

A TAXONOMIC REVIEW OF BRAZILIAN DENDROCEROS NEES (DENDROCEROTACEAE)

Leandro de A. Amélio¹
Aline M. de Souza²
Denilson F. Peralta³
Emilia de B. Valente⁴

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ABSTRACT

In this paper we present a taxonomic revision of Brazilian *Dendroceros* Nees and recognize three species: *Dendroceros breutelii* Nees, *D. crispatus* (Hook.) Nees, and *D. crispus* Nees. In Brazil, the genus is restricted to the Atlantic Forest in humid montane forests and cloud forests from 1,000 to 1,700 m a.s.l., mainly on shaded bark or leaves. Fragments dropping from the involucrem are reported for the first time and represent the first report of this type of asexual reproduction in the genus. Descriptions and illustrations, as well as comments on geographic distribution are provided here. The ecology, palynology and conservation of the species are discussed. *Dendroceros rigidus* is considered as a new synonym, and *D. exalatus* as extinct in wild.

Keywords: Anthocerotophyta, capsule morphology, extinct species, hornworts, spore ornamentation.

RESUMO

Neste trabalho apresentamos uma revisão taxonômica Brasileira de *Dendroceros* Nees, reconhecemos três espécies: *Dendroceros breutelii* Nees, *D. crispatus* (Hook.) Nees e *D. crispus* Nees. No Brasil, o gênero é restrito à Mata Atlântica em florestas montanas úmidas e florestas nebulares de 1.000 a 1.700 m a.s.l., principalmente em troncos ou folhas sombreadas. Fragmentos caindo do invólucro são relatados pela primeira vez e representam o primeiro relato desse tipo de reprodução assexuada no gênero. Descrições e ilustrações, bem como comentários sobre a distribuição geográfica são fornecidos nesse estudo. A ecologia, palinologia e conservação das espécies são discutidas aqui. *Dendroceros rigidus* é considerado um novo sinônimo e *D. exalatus* como espécie extinta na natureza.

Palavras-chave: Anthocerotophyta, morfologia da capsula, espécie extinta, antóceros, ornamentação dos esporos.

1 Doutorando em Botânica. Departamento de Biologia, Universidade Estadual de Feira de Santana. Av. Transnordestina, s/n, Novo Horizonte - BA, 44036-900. Feira de Santana, BA, Brasil. Corresponding author's e-mail: ednlora@gmail.com.

2 Doutora em Botânica. Secretaria de Educação do Estado da Bahia, Centro Estadual de Educação Profissional em Saúde Adélia Teixeira. Av. Jorge Teixeira, 16 - Candeias, Vitória da Conquista - BA, 45028-536. ninedesouza@gmail.com.

3 Pesquisador, Curador do Herbário de SP, Instituto de Botânica, Av. Miguel Stéfano, 3687 - CEP04301-902, São Paulo, SP, Brasil. denilsonfperalta@gmail.com.

4 Doutora e Professora Titular do Programa de Pós-Graduação em Botânica. Universidade Estadual de Feira de Santana. Av. Transnordestina, s/n, Novo Horizonte - BA, 44036-900. Feira de Santana, BA, Brasil. ebvalente@gmail.com

INTRODUCTION

Anthocerotophyta is considered the most derived group in the bryophytes, being singled out by many phylogenetic studies as the sister group to all tracheophytes (Qiu *et al.*, 2006; Renzaglia *et al.*, 2009; Shaw & Goffinet 2009; Shaw *et al.*, 2011). This group includes gametophytes with one to eight chloroplasts per epidermal cell, common colonies of the bacteria (*Nostoc* sp.) immersed in the thallus, long cylindrical bivalved capsules with the foot completely immersed in the thallus, stomata on the sporophyte and asynchronous spore development (Gradstein *et al.*, 2001).

There are about 300 species of hornworts in the world (Duff *et al.*, 2007), with 5 families and 14 genera (Renzaglia *et al.*, 2009). Eleven species have been reported from Brazil, and these belong to three families: Anthocerotaceae Dumort. (4 spp.), Dendrocerotaceae (Milde) Hässel (2 spp.) and Notothyladaceae Müll. Frib. (5 spp.) (Gradstein & Costa, 2003; Costa, 2017 a). The hornworts of Brazil have never been systematically investigated and the treatment for the Flora do Brasil (2020) was based on old lists without examination of specimens.

Dendrocerotaceae includes four genera worldwide: *Dendroceros* Ness, *Megaceros* Campb., *Nothoceros* (R. M. Schust.) J. Haseg. and *Phaeomegaceros* Duff *et al.* (Duff *et al.*, 2007; Renzaglia *et al.*, 2009; Söderström *et al.*, 2016). The four genera share the characters of having a capsule without stomata, pseudoelaters with helical thickening bands and a single antheridium per antheridial chamber (Hasegawa, 1994; Renzaglia *et al.*, 2009).

Dendroceros is distinguished by the presence of a midrib in the thallus, wings with perforations, multicellular spores with endosporic development and the presence of a conspicuous pyrenoid per cell (Vaughn *et al.*, 1992; Hasegawa, 1994; Duff *et al.*, 2007; Villarreal *et al.*, 2007; Renzaglia *et al.*, 2009). The epiphytic and epiphyllous habits of *Dendroceros* are remarkable and unique (Gradstein *et al.*, 2001; Frahm, 2005; Villarreal *et al.*, 2010). The genus comprises 43 species with mainly tropical distributions (Duff *et al.*, 2007; Villarreal *et al.*, 2010; Villarreal *et al.*, 2012). In Brazil occur exclusively in ombrophilous forests of the Atlantic Forest Biome, having been recorded in six Brazilian states of the South and Southeastern geopolitical regions of the country (Yano, 2008, 2010; Peñaloza Bojacá *et al.*, 2016; Costa, 2017 b).

The species *D. crispus* (Sw.) Nees, has been widely found in Brazil, but nine other species had also been described for the country (Gottsche *et al.* 1844; Stephani 1909, 1917, 1923), most of which are currently considered to be synonyms.

Historically, all *Dendroceros* on tree trunks were identified as *D. crispus*, even in the field. However, after analyzing specimens from herbaria we were able to recognize three morphotypes, which prompted us to revisit the literature and reexamine type specimens. Here we revise *Dendroceros* from Brazil based on field studies, type materials and herbarium specimens, providing a key and a morphological characterization of the species.

MATERIAL AND METHODS

We presented here a treatment taxonomic for *Dendroceros* based on all literature concerning this genus, field studies and data of 77 herbarium specimens from the following herbaria: G, HUEFS, NY, SJRP, SP and RB. The herbarium samples were collected since 1977, integrating floristic lists of bryophytes to country.

We observed and measured characters such as thallus size, thallus cells and the chloroplast quantities, cells of the capsule at the margin and centrally, the length of the

columella, pseudoelater structure, colors and size under optical and stereo microscopes. The taxonomic treatment included the measures of the morphology and notes to easy identification characters to the species. The cell walls of the capsule were measured with a micrometer eyepiece on a ZEISS microscope Primo Star. The observations of dry plant material were made with ZEISS microscope Primo Star and the Scanning Electron Microscopy (SEM) observations of materials were made with Philips XL-20.

