa.

THE GENUS *CAMPYLOCENTRUM* IN COSTA RICA

The beginning of orchid botanical exploration in Costa Rica started with the Dane Anders Sandoe Oersted in 1846 (Pupulin & Ossenbach 2005). In his publication, *L'Amérique Centrale* (Oersted 1863), no collections from Costa Rica are referable to *Campylocentrum*. Herman Wendland, Josef Ritter von Rawicz Warszewicz and Carl Hoffman, who came to Costa Rica in the second half of the eighteenth century, apparently did not collect specimens of *Campylocentrum* (Reichenbach 1866). The earliest botanist to collect specimens of *Campylocentrum* in Costa Rica was A.R. Endrés, ostensibly between 1867 and 1871. Among his gatherings, kept in the Reichenbach Herbarium in Vienna, there are several collections of *C. schiedei* (W-*Rchb Orch* 18852, 19056, 19057) (Figure 15), all without specific locality and W-*Rchb Orch* 19057 collected in San Ramón de Alajuela . He also depicted three collections of *C. brenesii* (a species described by R. Schlechter in 1923, but still undescribed at that time). The specimens W- *Rchb Orch* 18850, 18851 and 19059 have detailed sketches of floral segments (Figure 16). Endrés also prepared a description of the species, mounted on the sheet W-*Rchb Orch* 19059. This specimen came from San Ramón de Alajuela, his home in Costa Rica, where it was ostensibly collected (or it flowered) in October or November. We were unable to identify the specimen on sheet W- *Rchb Orch* 18853, another collection by Endrés, because the material is severely damaged. It is

probably a leafy species (aff. *C. schiedei*), but it lacks both leaves and inflorescences.

During the nineteenth century, Reichenbach (1866) only recorded *C. schiedei* for the Mesoamerican region, but he never reported any of the Costa Rican collections he received from Endrés. It was not until the beginning of the decade of 1920s, when a period of great botanical activity in Costa Rica took place, 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. The first mentions of a species referable to *Campylocentrum* appeared in Ames' *Schedulae Orchidianae* and Schlechter's *Beiträge zur Orchideenkunde von Zentralamerika* (Ames 1923; Schlechter 1923a, 1923b, 1923c, 1923d). By this time, A. and C. Brade had collected three different species of *Campylocentrum* in 1910. They sent the material to Schlechter, who described two of the specimens and cited a new record for Costa Rica in his *Orchidaceae Bradeanae Costaricensis* (Schlechter 1923b). Among Brade's collections, Schlechter described a leafless species, *C. multiflorum*, from Cerro Turubales [Turrubares] in central Pacific Costa Rica (*A. Brade & C. Brade 1316*, B, destroyed; drawing, AMES) (Figure 18). In La Palma region the two German brothers collected a small leafy species, later described by Schlechter as *Campylocentrum parvulum* (=*Campylocentrum brenesii* Schltr.) (*A. Brade & C.*

Brade 1294, B, destroyed; drawing, AMES) (Figure 19). The third collection, from San Jerónimo de Grecia, Alajuela (now part of Naranjo), was identified by Schlechter as *Campylocentrum peniculus* Schltr. (=*C. micranthum*), a species described by him in 1922, based on a collection by C.H Powell in Panama in 1921.

During this period, and for the following 20 years, there was a flourish of field activity by the resident English naturalist Charles H. Lankester, who started to collect orchids in Costa Rica and established a fruitful scientific cooperation firstly with Robert A. Rolfe at the Royal Botanic Gardens, Kew. Then, most notably, Lankester cooperated with Oakes Ames at the Botanical Museum of Harvard University, who described hundreds of orchid species in the same years as R. Schlechter, his strong competitor. As part of the results of that fieldwork activity, Charles H. Lankester found in 1919 an aphyllous *Campylocentrum* near the Reventazú [Reventazón] river in the Atlantic watershed of the Costa Rican continental divide (*C.H. Lankester 71*, K) (Figure 20). He sent this specimen together with his first orchid collections to R.A. Rolfe at Kew. However, it was not until Ames's visit to Kew, when it was described as *C. lankesteri* (Ames 1923). This species is here considered a synonym of the widespread *C. fasciola*. Nevertheless, it was the second report of an aphyllous species in the country together with *C. multiflorum*, its Pacific counterpart.

Based on Alberto Brenes's collections, Rudolf Schlechter described in *Orchidaceae Brenesianae* hundreds of new species of Costa Rican orchids (Schlechter 1923c). In 1921, Brenes found two species of *Campylocentrum*. One is

the type specimen of *Campylocentrum acutum* Schltr. (=*C. schiedei*), collected at Santiago de San Ramón, Alajuela (*A. Brenes 147*, B, destroyed, drawing, AMES) (Figure 21). The other specimen (*A. Brenes 127*, destroyed, drawing, AMES), collected at San Pedro de San Ramón, Alajuela, honoured A.M. Brenes as *Campylocentrum brenesii* Schltr. (Figure 22). A specimen now referable to *C. brenesii* was collected by A.R. Endrés in the second half of the nineteenth century, but the species remained undescribed until 1923 (W-*Rchb Orch* 18850, 18851 and 19059) (Figure 16). Between 1925 and 1927, A.M. Brenes collected three specimens of *C. brenesii*, one at La Palma de San Ramón and two at La Paz de San Ramón (CR). In 1925, C. H. Lankester collected a small leafy *Campylocentrum* around La Estrella, at El Guarco of Cartago. Oakes Ames and Charles Schweinfurth described it as *Campylocentrum longicalcaratum* in *Schedulae Orchidianae* in 1930 (*C.H. Lankester 1013*, AMES-33651) (Figure 23).

Five years later, two Austrians of the Oesterreich Costarica-Expedition, Otto Porsch and Georg Cufodontis, collected the aphyllous *C. multiflorum* in Finca Santa María in Peninsula de Osa, near Puerto Jiménez, Puntarenas (*G. Cufodontis 155*, W-R 1767). The specimen was identified in 1931 by O. Ames as *Campylocentrum sullivanii*, a species described by Fawcett and Rendle and considered here conspecific with *C. fasciola*. R.L. Dressler identified the same specimen as *Campylocentrum tyrridion* Garay & Dunst., a species originally described from Venezuela (Dunsterville & Garay 1961). In the same year, A. Brenes collected another specimen of *C. multiflorum* between Puerto Jiménez and Río Tigre in the

Osa Peninsula, Puntarenas (*A. Brenes s.n.*, CR). Further collections recorded before the end on the first half of the twentieth century had been made by Marlon Valerio in 1934, who collected a *C. multiflorum* around Buenos Aires de Puntarenas (*M. Valerio s.n.*, CR). One year later, in 1935, A.M. Brenes collected *C. micranthum* in San Ramón de Alajuela. This fruitful period in the history of the orchids in Costa Rica fell into decline when Schlechter died in 1925 and O. Ames lost his interest in Neotropical orchids, followed by his death in 1950 (Ossenbach 2003).

By 1937, in his treatment of the Orchidaceae for Standley's Flora of Costa Rica, Ames (1937) listed 7 species: *C. acutum* (=*C. schiedei*), *C. brenesii*, *C. longicalcaratum* (=*C. brenesii*), *C. micranthum*, *C. parvulum* (=*C. brenesii*), *C. schiedei* and *C. sullivanii* (=*C. fasciola*). Here he considered *C. lankesteri* (*Lankester 71*, K-L) and *C. multiflorum* (*A & C Brade 1316*, B, destroyed; illustration, AMES and *Cufodontis 155*, W) conspecific with *C. sullivanii* (=*C. fasciola*) by Ames (1937).

The second half of the twentieth century constitutes a new period of botanical activity in Costa Rica, starting with the German gardener Clarence K. Horich (Pupulin & Ossenbach 2005). He collected orchids in Costa Rica in the beginning of the 1950's, settling permanently in Costa Rica in 1957 (Ossenbach 2003). Horich discovered many new species and new records for the country and became one of the most important collectors of the time. He was the owner of a property near San Carlos, Alajuela. There, he was the first to collect *C. poeppigii* in Costa Rica. He provided a detailed account on the particular habitat of this species,

which grows on *Psidium guajava* (Myrtaceae) and *Crescentia* sp. (Bignoniaceae) trees. In the same kind of habitat, where the plants are mostly restricted on twigs in disturbed, low elevation wet areas, Horich also recorded *C. C. fasciola* (he identified it as *C. sullivanii*) and *C. micranthum*, growing sympatrically with *C. poeppigii* (Horich 1980, 1982).

Todzia (1980) published the first taxonomic revision of Costa Rican *Campylocentrum*. She reported seven species and discussed the anatomy, ecology and biology of the genus. Among the results, she included *Todaroa* Rich & Galeotti in *Campylocentum* Benth., but never discussed the status of *T. micrantha*. Todzia recognized seven species: *C. brenesii, C. fasciola, C. longicalcaratum, C. micranthum, C. parvulum, C. poeppigii* and *C. schiedei*. She also suggested that *C. pachyrrhizum* might occur in Costa Rica, based on a record of this species from the región of Colón, in central Panama. *Campylocentrum longicalcaratum* and *C. parvulum* were considered distinct from *C. brenesii*, and *C. acutum* was reduced to the synonymy with *C. schiedei*. Todzia (1980) also reduced *C. lankesteri* and *C. multiflorum* under synonymy with *C. fasciola*. In this sense, she accepted only one aphyllous species of *Campylocentrum* in Costa Rica.

Mora-Retana & Castro (1992) listed eight species for Costa Rica, *C. brenesii, C. fasciola, C. longicalcaratum, C. micranthum, C. pachyrrhizum, C. parvulum, C. poeppigii* and *C. schiedei*. As they did not base their list on herbarium vouchers, the presence of *C. pachyrrhizum* in Costa Rica remained doubtful. They

followed Todzia's (1980) conclusion about the synonymy of *C. multiflorum* with *C. fasciola*.

Dressler (1993b) reported the same eight species and noted that *C.tyrridion* and *Campylocentrum dressleri* H.Dietr. & M.A.Díaz occur in Panama. Later, Pupulin (1998), added *Campylocentrum panamense* Ames. This species is very similar to *C. micranthum* and sometimes could be overlooked or misidentified in the field. In his floristic projects around Quepos region in central Pacific, Pupulin (2001) also recorded an aphyllous *Campylocentrum* identified as *C. tyrridion*. With this record, the suspicion about the presence of two aphyllous species with cylindrical roots in Costa Rica arose again. Then, in his catalogue of Costa Rican orchids, Pupulin (2002) reported nine species in the genus. He reduced *C. parvulum* and *C. longicalcaratum* to the synonymy of *C. brenesii*. Also, he reported four aphyllous species. Three of them were based on collections from the Pacific region. *Campylocentrum dressleri* (a Panamanian species) was a new record, based on a collection from the vicinity of Buenos Aires of Puntarenas (*Villalobos* s.n., USJ); *C. multiflorum* was recorded on the basis on *Brenes* 12123 (CR), collected around Puerto Jiménez, and *C. tyrridion* from the region of Quepos (*Pupulin 1029*, drawings). The other leafless species was the previously reported Atlantic species, *C. fasciola*. He was right in reporting the specimen *Brenes 12123* (CR) under *C. multiflorum*. Due to the absence of a voucher, *C. pachyrrhizum* was excluded from the list (Pupulin 2002).

With few changes with respect to Pupulin's work (2002), Dressler's treatment for the Manual de Plantas de Costa Rica (Dressler 2003) reported seven species. He recognized two aphyllous species with cylindrical roots in Costa Rica, reducing *C. multiflorum* and *C. dressleri* to *C. tyrridion*, a species otherwise known from Venezuela. The other is the previously recorded *C. fasciola*. Even though no vouchers were available, he predicted the presence of *C. pachyrrhizum* in the lowlands of the Caribbean watershed.

In 2005, in their treatment of the genus for *Vanishing Beauty—Native Costa Rican Orchids*, the authors included 8 previously known species. They accepted both *C. multiflorum* and *C. tyrridion* (Pupulin & Bogarín 2005). The treatment offers short ecological and geographical notes for most of the species and illustrates with photographs four of the taxa. Most recently, Bogarín & Pupulin (2009) pointed out the main taxonomic problems within the genus in Costa Rica.

SYSTEMATIC TREATMENT

Campylocentrum Bentham, J. Linn. Soc., Bot. 18: 337. 1881; Benth & Hook. Gen. Pl. 3: 585. 1883 (as *Campylocentron*).

Type species: ***Campylocentrum schiedei*** (Rchb.f.) Benth. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 292 1884. *Angraecum schiedei* Rchb.f. in W.G.Walpers, Ann. Bot. Syst. 6: 901.1864.

Todaroa A. Rich & Galeotti, Ann. Sci. Nat., Bot., III, 3: 28. 1845., *nom. illeg.* Type species: nom. illeg. =*Todaroa micrantha* A. Rich & Galeotti, Ann. Sci. Nat., Bot., II, 3: 28. 1845. non ***Campylocentrum micranthum*** (Lindl.) Maury, J. Bot. (M. Louis Morot) 3: 273. 1889. non *Todaroa* Parlatore, Hist. Nat. Îles Canaries. 155. 1843. Apiaceae (= Umbelliferae).

Plants epiphytic, monopodial (with indefinite terminal growth), with either elongated, distichously leafy, suberect to pendent, often branching stems or acaulescent, leafless, condensed stems. ***Roots*** fleshy, cylindrical or flattened, 1-4 mm in diameter, to 50 cm long, with green or yellowish (rarely reddish-brown) tips, often chlorophyllous inside and striped with white bands in leafless species, produced along the stem opposite the leaves. ***Leaves***, if present, elliptic, oblong-ovate, oblong-elliptic, lanceolate or ligulate, fleshy to coriaceous, rarely terete, conduplicate, articulate with the sheath envolving the stem, sometimes absent or reduced into scale-like leaves along an elongated stem. ***Inflorescence*** a lateral raceme, loose or densely flowered, produced opposite to the leaves at the point of emergence of the roots, or from the short stem at the center of the root cluster. ***Flowers*** distichously arranged on the rachis, often facing the same direction so appearing secund, white with greenish to yellowish spur, the sepals sometimes adaxially provided with small, black warts. ***Sepals*** subequal, free or partially connate, elliptic, oblong or ovate, acute or obtuse, usually spreading only at apex. ***Petals*** subequal to the sepals, acute or obtuse. ***Lip*** 1- to 3-lobed, the midrib of the

lamina often sparsely pubescent toward the apex, adnate to the base of the column, sessile, forming an elongate or saccate spur at the base. ***Column*** very short, less than 1 mm long, with terminal anther, wingless, without a foot. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe. ***Anther cap*** flat or subcucullate, 2-celled. ***Capsule*** ovoid to narrowly oblong, with ridges, 6-valved. ***Seed*** filiform to fusiform.

KEY TO THE COSTA RICAN SPECIES OF *CAMPYLOCENTRUM*

1. Plants caulescent, the stems provided with distichously arranged leaves, the leaves flat or scale-like ------2

    2. Leaves rudimentary, caducous, tiny, narrowly conical------ (Sect. *Pseudocampylocentrum*) *C. poeppigii*

    2. Leaves well developed, conduplicate, persistent, dorsiventrally flattened------ Sect. *Campylocentrum*) ------3

        3. Leaves less than 2 cm long ------4

            4. Leaves linear to elliptic-lanceolate, with distinctly lacerate sheaths ------ *C. tenellum*

            4. Leaves ovate to elliptic, the margins of the sheaths entire ------*C. brenesii*

        3. Leaves more than 3 cm long ------5

            5. Leaves subcoriaceous, lip with the mid-lobe rectangular-acute, sepals and petals spatulate at apex ------*C. panamense*

5. Leaves coriaceous, lip with the mid-lobe always acute, sepals and petals acute ------6

6. Inflorescence congested, the lip with the mid-lobe three times larger than the lateral lobes, the spur distinctly larger than the blade of the lip ------*C. micranthum*

6. Inflorescence lax, the lip with the mid-lobe twice larger than the lateral lobes, the spur equal to scarcely larger than the blade of the lip ------*C. schiedei*

1. Plant acaulescent, without conduplicate or scale-like leaves ------ (Sect. Dendrophylopsis) 7

7. Roots flattened; inflorescence congested; floral bracts covering the ovary ------ *C. generalense*

7. Roots cylindrical; inflorescence lax; floral bracts partially covering the ovary ------8

8. Spur wider at the base and progressively narrowing to the apex, without keels, the midlobe of the lip acute, sepals acute or rounded ------*C. multiflorum*

8. Spur narrow at the base and wider at the apex, with conspicuous longitudinal keels, the midlobe truncate, sepals cuspidate ------*C. fasciola*

SPECIES DESCRIPTION

1. ***Campylocentrum brenesii*** Schltr. Repert. Spec. Nov. Regni Veg. Beih. 19: 268. 1923. Type: Costa Rica. Alajuela: San Pedro de San Ramón, 1075 m *A.M. Brenes 127*, Sep 1921. (holotype B†; lectotype duplicate of the holotype, AMES-10645 selected by Barringer 1986; isolectotypes CR-18479, NY, pohotograph, F ex CR). Figure 24—26

Campylocentrum parvulum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 157.1923. Type: Costa Rica. La Palma, 1400 m, blühend im Juni 1910, *A. Brade & C. Brade 1294* (holotype B†; drawing of type, based on *A. Brade & C. Brade 1294*, AMES-106464) (Figure 19).

Campylocentrum longicalcaratum Ames & C. Schweinf., Schedul. Orchid. 10: 111. 1930. Type: Costa Rica. La Estrella, July 1925, *C.H. Lankester 1013* (holotype AMES-33651) Figure 23

Plant epiphytic, pendent, with terete, leafy stem to 15 cm long. ***Roots*** fleshy, up to 30 cm long, less than 1.5 mm in diameter, white to greenish, with green or orange-yellowish tips. ***Leaves*** many (to 13), distichous, ovate to elliptic-oblong to suborbicular, acute to obtuse or emarginate, unequally 2-lobed at the apex, conduplicate, coriaceous to fleshy, articulate with the sheath envolving the stem, to about 4.0 x 2.2 cm. ***Inflorescence*** a many-flowered (to 17) raceme usually larger than the leaves, produced along the stem, opposite to the leaves, the flowers distichously arranged on the rachis, about 4 cm long; ***pedicel*** inconspicuous, less

than 0.5 mm long; ***floral bracts*** triangular, scarious. ***Ovary*** cylindric, less than 1 mm long, usually covered with sparsely minute trichomes. ***Flowers*** small, about 4 mm in length, secund, white with greenish spur. ***Dorsal sepal*** subequal to the lateral sepals, elliptic, rectangular, ovate, acute, 1.8 x 0.9 mm. ***Lateral sepals*** ovate, lanceolate, acute, concave towards the base, 2 x 0.7 mm. ***Petals*** ovate, lanceolate, acute, 1.8 x 0.5 mm. ***Lip*** 3-lobed, the lateral lobes triangular, acute, small, less than 0.7 mm long, the midlobe triangular, acute, subequal to the lateral lobes, slightly conduplicate, concave, with a very small hairly callous along the midrib, extended at the base into a cylindric, clavate, porrect, more or less continuous with the lip, subequal than the blade of the lip (to 2.2 mm long, 0.5 mm wide); entire lip 2.8 mm long including the spur, 2.2 mm wide between the lateral lobes. ***Column*** very short, to 1 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe; viscidium elliptic. ***Anther cap*** subquadrate-cucullate, 2-celled.

Distribution. Guatemala, Costa Rica and Panama.

Additional material examined: COSTA RICA. **Alajuela**: San Ramón, La Palma de San Ramón, pasture, 1260 m, epiphyte, flowers white, 8 June 1969, *R. W. Lent* s.n. (CR); San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'N 84°37'W, 850 m, bosque muy húmedo tropical transición a premontano, sobre el Sendero Pájaro Sombrilla, epífita en bosque secundario con remanentes de primario, 3 octubre 2003, *D. Bogarín 436* (JBL-Spirit, Figure 24); Límite entre Alajuela y Heredia: Grecia, Sarapiquí, Colonia Virgen del Socorro, camino a

Cariblanco, puente sobre el Río San Fernando, 10°16'32"N 84°10'16"W, 750 m, orillas del Río San Fernando, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario, 13 febrero 2004, *D. Bogarín 755, H. León-Páez, F. Pupulin & E. Salas* (JBL-Spirit, USJ); San Carlos, Quesada, cerca de 6 km al este de Sucre, límite oeste del P.N. Juan Castro Blanco, faldas del Cerro Platanar, 10°17'38.7"N 84°22'33.7"W, 1738 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 30 enero 2009, *D. Bogarín 6223 & F. Pupulin* (CR). San Ramón, Santiago, mountains towards San Rafael, ca. 10º01'N 84º30'W, 1300 m, lower montane wet forest, epiphytic in secondary vegetation and scattered trees in pastures, 1 February 2004, *F. Pupulin 5086 & E. Salas* (JBL-Spirit, USJ); Same locality: *F. Pupulin 5088* & *E. Salas* (JBL-Spirit, USJ); Alajuela: San Ramón, Piedades Norte, La Paz, desviación a la izquierda, hacia el Cerro Azahar, km 2.6, orillas del Río San Pedro, 10°08'59.4"N 84°34'00.8" W, 1312 m, bosque pluvial premontano, en cercas y árboles en potreros y bosque secundario, 30 enero 2005, *D. Bogarín* 1292*, F. Pupulin, M. Salas & P. Seaton* (JBL-Spirit, USJ); **Cartago**: Cartago, San Francisco, Muñeco, 4.5 km al sur de Muñeco, camino a Alto Belén, 9°45'15.7"N 83°53'50.6"W, 1968 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 27 mayo 2009, *D. Bogarín 6577, R. Gómez, Y. Kisel & R. Trejos* (JBL-Spirit, CR); Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, 9°48'36.7"N 83°45'16.2"W, 1396 m, bosque pluvial montano bajo, epífitas en ramitas de árboles aislados de *Psidium guajava* (Myrtaceae) en potreros, 24 noviembre 2008, *D. Bogarín* 5845, *R.L. Dressler, R. Gómez & R. Trejos* (JBL-Spirit); Cartago: Jiménez,

Pejivalle, Tausito, cerca del Río Tausito, 1.5 km antes de Tausito, 9°46'00.7"N 83°46'48.7"W, 1020 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 16 Octubre 2009, *D. Bogarín 7398 & A. Karremans* (JBL-Spirit); La Unión, San Rafael, Cerros de La Carpintera, Campamento Escuela Iztarú, 9°53'08.2"N 83°58'15.6"W, 1778 m, bosque húmedo premontano, epífitas en potreros arbolados, 30 octubre 2008, *D. Bogarín 5417, R.L. Dressler, R. Gómez, F. Pupulin, & R. Trejos* (CR); La Unión, San Rafael, campo Escuela Iztarú, 9°53'26.8"N 83°58'7.1"W, 1638 m, epífita en bosque secundario, 13 Mayo 2008, *A. Cascante 1945* (CR); Cartago: Límite entre Turrialba y Jiménez, La Suiza, Pejibaye, camino a Esperanza, orillas de la Quebrada Regada, 9°48'21.4"N 83°39'10.6" W, 726 m, bosque muy húmedo premontano, epífitas en bosque secundario a la orilla del río en sitio sombreado, 28 agosto 2004, *D. Bogarín* 953 & *J. Carmona* (JBL-Spirit, USJ); Same Locality, *D. Bogarín* 952 & *J. Carmona* (JBL-Spirit, USJ); 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 ramas jóvenes y troncos de *Oreamunnea* (Junglandaceae), bosque pluvial premontano, 24 agosto 2004, *D. Bogarín 921, H. León-Páez & E. Hoppe* (JBL-Spirit, USJ); Paraíso, Orosi, Tapantí, 9°46'13.7"N 83°49'43.08"W, 1165 m, orilla del Río Grande de Orosi, epífitas en cafetal abandonado, bosque pluvial montano a montano bajo, bosque secundario y remanentes de primario, 25 Febrero 2009, *D. Bogarín 6256, R. Gómez & R. Trejos*; Same locality, 3 marzo 2009, *D. Bogarín 6363, R.L. Dressler, R. Gómez & R. Trejos* (JBL-Spirit); **Guanacaste**: Parque Nacional Guanacaste, Estación Cacao, bosque primario y orilla de bosque, 10°55'45"N 85°28'15"W, 1100

m, epífita, flor blanca, 2 Junio 1990, *E. Bello 2259* (INB); **Heredia**: Barva, La Legua, Finca Montreal, ridge between headwaters of Río Volcán and Río San Fernando, just obove trail to refugio at 1800 m, primary montane wet forest, 10°12'39"N 84°06'45"W, epiphyte on fallen branch, 9 October 1992, *B. Boyle 1090* (CR); Vara Blanca, pastures 1.5 km East of Vara Blanca, NW slopes of Barba Volcano, 1 June 1969, 1820 m, *R.W. Lent 1968* (CR); Vara Blanca, 1600-1800 m, 27 June 1979, *C. Todzia* 624 (CR); Same Locality: the Finca of Mike Canon, near the junction of Highways 9 and 120, 1900 m, 20 July 1975, *J & K Utley s.n.* (CR); Heredia, Vara Blanca, carretera a San Rafael, km 3, 10°10'39.9"N 84°08'36.0" W, 1811 m, bosque pluvial montano bajo, epífitas en cercas a orillas de la carretera, 23 diciembre 2004, *D. Bogarín 1164, 1165, 1166* & *M. Blanco* (JBL-Spirit, USJ, (Figure 25); Heredia: San Rafael, Concepción, Residencial El Castillo, Calle Lobo, falda sur del Cerro Tibás, 10°4'07.7"N 84°03'56.6"W, 1940 m, bosque muy húmedo montano bajo, epífitas en potreros arbolados, 19 marzo 2009, *D. Bogarín 6420, R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (CR, JBL-Spirit); Heredia: San Rafael, Concepción, Residencial El Castillo, Calle Lobo, falda oeste del Cerro Turú, 10°3'52.2"N 84°03'43.2"W, 1840 m, bosque muy húmedo montano bajo, epífitas en epífitas en potreros arbolados, 19 marzo 2009, *D. Bogarín 6488, R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (CR, JBL-Spirit). **Puntarenas**: Puntarenas, Reserva Biológica Monteverde, Cordillera de Tilarán, Río Guacimal, 10°18'00"N 84°48'00"W, 1500 m, epífita en rama caida en claro del bosque, 31 mayo 1989, *E. Bello 929.* (INB); Same locality: Río Veracruz, 10°16'N 84°22'W, 1300 m, epífita en potero, 4 Mayo 1991, *E. Bello 2763, E. Cruz* & *R. Cruz.* (INB); Puntarenas, Santa Elena, camino hacia el

Cerro Amigos, 1700 m, 10°19'20"N 84°48'01"W, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 30 julio 2003, *D. Bogarín 379 M. Blanco* & *M. Whitten*. (JBL-Spirit, USJ); Same locality: *D. Bogarín 380, M. Blanco* & *M. Whitten*. (JBL-Spirit, USJ).

Habitat and ecology. Epiphytic in tropical wet forest, premontane belt transition and premontane rain forest in secondary vegetation and disturbed areas from 700 to 1900 m of elevation. Populations have been observed on twigs of *Coffea arabica* (Rubiaceae), *Eugenia* sp. (Myrtaceae), *Psidium guajava* (Myrtaceae) in humid areas. Often they are growing on exposed conditions such as fences in pastures, or in deep shade on secondary vegetation.

Eponymy. It is named in honour of the Costa Rican orchidologist Alberto Brenes who collected the type specimen.

Phenology: plants flower from March to May and September to November but sporadic flowering has been observed throughout the year. It is common to observe plants bearing several infructescences in the field.

Discussion. The species is easily distinguished by the small size of the leaves, less than 2 cm in length and the relative size of the plant, which is shorter (<15 cm) than any other species of the genus of the section *Campylocentrum*, excluiding *C. tenellum*. The flowers are also smaller, up to 3 mm in length. Although *C. brenesii* could be as tiny as *C. tenellum*, the latter differs in having lacerate leaf sheaths (not present in *C. brenesii*) and linear leaves (vs. ovate or elliptic in *C. brenesii*). Also, in

C. tenellum, the spur is slightly curved upward, wider at the base and progressively narrowing towards the apex (vs. oblong, curved downward in *C. brenesii*).

