

Edlley Pessoa

**SISTEMÁTICA E HISTÓRIA EVOLUTIVA DE *Campylocentrum* Benth. (ORCHIDACEAE)**

Recife  
2017

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Tese apresentada ao Programa de Pós-Graduação o em Biologia Vegetal – PPGBV/UFPE, como parte dos requisitos para obtenção do título de doutor em Biologia Vegetal.

Orientador: Prof. Dr. Marccus Alves

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## RESUMO

**Sistemática e história evolutiva de *Campylocentrum* (Orchidaceae)** – Este estudo se propôs a elucidar o complexo gênero *Campylocentrum*, utilizando diversas ferramentas como morfologia externa, anatomia, genética molecular, relógio molecular e biogeografia num ensaio à taxonomia integrativa. Os estudos desenvolvidos evidenciaram a necessidade de maior atenção com as coleções científicas visto que das oito novas espécies descritas cinco já tinham sido previamente coletadas. A análise de caracteres anatômicos das raízes se mostrou importante para distinguir grupos taxonômicos dentro do gênero. O estudo filogenético baseado em dados moleculares nucleares (ITS e *Xdh*) e plastidiais (*matK*, *rpl32-trnL*, *trnL-F* e *ycf1*) mostrou que a classificação infra-generica previamente conhecida não se sustentava, e duas novas seções foram propostas, sendo reconhecidas cinco no total. A maioria dos caracteres amplamente utilizados na taxonomia de Orchidaceae foi indicada como homoplásicas em *Campylocentrum*, por outro lado outros sub-utilizados como raízes e cápsulas são apresentados como mais consistentes. Através de uma análise de datação, ficou evidente que *Campylocentrum* assim como seu gênero irmão *Dendrophyllax* são recentes, e suas diversificações estão ligadas a eventos ocorridos principalmente no Plioceno e Pleistoceno. A análise biogeográfica indicou eventos sucessivos de dispersão a longa distancia. Embora apenas uma espécie tenha sido citada anteriormente como ameaçada, após análise das distribuições seguindo as normas da IUCN concluímos que *Campylocentrum* inclui três espécies “quase ameaçadas” (NT), três vulneráveis (VU), uma ameaçada (EN) e duas criticamente ameaçadas (CR). O gênero compreende 72 espécies, sendo 37 da seção *Campylocentrum*, 13 da seção *Dendrophylopsis*, 15 da seção *Laevigatum*, uma da seção *Pseudocampylocentrum* e seis da seção *Teretifolium*. Considera-se o Brasil o país com maior diversidade onde podem ser encontradas 36 espécies.

**Palavras-Chave:** Angraecinae, Vandaeae, Filogenia, Taxonomia, Biogeografia, Anatomia.

## ABSTRACT

**Systematics and evolutionary history of *Campylocentrum* (Orchidaceae)** – This study proposes elucidate the complex genus *Campylocentrum*, using different tools, such as external morphology, anatomy, molecular genetics, molecular clock and biogeography, in an assay to integrative taxonomy. Here is indicated the need of attention to scientific collections, since from eight new taxa described five were previously collected and deposited in herbaria. The analysis of anatomic features of roots shows important characters to distinguish taxonomic groups under the genus. The phylogenetic study based in nuclear (ITS e *Xdh*) and plastidial datasets (*matK*, *rpl32-trnL*, *trnL-F* e *ycf1*) indicates that the previously known infra-generic classification is not supported, and two new sections were proposed, recognizing five in total. Majority of the characters widely used on orchid taxonomy were indicated as homoplastic to *Campylocentrum*, moreover underused features such as roots and capsules seems to have a better phylogenetic signal. The dating analysis revealed *Campylocentrum* and its sister genus *Dendrophyllax* as relatively young, their diversifications are linked to events occurred at Pliocene and Pleistocene. The biogeography analysis indicated successive events of long-distance dispersal. Although only one species had been cited before as endangered, after the analysis of the distributions following the instructions of IUCN we concluded that *Campylocentrum* includes three species classified as near threatened (NT), three vulnerable (VU), one endangered (EN) and two critically endangered (CR). The genus is composed by 72 species, 37 from *C.* sect. *Campylocentrum*, 13 from *C.* sect.. *Dendrophyllaxis*, 15 from *C.* sect.. *Laevigatum*, one from *C.* sect. *Pseudocampylocentrum* and six from *C.* sect. *Teretifolium*. Brazil is pointed out with the greatest diversity with 36 species.

**Key-Words:** Angraecinae, Vandaeae, Phylogeny, Taxonomy, Biogeography, Anatomy.



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## **1. Fundamentação Teórica**

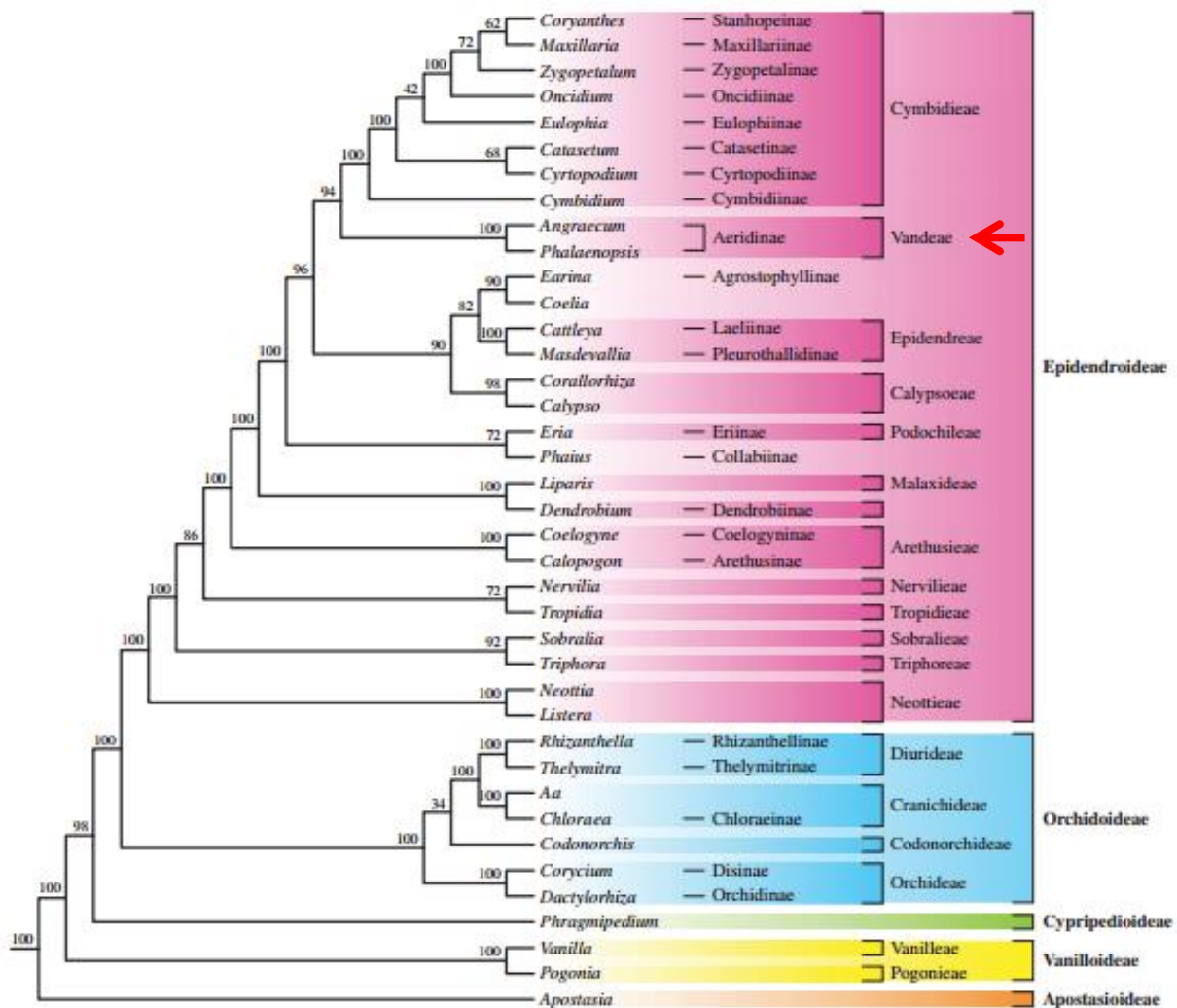
### **1.1. Breve sistemática de Orchidaceae**

Orchidaceae pode ser considerada a família de plantas com maior número de estudos filogenéticos publicados. O resultado desse esforço é apresentado nos seis volumes do *Genera Orchidacearum* (Pridgeon et al. 1999, 2001, 2003, 2005, 2009, 2014), que são tratados em conjunto como o sistema de classificação mais atual seguido pela maioria dos orquidólogos no mundo. De acordo com os autores, a família é dividida em cinco sub-famílias: Apostasioideae, Cypripedioideae, Vanilloideae, Orchidoideae e Epidendroideae.

Epidendroideae é a sub-família mais diversa e é amplamente distribuída, inclui principalmente grupos epifíticos, sendo composta por 14 tribos (Freudenstein et al. 2015). As tribos mais diversas em número de espécies são Vandae (quatro subtribos), Epidendreae (sete subtribos) e Cymbidieae (onze subtribos), todas com distribuição pantropical (Pridgeon et al. 2005, 2009, 2014).

### **1.2. Sistemática da Tribo Vandae e Subtribo Angraecinae (Epidendroideae-Orchidaceae).**

Vandae foi descrita por Lindley (1826) baseado no gênero *Vanda* (subtribo Aeridinae) e inclui as tribos outrora aceitas Adrorhizeae (Schltr.) Szlach., Polyrhizeae Small, Polystachyeae Pfitzer e Sarcantoeae Pfitzer. Está inserida na subfamília Epidendroideae sendo filogeneticamente relacionada à tribo Cymbidieae (Givnish et al. 2015) (Fig.1).

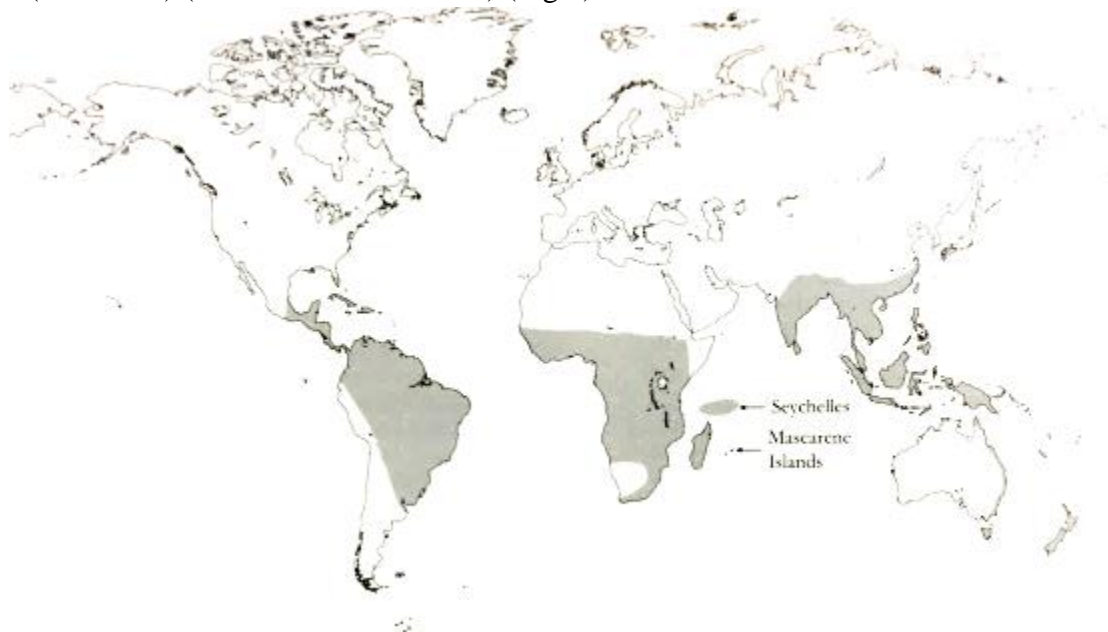


**Figura 1.** Filogenia plastômica para Orchidaceae, baseada em análise de verossimilhança (retirado de Givnish et al. 2015). A tribo Vandaeae é apontada com a seta vermelha.

O monofiletismo de Vandaeae é sustentado por alguns estudos recentes utilizando dados moleculares (Chase et al. 2003, Carlsward et al. 2006, Freudenstein et al. 2015). Morfologicamente, a tribo é caracterizada por possuir crescimento monopodial (excluindo Polystachyinae), estigmas esféricos e sementes com paredes lateralmente comprimidas (Freudenstein & Rasmussen 1999).

A tribo apresenta ca. de 2.600 espécies e 139 gêneros (Schuiteman et al. 2014), sendo segregada em quatro subtribos: Aeridinae, Adrorhizinae, Angraecinae e Polystachyinae (Carlsward et al. 2006, Freudenstein et al. 2015). Tem distribuição

Pantropical, porém mais diversificada na África (principalmente Angraecinae) e Ásia (Aeridinae) (Schuiteman et al. 2014) (Fig.2).



**Figura 2.** Distribuição de Vandae. (retirado de Schuiteman et al. 2014).

Embora vários gêneros apresentem a condição áfila dentro da Tribo Vandae (ex. *Campylocentrum* Benth., *Chiloschista* Lindl., *Dendrophylax* Rchb.f., *Microcoelia* Lindl., *Taeniophyllum* Blume e *Taeniorrhiza* Summerh.), estudos filogéticos vêm apontando que estes não são relacionados, tendo o caráter surgido diversas vezes no grupo (Carlsward et al. 2006, Freudenstein et al. 2015).

A subtribo Angraecinae (incluindo Aerangidinae, *sensu* Carlsward et al. 2006) é representada por 760 espécies e 49-64 gêneros (Carlsward & Cribb 2014; Szlachetko et al. 2013) sendo a maioria africana. Apenas dois desses são endêmicos da região neotropical: *Campylocentrum* Benth. e *Dendrophylax* Rchb. f. (incluindo *Harrisella* Fawc. & Rendle, *Polyradicion* Garay e *Polyrrhiza* Pfitz, *sensu* Carlsward et al. 2003).

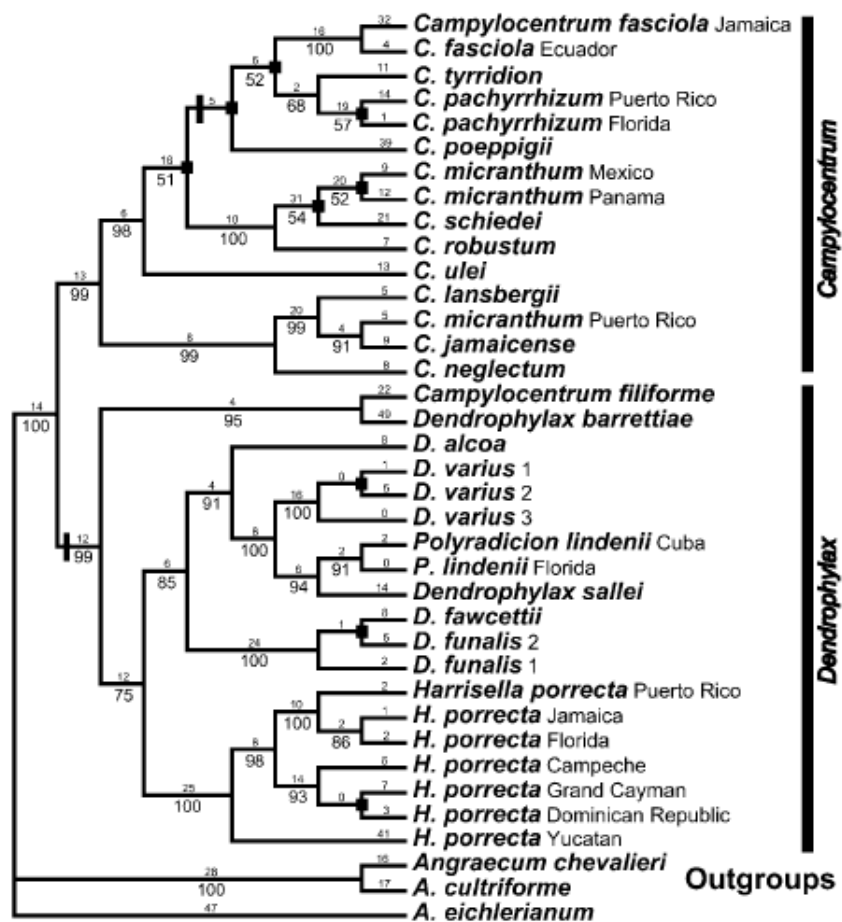
É caracterizada pelo crescimento monopodial e ausência de pseudobulbos, inflorescências laterais, flores frequentemente calcaradas, duas polínias com 1-2 estipes e 1-2 viscídios (Carlsward & Cribb 2014). A filogenia de Angraecinae vem sendo



confirmada por subsequentes estudos filogenéticos moleculares (Carlsward et al. 2003, Carlsward et al. 2006, Freudenstein et al. 2015), tendo Aeridinae como grupo irmão.

Dentre os gêneros da subtribo, se destacam *Campylocentrum* e *Dendrophyllax* por serem filogeneticamente relacionados e formarem o “clado Neotropical” dentro de Angraecinae, sugerindo um único evento de dispersão da África em direção às Américas (Carlsward et al. 2003).

Como citado acima, a condição áfila está presente em ambos os gêneros, porém *Campylocentrum* apresenta tanto representantes com folhas como alguns áfilos, e *Dendrophyllax* é exclusivamente áfilo (Carlsward et al. 2003). O estudo de Carlsward et al. (2003) apresentou ambos os gêneros como monofiléticos, e sugere que assim como nos demais gêneros de Vandeeae, a condição áfila surgiu mais de uma vez (Fig. 3).



**Figura 3.** Filogenia de Angraecinae Neotropicais baseada numa análise de MP de dados nucleares (ITS) e plastidiais (*trnL-F*, *matK*) (retirado de Carlsward et al. 2003).

### 1.3. O gênero *Campylocentrum* Benth.

#### 1.3.1. Histórico

*Campylocentrum* foi descrito por Bentham (1881) como um novo nome para *Todaroa* A. Rich. & Galeot., um nome ilegítimo previamente ocupado em Apiaceae. Embora o autor cite 15 espécies para o gênero, as novas combinações requeridas não foram apresentadas.

O *typus* de *Todaroa* é *T. micranta* A. Rich. & Galeot. No entanto, uma combinação anterior de *Angraecum micranthum* Lindl. em *Campylocentrum* foi proposta por Maury (1889), tornando uma possível nova combinação de *T. micranta* para o gênero ilegítima. Desta forma, o gênero foi tipificado com o próximo nome disponível para *T. micranta*, *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsl., baseado em *A. schiedei* e até então considerado sinônimo (Bogarín & Pupulin 2010).

Segundo Bentham (1881), *Campylocentrum* incluiria as espécies neotropicais descritas em *Angraecum* por Lindley e em *Aeranthus* por Reichenbach f., tendo *Dendrophyllax* Rchb.f. como gênero relacionado. O gênero se manteve praticamente negligenciado até o início do século XX, quando Rolfe (1903) e Cogniaux (1906) propuseram as combinações necessárias.

Cogniaux (1906) propôs uma classificação infragênerica para o gênero organizando em três seções: *Eucampylocentrum* Cogn. para espécies com caules alongados e folhas desenvolvidas, *Dendrophylopsis* Cogn. para espécies com caules reduzidos e áfilas, e *Pseudocampylocentrum* Cogn. com caule alongado e folhas cilíndricas reduzidas.

Nas décadas seguintes, dezenas de espécies foram descritas no gênero, a maioria delas por Schlechter (1920, 1921, 1922, 1925, 1926, 1929) principalmente para América Central e Noroeste da América do Sul. Atualmente, *Campyloctrum* inclui ca. de 70 espécies (Carlsward 2014), porém esse número precisa ser revisto, uma vez que um maior esforço de coleta e de estudos taxonômicos vem apontando a existência de espécies ainda não descritas e nomes atualmente em sinonímia que devem ser reestabelecidos como espécies, assim como outros sinonimizados (Bogarín & Pupulin 2010).

### **1.3.2. Etimologia**

O nome deriva do grego *campylos* (“curvado”) e *kentron* (“cálcar”), em referência à forma do cálcar de *Campyloctrum shiedei*, a espécie tipo.

### **1.3.3. Morfologia externa**

#### ***Raízes***

Existe uma grande variação nesse órgão em *Campyloctrum*. As raízes podem ser cilíndricas (mais frequente) ou achatadas dorso-ventralmente (em algumas espécies áfilas) e àquelas cilíndricas podem ter superfície lisa (mais frequente) ou granulosa (espécies com folhas cilíndricas) (Fig. 4). Esses caracteres se mantem mesmo nos espécimes desidratados depositados em coleções científicas, sendo bastante úteis na identificação de grupos taxonômicos dentro do gênero.



**Figura 4.** Raízes de *Campylocentrum*. A-B. Raízes cilíndricas com superfície lisa; C-D. Raízes cilíndricas com superfície granulosa.

### *Folhas*

Este é possivelmente o órgão com maior variabilidade morfológica no gênero. Nas plantas consideradas “áfilas”, as folhas estão reduzidas a escamas acolorofiladas geralmente deltoides e agrupadas no ápice do caule, enquanto que as plantas foliosas podem ser divididas em dois grupos morfológicos: 1. folhas conduplicadas e 2. folhas cilíndricas (Fig. 5).



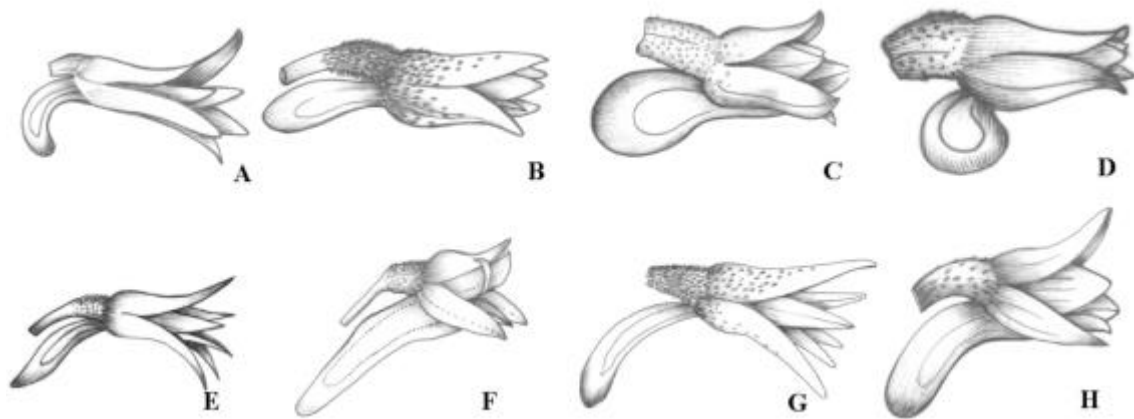
**Figura 5.** A. Folhas conduplicadas. B. Áfila C. Folhas cilíndricas.

As espécies com folhas conduplicadas são a maioria no gênero, compondo dois terços das espécies e são amplamente distribuídas nos neotrópicos. Estas folhas são em sua maioria assimetricamente 2-lobadas, e assumem consistência diversa desde membranáceas a crassas. Aquelas espécies de folhas cilíndricas são, em sua maioria, endêmicas da Floresta Atlântica com exceção de *C. poeppigii*, espécie que tem as menores folhas no grupo e é amplamente distribuída desde as Antilhas ao Norte do Brasil (BFG 2015, Govaerts et al. 2016).

### ***Inflorescências e flores***

Em contraste com a porção vegetativa, as inflorescências e flores de *Campylocentrum* são bastante conservadas. As inflorescências são racemos curtos com 4-30 flores disticamente arranjadas, e mais comumente congestas, embora em algumas espécies as flores não estejam justapostas. Na maioria das espécies, as flores apresentam-se mais curtas que as folhas, embora naquelas áfilas e em alguns grupos de plantas foliosas tenham maior comprimento. As brácteas florais são em sua maioria deltoides e reduzidas ( $\leq 1$  mm compr.), porém em algumas espécies essas são desenvolvidas e assumem outras formas (ex. ovada, orbicular), sendo este caráter importante para reconhecimento das mesmas.

As flores tem perianto muito similar entre si. Entre os caracteres importantes para reconhecimento de espécies no gênero estão: 1. número de nervuras das peças do perianto; 2. forma do labelo (inteiro vs. 3-lobado); e 3. forma, comprimento e curvatura do cálcio. Embora úteis, esses caracteres não representam sinapomorfias para quaisquer grupos dentro do gênero, sendo impossível a determinação de uma espécie dentro de uma das seções propostas do Cogniaux (1906) baseado unicamente em caracteres florais (Fig. 6).



**Figura 6.** Variação na forma e comprimento do calcar em espécies de *Campylocentrum*.

A. *C. micranthum* (Lindl.) Maury, B. *C. pauloense* Hoehne & Schltr., C. *C. itatiaiae* Pessoa & Alves, D. *C. schlechterianum* Pessoa & Alves, E. *C. ornithorrhynchum* (Lindl.) Rolfe, F. *C. sellowii* (Rchb.f.) Rolfe, G. *C. hirtellum* Cogn., H. *C. brevifolium* (Lindl.) Pessoa & Alves

#### 1.3.4. Anatomia

Carlswald et al. (2006) estudaram órgãos vegetativos de integrantes da tribo Vandeeae. Numa descrição geral, *Campylocentrum* é caracterizado anatomicamente por raízes com velame com uma a três camadas; células exodérmicas espessadas em  $\cap$ - ou  $\circ$ ; células endeodérmicas espessadas em  $\circ$ , e cilindro vascular com seis até nove polos de xilema, com tecido vascular embebido no esclerênquima. As folhas têm estômatos na face abaxial, a hipoderme é adaxial- e abaxialmente composta por uma fileira de idioblastos espalhados no clorênquima do mesófilo. O mesófilo é heterogêneo com várias fileiras de células colunares ao redor de células isodiamétricas centrais. Corpos de sílica são encontrados em associação com o floema e xilema.

### 1.3.5. Distribuição

O gênero é amplamente distribuído na região neotropical, excluindo apenas o Chile (Carlsward et al. 2014, Primavera 2013). No Brasil ocorrem mais de metade das espécies, principalmente na Floresta Atlântica (BFG 2016), que é citada como seu centro de diversidade (Todzia 1980). A América Central e noroeste da América do Sul em conjunto também representam uma área de grande diversidade do gênero (Bogarín & Pupulin 2010) (Fig. 7).

Vinte táxons (ca. 30%) são endêmicos da Floresta Atlântica do Brasil, sendo os estados do Espírito Santo (11 spp.), Minas Gerais (15 spp.) e Rio de Janeiro (17 spp.) os mais diversos (BFG 2016). Estudos recentes vêm demonstrando que a Colômbia possivelmente é o segundo país com maior riqueza de espécies do gênero (Kolanowska & Szlachetko 2013).



**Figura 7.** Distribuição de *Campylocentrum*. (baseado em Bogarín & Pupulin 2010).

De uma forma geral as espécies do gênero ocorrem principalmente em áreas florestais como a Bacia Amazonica, Chocó, Floresta Atlântica e Florestas secas das

Antilhas e América Central. No entanto, embora sejam mais raras, algumas espécies ocorrem em ecossistemas secos como a Caatinga, Cerrados e Chaco (BFG 2015).

### 1.3.6. Polinização

Poucas espécies do gênero já foram alvo de estudos ecológicos, que são especialmente relativos à sua biologia floral e polinização. Para *Campylocentrum densiflorum* Cogn. (tratado na obra original como *C. aromaticum* Barb. Rodr.) foi registrada a polinização por abelhas, principalmente do grupo das Halictidae, no entanto algumas moscas também foram observadas sendo estas consideradas “polinizadores acessórios” (Singer & Cocucci 1999). Abelhas também são o principal grupo de polinizadores de *C. grisebachii* Cogn. (tratado na obra original como *C. burchellii* Cogn.), porém visitantes dessa espécie são do grupo das Meliponini (Singer & Cocucci 1999).

Entretanto, outros estudos indicam a fraca visitação por polinizadores, sugerindo que algumas espécies se reproduzem por autogamia, sendo observado alto índice de frutificação, como tratado por Damon & Dalas-Reblero (2007) para *C. stenanthum* Schltr. [tratado na obra original como *C. micranthum* (Lindl.) Maury].

Mais recentemente, a biologia reprodutiva de *C. crassirhizum* Hoehne [tratado na obra original como *C. micranthum* (Lindl.) Maury] foi estudada por Cabral & Pansarin (2016), onde foram observadas abelhas dos grupos Tapinotaspidiinae e Xylocopinae. Essa espécie é autocompatível, porém não autógama como observado em *C. stenanthum* Schltr. por Damon & Dalas-Reblero (2007), e possui altos níveis de sucesso reprodutivo em condições naturais (ca. 35% de formação de frutos).

Levando em consideração que flores da subtribo Angraecinae tem características que sugerem que sejam polinizadas por mariposas (Dressler 1981), como os longos cálcres, coloração esbranquiçada e antese noturna, no gênero *Campylocentrum* houve

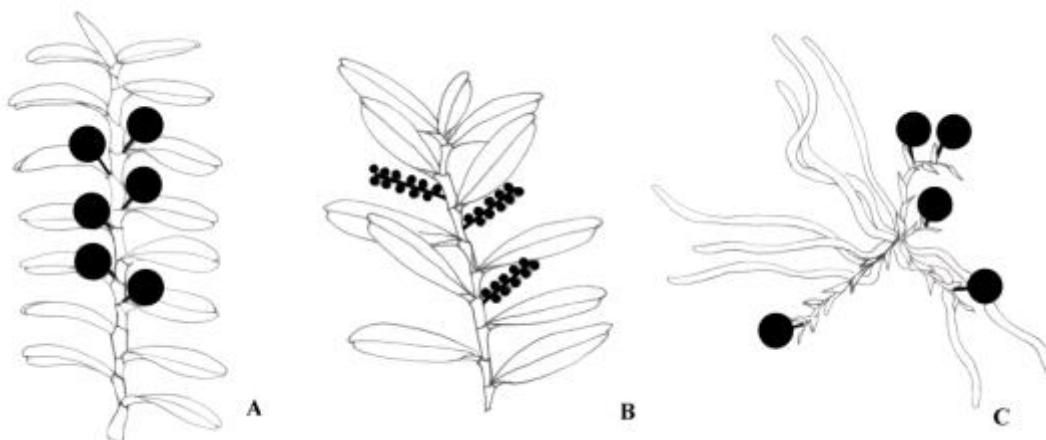


uma adaptação à polinização por abelhas, como a redução do tamanho das flores e antese diurna (Singer & Cocucci 1999; Damon & Dalas-Reblero 2007; Cabral & Pansarin 2016).

### 1.3.7. Relações filogenéticas

Estudos filogenéticos moleculares envolvendo *Campylocentrum* ainda são incipientes e aqueles existentes tem como foco as categorias supra-genéricas. No entanto, indicam o monofiletismo do gênero, que é bem sustentado (99% BS) baseado em dados nucleares e plastidiais combinados (Carlsward et al. 2003, 2006). *Dendrophylax* surge como seu grupo irmão, e juntos formam o “clado atlântico” (100% BS), que aparece embebido no reconhecidamente polifilético gênero *Angraecum* (Carlsward et al. 2006, Szlachetko et al. 2013).

As espécies de *Angraecum* mais próximas ao “clado atlântico” pertencem à *A.* sect. *Angraecoides* (Cordem.) Garay, que inclui cerca de 25 espécies endêmicas do oeste da África (Garay 1972). O hábito dessas espécies lembram aqueles dos *Campylocentrum* de folhas conduplicadas, enquanto que as flores parecem com as de *Dendrophylax* (Fig.8).



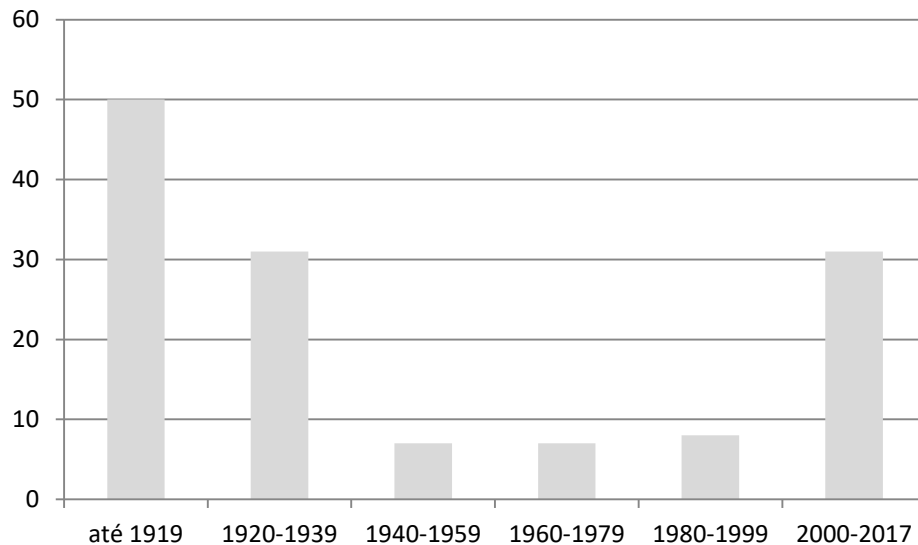
**Figura 8.** Hábitos. A. *Angraecum* sect. *Angraecoides*; B; *Campylocentrum*; C. *Dendrophylax*. Círculos pretos representam flores.

Relações filogenéticas entre espécies de *Campylocentrum* são pouco conhecidas, pois somente nove espécies já foram alvo de estudos filogenéticos (Carlsward et al. 2003). Sabe-se porém que dentre as seções propostas por Cogniaux (1906), *C. sect. Campylocentrum*, não é monofilética (Carlsward et al. 2003). Vale ressaltar que no estudo desenvolvido por Carlsward et al. (2003), vários espécimes foram erroneamente identificados, comprometendo a discussão e evidenciando a necessidade de estudos taxonômicos no grupo.

### 1.3.8. Circunscrição

Quando descrito ainda no séc. XIX, *Campylocentrum* era composto por apenas uma espécie, *C. schiedei*, e assim permaneceu praticamente negligenciado até os estudos de Rolfe (1903) e Cogniaux (1906) no início do século XX, quando dezenas de combinações e novas espécies foram propostas. Nas décadas de 20 e 30 do século passado muitas novas espécies foram propostas, especialmente por Schlechter (1920, 1921, 1922, 1925, 1926, 1929). As seis décadas seguintes foram marcadas pela pouca atenção dada ao grupo, com uma média de 3,5 espécies descrita por década.

Por outro lado, já no séc. XXI, muitas espécies áfilas descritas em *Campylocentrum* foram combinadas para *Dendrophylax* baseados nos estudos de filogenia molecular de Carlsward et al. (2003). Especialmente na última década (2010-2017) houve um novo surto de estudos taxonômicos para o gênero, sendo 26 novas espécies descritas nesse período (ver Gráfico 1). Apesar de ca. de 130 nomes já terem sido propostos para o gênero, somente 70 são aceitos, porém esse número tende a diminuir através de revisões taxonômicas necessárias, especialmente no complexo *C. micranthum*.



**Gráfico 1.** Número de espécies novas de *Campylocentrum* descritas por períodos determinados. (Fonte: IPNI)

#### 1.4. Objetivo

Este estudo se propõe a elucidar o complexo gênero *Campylocentrum*, utilizando diversas ferramentas na taxonomia como morfologia externa, anatomia, genética molecular, relógio molecular e biogeografia num ensaio à taxonomia integrativa. Desta forma, objetiva a resolução de problemáticas nomenclaturais e sistemáticas através de uma filogenia molecular e revisões taxonômicas do grupo.

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# CAPÍTULO 1

## Novas espécies e Notas Taxonômicas

**Manuscrito 1** – Notes on *Campylocentrum* (Vandaeae; Epidendroideae; Orchidaceae): Reestablishment of two South American species.

**Phytotaxa 204(1): 85-90 (2015).**

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**Manuscrito 2** – The identity of *Campylocentrum sellowii* (Angraecinae - Orchidaceae): clarifying on its circumscription and lectotypifications.

**Feddes Repertorium 126: 67-72 (2015).**

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**Manuscrito 3** – A new *Campylocentrum* (Vandaeae; Epidendroideae; Orchidaceae) from submontane Atlantic Forest of northeastern Brazil.

**Phytotaxa 197(1): 54-58 (2015).**

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**Manuscrito 4** – *Campylocentrum benellii* and *C. paludosum* spp. nov. (Angraecinae – Orchidaceae): two new leafless species from Brazil.

**Nordic Journal of Botany 34: 376-379 (2016).**

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**Manuscrito 5** – The Smallest Angraecoid Species from the Neotropics: A New *Campylocentrum* (Orchidaceae) from a Brazilian Subtropical Forest.

**Systematic Botany 40(1): 79-82 (2015).**

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**Manuscrito 6** – *Campylocentrum brevifolium* (Lindl.) E. M. Pessoa & M. Alves, a neglected and critically endangered orchid from the Atlantic Forest of Brazil.

**Kew Bulletin 70: 42 (2015).**

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**Manuscrito 7** – Three new species of *Campylocentrum* (Vandaeae, Orchidaceae) from Brazil.

**Phytotaxa 217(3): 265-272 (2015).**

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**Notes on *Campylocentrum* (Angraecinae-Orchidaceae): Re-establishment of two South American species**

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**Abstract**

During research on the taxonomical review of the genus, two South American species, *C. kuntzei* and *C. mattogrossense*, previously considered synonyms of *Campylocentrum micranthum*, were recognized as distinct species. Descriptions and illustrations, in addition to typifications, new synonyms, an identification key and the conservation statuses are provided.

**Keywords:** Amazon, Brazil, Cerrado, Neotropics, Vandae.



## Introduction

*Campylocentrum* was proposed by Bentham (1881: 337) for American species placed in *Angraecum* Bory (1804: 359) by Lindley and *Aeranthes* Lindley (1824: 817) by Reichenbach f., and *C. micranthum* (Lindley 1835: 1772) Maury (1889: 273) is the first species described which belongs to the genus, although it is not the type species of the genus.

The species was originally described under *Angraecum* by Lindley (1840), and after being replaced by Maury (1889), 14 new names were proposed based on specimens closely related to *C. micranthum*, most of which are nowadays considered synonyms.

During studies for the taxonomical review of the genus, two South American species, *C. kuntzei* Cogniaux. ex Kuntze (1898: 298) and *C. mattogrossense* Hoehne (1941: 62) were recognized as distinct species, although currently being cited as synonyms of *C. micranthum* (Brako & Zarucchi 1993, CONABIO 2009, D'Arcy 1987, Dodson & Dodson 1980, Hamer 1982, Ibisch 1996, Jørgensen *et al.* 2010, McLeish *et al.* 1995, Stevens *et al.* 2001) or *C. robustum* Cogniaux (1906: 509) (Brako & Zarucchi 1993, Jørgensen & León-Yáñez 1999, Zuloaga 2008).

This study reinforces the significant morphological differences among the taxa and proposes the re-establishment of *C. kuntzei* and *C. mattogrossense*.

Complete descriptions of the species, illustrations, typifications, new synonyms, an identification key and the conservation statuses (IUCN 2013) are also included. A discussion of morphological affinities is also presented.

## Taxonomic treatment

*Campylocentrum kuntzei* Cogniaux ex Kuntze (1898: 298).

Type: BOLIVIA. Rio Juntas, 500 m alt., 13 April 1892, *C.O. Kuntze s.n.* [lectotype: BR! **designated here**, isolectotypes: F (not seen), NY 8632 (not seen), NY 8631 (not seen), **designated here**). (Fig. 1)

Epiphytic herbs. Roots 1.5–3.0 mm diam., cylindrical, fibrous, smooth, whitish to dark grey. Stem 11.0–20.0 cm long, cylindrical, rarely branched. Leaves 60.0–85.0 ×

14.0–27.0 mm, greenish, oblong-elliptical to oblanceolate, the apex asymmetrically slightly 2-lobed, lobes acute, margin entire. Inflorescences 16.0–40.0 mm long, peduncle 2.0–4.0 mm long, partially covered by bracts, glabrous, brownish; rachis 12.0–38.0 mm long, glabrous, brownish; floral bracts 1.5–2.0 × 1.0–1.5 mm, deltoid, margin minutely denticulate, the apex acute, membranaceous. Flowers 14–30 (per inflorescence), pale green with a cream-colored spur, distichous, ovary pedicellate, 0.8–1.2 mm long; dorsal sepal 3.8–5.1 × 1.0–1.2 mm, oblong, the apex acute, 3-nerved, base slightly papillate, margin entire, membranaceous; lateral sepals 4.5–6.5 × 1.0–1.5 mm, oblong-subfalcate, the apex acute, 3-nerved, base slightly papillate, margin entire, membranaceous; petals 3.5–5.0 × 0.8–1.0 mm, oblong, the apex acute to obtuse, 3-nerved, glabrous, margin entire, membranaceous; lip 4.0–6.0 mm long, 1.3–2.0 mm wide between the lateral lobes, 3-lobed, membranaceous, 7–9-nerved, margin entire, producing a spur at base, lateral lobes 0.1–0.2 × 0.2–0.3 mm, subdeltoid, the apex truncate to obtuse, middle lobe 3.0–4.0 × 0.8–1.0 mm, narrowly lanceolate, the apex acute, pilose on the abaxial surface, spur 4.8–6.0 mm long, 1.0–1.3 mm diam., cylindrical-clavate, slightly curved, the apex rounded, cream colored, occasionally slightly papillate; gynostemium 0.6–0.8 mm long, anther cap apex rounded, pollinia 2, globose. Capsule 7.0–12.0 × 2.5–3.2 mm, fusiform, 6-ribbed, pedicellate, pedicel 0.5–0.8 mm long.

**Distribution and Ecology:** — *Campylocentrum kuntzei* is known from central-western South America, specifically in Bolivia, Brazil and Paraguay. It grows in lowland to sub-montane forests (200–760 m alt.), in Amazon and Cerrado (gallery forest) vegetation. The flowering period is from September to November, and fruits can be observed throughout the whole year.

**Conservation Status:** — This species falls under the Least Concern (LC) category.

**Nomenclatural and Taxonomic notes:** —Although Kuntze (1898) did not indicate type material for this name, specimens collected by him from the same locality cited in the protolog and named by Cogniaux as *Campylocentrum kuntzei* were found in BR (handwritten by Cogniaux), F, and NY herbaria. Here, we select a specimen from BR as the lectotype of the name, due to the presence of flowers and Cogniaux's handwriting.

Dodson & Dodson (1980) considered *Campylocentrum kuntzei* as a synonym of *C. micranthum*, yet without any morphological explanation. This was followed by several authors (Brako & Zarucchi 1993, CONABIO 2009, Hamer 1982, Ibisch 1996, Jørgensen *et al.* 2014, McLeish *et al.* 1995, Stevens *et al.* 2001). Indeed, *C. kuntzei* is morphologically related to *C. micranthum* but it can be easily distinguished by characters from the spur such as color (cream colored vs. pale green), curvature (slightly curved vs. inflexed) and size [ $> 4.8$  mm (as long as to longer than the sepals) vs.  $< 3.5$  mm (shorter than the sepals)]. (Fig. 2)

Additionally, *C. kuntzei* is restricted to central-western South America, while *C. micranthum* occurs in the Lesser Antilles, northern (Amazon) and eastern (Atlantic Forest) South America.

**Additional specimens examined:** — BOLIVIA. La Paz: Sud Yungas, Santa Rosa, Alto Beni, 18 May 1999, *T. Kromer & A. Acebey 417* (LPB not seen, GOET); San Carlos: Mapiri, Sep 1907, *O. Buchtien 1284* (HGB). BRAZIL. Acre: Alto Juruá, Reserva extrativista, Nov 1993, *L. Bernacci 3181* (IAC); Senador Guiomard, Rio Iquiri, 17 Apr 2010, *H. Medeiros et al. 374* (RB); *ibid.*, 19 Mar 2011, *M. H. Terra-Araújo et al. 651* (RB); Tarauacá, 18 Sep 1968, *G. Prance et al. s.n.* (INPA, HB); Goiás: Alexania, lago Corumbá, 7 Jun 2005, *G. Pereira-Silva et al. 10114* (CEN); Corumbaba, Córrego Lobórea, 14 Nov 1997, *S. P. C. Silva et al. 730* (CEN); Pirenópolis, Santuário de Vida Silvestre Vaga Fogo, 27 Nov 2002, *M. L. Fonseca et al. 3856* (CEN, IBGE, SP). PARAGUAY. Guairá: Colonia Independencia, 17 Mar 1966, *G. Esser 14519* (B, HEID).

***Campylocentrum mattogrossense* Hoehne (1941: 62).**

Type: BRAZIL. Mato Grosso: São Luiz de Cáceres, Lava Pés, August 1911, *F.C. Hoehne in Comissão Rondon 4473* (lectotype R! **designated here**). (Fig. 1)

***Campylocentrum cuyuniae* Szlachetko & Kolanowska (2013: 265). *syn. nov.***

Type: GUYANA. Cuyuni-Mazaruni: Cuyuni River, Kauri Creek, Mora Forest, 17 May 1933, *Tutin 118* (holotype BM!)

Epiphytic herbs. Roots 1.5–2.0 mm diam., cylindrical, fibrous, smooth, whitish to dark grey. Stem 3.5–34.0 cm long, cylindrical, rarely branched. Leaves 32.0–113.0 × 9.0–20.0 mm, greenish (usually dark brown when dried), oblong-elliptical, oblanceolate, or widely elliptical, the apex asymmetrically slightly 2-lobed, lobes obtuse to rounded, margin entire. Inflorescences 12.0–25.0 mm long, peduncle 1.0–3.0 mm long, partially covered by bracts, glabrous, brownish; rachis 11.0–22.0 mm long, glabrous, brownish; floral bracts 1.0–1.5 × 0.7–0.9 mm, deltoid, margin minutely denticulate, the apex acute, membranaceous. Flowers 11–22 (per inflorescence), pale orange, distichous, pedicellate ovary 0.8–2.0 mm long; dorsal sepal 4.9–5.1 × 1.0–1.2 mm, oblong, the apex acute, 3-nerved, adaxially glabrous to slightly papillate, margin entire, membranaceous; lateral sepals 5.0–5.1 × 1.0–1.1 mm, oblong-subfalcate, the apex acute, 3-nerved, adaxially glabrous to slightly papillate, margin entire, membranaceous; petals 4.5–4.8 × 0.8–0.9 mm, oblong, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; lip 5.0–5.2 mm long, 2.2–2.3 mm wide between the lateral lobes, 3-lobed, membranaceous, 7–9-nerved, margin entire, producing at base a spur, lateral lobes 0.3–0.5 × 0.4–0.6 mm, suborbicular, the apex rounded, mid-lobe 3.2–3.3 × 0.9–1.0 mm, narrowly lanceolate, the apex acute, glabrous, spur 5.0–5.2 mm long, 1.0–1.2 mm diam., cylindrical-clavate, straight, the apex attenuate to rounded, pale orange, glabrous to slightly papillate; gynostemium 0.7–0.8 mm long, anther cap apex truncate, pollinia 2, globose. Capsule 7.0–9.0 × 2.0–3.0 mm, fusiform, 6-ribbed, pedicellate, pedicel 0.8–1.0 mm long.

**Distribution and Ecology:** — *Campylocentrum mattogrossense* is known from northern and central South America, in Brazil, French Guiana and Guyana. It probably occurs in Bolivia as populations are known from the Brazilian portion of the Abunã river, which forms the border between both countries. It grows in lowland forests (6–300 m alt.) in Amazon and Cerrado (gallery forest) vegetation. The flowering period is from December to April, and fruits can be observed throughout the year.

**Conservation Status:** — This species falls under the Least Concern (LC) category.

**Nomenclatural and Taxonomic notes:** — Hoehne (1941) cited two specimens as types (syntypes) of *Campylocentrum mattogrossense*, *Hoehne in Com. Rondon 4473*

and *Hoehne in Com. Rondon 570*, both from the same locality and deposited at R herbarium. Here we selected the number “4473” as the lectotype due the better preservation of the specimen. Recently, Szlachetko & Kolanowska (2013) described *C. cuyuniae* from Guyana, and compared it with *C. colombianum* Schltr. but neglected the existence of *C. matogrossense*. After the examination of the holotype of the new proposed species at BM herbarium, it is considered here a synonym.

*C. matogrossense* was included as a synonym of two different names. It was placed under *C. micranthum* by Dodson & Dodson (1980), which was followed by CONABIO (2009), Hamer (1982), Jørgensen *et al.* (2014) and McLeish *et al.* (1995), and under *C. robustum* by Pabst & Dungs (1977), which was followed by Brako & Zarucchi (1993), Jørgensen & León-Yáñez (1999) and Zuloaga (2008).

*Campylocentrum matogrossense* is easily distinguished among species morphologically related to *C. micranthum* by the straight spur which is often curved in the other taxa. It also differs from *C. micranthum* in the color of the flowers (pale orange vs. pale green), the lateral lobes of the lip (suborbicular with a rounded apex vs. deltoid with an acute to obtuse apex), size and curvature of the spur ( $\geq 5.0$  mm, straight vs.  $< 3.5$  mm, inflexed). (Fig. 2)

*Campylocentrum robustum* belongs to another group of species, and its vegetative portion can be distinguished from the *C. micranthum* group, as well as from *C. matogrossense*, by the form and apex of the leaves (oblong with a strongly 2-lobed apex vs. oblong-elliptical to oblanceolate with a slightly 2-lobed apex) (Fig. 3), the flowers differ by the entire lip (vs. 3-lobed). *Campylocentrum robustum* is endemic to the Brazilian Atlantic Forest, eastern South America (Barros *et al.*, 2014).

**Additional specimens examined:** — BRAZIL. Amazonas: Lago Cauaçu, 16 Jun 1965, *R. Richter s.n.* (HB); Alto Rio Negro, Jul 1972, *R. Richter s.n.* (HB); Goiás: Paraúna, Ponte de Pedra, 10 Jan 1993, *J. A. N. Batista 375* (CEN); Maranhão: Rio Maracaçume, Jul 1958, *R. Fróes 34394* (IAN); Mato Grosso: Cuiabá, Coxipó, Dec 1978, *J. Lima 50* (HB); São Luiz de Cáceres, Lava Pés, Sep 1908, *Hoehne in Com. Rondon 570* (R); Pará: Belém, Boa Vista, 22 May 1968, *J. Pires & N. Silva 11740* (IAN); Tucuruí, Vila Santa Rosa, Apr 1981, *N. Bastos & C. Motta 420* (MG); Altamira, Rio Iriri, 18 Aug 1986, *R. Vasconcelos et al. 8* (MG); São Félix do Xingú, Serra de Campo, 12 Aug 2001, *A. Salles et al. 2178* (HEPH); Rondônia: Abunã, Madeira-

Mamoré, 13 Jul 1968, *G. Prance et al. s.n.* (INPA); Presidente Médici, 31 May 1985, *U. Maciel 1476* (MG); Tocantins: *sine loco acurato*, 16 Aug 1978, *E. Mileski s.n.* (RB); Araguaçu, estrada para Alvorada, 16 Feb 1997, *J. A. N. Batista et al.* (CEN, UB). FRENCH GUIANA. Lieu de Récolte: Inselberg Mont Chauve, 265 m alt, 19 Apr 1997, *J. F. Villiers & C. Sarthou 6126* (P); *ibid.*, 11 Apr 1997, *G. Cremers & F. Crozier 14860* (CAY not seen, P). GUYANA. *sine loco acurato*, 1898, *E. F. Thurn 92 p. part.* (K).

### Key to the cited species

1. Leaves oblong with a strongly 2-lobed apex; lip entire.....*C. robustum*  
 - Leaves oblong-elliptical, elliptical, oblanceolate or widely elliptical with a slightly 2-lobed apex; lip 3-lobed.....2
2. Lateral lobes of the lip suborbicular, rounded apex; spur straight.....*C. mattogrossense*  
 - Lateral lobes of the lip deltoid to subdeltoid, the apex acute, obtuse, or truncate; spur slightly curved to inflexed.....3
3. Spur  $\leq 3.5$  mm, shorter than the sepals, inflexed.....*C. micranthum*  
 - Spur  $\geq 4.8$  mm, as long as to longer than the sepals, slightly curved.....*C. kuntzei*

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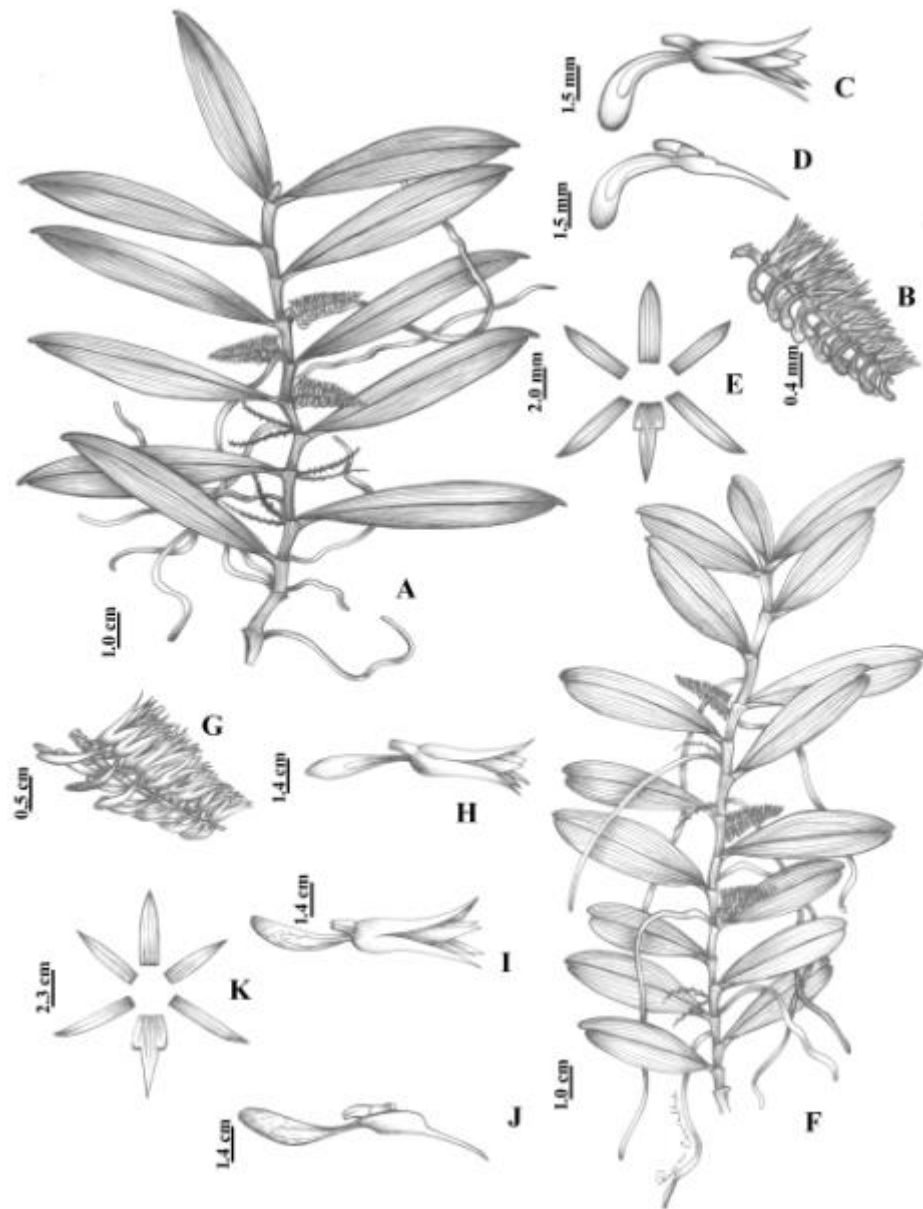
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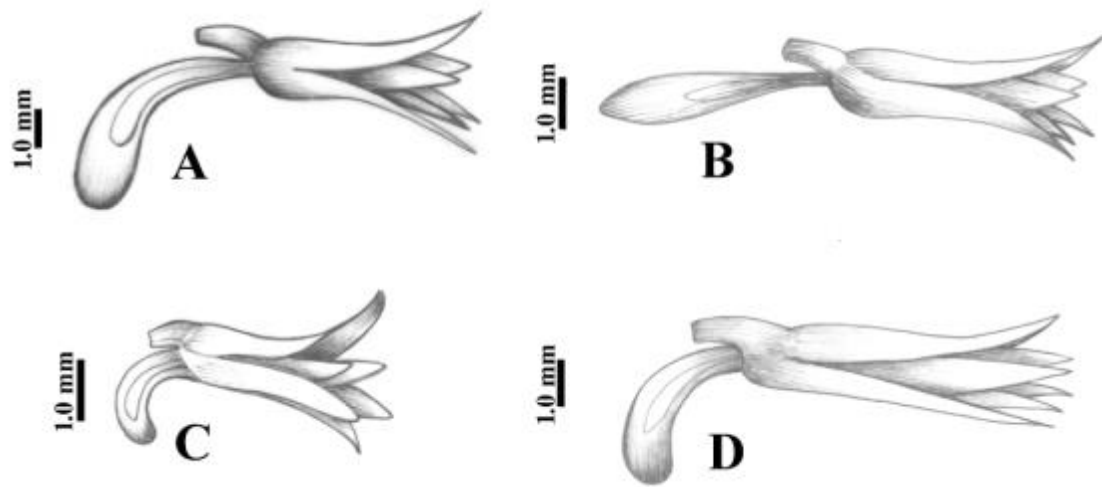
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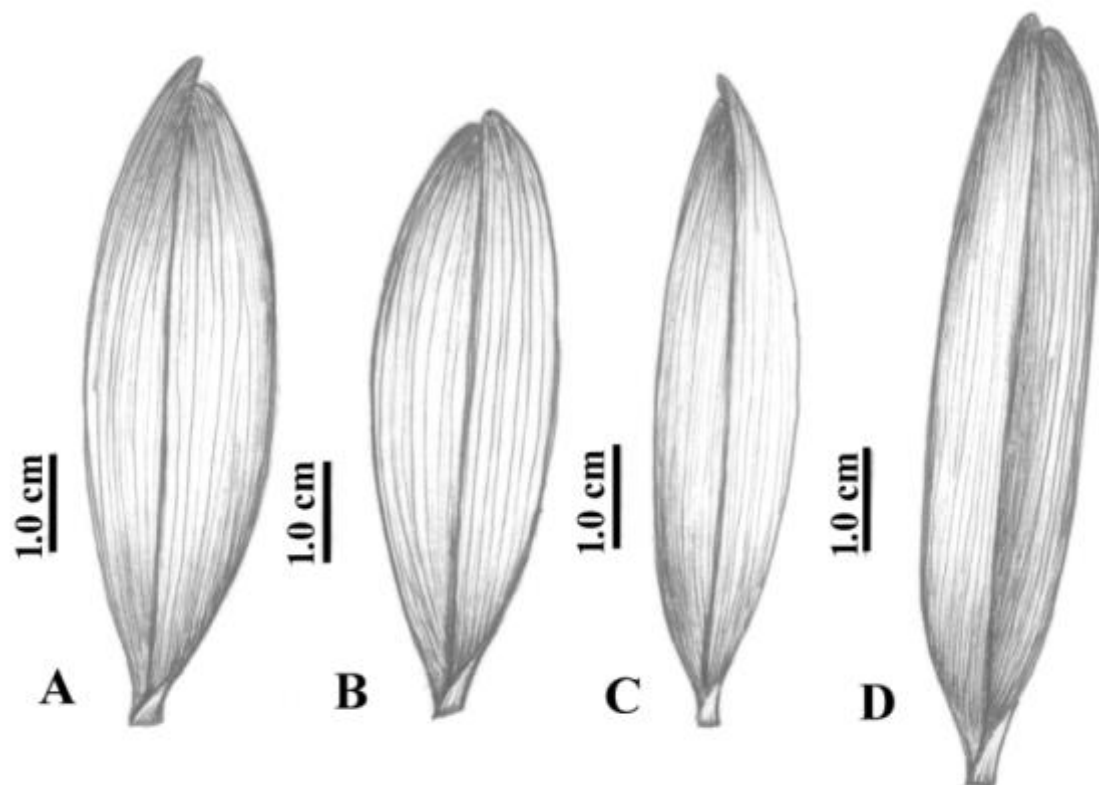




**FIGURE 1.** A-E. *Campylocentrum kuntzei*, A. Habit; B. Inflorescence; C. Flower; D. column and lip, lateral view; E. Dissected perianth. F-K. *C. mattogrossense*., F. Habit; G. Inflorescence; H-I. Flowers; J. column and lip, lateral view; K. Dissected perianth. [A-E. Drawn from *H. Medeiros* 374 (RB); F-H and K. Drawn from *U. N. Maciel* 1476 (MG); I-J Drawn from *J. F. Villiers & C. Sarthou* 6126 (P)].



**FIGURE 2.** Flowers. A. *Campylocentrum kuntzei*; B. *C. mattogrossense*; C. *C. micranthum*; D. *C. robustum*.



**FIGURE 3.** Leaves. A. *Campylocentrum kuntzei*; B. *C. mattogrossense*; C. *C. micranthum*; D. *C. robustum*.

**The identity of *Campylocentrum sellowii* (Angraecinae-Orchidaceae): clarifying on its circumscription and lectotypifications**

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Running title: The identity of *Campylocentrum sellowii*.

Keywords: Vandae, Neotropics, Brazil, Atlantic Forest, Cerrado.

**Abstract.** Cogniaux reviewed the Brazilian species of *Campylocentrum* and recognized *Campylocentrum aciculatum* and *C. sellowii* as distinct species. In his study, he also included two specimens of *C. ornithorrhynchum* among the material of *C. sellowii*. Examination of the type specimens shows that *C. sellowii* and *C. aciculatum* are the same species, and *C. ornithorrhynchum* is a distinct species. The aim of this study is to clarify the identity of *C. sellowii* and expand the description to include the concept of *C. aciculatum* and exclude the floral characters of *C. ornithorrhynchum*. It also provides an illustration, distribution map, key, lectotypifications of the treated names and discussion of its affinities with related species.

## Introduction

*Campylocentrum* Benth. comprises about 70 Neotropical species (Govaerts et al. 2015, Carlswald 2014) that exhibit great variation in habit, especially the presence/absence and form of the leaves (leafless/leafy; terete/conuplicate) (Bogarín & Pupulin 2010).

Currently, seven species with terete leaves are recognized, six of them endemic to eastern South America, mainly in the Atlantic Forest or areas transitional to *cerrado* vegetation (Barros et al. 2015; Govaerts et al. 2015). *Campylocentrum poeppigii* (Rchb.f.) Rolfe is the only widely distributed species, occurring from Mexico to northern South America (Govaerts et al. 2015).

In addition to terete leaves, the seven species share roots with a muricate to tuberculate surface, a feature first described by Reichenbach & Warming (1881) as slightly verrucose (“*paucis verrucosis*”) to describe *C. aciculatum* (Rchb.f. & Warm.) Cogn., later described by Barbosa Rodrigues (1882) as granulose (“*granulosae*”) in *C. parahybunense* (Barb. Rodr.) Rolfe and by Cogniaux (1906) as minutely to densely papillose (“*subtiliter, denseque, longiusculis, papillosis*”) in other species.

*Campylocentrum sellowii* (Rchb.f.) Rolfe was first described as *Angraecum* Bory based in a specimen from Brazil (without precise location) collected by Sellow (Reichenbach 1850). Rolfe (1903) proposed the currently accepted nomenclatural combination and mentioned the absence of flowers (only fruits were available) in all specimens analyzed: “...*I have seen being in fruit only.*” He probably did not have access to the Reichenbach herbarium which was closed from 1889 to 1915 (Stafleu & Menega 1992) and where a type specimen with flowers was deposited.

Later, Reichenbach & Warming (1881) described *C. aciculatum* (Rchb.f. & Warm.) Cogn. under *Aeranthus* Lindl. based on a specimen collected by Warming from Minas Gerais, Brazil, which is available at C. After a morphological examination of the type specimens for a taxonomic review of the genus, we recognized that *C. sellowii* and *C. aciculatum*, although described originally in different genera, are in fact the same species.

Cogniaux (1906) reviewed the Brazilian species of *Campylocentrum* and recognized *C. aciculatum* and *C. sellowii* as distinct species. In this study he interpreted

two specimens [Glaziou 6722 and J. de Moura 50] that are in fact a third species, *C. ornithorrhynchum* (Lindl.) Rolfe, as specimens of *C. sellowii*. He probably also did not have access to the Reichenbach collection, and consequently the description of the flowers of *C. sellowii* in Cogniaux's study is actually based on *C. ornithorrhynchum*.

The confusion caused by his misinterpretation of *C. sellowii* can be seen in several subsequent studies (Hoehne 1945; Pabst & Dungs 1977) and more often in local herbaria. The aim of this note is to clarify the identity of *C. sellowii* and expand the description to include the concept of *C. aciculatum* and exclude the floral characters of *C. ornithorrhynchum*.

This study also provides an illustration of the morphological variation in *C. sellowii*, a distribution map, lectotypifications of names, and discussion of its affinities with related species. Additionally, a key for species of *Campylocentrum* with terete leaves is presented.

## **Material and Methods**

This study was based on an examination of living and dried specimens deposited in herbaria. The measurements of vegetative and floral parts were made using fresh material and flowers in spirit, and the illustration was produced based on collections from different locations aiming to show the morphological variation across the distribution of the species.

The identification key was based on an analysis of type specimens and other materials deposited at the herbaria BHCB, BR, C, CESJ, E, EAN, ESA, HB, HUEFS, K, MBML, NY, P, R, RB, SP, SPF, UFP and W (acronyms according to Thiers 2015). We used georeferenced records of collections of the above-mentioned herbaria for the construction of the map, records without information about coordinates were based on the center of the municipality, obtained by the geoLoc tool (available at <http://splink.cria.org.br/geoloc>).

## **Results and Discussion**

*Campylocentrum sellowii* (Rchb.f.) Rolfe, Orchid Review 11: 246. 1903. Fig. 1

≡ *Angraecum sellowii* Rchb.f., Linnaea 22: 857. 1850. Type: BRAZIL. *Sine loco acurato*, s.d., Sellow B 1337 – C 346 (Lectotype: W 39239! Isolectotypes: W 17516!, K!, BR! **designated here**).

= *Campylocentrum aciculatum* (Rchb.f. & Warm.) Cogn. in C. F. P. von Martius & auct. Sec. (eds.), Fl. Bras. 3(6): 516. 1906. *Aeranthus aciculata* Rchb.f. & Warm., Otia Bot. Hamburg.: 91. 1881. Type: BRAZIL. Minas Gerais, Lagoa Santa. s.d., *Warming s.n.* [lectotype: C! (in spirit), isolectotype: W! **designated here**]. *syn. nov.*

Epiphytic or rupicolous herb. Roots 1.5–2.5 mm diam., terete, fibrous, whitish-gray, surface minutely muricate. Stem 7.5–62.0 cm long, 1.2–3.0 mm diam., terete. Leaves caducous in older portions, usually present in the young branches; the sheaths 5.0–17.0 mm long, striate; the blades 8.0–30.0 × 1.0–2.0 mm, distichous, terete, straight or arched, the apex acuminate, fleshy. Inflorescence 5.0–15.0 mm long, a raceme; peduncle 0.8–1.5 mm long, the surface minutely papillose; rachis 4.2–13.5 mm long, the surface minutely papillose; floral bracts 0.5–0.8 × 0.3–0.4 mm, deltoid, the margin ciliate, the apex acute, membranaceous; flowers 6–18 per inflorescence, pale orange, distichous; the ovary pedicellate, 0.8–1.2 mm long, smooth to minutely papillose; dorsal sepal 1.0–1.8 × 0.7–1.0 mm, ovate to lanceolate, the apex acute, 1-nerved, glabrous, the margin entire, membranaceous; lateral sepals 1.1–2.1 × 0.5–0.6 mm, elliptical to lanceolate, the apex acute, 1-nerved, glabrous, the margin entire, membranaceous; petals 1.0–1.8 × 0.3–0.5 mm, elliptical to lanceolate, the apex acute, 1-nerved, glabrous, the margin entire, membranaceous; lip 1.0–1.8 × 1.0–1.5 mm, entire to obscurely 3-lobed, membranaceous, 5–7-nerved, the margin entire, producing at base a slender spur, the spur 1.6–3.5 mm long × 0.5–0.6 mm diam., conic, sub-patent, the apex obtuse; column ca. 0.5 mm long, pollinia 2, globose, viscidium with two parts. Capsule 4.0–6.0 × 1.0–1.8 mm, elliptical to obovoid, the surface rugose, pedicellate, the pedicel 1.0–1.6 mm long.

Distribution and Ecology: *Campylocentrum sellowii* is endemic to Brazil (states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) (Fig. 2). It grows in lowland to sub-montane forests (150-1100 m alt.), in Atlantic Forest (including *restingas*), *Caatinga* and *Cerrado* (gallery forest) vegetation. The flowering period is from January to May and fruits can be observed from May to November.

Conservation Status: According to the IUCN (2013), this species is classified as Vulnerable due to its very reduced (B2) and very impacted (B2a) area of occupancy.

Morphological affinities: *Campylocentrum sellowii* has a large variation in the size of its flowers (Fig. 1), which can be found in the same inflorescence (comparing flowers from the base and from the top), in different specimens of the same population, and among populations (the largest flowers are found in plants from the states of Bahia and northern Minas Gerais).

Although the majority of the specimens of *C. ornithorrhynchum* have longer leaves (> 30.0 mm), some examined plants has shorter leaves (< 20.0 mm), very similar in size to those of *C. sellowii*. The two species are easily distinguished by lip shape, clearly 3-lobed in *C. ornithorrhynchum*, and entire to obscurely 3-lobed in *C. sellowii*, and by the capsules, pedicellate in *C. sellowii* (pedicel 1.0–1.6 mm long), and sessile in *C. ornithorrhynchum* (pedicel ca. 0.1 mm long).

A lip shape similar to that of *C. sellowii* (obscurely 3-lobed) is present in *C. poeppigii* (Rchb.f.) Rolfe, which can be distinguished by its shorter leaves (3–7 mm long vs. 8–30 mm long) and spur as long as or slightly longer than the pedicellate ovary (vs. two times longer or more than the pedicellate ovary).

*Campylocentrum sellowii* can be confused with *C. wawrae* (Rchb.f. ex Beck) Rolfe by the short, arched leaves. The latter is recognized by shorter inflorescences ( $\leq$  5.0 mm long vs. 5.0–15.0 mm long) with 3–5 flowers (vs. 6–18 flowers per inflorescence) with a clearly 3-lobed lip (vs. entire to obscurely 3-lobed) and a shorter spur (about 1.0 mm long vs. 1.6–3.5 mm long).

Nomenclatural notes: Reichenbach cited a specimen collected by Sellow (without number) from Brazil as a type of *Angraecum sellowii*. The authors were able to find four specimens belonging to this collection, two at W, one at BR and one at K.

Although he did not cite the herbarium in the protolog, a specimen of his collection (currently at W) should be selected as a lectotype. While there are two specimens collected by Sellow deposited at W, the specimen W no. 39239 is herein selected as a lectotype for the name (instead W no. 17516) due to its better conservation.

When Reichenbach described *Aeranthes aciculata*, he studied a collection by Warming from Lagoa Santa (Brazil). Although the Reichenbach herbarium is currently at W, the Warming specimen is deposited at C (in spirit) which is here designated as lectotype, with a fragment deposited at W designated as isolectotype.

Additional specimens examined: BRAZIL. Bahia. Abaíra, Morro do Zabumba, 13 Mar 1992, *B. Stannard et al. H51941* (E, HUFS, K, SPF, UFP); Maracás, Estrada para Cruzeiro, 19 Jul 2013, *E. Melo et al. 11317* (HUEFS); Morro do Chapéu, Buraco do Possodônio, 7 Apr 2008, *C. Bastos & C. Vandenberg 178* (HUEFS); *ibid.*, 5 Mar 2007, *C. Bastos 130* (HUFS); *ibid.*, Sítio Novo Horizonte, 8 Apr 2008, *C. Bastos & C. Vandenberg 182* (HUEFS); *ibid.*, 8 Apr 2008, *C. Bastos & C. Vandenberg 204* (HUEFS); Vitória da Conquista, Serra do Tromba, 10 Nov 2008, *C. Azevedo et al. 351* (HUEFS); Espírito Santo. Alfredo Chaves, 27 May 1974, *R. Kautsky 436* (HB); Guaraparí, Setiba, 12 Mar 1995, *C.N. Fraga 128* (MBML); *ibid.*, 12 Mar 1995, *C.N. Fraga 129* (MBML); *ibid.*, 5 Apr 1996, *C.N. Fraga 312* (MBML); *ibid.*, 5 Apr 1995, *C.N. Fraga et al. 147* (MBML); Linhares, Reserva Natural da CVRD, 14 Jun 1993, *G.L. Farias 610* (RB); Santa Isabel, Pedra do Vento, 15 May 1974, *B. Ghillany 2-74* (HB); Minas Gerais. between Rio Grande and Diamantina, s.d., *Burchell 5366* (K, W); Conceição do Mato Dentro, PCH Sumidouro, 25 Sep 2005, *P. Viana et al. 1886* (CESJ); Coronel Pacheco, Fazenda Liberdade, 13 Feb 1942, *E.P. Heringer 936* (SP, SPF); *ibid.*, Fazenda da Companhia, 27 Jun 1944, *E.P. Heringer s.n.* (SP); Cristais, Sítio Barreiro, 21 Jul 2013, *E. Pessoa & B.M. Carvalho 1189* (BHCB, NY, RB, SP, UFP); *ibid.*, Sítio Barreiro, 20 Jul 2014, *B.M. Carvalho 119a* (BHCB); Espinosa/Montezuma, Serra do Pau D'arco, 15 Mar 1994, *C. Sakuragui et al. CFCR 15089* (ESA, K, SPF, UFP); Formiga, Baiões Mar 1956, *N. Welter 164* (HB); Paraoapeba, 4. Jan 1958, *E.P. Heringer s.n.* (HB); *ibid.*, 30 Jan 1959, *E. P. Heringer 5764* (K); *ibid.*, Fazenda Funil, 9 Feb 1957, *E.P. Heringer s.n.* (HB); *ibid.*, Aracaí, 19 Mar 1957, *E.P. Heringer s.n.* (HB); Serro, Serra do Espinhaço, Feb 1956, *L.P. Felix & G. Dornelas 77* (EAN); Rio de Janeiro. Araruama, APA Massambaba, 14 Mar 1996, *L. Emygdio 5906* (R); Armação de



Búzios, Serra das Emeranças, 17 Mar 2001, *C. Farney & A. Terra 4365* (RB); Bordas do Rio Paraíba, 28 Jul 1881, *A. Glaziou 13233* (BR, C, P); Ilha do Rio Paraíba, 4 Mar 1966, *J. Laranja s.n.* (HB); Macaé, s.d., *Riedel s.n.* (BR); Petrópolis, Areal, 17 May 1928, *C. Spannagel 161* (SP); Rio de Janeiro, Estação de Comércio, s.d., *L. Rangel s.n.* (R); São Paulo. São José do Berreiro, 3 May 1968, *D. Sucre et al. 3046* (RB).

### Key to species of *Campylocentrum* with terete leaves

1. Leaves  $\leq 7.0$  mm long; inflorescence longer than the leaves (plants from Mexico to northern South America).....*C. poeppigii*
  - Leaves  $> 7.0$  mm long; inflorescence shorter than the leaves (plants from eastern South America).....2
2. Lip entire to obscurely 3-lobed; spur half longer than the sepals.....*C. sellowii*
  - Lip clearly 3-lobed; spur shorter to slightly longer than the sepals.....3
3. Mid-lobe of the lip as long as the lateral lobes; spur obovoid, shorter than the pedicellate ovary.....*C. wawrae*
  - Mid-lobe of the lip longer than the lateral lobes; spur clavate to cylindrical, as long as or longer than pedicellate ovary.....4
4. Sepals  $\geq 1.3$  mm long, 1-nerved.....*C. pernambucense*
  - Sepals  $\geq 1.6$  mm long, 3-nerved.....5
5. Roots slightly muricate, leaves distichous; lateral lobes of the lip  $> 0.7$  mm wide.....*C. ornithorrhynchum*
  - Roots densely tuberculate, leaves secund (distichous only in the top leaves); lateral lobes of the lip  $\leq 0.5$  mm wide.....*C. parahybynense*

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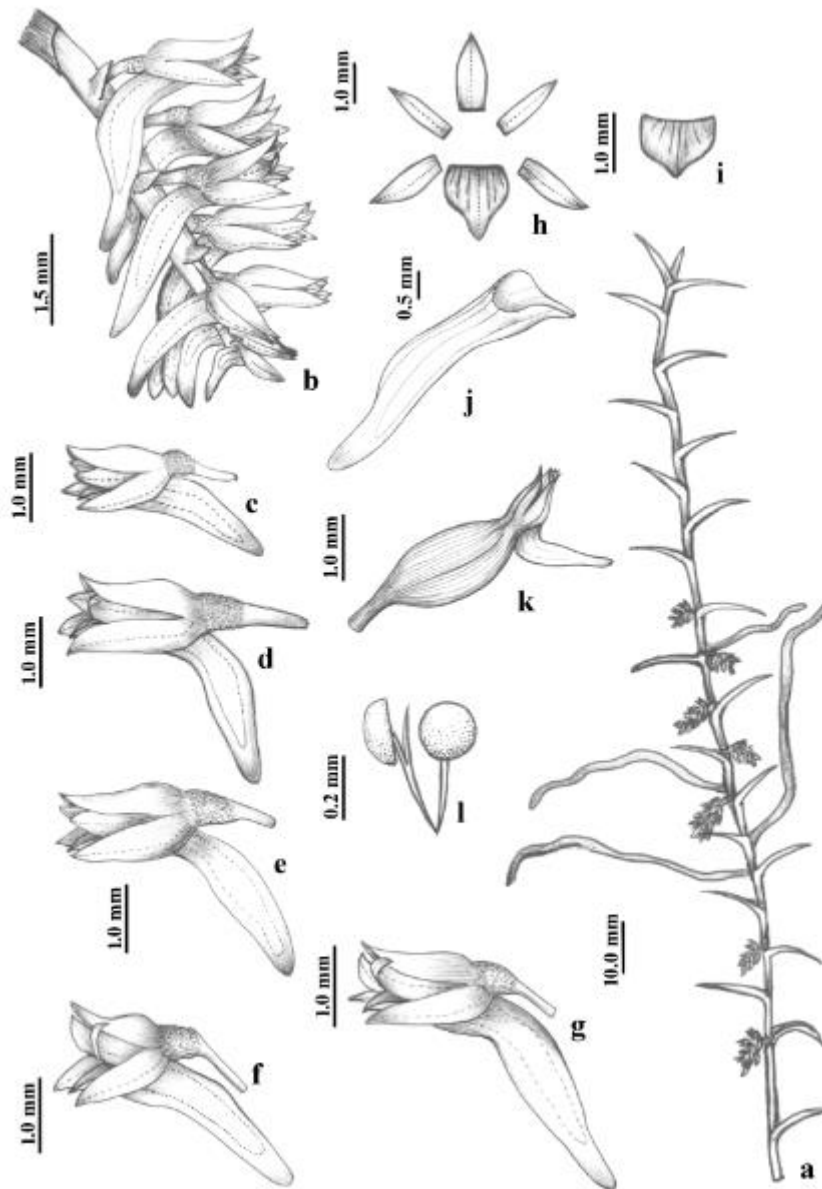
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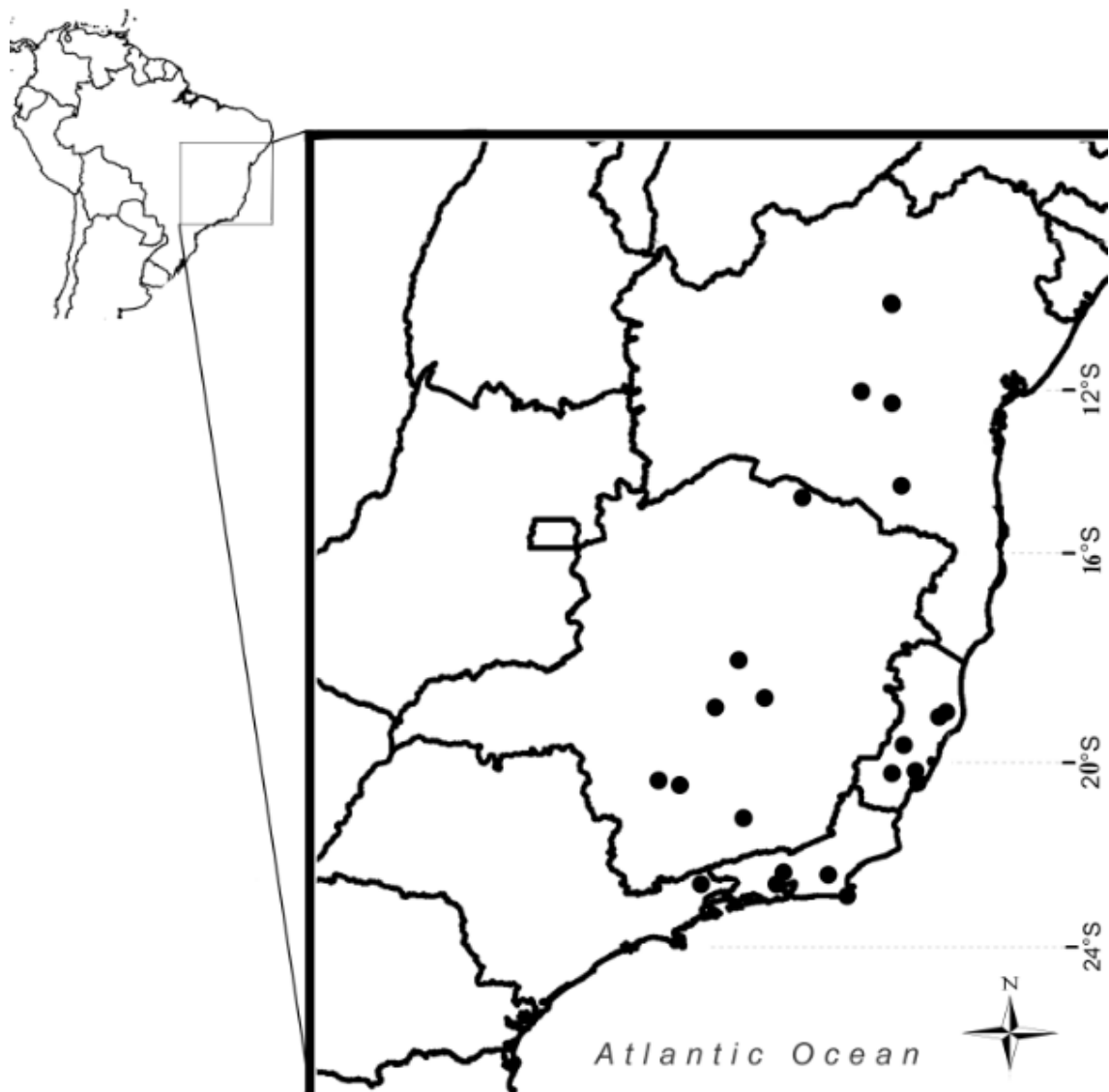
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**Figure 1.** *Campylocentrum sellowii*. a. Habit; b. Inflorescence; c. Flower (from Minas Gerais); d. Flower (from Minas Gerais); e. Flower (from Rio de Janeiro); f. Flower (from Espírito Santo); g. Flower (from Bahia); h. Dissected perianth; i. Lip; j. Lip and spur in profile; k. Capsule (perianth persistent), l. Pollinarium. [a–b, g–h, j and l: drawn from *B. Stannard et al. H51941* (SPF); c and i: from *L.P. Felix & G. Dornelas 77* (EAN); d: from *C. Sakuragui et al. CFCR 15089* (SPF); e: from *C. Farney & A. Terra 4365* (RB); f: from *C.N. Fraga 128* (MBML); k: from *E. Pessoa & B.M. Carvalho 1189* (UFP)].



**Figure 2.** Map of the known distribution of *Campylocentrum sellowii* (Rchb.f.) Rolfe.

**A new *Campylocentrum* (Vandaeae; Epidendroideae; Orchidaceae) from submontane Atlantic Forest of northeastern Brazil.**

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**Abstract**

A new species of *Campylocentrum* with reduced stems, small conduplicate leaves and long inflorescences is described from submontane Atlantic forest of Pernambuco state, northeastern Brazil. It is related to *C. hirtellum*, but differs by having a pedicellate ovary and slightly papillate base of the perianth, smaller sepals, mid-lobe of the lip less than three times longer than the lateral lobes, lip 5-nerved, spur slightly longer than the pedicellate ovary and a glabrous capsule. It is illustrated and its affinities with allied species are also discussed.

**Keywords:** New species, Epiphytes, Montane Forest, Pernambuco

## Introduction

*Campylocentrum* Benth (1881: 337) comprises about 70 species (Govaerts 2014). According to Todzia (1980), the Atlantic Forest of Brazil is the endemism centre of the genus with ca. 30 species (Barros *et al.* 2014, Siqueira *et al.* in press, Pessoa *et al.* in press).

Cogniaux (1906) proposed three sections within the genus: *C.* sect. *Campylocentrum* [originally *C.* sect. *Eucampylocentrum*, Cogniaux (1906: 504)], species with stems and leaves developed, *C.* sect. *Dendrophylopsis* Cogniaux (1906: 504), leafless species, and *C.* sect. *Pseudocampylocentrum* Cogniaux (1906: 504), species with developed stems and reduced leaves.

*Campylocentrum hirtellum* Cogniaux (1906: 521), *C. hondurensense* Ames (1923: 37) and *C. steyermarkii* Foldats (1968: 316) have reduced stems ( $\leq 10.0$  mm long) and small conduplicate leaves. These plants occasionally lose their leaves in the drying procedure, and they look like leafless plants. This could possibly explain the mistaken placement of *C. hirtellum* by Cogniaux (1906) under *C.* sect. *Dendrophylopsis*. Subsequently, the species, which actually belongs to *C.* sect. *Campylocentrum*, was better illustrated by Hoehne (1941). Among the species of the Atlantic Forest only *C. hirtellum* shows the characters mentioned above. It is known from Rio de Janeiro (Brazilian Southeast) and Santa Catarina states (Brazilian South, Barros *et al.* 2014).

During the studies for a taxonomical review of *Campylocentrum*, a new species with reduced stems and long inflorescences was found in submontane forest in Pernambuco state, Brazilian Northeast. It is described and illustrated below, and its affinities with the allied species are also discussed.

### ***Campylocentrum serranum* E. Pessoa & M. Alves, *sp. nov.* (Fig. 1, 2)**

Type: —BRAZIL. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 8°43'12"S, 35°50'38"W, 700 m, 30 May 2012, E. Pessoa *et al.* 945 (fl.) (holotype UFP, isotypes K, NY, RB).

*C. serranum* is morphologically related to *C. hirtellum*, but differs by having a pedicellate ovary and slightly papillate base of the perianth, smaller sepals, mid-lobe of the lip less than three times longer than the lateral lobes, lip 5-nerved, spur slightly longer than the pedicellate ovary and a glabrous capsule.

Epiphytic herb. Roots 1–1.5 mm diam., dorso-ventrally flattened, fibrous, smooth, whitish to dark grey. Stem 3–7 mm long, cylindrical, completely covered by the leaf sheaths. Leaves 2–4, sheath 2–3.5 mm long, blade 10–31 mm long, 2–4 mm wide, dark green, elliptical, falcate, the apex asymmetrically 2-lobed, lobes acute, margin entire, caducous. Inflorescence 25–40 mm long, peduncle 7–12 mm long, papillate, brownish; rachis 15–30 mm long, papillate, brownish; floral bracts 0.5–1.2 mm long, 0.3–0.5 mm wide, lanceolate to deltoid, margin ciliate, the apex acute, membranaceous. Flowers 8–15 (per inflorescence), whitish, distichous, ovary 1.3–1.5 mm long, pedicellate, slightly papillate; dorsal sepal 1.2–1.5 mm long, 0.3–0.5 mm wide, oblong-elliptic, the apex acute to obtuse, 1-nerved, adaxially slightly papillate in the base, margin entire, membranaceous; lateral sepals 1.4–1.6 mm long, 0.4–0.5 mm wide, oblong-elliptical, the apex acute, 1-nerved, adaxially slightly papillate in the base, margin entire, membranaceous; petals 1.1–1.3 mm long, 0.4–0.5 mm wide, oblong-elliptical, the apex acute, 1-nerved, glabrous, margin entire, membranaceous; lip 1–1.2 mm long, 1–1.1 mm wide between the lateral lobes, 3-lobed, membranaceous, 5-nerved, margin entire, producing at base a spur, lateral lobes 0.2–0.3 mm long, 0.3–0.4 mm wide, orbicular, the apex rounded, mid-lobe 0.5–0.6 mm long, ca. 0.3 mm wide, deltoid, the apex acute, spur 1.5–1.6 mm long, 0.3–0.5 mm diam., cylindrical, slightly curved, the apex rounded; gynostemium 0.2–0.3 mm long,, anther cap apex 2-lobed, pollinia 2, globose. Capsule 5.0–6.0 mm long, 1.5–2 mm wide, fusiform, 6-ribbed, glabrous, pedicel ca. 1 mm long.

**Distribution and Ecology:** —It is known only from the type locality, an area of submontane Atlantic forest along the eastern border of the Borborema plateau, Pernambuco state, northeastern Brazil. The area is part of the Serra do Urubu, which is mainly covered by ombrophilous forest (Veloso 1992) with some exposed rocky outcrops at 600–800 m altitude. Some new species of orchids have been recently described from the area (Amorim & Alves 2012, Sobral 2013, Gregório *et al.* 2014, Pessoa *et al.* 2014a, Pessoa *et al.* 2014b.). The



flowering period is poorly known, but based on the specimens cited, flowers can be found in May, and fruits in January.

**Etymology:** —It is named on behalf of the area of occurrence, highlands of Pernambuco state (Serra do Urubu).

**Morphological affinities:** —*Campylocentrum serranum* is morphologically related to species with reduced stems and small conduplicate leaves like *C. hirtellum*, *C. hondurensis* and *C. steyermarkii*. The latter two species are restricted to the Amazon Basin and Central America, and have inflorescences as long as to slightly shorter than the leaves and an entire to obscurely 3-lobed lip. *C. hirtellum* and *C. serranum* grow in the Atlantic Forest of Brazil, and have inflorescences longer than the leaves and a distinctly 3-lobed lip.

The new species differs from *C. hirtellum* by having a slightly papillate pedicellate ovary and base of the perianth (vs. pedicellate ovary and base of perianth densely hirtellous), smaller sepals ( $\leq 1.6$  mm long vs.  $\geq 2.0$  mm long), mid-lobe of the lip less than three times longer than the lateral lobes (vs. more than four times longer), lip 5-nerved (vs. 9-nerved), spur slightly longer than the pedicellate ovary (vs. spur more than two times longer than the pedicellate ovary) and glabrous capsule (vs. densely hirtellous capsule) (Fig. 1).

The comparison of diagnostic features between *C. serranum* and allied species is presented in Table 1.

**Additional specimens examined (paratypes):** — BRAZIL. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 8°43'53"S, 35°50'34"W, 752 m, 29 January 2013, *E. Pessoa et al. 1051* (fr.) (UFP); *ibid.*, 776 m, 25 November 2014, *E. Pessoa et al. 1279* (fr.) (UFP).

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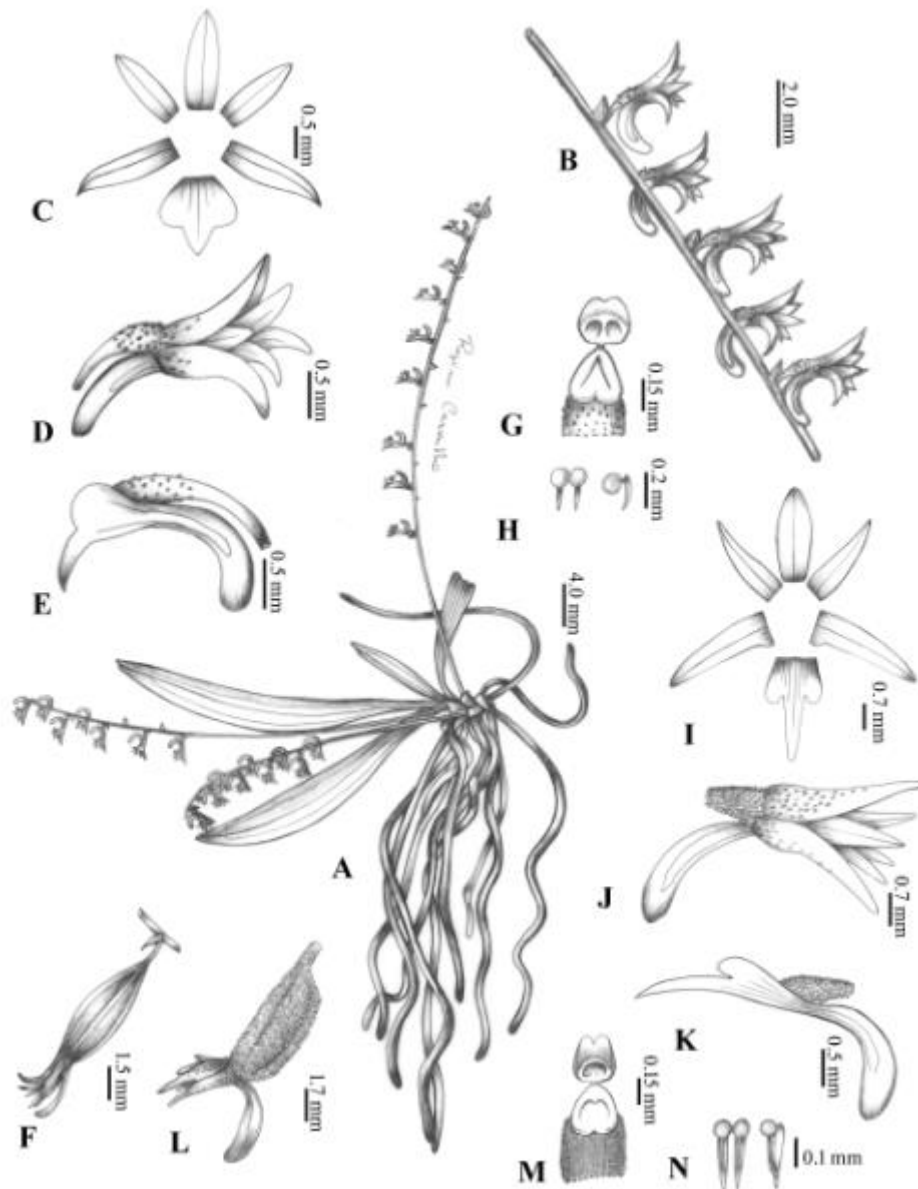
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**TABLE 1.** Comparison of morphological characteristics of *Campylocentrum serranum* and related species.

<b>Characters</b>	<i>C. hirtellum</i>	<i>C. hondurensis</i>	<i>C. serranum</i>	<i>C. steyermarkii</i>
<b>Inflorescence length (I) × leaf length (L)</b>	I > L	I < L	I ≥ L	I < L
<b>Lip form</b>	distinctly 3-lobed	entire	distinctly 3-lobed	obscurely 3-lobed
<b>Spur length (S) × pedicellate ovary length (P)</b>	S > P	S > P	S > P	S < P
<b>Capsule surface</b>	hirtellous	sparsely glandulose	glabrous	sparsely glandulose



**FIGURE 1.** *Campylocentrum serranum*. A. Habit. B. Detail of inflorescence. C. Dissected perianth. D. Flower. E. Lip and pedicellate ovary. F. Capsule. G. Column. H. Pollinarium. *Campylocentrum hirtellum*. I. Dissected perianth. J. Flower. K. Lip and pedicellate ovary. L. Capsule. M. Column. N. Pollinarium. [A-E, G-H drawn from *E. Pessoa et al.* 945; F from *E. Pessoa et al.* 1051; I-K, M-N from *Reitz & Klein* 1152 (HBR); L from *H. Shenck* 2718 (BR)].



