

# *Campyloneurum atrosquamatum* (Polypodiaceae), a new species from Amazonia

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**Abstract.** A new species, *Campyloneurum atrosquamatum*, is described from the western Amazonian region of Ecuador to Bolivia, and from French Guiana and northeastern Brazilian Amazon. The new species belongs to the Repens Clade of *Campyloneurum*. Previously, it had been identified as *C. coarctatum* because of its similar lamina size and shape. An earlier phylogenetic study, however, resolved it as sister to *C. fuscusquamatum*, a species with nearly identical rhizome scales and a similar geographic distribution. We describe the new species, compare it to related species, and provide illustrations, distribution maps, and a key to similar species. A lectotype is chosen for *C. coarctatum*.

**Keywords:** ferns, floristics, pteridophytes, South America, taxonomy.

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*Campyloneurum* C. Presl is entirely Neotropical and contains about 60 species (León, 1992; Lellinger, 1988; Labiak & Moran, 2018). Phylogenetically, it forms a clade with *Microgramma* C. Presl and *Niphidium* J. Sm. (Schneider et al. 2004; Kreier et al. 2007; Schuettpelz and Pryer 2007; Labiak & Moran, 2018). The clade is characterized by simple, entire leaves, the only exceptions being three 1-pinnate species that compose *C. sect. Decurrentia* R. C. Moran & Labiak (Moran & Labiak, 2017). The veins of all three genera are anastomosed, but they form different patterns, as has been documented for *Campyloneurum* (Moran & Labiak, 2017), *Microgramma* (de la Sota & Pérez-García, 1982), and *Niphidium* (Lellinger, 1972). The venation of *Campyloneurum* differs from that of *Microgramma* and *Niphidium* by the main lateral veins cross-connected by finer arcuate veins, creating a series of areoles between the costae and margins (Labiak & Moran, 2018). The areoles along the costae have only one included, excurrent veinlet, but the supra-costular areoles typically include two excurrent veinlets. When fertile, excurrent veinlets bear round sori near or at the

tips of these veinlets. This distinctive venation pattern is lost in the Pruinoso clade of *Campyloneurum*, which is characterized by pruinose rhizomes (Labiak & Moran, 2018). Although it has anastomosing veins, the Pruinoso clade often lacks conspicuous main lateral veins between the costa and margin, and for this reason the characteristic cross-venation pattern of the genus cannot develop.

Species recognition within *Campyloneurum* has proved challenging. Although character-state reconstructions show that some characters in the genus exhibit little homoplasy (e.g., 1-pinnate laminae, rhizome pruinosity, and the presence of hairs on the laminae abaxially), many characters are highly homoplastic (Labiak & Moran, 2018). These include rhizome habit, growth form, cell shape of the rhizome scales, lamina shape, and prominence of lateral veins between the costa and margin (Labiak & Moran, 2018). High levels of homoplasy and the similarities they impart to unrelated species appear to be one of the main reasons many species in *Campyloneurum* have gone undetected.

A previous phylogenetic analysis suggested that at least 15 species of *Campyloneurum* are still undescribed (Labiak & Moran, 2018). Some of these species were described by us for southeastern Brazil (Labiak et al., 2017) and for Costa Rica and Panama (Moran & Labiak, 2018). In the present paper, we describe yet another new species. It occurs in Amazonia and belongs to the Repens Clade, which is characterized by long-creeping, non-pruinose rhizomes (Labiak & Moran, 2018). Specimens of this new species had been previously identified as *C. coarctatum* primarily because of their similarities to that species in lamina size and shape.

### Methods

*Herbarium studies.*—A total of 81 specimens were studied from B, F, MO, NY, QCA, UC, USM, TEX, TUR and on-line images from BM, COL, F, US (respectively, <http://www.nhm.ac.uk/our-science/data/spruce/>; <http://www.biovirtual.unal.edu.co/en/collections/search/plants/>; <http://emuweb.fieldmuseum.org/botany/detailed.php>; <https://collections.nmnh.si.edu/search/botany>), and JSTOR Global Plants (<https://plants.jstor.org/>). In citing type specimens, we give barcode numbers in brackets. In citing type and non-type specimens, we supply geographic coordinates in brackets when those coordinates were not given on the original herbarium label. The dot-distribution maps were based on all specimens studied and generated with QGIS version 2.0.1 (Quantum GIS Development Team, 2013). Layers included a delimited text file compiled from all specimens studied, shape files (political units and rivers) obtained from the Organization for Flora Neotropica ([www.nybgpress.org](http://www.nybgpress.org)), and a raster file (1: 10,000,000) from Natural Earth ([www.naturalearthdata.com](http://www.naturalearthdata.com)).

### New species

***Campyloneurum atrosquamatum*** Labiak, B. León & R. C. Moran, **sp. nov.** Type: Ecuador. Napo: just outside of Parque Nacional Yasuní, ca. km 26.1 on Maxus Oil Road, transect 18, 0°35'S, 76°31'W, floodplain forest, ca. 300 m, 20 Apr 1996, R. C. Moran, H. Tuomisto, K. Ruokoleinen & A. Poulsen 6248 (holotype,

QCA; isotypes, AAU, NY [barcode 04061672], QCNE, TUR). (Figs. 1, 2 and 3.)

**Diagnosis:** *Campyloneurum atrosquamatum* differs from *C. coarctatum* by rhizome scales linear to linear-lanceolate and dark brown, and by its occurrence at lower elevations (100–700 m vs. (450–)1000–2370 m).