Campylocentrum brenesii is the most variable species in the study area, both in vegetative architecture (particularly in plant size, a well as the shape and length of the leaves that range from ovate to orbicular or elliptic) (Figure 27) and flower morphology (Figure 24, 25). Several specimens were examined and documented by means of analytical drawings. Because of their exceeding variability, the living and dried specimens were grouped into two main morphs, according to leaf shape, plant size, and spur length. Morph 1 included short plants (<10 cm tall) with slightly congested-overlapping, ovate leaves, oblong sepals and small rounded spurs. This morph fits well Schlechter's concept of *C. brenesii* (*A.M. Brenes 127*, AMES) (Figure 22). It had been depicted by Endrés (W-*Rchb Orch* 0018850, 0018851, Figure 16) and is represented here by the figure 24. This morph has been observed mostly at lower elevations (700 to 800 m) in humid areas. Morph 2 (Figure 25) included plants longer than those of morph 1 (<15 cm tall) with lax, elliptic-linear leaves and longer spurs (more than 2 mm). They were observed mostly at higher elevations (800-1700 m). This morph fits Ames's concept of *C. longicalcaratum* (*C.H. Lankester 1013*, AMES) (Figure 23). However, some populations cannot be placed in any of the previously disccussed morphs. Throughout their range, spur length varies between individuals from short (morph 1) to long (morph 2), while the leaves can be either ovate or linear. A good example of this variation is represented by the type specimen of *C. parvulum* (*A. Brade & C.*

Brade 1294, AMES) (Figure 19). It is a small plant with linear leaves but the flowers have small spurs. No correlation was observed between the formerly discussed features, as well as and between character variations and the specific habitat where the specimens were found. In the area of Orosi Valley and vicinity of Tapantí, plants with linear and ovate leaves grow sympatrically, and plant size and shape of floral parts vary within the same population (i.e., *D. Bogarín 921*, USJ, *D. Bogarín 6256,* CR, *D. Bogarín 6363,* JBL-Spirit). Other characters previously used to distinguish *C. brenesii*, *C. longicalcaratum* and *C. parvulum*, like the length of the spur against the length of sepals, the sparsely or congested inflorescences, the lateral compression of the spur, the shape of the perianth parts, and the length of the inflorescences (larger or shorter than the leaves), proved to be variable, and no correlation were observed between those features. Todzia (1980) and Dressler (1993b) accepted *C. longicalcaratum* and *C. parvulum* as distinct species, according to the differences in the relative length of the leaves, the inflorescences and the spur, a highly variable set of features. Pupulin (2002) reduced *C. longicalcaratum* and *C. parvulum* under *C. brenesii*, an idea later supported by Dressler (2003). On the sole basis of morphological characters, we can not maintain a distinction between the three formerly proposed species, and we favor the use of a broad concept of *C. brenesii* until more information becomes available to assess the specific limits in this complex.

According to art. *11.5.* of the Code of Botanical Nomenclature, when, for any taxon, a choice is possible between legitimate names of equal priority in the

corresponding rank (*C. brenesii* and *C. parvulum* have equal priority since they were described by Schlechter (1923b) in the same publication), or between available final epithets of names of equal priority in the corresponding rank, the first such choice to be effectively published establishes the priority of the chosen name (see, in particular, *Ex. 20.*). As *C. brenesii* has been previously chosen against *C. parvulum* by Pupulin (2002) and Dressler (2003), this name is accordingly treated as having priority over *C. parvulum.*

2. ***Campylocentrum fasciola*** (Lindl.) Cogn., Fl. Bras. 3(6): 520. 1906. Type: Guyana: Demerara, *Schomburgk s.n.* (holotype K-L) (Figure 28, 29).

Angraecum fasciola Lindl., Edward's Bot. Reg. 26: sub t. 68. 1840.

Aeranthes fasciola (Lindl.) Rchb.f., Walp. Ann. Bot. Syst. 6: 902. 1864.

Campylocentrum sullivanii Fawc. & Rendle, J. Bot. 47: 128. 1909. Type: Jamaica. Belvedere, Hanover, 500 ft, *Harris* 7523 (holotype K; isotype W).

Campylocentrum lankesteri Ames, Schedul. Orch. 4: 57. 1923. Type: Costa Rica: Reventazu [Reventazón] River, alt. 100 ft, *C.H. Lankester* 71 (holotype K; illustration of type, AMES) (Figure 20).

Plant epiphytic, acaulescent, a core of scale-like leaves less than 5 mm long, with a cluster of roots. ***Roots*** cyclindric, conspicuous, flexuous, white to greenish, glabrous, up to 35 cm long, less than 2.5 mm in diameter, striped with white bands,

produced from the obsolescent stem, with green tips. ***Inflorescence*** 1 to many, a patent raceme with 5-24 flowers, erect to suberect; ***peduncle*** filiform, mamillate, to 5 cm long; ***floral bracts*** inconspicuous, scarious, triangular, acute. ***Ovary*** sessile, curved, less than 1.5 mm long. ***Flowers*** small, about 3 mm in length, disthichous, nonresupinate, white with greenish-white spur. ***Dorsal sepal*** ovate-elliptic, cuspidate, subequal to the lateral sepals, 1.5 x 0.5-1 mm. ***Lateral sepals*** ovate-elliptic, cuspidate, 1.7 x 0.5-1 mm. ***Petals*** ovate-elliptic, obtuse to acute, about 1.0 x 0.4-0.8 mm. ***Lip*** 3-lobed, the lateral lobes rounded to acute, the midlobe triangular, truncate, retuse or subacute, conduplicate, with a very small hairly callus, extended at the base into a curved, saccate, clavate, 3-lobuled spur, provided with conspicuous longitudinal keels; entire lip 3 mm long including the spur, 2.3 mm wide across the lateral lobes. ***Column*** very short, to 0.5 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on short hyaline stipe; viscidium elliptic. ***Anther cap*** cucullate, subquadrate, 2-celled.

Distribution. Belize and Guatemala to Brazil and Antilles.

Additional material examined: COSTA RICA. **Alajuela**: Alajuela, San Carlos, Pocosol, Santa Rosa Centro, Barrio Jasmín, Finca Rosibel, 115 m, 10°37'18.1"N 84°31'17.6"W, bosque muy húmedo tropical, transición a basal, epífitas en árboles aislados de *Psidium guajava* en potreros, 14 diciembre 2005, *D. Bogarín* 2220, *F. Pupulin* & *E. Vargas* (JBL-Spirit, USJ); **Cartago**: Turrialba, Turrialba, Campus de la Universidad de Costa Rica, Sede Atlántico, 9°54'03"N 83°40'04"W, 643 m, bosque muy húmedo premontano, epífitas en zonas verdes y jardines, sobre *Terminalia*

catappa (Combretaceae), 20 diciembre 2004, *D. Bogarín 1119 & 1120, A. Karremans,* & *A. Prendas* (JBL-Spirit, USJ); **Heredia**: Sarapiquí, Horquetas, en jardín de Doña Otilia Vargas, sobre árbol de guayaba (*Psidium guajava*), 30 Diciembre 2004, *C. Ossenbach* 336 (JBL-Spirit, USJ, Figure 28); Sarapiquí. Horquetas, Buenos Aires, en jardines de la casa de Doña Otilia Vargas, 10°20'34.3"N 83°57'32.5"W, 100 m, bosque muy húmedo tropical, epífita en *Citrus* spp., 12 abril 2008, *D. Bogarín* 4481 (JBL-Spirit). **Limón**: Siquirres, Siquirres, Guayacán, en potreros bajando el camino frente el bar Guayacán, en las orillas de la Quebrada Quebrador, 10°02'1.44"N 83°32'13.5" W, 477 m, bosque muy húmedo tropical transición a premontano, epífita en *Psidium guajava* en potrero, 25 enero 2008, *D. Bogarín 4051* & *A. Karremans* (JBL-Spirit). Siquirres, Florida, San Antonio, rivera del Río Reventazón, entre los ríos Blanco y Pascua, 10°02'38.7"N 83°36'47"W, 650 m, bosque muy húmedo tropical transición a premontano, epífita en árboles *de Psidium guajava*, aislados en potreros, 2 abril 2008, *D. Bogarín 4245, R.L. Dressler, A. Karremans, A. Russell & R. Samuel* (JBL-Spirit).

Phenology. February to May and October to November.

Habitat. Epiphytic in premontane wet forest along the Caribbean watershed between 100-650 m of elevation. Plants can be found growing in secondary vegetation, disturbed areas, gardens and pastures. The populations were found mainly on twigs of *Citrus* spp. (Rutaceae), *Psidium guajava* (Myrtaceae) and *Terminalia catappa* (Combretaceae).

Etymology. Derived from the Latin *fascia,* "little bandage", in allusion to the characteristic bands of the spur.

Discussion. This species belongs to the section *Dendrophylopsis*, characterized by the aphyllous condition of the plants. Because vegetative characters are reduced in the aphyllous species, the taxonomy of this group has been based largely on gross floral morphology. *Campylocentrum fasciola* can be easily recognized by its spur, narrow at the base and wider at apex, with three longitudinal keels.

In Costa Rica, this species is restricted to the Caribbean watershed. It is distinguished from its relative, *C. multiflorum,* by the spur narrow at the base and wider at the apex (vs. spur wider at the base and progressively narrowing to the apex in *C. multiflorum*), with conspicuous longitudinal keels (vs. without keels), the midlobe of the lip truncate (vs. acute), and the cuspidate sepals (vs. acute or rounded in *C. multiflorum*).

Campylocentrum lankesteri was described by Oakes Ames in 1923 from the shores of the Reventazón River in the Atlantic lowlands of Costa Rica. Ames (1923) compared *C. lankesteri* with *Campylocentrum sullivanii* Fawc. & Rendle, a species described from Jamaica in 1909, stating that it "differs in the outline of the labellum which has the neuration less heavy". Later in 1937, in his treatment of the Orchidaceae for Standley's Flora of Costa Rica, Ames reduced *C. lankesteri* in synonymy under *Campylocentrum sullivanii*. An assessment of plants from the vicinity of Reventazón River in Turrialba (*D. Bogarín 1119*, JBL-spirit) together with

a direct examination of the type specimen of *C. lankesteri* (*C. Lankester 71*, K) (Figure 20), led us to support the previous inclusion of the former species under the synonymy of *C. fasciola* (Todzia 1980, Pupulin 2002, Dressler 2003).

3. *Campylocentrum generalense* Bogarín & Pupulin, **ined.**

Plant epiphytic, acaulescent, a leafless cluster of roots. *Roots* flat, conspicuous, flexuous, glabrous, with rather sharply defined edges, produced from the cormlike body of the obsolescent stem, to 5 mm wide with the tips orange. ***Inflorescence*** 1 to many patent racemes, many flowered (to 12) , congested, usually produced in pairs, with fíliform, glabrous or scurfy peduncle, to 2.5 cm long; ***floral bracts*** conspicuous, covering the ovary, scarious, ovate, acute, the margins erose. ***Ovary*** less than 1 mm long, scurfy. ***Flowers*** small, to 8 mm long, distichous, orange to yellowish with yellowish spur. ***Dorsal sepal*** rectangular, acute, 4.2 x 1.5 mm. ***Lateral sepals*** ovate to broadly ovate, acute, 4.2 x 1.8 mm. ***Petals*** elliptic, rectangular, acute, about 4.1 x 1 mm. ***Lip*** 3-lobed, the lateral lobes obtuse, small comparing with the midlobe, the midlobe triangular, acute, with pubescent callous extended at the base into a curved, slightly three-lobed, saccate, conspicuous, bulbous spur, narrow at the base, 1 mm, and wide at the apex 2 mm, curved upward the lip about 8 mm long including the spur, 2 mm wide. ***Column*** very short, with terminal anther, about 1 mm long. ***Pollinia*** 2, ovoid, on a short hyaline stipe; viscidium elliptic. ***Anther cap*** cucullate, ellipsoid, 2-celled.

Distribution. Only known from Costa Rica.

COSTA RICA. **San José**: San José: Pérez Zeledón, San Isidro de El General, Palmares, creciendo en *Citrus* sp. en zona alterada, 9°19'15"N 83°39'44"W, 600 m, colectada por Jorge Cambronero, floreció en cultivo en el jardín de J. Cambronero, en Palmares de San Isidro del General, setiembre 2005, flores en alcohol, 27 Octubre 2005, *D. Bogarín 2130*. (Figure 30, 31).

Habitat. Epiphytic in *Citrus* spp. trees in premontane wet forest in El General Valley in the Pacific lowlands of the Cordillera de Talamanca at 600 m of elevation.

Etymology. Named after the type locality of El General Valley in San Isidro de El General, Pérez Zeledón, located in the southern pacific side of San José province, Costa Rica.

Phenology. January to February.

Discussion. *Campylocentrum generalense* is similar to *Campylocentrum pachyrrhizum*, a species described by H. G. Reichenbach from Cuba. They are the only species of *Campylocentrum* which produce conspicuously flat roots with rather sharply defined edges from the leafless, obsolescent stem, and present conspicuous floral bracts that cover the ovary. *Campylocentrum generalense* differs from *C. pachyrrhizum* in having a congested inflorescence (vs. loose), the spur of the lip curved upward (vs. curved downward), narrow at base and wider at apex (vs. entire), and obscurely three lobed (vs. unlobed). Among the species of

Campylocentrum in Costa Rica, it is the only aphyllous species with conspicuously flattened roots.

A sketch of the type specimen of *C. pachyrrhizum* in Reichenbach Herbarium at Vienna shows a flower with an unlobed spur curved downward (*Wright 3207*, W-*Rchb Orch*) (Figure 17). Also the drawing of a Venezuelan voucher published by Dunsterville and Garay (1959), shows a specimen with lax inflorescence and flowers that present a cylindric, unlobed, downward curved spur. The same features are shown in the pictures of specimens from Florida (U.S.A) provided by Luer (1972: 275) and Brown (2002: 51), especially the lax inflorescences and the downward curved spur.

The presence of *C. pachyrrhizum* in Costa Rica has not been documented so far. Mora-Retana and García (1992) and Dressler (1993b) listed this species for Costa Rica without any specific reference to a voucher. Dressler (com. pers. 2008) observed a leafless flowerless specimen of *Campylocentrum* with flat roots in Milla 28, Finca Waldeck in Siquirres, along the Caribbean plains of Limón province, but no voucher was prepared at that time. In absence of voucher, we are unable to determine if this specimen corresponds to *C. generalense* or to a true *C. pachyrrhizum*. See excluded species for further discussion.

4. ***Campylocentrum micranthum*** (Lindl.) Maury, J. Bot. (M. Louis Morot) 3: 273. 1889. Type: Surinam, *G. Loddiges s.n.* (holotype K-L) (Figure 32—34).

Angraecum micranthum Lindl., Ann. Bot. Syst.6: 901. 1864.

Aeranthes micranthus (Lindley) Rchb.f., Ann. Bot. Syst. 6: 901. 1864.

Epidorchis micrantha (Lindl.) Kuntze, Revis. Gen. Pl. 2: 660. 1891.

Mystacidium micranthum (Lindl.) T.Durand & Schinz, Consp. Fl. Afr. 5: 54. 1895.

Campylocentrum micranthum Rolfe, Orchid Rev. 11(128): 245. 1903. *nom. superfl.*

Campylocentrum peniculus Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 91. 1922. Type: Panama: auf Hügeln bei Panama City, *C.W. Powell* 184 (holotype B†; lectotype, selected by Christenson 1991, AMES; isolectotype MO, photo).

Plant epiphytic, pendent, rarely suberect, with terete, leafy stem to 75 cm long. ***Roots*** fleshy, up to 30 cm long, less than 3 mm in diameter, white to greenish, with green tips. ***Leaves*** many (to 15), elliptic-oblong to suborbicular, obtuse or emarginate, unequally 2-lobed at the apex, conduplicate, coriaceous to fleshy, distichously arranged, to about 7.5 x 2-3 cm, articulate with the sheath envolving the stem, the sheaths lacerate at apex. ***Inflorescence*** a many-flowered (to 13) raceme usually shorter than the leaves, produced along the stem, opossite to the leaves, the flowers arranged distichously on the rachis, about 3.5 cm long; ***pedicel*** inconspicuous, less than 0.5 mm long; ***floral bracts*** subquadrate or triangular, scarious. ***Ovary*** cylindric, less than 2 mm long, covered with sparsely minute

trichomes. ***Flowers*** small, about 1.3 cm in length, disthichous, white with greenish spur. ***Dorsal sepal*** subequal to the lateral sepals, elliptic, oblong to linear-elliptic, lanceolate, acute, 5.5 x 1.5 mm. ***Lateral sepals*** elliptic-oblong, lanceolate, rectangular, acute, concave towards the base, 8.3 x 1.6 mm. ***Petals*** elliptic, lanceolate, acute, 5.6 x 1.5 mm. ***Lip*** 3-lobed; the lateral lobes triangular, acute, less than 1 mm long, clasping the column; the midlobe lanceolate, triangular, strongly acute, larger than lateral lobes, slightly conduplicate, concave, with a hairly callus along the midrib, extended at the base into a cylindric, clavate, porrect, down-curved spur, sometimes obscurely 3 lobed, more or less continuous with the lip, larger than the blade of the lip (to 5 mm long, 2 mm wide); entire lip 13 mm long including the spur, 2.3 mm wide between the lateral lobes. ***Column*** very short, to 1 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe; viscidium elliptic. ***Anther cap*** subquadrate-cucullate, 2-celled.

Distribution. Belize to Brazil and the Antilles.

Additional material examined: COSTA RICA. **Cartago**: Turrialba, Parque Central de Turrialba, ca. 600 m, bosque muy húmedo premontano, epífita, planta colectada por J. Carmona, floreció en cultivo en La Suiza de Turrialba, 28 agosto 2004, *D. Bogarín* 963 (JBL-Spirit, drawings); Turrialba, instalaciones del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 9°54'03"N 83°40'04"W, 650 m, bosque muy húmedo premontano, epífita en cercas de *Hibiscus* sp., 10 febrero 2004, *D. Bogarín* 696, *A. Karremans, H. León-Páez & F. Pupulin* (JBL-Spirit, drawings); Same locality, *D. Bogarín* 697, *A. Karremans, H. León-Páez & F. Pupulin*

(JBL-Spirit, drawings); **Heredia**: Sarapiquí, Finca La Selva. OTS Field Sstation near junction of Puerto Viejo and Sarapiquí rivers, 40-100 m, sendero oriental fallen from *Brosimum lactescens* (Moraceae), 2 April 1991, *K. Richardson 203* (CR). Sarapiquí, Horquetas, Buenos Aires, en jardines de la casa de Doña Otilia Vargas, 10°20'34.3"N 83°57'32.5"W, 100 m, bosque muy húmedo tropical, epífita en *Citrus* spp., 2002, *C. Ossenbach* s.n (JBL-Spirit). **Limón**: Pococí, Llanura de Santa Clara, Finca La Suerte, 10°26'30"N 83°47'20"W, 50 m, epífita, flores blancas, 5 agosto 1995, *R. Aguilar* 4257. (INB); Talamanca, San José Cabécar, 400 m, 9-3 March 1978, *C. Todzia* 183 (CR); **Puntarenas**: Aguirre, Quepos, La Managua, camino a Naranjito, 9°26'49.0"N 84°08'01.7" W, 51 m, bosque muy húmedo premontano transición a basal, epífitas en *Psidium* en jardines y plantaciones de *Citrus*, 31 marzo 2005, *D. Bogarín 1844, D. Castelfranco, F. Pupulin & A.C. Rodríguez* (JBL-spirit). Aguirre, Quepos, Manuel Antonio, trail to the beach south of Playa La Mancha, 100 m, epiphytic on *Crescentia cujete,* 28 July 1995, *F. Pupulin 332* (USJ, drawings, Figure 32); Osa-Golfito, "Bosque de Los Austriacos", Tropenstation La Gamba, 8°42'40"N 83°13'00"W, 125-400 m, bosque secundario, epífita en ramas caidas sobre el suelo y árboles a lo largo de los senderos, 3-4 julio 2004, *E. Serrano 137* & *M. Blanco* (USJ); Golfito, Golfito-Guaycará, camino a La Gamba, orillas de la Quebrada Gamba, 8°41'25.2"N 83°12'48.7" W, 205 m, bosque muy húmedo tropical transición a premontano, epífitas en *Psidium* y *Citrus* a orillas del camino, 24 octubre 2004, *D. Bogarín 1036* & *Botánica Forestal-UCR* (JBL-Spirit). Osa, Rancho Quemado, Sector Este, Sierpe, 8°42'20"N 83°33'40"W, 200-230 m, epífita, frutos verde claro, 9 noviembre 1991, *J. Marín* 283 (INB); Osa, Reserva

Forestal Golfo Dulce, entre Rincón y Chacarita, 8°46'00"N 83°22'00"W, 10-200 m, epífita en *Dialium*, flores anaranjado pálido, ca. 8 km de Chacarita hacia Rincón, 22 octubre 1990, *B. Hammel* 17942 (CR); **San José**: Turrubares, Carara, Bijagual, Villa Bijagual, 9°43'41.8"N 84°34'05.2" W, 452 m, bosque muy húmedo tropical transición a premontano, epífitas en plantaciones de *Citrus* detrás de la escuela, propiedad de la Sra. Ramírez, 16 enero 2005, *D. Bogarín 1272*, *I. Chaves & G. Bogarín* (JBL-Spirit); Same locality, 16 enero 2005, *D. Bogarín* 1263, *I. Chaves & G. Bogarín* (JBL-Spirit); Same locality, 16 enero 2005, *D. Bogarín* 1276, *I. Chaves & G. Bogarín* (JBL-Spirit, Figure 33).

Habitat. A widespread epiphyte in tropical wet forest, tropical moist forest, tropical moist forest premontane belt transition and tropical wet forest premontane belt transition from 0 to 900 m along both, the Caribbean and Pacific watersheds. It is found mainly associated with secondary vegetation, in open disturbed areas, gardens and pastures. The observed populations were found mostly in *Citrus* spp. (Rutaceae) plantations, *Hibiscus* spp. (Malvaceae) fences, and on trunks and twigs of *Terminalia catappa* (Combretaceae) and *Psidium guajava* (Myrtaceae). It has been rarely observed in understory secondary vegetation.

Etymology. Derived from the Latin *micranthum,* "small flowered", in allusion to the small flowers of this species compared with other members of *Angraecum*, the genus in which Lindley originally placed this species. In spite that its flowers are among the largest in *Campylocentrum*, the International Code of Nomenclature does not allow for changes in names arising from such errors (McNeill *et al.* 2006).

Phenology. Plants have been recorded in flower between January and October.

Discussion. *Campylocentrum micranthum* is a large leafy species that can be easily recognized by the conduplicate coriaceous leaves, the congested inflorescence, the acute perianth segments, the lip with the mid-lobe three times larger than the lateral lobes, and the spur distinctly larger than the blade of the lip. Although amply variable in plant and leaf size and shape, the features discussed here consistently to separate this species from its relatives.

This species belongs to the section *Campylocentrum*. Within this group, its closest relatives in Costa Rica are *C. panamense*, from which it differs by the coriaceous leaves (vs. subcoriaceous in *C. panamense*), the mid-lobe of the lip acute (vs. rectangular-acute), and the sepals and petals acute (vs. spatulate); and *C. schiedei*, from which differs by the congested inflorescences (vs. lax), the lip with the mid-lobe three times larger than the lateral lobes (vs. twice larger), and the spur distinctly larger than the blade of the lip (vs. equal to scarcely larger in *C. schiedei*).

Although recorded by Schlechter (1923b) from Costa Rica, *C. peniculus* should be considered as conspecific with *C. micranthum*. There are perhaps several other *Campylocentrum* species that have been described based on variant specimens of *C. micranthum*, but a carefully study is needed to clarify the status of species outside of Costa Rica (see Carnevali et al. 2001). For more information on the discussion and nomenclature of this species see above the chapter on *Campylocentrum* taxonomic history.

5. ***Campylocentrum multiflorum*** Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 156. 1923. Type: Costa Rica. [San José: Turrubares], Cerro Turubales [Turrubares], 500 m, bereits fruchtend im Februar 1910, *A. Brade & C. Brade 1316.* (holotype B†; drawing of the holotype, AMES-31555, based on *A. Brade & C. Brade 1316*). (Figure 18, 35—37).

Plant epiphytic, acaulescent, a leafless cluster of roots. ***Roots*** cyclindric, conspicuous, flexuous, glabrous, produced from the cormlike body of the obsolescent stem, less than 1 mm in diameter. ***Inflorescence*** 1 to many patent racemes, usually produced in pairs, with fíliform, glabrous peduncle, to 11 cm long; ***floral bracts*** inconspicuous, scarious, triangular, acute. ***Flowers*** small, distichous, white with yellowish spur. ***Dorsal sepal*** ovate to orbicular, acute, 0.8 x 0.7 mm. ***Lateral sepals*** ovate to broadly ovate, obtuse, 1-nerved, 1.2 x 0.5-1.0 mm. ***Petals*** oblique, elliptic-ovate, obtuse to acute, about 1.0 x 0.5 mm. ***Lip*** 3-lobed, the lateral lobes rounded to acute, the midlobe triangular, acute, rarely obtuse, with pubescent callous extended at the base into a curved, slightly three-lobed, saccate, conspicuous, bulbous spur, wider at the base, 0.8 mm, and narrow at the apex 0.3 mm, the lip about 2.5 mm long including the spur, 1.2 mm wide. ***Column*** very short, with terminal anther, about 0.5 mm long. ***Pollinia*** 2, ovoid, on a short hyaline stipe; viscidium elliptic. ***Anther cap*** cucullate, ellipsoid, 2-celled.

Distribution. Costa Rica and probably Panama.

Additional material examined: COSTA RICA. **Puntarenas**: Aguirre, near Naranjito, about 50 m, in *Citrus* orchard, 2 January 1999, flowered in cultivation at Gaia Botanical Garden, 9 May 1999, *F. Pupulin 1029 and 1030, D. Castelfranco & L. Spadari* (USJ, photo, drawings, Figure 35). Puntarenas: Aguirre, Quepos, La Managua, camino a Naranjito, 9°26'49.0"N 84°08'01.7" W, 51 m, bosque muy húmedo premontano transición a basal, epífitas en *Psidium* en jardines y plantaciones de *Citrus*, 31 marzo 2005, *D. Bogarín 1484, D. Castelfranco, F. Pupulin & A.C. Rodríguez* (JBL-Spirit, USJ, drawings, Figure 36). Same locality, *D. Bogarín et al.* 1485 and 1486 (JBL-Spirit, USJ). Aguirre, Quepos, road to Naranjito, La Managua, 09º26'48.1"N 84º08'02.1"W, 20 m, epiphytic in gardens and orchards along the roadside, tropical moist forest, *F. Pupulin 5638, D. Bogarín & A.C. Rodríguez*, 31 March 2005 (JBL-Spirit); Buenos Aires, Pilas, La Dibujada. Epífita en cítricos (*Citrus* spp.). Flores Blancas, Noviembre 1992. Floreció en mayo 2003. *J. Villalobos s.n.* (USJ); Orillas del Río Nuevo, cerca de Puerto Jiménez de Osa (Golfito), 20 m, 4 abril 1930, *A. Brenes s.n.* (CR); Buenos Aires de Osa, 480 m, 5 Abril 1934, *M. Valerio s.n.* (CR); Corredores, Laurel, flowers greenish white, epiphytic on *Citrus* sp. 100 m, 12 April, *C. Todzia* 219 (CR); Corredores, Corredor, Río Bonito, bosque muy húmedo tropical transición a premontano, 8°40'46.0"N 82°58'32" W, 116 m, 23 abril 2007, *R.L. Dressler* 6850 (JBL-spirit); Entre Puerto Jiménez y Río Tigre, 3 abril 1930, *A. Brenes s.n. (*CR).

Etymology. From the Latin *multiflorum*, "many flowered", in allusion to the several flowers and inflorescences of the specimen studied by Schlechter, unfortunately destroyed in Dahlem-Berlin in the Second World War.

Phenology. Plants have been recorded in flower from March to June.

Habitat. Epiphytic in tropical wet forest and tropical wet forest premontane belt transition along the Pacific watershed at 20-150 m of elevation. Populations are mainly found in orchards, pastures and commercial plantations of *Citrus* spp. and *Psidium guajava* trees. It has not been recorded from the northern region of Puntarenas and Guanacaste, and it ranges from Cerro Turrubares in Central Pacific to the Osa peninsula and the Burica region. Since some collections from Corredores, in southern Costa Rica have been made, it is highly probable that this species may occur in Chiriquí, Panama.

