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Source: *Willdenowia*, 50(2) : 279-304

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.50.50213>

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Taxonomy, distribution and conservation status of the fern genus *Cyclodium* (*Dryopteridaceae*)

Version of record first published online on 25 June 2020 ahead of inclusion in August 2020 issue.

Abstract: We present a taxonomic revision for *Cyclodium*, a neotropical fern genus that is most diverse in the Amazon lowlands, especially in the Guianas and Venezuela, but also extending to Central America, the western Andes and southeastern Brazil. The genus belongs to the *Dryopteridaceae* and is distinguished from other genera in this family by its dimorphic fronds and peltate indusia. We recognize 13 species of *Cyclodium*, for which we provide morphological descriptions, distribution maps, an identification key, illustrations and taxonomic comments. *Cyclodium pubescens* is described as new to science, *C. meniscioides* var. *paludosum* and *C. meniscioides* var. *rigidissimum* are synonymized under *C. meniscioides*, and *C. heterodon* var. *abbreviatum* is synonymized under *C. heterodon*. Lectotypes are designated for *Aspidium confertum*, *A. guianense*, *C. rigidissimum*, *Dryopteris calophylla* and *Polystichum inerme*. We also provide an assessment on conservation status for each species following IUCN categories and criteria.

Key words: Amazon, *Aspidium*, biodiversity, conservation status, *Cyclodium*, distribution, *Dryopteridaceae*, ferns, Guianas, Neotropics, nomenclature, *Peltochlaena*, polybotryoids, taxonomy, typification

Article history: Received 15 April 2020; peer-review completed 7 May 2020; received in revised form 28 May 2020; accepted for publication 2 June 2020.

Citation: Bohn A., Matos F. B. & Labiak P. H. 2020: Taxonomy, distribution and conservation status of the fern genus *Cyclodium* (*Dryopteridaceae*). – Willdenowia 50: 279–304. doi: <https://doi.org/10.3372/wi.50.50213>

Introduction

Cyclodium C. Presl is a neotropical genus in the *Dryopteridaceae*, occurring in Panama, Trinidad, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, northern Argentina and Brazil (Smith 1986; Tryon & al. 1991; Cremers & al. 1993; Smith & Moran 1995; Kessler & al. 2018; Bohn & al. 2019a) (Fig. 1). Most of its species occur between sea level and 800 m (Smith 1986), but some species can reach up to 1900 m in elevation (pers. obs.) (Fig. 2). The centre of diversity is the Guianas, where nearly half of the species are found (Smith 1986; Bohn & al. 2019b).

Cyclodium was originally described by Presl (1836) to accommodate three species of *Aspidium* Sw.: *C. confertum* (Kaulf.) C. Presl (= *A. confertum* Kaulf.), *C. glandulosum* (Blume) C. Presl (= *A. glandulosum* Blume) and *C. meniscioides* (Willd.) C. Presl (= *A. meniscioides* Willd.). Since *Cyclodium* was described, subsequent authors have changed its status, treating it either as a section of *Aspidium* (Hooker 1862; Hooker & Baker 1867) or under *Dryopteris* Adans. (Kuntze 1891; Morton 1939). Christensen (1913) treated the four species of *Cyclodium* known to him in *Dryopteris* subg. *Stigmatopteris* (C. Chr.) C. Chr. [unranked, “group”] *Peltochlaena* Fée ex C. Chr., namely *D. abbreviata* (C. Presl) Kuntze, *D.*

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sancti-gabrielii (Hook.) Kuntze, *D. subobliquata* (Hook.) Kuntze and *D. varians* (Fée) Kuntze. In the second part of his monograph, Christensen (1920) assigned *D. abbreviata* to the *Peltochlaena* group and included *D. trianae* (Mett.) Kunze (\equiv *C. trianae* (Mett.) A. R. Sm.) in *D.* [unranked, “subgroup”] *Polystichopsis* (J. Sm.) C. Chr. along with other species that are now commonly placed in *Arachniodes* Blume, *Lastreopsis* Ching and *Polystichopsis* (J. Sm.) Holttum. In his comments, however, he suggested that *D. trianae* could actually be another member of the *Peltochlaena* group (based on laminar shape, venation, and shape of lobes). More recently, Smith (1986) accepted *Cyclodium* as a separate genus, recognizing ten species and providing the most comprehensive taxonomic treatment to date. Molecular phylogenetic studies support the recognition of *Cyclodium* as monophyletic and sister to *Polybotrya* Humb. & Bonpl. ex Willd (e.g. Schuettpelz & Pryer 2007; Liu & al. 2015; Moran & Labiak 2015, 2016) or *Maxonia* C. Chr. (Lu & al. 2019).

Morphologically, *Cyclodium* is characterized by dictyostelic rhizomes, numerous vascular bundles in the stipe, 1–2-pinnate fronds (rarely simple or more divided), rachises with grooves more or less continuous onto the pinnae adaxially, chartaceous to subcoriaceous laminae, peltate or subpeltate (somewhat reniform) indusia, monolete and bilateral spores with a folded and echinulate perine, and a basic chromosome number of $x = 41$ (Smith 1986). Most of its species are terrestrial, occurring in rain forests and gallery forests, but some species have also been recorded as epiphytic, hemiepiphytic, epipetric and rheophytic (Smith 1986; Moran & Labiak 2015).

Hybridization seems to be common in *Cyclodium*. Besides some intrageneric hybrids reported by Smith (1986), there are two intergeneric hybrids recently described from Brazil, each involving a cross of *C. meniscioides* with different species of *Polybotrya* (Engels & Canestraro 2017; Schwartzburd & al. 2018). Even though examples of hybrids in *Cyclodium* do exist, little is known about them. Further studies are needed to assess the importance of hybridization in the genus.

The most recent and comprehensive taxonomic study on *Cyclodium* was published by Smith (1986), who recognized ten species and four varieties. Since then, the genus has received little study. *Cyclodium*, with its current circumscription, has been included in several Floras and regional checklists, such as Mickel (1985) for Trinidad, Tryon & al. (1991) for Peru, Cremers & al. (1993) for the Guianas, Smith (1995) for Venezuelan Guayana, Smith & Moran (1995) for Mesoamerica, Mori & al. (1997) for French Guiana, Peña-Chocarro & al. (1999) for Mbaracayú district of Paraguay, Navarrete (2001) for Amazonian Ecuador, Murillo-Pulido & al. (2008) and Forero & Gentry (1989) for Colombia, Kessler & al. (2018) for Bolivia and Bohn & al. (2019a) for Brazil. More recently, Bohn & al. (2019b) described a new species of *Cyclodium* and proposed some taxonomic changes, such as the

recognition of *C. trianae* var. *chocoense* A. R. Sm. at the species level.

In this study, we present a taxonomic revision of *Cyclodium* that includes typifications, morphological descriptions, a key to the species, illustrations, distribution maps, conservation status assessments and comments for all species. We recognize 13 species of *Cyclodium*, including *C. pubescens* Bohn & Labiak, which is described as new.

Material and methods

We examined a total of 686 specimens from the following herbaria: BHCN, CAY, INPA, MBM, NY, P, RB, RON, UC, UFP, UPCB and US (herbarium codes according to Thiers 2018+). Images of specimens and types were examined from additional Herbaria (B, BM, BR, C, COL, F, GH, HUA, MICH, MO, UEC, UNIR and Z) through online platforms such as JSTOR Global Plants (<https://plants.jstor.org/>), Re flora (<http://reflora.jbrj.gov.br/>) and SpeciesLink (<http://splink.cria.org.br/>). Selected specimens are listed in Appendix 1 (see Supplemental content online). Only one specimen was cited per municipality or equivalent administrative division (in alphabetical order) for each country (from north to south, from east to west). The list of all studied exsiccatae is provided in Appendix 2.

In the morphological descriptions, the smallest and largest frond on each specimen were measured for length and width. We used the proximal pinnae to assess the division of laminae, as well as for the number of veins and sori. Measurements of hairs and scales were made using a stereomicroscope (AmScope 3TX). Images of hairs, scales, microscales and indusia were made with an optical microscope (LEICA MZ16) coupled with a digital camera (LEICA DFC 500). To examine the perine ornamentation, spores were transferred with dissecting needles from herbarium specimens to aluminium stubs coated with asphalt adhesive. The stubs were then sputter-coated with gold for 2 min, and spores were imaged digitally using a JEOL JSM-6360LV scanning electron microscope at the Electron Microscopy Center of Universidade Federal do Paraná.

As for the habit, although the term “hemiepiphyte” is often used for *Cyclodium* species (e.g. Smith 1986), it seems that the term “terrestrial root climber” (sensu Canestraro & al. 2014) would be more appropriate and is therefore used here. In the hemiepiphytic plants, the gametophytes would have first established on the bases of trees and then, after fertilization, produced a climbing rhizome with long feeding roots extending to the soil. On the other hand, if the gametophytes were first established on the soil, then the plants would have climbed the tree trunks later on, without losing their connection to the soil – then constituting a terrestrial root climber (Canestraro & al. 2014; Testo & Sundue 2014; Moran & Labiak 2015; Labiak & al. 2017). Because there is evidence that many of the “hemiepiphytic” plants are also reported as terres-

trial, we have treated them as “terrestrial root climbers”. It is noteworthy that, in *Cyclodium*, little is known about the origin of the gametophytes and further studies are still needed to understand the actual habit of these plants.

Geographical coordinates were obtained from herbarium labels or estimated with Google Earth. When necessary, coordinates were converted to decimal degrees using the SpeciesLink converter tool (<http://splink.cria.org.br/conversor>). The distribution maps were made using the QGIS software 3.0.3 (QGIS Development Team 2013). Shape files were obtained from the Organization for Flora Neotropica (<https://www.nybg.org/bsci/ofn/ofn.html>) and a raster file (1: 10 000 000) was obtained from Natural Earth (<http://www.naturalearthdata.com/>). Preliminary conservation status assessments were made using the GeoCAT tool (Bachman & al. 2011) with 2 km of cell width. The results were analysed according to the IUCN Red List categories and criteria (IUCN 2012).

Taxonomic treatment

We recognize 13 species of *Cyclodium*. *Cyclodium pubescens* is here described as new to science. *Cyclodium meniscioides* var. *paludosum* (C. V. Morton) A. R. Sm. and *C. meniscioides* var. *rigidissimum* (C. Chr.) A. R. Sm. are synonymized under *C. meniscioides*, and *C. heterodon* var. *abbreviatum* (C. Presl) A. R. Sm. is synonymized under *C. heterodon* (Schrad.) T. Moore. Lectotypes are designated for *Aspidium confertum*, *A. guianense* Klotzsch, *C. rigidissimum* C. Chr., *Dryopteris calophylla* C. V. Morton and *Polystichum inerme* Fée. As for conservation status, most species are assessed (IUCN 2012) as Endangered (EN), except for five species that are considered Least Concern (LC) (*C. chocoense* (A. R. Sm.) Bohn & Labiak, *C. guianense* (Klotzsch) van der Werff ex L. D. Gómez, *C. inerme* (Fée) A. R. Sm., *C. meniscioides* and *C. trianae*), one considered Vulnerable (VU) (*C. akawaiaorum* A. R. Sm.) and another Data Deficient (DD) (*C. rheophilum* A. R. Sm.).

Cyclodium C. Presl, Tent. Pterid.: 85. 1836 ≡ *Aspidium* sect. *Cyclodium* (C. Presl) Hook., Sp. Fil. 4: 36. 1862. – Type (designated by J. Smith, Hist. Fil.: 203. 1875): *Aspidium confertum* Kaulf. [= *Cyclodium meniscioides* (Willd.) C. Presl].

= *Dryopteris* [unranked, “group”] *Peltochlaena* Fée ex C. Chr. in Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 7, 10: 74. 1913. – Type (designated by A. R. Smith, Amer. Fern J. 76: 73. 1986): *Dryopteris subobliquata* (Hook.) Kuntze [= *Cyclodium inerme* (Fée) A. R. Sm.].

– *Peltochlaena* Fée, Mém. Foug. 5 (Gen. Fil.): 289. 1852, nom. inval. (Turland & al. 208: Art. 36.1(a)).

Description — Plants terrestrial, terrestrial root climber, epipetric or rheophytic. *Rhizomes* short to long-creeping, 0.3–1.5 cm in diam., with 1–20 fronds per 3 cm of length,

scaly; *rhizome scales* basifixed, lanceate to lanceolate or ovate, 0.5–15 × 0.1–1.5 mm, concolorous or bicolorous, golden to black, sometimes with a darker centre, margins entire, glandular, dentate or fimbriate. *Fronds* monomorphic to dimorphic, lanceolate to elliptic, sterile fronds 16–150 × 3.5–47 cm, fertile fronds 23.5–184 × 6.5–47 cm; *petioles* stramineous to dark brown, with scales more abundant toward base, and linear, septate, dark brown microscscales, sometimes with bacilliform, translucent, yellowish hairs, 3–59 cm long in sterile fronds, 9.5–105.5 cm long in fertile fronds, 0.8–8 mm in diam.; *petiole scales* basifixed with sinus or peltate, ovate or lanceate to lanceolate, usually spreading, sometimes appressed, 1–12 × 0.2–3 mm, concolorous or bicolorous, golden to dark brown, sometimes with a darker centre, margins dentate to fimbriate; *laminae* 1-pinnate to 3-pinnate, rarely simple, chartaceous to coriaceous, with 3–25 pairs of lateral pinnae, these 7–60 cm long in sterile fronds, 13–112 cm long in fertile fronds conform or pinnatifid apex; *rachises* stramineous to tan, sometimes flexuous, grooved adaxially, grooves glabrescent or with bacilliform, translucent, yellowish or brownish hairs c. 0.1 mm long, abaxially glabrous or with linear, septate, dark brown microscscales and hairs similar to those of grooves, sometimes with lanceate, brown scales, 1–6 mm long and rarely with acicular, multicellular, translucent hairs; *pinna stalks* 0.5–8 mm long, with bacilliform, translucent, yellowish hairs, and microscscales similar to those of rachis; *pinnae* linear to lanceolate or elliptic, bases cuneate to truncate and larger acroscopically, or asymmetric, truncate acroscopically and cuneate basiscopically, sometimes auriculate, apices acute to acuminate or rounded, margins entire to pinnatisect, sterile proximal pinnae 1–25 × 0.3–7 cm, fertile proximal pinnae 2.5–26 × 0.4–8.5 cm, sterile medial pinnae 3.8–19 × 0.4–6.5 cm, fertile medial pinnae 2.6–23 × 0.3–4 cm; *costae* abaxially glabrescent or with septate, linear, brown microscscales, sometimes with lanceate scales 1–2 mm long and bacilliform, translucent, yellowish hairs c. 0.1 mm long, rarely with acicular, multicellular, translucent hairs; *laminar tissue* glabrescent or with microscscales similar to those on costae, rarely with acicular, multicellular, translucent hairs; *veins* free or anastomosing, conspicuous or inconspicuous, when free 1–12 pairs per segment, when anastomosed 1–8 rows between costa and pinna margins, sometimes proximal veinlets united with free tips or united to next veinlets, rarely with a commissural vein; *sori* discrete or confluent, impressed or not, medial on veins, forming 1–12 rows between costae and pinna margins, biseriate between two main lateral veins; *indusia* peltate or subpeltate, circular or somewhat reniform, 0.3–2.5 mm in diam., stramineous to brown, concolorous or bicolorous (sometimes with darker or lighter margins), margins entire or ciliate, rarely with ciliate surfaces; *spores* 35–75 × 28–64 µm, perine perforate or not, broadly folded, rarely without folds, densely echinulate, sometimes ridges anastomosing, folds low or high and continuous. $x = 41$.

