

# The 1-pinnate species of *Campyloneurum* (Polypodiaceae)

ROBBIN C. MORAN<sup>1</sup> AND PAULO H. LABIAK<sup>2</sup>

<sup>1</sup> The New York Botanical Garden, Bronx, NY 10456-5126, USA; e-mail: rmoran@nybg.org

<sup>2</sup> Universidade Federal do Paraná, Depto. de Botânica, C. P. 19031, 81531-980, Curitiba, Paraná, Brazil; e-mail: plabiak@ufpr.br

---

**Abstract.** *Campyloneurum* typically has simple and entire leaves; however, three of its species are 1-pinnate: *C. decurrentis*, *C. magnificum*, and *C. pentaphyllum*. These three species form a clade that is sister to the rest of the genus. The 1-pinnate clade is here named as **Campyloneurum** subgen. **Decurrentia**. This paper provides a taxonomic revision of the three species, presenting a key to distinguish them, descriptions, distribution maps, and specimens examined. A lectotype is designated for *C. decurrentis* var. *latifolium*, and a second-step lectotype for *C. magnificum*.

**KeyWords:** Ferns, Systematics, Taxonomy

---

*Campyloneurum* C. Presl is entirely Neotropical, occurring from southern Florida, the Antilles, and Mexico to southern Brazil and northern Argentina (Tryon & Tryon, 1982). Lellinger (1988) recognized 50 species in his provisional key to the genus. Since then, four additional species have been recognized or described as new (León, 1995, 2004; Rojas, 2005; León & Kessler, 2013). Also, the monotypic *Hyalotrichopteris* W. H. Wagner, recognized as distinct from *Campyloneurum* by Wagner and Farrar (1977) and Lellinger (1988), has been found nested in *Campyloneurum* (Kreier et al., 2007). Its sole species is now recognized as *C. anetoides* (Christ) R. M. Tryon & A. F. Tryon. Thus, the total number of species recognized in the genus now stands at 55.

*Campyloneurum* cannot be defined by a single morphological character present in all its species. Venation, however, is a synapomorphy for the genus. Typically—and there are significant exceptions, especially among those species with pruinose rhizomes—prominent lateral veins run from the midrib to the margin, and between them are finer cross-veins that create a series of areoles (Fig. 1). The basal areoles (those along the costa) contain a single excurrent veinlet, but the supra-costal areoles contain two or (in several large-leaved species) more excurrent veinlets.

The sori are typically borne at or near the apices of these excurrent veinlets (de la Sota & Pérez-García, 1982; León, 1992). This distinctive venation pattern has been lost in species of the genus that have narrower laminae, such as *C. angustifolium* (Sw.) Fée, *C. angustipaleatum* (Alston) M. Mey. ex Lellinger, and *C. chlorolepis* Alston (unpubl. data of the authors).

*Campyloneurum* forms a clade with *Microgramma* and *Niphidium*, but sister relationships among the three genera are still not well resolved. Schneider et al. (2004), Kreier et al. (2007), and Salino et al. (2008) recovered *Campyloneurum* as sister to *Niphidium*, whereas Schuettpelz and Pryer (2007) recovered it as sister to *Microgramma*. In all studies, however, support values were low. All three genera are characterized by simple, entire leaves, which represents a synapomorphy because the closest outgroup genera are generally 1-pinnate (i.e., *Pecluma*, *Pleopeltis*, *Polypodium* (s.s.), and *Serpocaulon*; Schuettpelz & Pryer, 2007). The simple-leaved species of *Pleopeltis* might appear to be an exception, but they are nested in the genus (Otto et al., 2009) and thus represent an independent evolution of simple leaves.

Within the *Campyloneurum-Niphidium-Microgramma* clade, only three species have 1-pinnate

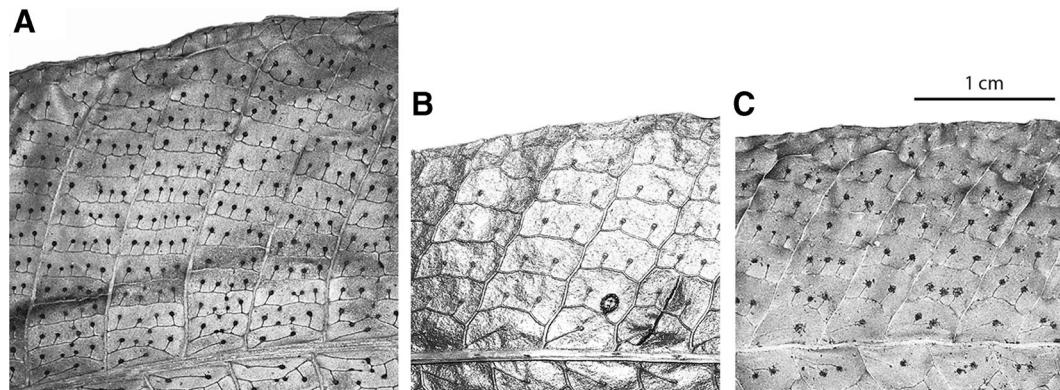


FIG. 1. Venation of the three 1-pinnate species of *Campyloneurum*. A. *C. magnificum*. B. *C. pentaphyllum*. C. *C. decurrens*. All same scale as in C. (A from Ortega & Smith 2449, NY; B from Smith 2456, NY; C from Prado 1512, SP.)

leaves: *C. decurrens* (Raddi) C. Presl, *C. magnificum* T. Moore, and *C. pentaphyllum* (Willd.) Pic. Serm. These species form a clade, and that clade is sister to the rest of *Campyloneurum* (unpubl. data of the authors). The three species seem to differ in no significant way from their congeners other than the division of the lamina. Their spores are verrucate as in many other species in the genus (Fig. 2; Tryon & Tryon, 1982; Tryon & Lugardon, 1991). The purpose of this paper is to provide a taxonomic treatment for these three species, including keys and illustrations to help identify them.

#### Materials and methods

Type specimens were examined at MO, NY, and P, and from on-line images available on JSTOR Global Plants. Field studies in southern Brazil were carried out by one of us (Labiak) to document growth habit and substrate. For measurements of pinnae in the keys and description,

the largest pinnae on a sheet was used. In the Additional Specimens Examined section, geographic coordinates not given on the specimen label, but estimated by us, are given in brackets.

#### Results

***Campyloneurum* subgen. *Decurrentia* R. C. Moran & Labiak, subgen. nov. Type: *Campyloneurum decurrens* (Raddi) C. Presl (basionym: *Polyodium decurrens* Raddi).**

Diagnosis: Differs from the rest of the genus by 1-pinnate leaves.

Plants terrestrial, epipetric, rarely rheophytic or epiphytic; rhizome scales appressed, dull brown, ovate-lanceolate, entire, the cells isodiametric or nearly so. Laminae 1-pinnate, imparipinnate, the terminal segment with more or less the same shape as the lateral pinnae.

