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PENSOFT

Leafy liverworts of Chapada das Mesas National Park: a floristic survey and checklist of the leafy liverworts of Maranhão state, Brazil

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Abstract

Chapada das Mesas National Park (CMNP) is the fourth largest conservation unit in Maranhão state and an important area for the study of bryophytes due to its geomorphological characteristics, predominant vegetation, and water potential. The aim of our study was to investigate the richness and composition of leafy liverwort species in CMNP, discuss the importance of this area in the state, and present an updated checklist of the leafy liverworts for Maranhão. Our botanical material was collected during four excursions to the park. The checklist was mainly based on literature reports. Forty-one species and two varieties in eight families and 20 genera were identified in CMNP. From the state of Maranhão, 106 species and two varieties in nine families and 39 genera are reported. Our survey of bryophytes in CMNP resulted in the first records from Maranhão of 19 species. *Lejeunea juruana* Gradst. & M.E.Reiner is also newly found in the Northeastern region of Brazil and in the Cerrado domain.

Keywords

Biodiversity, bryophyte flora, conservation units, Marchantiophyta, taxonomy

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Introduction

The Brazilian state of Maranhão is characterized by having large hydrographic basins (Montes et al. 1997; Bandeira 2013) and high biodiversity (Ab'Saber 1977; Muniz 2006; Dias et al. 2009; Spinelli-Araujo et al. 2016). Three of the six biomes in Brazil are present in Maranhão, as well as two transition zones: from the Amazon to Cerrado, and from Cerrado to Caatinga (Stella 2011).

Notwithstanding the high biological richness typical of transition zones (Odum 1988; Haidar et al. 2013; Spinelli-Araújo et al. 2016), little of Maranhão is legally protected (Araújo et al. 2011). Natural vegetation covers 75% of the state, but less than 19% of it is protected within 11 conservation units (five extractive reserves, three state parks, two national parks, and one biological reserve;

Spinelli-Araújo et al. 2016; Masullo et al. 2018). This number is very low when compared to other Brazilian states, such as Amapá, where 19 protected areas cover 72% of the territory (Drummond et al. 2008).

Chapada das Mesas National Park (CMNP) is the fourth largest conservation unit in Maranhão and extends over the territories of three municipalities. CMNP has Cerrado (sensu stricto) phytophysiognomy. Cliffs, predominant vegetation, and abundance of springs, waterfalls, and rivers in CMNP harbors a rich bryophyte flora which makes the exploration of this park all the more important.

Oliveira et al. (2018a) published the only study of bryophytes in CMNP, and it is on acrocarpic mosses. This study recorded 38 species, including 22 species found in Maranhão for the first time.

In the last 10 years, knowledge on the bryophyte flora of Maranhão has increased; new occurrences continue to be reported (e.g., Peralta et al. 2011; Macedo and Ilkiu-Borges 2014) and new species discovered (Brito and Ilkiu-Borges 2012). Altogether, studies provide records of leafy liverworts from the state.

The first species recorded in the state were *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. and *Xylolejeunea crenata* (Nees & Mont.) X.-L.He & Grolle (Yano et al. 1987; He and Grolle 2001). Yano et al. (2009) recorded 20 leafy liverwort species and Santos and Conceição (2010) 23 bryophyte species for Maranhão among which only *Monodactylopsis monodactyla* (Spruce) R.M.Schust. was a newly reported from the state. Peralta et al. (2011) added 15 species of leafy liverwort species out of a total of 49 bryophyte species added to the state's flora. Varão et al. (2011) recorded 22 species of bryophytes for the Bananal district, in the municipality of Governador Edison Lobão, but no species were new to the flora.

Brito and Ilkiu-Borges (2012) described *Ceratolejeunea maranhensis* Silva Brito & Ilk.-Borg. As part of a study of bryophytes in the city of Mirinzal; in the same study, four species were found for the first time in the state and one in the Northeast region. Macedo and Ilkiu-Borges (2014) added a new record of leafy liverworts collected in the Amazonia of Maranhão, totaling 37 new occurrences for the state.

Other studies of bryophytes conducted in Maranhão focused on the survey of bryophytes in diverse areas located in different municipalities (Costa et al. 2015; Vieira et al. 2017; Costa et al. 2018; Oliveira et al. 2018b, c; Silva et al. 2018; Bonfim et al. 2019). Of these works, only Oliveira et al. (2018b) recorded eight new leafy liverwort species for the state.

In our study, we investigate the richness and composition of leafy liverwort species in CMNP by including new collections and data from the literature. We discuss the importance of this area for the state and present an updated list of the leafy liverworts known to occur in Maranhão.

Study Area

Chapada das Mesas National Park (CMNP) is located in the state of Maranhão, northeastern Brazil. The park has an area of 159,954 ha in the municipalities of Carolina, Estreito, and Riachão (Fig. 1). Most of the park is on a plateau which at its base has an altitude of 250 m. There are high sandstone hills which were sculpted by the action of winds and rains. The relief is characterized by presence of sandstone and typical forms of paleokarst in sandstone. The soil is sandy, covered by vegetation physiognomies included in the Cerrado phytogeographic domain, among which savanna and gallery forest are notable. There are also Caatinga and Amazonian species intermingled, which increase the diversity of the area (Fig. 2) (Martins et al. 2017; ICMBio 2020).

CMNP has an abundance of water, including over 400 springs, and the Farinha and Itapecuru are the main rivers.

The region around CMNP has a very stable, tropical, humid climate, with high temperatures throughout the year. There are two well-defined seasons, the rainy season from December to May and the less rainy season from June to November. The average annual temperature and precipitation are 27 °C and 1,727 mm, respectively (INMET 2020).

Methods

We made four excursions to the study area, in March and October 2017, June 2018, and February 2020. Our methodology for collecting, herborizing, and preserving the botanical material follows Yano (1984). The samples were deposited in the CCAA herbarium of the Universidade Federal do Maranhão (UFMA).

Most of the samples were identified in the Biogeocycles/Limnology and Plant Systematics laboratories of the UFMA, but another part of the samples were identified in the Laboratory of Bryology at the Museu Paraense Emílio Goeldi.

Taxonomic identification was based on specialized literature (Gradstein et al. 2001; Gradstein and Costa 2003; Gradstein and Ilkiu-Borges 2009, 2015; Bastos 2017; Lima et al. 2018; Ilkiu-Borges and Oliveira-da-Silva 2018).

We adopted the taxonomic classification of Crandall-Stotler et al. (2009). However, for the classification of the genera *Dibrachiella* (Spruce) X.Q.Shi, R.L.Zhu & Gradst. and *Thysananthus* Lindenb., we followed Shi et al. (2015) and Sukkharak and Gradstein (2017), respectively. We also followed Söderström et al. (2016) to confirm all liverwort names.

To prepare the list of leafy liverworts of the state of Maranhão, we consulted taxonomic reviews and data available in online sources, such as the works by Yano et al. (1987), He and Grolle (2001), Yano et al. (2009), Santos and Conceição (2010), Peralta et al. (2011), Varão et al. (2011), Macedo and Ilkiu-Borges (2014), Brito and Ilkiu-Borges (2012, 2014), Costa et al. (2015), Costa and