Plants epiphytic; rhizomes (1.5–)2–3 mm wide, long-creeping, usually dark brown to blackish, not pruinose, the scales (1.5–)2–4 × 0.3–0.5 mm long, linear to narrowly lanceolate, ascending-appressed or sometimes (on phyllopodia) spreading, dark brown, concolorous, slightly clathrate or not, rarely clathrate at the distal parts of the scale, entire or nearly so, the cells elongated, usually with indistinct lumina; leaves 31–60 × 5–9 cm, internodes 1–3 cm long; petioles 5–19 cm long, 0.15–0.45 times the length of the laminae; laminae 29–41 cm long, oblong-lanceolate, chartaceous, glabrous or with inconspicuous scattered linear scales along the costa, the base gradually to abruptly concave (i.e., not long-decurrent), the apices acuminate; costae prominent and raised on the abaxial surface of the laminae; primary veins conspicuously prominent; secondary veins inconspicuous to obscure; areoles 9–13 between the costa and lamina margin.

*Distribution.*—French Guiana, Ecuador, Peru, Bolivia, Brazil; wet forests; 100–700 m.

*Etymology.*—The specific epithet is a compound of the Latin words *atro-*, dark, and *squamatum*, furnished with scales (Stearn, 1992), referring to the dark-brown, narrow scales that distinguish the species from *Campyloneurum coarctatum*.

**Additional specimens examined. BOLIVIA. La Paz:** Prov. Franz Tamayo, Parque Nacional Madidi, Río Hondo, Arroyo Negro, 14°40'21"S, 67°50'39"W, 400–700 m, 31 Mar 2002, *Fuentes 4226* (MO); Cochabamba: Prov. Chapare, Parque Machia, 1 km al E de Villa Tunari, 16° 58'S, 65° 24'W, 350 m, 14 Sep 1996, *Kessler et al. 8468* (UC).

**BRAZIL. Acre:** Município Caramari Amazonas, Río Juruá, N of Cruzeiro do Sul, Lago da Cigana (São Luis) S of Porto Alvaro Nestrinho, 07°37'S, 72°36'W, 150 m, 22 Aug 1986, *Croat 62,525* (MO, UC); Município Caramari Amazonas, vic. of Floresta, downstream from Cruzeiro do Sul, 07°37'S, 72°36'W, 150 m, 23 Aug 1986, *Croat 62,550* (MO, UC); Município Cruzeiro do Sul, Río Juruá, left bank, Igarapé Viseu, 15 minutes upstream by canoe, 8°18'S, 72°44'W, 21 Mar 1992, *Daly 7556* (NY). **Amapá:** Between first and second cachoeiras on Río Laué, Río Oiapoque, about 2 km east of confluence with Río Oiapoque, 2°53'N, 52°22'W, 27 Aug 1960, *Irwin 47,880* (NY); Amazonas: Juruá, [3°28'51" S, 66°4'8"W], Jun 1901, *Ule 5607* (B). **Pará:** Lageira, airstrip on Río Maicuru, varzea along Maicuru up to Igarapé Jangada,



FIG. 1. Four species of *Campyloneurum*. A–D. *Campyloneurum concavum*. E–H. *Campyloneurum atosquamatum*. I–L. *Campyloneurum coarctatum*. M–P. *Campyloneurum fuscusquamatum*. (A, from Costa Rica, W. R. Maxon 630, NY; B, from Costa Rica, A. Brenes s.n. in 1906, NY; C, holotype, from Panama, R. S. Williams 871, NY; D, from Costa Rica, J. T. Mickel 2050, NY; E, F, G, H, H, from Ecuador, A. Fay & L. Fay 3306, NY; I, from Peru, R. Vásquez 27,848, NY; J, from Bolivia, M. Sundue & M. Mendoza 899, NY; from Ecuador, K. J. Clark 7875, NY; L, from Peru, syntype, E. Poeppig s.n., P; M, from Peru, D. Washausen & F. Encarnación 621, NY; N, from Bolivia, M. Nee & I. Vargas C. 39,235, NY; O, from Ecuador, R. Moran et al. 6065, NY; from Bolivia, D. Smith & V. García 13,812, NY).