**FIGURE 2.** *Campylocentrum serranum*. A. Inflorescence. B. Habit. C. Lateral detail of inflorescence. D. Frontal detail of inflorescence. [A-D Pessoa *et al.* 945 (Holotype)]

***Campylocentrum benellii* and *C. paludosum* spp. nov. (Angraecinae-Orchidaceae):  
two new leafless species from Brazil.**

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**Abstract**

The leafless condition is present in two Neotropical epiphyte genera of Orchidaceae, *Campylocentrum* and *Dendrophyllax*. Only the first one is reported from Brazil, where seven leafless species are recorded, and four of them are endemic. This study describes two new species of *Campylocentrum* from the Atlantic forest of São Paulo state and Amazon forest of Acre, Mato Grosso and Rondônia states. It also provides a key to the Brazilian species of leafless *Campylocentrum*, illustrations, and a discussion of the affinities of the new species with allied ones.

**Keywords** –Atlantic Forest, Amazon Forest, *Dendrophylopsis*, Epidendroideae, Vandae

The Neotropical region has been indicated as one of the diversity centers of Orchidaceae (Dressler 1993), and in this area two genera with species of leafless epiphytes belonging to the subtribe Angraecinae, *Campylocentrum* Benth. and *Dendrophyllax* Rchb.f., are arousing the curiosity of botanists. Carlswald et al. (2003), using a molecular approach, delimited these genera; also suggesting that the leafless condition possibly has arisen twice in the subtribe.

The leafless species of *Campylocentrum* have short stems with leaves reduced to brownish, non-chlorophyllous scales (Boragín and Pupulin 2010). Cogniaux (1906) included the five species known at that time with this condition into *C.* sect. *Dendrophylopsis* Cogn.

Nowadays, the section *Dendrophylopsis* holds ca. 20 names, some of them are taxonomically unresolved. Among the species are *C. barrerarum* Kolan. & Szlach, *C. fernandezii* Kolan. & Szlach, *C. generalense* Boragín & Pupulin and *C. insulare* Siqueira & Pessoa (Boragín and Pupulin 2010, Kolanowska and Szlachetko 2013, Siqueira et al. 2015), which were recently described. The section is widespread in the Neotropics from the USA (Florida) to Argentina (Misiones) (Govaerts et al. 2015).

In Brazil seven species of leafless *Campylocentrum* are recorded, four of which are endemic to the country (Barros et al. 2015, Siqueira et al. 2015). This study describes two new species for this group, one from the Atlantic Forest of São Paulo state and other from the Amazon Forest of Acre, Mato Grosso and Rondônia states.

As part of a taxonomic review of the genus conducted by the first author, all type specimens of Brazilian leafless *Campylocentrum* were examined [herbaria BA, BR, C, FLOR, G, GOET, HB, K, L, M, P, R, RB, SP, SPF, U, and W (Thiers 2015)].

This study also provides a key to the Brazilian species of leafless *Campylocentrum*, illustrations, and a discussion of the affinities of the new species with their allies.

## **Taxonomic Treatment**

***Campylocentrum benellii* E. Pessoa & M. Alves, sp. nov. (Fig.1A–D, 2A)**



Similar to *C. pubirhachis* Schltr. based on the size of the spur but differs by having pale orange flowers, the mid-lobe of the lip smaller than the lateral lobes and a patent spur with a rounded apex .

**Type:** Brazil, Rondônia, Presidente Médici, Rio Machado, Near to the ferry [11°19'59"S; 61°53'50"W], 170 m elev., 21 Nov 2013, fl., A. Petini-Benelli & S.C. Freitas 925 (holotype: UFMT).

### *Etymology*

The name of the new species honors Adarilda Petini Benelli, the collector of the type specimen.

### *Description*

Epiphytic herbs. Roots 1.0–1.5 mm diam., cylindrical, fibrous, smooth, grey to whitish. Stem 5.0–8.0 mm long, cylindrical. Inflorescences 23.0–67.0 mm long, peduncle 6.0–18.0 mm long, minutely pubescent, ochre; rachis 17.0–49.0 mm long, minutely pubescent, ochre; floral bracts 0.5–0.8 mm × 0.4–0.6 mm, deltoid, membranaceous, ochre, margin minutely ciliate, acute at apex. Flowers 10–26 per inflorescence, pale orange, distichous, ovary pedicellate, 0.4–0.6 mm long, smooth; dorsal sepal 1.0–1.1 × 0.6–0.7 mm, ovate, membranaceous, acute at apex, 1-veined, margin entire; lateral sepals 1.0–1.2 × 0.6–0.7 mm, ovate, membranaceous, 1-veined, margin entire, acute at apex; petals 0.8–1.0 × 0.4–0.5 mm, ovate, membranaceous, 1-veined, glabrous, margin entire, acute at apex; lip 1.1–1.2 mm × 1.3–1.5 mm wide between the lateral lobes, entire to 3-lobed, membranaceous, 7-veined, margin entire, producing a spur at base, lateral lobes 0.7–0.8 × 0.2–0.3 mm, sub-orbicular, glabrous, rounded at apex, middle lobe 0.3–0.4 × 0.2–0.3 mm, widely deltoid, acute at apex, spur 1.9–2.1 mm long, 0.4–0.5 mm diam., cylindrical-clavate, patent, pale orange, rounded at apex; gynostemium 0.2–0.3 mm long, anther cap apex 2-lobed, pollinia 2, globose. Capsule 2.0–3.0 × 1.3–1.6 mm, globose to fusiform, 6-ribbed, pedicellate, pedicel 0.4–0.6 mm long.

### *Distribution and habitat*

The new species is known from the Brazilian states of Acre, Mato Grosso, Pará and Rondônia (Fig. 3). It probably also occurs in Bolivia and Peru, as these countries are adjacent to the Brazilian states cited, and have similar habitats. It grows in lowland areas of open, ombrophilous forests in the Amazon, or in gallery forest in *cerrado* vegetation.

### ***Phenology***

Based on herbarium specimens, flowers appear in November, and fruits from February to May.

### ***Similar species and notes***

Hoehne (1910) collected and illustrated a specimen from Tapirapoan [Tapirapoã] (state of Mato Grosso) as *C. tenue* (Lindl.) Rolfe. The sample was kept under this name for more than one hundred years. Although it was collected in flower, as illustrated by Hoehne, the specimen currently lacks flowers. A careful study showed that it is the species here described as *Campylocentrum benellii*.

Species with long-spurred flowers (> 1.8 mm long) are not common among the leafless species of *Campylocentrum*, but this characteristic is present in *C. pubirhachis*, which is endemic to the Atlantic Forest of Brazil (Barros et al. 2015) and *C. tyrridion* Garay & Dunst, distributed from Mexico to Venezuela (Govaerts et al. 2015).

The new species differs from *C. pubirhachis* by its pale orange flowers (vs. whitish flowers), the mid-lobe of the lip smaller than the lateral lobes (vs. mid-lobe as long as to longer than the lateral lobes) and a patent spur with a rounded apex (vs. sigmoid spur with an acute to obtuse apex), and from *C. tyrridion* by its glabrous, pedicellate ovary (vs. pubescent), mid-lobe of lip glabrous (vs. mid-lobe of the lip with a tuft of short hairs) and spur cylindrical-clavate with a rounded apex (vs. conical with an obtuse apex).

### ***Additional specimens examined (paratypes)***

Brazil. Acre, Cruzeiro do Sul, near the new airport, 12 Feb 1976, fr., O.P. Monteiro & C. Damião 327 (INPA); ibidem, 28 Feb 1976, fr., J. Ramos & G. Mota 146 (INPA). Mato Grosso, Cuiabá, Santa Carmem, Rio Azul, 5 May 1998, fr., M. Macedo & G. Guarim-Neto 6662 (UFMT); Tangará da Serra, Tapirapuã, Mar 1909, fl., Hoehne in

Com. Rondon 1408 (R). Pará, Tucuruí, Santa Rosa, 4 Oct 1983, fb., J. Revilla et al. 8532 (INPA, NY).

***Campylocentrum paludosum* E. Pessoa & M. R. Miranda sp. nov. (Fig. 1E–H, 2B)**

Similar to *C. fasciola* (Lindl.) Cogn. based on the shape and size of the perianth, but differs by a lip 5-veined and presence of short hairs on the mid-lobe of the lip, and spur wide-cylindrical.

**Type:** Brazil, São Paulo, Caraguatatuba, Lagoa do Capricórnio [23°36'22.6"S; 45°21'22.6"W], 6 m elev., 23 Nov 2014, fl., M. R. Miranda 87 (holotype: UFP; isotypes: NY, SP).

***Etymology***

The epithet is derived from the habitat where it occurs, a swamp forest, it is the English translation for the Latin word “palūdōsus”.

***Description***

Epiphytic herbs. Roots 1.0–2.0 mm diam., cylindrical, fibrous, smooth, grey to whitish. Stem 5.0–1.5 mm long, cylindrical. Inflorescences 15.0–50.0 mm long, peduncle 8.0–10.0 mm long, minutely pubescent, ochre; rachis 7.0–40.0 mm long, minutely pubescent, ochre; floral bracts 0.5–1.0 mm × 0.4–0.8 mm wide, deltoid, membranaceous, brown, margin minutely ciliate, acute at apex. Flowers 7–27 per inflorescence, whitish-green, distichous, ovary pedicellate, 1.5–1.8 mm long, smooth; dorsal sepal 1.3–1.5 × 1.0–1.1 mm, ovate-elliptical, membranaceous, acute to obtuse at apex, 1-veined, margin entire; lateral sepals 1.4–1.6 × 0.7–0.9 mm, ovate-lanceolate, membranaceous, 1-veined, margin entire, acute at apex; petals 0.9–1.2 × 0.6–0.8 mm, obovate-elliptical, rounded to obtuse at apex, membranaceous, 1-veined, glabrous, margin entire; lip 0.9–1.1 mm long, 1.2–1.5 mm wide between the lateral lobes, entire to 3-lobed, membranaceous, 5-veined, margin entire, producing a spur at base, lateral lobes 0.5–0.6 × 0.2 mm, sub-orbicular, rounded at apex, middle lobe 0.4–0.5 × 0.4–0.5 mm, deltoid, acute at apex, with short hairs, spur 1.6–1.8 mm × 0.8–1.0 mm diam.,

wide-cylindrical, straight to slightly curved, green, rounded at apex; gynostemium 0.5–0.6 mm long, anther cap apex 2-lobed, pollinia 2, globose. Capsule not seen.

***Distribution and habitat***

*Campylocentrum paludosum* is known only from the type locality, an area of swamp forest at sea level along the northern coast of the state of São Paulo, Brazil (Fig. 3). It grows as an epiphyte in shrubs, climbers and treelets in shady areas. It is locally rare, and only a small population with about 20 specimens was found in the type locality, an area that has been intensely deforested due to urbanization.

***Phenology***

Based on the type specimen flowers appear in November.

***Similar species and notes***

Among the Brazilian leafless *Campylocentrum*, *C. paludosum* is related to Amazonian species such as *C. amazonicum* Cogn., *C. fasciola* and *C. tenue*. From *C. amazonicum* it differs by its wide-cylindrical spur with a rounded apex (vs. conical spur with an acute apex); from *C. fasciola* by its lip 5-veined (vs. 7-veined) and a spur wide-cylindrical (vs. obovoid to clavate); and from *C. tenue* by its 3-lobed lip (vs. entire), a wide-cylindrical spur longer than the sepals (vs. globose spur shorter than the sepals).

Barros et al. (2015) cited *C. grisebachii* Cogn. and *C. pubirhachis* as being from the state of São Paulo. The first species is easily distinguished by its ovate floral bracts with the apex obtuse to rounded (vs. deltoid with an apex acute), the unveined sepals (vs. 1-veined) and spur two times (or more) longer than the sepals (vs. slightly longer than the sepals). The second species is distinguished by a longer sigmoid spur ( $\geq 2.0$  mm long vs.  $\leq 1.8$  mm long) with an acute to obtuse apex (vs. rounded apex).

**Key to species of *Campylocentrum* sect. *Dendrophyloopsis* in Brazil**

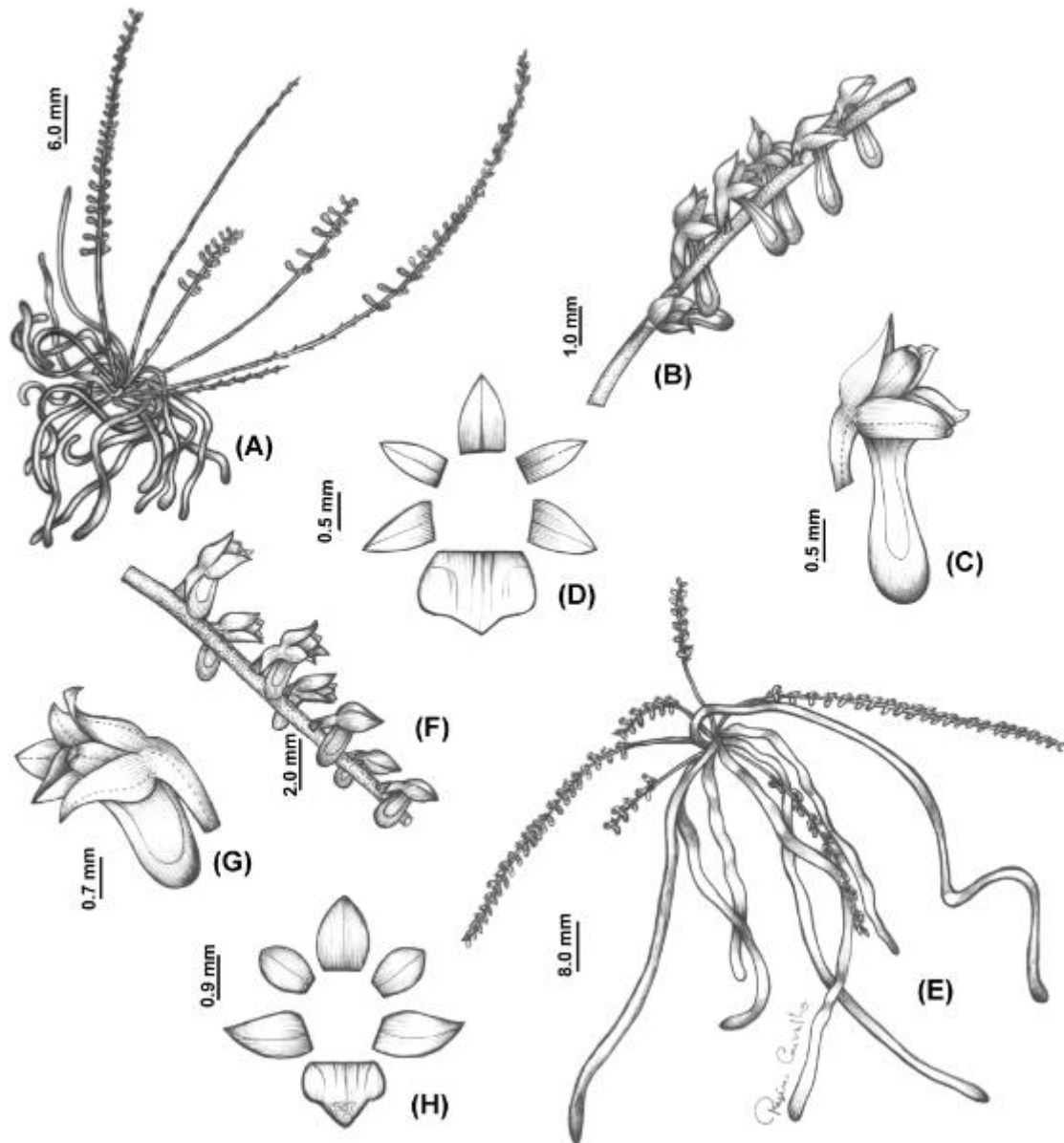
1. Roots dorso-ventrally flattened,  $\geq 3$  mm wide; floral bracts  $\geq 1.3$  mm wide, covering the base of the the inflorescence .....*C. pachyrrhizum* (Rchb.f.) Rolfe  
 – Roots cylindrical,  $\leq 2$  mm wide; floral bracts  $\leq 1.2$  mm wide, base of the inflorescence exposed.....2
2. Spur shorter than the sepals.....3  
 – Spur as long as or longer than the sepals.....4
3. Lip distinctly 3-lobed, spur conical .....*C. insulare*  
 – Lip entire, spur globose to obovoid.....*C. tenue*
4. Floral bracts ovate, the apex obtuse to rounded; sepals unveined,  $\leq 0.8$  mm long.....*C. grisebachii*  
 – Floral bracts deltoid, the apex acute; sepals 1-3-veined,  $\geq 1.2$  mm long; .....5
5. Lip longer than wide, spur sigmoid.....*C. pubirhachis*  
 – Lip wider than long, spur straight to slightly curved.....6
6. Spur conical, the apex acute .....*C. amazonicum*  
 – Spur obovoid, clavate or cylindrical, the apex rounded.....7
7. Spur patent, twice as long (or more) than the pedicellate ovary .....*C. benelli*  
 – Spur straight to slightly curved, as long as to slightly longer than the pedicellate ovary.....8
8. Lip 7-veined with a tuft of short hairs between the lateral lobes, spur obovoid to clavate.....*C. fasciola*  
 – Lip 5-veined with short hairs present on the mid-lobe, spur wide-cylindrical.....*C. paludosum*

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**Figure 1.** (A)–(D) *Campylocentrum benellii* sp. nov. (A) general aspect, (B) inflorescence, (C) flower, (D) dissected perianth. Drawn from A. Petini-Bebelli & S.C. Freitas 925. (E)–(H) *Campylocentrum paludosum* sp. nov. (E) general aspect, (F) inflorescence, (G) flower, (H) dissected perianth. Drawn from M. Rodrigues 87.





**Figure 2.** (A) *Campylocentrum benellii* sp. nov.; (B) *Campylocentrum paludosum* sp. nov.



**Figure 3.** Map of the known distribution of the new species. Circle – *Campylocentrum benellii* sp. nov.; Square – *C. paludosum* sp. nov.

**The Smallest Angraecoid Species from the Neotropics: A New *Campylocentrum* (Orchidaceae) from a Brazilian Subtropical Forest**

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**Abstract**—*Campylocentrum insulare* is a new species of *Campylocentrum* section *Dendrophyllopsis* from Santa Catarina, southern Brazil, a group of species characterised by the aphyllous condition. It is the smallest species known from this subtribe in the Neotropics, and is morphologically related to species of the *Campylocentrum fasciola* complex. It differs by its small size, an inflorescence and ovary that are minutely pubescent, a lip that is distinctly three-lobed, and a conic spur that is shorter than the sepals. A distribution map, illustrations and an identification key that includes species of this genus from southern Brazil are provided.

**Keywords**—Angraecinae, Atlantic Forest, conservation status, Santa Catarina, sect. *Dendrophyllopsis*.

*Campylocentrum* Benth. is a Neotropical genus with about 65 species that are distributed from Florida to Argentina (Govaerts et al. 2013). The Atlantic Forest of Brazil is cited as the center of diversity of the genus, and 26 species are already recorded (Barros et al. 2013). The genus has variable vegetative organs, especially the stem (reduced to elongated) and leaves (leafless to leafy, and conduplicate, cylindrical to fleshy scales) (Bogarín and Pupulin 2010).

A remarkable morphological group in the genus *Campylocentrum* is the aphyllous plants, which were included in sect. *Dendrophylopsis* by Cogniaux (1906). Species in this section are characterised by a short stem, leaves that are reduced to brown, membranaceous, and non-chlorophyllated scales, and longer inflorescences compared with the leafy species of the genus (Bogarín and Pupulin 2010).

Barros et al. (2013) recognized six species of sect. *Dendrophylopsis* in Brazil, *C. amazonicum* Cogn., *C. fasciola* (Lindl.) Cogn., *C. grisebachii* Cogn., *C. pachyrrhizum* (Rchb.f.) Rolfe, *C. pubirhachis* Schltr., and *C. tenue* (Lindl.) Rolfe. Only four are found in the Atlantic Forest (Barros et al. 2013; Pessoa and Alves 2012). Although *C. hirtellum* Cogn. has been included in sect. *Dendrophylopsis* by Cogniaux (1906), it was illustrated as a species with chlorophyllated and conduplicate leaves by Hoehne (1941).

Another Neotropical genus with leafless species is *Dendrophyllax* Rchb. f., phylogenetically it is the sister group of *Campylocentrum* (Carlswald et al. 2003). It can be distinguished by the inflorescence structure, in *Campylocentrum* it is unbranched with numerous flowers opening in rapid succession, while in *Dendrophyllax* it is sometimes branched with one or few flowers open at once (Bogarín and Pupulin 2010). Similarly to *Campylocentrum*, some species of *Dendrophyllax*, like *D. porrectus* (Rchb.f.) Carlswald & Whitten, represent extremes in flower reduction as adaptation to pollinator size (Carlswald et al. 2003, Whitten and Carlswald 2006).

The state of Santa Catarina has around 560 species of Orchidaceae, 11 of which are endemic and 24 are threatened species. *Campylocentrum* has 11 species cited for the state, and of these only *C. grisebachii* belongs to sect. *Dendrophylopsis* (C. E. Siqueira et al. unpubl. data). Today, the Atlantic Forest in the state of Santa Catarina covers about 31% of the total area, but Behling and Pillar (2007) suggested that the state was

entirely covered by dense forests in the past. Currently, the Atlantic Forest is represented by sparsely dispersed forest fragments that hardly exceed 50 ha and are mainly distributed along the coast (Ranta et al. 1998; Ribeiro et al. 2009; Vibrans et al. 2012).

*Campylocentrum insulare*, a new aphyllous species of the genus from the state of Santa Catarina, southern Brazil, is described and illustrated here. The taxonomic affinities are discussed, and an identification key for the species of this genus from southern Brazil is also provided.

#### MATERIALS AND METHODS

The description of the new species was based on the examination of a live plant. The illustration and the measurements of vegetative and floral parts were made on fresh material. The flowers were dissected under a stereomicroscope and photographed using a digital camera (Leica EZ4D with LAS 2.0).

The identification keys were produced based on the analysis of type materials and illustrations, as part of a review of the genus conducted by the second author, but also including other materials deposited at the Brazilian herbaria EAN, ESA, FLOR, HB, HBR, IAN, INPA, MG, R, RB, SP, and SPF, acronyms according to Thiers 2013. We used 103 georeferenced records of sect. *Dendrophylopsis* species deposited in the collections of the herbaria previously cited for the construction of the cartogram, using the software QGIS (available at <http://www.qgis.org>). Records without information about coordinates were based on the center of the municipality and obtained by the geoLoc tool (available at <http://smlink.cria.org.br/geoloc>).

#### TAXONOMIC TREATMENT

***Campylocentrum insulare*** C. E. Siqueira & E. Pessoa, sp. nov. —TYPE: BRAZIL. Santa Catarina: Florianópolis, Unidade de Conservação Desterro, 48° 30' 46" W, 27° 31' 53" S, 120 m elev., Dec. 2010 (st., fl. in cult.: 23 Dec. 2011), A. Zanin 1642 (holotype: FLOR).

Morphologically related to *C. tenue* but differs by its smaller size, an inflorescence, ovary and base of sepals minutely pubescent, a lip that is distinctly three-lobed, and a conic spur that is shorter than the sepals.

Epiphytic herb. Roots 0.8–1.0 mm diam, cylindrical, fibrous, smooth, whitish-green. Stem extremely reduced, ca. 0.5 mm long, cylindrical. Leaves reduced to achlorophyllated scales, brownish. Inflorescence ca. 8.5 mm long, ascendant raceme, inflorescence bract ca. 0.5 × 0.3 mm, deltoid, entire margin, the apex acute, membranaceous; peduncle ca. 2.5 mm, minutely pubescent, brownish; rachis 5–6 mm, minutely pubescent, brownish; floral bracts 0.4–0.6 × 0.3–0.4 mm, deltoid, ciliate margin, the apex acute, membranaceous. Flowers ca. 7, whitish with a brownish base, alternate, pedicellate ovary 0.5–0.6 mm long, minutely pubescent; dorsal sepal 1.4–1.5 × 0.6–0.7 mm, elliptic, the apex acuminate, 1-nerved, glabrous, entire margin, membranaceous; lateral sepals 1.3–1.4 × 0.5–0.6, oblong-elliptic, the apex acuminate, 1-nerved, glabrous, entire margin, membranaceous; petals ca. 1.25 × 0.55 mm, elliptic, the apex acute to obtuse, 1-nerved, glabrous, entire margin, membranaceous; labellum 1.9–2 × 1.35–1.4 mm, trilobed, membranaceous, 3-nerved, slightly serrate margin, producing at base a spur, lateral lobes 0.3–0.45 × 0.3–0.4 mm, deltoid, the apex obtuse, mid-lobe ca. 0.7 mm × 0.7 mm, deltoid, the apex acute, spur 0.5–0.7 mm long, 0.35–0.4 mm diam, conic, straight, the apex rounded; gynostemium ca. 0.4 mm long, pollinia 2, globose. Capsule not seen. Figures 1–2.

***Distribution and Ecology***—This species was found growing as epiphyte in remnants of the Atlantic Forest at medium to advanced succession stage in the Unidade de conservação Desterro at 100–120 m (Fig. 3). It probably occurs in adjacent areas but due to the extremely reduced size of the plants, it is difficult to find. The only collected specimen was found growing on the roots of *Pabstiella fusca* Chiron & Xim. Bols. (Orchidaceae) and cultivated at the Universidade Federal of Santa Catarina. The species has not been found in the area since then.

***Phenology***—Flowering period is poorly known, but based on the type material, it blooms in December.

***Conservation Status***—Due to the rarity and restricted distribution in the central-east in the state of Santa Catarina and the apparent vulnerability to human activities, the species can be classified as vulnerable (VU) using the criterion D2 (IUCN 2013).

***Etymology***—The new species is named on behalf of the type locality, the island of Santa Catarina.

**Morphological Affinities**—The new species belongs to *Campylocentrum* sect. *Dendrophylopsis*, and it is smaller than other species in the genus, as well as possibly of all Angraecinae. It is easily distinguished among the aphyllous species by its short conic spur that is smaller than the sepals (Tab. 1).

The most morphologically similar species are *C. amazonicum*, *C. fasciola*, *C. minutum* C. Schwinf., *C. multiflorum* Schltr, and *C. tenue* (Lindl.) Rolfe. (*C. fasciola* complex). However, it is distinguishable from them by its small size (9 mm vs. plants  $\geq$  35.0 mm long), an inflorescence, ovary and base of sepals minutely pubescent (vs. glabrous to minutely sparse puberulent), and conic spur shorter than the sepals (vs. an obovoid or linear-conic spur that is as long as, or longer than the sepals).

The pubescent inflorescence is also found in *C. pubirhachis*, which is known from the Atlantic Forest in the state of Sao Paulo (Barros et al. 2013). However, *C. insulare* has a longer and cylindrical spur ( $\geq$  1.8 mm long).

Other leafless species of the genus, *C. grisebachii* Cogn., has distribution from the southern Brazil, it can be easily distinguished from the new species by the indument of ovary and sepals (glabrous vs. minutely pubescent), the lip shape (entire to obscure 3-lobed vs. distinctly 3-lobed), and size of spur if compared with the perianth (two times longer than the perianth vs. shorter than the perianth).

#### KEY TO *CAMPYLOCENTRUM* SPECIES FROM THE SOUTHERN REGION OF BRAZIL

1. Stems extremely reduced ( $\leq$  7.0 mm long).....2
2. Leafy plants (leaves often caducous); sepals  $\geq$  2.3 mm long..... *C. hirtellum*
2. Aphyllous plants; sepals  $\leq$  1.4 mm long.....3
3. Ovary and sepals glabrous, labellum entire to obscure 3-lobed..... *C. grisebachii*
3. Ovary and base of the sepals minutely pubescent, labellum 3-lobed..... *C. insulare*
1. Stems well developed ( $>$  15.0 mm)
4. Leaves cylindrical, apex acute.....5
5. Roots slightly granulose, distichous leaves..... *C. ornithorrhynchum*
5. Roots strongly muricate, secund leaves . . . . . *C. parahybunense*
4. Leaves dorso-ventrally flattened, apex bilobed.....6
6. Inflorescences larger than the leaves..... *C. ulaei*

6. Inflorescences shorter than the leaves.....7
7. Labellum entire to obscure 3-lobed.....8
8. Labellum oblong, spur cylindrical, curved. . . . . *C. robustum*
8. Labellum ovate, spur obovoid, strongly geniculated.....9
9. Sepals  $\leq$  1.3 mm long; lip entire . . . . . *C. brachycarpum*
9. Sepals  $>$  2.0 mm long; lip obscure 3-lobed . . . . . *C. densiflorum*
7. Labellum distinctly 3-lobed.....10
10. Leaves  $\leq$  6.0 mm wide, spur obovoid. . . . . *C. pauloense*
10. Leaves  $>$  7.0 mm wide, spur cylindrical to sub-obclavate.....11
11. Flowers open successively, the ones more developed at base; fruits  $\leq$  0.7 mm long. .  
 . . . . . *C. neglectum*
11. Flowers open all together; fruits  $>$  7.0 mm long.....12
12. Leaves oblong-elliptic, the apex slightly emarginated; sepals and spur externally  
 sparsely pubescent (only available in fresh material)..... *C. spannagelii*
12. Leaves oblong, the apex strongly bilobed; sepals and spur externally  
 glabrous.....*C. crassirhizum*

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TABLE 1. Comparison of morphological features of *Campylocentrum insulare* and other species of the *Campylocentrum* sect. *Dendrophylopsis* from Brazil.

Measurements are in mm.

	Root width	Inflorescence length	Spur length	Perianth (P) x Spur (S)
<i>C. amazonicum</i>	1.0–1.5	50.0–65.0	1.4–1.8	P < S
<i>C. fasciola</i>	1.5–2.0	35.0–85.0	1.3–1.4	P ≥ S
<i>C. grisebachii</i>	1.0–1.5	13.0–55.0	0.9–1.4	P < S
<i>C. insulare</i>	0.8–1.0	13.0	0.5–0.7	P > S
<i>C. pachyrrhizum</i>	2.8–6.0	20.0–43.0	2.2–2.8	P > S
<i>C. pubirhachis</i>	1.0–1.5	20.0–50.0	1.8–2.0	P < S
<i>C. tenue</i>	1.0–1.5	25.0–70.0	0.8–1.0	P ≥ S

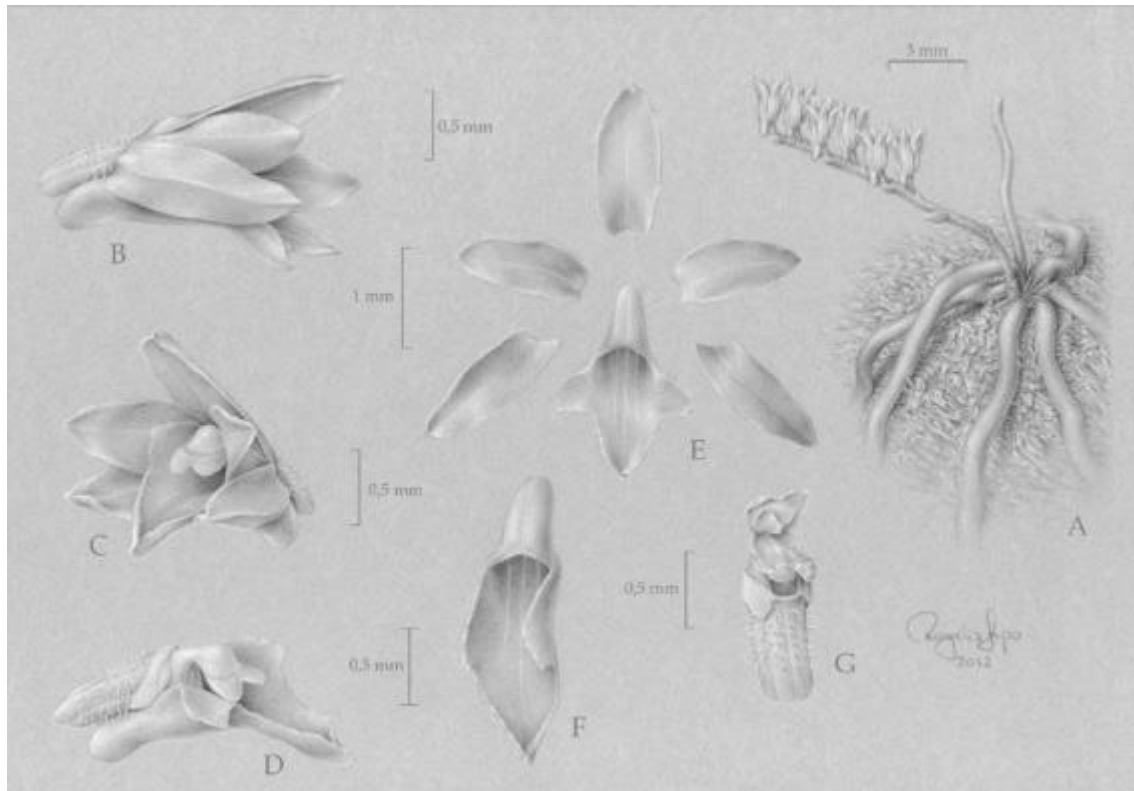


FIG. 1. *Campylocentrum insulare* C. E. Siqueira & E. Pessoa (A. Zanin 1642). A. Habit. B. Flower, lateral view. C. Flower, front view. D. Ovary, gynostemium and labellum. E. Dissected flower. F. Labellum. G. Ovary and gynostemium. Drawn by Rogério Lupo.



FIG. 2. *Campylocentrum insulare* C. E. Siqueira & E. Pessoa (A. Zanin 1642). A. Habit.

B. Flower, front view. C. Flower, lateral view. Photos by C. E. Siqueira.

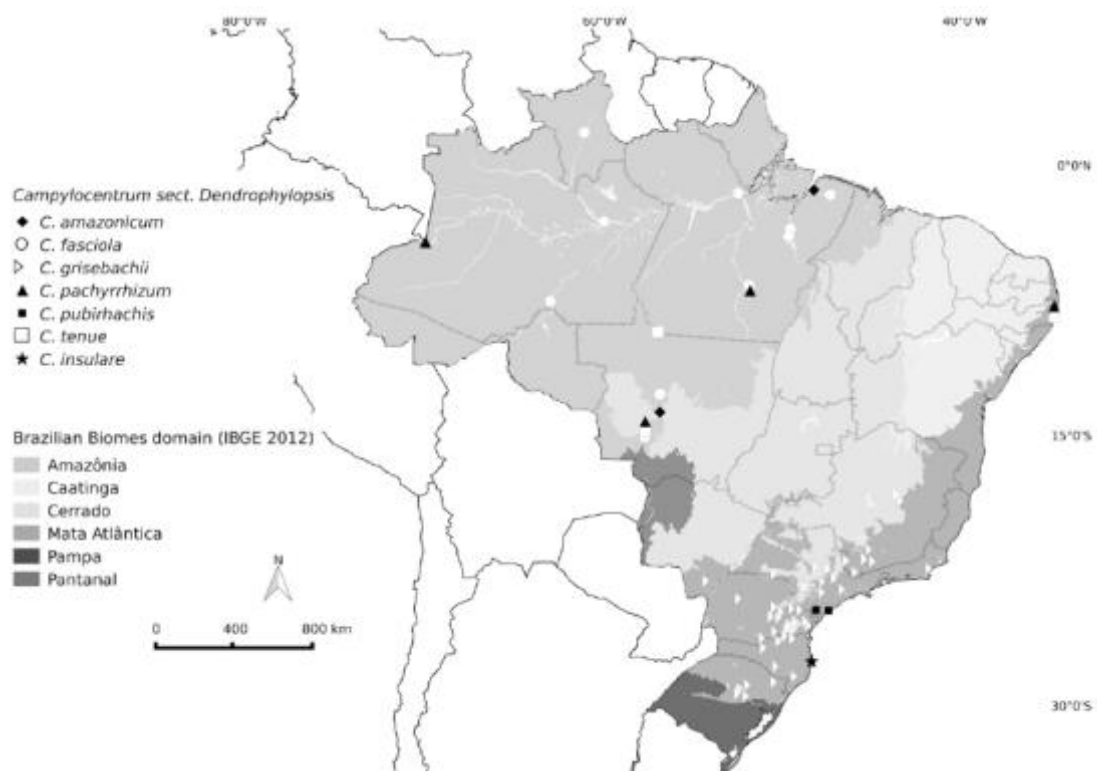


FIG. 3. Distribution map of the Brazilian species of *Campylocentrum* sect.

*Dendrophyloopsis*.

***Campylocentrum brevifolium* (Lindl.) E. Pessoa & M. Alves, a neglected and critically endangered orchid from the Atlantic Forest of Brazil.**

**Edley Pessoa<sup>1</sup>; Jefferson Rodrigues Maciel<sup>2</sup>; Marccus Alves<sup>3</sup>**

**Summary.** New morphological, ecological and geographical data support the recognition of *Campylocentrum brevifolium* as a distinct species. This study aims to provide a nomenclatural update including a new combination and typifications, discuss its morphological affinities to allied Brazilian species (*C. crassirhizum*, *C. micranthum* and *C. pauloense*), and provide the conservation status of the threatened species. It also includes descriptions, illustrations, distribution maps and an identification key.

**Key-words.** Angraeciinae, new combination, nomenclature, Orchidaceae, typification.

## Introduction

The subtribe Angraeciinae is represented in the Neotropics by two genera, *Campylocentrum* Benth., comprised by leafy and leafless plants, and *Dendrophylax* Rchb.f., with only leafless species (Carlsward *et al.* 2003).

Certain american species placed in *Angraecum* by Lindley and *Aeranthus* by Reichenbach f., were later grouped into *Campylocentrum* (Bentham 1881). Nowadays, the genus is composed of about 65 species (Govaertes *et al.* 2014), and the Atlantic Forest of Brazil has been indicated as the diversity center (Todzia 1980).

*Angraecum brevifolium* Lindl. was described by Lindley (1840) with another five species (*A. fasciola*, *A. gladiifolium*, *A. ornithorrhyncum*, *A. polystachyum*, *A. tenue*). Most of them were transferred by Rolfe (1903) and Cogniaux (1906) to *Campylocentrum*.

Rolfe (1903) considered *Angraecum brevifolium* allied to *Campylocentrum micranthum* (Lindl) Maury, but a new combination was not proposed. On the other hand, Cogniaux (1906) considered *A. brevifolium* and *C. micranthum* as conspecific, and this broad concept persists up to now (Brako & Zarucchi 1993; CONABIO 2009; D'Arcy 1987; Dodson & Dodson 1980; Hamer 1982; Jørgensen *et al.* 2010; McLeish *et al.* 1995; Stevens *et al.* 2001).

New morphological, ecological and geographical data support the recognition of specimens belonging *A. brevifolium* as a distinct species, making a new combination in *Campylocentrum* necessary. The aims of this study are the following: 1 – provide a nomenclatural update including new combination and typification, 2 – discuss morphological affinities to allied Brazilian species, and 3 – provide the conservation status. Descriptions, illustrations, distribution maps and an identification key are provided.

## Material and Methods

During preparation of a taxonomic revision of *Campylocentrum*, extensive studies in Brazilian and European herbaria were recently conducted. Specimens from 64 collections were studied: ALCB, ASE, B, BA, BAF, BHCb, BHZB, BM, BR, C, CEN, CEPEC, CESJ, COR, E, EAC, EAN, ESA, FLOR, FR, FUEL, FURB, G, GOET, HAMAB, HB, HBG, HBR, HEID, HEPH, HRCB, HUEFS, HST, IAC, IAN, IBGE, ICN, INPA, IPA, JPB, K, L, M, MAC, MBML, MG, MIRR, P, PEUFR, R, RFA, RB,

SP, SPF, U, UB, UEC, UFP, UFRN, UFRR, UPCB, VIES, W, WU (Thiers 2014, continuously updated). Names in boldface are currently accepted.

Data from the specimen labels were used to construct a geographic distribution map. Specimens with no geo-referenced data had their distributions corrected manually using online gazetteers (Google Earth). The distribution data were plotted in Diva-GIS (Hijmans *et al.* 2001). The extent of occurrence (EOO) and the area of occupancy (AOO, grid cell width = 2 km) was calculated with Geocat tools (Bachman *et al.* 2011). Species conservation status is based on the IUCN criteria (IUCN 2013).

## Taxonomic treatment

### Key for *Campylocentrum brevifolium* and allied species

1. Leaves oblong-elliptic to oblanceolate, the apex slightly bi-lobed; spur inflexed; fruits 6-ribbed.....**C. micranthum**
- 1'. Leaves oblong to linear-oblong, the apex strongly bi-lobed; spur slightly curved; fruits not ribbed
  2. Pedicellate ovary  $\geq 1.3$  mm long; sepals  $\geq 3.0$  mm; mid-lobe of lip  $\geq 1.3$  mm long.....**C. crassirhizum**
  - 2.' Pedicellate ovary  $\leq 1.2$ ; sepals  $\leq 2.1$  mm; mid-lobe of lip  $\leq 1.0$  mm long
    3. Lobes of the leaves acute to obtuse; lip 9-11 nerved; spur as long as to slightly longer than the pedicellate ovary.....**C. pauloense**
    - 3'. Lobes of the leaves rounded; lip 5 nerved; spur two times longer than the pedicellate ovary .....**C. brevifolium**

### ***Campylocentrum brevifolium*** (Lindl.) E. Pessoa & M. Alves, **comb. nov.**

*Angraecum brevifolium* Lindley, *Edwards's Bot. Reg.* 26: 68 (1840). Type: Brazil, Rio de Janeiro, [probably near Cabo Frio], Sept. 1815, *M. Wied s. n.* (holotype BR!; isotypes GOET!; W-R!).

Epiphytic herb. *Roots* 1.0–2.0 mm diam., cylindrical, fibrous, smooth, whitish to dark grey. *Stem* 10.5–38.0 cm long, cylindrical, rarely branched. *Leaves* 11.0–28.0 mm long, 4.0–7.0 mm wide, greenish, oblong, the apex asymmetrically strongly 2-lobed, lobes

rounded, margin entire, occasionally curved. *Inflorescence* 3.0–11.0 mm long, *peduncle* ca. 1.0 mm long, completely covered by bracts, glabrous, brownish; *rachis* 2.0–10.0 mm long, glabrous, brownish; *floral bracts* 0.5–0.8 mm long, 0.3–0.5 mm wide, deltoid, margin entire, the apex acute, membranaceous. *Flowers* 6–14 (per inflorescence), cream colored, distichous, *pedicellate ovary* 0.9–1.2 mm long, papillate; *dorsal sepal* 1.6–2.1 mm long, 0.7–0.8 mm wide, oblong-elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lateral sepals* 1.6–2.1 mm long, 0.7–0.8 mm wide, oblong-elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *petals* 1.3–1.5 mm long, 0.6–0.8 mm wide, wide elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lip* 1.3–1.5 mm long, 1.2–1.4 mm wide between the lateral lobes, obscurely 3-lobed, membranaceous, 5-nerved, margin entire, producing a spur at base, lateral lobes 0.8–0.9 mm long, 0.35–0.4 mm wide, sub-orbicular, the apex rounded, mid-lobe 0.5–0.6 mm long, 0.5–0.6 mm wide, deltoid, the apex obtuse, *spur* 1.8–2.3 mm long, 0.4–0.6 mm diam., cylindrical, slightly curved, the apex rounded, pale orangish; gynostemium 0.5–0.6 mm long, anther cap apex truncate, pollinia 2, globose. *Capsule* 6.0–10.0 mm long, 1.3–1.8 mm wide, fusiform, straight to curved, not ribbed, pedicellate, pedicel 0.5–1.0 mm long. Fig. 1.

**DISTRIBUTION.** Brazil, state of Rio de Janeiro (southeastern Brazil). (Map 1).

**SPECIMENS EXAMINED. BRAZIL.** *Sine loco accurately.* s.d., *Martius* s.n. [M, K (Illustration of the specimen), W-R (Illustration of the specimen)]. Rio de Janeiro: Armação de Búzios, Serra das Emeranças, 21 Aug. 1998, *C. Farney et al.* 3817 (RB); Arraial do Cabo, Morro do Atalaia, 2 Feb. 1950, *G. Pabst* 493 (HB, M); Cabo Frio, Restinga de Cabo Frio, 15 Aug 1966, *D. Sucre* 986 (HB, RB); Morro da Gamboa, 11 Aug 1967, *D. Sucre* 1539 (RB, UFP); Morro da Piaçava, 31 Aug 2004, *C. Farney & J.C. Silva* 4536 (RB); Ilha do Cabo Frio, 11 May 1887, *H. Schenck* 3971 (BR).

**HABITAT.** *Campylocentrum brevifolium* grows in “restinga” vegetation (coastal lowland forest and savanna physiognomies often on sandy soils).

**CONSERVATION STATUS.** Based on criterion B1a, this species is considered Critically Endangered (CR).

**PHENOLOGY.** Flowers can be observed in August and September, fruits from February to May.



**NOMENCLATURAL NOTES.** Lindley (1840) describes *A. brevifolium* based on a specimen from Rio de Janeiro, Brazil (without precise location) collected by the Prince Maximilian of Wied-Newied. According to Urban (1906), M. Wied collected along the coast of the state of Rio de Janeiro (Praia Grande, Cabo Frio, Macaé and São João da Barra) between July and October 1815. Recent collections of *C. brevifolium* from Cabo Frio and Armação de Buzios suggest this area as the possible type locality (according to the label of the type specimen, it was collected in September 1815). It is corroborated by other samples collected by him in the same month in Cabo Frio, such as *Oxalis fruticosa* Raddi, Wied s.n., Sep 1815 (Moraes 2013). Three collections of *C. brevifolium* made by M. Wied from the same date and location were found at BR, GOET, and W-R herbaria. The protolog of *A. brevifolium* (Lindley 1840) cites “*Herbarium Regium Monacense*” (herbarium M), but H. Esser (pers. com.) confirmed that the sample was never placed at M, and it probably belongs to the “*Herbarium Martii*”. This collection was acquired by the Belgian government in 1870, and today is part of the BR herbarium (Forther 1994).

**TAXONOMIC NOTES.** Rolfe (1903) is the first author to discuss *A. brevifolium* and he stresses that it is very closely allied to *C. micranthum*. However, placement at that time within *Campylocentrum* was not possible due to the lack of flowers on the studied specimens. Later, Cogniaux (1906) included it in a broad concept of *C. micranthum*.

Here, after analyzing a large set of specimens, *C. brevifolium* is recognized as a distinct species which is morphologically distinct from *C. micranthum*.

*C. brevifolium* and *C. micranthum* belong to *Campylocentrum* sect. *Campylocentrum* (= *Eucampylocentrum* sensu Cogniaux, 1906) which includes plants with developed stems and leaves (conduplicate or cylindrical) and is represented in Brazil by 25 species (Barros *et al.* 2014).

Morphologically, *C. brevifolium* is similar to *C. crassirhizum* Hoehne and *C. pauloense* Hoehne & Schltr. (comments under the cited species). They differ from *C. micranthum* by the shape of the leaves (oblong to linear-oblong vs. oblong-elliptic to oblanceolate), the leaf apex (strongly bi-lobed vs. slightly bi-lobed), spur curvature (slightly curved vs. inflexed), and fruits (not ribbed vs. 6-ribbed). The perianth morphology in *C. brevifolium* is considerably different from *C. micranthum* (comments under the cited species) (Figs. 1, 2).

**Campylocentrum crassirhizum** *Hoehne* (1939: 44). Type: Brazil, Espírito Santo, Santa Teresa, April/1939 (*fl. in cult.*), *A. Ruschi* 05 (holotype SP!).

*C. iglesiasii* Brade (Brade 1941: 2). **synon. nov.** Type: Brasil, São Paulo, São José de Barreiras, Feb. 1940, *A. Iglesias* s. n. (holotype RB!).

Epiphytic herb. *Roots* 1.5–4.0 mm diam., cylindrical, fibrous, smooth, whitish to grey. *Stem* 3.0–55.0 cm long, cylindrical, rarely branched. *Leaves* 15.0–85.0 mm long, 5.0–16.0 mm wide, greenish, oblong, the apex asymmetrically 2-lobed, lobes rounded, margin entire. *Inflorescence* 6.0–25.0 mm long, *peduncle* 1.0–3.0 mm long, completely covered by bracts, glabrous, brownish; *rachis* 5.0–22.0 mm long, glabrous, brownish; *floral bracts* 0.8–1.0 mm long, 0.4–0.6 mm wide, deltoid, minutely denticulate margin, the apex acute, membranaceous. *Flowers* 7–21 (per inflorescence), cream-colored to orangish, distichous, *pedicellate ovary* 1.3–2.0 mm long, slightly papillate; *dorsal sepal* 3.0–5.0 mm long, 0.8–1.5 mm wide, oblong, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lateral sepals* 3.0–5.2 mm long, 0.8–1.5 mm wide, oblong-falcate, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *petals* 2.5–4.2 mm long, 0.8–1.5 mm wide, oblong-elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lip* 2.5–4.8 mm long, 1.5–3.2 mm wide between the lateral lobes, 3-lobed, membranaceous, 11-nerved, margin entire, producing at base a spur, lateral lobes 1.2–2.6 mm long, 0.5–1.1 mm wide, orbicular, the apex rounded, mid-lobe 1.3–2.2 mm long, 0.5–0.9 mm wide, narrowly lanceolate, the apex acute, *spur* 2.0–4.0 mm long, 0.6–1.3 mm diam., cylindrical, slightly curved, the apex rounded, orangish; gynostemium 0.6–1.0 mm long, anther cap apex slightly emarginate, pollinia 2, globose. *Capsule* 6.0–15.0 mm long, 1.5–2.1 mm wide, fusiform, occasionally curved, not ribbed, pedicellate, pedicel 0.5–1.0 mm long. Fig. 1

**DISTRIBUTION.** Brazilian coast, from the state of Rio Grande do Norte to Santa Catarina. (Map 2).

**SPECIMENS EXAMINED. BRAZIL:** *sine loco acurato*: Feb. 1937, *Gardner* 668 (K). Alagoas: Murici, 1 April 2013, *E. Pessoa et al.* 1082 (UFP). Bahia: Amargosa, Serra do Timbó, 29 April 2007, *J.L. Paixão et al.* 1174 (HUEFS); Jequié, Serra do Brejo Novo, 22 Aug. 2011, *E. Pessoa et al.* 618 (UFP); Lençóis, Serra Larga, 19 Dec. 1984, *G. Lewis et al.* s.n. (SPF); Maracás, Fazenda Lagoa de Dentro, 5 Dec. 2011, *M.N. Oliveira* 329 (UFP); Morro do Chapéu, estrada para Bonito, 23 July 2008, *C. Bastos &*

*J. Pinto* 244 (HUEFS); Paulo Afonso, Reserva Ecológica Raso da Catarina, 23 June 1982, *L.P. Queiroz* 327 (ALCB). Ceará: Guaramiranga, Pico Alto, 22 April 2013, *E. Pessoa et al.* 1111 (UFP); Maranguape, Serra de Maranguape, 4 May 1991, *L. P. Felix* 3386 (EAN); Pacotí, 31 Aug. 1986, *L. Lima-Verde* s.n. (EAC); Baturité, Sítio São João, 14 Dec. 1939, *J. Eugênio* 455 (RB). Espírito Santo: Fundão, 9 March 2003, *A. P. Fontana & F. C. Sarmiento* 519 (MBML); Linhares, 15 April 2011, *J. Meirelles* 527 (ESA); Santa Maria de Jetibá, 13 March 2003, *L. Kollmann & M. V. Berger* 6036 (MBML); Santa Teresa, Mata do Melo Leitão, 28 July 2013, *E. Pessoa et al.* 1192 (UFP); Vargem Alta, 9 Dec. 1956, *E. Pereira* s.n. (RB). Minas Gerais: Barroso, Mata do Baú, 24 May 2003, *L. Menini-Neto et al.* 10 (CESJ); Carmópolis, Estação Ecológica Mata do Cedro, 25 Nov. 2004, *L. Echtermacht & T. Dornas* 651 (BHCB); Catas Altas, Serra do Caraça, 5 Jan 2005, *R. Mota* 2382 (BHCB); Coronel Pacheco, Fazenda da Campanhia, 27 June 1944, *E. P. Heringer* s.n. (SP); Cristais, Sítio Estreito, 20 July 2013, *E. Pessoa et al.* 1187 (UFP); Mariana, Oct. 1840, *Gardner* 5202 (BM, K); Lagoa Santa, s.d., *Warming* s.n. (C); Barbacena, Nov. 1843, *M. Weddel* 1193 (P). Mato Grosso do Sul: Bonito, Parque Nacional da Serra da Bodoquena, 5 Dec. 2010, *A. Quinet* 2286 (RB). Paraíba: Areia, Fazenda Junco, 6 March 1989, *L. Felix & G. Dornelas* 1926 (EAN); Paraná: Guaratuba, Rio da Praia, 2 May 1976, *M. Leinig* 584 (HB); Paranaguá, Tabuleiro do Guaraní, 31 Jan. 1966, *G. Hatschbach* s.n. (HB); Praia Leste, 21 April 1975, *M. Leinig* 561 (HB). Pernambuco: Agrestina, Pedra Cabeça de Velho, 28 March 2008, *P. Gomes* 765 (UFP); Belo Jardim, Pedra do Caboclo, 11 Jan. 2012, *E. Pessoa et al.* 904 (UFP); Igarassu, Usina São José, 1 March 2010, *E. Pessoa et al.* 257 (UFP); Jaqueira, Usina Colônia, 31 Jan. 2013, *E. Pessoa et al.* 1063 (UFP); Sanharó, Jenipapo, 7 May 1966, *A. Giuliatti* 4543 (HUEFS). Rio de Janeiro: Búzios, Fazenda José Gonçalves, 7 Aug. 1997, *P. R. Farág & A. Lobão* 425 (RB); Guanabara, Morro do Rangel, 31 May 1973, *D. Sucre* s.n. (RB); Itatiaia, Rio Campo Belo, Feb 1955, *A. Brade* s.n. (HB); Niterói, Itaciatiara, 26 May 1998, *F. Pinheiro* 159 (HB); Vassouras, Ponte Funda, 14 Sept. 2013, *E. Pessoa & S. Wangler* 1194 (UFP). Rio Grande do Norte: Tibau do Sul, Trilha L do Polígono do Parque, 2 Aug. 2012, *J. G. Jardim* 6352 (UFRN). Santa Catarina: Balneário Camboriú, Parque Interpraias, 5 May 2010, *A. Stival-Santos et al.* 2728 (FURB); Florianópolis, Campeche, 2 Oct. 2013, *E. Pessoa & C. E. Siqueira* 1198 (UFP); Navegantes, Costa Azul, 24 Feb. 2011, *A. Korte* 5999 (FURB); Pomerode, Ouro Preto Mineração, 4 Oct. 2011, *T. Cadornin* 3276 (FURB). São Paulo: Araras,

Fazenda Nova Santa Cruz, 28 Sept. 2006, *C. Moraes* 11 (HRCB); Bananal, Serra da Bocaína, 14 April 2007, *C. N. Fraga & M. C. Nadruz* 1689 (RB); Bertioga, Itaquaré, 30 Oct. 2001, *S. E. Martins* 752 (SP); Cananéia, Parque Estadual da Ilha do Cardoso, 18 March 2003, *T. Brier* 926 (UEC); Eldorado, Parque Estadual de Jacupiranga, 23 March 2005, *A. Oriani et al.* 526 (UEC); Sete Barras, Parque Estadual Carlos Botelho, 22 April 2002, *R. Farias et al.* 678 (ESA). Sergipe: Areia Branca, Parque Nacional Serra de Itabaiana, 1 Aug. 2007, *J. E. Nascimento* 145 (ASE); Capela, Refúgio da Vida Silvestre Mata do Junco, 18 Oct. 2012, *M. C. Pessoa et al.* 776 (UFP); Lagarto, Povoado Rio das Vacas, 12 March 2010, *L. A. Santos* 99 (ASE), Simão Dias, Fazenda Mercador, 11 March 2011, *T. Carregosa* 184 (ASE).

**HABITAT.** *Campylocentrum crassirhizum* is common in Atlantic Forest, Caatinga and Cerrado biomes, and grows in lowland to highland forest or savannas, up to 900 m alt.

**CONSERVATION STATUS.** This species falls under the Least Concern (LC) category.

**PHENOLOGY.** Flowers can be observed from December to June, fruits during the whole year.

**NOMENCLAURAL NOTES.** *Campylocentrum crassirhizum* was described based on a specimen that flowered in cultivation in the São Paulo Botanical Garden originally from Santa Teresa, Espírito Santo.

**TAXONOMIC NOTES.** Warming (1884) cited and illustrated a specimen based on the samples *Warming s.n.* (C spirit no. 8309!, no. 8313!) from Lagoa Santa, Minas Gerais, as *Aeranthus lansbergii* Rchb.f., although it is clearly *C. crassirhizum*. In the same way, several other specimens cited by Cogniaux (1906) as *C. micranthum* - *Gardner* 5202, K! no. 79741, BM! no. 539086; *Gardner* 668, K! no. 886225; *Weddel* 1193, P! no. 361615- were misidentified.

Specimens of *C. crassirhizum* have been wrongly identified as *C. micranthum*, *C. neglectum* (Rchb.f. & Warm.) Cogn., or *C. linearifolium* Schltr. ex Mansf., leading some authors to recognize a small distribution for the species (Pabst & Dungs 1977), but currently we know that it is widely distributed along the Brazilian coast (Barros *et al.* 2014) (Map 2).

It is morphologically similar to two Jamaican species, *C. barrettiae* Fawc. & Rendle and *C. jamaicense* (Rchb.f. ex Wullschl.) Benth. ex Fawc. The vegetative

portions of these species are indistinguishable, but the lip shape and size of spur (larger in *C. crassirhizum*) are useful to recognize them.

*Campylocentrum crassirhizum* is widely variable in size and small specimens are common and can be confused with *C. brevifolium*. It can be easily distinguished by the longer sepals ( $\geq 3.0$  mm, vs.  $\leq 2.1$  mm long), and middle lobe of lip more than five to six times longer than the lateral lobes (vs. slightly longer). Sympatric populations are found in Cabo Frio and Buzios, state of Rio de Janeiro.

Brade (1941), based on a specimen of *C. crassirhizum* with small leaves, described the name *C. iglesiasii* which is here synonymized.

***Campylocentrum micranthum* (Lindl.) Maury (1889: 273).**

*Angraecum micranthum* Lindley (1835: t. 1772). *Aeranthes micranthus* (Lindl.) Rchb. f. (Reichenbach fil. 1864: 901). *Epidorchis micrantha* (Lindl.) Kuntze (Kuntze 1891: 660). *Mystacidium micranthum* (Lindl.) T. Durand & Schinz (T. Durand & Schinz 1895: 54). *Campylocentrum micranthum* (Lindl.) Rolfe (Rolfe 1903: 245).  
Type: Surinam, *G. Loddiges* s.n. (holotype K–L!).

Epiphytic herb. *Roots* 1.0–2.0 mm diam., cylindrical, fibrous, smooth, whitish to dark grey. *Stem* 8.0–47.0 cm long, cylindrical, rarely branched. *Leaves* 26.0–90.0 mm long, 9.0–22.0 mm wide, greenish, oblong-elliptic to oblanceolate, the apex asymmetrically slightly 2-lobed, lobes obtuse, margin entire. *Inflorescence* 10.0–30.0 mm long, *peduncle* 1.0–3.0 mm long, completely covered by bracts, glabrous, brownish; *rachis* 8.0–27.0 mm long, glabrous, brownish; *floral bracts* 0.9–1.3 mm long, 0.5–0.8 mm wide, deltoid, minutely denticulate margin, the apex acute, membranaceous. *Flowers* 8–21 (for inflorescence), white greenish, distichous, *pedicellate ovary* 2.0–3.0 mm long, slightly papillate; *dorsal sepal* 3.8–5.0 mm long, 1.0–1.5 mm wide, oblong, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lateral sepals* 4.0–5.5 mm long, 0.8–1.1 mm wide, oblong-falcate, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *petals* 3.0–5.0 mm long, 0.7–1.0 mm wide, oblong-elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lip* 3.5–5.0 mm long, 1.8–2.0 mm wide between the lateral lobes, 3-lobed, membranaceous, 9-nerved, margin entire, producing at base a spur, lateral lobes 1.3–1.9 mm long, 0.55–0.65 mm wide, deltoid, the apex acute to obtuse, mid-lobe 2.3–3.1 mm long, 0.5–0.9 mm wide,

narrowly lanceolate, the apex acute, pilose along the midrib, *spur* 2.5–3.5 mm long, 1.0–1.5 mm diam., cylindrical-clavate, inflexed, the apex rounded, greenish; gynostemium 0.8–1.0 mm long,, anther cap apex rounded, pollinia 2, globose. *Capsule* 7.0–11.0 mm long, 2.0–2.5 mm wide, fusiform, 6-ribbed, pedicellate, pedicel 0.8–1.0 mm long. Fig. 2.

**DISTRIBUTION.** South America (Amazon and northern Atlantic Forest), and Lesser Antilles. (Map 3).

**SPECIMENS EXAMINED. BRAZIL.** Alagoas: Ibateguara, Coimbra. 15 June 2002, *M. Oliveira* 975 (UFP); Murici, Serra do Ouro. 18. Feb. 2004, *A. Pinheiro* 245 (MAC). Amapá: Amapá, Rebio Lago Piratuba. 4 June 2006, *A. Rocha et al.* 529 (HAMAB); Calçoene, Rio Cassiporé. 18 Sept. 2005, *S. Costa-Neto* 2158 (HAMAB, MG); Oiapoque, Clevelândia. 23 April 1960, *W. Egler* 1402 (MG). Amazonas: Manaus, Reserva Ducke. 13 April 1998, *J. Ribeiro* 1972 (INPA); Presidente Figueiredo, Rebio Uatumã. 6 July 2007, *Carvalho-Sobrinho & Mesquita* 1534 (INPA). Bahia: Canavieiras. 15 Nov. 2002, *J. G. Jardim et al.* 4067 (UFP); Ipiaú, estrada a Ibirataia. 30 Oct. 1970, *T. Santos* 1242 (CEPEC); Santa Cruz de Cabrália, Rebio Pau Brasil. 1 Oct. 1971, *A. Eupunino* 12 (CEPEC); Serra de Sincorá. s.d., *Martius* s.n.(M). Ceará: Maranguape, Trilha da Rajada. 23 April 2013, *E. Pessoa et al.* 1120 (RB, UFP); Pedra do Derretido. 25 May 2005, *L. Lima-Verde et al* 2491 (EAC). Pará: Belém, Reserva do Guamá. Nov. 1980, *P. Braga* 3600 (INPA); Castanhal. 2 June 1995, *M. Silva* 17 (MG); Barcarena, Rio Tauá. 26 Aug. 1985, *A. Lins et al.* 310 (MG); Marabá, Serra Norte. 24 May 1982, *R. Secco et al.* 319 (MG). Pernambuco: Olinda. 30 May 1925, *B. Pickel* 970 (SP); Igarassu, Usina São José. 21 Jan. 2014, *E. Pessoa et al.* 1217 (RB, UFP); Jaqueira, RPPN Frei Caneca. 30 May 2012, *E. Pessoa et al.* 952 (RB, UFP). Roraima: Alto Alegre, Serra dos Surucucus. 14 Oct 1991, *J. Silva* 256 (MG); Caracarái, Rio Anauá. 25 Aug 2012, *E. Pessoa et al.* 1001 (INPA, RB, UFP). **FRENCH GUYANA.** Cayenne, s.d., *Poiteau* s.n. (W); Montagnes Plomb, 7 Dec. 1993, *B. Bordenave* 624 (CAY, P); Nouragues, Basin de L'Arataye. 16 March 1989, *C. Sarthou* 498 (CAY, P); *ibid.*, 23 April 1992, *D. Larpin* 1045 (CAY, P); Pays Indien. 18. Nov. 1976, *Y. Veyret* s.n. (HB); Saint-Elie. May 1989, *D. Larpin* 330 (CAY, P); Oyapock River. March 1976, *M. Fily* 05 (P). **GUADALOUPE.** Vernou, 10 June 1936, *H. Stehlé* 963 (P). **GUYANA.** *Sine loco acurato*, 1898, *E. F. Thurnefort* s.n. (K); *Sine loco acurato*, 1898, *E. F. Thurnefort*

92 (K); *Sine loco acurato*, July 1824, *Poiteau* s.n. (K); Aruka River, 8 March 1945, *s.col* (K); Mabaruma, 9 Nov. 1990, *M. Polak et al.* 178 (U). **MARTINIQUE.** Grand-Rivière, 10 June 1982, *C. Sastre* 7544 (P). **SURINAM.** *Sine loco acurato*, s.d., *W. E. Vriese* s.n. (K, P); *Sine loco acurato*, s.d., *G. Loddiges* s.n. (K); *Sine loco acurato*, 1846, *Hostmann* s.n. (P, W); Beekhuizen, Paramanibo, s.d., *Wullschlagel* 532 (BR, W); Anansitabbetje, Gran Holo Soela, 2 Aug. 1973, *M. Teunissen* 1138 (U); La Recontre. May 1830, *Spittgerber* 955 (W); Nassau, Marowijne, 29 March 1949, *J. Lanjouw & J. Lindeman* 2968 (U); Surinam River, 12 Dec. 1971, *M. Teunissen & P. Teunissen* 1139 (U). **TOBAGO.** Adelphi, 13 May 1913, *W. E. Broadway* s.n. (BM); Widow Forest, 20 Feb. 1912, *W. E. Broadway* 3915 (K). **TRINIDAD.** *Sine loco acurato*, 1985, *Bradford* s.n. (BM); *Sine loco acurato*, 4 Feb. 1927, *W.E. Broadway* 7382 (BM); Valencia. 13 March 1925, *W.E. Broadway* s.n. (K). **VENEZUELA.** Cerro Copey, Isla Margarita, 18 April 1983, *A. Sudgen* 1163 (K); Delta do Amacuro, Antonio Díaz, 19 Oct. 1977, *J. A. Steyermark et al.* s.n. (HB); Monagas, Naturin, 20 Oct. 1965, *F. Breteler* 4668 (U).

**HABITAT.** *Campylocentrum micranthum* is found in dense, shady, and humid lowland forests.

**CONSERVATION STATUS.** This species is classified as of Least Concern (LC).

**PHENOLOGY.** Flowers can be observed from March to June, fruits during the whole year.

**NOMENCLATURAL NOTES.** *Campylocentrum micranthum* is the first species described which belongs to the genus *Campylocentrum*. However, the species was originally placed under *Angraecum* by Lindley (1840), although it is not the type-species of the genus. The type specimen of this name was erroneously associated by Lindley with a collection by Loddiges from Sierra Leone (Africa). According to Rolfe (1903), Lindley mounted the original drawing together with Surinam specimens, and corrected the record on the herbarium sheet. Although the name *C. micranthum* (Lindl.) Rolfe (1903) has been widely used, it must be disregarded because a new combination had previously been proposed by Maury (1889) as *C. micranthum* (Lindl.) Maury (Borarin & Pupulin 2010).

**TAXONOMIC NOTES.** Several taxa have been included in a broad concept of *C. micranthum*, such as *C. barrettiae* Fawc. & Rendle and *C. jamaicense* (Rchb.f. ex Wullschl.) Benth. ex Fawc. from Jamaica, *C. brevifolium* (Lindl.) E. Pessoa & M. Alves and *C. mattogrossense* Hoehne from Brazil, *C. colombianum* Schltr. from Colombia, *C.*

*ecuadorensis* Schltr. from Ecuador, *C. kuntzei* Cogn. ex Kuntze from Bolivia, *C. lansbergii* from Venezuela, *C. panamense* Ames and *C. peniculus* Schltr. from Panama, and *C. stenanthum* Schtr. from Guatemala. These names can easily be placed under the *C. micranthum* complex, which requires an indepth taxonomic review based on molecular tools.

Although some authors follow the broad concept explained above of *C. micranthum* (Brako & Zarucchi 1993; CONABIO 2009; D'Arcy 1987; Dodson & Dodson 1980; Hamer 1982; Ibisch 1996; Jørgensen *et al.* 2010; McLeish *et al.* 1995; Stevens *et al.* 2001; Zuloaga 2008), here we accept that *C. micranthum* is restricted to South America and the Lesser Antilles (Map 3). In Venezuela, Trinidad & Tobago, Martinique and Guadeloupe Islands more than one species of the *C. micranthum* complex occur.

*Campylocentrum micranthum* can be distinguished from *C. brevifolium* by the size of the sepals ( $\geq 3.5$  mm long vs.  $\leq 2.1$  mm long), and middle lobe of the lip several times longer than the lateral lobes (vs. slightly longer). Both species can be distinguished from *C. crassirhizum* by the form of the lateral lobes of the lip (deltoid vs. orbicular), spur curvature (inflexed vs. slightly curved), color of the spur (greenish vs. orangish). They can also be distinguished from *C. pauloense* by the size of the sepals ( $\geq 3.5$  mm long vs.  $\leq 2.2$  mm long), and form of the spur (cylindrical-clavate vs. clavate).

***Campylocentrum pauloense* Hoehne & Schlechter** (1926: 297). Type: Brazil, São Paulo, São Paulo, Butantan, March 1921, A. Gehrt s. n. (holotype SP!; isotypes SPF!, B†).

*C. linearifolium* Schltr. ex Mansf., (Mansfeld 1928: 264). **synon. nov.** Type: Brazil, São Paulo, São Paulo, Vila Emma, Dec. 1921, Brade, A.C. 8126 (Holotype B†); Brazil, São Paulo, São Paulo, Vila Emma, April 1940, A. C. Brade 16.255 (neotype RB! **here designated**; isoneotypes SPF!, UFP!).

*C. minutum* Dutra, **nom. ms.**

Epiphytic herb. *Roots* 1.0–2.0 mm diam., cylindrical, fibrous, smooth, whitish to dark grey. *Stem* 2.0–21.0 cm long, cylindrical, occasionally branched. *Leaves* 15.0–33.0 mm long, 3.0–6.0 mm wide, greenish, oblong to linear-oblong, the apex asymmetrically 2-lobed, lobes acute to obtuse, margin entire, frequently curved. *Inflorescence* 4.0–12.0



mm long, *peduncle* 2.0–4.0 mm long, glabrous, brownish; *rachis* 2.0–8.0 mm long, glabrous, brownish; *floral bracts* 0.8–1.0 mm long, 0.3–0.7 mm wide, deltoid, margin entire to minutely denticulate, the apex acute, membranaceous. *Flowers* 3–10 (for inflorescence), white greenish, distichous, *pedicellate ovary* 0.7–1.2 mm long, papillate; *dorsal sepal* 1.5–2.1 mm long, 0.3–0.4 mm wide, oblong-elliptic, the apex acute, 3-nerved, adaxially sparsely papillate, margin entire, membranaceous; *lateral sepals* 1.5–2.2 mm long, 0.3–0.4 mm wide, oblong, the apex acute, 3-nerved, adaxially sparsely papillate, margin entire, membranaceous; *petals* 1.4–1.7 mm long, 0.3–0.4 mm wide, oblong-elliptic, the apex acute, 3-nerved, glabrous, margin entire, membranaceous; *lip* 1.5–2.0 mm long, 1.3–1.7 mm wide between the lateral lobes, 3-lobed, membranaceous, 9–11-nerved, margin entire, producing at base a spur, lateral lobes 1.0–1.1 mm long, 0.5–0.65 mm wide, sub-orbicular, the apex rounded, mid-lobe 0.5–1.0 mm long, 0.3–0.4 mm wide, deltoid to ovate, the apex acute, *spur* 1.1–1.5 mm long, 0.5–0.8 mm diam., clavate, slightly curved, the apex rounded, greenish; gynostemium 0.1–0.2 mm long, anther cap apex rounded, pollinia 2, globose. *Capsule* 7.0–10.0 mm long, 1.3–2.0 mm wide, fusiform, straight to curved, not ribbed, pedicellate, pedicel 0.5–1.0 mm long. Fig. 2.

**DISTRIBUTION.** This species is endemic from southeastern and southern Brazil. (Map 4).

**SPECIMENS EXAMINED. BRAZIL.** Espírito Santo: Pedra Azul, 12 Feb. 1970, *R. Keutzky* 234 (HB); Santa Maria de Jetibá, Rio Nove, 24 Feb. 2000, *V. Demunner et al.* 806 (MBML); Santa Teresa, Sítio Canaã, 27. Feb. 2003, *U. Zottich* 4 (MBML). Minas Gerais: Lima Duarte, P.E. de Ibitipoca, 18 Oct. 2003, *L. Menini-Neto et al.* 28 (CESJ); São Francisco de Paula, 14 Dec. 1994, *E. Tameirão* 961 (BHCB). Rio de Janeiro: Teresópolis, Morro da estação, 7 Jan. 1959, *A. Abendroth* P-135 (HB). Rio Grande do Sul: Emboaba, Osório, 25 Nov 1983, *J. Waechter* 1993 (ICN); Torres, Caqueira, Feb 1927, *Dutra* 987 (ICN); Santa Catarina: Alfredo Wagner, Alto Limeirinha, 25 Nov 2009, *A. Korte & A. Kniess* 992 (FURB); Brusque, Azambuja, 23 Sept. 1981, *R. Reitz* 4163 (HB); Florianópolis, Campeche, 2 Oct. 2013, *E. Pessoa & C. E. Siqueira* 1197 (RB, UFP); Taió, Fazenda Tarumã, 24 Feb. 2010, *J. Schmitt et al.* 1532 (FURB). São Paulo: Assis, ESEC Assis, 7 Jan. 2003, *T. Breier & A. Bahrami* 811 (UEC); São

Lourenço da Serra, RPPN Paiol Maria, 26 April 2011, *J. Lombardi et al.* 8515 (HRCB); São Paulo, Villa Emma, March 1937, *A. Brade* 15727 (RB).

**HABITAT.** *Campylocentrum pauloense* grows in “restinga” vegetation (coastal lowland forest and savanna physiognomies often on sandy soils) and ombrophilous forest (Atlantic Forest), occasionally in highlands, up to 700m alt.

**CONSERVATION STATUS.** Due to its very reduced (B2) and very impacted (B2a) area of occupancy, this species is classified as Vulnerable.

**PHENOLOGY.** Flowers can be observed from July to March, fruits from April to October

**NOMENCLATURAL NOTES.** Schlechter & Hoehne (1926) cited material collected by Gehrt in the city of São Paulo as the type of *C. pauloense* without a herbarium citation, though they did cite the catalog number (n° 5506) which refers to a specimen of the SP herbarium. The authors in this study found another specimen in SPF, and according to the data of the SP herbarium another specimen would have been available at B, but it was destroyed. *C. linearifolium* was described by Mansfeld (1928) based on a specimen collected in São Paulo by Brade and sent to Schlechter who died before having published it. The type collection deposited at B herbarium was *destroyed, a neotype from the same locality and collector is here proposed.*

**TAXONOMIC NOTES.** Mansfeld (1928) distinguishes *C. linearifolium* from *C. pauloense* by its wider and more elliptic leaves, more vigorous inflorescences, and an ovate mid-lobe of the lip. After observation of several specimens, in collections and in the field, we are able to say that this species has large inter- and intrapopulational variations in leaf shape and curvature (the type specimen of *C. pauloense* has curved leaves). Some slight variation was also found in the shape of the lip mid-lobe (deltoid to ovate).

Among the species treated here, *C. pauloense* is the most similar to *C. brevifolium*, due to the small size of the plant and flowers. Although both species can be found in “restinga” vegetation, *C. pauloense* may be distinguished by the apex of the lobes of the leaves (acute to obtuse vs. rounded), number of nerves in the lip (9–11 nerved vs. 5 nerved), spur size if compared with the pedicellate ovary (as long as to slightly longer vs. two times longer).

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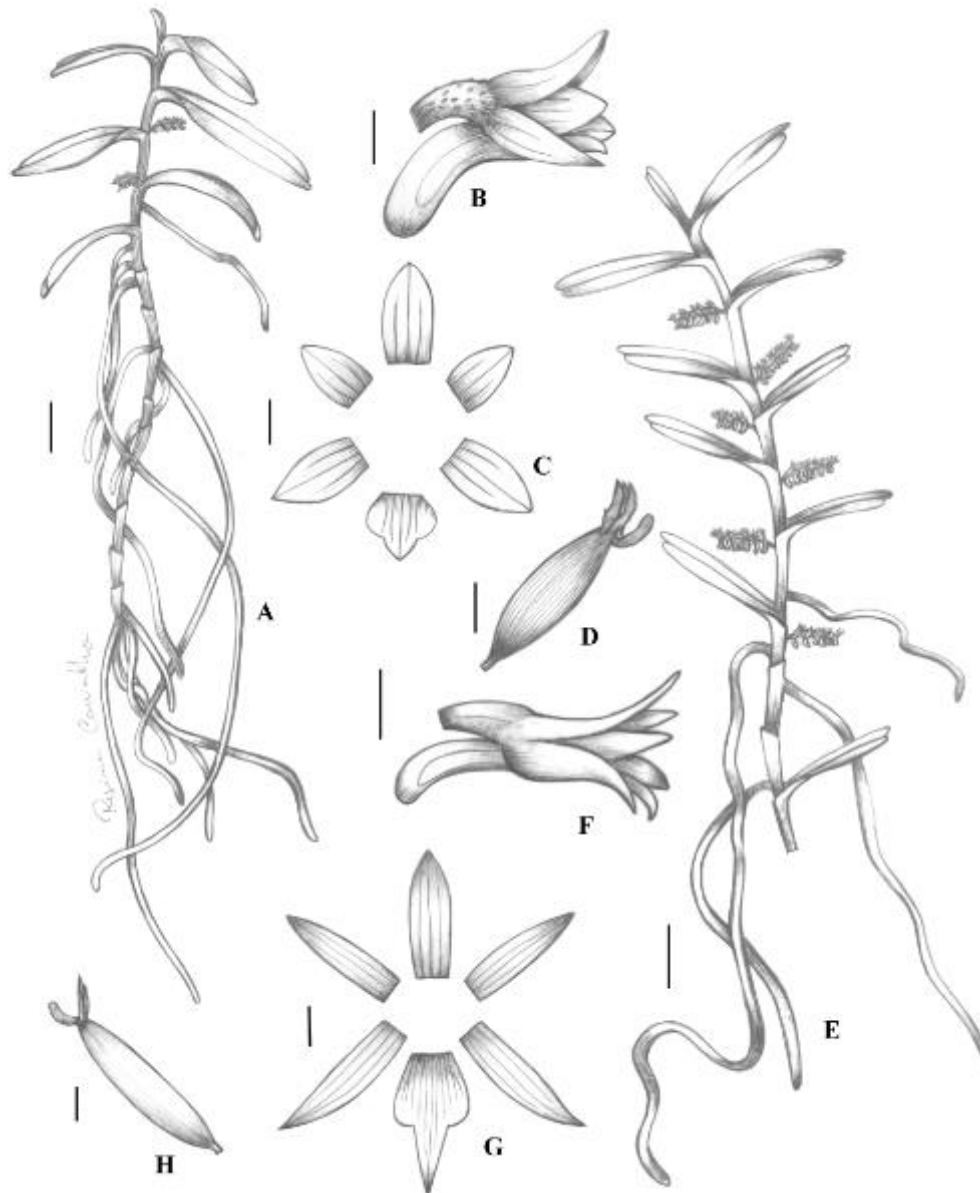


Figure 1. A–D. *Campylocentrum brevifolium*. A. Habit (scale bar = 7.0 mm). B. Flower (scale bar = 0.5 mm). C. Dissected perianth (scale bar = 1.0 mm). D. Capsule (scale bar = 2.0 mm). E–H. *Campylocentrum crassirhizum*. E. Habit (scale bar = 15.0 mm). F. Flower (scale bar = 1.5 mm). G. Dissected perianth (scale bar = 1.0 mm). H. Capsule (scale bar = 1.0 mm). [A–D drawn from *M. Wied s. n.* (BR); E–H drawn from *A. Ruschi 05* (SP)] (Drawn by Regina Carvalho).

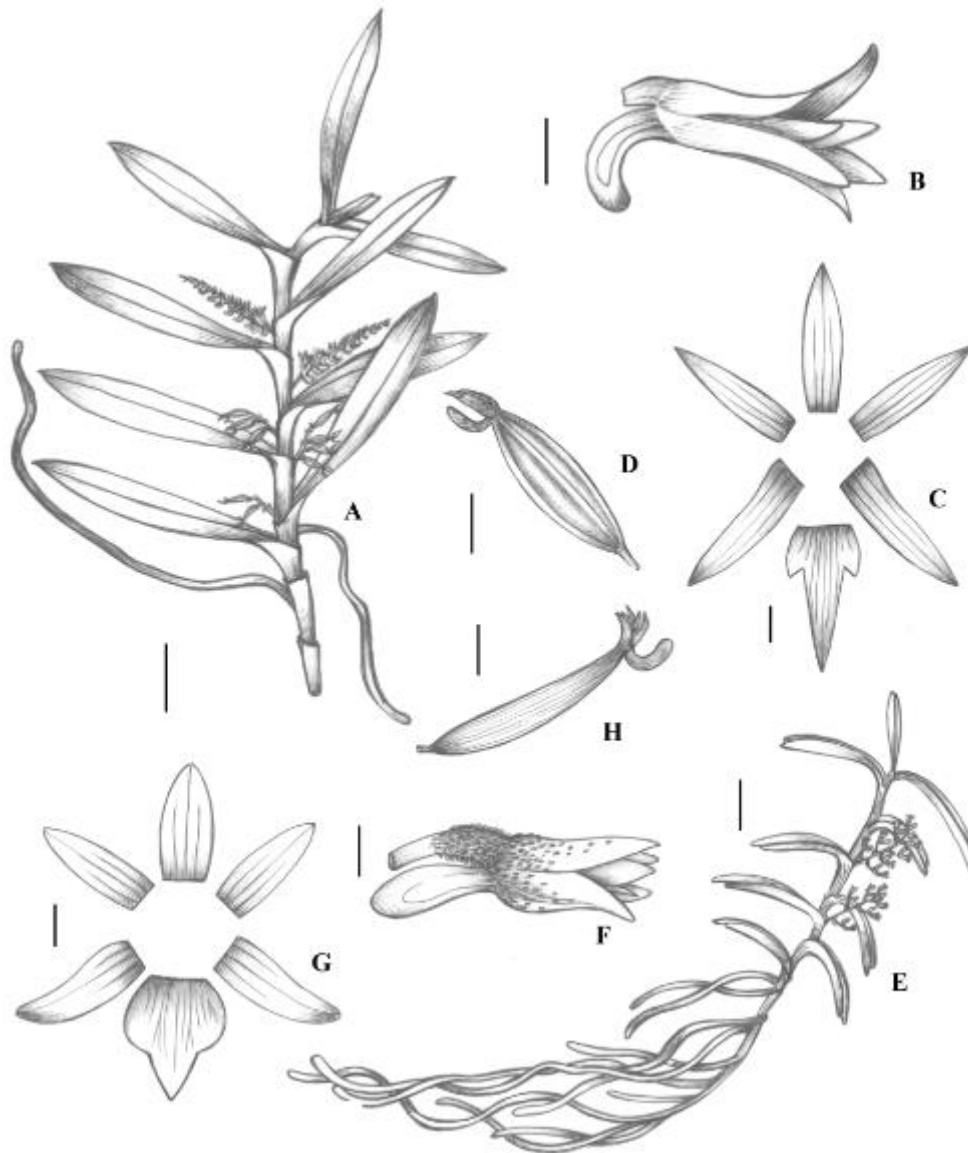


Figure 2. A–D. *Campylocentrum micranthum*. A. Habit (scale bar = 15.0 mm). B. Flower (scale bar = 1.5 mm). C. Dissected perianth (scale bar = 1.0 mm). D. Capsule (scale bar = 2.0 mm). E–H. *Campylocentrum pauloense*. E. Habit (scale bar = 8.0 mm). F. Flower (scale bar = 0.5 mm). G. Dissected perianth (scale bar = 0.5 mm). H. Capsule (scale bar = 2.0 mm). [A–D drawn from *s. coll.* 682a (K); E–H drawn from *A. Gehrt s. n.* (SP)] (Drawn by Regina Carvalho).

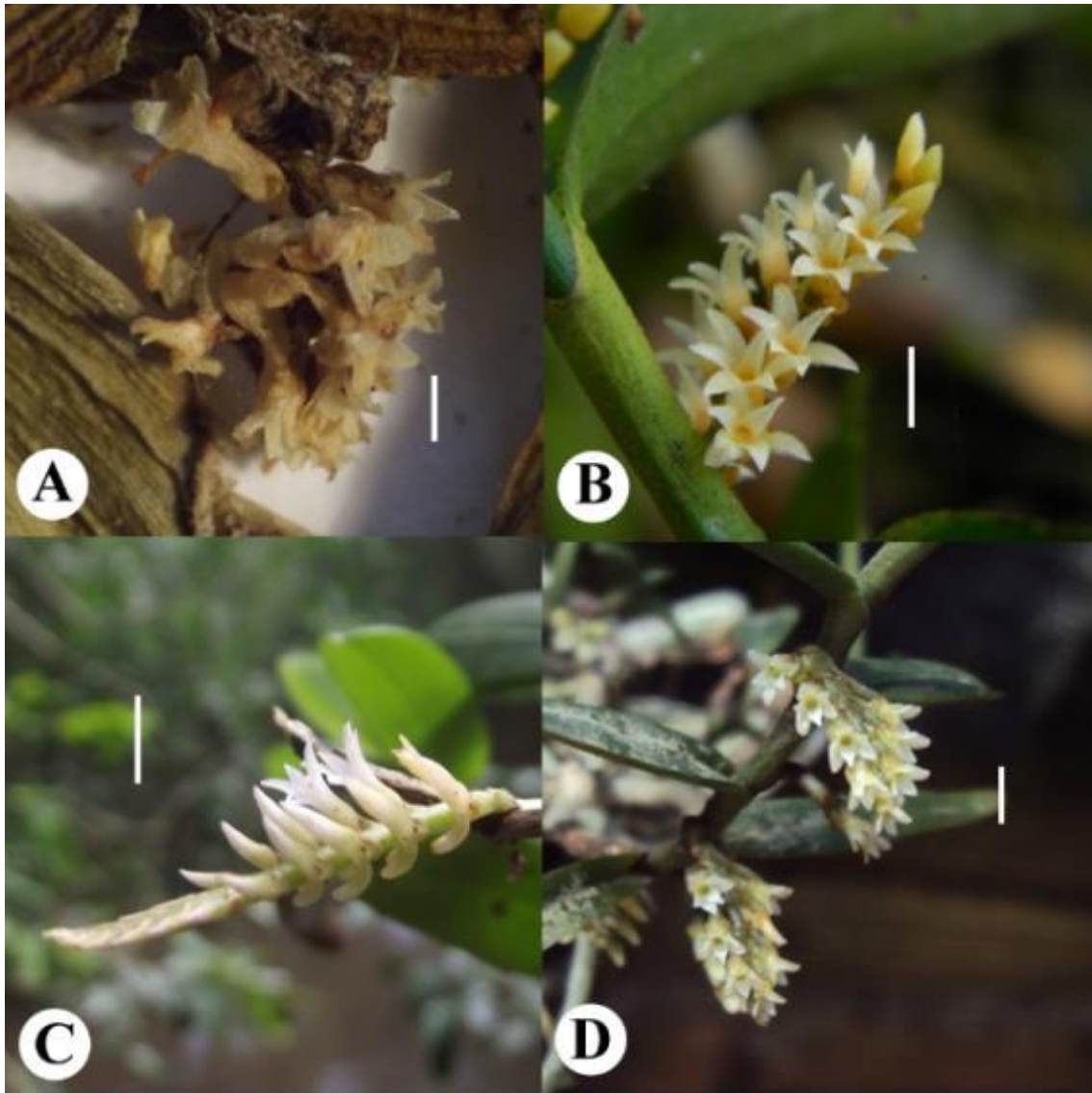
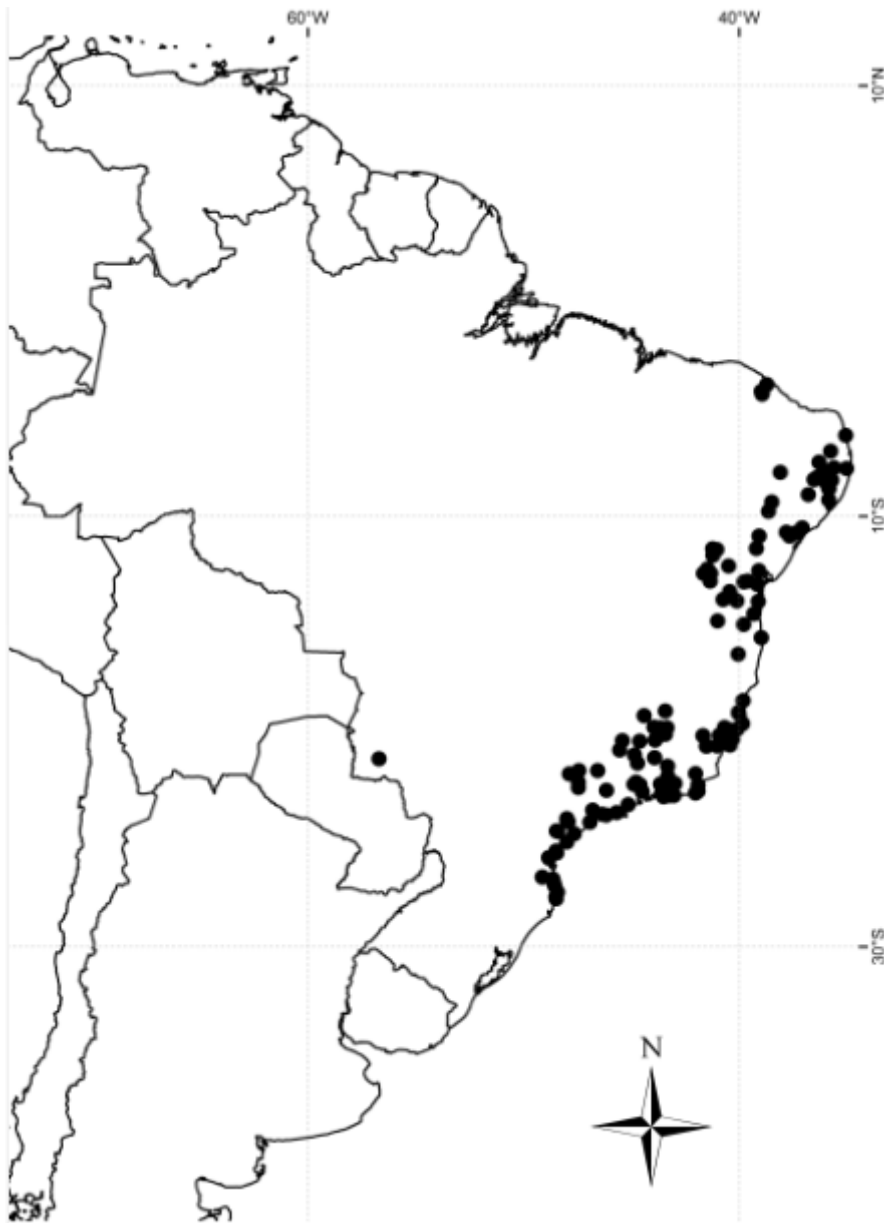


Figure 3. A. *Campylocentrum brevifolium* [C. Farney & J. C. Silva 4536 (RB); scale bar = 1.8 mm]. B. *Campylocentrum crassirhizum* [E. Pessoa et al. 1063 (UFP); scale bar = 3.5 mm]. C. *Campylocentrum micranthum* [E. Pessoa et al. 952 (RB, UFP); scale bar = 4.0 mm]. D. *Campylocentrum pauloense* [J. Caetano s.n. (FURB); scale bar = 2.0 mm].





Map 1. Map of the known distribution of *Campylocentrum brevifolium*.



Map 2. Map of the known distribution of *Campylocentrum crassirhizum*.



Map 3. Map of the known distribution of *Campylocentrum micranthum*.



Map 4. Map of the known distribution of *Campylocentrum pauloense*.

**Three new species of *Campylocentrum* Benth. (Angraecinae-Orchidaceae) from Brazil.**

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**Abstract**

*Campylocentrum* is composed by about 70 species, half of them cited from Brazil. In recent studies for the taxonomical review of the genus three new species from the country belonging to *C.* sect. *Campylocentrum* were recognized and were described here. Two from Atlantic forest, *C. itatiaie* and *C. schlechterianum*, and one from “cerrado”, *C. carvalhoi*. This study also provides illustrations, a map of distribution, a key of identification and discuss about their affinities with the allied species.

**Keywords:** Neotropics, Atlantic Forest, Cerrado, Vandae.

## Introduction

In the Neotropics the subtribe Angraecinae Summerhayes (1966: 188) is represented by the genera *Campylocentrum* Bentham (1881: 337) and *Dendrophyllax* Reichenbach f. (1864: 903), whose taxonomic limits were studied with a molecular approach by Carlswald *et al.* (2003).

*Campylocentrum* is composed by about 70 species (Govaertes *et al.* 2014) and 35 of them are cited by Barros *et al.* (2015) to Brazil. More than two-thirds of the Brazilian species grows in the Atlantic Forest, which according to Todzia (1980) is the endemism center of the genus.

The Brazilian species of *Campylocentrum* were reviewed by Cogniaux (1906), who proposed three sections for the genus: *C.* sect. *Campylocentrum* (1906: 504), *C.* sect. *Dendrophyllaxis* (1906: 504), and *C.* sect. *Pseudocampylocentrum* (1906: 504). Along the XXth century, 15 new names based on Brazilian specimens were proposed (Brade 1941, Hoehne 1938, Hoehne 1941, Hoehne & Schlechter 1922, Mansfeld 1928, Schlechter & Hoehne 1926) but nowadays most of which are considered synonyms. Recently, two new species: *C. insulare* Siqueira & Pessoa (2015: 79) and *C. serranum* Pessoa & Alves (2015: 54) were described from the states of Santa Catarina and Pernambuco.

In recent studies for the taxonomical review of the genus, three new species from Brazil of *C.* sect. *Campylocentrum*, which is characterized by conduplicate leaves, were recognized. Two of them are from the Atlantic forest were found among previous and indeterminate collection in local herbaria, and one from “*cerrado*” vegetation that was found in a fieldwork expedition carried on in 2013–2014.

This study aims to describe the new discoveries and it provides illustrations, a map of distribution and discuss the morphological affinities of the new taxa with their allied species.

***Campylocentrum carvalhoi* E. Pessoa & M. Alves, *sp. nov.* (Fig. 1A–F)**

Type:—BRAZIL, Minas Gerais: Cristais, Propriedade do Sr. Lázaro de Assis Carvalho (Sítio Barreiro), 876m a.s.l., 20 July 2014, fl., fr., *B. M. Carvalho 119b* (holotype: UFP, isotype, BHCB).

Morphologically related to *C. intermedium* (Reichenbach & Warming 1881: 91) Rolfe (1903: 245), but differs by shorter floral organs as sepals (1.3–1.8 mm vs. 3.0 mm long), petals (1.2–1.3 mm vs. 2.5–2.7 mm long), and lip (3-lobed and 1.6–1.7 mm vs. entire and 3.0 mm long).