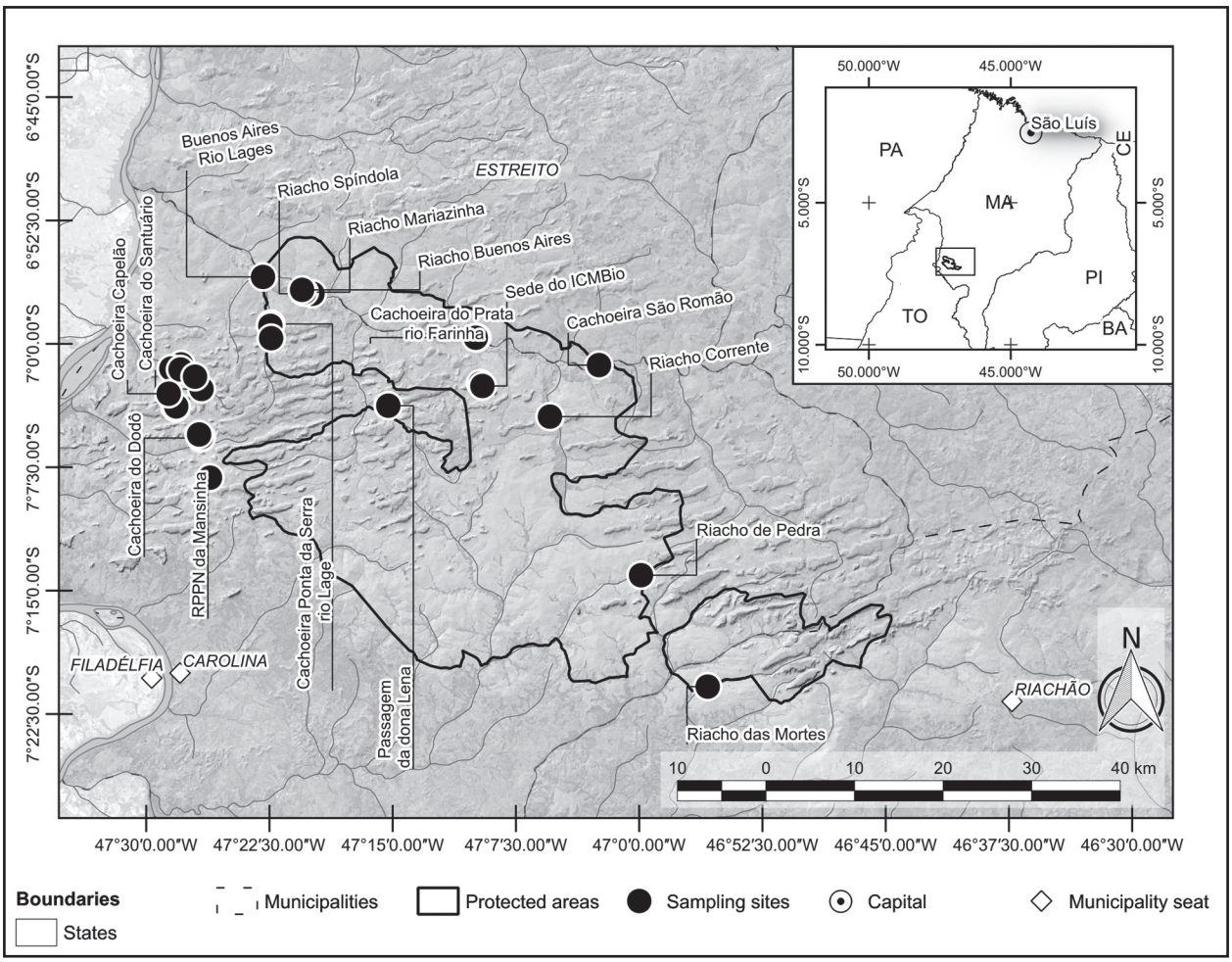

Figure 1. Map of the study area, showing sampling sites, both inside and outside of Chapada das Mesas National Park.

Conceição (2015), Vieira et al. (2017), Costa et al. (2018), BFG (2018), Oliveira et al. (2018b, 2018c), and Bonfim et al. (2019).

The distribution pattern (Neotropical, Pantropical, endemic to Brazil, Afro-American, South American, or Tropical South and Central American) of each species is based on Gradstein and Costa (2003), Costa et al. (2011), Yano (2011), Gradstein (2013), and BFG (2018). We classified species as South American when present in more than one country of South America.

Results

We examined 388 specimens of leafy liverworts collected from CMNP and identified 41 species and two varieties distributed in eight families and 20 genera. Lejeuneaceae Cavers had the greatest species richness and abundance (25 spp. and two varieties; 181 specimens), which was followed by Frullaniaceae Lorch (5 spp.; 15 specimens). These families together represented 73% of the leafy liverwort flora of the study area.

The most representative genera were *Cheilolejeunea* (Spruce) Steph., *Frullania* Raddi, and *Lejeunea* Lib., with seven, five, and four species, respectively. The most abundant species were *Lejeunea glaucescens* Gottsche, *Cheilolejeunea trifaria* (Reinw, Blume & Nees) Mizut., *Ceratolejeunea cubensis* (Mont.) Schiffn., and *Zoopsidella integrifolia* (Spruce) R.M.Schust., with 53, 23, 22, and 21 occurrences, respectively.

As for distribution in substrates (Fig. 2G–I), rupicolous species predominated (32 spp.; 95 specimens), followed by corticolous (22 spp.; 48 specimens), epixylic (13 spp.; 16 specimens), terrestrial (9 spp.; 30 specimens), and epiphyllous (5 spp.; 12 specimens) species.

We added 19 species of leafy liverworts to the bryoflora of Maranhão: *Cylindrocolea planifolia* (Steph.) R.M. Schust., *Odontoschisma variabile* (Lindenb. & Gottsche) Trevis., *Frullania intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb., *F. rio-janeirensis* (Raddi) Ångstr., *Ceratolejeunea cubensis*, *Cheilolejeunea acutangula* (Nees) Grolle, *C. intertexta* (Lindenb.) Steph., *C. trifaria*, *Lejeunea controversa* Gottsche, *L. quinqueumbonata* Spruce, *L. juruana*, *Metalejeunea cucullata* (Reinw, Blume & Nees) Grolle, *Otigoniolejeunea huctumalcensis* (Lindenb. & Gottsche) Y.M.Wei, R.L.Zhu & Gradst., *Schiffneriolejeunea polycarpa* (Nees) Gradst., *Zoopsidella integrifolia*, *Lophocolea bidentata* (L.) Dumort., *Plagiochila exigua* (Taylor) Taylor, *P. raddiana* Lindenb., and *P. simplex* (Sw.) Lindenb. *Lejeunea juruana*, which was previously known only from Amazonas, Mato Grosso, and São Paulo, is newly reported from the Northeastern region of Brazil.

Figure 2. Diversity of environments and substrates of leafy liverworts in the Chapada das Mesas National Park. **A.** Waterfall São Romão; **B.** Waterfall Prata; **C.** Meeting of the Lage River with the Farinha River; **D.** Stream Bueno Aires; **E.** Waterfall Pedra Caída; **F.** Body of water near the ICMBio headquarters; **G.** *Acrolejeunea* (Spruce) Steph. and *Frullania* Raddi species on the live tree trunks; **H.** *Fossombronia porphyrorhiza* (Nees) Prosk. on decomposing trunks; **I.** *Lejeunea* Lib. species on soil; **J.** *Cololejeunea* (Spruce) Steph. species on leaves; **K.** *Cheilolejeunea* (Spruce) Steph. species on rocks; **L.** Bryophyte species on rocks and live trunks near the waterfall.

Noteworthy species in CMNP are illustrated (Fig. 3). Species with one asterisk are selected records from our collection in the Chapada das Mesas National Park, species with two asterisks are newly recorded from Maranhão, and the one species with three asterisks is newly recorded from the Northeast region of Brazil.

Cephaloziellaceae

***Cylindrocolea planifolia* (Steph.) R.M.Schust.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída–Cachoeira Pedra Furada, rupícola; 07°03′S, 047°28′W; alt. 200 m; 7 Feb. 2020; JAS Silva 579; CCAA 2353.

Identification. Plants light green to brownish, ca. 1 mm wide. Leaves succubous, inserted laterally on the stem, ovate, 2-lobed with acute or somewhat obtuse apex, margin entire, plane to slightly recurved; cells rectangular, trigones absent or minute, cuticle smooth. Underleaves lacking.

In Brazil, three species are recognized, *Cylindrocolea planifolia*, *C. ryzantha*, and *C. brasiliensis* Costa et al. Differences between them are presented in the key by Costa et al. (2008).

Description and illustration. Fulford (1976: 399–401, fig. 2).

***Cylindrocolea rhizantha* (Mont.) R.M.Schust.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída–Cachoeira Pedra Furada, rupícola; 07°03′S, 047°28′W; alt. 200 m; 7 Feb. 2020; JAS Silva 578; CCAA 2352.

Cephaloziaceae

***Odontoschisma variabile* (Lindenb. & Gottsche) Trevis.**

Material examined. BRAZIL • Maranhão, Parque Nacional Chapada das Mesas, Cachoeira do Dodô, rupícola; 07°05′S, 047°26′W; alt. 234 m; 5 Feb. 2020; JAS Silva 512; CCAA 2343. Maranhão, Parque Nacional Chapada das Mesas, Constância Ecológica, Vereda Bonita, corticícola, próximo à queda d'água; 07°03′S, 047°15′W; alt. 191 m; 5 Feb. 2020; JAS Silva 497; CCAA 2332.

Identification. Plants pale green. Leafy branches predominantly ventral-intercalary, stolons frequent, sometimes with rudimentary leaves. Leaves distant to imbricate, ovate to oblong-ovate, asymmetric, apex rounded to short bifid, margin frequently incurved, slightly bordered by one row of subquadrate cells; cells isodiametrical-hexagonal, usually becoming smaller towards the margin, trigones usually large, inflated, cuticle papillose.