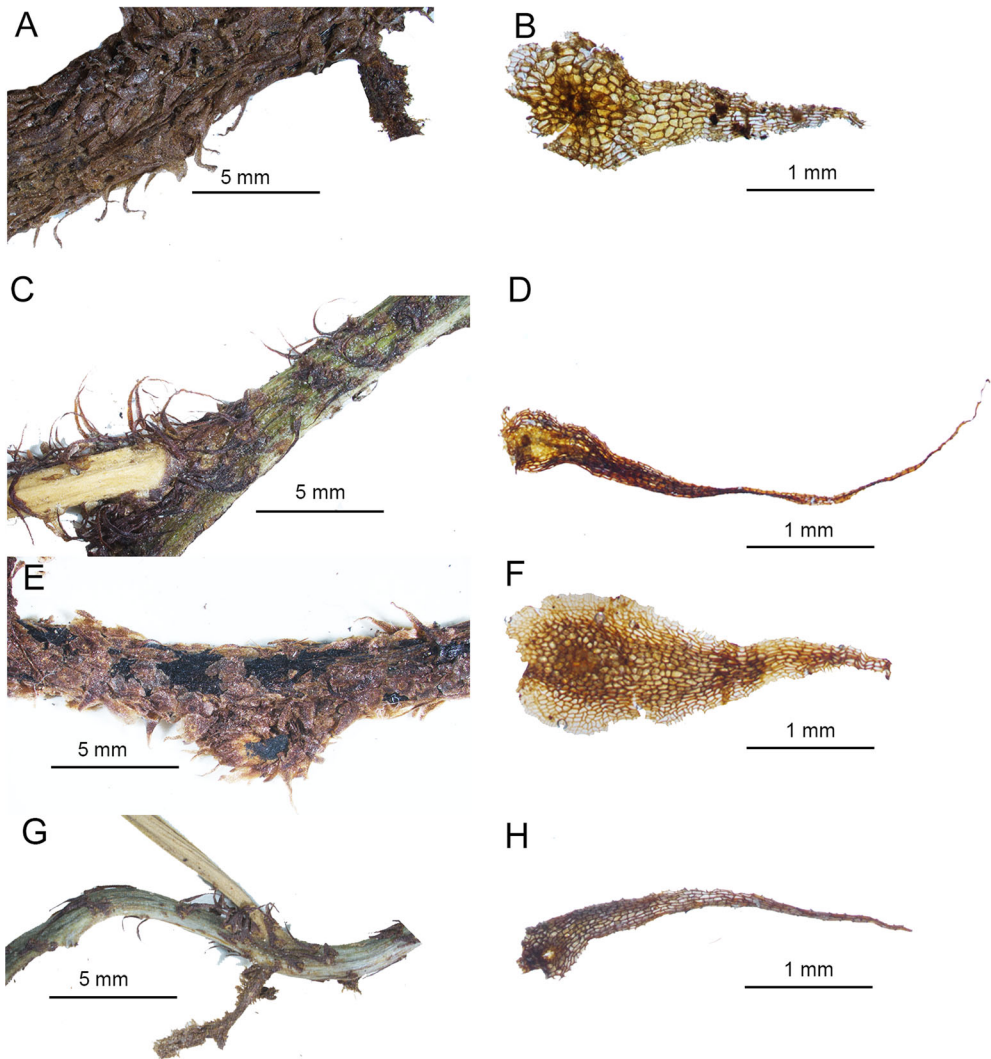


FIG. 2. Rhizome and rhizome scales of four species of *Campyloneurum*. **A, B.** *Campyloneurum concavum*. **C, D.** *Campyloneurum atosquamatum*. **E, F.** *Campyloneurum coarctatum*. **G, H.** *Campyloneurum fuscusquamatum*. (A and B, from Costa Rica, *J. T. Mickel 2050*, NY; C and D, from Ecuador, *R. M. Mirabai & E. Tepe 195*, NY; E and F from Peru, *H. van der Werff et al. 25,327*, NY; G and H, from Bolivia, *L. Arroyo P. 26*, NY).

0°55'S, 54°26'W, 280 m, 1 Aug 1981, *Strudwick & Sobel 3985* (NY).

**ECUADOR. Morona-Santiago:** Cantón Mendez, E of Mendez on Bella-Union road, trail to river at sign for Mendez, along steep banks, 483 m, 27 Jul 2011, *McCarthy & Tepe 195* (NY). **Napo:** Nor-oriente, Nuevo Rocafuerte, colecciones al sur-oeste de la población, en pica que va al río Braga, zona pantanosa, [5°60'S, 76°24'W], 200–230 m, 2 Mar 1981, *Jaramillo & Coello 4629* (NY, QCA); Parque Nacional Yasuni, Km 36.6 on the oil road starting at Pompeya, Transect 8, 0°39'S, 76°2'W, 300 m, 15 Apr 1996, *Moran 6177* (NY, QCA, TUR); Añangu, Río Napo, trail to tierra firme line, 0 31'S, 76 23'W, 260–300 m, 6 Jul 1983, *Lawesson et al. 39,775* (QCA); Añangu, well drained hilly ground in the Parque

Nacional Yasuni, 0°31–32'S, 76°23'W, 260–350 m, 2 Mar 1981, *Øllgaard et al. 38,827* (QCA, UC). **Pastaza:** Montalvo, on the Río Bobonaza, disturbed rain forest round the military camp, 2°5'S, 76°58'W, 300 m, 28 Jul 1980, *Øllgaard et al. 35,411* (QCA, UC).

**FRENCH GUIANA.** Pied du mont Galbao, entre Crique Canal Panamá, 3°37'N, 53°17'W, 180 m, 8 Jan 1986, *Granville 8477* (NY); Pied du Mont Galbao, Crique Canal Panamá, 10 km à l'ouest de S, 3°37'N, 53°17'W, 180 m, 9 Jan 1986, *Granville 8500* (NY).

**PERU. Cuzco:** La Convención, Echarate, San Martín norte, 11°44'19"S, 72°42'31"W, 479 m, 19 Feb 2011, *Mendoza & Fernández-Baca 6302* (USM); La Convención, Echarati, Pagoreni well site, [11°42'53"S, 72°54'1"W], 350 m, 18

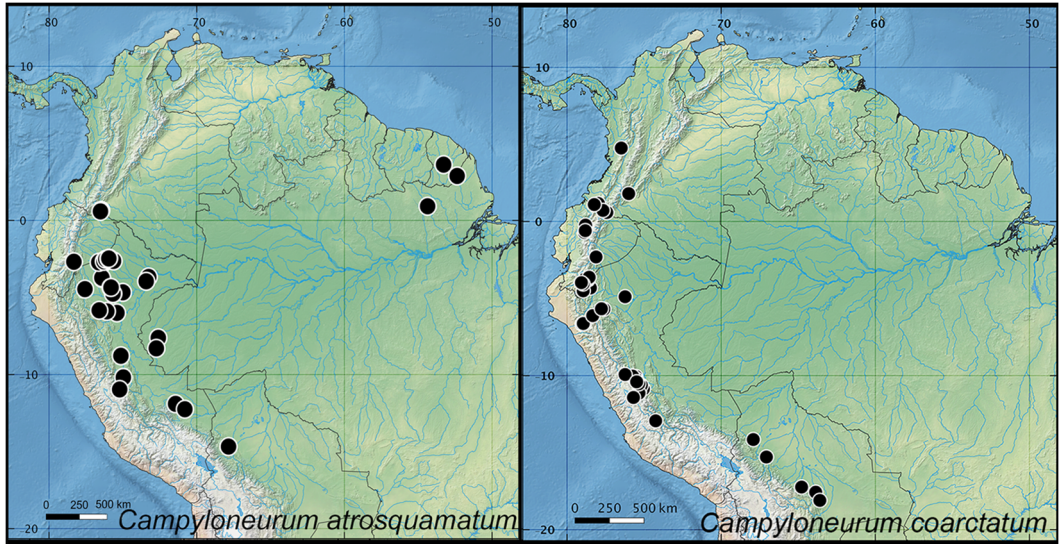


FIG. 3. Geographic distribution of *Campyloneurum atosquamatum* and *C. coarctatum*.