Discussion. This species belongs to the section *Dendrophylopsis*. It differs from *C. fasciola*, its Caribbean counterpart, by the spur wider at the base and progressively narrowing to the apex, without longitudinal keels (vs. spur narrow at the base and wider at the apex, with conspicuous longitudinal keels in *C. fasciola*), the midlobe of the lip acute (vs. truncate) and the sepals acute or rounded (vs. cuspidate). Moreover, both species are clearly isolated geographically. *Campylocentrum fasciola* is restricted to the lowlands of the Caribbean watershed and *C. multiflorum* is only found along the Pacific watershed, ranging from Cerro Turrubares, in Central Pacific (the type locality of *C. multiflorum*) to the south (Figure 37). Material

available for this study showed that the morphological features discussed previously consistently separate both species but also they have a strong correlation with the geographic data. Whilst the taxonomy of the Caribbean *C. fasciola* provokes no discussion, the identity of the leafless *Campylocentrum* from the Pacific lowlands is still debatable.

Since several authors have misidentified this species as *C. fasciola,* reducing *C. multiflorum* in synonymy under *C. fasciola* (Todzia 1980, Dressler 2003, Romero-González & Carnevali 2005), the name *C. multiflorum* remained in the oblivion. Schweinfurth was the first in treating this species as synonym of *C. fasciola,* writing that name on the herbarium sheet of the lectotype (AMES-31555). As a consequence of this mistake, the name *C. tyrridion*, a species described by Dunsterville & Garay (1961) based on Venezuelan material, has been applied to the aphyllous *Campylocentrum* of the Pacific lowlands in Costa Rica (Pupulin 2002, Dressler 2003, Romero-González & Carnevali 2005).

Definitely, the loss of the type specimen in Dahlem-Berlin and the small and inconspicuous condition of the aphyllous specimens have traditionally precluded a clear understanding of the species circumscription of *C.multiflorum*. No duplicates of the type collection cited by Schlechter (*A. Brade & C. Brade 1316*, B†) (Figure 18) are known. The drawing kept at the Ames Orchid Herbarium is the only known material referable to this species since its destruction. Consequently it has been chosen here as lectotype. Together with the protologue, it is the only evidence to aid in understanding Schlechter's concept of *C. multiflorum*. The drawing of the

lectotype shows the mid-lobe of the lip acute as in the specimens studied. In the protologue, Schlechter noted that the plant available had many fruits but there were few flowers that could be used for adequate analysis (Schlechter 1923). He compared this species with *C. sullivanii,* a species otherwise known from the Antilles. However, we consider that the clearly distinction between *C. fasciola* and *C. multiflorum*, together with the geographic distribution data (in which the type locality of *C. multiflorum* fits and agrees with the hypothesis discussed above) are enough evidence to reconsider the name *C. multiflorum*. Having priority, *C. multiflorum* is the correct name for the Costa Rican Pacific leafless species, while the name *C. tyrridion* (if the two species are distinct) should be best applied to the Venezuelan species.

6. ***Campylocentrum panamense*** Ames, Orchidaceae 17: 88. 1922. Type: Panamá. In woods near Gatún, on trees, 10 Jan. 1860, *Sutton Hayes* 988 (holotype NY, photo, illustration of type AMES) (Figure 38—40).

Plant epiphytic, pendent, with terete, leafy stem up to 50 cm long. ***Roots*** fleshy, up to 40 cm long, less than 2.5 mm in diameter, white to greenish, with green tips. ***Leaves*** many (to 22), elliptic to linear-elliptic, subcoriaceous, conduplicate, emarginate, unequally 2-lobed at the apex, articulate with the sheath envolving the stem, to 10 x 2.5 cm. ***Inflorescence*** a many-flowered (to 10) raceme shorter than the leaves, produced along the stem, opossite to the leaves, the flowers arranged

distichously on the rachis, 1.5-4 cm long; ***pedicel*** conspicuously globose at the base; ***Floral bracts*** triangular, scarious. ***Ovary*** cylindric, less than 2 mm long. ***Flowers*** small, about 1.3 cm in length, disthichous, white with yellowish spur. ***Dorsal sepal*** spathulate, oblong to linear-elliptic, obtuse, wide at apex, 7.5 x 1.8-2.0 mm. ***Lateral sepals*** linear-spathulate to oblong, obtuse to acute with a small apicule, concave, 8.3 x 1.6 mm. ***Petals*** oblong-elliptic, acute, 7.0 x 1.5 mm. ***Lip*** obscurely 3-lobed; the lateral lobes triangular, rounded at apex, less than 0.7 mm long, clasping the column, the midlobe lanceolate to oblong, acute, slightly conduplicate, concave, with a very small hairly callus along the midrib, extended at the base into a cylindric, saccate, slightly curved spur, more or less continuous with the lip, shorter or equal to the blade of the lip (to 5.6 mm long); entire lip 12 mm long including the spur, 2.5 mm wide between the lateral lobes. ***Column*** very short, to 0.8 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on a short, ligulate, hyaline stipe; viscidium elliptic. ***Anther cap*** cucullate, subquadrate, 2-celled.

Distribution. Costa Rica, Panama and Ecuador.

Additional material examined: COSTA RICA. **Alajuela**: Reserva Biológica Monteverde, Estación Eladio's, 10°19'N 84°43'W, 820 m. Epífita en árbol caido. Flor blanca, 2 octubre 1990, *E. Bello 2381* (INB); Sarapiquí, San Miguel, camino a Colonia Carvajal, puente sobre el Río Sarapiquí, 10°19'16"N 84°10'34"W, 380-400 m, orillas del Río Sarapiquí, bosque muy húmedo tropical transición a premontano, epífita en bosque secundario, 13 febrero 2004, *D. Bogarín 725, H. León-Páez, F. Pupulin* & *E. Salas* (JBL-Spirit); **Cartago**: Límite entre Turrialba y Jiménez, La

Suiza, Pejivalle, camino a Esperanza, orillas de la Quebrada Regada, 9°48'21.4"N 83°39'10.6" W, 726 m, bosque muy húmedo premontano, epífita en bosque secundario a la orilla del río en sitio sombreado, 28 agosto 2004, *D. Bogarín* 954 & *J. Carmona* (JBL-Spirit, drawings); **Limón**: Pococí, Guápiles, carretera Braulio Carrillo, 300 m hacia abajo de la entrada del Teleférico del Bosque Lluvioso, 511 m, 10°10'57"N 84°54'53"W, bosque muy húmedo tropical transición a premontano, epífita en lianas a orilla de la carretera, 9 julio 2004, *D. Bogarín* 871 & *F. Pupulin* (CR, JBL-Spirit, USJ, drawings, Figure 39); **Puntarenas**: Aguirre, Villa Nueva, road to Cerro Carpintera, 250 m, 5 July 1995, *F. Pupulin* 305 & *D. Castelfranco* (USJ, drawings, Figure 38).

Habitat. Epiphytic in tropical wet forest transition to premontane along the Pacific and Caribbean watersheds of the country at 250-820 m of elevation. It is associated with secondary vegetation along rivers or small creeks and it is less often seen in disturbed areas such as open pastures or plantations.

Etymology. Derived from Panama, the country where the type specimen was collected.

Phenology. Plants have been recorded in flower from July to October.

Discussion. This species belongs to the section *Campylocentrum*. It is closest in appearance to *C. micranthum*, especially in plant size (Ames 1922). Both species are often robust plants and might look like the same, being treated as conspecific (Williams & Allen 1980). However, *C. panamense* differs in having subcoriaceous

leaves (vs. coriaceous in *C. micranthum*), spathulate sepals and petals (vs. acute), the spur shorter than the length of the lip's blade (vs. longer) and the inflorescence lax (vs. congested).

7. ***Campylocentrum poeppigii*** (Rchb.f.) Rolfe, Orchid Rev. 11: 246. 1903. Type: Cuba: Savana de Macuriyes, Apr. 1824 ("*Limodorum*"), *Poeppig s.n.* (holotype W, isotypes MO, P, W) Figure 41, 42.

Angraecum poeppigii Rchb.f., Linnaea 22: 858. 1849.

Plant epiphytic, forming a mass of stems and roots. ***Roots*** white, flexuous, attached to the tree or free along the stems, to 3 mm wide. ***Stem*** simple or sometimes branched, partially covered by the old sheathing leaf bases, to 25 mm long, terete, 1 to 2 mm wide. ***Leaves*** very reduced, triangular, acute, caducous, persisting only at the apex, subterete, 3 to 5 mm long. ***Leaf sheaths*** tubular, adpressed to the stem, lacerate to smooth along the apical margin. ***Inflorescence*** distichous, many flowered (to 10), produced from the sides of the stem directly below the point of emergence of the roots, less than 1.5 cm long. ***Floral bracts*** ovate, concave, acute, brown. ***Flowers*** distichously arranged on the rachis, facing the same direction so appearing secund, white to yellowish. ***Dorsal sepal*** ovate, acute, conduplicate, 1.6 x 1 mm. ***Sepals*** subequal, elliptic, oblong to ovate, acute, conduplicate, usually spreading only at apex, minutely denticulate at base, 2 x 1 mm. ***Petals*** subequal to the sepals, ovate, acute, 1.4 x 0.7 mm. ***Lip*** 3-lobed; the lateral lobes triangular,

rounded at apex, less than 0.7 mm long, clasping the column, the midlobe trialgular, acute, slightly conduplicate, concave, without hairly callus along the midrib, extended at the base into a cylindric, saccate, slightly curved spur, more or less continuous with the lip, shorter or equal to the blade of the lip (to 1.7 mm long); entire lip 3 mm long including the spur, 1.8 mm wide between the lateral lobes. ***Column*** very short, less than 0.5 mm long, with terminal anther, wingless, without a foot. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe. ***Anther cap*** flat or sub cucullate, 2-celled. ***Capsule*** ovoid to narrowly oblong, with ridges. ***Seed*** filiform to fusiform.

Distribution. Guatemala to Ecuador, Venezuela, Brazil and Antilles.

Additional material examined: COSTA RICA. **Alajuela**: North of San Carlos Basin, San Pedro de Cutris (San Pedro de Arenal), 1 km from Río San Carlos, 100 m, growing on *Psidium,* on dead branches, tiny twigs with *Rodriguezia compacta*, *Ionopsis paniculatum*, *Trigonidium egertonianum*, 28 April 1979, *C.K. Horich s.n.* (CR); San Carlos, Pocosol, Santa Rosa Centro, Barrio Jasmín, Finca Rosibel, 10°37'18.1"N 84°31'17.6"W, 115 m, bosque muy húmedo tropical, transición a basal, epífita en árboles aislados de *Psidium guajava* en potreros, 14 diciembre 2005, *D. Bogarín 2218, F. Pupulin* & *E. Vargas* (JBL-Spirit, CR, Figure 41).

Habitat. This species is associated with disturbed areas like pastures and agricultural plantations along the wet plains of the Caribbean watershed in tropical

wet forest, basal belt transition at 100-150 m of elevation. It has been recorded growing on *Psidium guajava* trees as a mass of roots and stems.

Eponymy. Named after the German Eduard Friedrich Poeppig (1798-1868), who collected the type specimen.

Phenology. Plants have been recorded in flower from April to August.

Discussion. *Campylocentrum poeppigii* is readily distinguished by its elongate stems with rudimentary, caducous, tiny (less than 5 mm long), acute and narrowly conical scale-leaves. Cogniaux (1906) used that set of features to classify this species under the Section *Pseudocampylocentrum*. The inflorescences are inconspicuous, having whitish flowers with a three lobed spur and the lip lacks the characteristic pubescent callous of most of the species of the genus, at least in the studied specimens listed here.

8. ***Campylocentrum schiedei*** (Rchb.f.) Benth. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 292 1884. Type: Mexico. Daselbst bei Xalapa, *C.J.W. Schiede, C.A. Ehrenberg* & *F.E. Leibold s.n.* (holotype W) Figure 43, 44.

Angraecum schiedei Rchb.f. Linnaea 22: 857-858. 1849.

Aeranthes schiedei (Rchb.f.) Rchb.f., Ann. Bot. Syst.6: 901. 1864.

Campylocentrum acutum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 268. 1923. Type: Costa Rica: Arbres des bois, paturages et des haies, Santiago de

San Ramón, alt. 1075-1100 m, Nov 1921. Semipendante. Fleurs petites, blanches, *A.M. Brenes 147* (holotype B†; lectotype, ,selected by Barringer 1986, AMES; isolectotypes CR-18480, NY, photo of type, F ex CR) (Figure 21).

Todaroa micrantha A. Rich & Galeott., Ann. Sci. Nat. Bot., sér. 3 3: 28. 1845. Type: Mexico. *H. Galeotti s.n.* (holotype P, drawings K, W) (Figure 12, 13).

Plant epiphytic, pendent, with terete, leafy stem to 30 cm long. ***Roots*** fleshy, up to 30 cm long, less than 3.5 mm in diameter, white to greenish, with green or orange-yellowish tips. ***Leaves*** many (to 16), distichous, ovate to elliptic-oblong to suborbicular, acute to obtuse or emarginate, unequally 2-lobed at the apex, conduplicate, coriaceous to fleshy, articulate with the sheath envolving the stem, to about 4.0 x 2.2 cm. ***Inflorescence*** a many-flowered (to 25) raceme usually larger than the leaves, produced along the stem, opposite to the leaves, the flowers distichously arranged on the rachis, about 5 mm long; ***pedicel*** inconspicuous, less than 0.4 mm long; ***floral bracts*** triangular, scarious. ***Ovary*** cylindric, less than 1 mm long, covered with sparsely minute trichomes. ***Flowers*** small, about 1.3 cm in length, disthichous, white with greenish spur. ***Dorsal sepal*** subequal to the lateral sepals, elliptic, rectangular, ovate, subacute to rounded, 2.6 x 1.6 mm. ***Lateral sepals*** elliptic-oblong, lanceolate, acute, concave towards the base, 3.2 x 1.2 mm. ***Petals*** ovate, lanceolate, acute, 2.2 x 1.2 mm. ***Lip*** 3-lobed, the lateral lobes triangular, acute, small, rounded at apex, less than 1 mm long, the midlobe

triangular, acute, subequal to the lateral lobes, slightly conduplicate, concave, with a very small pubescent callous along the midrib, extended at the base into a cylindric, clavate, porrect, 3-lobed spur, more or less continuous with the lip, about, subequal than the blade of the lip (to 1.8 mm long, 1 mm wide); entire lip 4.2 mm long including the spur, 2.3 mm wide between the lateral lobes. ***Column*** very short, to 1 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe; viscidium elliptic. ***Anther cap*** subquadrate-cucullate, 2-celled.

Distribution. Mexico to Panama.

Additional material examined: COSTA RICA. **Alajuela**: San Carlos, above Ciudad Quesada, toward San Vicente, 1200-1300 m, flowered in cultivation, 20 September 1994, epiphyte, flowers cream, *R.L. Dressler* 6172 (CR); San Ramón, Piedades, 1100 m, 29 Setiembre 1925, *A. Brenes* s.n. (CR); San Ramón, La Palma 1100 m, 10 noviembre 1927, *A. Brenes* s.n. (CR); San Ramón, San Miguel, 6 Noviembre 1923, *A. Brenes* s.n. (CR); **Cartago**: Cartago, Cartago, Dulce Nombre, bosque secundario del Jardín Botánico Lankester, 1200 m, bosque húmedo premontano, epífita creciendo espontáneamente en *Conostegia xalapensis* (Melastomataceae), 21 octubre 2003, *D. Bogarín* 494 (JBL-spirit); Cartago, Dulce Nombre, Jardín Botánico Lankester, bosque secundario, ca. 1370 m, 18 Diciembre 2004, *G. Rojas* 26 (JBL-Spirit); Paraíso, Cachí, camino de Loaiza hacia el Alto Araya, 1000-1300 m, 9°49'23"N 83°49'58"W, bosque muy húmedo premontano, epífita en cercas de potreros y cafetales, 12 julio 2003, *D. Bogarín* 311, *D. Kikut* & *A. Prendas* (JBL-Spirit, drawings); Cartago-La Unión, Guadalupe-San Rafael, Coris,

Cerros de La Carpintera, detrás del Parque Industrial de Cartago, 9°52'16.7"N 83°58'42.0"W, 1504 m, bosque húmedo premontano, epífitas en bosque secundario, 30 octubre 2008, *D. Bogarín* 5496, *R.L. Dressler, R. Gómez, F. Pupulin, & R. Trejos* (CR) La Unión, Tres Ríos, San Vicente, Zona Protectora La Carpintera, Finca La Carpintera, bosque húmedo premontano, 9°53'35"N 83°58'44"W, ca. 1550 m, 13 agosto 2006, *E. Serrano 411* & *W. Salazar* (JBL-Spirit); Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1542 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 22 abril 2008, *D. Bogarín 4532, A. Gaillard, R. Gómez, Y. Kisel, R. Phillips & R. Trejos* (JBL-spirit); Jiménez, Tucurrique, Sabanillas, camino hacia Cerros Duán, márgen de la Quebrada Honda, 9°50'39.9"N 83°45'19.2" W, 1264 m, bosque pluvial premontano, en bosque secundario en cercas de potreros próximos a la quebrada, 6 febrero 2005, *D. Bogarín* 1376 & *J.C. Cervantes* (JBL-spirit); Same locality, 6 febrero 2005, *D. Bogarín* 1372 & *J.C. Cervantes* (JBL-spirit); Paraíso, Orosi, camino entre Alto Araya y Guábata, 1317 m, 9°47'99.2" N 83°49'68.5"W, bosque muy húmedo premontano, creciendo en sitio pantanoso alrededor de plantaciones y cafetales, 28 marzo 2008, *D. Bogarín 4149*, *R.L. Dressler, S. Gamboa, A. Russell & R. Samuel* (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, *D. Bogarín* 1834, *R.L. Dressler, M.G. Gei, R. Gómez & G. Rojas* (JBL-spirit); **Guanacaste**: Parque

Nacional Rincón de La Vieja, Hacienda Santa María, de la planta hidroeléctrica siguiendo el canal hasta "El Chagüite", 10°48'N 85°19'W, 1550 m, epífita, flores blancas, 22 octubre 1987, *G. Herrera 941* (CR). **Puntarenas**: Coto Brus, Las Alturas de Cotón, Fila Cedro, unpaved road to Río Cedro, 8º58'20"N 82º52'40"W 8º59'03"N 82º54'20"W, 1670-1240 m, lower montane moist forest, primary vegetation, 20 March 2003, *F. Pupulin* 4446, *H. Léon-Páez* & *A.C. Rodríguez* (JBL-Spirit, USJ, drawings). Same locality: *F. Pupulin 4409, H. Léon-Páez* & *A.C. Rodríguez* (JBL-Spirit, USJ, drawings); San Vito de Coto Brus, Altamira de Biolley, Parque Internacional La Amistad, Sector Altamira, ca. 1500 m, bosque tropical nuboso, hábito epífito, 26 julio 2005, *G. Rojas 45* (JBL-spirit); Puntarenas: Coto Brus, Sabalito, Las Alturas de Cotón, Zona Protectora Las Tablas, Estación Biológica Las Alturas, camino al Cerro Chai, 8°59'00.9" N 82°50'01.5" W, 1650 m, bosque muy húmedo premontano, en bosque secundario a orillas del camino, 26 octubre 2005, *D. Bogarín* 2085, *R.L. Dressler, R. Gómez, F. Pupulin, A. y S. Rambelli* (JBL-Spirit); Same locality, *D. Bogarín 2102* (JBL-Spirit); Monteverde, 1400-1700 m, 18 October 1979, *C. Todzia 497* (CR). **San José**: Acosta, Bijagual, bosque tropical seco, vegetación secundaria madura, 135-200 m, 8 diciembre 2004, *R.A. Valverde 1460* (JBL-Spirit); San José: Aserrí, Salitrillos, márgenes del Río El Chiflón, cataratas El Chiflón, Lajas, camino hacia Tarbaca, 1650 m, floreció en agosto 2003 en el cultivo de la familia Valverde Arias, Desamparados, 29 setiembre 2002, *R.A. Valverde 572* (JBL-Spirit); San José: Aserrí, Distrito Central, Barrio Las Mercedes, Barrio Los Ángeles, floreció en agosto 2003 en cultivo de la familia Valverde Arias, Desamparados, 18 setiembre 2002, *R.A. Valverde 573* (JBL-Spirit);

Montes de Oca, San Pedro, Ciudad Universitaria Rodrigo Facio, Universidad de Costa Rica, cerca de la Biblioteca L. Demetrio Tinoco, 1200 m, 9°57'39"N 84°3'00" W, bosque húmedo premontano, epífitas en *Parmentiera* sp. (Bignoniaceae), 22 setiembre 2003, *D. Bogarín 425 & A. Rodríguez* (USJ, Drawings, Figure 43). Montes de Oca, San Pedro, Ciudad Universitaria Rodrigo Facio, Universidad de Costa Rica, 9°56'33"N 84°03'06" W, 1232 m, bosque húmedo premontano, epífita en zonas verdes sobre *Murraya paniculata* (Rutaceae), 8 setiembre 2004, *D. Bogarín 1006* & *A. L. Chacón* (JBL-Spirit, USJ, drawings). Puriscal, Santiago, cuadrante de la ciudad, en jardines de la iglesia antigua, 9°50'58.7"N 84°18'27.8" W, 1100 m, bosque muy húmedo premontano, epífitas en *Cupressus lusitanicus*, 12 diciembre 2004, *D. Bogarín 1101, A. Prendas* & *D. López Kikut* (CR); Tarrazú, San Lorenzo, camino de San Joaquín y Santa Marta, 9°35'15"N 84°59'10" W, 1300-1400 m, epífita, botones florales blancos, creciendo a orilla del camino, 22 agosto 1997, *A. Estrada 1143* & *O. Valverde* (CR).

Habitat. Plants have been found in disturbed or young secondary forest in shady vegetation in lower montane moist forest, premontane wet forest and premontane moist forest from 1000 to 1670 m of elevation. Common phorophytes of *C. schiedei* are: *Cupressus lusitanicus* (Cupressaceae), *Murraya paniculata* (Rutaceae), *Conostegia xalapensis* (Melastomataceae) and *Parmentiera* sp. (Bignoniaceae); however, it seems that no host-specificity occurs.

Eponymy. Dedicated to the German physician and botanist Christian Julius Wilhelm Schiede (1798-1836), who participated in the type collection.

Phenology. Plants have been recorded in flower from January to March and July to November.

Discussion. This species belongs to the section *Campylocentrum*. During the nineteenth century, A.R. Endrés was the first to collect *C. schiedei* (at that time still undescribed) in Costa Rica. It might be confused with *C. micranthum*, but the relatively small habit, the lax inflorescence often surpassing the leaf length (vs. congested and shorter than the leaves in *C. micranthum*), the lip with the mid-lobe twice larger than the lateral lobes (vs. three times larger) and the spur equally to scarcely larger than the blade of the lip (vs. distinctly larger) are useful features to distinguish this species. Also, its coriaceous leaves, and the lax inflorescence larger than the leaves, easily distinguish this species from *C. panamense*.

Campylocentrum acutum was published by Schlechter based on a plant collected in Santiago de San Ramón by A.M Brenes (*147*, isolectotype CR-18480) (Figure 21). According to Schlechter, this species is distinguished from *C. schiedei* by the loose flower clusters and other minor flower details.

The type of *Todaroa micrantha* matchs well the concept of *C. schiedei* and this name is treated here as synonym. Although the former name is earlier than *A. schiedei*, the name was based on the illegitimate *Todaroa* (see introduction).

9. ***Campylocentrum tenellum*** Todzia, Ann. Missouri Bot. Gard. 72(4): 877, f. 1. 1985. Type: Panama: Panama. La Eneida, region of Cerro Jefe, 26 Oct 1969, *R.L Dressler 3758* (holotype CR) (Figure 45, 46).

Plant epiphytic, pendent or ascending, with terete, slightly fractiflex, leafy stem to 5.5 cm long. ***Roots*** basal, flexuous, glabrous, up to 15 cm long, less than 1.5 mm in diameter, white to greenish, with green or orange-yellowish tips. ***Leaves*** many (to 24), distichous, linear-lanceolate to elliptic-oblong, acute, emarginate, green-orangish unequally 2-lobed at the apex, conduplicate, coriaceous, the margin denticulate or crenulate, articulate with the persistent sheath envolving the stem, to about 0.7-1 x 0.1-0.3 cm. ***Leaf sheath*** tubular, compressed, distinctly lacerate. ***Inflorescence*** a many-flowered (to 10) raceme usually larger than the leaves, produced along the stem, opposite to the leaves, the flowers distichously arranged on the rachis, minutely puberulent, about 1.4 cm long, the rachis 7-10 mm long, minutely puberulent; ***pedicel*** inconspicuous, less than 1 mm long; ***floral bracts*** concave, triangular, acuminate, ciliate, scarious. ***Ovary*** cylindric, less than 1 mm long, covered with sparsely minute trichomes. ***Flowers*** small, about 1.5 mm in length, disthichous, greenish or white-cream colored, the anther cap yellow. ***Dorsal sepal*** subequal to the lateral sepals, ovate-elliptic to oblong, subacute to rounded, outer surface pubescent, 2.1 x 1 mm. ***Lateral sepals*** ovate, acute, subfalcate, concave towards the base, outer surface densely pubescent, 2.5 x 1 mm. ***Petals*** elliptic-oblong, acute, outer surface densely pubescent, 1.8 x 0.7 mm. ***Lip*** 3-lobed,

the lateral lobes oblong, small, rounded at apex, less than 1 mm long, the midlobe triangular, acute, subequal to the lateral lobes, slightly conduplicate, concave, with a densely pubescent callous along the midrib, extended at the base into a cylindric, porrect, obscurely 3-lobed spur, basally wider and narrowing towards the apex, more or less continuous with the lip, about, subequal than the blade of the lip (to 2.8 mm long, 1.2 mm wide); entire lip up to 6 mm long including the spur, 2 mm wide between the lateral lobes. ***Column*** very short, to 1 mm long, with terminal anther. ***Pollinia*** 2, ovoid, on short, ligulate, hyaline stipe; viscidium elliptic. ***Anther cap*** subquadrate-cucullate, 2-celled. Capsule not seen.

Distribution. Known only from Costa Rica and Panama.

Additional material examined: COSTA RICA. **Cartago**: Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, 9°48'36.7"N 83°45'16.2"W, 1396 m, bosque pluvial montano bajo, epífita en ramitas de árboles aislados de *Psidium guajava* (Myrtaceae) en potreros, 24 noviembre 2008, *D. Bogarín 5844*, *R.L. Dressler, R. Gómez & R. Trejos* (JBL-Spirit, Figure 45); Jiménez, Pejibaye, Tausito, cerca del Río Tausito, 1.5 km antes de Tausito, 9°46'00.7"N 83°46'48.7"W, 1020 m, bosque pluvial premontano, epífita en *Citrus* sp. a orillas del camino, 16 octubre 2009, *D. Bogarín 7395 & A. Karremans* (JBL-Spirit). Límite entre Turrialba y Jiménez, La Suiza, Pejivalle, camino a Esperanza, en lomas cerca de la Quebrada Puente, 9°48'46.0"N 83°39'10.0" W, 738 m, bosque muy húmedo premontano, epífita en bosque secundario a la orilla de cañaverales, 28 agosto 2004, *D. Bogarín 960* & *J. Carmona* (USJ-drawings);

Limón: Pococí, Guápiles, Hacienda La Cuenca, 600-650 m, 10°08'78"N 83°46'46" W, 1-3 enero 2005, *M. Blanco* 2745, *A. Chávez, L. duToit* & *C. Ugalde* (USJ-drawings, Photo). **PANAMA**. Panama: El Llano-Carti Highway, 15-20 km N of El Llano, 30 Sept. 1973, *R.L Dressler* s.n. (paratype, CR).

Habitat. Plants grow in secondary disturbed vegetation, forest edges and twigs of cultivated trees like *Psidium guajava* in premontane tropical wet forest and lower montane rain forest along the Caribbean watershed of Talamanca range from 600 to 1400 m of elevation.

Etymology. From the Latin *tenellus*, "delicate", in reference to the small and delicate habit of this species.

Phenology. Plants have been recorded in flower from October to December.

Discussion. *Campylocentrum tenellum* is easily recognized by its lacerate leaf sheaths and the small plant size. Other distinguishing features include the linear-elliptic leaves, the spur wider at base and narrowing towards the apex, the pubescent upper surface of sepals and the conspicuous pubescent callus.