Key to the species of *Cyclodium*

1. Veins anastomosing 2
 - Veins free 7
2. Lamina apex pinnatifid 3
 - Lamina apex conform 4
3. Fronds hemidimorphic, sterile at base and fertile at apex; costa abaxially with scales composed of 2 or 3 cells at base, up to 0.1 mm wide ... **6. *C. heterodon***
 - Fronds monomorphic or holodimorphic; costa abaxially with scales composed of more than 3 cells at base, c. 0.3 mm wide **3. *C. calophyllum***
4. Pinna margins with a commissural vein **1. *C. akawaiaurum***
 - Pinna margins without a commissural vein 5
5. Rhizome scales dark brown to black, usually with twisted apices; proximal pinnae of sterile fronds with 1–2.5 cm wide **13. *C. varians***
 - Rhizome scales golden to dark brown, without twisted apices; proximal pinnae of sterile fronds up to 3 cm wide 6
6. Rachis, costa and lamina pubescent, hairs spreading, acicular, multicellular and translucent **9. *C. pubescens***
 - Rachis, costa and lamina glabrous or with scales only **8. *C. meniscioides***
7. Laminae 1-pinnate-pinnatisect or more divided; indusia peltate or subpeltate 8
 - Laminae 1-pinnate to 1-pinnate-pinnatifid; indusia peltate only 10
8. Rhizome scales up to 3 mm long, dark brown to black, cordiform; rachis and costae with several multicellular, acicular, translucent hairs **11. *C. seemannii***
 - Rhizome scales 5–10.5 mm long, golden to brown, linear-lanceate; rachis and costae without multicellular, acicular, translucent hairs 9
9. Proximal pinnae 2-pinnate-pinnatifid; usually more than ten rows of sori between base and apex of each segment; margin of segments crenate to pinnatifid ... **12. *C. trianae***
 - Proximal pinnae 1-pinnate-pinnatisect to 2-pinnate; usually less than nine rows of sori between base and apex of each segment; margin of segments entire or slightly crenulate at apex **4. *C. chocoense***
10. Costae abaxially with at least a few scales 11
 - Costae abaxially lacking scales 12
11. Fertile fronds 25–34 cm long; proximal pinnae less than 1 cm wide; one row of sori between costa and margin; perine of spores lacking folds **10. *C. rheophilum***
 - Fertile fronds larger than 34 cm; proximal pinnae more than 1 cm wide; 2–5 rows of sori between costa and margin; perine of spores with conspicuous folds **5. *C. guianense***
12. Rhizome scales ovate-lanceolate, bicolorous; 11–25 pairs of lateral pinnae; indusia non-ciliate **2. *C. alansmithii***

- Rhizome scales lanceate, concolorous; 9–16 pairs of lateral pinnae; indusia ciliate **7. *C. inerme***

1. *Cyclodium akawaiaurum* A. R. Sm. in Amer. Fern J. 76: 71. 1986. – Holotype: Guyana, Roraima, NW-facing slopes of Mt Roraima, vicinity of Camp 6, near end of the Waruma Trail, c. 1 mile N of the prow, 05°16'30"N, 60°44'45"W, [1280–1310] m, 27 Mar 1978, J. F. Warrington, K. Burras, J. R. Woodhams & P. J. Edwards K.E.R. 76 (UC barcode UC1484715!; isotype: K n.v.). – Fig. 1A, 4D–G, 8A.

Morphological description — Plants terrestrial or terrestrial root climber. *Rhizomes* long-creeping, 0.6–1.5 cm in diam., with 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate to lanceolate, 5–10.5 × 0.4–1(–1.5) mm, concolorous or bicolorous, golden to brown, sometimes with a darker centre, margins minutely to strongly dentate. *Fronds* subdimorphic to dimorphic, lanceolate, sterile fronds 43–57(–71.5) × 12–22 cm, fertile fronds 23.5–63(–107.5) × 9–16 cm; *petioles* stramineous to dark brown, with several scales more abundant toward base and sometimes with septate, linear, dark brown microscscales, 15–25 cm long in sterile fronds, 21–32(–48) cm long in fertile fronds, 1.5–3(–6) mm in diam.; *petiole scales* basifixed with a narrow sinus, similar to those of rhizome, 2–7(–10.5) × 0.3–1.5 mm, margins dentate to fimbriate; *laminae* 1-pinnate, subcoriaceous to coriaceous, with 8–15 pairs of lateral pinnae, gradually reduced to a conform apex, sometimes with a small auricle at base, 22–33(–47) cm long in sterile fronds, 23.5–27(–35) cm long in fertile fronds; *rachises* stramineous to tan, sometimes flexuous, adaxially with yellowish hairs, c. 0.1 mm long, abaxially glabrous or with linear, septate, dark brown microscscales and hairs similar to those of grooves, sometimes with lanceate, brown scales, composed of few cells at base, 1–2 mm long, with dentate margins; *pinna stalks* 3–6 mm long, with hairs and microscscales similar to those of rachises; *pinnae* linear to lanceolate, bases cuneate to truncate and larger acroscopically, or truncate acroscopically and cuneate basiscopically, apices acute to acuminate, sometimes rounded, margins entire to crenulate, sterile proximal pinnae 6–11(–15) × 1.7–2.2(–3.5) cm, fertile proximal pinnae 5–6(–9) × 0.5–1.1(–1.7) cm, sterile medial pinnae 6–9.5(–11.5) × 1.6–2(–3) cm, fertile medial pinnae 4–7(–9) × (0.3–)0.7–1(–1.5) cm; *costae* abaxially with microscscales similar to those of rachises and rarely with scales composed of few cells at base, 1–2 mm long; *laminar tissue* with microscscales similar to those of rachises; *veins* anastomosing, conspicuous, with 1–3 anastomoses between costae and pinna margins, sometimes proximal veinlets united with tips free or united to next veinlets, veins projecting at end, forming a commissural vein; *sori* discrete or confluent near costae, impressed, medial on veins, forming 1–3 rows between costae and pinna margins, biserial between two main lateral veins;

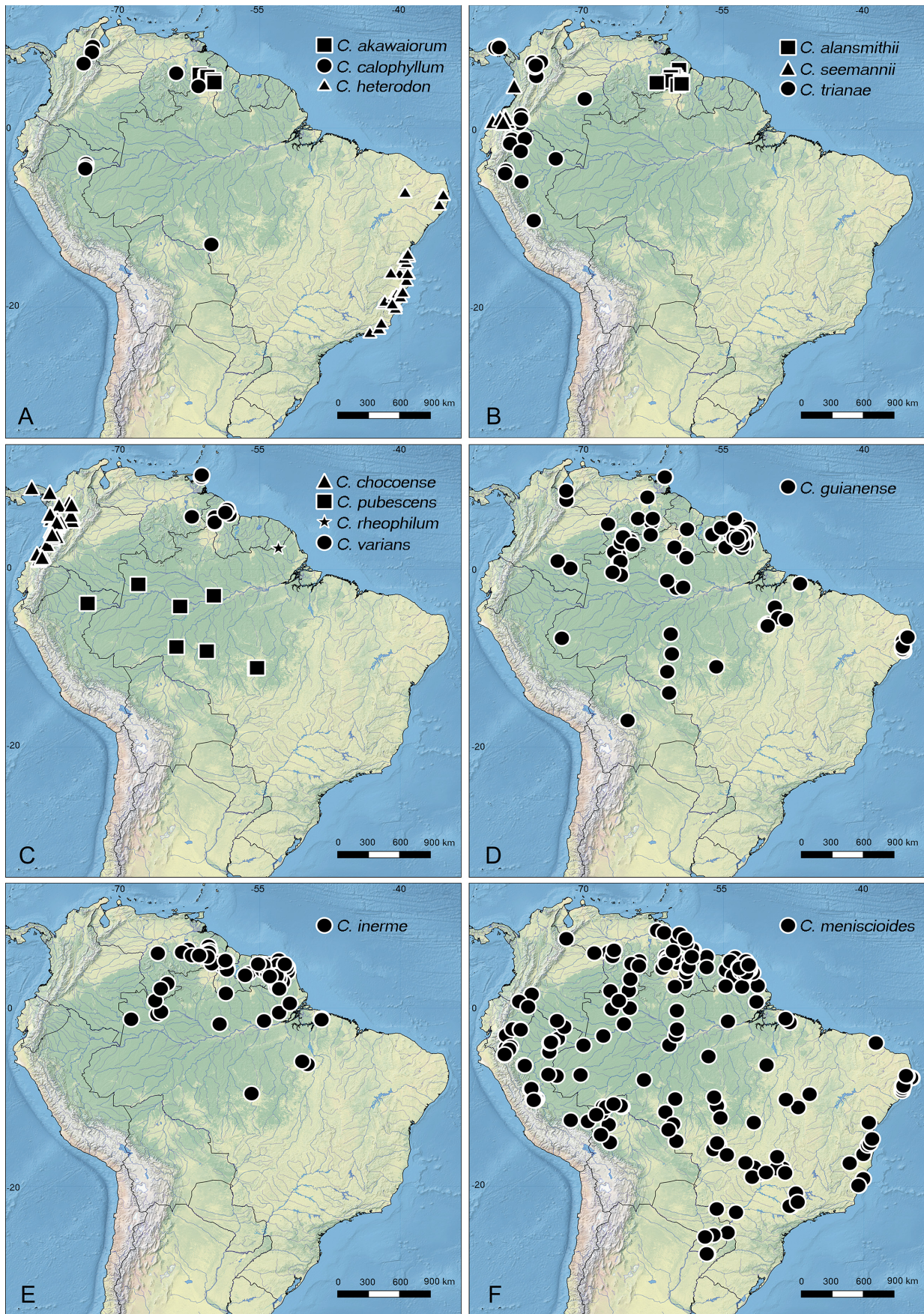


Fig. 1. Distribution of *Cyclodium* in the Neotropics. – A: *C. akawaiaorum*, *C. calophyllum*, *C. heterodon*; B: *C. alansmithii*, *C. seemannii*, *C. trianae*; C: *C. chochoense*, *C. pubescens*, *C. rheophilum*, *C. varians*; D: *C. guianense*; E: *C. inerme*; F: *C. meniscioides*.

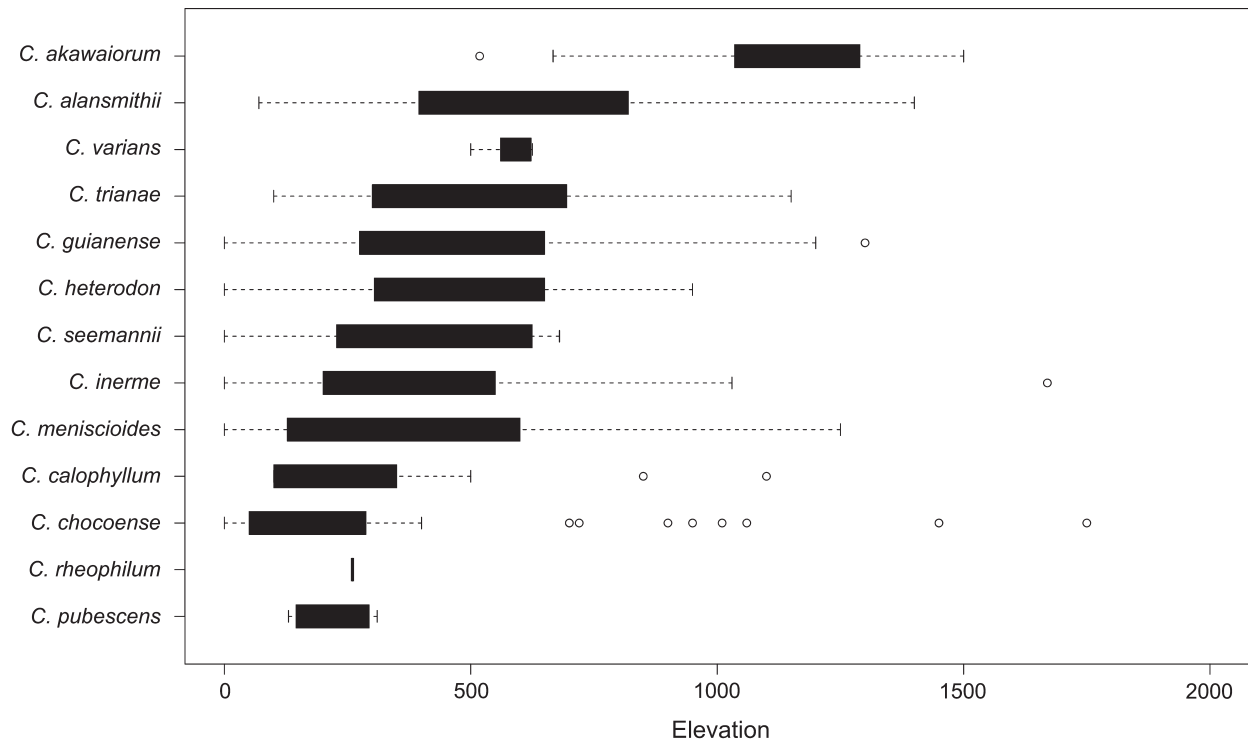


Fig. 2. Boxplot representing the elevational ranges (in metres) of the species of *Cyclodium*. The dashed lines extending from the boxes (whiskers) indicate the variability outside the upper and lower quartiles. The circles indicate the outliers.

indusia peltate, circular, 1–2.5 mm in diam., concolorous or bicolorous, stramineous to brown, sometimes with darker margins, margins entire or ciliate; *spores* 44–56 × 28–30 µm, perine perforate, broadly folded and densely echinulate, folds low and continuous.

Distribution and ecology — *Cyclodium akawaiaorum* is known from Guyana and Venezuela (Bolívar) (Fig. 1A) and grows as a terrestrial root climber on tree trunks in montane rain forests, between 670–1500 m (Fig. 2). Some specimens were also recorded as epiphytic (e.g. *Boom* 8931, NY; *Boom* 8942, NY; *Clarke* 9150, CAY; *Clarke* 10414, US; *Hahn* 5424, CAY).

Conservation status — The extent of occurrence (EOO) of *Cyclodium akawaiaorum* is 7892 km², which is less than the 20000 km² threshold of the B1 criterion of the Vulnerable category. Although the area of occupancy (AOO) was estimated as 44 km², which would suggest it could be Endangered, only one criterion was met: B2b(ii). Considering that this species occurs in non-populated areas, near the National Parks of Canaima (Venezuela), Mount Roraima (Brazil) and Kaieteur (Guyana), *C. akawaiaorum* is assessed here as Vulnerable: VU B1ab(i).

Remarks — *Cyclodium akawaiaorum* can be recognized by its 1-pinnate fronds, coriaceous laminae, conform distal pinna and anastomosing veins. It is most similar to *C. meniscioides*, from which it differs by thicker laminae (coriaceous vs chartaceous to subcoriaceous), fewer

areoles between costae and pinna margins (1–3 vs 4–7 rows) and the presence of a marginal commissural vein. Some specimens have flexuous rachises (*Henkel* 1372, CAY; *Henkel* 4349, CAY and US; *Boom* 8931 and 8942, NY), but we were unable to correlate this character with any other differences in morphology or distribution. Notwithstanding, this character seems to be plastic within some specimens, such as in *Henkel* 4349 (CAY, US). Preliminary phylogenetic analysis shows that *C. akawaiaorum* is sister to *C. meniscioides*, a relationship that was previously suggested by Smith (1986) on the basis of morphology.

2. *Cyclodium alansmithii* Bohn & Labiak in Pl. Ecol. Evol. 152: 522. 2019. – Holotype: Guyana, upper Mazaruni river basin, Mt Ayanganna, 800 m, 27 Jul 1960, S. S. Tillett, C. L. Tillett & R. Boyan 44942 (NY barcode NY02859537!; isotype: MO barcode MO1858729 n.v., US barcode US00719099!). – Fig. 1B, 6, 8B.

Morphological description — Plants terrestrial or epipetric. *Rhizomes* short-creeping, 0.3–0.5(–1) cm in diam., with 6–10 fronds per 3 cm, scaly at apex; *rhizome 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–)37–50(–63) × 8–10.5(–17) cm, fertile fronds (29–)37–65(–80) × (8–)10–14 cm; *petioles* stramineous to tan, with scattered scales, rarely with septate, lin-

ear, brown microscales, 11–18(–36) cm long in sterile fronds, 16–37(–48) cm long in fertile fronds, 1.5–3 mm in diam.; *petiole scales* basifixed with a sinus or peltate, ovate-lanceolate, appressed, 1.5–5 × 0.5–3 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly fimbriate; *laminae* 1-pinnate-pinnatifid, chartaceous, with (11–)15–25 pairs of lateral pinnae, sometimes overlapped toward apex, gradually reduced to a pinnatifid apex, (18–)23–33 cm long in sterile fronds, (13–)17–34 cm long in fertile fronds; *rachises* stramineous to tan, adaxially with yellowish hairs c. 0.1 mm long, abaxially glabrous or with brown to dark brown, scattered microscales, rarely with brown scales, 1.5–2 cm long; *pinna stalks* 1.5–3(–4) mm long, with hairs and microscales similar to those of rachis; *pinnae* linear to elliptic, bases truncate, sometimes subauriculate acroscopically, apices acute to rounded, margins undulate or crenate to pinnatifid, pinnae more dissected in fertile fronds, sterile proximal pinnae (3.8–)4.5–8 × 1.3–2 cm, fertile proximal pinnae (2.5–)3.5–6(–8) × (0.7–)1–1.4(–2) cm, sterile medial pinnae 3.8–5.3(–7) × 1–1.6 cm, fertile medial pinnae (2.6–)3–6 × 0.7–1.6 cm; *costae* abaxially with brown microscales; *laminar tissue* glabrescent, with microscales similar to those of costae; *veins* free, conspicuous, 3- or 4-furcate between costae and pinna margins, proximal veins ending below or immediately above sinus, rarely reaching pinna margins; *sori* discrete, impressed, medial on veins, forming 2 or 3(or 4) rows of sori between costae and pinna margins, biseriate between two main lateral veins; *indusia* peltate, sometimes with stalk slightly off-centre, round, 0.5–1 mm in diam., concolorous, stramineous, entire to erose margins; *spores* 47–55 × 37–40 µm, perine with few perforations, broadly folded and densely echinulate, folds low and continuous.

