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REGULAR PAPER

Taxonomic novelties in *Cyclodium* (Dryopteridaceae) and a key to the species with free veins

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Background – *Cyclodium* is a neotropical fern genus comprising about ten species. Most species are found in northern South America, and the foothills of the Guiana Shield is an important region for species diversification. Our phylogenetic and taxonomic studies of the genus demonstrated the need to describe a new species and to recognize a variety at species level.
Methods – This study is based on herbarium specimens from CAY, HUA, INPA, MBM, NY, P, RB, UC, UFP, UPCB, and US. Morphological characters were analyzed using standard procedures. The indumentum and spores of the new species were studied using a scanning electron microscope. Species delimitation is proposed based on our preliminary phylogenetic studies, as well as on morphology and geographical distribution.
Key results – *Cyclodium alansmithii* Bohn & Labiak is recognized as a new species, described, and illustrated. The most similar species is *Cyclodium inerme* (Fée) A.R.Sm., from which it differs by ovate-lanceolate and bicolored scales, reduced fronds, truncate pinna bases, and non-ciliate indusia. *Cyclodium alansmithii* is currently assessed as Endangered (EN) using IUCN criteria, but more fieldwork and herbarium studies are necessary to establish a more accurate conservation assessment. *Cyclodium trianae* (Mett.) A.R.Sm. var. *chocoense* A.R.Sm. is here elevated to species rank. A key to species of *Cyclodium* with free veins is provided.

Keywords – Amazon; biodiversity; ferns; Guayana Shield; polybotryoids; taxonomy.

INTRODUCTION

Cyclodium C.Presl (Dryopteridaceae) is entirely neotropical, with about ten species distributed from Trinidad and Panama to northeastern Argentina and eastern Brazil, usually below 1500 m of altitude (Smith 1986). The greatest diversity is found in the Guianas, where six species and many putative hybrids occur (Cremers et al. 1993). The most recent comprehensive study of *Cyclodium* is that of Smith (1986), and since then the genus has appeared in numerous regional floras and checklists (e.g., Tryon & Stolze 1991; Cremers et al. 1993; Smith & Moran 1995; Smith et al. 1995; Mori et al. 1997; Santiago & Barros 2003; Garcia & Salino 2008; Almeida & Salino 2015; Kessler et al. 2018). Additionally, two intergeneric hybrids involving a cross of *Cyclodium meniscioides* (Willd.) C.Presl with different species of *Polybotrya* Humb. & Bonpl. ex Willd. have been recently described from Brazil (Engels & Canestraro 2017; Schwartsburd et al. 2018), suggesting that hybridization may have played an important role in the evolution and diversification of *Cyclodium*.

The genus is characterized by short- to long-creeping rhizomes, 1–2-pinnate fronds (rarely more divided), chartaceous to subcoriaceous laminae, and peltate indusia. Most of its species are terrestrial, but there are records of hemie-

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piphytic, epiphytic, epipetric, and rheophytic plants (Smith 1986). Some of these characters are also present in other dryopteroid genera, such as *Maxonia* C.Chr., *Olfersia* Raddi, *Polybotrya*, and *Stigmatopteris* C.Chr. Some earlier authors (e.g., Christensen 1913, 1920; Tryon & Tryon 1982; Smith 1986; Moran 1987, 1991a) have used these similarities to suggest affinities between these genera on the basis of morphology. More recently, phylogenetic studies based on plastid DNA recovered *Cyclodium* as monophyletic and sister to *Polybotrya*, forming a clade with other dryopteridoid ferns that have creeping rhizomes and (often) fertile-sterile leaf dimorphism (Moran & Labiak 2015; PPG I 2016).

During our phylogenetic (ten taxa of the genus, five chloroplastidial markers) and taxonomic studies on *Cyclodium* (Bohn et al. in prep.), we found some taxonomic novelties that we present herein. They include a new species, *Cyclodium alansmithii,* and a new status for *C. trianae* (Mett.) A.R.Sm var. *chocoense*. Because both species have free veins, we also provide a dichotomous key to all free-veined species of *Cyclodium*.

MATERIALS AND METHODS

Herbarium specimens were obtained as loans from CAY, HUA, INPA, MBM, NY, P, RB, UC, UFP, UPCB, and US (Thiers 2018). Additional images of type specimens were accessed on JSTOR (https://plants.jstor.org/). For morphological descriptions, the largest fertile and sterile pinnae were measured. Measurements of hairs and scales were made using a trinocular stereo microscope (AmScope SM-3TX) equipped with a 54-bulb LED illumination and MU500 5MP digital camera. SEM images of the spores, scales, and hairs were obtained using a JEOL JSM-6360LV scanning electron microscope at the Electron Microscopy Center of Universidade Federal do Paraná. The material was transferred with dissecting needles from herbarium specimens to aluminum stubs coated with asphalt adhesive. The stubs were sputter-coated with gold for two minutes. Hairs, scales, proscales, and indusia were imaged digitally with an optical microscope LEICA MZ16 equipped with a camera (LEICA DFC 500) at the Department of Zoology, Universidade Federal do Paraná. Information about the geographical distribution was obtained from herbarium labels, and the maps were made using QGIS ver. 3.2.0 software (Quantum GIS Development Team 2013). When not provided, geographical coordinates were estimated, and are presented within brackets. The layers included a raster file (1: 10,000,000), from Natural Earth (www.naturalearthdata.com), and shape files (political units and rivers), obtained from the Organization for Flora Neotropica (www.nybgpress.org). The conservation status of the new species was obtained using the GeoCAT tool from Kew (http://geocat.kew.org/).

TAXONOMIC TREATMENT

Cyclodium alansmithii Bohn & Labiak, **sp. nov.**

Figs 1–4

This species is similar to *Cyclodium inerme* (Fée) A.R.Sm. by having 1-pinnate laminae, pinnae with crenate margins, and free veins, with the basal veinlets arising from costules and ending below or right above the sinuses. It differs from *C. inerme* by its smaller fronds, ovate-lanceolate and bicolorous rhizome scales, pinnae with truncate bases, and indusia with non-ciliate margins. It is also similar to *Cyclodium guianense* (Klotzsch) A.R.Sm., from which it differs by the absence of conspicuous costal scales. – **Type**: Guyana, Upper Mazaruni River Basin, Mt. Ayanganna, [05°22′03.4″N, 59°56′51.8″W], alt. 800 m, 27 Jul. 1960, *Tillett 44942* (holotype: NY, barcode 2859537; isotype: US, barcode 00719099).

