

UNIVERSIDAD DE COSTA RICA  
SISTEMA DE ESTUDIOS DE POSGRADO

TRATAMIENTO SISTEMÁTICO DEL GÉNERO *TRICHOSALPINX*  
(ORCHIDACEAE: PLEUROTHALLIDINAE) EN COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado  
en Biología para optar al grado y título de Maestría Académica en Biología

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## **Dedicatoria**

Este trabajo está dedicado a Emilia Campos Gaitán, mi mamá, quien me ha acompañado por el hermoso camino de la vida, siempre de la mano. Mi esfuerzo y empeño son inspirados por su ejemplo, y esta es mi manera de reconocerle desde lo más profundo.

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## **PREFACIO**

La revisión taxonómica de *Trichosalpinx* (Orchidaceae) en Costa Rica es presentada. La historia taxonómica del género, su posición filogenética y problemas nomenclaturiales son discutidos. El género es tratado como un grupo de 23 especies en el país, y claves dicotómicas a nivel de subgénero y especies son proveídas. Los taxa son descritos e ilustrados con base en material costarricense, y su distribución en el país es evaluada. Se proveen mapas de distribución para todos los taxa. Se presenta la distribución general, la derivación del nombre, notas sobre su ecología y caracteres diagnósticos para cada taxon.

## **ABSTRACT**

A taxonomic revision of *Trichosalpinx* (Orchidaceae) in Costa Rica is presented. The taxonomic history of the genus, its phylogenetic position and nomenclatural issues are discussed. Characters of vegetative and floral morphology are addressed and illustrated, and their taxonomic significance is discussed. The genus is treated as comprising 23 species in the country, and a key to subgenera and species is provided. Taxa are described and illustrated on the basis of Costa Rican material, and their 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.

## I. INTRODUCTION

The Neotropical subtribe Pleurothallidinae Lindl. comprises about 60–80 genera and approximately 4100 species (Pridgeon *et al.* 2005). The group represents about 15–16% of all known orchid species worldwide. It is distributed from south Florida to northern Argentina, with peaks of diversity in the montane and sub-montane rain and cloud forests of Central America and the Andes (Jørgensen & León-Yáñez 1999, Vásquez & Ibisch 2000, Dodson 2004, Stenzel 2004). In Mesoamerica, Costa Rica holds the highest number of genera within the Pleurothallidinae (Ossenbach *et al.* 2007). The hyperdiversity of the subtribe, which represents one of the most diverse monophyletic groups of plants on Earth, poses extremely interesting questions from the evolutionary point of view. Despite the several efforts, none of the morphological, anatomical or molecular approaches (Pridgeon 1982, Luer 1986, 2002, Neyland *et al.* 1995, Pridgeon *et al.* 2001, Pridgeon & Chase 2001, 2005, van den Berg *et al.* 2005) have been able to achieve an establish generic and subgeneric classification in this monophyletic subtribe (*sensu* Pridgeon *et al.* 2001, 2005).

Members of this subtribe are distinguished by the sympodial growth, unifoliate (except for *Dilomilis* Raf., *Fronitaria* Luer and *Tomzania* Nir.), nonpseudobulbous ramicauls (the term used to designate the part of the stem above of the last reiteration bud in Pleurothallids; see Stern & Pridgeon 1984), conduplicate leaves, velamentous roots, and an articulation between the pedicel and the ovary (except for *Dilomilis*, *Neocogniauxia* Schltr. and *Tomzania*) instead of at the base of the pedicel as in most the other orchids (Luer 1986, van den Berg *et al.* 2005, Pridgeon *et al.* 2005). Genera in the Pleurothallidinae have been traditionally defined on the basis of number of pollinia, number of stigma lobes, degree of sepal connation, resupination, shape of the various perianth

parts, and presence or absence of lip mobility (Garay 1979, Luer 1986, 1987, 2000, Stenzel 2004).

Plants in the Pleurothallidinae are epiphytic, terrestrial or lithophytic, and inhabit dry, humid, and cloud forests, mangroves and paramo. In Costa Rica, they are mainly epiphytic, and inhabit forests between 0 to more than 3000 m elevation, although many have restricted distributions in humid forests between 1000 and 2000 m. Plants can be as long as 1 m, but most of them are less than 30 cm long.

The pollination system of most species remains unknown. The vast majority of the documented cases represent pollination by dipterans, some by deceit (Borba & Semir 2001, Borba *et al.* 2001, Blanco & Barboza 2005, Pupulin *et al.* 2012). Pollination studies in *Acianthera* Scheidw. (Singer & Cocucci 1999, Borba & Semir 2001, Borba *et al.* 2001), *Dracula* Luer (Endara *et al.* 2010), *Lepanthes* Sw. (Blanco & Barboza 2005, Blanco & Vieira 2011), *Masdevallia* Ruiz & Pav. (Cuervo 2012, Dodson 1962), *Pleurothallis* R.Br. (Duque-Buitrago *et al.* 2014) and *Specklinia* Lindl. (Pupulin *et al.* 2012) have mostly revealed myophily, or pollination by flies. Instead of a single strategy, Pleurothallids use a variety of different ways of attracting pollinators, including odor attractants and structural mimicry (e.g. fungus or flesh-like structures and insect sexual parts). Although myophily and self-incompatibility have been reported to be basal characteristics in the former delimitation of the Pleurothallidinae and possibly have been kept in the derived lineages (Barbosa *et al.* 2009), alternative pollinators, including pollination by microhymenoptera and Coleoptera, have also been reported to occur (Duque 1993).

Pleurothallidinae include several of the largest genera within Orchidaceae, such as *Pleurothallis*, *Stelis* Sw. and *Lepanthes*. The latter is one of the genera bearing lepanthiform sheaths on the ramicauls, along with *Lepanthopsis* (Cogn.) Ames,

*Draconanthes* (Luer) Luer and *Trichosalpinx* Luer. Lepanthiform sheaths are tubular sheaths that cover the ramicaul, more or less imbricate, with longitudinal ribs and dilated ostia with thickened, ciliate margins.

*Trichosalpinx* was described in 1983 and typified by the widely distributed *Specklinia ciliaris* Lindl. (Luer 1983). The name comes from the Greek *trichos*, “hair”, and *salpinx*, “a trumpet”, referring to the ciliate ribs and margins of the trumpet-like sheaths of the ramicaul (Luer 1983). At present, around 160 species have been described in *Trichosalpinx* after Luer (1997) relegated 20 names to the synonymy of other species, and transferred 10 species to other genera such as *Lepanthopsis*, *Pabstiella* Brieger & Senghas and *Pleurothallis*.

Populations of *Trichosalpinx* are found throughout the Neotropics, with evident species concentration in the Andes and the high mountain ranges of Costa Rica and western Panama. The moist and wet forests of the Andes between 1600 m and 2700 m harbor the majority of the *Trichosalpinx* species described to date (Luer 1997; Fig. 1).

Species distribution in *Trichosalpinx* is variable. Some species are found all throughout the Neotropics, as in the cases of *T. memor* (Rchb.f.) Luer and *T. dura* (Lindl.) Luer. Other species are restricted to a regional scale (e.g. *T. pergrata* [Ames] Luer, found only in Costa Rica and Panama). Furthermore, regional endemisms occur on a regular basis, as in the cases with *T. reflexa* Mel.Fernández & Bogarín, restricted to the Pacific lowlands of Costa Rica, and *T. systremmata* (Luer) Luer, only located in the rich, cloud forests of Loja in Ecuador.

Before the beginning of this study, 20 species were recognized to be represented in Costa Rica (Luer 1997, Ossenbach *et al.* 2007). After that, two new species, *Trichosalpinx reflexa* (Fernández & Bogarín 2011), and *T. sanctuarii* Mel.Fernández & Bogarín (Fernández & Bogarín 2013) were added, while *T. minutipetala* (Ames & C.Schweinf.) Luer (previously considered a synonym of *T. memor*) was recognized as a distinct species (Fernández 2011). Therefore, the present study recognizes a total of 23 species, twelve of them belong to the subgenus *Trichosalpinx*, and 11 belong to the subgenus *Tubella* Luer. No species of the other two subtribes, *Pseudolepanthes* Luer and *Xenia* Luer, which are essentially South American, are known in Costa Rica.

In Costa Rica, the elevational distribution of *Trichosalpinx* ranges from 100 m in the northwestern Pacific lowlands to 2500 m in the cloud forests of the Cordillera de Tilarán and the Cordillera Volcánica Central, with a maximum concentration of species between 800 and 1500 m (Fig. 2). Individuals are commonly found growing epiphytically in scattered trees in open areas and riparian forests, as well as in secondary and primary premontane and lower montane forests (life zones according to Holdridge 1967, 1987).

Pollination of *Trichosalpinx* species is unknown (Blanco & Barboza 2005, Pridgeon *et al.* 2005). Nevertheless, floral morphology suggests myophily, especially because of the brownish or dull reddish floral colors and mobile lip, similar to those of other fly-pollinated orchids such as *Bulbophyllum* Thouars (Teixeira *et al.* 2004, Jersáková *et al.* 2006) and *Acianthera* (Borba & Semir 2001). Further studies on scent and reward recognition are still needed.

Plants of *Trichosalpinx* are epiphytic and caespitose or repent; some species are prolific (with ramicauls borne on top of each other), and all of them bear lepanthiform sheaths.

The leaves are apical on the ramicauls, and shape varies from broadly to narrowly elliptical, with acute to obtuse apexes; the inflorescence is apical, racemose and rarely single-flowered. The flowers are resupinate, with the lateral sepals separate or partially or completely connate, while the petals are membranous. The lip is entire or basally lobed, and is attached to the column foot by a flexible articulation. The column is semi-cylindrical, with a short foot. The anther is incumbent, operculate with two pyriform pollinia (Luer 2003).

Luer proposed an infrageneric classification that has been used for more than 30 years now (Luer 1983, 1997). He organized *Trichosalpinx* in four subgenera: *Tubella*, *Trichosalpinx*, *Xenia* and *Pseudolepanthes*. Differences are based on the presence of prolific ramicauls, the relationship between the length of the leaf and that of the inflorescence, the shape and margins of the petals and the presence of a column-foot. Morphological and anatomical data was used by Archila (2000) to support the elevation of *Tubella* (to which he also added species from subgenus *Xenia* without providing evidence) and *Pseudolepanthes* to generic status.

*Trichosalpinx* was included in recent phylogenetic analyses. Based on molecular data, Pridgeon and colleagues (2001) revealed that *Trichosalpinx* (*sensu* Luer) is a polyphyletic genus. Moreover, their results in the consensus tree show that subgenus *Trichosalpinx* is also polyphyletic, with two member of the subgenus strongly supported in one clade but separated from a third member, *T. berlineri* (Luer) Luer, which was found to be close to *Zootrophion* Luer with low support. The only species of subgenus *Tubella* evaluated, the widely distributed *T. arbuscula* (Lindl.) Luer, failed to provide phylogenetic information in the consensus tree. In a more recent study, Karremans (2014) evaluated the phylogenetic

relationships within *Anathallis* Barb.Rodr. and related genera, which confirmed the polyphyletic nature of genus and subgenus *Trichosalpinx*, and the need for a recircumscription to attain monophyly. His study also included a sample of *T. arbuscula* sister to the other *Trichosalpinx* species, with low bootstrap support (0.44). A phylogenetic analysis of genus *Trichosalpinx* (Fernández *et al.* in prep.), including several species of subgenera *Trichosalpinx* and *Tubella*, further evidences the need for a complete recircumscription of this highly polyphyletic genus, which is diversely interrelated with other genera as *Anathallis*, *Lepanthes*, *Zootrophion* and the recently proposed *Lankesteriana* Karremans. Since the systematic relationships of *Trichosalpinx* sensu lato (i.e., including all the taxa that in some moment were assigned to it) are still unclear, I prefer to maintain the traditional circumscription of *Trichosalpinx* in the present contribution.

Although Costa Rica has a well-established tradition in orchidology, the local knowledge on genus *Trichosalpinx* has been based on a relatively low number of herbarium collections, which naturally limits the understanding of their natural variation and the geographical and ecological patterns associated to their distribution. Additionally, many herbarium specimens are erroneously identified due to the difficulty in recognizing characters in their small, dried flowers. Likewise, major difficulties in delimiting taxa in the several species complexes of the genus have not yet been resolved, so a taxonomic revision of the genus in Costa Rica is needed. As part of a major project aimed toward the completion of the treatment of Pleurothallidinae for the *Flora Costaricensis*, the present work aims to produce the first taxonomic revision of *Trichosalpinx* in Costa Rica, based on an extensive survey of living and preserved specimens and their corresponding morphological variation and distributional and ecological data.

## II. METHODOLOGY

The taxonomic work was mainly conducted at Lankester Botanical Garden, University of Costa Rica (located in Dulce Nombre, Cartago province, 9°50'25.9" N 83°53'19.4" W at 1370 m), from 2011 to 2014.

### **Collection of samples**

In this study live plants from fieldtrips were acquired. Different localities were visited according to the following cri

teria: 1) their type locality (for species described from Costa Rican plants), 2) other Costa Rican localities reported in the protologue, 3) other Costa Rican localities recorded in herbarium samples and the literature. Botanical exploration in several traditionally under-collected areas of Costa Rica was also conducted. Whenever possible, at least 5 plants per locality and/or population were collected. For the purposes of the present work, a population was defined as all the individuals occupying the same phorophyte (following Tremblay 1997). Flowerless plants were cultivated at the Lankester Botanical Garden facilities until floral material was obtained for study. The herbarium specimens saved in the dried and spirit-preserved collections of the Costa Rican National Herbarium (CR), the Luis Fournier Oraggi Herbarium (USJ), the National Biodiversity Institute Herbarium (INB) and the Lankester Botanical Garden Herbarium (JBL) were studied. Digital images of type specimens, when deposited outside Costa Rica, were also studied.

A database associated with the geographical information from living plants and herbarium specimens was created, which includes the following information: a) name of the species; b) locality (province, county, district, other locality data); c) geographic coordinates; d) vegetation type and life zone; e) habit; f) collecting date; g) collector name and number; h) herbarium of deposition. For spirit-preserved specimens at JBL lacking collector, the term “JBL-” followed by the Living Plants Collection identification number, all in italics, was used. For plants collected in the field during the course of this study, geographical reference data were obtained with a Garmin eTrex Vista GPS unit. Life zone classification was based on Holdridge’s Life Zone System (Holdridge 1967, 1987). Collecting data are partially available through the Lankester Botanical Garden Herbarium web site (<http://www.jbl.ucr.ac.cr/php/investigacion/herbConsultEspecif.php>).

### **Description and documentation of specimens**

Unless indicated otherwise, botanical descriptions were prepared from living plants and spirit-preserved specimens at JBL, supplemented with information from preserved material at the other national herbaria. All herbarium material studied was annotated.

Each plant collected from the field or otherwise flowered in cultivation at JBL was photographed, illustrated, preserved in spirit, and deposited in the Spirit Collection at JBL. The date indicated in all specimens deposited at JBL cited in the section “Additional Material Studied” refer to the collecting dates, not to flowering dates as in the material from other herbaria. When duplicates were available, they were dried and deposited at CR or USJ.

Recording of morphological characters, including size and shape, as well as drawings and photographs, were executed using Leica MZ 9.5 and M80 stereomicroscopes, provided with a drawing tube and Leica IC80 and Leica DFC295 digital cameras. Images of stems, flowers and fruits were obtained using Epson Perfection 2400 and Epson Perfection V600 scanners, at resolutions between 1000 and 3000 dpi. When live plants were available, taxa were illustrated with a composite line drawing based on living material. Composite plates were diagrammed by using Adobe Photoshop®. Ink drawings were prepared in smooth Fabriano® paper of 240 g/m<sup>2</sup> with a Rotring® Rapidograph 0.1mm using black capillary cartridges and traced in Artograph LightPad® A920. Character variations of morphologically variable species were also drawn. Illustrations include at least the plant habit, flower, dissected perianth, column, anther and pollinaria. When possible, uniformity in floral views and plate composition was maintained to facilitate species comparisons.

When the flower structure of a herbarium specimen was not easily observed, or if it did not seem to correspond to any of the species of *Trichosalpinx* studied from living plants, one or (preferably) two flowers were rehydrated by placing them in concentrated ammonia (NH<sub>3</sub>) in a closed vial for 6 to 24 hours, and then transferred to tap water. These flowers were examined, dissected and drawn using a stereomicroscope as specified above. Once completed, the flower parts were put in a lignin-free paper envelope, dried, and returned to the herbarium specimen along with a copy of the drawing and identification label where necessary.

Phenological data (specifically flowering dates) were acquired from field collections and exsiccata. Phenological data obtained from cultivated plants were summarized separately

from that of plants in the field, as their phenology can be influenced by the conditions in cultivation. Phenology of populations from the Caribbean and Pacific versants was summarized separately to detect any differences for those species that occur in both sides of the continental divide.

After documentation, individuals were classified based on their morphological similarities. Descriptions were made based on Stearn (1987). For the application of species names, type specimens or the corresponding images of species of *Trichosalpinx* found in Costa Rica were studied. The documented material and descriptions were compared with protologue descriptions and available type material of *Trichosalpinx* species known. Interpretation of size, shape, texture, arrangement and position characters were based on Stearn (1987) and Harris & Harris (2001).

Reference material, illustrations, descriptions and images, as well as the articles generated from this project, are available online through the web site [www.epidendra.org](http://www.epidendra.org) (Pupulin 2007, 2009).

### III. TAXONOMIC HISTORY OF *TRICHOSALPINX*

#### 1. The first discoveries

The first species that would be eventually assigned to *Trichosalpinx* was described in 1816 as *Dendrobium pusillum* by Kunth, from a collection made by Humboldt, Bonpland & Kunth in Loja, Ecuador (Humboldt & Bonpland 1815; Fig. 3). Lindley (1835) transferred the species to *Specklinia* on the basis of its partially connate sepals that form a hump. Shortly later the same author transferred it to *Pleurothallis* (Lindley 1842: 82–83). Almost fifty years later Kuntze made a new combination of the species in *Humboldtia* Ruiz & Pav. (Kuntze 1891). Nonetheless, this genus is illegitimate in the Orchidaceae for being a later homonym (for a few months) of another genus proposed in 1794 in the Fabaceae (Vahl 1794). Finally, Luer (1983) made it the type species of his new genus *Trichosalpinx* Luer (Luer 1983). The type material is preserved at the National Museum of Natural History in Paris, where Humboldt and Bonpland deposited much of the material gathered during their voyage through South and North America.

Lindley described *Pleurothallis arbuscula* Lindl. in 1842, and *P. dura* Lindl. in 1859. They were found in Loja (Ecuador) and Peru respectively (Lindley 1842, 1859; Figs. 8, 9). In 1838, Lindley added *Specklinia ciliaris* and *S. orbicularis* Lindl. (now *Trichosalpinx ciliaris* and *T. orbicularis*, respectively; Figs. 4, 5), two species described from plants cultivated in the greenhouses of the Loddiges family (Lindley 1838). Apparently, *S. ciliaris* was imported from somewhere in Mexico, while *S. orbicularis* was brought to the greenhouses from Demerara in the Guyanese coast. Shortly after, *Pleurothallis memor* Rchb.f. (now *Trichosalpinx memor*) was described by Reichenbach (1856). It was based on a plant with doubtful locality, cultivated by Forkel in Hamburg (Fig. 6). The species is rather common

from Mexico to the Andes and the Antilles. Its high morphological variability promoted the proliferation of synonyms, which according to Luer (1997) includes *P. brevis* Schltr., *P. gnomonifera* Ames, *Trichosalpinx greenwoodiana* Soto Arenas and *T. nageliana* Soto Arenas), as well as the entangling with other similar species in herbaria and literature (e.g., *T. ciliaris* [Lindl.] Luer and *T. blaisdellii* [S.Watson] Luer).

*Pleurothallis blaisdellii* S.Watson (now *Trichosalpinx blaisdellii* [S.Watson] Luer) was described by Watson (1888) from a plant collected in the Chocón forests of Guatemala (Fig. 7). It is distributed from Mexico to Panama and grows in sites located between 300 and 1800 m of elevation (Luer 1997). At least five species names have been considered synonyms of *T. blaisdellii* afterwards (Luer 1997).

## **2. History of Costa Rican *Trichosalpinx* species**

Auguste R. Endrés documented the first records of *Trichosalpinx* in Costa Rica. He botanized in the country between the end of 1866 and the beginning of 1874. His specimens, descriptions and illustrations were sent to his principal correspondent, Professor Reichenbach in Hamburg. Today, the materials of Endrés are preserved at the Museum of Natural History of Wien, where Reichenbach's orchid herbarium was deposited after his death (Ossenbach *et al.* 2013). Amongst those materials the type of *Pleurothallis moschata* Rchb.f., the first species of *Trichosalpinx* described from Costa Rica, is found. Although the type locality is unknown, Endrés collected this plant during one of his many expeditions to the interior of Costa Rica. He described it as having “[...] prolific stems [...] with obtuse, oblong leaves [...] and inflorescences of white-yellowish flowers [...]” (Fig. 10) (Pupulin *et al.* 2011). As usual, Endrés elaborated a set of fine sketches of the plant and

flower parts, which he sent to Reichenbach, along with the type material (Ossenbach *et al.* 2013) (Figs. 11 & 12). Reichenbach published the species in 1881 in his *Xenia Orchidacea*. After transferring it to *Trichosalpinx*, Luer (1997) reduced *T. moschata* (Rchb.f.) Luer to the synonymy of *T. arbuscula*, considering that “the collections from Central America known as *T. moschata* [...] are not specifically different from those from the Andes, although the habit is smaller”.

In 1923 Ames and Schlechter described *Pleurothallis cedralensis* Ames (1923), *P. pergrata* Ames (1923) and *P. trachystoma* Schltr. (Schlechter 1923) (Figs. 13, 14 & 15, respectively). The first two were collected around 1919 by Charles Lankester at El Guarco, south of Cartago in the Cordillera de Talamanca. *Pleurothallis cedralensis* is a commonly found species in Costa Rica, Panama, Ecuador, Venezuela and Bolivia with multiple inflorescence axes and plain yellow flowers (Luer 1997). *Trichosalpinx pergrata* is perhaps the most attractive species of the genus in Costa Rica; Ames called it “*pergrata*” in reference to the “very pleasant” appearance of the plant, characterized by the flowers with short peduncles and long, pink to red sepals. *Trichosalpinx trachystoma* (Schltr.) Luer was collected in 1921 in the vicinity of San Pedro de San Ramón, in the Cordillera de Tilarán, by Alberto M. Brenes, and sent to Schlechter for description. The type specimen at Berlin was destroyed during World War II, forcing it to be neotypified based on a drawing of the species (Barringer 1986).

Two years later Ames and Schweinfurth described *Pleurothallis nana* Ames & C.Schweinf. naming it from the Latin *nanus*, or dwarf, in allusion to the tiny size of the plant (Ames & Schweinfurth 1925; Fig. 16). Lankester collected it at “Pejibaye de Turrialba” [now Jiménez], along the Caribbean watershed of the Cordillera de Talamanca. For several decades this was the only sample known, until he found it again in 1963 in Heredia,

somewhere between Poás and Barva volcanoes in the Cordillera Volcánica Central (Luer 1997).

The same year Ames described *Pleurothallis navarrensis* Ames from plants collected by P.C. Standley at Navarro de El Muñeco in Cartago, now deposited at AMES and US (Ames 1925; Fig. 17). Ames compared this species with *Pleurothallis abjecta* Ames [today considered a synonym of *Lankesteriana barbulata* (Lindl.) Karremans, Karremans (2014)], from which it differs mainly by the abbreviate peduncle and the fimbriate, lanceolate petals.

Schweinfurth (1937) described *Pleurothallis rotundata* C.Schweinf. on the basis of a plant found by Hunter and Allen in the mountains of La Pintada, Coclé, Panama (Fig. 18). The description was based on a flower in advanced state of anthesis. In 1981, Luer described *Trichosalpinx operculata* Luer, also from Panama, distinguishing it from *T. rotundata* (C.Schweinf.) Luer by the lip that is not fimbriate in the last third, as opposed to *T. rotundata*. Nevertheless, after rehydrating the flowers of the type of *T. rotundata*, Luer reduced his *T. operculata* to the synonymy of the former species (Luer 1997).

In one of his many collecting expeditions around San Ramón de Alajuela, Brenes found a small plant with inflorescences of few pale flowers, which he sent to Harvard University. There, Schweinfurth described it as *Pleurothallis membraniflora* C.Schweinf. (Schweinfurth 1938; Fig. 19).

In 1940 Schweinfurth described *P. broadwayi* var. *tricarinata* C.Schweinf. (Fig. 20) from a plant collected in Palmira, Alajuela by A. Smith. More recently, Luer (1977) recognized this variety at the species level but the epithet *tricarinata* had been previously used for a species in *Pleurothallis*, and it was necessary to propose a new name. Luer named it *Pleurothallis carinilabia* (Luer) [now *Trichosalpinx carinilabia* (Luer) Luer].

In 1996, Luer described *Trichosalpinx fruticosa* Luer, *T. lankesteriana* Luer, *T. ringens* Luer and *T. todziae* Luer (Figs. 21–24). The first, apparently rare, was found at Cerro de la Muerte (type locality), on the highlands of the Cordillera de Talamanca in Costa Rica (Luer 1996), as well as in Guatemala and El Salvador. *Trichosalpinx lankesteriana* was described from a plant in cultivation at Lankester Botanical Garden with no collecting data. In the description, Luer indicated that *T. lankesteriana* is barely something more than a geographical variation of *T. blaisdellii* (Luer 1996), which presents ample distribution from Mexico to Panama. *Trichosalpinx blaisdellii* has been considered a morphologically very variable species, thus it is not surprising that the few morphological differences of *T. lankesteriana* had made the author reconsider the species and add it to the long list of synonyms of *T. blaisdellii* just a year later (Luer 1997).

In 1997 *Trichosalpinx parsonsii* Luer & Dod was described by Luer and Dod based upon a plant collected in 1990 by Grantham and Parsons at Santa María de Dota, on the Pacific side of the Cordillera de Talamanca (Luer 1997). The type was the only specimen known, until a plant from San Ramón de Alajuela was recently found and preserved at JBL.

#### IV. CURRENT PHYLOGENETIC CIRCUMSCRIPTION

In their phylogenetic study of Pleurothallidinae based on molecular evidence, Pridgeon and colleagues (2001) carried out separate and combine analyses of nuclear and plastid DNA sequences. Four species of *Trichosalpinx*, *T. arbuscula* (subgenus *Tubella*), *T. berlineri*, *T. blaisdellii* and *T. orbicularis* (Lindl.) Luer (subgenus *Trichosalpinx*) were incorporated in the survey, although only the last three were included in the combined tree. According to the results, *Trichosalpinx* belongs to the *Lepanthes* clade, which includes *Fronitaria*, *Lepanthes*, *Lepanthopsis*, *Pleurothallis* subgenus *Acuminatia* Luer and *Specklinia* section *Muscosae* Lindl., and *Zootrophion*. This clade had 100% bootstrap support in the combined tree. According to the authors, a unique feature identifies the clade: the existence of imbricating or sclerotic sheaths covering the stem (Pridgeon *et al.* 2001).

In the particular case, the results show that *Trichosalpinx* is a polyphyletic group. The tree from the ITS matrix shows *T. arbuscula* isolated from the other four *Trichosalpinx* species included in the analysis, and placed next to members of *Pleurothallis* subgenus *Acuminatia* [= *Pleurothallis* section *Acuminatae* Lindl. (Lindley 1859)], presently classified in the genus *Anathallis* (Pridgeon & Chase 2001). Lindley had already recognized the affinities of *T. arbuscula* with members of *Anathallis*, having placed both groups in *Pleurothallis* section *Acuminatae*. According to Lindley, these affinities are based upon the presence of racemes longer than the leaf and acuminate sepals (Lindley 1859, Pridgeon *et al.* 2001).

Furthermore, the tree from the ITS matrix shows *T. orbicularis* and *T. blaisdellii* together in a subclade of their own, with complete bootstrap support in the combined tree. For a

trained eye, the morphological affinities of *T. orbicularis*, *T. blaisdellii* and *T. berlineri* are evident, with all three species having caespitose habits with no prolific ramicauls, racemes shorter than the leaf, relatively fleshy, ciliate sepals, and an oblong lip with a central callus. However, in the study of Pridgeon and colleagues (2001), *T. berlineri* forms a subclade (although weakly supported in the combined tree) along with members of *Zootrophion* (a genus with which *Trichosalpinx* shares few morphological traits), and isolated from the group formed by *T. blaisdellii* and *T. orbicularis* (Pridgeon & Chase 2001).

A recent analysis carried out by Karremans (2014) including five species of *Trichosalpinx* confirms Pridgeon *et al.*'s (2001) results and shows that *Trichosalpinx* is, at least, biphyletic, and probably triphyletic. A first clade formed by *T. blaisdellii* and *T. orbicularis* is found (with low bootstrap support) to be sister to *Anathallis*, in turn sister to the clade formed by *Lepanthes*, *Fronitaria* and *Lepanthopsis*. A second clade formed by *T. berlineri* and *T. dependens* (Luer) Luer is sister to the recently proposed genus *Lankesteriana* Karremans, and in turn sister to *Zootrophion*. An accession of *T. arbuscula* is sister to all clades except for the outgroup species. The need of a better representation of *Trichosalpinx* taxa in phylogenetic analysis to correctly assess their evolutionary position is evident, but it is almost certain that *Trichosalpinx*, as currently circumscribed, is polyphyletic.

## V. MORPHOLOGY

### Roots

Roots are cylindrical, measuring 1–3 mm in diameter, developing from the nodes of the rhizome, with greenish or yellowish tips (Fig. 26). The formation of aerial roots was frequently observed in species of subgenus *Tubella* (Fig. 26-A). They anchor the plant to the substrate and entangle with tufts of lichens and mosses, serving an important structural function. In species of subgenus *Trichosalpinx*, only a few plants of *T. memor* and *T. blaisdellii* produced aerial roots.

Pridgeon (1982) made several observations on the root, stem and leaf anatomy of *Trichosalpinx*. In the transverse section of *T. carinilabia* he found that the velamen is uniseriate with elliptical or rectangular cells; the exodermis is uniseriate with long, rectangular, polygonal or elliptical cells with U-shaped wall thickenings (no details to the identity of the wall are mentioned), while the passage cells have thin walls. The cortical parenchyma cells are isodiametric to elliptical in cross section, and the endodermis is uniseriate with O- or U-shaped periclinal wall thickenings. The pericycle is also uniseriate; the stele is tetrarch and the pith sclerotic (Pridgeon 1982, Pridgeon *et al.* 2005).

Root morphology showed no special value in the taxonomy of the group at the specific level. Characters evaluated (color, length and diameter) varied regardless of the species. However, production of aerial roots was representative of subgenus *Tubella*.

### Stems

Although there is some agreement in the application of the term rhizome to designate the horizontal portion of the stem, the application of a name to designate the vertical portion that bears leaves and inflorescences is more controversial. It has been called a “secondary stem” (), but the term contradicts the concept that both the horizontal and vertical portions are formed by a succession of nodes and internodes, and thus, refers to a single organ, a unique stem (Dressler 1981). Stern and Pridgeon (1984) proposed the term “ramicaul” to distinguish it from the rhizome; nevertheless, the word itself has been considered inappropriate because the first part refers to a (not necessarily present) branching property of the term (Rasmussen 1985). Soto Arenas (1987) used “stem” to name the vertical portion after considering that it was impossible for it to be confused with any other organ of the plant. Here, I use the terms rhizome and ramicaul, the latter defined as the part of the stem above of the last reiteration bud in Pleurothallids. This term has been used extensively in the most thorough taxonomic treatments of *Trichosalpinx* (Luer 1983, 1986, 1994), which are baselines for this systematic study.

The first internodes of each sympodial unit are somewhat thickened and grow horizontally, and make up the segment of stem called the rhizome. In this portion of the stem, meristems produce new shoots and roots. The ramicauls produced are terete, from 7 mm (as in *T. parsonsii*) to 20 cm long (as in *T. minutipetala*), mostly slender and elongated (Fig. 27). In subgenus *Tubella* prolific stems are present in all the species except for *T. pergrata*. The ramicauls are frequently longer than the leaves, and have three or more internodes. The presence of a conspicuous annulus is consistent in all species. Although production of new shoots from the apical meristems is characteristic in subgenus *Tubella* (Fig. 28A), the same phenomenon was observed in some plants of subgen.

*Trichosalpinx* in the wild and in cultivation. Producing proliferations may enhance the plant photosynthetic capability.

The ramicaul cortex is composed of sclerified subepidermal layers and parenchymatous inner cells. The vascular bundles are colateral and arranged in one or two concentric rings, with sclerenchyma bundle caps mostly developed at the outer (phloem) flank. The outermost ring of vascular bundles is continuous with the sclerenchyma sheath, and there can be up to eight cell layers between bundles (Pridgeon 1982).

Ramicaul size and shape are diagnostic for some Costa Rican taxa. The fractiflex ramicaul of *Trichosalpinx ciliaris* is unique to that species. The ramicauls of the prolific *T. arbuscula*, which forms long chains of superposed ramicauls, reach as long as 23 cm altogether, and easily exceed the length of all other Costa Rican species. In *T. pergrata*, the absence of prolific ramicauls separates this species from other Tubellas.

### **Ramicaul sheaths**

Ramicauls are covered with lepanthiform sheaths, a term used to describe the sheaths of several taxa including *Draconanthes*, *Lepanthes*, *Lepanthopsis* and *Trichosalpinx*.

Lepanthiform sheaths are tubular, more or less imbricate, longitudinally ribbed with oblique ostia, frequently dilated and thickened at the margins; the ribs and margins can be ciliate, scabrous or rarely glabrous.

When young, sheaths are glumaceous and frequently densely covered with purplish cilia. When old, sheaths turn dry and fibrous with less numerous, harder cilia. The apical sheath of the ramicaul is longer and wider than the rest (although this is less evident in *Tubella*),

and the apex is often elongated to cover both the petiole and the base of the leaf blade. The distalmost sheath tissue can be broken by the emergence of new organs, like leaves, inflorescences and roots.

Taxonomically, sheath morphology is only significant to distinguish the two subgenera of *Trichosalpinx* present in Costa Rica. In subgenus *Trichosalpinx*, the sheaths are mostly funnel-shaped, and the ostia has particularly thickened margins; plants of *T. minutipetala* bear amply dilated ostia. In species like *T. blaisdellii*, *T. memor* and *T. minutipetala* the distalmost sheath of a ramicaul is reticulated (Fig. 28C).

In subgenus *Tubella* the sheaths are more tubular and adpressed. The longitudinal ribs are more evident when the sheaths have recently developed (Fig. 28B).

### **Leaves**

Most *Trichosalpinx* species show well developed, conduplicate, erect to suberect, thin to fleshy or coriaceous, glabrous, ovate to elliptic, acute to obtuse leaves. Members of subgenus *Trichosalpinx* bear mainly coriaceous, fleshy, ovate to elliptic, acute leaves with short (5–15 mm) petioles (Fig. 27). In this subgenus, overall leaf size is greater than in members of *Tubella*. The leaves of some species (as *T. blaisdellii*, *T. memor* and *T. rotundata*) are suffused with purple beneath, more intensively along the veins.

Some leaf characters are of diagnostic use. Only plants of *T. ciliaris*, *T. minutipetala* and *T. reflexa* develop narrowly elliptical, acute leaves. Along with distribution data and the shape of ramicaul sheaths, the coriaceous, convex, orbicular leaves of *T. caudata*, *T. orbicularis* and *T. rotundata* are helpful when determining specimens.

On the other hand, species of *Tubella* bear ascending to erect, coriaceous, glabrous, orbicular to ovate, acute to subacute leaves, with short petioles 0.3–5.5 cm long. The leaves of this group tend to be smaller than those of subgenus *Trichosalpinx* (1.2–8.1 cm).

Young leaves frequently show purple-stained veins, more evident abaxially, as in *T. cedralensis*, *T. dura* and *T. pusilla* (Kunth) Luer. This peculiarity is also observed in some species of *Lepanthes* and *Zootrophion*.

Iridescence was observed on the adaxial leaf surface of several individuals of *T. blaisdellii* and *T. memor*, frequently found in the main trunk of trees and bushes at understory level. This phenomenon may be an adaptation for the capture of photosynthetically active light in leaves that have grown in low light conditions (Glover & Whitney 2010).

As summarized in Pridgeon *et al.* (2005), there are hairs present on both surfaces (glandular, sunken, consisting of two or three cells), while the stomata are restricted to the abaxial surface. The epidermal cells are polygonal, rectangular or elliptical, usually with conspicuous primary pit-fields. In the transverse sections the cuticle is of variable thickness, often minutely papillose; the epidermal cells are elliptical, rectangular, or peg-shaped, and adaxial cells are larger than abaxial cells. The stomata are flushed with the abaxial surface. The hypodermis presents spiral thickenings; the chlorenchyma is heterogeneous, the pallisade mesophyll 1-3 layers, spongy 4-10 layers; spirally thickened idioblasts are present. Vascular bundles are collateral and arranged in a single row in the centre of the mesophyll; the largest bundles with sclerenchyma caps of 1–2 files of fibers adaxially and up to four files of fibers abaxially. Fiber bundles are absent. For more details on the anatomical structure of *Trichosalpinx*, see Pridgeon (1982) and Pridgeon *et al.* (2005).

## Inflorescences

Inflorescences of *Trichosalpinx* are alternate, distichous, mostly secund, erect, descending or pendulous, terminal racemes (except for the fascicles produced by *T. ringens* and *T. sanctuarii*). The structure is remarkably similar throughout the examined species.

Peduncles are produced at the apex of the ramicaul near the base of the adaxial face of the leaf from a conduplicate, papyraceous, ovate to triangular, acute spathe, 1–2 mm long. Although most examined inflorescences grow adpressed against the abaxial leaf surface, the peduncles occasionally turned around the petiole and grow facing the adaxial leaf surface. The rachis is terete, glabrous and persistent, and is covered with small, papyraceous floral bracts. Ovaries and pedicels are terete, glabrous, from 1 to 3.5 mm long and exhibit no ornamentation. Ovaries are shallowly, longitudinally channeled. In most species, peduncles shift direction, positioning flowers in a secund or subsecund accommodation. After flowering, the pedicels remain photosynthetic and are persistent until they become dry.

With the exceptions of the few-flowered *Trichosalpinx pergrata*, *T. ringens* and *T. sanctuarii*, inflorescences of Costa Rican *Trichosalpinx* species produce three or more flowers per inflorescence (Fig. 29). Furthermore, one to three racemes can develop simultaneously from the same ramicaul.

As noted by Luer (1997) inflorescence/leaf length ratio is diagnostic at the subgeneric level. Inflorescences of the nominal subgenus are mostly shorter than the leaf, while in species of *Tubella* the inflorescence is commonly longer than the leaf, except in *T. pergrata*.

## Flowers

Dorsal sepals are mostly broadly ovate to narrowly triangular with acuminate to attenuate apices. Lateral sepals frequently form a mentum at the base to accommodate the column-foot. The sepals of subgenus *Trichosalpinx* are fleshy, ciliate and colorful (dark vinaceous, red, purple), with a white base and discolored, thickened apices. The lateral sepals in this subgenus are fully or partially connate, and sometimes form a concave synsepal or bifid laminae, as in *T. ciliaris* and *T. blaisdellii*, respectively. In subgenus *Tubella*, the sepals are membranous, free to partially free, carinate, glabrous and mostly unicolor, white to yellowish or greenish, except for the fuchsia to pink coloration of *T. pergrata*. (Fig. 30).

Petals are very similar among species; they are consistently straight, flat, membranous (except for the fleshy petals of *T. pergrata*, *T. ringens* and *T. sanctuarii*), 1-veined, mostly ovate to elliptical, oblique in shape, and acute to acuminate or obtuse, often with fimbriate or denticulate apical margins.

Lips are ovate to oblong with the disc broadened in, at least, half of the species, but simpler or more complex lips also occur. Lips in subgenus *Trichosalpinx* are mostly brown-purple to dark purple, marginally ciliate, oblong, orbicular or triangular, from 2 to 4 mm long. The disc (in this treatment, the central area along the basal half of the lip) usually bears a keel or callus from the base to the middle where it disappears or forks in two. The base presents two retrorse auricles; the apex is usually not thickened, softly descendent. The lip is attached to the column-foot by a flexible, membranous hinge (except in *T. ringens* and *T. sanctuarii*, where the lip is rigidly attached to the column foot) that enables it to move up and down with the help of wind or pressure, as in some species of *Bulbophyllum* (Teixeira *et al.* 2004) and *Lankesteriana* (Karremans 2014). In subgenus

*Tubella*, lips are yellow or white, glabrous, elliptical-oblong, flat to slightly arcuate; the base is frequently broadened, with erect, lateral lobes; the apex is thickened in most species. The presence and shape of a longitudinal callus in the disc area, as well as the thickening of the midvein and apex are of diagnostic value in species of both subgenera.

Although they belong to subgenus *Trichosalpinx*, *T. ringens* and *T. sanctuarii* have a general flower architecture that differ significantly from the rest of the group. The dorsal sepals are narrowly ovate, thick and erect, and the veins are profusely stained. Petals are ciliate, thick and 3-veined. The lips are fleshy, arcuate and the adaxial surface is partially pillose; they lack the basal, retrorse lobules and the flexible hinge present in other species, which suggests a different pollination syndrome (Fernández & Bogarín 2013).

In general terms, columns are white, straight, terete, with a variously irregular apex, and with a projected basal portion forming a conspicuous column foot, to which the lip attaches by a membranous articulation. The apical portion of the column can be provided with lateral appendages called wings, more frequently in subgenus *Trichosalpinx*. The anther is apical and the stigma ventral in subgenus *Trichosalpinx*, while both are mostly ventral in subgenus *Tubella* (Fig. 31). The anther cap is incumbent, ovate and emarginate.

### **Pollinaria**

Pollinaria are formed by two ovoid to pyriform pollinia. Their structure can be of three basic kinds: a) pollinia with a flat pair of suborbicular to ovate, basally adjoined caudicles (“whale-tail” pollinaria *sensu* Karremans *et al.* 2013), as in subgenus *Trichosalpinx* (Fig. 32A); b) pollinia free or adjoined by the cellular, oval caudicles, as in subgenus *Tubella* (Fig. 32B); c) pollinia free with no evident joining structure upon removal from the anther,

as in *T. sanctuarii*. As in other orchids lacking a viscidium, the viscous, hyaline substance present in the rostellum presumably allows the attachment of the pollinia to the back of the pollinator, enabling their removal when the pollinator recedes to leave the flower (Fernández & Bogarín 2013).

## **Fruits**

Fruits are fleshy, ovoid, 3-valved, dehiscent capsules with parietal placentation. The external surface is smooth, shiny and not ornamented; in subgenus *Trichosalpinx* it is usually pigmented with pink or fuchsia, while in species of *Tubella* it remains green. Dehiscence is loculicidal, but the capsules split along only two functional longitudinal slits, as observed in most pleurothallids (Fernández *et al.*, in prep.). The dehiscence lines are incomplete, so that the two valves of the capsule remain united at both ends. Perianth remnants are persistent at the apex of the fruit (Fig. 33).

Hygroscopic endocarpic trichomes occur in the fruits of *Trichosalpinx*. The trichomes are unicellular, borne in two rows on either side of each carpel midrib. The capillitium (the aggregation of the trichomes) is responsible for dispersing seeds when they twist and recoil with changes of humidity as soon as the fruit opens (Dunsterville 1969, Blanco *et al.* 2006, Rasmussen & Johansen 2006). The seeds form masses that are densely attached around the prolongations of the placentae. Each mass is interspersed by several trichomes, but not all trichomes intersperse masses of seeds. The seeds of *Trichosalpinx* subgenus consist of an oval embryo that occupies nearly a fourth of the total length of the fusiform testa. The testa bears subquadrate to linear periclinal walls. The seeds of species in subgenus *Tubella* are unknown.

Fruits have been uncommonly found in the wild. However, plants of *T. blaisdellii*, *T. memor* and *T. reflexa* cultivated in the greenhouses at Lankester Botanical Garden produce fruits abundantly.

Diagnostic fruit characters at the specific level were not found during the course of this study, especially because of the lack of fruit production in most species. However, some tendencies can be inferred at the subgeneric level. Fruits of subgenus *Trichosalpinx* tend to be bigger, ellipsoid and suffused with red or pink externally. In subgenus *Tubella* fruits are smaller, spheroid and green with no red stains. Further studies are needed to evaluate their diagnostic use in taxonomy.

## VI. SYSTEMATIC TREATMENT

In 1983, Luer created the genus *Trichosalpinx* to allocate species with lepanthiform sheaths, which are also present in *Draconanthes*, *Lepanthes* and *Lepanthopsis*. Nevertheless, *Trichosalpinx* is differentiated by the longer rather than broader petals (transversely bilobed in *Lepanthes*), the lip with an elongate mid lobe (absent or turned into a small appendix in *Lepanthes*), trilobed, usually membranous petals (simple in *Lepanthopsis*, fleshy in *Draconanthes*), and an elongate column with an elliptical stigma (short, with a transversally bilobed stigma in *Lepanthopsis*) usually provided with a foot (without a foot in *Lepanthes*, *Lepanthopsis* and *Draconanthes*; Luer 1997, Luer & Thorerle 2010).

According to the classification of Luer (1986, 1997), the genus is subdivided in four subgenera: *Trichosalpinx*, *Tubella* Luer, *Pseudolepanthes* Luer and *Xenia* Luer. Subgenus *Trichosalpinx* is composed of species of caespitose habit with non-prolific ramicauls and usually coarse lepanthiform sheaths, racemes shorter than the leaf (except for *T. pringlei*), petals that are frequently ciliate, denticulate, erose, fimbriate or serrate, a lip with two basal, retrorse auricles (except for *T. pringlei*), and a straight column with a foot (Luer 1997). Species belonging to subgenera *Tubella* are mostly provided with prolific stems, racemes commonly longer than the leaf, an oblong, ovate, entire or trilobed lip with 2 or 3 longitudinal calli and no basal auricles, and a column foot, to which the lip is attached.

Subgenus *Pseudolepanthes* is characterized by the non-prolific stems, racemes longer than the leaf, sepals more or less spiculate, a thick, wide, basally unguiculate lip with a conspicuous, verrucose callus, and a footless column (Luer 1997). Finally, subgenus *Xenia* clusters species with no resemblance to the other three subgenera. Few are the

characteristics shared among the species of subgenus *Xenia*, including non-prolific ramicauls, racemes longer than the leaf, glabrous sepals, a variously lobed lip with a callus, and a footless column (Luer 1997). All known species belonging to this two subgenera are found in South American countries, with emphasis in Colombia and Ecuador.

While some *Trichosalpinx* species present low morphological variability, others (generally those with ample distribution) appear to form complexes characterized by numerous morphological variations. In Costa Rica, may be observed among populations of *T. blaisdellii*, *T. dura*, *T. memor* and *T. orbicularis*. Luer emphasized his opinion that the recognition of these variations as different taxa, far from clarifying relationships, can lead to a major confusion in the taxonomy of the group (Luer 1997). Nonetheless, the systematic study of morphological, anatomical biogeographical and molecular data sets, supported by an ample sampling of these species complexes, can offer relevant information about the variation allowing, in some cases, the recognition of well-defined entities.

Archila (2000) elevated subgenera *Tubella* (to which he also added species from subgenus *Xenia*) and *Pseudolepanthes* to the generic level. These transfers were based on morphological differences –some of which previously recognized by Luer (1997)– including the inflorescence/leaf length ratio in relation to that of the leaf, ramicaul branching degree, presence of roots growing from the base of proliferating ramicauls, anther position, and shape and size of the rostellum and caudicle. To further support his proposal, Archila cited differences in the type of leaf venation and the composition of flavonoids, but he did not indicate which species and how many samples per species were

analyzed. In the present treatment, the traditional circumscription of *Trichosalpinx* is provisionally accepted (i.e., including subgenus *Tubella* and *Pseudolepanthes*).

***Trichosalpinx*** Luer, *Phytologia* 54(5): 393–394. 1983. TYPE SPECIES: *Trichosalpinx ciliaris* (Lindl.) Luer, *Phytologia* 54(5): 395. 1983. BASIONYM: *Specklinia ciliaris* Lindl. Edwards's Bot. Reg. 24: Misc. 31. 1838.

***Trichosalpinx*** subgenus ***Trichosalpinx*** Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 15: 1–81. 1986.

= *Pleurothallis* section *Lepanthiformes* (Lindl.) Cogn., *Flora Bras.* 3(4): 579. 1896, in part. BASIONYM: *Pleurothallis* section *Brachystachyae* subsection *Lepanthiformes* Lindl., *Fol. Orch.*, *Pleurothallis* 25. 1859. LECTOTYPE SPECIES, designated by Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 15: 65. 1986: *Specklinia ciliaris* Lindl., Edwards's Bot. Reg. 24: Misc. 31. 1838.

= *Pleurothallis* section *Bipaleolatae* Pabst, *Orchid. Bras.* 1: 162. 1975. TYPE SPECIES: *Specklinia orbicularis* Lindl., Edwards's Bot. Reg. 24: 31. 1838.

***Trichosalpinx*** subgenus ***Tubella*** Luer, *Monogr. Syst. Bot.* 15: 66. 1986. TYPE SPECIES: *Pleurothallis acremona* Luer, *Selbyana* 5(2): 157. 1979.

= *Pleurothallis* sect. *Elongatae* subsect. *Lepanthiformes* Lindl., *Fol. Orch.*, *Pleurothallis* 26. 1859. LECTOTYPE SPECIES, designated by Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 15: 65. 1986: *Pleurothallis chamaelepanthes* Rchb.f., *Bonplandia* 3: 240. 1855.

= *Pleurothallis* sect. *Acuminatae* subsect. *Lepanthiformes* Lindl., Fol. Orch. Pleuroth.

32. 1859. LECTOTYPE SPECIES, designated by Luer, Monogr. Syst. Bot. Missouri Bot. Gard.

15: 65. 1986: *Pleurothallis arbuscula* Lindl. Edwards's Bot. Reg. 28: Misc. 72-73. 1842.

= *Trichosalpinx* subgen. *Tubella* sect. *Tubellae* Luer, Monogr. Syst. Bot. Missouri Bot.

Gard. 15: 68. 1986.

= *Tubella* Archila, Revista Guatemalensis 3(1): 46. 2000. TYPE SPECIES: *Pleurothallis*

*acremona* Luer, Selbyana 5: 157. 1979.

***Trichosalpinx*** subgen. ***Pseudolepanthes*** Luer, Monogr. Syst. Bot. Missouri Bot. Gard.

64: 5. 1997. TYPE SPECIES: *Trichosalpinx pseudolepanthes* Luer & Escobar, Orquideología

16(2): 183. 1984.

= *Trichosalpinx* subgen. *Tubella* sect. *Pseudolepanthes* Luer, Monogr. Syst. Bot. Missouri

Bot. Gard. 15: 68. 1986. TYPE SPECIES: *Trichosalpinx pseudolepanthes* Luer & R.Escobar,

Orquideología 16(2): 183. 1984.

= *Pseudolepanthes* Archila, Revista Guatemalensis 3(1): 76. 2000. TYPE SPECIES:

*Trichosalpinx pseudolepanthes* Luer & R.Escobar, Orquideología 16(2): 183. 1984.

***Trichosalpinx*** subgen. ***Xenia*** Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 6. 1997.

TYPE SPECIES: *Trichosalpinx escobarii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64:

114. 1997.

= *Tubella* Archila, Revista Guatemalensis 3(1): 46. 2000. TYPE SPECIES: *Trichosalpinx*

*escobarii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 114. 1997.

### 1. Key to the Costa Rican subgenera and species of *Trichosalpinx*

Out of the four subgenera, only subgen. *Trichosalpinx* and *Tubella* have representatives in Mesoamerica. Based on the morphological differences given in this treatment, three keys to the Costa Rican *Trichosalpinx* are presented. Species not found during the course of this study were included in the keys based on the protologue and exsiccata material, and marked with an asterisk (\*).

Key to the subgenera of Costa Rican *Trichosalpinx*

1 Ramicauls not prolific, with coarse lepanthiform sheaths; racemes shorter than the leaf; petals frequently ciliate, denticulate, or fimbriate; lip entire, the base with two auricles, the disc with one central callus ..... subgenus ***Trichosalpinx***

1' Ramicauls prolific (except in *T. pergrata*), with papyraceous to coarse lepanthiform sheaths; racemes longer than the leaf (except in *T. pergrata*); petals entire; lip entire or trilobed, the base without auricles, the disc with or without a prominent midvein, and frequently with two lateral, longitudinal calli ..... subgenus ***Tubella***

Key to the Costa Rican species of subgenus *Trichosalpinx*

- 1 Leaves ovate, orbicular or elliptic ..... 2
- 2 Inflorescence a successive 1- or 2- simultaneously flowered fascicle, present on the adaxial leaf surface ..... 3
- 3 Sepals longitudinally veined, yellow with brown-red along the veins; petals translucent with red stripes; lip trilobed, with a central callus that forks in two below the middle, gently arcuate, with no plates ..... ***T. sanctuarii***
- 3' Sepals purple-brown and pale yellow toward the apices; petals entirely brown-red; lip entire with no callus, deeply arcuate, with a pair densely ciliate lamellate plates ..... ***T. ringens***
- 2' Inflorescence a several-flowered raceme, presented on the abaxial leaf surface ..... 4
- 4 Sepals connate to near their apex, forming a concave synsepal ..... 5
- 5 Lip apex broadened, without a longitudinal keel ..... ***T. trachystoma***
- 5' Lip apex acute to obtuse, with a longitudinal, apically bifid keel from the base to near the middle ..... ***T. memor***
- 4' Sepals connate to the middle of their length or less, forming a bifid blade ..... 6
- 6 Sepals glabrous ..... 7
- 7 Dorsal sepal narrowly triangular; lateral sepals fleshy, thickened at the apex ..... ***T. caudata***
- 7' Dorsal sepal ovate; lateral sepals membranous, not thickened at the apex ..... ***T. orbicularis***
- 6' Sepals pubescent ..... 8
- 8 Petals almost as long as sepals; lip with the margin ciliate or fimbriate, the adaxial surface glandular-pubescent ..... ***T. navarrensis\****

- 8' Petals half or less as long as sepals; lip with the margin entire, the surface  
smooth ..... 9
- 9 Lip yellow, narrowly triangular ..... ***T. rotundata***
- 9' Lip purple, oblong ..... ***T. blaisdellii***
- 1' Leaves narrowly elliptic to lanceolate ..... 10
- 10 Synsepal reflexed ..... ***T. reflexa***
- 10' Synsepal concave ..... 11
- 11 Petals quadrate; lip sharply reflexed ..... ***T. minutipetala***
- 11' Petals oblong; lip straight ..... ***T. ciliaris***

Key to the Costa Rican species of subgenus *Tubella*.

- 1 Ramicauls not prolific, with the sheaths densely hispid along ribs and margins; sepals fuchsia-rose to dark-rose (exceptionally yellow) ..... ***T. pergrata***
- 1' Ramicauls prolific, with the sheaths minutely ciliate along ribs and margins; sepals yellow or white ..... **2**
- 2 Leaves fleshy, obovate to obelliptic, surface convex, dark green to purple .. ***T. pusilla***
- 2' Leaves coriaceous, elliptic, flat, green or stained with purple only along the veins ... **3**
- 3 Lateral sepals reflexed ca. 90 degrees at the base; petals crenate .. ***T. carinilabia***
- 3' Lateral sepals straight or slightly reflexed in the apical half; petals entire or occasionally serrate ..... **4**
- 4 Petals ovate ..... ***T. fruticosa***
- 4' Petals obovate or elliptical ..... **5**
- 5 Lip apex not thickened ..... **6**
- 6 Lip without lateral lobes ..... ***T. arbuscula***
- 6 Lip with lateral lobes ..... ***T. membraniflora***
- 5' Lip apex thickened ..... **7**
- 7 Lip with lateral, erect lobes, the disc without calli or thickened midvein ..... ***T. cedralensis***
- 7' Lip with no lobes or subtle lateral lobes, these not erect ..... **8**
- 8 Lip disc flat ..... ***T. parsonsii***
- 8 Lip disc with a central calli or thickened midvein ..... **9**
- 9 Lip with two submarginal, longitudinal calli and a thickened midvein; column broadly winged apically ..... ***T. dura***

- 9' Lip with two shallow thickenings at the forward angle between the lateral lobes and the papillous inferior lobe; column obtusely winged apically ..... 10
- 10' Plants erect; pedicels 1.5-4.0 mm; sepals long-attenuate; lip flat or inconspicuously thickened apically ..... ***T. todziae***
- 10' Plants descendent or pendulous; pedicels 2.5-6.0 mm long; sepals acute; lip conspicuously thickened apically ..... ***T. nana***

## 2. Species description and discussion

The most recent published catalogue of Costa Rican orchid species (Ossenbach *et al.* 2007) recorded twenty species of *Trichosalpinx* for the country. Since then, two new species have been added (Fernández & Bogarín 2011, 2013) and another one, previously considered a synonym, has been shown to be a good species (Fernández 2011), all as part of the present study. In the following account, species are presented alphabetically by their currently accepted name. Square brackets [ ] indicate entries made by the author that do not necessarily reflect data present on the specimen labels or the protologue.

### 1. *Trichosalpinx arbuscula* (Lindl.) Luer, *Phytologia* 54(5): 394. 1983.

BASIONYM: *Pleurothallis arbuscula* Lindl., Edwards's Bot. Reg. 28: Misc. 72–73.

1842. *Humboldtia arbuscula* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891, *nom. illeg.*

TYPE: Perú [Ecuador] found near Loja, *Hartweg s.n.* (holotype, K-79691; isotype, AMES-118556; photo of type, AMES, LD, W). Fig. 34.

*Trichosalpinx dinotherii* (Rchb.f.) Luer, *Phytologia* 54: 395. 1983. BASIONYM:

*Pleurothallis dinotherii* Rchb.f & Warsc., *Bonplandia* 2: 114. 1854. *Humboldtia*

*dinotherii* (Rchb.f.) Kuntze, *Rev. Gen. Pl.* 2: 667. 1891, *nom. illeg.* TYPE: Perú,

*Warscewicz s.n.* (holotype, K; isotype, AMES; drawing of type, AMES-38011).

*Pleurothallis diptera* Lindl., *Fol. Orchid. Pleurothallis* 44. 1859. *Humboldtia diptera*

(Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 667. 1891, *nom. illeg.* TYPE: Ecuador: Pichincha,

forest on the road to Nanegal, *Jameson s.n.* (holotype, K; drawing of type, AMES).

*Trichosalpinx moschata* (Rchb.f.) Luer, Phytologia 54: 396. 1983. BASIONYM:  
*Pleurothallis moschata* Rchb.f., Xenia Orchid. 3(2): 42–43, t. 217. 1881. TYPE:  
 Costa Rica: Cultivated at Hamburger Botanischen Garten, collected by Endres in  
 Costa Rica, *Endres s.n.* (holotype, W).

*Pleurothallis lepanthoides* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 106.  
 1920. TYPE: Colombia: Cauca, *M. Madero s.n.* (holotype, B, destroyed; neotype  
 designated by Luer (1997, as “lectotype”), AMES-28789, illustration of type).

*Pleurothallis tricaudata* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 77. 1921.  
 TYPE: Peru: Huánuco, Huánuco, mountains between Chinchao and Acomayo, Sept  
 1913, 3100–3200 m, *Weberbauer 6827* [holotype, B, destroyed; lectotype, selected  
 by Christenson (1996), MOL; isolectotypes, AMES, MOL, US].

*Trichosalpinx arbusculoides* (Hashimoto) Luer, Phytologia 54: 394. 1983.  
 BASIONYM: *Pleurothallis arbusculoides* Hashimoto, Bull. Natl. Sci. Mus. 4: 9. 1978.  
 TYPE: Bolivia: Pampatambo, Chapare, division to Ende Planta Corani, 68 km  
 northeast of Cochabamba, 7 Dec 1974, *Nishida, Ono, Hashimoto & Ohga 01043*  
 (holotype, TNS).

**Herb** epiphytic, caespitose, erect, up to 33 cm tall including the inflorescence. **Roots**  
 slender, flexuous, to 1 mm in diameter. **Ramicauls** erect to ascendent, slender to stout,  
 prolific, 2–7 cm long, enclosed by 3–9 tubular, papyraceous, ribbed, microscopically ciliate,  
 lepanthiform sheaths, 4–15 mm long, pale to dark brown, basally adpressed, obtuse and  
 dilated apically. **Leaves** elliptical to obovate, apiculate, erect, coriaceous, 0.7–3.5 × 0.4–  
 1.5 cm, basally cuneate, narrowing into a petiole up to 1 cm long. **Inflorescence** a 9–13

successively flowered, distichous raceme, 6–10 cm long including the peduncle 2–4 cm long, produced at the apex of the ramicauls from a conduplicate, ovate, acute spathe.

**Floral bracts** cuneiform, conduplicate, papyraceous, 1–2 × 2 mm. **Pedicels** 2–6 mm long, persistent. **Ovary** cylindrical, 1 mm long. **Flowers** with the sepals basally white, green towards the apex, occasionally suffused with pink-purple along the veins; petals translucent white; the lip brown at the base and greenish-yellow towards the apex, the column green, the column-foot brown, the anther yellow. **Dorsal sepal** narrowly ovate, basally concave, acute, attenuate, glabrous, carinate, 7–10 × 2–3 mm, 3-veined. **Lateral sepals** narrowly ovate to triangular, basally concave, oblique, glabrous, carinate, 7.0–9.6 × 1.3–2.0 mm, 3-veined. **Petals** elliptic to obovate, attenuate, obtuse, entire, repand towards the apex, 1.8–2.3 × 0.6–1.0 mm. **Lip** oblong, obtuse, arcuate, glabrous, 2.0–2.5 × 1 mm; disc with two longitudinal, lateral calli; midvein thickened; submarginal surface papillose. **Column** semiterete, broadly and deeply winged above the middle, 1.2–1.8 mm long; clinandrium apical; stigma ventral. **Anther cap** incumbent, broadly ovate, emarginate. **Pollinia** 2, pyriform, on a pair of cellular, ovate caudicles. **Fruit** not seen.

**Distribution.** Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru and Bolivia (Luer, 1997).

**Additional material examined. Costa Rica.** – **Alajuela:** San Ramón, Piedades Sur, San Miguel (La Palma), en El Alto después de San Bosco, 10°07'43.7"N 84°33'13.5"W, 1289 m, en árboles solitarios en potrero, 21 Dic 2010, A. Karremans 3303, J.A.J. Karremans & M. Contreras (JBL-D4775); A. Karremans 3304, J.A.J. Karremans & M. Contreras (JBL-D4774); – San Ramón, Reserva Biológica A. M. Brenes, 900 m, 23 May 1998, flowered in cultivation at Jardín Botánico Lankester, Oct 2001, M.A. Blanco 872 (USJ-80003); – San

Ramón, Angeles, Reserva Biológica A.M. Brenes, alrededores de la Estación Biológica del Río San Lorencito, 900-1100 m, 27-28 agosto 2011, *M. Blanco 4047* (JBL-D6219); *M. Blanco 4048*, *J. Abarca*, *M. Díaz*, *M. Chavarría* & *J. Gómez-Laurito* (JBL-D5757); – *M. Blanco 4049*, *J. Abarca*, *M. Díaz*, *M. Chavarría* & *J. Gómez-Laurito* (JBL-D5758); – *M. Blanco 4050*, *J. Abarca*, *M. Díaz*, *M. Chavarría* & *J. Gómez-Laurito* (JBL-D5759); – *M. Blanco 4052*, *J. Abarca*, *M. Díaz*, *M. Chavarría* & *J. Gómez-Laurito* (JBL-D5763). –

**Cartago:** Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1542 m, bosque pluvial premontano, epifitas en bosque secundario y árboles en zonas abiertas, 22 abr 2008, *D. Bogarín 4500*, *A. Gaillard*, *R. Gómez*, *Y. Kisel*, *R. Phillips* & *R. Trejos* (JBL-D3831); – Paraíso, Orosi, P.N. Tapantí, estribaciones Sur, Alto Peralta, 9.75 -83.783, 1400 m, 21 Dic 1992, *G. Herrera 5816* (CR-169702, USJ-050992); – Turrialba, Tayutic, Moravia de Chirripó, unos 3 Km después de un albergue en Hacienda Moravia, siguiendo la calle hacia platanillo, 500 m más arriba de la única pulpería que hay en el lugar, sobre unos trechos al lado de la calle, bosque perturbado, 9°50'12" N - 83°25'35" W, 1000-1200 m, 30 jul 2005, *A. Karremans 870* & *P. Ferreira* (JBL-D4398). – **Heredia:** [Santa Bárbara], Los Cartagos, 10.139 -84.172, 1900 m, flores de color amarillo, *C.A. Todzia 909* (CR-73525). – **Limón:** Talamanca, Bratsi, P.N. La Amistad, río Coén, río Lori, cerro junto al paso del Sendero de Ujarrás a San José Cabecar, 9.356944 -83.222222, 1800 a 1900 m, epífita, botones verde amarillentos, crece sobre troncos, 22 mar 1993, *A. Fernández 788* (INB-572816); – Límite entre Limón y Puntarenas: Talamanca-Buenos Aires, Bratsi-Potrero Grande, Parque Internacional La Amistad, Sector Altamira, sendero al Valle del Silencio, Cerro Hoffman, sobre la divisoria de aguas, 9°05'38.2" N 82°58'37.73" W, 2553 m, bosque pluvial montano, 14 ago 2012, *D. Bogarín 9780*, *M. Fernández*, *J. Godínez*, *A.*

*Karremans, J. Kruizinga & C. Smith* (JBL-E1026). – **San José:** Aserrí, Legua, La Legua, camino desde Fila El Alto hacia la cumbre del Cerro Caraigres (Cerro Dragón), 9°43'01.0"N 84°07'43.5"W, 2266 m, bosque pluvial montano bajo, epífitas en bosque secundario sobre el borde de bosque y potrero, 23 abr 2009, *D. Bogarín 6861*, *Y. Kisel*, *P. Renshaw*, *R. Trejos & M. Turjak* (JBL-D3871); – Aserrí, Legua, Z.P. Caraigres, Fila Aguabuena, Faldas cerro Dragón, 9.716667 -84.125, 2000 a 2100 m, epífita, flores verde claro, 7 mar 1997, *Q. Jiménez 2254* (INB-828373); – Moravia, San Jerónimo, P.N. Braulio Carrillo, río Sucio, Zurqui Station, about 0.5 km SE of Estación de Peaje, at Park border, epiphytic at base of tree trunk at pasture/ 2' forest edge, 10.052778 -84.005556, 1600 a 1700 m, 26 Oct 1990, *S. Ingram 631* (INB-563177); – Vásquez de Coronado, Jesús, hacia Montserrat (mismo lugar del # 11 del 09.04.2002), 10°01'02" N 83°56'27" W, 1845 m, en musgo, en la sombra, en ca. 1 m en el tronco, 18 Apr 2003, *W. Schug 98*, *W. Tresch & J. Wurmet* (JBL-D0469); – Vásquez de Coronado, Jesús (Dulce Nombre), río Blanco, camino a Los Juncos, R.F. Cordillera Volcánica Central, 10.036111 -83.922222, 1500 a 1600 m, epífita, flores crema con líneas rosadas, 23 nov 2003, *J.F. Morales 10117* (INB-4008418, 4008419, 4008420, 4008421; CR-271114). Fig. 35.