Distribution and ecology — *Cyclodium alansmithii* occurs from Guyana to Venezuela (Fig. 1B). Most specimens were recorded as terrestrial, but some have been recorded as epipetric. This species often occurs near creeks and on hillsides, growing on sandstone soils, between 170–1400 m (Fig. 2). One specimen (Gillespie 2288, INPA) is unusual in occurring in a “terra firme forest”, at 70–75 m.

Conservation status — The extent of occurrence (EOO) of *Cyclodium alansmithii* is 29 142 km², which exceeds the 20 000 km² threshold of the B1 criterion of the Vulnerable category, and would give it the status of Least Concern. However, the area of occupancy (AOO) was estimated at 60 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category, and the species is therefore assessed as Endangered: EN B2ab(ii).

Remarks — *Cyclodium alansmithii* is characterized by its ovate-lanceolate, bicolorous scales, 1-pinnate lami-

nae, pinnae with truncate bases and crenate margins, and free veins. It is similar to *C. inerme*, from which it differs by its ovate-lanceolate and bicolorous rhizome scales (vs lanceate and concolorous), reduced fronds (the measurements overlap, but *C. alansmithii* is typically smaller overall), pinna bases truncate on both sides (vs truncate acroscopically, cuneate basiscopically), non-ciliate indusia (vs ciliate) and spores with perforated perine (vs non-perforate). Furthermore, *C. alansmithii* occurs only in Guyana and Amazonian Venezuela, whereas *C. inerme* is known from Amazonian Venezuela and Brazil, Guyana, Suriname and French Guiana.

3. *Cyclodium calophyllum* (C. V. Morton) A. R. Sm. in Amer. Fern J. 76: 73. 1986 ≡ *Dryopteris calophylla* C. V. Morton in Bull. Torrey Bot. Club 66: 49. 1939. – **Lectotype (designated here)**: Colombia, Santander, vicinity of Barranca Bermeja, Magdalena valley, between Sogamoso and Colorado rivers, 100–500 m, 4 Sep 1934, O. L. Haught 1353 (US barcode US00067163 [image!]; isoelectotypes: GH barcode GH00342738 [image!], MICH barcode MICH1190409 [image!], US barcodes US00067161!, US00067162 [image!]). – Fig. 1A, 4H–J, 8C.

Morphological description — Plants terrestrial. *Rhizomes* long-creeping, c. 1.5 cm in diam., with 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 2–5 × 0.5–1.5 mm, concolorous, dark brown to black, margins entire. *Fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 70–75 × 25–26 cm, fertile fronds 104–116 × 31.5–38 cm; *petioles* stramineous to dark brown, with scattered scales more abundant toward base, and dark brown microscales, sometimes with hairs, 28–30 cm long in sterile fronds, 40.5–56 cm long in fertile fronds, 5–6 mm in diam.; *petiole scales* basifixed with a sinus, lanceate to lanceolate, 4–10 × 0.5–1 mm, concolorous, light brown, margins dentate; *laminae* 1-pinnate, chartaceous to coriaceous, with 10–14(–18) pairs of lateral pinnae and pinnatifid apex, 42–45 cm long in sterile fronds, 50–64(–74) cm long in fertile fronds; *rachises* tan, with yellowish hairs, and golden microscales, also with lanceate scales, 1–6 mm long, concolorous, golden to brown, margins dentate; *pinna stalks* (2–)4–6 mm, with hairs, microscales, and scales similar to those of rachises; *pinnae* linear to elliptic, bases truncate acroscopically and cuneate basiscopically, asymmetric at bases, subauriculate or auriculate acroscopically, apices acute and crenate to serrate, margins crenate to pinnatifid, sterile proximal pinnae 12–14 × 2–4 cm, fertile proximal pinnae 14–19 × 1.7–2.4 cm, sterile medial pinnae 10–13 × 1.5–2 cm, fertile medial pinnae 13–16 × 1.4–1.8 cm; *costae* abaxially with linear, golden scales, some of them with few cells at base, and golden microscales; *laminar tissue* with microscales similar to those of costae; *veins* highly variable, free to anastomosing, conspicuous, sometimes with one or two

pairs of veinlets united just below sinus or running to sinus, remaining veinlets ending before margin; *sori* discrete, not impressed, medial on veins, forming 4–6 rows between costae and pinna margins, biseriate between two main lateral veins; *indusia* peltate, circular, 1–1.5 mm in diam., bicolorous, brown with a blackish centre, margins entire; *spores* 57–75 × 42–58 µm, perine perforate, broadly folded and densely echinulate, forming anastomosing areoles, folds high and continuous.

Distribution and ecology — *Cyclodium calophyllum* is known from Venezuela, Colombia, Peru and Brazil (newly recorded here for the last two countries) (Fig. 1A). This distribution is quite unusual within the genus, with specimens occurring on borderline regions of the Amazon Basin. It is terrestrial, sometimes growing on stream margins, occurring in evergreen forests between 100–500 m (Fig. 2). One specimen (Aymard 4862, UC) is unusual because it occurs on the tepuis of Venezuela, between 850–1100 m.

Conservation status — The extent of occurrence (EOO) of *Cyclodium calophyllum* is 2 490 388 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 36 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category. Considering that this species has a small elevational range and a small AOO within its EOO, we classify it here as Endangered: EN B2ab(i).

Remarks — *Cyclodium calophyllum* can be distinguished by its 1-pinnate laminae, pinnatifid apex, irregularly anastomosing veins and presence of conspicuous scales on costae abaxially. It most resembles *C. guianense*, which differs in having subdimorphic laminae, anastomosing veins, and spores with perforate perine. It is also similar to *C. meniscioides*, from which it differs by having rhizome scales with entire margins (vs dentate to fimbriate), more pairs of lateral pinnae (10–18 vs 3–8) and pinnatifid apices (vs conform).

Although the examined specimens demonstrate clear characters to be included within the genus, we found some morphological differences between them. For example, some specimens from Colombia (e.g. Haught 1353) and Venezuela (e.g. Liesner & González 13307) have larger fronds, and the Peruvian specimens (e.g. Flores 1602 and Tuomisto 8113 and 10060) have more dissected pinnae margins. These specimens could be a product of polyploidy (as already indicated by Smith 1986), hybridization or could even represent a complex of species. However, the current data about this species, and the limited number of specimens available in herbaria, preclude us from fully understanding the morphological variation and the unusual distribution of this taxon.

The protologue of *Dryopteris calophylla* cited three syntypes at US (“[accession] nos. 1662621–3”). In 1983–1984, Smith labelled one of these specimens (US

00067163) as “lectotype”. However, this was not effectively published, and therefore the designation of a type was not achieved (Turland & al. 2018: Art. 7.10). In his monograph of *Cyclodium*, Smith (1986) cited the same three syntypes at US (“[holotype]: US, 3 sheets!”) without choosing a lectotype. Because there is nothing indicating that these syntypes are parts of a single specimen, they should be treated as duplicate specimens belonging to a single gathering from among which a lectotype must be chosen (Art. 8.3). We chose US 00067163 as the lectotype because it is the only fertile specimen in the gathering.

4. *Cyclodium chocoense* (A. R. Sm.) Bohn & Labiak in Pl. Ecol. Evol. 152: 527. 2019 ≡ *Cyclodium trianae* var. *chocoense* A. R. Sm. in Amer. Fern J. 76: 93. 1986. – Holotype: Colombia, Chocó, Corcovada region, upper Río San Juan, ridge along Yeracúí valley, 200–275 m, 24–25 Apr 1939, E. P. Killip 35287 (US barcode US01050249 [image!]; isotype: COL barcode COL000006256 [image!]). – Fig. 1C, 5N–R, 8D.

Morphological description — Plants terrestrial. *Rhizomes* short-creeping, 1–1.5 cm in diam., with 6 or 7 fronds per 3 cm, scaly; *rhizome scales* basifixed, linear to lanceate, 5–10 × 0.2–0.4(–0.6) mm, concolorous, brown to golden, apices somewhat twisted, margins entire. *Fronds* monomorphic, lanceolate-ovate, sterile fronds c. 49 × 12 cm, fertile fronds 81–97(–129) × 14–30 cm; *petioles* stramineous to dark brown, with scales more abundant toward base, also with brown microscs and yellowish hairs, c. 21 cm long in sterile fronds, (22–)45–76 cm long in fertile fronds, 2.5–5 mm in diam.; *petiole scales* basifixed with a sinus, lanceate, 4–7 × 0.5–1 mm, concolorous, brown to dark brown, margins entire; *laminae* 1-pinnate-pinnatifid to 2-pinnate, subcoriaceous to coriaceous, with 13–16(–21) pairs of lateral pinnae and apex pinnatifid, c. 28 cm long in sterile fronds, 25–48(–53) cm long in fertile fronds; *rachises* stramineous to tan, with yellowish hairs and dark brown, scattered microscs and sometimes with linear to lanceate, brown scales, with few cells at base, 0.5–1 mm long; *pinna stalks* 3–8 mm long, with hairs and microscs similar to those of rachises; *pinnae* lanceolate to elliptic, with 7–11 pairs of lateral pinnales, bases asymmetric, with first segment larger acroscopically, apices pinnatifid, sterile proximal pinnae 7 × 2.3 cm, fertile proximal pinnae 8–10 × 2.3–5 cm, sterile medial pinnae 6 × 1.5 cm, fertile medial pinnae 7–13 × 1.5–4 cm; *costae* abaxially with scales and microscs similar to those of rachises; *laminar tissue* scales and microscs similar to those of costa; *pinnules* lanceolate to elliptic, bases truncate acroscopically and frequently adnate to costae basiscopically, apices acute or rounded and sometimes crenate, margins entire to slightly undulate, 1.5–2.2 × 0.5–0.6 cm; *costules* with scales and microscs similar to those of costae; *veins* free, conspicuous, 6–12 pairs of furcate veins between costae and pinna

margins, or proximal veins, when veinlets arising from main veins 1-furcate, ending below margin basiscopically; *sori* discrete, not impressed, terminal on veins, forming 6–12 rows between costae and pinna margins, biseriate between two main lateral veins; *indusia* subpeltate to peltate, c. 1 mm in diam., concolorous, stramineous to tan, margins entire to undulate, sometimes ciliate; *spores* 44–56 × 28–30 µm, perine non-perforate, broadly folded and densely echinulate, folds low and continuous.

Distribution and ecology — *Cyclodium chocoense* is known from Panama, western Colombia (east to Cordillera Central) and western Ecuador (Fig. 1C). It shows a Mesoamerican-Chocó distribution pattern, which is found in many other groups of ferns such as *Asplenium* L. (Muramaki & Moran 1993), *Lellingeria* A. R. Sm. (Labiak 2013), *Lomariopsis* Fée (Moran 2000) and *Megalastrum* Holttum (Moran & Prado 2010). Most of the specimens are terrestrial, occurring in wet, evergreen forests, between 0–1750 m (Fig. 2), sometimes near rivers. One specimen was recorded as epiphytic (*Forero 4813*, COL).

Conservation status — Our conservation assessment shows that, although the species is threatened by area of occupancy (AOO), its extent of occurrence (EOO) is large (265 669 km²), far exceeding the 20 000 km² threshold of the B1 criterion of the Vulnerable category. Considering its wide EOO, its wide elevational range and the ecology of the species, a more accurate estimation of its AOO would be likely higher than the 2000 km² threshold of any threat category. As neither of the criteria B1 or B2 is met, *Cyclodium chocoense* is assessed here as Least Concern (LC).

Remarks — *Cyclodium chocoense* is characterized by its 1-pinnate-pinnatifid to 2-pinnate laminae and free veins. It has been considered a variety of *C. trianae* because, like that species, it has 2-pinnate laminae and a 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. Besides morphology, *C. trianae* is found only on the eastern side of the Andes, whereas *C. chocoense* occurs only on the western side. Another similar species is *C. seemannii*, which differs by its cordiform and blackish rhizome scales, more dissected laminae and presence of multicellular, acicular and translucent hairs on costae and rachises. Two specimens from Ecuador (*Hoover 3935* and *Neill 12453*, both at UC) are unusual by having more dissected laminae than typical specimens from Colombia and Panama.

5. *Cyclodium guianense* (Klotzsch) van der Werff ex L. D. Gómez in *Phytologia* 60: 371. May 1986 ≡ *Aspidium guianense* Klotzsch in *Linnaea* 20: 364. 1847 ≡ *Poly-*

stichum guianense (Klotzsch) C. Presl., *Epimel. Bot.*: 58. 1851 ['*guianense*'] ≡ *Aspidium abbreviatum* var. *guianense* (Klotzsch) Baker in Martius, *Fl. Bras.* 1(2): 464. 1870 ≡ *Dryopteris guianensis* (Klotzsch) Posth., *Ferns Surinam*: 51. 1928 ≡ *Stigmatopteris guianensis* (Klotzsch) C. Chr., *Index Filic.*, *Suppl.* 3: 174. 1934 ≡ *Cyclodium guianense* (Klotzsch) A. R. Sm. in Amer. Fern J. 76: 75. Apr–Jun 1986. – **Lectotype** (first-step designated by Smith 1986: 76; **second-step designated here**): Guyana, s.d., *M. R. Schomburgk 1157* (B barcode B200137414 [image!]; isolectotypes: B barcode B200137415 [image!]; K barcode K000590373 [image!]; UC barcode UC416949!). – Fig. 1D, 4R–T, 8E–G. = *Polypodium sancti-gabrielii* Hook., *Sp. Fil.* 4: 233. 1863 ≡ *Nephrodium sancti-gabrielii* (Hook.) Baker in Martius, *Fl. Bras.* 1(2): 469. 1870 ≡ *Dryopteris sancti-gabrielii* (Hook.) Kuntze, *Revis. Gen. Pl.* 2: 813. 1891 ≡ *Stigmatopteris sancti-gabrielii* (Hook.) C. Chr., *Index Filic.*, *Suppl.* 3: 175. 1934. – **Lectotype** (designated by Christensen 1913: 80): Brazil, Amazonas, São Gabriel da Cachoeira, Feb 1852, *R. Spruce 2153* (K barcode K000590374 [image!]; isolectotypes: BM barcodes BM000937905 [image!], BM000937906 [image!]; BR barcode BR0000006869885 [image!], BR0000006870911 [image!]; G barcode G00348381 n.v.; P barcode P00630605 [image!]).

Morphological description — Plants terrestrial, terrestrial root climber or epipetric. *Rhizomes* short-creeping, 0.5–1.5 cm in diam., with 5–14 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 4–12 × 0.4–1.5 mm, concolorous, light to dark brown, margins entire to minutely denticulate. *Fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 55–110 × 12–34 cm, fertile fronds 65–140 × (13–)20–36(–46) cm; *petioles* stramineous to tan, sometimes darker at base, with scales more abundant toward base, (12–)20–47 cm long in sterile fronds, (13–)20–84 cm long in fertile fronds, 0.8–6 mm in diam.; *petiole scales* basifixed with a narrow sinus, lanceate to ovate, 2–7 × 0.5–1.5 mm, concolorous or bicolorous, golden to light brown, with a somewhat darker centre, margins entire to slightly dentate, rarely fimbriate; *laminae* 1-pinnate to 1-pinnate-pinnatifid, chartaceous to subcoriaceous, with 16–23 pairs of lateral pinnae and apex pinnatifid, (23–)30–60 cm long in sterile fronds, (22–)30–64 cm long in fertile fronds; *rachises* stramineous to tan, adaxially with yellowish hairs, c. 0.1 mm long, abaxially with lanceate, bicolorous, golden to brown scales, or scales black and with lighter margins, 0.3–2 mm long, margins fimbriate, also with golden microscs; *pinna stalks* 1–4 mm long, with hairs, scales and microscs similar to those of rachises; *pinnae* linear to lanceolate, sometimes elliptic, bases truncate, or truncate acroscopically and cuneate basiscopically, slightly asymmetric at base, subauriculate acroscopically, apices acute to acuminate and crenate to serrate, margins undulate to crenate, sterile proximal pinnae 7–14(–17.5) ×

1.2–2.5(–3.1) cm, fertile proximal pinnae 7–18(–23) × 0.8–2.6 cm, sterile medial pinnae 7–17 × 1–2.5 m, fertile medial pinnae 8–18(–23) × 0.8–2.5 cm; *costae* abaxially with linear to lanceolate, brown scales, and light to dark brown microscs; *laminar tissue* glabrescent or with scales and microscs similar to those on *costae*, often with yellow to reddish, resinous, circular excretions; *veins* free, inconspicuous, 3–5-furcate between *costae* and margins, anterior proximal one of each segment ending in lamina below sinus, remaining veinlets ending near margin; *sori* discrete, impressed, medial to terminal on veins proximally, forming 2–4(or 5) rows of sori between *costae* and pinna margins, biseriate between two main lateral veins; *indusia* peltate, circular, 0.3–1.5 mm in diam., concolorous or bicolorous, stramineous with a darker centre, margins entire to glandular; *spores* 35–65 × 33–52 µm, perine non-perforate, broadly folded and slightly to densely echinulate, folds high and continuous.