Plants terrestrial or epipetric. Rhizomes short-creeping, 0.3–0.5(–1) cm diam., with ca. 6–10 fronds per 3 cm, scaly at apex; scales basifixed, ovate-lanceolate, 3–5 × 0.5–1 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly erose. Fronds monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds (31–)37.5–50(–63) × 8.5–10.5(–17) cm, fertile fronds (29.5–)37–64.5(–80) × (8–)10–14 cm; petioles stramineous to tan, with scattered scales, rarely with septate, linear, brown proscales, 11–18(–36) cm long in sterile fronds, 16.5–36.5(–48) cm long in fertile fronds, 1.5–3 mm diam.; petiole scales basifixed and with a sinus or peltate, ovate-lanceolate, adpressed, 1.5–5 × 0.5–3 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly fimbriate; laminae 1-pinnate pinnatifid, with (11–)15–25 pairs of lateral pinnae, sometimes overlapping towards apex and gradually reduced to a pinnatifid apex; (18–)23.5–32.5 × 8.5–10.5(–17) cm in sterile fronds, (13–)17.5–34 × (6.5–)7.5–12.5 cm in fertile fronds; rachises stramineous to tan, with an elevated center and two shallow lateral grooves abaxially and a central groove adaxially, the grooves with bacilliform, translucid, yellowish hairs ca. 0.1 mm long, abaxially glabrous or with septate, linear, brown to dark brown, scattered proscales, rarely with brown scales, ca. 1.5–2 cm long; pinna stalks 1.5–3(–4) mm long, with bacilliform, translucid, yellowish, glandular hairs and proscales similar to those of the rachises; pinnae linear to elliptic, bases truncate, sometimes subauriculate acroscopically, apices acute to round, margins undulate or crenate to pinnatifid margins, more dissected in fertile fronds, sterile basal pinnae (3.8–)4.5–8 × 1.3–2 cm, fertile basal pinnae (2.5–)3.5–6(–8) × (0.7–)1–1.4(–2) cm, sterile medial pinnae 3.8–5.3(–7) × 1.1–1.6 cm, fertile medial pinnae (2.6–)3–6 × 0.7–1.6 cm; costae abaxially with linear, septate, brown to dark brown proscales; laminar tissue glabrescent, with septate, light brown proscales; veins free, conspicuous, 3–4-furcate, the basal veins ending below or immediately above the sinuses, rarely reaching the margins; sori discrete, impressed, medial on veins, forming 2 or 3(–4) rows between costae and margins, biseriate between two main lateral veins; indusia peltate, sometimes with stalks slightly dislocated from center, circular, ca. 0.5–1 mm diam, concolorous, stramineous, with entire to erose margins; spores monolete, 50–55 µm diam., perines broadly folded and densely echinulate, the folds low and continuous. Figs 1–3.

Distribution – Guyana (Cuyuni-Mazaruni and Potaro-Siparuni Regions) and Venezuela (Bolívar) (fig. 4).

Other collections examined – **Guyana**: Cuyuni-Mazaruni Region, Aurora, creek ± 1 km WSW of camp, 06°47′N, 59°44′W, alt. 70–75 m, 12 Oct. 1989, *Gillespie 2288* (INPA); Cuyuni-Mazaruni Region, at headwaters of Kangu River, W

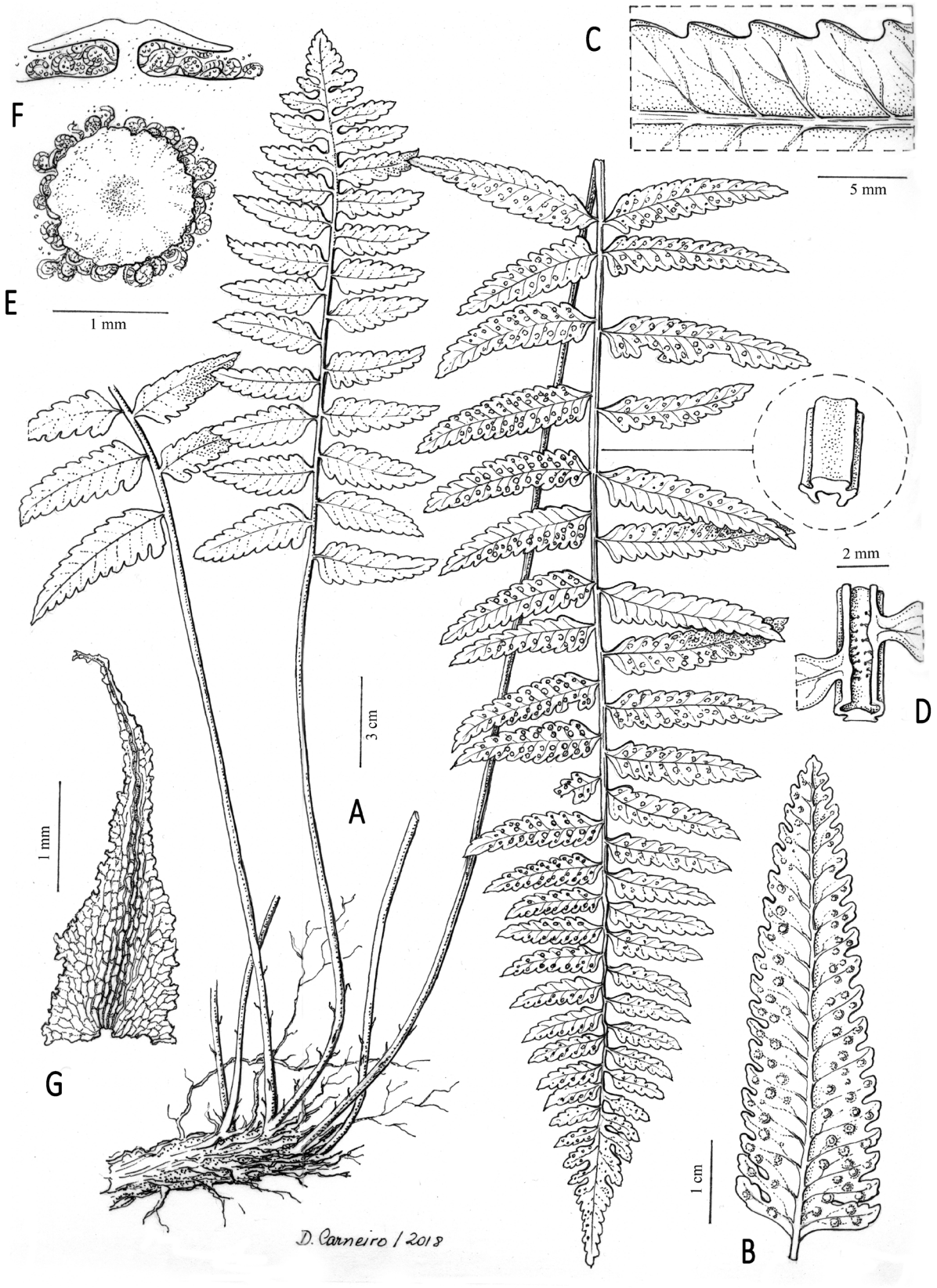

Figure 1 – *Cyclodium alansmithii*. **A**. Habit with detail of abaxial side of rachis. **B**. Detail of a fertile pinna. **C**. Detail of free venation. **D**. Detail of adaxial side of rachis groove with bacilliform hairs. **E**. Top view of peltate indusium. **F**. Transversal view of peltate indusium and sporangia. A–F from *Tillet 44942* (NY); Drawn by Diana Carneiro.