**Habitat and ecology.** Epiphytic in premontane wet and lower montane wet forests in borders of secondary vegetation and in scattered trees in open areas, from 900 to 2300 m of elevation.

**Etymology.** From the Latin *arbusculus*, “a little tree”, in allusion to the branching habit.

**Phenology.** Plants flower mainly between November and February, but sporadic flowering occurs at any time of the year in cultivation. Based on exsiccata material, plants flowered continuously from October to March. Fruits were collected from February to March.

**Discussion.** When not in flower, plants of *Trichosalpinx arbuscula* are distinguished by the long chains of ramicauls that size >20 cm long altogether, and the elliptical to obovate leaves up to 3.5 cm long. The habit can be confused with that of *Lepanthopsis floripecten* (Rchb.f.) Ames; however, ramicauls of *L. floripecten* are not prolific. Flowering plants of *T. arbuscula* often bear several large, distichous, simultaneously 9–13 flowered racemes. The carinate sepals are frequently white at the concave base, but turn into green towards the thickened apices. The lip shows a thickened midvein and two longitudinal calli along its entire length, unlike the lip of *T. dura* (Lindl.) Luer, thickened only near the glandular-papillose apex. The lip base in *T. arbuscula* is commonly suffused with brown or purple, but the rest is greenish-yellow. Besides variation in length of the racemes, leaves and sepals, morphology of flower parts in *T. arbuscula* is constant, and readily recognizable from any other *Trichosalpinx* species found in Costa Rica.

The lower montane and premontane wet forests of Costa Rica represent the northern limit of this species. Specimens found in Costa Rica are smaller and inhabit lower elevations than those in the Andes (Luer 1997). The floral features of the type specimen of *Pleurothallis moschata* Rchb.f., described from a plant found by Endrés in Costa Rica (no specific locality reported), agrees with those of the type specimen of *T. arbuscula* (described from Ecuador).

## **2. *Trichosalpinx blaisdellii* (S.Watson) Luer, *Phytologia* 54: 394. 1983.**

BASIONYM: *Pleurothallis blaisdellii* S.Watson, Proc. Amer. Acad. Arts 23: 284. 1888.

TYPE: Guatemala. Chocón forests, flowered in cultivation at Cambridge, Nov 1887,

*S. Watson s.n.* (holotype, AMES-74086; isotypes, AMES, K-463156). Figs. 36 & 37.

*Pleurothallis peraltensis* Ames, Sched. Orchid. 6: 65–67. 1923. TYPE: Costa Rica. Peralta, 2500 ft [762 m], 13 Jul 1923, *C.H. Lankester 484* (holotype, AMES).

*Pleurothallis standleyi* Ames, Sched. Orchid. 9: 37–41, f. 7. 1925. TYPE: Costa Rica. Cartago: El Muñeco, south of Navarro, 1400 m, Feb 1924, *P.C. Standley 33607* (holotype, AMES; isotypes, MO, US).

*Trichosalpinx tamayoana* Soto Arenas, Orquídea (Mexico City) 10(2): 264–266. 1987. TYPE: Mexico. Sinaloa: km 223 de la carretera Durango-Mazatlán, ca. de Potrerillos, 1350 m, cañada húmeda con selva mediana subcaducifolia-bosque mesófilo de montaña, rodeada de encinares secos y abiertos, epífita sobre *Annona* sp. a la orilla de arroyo, 30 Apr 1986, *Soto Arenas & Salazar 2121* (holotype, AMO; isotype, MO).

*Trichosalpinx lankesteriana* Luer, Lindleyana 11(2): 108, f. 35. 1996. TYPE: Costa Rica. Without collection data, flowered in cultivation at the Lankester Botanical Garden, Cartago, 18 Mar 1995, *C. Luer 17411* (holotype, CR; isotype, MO; drawing of type, MO; photo of the clonotype, JBL).

**Herb** epiphytic, caespitose, erect to suberect, up to 17.3 cm tall. **Roots** slender, flexuous, to 1.5 mm in diameter. **Ramicauls** erect, stout, not prolific, 0.6–10.7 cm long, enclosed by 2–8 infundibuliform, fibrous, ribbed, microscopically ciliate, lepanthiform sheaths, 3–23 mm long, brown, partially purple when immature, basally adpressed, apiculate and dilated apically. **Leaves** erect, elliptic to ovate, obtuse to acute, coriaceous, flat to shallowly

concave, the margins entire and sharp, 1.0–6.8 × 0.6–2.8 cm, commonly purple abaxially; base cuneate, narrowing into a terete to sulcate petiole up to 3 mm long; apex with an apiculus projected ca. 1 mm. **Inflorescence** a dense, distichous, simultaneously 5–8 flowered raceme, 1–4 cm long including the peduncle 4–11 mm long, produced at the apex of the ramicaul from a lanceolate, acute, conduplicate, adpressed spathe, ca. 1.5 mm long. **Floral bracts** membranaceous, cylindrical, ovate, obtuse, 1.5–1.7 × 1.0 mm. **Pedicels** 1.0–1.5 mm long, persistent. **Ovary** shallowly channeled, up to 1.5 mm long. **Flowers** with purple, vinaceous or flesh colored sepals, basally white, apically commonly washed-out; petals translucent white to light yellow; lip dark purple; column and anther white. **Sepals** fleshy, polished, entire, margins scarcely fimbriate. **Dorsal sepal** narrowly elliptical to ovate, obtuse to subacute, truncate, suberect to erect, 5.3–12.0 × 1.8–2.4 mm, 3-veined, shallowly concave basally, variously thickened apically. **Lateral sepals** narrowly elliptical to narrowly ovate, acute, recurved, 4.6–9.6 × 1.3–1.9 mm, connate from the base up to the middle forming a mentum basally, 4-veined all together. **Petals** membranous, oblong, broadly obtuse, truncate, lacerate towards the apex, straight, 1.7–3.1 × 0.7–1.4 mm, 1-veined. **Lip** gently arcuate, oblong to ligulate, rounded, ciliate along the margins, 1.7–3.8 × 0.6–1.1 mm, the lower third broadly dilated with the flanks suberect, the disc with a prominent central carina borne at the base base and disappearing towards the middle, the base with two retrorse auricles and a central membrane that is hinged to the column-foot, the apex with a shallow groove from the middle towards the apex, the margins deflexed. **Column** stout, semiterete, denticulate to lacerate at the apex, 1.4–2.3 mm long, longitudinally winged, the clinandrium subapical, the stigma ventral. **Anther** cap incumbent, ovate, emarginate. **Pollinia** 2, yellow, obovate to pyriform, on a cellular, oval caudicle. **Fruit** a pink to purple, 2-valved, glabrous, subglobose capsule, 7.0–9.0 × 3.0–6.5

mm, laterally dehiscent, with two prominent dehiscence lines running along the carpel midribs, perianth persistent.

**Distribution.** From Mexico to Panama (Luer 1997).

**Additional material examined. Costa Rica.** – **Alajuela:** San Carlos, Boca Tapada, 10 set 2004, 225 m, *C. Ossenbach* 369 (JBL-D0407); – San Ramón, Ángeles, Reserva Biológica Alberto Manuel Brenes, alrededores de la Estación Biológica del Río San Lorencito, 900-1100 m, 27-28 ago 2011, *M. Blanco* 4036, *J. Abarca*, *M. Díaz*, *M. Chavarría* & *J. Gómez Laurito* (JBL-D5761); – San Ramón, Ángeles, Los Lagos, desvío a la Reserva Biológica Alberto M. Brenes desde la carretera San Ramón-La Fortuna, 10°14'26" N 84°31'47" W, 850 m, bosque muy húmedo tropical transición a premontano, en cercas de fincas, 26 may 2008, *D. Bogarín* 5022 (JBL-D2702); – San Ramón, Ángeles, Los Lagos, desvío a la Reserva Biológica Alberto M. Brenes, 14 oct 1995, *A. Q.* [probably, *Alonso Quesada*] *s.n.* (JBL-D3404); – San Ramón, Angeles, Camino entre Los Lagos y entrada a la Reserva Biológica Alberto Manuel Brenes, en parche boscoso, planta con hojas iridiscentes, 10°14'06"N 84°31'56"W, 800 m, 23 ene 2001, *M. Blanco* 1806, *R.C. Moran*, *J.E. Watkins*, & *E. Vega* (JBL-D4885; USJ-76579); – [San Ramón], Reserva de San Ramón, along a minor tributary of the Rio Lorencito, 1070m, 15 ago 1991, *M. Germani* 15 (USJ-039905); – San Ramón, Reserva Biológica Alberto Manuel Brenes, Sendero Cascada, epífita, luz media a abundante y materia orgánica abundante, 10°12'40"N 84°36'40"W, 1000 m, 10 mar 2006, *A. Rojas* 6858, *J. Gómez* & *V. Mora* (JBL-D2692); – San Ramón, Piedades Sur, San Miguel (La Palma), camino a San Bosco, a orillas y dentro de un pequeño bosque secundario. 10°07'18.8"N 84°31'13.1"W, 1062 m, 21 dic 2010, *A. Karremans* 3278, *J.A.J. Karremans* & *M. Contreras Fernandez* (JBL-D5703). – **Cartago:** Cartago, Copalchí, 1800

m, floreció el 28 oct 1993 en el Jardín Lankester, Cartago, 1350 m, *Dora E. Mora s.n.* (USJ-049934); – Jiménez, Pejibaye, unpaved road from Purisil to Tausito, Reserva Sura Mina Iriria Tsochok Doboni Meye (La Madre Tierra), 09°46'38"N 83°46'30"W, 1295 m, premontane wet forest, secondary vegetation and remnants of primary, 25 Jul 2006, *F. Pupulin 6267, D. Bogarín, M. Dix, R.L. Dressler & A. Karremans* (JBL-D3427); – Jiménez, Reserva El Copal, 9°47'00"N 83°45'20"W, 1000 – 1200 m, 2 jun 2001, *M. Blanco 1912 & R. Narit* (JBL-D2716, USJ-); – Jiménez, Pejibaye, La Selva, Reserva Biológica El Copal, 500 m siguiendo el sendero Mariposa, 1020 m, bosque pluvial premontano, epífitas en bosque secundario sobre árbol caído a orillas del sendero, 14 jun 2009, *M. Fernández 1, L. Sandoval, E. Biamonte & O. Morrison* (JBL-D3570); – *M. Fernández 2, L. Sandoval, E. Biamonte & O. Morrison* (JBL-D3685); – [La Unión], Tres Ríos, Cerro La Carpintera, *D. E. Mora s.n.* (USJ-049933); – Turrialba, Tuis, Cien Manzanas, alrededor de 1 km sobre el camino en San Juan Bosco y San Vincente. 9°51'59"N 83°34'02"W, 1000–1100 m, bosque pluvial premontano, epífitas al lado del camino, a orillas de quebrada y en árboles solitarios de potrero, 15 de may 2010, *A. Karremans 2666* (JBL-D5608); – [idem] *A. Karremans 2681* (JBL-D5609); – Turrialba, Moravia de Chirripó, Tsipirí, 9°48'N 83°23'W, 1050 m, along a small creek and in disturbed primary forest, plants epiphytic, mostly in shade on understory vegetation and lower branches, 3 May 2002, *F. Pupulin 3749, J. Warner & R. Gómez* (JBL-D3408); Jiménez, Taos, 1000 m, 1984, *R. L. Dressler 300* (USJ-026170); – Turrialba, P.N. Barbilla, cuenca del Matina, sendero Científico Barthón, sección Cerro Tigre, río Barbilla, 9:55:15.000 N – 83:23:55.000 W, 12 Mar 2001, *E. Mora Castro 1961* (CR-262881). – **Guanacaste**: Tilarán, Tierras Morenas, desviación a la izquierda después del Río Cabuyo, camino al Proyecto Geotérmico Tenorio y Cerro Jilguero, ca. 4.5 km norte de Tierras Morenas, ladera sureste del Volcán Tenorio, 10°36'11.6"N

85°00'05.3"W, 900-1000 m, bosque pluvial premontano, epífitas a orillas del camino y en bordes de potreros, 2 Feb 2006, *D. Bogarín 2402, R.L. Dressler, R. Gómez & A. Rojas* (JBL-D2641). – **Heredia**: Sarapiquí, Rara Avis, 15 km suroeste de Las Horquetas, 10°17'03"N 84°02'47"W, 500-800 m. 20 oct 1997, *G. Beckers 23* (CR-217033); – Sarapiquí, Puerto Viejo, Estación Biológica La Selva, a orillas del Río Sarapiquí, 10°26'29"N 84°00'53"W, 40 m, bosque muy húmedo tropical, epífitas sobre troncos y ramas caídas en bosque secundario, 7 jun 2003, *D. Bogarín 212* (JBL-D2900); *D. Bogarín 23* (JBL-D2458); – Sarapiquí, Puerto Viejo, Estación Biológica La Selva, 1 oct 2000, *M. Blanco 1615* (JBL-D2845); Sarapiquí, Finca La Selva, OTS field station near junction of Puerto Viejo and Sarapiquí rivers, 40–100 m, sendero Hartshorn (SHA) 250, just before the river, 19 mar 1991. *K. Richardson K-123B* (CR-154593); – Sarapiquí, laguna, camino a Puerto Viejo, 8 ene 1992, *JBL-00390* (USJ-). – **Limón**: Pococí, Guápiles, 1 km después del puente sobre el Río Corinto en dirección a Guápiles, 10°12'40.9"N 83°52'38.5" W, 300 m, bosque muy húmedo tropical, epífitas en bosque secundario, 15 jun 2006, *D. Bogarín 2894, R.L. Dressler, J. Gómez-Laurito & F. Pupulin* (JBL-D2454); – Siquirres, Florida, San Antonio, rívera 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, epífitas en árboles aislados en potreros, 2 abr 2008, *D. Bogarín 4244, R.L. Dressler, A. Karremans, A. Russell & R. Samuel* (JBL-D2632); – Talamanca, Sixaola, Área no protegida, fila entre Gandoca y Manzanillo frente a Punta Mona, 9°36'0"N 82°39'0"W, 50 m, 29 mar 1995, *G. Herrera 7627* (CR-233801). – **Puntarenas**: Buenos Aires, Volcán, 09°13'N, 83°26'W, bosque secundario muy alterado a orillas de un riachuelo, ca. 450 m, 17 abr 2012, *A. Karremans 5308, C. Cambrero, J. Gemmel* (JBL-D5700); – [idem], *A. Karremans 5309* (JBL-D5590); – Buenos Aires, Fila Cabagra, 10 km al norte de Brujo, Cerro Pelón,

9°10'12.78" N 83°13'25.45" W, 868 m, bosque muy húmedo premontano, colectadas por Y. Kisel, P. Renshaw & R. Trejos, 9 mayo 2009, en cultivo en el Jardín Botánico Lankester, 20 may 2009, *D. Bogarín 7251* (JBL-D3554); – Golfito, Jiménez, P.N. Corcovado, Carate, 8.497222 -83.481944, 500 m, Dos Brazos de Río Tigre, cuenca superior del Río Madrigal, margen derecha, 8 dic 1990, *G. Herrera 4747* (INB-1593593; CR-201912); – Golfito, Puerto Jiménez, P.N. Esquinas, Fila way, 8°41'N 83°13'W, 200 m, epiphyte, dark purple, 14 feb 2000. *P. Hietz 5* (CR-230304); – Osa, Sierpe, unos 6 km de Bahía Drake, frente a la torre de telecomunicaciones, parte más alta sobre el camino entre Bahía Drake y Rancho Quemado, bosque muy húmedo tropical, 8°41'48" N 83°35'47" W, ca. 400 m, 20 abr 2012, *A. Karremans 5330 & J. Gemmel* (JBL-D5591); – Osa, Rancho Quemado, 250 m, 15 Sept 1993, *R. L. Dressler s.n.* (JBL-D3480); – Puntarenas, Monteverde, 10°18'N 84°48'W, 1450 m, 16 Mar 1989, *J. T. Atwood 8984* (CR-137874); – Puntarenas, Monteverde, Bajos de La Lindora, Río Guacimal, 10°18'N 84°48'W, 1000 m, epífita en árbol de bosque, 19 Feb 1988, *W. Haber 8268* (CR-135231). – **San José**: Dota, San Joaquín, 1km después de la escuela de San Joaquín yendo hacia Quepos, 09°34'32.88"N, 84°00'18.06"W, en árboles esparcidos en potreros, 20 feb 2012, *A. Karremans 5150* (JBL-D5480); – Dota, eastern slopes of Cerro Nara, in premontane rain forest, disturbed primary forest, 9°29'01"N, 84°00'25"W, 840-740 m, 14 Jan 1999, *F. Pupulin 1092, D. Castelfranco & L. Spadari* (JBL-D4244); – Escazú, San Antonio, Cerros de Escazú, Z. P. Cerros de Escazú, camino hacia Londres, Alto Jorge Zeledón, a 1.3 km NE en línea recta de Cerro Cedral, zona con ciprés y jaúl, rodeado de bosque semi intervenido, 9°52'10,1"N – 84°8'12.7"W, 2051 m, 26 Ago 2010, *S. Lobo 2685* (CR-263528); – Pérez Zeledón, Refugio de Vida Silvestre Boracayán, in the Fila Costeña along the San José-Puntarenas Province border, ca. 10 km E of Dominical, southern Fila

Tinamastes near Cuesta Yeguas, epiphyte, abundant, 9°14.9' N 83°45.2' W, 800-1000 m, 26 May 2003, *J. Clarke 110, B.K. Holst, M. Blanco, S. Dalström, N. Edmondson, J.M. Heaney & W. Higgins* (JBL-D3265); – Vásquez de Coronado, Braulio Carrillo Nat. Park, sobre el sendero La Botella, 750m, 5 ene 1990, *S. Ingram 560 & K. Ferrell* (USJ-037628); – Vásquez de Coronado, Braulio Carrillo NP, along the Terciopelo trail occurring with *Trichosalpinx orbicularis, Pleurothallis verecunda*, 29 mar 1991, *K. Richardson K-182* (CR-154592); – cultivado en San José, 27 oct 1938, *E. Span 16* (CR-26414). – **Sin datos de colecta:** *C. A. Luer 17411* (JBL-D1597; USJ-79276); – *A. Karremans 1003* (JBL-B1122); – *JBL-00417* (JBL-D3369); – *JBL-00421* (JBL-D4607); – *JBL-01710* (JBL-D2448); – *JBL-01781* (JBL-D3516); – *JBL-01855* (JBL-D2636). Fig. 38.

**Habitat and ecology.** A widespread epiphyte in tropical wet forest, tropical wet forest premontane belt transition, premontane wet forest basal belt transition, premontane wet forest, premontane rain forest and lower montane rain forest from 0 to 1300 m along the Caribbean and Pacific watersheds. It was found mainly associated with secondary roadside and riverine vegetation on shaded branches, and on scattered trees of open disturbed areas and pastures.

**Eponymy.** Named after F. E. Blaisdell, companion of S. Watson, co-discoverer of the species.

**Phenology.** Plants in cultivation flower throughout the year, independently of the population, with bloom peaks between June and September. Plants found in the Pacific watershed were found in flower between January and March, and from August to December. On the other hand, plants collected in the Caribbean watershed were found in

flower mainly between January and March, and one specimen was collected in flower in October.

Production of fruits *in situ* was not recorded, but few plants in cultivation produced fruits between July and August.

**Discussion.** *Trichosalpinx blaisdellii* is a common and morphologically, highly variable species, widespread in Costa Rica along both the Caribbean and Pacific watersheds from sea level to 1300 m. Vegetative and floral characters vary greatly between and within populations, as well as size, shape and color of sepals, and size of petals and lip, just to mention the most conspicuous shifts (Fig. 39). No pattern relating morphology to locality, elevation or type of forest was found. Despite variability, *T. blaisdellii* can be recognized by the variously recurved lateral sepals connate from the base to the middle, forming a bifid synsepal; the basal mentum; the membranous, translucent, lacerate petals; and the densely ciliate, dark purple lip with a central callus and two basal lobules. Iridescence was noted on the adaxial surface of young leaves. Further studies may elucidate the ecological and structural implications of this character.

*Trichosalpinx orbicularis* and *T. rotundata* can be confused because of similar habit and color and disposition of sepals, but these two species bear orbicular, deeply concave leaves (vs. flat to shallowly concave in *T. blaisdellii*), as well as narrowly ovate dorsal sepals and distinct lateral sepals that are connate below the middle (vs. above or to the middle in *T. blaisdellii*). *Trichosalpinx memor* is also similar to *T. blaisdellii*, but the first can be easily distinguished by the concave, externally papillose, green, brown or purple synsepal (vs. recurved, smooth and reddish), the absence of a mentum at the base of the densely ciliate sepals (vs. provided with a distinct mentum at the base of the scarcely

fimbriate sepals), and the lip with a central callus that is bifid above the middle (vs. central callus disappearing gradually towards the middle).

*Trichosalpinx blaisdellii* was first collected in Costa Rica by Auguste R. Endrés (1838–1874), but it was not until 1888 when Sereno Watson described the species from the Chocón forests in Guatemala. Since then, at least four posterior species have been considered synonyms of *T. blaisdellii*, including three described names from Costa Rica. Between 1923 and 1925, Ames described *Pleurothallis peraltensis* and *Pleurothallis standleyi*, from Peralta (north of Turrialba) and Navarro, respectively. In 1996 Luer described *Trichosalpinx lankesteriana* from a Costa Rican plant without specific locality, distinguished by the longer and fleshy sepals and broader, recurved lateral sepals. The extensive collections of specimens of *T. blaisdellii* carried out as part of this project allowed the recognition of a wide range of morphological variations that includes gradual shifts of form, size and aspect of both vegetative and floral features. After a detailed revision of protologues and physical and digital images of the type specimens of *P. peraltensis*, *P. standleyi* and *T. lankesteriana*, I conclude that they represent morphological variations that fit in the concept of *T. blaisdellii* treated here, and so they are treated as synonyms.

### **3. *Trichosalpinx carinilabia* (Luer) Luer, *Phytologia* 54: 394. 1983.**

BASIONYM: *Pleurothallis carinilabia* Luer, *Selbyana* 3: 256. 1977. Syn.: *Pleurothallis broadwayi* Ames var. *tricarinata* C.Schweinf., *Bot. Mus. Leafl.* 8: 42. 1940. TYPE: Costa Rica. Alajuela: Palmira, epiphyte on oak, 2000 m, 27 May 1938, A. Smith H 668 (holotype, AMES). Fig. 40.

**Herb** epiphytic, up to 6.5 cm tall including the inflorescence. **Roots** white, slender, flexuous. **Ramicauls** straight to ascendent, prolific (2–3 superposed in a chain), each 4–13 cm long, enclosed by 2–5 tubular, adpressed at the base, ribbed, minutely hispid, brown lepanthiform sheaths, 4–7 mm long, with dilated, minutely hispid ostia. **Leaves** erect, elliptical, retuse, thickly coriaceous, 8–11 × 5–7 mm, narrowing at the cuneate base into a petiole 1 mm long. **Inflorescence** a dense, distichous, successively 3–7 flowered raceme, up to 3.8 cm long including the peduncle 1.3–1.5 cm long. **Floral bracts** translucent hazel, obdeltoid, truncate, 1.0–1.3 × 1.2–1.5 mm. **Pedicels** 2–3 mm long. **Ovary** 0.5 mm long, glabrous. **Flowers** with the sepals yellowish-white, the petals translucent yellow, the lip greenish white and the column white. **Sepals** glabrous, carinate, concave at the base and thickened toward the apex. **Dorsal sepal** ovate, truncate, acute, 3.5–4.0 × 1.6–1.8 mm, 3-veined. **Lateral sepals** free, reflexed, triangular, truncate, acute, 2.8–4 × 0.9–1.2 mm, 1-veined. **Petals** membranaceous, obovate, truncate, broadly acute, crenate towards the apex, 1.6–2.1 × 0.8–0.9 mm, 1-veined. **Lip** fleshy, oblong, truncate, obtuse; the base broadened forming two low, erect lobes, hinged to the column-foot; the apex thick, papillose, the disc with two lateral thickenings above the middle; the midvein thickened basally; 2.2–2.3 × 0.8–1.2 mm, 1-veined. **Column** semiterete, slightly arcuate, 1.0–1.3 mm, the clinandrium shallowly winged, the stigma ventral, the anther cap subapical, incumbent, ovate, emarginate. **Pollinia** 2, pyriform, on an oval caudicle. **Fruit** not seen.

**Distribution.** Costa Rica and Panama (Luer 1997).

**Additional material examined. Costa Rica. – Alajuela:** San Ramón, Piedades Sur, aprox. 5 km sobre la carretera a Bureal en dirección este a oeste, 10°07'43.7"N 84°33'13.5"W, 1289 m, bosque muy húmedo premontano, epífitas en bosque alterado, 19 jul 2012, *M. Fernández 631 & A.P. Karremans* (JBL-D5620). – **Heredia:** San Rafael, from Residencial El Castillo, about 3 km towards Cerro Chompipe, finca Martin Prada, 1600 m, 30 abr 2000, *F. Pupulin 2306 & M. L. Spadari* (USJ-80898); – San Rafael, road from Residencial El Castillo to Monte de la Cruz, along Río Tibás, slopes of Cerro Tibás, 10°04'N, 84°03'W, 2000 m, lower montane moist forest, primary vegetation, 31 Mar 2003, *F. Pupulin 4548* (JBL-B0286); – San Rafael, Concepción, Residencial El Castillo, Calle Lobo, southern slope of Cerro Tibás, 10°4'07.7"N 84°03'56.6"W, 1940 m, lower montane wet forest, epiphytic on scattered trees in pastures, 19 Mar 2009, *F. Pupulin 7662, D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D2895); San Rafael, Cerro de la Cruz, Arthur Weston, Abril 28 1967, *L. Rodríguez Caballero 507* (USJ-10855). – **Puntarenas:** Monteverde, in sub-elfin woodland of cloud forest on road to TV towers at about 1700 m, plants in bud, some flowers nearly open, 9 Mar 1989, *J. T. Atwood 8941* (CR-137875); – Monteverde, common epiphyte in pastures of south part of Monteverde at about 1400 m, 14. Mar 1989, *J. T. Atwood 8974* (CR-141841); Reserva Monteverde, 4 nov 1984, *Robert L. Dressler 128* (USJ-025692). Fig. 41.

**Habitat and ecology.** Epiphytic in wet premontane and lower montane moist forests in primary vegetation and disturbed areas from 1200 to 2000 m of elevation. Frequently found growing on exposed conditions such as scattered trees in pastures.

**Etymology.** From the Latin "*carinilabius*", "with a carinate lip", in reference to the tricarinate lip.

**Phenology.** Plants of *T. carinilabia* kept in the greenhouse flowered during June, July and November. Data from exsiccata indicate flowering in March, April and November.

**Discussion.** *Trichosalpinx carinilabia* is distinguished by the growth habit with few successive ramicauls, the long racemes two to three times as long as the leaf, the long pedicels, the carinate sepals, the lateral ones bent backwards, the lip with two marginal carinae, thickened midvein and papillose-glandular apex, and the column with short wings. The most similar Costa Rican species is *T. todziae*, which has the same vegetative architecture. *Trichosalpinx todziae* is distinguished by the narrowly triangular, larger sepals, and the arcuate, fleshy lip with two erect basal lobes and a thick apex.

*Trichosalpinx carinilabia* could also be mistaken with *T. dura*, since both share some vegetative and floral traits. However, plants of *T. dura* usually produce shorter ramicauls, longer peduncles with shorter pedicels, while flowers bear erect, yellow sepals with frequently orange apices, spatulate petals and a rhomboid, trilamellate, apically orange lip. The column of *T. dura* is straight with the apex broadly winged.

*Trichosalpinx carinilabia* can also be misidentified for *T. cedralensis* because of its prolific ramicauls, elliptical leaves and small light-colored flowers. Nevertheless, plants of *T. cedralensis* produce long chains of superposed ramicauls, straight, sulphur yellow petals, and an ecarinate, membranaceous lip.

Schweinfurth (1940) described the variety "tricarinata" of *Pleurothallis broadwayi* based on several Costa Rican collections. According to him, these collections differed from typical *P. broadwayi* by the longer pedicels, a fractiflex raceme, a central lip keel ending below the fleshy apex, and the absence of distinct column wings. Luer (1977) elevated *P. broadwayi* var. *tricarinata* to the rank of species as *Pleurothallis carinilabia*. Although the name was validly published, the discussion and drawing (locality unknown) were erroneously based

on a specimen of *T. tropida* (Luer) Luer, a different, Panamanian species. The plant on which the drawing of *T. carinilabia* included in the present treatment is based, was collected in Piedades de San Ramón, just a few kilometers southwest from the type locality of *Pleurothallis broadwayi* var. *tricarinata*.

**4. *Trichosalpinx caudata* Luer & R.Escobar, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 20, f. 5. 1997.**

TYPE: Colombia. Antioquia: La Tebaida, collected by E. Valencia, July 1988, flowered in cultivation at Colomborquídeas, 16 May 1993, *C. Luer 16907* (holotype, MO; drawing of type, MO). Fig. 42.

**Herb** epiphytic, caespitose, erect, up to 10 cm tall. **Roots** slender, flexuous, to 2 mm in diameter. **Ramicauls** erect, stout, not prolific, 1.5–8.0 cm long, enclosed by 3–6 tubular, fibrous, ribbed, microscopically hispid, imbricating, lepanthiform sheaths, 0.7–2.0 cm long, brown, basally adpressed, with broadly dilated ostia, the apical sheath 1.0–2.4 cm long, covering the petiole, leaf base and pedicels. **Leaves** erect to suberect, orbicular to elliptic, obtuse, flat to shallowly concave, coriaceous, apiculate, 1.3–4.1 × 0.6–2.5 cm, occasionally purple abaxially, the cuneate base narrowing into a petiole up to 4 mm long, **Inflorescence** a congested raceme, bearing 2–3 distichous, simultaneous flowers, 11–17 mm long including the peduncle 7–10 mm long, adpressed against the abaxial leaf surface, 2–3 racemes flowerig simultaneously. **Floral bracts** cuneiform, conduplicate, 1.2 × 1.0 mm. **Pedicels** 0.6–1.0 mm long, persistent. **Ovary** cylindric, 1 mm long. **Flowers** with the sepals vinaceous, suffused with yellow towards the apex, white at the base, the

petals translucent vinaceous, the lip dark vinaceous, the column white, the anther pinkish. **Dorsal sepal** membranous, entire, descendent, narrowly triangular, acute, 7.2–8.5 × 1.3–2.1 mm, 3-veined, the apical half commonly serrulate. **Lateral sepals** fleshy, entire, narrowly ovate, connate to the middle into a bifid lamina deeply concave at the base, forming a mentum with the column foot, 5.8–6.8 × 4.3–5 mm, 4-veined altogether, the margins scarcely ciliate, the apices elongated, thickened, semiterete. **Petals** straight, horizontally parallel, membranaceous, oblong, acute, truncate, 0.8–1.0 × 0.8–1.0 mm, the apex fimbriate. **Lip** descending, membranaceous, oblong, acute, 2.0–2.7 × 0.8–1.3 mm, the basal margins dilated and minutely ciliate, the disc with a central carina from the base to the first third of the lamina, the base with two retrorse lobules and a central membrane that is hinged to the column-foot, the apex long-attenuate, acute, fimbriate. **Column** semiterete, straight, deeply fimbriate at the apex, 2.3–2.7 mm long, perpendicular to the column-foot, the clinandrium apical, the stigma rounded, ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform to globose, each with a cellular, irregular, minute caudicle. **Fruit** not seen.

**Distribution.** Costa Rica, Panama and Colombia.

**Additional material examined. COSTA RICA.** – **Alajuela:** San Carlos, Boca Tapada, alrededores del Hotel Laguna de Río Lagarto, en jardín del hotel Arenal Paraíso, 100 m, 10 oct 2004, *C. Ossenbach 368 & P. Casasa* (JBL-E0264). – **Puntarenas:** Osa, Cortés, fila Dominicalito, 250 m, *D. Jiménez invenit, M. Fernández 546* (JBL-D4606; USJ-); Osa, San Juan, cuenca media del río San Juan, siguiendo el curso aguas arriba, 200 m, flor morada de ápice anaranjado, conspicuo, 5 nov 1990, *G. Herrera 4568* (CR-177634). Fig. 43.

**Habitat and ecology.** *Trichosalpinx caudata* has been found growing epiphytically in disturbed areas close to water bodies at low elevations of the northern Caribbean plains, and in open areas of the Osa Peninsula at low elevations.

**Etymology.** From the Latin *caudatus*, “caudate”, referring to the elongated lateral sepals.

**Phenology.** In the wild, plants flowered in July and November. Costa Rican specimens flowered between June and September under cultivation.

**Discussion.** *Trichosalpinx caudata* and *T. orbicularis* are vegetatively undistinguishable. However, *T. caudata* can be distinguished by its long, caudate sepals, the longer (up to 8.5 mm long vs. less than 6 mm in *T. orbicularis*), narrowly triangular (vs. ovate) dorsal sepal; the lateral sepals are narrowly ovate, elongated, connate only at the base (vs. broadly ovate, not elongated, connate from the base up to the middle), and the apex is widened, semiterete and fleshy (vs. not widened, flat and not thickened); the petals are narrowly acute to acuminate and densely fimbriate (vs. acute to obtuse and scarcely fimbriate in *T. orbicularis*). The lip is usually twice longer than the column (vs. one-third longer than column in *T. orbicularis*; Fernández *et al.* 2014).

**5. *Trichosalpinx cedralensis* (Ames) Luer, *Phytologia* 54(5): 394. 1983.**

BASIONYM: *Pleurothallis cedralensis* Ames, *Schedul. Orch.* 4: 1 8. 1923. TYPE:

Costa Rica. Cartago: Cedral, 1700 m, 28 Jul 1919, *C. H. Lankester* 352 (holotype, K; isotype, K; drawing of the holotype, AMES; photo of the holotype, AMES). Fig.

44.

*Pleurothallis myrtilus* Schltr. Repert. Spec. Nov. Regni Veg. 19: 25, 108. [Dec]

1923. TYPE: Costa Rica. La Palma, 1800 m, blühend im Dezember 1908, A. Brade & C. Brade 1106 (holotype, B, destroyed; neotype designated by Luer [1997, as the 'lectotype'], drawing, AMES).

**Herb** epiphytic, caespitose, erect, up to 18 cm tall including the inflorescence. **Roots** slender, flexuous, to 1 mm in diameter. **Ramicauls** erect to pendent, stout, forming a tree-like structure with a primary ramicaul 1.3–9.0 cm long, and several secondary, prolific ramicauls, 1.0–7.5 cm long, each enclosed by 3–10 tubular, lepanthiform sheaths, adpressed, ribbed, light brown, 0.5–1.4 cm long. **Leaves** elliptical, acute, apiculate, coriaceous, 0.8–1.8 × 0.3–0.7 cm, the cuneate base narrowing into a petiole up to 1.5 mm long. **Inflorescence** distichous, a 6–8 successively flowered raceme, 2.8–3.2 cm long including the peduncle 3–4 mm long, produced at the apex of the ramicaul from a conduplicate, oblanceolate, acute spathe, 5–9 mm long. **Floral bracts** narrowly cuneiform, conduplicate, papyraceous, 1 mm long. **Pedicels** 1 mm long, persistent. **Ovary** cylindrical, 1 mm long. **Flowers** with the sepals white to pale yellow, the petals translucent white, the lip pale yellow, the column greenish-white, the anther white. **Dorsal sepal** ovate, concave at the base, acute to obtuse, truncate, glabrous, carinate, 5.0–6.8 × 1.9–2.4 mm, 3-veined. **Lateral sepals** narrowly triangular, concave at the base, oblique, glabrous, carinate, 4.5–6.2 × 0.8–1.1 mm, 2-veined. **Petals** oblong, truncate, obtuse, entire 2.5–3.6 × 0.8–1.2 mm, 1-veined. **Lip** narrowly oblong, obtuse, truncate, trilobate, glabrous, 3.1–4.2 × 0.8–1.1 mm, the two basal lobes erect, borne at the apex, the apical lobe convex, thickened, glandulose, the disc flat. **Column** semiterete, 1.6–1.7 mm long, the apex with two obtuse wings, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, broadly ovate, emarginate. **Pollinia** 2, pyriform, on cellular, suborbicular caudicles. **Fruit** not seen.

**Distribution.** Costa Rica, Panama, Venezuela, Ecuador and Bolivia.

**Additional material examined. Costa Rica. – Alajuela:** Naranjo, Palmira, Bajo del Toro, road to Río Toro waterfall, ca. km 2.5, 10°15'00"N, 84°16'23"W, 1230 m, premontane wet forest, epiphytic on short trees along the roadside, 13 Apr 2003, *F. Pupulin 4608*, *E. Salas & H. Leon-Paéz* (JBL-B0208); – [San Ramón], cerca de San Ramón, 1050 m, nov 1921, *A. M. Brenes 23* (CR-26105); – [San Ramón], La Palma de San Ramón, 1190 m, 23 nov 1922, *A. M. Brenes 473* (CR-26154); – [San Ramón], Piedades, cerca de San Ramón, 1025 m, 5 nov 1925, *A. M. Brenes 1253* (CR-26106); – San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10°08'58.7"N 84°34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, 19 Feb 2008, *F. Pupulin 7049*, *R.L. Dressler & A. Karremans* (JBL-D3428); – San Ramón, Piedades Sur, San Miguel (La Palma), en El Alto después de San Bosco, en árboles solitarios en potrero, 21 dic 2010, 10°07'43.7"N 84°33'13.5"W, 1289 m, *A. Karremans 3307*, *J.A.J. Karremans & M. Contreras Fernandez* (JBL-D4791); – San Ramón, R.B. Alberto Manuel Brenes, Los Angeles, 20 km norte de la Estación, 10.211 - 84.606, 21 oct 1993, *G. Herrera 6628* (CR-171856); – San Ramón, R.B. Alberto Manuel Brenes, U.C.R., sobre rama de árbol caído, 10.211 -84.605, 1000 m, 12 oct 1995, *A. Cascante 785* (CR-197118); – San Ramón, R. B. Alberto Manuel Brenes, creciendo sobre árbol caído, 10.211 -84.605, 1000 m, 14 oct 1995, *A. Quesada 199* (CR-223497); –

**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 may 2009, *D. Bogarín 6566*, *R. Gómez, Y. Kisel & R. Trejos* (JBL-D3857); – [Cartago], Z.P. La Carpintera, bosque en parte alta de los cerros, propiedad del campo Escuela Istarú, 9.883 -83.979, 1873 m, epífita entre

musgos sobre rama de un roble, *A. Cascante 1737* (CR-254985); – Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, sendero Oropéndola, orillas del Río Grande de Orosi, 9°44'13.5"N 83°46'49.6" W, 1376 m, epífitas en sitio sombreado en bosque secundario alrededor del sendero, bosque pluvial premontano, 28 dic 2004, *D. Bogarín 1216*, *M.A. Blanco*, *S. Dälstrom*, *F. Pupulin* & *C. Lewis* (JBL-C0495); – Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, El Mirador, 9°44'13.5"N 83°46'49.6" W, 1376 m, epífitas en sitio sombreado en ramas jóvenes y troncos de *Oreamunnea* (Junglandaceae), bosque pluvial premontano, 24 ago 2004, *D. Bogarín 929*, *H. León-Páez* & *E. Hoppe* (JBL-C0328); – Paraíso, Tapantí, *D. E. Mora 5* (USJ-027467); – *D. E. Mora 6* (USJ-027466); – Paraíso, Cachí, Peñas Blancas, 9°49'51.3"N 83°46'13.1"W, 1400 m, premontane wet forest, epiphytic on trees in pastures and secondary mature vegetation, 13 Nov 2008, *F. Pupulin 7498*, *D. Bogarín*, *R.L. Dressler*, *R. Gómez* & *R. Trejos* (JBL-D3989); – *F. Pupulin 7505*, *D. Bogarín*, *R.L. Dressler*, *R. Gómez* & *R. Trejos* (JBL-D3323); – Paraíso, Cachí, Peñas Blancas, entre Cerros Duán y Alto Velo de Novia, 9°48'43.76" N 83°46'36.61" W, 1829 m, bosque muy húmedo premontano, epífitas en árboles en potreros y borde de bosque, 11 may 2009, *D. Bogarín 7199*, *R. Gómez*, *Y. Kisel*, *P. Renshaw* & *R. Trejos* (JBL-D3519); – *D. Bogarín 7219*, *R. Gómez*, *Y. Kisel*, *P. Renshaw* & *R. Trejos* (JBL-D3481); – Paraíso, remnant trees in pasture along Río Grande de Orosí, 1.5 km SW of Tapantí, 1220 m, 1 Jan 1970, 9.76245 -83.812642, *R. W. Lent 1812* (CR-62933); – Paraíso, Cachí, 1600 m, camino al Cerro Duán, en fincas y potreros en la cima de la vertiente del río Naranjo, 9°49'56"N 83°45'50"W, bosque muy húmedo premontano, epífitas al lado del río, 9 Feb 2013 *A. Karremans 6010* (JBL-D5745); – P.N. Tapantí-Macizo Cerro de la Muerte, sendero Oropéndola, bosque secundario, 9.902 -83.790, 1300 m, 20 agosto 1992, *J. F. Morales 403* (CR-165149). – **Guanacaste**, R. B. Monteverde, 3 km N Santa Elena,

Atlantic exposure near continental divide on Bello farm, lower montane wet forest, 1500 m, 10.333 -84.833, 20 Dec 1985, *W. Haber 3811* (CR-129061); – Abangares, 5 km NNW Monteverde, on road to Las Nubes, continental divide, 10.35 -84.817, 1450 m, *W. Haber 9027* (CR-151875); – [Abangares], road to [finca] San Gerardo, lower montane rainforest, 10.35 -84.8, 1580m, *W. Morris 4034* (CR-143011). – **Heredia**: Santa Bárbara, Santo Domingo, Los Cartagos, carretera a Vara Blanca, km 25, 10°08'39.3"N 84°09'30.1" W, 2120 m, bosque pluvial montano bajo, epífitas en cercas a orillas de la carretera, 23 dic 2004, *D. Bogarín 1134 & M. Blanco* (JBL-D3370); Barva, Parque Nac. Braulio Carrillo, at refugio- 2050m slope of V. Barva, on road from San Rafael, about 0.5 km E of refuge, 20 nov 1990, *S. Ingram 740 & K. Ferrell* (USJ-037735); – **Limón**: Siquirres, Las Brisas de Pacuarito, subiendo por las fila superior de la margen izquierda de quebrada Jesús, hasta Cerro Tigre, 9.922 -83.40, 1550 m, *G. Herrera 8671* (CR-210992); – Talamanca, Bratsi, P.N. La Amistad, Río Lari, 9.384167, -83.110278, 1800 m, Alto Lari, siguiendo la fila entre Rios Lari y Dapari (Pare), 24 mar 1992, *R. Aguilar 1164* (INB-1573235). – **Puntarenas**: Puntarenas, Monteverde, Guacimal, Altos de Rio Veracruz, finca Brenes, 10.25 -84.8, 1300 m, 12 ene 1990, *E. Bello 1783* (INB-1568779); Monteverde community, "The Bullpen" pasture on John Campbell property, Pacific slope, 1540 m, 14 abr 1989, *B. Boyle 51-89* (USJ-038200, 038201); Reserva de Monteverde, 4 nov 1984, *Robert L. Dressler B-350 #128a* (USJ-75002); – [Monteverde], Reserva Monteverde, *D. E. Mora s.n.* (USJ-030731). – **San José**: Coronado, San Rafael, calle de lastre de Las Nubes bajando a San Pedro, 10°00' 00" N, 83° 58' 17" W, 1645 m, 17 nov 2002, *W. Schug 84, J. J. Zúñiga, J. Röth & B. Röth* (JBL-C0170); – Moravia, San Jerónimo, 2.5 km después del peaje de la carretera Braulio Carrillo ruta 32, frente al restaurante La Fonda, 10°02'53.26"N 84°00'23.78"W, 1584 m, bosque pluvial montano bajo, epífitas en cercas de fincas y

bosque secundario “supra arbores ad agros versus viam Braulio Carrillo in praedio San Jerónimo prope La Fonda”, 10 Abr 2011, A. *Karremans* 3926 & D. *Bogarín* (JBL-D4793); – [idem], A. *Karremans* 3941 & D. *Bogarín* (USJ-); – [idem], D. *Bogarín* 8581 & A. *Karremans* (JBL-E0830); – Tarrazú, camino a San Josecito, creciendo en tronco a baja altura, en orilla del bosque, 9.622 -84.125, 1400 m, 23 set 1997, O. *Valverde* 237 (CR-211558). Fig. 45

**Habitat and ecology.** Plants of *T. cedralensis* have been found in tropical wet premontane belt transition, moist and wet premontane, lower moist montane and wet forests, from 1000 to 2120 m. This species can frequently be found growing alongside mosses and ferns in exposed parts of trees scattered in pastures, as well as in trees bordering secondary forests.

**Eponymy.** In reference to Cedral, the locality where C. H. Lankester collected the plant that served as the type specimen.

**Phenology.** Flowering plants of *T. cedralensis* have been collected from July through January, both in the wild and in cultivation. Material from exsiccata indicate flowering from September to April.

**Discussion.** *Trichosalpinx cedralensis* is distinguished by the prolific ramicauls that form a tree-like structure; the lepanthiform sheaths completely adpressed to the ramicaul, the elliptical to narrowly elliptical, acute leaves, the racemes at least three times longer than the leaf; the white flowers with carinate sepals and oblong, translucent petals, and by the narrowly oblong lip with two basal, erect lobes truncate above the middle and with a thickened, glandular apex.

*Trichosalpinx acremona* (Luer) Luer, a species described from Ecuador, is similar to *T. cedralensis* because of its branching ramicauls, leaf shape and general floral morphology and coloration. Nevertheless, plants of *T. cedralensis* bear smaller (<1.9 vs 1.5–2.5 cm long in *T. acremona*), elliptical leaves (vs narrowly elliptical), shorter racemes (2.8–3.2 vs 3–4 cm long) of 6 to 8 flowers (vs 5–7 flowers), shorter dorsal (5–6.8 vs 8 mm) and lateral sepals (4.5–6.2 vs 8 mm), larger petals (2.5–3.6 vs 2.75 mm long), and a column with apical, obtuse (vs acute) wings. In Costa Rica, plants of *T. cedralensis* and *T. dura* have been found sympatrically in premontane wet forests (i.e., Reserva Biológica Alberto M. Brenes in San Ramón, and Muñeco in Cartago), but the former can usually be distinguished by its shrubby habit, caused the production several prolific secondary ramicauls from each basal ramicaul, while *T. dura* produces a single series of superposed ramicauls from each basal ramicaul instead. Plants of *T. cedralensis* are variable in terms of size, but floral and vegetative morphology is constant.

*Pleurothallis myrtilus*, described from a plant collected in La Palma (San Ramón, province of Alajuela) by the Brade brothers and described by Schlechter in late 1923; the type was deposited in Berlin-Dahlem Botanical Museum where it was destroyed in WWII. A drawing of the type, deposited at AMES under accession number 28789, was designated by Luer (1997) as the lectotype. The drawing shows the carinate, narrowly triangular lateral sepals, the elliptical petals, the 3-lobed, 3-veined lip with a featureless disc, and the column with obtuse wings, agreeing with Ames's original concept of *P. cedralensis*. There, *Pleurothallis cedralensis* was compared to *P. cabellensis*, a species described from a plant found in Venezuela, and treated as part of *Specklinia* and recently transferred to *Sylphia* (Luer 2006).

*Trichosalpinx cedralensis* is frequently found in Costa Rica (13 different populations here accounted) mainly in premontane wet forests, where it grows exposed to the sun. The species is also known from Panama, Ecuador, Venezuela and Bolivia.

**6. *Trichosalpinx ciliaris* (Lindl.) Luer, *Phytologia* 54(5): 395. 1983.**

BASIONYM: *Specklinia ciliaris* Lindl., Edwards's Bot. Reg. 24: Misc. 31. 1838.

*Pleurothallis ciliaris* (Lindl.) L.O. Williams, *Caldasia* 1(5): 14. 1942. TYPE: Mexico, *Loddiges s.n.* (holotype, K-79852; drawing of type, AMES-23687). Fig. 46.

*Pleurothallis lepanthiformis* Rchb.f., *Linnaea* 18: 398–399. 1844[1845], *nom. illeg.*

*Humboltia lepanthiformis* (Rchb.f.) Kuntze, *Revis. Gen. Pl.* 2: 667. 1891, *nom. illeg.*

TYPE: Mexico. Temperirtes, *Leibold 22* (syntype, HAL, not found). Mexico.

Temperirtes, *Leibold 23* (syntype, HAL; lectotype, designated by Luer (1993), AMES).

*Pleurothallis purpusii* Schltr. *Orchis* 9(3): 49. 1915. TYPE: Mexico. "Wurde von C.A. Purpus im Jahre 1912 bei Zacnapam gesammelt und blühte im Sept 1913 im Botanischen Garten zu Darmstadt, von wo ich die Art durch Herrn Garteninspektor J.A. Purpus, den Bruder des Sammlers, erhielt", *J. A. Purpus s.n.* (holotype, destroyed at B; neotype designated by Luer [1997, as the 'lectotype'], *J. A. Purpus 7712*, UC, not found).

**Herb** epiphytic, caespitose, descendent, up to 7 cm tall. **Roots** slender, flexuous, to 1 mm in diameter. **Ramicauls** slender, erect, fractiflex, 3.5–4.0 cm long, enclosed by 5–9

tubular, adpressed at the base, ribbed, glabrous, brown lepanthiform sheaths, 1 cm long, with dilated, minutely ciliate ostia. **Leaves** suffused with purple beneath along the veins, erect, coriaceous, narrowly elliptical, ovate or orbicular, acute, shortly apiculate, 3.5–4.5 × 0.9–1.1 cm, the cuneate base narrowing into a petiole up to 0.4 cm long.

**Inflorescence** a dense, distichous, 5–7 simultaneously flowered raceme, 1.5–2.0 cm long including the peduncle 0.8 mm long, produced at the apex of the ramicaul from a lanceolate, acute spathe 1 cm long. **Floral bracts** tubular, cuneiform, conduplicate, 1 × 1 mm. **Pedicels** 1 mm long, persistent. **Ovary** cylindric, 1 mm long. **Flowers** with the dorsal sepal yellow, suffused with purplish-red toward the apex, the synsepal white at the base suffused with purplish-red, the petals purplish-red, the lip dark purple, the column and anther white. **Dorsal sepal** flexuous, oblong, acute, ciliate, 3.4–3.7 × 1.9–2.1 mm, 3-veined. **Lateral sepals** fleshy, connate close to the apex into a broadly ovate, retuse, entire, ciliate along the margin, concave synsepal, 2.7–2.9 × 1.9–2.1 mm, 3-veined. **Petals** oblong, acute to obtuse, fimbriate, 1.0 × 0.5 mm, 1-veined. **Lip** oblong, rounded, shallowly arcuate, ciliate along the first half, 1.7 × 0.5 mm, the margins of the apex incurved; the disc with a central carina from the base that disappears below the middle, after which it turns into a furrow; the basal lobes short, erect. **Column** short, semiterete, curved and fimbriate at the apex, broadly winged toward the apex, 1.7 mm long, the clinandrium subapical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, on a cellular, oval caudicle. **Fruit** not seen.

**Distribution.** From Mexico to Costa Rica, with the exception of El Salvador.

**Additional material examined. Costa Rica.** – **Cartago:** Fajardo de Cachí, margen norte del río Reventazón, terreno muy pedregoso con cobertura de bosque secundario sobre las paredes de acantilado del río, 9°50'49.46"N 83°48'11.62"W, colectado por D. Jiménez, 16

jul 2010, *M. Fernández 328*, (JBL-D4288); – Paraíso, Cachí, camino al Cerro Duán, orillas del río Naranjo, 1300 m, 9°49'43"N 83°46'31"W, bosque muy húmedo premontano, epífitas al lado del río, 9 feb 2013, *A. Karremans 6000* (JBL-D6122). Fig. 47.

**Habitat and ecology.** Plants were found in the lowlands of the Caribbean watershed in premontane wet forest, growing epiphytically in riverine forests where humidity is high and temperature is warm. The plants collected in the zone of Cachí were found in the main tree trunks in shaded conditions.

**Etymology.** From the Latin *ciliaris*, "ciliate", in reference to the floral parts.

**Phenology.** Plants flower from September to November under greenhouse conditions.

**Discussion.** *Trichosalpinx ciliaris* is recognized by the fractiflex ramicauls that bear 5-9 lepanthiform sheaths that are mostly glabrous except for the minutely ciliate ostia. The leaves are narrowly lanceolate, acute, with the base constricted into a short petiole, the midvein is commonly stained with purple beneath. It is evident that the flowers resemble those of *T. memor* in color patterns, the concave synsepal and the lip with a central carina. Nevertheless, the ramicauls of *T. memor* are straight (vs. fractiflex), the leaves are mostly ovate to oblong (vs. narrowly lanceolate), the petals are suffused partially or totally with purple or brown-red (vs. translucent white or pale yellow), and the lip is shallowly arcuate with the apical margins incurved (vs. flat throughout all its extension). Also, the habit of the recently described *T. reflexa* is almost indistinctive from that of *T. ciliaris*, but the flowers with an erect dorsal sepal and a reflexed synsepal, as well as a densely long-ciliate lip allow rapid identification. Although *T. ciliaris* is morphologically variable along its wide

distribution (according to Luer 1997 and Soto Arenas 1987), the phenotype of Costa Rican populations is apparently constant.

With morphologically variable species come a vast number of synonyms, and *T. ciliaris* is no exception. The protologues of both *Pleurothallis purpusii* (Reichenbach 1844 [1845]) and *P. lepanthiformis* (Schelchter 1915) agree with the concept of *T. ciliaris*. On the other hand, several names were previously located under the synonymy of *T. ciliaris* but have been revised and are currently assigned to the synonymy of other species: *P. gnomonifera* and *T. brevis* are synonyms of *T. memor*, *P. ciliata* Knowles & Westc. is a synonym of *Acianthera aphyta* (Lindl.) Pridgeon & M.W.Chase and *Pleurothallis villosa* agrees with the concept of *Stelis villosa* (Knowles & Westc.) Pridgeon & M.W.Chase.

**7. *Trichosalpinx dura* (Lindl.) Luer, *Phytologia* 54: 395. 1983.**

BASIONYM: *Pleurothallis dura* Lindl., *Folia Orch. Pleuroth.* 32. 1859. *Humboltia dura* (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 667. 1891. TYPE: Peru [Ecuador?]. Forests of the Andes, *Jameson s.n.* (holotype, K; isotypes, AMES, W). Fig. 48.

*Pleurothallis foliata* Griseb., *Fl. Brit. W. Ind.* 610. 1864. *Trichosalpinx foliata* (Griseb.) Luer, *Phytologia* 54: 395. 1983. *Humboltia foliata* (Griseb.) Kuntze, *Rev. Gen. Pl.* 2: 667. 1891, *nom. illeg.* TYPE: Jamaica. *N. Wilson s.n.* [160] (holotype, not located [K and GOET mentioned as possible sites by web database [www.TROPICOS.org](http://www.TROPICOS.org)]; drawing of type, AMES).

*Pleurothallis corazonica* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 443. 1899.

TYPE: Ecuador. Terrestris in silvis densis humidis circa Silante et Michigalli, in declivitatibus occidentalibus montis Corazon, 2000-2300 m, *F. C. Lehmann 4501* (holotype, destroyed at B; neotype, designated by Luer 1997: Ecuador. Below Chiriboga, 2000 m, *C. Luer, A. Hirtz et al. 9870C* [MO]).

*Pleurothallis broadwayi* Ames, Orchid. 2: 267. 1908. TYPE: Annandale, St.

George's, Grenada, W. I. on cocoa trees, growing here and there among

*Pleurothallis pruinosa* Lindl., flos. yellow, March, 1906, *W. E. Broadway 1846*

(lectotype, selected by Schweinfurth 1940).

*Pleurothallis guadalupensis* Cogn., Symb. Antill. 6: 432. 1909. TYPE: Guadeloupe.

Supra arbores in sylvis ad Bonbariman in monte Haut-Matouba, alt. 810 m, *Duss 4192* (holotype, BR; isotypes, AMES, NY).

*Pleurothallis lepanthopsis* Schltr., Repert. Spec. Nov. Regni Veg. 14: 386. 1916.

TYPE: Ecuador. In silvis montis Carazon prope Milligali, *A. Sodiro 27* (holotype, BR).

*Pleurothallis williamsii* Ames, Orchid. 7: 120. 1922. TYPE: Panama. Cana and

vicinity, Apr 17-June 8, 1908, 2000-6500 feet altitude, *R.S. Williams 976* (holotype, AMES; isotype, NY).

*Pleurothallis anomala* Hoehne, Arch. Inst. Biol. (São Paulo) 2: 43. 1929.

*Pleurothallis broadwayi* ssp. *anomala* (Hoehne) Garay, Arch. Bot. São Paulo 11:

53. 1951. TYPE: Brazil. São Paulo: Estação Biologica do Alto da Serra, 2 Oct 1921, A. Gehrt 7965 (holotype, SP).

*Pleurothallis amygdalina*, *nomen nudum* (cited by Schlechter in the protologue of *Pleurothallis lepanthopsis*, Repert. Spec. Nov. Regni Veg. 14: 386. 1916).

**Herb** epiphytic, branching, up to 8 cm long. **Roots** slender, flexuous, to 0.7 mm in diameter. **Ramicauls** erect, prolific, 1–4 (–6) superposed ramicauls, each ramicaul 1–5 cm long, enclosed by 3–7 tubular, grey to light brown lepanthiform sheaths, adpressed, shallowly ribbed, 0.3–0.8 cm long, the margin ciliate, dilated. **Leaves** entire, narrowly elliptical to obovate, obtuse, fleshy, with an apiculus projecting abaxially, 3–18 × 3–7 mm, with the three veins commonly suffused with purple abaxially, the cuneate base narrowing into a petiole 1.0–2.5 mm long. **Inflorescence** suberect to descending, distichous, a 6–11 simultaneously flowered raceme, 1.5–6.0 cm long including the peduncle 0.4–1 cm long, produced at the apex of the ramicaul from a conduplicate, ovate, acute, basally adpressed spathe. **Floral bracts** cuneiform, conduplicate, papyraceous, 0.5–0.9 mm long. **Pedicels** 1.0–2.5 mm long, persistent. **Ovary** cylindric, 0.5 mm long. **Flowers** with the sepals yellow, the apex orange, the petals translucent yellow, occasionally suffused with vinaceous along the margins and central vein; the lip yellow, with the base yellow or vinaceous and the apex commonly orange; the column yellow or partially suffused with vinaceous, the column-foot vinaceous, the anther cap white. **Dorsal sepal** glabrous, ovate to triangular, acute to acuminate, the lower third concave, the apex thickened, carinate dorsally, 3.9–5.4 × 1.2–1.9 mm, 3-veined. **Lateral sepals** free, glabrous, reflexed, narrowly triangular to falcate, acute, carinate dorsally, thickened towards the apex, 3.5–5.0

× 1.0–1.3 mm, 1-veined. **Petals** glabrous, slightly turned outwards, elliptic to obovate, rounded to subacute, the apex variable from shallowly lobed to serrate, 1.2–1.5 × 0.6–0.8 mm. **Lip** glabrous, oblong, obtuse, slightly arcuate, cellular-glandular, 1.7–2.5 × 0.7–0.9 mm, the lower third broadly rounded forming a pair of low, erect lobes, the disc with the lateral veins shortly thickened, the apex thickened. **Column** terete, broadly winged above the middle, 0.9–1.2 mm long, with a column foot 0.8–1.2 mm long, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, broadly ovate, emarginate. **Pollinia** 2, yellow, ovate, on cellular, ovate caudicles. **Fruit** a green, glabrous, 2-valved, globose capsule, 2.5–3.0 × 3.0 mm, with two prominent dehiscent lines along the carpel midribs, perianth remnants persistent.

**Distribution.** Mexico to Panama, into the Andes south to Bolivia, and the Antilles (Cuba, Jamaica, Dominican Republic, Haiti, Grenada, Guadalupe, Martinique, Trinidad and St. Kitts).

**Additional material examined. Costa Rica.** – **Alajuela:** Alajuela, Sarapiquí, Cinchona, bosque a la orilla de la calle, bosque húmedo [bosque pluvial premontano], 15 May 2005, *E. Serrano 232 & Grupo de Asociación de Aves AOS* (JBL-B1555); – San Ramón, Angeles, Reserva Biológica A. M. Brenes, alrededores de la Estación Biológica del río San Lorencito, [10°13'08"N 84°35'48"W] 900-1100 m, [bosque muy húmedo tropical transición a premontano], 27-28 ago 2011, *M. Blanco 4042, J. Abarca, M. Díaz, M. Chavarría & J. Gómez-Laurito* (JBL-D5760); – San Ramón, San Lorenzo, road between San Ramón and La Fortuna, Los Lagos, Centro educativo Los Lagos, 780 m, 11 may 2002, *F. Pupulin 3806, H. Montealegre & A. C. Rodríguez* (USJ-80848, 80179); – Upala, Bijagua, en la calle nueva desde el Celeste Mountain Lodge al parque Volcán Tenorio, sobre árboles al

lado de camino en bosque primario, bosque húmedo premontano, 10°42'59"N 85°01'23"W, 800 m 28 mar 2011, A. Karremans 3794, M. Contreras y P. Aguilar (JBL-D5857). – **Cartago**: Jiménez, Selva, Reserva El Copal, 1000-1200 m, 2 jun 2001, M. Blanco 1937 & R. Narit (USJ-80286); – Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 9°46'51.7"N 83°43'00.4"W, 707 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del río, 16 oct 2009, A. Karremans 2468 & D. Bogarín (JBL-C1066); – [Idem], A. Karremans 2490 & D. Bogarín (JBL-C1067). Idem, 29 ene 2012, A. Karremans 4885, R.J.C.M. Ferrerira Lok & I.V. Ferreira Lok (JBL-D5483); – [Idem], 30 abr 2009, D. Bogarín 6945, M. Fernández, R. Gómez, Y. Kisel, F. Pupulin, P. Renshaw & R. Trejos (JBL-D3271); – Jiménez, Pejibaye, Taus, margen del río Tausito, 500 m después de la Escuela de Taus, bosque pluvial premontano, epífitas en bosque secundario a lo largo del río, 9°47'09"N 83°43'04"W, jun 2011, M. Fernández 547 & L. Sandoval (JBL-E0791); – Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, senderos La Pava y La Catarata, orillas del río Grande de Orosi, 9°44'04.3"N 83°46'55.04" W, 1341 m, epífitas en bosque secundario y árboles a orillas del río, bosque pluvial montano bajo, 8 feb 2012, A. Karremans 4973, D. Bogarín, M. Fernández, F. Pupulin & C.M. Smith (JBL-D5372); – A. Karremans 4974, D. Bogarín, M. Fernández, F. Pupulin & C.M. Smith (JBL-D5365); – [Jiménez], pasture near río Pejibaye, 2 km S.W. of Taus, 9.783 -83.733, 750 m, R. W. Lent 2965 (CR-54317). – **Heredia**: Varablanca, San Rafael, km 1.7 after the village of San Rafael, along the Río San Rafael, 10°10'N 84°07'W, ca. 1750 m, lower montane wet forest, epiphytic in secondary mature vegetation, riparian gallery forest, 6 Jul 2002, F. Pupulin 4077, E. Salas & H. León-Páez (JBL-B0179). Fig. 49.