This species was first collected by Robert L. Dressler in region of Cerro Jefe in Central Panama, in 1969. When described the species, Todzia (1985) mentioned the straight, acute spur, the thin lanceolate leaves and the small size of the plant as useful features to separate this species from *C. parvulum* (=*C. brenesii*). Otherwise, both *C. brenesii* and *C. tenellum* are vegetatively similar in plant size, but *C. brenesii* lacks the leaf sheath lacerations of *C. tenellum*. The illustration published in

the protologue of *C. tenellum* is somewhat schematic and does not represent accurately the critical characters of the species, like the lip shape and the lacerate margin of the leaf sheaths. However, direct examination of the type plant and rehydrated flowers from the holotype (*R.L Dressler 3758*, CR) leaves no doubt about the identity of Costa Rican gatherings (Figure 47).

The vegetative characters such as the lacerate leaf sheaths and the linear leaves are enough to recognize *C. tenellum* even when sterile. The collections cited here as *D. Bogarín 960 & J. Carmona* (USJ-drawings) and *M. Blanco 2745* (USJ-drawings, Photo) are in sterile condition, but both plants are unmistakable by their leaf sheaths lacerations. Fortunately, the collection *D. Bogarín 5844* (JBL-Spirit, Figure 45) allowed the documentation of this species in fertile condition. This is the first flowering record of this species in Costa Rica.

EXCLUDED SPECIES

Campylocentrum dressleri H. Dietr. & M.A. Díaz, Die Orchidee (Hamburg) 35(1): 28. 1984. Type: Panama. Darién: margins of the Tschkonake river, 5 km W of Yavisa, tropical rain forest, April 1980, flowering in cultivation in Jardín Botánico Nacional de Cuba, May 1983, *J. Bisse, A. Álvarez & A. Díaz s.n. sub H. Dietrich s.n.* (holotype, HAJB).

Pupulin (2002) cited *C. dressleri*, based on a plant collected in Buenos Aires de Puntarenas by *J. Villalobos s.n.* (USJ). A careful examination of this specimen revealed that it better corresponds to *C. multiflorum* (see discussion of *C.*

multiflorum). *Campylocentrum dressleri* has been described from Panama and its main feature is the cochleiform unlobed lip (Dietrich & Díaz 1984). This feature has not been observed in the material examined from Costa Rica.

Campylocentrum pachyrrhizum (Rchb.f.) Rolfe, Orchid Rev. 11: 246. 1903. Type: Cuba. *Wright 3207* (holotype, W; illustration of type, W; illustration of type, K).

The species has been listed by Mora-Retana & García (1992) and Dressler (1993b) but without citing a specific voucher. The material studied from El General Valley in the Pacific watershed of Talamanca in Costa Rica proved to be a different species.

Campylocentrum tyrridion Garay & Dunsterv. ex Foldats, Flora of Venezuela 15, 5: 441. 1970.

Bas.: *Campylocentrum tyrridion* Garay & Dunsterv., Venez. Orchid. Ill. 2: 54-55. 1961.

Type: Venezuela. Miranda: "cerca de Higuerote" (holotype, AMES).

This species has been attributed to Costa Rica by Pupulin (2002), Dressler (2003) and Romero & Carnevali (2005). However, all the vouchers cited by the former authors are *C. multiflorum*. Having priority, the name *C. multiflorum* should be applied for the Costa Rican Pacific leafless species, leaving the name *C. tyrridion* for the Venezuelan species.

CONCLUSIONS

1. *Campylocentrum brenesii* is accepted, while *C. longicalcaratum* and *C. parvulus* are maintained under synonymy of that name. Todzia (1980) and Dressler (1993) accepted both as distinct species, using the relative length of leaves, inflorescences and lip spur to separate between the three species. However, that set of features proved to be variable. Pupulin (2002) reduced *C. longicalcaratum* and *C. parvulum* under *C. brenesii*, an idea later supported by Dressler (2003). According to art. *11.5.* of the Code of Botanical Nomenclature*,* when, for any taxon, a choice is possible between legitimate names of equal priority in the corresponding rank (*C. brenesii* and *C. parvulum* have equal priority since they were described by Schlechter (1923b) in the same publication), the first such choice to be effectively published establishes the priority of the chosen name (see, in particular, *Ex. 20.*). As *C. brenesii* has been previously chosen against *C. parvulum* by Pupulin (2002) and Dressler (2003), this name is accordingly treated as having priority over *C. parvulum.*

2. *Campylocentrum fasciola* is accepted. It is distinguished by the spur narrow at the base and wide at apex with three longitudinal keels along it. *Campylocentrum lankesteri* is here considered conspecific with *C. fasciola*. This species is restricted to the lowlands of the Caribbean watershed.

3. *Campylocentrum multiflorum* is accepted. It differs from *C. fasciola*, its Caribbean counterpart, by the spur wider at the base and progressively narrowing to the apex, without longitudinal keels (vs. spur narrow at the base and wider at the apex, with

conspicuously longitudinal keels in *C. fasciola*), the midlobe of the lip acute (vs. truncate) and the sepals acute or rounded (vs. cuspidate). Moreover, both species are clearly isolated geographically. *Campylocentrum fasciola* is restricted to the lowlands of the Caribbean watershed and *C. multiflorum* is only found along the Pacific watershed, ranging from Cerro Turrubares, in Central Pacific (the type locality of *C. multiflorum*) to the south. Whilst the taxonomy of the Caribbean *C. fasciola* provokes no discussion, the identity of the leafless *Campylocentrum* from the Pacific lowlands is still debatable. If the two species are distinct, *C. multiflorum* should be the correct name for the Costa Rican Pacific leafless species, while the name *C. tyrridion* should be applied to the species from Venezuela. In the case they will prove to be conspecific, *C. multiflorum* has nomenclatural priority.

4. The Costa Rican voucher of *C. dressleri*, *J. Villalobos* s.n. (USJ) clearly correspond to *C. multiflorum,* so *C. dressleri* is excluded from Costa Rica.

5. *Campylocentrum panamense*, closely allied to *C. micranthum* is clearly distinct by the subcoriaceous leaves, the spathulate sepals and petals, the spur shorter than the length of the lip's blade and the lax inflorescence. After its first record from Costa Rica, this species is now known by several other collections.

6. *Campylocentrum poeppigii* was first recorded in Costa Rica by Horich (1980). It is easily distinguished by the elongate stems with rudimentary, caducous, tiny and narrowly conical scale-leaves. This feature has been used to classify this species under the Section *Pseudocampylocentrum* by Cogniaux (1906) in *Flora Brasiliensis*.

7. *Campylocentrum schiedei* is distinguished by the lax inflorescences often surpassing the length of the leaves. Geographically, *C. schiedei* grows from 1000 to 1500 m of elevation, contrasting with *C. micranthum* and *C. panamense*, which grow in lowlands up to 900 m of elevation.

8. *Campylocentrum tenellum* Todzia, is recorded for a first time in Costa Rica. This species was described from Panama by Todzia (1985). Two specimens of *C. tenellum* from different localities in Costa Rica are known, but unfortunately they never flowered. As noted by Todzia (1985) the vegetative features such as the lacerate leaf sheaths and the linear leaves are enough to recognize this species in sterile condition.

9. An aphyllous species with flat roots has been recorded from El General Valley in the Pacific watershed of Talamanca range. Although *C. pachyrrhizum* is expected to occur in Costa Rica, the material collected suggests that it may correspond to an undescribed species. Specimens from Antilles and Venezuela have a downward curved spur and lax inflorescenses, while the Costa Rican record has an upward curved spur and congested inflorescences. This species is apparently rare and constitutes another new record for Costa Rica.

10. As the types of *C. parvulum* and *C. multiflorum* were destroyed in Dahlem-Berlin in the Second World War the two species need to be lectotipifyed.

LIST OF SPECIES OF *CAMPYLOCENTRUM* IN COSTA RICA

1. *Campylocentrum brenesii* Schltr.
2. *Campylocentrum fasciola* (Lindl.) Cogn.
3. *Campylocentrum generalense* Bogarín & Pupulin
4. *Campylocentrum micranthum* (Lindl.) Maury
5. *Campylocentrum multiflorum* Schltr.
6. *Campylocentrum panamense* Ames
7. *Campylocentrum poeppigii* (Rchb.f.) Rolfe
8. *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsl.
9. *Campylocentrum tenellum* Todzia

INDEX TO EXSICCATAE AND SPIRIT-PRESERVED SPECIMENS

Numbers in parentheses refer to the species number in the treatment. Type specimens in boldface.

Aguilar 4257 (4).

Bello 929 (1); *Bello 2259* (1); *Bello 2381* (6).

Bello 2763, Cruz & *Cruz* (1).

Blanco 2745, Chávez, duToit & Ugalde (9).

Bogarín 436 (1); *494* (8); *2102* (8); ***2130* (3)**; *4481* (2).

Bogarín & *Blanco 1164* (1); *1165* (1); *1166* (1).

Bogarín 379, *Blanco* & *Whitten* (1); *380* (1).

Bogarín 1036 & *Botánica Forestal-UCR* (4).

Bogarín 953 & *Carmona* (1); *952* (1); *954* (6); *960* (9).

Bogarín 1484, Castelfranco, Pupulin & Rodríguez (5); *1844* (4).

Bogarín 1372 & *Cervantes* (8); *1376* (8).

Bogarín 1006 & *Chacón* (8).

Bogarín 1272, *Chaves & Bogarín* (4); *1263* (4); *1276* (4).

Bogarín 4149, *Dressler, Gamboa, Russell & Samuel* (8).

Bogarín 1834, *Dressler, Gei, Gómez & Rojas* (8).

Bogarín 2085, *Dressler, Gómez, Pupulin & Rambelli* (8).

Bogarín 5417, *Dressler, Gómez, Pupulin, & Trejos* (1); *5496* (8)

Bogarín 5844, Dressler, Gómez & Trejos (9); *5845* (1); 6363 (1).

Bogarín 4245, *Dressler, Karremans, Russell & Samuel* (2).

Bogarín 4532, Gaillard, Gómez, Kisel, Phillips & Trejos (8).

Bogarín 6256, Gómez & Trejos (1).

Bogarín 4051 & *Karremans* (2).

Bogarín 7359 & *Karremans* (9).

Bogarín 7398 & *Karremans* (1).

Bogarín 963, Karremans, León-Páez & *Pupulin* (4); *697* (4).

Bogarín 1119, Karremans, & *Prendas* (2); *1120* (2).

Bogarín 311, Kikut & *Prendas* (8).

Bogarín 921, León-Páez & *Hoppe* (1).

Bogarín 725, León-Páez, Pupulin & *Salas* (6); 755 (1).

Bogarín 1101, Prendas & *López Kikut* (8).

Bogarín 871 & *Pupulin* (6); *6223* (1).

Bogarín 1292, Pupulin, Salas & *Seaton* (1).

Bogarín 2218, Pupulin & *Vargas* (7); *2220* (2).

Bogarín et al. 1485 (5); *1486* (5).

Boyle 1090 (1).

***Brade & Brade 1294* (1); *1316* (5).**

***Brenes 127* (1); *147* (8)**; *s.n.* (5); *s.n.* (5); *s.n.* (8); *s.n.* (8).

Cascante 1945 (1).

Dressler 3758 **(9);** *Dressler 6172* (8); *Dressler 6850* (5); *Dressler s.n.* (9).

Ehrenberg & Leibold s.n. **(8).**

Estrada 1143 & *Valverde* (8).

Galeotti s.n. **(8).**

Hammel 17942 (4).

Hayes 988 **(6).**

Herrera 941 (8).

Horich s.n. (7).

Lankester 71 **(1);** ***1013*** **(1).**

Lent s.n. (1).

Loddiges s.n. **(4).**

Marín 283 (4).

Ossenbach 336 (2); *s.n.* (4)

Poeppig s.n. (7).

Powell 184 (4).

Pupulin 332 (4).

Pupulin 5638, Bogarín & Rodríguez (5).

Pupulin 307 & *Castelfranco* (6).

Pupulin 1029, Castelfranco & Spadari (5); *1030* (5).

Pupulin 4409, Léon-Páez & *Rodríguez* (8); *4446* (8).

Pupulin 5086 & Salas (1); *5088* (1).

Richardson 203 (4).

Rojas 26 (8); *45* (8).

***Schomburgk s.n.* (2).**

Serrano 137 & *Blanco* (4).

Serrano 411 & *Salazar* (8).

Todzia 183 (4); *219* (5); *497* (8); *624* (1).

Utley s.n. (1).

Valerio s.n. (5).

Valverde 1460 (8); *572* (8); *573* (8).

Villalobos s.n. (5).

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Fig. 1. Distribution map of *Campylocentrum*

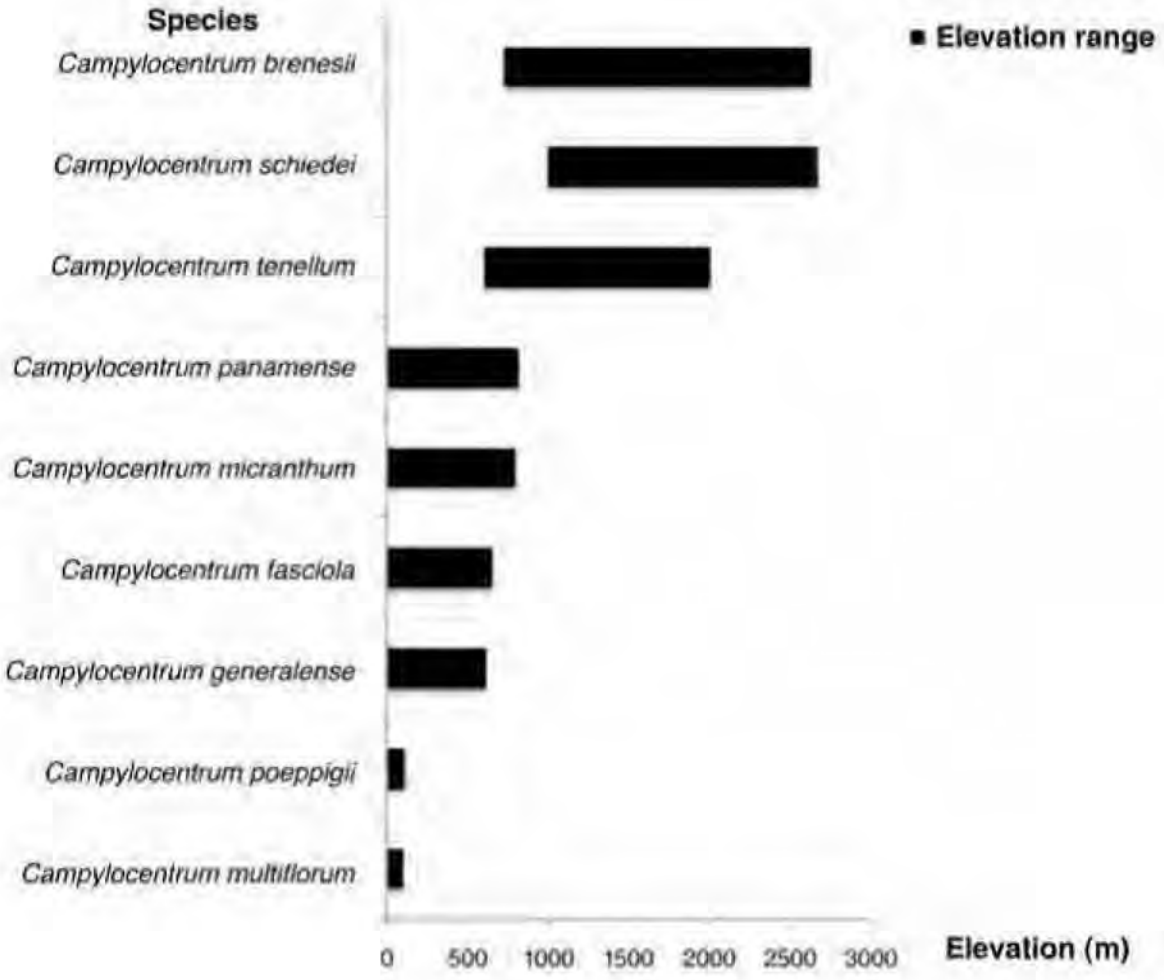

Fig. 2. Elevation range of the species of *Campylocentrum* in Costa Rica calculated with the data available in this study. Vertical axis = taxa; horizontal axis = elevation in meters above sea level

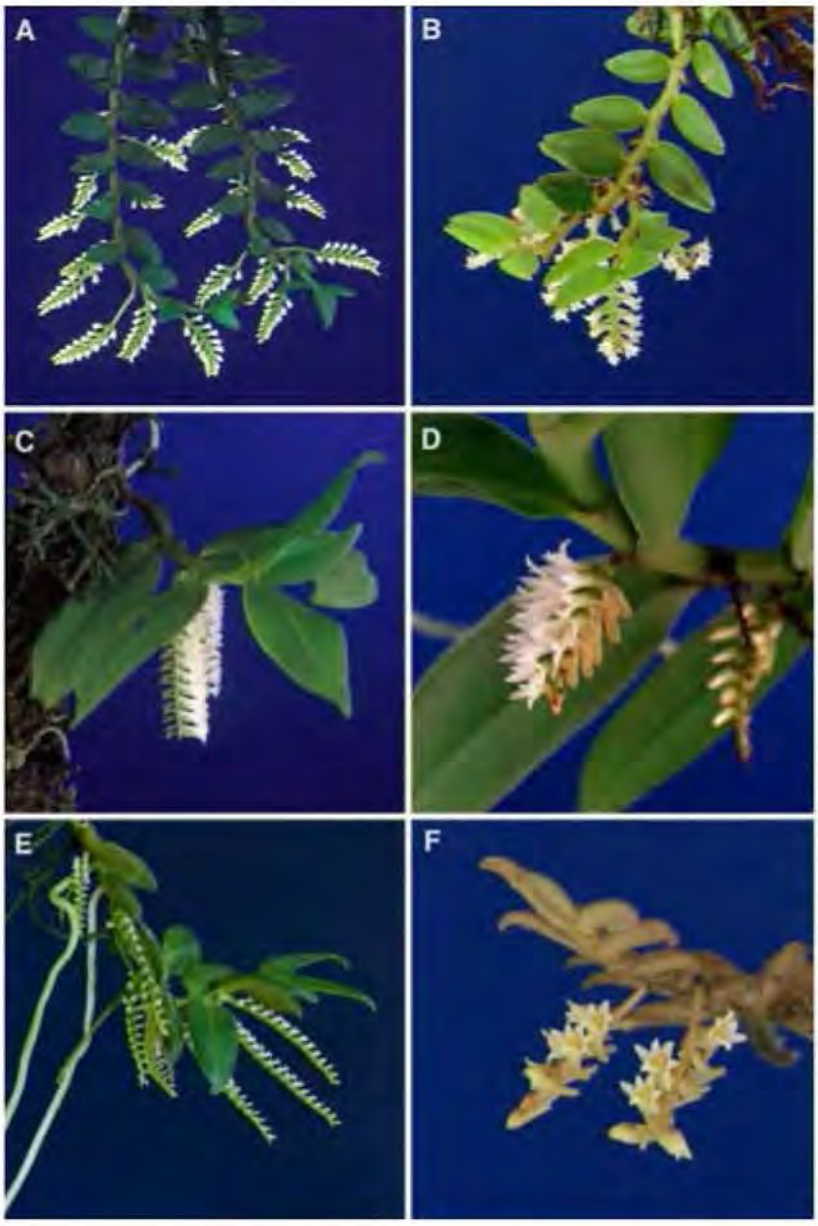

Fig. 3. Plant morphology in Costa Rican leafy *Campylocentrum*. A — *C. brenesii* (*Bogarín 1292*). B — *C. brenesii (Pupulin 3200*). C — *C. panamense* (*Bogarín 725*). D — *C. micranthum* (*Castelfranco s.n.*). E — *C. schiedei* (*Serrano 411*). F — *C. tenellum* (*Bogarín 5844*). Photo: A, B, D by F. Pupulin; C, E, F by D. Bogarín.

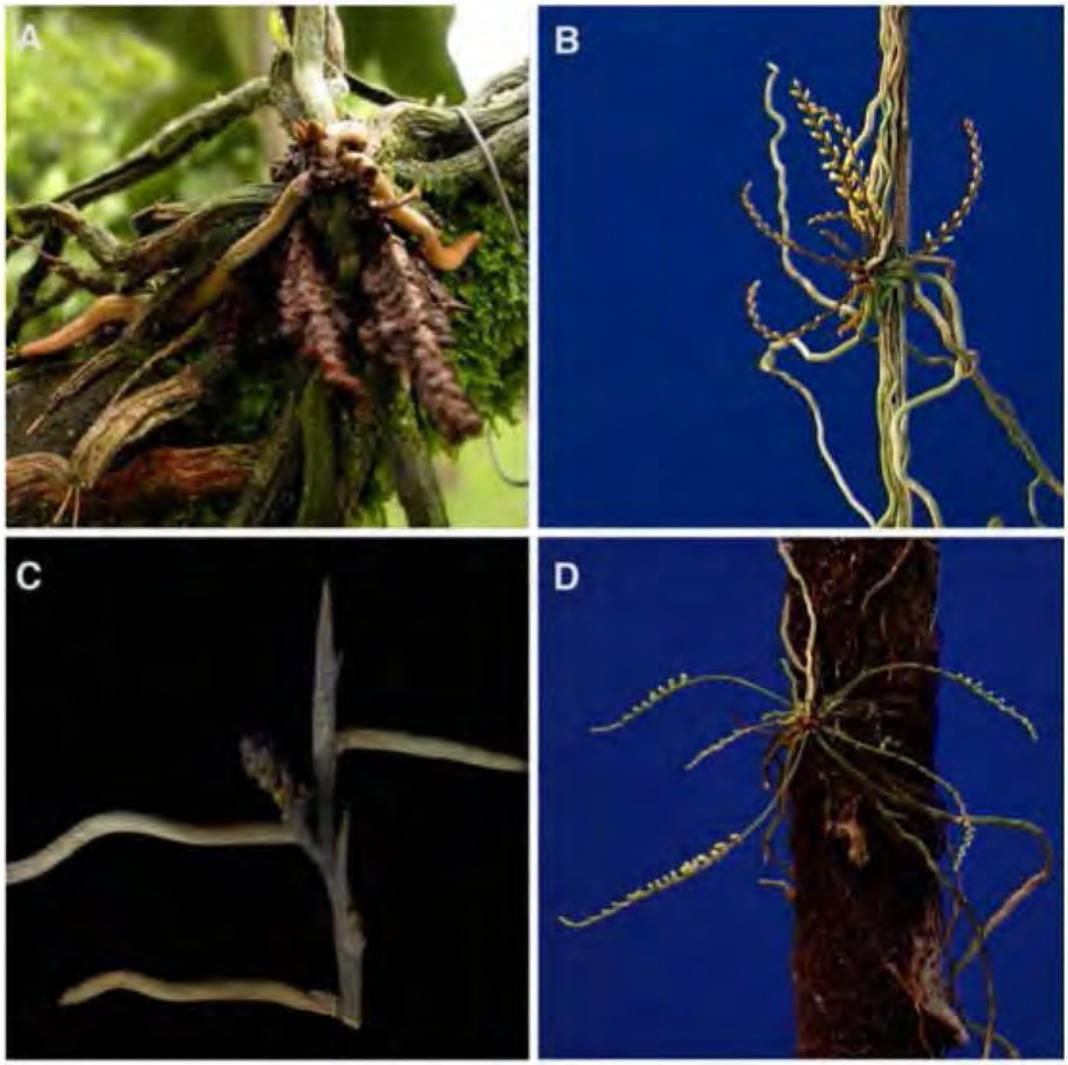

Fig. 4. Plant morphology in Costa Rican leafless *Campylocentrum*. A — *C. generalense* (*Bogarín 2130*). B — *C. fasciola (Ossenbach s.n.*). C — *C. multiflorum* (*Pupulin 1029*). Photo by F. Pupulin.

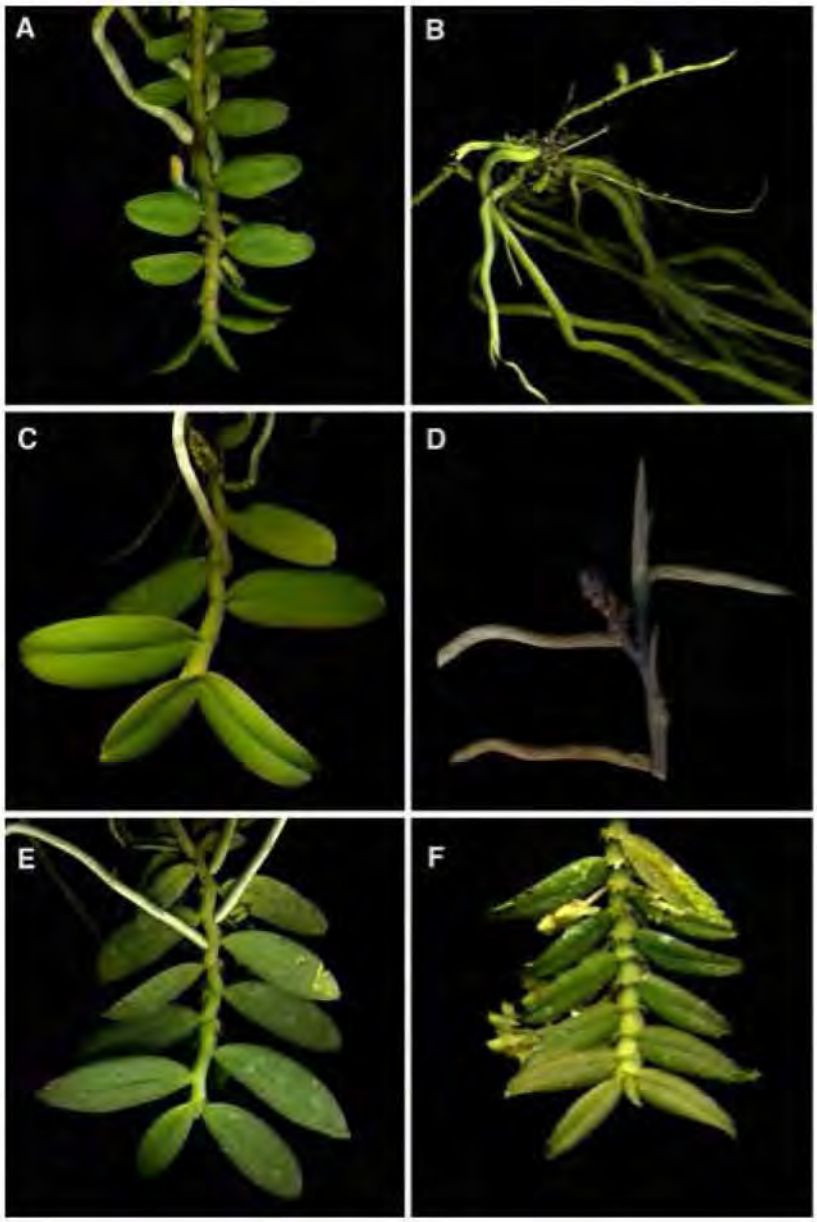

Fig. 5. Stems in Costa Rican *Campylocentrum*. A — *C. brenesii* (*Bogarín 6488*). B — *C. fasciola* (*Bogarín 4481*). C — *C. micranthum* (*Pupulin 4809*). D — *C. poeppigii* (*Bogarín 2218*). E — *C. schiedei* (*Bogarín 2085*). F — *C. tenellum* (*Bogarín 7395*).