Distribution and ecology — *Cyclodium guianense* is distributed in French Guiana, Suriname, Guyana, Trinidad, Venezuela, Colombia, Brazil and Bolivia (Fig. 1D). The occurrence in Rondônia and Mato Grosso are new records for Brazil. Most specimens are terrestrial or epipetric and frequently grow near creeks in highly humid environments. Plants occur in evergreen forests on sandy soil, between 100–1300 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium guianense* is 7812998 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 400 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category. However, considering that *C. guianense* has a large EOO, a wide elevational range and occurs in many different ecosystems, it is more likely that its AOO exceeds the threshold of any threat category. Therefore, *C. guianense* is assessed here as Least Concern (LC).

Remarks — *Cyclodium guianense* is characterized by 1-pinnate fronds, free veins, and conspicuous scales on *costae* abaxially. It is one of the most widespread species of *Cyclodium*, with a considerable variation in pinna size along its distribution, from 8 × 1.5 cm (Zuquim 237, INPA; Amazonas) to 21 × 3 cm (Prance 1825, NY and RB; Pará). Also, most specimens from Trinidad have strongly truncate pinna bases and fewer costal scales and microscs, differing from the continental specimens in these characters. Some specimens (e.g. Croizat 782, NY; Cremers 10271, CAY, UC, US) bear a thick and resinous indusial margin, but we were unable to correlate this character with any geographical patterns or other morphological characters.

Cyclodium guianense most resembles *C. calophyllum*, *C. inerme* and *C. rheophilum*. It differs from these species by the presence of conspicuous costal scales abaxially and a generally higher number of lateral pin-

nae (16–23 vs 9–16 pairs). See *C. rheophilum* for a more detailed comparison with that species.

6. *Cyclodium heterodon* (Schrad.) T. Moore, Index Fil.: 275. 1861 = *Aspidium heterodon* Schrad. in Gött. Gel. Anz. 1824: 869. 1824 = *Polystichum heterodon* (Schrad.) C. Presl, Epimel. Bot.: 58. 1851 = *Cyrtomium heterodon* (Schrad.) T. Moore ex C. Chr., Index Filic.: 197. 1905. – Lectotype (designated by Smith 1986: 79): Brazil, Bahia, [Ilhéus], “in sylvis ad Almadam et in via Felisbertia”, 1820, M. Wied s.n. (BR barcodes BR0000006977009 [image!]; isolectotypes: BR barcodes BR0000006976941 [image!], BR0000006976910 [image!], BR0000006976972 [image!]). – Fig. 1A, 3A–D, 8H, I.

= *Aspidium abbreviatum* Schrad. in Gött. Gel. Anz. 1824: 869. 1824, nom. illeg. [non *Aspidium abbreviatum* (Lam. & DC) Poir. in Lamarck & al., Encycl. Suppl. 4: 516. 1816] = *Polystichum abbreviatum* J. Sm. in London J. Bot. 1: 199. 1842, nom. illeg. [non *Polystichum abbreviatum* Lam. & DC., Fl. Franç., ed. 3, 2: 560. 1805] = *Cyclodium abbreviatum* C. Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 620. 1851 = *Nephrodium abbreviatum* (C. Presl) Fée, Mém. Foug. 5 (Gen. Filic.): 306. 1852 = *Cyrtomium abbreviatum* (C. Presl) J. Sm., Ferns Brit. Foreign, ed. 2: 304. 1877 = *Dryopteris abbreviata* (C. Presl) Kuntze, Revis. Gen. Pl. 2: 812. 1891 = *Cyclodium heterodon* var. *abbreviatum* (C. Presl) A. R. Sm. in Amer. Fern J. 76: 80. 1986. – Lectotype (designated by Smith 1986: 81): Brazil, Bahia, “ad ripas fluv. Mucuri”, 1816, M. Wied s.n. (BR barcode BR0000006870799 [image!]; isolectotypes: BR barcodes BR0000006977030 [image!], BR0000006978686 [image!]).

Morphological description — Plants terrestrial or terrestrial root climber. *Rhizomes* long-creeping, 0.5–1.6 cm in diam., with 1–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 0.5–2 × 0.3–1 mm, concolorous, golden to dark brown, margins entire to denticulate. *Fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 42–53 × 16.5–18 cm, fertile fronds 90–99 × (34–)40–45 cm; *petioles* stramineous, darker at base, with scales more abundant toward base and few reddish brown microscs, 21–25 cm long in sterile fronds, (39–)46–58 cm long in fertile fronds, 3–7 mm in diam.; *petiole scales* basifixed with a sinus, linear to lanceolate, 3–12 × 0.2–1.5 mm, concolorous, golden to brown, margins entire to denticulate; *laminae* 1-pinnate to 2-pinnate, subcoriaceous, with (9–)13–21 pairs of lateral pinnae and apex gradually or subabruptly reduced and pinnatifid, 19–28 cm long in sterile fronds, (41–)53–77(–112) cm long in fertile fronds; *rachises* stramineous to tan, with an elevated centre and two shallow lateral grooves abaxially, with yellowish hairs, c. 0.1 mm long, abaxially with linear, golden to brown scales, with few cells at base, 1–5 mm long, also with brown microscs 0.5–1 mm long; *pinna stalks*

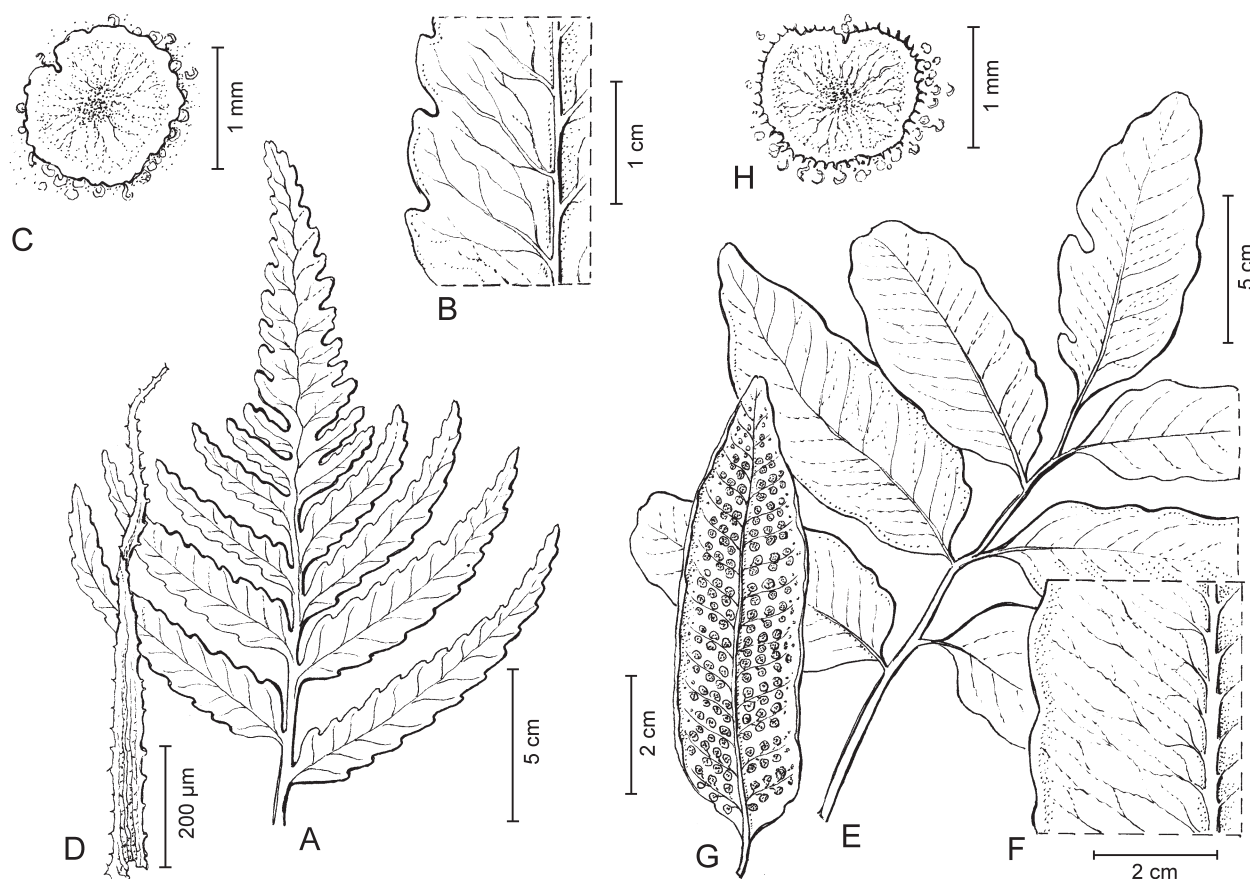


Fig. 3. A–D: *Cyclodium heterodon*; A: frond apex; B: detail of veins abaxially; C: indusium; D: rhizome scale. – E–H: *C. meniscioides*; E: frond apex; F: detail of veins abaxially; G: fertile pinna; H: indusium. – A–D from Matos & al. 228 (UPCB) and Fiaschi & al. 2938 (UPCB); E–H from Jardim & al. 4843 (UPCB) and Labiak & al. 3706 (UPCB). – Drawn by Diana Carneiro.

0.5–2 cm long, with hairs, scales, and microscales similar to those of rachises; *pinnae* linear-lanceolate to elliptic, bases cuneate or truncate acroscopically and cuneate basiscopically, sometimes asymmetric at base with an expanded auricle acroscopically, apices acute to attenuate and crenate, margins undulate to crenate or pinnatifid, sterile proximal pinnae 8–9 × 1.5–1.6 cm, fertile proximal pinnae (13–)16–24 × 2.3–3.6 cm, sterile medial pinnae (6–)7–18 × 1.4–3 cm, fertile medial pinnae 14–16 × 1.5–3.2 cm, often with sori distributed from base to middle of pinna; *costae* abaxially with linear, brown scales, with few cells at base, and brown microscales; *laminar tissue* with microscales similar to those of costae; *veins* anastomosing, conspicuous, 1–6(–8) anastomoses between costae and pinna margins, at least proximal veinlets arising from costae united; *sori* discrete, impressed, medial on veins, forming 2–6(–8) rows between costae and pinna margins, biserrate between two main lateral veins, sometimes connivent toward costae; *indusia* peltate or sometimes with a narrow sinus, circular, 0.7–1.5 mm in diam., concolorous or bicolorous, stramineous to brown, with thinner, lighter, entire margins; *spores* 51–54 × 35–43 µm, perine perforate, broadly folded and echinulate, forming anastomosing areoles, folds high and continuous.

Distribution and ecology — *Cyclodium heterodon* is endemic to Brazil, occurring in the eastern Amazon (Pará), and disjunctly in the Atlantic rain forest (Ceará, Pernambuco, Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro) (Fig. 1A). Most of the specimens are terrestrial, rarely epipetric (Lopes 184, MBM and UFP), and are often associated with shaded and humid habitats, between 0–950 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium heterodon* is 524 230 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 148 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category. Although some specimens are often recorded in or near some protected areas of Atlantic rain forest, most of these areas are disturbed by human activity, and therefore we classify this species as Endangered: EN B2b(ii,iii).

Remarks — *Cyclodium heterodon* is characterized by monomorphic to subdimorphic sterile/fertile fronds, 1-pinnate to 2-pinnate laminae, anastomosing veins (at least a few veins uniting on some pinnae) and glabrous, peltate indusia. Smith (1986) recognized two varieties for this species based on the laminar cutting and number

of anastomoses: (1) var. *heterodon*, with sinuate pinnae margins and two to three pairs of united veins between the costae and pinna margins; and (2) var. *abbreviatum*, with pinnatifid pinnae and only one pair of united veins between the costae and pinna margins. We noticed, however, that these characters are not related to geography and there is a continuum of morphotypes between the types of these two varieties. Our preliminary phylogenetic analysis has shown that *C. heterodon* is monophyletic, but its varieties are not. It most resembles *C. meniscioides*, with which it overlaps in distribution in Pará, Pernambuco, Bahia, Espírito Santo and Minas Gerais. *Cyclodium heterodon* differs from *C. meniscioides* by its monomorphic to subdimorphic fronds (vs strongly dimorphic), pinnatifid apex (vs conform), fewer anastomoses between the costae and pinna margins, and indusial margins entire (vs ciliate). Another similar species is *C. guianense*, which also occurs in Pará and Pernambuco. *Cyclodium heterodon* differs from it by having wider sterile pinnae (1.5–3.5 vs 1.2–2.5 cm wide) with entire to crenate apex (vs strongly serrate apex) and anastomosing veins (vs free veins).

Cyclodium heterodon occurs sympatrically with *C. meniscioides* and *C. guianense* in the Brazilian state of Pernambuco. Because natural hybridization seems to be common in *Cyclodium*, hybrids of intermediate morphology between these species are expected. One probable hybrid between *C. heterodon* and *C. meniscioides* is *Lopes 628* (UFP), which has the elliptic pinnae and regular anastomosing veins of *C. meniscioides* combined with the pinnatifid pinnae margins of *C. heterodon*. Another specimen, *Lopes 184* (HUEFS, MBM, UFP), is possibly a hybrid between *C. heterodon* and *C. guianense*; it has large, coriaceous pinnae (like *C. heterodon*) and free veins (like *C. guianense*). Both specimens are sterile, so no spores were seen. Further collections are needed to confirm whether hybridization is happening among these taxa.

7. *Cyclodium inerme* (Fée) A. R. Sm. in Amer. Fern J. 76: 82. 1986 \equiv *Polystichum inerme* Fée, Mém. Foug. 5 (Gen. Filic.): 281. 1852. – **Lectotype** (first-step designated by Smith 1986: 82; **second-step designated here**): French Guiana, 1850, F. M. R. Leprieur 188 (P barcode P00630602 [image!]; isolectotypes: P barcodes P 00630601 [image!], P00630603 [image!], MPU n.v.). – Fig. 1E, 4O–Q, 8J.

= *Polypodium subobliquatum* Hook., Sp. Fil. 4: 240. 1863 \equiv *Nephrodium subobliquatum* (Hook.) Baker, Syn. Fil.: 261. 1867 \equiv *Dryopteris subobliquata* (Hook.) Kuntze, Revis. Gen. Pl. 2: 813. 1891 \equiv *Thelypteris subobliquata* (Hook.) Ching in Bull. Fan Mem. Inst. Biol., Bot. 10: 254. 1941. – **Lectotype** (designated by Christensen 1913: 81): Suriname, s.d., F. W. R. Hostmann 15 (K barcode K000590375 [image!]; isolectotypes: BM barcodes BM000937907 [image!], BM000937904 [image!], P barcode P00630604 [image!]).

Morphological description — Plants terrestrial or epipetric. *Rhizomes* short-creeping, 0.5–1.2(–2) cm in diam., with (7–)9–15 fronds per 3 cm, scaly at apex; *rhizome scales* basifixed, lanceate, 3–5 \times 0.4–0.6 mm, concolorous, dark brown, margins entire or slightly fimbriate. *Fronds* monomorphic to subdimorphic, lanceolate to elliptic, sterile fronds (33–)44–72(–76) \times (11–)14–25(–29) cm, fertile fronds 50–96 \times (10–)14–28 cm; *petioles* stramineous to tan, with scales more abundant proximally, (15–)18–37(–42) cm long in sterile fronds, (15–)29–61 cm long in fertile fronds, (1–)2–3(–5) mm in diam.; *petiole scales* basifixed, lanceate, (2–)3–5 \times 0.5–0.7 mm, concolorous or bicolorous, light to dark brown, sometimes with a darker centre, margins slightly to strongly fimbriate; *laminae* 1-pinnate to 1-pinnate-pinnatifid, chartaceous to subcoriaceous, with 9–16(–21) pairs of lateral pinnae and apex pinnatifid, (17–)20–40 long in sterile fronds, (21–)32–45 cm long in fertile fronds; *rachises* stramineous, rounded abaxially, with yellowish, hairs c. 0.1 mm long, abaxially with brown microscales, also with linear scales 0.3–1 mm long; *pinna stalks* (0.5–)3–7 mm long, with hairs and microscales similar to those of rachises; *pinnae* linear to elliptic or lanceolate, bases strongly truncate acroscopically and cuneate basiscopically, asymmetric and with an expanded auricle acroscopically, apices acute to acuminate and crenate to serrate, margins undulate to crenate or pinnatifid, sterile proximal pinnae 5–12(–17) \times 1.7–3.5(–4) cm, fertile proximal pinnae (5–)7–17 \times 1.7–3.7(–4.5) cm, sterile medial pinnae 6–14 \times 1.5–3 cm, fertile medial pinnae (5–)7–12(–15) \times 1.3–3.5 cm; *costae* abaxially with brown microscales; *laminar tissue* with microscales similar to those of costae; *veins* free, conspicuous, 3–6 furcate between costae and pinna margins, proximal of each segment ending just below sinus or at sinus; *sori* discrete, impressed, median on veins proximal to costae, terminal on distal veins, forming 4–6 rows of sori on each segment, biserial between two main lateral veins; *indusia* peltate, circular, 0.5–1 mm in diam., concolorous, stramineous, entire or minutely ciliate margins; *spores* 51–68 \times 37–46 μ m, perine non-perforate, broadly folded and echinulate, folds high and continuous.