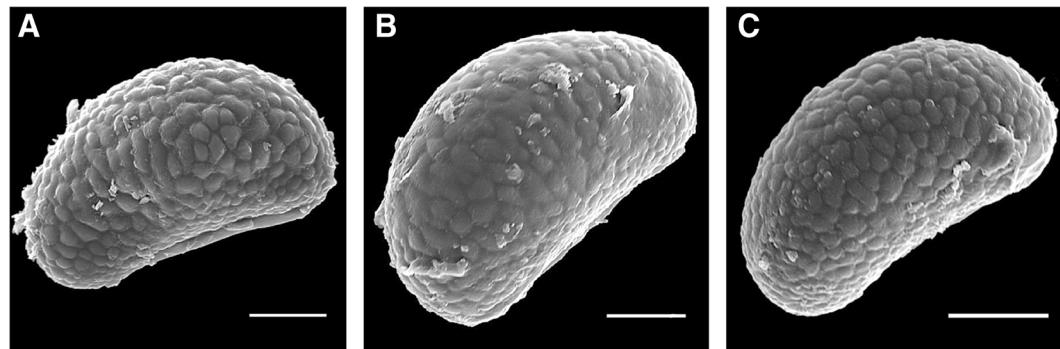


FIG. 2. Spores of two species of 1-pinnate *Campyloneurum*. A. *C. magnificum*. B, C. *C. decurrens*. Scale bars = 10 micrometers. (A, from Colombia, Sanin et al. 5153, NY; B, C. from Brazil, Matos et al. 290, NY.)

**Distribution.**—Costa Rica and Panama, Martinique, Venezuela to Bolivia, and southeastern Brazil; wet shaded forests, terrestrial or terrestrial root-climbers (sensu Canestraro et al., 2014) on the bases of trunks, or (in *C. decurrens*) on rocks or boulders and sometimes rheophytic; 0–2750 m.

The new subgenus name refers to the 1-pinnate species of the genus. The other species in the genus, including the type species *C. repens*

(Aublet) Ching, all have simple and entire leaves. To these latter species the autonym “*Campyloneurum* subg. *Campyloneurum*” applies.

*Campyloneurum* subgen. *Decurrentia* is known from a Tertiary fossil (Fig. 3) found in Italy and described as “*Polypodium (Campyloneurum) morellii*.” (Squinabol, 1889–1891). The fossil is 1-pinnate and has venation typical of the genus.

#### Key to the species of *Campyloneurum* subgen. *Decurrentia*

1. Pinnae 32–44 × 6.5–11.5 cm; areoles 10–14 between costa and pinna margin; included veinlets 3 or 4(–5) per areole. . . . . 2. *C. magnificum*
1. Pinnae 21–32 × 3–4.5 cm wide; areoles 6–8 between costa and pinna margin; included veinlets 2 or 3 per areole.
  2. Distal pinnae and terminal segment strongly decurrent; plants typically on boulders, sometimes terrestrial or rheophytic, rarely epiphytic at base of trunks; southeastern Brazil. . . . . 1. *C. decurrens*
  2. Distal pinnae and terminal segment sessile and not or only very shortly decurrent; plants terrestrial to climbing 6 m on trunks; Martinique, northern Colombia, northern Venezuela . . . . . 3. *C. pentaphyllum*

- 1. *Campyloneurum decurrens* (Raddi) C. Presl,**  
Tent. Pterid. 190. 1836. *Polypodium decurrens* Raddi, Syn. Fil. Bras. 287. 1819.  
*Campyloneurum decurrens* (Raddi) J. Sm., J. Bot. 4: 58. 1841, comb. superfl. Type: Brazil. Rio de Janeiro: s.d., *G. Raddi* s.n. (holotype: FI). (Figs. 1C, 2B, C, 4, 5)

*Campyloneurum juglandifolium* Fée, Crypt. Vasc. Brésil 1: 117, t. 45, f. 1. 1869. Type: Brazil. Rio de Janeiro: s.d., *A. Glaziou* 1750 (holotype: P [barcode P00624658]).

*Campyloneurum decurrens* var. *latifolium* Fée, Crypt. Vasc. Brésil 1: 117. 1869. Type: Brazil. Rio de Janeiro: s.d., *A. Glaziou* 404 (lectotype,