Apr 1998, Núñez et al. 21,554 (USM). **Junín:** Puerto Bermúdez, [10°11'S, 74°58'W], 375 m, 14–17 Jul 1929, Killip & Smith 26,444 (NY); Río Paucartambo Valley, near Perene Bridge, [10°58'S, 75°13'W], 700 m, 19 Jun 1929, Killip & Smith 25,200 (NY). **Loreto:** Prov. Alto Amazonas, cerca a la comunidad de Andoas, 2°49'11.9"S, 76°24'0"W, 246 m, 4 Mar 2001, Cárdenas et al. 792 (TUR); Prov. Loreto, near Sungachi, 43°12'S, 76°25'12"W, 110 m, 7 Aug 2003, Cárdenas & Vormisto 1509 (TUR); Prov. Loreto, near Juan Velasco Alvarado, 4°45'S, 75°39'W, 110 m, 7 Aug 2003, Cárdenas & Vormisto 1545 (TUR); Prov. Loreto, near Juan Velasco Alvarado, 4°45'S, 75°39'W, 110 m, 10 Aug 2003, Cárdenas & Vormisto 1562 (TUR); Prov. Loreto, near Juan Velasco Alvarado, 4°45'S, 75°39'W, 110 m, 12 Aug 2003, Cárdenas & Vormisto 1576 (TUR); Prov. Loreto, near Juan Velasco Alvarado, 4°45'S, 75°39'W, 110 m, 12 Aug 2003, Cárdenas & Vormisto 1576 (TUR); Prov. Loreto, near Juan Velasco Alvarado, 4°45'S, 75°39'W, 110 m, 28 Feb 1996, Cárdenas & Vormisto 1577 (TUR); Prov. Loreto, near Guineal, 4°20'59.9"S, 75° 49' 48"W, 110 m, 11 Oct 1998, Cárdenas & Vormisto 1637 (TUR); Prov. Loreto, near Guineal, 4°20'59.9"S, 75°47'59"W, 110 m, 25 Oct 1998, Cárdenas & Vormisto 1666 (TUR); Prov. Requena, Reserva Nacional Pacaya-Samiria, Campamento Grado 6, 5°59'43"S, 75°11'00"W, 25 Apr 1993, Del Carpio 1886 (USM); Río Marañón, una hora arriba del caserío de Saramuro, 4°40'S, 75°00'W, [300 m], 22 Jan 1979, Diaz & Ruiz 875 (MO); Prov. Loreto, upper Río Pastaza, ca 23 km NW of Nuevo Andoas community and Lote 1AB airfield, 2°43'12"S, 76°37'47.9"W, 250 m, 25 Apr 2005, Higgins & Ruiz 12 (TUR); Prov. Loreto, upper Río Pastaza, ca. 23 km NW of Nuevo Andoas community and Lote 1AB airfield, 2°43'12"S, 76°37'47.9"W, 250 m, 1 May 2005, Higgins & Ruiz 40 (TUR); Prov. Loreto, Río Tigre, adjacent to Nuevo Remanente community, 2°37'47.9"S, 76°37'47.9"W, 250 m, 23 May 2005, Higgins & Ruiz 196 (TUR); Prov. Loreto, ca. 20 km NE of Nuevo Andoas, along road between Río Pastaza and Río Tigre in Lote 1AB, 2°38'59.9"S, 76°16'48"W, 250 m, 5 Mar 2006, Higgins & Ruiz 513 (TUR); Prov. Loreto, adjacent to Shiviayacu, along road

