Leandro de Almeida Amélio

REVISÃO DA FAMÍLIA LEPIDOZIACEAE LIMPR. (MARCHANTIOPHYTA)

ENTENDENDO A EVOLUÇÃO NA MORFOLOGIA DESTA MEGA DIVERSA FAMÍLIA DE HEPÁTICAS FOLHOSAS

Feira de Santana - BA
Dezembro 2022

Ficha Catalográfica - Biblioteca Central Julieta Carteado - UEFS

A534 Amélio, Leandro de Almeida
Revisão da família Lepidoziaceae Limpr. (Marchantiophyta) entendendo a evolução na morfologia desta mega diversa família de hepáticas folhosas / Leandro de Almeida Amélio. – 2022.
135 f.: il.

Orientadora: Emilia de Brito Valente.
Coorientador: Denilson Fernandes Peralta.
Tese (doutorado) – Universidade Estadual de Feira de Santana, Programa de Pós-graduação em Botânica, Feira de Santana, 2022.

1. Lepidoziaceae. 2. Taxonomia. 3. Hepáticas folhosas - morfologia. I. Título. II. Valente, Emilia de Brito, orient. III. Peralta, Denilson Fernandes, coorient. IV. Universidade Estadual de Feira de Santana.

CDU 582.32

Daniela Machado Sampaio Costa - Bibliotecária - CRB-5/2077

Universidade Estadual de Feira de Santana

Departamento de Ciências Biológicas

Programa de Pós-graduação em Botânica

Leandro de Almeida Amélio

REVISÃO DA FAMÍLIA LEPIDOZIACEAE LIMPR. (MARCHANTIOPHYTA)

ENTENDENDO A EVOLUÇÃO NA MORFOLOGIA DESTA MEGA DIVERSA FAMÍLIA DE HEPÁTICAS FOLHOSAS

Feira de Santana – BA

Dezembro 2022

Universidade Estadual de Feira de Santana
Departamento de Ciências Biológicas
Programa de Pós-graduação em Botânica

REVISÃO DA FAMÍLIA LEPIDOZIACEAE LIMPR. (MARCHANTIOPHYTA)

ENTENDENDO A EVOLUÇÃO NA MORFOLOGIA DESTA MEGA DIVERSA FAMÍLIA DE HEPÁTICAS FOLHOSAS

Leandro de Almeida Amélio

Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Estadual de Feira de Santana como parte dos requerimentos para a obtenção do título de *Doutorado em Botânica.*

Orientadora: Dra. Emilia de Brito Valente (UEFS)
Coorientador: Dr. Denilson Fernandes Peralta

Feira de Santana – BA
Dezembro 2022

Leandro de Almeida Amélio

REVISÃO DA FAMÍLIA LEPIDOZIACEAE LIMPR. (MARCHANTIOPHYTA)

ENTENDENDO A EVOLUÇÃO NA MORFOLOGIA DESTA MEGA DIVERSA FAMÍLIA DE HEPÁTICAS FOLHOSAS

Banca examinadora

Dr. Diego Knop Henriques
Universidade Federal do Paraná (UFPR)

Dra. Emanuelle Lais dos Santos
Universidade Cesumar (UNICESUMAR)

Dra. Julia Viegas Mundim
Colégio Militar de Brasília - Exército Brasileiro (CMB - EB)

Dra. Juçara Bordin
Universidade Estadual do Rio Grande do Sul (UERGS)

Dra. Emilia de Brito Valente
Universidade Estadual de Feira de Santana (UEFS)
Orientadora e Presidente

2022

Dedico esse trabalho a todos que incentivam e apoiam a ciência e a educação.

“Many botany student has had it explained to him that the bryophytic way of life is rather a poor idea without a glorious future in the full exploitation of the land habitat.... On the contrary, it is an excellent idea with so much future that the plants which adopted it have rigorously stayed with it, finding ample opportunity for themselves in a succession of geological epochs.”

Johannes Proskauer 1964

Agradecimentos

Agradeço imensamente a todos que contribuíram não apenas para conclusão desse trabalho, mas para minha formação profissional e moral.

Sou muito grato à pós-graduação da Universidade Estadual de Feira de Santana, pela oportunidade, e logo parabenizo por sustentar de forma tão agregadora o ensino e a pesquisa. Agradeço à minha orientadora Emilia de Brito Valente, por me aceitar como seu aluno e seguir comigo durante esse período. Agradeço ao meu coorientador Dr. Denilson Fernandes Peralta, por ter me passado uma bagagem enorme de conhecimento, por ter aceitado me coorientar, por ter sempre me respondido e me acompanhado nessa trajetória.

Aos meus amigos que, além de companhia de sala de aula e laboratório, foram parceiros para inúmeros trabalhos e dificuldades, com vocês passei ótimos momentos, todo meu aprendizado dentro da academia. Com vocês os dias tornavam-se ainda mais interessantes. Amigos que levarei para sempre no meu coração e que nessas palavras espero demonstrar meu profundo agradecimento e admiração a Adele, Aldinne, Aline, André, Andreza, Ariadne, Diogo, Douglas, Evandro, Juan, Gabriel, Iasmim, Jéssica, João, Maria, Marina, Milena, Ray, Sheila que estiveram comigo durante todo esse ciclo, me apoiaram e sempre estiveram ao meu lado para enfrentar as barreiras da vida acadêmica.

Agradeço também às pessoas lindas que encontrei nessa jornada que me ajudaram muito na concretização desse projeto, por ter me ajudado nas minhas viagens e coletas, grande abraço e admiração principalmente aos curadores dos herbários e às secretárias do programa de pós-graduação em Botânica da UEFS.

Sou muito grato à minha mãe Aluiza, por tudo que me ajudou e me ensinou para encarar meus problemas, que sempre me incentivou a estudar e que agora cuida de mim em espírito, te amo mãe. Às minhas irmãs e meus sobrinhos pelo apoio e admiração.

Por fim muito obrigado à Capes pela bolsa de estudo concedida, pois sem ela seria muito difícil ter feito tudo que consegui.

Agradeço aos professores responsáveis pelo conhecimento adquirido na minha formação. E agradeço a Deus por ter me dado capacidade de concluir mais uma etapa na minha vida.

Resumo

Lepidoziaceae é a segunda família mais diversa de hepáticas folhosas do mundo. A família é atualmente considerada monofilética e apresenta ampla diversidade morfológica, são plantas de 0,5-4,0 cm com filídios extremamente reduzidos, podendo ainda possuir dentes ou não como anexos aos filídios e, com ou sem a presença de anfigastros. Este projeto foi motivado pela necessidade de revisão taxonômica, visando entender a diversidade morfológica e clarear o posicionamento filogenético de algumas subfamílias e o que causa o polifiletismo de alguns gêneros. A revisão taxonômica começou com a análise das descrições originais e materiais tipo. Esse conhecimento direcionou o estudo dos materiais depositados nos herbários nacionais e internacionais, visando estabelecer os limites morfológicos das espécies e direcionar as coletas em áreas pouco amostradas para o Brasil. No estudo de revisão taxônomica, o foco foi o gênero *Lepidozia*, dentro do qual foram reconhecidas oito espécies, sendo três novas ocorrências e um táxon que retoma à flora após 20 anos sendo considerado sinônimo, ainda que nunca houvesse tal confirmação. A distribuição geográfica da família apresenta concentração na Amazônia e Mata Atlântica, sendo as espécies endêmicas mais fortemente encontradas ao norte do Brasil. Para o estudo filogenético foram analisadas quatro regiões: os genes do cloroplasto rbcL, trnL-F e rps4, e os genes de núcleo 26s. A hipótese filogenética obtida mostra que o gênero *Micropterygum*, nunca amostrado molecularmente, forma um grupo monofilético, irmão de *Acromastigum* e juntos formam grupo irmão do clado *Bazzania* e ainda estamos inferindo que o período de diversificação e evolução dos caracteres vegetativos foi de 120 milhões de anos atrás. Paralelamente estão sendo caracterizados pela primeira vez os esporos de *Micropterygium,* sendo representadas sete espécies.

Palavras chaves: Diversidade, diversificação, endemismo, esporos, evolução, filídios, hepáticas, palinologia, revisão taxonômica.

Abstract

Lepidoziaceae is the second most diverse family of leafy liverworts in the world. The family is currently considered monophyletic and presents a wide morphological diversity, they are tinny to medium plants with a large dirversity of reduced leaves, with or without teeth on the leaves and, the underleaves are reduce or well developed. This project was motivated by the need for a taxonomic revision, aiming to understand the morphological diversity, and to clarify the phylogenetic position of some subfamilies and what causes the polyphyly of some genera. The taxonomic review began with analysis of original descriptions and type materials. This knowledge guided the study of the materials deposited in national and international herbaria, aiming to establish the morphological limits of the species and direct the collections in areas few sampled for Brazil. In the taxonomic review study, the focus was on the genus *Lepidozia*, within which eight species were recognized, three of which are new occurrences and a taxon that resumes to the brasilian flora after 20 years being considered synonymous, even though there was never such confirmation. The geographic distribution of the family is concentrated in the Amazon and Atlantic Forest, with the endemic species strongly found in the north of Brazil. For the phylogenetic study, four regions were analyzed: the chloroplast genes rbcL, trnL-F and rps4, and the 26s nuclear genes. The phylogenetic hypothesis obtained shows that the genus *Micropterygum*, never sampled molecularly, forms a monophyletic group, sister of *Acromastigum* and together they form a sister group of the clade *Bazzania* and we are still inferring that the period of diversification and evolution of the vegetative characters was 120 million years. At the same time, *Micropterygium* spores are being characterized for the first time, with seven species being represented.

Keywords: Endemism evolution, diversification, liverworts, palynology, taxonomic revision.

Sumário

1. Introdução

1.1. Atual taxonomia de Lepidoziaceae

Lepidoziaceae pertence à Divisão Marchantiophyta, é a segunda maior família de hepáticas folhosas, atualmente possui 28 gêneros e cerca de 950 espécies (Gradstein *et al.* 2011; Söderström *et al*. 2016; GBIF 2022). Atualmente Lepidoziaceae pertence à Classe Jungermanniopsida Stotler & Crandal–Stotler; subclasse Jungermanniidae Engl.; Ordem Jungermanniales H. Klinggr.; subordem Lophocoleinae Schljakov (Crandall-Stotler et al. 2009; Söderström et al. 2016). E a família é considerada grupo irmão de Lophocoleaceae De Not. (Heinrichs et al. 2007).

Para o Brasil são citados em literatura 12 gêneros de Lepidoziaceae (Meagher 2010; 2011a; 2011b; 2011c; 2015; Gradstein *et al.* 2003; Costa 2010; Costa & Peralta 2015; Söderström et al. 2016; Peralta et al. 2020: *Amazoopsis* J.J.Engel & G.L.Merr., *Arachniopsis* Spruce, *Bazzania* Gray, *Kurzia* G.Martens, *Lepidozia* (Dumort.) Dumort., *Micropterygium* Gottsche, *Mytilopsis* Spruce, *Paracromastigum* Fulford et J.Taylor, *Protocephalozia* (Spruce) K.I.Goebel, *Pteropsiella* Spruce, *Telaranea* Spruce ex Schin., e *Zoopsidella* R.M.Schust.

Estas plantas são elementos comuns nas florestas úmidas temperadas e tropicais, onde estão entre as espécies dominantes de hepáticas folhosas, juntamente com Lejeuneaceae e Plagiochilaceae (Meagher 2012; Gleny & Bartlett 2008). Gradstein *et al.* (2001) estimam que nas Américas ocorram cerca de 170 espécies da família, e para o Brasil já são citadas 48 (Costa 2010; Peralta et al. 2020).

O reconhecimento morfológico de Lepidoziaceae é feito pelas características do gametófito folhoso, usualmente pinado ou bifurcado, com ramificação tipo- *Frullania*, ramos fracamente diferenciados, podendo ter hialoderme presente ou não, o tamanho dos indivíduos são de pequenos até robustos, verde brilhante, amarelados até acastanhados, o crescimento é ereto até prostrado, sempre aplanados dorsiventralmente, e as ramificações apresentam os ramos ginoeciais, ventrais e flageliformis (Fulford 1966; Gradstein & Costa 2003; Cleavitt et al. 2007; Zhou et al. 2012; Peralta et al. 2020).

Os filídios apresentam ampla variação morfológica. Eles podem ser divididos em segmentos filiformes ou simples, apresentam aspecto espalhados ou imbricados, com a inserção transversal ou obliqua (Schuster 1993). É a única família onde os filídios podem ser íncubos ou súcubos, com aspectos planos ou côncavos, simétricos ou assimétricos e o ápice agudo ou obtuso, a margem pode ser serreada acima ou variadamente dividida, desde bífidos a quadrífidos ou em muitos segmentos e a lâmina do filídio pode apresentar ou não quilhas. As células da lâmina do filídio podem ser romboide, quadráticas até retangulares, as paredes celulares delgadas ou espessas, lisas ou papilosas, e a cutícula lisa ou verrucosa. É uma das poucas famílias onde o anfigastro pode estar presente ou ausente, e ser semelhante ou não aos filídios. E o perianto apresentando três quilhas (Fulford 1966; Schuster 1993).

O esporófito possui seta apresentando de oito a dezesseis fileiras de células geralmente pequenas em secção transversal.

Os gêneros *Micropterygium* Lindenb., *Lepidozia* Dumort. e *Kurzia* G.Martens, apresentam muitas espécies e são sempre indicados como necessitando de revisão taxonômica, eles são muito expressivos nos Dominios fitogeográficos brasileiros, principalmente na Mata Atlântica, Cerrado e Amazônia (Söderström *et al*. 2016; Peralta et al. 2020; Peralta *et al*. 2022).

Dentro da abordagem filogenética, Lepidoziaceae foi objeto de poucos estudos. Davis (2004), por exemplo, ofereceu possíveis relações intrafamiliares a partir do estudo que incluiu *Trichocolea tomentosa* (Sw.) Gottsche (Trichocoleaceae) como um táxon irmão para *Lepidozia reptans* (L.) Dumort. e *Herbertus* Gray (Herbertaceae). Davis (2004) apresentou uma estimativa de filogenia na qual um clado de quatro espécies de Lepidoziaceae formaria uma politomia com *Herbertus*, *Triandrophyllum* Fulford & Hatcher, *Mastigophora* Nees (Herbertaceae) e *Lepicolea* Dumort. (Lepicoleaceae).

He-Nygre'n *et al*. (2004), baseado em três regiões do cloroplasto, obtiveram resultados que agruparam Lepidoziaceae com *Temnoma pilosum* (A. Evans) R.M.Schust. e estas em um clado que inclui membros das Lophocoleaceae (He-Nygre'n & Piippo 2003; Hentschel *et al*. 2006), Herbertaceae e *Plagiochila* (Dumort.) Dumort. He-Nygre´n *et al*. (2006) colocaram Lepidoziinae como espécies próximas de Lepicoleineae e Herbertineae, assim como o trabalho de Heinrichs *et al*. (2005).

O último e mais expressivo estudo sobre a família a nível molecular foi feito por Cooper (2011, 2012a,b, 2013). Os objetivos desses estudos foram dimensionar as relações entre os subgêneros de *Lepidozia* (incluindo espécies majoritariamente orientais) e inferir sua relação filogenética (Cooper 2011; 2012a; 2012b; 2013). O mesmo autor levanta questões muito pertinentes com relação à diversificação da divisão Marchantiophyta e das grandes famílias (Cooper 2013) de hepáticas folhosas.

Apesar desses esforços, entendemos que a classificação de Lepidoziaceae está em estado de fluxo. O último levantamento de táxons (Söderström *et al*. 2016) segue a classificação proposta por Cooper (2013) com base nos estudos moleculares recentes (Heslewood & Brown 2007; Cooper *et al.* 2011; 2012 a, b), incorporando alterações nomenclaturais de Cooper *et al.* (2013).

Entretanto, Cooper *et al.* (2013) trazem a discussão sobre a insuficiência de dados para se conhecer as unidades monofiléticas em Lepdoziaceae ou para recircunscrever as subfamílias e gêneros duvidosos (Cooper 2013), como por exemplo, as espécies ocidentais em *Lepidozia, Micropterygium*, e os gêneros *Kurzia* e *Pteropsiella*.

1.2. Contexto histórico de Lepidoziaceae

Lepidoziaceae é a segunda maior família de hepáticas folhosas e se destaca pela ampla diversidade morfológica e ecológica (Cooper et al. 2011).

Embora hipóteses apontem que foi na Gondwana o início da diversificação desta família, Cooper *et al.* (2012), indicam que Lepidoziaceae surgiu durante o Cretáceo inferior (137 Ma.) com a primeira divergência do grupo ocorrendo em torno de 116 Ma. Porém, para estimar o tempo de diversificação dos clados principais, falta a resolução filogenética dos ramos basais.

Cooper *et al.* (2012b) indicam que a diversificação de espécies existentes em *Bazzania* e *Lepidozia* é menor que 70 Ma. e 50 Ma., respectivamente. Ambos os gêneros ocupam habitats florestais, e a diversidade dessas linhagens dentro desses ambientes podem estar relacionadas a mudanças na composição das florestas. Além disso, são geograficamente difundidos em massas de terra que já abrigaram o antigo continente Gondwana.

Apesar disso, as idades desses gêneros não parecem ser consistentes com explicações pragmáticas para a atual distribuição geográfica. As quatro subordens de Jungermanniales, divergiram entre 188-265 Ma. Estima-se que Lepidoziaceae tenha divergido de Aphaloziinae e Jungermanniieae próximo de 198.7 (172.3-224.9) Ma., e começou a diversificar em 174.1 (143.1-203.3) Ma. (Cooper *et al.* 2012b). Os ramos de Lepidoziaceae se originaram por volta de 137.2 (108.7-155.9) Ma. Os primeiros grupos que divergiram datam de 116 (95.4-126.5) Ma. Sequências sobre a divergência inicial em Lepidoziaceae não são sustentadas, e estimativas de tempo de divergências precisas não foram possíveis. Várias das linhagens ricas em espécies, têm origem relativamente recente e *Bazzania* e *Lepidozia* são linhagens que aparentemente diversificaram subsequentemente ao Cretáceo. Linhagens com poucas espécies se originaram durante o início da fase de diversificação em Lepidoziaceae (Cooper *et al.* 2012b).

A taxonomia da família variou muito desde sua descrição em 1877, por Limpricht, e atualmente (Crandall-Stotler e Stotler 2000; Schuster 2000; Cooper 2011, 2012a, 2013) inclui membros anteriormente alocados em outras famílias, tais como Zoopsidaceae, Bazzaniaceae, Paracromastigaceae, Hyalolepidoziaceae e Cephaloziaceae (Evans 1939; Fulford 1963, 1966, 1968).

Ao definir e descrever a família como "natural", Schuster (1969) listou uma série de caracteres, sendo os mais importantes: ramos isofílicos, os rizóides restritos a bases subjacentes e morfologia da seta.

Atualmente, a organização em nível subfamiliar e genérico apresenta os relacionamentos submetidos a uma série de interpretações subjetivas e com ênfases muito diferentes na importância relativa dos caracteres.

Apesar do considerável trabalho na família (por exemplo, Grolle 1963, 1964; Schuster & Engel 1974; Schuster 1980, 1993, 1999a, b, c, 2000; Engel & Schuster 2001; Engel & Smith Merrill 2004), os limites genéricos continuam a ser fluidos como discutido por Engel e Smith Merrill (2004). Houveram poucas tentativas de aplicar cladística às hepáticas folhosas, e menos ainda dentro de Lepidoziaceae. Em seu lugar, houve uma série de discussões intuitivas sobre evolução e classificação apresentadas por Schuster (1966, 1972, 1979, 1984, 2000).

A plasticidade dos caracteres morfológicos no gametófito e a incerteza dos limites genéricos em Lepidoziaceae fazem desta família o grupo alvo neste estudo usando técnicas moleculares.

Na última década, mais de 30 novas espécies foram descritas para o Neotrópico, e juntamente com elas novas espécies foram implementadas a flora nacional, assim como novos registros para o Brasil (Söderström, et al. 2016; Peralta, et al. 2022). Os grupos taxonômicos estão em constante estado de fluxo, sendo implementado a cada nova observação uma ferramenta mais recente e moderna para novas análises. Lepidoziaceae, como a segunda maior família de hepáticas do mundo, abriga uma das maiores diversidades morfológicas entre os gêneros.

Assim, a) tendo em vista que em Lepidoziaceae os gênero e espécies conhecidos para o Brasil não são delimitados através de inferências moleculares; b) tendo em vista a necessidade da morfologia para auxiliar estudos com a família, c) e o entender a diversificação observada nos filídios, buscando localizar o período de diversificação desse caráter morfológico extremamente expressivo para a família.

1.3. Status de Lepidoziaceae para o Brasil

Um dos primeiros estudos que abarcou Lepidoziaceae para a América do Sul foi o trabalho de Margareth Fulford (Fulford 1966), que reuniu uma série de famílias em uma grande sinopse de Marchantiophyta para a América Latina. Para Lepidoziaceae foram considerados 14 gêneros e 137 espécies.

O estudo mais extenso feito para o Brasil com Lepidoziaceae foi o de Gradstein e Costa (2003), que considerou, 12 gêneros e 42 espécies. Este trabalho foi importante porque apresentou descrição para os gêneros, chave para as espécies e algumas ilustrações.

O trabalho de Gradstein e Costa (2003) é um excelente marco, sendo a principal referência quando se trata da identificação de espécies de hepáticas no Brasil. Infelizmente, o trabalho traz alguns problemas, pois indicam sinônimos sem apresentar materiais examinados, como é o caso de *Lepidozia brasiliensis* Steph. e *Lepidozia cupressina* (Sw.) Lindenb.

Para a América Latina, recentemente foram apresentados estudos taxonômicos que trazem descrições e ilustrações para alguns gêneros, como nos estudos de Gradstein (2017) sobre *Bazzania* da América do Sul; Costa (2021) apresentou uma nova espécie do mesmo gênero para a ciência; Ilkiu-Borges et al. (2016) apresentando o gênero *Telaranea* para a região norte do Brasil. Existem ainda inúmeras listagens brioflorísticas para o Brasil, como por exemplo: Ilkiu-Borges e Oliveira-da-Silva (2016), Faria et al. (2020), Koga e Peralta (2021), Soares e Peralta (2021), Dewes et al. (2021), Fernandes et al. (2021). Atualmente, contamos com a Flora e Funga do Brasil (2022), que reúne em um projeto integrado vários taxonomistas para monografar toda a flora nacional, projeto este que concentra as informações das revisões e listagens florísticas. Nesse contexto, Lepidoziaceae conta com descrição e ilustrações para os doze gêneros (*Amazoopsis* Engel & Merr., *Arachniopsis* Spruce, *Bazzania* S. F. Gray, *Kurzia* G. Martens, *Lepidozia* Dumort., *Micropterygium* Lindenb., *Mytilopsis* Spruce, *Paracromastigum* Fulford & Taylor, *Protocephalozia* (Spruce) Schiffn., *Pteropsiella* Spruce, *Telaranea* (Spruce) Schiffn. e *Zoopsidella* R.M.Schust.) e para 53 espécies, sendo oito indicadas como endêmicas (Peralta et al. 2020).

A distribuição geográfica da maioria das espécies no território nacional apresenta concentração em lugares úmidos e com alto índice de pluviosidade, e estão distribuídas em três domínios fitogeográficos: Amazônia, Cerrado e Mata Atlântica (Fiaschi & Pirani 2009).

Lepidozia é o segundo maior gênero em Lepidoziaceae, com cerca de 450 espécies em todo mundo. Este gênero foi proposto por Dumortier (1831), tem ampla distribuição, e apresenta grande plasticidade morfológica e amplitude ecológica. Atualmente a classificação de *Lepidozia* segue Schuster (1984). Na última década o gênero foi alvo de estudos filogenéticos (Cooper 2011, 2012a,b), mas estes estudos não compreendem toda variação morfológica do gênero (Cooper et al. 2013).

Atualmente são reconhecidas quatro espécies para o Brasil (*Lepidozia cupressina*, *L. coilophylla*, *L. inaequalis*, *L. incurvata*), as quais são apresentadas no estudo de Gradstein e Costa (2003), predominantemente ocorrendo no domínio da Mata Atlântica (Valente *et al.* 2006; Santos & Costa 2010; Carmo *et al.* 2016, 2018; Yano et al. 2019; Amélio 2019; Lima & Peralta 2021; Koga & Peralta 2022).

As espécies em sua maioria são dioicas com cápsulas diminutas e muitas espécies são conhecidas apenas pelo material gametofitico (Engel & Schuster 2001), por esse motivo ainda falta tanto conhecimento com relação aos esporos deste gênero, assim como em outros em Lepidoziaceae. É válido à observação em campo se há presença de esporófitos, assim essas estruturas devem ser preservadas em envelopes distintos da amostra principal. Tal preocupação viabiliza estudos futuros com relação à morfologia do esporófito e esporos.

Os segmentos são os principais caracteres a serem observados na identificação de *Lepidozia*, tais segmentos variam de curtos como observado em *L. incurvata*, a muito longos como em *L. inaequalis*, de finos em *L. brasiliensis* a largos como em *L. cupressina*. Apesar da maioria das espécies terem como padrão um perfil de quatro segmentos, espécies como *L. macrocolea* pode apresentar usualmente mais de cinco (Fulford 1966).

1.4. Morfologia como auxílio e complemento em estudos evolutivos

A visão de um mundo caracterizado extraordinariamente por formas, e que foram as estruturas morfológicas, órgãos, tecidos e acessórios que premeditaram a distinção entre os indivíduos, é tratada desde Lineu, que observava os caracteres, e esses não exclusivamente em vegetais, para realizar suas classificações. Para a ciência, essa ainda é a principal explicação para a diversidade no mundo. A morfologia sempre esteve presente na ciência e o advento de novas tecnologias corroboram para a implementação e aperfeiçoamento de técnicas utilizadas para a morfologia (Rouhan & Gaudeul 2014).

Considerada ciência da diversidade da vida, a Sistemática abrange a descoberta e a interpretação da biodiversidade, na forma de um sistema de classificação preditivo, com o propósito fundamental de desvendar a evolução dos organismos, além de buscar identificar os processos responsáveis por esta diversidade (Judd et al. 2009).

Ancorada em quatro princípios básicos: classificação, descrição, identificação e nomenclatura, a sistemática filogenética é baseada no critério de que as classificações precisam refletir a história evolutiva dos organismos e, atualmente, adicionando a reconstrução filogenética como um de seus elementos (Judd et al. 2009). A descrição é o detalhamento de todos os atributos do organismo, sendo, no caso de briófitas a geração gametofítica, vegetativa e predominantes e a esporofítica, sexual e efêmera.

A nomenclatura é essencial para que o nome seja aplicado ao organismo reconhecido de forma única e universal, rigidamente estabelecido pelo Código Internacional de Nomenclatura para Algas, Fungos e Plantas (Bicudo et al. 2018). E a classificação consiste em ordenar sob níveis hierárquicos de acordo com suas características (atualmente, priorizando as relações filogenéticas).

Todos esses princípios são baseados praticamente em estudos morfológicos, isso desde que o processo de identificação fora do reconhecimento filogenético é praticamente amparado em informações de morfologia. Apesar de todo rigor na descrição dos métodos, a inclusão de dados morfológicos deve seguir uma proposta onde pode ser explorado um conjunto específico de caracteres, limitando o número de características, ainda que toda morfologia do grupo não tenha sido explorada o objetivo poderá ser (Queiroz 2010).

Em Lepidoziaceae, microestruturas como os esporos e elatérios ainda são pouco conhecidos, isso porque estas estruturas são raras nos espécimes coletados, ou o acondicionamento das amostras nas coleções não são preservadas.

Lindenberg (1846) apresentou pela primeira vez ilustrações, incluindo pranchas coloridas, e demonstrou a amplitude morfológica do gênero *Lepidozia*. Consecutivamente, Reinner (1933) estudou *Micropteryium*, Fulford (1963, 1966, 1968), *Bazzania*, e Schuster (2000), *Telaranea*. A morfologia para esse grupo sempre foi marcante, o que torna Lepidoziacae um grupo fácil de identificar, principalmente no que consiste a plasticidade morfológica.

1.5. Estudo dos esporos em hepáticas

Os esporos são produzidos, após a meiose, nos esporângios dos esporófitos e funcionam como unidade de propagação e disseminação das briófitas. A morfologia e a ultraestrutura dos esporos das briófitas são significativas na taxonomia de vários grupos (Jing et al. 2007) e têm demonstrado importante papel para o tratamento sistemático e caracterização de gêneros e espécies. No entanto, antigamente os esporos eram negligenciados e poucas características eram incluídas em trabalhos científicos, sendo que alguns autores citaram apenas coloração e tamanho (Bruch et al.1855; Britton 1913).

Os estudos ganharam mais destaque à medida que novas técnicas eram desenvolvidas, McClymont (1954) e Terasme (1955) foram os primeiros a aplicarem o método da acetólise de Erdtman (1952) para analisar esporos de musgos e acreditaram no valor taxonômico deste caráter para auxiliar durante as descrições e identificações de espécies. Erdtman (1952), o desenvolvedor do método, apresentou estudo detalhado dos esporos de algumas espécies de briófitas (Erdtman 1957, 1965), demonstrando a diversidade e variabilidade existente entre algumas espécies.

De acordo com Clarke (1979), a morfologia dos esporos nunca desempenhou um papel tão significativo na sistemática das briófitas como nos tempos modernos. E Mogensen (1981) apontou que o estudo com esporos de briófitas era ainda muito recente em muitos países e que faltam cientistas especialistas com ampla experiência neste campo. É notório o aumento exponencial da palinologia na taxonomia vegetal, graças à aplicação da Microscopia Eletrônica de Varredura (MEV). A maioria dos estudos foram aplicados aos pólens das angiospermas (Skvarla et al. 1988; Harley & Ferguson 1990), enquanto os esporos das briófitas receberam menos atenção, devido seu tamanho diminuto, aparentemente uniforme, e pela ornamentação de esporos serem, muitas vezes, mais difícil de correlacionar com caracteres macroscópicos (Saito & Hirohama 1974).

De acordo com os registros, foi Lindenberg (1846) o primeiro a observar esporos em briófitas e os primeiros estudos extensos com esporos de diversas espécies de briófitas foram publicados por Roth (1905). No Japão, os trabalhos de Miyoshi (1973) e Hirohama (1970, 1975, 1976, 1977, 1978), são de particular importância, porque apresentam a caracterização dos esporos de 42 espécies.

Clarke (1979), tentando estabelecer os padrões de ornamentação dos esporos de briófitas, comenta que eles são irregulares e é improvável que um sistema verbal de terminologia os descreva adequadamente. Olesen & Mogensen (1978) e Mogensen

(1981) estudaram a morfologia dos esporos das briófitas e apresentaram métodos para a tomada de medidas dos esporos.