**Habitat and ecology.** Plants were found inhabiting the premontane rain, premontane wet, and low montane rain forests of the northern (Caribbean) slopes of the Cordillera de

Talamanca; the premontane rain and low montane wet forests of the Desengaño gap in the Cordillera Volcánica Central, and the tropical wet (transitional premontane) forests of San Ramón in the east edges of the Cordillera de Tilarán in the Pacific watershed.

**Etymology.** From the Latin *durus*, “hard”, in reference to the consistency of the leaves.

**Phenology.** Under greenhouse conditions, plants of *Trichosalpinx dura* flower mainly between June and October, but sporadic flowering was observed in January. Two plants from different localities produced fruits between December and January while in the greenhouses. Exsiccata indicate flowering in May and June.

**Discussion.** *Trichosalpinx dura* is recognized by the prolific ramicauls that produce long, tangled chains of stems, which bear elliptical to obovate leaves with purple colored veins. The racemes bear several yellow flowers with a dorsal sepal concave at the base and narrowed towards the apex, and reflexed lateral sepals. The petals are slightly deflexed, and the lip bears two short, erect lobes in the lower third and two longitudinal calli, and the apex is always thickened and cellular-glandulose.

This species is most similar to *Trichosalpinx membraniflora*, but the latter has a flat lip with no evident thickenings and the apical portion of the column is elongated forward with the anther seemingly dorsal. Unfortunately, additional specimens of *T. membraniflora* were not found during the course of this study.

The also widely distributed *Trichosalpinx cedralensis* may be confused with *T. dura*.

Vegetatively, both share the long, prolific ramicauls, the ribbed, adpressed sheaths and the elliptical leaves. Nevertheless, plants of *T. dura* usually produce long chains with only

one ramicaul borne from the apex of the preceding, while most individuals of *T. cedralensis* form erect, tree-like structures with a lower production of successive ramicauls. Although flowers of both species may be confused at first sight because of similar shape and arrangement, flower color is particularly useful. The sepals of *T. dura* are yellow with apices usually orange (vs. entirely white to light yellow), petals are translucent yellow and occasionally suffused with vinaceous purple along the margins and central vein (vs. translucent white), the lip is yellow with the base suffused with wine-purple (vs. light yellow), and has two shallow, erect lobes in the basal third (vs. two comparatively high, erect lobes) and two lateral, parallel calli (vs. no calli).

As reported by Luer (1997), plants of *Trichosalpinx dura* vary greatly even within a limited area. In Costa Rican specimens, vegetative variations are evident, including changes in length of ramicauls, diameter of ostia and size and shape of leaves. Although to a lesser extent, variations in flower morphology were also noticed, including number of flowers per raceme, length of rachis, pedicels and sepals, shape and color of petals and color of the basal portion of lips (Fig. 50). Compared to South American data cited in Luer (1997), Costa Rican populations bear shorter inflorescences caused mainly by shorter peduncles (0.4–1.0 cm vs. 1.0–4.0 cm). On average, flowers are also smaller due to the comparatively shorter and narrower sepals. Eventhough Lindley described the stems of *P. dura* as non-prolific (a non-conventional character in subgenus *Tubella*), in the majority of the specimens the stems are in fact superposed, forming long chains (Luer 1997).

It is important to notice that Lindley annotated in the protologue that Peru was the country of origin of the type specimen. Nevertheless, the holotype material has no indication of the country of origin of this material, while the isotype deposited at AMES indicates Ecuador

as the original country of collection, which is used by Luer (1997) in his treatment of *Trichosalpinx*.

**8. *Trichosalpinx fruticosa* Luer, *Lindleyana* 11(2): 105. 1996.**

*Trichosalpinx fruticosa* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 59–60. 1997, *nom. illeg.* homonym.

TYPE: Costa Rica. San José: epiphytic on Cerro del Muerte, alt. 2400 m, 21 Mar 1986, collected by W. Ballesteros, C. Luer 12135 (holotype, MO). Fig. 51.

**Herb** epiphytic, branching, erect, up to 18 cm tall including the inflorescence. **Roots** slender, flexuous, to 1.5 mm in diameter. **Ramicauls** slender, suberect to ascending, prolific, 0.6 to 9 cm long, enclosed by 2–8 tubular, closely adpressed, greyish, glabrous to minutely scabrous lepanthiform sheaths, 0.3–1.1 cm long. **Leaves** ascending, thickly coriaceous, elliptical, obtuse, entire, 10–18 × 3–6 mm, the attenuate base narrowing into a petiole up to 2 mm long. **Inflorescence** a congested, fractiflex, simultaneously 5–9 flowered raceme, 2.6–3.8 cm long including the peduncle up to 1 cm long, produced at the apex of the ramicaul from a conduplicate, lanceolate, acute spathe. **Floral bracts** tubular, ovate, narrowly acuminate, papyraceous, 2.4–2.6 mm long. **Pedicels** 0.3–0.6 mm long, persistent. **Ovary** cylindrical, sulcate, 0.5–0.7 mm long. **Flowers** with the sepals entire, glabrous, carinate, white to light yellow, the petals translucent white, the lip white or light yellow, the column and anther white. **Dorsal sepal** ovate, acuminate to caudate, free, 5.9–8.8 × 1.4–1.6 mm, 3-veined, the base slightly concave, truncate. **Lateral sepals** narrowly

triangular, concave at the base, oblique, narrowly obtuse, 6.4–8.1 × 0.7–0.9 mm, 2-veined. **Petals** membranous, narrowly ovate to lanceolate, acute, minutely erose, 1.6–2.2 × 0.6–0.8 mm, 1-veined. **Lip** glabrous, narrowly oblong, obtuse, 1.8–2.8 × 0.9–1.3 mm across the lobes, the basal half with two lateral erect lobes, the disc with a shallow, central carina from the base to near the apex, the apex thick, papillate, convex beneath, the base truncate, hinged to the column-foot. **Column** terete, 1.2–1.6 mm long, the apex wingless, the clinandrium subapical, the stigma ventral. **Anther cap** incumbent, broadly ovate, emarginate. **Pollinia** 2, ovoid, on cellular, ovate caudicles. **Fruit** not seen.

**Distribution.** Guatemala, El Salvador and Costa Rica.

**Additional material examined. Costa Rica – Alajuela:** Naranjo, Palmira, Bajo del Toro, Río Toro waterfall, 10°15'15"N, 84°16'17"W, 1220 m, premontane wet forest, secondary mature vegetation, 13 Apr 2003, *F. Pupulin 4586, E. Salas & H. Leon-Paéz* (JBL-B0213). – **Cartago:** El Guarco, San Isidro, Macizo Cerro de La Muerte, Vara de Roble, en camino que entra a la estación eléctrica, 09°46'20.00"N 83°59'13.10"W, 1940 m, bosque pluvial montano, epífita en árboles en finca, 4 abr 2012, *M. Fernández 617, M. Contreras, A. Karremans & L. Sandoval* (JBL-D4956); – *M. Fernández 623, M. Contreras, A. Karremans & L. Sandoval* (JBL-D4968); – *M. Fernández 624, M. Contreras, A. Karremans & L. Sandoval* (JBL-D5000); – Cartago, San Francisco, Muñeco, 3 km al sur de Muñeco, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'0.6"N 83°53'55.4"W, 1621 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 27 may 2009, *D. Bogarín 6509, R. Gómez, Y. Kisel & R. Trejos*; – San Nicolás, Cerros de La Carpintera, bosques remanentes en la parte alta y árboles en potreros cercanos, 1770 m, 9 may 2012, *A. Cascante 2338* (USJ-100702). – **Puntarenas:**

Monteverde, 1450 m, 9 jun 1989, *J. T. Atwood 89-149* (CR-031040). – **Sin datos de colecta**: flowered in cultivation at Lankester Botanical Garden, *JBL-11580* (JBL-D2961).

Fig. 52.

**Habitat and ecology.** *Trichosalpinx fruticosa* was found inhabiting the premontane and montane rain forests of the Cordillera de Talamanca, as well as the premontane wet forests of the Cordillera Volcánica Central in Costa Rica, between 1200 and 2000 m elevation. It grows epiphytically mainly on branches and twigs of scattered *Quercus* sp. trees as well as in the boundaries of secondary mature forests.

**Etymology.** From the Latin *fruticosus*, “bushy”, in reference to the habit (Luer 1996).

**Phenology.** Plants bearing inflorescences were found during field work in April 2012, while *exsiccata* shows flowering in May and June. In cultivation, plants flowered several times on January, April and September.

**Discussion.** *Trichosalpinx fruticosa* is most similar to *T. cedralensis*, particularly in the growing habit. Both produce tree-like structures of long, prolific ramicauls covered by adpressed sheaths with terminal, elliptical, thickly, coriaceous leaves, tangled with mosses and lichens. Flowers of *T. fruticosa* can be recognized by the longer sepals (5.9–8.8 mm vs. 5–6.8 mm in *T. cedralensis*), the laterals triangular and free (vs. ovate and connate above the middle), the equal petals (vs. oblique), and the lip with a central, though shallow, carina. They both share similar environments in the montane to premontane rain forests of Costa Rica.

In his treatment of the genus, Luer (1997) erroneously published *Trichosalpinx fruticosa* as a new species. According to the International Code of Nomenclature for algae, fungi, and plants (McNeill *et al.* 2011), this publication is a homonym since it was validly published in a previous work (Luer 1996).

**9. *Trichosalpinx membraniflora* (C.Schweinf.) Luer, *Phytologia* 54(5): 396. 1983.**

BASIONYM: *Pleurothallis membraniflora* C.Schweinf., Bot. Mus. Leaflet. 5(6): 91.

1938. TYPE: Costa Rica. Alajuela: San Pedro de San Ramón, 29 Jul. 1935, A.M.

*Brenes 20.571* (holotype, AMES). Fig. 19.

**Herb** epiphytic, caespitose, up to 4.8 cm tall. **Roots** fibrous, glabrous, stout, to 1 mm diameter. **Ramicauls** slender, prolific, 5.0-8.8 cm, enclosed by usually 4–7 tubular, nervose-angulate, minutely hispid, basally adpressed lepanthiform sheaths, up to 7 mm long, ovate and ciliate apically. **Leaves** erect, obovate, marginate, apiculate, rounded, coriaceous, 9 × 4–5 mm, minutely cartilaginous-serrulate apically, base gradually narrowing into a short petiole. **Inflorescences** a loose, up to 4-flowered fascicle, borne at the apex of the ramicaul. **Flowers** membranaceous. **Sepals** parallel, about equally long. **Dorsal sepal** oblong-lanceolate, subacute, concave, 3.0 × 1.5 mm, carinate adaxially, 3-nerved. **Lateral sepals** free, narrowly triangular-lanceolate, slightly falcate, acute, 8.0 × 0.9 mm, carinate adaxially, 1-nerved. **Petals** diaphanous, narrowly elliptic-ligulate, acute or subacute, oblique at the apex, about 1.0 × 0.2 mm, about equaling the column, 1-nerved. **Lip** simple, oblong, membranaceous, subsessile, undulate marginally, 1.4 × 0.6 mm, slightly broader near the base, broadly rounded basally and apically, 3-nerved. **Column**

inconspicuous, about 1 mm long, winged on each side throughout. **Anther cap, pollinia** and **fruit** not seen. (Description based on the protologue [Schweinfurth 1938], holotype and drawing of the holotype [AMES-74431]).

**Distribution.** Known only from Costa Rica and Panama.

**Additional material examined.** Other than the type specimen, no material was found during this project. (Fig. 53).

**Habitat and ecology.** The type specimen (and only Costa Rican material found so far) was growing epiphytically in the premontane wet forests at 950 m in the San Ramón area, in the Cordillera de Tilarán.

**Etymology.** From the Latin *membraniflorus*, “with membranous flowers”, referring to the delicate consistence of the flower.

**Phenology.** The type specimen was collected in flower in July. The two known Panamanian specimens were collected (presumably in flower) in September and February.

**Discussion.** *Trichosalpinx membraniflora* is a Central American species, known from the type specimen –collected in San Ramón in the province of Alajuela, Costa Rica-, and from two plants collected at mid-elevations in Coclé, Panamá. *Trichosalpinx membraniflora* mostly resembles *T. dura*, from which it is distinguished by the inflorescence as long as the leaf (twice or more times longer than the leaf), the barely longer and somewhat broader petals ( $1 \times 0.25$  mm vs  $1.2\text{--}1.5 \times 0.6\text{--}0.8$  mm in *T. dura*) the lip without

thickenings (vs. two shallowly thickened lateral veins), and a column with two wings elongated to the front (vs. a column with short wings projecting downwards).

The surroundings of San Pedro of San Ramón were among the favorite collecting sites of Brenes and Endrés in Costa Rica. Today, pastures, coffee plantations and housing development take over the majority of the landscape, where scarce patches of riverine forest persist. Although visited in several occasions accompanied by numerous trained collectors, no plants resembling *T. membraniflora* were found. Nearby localities with similar type of forest (sensu Holdridge 1986) such as Palmira, Balsa, San Miguel, Naranjo and the Alberto M. Brenes Biological Reserve, were visited unsuccessfully. Accordingly, the description cited here is a transcript of the original one by Schweinfurth. It is expected that the Costa Rican populations, if any, have diminished drastically or have disappeared. Some of the surrounding forests at the zone of El Valle de Antón in Coclé, Panama, where two specimens were collected in 1976 and 1985, are protected territories, and populations of *T. membraniflora* are probably still found there.

**10. *Trichosalpinx memor* (Rchb.f.) Luer, *Phytologia* 54(5): 396. 1983.**

BASIONYM: *Pleurothallis memor* Rchb.f., *Bonplandia* 4(20-21): 330. 1856.

*Humboldtia memor* (Rchb.f.) Kuntze, *Revis. Gen. Pl.* 2: 667. 1891, *nom. illeg.*

TYPE: Colombia. Without collection data, flowered in cultivation in Hamburg Bot. Garden by *H. Forkel s.n.* (holotype, W-R). Figs. 54–55.

*Pleurothallis brevis* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 19: 183. 1923.

TYPES: Costa Rica, troncs humides, Los Angeles de Heredia, alt. 1500 m, May

1921, *A.M. Brenes 13* (syntype at B, destroyed); Costa Rica, bois à San Pedro de San Ramon, alt. 950 m, Jun 1921, *A.M. Brenes 40* (syntype at B, destroyed). NEOTYPE, designated by Barringer, *Fieldiana, Bot. n.s. 17: 13* (1986): Costa Rica, Cartago: near Cartago, 1450 m, Apr 1922, drawing of *A.M. Brenes 276* (AMES-29918); also designated as 'lectotype' by Luer, *Icon. Pleur. 15: 26-28* (1997).

*Pleurothallis gnomonifera* Ames, *Sched. Orchid. 6: 61–63*. 1923. TYPE: Panama. Chiriqui: Cerro Norquita, alt 5000-6000 ft, *C.W. Powell 311* (holotype, AMES-26928).

*Trichosalpinx greenwoodiana* Soto Arenas, *Orquídea* (Mexico City), n.s., 10(2): 257–259. 1987. TYPE: Mexico. Chiapas: Cerro Tres Picos, al norte de Tonalá, selva mediana-baja perennifolia de montaña, con *Oreopanax*, lauráceas y ericáceas, ca. 2150 m, ejemplar preparado de material cultivado, 20 Oct 1986, *Soto Arenas, E. Martínez & A. Mendoza 2763* (holotype, AMO).

*Trichosalpinx nageliana* Soto Arenas, *Orquídea* (Mexico City), n.s., 10(2): 259–262. 1987. TYPE: Mexico. Guerrero: ca. 2 km antes de Omiltemi, bosques húmedos, deciduos, de encinos (*Quercus castanea*) sobre calizas aflorantes, ca. 1900 m, 7 Jul 1984, *M.A. Soto, J. Meave, L.M. Calvo & H. Paz 3075* (holotype, AMO; isotype, MO).

**Herb** epiphytic, caespitose, erect, up to 12 cm tall. **Roots** slender, flexuous, 1 mm in diameter. **Ramicauls** slender, erect, 1–9 cm long, enclosed by 3–6 tubular, adpressed at the base, ribbed, ciliate, lepanthiform sheaths, 1.5–3 cm long, with dilated, ciliate ostia. **Leaves** suffused with purple beneath, fleshy, elliptic to narrowly ovate, obtuse, apiculate,

1.2–3.5 × 0.9–2.3 cm, the cuneate base narrowing into a petiole up to 4 mm long.

**Inflorescence** a dense, distichous, 2–6 simultaneously flowered raceme, 1–2.5 cm long including the peduncle 4–8 mm long, THE APEX OF THE RAMICAUL of the leaf from a lanceolate, acute, conduplicate spathe. **Floral bracts** cuneiform, conduplicate, 1 × 1 mm.

**Pedicels** 1 mm long, persistent. **Ovary** cylindrical, 1 mm long. **Flowers** with the sepals dark purple, purple or greenish-purple, white at the base, papillate externally, ciliate along the margins, the petals translucent yellowish, the lip dark purple, sometimes suffused with yellow toward the apex, the column white, the clinandrium white (occasionally pinkish apically), the anther white. **Dorsal sepal** more or less membranaceous, erect to descendent, oblong to ovate, acute, truncate, 3.3–3.7 × 1.7–2.1 mm, shallowly concave at the base, 3-veined. **Lateral sepals** fleshy, connate into a broadly ovate, retuse, entire, concave synsepal, 3.1–3.7 × 3.3–3.7 mm, 4-veined. **Petals** membranaceous, oblong to elliptic, obtuse, truncate, fimbriate, 1.1–1.3 × 0.6–0.7 mm, 1-veined. **Lip** gently arcuate, narrowly oblong to ligulate, rounded, ciliate, 2.1–2.3 × 0.5–0.6 mm, the basal margins shortly dilated, suberect, the apical margins deflexed, the disc with a central carina from the base, decreasing in height in the basal third, where it divides into two low, longitudinal keels which disappear distally, the base with two retrorse lobules and a central membrane that is hinged to the column-foot, the apex with a shallow groove from the middle towards the end. **Column** straight, semiterete, fimbriate at the apex, 1.5–1.9 mm long, the clinandrium subapical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, on a cellular, oval caudicle. **Fruit** a pinkish, 2-valved, glabrous, globose capsule, 7.0–8.0 × 5.0–5.5 mm, laterally dehiscent, with two prominent dehiscence lines running along the carpel midribs, the perianth persistent.

**Distribution.** From Mexico to Colombia, Peru, Ecuador and Bolivia, and in Grenada and Cuba in the Antilles (Luer 1997).

**Additional material examined. Costa Rica. – Alajuela:** Alfaro Ruiz, Palmira, Reserva Biológica Bosque de Paz, 10°12'17"N 84°19'02", 1541 m, bosque muy húmedo montano bajo, 11 ago 2011, *A. Karremans 4580, D. Bogarín & M. Muñoz* (JBL-D4805); – *A. Karremans 4599, D. Bogarín & M. Muñoz* (JBL-D5593); – Alfaro Ruiz, distrito Palmira, Pueblo Nuevo, Fila La Picada, Zona Protectora El Chayote, 1920 m, remnants of primary forest in pastures, 21 Nov 1999, *F. Pupulin 1819, L. Spadari, S. Méndez & V. Blanco M.* (JBL-E0827); – Alfaro Ruiz, Palmira, Reserva Biológica Bosque de Paz, orillas del sendero Jaulares, 10°12'17.00"N 84°19'02.10"W, 1541 m, bosque muy húmedo montano bajo, "crescit in locis umbrosis in arborum vetustarum vel collapsarum truncis per tramitem Jaluares ad Bosque de Paz", 11 ago 2011, *D. Bogarín 9032, A. Karremans & M. Muñoz* (JBL-D5449); – San Ramón, sin más datos de colecta, floreció en cultivo en el Jardín Botánico Lankester, A. Q. [probably, *Alonso Quesada*] *s.n.* (JBL-D3335); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06" N 84°36'11" W, 850 m, bosque muy húmedo tropical transición a premontano, sobre el Sendero Pájaro Sombrilla, epífitas en bosque secundario con remanentes de primario, 3 oct 2003, *D. Bogarín 441* (JBL-D0085); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'12" N 84°36'13" W, 800-900 m, camino por el sendero La Catarata, orillas del Río San Lorencito, bosque muy húmedo tropical transición a premontano, epífitas en bosque primario y secundario, 24 may 2008, *D. Bogarín 4975* (JBL-D3269); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06" N 84°36'11" W, 800-900 m, camino por el sendero La Fila, bosque muy húmedo tropical transición a premontano, epífitas en ramas caídas alrededor del sendero, 25 may 2008, *D. Bogarín 5009* (JBL-D2462); *D. Bogarín 5016*

(JBL-D3342); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06" N 84°36'11" W, 850 m, bosque muy húmedo tropical transición a premontano, sobre el Sendero La Catarata, epífitas en borde de bosque secundario a orillas del Río San Lorencito, 24 set 2005, *D. Bogarín 1880* (JBL-D3326); – San Ramón, Reserva Forestal de San Ramón, 850-1000 m, floreció en cultivo en Italia, 25 set 1992, *M. Germani 41* (USJ-91717); – *JBL-01546* (JBL-D3464); San Ramón, Piedades Sur, San Miguel (La Palma), en El Alto después de San Bosco, en árboles solitarios en potrero, 21 dic 2010. 10°07'43.7"N 84°33'13.5"W, 1289 m, *A. Karremans 3044, J.A.J. Karremans & M. Contreras Fernandez* (JBL-D5371); – San Ramón, La Balsa, road from San Ramón to La Fortuna, proximity of Río La Balsa, 10°11'52.2"N 84°30'54.4"W, 990 m, premontane wet forest, epiphytic in secondary vegetation along the edges of *Dracaena* plantations, 26 Dec 2004, *F. Pupulin 5472, E. Salas-Pupulin, S. Dalström & C. Lewis* (JBL-D3255); – San Ramón, Piedades, Piedades Norte, road to Bajo de La Paz, km 2.6, along the Río San Pedro, 10°08'59.9"N 84°33'53.3"W, 1307 m, premontane wet forest, epiphytic along th shores of the river, 30 Jan 2005, *F. Pupulin 5500, D. Bogarín, M. Salas & P. Seaton* (JBL-D3341); – San Ramón, Santiago, finca of Jesús Salas Jiménez, mountains toward the towers of Berlín, 10°02'21"N 84°12'02"W, 1300 m, lower montane rain forest, epiphytic in old tress along coffee plantations, 14 Sep 200, *F. Pupulin 7166, E. Salas-Pupulin & Jesús Salas* (JBL-D2841); – San Ramón, Reserva Biológica Alberto Manuel Brenes, entrando por Miramar, El Cedral, cercanías de la casa, epífitas, luz media a abundante y materia orgánica escasa, con musgos, 10°16'30" N 84°39'10" W, 1200 m, 17 mar 2006, *A. Rojas 7026, J. Gómez & V. Mora* (JBL-D3403); – Upala, Aguas Claras de Buenos Aires, hotel Termales Azules, camino por la ladera del Volcán Rincón de La Vieja, hasta las cataratas, 10°49' N - 85°16' W, 700-1500 m de altura, 6 abr 2004, *A. Karremans 292 & familia* (JBL-B1166); – [Upala],

PN Rincón de la Vieja, rd. to Colonia Blanca by Quebrada Rancho Grande, Alajuela, 700 m, 14 Jul 1978. *C. Tozia* 363 (CR-66769); – [Upala], PN Rincón de la Vieja, rd. to Colonia Blanca by Quebrada Rancho Grande, 700 m, 15 Aug 1978, *C. Todzia* 398 (CR-70124); – Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, sobre los principales senderos, bosque húmedo tropical montano bajo, transición a montano, 10°12'35" N - 84°18'44" W, 1500 m, 18 ene 2011, *A. Karremans* 3487 (JBL-D4916); – Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, sobre los principales senderos, bosque húmedo tropical montano bajo, transición a montano, 10°12'35" N -84°18'44" W, 1500 m, 18 ene 2011, *A. Karremans* 3468 (JBL-D5706). – **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 may 2009, *D. Bogarín* 6580, *R. Gómez, Y. Kisel & R. Trejos* (JBL-D2861); – Orosí, Muñeco de Navarro, finca de Luis Espinoza, 1300 m, 12 abr 1998, *M. Blanco* 803 & *L. G. Espinoza* (USJ-068181); – Jiménez, Pejibaye, La Selva, Reserva Biológica El Copal, 500 m siguiendo el sendero Mariposa, 1020 m, bosque pluvial premontano, epífitas en bosque secundario sobre árbol caído a orillas del sendero, 14 jun 2009, *M. Fernández* 3, *L. Sandoval, E. Biamonte & O. Morrison* (JBL-D3462); – Paraíso, Cachí, Peñas Blancas, entre Cerros Duán y Alto Velo de Novia, 9°48'43.76" N 83°46'36.61" W, 1829 m, bosque muy húmedo premontano, epífitas en árboles en potreros y borde de bosque, 11 mayo 2009, *D. Bogarín* 7193, *R. Gómez, Y. Kisel, P. Renshaw & R. Trejos* (JBL-D5689); – Paraíso, Orosí, Tapantí, Parque Nacional Tapantí, senderos La Pava y La Catarata, orillas del río Grande de Orosí, 9°44'04.3"N 83°46'55.04"W, 1341 m, epífitas en bosque secundario y árboles a orillas del río, bosque pluvial premontano, 8 feb 2012, *D. Bogarín* 9462, *M.*

*Fernández, A. Karremans, F. Pupulin & C.M. Smith* (JBL-D5273); – Paraíso, Fajardo de Cachí, margen norte del río Reventazón, terreno muy pedregoso con cobertura de bosque secundario sobre las paredes de acantilado del río, exactamente en este árbol, 9°50'49.46"N 83°48'11.62"W, colectada por D. Jiménez, en cultivo en el Jardín Botánico Lankester, *M. Fernández* 330 (JBL-E0828); – Turrialba, La Suiza, Llanos del Quetzal, camino a Chirripó Abajo, 9°46'55.4"N 83°24'21.0"W, 1411 m, epífitas en bosque secundario alrededor del camino, bosque muy húmedo premontano, 17 jun 2011, *M. Fernández* 454, *A. Karremans & D. Bogarín* (JBL-D5627); *M. Fernández* 457, *A. Karremans & D. Bogarín* (JBL-D4794); – Turrialba, La Suiza, Llanos del Quetzal, ca. 1 km sobre el camino detrás de la Escuela de Kabébata (Alto Quetzal), 9°46'43.6"N 83°24'41.6"W, 1449 m, epífitas en bosque primario y secundario, bosque muy húmedo premontano "supra arbores in nemoribus Llanos del Quetzal ad Turrialba in Cartago", 17 jun 2011, *A. Karremans* 4246, *M. Fernández & D. Bogarín* (JBL-D5479); – 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, epífitas en bosque secundario a orillas del camino, 1 may 2008, *D. Bogarín* 4750, *A. Karremans, Y. Kisel & R. Phillips* (JBL-D3181); – Paraíso, Cachí, Peñas Blancas, 9°49'51.3"N 83°46'13.1"W, 1400 m, premontane wet forest, epiphytic on trees in pastures and secondary mature vegetation, 13 Nov 2008, *F. Pupulin* 7501, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D2680, USJ-). – **Guanacaste**: Tilarán, San Miguel, aproximadamente 2,5 Km de la Escuela de San Miguel hacia La Florida, finca La Trinidad, en potreros de la familia Durán Rivera, 10°24'56"N 84°54'23"W, 900 m, 1 ag 2011, *M. Fernández* 535 & *L. Sandoval* (JBL-D4796); – Monteverde, 1450m, 9 jun 1989, *J. T. Atwood* 89-156 (USJ-031005). – **Heredia**: Sarapiquí, La Selva, Jun 1995, *G. Carnevali s.n.* (JBL-D3908); Sarapiquí, Puerto Viejo, La

Selva, 50 m, 1 Oct 2000, *M. Blanco* 1617 (JBL-D3461); [San Rafael] road south of Cerro Chompipe, NE Concepción, wet montane forest, epiphytic on mossy limbs, 10°5'0.8" N 84°04'40.7" W, 2015 m, *M. Whitten* 2232 (JBL-D3463); – San Rafael, camino al Monte de La Cruz, desviación al Residencial El Tirol, 10°4'27"N 84°5'8"W, 1800 m, bosque húmedo premontano, epífitas a la orilla del Río Segundo, 17 abr 2003, *D. Bogarín* 165 (JBL-B0130); – San Rafael, high along the Río Tibás, toward Cerro Tibás, abr 1998, *F. Pupulin* 538 (USJ-071064); – San Rafael, Ángeles, camino al Monte de La Cruz, desviación al Residencial El Tirol, orillas del Río Segundo, cerca de Finca Villa Delia, 1840 m, 10°4'27"N 84°5'8"W, bosque húmedo premontano, epífitas en bosque secundario a lo largo del río, 1 jul 2007, *D. Bogarín* 3955 (JBL-D4194, USJ-); – *D. Bogarín* 3956 (JBL-D3556); – *D. Bogarín* 3962 (JBL-D3324); 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 mar 2009, *D. Bogarín* 6409, *R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (JBL-D3183); – 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 mar 2009, *D. Bogarín* 6461, *R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (JBL-D3336); – *D. Bogarín* 6462, *R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (JBL-D3124); – *D. Bogarín* 6470, *R.L. Dressler, R. Gómez, F. Pupulin & R. Trejos* (JBL-D2800); San Rafael, Cuatro Cruces, cerca del cauce del río Tibás, 1700-1900 m, bosque húmedo premontano, epífitas en árboles a orillas de la calle, 5 jul 2009, *M. Fernández* 8, *L. Sandoval, X. Sandoval & O. Sandoval* (JBL-D3423); – *M. Fernández* 12, *L. Sandoval, X. Sandoval & O. Sandoval* (JBL-D3310); – finca Martín Prada, under Cerro Chompipe, 1620 m, mature secondary montane cloud forest, along a river, 17 Aug 1997, *F. Pupulin* 462, *J. Warner, M.*

*Prada et al.* (JBL-B0224); – San Isidro, Concepción, falda sur del Cerro Zurquí, ca. 3 km al norte de Concepción, entre dos afluentes de la Quebrada Caricias, 10°02'56.6"N 84°02'23.9"W, 1688 m, bosque pluvial montano bajo, epífitas en árboles aislados principalmente *Quercus* sp. y *Cupressus lusitanicus* en poteros, 26 oct 2011, *D. Bogarín* 9268, *D. Jiménez, D. Matamoros & G. Villalobos* (JBL-D5448); – San Rafael, road from Residencial El Castillo to Monte de la Cruz, along Río Tibás, slopes of Cerro Tibás, 10°04'N, 84°03'W, 2000 m, lower montane moist forest, primary vegetation, 31 Mar 2003, *F. Pupulin* 4542 (JBL-D3424); – San Rafael, Concepción, Residencial El Castillo, Calle Lobo, southern slope of Cerro Tibás, 10°4'07.7"N 84°03'56.6"W, 1940 m, lower montane wet forest, epiphytic on scattered trees in pastures, 19 Mar 2009, *F. Pupulin* 7674, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D3402); – *F. Pupulin* 7675, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D3400); – *F. Pupulin* 7676, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D3268); – *F. Pupulin* 7677, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D3216); – *F. Pupulin* 7680, *D. Bogarín, R.L. Dressler, R. Gómez & R. Trejos* (JBL-D3405); – finca Martín Prada, under Cerro Chompipe, 1620 m, mature secondary montane cloud forest, along a river, 17 Aug 1997, *F. Pupulin* 455, *J. Warner, M. Prada et al.* (JBL-D3318); – Vara Blanca, San Rafael, puente sobre el Río San Rafael, 10°10'37.7" N 84°07'52.5" W, 1755 m, bosque pluvial montano bajo, en potreros arbolados y bosque secundario a orillas, 17 jun 2009, *D. Bogarín* 7330, *R.L. Dressler, F. Pupulin & R. Trejos* (JBL-D3830). – **Puntarenas:** Osa, Ganado de Sierpe, Península de Osa, 10-50m, 27 Aug 1979, *C. Todzia* 977 (CR-73514); – Puntarenas, Monteverde, Estación Biológica Monteverde, entre los senderos Jilguero y Cariblancos, 10°19'15.9" N 84°47'37.8" W, 1817 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del sendero, 7 ago 2010, *D. Bogarín* 8004 & *M. Fernández*

(JBL-D4198); – [Monteverde], Cordillera de Tilarán. Reserva Biológica de Monteverde, Marzo de 1990, floreció en cultivo el 17 feb 1994 en Jardín Lankester Cartago, 1350 m, *D. E. Mora s.n.* (USJ-050993); – Santa Elena, Cerro Plano, finca Beeche, 10°19'13"N 84°48'35"W, 1580 m, epiphytic on old trees in pastures, lower montane cloud forest, 30 Apr 2003, *F. Pupulin 4736 & G. Barboza* (JBL-D3401). – **San José:** Dota, San Joaquín, 1km después de la escuela de San Joaquín yendo hacia Quepos, 09°34'32.88"N, 84°00'18.06"W, 1100 m, en árboles esparcidos en potreros, 4 abr 2012, *M. Fernández 615, M. Contreras, A. Karremans & L. Sandoval* (JBL-D6024); – Vásquez de Coronado, Parque Nac. Braulio Carrillo, Zurqui station, between station and Tajo Santa Cecilia, about 3km WSW of station, in pasture, 1750 m, 29 oct 1990, *S. Ingram 646 & K. Ferrell* (USJ-037651). – **Sin datos de colecta**, floreció en cultivo en el Jardín Botánico Lankester, *JBL-01388* (JBL-D2894); – *JBL-01432* (JBL-D2830); – *JBL-01864* (JBL-D3558); – *JBL-11592* (JBL-D3254); – Sin datos de colecta, *JBL-01575* (JBL-D2710). – **Panamá:** Llano-Carti rd. 1 mile past saw mil on dirt roads, 300-500 m, 11 Nov 1979, *C. Todzia 1020 et al.* (CR-73663). Fig. 56.

**Habitat and ecology.** This is a common, morphologically variable species. Plants were found inhabiting tropical wet forests (premontane belt transition), tropical moist forests (premontane belt transition), premontane rain forest, premontane wet forest, premontane moist forest, montane wet forest, montane cloud forest, lower montane wet forest, lower montane moist forest, and lower montane cloud forest, between 600 and 2500 m elevation in both watersheds. Only one specimen was found inhabiting much lower elevations in the trunks of the tropical wet forest of La Selva Biological Station in the Caribbean watershed.

*Trichosalpinx memor* grows epiphytically in primary and secondary forests along rivers and roadsides, on the limbs and trunks of *Quercus* spp., *Cupressus lusitanicus*, and some Anacardiaceae, among others. Few plants were found growing in scattered trees in pastures and coffee plantations.

**Eponymy.** From the Latin *memor*, “mindful”, in allusion to its resemblance to *Trichosalpinx ciliaris*.

**Phenology.** Plants in cultivation flowered throughout the year, with a clear peak between July and September. In the wild, plants bearing flowers were also common throughout the year. Although rare, production of fruits was recorded in April, and from August to November in cultivation.

**Discussion.** *Trichosalpinx memor* is distinguished by the fleshy, coriaceous, elliptic to narrowly ovate, obtuse leaves commonly suffused with purple beneath, and the long, dense, secund inflorescences with dark purple to greenish purple flowers. The sepals are long-ciliate along the margins, and glandulose-papillate externally. The dorsal sepal is white at the base with the apex suffused with purple or pink towards the apex; the lateral sepals connate into a concave synsepal. The membranaceous petals are ciliate to fimbriate at the apex. The dark purple lip (sometimes yellow at the base) is narrowly oblong to ligulate, rounded, minutely ciliate, and bears a longitudinal, central carina borne at the base and decreasing towards the middle where it bifurcates. The column is straight, fimbriate and suffused with pink at the apex.

Although *T. minutipetala* may be confused with *T. memor*, the long ramicauls (up to 23 cm) covered by coarse, densely hispid sheaths, the quadrate petals and the shorter lip sharply

reflexed near the middle, are distinctive in the former species. Also, the flowers of *T. ciliaris* resemble those of *T. memor*, but the former is easily distinguished by the fractiflex (vs straight) ramicauls and the narrowly lanceolate (vs ovate to oblong) leaves. Finally, the habit of the rare *T. trachystoma* is similar to that of *T. memor*, but the former is easily distinguished by the declining lateral sepals, connate only at the base (vs entirely connate) and the spatulate, apically broadened (vs narrowly oblong to ligulate) lip.

*Trichosalpinx memor* is a common and morphologically highly variable species (Fig. 57), with populations present in both the Caribbean and Pacific watersheds of Costa Rica. Vegetative and floral characters are conspicuously variable between and within populations. Nevertheless, two morphs (representing the extremes of this variational range), based primarily on color patterns, are detailed here. Morph 1 is recognized by the shorter ramicauls, the ovate leaves abaxially stained with purple mostly along the veins, the profusely ciliate flowers with the sepals purple and the base white, the dark purple or yellow lip, and the column with the apex stained with pink. This morph inhabits mainly the high mountains of the Cordillera Volcánica Central, with large populations in the eastern slopes of the Barva volcano.

Morph 2 presents more narrowly ovate to narrowly elliptical leaves barely stained with purple along the veins, and flowers with a distinctive color pattern: the external surface of the lateral sepals is yellow or greenish, and the internal surface is white at the base forming a trident-like shape, while the rest is dark purple; the lip is usually dark purple and the clinandrium is white. Plants resembling this morph were found mainly in the low montane wet tropical forests of the southwestern foothills of Poas volcano, and in the premontane wet forests of Paraiso county in the Costa Rican Caribbean watershed.

*Trichosalpinx memor* is perhaps the most representative species of subgenus *Trichosalpinx* in Costa Rica in terms of distribution, habitat occupancy and population size. Nonetheless, the most interesting characteristic of this species was perfectly resumed by Luer (1997): "no two populations are alike". Further anatomical, molecular and ontogenic studies including representatives from other Neotropical populations may help elucidate the evolutionary history of the species.

**11. *Trichosalpinx minutipetala* (Ames & C.Schweinf.) Luer, *Phytologia* 54(5): 396. 1983.**

BASIONYM: *Pleurothallis minutipetala* Ames & C.Schweinf., *Schedulae Orchidiana*e 10 (32-33). 1930. TYPE: Costa Rica: Alajuela. Bosque de C. Laguna [Cruzada Laguna?], alt. 1190 m, Nov 1922, A.M. Brenes (102) 432 (holotype, AMES-31111; isotype, CR-26170). Fig. 58.

**Herb** epiphytic, caespitose, erect, up to 23 cm tall. **Roots** slender, flexuous, to 2 mm in diameter. **Ramicauls** erect, 1.5–20 cm long, enclosed by 5–11 tubular, adpressed at the base, ribbed, densely hispid, brown lepanthiform sheaths, 1.5–3.0 cm long, with broadly dilated, ciliate ostia, the apical 2.8–3.6 cm long, adnate to the petiole and peduncles. **Leaves** erect, coriaceous, narrowly elliptic to lanceolate, acute, apiculate, 1–8.1 × 0.8–1.9 cm, the cuneate base narrowing into a petiole up to 0.8 cm long. **Inflorescence** a dense,

distichous, 7–8 successively flowered raceme, 2.8–4.0 cm long including the peduncle 1.0–1.5 cm long. **Floral bracts** cuneiform, conduplicate, 2 × 2 mm. **Pedicels** 1 mm long, persistent. **Ovary** cylindric, 1 mm long. **Flowers** with the dorsal sepals white, suffused with pink along the 3 veins and towards the apex, the synsepal purple, white at the base, the petals translucent white, the lip dark purple, the column and anther white. **Sepals** papillate externally, densely ciliate along the margins. **Dorsal sepal** descending, widely ovate, triangulate, acute, 3.8–4.5 × 2.1–2.6 mm, 3-veined. **Lateral sepals** fleshy, connate into a broadly ovate, retuse, entire, strongly concave synsepal, 4.8–5.5 × 4.3–5.0 mm, 3-veined. **Petals** quadrate, obtuse, ciliate-fimbriate, 0.8–1.0 × 0.8–1.0 mm. **Lip** oblong, rounded, fimbriate in the proximal half, minutely ciliate apically, slightly bent in the middle, 2.0–2.7 × 0.8–1.3 mm; the disc with a high central carina running from the base to the middle, where it divides into two low keels; with two short basal lobes. **Column** short, semiterete, straight, deeply fimbriate apically, 2.3–2.7 mm long, the clinandrium subapical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, on a cellular, oval caudicle. **Fruit** a pink, 2-valved, glabrous, elliptic capsule, 8.5–9.0 × 4.5–5.5 mm, laterally dehiscent, with two prominent dehiscence lines running along the carpel midribs, the perianth persistent.

**Distribution.** Known only from the Costa Rican highlands of the Talamanca, Central Volcanic and Tilarán mountain ranges. Probably present in western Panama as well.

**Additional material examined. Costa Rica:** – Sin más datos de colecta, floreció en cultivo en el Jardín Botánico Lankester, A. *Karremans s.n.* (JBL-18631); A. *Karremans s.n.* (JBL-18633). – **Alajuela:** Alvaro Ruiz, Palmira, Reserva Biológica Bosque de Paz, 10°12'17"N 84°19'02, 1541 m, bosque muy húmedo montano bajo, 11 ago 2011, A.

*Karremans 4578, D. Bogarín & M. Muñoz* (JBL-E0961); – Bajos del Toro, along a minor tributary of río Toro, 1410–1500 m, 12 Feb 2000, *F. Pupulin & M. L. Spadari 2031* (USJ-78992); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'12" N 84°36'13" W, 800-900 m, camino por el sendero La Catarata, orillas del Río San Lorencito, bosque muy húmedo tropical transición a premontano, epífitas en bosque primario y secundario, 24 may 2008, *D. Bogarín 4970* (JBL-D4062); – San Carlos, Quesada, cerca de 5 km al este de Sucre, límite oeste del P.N. Juan Castro Blanco, faldas del Cerro Platanar, 10°17'00.3"N 84°23'05.1"W, 1608, bosque pluvial montano bajo, epífitas en potreros arbolados, 30 ene 2009, *D. Bogarín 6192 & F. Pupulin* (JBL-D3174); – Valverde Vega, Toro Amarillo, en potreros frente a la Reserva Biológica Bosque de Paz, orillas Río Toro, 10°12'10.80"N 84°18'54.75"W, 1561 m, bosque muy húmedo tropical "supra arbores in pascuis, campis et collibus nemorosis juxta fluvium Toro ad Bosque de Paz", 11 ago 2011, *D. Bogarín 9030, A. Karremans & M. Muñoz* (JBL-E0938); – Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, sobre los potreros frente a la entrada principal de la reserva, 1500-2000 m, bosque húmedo tropical montano bajo, transición a montano. 10°13'07" N - 84°17'53" W, 19 ago 2007, *A.P. Karremans 2098 & M. Muñoz* (JBL-D2649); – Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, al lado de la calle principal, árboles solitarios en potrero, bosque húmedo tropical montano bajo, transición a montano, 10°12'35" N - 84°18'44" W, 1500 m, 27 nov 2010, *A.P. Karremans 3077* (JBL-D4504); – Valverde Vega, Toro Amarillo, en potreros frente a la Reserva Biológica Bosque de Paz, orillas Río Toro, 10°12'10.80"N 84°18'54.75"W, 1561 m, bosque muy húmedo tropical "supra arbores in pascuis, campis et collibus nemorosis juxta fluvium Toro ad Bosque de Paz", 11 ago 2011, *A. Karremans 4551, D. Bogarín & M. Muñoz* (JBL-D4929, E0938); –

San Carlos, Quesada, about 5 km east of Sucre, western limit of Juan Castro Blanco National Park, slopes of Cerro Platanar, 10°17'00.3"N 84°23'05.1"W, 1600 m, lower montane rain forest, epiphytic on scattered trees in pastures, 30 Jan 2009, *F. Pupulin* 7581 & *D. Bogarín* (JBL-D3395); – *F. Pupulin* 7582 & *D. Bogarín* (JBL-D3258); – Alajuela: San Carlos, Jul 2004, *J. Vega s.n.* (JBL-D3816); – **Cartago**: El Guarco, San Isidro, Casa Mata, Carretera Interamericana, km 40, desvío a San Cristóbal Norte, 9°46'32.21"N 83°56'34.40" W, 1869 m, epífitas en árboles a orillas de la calle, bosque muy húmedo montano bajo, 24 abr 2008, *D. Bogarín* 4643, *A. Karremans*, *Y. Kisel* & *R. Phillips* (JBL-D2658); – [El Guarco?], road to Cerro de la Muerte, km 41, below the Empalme, 1900 m, 10 Jul 1983, *R. Escobar* & *K. Anderson* 2747 (CR-94777); – Turrialba, Santa Cruz, Las Abras, 10°00'07"N, 83°44'00"W, entre 1900-2100 m, en la Finca de Emma Quesada Chinchilla – Rossana Lok, subiendo en los potreros sobre la lechería. Bosque nuboso de las faldas del volcán Turrialba, con algunos parches de potreros con árboles solitarios, 6 de may del 2007, *A. Karremans* 1744 & *Diego Bogarín* (JBL-D3340); – Turrialba, Santa Cruz, finca de los Santiago, camino a las Virtudes, bosque nuboso montano, en árboles de potrero y dentro del bosque, 9°59'40" N 83°44'10" W, 2000 m, 30 oct 2010, *A. P. Karremans* 3017 (JBL-D5486); – Alvarado, Capellades, Santa Teresa, al lado del río del parque de aventuras, en árboles de potreros, bosque muy húmedo montano, 09°56'25.2"N 83°47'18.14"W, 1874 m, 1 may 2011, *A. P. Karremans* 4071 (JBL-G0074); – Macizo de la Muerte, southern Panamerican Highway, km 47, Palo Verde, ca. 2000 m, epiphytic on large trees, remnants of primary and secondary vegetation, lower montane wet forest, 16 Nov 2002, *F. Pupulin* 4286, *E. Salas*, *H. León-Páez* & *A.C. Rodríguez* (JBL-D2977). – **Guanacaste**: Monteverde, Tilarán, Tronadora, Area de Conservación Arenal, Sierra de Tilarán, 10°21' N -84°48' W, 1500 a 1600 m, 20 Nov 1988, *W. Haber* 8824 (INB-

1564884). – **Heredia**: Heredia, Vara Blanca, en los potreros y partes de bosque secundario pertenecientes al Poas Volcano Lodge cerca del centro de Vara Blanca, 10°10'00" N - 84°10'06" W, altura alrededor de 1700 y 1900 m, 3-4 ago 2006, A. *Karremans 1333 & D. Karremans* (JBL-E0829); [San Rafael], Monte de la Cruz, above Finca Monte Cristo, pasture and remnant forest; 02 Aug 1982, C. *Todzia 2065 & R. C. Moran* (CR-91688). – **Puntarenas**: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, 8°56'46.1" N 82°44'30.9" W, 1778 m, finca "El Capricho" de Miguel Sandí, principalmente en árboles de *Quercus* en las lomas y potreros al margen del río Sutú, bosque muy húmedo premontano, 6 oct 2010, M. *Fernández 407, R.L. Dressler, D. Bogarín & F. Pupulin* (JBL-D4928); – Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km NE of Lucha, Sitio Coto Brus, finca Sandí "El Capricho", 8°56'46.1" N 82°44'30.9" W, 1778 m, epiphytic, mostly on *Quercus* in pastures and along the river Sutú, wet premontane forest, 6 Oct 2010, F. *Pupulin 7912, D. Bogarín, R.L. Dressler and M. Fernández* (JBL-D5785); – Puntarenas-Chiriquí: Coto Brus-Renacimiento, línea fronteriza hacia el Cerro Pando, después del mojón N.338, 8°55'11.22" N 82°43'18.18" W, 2446 m, bosque muy húmedo montano bajo, epífitas en bosque primario, "in sylvis virginis versus montium Pando in itinere ad summum Costa Rica austro-orientalis in finibus utrimque Costa Rica et Panama", 19 abr 2011, D. *Bogarín 8696, D. Jiménez & A. Karremans* (JBL-D4587); D. *Bogarín 8703, D. Jiménez & A. Karremans* (JBL-E0833); – Puntarenas, Santa Elena, camino hacia el Cerro Amigos, 1700 m, 10°19'N 84°48'W, bosque pluvial premontano, epífitas en bosque secundario a orillas del sendero, colectado por L. Sandoval, 20 may 2011, M. *Fernández 446* (JBL-D4723); – 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, 6 ago 2010, *M. Fernández 282 & D. Bogarín* (JBL-D5744); – Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1" N 82°44'30.9" W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 jun 2010, *A. P. Karremans 2836 & D. Bogarín* (JBL-D5610); – Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1" N 82°44'30.9" W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 oct 2010, *M. Fernández 408, D. Bogarín, R.L. Dressler & F. Pupulin* (JBL-D5610); – *F. Pupulin 7901, D. Bogarín, R.L. Dressler & M. Fernández* (JBL-D4914); – Puntarenas, Santa Elena, camino hacia el Cerro Amigos, 1700 m, 10°19'N 84°48'W, bosque pluvial premontano, epífitas en bosque secundario a orillas del sendero, colectado por L. Sandoval, 20 may 2011, *M. Fernández 444* (JBL-D5718). – **San José:** Dota, Pan American Highway, km 55 South, between Casa Mata and Tres de Junio, La Chonta, 9°41'57.3"N 83°56'34.8"W, 2450 m, montane rain forest, epiphytic on old *Quercus* trees scattered in pastures, 12 Mar 2012, *A. Karremans 5238, F. Pupulin, G. Strigari and S. Strigari* (JBL-E0857). Fig. 59.

**Habitat and ecology.** Plants of this species were found growing epiphytically in scattered trees in pastures and in secondary lower montane rain forests, very humid premontane, montane and lower montane forests, and tropical humid low montane forest in Costa Rica, at elevations of 850–2450 m.

**Etymology.** From the Latin *minutipetalus*, “with a small petal”, in reference to the minute size of these organs.

**Phenology.** In the wild, plants were found flowering in February, July, August and November. The species flowers throughout the year under greenhouse conditions.

**Discussion.** Morphologically, *Trichosalpinx minutipetala* is most similar to *T. memor* and has been considered a synonym of the latter mainly because of the purple ciliate flowers and the lip with a forked central callus. However, *T. minutipetala* can be distinguished by the much longer ramicauls, hispid margins and ribs of the ramicaul's sheaths, the narrowly lanceolate leaves, the quadrate petals and the shorter lip bent near the middle. Even though *T. minutipetala* is morphologically similar to *T. memor*, its features are consistent among all the specimens collected in Costa Rica. A morphological variation of *T. minutipetala* with pink-orange sepals was found during the course of this study. Populations were located in Cerro Pando (close to the border with Panama) and the Macizo de la Muerte forests in the Cordillera de Talamanca, at 1900-2500 m, and may perhaps represent a different taxon. I refrain, however, to name it until further specimens may be studied to understand the range of variation at the specific level.

**12. *Trichosalpinx nana* (Ames & C.Schweinf.) Luer, *Phytologia* 54(5): 396. 1983.**

BASIONYM: *Pleurothallis nana* Ames & C.Schweinf., *Schedul. Orchid.* 8: 29. 1925.

TYPE: Costa Rica. Cartago: Pejivalle [Pejibaye], 16 May 1924, *C.H. Lankester 865* (holotype, AMES). Fig. 60.

**Herb** epiphytic, caespitose, pendulous, up to 4,2 cm long. **Roots** white, glabrous, slender, flexuose, to 0.8 mm in diameter. **Ramicauls** prolific, pendulous, 1.0–3.7 cm long, enclosed by 3–6 infundibuliform, shallowly striated, basally adpressed, light-brown lepanthiform sheaths, 2–4 mm long, the ostia hispid. **Leaves** elliptical, obtuse, apiculate, fleshy to coriaceous, 4–10 × 3–6 mm, the cuneate base narrowing into a partially twisted petiole up to 1 mm long. **Inflorescence** a descending, alternate, 3–4 successively-flowered raceme, 1.0–2.4 cm long including the peduncle 5–8 mm long, produced at the apex of the ramicaul from a conduplicate, ovate, truncate, narrowly acuminate, papyraceous spathe, 1 mm long. **Floral bracts** conduplicate, ovate, truncate, acute, membranaceous, 0.8 mm long. **Pedicels** straight, 2.5–6.0 mm long, persistent. **Ovary** shallowly channeled longitudinally, 1 mm long. **Flowers** with the sepals white and basally greenish, petals white, the lip white and basally yellowish, the column white, the anther white. **Dorsal sepal** ovate, acute to acuminate, truncate, glabrous, externally carinate, 3.7 × 1.0–1.2 mm, concave at the base, 3-veined. **Lateral sepals** narrowly triangular to subovate, acute, truncate, glabrous, externally carinate, 3.2–3.4 × 0.7 mm, 1-veined. **Petals** membranous, elliptic-oblong, truncate, obtuse, oblique, 1.6–1.7 × 0.5–0.6 mm, margin undulate towards the apex, 1-veined. **Lip** fleshy, glabrous, narrowly elliptic to oblong, obtuse, trilobed, 1.6–1.8 × 0.6 mm, the dilated base forming two short, lateral, erect lobes, and a pair of shallow thickenings at the forward angle between the lateral

lobes and the papillose inferior lobe. **Column** terete, 0.8–0.9 mm long, the apex shallowly winged, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, broadly ovate, emarginate. **Pollinia** 2, broadly ovate, on a cellular, suborbicular caudicle. **Fruit** not seen.

**Distribution.** Known only from the Costa Rican Caribbean watershed.

**Additional material examined. Costa Rica.** – **Cartago:** Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 9°46'51.7"N 83°43'00.4"W, 707 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del río, 29 ene 2012, A. *Karremans 4882, R.J.C.M. Ferrerira Lok & I.V. Ferreira Lok* (JBL-D5399); – A. *Karremans 4883, R.J.C.M. Ferrerira Lok & I.V. Ferreira Lok* (JBL-D5852); – A. *Karremans 4884* (JBL-E1078); A. *Karremans 4902* (JBL-D6123); A. *Karremans 4904* (JBL-D5802); – Jiménez, Pejibaye, Taus, orillas del Río Pejibaye, 9°46'55.86"N 83°43'01.63"W, 733 m, bosque pluvial premontano, epífitas bosque secundario alrededor del río, 11 may 2014, D. *Bogarín 11078 & M. Bonilla* (JBL-D6245); – [La Unión], Z.P. La Carpintera, parte alta de los cerros, bosque de Campo Istarú colindante con potrero arbolado, 9.883 -83.979, 1785 m, epífita en tronco de árbol achaparrado sobre fila, sitio expuesto al viento, jul 2007, A. *Cascante 1701* (CR-254875); – La Unión, Z.P. La Carpintera, 9.883 -83.979, 1871m, epífita creciendo en substratos lanosos en el piso del sotobosque nuboso, 3 jun 2008, A. *Quesada 2649* (CR-257756). – **San José:** Vásquez de Coronado, Jesús, Parque Nacional Braulio Carrillo, Sendero La Botella, 10°09'34"N 83°57'14.8"W, 702 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario y primario, 22 mar 2012, M. *Fernández 580, D. Bogarín, A. Karremans & C. Smith* (JBL-D6284). Fig. 61.

**Habitat and ecology.** Plants were found at the type locality of Pejibaye, where premontane rainforests have been reduced severely to scattered patches and riverine fringes, growing on branches in riverine, secondary forests.

**Etymology.** From the Latin “*nanus*”, dwarf, in reference to the small habit.

**Phenology.** Plants kept in greenhouse conditions flowered successively between late May and mid June, along with the rainy season onset. Accordingly, data from exsiccata indicate a flowering period between June and July.

**Discussion.** Some specimens collected and examined here were found in the same locality where Lankester found the type plant ninety years ago. Apparently, the species has been able to cope with human alterations in the fringes of riverine forests along the Pejibaye river. Patches of young and mature secondary forests, where *T. nana* may be seen, are being protected in nearby areas due to conservation efforts of the community, international organizations and national institutions.

*Trichosalpinx nana* may be confused with specimens of *T. todziae* because of the caespitose habit, similar leaves and comparable size and color of the inflorescences. However, the habit of *T. nana* is descendent to pendulous (vs. erect), the successively branching ramicauls form long chains (vs. basal ramicauls that produce only one or two subsequent superposed ramicauls), the leaves are ventrally stained with purple along the veins (no stains noted in leaves of *T. todziae*), and the flowers are long-pedicellate (2.5–6.0 mm vs. 1.5–4.0 mm) with acute (vs. long-attenuate) sepals and a flat (vs. arcuate) lip.

The concept of *T. nana* is similar to that of *T. scabridula* (Rolfe) Luer since both species present relatively small habits (5–20 cm long) with elliptical, coriaceous leaves, branching ramicauls and inflorescences with pale flowers. However, *T. nana* is distinguished by the smaller flowers with sepals up to 3.5 mm (vs. 4.5–7.0 mm), and petals up to 1 mm (vs. 2–3 mm). The lip is membranous and has two lateral lobes with shallow thickenings in the inner zone (vs. fleshy with evident calli). The column is thicker and wingless, while in *T. scabridula* the column is thinner and bears a pair of shallow wings at the apex.

When the flower is fresh or preserved in liquid, the calli at the junction between the lateral lobes and the apical lobe are easily distinguished. After dehydration for herbarium purposes, those calli almost disappear, as noted by Luer (1997).

**13. *Trichosalpinx navarrensis* (Ames) Mora-Ret. & J.García, Brenesia 37: 125. 1992.**

BASIONYM: *Pleurothallis navarrensis* Ames, Sched. Orchid. 9: 34. 1925. TYPE:

Costa Rica. Cartago: Muñeco, south of Navarro, alt. 1400 m, 8–9 Feb 1924, P.C.

*Standley* 33888 (holotype, AMES). Fig. 17.

**Herb** epiphytic, repent, approx. up to 3.5 cm long. **Ramicauls** repent, prolific, much abbreviated, more or less decumbent, about 5 mm long, enclosed by infundibuliform, rufous sheaths, dilated and marginate with hispidulous emergences on the nerves apically. **Leaves** elliptical or suborbicular, obscurely marginated, coriaceous, conspicuously and deeply rugose when dry, up to 12.0 × 5.5–6.5 mm, purplish beneath, much exceeding the inflorescence. **Inflorescence** a single flowered fascicule, abbreviated, about 4 mm long

including the peduncle, partly concealed by sheaths. **Pedicel** and **ovary** not seen.

**Flowers** dark red-purple. **Dorsal sepal** ovate, broadly acute, truncate, descendent, 3.25 × 1.75 mm, base broad, 3-nerved. **Lateral sepals** ovate-oblong, subacute, glandular-ciliate, 3.25 × 1.00 mm, connate and forming a mentum basally, thickened apically, sparsely glandulose abaxially, 3-nerved. **Petals** narrowly lanceolate, acute, glandular-ciliate, 2.25 mm long, 1-nerved. **Lip** narrowly linguiform, acute, glandulose-ciliolate, 2.5 mm × 0.5 mm, the disc with a conical, glandulose, callus-like thickening disappearing near the middle of the lamina; upper surface densely glandulose; margin more or less erect in the basal half and deflexed in the apical half; the base with two auriculiform introrse lobules formed by the base of the expanded portion of the labellum, hinged to the column foot by a abbreviate, equaled membrane. **Column** semiterete, 2 mm long, dilated apically, with a 5-toothed and fringed clinandrium. **Anther cap, pollinia** and **fruit** not seen. (Description based on the protologue [Ames 1925], holotype and drawing of the holotype [AMES-74493]).

**Distribution.** Known only from two plants found in the premontane rain forests of El Muñeco, south of Navarro, in the province of Cartago.

**Additional material examined.** No material was found in the wild or among the exsiccata kept in the examined herbaria. Fig. 62.

**Habitat and ecology.** The site where *T. navarrensis* was collected in 1924 is today highly disturbed by deforestation and urban expansion. According to Holdridge (1987), it corresponds to premontane rain forests. Nearby areas with similar type of forest were visited unsuccessfully.

**Eponymy.** Named after the locality of Navarro, where the species was collected.

**Phenology.** The original specimens were found flowering in February.

**Discussion.** The morphological concept of *T. navarrensis* places it in the *T. memor* - *T. blaisdellii* group, characterized by the dilated, minutely ciliate ostiae of the lepanthiform sheaths, the coriaceous leaves with short petioles, the fleshy, ciliate, oblong to broadly ovate sepals, the membranous petals, and the ligulate, oblong or ovate lip bearing a low callus borne at the base and disappearing variously towards the middle. Within this group, *T. navarrensis* can be distinguished by the small habit, the 1-flowered inflorescences one-third the length of the leaves, the pubescent sepals, the larger and narrower petals ( $2.25 \times 0.50$  mm vs.  $1.1-1.3 \times 0.6-0.7$  in *T. memor*), and the lip with a not-bifurcate central keel.

Although *Trichosalpinx navarrensis* is today considered under *Trichosalpinx* subgenus *Trichosalpinx*, several characters do not agree with the subgeneric concept: the repent habit (vs. caespitose); the very coriaceous leaves (vs. fleshy to coriaceous); the single-flowered inflorescences (vs. commonly successively or simultaneously multi-flowered inflorescences); the lateral sepals connate only at the base by a few millimeters (vs. connate more or less throughout, sometimes forming a concave synsepal); the sepals pubescent in the inner surface (vs. sepals glabrous); the petals as long as the lip (vs. shorter than the lip); the lip densely glandulose to pubescent on the upper surface (vs. glabrous or papillate); the column with the clinandrium 5-lobuled (vs. deeply fringed with no lobules).

Interestingly, *T. navarrensis* is remarkably similar to *Anathallis lewisae* (Ames) Solano & Soto Arenas, a widely distributed species. The similarities to *Anathallis* Barb.Rodr. (as

apposed to *Trichosalpinx* subgen. *Trichosalpinx*) include the repent habit; the abbreviated ramicauls; the single-flowered inflorescence; the almost free, spreading sepals, pubescent in the inner surface; and the pubescent lip. Ames (1925) compared it to *Pleurothallis abjecta* Ames, previously included by Pridgeon & Chase (2001) under their concept of *Anathallis*, and recently included in genus *Lankesteriana* (Karremans 2013). The inclusion of a sample of this species in a comprehensional phylogenetic analysis of *Trichosalpinx* and related genera may help in the understanding of this rare species.

The area of Navarro is highly disturbed with artificial thicket habitats, young secondary forests and few areas with mature secondary forests where selective logging has occurred. Although visited in several occasions accompanied by numerous trained collectors, no specimen resembling *T. navarrensis* was found. Nearby localities with a similar type of forest such as Purisil and the surroundings of the Tapantí National Park were visited unsuccessfully. It is suspected that the populations, if there are any remaining, have diminished drastically. Accordingly, the description is based on the species protologue and type material.

**14. *Trichosalpinx orbicularis* (Lindl.) Luer, *Phytologia* 54(5): 396. 1983.**

BASIONYM: *Specklinia orbicularis* Lindl., Edwards's Bot. Reg. 24: Misc. 31. 1838.

*Pleurothallis orbicularis* (Lindl.) Lindl., Edwards's Bot. Reg. 28: Misc. 79. 1842.

*Humboltia orbicularis* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 668. 1891, *nom. illeg.*

TYPE: Guayana. Demerara, imported by Messrs. Loddiges, March 1830, *Loddiges s.n.* (holotype, K-Lindl.). Fig. 63.

*Lepanthes orbiculata* Lindl. ex Rchb.f., Xenia Orchid. 1: 152. 1856. TYPE: Hab. ic. ab. ill. ["Habeo iconam ab illustratio", or "I have a figure from an illustration"; illustration mentioned not found], (holotype, K-Lindl.).

*Pleurothallis biflora* H.Focke, Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 2: 197–198. 1849. *Humboltia biflora* (H.Focke) Kuntze, Revis. Gen. Pl. 2: 667. 1891, *nom. illeg.* TYPE: Surinam, Paramaribo, habitat in sylvis pl. Berlijn, ad rivum Para, supra arbores. Florebat junio, julio, octobri & novembri, 3 Jan. 1845, *H. C. Focke s.n.* (holotype, W).