between Río Pastaza and Río Tigre in Lote 1AB, 2°31'12"S, 76°9'0"W, 250 m, 6 Mar 2006, Higgins & Ruiz 597 (TUR); Prov. Loreto, ca. 15 km NE of Shiviayacu, along road between Río Pastaza and Río Tigre in Lote 1AB, 2°28'47.9"S, 75°58'48"W, 200 m, Higgins & Ruiz 818 (TUR); Prov. Loreto, ca. 25 km NE of Shiviayacu, along road between Río Pastaza and Río Tigre in Lote 1AB, 2°27'0"S, 75°55'48"W, 200 m, Higgins & Ruiz 1083 (TUR); Prov. Loreto, ca. 20 km NE of Shiviayacu, along road between Río Pastaza and Río Tigre in Lote 1AB, 2°28'12"S, 75°57'0"W, 200 m, Higgins & Ruiz 1100 (TUR); Yurimaguas, lower Río Huallaga, [5°54'S, 76°05'W], 135 m, 23 Aug–7 Sep 1929, Killip & Smith 27,668 (F, NY); Balsapuerto, lower Río Huallaga basin, [5°50'S, 76°36'W], 150–350 m, 28–30 Aug 1929, Killip & Smith 28,472 (NY); Santa Rosa, lower Río Huallaga below Yurimaguas, [3°46'S, 76°24'W], 175 m, 1–5 Sep 1929, Killip & Smith 28,854 (F, NY); Balsapuerto, lower Río Huallaga basin, [5°50'S, 76°36'W], 150–350 m, 28–29 Aug 1929, Killip & Smith 28,427 (F, NY, P, US); Balsapuerto, Lower Río Huallaga basin, [5°50'S, 76°36'W], 150–350 m, 28–30 Aug 1929, Killip & Smith 28,573 (NY); above Pongo de Manseriche, left bank of Río Santiago, 4°27'30"S, 77°34'51" W, 200 m, 23 Nov 1931, Mexia 6141a (MO); Prov. Maynas, Experimental Station Allpahuayo, 3°57'S, 73°21'W, 100–200 m, 27 Feb 1996, Tuomisto et al. 9627 (TUR, UC); Prov. Maynas, Experimental station 'Allpahuayo' of IAP, Km 20 of the road Iquitos-Nauta, 3°57'S, 73°21'W, 100 m, 21 Mar 2005, Tuomisto et al. 9647 (TUR); Dtto. Iquitos, Río Nanay, trail from Astoria to Río Mazan, [3°40'S, 73°15'W], [300 m], 26 Mar 1976, Rimachi 2139 (MO); Provincia Maynas, Dtto. Iquitos, Allpahuayo, Estación Experimental del Instituto de Investigaciones de la Amazonia Peruana (IAP), 04°10'S, 73°30'W, 150–180 m, 27 May 1991, Vásquez & Jaramill 16,627 (USM); **Madre de Dios:** Manu, S side of rio Manu, close to Cocha Cashu Biological station, 11°54'S, 71°26'W, 400 m, 7 Oct 1998, Tuomisto et al. 13,095 (TUR, UC); Prov. Manu, S side of Río Manu, close to Cocha Cashu Biological Station, 11°54'0"S, 71°25'48"W, 300 m, 21 Mar 2005, Tuomisto et al. 13,184 (TUR); Prov. Manu, N bank of Río

Madre de Dios, 10 km E from the mouth of Río Manu, 12°15' 0"S, 70°47' 59.9W, 250 m, 1 Apr 2005, Tuomisto et al. 13,396 (TUR). **Ucayali:** Prov. Coronel Portillo, Bosque von Humboldt, Km 28 on Carretera Marginal, in construction, heading towards Puerto Bermúdez, 8°47'S, 75°08'W, 200 m, 22 Jun 1981, Young & Salazar 1015 (F, MO).

*Campyloneurum atosquamatum* belongs to the Repens Clade (Labiak & Moran, 2018), which is characterized by long-creeping, non-pruinose rhizomes, and internodes 10–20 times the width of the rhizomes. Resembling *C. coarctatum* in lamina size and shape, it was previously identified as that species, but in a previous phylogenetic analysis it was recovered as sister to *C. fuscusquamatum* Lellinger (Labiak & Moran, 2018).

*Campyloneurum atosquamatum* resembles both *C. coarctatum* and *C. fuscusquamatum*. It resembles *C. coarctatum* by size of the leaves and oblong-lanceolate laminae with concave bases (Fig. 1). Because of these characters, most specimens of *C. atosquamatum* were previously identified as *C. coarctatum* (e.g., León, 1992, 1993). *Campyloneurum atosquamatum*, however, differs from *C. coarctatum* by stiff, narrow, dark brown rhizome scales (vs. more flaccid, wider, and paler brown in *C. coarctatum*; Fig. 2). Instead, the rhizome scales of *C. atosquamatum* greatly resemble those of the species it was resolved sister to *C. fuscusquamatum* (Fig. 2G, H). The latter species differs from *C. atosquamatum* by shorter petioles (1–5 vs. 5–19 cm long), narrower oblong laminae, and tapered (not concave) lamina bases (Fig. 1).

Another species from the same Clade that resembles *Campyloneurum atosquamatum* is *C. abruptum* (Lindm.) B. León (León, 1992, 1993, 2018; Moran & Labiak 2018). *Campyloneurum abruptum* differs by having a longer and wider decurrent wing along the petioles, and more oblong laminae and acute apices (see Moran & Labiak, 2018, Fig. 1G–E), whereas *C. atosquamatum* has a truncate base and relatively shorter laminae with acuminate or cuspidate apices. Additionally, the rhizomes are more than 5 mm wide in *C. abruptum*, and 2–3 mm wide in *C. atosquamatum*. Illustrations of *C. abruptum* are available in Moran & Labiak (2018).

Those specimens of *Campyloneurum atosquamatum* that provided growth-habit information on their labels were said to be epiphytic; none were recorded as terrestrial or epipetric. In contrast, *C. coarctatum* is more variable in growth habit: 10 specimens

were recorded as epiphytic, five epipetric, and six terrestrial.

Like *Campyloneurum atosquamatum*, another species separated from *C. coarctatum* is *C. concavum* R. C. Moran & Labiak. It differs from the new species, *C. atosquamatum*, by generally larger size, with wider rhizomes (3–5 vs. 2–3 mm), larger rhizome scales (2.5–3.5 × 0.5–2.6 mm vs. (1.5–)2–4 × 0.3–0.5 mm), and typically wider laminae ((7–)10–12 vs. 5–9 cm). *Campyloneurum concavum* is endemic to Costa Rica and Panama (Moran & Labiak, 2018), whereas *C. atosquamatum* occurs only in Amazonia (Fig. 3).

Because *Campyloneurum atosquamatum* is being distinguished in this paper from *C. coarctatum*, the species with which it has been previously identified, we provide the following description of the latter species for comparison.