De modo geral, os esporos das briófitas podem ser inaperturados, leptomados ou apresentar uma abertura (Brown & Lemmon 1984, 1988). O leptoma é uma região disposta no pólo proximal dos esporos que permite a saída do tubo germinativo. Ele é caracterizado pelo aumento da espessura da intina, diminuição da espessura da exina e a ausência dos elementos da perina (Olesen & Mogensen 1978). No esporo adulto ou maduro, a abertura está recoberta por uma camada de exina e pode apresentar distinções estruturais de acordo com a espécie (Olesen & Mogensen 1978; Mogensen 1983).

Muitos estudos com base no método de MEV sobre esporos de briófitas foram publicados no Brasil e no mundo (Udar & Srivastava 1984; Udar & Agarwal 1985; Blackmore & Barnes 1991; Brown & Lemmon 1988; 1991; Brown et al. 2015; Estébanez et al. 1997; Luizi-Ponzo & Barth 1998; 1999; Luizi-Ponzo & Melhem 2006; Caldeira et al. 2006, 2009, 2013; Yano & Luizi-Ponzo 2006, 2011; Rocha et al. 2008; Rodrigues & Luizi-Ponzo 2015; Savaroğlu 2015; Savaroğlu et al. 2017; Silva-e-Costa et al. 2017). Estes estudos vêm contribuindo para novidades científicas, como por exemplo Silva-e-Costa & Luizi-Ponzo (2019) e Passarella & Luizi-Ponzo (2022) que descrevem e ressaltam a importância morfológica das ultraestruturas para estudos ambientais, de biodiversidade e evolutivos.

Blackmore & Barnes (1991), demonstraram a importância dos caracteres de polén na determinação de homologias entre as plantas terrestres e Rushing (1985), a sua relevância na caracterização taxonômica de briófitas, especificamente dentro da família de musgos Bruchiaceae. Apesar de todo conhecimento sobre os esporos, é perceptível a necessidade de mais pesquisas nesta área, para obtenção de novos dados e caminhos a serem explorados.

1.6. Morfologia e ambiente

As briófitas são consideradas as plantas terrestres mais antigas, e desde seu surgimento, especiaram e se transformaram, ocupando todos os continentes e tipos de substratos. As hepáticas, como são popularmente conhecidas, se diferenciaram, de forma bem marcante, entre plantas talosas e folhosas (Richards 1984; Fudali 2001).

Com a rápida diversificação das angiospermas, as hepáticas ganharam, como substratos de colonização, os troncos vivos e em decomposição, os galhos e as folhas.

Nestes substratos, com novas condições ambientais em curto período diversificarm grupos grandes como Lejeuneaceae (Schäfer-Verwinp et al. 2014; Bechteler 2016 a, b).

Dessa maneira, o período de especiação atual é marcado por muitas dúvidas e incertezas, uma vez que os caracteres morfológicos podem ou não serem considerados autapomorfias ou plesiomorfias. Como grande exemplo, a ausência de estômatos nas hepáticas.

Harris et al. (2020) mostram que o desenvolvimento e evolução dos estômatos precede as briófitas e as evidências apontam que o ancestral comum das criptógamas com as fanerógamas já possuía estômatos. Por algum motivo os estômatos não teriam se desenvolvido em todos seus descendentes, ainda que musgos e os antóceros apresentam estômatos não funcionais, e as hepáticas não teriam nem vestígios morfológicos. Os estômatos são largamente difundidos como estrutura chave na entrada e saída de gases nas fanerógamas. No entanto, nestas, tudo o que vemos é esporófito, e esta, sendo uma fase grande e dominante. Já nas, briófitas apenas naqueles que o esporófito é mais duradouro, como musgos e antóceros, eles estão presentes e são visíveis. Nas hepáticas, a seta é bem efêmera, hialina e se fragmenta bem rápido.

Outra estrutura que ganhará função similar à desempenhada pelos estômatos seriam os poros, mas estes não são controlados por nenhum tipo de mecanismo e o surgimento ainda é incerto, requerendo mais investigações (Harris et al. 2020).

A morfologia das briófitas tem impressionado pela capacidade dessas plantas de se adaptarem, até mesmo nas condições mais adversas, e de conseguirem alcançar longas distâncias, como os musgos do Polo Norte e do Polo Sul. Evidências indicam que a capacidade de reprodução pela via assexuada é tão eficiente quanto sexuadamente e que essas espécies seriam propagadas e não teriam evoluído por convergência, o que as tornaria muito similar a outras espécies geneticamente distintas. Esta teoria explicaria cerca de 13% não apenas da flora das criptógamas, mas de toda vida selvagem endêmica do planeta (Silva, 2007).

1.7. Os estudos filogenéticos com hepáticas

A nomenclatura das hepáticas começou com Linnaeus (1753), que as subdividiu em dois grupos morfológicos. Crandall-Stotler e Stotler (2000), testaram a hipótese de Linnaeus e reconheceram duas classes, de acordo com as análises morfológicas e filogenéticas. No entanto, estudos filogenéticos desde então têm mostrado extensa homoplasia com muitos dos caracteres usados para definir gêneros ou famílias (Crandall-

Stotler et al. 2005), com a classificação mais recente de Marchantiophyta sendo baseada na filogenia de Crandall-Stotler et al. (2009 a, b). O alto teor de homoplasia e a falta de caracteres diagnósticos morfológicos estáveis dificultam a delimitação dos gêneros e a reconstrução de suas relações, como em Lejeuneaceae (Sukkharak et al. 2011).

A classificação biológica contemporânea, é largamente produto direto da nomenclatura de Linnaeus e da teoria da evolução de Darwin. As bases que compõem a nomenclatura de Linnaeus por regras são amplamente aceitas e a classificação pode refletir a evolução e esta, por sua vez, seria um fato. As relações evolutivas podem ser identificadas, e essas relações poderiam ser traduzidas em um sistema de classificação (WILEY & LIBERMANN 2011).

Possível abordagem para a filogenia de hepáticas foi dada por Wettstein (1903-1908). O sistema Wettstein, posiciona os gametófitos folhosos eretos antes das formas achatadas bilateralmente. A motivação para tal sistema vem da suposição de que musgos e hepáticas são derivados de um ancestral comum e, portanto, as hepáticas ancestrais seriam as mais parecidas com os musgos. Pensamento parecido com o de Wettstein foi apresentado na tese de Church (1919), que argumentou que as hepáticas folhosas se originaram repetidamente de ancestrais talosos de algas marinhas. Devido às diferenças ambientais dramáticas, é improvável que uma transformação evolutiva semelhante tivesse ocorrido em ambiente terrestre. Portanto, essas plantas frondosas devem ter apresentado tal estado já em seu ancestral.

Desta forma, espécies com eixos sem filídios ou talos seriam derivadas de ancestrais folhosos. Assim, a condição ancestral teria sido de alternância isomórfica de gerações folhosas e indícios evolutivos indicam redução para caracteres folhosos ou talosos. A teoria de Church foi aplicada às hepáticas por Evans (1939) e foi desenvolvida por Schuster (1972, 1984), um dos principais responsáveis da classificação filogenética pré-molecular das hepáticas. As classificações compreendidas de hepáticas por Crandall-Stotler et al. (2000) e Schuster (2000) expõem nitidamente os pensamentos de Church sobre evolução morfológica redutiva.

A diversidade de hepáticas no Brasil é representada por cerca de 663 espécies, com 125 endêmicas (Peralta et al. 2020). No entanto, os estudos filogenéticos são escassos frente a essa riqueza. Forrest et al. (2006) montaram uma grande filogenia molecular de Marchantiophyta e, com suas análises, forneceram suporte para o monofiletismo de hepáticas e para a base previamente resolvida dos relacionamentos dentro de Marchantiophyta.

Heinrichs et al. (2014), Schäfer-Verwinp et al. (2014), Yu et al. (2014) e Bechteler et al. (2016a e b) testaram o monofiletismo de Lejeuneaceae, a maior família de hepáticas folhosas, e obtiveram a definição de quatro subtribos que foram adicionadas com base em extensões dos conjuntos de dados moleculares. Antes destes estudos, a classificação dos gêneros de Lejeuneeae era amplamente baseada em caracteres gametofíticos.

Villareal et al. (2016), apresentou uma filogenia completa em nível genérico das hepáticas talosas complexas, que usaram para estimar tempos de divergência e analisar tendências evolutivas. Este estudo, apesar de incluir algumas amostras do Brasil, não teve como alvo táxons nativos.

Inicialmente, relações filogenéticas foram inferidas com intuito de interpretar os estados de caráter. Dentre as primeiras hipóteses evolutivas propostas por Haeckel (1866), abordagens especulativas forneceram um bom ponto de partida. Ocasionalmente essa abordagem ainda é utilizada para interpretar as relações, particularmente entre as linhagens extintas (Stuessy 2004, 2010).

2. Objetivos

2.1 Objetivo Geral

- Fornecer estudo taxonômico e filogenético abarcando parte da família Lepidoziaceae.

2.2 Objetivos Específicos

- Fornecer estudo taxonômico do gênero *Lepidozia* para o Brasil.
- Investigar a morfologia dos esporos de *Micropterygium*.
- Analisar as características morfológicas diagnósticas dos gêneros de Lepidoziaceae no Brasil e correlacionar com a distribuição geográfica, com ênfase nas espécies endêmicas;
- Investigar período de diversificação das espécies de *Micropterygium* Lindenb. e *Lepidozia* (Dumort.) Dumort. do Brasil;
- Verificar quais autopomorfias e sinapomorfias que caracterizam e diferenciação os gêneros em Lepidoziaceae;

3. Materiais e Métodos

3.1 Levantamento bibliográfico

O levantamento bibliográfico foi realizado ao longo de toda a pesquisa, através da consulta às obras originais, revisões taxonômicas e monografias, levantamentos florísticos e demais publicações sobre a família. Esses materiais consultados foram provenientes de arquivos digitais das bases do Biodiversity Heritage (http://www.biodiversitylibrary.org/), Botanicus (http://www.botanicus.org/), Internet Archive (https://archive.org) e Jardim Botânico Real de Madri (http://bibdigital.rjb.csic.es/ing/). Além de consultas a materiais depositados em bibliotecas físicas, como a Biblioteca do Instituto de Pesquisas Ambientais (São Paulo), Instituto de Pesquisas da Amazônia (Manaus) e no Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (Rio de Janeiro).

3.2 Coletas

Foram realizadas oito coletas, uma no Estado de Minas Gerais (município de Passa Quatro); duas em São Paulo (Serra da Bocaina e no Parque Estadual do Rio Turvo); três no Estado do Amazonas (no Museu da Amazônia (MUSA) e na Reserva Florestal Adolpho Ducke e na Reserva biológica da Campina), e duas no estado da Bahia (Chapada Diamantina e no município de Serrinha). As coletas foram realizadas em busca das espécies endêmicas de Lepidoziaceae, de acordo com estudos florísticos, também foram aproveitadas idas a campo provenientes de outros projetos. As amostras coletadas encontram-se depositadas nos herbários SP e HUEFS.

3.3 Consulta aos herbários

Foram examinados 3089 espécimes, incluindo os 15 tipos nomenclaturais, os quais se concentraram nos objetivos do primeiro capítuo desse estudo. A análise dos tipos foi a partir das visitas aos herbários (SP, INPA, RB, HUEFS, MG e G) e empréstimos, os quais foram armazenados temporariamente no Herbário SP do Instituto de Pesquisas Ambientais, eles estão listados no tratamento taxonômico e os acrônimos dos herbários seguem Thiers (2019). Foram consultados também espécimes digitalizados no JSTOR Types, com obetivo de confirmar os espécimes tipos (plants.jstor.org).

3.4 Análise nomenclatural

Neste trabalho as decisões nomenclaturais foram tomadas seguindo o Código Internacional de Nomenclatura para Algas, Fungos e Plantas (Bicudo et al. 2018). Os espécimes tipo foram encontrados através de consultas ao Tropicos.org, e o Checklist of liverworts and hornworts to world (Sordestron et al. 2016), Biodiversity Heritage (http://www.biodiversitylibrary.org/), Botanicus (http://www.botanicus.org/), Internet Archive (https://archive.org) e Jardim Botânico Real de Madri (http://bibdigital.rjb.csic.es/ing/) e JSTOR Types.

Nomes e citações bibliográficas dos táxons foram conferidos nas obras príncipes e confrontadas com as bases do Index Hepaticarum (https://www.ville-ge.ch/musinfo/bd/cjb/hepatic/index.php) e do Tropicos (http://www.tropicos.org/).

A identidade das espécies foi baseada além dos dados moleculares deste estudo também na análise detalhada dos materiais-tipo examinados, dos protólogos disponíveis e os espécimes coletados e de herbário ajudaram a definir os limites morfológicos e fitogeográficos das espécies.

3.5 Análise morfológica e taxonômica

As análises morfológicas ocorreram no Laboratório de Taxonomia da UEFS (TÁXON), e no Núcleo Coleções Biológicas no Instituto de Pesquisas Ambientais. As análises morfológicas, descrições, chaves de identificação, ilustrações, comentários morfológicos basearam-se em materiais herborizados reidratados de coletas recentes. A observação dos caracteres gametofíticos e esporofíticos foi auxiliada por estereomicroscópios e microscópios ópticos presentes nos referidos laboratórios.

A terminologia para as formas de estruturas planas e tridimensionais segue as recomendações do Systematics Association Committee for Descriptive Biological Terminology (1962) e a literatura específica para briófitas, como por exemplo Luizi-Ponzo *et al.* (2006), Punt et al. (2007) e Erdtman (1952) para nomenclatura palinológica.

As estruturas foram observadas sob o estereomicroscópio utilizando-se pinças e lâminas de barbear (para seccionar o caulídio), tendo sido observadas e medidas em microscópio óptico com lente milimetrada acoplada e em escala com auxílio do software Cells, instalado em máquina com microscópio acoplado.

As micrografias foram tomadas com base em material herborizado, utilizando-se estereomicroscópio e microscópio. As micrografias foram vitais para construção da tabela morfológica e para as pranchas das espécies que ilustram o capítulo 1 desta Tese. Foram incluídos os caracteres fundamentais na identificação (hábito, disposição dos filídios, filídios e anfigastros), imagens disponíveis no primeiro capítulo deste trabalho.

3.6 Distribuição geográfica e substratos colonizados

Os dados relativos aos hábitats e à distribuição geográfica foram baseados nas etiquetas das exsicatas depositadas nos herbários, bem como nas observações em campo. Considerou-se o manual técnico da vegetação brasileira (IBGE, 2012), assim como as definições de Domínios morfoclimáticos do Brasil proposta por Ab'saber (1967, 2003), discutida e atualizada por Oliveira-Filho (2009; 2015) e Castuera-Oliveira et al. (2020). A nomenclatura para os substratos colonizados seguiu Richards (1984) e Fudali (2001).

Os mapas de distribuição das espécies foram gerados a partir do Mapa Base Global GIS no programa ArcMapGIS (Esri, 1999) com base nas coordenadas disponíveis nas etiquetas das exsicatas. Aquelas que não apresentaram esta informação tiveram suas coordenadas definidas por aproximação, utilizando-se o site do IBGE (https://www.ibge.gov.br/).

3.7 Preparo do banco de dados

Os espécimes que foram utilizados neste trabalho foram elencados de acordo com os caracteres morfológicos, coordenadas geográficas, e marcador. Estas informações foram retiradas de bancos de dados dos herbários brasileiros, com o auxílio do *speciesLink* e o gerenciador de coleções BRAMS (IPA-SP). As sequências produziadas foram disponibilizadas no GenBank, analisadas e filtradas de acordo o marcador utilizado, levando em consideração sequências inteiras e parciais.

3.8 Análise molecular e filogenética

Considerando que as várias coleções contam com espécimes recém-coletados e, não sendo possível retirar material para análise molecular de espécimes tipos, foram utilizadas no total 18 amostras recentes das espécies de Lepidoziaceae. As espécies selecionadas foram determinadas de acordo com a ausência de dados no banco de dados, como as espécies brasileiras de *Lepidozia* e o gênero Sul Americano *Micropterygium*. Como grupos externos foram incluídas as espécies de Lophocoleaceae e Geocalycaceae.

O arranjo observado nas hipóteses filogenéticas obtidas a partir destes materiais foi essencial para embasar a eleição de características que sustentem o monofiletismo ou não dos clados e que ajudaram na delimitação taxonômica dos táxons.

O DNA total foi extraído por meio do método CTAB (Doyle & Doyle, 1987, 1990) com modificações de Câmara (2006, 2009). Após a extração, o DNA foi amplificado por meio da Reação em Cadeia da Polimerase (PCR) e foram analisadas quatro regiões (tabela 1), seguindo, Heslewood *et al.* (2007), Liu et al. (2010) e Cooper (2012a,b).

O produto de PCR foi purificado utilizando polietilenoglicol (PEG) e sequenciados diretamente na FioCruz®. As sequências foram comparadas com as obtidas do GenBank utilizando BLAST (Altschul *et al.* 1990). Esta comparação é indicada para confirmação da filiação das sequências extraídas. Atualmente, o banco de dados genômicos online conta com uma gama de sequências de Lepidoziaceae, que foram filtradas e analisadas em conjunto com os 12 terminais provenientes desse estudo. O alinhamento e edição das sequências foi verificado com o auxílio dos programas BioEdit 7.2.5 (Hall 1999).

As análises de máxima verossimilhança (MV) foram realizadas com os softwares MEGA (Kumar, Stecher e Tamura 2016), RAxML v.8 (Stamatakis 2014) e a plataforma CIPRES. Estas análises se baseiam na busca heurística, 10.000 (random-addition-sequence replicates), troca de ramo (tree bisection-reconnection), MULTrees ativado, e *collapse zero-length branches* desativado. Os caracteres foram tratados como equilibrados e não ordenados. Ao se encontrar mais de uma árvore de verossimilhança, estas foram resumidas a apenas uma árvore de consenso estrito. Valores de *bootstrap* não paramétricos (Felsenstein 1985) foram gerados como buscas heurísticas com 1.000 repetições, cada uma com dez réplicas aleatórias. Rearranjos foram restritos a 1.000.000

por repetição. Valores percentuais *Bootstrap* (BPV) ≥ 70 foram considerados como um bom suporte (Hillis & Bull 1993).

As análises Bayesianas foram realizadas com o software MrBayes 3.0 (Ronquist & Huelsenbeck, 2003) e na plaforma CIPRES. Nestas análises, os valores de similaridade foram acompanhados graficamente para examinar os parâmetros e determinar o número de árvores necessárias para alcançar a estacionalidade (*burn-in*), já a plaforma Cipres gera os resultados da análise com o *burn-in*. A seleção do modelo foi concluída usando iqtree-1.6.12. (Minh et al. 2020). O modelo mais bem classificado de acordo com o critério de informação de Akaike (AIC, Akaike, 1973; Burnham e Anderson, 2004) foi usado para análises bayesianas. Nestes casos o modelo com classificação mais alta foi o GTR + C + I, e seu desempenho comparado por meio de fatores de Bayes (Kass e Raftery, 1995). Clados com probabilidade posterior P0.9 são considerados suportados e aqueles com probabilidade posterior P0.95 são considerados fortemente suportados.

A inferência bayesiana (BI) foi executada usando o Mr. Bayes (Huelsenbeck e Ronquist, 2003) conforme implementado no Portal CIPRES (Miller et al., 2010). Duas cadeias independentes de Markov Monte Carlo (MCMC), cada uma é executada por dez milhões de gerações, amostrando a cada 1.000 gerações. Depois de plotar os valores de log verossimilhança e calcular o desvio padrão das frequências divididas para verificar a convergência, as primeiras 1001 amostras foram descartadas.

As As árvores selecionadas foram resumidas em uma única árvore de consenso de maioria e as probabilidades posteriores foram utilizadas para estimar a sustentação das bipartições (Ronquist & Huelsenbeck, 2003). No caso das análises Bayesianas só foram considerados como bem sustentados os ramos com probabilidades > 90%.

3.9. Estimação de tempo de divergência

Para estimar o tempo de divergência foi utilizado o programa BEAUTY e BEAST v1.8 (Drummond & Rambaut, 2007) e a plaforma CIPRES, utilizando como árvore inicial o melhor resultado obtido nas análises bayesianas.

Devido à escassez de fósseis de Lepidoziaceae e briófitas de modo geral, o tempo de divergência foi calibrado baseando-se em um espectro geral da família proposto por Cooper et al. (2012a), como *Bazzania* (70 Milhões de anos), *Lepidozia* (50 milhões de anos), Lepidoziaceae (116 milhões de anos), Marchantiophyta (492.7 milhões de anos). Outros pontos de calibração secundária foram baseados em Heinrichs et al. (2018) (Lophocoleaceae, Plagiochilaceae) e Cooper (2013) seguindo os métodos propostos por Cervantes et al. (2016).

Tabela 1. Descrição dos marcadores utilizados neste estudo

Marcador	Genoma	Primer [sequência 5'-3']	Referência:
nr26S	nuclear	LS0F [ACCCGCTGTTTAAGCATAT]	Shaw 2000
		LS12R [ATCGCCAGTTCTGCTTACCA]	Shaw 2000
rbcL	cloroplasto	mtrnRR [GCTCTAATCCACTGAGCTAC]	Cox et al., 2001
		nm34 [GTTGTTGGGATTTAAAGCTGGTGTT]	Cox et al., 2001
		rcbL1 [GGGATTTATGTCACCACAAACAGA]	Gadek & Quinn 1993
		rbcL2 [GATCTCCTTCCATACTTCACAAGC]	Gadek & Quinn 1993
rps4	cloroplasto	rps5 [ATGTCCCGTTATCGAGGACCT]	Nadot et al. 1994
		trnas [TACCGAGGGTTCGAATC]	Souza-Chies et al. 1997
trnL-trnF	cloroplasto	trnF [ATTTGAACTGGTGACACGAG]	Taberlet et al. 1991
		trnC [CGAAATCGGTAGACGCTACG]	Taberlet et al. 1991

4. Referências bibliográficas

Ab'Saber, A. N. 1967. Domínios morfoclimáticos e províncias fitogeográficas no Brasil. Orientação 3: 45-48.

Ab'Saber, A. N. 2003. Os Domínios de Natureza no Brasil: potencialidades paisagísticas. São Paulo: Ateliê Editorial.

Akaike, H. 1973. Information Theory as an Extension of the Maximum Likelihood Principle. In: Petrov, B. N. F., Csaki, F. (eds.). Second International Symposium on Information Theory. Akademiai Kiado., Budapest, pp. 267-281.

Amélio, L. A.; Peralta, D. F.; Carmo, D. M. 2019. Briófitas do Parque Estadual de Campos do Jordão, Estado de São Paulo, Brasil. Hoehnea 46: e962018. doi: 10.1590/2236-8906-96/2018

Altschul, S. F.; Gish, W.; Miller, W.; Myers, E. W.; Lipman, D. J. 1990. Basic local alignment search tool. Journal of Molecular Biology 215:403–410.

Bechteler, J.; Lee, G. E.; Schafer-Verwimp, Renner, M. A. M.; Peralta, D. F.; Heinrichs, J. 2016a. Towards a monophyletic classification of Lejeuneaceae V: the systematic position of *Pictolejeunea*. Phytotaxa doi: 10.11646/phytotaxa.280.3.4.

Bechteler, J.; Lee, G. E.; Schafer-Verwimp, Pócs, T.; Peralta, D. F.; Renner, M. A. M.; Heinrichs, J.; Schneider, H. 2016b. Towards a monophyletic classification of Lejeuneaceae IV: reinstatement of *Allorgella*, transfer of *Microlejeunea aphanella* to *Vitalianthus* and refinements of the subtribal classification. Plant Systematic. Evolution. doi: 10.1007/s00606-015- 1252-8

Bicudo, C. E. M.; Prado, J.; Hirai, R. Y. 2018. Código Internacional de Nomenclatura Botânica para algas, fungos e plantas (Código de Shenzhen, 2018). RIMA.

Blackmore, S.; Barnes, S. H. 1991. Pollen and spores. Patterns of diversification. The systematics association. Special volume No. 44. Clarendon Press, Oxford, pp. 1–402.

Brown, R. C; Lemmon B. E. 1988. Sporogenesis in bryophytes. Advances in Bryology 3: 159-223.

Brown, R. C.; Lemmon, B. E. 1991. Sporogenesis in simple land plants. In: BLACKMORE S, BARNES S.H. (eds.) Pollen and spores. patterns of diversification. Oxford, Clarendon Press. p 9-24.

Brown, R. C.; Lemmon, B. E.; Shimamura, M.; Villarreal, J. C.; Renzaglia, K. S. 2015. Spores of relictual bryophytes: Diverse adaptations to life on land. Review of Palaeobotany and Palynology 216: 1-17.

Burnham, K. P., Anderson, D. R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33: 261-304.

Caldeira, I.C.; Gonçalves-Esteves, V.; Luizi-Ponzo, A.P. 2006. Morfologia dos esporos das espécies de Leucobryaceae Schimp. (Bryophyta) do Parque Estadual de Ilha Grande, Município de Angra dos Reis, Estado do Rio de Janeiro. Revista Brasileira de Botânica 29: 301-307.

Caldeira, I.C.; Gonçalves-Esteves, V.; Luizi-Ponzo, A.P. 2009 Morfologia dos esporos de Sematophyllaceae Broth. ocorrentes em três fragmentos de Mata Atlântica, no Rio de Janeiro, Brasil. Revista Brasileira de Botânica 32: 299-306.

Caldeira, I.C.; Gonçalves-Esteves, V.; Luizi-Ponzo, A.P. 2013. Palynology of selected species of Fissidens (Hedw.). Plant Systematics and Evolution 299: 187-195.

Câmara, P. E. A. S. 2006. Molecular contribution on the systematics placement of the moss genus Paranapiacabaea. Bol Inst Bot. (São Paulo) 18: 159-162 **Câmara, P. E. A. S.** 2009. Métodos de extração de DNA de Bryophyta para análises filogenéticas. Heringeriana, Brasília, V. 3, n. 2, p. 11-17.

Carmo, D.M.; Lima, J.S.; Amélio, L.A.; Peralta, D.F. 2016. Briófitas do Parque Estadual da Serra do Mar, Núcleo de Santa Virgínia, Estado de São Paulo, Brasil. Hoehnea 43(2): 265-287.

Carmo, D.M.; Lima, J.S.; Amélio, L.A.; Peralta, D.F. 2018. Briófitas da Reserva Particular do Patrimônio Natural da Serra do Caraça, Estado de Minas Gerais, Brasil. Hoehnea 45(3): 484-508.

Castuera-Oliveira, L.; Oliveira-Filho, A.T.; Eisenlohr, P.V. 2020. Emerging hotspots of tree richness in Brazil. Acta Botanica Brasilica - 34(1): 117-134.

Cervantes, A.; Fuentes, S.; Gutierrez, J.; Magallon, S.; Borsch, T. 2016. Successive arrivals since the Miocene shaped the diversity of the Caribbean Acalyphoideae (Euphorbiaceae). Journal of Biogeography (J. Biogeogr.) (2016) 43, 1773–1785

Church, A. H. 1919. Thalassiophyta and the subaerial transmigration. Oxford Botanical Memoirs 3, 1-95.

Clarke, G.C.S. 1979. Spore morphology and Bryophyte Systematics. In: Clarke, G.C.S. & Duckett, J.G. (Eds.), Bryophyte Systematics. Academic Press, London and New York, pp. 231–250.

Cooper, E. D.; Shaw, A. J.; Shaw, B.; Henwood M. J.; Heslewood, M. M.; Brown, E. A. 2011. A multi-locus molecular phylogeny of the Lepidoziaceae: Laying the foundations for a stable classification. Molecular phylogenetics and evolution. 59. 489-509.

Cooper, E. D.; Henwood, M. J.; Brown, E. 2012a. A molecular phylogeny of the *Lepidozia* generic complex supports re-circumscription of the Lepidozioideae. Molecular Phylogenetics and Evolution. 65, 10-22.

Cooper, E. D.; Henwood, M. J.; Brown, E. A. 2012b. Are the liverworts really that old? Cretaceous origins and Cenozoic diversification in Lepidoziaceae reflect a recurrent theme in liverwort evolution. Biological Journal of the Linnean Society, 107, 425-441.

Cooper, E. D. 2013a. Notes on Early Land Plants Today. 37. Towards a stable, informative classification of the Lepidoziaceae (Marchantiophyta). Phytotaxa, 97 (2): 44-51.

Costa, D. P., coord. Lista de espécies: briófitas. In: FORZZA, RC., org., *et al.* INSTITUTO DE PESQUISAS JARDIM BOTÂNICO DO RIO DE JANEIRO. *Catálogo de plantas e fungos do Brasil* [online]. Rio de Janeiro: Andrea Jakobsson Estúdio: Instituto de Pesquisa Jardim Botânico do Rio de Janeiro, 2010. p. 452-521. Vol. 1. ISBN 978-85-8874-242-0. Available from SciELO Books

Costa, D. P. 2021. A New Species of *Bazzania* (Lepidoziaceae, Marchantiophyta) from the Guiana Highlands of Brazil. Systematic Botany, Volume 46, Number 3, July-September 2021, pp. 728-731(4)

Crandall-Stotler, B.; Stotler, R. E. 2000. Morphology and classification of the Marchantiophyta. In: Shaw A. J., Goffinet B. (eds.) Bryophyte biology. Cambridge University Press, Cambridge, pp. 21–70.

Crandall-Stotler, B. J.; Forrest, L. L.; Stotler, R. E. 2005. Evolutionary trends in the simple thalloid liverworts (Marchantiophyta, Jungermanniopsida subclass Metzgeriidae). Taxon. doi: 10.2307/25065359

Crandall-Stotler, B.; Stotler, R. E.; Long, D. G. 2009a. Morphology and classification of the Marchantiophyta. In: Goffinet B and AJ Shaw (eds) Bryoph Biol, 2nd edn. Cambridge University Press, Cambridge, pp 1-54

Crandall-Stotler, B.; Stotler, R.E.; Long, D.G. 2009b. Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66(1):155-198.

Davis, E. C. 2004. A molecular phylogeny of leafy liverworts (Jungermanniidae:Marchantiophyta). In: Goffinet B., Hollowell V., Magill R. (eds.) Molecular systematics of bryophytes. Missouri Botanical Garden Press, St. Louis, pp. 61–86.

Doyle, J. J.; Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf
tissue. Phytochemistry Bulletin 19: 11-15.

Doyle, J.J.; Doyle, J.L. 1990. Isolation of plant DNA from fresh tissue. Focus 12: 13-15.

Dumortier, B. C. 1835. Recueil d'Observations sur les Jungermanniacées. I. Révision des genres. J.-A. Blanquart, Tournay, 27 pp. http://dx.doi.org/10.5962/bhl.title.731

Engel, J.J.; Schuster, R.M. 2001. Austral Hepaticae. 32. A revision of the genus Lepidozia (Hepaticae) for New Zealand. Fieldiana, Botany, n.s. 42: 1–107

Engel, J. J.; Smith Merrill, G. L. 2004. Austral Hepaticae 35. A taxonomic and phylogenetic study of *Telaranea* (Lepidoziaceae), with a monograph of the genus in temperate Australasia and commentary on extra-Australasian taxa. Fieldiana, Bot. 44:1–265.