The pantropical–holarctic genus *Odontochisma* is represented by 21 species, of which five occur in Brazil. Gradstein and Ilkiu-Borges (2015) presented a taxonomic revision of this genus.

Description and illustration. Gradstein and Ilkiu-Borges (2015: 72–78, fig. 26).

Fossombroniaceae

***Fossombronia porphyrorhiza* (Nees) Prosk.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, sobre solo na trilha da cachoeira do Prata; 06° 59′S, 049°09′W; alt. 197 m; 6 Jun. 2018; JAS Silva 205; CCAA 1763.

Frullaniaceae

***Frullania ericoides* (Nees) Mont.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho Buenos Aires, corticícola, ilha da cachoeira do Prata; 06°56′S, 047°20′W; alt. 228 m; 30 Oct. 2017; JAS Silva 149; CCAA 1567.

***Frullania gibbosa* Nees**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Buenos Aires, sobre serrapilheira, mata de galeria, próxima a margem do rio; 06°56′S, 047°20′W; alt. 228 m; 29 Oct. 2017; JAS Silva 156; CCAA 1585.

***Frullania intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb.**

Figure 3A

Material examined. BRAZIL • Maranhão, Parque Nacional Chapada das Mesas, Rio Laje, sobre rochas próximo à casa do Síduca; 06°59′S, 047°22′W; alt. 243 m; 4 Feb. 2020; JAS Silva 467; CCAA 2343. Maranhão, Parque Nacional Chapada das Mesas, Trilha morro do Dodô, sobre rochas; 07°05′S, 047°26′W; alt. 256 m; 5 Feb. 2020; JAS Silva 515; CCAA 2337.

Identification. Plants green, brown, or reddish-brown, irregularly pinnate, bipinnate to tripinnate branched. Hemiphyll entire associated with a lobule. Leaves imbricate, ovate, strongly convex, margins entire, dorsal base auriculate, apex slightly acute to apiculate, incurved; median cells elongated, trigones nodulose. Lobules erect, subparallel to the stem, subcylindrical (attenuated at base), rarely laminate, beak absent. Stylus filiform, 2–4 cells in a row, 1 cell wide at base. Underleaves subimbricate to imbricate, ovate, ⅓–¼ bifid, margins entire, recurved, apex acute, base rounded to auriculate, recurved, insertion line curved.

Frullania intumescens is characterized by leaf lobes strongly convex, with strongly incurved, acute to apiculate margin, underleaves usually subimbricate, with margin recurved and base varying from rounded to auriculate.

Description and illustration. Lima et al. (2018: 978–980, fig. 5).

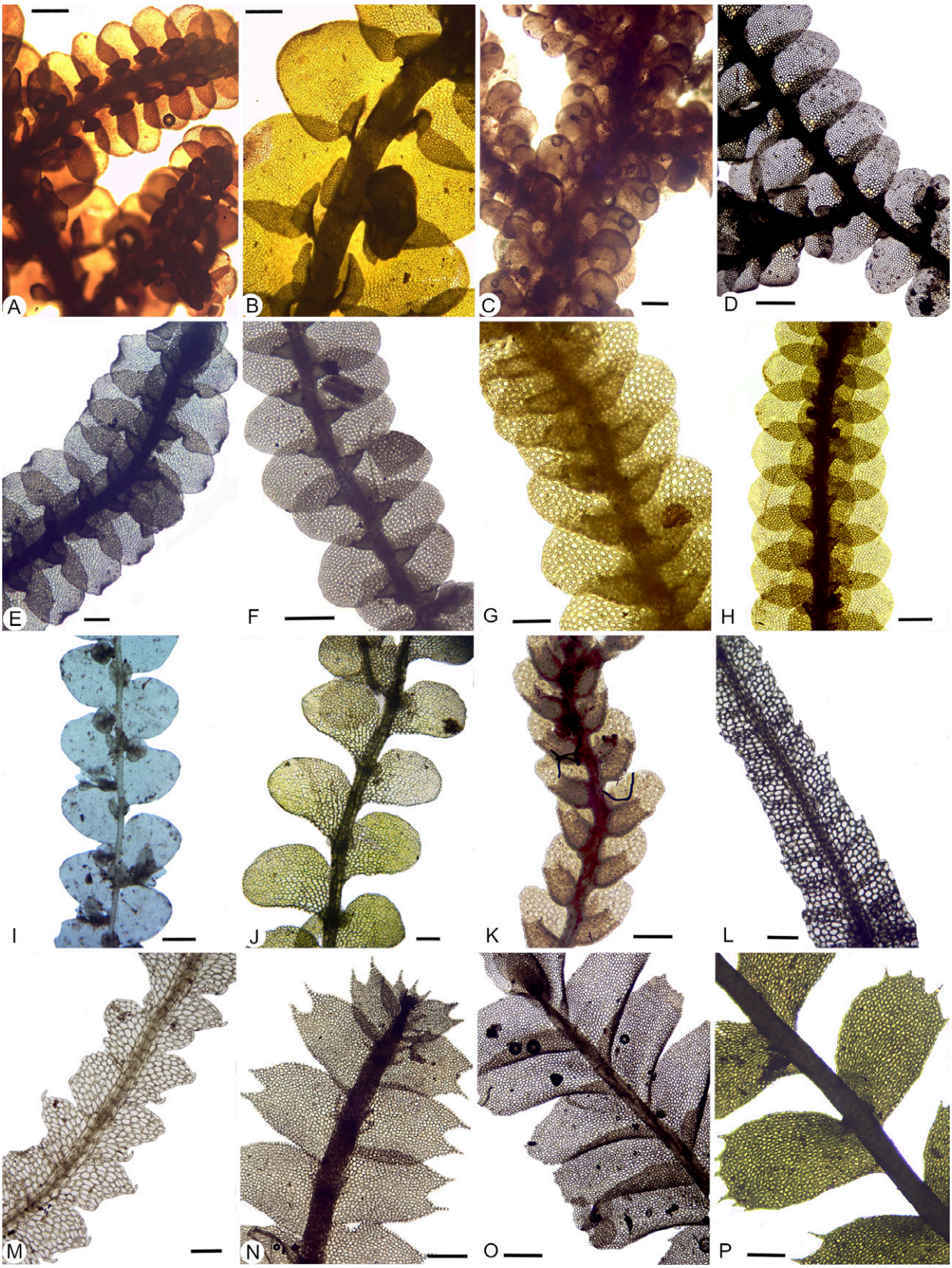

Figure 3. Leafy liverworts of the Chapada das Mesas National Park; **A.** *Frullania intumescens*; **B.** *Frullania platicalyx*; **C.** *Frullania rio-janeirensis*; **D.** *Ceratolejeunea cubensis*; **E.** *Cheilolejeunea acutangula*; **F.** *Cheilolejeunea adnata* var. *adnata*; **G.** *Cheilolejeunea intertexta*; **H.** *Cheilolejeunea trifaria*; **I.** *Lejeunea juruana*; **J.** *Lejeunea quinqueumbonata*; **K.** *Metalejeunea cucullata*; **L.** *Zoopsidella integrifolia*; **M.** *Zoopsidella macella*; **N.** *Lophocolea bidentata*; **O.** *Plagiochila raddiana*; **P.** *Plagiochila simplex* (Scale bar: A-B, F-G, P= 20 µm; C-D, H-O= 100 µm; E= 300 µm).

***Frullania platicalyx* Herzog**
Figure 3B

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Prata, Rio Farinha, corticícola, ramos parcialmente eretos; 06°59′S, 047°09′W; alt. 231 m; 5 Feb. 2020; JAS Silva 473; CCAA 2339.

****Frullania rio-janeirensis* (Raddi) Ångstr.**
Figure 3C

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, sobre tronco de árvore próximo à corrente d´água; 06°59′S, 049°09′W; alt. 197 m; 6 Jun. 2018; JAS Silva 203; CCAA 1645.

Identification. Plants green to brown, irregularly (bi)pinnate branched. Hemiphyll entire associated with a lobule. Leaves subimbricate to imbricate, orbicular, slightly convex, margins entire, dorsal base auriculate, apex rounded, slightly plane; median cells isodiametric, trigones nodulose. Lobules erect, subparallel to the stem, galeate with an oblong laminal portion, rarely laminate, beak long, not decurrent. Stylus filiform, 2–3 cells in a row, 1–2 cell wide at base. Underleaves imbricate, orbicular, ⅙ bifid, margins entire, recurved, apex rounded, base rounded to auriculate, plane to recurved, insertion line curved.