We are presenting in this study key to species, description and illustrations are for each species, following Chantanaorrapint (2015). The specimens analyzed are mainly from protected areas. The geographic distributions follow the Brazilian geopolitical states (IBGE 2012) and was analyzed using the GBIF website (<https://www.gbif.org>).

RESULTS AND DISCUSSION

We recognize three species from Brazil: *Dendroceros breutelii* Nees, *D. crispatus* (Hook.) Nees, *D. crispus* Nees and *Dendroceros exalatus* Steph. was proposed as extinct species (Table 1). *Dendroceros rigidus* was described by Stephani (1917) to the State of São Paulo and here we proposed as a new synonym to *D. breutelii*, and the other four names suggested in the literature to the occurrence in Brazil were confirmed the synonymization made before. We observed that *Dendroceros* Nees has its occurrence restricted to Atlantic Forest in the sub formations of the humid montane forest and cloud forest from 1,000 to 1,700 *m a.s.l.*, mainly in shaded on bark or leaves.

Individuals can vary in color, ranging from yellow-green to dark green, with thallus margin varying from slightly to strongly crisped-undulating. Samples collected in open and illuminated areas are lighter and strong crisped margins, while those from shaded areas are darker and plane margins.

As additional data concerning the morphological characteristics of the genus *Dendroceros*, we observed several fragments dropping from the involucrem. When the involucrem is young there is a large number of fragments in folds, which stretch with capsule maturation such that the fragments stand out and fall to the substrate. We observe the germination these fragments and it is the first report of these asexual reproduction in the genus. There has been no study describing gemmae or propagules of hornworts, or of this genus, thus further investigation of this feature would be very interesting.

Table 1. Morphological comparison of the four Brazilian species of *Dendroceros* Nees.

Characters	<i>D. breutelii</i>	<i>D. crispatus</i>	<i>D. crispus</i>	<i>D. exalatus</i>
Number of cells in the spore	4–6	8–12	4–6	--
Format of capsule cell	long-rectangular	rectangular	rectangular	--
Capsule cell thickening	uniform	trigons and intermediates	uniform	--
Pores in Capsule Cells	present	absent	present	--
Margin of the gametophyte	crispate, wavy	crispate or forming a hood-like structure	crispate, wavy	--
Margin of the involucrem	fragments in the folds	fragments in the folds	smooth	--
Parts of the capsule cylindrical after opening	channelized	flat, revoluta	channelized	--
Cavernous midrib	none	none	none	present

Key to the Brazilian species of *Dendroceros*

1. Midrib cavernous with chambers (either empty, or containing *Nostoc*); thallus thin, with sparse and filamentary branches (with the appearance of *Riccardia*)..... *D. exalatus*
1. Midrib solid (without chambers); thallus large, with short and not filamentous branches.2
2. Thallus with perforations, irregular or with hood-like structures; capsule with valves attached at one side; involucre with 4–6 layers of cells; epidermal cells of the capsule with confluent thickenings *D. crispatus*
2. Thallus without perforations (without perforations), thallus plane or weakly crispate; capsule with split valves; involucre with 1–2 layers of cells; epidermal cells of the capsule with uniform thickenings.....3
3. Wings plane to slightly crispate; involucre entire; epidermal cells of the capsule short with uniformly thickened cells *D. breutelii*
3. Wings crispate; involucre crispate with ramenta (with deciduous parts); epidermal cells of the capsule long with irregularly thickened cells (similar to collenchyma) *D. crispus*

Dendroceros breutelii Nees, Syn. Hepat. 4: 581.1846 (Gottsche *et al.*, 1846). Type: [São Cristóvão Island] St. Kitts. *Breutel s.n.* (holotype G00115617!).

=*Dendroceros macrosporus* Steph., Spec. Hepat. 5: 1014. 1917. Type: Brazil, São Paulo: Rio Grande, ad São Paulo Railway, 7 June 1901, *Schiffner 700* (lectotype G00067711 (hb - Stephani no. 24035), designated by Villarreal *et al.* (2015)).

=*Dendroceros angustifrons* Steph., Spec. Hepat. 5:1016. 1917. Type: Brazil, São Paulo: “in sylvaticus ad Rio Mambu in districts urbis Conceição de Itanhaém”, 30 June 1901, *Schiffner 726*, (lectotype G00060906 (hb - Stephani no. 24025) [<http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=115857&lang=en>], designated by Villarreal *et al.* (2015)).

=*Dendroceros ecuadorensis* Steph., Spec. Hepat. 6: 429. 1923. Type: Ecuador, Gualaquiza, “Llionis salesianum”, 1908, *Allioni 6511* (lectotype G00060904, designated by Villarreal *et al.* (2015)).

=*Dendroceros rigidus* Steph., Spec. Hepat. 5: 1017. 1917. Type: Brazil, prov. São Paulo, prope Raiz da Serra, VI-1901, *Schiffner 992* (Isotype S-B22423), *syn. nov.*

=*Dendroceros schiffneri* Steph., Spec. Hepat. 5: 1017. 1917. Type: Brazil, São Paulo: “ad flumen Rio Branco prope Santos”, 13 September 1901, *Schiffner 2147* (lectotype G00067709 (hb - Stephani no. 24037) [<http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=127941&lang=en>], designated by Villarreal *et al.* (2015)).

Fig. 1 and 4 A–B.

Description: Gametophytes medium sized, green to dark green, adherent to bark. Thallus (0.8–) 1–2 (–3.0) cm wide, (2–) 3–4 cm long, irregularly sub-pinnately branched, branches divergent. Midrib 150–200 µm wide, solid; in cross section (not including *Nostoc* colonies), 0.3–0.9 mm wide when mature and 7–10 cells long, midrib flat, margin entire; in cross-section cells 17.5–35.5 × 17–25 µm. Lamina unistratose, crispate, with some small perforations especially conspicuous near the margin, margins nearly entire; cells 17–35 × 18–35 µm at the margin, 17–28 × 20–38 µm in the middle part, thin-walled, trigones, very small 3–10 × 4–12 µm. Rhizoids small and pale, 7–12 µm wide, present on the midrib. *Nostoc* colonies embedded in the thallus, commonly in older parts, scattered on dorsal and ventral sides of midrib. Monoecious; androecia scattered on main branches;

antheridia solitary, rounded-ovoid, 150–140 μm wide. Involucrum medium-sized, squamulose (0.5) 0.7–0.9 mm long. Capsules long and not very wide, 1.0–2.0 cm long, 450–480 (–520) μm in diameter, bivalved when mature; epidermal cells short (30), 38–68 \times 10–15 μm , rectangular, with thickened walls. Spores rounded globose, 35–60 \times 40–60 (–65) μm , green, multicellular with 4–6 cells, densely papillose. Pseudoelaters pale yellow, unbranched, 380–400 (–450) μm long, 7–10 μm wide, without papillae, with a single helical band.

Notes: *Dendroceros breutelii* is characterized by having a thallus with wings, perforated or not, with nodule thickened (trigones); capsule with papillose cuticle with rectangular cells and strong and uniform thickenings. *Dendroceros breutelii* is very similar to *D. crispus*, differing mainly in characters of the cells of the capsule wall and spores, which according to Campbell (1898) remain unicellular in *D. breutelii* until dehiscence of the capsule.

