A REVISION OF THE GENUS TRICHOCENTRUM (ORCHIDACEAE: ONCIDIINAE)\textsuperscript{1}

FRANCO PUPULIN

Via Correggio 57, 20149 Milano, Italy

ABSTRACT: A taxonomic revision of the genus Trichocentrum is presented. The history of the genus is highlighted and phylogenetic relationships are discussed. Twenty-three species are recognized, pertaining to seven natural groups. Characters of each group are discussed and keys to groups and species are included. Two new species, \textit{T. estrellense} and \textit{T. wagneri}, are described.

\textbf{The Discovery} of the first species of \textit{Trichocentrum} predates its formal description by some 50 years. It was found by Hipólit Ruiz and José Pavón during the Spanish Expedition Botánica of 1777–1788 to the vice-kingdom of Peru (now Peru and Chile). A plate of what would later be described as \textit{Trichocentrum pulchrum} Poepp. \& Endl., by Isidro de Gálvez, second illustrator of the expedition, is kept at Royal Botanic Garden of Madrid under the name \textit{Orchis punctata} (Real Jardín Botánico, IV, 1252). This watercolor well illustrates the habit of the species and has a floral detail showing the column and the spurred lip with pedicel. Though it bears no date, the plate was most likely completed before March 1778 when Gálvez left Lima and returned to Spain together with Ruiz and Pavón. Unfortunately this plate, as well as most of the drawings intended for Ruiz and Pavón’s \textit{Flora Peruiana et Chilenis}; was never published; only three volumes of the projected series of twenty were printed between 1798 and 1802 (Cabello Martín et al., 1988).

Eduard Friedrich Poeppig and Stephan Ladislaus Endlicher proposed the genus \textit{Trichocentrum} in 1837 based on a flowering plant Poeppig collected in Peru in 1830 near Pampayacu in northern Huánuco province along the eastern slopes of Cordillera Central. In 1881 Bentham assigned the genus to subtribe Oncидеae, encompassing only New World genera. Later Schlechter (1926) divided the genera of Bentham’s Oncidéeae into twelve different subtribes; \textit{Trichocentrum} was referred to subtribe Trichocentreae on account of its spurred lip, excavated stigma and the absence of a column foot. In Schlechter’s posthumous classification this subtribe appears closely related to Comparettieae, from which it may be easily separated on the basis of the free lateral sepals and the lack of any appendages at the base of the lip (Schlechter, 1926). This classification was largely followed by Schweinfurth (1959). Dressler and Dodson (1960) restored subtribe Oncidéeae \textit{(sensu Bentham)}, dividing it into three major alliances; \textit{Trichocentrum} was placed in the \textit{Oncidium} complex. Dressler (1981), examining phylogenetic relationships within Oncidéeae, considered the spur of \textit{Trichocentrum} primitive for the subtribe, and stressed the close relationships of \textit{Trichocentrum} with the so-called “rat-tail” \textit{Oncidium} section \textit{Cebolleta} and “mule-ear” \textit{Oncidiums}, \textit{Oncidium} section \textit{Plurituberculata}, and proposed these two sections may be separated as the genus \textit{Loipharis} Raf. Williams and Dressler (ined., cited in Dressler, 1981) suggested that the whole \textit{Oncidium} complex evolved from a common \textit{Trichocentrum}-like ancestor, the tabula infrastigmatica being derived from a partial fusion of the lip with the column base, as in \textit{Trichocentrum}.

Chase (1986, 1986b) proposed a new realignment of the oncioidi genera based on a series of previously overlooked and/or underutilized floral and vegetative characters, including chromosome number and life history. In this preliminary scheme \textit{Trichocentrum} is considered to be an

\textsuperscript{1} Gratitude is extended to the curators at AMES, BR, CR, FLAS, K, P, RPSC, SEL, USJ, and W for the loan of photographs and critical specimens. Special thanks are acknowledged to J. T. Atwood, C. H. Dodson, R. L. Dressler and G. A. Romero for their useful suggestions and critical comments to the manuscript.
anomalous genus. The unique combination of floral features, vegetative morphology and low chromosome numbers (2n=24, 28) suggest an evolutionary path independent from other oncidioioid orchids. However, the convex structure of Trichocentrum stipe is also represented in Oncidiinae in Oncidium sections Cebolleta and Plurituberculata. This shared character, together with a low chromosome count, vegetative architecture (i.e. pseudobulb reduction), and site preferences (i.e. eliophytism) seems to support Dressler's hypothesis that placed Trichocentrum close to Oncidium sections Cebolleta and Plurituberculata (Dressler, 1981). A recent study by Chase and Palmer (1992), using chloroplast DNA (cpDNA) restriction sites of the Oncidiinae, effectively reduces the gap between the two schemes of phyletic relationships. As suggested by Dressler (1981), Trichocentrum is assigned to the Lophiarias clade, but on the basis of its low chromosome number, it now occupies a derived position within the group. Based on these findings, Dressler (1993) treated Trichocentrum as a subgroup of section Plurituberculata. If this clade were elevated to the rank of genus, Trichocentrum would have priority over Lophiarias (Dressler, 1993). The genus Lophiarias, however, was recently resurrected by Braem (1993) applying it only to the species of Oncidium section Plurituberculata, with the exception of Oncidium splendidum A. Rich. Braem (1993) did not refer the species of Oncidium sect. Cebolleta to Lophiarias based on differences in vegetative habit and pollinarium morphology.

Trichocentrum, as circumscribed herein, includes some 23 species of epiphytic plants found from southern Mexico to Brazil, Bolivia and Peru. The generic name Trichocentrum refers to the presence of a slender and flexuous spur (from the Greek words trichos, hair, and kentron, spur), a feature characteristic of T. pulchrum and its close relatives. However, only half of the Trichocentrum species currently recognized fit this generic concept. The other species vary greatly in spur morphology, presenting a short and gibbose, plurilobulate, saccate, or clavate spur. Differences in spur shape are consistently associated with gross floral and micromorphological traits. An attempt to group the different taxa on the basis of such unique sets of shared floral features is supported by their geographic distribution that shows at least four major patterns (Fig. 3, 7, 10, 12).