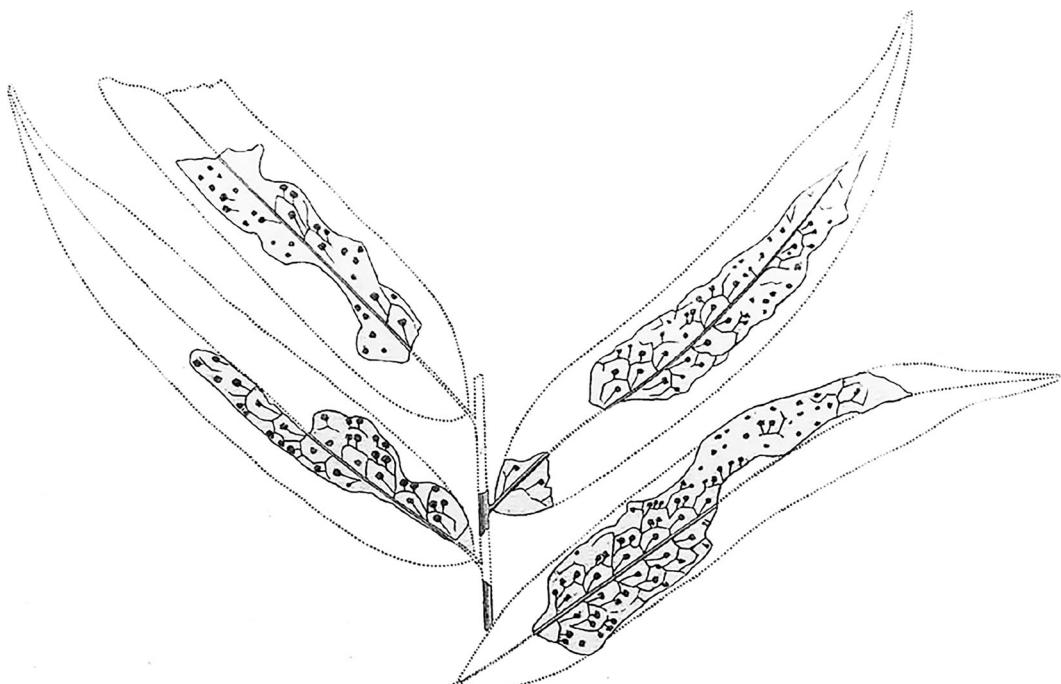
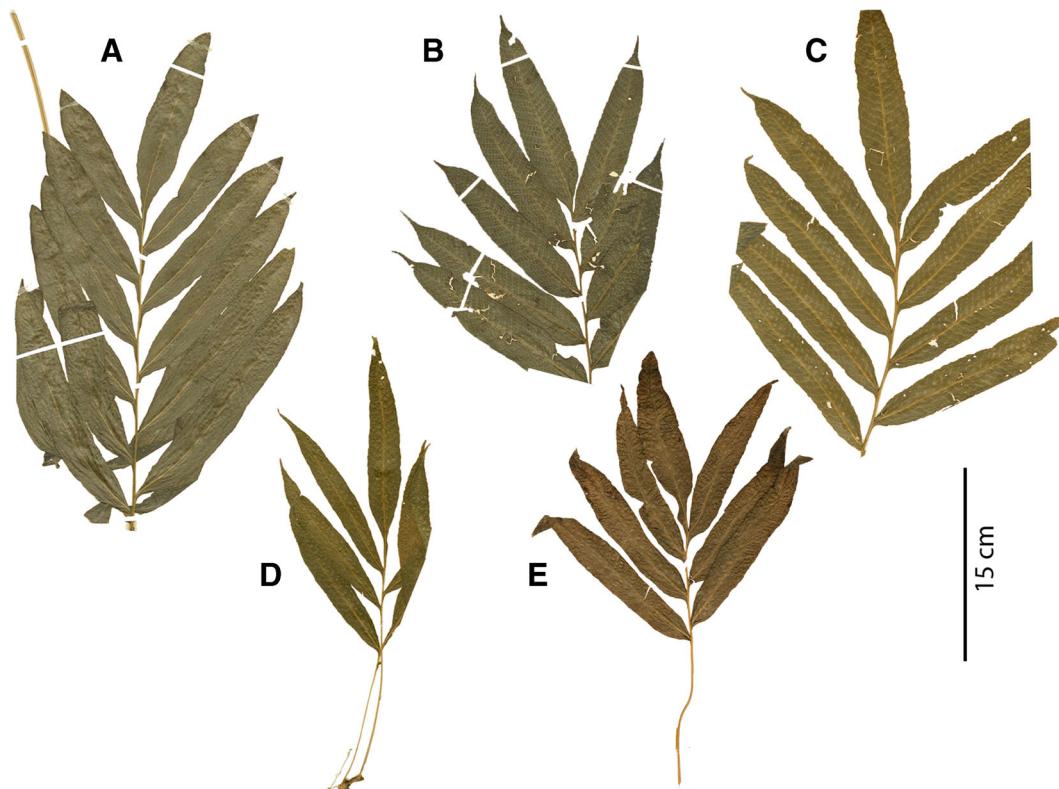


FIG. 3. *Campyloneurum morellii*, a Tertiary fossil from Italy belonging to *Campyloneurum* subgen. *Decurrentia*. (From Squinabol, 1889–1891.)



**FIG. 4.** *Campyloneurum decurrens* from southeastern Brazil. (A, Brackenridge s.n., PH; B, Glaziou 1749, P; C, Glaziou 1684, RB; D, Glaziou 403, RB; E, collector unknown (cultivated), RB.)

here designated: P [barcode P00637539]; isolectotype: RB [barcode 00682032]).  
*Campyloneurum decurrens* var. *tenerum* Féé, Crypt. Vasc. Brésil 1: 117. 1869. Type: Brazil. Rio de Janeiro: s.d., A. Glaziou 403 (holotype: RB barcode 00681994).

Pinnae 24–32 × 3–4 cm, pairs 3–12, the distal ones and the terminal segment strongly decurrent; areoles 6–8 between the costa and margin; included veinlets 2 or 3 per areole.

**Distribution.**—southeastern Brazil; wet shaded forests, typically on boulders, sometimes terrestrial or rheophytic, rarely on the base of trunks; 0–1600 m.

**Additional specimens examined. BRAZIL. Bahia:** Camacã, Fazenda Serra Bonita, 9.7 km W de Camacã na estrada para Jacarecí, daí 6 km SW na estrada para a RPPN e Torre da Embratel, 15°23'30"S, 39°33'55"W, 835 m, 3 Feb 2005, Matos et al. 290 (NY, UPCB); RPPN Serra do Teimoso, Rod. Jussarí/Palmira, Fazenda Teimoso, entrada à esq. ca. 7.5 km de Jussarí Trilha para o topo da serra., 11°02'49"S, 41°58'08"W, s.d., Matos 808 (BHCB, CEPEC, UPCB).

**Espirito Santo:** Castelo, Parque Estadual do Forno Grande, trilha do Rio Manso, 20°31'28"S, 41°07'14"W, 1480 m, 20 Jul 2008, Labiak et al. 4872 (MBML, UPCB); Alto Liberdade, Prop. Delcelcio, Marilândia, 19°24'46"S, 40°32'31"W, 150 m, 13 Sep 2007, Vervloet 3501 (MBML). **Minas Gerais:** Mun. Viçosa, Mata Atlântica de planalto, Sítio Bom Sucesso, Mata do Sr. Nico, 20°47'42"S, 42°50'44"W, 730 m, 29 Jul 2009, Prado & Valente 2027 (NY). **Paraná:** Guaratuba, Serra da Prata, estrada para chácara do INRI Cristo, 25°34'40"S, 48°42'07"W, 150 m, 10 Dec 2004, Labiak et al. 3480 (NY, UPCB); Antonina, Reserva Natural do Rio Cachoeira (SPVS), Trilha da Rede, 25°18"S, 48°41"W, 400 m, 28 Oct 2006, Matos et al. 1269 (NY, UPCB). **Rio de Janeiro:** Parque Nacional do Itatiaia, trilha para a Cachoeira Itaporani, Itatiaia, 22°29'46"S, 44°33'48"W, 1150 m, 1 Sep 2008, Labiak 4412 (UPCB); Itatiaia, Serra da Mantiqueira, Itatiaia National Park (lower portion), off Estrada do Parque Nacional (BR-485), along trail to the Cachoeira Véu da Noiva, 22°29'46"S, 44°33'48"W, 1065 m, 19 Jan 2010, Schuettpelz et al. 1439 (MO, NY, SP). **Santa Catarina:** Município de São Francisco do Sul, Vila da Glória, 100 m, Apr 2004, Heissner G08L2 (UPCB); Antonio Carlos, Biguaçu, 27°29'41"S, 48°39'22"W, 25 Jan 1943, Reitz 239 (PACA). **São Paulo:** Iporanga/Apiaí, Parque Estadual Turístico do alto Ribeira, Núcleo Santana, 24°32'22"S, 48°41'36"W, 4 Dec 2011, Mazziero & Soller 919 (NY, UPCB); Mun. Ubatuba, Ilha Anchieta, trilha para a praia do leste. Mata Atlântica, 23°32'67"S, 45°02'72"W, 18 Feb 2004, Prado et al. 1512 (NY, SP).