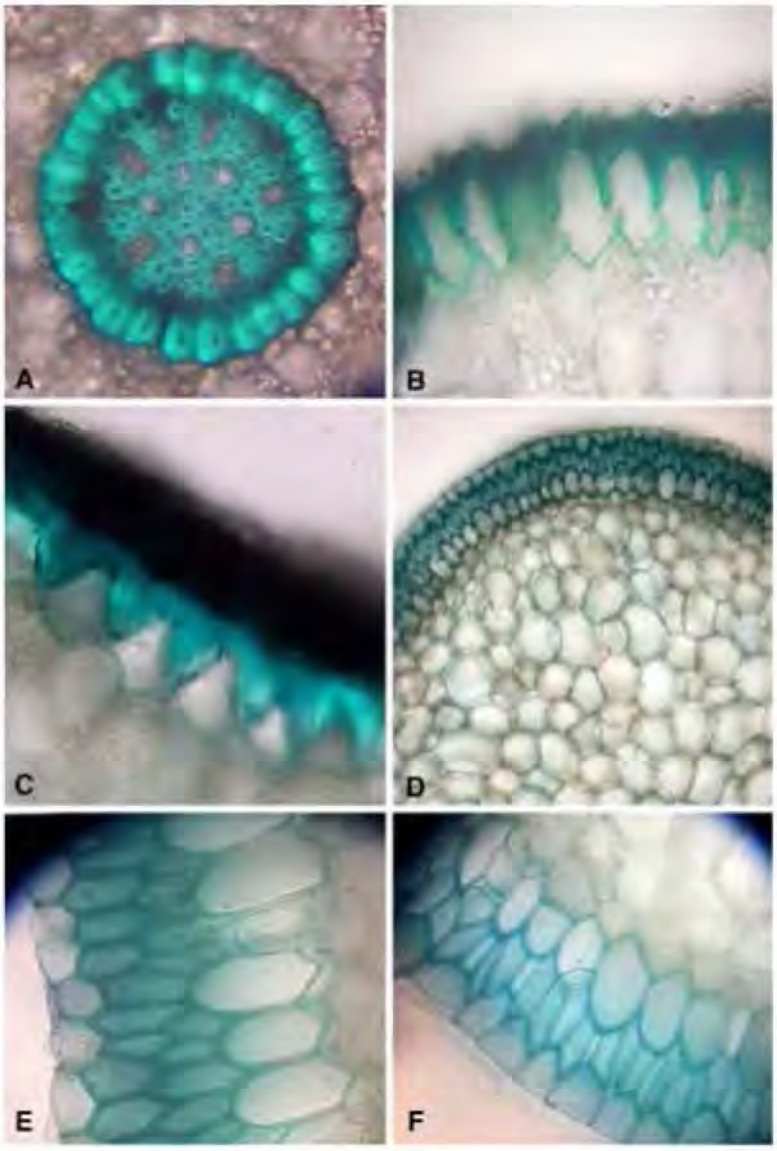

Fig. 6. Root transverse section (TS) using light micrograph showing: A — Endodermis (En) of *C. fasciola* (*Bogarín 4481*). B — Exodermis (Ex) in *C. multiflorum* (*Pupulin 5638*). C — Velamen and exodermis (Ex) in *C. generalense* (*Bogarín 2130*). D — Velamen cell layers (V), exodermis (Ex) and parenchyma (P) in *C. panamense* (*Bogarín 725*) E — Velamen (V) and exodermis (Ex) in *C. panamense* (*Bogarín 725*). F. Velamen (V) and exodermis (Ex) in *C. schiedei* (*Bogarín 2085*)

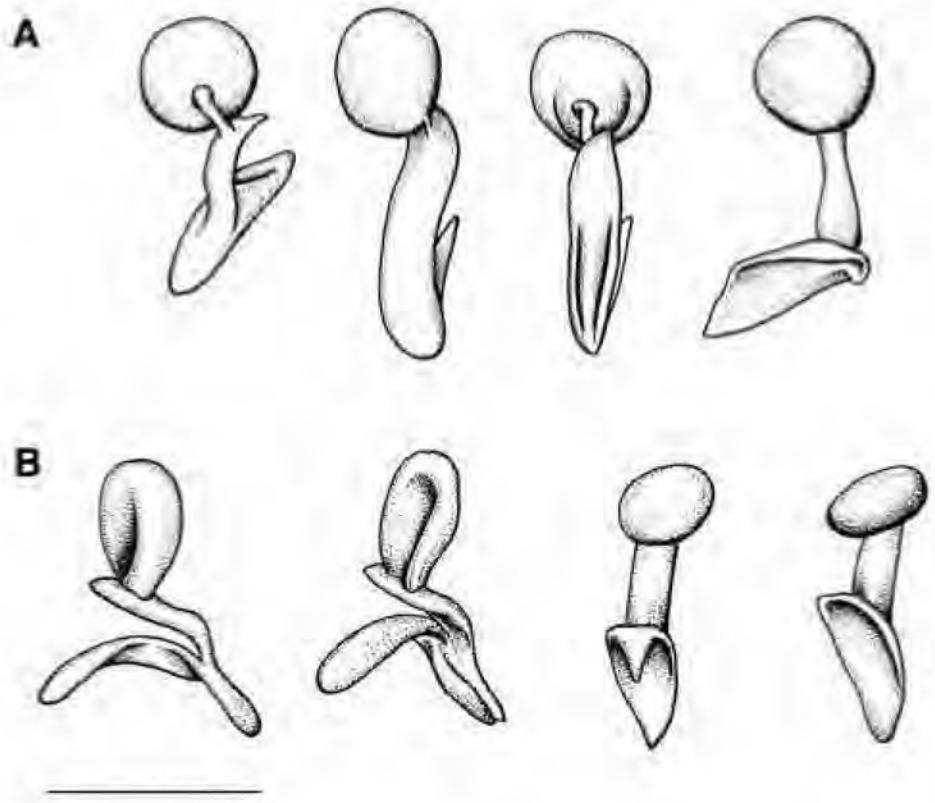

Fig. 7. Hemipollinarium of: A — *C. micranthum* (*Pupulin 4809*). B — *C. tenellum* (*Bogarín 7395*). Scale bar = 1 mm

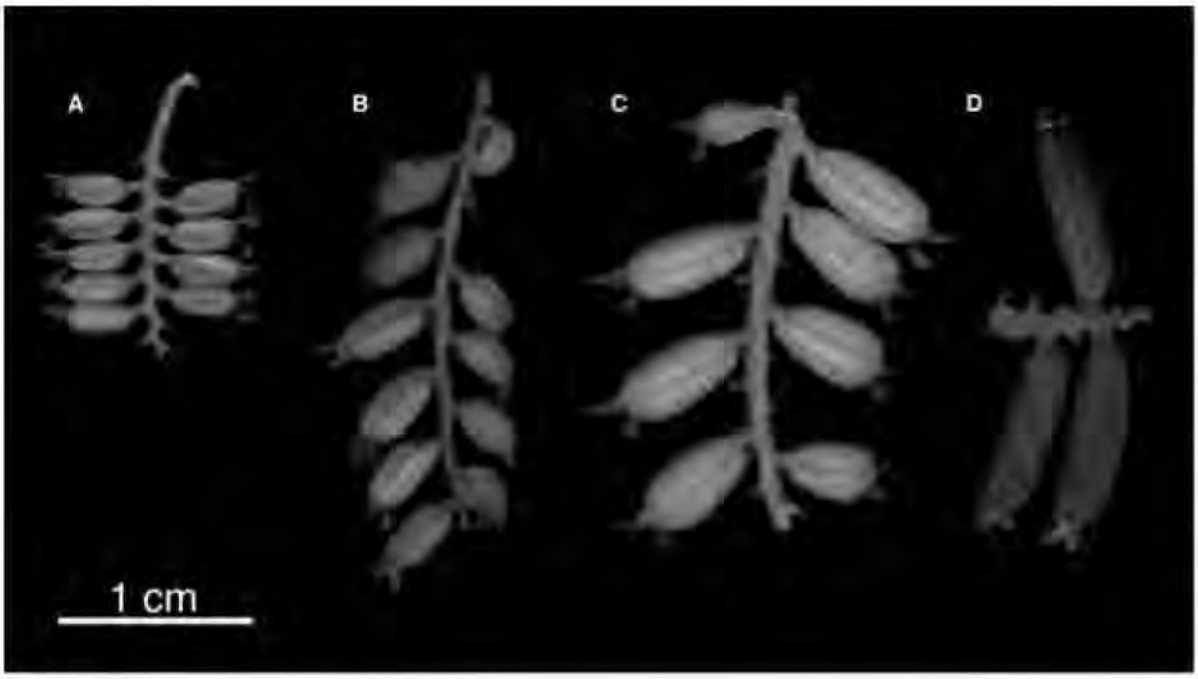

Fig. 8. Fruit morphology in *Campylocentrum*. A — *C. brenesii* (*Bogarín 6488*). B — *C. fasciola* (*Bogarín 4481*). C — *C. schiedei* (*Bogarín 2085*). D — *C. poeppigii* (*Bogarín 2218*).

Fig. 9. A specimen of *C. brenesii* (*Bogarín 6488*) bearing infructescences and developing new inflorescences

Fig. 10. Photo of the type specimen of *Angraecum micranthum* Lindl. (Kew-Lindley Orchid Herbarium, K000079739, K000079738). Reproduced with the kind permission of the Board of Trustees of the Royal Botanic Gardens, Kew.

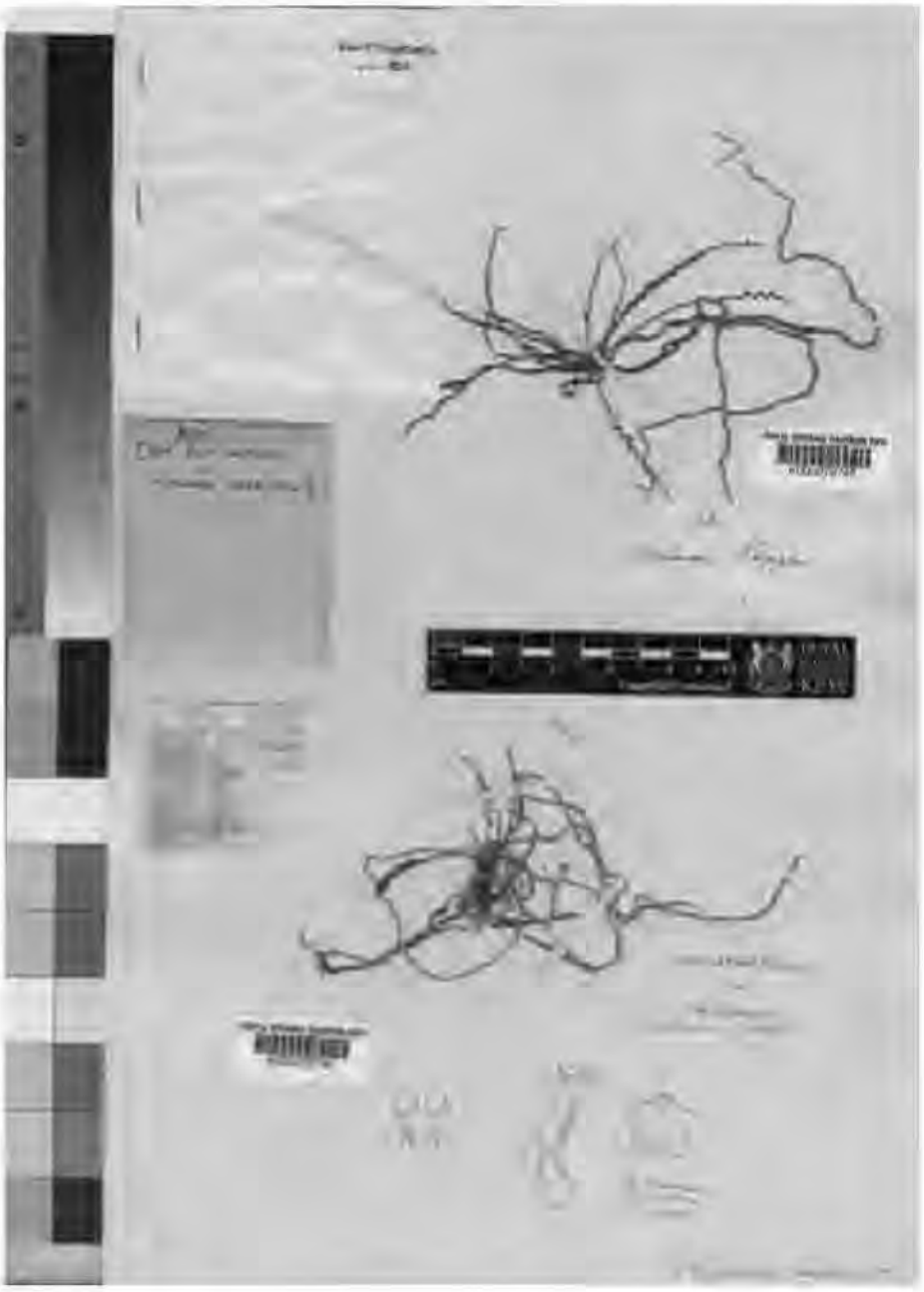

Fig. 11. Photo of the type specimen of *Angraecum fasciola* Lindl. (Kew-Lindley Orchid Herbarium, K000079746). Reproduced with the kind permission of the Board of Trustees of the Royal Botanic Gardens, Kew.

Fig. 12. Tracing of the type specimen of *Todaroa micrantha* A. Rich. & Galeotti (Kew-Lindley Orchid Herbarium, K000079743). Reproduced with the kind permission of the Board of Trustees of the Royal Botanic Gardens, Kew.

Fig. 13. Tracing of the type specimen of *Todaroa micrantha* A. Rich. & Galeotti. (Reichenbach Herb. Orchid. Vienna, W-R 21249). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

Fig. 14. Photo of the type specimen of *Angraecum schiedei* Rchb.f. (Reichenbach Herbarium-W, W-R 23671). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

Fig. 15. Photo of a specimen of *C. schiedei* collected by A.R. Endrés ostensibly between 1867 and 1871 (Reichenbach Herbarium-W, W-R 18852). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

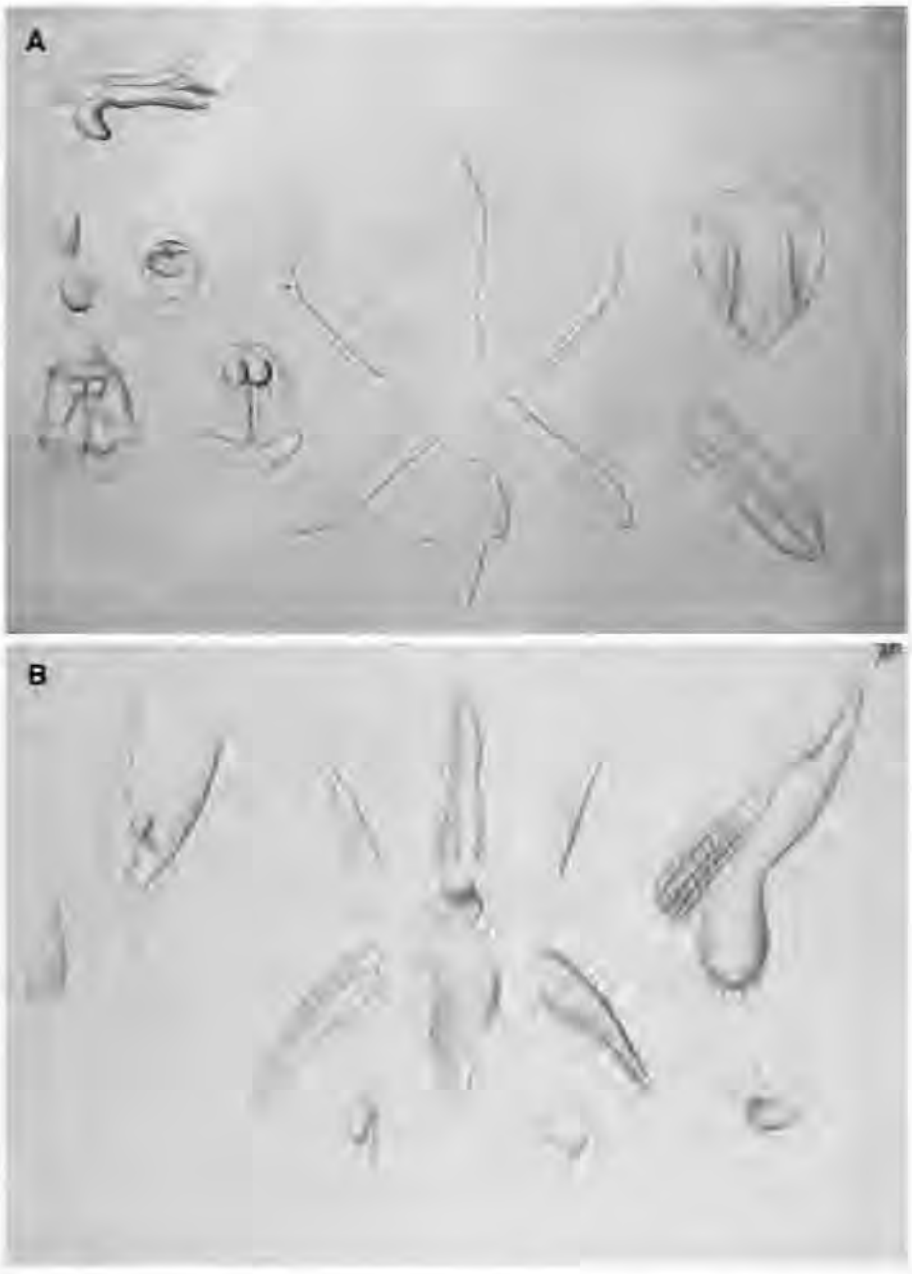

Fig. 16. Drawings of two specimens of *C. brenesii* by A.R. Endrés ostensibly collected between 1867 and 1871, Reichenbach Herbarium. A —W-R 18850; B —W-R 18851. Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

Fig. 17. Tracing of the type specimen of *Aeranthus pachyrrhizus* Rchb.f. (Reichenbach Herb. Orchid. Vienna, W-R 22290). Reproduced with the kind permission of the Herbarium, Naturhistorisches Museum, Wien.

Fig. 18. Tracing of the type specimen of *Campylocentrum multiflorum* Schltr. (AMES-106462). Reproduced with the kind permission of the Director, Harvard University Herbaria.

Fig. 19. Tracing and photograph of the type specimen of *Campylocentrum parvulum* Schltr. (AMES-106464). Reproduced with the kind permission of the Director, Harvard University Herbaria.

Fig. 20. Photo of the holotype of *Campylocentrum lankesteri* Ames (Kew Orchid Herbarium, K0000463303). Reproduced with the kind permission of the Board of Trustees of the Royal Botanic Gardens, Kew

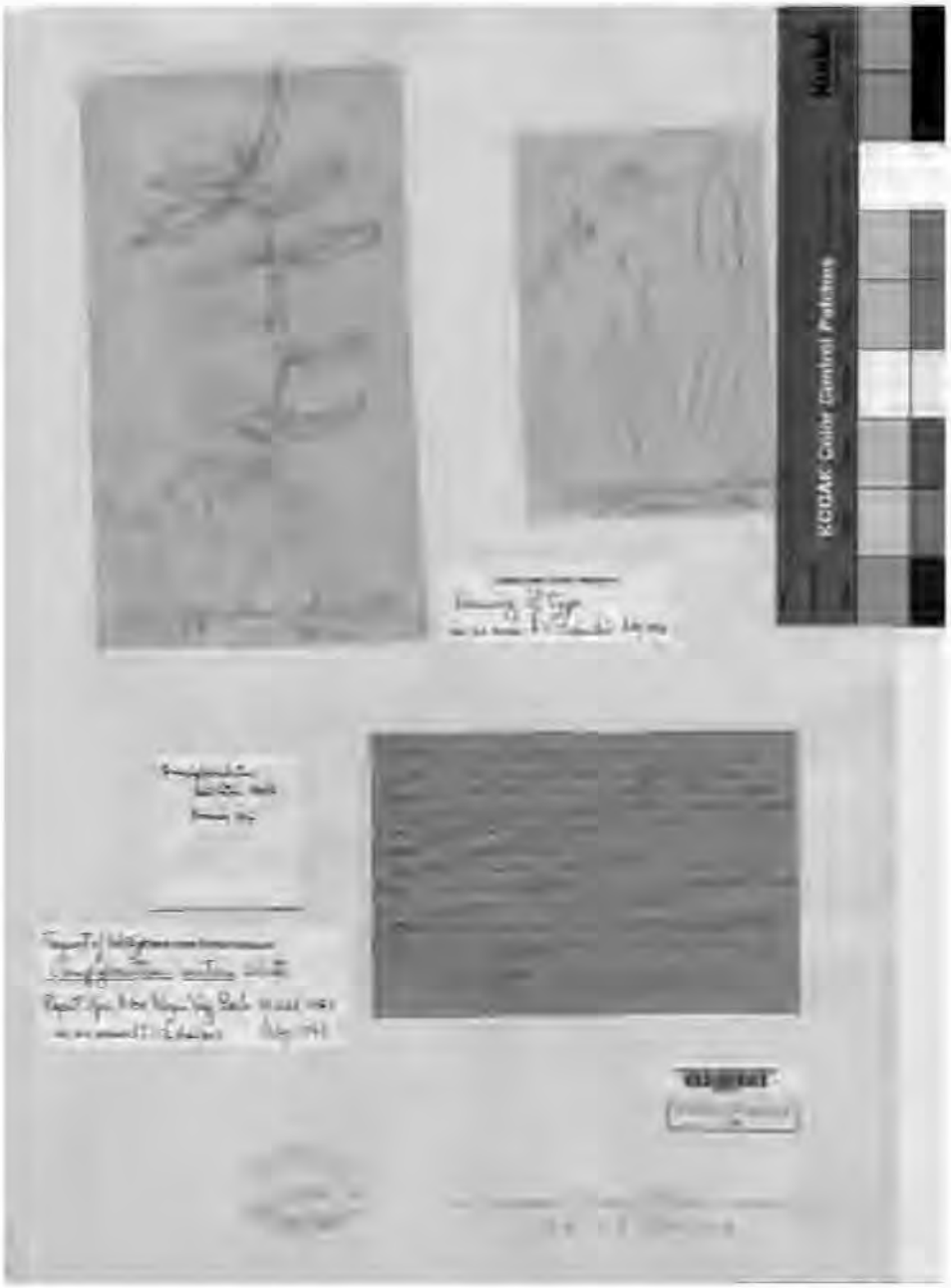

Fig. 21. Tracing of the type specimen of *Campylocentrum acutum* Schltr. (AMES-106451). Reproduced with the kind permission of the Director, Harvard University Herbaria.

Fig. 22. Photo of the isotype of *Campylocentrum brenesii* Schltr. (AMES-106453). Reproduced with the kind permission of the Director, Harvard University Herbaria.

Fig. 23. Photo of the holotype of *Campylocentrum longicalcaratum* Schltr. (AMES-106459). Reproduced with the kind permission of the Director, Harvard University Herbaria

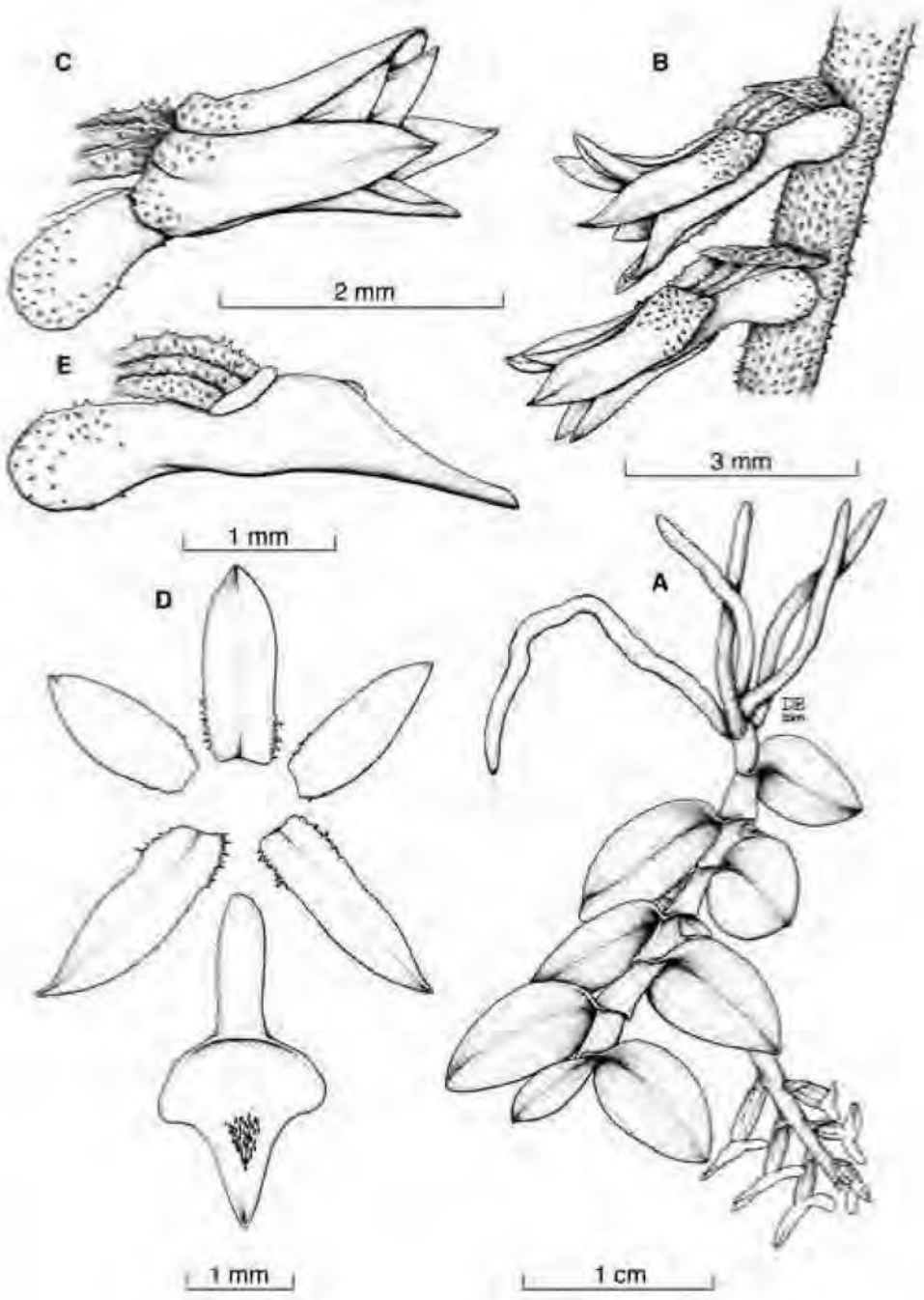

Fig. 24. *Campylocentrum brenesii* Schltr. A — Habit. B — Segment of the inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 436* (JBL-Spirit).

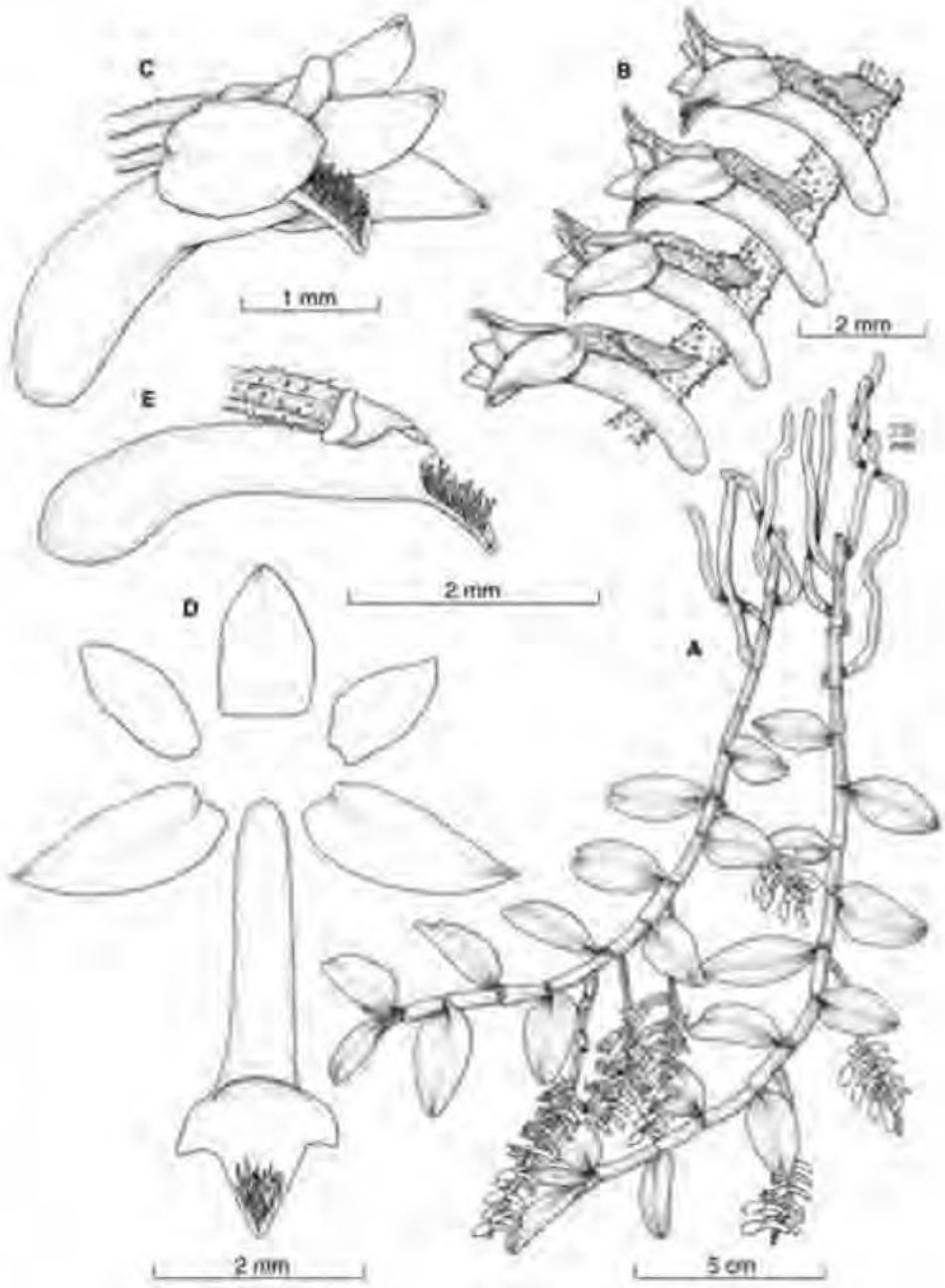

Fig. 25. *Campylocentrum brenesii* Schltr. A — Habit. B — Segment of the inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 1164* (JBL-Spirit).