Evolution of the spur in Subtribe Oncidiinae

In spite of the unique habit it shares with members of the Lophiarias clade, Trichocentrum presents a radically different floral morphology and its pollination is carried out by fragrance-collecting euglossine bees (van der Pijl and Dodson, 1966), whereas the Lophiarias clade has evolved deceit pollination. Furthermore, the spur of Trichocentrum, a non-functional nectary involving only labellum tissue, is unique among the Oncidinae. The papillose-hirsute internal walls of the spur in some Trichocentrum species (Pupulin & Mora-Retana, 1994) is also a unique feature in the subtribe. A labellar spur is common in many vandoid genera, mainly in Andraeanae and Aerangidinae and in their Neotropical relatives (Campylocentrum and Dendrophyllax), and is found in members of Cyrtopodinae (Galeandra), but it represents an exception among the Oncidinae, if not among the whole tribe Maxillariae (sensu Dressler, 1993). A labellar nectar cavity is present in Leochilus, Goniochilus and Ionopsis, but this cavity is merely a receptacle to collect the nectar secreted by the column, and it is perhaps primitive in the rodriguezioid group. Also the presence of a tubular spur is not uncommon in the Oncidinae, and it can be found in many genera such as Rodrigueza, Comparetia, Dian- dienium, and Plectropha. A somewhat rudimentary cavity is also present in the distant genus Brchtia, strictly related to the Ada, Brassia and Aspasia complex. In Oncidinae genera, however, the spur is mainly formed by the partial fusion of lip base and lateral sepals, while columnar tissue may sometimes produce one or more “horns” within the sepals cavity, as in the case of Comparetia, Sceochilus, Dianidium and other rodriguezioid genera. A somewhat complete and graduate succession of nectary shapes can be observed in Oncidinae, from the simple nectar cavity of Leochilus, Goniocithus and Ionopsis, through the tubular nectar cavity of Plectropha to the tubular nectar spur with lip-column “horns” of Comparetia, Rodrigueza, Sceochilus, etc. (Fig. 1). The characteristic spur of Trichocentrum, derived of labellum tissue alone, is unique among strictly Neotropical orchids. Recent molecular studies (Chase and Palmer, 1992) highlight the different origins of the Trichocentrum spur, grouping together all the “spurred” Onci-
Fig. 1. Longitudinal section of column, lip and lateral sepals in some “spurred” Oncidiinae. A. Brachitia sulfurea, Venezuela (from Dunsterville & Garay, 1979); B. Leochilus tricuspidatus, Costa Rica (adapted from Chase, 1986b); C. Goniochilus leochilinus, Costa Rica (F. Pupulin 171); D. Rodriguezia compacta, Costa Rica (F. Pupulin s.n.); E. Scelochilus paraguaënsis, Venezuela (adapted from Dunsterville & Garay, 1979); F. Comparattia speciosa, Brazil (cult. A. Wagner s.n.); G. Trichocentrum candidum, Guatemala (O. Mittelstaedt s.n.); H. Trichocentrum dianthum, Costa Rica (F. Pupulin 20); I. Trichocentrum fuscum, Brazil (Seidel s.n.). Bars = 1 cm.
diinae into a unique Rodriguezia clade (mainly composed by twig-epiphytes), with the unique exception of Trichocentrum, that the authors consider, phylogenetically, an artificial genus. I hope a revision of Trichocentrum may contribute to better understand its relationships with the main corpus of the Oncidiinae and Lophiariu complex. In spite of a certain number of common features, Trichocentrum species in fact present very different traits, and some of these characters may prove useful to recognize the occurrence of several, different natural groups within the genus.

Characters used in groups and species delimitation

Habit and size—Species of Trichocentrum have a generally similar habit and are extremely variable with respect to plant size. Gross differences in size do exist among different groups of taxa (i.e., plants of Trichocentrum candidum group are generally smaller than taxa pertaining to Trichocentrum fuscum group). However, the size of individual plants can be excessively influenced by environmental elements, and the great variation within populations results in size being of no practical utility for taxonomic purposes.

Roots—Trichocentrum species share the same basic root structure which is typical of the subtribe, with long pericyclic cells, a broad-celled cortex, a thin layer of endodermis cells and 3—4 layers of velamen cells. Major variations are associated to the thickness of the cortex, resulting in different root diameters, that can vary from 0.8 to 1.9 mm. Such a difference, however, is chiefly consistent within well defined species complexes, and the character has but a little practical value in delimiting species.

Pseudobulbs—Trichocentrum pseudobulbs are very small, usually less than 0.5 cm in diameter, and vary in shape from subglobose to elliptical—ovate to cylindrical. The latter type is generally longer, being sometimes 1.0 cm long. Variations in pseudobulb size, however, appear to be consistently associated to the dimension of the apical leaf, thus resulting of no value in species delimitation.

Leaves—Leaf shape, coloration and thickness are variable characters in most of Trichocentrum species. As a general rule, T. tigrinum and some other species show leaf adaptation to eliohyphyism (i.e., red-purple pigmentation) or hydic stress, whereas leaves of most of the species are typical of shadow-growing, moist dependent epiphytes. Although such differences have been used to delimit species (Reichenbach, 1876; Rolfe, 1893; Beckner, 1961; Schweinfurth, 1945), variations in these characters are mainly dependent on environmental elements and may also vary within individuals.