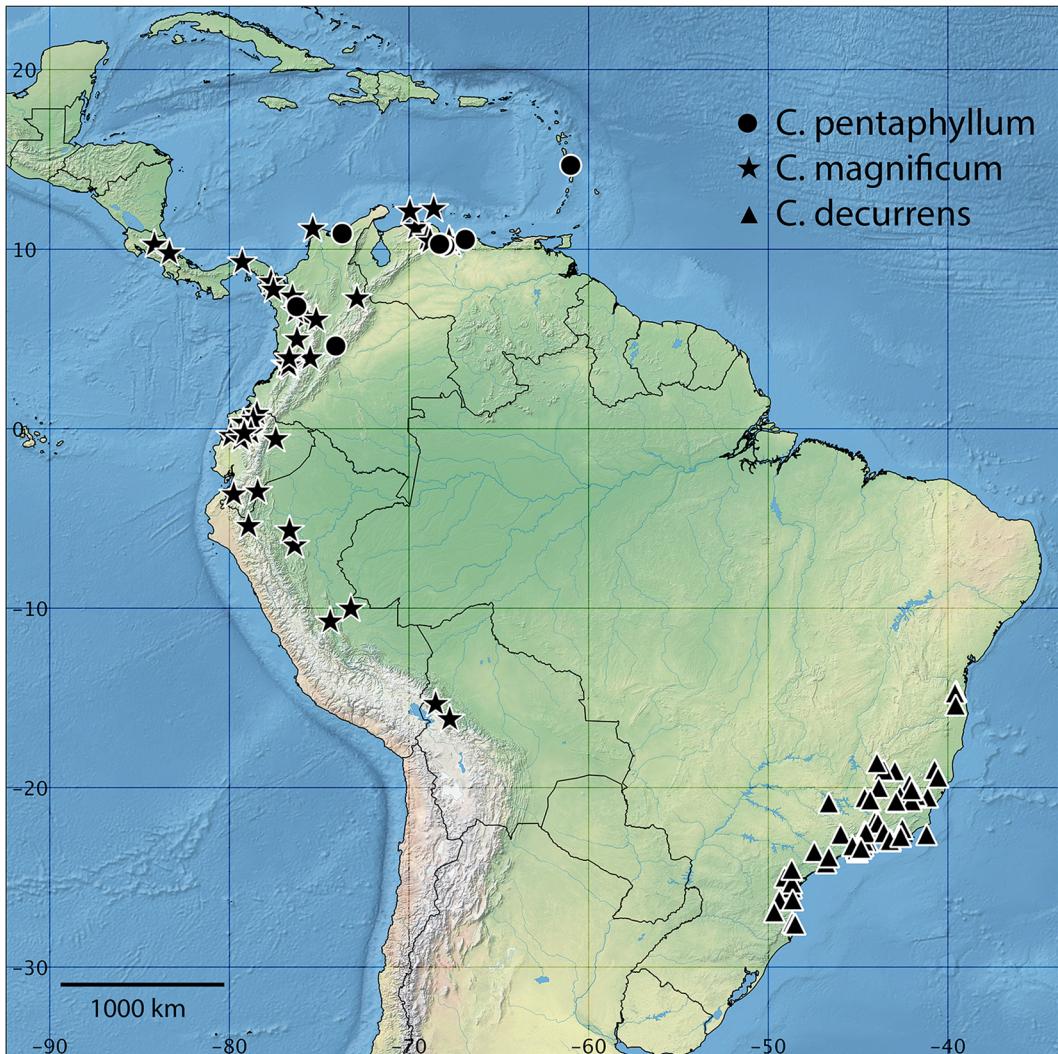


FIG. 5. Distribution of the three species belonging to *Campyloneurum* subgen. *Decurrentia*.

The type of *Campyloneurum juglandifolium* (Glaziou 1750, P) consists of only a single sheet. According to Windisch (1982), no duplicate of this collection is at RB. Therefore, because there is apparently only a single sheet, it must be considered a holotype.

Fée (1869) described var. *latifolium* as differing by pinnae about 3 cm wide, but this seems to be within the variation for the species. Also, var. *tenerum* Fée (1869) seems to us typical in all respects for the species. Accordingly, we have placed Fée's varieties in synonymy.

Spruce 3963 (BR) was previously identified as “*Campyloneurum decurrens*” from Peru, Prov.

San Martín, Tarapoto. We agree with this identification but believe that a label mix-up has occurred because all other specimens of *C. decurrens* are from southeastern Brazil. The specimen came from the herbarium of Martius, who collected in southeastern Brazil. We suspect that the sheet was actually collected by Martius and later mislabeled as a Spruce collection.

**2. *Campyloneurum magnificum* T. Moore, Index Fil. 226. 1861. New name for *Polypodium fendleri* D. C. Eaton, Mem. Amer. Acad. Arts n.s. 8: 199. 1860. *Polypodium decurrens* Raddi var. *fendleri***

(D. C. Eaton) Hook., Sp. Fil. 5: 43: 1864. *Campylooneurum fendleri* (D. C. Eaton) J. Sm., Hist. Fil. 97: 1875, nom. illegit., non T. Moore 1861. *Polyodium magnificum* (T. Moore) Hieron., Bot. Jahrb. Syst. 34: 535. 1904. Type: Venezuela, Aragua: Colonia Tovar, about 1300 m, 1856–57, A. Fendler 410 (lectotype, designated by León, 1993: YU, second-step lectotype here designated: YU [barcode YU000826]; isolectotypes, B [barcode B 20 0093583], BR [barcode BR0000006970314], F [barcode F0075636F], GH [barcode GH00112615], GOET [GOET009061], K [K000590792], MO [accession numbers MO-255910, MO-255911], NY [barcodes NY00144810, NY00144812], PH [barcode PH00021018]); YU [barcodes YU000825, YU000827, YU000828]. (Figs. 1A, 2A, 5, 6D–F, 7)

Pinnae 32–44 × 6.5–11.5 cm, pairs ca. 4, the distal ones slightly adnate for 3–5 mm on the basiscopic side and slightly decurrent; areoles 10–14 between the costa and margin; included veinlets 3 or 4(–5) per areole.

**Distribution.**—Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia; terrestrial in wet shaded forests, rarely as a terrestrial root climber (sensu Canestraro et al., 2014) on the bases of trunks; 200–2200 m. León (1992) listed Trinidad for this species but did not cite a voucher, and we have not seen any specimens from this island.