branch, ± 4 km NW of E peak of Mt. Ayanganna, first talus slope of plateau, 05°25′N, 60°00′W, alt. 700 m, 5 Mar. 1987, *Pipoly 11045* (US); Cuyuni-Mazaruni Region, below 1st escarpment (of four) of Kamakusa Mt., 0–1.5 mi SW of Micrandra (4th) Camp, 05°51′08″N, 60°11′17″W, alt. 840 m, 29 May 2012, *Wurdack 5749* (CAY); Cuyuni-Mazaruni Region, Kako river, Chinakuruk Mountain, cliff foot of mountain, [05°31′47″N, 60°42′39″W], alt. 1226 m, 21 May 2009, *Redden 6709* (NY); Cuyuni-Mazaruni Region, Pakaraima Mtns, Kumarau Falls on Kurupung R, 0.2–1.0 km N along river gorge edge, 06°06′N, 60°21′W, alt. 300–340 m, 1 Aug. 1992, *Hoffmann 2248* (CAY); Cuyuni-Mazaruni Region, Pakaraima Mountains, Kurupung-Membaru trail, 2.75 km from Kumarau Falls, 06°05′N, 60°23′W, alt. 650 m, 22 Jul. 1992, *Hoffman 2109* (CAY); Potaro-Siparuni Region, Kaieteur National Park, W bank Potaro River, 0.5 km from falls in gorge, 05°11′N, 59°28′W, alt. 170 m, 12 Jul. 1993, *Henkel 2174* (CAY); Potaro-Siparuni Region, Marina Falls, 05°22′43″N, 59°28′93″W, alt. 449 m, 28 Mar. 2011, *Zartman 9359* (INPA); Potaro-Siparuni Region, Mt. Ayanganna, east face, camp at base of first of four escarpments, 05°22′22″N, 59°57′34″W, 16 Jun. 2001, *Clarke 9199* (NY); Potaro-Siparuni Region, Pakaraima Mts., Mt. Korak, Mazaruni R., 05°59′N, 60°37′W, alt. 600 m, 14 Nov. 1979, *Maas 4436* (NY); Potaro-Siparuni Region, Pakaraima Mts, Mt. Wokomung, Suruwabaru Creek, 2–3 km upstream from its juncture with Yuarka R, 05°03′N, 59°53′W, alt. 675–750 m, 10 Feb. 1993, *Henkel 1222* (CAY, NY); Potaro-Siparuni Region, Pakaraima mts., Mt. Wokomung; Suruwabaru Creek, 12 km from juncture with Yuarba River, 05°02′N, 59°54′W, alt. 675–750 m, 7 Nov. 1993, *Henkel 4106* (NY); Potaro-Siparuni Region, upper Kuribrong River, 05°34′20″N, 59°54′22″W, 20 Mar. 2011, *Zartman*