Inflorescence—Most Trichocentrum species present successive inflorescences producing three to many flowers over a long period. In many cases, if pollination does not take place along the principal axis of the inflorescence, racemes may freely branch becoming paniculate, but T. caloreras also show primarily paniculate inflorescence. Single-flowering inflorescences are not uncommon in South American taxa. Simultaneous, two-flowered, sometimes multi-branched inflorescences can be found in some species complexes; a multiflowered and simultaneous inflorescence type has been also recorded (Schweinfurth, 1946). Though generally ignored, inflorescence type and number of flowers are useful characters to distinguish species.

Ovary—Most of Trichocentrum species possess terete to subclavate ovaries, with the exception of the species closely related with Trichocentrum pulchrum, that can be easily distinguished from Trichocentrum fuscum group on the basis of their unique triquetrous ovary.

Sepals and petals—Differences in shape and size of the sepals and petals have been used in differentiating species (Lindley, 1850; Reichenbach, 1883; Schlechter, 1923). Flowers of Trichocentrum generally bear similar sepals and petals, varying in shape from elliptic to linear-elliptic to elliptic-ovate. Sepals vary in length from 5 mm to about 30 mm. Spreading or closed sepals and petals permit to delimit some taxa. Size differences among species can be observed and utilized in delimiting species complexes, but the strong dependence of flower size on environmental elements reduces the practical value of this character for species delimitation.

Labellum—Shape and ornamentation of the labellum are some of the most useful characters to distinguish groups and species within Trichocentrum. Labellum morphology has been extensively used in the classification of the genus (Reichenbach, 1876; Kränzlin, 1897; Lindley, 1850; Schlechter, 1923; Garay, 1970; Pupulin, 1994; Pupulin
& Mora-Retana, 1994), and differences among taxa are sufficiently consistent to assume practical value in species delimitation. General shape of the lip, shape and number of the basal calli, presence or absence of lateral lobes, degree of apical and lateral margins of the labellum were used in the present analysis.

Spur—The length of the spur has been used to distinguish similar taxa (Rolfe, 1894, 1913; Teuscher, 1961), but this sole character proved to be rarely critical in distinguishing species pertaining to the same group. Shape characters that proved to be useful in delimitation of species complexes include lobulate, cylindric, and clavate spurs. Also the indumentum of the internal walls of the spur may be utilized to distinguish groups of taxa. On the contrary, number of spur lobes in taxa presenting lobulate spurs has not practical value in differentiating species, and many observations confirmed the variability of this character also within different flowers on the same inflorescence. Although some early workers emphasized the grade of spur sinuosity in long-spurred taxa as a diagnostic character (Lindley, 1843; 1854; Reichenbach, 1883), the great variability of this character within populations results of unpractical value for taxonomic work.

Column—Apart from a few cases (Reichenbach, 1854; 1869; 1881; 1883), morphological characters of the column have been largely neglected in delimiting species concepts within Trichocentrum. Columnar characters contributed to the delimitation of some taxa in this treatment. Trichocentrum species generally share the same basic structure of the gynostemium, with a short, stout, winged column and a broad stigma, but the wings may show considerably differences between closely related taxa. Useful characters include presence or absence of glandular appendages at the column apex, shape, color and margins of the wings.

Anther—Indumentum type of the operculum is a consistent character and it has been used in this treatment to delimit species within some groups.

Pollinarium—Although generally ignored in species descriptions, pollinarium characters may prove to be useful in delimiting different taxa within the genus. The main differences in pollinarium involve stipe morphology and the degree of movement after it is removed from the column. These include the grade of reflexion of distal margins and the placement of pollinia in various positions. Such characters were not used here to distinguish different taxa because of the limited information available on the pollinarium morphology of many Trichocentrum species.

**TAXONOMY**


Perennial herbs, epiphytic, with vegetative buds developing from the base of the previous growth on a reduced rhizome. Pseudobulbs more or less inconspicuous, ovoid or rounded to cylindric, generally concealed by scarios. Roots filiform or fleshy, glabrous, somewhat branched, arising from the base of the new pseudobulb, whitish with green apex. Leaves single, only occasionally in pairs, articulate at the apex of the pseudobulb, fleshy to coriaceous, usually small, suberect to arcuate or pendent, persistent; varying in outline from ovate to oblong-elliptic to ligulate, usually widest in basal half, mor or less gradually narrowing to a sessile base. Inflorescence basal or terminal, simple or racemose, somewhat branched, arising from the base or near the insertion of the leaf of the last pseudobulb; peduncle terete suberect, arching or pendent with two or more lanceolate acute bracts; rhachis usually fruticul. Flowers often large, showy and sometimes fragrant. Sepals and petals free, subsimilar, usually spreading, with acute to emarginate apex. Lip adnate to the base of the column, suberect, simple or obscurely three-lobed, concave, flat or convex, with or without calli or ridges near the base, producing with the column base a slender or gibbous or clavate, short or elongate spur. Column short, stout, adnate to the lip, auriculate or winged above, without a foot. Clinandrium commonly shallow, with entire margins. Anther cuculate to emispherical, with 2 cells, glabrate to hirsute. Pollinia 2, notched to complanate, on a triangular more or less elongate stipe often with reflexed margins; viscidium peltate or ovoid.

**DISTRIBUTION:** About 23 species wide-

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spread from southern Mexico through Central America southward to Brazil, Bolivia, and Peru.

**Key to the Groups of Trichocentrum**

1a. Spur gibbous, 2–4-lobed, or clavate .......................... 2
2a. Spur short, less than 5 mm long, 2–4 lobed; lip elliptic-ovate .................................................. *T. candidum* group
2b. Spur longer than 10 mm, clavate; lip pandurate ........................................... *T. hoegelii* group
1b. Spur slender, conic or tubular .......................... 3
3a. Lip with two lateral, erect, falcate lobes near the base .................................................. *T. pflavii* group
3b. Lip without lateral, erect, falcate lobes near the base .................................................. 4
4a. Spur longer or equaling the lip, flexuous to uncinate .................................................. 5
5a. Ovary triquetrous; disc thickly bicarinate .................................................. *T. puelchrum* group
5b. Ovary not triquetrous; disc with two to four slender carines ........................................... *T. fascum* group
4b. Spur shorter than lip, linear .................................................. 6
6a. Lip concave, strongly narrowed above; flowers campanulate, produced on successive inflorescence .................................................. *T. brachyceras* group
6b. Lip flat to slightly convex, with dilated lamina; flowers spreading on 1–2-flowered, simultaneous inflorescences .................................................. *T. tigrinum* group

Relationships between *Trichocentrum* groups suggested here are summarized in Fig. 2.