Dendroceros rigidus was described to Brazil for the State of São Paulo, by Stephani (1917), mainly by the margin crispate, capsule long and the spores 54 μm rough. Our study of type material of both species shows that they overlap in sporophytic characters, such as the characters to capsule, and the spores. Additionally, the yellow rough spores are nearly identical in both species. For the moment, we suggest to synonymize both species, based on morphological studies. The authors encourage molecular work to define whether *D. rigidus* is a single widespread species or it represents a cluster of cryptic species.

Several specimens analyzed possess a characteristic one pore per cell, independent of maturity, and a squamulose involucrum, which we believe may be propagules or gems, but further study is needed.

Distribution and ecology: *Dendroceros breutelii* occurs in Cuba, Leeward Islands, Suriname, Ecuador. In Brazil the species occurs in the Northeast and Southeast regions in the states of Bahia, São Paulo, Paraná. The species grows on bark in rainforests.

Specimens Examined. Brazil. Bahia: Boa Nova, Parque Nacional de Boa Nova 14° 24' 46.6"S & 40° 07' 47.8"W, 26 Jul 2013, A.M. Souza et al. 728 (HUEFS). Paraná: Antonina, Bairro Alto, 18 nov 2012, A. Schäfer-Verwimp 33985 (SP), 18 Nov 2012, D.F. Peralta et al. 13114 (SP); Morretes, Serra da Graciosa, 21 Aug 1999, D.F. Peralta 387 (SP, SJRP); 23 Jul 2014, D.F. Peralta et al. 16121 (SP); Quatro Barras, 18 Nov 2012, D.F. Peralta et al. 12950 (SP). São Paulo: Biritiba Uçu, 25 Jul 1983, O. Yano et al. 7814, 7853 (SP); Cananéia, Ilha do Cardoso, 10 Dez 1981, D.M. Vital 10262 (SP), 20 Jan 1981, O. Yano 3191 (SP), 29 Jan 1985, D.M. Vital 12832 (SP); Iporanga, 25 Jul 2009, D.M. Vital & W.R. Buck 20579 (SP, NY); Mogi das Cruzes, distrito de Taiacupeba, 16 Jun 2007, D.F. Peralta & J. Bordin 5345 (SP), 1 Nov 2008, D.F. Peralta et al. 7321 (SP); Natividade da Serra, 11 Jun 2013, D.M. Carmo & D.F. Peralta 589 (SP); São Luiz do Paraitinga, 16 Jun 1983, O. Yano et al. 7778 (SP); 16 Jun 2007, D.F. Peralta & J. Bordin 5267 (SP); 7 Set 2009, D.F. Peralta et al. 9295 (SP), 11 Jun 2013, D.F. Peralta & D.M. Carmo 14170 (SP), 17 Apr 2013, D.F. Peralta & A.M. Gugliotta 13725 (SP), 12 Jun 2013, D.F. Peralta & D.M. Carmo 14830 (SP).

Dendroceros crispatus (Hook.) Nees, Syn. Hepat. 579. 1844. *Monoclea crispata* Hook., Bot. Misc. 1: 117. 1830. Type: [Saint Vincent Island] in ramis arborum, insulae Sancti vincenti, L. Guilding (lectotype S-B1983, designated by Peñaloza-Bojacá et al. (2019), n.v.), Brazil, Serra dos Órgãos, Gardner [s.n.] (BM000746080), cited by Garcia et al. (2012).

Fig. 2 and 4 C–D.

Description: Gametophytes medium sized, pale to dark green, strongly adherent to bark. Thallus (0.8–) 1–2 (–3.0) mm wide, (2–) 3–4 cm in diam., irregularly sub-pinnately branched, branches divergent. Midrib 150–200 μm wide, solid; in cross section (not including *Nostoc* colonies), 0.3–0.9 mm wide when mature and 8–10 cells long, midrib flat, margin entire; in cross-section cells 17.5–37.5 \times 17–25 μm . Lamina unistratose, strongly crispate or forming a hood-like or galeade structures, with some small perforations especially conspicuous near the margin, margins nearly entire; cells 17–37 \times 18–35 μm at margin, 17–28 \times 20–38 μm in middle part, thin-walled, trigones, very small 3–10 \times 4–12 μm . Rhizoids small and pale, 8–12 μm wide, present on midrib. *Nostoc* colonies embedded in the thallus, especially in older parts, scattered on dorsal and ventral sides of midrib. Monoecious; androecia scattered on main branches; antheridia solitary, rounded-ovoid, 150 μm wide. Involucrum shortly squamulose (0.5–) 0.7–0.8 mm long. Capsules long and wide, 1.5–2 cm long, 460–480 (–550) μm in diameter, bivalved when mature, but just one side of capsule completely open, dehiscence line weaker on one side; epidermal cells short (25–) 30–55 \times 12–25 μm , with space, without thickened walls, but with trigones-like spaces beyond the cells of capsule. Spores rounded globose, 40–65 \times 70–100 μm , green, multicellular with 10 or more cells, densely papillose. Pseudoelaters pale brown, unbranched, 450–500 (–550) μm long, 7–10 μm wide, without papillae, with a single helical band.

Notes: *Dendroceros crispatus* (Hook.) Nees has distinctive capsule cells with large trigones and intercalary thickenings. This feature is found in five other species: *D. africanus* Steph. differs in the number of spore cells (to ten), and the smaller size of the spores reaching to 65.5–87.5 \times 45–62.5 μm (Infante 2010); *D. borbonicus* Steph. differs by the small cells of the capsule that reach to 25–50 \times 15.5–25 μm (Hasegawa 1981); *D. japonicus* Steph. differs because it has the lamina undulate (Hasegawa 1980), and *D. granulatus* Mitt. differs by a large number of small cells (more than 20) of the spore and the margin undulate (Hasegawa, 1982).

These taxa seem as a continuum and the characters to recognize the species in *Dendroceros* need to be evaluated using molecular tools, as all as Sérgio *et al.* (2012) emphasize the needs of phylogenetic studies to understanding the relationships among the taxa with nodulose epidermal cells.

Distribution and ecology: *Dendroceros crispatus* occurs in Australia, Belize, Costa Rica, Cuba, Ecuador, French Polynesia, New Caledonia, Panama, Peru, Puerto Rico. In Brazil is known to the South and Southeast regions, in the states of Paraná, Rio de Janeiro, Santa Catarina and São Paulo. This species grows on bark in rainforests, where it develops numerous sporophytes.

Specimens Examined. Brazil. Paraná: Road to Graciosa, between Morretes and Paranaguá, 27 Sep 1993, O. Yano *et al.* 20593, 20596, 20659 (SP), 27 Nov 1994, O. Yano *et al.* 23160 (SP), 18 Nov 2012, A. Schafer Verwimp 22920 (SP), 18 Nov 2012, D.F. Peralta *et al.* 12953 (SP). Rio de Janeiro: Nova Friburgo, Road to Lumiar, 22 Jul 1996, O. Yano & S.R. Gradstein 24750 (SP). Santa Catarina: Urubici, Parque Nacional de São Joaquim, 10 Mar 2009, D.F. Peralta & M.A. Barros 7715 (SP). São Paulo: Cunha, Parque Estadual da Serra do Mar, 22 Jun 2006, D.F. Peralta *et al.* 3956 (SP); Serra da Paranapiacaba, 30 Apr 1989, A. Schafer Verwimp & I. Verwimp 11118 (SP).