Distribution and ecology — *Cyclodium inerme* occurs in Amazonian Venezuela, Guyana, Suriname, French Guiana and Brazil (Amapá, Amazonas, Pará and north of Mato Grosso) (Fig. 1E). This species is often recorded as terrestrial, but numerous specimens are epipetric as well. One specimen was recorded as epiphytic (*Pereira 627*, BHCB). *Cyclodium inerme* is often associated with sandstone and streams, in evergreen forests, between 10–1900 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium inerme* is 2759 584 km², which would give it the status of Least Concern. The area of occupancy

(AOO) was estimated at 392 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category. However, the species has a large EOO, a wide elevational range and occurs in several ecosystems, in or near protected areas. For these reasons, this species is assessed here as Least Concern (LC).

Remarks — *Cyclodium inerme* is characterized by its short, crenate to pinnatifid pinnae, free veins and lack of conspicuous scales on the costae. It most resembles *C. alansmithii* (which see for differences). Another similar species is *C. guianense* (see for differences), which has a wider distribution, but overlaps in nearly all areas, except Colombia, Bolivia and some Brazilian states. *Cyclodium inerme* seems to be more frequent than *C. guianense* in Guyana and Venezuela.

Cyclodium inerme is relatively uniform in morphology across its distribution. Both crenate to deeply pinnatifid fronds occur in all localities, but more dissected laminae seem to be more common in Brazil, and specimens from Suriname often have shorter pinnae.

Four specimens with the same collector's number (8913) and with the same label, are probably mixed. Two are *Cyclodium inerme* (Cremers 8913, UC; Granville 8913, INPA), whereas two others are *C. guianense* (Cremers 8913, CAY; Granville 8913, NY). Another gathering (Cremers 12096, CAY) is partly *C. inerme* (barcodes 052160 and 052161) with also a fertile frond of *C. meniscioides* (barcode 052162). Lastly, one gathering (Cremers 10180) is a mixture of *C. guianense* (CAY 018483) and *C. inerme* (UC 1556093).

The protologue of *Polystichum inerme* Fée (1852) cited the following information: “Habitat in Guyanâ gallicâ (Leprieur, n. 188, Herb. clar. Mougeot.)”. According to Stafleu & Cowan (1981), the Mougeot Herbarium is now in MPU. This specimen was not located by Smith (1986), who cited an “isotype” in P. We also did not find this specimen in MPU, so we designate the specimen in P as the lectotype. There are two other duplicates of Leprieur 188 in P, and we consider these islectotypes.

8. *Cyclodium meniscioides* (Willd.) C. Presl, Tent. Pterid.: 85. 1836 ≡ *Aspidium meniscioides* Willd., Sp. Pl. 5: 218. 1810 ≡ *Nephrodium meniscioides* (Willd.) J. Sm. in J. Bot. (Hooker) 4: 188. 1841 ≡ *Dryopteris meniscioides* (Willd.) Kuntze, Revis. Gen. Pl. 2: 813. 1891 ≡ *Stigmatopteris meniscioides* (Willd.) K. U. Kramer in Proc. Kon. Ned. Akad. Wetensch. C, 71: 521. 1968. – Holotype: Brazil, s.d., J. C. von Hoffmannsegg s.n. (B barcode B-W 19737-010 [image!]). – Fig. 1F, 3E–H, 8K, L, 9A.

= *Aspidium confertum* Kaulf., Enum. Filic.: 232. 1824 ≡ *Cyclodium confertum* (Kaulf.) C. Presl, Tent. Pterid.: 85. 1836 ≡ *Nephrodium confertum* (Kaulf.) J. Sm. in J. Bot. (Hooker) 4: 188. 1841 ≡ *Dryopteris meniscioides* var. *conferta* (Kaulf.) C. V. Morton in Bull. Torrey Bot. Club 66: 51. 1939. – **Lectotype (designated**

here): French Guiana [“Cayenna”], L. C. Richard s.n. (P barcode P00630615 [image!]; islectotypes: P barcodes P00630616 [image!], P00630617 [image!], P00630618 [image!], P00630619 [image!]; probable islectotype: LE n.v.).

= *Aspidium hookeri* Klotzsch in Linnaea 20: 364. 1847, nom. illeg. [non *Aspidium hookeri* Sweet in Hort. Brit., ed. 2: 579. 1830]. – Type: “Guyana, R. Schomburgk 16174” (not found).

= *Cyclodium rigidissimum* C. Chr. in Bot. Tidsskr. 25: 79. 1903 ≡ *Cyclodium meniscioides* var. *rigidissimum* (C. Chr.) A. R. Sm. in Amer. Fern J. 76: 87. 1986. – **Lectotype (designated here)**: Guyana (“Brazil”), C. F. Appun (“A. F. M. Glaziou”) 12374 (C barcode C10020678 [image!]; islectotypes: B barcodes B200040062 [image!], B200040063 [image!], C barcodes C10020676 [image!], C10020677 [image!], G [3 sheets] n.v., P barcode P00630614 [image!]). – According to Smith (1986), the syntypes were actually collected in Guyana by Appun and later distributed by Glaziou under his number; Appun 1176 (K) may be part of the same gathering.

= *Campium molle* Copel. in Philipp. J. Sci. 37: 390. 1928 ≡ *Bolbitis mollis* (Copel.) Ching in C. Chr., Index Filic., Suppl. 3: 49. 1934. – Holotype: Brazil [“Ceylon”], s.d., G. Gardner s.n. (K barcode K000590377 [image!]). – See Hennipman (1977: 314) for discussion.

= *Dryopteris paludosa* C. V. Morton in Bull. Torrey Bot. Club 66: 50. 1939 ≡ *Stigmatopteris paludosa* (C. V. Morton) R. M. Tryon & A. F. Tryon in Rhodora 83: 136. 1981 ≡ *Cyclodium meniscioides* var. *paludosum* (C. V. Morton) A. R. Sm. in Amer. Fern J. 76: 87. 1986. – Holotype: Colombia, Dept. Antioquia, Puerto Berrío, 130–140 m, 11–13 Jan 1918, F. W. Pennell 3723 (NY barcode NY00149458 [image!]; isotype: US barcode US00067164 [image!]).

– *Aspidium rigidissimum* C. Chr. in Bot. Tidsskr. 25: 79. 1903, nom. inval. (Turland & al. 2018: Art. 36.1(b)).

Morphological description — Plants terrestrial or terrestrial root climber. *Rhizomes* short- to long-creeping, 0.5–1.5 cm in diam., with 3–5(–8) fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 4–15 × 0.4–1 mm, concolorous, light to dark brown, margins dentate to fimbriate. *Fronds* subdimorphic to dimorphic, lanceate to lanceolate; sterile fronds (34–)46–137(–150) × (14–)26–40 cm, fertile fronds (68–)75–150(–184) × (6–)14–27 cm; *petioles* stramineous to dark brown, with several scales more abundant proximally and sometimes with dark brown microscales, 22–38 cm long in sterile fronds, (28–)46–77(–121) cm long in fertile fronds, 2–6(–10) mm in diam.; *petiole scales* similar to those of rhizomes, basifixed with a narrow sinus, 3–12 × 0.2–3 mm; *laminae* rarely simple to usually 1-pinnate, subcoriaceous to coriaceous, with (1–)3–8(–13) pairs of lateral pinnae, often with a reduced pinna before dis-

tal and conform apex; 29–47 cm long in sterile fronds, (21–)32–80 cm long in fertile fronds; *rachises* stramineous to tan, adaxially with yellowish hairs 0.1–0.2 mm long, and sometimes with light to dark brown microscales 0.3–0.4 mm long, abaxially with hairs and microscales similar to those of grooves, also sometimes with scales composed of few cells at base, c. 2 mm long; *pinna stalks* 2–4(–6) mm long, with hairs, microscales, and sometimes scales similar to those of rachises; *pinnae* lanceate to lanceolate, sometimes ovate, bases cuneate or truncate, sometimes slightly asymmetric, truncate and larger acroscopically, cuneate basiscopically, apices acute to acuminate, margins entire to crenate, fertile more dissected, sterile proximal pinnae 1.2–25 × 3.5–7 cm, fertile proximal pinnae 7–17(–26) × (0.7–)1.5–3.5(–8.5) cm, sterile medial pinnae 11–19 × 3.5–6.5 cm, fertile medial pinnae (5–)11–16 × 1–3.5 cm; *costae* abaxially with dark brown microscales, and light to dark brown scales, composed of few cells at base, c. 1 mm long; *laminar tissue* with scales and microscales similar to those of costae; *veins* anastomosing, inconspicuous, with 4–7 areoles between costae and pinna margins, sometimes from united veinlets there is a free tip, or tip is united with next veinlets; *sori* discrete, impressed, medial on veins, forming 4–7 rows between costae and pinna margins, biseriate between two main lateral veins, frequently confluent at maturity with two proximal ones united; *indusia* peltate, circular, 1–1.5 mm in diam., concolorous, light to dark brown, margins entire, or minutely to densely ciliate; *spores* 53–63 × 36–47 µm, perine perforate, broadly folded and densely echinulate, forming anastomosing areoles, folds high and continuous.

Distribution and ecology — *Cyclodium meniscioides* has the widest distribution of any species of *Cyclodium*, occurring from Colombia to Paraguay and NE Argentina, Trinidad, Venezuela, Guyana, Suriname, French Guiana and nearly all of Brazil (Fig. 1F). This species is often recorded as terrestrial or climbing on tree trunks up to 1–2 m high. Also, some specimens have been cited as epiphytic (e.g. Tillett 44945, NY; Morales 1205, UC; Granville 2894, CAY; Prance 15945, INPA; Croat 18579, UC) or epipetric (*Cremers* 10851, UC; *Granville* 15488, CAY; *Delnatte* 722, CAY). In general, *C. meniscioides* occurs in humid and shaded forests, between 0–1250 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium meniscioides* is 12 226 986 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 852 km², which is less than the 2000 km² threshold of the B2 criterion of the Vulnerable category. Because this species is widely distributed, has a large EOO, a wide elevational range and occurs in many different ecosystems, it is more likely that its AOO exceeds the threshold of any threat category. *Cyclodium meniscioides* is therefore assessed here as Least Concern (LC).

Remarks — *Cyclodium meniscioides* is characterized by its subdimorphic to dimorphic 1-pinnate fronds, anastomosing veins and peltate indusia with ciliate margins. It mostly resembles *C. heterodon* and *C. akawaorum* (which see for differences). This species is highly variable in morphology, and nearly all characters seem to be plastic and not restricted to a particular geographical region. In other words, we found no correlation between these morphological characters and the geographical areas where *C. meniscioides* occurs.

For the varieties recognized by Smith (1986) for *Cyclodium meniscioides* (i.e. *C. meniscioides* var. *paludosum* and *C. meniscioides* var. *rigidissimum*), we found a considerable number of intermediates between morphological extremes, even in a same geographical region. Therefore, we here subsume these varieties under *C. meniscioides*.

One specimen from Brazil (*Salino* 412b, UC) is noteworthy for having smaller and simple sterile and fertile fronds, an unusual character in this species. The plasticity of size and number of lateral pinnae can be seen in two specimens from French Guiana (*Bordenave* 7248, CAY). In these specimens the petiole length of the sterile fronds varies almost 20 cm, and the number of lateral pinnae varies from 1 to 6 pairs.

Recently, two intergeneric hybrids involving this species were described: one from the southern Amazon, with *Polybotrya goyazensis* Brade (×*Cyclobotrya telespirensis* Engels & Canestraro) (Engels & Canestraro 2017), and another from the state of Ceará, with *P. osmundacea* Humb. & Bonpl. ex Willd. (×*Cyclobotrya amalgamata* Schwartsb. & Canestraro) (Schwartzburd & al. 2018). According to Bohn & al. (unpublished data), *Cyclodium meniscioides* is monophyletic and sister to *C. akawaorum*, a clade supported by dimorphic fertile/sterile fronds and conform distal pinnae.

Smith (1986) included *Soromanes integrifolium* Fée [= *Polybotrya serratifolia* (Fée) Klotzsch] in the synonymy of *Cyclodium meniscioides* because the illustration in the protologue of *S. integrifolium* showed a sterile frond of *C. meniscioides* mixed with a fertile frond of *P. serratifolia*. When Moran (1987) designated only the fertile frond as lectotype of *S. serratifolium*, he disregarded the admixture and fixed the application of the name concerned (Turland & al. 2018: Art. 8.2).

9. *Cyclodium pubescens* Bohn & Labiak, sp. nov. – Holotype: Brazil, Mato Grosso, Itaúba, Resgate de FLORA da UHE Colíder, estrada de acesso para Lote F de supressão, 18 Aug 2016, M. E. Engels & L. M. S. Aquino 4763 (MBM barcode MBM382725!; isotypes: HERBAM n.v., TANG n.v.). – Fig. 1C, 7, 9B.

Diagnosis — *Cyclodium pubescens* resembles *C. meniscioides* by having 1-pinnate laminae, conform apices and anastomosing veins. It differs from that species by the presence of abundant, erect hairs on laminar tissue and veins.

Morphological description — Plants terrestrial or terrestrial root climber. *Rhizomes* short-creeping, 0.8–1.5 cm in diam., with 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 5–15 × 0.2–0.6 mm, bicolorous, light to dark brown, with a discrete darker centre, margins slightly dentate to fimbriate. *Fronds* dimorphic, lanceate to lanceolate; sterile fronds (56–)96–118 × (18–)27–44 cm, fertile fronds (82–)123–144 × 18–26 cm; *petioles* stramineous to tan, with scales more abundant toward base, and dark brown microscs, also with acicular, erect, septate, translucent hairs, 0.5–1 mm long, (26–)33–52 cm long in sterile fronds, (46–)61–91 cm long in fertile fronds, 2–6 mm in diam.; *petiole scales* similar to those of rhizomes, basifixed with a narrow sinus, 3–12 × 0.2–0.5 mm, concolorous; *laminae* 1-pinnate, subcoriaceous to coriaceous, with 5–9(–12) pairs of lateral pinnae, sometimes with a reduced pinna before distal and conform apex, (28–)34–60 cm long in sterile fronds, (21–)34–79 cm long in fertile fronds; *rachises* stramineous to tan, adaxially with yellowish hairs 0.1–0.2 mm long, and light to dark brown microscs 0.3–0.4 mm long, abaxially with several hairs and sometimes with microscs similar to those of grooves, also with linear scales c. 2 mm long, these comprising a few cells at base; *pinna stalks* 2–4(–6) mm long, with hairs, microscs, and scales similar to those of rachises; *pinnae* lanceate to lanceolate, slightly asymmetric, truncate acroscopically and cuneate basiscopically, apices acute to acuminate, margins entire to crenate, fertile more dissected, sterile proximal pinnae 13–16(–23) × 3.5–5.5 cm, fertile proximal pinnae 8–12 × 1.5–3 cm, sterile medial pinnae 12–15(–18) × 3.5–5 cm, fertile medial pinnae 9–12 × 1.5–3 cm; *costae* abaxially with hairs and brown microscs similar to those of rachises, also with light to dark brown scales, composed of few cells at base, c. 1 mm long; *laminar tissue* with hairs and microscs similar to those of costae; *veins* anastomosing inconspicuous, with 4–6 anastomoses between costae and pinna margins, sometimes veins with a free tip distal to united veinlets, or vein-tips united with most distal veinlets; *sori* discrete, not impressed, medial on veins, forming 4–6 rows of sori between costae and pinna margins, biseriate between two main lateral veins, often confluent; *indusia* peltate, 0.5–1.5 mm in diam., concolorous, light to dark brown, margins densely ciliate, often with cilia covering outer surface; *spores* 60–71 × 48–64 µm, perine perforate, broadly folded and densely echinulate, forming anastomosing areoles, folds high and continuous.

Distribution and ecology — *Cyclodium pubescens* occurs in the western portion of the Amazon basin, in Peru (Loreto) and Brazil (Amazonas, Rondônia and Mato Grosso) (Fig. 1C). All specimens are terrestrial, with the exception of *Cid* 3722 (INPA), which was recorded as epiphytic on a living tree. This species often grows on wet soils composed of sand or clay, near streams, between 130–310 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium pubescens* is 977 660 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 36 km², which is less than the 500 km² threshold of the B2 criterion of the Endangered category. Moreover, this species is often recorded from transitional areas between the Amazon rain forest and the Brazilian Cerrado. These areas are currently considered the “deforestation frontier”, on the southern border of the Amazon. For these reasons, *C. pubescens* is assessed here as Endangered: EN B2b(ii,iii).