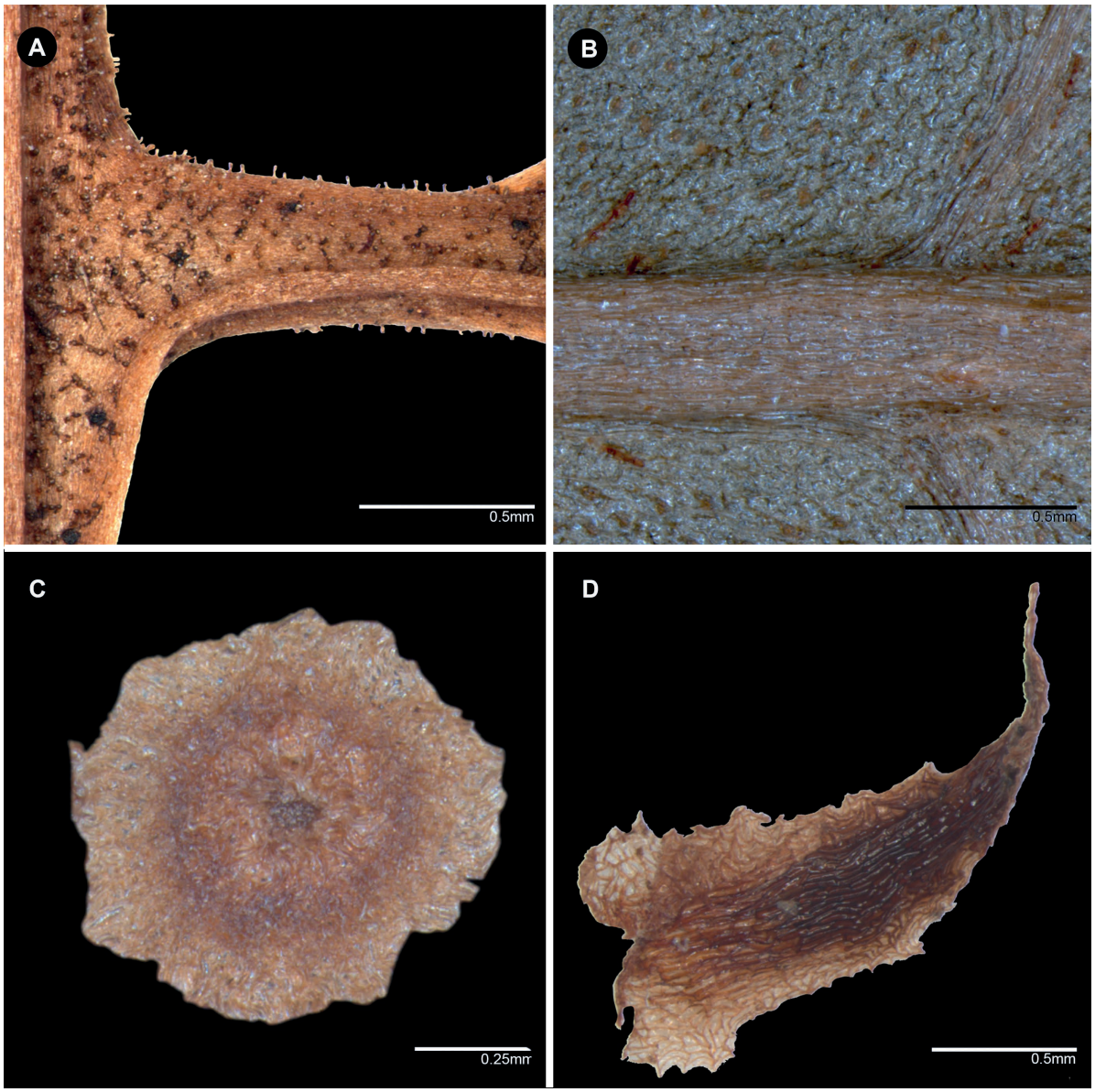

Figure 2 – Pinna stalk, costa, indusium and scale of *Cyclodium alansmithii*. **A**. Pinna stalk with hairs. **B**. Costa with proscales. **C**. Top view from indusium. **D**. Petiole scale. A, C from *Henkel 2174* (CAY); B, D from *Zartman 9172* (NY).

9172 (INPA); Potaro-Siparuni Region, Potaro River gorge, [05°10′0.72″N, 59°28′0.71″W], 17 May 1944, *Maguire 23525* (NY).

Venezuela: Bolívar, Chimantá Massif, southwestern-facing forested slopes of Chimantá-tepuí (Torono-tepuí), between Base Camp and steep slopes above valley of Río Tirica, [05°18′43″N, 62°07′23″W], alt. 1000–1400 m, 15 May 1953, *Steyermark 75376* (US).

Habitat and ecology – This new species is often associated to creeks and hillsides, growing on sandstone soils between 170–1400 m in elevation. Most specimens are terrestrial, but some are epipetric. One specimen (*Steyermark 75376*, US, barcode 00798729), is unusual because it occurs at lower elevations, between 70–75 m, in "terra firme" forest. The region where *C. alansmithii* occurs is part of the Guiana Shield, the remainder of an ancient craton older than the Gondwana dissociation, that extends from southwestern Venezuela, Guyana, Suriname, French Guiana, to northern Brazil and southeastern Colombia (Funk & Berry 2005). The most comprehensive work for the Guiana Shield region is from Berry et al. (1995), which analyzed the Venezuelan Guayana, and found high diversity and endemicity of fauna and flora. This region is known to have diverse geological formations, such as tepuis and inselbergs, with several habitats, as tropical savannas, lowland and montane forests, as well as shrub, and herbaceous formations (Berry et al. 1995). Most regions from the Guiana Shield are still untouched (ca. 60–70%), and programmes to encourage conservation are recent. The most comprehensive of them is The Biological Diversity of the Guiana Shield (BDG), which since 1983 is conducted by

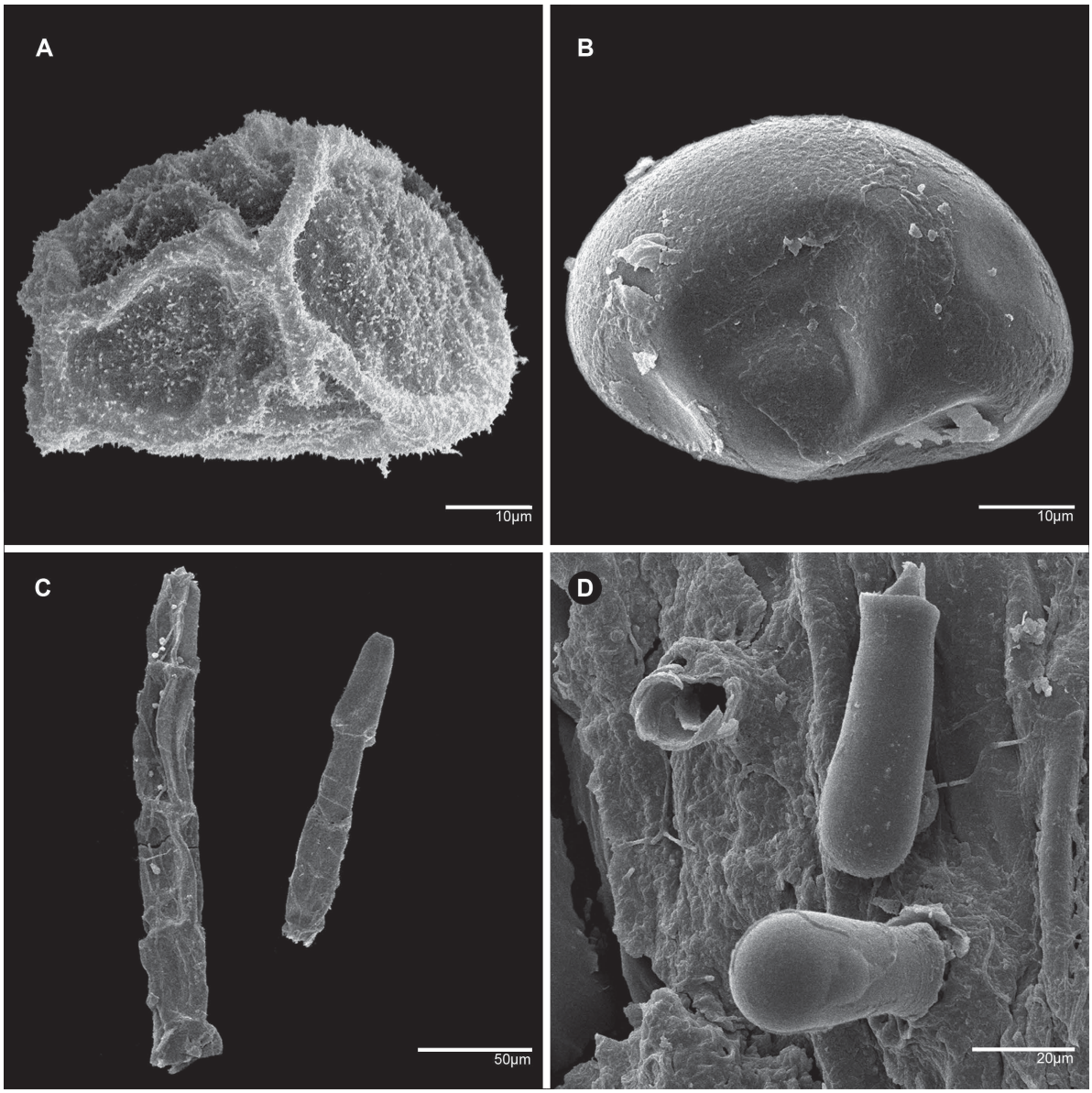

Figure 3 – Spores, proscale, and hairs of *Cyclodium alansmithii* (SEM). **A**. Spore. **B**. Spore without perispore. **C**. Proscales. **D**. Bacilliform hairs of pinna stalk. A–D from *Zartman 9172* (NY).

the Smithsonian Institution's National Museum of Natural History.