Epiphytic herb. Roots 1–2 mm diam., cylindrical, fibrous, smooth, whitish to grey. Stem 5.5–23 cm long, cylindrical, unbranched. Leaves 25–45 mm long, 2.5–4 mm wide, greenish, linear, the apex minutely 2-lobed, lobes acute to obtuse, entire margin. Inflorescence 7–11 mm long, peduncle 1–2 mm long, glabrous, brownish; rachis 6–9 mm long, glabrous, brownish; floral bracts 0.5–0.9 mm long, 0.5–0.7 mm wide, deltoid, covering the base of the pedicellate ovary, minutely denticulate margin, the apex acute, membranaceous. Flowers 7–15 (for inflorescence), pale orange, distichous, pedicellate ovary 0.7–1 mm long, glabrous; dorsal sepal 1.3–1.5 mm long, 0.7–0.8 mm wide, ovate-oblong, the apex acute, 3-nerved, glabrous, entire margin, membranaceous; lateral sepals 1.6–1.8 mm long, 0.7–0.8 mm wide, ovate-oblong, subfalcate, the apex acute, 3-nerved, glabrous, entire margin, membranaceous; petals 1.2–1.3 mm long, 0.5–0.6 mm wide, elliptic-lanceolate, the apex acute, 3-nerved, glabrous, entire margin, membranaceous; lip 1.6–1.7 mm long, 1–1.2 mm wide between the lateral lobes, 3-lobed, membranaceous, 7-nerved, entire margin, producing at base a spur, lateral lobes 0.1 mm long, 0.3–0.4 mm wide, suborbicular, the apex rounded, mid-lobe 0.5–0.7 mm long, 0.4–0.5 mm wide, deltoid, the apex acute, glabrous, spur 1.8–2 mm long, 0.5–0.7 mm diam., ellipsoid to sub-conic, patent, the apex obtuse to acute, orangish, glabrous; ginostemium ca. 0.2 mm long, anther cap apex rounded, pollinia 2, globose. Capsule 4–6 mm long, 1.5–2 mm wide, fusiform, smooth, pedicellate, pedicel 0.5–0.8 mm long.

**Distribution and Ecology:**—*Campylocentrum carvalhoi* is known only from type locality in the state of Minas Gerais (Southeastern Brazil). It grows in sub-canopy of Gallery Forest in “*cerrado*” vegetation, and it is locally rare. Other four species of the genus occur in the area, *C. brachycarpum* Cogniaux (1906: 512), *C. crassirhizum* Hoehne (1939: 44), *C. grisebachii* Cogniaux (1906: 522) and *C. sellowii* (Reichenbach

f. 1850: 857) Rolfe (1903: 246). The area is not formally protected and is surrounded by farms. The flowering period is poorly known, fruits and late flowers can be observed in July.

**Etymology:**—The specific name honors the collector of the type specimen, Bruno Moraes de Carvalho, a Brazilian orchidologist from the state of Minas Gerais.

**Morphological affinities:**—Only eight species of *Campylocentrum* grow in the “*cerrado*” vegetation (Barros et al. 2015), generally they prefer areas of gallery forest. *C. carvalhoi* is the ninth species described from this ecosystem, and due the form of the spur (ellipsoid to sub-conic with an obtuse to acute apex), it is closely related with *C. intermedium*, a rare species known only from the type specimen collected by Warming in Lagoa Santa (Minas Gerais). It is distinguished by shorter length of the floral organs (sepals, petals, and lip) and the shape of the lip.

The vegetative portion, with relatively short and linear leaves, is similar to other Brazilian species which grow Atlantic Forest such as *C. pauloense* Hoehne & Schlechter (1926: 297), *C. brevifolium* (Lindley 1840: 68) Pessoa & Alves (2015: *in press*) and the other two species described in this study, *C. itatiaie* and *C. schlechterianum*. The new species differs from them mainly by the shape of the spur (ellipsoid to sub-conic, patent, with an apex obtuse to acute).

**Additional specimen examined (paratype):**—BRAZIL. Minas Gerais: Cristais, Sítio Barreiro, 814 m alt., 21 July 2013, *E. Pessoa & B. M. Carvalho 1190* (fl., fr.) (UFP).

***Campylocentrum itatiaie* E. Pessoa & M. Alves, *sp. nov.* (Fig. 1G–L)**

Type:—BRAZIL. Rio de Janeiro: Parque Nacional do Itatiaia, Pinheiral, 2,000 m a.s.l., Jan 1938, *L. Lanstyk s.n.* (fl.) (holotype: RB).

Morphologically related to *C. brachycarpum* Cogniaux, but differs by shorter floral bracts (0.3–0.4 mm vs. 1.0–1.5 mm long) and 3-lobed lip (vs. unlobed).



Epiphytic herb. Roots 1.5–2 mm diam., cylindrical, fibrous, smooth, whitish to grey. Stem 15.5 cm long, cylindrical, unbranched. Leaves 18.0–21 mm long, 3–5 mm wide, greenish, linear-oblong, the apex minutely 2-lobed, lobes obtuse, entire margin. Inflorescence 6–15 mm long, peduncle 1–2 mm long, glabrous, brownish; rachis 5–13 mm long, glabrous, brownish; floral bracts 0.3–0.4 mm long, 0.2–0.3 mm wide, deltoid, covering the base of the pedicellate ovary, minutely denticulate margin, the apex acute, membranaceous. Flowers 12–20 (for inflorescence), color unknown, distichous, pedicellate ovary 0.6–1 mm long, sparsely papillose; dorsal sepal 0.9–1 mm long, 0.6–0.7 mm wide, ovate, the apex obtuse, 1-nerved, glabrous, entire margin, membranaceous; lateral sepals 1.2–1.4 mm long, 0.7–0.8 mm wide, oblong, subfalcate, the apex acute, 1-nerved, glabrous, entire margin, membranaceous; petals 0.9–1 mm long, 0.6–0.7 mm wide, oblong, the apex rounded, 1-nerved, glabrous, entire margin, membranaceous; lip 1.1–1.2 mm long, 1.2–1.4 mm wide between the lateral lobes, 3-lobed, membranaceous, 5-nerved, entire margin, producing at base a spur, lateral lobes 0.1 mm long, 0.3–0.35 mm wide, suborbicular, the apex rounded, mid-lobe 0.4–0.5 mm long, 0.4–0.5 mm wide, deltoid, the apex obtuse, glabrous, spur 0.8–1.1 mm long, 0.5–0.7 mm diam., obovoid, straight to slightly curved, the apex rounded, glabrous; ginostemium ca. 0.2 mm long, anther cap apex rounded, pollinia 2, globose. Capsule not seen.

**Distribution and Ecology:**—It is known only from type locality in the Itatiaia National Park, in the state of Rio de Janeiro (Southeastern Brazil). It is an important remaining of montane Atlantic Forest of the Serra da Mantiqueira with elevations upper 2,000 m a.s.l. (IBDF 1997). Although extensive botanical studies have been performed in the area (Barberena *et al.* 2008, Lima & Guedes-Bruni 2004, Morin & Barroso 2007, Monteiro & Guimarães 2009, Monteiro & Guimarães 2008) only one specimen collected in 1938 is known, probably it is a rare species from areas of difficult access. The flowering period is poorly known, but according with the specimen label flowers can be observed in January.

**Etymology:**—The name of the new species refers to the type locality of the new taxon.

**Morphological affinities:**—*Campylocentrum itatiaie* has an obovoid spur, this characteristic is present in species such as *C. brachycarpum* Cogniaux, *C. densiflorum*

Cogniaux (1906: 511), *C. organense* (Reichenbach f. 1864: 901) Rolfe (1903: 245). Nevertheless, all three have longer floral bracts (> 1.0 mm long), and *C. itatiaie* has floral bracts with 0.3–0.4 mm long. Tiny flowers with sepals < 1.5 mm long are shared by the new species and *C. brachycarpum*, but it differs by the 3-lobed lip (vs. entire). Additionally in *C. brachycarpum*, the pedicellate ovary and part of perianth are covered by the floral bract and in *C. itatiaie* the floral bract covers only the base of the pedicellate ovary.

***Campylocentrum schlechterianum* E. Pessoa & M. Alves, *sp. nov.* (Fig. 1A–H)**

Type:—BRAZIL. Santa Catarina: São Martinho, Chicão, 526 m a.s.l., 26 Jan 2010, *J. Schmitt et al. 1020* (fl.) (holotype: FURB).

Similar to *C. pauloense* but differs by the globose and patent spur (vs. clavate and slightly curved).

Epiphytic herb. Roots 1–1.5 mm diam., cylindrical, fibrous, smooth, whitish to grey. Stem 3–13 cm long, cylindrical, rarely branched. Leaves 10–28 mm long, 3–4 mm wide, greenish, linear-oblong, the apex 2-lobed, lobes acute to obtuse, entire margin. Inflorescence 5–8 mm long, peduncle ca. 1 mm long, glabrous, brownish; rachis 4–7 mm long, glabrous, brownish; floral bracts 0.3–0.5 mm long, 0.2–0.3 mm wide, deltoid, covering the base of the pedicellate ovary, minutely denticulate margin, the apex acute, membranaceous. Flowers 4–8 (for inflorescence), cream colored, distichous, pedicellate ovary 0.8–1.2 mm long, papillose; dorsal sepal 1.8–2.1 mm long, 0.9–1 mm wide, oblong, the apex obtuse, 3-nerved, glabrous, entire margin, membranaceous; lateral sepals 2–2.5 mm long, 0.7–0.8 mm wide, oblong, subfalcate, the apex acute to obtuse, 3-nerved, glabrous, entire margin, membranaceous; petals 1.7–1.9 mm long, 0.7–0.8 mm wide, oblong, the apex acute to obtuse, 3-nerved, glabrous, entire margin, membranaceous; lip 1.9–2.1 mm long, 1.5–1.8 mm wide between the lateral lobes, 3-lobed, membranaceous, 9-nerved, entire margin, producing at base a spur, lateral lobes 0.1 mm long, 0.4–0.5 mm wide, suborbicular, the apex rounded, mid-lobe 0.9–1 mm long, 0.6–0.8 mm wide, deltoid, the apex acute, glabrous, spur 1–1.2 mm long, 0.9–1.1 mm diam., globose, patent, the apex rounded, glabrous; ginostemium ca. 0.2 mm long., anther cap apex rounded, pollinia 2, globose. Capsule not seen.

**Distribution and Ecology:**—It occurs in the state of Santa Catarina (Southern Brazil) and São Paulo (Southeastern Brazil) in areas of Atlantic Forest with elevation of 500–700 m a.s.l. It probably also occurs in the State of Paraná (Southern Brazil), since it is geographically between the previous cited states. The flowering period is poorly known, but according analyzed specimens flowers can be observed between January and March.

**Etymology:**—The name of the new species honors Rudolf Schlechter, a botanist from Germany, who described several species of *Campylocentrum* in the first decades of the XXth century.

**Morphological affinities:**—*Campylocentrum schlechterianum* is vegetatively similar to *C. pauloense*, in that point the species are undistinguishable. The inflorescence with few flowers (4-8), and the shape of the sepals and petals confirms it. Nevertheless the shape and position of the spur (globose and patent vs. clavate and slightly curved) become *C. schlechterianum* similar to *C. brachycarpum* or *C. itatiaie*. It differs from *C. brachycarpum* by the length of the floral bracts (0.3–0.5 mm vs. 1–1.5 mm) and shape of the lip (3-lobed vs. entire), and from *C. itatiaie* by the number of flowers for inflorescence (4–8 vs. 12–20) and length of the sepals (1.8–2.5 mm vs. 0.9–1.4 mm).

**Additional specimens examined (paratypes):**—BRAZIL. São Paulo: Barra do Turvo, Parque Estadual de Jacupiranga, Núcleo Cedro, 24 Mar 2005, A.C.C. Destefani *et al.* 111 (fl.) (ESA); *ibid.*, 24 Mar 2005, Destefani *et al.* 115 (st.) (ESA).

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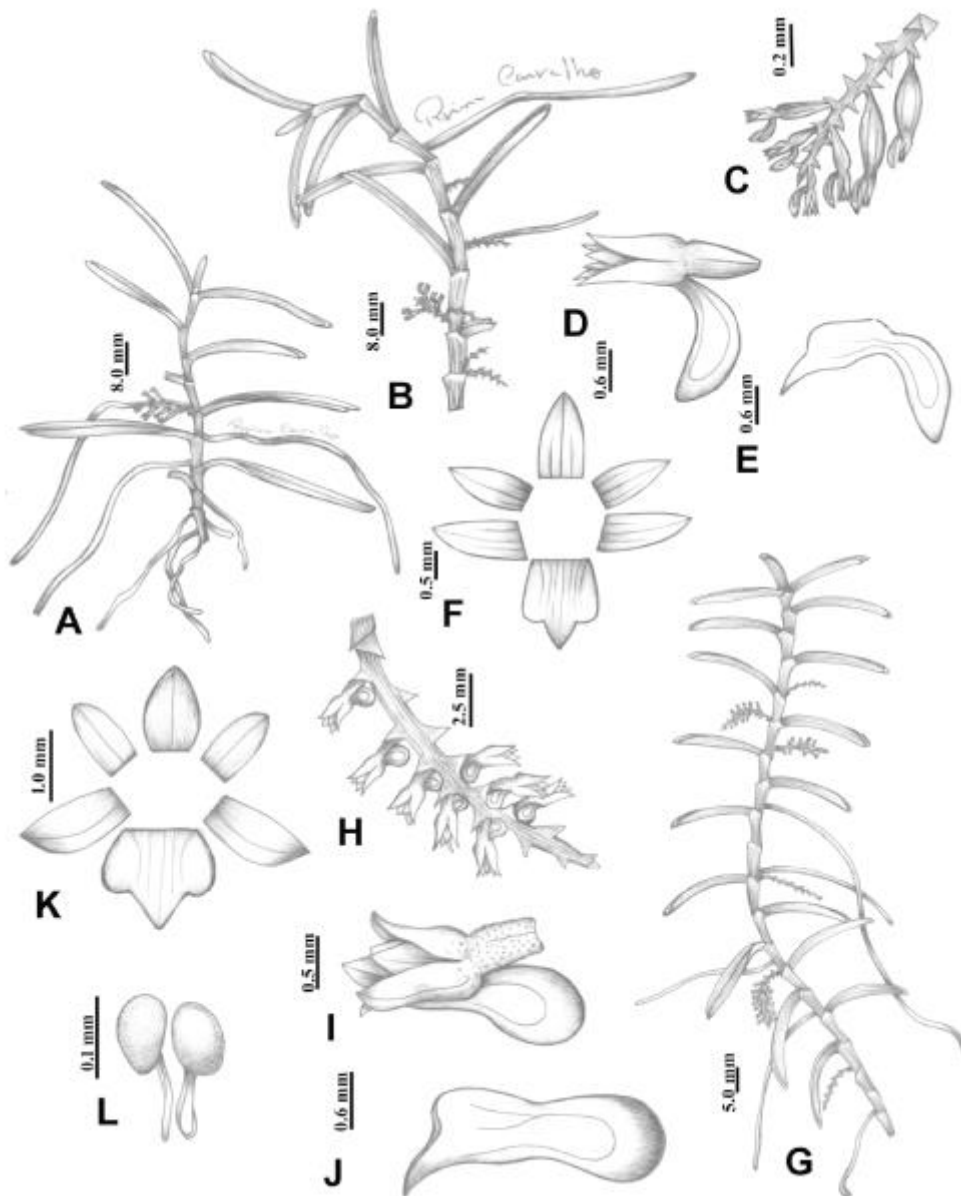
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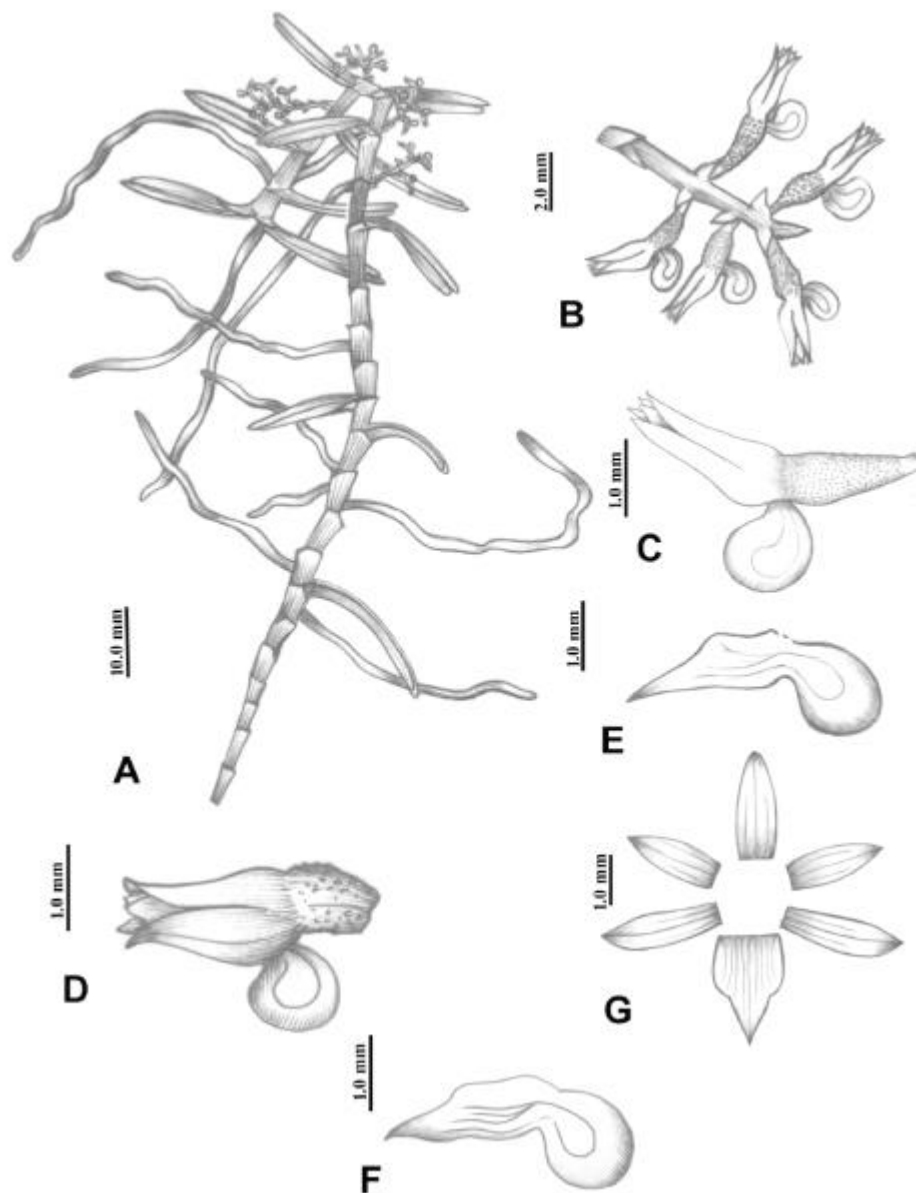
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**TABLE 1.** Comparison of morphological characteristics of the new species and their allied.

	<i>C. carvalhoi</i>	<i>C. intermedium</i>	<i>C. itatiaie</i>	<i>C. brachycarpum</i>	<i>C. schlechterianum</i>	<i>C. pauloense</i>
<b>Leaves: Length x width</b>	25.0–45.0 × 2.5–4.0 mm	30.0–40.0 × 4.0–6.0 mm	18.0–21.0 × 3.0–5.0 mm	20.0–50.0 × 4.0–9.0 mm	10.0–28.0 × 3.0–4.0 mm	15.0–33.0 × 3.0–6.0 mm
<b>Flowers/Inflorescence</b>	7–15	10–12	12–20	8–22	4–8	3–10
<b>Sepals length</b>	1.3–1.8 mm	3.0 mm	0.9–1.4 mm	1.0–1.2 mm	1.8–2.5 mm	1.5–2.2
<b>Sepals (nerves)</b>	3-nerved	1-nerved	1-nerved	3-nerved	3-nerved	3-nerved
<b>Lip (nerves)</b>	7-nerved	(not observed)	5-nerved	5-nerved	9-nerved	9–11-nerved
<b>Spur form</b>	Ellipsoid to sub- conic, obtuse to acute apex	Sub-conic, acute apex	Obovoid, rounded apex	Obovoid, rounded apex	Obovoid, rounded apex	Clavate
<b>Spur position</b>	Patent	Straight	Straight to slightly curved	Slightly curved to patent	Patent	Slightly curved

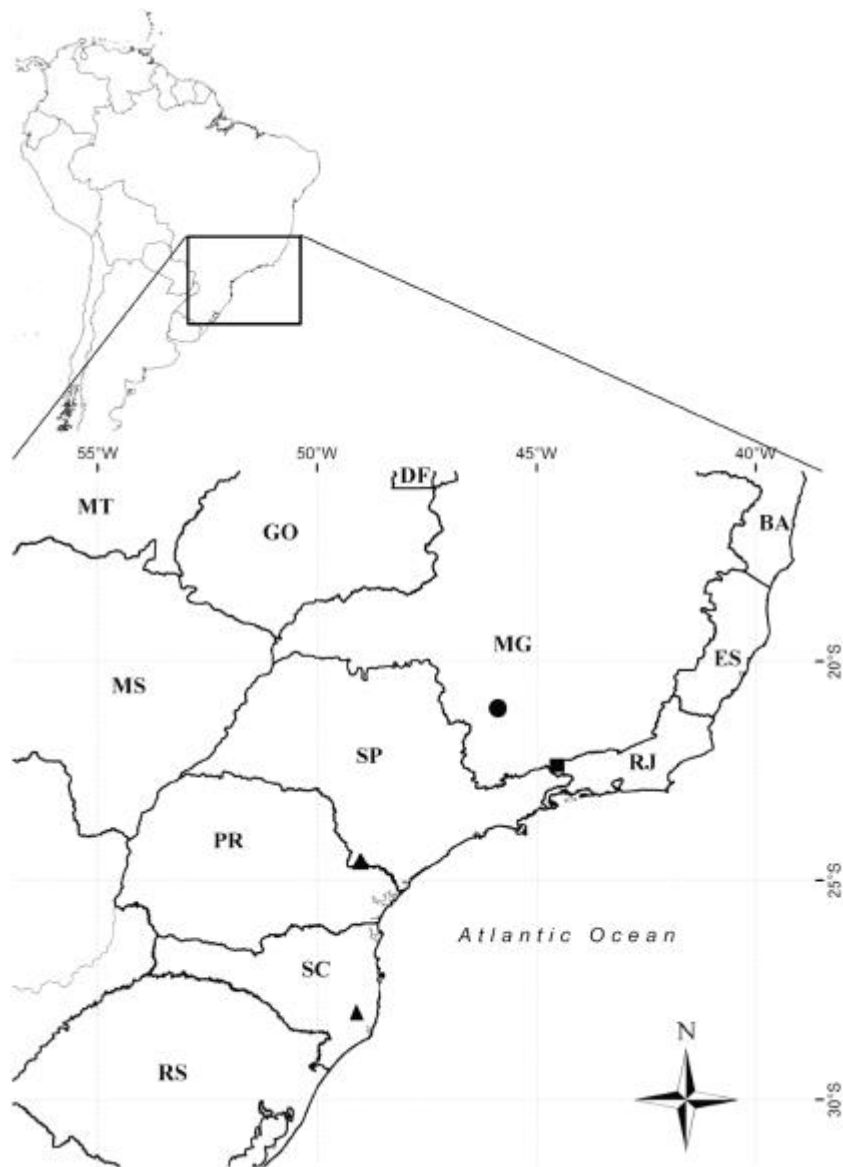


**FIGURE 1.** A–F. *Campylocentrum carvalhoi*. A–B. Habit. C. Inflorescence. D. Flower. E. Lip and spur in profile. F. Dissected perianth. G–L. *Campylocentrum itatiaie*. G. Habit. H. Inflorescence. I. Flower. J. Lip and spur in profile. K. Dissected perianth. L. pollinarium. [A. drawn from E. Pessoa & B. M. Carvalho 1190 (UFP); B–F drawn from B. M. Carvalho 119 (UFP); G–L drawn from L. Lanstyak s.n.(RB)].



**FIGURE 2.** *Campylocentrum schlechterianum* A. Habit. B. Inflorescence. C–D. Flowers, E–F. Lip and spur in profile. G. Dissected perianth. [A–C., E. and G. drawn from Schmitt *et al.* 1020 (FURB); D. and F. drawn from A.C.C. Destefani *et al.* 111 (ESA)].





**FIGURE 3.** Map of the known distribution of the new species. Circle – *Campylocentrum carvalhoi*; Square – *C. itatiaie*; Triangle – *C. schlechterianum*.

# CAPÍTULO 2

## Anatomia

**Manuscrito 1** – The odd roots of *Campylocentrum* (Angraeciinae-Orchidaceae): a descriptive anatomical study of its morphologically variable roots

**Submetido a: Rodriguésia**

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**Título: The odd roots of *Campylocentrum* (Angraeciinae-Orchidaceae): a descriptive anatomical study of its morphologically variable roots.**

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Título abreviado: The roots of *Campylocentrum*.

*Abstract* – (The odd roots of *Campylocentrum*: a descriptive anatomical study of its morphologically variable roots). Although some anatomical studies have been performed in Angraecinae, knowledge about the anatomy of the genus *Campylocentrum* is as yet incipient. The aim of this study is to anatomically characterize the structure of the different kinds of roots in the genus. Roots from 12 species were analyzed, including all the morphological variation in the genus (smooth and granulose surface). The leafless species are characterized by endovelamen, exodermal and endodermal cell walls thicker than in the leafy species. The species with terete leaves can be split in two groups: one constituting *C. poeppigii*, whose roots have a granulose surface produced by numerous unicellular, absorbent hairs; the second formed by six species from the Atlantic Forest. In this second group, the same granulose root appearance is produced by tufts of epivelamen in addition to the unicellular, absorbent root hairs. The other species in the genus, with conduplicate leaves, do not present a pattern for grouping. Some of them, such as *C. serranum* and *C. micranthum*, share a similar structure with the leafless species, but with thinner exodermal and endodermal cell walls. Other species, such as *C. crassirhizum* and *C. jamaicense*, are the only ones in the genus with  $\circ$ -thickened cells in the exodermis.

**Key words:** Vandeeae, anatomy, velamen, Neotropics.

*Resumo* – (As raízes bizarras de *Campylocentrum*: um estudo anatômico descritivo das suas raízes morfológicamente variáveis). Embora alguns estudos anatômicos tenham sido produzidos para Angraecinae, o conhecimento sobre a anatomia do gênero *Campylocentrum* ainda é incipiente. O objetivo desse estudo é caracterizar anatomicamente a estrutura dos diferentes tipos de raízes do gênero. Raízes de 12 espécies foram analisadas, incluindo toda a variação morfológica do gênero (superfície granulosa e lisa). As espécies áfilas são caracterizadas pelas paredes das células do endovelame, exoderme e endoderme mais espessadas que aquelas das espécies foliosas. As espécies com folhas cilíndricas podem ser separadas em dois grupos: um constituído por *C. poeppigii*, que possuem raízes com superfície granulosa produzida por numerosos pelos radiculares unicelulares; um segundo grupo formado por seis espécies da floresta Atlântica, onde a mesma aparência granulosa das raízes é produzida por tufos de epivelame, além da presença de pelos radiculares unicelulares. As outras espécies do gênero, com folhas conduplicadas, não apresentam um padrão para agrupamento. Algumas delas, como *C. serranum* e *C. micranthum*, compartilham uma estrutura similar a das espécies áfilas, mas com paredes das células da exoderme e endoderme mais finas. Outras espécies, como *C. crassirhizum* e *C. jamaicense*, são as únicas no gênero com células da exoderme espessadas em o.

Palavras-chave: Vandaeae, anatomia, velame, Neotrópicos.

## Introduction

Being a group of epiphytic orchids, *Campylocentrum* has several adaptations for the life form. Some of them permit the existence of leafless plants with chlorophyll-containing roots and with aeration units regulating gas exchange which are analogous to the stomatal complexes of leaves, making the roots the major photosynthetic organ in this group (Schimper 1888; Benzing & Ott 1981; Benzing *et al.* 1983; Pridgeon 1987).

Although some anatomical studies have been performed in subtribe Angraeciinae (tribe Vandeeae), knowledge about the anatomy of the Neotropical genera is still rudimentary. Within the vegetative portion, especially the roots, morphological descriptions are available for nine species of *Campylocentrum* (Carlswald *et al.* 2006; Bogarin & Pupulin 2010).

The first species to be anatomically described was *C. grisebachii* Cogn., a leafless species studied by Goebel (1922). Four other leafless ones were analyzed by Bogarin & Pupulin (2010), Carlswald *et al.* (2006), Stern (2014) and Winter *et al.* (1985). Roots of four leafy species have also been described (Bogarin & Pupulin 2010; Carlswald *et al.* 2006).

A general description of the root anatomy in the genus (in TS - transverse section) was provided by Carlswald (2006, 2014). *Campylocentrum* is characterized by a velamen with one to three layers; exodermal cells  $\cap$ - to  $\circ$ -thickened; endodermal cells  $\circ$ -thickened, and a vascular cylinder with six to nine xylems poles and vascular tissue embedded in sclerenchyma.

*Campylocentrum* is a Neotropical genus comprising about 70 species which belongs to the subtribe Angraeciinae (Carlswald 2014). According to Cogniaux (1906), the genus can be organized into three sections: *C.* sect. *Campylocentrum* (originally *C.* sect. *Eucampylocentrum*), species with well developed stems and leaves, *C.* sect. *Dendrophylopsis*, leafless species, and *C.* sect. *Pseudocampylocentrum*, species with developed stems but reduced leaves.

*Campylocentrum* sect. *Campylocentrum sensu* Cogniaux (1906) includes two groups with different leaf and root morphology, one with conduplicate leaves and a smooth external root surface (the typical velamen in orchids), and another group with terete leaves and a granulose to tuberculate external root surface (an unusual velamen) (Pessoa & Alves 2016) (Fig. 1A-D).

The group of species with terete leaves, included by Cogniaux (1906) in *C.* sect. *Campylocentrum*, has never been analyzed anatomically before. However, roots with a granulose surface are present in at least one genus of Vandeeae (*Microcoelia* Lindl., *vide* Cribb 2015), but is not clear if this feature is analogous in these genera.

The aim of this study is to anatomically describe the roots in species of *Campylocentrum* and their variation. This information will provide a better understanding of the genus and possibly support the taxonomic groups proposed by Cogniaux (1906) based on anatomical variation.

### **Material and Methods.**

Roots from 12 species were studied, eight of which were collected in the field and four from herbarium specimens (Tab. 1). Sampling included the three sections of the genus, organized here in three morphological groups: leafless plants (2 spp.); leafy with smooth velamen (3); leafy with granulose velamen (7). For ten species, only one specimen was analyzed due to their rarity (Tab. 1).

Samples of the median area of young roots of species collected in the field were fixed in 50% formaldehyde-Acetic acid- Alcohol (50% FAA) or in 1% glutaraldehyde + 4% formaldehyde in 0.1M sodium phosphate buffer, at pH 7.2 for 48h (McDowell & Trump 1976), then washed and stored in 70% ethanol (Johansen 1940). Materials obtained from herbarium specimens were rehydrated in boiled water with 50% glycerin, then washed thoroughly in tap water, and stored in 70% ethanol (Smith & Smith 1942, modified).

All samples were dehydrated in an increasing ethanol/tertiary butyl alcohol series and embedded in paraffin (Ruzin 1999). Transverse (TS) and longitudinal (LS) sections of the roots were cut on a rotary microtome (10–12  $\mu$ m) and stained with Astra blue and safranin (9:1), a modification of the methodology described by Bukatsch (1972). The slides were mounted in Canada balsam. The sections were submitted to histochemical analyses with Ferric chloride (Johansen 1940), Lugol (Johansen 1940), Sudan IV (Pearse 1985), for the detection of phenolic substances, starch and lipids respectively. The material was analyzed and all images captured by an Olympus CX31 and Leica DM500 microscope with the aid of Leica software.

## Results

**Velamen** - In *Campylocentrum* the velamen comprises two layers in the majority of the species studied (Figs. 2A-E, 3A-C), except to *C. crassirhizum* and *C. ornithorrhynchum* with two to three layers of cells (Tab. 2, Fig. 3D).

The epivelamen is composed of only one layer in all species analyzed, the cells were isodiametric (Fig. 3A-C) to radially elongated (Fig. 3D), and U-thickened in almost all species analyzed (Fig. 3A-D), except in *C. ornithorrhynchum* (not thickened) (Figs. 2-3). Although epivelamen tufts were not cited by Carlswald (2006, 2014) for the genus, they occur in *C. labiakii* Pessoa & Alves, *C. ornithorrhynchum*, *C. parahybunense* (Barb. Rodr.) Rolfe, *C. pernambucense* Hoehne and *C. wawrae* (Rchb.f. & Warm.) Rolfe (Tab. 2, Figs. 2C-D). The tufts are formed by randomly distributed cells which extend externally from the epivelamen; the subtending cells in the tufts are sometimes elongated as well (Fig. 2B-D).

On the other hand, absorbent root-hairs were observed in *C. labiaki*, *C. parahybunense*, *C. poeppigii* (Rchb.f.) Rolfe, *C. sellowii* and *C. wawrae* (Tab. 2, Fig. 2E). Linear thickenings, forming pores in the cell walls of the epivelamen, were observed in almost all species analyzed (Fig. 3A).

The endovelamen comprised one or two layers of cells in *C. crassirhizum*, *C. ornithorrhynchum*, and only one layer of cells in all other species examined (Tab. 2, Figs. 2-3). Endovelamen cells were radially elongated, the external layer was  $\circ$ -thickened, and the internal layer, when present, was  $\cap$ -thickened (Figs. 2C, 3A-D).

**Cortex** - The number of cell layers in the cortex varies from six to 14 - *C. grisebachii*, *C. micranthum*, *C. pernambucense*, *C. sellowii*, and *C. serranum* have up to seven layers, while only *C. poeppigii* and *C. wawrae* have 11 to 14 (Tab. 2, Fig. 2 A-B).

Exodermal cells were radially elongated in all species, being  $\circ$ -thickened in *C. crassirhizum* and  $\cap$ -thickened in all other species analyzed (Tab. 2, Figs. 2-3). Aeration complexes were observed only in *C. grisebachii* and *C. pernambucense* (Fig. 3B). The endodermis consisted of one layer of hexagonal cells in all species, being  $\circ$ -thickened with the presence of passage cells in almost all of them, except in *C. parahybunense*, *C. sellowii*, and *C. serranum*, whose cells were not thickened and passage cells were absent (Tab. 2, Figs. 4A-E).



Fungal hyphae were observed only in *C. crassirhizum* (cortex and velamen), *C. grisebachii* and *C. serranum* (cortex) (Fig. 5A). Water-storage idioblasts were present in the cortical parenchyma of *C. grisebachii* and *C. ornithorrhynchum* (Fig. 5B).

Raphides and starch grains were observed in the cortex and pith of all species analyzed (Fig. 5C-D).

**Stele** - Steles were composed of alternating clusters of xylem and phloem cells with six protoxylem poles in *C. crassirhizum*, *C. labiaki*, *C. pernambucense*, *C. serranum* and *C. wawrae*; seven poles in *C. grisebachii* and *C. paludosum*; eight poles *C. sellowii*; nine poles in *C. micranthum*, *C. parahybunense* and *C. poeppigii*; and eleven poles in *C. ornithorrhynchum* (Tab. 2, Fig. 4A-E).

The pericycle had one cell layer in *C. grisebachii*, *C. labiaki*, *C. ornithorrhynchum*, *C. parahybunense*, *C. poeppigii*, *C. sellowii* and *C. wawrae* (Figs. 4A-E), and one to two layers of cells in *C. crassirhizum*, *C. paludosum*, *C. pernambucense*, *C. micranthum*, and *C. serranum* (Figs. 4A-E). Pericyclic cells were thin-walled opposite xylem and thick-walled opposite phloem tissue (Fig. 4A-E). Pith cell walls were thickened in *C. crassirhizum*, *C. grisebachii*, *C. ornithorrhynchum*, and *C. pernambucense* (Figs. 4A-E).

## Discussion

According to Porembski & Barthlott (1988) the velamen of orchids is classified into 12 types. *Campylocentrum* fits within the “*Vanda* Type”, which is characterized by a less than five-layered velamen, differentiated into large-celled epivelamen and comparatively small-celled endovelamen, the latter with cell walls thicker than those of the epivelamen; exodermis cells often much larger than the velamen cells; and tracheoidal idioblasts in the cortex occasionally present. The structure of the roots of *Campylocentrum* and its sister genus *Dendrophylax* (Carlsward *et al.* 2003) is very similar, making it impossible to distinguish them solely by these overlapping characters (Carlsward *et al.* 2006).

Although absorbent root hairs were observed here in four species and also in *C. generalense* by Bogarin & Pupulin (2010) and *C. pachyrrhizum* by Carlsward *et al.* (2006), they were more numerous in *C. poeppigii* and gave the velamen surface a slightly granulate texture (Fig. 1D). On the other hand, the same surface texture is

found in other species, where it is produced by tufts of epivelamen, and according to Carlsward *et al.* (2006), it can also be found in *Tridactyle* Schltr., an African genus of Angraeciinae.

According to the general anatomical description of the root structure in the genus provided by Carlsward *et al.* (2006),  $\circ$ -thickened cells in the exodermis had only been observed in *C. jamaicense* [published as *C. micranthum*, voucher checked and corrected (*Ackerman 3341*)] by Carlsward *et al.* (2006). Such cells were found here also in *C. crassirhizum*, which is morphologically related to *C. jamaicense*. Both species share oblong, conduplicate leaves with a strongly 2-lobed apex (Pessoa *et al.* 2015).

The majority of species have the exodermis with  $\cap$ -thickened cell walls, however they were apparently thicker in the leafless species (although we did measure it), a state which was also observed by Bogarin & Pupulin (2010) in *C. generalense*. The function of the thicker endovelamen, exodermal and endodermal cell walls in this group is unclear, but may be indicative of a means to prevent water loss via transpiration and also to provide support and protect the cortex and the vascular tissue from mechanical damage and cell collapse during periods of drought dryness (Noel 1974; Benzing & Ott 1981; Benzing *et al.* 1982; Benzing *et al.* 1983; Carlsward *et al.* 2006).

Although Carlsward *et al.* (2006) describe the endodermal cells as  $\circ$ -thickened for all species in the genus, in *C. parahybunense*, *C. sellowii* and *C. serranum* the endodermal cells were not thickened. The walls of the endodermal cells in the leafless species were thicker, as also observed by Bogarin & Pupulin (2010).

Carlsward *et al.* (2006) analyzed roots with six to nine poles in the vascular cylinder but *C. ornithorrhynchum*, with 11 poles, holds the record for the highest number found in the genus. According to Pridgeon (1987), the number of poles is consistent and is useful for delimiting species of Orchidaceae. However, according to Rütter & Stern (1992) it can vary among different specimens of the same species and also in the same root at different height levels. Meanwhile, Rütter & Stern (1992) and Rosso (1966) indicated that root diameter and the number of poles of protoxylem are related. Ontogenetic studies must confirm the variation of number of poles and its use as diagnostic character in the family. This is the main reason why no claim for species delimitation in *Campylocentrum* can be stated yet on this matter. Additionally, no correlation between the number of poles root diameter has been found too which is

exemplified in *C. crassirhizum* and *C. sellowii*. For these two species which have thicker roots, six and eight poles respectively were found. For other species of *Campylocentrum* with thinner roots, nine and eleven poles were found.

In summary, the leafless species analyzed show the same basic structure, with a two-layered velamen, endovelamen, exodermal and endodermal cell walls thicker than those in the leafy species, and vascular cylinder with six or seven xylem poles (Fig. 6 C, G).

The group of species with terete leaves and granulose roots can be split in two. One group comprises a single species, *C. poeppigii*, known from Mexico to northern Brazil and included in *C. sect. Pseudocampylocentrum*, in which the granulose surface is produced by numerous unicellular, absorbent hairs (Fig. 6 D, H). The second sub-group is formed of six species distributed along the Atlantic coast of Brazil and included in *C. sect. Campylocentrum*, their roots have a similar external morphology, but in this case all species have tufts of epivelamen in addition to unicellular, absorbent root hairs (Fig. 6 B, F). This second sub-group had not been anatomically analyzed before, making this study the first to describe its roots.

The other species in the genus (with conduplicate leaves and smooth roots) do not present any patterns for grouping. Some of them, such as *C. serranum* and *C. micranthum*, have a structure similar to the leafless species, but with thinner exodermal and endodermal cell walls. Other species, such as *C. crassirhizum* and *C. jamaicense*, are the only ones in the genus known to have  $\alpha$ -thickened cells in the exodermis (Fig. 6 A-E).

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Table 1. Species studied (LL: Leafless; SM: leafy with smooth roots; GR: leafy with granulose roots/ CA: *C. sect. Campylocentrum*; DE: *C. sect. Dendrophylopsis*; PS: *C. sect. Pseudocampylocentrum*).

Species	Voucher	LL	SM	GR	CA	DE	PS
<i>C. crassirhizum</i>	<i>E. Pessoa et al. 1092</i> (UFP)		×		×		
<i>C. grisebachii</i>	<i>E. Pessoa &amp; B.M. Carvalho 1188</i> (UFP)	×				×	
<i>C. labiaki</i> *	<i>D.A. Folli 2150</i> (RB)			×	×		
<i>C. micranthum</i>	<i>E. Pessoa et al. 1217</i> (UFP)		×		×		
<i>C. ornithorrhynchum</i>	<i>E. Pessoa et al. 1239</i> (UFP)			×	×		
<i>C. paludosum</i>	<i>M. Mirana 87</i> (UFP)	×				×	
<i>C. parahybunense</i> *	<i>A. Korte &amp; A. Kniess 2230</i> (FURB)			×	×		
<i>C. pernambucense</i>	<i>E. Pessoa et al. 1085</i> (UFP)			×	×		
<i>C. poeppigii</i> *	<i>E. Pessoa et al. 693</i> (UFP)			×			×
<i>C. sellowii</i>	<i>E. Pessoa &amp; B.M. Carvalho 1189</i> (UFP)			×	×		
<i>C. serranum</i>	<i>E. Pessoa et al. 945</i> (UFP)		×		×		
<i>C. wawrae</i> *	<i>R.C. Mota 3153</i> (BHCB)			×	×		

\*Herbarium specimens

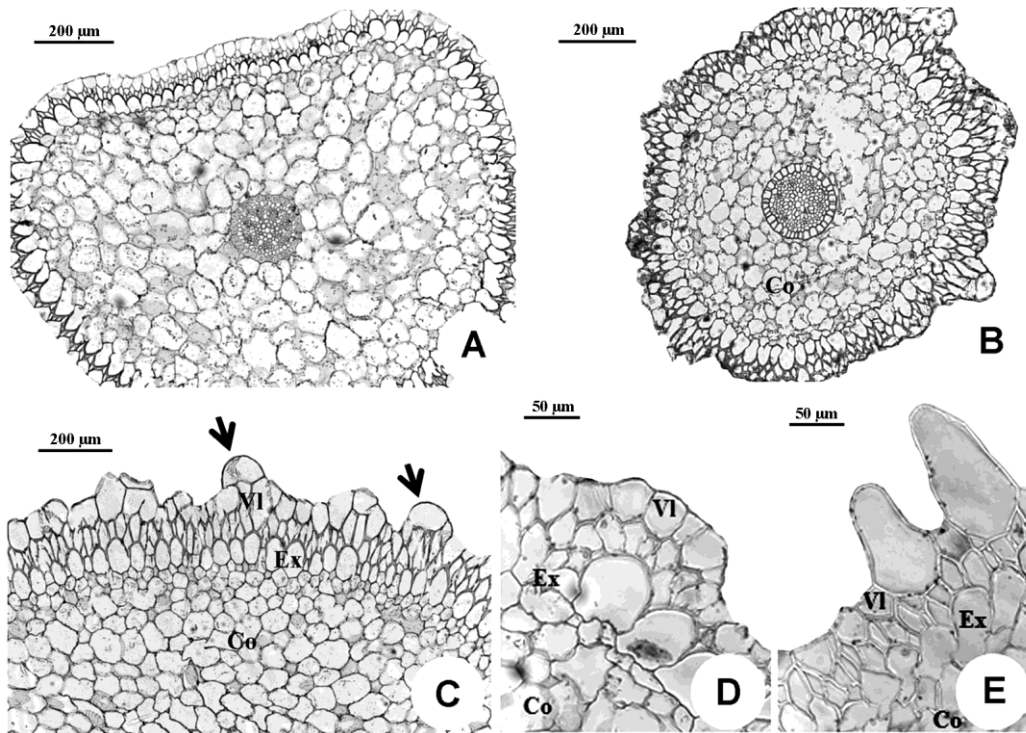
Table 2. Principal anatomical root characters used to distinguish species of *Campylocentrum*.

	Velamen	Absorbent root hairs	Tufts	Exodermis	Cortex	Endodermis	Number of poles
<i>C. crassirhizum</i>	2-3-layered	Absent	Absent	○-thickened	7-10-layered	○-thickened	6
<i>C. grisebachii</i>	2-layered	Absent	Absent	∩-thickened	6-7-layered	○-thickened	7
<i>C. labiaki</i>	2-layered	Present	Present	∩-thickened	7-layered	○-thickened	6
<i>C. micranthum</i>	2-layered	Absent	Absent	∩-thickened	6-7-layered	○-thickened	9
<i>C. ornithorrhynchum</i>	2-3-layered	Absent	Present	∩-thickened	8-10-layered	○-thickened	11
<i>C. paludosum</i>	2-layered	Absent	Absent	∩-thickened	9-10-layered	○-thickened	7
<i>C. parahybunense</i>	2-layered	Present	Present	∩-thickened	8-10-layered	Not thickened	9
<i>C. pernambucense</i>	2-layered	Present	Present	∩-thickened	7-layered	○-thickened	6
<i>C. poeppigii</i>	2-layered	Present	Absent	∩-thickened	11-layered	○-thickened	9
<i>C. sellowii</i>	2-layered	Absent	Present	∩-thickened	6-7-layered	Not thickened	8
<i>C. serranum</i>	2-layered	Absent	Absent	∩-thickened	6-7-layered	Not thickened	6
<i>C. wawrae</i>	2-layered	Present	Present	∩-thickened	11-14-layered	○-thickened	6

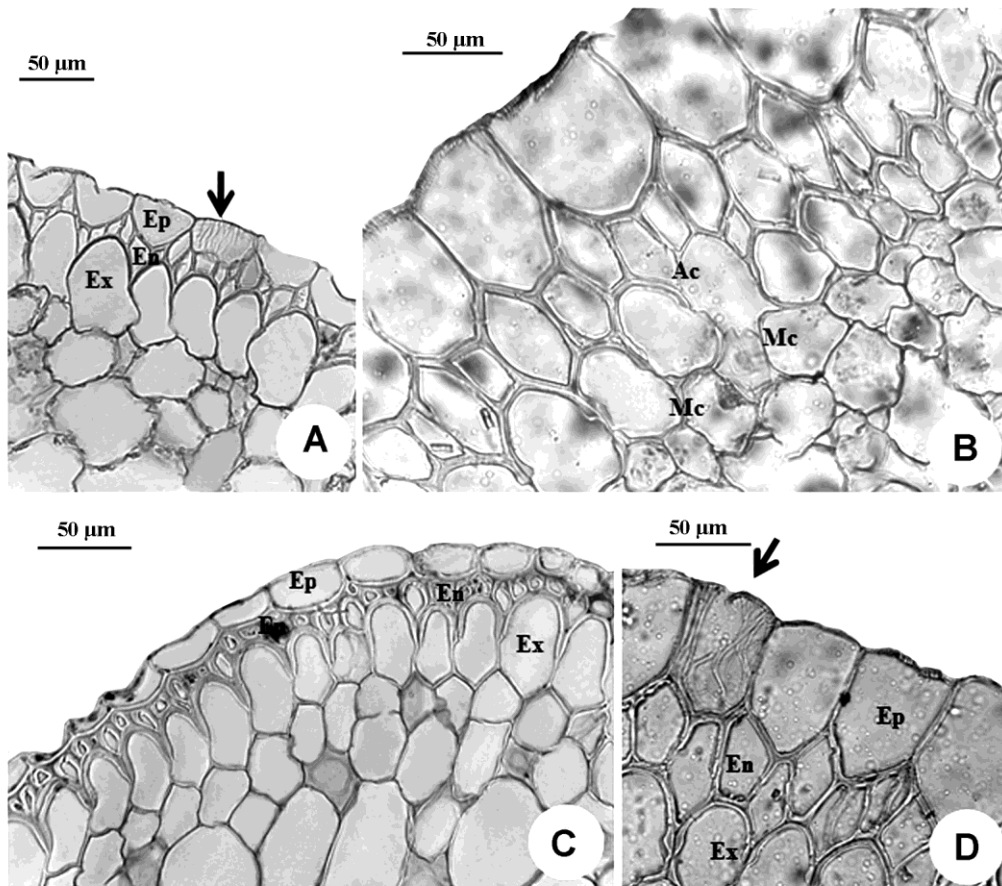


**Figure 1A–D.** Fresh roots. A. *C. crassirhizum*; B. *C. paludosum*; C. *C. ornithorrhynchum*; D. *C. poeppigii*.

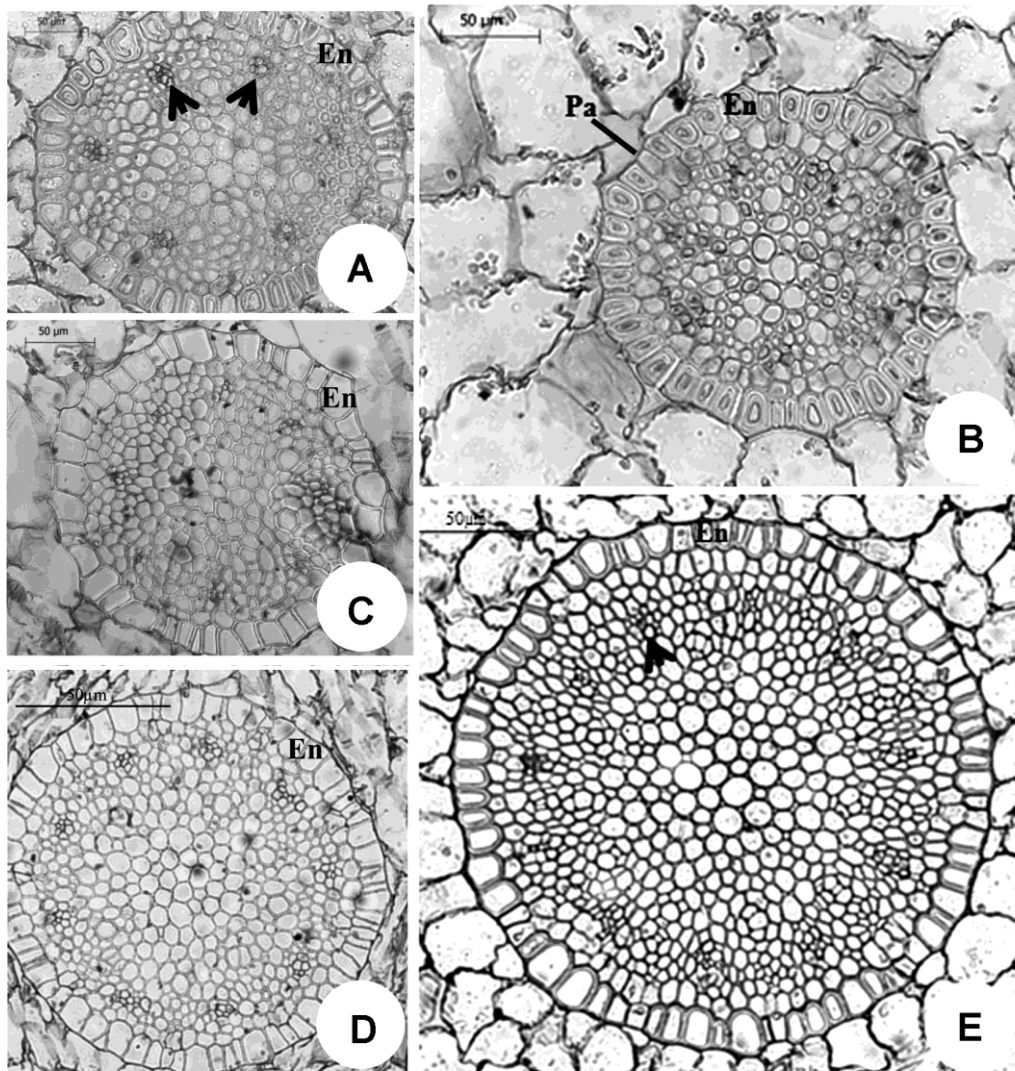




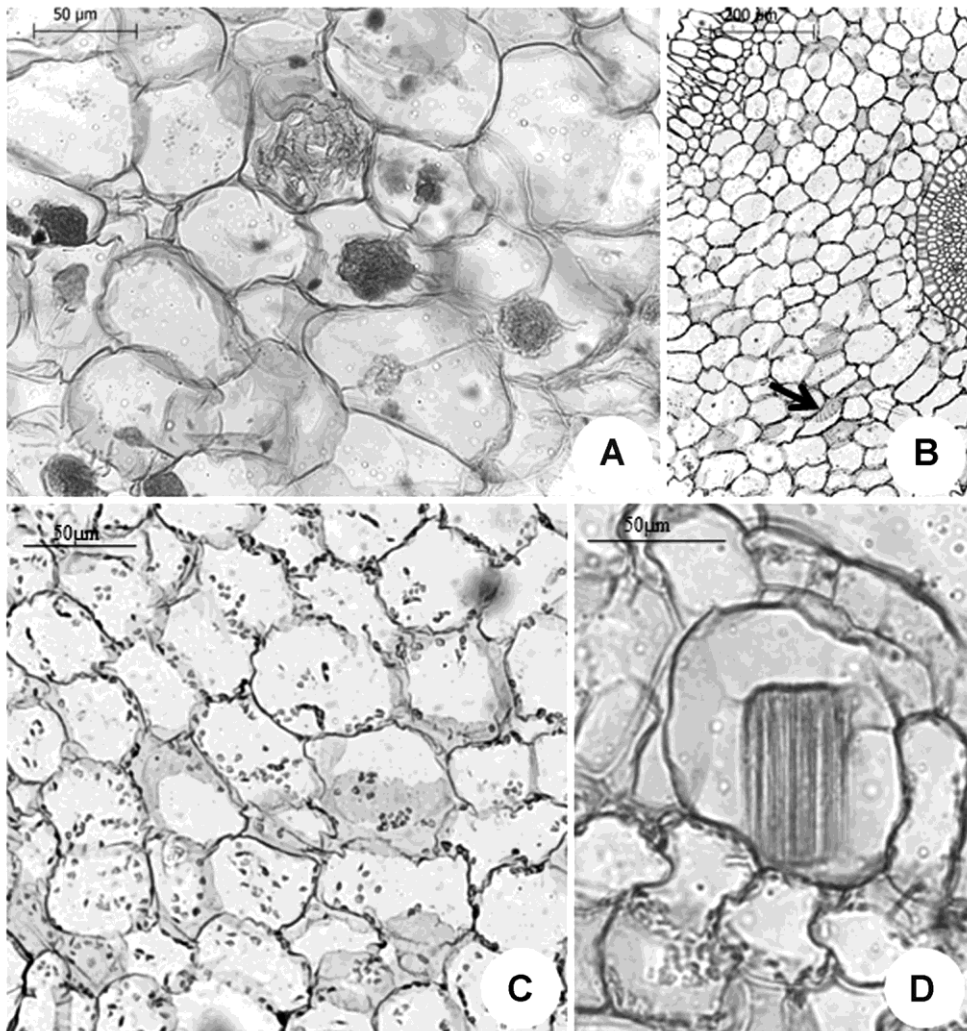
**Figure 2A–E.** Roots, TS. A. General aspect of *Campylocentrum grisebachii*; B. General aspect of *Campylocentrum pernambucense* C. Undulating epivelamen with tufts in *Campylocentrum ornithorhyncum*; D. Undulating epivelamen with tufts in *Campylocentrum pernambucense*; E. Epivelamen showing absorbent root-hairs in *Campylocentrum poeppigii*. Co - Cortex, Ex - Exodermis, VI - Velamen, Arrows – tufts.



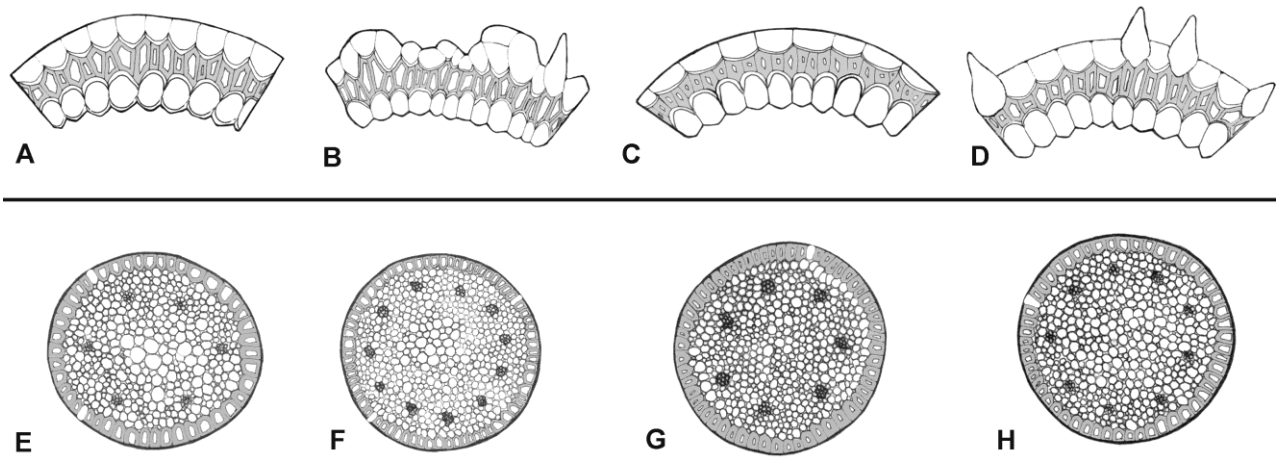
**Figure 3A–E.** Roots, LT. A. *Campylocentrum parahybunense*, endovelamen (En) cells radially elongate and exodermis (Ex) showing  $\cap$ -thickened cell walls, cells with linear thickening forming pores in the cell walls (arrow); B. Aeration complex (Ac) in *Campylocentrum grisebachii*, endovelamen (En) showing one layer of  $\circ$ -thickened cells. C. *Campylocentrum paludosum* showing endovelamen with thicker cell walls. D. Cells with linear thickening forming pores in the cell walls (arrow) in *Campylocentrum crassirhizum*. En-Endovelamen; Ep-Epivelamen; Ex-Exodermis; Mc-Modified cortical cell.



**Figure 4A–E.** Roots, TS showing stele. A. Six protoxylem poles in *Campylocentrum crassirhizum*. Note endodermis (En) cells  $\circ$ -thickened. B. Seven protoxylem poles and endodermis (En) cells  $\circ$ -thickened in *Campylocentrum grisebachii*. Note passage cells (Pa) in the endodermis. C. Eight protoxylem poles in *Campylocentrum sellowii*. Note endodermis (En) cells are not thickened. D. Nine protoxylem poles and endodermis (En) cells not thickened in *Campylocentrum poeppigii*. E. Eleven protoxylem poles and endodermis (En) cells  $\circ$ -thickened in *Campylocentrum ornithorhynchum*. Arrow-Phloem; En-Endodermis.



**Figure 5A–D.** Roots, TS. A. Fungal hyphae in cortex of *Campylocentrum serranum*. B. Water-storage idioblasts (arrow) in cortex of *Campylocentrum ornithorrhyncum*. C. Starch grains in cortex of *Campylocentrum wawrae*. D. Root LS showing one raphide crystal in cortex of *Campylocentrum grisebachii*.



**Figure 6A–H.** Schemes of the main types of roots in TS. A-D: Velamen + exodermis. A. *C. crassirhizum*; B. *C. paludosum*; C. *C. ornithorrhynchum*; D. *C. poeppigii*. Epivelamen – light gray; Endovelamen – Dark gray; Exoderm – White. E-H: Endodermis + stele. E. *C. crassirhizum*; F. *C. paludosum*; G. *C. ornithorrhynchum*; H. *C. poeppigii*. Endodermis – Dark gray; Xylem poles – Black.

# CAPÍTULO 3

## Filogenia e biogeografia

**Manuscrito 1** – Evolutionary history and systematics of *Campylocentrum* (Orchidaceae: Vandaeae: Angraecinae): a phylogenetic and biogeographical approach

**Submetido a: Molecular Phylogenetics and Evolution**

**Evolutionary history and systematics of *Campylocentrum* (Orchidaceae: Vandaeae: Angraecinae): a phylogenetic and biogeographical approach**

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## Abstract

Subtribe Angraecinae (Orchidaceae: Vandae) are mainly distributed in Africa, with two genera, *Campylocentrum* and *Dendrophylax*, restricted to the Neotropics. As a Neotropical widespread genus, *Campylocentrum* constitutes an appropriate model to reveal biogeographic patterns in this area and investigate routes of colonization and dispersion. In this study, we reconstructed phylogenetic relationships of the genus through Bayesian inference and maximum parsimony analyses of combined nuclear (ITS and *Xdh*) and plastid (*matK* exon, *rpl32-trnL* spacer, *trnL* intron, *trnL-trnF* spacer, and *ycf1* exon) DNA datasets, aimed at establishing a new infrageneric classification for this taxonomically complex genus. Based on the most comprehensive phylogenetic tree, we investigated *Campylocentrum* biogeographic history by estimating divergence times, inferred using fossil and secondary calibrations applying a relaxed-clock model approach, and reconstructing ancestral areas of distribution under a time-stratified likelihood model. The phylogenetic analyses provided strong support to the majority of the clades. *Campylocentrum* is monophyletic; we recognize five sections based upon strongly supported clades. We conclude that the African angraecoid ancestor of *Campylocentrum* and *Dendrophylax* dispersed to the Antilles. *Campylocentrum* is estimated to be a relatively young genus (Late Miocene, ca. 8.2 million years ago) and its most recent common ancestor had a disjunctive distribution in the Antilles and Parana dominion. During the Pliocene, the five sections diverged and expanded their distributions in the Neotropics, and in the Pleistocene radiations were experienced by some of the terminal clades. We hypothesize that the evolutionary history of *Campylocentrum* was highly influenced by orogenic events that occurred during the Pliocene and by the climatic fluctuations in the Pleistocene.

Keywords: Antillean floras; Caribbean biodiversity; molecular clock; Neotropical biogeography; Neotropical flora.



## 1. Introduction

Orchidaceae are one of the two largest plant families and occur on all continents except Antarctica (Dressler, 2005). They are particularly diverse in the Neotropics and Southeast Asia (Dressler, 1993). The Neotropical region houses the highest terrestrial biodiversity in the globe (Myers et al., 2000; Maiti and Maiti, 2011), including some hyper-diverse orchid groups such as subtribes Laeliinae, Maxillariinae, Oncidiinae and Pleurothallidinae, all endemic to this region (Pridgeon et al., 2005, 2009). Other taxa, such as tribe Vandeeae, are almost entirely Paleotropical, including the mostly Afromalagasy subtribe Angraecinae (Vandeeae; Carlswald et al., 2006a; Pridgeon et al., 2014) that includes two Neotropical genera, *Campylocentrum* and *Dendrophylax* (Carlswald et al., 2006a; Pridgeon et al., 2014).

Angraecinae comprise 49 genera (Pridgeon et al., 2014; but see also Szlachetko et al., 2013, who recognizes many more). Variation in number of genera recognized depends on the concept of the large genus *Angraecum*, which in a recent molecular phylogenetic studies was found to be non-monophyletic (Carlswald et al., 2006a; Szlachetko et al., 2013). *Campylocentrum* and *Dendrophylax* are embedded within *Angraecum s.l.* as sister to *Angraecum* sects. *Conchoglossum* and *Arachnangraecum* or the genera *Angraecoides* and *Eichlerangraecum* as proposed by Szlachetko et al. (2013). Because the study by Szlachetko et al. (2013) did not include many of the other genera in subtribe Angraecinae, it cannot be considered definitive in terms of resolving the taxonomic complications of this subtribe. We prefer instead to follow the taxonomy of Pridgeon et al. (2014).

The Neotropical genera *Campylocentrum* and *Dendrophylax* include the only leafless taxa within Angraeciinae, the phylogenetic relationships of which were studied by Carlswald et al. (2003). They found that leaves were lost twice in this clade. *Campylocentrum* has both leafy and leafless species, whereas *Dendrophylax* comprises only leafless species (Carlswald et al., 2003).

*Campylocentrum* currently includes 70 species (Carlswald, 2014a; Kolanowska and Szlachetko, 2013; Pessoa and Alves, 2015; Pessoa and Alves, 2016a, 2016b) occurring in all Neotropical countries with exception of Chile (Carlswald, 2014a; Primavera, 2013). *Campylocentrum* and *Dendrophylax* are most easily distinguished by their inflorescences. *Campylocentrum* have racemes with numerous, relatively small flowers that open simultaneously, whereas in *Dendrophylax* the flowers are fewer and

larger and have inflorescences that are often fractiflex, occasionally branched, with one to few flowers opening successively. *Dendrophylax* flowers vary in size among species from a few mm to several cm, including some with long nectar spurs. (Carlsward and Cribb, 2014). Cogniaux (1906) proposed an infra-generic classification of the genus, organizing it in three sections based on vegetative characters (Table 1; Bogarín and Pupulin, 2010).

Although extensive efforts to produce molecular analyses have clarified higher taxonomic levels of Orchidaceae (reviewed in Chase et al., 2015), the majority of Neotropical genera remain unstudied at the species level. *Campylocentrum* constitutes an appropriate model to reveal biogeographic patterns in this area, as it is a widespread genus.

The previously published phylogenetic analyses (Carlsward et al., 2003; 2006a; Neubig et al., 2009) included only a few species of *Campylocentrum*. Therefore, a more comprehensive and well-supported molecular analysis is needed to provide a robust background to study the evolution of traits and the systematics of the group. The main goals of this study are: 1. provide a phylogenetic tree based on both nuclear (ribosomal ITS and low-copy *Xdh* exon) and plastid (*matK* exon, *rpl32-trnL* spacer, *trnL* intron *trnL-F* spacer, and *ycf1* exon) DNA data; 2. establish a new infrageneric classification for *Campylocentrum*; 3. estimate the divergence times of its clades, and relate these dates to events in Earth history and; 4. produce a likelihood-based biogeographical analysis to reconstruct ancestral areas of distribution and estimate the dispersal, vicariance and peripheral isolation events that may have occurred.

## **2. Material and methods**

### *2.1. Taxon sampling*

This study includes samples for 30 of the 70 recognized species of *Campylocentrum* (Carlsward, 2014a; Kolanowska and Szlachetko, 2013; Pessoa and Alves, 2015; Pessoa and Alves, 2016a, 2016b), with a total of 55 samples, which includes all habits in the genus and all taxonomic sections proposed by Cogniaux (1906). Multiple accessions were used for fourteen species with wide distributions to encompass their putative morphological and genetic variation. Outgroups were chosen based on Carlsward et al. (2003, 2006a) and Szlachetko et al. (2013) and included three species of the Neotropical sister genus *Dendrophylax* in addition to three representatives

of the African *Angraecum s.l.* (*Angraecoides*, *Dolabrifolia* and *Humblotiangraecum sensu* Szlachetko et al., 2013), with a total of nine samples in the outgroup (Appendix A).

Samples were obtained during fieldwork except for two herbarium specimens and some living collections (all dried and stored in silica gel) in addition to DNA samples of specimens available from the DNA Bank at the University of Florida, which were used to produce sequences of the additional markers used in this study (*rpl32-trnL*, *Xdh*, *ycf1*). The sequences of *Campylocentrum* previously published by Carlswald et al. (2003, 2006a) and available in GenBank (ITS, *matK* and *trnL* intron and *trnL-trnF* spacer) were also included, although we have corrected the taxonomic names used in that study.

## 2.2. DNA extraction, amplification, and sequencing

DNA was extracted following a CTAB “mini-extraction” procedure (Doyle and Doyle, 1987, 1990). Total DNA was then purified using QIAquick silica columns (QIAGEN Ltd., Crawley, UK).

The primers of Sun et al. (1994) were used to amplify the internal transcribed spacer region (ITS1 + 5.8S rDNA + ITS2). Amplifications were performed in a volume of 25  $\mu$ l, with 12.5  $\mu$ l of DreamTaq Green Master Mix (Thermo Fisher Scientific, Leicestershire, UK), 4  $\mu$ l of TBT-PAR, 0.5  $\mu$ l of DMSO, 6.0  $\mu$ l nuclease free water, 0.5  $\mu$ l of each primer mix (10  $\mu$ M) and 1  $\mu$ l of template DNA (30-90 ng/ $\mu$ l). The reaction conditions were: initial denaturation of 94  $^{\circ}$ C for 1 min, followed by 30 cycles of 94  $^{\circ}$ C for 1 min, 48  $^{\circ}$ C for 1 min and 72  $^{\circ}$ C for 90 s, and a final extension of 72  $^{\circ}$ C for 4 min.

The low copy nuclear gene xanthine dehydrogenase (*Xdh*) was amplified using primers X551 and X1591 of Górnjak et al. (2010). Amplifications were performed in the same volume and using the same reagents as ITS. The PCR program followed the touchdown procedure proposed by the authors: initial denaturation of 94  $^{\circ}$ C for 2 min, followed by six cycles of 94  $^{\circ}$ C for 45 s, 55 - 49  $^{\circ}$ C (reducing 1  $^{\circ}$ C per cycle) for 45 s and 72  $^{\circ}$ C for 90 s, then 28 cycles of 94  $^{\circ}$ C for 45 s, 49  $^{\circ}$ C for 45 s and 72  $^{\circ}$ C for 90 s, and a final extension of 72  $^{\circ}$ C for 5 min.

The plastid spacer *rpl32-trnL* was amplified with the primers UAG and F of Shaw et al. (2007); the *trnL* intron and *trnL-F* spacer were amplified as one fragment with the primers c and f or separately in some cases with the pairs e/f and c/d of

Taberlet et al. (1991). Portions of the plastid *matK* gene were amplified using the primers 5R and XF of Ford et al. (2009). Portions of the plastid *ycfI* gene were amplified with the primers 3720F and 5500R and the internal IntF and IntR of Neubig et al. (2009). Amplification of the five plastid regions was performed in a volume of 25  $\mu$ l containing 12.5  $\mu$ l of DreamTaq Green Master Mix, 4  $\mu$ l of TBT-PAR, 6.5  $\mu$ l nuclease free water, 0.5  $\mu$ l of each primer mix (10  $\mu$ M), and 1  $\mu$ l of template DNA (30-90 ng/ $\mu$ l).

The PCR program used to amplify *rpl32-trnL* and *trnL-F* (both intron and spacer) was: initial denaturation step of 80 °C for 5 min, followed by 30 cycles of 95 °C for 1 min, 50 °C for 1min and 65 °C for 4 min, and a final extension of 65 °C for 5 min. Amplification of *matK* had an initial denaturation step of 94 °C for 1 min, followed by 35 cycles of 94 °C for 30 s, 46–48 °C for 40 s and 72 °C for 40 s, and a final extension of 72 °C for 5 min. Amplification of *ycfI* was carried out using a touchdown protocol following Neubig et al. (2009): 94 °C for 3 min, followed by eight cycles of 94 °C for 30 s, 60 to 52° C (reducing 1 °C per cycle) for 1 min and 72 °C for 3 min, then 30 cycles of 94 °C for 30 s, 50°C for 1 min and 72 °C for 3 min, and a final extension of 72 °C for 3 min.

All PCR products were purified using the QIAquick PCR purification kit (Qiagen, Crawley, UK) following the manufacturer's protocol. Amplifications from DNA of herbarium specimens collected less than five years ago were all successful.

Cycle sequencing was carried out using Big Dye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Inc., ABI, Warrington, Cheshire, UK) using the same primers as the amplifications. The reaction mix for the nuclear markers contained 1.5  $\mu$ l of 5 $\times$  sequencing buffer, 0.25  $\mu$ l of Big Dye terminator, 0.75  $\mu$ l of 10  $\mu$ M primer (1.5 pmol), 1-2  $\mu$ l of amplified product (30-90 ng/ $\mu$ l), 0.2  $\mu$ l of DMSO, and 1.3  $\mu$ l of H<sub>2</sub>O, in a total of 5  $\mu$ l reaction volume. The reaction mix for the plastid markers contained 1.5  $\mu$ l of 5 $\times$  sequencing buffer, 0.25  $\mu$ l of Big Dye terminator, 0.75  $\mu$ l of 10  $\mu$ M primer, 1-2  $\mu$ l of amplified product (30-90 ng/ $\mu$ l), and 1.5  $\mu$ l of H<sub>2</sub>O, in a total of 5  $\mu$ l reaction volume. The cycle sequencing program consisted in 25 cycles of denaturation of 94 °C for 15 s, annealing of 50 °C for 5 s and elongation of 60 °C for 4 min. The cycle sequencing products were sequenced on an ABI 3720 automated DNA sequencer according to the manufacturer's protocol. Chromatograms were edited and contigs assembled using Geneious 8.0.4 (Biomatters Ltd., New Zealand).

### 2.3. Phylogenetic analysis

Sequences were aligned initially using Geneious 8.0.4 (Biomatters Ltd., New Zealand), and a second alignment was carried out using MUSCLE (Edgar, 2004), which was subsequently manually optimized. Independent sequence matrices were compiled for each DNA region, including the sequences from GenBank. In order to observe significant conflicts between independent DNA data matrices, congruence was estimated by looking for well-supported incongruent clades among the phylogenetic trees obtained for each of the regions separately. All plastid regions were treated as a single matrix, whereas the two nuclear regions, ITS and *Xdh*, were analyzed separately.

Bayesian inference (BI) and maximum parsimony (MP) analyses were performed for combined data set using, respectively, MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) on the CIPRES Science Gateway portal (Miller et al., 2010), and PAUP 4.0b10 (Swofford, 2002). *Angraecum leonis* (A. sect. *Humblotiangaecum* Schltr.) was selected as the single outgroup based on the previous phylogenetic studies of Carlswald et al. (2006a) and Szlachetko et al. (2013).

The MP analyses were performed via heuristic searches using 40,000 random taxa additions and tree bisection reconnection (TBR) branch swapping. Bootstrap percentages (BP) were estimated with 1,000 non-parametric replicates and TBR swapping. Clades with BP  $\geq$  85 and 0.95 posterior probability (PP; Cummings et al. 2003, Simmons et al. 2004) were considered well supported (Erixon et al., 2003).

The best-fitting nucleotide substitution model for BI were selected using JModelTest 0.1.1 (Posada, 2008) under the Bayesian information criterion (BIC; Brown and Lemmon, 2007). The most appropriate models for each region were TrNef+G for nrITS, TrN+G for *Xdh*, TPM1uf+G for *matK*, TPM1uf for *rpl32-trnL*, TPM1uf+G for *trnL-F*, and TVM+G for *ycf1* (Appendix B). The best model was adapted for the options available at MrBayes 3.1. and partitioned by region (see Appendix B).

BI included two independent runs with four chains each with the Markov Chain Monte Carlo (MCMC) parameters set to 20 million generations with sampling each 10.000<sup>th</sup> tree. We discarded as burn-in the first ten thousand sampled trees. Convergence between the two independent runs was checked using Tracer 1.6 (Rambaut et al., 2013).

### 2.4. Time divergence estimates and biogeographical analysis

Due the lack of orchid fossils assigned to closely related species of subtribe Angraecinae (Iles et al., 2015), we built a phylogenetic tree including five additional species of orchids (Appendix S1) that represent the major clades between Angraecinae and the closest available fossil genus (*Earina*; Conran et al., 2009). This matrix included only the nuclear region ITS and two plastid regions, *matK* and *ycf1*, due to the unavailability of the remaining regions included in this study in GenBank for the additional five species. One specimen per species of *Campylocentrum* and *Dendrophylax* was included, except for two widespread species, *C. fasciola* and *C. pachyrrhizum*, for which were included two specimens to represent the whole distribution range based on the phylogenetic results (Fig.1).

Absolute divergence times were estimated with a relaxed-clock Bayesian approach in BEAST 1.8.0 (Drummond et al., 2012) on CIPRES. A relaxed molecular clock analysis with uncorrelated log-normal model was performed, which takes into consideration rate heterogeneity between lineages with substitution rates uncorrelated across the tree (Drummond et al., 2006), allowing the mutation rate to vary among partitions. We used BEAUti 1.8 to create input files, assigning the same best-fitting models used for BI (appendix B), and constraints in topology were applied as necessary (Drummond et al., 2012) to match the topology of subfamily Epidendroideae in Freudenstein and Chase (2015) and the topology found for the species of *Campylocentrum* in the previous results (Fig.1). The tree speciation prior followed the Yule Process, and two MCMC chains were run for 100 million generations sampling every 10,000<sup>th</sup> generations. Convergence and mixing were assessed using the effective sampling size criterion (ESS > 200) in Tracer 1.6, and post-burnin of trees was performed with TreeAnnotator 1.8 (Drummond and Rambaut, 2007) to obtain a maximum clade credibility tree with mean values and 95% confidence intervals for nodal ages.

Three nodes were calibrated (see Fig. 2,  $\alpha$ ,  $\beta$  and  $\gamma$ ). Both primary and secondary calibrations were applied in BEAST. Only one fossil, *Earina fouldenensis*, from the early Miocene (23–20 ma) of New Zealand was used (Conran et al., 2009), and it was assigned a log-normal prior distribution (Fig. 2,  $\alpha$ ). In addition, we used two secondary calibrations obtained from Givnish et al. (2015): the divergences of the Angraecinae + Aeridinae clades from their sister clade in tribe Vandaeae ( $21.21 \pm 4.2$  ma) and

Angraecinae and Aeridinae ( $13.25 \pm 4$  ma), which were both assigned normal prior distributions (Fig. 2,  $\beta$ ,  $\gamma$ ).

The biogeographic history of *Campylocentrum* was analyzed using the likelihood-based dispersal-extinction-cladogenesis (DEC) model implemented in LAGRANGE 20151128 (Ree et al., 2005; Ree and Smith, 2008), calculating global extinction and dispersal rates and ancestral range reconstructions for each node in the maximum clade credibility tree obtained from Beast, excluding the five additional orchid species added for calibration purposes.

The distribution of the genus and related genera was split into seven operational areas (Fig. 3) adapted from Morrone (2014): Sub-Saharan Africa (G), Antillean sub-region (A), Brazilian dominion (D), Chacoan dominion (E), Mesoamerica dominion (B), Pacific dominion (C), and Parana dominion (F). Species distribution ranges (presence/absence) included a maximum of three areas per species except for two widespread species, *C. fasciola* and *C. pachyrrhizum*, which included two specimens from the extremes of their distributions.

We performed a stratified model that contained two time slices (TS): TSI (11-7 ma, Tortonian to Late Miocene) reflecting the presence of a large lake in the Amazon basin (the Acre System), and TSII (7-0 ma, Late Miocene to present) capturing the final drainage of Acre System forming the modern Amazon and Orinoco Basins (Figure 3), (Hoorn et al., 2010). For each TS, a different matrix of bidirectional dispersal rates reproducing the geographical connectivity among the areas was applied (Viruel et al., 2015) (Appendix S2).

### 3. Results

#### 3.1. Molecular datasets

This study produced 318 new sequences for *Campylocentrum* and related genera (Appendix A), which were combined with 57 previously published sequences (Carlsward et al., 2003, 2006a) with their species names adjusted in line with current taxonomic concepts. All six analyzed regions were generated for all accessions except for nine; five of them lack only *Xdh*, but none lacks more than one sequence. The complete matrix has a total of 6,128 bp, of which 782 (12.7%) were potentially parsimony informative. ITS (20.1% of positions), *trnL-F* (15.1%) and *ycfI* (17.4%)

were the most informative. Due its greater length (1729 bp aligned), *ycf1* provided the greatest absolute number of informative sites (301; Appendix B).

### 3.2. Phylogenetic relationships

In the parsimony analysis, the complete dataset produced 16 most parsimonious trees, length 1997 steps with a consistency index (CI) = 0.75 and retention index (RI) = 0.90. Analyses performed separately for each region show similar indices (Appendix B).

The BI and MP trees obtained from all data combined provided similar topologies (Fig. 1, supplementary material, Fig. S1). Most relationships among clades were similar as well to the combined plastid dataset (supplementary material, Fig. S4); however, the independent nuclear analyses (ITS and *Xdh*) were less resolved (supplementary material, Fig.S2-S3). The most congruent topology among all analyses resolved both *Campylocentrum* (BP 100, PP 1.00) and *Dendrophylox* (BP 97, PP 1.00) as sister clades (Fig. 1). Successively diverging from the base are *Angraecum moandense* (BP 100, PP 1.00), *A. distichum* (BP 100 %, PP 1), and *A. leonis*. When performed separately, the *Xdh* and ITS analyses show *A. moandense* in a polytomy with *Campylocentrum* and *Dendrophylox*, so consequently these nuclear regions did not identify the Neotropical clade (*Campylocentrum* + *Dendrophylox*) observed with the plastid regions (supplementary material, Fig. S2, S3 and S4).

Two major clades occur within *Campylocentrum* (A and B), both strongly supported in the combined BI and MP trees (BP 100, PP 1.00). A similar strongly supported topology is observed in the ITS, *Xdh* and plastid (combined) trees (Fig. 1-2, supplementary material, Fig. S2, S3 and S4). However the ITS analysis did not produce a monophyletic *Campylocentrum*; clades A and B fall in a polytomy with *Dendrophylox* and *A. moandense* (supplementary material, Fig. S2).

Clade A comprises *C.* sect. *Campylocentrum* as sister of *C.* sects. *Dendrophylopsis* + *Pseudocampylocentrum* in the combined BI tree, a result also observed in the plastid tree (Fig. 1, supplementary material, Fig. 1 and 4), but the *Xdh* and ITS (individual) trees make these into polytomies (supplementary material, Fig. 2–3). Although section *Campylocentrum* has a high PP (0.98) with all data combined, in the combined MP analysis it is split in two clades along a polytomy: one includes *C. calostachium*, *C. serranum* and *C. ulaei* (BP 100, PP 1.00) and other with the remaining species (BP 92, PP 1.00). Among these two clades in the same polytomy is also *C.*



sects. *Dendrophylopsis* + *Pseudocampylocentrum* with a moderate to strong support (BP 83, PP 0.99; Fig. 1, supplementary material, Fig. S1). Conversely, the plastid tree provides good resolution for *C.* sect. *Campylocentrum* with a strong support in both BI and MP (BP 97, PP 1.00; supplementary material, Fig. S4).

Clade B includes two new sections described in Appendix C, *C.* sects. *Levigatum* and *Teretifolium*, both strongly supported in the combined BI and MP (BP 99, PP 1.00 and BP 100, PP 1.00, respectively; Fig. 1, supplementary material, Fig. S1). Both sections are also highly supported in the plastid tree (BP 99, PP 1.00 and BP 100, PP 1.00, respectively; supplementary material, Fig. S4). The ITS and *Xdh* trees include only *C.* sect. *Teretifolium* as monophyletic with good support (BP 88, PP 1.00 and BP 86, PP 1.00, respectively) (supplementary material, Fig. S2–S3).

The datasets used in this study were not able to clarify relationships among taxa within *C.* sect. *Teretifolium*, except for *C. sellowii* as sister to the rest of this clade (BP 100, PP 1.00), which is internally unresolved due to low genetic variation. A similar topology is provided by the plastid combined tree (supplementary material, Fig. S4).

### 3.3. Dating and Biogeography

The divergence time between African *Angraecum moandense* and the Neotropical clade formed by *Campylocentrum* and *Dendrophyllax* was estimated to the late Miocene at 8.53 million years ago (mya; 95% HPD = 10.7–6.4 mya). The ancestral area reconstruction suggests a first long-distance dispersion from Africa (G) to the Antilles (A) in the Neotropics (node 3, probability = 0.7, Fig. 2-3). The ancestor of *Campylocentrum* and *Dendrophyllax* was most probably restricted to the Antilles (A), and the estimated split for these two genera was almost contemporary with the previous node, 8.21 mya (95% HPD = 10.5–5.9 mya), supporting a hypothesis of rapid divergence after colonization of the Neotropics (node 4, prob. = 0.61, Fig. 2-3).

The most recent common ancestor (MRCA) of *Campylocentrum* had a possible disjunct distribution between the Antilles (A) and Parana (F), suggesting a second long-distance dispersal (A→F; node 7, prob. = 0.2, Fig. 2-3). Clades A (*C.* sect. *Campylocentrum* + *C.* sect. *Dendrophylopsis* + *C.* sect. *Pseudocampylocentrum*) and B (*C.* sect. *Laeligatum* + *C.* sect. *Teretifolium*) also diverged in Late Miocene, 7.22 mya (95% HPD = 9.2–5.2 mya), with a subsequent dispersal and expansion to the Chacoan dominion (E) and Central America (B), respectively (node 8, prob. = 0.4, and node 20,

prob. = 0.26, Fig. 2-3). Both clades start their diversification in the late Miocene/Pliocene, 2.9 mya (95% HPD = 4.2–1.7 mya) and 5.38 mya (95% HPD = 6.79–3.97 mya), respectively (nodes 8 and 20, Fig. 2-3).

Divergence of the MRCA of *C.* sects. *Dendrophylopsis* + *Pseudocampylocentrum* was likely 4.79 mya (95% HPD = 6.1–3.48 mya), and it was most probably distributed exclusively in Central America (B), the case as well for the MCRA of these sections separately. The wide distribution of some species in these sections was probably reached in the Pleistocene (node 21, prob. = 0.43, and node 22, prob. = 0.47, Figs. 2-3).

Within *C.* sect. *Campylocentrum* two main clades diverged also in the Late Miocene/Pliocene due to vicariance, 5.16 mya (95% HPD = 6.6–3.7 mya; node 27, prob. = 0.42, Figs. 2-3), one clade formed by *C. calostachium*, *C. serranum* and *C. ulaei* with origin in Parana (F), and a MRCA from 2.69 mya (95% HPD = 3.8–1.6 mya; node 28, prob. = 0.96, Fig. 2-3), and the second clade with a MCRA from 4.28 mya (95% HPD = 4.6–2.32 mya) originating in Central America (B), after which it diversified rapidly in the Pleistocene (node 30, prob. = 0.35, Fig. 2-3). In clade B, the MRCA of both *C.* sects. *Laevigatum* and *Teretifolium* also had an estimated origin and diversification in the Pleistocene, 1.76 (95% HPD = 2.7–0.8 mya) and 2.04 (95% HPD = 2.9–1.18 mya), respectively, mainly in Parana (F) (node 9, prob. = 0.83, and node 13, prob. = 0.46, Fig. 2-3).

Low resolution in reconstructing distributions in the terminal clades of *C.* sect. *Dendrophylopsis* and “*C. micranthum* complex” were observed due the wide distribution of the species and poor sampling of the leafless species. Only the original area is known at this point and considering the putative subsequent expansions, more detailed studies focused on these groups might provide a better understanding of their evolutionary history. Divergence times, 95% HDP and ancestral areas with their probabilities for all tree nodes are presented in Appendix D.

## 4. Discussion

### 4.1. Phylogenetic relationships

Phylogenetic analysis of the combined data provides good resolution for the majority of clades, which allowed us to discuss and define with a high level of

confidence some taxonomic groups. The results support the African *Angraecum moandense* (cited as *A. chevalieri* by Carlswald et al., 2006; see Pessoa & Alves 2016c; *A. sect. Angraecoides sensu* Garay, 1973, or genus *Angraecoides sensu* Szlachetko et al., 2013) as sister to the Atlantic clade (*Campylocentrum*+*Dendrophylax*; Carlswald et al., 2006a; Szlachetko et al., 2013). *Angraecum sect. Angraecoides* includes species mainly distributed in West Tropical Africa (Govaerts et al., 2016) and is characterized by an often one-flowered inflorescence, green to greenish-yellow flowers and cylindrical or clavate spurs (Garay, 1973). Their flower morphology resembles that of *Dendrophylax* (e.g. *D. barrettiae*), although their leafy habit is similar to species of *Campylocentrum* (e.g. *C. crassirhizum* Hoehne).

*Campylocentrum* and *Dendrophylax* are demonstrated to be monophyletic, as first shown by Carlswald et al. (2003, 2006a). Despite the shared leafless condition, the genera are easily distinguished by their inflorescence arrangement, mainly many-flowered with flowers densely and distichously arranged in *Campylocentrum* in contrast to few-flowered, loosely and not distichously arranged in *Dendrophylax*. They can also be recognized as distinct from their African relatives by their tiny flowers with a similar morphology among species *versus* larger flowers and morphologically variable among species, respectively (Carlswald, 2014a, 2014b). Inflorescence structure and flower size can be considered as synapomorphies for *Campylocentrum* in subtribe Angraecinae.

This study presents the first phylogenetic analysis of *Campylocentrum* including a representative sampling of its morphological diversity and distribution. Within the genus, two major clades are strongly supported (A and B). Both were also present in Carlswald et al. (2003). However, this previous study included only six species, of which samples of *C. stenanthum* were misidentified as *C. micranthum*, *C. robustum* and *C. schiedei*. For clade B, those authors used three samples including *C. jamaicense* misidentified as *C. micranthum*, and *C. crassirhizum* as *C. lansbergii*. The lack of a generic revision is the main reason for this misinterpretation of species identities. Pessoa et al. (2015) and Pessoa and Alves (2015a, b) studied “*C. micranthum*”, which was recognized as a “nomenclatural complex” requiring new combinations, re-establishments of some old names and re-circumscription of most species.

The majority of vegetative and floral features traditionally used in taxonomic treatments in the genus (Cogniaux, 1906; Todzia, 1980; Bogarín and Pupulin, 2010;

Pessoa and Alves, 2016a; Pessoa and Alves, 2016b) are here considered homoplastic, consequently having limited use. However, the capsule surface morphology clearly distinguishes clade A (6-ribbed capsule) from clade B (non-ribbed). A non-ribbed capsule is accepted here as the synapomorphy for clade B, whereas a 6-ribbed capsule is a symplesiomorphy for clade A since it is similar to those of *Dendrophylax* and *Angraecum*.

Clade A is widespread in the Neotropics and composed of the three sections proposed by Cogniaux (1906). The sister of the rest of this clade, *C.* sect. *Campylocentrum*, is the most diverse section in the genus. This section includes species with conduplicate leaves and elongate stems, and its circumscription *sensu* Cogniaux (1906) is found not to be monophyletic. It is re-circumscribed here, excluding species with non-ribbed capsules (clade B). The section with this new circumscription is highly supported in the combined BI analysis as well as in MP and BI for the plastid data. However, it is not supported in the combined MP analysis, a result of the polytomy including the *C. ulaei* group (*C. calostachium*, *C. serranum* and *C. ulaei*).

Three strongly supported major subclades are recognized in *C.* sect. *Campylocentrum*. Sister to the rest is the *C. ulaei* group, endemic to Parana (F) and characterized by relatively longer inflorescences. Its sister is mainly distributed outside Parana (F, except for *C. micranthum*) and is split into two subclades. The first one (*C. tenellum*, *C. brenesii*) has species from the Antilles (A), Central America (B) and the Pacific dominions (C). The other is the *C. micranthum* complex (Pessoa et al., 2015) that includes seven species sampled here with relatively shorter and congested inflorescences.

Within the *C. micranthum* complex, *C. huebneri* + *C. mattogrossense* are sister to the rest, which includes the other five species sampled. One of the latter is *C. schiedei*, the type species of the genus. Among *C. panamense*, *C. micranthum*, *C. kuntzei* and *C. stananthum*, there is a clear difference in spur morphology; *C. huebneri* has the longest spur in the genus (1.0-2.0 cm long vs. 0.2–0.6 cm long), and *C. mattogrossense* has a straight spur (*vs.* commonly slightly curved to inflexed in the other species; Pessoa and Alves, 2015). The concept of *C. micranthum* has been widely and incorrectly applied (Pessoa and Alves, 2015; Pessoa et al., 2015; Bogarín and Pupulin, 2010), and these results support some of the proposed names in the complex,

although many others were not included in this study. A broad study of the group is required to a better understand the species boundaries.

*Campylocentrum* sect. *Campylocentrum* is sister to a clade formed by *C.* sects. *Dendrophylopsis* + *Pseudocampylocentrum*. The leafless species of *Campylocentrum* are included in *C.* sect. *Dendrophylopsis*, and it is also distinguished by having the viscidium comprised of a single part (Pessoa and Alves, 2016b) and roots with thicker cell walls found in the endovelamen, exoderm and endoderm (Pessoa et al., 2017). All these features are unique for species of the section and are considered synapomorphies. Two subclades occur in this section, one formed by *C. grisebachii* + *C. pachyrrizum* and characterized by the apex of the anther cap rounded or truncate and a second one with *C. fasciola* + *C. tyrridion* that has a bilobed anther cap (Pessoa and Alves, 2016b). Both clades are supported in the BI analyses but not by MP.

Monospecific *C.* sect. *Pseudocampylocentrum* morphologically resembles species placed in this study in *C.* sect. *Teretifolium* (clade B) based on its cylindrical leaves and granulose root surface. Although externally similar, the root surface is composed of unicellular absorbent hairs, whereas in *C.* sect. *Teretifolium* the roots have tufts of epivelamen (Pessoa et al., 2017). Terete leaves seem to be an adaptive convergence and are also found in other genera in Angraecinae (e.g. *Nephrangis* and *Solenangis*). Our results confirm that leaflessness and terete leaves are homoplastic, arising more than once in the subtribe (Carlsward et al., 2006a; Pessoa et al., 2016a).

Clade B is almost restricted to Parana (F), except for *C. jamaicense* endemic to the Antilles. It includes *C.* sects. *Laevigatum* and *Teretifolium*, both strongly supported and characterized by non-ribbed capsules. *Campylocentrum* sect. *Teretifolium* is distinguished from its sister by having cylindrical leaves and granulose to tuberculate root surfaces. Although a taxonomic treatment exists for the group (Pessoa and Alves, 2016a), relationships among its species are still poorly resolved. Our study was unable to disentangle it, except to recognize *C. sellowii* as sister to the other four representative species included. Low interspecific genetic divergence probably reflects rapid and recent diversification producing lack of resolution (Snak et al., 2016; Vatanparast et al., 2011; Liu et al., 2016; Maravi et al., 2013).

Two species of *C.* sect. *Laevigatum* have been previously considered synonyms of *C. micranthum* (*C.* sect. *Campylocentrum*), *C. brevifolium* and *C. jamaicense*. Both

are similar in habit, especially their conduplicate leaves with asymmetrically bilobed apices, as observed in the majority of genera in Angraecinae. However, contrary to expectation, species of these sections are not closely related in the tree. *Campylozentrum* sect. *Laevigatum* is distinguished mainly by non-ribbed capsules in contrast to 6-ribbed in *C.* sect. *Campylozentrum*. It also differs by roots with  $\ominus$ -thickened cell walls in the exoderm instead of  $\cap$ -thickened as in other species of the genus (Pessoa et al., 2017). Although only two species have been anatomically analyzed, *C. jamaicense* by Carlswald et al. (2006b) and *C. crassirhizum* by Pessoa et al. (2017), this character is suggested here as a possible synapomorphy for the section.

*Campylozentrum* sect. *Laevigatum* has two subclades. One of them is *C. pauloense* + *C. spannagelii* + *C. densiflorum* + *C. brachycarpum*, all four endemic to southern Parana (F, northern Argentina, southern Brazil and Paraguay). *Campylozentrum brachycarpum* and *C. densiflorum* represent in this study the *C. organense* group (*organense* absent from this study) characterized by relatively large, ovate floral bracts that cover all or most of the ovary (vs. relatively shorter and deltoid in other leafy species).

The second subclade includes *C. neglectum* + *C. robustum* + *C. crassirhizum* + *C. jamaicense*, mainly distributed in the Atlantic Forest and the South American “dry diagonal” (E, formed by caatinga, cerrado and chaco vegetation *sensu* Prado and Gibbs, 1993, the Chacoan domain), except for *C. jamaicense*, which occurs in the Antilles. *Campylozentrum crassirhizum* and *C. jamaicense*, in spite of their large disjunction, are similar morphologically and have been distinguished only by the spur length. Our analyses did not provide a clear understanding of the relationship between these species. The two accessions of *Campylozentrum crassirhizum* did not fall together, the one from southeastern Brazil is sister to the other accession from northeastern Brazil plus the specimens of *C. jamaicense*. However, this topology is not supported by MP, and more studies including population genetics will be important to understand the relationships of these two species.