Erdtman, G. 1952. On pollen and spore terminology. Palaeobotanist 1: 169–176.

Erdtman, G. 1957. Pollen and spore morphology/Plant taxonomy. Gymnospermae, Pteridophyta, Bryophyta (illustrations). An introduction to palynology, II. Almqvist and Wiksell, Stockholm, pp. 1–151.

ESRI – Environmental Systems Research Institute. 1999. ArcView GIS, version 3.2. Redlands, California.

Estebanez, B.; Alfayate, C.; Ron, E. 1997. Observations on spore ultrastructure in six species of Grimmia (Bryopsida). Grana 36: 347–357.

Evans A. W. 1939. The classification of the Hepaticae. Bot. Rev. 5: 49–96.

Faria, A. L. A.; Valente, D. V.; Silva, A. L.; Cunha, M. J.; Amorin, E. T.; Peralta, D. F. 2020. Briófitas Do Parque Estadual Do Forno Grande, Espírito Santo - Mata Atlântica, Brasil. PESQUISAS, Botânica, N° 74.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Fernandes R. S; Silva J. A. S; Ottoni F. P; Costa D. P. 2021. Diversity of thalloid liverworts in Brazilian Savanna of Parque Nacional da Chapada das Mesas, Maranhão, Brazil. Check List 17 (1): 45-58. https://doi.org/10.15560.17.1.45.

Fiaschi, P. ; Pirani, J. R. 2009. Review of plant biogeographic studies in Brazil. Journal of Systematics and Evolution 47:477-496.

Forrest L. L.; Christine D. E.; Long D. G.; Crandall-Stotler B. J.; Clark A.; Hollingsworth M. L. 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta): multiple taxa, genomes and analyses. The Bryologist. doi.org/10.1639/0007-2745(2006)109[303:UTEHOT]2.0.CO;2

Frahm, J.P. 2003. Manual of Tropical Bryology. Tropical Bryology 23:1-195.

Frahm, J.P.; Gradstein, S.R. 1991. An altitudinal zonation of tropical rain forests using bryophytes, Journal of Bryology 18: 669-678.

Fudali E. 2001. The ecological structure of the bryoflora of Wroclaw's parks and cemeteries in relation to their localization and origin. Acta Societatis Botanicorum Poloniae 70(3): 229-235.

Fulford, M. 1946. The genus Bazzania in Central and South America. Chronica Botanica Company. Waltham, Mass., U.S.A. pp. 187.

Fulford, M. 1963. Manual of the leafy Hepaticae of Latin America. Part I. Mem. New York Bot. Gard. 11: 1–172.

Fulford, M. 1966. Manual of the leafy Hepaticae of Latin America. Part II. Mem. New York Bot. Gard. 11: 173–276.

Fulford, M. 1968. Manual of the leafy Hepaticae of Latin America. Part III. Mem. New York Bot. Gard. 11: 277–392.

GBIF.2022. //www.gbif.org/species/2280. Acesso em maio de 2022.

Glenny, B. 2008. A New Bazzania species (Lepidoziaceae) from Stockton Plateau, Nelson, South Island, New Zealand. Fieldiana: Botany, N.S., 47: 175-180.

Gradstein, S. R. 2017. *Bazzania* (Marchantiophyta) in South America. DOI: 10.1127/nova_hedwigia/2017/0409

Gradstein, S. R.; Costa D. P. 2003. The Hepaticae and Anthocerotae of Brazil. Memoirs of the New York Botanical Garden 87: 1-318.

Grolle R. 1963. (1964). Uber *Kurzia* v. Martens: Rev. Bryol. Liche´nol. 32 166–180.

Grolle R. 1964 Notulae hepaticologicae XV. Neue Notizen u¨ ber *Kurzia* v. Mart. und Verwandte. J. Jap. Bot. 39: 79–81.

Haeckel, E. 1866. Allgemeine Entwicklungsgeschichte der organismen. Reimer, Berlin.

Hall, T.A. 1999. BioEdit: a user-friendly biological alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.

Hammer, O.; Harper, D.A.T.; Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 9pp.

Harley, M.; Ferguson I. K. 1990. The role of the SEM in pollen morphology and plant systematics. In: Claugher, D. (Ed.) Scanning electron microscopy in taxonomy and functional microscopy. Clarendon Press, Oxford, pp. 45–68.

Harris, B. J.; Harrison, C. J.; Hetherington, A. M.; Williams, T. A. 2020. Phylogenomic evidence for the monophyly of Bryophytes and the Reductive Evolution of Stomata. Current Biology, 23 pp.

Heinrichs, J.; Gradstein, S. R.; Wilson, R.; Schneider, H. 2005. Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene rbcL. Crypt. Bryol. 26: 131– 150.

Heinrichs J.; Dong S.; Schäfer-Verwimp A.; Peralta D. F.; Feldberg K.; Schmidt A.; Schneider H. 2014. Towards a monophyletic classification of Lejeuneaceae II: subtribes Pytnolejeuneinae and Xylolejeuneinae sbtr. nov., transfer of Octolejeunea to 41 Lepidolejeuninae, and generic refinements. Phytotaxa. doi: 10.11646/phytotaxa.163.2.1.

He-Nygren, X.; Piippo, S. 2003. Phylogenetic relationships of the generic complex *Chiloscyphus– Lophocolea–Heteroscyphus* (Geocalycaceae, Hepaticae): insights from three chloroplast genes and morphology. Ann. Bot. Fennici 40: 317–329.

He-Nygre´n, X.; Ahonen, I.; Jusle´n, A.; Glenny, D.; Piippo, S. 2004 Phylogeny of liverworts – beyond a leaf and a thallus. In: Goffinet B., Hollowell V., Magill R. (eds.) Molecular systematics of bryophytes. Missouri Botanical Garden Press, St. Louis, pp. 87–118.

He-Nygre´n, X.; Jusle´n, A.; Ahonen, I.; Glenny, D.; Piippo S. 2006 Illuminating the evolutionary history of liverworts (Marchantiophyta) towards a natural classification. Cladistics 22:1–31.

Heinrichs, J.; Feldberg, K.; Bechteler, J.; Regalado, L.; Renner, M. A. M.; Schäfer-Verwimp, A.; Krings, M. 2018. A Comprehensive Assessment of the Fossil Record of Liverworts in Amber. Transformative Paleobotany, 213–252. doi:10.1016/b978-0-12-813012-4.00012-7

Hentschel, J.; Wilson, R.; Burghardt, M.; Zundorf, H.J.; Schneider, H.; Heinrichs, J. 2006. Reinstatement of Lophocoleaceae (Jungermanniopsida) based on chloroplast gene rbcL data: exploring the importance of female involucres for the systematics of Jungermanniales. Pl. Syst. Evol. 258: 211–226.

Heslewood, M. M.; Brown, E. A. 2007. A molecular phylogeny of the liverwort family Lepidoziaceae Limpr. in Australasia. Pl. Syst. Evol. 265: 193–219.

Hillis, D.M.; Bull, J.J. 1993. An empirical test of bootstrapping as a method for assessing the confidence in phylogenetic analysis. Systematic Biology 42:182–192.

Hirohama, T. 1975. Spore morphology of bryophytes observed by scanning electron microscopy, I Dicranaceae. Bulletin of National Science Museum. Tokyo 2(B): 61–72.

Hirohama, T. 1977. Spore morphology of bryophytes observed by SEM, II Bartramiaceae. Bulletin of National Science Museum. Tokyo 3(B): 37–44.

IBGE 2012. Manual Técnico da Vegetação Brasileira, ed 2. Rio de Janeiro, Fundação Instituto Brasileiro de Geografia e Estatística, Departamento de Recursos Naturais e Estudos Ambientais.

Ilkiu-Borges, A.L.; Oliveira-da-Silva, F. R. 2016. Flora das cangas da Serra dos Carajás, Pará, Brasil: Lepidoziaceae. Rodriguésia: 67.

Jing, Y.; Tong, C; Xi, W.Q. 2007. Study of spore types of Chinese mosses. In: Nath, V. & Asthana, A.K. (Eds.), Current trends in Bryology. Bishen Singh Mahendra Pal Singh, Dehra Dun., pp. 1–15.

Judd W.; Singer R.; Singer R. 2009. Sistemática vegetal: um enfoque filogenético. 3ed. Artmed.

Kass, R. E., Raftery, A. E. 1995. Bayes Factors. Journal of the American Statistical Association 90: 773-795.

Kumar, S.; Stecher, G.; Tamura, K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. Mol. Biol. Evol. 33(7):1870–1874

Koga, M. L.; Peralta, D. F. 2021. Bryophytes of Rio Turvo State Park (SP), Brazil: integrating floristics, geographical distribution, reproduction and ecological traits to support the conservation of an Atlantic Forest fragmente. Acta Botânica Brasilica. 35 (3): 389-417.

Lepidoziaceae in Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro.Disponível em: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB97679>. Acesso em: 08 Mar. 2018

Limpricht, K. G. 1877. Lebermoose. In: Cohn F. (1876–1877) Kryptogamen-Flora von Schlesien. Vol. 1. Breslau, pp. 225–352.

Lima, J. S.; Peralta, D. F. 2021. Brioflora do Parque Nacional da Serra da Bocaina, de São Paulo, Brasil. Hoehnea. vol.48.

Lindenberg, J. B. W. 1846. Species Hepaticarum. Bonnae. Phyt. 197.

Linnaeus, C. 1753. Species Plantarum 1. Laurentius Salvius, Stockholm, pp 28

Luizi-Ponzo, A.P.; Bastos, C.J.P., Costa. D.P.; Pôrto, K.C.; Câmara, P.E.A.S., Lisboa, R.C.L.; Bôas-Bastos, S.V. 2006. Glossarium Polyglottum Bryologiae. Editora UFJF. Juiz de Fora.

Liu, Y.; Yan, Hai-Fei.; Tong C.A.O.; Xue-Jun G.E. 2010. Evaluation of 10 plant barcodes in Bryophyta (Mosses). Journal of Systematics and Evolution 48 (1): 36–46.

Luizi-Ponzo, A. P.; Barth, O. M. 1998. Spore morphology of some Bruchiaceae species (Bryophyta) from Brazil. Grana 37: 222–227.

Luizi-Ponzo, A. P.; Barth, O. M. 1999. Spore morphology of some Dicranaceae species (Bryophyta) from Brazil. Grana 38: 42–49.

Luizi-Ponzo, A. P.; Melhem, T. S. 2006. Spore morphology and ultrastructure of the tropical moss *Helicophyllum torquatum* (Hook.) Brid. (Helicophyllaceae) in relation to systematics and evolution. Cryptogamie, Bryologie 27: 413-420.

Luizi-Ponzo, A.P.; Bastos, C.J.P.; Costa. D.P.; Pôrto, K.C.; Câmara, P.E.A.S.; Lisboa, R.C.L.; Bôas-Bastos, S.V. 2006. Glossarium Polyglottum Bryologiae. Editora UFJF. Juiz de Fora.

McClymont, J. W. 1955. Spore studies in the Musci with special reference to the genus Bruchia. Bryol. 58: 28-306.

Meagher, D. 2011a. Studies on *Bazzania* 4. *Bazzania mittenii* (Steph.) Steph. (Lepidoziaceae, Marchantiophyta), a re-instated Australasian liverwort and its synonyms. Nova Hedwigia Vol. 93 issue 1–2, 183–190.

Meagher, D. 2011b. Studies on *Bazzania* (Lepidoziaceae, Marchantiophyta) 3. Four new species from Australia. Nova Hedwigia Vol. 92 issue 3–4, 487–495.

Meagher, D. 2015. Studies on *Bazzania* (Marchantiophyta: Lepidoziaceae) 8. *Bazzania wooroonooran* sp. nov. and seven other rare species from tropical Australia. Nova Hedwigia. DOI: 10.1127/nova_hedwigia/2015/0247.

Miller, M. A., Holder, M. T., Vos, R., Midford, P. E., Liebowitz, T., Chan, L., Hoover, P., Warnow, T. 2010. The CIPRES Portals. www.phylo.org.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A., Lanfear, R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37: 1530-1534.

Mogensen, G. S. 1981. The biological significance of morphological characters in Bryophytes: The Spore. Bryologist 84(2): 187–207.

Miyoshi, N. 1973. Scanning electron microscopic observation of spores in Musci. Japanese Journal of Palynology 12: 13–18.

Myers, N.; Mittermeier, R. A.; Mittermeier, C. G.; da Fonseca, G. A. B.; Kent, J. 2000. Biodiversity hotspots for conservation priorities. NATURE, vol. 403.

Neumann, A. J.; Rushing, A. E.; Mueller, D. M. J. 1982. A Modified, Short Protocol for Preparation of Bryophytes for Scanning Electron Microscopy. The Bryologist 85(1): 74-78.

Olesen, P.; Mogensen, G. S. 1978. Ultrastructure, histochemistry and notes on germination stages of spores in selected mosses. Bryologist 81(4): 493–516.

Oliveira-Filho, A. T. 2009. Classificação das fitofisionomias da América do Sul cisandina tropical e subtropical: proposta de um novo sistema – prático e flexível – ou uma injeção a mais de caos? Rodriguésia 60: 237-258.

Oliveira-Filho, A. T. 2015. Um Sistema de classificação fisionômico-ecológica da vegetação Neotropical. In: Eisenlohr P.V, Felfili J.M, Melo M.M.R.F, Andrade L.A, Neto J.A.A.M. (eds.) Fitossociologia no Brasil: métodos e estudos de casos. Vol. 2. Belo Horizonte, Editora UFV. p. 452-473.

Passarella, M.A.; Luizi-Ponzo, A.P. 2022. Oncophoraceae (Bryophyta): a palynological treatment of species occurring in the Americas. Anais da Academia Brasileira de Ciências 94(1).

Peralta, D.F.; Amelio, L.A.; Souza, A.M.; Carmo, D.M.; Santos, E.L.; Valente, E.B.; Oliveira, H.C.; Lima, J.S.; Prochazka, L.S. 2020. Lepidoziaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available at: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB97671>. Accessed on: 03 fev. 2022

Proskauer, J. 1964. *Riccia tuberose* Taylor = *Anogramma leptophylla* (L.) Link, oro n the importance of being bryophytic. Journal of Indian BOtanical SOciety 42ª: 185-188.

Reimers, Von H. 1933. Revision der Lebermoos gattung *Micropterygium*. Hedwigia 76: 165–168.

Richards, P.W. 1984. The ecology of tropical Forest bryophytes. In: R.M. Schuster (ed.). New Manual Bryology, v.2. Nichinan, The Hattori Botanical Laboratory. pp.1233-1970.

Rocha, L.M.; Gonçalves-Esteves, V.; Luizi-Ponzo, A.P. 2008. Morfologia de esporos de espécies de Polytrichaceae Schwägr. (Bryophyta) do Brasil. Revista Brasileira de Botânica 31: 537-548.

Rodrigues, R.S.; Luizi-Ponzo, A.P. 2015. Palinologia de espécies selecionadas da família Pottiaceae (Bryophyta). Pesquisas, Botânica 67: 303-317.

Ronquist, F.; Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572-1574

Rouhan G; Gaudeul M. 2014. Plant taxonomy: A historical perspective, current challenges, and perspectives. In Pascale Besse (ed.), Molecular Plant Taxonomy: Methods and Protocols, Methods in Molecular Biology 1115: 1-37.

Roth, G. 1905. Die Europäischen Laubmoose beschrieben und gezeichnet von. Vol II, Leipzig Verlag von Wilhelm Engelmann, pp. 38–175.

Rushing, A. E. 1985. Spore morphology in the genus Bruchia Schwaegr. (Musci). Am. J. Bot. 72 (1): 75-85.

Santos N.D.; Costa D.P. 2010. Altitudinal zonation of liverworts in the Atlantic Forest, Southeastern Brazil. The Bryologist 113: 631-645.

Savaroğlu, F. 2015 Spore morphology of some Orthotrichaceae Arn. Species (Bryophyta) from Turkey. Bangladesh Journal of Botany 44: 499-506.

Savaroğlu, F.; Erkara, I. P.; Koyuncu, O. 2017. Observations of spore morphology of some species of Hypnaceae Schimp. (Bryophyta) in Turkey. Bangladesh Journal of Botany 46: 9-17.

Schäfer-Verwimp, A.; Feldberg, K.; Dong, S.; van Melick, H.; Peralta, D. F.; Schmidt, A.; Schneider, H.; Heinrichs, J. 2014. Towards a monophyletic classification of Lejeuneaceae III: the systematic position of Leiolejeunea. Phytotaxa. doi: 10.11646/phytotaxa.170.3.4.

Schuster, R. M. 1966. The Hepaticae and Anthocerotae of North America. Vol. 1. Columbia University Press, New York, pp. 1–801.

Schuster, R. M. 1969. The Hepaticae and Anthocerotae of North America. Vol. 2. Columbia University Press, New York, pp. 1–1062.

Schuster, R. M. 1972 (1973). Phylogenetic and taxonomic studies on Jungermanniidae. J. Hattori Bot. Lab. 36: 321–405.

Schuster, R. M. 1979. The phylogeny of the Hepaticae. In: Clarke G. C., Duckett J. G. (eds.) Bryophyte systematics, Systematics Association 14. Academic Press, London and New York, pp. 41–82.

Schuster, R. M. 1980. Studies on Hepaticae, LIVLVIII. Kurzia v. Mart. [*Microlepidozia* (Spr.) Joerg.], *Megalembidium* Schust., *Psiloclada* Mitt., Drucella Hodgs., and *Isolembidium* Schust. J. Hattori Bot. Lab. 48: 337–421.

Schuster, R. M. 1984. Evolution, phylogeny and classification of the Hepaticae. In: Schuster R. M. (ed.) New manual of bryology Vol. 2. Hattori Botanical Laboratory, Nichinan, pp. 892–1070.

Schuster, R. M. 1993. Studies on Hepaticae, LXIILXIV. Lepidoziaceae subf. Zoopsidoideae (1). Nova Hedwigia 56: 35–59.

Schuster, R. M. 1999a. Studies on Hepaticae, LXV Lepidoziaceae subf. Zoopsidoideae (2): *Zoopsis*. Nova Hedwigia 68: 1–63.

Schuster, R. M. 1999b Studies on Hepaticae, LXVI Lepidoziaceae subf. Zoopsidoideae (3): *Zoopsidella*. Nova Hedwigia 69: 101–149.

Schuster, R. M. 1999c. Studies on Hepaticae, LXVII-LXVIII Lepidoziaceae subf. Zoopsidoideae (4): *Monodactylopsis* and *Pteropsiella*. Nova Hedwigia 69: 517–540.

Schuster, R. M. 2000. Austral Hepaticae Part I. Nova Hedwigia 118: 1–524.

Schuster, R. M.; Engel, J. J. 1974. A monograph of the genus *Pseudocephalozia* (Hepaticae). J. Hattori Bot. Lab. 38: 665–701.

Silva, A. S. M.; Simabukuro, E. A. 2007. Ecofisiologia de briófitas de floresta atlântica nordestina. 2007. Dissertação (Mestrado). Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife

Silva-E-Costa, J.C.; Luizi-Ponzo, A.P.; Resende, C.F.; Peixoto, P.H.P. 2017. Spore germination, early development and some notes on the effects of in vitro culture medium on *Frullania ericoides* (Nees) Mont. (Frullaniaceae, Marchantiophyta). Acta Botanica Brasilica 31: 19-28

Silva-E-Costa, J.C.; Luizi-Ponzo, A.P. 2019. Spores of *Plagiochila* (Dumort.) Dumort.: the taxonomic relevance of morphology and ultrastructure. Acta Botanica Brasilica - 33(3): 391-404.

Skvarla, J. J.; Rowley, J. R.; Chissoe, W. F. 1988. Adaptability of scanning electron microscopy to studies of pollen morphology. Aliso 12: 119–175.

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.; Xiaolan He; Heinrichs, 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.; Tiers, B.M.; Uribe, J.;

Váňa, J.; Villarreal, J.C.; Wigginton, M.; Zhang, L.; Rui-Liang, Z. 2016. World checklist of hornworts and liverworts. PhytoKeys 59: 1-828.

Schiffner, V. 1893. Lebermoose. In: Engler & Prantl., Die Natürlichen Pflanzenfamilien 1': 3-141. fig. 1-73. Leipzig.

Spruce, R. 1885. Hepaticae of the Amazon and the Andes of Peru and Ecuador. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 1-589.

Stamatakis, A. (2014) RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.Stephani, F. 1901. Species Hepaticarum, Vol. II. Acrogynae. Geneva: George & C.

Stuessy, T. F. 2004. A transitional-combinational theory for the origin of angiosperm. Taxon 53 (1), 3-16.

Stuessy, T. F. 2010. Paraphyly and the origin and classification of angiosperms. Taxon 59 (3), 689-693.

Sukkharak P; Gradstein S.R; Stech M. 2011. Phylogeny, taxon circumscriptions, and character evolution in the core Ptychanthoideae (Lejeuneaceae, Marchantiophyta). Taxon 60:1607–1622

SYSTEMATICS ASSOCIATION COMMITTEE FOR DESCRIPTIVE BIOLOGICAL TERMINOLOGY, IIa. 1962. Terminology of Simple Symmetrical Plane Shapes (Chart 1a), Addendum. Taxon 11: 245-247.

Taberlet, P.; Gielly, L.; Pautou, G.; Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17: 1105-1109.

Terasmae, J. 1955. On the spore morphology of some Sphagnum species. Bryol. 58: 306-311.

Thiers, B. 2009. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. http://sweetgum.nybg.org/ih/

TROPICOS. 2018. http://www.tropicos.org/ 8 de março 2018.

Udar, R.; Srivastava, S.C. 1984. Scanning electron microscopy of spores of Indian liverworts. Journal of Hattori Botanical Laboratory 56: 97–103.

Udar, R.; Agarwal, A. 1985. The genus Riccia in Pachmarhi with SEM details of spores of two species. Journal of Indian Botanical Society 64: 246–250.

Valente, E.B.; Pôrto, K.C. 2006. Hepáticas (Marchantiophyta) de um fragmento de Mata Atlântica na Serra da Jibóia, Município de Santa Teresinha, BA, Brasil. Acta Botanica Brasilica 20: 433-441.

Valente, E. B.; Pôrto, K.C.; Bastos, C. J. P. 2011. Checklist de briófitas da Chapada Diamantina, Bahia, Brasil. Boletim do Instituto de Botânica 21: 111-124.

Verdoon, F. 1932. Classification of hepatics. pp. 413 432. In.: Verdoorn, F. (ed.). Manual of Bryology. The Hague.

Villareal, J. C.; Crandall-Stotler, B. J.; Hart, M. L.; Long, D. G.; Forrest, L. L. 2016. Divergence times and the evolution of morphological complexity in an early land plant lineage (Marchantiopsida) with a slow molecular rate. New Phytologist. doi: 10.1111/nph.13716

Wettstein, R. 1903-1908. Handbuch der systematischen botanik. II. Band. 1.

Wiley, E. O.; Libermann, B. 2011. Phylogenetics: Theory and Practice of Phylogenetic Systematics. New Jersey: Wiley-Blackwell.

Yano, O.; Luizi-Ponzo, A.P. 2006. *Chonecolea doellingeri* (Chonecoleaceae, Hepaticae), taxonomia e distribuição geográfica no Brasil. Acta Botanica Brasilica 20: 783-788.

Yano, O.; Luizi-Ponzo, A.P. 2011. *Dumortiera hirsuta* (Dumortieraceae, Marchantiophyta), taxonomy, palynology and geographic distribution. Boletim do Instituto de Botânica 21: 9-18.

Yano, O.; Peralta, D.F.; Bordin, J. 2019. Brioflora da Ilha do Cardoso. São Paulo, RiMa Editora.

Zhou, Lan-Ping; Zhang, L.; Xing, Fu-Wu, 2012. The genus *Bazzania* in China and adjacent regions. 1. *Bazzania dulongensis* L.-P.Zhou & L.Zhang sp. nov. and *Bazzania hainanensis* L.-P.Zhou & L.Zhang sp. nov. Journal of Bryology. 34(1): 1-10.

CAPÍTULO 1

THE BRAZILIAN REVIEW OF *LEPIDOZIA* (DUMORT.) DUMORT. (LEPIDOZIACEAE)

Rodriguesia

CAPÍTULO 1

The Brazilian review of *Lepidozia* (Dumort.) Dumort. (Lepidoziaceae)

Leandro de A. Amélio[1*], Emilia de B. Valente[1], Denilson F. Peralta[2]

[1] Departamento de Biologia, Universidade Estadual de Feira de Santana, Feira de Santana, BA, Brazil

[2] Instituto de Pesquisas Ambientais, Av. Miguel Stéfano, 3687 - CEP 04301902 - São Paulo, SP, Brazil

[*] Corresponding author's email: ednlora@gmail.com

Short title: *Lepidozia* in Brazil

Abstract: The genus *Lepidozia* (Dumort.) Dumort. is reviewed for Brazil based on type material, herbarium specimens and recent collections. Eight species are recognized to the genus, plus one variety. *Lepidozia pseudocupressina* is synonymized with *L. cupressina*, just as *L. densa* was synonymized to *L. brasiliensi*s. Two species are new occurrence to the country (*L. alstonii* and *L. patens*) and *L. aequiloba* is reinstated to the Brazilian flora. A diagnostic key, descriptions, illustrations and taxonomic comments are provided.

Key words: Biodiversity, Cryptogam taxonomy, Leafy liverworts, Neotropics, New occurrence.

Introduction

The leafy liverworts are a large and complex group widespread in the world, with numerous life-forms and large morphological variation (e.g., Schuster, 1984; Gradstein, 2013). *Lepidozia* (Dumort.) Dumort., with approximately 30 accepted species in Neotropical region, is a large genus of liverworts (Marchantiophyta) and the most diverse morphologically in the Lepidoziaceae, together with *Bazzania* Gray, *Kurzia* G. Martens and *Telaranea* Spruce ex Schiffn. (Söderström, et al. 2016; Schuster, 2000; Fulford, 1966). The genus is readily recognized by the pinnately branched stems, from creeping to loosely attached to the substratum, or somewhat ascending; the leafy shoots are mostly loosely attached to substrate, yellowish or whitish to olive-green, rarely brownish in life, usually relatively opaque and greenish. The plants are small to medium-sized, usually 0.5–2.5(–4) mm wide. Branching is regular to irregularly *Frullania* type, and copiously 1-3 pinnate.

The genus *Lepidozia* was proposed by Dumortier in 1835, based on the *Pleuroschisma* sect. *Lepidozia* (Dumortier, 1831). The family (Lepidoziaceae) contains genera with a wide distribution, is nearly cosmopolitan and expresses a large array of morphological characters and an equally large ecological amplitude. Reproductive organs and spores are rare in *Lepidozia* species as well as asexual reproduction in the genus. The plants are mostly dioicous and the capsule and seta tiny, and susceptible to damage; many species are only known from gametophytic material (Fulford 1966, Engel & Schuster 2001).

The present classification of the family is largely based on the studies of Rudolph M. Schuster, who used morphological intuitive phylogenetic relationships to propose classifications (Schuster 1984). The systematics and taxonomy of liverworts has been considerably revised in recent decades based on molecular data (e.g., Crandall-Stotler *et al*. 2008, 2009), and the delimitation of the Lepidoziaceae has been refined (Cooper 2011, 2012a). However, the current classification does not accommodate all morphological variations within the genera (Cooper *et al*. 2013a).

A brief taxonomic treatment of the genus *Lepidozia* in Brazil with a key to four species was presented by Gradstein & Costa (2003). In this paper, new herbarium material from Brazil has been revised and our knowledge of the geographic distribution and diagnostic characters has been improved and updated, since a considerable number of species have proven to be synonyms (Söderström *et al*., 2016) or were transferred to other genera.

Till now, the same four species were recognized in Brazil (Costa & Peralta, 2015), most of them occurring in the Atlantic rainforest (Fulford 1966; Gradstein & Costa 2003; Valente *et al.* 2011, 2013; Santos & Costa 2010; Yano 2019; Carmo 2016a, 2016b, 2018; Amélio 2019).

While analyzing herbarium specimens of *Lepidozia* we found that the number of species in Brazil is larger than hitherto accepted. In this study, we present a treatment to *Lepidozia* and comment on the Brazilian ranges of the species, providing data that will hopefully be useful in the identification of collections, and in indicating how rich is the Brazilian liverwort flora.

Materials and methods

We examined types and samples from the following herbaria G, HUCS, HUEFS, ICN, INPA, JE, NY, RB, SJRP, SP, and UB. The total of 500 samples were analyzed in this study. The terminology used in the morphological descriptions, habitat, geographic distribution and ecological comments follow Fulford (1966), Engel & Schuster (2001), Gradstein & Costa (2003) and Cooper (2013b).

Gametophytes were examined under simple optical and stereo microscopes for all samples listed in specimens examined. We observed and measured gametophyte size, number of leaf lobes, cells of the leaf, both those of the margin and midleaf, the length of the leaf, underleaf, and stem. Taxonomic and ecological notes, a key to species, diagnostic descriptions and illustrations are provided for each species, following Gradstein (2017). All structures were measured with a micrometer eyepiece using an optical microscope. The geographic distribution follows the Brazilian geopolitical states (IBGE 2012).

Results

We recognize eight species of *Lepidozia* in Brazil, and a variety of the *L. coilophylla*, and we propose the synonymization of *L. pseudocupressina* (Schiffn. 1919) under *L. cupressina*.

The Brazilian *Lepidozia* species are found often on bark, but may be found on soil and rocks, ranging from 100 to 1500 m above sea level. The genus is widely distributed in biomes of Amazon, Atlantic rainforest and Savannas and has scattered occurrences in the Caatinga.

This is an important study in the Brazilian flora of the liverworts, extending the *Lepidozia* distribution to five new states: *L. aequiloba*, which was found in Minas Gerais. The species *Lepidozia coilophylla* has new records in Bahia, Espírito Santo, Paraná and Pernambuco. *L. cupressina* was identified in Amazonas, Distrito Federal, Paraná; and *L. inaequalis* in Amazonas, Pará, Rio Grande do Sul and Roraima. *Lepidozia alstonii* and *L. patens* are new records to the country, and the species *L. brasiliensis* has been appointed as *L. cupressina* synonyms which return to Brazilian flora. This represents how the liverwort flora may be underestimated.

Taxonomic treatment

Lepidozia (Dumort.) Dumort.