Remarks — *Cyclodium pubescens* is characterized by its anastomosing veins and 1-pinnate, pubescent fronds, with several acicular, multicellular, translucent hairs on the laminae, costae and rachises. It most resembles *C. meniscioides* in laminar size and venation, but hairs are lacking in *C. meniscioides*. The only other species of *Cyclodium* that is pubescent (with acicular, multicellular hairs that are distinct from the bacilliform hairs found in all species) is *C. seemannii*, which differs from *C. pubescens* by cordiform (vs lanceate) rhizome scales, 1-pinnate-pinnatisect to 3-pinnate (vs 1-pinnate) laminae and free (vs anastomosing) veins.

10. *Cyclodium rheophilum* A. R. Sm. in Amer. Fern J. 76: 88. 1986. – Holotype: French Guiana, Upper Oyapock, Mt St Marcel, torrent on the S slope, 260 m, 27 Jul 1975, J.-J. de Granville 2586 (F barcode F0075677F [image!]; isotypes: K barcodes K000590378 [image!], K000590379 [image!], NY barcode NY00842334 [image!], P barcode P00630613 [image!], UC barcode UC1542815!, Z n.v.). – Fig. 1C, 4A–C, 9C.

Morphological description — Plants epipetric or rheophytic. *Rhizomes* short-creeping, 0.3–0.7 cm in diam., with 8–12(–20) fronds per 3 cm, scaly at apices; *rhizome scales* basifixed, thin, lanceolate, 2–4 × 0.5–1 mm, concolorous, light brown, margins entire to slightly fimbriate. *Fronds* monomorphic to subdimorphic, linear or lanceolate to elliptic, sterile fronds 16–21(–29) × 3.5–5(–9) cm, fertile fronds (25–)30–34 × 6–9 cm; *petioles* stramineous to tan, with scattered scales and several reddish brown dots, 3–5(–8) cm long in sterile fronds, 9–10 cm long in fertile fronds, 0.5–1.5 mm in diam.; *petiole scales* basifixed with a sinus, ovate-lanceolate, appressed, 1–2.5 × 0.3–1 mm, concolorous, light brown, margins thin and entire to fimbriate; *laminae* 1-pinnate, chartaceous, with 11–18(–21) pairs of lateral pinnae and pinnatifid apex, 7–16(–20) cm long in sterile fronds, 20–24 cm long in fertile fronds; *rachises* stramineous to tan, rounded abaxially, with yellowish, hairs, c. 0.1 mm long, abaxially with brown to dark brown microscs, also with lanceate, brown scales, with few cells at base, 0.5–2 mm long; *pinna stalks* 0.5–2 mm long, glabrescent or with microscs similar to those of rachises; *pinnae* linear to elliptic, bases truncate acroscopically and

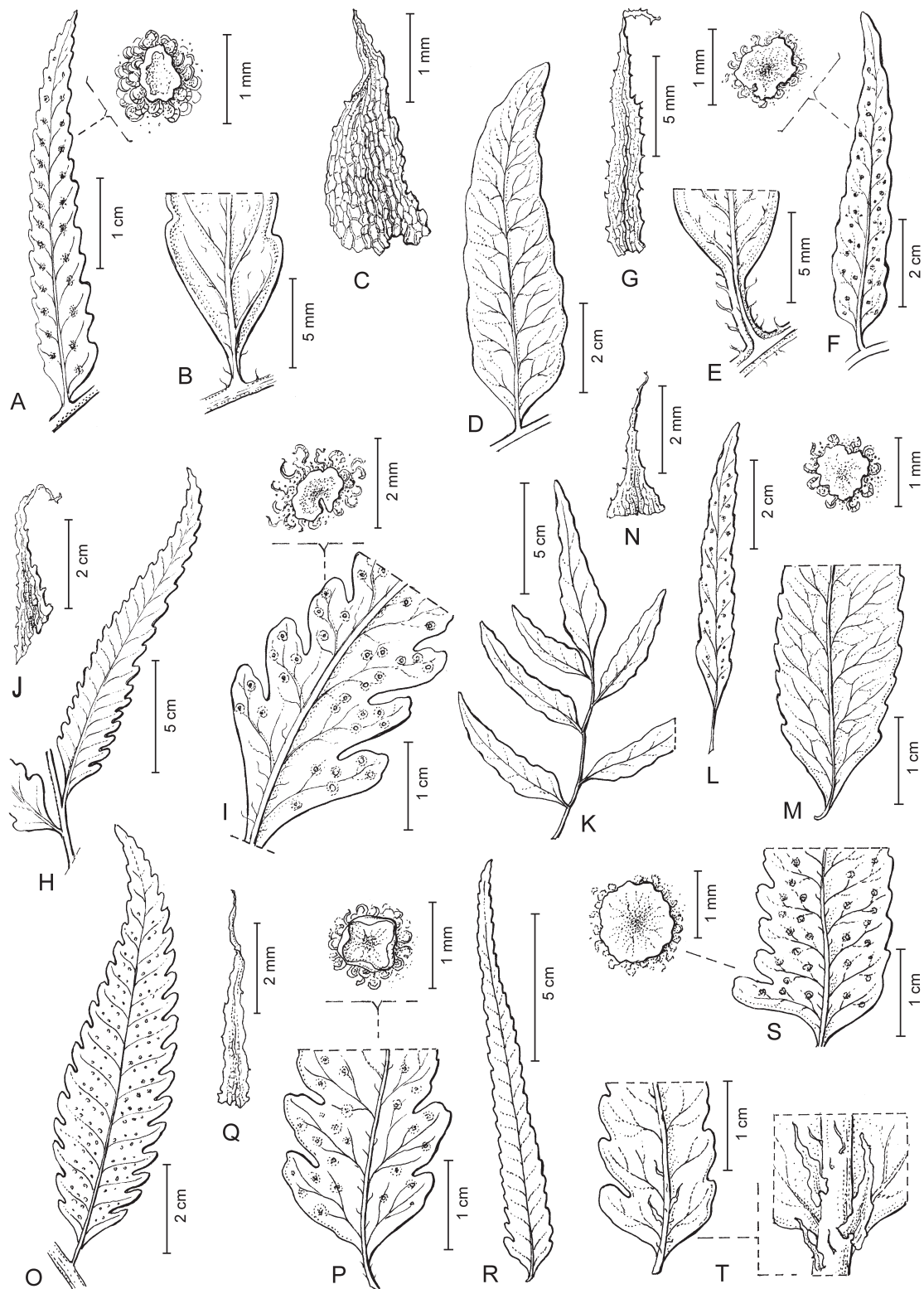


Fig. 4. A–C: *Cyclodium rheophilum*; A: fertile pinna with detail of indusium; B: detail of scales of pinnule and costa abaxially; C: rhizome scale. – D–G: *C. akawaiorum*; D: sterile pinna; E: detail of scales of pinna stalk and costa abaxially; F: fertile pinna with detail of indusium; G: rhizome scale. – H–J: *C. calophyllum*; H: sterile pinna; I: fertile pinna with scales and detail of indusium; J: rhizome scale. – K–N: *C. varians*; K: frond apex; L: fertile pinna with detail of indusium; M: sterile pinna; N: rhizome scale. – O–Q: *C. inerme*; O: fertile pinna; P: fertile pinna with detail of indusium; Q: rhizome scale. – R–T: *C. guianense*; R: sterile pinna; S: fertile pinna with detail of indusium; T: sterile pinna with detail of costal scales. – A–C from Granville 15523 (NY); D–G from Clarke & al. 9150 (CAY) and K. E. R. 1207 (UC); H–J from Stergios 10604 (UC) and Liesner & González 13307 (UC); K–N from Clarke & al. 9964 (US) and 10037 (NY); O–Q from Cremers 7828 (CAY) and Granville & al. 12708 (CAY); R–T from Cremers & al. 10271 (UC) and Costa 33 (UPCB). – Drawn by Diana Carneiro.

cuneate basiscopically, sometimes asymmetric at base, narrowly subauriculate acroscopically, apices acute to obtuse, margins crenate to dentate, sterile proximal pinnae $1.5\text{--}5 \times 0.3\text{--}0.7$ cm, fertile proximal pinnae $2.7\text{--}4.8 \times 0.4\text{--}0.5$ cm, sterile medial pinnae $2.5\text{--}5 \times 0.4\text{--}0.6$ cm, fertile medial pinnae $3.2\text{--}5 \times 0.45\text{--}0.5$ cm; *costae* with light to dark brown microscales; *laminar tissue* with microscales similar to those of *costae*, also abaxially sometimes with several reddish, resinous dots; *veins* free, inconspicuous, simple to 1-furcate between *costae* and pinna margins; *sori* discrete, impressed, median on veins, forming 1 row of sori between *costae* and pinna margins, uniseriate between two main lateral veins; *indusia* reniform, $0.5\text{--}0.8$ mm in diam., bicolorous, stramineous, margins darker and glandular; *spores* $59\text{--}64 \times 39\text{--}41$ μm , perine perforate, not folded, densely echinulate.

Distribution and ecology — *Cyclodium rheophilum* is known only from French Guiana (Fig. 1C). As its name suggests, this species is rheophytic, growing on rocks associated with creeks in rain forests, at 260 m (Fig. 2).

Conservation status — *Cyclodium rheophilum* is known from only two gatherings, which suggests it is a rare and narrow endemic to French Guiana. Because there is insufficient information for a proper assessment of conservation status, we here classify this species as Data Deficient (DD).

Remarks — *Cyclodium rheophilum* is characterized by the reduced fronds, conspicuous scales on *costae*, and peltate indusia with minutely glandular margins. It is also the only rheophytic species in the genus.

Among the species that occur in French Guyana, the most similar ones are *Cyclodium guianense* and *C. inerme*. *Cyclodium rheophilum* differs from *C. guianense* by its smaller fronds ($16\text{--}34$ vs $55\text{--}140$ cm long), and spores with non-folded and perforate perine (vs folded and non-perforate in *C. guianense*). Some specimens of *C. guianense* are more similar to *C. rheophilum* in having reduced fronds and narrower pinnae, but their spores agree with typical *C. guianense*. From *C. inerme*, *C. rheophilum* differs by the presence of costal scales and by its non-folded and perforated perine (vs folded and non-perforated). *Cyclodium rheophilum* was included in a phylogeny of the genus by Bohn & al. (unpublished data), where it was recovered in an unresolved clade with *C. guianense* (which see for further discussion).

11. *Cyclodium seemannii* (Hook.) A. R. Sm. in Amer. Fern J. 76: 89. 1986 \equiv *Aspidium seemannii* Hook., Sp. Fil. 4: 34. 1862 [*‘Seemannii’*] \equiv *Polystichum seemannii* (Hook.) J. Sm., Hist. Fil.: 220. 1875 [*‘Semani’*] \equiv *Dryopteris seemannii* (Hook.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. – Lectotype (designated by Smith 1986: 89): Colombia, Dept. Chocó, Bay of Ardita, Dec 1947, B. C. Seemann s.n. (K barcode K000590380 [image!]; isolec-

totypes: P barcodes P00630611 [image!], P00630612 [image!]). – Fig. 1B, 5A–G, 9D.

Morphological description — Plants terrestrial. *Rhizomes* short-creeping, $0.5\text{--}1$ cm in diam., with 7–14 fronds per 3 cm, scaly; *rhizome scales* basifixed with a sinus, thickened, slightly raised and overlapping, sometimes with a creased centre, cordiform, $1.5\text{--}3 \times 0.3\text{--}0.7$ mm, concolorous, dark brown to black, margins entire. *Fronds* monomorphic to subdimorphic, lanceolate-ovate, sterile fronds $58\text{--}83 \times 22\text{--}40$ cm, fertile fronds $102\text{--}110 \times 24\text{--}65$ cm; *petioles* stramineous to tan, with scattered scales and golden to light brown microscales, also with yellowish hairs, $25\text{--}50$ cm long in sterile fronds, $65\text{--}73$ cm long in fertile fronds, $2\text{--}4$ mm in diam.; *petiole scales* similar to those of rhizomes $1.5\text{--}3 \times 0.3\text{--}0.6$ mm, light brown to brown; *laminae* 1-pinnate-pinnatissect to 3-pinnate, subcoriaceous, with 12–18 pairs of lateral pinnae, apex gradually reduced and pinnatifid, $27\text{--}34$ cm long in sterile fronds, $47\text{--}75$ cm long in fertile fronds; *rachises* stramineous to tan, rounded abaxially, adaxially with several blackish hairs c. 0.1 mm long, abaxially with light brown microscales, and lanceate to cordate, dark brown scales, $1\text{--}2$ mm long, and some smaller scales with few cells at base, $0.3\text{--}0.8$ mm long, also with yellowish hairs, and several multicellular, acicular, translucent hairs; *pinna stalks* $5\text{--}8$ mm long, with hairs and microscales similar to those of rachises; *pinnae* linear to lanceolate or elliptic, with 8–14 pairs of lateral pinnules, bases asymmetric, with first segment larger and arising acroscopically, sometimes at base with an expanded auricle acroscopically, often 3-pinnate, apices pinnatifid, sterile proximal pinnae $12\text{--}19(\text{--}22) \times 4.5\text{--}7.5$ cm, fertile proximal pinnae $(8\text{--})14\text{--}24 \times (2.7\text{--})5\text{--}8$ cm, sterile medial pinnae $9\text{--}14 \times 2\text{--}3$ cm, fertile medial pinnae $(7\text{--})11\text{--}14 \times (1.5\text{--})2.5\text{--}3.5$ cm; *costae* abaxially with hairs, scales, and microscales similar to those of rachises, sometimes with sessile, globose, yellowish to reddish glands; *laminar tissue* with hairs, scales, microscales, and glands similar to those of *costae*; *pinnules* elliptic to slightly spatulate, bases larger acroscopically and cuneate basiscopically, asymmetric at base with an expanded auricle acroscopically, apices obtuse to rounded and crenate to serrate, margins crenate to pinnatifid, sterile proximal pinnules $2\text{--}3 \times 0.7\text{--}1$ cm, fertile proximal pinnules $1.5\text{--}4 \times 0.5\text{--}1.5$ cm; *costules* abaxially with reddish brown microscales, these more frequent proximally of pinnule; *veins* free, inconspicuous, 7–10 furcate between *costae* and pinna margins; *sori* discrete, inconspicuous, terminal on veins, forming 6–10 rows of sori between *costae* and pinna margins, uniseriate or biseriate between two main lateral veins; *indusia* subpeltate to peltate, $1\text{--}2$ mm in diam., concolorous, stramineous, margins and surfaces with several glandular trichomes; *spores* $52\text{--}54 \times 39\text{--}44$ μm , perine non-perforate or not, broadly folded and densely echinulate, folds high and continuous.