#### 4.2. Divergence time and biogeography

The MRCA of *A. moandense* and the Neotropical genera of Angraecinae arrived in the Antilles (A) during the late Miocene (ca. 8.53 mya; Fig. 3). A relatively recent trans-Atlantic long-distance dispersion event like that is also cited for *Pitcairnia*

*feliciana*, Bromeliaceae (ca. 9.3 Ma; Givnish et al., 2011), and *Maschalocephalus*, Rapateaceae (ca. 7.3 Ma; Givnish et al. 2004). However, for these two species the migration events occurred in the opposite direction from that proposed here for Angraecinae and were not followed by diversification (Givnish et al., 2004, 2011). Moreover, although it occurred much earlier in the Oligocene/Miocene (ca. 35 Ma), the papaya family (Caricaceae) is a good example of an African taxon that experienced a radiation in Neotropics (Carvalho and Renner, 2012; Christenhusz and Chase, 2013). Carvalho and Renner (2012) suggested that the ancestor of the group arrived first in the Antilles, in agreement with the results here for Angraecinae.

In the Antilles (A), divergence of *Campylocentrum* and *Dendrophyllax* (ca. 8.22 mya) was almost concomitant with dispersal of their MRCA from Africa (ca. 8.53 Ma). The MRCA of *Campylocentrum* reached Parana (F) through a second long-distance dispersal also in late Miocene (ca. 7.22 mya; Fig. 3). According to Pound et al. (2011) in this subepoch a portion of the present northern coast of Brazil (Maranhão and Piauí states) was inundated. The authors indicated that, based on a data/model biome reconstruction, the ancient coast was covered by tropical evergreen forests. It is possible that the MRCA of *Campylocentrum* arrived in that region instead of the coast of the Guyanas, which even though closest to the Antilles was covered at that time by tropical savannas. The once flooded area and the ancient coast were probably where the ancestor arrived first in South America and are currently occupied by cerrado and caatinga vegetation (Chacoan dominion *sensu* Morrone, 2014). Extinction events caused by climate and consequently vegetation changes could explain the current absence of the genus in this area.

In the Pliocene, clade A expanded its distribution from the Antilles (A) to Mesoamerica (B) and clade B from Parana (F) to Chacoan dominion (E). In both cases, they were followed by a radiation, originating by peripheral isolation events the five main clades recognized in the genus (here considered as *C.* sects. *Campylocentrum*, *Dendrophyllaxis*, *Laevigatum*, *Pseudocampylocentrum* and *Teretifolium*; Fig. 3). According to Turchetto-Zolet et al. (2013), climate changes and orogenic events with consequent changes in the drainage systems and vegetation (Salzmann et al., 2008) occurred in Pliocene and contributed to shaping the current diversity of plant lineages in the Neotropics. In this region, several taxonomic groups exhibited diversification in this epoch, including bellflowers (Campanulaceae; Lagomarsino et al., 2016), tank-epiphytic

bromeliads (Givnish et al., 2011, 2014), some Fabaceae such as *Chamaecrista* ser. *Coriaceae* (Rando et al., 2016), *Platymiscium* (Saslis-Lagoudakis et al., 2008) and *Carnivalia* (Snak et al., 2016), the orchid subtribe Stanhopeinae (Givnish et al., 2015) and Solanaceae subtribe Physalinae (Zamora-Tavaraes et al., 2016).

Central America (B) was an important center of origin for some clades of *Campylocentrum*, especially those in clade A. During the Pliocene, sections *Campylocentrum* (in part, ca. 4.28 mya, node 30, except for the *C. ulaei* group), *Dendrophylopsis* (ca. 4.06 mya), and *Pseudocampylocentrum* (ca. 4.79 mya) expanded their distributions from this area followed by radiations (Fig. 3). Orogenic events occurring in Pliocene, such as the definitive closure of Isthmus of Panama (Knowlton and Weigt, 1998; although other authors have stated recently that it was earlier, Montes et al., 2015) and volcanism (Mann, 2007; Vogel et al., 2006; Weinberg, 1992) seem to be relevant to the diversification of these groups in the area.

Nevertheless, Parana (F) was the center of origin for *C. sect. Teretifolium* (ca. 1.76 mya) and part of *C. sect. Laevigatum* (node 17, ca. 1.23 mya), with evidence of in-situ diversification in the Pleistocene. The *C. ulaei* group (clade A, *C. sect. Campylocentrum*) is also endemic to Parana (F). It diverged from its sister by a vicariant event (B/F) in the early Pliocene, and the species diverged during the Plio-Pleistocene, which matches groups in clade B (Fig. 3). Pleistocene climatic fluctuations (Behling and Negrelle, 2001) played an important role in speciation in Parana (F), as argued by Hooghiemstra and van der Hammern (1998). At that time, the glacial and interglacial periods may have resulted in successive fragmentation and expansion of forests, promoting allopatric and parapatric speciation, also termed as refuge theory (Haffer, 1969; Prance, 1973).

The climatic fluctuations that occurred in Pleistocene were also important in evolution of the *C. micranthum* complex (clade A, *C. sect. Campylocentrum*). It experienced an extensive radiation with expansion of its distribution from Mesoamerica (B), Pacific (C) and Brazil (D), ranging to the Antilles (A), Chacoan (E) and Paraná dominions (F) in the last one million years (Fig. 3). Kolanowska (2015) in a study of ecological niche modeling for two species of the *C. micranthum* complex in the last glacial maximum, although with a restricted approach, indicated the presence of several refugia for the group in the Mesoamerica (B) and Pacific (C), a result confirmed by our study. Similar rapid diversification in the last one million years was experienced by



some Andean clades of Campanulaceae (Lagomarsino et al., 2016) and Brazilian saxicolous *Chamaecrista* ser. *Coriaceae* (Rando et al., 2016). However, these were not followed by range expansion, and their diversity more likely arose in situ.

## 5. Conclusions

Phylogenetic reconstruction of *Campylocentrum* confirmed it as monophyletic in its current circumscription. It is composed of two major clades, one that includes the three sections previously proposed by Cogniaux (1906) and the second with two new sections, *C. sects. Laevigatum* and *Teretifolium*, recognized in this study (these species had been included previously in *C. sect. Campylocentrum*). Although the majority of the morphological characters are here considered homoplastic, the two main clades included in the genus are distinguished by their capsules (6-ribbed vs. non-ribbed, respectively). The sections are recognized only by sets of features, except for *C. sect. Dendrophyloopsis* that exhibits clear synapomorphies such as leaflessness, one-parted viscidia, and roots with endovelamen, exoderm and endoderm cell walls thicker than those in the leafy species.

The divergence time analysis and ancestral distribution reconstruction indicated that *Campylocentrum* is relatively young and arose in late Miocene. Its most recent common ancestor probably had a disjunct distribution between the Antilles and Paraná dominions. During the Pliocene, the five sections of the genus had already diverged and expanded their distributions to Mesoamerican, Chacoan, Pacific and Brazilian dominions. Climatic fluctuations in the Pleistocene played an important role in spurring radiation, especially in the sections of clade B in Parana (F) and the *C. micranthum* complex (clade A) in the Mesoamerican, Pacific and Brazilian dominions. Therefore, the evolutionary history of *Campylocentrum* confirms the importance of orogenic events occurring in the Pliocene as well as climatic fluctuations in Pleistocene for diversification in the Neotropics.

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**Table 1.** Sections of *Campyloctrum sensu* Cogniaux (1906) and their main vegetative features.

	<b>Roots</b>	<b>Stem</b>	<b>Leaves</b>
<i>C. sect. Campyloctrum</i>	smooth/granulosae	elongated	conduplicate/terete and developed
<i>C. sect. Dendrophyloopsis</i>	smooth	reduced	absent
<i>C. sect. Pseudocampyloctrum</i>	granulosae	elongated	terete and reduced

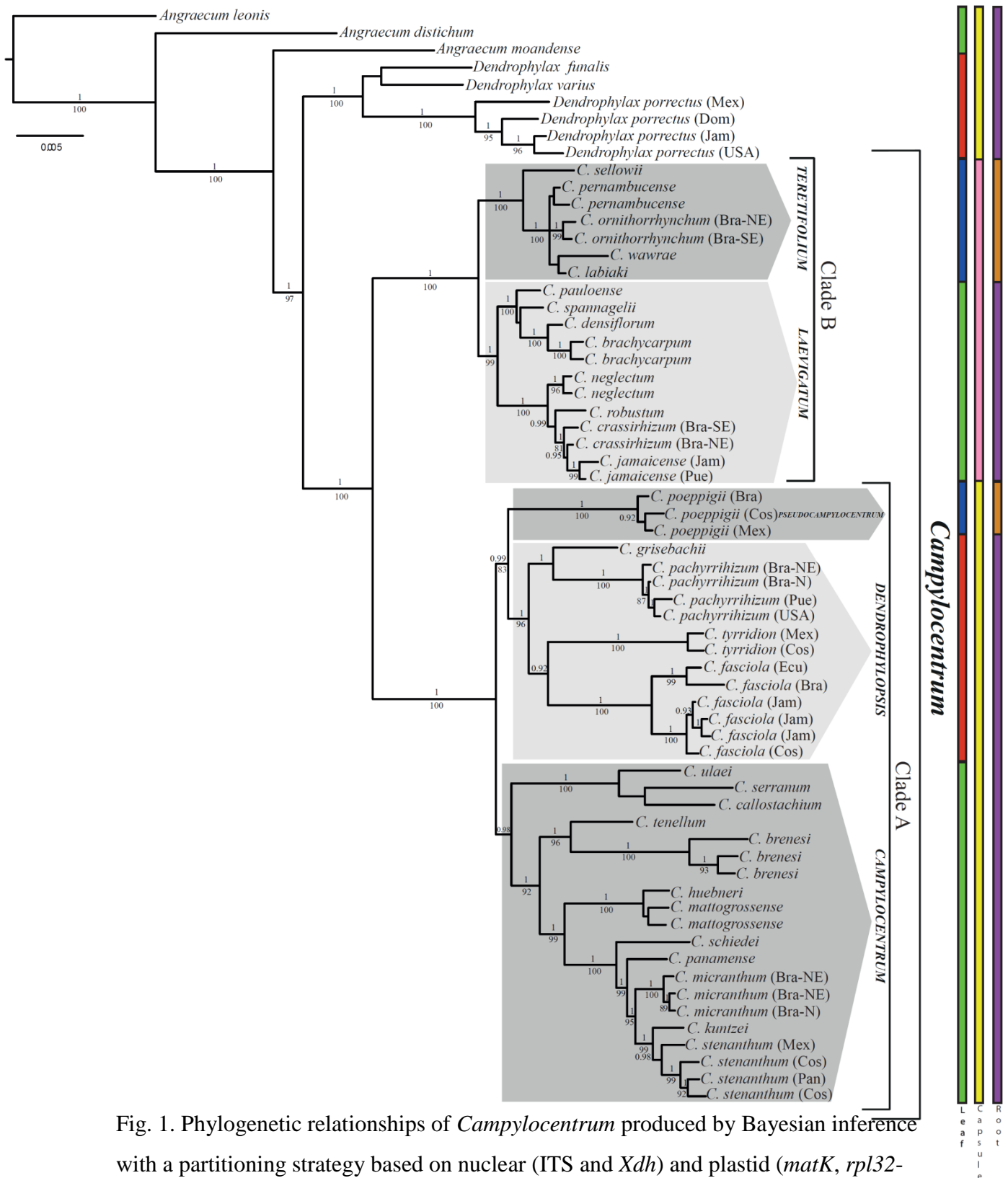


Fig. 1. Phylogenetic relationships of *Campylocentrum* produced by Bayesian inference with a partitioning strategy based on nuclear (ITS and *Xdh*) and plastid (*matK*, *rpl32-trnL*, *trnL-F*, *ycf1*) regions combined. Posterior probabilities ( $\geq 0.9$ ) are indicated above branches and maximum parsimony bootstrap percentages ( $\geq 80$ ) are indicated below branches. Lateral bars: green – leaves conduplicate; red – leafless; blue – leaves cylindrical; yellow – capsules 6-ribbed; pink – capsules non-ribbed; purple – roots smooth; orange – granulose.



Fig. 2. Divergence time estimates for *Campylocentrum* and related genera based on nuclear ITS, and plastid *matK* and *ycf1* performed with BEAST. Bars represent 95% highest posterior density (HPD) estimates. The asterisk indicates a fossil calibration ( $\alpha$ ), diamonds indicates secondary calibrations,  $\beta$  = divergence of the clade Angraecinae+Aeridinae within the tribe Vandeae;  $\gamma$  = divergence of subtribes Angraecinae and Aeridinae. A geological timescale is placed at the top, vertical discontinuous grey lines separate two time slices (TSI–TSII) used in the biogeographical analysis.

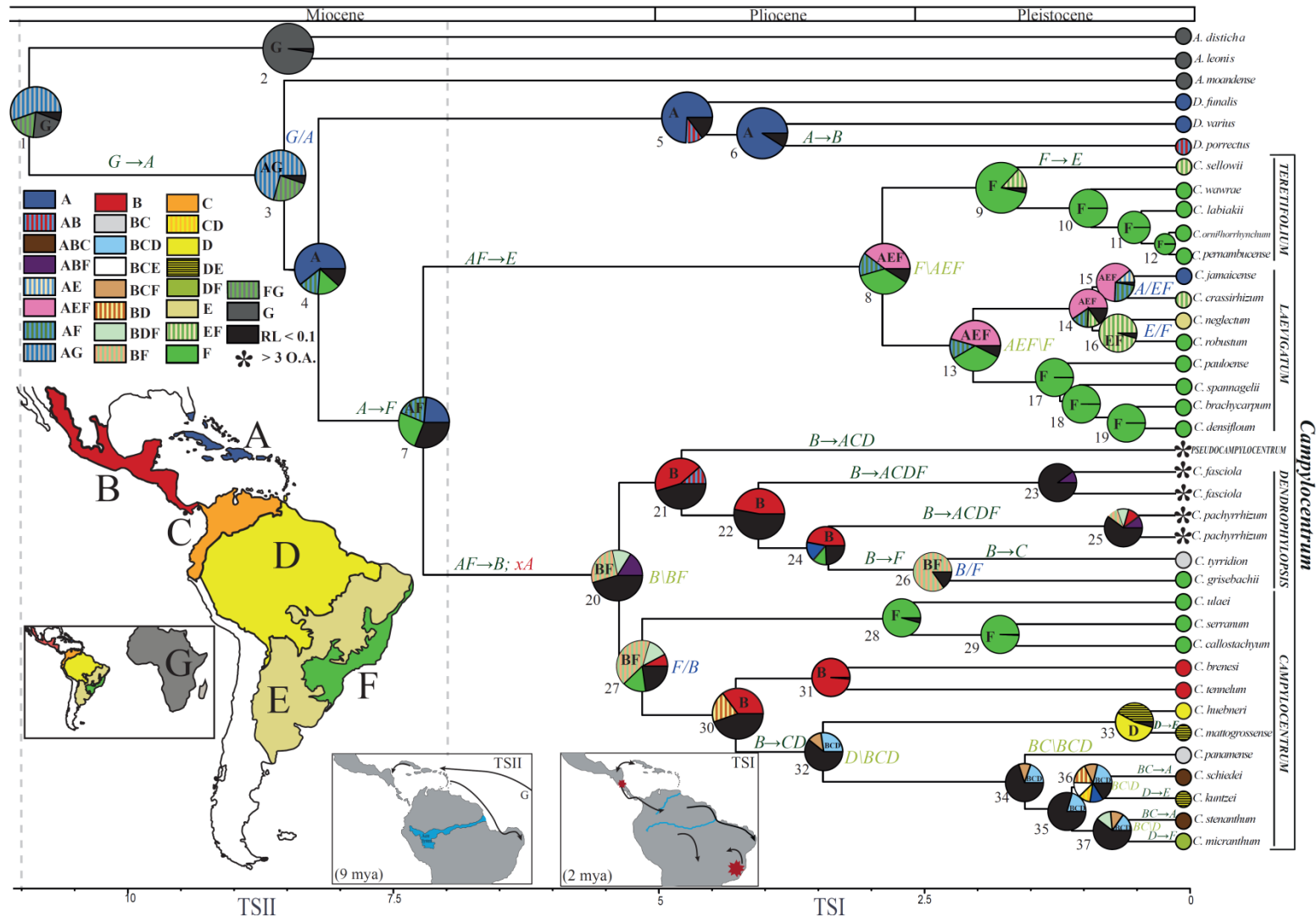
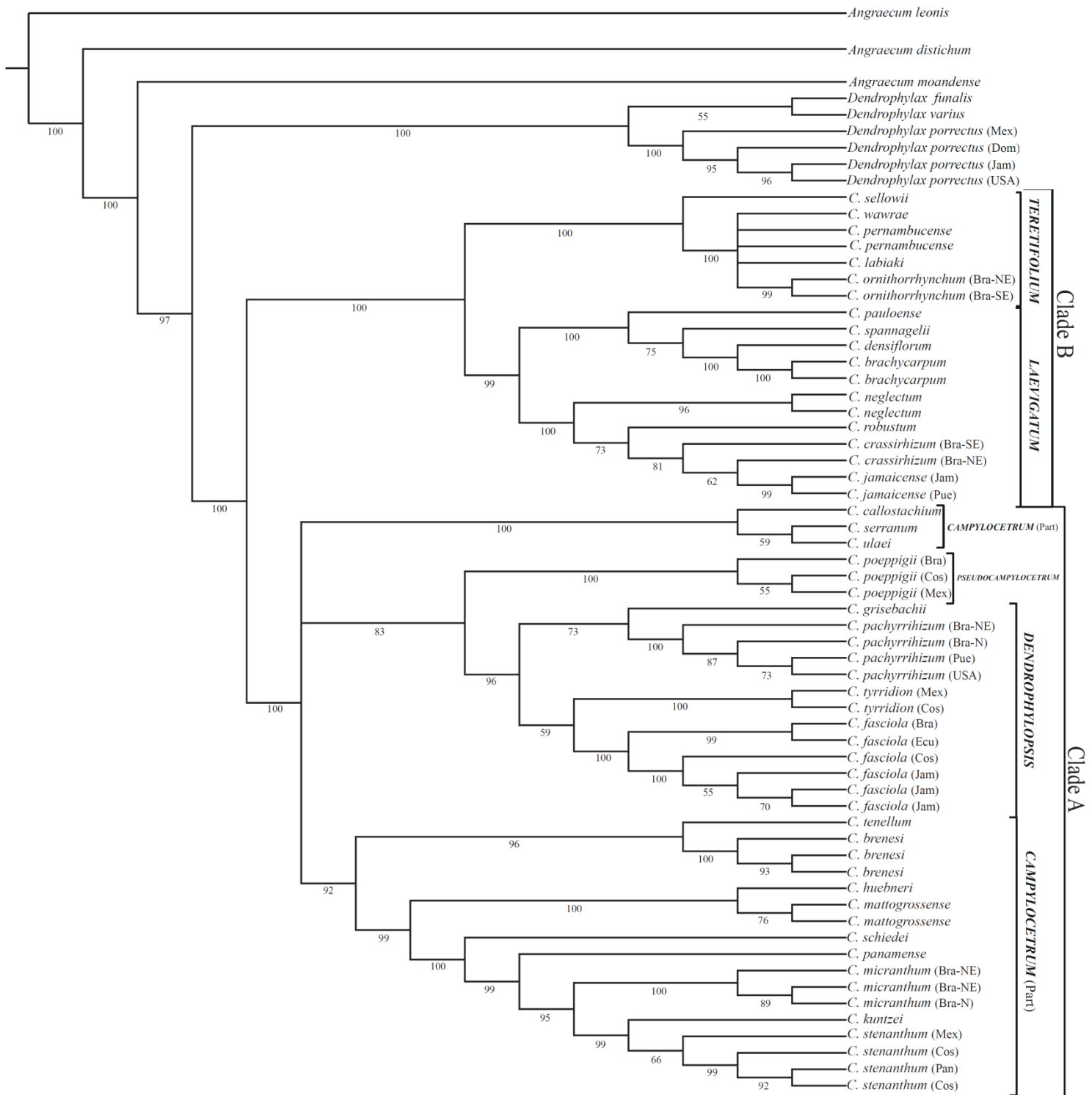
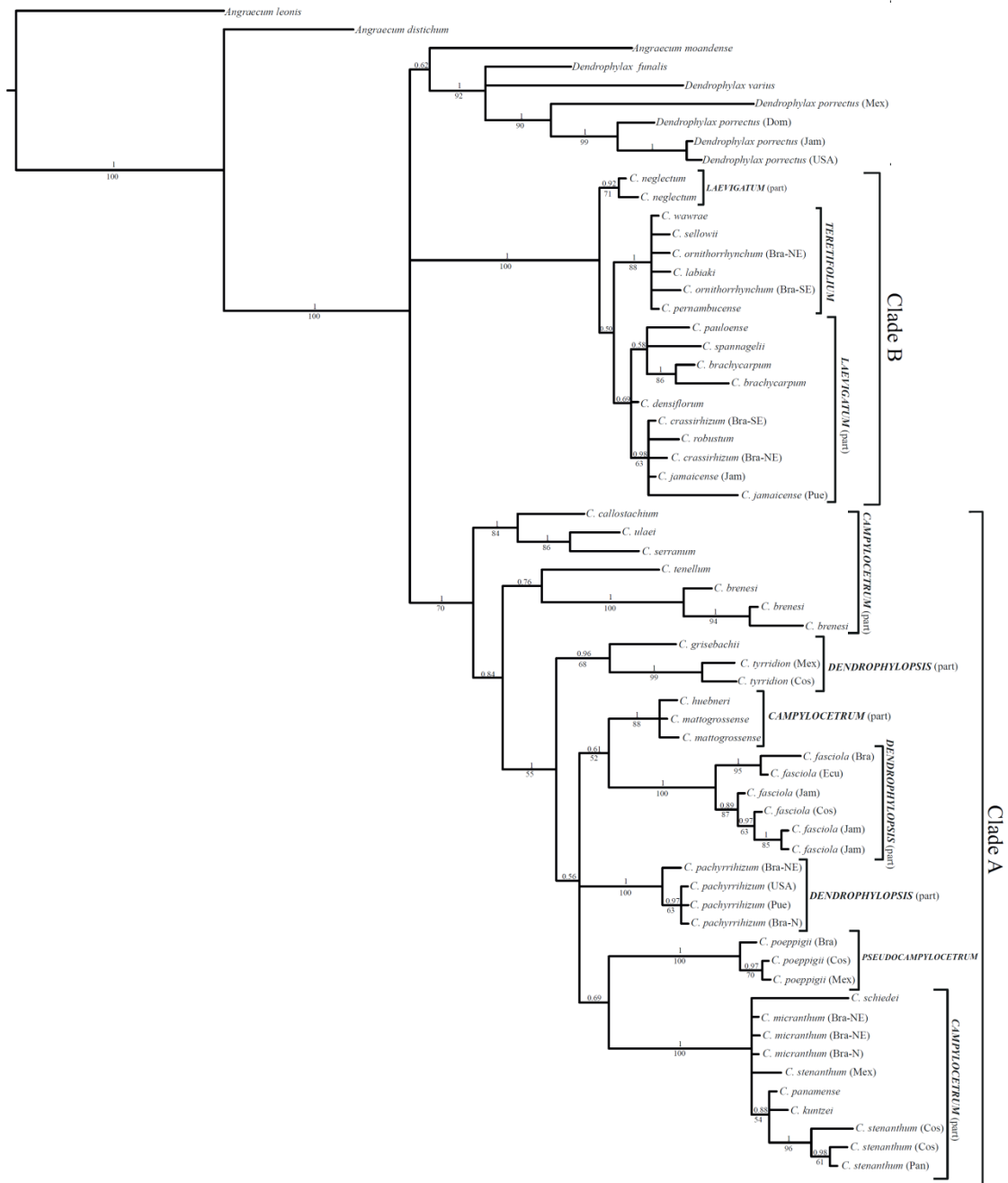


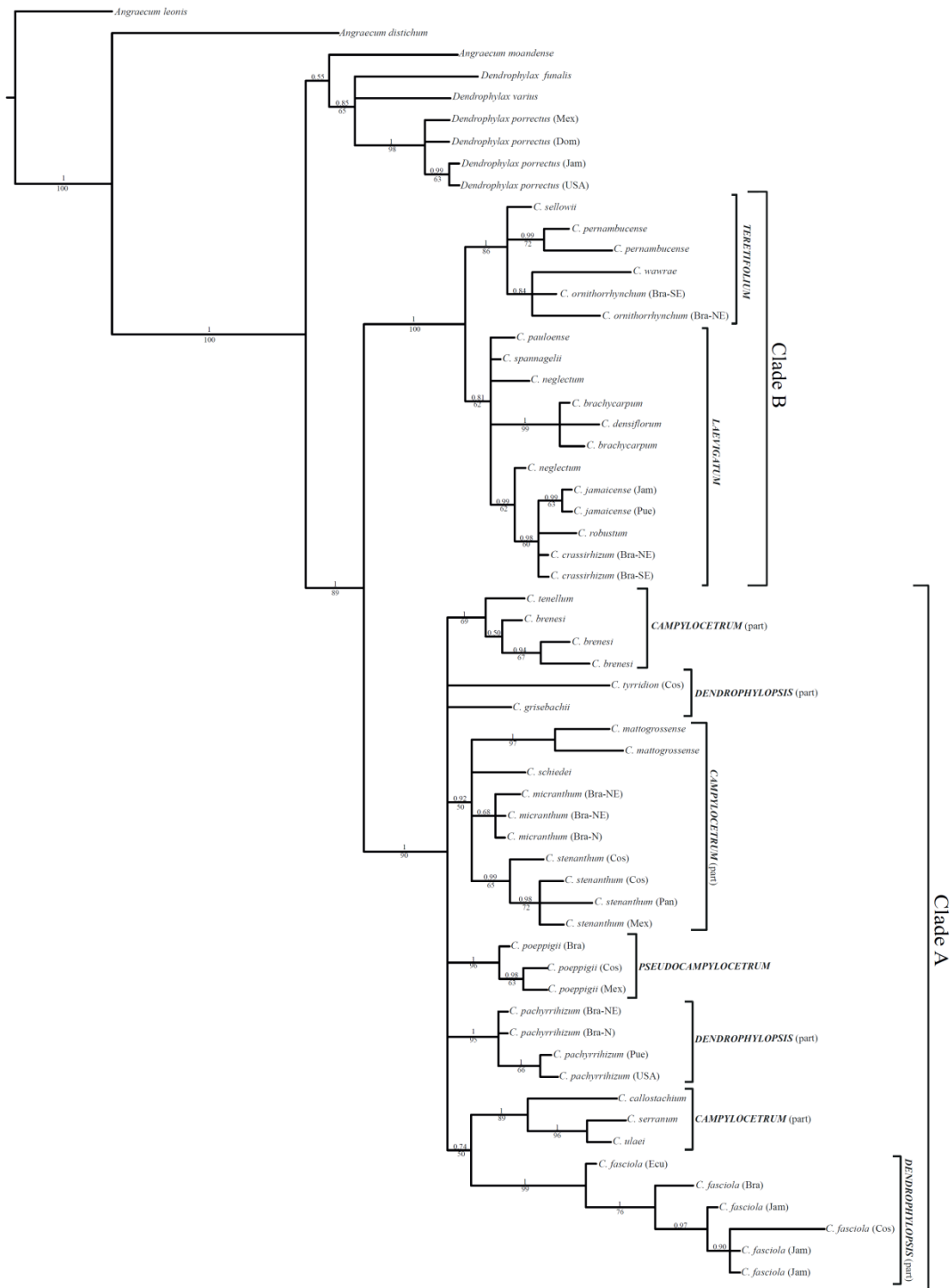
Fig. 3. Ancestral area reconstruction inferred by LAGRANGE. Pie charts at nodes indicate the probabilities of ancestral areas, when lower than 0.1 where combined in the “remainder” category (black sections). A = Antillean sub-region; B = Mesoamerica dominion; C = Pacific dominion; D = Brazilian dominion, E = Chacoan dominion; F = Parana dominion; G = Africa. A geological timescale is placed at the top, node numbers are indicated below branches. Vertical discontinuous grey lines separate two time slices (TSI = 7–0 Ma and TSII = 7–11 Ma), inset maps represent the Palaeogeographical configuration of the Neotropical region and Amazon Basin in these time slices. Inferred dispersal ( $X \rightarrow Y$ ), vicariance ( $X/X$ ) and peripheral isolated speciation ( $X \setminus Y$ ) events are represented also in the tree.



Supplementary Fig. 1. Strict consensus tree from MP analysis based on nuclear (ITS and *Xdh*) and plastid (*matK*, *rpl32-trnL*, *trnL-F*, *ycf1*) regions combined (length = 1997 steps, CI = 0.75 and RI = 0.90). Numbers below the branches are bootstrap percentages ( $\geq 50$ ).

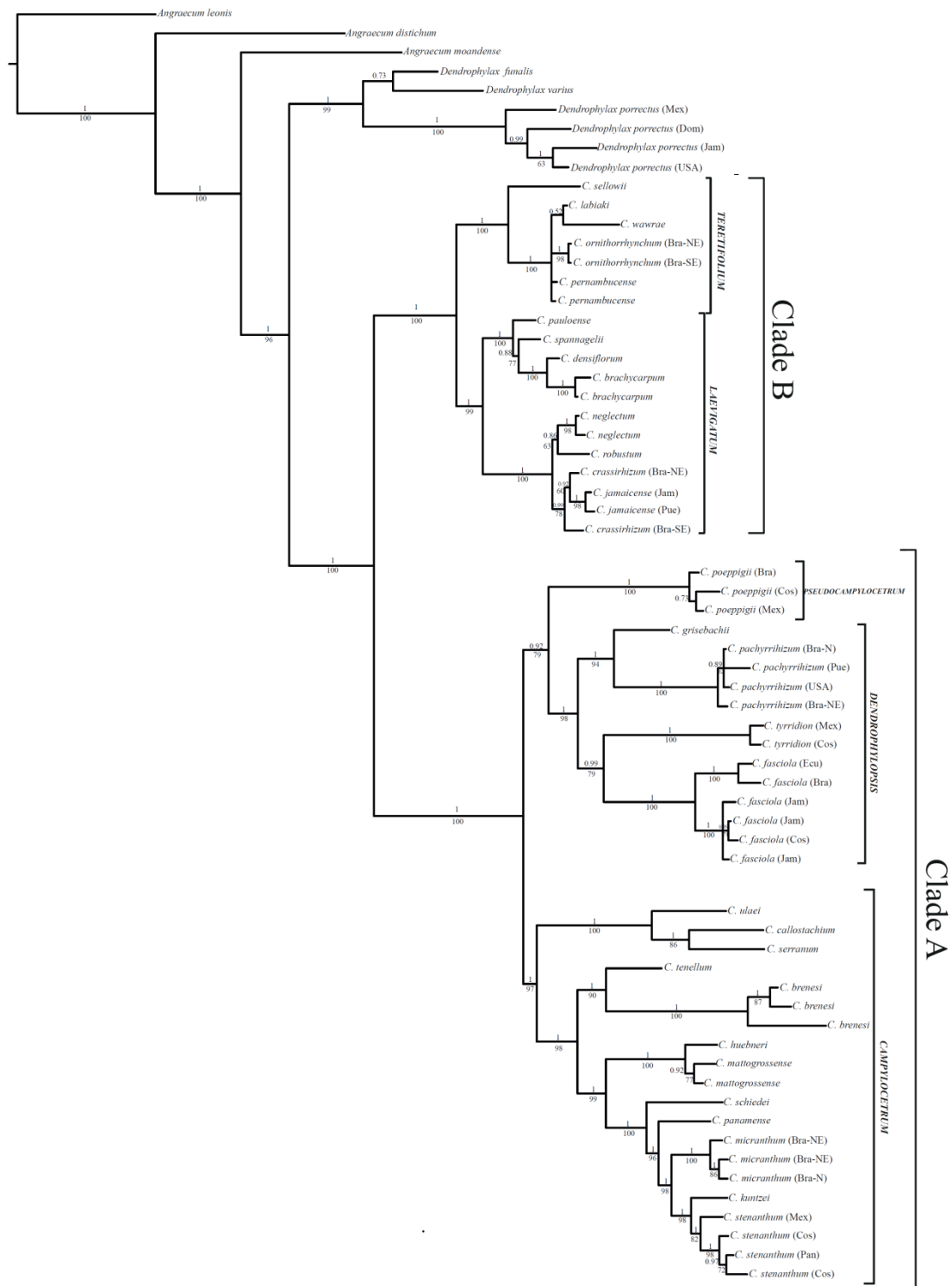


Supplementary Fig. 2. Phylogenetic relationships of *Campylocentrum* obtained by Bayesian inference based on ITS. Posterior probabilities ( $\geq 0.5$ ) are indicated above branches, and maximum parsimony bootstrap percentages ( $\geq 50$ ) are indicated below branches.



Supplementary Fig. 3. Phylogenetic relationships of *Campylocentrum* obtained from a Bayesian inference based on *Xdh*. Posterior probabilities ( $\geq 0.5$ ) are indicated above branches, and maximum parsimony bootstrap percentages ( $\geq 50$ ) are indicated below branches.





Supplementary Fig. 4. Phylogenetic relationships of *Campylocentrum* obtained from by Bayesian inference with a partitioning strategy based on combined plastid regions (*matK*, *rpl32-trnL*, *trnL-F*, *ycf1*). Posterior probabilities ( $\geq 0.5$ ) are indicated above branches, and maximum parsimony bootstrap percentages ( $\geq 50$ ) are indicated below branches.

Taxon	Voucher Origin: Collector (Herbarium)	Markers					
		ITS	XDH	matK	rpl32-trnL	trnL-F	ycf1
<i>Angraecum distichum</i> Lindl.	Garden origin (Cal-Orchid): B. Carlsward 237 (FLAS)						
<i>Angraecum leonis</i> Rchb.f.	Garden Origin: B. Carlsward 390 (FLAS)						
<i>Angraecum moandense</i> de Wild.	Garden origin (Selby Botanical Gardens): B. Carlsward 208 (FLAS)	AF506320*		AF506363*		AF506339*	
<i>Campylocentrum brachycarpum</i> Cogn.	Brazil, Espírito Santo: E. Pessoa 1191 (UFP)						
<i>C. brachycarpum</i> Cogn.	Brazil, São Paulo: Orquidário do Estado - LZ53 (SP)						
<i>C. brenesi</i> Schltr.	Costa Rica: M. Blanco 2139 (USJ)						
<i>C. brenesii</i> Schltr.	Costa Rica: D. Bogarin 11119 (CR)						
<i>C. brenesii</i> Schltr.	Costa Rica: D. Bogarin 6363 (CR)						
<i>C. callostachium</i> (Barb.Rodr.) Cogn.	Brazil, São Paulo: M.R. Miranda 02 (UFP)						
<i>C. crassirhizum</i> Hoehne	Brazil, Sergipe: E. Pessoa 1243 (UFP)						
<i>C. crassirhizum</i> Hoehne	Brazil, Espírito Santo: E. Pessoa 1192 (UFP)						
<i>C. densiflorum</i> Cogn.	Brazil, Santa Catarina: E. Pessoa 1196 (UFP)						
<i>C. fasciola</i> (Lindl.) Cogn.	Jamaica, Claude Hamilton: B. Carlsward 301 (FLAS)	DQ091564*		DQ091321*		DQ091445*	
<i>C. fasciola</i> (Lindl.) Cogn.	Brazil, Mato Grosso: A.P. Beneli 966 (UFP)						
<i>C. fasciola</i> (Lindl.) Cogn.	Jamaica: M. Witten 711						
<i>C. fasciola</i> (Lindl.) Cogn.	Jamaica, Claude Hamilton: B. Carlsward 185 (FLAS)	AF506294*		AF506342*		AF147226*	
<i>C. fasciola</i> (Lindl.) Cogn.	Costa Rica: D. Bogarin 10415 (CR)						
<i>C. fasciola</i> (Lindl.) Cogn.	Ecuador: M. Witten 1933	AF506295*		AF506343*			

	(QCNE)					
<i>C. grisebachii</i> Cogn.	Brazil, Minas Gerais: E. Pessoa 1188 (UFP)					
<i>C. huebneri</i> Mansf.	Brazil, Roraima: E. Pessoa 701 (UFP)		n.s.			
<i>C. jamaicense</i> (Rchbf. ex Griseb.) Benth. ex Fawc	Jamaica: M. Witten 1934 (FLAS)	AF506299*		AF506348*		AF506326*
<i>C. jamaicense</i> (Rchbf. ex Griseb.) Benth. ex Fawc.	Puerto Rico: D. Ackerman 3341 (UPRRP)	AY147219*		AF506325*		AF506346*
<i>C. kuntzei</i> Cogn. ex Kuntze	Paraguay, Guairá: G. Esser 14519 (HEID)		n.s.			
<i>C. labiakii</i> Pessoa & Alves	Brazil, Espírito Santo: J. Meireles 545 (ESA)					
<i>C. mattogrossense</i> Hoehne	Brazil, Mato Grosso: A. P. Beneli 968 (UFP)					
<i>C. mattogrossense</i> Hoehne	Brazil, Pará: A. K. Koch 566 (SP)					n.s.
<i>C. micranthum</i> (Lindl.) Maury	Brazil, Roraima: E. Pessoa 1001 (UFP)					
<i>C. micranthum</i> (Lindl.) Maury	Brazil, Permambuco: E. Pessoa 1062 (UFP)					
<i>C. micranthum</i> (Lindl.) Maury	Brazil, Ceará: E. Pessoa 1115 (UFP)					
<i>C. neglectum</i> (Rchb.f. & Warm.) Cogn.	Brazil, Distrito Federal: E. Pessoa 1278 (UFP)					
<i>C. neglectum</i> (Rchb.f. & Warm.) Cogn.	Brazil: B. Carlswald 272 (FLAS)	AF506297*		AF506345*		AF506324*
<i>C. ornithorrhinchum</i> (Lindl.) Rolfe	Brazil, Permambuco: E. Pessoa 1239 (UFP)					
<i>C. ornithorrhinchum</i> (Lindl.) Rolfe	Brazil, São Paulo: RR18135					
<i>C. pachyrrhizum</i> (Rchb.f.) Rolfe	Brazil, Sergipe: E. Pessoa 1245 (UFP)					
<i>C. pachyrrhizum</i> (Rchb.f.) Rolfe	Brazil, Pará: A.K. Koch 565 (SP)					
<i>C. pachyrrhizum</i> (Rchb.f.) Rolfe	USA, Florida: No voucher			AF506349*		AF506327*
<i>C. pachyrrhizum</i> (Rchb.f.) Rolfe	Puerto Rico: D. Ackerman s.n. (UPRRP)	AF506301*		AF506350*		AF506328*
<i>C. panamense</i> Ames	Costa Rica: D. Bogarin 871 (CR)		n.s.			

<i>C. pauloense</i> Hoehne & Schltr.	Brazil, Santa Catarina: E. Pessoa 1197 (UFP)					
<i>C. pernambucense</i> Hoehne	Brazil, Sergipe: E. Pessoa 1244 (UFP)	n.s.				
<i>C. pernambucense</i> Hoehne	Brazil, Pernambuco: E. Pessoa 1287 (UFP)					
<i>C. poeppigii</i> (Rchb.f.) Rolfe	Brazil, Roraima: E. Pessoa 968 (UFP)					
<i>C. poeppigii</i> (Rchb.f.) Rolfe	Mexico: B. Carlswald 307(FLAS)	AF506302*		AF506351*		AF506329*
<i>C. poeppigii</i> (Rchb.f.) Rolfe	Costa Rica: D. Bogarin 2218 (CR)					
<i>C. robustum</i> Cogn.	Brazil, Minas Gerais: Museu de História Natural 0967 (MHN)					
<i>C. schiedei</i> (Rchb.f.) Benth. ex Hemsl.	Costa Rica: D. Bogarin 494 (CR)					
<i>C. sellowii</i> (Rchb.f.) Rolfe	Brazil, Minas Gerais: E. Pessoa 1189 (UFP)					
<i>C. serranum</i> Pessoa & Alves	Brazil, Pernambuco: E. Pessoa 945 (UFP)					
<i>C. spannagelli</i> Hoehne	Brazil, Rio de Janeiro: E. Pessoa 1195 (UFP)		n.s.			
<i>C. stenanthum</i> Schltr.	Costa Rica: M. Witten 1822 (FLAS)	AF506304		AF506352*		
<i>C. stenanthum</i> Schltr.	Mexico: B. Carlswald 180 (FLAS)	AF506298*		AF506347*		AY147227*
<i>C. stenanthum</i> Schltr.	Panama: B. Carlswald 315 (FLAS)	AY147220*		AY147228*		AY147235*
<i>C. stenanthum</i> Schltr.	Costa Rica: D. Bogarin 1263 (CR)					
<i>C. tenellum</i> Todzia	Costa Rica: D. Bogarin 5844 (CR)					n.s.
<i>C. tyrridion</i> Garay & Dunst. ex Foldats	Mexico: G. Carnevali 5145 (CICY)	AF506305*	n.s.	DQ091322*		DQ091446*
<i>C. tyrridion</i> Garay & Dunst. ex Foldats	Costa Rica: D. Bogarin 1486 (CR)					
<i>C. ulaei</i> Cogn.	Brazil, São Paulo: M.R. Miranda 01 (UFP)					
<i>C. wawrae</i> (Rchb.f. ex Beck) Rolfe	Brazil, Minas Gerais: D. Barbosa 13 (CESJ)		n.s.			
<i>Dendrophyllax funalis</i> (Sw.)	Jamaica: B. Carlswald	AY147221*		AF506355*		AY147229*

Benth. ex Rolfe	302 (FLAS)					
<i>D. porrectus</i> (Rchb.f.) Carlsward & Whitten	Mexico, Yucatán: G. Cernevali 5907 (CICY)	AF506314*		AF506357*		AF506335*
<i>D. porrectus</i> (Rchb.f.) Carlsward & Whitten	USA, Florida: B. Carlsward 329 (FLAS)	AY147223*		AY147237*		AY147232*
<i>D. porrectus</i> (Rchb.f.) Carlsward & Whitten	Dominican Republic: M. Witten 1950 (JBSD)	AY147224*		AY147238*		AY147233*
<i>D. porrectus</i> (Rchb.f.) Carlsward & Whitten	Jamaica: B. Carlsward 184 (FLAS)	Af506315*		Af506358*		AY147231*
<i>D. varius</i> (J.F. Gmel.) Urb.	Dominican Republic: M. Whitten 1960 (JBSD)	AY147222*		AY147236*		AY147230*

## Appendix A

Taxa, voucher information, and Genbank accessions used in this study (previously published sequences are indicated with an asterisk).

## Appendix B

Features of DNA datasets used in this study, and best fit models used to BI for each marker.

	ITS	XDH	<i>matK</i>	<i>rpl32-trnL</i>	<i>trnL-F</i>	<i>ycfI</i>	Plastid combined	All data combined
<b>No. of taxa</b>	63	59	62	64	63	63	64	64
<b>Aligned length</b>	660	908	647	688	1496	1729	4560	6128
<b>No. variable positions</b>	218 (33%)	179 (19.7%)	112 (17.1%)	68 (9.8%)	453 (22.3%)	419 (24.2%)	935 (20.5%)	1326 (21.6%)
<b>No. potentially parsimony informative sites</b>	132 (20.1%)	89 (9.8%)	53 (8.2%)	30 (4.3%)	227 (15.1%)	301 (17.4%)	561 (12.3%)	782 (12.7%)
<b>No. of changes/variable sites</b>	1.66	1.25	1.35	1.13	1.34	1.58	1.47	1.51
<b>Fitch tree length</b>	361	225	151	77	609	664	1374	1997
<b>CI</b>	0.72	0.86	0.82	0.91	0.80	0.72	0.75	0.75
<b>RI</b>	0.90	0.93	0.92	0.95	0.90	0.91	0.90	0.90
<b>Best fit model</b>	HKY+G	HKY+G	GTR+G	GTR	GTR+G	GTR+I+G	-	-

(BI)

## Appendix C

### Taxonomic treatment

#### 1. *Campylocentrum* Benth., J. Linn. Soc. Bot. 18: 337. 1881.

Type species: *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsl. (Basionym: *Angraecum schiedei* Rchb.f.; originally published as *Todaroa micrantha* A. Richard & Galeotti).

*Todaroa* A. Rich. & Galeotti, Ann. Sci. Nat. Bot. 3: 28. 1845. *nom. illeg.* [non *Todaroa* Parl. Hist. Nat. îles Canaries 2: 155. 1843. Apiaceae (= Umbelliferae)].

Type species: *Todaroa micrantha* A. Rich. & Galeotti, *nom. illeg.*

##### 1.1. *Campylocentrum* sect. *Campylocentrum* Cogn. in Mart., Fl. bras. 3(6): 504.

1906.

Type species: *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsl.

This widespread section is characterized by leafy species, with roots cylindrical and smooth, leaves conduplicate and capsules 6-ribbed. It includes half of the genus (ca. 35 species).

##### 1.2. *Campylocentrum* sect. *Dendrophylopsis* Cogn. in Mart., Fl. bras. 3(6): 504.

1906.

Type species: *Campylocentrum fasciola* (Lindl.) Cogn., designated by Pessoa & Alves (2016).

This widespread section includes the leafless species with roots dorso-ventrally flattened or cylindrical, and always smooth, leaves reduced to achlorophylated scales, and capsules 6-ribbed. It is composed by 13 species.

##### 1.3. *Campylocentrum* sect. *Laevigatum* E. Pessoa & M. Chase, *sect. nov.*

Type species: *Campylocentrum brevifolium* (Lindl.) E. Pessoa & M. Alves, Kew Bull. 70: 43. 2015.

Similar to *C.* sect. *Campylocentrum* but differs by its not ribbed capsules (*vs.* 6-ribbed).

This section is almost restricted to Eastern South America, except to *C. jamaicense* from the Antilles, it includes leafy species, with roots cylindrical and smooth, leaves conduplicate and capsules not ribbed. It is composed by 15 species.

**1.4. *Campylocentrum* sect. *Pseudocampylocentrum*** Cogn. in Mart., Fl. bras. 3(6): 504. 1906.

Type species: *Campylocentrum poeppigii* (Rchb.f.) Rolfe.

This monospecific section is distributed in the Antilles, Central America and Northern South America. The only taxon recognized so far is a leafy species, with roots cylindrical and minutely granulosae, leaves terete and capsules 6-ribbed.

**1.5. *Campylocentrum* sect. *Teretifolium*** E. Pessoa & M. Chase, *sect. nov.*

Type species: *Campylocentrum ornithorrhynchum* (Lindl.) Rolfe, Orchid Review 11: 246. 1903.

Similar to *C. sect. Pseudocampylocentrum* but differs by its roots's surface granulosae composed by tufts of epivelamen (*vs.* composed by unicellular absorbent hairs), and not ribbed capsules (*vs.* 6-ribbed).

This section is endemic to Eastern South America, it includes leafy species, with roots cylindrical and minutely granulosae to tuberculate, leaves terete and capsules not ribbed. It is composed by seven species.

## Appendix D

Divergence time estimates and ancestral areas for nodes indicated in the figures 2-3.

HPD = highest posterior density; A = Antillean sub-region; B = Mesoamerica dominion; C = Pacific dominion; D = Brazilian dominion, E = Chacoan dominion; F = Parana dominion; G = Africa.

Node	Ages (Mya)		Ancestral areas	
	Mean	95% HPD	Area	Probability
1	10.93	13.7–8.2	G	0.21
2	8.47	11.4–5.6	G	0.97
3	8.53	10.7–6.4	AG	0.70
4	8.21	10.5–5.9	A	0.61
5	4.7	6.7–2.7	A	0.74
6	4.01	6.0–2.1	A	0.91
7	7.22	9.2–5.2	AF	0.20
8	2.9	4.2–1.7	AEF	0.40
9	1.76	2.7–0.8	F	0.83
10	0.93	1.53–0.4	F	1
11	0.46	0.76–0.26	F	1
12	0.2	0.27–0.13	F	1
13	2.04	2.9–1.18	AEF	0.46
14	0.92	1.4–0.44	AEF	0.59
15	0.71	1.07–0.35	AEF	0.63
16	0.64	1.08–0.2	EF	0.95
17	1.23	1.83–0.63	F	1
18	1.04	1.63–0.45	F	1
19	0.56	0.95–0.17	F	1
20	5.38	6.79–3.97	BF	0.26



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21	4.79	6.1–3.48	B	0.43
22	4.06	5.2–2.92	B	0.47
23	1.25	2.0–0.5	ABF	0.1
24	3.4	4.64–2.16	B	0.47
25	0.61	1.2–0.2	ABF	0.1
26	2.4	3.4–1.4	BF	0.84
27	5.16	6.6–3.7	BF	0.42
28	2.69	3.8–1.6	F	0.96
29	1.82	2.7–0.94	F	0.99
30	4.28	5.5–3.06	B	0.35
31	3.29	4.4–2.18	B	0.99
32	3.46	4.6–2.32	BD	0.27
33	0.52	1.0–0.1	D	0.42
34	1.56	2.2–0.92	BCD	0.2
35	1.11	1.7–0.52	BCD	0.21
36	0.81	1.3–0.32	BCD	0.21
37	0.73	1.2–0.26	BCD	0.15

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## Appendix S1

Taxa, voucher information, and Genbank accessions used to the dating analysis in this study (sequences on GenBank but not published yet in papers are indicated with an asterisk, the voucher information is not available).

Taxon	Collector (Herbarium)	Markers		
		ITS	<i>matK</i>	<i>ycf1</i>
<i>Earina autumnalis</i> (G. Forst.) Hook.f.	M. W. Chase O-298 (K)	AF260149	AF263656	none
<i>Cattleya bicolor</i> Lindl.	F.G. Brieger 4333 (ESA)	JN600949	none	JN600718
<i>Cattleya bicolor</i> Lindl.	F.G. Brieger 895 (ESA)	none	EU139961	none
<i>Maxillaria splendens</i> Poepp. & Endl.	W.M. Whitten 2940 (FLAS)	none	none	KF660506
<i>Maxillaria splendens</i> Poepp. & Endl.	S. Koehler 144 (UEC)	DQ210252	DQ210684	none
<i>Cymbidium eburneum</i> Lindl.	J. Luo*	none	KF361650*	KF361650*
<i>Cymbidium eburneum</i> Lindl.	M.W. Chase 1505 (K)	AF470503	none	none
<i>Phalaenopsis wilsonii</i> Rolfe	B. Carlsward 331 (FLAS)	DQ091672	none	EU490763
<i>Phalaenopsis wilsonii</i> Rolfe	TBG 144214*	none	AB217751*	none

## Appendix S2

Palaeogeographical models for dispersal rates across areas implemented in the biogeographical analysis. A = Antillean sub-region; B = Mesoamerica dominion; C = Pacific dominion; D = Brazilian dominion, E = Chacoan dominion; F = Parana dominion; G = Africa.

### Time Slice 1: 11–7 Ma

	A	B	C	D	E	F	G
A	1	0.1	0.1	0.05	0.0001	0.001	0.001
B		1	0.1	0.01	0.0001	0.0001	0.0001
C			1	0.1	0.0001	0.0001	0.0001
D				1	0.1	0.1	0.0001
E					1	0.5	0.0001
F						1	0.001
G							1

### Time Slice 2: 7–0 Ma

	A	B	C	D	E	F	G
A	1	0.5	0.5	0.1	0.005	0.001	0.001
B		1	0.5	0.05	0.001	0.001	0.0001
C			1	0.5	0.01	0.001	0.0001
D				1	0.5	0.1	0.0001
E					1	0.5	0.0001
F						1	0.001
G							1

# CAPÍTULO 4

## Revisões taxonômicas

**Manuscrito 1** – Taxonomic revision of *Campylocentrum* (Orchidaceae–Vandae–Angraecinae): species with terete leaves.

**Systematic Botany 41(3):700-713 (2016).**

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**Manuscrito 2** – Taxonomic revision of *Campylocentrum* sect. *Dendrophylopsis* Cogn. (Orchidaceae–Vandae–Angraecinae).

**Phytotaxa 286(3): 131-152 (2016).**

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**Manuscrito 3** – *Campylocentrum* sect. *Campylocentrum* Cogn. (Orchidaceae–Angraecinae) in Brazil.

**a ser submetido ao periódico Phytotaxa.**

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**Manuscrito 4** – Taxonomic revision of *Campylocentrum* sect. *Laevigatum* E. Pessoa & M. Chase (Orchidaceae–Vandae–Angraecinae).

**a ser submetido ao periódico Phytotaxa.**

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## Taxonomic Revision of *Campylocentrum* (Orchidaceae–Vandaeae–Angraecinae): Species with Terete Leaves

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**Abstract** –This study has the purpose of reviewing the species of *Campylocentrum* with terete leaves. While 15 names have been proposed in the group, here we recognize only six species. Herein, we also describe a seventh new species, *C. labiakii*, which is endemic to the Brazilian state of Espírito Santo. Finally, this study also provides typifications, complete synonymies, conservation statuses, complete descriptions, distribution maps and an identification key to the species in question.

**Keywords**– Atlantic Forest, Brazil, Epidendroideae, Monocots, Neotropics .

*Campylocentrum* Benth. is one of the Neotropical genera belonging to the subtribe Angraecinae (Carlsward 2014) and comprises about 70 species (Govaerts et al. 2015). According to Carlsward et al. (2003), it is a monophyletic group and *Dendrophyllax* Rchb. f. is its sister genus. Together, they form a “Neotropical clade” under the subtribe, composed almost completely by African genera. Recently, the genus *Angraecum* Bory was split into 18 genera, among which *Angraecoides* (Cordem.) Szlach., Mytnik & Grochocka is the most related to the “Neotropical clade” (Szlachetko et al. 2013).

Three sections are recognized within the genus, *C.* sect. *Campylocentrum* Cogn., *C.* sect. *Dendrophyllaxis* Cogn. and *C.* sect. *Pseudocampylocentrum* Cogn. (Cogniaux 1906; Todzia 1980; Bogarín and Pupulin 2010). Phylogenetic studies have shown that among the sections *sensu* Cogniaux (1906), only *C.* sect. *Dendrophyllaxis* (leafless species) and *C.* sect. *Pseudocampylocentrum* [monospecific, including only *C. poeppigii* (Rchb. f.) Rolfe, *sensu* Cogniaux (1906)] are monophyletic groups (Carlsward et al. 2003). *Campylocentrum* sect. *Campylocentrum* (*sensu* Cogniaux 1906) includes species with conduplicate and terete leaves. It is a non-monophyletic group and should be split into two or three sections (Carlsward et al. 2003).

Therefore the species with terete leaves were included in two sections by Cogniaux (1906), which he structured geographically, *C. poeppigii*, in that time, was known only from Cuba, and the other species from the Brazilian Coast. Moreover these species share two important morphological characters, 1. terete leaves and 2. roots with a minutely granulate to densely tuberculate surface (Fig. 1A–G). No species from the Atlantic forest were included in the phylogenetic study performed by Carlsward et al. (2003).

The first discovered member of the group, *C. ornithorrhynchum*, was first placed in *Angraecum* by Lindley (1840), followed by Reichenbach (1850) who described *C. poeppigii* and *C. sellowii* in the same genus. Another two species, *C. parahybunense* and *C. wawrae* were described in *Aeranthus* Lindl. (Barbosa Rodrigues 1882; Beck 1888). Although the genus *Campylocentrum* had been described in 1881 by Bentham, these species remained under other genera for more than 20 years, finally having five names transferred to the genus by Rolfe (1903). *Campylocentrum pernambucense* Hoehne ex Hoehne (1938) was the only new species described since Cogniaux (1906).

The group has a disjunct distribution, with the majority of the species occurring in eastern and southern South America, ranging from northeastern Brazil to northern

Argentina and Paraguay, and one species, *C. poeppigii*, ranging from northern South America to Nicaragua and the Antilles (Barros et al. 2015; Govaerts et al. 2015). The Atlantic Forest is the center of diversity and endemism, where five species are found. Gallery forest in “*cerrado*” vegetation has a few species, while *C. poeppigii* has the widest distribution, growing from the Amazon Basin as far as Central American forests and the Antilles (Barros et al. 2015; Bogarín and Pupulin 2010). A similar disjunct distribution is known in another orchid genus, *Christensonella* Szlach., Mytnik, Górniak & Smiszek (subtribe Maxillariinae), wherein only *Christensonella uncata* (Lindl.) Szlach., Mytnik, Górniak & Smiszek has a wide area of occurrence in northern South America to Mexico, and the other species are endemic to southeastern Brazil to northern Argentina (Koehler et al. 2012). The species are predominantly epiphytes, rarely accidentally saxicolous, growing from sea level to elevations of up to 1,500 m.

Roots with a minutely granulose to densely tuberculate surface (Fig. 1) and terete leaves are the diagnostic characters of the group. However, identification of the species is complex, especially due to overlap in many floral and vegetative characters. After Cogniaux (1906), who included four species, Pabst and Dungs (1977) presented a list of Brazilian orchids, and recognized seven species in the genus. The species concepts adopted by Cogniaux (1906) and Pabst and Dungs (1977) are quite different from that which is followed here and some misunderstandings and mistakes led to confusions in their studies. These misconceptions were previously clarified by Pessoa and Alves (2016).

Considering the taxonomic complexity of the group, this study has a purpose to confirm the species by reviewing all the names proposed earlier, combined with a morphological analysis that examined the geographical extremes of morphological variation. The taxonomic treatment offers a review of 15 names among six accepted species, and a description of a seventh, new species. It also provides an identification key to all seven species and descriptions that include typification, complete synonymy, conservation status, and a distribution map for each species.

## MATERIALS AND METHODS

Principally herbarium samples and live specimens were the basis for the morphological studies. Expeditions were carried out between 2011–2015 in the Brazilian Atlantic Forest and Amazon Basin.

All type materials were examined by the authors. Collected specimens were deposited at UFP with duplicates sent to K, NY, and RB. Specimens from 71 herbaria were analyzed: ALCB, \*AMES, ASE, B, BA, BAF, BHCb, BHZB, BM, BR, C, CEN, CEPEC, CESJ, COR, CR\*, E, EAC, EAN, ESA, \*F, FLOR, FR, FUEL, FURB, G, GOET, HAMAB, HB, HBG, HBR, HEID, HEPH, HRCB, HUEFS, HST, IAC, IAN, IBGE, ICN, INPA, IPA, JPB, K, L, M, MAC, MBML, MG, MIRR, MO, \*NY, P, PEUFR, R, RFA, RB, \*SEL, SP, SPF, U, UB, UEC, UFP, UFRN, UFRR, UPCB, US, VIES, W, and WU; acronyms according to Thiers (2015), [“\*” only images].

The conservation status of each species was defined according to the categories proposed by the IUCN (2015), including field observations and data from herbaria. Geographic distribution maps were produced by the software SimpleMappr (Shorthouse 2010) using a database of geographical coordinates from herbarium material and field collections. Morphological terminology follows Harris and Harris (2001) and Stearn (1995).

#### TAXONOMIC TREATMENT

CAMPYLOCENTRUM Benth., J. Linn. Soc., Bot. 18: 337. 1881; Benth. & Hook. Gen. Pl. 3: 585. 1883 (as *Campylocentron*).—TYPE SPECIES: *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 292. 1884. (Basionym: *Angraecum schiedei* Rchb.f.; originally published as *Todaroa micrantha* A. Rich & Galeotti).

*Todaroa* A. Rich. & Galeotti, Ann. Sci. Nat., Bot., III, 3: 28. 1845, nom. illeg. [non *Todaroa* Parlatores, Hist. Nat. Îles Canaries:155. 1843. Apiaceae (= Umbelliferae)].  
—TYPE SPECIES: *Todaroa micrantha* A. Rich & Galeotti, Ann. Sci. Nat., Bot., II, 3: 28. 1845, nom. illeg.

#### ***Description Including Only Species with Terete Leaves—***

Epiphytic or rupicolous, monopodial herbs. Roots cylindrical, fibrous, whitish-gray, the surface minutely granulose to densely tuberculate. Stem cylindrical, partially covered by the leaf sheaths. Leaves caducous or persistent in older portions; the sheaths striate; the



blades distichous or secund, terete, straight to arched, the apex acute to acuminate, fleshy. Inflorescences lateral, racemose; peduncle smooth to minutely papillose; the rachis smooth to minutely papillose; floral bracts deltoid, the margin entire to minutely ciliate, the apex acute, membranaceous; flowers 3–18 per inflorescence, distichous; pedicellate ovary minutely papillose; dorsal sepal elliptic-ovate, lanceolate, obovate, oblong, oblong-lanceolate or ovate, the apex acute to obtuse, 1-3-nerved, glabrous, entire margin, membranaceous; lateral sepals elliptic, elliptic-ovate, oblong or lanceolate, sub-falcate, the apex acute to obtuse, 1-3-nerved, glabrous, margin entire, membranaceous; petals elliptic, oblong or lanceolate, the apex acute, 1-3-nerved, glabrous, margin entire, membranaceous; lip entire to 3-lobed, membranaceous, 5-11-nerved, the margin entire, produced at base into a slender spur, lateral lobes orbicular, oblong or sub-orbicular, the apex rounded to truncate, middle lobe deltoid, the apex acute, spur conical, cylindrical, cylindrical-clavate, cylindrical-ellipsoid, oblong-obovoid, or wide ellipsoid, straight, slightly curved or sub-patent, the apex obtuse to rounded; column erect, wingless, footless, anther cap apex 2-lobed, viscidium 2, pollinia 2, globose, slightly dorsi-ventrally compressed. Capsule ellipsoid to obovoid, pedicellate to sub-sessile, perianth persistent.

#### KEY TO SPECIES OF *CAMPYLOCENTRUM* WITH TERETE LEAVES

1. Leaf blades  $\leq$  7.0 mm long; spur wide-ellipsoid; capsule subsessile (plants from Nicaragua and the Antilles to northern South America).....5. *C. poeppigii*
1. Leaf blades  $\geq$  9.0 mm long; spur conical, cylindrical, cylindrical-clavate or oblong-obovoid; capsule pedicellate (plants from eastern South America).....2
2. Lip entire to obscurely 3-lobed; spur conical, two times (or more) longer than the pedicellate ovary; pedicel of the capsule around  $\frac{1}{4}$  of the whole length.....6. *C. sellowii*
2. Lip clearly 3-lobed; spur cylindrical, cylindrical-clavate or oblong-obovoid, shorter to slightly longer than the pedicellate ovary; pedicel of the capsule  $\leq$   $\frac{1}{6}$  of the whole length.....3
3. Lip wider than long; spur oblong-obovoid .....7. *C. wawrae*
3. Lip longer than wide; spur cylindrical, cylindrical-clavate or cylindrical-ellipsoid.....4
4. Leaves secund (distichous only at the stem apex).....5
4. Leaves distichous.....6

5. Roots granulose; inflorescence 3–5 flowered; petals  $\leq 1.4$  mm long, spur  $\leq 1.2$  mm long.....1. *C. labiakii*
5. Roots densely tuberculate; inflorescence 6–10 flowered; petals  $\geq 1.7$  mm long, spur  $\geq 1.8$  mm long.....3. *C. parahybunense*
6. Pedicellate ovary  $\leq 1.5$  mm long; base of the perianth pale orange; spur cylindrical, apex rounded.....4. *C. pernambucense*
6. Pedicellate ovary  $\geq 1.5$  mm long; base of the perianth pale green; spur cylindrical-ellipsoid, apex obtuse.....2. *C. ornithorrhynchum*

**1. *Campylocentrum labiakii*** E. Pessoa & M. Alves, sp. nov.—TYPE: BRAZIL.

Espírito Santo: Nova Venécia, Área de Proteção Ambiental da Pedra do Elefante, 18°46'13" S, 40°26'51" W, 300–600 m elev., 14 Jan. 2009, P. H. Labiak et al. 5087 (fl.) (holotype: RB!; isotypes: CEPEC!, MBML!, UPCB!).

Similar to *C. pernambucense* but differs by its secund leaves (vs. distichous), sepals 3-nerved (vs. 1-nerved) and shorter spur ( $\leq 1.2$  mm vs.  $\geq 1.3$  mm), and similar to *Campylocentrum parahybunense* (Barb.Rodr.) Rolfe but differs by its granulose root surface (vs. densely tuberculate),  $\leq 3$  mm long inflorescence (vs.  $\geq 3.5$  mm long), and smaller flowers (sepals  $\leq 1.7$  mm long vs.  $\geq 1.8$  mm long).

Epiphytic herbs. Roots 1.0–1.5 mm diam., the surface granulose. Stem 10.0–24.5 cm long, 1.0–1.5 mm diam. Leaves persistent in older portions; the sheaths 3.0–9.0 mm long; the blades 17.0–45.0 mm long, 0.5–1.0 mm wide, secund, distichous near the stem apex, straight to slightly arched, the apex acuminate. Inflorescences 2.0–3.0 mm long; peduncle 0.1–0.3 mm long, the surface smooth; rachis 1.9–2.7 mm long, the surface smooth; floral bracts 0.2–0.3 mm long, 0.2–0.3 mm wide, deltoid, the margin entire; flowers 3–5 per inflorescence, whitish; pedicellate ovary 0.7–0.8 mm long, minutely papillose; dorsal sepal 1.2–1.5 mm long, 0.3–0.5 mm wide, lanceolate, the apex acute, 3-nerved; lateral sepals 1.3–1.7 mm long, 0.5–0.6 mm wide, oblong to lanceolate, sub-falcate, the apex acute, 3-nerved; petals 1.1–1.4 mm long, 0.3–0.4 mm wide, oblong to lanceolate, the apex acute, 1-nerved; lip 1.1–1.5 mm long, 1.0–1.5 mm wide, 3-lobed, 9-nerved, lateral lobes 0.4–0.7 mm long, 0.2–0.3 mm wide, orbicular, the apex rounded, middle lobe 0.7–0.8 mm long, 0.3–0.4 mm wide, deltoid, the apex acute, spur 1.0–1.2 mm long, 0.3–0.4 mm diam., cylindrical-clavate, slightly curved,

the apex rounded; column 0.4–0.7 mm long. Capsule 3.0–7.0 mm long, 0.8–1.5 mm wide, ellipsoid, pedicellate, pedicel 0.2–0.7 mm long. Figures 1A, H, 2A–D.

**Distribution and Ecology** — *Campylocentrum labiakii* is endemic to the northern portion of the state of Espírito Santo (Fig. 3), in Atlantic Forest in habitats locally called *Floresta de Tabuleiro* or in sub-montane forest close to rock outcrops. The flowering period is poorly known but based on the specimens analyzed flowers can be observed in January and fruits in April.

**Conservation Status**— Based on criterion B1a (extent of occurrence less than 100 km<sup>2</sup>, and severely fragmented), this species is considered critically endangered (CR).

**Etymology**— It honors the collector of the type specimen, Dr. Paulo Henrique Labiak, a Brazilian botanist who has dedicated his career to the study of Neotropical ferns.

**Nomenclatural and Taxonomic Notes**— Samples of the new species were misidentified under *C. parahybunense* in four herbaria, a misidentification that can be explained by the two species being the only ones with secund leaves. In general, the vegetative portion of *C. labiakii* is smaller than *C. parahybunense*, as well as the flowers, but the key character to distinguish this species is the surface of the roots, which is granulose in the new species and densely tuberculate in *C. parahybunense*. Based on the general size of the plant and floral portions, it is related to *C. pernambucense* but differs by its secund leaves (vs. distichous), 3-nerved sepals (vs. 1-nerved) and shorter spur ( $\leq 1.2$  mm vs.  $\geq 1.3$  mm) (Table 1).

**Representative Specimens Examined**—BRAZIL. Espírito Santo: Linhares, Reserva Natural da Companhia Vale do Rio Doce, 6 Jan 1994, D.A. Folli 2150, fl. (CVRD, RB); *ibid.*, 15 Apr 2011, J. Meirelles *et al.* 545, fr. (ESA); Sooretama, Reserva de Sooretama, 17 Jul. 1969, D. Sucre 5706, fr. (RB).

2. *CAMPYLOCENTRUM ORNITHORRHYNCHUM* (Lindl.) Rolfe, *Orchid Rev.* 11: 246. 1903.

*Angraecum ornithorrhynchum* Lindl., *Edwards's Bot. Reg.* 26: 68.1840. *Aeranthes ornithorrhyncha* (Lindl.) Rchb.f., *Ann. Bot. Syst.* 6: 903. 1864. — TYPE: BRAZIL. Santa Catarina: s.d., J. Tweedie *s. n.* (fl./fr.) (holotype: K!; isotype: BR!).

Epiphytic herbs. Roots 1.5–3.0 mm diam., the surface granulose. Stem 5.0–57.5 cm long, 1.3–2.0 mm diam. Leaves persistent in older portions; the sheaths 6.0–16.0 mm

long; the blades 12.0–75.0 mm long, 1.0–1.5 mm wide, distichous, straight to slightly arched, the apex acuminate. Inflorescences 3.0–11.0 mm long; peduncle 0.6–1.5 mm long, surface smooth; the rachis 2.4–9.5 mm long, surface smooth; floral bracts 0.5–1.0 mm long, 0.3–0.6 mm wide, deltoid, the margin entire; flowers 4–10 per inflorescence, whitish, base of perianth pale green; pedicellate ovary 1.5–2.5 mm long, minutely papillose; dorsal sepal 1.4–2.8 mm long, 0.6–0.8 mm wide, obovate to oblong-lanceolate, the apex acute to obtuse, 1–3-nerved; lateral sepals 1.6–3.1 mm long, 0.4–0.6 mm wide, oblong to lanceolate, sub-falcate, the apex acute, 1–3-nerved; petals 1.3–2.8 mm long, 0.4–0.5 mm wide, oblong to lanceolate, the apex acute, 1–3-nerved; lip 1.8–3.2 mm long, 1.2–1.8 mm wide, 3-lobed, 7–9-nerved, lateral lobes 1.0–1.2 mm long, 0.3–0.4 mm wide, orbicular to oblong, the apex rounded, middle lobe 0.8–2.0 mm long, 0.7–1.0 mm wide, deltoid, the apex acute, spur 1.7–2.7 mm long, 0.4–0.5 mm diam., cylindrical-ellipsoid, straight to slightly curved, the apex obtuse; column 0.3–0.6 mm long. Capsule 6.0–12.0 mm long, 1.3–2.0 mm wide, ellipsoid, pedicellate, pedicel ca. 0.8–1.0 mm long. (Figures 1B, I, 4A–F).

***Distribution and Ecology***— This species is endemic to the Atlantic Forest and has a wide distribution covering almost the whole area of this ecosystem in Brazil (states of Bahia, Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo) and Paraguay (Department of Misiones) (Fig. 5). It probably occurs in Argentina (province of Misiones) due to the geographical proximity, but no specimen has been located so far to confirm this. Abundant collections are available from the states of Espírito Santo, Rio de Janeiro, Rio Grande do Sul and Santa Catarina but it appears rare in the other states. It grows mainly in montane to submontane areas, but in southern Brazil it is also found in lowland forests. Based on the analyzed specimens, flowers and fruits can be observed throughout the year with a peak of flowering from June to October, we have not observed a peak for fruits.

***Conservation Status***— This species falls under the least concern (LC) category, based on its wide distribution.

***Nomenclatural and Taxonomic Notes***— Although the basionym was described by Lindley (1840), the type specimen of *C. ornithorrhynchum* was cited in the protolog as part of the Hooker collection (currently at K) and not in the Lindley collection

(currently also at K), additionally a fragment was found at BR and it is listed here as an isotype. A second specimen from Lindley's collection (K-L), which is indicated on the sheet as collected by *J. Tweedie* from the same locality (apparently an isotype), is actually another species. The secund leaves and densely tuberculate roots clearly support its identification as *C. parahybunense*.

As the most widely distributed species in the Atlantic Forest, there is a large variation in the size of the flower among the different populations. No geographic correlation with this variation was found, showing that populations with large and small flowers are randomly distributed. This species can be confused with *C. parahybunense* but differs by its granulose roots (vs. densely tuberculate), distichous leaves (vs. leaves secund, distichous only at the stem apex), and  $\geq 0.7$  mm wide mid-lobe of the lip (vs.  $\leq 0.6$  mm wide).

Several specimens of *C. ornithorrhynchum* were found under the name *C. sellowii*. This is probably the result of a sequence of taxonomical mistakes started by Cogniaux (1906). He cited two specimens of *C. ornithorrhynchum* (*Glaziou 6722* and *J. de Moura 50*) among the studied material of *C. sellowii* and a wrong concept of this species was followed by Hoehne (1949) and Pabst and Dungs (1977), which has subsequently been misapplied in the Brazilian herbaria (Pessoa and Alves 2016; Table 1).

**Representative Specimens Examined**—BRAZIL. Bahia: Boa Nova, Fazenda São José, 25 Oct. 2001, W.W. Thomas *et al.* 12627, fl. (CEPEC, NY); Espírito Santo: Alegre, Parque Nacional do Caparaó, Pedra Roxa, 18 Oct. 2000, W. Forster & G.O. Romão 748, fl. (ESA); Cachoeira do Itapemirim, 4 Sep. 1948, A.C. Brade 19127, fl. (RB); Cariacica, Reserva Biológica Duas Bocas, 6 May 2008, A.P. Fontana *et al.* 5208, fr. (MBML, RB); Castelo, Parque Estadual do Forno Grande, 12 Jul. 2004, L. Kollmann & R.L. Kollmann 6885, fl. (MBML); Domingos Martins, Biriricas, 2010, J. Guiard 10244, fl. (MBML); Fundão, Goiaba-açu, 11 Oct. 2003, A.P. Fontana & N. Toniato 618, fl. (MBML); João Neiva, Cavalinhos, 6 Jun. 2006, A.P. Fontana & K.A. Brahim 2154, fr. (RB); Mimoso do Sul, Pedra dos Pontões, 5 Sep. 2008, D.R. Couto *et al.* 909, fr. (MBML); Santa Leopoldina, Cachoeira da Fumaça, 6 Jul. 1988, L. Kollmann 17, fl. (MBML); Santa Maria de Jetibá, Pedra do Garrafão, 10 Aug. 2003, M.V.S. Berger & A. Belz 110, fl. (MBML); Santa Teresa, Estação Biológica de Santa Lúcia, 16 Oct. 2003, R.R. Vervloet & V. Demuner 2561, fl. (MBML); Mato Grosso do Sul: Bodoquena, Estação de Bodoquena, Dec. 1941, N. Santos *s.n.*, fl. (R); Minas Gerais: Bandeira, Mata do Boi Rajado, 4 Oct. 2003, A. Salino *et al.* 8999, fl. (BHCB); Santa Maria do Salto, Distrito Talismã, Fazenda Duas Barras, 10 Oct. 2003, A. Salino *et al.* 9211, fl. (BHCB); Paraná: Antonina, Serra Capivari Grande, 14 Apr. 1967, G. Hatschbach 16354, fr. (HB, HBR, MBM, US); between Curitiba and Paranaguá, Serra do Mar, 18 Jun. 1969, M. Leining 399, fl. (HB); Pernambuco: Belo Jardim, Santa Rosa, 14 Jan. 1989, L.P. Felix & G.V. Dornelas 1928, fl., fr. (EAN, UFP); Brejo da Madre de Deus, Reserva Particular do Patrimônio Natural Fazenda Bitury, 16. Jul.

2014, *E. Pessoa et al.* 1239, fr. (UFP); Caruaru, Brejo dos Cavalos, 15 Oct. 2002, *A.M. Miranda et al.* 4035, fr. (EAC, HST); Rio de Janeiro: Itatiaia, Parque Nacional do Itatiaia, 12 Jul. 2006, *C.O. Azevedo et al.* 201, fl. (RB); Mangaratiba, Reserva Particular do Patrimônio Natural de Rio das Pedras, 22 Apr. 2003, *E. Saddi & C.A. Zaldini* 56, fl. (RB); Petrópolis, Meio da Serra, s.d., *C. Spannagel* 16, fl. (SP); Queimados, Reserva Biológica do Tinguá, 9 Feb. 2007, *C.N. Fraga et al.* 1719, fl. (RB); Rio de Janeiro, Corcovado, Jul. 1887, *J. de Moura* 50, fl. (BR, RB); *ibid.*, *ibid.*, s.d., *Glaziou* 6722, fl. (BR, C, K, P), *ibid.*, Pico do Papagaio, May 1895, *E. Ule* 4021, fl. (BR, HBG, SP); Teresópolis, Soberbo, 20 Jul. 1918, *F.C. Hoehne s.n.*, fl. (SP); Rio Grande do Sul: Montenegro, Morro do Cabri, 29 Sep. 1987, *I. Fernandes* 363, fl. (ICN); Nova Petrópolis, Mosseck, Oct. 2009, *M. Grings* 1195, fl. (ICN); Pelotas, Cerrito Alegre, 11 Jun. 1959, *J.C. Sacco* 1351, st. (HB); Porto Alegre, Morro do Sabiá, 28 Dec. 1948, *B. Rambo* 39245, fr. (ICN); Santa Cruz do Sul, Trombado, 11 Sep. 1977, *J.L. Waechter* 594, fl. (ICN); São Francisco de Paula, Sep. 1952, *G. Karl s.n.*, fl. (HB); São Leopoldo, Dois Irmãos, 13 Sep. 1934, *C. Orth s.n.*, fl. (B, HBR, SP); São Sebastião do Caí, Oct. 1927, *J. Dutra* 997, fl. (ICN); Torres, Morro Azul, 16 Sep. 1978, *J.L. Waechter* 990, fl. (ICN); Santa Catarina: Florianópolis, Ribeirão, Tapera, 5 Jun. 1970, *A. Bresolin* 21, fl. (FLOR, HBR, ICN, M); Itajaí, Morro da Fazenda, 6 Sep. 1958, *R. Reitz* 5858, fl. (HB, HBR); Joinville, Morro da Tromba, 16 Sep. 2010, *W.S. Mancinelli* 1289, fl. (UPCB); Governador Celso Ramos, Jordão, 19 May 1971, *R.M. Klein & A. Bresolin* 9453, fl. (FLOR, HBR); Lauro Muller, Novo Horizonte, 22 Aug. 1958, *R. Reitz & R. Klein* 7019, fl. (FLOR, HB, HBR); Luiz Alves, Braço Joaquim, 11 May 1956, *R. Reitz & R. Klein* 3237, fl. (HBR); Morro Grande, Três Barras, 11 Dec. 2009, *J.L. Schmitt et al.* 967, fl. (FURB); Palhoça, Morro do Cambirela, 22 Sep. 1971, *R.M. Klein & A. Bresolin* 9717, fl. (FLOR, HB, HBR, UFP); Paulo Lopes, Bom Retiro, 20 Sep. 1973, *A. Bresolin* 828, fl. (FLOR, HBR, ICN); Presidente Nereu, Rio Pequeno, 8 Oct. 2009, *A. Korte & A. Kniess* 404, st. (FURB); Siderópolis, São Bento, 5 Nov. 2009, *M. Verdi et al.* 3053, fr. (FURB, UPCB); São Paulo: *sine loco acurato*, 3 May 1895, *Loefgren in Comm. Geogr. E Geol. S. Paulo* 3105, fl. (BR); Cananéia, Parque Estadual da Ilha do Cardoso, 22 May 2002, *T.B. Breiner* 108, fl. (UEC); Pilar, Fazenda Moquem, 1 Apr. 1945, *H.P. Krug s.n.*, st. (IAC); São Paulo, Alto da Serra, Estação Biológica, 18 Jul. 1935, *O. Handro s.n.*, fl. (SP, SPF). PARAGUAY. Misiones: *sine loco acurato*, 12 Aug. 1971, *F. Dungs s.n.*, fl. (HB).

3. *CAMPYLOCENTRUM PARAHYBUNENSE* (Barb. Rodr.) Rolfe, *Orchid Rev.* 11: 246. 1903.

*Aeranthes parahybunensis* Barb. Rodr., *Gen. Sp. Orchid.* 2: 245. 1882. Type: Brazil. Minas Gerais, Margens do Rio Parahybuna, s.d. [destroyed, fide Sprunger et al. (1996), lectotype, here designated: Barbosa Rodrigues J., *Gen. Sp. Orchid.* 2: tab. 706, original illustration at Jardim Botânico do Rio de Janeiro; reproduced by Sprunger et al. (1996), *Iconographie des Orchidées du Brésil* 5: 397, tab. 269]

*Campylocentrum parahybunense* var. *gracile* Cogn., in *Mart., Fl. bras.* 3(6): 520. 1906.

— TYPE: BRAZIL. Santa Catarina: Blumenau, Oct 1886, *J. H. R. Schenck* 889 [holotype: B, destroyed; neotype, **here designated**: Brazil. Santa Catarina, Blumenau, Feb 1939, *F. Muller s.n.* (RB!)]

Epiphytic herbs. Roots 1.5–2.0 mm diam., the surface densely tuberculate. Stem 20.0–65.0 cm long, 1.0–1.5 mm diam. Leaves persistent in older portions; the sheaths 8.0–22.0 mm long; the blades 22.0–65.0 mm long, 0.5–1.5 mm wide, secund, distichous near the stem apex, straight to slightly arched, the apex acuminate. Inflorescences 3.5–7.0 mm long; peduncle 0.1–0.6 mm long, the surface smooth; the rachis 2.9–6.4 mm long, the surface smooth; floral bracts 0.4–0.7 mm long, 0.3–0.4 mm wide, deltoid, the margin entire; flowers 6–10 per inflorescence, whitish, base of perianth pale green; pedicellate ovary 1.3–2.0 mm long, minutely papillose; dorsal sepal 1.8–3.0 mm long, 0.5–0.8 mm wide, oblong to lanceolate, the apex acute to obtuse, 3-nerved; lateral sepals 1.9–3.2 mm long, 0.5–0.8 mm wide, oblong to lanceolate, sub-falcate, the apex acute, 3-nerved; petals 1.7–3.0 mm long, 0.4–0.5 mm wide, oblong to lanceolate, the apex acute, 3-nerved; lip 1.8–3.1 mm long, 1.2–1.7 mm wide, 3-lobed, 9–11-nerved, lateral lobes 0.8–1.5 mm long, 0.3–0.5 mm wide, orbicular to oblong, the apex truncate to rounded, middle lobe 1.0–2.0 mm long, 0.4–0.6 mm wide, deltoid, the apex acute, spur 1.8–3.0 mm long, 0.4–0.6 mm diam., cylindrical-ellipsoid, slightly curved, the apex rounded; column 0.4–0.7 mm long. Capsule 7.0–13.0 mm long, 1.5–2.5 mm wide, ellipsoid, pedicellate, pedicel ca. 0.4–1.5 mm long. (Figures 1C, J, 4G–J).

***Distribution and Ecology***— Endemic to the Atlantic Forest of Brazil, the species is known from the states of Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina and São Paulo (Fig. 5). Although it has a wide distribution, it is rare outside the states of Espírito Santo, Santa Catarina and São Paulo. In northeastern and southeastern Brazil, it grows mainly in submontane or montane forests, while in southern Brazil it also grows in lowland forests. The flowering period varies among areas and it is possible to find flowers and fruits throughout the year with a peak from March to May for flowers and between August and December for fruits.

***Conservation Status***— Because of its distribution along the Atlantic Forest from northeastern to southern Brazil, this species is classified as least concern (LC).

***Nomenclatural and Taxonomic Notes***— The holotype of *C. parahybunense* was accidentally destroyed by a flood (Sprunger *et al.* 1996). Therefore, a lectotype for this

name is here proposed based on the original illustration made by Barbosa Rodrigues and cited in the original publication.

Careful examination of several specimens from the entire distribution of this species led us to discredit the existence of the variety proposed by Cogniaux (1906). *Campylocentrum parahybunense* var. *gracile* was described based on a specimen from Blumenau (State of Santa Catarina, Brazil), collected by *H. Schenck*. The description suggests a plant with smaller leaves and linear capsules which are interpreted here as part of the morphological variation of the species, or even as young stages of development (for the capsules). The specimen collected by *H. Schenck*, deposited at B was destroyed during WWII. Therefore, a neotype from the same locality (Blumenau) is here chosen for the name.

*Campylocentrum parahybunense* can be confused with *C. labiakii* based on the second leaves, and with *C. ornithorrhynchum* based on the very similar flowers. It can be recognized by the densely tuberculate roots (vs. granulose in *C. labiakii* and *C. ornithorrhynchum*), which is the key character to identify it (Table 1).

**Representative Specimens Examined**—BRAZIL. Bahia: Elísio Medrado, Reserva Jequitibá, Serra da Jibóia, 24 Jul. 2004, *J.G. Jardim 4257*, fr. (CEPEC, HUEFS); Espírito Santo: Castelo, Parque Estadual do Forno Grande, 1 Feb. 1973, *E. Lagasa 177*, st. (MBML); Santa Teresa, Área de Proteção Permanente São Lourenço, 20 Apr. 2002, *A.P. Fontana et al. 336*, fl. (MBML); Vargem alta, Cachoeira de Itapemirim, 4 May 1949, *A.C. Brade 19742*, fl. (RB); Paraná: Adrianópolis, Parque Estadual das Lauráceas, 12 Dec. 2006, *F.B. Matos et al. 1281*, fr. (UPCB); Rio de Janeiro: Nova Friburgo, Lumiar, 1 Aug. 1974, *F. Dungs s.n.*, fr. (HB); Petrópolis, Apr. 1928, *C. Spannagel 140*, fl. (SP); Serra dos Orgãos, s.d., *Miers s.n.*, st. (K); Santa Catarina: *sine loco acurato*, s.d. *J. Tweedie s.n.*, fr. (K); Alfredo Wagner, Alto Limeirinha, 25 Nov. 2009, *A. Korte & A. Kniess 1027*, fr. (FURB); Apiúna, Jundiá, 19 Mar. 2010, *A. Korte & A. Kniess 2230*, fl. (FURB); Benedito Novo, Ceesan Liberdade, 11 Feb. 2013, *J. Caetano s.n.*, fl. (FURB); Florianópolis, Parque Municipal da Lagoa do Peri, 10 Mar. 2010, *T.J. Cadorin et al. 1491*, fl. (FURB); Passo Manso, Taió, 27 Jan. 2012, *A. Korte 7102*, fl., fr. (FURB); Pomerode, Ouro Preto Mineração, 5 Oct 2011, *T.J. Cadorin 3312*, st. (FURB); Pouso Pombinas, Alto Pombinas, 7 May 2010, *A. Korte & A. Kniess 3171*, fr. (FURB); Santo Amaro da Imperatriz, Área do Hotel Plaza Caldas da Imperatriz, 25 Apr. 2008, *J.Z. Matos s.n.*, fl. (FLOR); Vitor Meireles, 11 Oct 2010, *J.L. Schmitt & E. Caglione 3007*, fl.(IBGE); São Paulo: *sine loco acurato*, s.d., *Loefgren in Comm. Geogr. Geol. S. Paulo 2523*, st. (BR); Barra do Turvo, Parque Estadual de Jacupiranga, Núcleo Cedro, 24 Mar. 2005, *A.C.C. Destefani et al. 109*, fl. (ESA); Eldorado, Parque Estadual de Jacupiranga, Núcleo Caverna do Diabo, 25 Mar. 2005, *J.C. Braidotti et al. 60*, fl. (ESA); São Paulo, Agua Funda, 10 Apr. 1940, *O. Handro s.n.*, fl. (SPF).



4. *CAMPYLOCENTRUM PERNAMBUCENSE* Hoehne ex Hoehne, Arq. Bot. S. Paulo 1: 22. 1938. — TYPE: BRAZIL. Pernambuco: Vitória, 5 Jul 1935, *B. Pickel* 3928 (fl.) (holotype: SP!).

*Campylocentrum pernambucense* Hoehne, Res. Hist. Secc. Bot. Agron. Inst. Biol. S. Paulo: 140. 1937. nom. nuda.

Epiphytic herbs. Roots 1.0–1.5 mm diam., the surface granulose. Stem 2.5–33.0 cm long, 1.0–1.5 mm diam. Leaves persistent in older portions; the sheaths 4.0–12.0 mm long; the blades 12.0–50.0 mm long, 0.8–1.5 mm wide, distichous, straight to arched, the apex acuminate. Inflorescences 2.0–5.0 mm long; peduncle 0.3–0.6 mm long, the surface smooth; the rachis 1.7–4.4 mm long, glabrous to sparsely papillose; floral bracts 0.4–0.8 mm long, 0.3–0.6 mm wide, deltoid, the margin entire; flowers 4–7 per inflorescence, whitish, base of perianth pale orange; pedicellate ovary 1.0–1.5 mm long, minutely papillose; dorsal sepal 1.1–1.3 mm long, 0.7–0.8 mm wide, ovate to lanceolate, the apex acute, 1-nerved; lateral sepals 1.3–1.5 mm long, 0.5–0.7 mm wide, elliptic to lanceolate, sub-falcate, the apex acute, 1-nerved; petals 1.0–1.3 mm long, 0.3–0.4 mm wide, lanceolate, the apex acute, 1-nerved; lip 1.2–1.4 mm long, 1.0–1.1 mm wide, 3-lobed, 7-nerved, lateral lobes 0.6–0.7 mm long, 0.2–0.3 mm wide, orbicular, the apex rounded, middle lobe 0.5–0.7 mm long, 0.4–0.5 mm wide, deltoid, the apex acute, spur 1.3–1.4 mm long, 0.6–0.7 mm diam., cylindrical, slightly curved, the apex rounded; column 0.3–0.4 mm long. Capsule 5.0–7.0 mm long, 1.5–2.0 mm wide, ellipsoid, pedicellate, pedicel ca. 0.3–0.6 mm long. (Figures 1D, K, 6A–E).

***Distribution and Ecology***— The species is endemic to the Atlantic Forest of northeastern Brazil. While it is known from the states of Alagoas, Bahia, Paraíba, Pernambuco and Sergipe (Fig. 7), the species is clearly more abundant in Pernambuco, and rare in the other states. It grows in the sub-canopy of protected areas, where it has small populations. Based on the specimens analyzed, flowers can be observed between September and January, and fruits during the whole year.

***Conservation Status***— Because of its reduced (B2) and very fragmented (B2a) area of occupancy, this species is classified as vulnerable (VU).

***Nomenclatural and Taxonomic Notes***— Although the name *C. pernambucense* Hoehne had often been cited in checklists or local floras, it is actually a *nomen nudum*.

It was published with no type material or diagnosis in a commemorative list of the herbarium SP (Hoehne 1937), the complete description, illustration and type citation for the name were published in the next year (Hoehne 1938), the correct name for this species is *C. pernambucense* Hoehne ex Hoehne.

This species is similar to *C. labiakii* and *C. wawrae* based on the size of the vegetative portion, which is smaller than the other species of the group. From *C. labiakii*, it differs by its distichous leaves (vs. secund), 1-nerved sepals (vs. 3-nerved) and longer spur ( $\geq 1.3$  mm vs.  $\leq 1.2$  mm) and from *C. wawrae* by the lip longer than wide (vs. wider than long), the cylindrical spur (vs. oblong-obovoid). It can also be confused with young specimens having small flowers of *C. ornithorrhynchum* but it can be distinguished by the size of the pedicellate ovary ( $\leq 1.5$  mm long vs.  $\geq 1.5$  mm long), the color of the perianth base (pale orange vs. pale green), and the form of the spur (cylindrical, apex rounded vs. cylindrical-ellipsoid, apex obtuse) (Table 1).

**Representative Specimens Examined**—BRAZIL. Alagoas: Iateguara, Usina Serra Grande, Engenho Coimbra, 2 Jun. 2005, *J.A. Siqueira-Filho et al. 1508*, st. (UFP); Murici, Estação Ecológica Murici, Bananeiras, 2 Apr. 2013, *E. Pessoa et al. 1085*, fr. (RB, UFP); Bahia: Jequié, Serra do Castanhão, 23 Oct. 2001, *W.W. Thomas et al. 12551*, fl.,fr. (CEPEC, HUEFS, NY); Paraíba: Areia, Sep. 1983, *L.P. Felix & G.V. Dornelas 17*, fl. (EAN); Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 29 Jan. 2013, *E. Pessoa et al. 1050*, fl.,fr. (K, NY, RB, UFP); Lagoa dos Gatos, Reserva Particular do Patrimônio Natural Pedra D'Anta, 17 Dec. 2010, *E. Pessoa & A. Melo 429*, fl.,fr. (RB, UFP); Sergipe: Capela, Refúgio da Vida Silvestre Mata do Junco, Trilha do Estreito, 18 Oct. 2012, *M.C. Pessoa et al. 768*, fl. (UFP); *ibid.*, *ibid.*, 5 Aug. 2014, *E. Pessoa et al. 1244*, fr. (UFP).

5. *CAMPYLOCENTRUM POEPPIGII* (Rchb.f.) Rolfe, *Orchid* ver. 11: 246. 1903. *Angraecum poeppigii* Rchb.f., *Linnaea* 22: 858. 1850. — TYPE: CUBA. Savana de Macuriyes: Apr. 1824, *E. F. Poeppig s.n.* (fr.) (lectotype: W! no. 39225; isolectotypes: BR!, G!, L!, M!, MO photograph!, P!, W! no. 39227, here designated).

*Campylocentrum kuhlmannii* Brade, *Arq.Serv. Florest.* 1(2): 3. 1941. — TYPE: BRAZIL. Roraima: Rio Branco, Ilha do Ajarani, Mar 1913, *J. Kuhlmann 263* (fr.) (Holotype: RB!).

*Limodorum opuntioides* Poepp., nom. ms.

Epiphytic herbs. Roots 1.5–3.0 mm diam., the surface minutely granulose. Stem 21.0–56.0 cm long, 2.0–3.0 mm diam. Leaves caducous in older portions, usually present on young branches; the sheaths 6.0–9.0 mm long; the blades 2.0–7.0 mm long,

0.8–1.0 mm wide, distichous, straight, the apex acute. Inflorescences 8.0–15.0 mm long; peduncle 1.0–2.0 mm long, the surface smooth; the rachis 7.0–13.1 mm long, smooth surface; floral bracts 0.5–0.8 mm long, 0.3–0.5 mm wide, deltoid, the margin minutely ciliate; flowers 8–14 per inflorescence, whitish; pedicellate ovary 2.0–3.0 mm long, minutely papillose; dorsal sepal 1.6–2.1 mm long, 1.0–1.2 mm wide, elliptic-ovate, the apex obtuse, 1-nerved; lateral sepals 1.9–2.2 mm long, 1.0–1.1 mm wide, elliptic-ovate, sub-falcate, the apex obtuse, 1-nerved; petals 1.4–1.8 mm long, 0.8–1.0 mm wide, oblong, the apex acute, 1-nerved; lip 1.2–1.7 mm long, 1.5–1.8 mm wide, obscurely 3-lobed, 7-nerved, lateral lobes 1.0–1.2 mm long, 0.4–0.6 mm wide, sub-orbicular, the apex rounded, middle lobe 0.3–0.6 mm long, 0.3–0.4 mm wide, deltoid, the apex acute, spur 1.8–2.0 mm long, 0.8–1.0 mm diam., wide-ellipsoid, slightly curved, the apex obtuse to rounded; column 0.6–0.7 mm long. Capsule 7.0–11.0 mm long, 2.0–2.5 mm wide, ellipsoid, sub-sessile, pedicel ca. 0.1 mm long. (Figures 1E, L, 6F–I).

***Distribution and Ecology***— *Campylocentrum poeppigii* is known from southern Mexico to the Brazilian Amazon (States of Amazonas, Mato Grosso, Pará, Rondônia, and Roraima) (Fig. 7). Govaerts et al. (2015) cite it from Honduras, French Guyana, Guyana, Suriname, and Ecuador, but no vouchers were located from these countries. Specimens collected from Cuba and the Brazilian state of Roraima (where the type locality of *C. kuhlmannii*, a synonym, is located) are particularly common, which is an exception compared to the other countries and states of Brazil where the species is found. It grows in the canopy and sub-canopy of lowland forests and also in flooded areas in Brazil. Although the majority of the collections are in fruit, a few are in flower, which leads us to assume that the species blooms throughout the year but in different periods according to the geographical location of the population.

***Conservation Status***— This species falls under the least concern (LC) category, based on its wide distribution.

***Nomenclatural and Taxonomic Notes***— *Campylocentrum poeppigii* was described under *Angraecum* based on a specimen collected by *E. Poeppig* (s.n.) from Cuba, which had been identified on the label as *Limodorum opuntioides* Poepp., a name never published. Although Todzia (1980) and Bogarín and Pupulin (2010) had cited a specimen from W as the holotype of this name, there is no citation of a collection in the

original publication, furthermore two specimens are available at W. As a result, “W no. 39225” was chosen instead of “W no. 39227”, as it is better preserved.