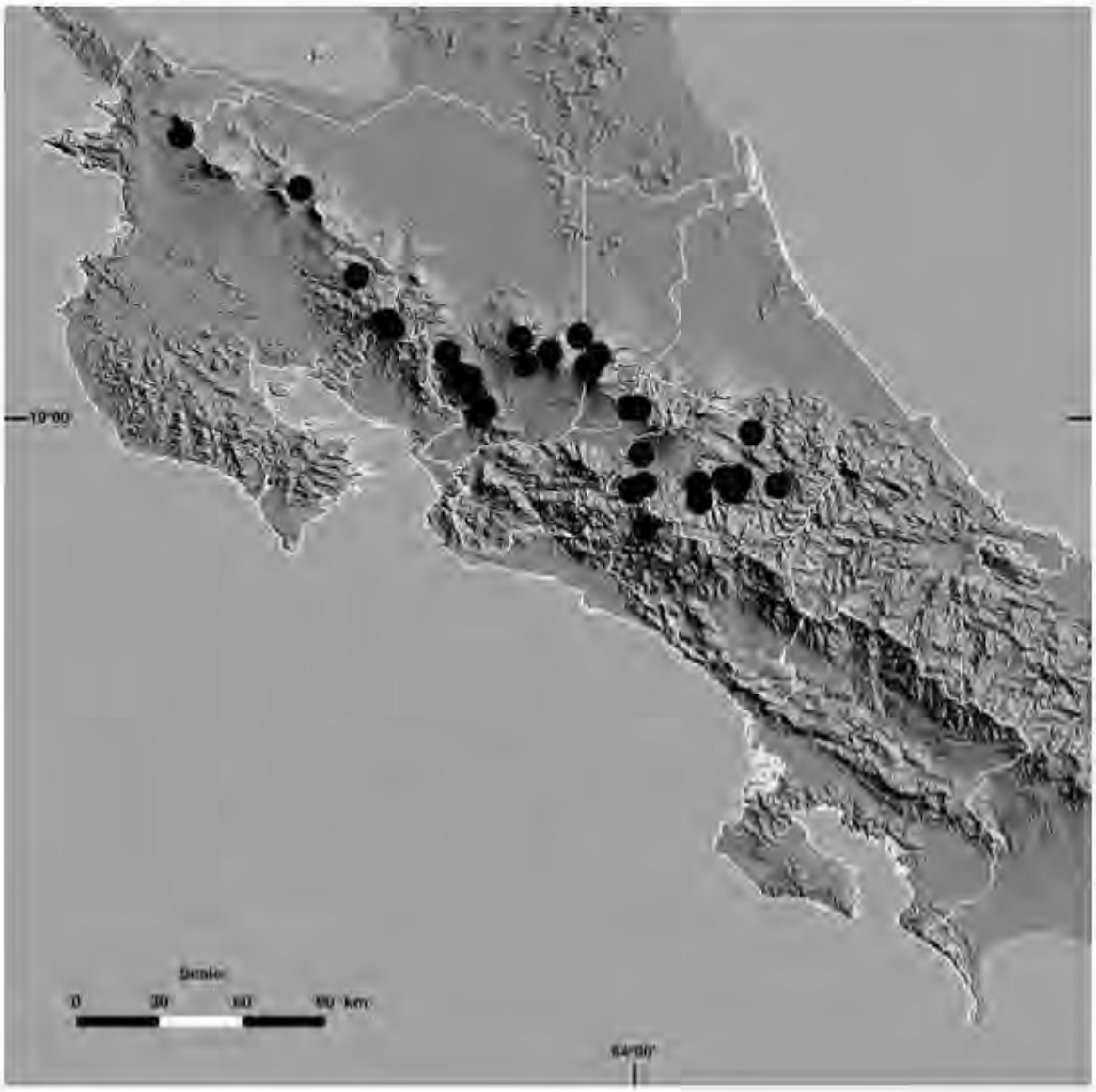

Fig. 26. Distribution map of *C. brenesii* in Costa Rica.

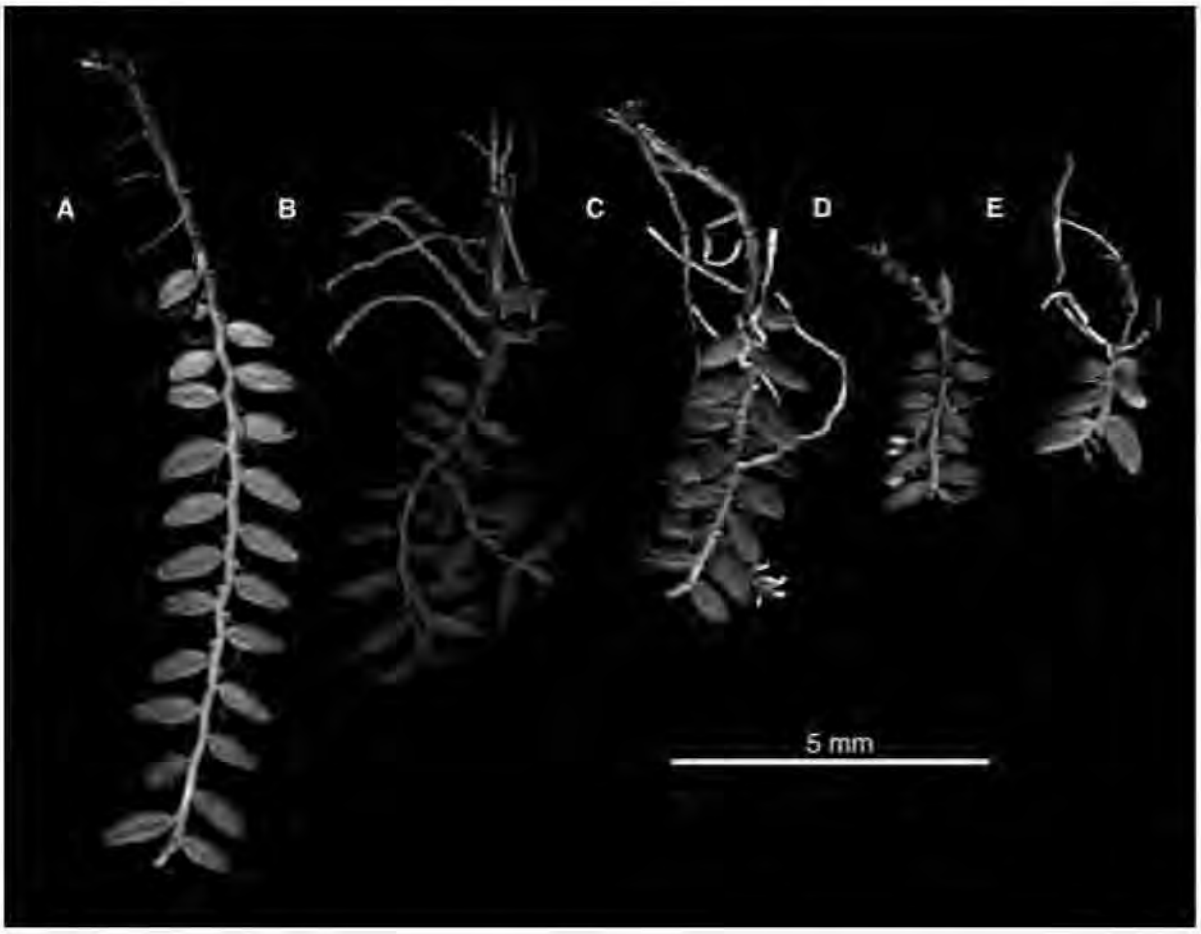

Fig. 27. Morphologic variation in *C. brenesii*: A — *Pupulin 6053*. B- *Karremans 1329* . C —*Bogarín 755*. D — *Bogarín 5408*. E — *Bogarín 5845*.

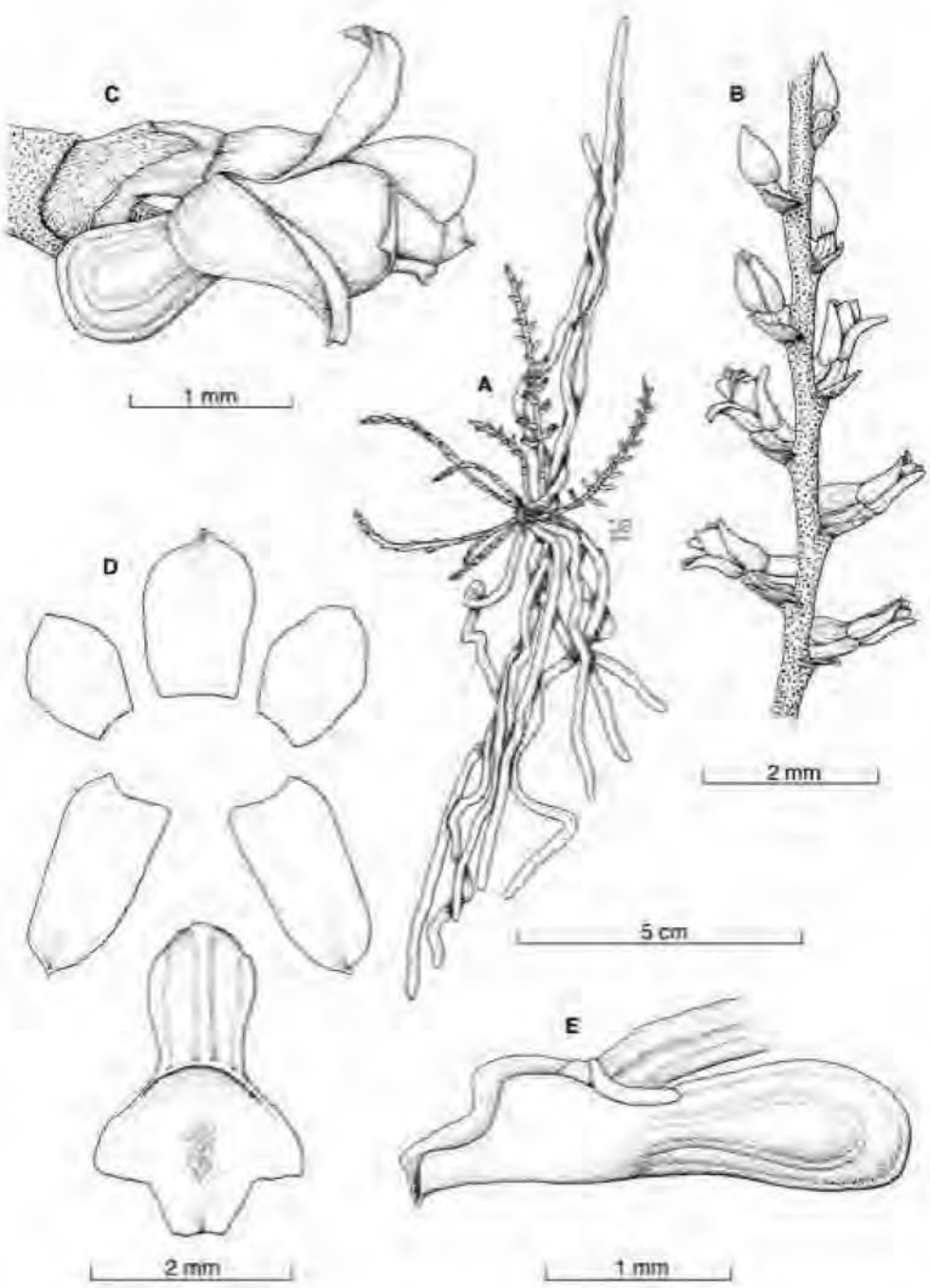

Fig. 28. *Campylocentrum fasciola* (Lindl.) Cogn. A — Habit. B —Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *C. Ossenbach 336* (JBL-Spirit).

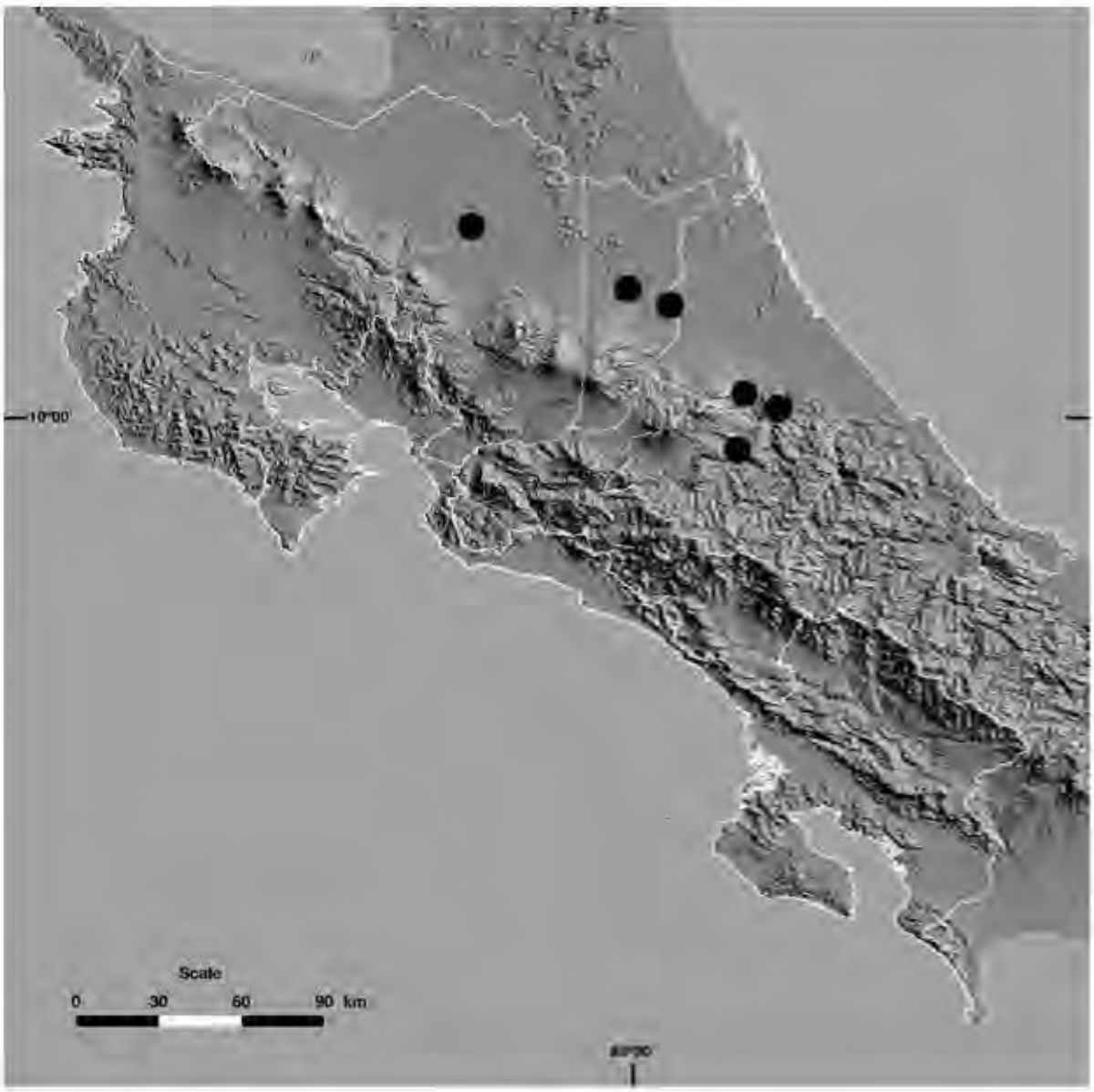

Fig. 29. Distribution map of *C. fasciola* in Costa Rica

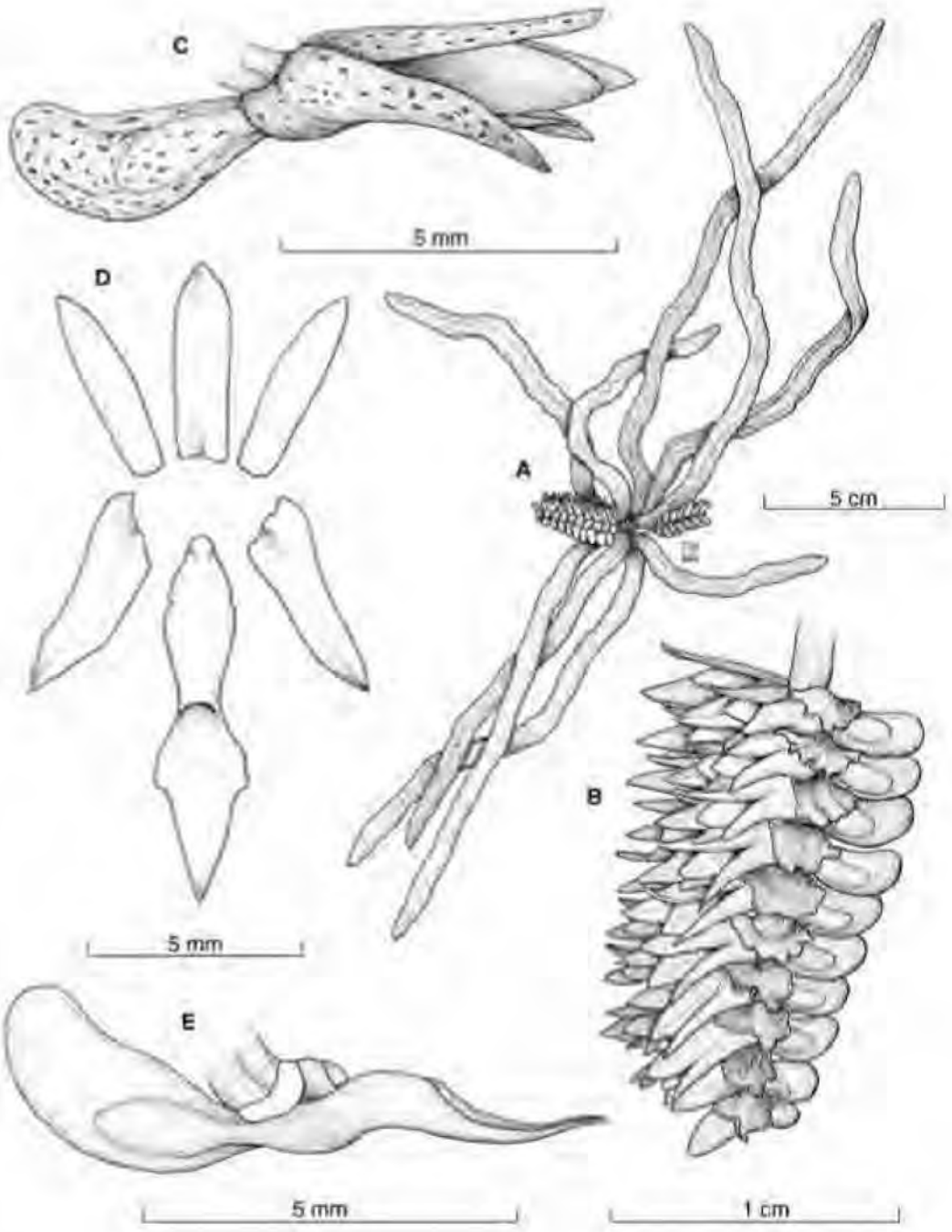

Fig. 30. *Campylocentrum generalense* Bogarín & Pupulin, ined. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 2130* (JBL-Spirit).

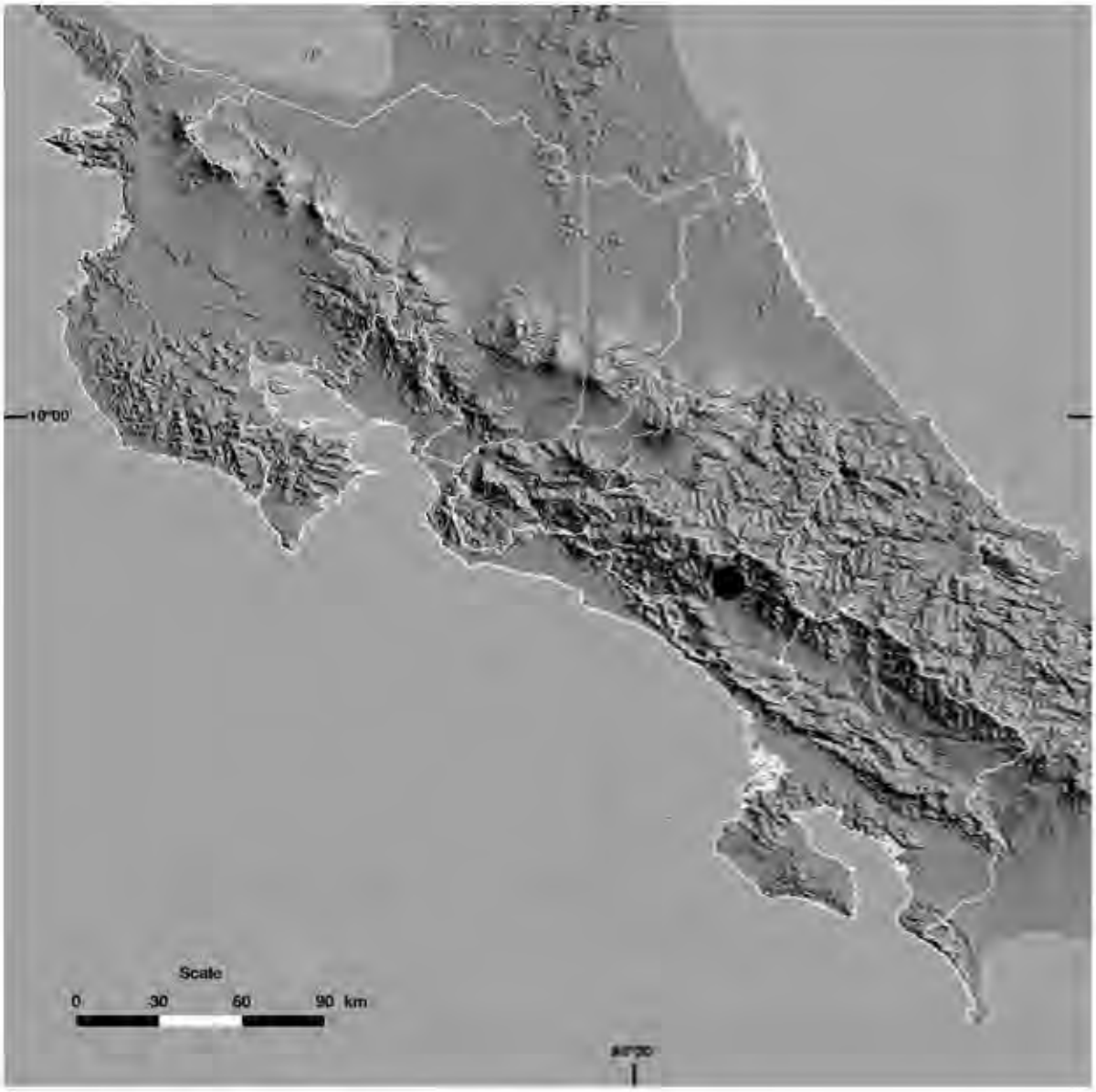

Fig. 31. Distribution map of *C. generalense* in Costa Rica

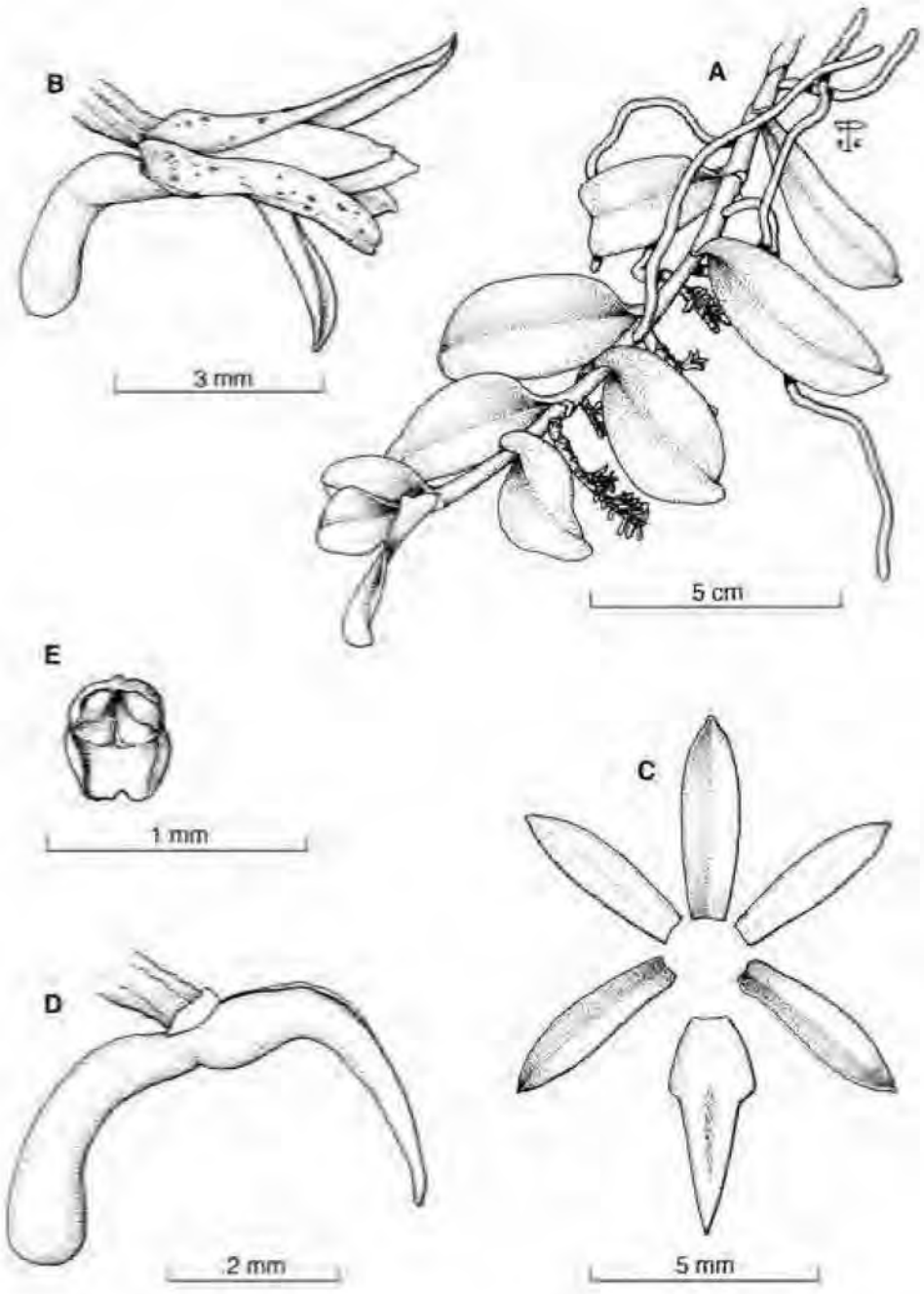

Fig. 32. *Campylocentrum micranthum* (Lindl.) Maury. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Operculum. Drawn by F. Pupulin from *F. Pupulin 332* (USJ)

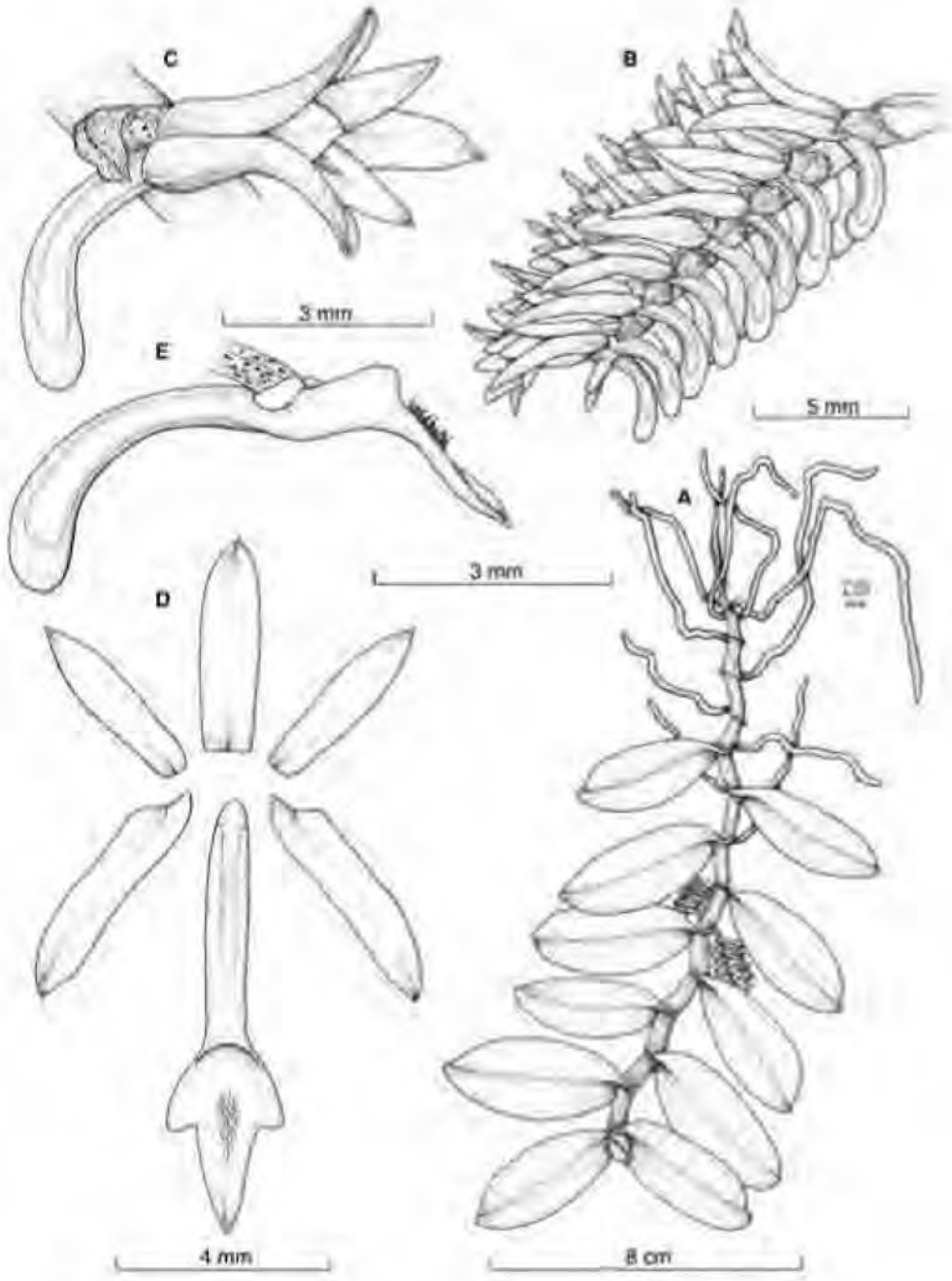

Fig. 33. *Campylocentrum micranthum* (Lindl.) Maury. A — Habit. B —Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 1276* (JBL-Spirit).