*Pleurothallis trachythea* F.Lehm. & Kraenzl., Bot. Jahrb. Syst. 26(3–4): 444–445. 1899. TYPE: Colombia. Epiphytica in silvis densis humidis circa las Juntas del Dagua, in Andibus occident. ditionis Cali, 300–500 m, *Lehmann 8224* (holotype, destroyed at B; lectotype designated by Luer [1997], K; isolectotypes, AMES, NY).

*Trichosalpinx lancifera* (Schltr.) Luer, Phytologia 54(5): 396. 1983. BASIONYM: *Pleurothallis lancifera* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 48–49. 1924. TYPE: Colombia: Putumayo, epiphyte bei Mocoa (Territorio del Caqueta), 530 m, June 1921, *W. Hopp 67* (holotype, destroyed at B; lectotype not designated).

*Trichosalpinx oxychilos* Carnevali & G.A.Romero-Gonzalez, Novon 3(1): 21. 1993. TYPE: Venezuela. Bolívar: Cerro Jaua, ca. 1800 m, Feb. 1976, *G. C. Dunsterville & E. Dunsterville 1347* (holotype, AMES).

**Herb** epiphytic, caespitose, erect, up to 12 cm tall. **Roots** slender, flexuous, to 2 mm in diameter. **Ramicauls** erect, 1.3–7.5 cm long, enclosed by 2–5 infundibuliform, ribbed,

microscopically hispid, fibrous, imbricating, persistent, brown lepanthiform sheaths, 0.7–2.0 cm long, with broadly dilated ostia, the apical covering the petiole and leaf base. **Leaves** erect, shallowly concave, coriaceous, orbicular to elliptic, apiculate, obtuse, 12–39 × 5–22 mm, occasionally purple beneath, the cuneate base narrowing into a petiole up to 3 mm long. **Inflorescence** a congested, 3–5 simultaneously flowered raceme, distichous, 8–15 mm long including the peduncle 4–7 mm long, born from behind the leaf base. **Floral bracts** cuneiform, conduplicate, 1 × 1 mm. **Pedicels** 0.4–1.0 mm long, persistent. **Ovary** cylindric, 1 mm long. **Flowers** with the sepals yellow suffused with brown purple or dark red towards the thickened apex, the petals dark red, the lip dark red or vinaceous, the column white, the anther light yellow with pink stains. **Dorsal sepal** fleshy, entire, suberect, broadly ovate, acute, 5.1–5.7 × 2.2–2.3 mm, 3-veined, the apex thickened and broadened. **Lateral sepals** fleshy, entire, ovate, broadly acute to obtuse, connate from the base up to one third into a bifid lamina, deeply concave at the base forming a mentum with the column-foot, 5.2–6.5 × 2.5–3.1 mm, 4-veined together, the margins minutely ciliate, the apices thick. **Petals** straight, horizontally parallel, membranaceous, oblong, obtuse, 1.7–2.1 × 1.0 mm, the apex fimbriate. **Lip** straight, narrowly oblong, acute, 2.8–3.0 × 0.8 mm, the basal margins dilated, erect and minutely ciliate, the disc with a central carina from the base and disappearing towards the apex, the base with two retrorse lobules and a central membrane that is hinged to the column-foot, the apex shortly fimbriate. **Column** semiterete, straight, the apex deeply fimbriate above, 1.5–1.6 mm long, forming a right angle with the column-foot, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, ovate, on a cellular, irregular, minute caudicle. **Fruit** not seen.

**Distribution.** From Mexico to Panama into the Andes from Colombia and Venezuela to Bolivia, and in the Antilles in Grenada and Cuba.

**Additional material examined. Costa Rica.** – **Limón:** Pococí, Parismina, recolectada por G. Villalobos, 100 m, floreció en cultivo en el Jardín Botánico Lankester, 30 oct 2009, *D. Bogarín* 7403 (JBL-D3890); – Pococí, Guápiles, Reserva Teleférico del bosque lluvioso, parque atlántico, 10°10'24.5"N 83°54'48.3"W, 546 m, 14 oct 2008. *A. Quesada* 2716 (CR-257799); – Talamanca, Bratsi, R.I. Talamanca, Río Lari, Amubri, Alto Lari, 9.448611 - 83.044444, 300 m, siguiendo el camino entre Surayo y el río Dapari (Rio Pare), margen izquierda del río Lari, 25 Feb 1992, *G. Herrera* 5058 & *G. Carnevali* (INB-2922429). – **Puntarenas:** Puntarenas, Aguirre, Quepos, Quebrada Arroyo, flowered in cultivation, 100 m, 1 ago 2000, *D. Castelfranco* 68 & *P. Seaton* (JBL-B0405). – **San José:** Acosta, Gravilias, Cerro El Dragón, 23 set 2003, colectada por Jorge Chinchilla, floreció en cultivo de la familia Valverde Arias, Desamparados, 1800 m, nov 2003, *R. Valverde* 615 (JBL-D0453); – *R. Valverde* 617 (JBL-D0437); – Pérez Zeledón, Carretera Interamericana, La Ese, km 114-122, orilla de la carretera, 9°26'N 83°35'W, 1200-1400 m, 12 jul 2005, *A. Rojas* 6474 & *H. Kennedy* (JBL-D2802); – Vázquez de Coronado, Jesús, Parque Nacional Braulio Carrillo, Sendero La Botella, 10°09'33.9"N 83°57'14.8"W, 702 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario y primario, 2 jun 2010, *M. Fernández* 65, *D. Bogarín* & *A. Karremans* (JBL-D4214); – Vázquez de Coronado, Cascajal, P.N. Braulio Carrillo, Río General, 10.166667 -83.955556, 750 m, epiphytic on bark of fallen tree trunk along Sendero La Botella, in primary forest, 5 Jan 1991, *S. Ingram* 838 (CR-148400, INB-2923259); – [Vázquez de Coronado], Braulio Carrillo N.P. along the Terciopelo trail occurring with *Trichosalpinx orbicularis*, *Pleurothallis verecunda*, 29 Mar 1991, *K. Richardson* K-184 (CR-154602). Fig. 64.

**Habitat and ecology.** Growing epiphytically in primary and mature secondary forests of the tropical wet and premontane wet forests of the Caribbean watershed at less than 800 m. Frequently found near water bodies. Two plants growing as high as 1800 m were found in 2003 in the Cerro Dragón area (also known as Carraigres); although the area was re-visited twice, no plants of *T. caudata* or similar were found.

**Etymology.** From the Latin *orbicularis*, referring to the shape of the leaves.

**Phenology.** Flowers are produced between August and November in cultivation, while blooming in the wild was documented from January to March and October.

**Discussion.** *Trichosalpinx orbicularis* and *T. caudata* Luer are vegetatively almost indistinguishable. Nevertheless, the long, caudate sepals of the latter is the most conspicuous differentiating character. In *T. caudata* the dorsal sepal is narrowly triangular (vs. ovate) and can reach up to 8.5 mm long (vs. up to 5.7 mm in *T. orbicularis*), the lateral sepals are narrowly ovate, elongated, as long as 6.8 mm, connate only at the base (vs. broadly ovate, not elongated, up to 6.5 mm, connate from the base up to the middle), and not thickened apically (vs. apically thickened). The petals are narrowly acute to acuminate (acute to obtuse in *T. orbicularis*), densely fimbriate marginally. The lip is usually twice longer than the column (vs. one-third longer than column in *T. orbicularis*).

In his revision of *Trichosalpinx*, Luer (1997) treats this species as a morphologically complex group. Variations in terms of length, outline and general shape of perianth parts occur throughout its wide distribution. Considering the morphological differences between populations of *T. caudata* and *T. orbicularis*, and the apparent allopatric distribution (*T. orbicularis* restricted to the Caribbean watershed and *T. caudata* mainly established in the

south Pacific watershed), the two concepts are here treated separately. Further anatomical and molecular studies including plants that represent the entire geographical range of both concepts may help elucidate the evolutionary relationships and define the specific circumscription of *T. orbicularis*.

**15. *Trichosalpinx parsonsii* Luer & Dod, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 72, f. 68. 1997.**

TYPE: Costa Rica: San José, near Santa Maria de Dota, 13 June 1990, flowered in cultivation in Berkeley, CA, by D. Dod, June, 1997, *M. Grantham & J. Parsons 03 93 90* (holotype, UC; isotype, MO). Fig. 65.

**Herb** epiphytic, caespitose, ascending, up to 13 cm tall including the inflorescence. **Roots** slender, flexuous, to 0.5 mm in diameter. **Ramicauls** ascending, branching, 3–23 mm long, enclosed by 2–4 tubular, lepanthiform sheaths, adpressed, ribbed, greyish-brown, 2–6 mm long, the ribs microscopically pubescent, the ostia inconspicuously dilated and microscopically ciliate. **Leaves** coriaceous, elliptic, acute, apiculate, 5.0–12.0 × 2.5–7.0 mm, the veins commonly suffused with purple ventrally, the cuneate base narrowing into a petiole up to 1 mm long. **Inflorescence** distichous, a 3–4 successively flowered raceme, 2.0–3.8 cm long including the peduncle 8 mm long, borne at the apex of the ramicauls from a conduplicate, ovate, acute spathe, 1 mm long. **Floral bracts** narrowly cuneiform, conduplicate, papyraceous, 1 mm long. **Pedicels** 1.5–2.5 mm long, persistent. **Ovary** cylindrical, superficially channeled, 1 mm long. **Flowers** white to pale yellow. **Sepals** glabrous, attenuate, carinate. **Dorsal sepal** narrowly ovate to triangular, shallowly concave

at the base, acute, truncate, 3.2–4.0 × 1 mm, 3–veined. **Lateral sepals** narrowly triangular, oblique, acute, free, 3.1–3.8 × 0.6 mm, 1-veined. **Petals** membranous, glabrous, entire, elliptical, oblique, obtuse, 1.3–1.5 × 0.6 mm, 1-veined. **Lip** glabrous, entire, oblong, obtuse, 1.3 × 0.6 mm, concave in the distal half, the disc flat, the apex thickened, rounded, the base truncate, hinged to the column foot. **Column** terete, 1 mm long, barely widened apically, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, convex externally, shallowly concave internally, on cellular, ovate caudicles. **Fruit** not seen.

**Distribution.** Known only from Costa Rica.

**Additional material examined. COSTA RICA.** – **Alajuela:** San Ramón, Piedades Sur, San Miguel (La Palma), en El Alto después de San Bosco, en árboles solitarios en potrero, 21 dic 2010, 10°07'43.7"N 84°33'13.5"W, 1289 m, *A. Karremans 3305, J.A.J. Karremans & M. Contreras Fernandez* (JBL-D4392). Fig. 66.

**Habitat and ecology.** *Trichosalpinx parsonsii* was described from the montane wet forests of Santa María de Dota, a region from 1600 to 1800 m elevation, whereas the material deposited at JBL was found growing epiphytically in the premontane wet forests of the species-rich area of San Ramón at about 1300 m. The two collections, both from the Pacific watershed, are from different mountain chains, and the paucity of available material suggests that populations of *T. parsonsii* may be scattered and formed by a few individuals.

**Eponymy.** Named after Jerry Parsons of Berkeley, California, co-collector of this species.

**Phenology.** Luer and Dod (1997) reported that the plant that served as type flowered in June at Berkeley in California, while the plant collected recently by A. Karremans flowered in April in cultivation.

**Discussion.** Although the vegetative parts of this small species are similar to those of other species of *Tubella* with small habit (e.g. *T. nana*), *T. parsonsii* is recognized by the barely open flowers, the entire lip with no ornamentation, and the column barely widened apically. These features, along with the simple appearance of the flower, may indicate a syndrome of autopolination.

**16. *Trichosalpinx pergrata* (Ames) Luer, *Phytologia* 54: 396. 1983.**

BASIONYM: *Pleurothallis pergrata* Ames, Sched. Orchid. 4: 24. 1923.

TYPE: Costa Rica. Cartago: La Estrella de Cartago, alt. ca. 5000 ft., C.H. Lankester & A. Sancho 436 (holotype, AMES). Fig. 67.

*Trichosalpinx falcipetala* (Schltr.) Luer, *Phytologia* 54: 395. 1983. BASIONYM:

*Pleurothallis falcipetala* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27: 163. 1924.

TYPE: Colombia. Cauca: Ohne nähere Standortsangabe, F.C. Lehmann 2045 (holotype, B destroyed; neotype, F.C. Lehmann 8245, K, designated by Luer, Monogr. Syst. Bot. Missouri Bot. Gard., 64: 72-73, 1997).

**Herb** epiphytic, caespitose, erect, up to 7 cm long. **Roots** slender, flexuous, to 0.8 mm in diameter. **Ramicauls** erect, not prolific, 0.7–4.0 cm long, enclosed by 3–7 tubular, adpressed, shallowly ribbed, densely ciliate, cinnamon brown lepanthiform sheaths, 0.5–1.4 cm long, widened towards the apex. **Leaves** erect, coriaceous, elliptical, acute to

obtuse, 7–22 × 2.5–7.0 mm, the cuneate base narrowing into a petiole up to 1.5 mm long, the apex apiculate. **Inflorescence** a congested, successively single-flowered raceme, 3.0–4.6 mm long, produced at the apex of the ramicaul, the spathe not seen. **Floral bracts** cylindric, fleshy, 1.0–1.5 mm long, covering both pedicel and ovary. **Pedicels** 1.2–1.5 mm long, persistent. **Ovary** 0.8–1.0 mm long. **Flowers** with sepals fuchsia-rose or yellow, petals flesh red to coral or yellow, the lip rose to dark rose or light yellow, column light rose, anther light yellow. **Dorsal sepal** glabrous, ovate, acute to narrowly obtuse, basally concave, shallowly carinate externally, 13.8–24.5 × 2.1–3.2 mm, 3-veined, the apex elongated, filiform. **Lateral sepals** descending, glabrous, ovate to triangular, oblique, narrowly obtuse, basally concave, 13.8–23.0 × 1.3–1.4 mm, connate for 2.5–3.0 mm, 1-veined. **Petals** succulent, entire, elliptical to obovate, oblique, obtuse, apically concave, hispid to long-papillate externally, 2.2–2.3 × 1.0–1.3 mm, 1-veined. **Lip** glabrous, thick, narrowly elliptical to ovate, retuse, basally trilobed, 3.1–3.6 mm long, 1.0–1.8 mm wide across the erect lobes, the apex descending, glandulose, the disc shallowly depressed, the base truncate, unguiculate, hinged to the column-foot. **Column** terete, 1.5–1.9 mm long, wingless, the basal third with two small, lateral, round projections, the clinandrium subapical, the stigma ventral, as wide as the column. **Anther cap** incumbent, broadly ovate, the apex emarginate internally, inflated externally. **Pollinia** 2, pyriform, flattened dorsally, on cellular, orbicular caudicles. **Fruit** not seen.

**Distribution.** Costa Rica, Panama and Colombia.

**Additional material examined. Costa Rica.** – **Cartago:** Cartago, San Francisco, Muñeco, 3 km al sur de Muñeco, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'0.6"N 83°53'55.4"W, 1621 m, bosque pluvial premontano, epífitas en bosque

secundario y árboles en zonas abiertas, 27 may 2009, *D. Bogarín 6502*, *R. Gómez, Y. Kisel & R. Trejos* (JBL-D3406); – Guarco, San Isidro, Z.P. Río Navarro y Río Sombrero, La Cangreja, cabeceras del Río La Estrella, 9.758333 -83.965278, 1713 m, epífita, flores moradas, 12 nov 2007, *J. F. Morales 15794* (INB-4187489); – Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, 9°48'36.7"N 83°45'16.2"W, 1396 m, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque, 24 nov 2008, *D. Bogarín 5784*, *R.L. Dressler, R. Gómez & R. Trejos* (JBL-D2653); – Paraíso, Orosi, Purisil, Parque Purisil, behind the “cabaña”, 9°46'N 83°48'W, 1450 m, lower montane wet forest, secondary vegetation, collected by H. León-Páez, A.C. Rodríguez & E. Salas, 12 Jun 2003, *F. Pupulin 3861* (JBL-C0574); – Paraíso, Orosi, Purisil, 1 km sur del centro, 9°45'13.11"N 83°48'57.56" W, 1291 m, epífitas en cafetos y árboles solitarios en cafetales abandonados, bosque pluvial premontano, 12 feb 2012, *A. Karremans 5032* (JBL-D5485). – **Puntarenas**: Coto Brus, San Vito de Java, road from Las Cruces to Río Claro, Fila Cruces-Zapote, 8°47'04"N 83°02'02"W, 1530 m, región templada tropical muy húmeda, with E. Salas, H. León-Páez & A.C. Rodríguez, 13 Nov 2002, *F. Pupulin 4233* (JBL-B1697). – **San José**: Tarrazú, San Lorenzo, Naranjillo, Nara, 2 km camino a San Isidro, 9.504167 -84.0, 800 m, epífita, flores moradas, 5 mar 2008, *J. F. Morales 15987* (INB-4189382, INB-4189383); – Tarrazú, San Lorenzo, ca. 4 km al sureste de Santa Marta, camino a Bajo Reyes, 9°36'38.2"N 84°00'52.1"W, 1475 m, bosque muy húmedo premontano, epífitas en cercas de potreros a orillas de la carretera, 20 nov 2008, *D. Bogarín 5635*, *R.L. Dressler, M. Fernández, R. Gómez & R. Trejos* (JBL-D3317); – *idem*, *D. Bogarín 5636*, *R.L. Dressler, M. Fernández, R. Gómez & R. Trejos* (JBL-D3316); – Tarrazú, San Lorenzo, camino entre Nápoles y Rodeo, 9°35'08.4"N 84°03'34.7" W, 1439 m, bosque pluvial premontano, epífitas en bosque secundario a

orillas del camino, 13 jun 2009, *D. Bogarín 7281 & F. Pupulin* (JBL-D4505); – Tarrazú, Alto de San Jerónimo, carretera entre ríos Paraíso y San Marcos, 9.579 N -84.085 W, 1600 m, 24 set 2004, *S. Lobo 859* (CR-248730). Fig. 68.

**Habitat and ecology.** *Trichosalpinx pergrata* grows epiphytically in the premontane and lower mountain rain forests, and the premontane and lower montane wet forests of Costa Rica (Holdridge 1987), from 1200 to 1650 m elevation. Plants are usually found growing exposed on scattered trees and fences of pastures and plantations, and partially shaded in borders of secondary forests and coffee plantations.

**Etymology.** From the Latin *pergratus*, meaning “very pleasant”, in allusion to the aspect of the plant.

**Phenology.** Flowering period from September to November, and February to March, under both wild and greenhouse conditions.

**Discussion.** Among the Costa Rican *Trichosalpinx*, *T. pergrata* is the most distinctive species. The pinkish-red color (sometimes yellow) of the flowers, the very short, sequential, few-flowered inflorescences, the elongate, filiform sepals and the succulent petals and lip are unique characters of this species. Luer assigned it to subgenus *Tubella*, but several morphological discrepancies suggest a different phylogenetic affinity. Tubellas are characterized by prolific ramicauls and glabrous or microscopically ciliate lepanthiform sheaths (Luer 1986), while *T. pergrata* produces non-prolific ramicauls with densely ciliate sheaths. Also, Tubellas produce several simultaneously-open flowers on inflorescences that are consistently longer than the leaf; the flowers bear flat, membranous, entire petals and membranous lips with a pair of calli on the disc (similar to those of some *Anathallis*).

On the contrary, the inflorescence of *T. pergrata* is much shorter than the leaf, produces only one or two flowers at the same time, has concave, succulent and externally-papillate petals, and has a thick, ecallous lip. Thus, *Trichosalpinx pergrata* does not fit well in either of the other subgenera proposed.

**17. *Trichosalpinx pusilla* (Kunth) Luer, *Phytologia* 54(5): 397. 1983.**

BASIONYM: *Dendrobium pusillum* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 357.

1815[1816]. *Humboltia pusilla* (Kunth) Kuntze, Revis. Gen. Pl. 2: 668. 1891, *nom.*

*illeg.* *Specklinia pusilla* (Kunth) Lindl., Edwards's Bot. Reg. 21: sub. t. 1797. 1835.

*Pleurothallis pusilla* (Kunth) Lindl., Edwards's Bot. Reg. 28: Misc. 82-83. 1842.

TYPE: Ecuador. Loja: in small trees near Loja, 1802, *Humboldt & Bonpland s.n.*

(holotype, P-Bonpl.; isotypes, AMES, W). Fig. 69.

*Trichosalpinx roraimensis* (Rolfe) Luer, *Phytologia* 54: 397. 1983. BASIONYM:

*Pleurothallis roraimensis* Rolfe, Trans. Linn. Soc. London, Bot. 6(1): 58–59. 1901.

TYPE: Guyana: Roraima, summit, 8600 ft., 1898, *McConnell & Quelch 687*

(holotype, K).

**Herb** epiphytic, caespitose, erect, up to 10 cm long, including the inflorescence. **Roots** greyish, slender, flexuous, 1 mm diameter. **Ramicauls** prolific, erect, 3.2–6.0 cm long, enclosed by 3–4 cylindrical, imbricate, fibrous, shallowly striated, adpressed, light-brown lepanthiform sheaths, 4–10 mm long each, ostia 1–2.5 mm in diameter, with the apical margin dilated, thickened, microscopically hispid, the apical sheath covering the base of the leaf and inflorescence. **Leaves** thick, entire, obovate to obelliptic, retuse, 8–17 × 4–5

mm, suffused with purple abaxially, mucronate, the base narrowing into a cuneate petiole, 1.5 mm long. **Inflorescence** an erect, alternate, 3–4 successively-flowered raceme, 2.5–4.0 cm long including the peduncle 1.2 cm long, borne at the apex of the ramicaul from a papyraceous, ovate, obtuse, truncate spathe, 0.5 mm long. **Floral bracts** tubular, membranaceous, 0.7 mm long. **Pedicel** straight, 5–7 mm long, persistent. **Ovary** pinkish to purple, cylindrical, channeled longitudinally, 0.4–0.6 mm. **Flowers** with the sepals and petals yellowish white, the lip translucent white and stained with yellow along the central zone, column white. **Dorsal sepal** ovate, narrowly acute to caudate, glabrous, externally shallowly carinate,  $2.5\text{--}6.3 \times 1.1\text{--}1.8$  mm, concave at the base, 3-veined. **Lateral sepals** triangular, elongate, glabrous, externally carinate along the vein,  $3.0\text{--}5.8 \times 0.4\text{--}0.6$  mm, connate at the base forming a mentum, 1-veined. **Petals** straight, membranous, elliptic, broadly obtuse, unequal,  $1.2\text{--}1.6 \times 0.6\text{--}0.8$  mm, the apex irregular, 1-veined. **Lip** glabrous, oblong, trilobed, the lateral lobes rounded, erect, the apical lobe glandulous, oblong, rounded, 1.6–2.2 mm long, 1.0–1.2 mm wide across the lateral lobes, 0.4–0.5 mm wide across the apical lobe, with two lateral thickenings in the junction of the lateral and apical lobe. **Column** terete, 1.3–1.4 mm long, the clinandrium subapical, the stigma ventral. Anther cap incumbent, transversely ovate, emarginate. **Pollinia** 2, round, on cellular, irregular caudicles. **Fruit** a dark green, glabrous, 2-valved, ovoid capsule,  $3.0\text{--}4.0 \times 2.0\text{--}2.5$  mm, with two dehiscent lines along the carpel midribs, perianth remnants persistent.

**Distribution.** Costa Rica, Colombia, Venezuela, Guyana, Ecuador and Peru.

**Additional material examined.** Costa Rica. – **Alajuela:** Poás, San Juan, 1.6 km antes de la entrada principal al Parque Nacional Volcán Poas,  $10^{\circ}10'3.32''\text{N}$   $84^{\circ}13'46.19''\text{W}$ , 2445 m, epífitas en robles esparcidos en potreros junto a camino de finca, bosque pluvial

montano, 19 may 2014, *M. Fernández 911, D. Bogarín & L. Sandoval* (JBL-D6243). –

**Heredia:** Barva, San José de la Montaña, 10.1147 N 84.13 W, 2200-2300 m, en bosques remanentes cerca de Sacramento, colectada por R. J. Abarca, 15 ago 1994, *J.F. Morales 4065* (INB-1574472!). – **Limón-Puntarenas:** Talamanca-Buenos Aires, Bratsi-Potrero

Grande, Parque Internacional La Amistad, Sector Altamira, sendero al Valle del Silencio, Cerro Hoffman, sobre la divisoria de aguas, 9°05'38.2" N 82°58'37.73" W, 2553 m, bosque pluvial montano, 14 ago 2012, *A. Karremans 5642, D. Bogarín, M. Fernández, J. Godínez, J. Kruizinga & C.M. Smith* (JBL-D5392); – Buenos Aires, Buenos Aires, Olán, cumbre del Cerro Tinuk, 9°17'29.1" N 83°10'11.2" W, 1417 m, bosque pluvial premontano, epífitas en bosque de páramo, 25 jul 2012, *A. Karremans 5541, D. Bogarín, D. Jiménez, & V.H.*

*Zúñiga* (JBL-D5381); – Cordillera de Talamanca, cerro Kamuk-cerro Dudu, on the continental divide, 9°14'30"N 83°4'30"W, 3050 m, edge of elfin forest and paramo, 26 Mar 1984, *G. Davidse 26069, G. Herrera & R.H. Warner* (CR-105437). Fig. 70.

**Habitat and ecology.** This species is frequently found growing in mature secondary and primary forests on the main tree trunks, shaded and amongst mosses and lichens. It inhabits the rain mountain forests up to the paramo between 2500 m and 3050 m elevation, where cold wind and showers, as well as high solar radiation, are the constant.

**Etymology.** From the Latin *pusillus*, “very small”, referring to the size of the plant.

**Phenology.** Flowering is reported to occur in March and August, according to exsiccata material. It was observed that flowers of most plants also bore fruits or were developing a fruit when collected, while the perianth never went through anthesis; the plants also produced flowers and fruits under greenhouse conditions, all of which may indicate a self-pollination mechanism involved.

**Discussion.** Although widely distributed throughout the Neotropics, *Trichosalpinx pusilla* is a relatively uncommon species in Costa Rica. It is restricted to the high elevation mountain rain forests of the Cordillera de Talamanca and Cordillera Volcánica Central, close to the continental divide.

The species can be recognized by the shortly prolific ramicauls that bear elliptic to obovate thickly coriaceous leaves, which are commonly suffused with purple abaxially. The flowers are yellowish white -a common trait in subgenus *Tubella*-, the sepals are usually elongated and the membranous petals are elliptic and unequal. More distinctive is the trilobed lip with the lateral lobes round and erect, and the apical lobe oblong and microscopically glandulous; the junction between the apical and lateral lobes bear two shallow calli that are difficult to see in dried specimens (the probable reason why Kunth overlooked this trait in the holotype material); the area all around the midvein is bright yellow, while the lip lateral lobes are translucent white.

*Trichosalpinx pusilla* is more likely to be confused with *T. todziae* because of their similar floral architecture and color, and membranous oblong petals. Their lips are also similar with the two lateral, erect projections at the basal half and the two thickenings at or near the lobular angles. Nevertheless, the plants of both species are quite easy to distinguish, which is uncommon among species of *Tubella*; while plants of *T. pusilla* have erect ramicauls and oblanceolate to obovate thickly coriaceous leaves stained with purple abaxially, the plants of *T. todziae* have pendant ramicauls with shorter, herbaceous, elliptical leaves (8–17 mm in *T. pusilla* vs 7–12 mm in *T. todziae*).

Plants of *T. pusilla* collected in the Cordillera de Talamanca and Cordillera Volcánica Central showed cleistogamous flowers. The swollen ovaries and the perianth parts (in

early fruit developmental stages) were drawn, digitally documented and compared with not pollinated flowers from other populations. Cleistogamous flowers had comparatively shorter sepals, narrower petals and swollen columns. Divergence in the phenotypes of flowers (caused by, e.g., heterochrony) undergoing cleistogamy has been registered as part of plant developmental studies (Li & Johnston 2000), but infrequently mentioned in taxonomical treatments.

**18. *Trichosalpinx reflexa* Mel.Fernandez & Bogarín, Phytotaxa 38: 42. 2011.**

TYPE: Costa Rica. Guanacaste: Nicoya, San Antonio, Barra Honda National Park, Ceiba trail, area of Las Cascadas, 10°11'15"N 85°20'36.1"W, 210 m, basal transition to premontane wet forest, epiphytes in fallen *Ficus* sp. (Moraceae) tree, 11 July 2005, D. Bogarín 1674 & F. Paniagua (holotype, JBL-C0621; isotype CR-251812). Fig. 71.

**Herb** epiphytic, caespitose, erect to suberect, up to 10 cm tall. **Roots** slender, flexuous, to 2 mm in diameter. **Ramicauls** slender, 1.5–5.5 cm long, enclosed by 2–7 tubular lepanthiform sheaths; the sheaths acute, adpressed at the base, ribbed, minutely ciliate at the dilated margins, brown, 0.8–1.4 cm long. **Leaves** narrowly elliptical to narrowly obovate, apiculate, erect, fleshy, coriaceous, green suffused with purple beneath, 2.7–5.4 × 0.7–1.4 cm, the cuneate-attenuate base narrowing into a petiole up to 0.7 cm long, the petiole enclosed by the tip of the apical ramicaul bract. **Inflorescence** distichous, a successively flowering raceme with four to eight flowers, 1.2–1.6 cm long including the peduncle 4 mm long, THE APEX OF THE RAMICAUL of the leaf from a conduplicate, linear-ovate, acute spathe, 1.0–1.5 × 0.2–0.3 mm. **Floral bracts** cuneiform, conduplicate, 1 × 1

mm. **Pedicels** 1 mm long, persistent. **Ovary** cylindrical, 1 mm long. **Flowers** with the sepals white suffused with dark purple toward the apex, petals translucent white, the lip blackish purple, the column and anther white. **Dorsal sepal** erect, oblong, obtuse, convex toward the apex, 3.5–4.5 × 2.0–2.5 mm, 3-veined. **Lateral sepals** connate into an ovate-oblong, retuse, entire synsepal, concave at the base and reflexed toward the apex, 3.0–4.0 × 2.0–2.5 mm, 3-veined. **Petals** oblong, acute, entire or serrulate, the apex erose, 1.3–2.0 × 1.0–1.8 mm. **Lip** oblong, obtuse, ciliate, 2.0–3.0 × 1.5 mm, the disc with a central carina in the proximal third, that divides into two low keels close to the middle third, the basal lobes erect. **Column** semiterete, deeply erose-fimbriate at the apex, broadly winged near the apex, 2 mm long, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, on a cellular, oval caudicle. **Fruit** a reddish, glossy, 2-valved, glabrous, subglobose capsule, 5.5 × 4.0–4.5 mm, laterally dehiscent, with two prominent dehiscence lines running along the carpel midribs, the apex with persistent perianth.

**Distribution.** Known only from Costa Rica.

**Additional material examined. Costa Rica.** – **Guanacaste:** Nandayure, 9°54' N 85°20' W, *JBL 00401* (JBL-D3479); – Nicoya, San Antonio, Barra Honda National Park, Las Cascadas (the waterfalls), entering from Finca San Diego (Finca Los Trejos), 10°10'59.86"N 85°20'17.41"W, 86 m, premontane moist, transition to tropical moist forest, epiphytic in gallery forest on *Brosimum alicastrum* "Ojoche" (Moraceae) close to a water stream, 22 Feb 2012, *F. Pupulin 8191* & *D. Bogarín* (JBL-D5716); – Santa Cruz, distrito primero, Parque Nacional Diriyá, cuenca del río Enmedio, sendero a la catarata Santa Fe, ca. 300 m, 10°8'50"N 85°36'19"W, bosque de galería a orilla del río, 29 Jan 2009, *D.*

*Barrantes & M. Rojas s.n.* (USJ-93387). – **Puntarenas**: Esparza, San Rafael, Río Jesús María, cerca de 500 m río arriba a partir del Puente de Las Damas, 9°57'48.7"N 84°36'35.7"W, 170 m, bosque húmedo tropical, en troncos caídos de *Anacardium excelsum* (Anacardiaceae), 29 dic 2000, *D. Bogarín 19, A. Prendas & P. Rodríguez* (JBL-C0071); – Garabito, Jacó, Parque Nacional Carara, sobre el sendero Quebrada Bonita, 9°46'24.1"N 84°36'03.4" W, 110 m, bosque húmedo tropical, epífitas en bosque secundario en ramas caídas cerca de la toma de agua, 19 mar 2008, *D. Bogarín 4075* (JBL-D3957); – Cóbano, Cabo Blanco Absolute Natural Reserve, southern tip of the Nicoya Peninsula, secondary vegetation on former plantations and pasture, and remnants of original tall evergreen forest on steep slopes and stream edges in the Cabo Blanco Nature Reserve, 0–200 m, 9°35' N 85°6'W, 1–7 Dec 1969, *W.C. Burger & R.L. Liesner 6637* (CR-063105). – **San José**: Turrubares, San Luis, 1 km después de Pital hacia San Luis, orillas del Río Turrubaritos, 9°49'37.2" N 84°27'45.4" W, 450 m, bosque muy húmedo tropical transición a premontano, epífitas en *Anacardium excelsum* (Anacardiaceae), 28 jul 2010, *M. Fernández 195, D. Bogarín, R.L. Dressler & C. Smith* (JBL-D4221); – Without locality data, *JBL-10236* (JBL-D2643). Fig. 72.

**Habitat and ecology.** *Trichosalpinx reflexa* is restricted to the lowland semi-deciduous forests of the northern Pacific watershed of the Costa Rican mountains. Plants inhabit tropical wet, very wet and transitional premontane forests, between 100 and 500 m elevation.

**Etymology.** From the Latin *reflexus*, referring to the reflexed synsepal of the flowers.

**Phenology.** Plants of *Trichosalpinx reflexa* flower from September to February, and production of fruits was observed in February, under greenhouse conditions. In nature, plants bearing flowers were seen in January, July and December.

**Discussion.** According to the subgeneric classification of Luer (1997), *Trichosalpinx reflexa* belongs to subgenus *Trichosalpinx*. It is most similar to *Trichosalpinx ciliaris* and *T. memor*. *Trichosalpinx reflexa* can be distinguished from *T. memor* mainly by the narrow elliptic-lanceolate leaves (vs. elliptic-ovate), glabrous sepals (vs. densely ciliate), the erect dorsal sepal (vs. porrect), the synsepal reflexed towards the apex (vs. straight), the longer and narrower petals  $2.0\text{--}2.6 \times 0.6\text{--}1.0$  mm (vs.  $1.3\text{--}2.0 \times 1.0\text{--}1.8$  mm), and the low central keel in the proximal third of the lip (vs. a prominent central keel ending in the middle of the lip). In habit, *T. ciliaris* is similar to *T. reflexa*, mainly because the plants are of similar size and have narrowly lanceolate leaves, but the first species can be readily distinguished by the long fractiflex ramicauls and the concave, non-reflexed synsepal. In Costa Rica, *T. ciliaris* has only been found in the Caribbean watershed between 100 and 1000 m of elevation, whereas *T. reflexa* is restricted to the semi-deciduous tropical wet, very wet and transitional forests of the Pacific watershed between 100 and 500 m of elevation.

**19. *Trichosalpinx ringens* Luer, Lindleyana 11(2): 108. 1996.**

TYPE: Panama. Chiriquí: epiphytic in cloud forest, Cerro Colorado, alt. 1670 m, 15 Feb 1985, C. Luer, J. Luer, R. Dressler & K. Dressler 10539 (holotype, MO). Fig. 73.s

**Herb** epiphytic, caespitose, erect, up to 10 cm long. **Roots** slender, flexuous, 1 mm in diameter. **Ramicauls** slender, erect, 5–9 cm long, enclosed by 6–10 tubular, adpressed, densely long-ciliate, coarse lepanthiform sheaths, 1.0–1.5 cm long. **Leaves** ovate, acute, apiculate, coriaceous, 2.3–4.2 × 1.1–2.2 cm, the cuneate-attenuate base narrowing into a petiole up to 0.3 cm long, the petiole enclosed by the tip of the apical ramicaul bract.

**Inflorescence** a successively single or two-flowered fascicle, 5–8 mm long including the peduncle 1–2 mm long, produced at the apex of the ramicauls from a conduplicate, papyraceous spathe. **Floral bracts** cylindric, conduplicate, 5.0 × 1.5 mm. **Pedicels** 2.5–4.2 mm long, persistent. **Ovary** cylindric, channeled, 1.2–1.6 mm long. **Flowers** with the sepals purple-brown and pale yellow toward the apices, the petals mostly translucent yellow, the lip pinkish with the base and plates suffused with purple-brown, the column yellow with the clinandrium suffused with pink, and the anther white. **Dorsal sepal** erect, entire, glabrous, oblong, rounded, 6.3–7.2 × 2.2–2.5 mm, three-veined. **Lateral sepals** carinate, connate into a broadly obovate, retuse, entire, concave synsepal, 3.9–4.2 × 5.0–5.6 mm, 4 or 6-veined, the base forming a mentum. **Petals** thin, oblong, obtuse, ciliate to erose at the apex, 2.1–2.6 × 1.0–1.3 mm, 3-veined. **Lip** thick, trilobed, rounded, arcuate, 2.9–3.3 × 1.3–1.6 mm, the lateral lobes erect, densely ciliate along the margins, the base truncate, the apical lobe rounded, the disk deeply cleft longitudinally between two lamellar plates, densely ciliate in the middle zone. **Column** stout, semiterete, the apex deeply cleft, 2.5–2.9 mm long, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, the base transversally flattened with no apparent caudicle. **Fruit** not seen.

**Distribution.** Costa Rica and Panama.

**Additional material examined. Costa Rica. – Cartago:** Paraíso, Cachí, Peñas

Blancas, entre Cerros Duán y Alto Velo de Novia, 9°48'43.76" N 83°46'36.61" W, 1829 m, bosque muy húmedo premontano, epífitas en árboles en potreros y borde de bosque, 11 may 2009, *D. Bogarín 7187, R. Gómez, Y. Kisel, P. Renshaw & R. Trejos* (JBL-D3472); – *D. Bogarín 7188, R. Gómez, Y. Kisel, P. Renshaw & R. Trejos* (JBL-D3259); – Casamata, cruce a San Cristóbal, árbol en parche de bosque secundario a la orilla del potrero, frente a terreno de la estación eólica, 9°46'56.03"N 83°59'39.84"W, 1970 m, colectada por D. Jiménez, en cultivo en el Jardín Botánico Lankester, *M. Fernández 338* (JBL-D4532).

**Heredia:** Sarapiquí, Horquetas, Reserva Biológica Rara Avis, bosque muy húmedo tropical, epífitas en bosque primario alrededor del sendero Bromelia y

Morpho, 10°16'55.21"N 84°02'51.88"W, 756 m, 24 mar 2013, *D. Bogarín 10075* (JBL-D5804). – **Limón:** Guácimo, Parismina [300 m], colectada por G. Villalobos, sin más datos de colecta, *M. Fernández 551* (JBL-D4792). – **Puntarenas:** Coto Brus-Valle del Risco, línea fronteriza sobre la divisoria de aguas ingresando por el camino de la Finca Sandí-Hartmann "El Capricho", alrededores de riachuelo, 8°57'14"N 82°43'39"W, 2107 m, bosque pluvial montano bajo, 11 dic 2013, *M. Fernández 811, A. Karremans, D. Bogarín & L. Sandoval* (JBL-D6247). – **San José:** Vásquez de Coronado, Jesús, Parque Nacional Braulio Carrillo, Sendero La Botella, 10°09'34"N 83°57'14.8"W, 702 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario y primario, 22 mar 2012, *M. Fernández 577, D. Bogarín, A. Karremans & C. Smith* (JBL-D5717). Fig. 74.

**Habitat and ecology.** *Trichosalpinx ringens* inhabits the premontane wet, montane wet and tropical wet forests of the Caribbean plains and foothills north of the Cordillera Volcánica Central, as well as the premontane wet and low montane rain forests of the northern midlands and central highlands of the Cordillera de Talamanca. In terms of

elevation, *T. ringens* is distributed from 300 to 2100 m; such a broad elevational range is uncommon among *Trichosalpinx* species, and shows a high adaptability to varied environmental conditions.

**Etymology.** From the Latin *ringens*, “gaping”, referring to the bilabiate flower.

**Phenology.** Plants were observed in flower during July, November and March, under greenhouse conditions. No material of this species was found in national herbaria.

**Discussion.** Although several characters place them in subgenus *Trichosalpinx*, both *T. ringens* and *T. sanctuarii* form a morphologically distinctive group, which probably deserves recognition as a distinct taxonomic unit. Whilst subgen. *Trichosalpinx* is distinguished by the caespitose habit (except for *T. navarrensis*), non-proliferous ramicauls, multi-flowered racemes shorter than the leaf, fleshy sepals, erose petals, and a lip with a longitudinal callus and basal, retrorse lobules (Luer 1997). *Trichosalpinx ringens* as well as the less frequent *T. sanctuarii*, produce one- or two- flowered inflorescences, and their lips lack the basal auricles, a feature shared by most other members of the subgenus. Furthermore, the lip of *T. ringens* is deeply arcuate and bears a pair of lamellar plates on the disk zone separated by a deep cleft; these plates are pubescent on the ventral surface, a feature not seen in the rest of the subgenus. Ecological and molecular studies may reflect a distinct evolutionary path taken by this subgroup of *Trichosalpinx*.

*Trichosalpinx ringens* can be distinguished from *T. sanctuarii* by the color pattern of sepals and petals. The sepals of *T. sanctuarii* are yellow, longitudinally striped with brown-red along the veins, and its petals are brown-red. In contrast the sepals of *T. ringens* are purple-brown and pale yellow toward the apices, and the petals are mostly translucent

white. Also, the taller habit with flowers that bear longer dorsal sepals and synsepals, and the lip with two ciliate, lamellar plates on the ventral zone (vs. a lip with erect lateral lobes only ciliate along the margins and a bifid mid central callus) are also helpful to differentiate these species. In the protologue of *T. ringens*, Luer (1996, 1997) indicated that the specimen has single-flowered inflorescences per ramicaul. Nonetheless, specimens examined in this project constantly produced one or two simultaneously opened flowers per ramicaul. This was observed both in the field and under greenhouse conditions.

**20. *Trichosalpinx rotundata* (C.Schweinf.) Dressler, Novon 7(2): 124. 1997.**

BASIONYM: *Pleurothallis rotundata* C.Schweinf., Bot. Mus. Leafl. 4(7): 115. 1937.

TYPE: Panama. Coclé: mountains beyond La Pintada, alt. 400–600 m, Feb 1935, A.A. Hunter & P.H. Allen 561 D (holotype, AMES; isotype, MO). Fig. 75.

*Trichosalpinx operculata* (Luer) Luer, Phytologia 54(5): 396. 1983. BASIONYM:

*Pleurothallis operculata* Luer, Phytologia 49(3): 213. 1981. TYPE: Panama. Coclé: epiphytic in cloud forest, El Copé, collected by R.L. Dressler, cultivated at [The Mary Selby Botanical Garden] SEL-78-480, flowered 18 Jul 1979, C. Luer 4075 (holotype, SEL).

**Herb** epiphytic, caespitose, up to 12 cm. **Roots** slender, light brown, up to 1 mm in diameter. **Ramicauls** erect, 1.5–9.0 cm long, enclosed by four to nine cinnamon-brown lepanthiform sheaths; the sheaths acute, tubular, coriaceous, ribbed, adpressed at the base, broadly dilated at the apex, the margin and ribs densely hispid, 0.3–2.0 cm long, the

distalmost sheath apically cuneate. **Leaf** suberect, convex, widely ovate to circular, rounded, retuse, coriaceous, dark green above and green suffused with purple beneath, leaves green when young, 1.6–3.5 × 1.3–2.9 cm, contracted below into a petiole 1.0–3.5 mm long. **Inflorescence** a congested, distichous, 2 to 5 simultaneously flowered raceme, up to 12 mm long including the filamentous peduncle up to 10 mm long. **Floral bracts** cuneiform, conduplicate, 1.5–2.0 mm long. **Pedicels** 1.5 mm, persistent. **Ovary** cylindrical, 1 mm. **Flower** with the sepals membranous, yellow suffused with flesh-red from near the base towards the apex, the basal and apical margins fringed, the petals translucent yellow, the lip yellow and basally red, the column white, the anther reddish. **Dorsal sepal** slightly incurved, narrowly ovate, truncate, acute, microscopically ciliate, 5.6–6.3 × 1.5–1.6 mm, 3-veined. **Lateral sepals** narrowly ovate to triangular, truncate, acute, densely ciliate along the external margins, connate from the base up to the middle forming a bifid lamina, the center papillate internally, 4.7–6.5 × 2.1–2.5 mm, 4-veined altogether, the apex reflexed, thickened. **Petals** elliptic to narrowly ovate, truncate, narrowly obtuse, 2.2–2.8 × 0.6 mm, the apex deeply erose-ciliate. **Lip** narrowly ovate, obtuse, acuminate, 3.0 × 0.8 mm, the basal margins minutely denticulate, forming a pair of erect lobules, the disc with a longitudinal callus borne at the base and descending towards the middle and two auricles, hinged to the column-foot by a flexible claw, the apex fimbriate. **Column** semiterete, 1.9–2.0 mm long, deeply fimbriate at the apex, widened apically. **Anther** ventral. **Anther cap** incumbent, ovate, emarginate. **Stigma** ventral. **Pollinia** 2, pyriform, on an oval caudicle. **Fruit** not seen.

**Distribution.** Costa Rica and Panama.

**Additional material examined. Costa Rica.** – **Alajuela:** San Carlos, Fortuna, Volcán Chato, sobre el sendero a la laguna de la cima de volcán, en bosque primario, muy húmedo premontano, 10°26'34"N 84°40'51"W, 899 m, 27 de jul 2011, A. Karremans 4385 (JBL-D4895); – A. Karremans 4386 (JBL-D4737). – **Cartago:** Cartago, San Francisco, Muñeco, Navarro, 3 km al sur de la iglesia de Navarro, entre Río Sombrero y Quebrada Patarrá, 9°45'54.84"N 83°54'22.51"W, 1579 m, bosque pluvial premontano, “ad sylva secundaria et primaria prope oppidum Navarro ad margines viam ubi Standley probabiliter *Trichosalpinx navarrensis*, *Eurystyles standleyi* et *Coccineorchis navarrensis* invenit”, 12 may 2011, A. Karremans 4120, M. Fernández, R. Gómez, D. Bogarín & C. Smith (JBL-E0817). – **Limón:** Pococí, Guápiles, Pocora, La Argentina Sur, epífita en troncos musgosos, floreció en may 2004 en cultivo de la familia Valverde Arias, Desamparados, 600 m, 15 feb. 2004, R. Valverde 1189 (JBL-B0863). Fig. 76.

**Habitat and ecology.** This species is found in the premontane wet and rain forests, as well as in the premontane wet forest, basal belt transition of the Caribbean watershed between 600 and 1600 m. It has been found growing in the humid shaded environments of densely moss-covered tree trunks of primary and secondary forests.

**Etymology.** From the Latin *rotundatus*, meaning “rounded”, in allusion to the round leaves.

**Phenology.** When cultivated, plants of this species flower all year round, with a peak in September and October, towards the end of the Costa Rican rainy season.

**Discussion.** This species, described from the lowlands of central Panama, was initially compared to *Pleurothallis trachytheca* F.Lehm. & Kraenzl., considered by several authors

as a synonym of *T. orbicularis* (Luer 1975, 1983, 1997, 2003, Stevens *et al.* 2001, Funk *et al.* 2007). In fact, *T. orbicularis* is the most similar species to *T. rotundata*, mainly because of the densely ciliate sheaths of the erect ramicauls, the sub-orbicular leaves and the reddish flowers bearing a large lip with the apex acuminate and fimbriate.

Nevertheless, *T. rotundata* can be easily distinguished by the deeply convex, circular leaves suffused with purple beneath, the short racemes bearing commonly 2 or 3 flowers, the red and yellow lateral sepals with reflexed, thick apices and the fimbriate, membranous petals projecting outwards.

**21. *Trichosalpinx sanctuarii* Mel.Fernández & Bogarín, *Brittonia* 65(1): 96–101. 2013.**

TYPE: Costa Rica. Guanacaste: Tilarán, Arenal, Nuevo Arenal, en parcelas del Santuario Católico de la Divina Misericordia, 1.5 km noreste del puente sobre el río Dos Bocas, 10°33'N 84°53'W, 650 m, bosque muy húmedo premontano, Hermano Jorge de la Cruz *invenit*, Mar 2011, *M. Fernández* 529 (holotype: JBL; isotype: NY). Fig. 77.

**Herb** epiphytic, caespitose, erect, up to 6.8 cm long. **Roots** slender, flexuous, 1 mm in diameter. **Ramicauls** slender, 2.0–4.2 cm long, enclosed by 3–6 tubular, lepanthiform sheaths; the sheaths cylindrical, adpressed, ribbed, minutely ciliate along ribs and margins of the dilated ostia, brown, 0.8–1.1 cm long. **Leaves** ovate, acute, apiculate, semi-coriaceous, 2.0–2.6 × 0.9–1.3 cm, the cuneate-attenuate base narrowing into a petiole up to 0.2 cm long, the petiole enclosed by the tip of the apical ramicaul bract. **Inflorescence** a successively single or 2-flowered raceme, 8 mm long including the peduncle 1 mm long, borne at the apex of the ramicaul from a conduplicate, papyraceous spathe. **Floral bracts**

cylindric, conduplicate, 1 × 1 mm. **Pedicels** 5 mm long, persistent. **Ovary** cylindric, 1 mm long. **Flowers** with the sepals and petals yellow, brown-red along the veins, the lip dark red, the column yellow and the anther white. **Dorsal sepal** erect, oblong, obtuse, 6.6 × 2.5 mm, three-veined. **Lateral sepals** carinate, connate into a broadly obovate, retuse, entire, concave synsepal, 3.7 × 4.1 mm, 4-veined. **Petals** oblong, obtuse, erose towards the apex, 2.3 × 1.0 mm. **Lip** oblong, obtuse, 3.9 × 1.6 mm, with two short, erect, ciliate lateral lobes and a mid-central callus that bifurcates into 2 low keels. **Column** stout, semiterete, the apex cleft, 2.5 mm long, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, pyriform, the base transversally flattened with no caudicle. **Fruit** not seen.

**Distribution.** Endemic to Costa Rica.

**Additional material examined. Costa Rica.** – **Guanacaste:** Tilarán, Arenal, Nuevo Arenal, en parcelas del Santuario Católico de la Divina Misericordia, 10°33'N 84°53'W, 650 m, bosque muy húmedo premontano, Hermano Jorge de la Cruz *invenit*, May 2011, M. Fernández 545 (paratype, JBL). Fig. 78.

**Habitat and ecology.** Epiphyte on scattered trees in pastures, in very humid pre- montane forest in the Caribbean watershed of Cordillera de Tilarán.

**Eponymy.** The specific epithet, from the Latin *sanctuarium*, sanctuary, refers to the Santuario Católico de la Divina Misericordia (Catholic Sanctuary of the Divine Mercy), where the plants studied were collected.

**Phenology.** Plants flower from July to October under wild conditions.

**Discussion.** *Trichosalpinx sanctuarii* belongs to subgenus *Trichosalpinx*, distinguished by the caespitose habit, non proliferous ramicauls, racemes shorter than the leaf, fleshy sepals, and erose petals (Luer 1997). Nevertheless, *T. sanctuarii*, as well as *T. ringens*, lack the basal lobes of the lip, a feature shared by most other members of this subgenus. *Trichosalpinx sanctuarii* is most similar to *T. ringens*, mainly because of the coarsely long-ciliate, lepanthiform sheaths, ovate leaves, inflorescences with flowers produced near the base of the leaf, simultaneously few-flowered racemes (bearing one or two flowers), erect, obovate dorsal sepals, and oblong petals.

In describing *T. ringens*, Luer (1996, 1997) indicates that the specimen had single-flowered inflorescences per ramicaul. Nonetheless, plants examined in this study constantly produced one or two simultaneously opened flowers per ramicaul. This was observed both in the field and under greenhouse conditions. This feature was also observed in *T. sanctuarii*. *Trichosalpinx sanctuarii* can be distinguished from *T. ringens* by the smaller habit (up to 7 cm long vs. up to 10 cm tall) with flowers with differing color patterns in sepals and petals. The sepals of *T. sanctuarii* are yellow, longitudinally striped with brown-red along the veins, and the petals are brown-red; in contrast the sepals of *T. ringens* are purple-brown and pale yellow toward the apices, and the petals are mostly translucent white. The two species also differ in their lips; in *T. sanctuarii* the lip bends downwards approximately 20° (vs. deeply arcuate in *T. ringens*). Furthermore, the lip of *T. ringens* bears a pair of conspicuous, densely ciliate lamellate plates, whereas the lip of *T. sanctuarii* has no lamellae but a pair of short, ciliate, lateral lobes, and a central callus that bifurcates below the middle. Finally, the pollinarium of *T. sanctuarii* lacks a caudicle, thus the pollinia are separated from each other. A viscose hyaline substance was present along the ventral zone of the column. This sticky substance would allow the attachment of the

pollinia to the back of the pollinator, enabling their removal when the pollinator attempts to leave the flower.

**22. *Trichosalpinx todziae* Luer, *Lindleyana* 11(2): 111, 1996.**

TYPE: Costa Rica. San José: Bajo La Hondura, alt. 1100 m, 30 Jun 1978, C. *Todzia* 344 (holotype, CR). Fig. 79.

**Herb** epiphytic, caespitose, erect, up to 6.5 cm tall. **Roots** white, slender, flexuous, 0.5 mm diameter. **Ramicauls** prolific, erect to ascendent, 0.7–2.0 cm long, enclosed by 3–6 infundibuliform, imbricate, fibrous, shallowly striated, adpressed at the base, grey to light-brown, lepanthiform sheaths, 2–5 mm long each, ostia 1.5 mm in diameter, with apex dilated, margin hispid, the distalmost sheath slightly longer, dilated, covering the base of the leaf and inflorescence. **Leaves** elliptical, broadly acute to acuminate, entire, 7–12 × 4–7 mm, the midvein purple beneath, apiculate, the base narrowing into an attenuate petiole 1 mm long. **Inflorescence** distichous, an ascending, alternate, 5–7 successively flowered raceme, 1.8–4.0 cm long including the peduncle 0.5–1.4 cm, borne at the apex of any ramicaul from a papyraceous, ovate, obtuse spathe, 0.7 mm long. **Floral bracts** tubular, ovate, acute, basally truncate, membranaceous, 1.3–1.4 mm long. **Pedicels** straight, 1.5–5.0 mm long, persistent. **Ovary** green to purple, channeled longitudinally, 0.4–0.6 mm. **Flowers** white. **Dorsal sepal** ovate, narrowly obtuse, truncate, glabrous, externally carinate, 3.8–4.2 × 0.8–1.2 mm, concave at the base, the apex elongated, 3-veined. **Lateral sepals** narrowly ovate to triangular, narrowly obtuse, truncate, glabrous, externally carinate, 3.6–3.8 × 0.4–0.7 mm, connate just above the base forming a shallow mentum, 1-veined. **Petals** straight, membranous, narrowly elliptic to oblong, broadly obtuse,

truncate, unequal,  $1.2\text{--}1.9 \times 0.4\text{--}0.7$  mm, the margin undulate, 1-veined. **Lip** glabrous, oblong, broadly obtuse, attenuate,  $1.2\text{--}1.6 \times 0.5\text{--}0.8$  mm, 3-lobed, the apex fleshy, glandular, the disc with two lateral thickenings just above the middle, and a shallow longitudinal thickening from the base up below the middle. **Column** terete, 0.6–1.2 mm long, shortly broadened at the apex, the clinandrium apical, the stigma ventral. **Anther cap** incumbent, transversely ovate, emarginate. **Pollinia** 2, broadly ovate, on cellular, irregular caudicles. **Fruit** a green, glabrous, 2-valved, globose to ovoid capsule,  $3.0\text{--}3.5 \times 2.0\text{--}2.5$  mm, with 2 prominent dehiscent lines along the carpel midribs, perianth remnants persistent.

**Distribution.** Costa Rica and Panama.

**Additional material examined. Costa Rica.** – **Guanacaste:** Tilarán, San Miguel, aproximadamente 2,5 Km de la Escuela de San Miguel, finca La Trinidad, en potreros de la familia Durán Rivera,  $10^{\circ}24'56''\text{N } 84^{\circ}54'23''\text{W}$ , 900 m, 1 ago 2011, *M. Fernández 541 & L. Sandoval* (JBL-D5788). – **Puntarenas:** Coto Brus-Renacimiento, línea fronteriza entre Cerro Quijada del Diablo y Cerro Pando, entre mojones N.336-338,  $8^{\circ}54'51.9''\text{N } 82^{\circ}43'59.13''\text{W}$ , 2205 m, bosque muy húmedo premontano, epífitas en bosque primario, “in itinere per litem Costa Rica et Panama inter montis Quijada del Diablo et montis Pando”, 19 abr 2011, *A. Karremans 3983, D. Jiménez & D. Bogarín* (JBL-D5369); – Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí,  $8^{\circ}56'46.1''\text{N } 82^{\circ}44'30.9''\text{W}$ , 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 20 abr 2010, *A. Karremans 5410 & J. Geml* (JBL-D5370). – **San José:** Escazú, Bebedero, Cerros de Escazú, camino hacia el Cerro Pico Blanco,  $9^{\circ}52'34''\text{N } 84^{\circ}8'5''\text{W}$ , 2271 m, bosque muy

húmedo tropical montano bajo, 15 jun 2002, *D. Bogarín 49, A. Granados, J.P.*

*Jiménez & J.M. Matamoros* (JBL-B0107); – [Desamparados], Cerro de la Muerte, San Cristóbal Norte, 1750 m, may 1997, *Grettel Agüero s.n.* (USJ-63795); – [Desamparados] Cartago, Tablazo, 1500 m, 28 May 1978, *C. Todzia 291* (CR-66487). Fig. 80.

**Habitat and ecology.** Despite its rarity in terms of number of individuals per site, *Trichosalpinx todziae* is a widely distributed species that can be found from 900 m to 2500 m in elevation, in open areas or forest borders, and in primary and secondary forests. Following Holdridge's (1967, 1987) life zones classification, *T. todziae* occupies varied environments, from the premontane wet forests (rain forest transition) as in the northern foothills of Cordillera de Tilarán to the low montane wet forests of the southeast zone of the Cordillera de Talamanca. Although visited in several occasions, no plants of *T. todziae* were found at the type locality, where (mainly) deforestation has severely modified the natural landscape.

**Eponymy.** Named after Carol Todzia, collector of the type specimen.

**Phenology.** Plants in cultivation flowered between May and June, while flower and fruiting-producing plants were encountered during field trips between May and September. Exsiccata indicate flowering in May.

**Discussion.** This species is most similar to *Trichosalpinx nana*, but distinct in the erect habit (vs. descending), the flowers with sepals narrowly elongated that barely open (vs. triangular sepals with the apex variously reflexed), the arcuate lip with a papillate apex (vs. flat and apically smooth), and the straight column (vs. slightly arcuate). Luer (1997) compared *T. todziae* to *T. carinilabia* but *T. carinilabia* possesses longer pedicels, a

prominent mentum at the base of the lateral sepals (mentum absent in *T. todziae*), and a third, central carina on the lip (absent in *T. todziae*).

*Trichosalpinx todziae* is also similar to *T. parsonsii*, but the plants of the latter are usually shorter (up to 6.5 cm vs. up to 12 cm tall), and the simple lip has no ornamentations (vs. two lateral thickenings in the disc area, and a shallow longitudinal thickening in the basal half) and it is apically thickened (vs. apically not thickened).

Most flowers from various plants encountered in both Cordillera de Talamanca and Cordillera de Tilarán had developing fruits, possibly by self-pollination. Ovaries and columns were swollen and turning color from whitish green to purple, while the lips had partially lost the original arcuate shape. It is worth to mention that the columns of the southern populations were twice as long as the northern populations; further studies may reveal the implications of such a difference in length.

**23. *Trichosalpinx trachystoma* (Schltr.) Luer, *Phytologia* 54(5): 397. 1983.**

BASIONYM: *Pleurothallis trachystoma* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 196. 1923. TYPE: Costa Rica. Alajuela: San Pedro de San Ramón, 950 m, A. M. Brenes 40 (holotype at B, destroyed; neotype, designated by Barringer [1986, as 'lectotype'], AMES). Figs. 15, 81–82.

**Herb** epiphytic, caespitose, suberect, up to 9 cm tall. **Roots** slender, filiform, flexuose, glabrous. **Ramicauls** stout, suberect, 2.2–5.5 cm long, enclosed by 3–6 infundibuliform, fibrous, ribbed, tightly adpressed, ovate, acuminate sheaths, with the ostia muriculate to hispid, dilated. **Leaves** erect, flat to shallowly concave, coriaceous, entire, glabrous, ovate-

elliptic, apiculate, 1.8–5.5 × 0.7–2.3 cm long including the coriaceous petiole up to 2 mm long. **Inflorescence** an erect, lax, distichous, 4–7 simultaneously-flowered raceme, 1.1–2.8 cm long including the peduncle 0.5–0.8 cm long, produced at the apex of the ramicaul from a lanceolate, acute spathe. **Floral bracts** membranaceous, cucullate, ovate, obtuse, 0.8–1.2 mm long. **Pedicels** 1 mm long, persistent. **Ovary** shallowly channeled, up to 1 mm long. **Flowers** with the dorsal sepal light yellow suffused with purple or pinkish, the lateral sepals yellow at the base, purple towards the apex and greenish at the apices; the petals translucent white, the lip dark purple, the column white, the clinandrium white (occasionally pinkish apically), the anther white or pink. **Dorsal sepal** membranaceous, descendent, entire, oblong to ovate, acute, microscopically ciliate, 1.3–3.3 × 1.1–1.7 mm, shallowly concave at the base, 3-veined. **Lateral sepals** fleshy, entire, ovate, obtuse, oblique, connate only at the base forming a bifid lamina, microscopically ciliate along the margins, 2.9–4.0 × 1.8–2.8 mm, 2-veined altogether, the apex thick, declined. **Petals** membranaceous, broadly ovate to ligulate, more or less acute, fimbriate at the apex, 0.7–1.6 × 0.4–0.9 mm, 1-veined. **Lip** gently arcuate, spatulate, obtuse, sometimes microscopically ciliate along the margin, 3-veined, the apex broadened, 1.6–2.1 × 0.5–0.8 mm, the disc with a central carina from the base and disappearing near the middle, the base with two retrorse lobules and a central membrane that is hinged to the column-foot. **Column** slightly arcuate, semiterete, broadened and serrulate at the apex, 1.6–1.8 mm long, the clinandrium subapical, the stigma ventral. **Anther cap** incumbent, ovate, emarginate. **Pollinia** 2, globose to pyriform, on a cellular, oval caudicle. **Fruit** not seen.

**Distribution.** Costa Rica and Guatemala.

**Additional material examined. Costa Rica. Alajuela:** – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06"N 84°36'11"W, 800–900 m, orillas del Río San

Lorencito, cerca del Sendero Terciopelo, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario a orillas del río, 22 may 2004, *D. Bogarín* 822 (JBL-B0599, JBL-D3257); – San Ramón, Reserva Forestal de San Ramón, along the río [San] Lorencito, 1050 m, epiphytic in primary vegetation, premontane wet forest, 21 Aug. 1991, *F. Pupulin* 101, *E. Bianchi*, *M. Germani* & *D. Pedruzzi* (USJ, possibly lost; illustration, Fig. 81); – San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06" N 84°36'11" W, 800–900 m, camino por el sendero La Fila, bosque muy húmedo tropical transición a premontano, epífitas en ramas caídas alrededor del sendero, 25 may 2008, *D. Bogarín* 5012 (JBL-D3267, JBL-D5690). – **Cartago**: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, El Mirador, Alto Patillos, 9°44'04.22"N 83°46'41.17"W, 1468 m, bosque pluvial premontano "*occurit in arborum truncis ramulisque ad arborum versuras in prope Mirador in Tapantí*", 19 ene 2011, *D. Bogarín* 8355, *C. Montagnani* & *F. Pupulin* (JBL-D4799, JBL-D5265). – **Guanacaste**: Tilarán, San Miguel, aproximadamente 2,5 Km de la Escuela de San Miguel hacia La Florida, finca La Trinidad, en potreros de la familia Durán Rivera, 10°24'56"N 84°54'23"W, 900 m, 1 ago 2011, *M. Fernández* 536 & *L. Sandoval* (JBL-D6225). Fig. 83.

**Habitat and ecology.** Found inhabiting low and middle elevations in the premontane wet and tropical rain forests of Costa Rica. Two specimens were reported by Luer (1997) at low elevations in Patulul and Cubilguitz, Guatemala.