Although Cogniaux (1906) did not cite *C. poeppigii* as being from Brazil, a specimen at R, collected in the state of Mato Grosso and named by Cogniaux as *C. sellowii* was found during this study. This is yet another example of the several mistakes involving the identity of *C. sellowii*.

This species is easily distinguished from the others of the group by the reduced length of its leaf blades (2.0–7.0 mm long), and inflorescences 2-times (or more) longer than the leaves. These characters are shared only in rare cases with *C. sellowii*, from which it differs by a longer pedicellate ovary ( $\geq 2.0$  mm long vs.  $\leq 1.2$  mm long); a wide ellipsoid spur (vs. conical), and sessile capsule (vs. pedicellate) (Table 1).

**Representative Specimens Examined**—BELIZE. Stann Creek: Mullis River Road, 20 Mar. 1929, W.A. Schipp 5-39, fr. (AMES). BRAZIL. Mato Grosso: Tangará da Serra, Tapirapoan, Mar. 1909, F.C. Hoehne 2259, fl., fr. (R, SP); Pará: Vitória do Xingú, canteiro de obras da UHE Belo Monte, 05 Mar 2012, L.C. Antonio PSACF 118, fl. (MG); Rondônia: Alvorada D'Oeste, Linha 64, 23 Oct. 1986, L.C.B. Lobato et al. 274, fl., fr. (HAMAB, MG); Roraima: Amajari, Ilha de Maracá, 5 Feb. 1988, J. Ratter et al. 6222, fr. (K, MIRR); Caracaraí, Parque Nacional do Viruá, Rio Barauana, 21 Sep. 2011, E. Pessoa et al. 693, fr. (INPA, NY, RB, SP, UFP); Maracá, Rio Uraricoera, Cachoeira do Filhote, 23 Feb. 1979, J.M. Pires et al. 16774, fr. (INPA, MG). CUBA. *sine loco accurately*, Apr. 1860, Wright 3301, fl., fr. (AMES, BM, BR, G, K, NY, P, W); *sine loco accurately*, 1822, E. F. Poeppig s.n., fr. (K-L); Caibarién: Las Villas, 24 Aug. 1920, B. Ferdinand 508, fr. (US); Camaguey: Sierra Cibitas to Santa Rosa, 21 Feb. 1909, J.A. Shafer 543, fr. (NY); Pinar del Rio: El Ancón, Viñales, 19 May 1955, B. Alain 4255, fr. (US); *ibid.*, mountains north of San Diego de los Baños, 22 Apr. 1920, W. Palmer & J. H. Riley 637, fr. (US); Santa Clara: Lomines, Soledad, Cienfuegos, 8 Nov. 1928, J.G. Jack 6633, fr. (K, US); Caibarién, 24 Aug. 1920, B. Fernando 509, fr. (NY); COSTA RICA. Alajuela: North of San Carlos Basin, San Pedro de Cutris, 28 April 1979, C.K. Horich s.n., fl. (CR); San Carlos: Pocosol, Santa Rosa Centro, Barrio Jasmín, Finca Rosibel, 14 Dec. 2005, D. Bogarín et al. 2218, fr. (CR). GUATEMALA. Petén: Tikal National Park, Bajo Santa Fe, 24 Jul. 1959, E. Contreras 28, fr. (LL); *ibid.*, Bajo del Hormiguero 18 Feb. 1961, E. Contreras 1969, fr. (LL); JAMAICA. *sine loco accurately*, May 1845, A.C. Purdie s.n., fl., fr. (K). MEXICO. Quitana Roo, s.d., G. Carnevali & I.M. Ramírez 4288, fr. (SEL). PANAMA. Canal Area: Summit Gardens, 7 Jan. 1970, R.L. Dressler 3774, fr. (MO). PERU. Amazonas: Iquitos, 16 Oct. 1964, C.H. Dodson 2737, fr. (F); Loreto: Ucauali, Pampa del Sacramento, Santa Catalina 28 Nov. 1898, J. Huber s.n., fr. (SP). VENEZUELA. Amazonas: Atabapo, Raudel de Guaharibos, 7 Nov. 1982, F. Guánchez 2051, fr. (MO); Bolívar: Rio Caura, May 1882, G. Morillo & R. Leisner 8913, fl. (MO). TRINIDAD & TOBAGO. Trinidad: Aqua Santa, Arima, 5 Nov. 1908, W.E. Broadway 2323, fr. (AMES); *ibid.*, 14 Feb 1908, W.E. Broadway s.n., fr. (AMES).

6. *CAMPYLOCENTRUM SELLOWII* (Rchb.f.) Rolfe, Orchid Rev. 11: 246. 1903. *Angraecum sellowii* Rchb.f., Linnaea 22: 857. 1850. — TYPE: BRAZIL. *Sine loco acurato*, s.d., *Sellow B 1337 – C 346* (fl./fr.) (lectotype: W 39239!; isolectotypes: K!, BR!, W 17516!).

*Campylocentrum aciculatum* (Rchb.f. & Warm.) Cogn., in Mart., Fl. bras. 3(6): 516. 1906. *Aeranthes aciculata* Rchb.f. & Warm., Otia Bot. Hamburg.: 91. 1881. — TYPE: BRAZIL. Minas Gerais: Lagoa Santa. s.d., *Warming s.n.* [lectotype: C! (in spirit), isolectotype: W!].

Epiphytic or rupicolous herbs. Roots 1.5–2.5 mm diam., the surface minutely granulose. Stem 7.5–62.0 cm long, 1.2–3.0 mm diam. Leaves caducous in older portions, usually present on young branches; the sheaths 5.0–17.0 mm long; the blades 9.0–30.0 mm long, 1.0–2.0 mm wide, distichous, straight or arched, the apex acuminate. Inflorescences 5.0–15.0 mm long; peduncle 0.8–1.5 mm long, the surface minutely papillose; the rachis 4.2–13.5 mm long, the surface minutely papillose; floral bracts 0.5–0.8 mm long, 0.3–0.4 mm wide, deltoid, the margin ciliate; flowers 6–18 per inflorescence, pale orange; pedicellate ovary 0.8–1.2 mm long, minutely papillose; dorsal sepal 1.0–1.8 mm long, 0.7–1.0 mm wide, ovate to lanceolate, the apex acute, 1-nerved; lateral sepals 1.1–2.1 mm long, 0.5–0.6 mm wide, elliptic to lanceolate, the apex acute, 1-nerved; petals 1.0–1.8 mm long, 0.3–0.5 mm wide, elliptic to lanceolate, the apex acute, 1-nerved; lip 1.0–1.8 mm long, 1.0–1.5 mm wide, entire to obscurely 3-lobed, 5–7-nerved, lateral lobes 0.6–0.9 mm long, 0.3–0.5 mm wide, sub-orbicular, the apex rounded, middle lobe 0.4–0.8 mm long, 0.4–0.5 mm wide, deltoid, the apex acute, spur 1.6–3.5 mm long, 0.5–0.6 mm diam., conical, sub-patent, the apex obtuse; column ca. 0.5 mm long. Capsule 4.0–6.0 mm long, 1.0–1.8 mm wide, ellipsoid to obovoid, pedicellate, pedicel 1.0–1.6 mm long. (Figures 1F, M, 8A–D).

***Distribution and Ecology***— The species is endemic to Brazil (states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) (Fig. 9). It grows in lowland to sub-montane forests (150–1100 m alt.), in Atlantic Forest (including *restingas*), *Caatinga* and *Cerrado* (gallery forest) vegetation. The flowering period is from January to May and fruits can be observed from May to November. Our

observations in the field show that *C. sellowii* grows in massive populations concentrated on a few trees or treelets.

**Conservation Status**— This species is classified as vulnerable (VU) because of its reduced (B2) and impacted (B2a) area of occupancy.

**Nomenclatural and Taxonomic Notes**—It was described under *Angraecum* by Reichenbach, who did not cite any herbarium in the original publication. Four specimens assigned “*Sellow s.n.*” from Brazil (without precise localities) have been located, two at W, one at BR and one at K. One of the specimen at W (no. 39239) was selected by Pessoa and Alves (2016) as a lectotype. The synonymy of *C. aciculatum* under *C. sellowii*, as well as the typifications have been carefully explained by Pessoa and Alves (2016). The name *C. sellowii* was misapplied for a long time in collections for specimens of *C. ornithorrhynchum*. This was caused by mistakes in the citation of the analyzed material in Cogniaux’s study, this case is also treated by Pessoa and Alves (2015).

This species can be distinguished by its capsules (pedicel around  $\frac{1}{4}$  of the whole length), and the conical spur two times (or more) longer than the pedicellate ovary, which make it distinct from all the other species in the group. In some cases it can be confused with mature specimens of *C. wawrae* (Rehb.f. ex Beck) Rolfe, especially the ones with short and arched leaves, but it is recognized by its longer inflorescences (5.0–15.0 mm long vs.  $\leq 5.0$  mm long) with 6–18 flowers (vs. 3–5 flowers per inflorescence), the entire to obscurely 3-lobed lip (vs. clearly 3-lobed) and a longer spur (1.6–3.5 mm long vs. 0.8–1.4 mm long) (Table 1).

**Representative Specimens Examined**—BRAZIL. Bahia: Abaíra, Morro do Zabumba, 13 Mar. 1992, *B. Stannard et al. H51941*, fl. (E, HUFS, K, MO, SPF, UFP); Maracás, Estrada para Cruzeiro, 19 Jul. 2013, *E. Melo et al. 11317*, fr. (HUEFS); Morro do Chapéu, Buraco do Possodônio, 7 Apr. 2008, *C. Bastos & C. Vandenberg 178*, fl. (HUEFS); Vitória da Conquista, Serra do Tromba, 10 Nov. 2008, *C. Azevedo et al. 351*, fl. (HUEFS); Espírito Santo: Alfredo Chaves, 27 May 1974, *R. Kautsky 436*, fl. (HB); Guarapará, Setiba, 12 Mar. 1995, *C.N. Fraga 128*, fl. (MBML); Linhares, Reserva Natural da CVRD, 14 Jun. 1993, *G.L. Farias 610*, fr. (RB); Santa Izabel, Pedra do Vento, 15 May 1974, *B. Ghillany 2-74*, fl. (HB); Minas Gerais: between Rio Grande and Diamantina, s.d., *Burchell 5366*, fr. (K, W); Conceição do Mato Dentro, PCH Sumidouro, 25 Sep. 2005, *P. Viana et al. 1886*, fr. (CESJ); Coronel Pacheco, Fazenda Liberdade, 13 Feb. 1942, *E.P. Heringer 936*, fl. (SP, SPF); Cristais, Sítio Barreiro, 21 Jul. 2013, *E. Pessoa & B.M. Carvalho 1189*, fr. (BHCB, NY, RB, SP, UFP); Espinosa/Montezuma, Serra do Pau D’arco, 15 Mar. 1994, *C. Sakuragui et al. CFCR 15089*, fl. (ESA, K, SPF, UFP); Formiga, Baiões, Mar. 1956, *N. Welter 164*, fl. (HB); Paraopeba, 30 Jan. 1959, *E. P. Heringer 5764*, fl. (K); Serro, Serra do Espinhaço, Feb. 1956, *L.P. Felix & G. Dornelas 77*, fl. (EAN); Rio de Janeiro: Araruama, APA

Massambaba, 14 Mar. 1996, *L. Emygdio 5906*, fl. (R); Armação de Búzios, Serra das Emeranças, 17 Mar 2001, *C. Farney & A. Terra 4365*, fl. (RB); Bordas do Rio Paraíba, 28 Jul. 1881, *A. Glaziou 13233*, fr. (BR, C, P); Ilha do Rio Paraíba, 4 Mar. 1966, *J. Laranja s.n.*, fl. (HB); Macaé, s.d., *Riedel s.n.*, fl. (BR); Petrópolis, Areal, 17 May 1928, *C. Spannagel 161*, fl. (SP); Rio de Janeiro, Estação de Comércio, s.d., *L. Rangel s.n.*, fl. (R); São Paulo: São José do Barreiro, 3 May 1968, *D. Sucre et al. 3046*, fl. (RB).

7. *CAMPYLOCENTRUM WAWRAE* (Rchb.f. ex Beck) Rolfe., *Orchid Rev.* 11: 246. 1903.  
*Aeranthes wawrae* Rchb.f. ex Beck, *Itin. Princ. Sax Coburg.* 2: 156. 1888. — TYPE:  
 BRAZIL. Minas Gerais: Juiz de Fora, *H. Wawra ser 2-167a* (fl./fr.) (Holotype: W!).

Epiphytic herbs. Roots 1.0–1.5 mm diam., the surface granulose. Stem 6.0–26.0 cm long, 1.0–1.5 mm diam. Leaves persistent in older portions; the sheaths 5.0–10.0 mm long; the blades 9.0–30.0 mm long, 0.5–1.0 mm wide, distichous, arched, the apex acuminate. Inflorescences 2.0–5.0 mm long; peduncle 0.8–1.0 mm long, the surface sparsely papillose; the rachis 1.2–4.0 mm long, the surface sparsely papillose; floral bracts 0.4–0.7 mm long, 0.3–0.5 mm wide, deltoid, the margin entire; flowers 3–5 per inflorescence, cream colored, base of perianth pale orange; pedicellate ovary 1.2–2.0 mm long, minutely papillose; dorsal sepal 1.0–1.2 mm long, 0.5–0.7 mm wide, ovate to lanceolate, the apex acute, 1-nerved; lateral sepals 1.1–1.5 mm long, 0.4–0.6 mm wide, elliptic to lanceolate, sub-falcate, the apex acute, 1-nerved; petals 1.0–1.1 mm long, 0.3–0.4 mm wide, elliptic, the apex acute, 1-nerved; lip 0.9–1.4 mm long, 1.0–1.8 mm wide, 3-lobed, 5–9-nerved, lateral lobes 0.6–0.7 mm long, 0.2–0.4 mm wide, oblong-orbicular, the apex rounded, middle lobe 0.3–0.7 × 0.5–0.8 mm, deltoid, the apex acute, spur 0.8–1.4 mm long, 0.3–0.8 mm diam., oblong-obovoid, straight to slightly curved, the apex rounded; column ca. 0.5 mm long. Capsule 6.0–7.0 mm long, 2.0–3.8 mm wide, ellipsoid, pedicellate, pedicel ca. 1.0 mm long. (Figures 1G, N, 8E–I).

***Distribution and Ecology***— *Campylocentrum wawrae* is endemic to the Atlantic Forest of the state of Espírito Santo and eastern Minas Gerais (Fig. 9). It is a rare taxon and only nine specimens are known. The flowering period is from September to April, and fruits can be observed in July.

***Conservation Status***— Based on criterion B1a [extent of occurrence less than 5,000 km<sup>2</sup>, and severely fragmented), this species is considered endangered (EN).

**Nomenclatural and Taxonomic Notes**— *Campylocentrum wawrae* was described under *Aeranthes* by Beck (1888), based on notes and an illustration from Reichenbach made on the exsiccate of a specimen collected by *H. Wawra* from Minas Gerais (Brazil). Reichenbach was probably not able to publish the species as new since he died in the year following publication, when Beck was curator of the herbarium W (Stafleu and Mennega 1992).

This species can be confused with *C. pernambucense* but differs by its lip wider than long (vs. longer than wide), the oblong-obovoid spur (vs. cylindrical), and with *C. sellowii* by its shorter inflorescences ( $\leq 5.0$  mm long vs. 5.0–15.0 mm long) with 3–5 flowers (vs. 6–18 flowers per inflorescence), the clearly 3-lobed lip (vs. entire to obscurely 3-lobed) and a shorter spur (0.8–1.4 mm long vs. 1.6–3.5 mm long) (Table 1).

**Representative Specimens Examined**—BRAZIL. Espírito Santo: Alfredo Chávez, Córrego Fortuna, 2009, *J. Guiard 9764*, fl. (MBML); *ibid.*, 03 Apr. 2011, *G. Chiron 11003*, fl. (MBML); *ibid.*, 7 Jan. 1976, *R. Kautsky 524*, fl. (HB); Santa Maria de Jetibá, 6 Dec. 1982, *D. Martins 792*, fl. (HB); Vargem Alta, Sep. 1948, *A.C. Brade 19445*, fl. (RB); Minas Gerais: Chácara, Fazenda Fortaleza de Santana, 16 Jul. 2011, *D.E.F. Barbosa et al. 13*, fr. (CESJ); *ibid.*, 30 Nov. 1969, *V. Gomes 78*, fl. (HB, M); Mariana, Mina Alegria, 28 Nov. 2006, *R.C. Mota 3153*, fl. (BHCB).

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TABLE 1. Main morphological features of the species of *Campylocentrum* with terete leaves.

	<b>Roots's surface</b>	<b>Leaf</b>	<b>Inflorescence</b>	<b>Pedicellate ovary leght</b>	<b>Sepals</b>	<b>Petals</b>	<b>Lip</b>	<b>Spur</b>	<b>Capsule</b>
<i>C. labiakii</i>	Granulose	17.0–45.0 mm long, secund	2.0–3.0 mm long, 3–5 flowered	0.7–0.8 mm long	1.2–1.7 mm long, 3-nerved	1.1–1.4 mm long, 1-nerved	3-lobed, 9-nerved	1.0–1.2 mm long, cylindrical-clavate	3.0–7.0 mm long, pedicellate
<i>C. ornithorrhynchum</i>	Granulose	12.0–75.0 mm long, distichous	3.0–11.0 mm long, 4–10 flowered	1.5–2.5 mm long	1.4–3.1 mm long, 1–3-nerved	1.3–2.8 mm long, 1–3-nerved	3-lobed, 7–9-nerved	1.7–2.7 mm long, cylindrical-ellipsoid	6.0–12.0 mm long, pedicellate
<i>C. parahybunense</i>	Densely tuberculate	22.0–65.0 mm long, secund	3.5–7.0 mm long, 6–10 flowered	1.3–2.0 mm long	1.8–3.2 mm long, 3-nerved	1.7–3 mm long, 3-nerved	3-lobed, 9–11-nerved	1.8–3.0 mm long, cylindrical-ellipsoid	7.0–13.0 mm long, pedicellate
<i>C. pernambucense</i>	Granulose	12.0–50.0 mm long, distichous	2.0–5.0 mm long, 4–7 flowered	1.0–1.5 mm long	1.1–1.5 mm long, 1-nerved	1.0–1.3 mm long, 1-nerved	3-lobed, 7-nerved	1.3–1.4 mm long, cylindrical	5.0–7.0 mm long, pedicellate
<i>C. poeppigii</i>	Minutely granulose	2.0–7.0 mm long, distichous	8.0–14.0 mm long, 8–14 flowered	2.0–3.0 mm long	1.6–2.2 mm long, 1-nerved	1.4–1.8 mm long, 1-nerved	3-lobed, 7-nerved	1.8–2.0 mm long, wide ellipsoid	7.0–11.0 mm long, sub-sessile
<i>C. sellowii</i>	Minutely granulose	9.0–30.0 mm long, distichous	5.0–15.0 mm long, 6–18 flowered	0.8–1.2 mm long	1.0–2.1 mm long, 1-nerved	1.0–1.8 mm long, 1-nerved	entire to obscurely 3-lobed, 5–7-nerved	1.6–3.5 mm long, conic	4.0–6.0 mm long, pedicellate
<i>C. wawrae</i>	Granulose	9.0–30.0 mm long, distichous	2.0–5.0 mm long, 3–5 flowered	1.2–2.0 mm long	1.0–1.5 mm long, 1-nerved	1.0–1.1 mm long, 1-nerved	3-lobed, 5–9-nerved	0.8–1.4 mm long, oblong-obovoid	6.0–7.0 mm long, pedicellate

**APPENDIX 1.** Index of collectors: Numbers between parentheses correspond to the species numbers in the taxonomic treatment. The collection numbers for vouchers without collector's numbers are provided between square brackets.

Amaral, I. L. 1449 (5); Azevedo, C. et al. 201 (2), 351 (6); Barbosa, D. E. F. et al. 13 (7); Bastos, C. 130 (6); Bastos, C. & Vandenberg, C. 178 (6), 182 (6), 204 (6); Berger, M. V. S. & Belz, A. 110 (2); Bogarín, D. et al. 2218 (5); Bovini, M. G. 1010 (2); Brade, A. C. 11101 (2), 16828 (2), 19127 (2), 19445 (7), 19742 (3); Braidotti, J. C. et al. 60 (3); Breiner, T. B. 108 (2); Breiner, T. B. & Singer, R. B. 170 (2); Bresolin, A. 21 (2), 828 (2); Broadway, W. E. 2323 (5), [AMES 271795] (5); Burchell 5366 (6); Cadorin, T. J. et al. 1386 (2), 2073 (2), 1491 (3), 1491 (3), 3312 (3); Caetano, J. [FURB 40574] (3); Carboni, M. et al. 57 (3); Carnevali, G. & Ramírez, I. M. 4288 (5); Carvalho, B. M. 119a (6); Chiron, G. 11003 (7); Contreras, E. 28 (5), 580 (5), 1969 (5); Couto, D. R. et al. 909 (2), 128 (2); Couto, D. R. & Couto, T.R. 844 (2); Destefani, A. C. C. et al. 109 (3); Dodson, C. H. 2737 (5); Dressler, R. L. 3774 (5); Dungs, F. [HB 60999] (3), [HB 57786] (2); Dutra, J. 1021 (2), 997 (2); Emygdio, L. 5906 (6); Farias, G. L. 610 (6); Farney, C. & Terra, A. 4365 (6); Felix, L. P. & Dornelas, G.V. 17 (4), 77 (6), 1928 (2); Fernandes, I. 363. (2), 485 (2); Fernando, B. 509 (5); Folli, D. A. 2150 (1); Fontana, A.P. et al. 336 (3), 5208 (2); Fontana, A. P. & Brahim, K. A. 2154 (2); Fontana, A.P. & Esgario, C. 1451 (3); Fontana, A. P. & Silva, J. R. 32 (2); Fontana, A. P. & Toniato, N. 618 (2); Forster, W. & Romão, G. O. 748 (2); Fraga, C. N. 128 (6), 129 (6), 147 (6), 312 (6), 515 (2), 1719 (2); Ghillany, B. 2-74 (6); Glaziou, A. 6722 (2), 13233 (6); Gomes, V. 78 (7); Grings, M. 1195 (2); Guánchez, F. 2051 (5); Guiard, J. 9764 (7), 10244 (2); Handro, O. [SPF 72267] (3), [SPF 65065] (2); Hatschbach, G. 16354 (2); Heringer, E. P. 5764 (6), 936 (6), [HB 3138] (6), [HB 3168] (6), [HB 40828] (6); Hoehne, F. C. 2259 (5), [SP 2313] (2), [SPF 13100] (3).; Horich, C. K. [CR s.n.] (5); Huber, J. [SP 37589] (5); Jack, J. G. 6633 (5); Jardim, J.G. 4257 (3); Karl, G. [HB 1793] (2); Kautsky, R. 436 (6), 524 (7); Klein, R. 9541 (2), 9570 (2); Klein, R. M. & Bresolin, A. 6220 (2), 8697 (2), 9453 (2), 9717 (2); Atonio, L. C. 118 (5); Kollmann, L. et al. 17 (2), 11185 (2), 2854 (3); Kollmann, L. & Bausen, E. 4855 (2); Kollmann, L. & Kollmann, R.L. 6885 (2); Kollmann, L. & Vervloet, R.R. 2814 (3); Korte, A. 7102 (3); Korte, A. & Kniess, A. 404 (2), 1027 (3), 2230 (3), 3171 (3); Krug, H. P. [IAC 7796] (2); Kuhlmann, J. 263 (5); Labiak, P. H. et al. 5087 (1); Lagasa, E. 177 (3); Laranja, J. [HB 40925] (6); Laurênio, A. et al. 661 (2); Leining, M. 399 (2); Leitão-Filho, H. F. et al. 32893 (3); Lobato, L.C. B. et al. 274 (5), 345 (5); Loefgren in Comm. Geogr. Geol. S. Paulo 2523 (3), 3105 (2); Lombardi, J. et al. 5191 (3); Luederwaldt, H. [SP 27361] (3); Mancinelli, W. S. 1289 (2); Martins, D. 792 (7); Matos, F. B. et al. 1281 (3); Matos, J.Z. [FLOR 44097] (3), [FLOR 38669] (3); Meirelles, J. et al. 545 (1); Melo, E. et al. 11317 (6); Miers [K 886200] (3); Miranda, A. M. et al. 4035 (2); Morillo, G. & Leisner, R. 8913 (5); Mota, R. C. 3153 (7); Moura, J. de 50 (2); Orth, C. [SP 50497] (2); Pabst, G. F. [HB 1687] (2); Pessoa, E. et al. 380 (5), 693 (5), 863 (5), 960 (4), 1085 (4), 1050 (4), 1287 (4), 1244 (4), 1239 (2); Pessoa, E. & Carvalho, B. M. 1189 (6); Pessoa, E. & Melo, A. 429 (4), 968 (5); Pessoa, M.C. et al. 768 (4); Pickel, B. 3928 (4); Pires, J. M. et al. 16774 (5); Poeppig, E. F. [W 39225] (5); Purdie, A. C. [K s.n.] (5); Rambo, B. 39245. (2); Rangel, L. [R 3461] (6); Ratter, J. et al. 6222 (5); Reitz, R. 5858 (2); Reitz, R. & Klein, R. 3237 (2), 3627 (2), 7019 (2); Riedel [BR s.n.] (6); Rohr, J. A. 2243 (2), 452 (2); Romanini, R. P. 259 (2); Saddi, E. & Zaldini, C. A. 56 (2); Sacco, J. C. 1351 (2); Salino, A. et al. 8999 (2), 9211 (2); Santos, N. [R 35617] (2); Sakuragui, C. et al. CFCR 15089 (6);

Schenck, J. H. R. 889 (3); Schipp, W. A. 5-39 (5); Schmitt, J. L. et al. 967 (2); Schmitt, J. L. & Caglione, E. 3007 (3); Sellow B 1337 – C 346 (6); Shafer, J. A. 543 (5); Silva, A. G & Nascimento, L. M. 165 (2); Siqueira-Filho, J. A. et al. 1508 (4); Spannagel, C. 16 (2), 140 (3), 161 (6); Stannard, B. et al. H51941(6); Sucre, D. 5706 (1), 3046 (6); Thomas, W. W. et al. 12551 (4), 12627 (2); Tweedie, J. s.n. (3); Ule, E. 3460 (2), 4021 (2); Verdi, M. et al. 3053 (2); Vervloet, R. R. et al. 1175 (2), 1154 (2), 2186 (2); Vervloet, R. R. & Demuner, V. 2561 (2); Viana, P. et al. 1886 (6); Waechter, J. L. [ICN 32460] (2), 129 (2), 594 (2), 990 (2); Warming [C s.n.] (6); Wawra, H. ser. 2–167a (7); Welter, N. 164 (6); Wright 3301 (5).

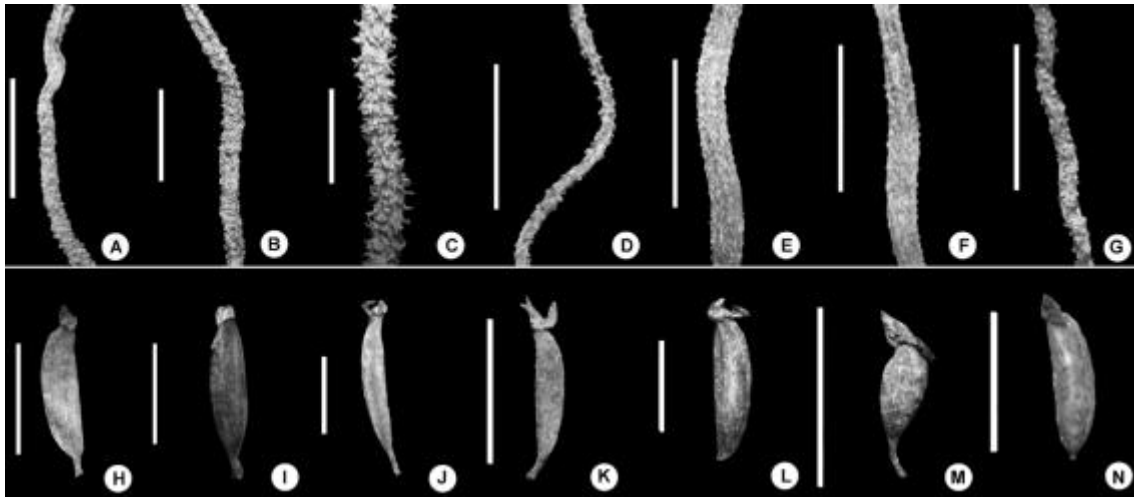


FIG. 1. A-G. Roots. A. *Campylocentrum labiakii*; B. *C. ornithorrhynchum*; C. *C. parahybunense*; D. *C. pernambucense*; E. *C. poeppigii*; F. *C. sellowii*; G. *C. wawrae*; H-N. Fruits. H. *Campylocentrum labiakii*; I. *C. ornithorrhynchum*; J. *C. parahybunense*; K. *C. pernambucense*; L. *C. poeppigii*; M. *C. sellowii*; N. *C. wawrae* (scale bar: 5.0 mm).

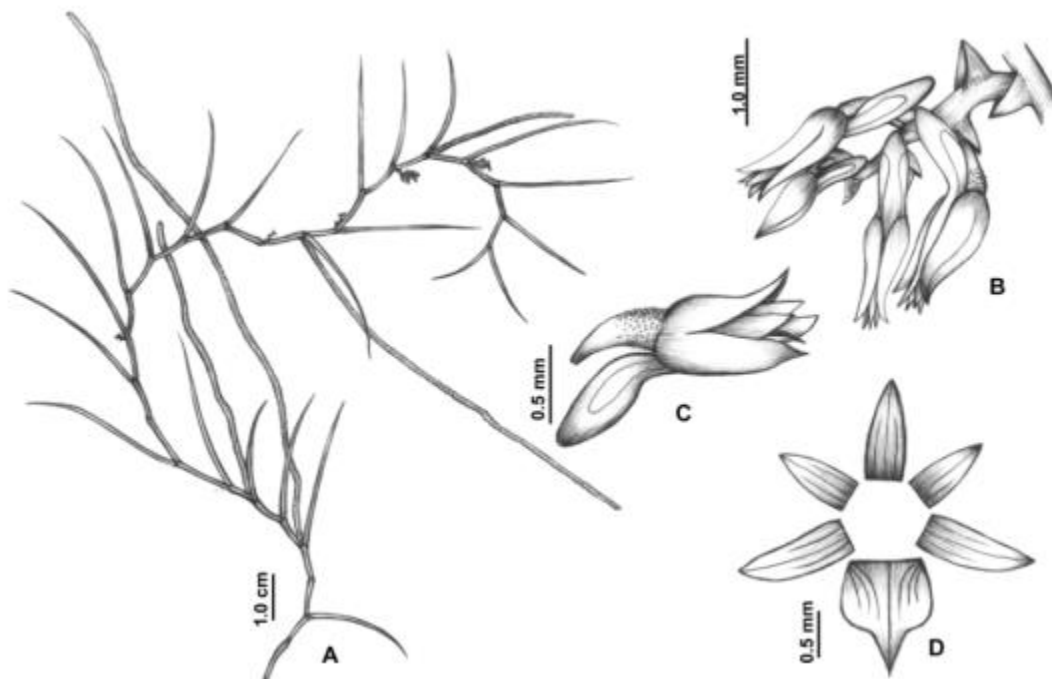


FIG. 2. A-D. *Campylocentrum labiakii*; A. Habit; B. Inflorescence; C. Flower; D. Dissected perianth. (Drawn from Labiak et al. 5087).

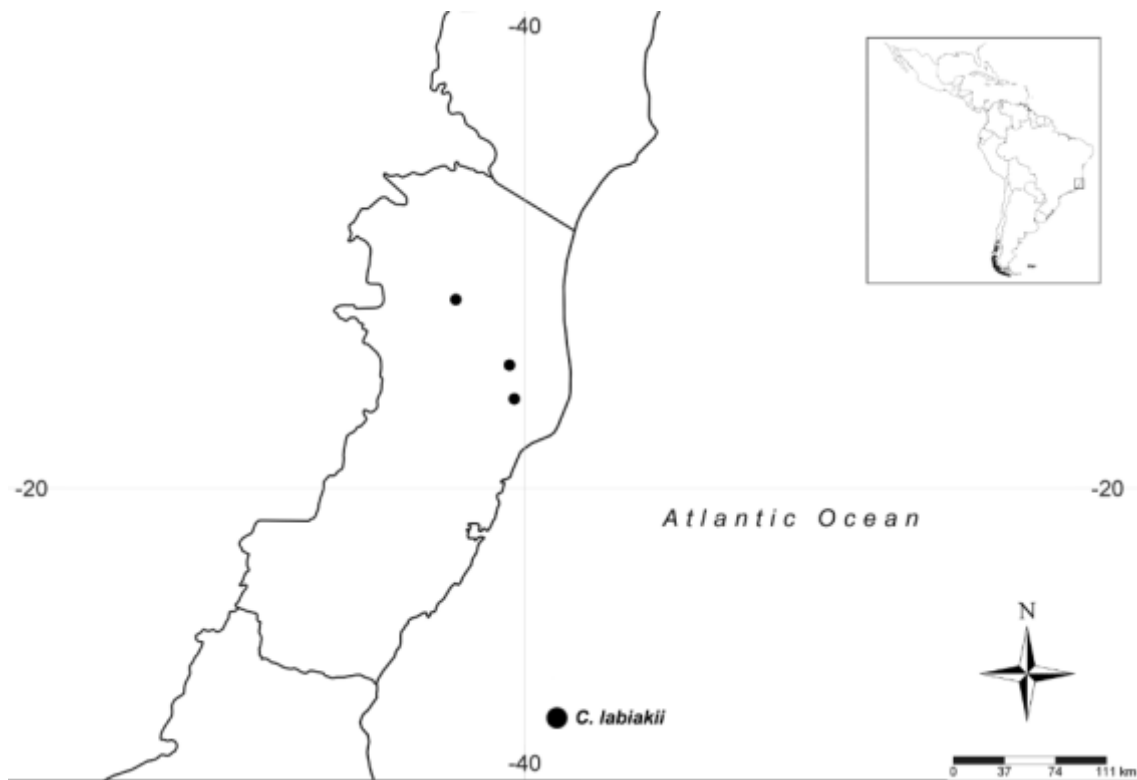


FIG. 3. Map of the known distribution of *C. labiakii* (black circle).

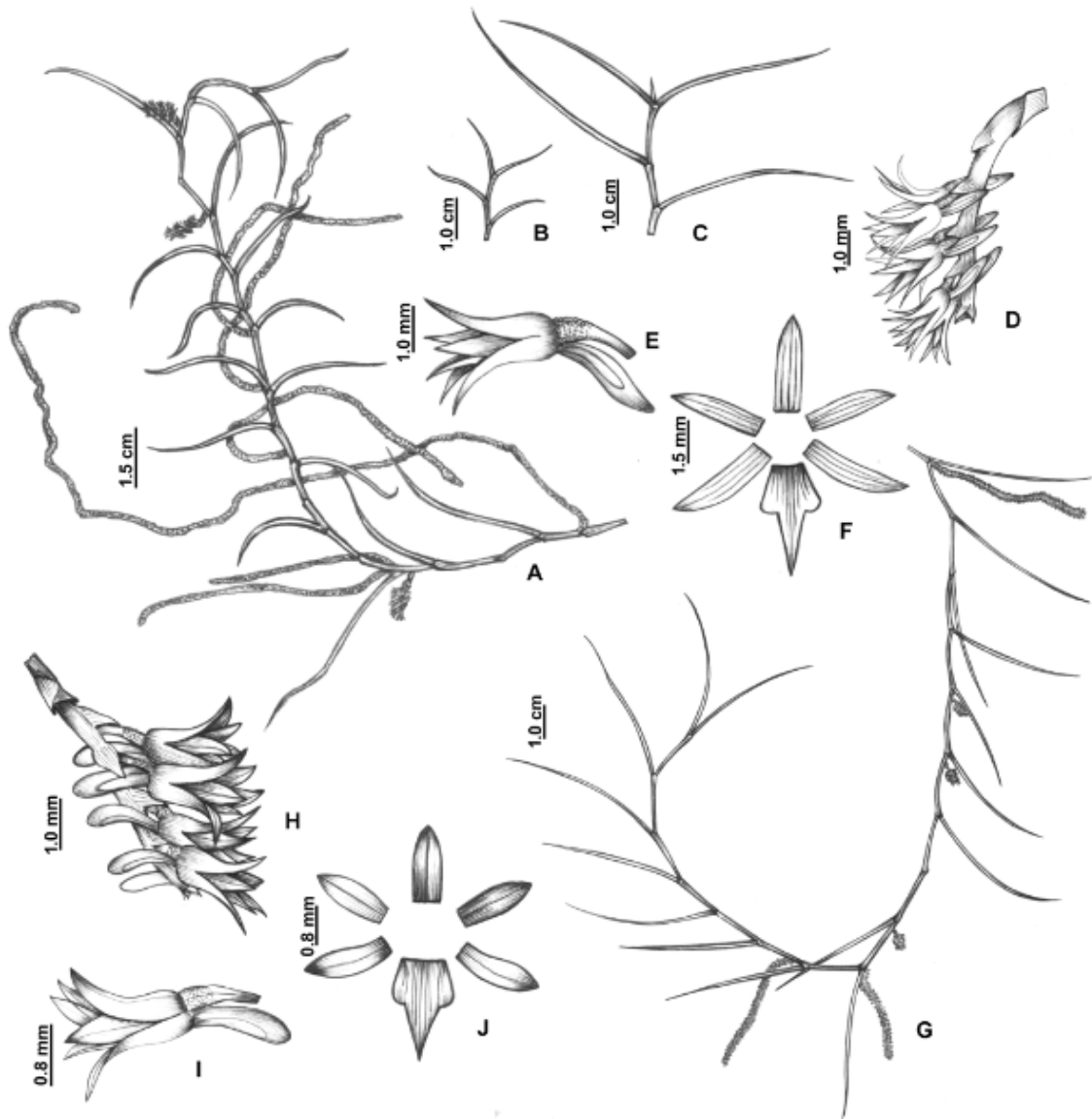


FIG. 4. A-F. *Campylocentrum ornithorrhynchum*; A. Habit; B-C. Variation in size of the leaves; D. Inflorescence; E. Flower; F. Dissected perianth; G-J. *Campylocentrum parahybunense*; G. Habit; H. Inflorescence; I. Flower; J. Dissected perianth. (A. Drawn from Tweedie s.n.; B. Drawn from Cadorin et al. 2073; C-F Drawn from Schmitt et al. 967)



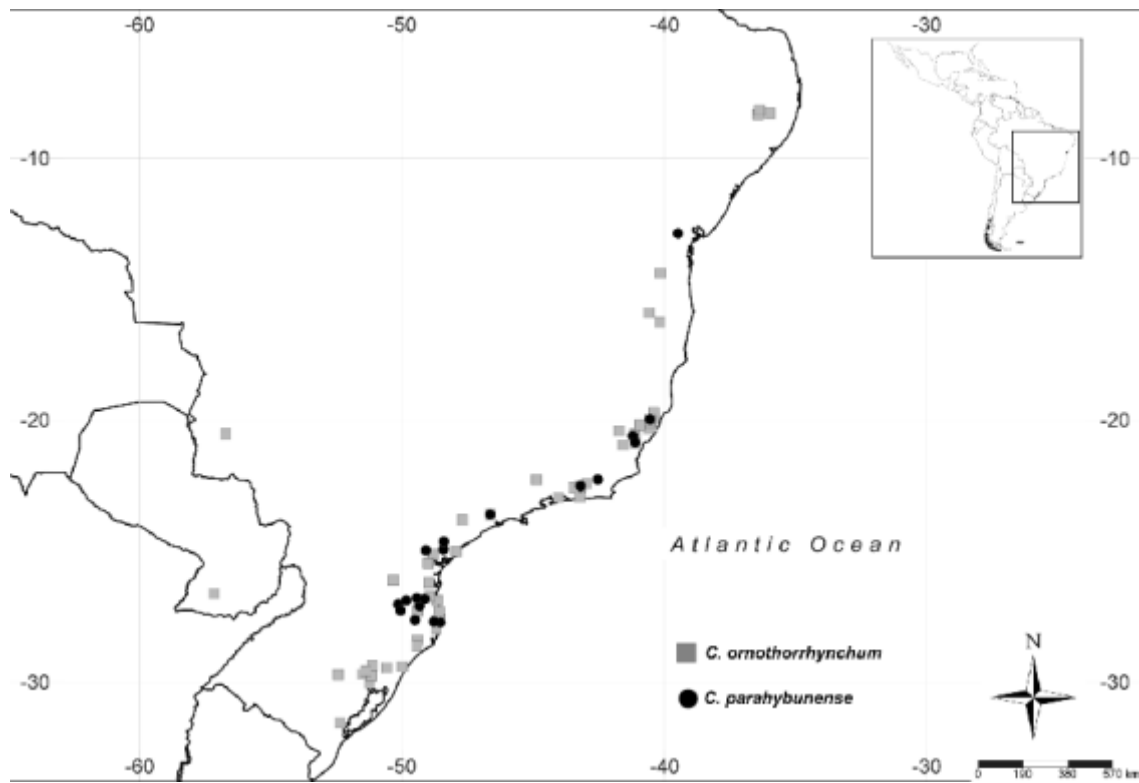


FIG. 5. Map of the known distribution of *C. ornithorrhynchum* (black circle) and *C. parahybunense* (gray square).

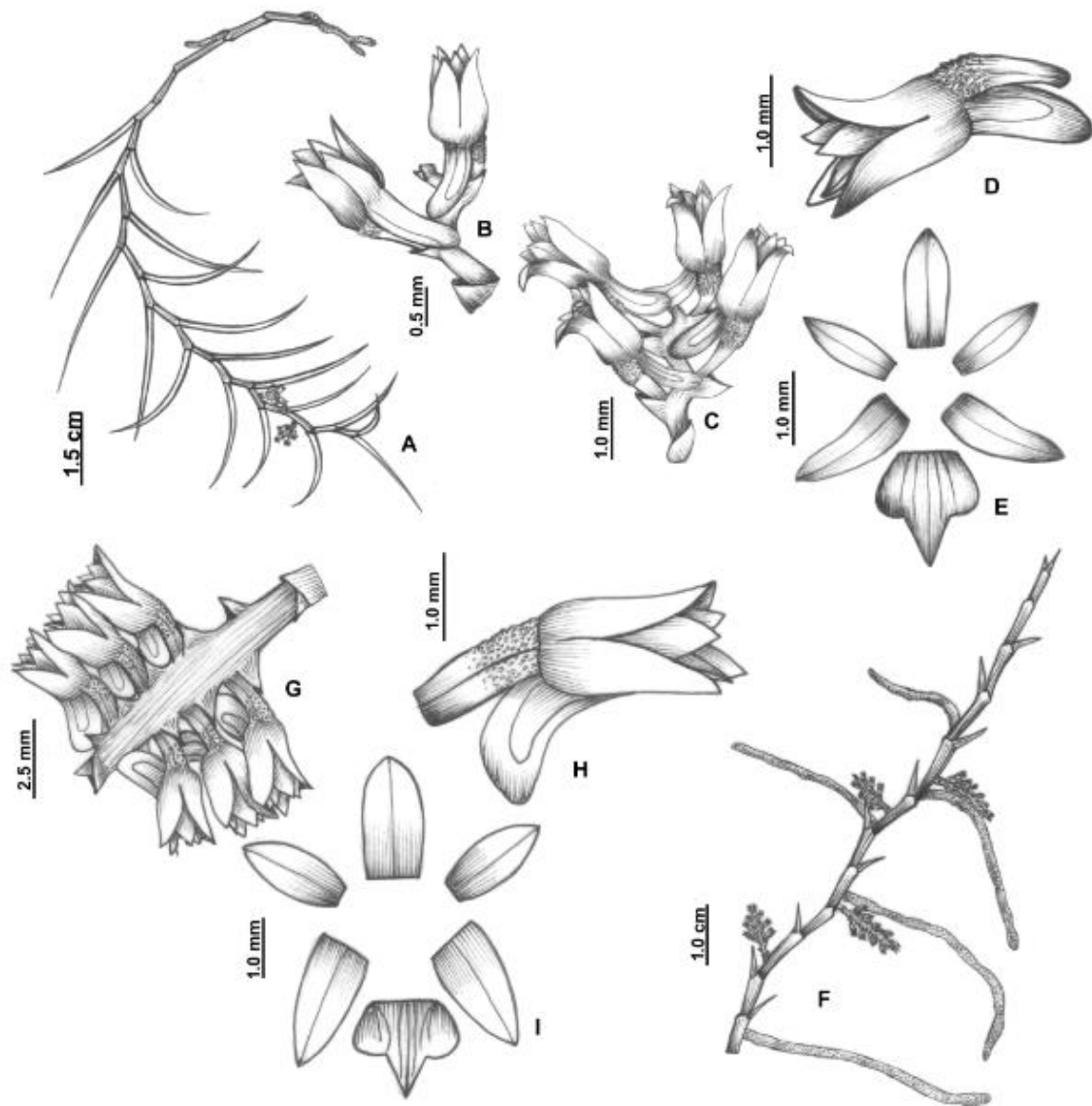


FIG. 6. A-F. *Campylocentrum pernambucense*; A. Habit; B-C. Inflorescences; D. Flower; E. Dissected perianth; F-I. *Campylocentrum poeppigii*; F. Habit; G. Inflorescence; H. Flower; I. Dissected perianth. (A-E. Drawn from *Pickel 3928*; F-I Drawn from *Lobato et al. 274*)

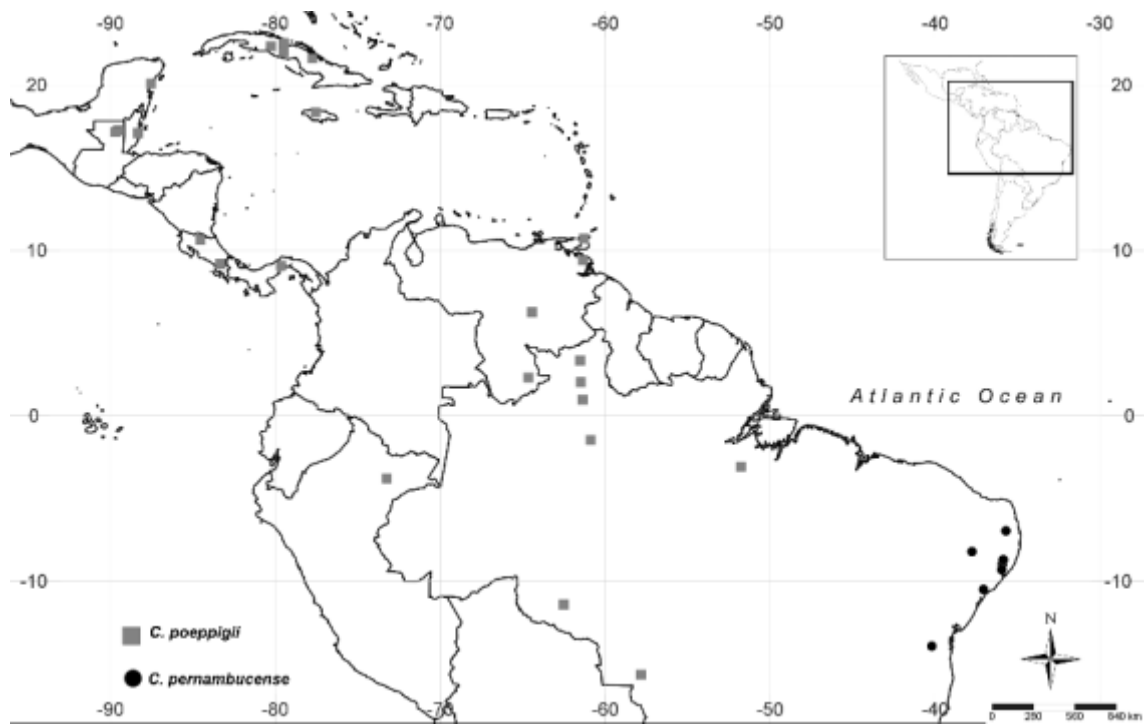


FIG. 7. Map of the known distribution of *C. pernambucense* (black circle) and *C. poeppigii* (gray square).

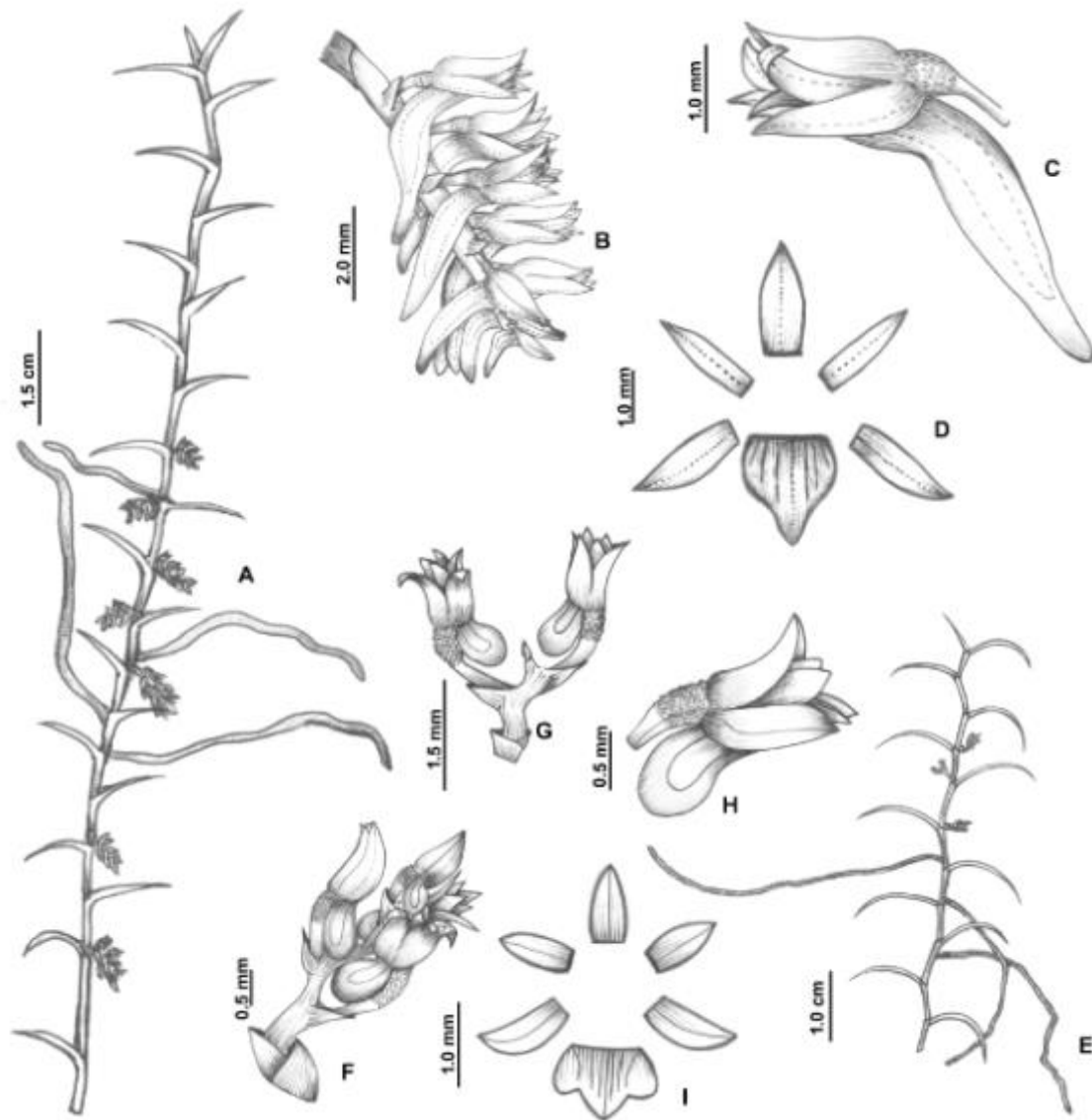


FIG. 8. A-D. *Campylocentrum sellowii*; A. Habit; B. Inflorescence; C. Flower; D. Dissected perianth. E-I. *Campylocentrum wawrae*; E. Habit; F-G. Inflorescences; H. Flower; I. Dissected perianth. (A-D. Drawn from *Heringer 936*; E-I. Drawn from *Kautsky 524*).



FIG. 9. Map of the known distribution of *C. sellowii* (gray square) and *C. wawrae* (black circle).

**Taxonomical revision of *Campyloctrum* sect. *Dendrophylopsis* Cogn. (Orchidaceae-Vandae-Angraecinae).**

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**Abstract** –This study reviews the leafless species of *Campyloctrum*, which belong to section *Dendrophylopsis*. Thirteen species are recognized. While the section has a wide distribution in the Neotropics, a majority of the species are known only from the type specimens or a few additional collections, suggesting a restricted distribution range. Members of *Dendrophylopsis* are easily distinguished but determination to species level is complicated by the low number of vegetative characters and similarity of the flowers, as well as the lack of a taxonomic revision of the group. These circumstances result in frequent misidentifications. This study provides typifications, complete synonymies, conservation statuses, complete descriptions, illustrations, distribution maps and an identification key to the species in question.

**Keywords:** Leaflessness, Epidendroideae, Monocots, Neotropics.

## Introduction

Although the leafless condition is present in several groups of orchids, it is often linked with terrestrial mycotrophic species, found in several Orchidoideae, some basal Epidendroideae Kosteletzky (1831: 233), and a few Cymbidieae Pfitzer (1887: 105) and Epidendreae Kunth (1815: 269) (Pridgeon *et al.* 1999, 2001, 2003, 2005, 2009, 2014). On the other hand, leaflessness in the tribe Vandeeae Lindley (1826: 14) is associated with epiphytes with a reduced shoot system. In this group, the roots form the main body of the plant and produce sugars using Crassulacean Acid Metabolism (CAM) (Carlswald *et al.* 2006, Winter *et al.* 1985).

About nine genera of Vandeeae contain leafless species, of which only two occur in the Neotropics: *Campylocentrum* Bentham (1881: 337) and *Dendrophyllax* Reichenbach (1864: 903), both from the subtribe Angraecinae Summerhayes (1966: 188) (Pridgeon *et al.* 2014). Using a molecular approach, Carlswald *et al.* (2003), delimited these genera and suggested that the leafless condition had possibly arisen twice in the subtribe.

*Campylocentrum* comprises about 70 species (Govaerts *et al.* 2016, Carlswald 2014), of which 13 are leafless. The first named, leafless species of the genus [*C. fasciola* (Lindley 1840: 68) Cogniaux (1906: 520) and *C. tenue* (Lindley 1840: 68) Rolfe (1903:246)] were described under *Angraecum* Bory (1804: 359) by Lindley (1840). Other species like *C. pachyrrhizum* (Reichenbach 1865: 279) Rolfe (1903: 246) were described under *Aeranthes* Lindley (1824: 817). The names were transferred to *Campylocentrum* in the beginning of the XXth century by Rolfe (1903) and Cogniaux (1906). According to Cogniaux (1906), these species are included in *C. sect. Dendrophylopsis* Cogniaux (1906: 504) which is also distinguished by having the viscidium formed of only one part. Other two sections were also proposed by him, *C. sect. Campylocentrum* and *C. sect. Pseudocampylocentrum* Cogniaux (1906: 504), which include leafy species whose viscidium is formed of two parts.

Phylogenetic studies have shown that *C. sect. Dendrophylopsis* is a monophyletic group (Carlswald *et al.* 2003, Pessoa *et al. in prep.*), *C. sect. Pseudocampylocentrum* is monospecific, and *C. sect. Campylocentrum* [*sensu* Cogniaux (1906)] is non-monophyletic and should be split into two or three sections (see Pessoa & Alves 2016).

*Campylocentrum sect. Dendrophylopsis* are widespread in the Neotropics from the United States (Florida) to Argentina (Misiones), but only three species (*C. fasciola*,

*C. grisebachii* Cogniaux (1906: 522) and *C. pachyrrhizum*) have wide distributions. Most of them (10 spp.) are known only from the type specimen or a few other samples, with a restricted to narrow distribution range. The species grow in several vegetation types (from Forests to Savannahs), from sea level to elevations up to 1,500 m. Although the Brazilian Atlantic Forest has been cited as the center of diversity of the genus (Todzia 1980), species of *C. sect. Dendrophylopsis* are more diversified in northwestern South America, including the Amazon Basin.

Members of the section are easily distinguished by their leafless condition, but specific determination is very complex, due to the low number of vegetative characters (basically shape and width of the roots) and similarity of the flowers. This study aims to review the names proposed for the section, including the leafless and recently described, new species (Bogarín & Pupulin 2010, Kolanowska & Szlachetko 2013, Siqueira *et al.* 2015, Pessoa *et al.* 2016) and combine this with an exhaustive morphological analysis covering the geographical and morphological variation. The taxonomic treatment provides typifications, synonymy, conservation statuses, descriptions, illustrations, distribution maps and an identification key.

## Material and Methods

Specimens were collected in expeditions carried out between 2011–2015 in the Brazilian Atlantic Forest, Amazon Basin, and “*cerrado vegetation*”. Samples were deposited at UFP with duplicates sent to K, NY, RB and SP.

Specimens, including all types, from 76 herbaria were analyzed: ALCB, \*AMES, \*AS, ASE, B, BA, BAF, BHCB, BHZB, BM, BR, C, CEN, CEPEC, CESJ, COAH, COL, COR, \*CR, E, EAC, EAN, ESA, \*F, FLOR, FR, FUEL, FURB, G, GOET, HAMAB, HB, HBG, HBR, HEID, HEPH, HRCB, HUEFS, HST, IAC, IAN, IBGE, ICN, INPA, IPA, JPB, K, L, M, MAC, MBML, MG, MIRR, MO, \*NY, P, PEUFR, R, \*RENTZ, RFA, RB, \*SEL, SP, SPF, U, US, UB, UEC, UFP, UFRN, UFRR, UPCB, \*VEN, VIES, W, WU; acronyms according to Thiers (2016), [“\*” only images].

Geographic distribution maps were produced using the software SimpleMapper (Shorthouse 2016) and the conservation status of the species was defined according to the categories proposed by IUCN (2016) using a database of geographical coordinates from herbarium material and field collections. Specimens with no georeferenced data



had their localities determined using online gazetteers (Google Earth). Due to the lack of sufficient collections, half of the species could not have their conservation statuses definitively classified, being treated as “Data deficient” (DD), while species with four or more collections were classified. The morphological terminology employed follows Harris & Harris (2001) and Stearn (1995).

### **Taxonomic Treatment**

*Campylocentrum* Bentham (1881: 337).

Type species: *Campylocentrum schiedei* (Rchb.f.) Benth. ex Hemsley (1884: 292). (Basionym: *Angraecum schiedei* Reichenbach (1850: 857); originally published as *Todaroa micrantha* Richard & Galeotti (1845: 28).

*Todaroa* Richard & Galeotti (1845: 28), *nom. illeg.* [non *Todaroa* Parlatores (1843: 155). Apiaceae (= Umbelliferae)].

Type species: *Todaroa micrantha* Richard & Galeotti (1845: 28), *nom. illeg.*

### **Key to the sections of *Campylocentrum***

1. Leafless plants (leaves reduced to achlorophyllous scales), stem reduced, viscidium of one part.....***C. sect. Dendrophyloopsis***
  - Leafy plants (leaves chlorophyllous), stem elongated, viscidium of two parts.....2
2. Leaf blades reduced to small, fleshy, cylindrical projections.....***C. sect. Pseudocampylocentrum***
  - Leaf blades developed.....***C. sect. Campylocentrum sensu lato***

*Campylocentrum sect. Dendrophyloopsis* Cogniaux (1906: 504). 1906.

Type species: *Campylocentrum fasciola* (Lindl.) Cogn., **here designated**.

Epiphytic herbs. Roots cylindrical or dorso-ventrally flattened, fibrous, smooth, greenish, grey or whitish. Stem cylindrical, reduced. Leaves reduced to achlorophyllous scales. Inflorescences arising from the top of the stem, minutely pubescent, ochre, brownish or dark brown, rachis exposed or covered by floral bracts; floral bracts deltoid or ovate, membranaceous, ochre, brownish or dark brown, margin minutely ciliate,

erose or entire, the apex acuminate, acute, obtuse or rounded. Flowers 7–64 (per inflorescence), cream-colored, ochre, pale orange, whitish, whitish-green or yellowish, distichous, ovary pedicellate, smooth or minutely papillose; dorsal sepal elliptical, oblong-lanceolate, ovate, ovate-elliptical, sub-orbicular or wide-elliptical, the apex acute, cuspidate, obtuse or rounded, unnerved to 1–3-nerved, glabrous or externally pubescent, membranaceous, margin entire; lateral sepals elliptical, elliptical-lanceolate, lanceolate, ovate, ovate-elliptical, oblong-elliptical or oblong-lanceolate, membranaceous, glabrous or externally pubescent, unnerved or 1–3-nerved, rarely 1-keeled, the apex acute or cuspidate, margin entire; petals elliptical, oblong, oblong-elliptical, oblong-lanceolate, obovate-elliptical, ovate or sub-orbicular, membranaceous, glabrous, the apex acute, rounded or obtuse, unnerved or 1–3-nerved, entire margin; lip entire to 3-lobed, margin entire or slightly serrate, membranaceous, glabrous, unnerved or 3–7-nerved, producing a spur at base, lateral lobes oblanceolate, sub-deltoid or sub-orbicular, glabrous, the apex truncate, obtuse or rounded, middle lobe deltoid or widely deltoid, the apex acute to obtuse, spur sub-globose, clavate, cylindrical, conical-cylindrical, conical-sigmoid, conical or cylindrical-ellipsoid, cylindrical-clavate, obovoid-clavate, slightly curved, curved, straight or patent, pale orange, yellowish or greenish, the apex acute, obtuse or rounded; gynostemium reduced, anther cap apex 2-lobed, rounded or truncate, pollinia 2, globose, viscidium of one part. Capsule globose to fusiform, 6-ribbed, pedicellate.

#### **Key to the species of *Campylocentrum* sect. *Dendrophylopsis***

1. Floral bracts ovate, completely covering the pedicellate ovary; anther cap apex rounded or truncate.....2
  - Floral bracts deltoid, covering only the base of the pedicellate ovary; anther cap apex 2-lobed.....4
2. Roots cylindrical,  $\leq 1.8$  mm wide; floral bracts entire  $\leq 1.2$  mm wide; sepals unnerved, spur two times (or more) longer than the sepals ..... *C. grisebachii*
  - Roots dorso-ventrally flattened,  $\geq 2.3$  mm wide; floral bracts erose  $\geq 2.5$  mm wide; sepals 3-nerved, spur shorter than the sepals.....3
3. Rachis completely covered by floral bracts; spur clavate, straight.....*C. generalense* Bogarín & Pupulin (2010: 385)

- Rachis exposed; spur cylindrical, curved.....*C. pachyrrhizum*
- 4. Spur cylindrical, cylindrical-clavate, ellipsoid, obovoid-clavate or sub-globose, wider close to the apex or similar width along the whole length .....5
  - Spur conical, conical-cylindrical or conical-sigmoid, wider at base.....9
- 5. Floral bracts acuminate at apex; spur sub-globose, shorter than the sepals.....*C. tenue*
  - Floral bracts acute or obtuse at apex; spur cylindrical, cylindrical-clavate, ellipsoid, obovoid-clavate, as long as or longer than the sepals.....6
- 6. Spur patent, twice as long (or more) than the pedicellate ovary .....*C. benelliae* Pessoa & Alves (2016: 376)
  - Spur straight to curved, shorter to slightly longer than the pedicellate ovary.....7
- 7. Petals acute at apex; lip entire, spur ellipsoid.....*C. fernandezii* Kolanoswka & Szlachetko (2013: 231)
  - Petals obtuse to rounded at apex; lip 3-lobed, spur cylindrical or obovoid-clavate.....8
- 8. Lip 7-nerved, spur obovoid-clavate.....*C. fasciola*
  - Lip 5-nerved, spur cylindrical.....*C. paludosum* Pessoa & Miranda (2016: 378)
- 9. Inflorescence  $\leq$  9.0 mm long; lip margin slightly serrate.....*C. insulare* Siqueira & Pessoa (2015:79)
  - Inflorescence  $\geq$  15.0 mm long; lip margin entire.....10
- 10. Spur twice longer than the lip.....11
  - Spur slightly longer than the lip .....12
- 11. Flowers 7–22 per inflorescence; dorsal sepal elliptical to ovate-elliptical; lip entire, spur glabrous.....*C. minutum* Schweinfurth (1948: 108)
  - Flowers 25–27 per inflorescence; dorsal sepal sub-orbicular; lip 3-lobed, spur slightly pubescent at apex.....*C. amazonicum* Cogn. in Martius (1906: 521)
- 12. Dorsal sepals obtuse to rounded at apex; lip 3-nerved.....*C. tyrridion* Garay & Dunst. ex Foldats (1970: 441)
  - Dorsal sepals acute at apex; lip 5-nerved.....*C. pubirhachis* Schlechter (1922: 67)

**1. *Campylocentrum amazonicum*** Cogn. in Martius (1906: 521). Type:—BRAZIL. Amazonas: Juruá, November 1901, *E. Ule 43b* (holotype: B destroyed, lectotype **here designated**: BR!). (Fig. 1A-D)

Roots ca. 1.0 mm diam., cylindrical. Inflorescence 50.0–80.0 mm long, peduncle ca. 30.0 mm long, brownish; rachis 30.0–50.0 mm long, brownish, exposed; floral bracts 0.8–1.0 × ca. 0.3 mm, deltoid, covering only the base of the pedicellate ovary, margin minutely ciliate, the apex acute. Flowers 25–27 (per inflorescence), whitish, distichous, ovary pedicellate 0.7–0.8 mm long, papillose; dorsal sepal 0.8–1.3 × 0.7–0.9 mm, sub-orbicular, 1-nerved, glabrous, margin entire, the apex obtuse; lateral sepals 1.0–1.3 × 0.7–0.9 mm, ovate, 1-nerved, glabrous, margin entire, the apex acute; petals 0.7–1.0 × 0.6–0.7 mm, sub-orbicular, 1-nerved, glabrous, margin entire, the apex obtuse; lip 0.8–1.2 × 1.7–2.2 mm between the lateral lobes, 3-lobed, 5-nerved, margin entire, lateral lobes 0.4–0.5 × 0.4–0.5 mm, sub-deltoid, the apex obtuse, middle lobe 0.25–0.3 × 0.4–0.5 mm, deltoid, the apex acute; spur 2.4–2.8 × 0.6–1.0 mm, wider at base, conical, straight, slightly pubescent, the apex acute; gynostemium ca. 0.3 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—*Campylocentrum amazonicum* is known only from the type specimen collected in the Brazilian Amazon. We have to highlight that the western Amazon Basin, characterized by dense ombrophilous forest, is poorly known and not well collected due to difficult access to the area. This fact can explain the lack of other specimens in scientific collections. Based on the collection locality, the species may also occur in Peru, as the Juruá River is shared by both countries (Fig. 2).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—In the original publication Cogniaux (1906) cited the type material collected by Ule as being in the *Herbarium Berolinense* (B). It was destroyed in the WWII, fortunately, an isotype at BR (one inflorescence) was found which we designated here as the lectotype.

Although it has not been collected again in the last century, *C. amazonicum* is a very distinctive species. Its conical spur wider at the base is similar to other species, such as *C. insulare*, *C. minutum*, *C. pubirhachis* and *C. tyrridion*, from which it can be distinguished by the dorsal sepal sub-orbicular, lip wider than long and spur slightly pubescent at apex.

2. *Campylocentrum benelliae* Pessoa & Alves (2016: 376). Type:—BRAZIL. Rondônia: Presidente Médici, Rio Machado, 21 November 2013, A. Petini-Benelli & S.C. Freitas 925 (holotype: UFMT!). (Fig. 1E-G)

Roots 1.0–1.5 mm diam., cylindrical. Stem 5.0–8.0 mm long, cylindrical. Inflorescences 23.0–67.0 mm long, peduncle 6.0–18.0 mm long, ochre, exposed; rachis 17.0–49.0 mm long, ochre, exposed; floral bracts 0.5–0.8 × 0.4–0.6 mm, deltoid, ochre, covering only the base of the pedicellate ovary, margin minutely ciliate, the apex acute. Flowers 10–26 (per inflorescence), pale orange, distichous, ovary pedicellate, 0.4–0.6 mm long, smooth; dorsal sepal 1.0–1.1 × 0.6–0.7 mm, ovate, 1-nerved, glabrous, margin entire, the apex acute; lateral sepals 1.0–1.2 × 0.6–0.7 mm, ovate, 1-nerved, glabrous, margin entire, the apex acute; petals 0.8–1.0 × 0.4–0.5 mm, ovate, 1-nerved, glabrous, margin entire, the apex acute; lip 1.1–1.2 × 1.3–1.5 mm between the lateral lobes, 3-lobed, 7-nerved, margin entire, lateral lobes 0.7–0.8 × 0.2–0.3 mm, sub-orbicular, glabrous, the apex rounded, middle lobe 0.3–0.4 × 0.2–0.3 mm, widely deltoid, the apex acute, spur 1.9–2.1 × 0.4–0.5 mm, wider close to the apex, cylindrical-clavate, patent, glabrous, the apex rounded; gynostemium 0.2–0.3 mm long, anther cap apex 2-lobed. Capsules 2.0–3.0 × 1.3–1.6 mm, globose to fusiform.

**Distribution and Habitat:**—*Campylocentrum benelliae* is endemic to Brazil (states of Acre, Mato Grosso, Pará and Rondônia) and occurs in lowland areas of open, ombrophilous forests in the Amazon Basin, or in gallery forest in *cerrado* vegetation. Although only a few specimens have been collected, based on the wide area of distribution in northern Brazil, it probably also occurs in Bolivia and Peru, as these countries are adjacent to the Brazilian states cited (Fig. 2).

**Conservation status:**—Based on its relatively wide distribution covering the Amazon Forest and the northern portion of *Cerrado* vegetation, this species falls under the Least Concern (LC) category.

**Nomenclatural and Taxonomic Notes:**—The species was illustrated by Hoehne (1910) and wrongly identified as *C. tenue*. More than one hundred years later, it was described as *C. benelliae* (as '*C. benellii*', Pessoa *et al.* 2016). Although several paratypes were cited in the protologue, the holotype is the only specimen known with completely developed flowers and in a good state of preservation.

This morphologically singular species is distinguished by the cylindrical-clavate, patent, spur which is twice as long (or more) than the pedicellate ovary. *Campylocentrum grisebachii* is the only species with similar characters but it has unnerved sepals and petals (vs. 1-nerved in *C. benelliae*), and an entire and unnerved lip (vs. 3-lobed and 7-nerved) (Table 1).

**Additional specimens examined:**—BRAZIL. Acre: Cruzeiro do Sul, próximo ao novo Aeroporto, 12 Feb 1976, *Monteiro & Damião 327* (INPA); *ibid.*, Aeroporto, 28 Feb 1976, *Ramos & Mota 146* (INPA); Mato Grosso: Cuiabá, Santa Carmem, Rio Azul, 5 May 1998, *Macedo & Guarim-Neto 6662* (UFMT); *ibid.*, Tangará da Serra, Tapirapuã, Mar 1909, *Hoehne in Com. Rondon 1408* (R); Pará: Tucuruí, Santa Rosa, 4 Oct 1983, *Revilla et al. 8532* (INPA, NY).

**3. *Campylocentrum fasciola*** (Lindl.) Cogn. in Martius (1906: 520). *Aeranthes fasciola* (Lindl.) Reichenbach (1864: 902). *Angraecum fasciola* Lindley (1840: 68). Type:—GUYANA. Demerara, s.d., *R. Schomburgk s.n.* (holotype: K!). (Fig. 1H-Q)

*Aeranthes filiformis* Grisebach (1864: 625). *Dendrophylax filiformis* (Griseb.) Benth. ex Fawcett (1898: 40). Type:—JAMAICA. Saint Mary: Calabash Tree, s.d., *McNab s.n.* [lectotype: K!, isolectotype: E!, designated by Ackerman (2014)]

*Campylocentrum barrerarum* Kolanowska & Szlachetko (2013: 225), **syn. nov.** Type:—COLOMBIA. Cundinamarca: Villa Gomes, Vereda Potosi, 10 June 1993, *A. C. Barrera & E. B. Torres 109* (holotype: COL!).

*Campylocentrum lankesteri* Ames (1923: 57). Type:—COSTA RICA. Reventazón River, July 1919, *C. H. Lankester 71* (holotype: K!; photograph and illustration at AMES!).

*Campylocentrum loretoense* Schlechter (1921: 118). Type:—PERU. Loreto: Moyobamba, s.d., *S. Filomeno s.n.* [holotype: B, destroyed, neotype **designated here**: Drawing of the holotype in Mansfeld (1929), Repert. Spec. Nov. Regni Veg. Beih. 57: Tab. 131 n. 514.

*Campylocentrum multiflorum* Schlechter (1923: 156). Type:—COSTA RICA. San José: Turrubares, Cerro Turubales, February 1910, *A. Brade & C. Brade 1316*. [holotype: B, destroyed; neotype: Schlechter's drawing of the holotype, AMES-31555, photograph!, designated by Bogarín & Pupulin (2010)].

*Campylocentrum sullivanii* Fawcett & Rendle (1909: 128). Type:—JAMAICA. Belvedere: Hanover, s.d., *J. A. Harris* 7523 [lectotype: BM! (539070); isolectotypes: BM! (539069), K!, NY!, designated by Ackerman (2014)].

*Campylocentrum weigeltii* (Rchb.f.) Szlachetko & Kolanowska (2013: 265), *syn. nov.* *Angraecum weigeltii* Reichenbach (1850: 857). Type:—SURINAM. s.d., *C. Weigelt s.n.* (lectotype **here designated**: W!, isolectotypes: BR!, K!).

Roots 1.0–1.5 mm diam., cylindrical. Inflorescences 16.0–152.0 mm long, peduncle 5.0–20.0 mm long, ochre; rachis 11.0–132.0 mm long, ochre, exposed; floral bracts 0.5–1.0 × 0.4–0.6 mm, deltoid, brown, margin minutely ciliate, covering only the base of the pedicellate ovary, the apex acute. Flowers 5–64 (per inflorescence), whitish-green to cream-colored, distichous, ovary pedicellate, 0.9–1.5 mm long, smooth; dorsal sepal 1.0–1.6 × 0.4–1.1 mm, ovate-elliptical to wide-elliptical, 1-nerved, glabrous, margin entire, the apex acute to obtuse; lateral sepals 1.2–1.8 × 0.4–0.9 mm wide, oblong-elliptical, 1-nerved, glabrous, margin entire, the apex acute; petals 0.9–1.4 × 0.3–0.7 mm, obovate-elliptical to elliptical, 1-nerved, glabrous, margin entire, the apex obtuse; lip 0.8–1.5 × 0.8–1.5 mm between the lateral lobes, 3-lobed, 7-nerved, margin entire, lateral lobes 0.5–1.0 × 0.3–0.4 mm, oblanceolate, the apex obtuse to rounded, middle lobe 0.3–0.6 × 0.5–0.7 mm, deltoid, the apex acute to obtuse, sometimes with a tuft of short hairs in the middle portion, spur 1.3–1.8 × 0.5–0.8 mm, wider close to the apex, obovoid-clavate, straight to slightly curved, glabrous, the apex rounded; gynostemium 0.4–0.6 mm long, anther cap apex 2-lobed. Capsules 4.0–6.0 × 2.0–3.0 mm, fusiform.

**Distribution and Habitat:**—Widespread in the Neotropics (Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, Guyana, Honduras, Jamaica, Martinique, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Surinam, Trinidad & Tobago and Venezuela), growing in forested environments (such as the Amazon Basin and Atlantic Forest) and Savannas. It has also been found in commercial plantations as indicated on specimen labels (eg. *Coffea*, *Citrus*, *Psidium*). Although Govaerts *et al.* (2016) indicated a distribution to Haiti and French Guyana, no samples have been found to confirm this (Fig. 2).

**Conservation status:**—Due to its wide distribution on the Neotropics including different ecosystems, this species is classified as of Least Concern (LC).

**Nomenclatural and Taxonomic Notes:**—This was one of the first species described for sect. *Dendrophylopsis*, based on a material from Guyana deposited at K. Due to its wide distribution, several other names have been proposed for specimens collected in the Antilles and Central and South America which are here considered synonyms.

Although recently transferred to *Campylocentrum* by Szlachetko & Kolanowska (2013), the combination of *A. weigeltii* lacks the citation of other type specimens, since only the material at W was cited as the holotype. We cite two other specimens deposited in K and BR. We designate the specimen at W as the lectotype, and the others as isolectotypes. We considered *A. weigeltii* a synonym of *C. fasciola*.

*Campylocentrum barreanum*, described from Colombia (Kolanowska & Szlachetko 2012), is also included among the synonyms. It was described based on a small specimen of *C. fasciola*. The authors in the protologue compare it with *C. pachyrrhizum*, but it is not morphologically related.

*Campylocentrum loretoense*, described by Schlechter (1921) from Peru, is also considered a synonym, unfortunately the holotype deposited in B was destroyed in WWII and no isotypes have been found. The drawing of the holotype provided by Mansfeld (1929) is designated here as a neotype of the name.

Bogarín and Pupulin (2010) designated the illustration of the type of *C. multiflorum* (AMES) as its neotype. The hypothesis created by the authors that *C. multiflorum* should be applied to Pacific Costa Rican, leafless *Campylocentrum* is not confirmed by us: firstly, because an analysis of several specimens from Mexico to Venezuela reveals continuous morphology, with an unusually small morphological variation for such a widespread species; secondly, based on a simple analysis of the neotype (illustration), which presents a dissected perianth clearly showing a spur obovoid-clavate with a rounded apex, also wider close to the apex, while *C. tyrridion*, the correct name to be applied to these plants (Romero-González & Fernández-Concha 2005), has a spur conical to conical-sigmoid, with an acute apex and wider at base. Based on this circumscription, *C. multiflorum* returns to synonymy under *C. fasciola*.



*Campylocentrum fasciola* is similar to *C. paludosum*, a species endemic to the southern portion of the Brazilian Atlantic Forest. It is easily distinguished by the lip 7-nerved (vs. 5-nerved) and spur obovoid-clavate (vs. cylindrical) (Table 1).

**Additional specimens examined:**—BELIZE. Stann Creek: *sine loco accurately*, 28 Feb 1929, *Schipp 544* (AMES). BOLIVIA. Cochabamba: Carrasco, between Ivirgarsama and Puerto Villarroel, 27 Oct 1996, *Ritter 3838* (MO); Santa Cruz: Rio Ichilo, 27 Oct 1993, *Billiet & Jadin 6009* (BR); Todos Santos: 15 Aug 1981, *Vasquez et al. 632* (Herbarium Vasquezianum). BRAZIL. Amazonas: Manaus, Reserva Ducke, 20 Feb 2001, *Knupp 1597* (INPA); Rio Purus, 1898, *Vaughan 60* (K); Mato Grosso: *sine loco accurately*, Jul 1845, *Weddell 3390* (P); Chapada dos Guimarães, Santana da Chapada, 9 Aug 1902, *Robert s.n.* (BM); Tangará da Serra, Tapirapoan, Mar 1909, *Hoehne in Comm Rondon 2255* (R, SP); Pará: *sine loco accurately*, Apr 1896, *Rand 289* (K); *sine loco accurately*, Oct 1895, *Huber 70* (MG); *sine loco accurately*, s.d., *Burchel 9709* (K, W); Almeirim, Reserva Biológica Maicuru, 28 Oct 2008, *Souza & Maciel 225* (MG); Ananindeua, 12 Apr 1991, *Silva & Silva 102* (MG); Belém, Rio Guamá, Nov 1980, *Braga 3599* (INPA); Santarém, planalto de Santarém, 10 Jan 1955, *Fróes 31505* (IAN); São Félix do Xingu, Serra do Campo, 10 Aug 2001, *Silva 2142* (EAN, HEPH, UFP); São Miguel do Guamá, 1 Nov 1948, *Black & Foster 48-3422* (IAC, IAN, HB); Tucuruí, 15 Nov 1981, *Daly et al. 1359* (INPA, K, MG, NY, SEL); Pernambuco: São Lourenço da Mata, Tapacurá, Mata do Toró, 27 Jan 1955, *Moraes s.n.* (EAN, HB); Roraima: Caracará, Parque Nacional do Viruá, 16 Sep 2010, *Pessoa et al. 633* (UFP); Ilha de Maracá, 29 Apr 1987, *Milliken et al. 154* (K). COLOMBIA. Chocó: Bahia Solano, May 1825, *no col.* (Klondu?) (W no. 17191); Valle del Cauca: Dagua, 5 May 1885, *Lehmann 3861* (G); Magdalena: *sine loco accurately*, Apr 1941, *Renz 3281* (RENZ). COSTA RICA. San Carlos: Llanuras de San Carlos, May 1910, *Brade & Brade 1297* (HB). CUBA. Guantánamo: Baracoa, Río Toa Valley, 18 Jun 1997, *Ackerman et al. 3081* (US). DOMINICAN REPUBLIC. Cevicos: Sanchez Ramirez, 12 May 1956, *Marcano & Jimenez 3356* (US); Distrito Nacional: Los Minas, Santo Domingo, 21 Apr 1969, *Marcano 14892* (NY); Bayaguana: Sierra de Agua, 1 May 1969, *Liogier & Marcano 15033* (NY, P); El Valle: Sabana de la Mar, Mar 1971, *Liogier 18104* (NY); Guamira: Hato Mayor to Sabana de la Mar, 28 Apr 1969, *Liogier 14997* (NY); Loma la Peguera: Bonaó, 17 Apr 1969, *Liogier s.n.* (NY); Samaná: Gran Estero, Sánchez, 12 Apr 1965, *Almonte 4988* (NY). ECUADOR. Napo: Cantón Tena, Estación Biológica

Jatun Sacha, 20 Jan 1990, *Cerón et al.* 8297 (MO). GUYANA. *sine loco acurato*: 1898, *Thurn* 58 (K); “*Macouria*”: Nov 1886, *Jenman* 2520 (K); Demerara: Mabura Hill, 189 km SSE of Georgetown, 25 Apr 1985, *Steege & Cornelissen* 166 (U). HONDURAS. Cortes: El Jaral, Lake Yoyoa, Mar 1933, *Edwards* 272 (K). JAMAICA. *sine loco acurato*, Jan 1823, *Purdie s.n.* (K); Saint Catherine: Riverhead, Ewarton, 12 Mar 1967, *Frootor* 27838 (U, US). MARTINIQUE. La Pagerie: Les Trois Llets, 18 Apr 1982, *Sastre & Colbrant* 7553 (P). MEXICO. Chiapas: *sine loco acurato*, s.d., *Soto et al.* B-275 (AMO). NICARAGUA. Atlántico Norte: Mosquito Coast, 1924, *Schramm s.n.* (AMES, US). PANAMA. Canal Zone: Rio Mendonza, 21 Aug 1971, *Dressler* 4085 (MO). PERU. Ayachcho: Provincia de la Mar, 22 Sep 1976, *Wasshausen & Encarnación* 836 (US); *ibid.*, San Miguel District of Ayna, San Pedro sector, 26 Sep 1995, *Castillo & Bennett* 7276 (USM); Cusco: Quispicanchis, Rio Araza, between Pande Azucar and Quince Mil Airport, 10 Aug 1991, *Núñez* 14120 (SEL, MO); Loreto: Iquitos, 5 Dec 1964, *Dodson* 2765 (SEL); Ucauali, Pampa del Sacramento, Santa Catalina, 28 Nov 1898, *Huber* 1523 (MG, G). PUERTO RICO. Cambalache Forest reserve, 27 Sep 1986, *Axelrod* 595 (NY); Indian Ceremonial Grounds, 1 Apr 1981, *Liogier et al.* 31873 (NY); Moca: Bo. Cruz, Finca Nir, 26 Apr 1996, *Nir* 55 (NY); Manati: Coto Sur, Poblado Polvorin, *Acevedo-Rodriguez* 12307 (US); Mayaguez: Hacienda Alicia, 13 Jul 1963, *Liogier* 9924 (NY); Utuado to Arecibo: Jun 1901, *Underwood & Griggs* 808 (NY, US). SURINAM. *Sine loco acurato*: 1823, *Leschenault s.n.* (P); Hannover: Zanderij, 31 Oct 1958, *Donselaar & Donselaar s.n.* (U); Jodensavanne: *sine loco acurato*, 12 Feb 1957, *Heyligers* 291 (U); Morea: s.d., *Wullschlagel* 546 (BR); Para: *sine loco acurato*, 2 Apr 1844, *Kappler* 1660 (W); Poelebantje: *sine loco acurato*, s.d., *Kegel* 700 (W); Republiek: *sine loco acurato*, Mar 1953, *Lindeman* 5712 (U). TRINIDAD & TOBAGO. Trinidad: Cedros, 17 Mar 1926, *Broadway* 6264 (BM, K, P, US); *ibid.*, Mar 1926, *Broadway* 6250 (K); *ibid.*, Milepost 54, 2 Apr 1979, *Philcox & Phillips* 8336 (K); Maraval, 14 Oct 1911, *Broadway* 6264 (K); *sine loco acurato*, 1846, *Bradford* 5342a (K). VENEZUELA. Amazonas: San Carlos de Rio Negro, 17 May 1979, *Liesner* 7486 (VEN); Aragua: Quebrada Las Adjuntas, Topo Golfo Triste, 20 May 1998, *Narvaéz et al.* 85 (VEN); Delta do Amacuro: Río Grande, close to the border with the state of Bolívar, 10 Feb, 1964, *Steyermark* 93133 (VEN); Zulia: *sine loco acurato*, Sep 1946, *Renz* 4194 (RENZ).

4. *Campylocentrum fernandezii* Kolanoswka & Szlachetko (2013: 231). Type:—COLOMBIA. Vaupés: Riberas del Rio Inirida, San Joaquin, 27 January 1953, A. Fernandez 2027 (holotype: COL!). (Fig. 3A-B).

Roots 1.0–1.2 mm diam., cylindrical. Inflorescences 15.0–25.0 mm long; peduncle 3.0–5.0 mm long, dark brown; rachis 12.0–20.0 mm long, dark brown, exposed; floral bracts 0.7–1.1 × 0.3–0.5 mm, deltoid, margin minutely ciliate, covering only the base of the pedicellate ovary, the apex acute to obtuse. Flowers 8–22 (per inflorescence), whitish, distichous, ovary pedicellate ca. 0.7 mm long, smooth; dorsal sepal 0.9–1.4 × 0.5–0.8 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; lateral sepals 1.4–1.8 × 0.5–0.8 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; petals 0.7–1.1 × 0.3–0.7 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; lip 0.7–1.2 × 0.8–1.2 mm, ovate, entire, 5-nerved, margin entire, the apex acute, spur 1.7–1.9 × 0.5–0.7 mm, wider close to the apex, ellipsoid, curved, glabrous, the apex rounded; gynostemium ca. 0.4 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Endemic to Colombia, it is known only from the type specimen collected in the Department of Vaupés (Colombian Amazon). Based on the type locality, the species grows in lowland Ombrophilous Forest close to river courses (Fig. 2).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—*Campylocentrum fernandezii* was described based on a single specimen from Colombia. It was misidentified as *C. burchellii* Cogniaux (1906: 522), a synonym of *C. grisebachii*, in 1954 by R. Schultes. This information was used by Kolanoswska & Szlachetko (2013) to compare it with *C. fernandezii*. However, these species are not morphologically related, *C. fernandezii* is similar to *C. fasciola* and *C. paludosum*, but is distinguished by its acute petals (vs. obtuse), entire lip (vs. 3-lobed) and ellipsoid spur (vs. cylindrical or obovoid-clavate) (Table 1).

Although the lip was described and illustrated as 3-lobed, during the analysis of a flower from the type, a fold in the apex was observed which probably confused the

authors of the species. When it is extended, the entire form of the lip is shown (Fig. 3A-E).

**5. *Campylocentrum generalense*** Bogarín & Pupulin (2010: 385). Type:—COSTA RICA. San José: Pérez Zeledón, San Isidro de El General, Palmares, February 2005, *D. Bogarín 2130* (holotype: JBL-spirit; isotype: CR, photograph!). (Fig. 3F-I)

Roots 2.3–3.5 mm diam., dorso-ventrally flattened. Inflorescences 15.0–20.0 mm long, peduncle 6.0–8.0 mm long, dark brown; rachis 9.0–12.0 mm long, dark brown, completely covered by floral bracts; floral bracts 2.5–3.0 × 3.0–3.2 mm, ovate, margin erose, dark brown, completely covering the pedicellate ovary, the apex acute. Flowers 13–25 (per inflorescence), congested, yellowish, distichous, ovary pedicellate, 1.0–1.2 mm long, scarious; dorsal sepal 4.0–4.2 × 1.1–1.5 mm, oblong-lanceolate, 3-nerved, externally pubescent, margin entire, the apex acute; lateral sepals 4.0–4.2 × 1.0–1.8 mm, oblong-lanceolate, 3-nerved, externally pubescent, margin entire, the apex acute; petals 4.0–4.1 × 1.0–1.1 mm, oblong-lanceolate, 3-nerved, glabrous, margin entire, the apex acute; lip 3.9–4.1 × 1.8–1.9 mm between the lateral lobes, 3-lobed, 7-nerved, margin entire, lateral lobes 1.3–1.5 × 0.4–0.5 mm, sub-orbicular, glabrous, the apex rounded, middle lobe 2.3–2.4 × 0.9–1.0 mm, deltoid, the apex acute, spur 3.0–4.0 × 1.2–2.0 mm, wider close to the apex, clavate, straight, yellowish, slightly pubescent, the apex rounded; gynostemium ca. 0.5 mm long, anther cap apex rounded. Capsules not seen.

**Distribution and Habitat:**—The species occurs in Costa Rica and Panama. This rare species was described by Bogarín & Pupulin (2010) and it is known only from two specimens, one from Pacific sub-montane forest (600 m of elevation) of the Cordillera de Talamanca, Costa Rica and another from lowland forest (less than 160 m of elevation) on Barro Colorado Island, Panama (Fig. 2).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—This species and *C. pachyrrhizum* are indistinguishable when observing only the vegetative portion, especially in terms of sharing the relatively wide dorso-ventrally flattened roots. The floral bracts are also very similar, but the arrangement of the flowers (congested vs. loose) and the form and

position of the spur (clavate and straight vs. cylindrical and curved) are important to distinguish them (Table 1).

**Additional specimens examined:**—PANAMA: Barro Colorado Island, 1963, *Dressler s.n.* (MO).

**6. *Campylocentrum grisebachii*** Cogn. in Martius (1906: 522). Type:—ARGENTINA. San Andres: Oran, 24 September 1873, *P. Lorentz & G. Hieronymus 284* (lectotype **here designated**: BR!, isoelectotypes: BA!, G!, GOET!, K!). (Fig. 3J-N)

*Campylocentrum filiforme* Cogn. ex Kuntze (1898: 298) **nom. illeg.** [non *Campylocentrum filiforme* (Swart 1788: 126) Cogniaux (1903: 184)]. Type:—ARGENTINA. San Andres: Oran, 24 September 1873, *P. Lorentz & G. Hieronymus 284* (lectotype **here designated**: BR!, isoelectotypes: BA!, G!, GOET!, K!).

*Campylocentrum burchellii* Cogn. in Martius, (1906: 522). *Aeranthus burchellii* Rchb.f., **nom. ms.** Type:—BRAZIL. Minas Gerais: between Rio Grande and Diamantina, s.d., *W. Burchell 5268* (lectotype **here designated**: K!).

*Campylocentrum chlororhizum* Porsch (1905: 162). Type:—BRAZIL. São Paulo: Sant'Ana da Lapa, July 1901, *R. Wettstein & V. Schiffner s.n.* (lectotype **here designated**: WU! no. 074728, isoelectotypes: BR!, M!, W!, WU! no. 074729.).

Roots 1.0–1.8 mm diam., cylindrical. Inflorescences 6.0–50.0 mm long, peduncle 2.0–15.0 mm long, ochre; rachis 4.0–35.0 mm long, ochre, exposed; floral bracts 0.7–1.2 × 0.6–10.9 mm, ovate, margin entire, pale ochre, completely covering the pedicellate ovary, the apex obtuse to rounded. Flowers 12–32 (per inflorescence), ochre, distichous; ovary pedicellate, 0.3–0.6 mm long, smooth; dorsal sepal 0.5–0.6 × 0.5–0.6 mm, ovate to sub-orbicular, unnerved, glabrous, margin entire, the apex rounded; lateral sepals 0.7–0.8 × 0.3–0.4 mm, elliptical, 1-keeled, glabrous, margin entire, the apex acute; petals 0.4–0.5 × 0.3–0.35 mm, oblong to ovate, unnerved, glabrous, margin entire, the apex rounded; lip 0.3–0.4 × 0.6–0.7 mm, ovate, entire, unnerved, margin entire, the apex obtuse to rounded, glabrous; spur 1.4–1.7 × 0.7–1.0 mm, wider close to the apex, obovoid-clavate, patent, glabrous, the apex rounded; gynostemium ca. 0.2 mm long, anther cap apex truncate. Capsules 3.0–4.0 × 1.5–2.0 mm, globose.

**Distribution and Habitat:**—South America (Argentina, Bolivia, Brazil and Paraguay), growing in Atlantic Forest and gallery forest in *Cerrado* and Chaco vegetation with preference for shaded forests, or partially open humid forests, generally close to rivers and streams. It has also been found in disturbed areas but then the populations are rare in short stretches of forest (Fig. 2).

Although some Amazonian specimens were cited among the syntypes of *C. burchellii* by Cogniaux (1906) [e.g. *Barbosa Rodrigues s.n.* (not located) and *G. Vaughan s.n.* (K!) both from Brazil and *Jenman 2520* (K!) from British Guyana], they actually belong to *C. fasciola*.

**Conservation status:**—Although the species has a wide distribution, including the Atlantic Forest, southern portion of *Cerrado* vegetation, and areas in the Chaco domain (southern Bolivia and Paraguay), all these areas suffer strong anthropic disturbance. Due to the fragmented and small populations, this species is classified in the Near Threatened (NT) category.

**Nomenclatural and Taxonomic Notes:**—*Campylocentrum grisebachii* was proposed to replace *C. filiforme* (Griseb.) Cogn. ex Kuntze, a combination based on *Aeranthus filiformis* Griseb. from Argentina, which is an illegitimate name and previously used for *C. filiforme* (Sw.) Cogn. [= *Dendrophyllax filiformis* (Sw.) Bentham ex Fawcett (1898: 40); Basionym: *Epidendrum filiforme* Swartz (1788: 126)] from the Dominican Republic.

*Campylocentrum burchellii* was described with several syntypes, here we designate the specimen *Burchell 5268* deposited in K as the lectotype due to its abundance of flowers and better preservation. Of *C. chlororhizum* we were able to find five specimens of *Wettstein & Schiffner s.n.* We wanted to choose a specimen from WU because it is the herbarium of the author, where two specimens are available. So, we herein designate WU no. 074728 as the lectotype due to its better preservation.

It is very easy to distinguish from the other species; the entire floral bracts and unnerved sepals, petals and lip are characters unique to *C. grisebachii* (Table 1).