**Trichocentrum candidum** group

This group includes six species presenting a gibbous, saccate, 2–4-lobed spur, namely *T. brevesii* Schltr., *T. caloceras* Endres & Rchb.f., *T. candidum* Lindl., *T. capistratum* Linden & Rchb.f., *T. costaricense* Mora-Retana & Pupulin, and *T. cymbiglossum* Pupulin. Apart from the rather obscure *T. brevesii*, known only from a copy of Schlechter’s drawing of the type, all the species within the group present a delicate, semi-hyaline texture, with similar sepals and petals varying in colour from white to greenish-white or brownish yellow. The lip is flat or concave, without any callosity or with two obscure thickened keels near the base. Furthermore, all the taxa invariably present filiform roots, a successive inflorescence and a gibbous, short, 2–4-lobed spur. The stipe is mobile in all the species, and strongly reflects its lateral distal margins after a few seconds from removal. Pollinia are entire, and they do not overlap after reflection of the stipe. All the species are morphologically very well differentiated from the main body of the genus, and their natural distribution confirms that they constitute a natural group. Besides *Trichocentrum capistratum*, the range of which extends southward to Colombia and Venezuela, all the remaining species in this group are restricted to Central America north of the Panama Canal. The greater concentration of species can be found in Costa Rica: only one species reaches the northern states of Veracruz and Guerrero in Mexico. This pattern suggests central Costa Rica is the center of distribution and the possibility of sympatric speciation in the group (Fig. 3).

**Key to the species of the Trichocentrum candidum** group

1a. Anther cap glabrous .................................................. *T. caloceras*
1b. Anther cap papilllose or hisrate .......................... 2
2a. Column wings decurrent, obtuse, with introrse apexes .................................................. *T. costaricense*
2b. Column wings ascending or porrect, acute, with somewhat revolute apexes .................................................. 3
3a. Lip narrow in the middle; flowers small (sepals and petals to 5–6 mm long); inflorescence erect to patent .................................................. *T. brevesii*
3b. Lip elliptic ovate or rhombic; flowers medium to large (sepals and petals longer than 15 mm); inflorescence pendulous .................................................. 4
4a. Lip shorter than sepals, acute to obtuse .................................................. *T. capistratum*
4b. Lip longer than sepals, retuse at apex .................................................. 5
5a. Lip obovate; column wings entire .................................................. *T. candidum*
5b. Lip broadly rhombic; column wings erose at the apex .................................................. *T. cymbiglossum*


**DISTRIBUTION:** Endemic to Costa Rica.
**REPRESENTATIVE SPECIMENS:** COSTA RICA. Alajuela: San Jerónimo, C. Wercklé 139 (B, destroyed). Without locality, Nehermann s.n. (B, destroyed).


**DISTRIBUTION:** Costa Rica and Panama.

**REPRESENTATIVE SPECIMENS:** COSTA RICA. San José: Perez Zeledón, San Juan de San Isidro, F. Pupulin 10 (USJ); Alto de San Juan, F. Pupulin & D.E. Mora-Retana 186 and 187 (USJ).
<table>
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<th>Group</th>
<th>Characteristic flower shape</th>
<th>Labellum shape</th>
<th>Spur shape</th>
<th>Type of inflorescence</th>
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Fig. 2. The subdivision of *Trichocentrum*. 


Fig. 4.


DISTRIBUTION: Mexico, Guatemala, El Salvador.


*T. pusillum* Lehm. in Herb. Kew., *Ms*.

DISTRIBUTION: Costa Rica, Panama, Colombia, and Venezuela.

REPRESENTATIVE SPECIMENS: COSTA
Fig. 4. *Trichocentrum candidum* Lindl. Voucher: GUATEMALA. Guanagasapa, Finca Santa María Buena Vista, O. Mittlstaedt s.n. (Herb. Pupulin).
PUPULIN—A REVISION OF TRICHOCENTRUM

RICA. San José: Pérez Zeledón, Alfombra de San Juan, F. Pupulin 3 (USJ); Las Nubes de Quizarrá, F. Pupulin & J. Cambronero 4 (USJ); Rivas, F. Pupulin & J. Cambronero 7 (USJ). Puntarenas: Cañas de Buenos Aires, J. Cambronero s.n. (USJ). PANAMA. Upper Chagres River, Powell 419 (AMES); Lake Gatún, Barro Colorado Is., J.D. Ackerman 1378 (SEL). Coclé: near the edge of El Valle de Antón, R. Dressler, C. Luer, J. Luer & P. Taylor 766 (SEL); lower part of El Valle de Antón, Hunter & Allen 384 (AMES); near Achiote, R. Dressler 3146 (FLAS); between Cerro Azul and Cerro Jefe, R. Dressler 3263 (FLAS); C. Luer, J. Luer & H. Butcher 9170 (SEL); El Valle de Antón, J. Cambronero s.n. (Herb. Pupulin); J.A. Fonseca s.n. (Herb. Pupulin). Without specific locality, R. Dressler 2832 (SEL). COLOMBIA. Boyaca: El Humbo, Lawrence 557 (AMES); Antioquia: Frontino, near Dabeiba, Lehmann 4633 (K, AMES); L.C. Vieira s.n. (Herb. Pupulin); San Carlos, G. Escobar 487 (AMES). VENEZUELA. Zulia: Cajimera, Perijá, C. Garcia E. s.n. (K); Colón, Río Catatumbo, D. Patrzek s.n.; Sierra de Perijá, Río Yasa, Steyermark & Fernandez 99625 (AMES).