**Etymology.** From the Greek *trachystoma*, a "coarse opening", probably referring to the sheaths covering the stem.

**Phenology.** Dates in exsiccata and living plants report a flowering period between November and March, during the country's dry season. No fruits were found.

**Discussion.** *Trichosalpinx trachystoma* is a Central American species, known from the type specimen –collected in San Ramón in the province of Alajuela, Costa Rica–, a few other Costa Rican specimens, and from two plants found in the lowlands of Guatemala. Since the holotype was presumably destroyed at B, the drawings of the type specimen, preserved at AMES, were chosen by Barringer (1986) as the lectotype. Although the drawings are no more than rough sketches, the protologue includes a detailed description.

As noted by Schlechter (1923), the original concept treated of *Trichosalpinx trachystoma* places it in the *T. memor* – *T. blaisdellii* group, characterized by the lepanthiform sheaths with dilated, minutely ciliate ostiae, the coriaceous leaves with short petioles, the flowers with fleshy, ciliate, oblong to broadly ovate sepals, membranous petals, bearing a low callus borne at the base and disappearing towards the middle of the ligulate, oblong or ovate lip. Nevertheless, *T. trachystoma* can be distinguished by the sepals connate only at the base with the apex declined and thickened; the spatulate lip widest near the apex, the disc with a central keel born at the base and disappearing near the middle of the lip, and the column broadly winged at the apex.

Plants collected in the surrounding areas of San Ramón (type locality), Tilarán and Tapantí at the same forest type and elevation as the type collection are in accordance with the concept proposed by Schlechter. Nonetheless, these specimens bore more flowers (4–8), had minute cilia along the margins (vs. glabrous) and were variable in terms of petal length and shape (all shorter than the column; from broadly ovate to ligulate). Based on the two Guatemalan collections, Luer (1997) also describes larger specimens (up to 10.3 cm tall) bearing two to four flowers in one raceme (vs. one or two), red-purple flowers (instead of

pale purple) and petals shorter than the column (vs. longer). Further studies including anatomical and molecular approaches will help to better circumscribe the concept of *T. trachystoma*, and its relationship with other members of the *T. blaisdellii* – *T. memor* complex.

## VII. EXCLUDED SPECIES

In the Checklist of the Orchids of the Western Hemisphere by Dodson (1992), *T. intricata* is included as present in Costa Rica, but no evidence was provided. After performing detailed examinations of literature and exsiccata, as well as extensive field work, no evidence of the presence of *T. intricata* in Costa Rica was found.

## VIII. CONCLUSIONS

1. Number and identity of Costa Rican species of *Trichosalpinx* was modified during the course of this study. Two new species (*Trichosalpinx reflexa* and *T. sanctuarii*) were described. Also, *Trichosalpinx minutipetala* was removed from the synonymy of *T. memor* and recognized as a distinct species. The total number of species rises up to 23. It is expected that this number increase by a few species in the next years, by the combination of Costa Rica's high diversity and intense botanical exploration (Karremans & Bogarín 2013).
2. *Trichosalpinx intricata* was excluded based on the lack of specimens that would demonstrate its presence in Costa Rica.
3. *Trichosalpinx arbuscula*, *T. blaisdellii*, *T. dura*, *T. memor* and *T. orbicularis* are here treated as species-complexes. Heterogeneity reflected in leaf shape and size, number of flowers per inflorescence, and sepal shape, size and color among and within populations, reveals high morphological variability. Further studies including samples from their Neotropical distributions are needed to understand and interpret the natural limits of each species concept.
4. *Trichosalpinx blaisdellii*, *T. caudata*, *T. ciliaris*, *T. memor*, *T. minutipetala*, *T. navarrensis*, *T. orbicularis*, *T. reflexa*, *T. ringens*, *T. rotundata*, *T. sanctuarii*, *T. trachystoma* are accepted for the *Flora Costaricensis*. Morphological evidence in exsiccata and fresh material revealed concordancy with each species' original concepts.
5. *Trichosalpinx arbuscula*, *T. carinilabia*, *T. cedralensis*, *T. dura*, *T. fruticosa*, *T. membraniflora*, *T. nana*, *T. parsonsii*, *T. pergrata*, *T. pusilla*, *T. todziae* are accepted

- for the *Flora Costaricensis*. Morphological evidence in exsiccata and fresh material revealed concordancy with each species' original concepts.
6. *Trichosalpinx ringens* and *T. sanctuarii* are included in *Trichosalpinx* sensu lato. Discrepancies at the generic level include the production of few flowers per ramicaul, the lack of the basal auricles in the lip base, and the presence of a pair of lamellar plates in the disc zone of the lip, separated by a deep cleft.
  7. *Trichosalpinx navarrensis* shows several features that agree with the concept of *Anathallis* as opposed to *Trichosalpinx* subgen. *Trichosalpinx*, including the repent habit, the abbreviated ramicauls, the single-flowered inflorescence, the pubescent, spreading sepals, and the pubescent lip. Comprehensive phylogenetic analysis of *Trichosalpinx* and related genera may help in the understanding of this rare species.
  8. Several characters including the single or two-flowered inflorescence much shorter than the leaf, the concave, succulent and externally-papillate petals, and the ecallous lip, disagree with the concept of subgenus *Tubella*. Further studies may help elucidate the phylogenetic affinities of this species.
  9. Based on the biological evidence provided in this treatment, it is clear that the full comprehension of the phylogenetic relationships (and the consequent taxonomical derivatives) involving *Trichosalpinx*, requires further studies. These must take in account a large species sampling, as internal relationships may be understood and interpreted only including all the possible lineages that explain the apparent and real misfits. Such a commitment, evidently, goes behind the scope of this study.
  10. As exemplified in this treatment, some (but not all) species form a natural assemblage within subgenus *Tubella*. However, other species, as in the case of *T. pergrata*, show morphological discrepancies to the original concept. The recognition

- of *Tubella* at the generic level, as presently circumscribed, would only contribute to nomenclatural inflation without promoting further understanding of the evolutionary aspects.
11. The conservative approach in the nomenclature of *Trichosalpinx* is the only possible and coherent at this stage of our knowledge of the group. This “biological treatment” of the involved groups represents a most useful framework for further systematic studies.

**IX. INDEX TO HERBARIUM SPECIMENS EXAMINED****1. Numerical list of species of *Trichosalpinx* in Costa Rica**

Numbers to the right correspond to those in the taxonomic treatment.

**Subgenus *Trichosalpinx***

2. *Trichosalpinx blaisdellii* (S.Wats.) Luer
4. *Trichosalpinx caudata* Luer & R.Escobar
6. *Trichosalpinx ciliaris* (Lindl.) Luer
10. *Trichosalpinx memor* (Rchb.f.) Luer
11. *Trichosalpinx minutipetala* (Ames & C.Schweinf.) Luer
13. *Trichosalpinx navarrensensis* (Ames) Luer
14. *Trichosalpinx orbicularis* (Lindl.) Luer
18. *Trichosalpinx reflexa* Mel.Fernández & Bogarín
19. *Trichosalpinx ringens* Luer
20. *Trichosalpinx rotundata* (C.Schweinf.) Dressler
21. *Trichosalpinx sanctuarii* Mel.Fernández & Bogarín
23. *Trichosalpinx trachystoma* (Schltr.) Luer

**Subgenus *Tubella***

1. *Trichosalpinx arbuscula* (Lindl.) Luer
3. *Trichosalpinx carinilabia* (Luer) Luer
5. *Trichosalpinx cedralensis* (Ames) Luer
7. *Trichosalpinx dura* (Lindl.) Luer
8. *Trichosalpinx fruticosa* Luer
9. *Trichosalpinx membraniflora* (C.Schweinf.) Luer
12. *Trichosalpinx nana* (Ames & C.Schweinf.) Luer
15. *Trichosalpinx parsonsii* Luer & Dod
16. *Trichosalpinx pergrata* (Ames) Luer

17. *Trichosalpinx pusilla* (Kunth) Luer

22. *Trichosalpinx todziae* Luer

## 2. List of Collections

Specimens are sorted according to herbaria of deposition. Numbers in parentheses refer to the numerical list of species presented above. Type specimens appear in bold face. For spirit-preserved specimens at JBL lacking a collector, the term "JBL-" followed by the Living Plants Collection identification number, all in italics, was used.

### CR

*Atwood* 8941 (3); 8974 (3); **8984** (2).

*Beckers* 23 (2).

*Bogarín* 1674 (18).

*Brenes* 1253 (5); 23 (5); **102-432** (11); 473 (5).

*Burger* 6637 (19).

*Cascante* 1701 (12); 1737 (5).

*Davidse* 26069 (17).

*Escobar & Anderson* 2747 (11).

*Haber* 3811 (5); 8268 (2); 9027 (5).

*Herrera* 4568 (4); 4747 (2); 5816 (1); 6628 (5); 7627 (2); 8671 (5).

*Hietz* 5 (2).

*Ingram* 838 (14).

*Lent* 1812 (5); 2965 (7).

*Lobo* 2685 (2); 859 (16).

*Mora Castro* 1961 (2).

*Morales* 403 (5); 10117 (1).

*Morris* 4034 (5).

*Quesada* 199 (5); 2649 (12); 2716 (14).

*Richardson* K-123B (2); K-182 (2); K-184 (14).

*Span* 16 (2).

*Todzia* 291 (22); **344 (22)**; 363 (2); 398 (2); 909 (1); 977 (2); 1020 (10); 2065 (11).

*Valverde* 237 (5).

## **INB**

*Aguilar* 1164 (5).

*Bello* 1783 (5).

*Fernández, A.* 788 (1).

*Haber* 8824 (11).

*Herrera* 4568 (4); 4747 (2); 5058 (14).

*Ingram* 631 (1); 838 (14).

*Jiménez* 2254 (1).

*Morales* 4065 (17); 10117 (1); 15794 (16); 15987 (16).

## **JBL**

A. Q. [probably, *Alonso Quesada*] s.n. (2); s.n. (10).

*Blanco* 1615 (2); 1617 (10); 1806 (2); 1912 (2); 4036 (2); 4042 (7); 4047 (1); 4048 (1);  
4049 (1); 4050 (1); 4052 (1).

*Bogarín* 19 (18); 23 (2); 49 (22); 165 (10); 212 (2); 441 (10); 822 (23); 929 (5); 1134 (5);

1216 (5); **1674 (18)**; 1880 (10); 2402 (2); 2894 (2); 3955 (10); 3956 (10); 3962 (10);  
 4075 (18); 4244 (2); 4500 (1); 4643 (11); 4750 (10); 4970 (11); 4975 (10); 5009 (10); 5012  
 (23); 5016 (10); 5022 (2); 5635 (16); 5636 (16); 5784 (16); 6192 (11); 6409 (10); 6461  
 (10); 6462 (10); 6470 (10); 6502 (16); 6509 (8); 6566 (5); 6580 (10); 6861 (1); 6945 (7);  
 7187 (19); 7188 (19); 7193 (10); 7199 (5); 7219 (5); 7251 (2); 7281 (16); 7330 (10); 7332  
 (10); 7403 (14); 8004 (10); 8355 (23); 8581 (5); 8696 (11); 8703 (11); 9030 (11); 9032  
 (10); 9268 (10); 9319 (10); 9462 (10); 9780 (1); 10075 (19); 11078 (12).

*Carnevali s.n.* (10).

*Castelfranco 68* (14).

Clarke 110 (2).

Dressler s.n. (2).

*Fernández 1* (2); 2 (2); 3 (10); 8 (10); 12 (10); 65 (14); 195 (18); 282 (11); 328 (6); 330  
 (10); 338 (19); 407 (11); 408 (11); 444 (11); 446 (11); 454 (10); 457 (10); **529 (21)**; 535  
 (10); 536 (23); 541 (22); 545 (21); 546 (4); 547 (7); 551 (19); 577 (19); 580 (12); 615 (10);  
 617 (8); 623 (8); 624 (8); 631 (3); 811 (19); 911 (17).

*JBL-00401* (18); 00417 (2); 00421 (2); 01388 (10); 01432 (10); 01546 (10); 01575 (10);  
 01710 (2); 01781 (2); 01855 (2); 01864 (10); 10236 (18); 11580 (8); 11592 (10).

*Karremans 292* (10); 870 (1); 1003 (2); 1333 (11); 1744 (11); 2098 (11); 2468 (7); 2490  
 (7); 2666 (2); 2681 (2); 2836 (11); 3017 (11); 3044 (10); 3077 (11); 3278 (2); 3303 (1);  
 3304 (1); 3305 (15); 3307 (5); 3468 (10); 3487 (10); 3794 (7); 3926 (5); 3983 (22); 4071  
 (11); 4120 (20); 4246 (10); 4385 (20); 4386 (20); 4551 (11); 4578 (11); 4580 (10); 4599  
 (10); 4882 (12); 4883 (12); 4884 (7); 4885 (7); 4902 (7); 4904 (12); 4973 (7); 4974 (7);  
 5032 (16); 5150 (2); 5238 (11); 5308 (2); 5309 (2); 5330 (2); 5410 (22); 5541 (17); 5642

(17); 6000 (6); 6010 (5); s.n. (11); s.n. (11).

*Luer* 17411 (2).

*Ossenbach* 368 (4); 369 (2).

*Pupulin* 101 (23); 455 (10); 462 (10); 1092 (2); 1819 (10); 3749 (2); 3861 (16); 4077 (7);  
4233 (16); 4286 (11); 4542 (10); 4548 (3); 4586 (8); 4608 (5); 4736 (10); 5472 (10); 5500  
(10); 6267 (2); 7049 (5); 7166 (10); 7498 (5); 7501 (10); 7505 (5); 7581 (11); 7582 (11);  
7662 (3); 7674 (10); 7675 (10); 7676 (10); 7677 (10); 7680 (10); 7901 (11); 7912 (11);  
8191 (18).

*Rojas* 6474 (14); 6858 (2); 7026 (10).

*Schug* 84 (5); 98 (1).

*Serrano* 232 (7).

*Valverde* 1189 (20); 615 (14); 617 (14).

*Vega* s.n. (11).

*Whitten* 2232 (10).

## **USJ**

*Aguero* s.n. (22).

*Atwood* 89-149 (8); 89-156 (10).

*Barrantes & Rojas* s.n. (18).

*Blanco* 803 (10); 872 (1); 1806 (2); 1937 (7).

*Boyle* 51-89 (5).

*Cascante* 2338 (8).

*Dressler & B-350* 128a (5); 128 (3); 300 (2).

*Fernández* 546 (4).

*Germani* 15 (2); 41 (10).

*Herrera* 5816 (1).

*Ingram* 560 (2); 646 (10); 740 (5).

*Luer* 17411 (2).

*Mora* 5 (5); 6 (5); *s.n.* (USJ-049934, USJ-049933 [2]); *s.n.* (USJ-030731 [5])

*Pupulin & Spadari* 2031 (11).

*Pupulin* 538 (10); 2306 (3); 3806 (7).

*Rodríguez* 507 (3).

*USJ-050993* (10).

## X. LITERATURE CITED

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## XI. FIGURES

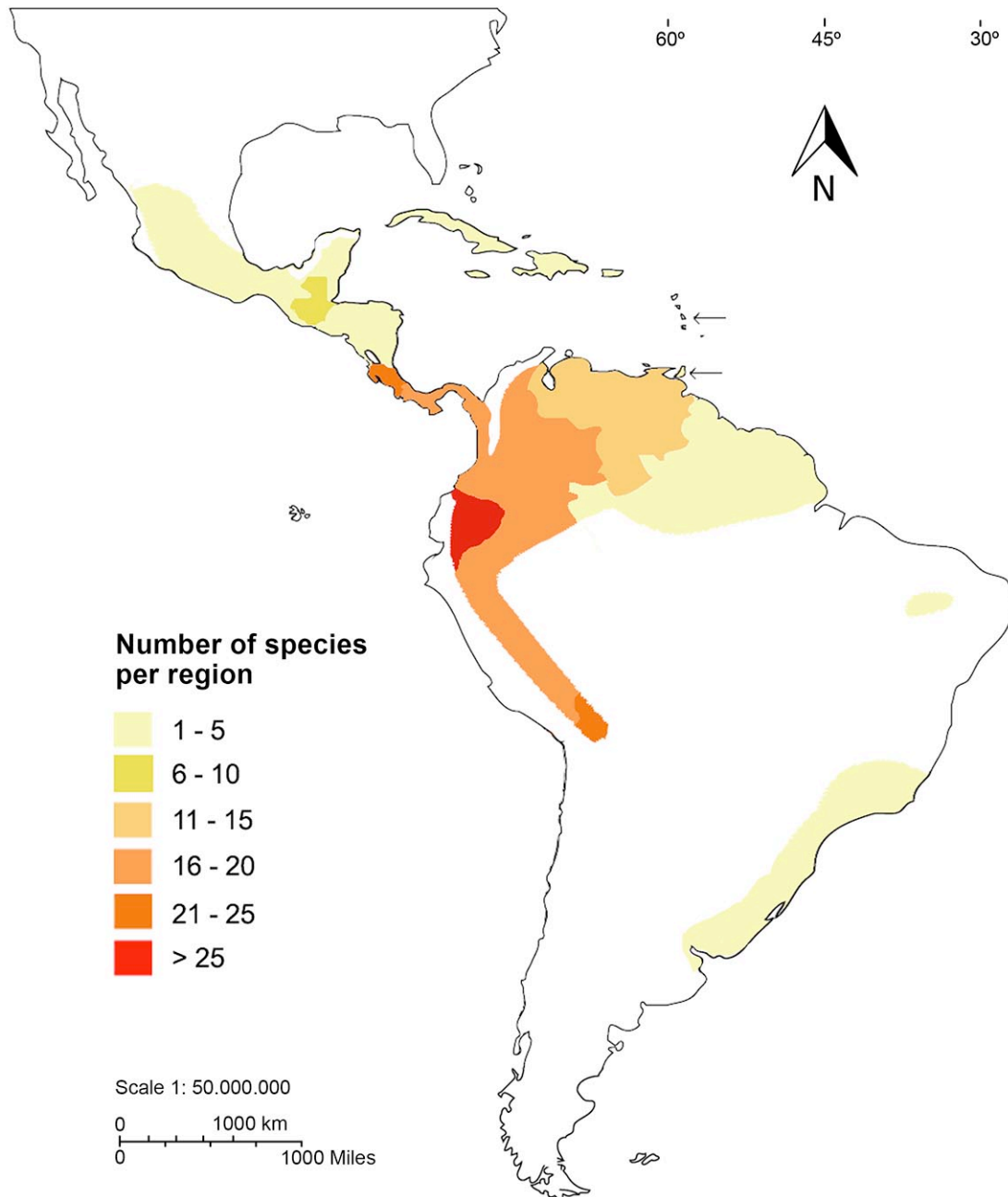


Figure 1. Geographic distribution of the genus *Trichosalpinx*, with the approximate number of species per region; modified from Pridgeon (2005).

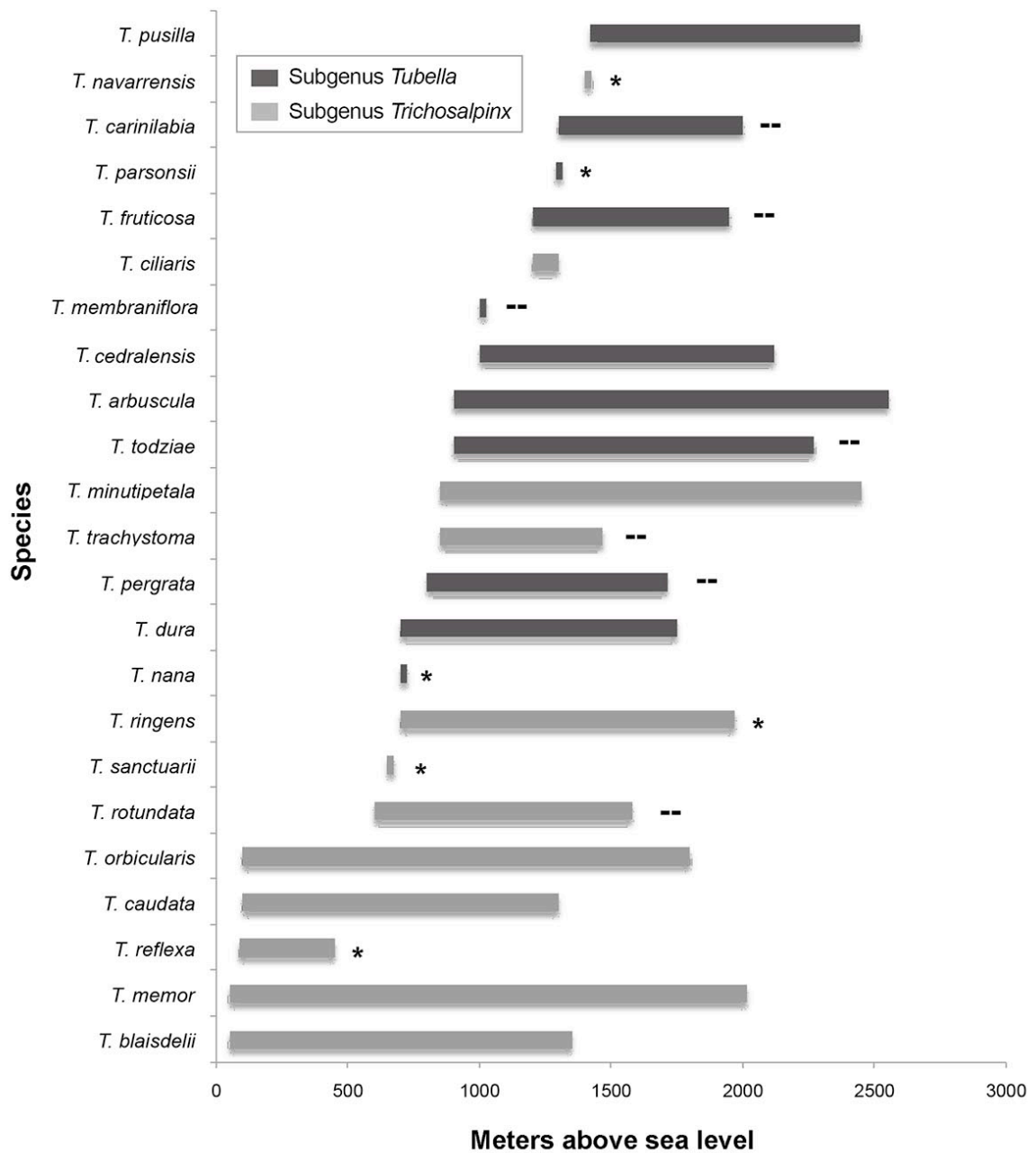


Figure 2. Elevational range of *Trichosalpinx* species in Costa Rica, based on herbarium records annotated in this treatment. \* indicates species endemic to Costa Rica. -- indicates regional endemisms.

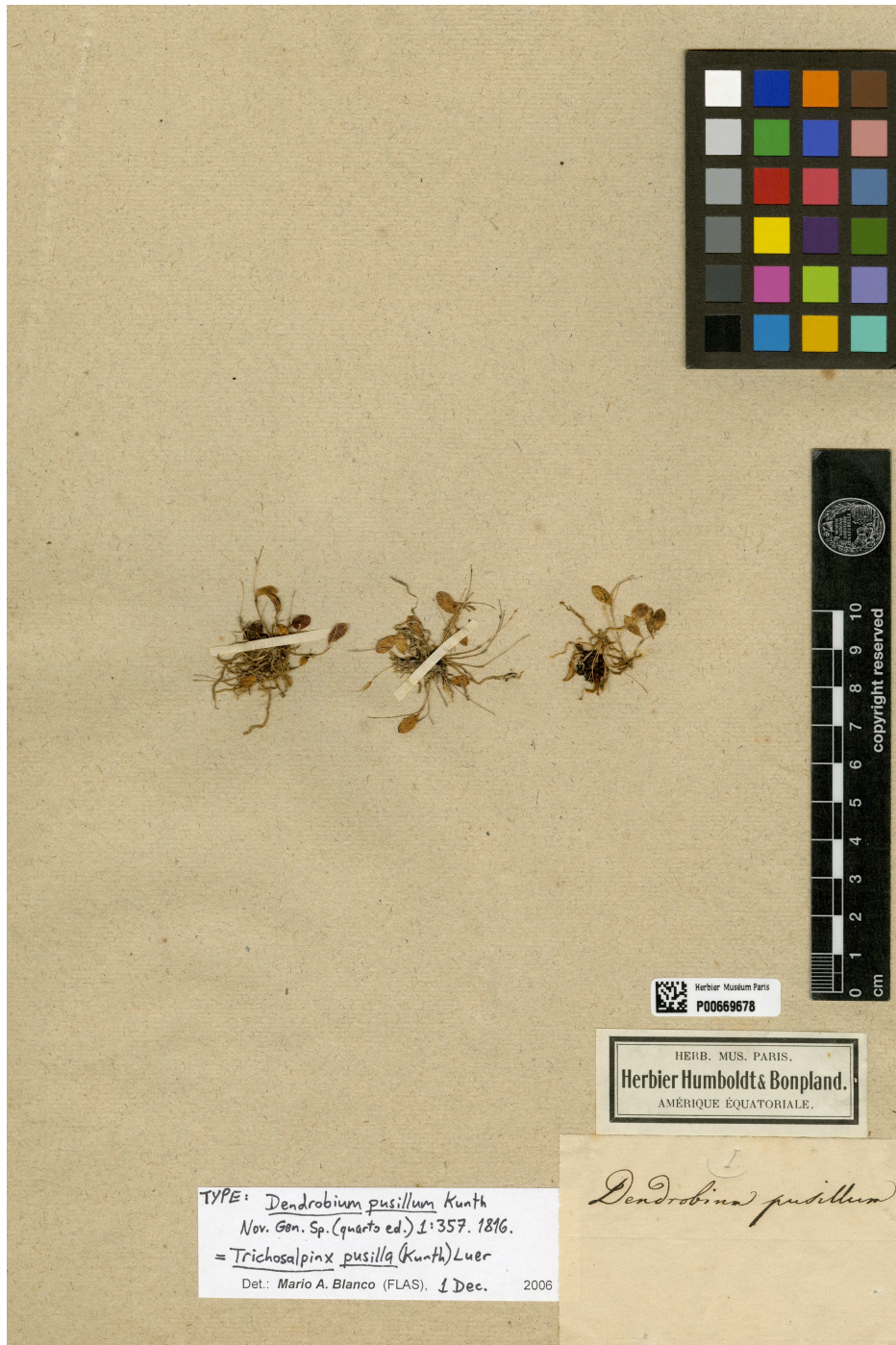


Figure 3. Holotype specimen of *Trichosalpinx pusilla* (Kunth) Luer (*Humboldt & Bonpland* s.n.; P-00669678). Credits to the Paris, Muséum National d'Histoire Naturelle, SM.



Figure 4. Holotype specimen and drawing of *Trichosalpinx ciliaris* (Lindl.) Luer (Loddiges s.n., K-000079852). Reproduced with the kind permission of the Board of Trustees, Royal Botanical Gardens, Kew.

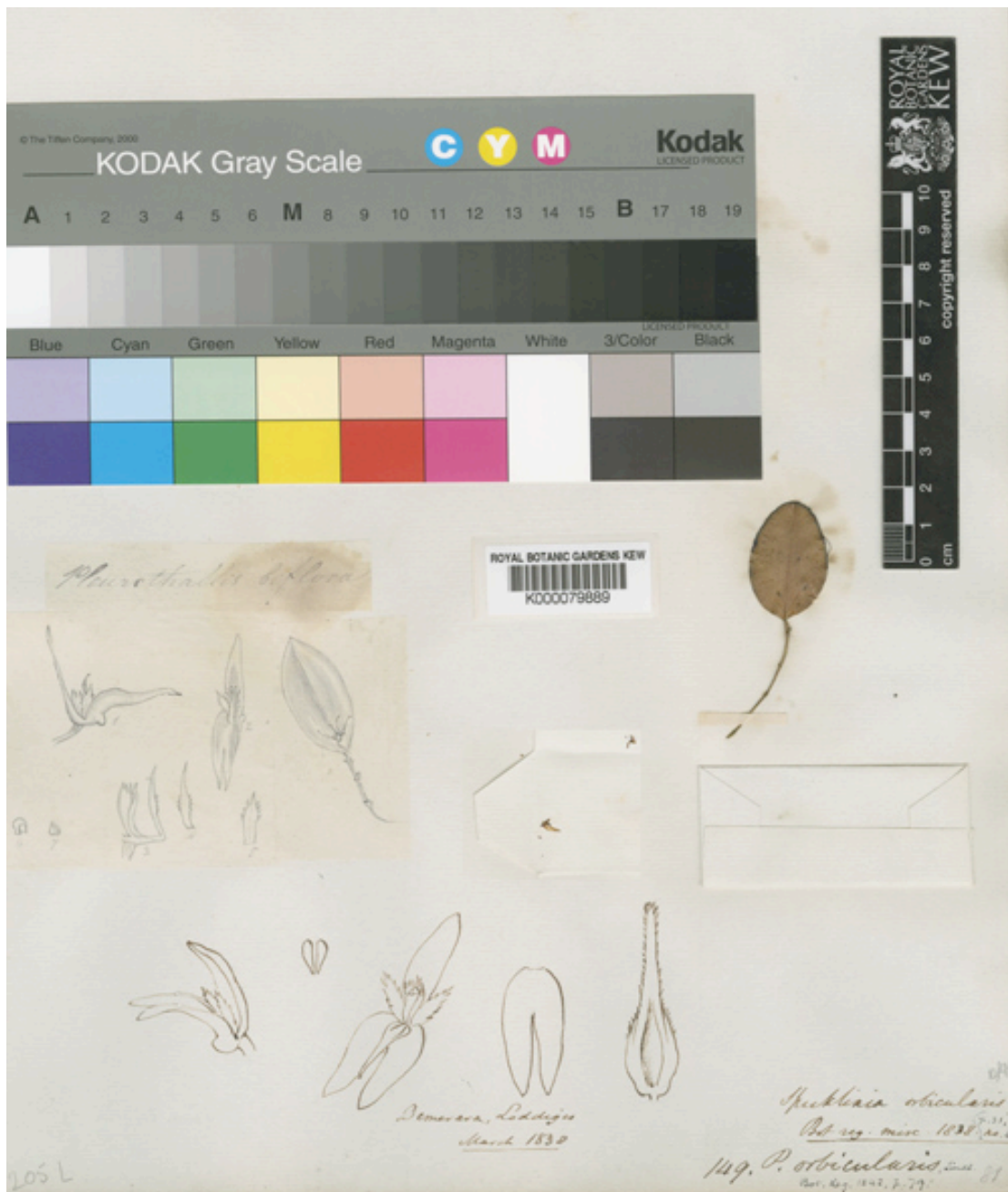


Figure 5. Holotype specimen and drawing of *Trichosalpinx orbicularis* (Lindl.) Luer (Loddiges s.n.; K-000079889). Reproduced with the kind permission of the Board of Trustees, Royal Botanical Gardens, Kew.



Figure 6. Holotype specimen of *Trichosalpinx memor* (Rchb.f.) Luer (*H. Forkel s.n.*; W-0053202). Reproduced with the kind permission of the Natural History Museum of Vienna.



Figure 7. Holotype specimen of *Trichosalpinx blaisdellii* (S. Watson) Luer (*Watson s.n.*; material framed) mounted in the same sheet (AMES-72460) as *Watson s.n.* (not a type, The Harvard University Herbaria code 00074089). Reproduced with the kind permission of the Harvard University Herbaria.



Figure 8. Holotype specimen and drawing of *Trichosalpinx arbuscula* (Lindl.) Luer (Hartweg s.n.; K-000079691). Reproduced with the kind permission of the Board of Trustees, Royal Botanical Gardens, Kew.



Figure 9. Holotype specimen and drawing of *Trichosalpinx dura* (Lindl.) Luer (Jameson s.n.; K-000079890). Reproduced with the kind permission of the Board of Trustees, Royal Botanical Gardens, Kew.

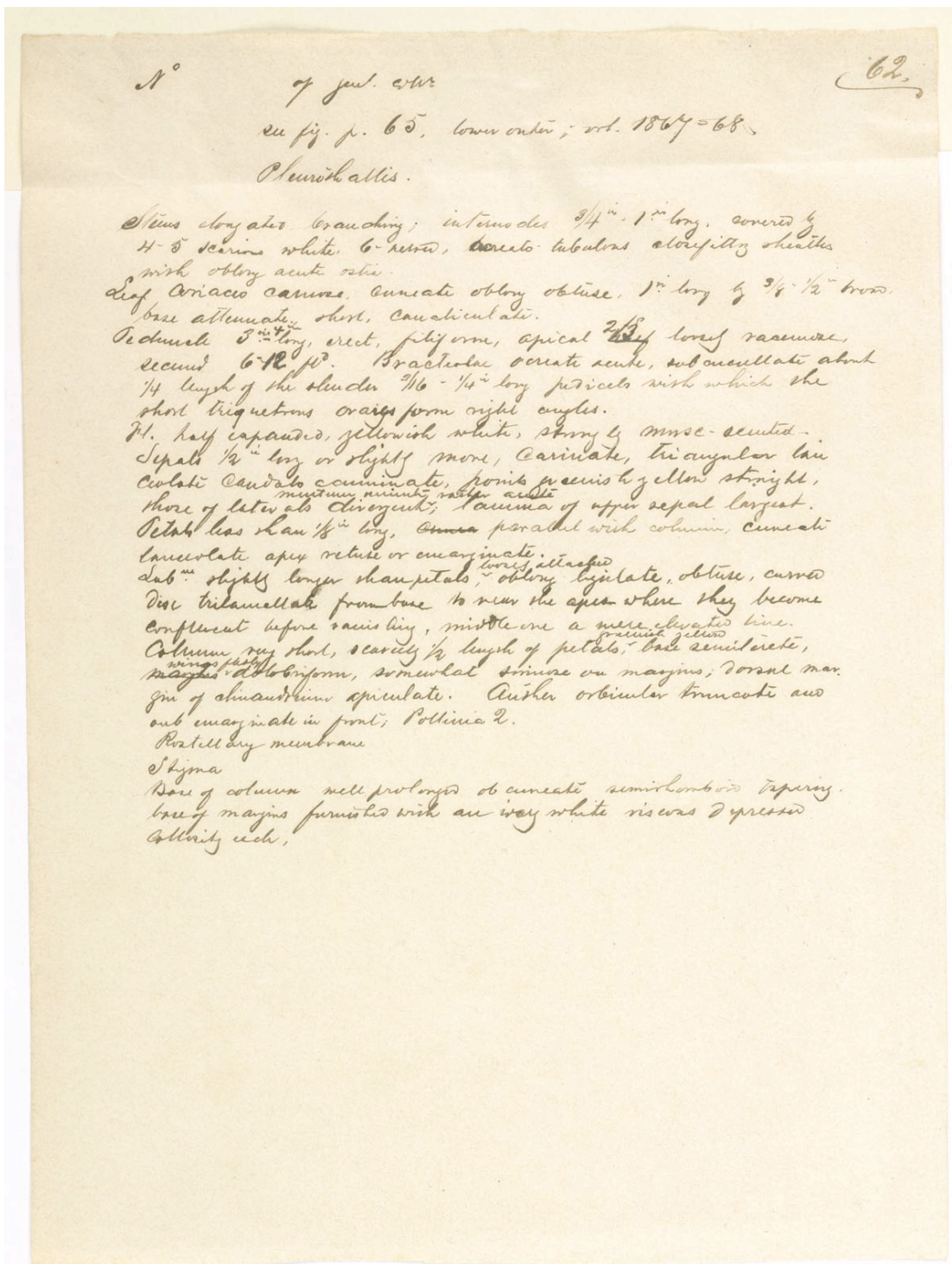


Figure 10. Description of *Pleurothallis moschata* Rchb.f. by Auguste R. Endrés (W-Rchb.f.-0020891). Reproduced with the kind permission of the Natural History Museum of Vienna.



Figure 11. Holotype specimen of *Pleurothallis moschata* Rchb.f., including color drawing by Reichenbach (Endres s.n.; W-Rchb.f.-0020892). Reproduced with the kind permission of the Natural History Museum of Vienna.



Figure 12. Drawing of *Pleurothallis moschata* Rchb.f. [= *Trichosalpinx arbuscula* (Lindl.) Luer] by Auguste R. Endrés (not a type drawing; W-Rchb.f.-0020889). Reproduced with the kind permission of the Natural History Museum of Vienna.

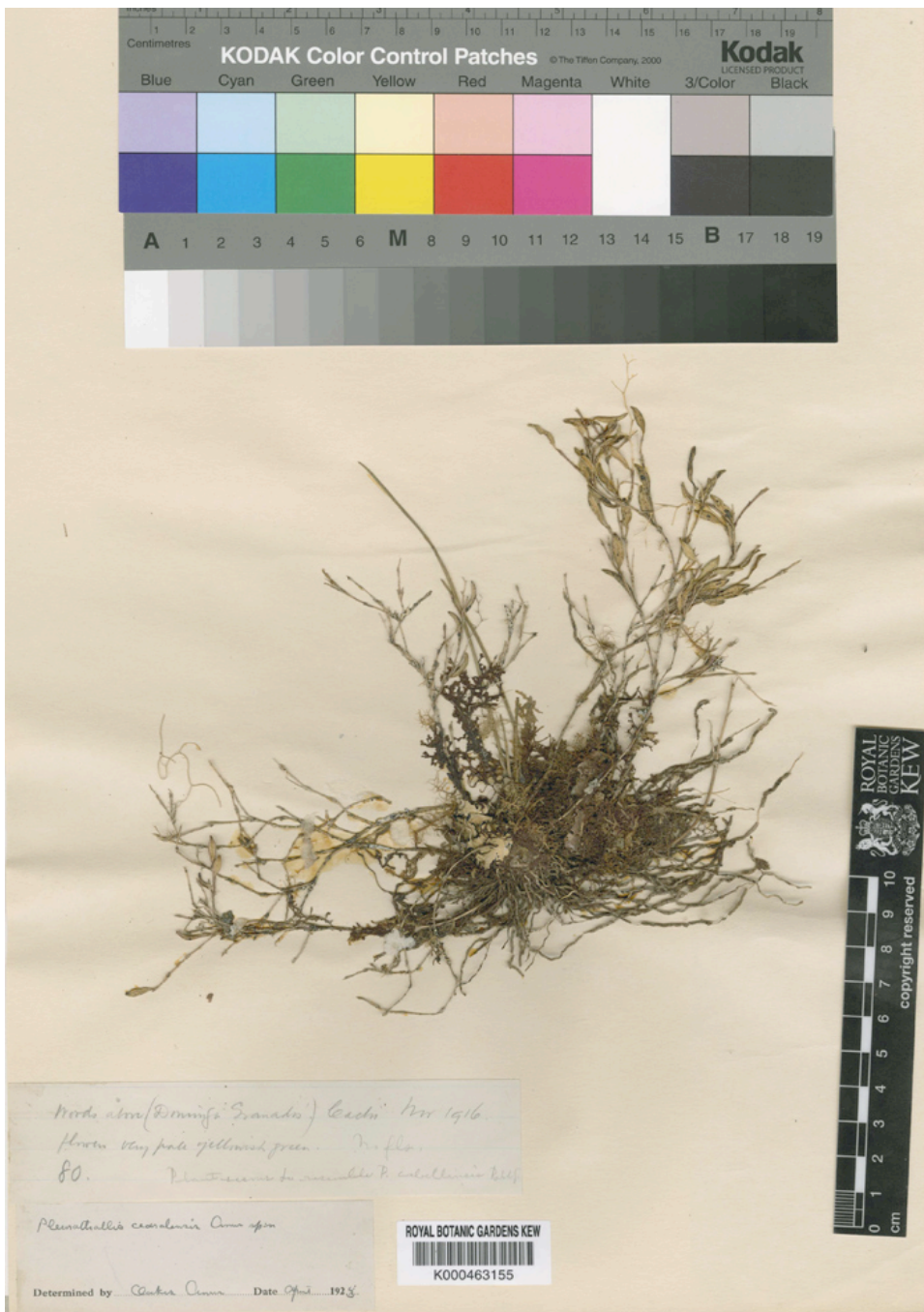


Figure 13. Holotype specimen of *Trichosalpinx cedralensis* (Ames) Luer (*Lankester 352*; K-000463155). Reproduced with the kind permission of the Board of Trustees, Royal Botanical Gardens, Kew.

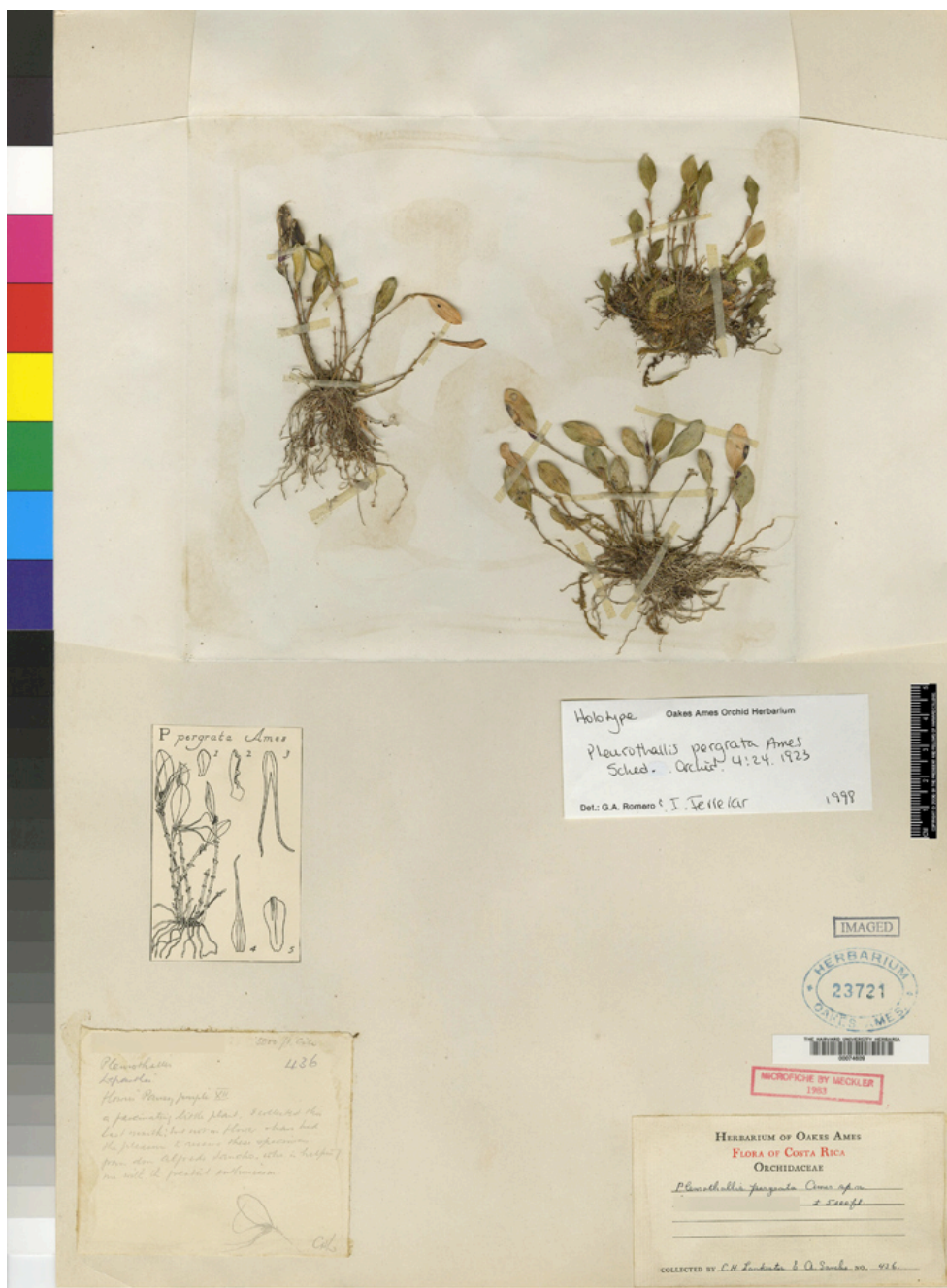


Figure 14. Holotype specimen and drawing of *Trichosalpinx pergrata* (Ames) Luer (Lankester & Sancho 436; AMES-23721). Reproduced with the kind permission of the Harvard University Herbaria.

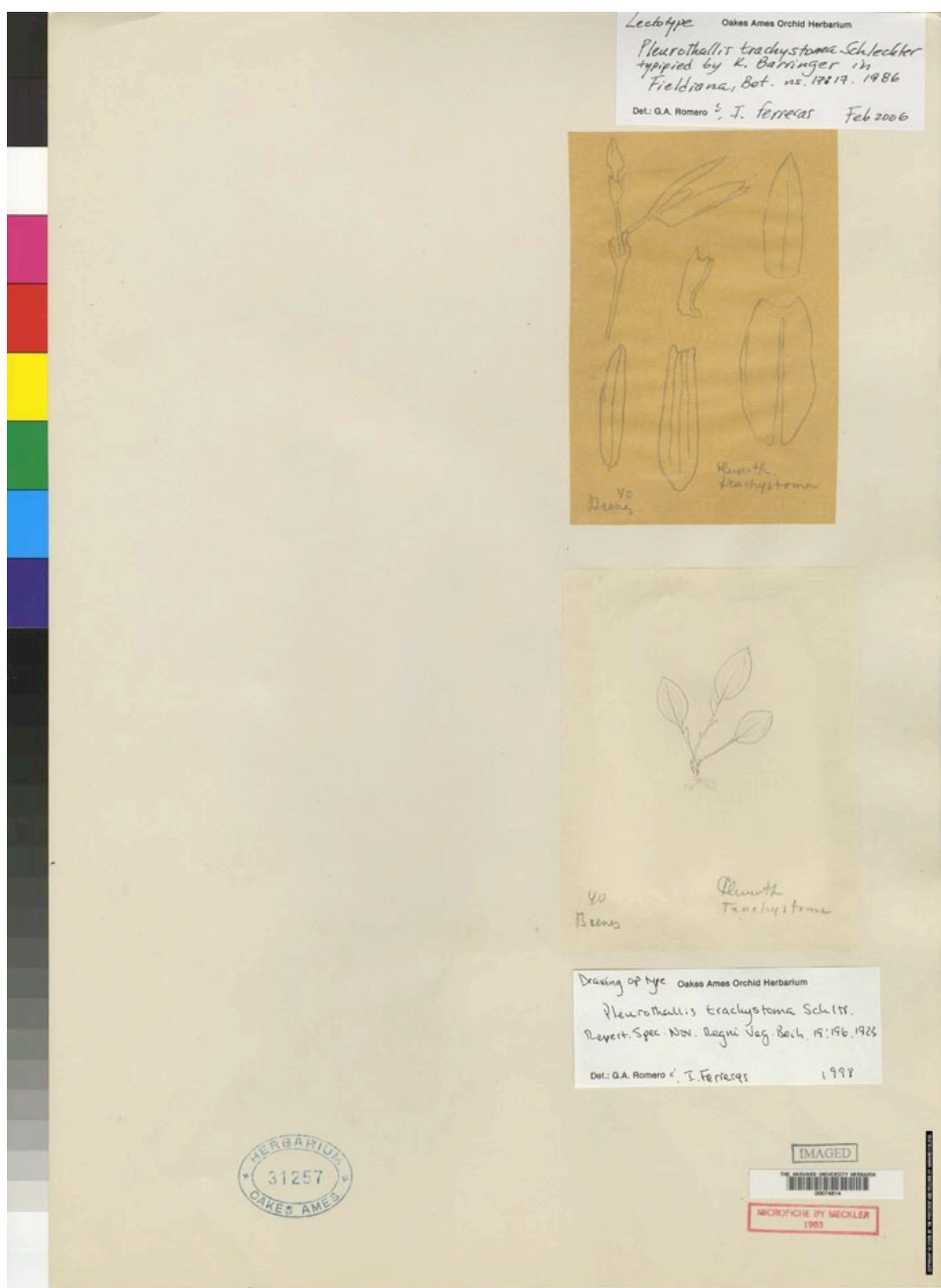


Figure 15. Lectotype specimen of *Trichosalpinx trachystoma* (Schltr.) Luer (*Brenes* 40; AMES-31257). Reproduced with the kind permission of the Harvard University Herbaria.

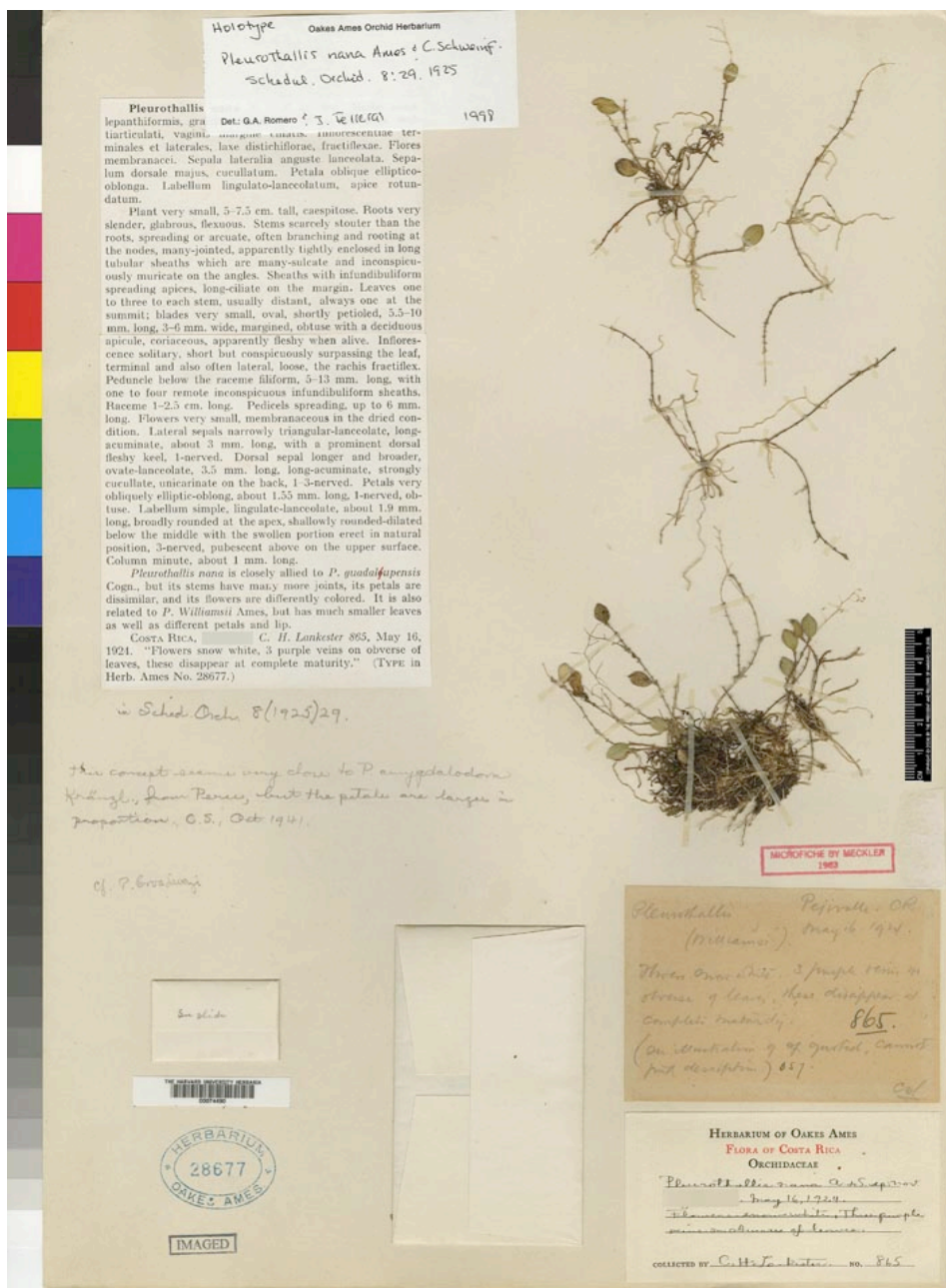


Figure 16. Holotype specimen of *Trichosalpinx nana* (Ames & C.Schweinf.) Luer (Lankester 865; AMES-28677). Reproduced with the kind permission of the Harvard University Herbaria.

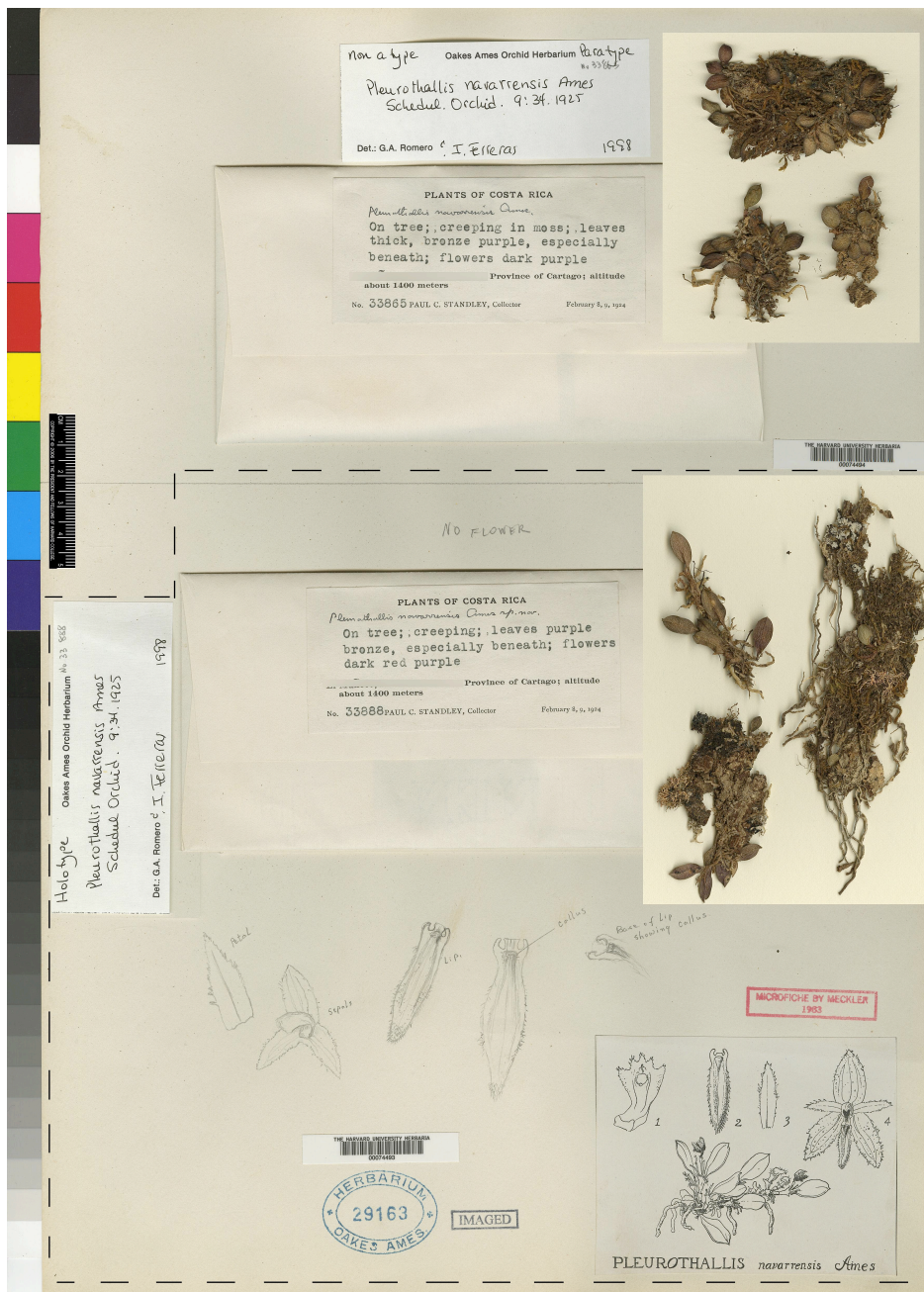


Figure 17. Holotype specimen and drawing of *Trichosalpinx navarrensisi* (Ames) Luer (Standley 33888; corresponding material framed) mounted in the same sheet (AMES-29163) as the paratype specimen of *T. navarrensisi* (Standley 33865). Reproduced with the kind permission of the Harvard University Herbaria.

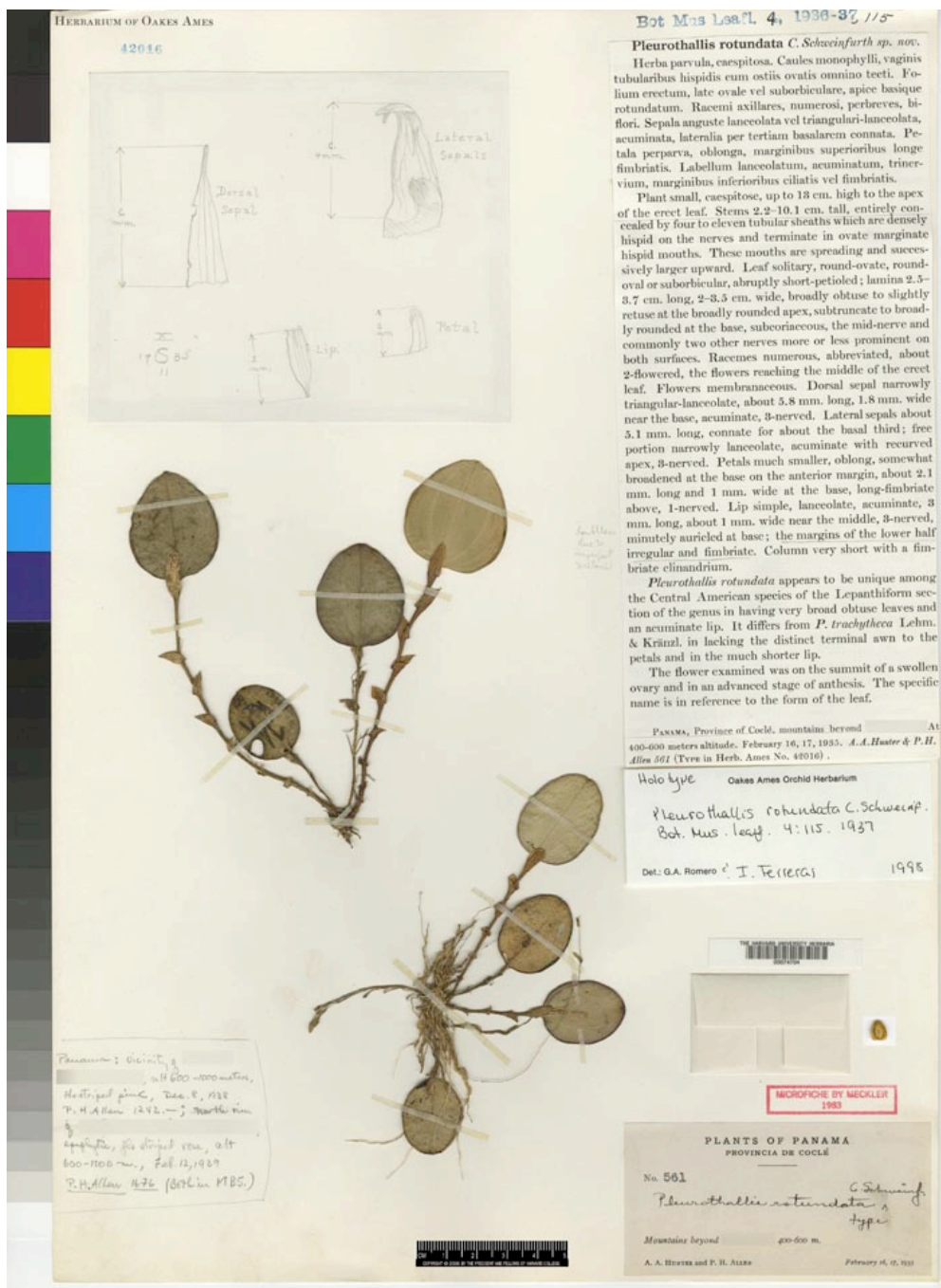


Figure 18. Holotype specimen of *Trichosalpinx rotundata* (C.Schweinf.) Luer (*Hunter & Allen 561 D*; AMES-42016). Reproduced with the kind permission of the Harvard University Herbaria.

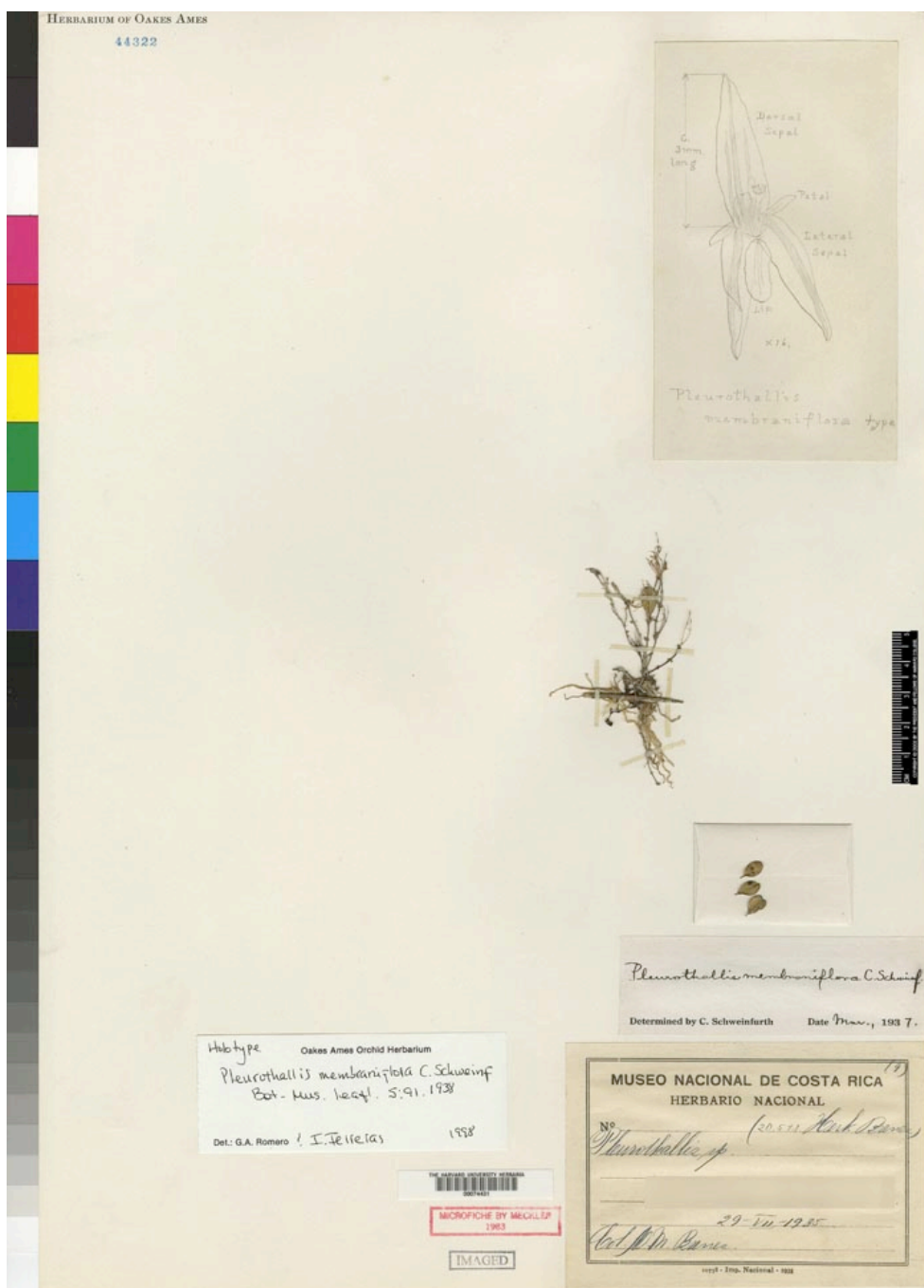


Figure 19. Holotype specimen and drawing of *Trichosalpinx membraniflora* (Ames Luer (Brenes 20.571; AMES-44322). Reproduced with the kind permission of the Harvard University Herbaria.