**Additional specimens examined:**—ARGENTINA. Misiones: Iguazú, Reserva Militar, 29 Jul 1973, *Correa et al 5079* (MO); General Manuel Belgrano, Reserva de Vida Silvestre, 12 Oct 2003, *Johnson 1058* (MO); Guarana, 31 Aug 1999, *Tressens et al. 6328* (MO). Jujuy: Ledesma, Higueritas, 20 Sep 1976, *Cabrera et al 28024* (K). Salta: Oran, São José, 28 Sep 1944, *William 382* (HB); *ibid.*, San Andres, 13 Jun 1945,

*Capurro 309* (BA, HB); Santa Victória, Los Toldos, 4 Dec 2007, *Cabral et al. 816* (HUEFS); *ibid.*, Parque Nacional del Baritu, 19 Sep 1990, *Novara 9983* (S), *ibid.*, 5 Sep 1997, *Johnson 784* (MO). BOLIVIA: Tarija: O'Connor, Narvaez, 2 Oct 1983, *Solomon 10982* (K, MO, SEL); Entre Rios, 2 Dec 1975, *Sloover 358* (BR); *ibid.*, 28 Oct 1993, *Ibisch & Ibisch 931257* (FR). BRAZIL. Minas Gerais: between Rio Grande and Diamantina, s.d., *Burchell 4785* (BR, K, W-R); Caldas, Capivary, 18 Jun/Set 1854, *Lindberg 522* (BR, S); *ibid.*, Ribeirão dos Bugres, 21 Sep 1869, *Regnell ser. III, 1141* (BR, S, W); *ibid.*, Aug 1903, *Edwall in Comm. Geogr. e Geol. São Paulo 6068* (BR); *ibid.*, 28 Aug 2009, *Rosa 110* (HRCB); Campanha, 1885, *Schreiner ex Schwake 4954* (BR, R,RB); Caxambú, Aug 1947, *Vaughan s.n.* (RB); Cristais, Sítio Estreito, 20 Jul 2013, *Pessoa & Carvalho 1188* (BHCB, RB, UFP). Paraná: Adrianópolis, Parque das Lauráceas, 27 Jan 2011, *Mancinelli & Soller 1389* (UPCB); Araucária, Campina dos Matins, 17 Sep 1993, *Silva et al. 2303* (UPCB); Castro, 19 Sep 1996, *Silva et al. 1973* (FUEL); Curitiba, 19 Apr 1909, *Dúsen 8524* (HB, K, L, MO, P, S); Lapa, São Carlos, 27 Sep 1970, *Xuaiyoshi 2374* (HB); Mandirituba, Passo Amarelo, 15 Sep 1991, *Dunaiski 145* (UPCB); Pinhais, Rio pequeno, 29 Aug 1998, *Silva et al. s.n.* (UPCB); Ponta Grossa, 22 Mar 1981, *Krieger 17973* (CESJ); Quatro Barras, Morro Anhangava, 22 Jul 1995, *Stehmann et al. 1619* (UEC); Tibagi, Rio Amparo, 18 Sep 1969, *Hatschbach & Guimarães 22203* (C, MBM, UPCB). Rio de Janeiro: Alto Macahé, 1892, *Glaziou s.n.* (BR, P). Rio Grande do Sul: *sine loco acurato*, s.d., *Garibaldi 4* (HB); Bom Jesus, 13 Jul 2009, *Buzatto 548* (ICN); São Leopoldo, Sep 1927, *Dutra 990* (ICN); Veranópolis, Retiro, 28 Jul 1984, *Silveira s.n.* (ICN). Santa Catarina: Caçador, Rio dos Bugres, 8 Jan 1962, *Reitz & Klein 11742* (HB, HBR); Campos Novos, 12 Sep 1963, *Reitz & Klein 16164* (HBR); Lajeado, Papanduva, 14 Sep 1962, *Klein 2993* (FLOR, HB, HBR, L, US); Lages, Encruzilhada, 13 Sep. 1962, *Klein 3155* (HBR) Mafra, Campo novo, 7 Sep 1957, *Reitz & Klein 4053* (HB, US); Orleans, Sep 1889, *Ule 4020* (BR, HBG); Porto União, 16 Sep 1962, *Klein 3062* (BR, FLOR, HB, HBR, ICN, K, L, M, UB, US);. São Paulo: s.loc., Sep 1892, *Glaziou 19887* (K, P, C); Faxina. Aug 1901, *Wettstein & Schiffner s.n.* (WU); Araras, Fazenda Nova Santa Cruz, 13 Oct 2006, *Moraes 33* (HRCB); Assis, Estação Ecológica Assis, 7 Jan 2003, *Breier & Bahrami 810* (UEC); Brotas, Fazenda Santa Elisa, 10 Aug 1991, *Queiroz & Salino 2834* (CEPEC, HUEFS, K); Campinas, Reserva Sta. Genebra, 28 Jul 1993, *Bernacci 109* (IAC). PARAGUAY. Alto Paraguay: Vista Alegre, Jul 1921, *Rojas 3871* (AS).

7. *Campylocentrum insulare* Siqueira & Pessoa (2015: 79). Type:—BRAZIL. Santa Catarina: Florianópolis, Unidade de Conservação Desterro, December 2010 (fl. in cult.: 23 Dec. 2011), A. Zanin 1642 (holotype: FLOR!). (Fig. 5A-E)

Roots 0.8–2.0 mm diam., cylindrical to dorso-ventrally flattened. Inflorescences 8.5–9.0 mm long, peduncle 2.5–3.0 mm long, brownish; rachis 5.0–7.0 mm long, brownish, exposed; floral bracts 0.4–1.0 × 0.3–0.6 mm, deltoid, margin minutely ciliate, ochre, covering only the base of the pedicellate ovary, the apex acute. Flowers 7–11 (per inflorescence), whitish, distichous, ovary pedicellate, 0.5–1.1 mm long, minutely papillose; dorsal sepal 1.0–1.5 × 0.6–1.0 mm, elliptical, 1-nerved, glabrous, margin entire, the apex obtuse to cuspidate; lateral sepals 1.1–1.8 × 0.5–0.7 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute to cuspidate; petals 0.9–1.5 × 0.55–0.9 mm, ovate to elliptical, 1-nerved, glabrous, margin entire, the apex acute to obtuse; lip 1.2–2.0 × 1.2–1.8 mm between the lateral lobes, 3-lobed, 3–5-nerved, margin slightly serrate, lateral lobes 0.3–0.6 × 0.3–0.5 mm, sub-deltoid to sub-orbicular, the apex obtuse to rounded, middle lobe 0.7–1.2 × 0.7–0.8 mm, deltoid, the apex acute, glabrous, spur 0.5–1.8 × 0.35–0.7 mm, wider at base, conical to conical-cylindrical, slightly curved, glabrous, the apex rounded, pale brown; gynostemium 0.3–0.4 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Endemic to Brazil (state of Santa Catarina). It is known only from two specimens collected in geographically close areas, both in Atlantic Forest (Fig. 4).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—*Campylocentrum insulare* was described based on a single specimen which flowered in cultivation. The type specimen was described with a conical spur shorter than the perianth (0.5–0.7 mm long). However, during this study, another specimen belonging to this species was found. It shares all other morphological characters with *C. insulare*, but the spur is longer (up to 1.8 mm long) and conical-cylindrical. We assume that the spur in this species varies in length and form, and the shorter spur in the type specimen was influenced by cultivation



This species is distinguished by its shorter inflorescence ( $\leq 9.0$  mm long) and slightly serrate lip. It is the smallest species in the section (Table 1).

**Additional specimens examined:**—BRAZIL. Santa Catarina: Joinville, Jurapê, 4 Dec 2009, *Mancinelli 1080* (UPCB).

**8. *Campylocentrum minutum*** Schweinfurth (1948: 108). Type:—PERU. Loreto: Mishuyacu, near Iquitos, February-March 1930, *G. Krug 923* (holotype: F, photograph! isotype: US, photograph!). (Fig. 5F-I)

Roots 0.8–1.7 mm diam., cylindrical. Inflorescences 23.0–50.0 mm long, peduncle 5.0–15.0 mm long, brownish; rachis 18.0–35.0 mm long, brownish, exposed; floral bracts 0.6–0.9  $\times$  0.4–0.6 mm, deltoid, ochre, covering only the base of the pedicellate ovary, margin minutely ciliate, the apex acute. Flowers 7–22 (per inflorescence), yellowish, distichous, ovary pedicellate, 0.5–0.9 mm long, glabrous; dorsal sepal 1.0–1.2  $\times$  0.5 mm, elliptical to ovate-elliptical, 1-nerved, glabrous, margin entire, the apex acute; lateral sepals 1.1–1.3  $\times$  0.5–0.6 mm, elliptical to ovate-elliptical, 1-nerved, glabrous, margin entire, the apex acute; petals 0.8–0.9  $\times$  0.35–0.4 mm, ovate to elliptical, 1-nerved, glabrous, margin entire, the apex acute; lip 1.0–1.2  $\times$  1.4–1.6 mm between the lateral lobes, ovate, entire, 5-nerved, margin entire, the apex acute, glabrous, spur 2.0–2.5  $\times$  0.7–0.8 mm, wider at base, conical-cylindrical, slightly curved, glabrous, the apex rounded, yellowish; gynostemium ca. 0.3 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Occurs in Ecuador and in the Peruvian Amazon, province of Loreto. Although described almost 70 years ago from an area with a relatively good knowledge of the flora (Martínez 1997), this species is known only from four specimens. The province of Loreto (type locality) is dominated by ombrophilous forests (Martínez 1997) (Fig. 4).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—It is similar to *C. amazonicum* but is distinguished by its inflorescences with 7–22 flowers (vs. 25–27), elliptical to ovate-elliptical dorsal sepal (vs. sub-orbicular), entire lip (vs. 3-lobed) and glabrous spur (vs.

slightly pubescent at apex). Other species such as *C. fernandezii* and *C. tenue* also have an entire lip, but *C. minutum* is easily distinguished by its conical-cylindrical spur (vs. ellipsoid or sub-globose) (Table 1).

**Additional specimens examined:**—Ecuador. Los Ríos: Quevedo a Santo Domingo, 12 Oct 1983, *Dodson 14129* (MO, SEL); Montalvo, 30-Mar-2 Apr 1973, *Holmnielsen et al. 2719* (AMES). Peru. Loreto: Maynas, Iquitos, 15 Dec 1988, *Vásquez & Jaramillo 11479* (MO).

**9. *Campylocentrum pachyrrhizum*** (Rchb.f.) Rolfe (1903: 246). *Aeranthus pachyrrhizus* Reichenbach (1865: 279). Type:—CUBA. s.d., *C. Wright 3207* (holotype: probably at W). (Fig. 5J-M)

*Aeranthus spathescens* Grisebach (1866: 264). Type:—CUBA. Guantánamo: Retiro, s.d., *C. Wright 3299* (lectotype **here designated**: K!, isolectotypes: BM!, G!, MA!, MO!, P!, , illustration at W!).

*Campylocentrum rimbachii* Schlechter (1921: 172). Type:—ECUADOR. Guayas: Ventanillas, April-May 1920, *A. Rimbach 5* (holotype: B, destroyed, neotype **here designated**: ECUADOR. Manabí: Monticristi, 3 August 1960, *C. Dodson 201* (SEL, photograph!).

Roots 2.3–4.0 mm diam., dorso-ventrally flattened. Inflorescences 15.0–43.0 mm long, peduncle 4.0–8.0 mm long, dark brown; rachis 11.0–35.0 mm long, dark brown, exposed; floral bracts 2.5–3.5 × 3.0–4.0 mm, ovate, margin erose, dark brown, completely covering the pedicellate ovary, the apex acute. Flowers 8–17 (per inflorescence), loose, yellowish, distichous, ovary pedicellate, 1.0–2.0 mm long, scarious; dorsal sepal 3.5–5.5 × 1.0–1.5 mm, oblong-lanceolate, 3-nerved, externally pubescent, margin entire, the apex acute; lateral sepals 4.1–5.5 × 1.0–1.5 mm, oblong-lanceolate, 3-nerved, externally pubescent, margin entire, the apex acute; petals 3.0–4.8 × 0.8–1.2 mm, oblong-lanceolate, 3-nerved, glabrous, margin entire, the apex acute; lip 3.2–4.5 × 1.5–2.0 mm between the lateral lobes, 3-lobed, 7-nerved, margin entire, lateral lobes 1.3–1.5 × 0.4–0.5 mm, oblanceolate, glabrous, the apex truncate to rounded, middle lobe 2.2–2.8 × 0.5–0.9 mm, deltoid, the apex acute, spur 2.0–3.0 × 0.7–0.8 mm, wider close to the apex, cylindrical, curved, slightly pubescent, the apex

rounded; gynostemium ca. 0.3 mm long, anther cap apex rounded. Capsules 6.5–8.0 mm long, 2.5–5.0 mm wide, fusiform.

**Distribution and Habitat:**—Widespread in the Neotropics (Brazil, Cuba, Dominican Republic, Ecuador, French Guyana, Guyana, Jamaica, Mexico, Panama, Puerto Rico, Surinam, Trinidad & Tobago, USA, Venezuela), although it has been cited to Guatemala and Haiti, no specimens were found to confirm this. It grows in different vegetation types including the Amazon Forest and Atlantic Forest, often in lowlands (Fig. 4).

**Conservation status:**—Based on its wide distribution, including several different ecosystems in the Neotropics, this species falls under the Least Concern (LC) category.

**Nomenclatural and Taxonomic Notes:**—It was described by Reichenbach in 1865 based on a specimen collected by Wright in Cuba (*Wright 3207*) one year after Grisebach described *Aeranthus spathescens* also based on a Wright specimen from Cuba (*Wright 3299*). These names are now considered synonyms. Although the type collection of *A. spathescens* is available and well distributed (K, BM, G, MA, MO, P), the type specimen of *C. pachyrrhizum* was not located at W, though it is probably there, as explained by Ackerman (2014) and Nir (2000). Neither those researchers nor us were successful in finding the type at W. Bogarín & Pupulin (2010) cited the holotype as being at W, with illustrations in W and K, but during our visits to these collections we observed the number “3299” in the top-right of the illustrations cited by these authors, suggesting that they are illustrations of the type of *A. spathescens*, not *C. pachyrrhizum*.

The type of *C. rimbachii*, collected in Ecuador, was destroyed in the WWII. We were unable to locate other specimens of this collection and there are no illustrations of the type in the protologue or in the herbarium, which are necessary to designate lectotypes. A specimen collected also in Ecuador was designated as neotype.

This species is very similar in the vegetative portion to *C. generalense*, while in terms of floral characters the form and position of the spur are especially important to distinguish them (see above in the comments of *C. generalense*) (Table 1).

**Additional specimens examined:**—BRAZIL. Amazonas: Tabatinga, Rio Solimões, s.d., *Braga et al. 3184* (INPA); Goiás: Aparecida do Rio Doce, Irara, 7 Mar 2007, *Guilherme et al. 564* (UB); Catalão, Fazenda Barra, s.d., *Salles et al. 2651* (HEPH); Iporá, Fazenda Jacuba, 11 Oct 2008, *Meneguzzo 12* (UB); Minaçu, estrada sul do

canteiro, 12 Dec 1991, *Walter et al. 1093* (CEN); Mato Grosso: Campinápolis, Paranatinga II, Rio Culene, 23 Apr 2006, *Petini-Benelli 17* (UFMT); Tangará da Serra, Tapirapoan, Mar 1909, *Hoehne in Comm Rondon 2258* (R, SP); Pernambuco: Igarassu, Usina São José, 21 Jan 2014, *Pessoa 1218* (UFP); *ibid.*, 4 Feb 2010, *Garcia 1430* (UFP); *ibid.*, 16 Dec 2009, *Pessoa & Souza 209* (UFP); Sergipe: Capela, Refúgio da Vida Silvestre Mata do Junco, 5 Aug 2014, *Pessoa et al. 1243* (UFP). DOMINICAN REPUBLIC. Dejabón: Cerro de chacuey, Partido, 4 Oct 1969, *Liogier 16256* (NY); *ibid.*, 22 Oct 1969, *Liogier 16453* (NY, P); El Aguacate: la Leanor, Banks of Mao River, 23 Oct 1968, *Liogier 13209* (NY); El Seibo: Margenes del Río Jauera, 16 Mar 1986, *Pimentel et al. 1734* (NY); La Vega: Bayacanes to San Isidro, 1 Feb 1969, *Liogier 13598* (NY); Samaná: Las Garitas, 12 Apr 1965, *Almonde & Marcano 4991* (NY). ECUADOR. El Oro: Malva, Zamura, 15 Jul 1979, *Dodson et al. 8428* (SEL). FRENCH GUYANA. Cayenne: *sine loco acurato*, s.d., *Poiteau s.n.* (BR, W). GUYANA. *sine loco acurato*, Jul 1824, *Poiteau s.n.* (K). JAMAICA. *Sine loco acurato*, 1865, *Morris 2326* (K, W); Cedar Hurst: *sine loco acurato*, s.d., *Jamaican Plants 2326* (NY). MEXICO. Chiapas: *sine loco acurato*, s.d., *Soto B111* (AMO). PANAMA. Barro Colorado: 20 Mar 1932, *Shattuck 844* (F). PUERTO RICO. Guajataca: *sine loco acurato*, 21 May 1966, *Woodbury s.n.* (NY); Guavate: *sine loco acurato*, 19 Jul 1961, *Woodbury s.n.* (NY); Mayaguez: *sine loco acurato*, Mar 1906, *Britton & Marble 629* (NY). SURINAM. Central Surinam Nature Reserve, 10 Jun 2003, *Herrera & Pinho 9843* (MO). TRINIDAD & TOBAGO. Trinidad: *sine loco acurato*, 1846, *Bradford 5342b* (BM, K). VENEZUELA. Aragua: Parque Nacional Henry Pittier, Nov 1983, *Ramírez & Carnevali 20* (VEN); Bolívar: Sucre, Santa Maria de Erebató, Feb 1989, *Fernandez & Sanoja 5029* (MO); *ibid.*, Feb 1989, *Sanoja 2526* (MO); Delta do Amacuro: Tucupita, Sierra Imata, 4-6 Apr 1979, *Davise & Gonzalez s.n.* (VEN); Miranda: Paz Castillo, Nov 1959, *Renz 9689* (RENZ); Zamora: Montana de los Indios, 23 Mar 1989, *Gonzalez 1979* (VEN). UNITED STATES OF AMERICA. Florida: Collier County, Deep Lake, 18 Mar 1937, *John s.n.* (FLAS); *ibid.*, 22 Sep 1965, *Ward 5364* (FLAS).

**10. *Campylocentrum paludosum*** Pessoa & Miranda (2016: 378). Type:—Brazil. São Paulo: Caraguatatuba, Lagoa do Capricórnio, 23 November 2014, *M. R. Miranda 87* (holotype: UFP!, isotypes: NY!, SP!). (Fig. 6A-C)

Roots 1.0–2.0 mm diam., cylindrical. Inflorescences 15.0–50.0 mm long, peduncle 8.0–10.0 mm long, ochre; rachis 7.0–40.0 mm long, ochre, exposed; floral bracts 0.5–1.0 × 0.4–0.8 mm, deltoid, brown, covering only the base of the pedicellate ovary, margin minutely ciliate, the apex acute. Flowers 7–27 (per inflorescence), whitish-green, distichous, ovary pedicellate, 1.5–1.8 mm long, smooth; dorsal sepal 1.3–1.5 × 1.0–1.1 mm, ovate-elliptical, 1-nerved, glabrous, margin entire, the apex acute to obtuse; lateral sepals 1.4–1.6 × 0.7–0.9 mm, ovate to ovate-elliptical, 1-nerved, glabrous, margin entire, the apex acute; petals 0.9–1.2 × 0.6–0.8 mm, obovate-elliptical, 1-nerved, glabrous, margin entire, the apex rounded to obtuse; lip 0.9–1.1 × 1.2–1.5 mm between the lateral lobes, obscurely 3-lobed to 3-lobed, 5-nerved, margin entire, lateral lobes 0.5–0.6 × 0.2 mm, sub-orbicular, the apex rounded, middle lobe 0.4–0.5 × 0.4–0.5 mm, deltoid, the apex acute, with short hairs, spur 1.6–1.8 × 0.8–1.0 mm, similar width along the whole length, cylindrical, straight to slightly curved, glabrous, the apex rounded; gynostemium 0.5–0.6 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Endemic to Brazil (states of Rio de Janeiro and São Paulo), growing in areas of lowland Atlantic Forest (Fig. 4).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—*Campylocentrum paludosum* is similar to *C. fasciola* and *C. fernandezii*, but it is distinguished by its petals obtuse to rounded (vs. acute in *C. fernandezii*), 3-lobed and 5-nerved lip (vs. entire in *C. fernandezii*, and 7-nerved in *C. fasciola*), and spur cylindrical (vs. obovoid-clavate in *C. fasciola* and ellipsoid in *C. fernandezii*) (Table 1).

**Additional specimens examined:**—BRAZIL. Rio de Janeiro: Magé, distrito de Citrolândia, 24 Jan 1984, *Guedes & Gonzaga 630* (RB).

**11. *Campylocentrum pubirhachis*** Schlechter (1922: 67). Type:—BRAZIL. São Paulo: Iguape, Morro das Pedras, December 1918, *A. C. Brade 7806* (lectotype **here designated**: HB!, isolectotypes: AMES!, R!, SP!, SPF!, US!). (Fig. 6D-G)

Roots 1.0–1.5 mm diam., cylindrical. Inflorescence 15.0–50.0 mm long, peduncle 4.0–15.0 mm long, brownish; rachis 11.0–35.0 mm long, brownish, exposed; floral bracts 0.8–1.0 × 0.3–0.4 mm, deltoid, margin minutely ciliate, covering only the base of the pedicellate ovary, the apex acute. Flowers 13–29 (per inflorescence), whitish, distichous, ovary pedicellate 1.2–1.6 mm long, glabrous; dorsal sepal 1.6–2.0 × 0.7–1.0 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; lateral sepals 1.8–2.2 × 0.7–1.0 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; petals 1.2–1.8 × 0.6–0.8 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; lip 1.7–2.0 × 1.8–2.0 mm between the lateral lobes, 3-lobed, 5-nerved, margin entire, lateral lobes 0.9–1.0 × 0.5–0.6 mm, sub-orbicular, the apex rounded, middle lobe 0.8–0.9 × 0.8–1.0 mm, deltoid, the apex acute, spur 2.8–3.1 × 1.0–1.2 mm, wider at base, conical-sigmoid, patent, glabrous, the apex obtuse; gynostemium 0.5–0.7 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Endemic to Brazil (state of São Paulo), rare and known only from two specimens collected in geographically close areas (micro-endemic), growing in lowland, ombrophilous Atlantic Forest (Fig. 4).

**Conservation status:**—Data deficient (DD).

**Nomenclatural and Taxonomic Notes:**—No herbarium citation is available in the original publication, but six specimens that belong to the type series (*A. C. Brade 7806*) were found. Although all samples are well preserved, the one deposited at HB has several specimens on the same sheet and was therefore chosen here as the lectotype.

Among the species in the group with conical spurs (including conical-cylindrical and conical-sigmoid), only *C. pubirhachis* and *C. insulare* occur in the Atlantic Forest. From this species, the former is easily recognized by its longer inflorescences (up to 50.0 mm long vs. ≤ 9.0 mm long) and the lip with entire margin (vs. serrate). It is morphologically related to *C. tyrridion* from which it can be distinguished by its sepals and petals acute at apex (vs. obtuse to rounded) and 5-nerved lip (vs. 3-nerved) (Table 1).

**Additional specimens examined:**—BRAZIL. São Paulo: Pariquera-Açu, Parque Estadual de Pariquera-Abaixo, 5 Jan 1999, *Sztutman 102* (ESA).

**12. *Campylocentrum tenue*** (Lindl.) Rolfe (1903: 246). *Angorchis tenuis* (Lindl.) Kuntze (1891: 652). *Angraecum tenue* Lindley (1840: 68). Type:—Brazil. Pará: *sine loco acurato*, s.d., *C. Martius s.n.* (holotype: M!, isotype: W!, illustration at K!). (Fig. 6H-K)

Roots 1.5–2.0 mm diam., cylindrical to dorso-ventrally flattened. Inflorescences 30.0–100.0 mm long; peduncle 5.0–10.0 mm long, dark brown; rachis 25.0–62.0 mm long, dark brown, exposed; floral bracts 1.0–1.5 × 0.5–0.7 mm, deltoid, margin minutely ciliate, covering only the base of the pedicellate ovary, the apex acuminate. Flowers 13–26 (per inflorescence), whitish, distichous, ovary pedicellate 0.8–1.0 mm long, smooth; dorsal sepal 1.5–1.6 × 0.8–0.9 mm, elliptical, 3-nerved, glabrous, margin entire, the apex acute; lateral sepals 1.8–2.0 × 0.8–1.0 mm, elliptical-lanceolate, 3-nerved, glabrous, margin entire, the apex acute; petals 1.3–1.5 × 0.6–0.7 mm, elliptical, 1-nerved, glabrous, margin entire, the apex acute; lip 1.5–1.7 × 1.4–1.5 mm, entire, ovate, 5-nerved, margin entire, apex acute, spur 1.2–1.3 × 0.9–1.0 mm, wider close to the apex, sub-globose, curved, glabrous, the apex rounded; gynostemium ca. 0.4 mm long, anther cap apex 2-lobed. Capsules not seen.

**Distribution and Habitat:**—Northern Brazil and Venezuela. It is a rare species and known from only four collections. Unfortunately, the majority of the Brazilian collections lack precise locality information. Based on the specimens collected in the vicinities of Belém and Santa Maria de Erebató in Venezuela, it probably grows in lowland forests in the northern portion of the Amazon Basin (Fig. 4).

**Conservation status:**—Although the type specimen has no precise location, the two Brazilian samples are located in the state of Pará, and the other from Venezuela, in the state of Bolívar, which is on the border with Brazil not far from Pará. Based on the low number of collections and the likely geographical closeness among them, we classified this species as Near Threatened (NT). We also highlight that the northern portion of Pará state is one of the most devastated areas in the Brazilian Amazon (Silva *et al.* 2005).

**Nomenclatural and Taxonomic Notes:**—A fragment of the original collection is deposited at W which is cited here as an isotype as well as an illustration of it at K. *Campylocentrum tenue* is a singular species easily recognized by its entire lip and subglobose spur. In general, it resembles *C. fasciola*, which has a 3-lobed lip and obovoid-clavate spur (Table 1).

**Additional specimens examined:**—BRAZIL. Pará: *sine loco acurato*, 16 Oct 1968, *Corrêa 43* (HB); Belém, 24 May 1901, *Huber 1523a* (MG). VENEZUELA. Bolivar: Sucre, Santa Maria de Erebató, Feb 1989, *Sanoja 2526* (MO).

**13. *Campylocentrum tyrridion*** Garay & Dunst. ex Foldats (1970: 441). Type:—VENEZUELA. Miranda: near to Higuero, s.d., *G. C. K. Dunsterville 435* (holotype: AMES, photograph!). (Fig. 6L-T)

*Campylocentrum dressleri* Dietrich & Díaz, (1984: 28). Type:—PANAMA. Darién: Orillas del Río Tschokonake, April 1980, *J. Bisse et al. s.n.* (holotype: HAJB, photograph!).

Roots 1.0–1.3 mm diam., cylindrical. Inflorescence 35.0–110.0 mm long; peduncle 12.0–25.0 mm long, brownish; rachis 23–70.0 mm long, brownish, exposed; floral bracts 1.0–1.5 × 0.3–0.6 mm, deltoid, covering only the base of the pedicellate ovary, margin minutely ciliate, the apex acute. Flowers 14–46 (per inflorescence), whitish, distichous, ovary pedicellate 0.8–1.5 cm long, smooth; dorsal sepal 0.8–1.5 × 0.6–0.8 mm, elliptical, ovate-elliptical to ovate, 1-nerved, glabrous, margin entire, the apex obtuse to rounded; lateral sepals 1.2–1.6 × 0.5–0.8 mm, elliptical to ovate-elliptical, 1-nerved, glabrous, margin entire, the apex acute to obtuse; petals 0.8–1.3 × 0.4–0.5 mm, elliptical, 1-nerved, glabrous, margin entire, the apex obtuse to rounded; lip 1.0–1.2 × 0.8–1.2 mm, 3-lobed, 3-nerved, margin entire, lateral lobes 0.4–0.5 × 0.2–0.3 mm, suborbicular, the apex rounded, middle lobe 0.5–0.9 × 0.2–0.3 mm, deltoid, the apex acute, spur 1.5–2.2 × 0.5–0.6 mm, wider at base, conical to conical-sigmoid, curved to patent, glabrous, the apex acute; gynostemium ca. 0.4 mm long, anther cap apex 2-lobed. Capsules 3.5–4.5 × 1.5–2.0 mm, fusiform to obovoid.



**Distribution and Habitat:**—Southern Mexico and northern South America (Colombia, Costa Rica, Mexico, Panama and Venezuela), although we have not seen specimens from the countries between Costa Rica and Mexico, Govaerts *et al.* (2016) cite this species to Belize and Guatemala, in addition to Ecuador and Peru in South America. It seems to be more common in southern Mexico and Central America, where we found a larger number of specimens than in South America. Due to its wide distribution, the species grows in different kinds of vegetation in lowland to montane forests (up to 1500 m elevation), and has also been found in commercial plantations as indicated on specimen labels (eg. *Coffea*, *Citrus*, *Psidium*). According to Romero-Gonzalez & Fernandez-Concha (2005) the species tends to grow on the twigs of tall trees and is often collected from fallen branches (Fig. 4).

**Conservation status:**—This species has a wide distribution, but southern Mexico and Central America in general (where it is more common) suffer strong anthropic disturbance, as well as the Caribbean coast of South America. Based on this fact, *C. tyrridion* is likely to be classified in a threatened category in the future, while being treated here as Near Threatened (NT).

**Nomenclatural and Taxonomic Notes:**—It was described based on a specimen from Venezuela. Its distribution along Central America and northern Mexico is controversial among authors (Romero-Gonzalez & Fernandez-Concha 2005, Bogarín & Pupulin 2010), but after an analysis of several specimens, we consider the species to have a wide distribution and include the concept of *C. dressleri*, described from Panama.

The specimen used to describe *C. dressleri* has five immature inflorescences, but based on the shape of the spurs it fits in *C. tyrridion*. A discussion about the use of *C. multiflorum* (synonym of *C. fasciola*) for specimens from the Pacific coast of Costa Rica is presented above (see comments under *C. fasciola*).

Its flowers are morphologically variable, and are similar to *C. pubirhachis* and *C. amazonicum*, from which it differs by the dorsal sepal elliptical (vs. sub-orbicular in *C. amazonicum*), with the dorsal sepal apex obtuse to rounded (vs. acute in *C. pubirhachis*), lip longer than wide (vs. wider than long in *C. amazonicum*), and 3-nerved lip (5-nerved in *C. amazonicum* and *C. pubirhachis*) (Table 1).

**Additional specimens examined:**—COLOMBIA. Guajira: Sierra Nevada de Santa Marta, s.d., *Purdie s.n.* (K). COSTA RICA. Buenos Aires de Osa, May 1925, *Lankester*

*s.n.* (K); *ibid.*, 5 Apr 1934, *Valerio s.n.* (CR); Corredores, Río Bonito, 23 Apr 2007, *Dressler 6850* (JBL); Puntarenas: Laurel, 12 Apr 1978, *Todzia 219* (CR, F, SEL); Puerto Jimenez, Peninsula Osa, Golfo Dulce, 31 Mar 1930, *Cufodonti 155* (W); San José: San Isidro de El General, 11 May 1932, *Kupper 1356* (M). MEXICO. Quintana Roo: Margarita Maza, 4 Aug 1998, *Carnevali et al. 5145* (AMES, AMO, CICY, F, K, MEXU, MO, SEL). PANAMA. *Sine loco acurato, s.d.*, *Philip s.n.* (SEL); Bocas del Toro: Rio Changuinola, community of Guayacan, 31 Aug 2007, *Laube et al. 376* (PMA); Canal Zone: Summit Gardens, 26 Jun 1970, *Dressler 3871* (PMA); Darién: El Real, *Duke 4865* (MO). VENEZUELA. Miranda: Páez, Rio Guapo, 8 Jun 1977, *Davidse & González 13757* (HB, MO, P, U, VEN); Zulia: Bolívar, between Pensano and Churugarita, 27 Apr 1982, *Bunting & Trujillo 11424* (VEN).

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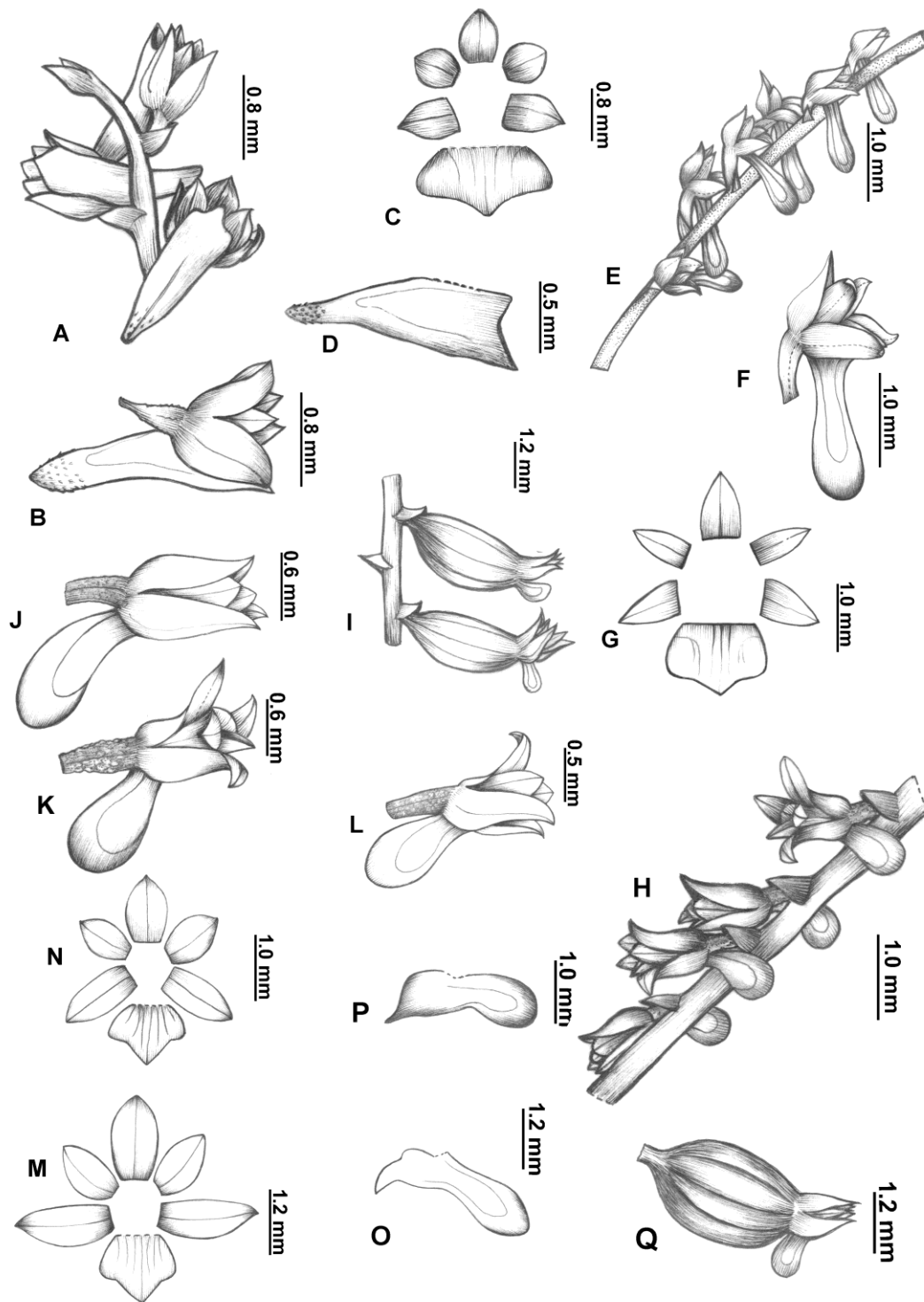


FIGURE 1. A–D. *Campylocentrum amazonicum*, A. Portion of the inflorescence, B. Flower, C. Dissected perianth, D. Lip and spur in profile; E–G. *C. benelliae*, E. Portion of the inflorescence, F. Flower, G. Dissected perianth; H–Q. *C. fasciola*, H–I. Portion of the inflorescence, J–L. Flower, M–N. Dissected perianth, O–P. Lip and spur in profile, Q. Fruit. [A–D. Drawn from *Ule 43b* (BR); E–G. Drawn from *Petini-Benelli & Freitas 925* (UFMT); H, J, M and O. Drawn from *Black & Foster 48-3422* (IAN); K. Drawn from; I, N, P and Q. Drawn from *no. col.* (W no. 17191)].



FIGURE 2. Distribution map of *Campylocentrum amazonicum* (grey triangle), *C. benellii* (white square), *C. fasciola* (black circle), and *C. fernandezii* (black square), *Campylocentrum generalense* (white circle), *C. grisebachii* (grey circle).



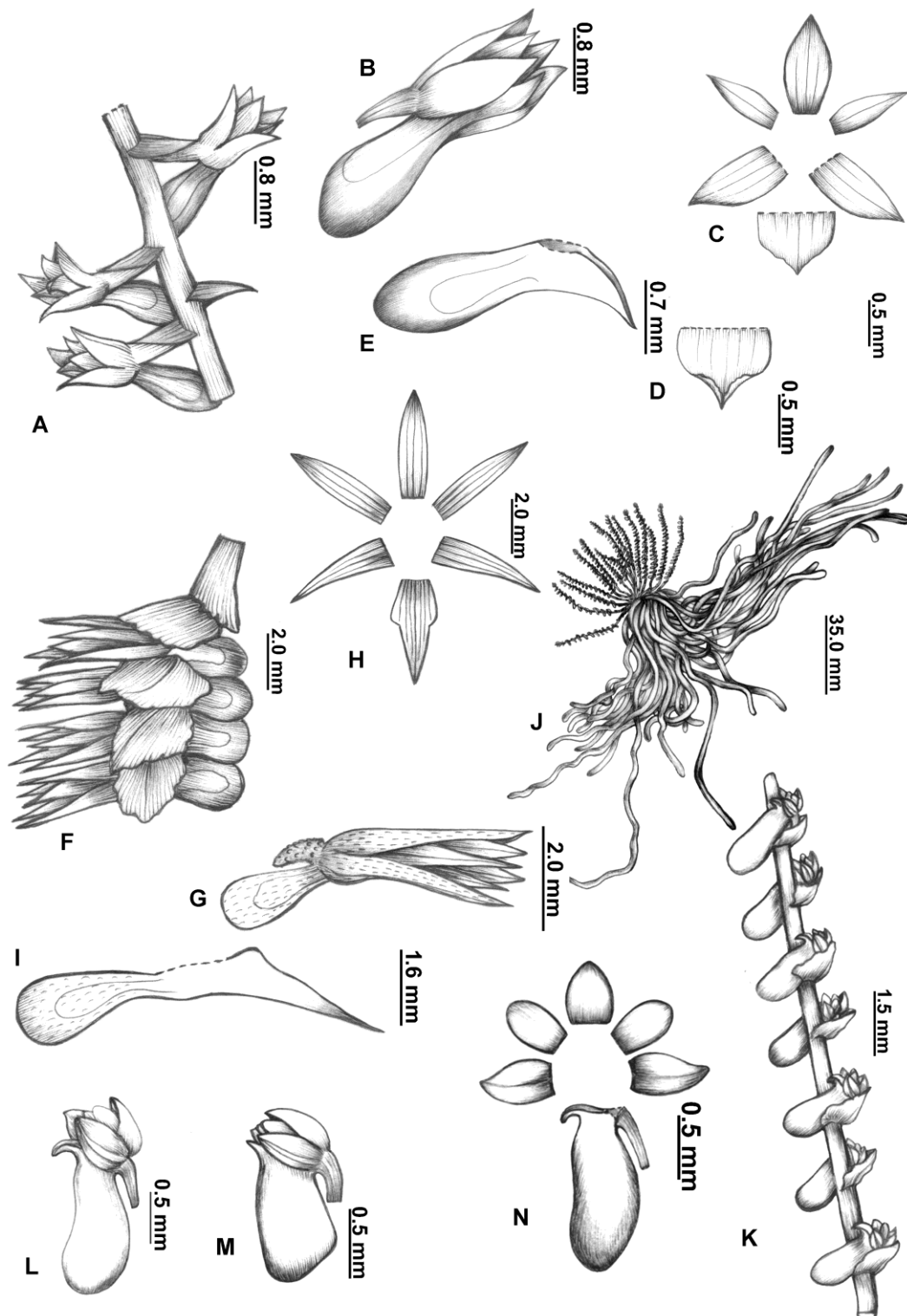


FIGURE 3. A–D. *C. fernandezii*, A. Portion of the inflorescence, B. Flower, C. Dissected perianth, D. Lip not extended, E. Lip and spur in profile, F–I. *Campylocentrum generalense*, F. Portion of the inflorescence, G. Flower, H. Lip and spur in profile, I. Dissected perianth; J–N. *C. grisebachii*, J. Habit, K. Portion of the inflorescence, L–M. Flower, N. Dissected perianth. [A–D. Drawn from *Fernandez 2027* (COL); F–I. Drawn from *Dressler s.n.* (MO); J–L and N. Drawn from *Wettstein & Schiffner s.n.* (WU); M. Drawn from *Rosa 110* (HRCB)].

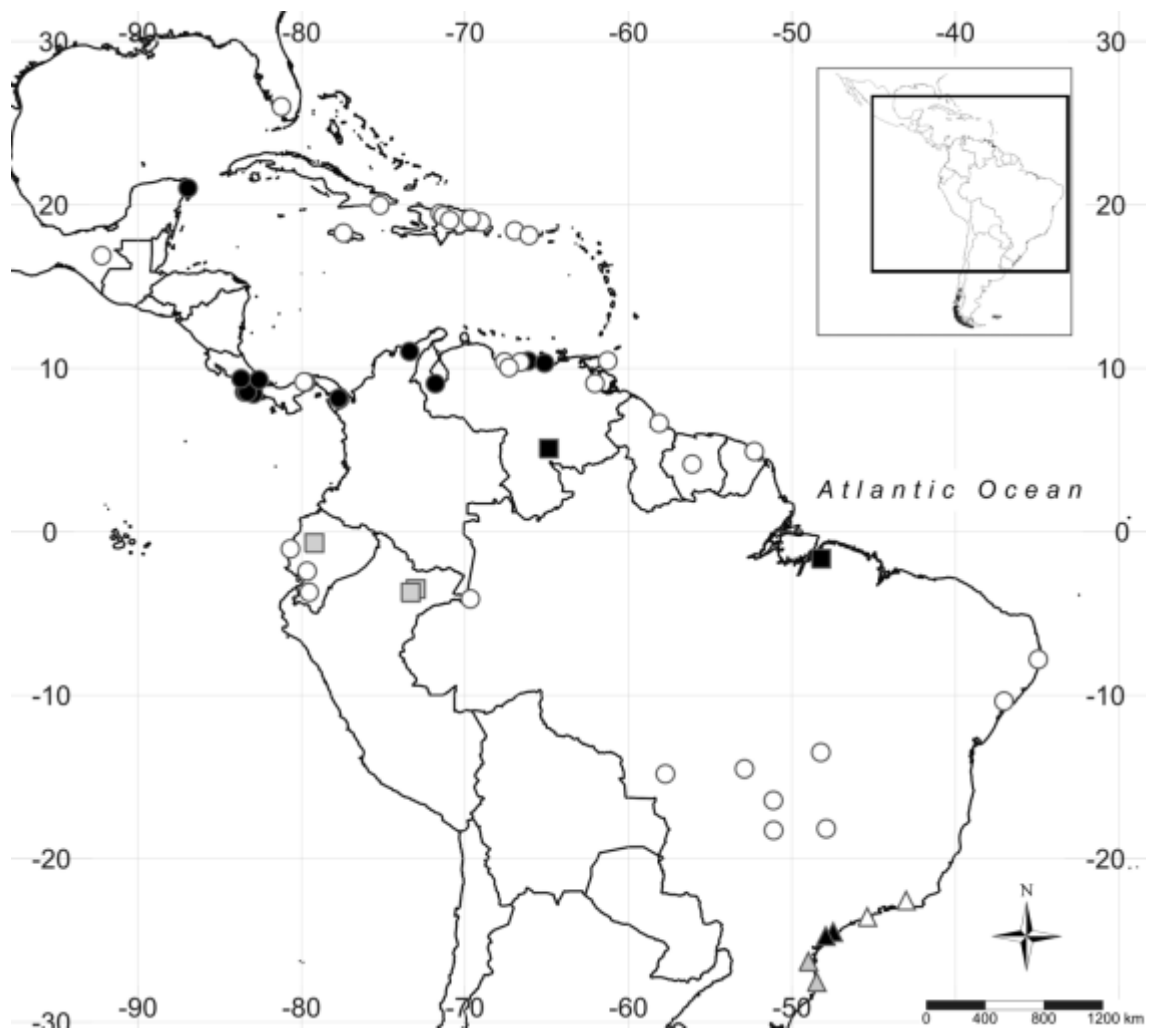


FIGURE 4. Distribution map of *Campylocentrum insulare* (grey triangle), and *C. minutum* (grey square), *C. pachyrrhizum* (white circle), *C. paludosum* (white triangle), *C. pubirhachis* (black triangle), *C. tenue* (black square), and *C. tyridion* (black circle).

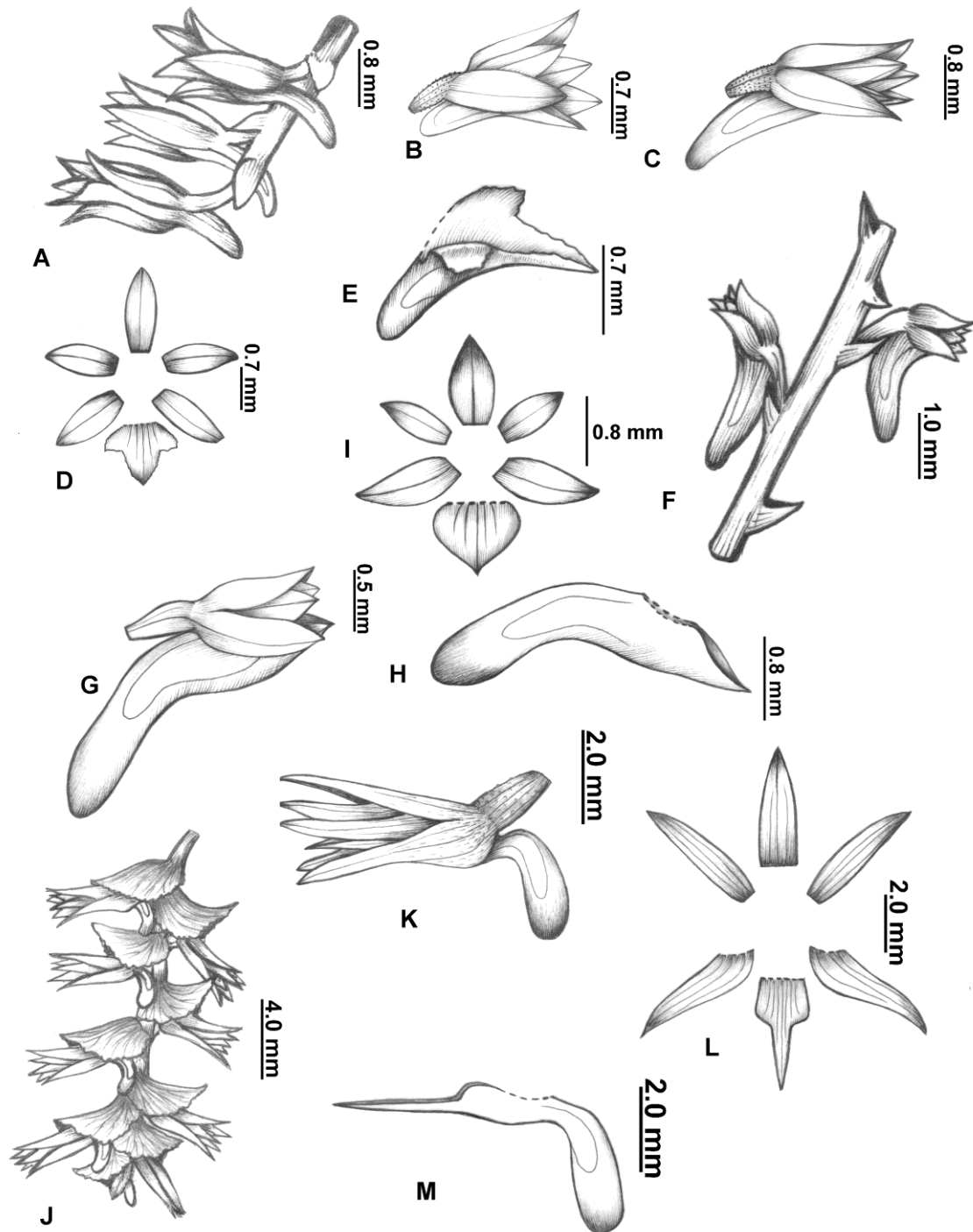


FIGURE 5. A–E. *C. insulare*, A. Portion of the inflorescence, B–C. Flower, D. Dissected perianth, E. Lip and spur in profile; F–I *C. minutum*, F. Portion of the inflorescence, G. Flower, H. Lip and spur in profile, I. Dissected perianth J–M. *Campylocentrum pachyrrhizum*, J. Portion of the inflorescence, K. Flower, L. Dissected perianth, M. Lip and spur in profile. [A and C–E. Drawn from *W. S. Mancinelli 1080* (UPCB); B. Drawn from *Zanin 1642* (FLOR); F–I. Drawn from *Vásquez & Jaramillo 11479* (MO); J–M. Drawn from *Braga et al. 3184* (INPA)].

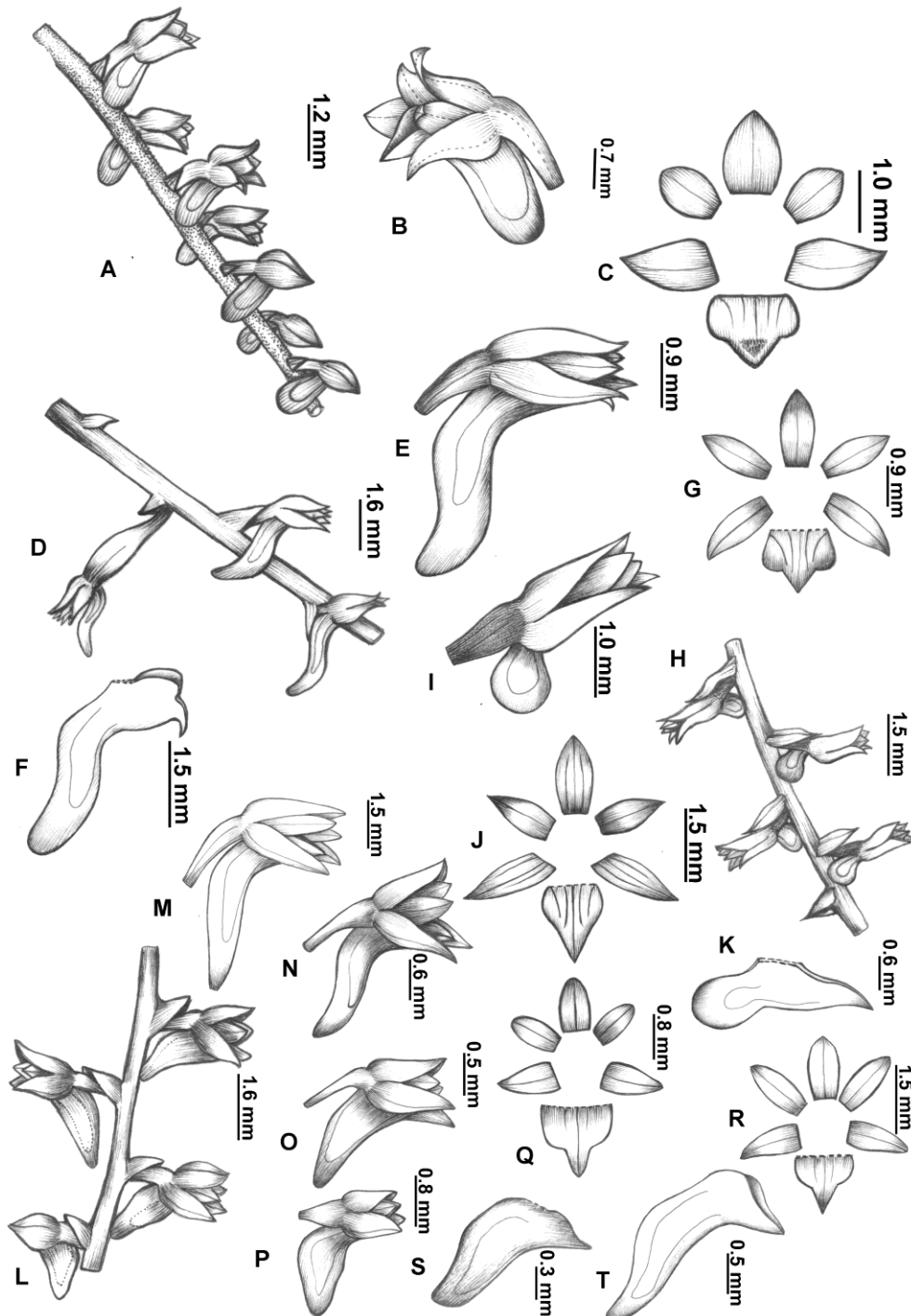


FIGURE 6. A–C. *C. paludosum*, A. Portion of the inflorescence, B. Flower, C. Dissected perianth; D–G. *C. pubirhachis*, D. Portion of the inflorescence, E. Flower, F. Lip and spur in profile, G. Dissected perianth; H–K. *C. tenue*, H. Portion of the inflorescence, I. Flower, J. Dissected perianth, K. Lip and spur in profile; L–T. *C. tyrridion*, L. Portion of the inflorescence, M–P. Flower, Q–R. Dissected perianth, S–T. Lip and spur in profile. [A–C. Drawn from *Miranda 87* (UFP); D–G. Drawn from *Sztutman 102* (ESA); H–K. Drawn from *Corrêa 43* (HB); L, O and Q. Drawn from *Lankester s.n.* (K); M, R and T. Drawn from *Davidse & González 13757* (HB); P and S. Drawn from *G. Cufodonti 155* (W); N. Drawn from *W. Purdie s.n.* (K)].

**TABLE 1.** Main morphological features of the species of section *Dendrophylopsis*.

Species	Roots	Inflorescences	Floral bracts	Sepals	Petals	Lip	Spur	Anther cap
<i>C. amazonicum</i>	1.0 mm, cylindrical	Rachis exposed, 25–27 flowered	Deltoid, minutely ciliate, acute	Sub-orbicular or ovate, 1-nerved	Sub-orbicular, 1-nerved	3-lobed, 5-nerved	Conical, straight, apex acute	2-lobed
<i>C. benellii</i>	1.0–1.5 mm, cylindrical	Rachis exposed, 10–26 flowered	Deltoid, minutely ciliate, acute	Ovate, 1-nerved	Ovate, 1-nerved	3-lobed, 7-nerved	Cylindrical-clavate, patent, apex rounded	2-lobed
<i>C. fasciola</i>	1.0–1.5 mm, cylindrical	Rachis exposed, 10–64 flowered	Deltoid, minutely ciliate, acute	Ovate-elliptical, wide-elliptical or oblong elliptical, 1-nerved	Obovate-elliptical to elliptical, 1-nerved	3-lobed, 7-nerved	Obovoid-clavate, straight to slightly curved, apex rounded	2-lobed
<i>C. fernandezii</i>	1.0–1.2 mm, cylindrical	Rachis exposed, 8–22 flowered	Deltoid, minutely ciliate, acute to obtuse	Elliptical, 1-nerved	Elliptical, 1-nerved	Entire, 5-nerved	Ellipsoid, curved, apex rounded	2-lobed
<i>C. generalense</i>	2.0–3.5 mm, dorso-ventrally flattened	Rachis covered by floral bracts, 13–25 flowered	Ovate, erose, acute	Oblong-lanceolate, 3-nerved	Oblong-lanceolate, 3-nerved	3-lobed, 7-nerved	Clavate, straight, apex rounded	Rounded
<i>C. grisebachii</i>	1.0–2.0 mm, cylindrical	Rachis exposed, 13–32 flowered	Ovate, entire, obtuse to rounded	Ovate to sub-orbicular or elliptical, unnerved	Oblong to ovate, unnerved	Entire, unnerved	Obovoid-clavate, patent, apex rounded	Truncate
<i>C. insulare</i>	0.8–2.0 mm, cylindrical to dorso-ventrally flattened	Rachis exposed, 7–11 flowered	Deltoid, minutely ciliate, acute	Elliptical, 1-nerved	Ovate to elliptical, 1-nerved	3-lobed, 3–5-nerved	Conical to conical-cylindrical, slightly curved apex rounded	2-lobed
<i>C. minutum</i>	0.8–1.7 mm, cylindrical	Rachis exposed, 7–14 flowered	Deltoid, minutely ciliate, acute	Elliptical to ovate-elliptical, 1-nerved	Ovate to elliptical, 1-nerved	Entire, 5-nerved	Conical-cylindrical, slightly curved, apex rounded	2-lobed
<i>C. pachyrrhizum</i>	2.0–4.0 mm, dorso-ventrally flattened	Rachis exposed, 8–16 flowered	Ovate, erose, acute	Oblong-lanceolate, 3-nerved	Oblong-lanceolate, 3-nerved	3-lobed, 7-nerved	Cylindrical, curved, apex rounded;	Rounded
<i>C. paludosum</i>	1.0–2.0 mm, cylindrical	Rachis exposed, 7–27 flowered	Deltoid, minutely ciliate, acute	Ovate or ovate-elliptical, 1-nerved	Obovate-elliptical, 1-nerved	3-lobed, 5-nerved	Cylindrical, straight to slightly curved, apex rounded	2-lobed
<i>C. pubirhachis</i>	1.0–1.5 mm, cylindrical	Rachis exposed, 13–29 flowered	Deltoid, minutely ciliate, acute	Elliptical, 1-nerved	Elliptical, 1-nerved	3-lobed, 5-nerved	Conical-sigmoid, patent, apex obtuse	2-lobed
<i>C. tenue</i>	1.5–2.0 mm, cylindrical to dorso-ventrally flattened	Rachis exposed, 13–26 flowered	Deltoid, minutely ciliate, acuminate	Elliptical or elliptical-lanceolate, 3-nerved	Elliptical, 1-nerved	Entire, 5-nerved	Sub-globose, curved, apex rounded	2-lobed
<i>C. tyrridion</i>	1.0–1.3 mm, cylindrical	Rachis exposed, 14–46 flowered	Deltoid, minutely ciliate, acute	Elliptical, ovate-elliptical or ovate, 1-nerved	Elliptical, 1-nerved	3-lobed, 3-nerved	Conical to conical-sigmoid, curved to patent, apex acute	2-lobed

**Taxonomic revision of *Campylocentrum* sect. *Campylocentrum* Cogn. (Orchidaceae–Vandae–Angraecinae) in Brazil.**

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**Abstract**

A taxonomical revision of the Brazilian species of *Campylocentrum* sect. *Campylocentrum* is provided. Ten species are recognized, three are endemic to the Atlantic Forest of Brazil. *Campylocentrum steyermarkii* is re-established, while *C. bonifaziae*, *C. christensonii*, *C. colombianum*, *C. flavum*, *C. gracile*, and *C. puyense* are synonymized. This study provides typifications, synonymies, conservation statuses (when possible), descriptions, illustrations, distribution maps and an identification key.

**Keywords:** Epidendroideae, Monocots, Neotropics, South America.

## Introduction

*Campylocentrum* Benth (1881: 337) and its sister genus *Dendrophylox* Reichenbach (1864: 903) are the only representatives of the subtribe Angraecinae in the Neotropics (Carlsward *et al.* 2003). The genus is composed by 73 species (Carlsward 2014, Govaerts *et al.* 2016, Pessoa *et al.* 2017) which are organized in five monophyletic sections, *C. sect. Campylocentrum* Cogniaux (1906: 504), *C. sect. Dendrophylopsis* Cogniaux (1906: 504), *C. sect. Laevigatum* E. Pessoa & M. Chase (2017: in press), *C. sect. Pseudocampylocentrum* Cogniaux (1906: 504), and *C. sect. Teretifolium* E. Pessoa & M. Chase (2017: in press).

The relationships of these clades were inferred using multiple markers (nuclear and plastidial), and shows that the previous infra-generic classification of *Campylocentrum* proposed by Cogniaux was not natural (Pessoa *et al.* 2017). *Campylocentrum sect. Campylocentrum sensu* Cogniaux (1906) was split in three clades: *C. sect. Laevigatum* and *C. sect. Teretifolium* include species with smooth capsules, while *C. sect. Campylocentrum* was re-circumscribed and includes only species with 6-ribbed capsules (Pessoa *et al.* 2017).

The section *Campylocentrum* is also characterized by leafy species. The leaves are conduplicate and the roots cylindrical and smooth. It includes half of the genus (38 species) and is widespread in the Neotropical region from the United States (Florida) to Argentina (Misiones) (Pessoa *et al.* 2017).

The type species of the genus, *C. schiedei* (Reichenbach 1850: 857) Benth ex Hemsley (1884: 292), was first described under *Angraecum* Bory (1804: 359), while other species like *C. calostachyum* (Barbosa Rodrigues 1881: 141) Cogniaux (1906: 514) under *Aeranthes* Lindley (1824: 817). The names published until the XIXth century were transferred to *Campylocentrum* mainly by Rolfe (1903) and Cogniaux (1906). The sections *Dendrophylopsis*, *Pseudocampylocentrum*, and *Teretifolium* were recently revised by Pessoa & Alves (2016a, 2016b) although the majority of species of *Campylocentrum* still need a taxonomic revision.

Many species of *C. sect. Campylocentrum* are cited as morphological and/or nomenclatural complexes (Pessoa *et al.* 2015, Pessoa & Alves 2015a, Pessoa *et al.* 2017). The systematic of the group is confuse mainly because of the proliferation in the

last 15 years of “new names” for species already described (eg. in Pessoa & Alves 2015b). We provide here a review of the Brazilian species which covers about 30% of the group but a major review of the remind species is mandatory. An exhaustive morphological analysis covering the geographical and morphological variation of the species was carried on the last five years and the taxonomic treatment provides typifications, synonymy, conservation statuses, descriptions, illustrations, distribution maps and an identification key.

## **Material and Methods**

Specimens from 74 herbaria were analyzed (including all types): ALCB, \*AMES, \*AS, ASE, B, BA, BAF, BHCB, BHZB, BM, BR, C, CEN, CEPEC, CESJ, COAH, COL, COR, E, EAC, EAN, ESA, \*F, FLOR, FR, FUEL, FURB, G, GOET, \*GUAY, HAMAB, HB, HBG, HBR, HEID, HEPH, HRCB, HUEFS, HST, IAC, IAN, IBGE, ICN, INPA, IPA, JPB, K, L, M, MAC, MBML, MG, MIRR, MO, \*NY, P, PEUFR, R, RFA, RB, \*SEL, SP, SPF, U, US, UB, UEC, UFP, UFRN, UFRR, UPCB, \*VEN, VIES, W, WU; acronyms according to Thiers (2016), [“\*” only images]. Additionally, specimens from six species were collected in expeditions carried out between 2011–2015 covering majority of the Brazilian states. Samples were deposited at UFP with duplicates sent to NY, RB and SP.

Maps with the geographic distribution were produced using SimpleMapp (Shorthouse 2016). The conservation status for species with more than four known specimens was defined according to the categories proposed by IUCN (2016) using a databank of geographical coordinates from field collections and herbarium material. Specimens with no geo-referenced data had their localities determined using online gazetteers (Google Earth).

The morphological analyses were based on examination of several live and dry (rehydrated) specimens. The flowers were dissected and the perianth was mounted between glass slides and cover slips using Entellan (Merck) or glycerin. The morphological terminology followed Harris & Harris (2001) and Stearn (1995).

## **Taxonomic Treatment**



***Campylocentrum*** Bentham (1881: 337).

Type species: *Campylocentrum schiedei* (Rchb. f.) Benth. ex Hemsley (1884: 292).  
(Basionym: *Angraecum schiedei* Reichenbach (1850: 857); originally published as  
*Todaroa micrantha* Richard & Galeotti (1845: 28).

*Todaroa* Richard & Galeotti (1845: 28), *nom. illeg.* [non *Todaroa* Parlatores (1843: 155).  
Apiaceae (= Umbelliferae)].

Type species: *Todaroa micrantha* Richard & Galeotti (1845: 28), *nom. illeg.*

### Key to the sections of *Campylocentrum*

1. Leafless plants (leaves reduced to achlorophyllous scales), viscidium of one part.....***C. sect. Dendrophylopsis***  
– Leafy plants (leaves chlorophyllous), stem elongated, viscidium of two parts.....2
2. Leaf blades reduced to small, fleshy and cylindrical projections.....***C. sect. Pseudocampylocentrum***  
– Leaf blades developed, cylindrical or conduplicate.....3
3. Leaves cylindrical.....***C. sect. Teretifolium***  
– Leaves conduplicate.....4
4. Capsules smooth.....***C. sect. Laevigatum***
4. Capsules 6-ribbed.....***C. sect. Campylocentrum***

***Campylocentrum sect. Campylocentrum Cogniaux*** (1906: 504). 1906.

Type species: *Campylocentrum schiedei* (Rchb. f.) Benth. ex Hemsl.

Epiphytic herbs. Roots cylindrical or dorso-ventrally flattened, fibrous, smooth, greenish, whitish, or dark grey. Stem cylindrical. Leaves pale to dark green, elliptical, oblanceolate, oblong to oblong-elliptical, sub-falcate, the apex asymmetrically 2-lobed, lobes acute, obtuse or rounded, margin entire. Inflorescences congest or lax, peduncle glabrous, hirtellous, minutely papillate to papillate, brownish, rachis glabrous, hirtellous, minutely papillate to papillate, brownish; floral bracts deltoid to lanceolate, margin entire to minutely denticulate, membranaceous, the apex acute to acuminate. Flowers cream colored, pale orange, whitish, white-greenish or yellowish, distichous,

pedicellate ovary glabrous, densely hirtelous to minutely papillate; dorsal sepal elliptical, oblong, oblong-elliptical, oblong-lanceolate to oblong-ovate, adaxially sparsely pilose or glabrous, 1–3-nerved, margin entire, membranaceous, the apex acute, obtuse or rounded; lateral sepals oblong, oblong-elliptical to oblong-lanceolate, subfalcate, adaxially sparsely pilose or glabrous, 1–3-nerved, margin entire, membranaceous, the apex acute, obtuse or rounded; petals elliptical-lanceolate, oblong to oblong-elliptical, adaxially pilose or glabrous, 1–3-nerved, margin entire, membranaceous, the apex acute, obtuse, or rounded; lip entire ovate or 3-lobed, 5–9-nerved, margin entire, membranaceous, producing a spur at base, lateral lobes oblanceolate, oblong to ovate, the apex obtuse, rounded to truncate, mid-lobe deltoid to lanceolate, the apex acute, spur clavate, cylindrical, cylindrical-clavate, ellipsoid or ovoid, curved, inflexed, patent, sigmoid, slightly curved or straight, pale green, pale orange or yellowish, glabrous to sparsely pilose, the apex acute, attenuate or rounded; gynostemium reduced, anther cap apex 2-lobed, pollinia 2, globose. Capsules fusiform, 6-ribbed, densely hirtellous, glabrous or minutely papillate, pedicelate.

The section is represented in Brazil by ten species, four are endemic to the Atlantic Forest, while six grow in Amazon forest. *C. micranthum* (Lindley 1835: t. 1772) Maury (1889: 273) is the only species disjunct between both forests. These plants grow commonly in the sub-canopy of moist environments.

#### **Key to species of *Campylocentrum* sect. *Campylocentrum* from Brazil.**

1. Inflorescence congest, glabrous; sepals and petals 3-nerved.....2
  - Inflorescence lax, hirtellous, minutely papillate or papillate; sepals and petals 1-nerved.....5
2. Spur  $\geq$  12 mm long, patent, the apex acute to obtuse.....*C. huebneri* Mansfeld (1928: 382)
  - Spur  $\leq$  6 mm long, slightly curved, inflexed or straight, the apex rounded.....3
3. Spur  $\leq$  3.5 mm long, shorter than the sepals, inflexed.....*C. micranthum*
  - Spur  $\geq$  4.8 mm long, as long as or longer than the sepals, slightly curved or straight.....4

4. Flowers pale green or cream-colored; spur slightly curved.....*C. kuntzei* Cogniaux ex Kuntze (1898: 298)  
 – Flowers pale orange; spur straight.....*C. mattogrossense* Hoehne (1941: 62)
5. Lip entire, spur ellipsoid or ovoid, inflexed or sigmoid.....6  
 – Lip 3-lobed, spur clavate, cylindrical or cylindrical-clavate, curved, slightly curved or straight.....7
6. Spur ellipsoid, sigmoid.....*C. hondurensense* Ames (1923: 37)  
 – Spur ovoid, inflexed.....*C. steyermarkii* Foldats (1968: 316)
7. Spur straight, longer than the sepals.....*C. calostachyum*  
 – Spur curved or slightly curved, as long as or shorter than the sepals.....8
8. Pedicellate ovary and capsules densely hirtelous; spur twice longer than the pedicellate ovary.....*C. hirtellum* Cogniaux (1906: 521)  
 – Pedicellate ovary minutely papillate; capsules glabrous; spur shorter to slightly longer than the pedicellate ovary.....9
9. Stem up to 0.7 cm long; sepals  $\leq$  1.6 mm long; spur cylindrical.....*C. serranum* E. Pessoa & M. Alves (2015b: 54)  
 – Stem up to 25 cm long; sepals  $\geq$  1.8 mm long; spur clavate to cylindrical-clavate.....*C. ulaei* Cogniaux (1906: 514)

**1. *Campylocentrum calostachyum* (Barb. Rodr.) Cogniaux (1906: 514).** *Aeranthes calostachya* Barbosa Rodrigues (1881: 141). Type:—BRAZIL. Rio de Janeiro: Paulo de Frontin (“Rodeio”), Serra de Santana, March 1881, *J. Barbosa Rodrigues s.n.* [holotype: destroyed, *fide* Sprunger et al. (1996), lectotype **here designated**: Barbosa Rodrigues J., *Revista de Engenharia* 3: tab. 719, original illustration at Jardim Botânico do Rio de Janeiro; reproduced by Sprunger et al. (1996), *Iconographie des Orchidées du Brésil* 5: 396, tab. 268]. (Fig. 1A-D, Fig. 2)

Roots 1–3 mm diam., cylindrical to dorso-ventrally flattened. Stem 0.7–6.5 cm long. Leaves 3–8.5 × 0.6–1.3 cm, oblong-elliptical, sub-falcate, lobes acute at apex. Inflorescences 3–9 cm long, lax, peduncle 1.1–2.2 cm long, papillate; rachis 1.9–6.8 cm long, papillate; floral bracts 1–1.5 × 0.4–0.7 mm, deltoid, margin entire to minutely denticulate, the apex acuminate. Flowers 12–42 (per inflorescence), whitish-green, pedicellate ovary 0.9–2 mm long, glabrous to minutely papillate; dorsal sepal 2.5–3 ×

0.6–1 mm, elliptical to oblong, 1-nerved, the apex obtuse, glabrous; lateral sepals 2.5–3 × 0.5–0.8 mm, oblong, subfalcate, glabrous, 1-nerved, the apex acute to obtuse; petals 2.5–2.8 × 0.5–1 mm, oblong-elliptical to oblong, 1-nerved, glabrous, the apex acute to obtuse; lip 2.3–2.7 mm long, 1.1–1.4 mm wide between the lateral lobes, 3-lobed, 5-nerved, margin entire, producing a spur at base, lateral lobes 1.1–1.2 × 0.3–0.5 mm, oblanceolate, the apex rounded, mid-lobe 1.2–1.5 × 0.5–0.9 mm, deltoid to lanceolate, the apex acute, spur 2.6–3.3 mm long, 0.6–1 mm diam., cylindrical, straight, pale green, glabrous, the apex rounded; gynostemium 0.3–0.5 mm long, anther cap apex 2-lobed. Capsules 4–6 × 1.5–2 mm, glabrous, pedicel ca. 1 mm long.

**Distribution and Habitat:**—Endemic to Brazil (states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo). This rare species grows in Atlantic forest from the sea level to montane areas (Itatiaia National Park).

**Conservation status:**—Due to its reduced and very fragmented area of occurrence and occupancy (B1a and B2a), this species is classified as Vulnerable (VU).

**Nomenclatural notes:**—The type specimen collected by Barbosa Rodrigues was accidentally destroyed by a flood (Sprunger *et al.* 1996). Then, a lectotype for this name is here proposed based on the original illustration made by Barbosa Rodrigues and cited in the original publication. Cogniaux (1906) included a wrong spelling variation of the name, “*C. callistachyum* Cogn.”, which is included in some important database of plants, such as The Plant List and IPNI. Besides that, the exclusion of Barbosa Rodrigues from the authority of the name is a mistake corrected here.

**Similar species:**—*Campylocentrum calostachyum* is morphologically related with the group of species with relatively longer and lax inflorescences, flowers with sepals and petals 1-nerved, and 3-lobed lip (represented in Brazil by *C. hirtellum*, *C. serranum* and *C. ulaei*). Among these species, it is distinguished by its straight spur, comparatively longer than the sepals. The vegetative portion is easily distinguished by its longer leaves of up to 8.5 cm (*vs.* up to 4.5 cm long).

**Additional specimens examined:**—BRASIL. Bahia: Arataca, Parque Nacional da Serra das Lontras, 4 Jul 2011, *Leitman et al.* 358 (RB); Espírito Santo: Domingos Martins, 15 Jun 1972, *Kautzky* 380 (HB); Minas Gerais: Itatiaia, Maromba, 21 Mar 1942, *Brade* 17235 (RB); Rio de Janeiro: Itatiaia, Parque Nacional do Itatiaia, lote 37, 27 Mar 1942, *sine col.* (RB); Guapimirim, Monte Olivete, 16 Mar 1994, *Figueredo s.n.* (RB); São Paulo: Caraguatatuba, 01 May 2015, *Miranda s.n.* (UFP).

**2. *Campylocentrum hirtellum* Cogniaux** (1906: 521). Type:—BRAZIL. Rio de Janeiro: Teresópolis, Serra dos Orgãos, 1886-1887, *H. Schenck 2718* (holotype: B, destroyed, letotype **here designated**: BR!). (Fig. 1E-H, Fig. 2)

Roots 0.5–2 mm diam., cylindrical to dorso-ventrally flattened. Stem 0.3–0.7 cm long. Leaves 0.5–2.1 × 0.2–0.5 cm, oblanceolate, sub-falcate, lobes acute at apex. Inflorescences 1.5–5 cm long, lax, peduncle 0.5–1 cm long, hirtellous; rachis 1–3.7 cm long, hirtellous; floral bracts 0.5–0.7 × 0.2–0.4 mm, deltoid, margin entire to minutely denticulate, the apex acute. Flowers 10–30 (per inflorescence), whitish, pedicellate ovary 0.8–1 mm long, densely hirtellous; dorsal sepal 2.2–3 × 0.7–1 mm, oblong-elliptical, adaxially sparsely pilose, 1-nerved, the apex obtuse; lateral sepals 2.5–3.2 × 0.5–0.8 mm, oblong, subfalcate, adaxially sparsely pilose, 1-nerved, the apex acute; petals 1.8–2.8 × 0.5–1 mm, oblong-elliptical, 1-nerved, glabrous, the apex acute; lip 2.2–2.8 mm long, 1–2 mm wide between the lateral lobes, 3-lobed, 7–9-nerved, margin entire, producing a spur at base, lateral lobes 0.8–1 × 0.3–0.5 mm, oblanceolate, the apex rounded, mid-lobe 1.3–1.8 × 0.3–0.7 mm, lanceolate, the apex acute, spur 1.6–2.5 mm long, 0.6–1 mm diam., cylindrical-clavate, curved, glabrous, the apex rounded; gynostemium 0.5–0.7 mm long, anther cap apex 2-lobed. Capsules 4–6 × 1.5–2 mm, densely hirtellous, pedicel 1–1.2 mm long.

**Distribution and Habitat:**—Endemic to Brazil (states of Rio de Janeiro and Santa Catarina). This rare species is known from few specimens and grows in Atlantic Forest. The labels of the specimens do not provide additional information about the habitat of this species, but possibly grows in dense ombrophilous forest.

**Conservation status:**—Based on criterion B1a and B2a, this species is considered Endangered (EN).

**Nomenclatural notes:**—The type specimen collected by H. Schenck was destroyed in the WWII and the lectotype designed here is constituted by a capsule with persistent perianth deposited in BR. Although it had been described under *C.* sect. *Dendrophylopsis* as a leafless species, the analysis of other specimens confirmed the presence of small leaves which are caduceus in some specimens.

**Similar species:**—*Campylocentrum hirtellum* is distinguished from all other species of the section by its densely hirtellous pedicellate ovary and capsules. The most

similar species is *C. serranum*, from which can be recognized also by the longer perianth ( $\geq 2.2$  mm long vs.  $\leq 1.6$  mm long), lip 7–9-nerved (vs. 5-nerved) and spur twice longer than the pedicellate ovary (vs. slightly longer). Its small leaves (0.5–2.1 cm long) are often absent in dried specimens.

**Additional specimens examined:**—BRAZIL. Rio de Janeiro: *sine loco acurato*, s.d., *no col.* (R, SP); Cantagalo, 1844, *Riedel s.n.* (W, P); Santa Catarina: Blumenau, Jun 1868, *Muller 84* (K); Ibirama, Horto Florestal, 2 Nov 1953, *Reitz & Klein 1152* (HB, HBR).

**3. *Campylocentrum hondurense* Ames (1923: 37).** Type:—HONDURAS. Lancetilla Farm, near Tela, 16 March 1923, AMES II-210 (holotype: AMES, photograph!).

(Fig. 1I-L, Fig. 2)

*Campylocentrum christensonii* Szlachetko & Kolanowska (2013: 264). *syn. nov.*

Type:—GUYANA. *Sine loco acurato*, s.d, *Thurn 552* (holotype: K!).

Roots 0.5–1 mm diam., cylindrical. Stem 0.2–4 cm long. Leaves 1.2–3.5 × 0.2–0.6 cm, elliptical, sub-falcate, lobes acute at apex. Inflorescences 0.8–2.7 cm long, lax, peduncle 0.3–0.8 cm long, minutely papillate; rachis 0.5–1.9 cm long, minutely papillate; floral bracts 1–1.3 × 0.4–0.5 mm, deltoid, margin entire to minutely denticulate, the apex acute. Flowers 3–15 (per inflorescence), whitish-green, pedicellate ovary 1–1.4 mm long, minutely papillate; dorsal sepal 1.8–2 × 0.8–1 mm, oblong-ovate, glabrous, 1-nerved, the apex acute; lateral sepals 2.1–2.3 × 0.7–1 mm, oblong, subfalcate, glabrous, 1-nerved, the apex acute; petals 1.3–1.7 × 0.5–0.8 mm, oblong-elliptical, 1-nerved, glabrous, the apex acute; lip 1.8–2.1 × 1–1.2 mm, entire, ovate, 5-nerved, margin entire, the apex acute, producing a spur at base, spur 2–3 mm long, 0.4–0.6 mm diam., ellipsoid, sigmoid, pale green, glabrous to sparsely pilose, the apex attenuate; gynostemium 0.6–0.7 mm long, anther cap apex 2-lobed. Capsules 5–7 × 1.2–2 mm, glabrous to minutely papillate, pedicel 0.8–1 mm long.

**Distribution and Habitat:**—Known to Brazil (states of Mato Grosso, Pará and Rondônia), Guyana, Honduras, Peru, Trinidad & Tobago and Venezuela. It grows in lowland ombrophylous forests, but is also found in seasonal forests.

**Conservation status:**—Based on its wide distribution, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—The analysis of the type specimen of the recently described *C. christensonii* confirms it as a synonym. Szlachetko and Kolanowska (2013) compared it to *C. steyermarkii* although morphologically related is easily distinguished. The authors argued in differences in the spur form (fusiform vs. cylindrical clavate) and size (distinctly longer than the lip vs. sub-equal in length to the lip) to distinguish *C. hondurensis* and *C. christensonii*. However, the variation was not confirmed after deep morphological analyses and it is probably another case of misinterpretation of the spur features in dried flowers.

**Similar species:**—*Campylocentrum hondurensis* and *C. steyermarkii* are the only species with entire lip from the section in Brazil, and also the only ones with relatively longer and lax inflorescences and flowers with sepals and petals 1-nerved that grow in the Brazilian Amazon basin. The morphology of spur is the only way to distinguish them: ellipsoid, sigmoid and attenuate at apex in *C. hondurensis* vs. ovoid, inflexed and rounded at apex in *C. steyermarkii*.

**Additional specimens examined:**—BELIZE. Toledo: Governor Creek, Monkey River, 15 Sep 1943, *Gentle 4472* (LL). BRAZIL. Mato Grosso: Paranaíta, 9 Mar 2012, *Soares et al. 1425461* (HERBAM); Pará: Jacareacanga, 24 Feb, 2012, *Soares et al. 1325382* (HERBAM); Rondônia: Porto Velho, Vista Alegre do Abumã, 23 Feb 2016, *Santos et al. 2842* (UFP). HONDURAS. Comayagua: Siguatepeque, 30 Apr 1947, *Williams & Molina 12545* (EAP). MEXICO. Chiapas: *sine loco acurato*, s.d., *Carnevali et al. 4399* (AMO). PERU. Madre de Dios: Tambopata, Cuzco Amazonico, 14 Jun 1989, *Núñez et al. 11029* (MO). TRINIDAD & TOBAGO. Lay Stretch, Valencia Road, 5 Dec 1924, *Broadway 9019* (BM). VENEZUELA. Amazonas: Río Mavaca, 23 Mar 1988, *Ramírez & Laskowski 246* (VEN).

**4. *Campylocentrum huebneri* Mansfeld** (1928: 382). Type:—BRAZIL. Amazonas: *sine loco acurato*, s.d., *G. Huebner 194* [holotype: B, destroyed, neotype **here designated**: BRAZIL. Amazonas, São Gabriel da Cachoeira, Rio Iamirim, 17 July 1999, *J.B. Silva 835* (neotype: MG!). (Fig. 3A-E, Fig. 4)

*Campylocentrum uroplectrum* Pabst (1955: 135). Type:—BRAZIL. Amazonas: Codajás, Rio Capitarí, 10 November 1950, *A. Fróes 26591* (holotype: IAN!, isotype: HB!, AMES, photograph!).

Roots 1.5–23 mm diam., cylindrical. Stem 5–23 cm long. Leaves 3.5–9 × 1–2 cm, usually dark brown when dried, oblong to oblong-elliptical, lobes obtuse to rounded. Inflorescences 1–2.5 cm long, congest, peduncle 0.2–0.5 cm long, glabrous; rachis 0.8–2 cm long, glabrous; floral bracts 0.7–1.2 × 0.4–0.6 mm, deltoid, margin minutely denticulate, the apex acute. Flowers 8–18 (per inflorescence), yellowish or pale orange, pedicellate ovary 1.8–2.2 mm long, glabrous or sparsely pilose; dorsal sepal 3.2–4.3 × 1.1–2 mm, oblong-lanceolate, 3-nerved, adaxially sparsely pilose, the apex obtuse to rounded; lateral sepals 3.5–5 × 1.1–2 mm, oblong-lanceolate, sub-falcate, 3-nerved, adaxially sparsely pilose, the apex acute, obtuse or rounded; petals 2.6–4 × 1–1.5 mm, oblong-elliptical, 3-nerved, glabrous to adaxially sparsely pilose, the apex acute to obtuse; lip 2.6–4.2 mm long, 3–3.5 mm wide between the lateral lobes, 3-lobed, 7-nerved, margin entire, producing a spur at base, lateral lobes 1–3 × 0.8–1 mm, deltoid to oblong, the apex obtuse to rounded, mid-lobe 1.8–2.1 × 1–1.1 mm, deltoid, the apex acute, spur 12–19 mm long, 1.2–1.5 mm diam., cylindrical, patent, yellowish or pale orange, sparsely pilose, the apex acute to obtuse; gynostemium 0.7–1 mm long, anther cap apex acute. Capsules 9–13 × 3–4 mm, glabrous to sparsely pilose, pedicel 0.8–1 mm long.

**Distribution and Habitat:**—South America (Brazil and Venezuela), in Brazil (states of Acre, Amazonas and Roraima). It grows in the Amazon basin in lowlands up to 200 m elev., often in flooded forests locally called *igapós* or *vázeas*.

**Conservation status:**—Based in the wide distribution and low fragmentation of habitat, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—The holotype of *C. huebneri* was destroyed in the WWII, any isotypes was located as well as no illustrations. A neotype was chosen among the samples collected by *G. Huebner* in state of Amazonas, Brazil.

**Similar species:**—*Campylocentrum huebneri* is part of the “*C. micranthum* complex” (Pessoa et al. 2015b) also represented in Brazil by *C. kuntzei*, *C. mattogrossense* and *C. micranthum*. The species is easily distinguished by its longer patent spur ( $\geq 12$  mm vs. up to 6 mm) and anther cap apex obtuse (vs. 2-lobed). The most similar species is endemic to Peru and Colombia, *C. huebnerioides* D.E. Bennett & Christenson (1998: 408), which differs by a shorter and arched spur.

**Additional specimens examined:**—BRAZIL. Acre: Parangaba, Rio Juruá-Mirim, 21 May 1971, *Mass 13191* (INPA); Amazonas: BR-174 sentido Boa Vista, Nov 1983,



*Hutchison 8758* (UEC); São Gabriel da Cachoeira, Rio Iamirim, 17 Jul 1999, *Silva 835* (MG); Roraima: Caracará, Parque Nacional do Viruá, Rio Barauana, 26 Jun 2010, *Pessoa et al. 355* (INPA); *ibid.*, 19 Sep 2011, *Pessoa et al. 670* (INPA, UFP); *ibid.*, 21 Sep 2011, *Pessoa et al. 701* (INPA, UFP). VENEZUELA. Amazonas: San Carlos de Rio Negro, 22 Sep 1975, *Berry & Brunig 1487* (MO); Atures, Río Coro-Coro, 23 Feb 1987, *Liesner & Holst 21338* (MO).

**5. *Campylocentrum kuntzei* Cogn. ex Kuntze** (1898: 298). Type:—BOLIVIA. Rio Juntas, 500 m alt., 13 April 1892, *C.O. Kuntze s.n.* [lectotype: BR!, designated by Pessoa & Alves (2015a), isoelectotypes: F, photograph!, NY 8632, photograph!, NY 8631, photograph]. (Fig. 3F-J, Fig. 4)

*Campylocentrum flavum* Kolanowska & Szlachetko (2013: 223). **syn. nov.** Type:—COLOMBIA. Antioquia: Between Frontino y Nutibara, 14 October 1989, *L.A. Escobar & F.X. Roldán 8631* (holotype: HUA, photograph!).

*Campylocentrum bonifaziae* Dodson (2003: 191). **syn. nov.** Type:—ECUADOR. Los Rios: Hacienda Clementina, s.d., *J. Cornejo & C. Bonifaz s.n.* (holotype: GUAY, photograph!).

*Campylocentrum colombianum* Schlechter (1920: 205). **syn. nov.** Type:—COLOMBIA. Vale del Cauca: *sine loco acurato*, s.d., *M. Madero s.n.* [holotype: B, destroyed, neotype **here designated**: Schlechter's drawing of the holotype, AMES-26788, isoneotype: Drawing of the holotype in Mansfeld (1929), *Repert. Spec. Nov. Regni Veg. Beih.* 57: Tab. 131 n. 514].

*Campylocentrum puyense* Dodson (2003: 195). **syn. nov.** Type:—ECUADOR. Sucumbios: Caño Zancudo del río Aguarico, 8 October 1991, *C.H. Dodson & G.A. Romero 18906* [holotype: transferred to MO! (originally in RPSC)].

Roots 1.5–3 mm diam., cylindrical. Stem 11–35 cm long. Leaves 4.5–9 × 1.4–2.7 cm, oblong-elliptical to oblanceolate, lobes obtuse. Inflorescences 1.5–4 cm long, congest, peduncle 0.2–0.3 cm long, glabrous; rachis 1.2–3.8 cm long, glabrous; floral bracts 1.5–2 × 1–1.5 mm, deltoid, margin minutely denticulate, the apex acute. Flowers 14–30 (per inflorescence), pale green or cream-colored, pedicellate ovary, 0.8–1.2 mm long,

glabrous; dorsal sepal  $3.8\text{--}5.1 \times 1\text{--}1.2$  mm, oblong, 3-nerved, base adaxially sparsely pilose, the apex acute; lateral sepals  $4.5\text{--}6.0 \times 1\text{--}1.5$  mm, oblong, sub-falcate, 3-nerved, base adaxially sparsely pilose, the apex acute; petals  $3.5\text{--}5 \times 0.8\text{--}1$  mm, oblong, 3-nerved, glabrous, the apex acute to obtuse; lip 4–6 mm long, 1.3–2 mm wide between the lateral lobes, 3-lobed, 7–9-nerved, margin entire, producing a spur at base, lateral lobes  $1.5\text{--}2.1 \times 0.2\text{--}0.4$  mm, oblong to oblanceolate, the apex obtuse, rounded to truncate, middle lobe  $3.0\text{--}4 \times 0.8\text{--}1$  mm, narrowly lanceolate, the apex acute, spur 4.8–6.2 mm long, 1–1.3 mm diam., cylindrical-clavate, slightly curved, cream colored, occasionally sparsely pilose, the apex rounded; gynostemium 0.6–0.8 mm long, anther cap apex rounded. Capsules  $7\text{--}12 \times 2.5\text{--}3.2$  mm, glabrous, pedicel 0.5–0.8 mm long.

**Distribution and Habitat:**—Widespread in South America (Bolivia, Brazil, Colombia, Ecuador, Paraguay and Peru), in Brazil (states of Acre and Goiás). It probably also occurs in the Brazilian states of Mato Grosso and Rondônia (Northern and Central-western Brazil), as cited by Pessoa and Alves 2015a. It grows in lowland to montane forests.

**Conservation status:**—Based on its wide distribution, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—The taxonomy of this species was treated by Pessoa and Alves (2015a), but here we expand its concept including several names once included under *C. micranthum* (Lindl.) Maury besides recently proposed species. “Sepals externally provided of small trichomes”, “size of the perianth”, “form of the spur apex”, and “size of the middle lobe compared with lateral lobes” are among the several features used by Schlechter (1920), Dodson (2003) and Kolanowska and Szlachetko (2013) to distinguish the species. Extensive morphological analyses of flowers show a continuous variation of the characters commonly used to recognize some of the names here synonymized. Its morphological variation is expected due its wide distribution as found in some species of *Campylocentrum* (Pessoa & Alves 2016a, 2016b).

**Similar species:**—*Campylocentrum kuntzei* is a morphologically variable species. Among the Brazilian species, it is similar to *C. mattogrossense* and *C. micranthum*, by their relatively shorter, glabrous and congest inflorescence and flowers with sepals and petals 3-nerved. It differs from *C. micranthum* by it is longer and slightly curved spur (up to 6.2 mm long vs. up to 3.5 mm and inflexed) longer than the sepals (vs. shorter than the sepals), and from *C. mattogrossense* by its pale green or cream-colored flowers

(vs. pale orange) and slightly curved spur (vs. straight). *Campylocentrum lansbergii* (Rchb.f.) Schltr., described and restricted to Venezuela is also morphologically similar but differs by the pendent inflorescences and shorter perianth and capsules.

**Additional specimens examined:**—BOLIVIA. La Paz: Sud Yungas, Santa Rosa, Alto Beni, 18 May 1999, *Kromer & Acebey 417* (LPB not seen, GOET); San Carlos: Mapiri, Sep 1907, *Buchtien 1284* (HGB). BRAZIL. Acre: Alto Juruá, Reserva extrativista, Nov 1993, *Bernacci 3181* (IAC); Senador Guiomard, Rio Iquiri, 17 Apr 2010, *Medeiros et al. 374* (RB); *ibid.*, 19 Mar 2011, *Terra-Araújo et al. 651* (RB); Tarauacá, 18 Sep 1968, *Prance et al. s.n.* (INPA, HB, NY, K); Goiás: Alexania, lago Corumbá, 7 Jun 2005, *Pereira-Silva et al. 10114* (CEN); Corumbáiba, Córrego Lobórea, 14 Nov 1997, *Silva et al. 730* (CEN); Pirenópolis, Santuário de Vida Silvestre Vaga Fogo, 27 Nov 2002, *Fonseca et al. 3856* (CEN, IBGE, SP). COLOMBIA. Antioquia: *sine loco accurately*, Jul 1891, *Lehmann 7623* (K); Betania, Vereda la Italia, 25 Jul 2013, *Fajardo & Zapata 893* (COL); Caquetá: Florencia, Corregimiento San Martín, 30 Sep 2011, *Estudiantes 7136* (COAH, HUAZ not seen); Casanare, Aguazul, Finca Namaste, 11 Apr 1995, *Jaramillo & Alvira 26* (COL); Chocó: Between Quibdó & Tutunendo, 23 Mar 1958, *Uribe 3116* (COL); Río Atrato, Quibdó, 2 May 1975, *Forero et al. 1471* (COL, MO); Cundinamarca: Sasaima, veredas La Herradura y Palacio, 13 Feb 1993, *Betancur et al. 3911* (COL); *ibid.*, Margen del rio Namay, 20 May 1989, *Barrera & Torres 312* (COL); San Luis, Vereda de Manizales, 12 Oct 1981, *Orozco et al. 654* (COL); Vale del Cauca: *sine loco accurately*, 23 Aug 1884, *Lehmann 1614a* (BM, G). ECUADOR. Esmeralda: Esmeralda-Santo Domingo Road, 1 Aug 1980, *Sauleda et al. 3834* (L); Guayaquil: *sine loco accurately*, 6 Aug 1878, *Lehmann s.n.* (W); Las Juntas: *sine loco accurately*, s.d., *Lehmann 8585* (K); Los Rios: Jauneche, Quevedo-Palenque, Canton Vinces, 23 Mar 1980, *Dodson & Gentry 9801* (MO); Manabi: Pedernales, Cerro Pata de Pájaro, 26 Aug 1998, *Neill 11318* (MO); Napo: Reserva biológica Jatun Sacha, Rio Napo, 17 Feb 1990, *Christensen 88248* (C). PARAGUAY. Guairá: Colonia Independencia, 17 Mar 1966, *Esser 14519* (B, HEID). PERU. Cuzco: Quispicanchis, 24 Jul 1991, *Núñez 13846* (MO); Echarate: Puyentimari, 25 January 2008, *Valenzuela et al. 10837* (MO); Junín: San Ramón, Aug 1923, *Schunke A66* (US); Loreto: Iquitos, August 1937, *Klug 10132* (US); Madre de Dios: Tambopata, Cuzco Amazonico, 14 Jun 1989, *Núñez et al. 11020* (MO); San Martín: Juan Jui, Alto Huallaga, Apr 1936, *Klug*

4317 (BM, K, U, US); Tumbes: Zarumilla, Matapalo, 2 Nov 1992, *Diaz et al.* 5531 (MO).

6. *Campylocentrum mattogrossense* **Hoehne** (1941: 62). Type:—BRAZIL. Mato Grosso: São Luiz de Cáceres, Lava Pés, August 1911, *Hoehne in Comissão Rondon* 4473 [lectotype: R!, designated by Pessoa & Alves (2015a)]. (Fig. 3K-O, Fig. 4)
- Campylocentrum cuyuniae* Szlachetko & Kolanowska (2013: 265). Type:—GUYANA. Cuyuni-Mazaruni: Cuyuni River, Kauri Creek, Mora Forest, 17 May 1933, *Tutin* 118 (holotype BM!).

Roots 1.5–2 mm diam., cylindrical. Stem 3.5–34 cm long. Leaves 3.2–11.3 × 0.9–2 cm, usually dark brown when dried, oblong-elliptical, oblanceolate, or widely elliptical, lobes obtuse to rounded. Inflorescences 1.2–2.5 mm long, congest, peduncle 0.1–0.3 cm long, glabrous; rachis 1.1–2.2 cm long, glabrous; floral bracts 1–1.5 × 0.7–0.9 mm, deltoid, margin minutely denticulate, the apex acute. Flowers 11–22 (per inflorescence), pale orange, pedicellate ovary 0.8–2 mm long, glabrous; dorsal sepal 4.9–5.1 × 1–1.2 mm, oblong, 3-nerved, adaxially glabrous to sparsely pilose, the apex acute; lateral sepals 5–5.1 × 1–1.1 mm, oblong, sub-falcate, 3-nerved, adaxially glabrous to sparsely pilose, the apex acute; petals 4.5–4.8 × 0.8–0.9 mm, oblong, 3-nerved, glabrous, the apex acute; lip 5–5.2 mm long, 2.2–2.3 mm wide between the lateral lobes, 3-lobed, 7–9-nerved, margin entire, producing a spur at base, lateral lobes 2.2–2.3 × 0.4–0.6 mm, oblong to oblanceolate, the apex rounded, mid-lobe 3.2–3.3 × 0.9–1 mm, narrowly lanceolate, the apex acute, glabrous, spur 5–5.2 mm long, 1–1.2 mm diam., cylindrical-clavate, straight, pale orange, glabrous to sparsely pilose, the apex rounded; gynostemium 0.7–0.8 mm long, anther cap apex truncate. Capsules 7–9 × 2–3 mm, glabrous, pedicel 0.8–1 mm long.