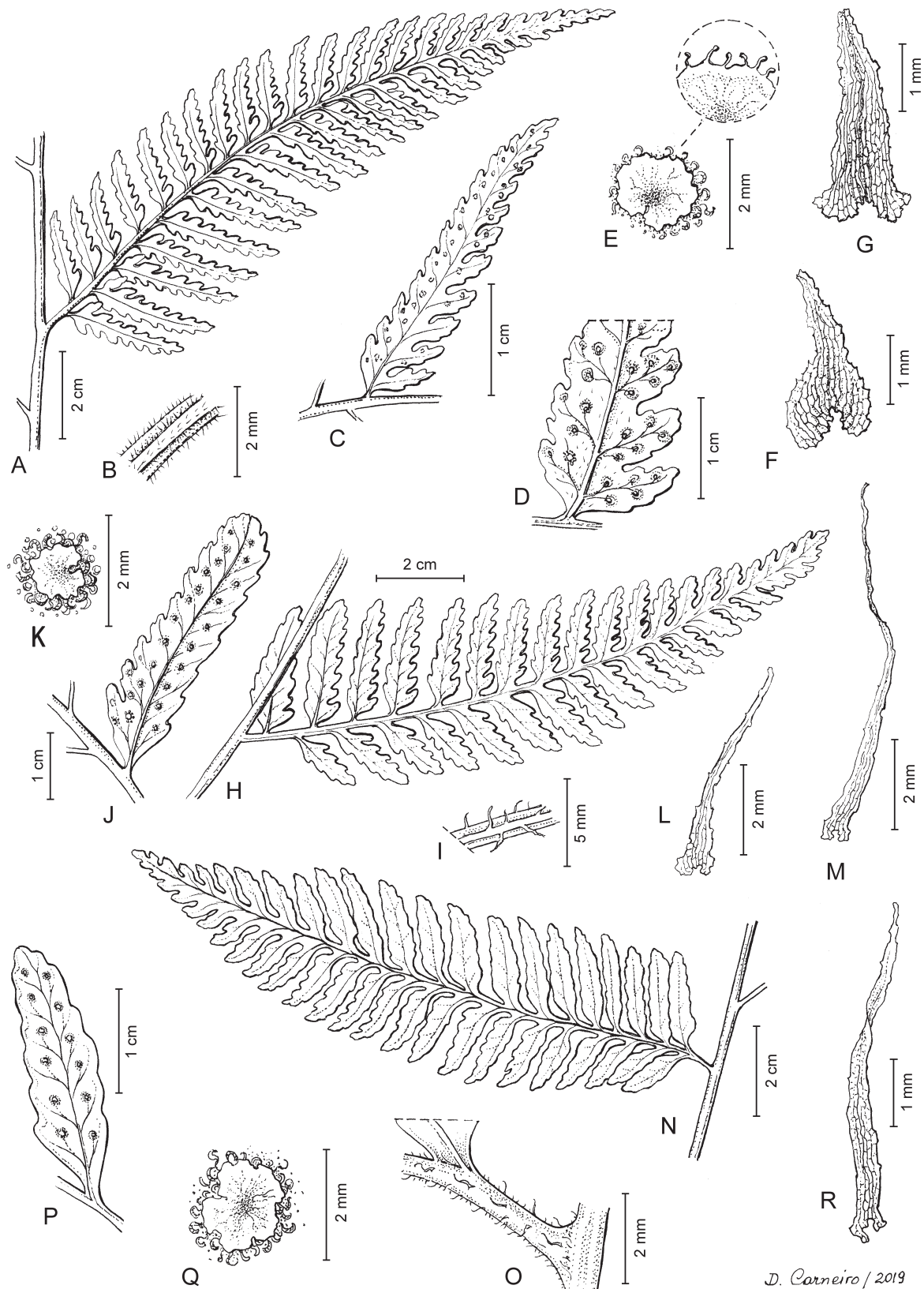


Fig. 5. A–G: *Cyclodium seemannii*; A: sterile frond; B: detail of costa abaxially; C: fertile pinnule; D: fertile pinnule with detail of veins and soral distribution; E: indusium; F: petiole scale; G: rhizome scale. – H–M: *C. trianae*; H: sterile pinna; I: detail of costa abaxially; J: fertile pinnule; K: indusium; L: petiole scale; M: rhizome scale. – N–R: *C. chocoense*; N: sterile pinna; O: detail of pinna stalk; P: fertile pinnule; Q: indusium; R: rhizome scale. – A–G from Øllgaard 99163 (P) and Mexia 8452 (US); H–M from Rojas & al. 102 (NY) and Rodríguez & al. 4210 (NY); N–R from Alverson & al. 143 (NY) and Hoover & al. 3935 (UC). – Drawn by Diana Carneiro.

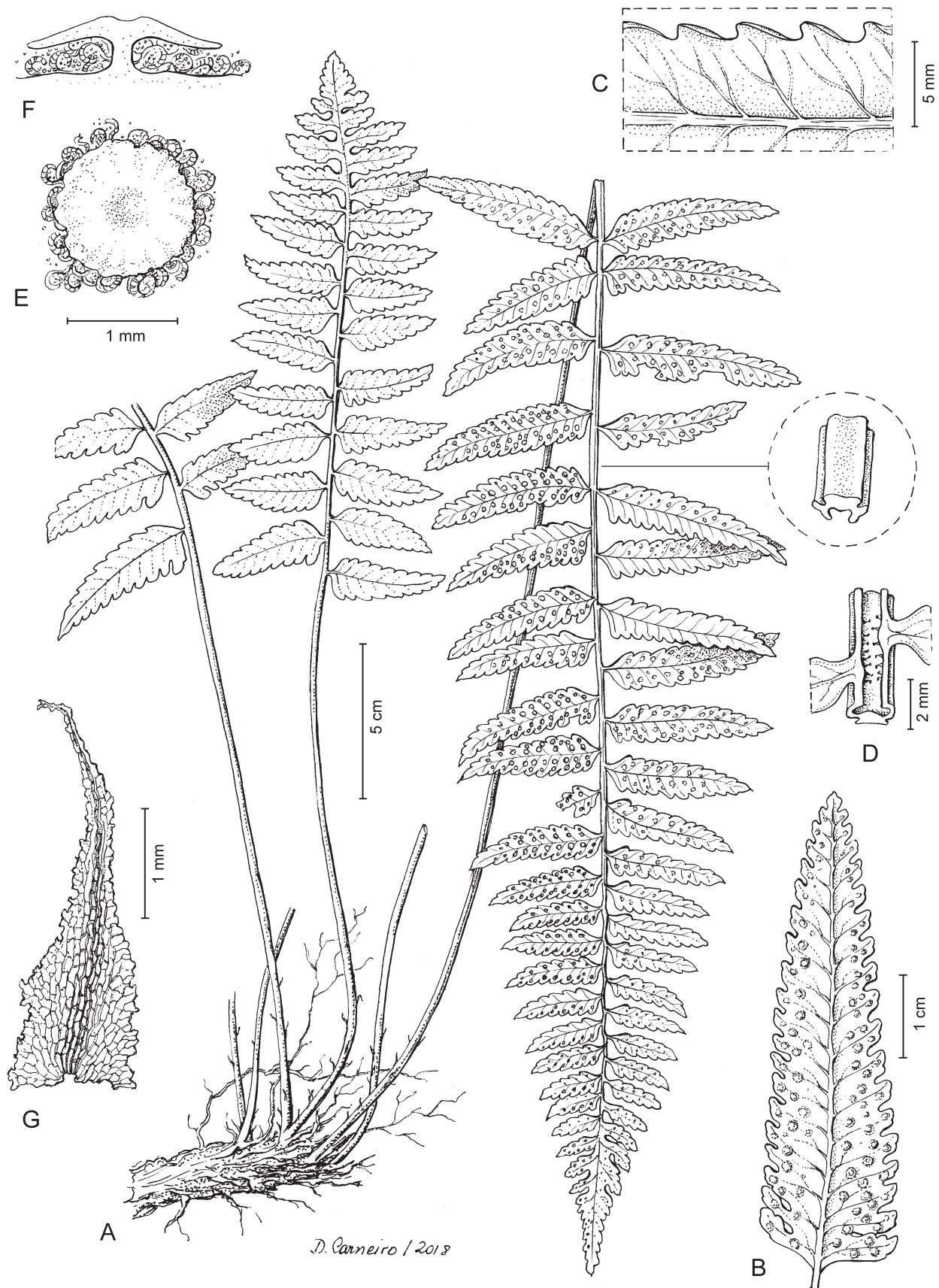


Fig. 6. A–F: *Cyclodium alansmithii*; A: habit with detail of rachis abaxially; B: fertile pinna; C: detail of veins; D: detail of rachis adaxially; E: indusium; F: lateral view of peltate indusium and sporangia. – A–F from Tillet 44942 (NY, US). – Drawn by Diana Carneiro; originally published in Bohn & al. (2019b: 523, fig. 1).

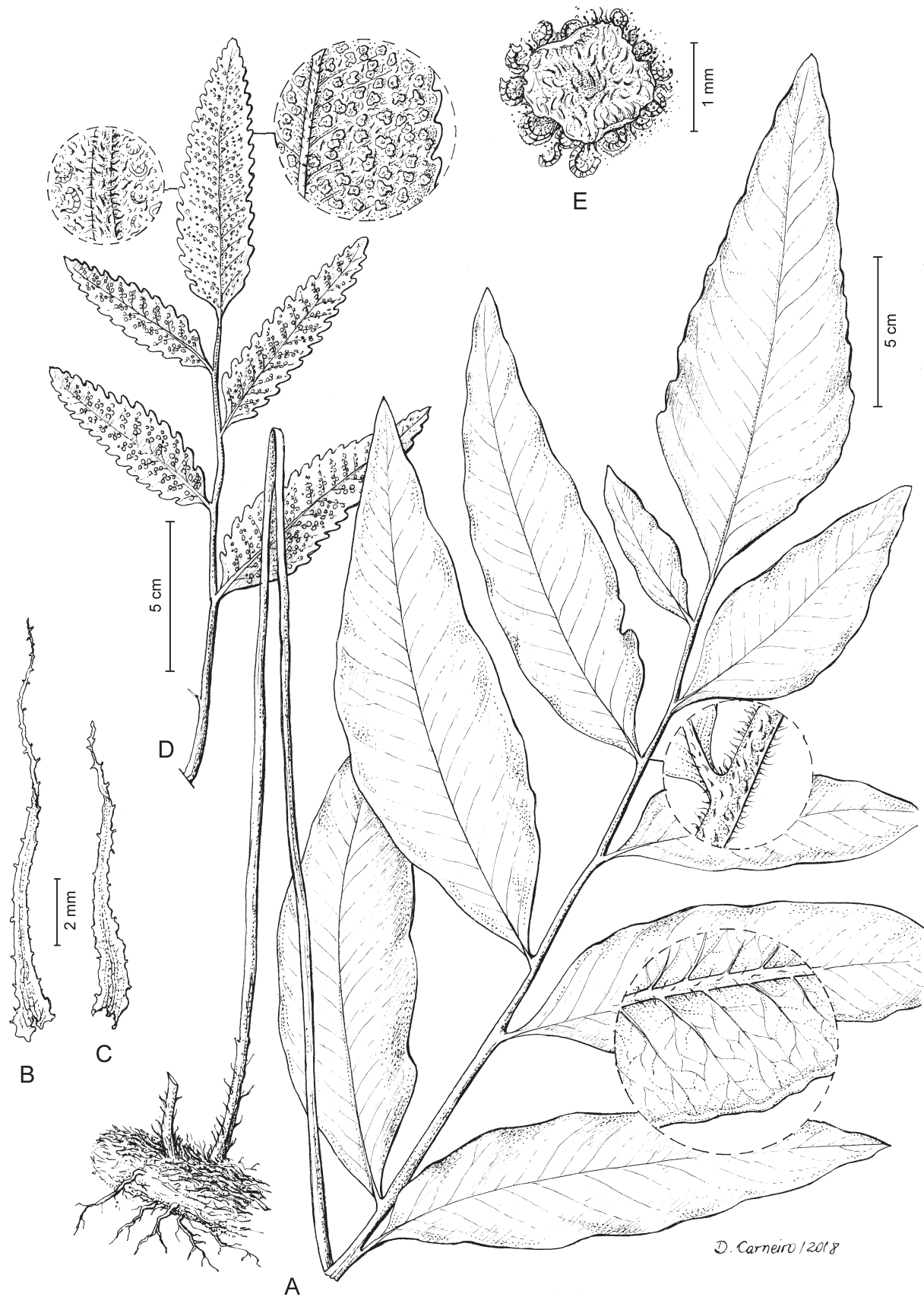


Fig. 7. A–E: *Cyclodium pubescens*; A: habit of sterile frond with detail of anastomoses and pubescence of rachis; B: rhizome scales; C: petiole scales; D: fertile frond with detail of pubescence of costa abaxially and laminar surface; E: indusium. – A–E from *Engels 4763* (MBM). – Drawn by Diana Carneiro.

Distribution and ecology — *Cyclodium seemannii* is restricted to the Pacific Coast of Colombia and Ecuador (Fig. 1B). In Colombia, it occurs in both highly humid (Chocó, San Juan river) and dryer (Pacific coast) regions (sensu Forero & Gentry 1989). All specimens are terrestrial, occurring on forest floors, more rarely in swamps, between 0–680 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium seemannii* is 41 883 km², suggesting that it is Near Threatened. The area of occupancy (AOO) was estimated at 36 km², suggesting it could be Endangered under criterion B2. *Cyclodium seemannii* and *C. chocoense* seem to be undercollected; they overlap in distribution in Chocó and northwestern Ecuador. *Cyclodium seemannii* seems to be more restricted and with a narrower elevational range. Therefore, it is assessed here as Endangered: EN B2b(ii,iii).

Remarks — *Cyclodium seemannii* is characterized by its thick, overlapping rhizome scales, dense indumentum on petioles, rachises and costae and also by bearing at least some round-reniform indusia with ciliate margins and surfaces. *Cyclodium seemannii* most resembles *C. trianae*, from which it differs by its cordiform, blackish rhizome scales, which are creased at mid-scale, and presence of multicellular, acicular and translucent hairs on costae and rachises. The only other species of *Cyclodium* with these hairs is *C. pubescens*, which differs by its 1-pinnate laminae and anastomosing veins. *Cyclodium seemannii* also resembles *C. chocoense* (which see for discussion).

12. *Cyclodium trianae* (Mett.) A. R. Sm. in Amer. Fern J. 76: 92. 1986 ≡ *Aspidium trianae* Mett. in Ann. Sci. Nat., Bot., sér. 5, 2: 243. 1864 ≡ *Nephrodium trianae* (Mett.) Baker, Syn. Fil.: 286. 1867 ≡ *Dryopteris trianae* (Mett.) Kuntze, Revis. Gen. Pl. 2: 814. 1891. – Lectotype (designated by Christensen 1920: 109): Colombia, Nova Granada, Prov. Barbacoas [Nariño], via de Túquerres, May 1853, J. J. Triana 32 (B barcode B200076883 [image!]; isoelectotype: BM barcode BM000937908 [also numbered as 615, image!] UC n.v., US n.v.). – Fig. 1B, 5H–M, 9E.

= *Nephrodium firmifolium* Baker, Syn. Fil., ed. 2: 501. 1874 ≡ *Dryopteris firmifolia* (Baker) Kuntze, Revis. Gen. Pl. 2: 812. 1891. – Lectotype (designated by Christensen 1920: 109): Peru, “In monte Guayrapurima, prope Tarapoto, Peruviae orientalis”, Aug 1856, R. Spruce 4662 (K barcode K000200351 [image!]; isoelectotypes: BM barcodes BM000777108 [image!], BM000777109 [image!], BR n.v., P barcodes P00630608 [image!], P00630609 [image!]).

Morphological description — Plants terrestrial. *Rhizomes* short-creeping, 0.6–0.8 cm in diam., with 5–7 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 5–11 ×

0.1–0.5 mm, concolorous, light brown, apices twisted and entire or slightly fimbriate, margins entire. *Fronds* monomorphic, lanceolate-ovate or elliptic, sterile fronds 72–84 × 27–34(–47) cm, fertile fronds 102–152 × 33–47 cm; *petioles* stramineous to tan, darker at base, with scales and microscscales more abundant proximally, 35–41(–59) cm long in sterile fronds, 54–85(–106) cm long in fertile fronds, 4–8 mm in diam.; *petiole scales* basifixed with a sinus, cordate at base and abruptly reduced to a filiform middle and apex, 3–10 × 0.4–0.8 mm, concolorous, light to dark brown, apices twisted, margins dentate to ciliate; *laminae* 1-pinnate-pinnatisect to 2-pinnate, rarely 3-pinnate, chartaceous to subcoriaceous, with 16–18 pairs of lateral pinnae and apex pinnatifid, 36–43 cm long in sterile fronds, 48–63 cm long in fertile fronds; *rachises* stramineous, with lanceate scales, these composed of few cells at base, 0.5–2 mm long, and brown, scattered microscscales; *pinna stalks* 5–7(–9) mm long, with yellowish hairs, also with scales and microscscales similar to those of rachises; *pinnae* linear to lanceolate-ovate or elliptic, with 9–15 pairs of lateral pinnules, bases asymmetric, with first segment larger and arising acroscopically, apices pinnatifid and crenate to dentate, sterile proximal pinnae 14–20 × 4.5–5 cm, fertile proximal pinnae 16–23 × 4.5–6.5 cm, sterile medial pinnae 12–13 × 3–4 cm, fertile medial pinnae 14–19 × 2.5–5 cm; *costae* abaxially with scales and microscscales similar to those of rachises; *laminar tissue* with microscscales similar to those of costae; *pinnules* lanceolate to elliptic, bases truncate acroscopically and frequently attached to costae basiscopically, apices acute or rounded, margins crenate, 2–4 × 0.5–1.3 cm in sterile fronds, 3–4 × 0.7–1 cm in fertile fronds; *costules* with scales and microscscales similar to those of costae; *veins* free, inconspicuous, 1- or 2(–4)-furcate between costa and margin; *sori* discrete, impressed, median on veins, forming 8–12 rows of sori between costa and margin, uniseriate between two main lateral veins; *indusia* subpeltate to peltate, 0.5–1.5 mm in diam., concolorous to bicolorous, stramineous to black, with a darker centre, entire to undulate margins; *spores* 39–47 × 30–39 µm, perine perforate, broadly folded and densely echinulate, folds high and continuous.

Distribution and ecology — *Cyclodium trianae* occurs in Panama, Colombia, Ecuador and Peru (Fig. 1B). In South America, it is mostly restricted to the eastern side of the Andes, except for a few records from Antioquia, Nariño and Putumayo departments. All specimens are terrestrial occurring in wet, evergreen forests, between 100–1150 m (Fig. 2).