Etymology – The specific epithet honours Alan R. Smith (1943–), American pteridologist and author of a detailed taxonomic revision of *Cyclodium* (Smith 1986).

Conservation assessment – According to IUCN categories and criteria (IUCN 2001), *Cyclodium alansmithii* is considered Endangered (EN). Its extent of occurrence (EOO) is 29,142.139 km², which exceeds the threshold of 20,000 km² for the Vulnerable category under criterion B1. The area of occupancy (AOO) was estimated at 60.000 km² (lower than the threshold of 500 km² of B2 criteria for Endangered category). The number of locations is estimated between 2 and 5, which qualify for Endangered category under B2a. Based on a decline of the habitat, the species is assessed as EN B2ab(iii).

Notes – *Cyclodium alansmithii* can be recognized by its ovate-lanceolate, bicolored rhizome and petiole scales, reduced fronds (generally ca. 30–65 × 8–14 cm), 1-pinnate laminae, pinnae with truncate bases and crenate margins, and free venation. From the six species that occur in Guyana (Cremers et al 1993), it mostly resembles *C. inerme* by its free veins with the basal veinlets arising from costules and ending below or right above sinus, pinnae with crenate margins, costal grooves virtually glabrous adaxially, and lack of

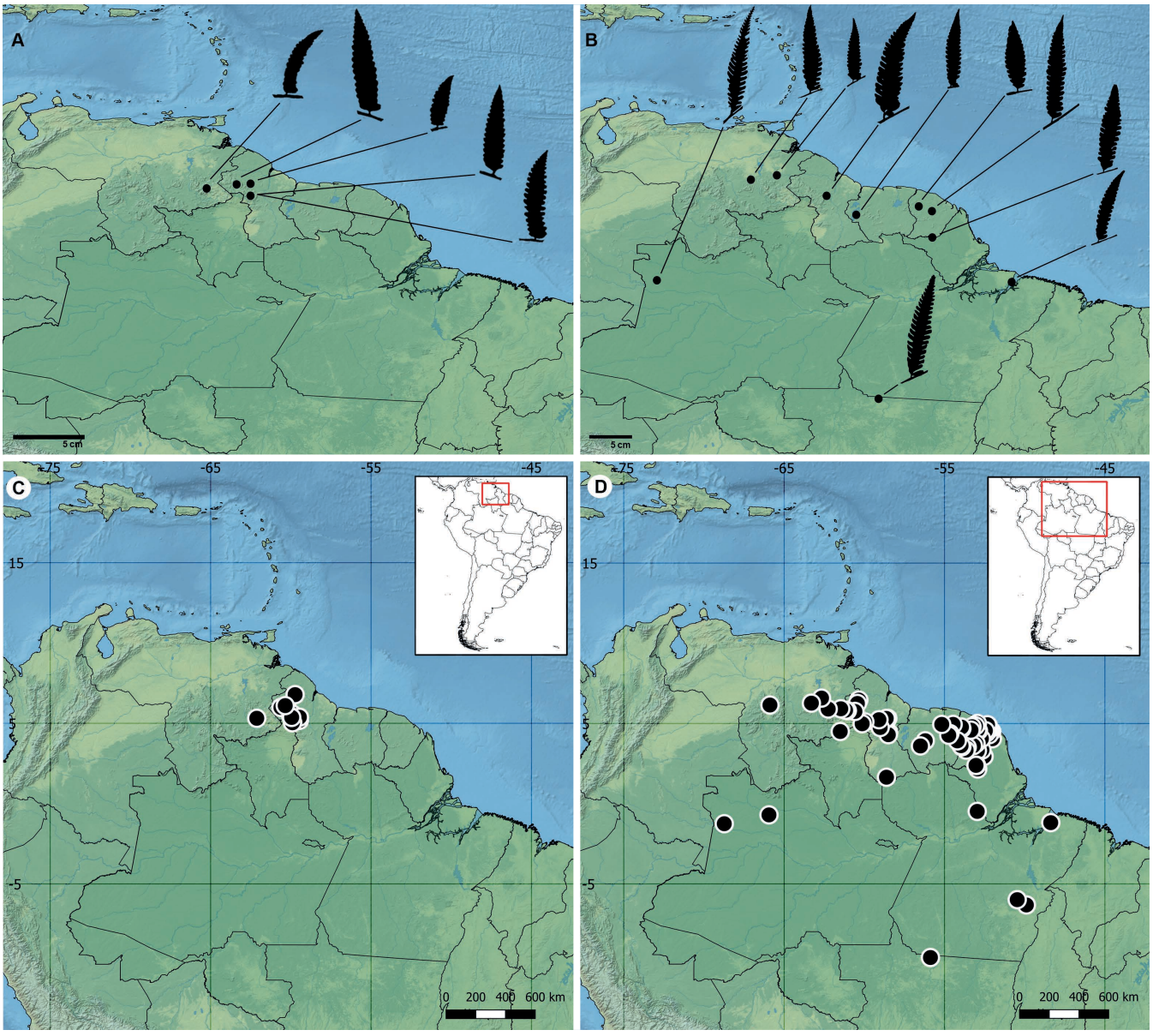

Figure 4 – Clinal variation and geographic distribution of *Cyclodium alansmithii,* and *Cyclodium inerme*. **A, C**. Clinal variation and distribution of *C. alansmithii*. **B, D**. Clinal variation and distribution of *C. inerme*. Images of *C. alansmithii* from *Henkel 2174* (CAY), *Hoffmann 2248* (CAY), *Maguire 23525* (NY), *Steyermark 75376* (US), *Tillet 44942* (NY). Images of *C. inerme* from *Aymard 6116* (UC), *Costa 383* (RB), *Cremers 5697* (CAY), *Froes 26025* (UC), *Henicka 293* (NY), *Hoff 6719* (CAY), *Irwin 54523* (NY), *Maas 5891* (NY), *Maia 441* (INPA), *Rivero 2347-A* (UC). Maps produced with QGIS (Quantum GIS Development Team 2013).

conspicuous scales abaxially. Also similar is the sympatric *C. guianense*. The main differences regarding *C. inerme* and *C. guianense* are given in the diagnosis above and in fig. 4. Two other species that also have bicolorous rhizome scales are *C. meniscioides*, and *C. akawaiorum* A.R.Sm. They both differ from *C. alansmithii* by having anastomosing veins. Another species from French Guiana, *Cyclodium rheophilum* A.R.Sm., also resembles *C. alansmithii*, but differs by having concolorous rhizome scales, narrower pinnae (1–2 cm vs. 0.3–0.6 cm), conspicuous costal scales, and reniform indusia.