Dendroceros crispus (Sw.) Nees, Syn. Hepat.: 581. 1844. *Anthoceros crispus* Sw., Prodrum: 146. 1788. Type: Jamaica, Swartz *s.n.* (lectotype S-B20564 [<http://andor.nrm.se/fmi/xsl/kryptos/kbo/publDetailItems.xsl?lay=webbkollekter&>]

token.nav=items&-db=kbo_mossregister&-recid=20141&-find=-find&-token.post=all&-token.languagecode=en-GB], designated by Proskauer (1960)).

=*Dendroceros brasiliensis* (Raddi) Nees, Syn. Hepat.: 581. 1844. *Anthoceros brasiliensis* Raddi, Memoria inserita nel tomo XVIII degli Atti della Società Italiana delle Scienze residente in Modena 18. 34. 1820. Type: Brazil, *Raddi s.n.* (Isotype E00002012)

=*Dendroceros foliatus* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 574, 1885. Type: Ecuador, Canelos, Cuesta de Mapoto, *Spruce s.n.* (holotype G00115607, isotype E-00002013).

[http://elmer.rbge.org.uk/bgbase/vherb/bgbasevherb.php?current__names_family=¤t__names_genus=Dendroceros¤t__names_species=foliatus&coll__name=&coll_núm=&specimens_barcode=&full__name=&specimens_region=&cfg=bgbase%2Fvherb%2Fbgbasevherb.cfg], designated by Villarreal et al. (2015)).

Fig. 3 and 4 E–F.

Description: Thallus green to dark green (0.8–) 1–2 (–3.0) mm wide, (2–) 3–5 cm long, irregularly sub-pinnately branched, branches divergent. Midrib 150–200 µm wide, solid; in cross section (not including *Nostoc* colonies), 0.3–0.9 mm wide when mature and 4–8 cells long, midrib flat and easily observed, margin entire; in cross-section cells 17.5–37.5 × 17–25 µm. Lamina unistratose, crispate, with some small perforations especially conspicuous near the margin, margins nearly entire; cells 17–37 × 18–35 µm at the margin, 17–28 × 20–38 µm in the middle part, thin-walled, trigones, 4–12 × 5–14 µm. Rhizoids, 8–14 µm wide, present mostly on the midrib. *Nostoc* colonies embedded in the thallus, especially usually in older parts, scattered on dorsal and ventral sides of midrib. Monoecious; androecium scattered on main branches; antheridia solitary, rounded-ovoid, 120–150 µm wide. Involucrum smooth-squamulose, 0.5–0.8 mm long. Capsules long, 1.0–1.7 cm, 450–500 (–550) µm in diameter, bivalved when mature, epidermal cells longer than in *D. breutelii* (70–) 75–110 × 8–17.5 µm, quadrate to rectangular. Spores rounded globose, 40–65 × 50–70 (–75) µm, green, multicellular with 4–6 (–8) cells, densely papillose. Pseudoelaters pale brown, unbranched, 390–420 (–450) µm long, 7–10 µm wide, without papillae, with a single helical band.

Notes: *Dendroceros crispus* is characterized by a crispate thallus with perforated wings and thickened nodules (trigones); capsules with long smooth cells, irregular thickening, multicellular and papillary spores. Several specimens analyzed possess a characteristic one pore per cell, independent of maturity, as in *D. breutelii*.

Distribution and ecology: *Dendroceros crispus* occurs in Moluccas, New Guinea, New Caledonia, Society Islands, Hawaii, Costa Rica, Panama, Cuba, Jamaica, Dominican Republic, Puerto Rico, Leeward Islands, Windward Islands, French Guiana, Surinam, Guyana, Colombia, Ecuador, Peru, Galapagos Islands, and Brazil. In Brazil the species occurs in the states of Minas Gerais, Paraná and São Paulo. The species grows on bark in rainforests.

Specimens Examined. Brazil. Minas Gerais: Itamonte, 27/4/2009, Yano, O. 31607 (SP). Paraná: Morretes, 23 Jul 2014, *D.F. Peralta et al.* 16094 (SP), 25 Jul 2014, *D.F. Peralta et al.* 16445 (SP). São Paulo: Cananéia, 29 Jul 1977, O. Yano 769 (SP), 3 Jun 1982, *D.M. Vital* 10506 (SP), 30 Nov 1983, *D.M. Vital* 11308 (SP); Guapiara, 8 Nov 1988, *S.R. Visnadi & D.M. Vital* 4977, 4985 (SP); Ibiuna, 30 Dez 1991, O. Yano & *M.P. Marcelli* 16126 (SP), 25 Feb 1993, O. Yano & *M.P. Marcelli* 18318 (SP); Itapeçerica da Serra, 29 Jun 1965, *D.M. Vital* 439 (SP); Mogi das Cruzes, 16 Jun 2006, *J. Bordin & D.F. Peralta* 709 (SP), 1 Nov 2008, *D.F. Peralta et al.* 7152, 7298 (SP); São Luiz do Paraitinga, 7 Sep 2009, *D.F. Peralta et al.* 9319 (SP), 11 Jun 2013, *D.F. Peralta & D.M. Carmo* 14358 (SP), 12 Jun 2013, *D.F. Peralta & D.M. Vital* 14597 (SP), 17 Apr 2013, *D.F. Peralta & A. Gugliotta* 13451, 13656 (SP); Ubatuba, 13 Oct 1995, *S.R. Visnadi & D.M. Vital* 2087 (SP).

Extinct species

Dendroceros exalatus Steph., Sitzungsber. Naturf. Ges. Leipzig 36: 14. 1909. Type: Brazil, Sellow s.n. (lectotype G00060902 (hb - Stephani no. 19702) [<https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00060902>], designated by Hasegawa (1980).

Description and illustration: Hasegawa (1980).

Dendroceros exalatus is recognized by cavernous midrib, described by Hasegawa (1980) that is unique among the Brazilian species of *Dendroceros*. Unfortunately, we could not find any other specimens of this species and this way our knowledge of this species is incomplete and based only in the notes of Hasegawa. He describes in the label attached to the type specimen features like verrucose involucrem and cavernous thallus, and so he probably studied the only and the last sporophyte of the sample, because the type specimen has no more sporophytes. The gametophytes are very tiny and branched very similar to gametophytes of *Riccardia*. Additional material of this species needs to be collected in order to discuss the ecology and geographical range.

Hasegawa (1980) explained that the citation of *Dendroceros exalatus* type specimen as from "Hab. Amboina" is erroneous and he finds only one specimen "Brasilia, Sello [w s.n.] (G19702)" that matches exactly with the original protologue by Stephani, which is used by Hasegawa (1980) to propose the lectotype.