Widely distributed in Brazil, this species is recognized by lobules galeate with a long beak and an oblong laminal portion (as large as the galeate portion) and perianth 4-keeled.

Description and illustration. Schuster (1992: 254–260, fig. 816).

Lejeuneaceae

***Acrolejeunea emergens* (Mitt.) Steph.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Prata, Rio Farinha, corticícola, na margem direita do Rio Farinha; 06°59′S, 047°09′W; alt. 228 m; 15 Mar. 2017; JAS Silva 82; CCAA 1773.

***Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Mata do Buenos Aires, epíxila, na mata ciliar; 06°55′S, 047°22′W; alt. 174 m; 4 Feb. 2020; JAS Silva 455; CCAA 2350.

***Ceratolejeunea cornuta* (Lindenb.) Schiffn.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Dodô, rupícola; 07°05′S, 047°26′W; alt. 234 m; 5 Feb. 2020; JAS Silva 514; CCAA 2349.

****Ceratolejeunea cubensis* (Mont.) Schiffn.**
Figure 3D

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Laje, Cachoeira Ponta da Serra, sobre rochas; 06°58′S, 047° 22′W; alt. 228 m; 11 Mar. 2017; JAS Silva 50; CCAA 1718.

Identification. Plants green to brown. Ventral merophyte of 2 cells wide. Leaves imbricate, ovate, apex rounded to widely acute, ± plane to ± incurved, margin entire to toothed near the apex; median cells isodiametric; ocelli usually 2(–8), suprabasal. Lobules ovate, ⅓–⅕ lobe length, rarely reduced, apical teeth short, falcate. Underleaves distant, bifid, ovate, usually longer than large, (2–)3 × stem width, base rounded, apex acute, margin ± entire.

Description and illustration. Dauphin (2003: 48–52, fig. 21); Gradstein and Ilkiu-Borges (2009: 58, fig. 32d–f).

****Cheilolejeunea acutangula* (Nees) Grolle**
Figure 3E

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho na RPPN da Mansinha, corticícola em mata de galeria; 07°08′S, 047°26′W; alt. 286 m; 3 Feb. 2020; JAS Silva 442; CCAA 2330.

Identification. Plants pale green. Ventral merophyte of 2 cells wide. Leaves subimbricate, ovate, apex acute to short acuminate, incurved, margin entire to slightly crenate, dorsal and ventral margin curved; median cells isodiametric, ca. 12–20 µm, trigones large, dorsal surface of the lobe slightly papillose. Lobules ovate, ¼ lobe length, apical tooth long, falcate. Underleaves distant, bifid, ovate to orbicular, larger than long or as large as long, 2–3 × stem width, base cuneate, apex acute, margin ± entire or with a lateral angular tooth. Gynoecia with a pycnolejeuneoid innovation, usually sterile. Perianth obovate, 5-keeled.

Cheilolejeunea acutangula is recognized by leaf lobe apex acute to short acuminate, leaf cells with large trigones and dorsal surface of the lobe slightly papillose. This species is commonly reported for xeric environments.

Description and illustration. Ilkiu-Borges and Oliveira-da-Silva (2018: 995–997, fig. 3a–c).

Cheilolejeunea adnata* (Kunze) Grolle var. *adnata
Figure 3F

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Mata do Buenos Aires, epíxila, na mata ciliar; 06°55′S, 047°22′W; alt. 174 m; 4 Feb. 2020; JAS Silva 455; CCAA 2350.

***Cheilolejeunea adnata* var. *autoica* Gradst. & Ilk.-Borg.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, corticícola, mata de galeria, Mansinha; 06°59′S, 047°09′W; alt. 195 m; 6 Jun. 2018; JAS Silva 334; CCAA 1754.

***Cheilolejeunea intertexta* (Lindenb.) Steph.**
Figure 3G

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, sobre troncos em decomposição próximo a cachoeira Buenos Aires; 06°56′S, 047°20′W; alt. 181 m; 11 Mar. 2017; JAS Silva 26; CCAA 1560.

Identification. Plants autoicous, green. Ventral merophyte of 2 cells wide. Leaves imbricate, ovate, apex rounded, plane to slightly incurved, margins entire, dorsal and ventral margin curved; median cells isodiametric to elongate, trigones small, cuticle smooth. Lobules ovate, ⅓ leaf length, apical tooth short. Underleaves distant, bifid to ½ of length, ovate-orbicular, 2(−3) stem width, base rounded with insertion line arched, apex acute, margin entire. Gynoecia with one pycnolejeuneoid innovation. Perianth obovate, 5-keeled.

Description and illustration. Bastos and Yano (2005, as *Cheilolejeunea paroica* Mizut.).

***Cheilolejeunea oncophylla* (Ångstr.) Grolle & M.E.Reiner**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Constância Ecológica, Vereda Bonita, corticícola, próximo à queda d'água; 07°03′S, 047°15′W; alt. 191 m; 5 Feb. 2020; JAS Silva 497; CCAA 2332.

***Cheilolejeunea rigidula* (Mont.) R.M.Schust.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Laje, terrícola, próximo ao curso d'água da cachoeira do Síduca, mata de galeria; 06°58′S, 047°22′W; alt. 241 m; 4 Feb. 2020; JAS Silva 464 (CCAA 2338).

***Cheilolejeunea savannae* L.P.Macedo, Ilk.-Borg. & C.J.Bastos**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Buenos Aires, sobre serapilheira, mata de galeria próximo a margem do riacho; 06°56′S, 047°20′W; alt. 228 m; 29 Oct. 2017; JAS Silva 156; CCAA 2350.

Cheilolejeunea savannae was recently described by Macedo et al. (2020). It occurrs in savanna vegetation, teso, várzea, and secondary forest in Amapá, Maranhão, and Pará states. This species was first identified as *Cheilolejeunea discoidea* (Lehm. & Lindenb.) Kachroo & R.M.Schust. by Ilkiu-Borges et al. (2009), Macedo and Ilkiu-Borges (2014), and Brito and Ilkiu-Borges (2014).

***Cheilolejeunea trifaria* (Reinw, Blume & Nees) Mizut.**
Figure 3H

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho Buenos Aires, corticícola, ilha da Cachoeira do Prata; 06°56′S, 047°20′W; alt. 228 m; 30 Oct. 2017; JAS Silva 149; CCAA 1567.

Identification. Plants olive-green. Ventral merophyte of 2 cells wide. Leaves subimbricate, suborbicular, apex rounded, plane to slightly incurved, margin entire or sinuate, dorsal and ventral margin curved; median cells isodiametric, ca. 20–25 µm, trigones small to large. Lobules ovate to elongate (usually hidden behind the underleaves), ⅓–½ lobe length, apical tooth short. Underleaves contiguous to subimbricate, bifid to ⅓–½ of length, ovate, larger than long, 3–6 × stem width, base broadly rounded with insertion line deeply arched, apex acute, margin entire. Gynoecia with 1–2 lejeuneoid innovation, often fertile. Perianth obovate, 5-keeled.

Cheilolejeunea trifaria is easily recognized by relatively large plants with suborbicular leaf lobes, lobules ovate to elongate, hidden behind the large underleaves (3–6 × stem width).

Description and illustration. Gradstein and Ilkiu-Borges (2009: 68, fig. 38e–g).

***Cololejeunea cardiocarpa* (Mont.) A.Evans**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho na RPPN da Mansinha, epífila em mata de galeria; 07° 08′S, 047°26′W; alt. 286 m; 4 Feb. 2020; JAS Silva 438; CCAA 2334.

***Cololejeunea diaphana* A.Evans**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho na RPPN da Mansinha, epífila em mata de galeria; 07° 08′S, 047°26′W; alt. 286 m; 4 Feb. 2020; JAS Silva 438; CCAA 2334.

***Dibrachiella parviflora* (Nees) X.Q.Shi, R.L.Zhu & Gradst.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, rupícola, próximo à queda d'água, trilha da cachoeira do Prata; 06°59′S, 049°09′W; alt. 197 m; 6 Jun. 2018; JAS Silva 214; CCAA 1562.

***Lejeunea controversa* Gottsche**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída–Cachoeira Pedra Furada, rupícola; 07°03′S, 047°28′W; alt. 200 m; 7 Feb. 2020; JAS Silva 578; CCAA 2352. Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída–Cachoeira Santuário, rupícola; 07°02′S, 047°26′W; alt. 128 m; 7 Feb. 2020; JAS Silva 554; CCAA 2358.