**Additional specimens examined. COSTA RICA.**  
**Alajuela:** Cantón de Alajuela, cordillera central Cariblanco, camino a Colonia Virgen del Socorro, 10°15'25"N, 84°10'20"W, 720–870 m, 11 Sep 1994, Rojas 1456 (MO, NY).  
**Limón:** Cantón de Limón, Cordillera de Talamanca, along divided Río Xikiari and Río Boyei, above Cabéca village of Admirante (not on current maps) 9°46'30"N, 83°20'00"W, 1100–1150 m, 13 Aug 1995, Grayum 10906 (MO, NY).

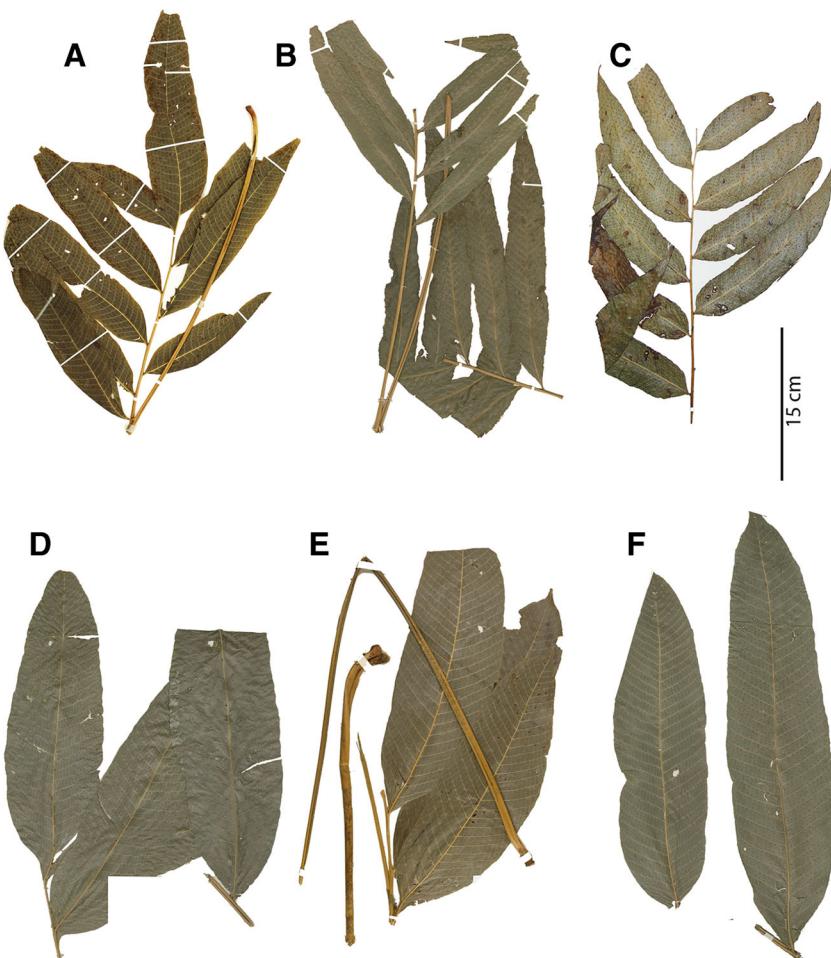
**PANAMA. Darién:** along headwater of Río Tuquesa, ca. 2 km air distance from continental divide, in vicinity of upper gold mining camp of Tyle Kittredge, 8°10'48"N 77°40'48"W, 600 m, 25 Aug 1974, Croat 27143 (MO, NY); Cerro Pirre, mountain and ridge just S of Pirre, 7°44'10"N 77°32'50"W, 10–20 Jul 1997, Folsom 4534 (MO, NY). **San Blas:** trail from end of road past Los Altos de Pacora región of Cerro Jefé, on to Cerro Brewster, 9°17'N, 79°17'W, 600–800 m, 20/25 Apr 1985, Hammel & de Nevers 13594 (MO, NY).

**VENEZUELA. Aragua:** Colonia Tovar, 10°15'N, 67°36'W, m, 1856–1857, Fendler 410 (B, F, GH, K, MO, NY); Río del Salto, Ocumare Valley, 10°29'N, 67°46'W, 600–700 m, 6 Nov 1937, Pittier 14173 (US). **Falcón:** Serranía de San Luiz, Fila

Norte, Hoya de Curimaguá and La Chapa, 12.5 km norte de Curimaguá 11°10'N, 69°37'W, 1300 m, 6 Mar 1993, Croat 74487 (MO, NY); Sierra de San Luis, arriba de Santa María, 12°5'28"N, 69°57'0"W, 1300 m, 1 Jan 1979, van der Werff et al. 126 (MO, NY). **Lara/Yaracuy:** área limítrofe entre los estados Lara y Yaracuy, distritos Urdaneta y Bolívar respectivamente, en la Finca Azul y Had. El Jaguar, 10°33'N, 68°56'W, 700–900 m, 16–17 Feb 1985, Ortega & Smith 2449 (NY); Sierra de Aroa, Cerro Tigre, 10 km E of Aroa air distance, Río Carabobo and adjacent slope up road, 10°26'N, 68°49'W, 800–1000 m, 30 Mar 1980, Liesner & González 9722 (MO, NY).

**COLOMBIA. Antioquia:** en los alrededores de Villa Arteaga, 7°21'21"N, 76°29'26"W, 200 m, 14 Aug 1948, Araque M. & Barkley 180738 (MEDEL, MO, US); Frontino, Parque Nacional Natural Las Orquídeas, vereda Venados Abajo, Finca de Gabriel Montoya, la margen derecha del Río Venados, 6°32'23"N, 76°19'9"W, 860–910 m, 23 Jul 2011, Sanín et al. 5153 (NY, US). **Chocó:** San José del Palmar, hoyo del Río Torito (afluente del Río Habita), declive occidental, Finca Los Guaduales, primera quebrada a orillas del Río Torito, 4°58'N, 76°14'W, 630–730 m, 13 Mar 1980, Forero et al. 7244 (COL); 0.2 km above the Ciudad Bolívar–Quibdo Road at ca. Km 139, 5°41'S, 76°39'W, 800 m, 3 Apr 1971, Lellingen & de la Sota 916 (US). **El Valle de Cauca:** valley of Río Dagua, 3°32'N, 76°52'03"W, 800 m, 2 Apr 1939, Alston 7824 (MO, NY); "Calima" on Río Calima, Cordillera Occidental, 3°55'N, 76°40'W, m, 14–15 Sep 1922, Killip 11223 (US); Mun. Calima, Vereda Campo Alegre, "Alto Calima," trocha paralela al Río Calima, cerca desembocadura Río Bravo, 3°55'N, 76°40'W, 900 m, 29 Aug 1981, Silverstone 539 (MO, NY). **Magdalena:** Sierra de Perijá, Espírito Santo Valley, 14 km E of Codazzi, 11 km from Venezuelan border, 10°02'S, 73°14'W, 1080 m, 12 Feb 1945, Grant 10910 (US). **Santander:** Tona, vereda Caragua, carretera a Tona, 7°15'N, 72°54'W, 1330–1390 m, 26 Jun 2004, Murillo & Forero 3732 (COL). **Tolima:** San Antonio, 3°55'N, 75°30'W, 2100 m, Lindig 307 (P, NY, US). **Department Unknown:** Vice-Regni Novae Granatae, 1783–1808, Mutis 3241 (MA, US).