**Distribution and Habitat:**—South America (Bolivia, Brazil, French Guyana and Guyana, probably also in Surinam), in Brazil (states of Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Rondônia and Tocantins). It grows in lowland forests in the Amazon basin and gallery forest in *Cerrado* vegetation.

**Conservation status:**—Based on its wide distribution, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—*Campylocentrum mattogrossense* was included for a long time under *C. micranthum* (Pessoa & Alves 2015a). Recently, Szlachetko and Kolanowska (2013) described *C. cuyuniae* based in a specimen clearly cospecific and neglecting the existence of the previous name. Pessoa and Alves (2015a) provided a re-establishment of *C. mattogrossense* and synonymized *C. cuyuniae* under it.

**Similar species:**—It is part of the “*C. micranthum* complex”. Species of this group are unrecognizable based on vegetative organs and parts of the perianth are also very similar. However, it is easily distinguished by its straight spur and the other ones have spurs curved, inflexed or slightly curved.

**Additional specimens examined:**—BOLIVIA: Pando: Manuripi, Puerto America, 10 Sep 1994, *Jardin 1061* (MO); BRAZIL. Amazonas: Lago Cauaçu, 16 Jun 1965, *Richter s.n.* (HB); Alto Rio Negro, Jul 1972, *Richter s.n.* (HB, M); Baixo Amazonas, Lago Cauaçu, 15 Jun 1965, *Richter s.n.* (HB); Goiás: Paraúna, Ponte de Pedra, 10 Jan 1993, *Batista 375* (CEN); Maranhão: Rio Maracaçume, Jul 1958, *Fróes 34394* (IAN); Mato Grosso: Chapada dos Guimarães, Manso, 12 Aug 1999, *Macedo & Gonçalves 7095* (UFMT); Cláudia, 1 Mar 2015, *Pezzini s.n.* (CNMT); Cuiabá, Coxipó, Dec 1978, *Lima 50* (HB, M); Between Cuiabá and Rondonópolis, Serra de São Vicente, 17 Nov 1977, *Lima 01* (HB, M); Jaciara, near BR-364 road, 11 Apr 2015, *Petini-Benellii 986* (CNMT); São Luiz de Cáceres, Lava Pés, Sep 1908, *Hoehne in Com. Rondon 570* (R); Pará: Altamira, Rio Iriri, 18 Aug 1986, *Vasconcelos et al. 08* (MG); Belém, Boa Vista, 22 May 1968, *Pires & Silva 11740* (IAN); São Félix do Xingú, Serra de Campo, 12 Aug 2001, *Salles et al. 2178* (HEPH); Tucuruí, Vila Santa Rosa, Apr 1981, *Bastos & Motta 420* (MG); Rondônia: Abunã, Madeira-Mamoré, 13 Jul 1968, *Prance et al. s.n.* (INPA); Presidente Médici, 31 May 1985, *Maciel et al. 1476* (MG); Tocantins: *sine loco acurato*, 16 Aug 1978, *Mileski s.n.* (RB); Araguaçu, estrada para Alvorada, 16 Feb 1997, *Batista et al. 686* (CEN, UB). FRENCH GUYANA. Lieu de Récolte: Inselberg Mont Chauve, 19 Apr 1997, *Villiers & Sarthou 6126* (P); *ibid.*, 11 Apr 1997, *Cremers & Crozier 14860* (CAY, P). GUYANA. *sine loco acurato*, 1898, *Thurn 92 p. part.* (K); Takutu-U: Essequibo, Kamoá, Kassikaityu, 25 May 1997, *Clarke 4952* (US).

**7. *Campylocentrum micranthum* (Lindl.) Maury** (1889: 273). *Angraecum micranthum* Lindley (1835: t. 1772). *Aeranthus micranthus* (Lindl.) Reichenbach (1864: 901). *Epidorchis micrantha* (Lindl.) Kuntze (1891: 660). *Mystacidium micranthum* (Lindl.)

T. Durand & Schinz (1895: 54). *Campylocentrum micranthum* (Lindl.) Rolfe (1903: 245). Type:—SURINAM. *sine loco acurato*, s.d., *G. Loddiges s.n.* (holotype: K–L!). (Fig. 5A–D, Fig. 6)

Roots 1–2 mm diam., cylindrical. Stem 8–47 cm long. Leaves 2.6–9 × 0.9–2.2 cm, oblong-elliptical to oblanceolate, lobes obtuse. Inflorescence 1–3 cm long, congest, peduncle 0.1–0.3 cm long, glabrous; rachis 0.8–2.7 cm long, glabrous; floral bracts 0.9–1.3 × 0.5–0.8 mm, deltoid, minutely denticulate margin, the apex acute. Flowers 8–21 (per inflorescence), white-greenish, pedicellate ovary 2–3 mm long, minutely papillate; dorsal sepal 3.8–5 × 1–1.5 mm, oblong, 3-nerved, glabrous, the apex acute; lateral sepals 4–5.5 × 0.8–1.1 mm, oblong, subfalcate, 3-nerved, glabrous, the apex acute; petals 3–5 × 0.7–1 mm, oblong-elliptical, 3-nerved, glabrous, the apex acute; lip 3.5–5 mm long, 1.8–2 mm between the lateral lobes, 3-lobed, 9-nerved, margin entire, producing a spur at base, lateral lobes 1.5–2 × 0.5–0.6 mm, oblong to oblanceolate, the apex acute to obtuse, mid-lobe 2.3–3.1 × 0.5–0.9 mm, narrowly lanceolate, the apex acute, spur 2.5–3.5 mm long, 1–1.5 mm diam., cylindrical-clavate, inflexed, greenish, the apex rounded; gynostemium 0.8–1 mm long, anther cap apex rounded. Capsules 7–11 × 2–2.5 mm, glabrous, pedicel 0.8–1 mm long.

**Distribution and Habitat:**—Antilles (Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Martinique, Puerto Rico and Trinidad & Tobago) and South America (Brazil, French Guyana, Guyana, Surinam and Venezuela), in Brazil (states of Alagoas, Amapá, Amazonas, Bahia, Ceará, Pará, Pernambuco and Roraima). It occurs in Antillean seasonal forests, and also in dense, and humid lowland forests in Amazon basin and northern Atlantic Forest.

**Conservation status:**—Based on its wide distribution, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—The name *C. micranthum* (Lindley 1835: t. 1772) Rolfe (1903) has been erroneously applied since Maury (1889) previously proposed a new combination (Bogarin & Pupulin 2010, Pessoa *et al.* 2015b). Many names have been included as synonyms of it and some of them have been reestablished and recognized as distinct species (Pessoa & Alves 2015a, Pessoa *et al.* 2015). Detailed study of the type specimen added by additional specimens from the type locality (Surinam) provide a

better understanding of its real morphological identity and excluded several synonyms whom the majority of them are now under *C. kuntzei*.

**Similar species:**—*Campylocentrum micranthum* is the species with the shorter spur (up to 3.5 mm) among the other from the “*C. micranthum* complex” in Brazil (*C. huebneri*, *C. kuntzei* and *C. mattogrossense*). *Campylocentrum antioquiense* Kolanowska & Szlachetko, described to Colombia is its most similar species based on the inflexed spur, but it differs by the vegetative portion (leaves and stem) much smaller than *C. micranthum*, and apex of the lateral lobes of the lip rounded (vs. acute to obtuse).

**Additional specimens examined:**—BRAZIL. Alagoas: Iateguara, Coimbra. 15 Jun 2002, *Oliveira 975* (UFP); Murici, Serra do Ouro, 18 Feb 2004, *Pinheiro 245* (MAC); Amapá: Amapá, Rebio Lago Piratuba, 4 Jun 2006, *Rocha et al. 529* (HAMAB); Calçoene, Rio Cassiporé, 18 Sep 2005, *Costa-Neto 2158* (HAMAB, MG); Mururú, Rio Aragarí, 22 Aug 1961, *Pires et al. 50426* (NY); Oiapoque, Clevelândia. 23 Apr 1960, *Egler 1402* (HB, MG); Rio Jari, Cachoeira Macacoara, 27 Aug 1961, *Egler & Irwin 46685* (NY); Amazonas: Caserío Natividad, Quebrada las Flores, 22 Sep 1977, *Morales 34* (COL). Humayta, Rio Madeira, 14 Sep 1934, *Krukoff 6539* (NY); Manaus, Reserva Ducke, 13 Apr 1998, *Ribeiro 1972* (INPA, K); *ibid.*, 23 Jun 1998, *Assunção & Silva 851* (INPA, K); Presidente Figueiredo, Reserva Biológica Uatumã. 6 Jul 2007, *Carvalho-Sobrinho & Mesquita 1534* (INPA); Bahia: Canavieiras, Transoricana, 15 Nov 2002, *Jardim et al. 4067* (HUEFS); Ipiaú, estrada a Ibirataia, 30 Oct 1970, *Santos 1242* (CEPEC); Santa Cruz de Cabralia, Reserva Biológica Pau Brasil, 1 Oct 1971, *Eupunino 12* (CEPEC, HB); Serra de Sincorá. s.d., *Martius s.n.*(M); Ceará: Maranguape, Trilha da Rajada; 23 Apr 2013, *Pessoa et al. 1120* (RB, UFP); *ibid.*, Pedra do Derretido, 25 May 2005, *Lima-Verde et al 2491* (EAC); *ibid.*, 4 May 1991, *Felix 4391* (EAN). Pará: *sine loco acurato*, 15 Jun 1908, *Baker 423* (BM, U); *sine loco acurato*, Apr 1896, *Rand s.n.* (K); Ananindeua, Mar 1991, *Silva & Silva 56* (MG); Belém, Reserva do Guamá, Nov 1980, *Braga 3600* (INPA); Barcarena, Rio Tauá. 26 Aug 1985, *Lins et al. 310* (MG); Castanhal, 2 Jun 1995, *Silva 17* (MG); Lageira, Rio Maicuru, 28 Jul 1981, *Strudwick & Sobel 3639* (NY); Marabá, Serra Norte. 24 May 1982, *Secco et al. 319* (MG); Vigia, Campina do Palha, 12 Jun 1966, *Pabst 8969* (HB); Pernambuco: Olinda, 30 May 1925, *Pickel 970* (SP); Igarassu, Usina São José, 21 Jan 2014, *Pessoa et al. 1217* (RB, UFP); Jaqueira, Reserva Particular Patrimônio Natural

Frei Caneca, 30 May 2012, *Pessoa et al.* 952 (RB, UFP); Roraima: Alto Alegre, Serra dos Surucucus, 14 Oct 1991, *Silva* 256 (MG); Caracarái, Rio Anauá, 25 Aug 2012, *Pessoa et al.* 1001 (INPA, RB, UFP). CUBA. Cuba Orientali, Sep 1859?, *Wright* 1619 (W); Guantánamo: Baracoa, Río Toa Valley, 18 Jun 1997, *Ackerman et al.* 3077 (US); Macuriyes, 1824, *Poeppig s.n.* (W). DOMINICAN REPUBLIC. Loma Isabel de Torres: Puerto Plata, 25 May 1969, *Liogier* 14575 (NY); Santo Domingo: Península de Jamaná, 1 Aug 1930, *Ekman* 15804 (K); *ibid.*, 27 Jan 1971, *Wright et al.* 572 (W); Santiago: Marcano, Arroyo Gurabo, 9 Oct 1954, *Jimenez* (US). FRENCH GUYANA. Cayenne: s.d., *Poiteau s.n.* (G, W); Montagnes Plomb: 7 Dec 1993, *Bordenave* 624 (CAY, P); Nouragues: Basin de L'Arataye. 16 Mar 1989, *Sarthou* 498 (CAY, P); *ibid.*, 23 April 1992, *Larpin* 1045 (CAY, P); Oyapock: Crique Gabaret, Mar 1976, *Fily* 05 (P); Pays Indien: 18 November 1976, *Veyret s.n.* (HB); Saint-Elie: May 1989, *Larpin* 330 (CAY, P); Oyapock River: Mar 1976, *Fily* 05 (P). GUADALOUPE. Vernou: 10 Jun 1936, *Stehlé* 963 (P). GUYANA. *Sine loco acurato*: 1898, *Thurnefort s.n.* (K); *Sine loco acurato*: 1898, *Thurnefort* 92 p. part. (K); *Sine loco acurato*: Jul 1824, *Poiteau s.n.* (K); Aruka River: 8 Mar 1945, *s.col* (K); Mabaruma: 9 Nov 1990, *Polak et al.* 178 (U). HAITI. *sine loco acurato*, 15 Aug 1903, *Nash* 455 (NY). JAMAICA. *sine loco acurato*, Nov 1881, *Morris s.n.* (K). MARTINIQUE. Grand-Rivière: 10 Jun 1982, *Sastre* 7544 (P). PUERTO RICO. Florida: Barrio Perol, Sector Los Caños, 30 Jun 2001, *Trejo-Torres et al.* 1241 (C). SURINAM. *Sine loco acurato*: s.d., *Vriese s.n.* (BM, G, L, K, P); *Sine loco acurato*: s.d., *Loddiges s.n.* (K); *Sine loco acurato*: 1846, *Hostmann* 682a (P, W); Anansitabbetje: Gran Holo Soela, 2 Aug 1973, *Teunissen* 1138 (U); Beekhuizen: Paramanibo, s.d., *Wullschlagel* 532 (BR, W); La Recontre: May 1830, *Splittgerber* 955 (L, P, W); Meerzorg: lower Surinam River, 15 Nov 1974, *Mennega & Koek-Noorman* 910 (U); Nassau: Marowijne, 29 Mar 1949, *Lanjouw & Lindeman* 2968 (U); *ibid.*, 1 Sep 1965, *Jones* 129 (K); Surinam River: 12 Dec 1971, *Teunissen & Teunissen* 1139 (U). TRINIDAD & TOBAGO. Tobago: Adelphi, 13 May 1913, *Broadway s.n.* (BM, G, NY); Widow Forest, 20 Feb 1912, *Broadway* 3915 (K); Trinidad: *Sine loco acurato*, 4 Feb 1927, *Broadway* 7382 (BM); *sine loco acurato*, 1877, *Fendler* 792 (E, NY); Caroni North Bank Road, 21 Mar 1920, *Britton & Mendelson* 822 (NY); Valencia, 13 Mar 1925, *Broadway s.n.* (K). VENEZUELA. Amazonas: Watchica Ridge, San Carlos de Rio Negro, 14 Apr 1979, *Liesner* 6623 (MO); Cerro Copey: Isla Margarita, 18 Apr 1983,



*Sudgen 1163* (K); Lower Orinoco: *sine loco acurato*, 18 Sep 1896, *Rusby & Squires 397* (K), Monagas: Naturin, 20 Oct 1965, *Breteler 4668* (U).

**8. *Campylocentrum serranum* E. Pessoa & M. Alves** (2015b: 54). Type:—BRAZIL.

Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 30 May 2012, *E. Pessoa et al. 945* (holotype: UFP!, isotypes: K!, NY!, RB!). (Fig. 5E-G, Fig. 6)

Roots 1–1.5 mm diam., dorso-ventrally flattened. Stem 0.3–0.7 cm long. Leaves 1–3.1 × 0.2–0.4 cm, elliptical, sub-falcate, lobes acute. Inflorescence 2.5–4 cm long, lax, peduncle 0.7–1.2 cm long, papillate; rachis 1.5–3 cm long, papillate; floral bracts 0.5–1.2 × 0.3–0.5 mm, lanceolate to deltoid, margin minutely denticulate, the apex acute. Flowers 8–15 (per inflorescence), whitish, ovary pedicellate 1.3–1.5 mm long, minutely papillate; dorsal sepal 1.2–1.5 × 0.3–0.5 mm, oblong-elliptical, 1-nerved, adaxially sparsely pilose in the base, the apex acute to obtuse; lateral sepals 1.4–1.6 × 0.4–0.5 mm, oblong-elliptical, 1-nerved, adaxially sparsely pilose in the base, the apex acute; petals 1.1–1.3 × 0.4–0.5 mm, oblong-elliptical, 1-nerved, glabrous, the apex acute; lip 1–1.2 mm long, 1–1.1 mm wide between the lateral lobes, 3-lobed, 5-nerved, margin entire, producing a spur at base, lateral lobes 0.2–0.3 × 0.3–0.4 mm, ovate, the apex rounded, mid-lobe 0.5–0.6 × 0.3 mm, deltoid, the apex acute, spur 1.5–1.6 mm long, 0.3–0.5 mm diam., cylindrical, slightly curved, whitish, the apex rounded; gynostemium 0.2–0.3 mm long, anther cap apex 2-lobed. Capsules 5–6 × 1.5–2 mm, glabrous, pedicel ca. 1 mm long.

**Distribution and Habitat:**—Endemic to Northeastern Brazil (state of Pernambuco). It was described recently and it is known only for the type locality, an area of submontane Atlantic forest.

**Conservation status:**—Due its extremely reduced and fragmented area of occupancy (criterion B1a and B2a) this species is considered Critically Endangered (CR).

**Similar species:**—*Campylocentrum serranum* is the only species from the group that occurs in the northern portion of Atlantic Forest characterized by relatively longer and lax inflorescences, flowers with sepals and petals 1-nerved, and 3-lobed lip. It is morphologically related to *C. hirtellum* from which differs by shorter sepals ( $\leq 1.6$  mm

vs.  $\geq 2.2$  mm long), lip 5-nerved (vs. 7–9-nerved) and spur slightly longer than the pedicellate ovary (vs. twice longer), and glabrous capsules (vs. hirtellous); and also related to *C. ulaei*, from which is easily distinguished by the shorter stems (up to 0.7 cm vs. 25 cm long), and spur cylindrical (vs. clavate to cylindrical-clavate).

**Additional specimens examined:**—BRAZIL. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 29 Jan 2013, *Pessoa et al. 1051* (UFP); *ibid.*, 25 Nov 2014, *Pessoa et al. 1279* (UFP).

**9. *Campylocentrum steyermarkii* Foldats** (1968: 316). Type:—VENEZUELA. Táchira: El Piñal, Río Frío, 27–30 August 1966, *J.A. Steyermark & M. Rabe 96715* (holotype: VEN, photograph!). (Fig. 7A–D, Fig. 6)

Roots 1–2 mm diam., dorso-ventrally flattened. Stem 0.2–0.8 cm long. Leaves 1–2.5  $\times$  0.2–0.7 cm, oblong-elliptical to oblanceolate, sub-falcate, lobes acute. Inflorescences 1.5–2.3 cm long, lax, peduncle 0.7–0.8 cm long, minutely papillate; rachis 0.8–1.5 cm long, minutely papillate; floral bracts 0.8–1.5  $\times$  0.3–0.5 mm, deltoid, margin entire to minutely denticulate, the apex acute. Flowers 10–16 (per inflorescence), pale green, pedicellate ovary 1–1.5 mm long, minutely papillate; dorsal sepal 1.5–2.0  $\times$  0.5–0.8 mm, oblong, glabrous, 1-nerved, the apex acute; lateral sepals 2–2.1  $\times$  0.5–0.7 mm, oblong, subfalcate, glabrous, 1-nerved, the apex acute; petals 1.2–1.5  $\times$  0.3–0.6 mm, elliptical-lanceolate, 1-nerved, glabrous, the apex acute; lip 1.5–1.8  $\times$  1–1.2 mm, entire, ovate, glabrous, 5-nerved, margin entire, the apex acute, producing a spur at base, spur 0.7–1.2 mm long, 0.5–0.7 mm diam., ovoid, inflexed, pale green, glabrous, the apex rounded; gynostemium 0.4–0.8 mm long, anther cap apex 2-lobed. Capsules 2.5–3.5  $\times$  1.5–2 mm, glabrous to minutely papillate, pedicel 0.3–0.5 mm long.

**Distribution and Habitat:**—South America (Brazil, Peru and Venezuela), in Brazil (state of Amazonas) it grows in lowland forest of the Amazon basin.

**Conservation status:**—Due to the few specimens known, it is not possible to classify this species under any IUCN status. Data deficient (DD).

**Nomenclatural notes:**—It was treated as a synonym of *C. hondurense* by Carnevali and Ramírez (1993). The authors argued that it was described based on a specimen with young buds and not fully developed spurs. However, specimens from Brazil (*J. Ribeiro et al. 1642*) and Peru (*G. Haxaire 873*) with fully developed flowers

were analyzed and both had kept the spur morphology as described to *C. steyermarkii*. It confirms the spur as diagnostic character to *C. steyermarkii*.

**Similar species:**—*Campylocentrum steyermarkii* is similar to *C. hondurensis* based on its entire lip. Although very similar on vegetative and majority of the perianth features, these species are easily distinguished by the spur morphology as cited above. *C. steyermarkii* has an ovoid and inflexed spur with rounded at apex, while in *C. hondurensis* it is ellipsoid, sigmoid and attenuate at apex.

**Additional specimens examined:**—BRAZIL. Amazonas: Manaus, Reserva Ducke, 17 Jun 1995, *Ribeiro et al.* 1642 (INPA, K). PERU. Loreto: Maynas, Rio Yubinetto, 4 Feb 1978, *Haxaire* 873 (P).

**10. *Campylocentrum ulaei* Cogniaux (1906: 514).** Type:—BRAZIL. Santa Catarina: Mauro Miller, Serra do Oratório, January 1890, *E. Ule* 1628 (lectotype **here designed**: BR! no. 997445, isoelectotypes: AMES, photograph!, BR! no. 997444, HBG!).

(Fig. 7E-H, Fig. 6)

*Campylocentrum ulaei* var. *parviflorum* Cogniaux (1906: 514). **syn. nov.** Type:—BRAZIL. Rio de Janeiro: Teresópolis, June 1887, *J. de Moura* 59 (lectotype **here designed**: BR!).

*Campylocentrum gracile* Cogniaux (1906: 513). **syn. nov.** Type:—BRAZIL. Minas Gerais: *sine loco acurato*, 1891, *A. Glaziou* 19895 (lectotype **here designed**: BR!, isoelectotypes: C!, K!, P!).

Roots 0.9–1 mm diam., cylindrical. Stem 0.8–25 cm long. Leaves 1–4.5 × 0.2–0.7 cm, oblong-elliptical, lobes acute. Inflorescences 2–11 cm long, lax, peduncle 0.6–2 cm long, minutely papillate; rachis 1.4–9 cm long, minutely papillate; floral bracts 1–1.2 × 0.4–0.5 mm, deltoid, margin entire to minutely denticulate, the apex acute. Flowers 16–52 (per inflorescence), whitish-green, pedicellate ovary 1.2–1.9 mm long, minutely papillate; dorsal sepal 1.8–3 × 0.8–1 mm, elliptical to oblong, glabrous, 1-nerved, the apex obtuse to rounded; lateral sepals 1.8–3.6 × 0.6–0.8 mm, oblong, subfalcate, glabrous, 1-nerved, the apex obtuse; petals 1.8–2.8 × 0.5–0.8 mm, oblong-elliptical, 1-nerved, glabrous, the apex obtuse to rounded; lip 1.8–3.1 mm long, 1.5–1.6 mm wide between the lateral lobes, 3-lobed, 5–7-nerved, margin entire, producing a spur at base,

lateral lobes 0.8–1.4 × 0.3–0.4 mm, oblong to oblanceolate, the apex rounded, mid-lobe 1–2 × 0.7–0.9 mm, deltoid to lanceolate, the apex acute, spur 1.5–2 mm long, 0.4–0.6 mm diam., clavate to cylindrical-clavate, curved, pale green, glabrous, the apex rounded; gynostemium 0.3–0.5 mm long, anther cap apex 2-lobed. Capsules 4–6 × 1.5–2 mm, glabrous, pedicel ca. 1 mm long.

**Distribution and Habitat:**—South America (Argentina, Brazil and Paraguay), in Brazil (states of Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo). It grows only in the Atlantic Forest and often found in montane ombrophilous forests, but also in lowland forests in Southern Brazil.

**Conservation status:**—Based on its wide distribution, this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—Cogniaux (1906) cited two specimens as types of *C. ulaei*, “*E. Ule 1628*” (AMES, BR, HBG) and “*J. de Moura s.n.*” (BR). Here, was chosen the collection of Ule as the lectotype based on the name of the species and duplicates available. A mistake on spelling of the name, “*C. ulei*”, has been used in some data bases such as The Plant List, and must be disregarded. *Campylocentrum gracile* and *C. ulaei* var. *parviflorum* are both part of the morphological variation of *C. ulaei* and are considered synonyms here. However, *C. ulaei* var. *peruvianum* C. Schweinfurth (1953:19) should be treated as a distinct species and a new combination changing the status of the species is provided below.

**Similar species:**—Among the Brazilian species of the section, *Campylocentrum ulaei* is similar to *C. calostachyum* and *C. serranum*, from which can be recognized by its clavate to cylindrical-clavate spur (*vs.* cylindrical). Mature specimens of *C. ulaei* are the largest among the group of lax inflorescences, with stems reaching 25 cm long.

**Additional specimens examined:**—ARGENTINA. Misiones: San Pedro, Parque Provincial Moconá, s.d., *Deginiani 1083* (SI); General Manuel Belgrano, 16 Dec 1997, *Múlgura 1913* (SI). BRAZIL. Espírito Santo: Vargem Alta, 2 Jun 1949, *Brade 20386* (RB); Paraná: Campina Grande do Sul, Sítio Belizário, 27 Dec 1966, *Hatschbach 15550* (F, HB, HBR, K, UPCB); Londrina, Parque Estadual Mata do Godoy, 14 Feb 2013, *Molina 38* (FUEL), *ibid.*, Serra do Cadeado, 2 Mar 1985, *Chagas & Silva 715* (CEN, FUEL, K); Piraquara, Haras Santo Antônio, 6 Nov 2003, *Kersten 713* (UPCB); Rio de Janeiro: Nova Friburgo, Reserva Ecológica de Macaé de Cima, 27 Nov 1990, *Toscano et al. 657* (RB); Serra dos Órgãos, 24 Nov 1942, *Pereira 172* (HB, RB); *ibid.*, 13 Dec

1891, *Ule s.n.* (R); *ibid.*, September 1949, *Brade s.n.* (RB); Teresópolis, 10 Nov 1980, *Orsnich s.n.* (HB); *ibid.*, Granja Comarí, 14 Nov 1929, *Brade 10000* (HB, SP); *ibid.*, 30 Oct 1929, *Brade 9844* (RB); *ibid.*, Feb 1888, *Moura 92* (BR!); Rio Grande do Sul: Faxinal, Cambará do Sul, Jan 1984, *Sobral 2859* (ICN); Santa Cruz do Sul, Trombudo, 22 Feb 1982, *Waechter 1869* (ICN); São Leopoldo, 1940, *Rohr s.n.* (RB); *ibid.*, s.d., *Dutra 983* (ICN); Santa Catarina: Ararangá, Serra da Pedra, 28 Dec 1943, *Reitz 397* (HB, HBR, RB); Imaruí, Águas Mornas, 16 Jan 1973, *Klein & Bresolin 10686* (FLOR); Joinville, Serra Dona Francisca, 10 Dec 2009, *Cadorin et al. 941* (FURB); São Paulo: Caraguatatuba, 1 May 2015, *Miranda s.n.* (UFP); Paraná-Piacaba, 25 Nov 1956, *Handro s.n.* (SP); São Paulo, Estação Biológica APA da Serra, 8 Dec 1925, *Kuhlmann s.n.* (SP). PARAGUAY. Alto Paraguay: Ñu-cañy, Mar 1919, *Fiebrig 6051* (AS); Santa Barbara: 1882, *Balansa 2997* (BAF!).

#### **Excluded name:**

#### ***Campylocentrum peruvianum* (C. Schweinfurth) Pessoa & Alves, *stat. nov.***

*Campylocentrum ulaei* var. *peruvianum* C. Schweinfurth (1953:19). Type:—PERU. Junin: Chanchamayo Valley, October 1924-1927, *C. Schunke 520* (holotype: F, photograph!).

**Nomenclatural notes:**—Although it resembles to *C. ulaei*, it is more related with other species with relatively longer and lax inflorescences which grow in Colombia, Ecuador, Peru and Venezuela, such as *C. schneeanum* Foldats (1968: 274) and *C. polystachyum* (Lindley, 1940: t68) Rolfe (1903: 245). According Pessoa et al. (2017), species from the Atlantic forest, and the ones from Amazon forest and Andean species emerge as separate monophyletic clades.

**Additional specimens examined:**—BOLIVIA. Santa Cruz: Ichilo, Parque Nacional Amboró, 28 Aug 1985, *Solomon & Urcullo 14095* (MO). PERU. Amazonas: Luya, Campore dendo, 25 Jun 1991, *Díaz & Campos 4466* (MO).

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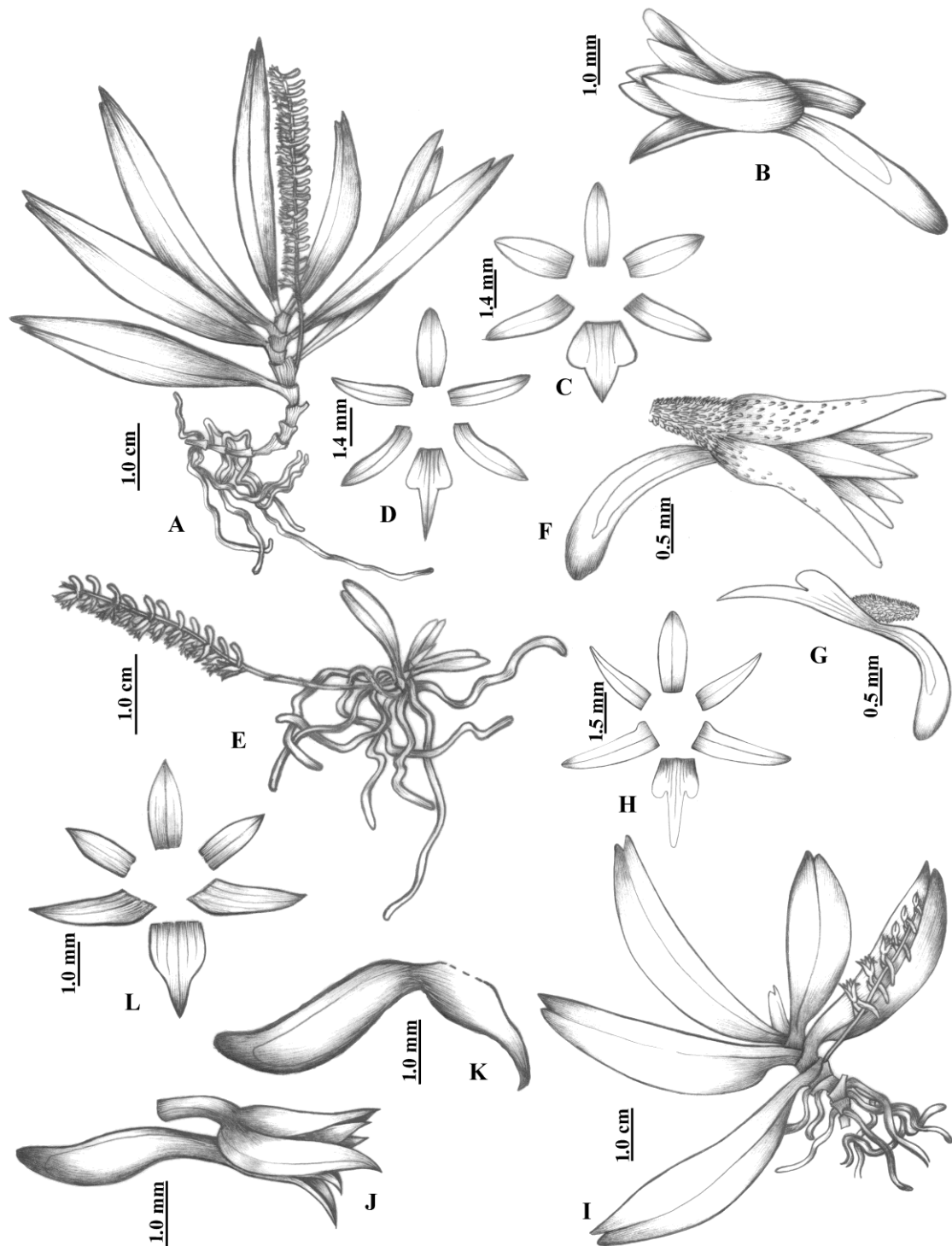


FIGURE 1. A-D. *Campylocentrum calostachyum*, A. Habit, B. Flower, C. Dissected perianth, D. Dissected perianth; E-H. *C. hirtellum*, E. Habit, F. Flower G. pedicellate ovary, lip and spur in profile, H. Dissected perianth; I-L. *C. hondurense*, I. Habit, J. Flower, K. lip and spur in profile, L. Dissected perianth. [A–C, drawn from A. C. Brade 17235 (RB), D. drawn from M.R. Miranda s.n. (UFP); E–H. drawn from Reitz & Klein 1152 (HBR); I–L. drawn from L.A.S. Santos et al. 2842 (UFP)].

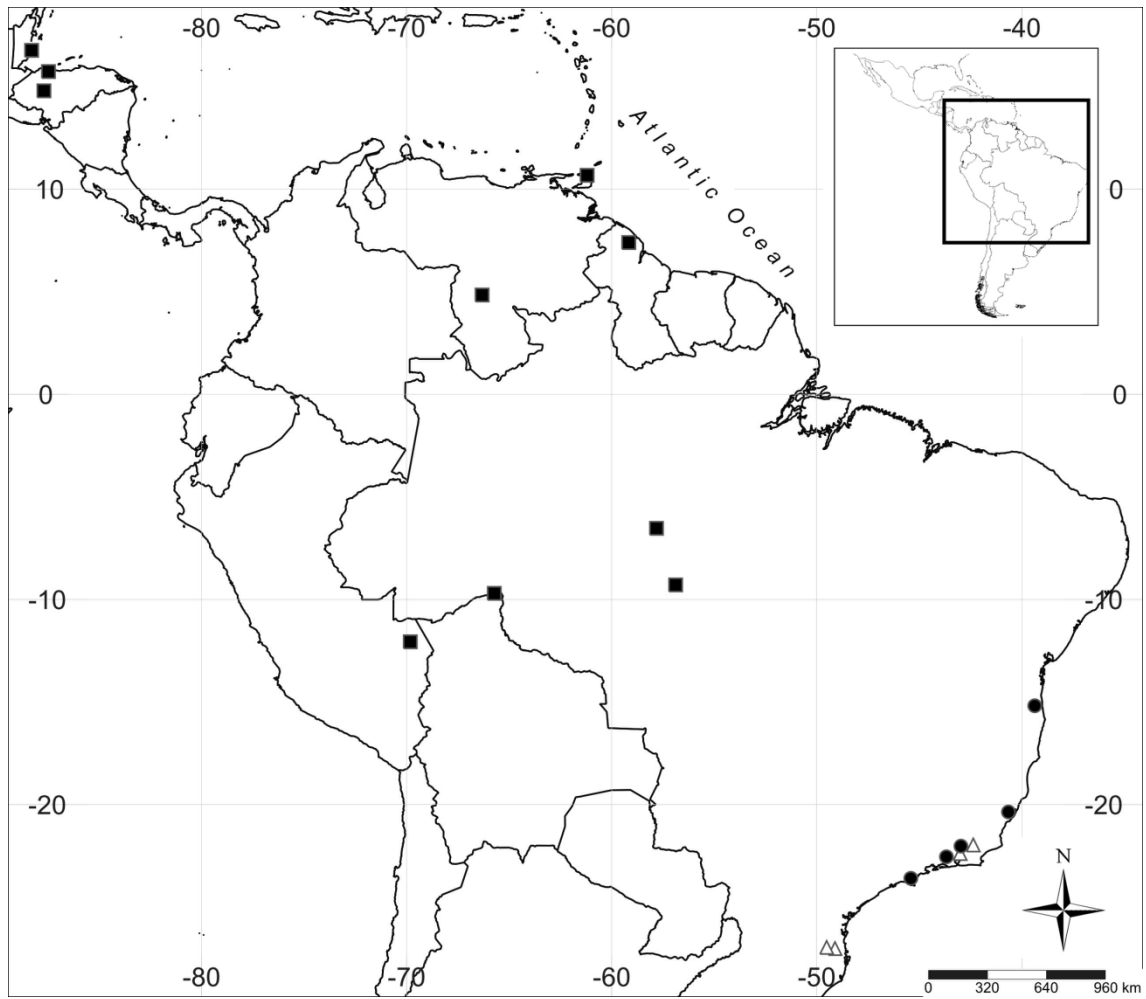


FIGURE 2. Distribution map of *Campylocentrum calostachyum* (black circle); *C. hirtellum* (white triangle) and *C. hondurensis* (black square).

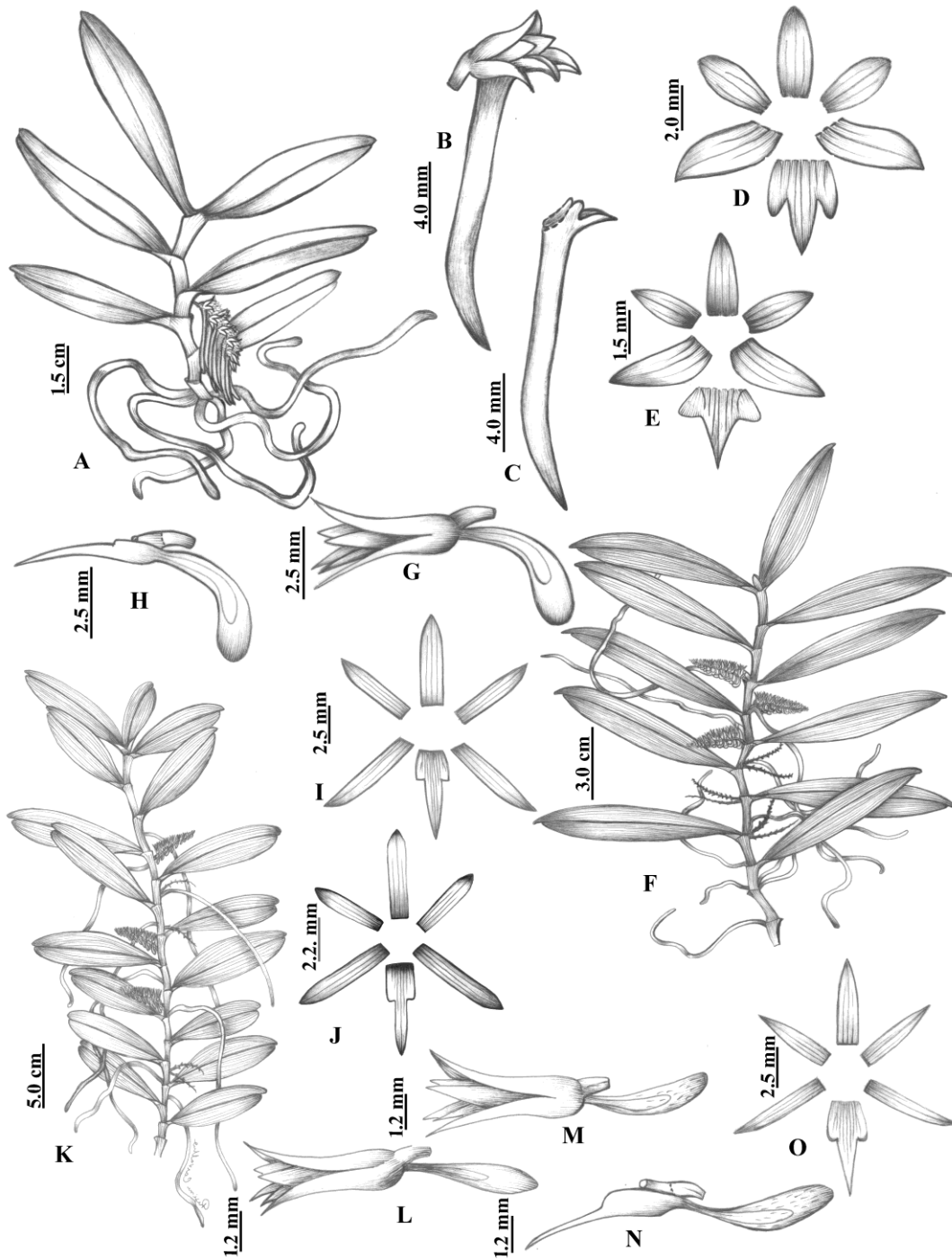


FIGURE 3. A-E. *Campylocentrum huebneri*, A. Habit, B. Flower, C. spur in profile, D. Dissected perianth; E. Dissected perianth; F-J. *C. kuntzei*, F. Habit, G. Flower, H. pedicellate ovary, lip and spur in profile, I. Dissected perianth, H. Dissected perianth; K-O. *C. mattogrossense*, K. Habit, L. Flower, M. Flower, N. pedicellate ovary, lip and spur in profile, O. Dissected perianth. [A–D, E. Pessoa *et al.* 670 (UFP), E. R.L. Liesner & B.K. Holst 21338 (MO); F–I. drawn from H. Medeiros 374 (RB), J. drawn from E. Esser 14519 (HEID); K–L and O. drawn from U.N Maciel 1476 (MG); M–N. drawn from J.F. Villiers & C. Sarthou 6126 (P)].

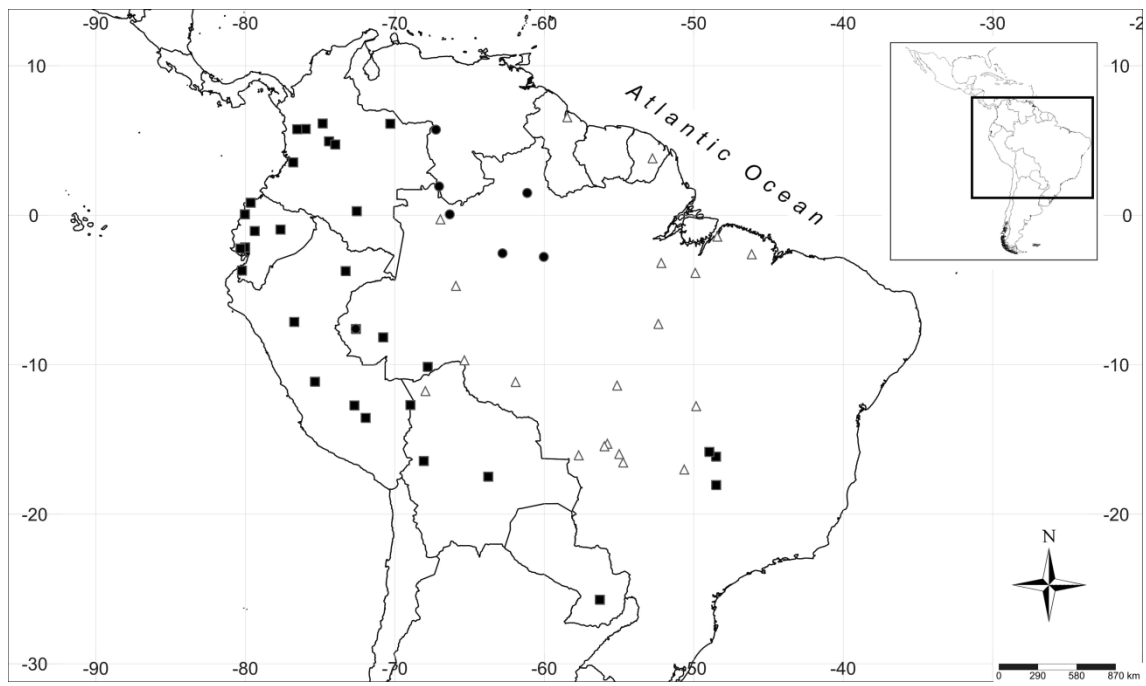


FIGURE 4. Distribution map of *Campylocentrum huebneri* (black circle); *C. kuntzei* (black square) and *C. mattogrossense* (white triangle).

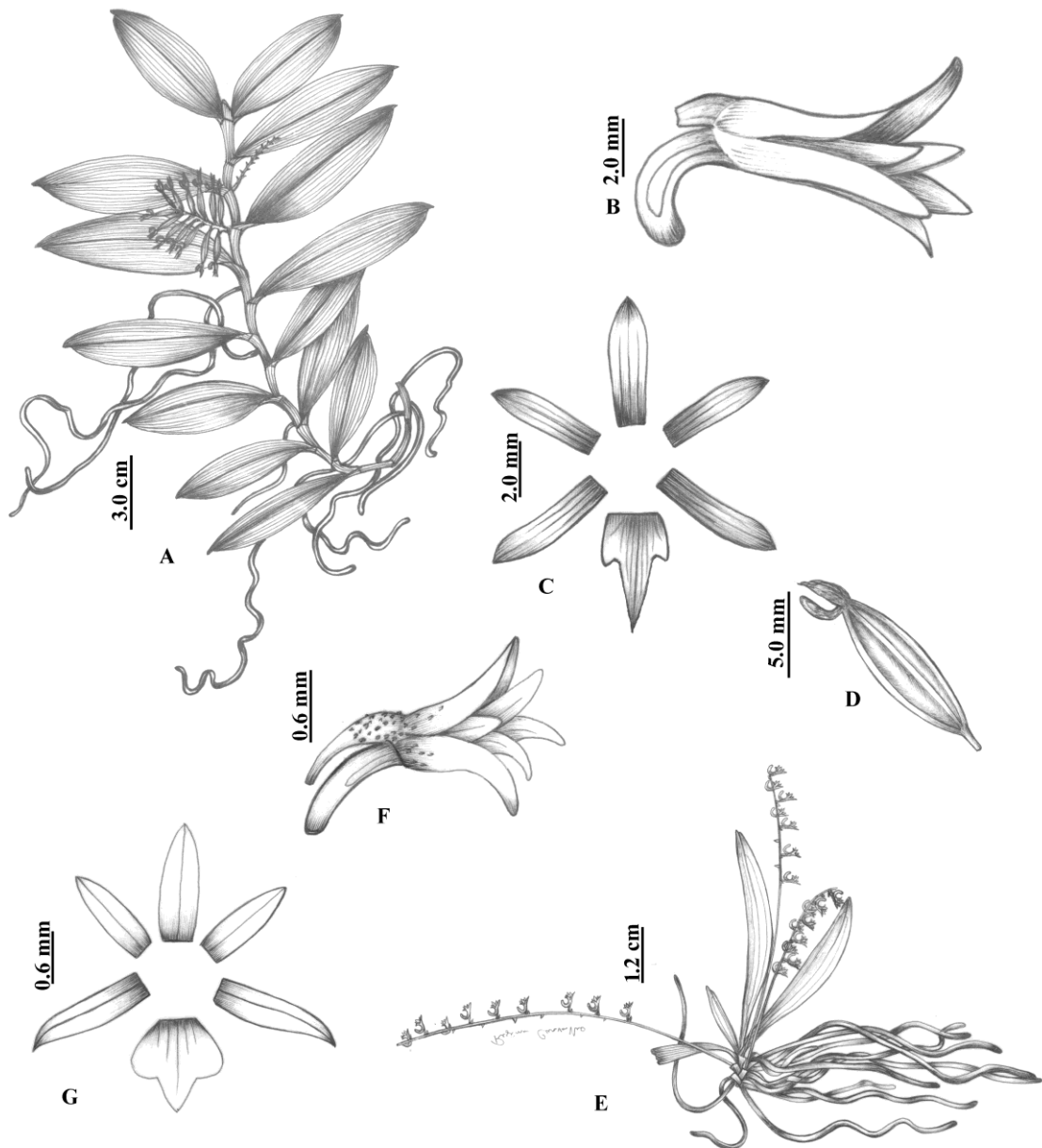


FIGURE 5. A-D. *Campylocentrum micranthum*, A. Habit, B. Flower, C. Dissected perianth, D. Capsule; E-H. *C. serranum*, E. Habit, F. Flower G. Dissected perianth, H. Capsule. [A-D. drawn from *E. Pessoa et al. 1217* (UFP); E-G. drawn from *E. Pessoa et al. 945* (UFP)].

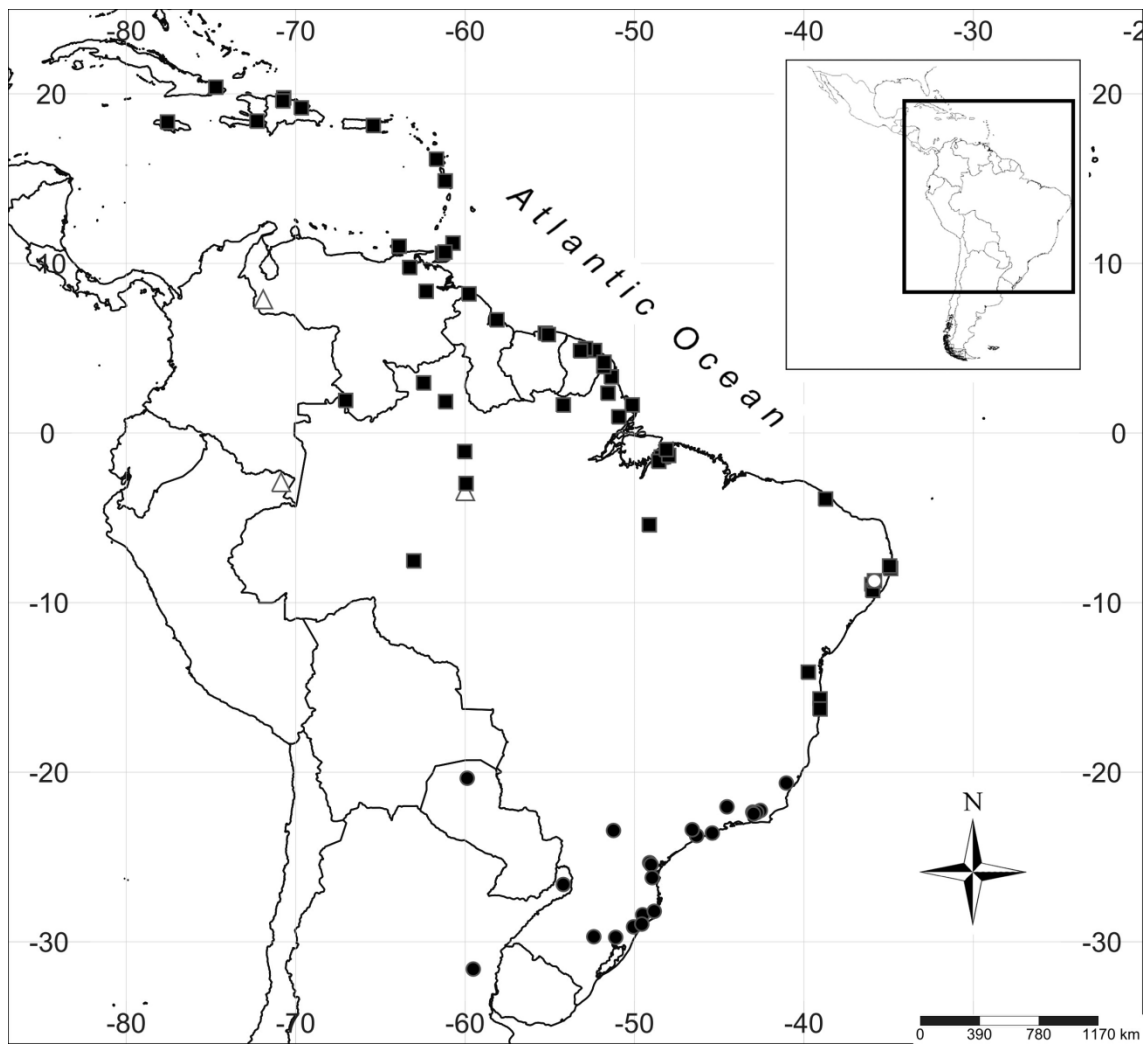


FIGURE 6. Distribution map of *Campylocentrum micranthum*, (black square); *C. serranum* (white circle), *C. steyermarkii* (white triangle) and *C. ulaei* (black circle).

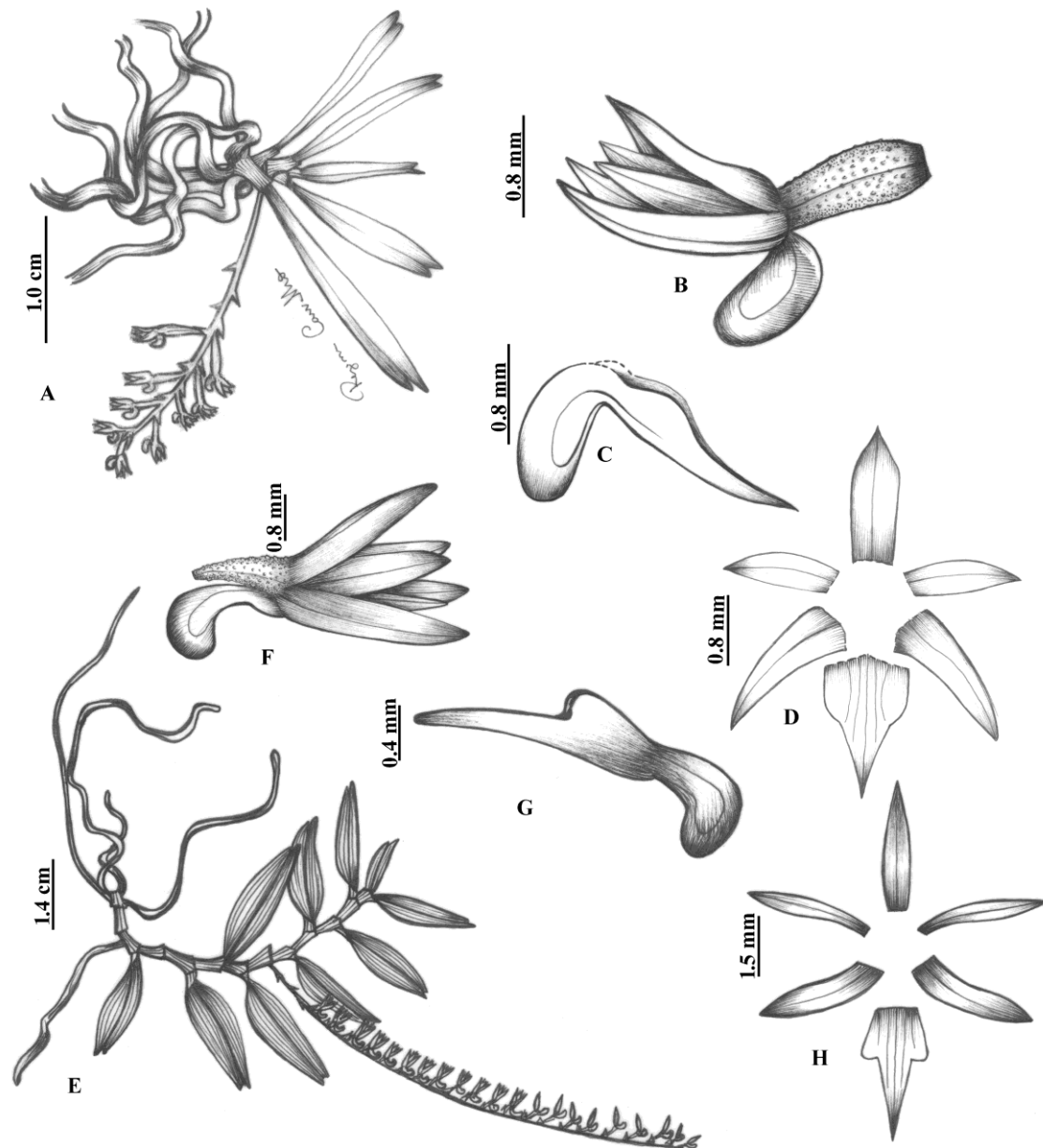


FIGURE 7. A-D. *Campylocentrum steyermarkii*, A. Habit, B. Flower, C. Lip and spur in profile, D. Dissected perianth; E-H. *C. ulaei*, E. Habit, F. Flower G. spur in profile, H. Dissected perianth. [A–D, drawn from *J. Ribeiro et al. 1642* (K); E–H, drawn from *A. C. Brade 10000* (HB)].



Table 1. Main morphological features of the species of section *Campylocentrum* in Brazil.

	Leaves width	Inflorescence	Sepals	Petals	Lip	Spur	Capsules
<i>C. calostachyum</i>	0.6–1.3 cm	lax, papillate	1-nerved, glabrous	1-nerved, glabrous	5-nerved, 3-lobed	cylindrical, straight to slightly curved	glabrous
<i>C. hirtellum</i>	0.2–0.5 cm	lax, hirtellous	1-nerved, sparsely pilose	1-nerved, glabrous	7–9- nerved, 3-lobed	cylindrical-clavate, curved	densely hirtelous
<i>C. hondurensense</i>	0.2–0.6	lax, minutely papillate	1-nerved, glabrous	1-nerved, glabrous	5-nerved, entire	ellipsoid, sigmoid	glabrous to minutely papillate
<i>C. huebneri</i>	1–2 cm	congest, glabrous	3-nerved, sparsely pilose	3-nerved, sparsely pilose	7-nerved, 3-lobed	cylindrical, patent	glabrous or sparsely pilose
<i>C. kuntzei</i>	1.4–2.7 cm	congest, glabrous	3-nerved, sparsely pilose	3-nerved, glabrous	7–9- nerved, 3-lobed	cylindrical-clavate, slightly curved	glabrous
<i>C. mattogrossense</i>	0.9–2 cm	congest, glabrous	3-nerved, sparsely pilose	3-nerved, glabrous	7–9- nerved, 3-lobed	cylindrical-clavate, straight	glabrous
<i>C. micranthum</i>	0.9–2.2 cm	congest, glabrous	3-nerved, glabrous	3-nerved, glabrous	9-nerved, 3-lobed	cylindrical-clavate, inflexed	glabrous
<i>C. serranum</i>	0.2–0.4 cm	lax, papillate	1-nerved, sparsely pilose	1-nerved, glabrous	5-nerved, 3-lobed	cylindrical, slightly curved	glabrous
<i>C. steyermarkii</i>	0.2–0.7 cm	lax, minutely papillate	1-nerved, glabrous	1-nerved, glabrous	5-nerved, entire	ovoid, inflexed	glabrous to minutely papillate
<i>C. ulaei</i>	0.2–0.7 cm	lax, minutely papillate	1-nerved, glabrous	1-nerved, glabrous	5–7- nerved, 3-lobed	clavate to cylindrical-clavate, curved	glabrous

**Taxonomic revision of *Campylocentrum* sect. *Laevigatum* E. Pessoa & M. Chase  
(Orchidaceae–Vandae–Angraecinae)**

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**Abstract**

Here we review the species included in *Campylocentrum* sect. *Laevigatum*, which are characterized by smooth roots, conduplicate leaves and unribbed capsules. Fourteen species are recognized, twelve of them are endemic to Brazil, while *C. jamaicense* is endemic to the Antilles. *Campylocentrum brevifolium* and *C. pauloense* were classified as Critically Endangered and Vulnerable, respectively. This study also provides typifications, complete synonymies, conservation statuses, descriptions, and an identification key to the species.

**Keywords:** Antilles, Epidendroideae, Monocots, Neotropics, South America.

## Introduction

*Campylocentrum* Bentham (1881: 337) is a Neotropical genus of epiphyte orchis that belongs to the subtribe Angraecinae Summerhayes (1966: 188) (Pridgeon *et al.* 2014). It is comprised by 73 species (Pessoa & Alves 2016a, 2016b, 2017) and is the second largest genus of the subtribe after *Angraecum* Bory (1804: 359).

Cogniaux (1906) proposed the first infra-generic classification to the genus, and organized it in three sections based on the vegetative portion. Leafless species were included under *C.* sect. *Dendrophylopsis* Cogniaux (1906: 504); *C. poeppigii* (Reichenbach f. 1850: 858) Rolfe (1903: 246) as the only species with elongated stems and reduced fleshy leaves was placed in *C.* sect. *Pseudocampylocentrum* Cogniaux (1906: 504), and all other species with elongated stems and developed leaves considered under *C.* sect. *Campylocentrum* Cogniaux (1906: 504).

This classification was tested by Pessoa *et al.* (2017) in a phylogenetic study using multiple markers (nuclear and plastidial) which showed that *C.* sect. *Campylocentrum sensu* Cogniaux (1906) was not a monophyletic group. Then, a new classification was stated. Species with unribbed capsules were included in two new sections, *C.* sect. *Teretifolium* E. Pessoa & M. Chase (2017: *in prep*) (species with terete leaves) and *C.* sect. *Laevigatum* E. Pessoa & M. Chase (2017: *in prep*) (species with conduplicate leaves).

Species of *C.* sect. *Laevigatum* are characterized by smooth roots, elongated stems, conduplicate leaves and unribbed capsules (Pessoa *et al.* 2017). It is distributed mainly in eastern South America, and only *C. jamaicense* is endemic to the Antilles with a disjunct distribution (Ackerman 2014).

Some species of this group were included under synonym of *C. micranthum* (Lindley 1835: t. 1772) Maury (1889: 273) (*C.* sect. *Campylocentrum*), such as *C. brevifolium* (Lindley 1840: 68) E. Pessoa & M. Alves (2015: 43) and *C. jamaicense* (Reichenbach & Wulfschlaegel 1864: 901) Fawcett (1893: 141). Misinterpretations like that were recently clarified by Pessoa *et al.* (2015) and Ackerman (2014) respectively, and also new species were recently proposed (Pessoa & Alves 2015).

Although the section *Campylocentrum* is the largest in the genus (Pessoa *et al.* 2017), the section *Laevigatum* is the most diverse in Brazil (BFG 2015) and identification mistakes in local herbaria are common. This study aims to review the

names proposed for the section by an exhaustive morphological analysis of its taxa covering the geographical and morphological variation. It provides typifications, synonymy, conservation statuses, descriptions, illustrations, distribution maps and identification keys.

### **Material and Methods**

Expeditions were carried out between 2011–2015 in Brazil (where the majority of the species are endemic). Eight species were found in the field (deposited at UFP, duplicates at RB and NY), and the other taxa were analysed with dried specimens from collections. The flowers were dissected and the perianth was mounted between glass slides and cover slips using Entellan (Merck) or glycerin. The morphological terminology followed Harris & Harris (2001) and Stearn (1995).

Specimens from 73 herbaria were analyzed (including all types): ALCB, \*AMES, \*AS, ASE, B, BA, BAF, BHCB, BHZB, BM, BR, C, CEN, CEPEC, CESJ, COAH, COL, COR, E, EAC, EAN, ESA, \*FMB, FLOR, FR, FUEL, FURB, G, GOET, HAMAB, HB, HBG, HBR, HEID, HEPH, HRCB, HUEFS, HST, IAC, IAN, IBGE, ICN, INPA, IPA, JPB, K, L, M, MAC, MBML, MG, MIRR, MO, \*MVFA, \*NY, P, PEUFR, R, RFA, RB, SP, SPF, U, US, UB, UEC, UFP, UFRN, UFRR, UPCB, VIES, W, WU; acronyms according to Thiers (2016), [“\*” only images].

The conservation status for species with more than four known specimens was defined according to the categories proposed by IUCN (2016) using a databank of geographical coordinates from field collections and herbarium material. Specimens with no geo-referenced data had their localities determined using online gazetteers (Google Earth). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCAT (Geospatial Conservation Assessment Tool - Bachman *et al.* 2011).

### **Taxonomic Treatment**

*Campylocentrum* Bentham (1881: 337).

Type species: *Campylocentrum schiedei* (Rchb. f.) Benth. ex Hemsley (1884: 292). (Basionym: *Angraecum schiedei* Reichenbach (1850: 857); originally published as *Todaroa micrantha* Richard & Galeotti (1845: 28).

*Todaroa* Richard & Galeotti (1845: 28), *nom. illeg.* [non *Todaroa* Parlatore (1843: 155).  
Apiaceae (= Umbelliferae)].

Type species: *Todaroa micrantha* Richard & Galeotti (1845: 28), *nom. illeg.*

**Key to the sections of *Campylocentrum* (adapted from Pessoa *et al.* 2016a)**

1. Leafless plants (leaves reduced to achlorophyllous scales), viscidium of one part.....***C. sect. Dendrophylopsis***
- Leafy plants (leaves chlorophyllous), stem elongated, viscidium of two parts.....2
2. Leaf blades reduced to small, fleshy and cylindrical projections.....***C. sect. Pseudocampylocentrum***
- Leaf blades developed, cylindrical or conduplicate.....3
3. Leaves cylindrical.....***C. sect. Teretifolium***
- Leaves conduplicate.....4
4. Capsules unribbed.....***C. sect. Laevigatum***
4. Capsules 6-ribbed.....***C. sect. Campylocentrum***

***Campylocentrum sect. Laevigatum* E. Pessoa & M. Chase (2017: in prep).**

Type species: *Campylocentrum brevifolium* (Lindley 1840: 68) E. Pessoa & M. Alves (2015: 43), designated by Pessoa *et al.* (2017).

Epiphytic herbs. Roots cylindrical, fibrous, smooth, whitish to grey. Stem elongated, cylindrical, unbranched to rarely branched. Leaves greenish, elliptic-oblong, linear-oblong or oblong, sometimes subterete, sometimes curved, the apex asymmetrically 2-lobed, lobes acute, obtuse or rounded, margin entire. Inflorescence raceme, peduncle glabrous, brownish; rachis glabrous, brownish; floral bracts deltoid, ovate or sub-orbicular, membranaceous, covering partially, completely, or only the base of the pedicellate ovary, margin minutely denticulate, the apex acute to obtuse. Flowers 3–26 (per inflorescence), with almost the same size in the base and apex, or bigger at the base and smaller at the apex, cream-coloured, white-yellowish or orangeish, distichous, ovary pedicellate, papillate; dorsal sepal elliptic, lanceolate, ovate, oblong, oblong-elliptic, membranaceous, 1–3–5-nerved, glabrous, glabrescent or sparsely pilose,

margin entire, the apex acute, obtuse or rounded; lateral sepals elliptic, oblong, oblong-elliptic or lanceolate, subfalcate, membranaceous, 1–3–5-nerved, glabrous, glabrescent or sparsely pilose, margin entire, the apex acute or obtuse; petals elliptic, elliptic-lanceolate, oblong, oblong-elliptic, oblong-oblancheolate or wide elliptic, membranaceous, 1–3–5-nerved, glabrous, margin entire, the apex acute, obtuse or rounded; lip entire to obscurely 3-lobed, oblong, ovate or lanceolate, or 3-lobed, 5–11-nerved, membranaceous, margin entire, producing at base a spur, glabrous, lateral lobes (when present) oblong, oblancheolate or sub-orbicular, the apex rounded, truncate, mid-lobe (when present) deltoid or narrowly lanceolate, the apex acute, obtuse or truncate, spur clavate, cylindrical, cylindrical-clavate, ellipsoid, globose, obovoid, ovoid-conical, sub-conical, curved, patent, slightly curved, straight or strongly inflexed, glabrous, glabrescent or sparsely pilose, the apex acute, obtuse, or rounded; gynostemium reduced, anther cap apex emarginated, retuse, rounded or truncate, pollinia 2, globose, viscidium with two parts. Capsules obovoid or ellipsoid, unribbed, glabrous or glabrescent, pedicellate.

#### **Key to species of *Campylocentrum* sect. *Laevigatum***

1. Floral bracts ovate to sub-orbicular, covering partially to completely the pedicellate ovary.....2
  - Floral bracts deltoid, covering only the base of the pedicellate ovary.....4
2. Lip entire to obscurely 3-lobed, spur curved.....
  - .....1. *C. brachycarpum* Cogniaux (1906: 512)
  - Lip distinctly 3-lobed, spur strongly inflexed.....3
3. Floral bracts  $\leq 2.5$  mm wide.....5. *C. densiflorum* Cogniaux (1906: 511)
  - Floral bracts  $\geq 2.8$  mm wide (up to 4.2 mm wide).....
    - .....10. *C. organense* (Reichenbach 1864: 901) Rolfe (1903: 245)
4. Spur ellipsoid, globose, obovoid, ovoid-conical or sub-conical.....5
  - Spur clavate, cylindrical-clavate or cylindrical.....8
5. Spur ellipsoid, ovoid-conical or sub-conical.....6
  - Spur globose or obovoid.....7
6. Sepals  $\leq 1.8$  mm long; lip 3-lobed...3. *C. carvalhoi* E. Pessoa & M. Alves (2015: 265)

- Sepals 3 mm long; lip entire to obscurely 3-lobed.....
- .....6. *C. intermedium* (Reichenbach & Warming 1881: 91.) Rolfe (1903: 245)
- 7. Flowers 12-20 for inflorescence; sepals  $\leq$  1.4 mm long, 1-nerved; lip 5-nerved
- .....7. *C. itatiaiae* Pessoa & M. Alves (2015: 267)
- Flowers, 4-8 for inflorescence; sepals  $\geq$  1.8 mm long, 3-nerved; lip 9-nerved
- .....13. *C. schlechterianum* E. Pessoa & M. Alves (2015: 268)
- 8. Lip entire to obscurely 3-lobed.....12. *C. robustum* Cogniaux (1906: 509)
- Lip distinctly 3-lobed.....9
- 9. Sepals  $\leq$  2.2 mm long; mid-lobe of the lip  $\leq$  1.0 mm long.....10
- Sepals  $\geq$  2.5 mm long; mid-lobe of the lip  $\geq$  1.3 mm long.....11
- 10. Lobes of the leaves acute to obtuse; lip 9 – 11-nerved; spur as long as to slightly longer than the pedicellate ovary.....11. *C. pauloense* Hoehne & Schlechter (1926: 297)
- Lobes of the leaves rounded; lip 5-nerved; spur two times longer than the pedicellate ovary .....
- .....2. *C. brevifolium*
- 11. Inflorescence with opened mature flowers larger at the base and smaller at the apex
- .....9. *C. neglectum* (Reichenbach & Warming 1881: 91) Cogniaux (1901: 425)
- Inflorescence with opened mature flowers almost the same size in the base and apex.....12
- 12. Flowers white-greenish; lateral lobes of the lip with truncate apex.....14. *C. spannagelii* Hoehne ex Hoehne (1938: 22)
- Flowers white-orangeish; lateral lobes of the lip with rounded apex.....13
- 13. Spur relatively slightly shorter than the lip.....4. *C. crassirhizum* Hoehne (1939: 44)
- Spur relatively twice shorter than the lip.....8. *C. jamaicense*

1. *Campylocentrum brachycarpum* Cogniaux (1906: 512). Type:—BRAZIL. São Paulo: São Paulo, February 1896, *Comm. Grogr. e Geol. São Paulo* 2871 (lectotype **here designated**: BR!). (Fig. 1A-G)

*Campylocentrum aromaticum* Barbosa Rodrigues (1907: 103). *syn. nov.* Type:—BRAZIL. Rio de Janeiro: Rio de Janeiro, December, *J. Barbosa Rodrigues s.n.* [destroyed, *fide* Sprunger *et al.* (1996), lectotype **here designated**: Barbosa Rodrigues J., *Contributions du Jardin Botanique de Rio de Janeiro* 4: tab. 23, fig. B, original illustration at Jardim Botânico do Rio de Janeiro].

Roots 1.5–2.5 mm diam. Stem 2–41 cm long, unbranched. Leaves 10–50 × 4–10 mm, linear-oblong to oblong, lobes obtuse to rounded. Inflorescence 6–17 mm long, peduncle 1–1.5 mm long; rachis 5–15.5 mm long; floral bracts 1–1.8 × 1.4–2 mm, ovate to sub-orbicular, covering partially to completely the pedicellate ovary, the apex acute to obtuse. Flowers 10–18 (per inflorescence), with almost the same size in the base and apex, white-yellowish, ovary pedicellate 0.8–1.5 mm long; dorsal sepal 1–1.8 × 0.7–0.8 mm, ovate to oblong, 3-nerved, glabrous, the apex acute to obtuse; lateral sepals 1.1–2 × 0.5–0.7 mm, elliptic to oblong, subfalcate, 3-nerved, glabrous, the apex acute; petals 1–1.8 × 0.5–0.6 mm, elliptic, 3-nerved, the apex acute to obtuse; lip 1.1–1.8 × 1.2–1.4 mm, entire to obscurely 3-lobed, ovate, 5–7-nerved, the apex acute to obtuse, spur 1–1.8 × 0.3–0.8 mm diam., obovoid to clavate, curved, the apex rounded, glabrous; gynostemium ca. 0.2 mm long, anther cap apex rounded to truncate. Capsules 3–5 × 1.5–2 mm, obovoid to ellipsoid, pedicel ca. 0.5 mm long.

**Distribution and ecology:**—This species is endemic to the Atlantic Forest of Southern and Southeastern Brazil. It grows in the subcanopy of dense to opened forests, mainly in submontane areas (Fig. 2).

**Conservation status:**—It has short and very fragmented extent of occurrence (EOO – B1a), but high number of populations are known (area of occupancy - AOO), here it is classified as Near Threatened (NT).

**Nomenclatural notes:**—Two syntypes are cited by Cogniaux in the original publication, *Campos-Novae s.n.* (BR) and *Comissão Geográfica e Geológica de São Paulo 2871* (BR), we choose the latest deposited as the lectotype by the presence of well preserved flowers, the specimen *Campos-Novae s.n.* is in fruit.

One year after the publication of *C. brachycarpum*, Barbosa Rodrigues (1907) proposed *C. aromaticum* based on a specimen from the state of Rio de Janeiro (Brazil). Unfortunately the original material was lost in a flooding (Sprunger et al. 1996), but based on the illustration provided in the protologue and measurements it should be included as a synonym of *C. brachycarpum*.

**Similar species:**—It is similar to other species with floral bracts ovate to sub-orbicular, covering partially to completely the pedicellate ovary, such as *C. densiflorum* and *C. organense* but differs by the lip entire to obscurely 3-lobed (*vs.* distinctly 3-lobed) and spur curved (*vs.* strongly inflexed).



It can also be confused with *C. itatiaiae* and *C. schlechterianum* due the shape of the spur (obovoid to clavate), but besides de floral bracts it can be distinguished by sepals 3-nerved (vs. 1-nerved in *C. itatiaiae*) and lip 5 nerved (vs. 9-nerved in *C. schlechterianum*). (Table 1).

**Additional specimens examined:**—BRAZIL. Espírito Santo: Mimoso do Sul, Santa Luzia, 20 May 2007, *Couto 323* (MBML); *ibid.*, Pedra dos Pontões, 29 June 2008, *Couto 622* (MBML); Pedra Azul, 9 March 1970, *Kautzky 234* (MBML); Santa Teresa, Estação Ecológica de Santa Lúcia, 30 March 2000, *Kollmann et al. 2785* (MBML); *ibid.*, Nova Lombardia, 9 April 2003, *Vervloet & Bausen 2182* (MBML); *ibid.*, Santo Henrique, 11 February 2005, *Fontana & Kollmann 1121* (MBML); *ibid.*, Serra do Gelo, 16 Agosto 2003, *Assis et al. 930* (MBML); *ibid.*, Valsugana Velha, 30 March 2000, *Kollmann et al. 2770* (MBML); *ibid.*, Sítio Canaã, 27 February 2003, *Zottich 21* (MBML); Venda Nova do Imigrante, Alto Caxias, 8 August 2009, *Mattedi 95* (MBML). Minas Gerais: Amarantina, 23 March 1989, *Reis et al. 91* (BHCB); Barroso, Mata do Baú, 3 November 2001, *Assis & Ladeira 350* (CESJ, UFP); *ibid.*, 19 April 2003, *Assis & Magalhães 816* (CESJ); Carandaí, Pedra do Sino Hotel Fazenda, 25 March 2006, *Mota & Viana 581* (BHCB, CESJ); Chácara, Fazenda Fortaleza de Santana, 16 July 2011, *Barbosa et al. 2* (CESJ, UFP); Cristais, Propriedade do Sr. Lázaro de Assis, 20 July 2014, *Carvalho 117* (BHCB); Itatiaiuçu, 7 February 2011, *Krahl 221* (VIES); Juiz de Fora, Mata da Fazenda Floresta, 24 September 2006, *Souza & Bastos 533* (CESJ); Paraopeba, 31 March 1959, *Heringer s.n.* (HB); São João del Rey, Serra de São José, 6 March 1988, *Alves 210* (RB). Rio de Janeiro: Nova Friburgo, Macaé de Cima, 17 July 1993, *Vieira & Gurken 296* (RB); *ibid.*, April 1948, *Polo 4* (RB); *ibid.*, Furnas do Catête, March 1954, *Lima s.n.* (HB); Santa Maria Magdalena, Pedra Dubois, 8 March 1935, *Brade 14316* (RB); Teresópolis, May 1917, *Sampaio 2496* (R); *ibid.*, Serra dos Orgãos, 15 March 1958, *Abendoroth 29* (HB); Vassouras, Ponte Funda, 14 September 2013, *Pessoa & Wangler 1193* (RB, UFP). São Paulo: Campinas, s.d., *Novaes s.n. (comm. el. Edwall) s.n.* (BR); Angatuba, Fazenda do Serviço Florestal, 23 February 1966, *Emmerich & Dressler 2842* (K, M, R); São José do Barreiro, 3 May 1968, *Sucre et al. 3047* (RB); São Paulo, Parque Estadual da Cantareira, Barrocada, 3 August 2005, *Arzolla 902* (SP, SPSF).

2. *Campylocentrum brevifolium* (Lindley) E. Pessoa & M. Alves (2015: 43).

*Angraecum brevifolium* Lindley (1840: 68). Type:—BRAZIL. Rio de Janeiro: [probably near Cabo Frio], September 1815, *M. Wied s. n.* (holotype: BR 518550!, isotypes: GOET!; W-R 23774!). (Fig. 1H-J)

Roots 1–2 mm diam. Stem 10.5–38 cm long, rarely branched. Leaves 11–28 × 4–7 mm, oblong, lobes rounded. Inflorescence 3–11 mm long, peduncle ca. 1 mm long; rachis 2–10 mm long; floral bracts 0.5–0.8 × 0.3–0.5 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 6–14 (per inflorescence), with almost the same size in the base and apex, cream-coloured, ovary pedicellate 0.9–1.2 mm long; dorsal sepal 1.6–2.1 × 0.7–0.8 mm, oblong-elliptic, 3-nerved, glabrous, the apex acute; lateral sepals 1.6–2.1 × 0.7–0.8 mm, oblong-elliptic, subfalcate, 3-nerved, glabrous, the apex acute; petals 1.3–1.5 × 0.6–0.8 mm, wide elliptic, 3-nerved, the apex acute; lip 1.3–1.5 × 1.2–1.4 mm, 3-lobed, 5-nerved, lateral lobes 0.8–0.9 × 0.35–0.4 mm, sub-orbicular, the apex rounded, mid-lobe 0.5–0.6 × 0.5–0.6 mm, deltoid, the apex obtuse, spur 1.8–2.3 × 0.4–0.6 mm diam., cylindrical, slightly curved, glabrous, the apex rounded; gynostemium 0.4–0.5 mm long, anther cap apex truncate. Capsules 6–10 × 1.3–1.8 mm, ellipsoid, straight to curved, glabrous, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Endemic to Brazil (state of Rio de Janeiro) with a restrict area of distribution in Atlantic Forest (micro-endemic) and grows in “*restinga*” vegetation (coastal lowland forest and savanna physiognomies often on sandy soils) in an region locally called “*Região dos Lagos*” (Fig. 2).

**Conservation status:**—Based on criterion B1a (extent of occurrence severely fragmented) and B2a (area of occupancy severely fragmented), this species is considered Critically Endangered (CR). The occurrence area also suffers a strong housing pressure, and the last collected specimen was found twelve years ago.

**Nomenclatural notes:**—It was described under *Angraecum* based on a specimen from Rio de Janeiro collected by the Prince Maximilian of Wied-Newied. Three collections were found at BR, GOET, and W-R herbaria. Although the original publication cites the “*Herbarium Regium Monacense*” (herbarium M), it probably belongs to the “*Herbarium Martii*” which was acquired by the Belgian government in 1870, and today is part of the BR herbarium (Forther 1994). The complete history of this taxon can be found in Pessoa *et al.* (2015).

**Similar species:**—It is similar to *C. crassirhizum* from which It can be easily distinguished by the shorter sepals ( $\leq 2.2$  mm, *vs.*  $\geq 2.5$  mm long), and lip 5 nerved (*vs.* 11-nerved) and to *C. pauloense* by the 5-nerved lip (*vs.* 9–11-nerved) and spur twice longer than the peicellate ovary (*vs.* as long as to slightly longer).

Its small plants can also be confused with *C. itatiaiae* and *C. schlechterianum*, but its cylindrical spur (*vs.* globose or obovoid) is very characteristic. (Table 1).

**Additional specimens examined:**—BRAZIL. *Sine loco acurato*. s.d., *Martius s.n.* [M, K (illustration of the specimen), W-R (illustration of the specimen)]. Rio de Janeiro: Armação de Búzios, Serra das Emeranças, 21 August 1998, *Farney et al. 3817* (RB); Arraial do Cabo, Morro do Atalaia, 2 February 1950, *Pabst 493* (HB, M); Cabo Frio, Restinga de Cabo Frio, 15 August 1966, *Sucre 986* (HB, RB); *ibid.*, Morro da Gamboa, 11 August 1967, *Sucre 1539* (RB, UFP); *ibid.*, Morro da Piaçava, 31 August 2004, *Farney & Silva 4536* (RB); *ibid.*, Ilha do Cabo Frio, 11 May 1887, *Schenck 3971* (BR).

**3. *Campylocentrum carvalhoi* E. Pessoa & M. Alves (2015: 265). Type:**—BRAZIL. Minas Gerais: Cristais, Propriedade do Sr. Lázaro de Assis Carvalho (Sítio Barreiro), 20 July 2014, *B. M. Carvalho 119b* (holotype: UFP!, isotype: BHCB!). (Fig. 1K-M)

Roots 1–2 mm diam. Stem 5.5–23 cm long, unbranched. Leaves 25–45 × 2.5–4 mm, linear-oblong, lobes acute to obtuse. Inflorescence 7–11 mm long, peduncle 1–2 mm long; rachis 6–9 mm long; floral bracts 0.5–0.9 × 0.5–0.7 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 7–15 (per inflorescence), with almost the same size in the base and apex, pale orange, ovary pedicellate 0.7–1.0 mm long; dorsal sepal 1.3–1.5 × 0.7–0.8 mm, lanceolate, 3-nerved, glabrous, the apex acute; lateral sepals 1.6–1.8 × 0.7–0.8 mm, lanceolate, subfalcate, 3-nerved, glabrous, the apex acute; petals 1.2–1.3 × 0.5–0.6 mm, elliptic-lanceolate, 3-nerved, the apex acute; lip 1.6–1.7 × 1–1.2 mm between the lateral lobes, 3-lobed, 7-nerved, lateral lobes 1–1.1 × 0.3–0.4 mm, suborbicular, the apex rounded, mid-lobe 0.5–0.7 × 0.4–0.5 mm, deltoid, the apex acute, spur 1.8–2 × 0.5–0.7 mm diam., ellipsoid to sub-conical, patent, glabrous, the apex obtuse to acute; gynostemium ca. 0.2 mm long, anther cap apex

rounded. Capsule 4–6 mm × 1.5–2 mm, ellipsoid, occasionally curved, pedicel 0.5–0.8 mm long.

**Distribution and ecology:**—Endemic to Brazil (state of Minas Gerais), and is known only from the type locality where it grows in the sub-canopy of gallery forests in *Cerrado* vegetation (around 870 m elev.) (Fig. 2).

**Conservation status:**—Data deficient (DD).

**Similar species:**—It is a very distinctive species, but the spur shape is similar to *C. intermedium* from which it can be distinguished by shorter perianth (1.3–1.8 mm vs. 3 mm long) and 3-lobed lip (vs. entire) (Table 1).

**Additional specimens examined:**—BRAZIL. Minas Gerais: Cristais, Sítio Barreiro, 21 July 2013, *Pessoa & Carvalho 1190* (UFP).

**4. *Campylocentrum crassirhizum* Hoehne** (1939: 44). Type:—BRAZIL. Espírito Santo: Santa Teresa, April 1939 (*fl. in cult.*), *A. Ruschi 05* (holotype: SP!). (Fig. 1N-P)

*Campylocentrum iglesiasii* Brade (1941: 2). Type:—BRAZIL. São Paulo: São José de Barreiras, February 1940, *A. Iglesias s.n.* (holotype: RB 42338!).

Roots 1.5–4 mm diam. Stem 3–55 cm long, rarely branched. Leaves 15–85 × 5–16 mm, oblong, lobes rounded. Inflorescence 6–25 mm long, peduncle 1–3 mm long; rachis 5–22 mm long; floral bracts 0.8–1.2 × 0.4–0.6 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 7–21 (per inflorescence), with almost the same size in the base and apex, cream-coloured to pale orange, ovary pedicellate, 1.3–2.0 mm long; dorsal sepal 3–5 × 0.8–1.5 mm, oblong, 3-nerved, glabrous, the apex acute; lateral sepals 3–5.2 × 0.8–1.5 mm, oblong, subfalcate, 3-nerved, glabrous, the apex acute; petals 2.5–4.2 × 0.8–1.5 mm, oblong-elliptic, 3-nerved, the apex acute; lip 2.5–4.5 × 1.5–3.2 mm between the lateral lobes, 3-lobed, 11-nerved, lateral lobes 1.2–2.6 × 0.5–1.1 mm, oblong, the apex rounded, mid-lobe 1.3–2.2 × 0.5–0.9 mm, narrowly lanceolate, the apex acute, spur 2–4 × 0.6–1.3 mm diam., cylindrical, slightly curved, glabrous, the apex rounded; gynostemium 0.6–1 mm long, anther cap apex retuse. Capsule 6–15 mm × 1.5–2.1 mm, ellipsoid, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Endemic to Brazil, it is one of the most common species of the genus and widespread in the Brazilian coast. It grows in Atlantic Forest, Caatinga and Cerrado, in lowland to highland forest or savannas, up to 900 m alt. (Fig. 2).

**Conservation status:**—Based on its wide distribution (EOO) and large number of known populations (area of occupancy - AOO) this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—It was described based on a specimen that flowered in cultivation in the São Paulo Botanical Garden, but it is originally from Santa Teresa, Espírito Santo. Brade (1941), based on a specimen of *C. crassirhizum* with small leaves, described *C. iglesiasii* which was synonymized by Pessoa et al. (2015).

Since the XIXth century specimens of *C. crassirhizum* have been misidentified. Reichenbach f. & Warming (1881) used the name *C. micranthum* (*C. sect. Campylocentrum*) to them, and were followed by Cogniaux (1906). As described in 1939 by Hoehne, Pabst & Dungs (1977) recognized the species, however they applied the names *C. iglesiasii* and *C. linearifolium* Schlechter for some of its specimens. This last one was recently synonymized under *C. pauloense* by Pessoa et al. (2015).

**Similar species:**—It is confused with other species with cylindrical to cylindrical clavate spur and lip 3-lobed, such as *C. spannagelii* from which it can be easily distinguished by the flower color (white-orangeish vs. white-greenish) and lateral lobes of the lip rounded (vs. truncate). However, the most similar species is *C. jamaicense*, from which almost all vegetative and floral features overlap besides the distribution but they can be distinguished by the spur relatively slightly shorter than the lip (vs. spur relatively twice shorter than the lip). (Table 1).

**Additional specimens examined:**—BRAZIL. *sine loco acurato*: February 1937, Gardner 668 (K). Alagoas: Murici, 1 April 2013, Pessoa et al. 1082 (UFP). Bahia: Almandina, Rodovia pra Ibitupã, 12 March 2005, Fiaschi et al. 2750 (CEPEC); Amargosa, Serra do Timbó, 29 April 2007, Paixão et al. 1174 (HUEFS); Boa Nova, Fazenda Pioneira, 23 October 2007, Ferreira 1589 (CEPEC); Brejões, Rodovia Amargosa-Brejões, 25 February 2000, Jardim et al. 2918 (CEPEC); Conceição do Coité, Serra do Mucambo, 11 January 2010, Carvalho 2 (HUEFS); Jequié, Serra do Brejo Novo, 22 August 2011, Pessoa et al. 618 (UFP); *ibid.*, Fazenda of Marcus Ludovico, 24 October 2001, Thomas et al. 12588 (CEPEC); Lençóis, Serra Larga, 19

December 1984, *Lewis et al. s.n.* (SPF); Maracás, Fazenda Lagoa de Dentro, 5 December 2011, *Oliveira 329* (UFP); Morro do Chapéu, estrada para Bonito, 23 July 2008, *Bastos & J. Pinto 244* (HUEFS); Mucugê, Parque Municipal de Mucugê, 27 January 2003, *Azevedo 173* (HUEFS); Palmeiras, Pai Inácio, 25 September 1994, *Giulietti et al. 769* (ALCB, HUEFS); Paulo Afonso, Reserva Ecológica Raso da Catarina, 23 June 1982, *Queiroz 327* (ALCB, HUEFS); Santa Cruz da Vitória, Fazenda Boa Fé, 26 May 2005, *Jardim et al. 4603* (CEPEC); Uruçuca, Distrito de Serra Grande, 28 April 1994, *Jardim et al. 431* (CEPEC); Ceará: Baturité, Sítio São João, 14 December 1939, *Eugênio 455* (RB); Guaramiranga, Pico Alto, 22 April 2013, *Pessoa et al. 1111* (UFP); Maranguape, Serra de Maranguape, 4 May 1991, *Felix 3386* (EAN); Pacotí, 31 August 1986, *Lima-Verde s.n.* (EAC); Sobral, Serra da Meruoca, 8 August 2016, *Pessoa et al. 1329* (UFP). Espírito Santo: Alegre, São João do Norte, 10 July 2008, *Couto & Altoé 630* (MBML); Aracruz, Barra Sahy, 13 November 1992, *Pereira et al. 2671* (VIES); Cariacica, Boqueirão, 28 October 1999, *Fraga 531* (MBML); Conceição da Barra, Itaúnas, 19 November 1999, *Fraga 553* (MBML); Fundão, 9 March 2003, *Fontana & Sarmiento 519* (MBML); Guarapari, Parque Estadual de Setiba, 3 September 1988, *Pereira et al. 1791* (VIES); Linhares, 15 April 2011, *Meirelles 527* (ESA); Santa Maria de Jetibá, 13 March 2003, *Kollmann & Berger 6036* (MBML); Santa Teresa, Mata do Melo Leitão, 28 July 2013, *Pessoa et al. 1192* (UFP); *ibid.*, Valsuna Velha, 6 April 2000, *Kollmann & Vervloet 2811* (MBML); Vargem Alta, 9 December 1956, *Pereira s.n.* (RB). Minas Gerais: Barbacena, November 1843, *Weddel 1193* (P); Barroso, Mata do Baú, 24 May 2003, *Menini-Neto et al. 10* (CESJ); Carmópolis, Estação Ecológica Mata do Cedro, 25 November 2004, *Echternacht & Dornas 651* (BHCB); Carrancas, Vargem Grande, 11 November 1998, *Simões et al. 441*(UEC); Catas Altas, Serra do Caraça, 4 December 1999, *Mota 113* (BHCB); Chácara, Fazenda Fortaleza de Santana, 16 July 2011, *Barbosa et al. 12* (CESJ); Coronel Pacheco, Fazenda da Campanhia, 27 June 1944, *Heringer s.n.* (SP); Cristais, Sítio Estreito, 20 July 2013, *Pessoa et al. 1187* (UFP); Itamonte, 22 November 2006, *Stehmann et al. 4504* (ESA); Lagoa Santa, s.d., *Warming s.n.* (C); Macaia, Bonsucesso, December 1991, *Tameirã Neto & Werneck 835* (BHCB); Mariana, October 1840, *Gardner 5202* (BM, K); Ouro Preto, Potreiro, 5 January 2006, *Rezende & Mendes 429* (BHCB); São Gonçalo do Rio Abaixo, 22 December 1993, *Borba 114* (BHCB). Paraíba: Areia, Fazenda Junco, 6 March 1989, *Felix & Dornelas 1926* (EAN); São João do

Tigre, Serra do Enjeitado, 25 February 2011, *Felix 13498* (EAN). Paraná: Guaratuba, Rio da Praia, 2 May 1976, *Leinig 584* (HB); Paranaguá, Tabuleiro do Guaraní, 31 January 1966, *Hatschbach s.n.* (HB); Praia Leste, 21 April 1975, *Leinig 561* (HB). Pernambuco: Agrestina, Pedra Cabeça de Velho, 28 March 2008, *Gomes 765* (UFP); Belo Jardim, Pedra do Caboclo, 11 January 2012, *Pessoa et al. 904* (UFP); Bezerros, Serra Negra, 18 March 1995, *Felix & Paula 7058* (EAN, UFP); Brejo da Madre de Deus, Reserva Particular do Patrimônio Natural Fazenda Bitury, 16 July 2014, *Pessoa et al. 1238* (UFP); Igarassu, Usina São José, 1 March 2010, *Pessoa et al. 257* (UFP); Jaqueira, Usina Colônia, 31 January 2013, *Pessoa et al. 1063* (UFP); Lagoa dos Gatos, Pedra D'Anta, 18 December 2010, *Pessoa & Melo 470* (UFP); Sairé, 3 April 1973, *Mariz 767* (UFP); Sanharó, Jenipapo, 7 May 1966, *Giulietti 4543* (HUEFS, IPA); São Caitano, Pedra do Cachorro, 7 March 2010, *Pessoa & Mendes 407* (RB, UFP). Rio de Janeiro: Búzios, Fazenda José Gonçalves, 7 August 1997, *P. R. Farág & A. Lobão 425* (RB); Cabo Frio, Morro da Ganboa, 24 June 1967, *Sucré 1507* (RB, UFP); Guanabara, Morro do Rangel, 31 May 1973, *Sucré s.n.* (RB); Niterói, Itaciatiara, 26 May 1998, *Pinheiro 159* (HB); Rio das Ostras, Praia Virgem, 1 May 1999, *Santos 122* (R); Rio de Janeiro, Gávea, 26 February 1941, *Brade 16768* (RB); *ibid.*, Restinga da Maranbaia, 12 November 2004, *Dias & Habibe 89* (RB); Santa Maria Magdalena, 8 March 1935, *Lima & Brade 14315* (RB); Teresópolis, Boa Fé, 15 June 1943, *Veloso 439* (R); Vassouras, Ponte Funda, 14 September 2013, *Pessoa & Wangler 1194* (UFP). Rio Grande do Norte: Tibau do Sul, Trilha L do Polígono do Parque, 2 August 2012, *Jardim 6352* (UFRN). Santa Catarina: Balneário Camboriú, Parque Interpraias, 5 May 2010, *Stival-Santos et al. 2728* (FURB); Florianópolis, Campeche, 2 October 2013, *Pessoa & Siqueira 1198* (UFP); Navegantes, Costa Azul, 24 February 2011, *Korte 5999* (FURB); Pomerode, Ouro Preto Mineração, 4 October 2011, *Cadorin 3276* (FURB); Porto Belo, 16 September 2009, *Schimitt et al. 63* (FURB). São Paulo: Araras, Fazenda Nova Santa Cruz, 28 September 2006, *Moraes 11* (HRCB); Bananal, Serra da Bocaína, 14 April 2007, *Fraga & Nadruz 1689* (RB); Bertiooga, Itaquaré, 30 October 2001, *Martins 752* (SP); Cananéia, Parque Estadual da Ilha do Cardoso, 18 March 2003, *Brier 926* (UEC); Eldorado, Parque Estadual de Jacupiranga, 23 March 2005, *Oriani et al. 526* (UEC); Iguape, 15 February, *Leitão & Rezende 33506* (UEC); Limeira, 1 November 1954, *Hoehne s.n.* (SPF); São Carlos, Ribeirão do Feijão, 22 September 1988, *Ribeiro 562* (HRCB); São José do Barreiro, Parque Nacional Serra da Bocaina, 16 February 2014,

*Amorim 1914* (UFP); São Paulo, Butantã, 12 December 1995, *Dislich 182* (SPF); Sete Barras, Parque Estadual Carlos Botelho, 22 April 2002, *Farias et al. 678* (ESA); Ubatuba, Praia da Fazenda, 26 June 2007, *Mania 140* (HRCB). Sergipe: Areia Branca, Parque Nacional Serra de Itabaiana, 1 August 2007, *Nascimento 145* (ASE); Capela, Refúgio da Vida Silvestre Mata do Junco, 18 October 2012, *Pessoa et al. 776* (UFP); Lagarto, Povoado Rio das Vacas, 12 March 2010, *Santos 99* (ASE), Simão Dias, Fazenda Mercador, 11 March 2011, *Carregosa 184* (ASE).