Identification. Plants dull green. Ventral merophyte of 2 cells wide. Leaves imbricate, ovate-oblong, apex rounded or acute to acuminate, margin entire to slightly crenate; median cells hexagonal, trigones large, cuticle strongly papillose. Lobules ovate, ⅕ lobe length, apical tooth

short, straight to falcate. Underleaves distant to contiguous, bifid, ovate, 2–3 × stem width, base cordate, apex narrowly triangular to acuminate ending of 2–5 cells in a row, margin entire, plane. Perianth obovate, 5-keeled, keels with teeth, cilia and lacinia.

Lejeunea controversa is mainly characterized by having the underleaves (2–3 × stem width) with the apex narrowly triangular to acuminate (ending of 2–5 cells in a row), a strongly papillose cuticle, and a 5-keeled perianth with teeth, cilia, and lacinia.

Description and illustration. Gradstein and Ilkiu-Borges (2009: 97, fig. 60a–c).

****Lejeunea glaucescens* Gottsche**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Mata do Buenos Aires, epíxila na mata ciliar; 06°55′S, 047°22′W; alt. 174 m; 4 Feb. 2020; JAS Silva 457; CCAA 2348.

The species has also been reported as *Lejeunea caulicalyx* (Steph.) M.E.Reiner & Goda in Maranhão (e.g., Macedo and Ilkiu-Borges 2014; Brito and Ilkiu-Borges 2014; Vieira et al. 2017; Oliveira et al. 2018b; Costa et al. 2018), which is now recognized as a synonym of *L. glaucecens* (Bastos and Gradstein 2020).

******Lejeunea juruana* Gradst. & M.E.Reiner**

Figure 3I

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira São Romão, sobre tronco vivo; 07°04′S, 047° 05′W; alt. 227m; 6 Jun. 2018; JAS Silva 305; CCAA 1518.

Identification. Plants pale green to brownish. Ventral merophyte of 4 cells wide. Leaves contiguous, insertion of leaf lobes very long, ovate, apex rounded, margin entire, dorsal margin slightly arched, ventral margin straight; median cells isodiametric, trigones small, cuticle smooth. Lobules frequently reduced, when well-developed with a 2–4 cells long tooth, keel straight. Underleaves distant, bifid, ovate, small, 1.5–2 × stem width, base cuneate, apex acute, margin entire, plane. Perianth obovate, 5-keeled, keels smooth.

Lejeunea juruana is a rare species mainly characterized by ventral merophyte of four cells wide, leaves with a very long insertion line, and underleaves very small. This species is also known by the numerous short male and female branches on both sides of the stem. All examined specimens of *L. juruana* in the study area were fertile.

This species was only known to the Amazonas (type locality), Mato Grosso (Bastos and Gradstein 2020) and São Paulo state (Peralta and Yano 2008, as *Neopotamolejeunea uleana* (Steph.) M.E.Reiner).

Description and illustration. Reiner-Drehwald (2000a: 452–455, fig. 2, as *Neopotamolejeunea uleana*).

*****Lejeunea quinqueumbonata* Spruce**

Figure 3J

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, cachoeira São Romão, sobre rochas; 06°59′S, 047°09′W; alt. 228 m; 11 Mar. 2017; JAS Silva 116; CCAA 1741.

Identification. Plants yellowish to light green. Ventral merophyte of 2 cells wide. Leaves contiguous to imbricate, ovate to ovate-oblong, apex rounded to obtuse, margin crenate, dorsal margin arched, ventral margin straight to slightly arched; median cells isodiametric to elongate, convex, trigones absent, cuticle smooth. Lobules frequently reduced or rectangular when well-developed, with a tooth 1 or 2 cells long. Underleaves distant, bifid, 2.5–4 × stem width, base cuneate to rounded, apex subacute, margin crenate, plane. Perianth subcylindrical, ⅓–½ emergent, 5-keeled, keels short.

The main characters that distinguish *L. quinqueumbonata* are the strongly crenate margins of the leaves, underleaves, and bracts and the slender cell walls (Reiner-Drehwald 2000b).

Description and illustration. Reiner-Drehwald (2000b: 112–115, fig. 14).

****Leptolejeunea elliptica* (Lehm. & Lindenb.) Besch.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira do Prata, Rio Farinha, epífila, borda da cachoeira da Prata, mata de galeira; 06°59′S, 047°09′W; alt. 228 m; 12 Mar. 2017; JAS Silva 91; CCAA 1503.

*****Metalejeunea cucullata* (Reinw, Blume & Nees) Grolle**

Figure 3K

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, corticícola na mata de galeria, Riacho Buenos Aires; 06°56′S, 047°20′W; alt. 181 m; 11 Mar. 2020; JAS Silva 35; CCAA 1572.

Identification. Plants green to olive green. Ventral merophyte of 2 cells wide. Leaves distant, suberect, ovate, apex rounded, margin entire, plane to slightly incurved; median cells isodiametric, ca. 15 µm, trigones small to medium sized, ocelli lacking. Lobules distant, ovate, ½–⅔ leaf length, keel crenate by convex cells, apical tooth sharp. Underleaves distant, 1.5–2 stem width, apex acute.

Metalejeunea cucullata is the only species of the genus that occur in Brazil. The species may be confused with species of *Microlejeunea*, but the latter genus present one or more ocelli at leaf base, innovations lejeuneoid, and usually dioicous plants (rarely monoicous), while in *Metalejeunea* the plants lack ocelli, innovations are pycnolejeuneoid, and monoicous plants.

Description and illustration. Gradstein and Ilkiu-Borges (2009: 111, fig. 69a–c).

*****Otigoniolejeunea huctumalcensis* (Lindenb. & Gottsche) Y.M.Wei, R.L.Zhu & Gradst.**

Material examined. BRAZIL • Maranhão, município de

Carolina, Parque Nacional Chapada das Mesas, Cachoeira São Romão, sobre rocha próximo à queda d'água; 07° 04′S, 047°05′W; alt. 227 m; 6 Jun. 2018; JAS Silva 277; CCAA 1834.

Identification. Plants greenish to pale brownish. Ventral merophyte of 2 cells wide. Leaves imbricate, ovate, apex rounded to subacute, margin entire to crenate; marginal cells convex, trigones medium-sized, cuticle slightly to strongly papillose; ocelli usually 1–4, suprabasal. Lobules oval to triangular, sometimes reduced, apical tooth obtuse, 1 cell long. Underleaves distant, suborbicular to ovate, 1.5–2.5 × stem width, bifid, base cuneate, apex subacute, margin entire. Perianth obovoid, 5-keeled, keels entire, bifid or more ramified laciniae. Vegetative reproduction by caducous leaves.

Otigoniolejeunea huctumalcensis is characterized by variable sized shoots, sometimes with narrow and wide shoot sectors occurring in a single plant, leaves with suprabasal ocelli (difficult to see in old herbarium specimens), 5-keeled perianths with ramified horns, vegetative reproduction often by regenerants on leaf margins and occasionally by caducous leaves (Reiner-Drehwald and Ilkiu-Borges 2007).

Description and illustration. Reiner-Drehwald and Ilkiu-Borges (2007, as *Lejeunea huctumalcensis* Lindenb. & Gottsche).

***Pycnolejeunea contigua* (Nees) Grolle**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, corticícola na mata de galeria, Riacho Buenos Aires; 06°56′S, 047°20′W; alt. 181 m; 11 Mar. 2020; JAS Silva 35; CCAA 1572.

****Schiffneriolejeunea polycarpa* (Nees) Gradst.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, sobre tronco em decomposição na borda de mata de galeria; 06°56′S, 047°20′W; alt. 181 m; 11 Mar. 2017; JAS Silva 22; CCAA 1604.

Identification. Plants green, brownish to brown (when dry), ca. 2 mm wide. Ventral merophyte of 5–8 cells wide. Leaves suberect to convoluted when dry, widely spreading and convex when moist, imbricate, suborbicular, apex rounded, slightly plane, margin entire; median cells elongated, trigones cordate, cuticle smooth. Lobules ovate, ½–⅓ lobe length, apex oblique, with 1 tooth. Underleaves contiguous to imbricate, entire, 4 × stem width, base rounded, apex truncate to rounded, margin entire. Perianth immersed to ⅓ emergent, obovate, 4 or 5-keeled.