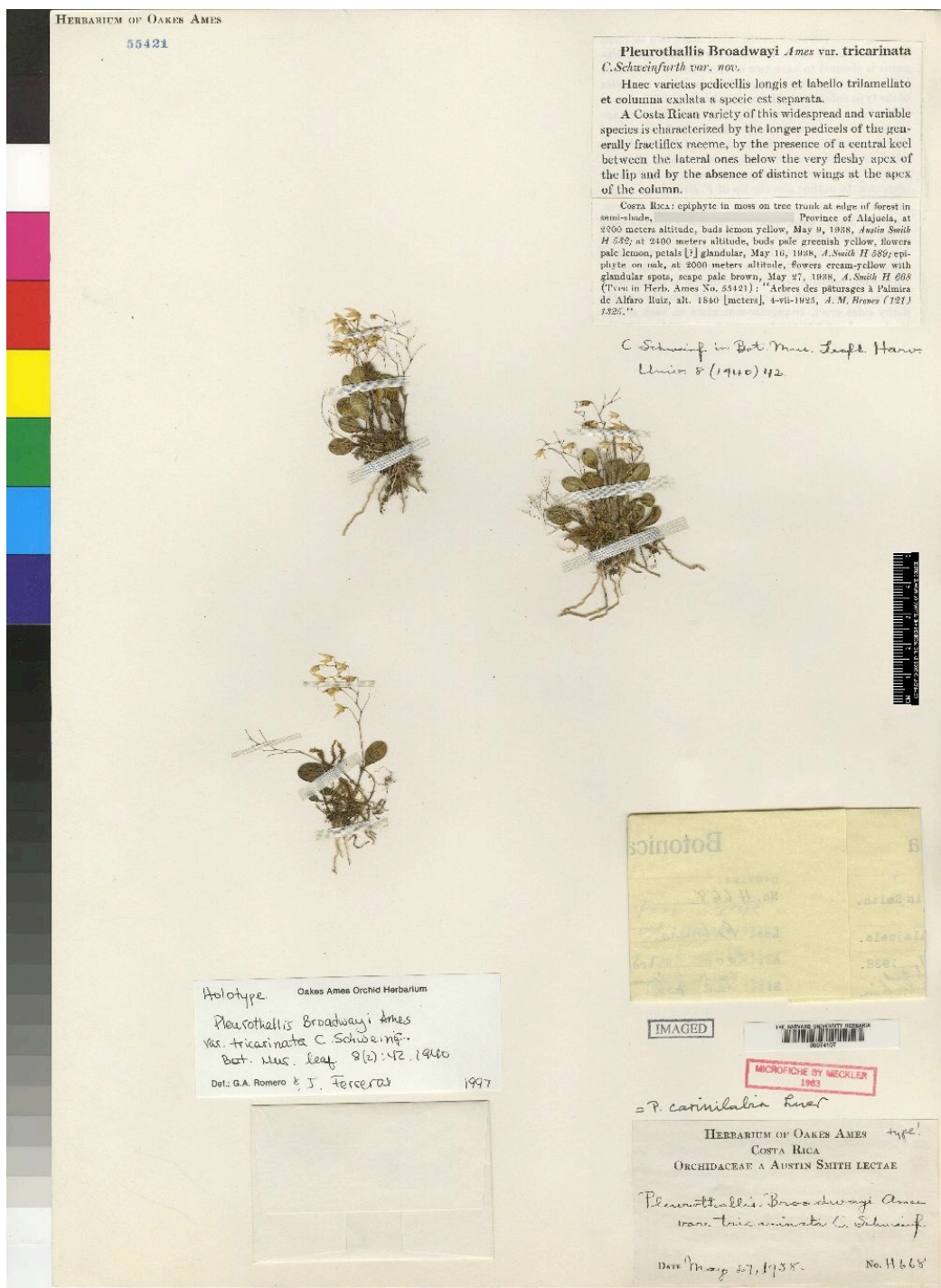


Figure 20. Holotype specimen of *Trichosalpinx carinilabia* (Luer) Luer (*Smith H 668*; AMES-55421). Reproduced with the kind permission of the Harvard University Herbaria.



Figure 21. Holotype specimen and drawing of *Trichosalpinx fruticosa* Luer (Luer 12135; MO-5122981). Reproduced with the kind permission of the Missouri Botanical Garden Herbarium.



Figure 22. Holotype specimen and drawing of *Trichosalpinx lankesteriana* Luer (Luer 17411; MO-5123145). Reproduced with the kind permission of the Missouri Botanical Garden Herbarium.



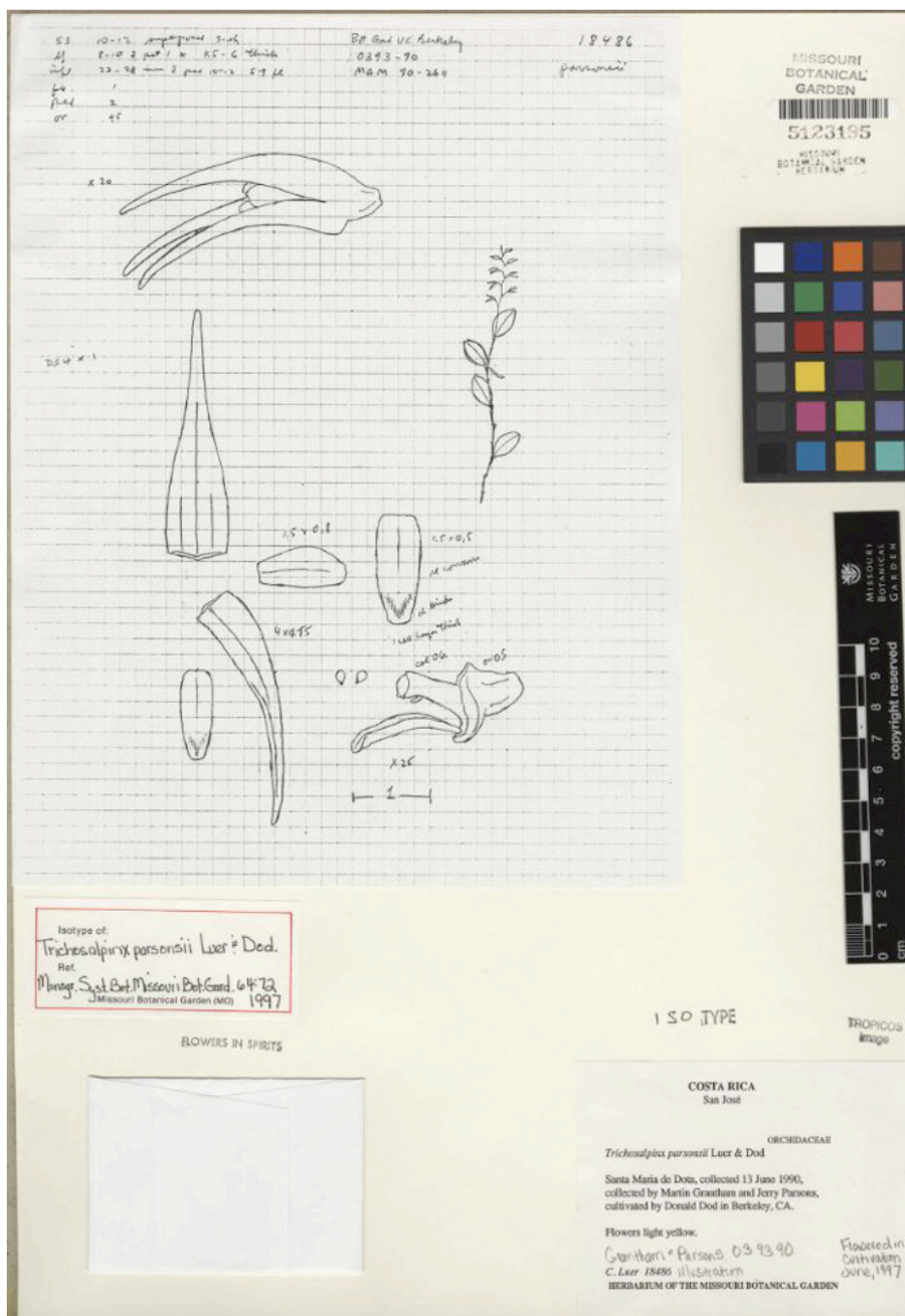


Figure 24. Isotype specimen of *Trichosalpinx parsonsii* Luer & Dod (*Grantham & Parsons* 03 93 90; MO-5123195). Reproduced with the kind permission of the Missouri Botanical Garden Herbarium.



Figure 25. Holotype specimen of *Trichosalpinx todziae* Luer (*Todzia* 344; CR-66495).

Reproduced with the kind permission of the Herbario Nacional de Costa Rica.



Figure 26. Root morphology in Costa Rican *Trichosalpinx*. A - *T. nana*; B - *T. cedralensis*; C - *T. blaisdellii*; D - *T. minutipetala*. A–B: Subgenus *Tubella*. C–D: Subgenus *Trichosalpinx*. White arrow points aerial root development. Scale bar = 2 cm.



Figure 27. Sheath and leaf morphology in Costa Rican *Trichosalpinx*. A. *T. blaisdellii*; B. *T. reflexa*; C. *T. memor*; D. *T. rotundata*; E. *T. arbuscula*; F. *T. dura*; G. *T. pergrata*; H. *T. cedralensis*. A–D Subgenus *Trichosalpinx*. E–H Subgenus *Tubella*. Prolific ramicauls are shown in E, F and H; in H, two proliferations were produced at the apex of the proximal ramicaul. Scale bar = 3 cm.

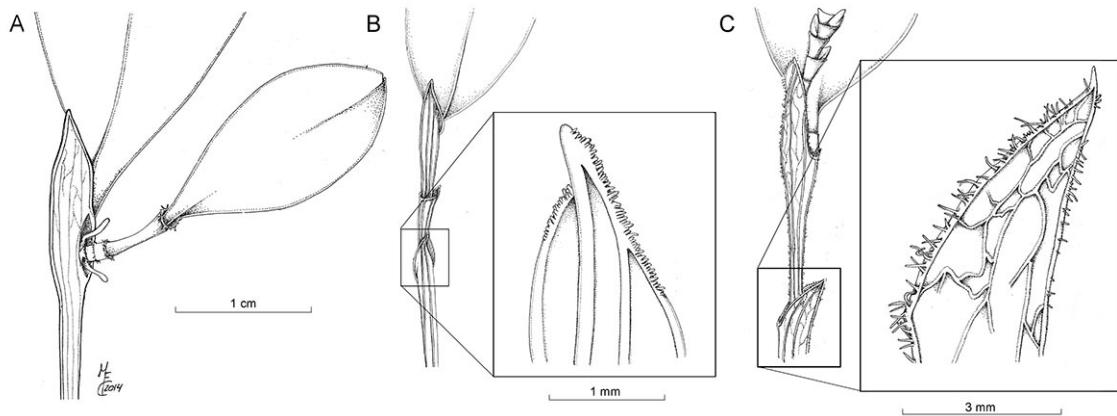


Figure 28. Details of sheath morphology in Costa Rican *Trichosalpinx*. A – Proliferation in *Trichosalpinx memor*. Note perforation of the distalmost sheath for emergence of new tissues. A–B Detail of the sheath morphology in B – subgenus *Tubella* and C – subgenus *Trichosalpinx*. Note vernal patterns and marginal ornamentation of the sheath.

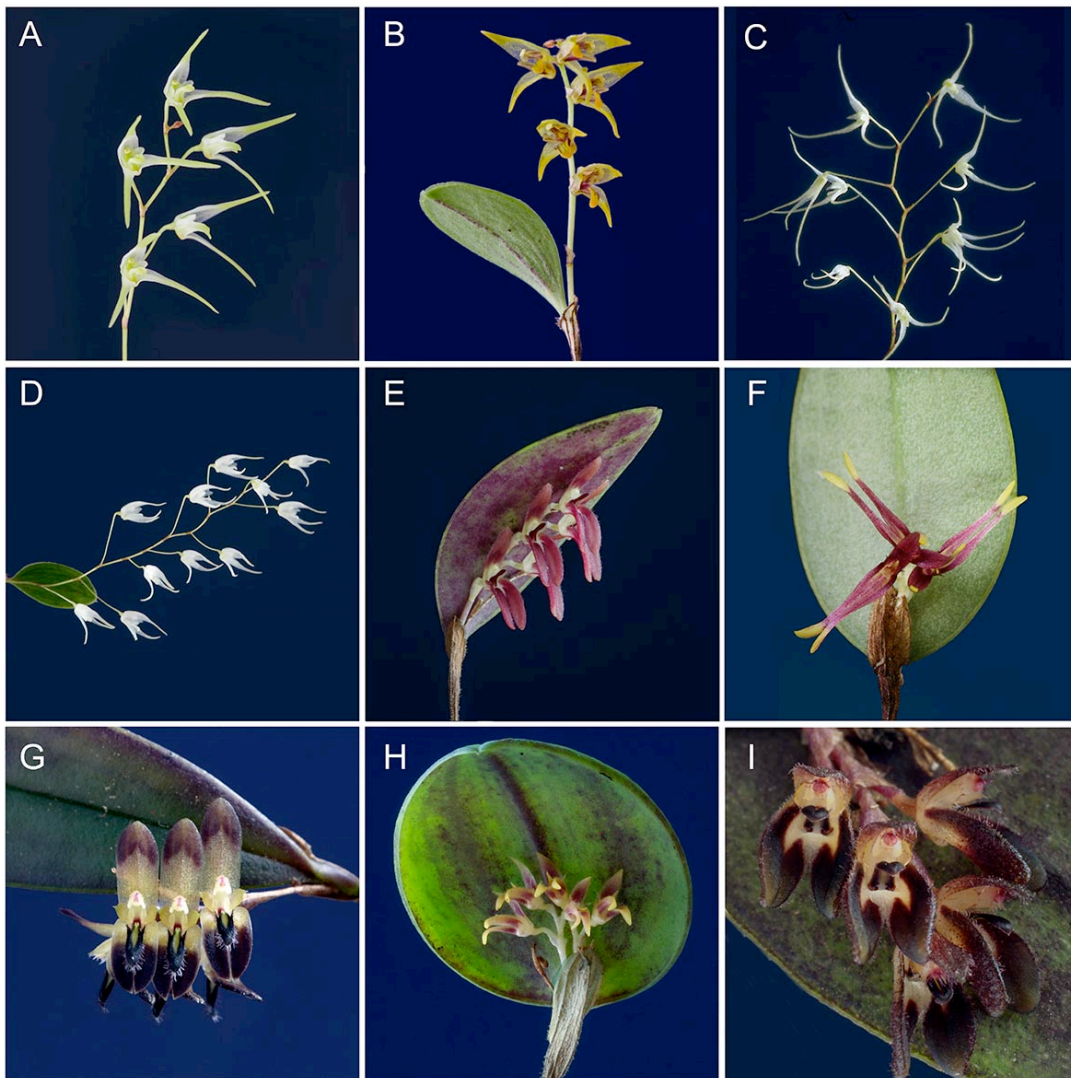


Figure 29. Inflorescence morphology in Costa Rican *Trichosalpinx*. Subgenus *Tubella*: A - *T. arbuscula*; B - *T. dura*; C - *T. fruticosa*; D - *T. todziae*. Subgenus *Trichosalpinx*: E - *T. blaisdellii*; F - *T. caudata*; G - *T. reflexa*; H - *T. rotundata*; I - *T. trachystoma*.

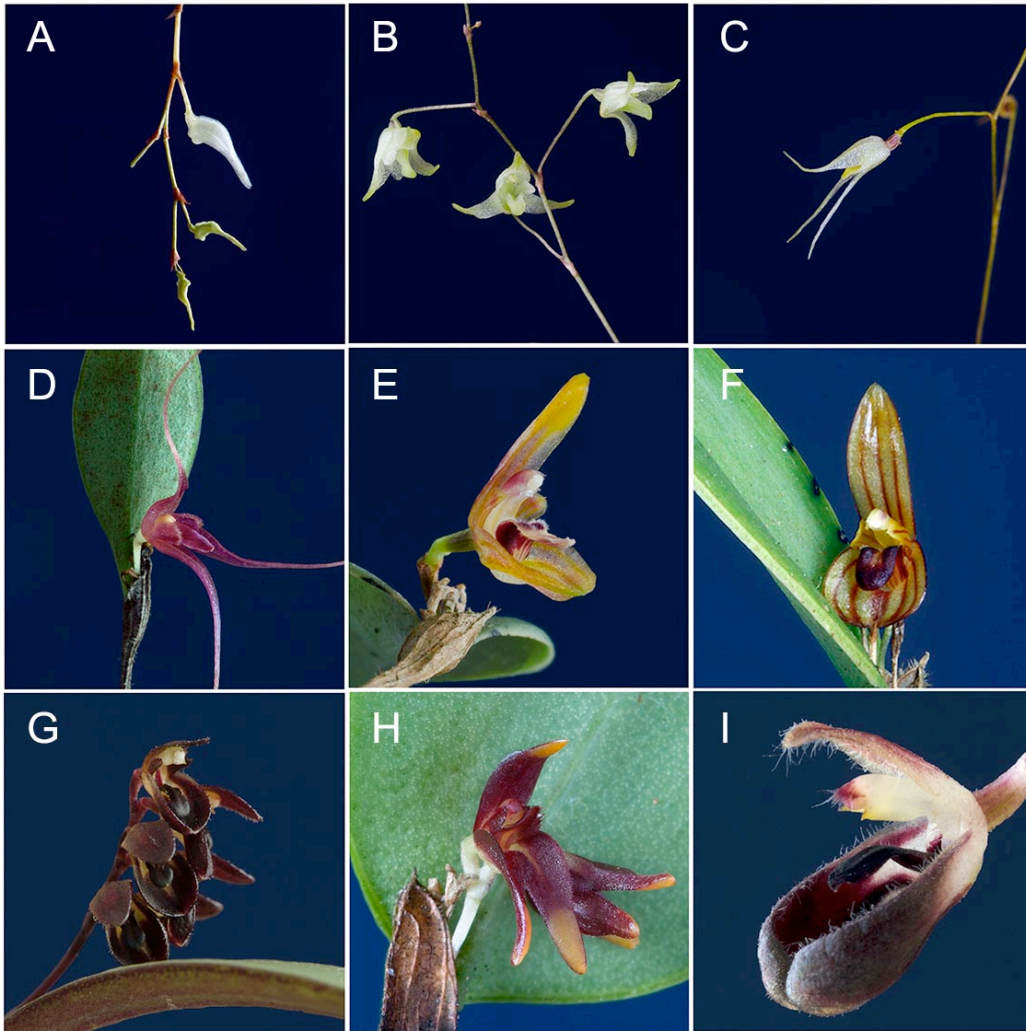


Figure 30. Flower morphology in Costa Rican *Trichosalpinx*. Subgenus *Tubella*: A - *T. parsonsii*; B - *T. carinilabia*; C - *T. pusilla*; D - *T. pergrata*. Subgenus *Trichosalpinx*: E - *T. ringens*; F - *T. sanctuarii*; G - *T. ciliaris*; H - *T. orbicularis*; I - *T. minutipetala*.

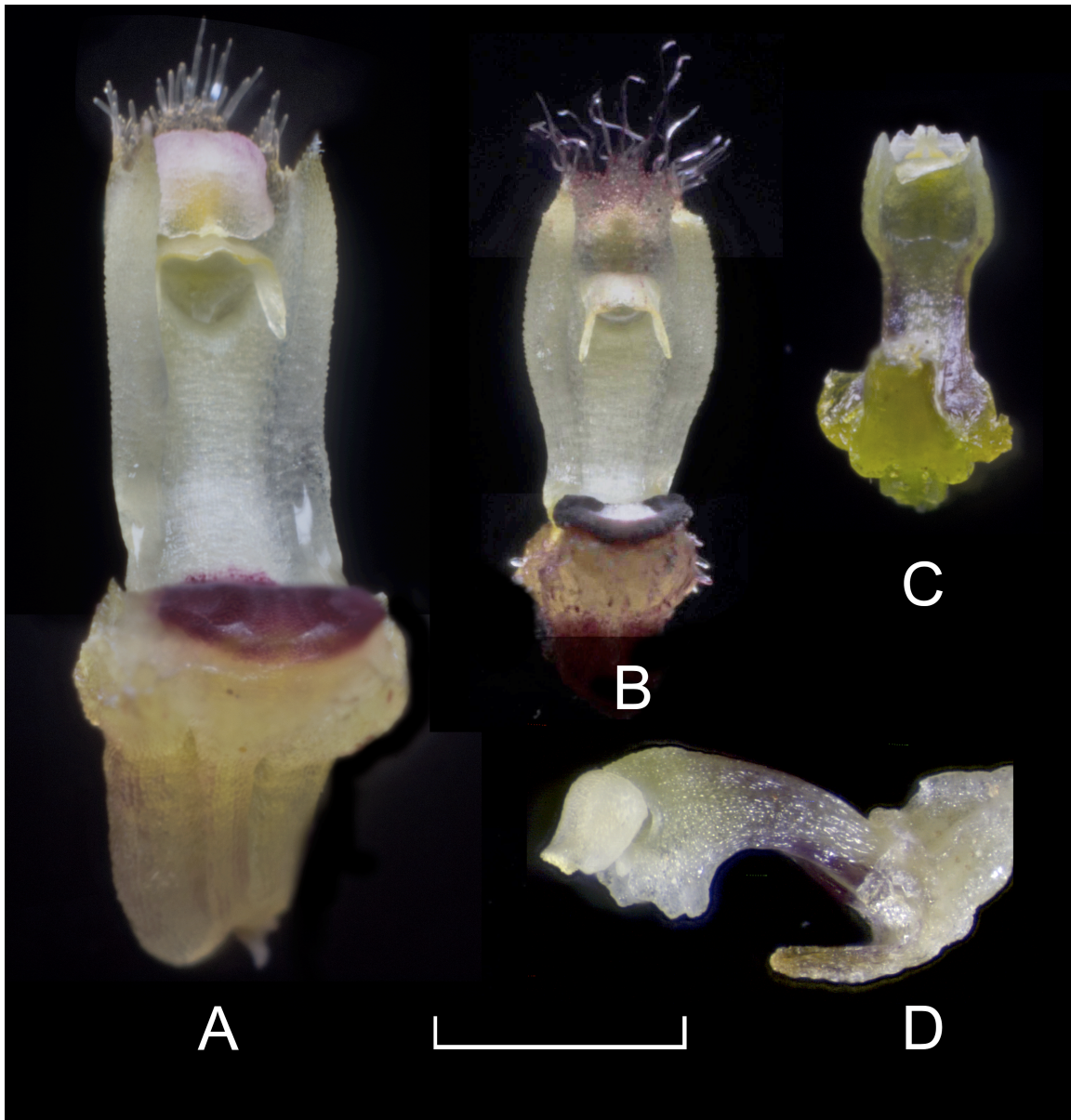


Figure 31. Column morphology in Costa Rican *Trichosalpinx*. Subgenus *Trichosalpinx*: A - *T. blaisdellii*; B - *T. memor*. Subgenus *Tubella*: C - *T. dura*; D - *T. arbuscula*. A–C: ventral view. D: dorsal view. Note the shape and position of the rostellum, and the shape of the column foot. Scale = 1 mm.

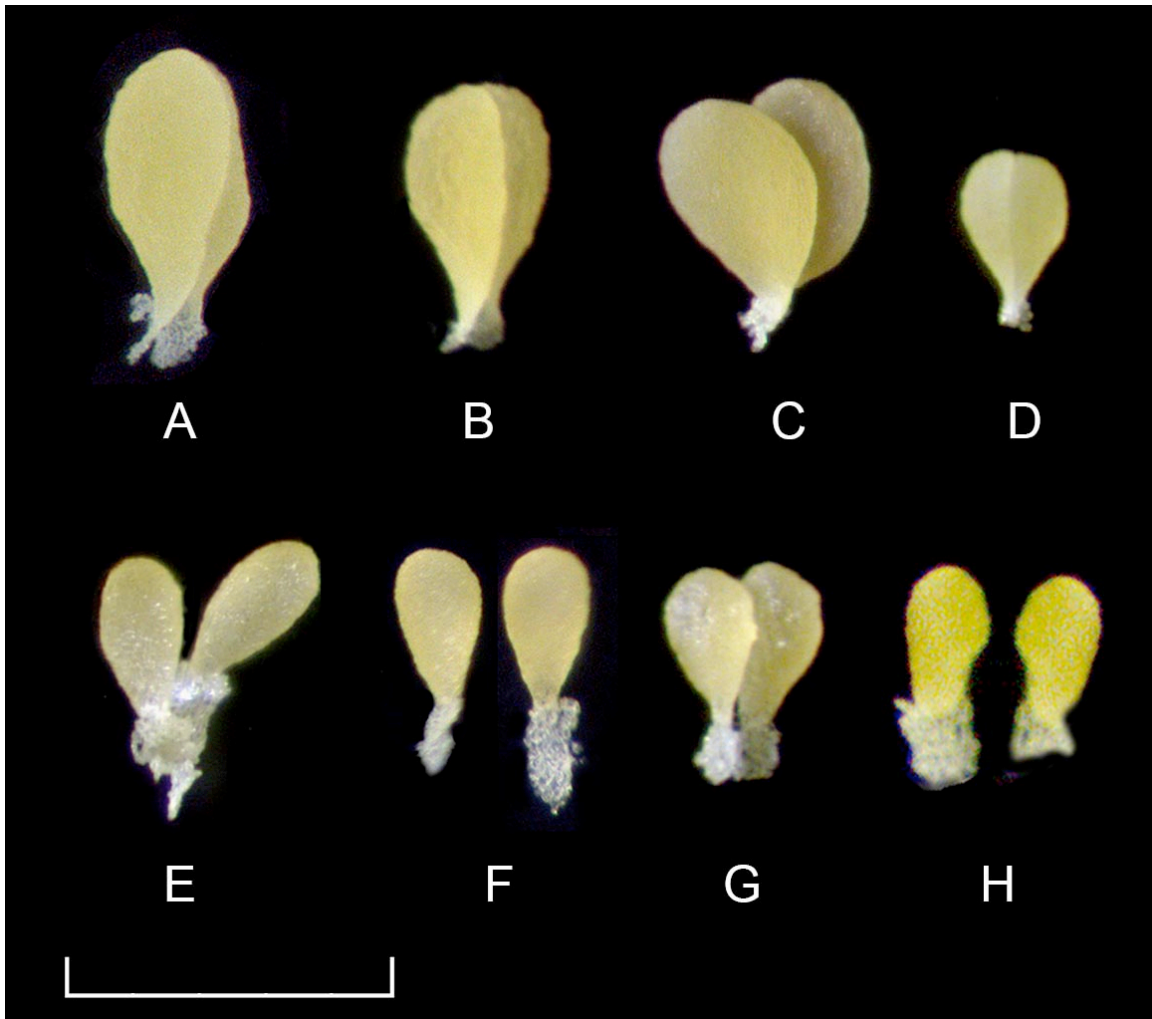


Figure 32. Pollinaria morphology in Costa Rican *Trichosalpinx*. Subgenus *Trichosalpinx*: A–B *T. blaisdellii*; C - *T. minutipetala*; D - *T. memor*. Subgenus *Tubella*: E–F *T. arbuscula*; G - *T. cedralensis*; H - *T. fruticosa*. Scale = 0.5 mm.



Figure 33. Fruit morphology in Costa Rican *Trichosalpinx*. Subgenus *Trichosalpinx*: A - *T. blaisdellii*; B - *T. memor*; C - *T. minutipetala*; D - *T. reflexa*. Subgenus *Tubella*: E–F *T. todziae*; G - *T. dura*. All fruits are shown undehisced. Top row, view from below; bottom row, transverse section. Scale = 1 cm.

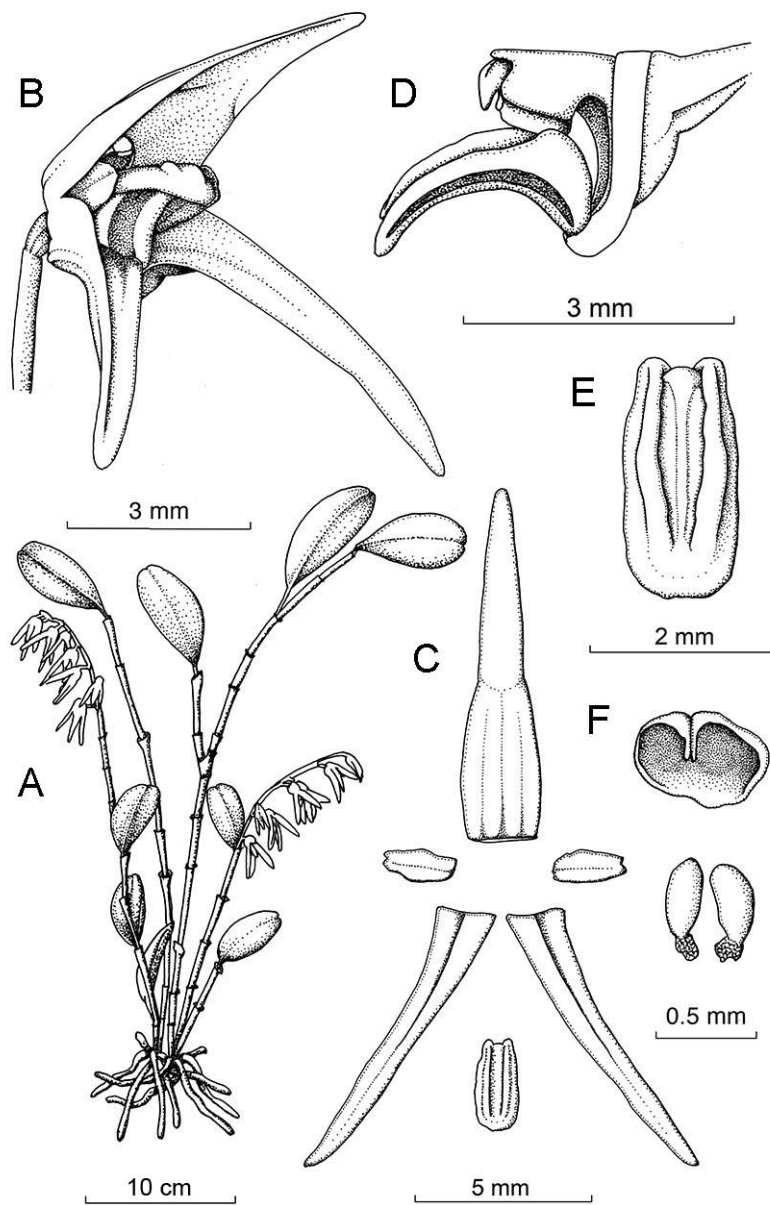


Figure 34. *Trichosalpinx arbuscula*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *F. Pupulin 4331* (JBL-spirit).

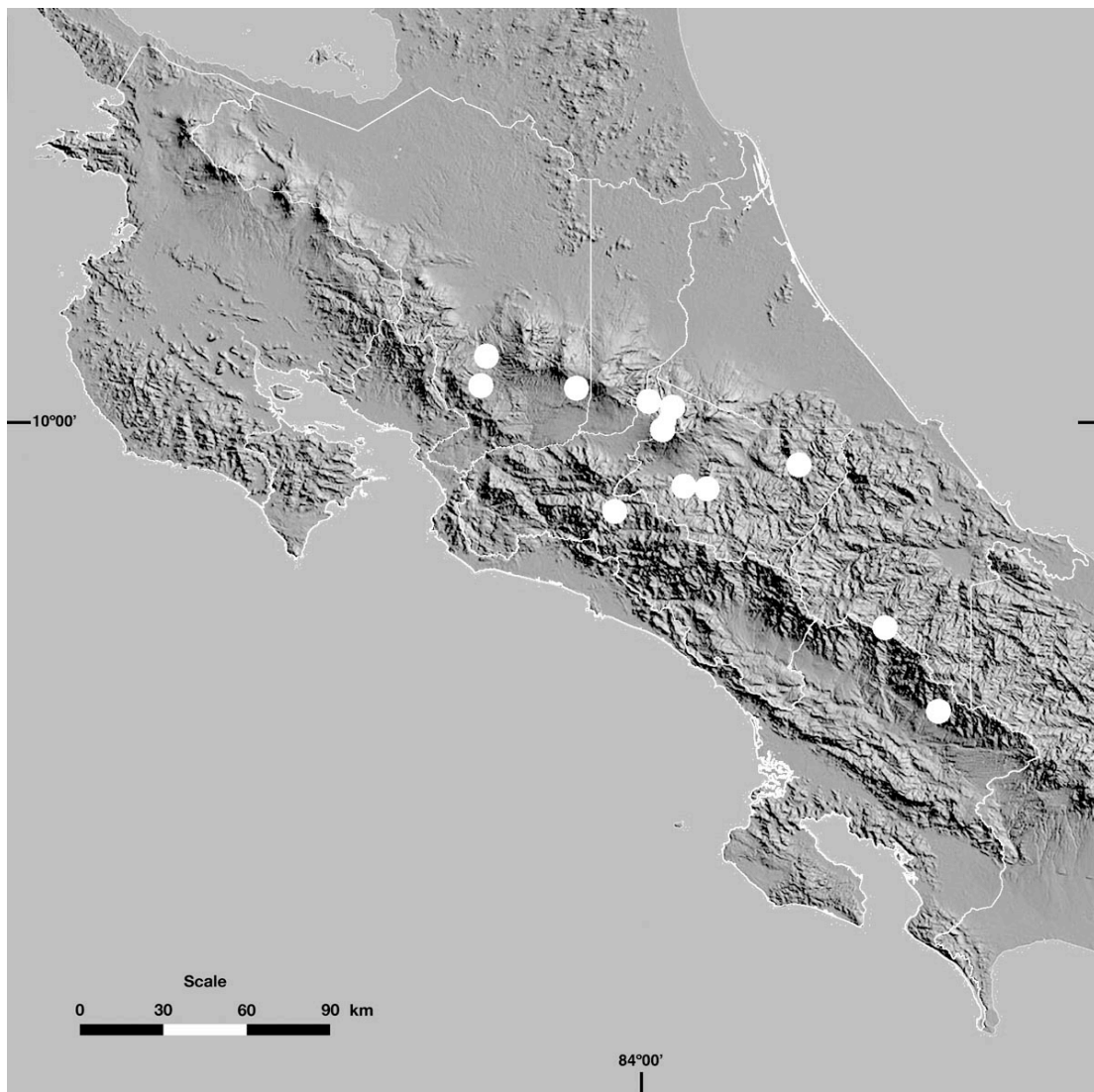


Figure 35. Distribution map of *Trichosalpinx arbuscula* in Costa Rica.

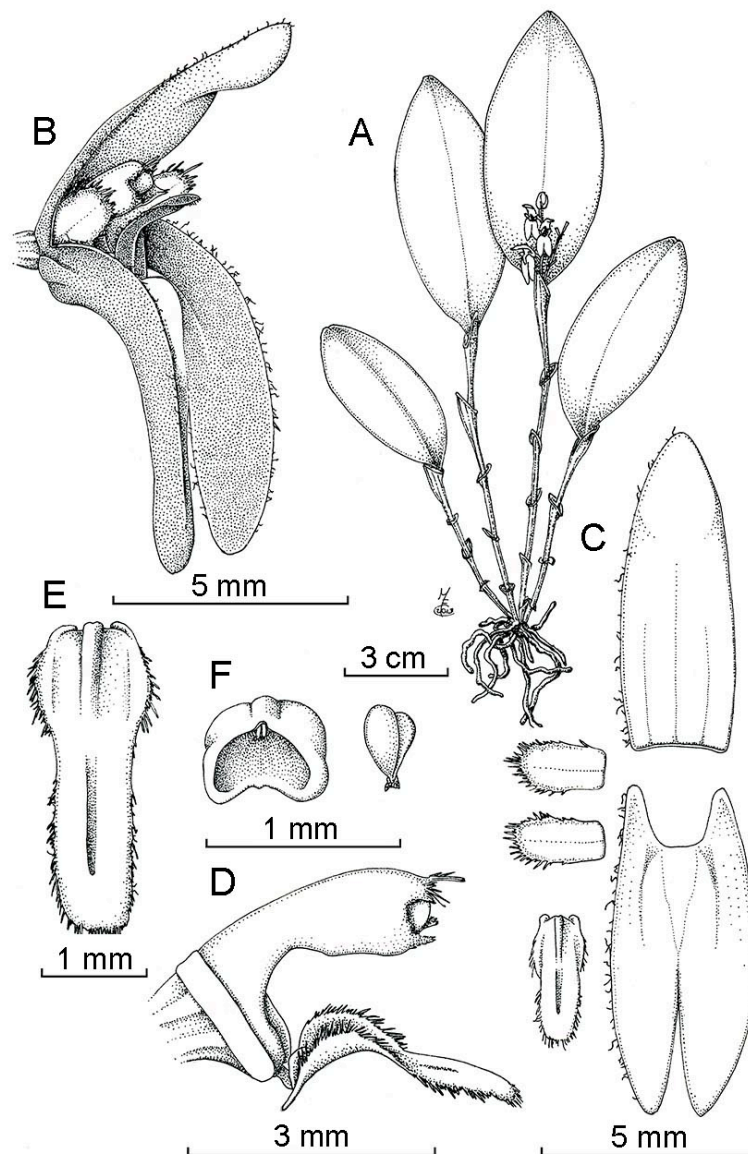


Figure 36. *Trichosalpinx blaisdelli*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *D. Bogarín 5022* (JBL-spirit).

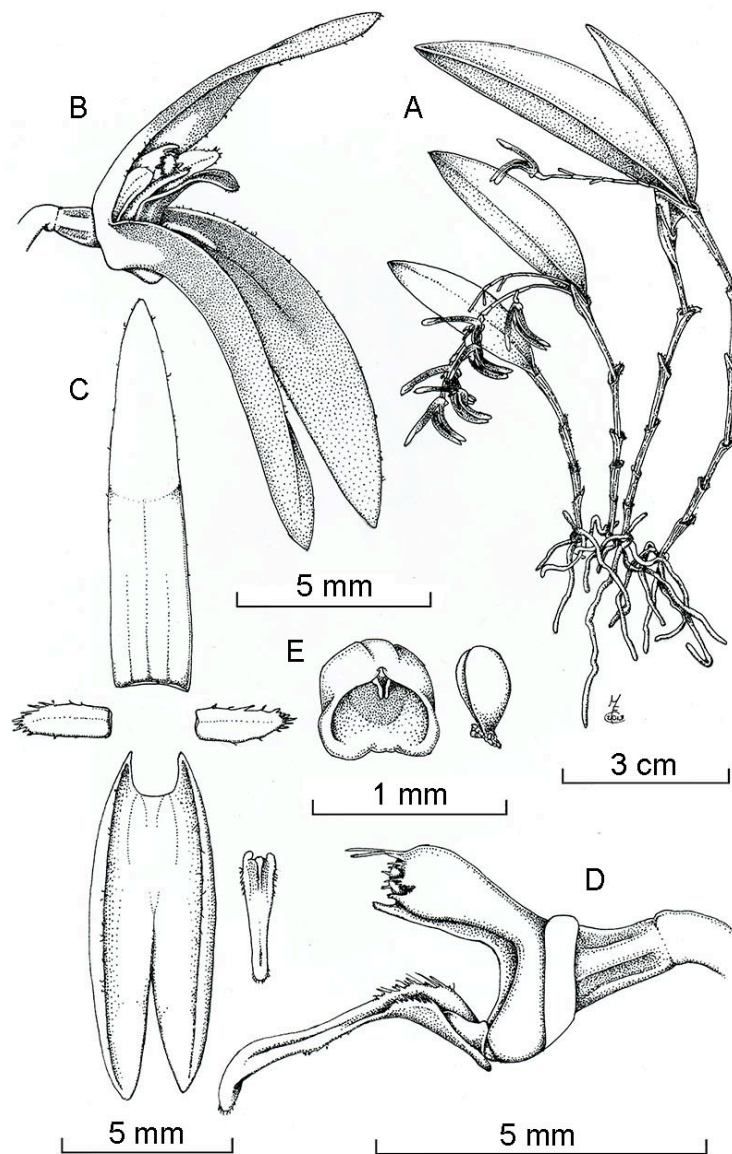


Figure 37. *Trichosalpinx blaisdellii* (form of *T. lankesteriana*). A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from Dressler s.n. [JBL-00404] (JBL-spirit).

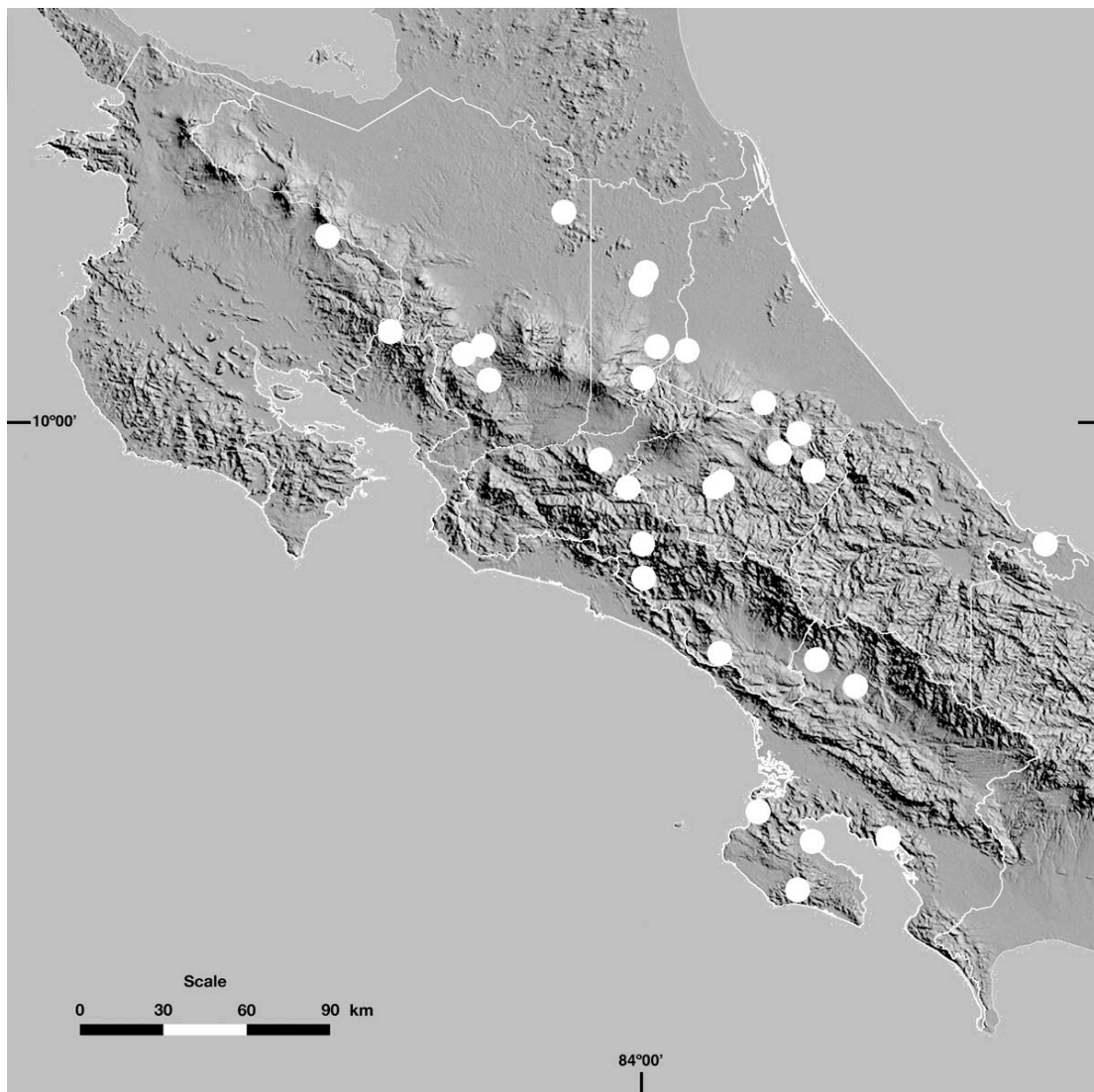


Figure 38. Distribution map of *Trichosalpinx blaisdellii* in Costa Rica.



Figure 39. Morphological variability in flowers of *Trichosalpinx blaisdellii*. A: size, shape and color variability in sepals and petals (Scale = 1 cm). B: Detail of size variations in dorsal sepals of *T. blaisdellii* (Scale = 5 mm).

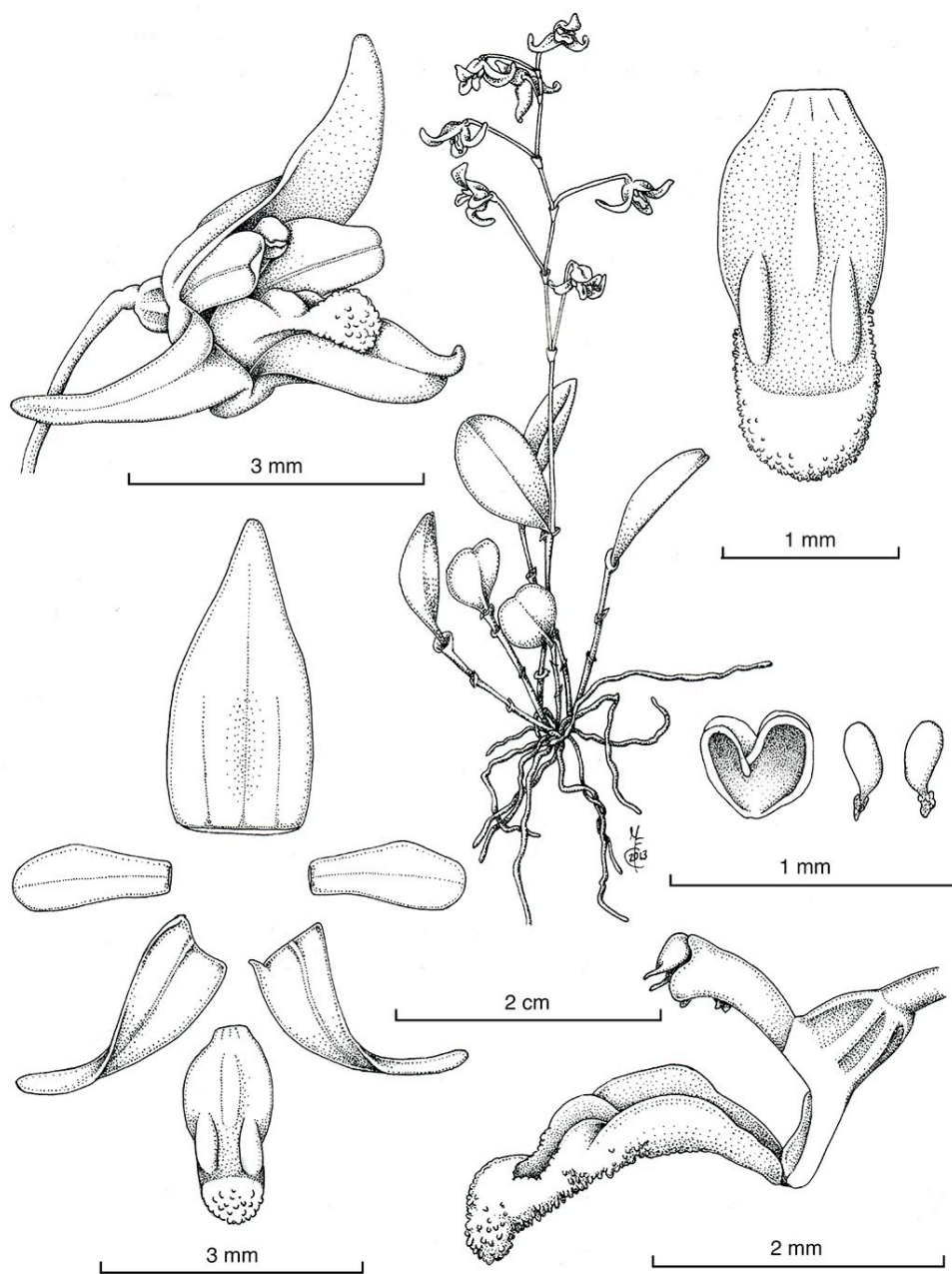


Figure 40. *Trichosalpinx carinilabia*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 631* (JBL-spirit).

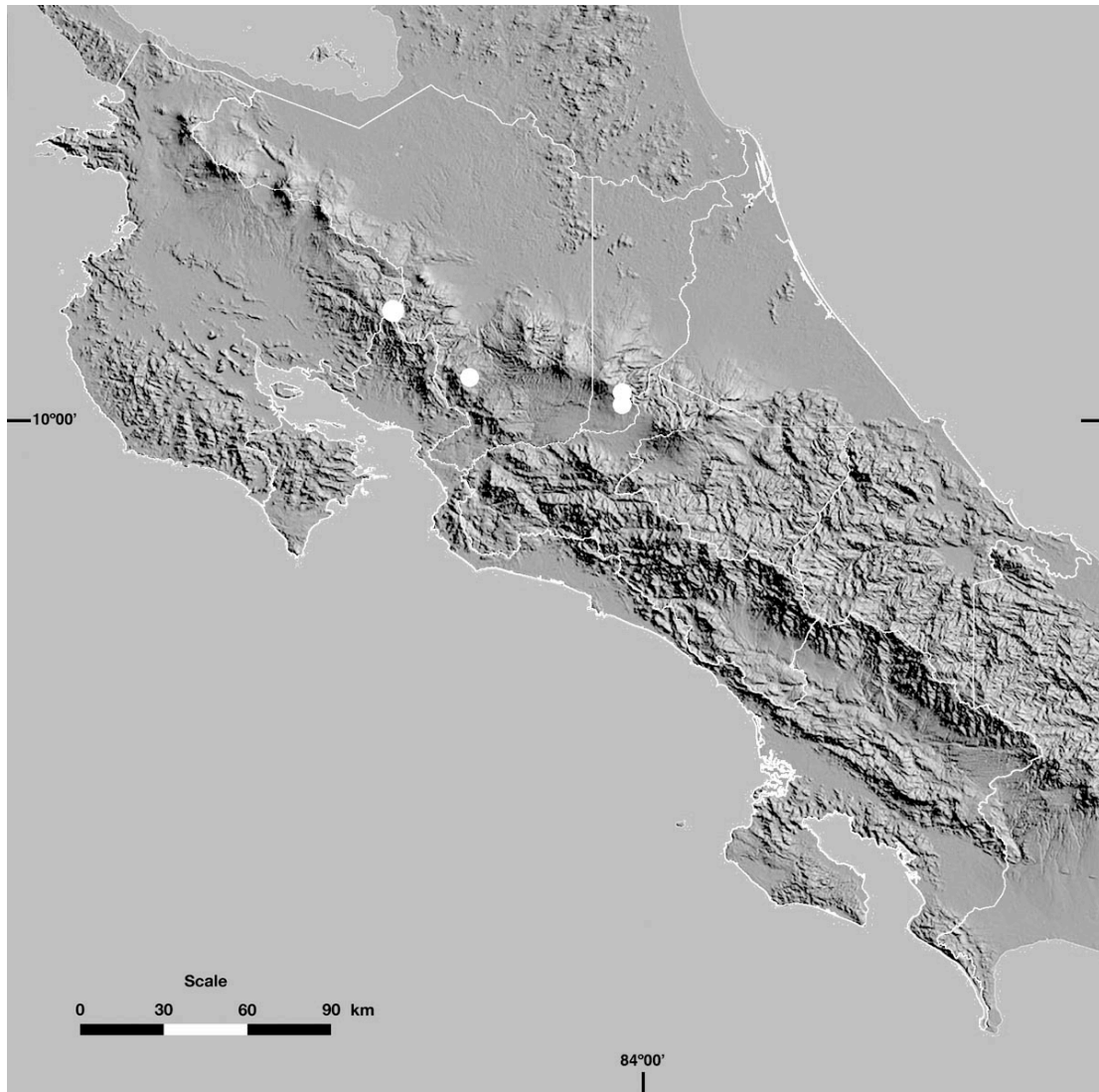


Figure 41. Distribution map of *Trichosalpinx carinilabia* in Costa Rica.

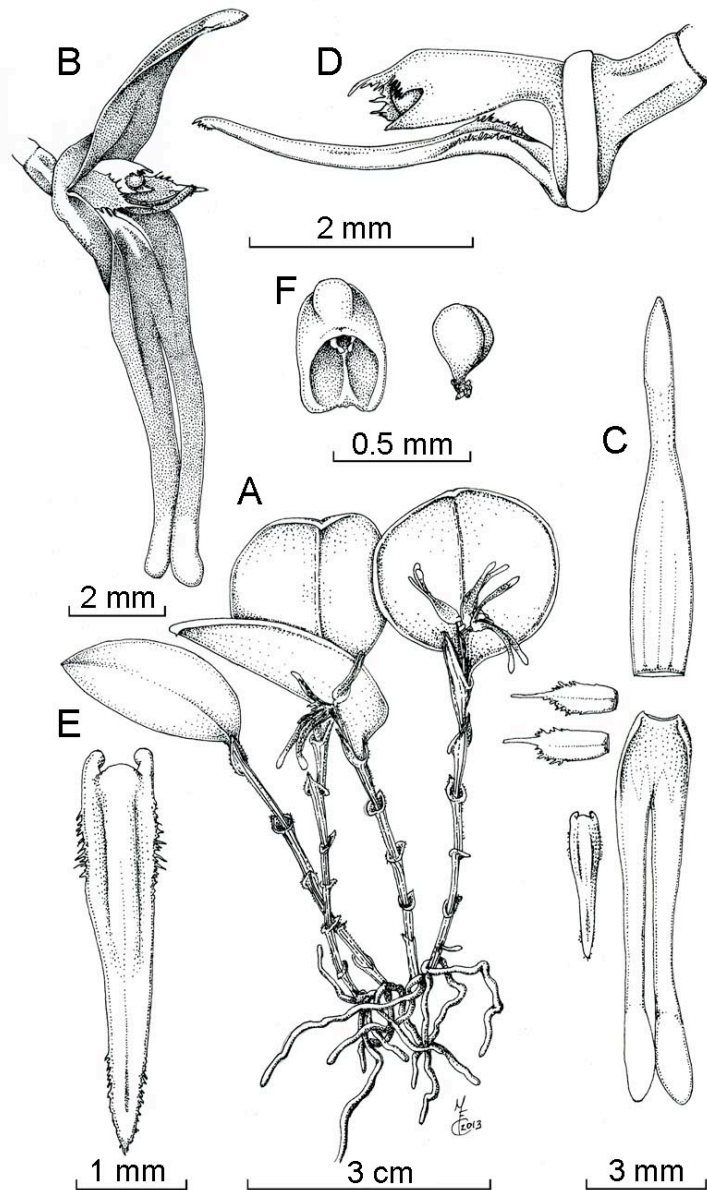


Figure 42. *Trichosalpinx caudata*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 546* (JBL-spirit).

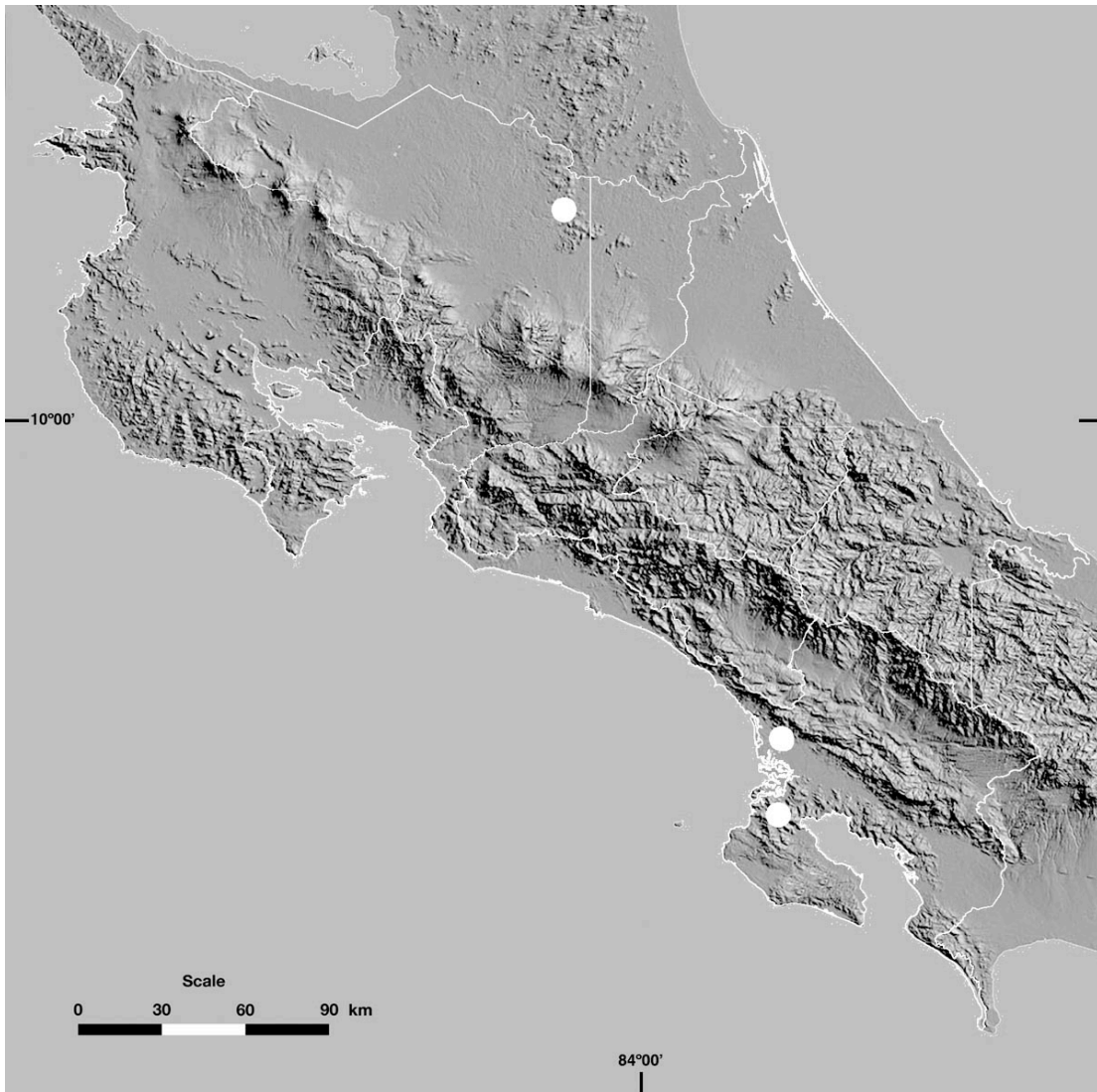


Figure 43. Distribution map of *Trichosalpinx caudata* in Costa Rica.

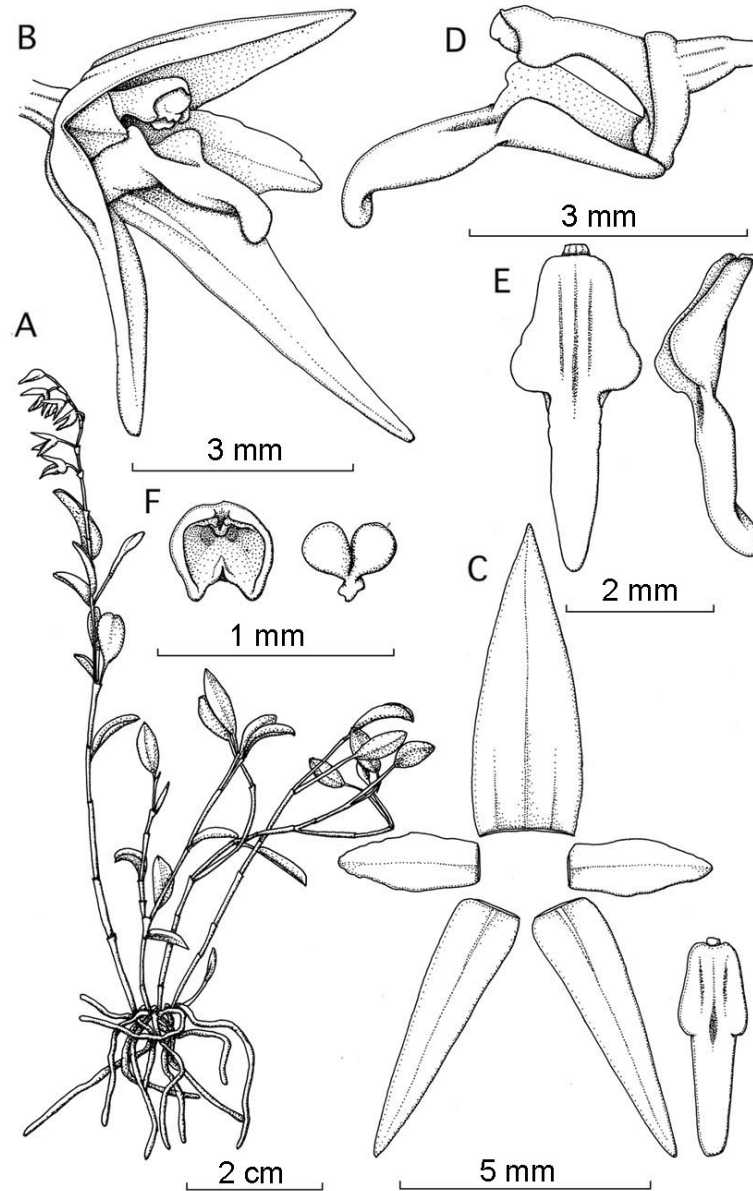


Figure 44. *Trichosalpinx cedralensis*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral and lateral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *F. Pupulin* 7498 (JBL-spirit).

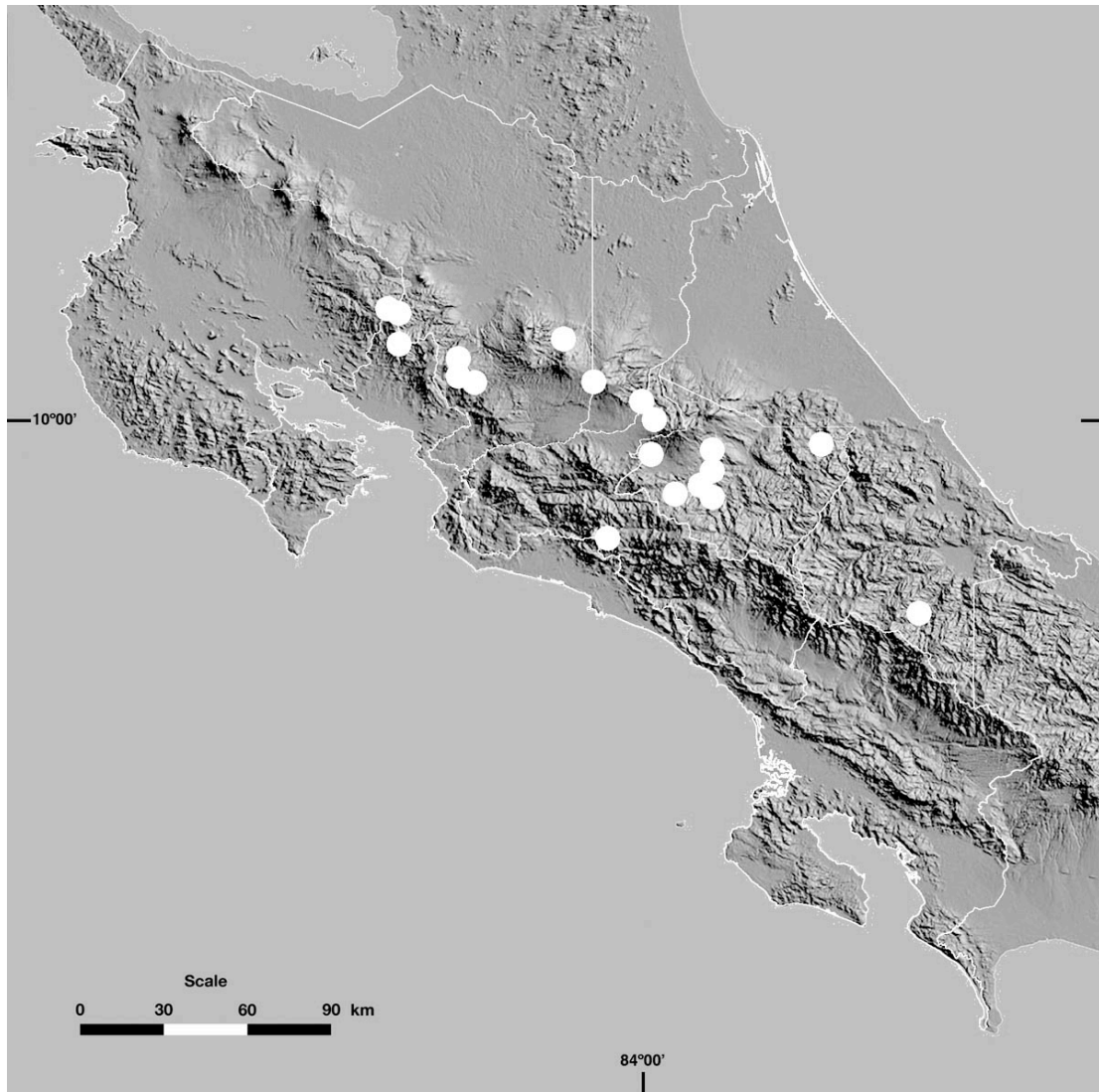


Figure 45. Distribution map of *Trichosalpinx cedralensis* in Costa Rica.