This species is Brazilian endemic (without locality). Conservation status Extinct (EX) because it is no longer collected since the period of Sellow collected (Sellow do not include date in his collection but we are adopting Mitten in 1869 because there is the citation of several species described on Sellow collections). Habitat occurrence in Atlantic Forest in South Brazil, near Rio Grande do Sul (where Sellow collected in Brazil).

The type specimens analyzed by Hasegawa (1980) described by Stephani (1909) were the only specimens known and after we analyzed specimens and visited several localities from all regions of Brazil including those probably visited by Sellow region we consider this species as extinct.

CONCLUSION

We recognize three species of *Dendroceros* to Brazil, and the first extinct species, *D. exalatus* knowledge only by the type specimen. The *Dendroceros* species combine a set of characters rarely found among other hornworts as they epiphyte and or epiphyll habits, absence of stomata, multicellular spores and pseudoelaters with helical thickening bands.

The phylogenetic and morphological interrelations among the genera of Anthocerotophyta have been discussed by Duff *et al.* (2007) and Villarreal *et al.* (2010). But it is important to emphasize that the hornworts have been underestimated for a long time.

The Brazilian hornworts flora is little known yet, and as a pantropical group there are always new species and occurrences when new collections are made. To *Dendroceros* species is the same and we believe that the species number is bigger than we know, and we reinforce the importance of floristic studies.

Additionally, the sampling of the genus in molecular phylogenies is rather limited (Villarreal *et al.*, 2015b; Peñaloza-Bojacá *et al.*, 2019). We hope with this study to stimulate further collections and research including molecular techniques to access species boundaries and geographical relationships in this widespread genus.

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REFERENCES

- CAMPBELL, D.H. 1898. On the Structure and Development of *Dendroceros*, Nees. *Botanical Journal of the Linnean Society* 33: 467-478.
- CHANTANAORRAPINT, S. 2015. Taxonomic studies in Thai Anthocerotophyta II. The genus *Nothothylas* (Nothothyladaceae). *Cryptogamie Bryologie* 36: 251-266.
- COSTA, D.P. 2017 a. Antóceros. In: Forzza, R.C. *et al.*, eds. Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro, Rio de Janeiro. Accessed 13 March 2017. Available at: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB128470>
- COSTA, D.P. 2017 b. Dendrocerotaceae. In: Forzza, R.C. *et al.*, eds. Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro, Rio de Janeiro. Accessed 13 March 2017. Available at: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB97157>
- DUFF, R.J.; VILLARREAL, J.C.; CARGILL, D.C. & RENZAGLIA, K.S. 2007. Progress and challenges toward developing a phylogeny and classification of the hornworts. *The Bryologist* 110 (2): 214-243.
- FLORA DO BRASIL ONLINE. 2020. Jardim Botânico do Rio de Janeiro. Disponível em: <<http://floradobrasil.jbrj.gov.br/>>. [access 2018 Jan 18]
- FRAHM, J.P. 2005. The First Record of a Fossil Hornwort (Anthocerotophyta) from Dominican Amber. *The Bryologist* 108(1): 139-141.
- GARCIA, C.; SÉRGIO, C.; VILLARREAL, J.C.; SIM-SIM, M. & LARA, F. 2012. The Hornworts *Dendroceros* Nees and *Megaceros* Campb. in São Tomé e Príncipe (Africa, Gulf of Guinea) with the Description of *Dendroceros paivae* sp. nov. *Cryptogamie, Bryologie*, 33(1):3-21 (2012). <https://doi.org/10.7872/cryb.v33.iss1.2012.003>
- GOTTSCHÉ, C.M.; LINDENBERG, J.B.G. & NEES, C.G. 1844. *Synopsis Hepaticarum. Hamburgi.* p. 581.
- GOTTSCHÉ, C.; J.B.G. LINDENBERG, & C.G. NEES AB ESENBECK. 1846. *Synopsis Hepaticarum* 4: 581.
- GRADSTEIN, S.R.; CHURCHILL, S.P. & SALAZAR-ALLEN, N. 2001. Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* 86: 1-577.
- GRADSTEIN, S.R. & COSTA, D.P. 2003. Liverworts and hornworts of Brazil. *Memoirs of The New York Botanical Garden* 87: 1-301.
- HASEGAWA, J. 1980. Taxonomic studies on Asian Anthocerotae II. Some Asian species of *Dendroceros*. *Journal of the Hattori Botanical Laboratory* 68: 1-192.
- HASEGAWA, J. 1981. *Dendroceros borbonicus* Steph. - A new record for Sri Lanka. *Miscellanea Bryologica et Lichenologica* 9(2): 39-41.
- HASEGAWA, J. 1982. Note on Samoan species of *Dendroceros*. *Miscellanea Bryologica et Lichenologica* 9(5): 95-100.
- HASEGAWA, J. 1994. New classification of Anthocerotae. *Journal of the Hattori Botanical Laboratory* 76: 21-34.
- INFANTE, M. 2010. Notes on the genus *Dendroceros* in West Africa and South Atlantic Islands. *Journal of Bryology* 32: 283-287.