DISTRIBUTION: Endemic to Costa Rica.


DISTRIBUTION: Endemic to Costa Rica.


Trichocentrum hoegei group

This group includes a single species endemic to Mexico, the spur of which is not conic or tubular, but clavate: *Trichocentrum hoegei* Rchb.f. It represents an isolated taxon, seemingly without any close relative. The species presents a subquadrate lip, with two small basal calli, surrounded by purple red nectar-guides. Its pollinaria shows the shorter stipe of the entire genus, with reflected distal margins. Pyriform, complanate pollinia are wide, entire, and do not overlap after reflection of the stipe. *Trichocentrum hoegei* is the only known species to have a clavate spur, and its isolated distribution in Mexico (Fig. 5) seems to support the hypothesis of an early segregation of this taxon from the main complex of the genus.

* T. hoegei Rchb.f., Gard. Chron. n.s. 16: 717. 1881. TYPE: MEXICO. Veracruz: near Cordoba, Hoege s.n. (Holotype, W; Illustration in Xenia Orch. 3: 69, t. 234, Fig. 6. 1890).

DISTRIBUTION: Endemic to Mexico.
Fig. 6. *Trichocentrum hoegelii* Rehder. Voucher: MEXICO, Oaxaca: Río Salado, M.A. Soto 4324 (Herb. Pupulin).
**Trichocentrum pfavii group**

This group also appears to have originated in Central America, and its species are limited to central and southern Costa Rica and the Chiriquí province in northern Panama (Fig. 7). *Trichocentrum pfavii* Rchb.f., *T. dianthum* Pupulin & Mora-Retana, and *T. estrellense* Pupulin & J.B. García are the only three species within the genus presenting short, erect lobes near the base of the lip, such as papillose-hirsute internal walls of the spur. Due to their vegetative and floral morphology these species are more similar to each other than to any other taxon in the genus. *Trichocentrum dianthum* exhale a strong, herbaceous perfume, that may be associated with some special pollination syndrome. It is also likely that the structure of the papillose spur plays a fundamental role in pollination of these taxa. The pollinators of these three species, however, are still unknown.

**Key to the species of Trichocentrum pfavii group**

1a. Spur more than 5 mm long; column wings with longitudinal brown stripes
1b. Spur less than 5 mm long; column wings white with brown spots at margins

2a. Lip flabellate, with very crisped apex; lateral lobes of the lip digitate
2b. Lip obovate, fleshy, with plane apex; lateral lobes of the lip short and rounded

* T. dianthum Pupulin & Mora-Retana, Selbyana 15: 90. 1994. TYPE: COSTA RICA. San José: Perez Zeledón, Las Nubes de Quizarrá, 1000 m,
epiphytic on short trees along a little river, J. Cambronero s.n. (Holotype, USJ).

DISTRIBUTION: Endemic to Costa Rica.


_T. estrellense_ Pupulin & J.B. García sp. nov. TYPE: COSTA RICA. Cartago: El Guarco, in valleys under Palo Verde, epiphytic in shadow on tall trees along a minor tributary of Río Reventazón, 1250 m, 30 Apr. 1992, _F. Pupulin_ 209 (Holotype, USJ; Isotype, Herb. Pupulin). Fig. 8.

Species _Trichocentrum pfavii_ similis, sed labello minore marginibus planis, lobulis lateralis abbreviatis rotundatis, alis columnae abbreviatis marginibus laceratis et infloraeporta heterocronica differt.

Plant epiphytic, cespitose, pendant, with abbreviated rhizome. Roots filiform, flexuous, glabrous, silvery white with green apex. _Pseudobulb_ cylindric, up to 10 mm long, 5 mm wide, monophyllous. Leaf linear-elliptic to elliptic-oblong, obtuse to retuse, narrowed to a conduplicate, sessile base, light green, 8–12 cm long (to 20 cm), 2.5–3 cm wide. _Inflorescence_ lateral, basal, pendant, successive, sometime branched at the base, 5–to many-flowered; peduncle terete, 4 to 11.5 cm long, concealed by 2–3 concave, ovate bracts. Ovary linear-clavate, about 3 cm long including the pedical. Flowers rather large for the genus, with free sepals and petals, ivory white with a narrow chestnut brown blotch at the first third of their length and white lip, marked near the base by two rose-purple bars. _Dorsal sepal_ obovate-elliptic, obtuse to retuse, slightly concave toward the apex, to 16 mm long, 8.5 mm wide. _Lateral sepals_ obliquely elliptic, obtuse to retuse, with a short, rounded apicule, subcarinate towards the apex and slightly concave, to 16 mm long, 6.5 mm wide. _Petal_ linear-elliptic, obtuse, slightly concave towards the apex, 16 mm long, 6.5 mm wide. Lip obovate-subpandurate, adnate to the column, 21 mm long, with a short, linear claw 2 mm long, with two broad, subquadrature, pubescent lateral lobes at the base, expanding abruptly to the subpandurate blade, 16 mm long, 15.5 mm wide, deeply emarginate in front, with plane, entire margins, producing with the column base a very short, blunt, saccate spur, 2.6 mm long, 3.5 mm wide. Column short, stout, without a foot, 3 mm long, with a pair of short, erect, subdolabridiform, lacerate wings, spotted and blotched with brown along the margins. Anther white, ciliate, papillose. _Pollinia_ 2, pyriform, rugulose, on a short obtangular stipe; viscidium elliptic, brown when fresh.

ETYMOLOGY: Named from La Estrella, the region on northwestern slopes of the Cordillera de Talamanca, where the species was first found.

DISTRIBUTION: Endemic to Costa Rica.