Plants are green to brownish, in mats or tufts, pendulous or among other bryophytes; medium to large-sized, 0.6-2 mm wide, procumbent to slightly erect. Branches 1-3 pinnate, usually with alternate leaves. Vegetative leaf branches as Frullania type, branches in many taxa tending to become attenuate and microphyllous. Rhizoids are colorless and rarely branched from the bases of underleaves. Leaves are incubous, the margins of the lamina are entire or toothed, incised or ciliate, usually quadrifid (or trifid and in some species with five or more lobes), the lobes triangular. Underleaves transverse,

nearly as large as the leaves to much smaller, the lobes triangular, the margins entire, incised, toothed or ciliate. Plants dioicous, gametangia on abbreviated ventral intercalary branches. Androecia spicate. Gynoecial branches lacking normal leaves, isomorphic bracts and bracteoles, typically the innermost ones are larger than normal leaves and sheathing the perianth, usually elongated and ovate to oblong-ovate, apical lobing like the leaves, the lobes toothlike, sometimes vestigial. Perianth to 6 mm, cylindrical to fusiform, the mouth contracted, crenulated to long ciliate. Sporophyte stalk, seta 0.5-1.5 cm long, capsule spherical. the innermost layer with brown bands. Spores small, brown; elaters long, slender, bispiral. Asexual reproduction none or rare, via caducous leaf lobe apices.
Type: *Lepidozia reptans* (L.) Dumort.

Identification key

1. Plants slender; leaves scale-like, narrower than stem width, usually concave-incurved 2

1. Plants thick; leaves not scale-like, broader than stem width, almost plane (only concave when dry) 4

 2. Long plants, usually bronwish green, leaves scale-like 3

 2. Short plants, usually yellowish green, concave leaves .... *L. densa*

3. Plants usually green to yellowish; leaves strongly concave and the leaf lobes incurved, touching the stem; stem pinnately branched, branches usually short and not branched .... *L. incurvata*

3. Plants red, brownish to pale green; leaves with leaf lobes not strongly concave, not touching the stem; stems irregularly branched, branches longer and usually dichotomously branched .... *L. patens*

 4. Lobes with quadrate, thin-walled cells at the margin; leaves and underleaves with entire margins; lobes slightly divergent 5

 4. Lobes with rectangular, thick-walled cells at margin; leaves and underleaves with crenate margins; lobes not divergent .... *L. alstonii*

5. Leaves shallowly quadrifid; leaves with a sub-longitudinal insertion line 6

5. Leaves deeply quadrifid; leaves with an oblique to sub-transverse insertion line …... 7

 6. Leaves margins without teeth …………………………….....… *L. coilophylla*

 6. Leaves margins with 1–2-celled teeth ……..…. *L. coilophylla* var. *apiculiloba*

7. Leaves lobes ending in a long row of more than five cells long, cells distinctly longer than wide (3:1) ……………………………………..….…..……………... *L. inaequalis*

7. Leaves lobes ending in a short row of 1 (–2) cells, cells isodiametric to slightly elongate (1-2:1) 8

8. Leaf lobes truncate, ending with 1–2 cells; the leaf lobes short; underleaves narrower than stem .... *L. cupressina*

8. Leaf lobes ending with 1(–3) rows of 1–2 cells; the leaf lobes long; underleaves usually wider than stem ……………... 9

9. Underleaves lobes are usually narrower and long, forming a triangular, 3/5 longer than wide, 2–4-celled at the base ……………... *L. brasiliensis*

9. Underleaves narrower than the stem, lobes half of the underleaf length; the cells quadrate .... *L. aequiloba*

Lepidozia aequiloba Steph., Spec. Hepat.6: 319. 1922. Original Material: Brazil: Minas Gerais, Caraça. *E. A. Wainio (s.n.)* (barcode.G00069656 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069656)).
Fig. 1. A–D, Additional illustration and description in Fulford (1966).

Plants small, green or pale green, in mats or among others bryophytes, creeping, 2–4 cm long, pinnately branched, but the branches short and rarely flagelliform. Leaf insertion oblique. Stem leaves imbricate, longer than wide, 0.4–0.8 mm broad at the base, quadrifid; lobe length equal, short, divergent, the bases 4–5 cells broad, the apices acute, the sinus broad; lamina long, the margins entire with the dorsal base curved; leaf cells quadrate to rectangular, the walls thickened, the lumina round, the cuticle smooth. Underleaves narrower than the stem, cuneate, quadrifid to one half their length, the lobes widely divergent, narrowly triangular with uniseriate tips. Gametoecia and sporophyte not seen.

This species is recognized by the divergent lobes on the leaves and underleaves, with no more than four short cells. Gradstein & Costa (2003) suggested that it might be a synonym of *L. coilophylla* but they are distinct by the sub-longitudinal insertion of the leaf. *Lepidozia aequiloba* is often found on tree trunks, in the deep shaded forests. *L. aequiloba* was described by Stephani with the type collected in Brazil, but it was almost 100 years before it was collected in the country again. The type specimen is very delicate and without sporophytes. The species is known from Peru (Schultze-Motel & Menzel 1987), Venezuela (Fulford 1966) and Brazil. We increased its distribution within Brazil to Pernambuco, Rio de Janeiro, and São Paulo, in addition to the type locality in Minas Gerais.

Selected material: MINAS GERAIS: Caldas, 15.IV.2017, *O. Yano 34204* (SP). Catas Altas Reserva Particular do Patrimônio Natural, Parque Natural do Caraça, 20°5'56"S, 43°29'17"W, 30.V.2008, *D.F. Peralta 6402* (RB). PERNAMBUCO: Jaqueira. Serra do Quengo, 8°42'50"S, 35°50'"W, 2.IV.2002, *M.R. Pietrobom-Silva 5466* (SP). RIO DE JANEIRO: Itatiaia, Parque Nacional do Itatiaia, 22°25'25"S, 49°36'24"W 6.V.2016, *D.F. Peralta 18411* (SP). [Rio de Janeiro] Morro Queimado, 22º16'55"S, 42º31'52"W 12.X.1996, *D. Sucre 1099* (RB). [Rio de Janeiro] Parque Nacional da Tijuca, 22°55’S, 43°11’W 10.IX.1983, *D.P. Costa 29* (RB). SÃO PAULO: Mogi das Cruzes. Distrito de Taiaçupeba, Reserva Particular do Patrimônio Natural "Parque das Neblinas", 23°45'16"S, 46°09'39"W 1.XI.2008, *D.F. Peralta 7198* (SP).

Lepidozia alstonii Fulford, Mem. New York Bot. Gard. 11: 211. 1966. Original Material: Colombia: los Gagues, 10,700 ft., *Alston 7493* (Holotype BM); Ecuador: Pichincha, 15,000 ft., *Bell 408 p.p.* (Isotype CINC-B-0047125 - https://bryophyteportal.org/imglib/bryophytes/CINC/CINC-B-0047/CINC-B-0047125_lg.jpg).

Fig. 1. E–H, Additional illustration and description in Fulford (1966).

Plants are large, yellow to brown, in tufts or among other bryophytes, creeping, stems up to 5 cm or longer (but not longer than 8 cm), with leaves 0.8–1.2 mm broad, ascendant, pinnate, the lateral branches numerous, tending to become flagelliform at the tips, the ventral branches leafy or sexual. Line of leaf insertion sub transverse. Stem leaves imbricate, concave, 0.8–1.3 mm long, quadrate, quadrifid to one half or more; long lobes lanceolate, the margins irregular, undulate; dorsal margin of the lamina convex, with one or two conspicuous teeth, the ventral margin straight, with one or two teeth; leaf cells at the ventral margin straight, with one or two conspicuous teeth, the ventral margin straight, with one or two teeth. Plants dioicous. Perianth not seen.

The species is distinct and readily recognized because of the large size, brown pigmentation, the very deeply quadrifid leaves, the long, irregularly undulate lobes of the leaves and underleaves, the occurrence of teeth or spines on the margins of the lamina of both leaves and underleaves, and the uniformly thickened cell walls. *Lepidozia alstonii* grows on trees, and in crevices of rocks, at high altitudes in the northern Andes and was only known from Colombia and Ecuador (Bernal et al. 2016). Here we report the species new to Brazil, where it apparently is very rare and has been found only in São Paulo.

Selected material: RIO DE JANEIRO: Teresópolis, Parque Nacional da Serra dos Órgãos, 22°27'30"S, 43°01'32"W, 19.I.2022, *D.F. Peralta 27539* (SP). SÃO PAULO: Campos do Jordão. Parque Estadual de Campos do Jordão, 22°41'15"S, 45°27'58"W, 9.X.2009, *D.F. Peralta 9828* (SP). São Luiz do Paraitinga. Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 23°20'45"S, 45°7'47"W, 17.IV.2013, *D.F. Peralta 13893* (SP).

Lepidozia brasiliensis Steph., Spec. Hep. 3: 571. 1909. Original Material: Brazil: Minas Gerais. *P. K. H. Dusén [s.n]* (barcode G00069599 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069599)).

= *Lepidozia moritziana* Steph., Sv. Vet.-Akad. Handl. II. 23: 24. 1897. Original Material: Venezuela: *J.W.K. Moritz [s.n.]* (barcode G00280927 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g000280927), syn. fide Fulford (1966).

= Lepidozia fulva Steph., Spec. Hep. 3: 569. 1909; Original Material: Brazil. *E.H.G. Ule 231* (barcode G00069636 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069636), syn. fide Fulford (1966).

=Lepidozia densa Herzog, Repertoium Speciorum Novarum Regni Vegetabiilis. 20(3): 22-33. 1925. Original Material: Brasil, Serra dos Orgãos, Morro Assú: *Herzog 6381* (barcode JE04002088 - http://131.130.131.10/herbaria/jacq-viewer/viewer.html?rft_id=je_04002088&identifiers=je_04002088), *syn. nov.*

Fig. 2. A–D, Additional illustration and description in Fulford (1966).

Plants are small to medium-sized, yellow to green, in tufts or scattered among other bryophytes; creeping, sometimes long pendent, stems up to 2–5 cm, with leaves to 0.6 mm wide, pinnate. Lateral branches become flagelliform, the ventral branches usually long. Leaf insertion curved around the stem, slightly oblique. Stem leaves imbricate, squarrose, concave to incurved. Dorsal margin convex, quadrifid to 1/3 of the length;

lobes as a triangular form from 3–5-celled base, with an acute apex, 1–2-celled tip. Dioicous plants. Female bracts and bracteoles in three series, light green, the inner series orbicular, divided into 3–5 short and irregular lobes. Perianth 6 mm long, cylindrical, the mouth lobate, sometimes with some cilia.

After Gradstein & Costa (2003) suggested that *Lepidozia brasiliensis* was a synonym of *L. cupressina.* But this species differs from *L. cupressina* by its smaller size, the the underleaf lobes of *L. brasiliensis* are usually narrower and form a longer part of the underleaf, than those of *L. cupressina*, usually ending in 3-4 double cell row and 2-3 uniseriate row. Söderström et al. (2016) in the world wide checklist, accepted as a species, but with doubts about the morphological similarity with other species.

Additionally, we recognized *Lepidozia densa* Herzog, as a new synonym to *L. brasiliensis*. This species is known just by the original material, and after analyses we considered as a synonym.

Lepidozia. brasiliensis is often found on trunks, trees and decaying logs in moist forests. This species has a wide distribution in tropical America. Within Brazil the species is reported in Amazonas, Espírito Santo (Schäfer-Verwimp 1991), Distrito Federal, Goiás, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Roraima, Santa Catarina and São Paulo.

Selected material: AMAZONAS: São Gabriel da Cachoeira, Serra do Curicuriari, 0,2ºS, 66,5ºW. *W.R. Buck 2437* (INPA) DISTRITO FEDERAL: Brasília, Fazenda Água Limpa, 15°46'47''S, 47°55'47''W, 7.XI.1985, *D.M. Vital 13275, 13277* (SP). GOIÁS: Alto Paraíso de Goiás, Chapada dos Veadeiros, 19.III.1971, *H.S. Irwin 33205* (NY, SP). Pirenópolis, Parque Estadual dos Pireneus, base do Morro Cabeluda, 18.III.2006, *O. Yano 28690* (SP). MINAS GERAIS: Alto Caparaó, Parque Nacional de Caparaó, Vale Verde, 20°25'27''S, 41°50'20''W, 23.IV.2016 *D.F. Peralta 18215, 18382* (SP). Caeté, Serra da Piedade, 19°52'48''S, 43°40'11''W, 17.XI.1986, *O. Yano 10505* (SP). Catas Altas, Reserva Particular do Patrimônio Natural, 20°5'56''S, 43°29'17''W, 27.VII.2010, *D.F. Peralta 11611* (SP). Itamonte, 22°17'2''S, 44°52'12''W, 20.V.1988. *D.M. Vital 15868, 15893* (SP). Lima Duarte, Parque Estadual do Ibitipoca, 21°50'33''S, 43°47'35''W, 09.VIII.1993, *O. Yano 20298, 20324* (SP). Monte Verde, 22°30'54''S, 46°1'14''W, 14.I.2006. *D.F. Peralta 3463* (SP). [Conceição do Ibitipoca] Parque Estadual do Ibitipoca, 29.III.2013. *O. Yano 33383* (SP). Tiradentes, Serra de São José, 21°6'37''S, 44°10'41''W, 3.XII.1993. *O. Yano 21781, 21859* (SP). PARANÁ: Curitiba. 28.I.1987, *Schäfer-Verwimp 8264* (JE, SP). Foz do Iguaçu, 25°32'52''S, 54°35'17''W, 7.X.1979. *O. Yano 2188* (SP). Piraquara, Parque Estadual Pico do Marumbi, 25°30'55"S, 48°58'58"W, 18.VI.2015, *D.F. Peralta 17843* (SP). São Mateus do Sul, 25°52'27"S, 50°22'58"W, 20.IV.1983. *O. Yano 6442* (SP). RIO DE JANEIRO: Angra dos Reis, Ilha Grande, 23°0'24"S, 44°19'5"W, 21.III.1995. *O. Yano 23698* (SP). Resende, Parque Nacional do Itatiaia, 22°16'51"S, 44°15'53"W, 20.VI.1983, *O. Yano 7517* (SP). Teresópolis, Parque Nacional da Serra dos Órgãos, 22°24'44"S, 42°57'56"W, 21.X.1989. *O. Yano 13584* (SP). [Itatiaia] Parque Nacional do Itatiaia, 21.VI.1983, 22°16'51"S, 44°15'53"W. *O. Yano 7572* (SP). RIO GRANDE DO SUL: Bom Jesus, São José dos Ausentes, 19.V.1981, *R. Bueno 939* (ICN, SP). Serra da Rocinha, *14.I.1942, A. Sehnem 1003,* 29.X.1983, *R. Bueno 3539* (ICN, SP). Cambará do Sul, Fortaleza dos Aparados, 9.IV.1982. *R. Bueno 1324* (ICN, SP). São Francisco de Paula, Serra do Faxinal, 29°26'49"S, 50°34'45"W, 18.XII.1950. *A. Sehnem 5326* (RB). RORAIMA: Pacaraima, Monte Roraima. *M.R. Pereira 224* (INPA). SANTA CATARINA: Rancho Queimado, Serra da Boa Vista, 9.VII.1960, *P.R. Reitz 9885* (SP). SÃO PAULO: Apiaí, Parque Natural Municipal do Morro do Ouro, 24°31'2"S, 48°50'7"W, 23.IV.2007. *D.F. Peralta 4415* (SP). Barra do Turvo, Parque Estadual do Rio Turvo, Núcleo Cedro, 22°45'34"S, 48°25'18"W, 20.III.2019, *L.A. Amélio 818, 835* (SP). [Campos do Jordão] Parque Estadual de Campos do Jordão, 22°41'43"S, 45°28'52"W, 8.X.2009, *D.F. Peralta 9690, 10037* (SP). [Campos do Jordão] Horto Florestal, 22°41'32"S, 45°29'23"W, 3.X.2017. *D.M. Carmo 1744* (SP). Cunha, Parque Estadual da Serra do Mar, 23°14'12"S, 45°1'15"W, 22.VI.2006, *D.F. Peralta 3796* (SP). Moji das Cruzes, Parque Municipal da Serra de Itapety, 23°31'22"S, 46°11'18"W, 22.X.2005. *D.F. Peralta 3162* (SP). Peruíbe, Estação Ecológica da Juréia, 24°19'12"S, 46°59'54"W, 19.XI.1987, *D.M. Vital 15615* (SP). Pindamonhangaba, Eugênio Lefévre, 22°55'26"S, 45°27'42"W, 5.IV.1966. *D.M. Vital 851* (SP). São José dos Alpes, Serra da Mantiqueira, 22°33'9"S, 45°23'38"W, 16.IV.1999, *D.F. Peralta 177* (SP). Piquete, Morro do Careca, 22°36'49"S, 45°10'34"W, 23.IX.2006, *O. Yano 28880* (SP). Santo André, Reserva Biológica de Paranapiacaba, 23°39'50"S, 46°32'18"W, 26.XI.1980. *O. Yano 3161* (SP). Reserva Biológica do Alto da Serra, 23°39'50"S, 46°32'18"W, 9.VIII.1988, *C. Giancotti 118* (SP). São José do Barreiro, Parque Nacional da Serra da Bocaina, 22°42'49"S, 44°35'14"W, 15.V.2007. *D.F. Peralta 4667, 4668* (SP). [São Paulo] Parque Estadual da Cantareira, 23°19'30"S, 46°22'52"W, 6.XI.1991. *O. Yano 15832* (SP). Ubatuba, Núcleo Picinguaba do Parque estadual da Serra do Mar, 23°26'2"S, 45°4'16"W, 12.X.1995. *S.R. Visnadi 2067* (SP).

Lepidozia coilophylla Taylor**,** London J. Bot. 5: 370. 1846. Original Material: [Brazil] Brasilia, [Minas Gerais] Gongo soco. *C.J.F. Bunbury (s.n.)* (Isolectotype G (barcode G00115392 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00115392)).

= *Lepidozia laxepinnata* Spruce, Trans. Proc. Bot. Soc. Edinb. 15: 360. 1885. Original Material: Peru, Andes Peruvianos. M. Guayrapurina. *R. Spruce (s.n.)* (Isolectotype G (barcode G00280936 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00280936)), syn. fide Fulford (1966).

= *Lepidozia plumiformis* Spruce, Bull. Soc. Bot. France (Suppl.) 36: 199. 1889, Spruce, Rev. Bryol. 15: 33. 1888, *nom. inval*. Original Material: Brazil. Rio de Janeiro. *A.F.M. Glaziou 7135* (G (barcode G00115423 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00115423)), syn. fide Fulford (1966).

= *Lepidozia brevifissa* Steph., Spec. Hep. 3: 567. 1909. Original Material: [Brazil] Brasilia, Minas Gerais, Serra do Caraça. *E.A. Wainio 55* (barcode G00280855 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00280855)), syn. fide Fulford (1966).

= *Lepidozia cavifolia* Steph., Spec. Hep. 3: 577. 1909. Original Material: Brazil. Rio de Janeiro. *E.H.G. Ule 419* (barcode G00069611 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069611)), syn. fide Fulford (1966).

Illustration and additional description in Yano *et al*. (2019) and Fulford (1966).

Plants are medium size to large, light green to greenish brown, in mats or scattered among other bryophytes, creeping, prostate or sometimes long pendent. Stems 5–10 cm long, with leaves up to 1.2 mm wide, prostate, pinnate. Branches 1 cm long or longer, becoming flagelliform at the tips, and occasionally some ventral branches also flagelliform. Stem leaves are distant, ovate, truncate, 0.4–0.7 mm long; short lobes, triangular from a 3–4-celled base, incurved. Underleaves quadrate to longer than broad, not as wide as the stem, concave, the lobes triangle from 3–5-celled at the base, and the apex truncate or acute. Dioicous plants. Bracts and bracteoles in 6 or more series, large. Female bracts and bracteoles in 3–4 series, the inner bracts with 4–6 lobes with margins entire. Perianth mouth entire.

This species is recognized by the sub-longitudinal insertion of the leaf, the slithering quadrifid leaves, and the lobe and upper leaf margins without teeth. This species is often found on tree trunks, in deeply shaded forests and may be on rocks and soil, next to the base of trees up to 1000 m. *L. coilophylla* is extensively found in the neotropical zone: Bolivia, Guyana, Suriname, Venezuela, Peru and Brazil (Herzog 1925, Schiffner & Arnell 1964, Fulford 1996, Yano, 1984, Gradstein & Costa 2003). In Brazil it is reported in Amazonas (Costa et al. 2020), Minas Gerais, Paraná Rio de Janeiro, São Paulo, and Santa Catarina. In this study, *L. coilophylla* is reported as a new occurrence to Espírito Santo, and Pernambuco. This species typically occurs in the Atlantic rainforest. The var. *apiculiloba* (Steph.) Fulford differs by the lobes with scattered, hidden or few-celled teeth.

Selected material: BAHIA: Palmeiras, Pai Inácio. 12°18'52"S, 41°20'0"W. 12.VI.1981, *B.M. Boom 1180* (NY, SP). ESPÍRITO SANTO: Santa Teresa, Reserva Biológica Augusto Ruschi, 19°56'9"S, 40°36'W, 20.II.2003. *J. Rossilne 259* (SP). Santa Teresa, Nova Lombardia, 17.IX.2002, *R.R. Vervolet 989* (RB). MINAS GERAIS: Catas Altas, Reserva Particular do Patrimônio Natural, "Parque Natural do Caraça", 20°5'56"S, 43°29'17"W, 25.III.2016. *D.F. Peralta 18897, 18909, 18921* (SP). Passa Quatro, 22°23'25"S, 44°58'0"W, 27.V.1983. *J.F. Zikán 438* (SP). Santa Bárbara, Reserva Particular do Patrimônio Natural, "Parque Natural do Caraça", 19°57'34"S, 43°24'55"W*;* 23.X.1994. *O. Yano 21987* (SP). São Roque de Minas, Parque Nacional da Serra da Canastra, 20°10'32"S, 46°33'35"W, 17.VII.2013. *D.F. Peralta 15023, 15038* (SP). PARANÁ: Morretes, Parque Estadual do Marumbi, 25°26'11"S, 48°55'14"W, 23.VII.2014. *D.F. Peralta 16147* (SP). Serra da Graciosa, 21.VIII.1999. *D.F. Peralta 397* (SP). PERNAMBUCO: Jaqueira. Serra do Quengo. 8°42'50"S, 35°50'0"W, 2.IV.2002, *M.R. Pietrobom 5466* (SP). RIO DE JANEIRO: Santa Maria Madalena, Rancho da Mata Atlântica, trilha para o poço do Padre. 21°58′12″S, 41°59′57″W, 30.X.2008. *D.P. Costa 5001* (RB). Campos dos Goytacazes, mata à direita da estrada em direção ao Poço Parado, 21°45′16″S, 41°19′28″ W, 26.X.2006, *N.D. Santos 641* (RB). SÃO PAULO: Campos do Jordão, estrada de Campos do Jordão para Wenceslau Braz, 22°39'10"S, 45°26'6"W, 6.V.2012. *D.F. Peralta 12563* (SP). Cananéia, Ilha do Cardoso, 25°0'59"S, 47°56'23"W, 11.I.1977. *D.M. Vital 6816* (SP). Cubatão, Bairro Fabril, 23°53'42"S, 46°25'31"W, 18.IV.1993. *O. Yano 18778* (SP). Lago Azul, 23°53'42"S, 46°25'31"W, 18.IV.1993. *O. Yano 18804* (SP). Cunha, Parque Estadual da Serra do Mar, 23°14'12"S, 45°1'15"W, 22.VI.2006. *D.F. Peralta 3856* (SP). Guapiara, Parque Estadual Intervales, 24°11'6"S, 48°31'58"W, 8.XI.1988. *S.R. Visnadi 4765* (SP). Peruíbe, Estação ecológica Juréia-Itatins, 13.III.1990. *C. Giancotti 254* (SP). Santo André, Reserva Biológica do Alto da Serra de Paranapiacaba, 23°39'50"S, 46°32'18"W, 8.III.2007. *O. Yano 29442* (SP). São Paulo, Morro do Jaraguá, 23°32'51"S, 46°38'10"W, 30.IV.1921. *F.C. Hoehne 263* (SP).

Lepidozia coilophylla var. ***apiculiloba*** (Steph.) Fulford, Mem. New York Bot. pp. 194. 1966 ≡ *Lepidozia apiculiloba* Steph., Spec. Hep. 6: 321. 1922. Type: Bolivia. Pando. *O. Buchtien 12* (Holotype G (barcode G00069605 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069605).
= *Lepidozia kaulfussiana* . Steph., Hep. 6: 321. 1922. Type: Bolivia. La Paz. *O. Buchtien 10* (Holotype G (barcode G00069651 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069651)), syn. fide Fulford (1966).
Illustration and additional description in Fulford (1966).

The sub-longitudinal insertion of the leaf, and the quadrifid leaves are the main features of *L. coilophylla*. In this variety the margins of the leaves and underleaves have occasional blunt teeth formed by partly projecting cells. Usually it is found on tree trunks, but never found on rocks or barks. The variety occurs in South America in Bolivia (Fulford 1966), Peru (Stephani, 1905) and Brazil in São Paulo it is recognized as a new report.

Selected material: SÃO PAULO: Cananéia, Ilha do Cardoso, 25°0'59"S, 47°56'23"W, 26.II.1991, *O. Yano 8951*. Santo André, Reserva Biológica do Alto da Serra de Paranapiacaba, 23°39'50"S, 46°32'18"W, 24.IV.1987. *D.M. Vital 14828* (SP).

Lepidozia cupressina (Sw.) Lindenb. in Gottsche, Lindenberg & Nees. Syn. Hep. 207. 1845 ≡ *Jungermannia cupressina* Sw., Nov. Gen. Spec. Pl. Prodr.144. 1788 ≡ *Mastigophora cupressina* (Sw.) Trevis., Mem. Ist. Lom. III, 4: 416. 1877. Type: Jamaica. *Swartz [s.n.]* (Isotype G (barcode G00280987 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00280987)
= *Lepidozia pinnata* (Hook.) Dumort., Recueil Obs. Jungerm. 19. 1835 ≡ *Jungermannia reptans β pinnata* Hook., Brit. Jung. Pl. 75, 12. 1815. Type: United Kingdom, Long Crag. *Wilson & J. A. Wheldon [s.n.]* (Holotype BM), syn. fide Schiffner (1919), Fulford (1966).

= *Lepidozia pseudocupressina* Schiffn., Krit. Bemerk. Eur. Leberm. 14: 8–9. 1919. Type: Brazil. Santa Catarina. *E.H.G. Ule [s.n.] (Herbarium Brasiliense 339)* (Holotype G?), *syn. nov.*

= *Lepidozia allionii* Steph., Spec. Hep. 6: 320. 1922, Biblioth. Bot. 87: 225. 1916, *nom. inval*. Original material: Ecuador. Morona-Santiago. *M. Allioni 741* (Holotype G (barcode G00061365 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00061365), *syn. nov.*

Illustration and additional description in Pócs, Ochyra and Bednarek-Ochyra (2016)

Plants medium-sized, green to yellowish or brownish, in mats or scattered among bryophytes, creeping, stems 8 cm long, with leaves 1–1.5 mm wide, prostrate to suberect, pinnate or in few cases bipinnate, lateral branches frequent, densely leafy, up to 1.5–1.8 cm long, decurved to attenuate, long-flagelliform in the outer branches. Line of leaf insertion oblique. Stem leaves imbricate, asymmetric, widely ovate, concave, 0.5–0.8 mm long and up to 0.6–0.8 mm wide, the dorsal lamina arched, and the margins without or with 1-2 teeth, quadrifid to one half. Lobes long-triangular, incurved, the base 6–10 cells wide, apex of the lobes apiculate, with 2 cells, rarely with more than 3. Underleaves slightly wider than the main stem, and on branches the width similar to the leaves, imbricate, quadrifid to one half, the lobes with 2–6 cells at the base, and apex usually with one cell or two but no more than three. Plants dioicous. Male bracts in 4–6 series, the bracts concave, incised above. Female bracts in 3 series, usually hyaline to light green, divided above into 3–5 short and irregular lobes. Perianth 6 mm long, whitish, cylindrical, the mouth lobes ciliate or not.

Lepidozia pseudocupressina was described with the main distinguishing character being the long cilia (1–2 cells (-5)) on the perianth mouth. Taylor (1960), Fulford (1966) and Gradstein & Costa (2003) pointed out that the gametophyte of this species is identical to robust plants of *L. cupressina*, but their comments seem to be on the same observation as Schiffner on the original description, since they don't analyze the type. The curator of G herbaria was consulted and did not find the type specimen indicated by Fulford (1966).

The presence of perianth in the genus is rare in herbarium specimens, and thus Fulford (1966) indicated that *L. pseudocupressina* should be included in the species-complex of *L. cupressina;* and Gradstein and Costa (2003) suggest it as a variety of *L. cupressina*.

Our study on several hundreds of specimens show variable gametophyte characters of *L. cupressina*, such as the leaf and underleaf size, lobules, branching way, as well as the plant size, and the perianth variation used to describe *L. pseudocupressina* was found in other species (for exemple *L. brasiliensis*, *L. inaequalis*, *L. reptans*) and some specimens have perianth with or without cilia, therefore we believe that it is an ambiental variation.

L. cupressina is distinguished by the truncate lobes, ending with 1–2 cells, the lobes short and triangular, and underleaves somewhat wider than the stem. *L. cupressina* is often found in montane forests on soil, rocks, stumps and logs, trunks of trees, on bark and on rotten wood, the epiphytic form is rare, and it is extensively distributed in all tropical America: Bolivia, Ecuador, Cuba, Guatemala, Jamaica, Haiti, Honduras, Mexico, Peru, Venezuela (Spruce 1884; Fulford 1966, Pócs et al. 2016, Gradstein 2021), and in Brazil the known occurrence is in the states of Amazonas, Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco (Alvarenga et al. 2007), Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo and we report as new to Distrito Federal.

Selected material: AMAZONAS: São Gabriel da Cachoeira, Igarapé Arabú, 0°12'S, 66°30'W, 9.VII.1979. *R.M. Schuster 825* (SP). BAHIA: Abaíra, Campo de Ouro Fino, 13°8'45"S, 41°23'42"W, 25.I.1992. *D.J.N. Hind s.n* (SP). Riacho da Taquara, 14.II.1992. *B. Stannard, B., s.n.* (NY, SP.). Boa Nova, Recanto dos Pássaros, 22.IX.2013, *C.O. Azevedo 557* (SP), Lençóis Planalto, 12°33'47"S, 41°23'24"W, IX.1995, *A.M. Giulietii s.n.* (SP). DISTRITO FEDERAL: Brasília, Fazenda Água Limpa, 15°46'47"S, 47°55'47"W, 7.XI.1985. *D.M. Vital 13265* (SP). ESPÍRITO SANTO: Castelo, Parque Estadual Forno Grande, 20°30'56"S, 41°5'31"W, 1.X.2016. *D.F. Peralta 19379* (SP). MINAS GERAIS: Caldas, Pedra Branca, 15.IV.2017, *O. Yano 34204* (SP). Catas Altas, Reserva Particular do Patrimônio Natural, "Parque Natural do Caraça", 20°5'56"S, 43°29'17"W, 30.V.2008, D.F. *Peralta 6402, 6402* (SP). Conceição do Mato, Serra do Cipó, 19°2'14"S, 43°25'30"W, 14.III.1967, *D.M. Vital 1224* (SP). Diamantina, Gruta do Salitre, 14.XI.2010. *O. Yano 32976.* (SP). Lima Duarte, Parque Estadual do Ibitipoca, 21°41'32"S, 43°52'35"W, 15.X.1986. *H.C. Sousa s.n.* (SP). São Roque de Minas, Parque Nacional da Serra da Canastra, Cachoeira Casca d´Anta, 20°18'11"S, 46°31'25"W, 18.VII.2013, *D.F. Peralta 15196* (SP). PARANÁ: Morretes, Parque Estadual do Marumbi, Ponta do Tigre, 25°26'55"S, 48°54'54"W, 22.VII.2014. *D.F. Peralta 15910* (SP). Serra da Graciosa, 24.IX.1999. *D.F. Peralta 490* (SP). RIO DE JANEIRO: Angra dos Reis, Ilha Grande, 23°0'24"S, 44°19'5"W, 21.III.1995, *O. Yano 23657* (SP). Resende, Parque Nacional do Itatiaia, 22°28'8"S, 44°26'48"W, 23.VII.1966, *G. Eiten 7298* (SP).