- PEÑALOZA-BOCAJÁ, G.F.; MACIEL-SILVA, A.S.; OLIVEIRA, B.A.; ARAÚJO, C.A.T.; FANTECELLE, L.B. & VILLARREAL, J.C. 2016. Anthocerotophyta: Compilação monográfica das espécies de antóceros registradas no Brasil, Flora do Brasil 2020. Available in adaisesmaciel.wixsite.com/briofitasufmg [access 2018 Jan 27].
- PEÑALOZA-BOJACÁ, G.F.; VILLARREAL-AGUILAR, J.C. & MACIEL-SILVA, A.S. 2019. Phylogenetic and morphological infrageneric classification of the genus *Dendroceros* (Dendrocerotaceae; Anthocerotophyta), with the addition of two new subgenera. *Systematics and Biodiversity* 17(7): 712-727.
- PROSKAUER, J. 1953. Studies on Anthocerotales IV. *Bulletin of the Torrey Botanical Club* 80: 65-75.
- QIU, Y.L.; LI, L.; WANG, B.; CHEN, Z.; KNOOP, V.; GROTH-MALONEK, M.; DOMBROVSKA, O.; LEE, J.; KENT, L.; REST, J.; ESTABROOK, G.F.; HENDRY, T.A.D.; TAYLOR, W.; TESTA, C.M.; AMBROS, M.; CRANDALL-STOTLER, B.; DUFF, R.J.; STECH, M.; FREY, W.; QUANDT, D. & DAVIS, C.C. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. *Proceedings of the National Academy of Sciences* 103: 15511-15516.
- RENZAGLIA, K.S. 1978. A comparative morphology and developmental anatomy of the Anthocerotophyta. *Journal of the Hattori Botanical Laboratory* 44: 31-90.
- RENZAGLIA, K.S.; VILLARREAL, J.C. & DUFF, R.G. 2009. New insights into morphology, anatomy and systematics of hornworts. In: Goffinet, B. & A.J. Shaw (eds.). *Bryophyte Biology*. 2nd. Cambridge University Press, Cambridge.
- SÉRGIO, C.G.C.; VILLARREAL, J.C.; SIM-SIM, M. & LARA, F. 2012. The Hornworts *Dendroceros* Nees and *Megaceros* Campb. in São Tomé e Príncipe (Africa, Gulf of Guinea) with the Description of *Dendroceros paivae* sp. nov. *Cryptogamie, Bryologie* 33(1): 3-21.
- SHAW, A.J. & GOFFINET, B. 2009. *Bryophyte Biology*. Cambridge University Press, England.
- SHAW, A.J.; SZÖVÉNYI, P. & SHAW, B. 2011. Bryophyte diversity and evolution: windows into the early evolution of land plants. *American Journal of Botany* 98 (3): 1-18.
- SÖDERSTRÖM, L.; HAGBORG, A.; KONRAT, M.; BARTHOLOMEW-BEGAN, S.; BELL, D.; BRISCOE, L.; BROWN, E.; CARGILL, D.C.; COSTA, D.P.; CRANDALL-STOTLER, B.J.; COOPER, E.D.; DAUPHIN, G.; ENGEL, J.J.; FELDBERG, K.; GLENNY, D.; GRADSTEIN, S.R.; HE, X.; HEINRICH, J.; HENTSCHEL, J.; ILKIU-BORGES, A.L.; KATAGIRI, T.; KONSTANTINOVA, N.A.; LARRAÍN, J.; LONG, D.G.; NEBEL, M.; PÓCS, T.; PUCHE, F.; REINER-DREHWALD, E.; RENNER, M.A.M.; SASS-GYARMATI, A.; SCHÄFER-VERWIMP, A.; MORAGUES, J.G.S.; STOTLER, R.E.; SUKKHARAK, P.; THIERS, B.M.; URIBE, J.; VÁÑA, J.; VILLARREAL, J.C.; WIGGINTON, M.; ZHANG, L. & RUI-LIANG, Z. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828.
- SPRUCE, R. 1885. Hepaticae Amazonicae et Andinae. *Journal of the Linnean Botanical Society* 15: 1-574.
- STEPHANI, F. 1909. Sitzungsber. Naturf. Ges. Leipzig 36: p. 14.
- STEPHANI, F. 1917. *Species Hepaticarum*. Acrogynae 5: p. 1017.
- STEPHANI, F. 1923. *Species Hepaticarum*. *Bulletin de l'Herbier Boissier* 4: p. 429.
- VAUGHN, K.C.; LIGRONE, R.; OWEN, H.A.; HASEGAWA, J.; CAMPBELL, E.O.; RENZAGLIA, K.S. & MONGENAJERA, J. 1992. The Anthocerotae Chloroplast: a Review. *New Phytologist* 120: 169-190.
- VILLARREAL, J.C.; MENENDÉZ, G.H. & ALLEN, N.S. 2007. *Nothoceros superbus* (Dendrocerotaceae), a new hornwort from Costa Rica. *The Bryologist* 110(2): 279-285.

- VILLARREAL, J.C.; CARGILL, D.C.; HAGBORG, A.; SÖDERSTRÖM L. & RENZAGLIA, K.S. 2010. A synthesis of hornwort diversity: patterns, causes and future work. *Phytotaxa* 9: 150-166.
- VILLARREAL, J.C.; GOFFINET, B. & CARGILL, D.C. 2010. Phylogenetic delineation of *Nothoceros* and *Megaceros* (Dendrocerotaceae). *The Bryologist* 113(1): 106-113.
- VILLARREAL, J.C.; CAMPOS, L.V.; URIBE, J. & GOFFINET, B. 2012. Parallel evolution of endospory within hornworts: *Nothoceros renzagliensis* (Dendrocerotaceae), sp. nov. *Systematic Botany* 37(1): 31-37.
- VILLARREAL, J.C.; CARGILL, D.C.; SÖDERSTRÖM, L.; HAGBORG, A. & KONRAD, M.V. 2015a. Notes on Early Land Plants Today. 70. Nomenclatural notes in hornworts (Anthocerotophyta). *Phytotaxa* 208 (1): 92-96.
- VILLARREAL, J.C. & RENZAGLIA, K. . 2015b. The hornworts: important advancements in early land plant evolution. *Journal of Bryology* 37(3): 157-170.
- YANO, O. 2008. Catálogo dos Antóceros e Hepáticas brasileiros: literatura original, localidade-tipo e distribuição geográfica. *Boletim do Instituto de Botânica* 19: 1-119.
- YANO, O. 2010. Levantamento de novas ocorrências de briófitas brasileiras. Instituto de botânica. Publicação on-line do Instituto de Botânica. Accessed: 15 February 2016. Available at: www.i-bot.sp.gov.br/briófitasBrasileiras/BriófitasMIOLOECAPA.pdf