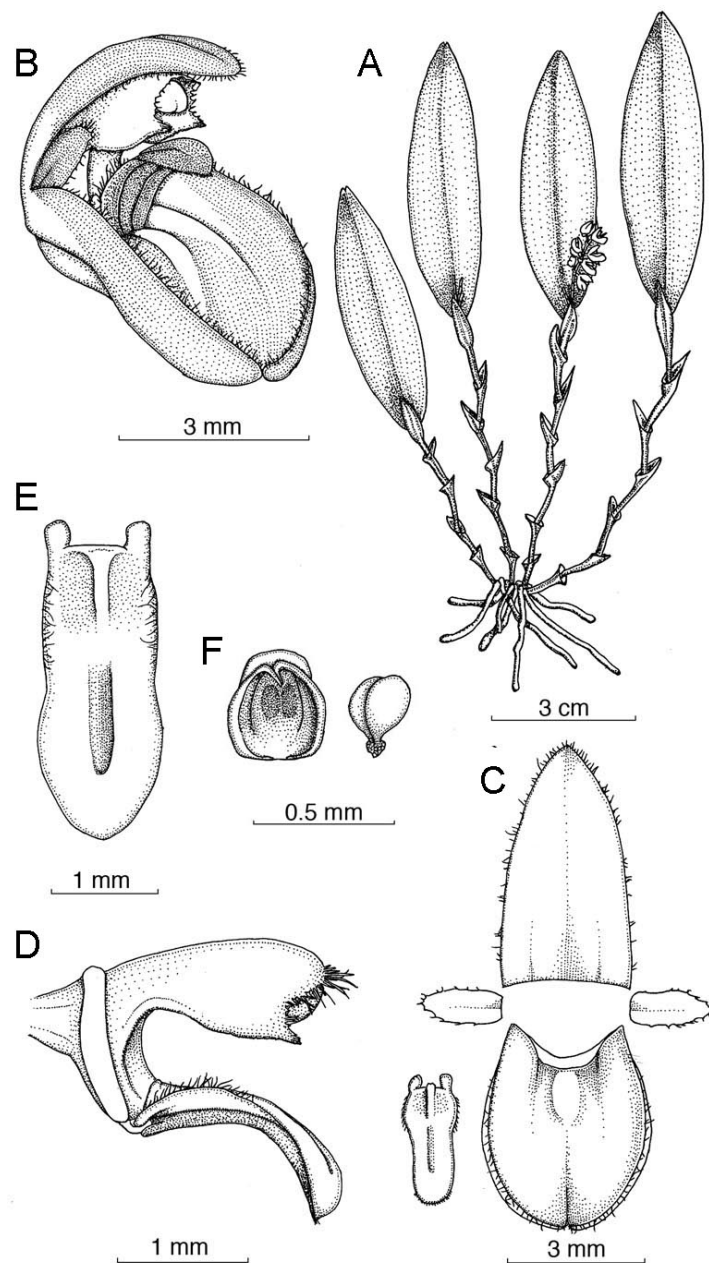


Figure 46. *Trichosalpinx ciliaris*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 328* (JBL-spirit).

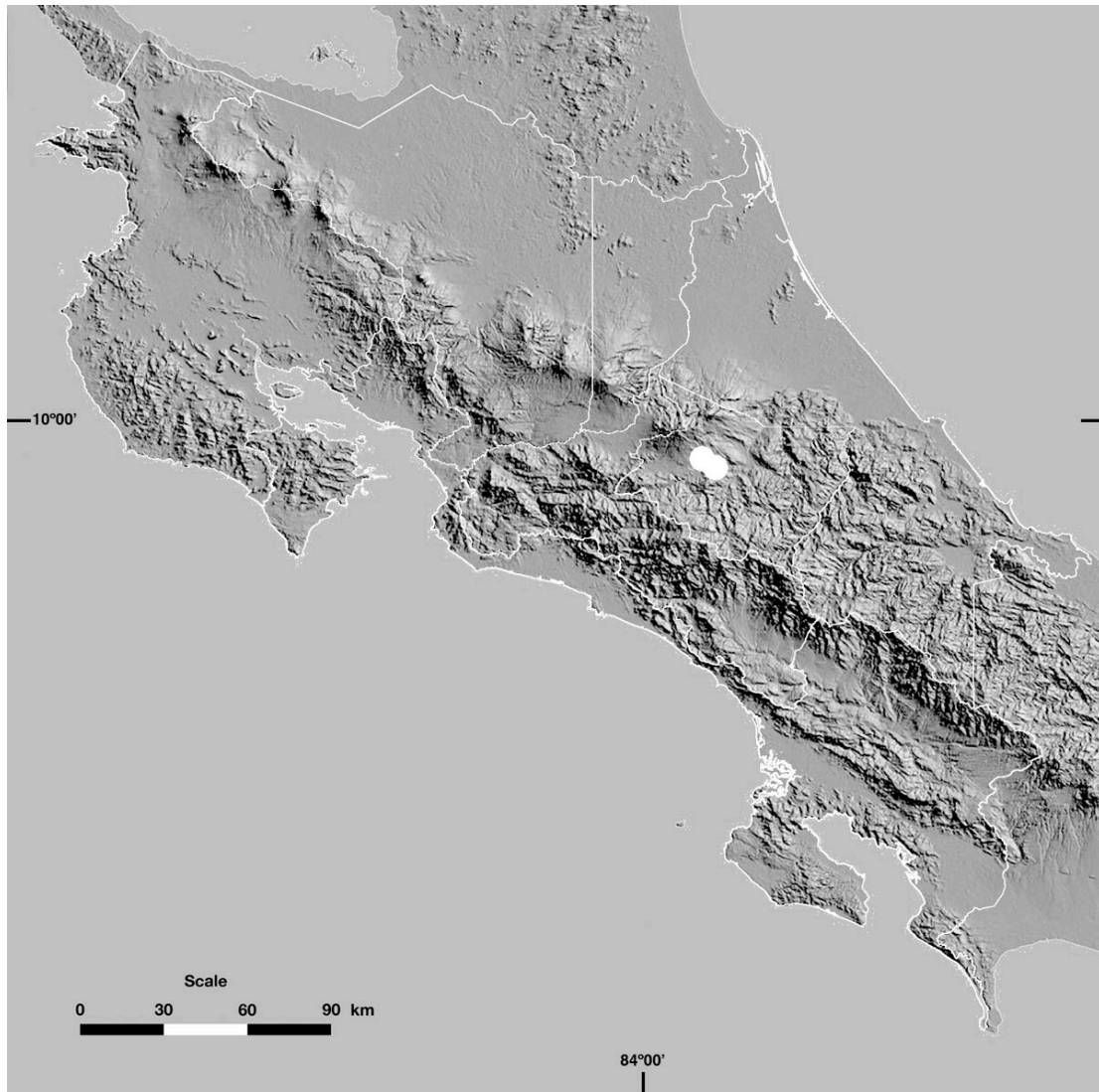


Figure 47. Distribution map of *Trichosalpinx ciliaris* in Costa Rica.

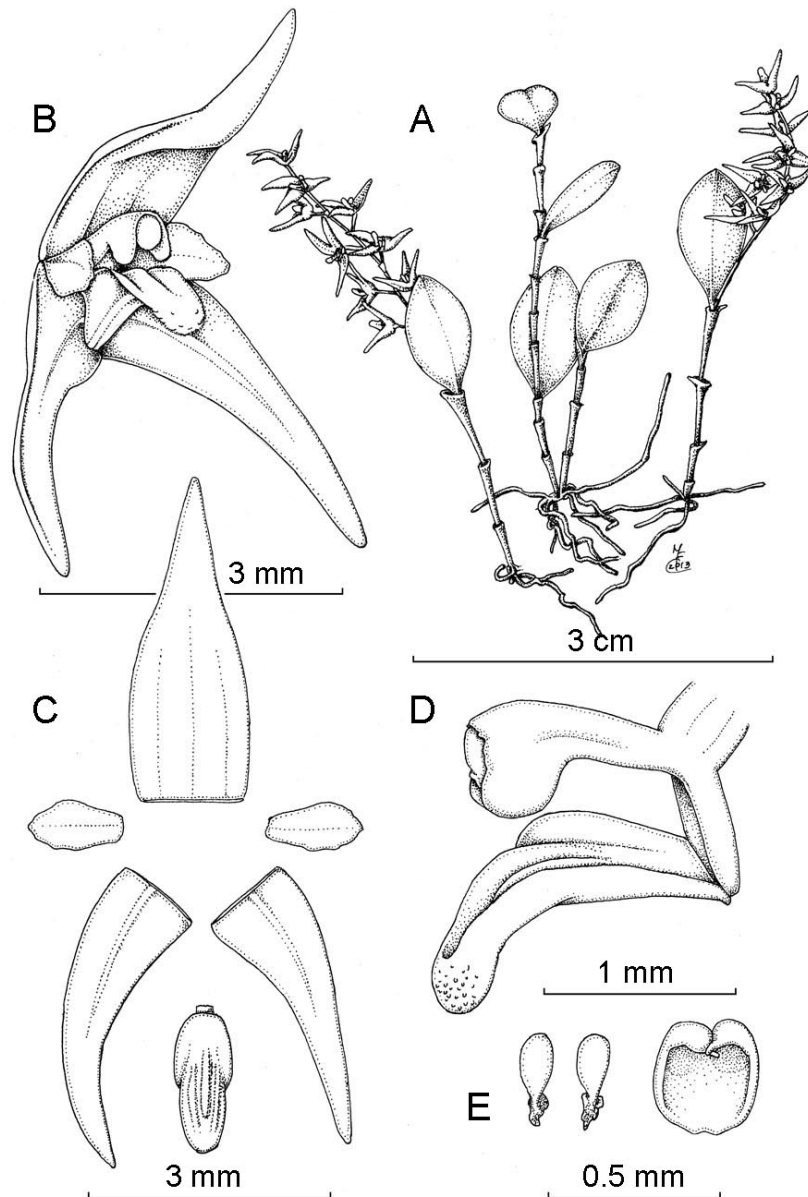


Figure 48. *Trichosalpinx dura*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 547* (JBL-spirit).

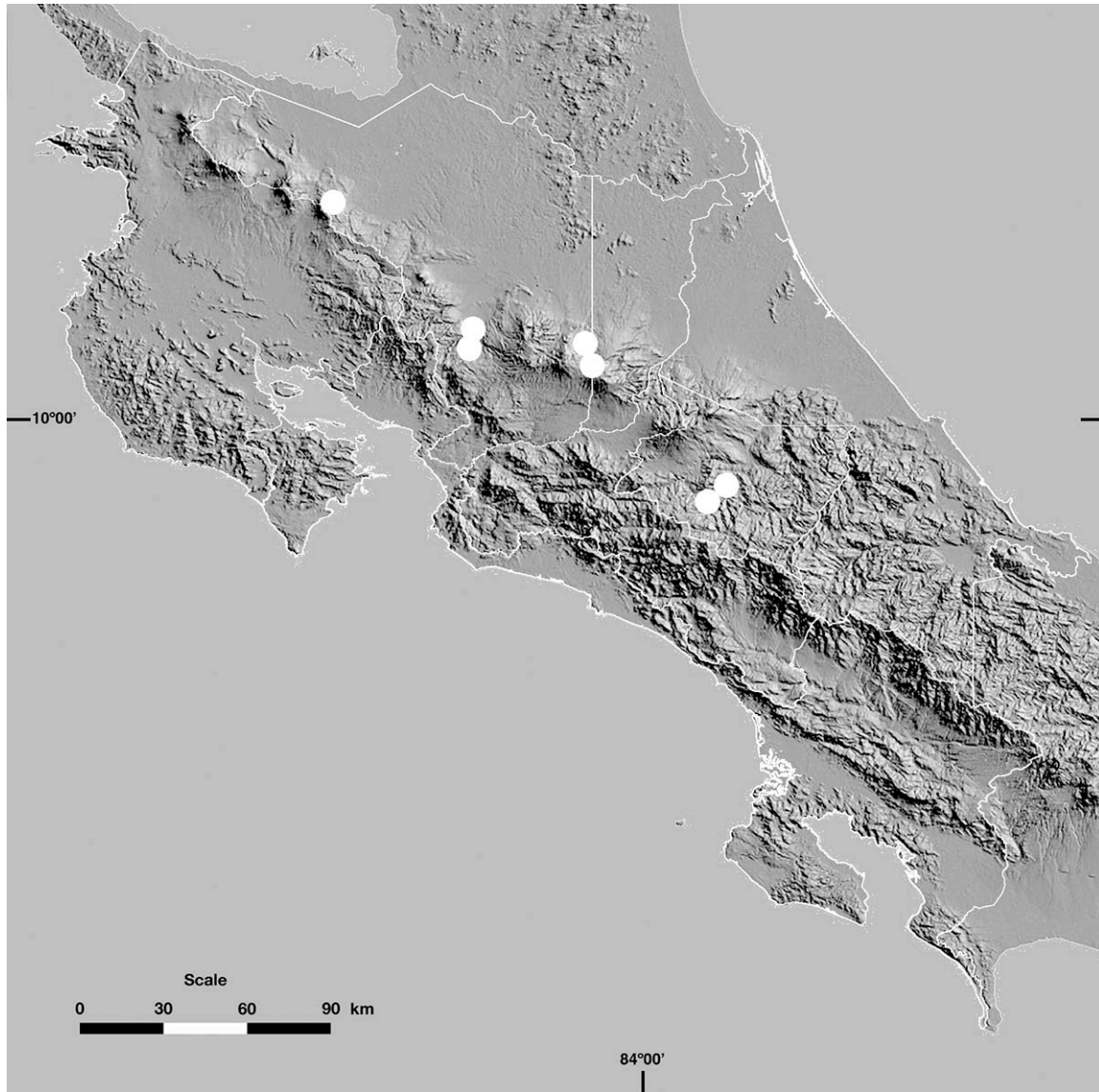


Figure 49. Distribution map of *Trichosalpinx dura* in Costa Rica.



Figure 50. Morphological variability of flowers of *Trichosalpinx dura*. Note variations of overall size, and red stains in the lips. Scale = 5 mm.

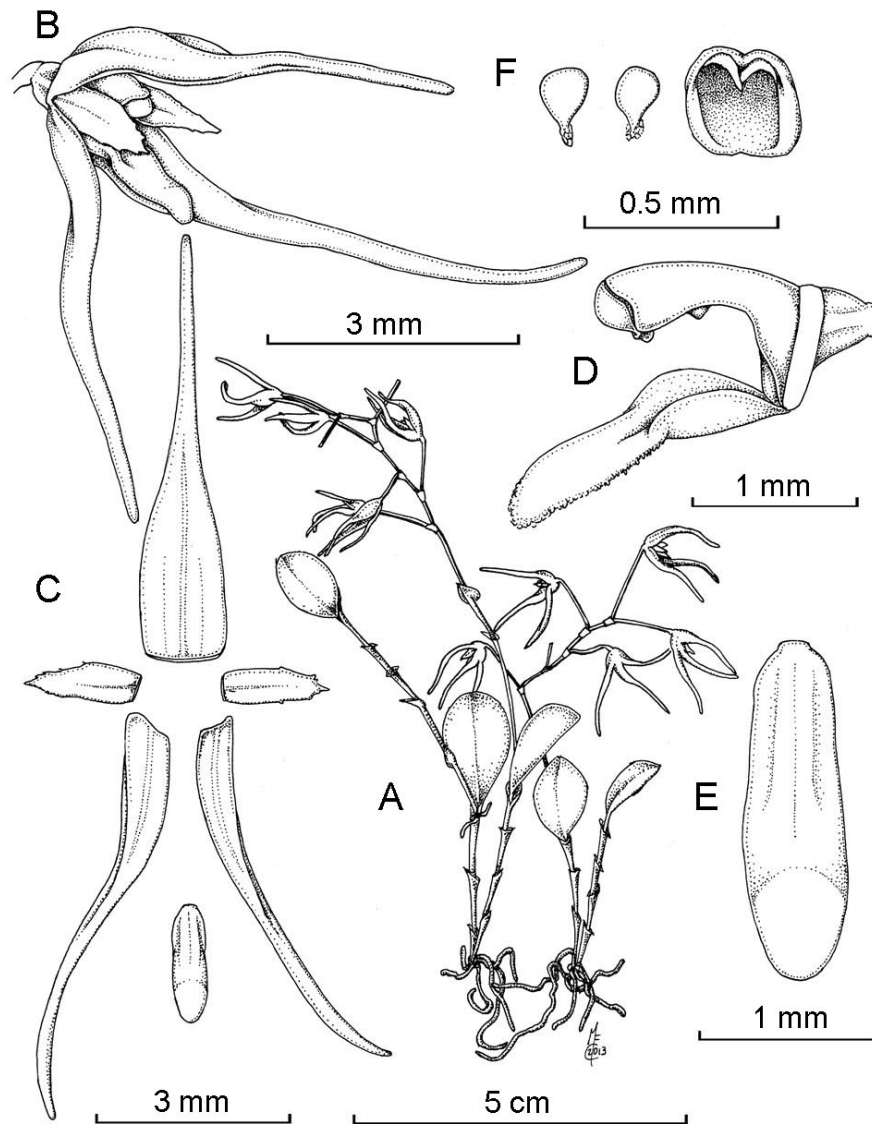


Figure 51. *Trichosalpinx fruticosa*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 617* (JBL-spirit).

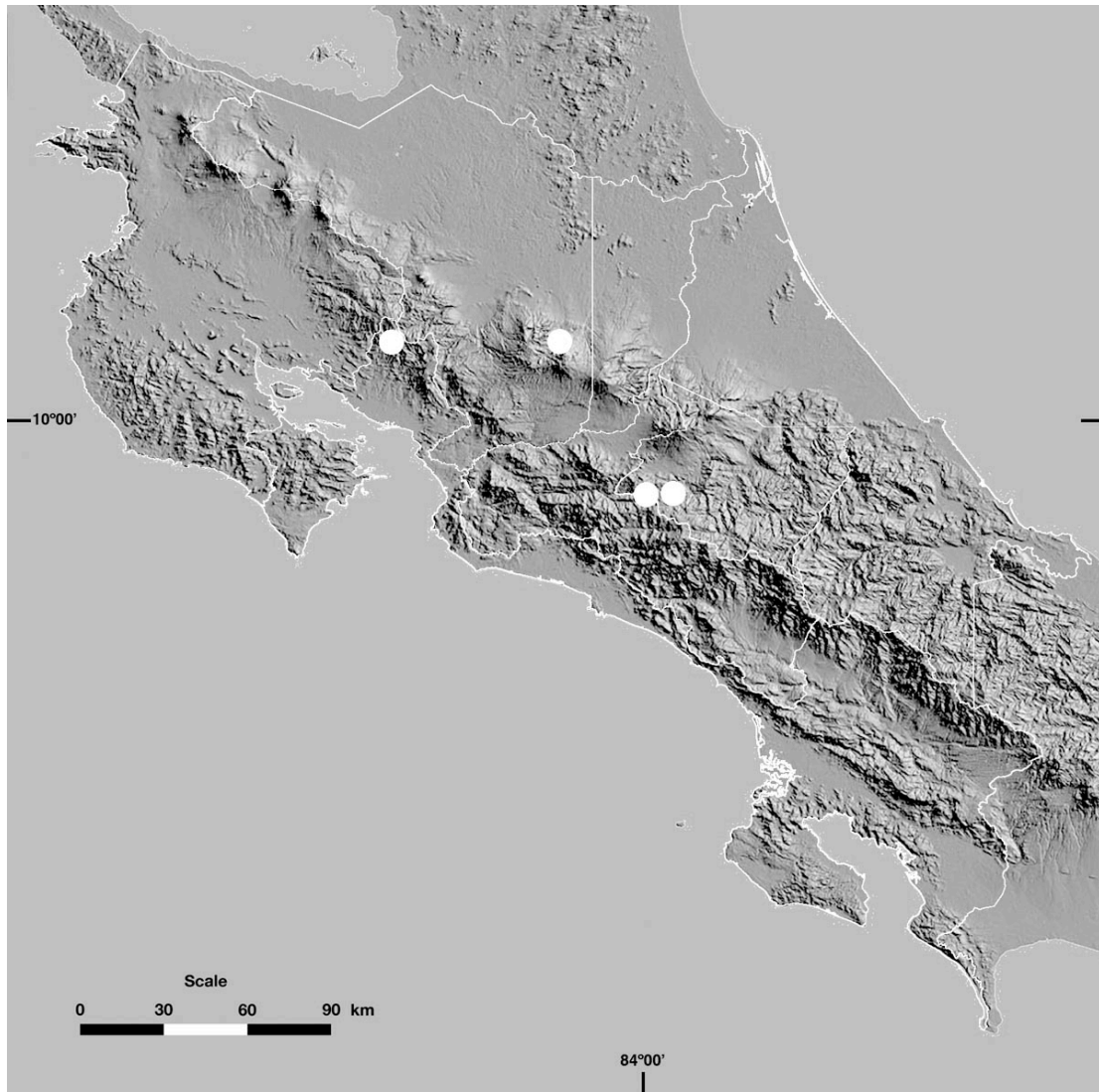


Figure 52. Distribution map of *Trichosalpinx fruticosa* in Costa Rica.

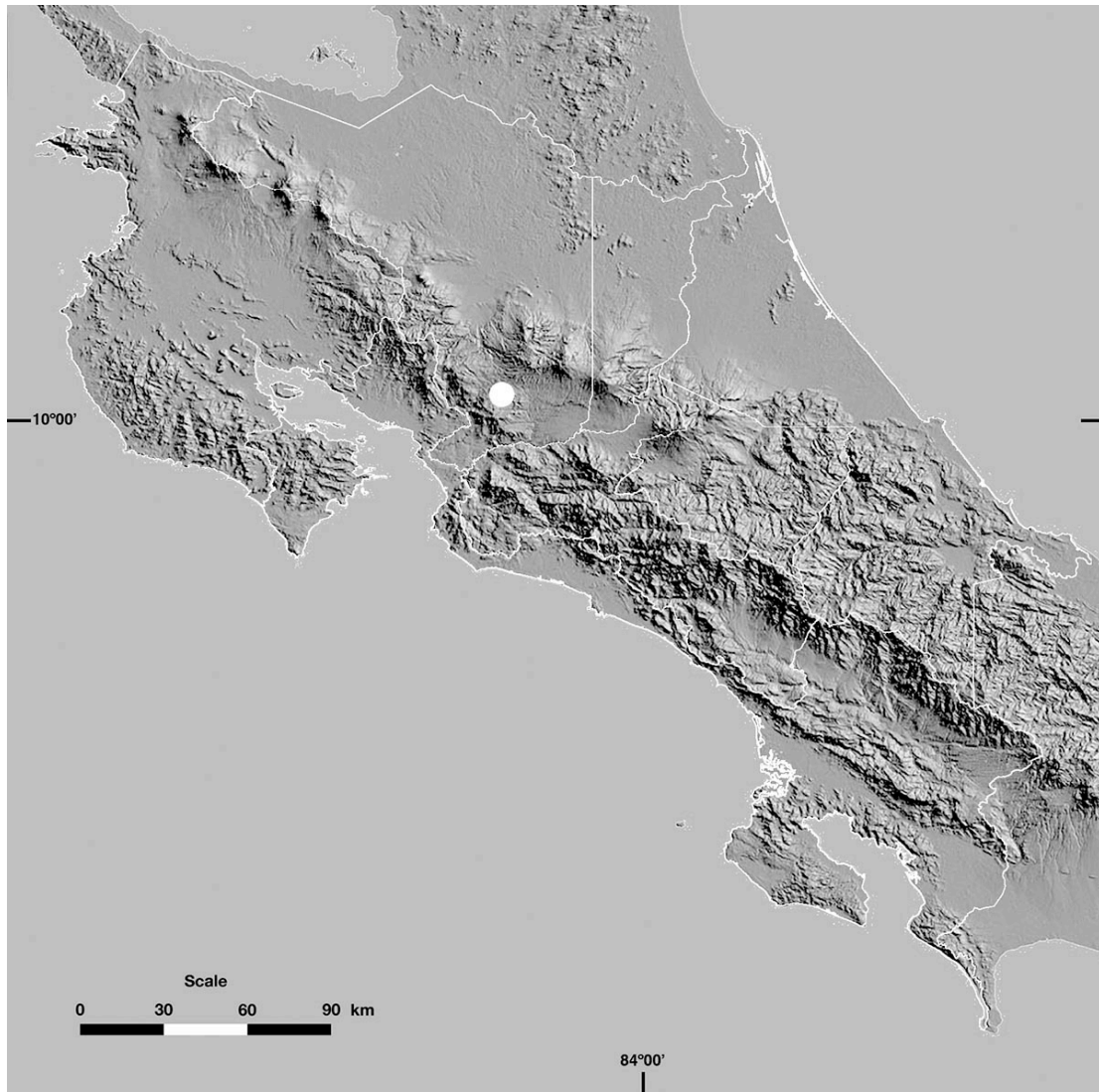


Figure 53. Distribution map of *Trichosalpinx membraniflora* in Costa Rica.

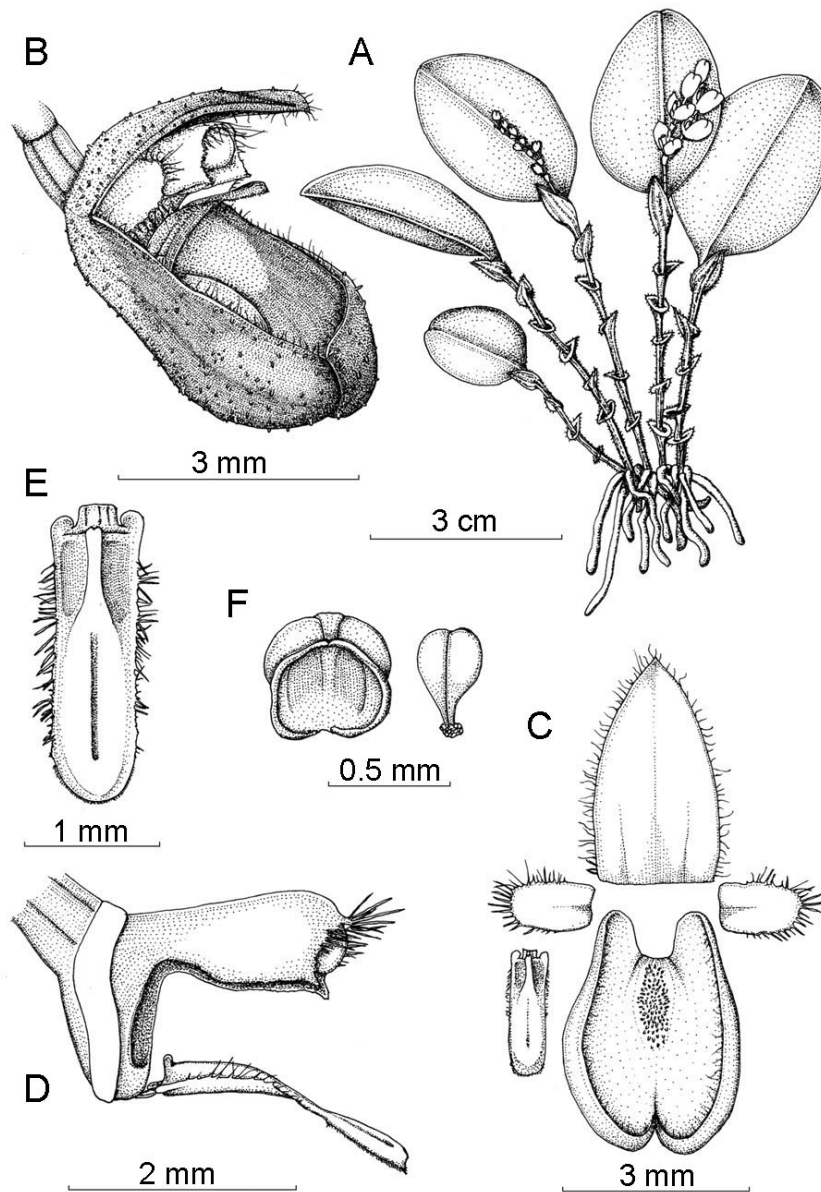


Figure 54. *Trichosalpinx memor*, morph 1. A – Habit. B – Flower. C – Dissected perianth.

D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria.

Drawn by M. Fernández from M. Fernández 12 (JBL-spirit).

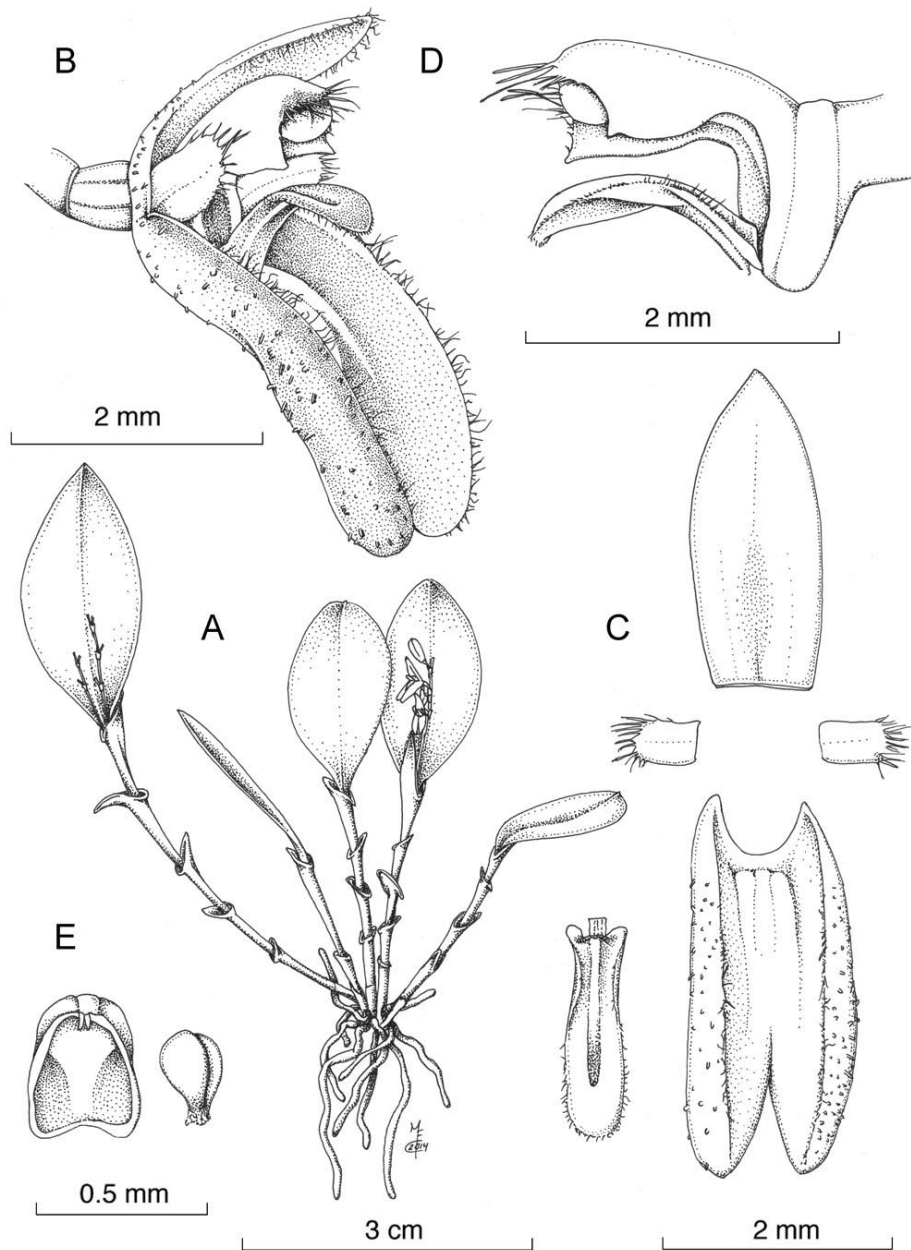


Figure 55. *Trichosalpinx memor*, morph 2. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Anther cap and pollinaria. Drawn by M. Fernández from *F. Pupulin* 5472 (JBL-spirit).

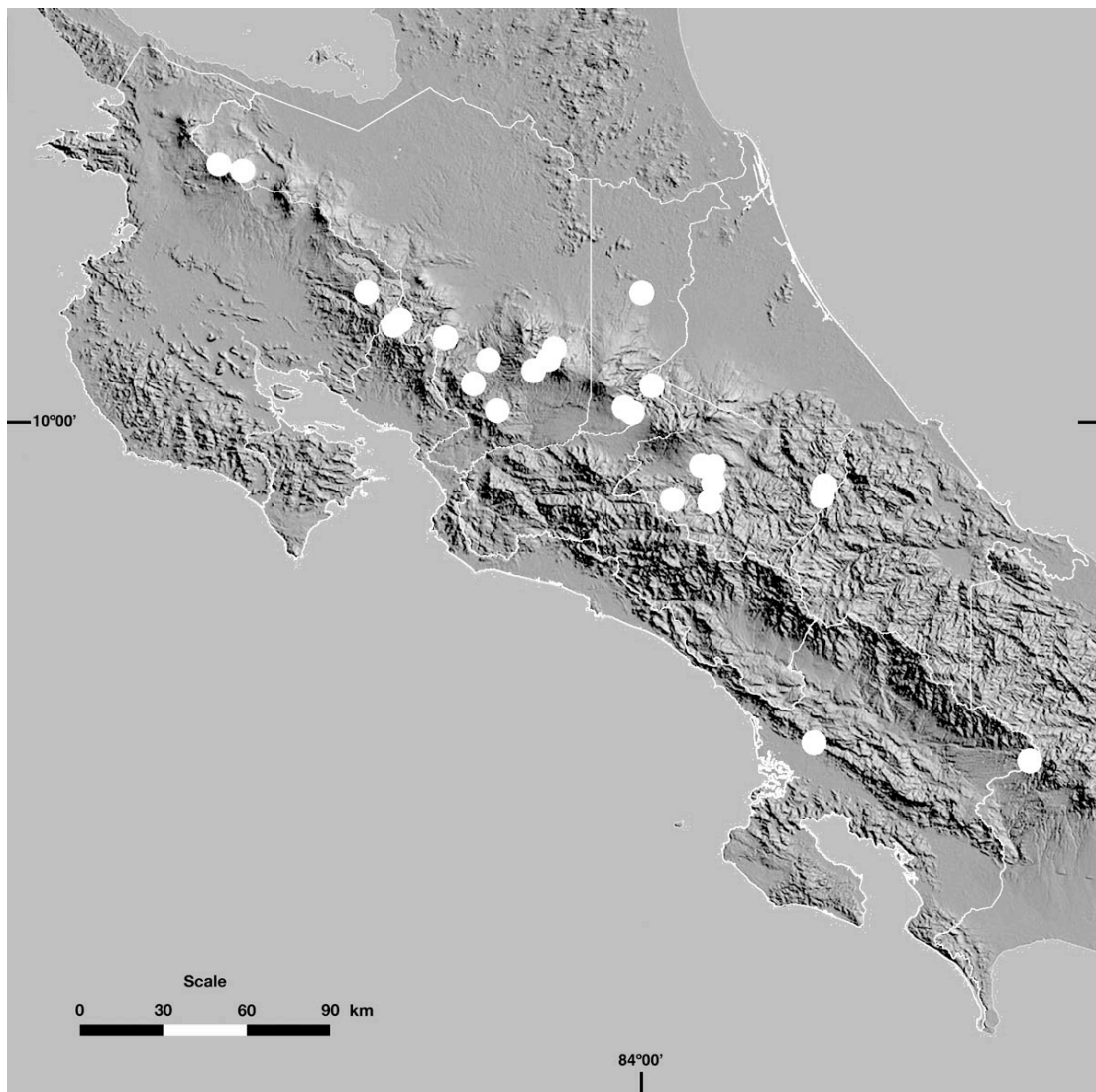


Figure 56. Distribution map of *Trichosalpinx memor* in Costa Rica.



Figure 57. Morphological variability of flowers of *Trichosalpinx memor*. A Morph 1. B Morph 2. Note differences in color of sepals, lip and anther cap. Scale = 3 mm.

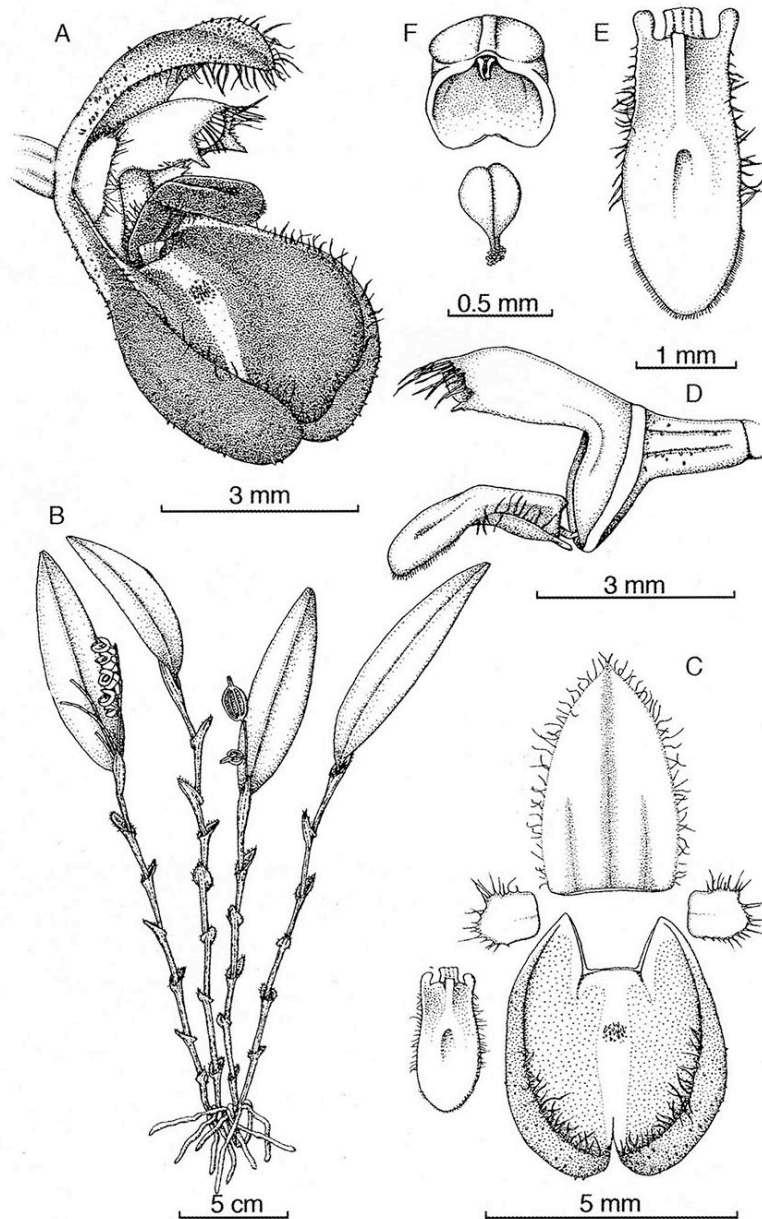


Figure 58. *Trichosalpinx minutipetala*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Column, ventral view. G – Anther cap and pollinaria. Drawn by M. Fernández from A. Karremans 1333 (JBL-spirit).

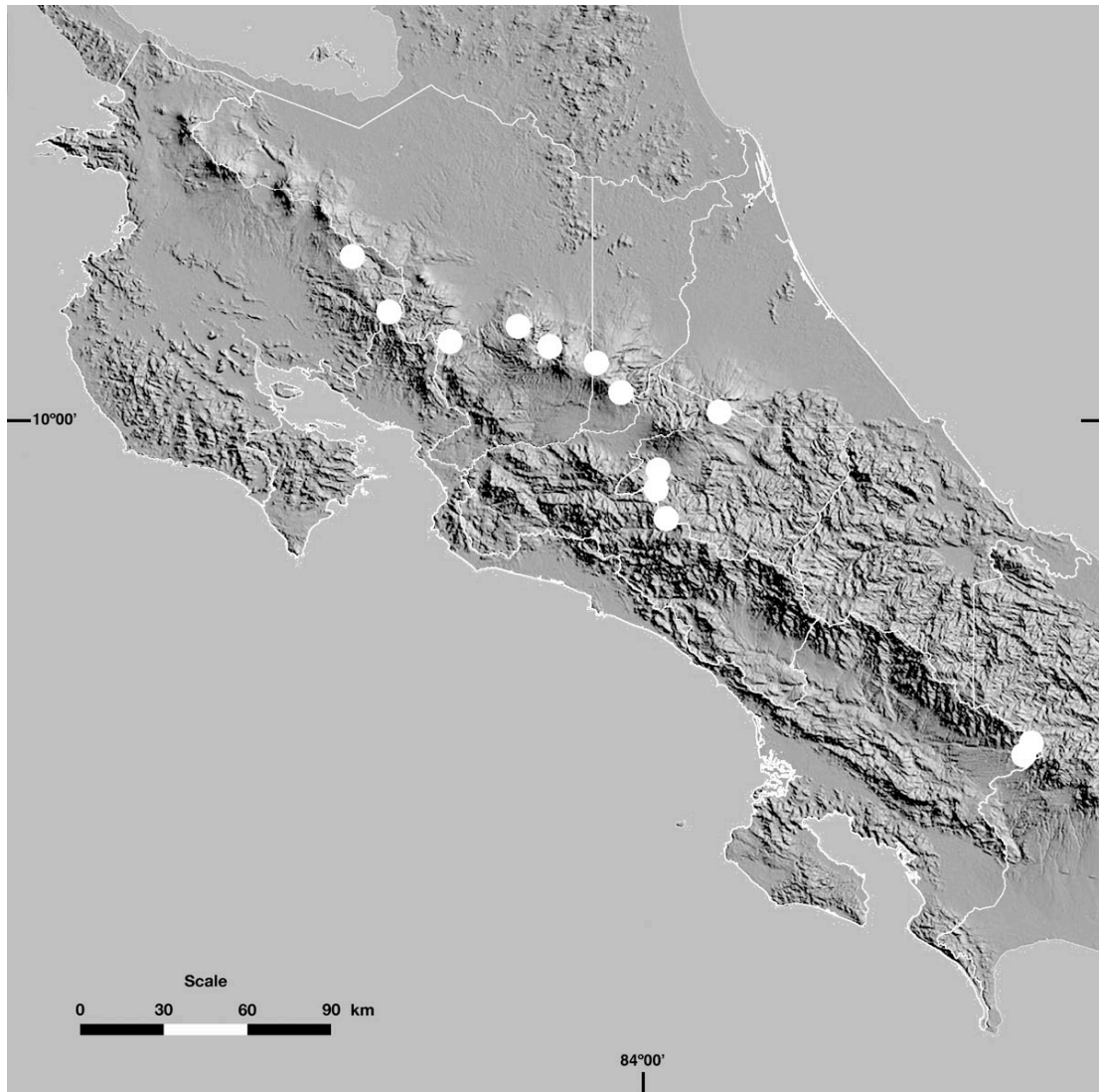


Figure 59. Distribution map of *Trichosalpinx minutipetala* in Costa Rica.

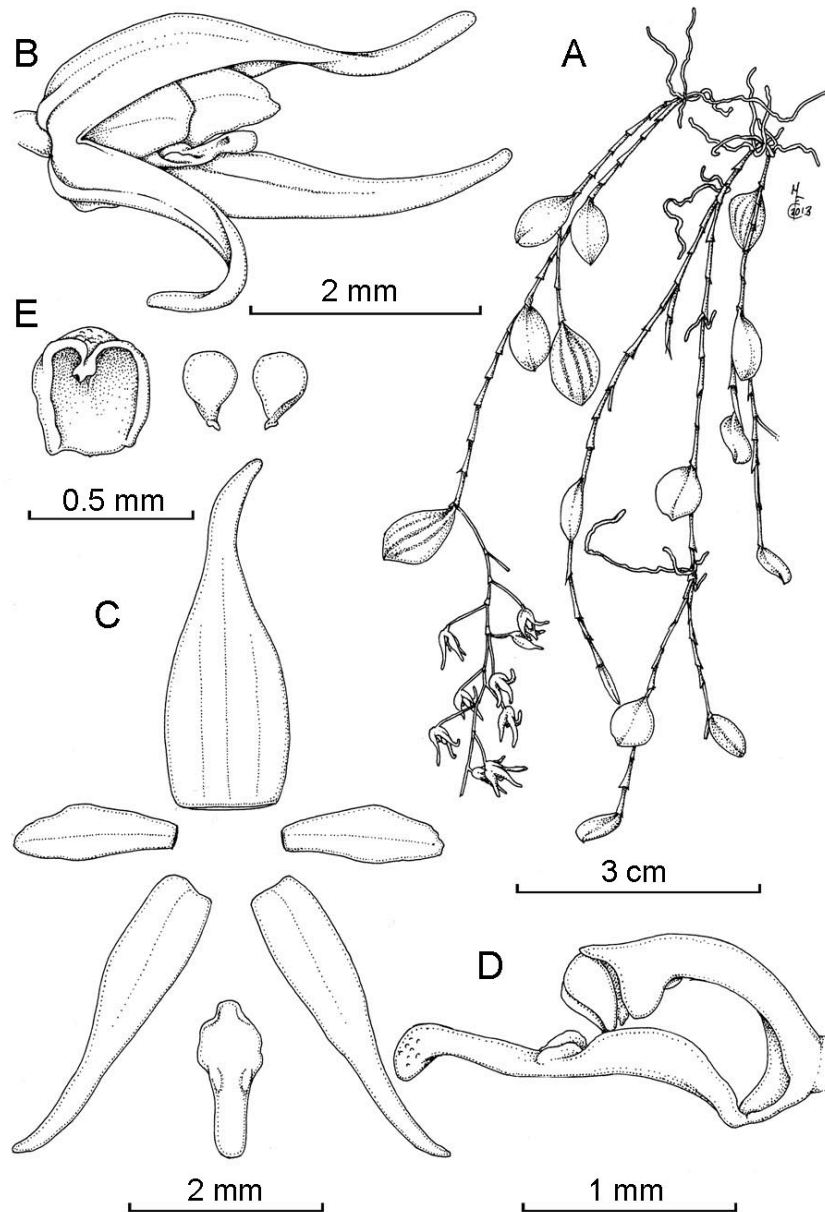


Figure 60. *Trichosalpinx nana*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Anther cap and pollinaria. Drawn by M. Fernández from A. *Karremans 4882* (JBL-spirit).

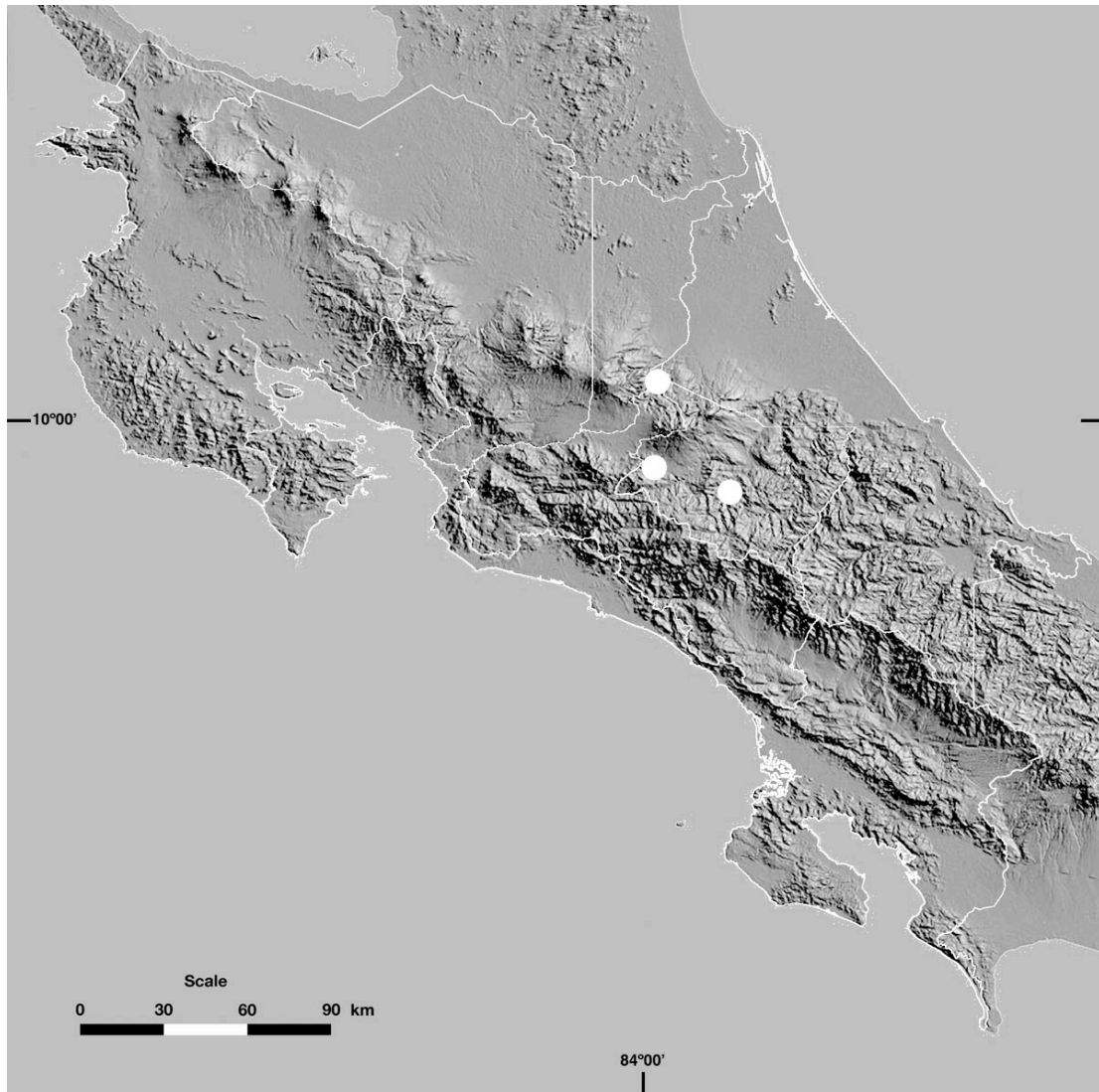


Figure 61. Distribution map of *Trichosalpinx nana* in Costa Rica.

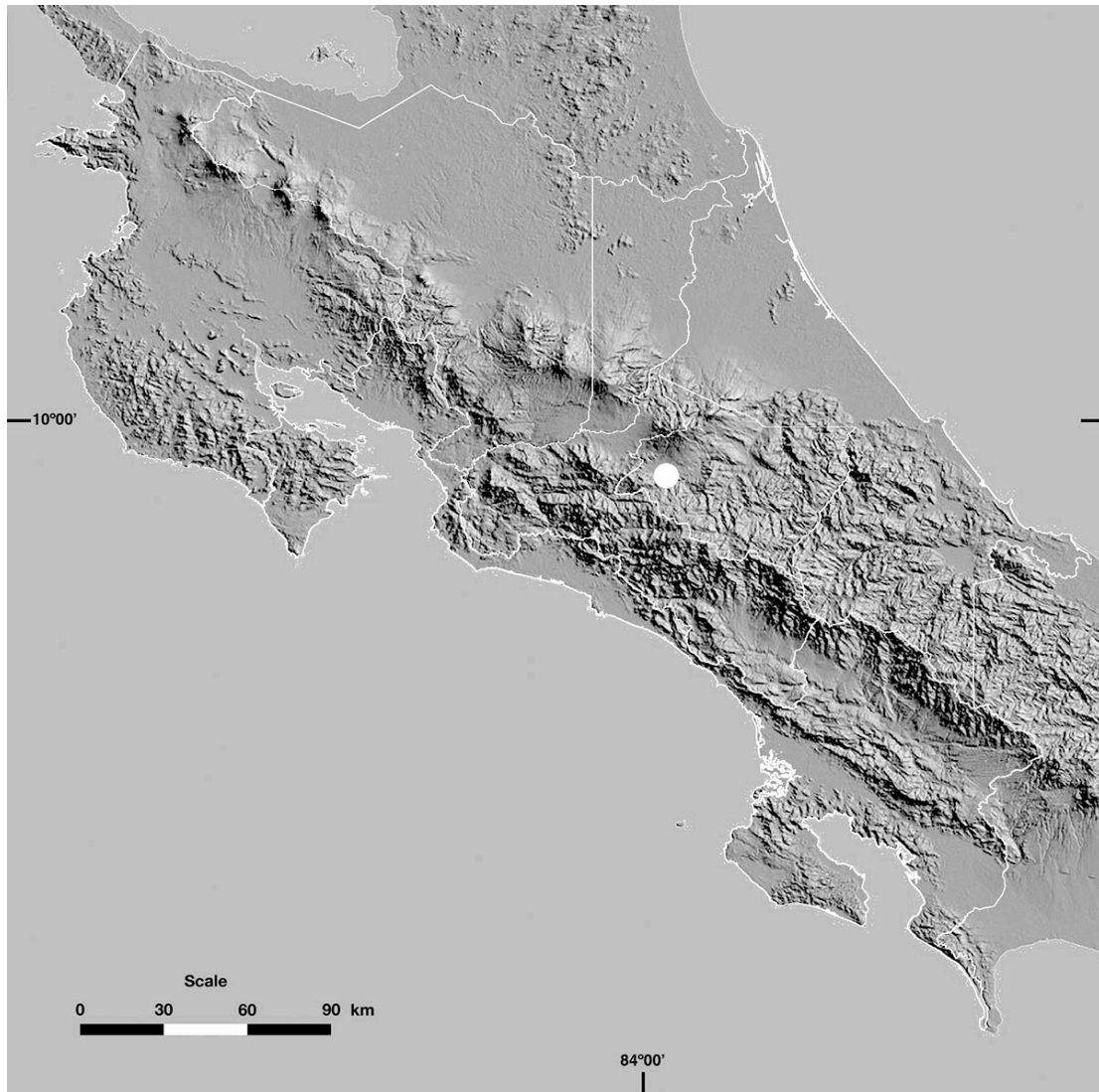


Figure 62. Distribution map of *Trichosalpinx navarrensis* in Costa Rica.

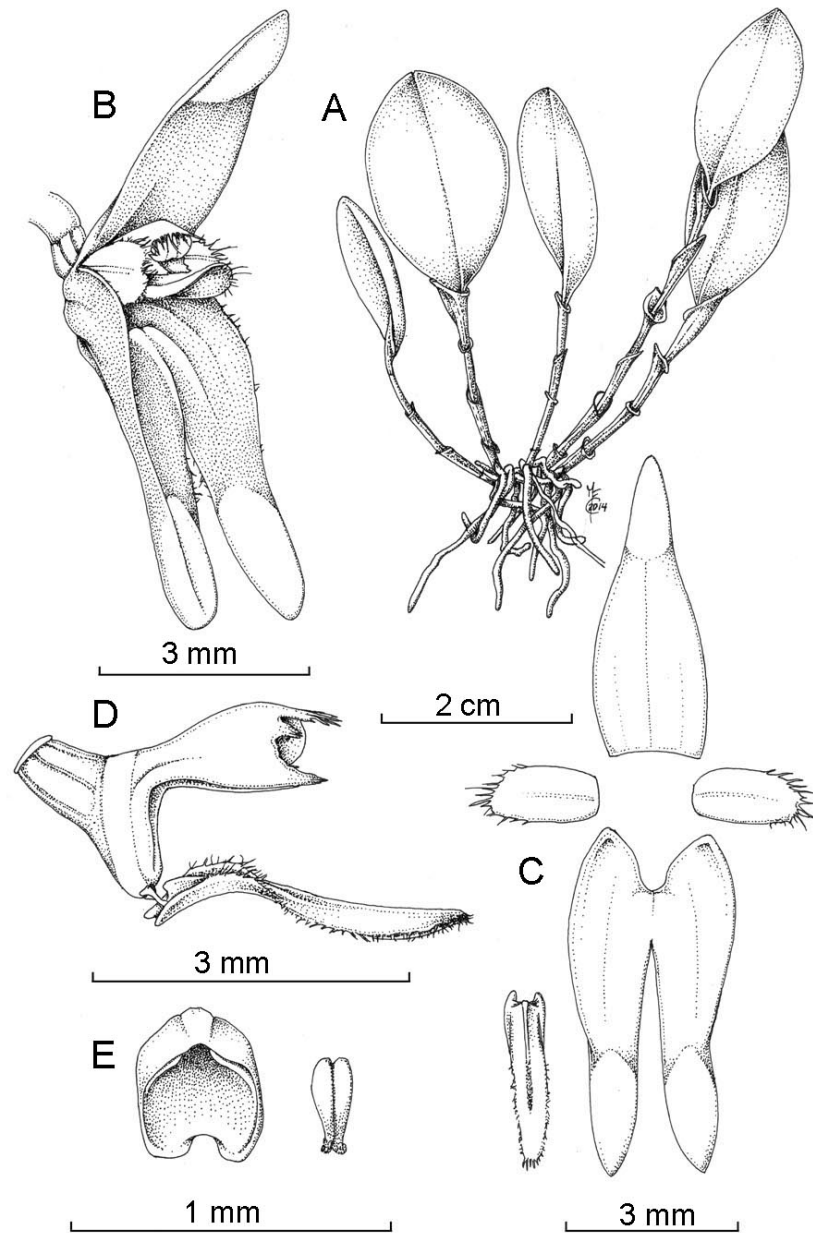


Figure 63. *Trichosalpinx orbicularis*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 65* (JBL-spirit).

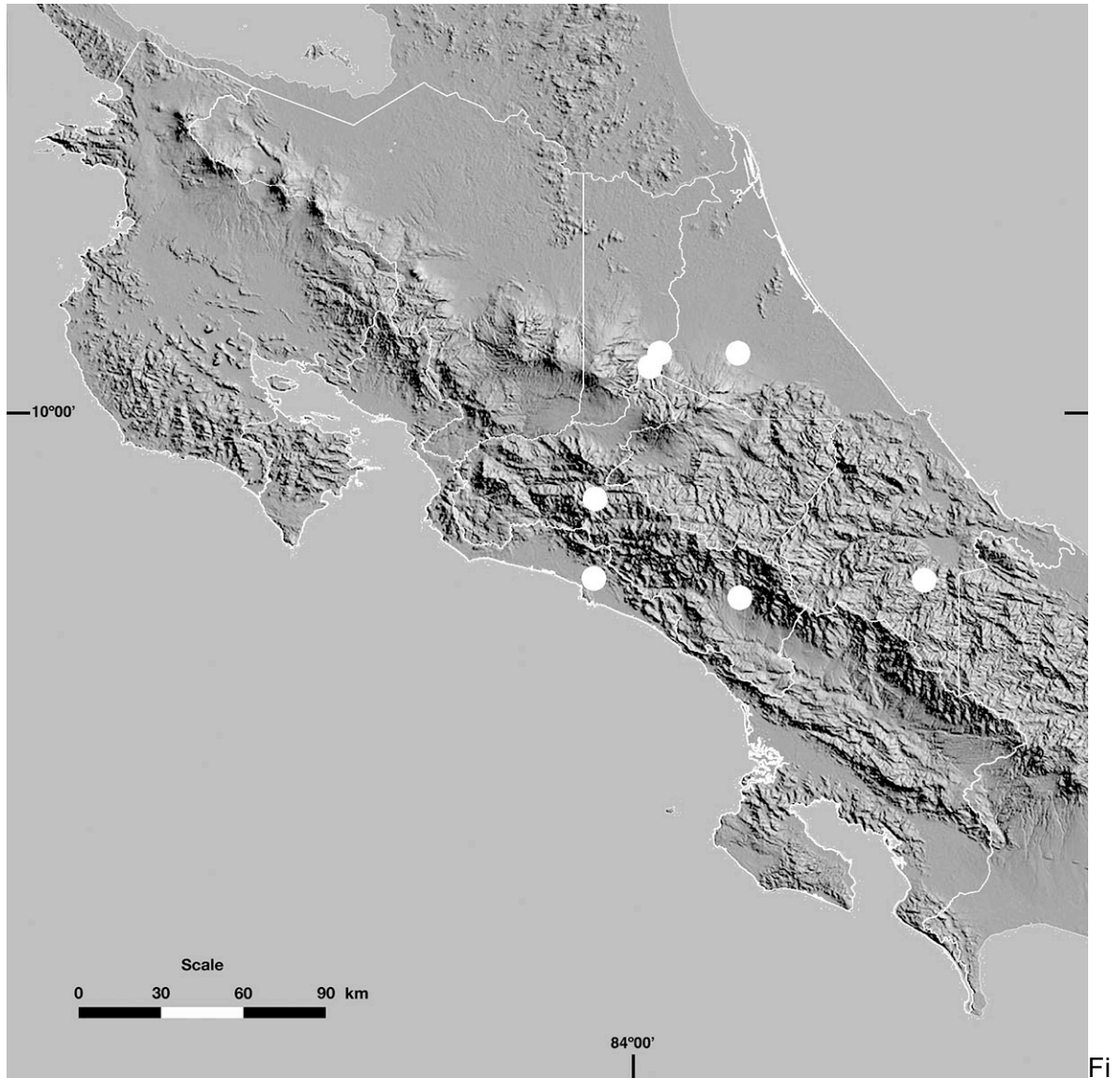


Figure 64. Distribution map of *Trichosalpinx orbicularis* in Costa Rica.

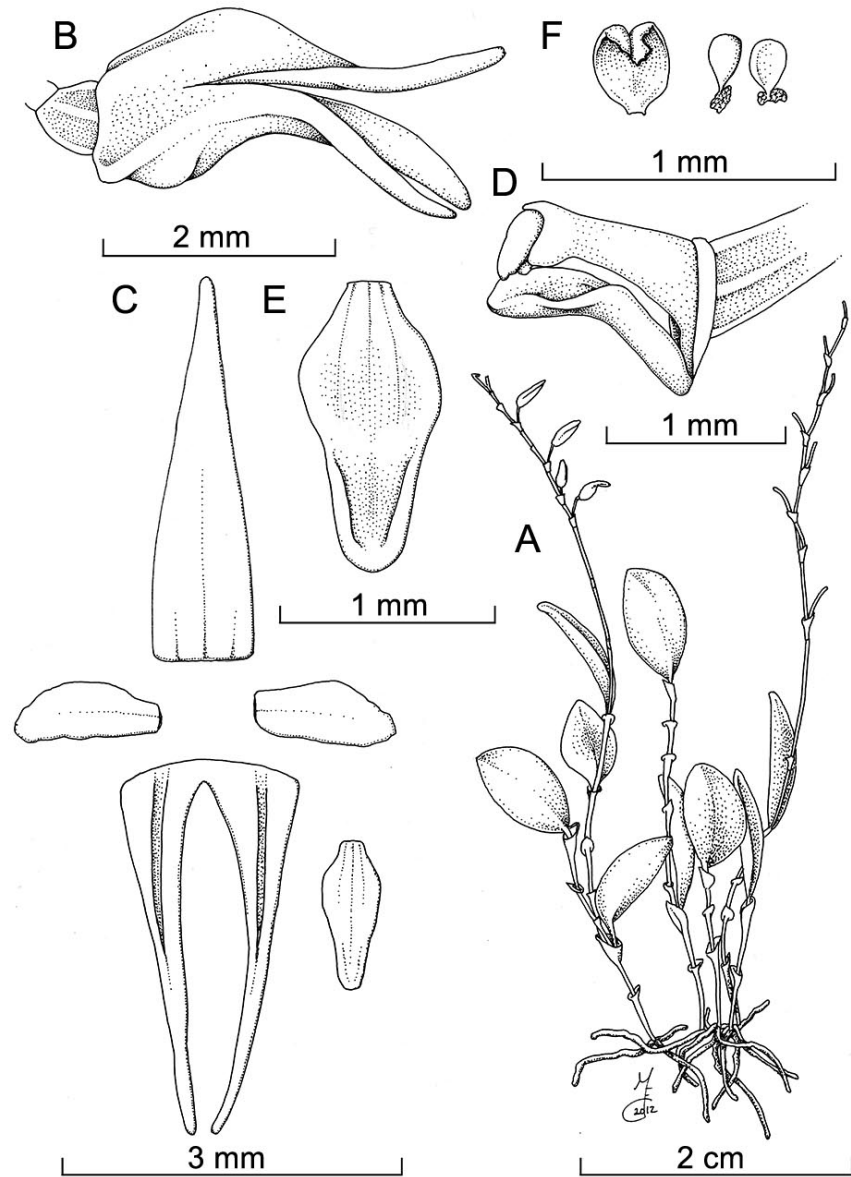


Figure 65. *Trichosalpinx parsonsii*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from A. Karremans 3305 (JBL-spirit).