RIO GRANDE DO SUL: Bom Jesus, Serra da Rocinha, 29.X.1983. *R. Bueno 3542* (SP). Cambará do Sul, Itaimbezinho, 8.II.1983. *R. Bueno 1435* (SP). SANTA CATARINA: São Joaquim, 27.IX.1987, *A. Schäfer-Verwimp 9147* (JE, SP). Parque Nacional de São Joaquim, 28°6'59"S, 49°29'54"W, 10.III.2009. *D.F. Peralta 7752, 7833* (SP). SÃO PAULO: Campos do Jordão, Bairro Jaguaribe, 22°43'48"S, 45°35'23"W, 08.XII.1993. *O. Yano 22055, 22063* (SP). Parque Estadual de Campos do Jordão, 22°41'15"S, 45°27'58"W, 9.X.2009. *D.F. Peralta 9828* (SP). Cananéia, Ilha do Cardoso, 25°0'59"S, 47°56'23"W, 01.XII.1983. *D.M. Vital 11316* (SP). Mogi das Cruzes, Parque das Neblinas, 23°27'9"S, 46°5'37"W, 1.XI.2008. *J. Bordin 1250* (SP). Santo André, Reserva Biológica de Paranapiacaba, 23°39'50"S, 46°32'18"W, 26.II.1985. *O. Yano 9396* (SP). São Bernardo do Campo, Parque Caminhos do Mar, 23°24'50"S, 46°20'7"W, 18.VI.1991. *O. Yano 15244* (SP). São José do Barreiro, Parque Nacional da Serra da Bocaina, Santo Isidro, 22°45'28"S, 44°39'10"W, 15.VIII.2018. *D.M. Carmo 1910* (SP). São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 23°20'45"S, 45°7'47"W, 17.IV.2013. *D.F. Peralta 13868* (SP). Parque Estadual das Fontes do Ipiranga, 23.IV.1974. *D.M. Vital 3081* (SP). Parque Estadual da Cantareira, 24.VIII.1992. *M.P. Marcelli 14028* (SP).

Lepidozia densa Herzog *in* Repertorium specierum novarum regni vegetabiilis, Brelin, 20(3): 26. 1925. Original Material: Brazil. Rio de Janeiro, Serra dos Orgãos, Morro Assú, 2400 m, *Lützelburg 6381* (barcode JE 04002088 - https://je.jacq.org/JE04002088). Figure 3. A-D. llustration and additional description in Herzog (1925).

Plants small, green to yellowish, in mats and among others bryophytes, creeping,, stems 0.5–1 cm long, with leaves 0.2–0.4 mm wide, prostrate to ascending, pinnate to bipinnate, often flagelliform at the tip, without or with scarce ventral flagelliform branches. Leaf insertion oblique. Stem leaves closely imbricate, squarrose, concave, 0.2–0.5 mm long to 0.25–0.6 mm wide at the base, with entire margins, divided to one fourth of their length into 4 lobes; lobes apiculate, triangular, often flexuose, ending in a uniseriate row of 5–8 cells, the base 3–5 cells wide, the walls thickened, the cuticle slightly verrucose. Underleaves wider than longer, up to 0.15 (0.18) mm wide, divided to one third the length, the lobes 4–5 cells long, 2 cells wide at the base. Dioicous plants. Male bracts in 4 - 6 or more series, the bracts concave, the lobes acuminate; antheridia solitary, large. Female bracts in 3–4 series, ovate, divided to one fourth their length into 4–5 lobes. Perianth with the mouth ciliate.

Lepidozia was described to Brazil in 1925 by Herzog, after that was collected by Hoenne. Fulford (1966) commented about this species, but she was not examined and the collections possibly were identified as another species as *L. incurvata* by the size, and *L. cupressina* by the curved leaves. According to Herzog (1925), *L. densa* occurs in Brazil at 2,400 m a.s.l. in Serra dos Órgãos mountains, and we confirm it, as a *Lepidozia* species to the higher altitudinal region in Rioi de Janeiro. It was rediscovered in a locality at 2,200 m of altitude indicates that its elevational range in the INP has narrowed over the last 98 years, maybe in response to climate change. Bergamini et al. (2009) demonstrated that climate warming can provoke alterations in the distributions of mosses and liverworts species present in cooler environments (cryophilous) and that they tend to migrate from mountainous sites to areas more favourable to their establishment. This is an endemic species of *Lepidozia* to Brazil, the only species of *Lepidozia* occurring in higher altitudes.

High-altitude fields in the Serra dos Orgãos harbor a high diversity of species, with elevated numbers of endemic and/or threatened liverwort, as Itatiaia National Park, other important conservation unid (Costa & Santos 2009; Rezende 2015; Gonçalves & Santos 2018). But this areas suffer with pastures, exotic species, several climate changes and wildfires (Aximoff 2011; Gonçalves et al. 2022). The case of *L. densa* and all liverworts, the habitat loss due to climate change is the main factor that makes it endangered, as this species has unique environmental requirements, that is, it depends on microenvironments for its establishment.

Selected material: RIO DE JANEIRO: Teresópolis, Parque Nacional da Serra dos Órgãos, 22°27'30"S, 43°01'32"W, 19.I.2022, *D.F. Peralta 27539, 27578* (SP).

Lepidozia inaequalis (Lehm. & Lindenb.) Lehm. & Lindenb. *in* Gottsche, Lindenberg & Nees. Syn. Hep. 209. 1845 ≡ *Mastigophora inaequalis* (Lehm. & Lindenb.) Trevis., Mem. Ist. Lomb. III, 4: 416. 1877 ≡ *Jungermannia inaequalis* Lehm. & Lindenb. *in* Lehmann, Pug. Pl. 5: 1. 1833. Original Material: Brazil. Rio de Janeiro, Nova Friburgo, *K. Beyrich [s.n.]* (barcode G00115412 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00115412).

= *Lepidozia cupressina* var. *tenuicuspis* Spruce, Trans. Proc. Bot. Soc. Edinb. 15: 358. 1885. ≡ *Lepidozia tenuicuspis* (Spruce) Spruce, Mem. Torrey Bot. Club. 1(3): 130. 1890

≡ (non *Lepidozia tenuicuspis* (Spruce) Steph., Spec. Hep. 6: 342. 1922, nom. inval. later homonym). Original Material: Peru. "Andes Peruviani", *R. Spruce [s.n.]* (barcode G00115411 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00115411), syn. fide Fulford (1966).

= *Lepidozia inaequalifolia* Spruce, Rev. Bryol. 15: 34. 1888, *nom. inval*. Original Material: Brazil, Rio de Janeiro. *A.F.M. Glaziou 11738* (G (barcode G00280968 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00280968), syn. fide Fulford (1966).

= *Lepidozia boliviensis* Steph., Spec. Hep. 3: 571. 1909. Original Material: Bolivia. Cochabamba. *T.K.J. Herzog [s.n.]* (barcode G00069800 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00069800), syn. fide Fulford (1966).

Illustration and additional description in Fulford (1966).

Plants large, green to yellowish to brownish, in mats and among others bryophytes, creeping, sometimes long pendent, stems 6–9 cm long, with leaves 1.2–1.4 mm wide, prostrate to ascending, pinnate to bipinnate, when densely leafy to 1.5–1.8 mm long, often flagelliform at the tip, without or with scarce ventral flagelliform branches. Leaf insertion oblique. Stem leaves closely imbricate, squarrose, concave, 0.8–1.4 mm long to 1–1.3 mm wide at the base, with entire margins, divided to one fourth of their length into 4–5 lobes; lobes very narrow, long apiculate, the largest of the genus, triangular, often flexuose, ending in a uniseriate row of 5–9 cells, the base 3–11 cells wide, the walls thickened, the cuticle verrucose. Underleaves large, wider than the stem, longer than wide, up to 0.5 mm wide, divided to one half or two thirds their length, slender, the lobes 5–9 cells long, very narrow, 2–5 cells wide at the base. Dioicous plants. Male bracts in 6 or more series, the bracts concave, the lobes acuminate; antheridia solitary, large. Female bracts in 3–4 series, ovate, divided to one fourth their length into 4–5 lobes. Perianth long, with the mouth ciliate.

This species is extensively known by the long and filiform lobes in the leaves and underleaves. It is often found in dense forests, in montane forests such as Atlantic rainforest for instance, on trunks of trees and rotten logs. *L. inaequalis* may be found throughout tropical America: Bolivia, Ecuador, Guatemala (Pèrez 2006), Peru, and in Brazil the occurrence is in Amazonas, Bahia, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina and São Paulo. We report as new occurrence to Pará and Roraima, Selected material: AMAZONAS: São Gabriel da Cachoeira, Igarapé Arabu, Serra Curicuriari, 09.VII.1970, *R.M. Schuster 608* (INPA, SP). BAHIA: Miguel Calmon, *E.B. Valente 1455* (HUEFS). MINAS GERAIS: Brejo da Lapa, 22°23'25"S, 44°58'W, III.1922. *J.F. Zikán 274* (SP). Itamonte, Parque Nacional do Itatiaia, 22°17'2"S, 44°52'12"W, 27.VI.1972. *D.M. Vital 3687* (SP). Santa Bárbara, Reserva Particular do Patrimônio Natural, “Parque Natural do Caraça”, 20°5'33"S, 43°28'24"W, 29.VII.2012. *D.F. Peralta 11941* (SP). PARÁ: Oriximiná. ESEC do Grão-Pará Serra do Acari, 2.IX.2008. *M.R. Pietrobom 8014* (SP). PARANÁ: Morretes, Parque Estadual do Marumbi, 25°26'55"S, 48°54'54"W, 22.VII.2012. *D.F. Peralta 15942* (SP). RIO DE JANEIRO: Angra dos Reis, Parque Nacional do Itatiaia, 22°25'25"S, 49°36'24"W, 6.V.2012, *D.F. Peralta 18355* (SP). Resende, Ilha Grande, 23°0'24"S, 44°19'5"W, 21.III.1992. *O. Yano 23659, 23705* (SP). RIO GRANDE DO SUL: Cambará do Sul, Itaimbezinho, 16.IV.1983. *R. Bueno 2533* (SP). São Francisco de Paula, Jaquirana, 39°26'53"S, 50°35'1"W, 26.X.1982. *R. Wasum s.n.* (HUCS, SP). RORAIMA: Boa Vista, Serra Parima, 28.VII.1974. *D. Griffin III 683, 687* (SP). SANTA CATARINA: Porto União, Porto União, 12.VII.1968. *P.R. Reitz 13159* (SP). SÃO PAULO: Campos do Jordão, Estação Biológica do Alto da Serra, 23°32'51"S, 46°38'10"W, IX.1922. *F.C. Hoehne 85*, 21.VII.1972, *D.M. Vital 7303* (SP). Cubatão, Estação Biológica da Boracéia, 23°31'56"S, 45°50'47"W, 23.III.1992, *O. Yano 22461* (SP). Cunha, Parque Estadual da Serra do Mar, Núcleo Picinguaba, 23°26'2"S, 45°4'16"W, 22.III.1992. *S.R. Visnadi 1527, 1700* (SP). Pindamonhangaba, Trilha de acesso ao Pico dos Marins, 22°36'49"S, 45°10'34"W, 15.VI.2002, *D.F. Peralta 3593* (SP). Parque Estadual do Rio Turvo, 24°33'49"S, 48°10'22"W, 16.V.2002. *D.F. Peralta 8272* (SP). São Paulo, 23°53'24"S, 46°25'11"W, 10.IX.1982, *D.M. Vital 13991*, (SP). Ubatuba, Serra da Mantiqueira, 22°55'S, 45°39'W, 16.IV.1992. *D.F. Peralta 177* (SP).

Lepidozia incurvata Lindenb. *in* Gottsche, Lindenberg & Nees., Syn. Hep. 203. 1845. ≡ *Mastigophora incurvata* (Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat. 4(13): 416. 1877. Original Material: Colombia. Mt. Quindío. *A. von Humboldt [s.n.]* (barcode G00265253 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g002652536).

= *Lepidozia lechleri* Steph., Spec. Hep. 3: 567. 1909. Original Material: Peru. *H.A. Weddell [s.n.]* (barcode G00060930 -

https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00060930), syn. fide Menzel (1984).

Illustration and additional description in Fulford (1966).

Plants long and filiform, slender, in green yellowish to olive-green, or brown to reddish, in mats or among others bryophytes, creeping, stems 7 cm long, with leaves up to 0.6 mm broad, tripinnate, the lateral branches long, flagelliform, the secondary branches frequently crowded, tufted, the ventral flagelliform branches long. Leaf insertion oblique, the leaves incubous. Stem leaves distant, imbricate, convex with the lobe incurved touching the stem, 0.2–0.5 mm long, 0.3–0.5 mm wide at the base. The dorsal margin of the lamina strongly arched and without teeth, quadrifid from one-fifth of their length, the lobes incurved, unequal, triangular from 2–6 cells at the base, the apex acute, of one or a row of several cells; leaf cells quadrate to rectangular, the walls thickened, the lumina rounded, with the cuticle smooth. Branch leaves often ascendant to spreading. Underleaves as wide as the stem or narrower, quadrate from one half of their length, the lobes uniseriate from 2–3 cells at the base. Dioicous plants. Male branches are slender with bracts in 4 or more series, wider than long, antheridia solitary, large. Female bracts in 3–4 series, bracts divided into 3–4(–5) lobes, without teeth at the margin. Perianth long, the mouth not ciliate.

L. incurvata is identified by the slender plants with concave leaves with incurved lobes, narrow underleaves, occurring usually on moist banks and sandstone rock faces, and on trunks of trees. However, it is not frequently collected and is apparently rare in Brazil. *L. subdichotoma* and *L. patens* may be confused but although slender, the leaves are smaller and reddish, usually convex. *Lepidozia incurvata* occurs mainly in open areas in humid montane forest, as in the Atlantic rainforest. It is widely distributed in the Neotropics: Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Peru, Venezuela and Brazil in the states of the Santa Catarina (Schäfer-Verwimp 1996), and new report to Minas Gerais, Rio Grande do Sul and São Paulo.

Selected material: MINAS GERAIS. Nova Lima, Reserva Particular do Patrimônio Natural, “Parque Natural do Caraça,” 20°5'50"S, 43°29'23"W, 27.VII.2012. *D.F. Peralta 11832* (SP). Catas Altas, Reserva Particular do Patrimônio Natural, 20°7'28"S, 43°27'31"W, 25.III.2012. *D.F. Peralta 20535*, *20562* (SP). RIO GRANDE DO SUL. Cambará do Sul, Parque Nacional Aparados da Serra, 29°9'30"S, 50°4'48"W, 29.VIII.2012. *D.F. Peralta 21039* (SP). SÃO PAULO. Santo André, Reserva Biológica de Paranapiacaba, 23°39'50"S, 46°32'18"W, 26.XI.1982. *O. Yano 3160* (SP).

Lepidozia patens Lindenb., Syn. Hepat. 202. 1845 ≡ *Mastigophora patens* (Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat. 4(13): 416. 1877. Original Material: Saint Kitts and Nevis. *J.C. Breutel [s.n.]* (barcode G00283295 - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g0028295).

Fig. 2. E–H. Additional illustration and description in Fulford (1966).

Plants slender, light brown, in mats or among other bryophytes; stems filiform, creeping, sometimes long pendent, to 10–15 cm long, pinnate or bipinnate, the lateral branches flagelliform, without leaves or very small ones. Leaf insertion transverse. Leaves distant, slightly quadrate to cuneate on older plants, margins without teeth, 0.2–0.4 mm long, 0.1–0.2 mm broad at the base, quadrifid or trifid, the lobes one half of the length, quickly divergent, triangular, 2–6 cells wide, the cell lumina rounded, the cuticle smooth. Underleaves very small, 0.1–0.2 mm long, 0.2 wide, quadrifid. Dioicous plants. Male branches usually near the type of flagelliform branches, the bracts and bracteoles in 5–6 series, the bracts larger than the leaves, imbricate, ovate, concave, bifid. Female branches usually with 3–5 series of bracts and bracteoles.

Known from Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, Guatemala, Guyana, Haiti, Jamaica, Lesser Antilles, Mexico, Panama, Peru, Puerto Rico and Venezuela (Reenen & Gradstein, 1984; Holz & Gradstein, 2005; Ramírez et al. 2007). To Brazil it is a new record.

Selected material: MINAS GERAIS**.** Nova Lima, Reserva Particular do Patrimônio Natural, “Parque Natural do Caraça,” 20°5'50"S, 43°29'23"W, 27.VII.2010, *D.F. Peralta 11832* (SP).

Discussion

While analyzing herbarium specimens of *Lepidozia* we found that the number of species in Brazil is larger than hitherto accepted. In this study, we present a treatment to *Lepidozia* and comment on the Brazilian ranges of the species, providing data that will hopefully be useful in the identification of collections, and in indicating how rich is the Brazilian liverwort flora.

We report eight species plus one variety of *Lepidozia* in Brazil, including *L. alstonii*, *L. aequiloba* and *L. patens* as new occurrences. These new reports in Brazil increase the richness of its liverwort biodiversity.

Lepidozia aequiloba was described as a Brazilian species, which is easily confused with *L. cupressina*, but differs from the latter in its divergent leaf lobes. For a long time, it had not been identified in the floristics studies, but it was accepted in Söderstrom et al. (2016) and confirm in this study. *Lepidozia alstonii,* described from the northern Andes (Colombia and Ecuador) by Fulford (1966), and *L. patens,* a species common in the West Indies, are new to Brazil. *Lepidozia pseudocupressina*, as a synonym of *L. cupressina*. The character (long cilia in perianth) that supposedly separated these species was found in other species, such as *L. brasiliensis, L. inaequalis, L. reptans*. Some specimens have perianth with cilia, becoming a weak character to distinguish the species. As well as *Lepidozia densa* which is known only from source material was synonymized to *Lepidozia brasiliensis*.

The most comprehensive taxonomic treatment of *Lepidozia* to date from Latin America is Fulford's (1966). Gradstein and Costa summarised the main diagnostic characters of the Brazilian species in *The Hepaticae and Anthocerotae of Brazil* (2003), and these studies are usually the main literature to identify *Lepidozia* and Lepidoziaceae in South America. In Gradstein and Costa (2003) the authors made an important point to reinforce the studies about the taxonomy and generic relationships. In this study, we conclude that the number of Lepidoziaceae species in Brazil may be underestimated, the main occurrence in Brazil is in the rich Atlantic rainforest.

The sampling of the Lepidoziaceae in molecular phylogenetic analyses has been mainly limited to European and Australasian species (Cooper *et al*. 2011, 2012a). We hope that further research on Lepidoziaceae taxonomy in the Neotropics will incorporate molecular techniques to assess species boundaries in widespread taxa (such *as L. cupressina*) and the relationships between South American genera (such as *Micropterygium*, and *Pteropsiella*) and European, Asiatic and Australasian Lepidoziaceae genera.

Others combinations within *Lepidozia*

Lepidozia digitisquama Herzog, Brotéria 6: 17. 1937. Type: Brazil, S. Paulo, Alto da Serra, Estação Biológica, *Gehrt [s.n.]* (JE). Synonym of *Telaranea apiahyna* (Steph.) Fulford according with Fulford (1966).

Excluded species:

Lepidozia degilisquarrea Herzog, herbarium name, this species was collected in Alto da Serra, São Paulo, but was never formally described (B300019578).

Lepidozia macrocolea Spruce, Trans. Proc. Bot. Soc. Edinb. 15: 36. 1884(5). Type: Ecuador, "Andes Quitenses", Mt. Tungurahua, *Spruce [s.n.]* (Original Material MANCH, isotypes BR, G). The specimen from Brazil *Burchell 3571* (BM), cited by Fulford (1966), does not indicate collection location. This is a species usually found in Andean regions, and in this study we did not recognize this species for these localities in Brazil.

Lepidozia ulothrix (Schwägr.) Lindenb., Syn. Hep. 210. 1845. Lindenberg & Gottsche (1846) reported this species in Brazil (herbaria Mougeot) without specimen citations. This species is known only from Australasia (Engel & Schuster, 2001) and from Mauritius Island (Pócs, 1984, based on a specimen from BM).

Acknowledgments

The authors are grateful to curators and staff of the herbaria cited in the text for the loan of specimens, to the CAPES for the grant of the first author and also to thank Dr. William R. Buck for advice and linguistic correction.

References

Alvarenga, L. D. P., Silva, M. P. P., Oliveira, J. R. P. M., Pôrto, K. C. (2007). Novas ocorrências de Briófitas para Pernambuco, Brasil. Acta botanica brasilica, 21(2): 349-360.

Amélio, L. A., Peralta, D. F, Carmo, D. M. (2019). Briófitas do Parque Estadual de Campos do Jordão, Estado de São Paulo, Brasil. Hoehnea 46, 2, 1–24.

Aximoff, I. (2011). O que perdemos com a passagem do fogo pelos Campos de Altitude do Estado do Rio de Janeiro? Biodiversidade Brasileira 2: 180-200.

Bernal, R., Gradstein, S. R., Celis, M. (2016). Catálogo de Plantas y Líquenes de Colombia. Bogotá: Universidad Nacional de Colombia. Facultad de Ciencias, Isntituto de Ciencias Naturales. p. 329.

Carmo, D. M., Peralta, D. F. (2016). Survey of bryophytes in Serra da Canastra National Park, Minas Gerais, Brasil. Acta Botanica Brasilica 30(2): 254–265.

Carmo, D. M., Lima, J. S., Amélio. L. A., Peralta, D. F. (2016). Briófitas do Parque Estadual da Serra do Mar, Núcleo de Santa Virgínia, Estado de São Paulo, Brasil. Hoehnea 43(2): 265–287.

Carmo, D. M., Lima, J. S., Silva, M. I., Amélio, L. A., Peralta, D. F. (2018). Briófitas da Reserva Particular do Patrimônio Natural da Serra do Caraça, Estado de Minas Gerais, Brasil. Hoehnea 45(3): 484–508.

Costa, D. P., Santos, N. D. (2009). Conservação de hepáticas na Mata Atlântica do sudeste do Brasil: uma análise regional no Estado do Rio de Janeiro. Acta Botanica Brasilica 23: 913-922.

Costa, D. P., Peralta, D. F. (2015). Bryophytes diversity in Brazil. Rodriguésia 66(4): 1–9.

Costa D. P., Nadal F., Rocha T. C. (2020). The first botanical explorations of bryophyte diversity in the Brazilian Amazon mountains: high species diversity, low endemism, and low similarity. Biodiversity and Conservation 29: 2663–2668.

Cooper, E. D., Shaw, A. J., Shaw, B., Henwood, M. J., Heslewood, M. M., Brown, E. A. (2011). A multi-locus molecular phylogeny of the Lepidoziaceae: Laying the foundations for a stable classification. Molecular Phylogenetics and Evolution 59: 489–509.

Cooper, E. D., Henwood, M. J., Brown, E. (2012a). A molecular phylogeny of the *Lepidozia* generic complex supports re-circumscription of the Lepidozioideae. Molecular Phylogenetics and Evolution 65: 10–22.

Cooper, E.D., Henwood, M. J., Brown, E. A. (2012b). Are the liverworts really that old? Cretaceous origins and Cenozoic diversification in Lepidoziaceae reflect a recurrent theme in liverwort evolution. Biological Journal of the Linnean Society 107: 425–441.

Cooper, E. D. (2013b). Notes on Early Land Plants Today. 37. Towards a stable, informative classification of the Lepidoziaceae (Marchantiophyta). Phytotaxa 97(2): 44–51.

Crandall-Stotler, B., Stotler. R. E., Long, D. G. (2008). Morphology and classification of the Marchantiophyta. In: Goffinet B, Shaw AJ (eds). Bryophyte Biology. New York, NY: Cambridge University Press, pp. 1–54.

Crandall-Stotler, B., Stotler, R. E., Long, D. G. (2009). Phylogeny and Classification of the Marchantiophyta. Edinburgh Journal of Botany 66: 155–198. http://dx.doi.org/10.1017/S0960428609005393

Dumortier, B. C. (1835). Recueil d'Observations sur les Jungermanniacées. I. Révision des genres. J.-A. Blanquart, Tournay, 27 pp. http://dx.doi.org/10.5962/bhl.title.731

Engel, J. J., Schuster, R. M. (2001). Austral Hepaticae. 32. A revision of the genus *Lepidozia* (Hepaticae) for New Zealand. Fieldiana: Botany, N.S., 42: 1–107

Fulford, M. H. (1966). Manual of the leafy Hepaticae of Latin America - part II. Memoirs of The New York Botanical Garden. 11. pp. 180-213.

Gonçalves, M. T. A., Santos, N. D. (2018). Campos de altitude do Parque Nacional do Itatiaia: um hotspot para briófitas. Diversidade e Gestão 2: 90-105.

Gonçalves, M. T. A., Peralta, D. F., Santos, N. D. (2022). Rediscovering *Andreaea subulata* Harv., a critically endangered moss in Brazil. Acta Botanica Brasilica. 36: 1-4.

Gottsche, C. M., Lindenberg, J. B. W., Nees, C. G. D. (1845). Synopsis Hepaticarum. Hamburgii.

Gradstein, S. R., Costa, D. P. (2003). The Hepaticae and Anthocerotae of Brazil. Memoirs of The New York Botanical Garden 87: 1–336.

Gradstein, S. R. (2013). Afro-American hepatics revisited. Polish Botanical Journal 58: 149–177.

Gradstein, S. R. (2017). *Bazzania* (Marchantiophyta) in South America. Nova Hedwigia 105: 1–23.

Gradstein, S. R. (2021). The liverworts and hornworts of Colombia and Ecuador. Memoirs of The New York Botanical Garden 121: 1-723.

Holz, I., Gradstein, S. R. (2005). Phytogeography of the bryophyte floras of oak forests and páramo of the Cordillera de Talamanca, Costa Rica. Journal of Biogeography, 32, 1591–1609

IBGE. (2012). Manual técnico da vegetação brasileira. Série: Manuais técnicos em geociências. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro

Lindenberg, J. B., Gottsche, C. M. (1846). Species Hepaticarum. Fasc. VI pp.1–78.

Menzel, M., Schultze-Motel Wolfram. (1987). Studies on Peruvian Bryophytes II. The Mosses Collected by Antonio Raimondi between the Years 1868 and 1879. Willdenowia, 16: 511-525

Pérez, M. E. P. (2006). Composicion de la hepatoflora en tres estados de sucesión vegetal: bosque, guamil y cultivo, en las comunidades de Chelemá I y II, Tucurú, Alta Verapaz, Guatemala. Tesis. Universidade de San Carlos de Guatemala.

Pócs, T. (1984). Synopsis of African Lepidoziacea K. Müll. Proceedings of the Third Meeting of the Bryologistgs from Central and East Europe, Praha, 14th – 18th June 1982: 107— 129.

Pócs, T., Ochyra, R., Bednarek-Ochyra, H. (2016). *Lepidozia cupressina* (Marchantiopsida, Lepidoziaceae) in Sub-Saharan Africa, with a Note on the Taxonomic Status of *L. Chordulifera*. Cryptogamie, Bryologie, 37 (2): 125-147.

Ramírez, B. R., Whittemore, A. T., Churchill, S. P. (2007). The bryophyte of the Department of Nariño, Colombia: II. Hepatics and hornworts. The bryoplogist 111 (3), 482-486.

Reener, G. B. A., Gradstein, S. R. (1984). An Investigation of Bryophyte Distribution and Ecology Along an Altitudinal Gradient in the Andes of Colombia. Journal Hattori Botany Laboratory 56: 79-84.

Rezende, M. A. (2015). Conservação de Briófitas na Mata Atlântica do sudeste do Brasil: uma análise das espécies de hepáticas endêmicas e/ou ameaçadas do Parque Nacional do Itatiaia. MSc Thesis, Escola Nacional de Botânica Tropical, Brazil.

Spruce, R. (1885). Hepaticae Amazonicae et Andinae. Transactions and Proceeding of the Botanical Society of Edinburgh 15: 1–588.

Santos, N. D., Costa, D. P. (2010). Phytogeography of the liverwort flora of the Atlantic Forest of southeastern Brazil. Journal of Bryology 32: 9–22.

Schäfer-Verwimp, A. (1991). Contribution to the knowledge of the bryophyte flora of Espírito Santo, Brasil. Journal Hattori Botanical Laboratory. 69: 147-170.

Schäfer-Verwimp, A. (1996). New or interesting records of Brazilian Bryophytes. V. Candottea 51: 283-302.

Schiffner, V. F. (1919). Kritische Bemerkungen über die Europäischen Lebermoose 14: 9.

Schuster, R. M. (1984). Evolution, phylogeny and classification of the Hepaticae. *In*: Schuster RM (ed). New Manual of Bryology, vol. 2. Hattori Botanical Laboratory, Nichinan, pp. 892–1070.

Schuster, R. M. (2000). Austral Hepaticae. Part 1. Nova Hedwigia. Beiheft 118: 1-530.

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., Xiaolan, He, Heinrichs, 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., Tiers, B. M., Uribe, J., Váňa, J., Villarreal, J. C., Wigginton, M., Zhang, L., Rui-Liang, Z. (2016). World checklist of hornworts and liverworts. PhytoKeys 59: 1–828.

Spruce, R. (1884). Hepaticae Amazonicae et Andinae. Trans. Proc. Botanical Society Edinburg. 15:1-588.

Stephani, F. (1922). Species Hepaticarum, vol. 6. *Lepidozia*: 319–436. Geneva.

Taylor, J. (1960). The genus *Lepidozia* in Latin America: A taxonomic monograph. Library of Congress Microcard no Jane Taylor. Mic. 60-3301.

Valente, E. B., Pôrto, K. C., Bastos, C. J. P. (2011). Checklist de briófitas da Chapada Diamantina, Bahia, Brasil. Boletim do Instituto de Botânica 21: 111–124

Valente, E. B., Pôrto, K., Bastos, C. J. (2013). Species richness and distribution of bryophytes within different phytophysiognomies in the Chapada Diamantina region of Brazil. Acta Botanica Brasilica 27(2): 294–310.

Yano, O., Peralta, D. F., Bordin, J. (2019). Brioflora da Ilha do Cardoso – Cananéia, São Paulo, Brasil. São Carlos. Rima editora. pp. 529–534.