_Trichocentrum estrellense_ inhabits submontane, evergreen, tropical rain forests of the Atlantic slopes of the Cordillera de Talamanca and Cordillera Central in Costa Rica, where the plants of this species grow on shady branches and trunks covered by live moss, mainly over streams. The climate of the high basin of Río Reventazón is wet, temperate, with a moderate water deficit (Herrera, 1985). Minimum and maximum temperature average at La Estrella region are 18 and 21°C, respectively. Flowering generally begins in early summer, and many flowers are produced successively from June to September. _Trichocentrum estrellense_ was first collected in January 1923 by C.H. Lankester near La Estrella, in the Province of Cartago, and a specimen was sent to Oakes Ames who identified it as _T. pfavii_ (AMES 26162). Another anomalous collection from the same area was illustrated in a delicate and delightful watercolor by Rafael Lucas Rodríguez Caballero. This plate, together with many other botanical drawings of Costa Rican orchids by Rodríguez, was posthumously published in 1986 as _T. pfavii_ (Rodríguez Caballero et al., 1986). Due to the variable regional forms of _T. pfavii_ (Pupulin & Mora-Retana, 1994) it is not surprising that herbarium material of _T. estrellense_ was overlooked for over 70 years. In fact, most of the morphological differences between the two taxa are better observed in living material, and the characteristic successive infloraeporta heterocronica differt.
cence, unique among the species close to *T. pfavii*, may be noticed only when plants are kept in cultivation. Joaquin B. García first pointed out the difference between plants native of La Estrella area and the typical form of *T. pfavii*. In April 1992 I had the opportunity to confirm the specific status of *T. estrellense* after a visit to the Valle del Guaro, in the high basin of Río Reventazón, where large colonies of this species were found. Within the genus, *T. estrellense* is so far the species with longer leaves; a leaf of the type specimen was 20 cm long.

*T. pfavii* Rchb.f., *Gard. Chron.* n.s. 16: 70. 1881. TYPE: PANAMA. Chiriquí: without specific locality, 19 Nov. 1880, Pfau 60 (Holotype, W). Fig. 9.


*T. saundersii* Endres & Rchb.f. in Reichenbach Herb., *Ms.*

*T. saundersii* Endres & Rchb.f. in Reichenbach Herb., *Ms.*

*T. zonalis* Rchb.f. in Reichenbach Herb., *Ms.*


**Trichocentrum pulchrum group**

The distribution of the three species in this group is limited to the Andes from Venezuela and Colombia to Peru (Fig. 10). These species can be easily recognized by their triquetrous ovaries, a unique character within the genus. Furthermore, they present two very thickened keels arising from the base of the disc, diverging at apex and somewhat intensely puberulent. The overall morphological similarity among the three species suggests a common ancestor for the group. The flowers are produced on single-flowered, arching to pendent inflorescences. *Trichocentrum pulchrum* is one of the most widespread species of the genus: it is known from Venezuela to Peru.

**Key to the species of Trichocentrum pulchrum group**

1a. Spur less than twice as long as the lip .... *T. pulchrum*

1b. Spur more than twice as long as the lip ....... 2

2a. Lip flabellate, with a broad, dark purple blotch on the disc ............... *T. brandiae*

2b. Lip obovate, with a yellow blotch on the disc .... *T. longicalcaratum*


DISTRIBUTION: Endemic to Colombia.


DISTRIBUTION: Colombia and Ecuador.


DISTRIBUTION: Colombia and Ecuador.
Fig. 9. *Trichocentrum pfavii* Rchb.f. Voucher: COSTA RICA. Puntarenas: Las Cruces, F. Pupulin & D. Castelfranco 2 (USJ).
Fig. 10. Distribution of the species of *Trichocentrum pulchrum* group.


*T. maculatum* Lindl., Orchid. Linden. 24. 1846. TYPE: COLOMBIA. Río Hacha, Sierra de Santa Marta, along the Río San Antonio (1300 m), 1844, *Linden* 1666 (Holotype, K; Isotypes, BR, P, W).

*T. speciosum* Schlim. in Herb. Kew., Ms. DISTRIBUTION: Colombia, Venezuela, Ecuador, and Peru.


**Trichocentrum fuscum** group

The six species of this group are found from Venezuela, through the Guianas, to southern Brazil, and from Ecuador to Bolivia and Peru along the Andean Cordilleras (Fig. 12). Apart from *T. panduratum*, the flowers of these six species are produced successively on generally pendulous inflorescences. The group shares the long, flexuous, slender spur and the relatively complex calli at the base of the lip, two features I believe are derived within *Trichocentrum*. The lip is generally wide, subpandurate to pandurate in outline, sometimes with brightly colored nectar guides toward the entrance of the spur. Though no data on the pollination of any of the species in this group are available, it is highly probable that the slender elongate spur is someway involved in attracting pollinators. *Trichocentrum fuscum* Lindl. is the most widely distributed species of the group: it is recorded from Venezuela through the Guianas to Brazil and the Amazonian regions of Ecuador, Bolivia and Peru.

**Key to the species of *Trichocentrum fuscum* group**

1a. Inflorescence simultaneously 2- to 5-flowered ......... *T. panduratum*

1b. Inflorescence successive ........................................ 2

2a. Column wings lanceolate to strictly triangular ....... 3

2b. Column wings oblong to broadly triangular ......... 4

3a. Disc of the lip with four keels ......................... *T. albo-coccineum*

3b. Disc of the lip with three keels ......................... *T. fuscum*
da Imperatriz, along Macurany lake, Barbosa Rodrigues s.n. (Holotype not located).


**DISTRIBUTION**: Brazil, Bolivia, and Peru.


**T. fuscin** Lindl., *Edwards’s Bot. Reg.* 23: sub t. 1951. 1837. TYPE: incorrectly said to be from Mexico, cultivated in the collection of Mr. Knight, *Warming* s.n. (Holotype not located; drawing, K). Fig. 13.