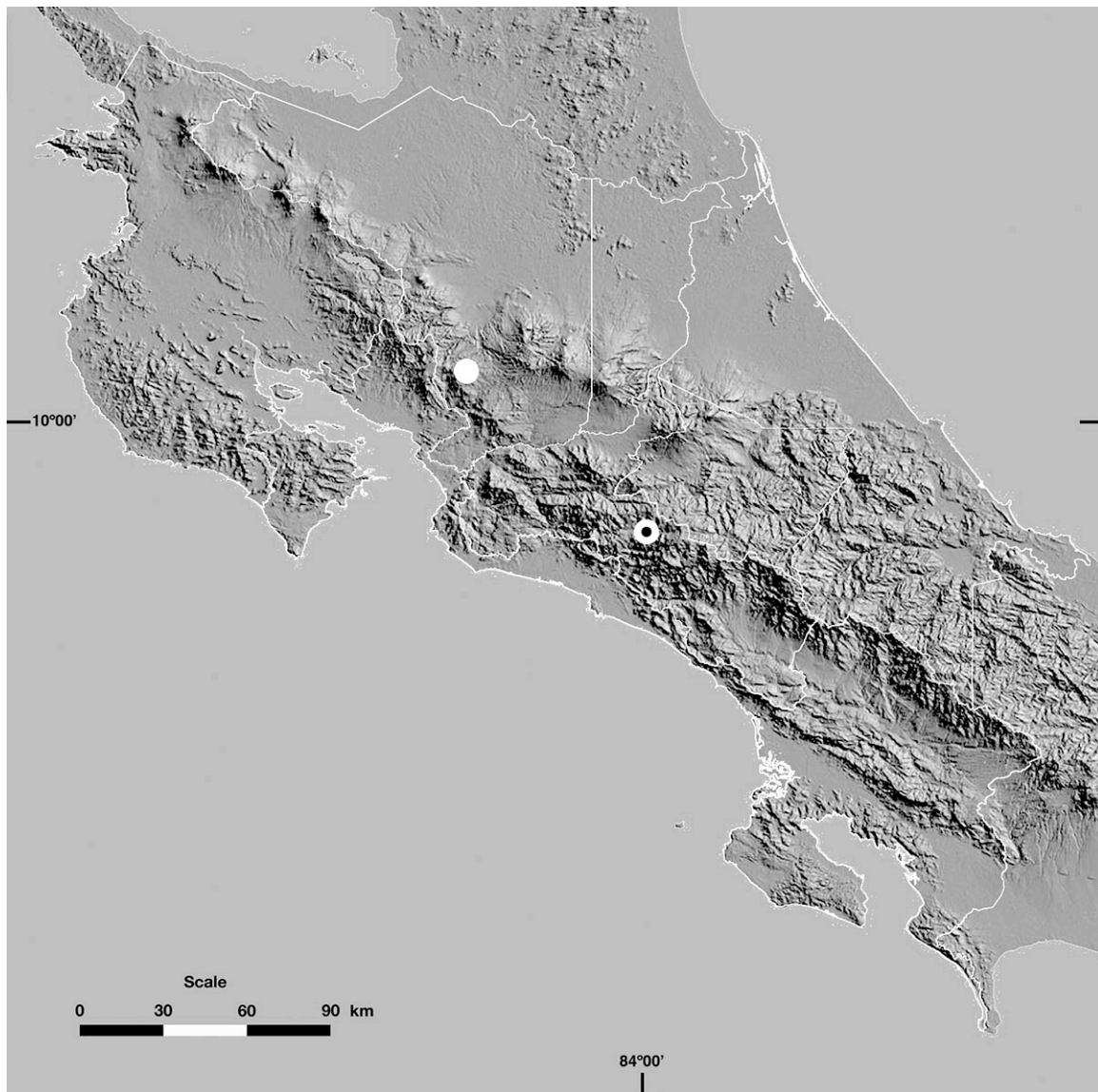


Figure 66. Distribution map of *Trichosalpinx parsonsii* in Costa Rica. White dot with center black indicates locality of the holotype.

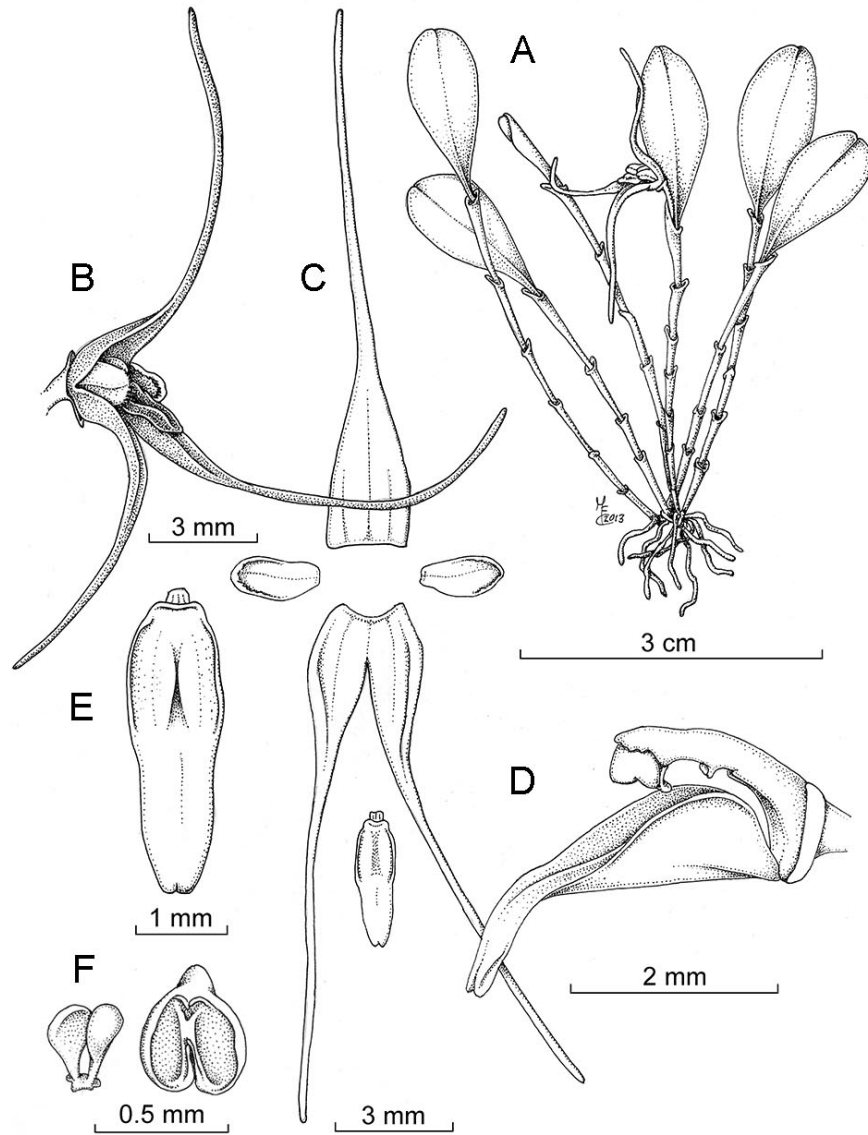


Figure 67. *Trichosalpinx pergrata*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view, not flattened. F – Anther cap and pollinaria. Drawn by M. Fernández from D. Bogarín 6502 (JBL-spirit).

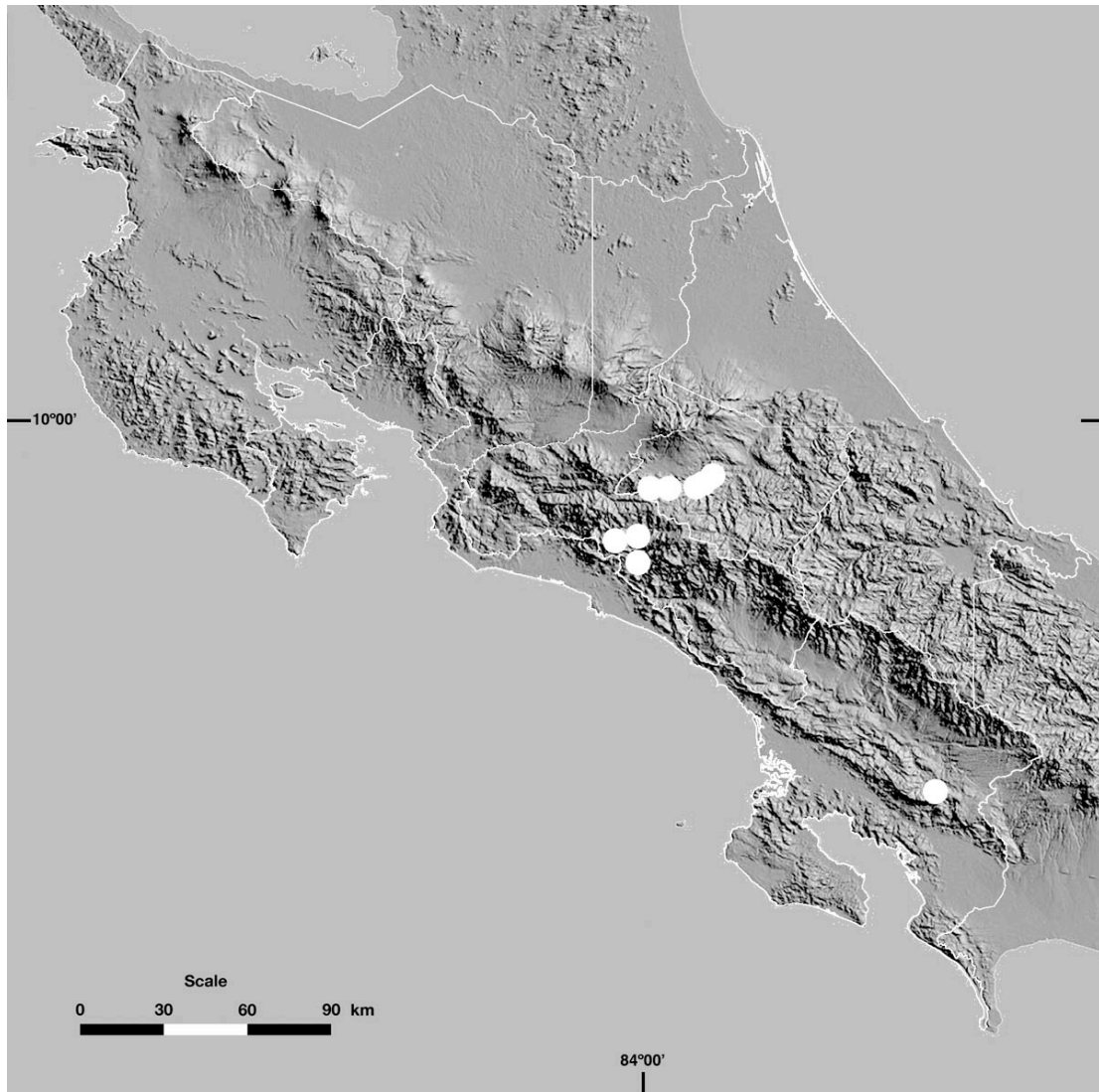


Figure 68. Distribution map of *Trichosalpinx pergrata* in Costa Rica.

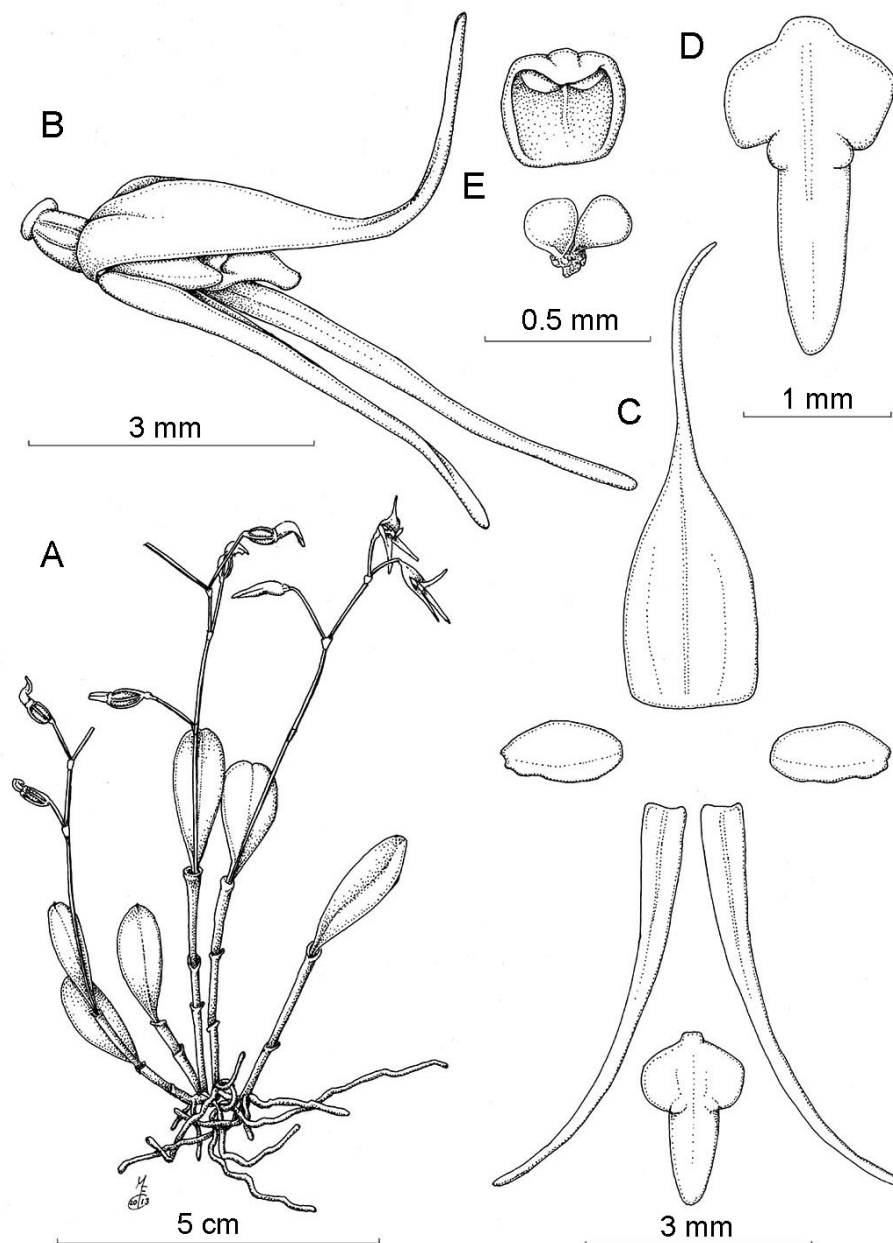


Figure 69. *Trichosalpinx pusilla*. A – Habit. B – Flower. C – Dissected perianth. D – Lip, ventral view. E – Anther cap and pollinaria. Drawn by M. Fernández from A. Karremans 5642 (JBL-spirit).

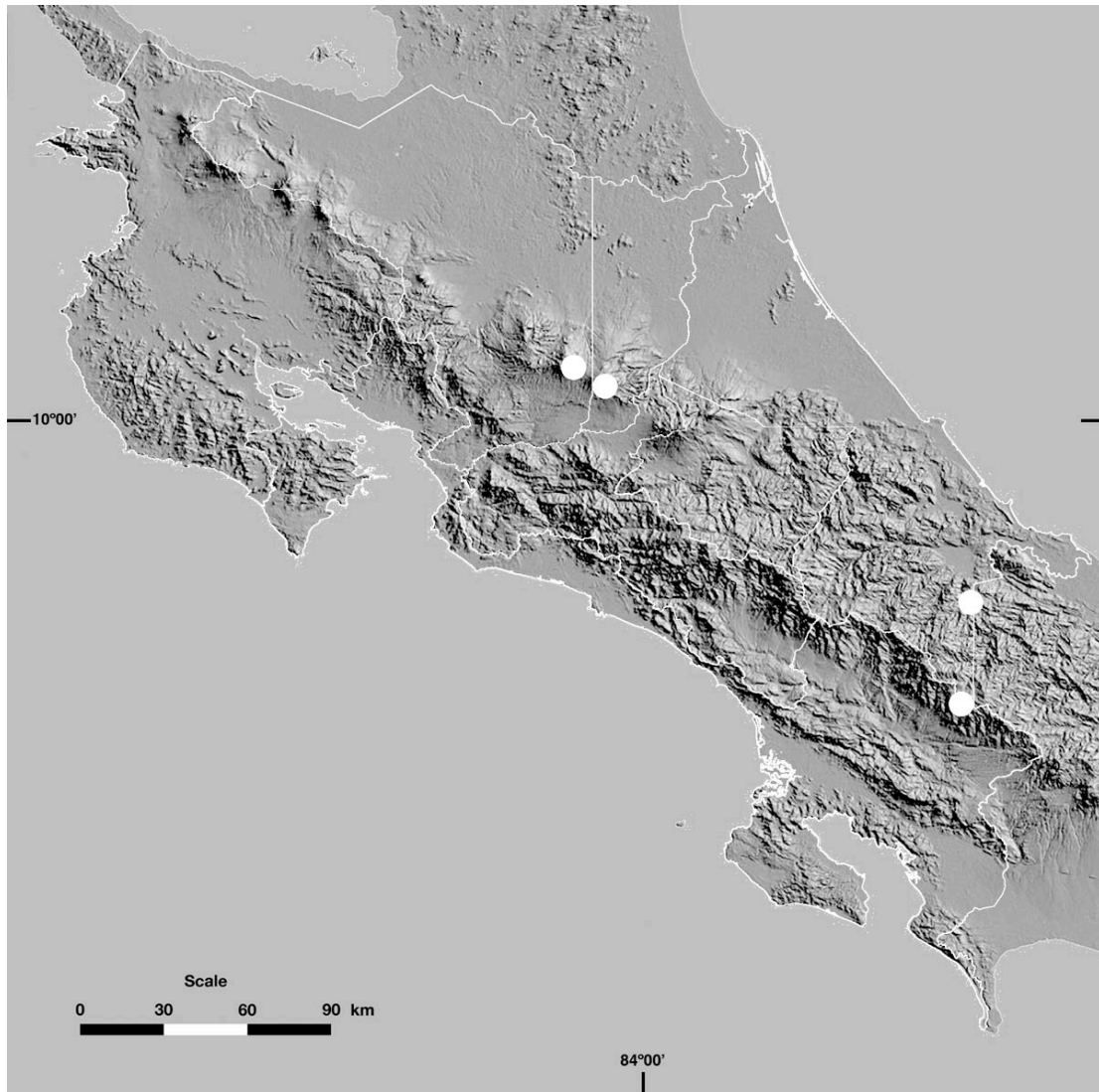


Figure 70. Distribution map of *Trichosalpinx pusilla* in Costa Rica.

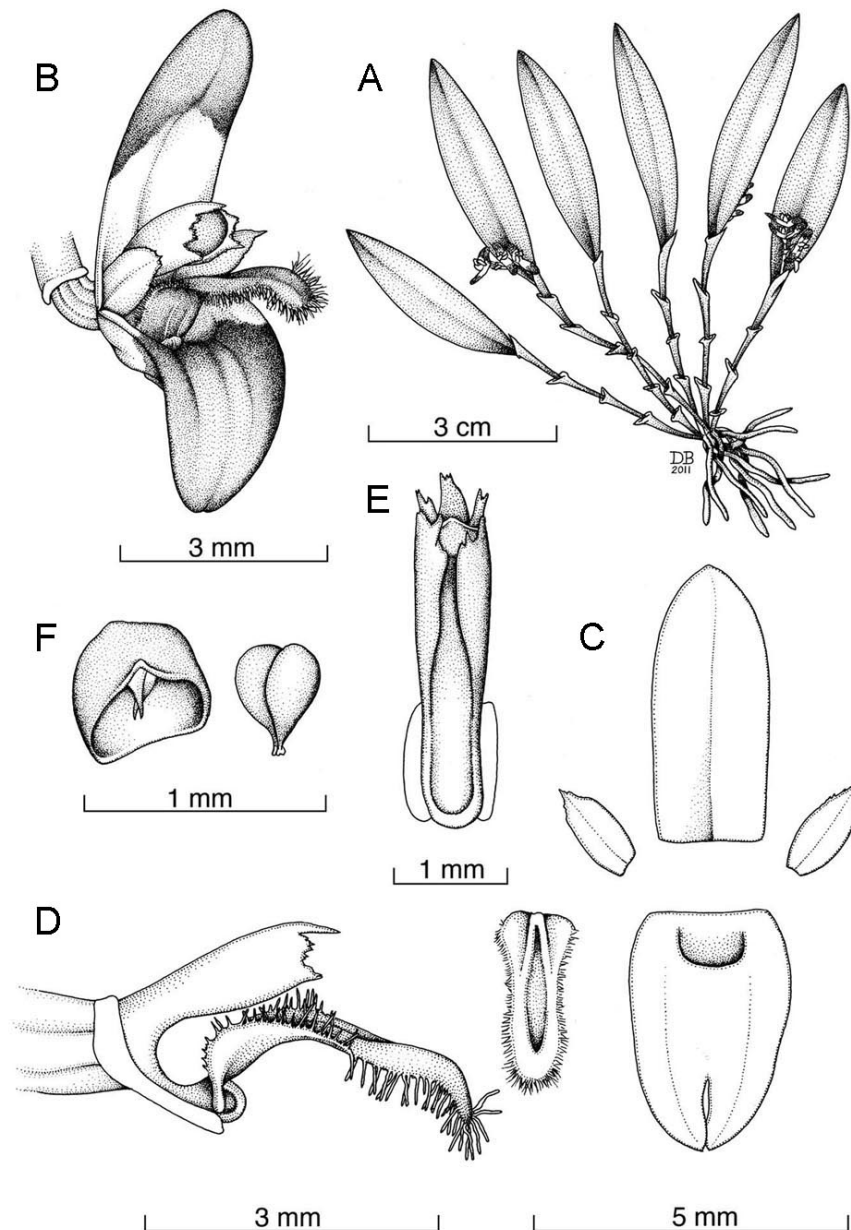


Figure 71. *Trichosalpinx reflexa*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Column, ventral view. F – Anther cap and pollinaria. Drawn by D. Bogarín from *D. Bogarín 1674* (JBL-spirit).

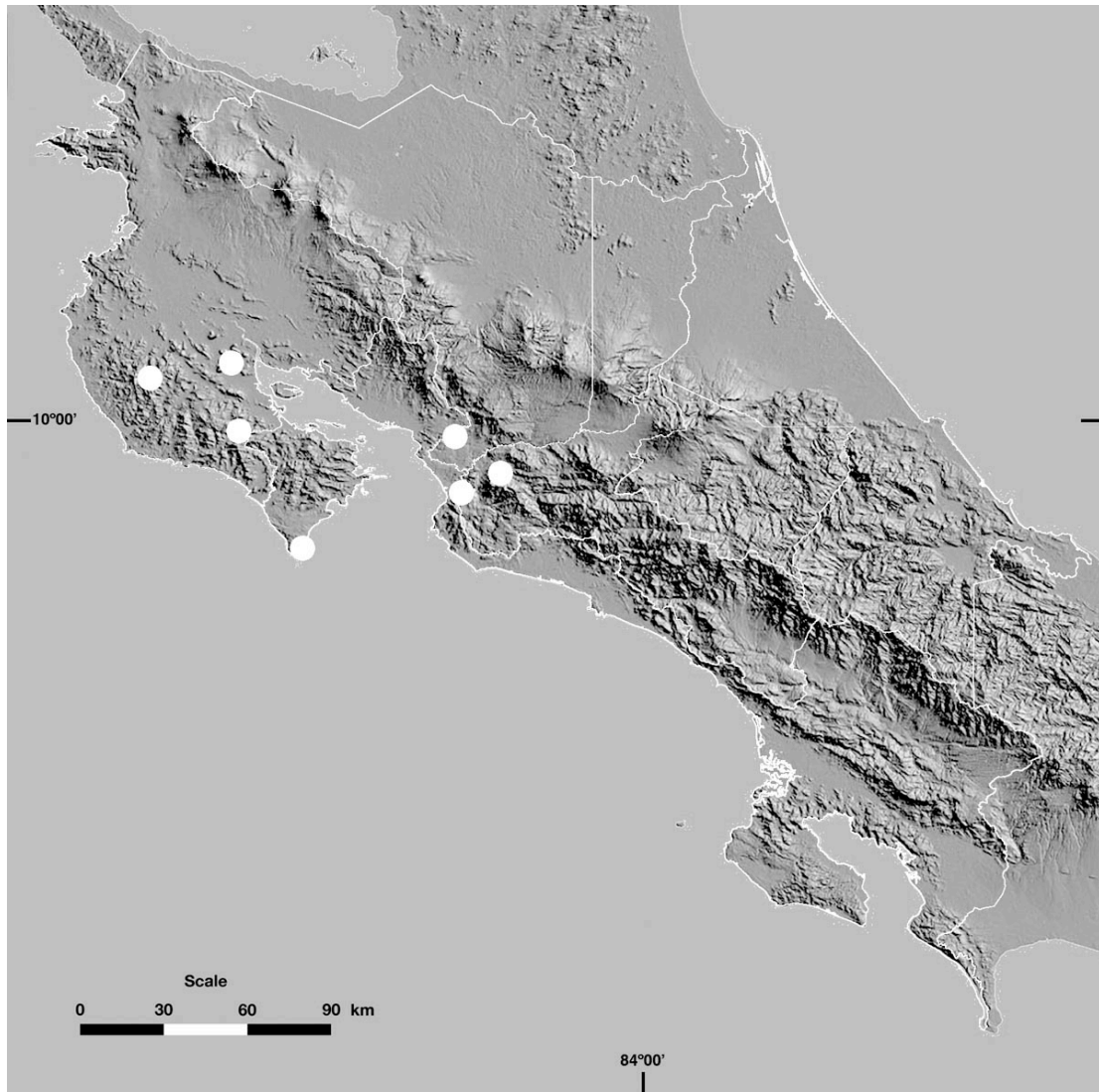


Figure 72. Distribution map of *Trichosalpinx reflexa* in Costa Rica.

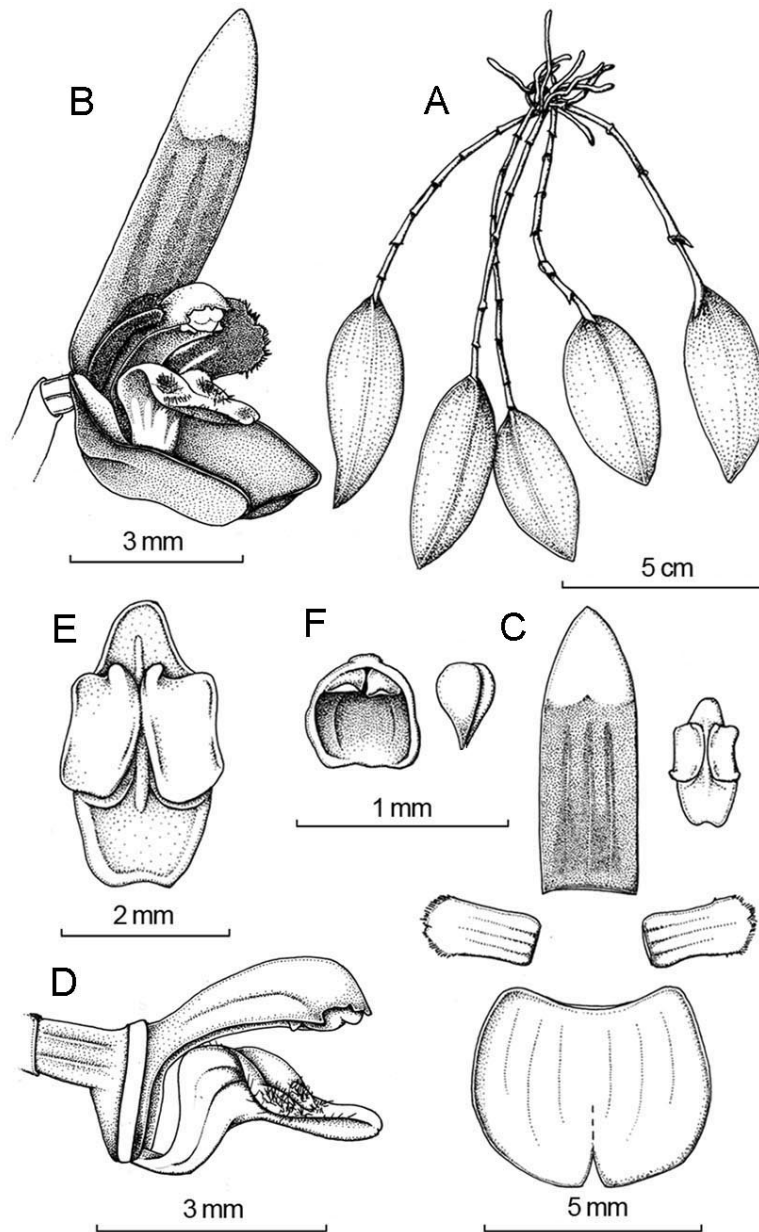


Figure 73. *Trichosalpinx ringens*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Anther cap and pollinaria. Drawn by M. Fernández from *D. Bogarín* 7187 (JBL-spirit).

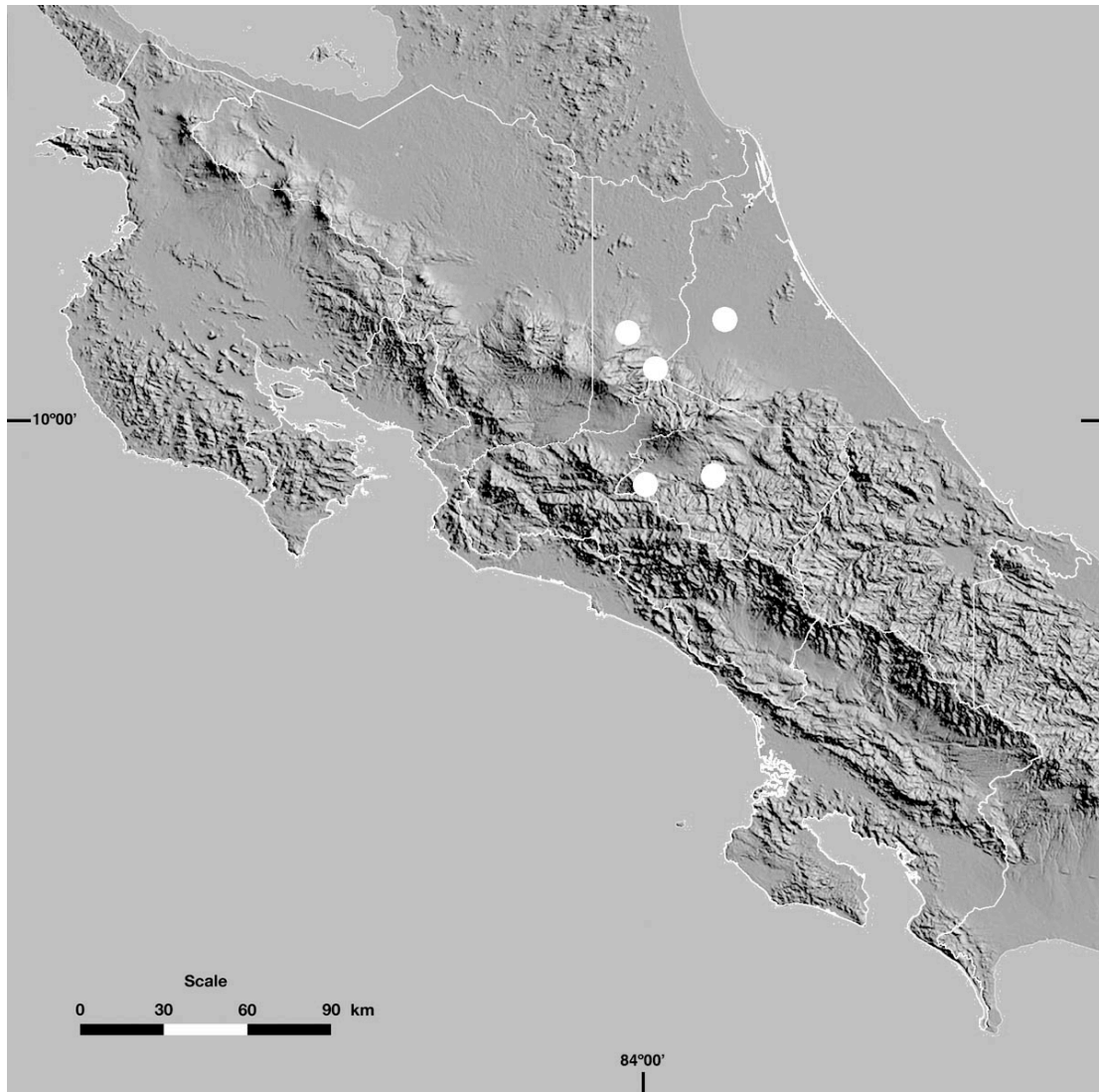


Figure 74. Distribution map of *Trichosalpinx ringens* in Costa Rica.

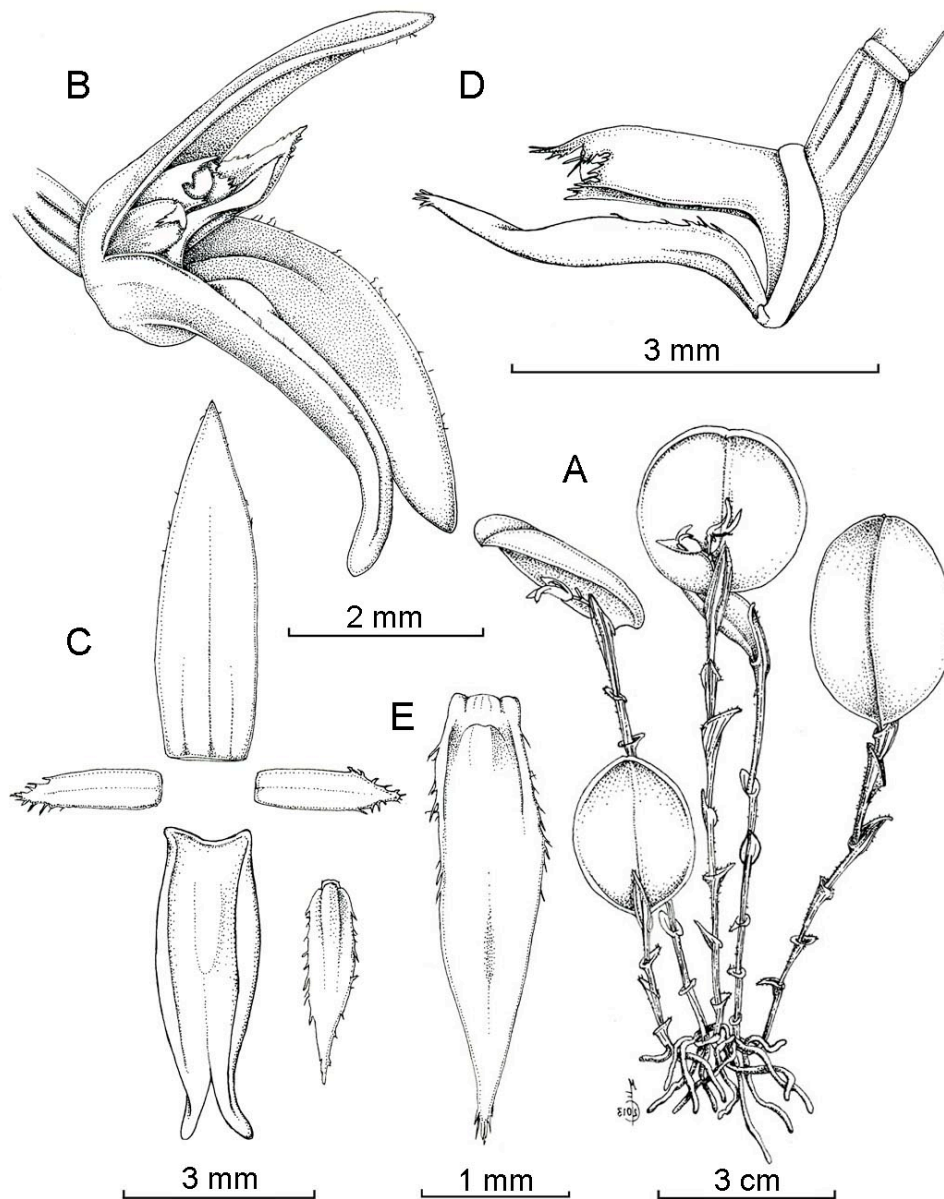


Figure 75. *Trichosalpinx rotundata*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. Drawn by M. Fernández from A. Karremans 4120 (JBL-spirit).

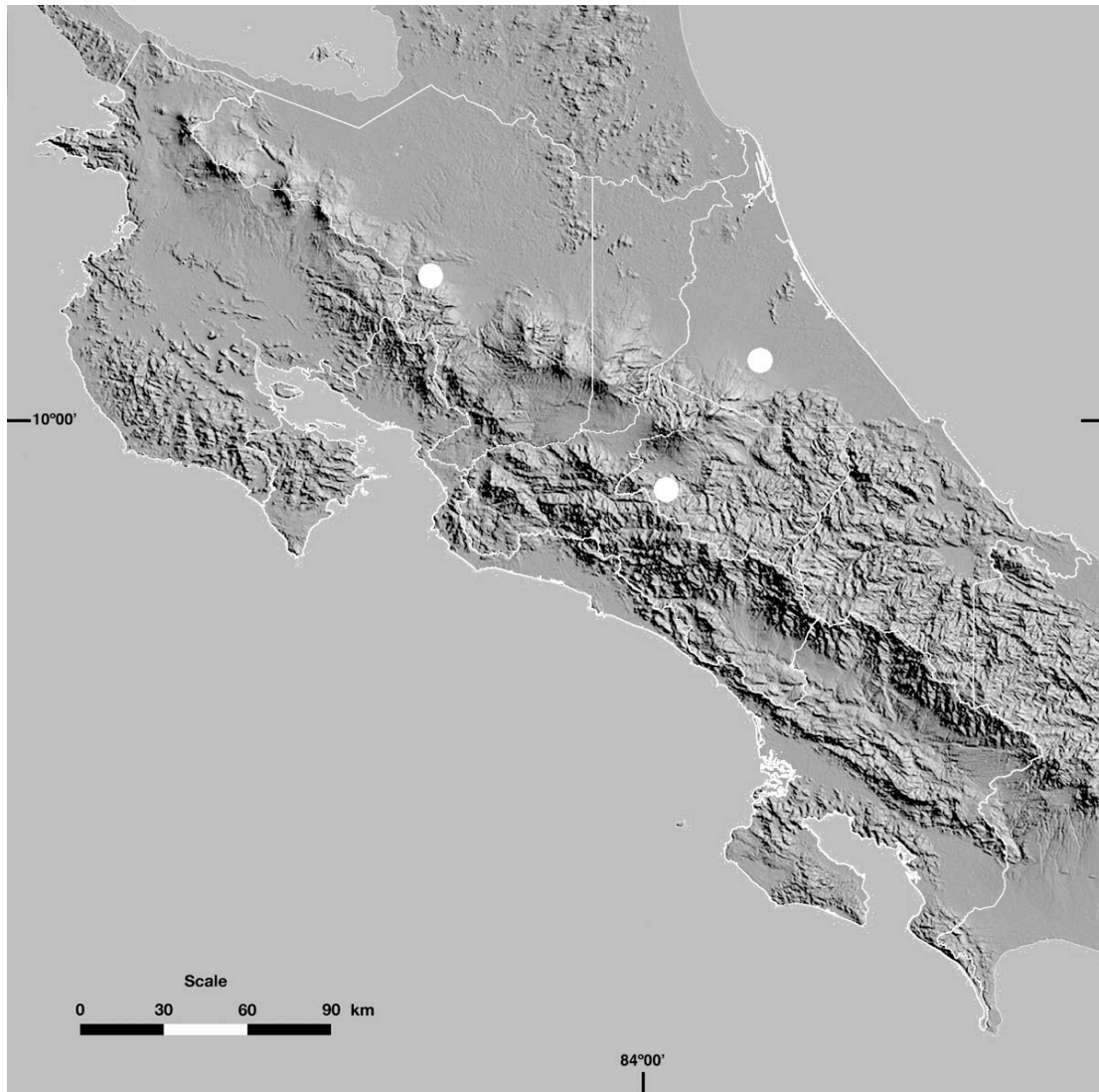


Figure 76. Distribution map of *Trichosalpinx rotundata* in Costa Rica.

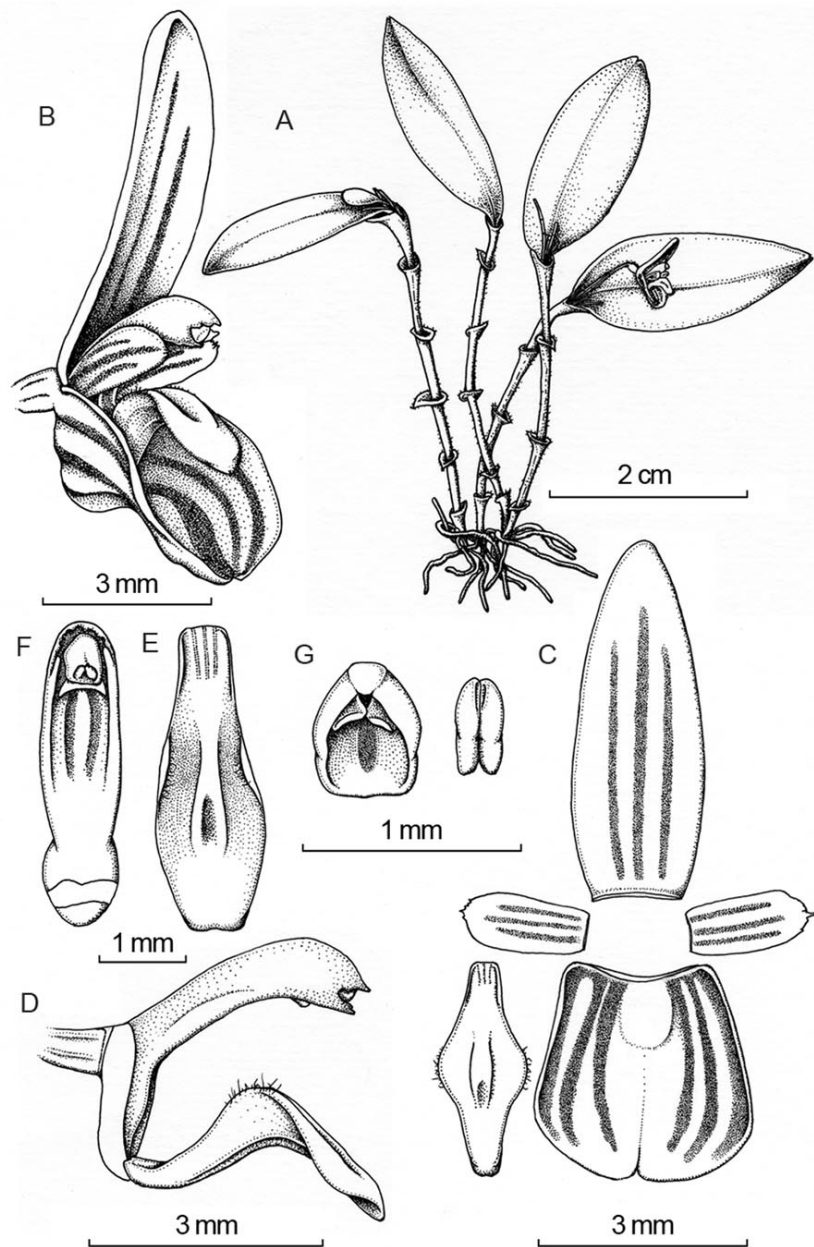


Figure 77. *Trichosalpinx sanctuarii*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Column, ventral view. G – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández 529* (JBL-spirit).

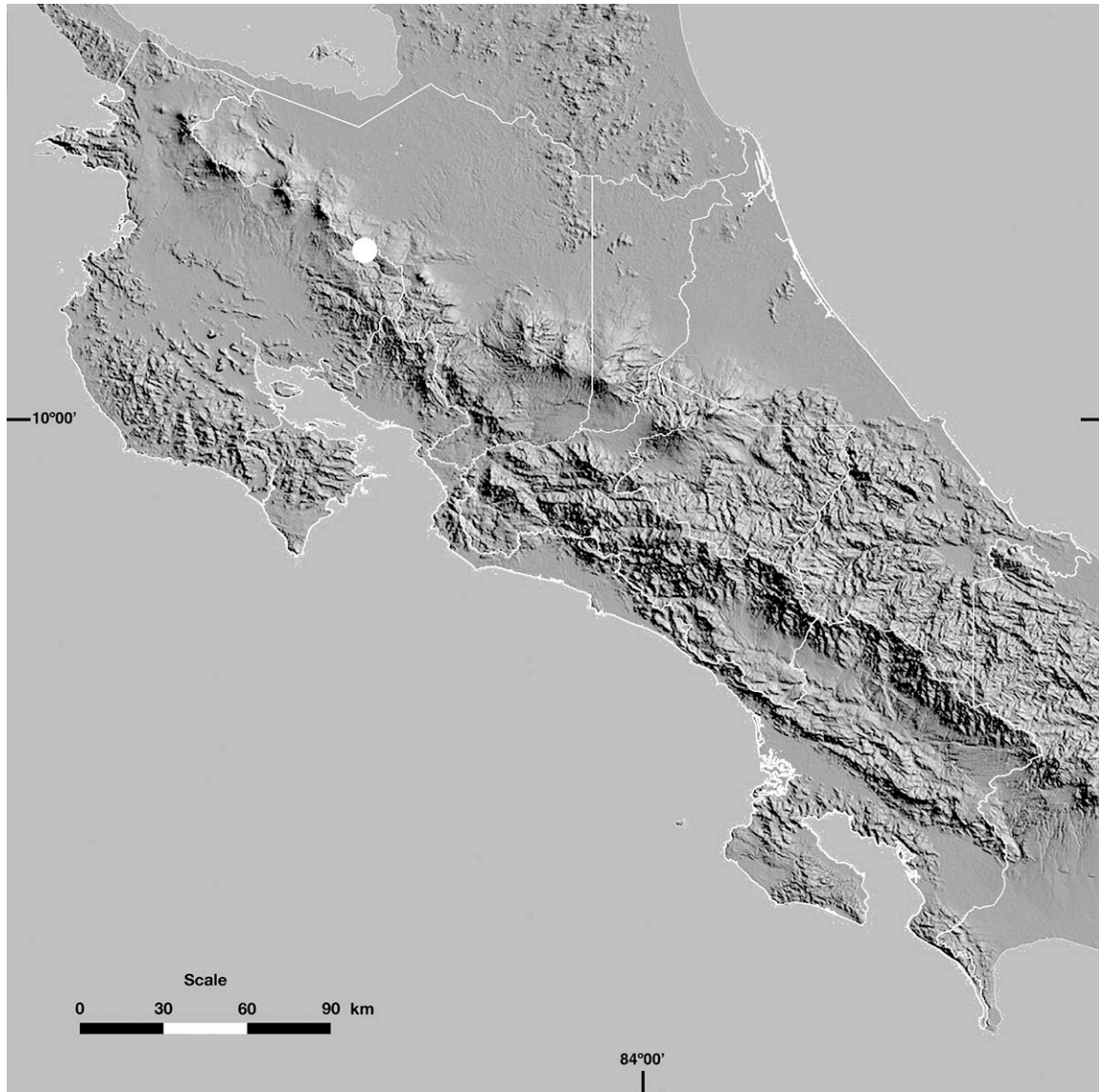


Figure 78. Distribution map of *Trichosalpinx sanctuarii* in Costa Rica.

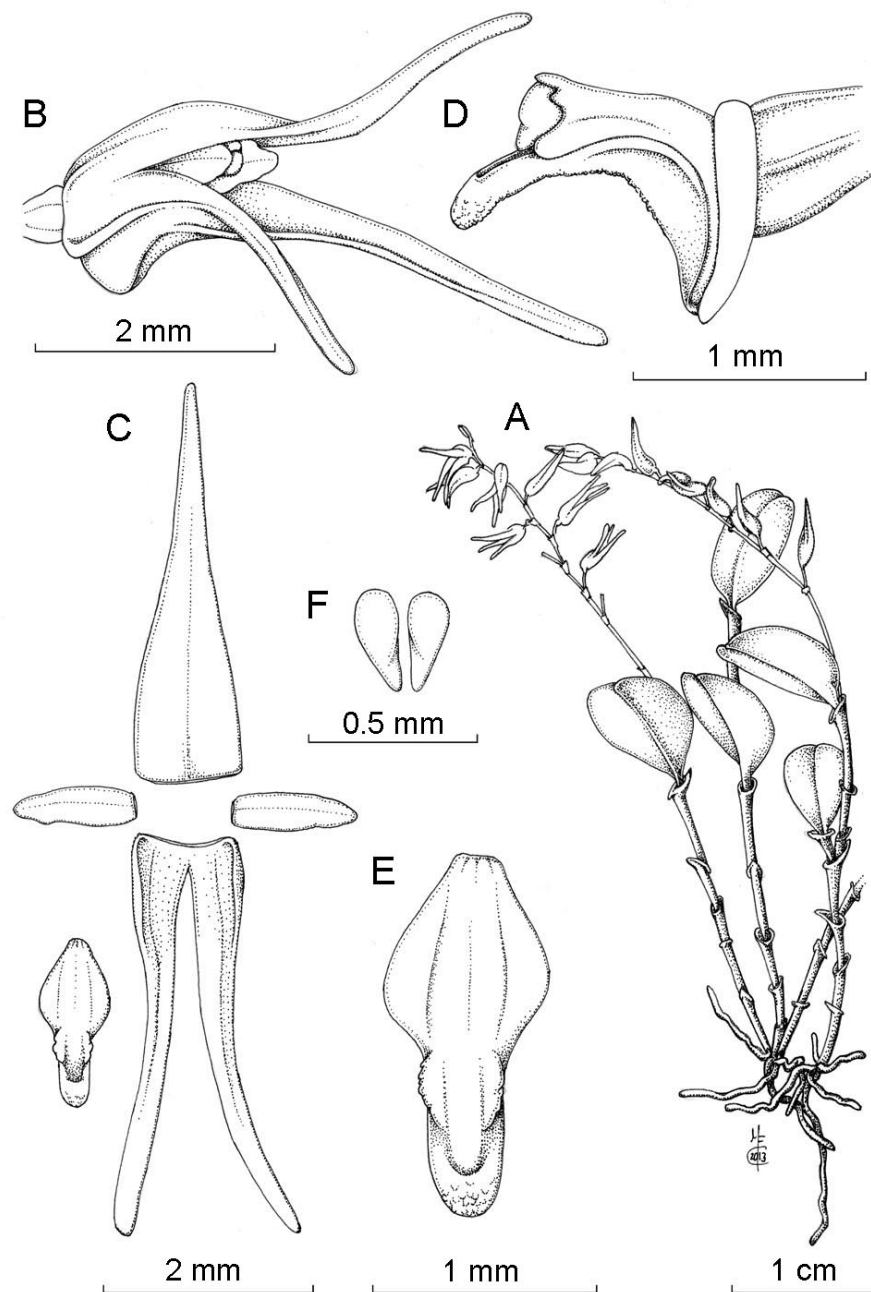


Figure 79. *Trichosalpinx todziae*. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Pollinaria. Drawn by M. Fernández from *D. Bogarín 49* (JBL-spirit).

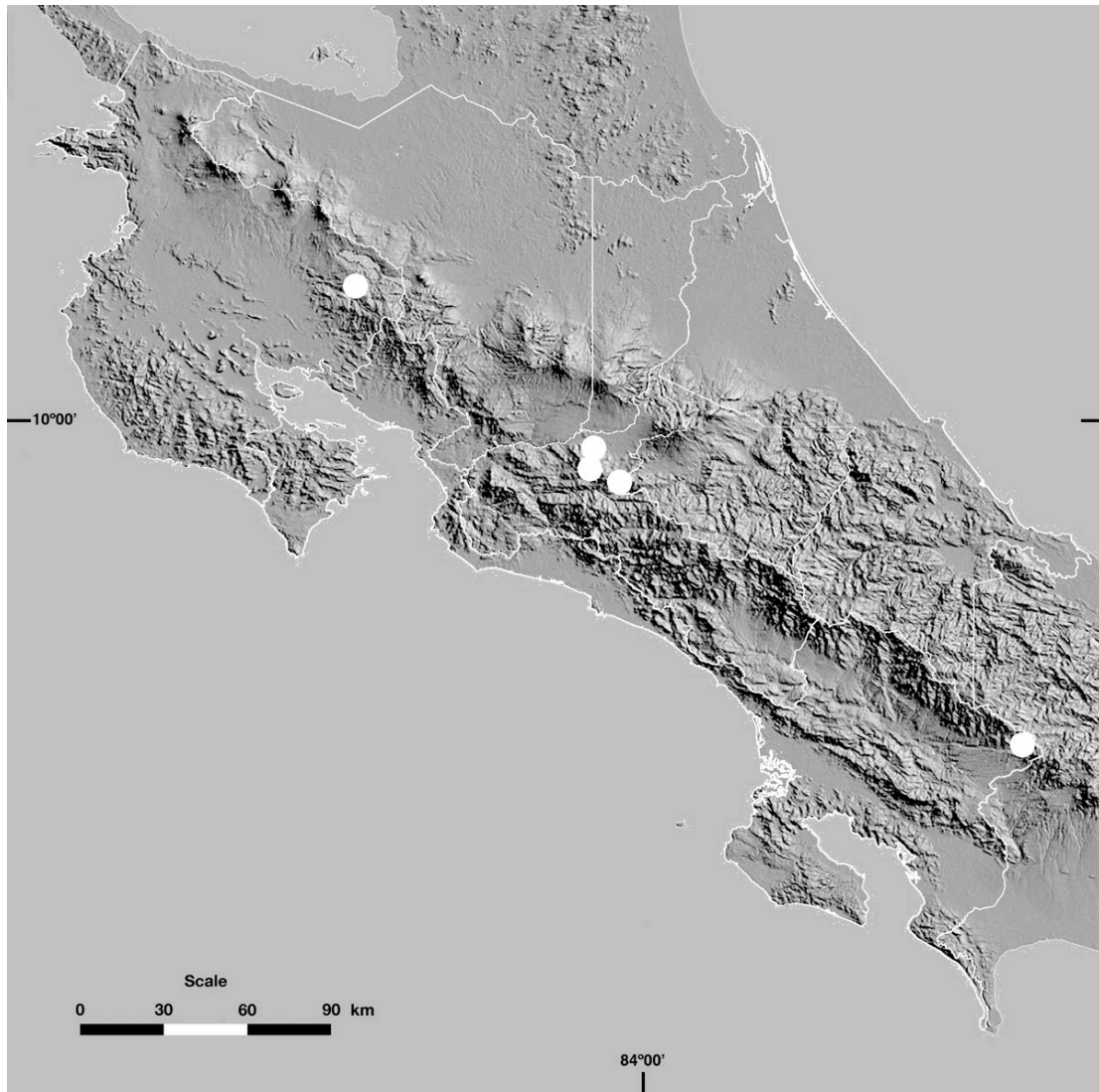


Figure 80. Distribution map of *Trichosalpinx todziae* in Costa Rica.

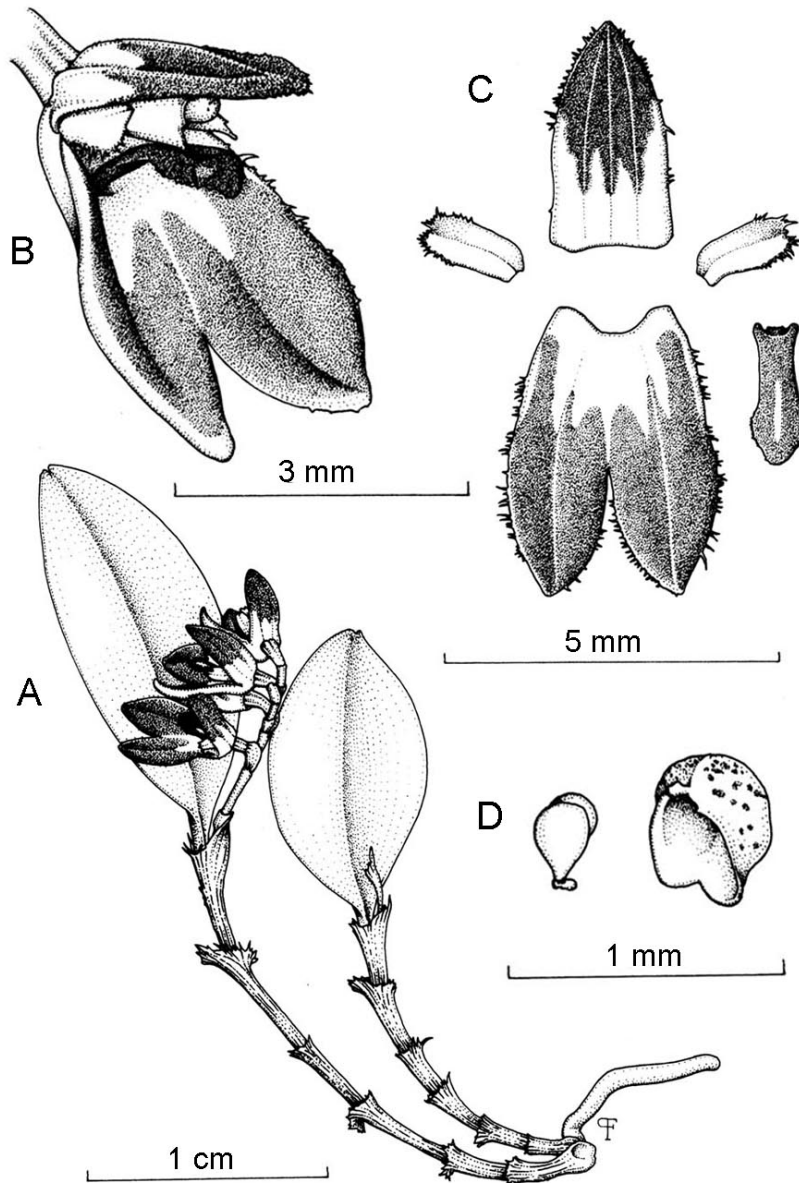


Figure 81. *Trichosalpinx trachystoma* from type locality. A – Habit. B – Flower. C – Dissected perianth. D – Pollinaria and anther cap. Drawn by F. Pupulin from F. Pupulin 101 (USJ, possibly lost).

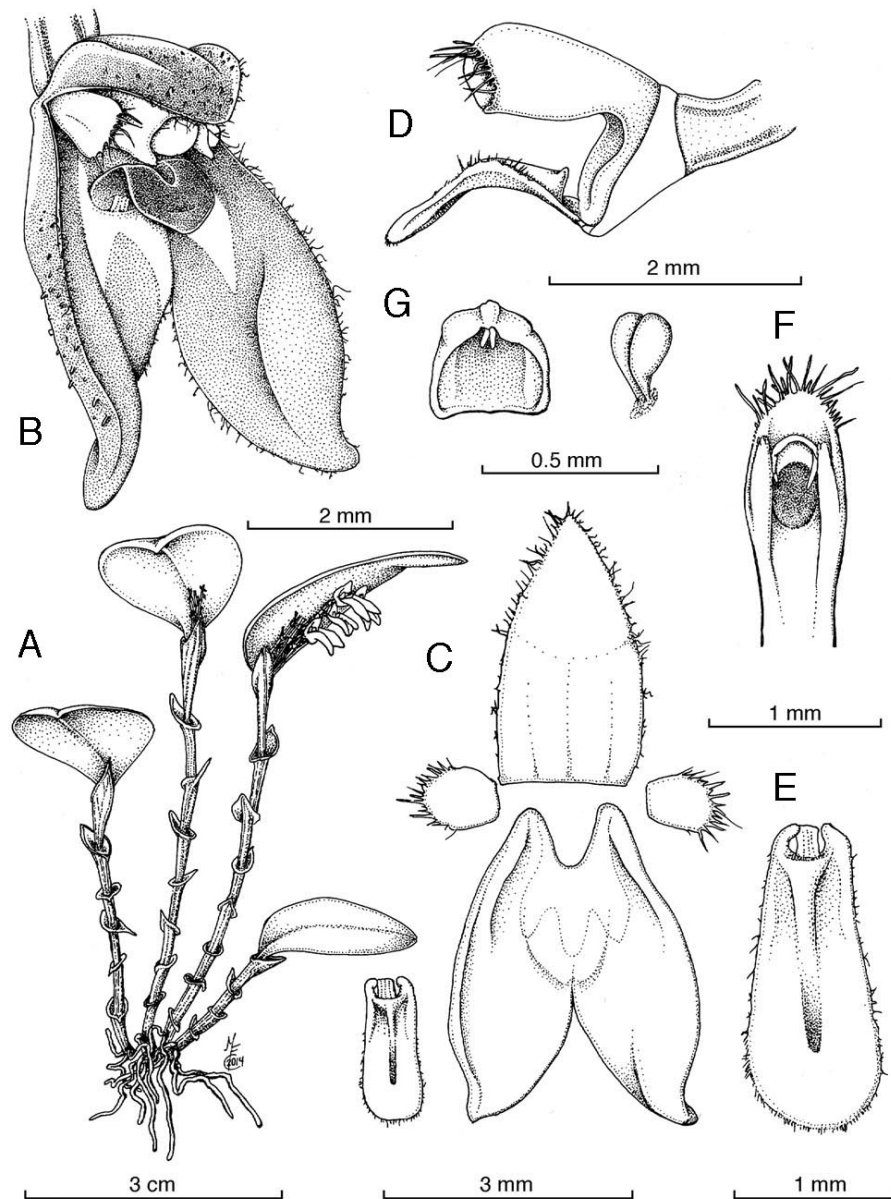


Figure 82. *Trichosalpinx trachystoma* from Tilarán, Guanacaste. A – Habit. B – Flower. C – Dissected perianth. D – Lip and column, lateral view. E – Lip, ventral view. F – Column, ventral view. G – Anther cap and pollinaria. Drawn by M. Fernández from *M. Fernández* 536 (JBL-spirit).

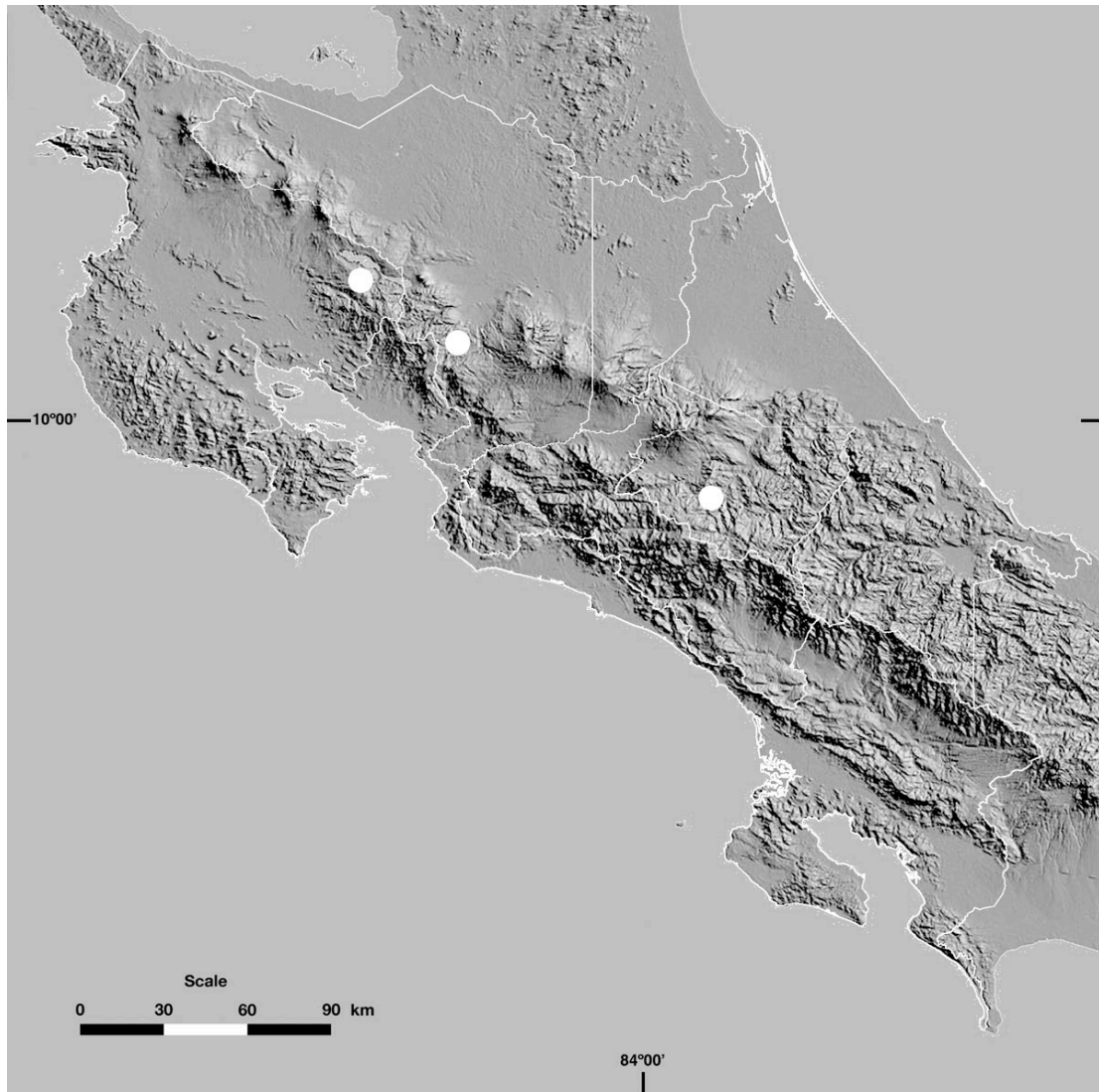


Figure 83. Distribution map of *Trichosalpinx trachystoma* in Costa Rica.