The pantropical genus *Schiffneriolejeunea* is comprised of 14 species, of which only two were recorded in Brazil, *S. polycarpa* and *S. amazonica* Gradst. Differences between these species are mainly in the leaf lobule; see the keys for *Schiffneriolejeunea* by Gradstein and Costa (2003) and Ilkiu-Borges and Oliveira-da-Silva (2018).

Description and illustration. Gradstein (1994: 71–75, fig. 19).

***Thysananthus auriculatus* (Wilson & Hook.) Sukkharak & Gradst.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho Buenos Aires, corticícola, ilha da Cachoeira do Prata; 06°56′S, 047°20′W; alt. 228 m; 30 Oct. 2017; JAS Silva 149; CCAA 1567.

***Xylolejeunea crenata* (Nees & Mont.) X.-L.He & Grolle**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Cachoeira São Romão, rupícola, cachoeira Ponta da Serra, Rio Laje; 07°04′S, 047°05′W; alt. 227 m; 8 Jun. 2018; JAS Silva 318; CCAA 1579.

Lepidoziaceae

***Monodactylopsis monodactyla* (Spruce) R.M.Schust.**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, próximo à sede do ICMBio, epíxila em mata de galeria; 07°02′S, 047°09′W; alt. 230 m; 5 Feb. 2020; JAS Silva 485; CCAA 2340.

****Zoopsidella integrifolia* (Spruce) R.M.Schust.**

Figure 3L

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Riacho na RPPN da Mansinha, rupícola em cachoeira caipora; 07°08′S, 047°26′W; alt. 286 m; 3 Feb. 2020; JAS Silva 451; CCAA 2336.

Identification. Dioicous. Plants whitish green, branches mostly ventral-intercalary. Leaves contiguous, ovate-triangular to oblong-rhomboidal in outline, margin rounded, 2 small rounded to sausage-shaped slime cells; median cells isodiametric to rectangular, thin walled, trigones absent to minute.

Description and illustration. Schuster (1999: 134–137, fig. 26).

***Zoopsidella macella* (Steph.) R.M.Schust.**

Figure 3M

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Laje, cachoeira Ponta da Serra, sobre rocha na trilha; 06°58′S, 047°22′W; alt. 228 m; 11 Mar. 2017; JAS Silva 48; CCAA 1542.

Lophocoleaceae

****Lophocolea bidentata* (L.) Dumort.**

Figure 3N

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio

Farinha, sobre rochas próximo à cachoeira São Romão; 06° 59′S, 047°09′W; alt. 228 m; 13 Mar. 2017; JAS Silva 109; CCAA 1609.

Identification. Plants pale green. Leaves alternate, distant to subimbricate, symmetrical, bifid ⅕–¼ lobe length, with a broad acuminate, rounded sinus, acuminate lobes, uniseriate tips 3–6 cells long, margin entire; median cells isodiametric, thin walled, trigones small, cuticle smooth. Underleaves distant, 1–2 × stem width, bifid near the base, with a short or long tooth on outer margin.

Description and illustration. Gradstein and Ilkiu-Borges [2009: 37, fig. 21 c–e, as *Chiloscyphus latifolius* (Nees) J.J. Engel & R.M. Schust.].

Plagiochilaceae

***Plagiochila exigua* (Taylor) Taylor**

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída, sobre solo; 07°02′S, 047°26′W; alt. 128 m; 7 Feb. 2020; JAS Silva 552; CCAA 2578.

Identification. Plants green to olive-green, poorly irregularly branched, branches predominantly intercalary. Leaves distant to contiguous, frequently caducous, oblong-elliptical to obovate, 1.5 × longer than wide; apex bifid, margins entire to 1–6 teeth; ventral base not ampliate, short decurrent, dorsal leaf base short decurrent; median cells isodiametric to slightly elongate, trigones small to large, cuticle smooth.

Description and illustration. Schuster (1980).

***Plagiochila raddiana* Lindenb.**
Figure 3O

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Rio Farinha, sobre rochas próximo a cachoeira São Romão; 06°59′S, 047°09′W; alt. 228 m; 13 Mar. 2017; JAS Silva 109; CCAA 1609.

Identification. Plants green to brownish green, dichotomously branched, branches predominantly terminal. Leaves subimbricate, rectangular, 2–2.5 × longer than wide; apex rounded to subtruncate, margin toothed by 3–8 teeth near apex, 1 or 2 teeth in lower ½ at tip of shoulder, teeth 1–5 cells long, 1–3 cells wide at base, ventral base without teeth, weakly ampliate, conspicuously recurved, forming a low crest (ventral stem surface not completely covered), long decurrent, dorsal leaf base short decurrent; median cells isodiametric to elongate, trigones small, cuticle smooth.

Description and illustration. Gradstein and Ilkiu-Borges (2009: 35, fig. 19a–b).

***Plagiochila simplex* (Sw.) Lindenb.**
Figure 3P

Material examined. BRAZIL • Maranhão, município de Carolina, Parque Nacional Chapada das Mesas, Pedra Caída–Cachoeira Pedra Furada, rupícola; 07°03′S, 047° 28′W; alt. 200 m; 7 Feb. 2020; JAS Silva 578; CCAA 2352.

Identification. Plants green to brownish, irregularly branched, branches predominantly intercalary. Leaves distant to subimbricate, frequently caducous, oblong-subrectangular, 1.5–2 × longer than wide; apex rounded, margin toothed by 3–10 spinose teeth, teeth 2–6 cells long; ventral base not ampliated, slightly recurved, short decurrent, dorsal leaf base short decurrent; median cells isodiametric, trigones narrowly radiate, cuticle smooth.

Description and illustration. Gradstein and Ilkiu-Borges (2009: 35, fig. 19g–i).

Discussion

The leafy liverwort species of CMNP represents 39% of the leafy liverworts recorded in the state and corresponds to 17% of the total number (236 species) of bryophytes (mosses and liverworts) occurring in the state (Yano et al. 1987, 2009; He and Grolle 2001; Conceição and Brito 2010; Santos and Conceição 2010; Peralta et al. 2011; Varão et al. 2011; Macedo and Ilkiu-Borges 2014; Brito and Ilkiu-Borges 2012, 2014; Costa et al. 2015; Vieira et al. 2017; Oliveira et al. 2018a, 2018b, 2018c, 2018d, 2018e; Costa et al. 2018; Silva et al. 2018a, 2018b; Bonfim et al. 2019). These results demonstrate the importance of CMNP to the bryophyte flora of Maranhão.

The predominance of Lejeuneaceae and Frullaniaceae in CMNP and in the state of Maranhão was already expected since these families present a wide diversity and distribution in Brazil (Gradstein and Costa 2003; Costa and Peralta 2015) and in the Neotropics (Gradstein et al. 2001). Some of species are generalists, adapted to various ecosystems and substrates (Gradstein et al. 2001; Gradstein and Costa 2003; Gradstein and Ilkiu-Borges 2009). Frullaniaceae species, in particular, usually develop in dry, places exposed to full sun and can be considered xerophytes among the liverworts (Lemos-Michel 1980; Hentschel et al. 2009; Lima et al. 2018).

The genera *Lejeunea*, *Cheilolejeunea*, and *Frullania* were the most representative in our study, as already reported in Maranhão (e.g., Peralta et al. 2011; Macedo and Ilkiu-Borges 2014; Brito and Ilkiu-Borges 2014; Oliveira et al. 2018b) and in the Northeast Region (e.g., Bôas-Bastos and Bastos 1998; Bastos and Yano 2006; Valente and Pôrto 2006; Yano and Peralta 2006; Siqueira et al. 2011; Oliveira and Bastos 2014; Silva et al. 2014; Germano et al. 2016).

Among the most frequently found species in CMNP, only *Lejeunea glaucescens* was already known from Maranhão (Peralta et al. 2011; Oliveira et al. 2018b); the other species we report for the first time from Maranhão. *Cheilolejeunea trifaria*, *Ceratolejeunea cubensis*, and *Zoopsidella integrifolia* are well known in other Brazilian phytogeographic domains and states (Gradstein and Costa 2003; BFG 2018), as well as elsewhere in the

Neotropics (Dauphin 2003; Gradstein and Ilkiu-Borges 2009; Bastos 2017).

Most studies of bryophytes in tropical forests report most species on live and decomposing tree trunks, which can be explained by the greater availability of these substrates and the more favorable conditions offered by them, such as high moisture (Richards 1988; Holz and Gradstein 2005). In CMNP, however, species were collected mostly on rocks; numerous rocks are available for the colonization by leafy liverworts, in our study area, which also has a more seasonal climate with a prolonged dry season. The same preference for rocks was found in a study of acrocarpous mosses in CMNP (Oliveira et al. 2018a), as well as in studies in the Brazilian Cerrado (Carmo and Peralta 2016) and in canga areas in Serra dos Carajás, Pará state (Oliveira-da-Silva and Ilkiu-Borges 2018).