**ECUADOR. El Oro:** Pinas, Parroquia el placer, reserva ecológica Buenaventura, propiedad fundación Jocotoco, Cerro las Bateas, Sendero White, 3°40'13"S, 79°45'32"W, 1230 m, 11 Apr 2005, Vargas et al. 5447 (MO, NY); Pinas, Parroquia el Placer, Reserva Ecológica Buenaventura, propiedad fundación Jocotoco, Cerro las Bateas, Sendero White, 3°40'13"S, 79°45'32"W, 1230 m, 12 Apr 2005, Vargas et al. 5447 (MO, NY). **Esmeraldas:** Lita, Cristal Road, 18 km beyond El Cristal, 0°50'N, 78°28'W, m, 7 Feb 1991, Moran & Rohrbach 5318 (MO, NY, QCNE); Quininde–Cantón, NE de las Golondrinas, Sitio La Bella Jungla, Cooperativa Unidos Venceremos, 300 Km aproximadamente, 00°20'N, 79°12'W, 300 m, 8 Oct 1993, Palacios 11451 (MO, NY). **Imbabura:** Playa Luisa, below Magnolia, lower Intag Valley, 0°30'N, 78°40'W, 1030 m, 17 Sep 1944, Drew 668 (COL, US). **Los Ríos:** Río Palenque Biological Station, Km 56 Quevedo–Santo Domingo road, 00°35'11"S, 79°21'52"W, 150–220 m, 6 Mar 1974, Dodson 5478 (US); Río Palenque field station halfway between Quevedo and Santo Domingo de los Colorados, 00°35'11"S, 79°21'52"W, 200 m, 16 Feb 1974, Gentry 9982 (MO, NY, US). **Manabí:** near Peripa, Pescadillo, 00°24'S, 79°55'W, Jul 1876, André 4230 (NY). **Morona-Santiago:** Gualاقiza, Cordillera del Condor, Valle del Río Quimi, orilla de Río Quimi, 3°30'24"S, 78°25'35"W, 1090 m, 13 Dec 2000, Cuascota 287



**FIG. 6.** Two 1-pinnate species of *Campyloneurum*. **A–C.** *C. pentaphyllum*. **D–F.** *C. magnificum*. (A, from Martinique, Duss 1568, US; B, from Colombia, Kaltbreyer s.n., S-1418543; C, from Venezuela, Alston 5263, MO; D, E, from Venezuela, Fendler 410, YU and K, respectively.)

(MO, NY); Gualaqueza, Cordillera del Condor, Valle del Río Quimi, Orilla de Río Quimi,  $3^{\circ}30'24"S$ ,  $78^{\circ}25'35"W$ , 2000 m, 13 Dec 2000, Guascota et al. 287 (MO, NY). **Napo:** Hollín-Loreto Road, 32 Km mark, 3–4 km S of road, path for permanent sampling plot,  $0^{\circ}35"S$ ,  $77^{\circ}25"W$ , 1200 m, 25 Jan 1991, Moran & Rohrbach 5132 (MEDEL, MO, NY). **Pichincha:** Reserva Florística-Ecológica Río Guajalito, Km 59 carretera antigua Quito-Santo Domingo,  $0^{\circ}01'3"S$ ,  $78^{\circ}48'W$ , 1800–2200 m, 24 Sep 1988, Jaramillo 3838 (MO, NY). **Táchilas:** vicinity of Santo Domingo de Los Colorados,  $00^{\circ}15'15"S$ ,  $79^{\circ}10'19"W$ , 500 m, 2–4 Apr 1943, Holdridge 1609 (US).

**PERU.** **Cajamarca:** San Ignacio, La Coípa, localidad Vista Florida (camino a la laguna)  $5^{\circ}26'10"S$ ,  $78^{\circ}56'00"W$ , 1900–2000 m, 20 Jun 1997, Campos & García 4043 (MO, NY, SPSF, USM). **Junín:** Schunke Hacienda, above San Ramón,  $11^{\circ}07'29"N$ ,  $75^{\circ}21'25"W$ , 1300–1700 m, Aug–Oct 1923, Schunke 170 (US). **Pasco:** Prov. Oxapampa, trail to Shumahuani from Chequitavo,  $10^{\circ}45'S$ ,  $74^{\circ}23'W$ , 1200 m, 24 Sep 1983, Smith 5212 (MO, NY, USM). **San Martín:** Prov.

San Martín, 4 mi E of Tarapoto,  $6^{\circ}30'05"S$ ,  $76^{\circ}21'56"W$ , 890 m, 6 Mar 1947, Woytkowski 35218 (MO, NY, UC).

**BOLIVIA.** **La Paz:** Prov. Larecaja, 6 km N (below) Casata,  $15^{\circ}20"S$ ,  $68^{\circ}31'W$ , 1300 m, 15 Dec 1981, Solomon et al. 6574 (MO, NY). **Nordiyungas:** Polo-Polo near Coroico,  $16^{\circ}11'S$ ,  $67^{\circ}44'W$ , 1100 m, Oct–Nov 1912, Buchtien 3490 (US).

### 3. *Campyloneurum pentaphyllum* (Willd.) Pic. Serm., Webbia 60(1): 128. 2005. *Aspidium pentaphyllum* Willd., Sp. Pl. ed. 4, 5: 216. 1810. *Cardiochlaena pentaphylla* (Willd.) Féé, Hist. Foug. Antill. 91. 1866. Type: Plumier, tab. 114. 1705, illustrating a plant from Martinique. (Figs. 1B, 5, 6A–C)

Pinnae 21–26 × 3.7–4.5 cm, pairs (3–)4 or 5(–)7, the distal ones and terminal segment not decurrent;



**FIG. 7.** Rhizome and petioles of *Campyloneurum magnificum*. **A.** Rhizome with some petioles still attached and others fallen to reveal the circular abscission scars on top of swollen phylloodia. **B.** Transverse section of rhizome showing meristoles. **C.** Transverse section of petioles, adaxial side oriented downward. Scale bars approximate. (Photos by David Sanín of a plant from Colombia; vouchered by Sanín 5153).

areoles 6 or 7 between the costa and margin; included veinlets 2 in each areole.