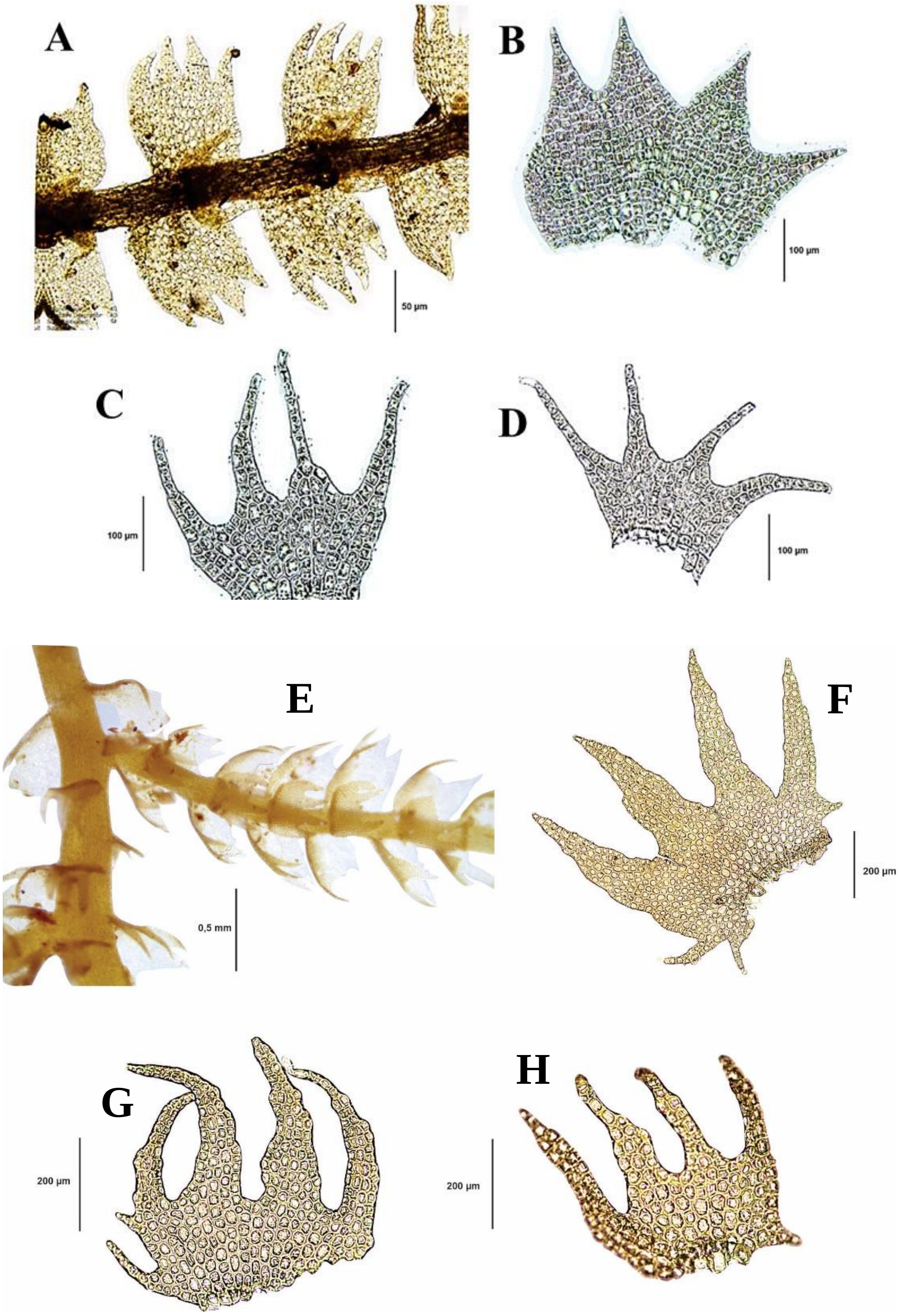


Figure 1. *Lepidozia aequiloba*. A. General aspect of the gametophyte. B. Leaf. C–D. Underleaves. *Lepidozia alstonii*. E. General aspect of the gametophyte, F. Leaf. G–H. Underleaves.

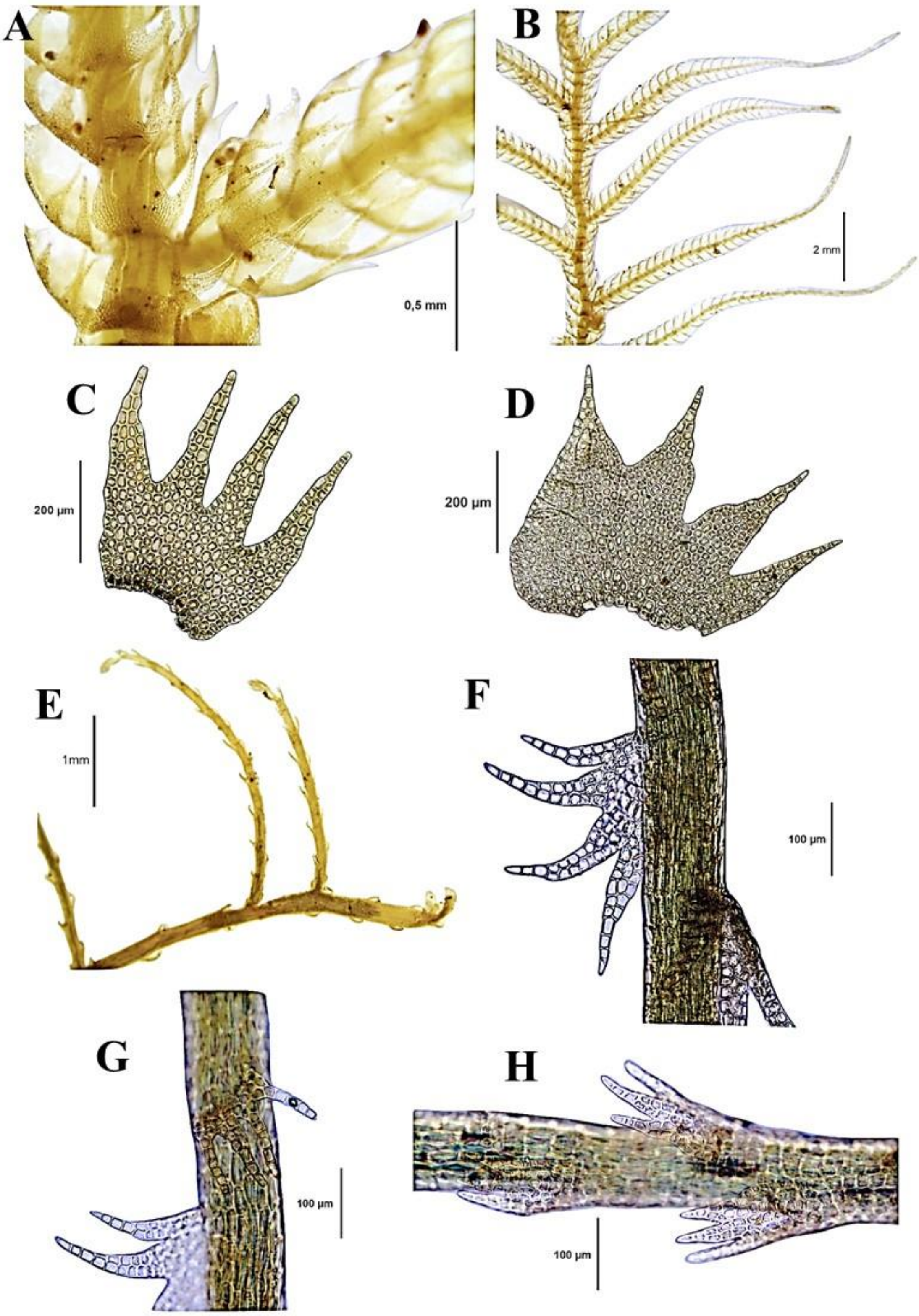


Figure 2. Lepidozia brasiliensis. A. Leaf and underleaf detail. B. General aspect of the gametophyte. C. Leaf, D. Underleaf. Lepidozia patens. E. General aspect of the gametophyte. F. Leaf of main branch. G. Underleaf detail. H. Leaf detail on secondary branch.

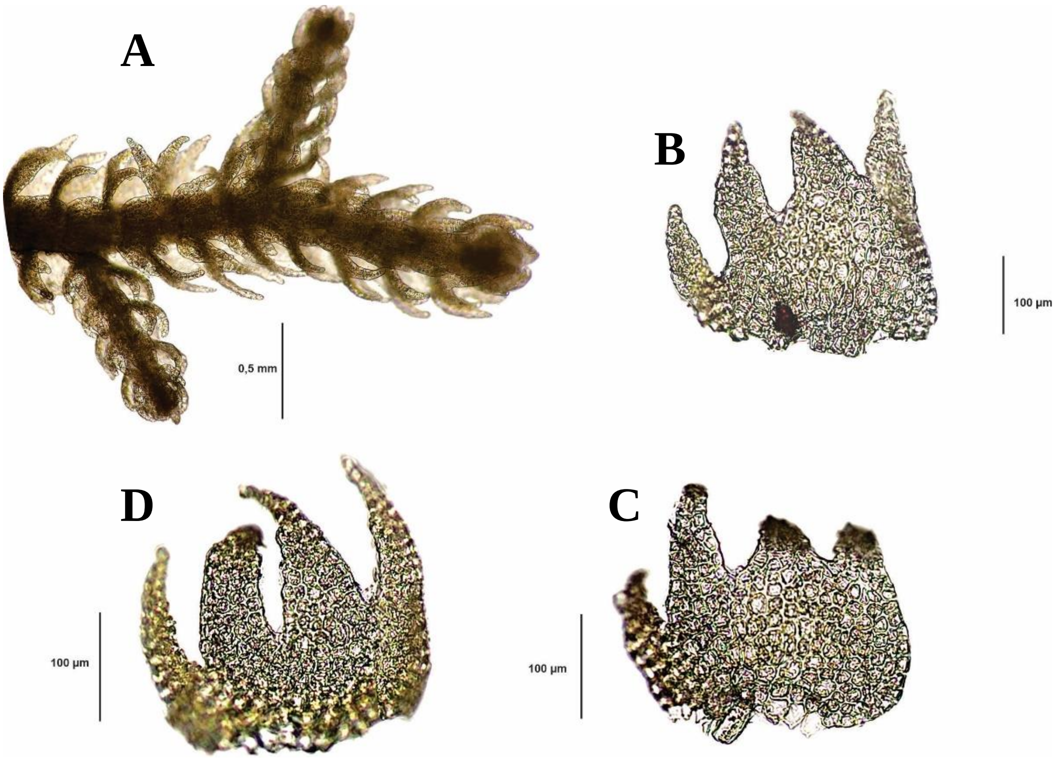


Figure 3. Lepidozia densa. A. General aspect of the gametophyte. B - C. Leaf, D. Underleaf.

CAPÍTULO 2

PALYNOLOGY OF THE BRAZILIAN SPECIES OF *MICROPTERYGIUM* LINDENBERG

Pesquisas Botânica

CAPÍTULO 2

PALYNOLOGY OF THE BRAZILIAN SPECIES OF *MICROPTERYGIUM* LINDENBERG

Leandro de Almeida Amélio[1]

Emilia de Brito Valente[1]

Denilson Fernandes Peralta[2]

[1] Departamento de Biologia, Universidade Estadual de Feira de Santana, Feira de Santana, BA, Brazil

[2] Instituto de Botânica, Av. Miguel Stéfano, 3687 - CEP 04301902 - São Paulo, SP, Brazil

[*]Corresponding author's email: ednlora@gmail.com

Abstract: *Micropterygium* Lindenb. is a leafy liverwort that are distributed mainly in South America. Lepidoziaceae is of great importance due to its taxonomic and ecological implications among bryophytes. There have been few palynological studies involving Lepidoziaceae and neither with *Micropterygium*. Here, we describe the spore morphology of seven species of *Micropterygium* and discuss the taxonomic value of palynological characters for these taxa. The spores were processed by standard palynological techniques and analyzed using light and electron microscopy. The spores were found to be isomorphic, apolar to weakly heteropolar, very small, vary in 7 μm to 13 μm (small size). The spore surface is reticule ornamented with nanogranules that vary in disposition. All the species was present with Scanning Electron Microscope for the first time.

Keywords: Bryophytes; Liverworts; Ornamentation, Scanning Electron Microscope; Sporoderm.

Introduction

Although bryophytes are among the oldest terrestrial plants on the Earth, they have highly evolved structures of gametophyte as well as sporophyte. Morphology and ultrastructure of liverworts are significant in the taxonomy and phylogeny of bryophytes (Jing, et al. 2007), and can be sucessfully utilized for systematic treatment of various taxa.

For bryophytes, spores are an important taxonomic tool, but for Marchantiophyta, palynology was never the focus of many investigations (Crandall-Stotler et al., 2009, Brown et al., 2015); however, these characters can be used to promote the analysis of evolutionary characters (Brown et al., 2015).

Micropterygium Lindenb. is a genus of the Lepidoziaceae, a family of leafy liverworts that includes robust plants (Gradstein & Costa, 2003, Peralta et al, 2022). Their leaves are alternate, succubous and with a toothed dorsal margin, with or without papillose cells. While underleaves are generally slim to small, with short segments, the leaves are asimetrical and succubous (Fulford, 1966; Gradstein & Costa, 2003; Peralta, et al. 2022). *Micropterygium* is an important group of bryophytes in the tropics due to its high level of endemicity (Désamoré, et al. 2010). The genus has ca. 50 published names (Fulford, 1966; Peralta, et al. 2022). The center of diversity for *Micropterygium* is in the Guiana Plateau, where about ten endemic species occur (Gradstein, et al. 2001). *Micropterygium* is the main liverwort of the tepuis of the Guiana Plateau, represented by 18 species (Désamoré, et al. 2010). Gradstein & Costa (2003) and the Peralta et al. (2022) reports ca seven species to Brazil (*Micropterygium campanense* Spruce ex Reimers, *Micropterygium lechleri* Reimers, *Micropterygium parvistipulum* Spruce, *Micropterygium reimersianum* Herzog, *Micropterygium trachyphyllum* Reimers) of which two are considered endemic (*M. leiophyllum* Spruce and *M. pterygophyllum* (Nees) Trevis.)

The study of bryophyte spores is still in it is infancy and very few scientists, claim a broad expertise in this field (Mogensen, 1981; Skvarla, et al. 1988; Harley & Ferguson, 1990). This is due to their usually small size, the apparent uniformity in surface characters when observed under light microscope, and also the spore ornamentation is quite often difficult to correlate with macroscopic characters (Saito & Hirohama, 1974; Hassel de Mennéndez, 1976).

Knowledge gaps remain in our understanding of spore morphology of mosses, liverwort, and hornworts. Although many researches are being conducted to overcome these major discontinuities, the morphology of spores is not a character in many phylogenies yet (Boros, et al. 1993). Many studies on spores have addressed different aspects of various groups (Udar & Srivastava, 1984; Udar & Agarwal, 1985; Blackmore & Barnes, 1991; Brown & Lemmon, 1988; 1991; Brown et al., 2015; Estébanez et al. 1997; Luizi-Ponzo & Barth, 1998; 1999; Luizi-Ponzo & Melhem, 2006; Caldeira et al., 2006; 2009; 2013; Yano & Luizi-Ponzo, 2006; Punt et al. 2007; 2011; Rocha et al., 2008; Rodrigues & Luizi-Ponzo, 2015; Savaroğlu, 2015; Savaroğlu et al., 2017; Silva-e-Costa et al., 2017; Silva-e-Costa & Luizi-Ponzo, 2019; Passarella & Luizi-Ponzo, 2022). However, little is known about morphology of the spores of the Lepidoziaceae. In fact, it is worthy to note that sporophytes are infrequente among species of liverworts (Vojtkó 1993; Zhao et al., 2011).

Lepidoziaceae is a broad family of leafy liverworts, which has a very brief description of spores, without illustratons (Schuster, 2000; Brown et al., 2015). The possibility of advancing and expanding the description of Lepidoziaceae stimulated this study for seven Brazilian species of *Micropterygium*. This paper presents a palynological study of the spores of *Micropterygium* scpecies: (i) describe spore ornamentation and size, (ii) sporoderm structure supported by spore morphology. This study also aims to provide data to assess their kinship and to support studies to identify spores in the environment and to implement them in phylogenetics research.

Materials and methods

We analyzed seven species of *Micropterygium* (*Micropterygium campanense* Spruce ex Reimers, *Micropterygium lechleri* Reimers, *Micropterygium parvistipulum* Spruce, *Micropterygium reimersianum* Herzog, *Micropterygium trachyphyllum* Reimers, *M. leiophyllum* Spruce and *M. pterygophyllum* (Nees) Trevis.), the available material which had mature capsules, totalling 14 botanical especimens from exsiccates kept in the following Brazilian herbaria: SP and HUEFS. The capsules were observed, and those in the best condition were selected. To obtain a better sampling of each specie, we analyzed at least two specimens.

The spores were characterized using the method of Wodehouse (1935). To compare the known specimens, 30 spores were measured on at least three slides following Bansal and Nath (2013) and Caldeira (2013). We measured the largest and smallest diameters in the proximal and distal polar views. The measurements were made with the Zeiss binocular microscope fitted with an ocular micrometer. Arithmetic mean (X), standard deviation (S), standard error (Sx), coefficient of variability (CV%), and 95% confidence interval (IC 95%) are presented, as well as the minimum and maximum spore size (Xmin-Xmax) of each analysed material.

Analyses of the spores by Scanning Electron Microscope (SEM) observation of the surface was made without critical point. The capsules were opened and the spores dispersed on stubs covered with double sided tape. A thin layer (20 nm) of gold palladium was coated in a PS–2 coating unit for about 15–20 minutes. These mounted samples were then stereo–scanned under SEM (Model Phillips XL 20). The SEM analyses were undertaken at the Electronic Microscopy Laboratory of the Fundação Osvaldo Cruz of the Salvador.

The classification system follows Erdtman’s terminology was applied to define the size classes in the bryophyte spores (Erdtman, 1952, 1965). Taxonomic notes, descriptions and illustrations are provided for each species, following Luizi-Ponzo and Melhem (2006), Punt et al. (2007), Bansal and Nath (2013) and Caldeira (2013).

Results

The observation of spores under light microscope and SEM provided a detailed analysis of the morphology and ornamentation of spores’s wall of the seven *Micropterigyum* species addressed in this study. The light microscope observations provide description of shape, scope, size, and general characteristics of ornamentation and coloring. While observations using SEM provided detailed description of exina, showing the morphology and the distribution pattern of the elements that make up the ornamentation.

General characteristics of spores: Spores isomorphic, apolar to slightly heteropolar, very small in size (8 – 13 μm; Tab. 1, Fig. 1), plane-convex. Spores surface ornamentation is formed by reticules and nanogranules. The observed differences were related to the distribution of the ornamentation elements, the measurements of the spores, and the thickness of the reticules.

Micropterygium campanense and *M. parvistipullum* showed the most variation in the largest diameter, and *M. reimersianum* the most variation in the smallest diameter (Table

1). In *M. lechkeri, M. leiophyllum*, *M. pterygophyllum* and *M. trachyphyllum*, the values of the largest and smallest diameters of the standard material did not fall within the confidence interval (Table 1). In the spores of the species analyzed inthis study, the exine is reticulate, smooth or with nanogranules arranged in different patterns.

Descriptions of spores: *Micropterygium lechleri* and *M. parvistipulum* showed the smallest reticules ornamentation. In this species, the reticula is continuous to each other and more uniform (Fig. 1).

The reticulum disposition in *Micropterygium campanense*, *M. pterygophyllum* and *M. reimersianum* (Fig. 1) is similar, and does not allow differentiation between these species. In both, the ornamental elements are distributed randomly over the sporoderm, and the exine is reticulate with nanogranules.

Micropterygium leiophyllum and *M. trachyphyllum* (Fig. 1) show similarities in the wide of reticula walls. In tboth, the reticula are widest and unevenly dispersed through the sporoderm, leaving the smooth exine exposed without nanogranules (Fig. l).

Discussion and conclusion

In this study sporoderm pattern of seven species *Micropterygium* (Lepidoziaceae) from the Brazilian region were investigated. The basis of their sporoderm ornamentation is reticulate type found to genus. All the spores of taxa studied were brownish, and reticulate. It is difficult to identify the species with *Micropterygium* spores just based on the sporoderm pattern, as the spores are very similar in size (8–10 µm), color, and have reticulate ornamentation.

Though spore ornamentation could play a role in the identification of these genus, other morphological characters also play an important role in separating them. For example, *Micropterygium* is usually recognized by the wing on the leave. Thus SEM studies in this paper emerged as an important taxonomic characters that present micromorphological related to sporoderm ornamentation that hardly are discerned under light microscopy (LM), and thus proved this characteristic could be used as a taxonomic tool in defining the status of this genus.

Studies like this increase the possibility of investigation in the field of genera and species. The knowledge of microstructures helps in the resolution of obstacles related to phylogeny and increases the range of characters in related studies (Hässel de Menendez, 1976; Brown et al., 2015). The characterization of the leafy liverwort flora has advanced considerably in recent years, showing the possibility that these reinforce the phylogenetic hypotheses.

Acknowledgment

The authors are thankful for the Fundação Oswaldo Cruz for the help with the infrastructure. This work was supported by the CAPES.

Specimens investigated

Micropterygium campanense Spruce ex Reimers. Brazil: Minas Gerais, Peralta, D.F., 11845, 11867, 28 August 2010 (SP).

Micropterygium lechleri Reimers. Brazil: Mato Grosso, Canarana, Mews, C.L., 10, 28 October 2006 (SP). Pará, Óbidos, Souza, M.G.C., 314, 18 January 2009 (SP).

Micropterygium leiophyllum Spruce. Brazil: Amazonas, Caracaraí, Yano O., 1474, 27 June 1979 (SP). Manaus, Prance G.T, s.n. 5 April 1971 (SP).

Micropterygium parvistipullum Spruce. Brazil: Amazonas, Reversa Duke, Flores A.M, 455, 9 June 1994 (SP). Manaus, Yano, O., 14586. 05 May 1990 (SP).

Micropterygium pterygophyllum (Nees) Trevis. Brazil: Amazonas, Presidente Figueiredo, Yano, O. 32712, 32751, 05 Setptember 2010 (SP).

Micropterygium reimersianum Herzog. Brazil. Mato Grosso, Chapada dos Guimarães, Yano, O., 27578, 16 May 2004 (SP). Bahia, Chapada Diamantina, Schäfer-Verwimp, A. 8709, 11 July 1987 (SP).

Micropterygium trachyphyllum Reimers. Brazil: Bahia, Lençois, Valente E-B, 554 1 November 2007 (HUEFS). Minas Gerais, Marcelli M-P, 11883, 28 July 2010 (SP).

References

BANSAL, P.; NATH, V. 2013. Study of sporoderm pattern under SEM in the genus Bryum. Phytotaxa 87 (1): 1–10.

BLACKMORE, S.; BARNES, S.H. 1991. Pollen and spores. Patterns of diversification. The systematics association. Special volume No. 44. Clarendon Press, Oxford, pp. 1–402.

BOROS, A.; JA´RAI-KOMLO´DI, M.; TOTH, Z.; NILSSON, S. 1993. An atlas of recent European bryophyte spores. Akadémiai Kiadó, Budapest, 244–249 pp.

BROWN, R.C, Lemmon BE. 1988. Sporogenesis in bryophytes. Advances in Bryology 3: 159-223.

BROWN, R.C.; LEMMON, B.E. 1991. Sporogenesis in simple land plants. In: BLACKMORE S, BARNES S.H. (eds.) Pollen and spores. patterns of diversification. Oxford, Clarendon Press. p 9-24.

BROWN, R.C.; LEMMON, B.E.; SHIMAMURA, M.; VILLARREAL, J.C.; RENZAGLIA, K.S. 2015. Spores of relictual bryophytes: Diverse adaptations to life on land. Review of Palaeobotany and Palynology 216: 1-17.

CALDEIRA, I.C.; GONÇALVES-ESTEVES, V.; LUIZI-PONZO, A.P. 2006. Morfologia dos esporos das espécies de Leucobryaceae Schimp. (Bryophyta) do Parque Estadual de Ilha Grande, Município de Angra dos Reis, Estado do Rio de Janeiro. Revista Brasileira de Botânica 29: 301-307.

CALDEIRA, I.C.; GONÇALVES-ESTEVES, V.; LUIZI-PONZO, A.P. 2009 Morfologia dos esporos de Sematophyllaceae Broth. ocorrentes em três fragmentos de Mata Atlântica, no Rio de Janeiro, Brasil. Revista Brasileira de Botânica 32: 299-306.

CALDEIRA, I.C.; GONÇALVES-ESTEVES, V.; LUIZI-PONZO, A.P. 2013. Palynology of selected species of Fissidens (Hedw.). Plant Systematics and Evolution 299: 187-195.

CRANDALL-STOTLER, B.; STOTLER, R.E.; LONG, D.G. 2009. Morphology and classification of the Marchantiophyta. In: Shaw JA, Goffinet B. (eds.) Bryophyte biology. Cambridge, Cambridge University Press. p. 1-54.

DÉSAMORÉ, A.; VANDERPOORTEN, A.; LAENEN, B.; GRADSTEIN, S.R.; KOK, P. J. R. 2010. Biogeography of the Lost World (Pantepui region, northeastern South America): Insights from bryophytes. Phytotaxa 9: 254–265

ERDTMAN, G. 1952. On pollen and spore terminology. Palaeobotanist 1: 169–176.

ERDTMAN, G. 1965. Pollen and spore morphology/ plant taxonomy. Gymnospermae, Bryophyta (Text). An introduction to palynology III. Stockholm, Almqvist and Wiksell.

ESTEBANEZ, B.; ALFAYATE, C.; RON, E. 1997 Observations on spore ultrastructure in six species of Grimmia (Bryopsida). Grana 36: 347–357. http://dx.doi.org/10.1080/00173139709362628.

FULFORD, M.H. 1966. Manual of the leafy Hepaticae of Latin America - part II. Memoirs of The New York Botanical Garden. 11. pp. 180-213.

GRADSTEIN, S.R.; CHURCHILL, S.P; SALAZAR, A.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. The Hepaticae and Anthocerotae of Brazil. Memoirs of The New York Botanical Garden 87: 1–336.

HARLEY, M.; FERGUSON, I.K. 1990. The role of the SEM in pollen morphology and plant systematics. In: Claugher, D. (Ed.) Scanning electron microscopy in taxonomy and functional microscopy. Clarendon Press, Oxford, pp. 45–68.

HÄSSEL DE MENENDEZ, G.G. 1976. Taxonomic problems and progress in the study of the Hepaticae. J Hattori Bot Lab 41:19–36.

JING, Y.; TONG, C.; XI, W.Q. 2007. Study of spore types of Chinese mosses. In: Nath, V. & Asthana, A.K. Eds. Current trends in Bryology. Bishen Singh Mahendra Pal Singh, Dehra Dun., pp. 1–15.

LUIZI-PONZO, A.P.; BARTH, O.M. 1998. Spore morphology of some Bruchiaceae species (Bryophyta) from Brazil. Grana 37: 222–227. http://dx.doi.org/10.1080/00173139809362670

LUIZI-PONZO, A.P.; BARTH, O.M. 1999. Spore morphology of some Dicranaceae species (Bryophyta) from Brazil. Grana 38: 42–49. http://dx.doi.org/10.1080/001731300750044690

LUIZI-PONZO, A.P.; MELHEM, T.S. 2006. Spore morphology and ultrastructure of the tropical moss Helicophyllum torquatum (Hook.) Brid. (Helicophyllaceae) in relation to systematics and evolution. Cryptogamie, Bryologie 27: 413-420.

MOGENSEN, G.S. 1981. The biological significance of morphological characters in Bryophytes: The Spore. Bryologist 84 (2): 187–207. http://dx.doi.org/10.2307/3242821

PASSARELLA, M.A.; LUIZI-PONZO, A.P. 2022. Oncophoraceae (Bryophyta): a palynological

treatment of species occurring in the Americas. Anais da Academia Brasileira de Ciências 94(1).

PERALTA, D.F.; AMELIO, L.A.; SOUZA, A.M.; CARMO, D.M.; SANTOS, E.L.; VALENTE, E.B.; OLIVEIRA, H.C.; LIMA, J.S.; PROCHAZKA, L.S. Lepidoziaceae in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro.Available at: <https://floradobrasil.jbrj.gov.br/FB97671>. Accessed on: 28 Jul. 2022

PUNT, W.; HOEN, P.; BLACKMORE, S.; NILSSON, S.; THOMAS, A. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143: 1-81.

ROCHA, L.M.; GONÇALVES-ESTEVES, V.; LUIZI-PONZO, A.P. 2008. Morfologia de esporos de espécies de Polytrichaceae Schwägr. (Bryophyta) do Brasil. Revista Brasileira de Botânica 31: 537-548.

RODRIGUES, R.S.; LUIZI-PONZO, A.P. 2015. Palinologia de espécies selecionadas da família Pottiaceae (Bryophyta). Pesquisas, Botânica 67: 303-317.

SAITO, K.; HIROHAMA, T. 1974. A comparative study of the spores of taxa in the Pottiaceae by use of scanning electron microscope. Journal of Hattori Botanical Laboratory 38: 475–488.

SAVAROĞLU, F. 2015 Spore morphology of some Orthotrichaceae Arn. Species (Bryophyta) from Turkey. Bangladesh Journal of Botany 44: 499-506.

SAVAROĞLU, F.; ERKARA, I.P.; KOYUNCU, O. 2017. Observations of spore morphology of some species of Hypnaceae Schimp. (Bryophyta) in Turkey. Bangladesh Journal of Botany 46: 9-17.

SCHUSTER, R.M. 2000. Austral Hepaticae, Part I. Nova Hedwigia Beiheft 118: viii, 1–524.

SILVA-E-COSTA, J.C.; LUIZI-PONZO, A.P.; RESENDE, C.F.; PEIXOTO, P.H.P. 2017. Spore germination, early development and some notes on the effects of in vitro culture medium on Frullania ericoides (Nees) Mont. (Frullaniaceae, Marchantiophyta). Acta Botanica Brasilica 31: 19-28

SILVA-E-COSTA, J.C.; LUIZI-PONZO, A.P. 2019. Spores of Plagiochila (Dumort.) Dumort.: the taxonomic relevance of morphology and ultrastructure. Acta Botanica Brasilica - 33(3): 391-404.

SKVARLA, J.J.; ROWLEY, J.R.; CHISSOE, W.F. 1988. Adaptability of scanning electron microscopy to studies of pollen morphology. Aliso 12: 119–175.

VOJTKÓ, A. 1993. The spore morphology of Hepaticae species. Acta Biologica Szegediensis 39: 59-69.

UDAR, R.; SRIVASTAVA, S.C. 1984. Scanning electron microscopy of spores of Indian liverworts. Journal of Hattori Botanical Laboratory 56: 97–103.