Cyclodium chocoense (A.R.Sm.) Bohn & Labiak, **stat. nov.**

Cyclodium trianae (Mett.) A.R.Sm. var. *chocoense* A.R.Sm. (Smith 1986: 93). – **Type**: Colombia, Chocó, Corcovado region, upper Río San Juan, ridge along Yeracüí Valley, alt. 200–275 m, 24–25 Apr. 1939, *Killip 35287* (holotype: US, barcode 01050249; isotype: COL, n.v.)

Distribution – *Cyclodium chocoense* is distributed from Panama through western Colombia and Ecuador (first record in Ecuador), whereas *C. trianae* occurs from Panama to Peru. Even though they co-occur in Panama and north of Colombia, *C. trianae* is found only on the eastern side of the Andes, whereas *C. chocoense* occurs only on the western side. Fig. 5.

Other collections examined – **Panama**: Panama, Cerro Azul, cabecera del río San Cristobal, [9°13′52″N, 79°21′02″W], alt. 900 m, 28 Dec. 1986, *Valdespino 289* (UC); Cerro Jefé, [9°13′58″N, 79°21′01″W], 16 Feb. 1985, *van der Werff 6986* (UC); San Blas, Kuna Yala, hills of Sperdi, near Puerto Obaldía, San Blas coast, [8°39′57″N, 77°25′05″W], alt. 20–200 m, Sep. 1911, *Pittier 4415* (US). **Colombia**: Antioquia, Anorí, vereda Puntiadero o la Concha abajo, quebradas El Salto y El Claro, sector la Concha abajo, 7°17′01.2″N, 75°05′17.1″W, alt. 720 m, 16 Jan. 2004, *Rodríguez 4461* (COL web); Mutatá, Finca El Dárien, [7°14′47″N, 76°26′00″W], alt. 200 m, 18 May 1976, *Atehortúa 216* (HUA web); Corregimiento Longaní, margem derecha del Rio Longaní, 2 km al norte de Mutatá, [7°14′21″N, 76°26′03″W], alt. 80–100 m, 19 Nov. 1987, *Alberláez 248* (HUA web); San Luis, vía Medellín-Bogotá, quebrada La Tebaída, 6°8′N, 75°10′W, alt. 1010–1060 m, 22 Jun. 1987, *Callejas 4002* (HUA web, NY); Vic. Planta Providencia, 26 km S & 23 km W (air) of Zaragoza, in valley of rio Anorí between dos Bocas & Anorí, 7°13′N, 75°03′W, alt. 400–700 m, 2 Mar. 1977, *White 140* (HUA web); Vic. Planta Providencia, 26 km S & 23 km W (air) of Zaragoza, in valley of rio Anorí between dos Bocas and Anorí, 7°13′N, 75°03′W, alt. 400–700 m, 13 Jun. 1976, *Sheperd 432* (HUA web); Vic. Planta Providencia, 28 km SW of Zaragoza, valley of Río Anorí in aread surronding the confluence of quebrada La Tirana and Río Anorí, approx. 3 km upriver from Plant Providencia, 7°18′N, 75°04′W, alt. 400–700 m, 4 Mar. 1977, *Alverson 143* (HUA web, NY); Bajo Calima, Buenaventura, Secretaria de Agricultura, [3°59′47″N, 76°58′35″W], alt. 80 m, 31 Mar. 1984, *de Escobar 4000* (HUA web); Bajo Calima, Buenaventura, Secretaria de Agricultura, [3°59′47″N, 76°58′35″W], alt. 70 m, 1 Apr. 1984, *de Escobar 4025* (HUA web); Caldas, Sanamá, El Carmén, 05°31′36″N, 75°02′26″W, 7 May 1992, *César 6973* (HUA web); Cauca, Timbiquí, east side of Gorgona Island, dense forest along stream, [2°49′58″N, 77°42′24″W], alt. 50–100