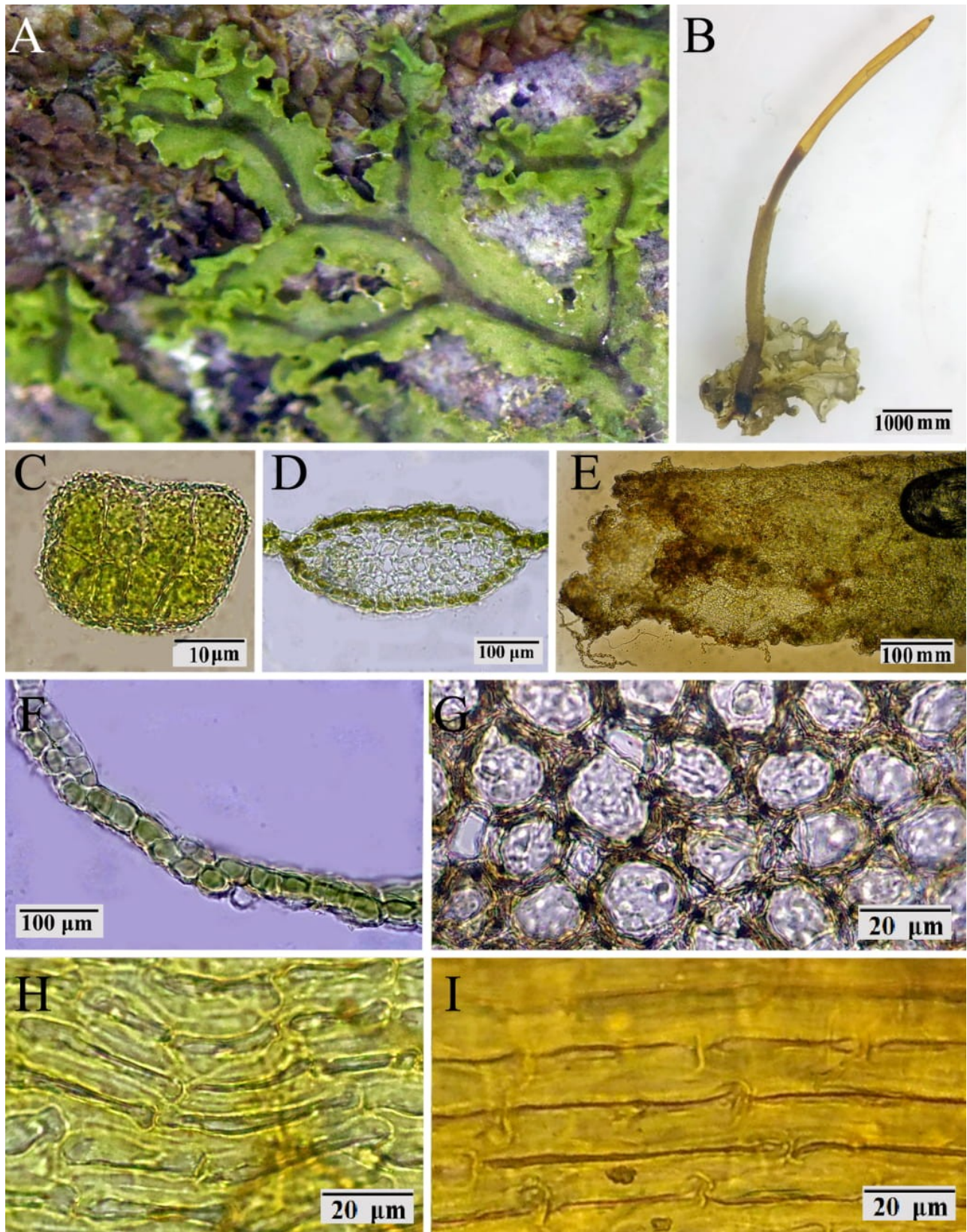


Figure 1. A–G. *Dendroceros breutelii* Nees **A.** Gametophyte on substrate. **B.** General aspect of the thallus with capsule. **C.** Spore. **D.** Cross section of midrib. **E.** Distal portion of the involucre. **F.** Cross section of the involucre. **G.** Epidermal cells of thallus. **H.** Epidermal cells of distal portion of capsule. **I.** Epidermal cells of the capsule.

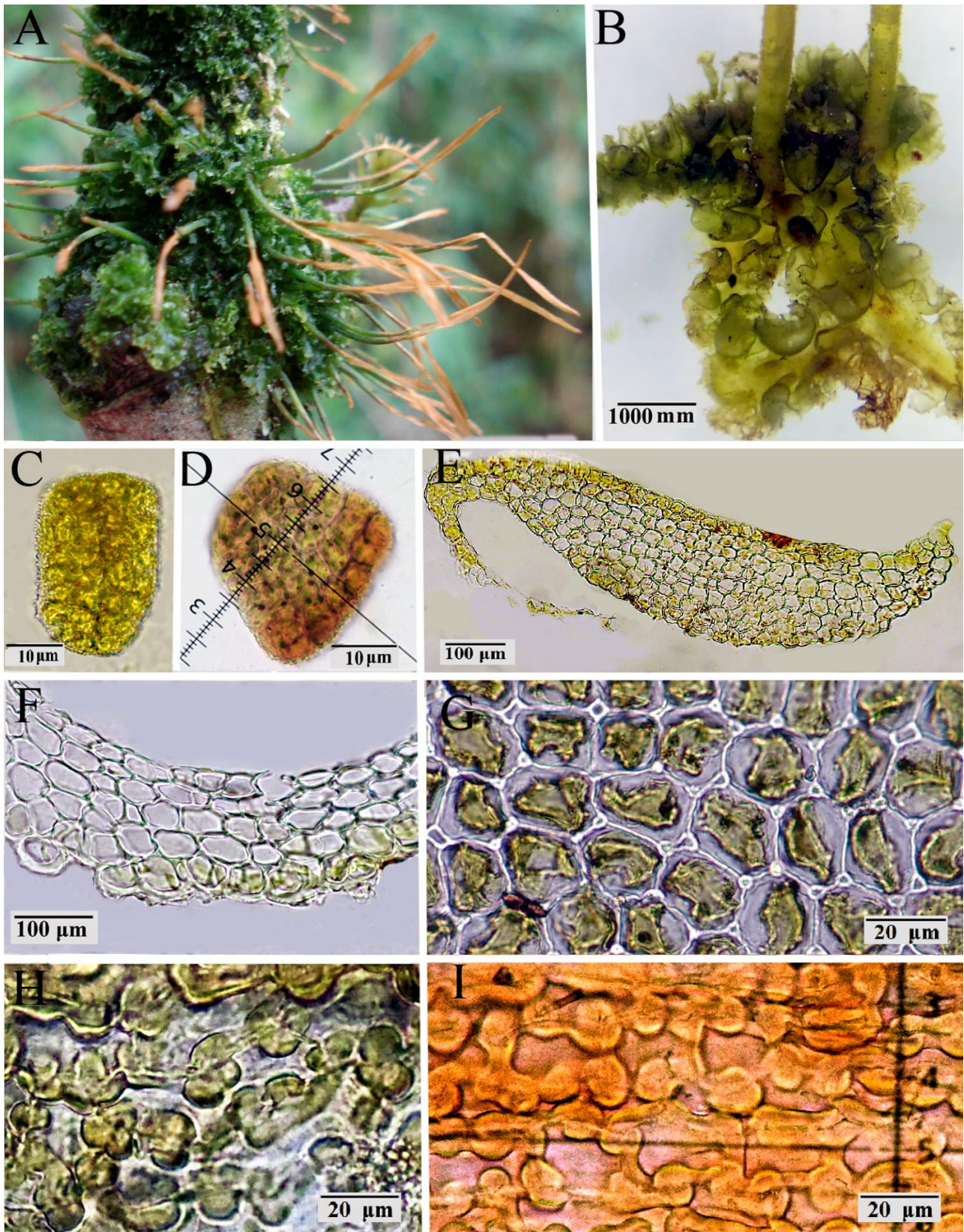


Figure 2. A–G. *Dendroceros crispatus* (Hook.) Nees. **A.** Gametophyte on substrate. **B.** General aspect of the thallus with capsule. **C–D.** Spore. **E.** Cross section of midrib. **F.** Cross section of the involucrem. **G.** Epidermal cells of thallus. **H.** Epidermal cells of distal portion of capsule. **I.** Epidermal cells of the capsule.