***Campyloneurum coarctatum*** (Kunze) Fée, Mém. Foug. 5 (Gen. Filic.) 258. 1852. *Polypodium coarctatum* Kunze, Linnaea 9: 39. 1834. Type: Peru. Huánuco: Cucheros, “subandin. in sylvis,” Jul 1829, E. Poeppig s.n. (lectotype, designated here: P [barcode P01354492]; isolectotype, W [accession number 0052620]). (Figs. 1, 2 and 3.)

Plants typically epiphytic, rarely terrestrial or epipetric; rhizomes 2–3 mm wide, long-creeping, usually brown to dark-brown, not pruinose, the scales 1.5–3.5 × 0.4–1 mm, broadly lanceolate, appressed, brown to pale-brown, concolorous or with paler borders, entire or nearly so, not clathrate, the cells elongated, indistinct; leaves 29–53 × 5–10 cm, internodes 2–8 cm long; petioles 7–22 cm long, 0.2–0.4 times the length of the laminae; laminae 22–33 cm long, oblong-lanceolate, chartaceous, glabrous, the base slightly concave-decurrent, the apices gradually attenuate to acuminate; costae prominent and raised on the abaxial surface of the laminae; primary veins conspicuously prominent; secondary veins inconspicuous to obscure; areoles 7–14 between the costa and lamina margin.

*Distribution and habitat.*—Colombia, Ecuador, Peru, Bolivia; known from both sides of the Andes; wet forests; (425–)1000–2370 m.

*Etymology.*—Kunze did not explain why he chose the specific epithet *coarctatum*, meaning pressed together, close-set, narrowed (Stearn, 1992). It might refer to the rhizome scales of the

lectotype, which are pressed close together, often overlapping—a condition that may be seen on other specimens where the scales have not been abraded (Fig. 2C). It might also refer to the abruptly narrowed lamina bases (Fig. 11–L).

**Additional specimens examined. BOLIVIA. Beni:** Prov. Beni, 25 km from Yucumo on Yucumo–Quiquibey road in the Pílon Lajas, [15°17'S, 67°04'W], 950 m, 15 Jul 1990, *Fay & Fay 2705* (US). **Cochabamba:** Prov. Tiraque. Localidad Los Guácharos, [17°24'S, 64°58'W], 490 m, 11 Sep 2003, *Zabalaga 117* (NY). **Santa Cruz:** Prov. Ichilo, Parque Nacional Ambaró, 1–2 km S from Campamento Mataracú, 17°34'S, 63°52'W, 425–600 m, 1 Jun 1998, *Nee 49,553* (NY); Prov. Florida. 4 km NE of Bermejo, in or near bottom of valley of “Refugio Los Volcánes”, 18°6'S, 63°36'W, 1070 m, 27 Jul 2003, *Sundue 733* (NY); Prov. Florida. 4 km NE of Bermejo, in or near bottom of valley of “Refugio Los Volcánes,” 18°6'S, 63°36'W, 1120 m, 28 Jul 2003, *Sundue 747* (NY).

**COLOMBIA. Chocó:** San José del Palmar, Cerro Torá, vertiente oriental, Río Negro, abajo del Helipuerto ca. 1 hora del Vereda de Río Negro, [04°53'S, 76°14'W], 1900 m, 16 Aug 1988, *Ramos et al. 1272* (NY); San José del Palmar, Cerro Torá, vertiente occidental, Hoya del Río Negro, Vereda de Río Negro, ca. 1 hora arriba del Helipuerto, 04°46'N, 76°29'W, 1900 m, 19 Aug 1988, *Ramos et al. 1362* (NY). **Huila:** Mun. Pilatito, Vereda El Triunfo. Finca El Pedregal, 300 m. arriba de la casa de Duena Isabel, 1°48'32"N, 76°0'59"W, 1550 m, 11 Jan 2005, *Rico et al. VMR0536* (COL). **Nariño:** Reserva La Planada, Quebradas El Mar - La Calladita, 1°10'N, 77°58'W, 1500–1800 m, 30 Apr 1988, *de Benavides 9694* (MO).

**ECUADOR. Carchi:** Cantón Tulcán, Reserva Indígena Awa, Comunidad San Marcos, 25 km NW de El Chical, parroquia Maldonado, 1°06'N, 78°14'W, 1500 m, 16–30 Nov 1990, *Rubio et al. 922* (MO). **Cotopaxi:** Cantón Sigchos, entre Río Escaleras y zona Escaleras, 0°35'40"S, 78°49'54"W, 2772 m, 17 Jul 2003, *Ramos et al. 6143* (NY); Cantón Sigchos, Bajo Triunfo Grande, bosque a mano izquierda de vía Triunfo Grande - Las Pampas, [0°42'S, 78°52'W], 2321 m, 9 Aug 2003, *Ramos et al. 7168* (NY). **Morona-Santiago:** Oeste de la ciudad de Macas, 2°18'S, 78°07'W, 1160 m, 24 Feb 1986, *Baker 6601* (NY); Pachicutza, at Escuela Fiscomisional Cardinal Döpfner, Km 140 on road Loja-Gualaquiza, 3°37'S, 78°34'W, 900–1000 m, 26–27 Apr 1973, *Holm-Nielsen et al. 4620* (F, NY). **Napo:** Hollín-Loreto road, Km 32, 3–4 km S of road, path to permanent sampling plot, 0°35'S, 77°25'W, 1200 m, 25 Jan 1991, *Moran & Rohrbach 5129* (MO); Hollín-Loreto road, Km 32, 3–4 km S of road, path to permanent sampling plot, 0°35'S, 77°25'W, 1200 m, 25 Jan 1991, *Moran & Rohrbach 5148* (MO); Cantón Archidona, faldas al S del Volcán Sumaco, Carretera Hollín-Loreto, Km 31, Comuna Challua Yacu, 00°43'S, 77°40'W, 1200 m, 20–25 Mar 1989, *Palacios 4112* (MO). **Pichincha:** Cantón Quito, Río Guajalito Reserve, 10 km W of Chiriboga; Km 69 of old road Quito–Santo Domingo, 0°14'S, 78°48'W, 1900 m, 9 Jul 1991, *Fay & Fay 3225* (NY); in sylvia subandinis, 2100 m, 1 Jul 1898, *Mille s.n.* (NY). **Zamora-Chinchipe:** road between Los Encuentros and El Sarsa, 4.7 km E of Los Encuentros, 3°46'42"S, 78°38'32"W, 822 m, 26 May 2003, *Croat & Menke 89,561* (NY, UC); Cantón Zamora, within 3 km of the town of Zamora, 4°03'5"S, 78°57'05"W, 1000 m, 17 Jul 1994, *Fay & Fay 4444*