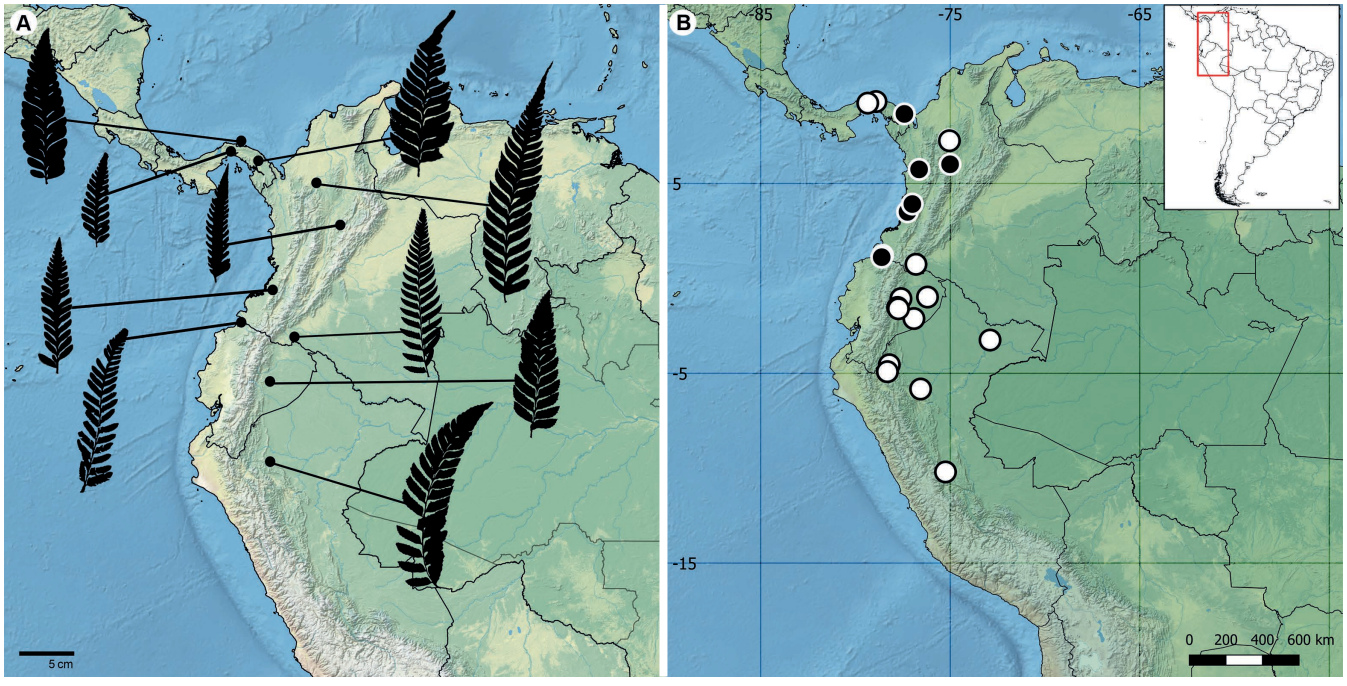

Figure 5 – Clinal variation and geographic distribution of *Cyclodium chocoense* (black circles) and *Cyclodium trianae* (white circles). **A**. Clinal variation of *C. chocoense* (five images on the left), and *C. trianae* (five images on the right). **B**. Distribution of *C. chocoense* and *C. trianae*. Images of *C. chocoense* from *Forero* 1342 (NY), *Hoover 3935* (UC), *Monsalve 433* (UC), *Pittier 4415* (US), *Valdespino 289* (UC). Images of *C. trianae* from *Alberlaéz 198* (NY), *Foster 9498* (NY), *Herrera 339* (UC), *Rodríguez 6865* (NY), *Tuomisto 11910* (UC). Maps produced with QGIS (Quantum GIS Development Team 2013).

Key to the species of *Cyclodium* with free venation

1. Laminae 1-pinnate-pinnatisect or more divided; indusia peltate, at least a few of them with a sinus, looking somewhat reniform 2
1'. Laminae 1-pinnate to 1-pinnate-pinnatifid; indusia always peltate 4

2. Rhizome scales to 3 mm long, dark brown to black, cordiform, folded lengthwise at center, and overlapping; several multicellular, acicular, translucent hairs on costae and rachis..... ***C. seemannii***
2'. Rhizome scales 5–10.5 mm long, golden to brown, linear to lanceate, planar and not overlapping; without multicellular, acicular, translucent hairs on costae and rachis 3

3. Proximal pinnae pair 2-pinnate-pinnatifid; usually more than ten rows of sori between the base and apex of each segment; segment margins crenate to pinnatifid..... ***C. trianae***
3'. Proximal pinnae pair 1-pinnate-pinnatisect to 2-pinnate; usually less than nine rows of sori between the base and apex of each segment; segment margins entire or slightly crenulate at apex..... ***C. chocoense***

4. Costae with scales more than two cells wide at their bases 5
4'. Costae lacking scales 6

5. Fertile fronds 25–34 cm long; proximal pinnae less than 1 cm wide; one row of sori between costae and margins; perine of spores lacking folds..... ***C. rheophilum***
5'. Fertile fronds larger than 34 cm; proximal pinnae more than 1 cm wide; 2–5 rows of sori between costae and margins; perine of spores with conspicuous folds ..... ***C. guianense***

6. Rhizome scales ovate-lanceolate, bicolorous; lateral pinnae 11–25 pairs; indusia non-ciliate ..... ***C. alansmithii***
6'. Rhizome scales lanceate, concolorous; lateral pinnae 9–16 pairs; indusia ciliate..... ***C. inerme***

m, 11 Feb. 1939, *Killip 33172* (COL web); Chocó, Bahía Solano, dense forest along Quebrada Jella, near ciudad Mutis, [6°12′34″N, 77°18′08″W], alt. 0–75 m, 21–23 Feb. 1939, *Killip 33622* (COL web); Chocó, Bahía Solano, km 11 between El Valle and ciudad Mutis, [6°13′47″N, 77°22′54″W], alt. 50 m, 15 Feb. 1986, *Wood 5296* (COL web); Chocó, Bahía Solano, low hills behind the beach 1–1.5 km NW of El Valle, N of the lagoon, [6°07′48″N, 77°26′26″W], alt. 25–75 m, 13 Feb. 1971, *Lellinger 343* (COL web); Chocó, Bahía Solano, near Punta San Francisco Solano, ca. 10 km NE of Puerto Mutis, [6°14′40″N, 77°23′15″W], alt. 10–100 m, 27 Jan. 1971, *Lellinger 82* (HUA web); Chocó, Bahía Solano, NW side of Alto del Buey, trail along ridge from the confluence of the forks of the rio Mutatá above Río Dos Bocas toward the top of Alto del Buey, [6°08′08″N, 77°19′38″W], alt. 950–1450 m, 8–10 Feb. 1971, *Lellinger 211*, *253* (COL web, HUA web); Chocó, Canton Del San Pablo, pan american Highway (under construction), ca. 10 km W of las Animas, [5°17′41″N, 76°41′01″W], alt. 100 m, 12 Jan. 1979, *Gentry 24057* (COL web); Chocó, carretera Andagoya-Condoto, cerca de Andagoya, 5°06′N, 76°40′W, 14 Apr. 1979, *Forero 5288* (COL web); Chocó, Istmina, dense forest near junction of Rio Condato and rio San Juan, [5°05′50″N, 76°41′47″W], alt. 100–150 m, 20 Apr. 1939, *Killip 35084* (COL web); Chocó, Istmina, río Bicordó, arriba de Noanamá, orillas del rio, 4°42′N, 76°55′W, 6 Apr. 1979, *Forero 4753* (COL web); Chocó, Istmina, rio El Salto (tributary of the Río Suruco), 9 km W of Andagoya, [5°05′32″N, 76°44′17″W], alt. 75–100 m, 23 Feb. 1971, *Lellinger 478* (COL web); Chocó, Istmina, Río Fujiadó, afluente del Río San Juan, 4°36′N, 76°54′W, 7 Apr. 1979, *Forero 4813* (COL web); Chocó, Litoral Del Bajo San Juan, Region del río Pichimá, comunidad indigena Waunana, 4°25′N, 77°17′W, 23 Nov. 1976, *Forero 746* (COL web); Chocó, Nóvita, quebrada Máncamo, afluente del Rìo Tamaná, cerrito em la margen izquierda, 4°57′N, 76°38′W, 11 Apr. 1979, *Forero 5051* (COL web); Chocó, Nuqui, corregimiento Termales, quebrada Piedra Piedra, [5°42′32″N, 77°15′55″W], alt. 0–25 m, 6 Sep. 1994, *Acevedo-Rodriguez 6807* (HUA web); Chocó, carretera Quibdó-Tutunendo, 15 km de Quibdó, [5°43′39″N, 76°36′10″W], alt. 45 m, 6 Sep. 1976, *Forero 2528* (COL web); Chocó, margem izquierda del río Munguidó, afluente del río Atrato, en pequeno cerro cerca de Altagracia, [5°42′38″N, 76°46′27″W], alt. 50 m, 4 May 1975, *Forero 1535* (COL web); Chocó, río Serrano, afluente del río Atrato, 4–6 km arriba del Guayabal, [5°44′37″N, 76°38′37″W], alt. 50 m, 29 Apr. 1975, *Forero 1342* (COL web, NY); Chocó, Tadó, Corcovada region, upper Río San Juan, ridge along Yeracüí Valley, [5°20′15″N, 76°15′05″W], alt. 200–275 m, 25–26 Apr. 1939, *Killip 35287* (COL web); Chocó, Mojarras de Tadó, 8.5 km E of Istmina, [5°16′14″N, 76°33′04″W], alt. 150–250 m, 20 Feb. 1971, *Lellinger 417* (COL web); Chocó, Unión Panamericana, quebrada Peña Negra, 8 km W of Quidbó-Istmina road on new Pan American Highway, [5°17′04″N, 76°39′33″W], alt. 90 m, 10 Jan. 1979, *Gentry 23937* (COL web, HUA web); Nariño, Barbacoas, al W de El Diviso, [1°22′40″N, 78°13′59″W], alt. 350 m, 3 Jun. 1973, *Leist 2158* (COL web); Nariño, carretera Barbacoas-Junin, km 8, [1°32′58″N, 78°05′44″W], alt. 140 m, 18 Dec. 1972, *Hagemann 1702* (COL web); Nariño, San Andres de Tumaco, km 80, [1°45′33″N, 78°47′07″W], alt.