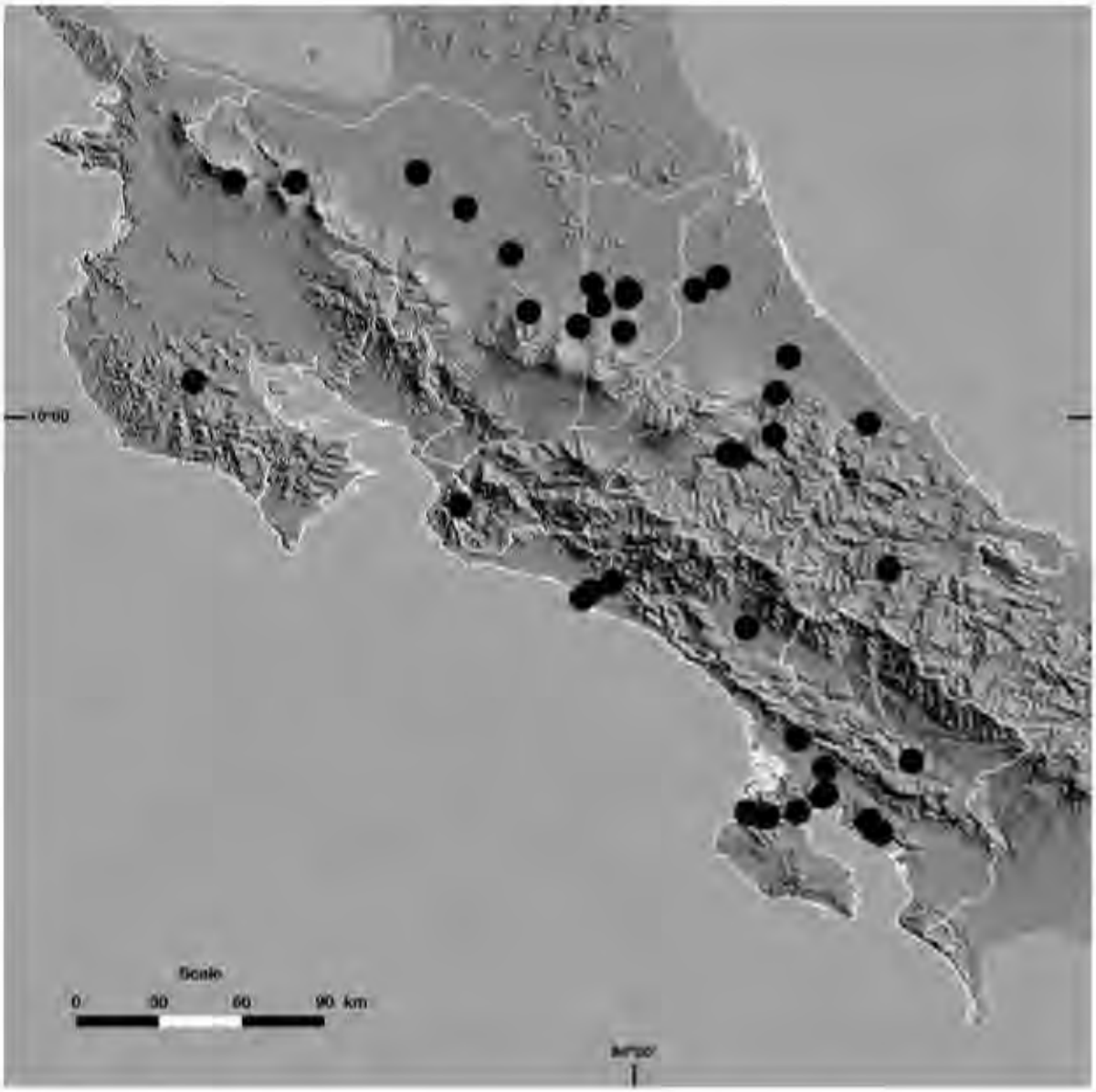

Fig. 34. Distribution map of *C. micranthum* in Costa Rica

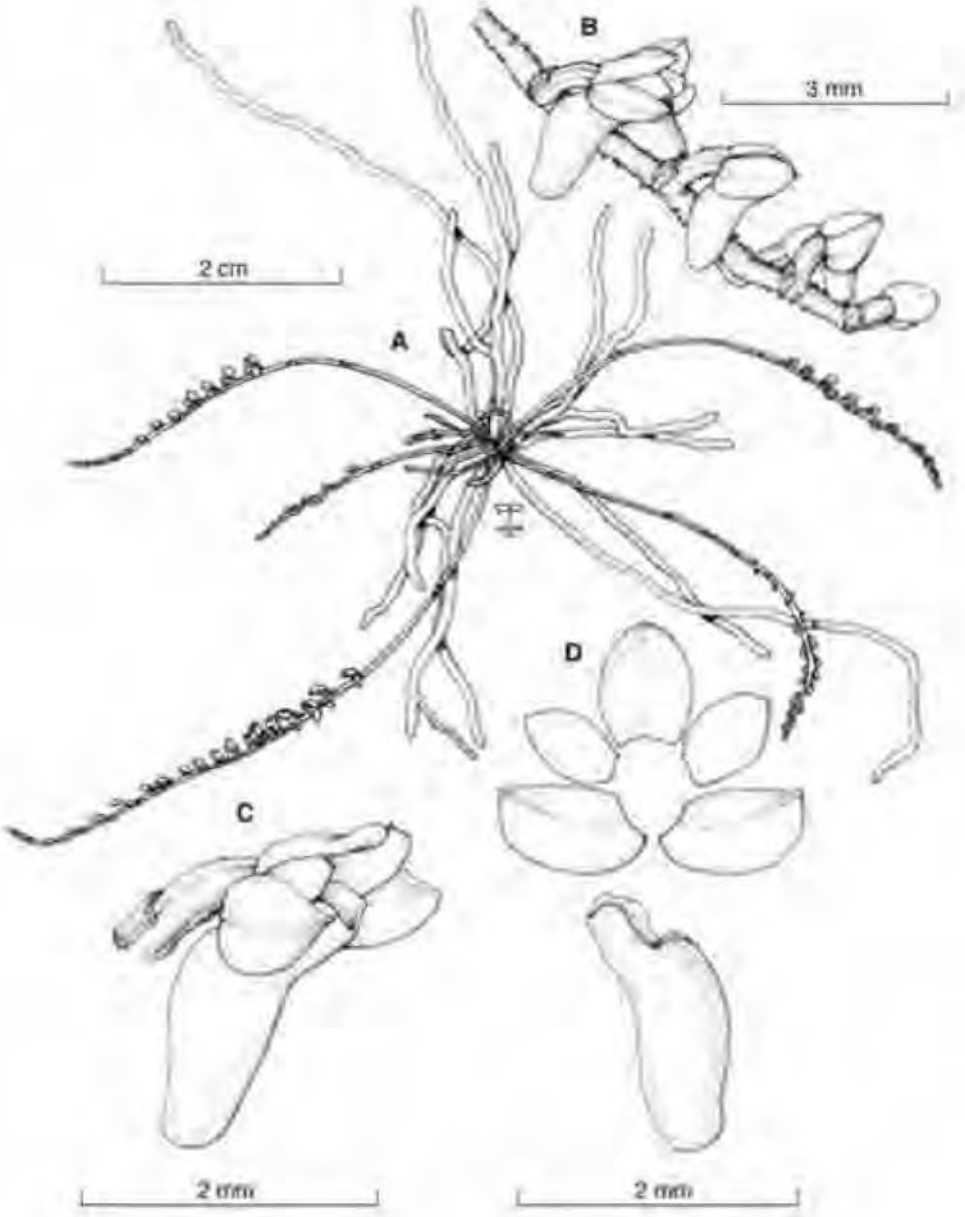

Fig. 35. *Campylocentrum multiflorum* Schltr. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. Drawn by F. Pupulin from *F. Pupulin 1029* (USJ).

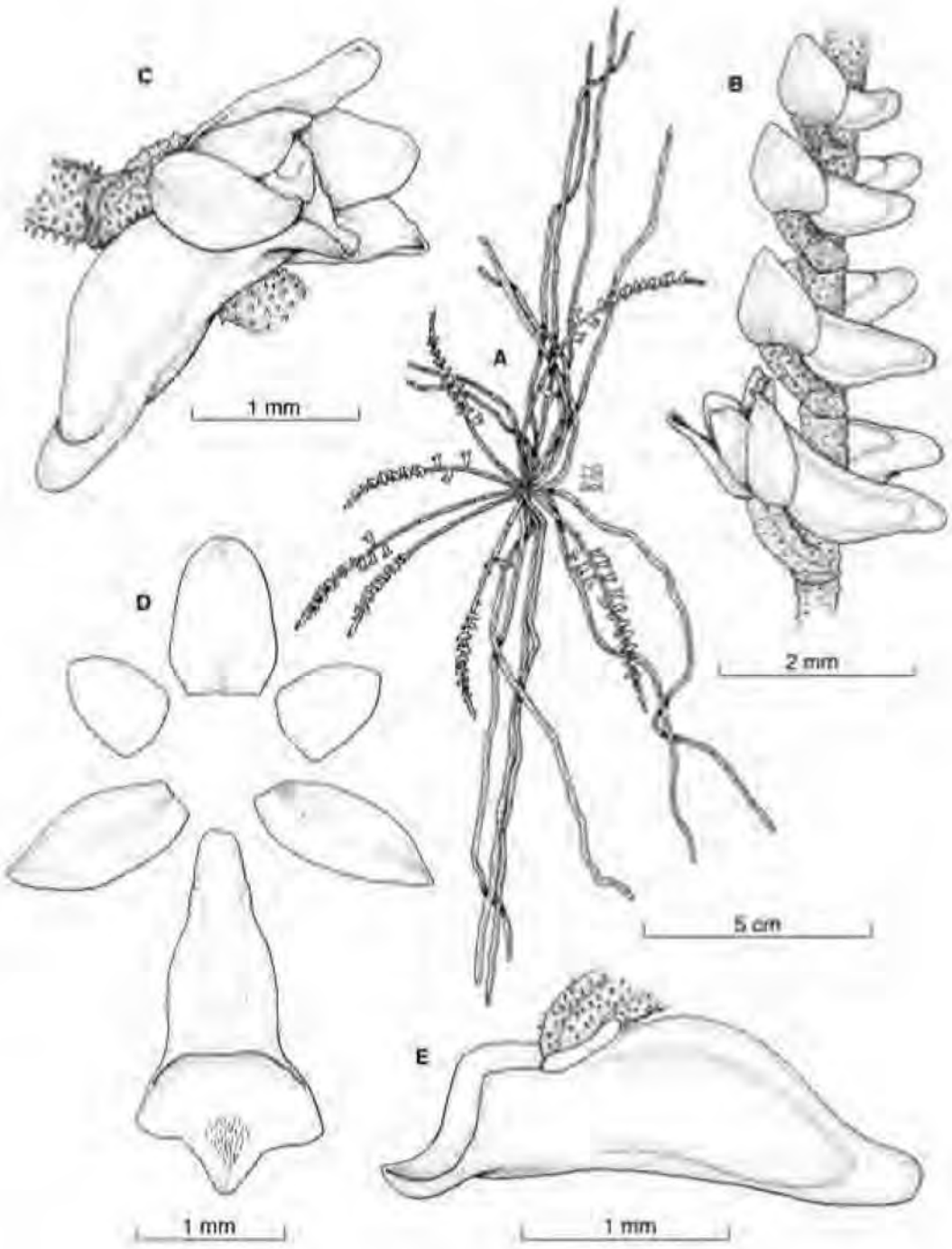

Fig. 36. *Campylocentrum multiflorum* Schltr. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 1484* (JBL-Spirit) .

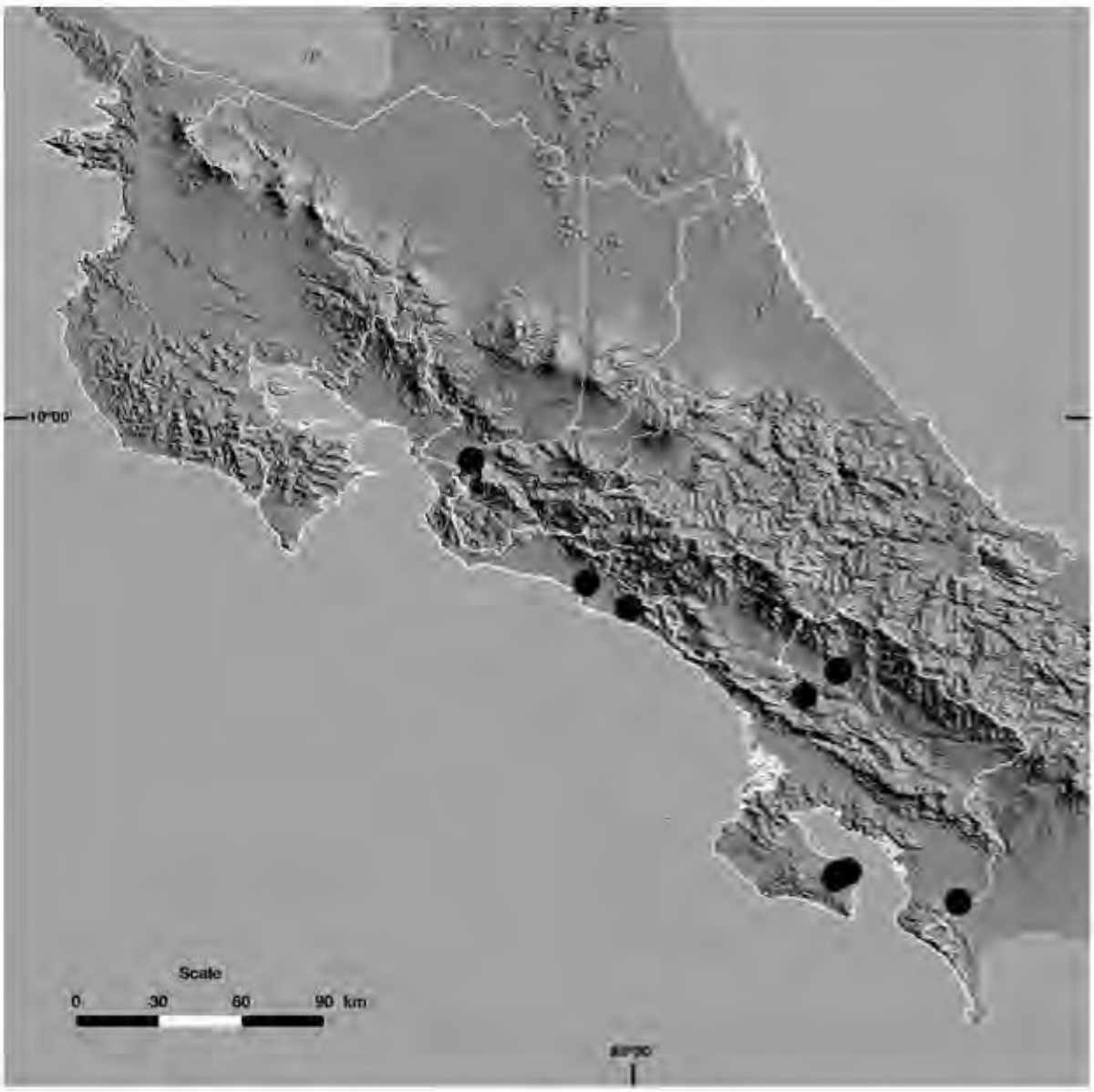

Fig. 37. Distribution map of *C. multiflorum* in Costa Rica

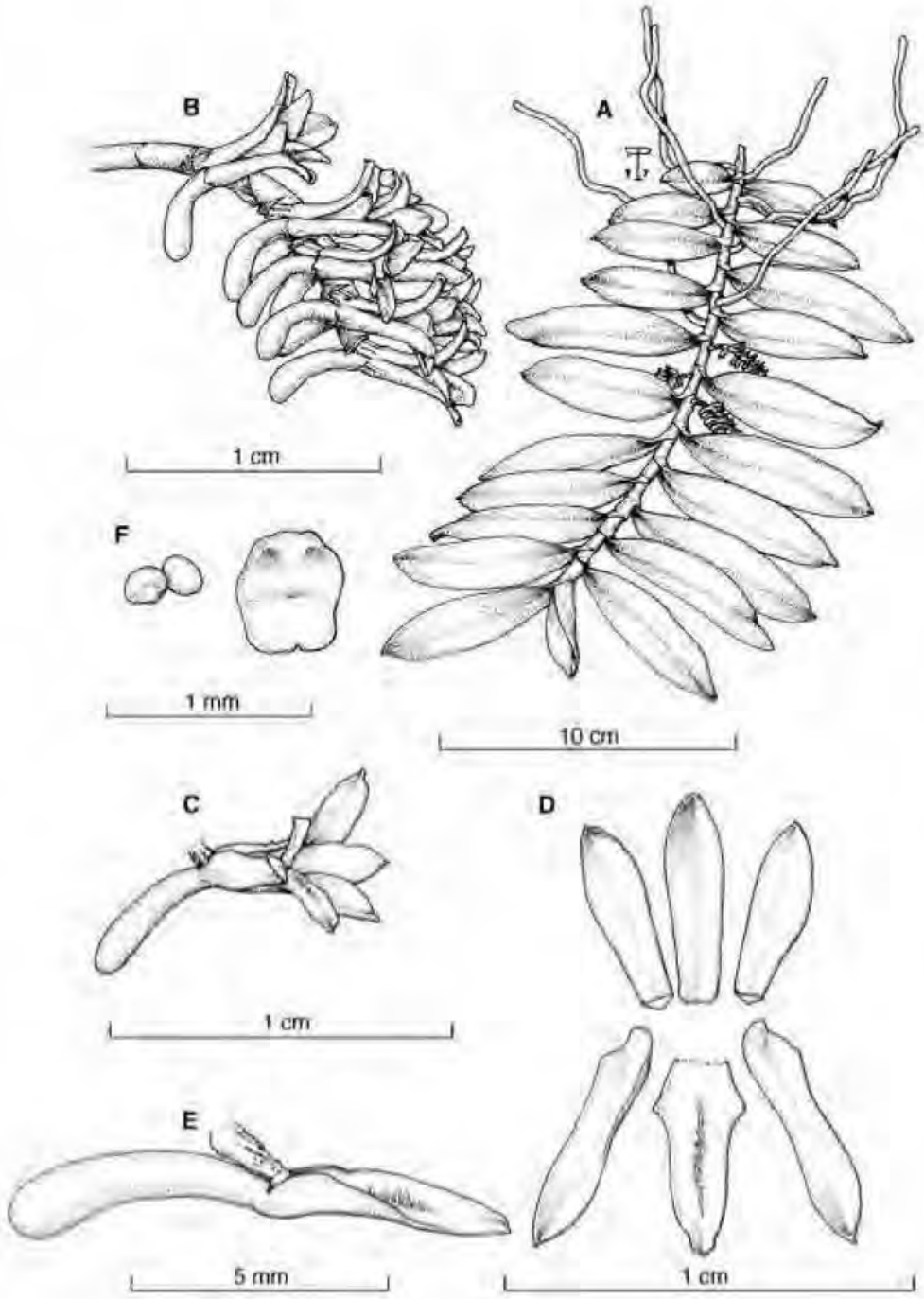

Fig. 38. *Campylocentrum panamense* Ames. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. F — Pollinarium and operculum. Drawn by F. Pupulin from *F. Pupulin 305* (USJ).

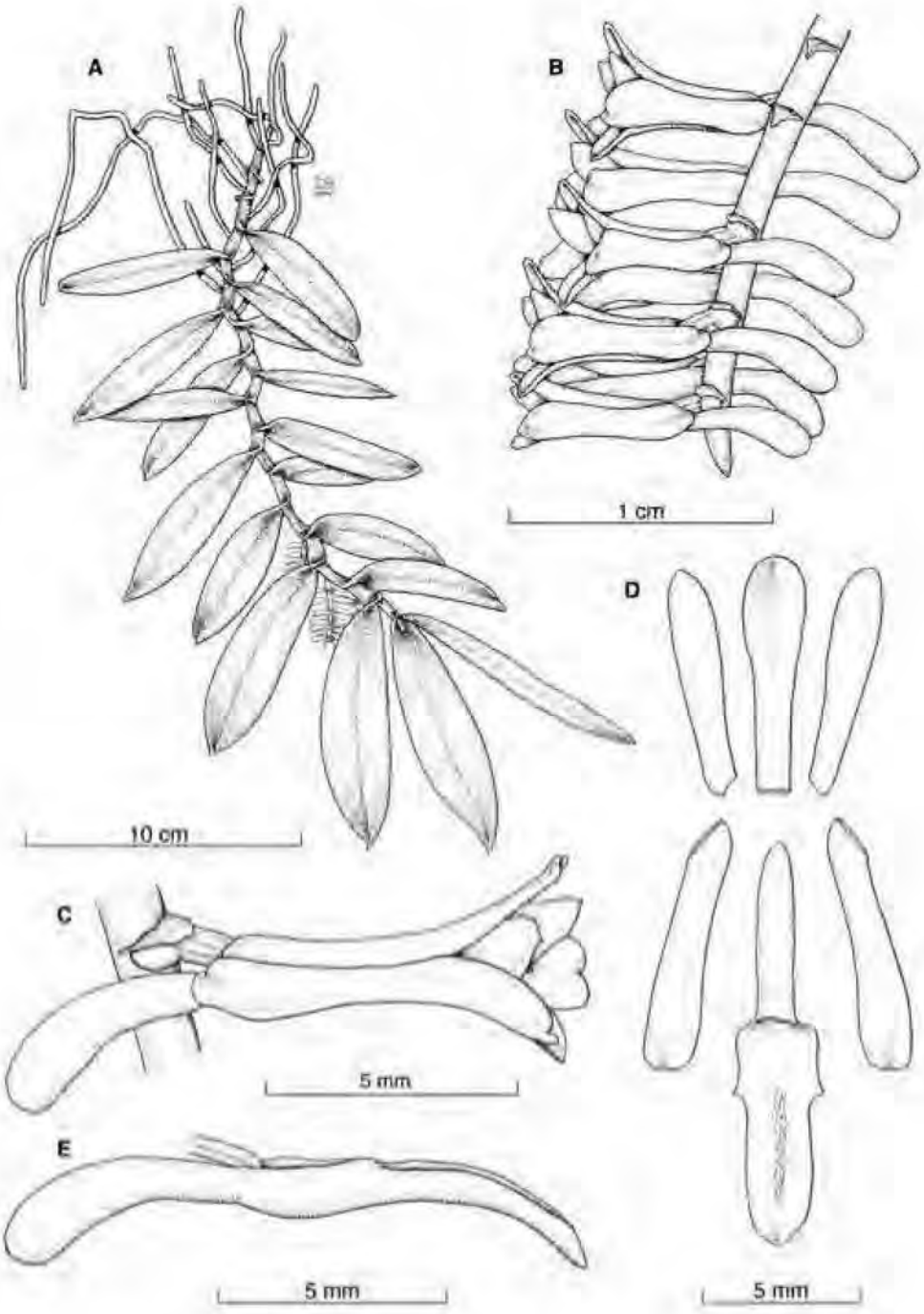

Fig. 39. *Campylocentrum panamense* Ames. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 871* (JBL-Spirit).