5. *Campylocentrum densiflorum* Cogniaux (1906: 511). Type:—BRAZIL. Southeastern Brazil, *sine loco acurato*, s.d., *Sellow s.n.* (lectotype **here designated**: W 23664!, isoelectotype: BR 13072575!). (Fig. 3A-G)

*Campylocentrum dutrae* Schlechter (1925: 108). *syn. nov.* Type:—BRAZIL. Rio Grande do Sul: São Leopoldo, Quinta do Manuel, Janeiro, *J. Dutra 846* (lectotype **here designated**: SP!, isoelectotype: ICN!). *Campylocentrum*

*hasslerianum* Hoehne (1938: 23). *syn. nov.* Type:—PARAGUAY. Guairá: Villa Rica, June 1931, *P. Jorgensen 3950* (holotype: SP!, isotypes: C!, US!).

*Campylocentrum hatschbachii* Schlechter (1926: 70). *syn. nov.* Type:—BRAZIL. Paraná: Curitiba, March-April 1925, *A. Hatschbach 50* [holotype: not found, probably destroyed at B, neotype **here designated**: BRAZIL. Paraná, Curitiba, *G. Pabst 551* (neotype: RB!, isoneotypes: HB!, HBR!,)].

*Campylocentrum rhomboglossum* Hoehne & Schlechter (1926: 297). *syn. nov.* Type:—BRAZIL. São Paulo: São Paulo, Butantã, 26 November 1920, *F.C. Hoehne s.n.* (holotype: SP 4591!, isotypes: AMES 106468 photograph!, F 895982 photograph!, SPF 72266!).

*Campylocentrum trachycarpum* Kraenzlin (1911: 87). *syn. nov.* Type:—BRAZIL. Paraná: Capão Grande, 28 February 1908, *P. Dúsen 7463* (holotype: S photograph!).

Roots 1.5–3 mm diam. Stem 12–48 cm long, rarely branched. Leaves 1.6–65 × 5–15 mm, oblong, lobes rounded. Inflorescence 7–15 mm long, peduncle 1–3 mm long; rachis 7–12 mm long; floral bracts 1.2–2.0 × 1.2–2.8 mm, ovate to sub-orbicular, covering partially the pedicellate ovary, the apex obtuse. Flowers 6–16 (per inflorescence), larger at the base, smaller at the apex, white-yellowish, ovary pedicellate



1–2.2 mm long; dorsal sepal 2.1–2.8 × 0.8–1.0 mm, oblong, 3-nerved, glabrescent to abaxially sparsely pilose, the apex acute; lateral sepals 2.1–3.2 × 0.8–0.9 mm, elliptic to oblong, subfalcate, 3-nerved, glabrescent to abaxially sparsely pilose, the apex acute; petals 1.6–2.8 × 0.7–1 mm, elliptic to oblong, 3-nerved, the apex acute to obtuse; lip 2–2.8 × 1.6–2.2 mm, 3-lobed, 7–9-nerved, lateral lobes 1.2–1.8 × 0.6–1.0 mm, sub-orbicular, the apex truncate to rounded, mid-lobe 0.8–1 × 0.4–0.6 mm, deltoid, the apex acute to obtuse, spur 1.8–2 × 0.8–1 mm diam., clavate, strongly inflexed, glabrescent to sparsely pilose, the apex rounded; gynostemium 0.5–0.8 mm long, anther cap apex emarginate. Capsules 7–11 × 1.5–2 mm, cylindrical to ellipsoid, often curved, pedicel ca. 0.5 mm long.

**Distribution and ecology:**—Northern Argentina, Southern and Southeastern Brazil, Southern Paraguay and Uruguay. It grows in Atlantic Forest from sea level to sub-montane forests, and also in submontane forest formations in Uruguay (Fig. 4).

**Conservation status:**—Based on its wide distribution (EEO) and large number of known populations (area of occupancy - AOO) this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—Three syntypes of *C. densiflorum* are cited by Cogniaux (1906) in the original publication, we choose *Sellow s.n.* deposited in W as the lectotype by the presence of a duplicate in BR (isolectotype). Although Cogniaux collection is in BR, the complete specimen collected by Sellow is in W, the isolectotype is a fragment.

Several names were proposed based in specimens with small morphological variations. As described, in the same inflorescence it has small (in the top) and large (in the base) flowers and besides that the size the number of nerves and shape of the lip is also variable. Curiously, to each state of Southeastern and Southern Brazil, a name was previously proposed to this group, such as: *C. hatschbachii* and *C. trachycarpum* from Paraná, *C. dutrae* from Rio Grande do Sul, *C. rhomboglossum* to São Paulo, and also a syntype of *C. densiflorum* to Minas Gerais.

**Similar species:**—It can be confused with *C. organense*, from which is distinguished only by the size of the floral bracts ( $\leq 2.5$  mm wide vs.  $\geq 2.8$  mm, up to 4.2 mm wide). All the other characters overlap. (Table 1)

**Additional specimens examined:**—ARGENTINA. Misiones: Iguazu, Parque Nacional del Iguazu, 16 April 1993, *Johnson 371* (MO); Santa Rosa, 12 February

1952, *Caburro 973* (BA). BRAZIL. *sine loco acurato* (probably Southeastern Brazil), s.d., *Burchell 1995* (K). Minas Gerais: *sine loco acurato*, Januray 1910, *Vincent 6963* (U); *sine loco acurato*, 1816-1821, *Saint-Hilaire C122* (P); Caldas, Serra de Caldas, 2 February 2009, *Batista et al. 2792* (BHCB), *ibid.*, s.d., *Regnell s.n.* (W). Paraná: Barigui de Santa Felicidade, 15 May 1958, *Leinig 30* (HB); Contenda, Rodovia do Xisto, 2 March 1982, *Hatschbach 44623* (ALCB, FUEL, HRB, MBM, SPF); Curitiba, 19 February 1950, *Pabst 551* (HBR); Guaratuba, Rio Saí, February 1957, *Hatschbach 3816* (MBM, HB); Jaguaraiva, Rio Sabiá, 28 November 1968, *Hatschbach 20458* (C, MBM, HBR, MO); *ibid.*, 23 December 1915, *Dusén 17470* (K, MO, P, U); Lapa, Santo Amaro, 16 November 1967, *Hatschbach 16163* (MBM, US); Piraquara, 3 April 1949, *Hatschbach 1430* (MBM, RB, SP); *ibid.*, Volta Grande, 15 April 1949, *Hertel 440* (FUEL); Quatro Barras, Borda do Campo, 9 May 1998, *França 2520* (HUEFS, UFP). Rio Grande do Sul: Arroio dos Ratos, Fazenda Faxinal, 3 February 1977, *Hagelund 10943* (C); Capão do Leão, Pedreira do Deprec, 12 December 1997, *Jarenkow & Garcia 3667* (ESA, PEL); Eldorado do Sul, Estação Experimental Agronômica, 28 August 2002, *Giongo & Knuppi 258* (ICN); Encruzilhada do Sul, 1 December 2012, *Verdi & Jarenkow 6311* (FURB); Guaiba, Passo do Petim, 22 December 1993, *Nunes 1380* (ICN); Pacheca, Camaquã, 28 May 1989, *Waechter 2386* (ICN); Pelotas, Horto Botânico, 30 September, 1959, *Sacco 1404* (FUEL, HB, K); Porto Alegre, Morro da Ponta Grossa, 31 December 1961, *Pabst 1290* (HB, K); *ibid.*, Morro da Glória, 14 December 1932, *Orth s.n.* (SP, SPF); Rio Grande, Taim, 5 December 1978, *Waechter 1072* (ICN, SP); Santa Cruz do Sul, Pinheiral, 24 July 1980, *Waechter 1664* (ICN); Santana da Boa Vista, Cerro do Diogo, 24 September 1985, *Brack & Irgang s.n.* (ICN); São Leopoldo, January 1942, *Leite s.n.* (SP); *ibid.*, 1942, *Eugenio 116* (R); Taim, 5 December 1978, *Waechter 1072* (ICN); Tenente Portela, Porque Florestal do Turvo, 3 October 1979, *Waechter 1388* (ICN); Torres, Faxinal, 21 December 1977, *Waechter 694* (ICN); Viamão, Parque St. Hillairie, 25 November 1978, *Guerreiro s.n.* (ICN). Santa Catarina: Brusque, Azambuja, 4 January 1950, *Reitz 3235* (HBR, SP, UFP); Concórdia. Barra dos Queimados, 4 May 2000, *Mackiewicz 40* (HBR); Florianópolis, Barreiros, Ribeirão, 29 December 1969, *Bresolin 18* (FLOR, HB, HBR, ICN); *ibid.* 16 January 1967, *Klein 7053* (FLOR, HB, HBR, ICN); *ibid.*, Campeche, 2 October 2013, *Pessoa & Siqueira 1196* (RB, UFP); Ibirama, Horto Florestal, 27 December 1954, *Klein 941*

(HBR); Lontras, Concórdia, 3 March 2011, *Korte 6120* (FURB); Matador, 17 December 1967, *Lourteig 2301* (P); Paulo Lopes, 12 February 1952, *Pabst 1362* (K, HBG, RB); Santa Terezinha, Imbuial, 8 July 2010, *Korte & Kniess 3661* (FURB); São Domingos, 13 September 2002, *Hoeltgibaum 135* (FLOR); São Martinho, Chicão, 26 January 2010, *Schmitt et al. 1066* (FURB); Tangará, Rio do Peixe, 15 June 2011, *Guimarães 1331* (FLOR). São Paulo: *sine loco acurato*, 1833, *Gaudichaud s.n.* (P); Barra do Turvo, Parque Estadual de Jacupiranga, 24 March 2005, *Destefani et al. 116* (ESA); Campinas, Fazenda Campo Grande, 4 December 1938, *Zagatto & Vetorato 3109* (IAC); Iguape, Morro das Pedras, 30 January 1921, *Brade 8080* (HB, K); Jaboticabal, s.d., *Frazão s.n.* (RB); Santo Amaro, Seminário Espírito Santo, 10 January 1943, *Krieger 317* (CESJ, SP); São Paulo, Água Funda, Jardim Botânico, 10 January 1936, *Handro s.n.* (SPF); *ibid.*, Villa Emma, March 1940, *Brade 16256* (RB); Sengés, Fazenda Pisa-Papel e Celulose, 18 December 1997, *Torezan et al. 758* (ESA, UEC, UFP). PARAGUAY. Alto Paraná: Itaipu Binacional, 17 July 2003, *Zardini et al. 60042* (MO); Canindeyu: Jujui-Mí, 19 June 1996, *Jiménez & Marín 1249* (BM, FMB); *ibid.*, Rumbo Norte, 19 June 1996, *Jiménez & Marín 1249* (BM, FMB, MO); Paraguari: La Rosada, Parque Nacional Ybycu'i, 12 July 1989, *Aguayo 356* (B); Santa Barbara, January 1882, *Balansa 2999* (BAF); *ibid.*, April 1876, *Balansa 632a* (P). URUGUAY. Treinta Y Três: Paso del Dragón, January 1980, *Izaguirre et al. s.n.* (MVFA).

6. *Campylocentrum intermedium* (Reichenbach f. & Warming) Rolfe (1903: 245). *Aeranthus intermedia* Reichenbach f. & Warming (1881: 91). Type:—BRAZIL. Minas Gerais: Lagoa Santa, s.d., *Warming s.n.* [lectotype **here designated**: C 8314! (in spirit), isoelectotype: W 23667!]. (Fig.3H-J)

Roots 3–4 mm diam. Stem 15 cm long, unbranched. Leaves 30–40 × 4–6 mm, linear-oblong, subterete, lobes acute to obtuse. Inflorescence 9–15 mm long, peduncle ca. 1.0 mm long; rachis 8–14 mm long; floral bracts 0.6–0.8 × 0.5–0.7 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 10–12 (for inflorescence), white orangish, pedicellate ovary 1.5–2 mm long; dorsal sepal 3 × 1 mm, elliptic, number of nerves unknown, glabrous, the apex acute; lateral sepals 3 × 0.8 mm wide, oblong-elliptic, number of nerves unknown, glabrous, the apex acute; petals

2.5–2.8 × 0.8 mm wide, elliptic, number of nerves unknown, the apex acute; lip 3 × 1.5–2 mm wide between the lateral lobes, entire to obscurely 3-lobed, lanceolate, number of nerves unknown, the apex acute to truncate, spur 1.5 × 0.8 mm diam., ovoid-conical, slightly curved, the apex obtuse, glabrous; ginostemium ca. 1 mm long, anther cap apex rounded. Capsules not seen.

**Distribution and ecology:**—Endemic to Brazil (state of Minas Gerais), it is probably an extinct species known only for the type specimen collected in the *Cerrado* of Lagoa Santa by Warming in the XIXth century. This area is currently extremely disturbed making almost impossible to find this species there again (Fig. 4).

**Conservation status:**—Data deficient (DD), probably exticted since it was not recollected in the last 150 years.

**Nomenclatural notes:**—It was described by Reichenbach f. and Warming under *Aeranthus* based in a collection of Warming from Lagoa Santa (Brazil). Although the Reichenbach herbarium is currently at W, the Warming collection is at C, the specimen is in spirit and is designated here as lectotype, with a fragment deposited at W designated as isolectotype.

**Similar species:**—It is a very distinctive species, but the spur shape is similar to *C. carvalhoi* from which it can be distinguished by longer perianth (3 mm vs. 1.3–1.8 mm long) and entire lip (vs. 3-lobed). (Table 1)

**7. *Campylocentrum itatiaiae* E. Pessoa & M. Alves (2015: 267).** Type:—BRAZIL. Rio de Janeiro: Parque Nacional do Itatiaia, Pinheiral, 2,000 m a.s.l., January 1938, *L. Lanstyak s.n.* (holotype: RB 35115!). (Fig. 3K-M)

Roots 1.5–2 mm diam. Stem 15.5 cm long, unbranched. Leaves 18–21 × 3–5 mm, linear-oblong, lobes obtuse. Inflorescence 6–15 mm long, peduncle 1–2 mm long; rachis 5–13 mm long; floral bracts 0.3–0.4 × 0.2–0.3 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 12–20 (per inflorescence), with almost the same size in the base and apex, color unknown, ovary pedicellate 0.6–1 mm long; dorsal sepal 0.9–1.0 × 0.6–0.7 mm, ovate, 1-nerved, glabrous, the apex obtuse; lateral sepals 1.2–1.4 × 0.7–0.8 mm, oblong, subfalcate, 1-nerved, glabrous, the apex acute; petals 0.9–1.0 × 0.6–0.7 mm, oblong, 1-nerved, the apex rounded; lip 1.1–1.2 × 1.2–1.4 mm between the lateral lobes, 3-lobed, 5-nerved, lateral lobes 0.6–0.7 ×

0.30–0.35 mm, suborbicular, the apex rounded, mid-lobe 0.4–0.5 × 0.4–0.5 mm, deltoid, the apex obtuse, spur 0.8–1.1 × 0.5–0.7 mm diam., obovoid, straight to slightly curved, glabrous, the apex rounded; gynostemium ca. 0.2 mm long, anther cap apex rounded. Capsules not seen.

**Distribution and ecology:**—Endemic to Brazil (state of Rio de Janeiro), it is known only from the type locality in the Itatiaia National Park (southeastern Brazil), an area of montane Atlantic Forest with elevations above 2,000 m a.s.l. (IBDF 1997) (Fig. 4).

**Conservation status:**—Data deficient (DD), although the typical area is an important and well preserved fragment of Atlantic Forest (IBDF 1997), maybe due the difficulty of access it was not recollected in the last 60 years.

**Similar species:**—It can be confused with *C. schlechterianum*, but is easily distinguished by the inflorescences with 12–20 flowers (vs. 4–8), shorter sepals ( $\leq 1.4$  mm long vs.  $\geq 1.8$  mm long) and lip 5-nerved (vs. 9-nerved). It is also similar to *C. brachycarpum* but differs by shorter floral bracts (0.3–0.4 mm vs. 1.0–1.8 mm long) and 3-lobed lip (vs. unlobed). (Table 1)

**8. *Campylocentrum jamaicense* (Reichenbach.f. & Wulfschlaegel) Fawcett (1893: 141). *Aeranthes jamaicensis* Reichenbach f. & Wulfschlaegel (1864: 901). Type:—JAMAICA. Fairfield, 1849, *H.R. Wulfschlaegel 1053* (lectotype **here designated**: W!, isolectotype: M!).** (Fig. 3N–O)

*Campylocentrum barrettiae* Fawcett & Rendle (1909: 127). Type:—JAMAICA. Charlemont near Ewarton, 26 February 1896, *W. Harris 6580* [lectotype: BM!, designated by Ackerman (2014)].

Roots 1–3 mm diam. Stem 2–48 cm long, rarely branched. Leaves 20–80 × 7–13 mm, oblong, lobes rounded. Inflorescence 4–25 mm long, peduncle 1–3 mm long; rachis 3–22 mm long; floral bracts 0.8–1 × 0.4–0.6 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 6–22 (per inflorescence), with almost the same size in the base and apex, cream-coloured to pale orange, ovary pedicellate 1.5–2.0 mm long; dorsal sepal 3.5–5.5 × 0.8–1.3 mm, oblong, 3-nerved, glabrous, the apex acute; lateral sepals 4.5–6 × 1–1.5 mm, oblong, subfalcate, 3-nerved, glabrous, the

apex acute; petals  $3\text{--}4.4 \times 0.9\text{--}1.2$  mm, oblong-elliptic, 3-nerved, the apex acute; lip  $4\text{--}5 \times 2.3\text{--}3.2$  mm between the lateral lobes, 3-lobed, 11-nerved, lateral lobes  $1.8\text{--}2.1 \times 0.5\text{--}1$  mm, lanceolate, the apex rounded, mid-lobe  $2.2\text{--}3 \times 0.7\text{--}1.2$  mm, narrowly lanceolate, the apex acute, spur  $1.7\text{--}2.7 \times 0.8\text{--}1.2$  mm diam., cylindrical, straight to slightly curved, the apex rounded; gynostemium 0.8–1 mm long, anther cap apex retuse. Capsule  $7\text{--}11$  mm  $\times$   $2.5\text{--}3.5$  mm, ellipsoid, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Endemic to the Antilles, it grows in Cuba, Jamaica, Puerto Rico and Trinidad & Tobago. Although Ackerman (2014) cites it to Dominica, Guadeloupe, and Martinica, neither specimens were cited for these localities and nor were found on herbaria. It grows in moist broadleaf forests from sea level to highlands (Fig. 4).

**Conservation status:**—It has short and very fragmented extent of occurrence (EOO – B1a), but high number of populations are known (area of occupancy area - AOO), here it is classified as Near Threatened (NT).

**Nomenclatural notes:**—It was the second species described from the section *Laevigatum*, and for a long time it was been considered a synonym of *C. micranthum* (*C. sect. Campylocentrum*). This mistake was corrected by Bogarín & Pupulin (2010) and Ackerman (2014).

Ackerman (2014) indicate a specimen from Fairfield (Jamaica) collected by *H.R. Wulfschlaegel* and deposited at W as the its holotype. A second specimen was found at M. The protologue did not cite any collection, so a lectotipification is needed and we choose the voucher from W as the lectotype since it is the the original collection of Reichenbach.

**Similar species:**—It is similar to *C. crassirhizum* from which almost all vegetative and floral features overlap, except by the spur relatively twice shorter than the lip (*vs.* spur relatively slightly shorter than the lip) distinguish it. The phylogenetic study performed by Pessoa *et al.* (2017) showed these species in the same clade mixed. However, based on the disjunct distribution (Antilles *vs.* eastern South America), and low support (81% BS) we recognize both species. More studies with population genetics approach is needed to understand the limits of these species. (Table 1)

**Additional specimens examined:**—CUBA. *sine loco accurately*, 1860-1864, *Wright* 3298 (AMES, BM, G, P); Pinar: San Diego de los Baños, 11 April 1900, *Palmer & Ridley* 379 (US); Road to Llagaruzá, vicinity of Soledad, 17 October 1941, *Gonzales*

297 (AMES). JAMAICA. *sine loco acurato*, March 1839, *Wilson s.n.* (E, K-L, W); *ibid.*, s.d., *Pundei 27* (K); *ibid.*, 12 February 1909, *Harris s.n.* (NY); Cockpit Country, 13-18 September 1906, *Britton 492* (NY); Dealele, February 1916, *Ridley s.n.* (K); Green Valey, 20 February 1901, *Harris 10405* (BM); Saint Ann Parish: Moneages, 16 January 1938, *Hunnewell 15236* (AMES); *ibid.*, 24 April 1995, *Ackerman & Melendez-Ackerman 2836* (NY); Reynolds mine, near Lydford, 30 June 1955, *Howard & Proctor 14211* (AMES). PUERTO RICO. Mayaguez: Hacienda Alicia, 13 July 1963, *Alain 9925* (AMES); Monte Galsa, 9 April 1886, *Sintenis 4193* (AMES, BM, C, G, K, L, M, NY, P, US, W); Junco, 24 June 1886, *Sintenis 4711* (C); Monte Bajaya, 30 April 1886, *P. Sintenis 4250* (G). TRINIDAD & TOBAGO. Trinidad: Valencia, 13 March 1913, *Broadway s.n. p.part.* (AMES, K, NY).

**9. *Campylocentrum neglectum* (Reichenbach f. & Warming) Cogniaux (1901: 425).**

*Aeranthes neglecta* Reichenbach f. & Warming (1881: 91). Type:—BRAZIL. Minas Gerais: Lagoa Santa, s.d., *Warming s.n.* [lectotype **here designated**: C 8324! (in spirit), original illustration at W!]. (Fig. 5A-F)

*Campylocentrum neglectum* var. *angustifolium* Cogniaux (1906: 508). *syn. nov.*

Type:—PARAGUAY. Cordillera de Altos: Rio Apa, s.d., *E. Hassler 1502* (lectotype **here designated**: P-361616!, isolectotypes: BM!, BR!, G!, K!, P-361622!).

*Campylocentrum acutilobum* Cogniaux (1906: 510) *syn. nov.* Type:—PARAGUAY.

Pirayu-bi: between Paraguari and Vila Rica, s.d., *Balansa 714* (holotype: P!, isotype: BR!).

*Campylocentrum zehntneri* Schlechter (1925: 342). *syn. nov.* Type: BRAZIL. Bahia:

Rio Preto, 21 October 1912, *Zehntner 3032(404)* (lectotype **here designated**: RB!, isolectotypes: M!, R!).

Roots 1.5–2.5 mm diam. Stem 5–45 cm long, rarely branched. Leaves 20–85 × 6–10 mm, oblong, lobes rounded. Inflorescence 9–45 mm long, peduncle 2–3 mm long; rachis 7–42 mm long; floral bracts 1–1.5 × 1–1.5 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute to obtuse. Flowers 7–26 (per inflorescence), larger at the base, smaller at the apex, cream-coloured to pale orange, ovary pedicellate 1.5–2.0

mm long; dorsal sepal  $2.5\text{--}3 \times 0.8\text{--}1$  mm, oblong, 3-nerved, glabrous, the apex acute to obtuse; lateral sepals  $3\text{--}3.5 \times 0.8\text{--}1$  mm, oblong, subfalcate, 3-nerved, glabrous, the apex acute to obtuse; petals  $2.2\text{--}2.8 \times 0.6\text{--}1$  mm, oblong-elliptic, 3-nerved, the apex acute to obtuse; lip  $2.8\text{--}3 \times 1.3\text{--}1.7$  mm between the lateral lobes, 3-lobed, 9-nerved, lateral lobes  $1.5\text{--}1.8 \times 0.4\text{--}0.6$  mm, oblong, the apex rounded, mid-lobe  $1.1\text{--}1.3 \times 0.3\text{--}0.6$  mm, narrowly lanceolate, the apex acute, spur  $2\text{--}2.6 \times 0.7\text{--}1$  mm diam., cylindrical to cylindrical-clavate, curved, glabrous, the apex rounded; gynostemium 0.4–0.6 mm long, anther cap apex retuse. Capsule 5–10 mm  $\times$  1.5–2.0 mm, ellipsoid, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Northern Argentina, Southern Bolivia, Southeastern and Central Brazil and Paraguay. It grows in Chaco, Cerrado vegetation and Atlantic Forest (Fig. 4).

**Conservation status:**—Based on its wide distribution (EEO) and large number of known populations (area of occupancy - AOO) this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—It was described by Reichenbach and Warming under *Aeranthus* based in a collection of Warming from Lagoa Santa (Brazil). Although the Reichenbach herbarium is currently at W, the Warming collection is at C, the specimen is in spirit and is designated here as lectotype, since no herbarium citation is present in the original publication.

After the examination of the types of *C. neglectum* var. *angustifolium*, *C. acutilobum* and *C. zehntneri*, we understand that their concept falls in the morphological variation of *C. neglectum*, and they are proposed here as synonyms. Additionally, we must highlight that one of the syntypes of *C. neglectum* var. *angustifolium* (*Balansa 632a*) belongs to *C. densiflorum*, and a specimen (*Schwacke 10412*) cited by Cogniaux (1906) as *C. neglectum* actually is *C. crassirhizum*.

*Campylocentrum zehntneri* was described based in a specimens possibly collected in Bahia. Although in the protologue the author cites *Zehntner 3032*, our observations on the types confirm a number “404” written on the sheets (or labels). The specimen at R is only marked with “404”, while at RB and M have both numbers (*Zehntner 3032* and *404*). Additionally, none locality called “Rio Preto” is known from the state of Bahia, meaning that it can be a mistake.



**Similar species:**—Among the species with cylindrical to/or cylindrical-clavate spurs and 3-lobed lip such as *C. crassirhizum*, *C. jamaicense*, *C. pauloense* and *C. spannagelii*, it is distinguished by opened mature flowers larger at the base of the axis of the inflorescence and smaller ones at the apex. It gives to the inflorescence a conic aspect. (Table 1)

**Additional specimens examined:**—ARGENTINA. Chaco: Campo del Nove, 14 December 1897, *Venturi s.n.* (BA); Colonia Benitez, December 1936, *Schulz 570* (SP); *ibid.*, July 1917, *Muello s.n.* (BAF); Las Palomas, November 1917, *Jorgesen 2067* (BA); Río Bermejo, Isleta de Selva, 14 November 1986, *Cristobal et al. 2088* (CTES, K). Corrientes: Capital, El Pericha, 6 November 1986, *Bliarpri 20181* (G); Estancia Santa Teresa, 13 January 1949, *Pederson 192* (C); General Paz, Lomas de Vallejos, 9 August 1973, *Schinini & Quarín 6973* (CTES, RB); Ituzaingó, Isla Apipé Grande, 11 December 1973, *Krapovickas et al. 24284* (CTES, G); Mburucuyá, Potrero, 18 October 2006, *Arbo et al. 9394* (CTES, HUEFS); Mercedes, Laguna Iberá, 24 February 1989, *Tressens et al. 3559* (CTES, BA, K); Saladas, 25 February 1917, L.K. s.n. (BA); San Cosme, Paso de la Patria, 31 January 2007, *Paula-Souza et al. 8107* (ESA, K), *ibid.*, 2 September 1970, *Pederson 9632* (C); San Luis de Palmar, 2 November 1975, *Cristobal et al. 1429* (CTES, G), San Miguel, Toro-y, 27 February 1990, *Vanni et al. 1455* (CTES, UB). Formosa: Formosa, 19 December 1900, *Kermes 473* (BA); *ibid.*, 1919, *Jorgensen 2074* (MO, US); El Ombu, 21 November 2004, *Maturo & Prado 181* (BM, CTES, MO); Pilcomayo, Riacho Negro, 16 May 1947, *Morel 2884* (K, W). Patiño: Formosa, El Cogoik, 19 February 2004, *Tressens et al. 6895* (CESJ, CTES, SP). Santa Fé: Rabón a Florencia, 11 January 1937, *Castellanos s.n.* (RB, UFP). BOLIVIA. Apolo: sine loco acurato, 11 March 1902, *Williams 50* (BM). Chiquitos: Tucavaca, Santiago de Chiquitos, 22 October 1994, *Vargas et al 3430* (F). Santa Cruz: Andrés Ibáñez, 27 July 1994, *Nee 45395* (G, MO); Nuflo de Chavez, Estancia San Miguelito, 18 March 1995, *Fuentes 526* (MO). BRASIL. Distrito Federal: Brasília, 13 November 1958, *Pereira & Pabst 4603* (RB, K); *ibid.*, Reserva Ecológica do IBGE, 31 May 1989, *Pereira Neto & Lopes 296* (BHCB, IBGE); *ibid.*, Rio Preto, 10 October 2002, *Rezende et al. 619* (CEN, HUEFS); *ibid.*, Formosa, Fazenda Manga, 27 November 2002, *Santos et al. 1699* (CEN); *ibid.*, Area de Proteção Ambiental do Gama, Cabeça de Veado, 23 October 2002, *Fonseca 3745* (CEN, IBGE). Goiás: Agua Fria, 4 February 2005, *Salles et al. 3591* (HEPH); Alto Paraíso de Goiás, Fazenda do Sr. Denezinho, 12 November 1996,

*Mendonça et al.* 2937 (IBGE); Cristalina, 15 May 2002, *Santos et al.* 1161 (CEN); Paraúna, Ponte de Pedra, 10 January 1993, *Batista* 375 (CEN); Sítio d'Abadia, Represa Mambái, 17 July 2009, *Peres-jr* 20 (UB). Mato Grosso do Sul: Bodoquena, Fazenda Rancho Branco, 31 October 2005, *Damasceno-Jr. et al.* 3644 (COR); Bonito, Parque Nacional da Serra da Bodoquena, 5 December 2010, *Quinet* 2286 (RB); Corumbá, Morro Santa Cruz, 23 July 1999, *Rodriguez* 08 (COR, SP). Minas Gerais: Cabeceira Grande, Rio Preto, 15 August 2002, *Santos et al.* 144 (CEN); Corinto, 4 March 1970, *Irwin et al.* 26907 (NY, UB); Cristais, propriedade do sr. Lázaro de Assis, 20 July 2014, *Carvalho* 116 (BHCB, UFP); Formoso, Rio Mato Grande, 6 November 1989, *Walter et al.* 533 (CEN); Funilândia, Lagoa da Gordura, 2 October 2007, *Batista et al.* 2134 (BHCB); Lagoa Santa, Area de Proteção Ambiental do Carste de Lagoa Santa, Poções, 1995, *Brina & Costa s.n.* (BHCB); *ibid.* Parque Estadual do Sumidouro, Gruta da Lapinha, 4 October 2007, *Batista* 2138 (BHCB); Manga, Gleba A, 23 October 1990, *Costa et al.* 381 (BHCB); Matozinhos, Sítio Retiro das Palmeiras, 13 October 2007, *Batista et al.* 2140 (BHCB); Paracatú, 21 October 1989, *Heringer et al.* 1382 (HEPH); Paraopeba, Horto Florestal, 12 October 1957, *Heringer* 5764b (UB); Pedro Leopoldo, Fazenda Jaguara, 7 November 1968, *Duarte* 11243 (BHCB); Queimados, Unaí, 20 January 1998, *Costa s.n.* (BHCB). PARAGUAY. *sine loco acurato*, February 1901, *Hassler* 8519 (G). Alto Paraguay: Puerto Casado, 16 October 1956, *Pederson* 4039 (C, K, P, U); San Pedro, 5 October 1956, *Woolston* 744 (C, K, P). Alto Parana: Reserva Itabó, Itaipú Binacional, August 1998, *Meireles* 7413 (G); Caaguazu: Arroyo Yakare, 8 February 1989, *Zardini & Aguayo* 10719 (G, K, MO). Caazapa: Tavai, Bosque Cercano al Hospital, 28 October 1988, *Dagen* 884 (G). Chaco: Cerro León, 15 April 1989, *Ramella* 6556 (G). Concepción: Paso Horqueta, Rio Aquidán, 19 February 1990, *Palacios* 1875 (AS, MO). Cordillera: *sine loco acurato*, s.d., *Hassler* 1502 (BR, K); Altos, 7 December 1902, *Friebrig* 562 (BM, E, G, K, M, U), *ibid.*, 1898, *Hassler* 3858 (G, K, P). Neembucú: Curupayty, Humaitá, 9 November 1978, *Bernardi* 18431 (G); Yacaré, Guazu Cuá, 26 October 1991, *Spichiger* 5350 (G); Paraguari: Isla del Tebicuary, Villa Florida, October 1980, *Casas & Molero s.n.* (MO); National Park Ybycu'i, 12 March 1992, *Zardini & Aquino* 31141 (AS, B, MO); Sapucay, November 1913, *Hassler* 12675 (BM, C, E, G, K, MO, U). Presidente Hayes: Estancia Maromba, 20 October 2004, *Juvenel et al.* 603 (BM); Villa Hayes, Estancia la Golondrina, 9

September 1982, *Hahn 700* (G, K, MO). San Lorenzo: *sine loco acurato*, 12 October 1919, *s.col.* (LP, SP).

**10. *Campylocentrum organense* (Reichenbach f.) Rolfe** (1903: 245). *Aeranthes organensis* Reichenbach f. (1864: 901). Type:—BRAZIL. Rio de Janeiro: Serra dos Órgãos, s.d., *J. Miers s.n.* (holotype: K-L 79737!, isotype: BM 539085!). (Fig. 5G-I)

Roots 2–4 mm diam. Stem 23–30 cm long, unbranched. Leaves 33–57 × 7–12 mm, oblong, lobes rounded. Inflorescence 9–15 mm long, peduncle 1–2 mm long; rachis 7–13 mm long; floral bracts 2–3 × 2.8–4.2 mm, ovate to sub-orbicular, covering partially to completely the pedicellate ovary, the apex rounded. Flowers 8–16 (for inflorescence), bigger at the base, smaller at the apex, color unknown, pedicellate ovary 1.3–2.2 cm long; dorsal sepal 1.8–3 × 0.8–1.2 mm, oblong to oblong-elliptic, 3-nerved, glabrescent to abaxially sparsely pilose, the apex obtuse; lateral sepals 2–3 × 0.6–1 mm, lanceolate to oblong, subfalcate, 3-nerved, glabrous to abaxially sparsely pilose, the apex acute to obtuse; petals 1.7–2.1 × 0.6–1 mm, elliptic to lanceolate, 3-nerved, the apex acute to obtuse; lip 1.7–2.2 × 1.8–2 mm, 3-lobed, 9-nerved, lateral lobes 1.2–1.4 × 0.5–0.8 mm, oblanceolate, the apex rounded, mid-lobe 0.5–1 × 0.5–0.7 mm, deltoid, the apex acute to obtuse, spur 1.8–2 × 0.8–1.2 mm diam., obovoid to clavate, strongly inflexed, glabrescent to sparsely pilose, the apex rounded; gynostemium 0.5–1 mm long, anther cap apex emarginate. Capsule not seen.

**Distribution and ecology:**—Endemic to Brazil (state of Rio de Janeiro), it is probably an extinct species since it has never been re-collected. Based on the type locality we can assume that it grew in highland ombrophilous Atlantic Forest (Fig. 6).

**Conservation status:**—Data deficient (DD), probably extinct since it was not re-collected in the last 150 years.

**Nomenclatural notes:**—The original publication cites the type specimen to the herbarium Lindley, which is currently at K-L (holotype). Additionally, we were able to find another specimen at BR (isotype).

**Similar species:**—It can be confused with *C. densiflorum*, from which it is distinguished only by the larger floral bracts (2.8 mm to 4.2 mm vs. ≤ 2.5 mm wide). (Table 1).

**11. *Campylocentrum pauloense* Hoehne & Schlechter** (1926: 297). Type:—BRAZIL. São Paulo: São Paulo, Butantan, March 1921, A. Gehrt s. n. (holotype: SP 5506!, isotypes: SPF 72263!, B destroyed). (Fig. 5J-L)

*Campylocentrum linearifolium* Schlechter ex Mansfeld (1928: 264). Type:—BRAZIL. São Paulo, São Paulo, Vila Emma, April 1940, A. C. Brade 16.255 (neotype: RB!, isoneotypes: SPF!, UFP!)], designated by Pessoa *et al.* (2015).

*Campylocentrum minutum* Dutra, *nom. ms.*

Roots 1–2 mm diam. Stem 2–21 cm long, occasionally branched. Leaves 15–33 × 3–6 mm, oblong to linear-oblong, frequently curved, lobes acute to obtuse. Inflorescence 4–12 mm long, peduncle 2–4 mm long; rachis 2–8 mm long; floral bracts 0.8–1.0 × 0.3–0.7 mm, deltoid, covering only the base of the pedicellate ovary the apex acute. Flowers 3–10 (per inflorescence), with almost the same size in the base and apex, white greenish, pedicellate ovary 0.7–1.2 mm long; dorsal sepal 1.5–2.1 × 0.3–0.4 mm, oblong-elliptic, 3-nerved, adaxially sparsely pilose, the apex acute; lateral sepals 1.5–2.2 × 0.3–0.4 mm, oblong, 3-nerved, adaxially sparsely pilose, the apex acute; petals 1.4–1.7 × 0.3–0.4 mm, oblong-elliptic, 3-nerved, the apex acute; lip 1.5–2.0 × 1.3–1.7 mm wide between the lateral lobes, 3-lobed, 9–11-nerved, lateral lobes 1.0–1.1 × 0.5–0.65 mm, sub-orbicular, the apex rounded, mid-lobe 0.5–1.0 × 0.3–0.4 mm, deltoid, the apex acute, spur 1.1–1.5 × 0.5–0.8 mm diam., clavate, slightly curved, glabrescent to sparsely pilose, the apex rounded; gynostemium 0.1–0.2 mm long, anther cap apex rounded. Capsule 7–10 × 1.3–2.0 mm, ellipsoid, sometimes curved, pedicel 0.5–1.0 mm long.

**Distribution and ecology:**—Endemic to South and Southeastern Brazil, it grows in “*restinga*” vegetation (coastal lowland forest and savanna physiognomies often on sandy soils), ombrophilous forest (Atlantic Forest) and less often in gallery forest in Cerrado, occasionally in highlands, up to 700m alt (Fig. 6).

**Conservation status:**—It has short and very fragmented extent of occurrence (EOO – B1a), and also short area of occupancy (AOO - B2a), here it is classified as Vulnerable (VU).

**Nomenclatural notes:**—A specimen collected by Gehrt was cited in the protologue as the only type specimen of *C. pauloense* (deposited at SP). We were able to find

another specimen in SPF (isotype), and according to the data of the SP herbarium another specimen would have been available at B, but it was probably destroyed. *Campylocentrum linearifolium* also described from São Paulo, was synonymized by Pessoa *et al.* (2015), and *C. minutum* a name used in some local herbarium sheets, but never published, is also cited here as a synonym.

**Similar species:**—Its vegetative portion is similar to *C. schlechterianum*, from which it is indistinguishable, but it differs by the clavate slightly curved spur (*vs.* globose and patent). The flowers can be confused with *C. brevifolium* but it differs by the 9–11-nerved lip (*vs.* 5-nerved) and spur as long as to slightly longer than the pedicellate ovary (*vs.* twice longer). (Table 1)

**Additional specimens examined:**—BRAZIL. Espírito Santo: Pedra Azul, 12 February 1970, *Keutzky 234* (HB); Santa Maria de Jetibá, Rio Nove, 24 February 2000, *Demunner et al. 806* (MBML); Santa Teresa, Sítio Canaã, 27 February 2003, *Zottich 4* (MBML); Minas Gerais: Lima Duarte, Parque Estadual de Ibitipoca, 18 October 2003, *Menini-Neto et al. 28* (CESJ); São Francisco de Paula, 14 December 1994, *Tameirão 961* (BHCB). Rio de Janeiro: Teresópolis, Morro da Estação, 7 January 1959, *Abendroth P-135* (HB). Rio Grande do Sul: Emboaba, Osório, 25 November 1983, *Waechter 1993* (ICN); Torres, Caqueira, February 1927, *Dutra 987* (ICN). Santa Catarina: Alfredo Wagner, Alto Limeirinha, 25 November 2009, *Korte & A.Kniess 992* (FURB); Brusque, Azambuja, 23 September 1981, *Reitz 4163* (HB); Florianópolis, Campeche, 2 October 2013, *Pessoa & Siqueira 1197* (RB, UFP); Taió, Fazenda Tarumã, 24 February 2010, *Schmitt et al. 1532* (FURB). São Paulo: Assis, Estação Ecológica Assis, 7 January 2003, *Breier & Bahrami 811* (UEC); São Lourenço da Serra, Reserva Particular Patrimônio Natural Paiol Maria, 26 April 2011, *Lombardi et al. 8515* (HRCB); São Paulo, Villa Emma, March 1937, *Brade 15727* (RB).

**12. *Campylocentrum robustum* Cogniaux** (1906: 509). Type:—BRAZIL. Rio de Janeiro: Rio de Janeiro, Copacabana, 1871, *A. Glaziou 5490* (lectotype **here designated**: C!, isoelectotypes: P!, W!). (Fig. 7A-F)

*Campylocentrum latifolium* Cogniaux (1906: 509). **syn. nov.** Type:—BRAZIL. *sine loco acurato* (probably southeastern Brazil), s.d., *Langsdorff s.n.* [holotype: LE photograph!, isotype: BR 989494!].

Roots 1–2 mm diam. Stem 6.5–60 cm long, unbranched. Leaves 35–110 × 6–23 mm, linear-oblong, lobes rounded. Inflorescence 8–20 mm long, peduncle 1–4 mm long; rachis 7–16 mm long; floral bracts 1–1.2 × 1.3–1.5 mm, deltoid, covering partially, completely the pedicellate ovary, the apex acute. Flowers 8–18 (per inflorescence), larger at the base, smaller at the apex, pale orange, ovary pedicellate 2.3–2.8 mm long; dorsal sepal 4.1–8 × 1.2–2.8 mm, oblong, 3–5-nerved, glabrous, the apex acute; lateral sepals 4.5–8.5 × 1–1.5 mm, oblong, subfalcate, 3–5-nerved, glabrous, the apex acute; petals 4–8 × 1–1.7 mm, oblong-ob lanceolate, elliptical, 3–5-nerved, the apex acute; lip 4.3–8.1 × 1.8–2.8 mm, entire to obscurely 3-lobed, oblong to lanceolate, 9–11-nerved, the apex acute to acuminate, spur 3.3–5.5 × 0.6–1.2 mm diam., cylindrical, curved, the apex rounded; gynostemium 0.5–1 mm long, anther cap apex rounded to truncate. Capsule 10–17 mm × 2–3 mm, ellipsoid, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Endemic to the Atlantic Forest of Northeastern and Southeastern Brazil. Although it has a wide distribution through the Brazilian coast, it is more common in Southeastern Brazil. It has been cited to Colombia, Ecuador and Peru, however those specimens actually belong to *C. kuntzei* Cogniaux *ex* Kuntze (Pessoa & Alves 2015) (Fig. 6).

**Conservation status:**—Based on its wide distribution (EOO) and large number of known populations (area of occupancy - AOO) this species falls under the Least Concern (LC) category.

**Nomenclatural notes:**—Two syntypes are cited by Cogniaux (1906) - *Glaziou 5490* and *Magalhães-Gomes 2115 – 2342* (both numbers in the same sheet), and we choose *Glaziou 5490* deposited at C as the lectotype by the presence of duplicates in P and W (isolectotypes). Although the material at P is more complete, Cogniaux cites the herbarium Warming (currently in C) in the protologue, and it is cited as the lectotype.

*Campylocentrum latifolium* was also described by Cogniaux (1906) based on a specimen of *C. robustum* with shorter and wider leaves. A careful analysis of flowers at BR (isotype) confirm it as vegetative variation and is treated here as a synonym.

**Similar species:**—It is a distinctive species and holds the largest flowers in the sect. *Laevigatum* (up to 8.5 mm long), and also the only species with cylindrical spur and entire to obscurely 3-lobed lip. The specimens from Northeastern Brazil are smaller

in floral and vegetative features, and can be confused with *C. crassirhizum* but its 3-lobed lip is very distinctive. (Table 1)

**Additional specimens examined:**—BRAZIL. Bahia: Almadina, Fazenda São Roque, 12 March 2005, *Fiaschi et al.* 2750 (CEPEC); Cachoeira, Vale dos Rios, October 1980, *Pedra-do-Cavalo* 809 (ALCB, HUEFS); Conceição do Coité, Serra do Mucambo, 4 October 2010, *Carvalho* 19 (HUEFS); Ipirá, Fazenda Recreio, 4 October 1986, *Queiroz et al.* 971 (HUEFS); Jequié, Fazenda de Marcus Ludovico and João Andrade, 24 October 2001, *Thomas et al.* 12588 (HUEFS, NY); *ibid.*, Morro da Torre, 13 April 2007, *Queiroz et al.* 12920 (HUEFS); Maracás, 9 July 1984, *Queiroz* 825 (HUEFS); *ibid.*, Fazenda Juramento, 27 April 1978, *Mori et al.* 10036 (CEPEC); Quijingue, Serra das Candeias, 13 November 2005, *cardoso et al.* 870 (HUEFS, UFP); Rui Barbosa, Serra do Orobó, 5 September 2004, *Queiroz et al.* 9535 (HUEFS); Santa Cruz da Vitória, Fazenda Boa Fé, 22 October 2005, *Jardim et al.* 4747 (CEPEC, HUEFS); Vitória da Conquista, Serra do Tromba, 18 October 2008, *Azevedo et al.* 350 (HUEFS). Espírito Santo: *sine loco acurato*, May 1961, *Machado* 51 (HB); Alegre, São João do Norte, 6 August 2004, *Couto* 162 (MBML); *ibid.*, 24 June 2008, *Couto et al.* 570 (MBML); *ibid.*, PCH Santá Fé, 10 July 2008, *Couto & Altoé* 630 (MBML); Aracruz, Bara do Riacho, 28 September 2010, *Vervoloet & Desanti* 3539 (MBML); *ibid.*, Picuã, 27 August 2011, *Sagrillo & Dalmonch* 15b (MBML); Guarapará, Setiba, 10 August 1996, *Fraga* 329 (MBML); *ibid.*, 18 October 1988, *Pereira & Gomes* 1858 (UFP, VIES); *ibid.*, Parque Estadual Paulo César Vinha, 26 August 1994, *Fraga* 32 (MBML); Santa Leopoldina, Colina Verde, 29 May 2007, *Demuner et al.* 4069 (MBML); *ibid.*, Morro do Agudo, 29 August 2007, *Vervloet et al.* 3344 (MBML); Vila Velha, Restinga de Interlagos, 14 September 1996, *Fraga* 343 (MBML); Vitória, Praia de Manginhos, 26 October 1970, *Kautsky* 297 (HB). Minas Gerais: Barroso, Mata do Baú, 19 April 2003, *Assis & Magalhães* 815 (CESJ); *ibid.*, 3 May 2003, *Assis et al.* 822 (CESJ); *ibid.*, 25 September 2001, *Assis & Ladeira* 257 (CESJ); Carrancas, Serra de Bicas, 30 April 1999, *Simões et al.* 822 (UEC); Coronel Pacheco, Fazenda Campanha, 27 June 1944, *Heringer* 1445 (SP); Jequeri, Usina de Providência, 29 September 1997, *Salino* 3511 (BHCB); Lavras, Terras do Seminário, 30 March 1958, *Welter* 225 (HB); Salto da Divisa, Fazenda Jabuti, 20 August 2003, *Lombardi et al.* 5311 (BHCB); Santana do Garambeu, Alto Rio Grande, 7 June 2001, *Salino & Mota* 6987 (BHCB). Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, 5

September 2013, *Buril et al. 645* (RB, UFP). Rio de Janeiro: *sine loco acurato*, 7 september 1894, *Magalhães Gomes 2115-2342* (BR); Araruama, Praia Seca, 23 August 2008, *Cavalcanti et al. 251* (RB); Aerial, Ilha do Rio Piabanha, 16 October 1949, *Pabst 428* (HB); Cabo Frio, Alcalis, 6 July 1973, *Sucre et al. 10024* (HB, RB); *ibid.* Armação de Búzios, 2 November 1983, *Martinelli & Soderstrom 9780* (RB); *ibid.*, Morro da Piaçava, 9 October 2002, *Farney & Fonseca 4491* (RB); *ibid.*, Perynas, 29 September 1993, *Emygdno 5781* (R); *ibid.*, Restinga do Peró, 17 September 1968, *Sucre 3684* (GUA, HB, RB, UFP); Carapebus, Praia de Carapebus, 23 September 1996, *Costa et al. 663* (R); *ibid.*, Lagoa Paulista, 23 April 1997, *Batista et al. 36* (R); Nova Friburgo, May 1955, *s.col. 215* (HB); Rio de Janeiro, Boca do Mato, August 1917, *Sampaio 2740* (R); *ibid.*, Botafogo, July 1914, *Hoehne s.n.* (R); *ibid.*, Praia de Grumari, 27 November 2005, *Ramos 14* (RFA); *ibid.*, Recreio dos Bandeirantes, September 1939, *Lutz 1500* (R); *ibid.*, Restinga de Grumari, 27 October 1998, *Angelo s.n.* (R); *ibid.*, Serra da Bica, 1886, *Schwaecke 5201* (RB); Rio das Ostras, Balneário das Garças, 25 September 1999, *Braga & Damasceno 527* (RB); Santa Maria Madalena, Rio Grande, 29 September 1979, *Martinho & Ventura 48* (HB); Saquarema, Reserva Ecológica de Jacarepiá, 29 October 1991, *Fontoura et al. 206* (RB, UFP).

**13. *Campylocentrum schlechterianum* E. Pessoa & M. Alves (2015: 268).** Type:— BRAZIL. Santa Catarina: São Martinho, Chicão, 526 m a.s.l., 26 January 2010, *J. Schmitt et al. 1020* (holotype: FURB!). (Fig. 7G-I)

Roots 1–1.5 mm diam. Stem 3–13 cm long, rarely branched. Leaves 10–28 × 3–4 mm, linear-oblong, lobes acute to obtuse. Inflorescence 5–8 mm long, peduncle ca. 1 mm long; rachis 4–7 mm long; floral bracts 0.3–0.5 × 0.2–0.3 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 4–8 (per inflorescence), with almost the same size in the base and apex, cream-colored, ovary pedicellate 0.8–1.2 mm long; dorsal sepal 1.8–2.1 × 0.9–1.0 mm, oblong, 3-nerved, glabrous, the apex obtuse; lateral sepals 2–2.5 × 0.7–0.8 mm, oblong, subfalcate, 3-nerved, glabrous, the apex acute to obtuse; petals 1.7–1.9 × 0.7–0.8 mm, oblong, 3-nerved, the apex acute to obtuse; lip 1.9–2.1 × 1.5–1.8 mm between the lateral lobes, 3-lobed, 9-nerved, lateral lobes 1.0–1.1 × 0.4–0.5 mm, suborbicular, the apex rounded, mid-lobe 0.9–1.0 × 0.6–0.8 mm, deltoid, the apex acute, spur 1.0–1.2 × 0.9–1.1 mm diam., globose, patent,



glabrous, the apex rounded; gynostemium ca. 0.2 mm long, anther cap apex rounded. Capsules not seen.

**Distribution and ecology:**—Endemic to Brazil (states of Santa Catarina and São Paulo), and recently described (Pessoa & Alves 2015). It grows in areas of Atlantic Forest with elevations of 500–700 m a.s.l. and probably also occurs in the State of Paraná (southern Brazil), as this state is geographically situated between the previous cited states (Fig. 8).

**Conservation status:**—Data deficient (DD).

**Similar species:**— Its vegetative portion is similar to *C. pauloense*, from which it is indistinguishable, but it differs by the globose and patent spur (*vs.* clavate slightly curved). The flowers can be confused with *C. itatiaie* and *C. brachycarpum* but it differs by sepals 3-nerved (*vs.* 1-nerved in *C. itatiaiae*) and 9-nerved lip (*vs.* 5-nerved in *C. brachycarpum*). (Table 1)

**Additional specimens examined:**—BRAZIL. São Paulo: Barra do Turvo, Parque Estadual de Jacupiranga, Núcleo Cedro, 24 March 2005, *Destefani et al. 111* (ESA); *ibid.*, 24 March 2005, *Destefani et al. 115* (ESA).

**14. *Campylocentrum spannagelii* Hoehne ex Hoehne (1938: 22). *Campylocentrum spannagelii* Hoehne (1937: 140) *nom. nud.* Type:—BRAZIL. Rio de Janeiro: Petrópolis, January 1933, *C. Spannagel 356* (holotype: SP!). (Fig. 7J-Q)**

*Campylocentrum toledo* Schlechter, *nom. ms.*

Roots 1–3 mm diam. Stem 5–76 cm long, unbranched. Leaves 16–65 × 5–11 mm, elliptical-oblong to oblong, lobes obtuse to rounded. Inflorescence 6–20 mm long, peduncle 2–4 mm long, glabrous, brownish; rachis 4–16 mm long, glabrous, brownish; floral bracts 0.8–1.2 × 0.5–0.7 mm, deltoid, covering only the base of the pedicellate ovary, the apex acute. Flowers 8–16 (per inflorescence), with almost the same size in the base and apex, white-greenish, ovary pedicellate 1.0–1.5 mm long; dorsal sepal 2.5–3.8 × 0.7–1 mm, elliptic, 3-nerved, adaxially sparsely pilose, the apex obtuse to rounded; lateral sepals 3–4 × 0.8–1 mm, oblong, subfalcate, 3-nerved, adaxially sparsely pilose, the apex acute to obtuse; petals 2.5–3.2 × 0.6–0.8 mm, oblong, 3-nerved, the apex acute; lip 2.7–3.8 × 2.5–2 mm between the lateral lobes, 3-lobed, 9–11-nerved,

lateral lobes 1.6–2 × 0.4–0.6 mm, oblong, the apex truncate, mid-lobe 1.1–1.9 × 0.8–0.9 mm, deltoid, the apex acute, spur 2.5–3.5 × 0.5–1.0 mm diam., cylindrical-clavate, straight to slightly curved, glabrescent to sparsely pilose, the apex rounded; gynostemium 0.6–1 mm long, anther cap apex retuse. Capsule 7–12 mm × 2–3 mm, ellipsoid, pedicel 0.5–1 mm long.

**Distribution and ecology:**—Endemic to the Atlantic Forest of Brazil (states of Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina e São Paulo). It is specially common in the east of the state of Minas Gerais and grows from sea level in areas of “*restingas*” to submontane forests (Fig. 8).

**Conservation status:**—Although it has a relatively medium distribution range (extent of occurrence – EOO), the high number of known populations provide wide area of occupancy (AOO), here it is classified as Least Concern (LC).

**Nomenclatural notes:**—Although the name *C. spannagelii* Hoehne had often been cited (eg. BFG 2015), it is actually a nomen nudum. It was published with no type material or diagnosis in a commemorative list of the herbarium SP (Hoehne 1937). The complete description, illustration and type citation for the name were published in the follow year (Hoehne 1938). The correct name for this species is *C. spannagelii* Hoehne ex Hoehne (see also Pessoa & Alves 2016).

**Similar species:**—This species has a wide variation on vegetative morphology (Fig. 4J-L), smaller plants are similar to *C. pauloense* (distinguished by larger flowers), while larger plants with wide leaves can be confused with *C. crassirhizum* (recognized by white-greenish flowers), a third “morphotype” with long thin leaves is very distinctive and were named in some herbarium sheets as “*C. toledo*”, but this name has never been published. The holotype includes two specimens with different morphologies. It is also confused with other species with cylindrical to cylindrical-clavate spur and lip 3-lobed, but is easily distinguished by white-greenish flowers (vs. yellowish, white orangish or cream coloured) and lateral lobes of the lip with truncate apex (vs. rounded). (Table 1)

**Additional specimens examined:**—BRAZIL. Espírito Santo: *sine loco acurato*, May 1961, *Machado 52* (HB); Fundão, Goiapaboa-Açu, 8 February 2003, *Fontana & Sarmiento 490* (MBML); Santa Leopoldina, Luxemburgo, 15 march 2005, *Fomntana et al. 1141* (MBML); Santa Teresa, Reserva Biológica de Nova Lombardia, 19 February 2002, *Kollmann et al. 5557* (MBML); *ibid.*, 26 March 2003, *Vervloet & Bausen 2071*

(MBML). Minas Gerais: Caeté, Serra da Piedade, 12 April 2001, *Mota & Marques 341* (BHCB); Catas Altas, RPPN Santuário do Caraça, 26 November 2008, *Viveros & Salino 58* (BHCB); *ibid.*, Serra do Caraça, 5 January 2005, *Mota 2382* (BHCB); *ibid.*, Mina de Fazendão, 28 July 2008, *Rezende & Pena 2782* (BHCB); Conceição do Mato Dentro, Parque Natural Municipal de Ribeirão do Campo, 15 December 2006, *Mota & Batista 3218* (BHCB); Descoberto, Reserva Biológica da Represa do Grama, 11 September 2003, *Assis et al. 878* (CESJ); Itamonte, 22 November 2006, *Stehmann et al. 4504* (BHCB); Lima Duarte, Parque Estadual de Ibitipoca, 11 March 2004, *Menini-Neto et al. 132* (CESJ); *ibid.*, 21 December 2003, *Menini-Neto & Ferreira 93* (CESJ); Olaria, Serra do Cruz, 21 December 2011, *Alves 169* (CESJ); Poços de Caldas, Morro são Domingos, 17 January 1968, *Rappa 1048* (R); Rio Preto, Serra Negra, 12 October 2007, *Roman et al. 01* (CESJ); *ibid.*, Ribeirão Santa, 1996, *Salimena s.n.* (CESJ, UFP); *ibid.*, Gruta do Funil, January 1999, *Caiafa & Ribeiro s.n.* (CESJ); Santa Barbara, Serra do Caraça, 14 December 1978, *Leitão-Filho et al. 9794* (UEC); Santa Maria do Salto, Fazenda Duas Barras, 23 August 2003, *Lombardi et al. 5446* (BHCB). Paraná: Paranaguá, Rio das Pombas, 13 March 1969, *Hatschbach 21247* (HB, MBM, MO). Rio de Janeiro: Itatiaia, Parque Nacional de Itatiaia, 17 March 1995, *Braga et al. 2180* (RB); *ibid.*, 13 March 1921, *Campos-Porto 1040* (RB); *ibid.*, 5 March 1942, *Brade 17201* (RB); *ibid.*, 15 March 2008, *Barberena 14* (RB); Majé, Santo Aleixo, 2 October 1983, *Guedes & Gonzaga 436* (RB); Nova Friburgo, Macaé de Cima, 29 August 1993, *Vieira & Gurken 392* (RB); Paty do Alferes, APA Palmares, 15 September 2013, *Pessoa & Wangler 1195* (RB, UFP); Petrópolis, Areal, s.d., *Spannagel 235* (SP); *ibid.*, Parque Nacional da Serra dos Orgãos, 30 January 2008, *Nadruz et al. 2152* (RB); *ibid.*, Serra da Estrela, November 1917, *Diogo 682* (R); Rio de Janeiro, Estrada das Paineiras, 9 May 1973, *Sucre 9975* (RB); *ibid.*, Morro Maxedo Sobrinho, 21 July 1968, *Sucre 3274* (RB, UFP); *ibid.*, Tijuca, February 1917, *Hoehne 209* (SP); Saquarema, October 1954, *Salarini & Araújo s.n.* (HB); Teresópolis, Jardim no Alto, 15 March 1958, *Abendroth p-28* (HB). Santa Catarina: Brusque, Barracão, 17 November 2009, *Stival-Santos et al. 1189* (FURB); Gaspar, Gasparinho, 15 October 2009, *Stival-Santos et al. 1052* (FURB); Joinville, Campo Alegre, 18 May 2008, *Verdi & Stival-Santos 686* (FURB); Luiz Alves, Braço Francês, 29 August 2009, *Gasper 2286* (FURB); Presidente Nereu, Braço do Salão, 27 October 2009, *Schmitt et al. 319* (FURB); Santo Amaro da Imperatriz, January 2005, *Matos 9* (FLOR, UFP); Siderópolis, Belvedere Baixo, 10 March 2010,

*Verdi et al.* 3475 (FURB); Treviso, Cirenáica, 10 March 2010, *Verdi et al.* 3376 (FURB). São Paulo: Cananéia, Parque Estadual Ilha do Cardoso, 18 March 2003, *Breier* 926 (ESA, UEC); Cubatão, Parque Estadual da Serra do Mar, 15 August 1998, *Singer* 98-79 (UEC); Cunha, Parque Estadual da Serra do Mar, 12 December 1996, *Bertoncini et al.* 755 (ESA, UFP); Eldorado, Parque Estadual de Jacupiranga, 28 March 2005, *Carboni et al.* 156 (ESA); Itanhaém, Loteamento Maramba, 18 April 2001, *Souza et al.* 253 (ESA); Lavrinhas, Vale do Ribeirão do Braço, 13 June 1996, *Goldenberg et al.* 356 (UEC); São Lourenço da Serra, Reserva Particular do Patrimônio Natural Paiol Maria, 9 March 2011, *Lombardi et al.* 8042 (HRCB); São Miguel Arcanjo, Parque Estadual de Carlos Botelho, 23 April 2002, *Udulutsch et al.* 673 (ESA); São Paulo, May 1913, *Toledo* 649 (RB); São Sebastião, Praia da Baleia, 23 April 2000, *Foster et al.* 516 (ESA).

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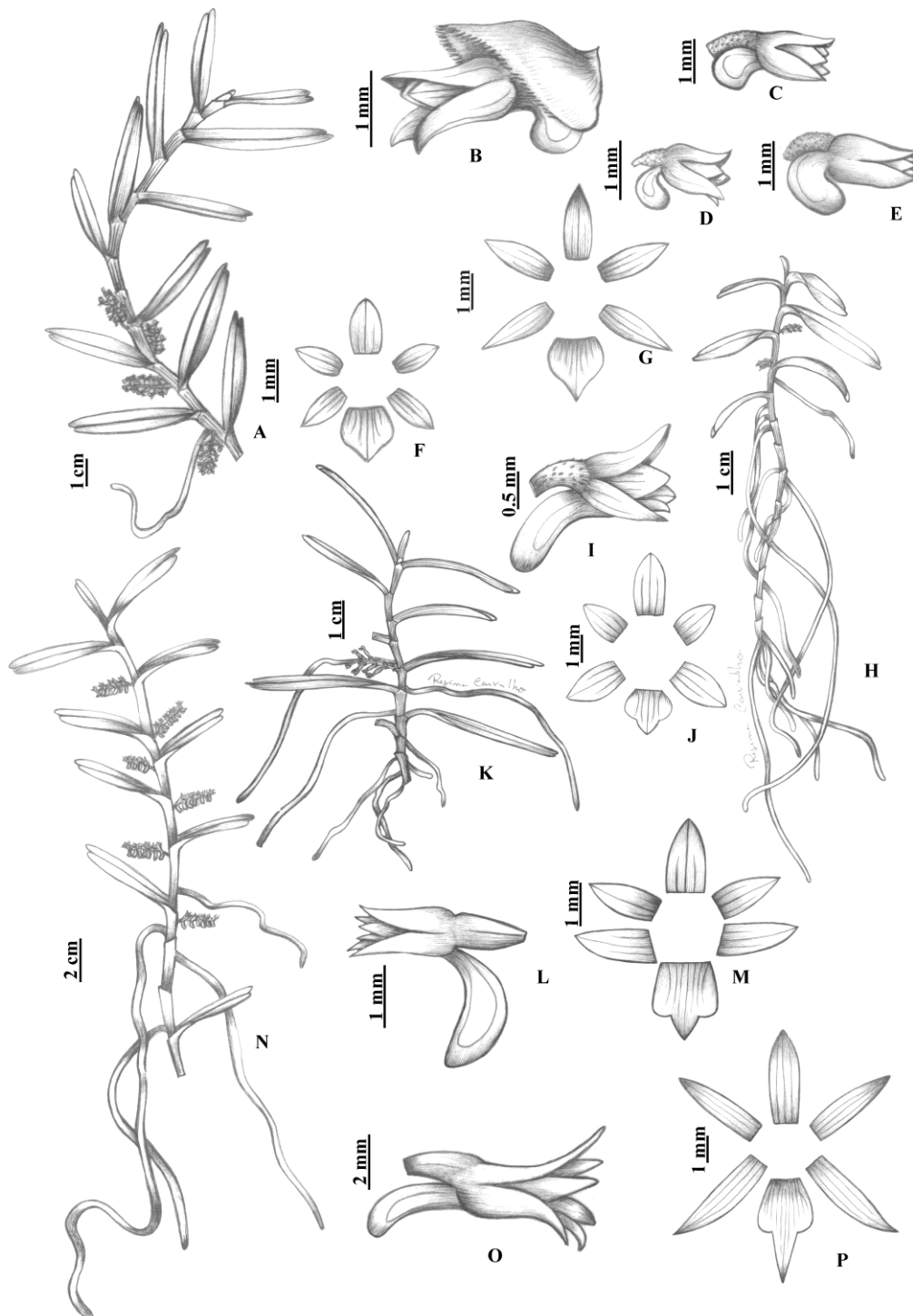


FIGURE 1. A–G. *Campylocentrum brachycarpum*, A. Habit, B–E. Flower, F–G. Dissected perianth; H–J. *C. brevifolium*, H. Habit, I. Flower, J. Dissected perianth; K–M. *C. carvalhoi*, K. Habit, L. Flower, M. Dissected perianth; N–P. *C. crassirhizum*, N. Habit, O. Flower, P. Dissected perianth. (A, B and G. Drawn from *Heringer 8794*, C. Drawn from *Duarte 01*, D and E. Drawn from *Polo 04*, E. Drawn from *Vesvloet 2182*; H, I and J. Drawn from *Wied s.n.*; K, L and M. Drawn from *Pessoa & Carvalho 1190*; N, O and P. Drawn from *Ruschi 05*).

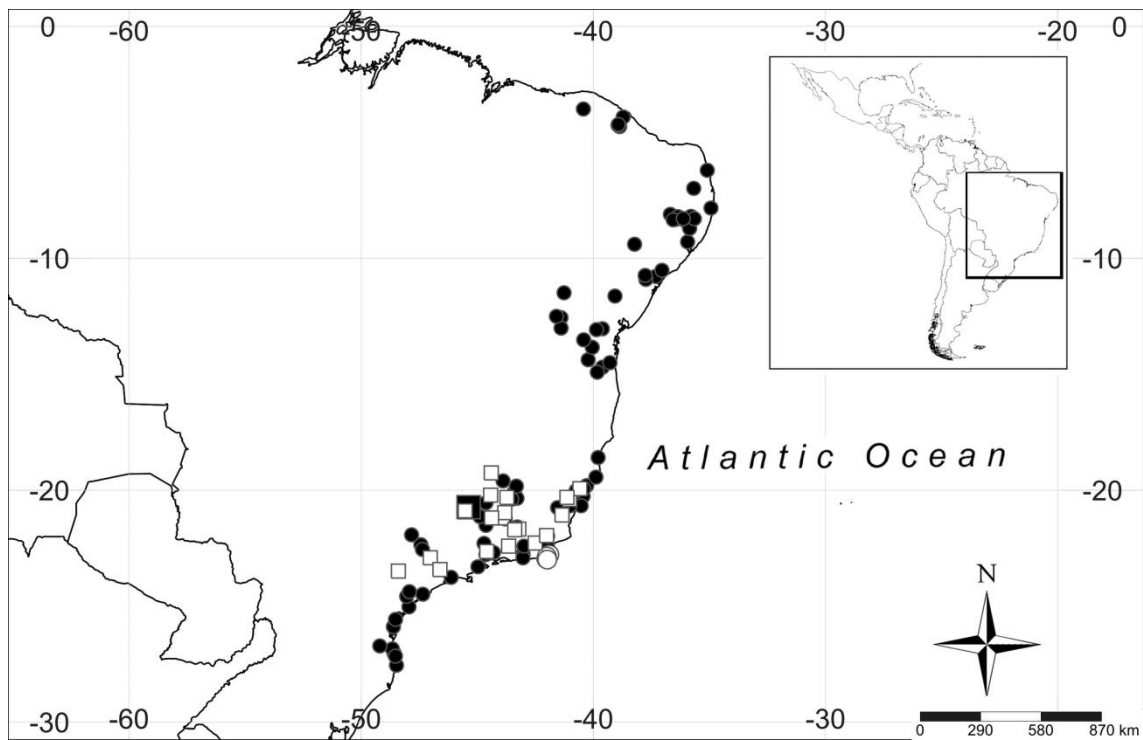


FIGURE 2. Distribution map of *Campylocentrum brachycarpum* (white square), *C. brevifolium* (white circle), *C. crassirhizum* (black circle) and *C. carvalhoi* (black square).

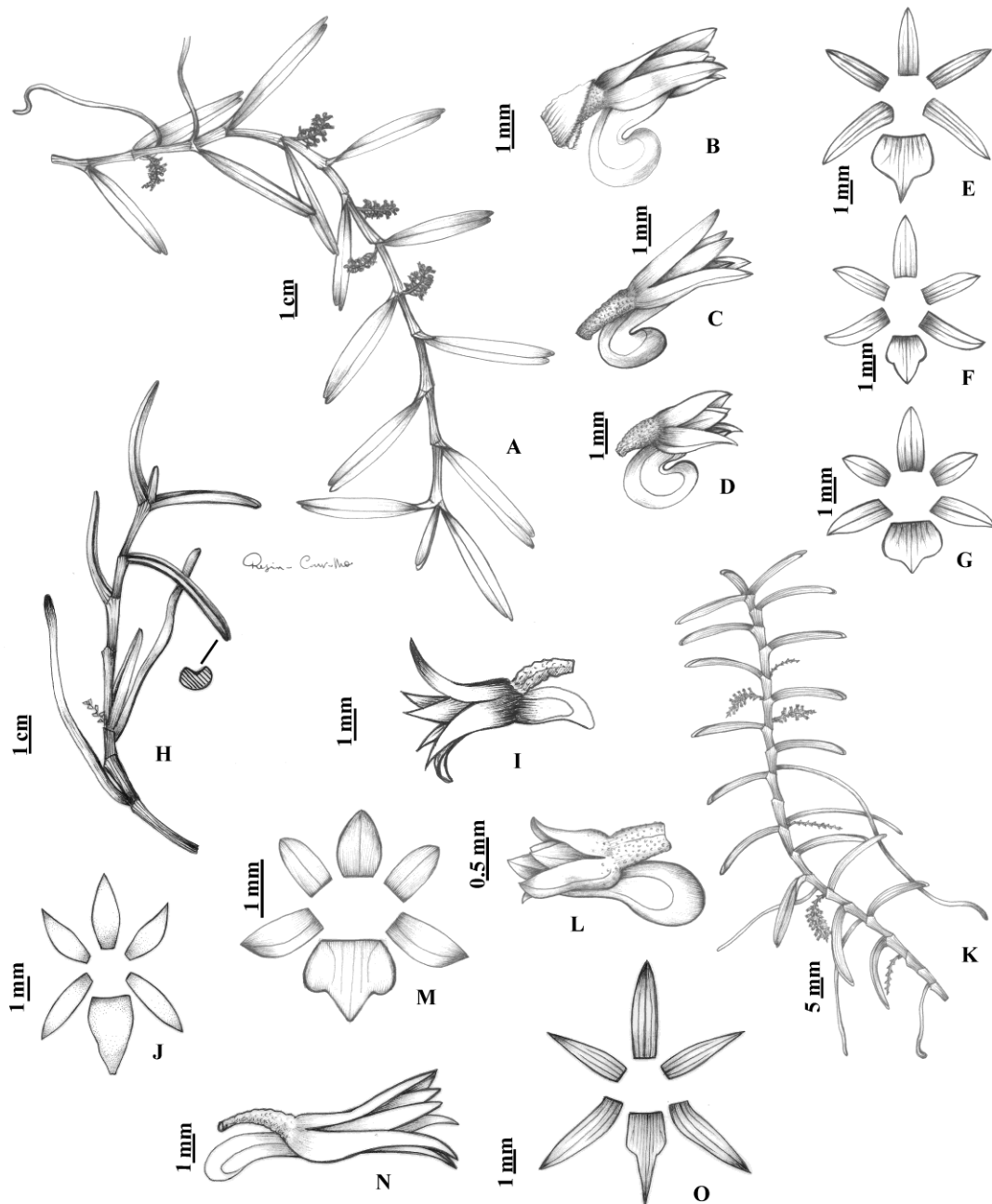


FIGURE 3. A–G. *Campylocentrum densiflorum*, A. Habit, B–D. Flower, E–G. Dissected perianth; H–J. *C. intermedium*, H. Habit, I. Flower, J. Dissected perianth; K–M. *C. itatiaiae*, K. Habit, L. Flower, M. Dissected perianth; N–O. *C. jamaicense*, N. Flower, O. Dissected perianth. (A and B. Drawn from *Burchell 1995*, C. and E. Drawn from *Handro s.n.*, D and G. Drawn from *Batista s.n.*, F. Drawn from *Jiménez & Marín 1249*; H. Drawn from *Warming s.n.*, I and J Copy from the original publication *Reichenbach f. & Warming (1881)*; K, L and M. Drawn from *Lanstyak s.n.*; N and O. Drawn from *Sintenis 4193*).

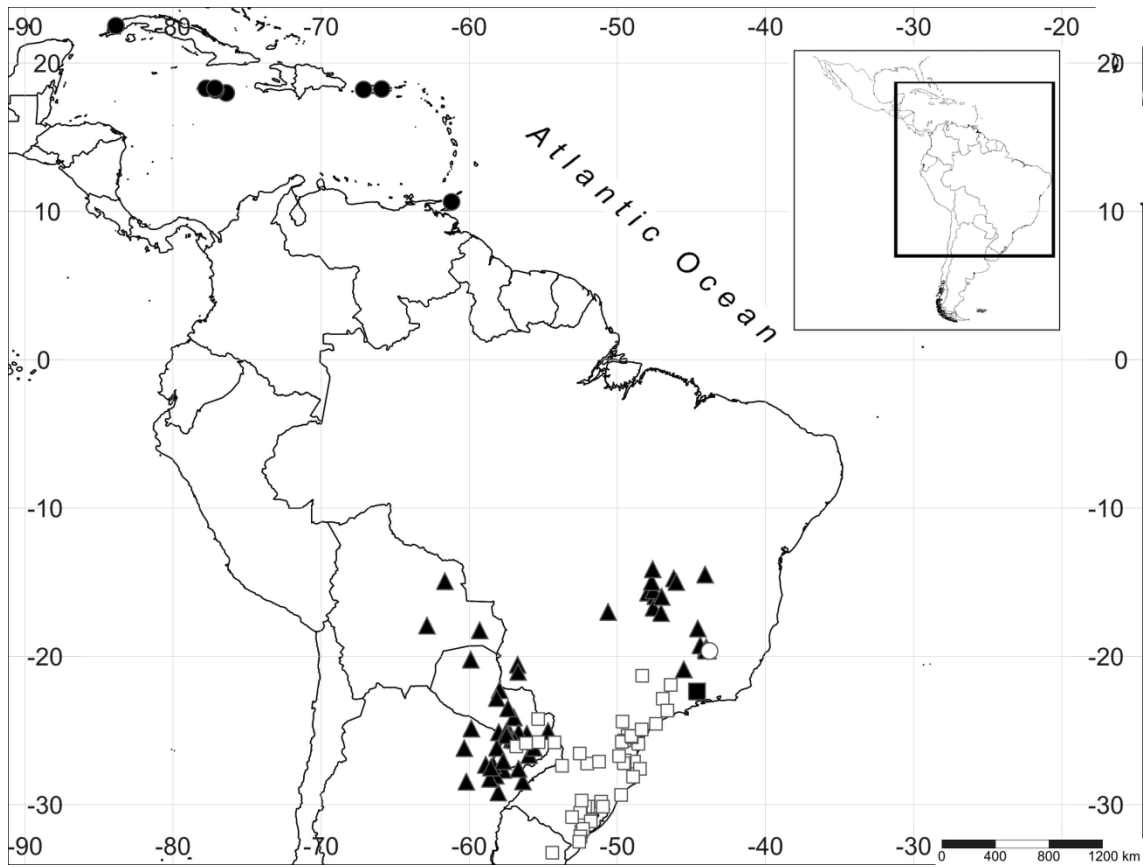


FIGURE 4. Distribution map of *Campylocentrum densiflorum* (white square), *C. intermedium* (white circle), *C. itatiaiae* (black square), and *C. jamaicense* (black circle), *C. neglectum* (black triangle).

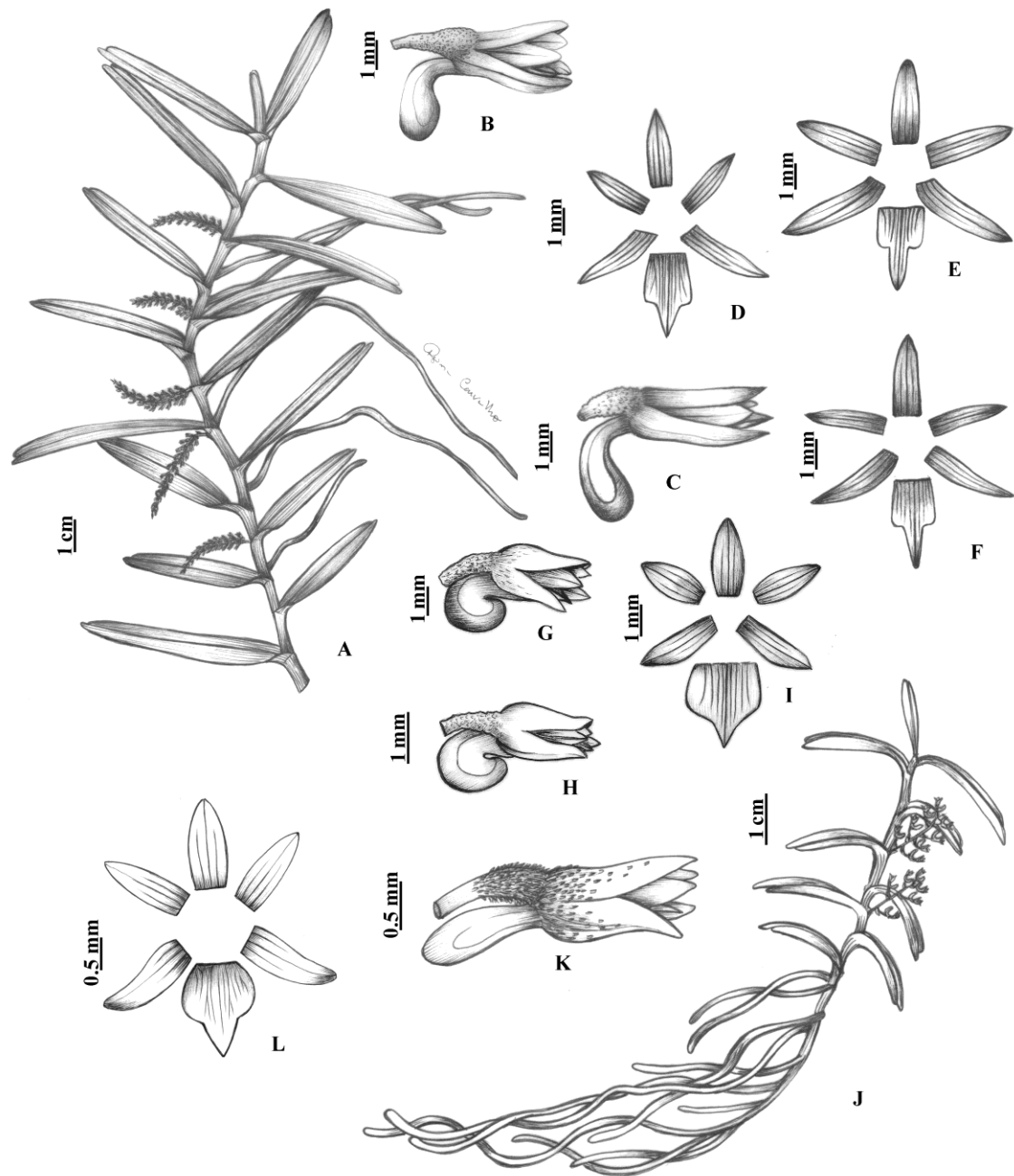


FIGURE 5. A–F. *Campylocentrum neglectum*, A. Habit, B–C. Flower, E–F. Dissected perianth; G–I. *C. organense*, G–H. Flower, I. Dissected perianth; J–L. *C. pauloense*, J. Habit, K. Flower, L. Dissected perianth. (A, C and D. Drawn from *Brina & Costa s.n.*; B and E. Drawn from *Paula-Souza et al. 8107*; F. Drawn from *Pederson 4039*; G, H and I. Drawn from *Miers s.n.*; J, K and L. Drawn from *Gehrt s.n.*).

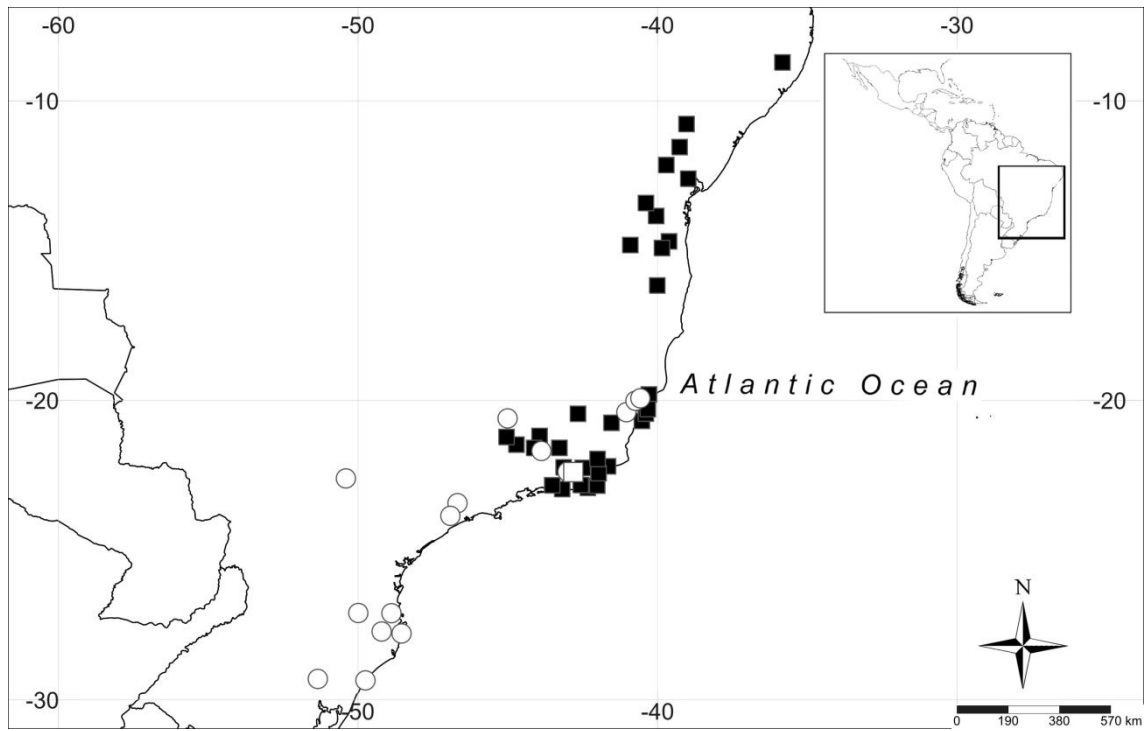


FIGURE 6. Distribution map of *Campylocentrum organense* (white square), *C. pauloense* (white circle) and *C. robustum* (black square).

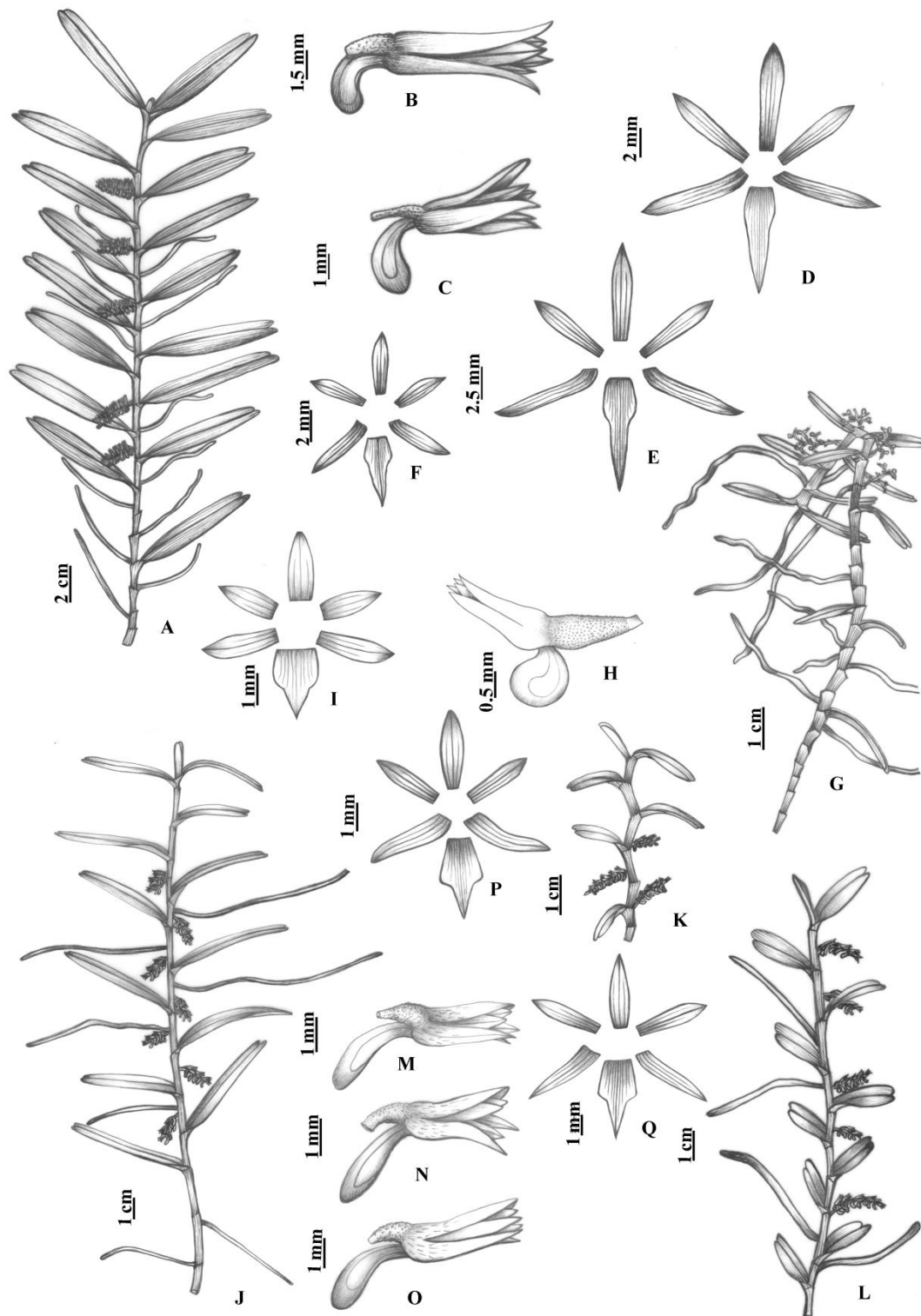


FIGURE 7. A–F. *Campylocentrum robustum*, A. Habit, B–C. Flower, D–F. Dissected perianth; G–I. *C. schlechterianum*, G. Habit, H. Flower, I. Dissected perianth; J–Q. *C. spannagelii*, J–L. Habit, M–O. Flower, P–Q. Dissected perianth. (A and E. Drawn from *Carvalho 19*, B and D. Drawn from *Assis et al. 822*, C and F. Drawn from *Buril et al. 645*, G, H and I. Drawn from *Destefani et al. 111*; J, M and P. Drawn from *Lombardi 8042*, K, N, Q. Drawn from *Mota & Batista 3218*, L and O. Drawn from *Brier 926*).

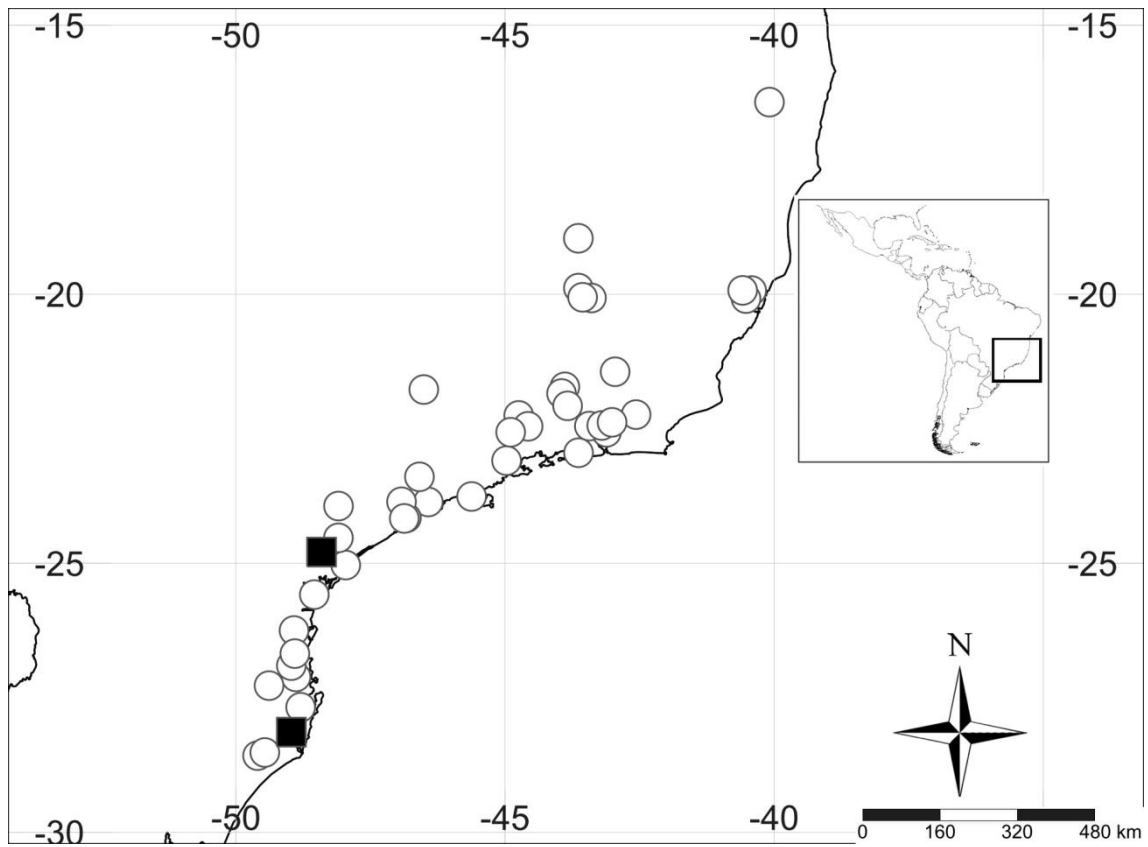


FIGURE 8. Distribution map of *Campylocentrum schlechterianum* (black square) and *C. spannagelii* (white circle).



Table 1. Main morphological features of the species of section *Laevigatum*.

	<b>Floral bracts</b>	<b>Sepals</b>	<b>Petals</b>	<b>Lip</b>	<b>Spur</b>
<i>C. brachycarpum</i>	ovate to sub-orbicular	3-nerved	3-nerved	entire to obscurely 3-lobed, 5–7-nerved	obovoid to clavate, curved
<i>C. brevifolium</i>	deltoid	3-nerved	3-nerved	3-lobed, 5-nerved	cylindrical, slightly curved
<i>C. carvalhoi</i>	deltoid	3-nerved	3-nerved	3-lobed, 7-nerved	ellipsoid to sub-conical, patent
<i>C. crassirhizum</i>	deltoid	3-nerved	3-nerved	3-lobed, 11-nerved	cylindrical, slightly curved
<i>C. densiflorum</i>	ovate to sub-orbicular	3-nerved	3-nerved	3-lobed, 7–9-nerved	clavate, strongly inflexed
<i>C. intermedium</i>	deltoid	unknown	unknown	Entire, unknown	ovoid-conical, slightly curved
<i>C. itatiaiae</i>	deltoid	1-nerved	1-nerved	3-lobed, 5-nerved	obovoid, straight to slightly curved
<i>C. jamaicense</i>	deltoid	3-nerved	3-nerved	3-lobed, 11-nerved	cylindrical, straight to slightly curved
<i>C. neglectum</i>	deltoid	3-nerved	3-nerved	3-lobed, 9-nerved	cylindrical to cylindrical-clavate, curved
<i>C. organense</i>	ovate to sub-orbicular	3-nerved	3-nerved	3-lobed, 9-nerved	obovoid to clavate, strongly inflexed
<i>C. pauloense</i>	deltoid	3-nerved	3-nerved	3-lobed, 9–11-nerved	clavate, slightly curved
<i>C. robustum</i>	deltoid	3–5-nerved	3–5-nerved	entire to obscurely 3-lobed, 9–11-nerved	cylindrical, curved
<i>C. schlechterianum</i>	deltoid	3-nerved	3-nerved	3-lobed, 9-nerved	globose, patent
<i>C. spannagelii</i>	deltoid	3-nerved	3-nerved	3-lobed, 9–11-nerved	cylindrical-clavate, straight to slightly curved

## Considerações Finais

- Os estudos desenvolvidos para *Campylocentrum* durante essa tese evidenciaram a necessidade de maior atenção com as coleções científicas para gêneros esquecidos da família Orchidaceae, visto que das oito novas espécies descritas aqui, cinco já tinham espécimes depositados em herbários.
- A análise anatômica das raízes se mostrou fundamental para busca de caracteres taxonomicamente informativos para distinguir grupos taxonômicos dentro do gênero.
- O estudo filogenético confrontou que a classificação previamente proposta para o gênero não se sustentava. As duas novas seções propostas aqui incluem algumas espécies (ex. *C. brevifolium* e *C. linearifolium*) anteriormente tratadas como sinônimos de espécies de outras seções (ex. *C. micranthum*), indicando o quão confusa estava a sistemática do gênero.
- A maioria dos caracteres amplamente utilizados na taxonomia de Orchidaceae foram indicados como homoplásicos, e outros sub-utilizados como raízes e frutos são apresentados com melhor sinal filogenético.
- Através da análise de datação, sugere-se fortemente que *Campylocentrum* assim como seu gênero irmão têm origem relativamente recente, e suas diversificações estão ligadas a eventos ocorridos principalmente no Plioceno e Pleistoceno. Já a análise biogeográfica indica eventos sucessivos de dispersão a longa distância como importantes na história de dispersão do grupo.
- Numa síntese das revisões apresentadas nessa tese os caracteres florais, especialmente aqueles ligados ao cálcio (tamanho, forma e curvatura), são muito importantes para distinção de espécies. Caracteres vegetativos (textura das raízes, tamanho e posição das folhas) são mais expressivos para distinção de espécies da seção *Teretifolium*. Embora ambos raramente sejam úteis para distinção de clados (sinapomorfias).
- No conjunto, embora apenas uma espécie tenha sido citada anteriormente como ameaçada, após análise das distribuições seguindo as normas da IUCN concluímos que o gênero inclui três espécies “quase ameaçadas” (NT), três vulneráveis (VU), uma ameaçada (EN) e duas criticamente ameaçadas (CR).
- O gênero compreende 72 espécies, sendo 37 da seção *Campylocentrum*, 13 da seção *Dendrophylopsis*, 15 da seção *Laevigatum*, uma da seção *Pseudocampylocentrum* e seis da seção *Teretifolium*, sendo o Brasil o país com maior diversidade com 36 espécies.

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## **Systematic Botany**

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