**DISTRIBUTION**: Venezuela, Surinam, Brazil, Ecuador, Peru, and Bolivia.


**T. recurvum** Lindl., Edward’s Bot. Reg. 29: misc. 9. 1843. TYPE: GUYANA. Ex hort. Lodigis s.n. (Holotype, K!).

**T. cornu-vaccae** Rchb.f. in Reichenbach Herb., Ms.


DISTRIBUTION: Ecuador (?), Guyana and Surinam.

REPRESENTATIVE SPECIMENS: ECUADOR. Morona-Santiago: Misión Bomboiza, Holm-Nielsen et al. 4197 (not seen, but very dubious). SURINAM. Paramaribo, 27 Feb. 1858, Focke s.n. (W). Concordia: Saramacca, without collector (as T. cornu-vaccae, BR); same locality, without collector (BR). Without locality, Wullschlægel s.n. (W); cult. Dull s.n. (W).


DISTRIBUTION: Brazil.

**Trichocentrum wagneri** Pupulin sp. nov. TYPE: BRAZIL. Without locality, introduced by A. Seidel, flowered in cultivation by A. Wagner in Santa Margherita, Italy, 25 Sept. 1990, F. Pupulin 289 (Holotype, SEL). Fig. 14.

Species ad Trichocentrum fusco Lindl. similis, sed calcarul multo magis longiore quam labeli, labello oblongo-panduralo rotundato marginibus leviter crenulatis, callis parallelis et alis columnae brunneo striatis differt.

**Plant** epiphythic, cespitose, pendent to suberect, with abbreviated rhizome. **Roots** filiform, flexuous, glabrous, silvery white with green apex. **Pseudobulbs** subglobose, up to 5 mm long, 3.5–4.5 mm wide, monophyllous. **Leaf** ovate-oblong to elliptic-oblong, retuse, narrowed to a conduplicate, sessile base, light green, 6–11 cm long, 3–3.5 cm wide. **Inflorescence** lateral, basal, pendent, successive, 1–many-flowered; peduncle terete, 7–9 cm long, concealed by 2–3 concave, ovate, papillose–bracts, to 8 mm long. **Ovaries** linear-clavate, terete, about 4 cm long including the pedicel. **Flowers** with free sepals and petals, dull brown with yellowish apexes and ivory white lip, marked near the base by yellow with purple–brown radiating lines and blotches. **Dorsal sepal** oblongo-late, acute, concave toward the apex, to 20 mm long, 6.5 mm wide. **Lateral sepals** obliquely subulate, acute to subobtuse, subparallel toward the apex and slightly concave, to 21 mm long, 5–
5.5 mm wide. Petals linear-obovate, obtuse, sometimes slightly concave towards the apex, 18.5 mm long, 5.5 mm wide. Lip from a cuneate base oblong-subpandurate, adnate to the column, to 26 mm long, 11.5 mm wide, emarginate in front, with plane to slightly crenulate margins, producing with the column base a slender, linear-attenuate, fouxious spur, 5 cm long, 0.35 cm wide at the base; disc with four slender, puberulent keels, the external ones shorter, extending parallel from the base to the middle of the lip. Column short, stout, without a foot, to 6 mm long, with a pair of large, erect, cuneate, subquadrate, irregularly erose-dentate wings, completely striped with brown. Anther white, subglobose, glabre. Pollinia 2, pyriform, deeply concave, on a short obtriangular stipe; viscidium peltate, brown.

ETYMOLOGY: Named in honor of Alessandro Wagner, of Milan, Italy, who first flowered the species in his collection.

DISTRIBUTION: Brazil.

REPRESENTATIVE SPECIMENS: BRAZIL. Without collection data, introduced by A. Seidel and flowered by F. Pupulin 290 (Herb. Pupulin); cultivated by A. Riboni, F. Pupulin 291 (Herb. Pupulin).

The species was introduced in Italy in early summer 1989 together with a group of *T. fuscam* plants coming from Brazil. Several specimens flowered in cultivation in 1990, showing flowers that only superficially resemble those of *T. fuscam* Lindl. *Trichocentrum wagneri* may be easily distinguished from *T. fuscam* mainly on the basis of spur length which is twice longer than the lip, whereas it is as long as the lip or slightly shorter in *T. fuscam*. The lip is oblong, plane, only slightly crenulate towards the middle. It presents on the disc four slender, puberulent keels, that run parallel from the entrance of the spur to the middle of the lamina. Column wings are wide, cuneate, subquadrate and concave; they are intensively striped by brown, whereas they are slightly spotted in *T. fuscam*. The species flowers in late autumn, from September through December.

**Trichocentrum brachyceras group**

Only two species belong in this group, one endemic to Colombia and Peru (Fig. 15), *Trichocentrum brachyceras* Schltr. is known only from a Schlechter's tracing of the type (published by Mansfeld, 1929). *Trichocentrum bra-

chyceras* flowers, as well as these of *T. brevicalcaratum* C. Schweinf., present a narrow, deeply concave lip with acute apex and short, tubular spur. Both the highly revolute margins of the lip and its acute to acuminate apex are useful characters to distinguish the taxa of this group from the main body of the genus. The two species can be easily distinguished by the length of the lip: it is longer than the sepals and with two keels near the base in *T. brachyceras*, while it is markedly shorter than the sepals and without keels in *T. brevicalcaratum*. Nothing is known about the vegetative morphology of *T. brachyceras*, but *T. brevicalcaratum* presents a typical habit for the genus, with short, 1-flowered inflorescences.

**Key to the species of **

**Trichocentrum brachyceras group**

1a. Lip longer than sepals, apiculate, with two distinct keels near the base .......................... *T. brachyceras*

1b. Lip markedly shorter than sepals, minutely retuse, without keels ........................... *T. brevicalcaratum*


DISTRIBUTION: Endemic to Colombia.


DISTRIBUTION: Endemic to Peru.

REPRESENTATIVE SPECIMENS: PERU. Junín: Chanchamayo Valley, C. Schunke 565 (F).