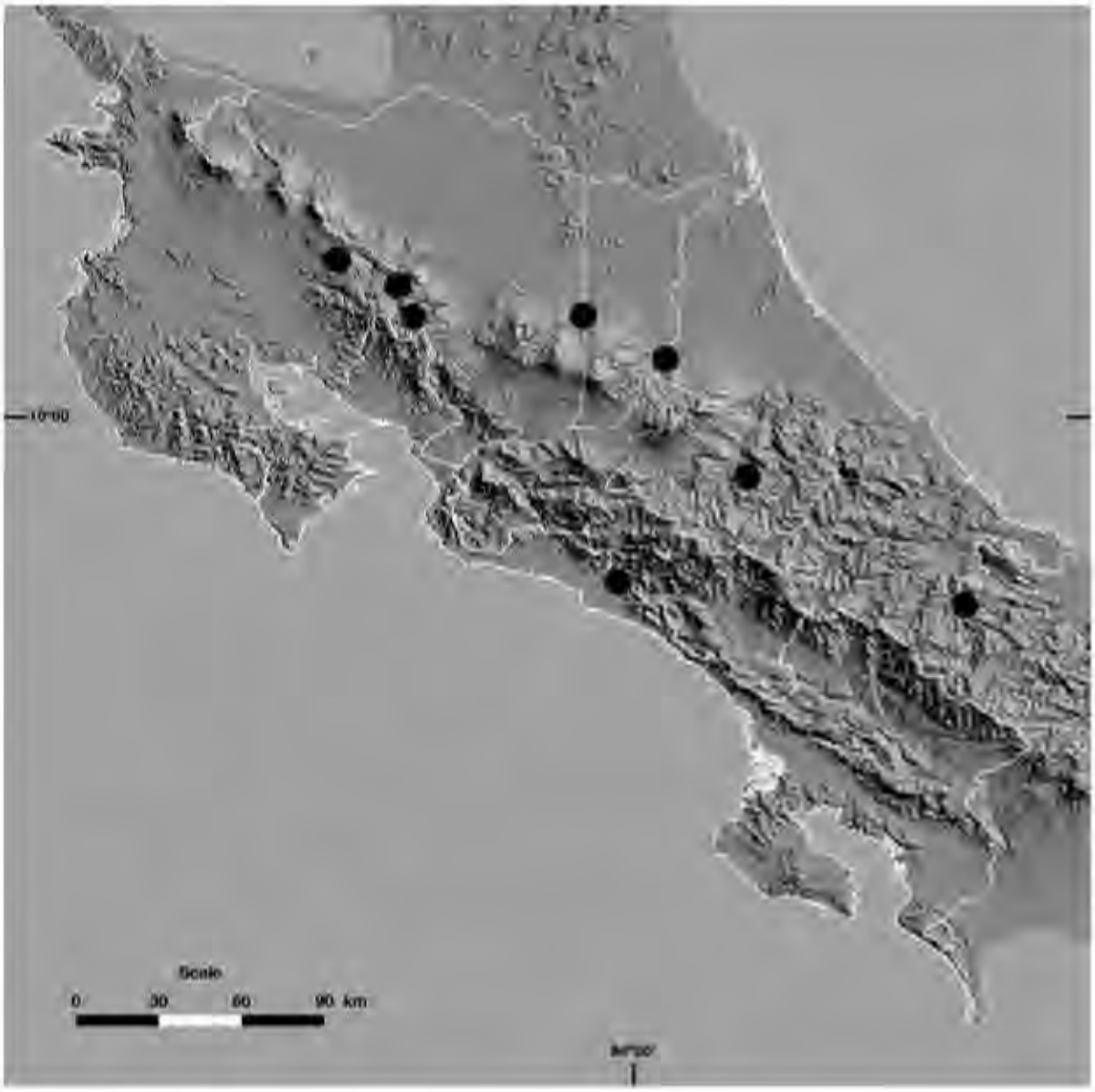

Fig. 40. Distribution map of *C. panamense* in Costa Rica.

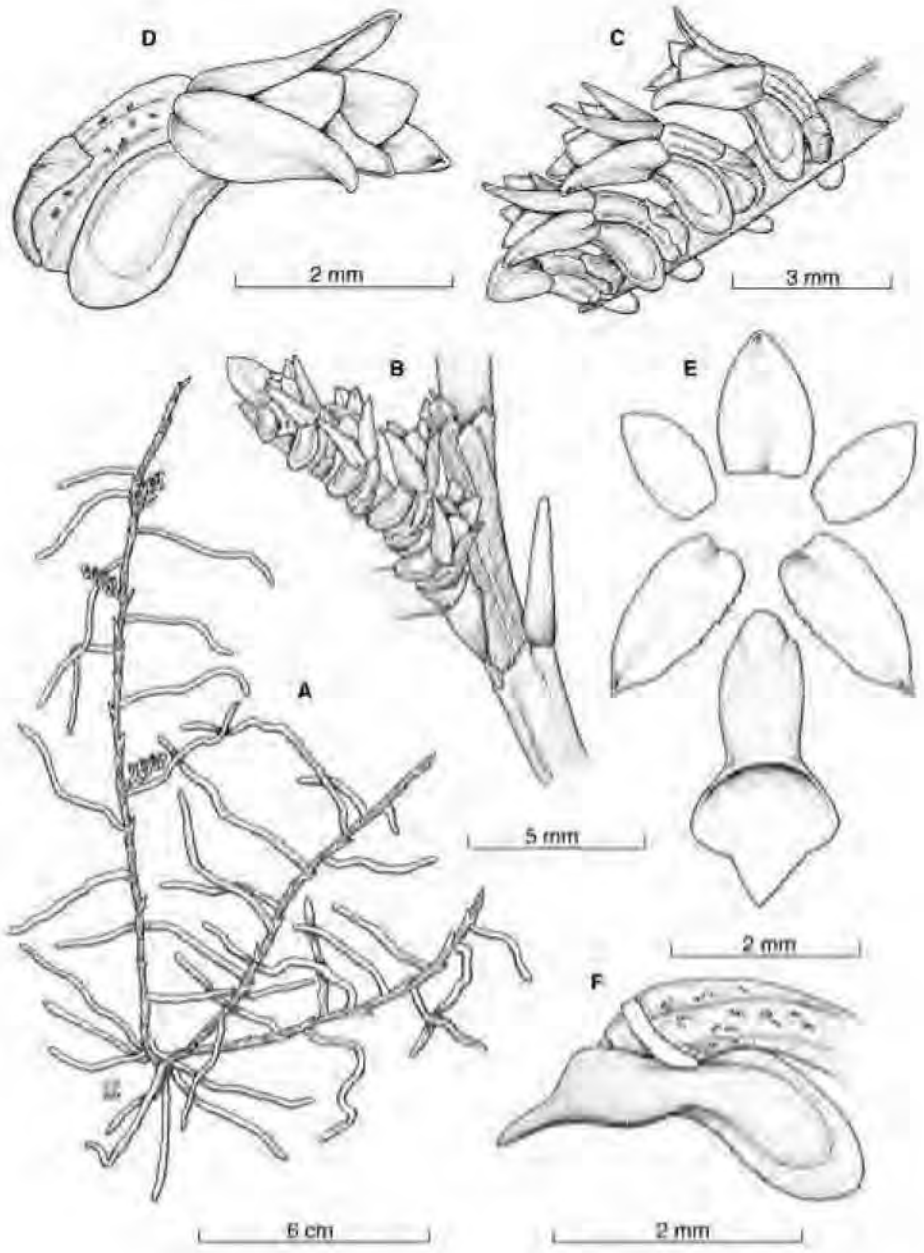

Fig. 41. *Campylocentrum poeppigii* (Rchb. f.) Rolfe. A — Habit. B — Stem and inflorescence. C — Inflorescence. D — Flower. E — Dissected perianth. F — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 2218* (JBL-Spirit).

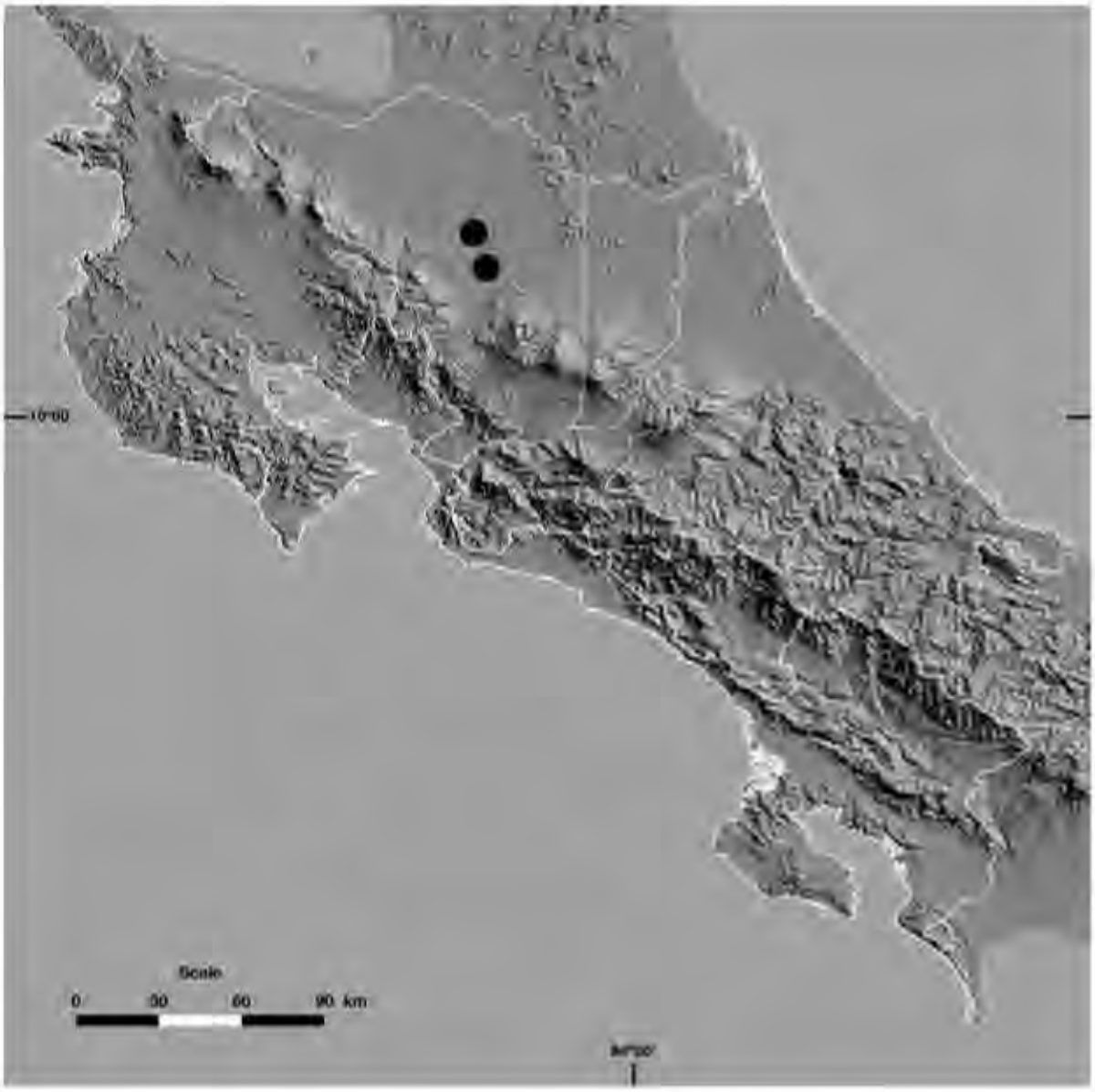

Fig. 42. Distribution map of *C. poeppigii* in Costa Rica.

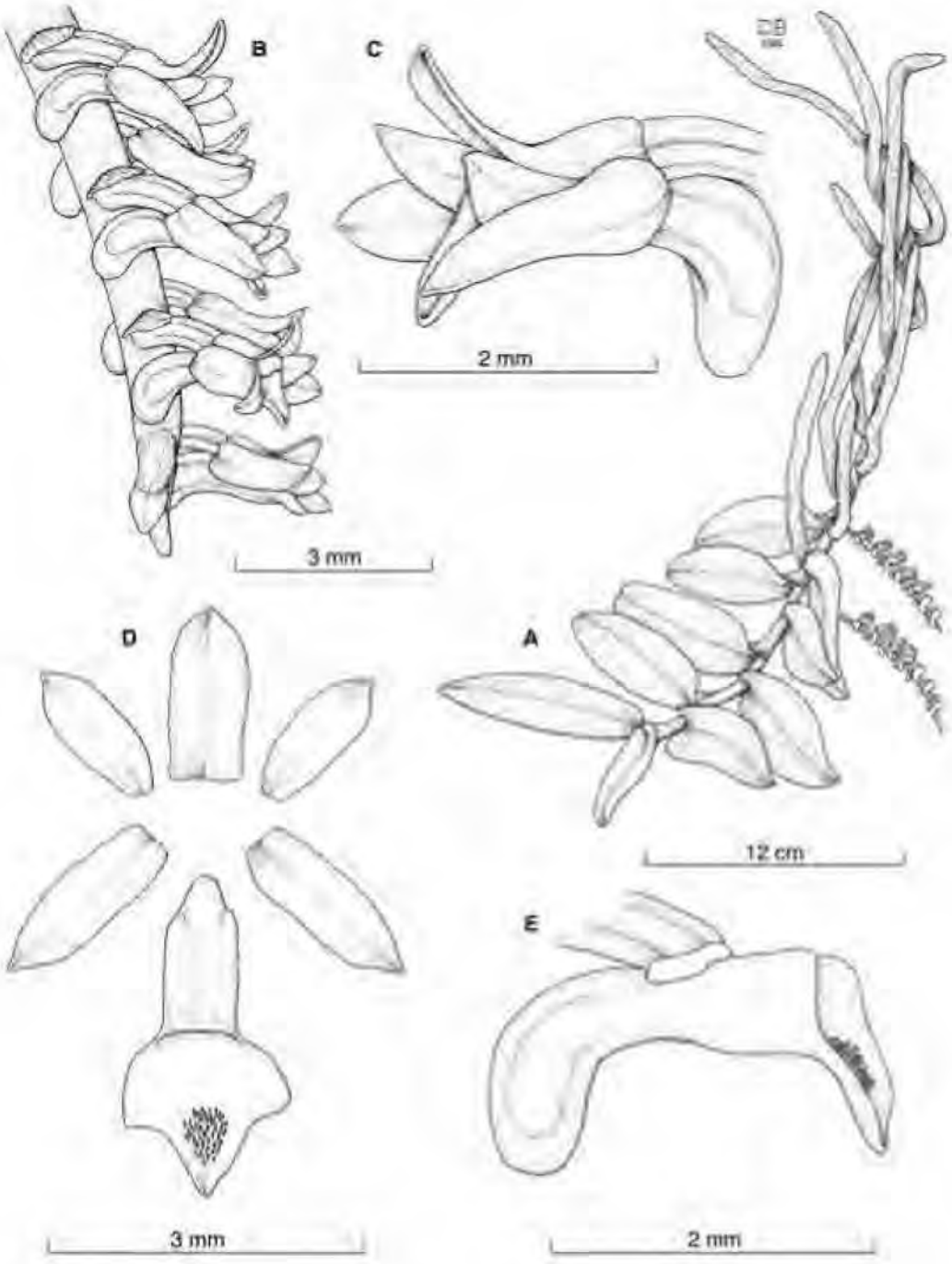

Fig. 43. *Campylocentrum schiedei* (Rchb. f.) Benth. ex Hemsl. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 425* (JBL-Spirit).

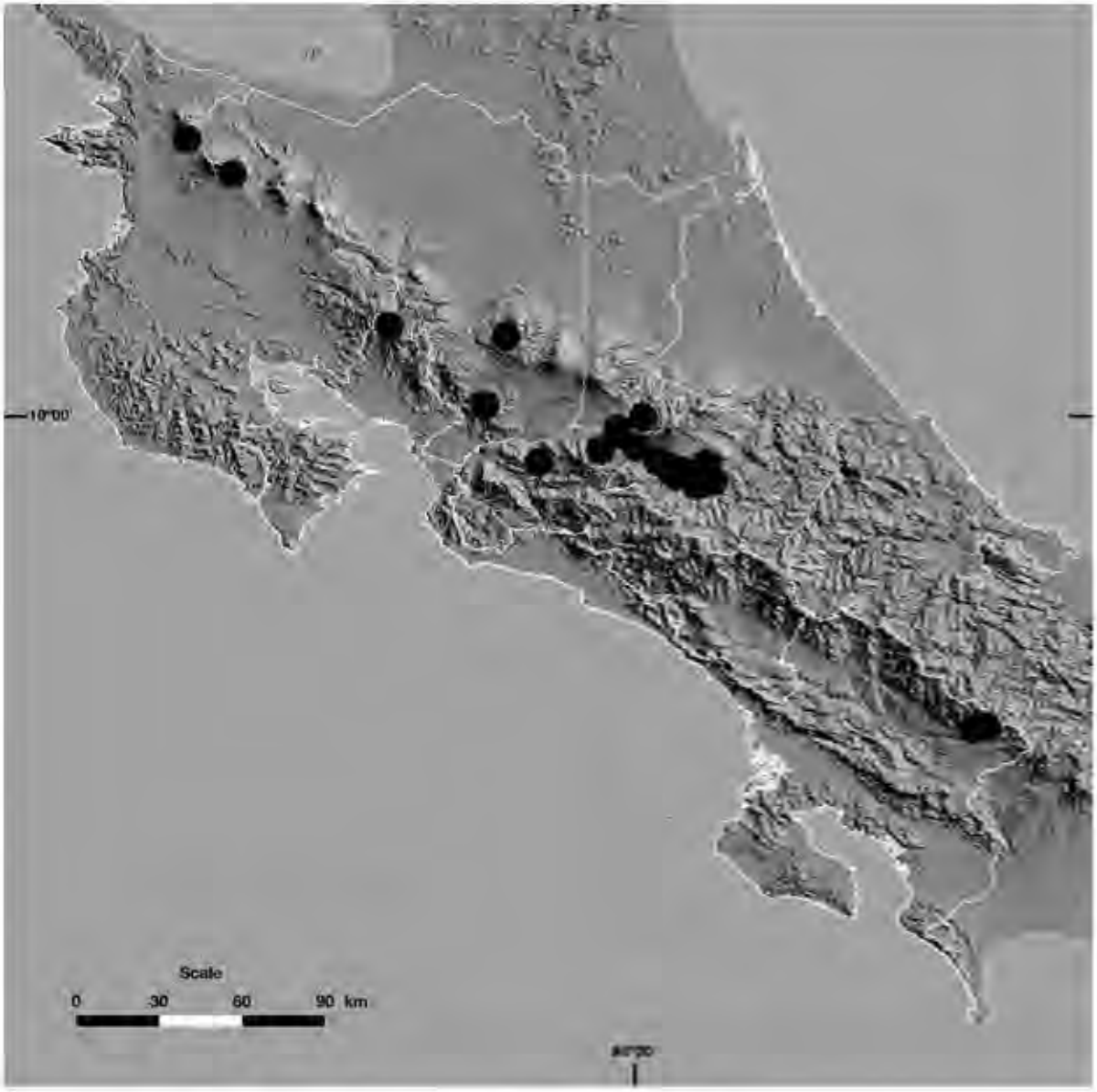

Fig. 44. Distribution map of *C. schiedei* in Costa Rica.

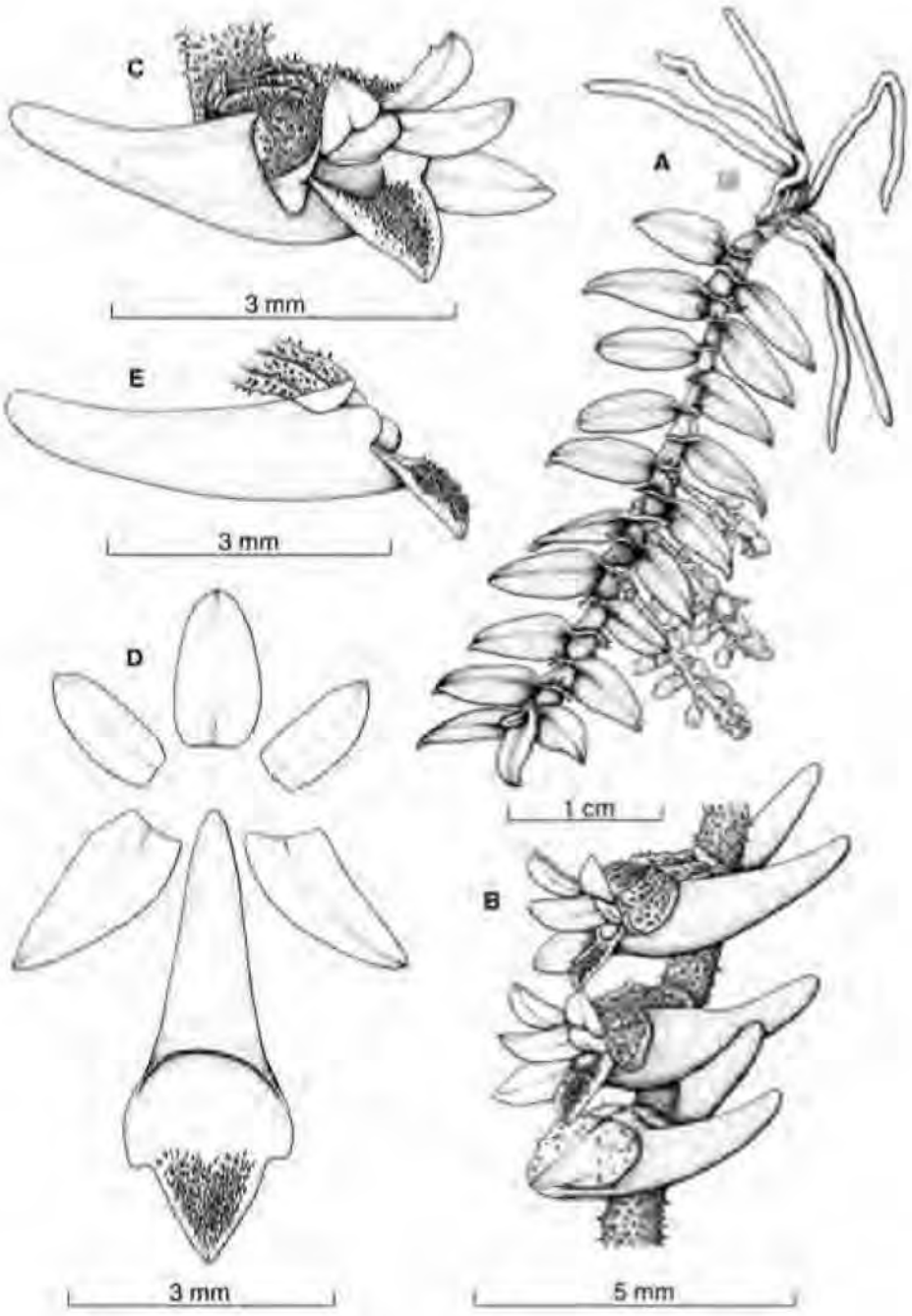

Fig. 45. *Campylocentrum tenellum* Todzia. A — Habit. B — Inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, lateral view. Drawn by D. Bogarín from *D. Bogarín 5844* (JBL-Spirit).

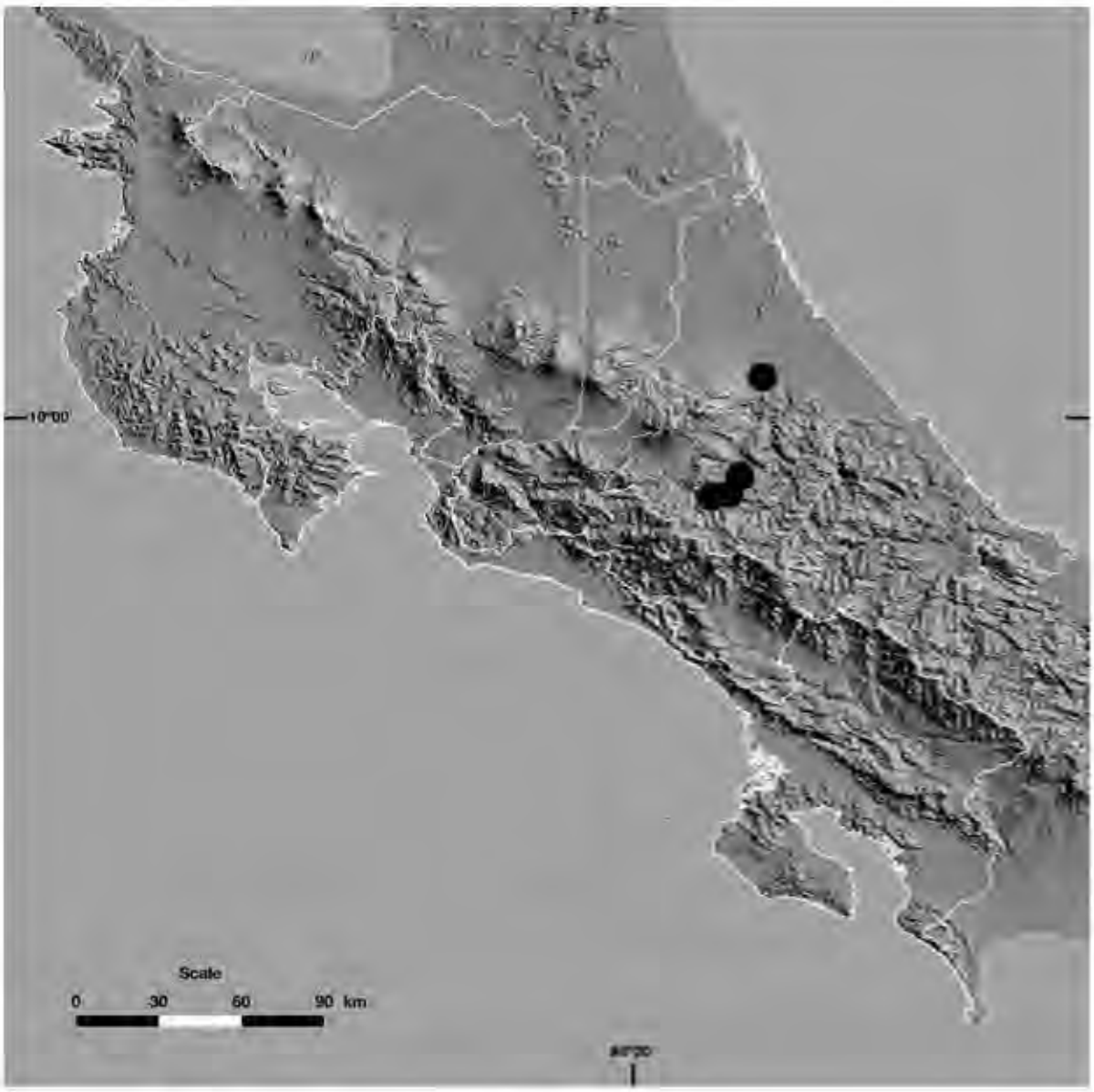

Fig. 46. Distribution map of *C. tenellum* in Costa Rica.

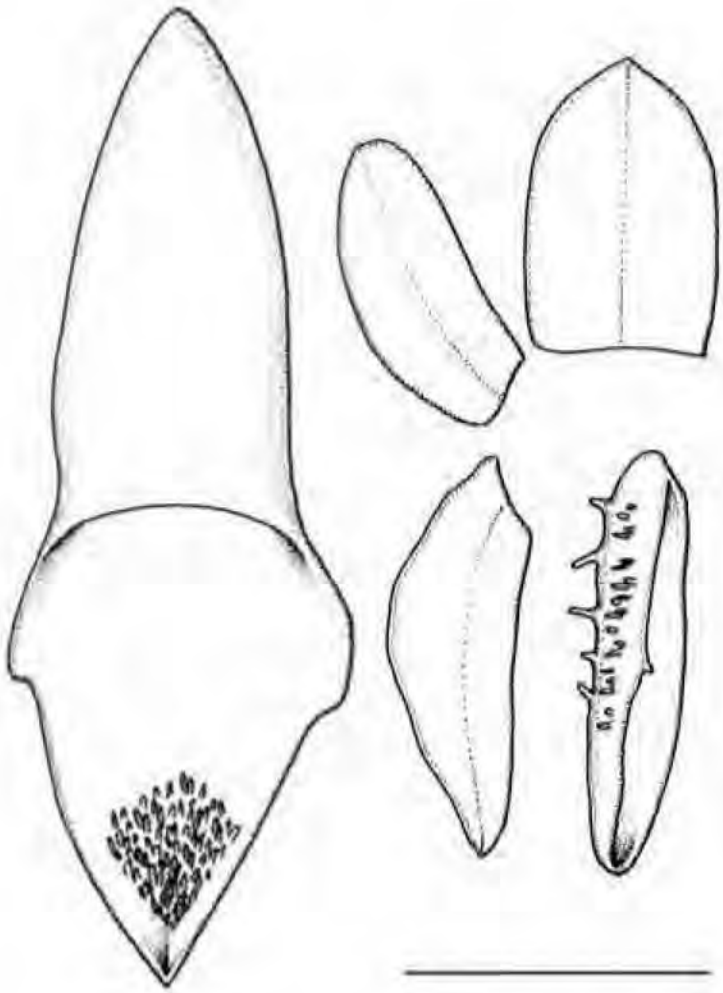

Fig. 47. Drawing of a flower from the holotype of *C. tenellum* based on *Dressler 3758* (CR). Scale bar = 1 mm .