Conservation status — The extent of occurrence (EOO) of *Cyclodium trianae* is 1 326 196 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 112 km², suggesting it could be Endangered under criterion B2. Like other species that occur in this region, *C. trianae* seems to be undercol-

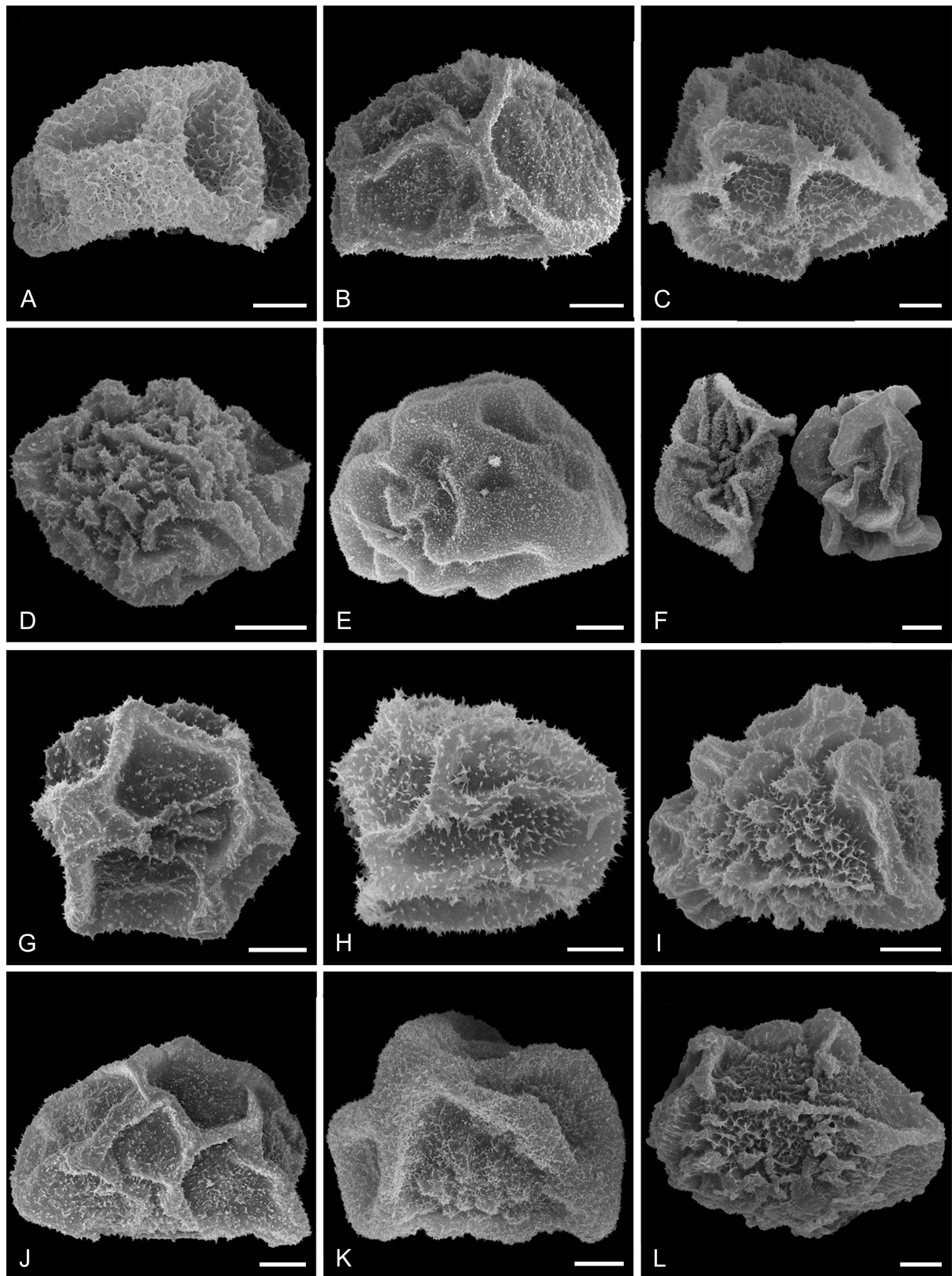


Fig. 8. Spores of *Cyclodium* – A: *C. akawaiaorum*; B: *C. alansmithii*; C: *C. calophyllum*; D: *C. chocoense*; E–G: *C. guianense*; H, I: *C. heterodon*; J: *C. inerme*; K, L: *C. meniscioides*. – A from Henkel & al. 4269 (NY); B from Zartman & al. 9172 (INPA), originally published in Bohn & al. (2019b: 525, fig. 3A); C from Liesner & González 13307 (UC); D from Hoover & al. 3935 (UC); E from Costa 33 (UPCB); F from Secco & al. 303 (NY); G from Cremers & al. 9193 (INPA); H from Pietrobom 4207 (NY, formerly as *C. heterodon* var. *abbreviatum*); I from Labiak & al. 4058 (UPCB, formerly as *C. heterodon* var. *heterodon*); J from Ingham & Ingham 33935 (NY); K from Zuquim & al. 355 (INPA, formerly as *C. meniscioides* var. *meniscioides*); L from García-Barriga 14347 (US, formerly as *C. meniscioides* var. *paludosum*). – Scale bars: A–L = 10 μ m.

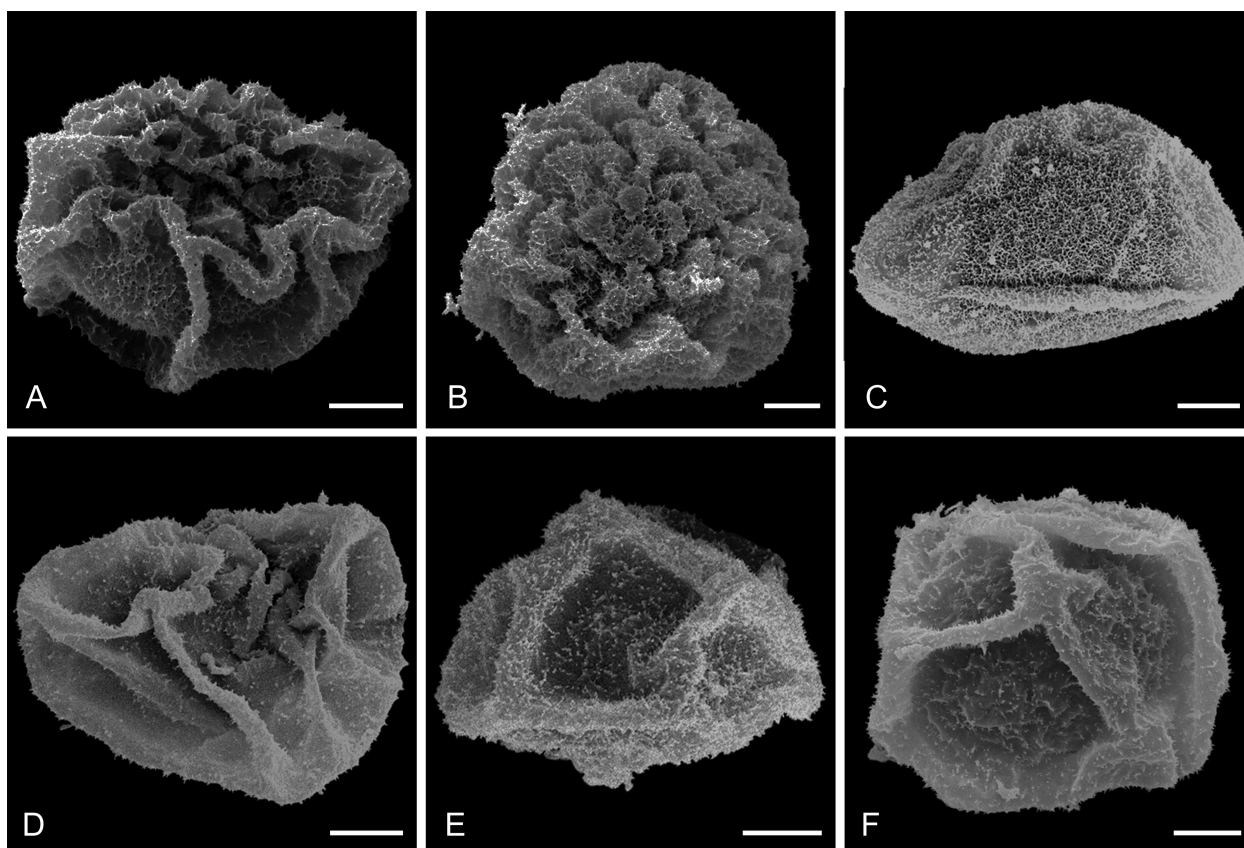


Fig. 9. Spores of *Cyclodium*. – A: *C. meniscioides*; B: *C. pubescens*; C: *C. rheophilum*; D: *C. seemannii*; E: *C. trianae*; F: *C. varians*. – A from Monteagudo & Francis 5309 (NY, formerly as *C. meniscioides* var. *rigidissimum*); B from Bronholi & al. 11-224 (UPCB); C from Granville & al. 15523 (NY); D from Ramírez & al. 9611 (UC); E from Rojas 0102 (NY); F from Clarke 10037 (NY). – Scale bars: A–F = 10 μ m.

lected. Nevertheless, the species is often recorded in primary or secondary forests, with a wide elevational range. Considering the ecology and the large EOO of this species, it is likely that its AOO exceeds the threshold of any threat category. *Cyclodium trianae* is therefore assessed as Least Concern (LC).

Remarks — *Cyclodium trianae* is characterized by its long fertile fronds (102–152 cm long) and free veins. It belongs to a group with highly dissected lamina (1-pinnate-pinnatisect to 3-pinnate), which includes *C. chocoense* and *C. seemannii* (see comments under these species for differences). Smith (1986) and Moran (1987) indicated *C. trianae* as a possible link between *Cyclodium* and *Polybotrya* based on morphology and anatomy of the petiole. Besides the highly dissected laminae and free veins, Moran (1987) found that *C. trianae* has vascular bundles shaped like a mushroom (as seen in cross-sections of petiole bases), with the base of the “mushroom” oriented adaxially, a trait also found in *Polybotrya*. Our preliminary phylogenetic analysis supports its placement within *Cyclodium*.

13. *Cyclodium varians* (Fée) A. R. Sm. in Amer. Fern J. 76: 94. 1986 \equiv *Nephrodium varians* Fée, Mém. Foug. 11: 88. 1866 \equiv *Dryopteris varians* (Fée) Kuntze, Revis.

Gen. Pl. 2: 814. 1891 \equiv *Stigmatopteris varians* (Fée) Alston in Bull. Misc. Inform. Kew 1932: 309. 1932 \equiv *Thelypteris varians* (Fée) C. F. Reed in Phytologia 17: 323. 1968. – Holotype: Trinidad and Tobago, La Trinité, s.d., M. Germain s.n. (P barcode P00630607 [image!]). – Fig. 1C, 4K–N, 9F.

– *Cyclodium varians* C. V. Morton ex Vareschi, Fl. Venez. 1: 368. 1969, nom. inval. (Turland & al. 2018: Art. 41.5).

Morphological description — Plants terrestrial or terrestrial root climber. *Rhizomes* short-creeping, 0.5–0.8 cm in diam., with 4–6 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 2–5 \times 0.3–1 mm, concolorous, dark brown to black, apices frequently twisted, margins denticulate. *Fronds* monomorphic to subdimorphic, elliptic to lanceolate; sterile fronds 36–51(–83) \times 17–19(–28) cm, fertile fronds (33–)45–75(–102) \times 10–19(–26) cm; *petioles* stramineous to tan or dark brown, with scales more abundant proximally, also with brown microscscales, and yellow to brownish hairs, 12–20(–33) cm long in sterile fronds, 17–37(–42) cm long in fertile fronds, 1–3(–5) mm in diam.; *petiole scales* similar to those of rhizomes, 2.5–5(–6) \times 0.2–0.5 mm; *laminae* 1-pinnate, subcoriaceous to coriaceous, with 8–15 pairs of lateral pinnae and a subconform apex, this subauricu-

late proximally, 22–28(–51) cm long in sterile fronds, 19–37(–62) cm long in fertile fronds; *rachises* stramineous, rounded abaxially, adaxially with yellowish, hairs, c. 0.1 mm long, also with dark brown, scattered micro-scales and hairs similar to those of grooves; *pinna stalks* 1–3(–7) mm long at proximal pinnae, with hairs and microscales similar to those of rachises; *pinnae* linear to lanceolate, bases truncate acroscopically and cuneate basiscopically, apices acute and crenate to serrate, margins entire to dentate, sterile proximal pinnae 6–10(–15) × 1.3–2.2(–2.5) cm, fertile proximal pinnae (4–)5–14(–20) × (0.6–)1–1.5(–4) cm, sterile medial pinnae 8–9(–15) × 1–1.5(–2) cm, fertile medial pinnae 5–12 × 0.7–1.5 cm; *costae* abaxially with linear to lanceolate, brown scales, sometimes with few cells at base, and brown microscales; *laminar tissue* with microscales similar to those of costae; *veins* anastomosing, conspicuous, with 2 or 3 anastomoses between costae and pinna margins; *sori* discrete, impressed, forming 1–3 rows between costae and pinna margins, biseriate between two main lateral veins, sometimes connivent toward costae; *indusia* peltate, round, 0.7–1 mm in diam., concolorous or bicolorous, brown or sometimes with a darker centre, ciliate margins; *spores* 51–63 × 37–47 µm, perine perforate, broadly folded, and densely echinulate, folds high and continuous.

Distribution and ecology — *Cyclodium varians* is known from Guyana, Venezuela (newly recorded here for this country) and Trinidad (Fig. 1C). Most specimens examined were collected from 1895–1986, and only two gatherings are recent (2003). Just three gatherings bear comments about the habit of this species: one terrestrial (Clarke 9964, US), one epiphytic (Clarke 10037, NY) and one with a creeping rhizome (Holst 2643, UC). As observed by Smith (1986), most of the rhizomes do not appear to have been buried in the ground and seem to be vertical, resembling the creeping habit of *C. meniscioides* and *C. akawaiaorum*. Furthermore, Smith (1995) described *C. varians* as “hemiepiphytic or terrestrial along muddy creek banks”, and most specimens seem to be associated with rivers, between 500–625 m (Fig. 2). One exception is Britton 1941 (US), which was recorded as growing in the Aripo savanna.

Conservation status — The extent of occurrence (EOO) of *Cyclodium varians* is 142 214 km², which would give it the status of Least Concern. The area of occupancy (AOO) was estimated at 40 km², suggesting the species could be Endangered under criterion B2. Besides the Guianas, this species also is distribution on Trinidad, which makes its EOO exceed the threshold of any threat category. However, most of the collections were made over 100 years ago, with little information on its ecology. Therefore, *C. varians* is assessed here as Endangered: EN B2b(ii,iii,iv).

Remarks — *Cyclodium varians* is characterized by its dark brown to black rhizome scales with twisted apices, 1-pin-

nate fronds and anastomosing veins. It resembles *C. akawaiaorum* and *C. meniscioides*, but overlaps in distribution only with the latter. *Cyclodium varians* differs from these two species by its shorter rhizome scales (2–5 mm long vs 5–10.5 mm long in *C. akawaiaorum*, and 4–15 mm long in *C. meniscioides*) that are twisted at the apex.

Cyclodium varians is also variable in division and length of its pinnae, sometimes also resembling *C. guianense* or *C. heterodon*. For instance, Jenman s.n. (NY 02859624) has wider and longer pinnae with deeply pinnatifid margins at the base (resembling some specimens of *C. heterodon* from northeastern Brazil), but the pinnae toward the apex are more like others of *C. varians*, decreasing to an atypical, small and pinnatifid apex. Another specimen (Jenman s.n., NY 02859623) was annotated as “*Cyclodium* sp. or hybrid” by Smith in 1985–1986, with a larger number of lateral pinnae, and a commissural vein (as *C. akawaiaorum*), but lanceate pinnae with serrulate margins (as *C. varians*). Most specimens have conform distal pinnae, with no gradual pinna reduction toward the apex, as *C. meniscioides*, but some from Guyana have a subconform to pinnatifid apex (Jenman s.n., NY 02859617, 02859618). Whether these specimens represent hybrids of *C. varians* with other species of this complex must await further studies. Likewise, the phylogenetic relationships of *C. varians* remain unknown.

Acknowledgements

We thank the curatorial staff of CAY, INPA, MBM, NY, P, RB, RON, UC, UFP, UCPB and US for loans of specimens. We also thank Felipe Cardona (HUA), Fernanda dos Santos (JOI), Libing Zhang (MO), Liz Brogan (K), Maria Salete Marchioretto (PACA) and Olof Ryding (C) for digital images of specimens. The line drawings were prepared by Diana Carneiro. We thank Raquel C. Marra for operating the SEM at Universidade Federal do Paraná and Duane Fernandes Lima for helping with the conservation status assessments. We also thank Alan Smith, Nicholas Turland and Weston Testo for their corrections and suggestions to improve this paper. This project was supported by a fellowship from CAPES to A.B. and by grants from CNPq to F.B.M. (155074/2018-0) and P.H.L. (307514/2016-1).

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Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2018 Journal Impact Factor 1.156

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

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