Trichocentrum tigrinum group

Trichocentrum tigrinum, a species from Ecuadorian and northern Peruvian Pacific regions is
the sole species referred to this group (Fig. 17). The very spreading flowers of this species, the showing coloration and sweet scent, which deserved it Reichenbach’s recognition as “Trichocentrum princeps,” can easily distinguish this monotypic group. According to van der Pijl and Dodson (1966), T. tigrinum is pollinated by Eu-

cola cingulata. The modified, very thick leaves of T. tigrinum allow the plants of this species to maintain a hydric balance in the sub-arid seasonal forests of the coastal plains of Ecuador and Peru, where the dry season may exceed five months.

T. tigrinum Linden & Rchb.f., Gard. Chron. 862. 1869. TYPE: ECUADOR. Guayas: Guayaquil, 1875, Wallis s.n. (Holotype, W). Fig. 18.

T. tigrinum var. splendens Linden & Rod., Lindenia 1: 53, t. 24. 1885.

DISTRIBUTION: Ecuador and Peru.

REPRESENTATIVE SPECIMENS: ECUADOR. Manabí: Montecristi, east of Manta, C.H. Dodson 113 and 340 (SEL), C.H. Dodson s.n.

(SEL); C.H. Dodson & L.B. Thien 1744 (SEL). Prov. Guayas: Manglaralto, C.H. Dodson 16252 (RPSC); Cordillera de Colonche-Chongón, 1500 m, E. Santiesteban sub F. Pupulin 287 (Herb. Pupulin). El Oro: Santa Rosa, E.F. André 4371 (K); F.C. Lehmann 1000 and 1001 (K); Rio Cal-

cara, between Ayabá and Zuruma, F.C. Lehmann s.n. (K). Prov. of Loja: Catamayo (K); Mar-


EXCLUDED SPECIES


TYPE: COLOMBIA. Millican s.n. = Plectropho-


urk. Amsterd. 1: 212, 1848.

T. plectrophora (Lodd. ex Lindl.) Rchb.f., Ann. Bot. Syst. 6: 544, 1863. = Plectrophora iridifolia (Lodd. ex Lindl.) Focke, Tijdscbr. Wiss. en Nat-

urk. Amsterd. 1: 212, 1848.


CHECKLIST OF SPECIES

AND SYNONYMS

Acoidium fuscum Lindl. = T. fuscum Lindl.

Orchis punctata Ruiz & Pavón = T. pulchrum Poepp. & Endl.

T. alatum Rolfe = Plectrophora alata (Rolfe) Garay

T. albo-coccineum Linden

T. albo-purpureum Linden & Rchb.f. = T. albo-

coccineum Linden

T. albo-purpureum var. striatum Linden & Rod. = T. albo-coccineum Linden
Fig. 18. *Trichocentrum tigrinum* Linden & Rchb.f. Voucher: ECUADOR. Loja: Macará, P. Andreetta s.n. (Herb. Pupulin).
T. alboviolaceum Schltr. = T. albo-coccineum Linden
T. brachyeras Schltr.
T. brandiaeae Krzl.
T. brevicalcaratum Schweinf.
T. caloceras Endres & Rchb. f.
T. candidum Lindl.
T. capistratum Linden & Rchb. f.
T. cornucopiæae Linden & Rchb.f. = T. fuscum Lindl.
T. cornu-vaccae Rchb.f. = T. recurvum Lindl.
T. costaricense Mora-Retana & Pupulin
T. cymbiglossum Pupulin
T. dianthum Pupulin & Mora-Retana
T. estrellense Pupulin & J.B. García
T. funale Lindl. = Dendrophyllax funalis
T. fuscum Lindl.
T. hartii Rolfe = T. fuscum Lindl.
T. hoegei Rchb.f.
T. ionophtalmum Rchb.f. = T. albo-coccineum Linden
T. iridifolium Lodd ex Lindl. = Plectrophora iridifolia (Lodd. ex Lindl.) Focke
T. leenanum Rchb.f. = T. albo-coccineum Linden
T. longicalcaratum Rchb.f.
T. maculatum Lindl. = T. pulchrum Poepp. & Endl.
T. mottagrossense Hoehne = T. fuscum Lindl.
T. orthoplectron Rchb.f. = T. albo-coccineum Linden
T. panamense Rolfe = T. capistratum Linden & Rchb.f.
T. panduratum Schweinf.
T. pfavii Rchb.f.
T. pfavii var. zonale Rchb.f. = T. pfavii Rchb.f.
T. pfavii f. album Henderson = T. pfavii Rchb.f.
T. pineli Lindl. = T. fuscum Lindl.
T. plectrophora (Lodd. ex Lindl.) Rchb.f. = Plectrophora iridifolia (Lodd. ex Lindl.) Focke
T. plectrophora Rchb.f. = T. recurvum Lindl.
T. porphyrio Rchb.f. = T. albo-coccineum Linden
T. pulchrum Poepp. & Endl.
T. purpureum Lindl. ex Rchb.f.
T. pusillum Lehm. = T. capistratum Linden & Rchb.f.
T. recurvum Lindl.
T. sandersianum Endres & Rchb.f. = T. pfavii Rchb.f.
T. saundersii Endres & Rchb.f. = T. pfavii Rchb.f.
T. speciosum Schlimg = T. pulchrum Poepp. & Endl.
T. tenuiflorum Lindl.
T. tigrinum Rchb.f.
T. tigrinum var. splendens Linden & Rod. = T. tigrinum Rchb.f.
T. triquetrum Rolfe = Plectrophora triquetera (Rolfe) Cogn.
T. verruciferum Schltr. = T. brandiaeae Krzl.
T. wagneri Pupulin
T. zonale Rchb.f. = T. pfavii Rchb.f.

LITERATURE CITED
——. 1850. Trichocentrum tenuiflorum, Paxton’s Fl. Gard. 1: 12.