**Distribution.**—Martinique, northern Venezuela, northern Colombia; terrestrial to climbing 6 m on trunks; 800–2750 m.

**Additional specimens examined.** MARTINIQUE. Piton Marcel, entre la montagne Pelee et la Pricheur, 14°40'N, 61°00'W, 1890, Duss 1568 (B, NY, US).

**VENEZUELA. Carabobo:** Río Aguada, 1500 m, 9 Jan 1939, Alston 6253 (MO); Distrito Bejuma, entre la Cumbre al oeste de la carretera Bejuma–Canoabo, entre la Cumbre

Paraguito y Cerro El Marquero, 1000–1250 m, 10°17'N, 60°18'W, 27 Jun 1999, Meier & Kunert 5020 (UC), 5033 (UC); Distrito Bejuma, Cordillera de la Costa, N de Bejuma, entre Cerro San Isidro y Cerro de Paja (Cariaprima), a lo largo de carretera, 1400–1650 m, 10°16'30"N, 68°13'30"W, 31 Dec 2001, Meier & Flauger 8837 (UC). **Distrito Federal:** vertiente sur a lo largo de la pica entre Hotel Humboldt y Papelón, 1730 m, 10°17'N–10°32'N, 60°18'W–66°52'W, 25 Oct 1992, Meier 2874 (UC).

**COLOMBIA. Antioquia:** Río Verde, 14 Jul 1889, Kalbreyer s.n. (S). **Bogotá:** Cordillera Oriental, Andes de Bogotá, 2750 m, [4°35'53"N, 74°04'33"W], 1 Nov 1856, Triana s.n. (COL). **Magdalena:** Sierra Nevada de Santa Marta, 1700–2200 m, 26 Aug 1898–

1901, *Smith* 2456 (F-n.v. [cited by León, 1992], MO, NY, TEX-LL).

*Campyloneurum pentaphyllum* has long been overlooked (e.g., Proctor, 1977). This probably happened because, after being described in *Aspidium*, it could not be combined in *Polypodium* (non *P. pentaphyllum* Baker, Ann. Bot. (Oxford) 5: 478. 1891), the genus most commonly used for species of *Campyloneurum* until about the 1970s. The species has sometimes been considered a synonym of *C. decurrents* (e.g., Proctor & Lourteig, 1990; Smith, 1985; León, 1992).

*Campyloneurum pentaphyllum* seems amply distinct from *C. decurrents*. Its distal pinnae are sessile and not or only very shortly decurrent, whereas those of *C. decurrents* are conspicuously decurrent. Also, *C. pentaphyllum* occurs on soil or trunks, whereas *C. decurrents* occurs primarily as terrestrial or on boulders along streams (pers. obs., Labiak). According to hand-written notes on *Smith* 2456 from Colombia, the rhizomes of *C. pentaphyllum* are long-creeping and terrestrial but may climb trees. Thus, it is a “terrestrial root climber” sensu Canestraro et al. (2014). The long-creeping rhizome of *C. pentaphyllum* was well illustrated by Plumier (1705).

The specific epithet *pentaphyllum* apparently refers to the fact that the plant illustrated by Plumier (1705) has five leaflets; namely, one apical pinna plus two pairs of lateral pinnae. Pichi Sermolli and Bizzarri (2005) discussed the typification of *Campyloneurum pentaphyllum* in connection with their treatment of Raddi’s type collection of *C. decurrents* in southeastern Brazil.

### Acknowledgements

We thank the following colleagues who kindly sent us images of specimens: William Javier Bravo Pedraza, Fernando Matos, Jefferson Prado, Germinal Rouhan, David Sanín, Eric Schuettpelz, Alan Smith, and Weston Testo. We thank Judith Garrison Hanks for help imaging the spores, and Fernando Matos for preparing the distribution maps. Blanca León and an anonymous reviewer provided helpful comments on the manuscript. David Sanín kindly allowed us to use his photographs for Fig. 5.

### Literature cited

- Canestraro, B., R. C. Moran & J. E. Watkins. 2014. Reproductive and physiological ecology of climbing and terrestrial *Polybotrya* (Dryopteridaceae) at the La Selva Biological Station, Costa Rica. International Journal of Plant Sciences 175: 432–441.
- de la Sota, E. R. & B. Pérez-García. 1982. Nerviación y dimorfismo foliar en *Microgramma* Presl (Polypodiaceae) s. str. Biotica 7: 45–64.
- Fée, A. L. A. 1869. Cryptogrammes vasculaires du Bésil. Veuve Berger-Levrault et Cie, Strasbourg, France.
- Kreier, H.-P., A. F. Rojas A., A. R. Smith & H. Schneider. 2007. *Hyalotrichopteris* is indeed a *Campyloneurum* (Polypodiaceae). American Fern Journal 97: 127–135.
- Lellinger, D. B. 1988. Some new species of *Campyloneurum* and a provisional key to the genus. American Fern Journal 78: 14–35.
- León, B. 1992. A taxonomic revision of the fern genus *Campyloneurum* (Polypodiaceae). Unpublished Ph.D. dissertation, Department of Systematic Botany, University of Aarhus, Denmark.
- León, B. 1995. A new species of *Campyloneurum* (Polypodiaceae) from northwestern Ecuador. Novon 5: 42–44.
- León, B. 2004. A new species of *Campyloneurum* (Polypodiaceae) from northern Peru. Revista Peruana de Biología 11: 135–137.
- León, B. & M. Kessler. 2013. *Campyloneurum poloense* (Polypodiaceae), a new combination and lectotypification for a Bolivian fern. Phytotaxa 119: 59–60.
- Otto, E. M., T. Janssen, H.-P. Kreier & H. Schneider. 2009. New insights into the phylogeny of *Pleopeltis* and related neotropical genera (Polypodiaceae, Polypodiopsida). Molecular Phylogenetics and Evolution 53: 190–201.
- Pichi Sermolli, R. E. G. & M. P. Bizzarri. 2005. A revision of Raddi’s pteridological collection from Brazil (1817–1818). Webbia 60: 1–393.
- Plumier, C. 1705. Traité des fougères de l’Amérique. Impr. Royale, Paris.
- Proctor, G. R. & A. Lourteig. 1990. The ascriptions of Plumier’s fern plates. Taxon 32: 565–571.
- Proctor, G. R. 1977. Pteridophytes. In: R. A. Howard (ed.), Flora of the Lesser Antilles, vol. 2. Arnold Arboretum, Jamaica Plain, Massachusetts.
- Rojas A., A. F. 2005. El complejo de *Campyloneurum angustifolium* (Sw.) Fée (Polypodiaceae) en Costa Rica. Lankesteriana 5: 41–48.
- Salino, A., T. E. Almeida, A. R. Smith, A. N. Gómez, H. P. Kreier & H. Schneider. 2008. A new species of *Microgramma* (Polypodiaceae) from Brazil and recircumscription of the genus based on phylogenetic evidence. Systematic Botany 33: 630–635.
- Schneider, H., A. R. Smith, R. Cranfill, T. J. Hildebrand, C. H. Haufner, & T. A. Ranker. 2004. Unraveling the phylogeny of polyproid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. Molecular Phylogenetics and Evolution 31: 1041–1063.
- Schuettpelz, E. H. & K. M. Pryer. 2007. Phylogeny of ferns inferred from 400 leptosporangiate species and three plastid genes. Taxon 56: 1037–1050.