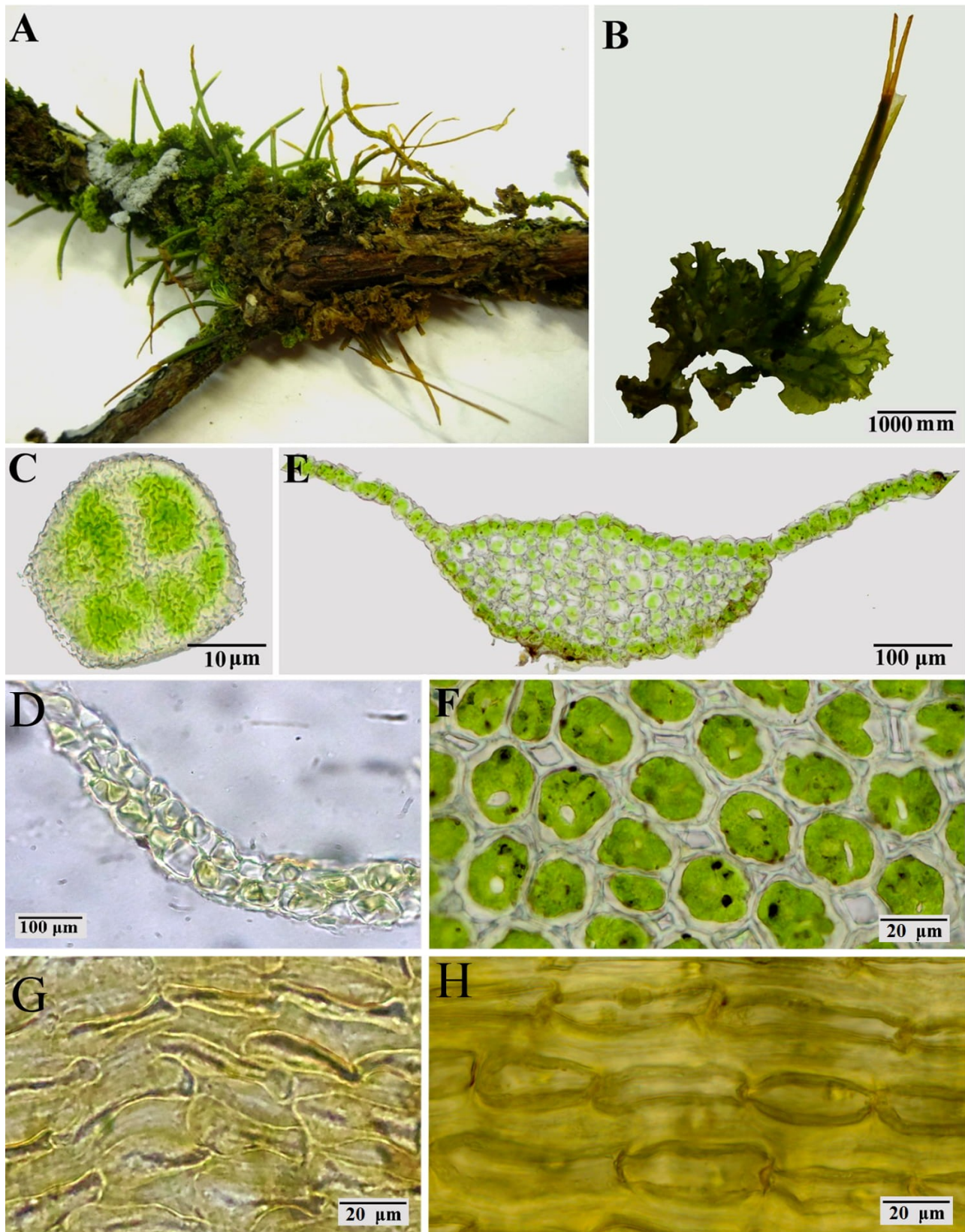


Figure 3. A–G. *Dendroceros crispus* (Sw.) Nees **A.** Gametophyte on substrate. **B.** General aspect of the thallus with capsule. **C.** Spore. **D.** Cross Section of the involucrem. **E.** Cross section of midrib. **F.** Epidermal cells of thallus. **G.** Epidermal cells of distal portion of capsule. **H.** Epidermal cells of capsule.

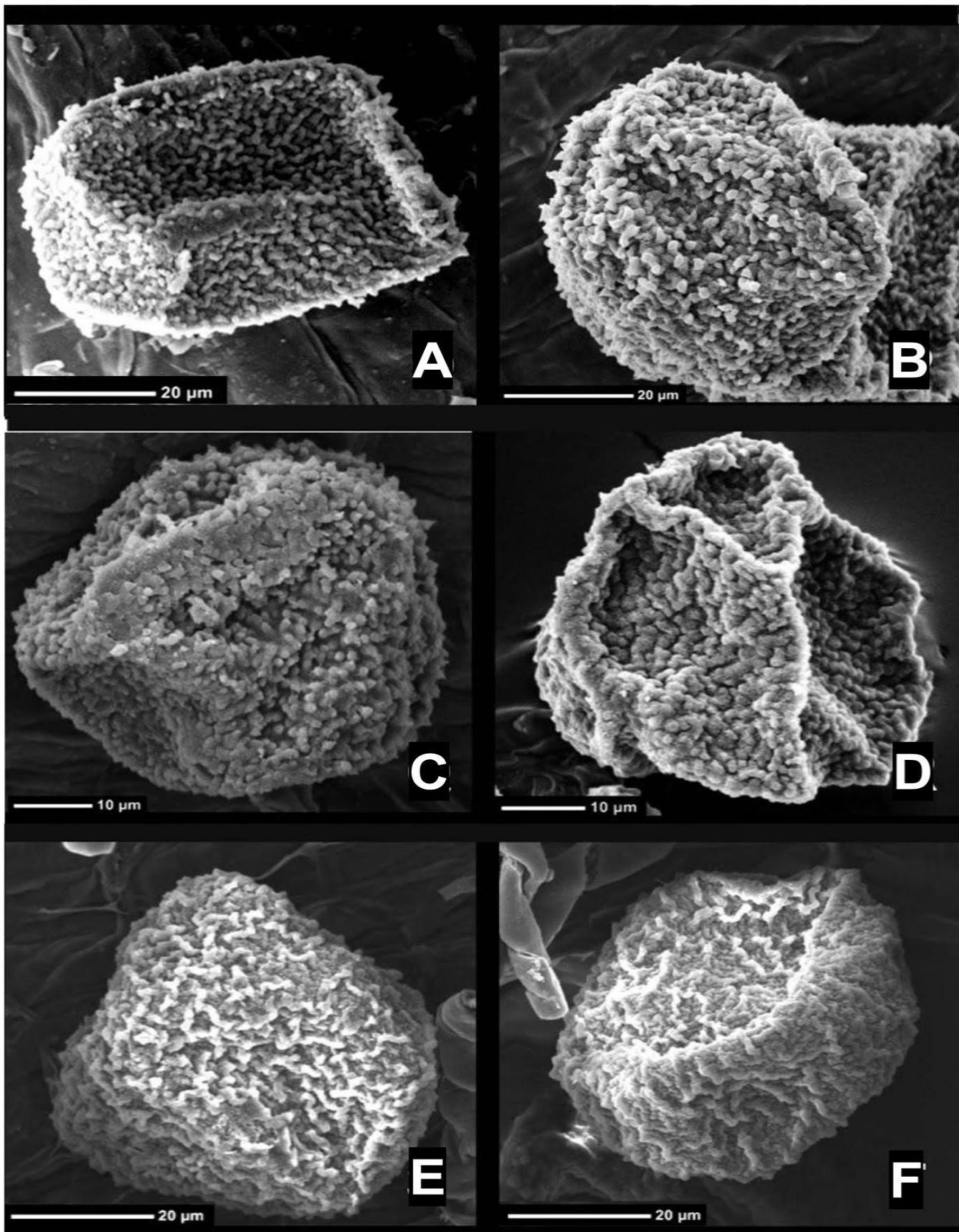


Figure 4. Spore Scanning Electron Microscopy characterization of the inner and outer view of the Brazilian *Dendroceros*. **A–B.** *Dendroceros breutelii* Nees **C–D.** *Dendroceros crispatus* (Hook) Nees **E–F.** *Dendroceros crispus* (Sw.) Nees.