The full list of leafy liverworts of Maranhão, which includes 106 species and two varieties in nine families and 39 genera, is presented in the Appendix, Table A1. This list collates species from the literature (Yano 1987; He and Grolle 2001; Yano et al. 2009; Santos and Conceição 2010; Peralta et al. 2011; Brito and Ilkiu-Borges 2012, 2014; Macedo and Ilkiu-Borges 2014; Oliveira et al. 2018b) as well as the results of our collections in CMNP.

Lejeuneaceae and Frullaniaceae were the families of greater richness in Maranhão (79 spp. and two varieties, and 9 spp., respectively), representing 83% of the leafy liverwort species known for the state. The most representative genera were *Lejeunea* (17 spp.), *Cheilolejeunea* (15 spp. and two varieties) and *Frullania* (9 spp.).

Six geographic distribution patterns were identified among the leafy liverworts of Maranhão. The Neotropical distribution was predominant (68 spp.), followed by Pantropical (25 spp.), South American (5 spp.), endemic to Brazil (*Ceratolejeunea maranhensis, Lejeunea juruana* and *Zoopsidella macella* (Steph.) R.M.Schust.), Afro-American (4 spp.), and Tropical South and Central American (*Lejeunea raddiana* Lindenb.).

The predominance of Neotropical species is common in floristic inventories in Brazil (Molinaro and Costa 2001; Imbassahy et al. 2009; Visnadi 2012; Oliveira-da-Silva and Ilkiu-Borges 2018, 2020). The majority of the liverwort species in the North and Northeast regions of Brazil have a Neotropical distribution pattern (e.g., Costa 2003; Valente and Pôrto 2006; Siqueira et al. 2011; Oliveira and Bastos 2014; Cerqueira et al. 2015; Oliveira-da-Silva and Ilkiu-Borges 2018, 2020).

With 75% of the territory covered by remnant vegetation of three different biomes, the state of Maranhão ranks 23rd in terms of bryophyte species richness among the 26 Brazilian states according to Costa and Peralta (2015). These data have changed since then, due to recent publications which have documented species from Maranhão for the first time (Costa et al. 2015, 2018; Vieira et al. 2017; Oliveira et al. 2018a, 2018b, 2018c, 2018d, 2018e;Silva et al. 2018a, 2018b; Bonfim et al. 2019), as in our study. Therefore, the state of Maranhão now ranks 14th among the states.

Published studies of the leafy liverworts of Maranhão show that more research is necessary in this state. Most of these studies were based on sporadic collections deposited in herbariums or records in taxonomic reviews (e.g., Yano et al. 1987; He and Grolle 2001; Yano et al. 2009; Peralta et al. 2011). Few studies have been carried out in large and important areas of the state, such as conservation units (Macedo and Ilkiu-Borges 2014; Oliveira et al. 2018a). Some important areas have already been surveyed, but not thoroughly sampled, such as the Mirador State Park . This park is the largest conservation unit in Maranhão (437,000 ha), but only eight leafy liverwort species are known from it (Santos and Conceição 2014).

Our survey of CMNP recorded 23 species from Maranhão, including 19 species recorded for the first time from the state (and one from the Northeastern region). We added one family (Cephaloziaceae) to the list of leafy liverworts of the state. In view of the fast demographic growth and the expansion of land use, additional studies of the state's bryophyte flora are sorely needed, especially unexplored areas, to increase knowledge about this group.

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Authors' Contributions

JPS, FROS, ALIB contributed to the identification of species, analysis and interpretation of the data, manuscript writing; FROS, ALIB, RSF contributed to critical revision and corrections; RSF contributed to the concept and design of the study.

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Appendix

Table A1. Leafy liverworts from Maranhão State, northeastern Brazil, with their respective worldwide distribution and first record for the State. *Species registered in the Chapada das Mesas National Park, ** New records for Maranhão, *** New records for the Northeast region of Brazil.

Family/species	Global distribution	First record from Maranhão state
Cephaloziellaceae		
***Cylindrocolea planifolia* (Steph.) R.M.Schust.	Neotropical	This study
**Cylindrocolea rhizantha* (Mont.) R.M.Schust.	Neotropical	Oliveira et al. 2018b
Cephaloziaceae		
***Odontoschisma variabile* (Lindenb. & Gottsche) Trevis.	Afro-American (rare in Africa)	This study
Fossombroniaceae		
**Fossombronia porphyrorhiza* (Nees) Prosk.	Neotropical	Yano et al. 2009
Frullaniaceae		
Frullania caulisequa (Nees) Nees.	Neotropical	Peralta et al. 2011
Frullania dusenii Steph.	Neotropical	Peralta et al. 2011
**Frullania ericoides* (Nees) Mont.	Pantropical	Yano et al. 2009
Frullania exilis Taylor	Pantropical	Macedo and Ilkiu-Borges 2014, as *Frullania apiculata* (Reinw., Blume & Nees) Nees
**Frullania gibbosa* Nees	Neotropical	Peralta et al. 2011
Frullania glomerata (Lehm. & Lindenb.) Nees & Mont.	Neotropical	Yano et al. 2009
***Frullania intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb.	Neotropical	This study
**Frullania platicalyx* Herzog	South American (Argentina and Brazil)	Oliveira et al. 2018b
***Frullania rio-janeirensis* (Raddi) Ångstr.	Pantropical	This study
Lejeuneaceae		
**Acrolejeunea emergens* (Mitt.) Steph.	Pantropical	Yano et al. 2009
**Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn.	Neotropical	Yano et al. 1987
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	Neotropical	Macedo and Ilkiu-Borges 2014
Caudalejeunea lehmanniana (Gottsche) A.Evans	Pantropical	Macedo and Ilkiu-Borges 2014
Ceratolejeunea coarina (Gottsche) Schiffn.	Neotropical	Yano et al. 2009
**Ceratolejeunea cornuta* (Lindenb.) Schiffn.	Pantropical	Macedo and Ilkiu-Borges 2014
***Ceratolejeunea cubensis* (Mont.) Schiffn.	Neotropical	This study
Ceratolejeunea guianensis (Nees & Mont.) Steph.	Neotropical	Macedo and Ilkiu-Borges 2014
Ceratolejeunea laetefusca (Austin) R.M.Schust.	Neotropical	Macedo and Ilkiu-Borges 2014
Ceratolejeunea maranhensis Silva Brito & Ilk.-Borg.	Endemic to Brazil, recorded only in Maranhão.	Brito and Ilkiu-Borges 2012
Ceratolejeunea minuta G.Dauphin	Neotropical	Macedo and Ilkiu-Borges 2014
***Cheilolejeunea acutangula* (Nees) Grolle	Neotropical	This study
**Cheilolejeunea adnata* (Kunze) Grolle var. adnata	Pantropical	Macedo and Ilkiu-Borges 2014
**Cheilolejeunea adnata* var. *autoica* Gradst. & Ilk.-Borg.	Pantropical	This study
Cheilolejeunea aneogyna (Spruce) A.Evans	Neotropical	Macedo and Ilkiu-Borges 2014
Cheilolejeunea clausa (Nees & Mont.) R.M.Schust.	Neotropical	Peralta et al. 2011
Cheilolejeunea comans (Spruce) R. M.Schust.	Neotropical	Macedo and Ilkiu-Borges 2014
Cheilolejeunea discoidea (Lehm. & Lindenb.) Kachroo & R.M.Schust.	Neotropical	Peralta et al. 2011
Cheilolejeunea filiformis (Sw.) W.Ye, R.L.Zhu & Gradst.	Neotropical	Oliveira et al. 2018b
Cheilolejeunea holostipa (Spruce) Grolle & R. L.Zhu	Neotropical	Macedo and Ilkiu-Borges 2014
***Cheilolejeunea intertexta* (Lindenb.) Steph.	Pantropical	This study
Cheilolejeunea neblinensis Ilk.-Borg. & Gradst.	South American (Brazil, Colombia and Venezuela)	Macedo and Ilkiu-Borges 2014
**Cheilolejeunea oncophylla* (Ångstr.) Grolle & M.E.Reiner	Neotropical	Macedo and Ilkiu-Borges 2014
**Cheilolejeunea rigidula* (Mont.) R.M.Schust.	Pantropical	Yano et al. 2009
**Cheilolejeunea savannae* L.P.Macedo, Ilk.-Borg. & C.J.Bastos	Endemic to Brazil	Macedo and Ilkiu-Borges 2014, as *Cheilolejeunea discoidea*.
***Cheilolejeunea trifaria* (Reinw, Blume & Nees) Mizut.	Pantropical	This study