- Smith, A. R.** 1985. Pteridophytes of Venezuela, an annotated list. Published by the author, Berkeley, California. [Photocopied manual]
- Squinabol, S.** 1889–1891. Contribuzione alla flora fossile del terreno terziario della Liguria. I, II, and III. Genova.
- Tryon, A. F. & B. Lugardon.** 1991. Spores of the Pteridophyta; surface, wall structure, and diversity based on electron microscope studies. Springer-Verlag, New York.
- Tryon, R. M. & A. F. Tryon.** 1982. Ferns and allied plants, with special reference to tropical America. Springer-Verlag, New York.
- Wagner, W. H., Jr. & D. R. Farrar.** 1977. The Central American fern genus *Hyalotrichia* and its family relationships. Systematic Botany 1: 348–362.
- Windisch, P. G.** 1982. Specimens from Féé's pteridological collection at the botanical garden of Rio de Janeiro. American Fern Journal 70: 56–60.
- Grant, M. L. 10910 (2)
- Grayum, M. 10906 (2)
- Guascota, M. et al. 287 (2)
- Hammel, B. & de Nevers 13594 (2)
- Heissner, K. G08L2 (1), PO1-5 (1)
- Holdridge, L. R. 1609 (2)
- Kalbreyer, W. s.n. (3)
- Killip, E. P. 11223 (2)
- Kollmann, L. 6685 (1)
- Korte, A. & Kniess 3925 (1)
- Labiak, P. H. et al. 3480 (1), 4872 (1)
- Labiak, P. H. 3906 (1), 4412 (1)
- Lellinger, D. B. & de la Sota 916 (2)
- Liesner, R. 9722 (2), 9738 (2)
- Lindig 307 (2)
- Magnago, L. F. S. 1650 (1)
- Matos, F. B. et al. 243 (1), 290 (1), 719 (1), 808 (1), 1078 (1), 1269 (1)
- Mazziero, F. F. F. & Soller 919 (1)
- Meier, W. 2874 (3)
- Meier, W. & Kunert 5019 (3), 5020 (3), 5033 (3)
- Meier, W. & Flauger 8837 (3)
- Meier, W. 17070 (2)
- Menezes, J. s.n. (1)
- Mexia, Y. 4892 (1)
- Mezzonato, A.C. 13 (1)
- Miers, J. s.n. (1)
- Moran, R. C. & Rohrbach 5132 (2), 5318 (2)
- Murillo, J. & Forero 3732 (2)
- Mutis, C. 3241 (2)
- Mynssen, C. M. & Bovini 676 (1)
- Mynssen, C. M. & Reis 1421 (1)
- Øllgaard, B. & Windisch 4650 (1)
- Ortega, F. & Smith 2449 (2), 2455 (2)
- Palacios, W. 11451 (2)
- Pittier, H. 14173 (2)
- Prado, J et al. 1512 (1)
- Prado, J. & Valente 2027 (1)
- Raddi s.n. (1)
- Reitz, R 239 (1)
- Rinnert, C. H. 937 (1)
- Rohr, J.A. 1060 (1)
- Rojas, A. 1456 (2)
- Salino, A. 696 (1), 1633 (1), 2226 (1), 4210 (1), 4277 (1), 5431 (1), 6214 (1), 6289 (1), 6289 (1), 6669 (1), 7159 (1), 7251 (1), 7349 (1), 11113 (1), 15555 (1)
- Sanín, D. et al. 5153 (2)
- Schuettpelz, E. et al. 1439 (1)
- Schunke, C. 170 (2)
- Sehnem, A. 9055 (1), 9057 (1), 9463 (1), 9464 (1)
- Silverstone, P. 539 (2)
- Smith, D. N. 5212 (2)
- Smith, H. H. 2456 (3)

**APPENDIX 1.** Index of Collectors' names and numbers. The number in parenthesis refers to the species: 1 = *Campyloneurum decurrens*; 2 = *C. magnificum*; 3 = *C. pentaphyllum*. Numbers in boldface indicate types.

- Almeida, T. E. 63 (1)
- Alston, A. H. G. 6253 (3), 7824 (2)
- André, E. 4230 (2)
- Araque M. & Barkley 180738 (2)
- Atehortúa, L. 111 (2)
- Athayade, F. P. F. 640 (1)
- Badini, J. 126 (1)
- Benalcazar, C. & Silva 222 (2)
- Brackenridge, W. D. s.n. (1)
- Brade, A. C. 6461 (1)
- Buchtien, O. 3490 (2)
- Bünger, M. O. 238 (1)
- Cadorin, T. J. et al. 628 (1), 2255 (1)
- Callejas, R. et al. 4057 (2)
- Campos, J. & García 4043 (2)
- Canestraro, B. et al. 619 (1)
- Christenhusz, M. J. M. et al. 4884 (1)
- Croat, T. B. 27143 (2), 74487 (2)
- Cuascota, M. 287 (2)
- Cuatrecasas, J. 13667 (2), 22735 (2)
- Dittrich, V.A.O. & Ribas 474 (1)
- Dittrich, V. A. O. et al. 1802 (1)
- Dodson, C. H. 5478 (2)
- Drew, W. B. 668 (2)
- Duss, P. 1568 (3)
- Echtermacht, L.A. 680 (1)
- Fendler, A. **410** (2)
- Folsom, J.P. 4534 (2)
- Forero, E. et al. 7244 (2)
- Gentry, A. 9982 (2)
- Glaziou, A. **403** (1), **404** (1), 970 (1), 1684 (1), 1749 (1), **1750** (1), 2388 (1)

- Smith, L. B. 2251 (1)  
Solomon, J. C. et al. 6574 (2)  
Souza, F. S. et al. 207 (1), 304 (1)  
Stehmann, J. R. 3748 (1)  
Triana, J. s.n. (3)  
Valente, G. E. 593 (1)  
van der Werff, H. et al. 126 (2)
- Vargas, H. et al. 5447 (2)  
Vervloet, R. R. 3248 (1),  
3501 (1)  
Vianna, M. C. 1162 (1)  
Windisch, P. 8480 (1)  
Woytkowski, F. 35218 (2)  
Zak, V. 3838 (2)