UDAR, R.; AGARWAL, A. 1985. The genus Riccia in Pachmarhi with SEM details of spores of two species. Journal of Indian Botanical Society 64: 246–250.

WODEHOUSE, R.P. 1935. Pollen grains: Their structure, identification and significance in science and medicine. New York, McGraw-Hill.

YANO, O.; LUIZI-PONZO, A.P. 2006. Chonecolea doellingeri (Chonecoleaceae, Hepaticae), taxonomia e distribuição geográfica no Brasil. Acta Botanica Brasilica 20: 783-788.

YANO, O.; LUIZI-PONZO, A.P. 2011. Dumortiera hirsuta (Dumortieraceae, Marchantiophyta), taxonomy, palynology and geographic distribution. Boletim do Instituto de Botânica 21: 9-18.

ZHAO, D.P.; BAI, X.L.; WANG, L.H. 2011. Observations of spore morphology of some hepatics species (Marchantiophyta) in China. Arctoa 20: 205-210.

Table I. Morphometric data of spores of *Micropterygium* (measurements in micrometers). Arithmetic mean (X), standard deviation (S), standard error (Sx), coefficient of variability (CV%), 95% confidence interval (IC 95%), minimum and maximum spore size (Xmin-Xmax).

	Xmin–Xmax	X+- Sx	S	CV%	IC 95%
Micropterygium campanense Spruce ex Reimers	11.00 – 14.00	13,21 ± 0.91	1.82	13.81	11.42 – 14.98
Micropterygium lechleri Reimers	8.10 – 10.50	9,34 ± 2.20	1.12	12.02	5.03 – 13.65
Micropterygium leiophyllum Spruce	11.00 – 12.00	11,7 ± 0.15	0.44	3.76	11.40 – 11.97
Micropterygium parvistipulum Spruce	12.50 – 13.40	13.08 ± 0.13	0.43	3.33	12.83 – 13.32
Micropterygium pterygophyllum (Nees) Trevis.	11.10 – 12.30	11.79 ± 0.17	0.60	5.15	11.47 – 12.12
Micropterygium reimersianum Herzog	5.40 – 7.00	5.95 ± 0.22	0.75	12.70	5.53 – 6.37
Micropterygium trachyphyllum Reimers	9.50 – 10.70	10.24 ± 0.21	0.55	5.34	9.84 – 10.64

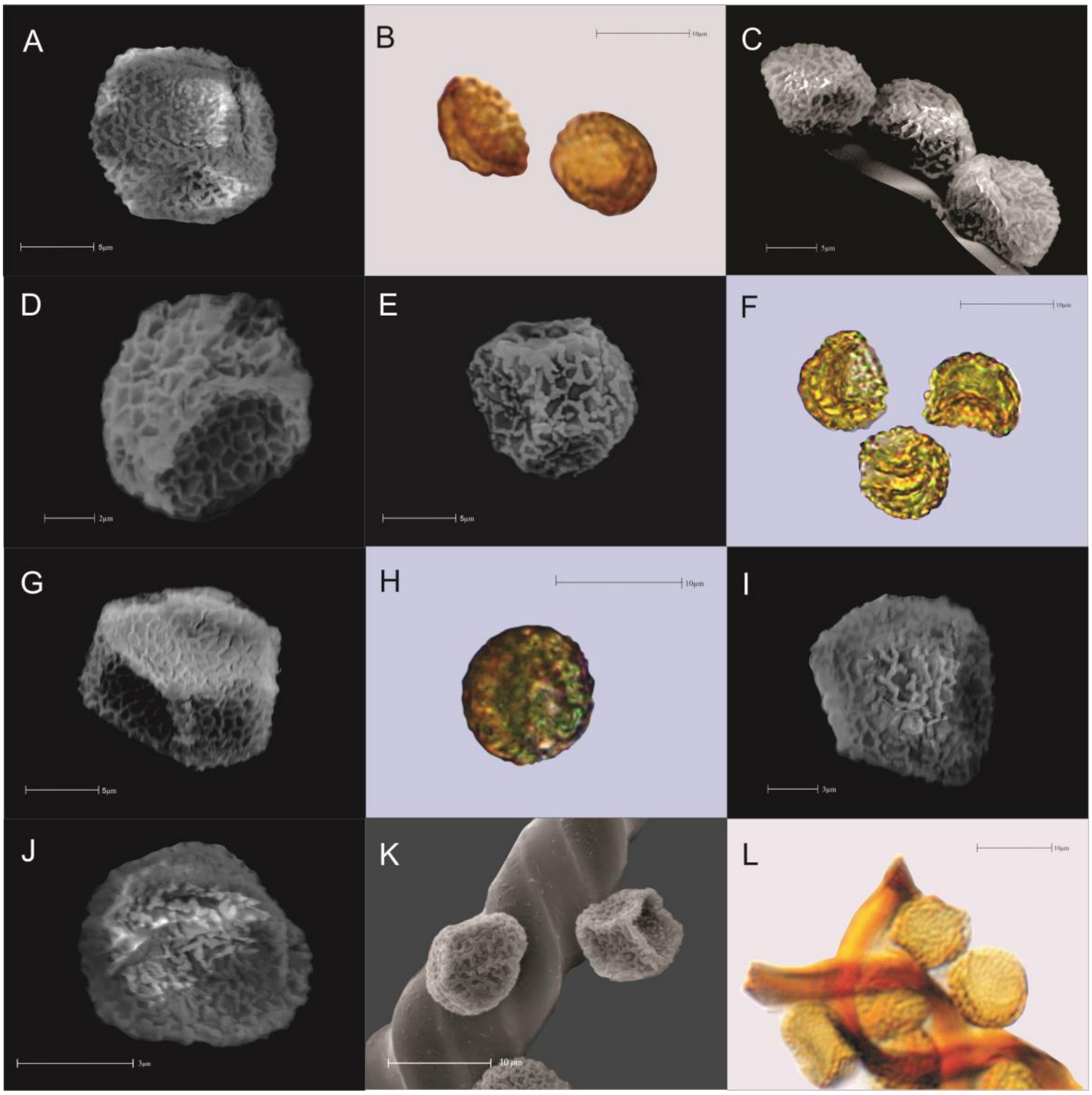


Figure 1: Photomicrographs and electromicrographs of spores of species of Micropterygium Lindenb. - A. *Micropterygium campanense*, SEM; B. *M. campanense*, LM; C-D. *M. lechleri*, SEM; E. *M. leiophyllum*, SEM; F. *M. leiophyllum*, LM; G. *M. parvistipulum*, SEM; H. *M. parvistipulum*, LM; I. *M. pterygophyllum*, SEM; J. *M. reimersianum*, SEM; K. *M. trachyphyllum*, SEM; L. *M. trachyphyllum*, LM.

CAPÍTULO 3

LEPIDOZIACEAE UPDATE, RECOGNIZING *MICROPTERYGIUM* CLADE

Molecular Phylogenetics and Evolution

CAPÍTULO 3

LEPIDOZIACEAE UPDATE, RECOGNIZING MICROPTERYGIUM CLADE

Leandro de Almeida Amélio, Emilia de Brito Valente and Denilson Fernandes Peralta

[1] Departamento de Biologia, Universidade Estadual de Feira de Santana, Feira de Santana, BA, Brazil

[2] Instituto de Pesquisas Ambientais, Av. Miguel Stéfano, 3687 - CEP 04301902 - São Paulo, SP, Brazil

[3] Corresponding author's e-mail: ednlora@gmail.com

Abstract: Four molecular markers (chloroplast rbcL, rps4 and trnL-trnF, and nuclear 26S) were used to investigate membership of the Lepidoziaceae, subfamily Bazzanioideae and relationships between its constituent species. The Bazzanioideae (comprising *Acromastigum*, *Bazzania*, *Micropterygium*) are polyphyletic as are two of its three constituent genera. We find strong support for a monophyletic lineage comprising *Acromastigum* and *Micropterygium*. Within this lineage we find support for Bazzanioideae. The Lepidozioideae are polyphyletic, *Lepidozia* is supported and *Telaranea* species form consecutive sister relationships to a monophyletic group. More data is necessary to determine whether or not this incongruence results from ancient hybridisation. We provide a re-circumscription of the Lepidoziaceae that includes *Micropterygium* as a Bazzanioideae genus.

Key words: DNA sequences, Liverworts, Phylogeny, Sister-clade.

Introduction

The Lepidoziaceae classification and the internal relationship of this family has been changing rapidly since the first molecular phylogenetics studies of Crandall-Stotler & Stotler (2000); Crandall-Stotler et al. (2009) and Vilnet et al. (2009). Molecular phylogenetics provides a means of deriving robust hypotheses of relationship where ambiguous characters, convergent and parallel morphological evolution, and overall structural simplicity combine to estimate phylogeny from morphology to the most liverworts (Devos et al. 2011).

The Lepidoziaceae are a cosmopolitan family of leafy liverworts. The total species number for liverworts is notoriously variable (von Konrat *et al*. 2010), the number of accepted species is nearly 860 (ELPT database). The taxonomic diversity is highest in post-gondwanan land fragments, but the family is cosmopolitan in distribution. In addition to being species-rich and exceptionally widespread, the family also encompasses a large portion of the total morphological range covered by the liverworts. As well as the typical leafy morphology of the type genus, *Lepidozia*, the family accommodates such morphotypes as, *Pteropsiella*, which is similar to the simple thalloid morphology of the Metzgeriales, and *Protocephalozia*, which resembles a charophycean alga with its branched filamentous protonema.

The Lepidoziaceae circumscription as we know actually came from Schuster (1969a) who organized the family based on isophyllous gynoecium branches, rhizoids restricted to underleaf bases and seta morphology. However, the gametophyte morphology is extremely variable, e.g. leaf insertion mostly incubous but also transverse and occasionally succubous; leaves 2–4(12) lobed, sometimes so deeply incised the 'disc' is less than a cell in length as *Arachniopsis* Spruce, or vestigial in some groups (*Zoopsis* (Hook. f. & Taylor) Gottsche et al.) and variability in branching modes.

Nowadays the classification of the family includes molecular evidence and it is based on Cooper (2011, 2012a,b, 2013). The studies including molecular phylogenies have supported the morphological Schuster's circumscription of the family (Heslewood & Brown 2007, He-Nygrén et al. 2006, Hendry et al. 2007, Cooper et al. 2011, 2012a, 2013), which includes seven subfamilies and 29 genera: 1. Subfam. Bazzanioideae Rodway (3 genera: *Acromastigum* A. Evans, *Bazzania* Gray, *Mastigopelma* Mitt.); 2. Subfam. Drucelloideae R. M. Schust. (monotypic: *Drucella* E.A.Hodgs.), 3. Subfam. Lembidioideae R. M. Schust. (7 genera: *Dendrolembidium* Herzog, *Hygrolembidium* R. M. Schust., *Isolembidium* R. M. Schust., *Kurzia* Mart., *Lembidium* Mitt., *Megalembidium* R.M.Schust., *Pseudocephalozia* R.M.Schust.); 4. Subfam. Lepidozioideae Müll.Frib. (4 genera: Ceramanus E. D. Cooper, *Lepidozia* (Dumort.) Dumort., *Neolepidozia* Fulford et J. Taylor, *Tricholepidozia* (R.M.Schust.) E. D. Cooper; 5. Subfam. Micropterygioideae Grolle (2 genera: *Micropterygium* Gottsche, *Mytilopsis* Spruce); 6. Subfam. Protocephalozioideae R. M. Schust. (monotypic: *Protocephalozia* (Spruce) K.I.Goebel); 7. Subfam. Zoopsidoideae R. M. Schust. (11 genera: *Amazoopsis* J. J. Engel et G.L.Merr, *Hyalolepidozia* S.W.Arnell ex Grolle, *Neogrollea* E.A.Hodgs., *Odontoseries* Fulford, *Paracromastigum* Fulford et J.Taylor, *Psiloclada* Mitt., *Pteropsiella* Spruce, *Telaranea* Spruce ex Schiffn., *Zoopsidella* R.M.Schust., *Zoopsis* Hook.f. ex Gottsche, Lindenb. et Nees).

The classification proposed in Cooper (2011, 2013) was mainly based on specimens from Australia and New Zealand, and the author indicates absence of molecular data, to the genera *Acrosmastigum*, *Bazzania*, *Kurzia*, *Lepidozia*, *Telaranea*, *Zoopsis* and, specially to the Subfamily Micropterygiodeae with the genera *Micropterygium*, *Mytilopsis*, *Pteropsiella* and *Protocephalozia*. Morphologically the best defined subfamily, Bazzanioideae is monophyletic. A close relationship between *Bazzania* and *Acromastigum* has long been hypothesized based on shared pseudo-dichotomous terminal branching and formation of frequent geotropic, flagelliform ventral branches (Evans 1939; Fulford 1963; Schuster, 2000), as also occur in *Micropterygium*. *Bazzania* is a genus of between 100 and 450 species (Stephani, 1909; Schuster, 2000), *Acromastigum* has around 65 species and *Micropterygium* around 18 species (Soderstron et al. 2016, Peralta et al. 2022).

Micropterygium was treated in the subfamily Micropterygioideae Grolle (1964) by Cooper (2013) but without molecular evidence, just based in the morphological characterization of the original description of Lindenb. et al. in Gottsche et al. (1845: 233), in the Reimers (1933) and Schuster (1969). These works split out the genus by its concave, bilobulate leaves, with a sharp keel, with a ventral wing present, absent or occasionally rudimentary. The subgeneric classification follows Reimers (1933) who recognized three sections within *Micropterygium*: Sect. Conchifolia Reimers (including plants with the insertion mostly arched, and less oblique, almost transverse.), sect. Subaequifolia Reimers (including plants characterized by radially symmetrical foliose stems; large underleaves, the dorsal wing very narrow, almost absent in some leaves), and sect. Genuina Reimers (including plants with lower lobe rarely reduced in extent, and the dorsal wing is prominently on the upper lobe, the two lobes together form an oblique pseudo lamina). Schuster (2000) proposed to divide the genus into two subgenera: *Pseudolembidium* (including plants isophyllous or sub isophyllous; underleaves similar or identical to lateral leaves in size and form), and *Micropterygium* (characterized by marked anisophylly).

Micropterygium is an endemic neotropical genus of 18–19 species, ranging from Cuba and Jamaica to south to Brazil, with its great diversity in Bolivia, Guiana and

Venezuela (Frey & Stech 2009, Peralta et al. 2022). Some of the species are restricted in distribution while others are widespread on Central and South America (Fulford 1966). The center of diversity of *Micropterygium* is in the Guiana Highlands, where about 10 endemic species occur (Gradstein et al. 2001, Désamoré et al. 2010), the genus is the main hepatic genus of the tepuis of the Guiana Highlands, with 18 species (Désamoré et al. 2010).

Since we are studying the family and analyzing recent specimens we provide molecular data of *Micropterygium* and here we present the results in order to improve its familial arrangement.

Material and methods

One nuclear and three chloroplast markers were sequenced (Table 1) for four species of the genus *Micropterygium*. The DNA extraction using modifications of the CTAB protocol (Doyle & Doyle, 1987; Camara, 2009) and all PCR reactions were completed under standard conditions, each 10 µm reaction contained 0.5 µm each primer, 5 µm Top Taq, 3 µm of H2O. Genomic DNA was added as 0.5 µm to each reaction without standardizing concentration. A standard temperature profile was used: 95ºC for 2 min, then 30 cycles of 95º C for 1 min, 50º C for 1 min and 72º C for 1 min, followed by a final extension step of 72º C for 10 min. The same primers were used for sequencing (table 1).

The sequences were aligned using MUSCLE (Edgar, 2004) and then manually edited in Mesquite v2.72 (Maddison and Maddison, 2009). Maximum likelihood (ML) analyses were run using RAx-ML v7.2.6 (Stamatakis, 2006) and on the CIPRES portal (Miller et al., 2010). Prior to Bayesian analysis, model selection was completed using iqtree-1.6.12. (Minh et al. 2020). The highest ranked model according to the Akaike information criterion (AIC, Akaike, 1973; Burnham and Anderson, 2004) was used for Bayesian analyses. Where the highest ranked model was not the GTR + C + I model, analyses were also performed with the GTR + C + I model and their performance compared using Bayes Factors (Kass and Raftery, 1995). Clades with a posterior probability P0.9 are considered supported and those with posterior probability P0.95 are considered strongly supported.

Bayesian inference (BI) was run using the Mr. Bayes (Huelsenbeck and Ronquist, 2001) as implemented on the CIPRES Portal (Miller et al., 2010). Two independent Markov chain Monte Carlo (MCMC) runs. Each run for ten million generations, using one heated and three cold chains, and sampling every 1000 generations. After plotting log likelihood values and calculating the standard deviation of split frequencies to check convergence, the first 1001 samples were discarded as burnin.

Results

We analyze our data in comparison with 150 taxonomic terminals, 143 representing five subfamilies and 22 genera, for four markers each in Lepidoziaceae and seven to outgroup. A total of 37 new sequences were generated for this study (Appendix tab. 2), of these sequences the genus *Micropterygium* was molecularly sampled for the first time, as well as the South American species of *Lepidozia.*

In this analises for 26S, rbcL, rps4 and trnL the GTR + I + gamma model was preferred, but the DAIC between it and the next best GTR + F + I model was within the interval of strongly supported models (Burnham and Anderson, 2004).

The single nuclear marker (26S) was the least variable of the four regions used. Sequences were available for 70 of the 150 ingroup accessions. Little incongruence is observed between the methods of analysis, which yield largely unresolved phylogenetic estimates with few supported nodes (figure 1). The subfamily is supported in ML and BI analyses of 26S (ML-BS 100) and it is well separated from the outgroup. The *Micropterygium* clade is supported in ML and BI analyses (ML-BS X).

The combined chloroplast data alignment had 3003 positions. A total of 333 sequences for 144 ingroup accessions represents a 72% complete sequence set. The trnL-trnF alignment had 666 positions of which 190 (35%) were informative. Sequences were obtained for 140 accessions. The rbcL alignment, which includes no insertions or deletions, had 1310 positions of which 288 (24%) were informative. The rps4 alignment had 625 positions of which 140 (22%) were informative. Sequences were obtained for 98 accessions. The combined dataset had 324 sequences from 151 accessions. The combined three chloroplast loci in a single analysis results in better resolution and support than individual analyses of either marker (figure 1). The sister clade *Telaranea* and Lepidozia recovered with support. The sister relationship between *Micropterygium* and

Acromastigum is supported and they are present as sister groups in Bazzanioideae with *Bazzania*.

Phylogenetic analyses

Our results support the genus *Micropterygium* as a sister clade of *Acromastigum* (ML-BS 100/1). *Acromastigum* and *Micropterygium* are paraphyletic with others groups non well delimited based on this markers analised, as *Lepidozia* and *Bazzania*. In the early divergent nodes are resolved and supported in ML and Bayesian analyses (nodes A–D, figure 1). The subfamilies corresponding approximately to current generic concepts shown for Cooper (2011) were recovered, Lepidozioideae, Lembidioideae and Drucelloideae (figure 1).

The monotypic genera used in this work *Neogrollea*, *Psiloclada*, *Sprucella*, *Megalembidium* and *Isolembidium* have supported relationships with other taxa. Even *Drucella*, however, persists in a phylogenetically isolated position like shown in Cooper (2011) (fig. 1).

Discussion

Our data incrise *Micropterygium* Lindenb. and *Acromastigum* A. Evans are sisters (ML 89, BI 1) with no differences in rps4 or rbcL, and ca. 10% bp difference in trnL-F. Accessions of *Bazzania* based only in plastidial regions (rps4, trnL and rbcL), and although in ML there is no well relation support between *Acromastigum* and *Micropterygium*.

Our sample also supports the species concepts of *Micropterygium* in South America. Where species have been significant to support the terminals in the clade. Just a few species of South America liverworts were molecularly evidentiated, and we reinforced the importance of projects focus on liverworts phylogeny.

The currently accepted broad definition of the Lepidoziaceae (Schuster, 2000; Cooper 2011) continued corroborated by the monophyly of the family in individual and concatenated analyses of four molecular markers across two genomic compartments. The monophyly of the Lepidoziaceae, gives some support to the main characters' appointment since Schuster (1969) to morphological as reliable predictors of phylogeny, i.e. a wide array of branching modes including distinct, usually large, underleaves with rhizoids restricted to the basal sector; general retention of lateral-terminal and ventral-intercalary branches; flagelliform/stoloniferous branches; strictly isophyllous gynoecium branches of determinate length; long, usually slender, sporophytes with the seta having a fixed number of cortical cell rows (8 or 16 cells); few rows of smaller, medullary cells; capsule wall with two-phase development and trigonous perianths.

A close relationship between *Acromastigum* and *Micropterygium* incrise new in Lepidoziaceae phylogeny. The pseudo-dichotomous terminal branching and often geotropic, flagelliform ventral branches as characters has hypothesized the morphological evidence.

Our data from 143 taxa, representing 22 genera in seven subfamilies, improves upon previous phylogenetic studies of the Lepidoziaceae (Engel and Merrill, 2004; Heslewood and Brown, 2007; Renner et al., 2006; Cooper 2011). *Micropterygium* and South America *Lepidozia* species representing new sequences to liverworts Marchantiophyta. In this work we classify *Micropterygium*.

The Clade Lepidozioideae presented in Cooper (2012a), was here supported by a new addition of *Lepidozia* from Brazil. It reinforces the monophyly of the subfamily and genus, even though these species are miles apart and do not co-occur in the same environment. The clade Bazzaniodeae presented in Cooper (2012a), with *Acromastigum* and *Bazzania* as paraphyletic clades. A core clade forms an apparently well-defined group, while some species group with *Micropterygium*, indicating the paraphyly of *Acromastigum.*

This new arrangement clarifies the possible position of *Micropterygium* on Lepidoziaceae. Understanding Lepidoziaceae, this hyper diverse family of hepatics, a stable classification with high predictive content requires evolutionary hypotheses. Phylogenetic studies at the family and subfamily level indicate that the existing classification does not reflect phylogenetic relationships. Understanding Lepidoziaceae, this hyperdiverse family of hepatics, a stable classification with high predictive content requires evolutionary hypotheses. Phylogenetic studies at the family and subfamily level indicate that the existing classification does not reflect phylogenetic relationships, and new dates may provide a chance to new topologies. This has important implications for understanding the diversity in the Lepidoziaceae.

Understanding the evolution of groups is essential for the classification and conservation of species, this indicates that the evolutionary relationships of groups that are still not well defined and, in some cases, advances in the studies of these relationships are responsible for solving this polytomy, as shown in Lepidoziaceae since the first studies with the family.

We suggest that new studies with *Pteropsiella* provide a plus to the phylogenies represented in Lepidoziaceae. Several phylogenetically important taxa remain unsampled or under-sampled. The inclusion of South and Central American species is necessary to improve the geographically biased sampling within the family.

Acknowledgments

The authors are grateful to the colleagues LAMOL UEFS lab, for their help in fieldwork and/or discussions. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil (CAPES) for fellowships given.

References

Akaike, H. 1973. Information Theory as an Extension of the Maximum Likelihood Principle. In: Petrov, B. N. F., Csaki, F. (eds.). Second International Symposium on Information Theory. Akademiai Kiado., Budapest, pp. 267-281.

Burnham, K. P., Anderson, D. R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33: 261-304.

Câmara, P. E. A. S. 2009. Métodos de extração de DNA de Bryophyta para análises filogenéticas. Heringeriana, Brasília 3(2): 11-17.

Cooper, E. D.; Henwood, M. J.; Brown, E. 2012a. A molecular phylogeny of the Lepidozia generic complex supports re-circumscription of the Lepidozioideae. Molecular Phylogenetics and Evolution 65: 10-22.

Cooper, E. D.; Henwood, M. J.; Brown, E. A. 2012b. Are the liverworts really that old? Cretaceous origins and Cenozoic diversification in Lepidoziaceae reflect a recurrent theme in liverwort evolution. Biological Journal of the Linnean Society 107: 425-441.

Cooper, E. D. 2013. Notes on Early Land Plants Today. 37. Towards a stable, informative classification of the Lepidoziaceae (Marchantiophyta). Phytotaxa 97(2): 44-51.

Cooper, E. D.; Shaw, A. J.; Shaw, B.; Henwood M. J.; Heslewood, M. M.; Brown, E. A. 2011. A multi-locus molecular phylogeny of the Lepidoziaceae: Laying the foundations for a stable classification. Molecular Phylogenetics and Evolution 59: 489-509.

Crandall-Stotler, B.; Stotler, R. E. 2000. Morphology and classification of the Marchantiophyta. In: Shaw A. J., Goffinet B. (eds.) Bryophyte biology. Cambridge University Press, Cambridge, pp. 21-70.

Crandall-Stotler, B.; Stotler, R.E.; Long, D.G. 2009b. Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66(1): 155-198.

Désamoré, A; Vanderpoorten, A; Laenen, B; Gradstein, S.R; Kok, P. J. R. 2010. Biogeography of the Lost World (Pantepui region, northeastern South America): Insights from bryophytes. Phytotaxa 9: 254-265.

Devos, N., Renner, M. A. M., Gradstein, R., Shaw, J., Vanderpoorten, A. 2011. Molecular data challenge traditional subgeneric divisions in the leafy liverwort Radula. Taxon 60(6): 1623–1632

Doyle, J. J.; Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemistry Bulletin 19: 11-15.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792-1797.

Engel, J. J.; Smith Merrill, G. L. 2004. Austral Hepaticae 35. A taxonomic and phylogenetic study of Telaranea (Lepidoziaceae), with a monograph of the genus in temperate Australasia and commentary on extra-Australasian taxa. Fieldiana, Botany 44: 1-265.

Evans A. W. 1939. The classification of the Hepaticae. Bot. Rev. 5: 49–96.

Frey, W., Stech, M. 2009. Marchantiophyta, Bryophyta, Anthocerotophyta. In: Frey, W. (Ed.) Syllabus of Plant Families. Borntraeger. Berlin, Stuttgart, pp. 73-74.

Fulford, M. 1963. Manual of the leafy Hepaticae of Latin America. Part I. Memoirs of The New York Botanical Garden 11: 1-172.

Fulford, M. 1966. Manual of the leafy Hepaticae of Latin America. Part II. Memoirs of The New York Botanical Garden 11: 173-276.

Gottsche, C.M, Lindenberg, J.B.W. & Nees von Esenbeck, C.G. 1845. Synopsis Hepaticarum, fasc. 2. Hamburg sumptibus Meissuerianis, pp. 145-304.

Gradstein, S.R.; Churchill, S.P.; Salazar, A.N. 2001. Guide to the Bryophytes of Tropical America. Memoirs of The New York Botanical Garden 86: 1-577.

Grolle R. 1964 Notulae hepaticologicae XV. Neue Notizen u¨ ber Kurzia v. Mart. und Verwandte. Journal of Japanese Botany 39: 79-81.

Hendry, T. A., Wang, B., Yang, Y., Davis, E.C., Braggins, J.E. Schuster, R.M., Qui, Y.L. 2007. Evaluating phylogenetic positions of four liverworts from New Zealand, *Neogrellea notabilis*, *Jackiella curcata*, *Goebelobryum unguiculatum*, and *Herzogianthus vaginatus* using three chloroplast genes. The bryologist 110: 738-751.

He-Nygre´n, X.; Jusle´n, A.; Ahonen, I.; Glenny, D.; Piippo S. 2006. Illuminating the evolutionary history of liverworts (Marchantiophyta) towards a natural classification. Cladistics 22: 1-31.

Heslewood, M. M.; Brown, E. A. 2007. A molecular phylogeny of the liverwort family Lepidoziaceae Limpr. in Australasia. Plant Systematics and Evol 265: 193–219.

Huelsenbeck, J. P., Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754-755.

Kass, R. E., Raftery, A. E. 1995. Bayes Factors. Journal of the American Statistical Association 90: 773-795.

Maddison, W. P., Maddison, D. R. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.72. http://mesquiteproject.org.

Miller, M. A., Holder, M. T., Vos, R., Midford, P. E., Liebowitz, T., Chan, L., Hoover, P., Warnow, T. 2010. The CIPRES Portals. www.phylo.org.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A., Lanfear, R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37: 1530-1534.

Peralta, D. F.; Amelio, L. A.; Souza, A. M.; Carmo, D. M.; Santos, E. L.; Valente, E. B.; Oliveira, H. C.; Lima, J. S.; Prochazka, L. S. 2020. Lepidoziaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro.Available at: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB97671>. Accessed on: 03 fev. 2022

Reimers, Von H. 1933. Revision der Lebermoos gattung *Micropterygium*. Hedwigia 76: 165–168.

Renner, M. A. M., Brown, E. A., Glenny, D. 2006. Two new Zoopsis species and their relationships to other zoopsids (Jungermanniopsida: Lepidoziaceae). Journal of Bryology 28, 331-334.

Schuster, R. M. 1969. The Hepaticae and Anthocerotae of North America. Vol. 2. Columbia University Press, New York, pp. 1-1062.

Schuster, R. M. 2000. Austral Hepaticae Part I. Nova Hedwigia 118: 1-524.

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.; Heinrichs, 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.; Tiers, B. M.; Uribe, J.; Váňa, J.; Villarreal, J.C.; Wigginton, M.; Zhang, L.; Rui-Liang, Z. 2016. World checklist of hornworts and liverworts. PhytoKeys 59: 1-828.

Stamatakis, A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312-1313.

Stephani, F. 1901. Species Hepaticarum, Vol. II. Acrogynae. Geneva: George & C.

Stephani, F. 1909. Species Hepaticarum, Geneva.

Vilnet, A. A., Konstantinova, N. A. Troitsky, A. V. 2009. Genosystematics and New Insight into the Phylogeny and Taxonomy of Liverworts. Molecular Biology 43(5): 783-793.