(MO, NY); road to La Saquea-Yacuamba, 1 km N Chapintza, [3°46'01"S, 78°52'15"W], 1100 m, 9 Apr 1995, *Harling & Andersson 23859* (QCA); 4 km W of Panguitza, on road to Panguitza, [3°53'55"S, 78°48'45"W], 1100–1200 m, 14 Apr 1985, *Harling & Andersson 24156* (QCA); Parque Nacional Podocarpus, Bombuscaro, MATRIX plot L5 along trail Higuerones, 4°07.37'S, 78°58.51'W, 1050 m, 20 Nov 2010, *Lehnert 2083* (TEX); Immediately N of Zamora, 4°4'S, 78°57'W, 1000–1200 m, 2–12 Jun 1984, *Øllgaard et al. 74813* (NY); NW of Zamora, 4°03'S, 78°58'W, 1100 m, 12 Mar 2013, *Øllgaard 100733* (QCA); stream ravine NW of Zamora, 4°30'S, 78° 57'W, 1000 m, 17 Feb 1993, *Øllgaard & León 100586* (QCA); new road Loja–Zamora, Km 38.6 E of the pass, 15 Feb 1991, *Øllgaard & Moran 98830* (QCA); area of Estación Científica San Francisco, road Loja–Zamora, ca. 35 km from Loja, 3°58'S, 79°04'W, 1850 m, 19 Dec 2003, *Werner 666* (UC); Area Estación Científica San Francisco, road Loja-Zamora, Quebrada San Ramón, 1750 m, 18 Sep 2005, *Werner & Knuth 1774* (QCA); Shaime, Cantón Nangaritzta, Pueblo Shaime on Río Nangaritzta, hill W of Shaime, 4°18'47"S, 78°29'59"W, 900 m, 20 Sep 2000, *Janovec et al. 1396* (NY).

**PERU. Amazonas:** Distrito Jumbilla, along road Jumbilla-Rioja, 5°39'58"S, 77°46'19"W, 1900–1940 m, 8 Nov 2012, *van der Werff et al. 25,327* (USM); Distrito Camporeddondo, Tullanya, Pascana, Pájaro Tigre, 6°6'33"S, 78°20'55"W, 2370 m, 4 Dec 1996, *Vásquez & Rojas 21,936* (NY). **Ayacucho:** Aina, between Huanta and Río Apurimac, [12°55'S, 74°15'W], 750–1000 m, 7–17 May 1929, *Killip & Smith 22,720* (NY, US). **Cajamarca:** Santa Cruz. Catache, Upper Río Ñaña valley, ca. 5 km above Monte Seco on path to Chorro Blanco, [06°40'S, 79°01'W], 1500–2000 m, 16–18 Mar 1986, *Dillon et al. 4355* (F, NY); Santa Cruz, alrededor del Choro Blanco, bosque del Monte Seco, 1950 m, 10 Oct 1993, *Leiva & Lazama 924* (F); Santa Cruz. ca. 3.2 km (por aire) ENE Monte Seco, 1900 m, 7 May 1987, *Santisteban & Guevara 32* (F). **Huánuco:** Las Cuevas de los Pavas on road to Lima, 625–1100 m, 30 Oct 1949–19 Feb 1950, *Allard 20,527* (US). Prov. Huánuco, Gorge of Río Chinchao, 5 km. above junction with Río Huallaga, 60 km NE of Huánuco, [9°55'50"S, 76°14'32"W], 1000 m, 11 Sep 1956, *Tryon & Tryon 5302* (F, US). **Junín:** Colonia Perene, [10°52'S, 75°03'W], 14–22 Jun 1929, *Killip & Smith 24,917* (NY); East of Quimiri Bridge, near La Merced, [11°02'S, 75°18'W], 800–1300 m, 1–3 Jun 1929, *Killip & Smith 23,896* (NY); Huacapistana, [11°14'S, 75°31'W], 1900 m, 28 Jun 1982, *León 242a* (USM); Prov. Chanchamayo, Schunke Hacienda, above San Ramón, 11°08'S, 77°20'W, 1300–1700 m, Aug–Oct 1923, *Schunke A167* (US); Prov. Tarma, Agua Dulce, 2000 m, 16 Apr 1948, *Woytkowski 37,025* (MO). **Pasco:** Prov. Oxapampa, Valle del Palcazú, Río Cacazú, Cacazú, bosque parcialmente alterado en ladera rocosa, [10°34'S, 75°06'W], 500–1000 m, 19 Aug 1985, *León 676* (F, USM); Distrito Oxapampa, Limite del Parque Nacional Yanachaga Chemillén, Quebrada San Alberto, 10°32'S, 75°21'W, 2310 m, 17 Aug 2002, *Monteagudo et al. 3639* (MO, NY); Prov. Oxapampa, Distrito Pozuzo, Huampal, 10°11'S, 75°34'W, 1250 m, 21 Sep 2002, *Monteagudo et al. 3964* (MO, NY, UC); Prov. Oxapampa, Distrito Pozuzo, Puesto de Vigilancia Huampal, 10°11'S, 75°34'W, 1250 m, 23 Sep 2002, *Monteagudo et al. 3992* (MO, NY); Prov. Oxapampa, Distrito Villa Rica, Localidad Centro Bocaz, trocha comunal, 10°38'S, 75°11'W, 1520 m, 22 Sep 2003, *Perea et al. 456* (MO, NY); Prov. Oxapampa, 4–5 km N of Mallampampa, 10°2'S, 75°45'W, 2400 m, 22 Jan 1984, *Smith*