300 m, 1 Nov. 1967, *Mora 4222* (COL web); Valle del Cauca, Buenaventura, about 18 km east of Buenaventura, dense forest, [3°53′56″N, 76°58′58″W], alt. 50 m, 14 Feb. 1939, *Killip 33246* (COL web); Valle del Cauca, Bajo Calima, [3°53′04″N, 77°00′39″W], 2 Apr. 1984, *de Escobar 4061* (HUA web); Valle del Cauca, Bajo Calima, Concesión Pulpapel/Buenaventura, 3°55′N, 77°00′W, alt. 100 m, 20 Sep. 1984, *Monsalve 433* (UC); Valle del Cauca, corregimiento San Cipriano, Reserva Natural de Escalerete, bajando de la casa blanca, [3°55′59″N, 77°10′00″W], alt. 100 m, 14 Apr. 1993, *Cruz 4044* (COL web); Valle del Cauca, costa del Pacífico, río Cajambre, quebrada del Corosal, [3°30′47″N, 77°14′03″W], 17 May 1944, *Cuatrecasas 17731* (UC); Valle del Cauca, dense forest near highway bridge over Río Dagua, about 20 km east of Buenaventura, [3°50′34″N, 76°47′26″W], alt. 40 m, 15 Feb. 1939, *Killip 33320* (COL web); Valle del Cauca, hoya del río San Juan, alrededores de Palestina, 4°10′N, 77°10′W, alt. 5 m, 26 Mar. 1979, *Forero 4035* (COL web); Valle del Cauca, quebrada Taparal, afluente del río San Juan, alrededores de la comunidad indigena Waunaná de Taparalito, 4°10′N, 77°10′W, alt. 5–10 m, 28 Mar. 1979, *Forero 4269* (COL web); Valle del Cauca, quebrada La Sierpe, afluente del Río San Juan, 4°10′N, 77°10′W, alt. 5 m, 1 Apr. 1979, *Forero 4449*, *4450* (COL web); Valle del Cauca, Dagua, Agua Clara, along highway from Buenaventura to Cali, [3°44′50″N, 76°43′11″W], alt. 100 m, 6 Jun. 1944, *Killip 38991* (US); Valle del Cauca, carretera Cali-Buenaventura, rio Danubio inferior, [3°43′38″N, 76°40′09″W], alt. 200 m, 15 Sep. 1967, *Hagemann 424* (COL web).

Ecuador: Esmeraldas, San Lorenzo, territorio Indígena Awá, Mataje village, 500 m west of Río Mataje, 01°13′00″N, 78°34′01″W, alt. 150 m, 14 Feb. 2000, *Neill 12453* (UC); Esmeraldas, San Lorenzo, further along trail to Rio Mataje (beginning at point where collecting ended previous day), Awá encampment from Rio Palaví encampment, 01°07′N, 78°37′W, alt. 200–230 m, 11 Feb. 1988, *Hoover 3935* (UC).

Habitat and ecology – *Cyclodium chocoense* is similar to *C. trianae* concerning habitat and ecology. Both species occur in primary or secondary wet evergreen forests, but *C. chocoense* seems to be often associated to rivers, and has a wider range of elevation, between 0 and 1750 m (vs. 100–1150 m). It is frequently recorded as terrestrial, but there are records of hemiepiphytic (*Alverson 143*) and epiphytic (*Forero 4813*) habits, whereas *C. trianae* seems to be exclusively terrestrial.

Conservation assessment – According to the IUCN categories and criteria (IUCN 2001), *C. chocoense* is considered Least Concern (LC). Although the species has a limited area of occupancy (AOO), its extent of occurrence (EOO) is large (265,668.199 km^2), far exceeding the 20,000 km^2 threshold for the Vulnerable category under criterion B1. Its AOO, is estimated at 192km^2, but it is largely under-estimated because of the species having been under-collected. Considering its wide EOO, its wide altitudinal range and the ecology of the species, a more accurate estimation of its AOO would be likely higher than the 2,000 km^2, the threshold forany threatened categories. As neither of B1 or B2 is met, *C. chocoense* is assessed as being Least Concern.

Notes – *Cyclodium chocoense* has been considered as a variety of *Cyclodium trianae* (besides the autonymic type variety) because, like that species, it has 2-pinnate laminae and somewhat reniform indusia (Smith 1986). We found, however, that these two taxa can be separated by a set of morphological characters that include degree of laminar division, number of sori, and dissection of the ultimate segments (fig. 5). The main differences are presented in the key below. Besides morphology, both species also have distinct patterns of distribution, as discussed in Distribution section. Our preliminary phylogenetic analysis (Bohn et al. in prep.) also recovered each taxon as monophyletic (three accessions of each were included), further supporting the recognition of *C. chocoense* as a distinct species. Furthermore, the existence of two morphologically distinct populations, in the east and western sides of the Andes, also suggests that they could be treated at the species level. Moran (1995) estimated that ca. 24% of the pteridophyte flora does not cross the physical barrier of the Andes, even though nearly all species are wind-dispersed. This creates an east-west pattern of distribution that is reflected in some morphological traits. This pattern has been recorded for species of *Alsophila* (Moran 1995), *Asplenium* (Murakami & Moran 1993), *Bolbitis* (Moran 2016), *Cyathea* (Moran 1991b), *Huperzia* (Øllgaard 1988), *Microgramma* (as *Solanopteris*; Moran 1992), *Stigmatopteris* (Moran & Labiak 2016), and *Trichomanes* (Moran 1995).

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