Family/species	Global distribution	First record from Maranhão state
Cheilolejeunea urubuensis (Zartman & I.L.Ackerman) R.L.Zhu & Y.M.Wei	South American (Brazil and Colombia)	Macedo and Ilkiu-Borges 2014, as *Vitalianthus urubuensis* Zartmann & I.L.Ackerman
Cololejeunea camillii (Lehm.) A.Evans	Neotropical	Peralta et al. 2011, as *Aphanolejeunea camillei* (Lehm.) R.M.Schust.
**Cololejeunea cardiocarpa* (Mont.) A.Evans	Pantropical	Brito and Ilkiu-Borges 2014
Cololejeunea contractiloba A.Evans	Neotropical	Macedo and Ilkiu-Borges 2014
**Cololejeunea diaphana* A.Evans	Pantropical	Macedo and Ilkiu-Borges 2014
Cololejeunea sintenisii (Steph.) Steph.	Neotropical	Brito and Ilkiu-Borges 2014
Cololejeunea submarginata P. Tixier	Neotropical	Oliveira et al. 2018b
Cololejeunea truncatifolia (Horik.) Mizut.	Pantropical	Peralta et al. 2011, as *Aphanolejeunea truncatifolia* Horik.
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	Neotropical	Yano *et al.* 2009
Dibrachiella auberiana (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	Neotropical	Macedo and Ilkiu-Borges 2014, as *Archilejeunea auberiana* (Mont.) A.Evans
**Dibrachiella parviflora* (Nees) X.Q.Shi, R.L.Zhu & Gradst.	Neotropical	Macedo and Ilkiu-Borges 2014, as *Archilejeunea parviflora* (Nees) Steph.
Diplasiolejeunea brunnea Steph.	Neotropical	Macedo and Ilkiu-Borges 2014
Diplasiolejeunea cobrensis Steph.	Pantropical	Peralta et al. 2011
Frullanoides tristis (Steph.) van Slageren	Neotropical	Oliveira et al. 2018b
Haplolejeunea amazonica Ilkiu-Borges & Gradst.	South American (Brazil, Guianas and Venezuela)	Macedo and Ilkiu-Borges 2014
Harpalejeunea stricta (Lindenb. & Gottsche) Steph	Neotropical	Macedo and Ilkiu-Borges 2014
Lejeunea adpressa Nees	Neotropical	Macedo and Ilkiu-Borges 2014
Lejeunea boryana Mont.	Pantropical	Macedo and Ilkiu-Borges 2014
Lejeunea cancellata Nees & Mont.	Neotropical	Yano et al. 2009
***Lejeunea controversa* Gottsche	Neotropical	This study
Lejeunea flava (Sw.) Nees	Pantropical	Yano et al. 2009
**Lejeunea glaucescens* Gottsche	Neotropical	Peralta et al. 2011
Lejeunea immersa Spruce	Neotropical	Oliveira et al. 2018b
****Lejeunea juruana* Gradst. & M.E.Reiner	Endemic to Brazil	This study
Lejeunea laeta (Lehm. & Lindenb.) Lehm. & Lindenb.	Neotropical	Peralta et al. 2011
Lejeunea laetevirens Nees & Mont.	Neotropical	Yano et al. 2009
Lejeunea parviloba Ångstr.	Neotropical	Macedo and Ilkiu-Borges 2014, as *Lejeunea tapajosensis* Spruce
Lejeunea phyllobola Nees & Mont.	Neotropical	Yano et al. 2009
***Lejeunea quinqueumbonata* Spruce	Neotropical	This study
Lejeunea raddiana Lindenb.	Tropical South American (Colombia, Ecuador, Bolivia and Brazil) and Central American (Panama).	Peralta et al. 2011
Lejeunea setiloba Spruce	Neotropical	Yano et al. 2009
Lejeunea trinitensis Lindenb.	Afro-American	Peralta et al. 2011
Lejeunea sp.	—	Macedo and Ilkiu-Borges 2014
**Leptolejeunea elliptica* (Lehm. & Lindenb.) Besch.	Neotropical	Macedo and Ilkiu-Borges 2014
Lopholejeunea nigricans (Lindenb.) Schiffn.	Pantropical	Yano et al. 2009
***Metalejeunea cucullata* (Reinw, Blume & Nees) Grolle	Pantropical	This study
Microlejeunea bullata (Taylor) Steph.	Neotropical	Yano et al. 2009
Microjeleunea epiphylla Bischler	Neotropical	Yano et al. 2009
Myriocoleopsis minutissima (Sm) R.L.Zhu, Y.Yu & Pócs	Pantropical	Peralta et al. 2011, as *Cololejeunea minutissima* (Sm.) Schiffn.
***Otigoniolejeunea huctumalcensis* (Lindenb. & Gottsche) Y.M.Wei, R.L.Zhu & Gradst.	Neotropical	This study
Pictolejeunea picta (Steph.) Grolle	Neotropical	Macedo and Ilkiu-Borges 2014
Prionolejeunea denticulata (F.Weber) Schiffn.	Neotropical	Macedo and Ilkiu-Borges 2014
Prionolejeunea scaberula (Spruce) Steph.	Neotropical	Yano et al. 2009
**Pycnolejeunea contigua* (Nees) Grolle	Pantropical	Brito and Ilkiu-Borges 2014
Rectolejeunea emarginuliflora (Gottsche) A.Evans	Neotropical	Macedo and Ilkiu-Borges 2014
Rectolejeunea fragelliformis A.Evans	Neotropical	Macedo and Ilkiu-Borges 2014
Rectolejeunea versifolia (Schiffn.) L.Söderstr. & A.Hagborg	Neotropical	Brito and Ilkiu-Borges 2014, as *Rectolejeunea berteroana* (Steph.) A.Evans
***Schiffneriolejeunea polycarpa* (Nees) Gradst.	Pantropical	This study
Schusterolejeunea inundata (Spruce) Grolle	South American (Brazil, Guyana and Peru)	Peralta et al. 2011
Stictolejeunea squamata (F.Weber) Schiffn.	Neotropical	Yano et al. 2009
Thysananthus amazonicus (Spruce) Schiffn.	Neotropical	Brito and Ilkiu-Borges 2014
**Thysananthus auriculatus* (Wilson & Hook) Sukkharak & Gradst.	Pantropical	Yano et al. 2009, as *Mastigolejeunea auriculata* (Wilson & Hook) Schiffn.
Thysananthus innovans (Spruce) Sukkharak & Gradst.	Neotropical	Yano et al. 2009, as *Mastigolejeunea innovans* (Spruce) Steph.
**Xylolejeunea crenata* (Nees & Mont.) X.-L.He & Grolle	Neotropical	He and Grolle 2001

Family/species	Global distribution	First record from Maranhão state
Lepidoziaceae		
**Monodactylopsis monodactyla* (Spruce) R.M.Schust.	Neotropical	Santos and Conceição 2010, as *Arachniopsis monodactyla* (Spruce) R.M.Schust.
Telaranea nematodes (Austin) M.Howe	Afro-American	Oliveira et al. 2018b
***Zoopsidella integrifolia* (Spruce) R.M.Schust.	Neotropical	This study
**Zoopsidella macella* (Steph.) R.M.Schust.	Endemic to Brazil	Yano et al. 2009
Lophocoleaceae		
Chiloscyphus liebmannianus (Gottsche) J.J.Engel & R.M.Schust.	Neotropical	Macedo and Ilkiu-Borges 2014
***Lophocolea bidentata* (L.) Dumort.	Pantropical	This study
Plagiochilaceae		
***Plagiochila exigua* (Taylor) Taylor	Neotropical	This study
Plagiochila martiana Nees	Neotropical	Peralta et al. 2011
Plagiochila montagnei Nees	Neotropical	Macedo and Ilkiu-Borges 2014
***Plagiochila raddiana* Lindenb.	Neotropical	This study
Plagiochila rutilans Lindenb.	Neotropical	Macedo and Ilkiu-Borges 2014
***Plagiochila simplex* (Sw.) Lindenb.	Neotropical	This study
Radulaceae		
Radula flaccida Lindenb. & Gottsche	Afro-American	Macedo and Ilkiu-Borges 2014
Radula mammosa Spruce	Neotropical	Macedo and Ilkiu-Borges 2014