& *Canne 5802* (MO, NY); Prov. Oxapampa, Pozuzu, [10°04'S, 77°32'W], 610 m, 20–22 Jun 1923, *Macbride 4581* (US); Parque Nacional Yanachaga Chemillén, Sector San Alberto, 10°32'S, 75°21'W, 2200 m, 20 Jan 2003, *Vásquez et al. 27,848* (MO, NY); Prov. Oxapampa, Yanachaga Parque Nacional, Yanachaga-Chemillén, Sector Quebrada Yanachaga, 10°24'13"S, 75°29'04"W, 1900 m, 11 Jan 2005, *Vásquez et al. 30,549* (MO, NY). **San Martín:** Tarapoto, [6°29'S 76°22'W], 1855–56 m, *Spruce 4646* (BM, K, NY); Moyobamba, 5°41.345'S, 77°41.179'W, 1306 m, 26 Jun 2015, *Suominen et al. 310* (USM); Prov. Rioja, along road Rioja–Pedro Ruiz, 5°40'27"S, 77°40'35"W, 1170 m, 23 Mar 1998, *van der Werff et al. 15,500* (MO); Aguas Verdes, 5°41'17"S, 71°37'52"W, 1100 m, 8 Nov 2012, *van der Werff et al. 25,327* (MO). **Department unknown:** s.d., *Matthews 1836* (NY).

*Campyloneurum coarctatum* belongs to the Repens Clade, which is characterized by long-creeping, non-pruinose rhizomes, and prominent main lateral veins between the costae and margins (Labiak & Moran, 2018). Within the clade, *C. coarctatum* is distinguished by pale to brown rhizome scales usually appressed to the rhizome surface, oblong-lanceolate laminae with concave bases, and petioles 0.2–0.4 times the length of the laminae (see Fig. 1H–K of Moran & Labiak, 2018).

There are two known syntypes collected by Poeppig, one at P and the other at W. We chose the specimen at P as the lectotype because it has a rhizome with scales, which is lacking in the W specimen.

All of the above species belong to the Repens Clade of *Campyloneurum* (Labiak & Moran, 2018), which is characterized by long-creeping rhizomes. Some of these species are hemiepiphytic, such as *C. serpentinum* (Christ) Ching from Central America (Labiak & Moran, 2018). Other species in the Repens Clade are

probably hemiepiphytic, but this needs to be documented by field studies.

The segregation of *Campyloneurum atosquamatum* from *C. coarctatum* has not changed the overall geographic distribution of the latter species. Specimens of *C. atosquamatum* were cited as *C. coarctatum* in recent floras for Peru (León, 1993), Bolivia (León, 2018), and Acre, Brazil (Prado et al., 2017). Both species are still known to occur in these regions (Fig. 2). All specimens of *C. coarctatum* cited by Sundue (2011) for Parque Nacional Amboró in southern Bolivia represent that species; *C. atosquamatum* is absent from central Bolivia, occurring only in the north of the country (Fig. 2). The only distribution that has changed is elevation, with *C. coarctatum* now recognized as occurring at generally higher elevations ((425–)1000–2370 m) than previously thought, with specimens from lower elevations (100–700 m) now understood to be a different species, *C. atosquamatum*.

The following key distinguishes the new species (*Campyloneurum atosquamatum*) from similar or related ones belonging to the Repens Clade (Labiak & Moran, 2018). *Campyloneurum concavum* is included in the key because, like *C. atosquamatum* here proposed, it was recently segregated from *C. coarctatum* (Moran & Labiak, 2017). Also, *C. abruptum* is included because its abruptly concave lamina bases (see Fig. 1E–G, in Moran & Labiak, 2017) resemble those of *C. atosquamatum* and *C. coarctatum*. Finally, *C. fuscusquamatum* is included because it was resolved as sister to the new species in a previous phylogenetic analysis (Labiak & Moran, 2018).

### Key to the species resembling *Campyloneurum coarctatum*

1. Rhizome scales broadly lanceolate, 0.4–1 mm wide, brown to pale brown.
  2. Rhizomes 3–5 mm wide; laminae 52–77 × (7–)10–12 cm wide; Costa Rica, Panama.....*C. concavum*
  2. Rhizomes 2–3 mm wide; laminae 29–53 × 5–10 cm wide; Colombia, Ecuador, Peru, Bolivia.....*C. coarctatum*
1. Rhizome scales linear to linear-lanceolate, 0.1–0.5 mm wide, brown to dark brown.
  3. Laminae 2.5–5 cm wide, linear-oblong, 7–11 times longer than wide.....*C. fuscusquamatum*
  3. Laminae 5–13 cm wide, lanceolate or elliptic lanceolate, 4–8 times longer than wide (not including the long decurrent wing in *C. abruptum*)
    4. Rhizomes more than 5 mm wide; lamina bases long-decurrent and forming a conspicuous wing along the petiole.....*C. abruptum*
    4. Rhizomes 2–3 mm wide; lamina bases gradually to abruptly concave, not forming a conspicuous wing along the petiole.....*C. atosquamatum*

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