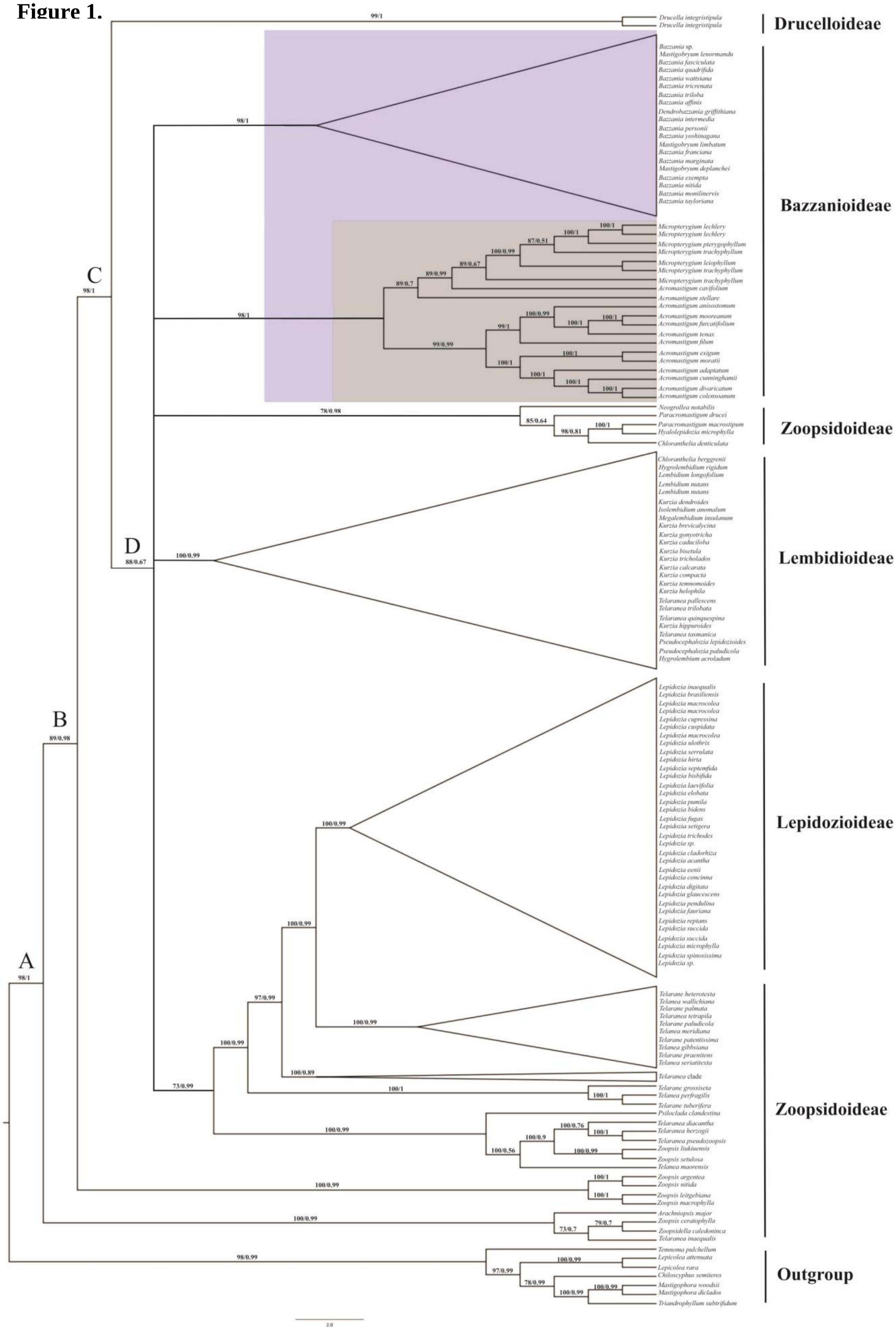
Von Konrat, M., Söderström, L., Renner M. A. M., Hagborg, A., Briscoe, L., Engel, J. J. 2010. Early Land Plants Today (ELPT): How many liverwort species are there? Phytotaxa 9: 22-40.

Table 1. Details of markers used in this study

Marker	Genome	Primer [sequence 5'-3']	Reference:
nr26S	nuclear	LS0F[ACCCGCTGTTTAAGCATAT]	Shaw 2000
		LS12R[ATCGCCAGTTCTGCTTACCA]	Shaw 2000
rbcL	chloroplast	mtrnRR[GCTCTAATCCACTGAGCTAC]	Cox *et al*., 2001
		nm34[GTTGTTGGGATTTAAAGCTGGTGTT]	Cox *et al*., 2001
		rcbL1[GGGATTTATGTCACCACAAACAGA]	Gadek & Quinn 1993
		rbcL2 [GATCTCCTTCCATACTTCACAAGC]	Gadek & Quinn 1993
rps4	chloroplast	rps5 [ATGTCCCGTTATCGAGGACCT]	Nadot *et al*. 1994
		trnas [TACCGAGGGTTCGAATC]	Souza-Chies *et al.* 1997
trnL-trnF	chloroplast	trnF [ATTTGAACTGGTGACACGAG]	Taberlet *et al.* 1991
		trnC [CGAAATCGGTAGACGCTACG]	Taberlet *et al.* 1991

Figure 1. Phylogram derived from the Bayesian inference (BI) total evidence analysis (26S+rbcL+rps4+trnL-F) PP > 0.95 are shown above branches and MLBS. The branches colapsed are those fully supported in the analyses and represent the subfamilies.

Figure 1.


Drucella integristipula
Drucella integristipula
Drucelloideae
Bazzania sp.
Mastigobryum lenormandu
Bazzania fasciculata
Bazzania quadrifida
Bazzania wattsiana
Bazzania tricrenata
Bazzania triloba
Bazzania affinis
Dendrobazzania griffithiana
Bazzania intermedia
Bazzania personii
Bazzania yoshinagana
Mastigobryum limbatum
Bazzania franciana
Bazzania marginata
Mastigobryum deplanchei
Bazzania exempta
Bazzania nitida
Bazzania monilinervis
Bazzania tayloriana
Micropterygium lechlery
Micropterygium lechlery
Micropterygium pterygophyllum
Micropterygium trachyphyllum
Micropterygium leiophyllum
Micropterygium trachyphyllum
Micropterygium trachyphyllum
Acromastigum cavifolium
Acromastigum stellare
Acromastigum anisostomum
Acromastigum mooreanum
Acromastigum furcatifolium
Acromastigum tenax
Acromastigum filum
Acromastigum exigum
Acromastigum moratii
Acromastigum adaptatum
Acromastigum cunninghamii
Acromastigum divaricatum
Acromastigum colensoanum
Bazzanioideae
Neogrollea notabilis
Paracromastigum drucei
Paracromastigum macrostipum
Hyalolepidozia microphylla
Chloranthelia denticulata
Zoopsidoideae
Chloranthelia berggrenii
Hygrolembidium rigidum
Lembidium longofolium
Lembidium nutans
Lembidium nutans
Kurzia dendroides
Isolembidium anomalum
Megalembidium insulanum
Kurzia brevicalycina
Kurzia gonyotricha
Kurzia caduciloba
Kurzia bisetula
Kurzia tricholados
Kurzia calcarata
Kurzia compacta
Kurzia temnomoides
Kurzia helophila
Telaranea pallescens
Telaranea trilobata
Telaranea quinquespina
Kurzia hippuroides
Telaranea tasmanica
Pseudocephalozia lepidozioides
Pseudocephalozia paludicola
Hygrolembium acroladum
Lembidioideae
Lepidozia inaequalis
Lepidozia brasiliensis
Lepidozia macrocolea
Lepidozia macrocolea
Lepidozia cupressina
Lepidozia cuspidata
Lepidozia macrocolea
Lepidozia ulothrix
Lepidozia serrulata
Lepidozia hirta
Lepidozia septemfida
Lepidozia bisbifida
Lepidozia laevifolia
Lepidozia elobata
Lepidozia pumila
Lepidozia bidens
Lepidozia fugax
Lepidozia setigera
Lepidozia trichodes
Lepidozia sp.
Lepidozia cladorhiza
Lepidozia acantha
Lepidozia eenii
Lepidozia concinna
Lepidozia digitata
Lepidozia glaucescens
Lepidozia pendulina
Lepidozia fauriana
Lepidozia reptans
Lepidozia succida
Lepidozia succida
Lepidozia microphylla
Lepidozia spinosissima
Lepidozia sp.
Lepidozioideae
Telarane heterotexta
Telanea wallichiana
Telarane palmata
Telaranea tetrapila
Telarane paludicola
Telanea meridiana
Telarane patentissima
Telanea gibbsiana
Telarane praenitens
Telanea seriatitexta
Telaranea clade
Telarane grossiseta
Telanea perfragilis
Telarane tuberifera
Psiloclada clandestina
Telaranea diacantha
Telaranea herzogii
Telaranea pseudozoopsis
Zoopsis liukiuensis
Zoopsis setulosa
Telanea maorensis
Zoopsis argentea
Zoopsis nitida
Zoopsis leitgebiana
Zoopsis macrophylla
Arachniopsis major
Zoopsis ceratophylla
Zoopsidella caledoninca
Telaranea inaequalis
Zoopsidoideae
Temnoma pulchellum
Lepicolea attenuata
Lepicolea rara
Chiloscyphus semiteres
Mastigophora woodsii
Mastigophora diclados
Triandrophyllum subtrifidum
Outgroup
A
B
C
D
2.0

Appendix

Table2. Genbank accesion numbers for sequences used in this study.

Taxon	Voucher (Collector, herbarium)	Source	*nr26S*	*rbcL*	*rps4*	*trnL-trnF*
Acromastigum adaptatum Hürl.	E. A. Brown, 06/ 137, NSW	New Caledonia	JF315899	JF316320	-	JF316589
Acromastigum anisostomum (Lehm. Et Lindenb.) A. Evans	E. C. Davis, NZ40, DUKE	New Zealand	JF316097	JF316321	JF316457	JF316588
Acromastigum cavifolium R. M. Schust.	E. A. Brown, 08/278, NSW	New Zealand	-	JF316302	JF316437	JF316585
Acromastigum colensoanum (Mitt.) A. Evans ex Reimers	E. A. Brown, NSW7224	Australia	-	EF100973	-	EF101080
Acromastigum cunninghamii (Steph.) A. Evans	J. J. Engel 23662, F	New Zealand	JF315888	-	JF316459	JF316590
Acromastigum divaricatum (Nees) A. Evans	E. A. Brown 04/ 84e, NSW	Papua New Guinea	-	-	JF316460	JF316591
Acromastigum exiguum (Steph.) A. Evans	E. A. Brown, NSW	Australia	-	EF100974	-	EF101081
Acromastigum filum (Steph.) A. Evans	E. A. Brown 03/ 139, NSW	New Caledonia	JF 315901	EF100975	-	EF101082
Acromastigum furcatifolium (Steph.) E. A. Br. Ms	E. A. Brown 02/ 100, NSW	Australia	-	EF100977	JF316547	EF101084
Acromastigum mooreanum (Steph.) E. A. Hodgs.	B. Shaw 6407, DUKE	Australia	JF315904	JF316318	JF316455	JF316587
Acromastigum moratii N. Kitag.	E. A. Brown, NSW 2000	Australia	-	EF100976	-	EF101083
Acromastigum stellare N. Kitag	E. A. Brown 03/184, NSW	New Caledonia	-	EF100978	-	EF101085
Acromastigum tenax (Steph.) A. Evans	E. A. Brown, NSW701861	New Caledonia	-	EF100979	-	EF101086
Arachniopsis major Herzog	E. A. Brown, NSW611656	New Caledonia	-	EF101021	-	EF101130
Bazzania affinis (Lindenb. & Gottsche) Trevis.	E. C. Davis, 146, DUKE	Jamaica	AY608200	DQ439680	AY608048	JF316633
Bazzania exempta J.J. Engel	Lange, P.J. 7881 DUKE	New Zealand	-	KF943623	KF943540	KF943105
Bazzania fasciculata (Steph.) Meagher	E. A. Brown, NSW605694	Australia	-	EF100980	-	EF101087
Bazzania francana (Steph.) N. Kitag.	E. A. Brown, NSW611491	New Caledonia	-	EF100981	-	EF101088
Bazzania involuta (Mont.) Trevis	J. J. Engel, 37 Tarn 1 F	New Zealand	JF315915	JF316323	JF316448	JF316631
Bazzania marginata (Steph.) N. Kitag.	E. A. Brown 03/140c NSW	New Caledonia	-	EF100982	KF851376	EF101089

Bazzania monilinervis (Lehm. & Lindenb.) Trevis.	E. A. Brown NSW490469	Australia	-	EF100983	-	EF101090
Bazzania nitida (F. Weber) Grolle	J. J. Engel, Bearley 36 F	New Zealand	JF315919	JF316322	JF316444	JF316630
Bazzania pearsonii Steph.	G. P. Rothero, 11022, E	Scotland	-	JF316282	JF316447	JF316632
Bazzania sp.	E. A. Brown NSW493373	Australia	-	EF100984	-	EF101091
Bazzania subtilis (Sande Lac.) Trevis.	E. A. Brown NSW706551	Australia	-	EF100985	-	EF101092
Bazzania tayloriana (Mitt.) Kuntze	E. A. Brown NSW712783	New Zealand	-	EF100986	KF851388	EF101093
Bazzania tricrenata (Wahlenb.)Lindenb.	D. Long, 34721, E	China	JF315877	JF316310	JF316451	JF316635
Bazzania trilobata (L.) Gray	D. Kosma, SIU culture IV	U.S.A.	JF315876	-	JF316453	JF316634
Bazzania wattsiana (Steph.) Meagher	E. A. Brown s.n. NSW494596	Australia	-	EF100987	-	EF101094
Bazzania yoshinagana (Steph.) Steph. ex. Yoshin.	T. Yamaguchi, 29079, F.	Japan	JF315878	-	JF316452	JF316637
Chloranthelia berggrenii (Herzog) R. M. Schust.	E. A. Brown, 08/ 282, NSW	New Caledonia	JF315931	JF316296	JF316423	JF316601
Chloranthelia denticulata (Steph.) R. M. Schust.	E. A. Brown 03/147, NSW	New Caledonia	-	EF100991	-	EF101100
Dendrobazzania griffithiana (Steph.) R.M. Schust. & W.B. Schofield	B. Shaw 9037 (DUKE)	Canada	KF851807	KF852413	KF851506	-
Drucella integristipula (Steph.) E.A. Hodgs.	E.A.Brown 08/219 NSW	New Zealand	-	JF316287	KF851385	JF316576
Drucella integristipula (Steph.) E. A. Hodgs.	E. A. Brown, 08/ 219, NSW	New Caledonia	JF315897	JF316287	JF316436	JF316576
Hyalolepidozia microphylla R. M. Shust. & J. J. Engel	E. A. Brown 08/ 301, NSW	New Zealand	-	JF316304	JF316435	JF316629
Hygrolembidium acrocladum (Berggr.) R.M. Schust.	Curnow 5587	Australia	-	AY462301	AY462356	AY463560
Hygrolembidium rigidum R. M. Schust. & J. J. Engel	E. A. Brown, 08/310, NSW	New Caledonia	JF315932	JF316299	JF316422	JF316602
Isolembidium anomalum (Rodway) Grolle	E. A. Brown 08286, NSW	New Caledonia	JF315926	JF316294	JF316416	JF316600
Kurzia brevicalycina (Steph.) Grolle	E. A. Brown, EAB 03/131, NSW	New Caledonia	JF315918	EF100993	JF316427	EF101102
Kurzia caduciloba R.M. Schust.	E.A. Brown NSW611386	New Caledonia	-	EF100994	-	EF101103
Kurzia calcarata (Steph.) Grolle	E. D. Cooper, 330, NSW	New Zealand	JF315921	JF316301	JF316428	JF316596
Kurzia compacta (Steph.) Grolle	M. A. M. Renner, 02102, AK	New Zealand	-	EF100995	-	EF101104

Kurzia dendroides (Carrington & Person) Grolle	E. A. Brown, 04/02, NSW	Australia	JF315920	EF100996	JF316418	EF101105
Kurzia gonyotricha (Sande Lac.) Grolle	M. von Konrat, 6/8-8b, F	Fiji	-	-	JF316426	JF316604
Kurzia helophila R. M. Schust.	E.D. Cooper, 383, NSW	New Zealand	JF315923	JF316300	JF316431	JF316597
Kurzia hippurioides (Hook. & Taylor) Grolle	E. A. Brown, 04/42, NSW	Australia	JF315924	EF100997	-	-
Kurzia temnomoides R.M. Schust.	E.A. Brown NSW709779	Australia	-	EF100998	-	EF101107
Kurzia trichoclados (Müll. Frib.) Grolle	G. P. Rothero, 11014, E	UK	JF315875	JF316319	JF316430	-
Lembidium longifolium R. M. Schust.	M. A. M. Renner,2530, F	New Zealand	JF315927	-	JF316425	-
Lembidium nutans (Hook. F & Taylor) Mitt. ex A. Evans	E. A. Brown, 02/ 322, NSW	New Zealand	JF315922	EF100992	JF316419	EF101046
Lembidium nutans (Hook. F. & Taylor) Mitt. ex A. Evans	J. J. Engel, 28415, F	New Zealand	JF315929	JF316295	JF316424	-
Lepidozia sp.	M.von Konrat 6/20-4	Fiji	JF3115909	JF316325	JF316478	-
Lepidozia sp.	B.Shaw 5789, DUKE	China	JF315934	JF316307	JF316477	-
Lepidozia acantha J.J. Engel	M.A.M.Renner 4253 NSW	New Zealand	-	JX289373	-	JX289510
Lepidozia bidens J.J. Engel	E.A.Brown 08/200 NSW	New Zealand	-	JX289377	-	JX289517
Lepidozia bisbifida Steph.	E. D. Cooper, 430, NSW	New Zealand	JF315940	JF316305	JF316480	JF316627
Lepidozia brasiliensis Steph.	This study	Brasil	*new*	*new*	*new*	*new*
Lepidozia cladorhiza (Reinw., Blume & Nees) Nees	A.Schafer-Verwimp 24878	Australia	-	JX289385	-	JX289423
Lepidozia concinna Colenso	E.D.Cooper 284 NSW	Australia	-	JX289407	-	JX289492
Lepidozia cupressina (Sw.) Lindenb.	D. G. Long, 29184, E	UK	-	-	JF316474	JF316623
Lepidozia cuspidata Steph.	J.-P.Frahm 15-4 GOET	Australia	-	JX289374	-	JX289468
Lepidozia digitata Herzog	M.A.M.Renner 2547 NSW	Australia	-	JX289411	-	JX289436
Lepidozia eenii S.W. Arnell	E.A.Brown NSW796723	Australia	-	JX289400	-	JX289516
Lepidozia elobata R.M. Schust.	E.A.Brown NSW745439	Australia	-	JX289391	-	JX289527
Lepidozia fauriana Steph.	T. Yamaguchi, 29076, F.	Japan	JF315933	-	JF316476	JF316620
Lepidozia fugax J.J. Engel	E.D.Cooper 350 NSW	Australia	-	JX289386	-	JX289480
Lepidozia glaucescens J.J. Engel	E.D.Cooper 239 NSW	Australia	-	JX289408	-	JX289435
Lepidozia hirta Steph.	E.D.Cooper 255 NSW	Australia	-	JX289378	-	JX289465

Lepidozia inaequalis (Lehm. & Lindenb.) Lehm. & Lindenb.	This study	Brazil	*new*	*new*	*new*	*new*
Lepidozia laevifolia (Hook. & Taylor) Gottsche, Lindenb & Ness	E. A. Brown, 04/ 08, NSW	Australia	JF315906	EF101000	JF316472	EF101109
Lepidozia macrocolea Spruce	This study	Patagonia	*new*	*new*	*new*	*new*
Lepidozia microphylla (Hook.) Lindenb.	J. J. Engel, 23699, F	New Zealand	JF315938	-	JF316475	-
Lepidozia pendulina (Hook.) Lindenb.	E.D.Cooper 421 NSW	Australia	-	JX289416	-	JX289463
Lepidozia pumila J.J. Engel	E.A.Brown NSW745437	Australia	-	JX289387	-	JX289526
Lepidozia reptans (L.) Dumort.	Sargent living culture collection, Berkeley	-	AY608229	JF316327	AY608083	-
Lepidozia septemfida Steph.	E.D.Cooper 76 NSW	Australia	-	JX289375	-	JX289472
Lepidozia serrulata J.J. Engel	E.D.Cooper 174 NSW	Australia	-	JX289384	-	JX289476
Lepidozia setigera Steph.	J. J. Engel, 41 Bog 20, F	New Zealand	JF315907	JF316326	JF316471	JF316625
Lepidozia spinosissima (Hook & Taylor) Mitt.	-	New Zealand	JF315935	EF101002	-	EF101111
Lepidozia succida Mitt.	T.Pocs 97108 - FATOL661	Uganda	-	KF852317	KF851420	JF316617
Lepidozia trichodes (Reinw. ex Blume & Nees) Gottsche	E.A.Brown, 04/67g, NSW	Papua New Guinea	JF315898	JF316324	JF316479	JF316624
Lepidozia ulothrix (Schwägr.) Lindenb.	E. A. Brown, 08/ 273, NSW	New Zealand	JF315939	JF316306	JF316473	JF316626
Mastigobryum deplanchei Gottsche ex Steph.	E.A. Brown NSW611525	New Caledonia	-	EF100988	-	EF101095
Mastigobryum lenormandii Steph.	E. A. Brown, 03/140c, NSW	New Caledonia	JF315916	EF100989	JF316449	EF101096
Mastigobryum limbatum Steph.	D. M. Crayn, 829, NSW	Australia	JF315908	EF100990	JF316446	EF101097
Mastigophora diclados (Brid. ex F. Weber) Nees	E. A. Brown NSW706536	Australia	-	EF100972	-	EF100971
Mastigophora woodsii (Hook.) Nees	D.Long 33696 E	China	JF315870	JF316313	JF316439	-
Megalembidium insulanum (W. Martin & E. A. Hodgs)	M. A. M. Renner, 02100a, NSW	New Zealand	JF315925	EF101005	JF316417	EF101115
Micropterygium lechleri Reimers	This study	Brazil	*new*	*new*	*new*	*new*
Micropterygium lechleri Reimers	This study	Brazil	*new*	*new*	*new*	*new*
Micropterygium leiophyllum Spruce	This study	Brazil	*new*	*new*	*new*	*new*
Micropterygium pterygophyllum (Nees) Trevis.	This study	Brazil	*new*	*new*	*new*	*new*

Micropterygium trachyphyllum Reimers	This study	Brazil	*new*	*new*	*new*	*new*
Micropterygium trachyphyllum Reimers	This study	Brazil	*new*	*new*	*new*	*new*
Micropterygium trachyphyllum Reimers	This study	Brazil	*new*	*new*	*new*	*new*
Neogrollea notabilis E. A. Hodgs	E. A. Brown, 08/ 312, NSW	New Zealand	JF315891	JF316288	JF316443	JF316605
Paracromastigum drucei (R. M. Schust.) R. M. Schust.	E. A. Brown, 08/315, NSW	New Zealand	JF315887	JF316283	JF316461	JF316586
Paracromastigum macrostipum (Steph.) R. M. Schust.	E. A. Brown, 08/ 218, NSW	New Zeland	JF315874	JF316303	JF316434	JF316628
Pseudocephalozia lepidozioides R. M. Schust.	E. A. Brown, 08/216, NSW	New Zeland	JF315893	JF316289	JF316413	JF316593
Pseudocephalozia paludicola R. M. Schust.	E. A. Brown, 08/ 293, NSW	New Zeland	JF315894	JF316290	JF316414	JF316594
Psiloclada clandestina Mitt.	E. A. Brown, 03/ 131c, NSW	New Caledonia	JF315868	EF101700	JF316458	EF101116
Sprucella succida (Mitt.) Steph.	T. Pocs, 97108/D, F	Uganda	-	-	JF316470	JF316617
Telaranea bisetula (Steph.) E.O. Campb.	E.A. Brown NSW611534	New Caledonia	-	EF101008	-	EF101117
Telaranea chaetocarpa (Pearson) Grolle	E. A. Brown, 03/ 146, NSW	New Caledonia	JF315886	EF101011	JF316462	EF101120
Telaranea diacantha (Mont.) J. J. Engel & G. L. Merr.	T. Pocs, 03156/N, F	Dominican Republic	JF315902	-	JF316454	-
Telaranea gibbsiana (Steph.) E.A. Hodgs.	E.D. Cooper, 205 NSW	Australia	-	JX289360	-	JX289454
Telaranea granulata J.J. Engel & G.L. Merr.	E.A. Brown 08/343 NSW	New Zealand	-	JX289324	-	JX289462
Telaranea grossiseta (Steph.) J.J. Engel & R.M. Schust.	E.A. Brown s.n. NSw	Australia	-	JX289340	-	JX289530
Telaranea herzogii (E. A. Hodgs.) E. A. Hodgs.	J. J. Engel, 23927, F	New Zealand	JF315903	JF316309	JF316440	JF316639
Telaranea heterotexta (Steph.) J. J. Engel & G. L. Merr.	E. A. Brown, 03/ 129, NSW	New Caledonia	JF315910	EF101012	JF316464	EF101121
Telaranea inaequalis R.M. Schust. ex J.J. Engel & G.L. Merr.	D. Glenny 10580 CHR	New Zealand	-	JX289444	-	JX289444
Telaranea lawesii (Steph.) Grolle	E. A. Brown, 04/ 84h, NSW	Papua New Guinea	JF315885	JF316332	JF316469	JF316606
Telaranea lindenbergii (Gottsche) J. J. Engle & G. L. Merr.	J. J. Engel, 23605, NSW	New Zealand	JF315884	JF316316	JF316482	JF316608
Telaranea martinii (E. A. Hodgs.) R. M. Schust.	J. J. Engel, 24903, F	New Zealand	JF315936	JF316330	JF316484	JF316615
Telaranea meridiana (E. A. Hodgs.) R. M. Schust.	J. J. Engel, 24863, F	New Zealand	-	-	JF316466	JF316610

Telaranea pallescens (Grolle) J. J. Engel & G. L. Merr.	J. J. Engel, 23623	New Zealand	JF315872	-	-	JF316598
Telaranea palmata J. J. Engel & G. L. Merr.	M. A. M. Renner, 2522, NSW	New Zealand	JF315914	JF316317	JF316468	JF316612
Telaranea paludicola (E.A. Hodgs.) E.A. Hodgs.	E.D. Cooper 286	New Zealand	-	JX289363	-	JX289456
Telaranea patentissima (Hook. & Taylor) E. A. Hodgs.	E. A. Brown, 03/61, NSW	Australia	JF315867	EF101016	JF316465	EF101125
Telaranea perfragilis J.J. Engel & G.L. Merr.	E.D.Cooper 3 NSW	New Zealand	-	JX289334	-	JX289489
Telaranea plumulosa (Lehm. & Lindenb.) Fulford	J. J. Engel, 26422, F	New Zealand	JF315889	JF316312	JF316483	-
Telaranea praenitens (Lehm. & Lindenb.) E.A. Hodgs.	E.D. Cooper 336 NSW	New	-	JX289357	-	JX289450
Telaranea pseudozoopsis (Herzog) Fulford	J. J. Engel, 25743, F	Chile	JF315900	JF316308	-	JF316638
Telaranea pulcherrima var. *mooreana* (Steph.) J. J. Engel & G. L. Merr.	M. A. M. Renner, 01-100, F	New Zealand	JF315883	-	JF316485	JF316619
Telaranea pulcherrima var. *pulcherrima* (Steph.) R. M. Schust.	H. Streimann, 59554, NY	Australia	AY608256	DQ439704	AY608114	JF316618
Telaranea quinquespina (J.J. Engel & G.L. Merr.) J.J. Engel & G.L. Merr.	E.A. Brown	Australia	-	EF101018	-	EF101127
Telaranea remotifolia E.A. Hodgs.	E.A.Brown 08/275 NSW	New Zealand	-	JX289369	-	JX289533
Telaranea remotifolia E.A. Hodgs.	E.D.Cooper 405 NSW	New Zealand	-	JX289370	-	JX289459
Telaranea seriatitexta (Steph.) J. J. Engel	J. J. Engel, 25953, F	Chile	JF315937	Jf316315	-	JF316621
Telaranea tasmanica (Steph.) J. J. Engel & G. L. Merr.	M. A. M. Renner, 1954, NSW	Australia	JF315879	JF316285	-	JF316592
Telaranea tetradactyla (Hook. & Taylor) E. A. Hodgs.	D. G. Long, 29502, E	UK	-	-	JF316481	JF316607
Telaranea tetradactyla (Hook. & Taylor) E. A. Hodgs.	D.G.Long 29502	United Kingdom	-	-	JF316481	JF316607
Telaranea tetrapila (Hook. & Taylor) J. J. Engel & G. L. Merr.	J. J. Engel, 24292, F	New Zealand	JF315913	JF316329	JF316467	JF316611
Telaranea trilobata (R. M. Schust.) J. J. Engel & G. L. Merr.	E. A. Brown, 08/250, NSW	New Zealand	JF315917	JF316293	JF316429	JF316599
Telaranea tuberifera J.J. Engel & R.M. Schust.	E.D.Cooper 11 NSW	New Zealand	-	JX289342	-	JX289488

Telaranea wallichiana (Gottsche) R. M. Schust.	E. A. Brown, 04/ 829, NSW	Papua New Guinea	JF315892	JF316328	JF316463	JF316609
Tricholepidozia chaetocarpa (Pearson) E.D. Cooper	E. A. Brown, NSW702433	New Caledonia	JF315886	EF101011	JF316462	EF101120
Zoopsidella caledonica (Steph.) R. M. Schust.	E. A. Brown, 03/ 179, NSW	New Caledonia	-	EF101022	-	EF101131
Zoopsis argentea (Hook. & Taylor) Gottsche, Lindenb. & Nees	J. J. Engel, 23962, F	New Caledonia	JF315880	-	-	JF316577
Zoopsis ceratophylla (Spruce)Hamlin	E. A. Brown, 08/ 320, NSW	New Zealand	-	JF316314	JF316412	JF316584
Zoopsis leitgebiana (Carrington & Person) Bastow	R. Coveny, sn, NSW [614795	Australia	-	EF101023	JF316432	EF101132
Zoopsis liukiuensis Horik.	E. A. Brown, 03/ 132, NSW	New Caledonia	JF315911	EF101024	JF316441	EF101134
Zoopsis macrophylla R. M. Schust.	E. A. Brown, 08/212, NSW	New Zealand	JF315882	JF316286	JF316433	JF316574
Zoopsis nitida Glenny, Braggins & R.M. Schust.	D. Glenny 10517 F	New Zealand	-	KF943568	KF943440	KF942990
Zoopsis setulosa Leitg.	E. A. Brown, 04/ 39, NSW	Australia	JF315912	EF101025	JF316525	EF101135
Chiloscyphus semiteres (Lehm.) Lehm. & Lindenb.	J. J. Engel, 24780, F	New Zealand	JF315869	JF316334	JF316438	-
Lepicolea attenuata (Miit.) Steph.	R. Stotler, 4586, ABSH	New Zealand	DQ268888	AY507410	AY507452	JF316578
Lepicolea rara (Steph.) Grolle	D. Norris, 66575, DUKE	Papua New Guinea	AY608227	DQ439691	AY608081	JF316578
Temnoma pulchellum (Hook.) Mitt. ex. Bastow	J.E.Braggins, 92/87, F	New Zealand	AY608257	DQ439705	AY608115	JF316575
Triandrophyllum subtrifidum (Hook & Taylor) Fulford & Hatcher	Ricardi, 9730/T, F	Venezuela	AY608259	DQ439706	AY608117	JF316580

CAPÍTULO 4

ON THE LEAF OF LEPIDOZIACEAE (MARCHANTIOPHYTA) A POLYMORPHIC CHARACTER

Biological Journal of the Linnean society

CAPÍTULO 4

ON THE LEAF OF LEPIDOZIACEAE (MARCHANTIOPHYTA) A POLYMORPHIC CHARACTER

Leandro de Almeida Amélio[1,3], Emilia de Brito Valente[1] and Denilson Fernandes Peralta[2]

[1] Departamento de Biologia, Universidade Estadual de Feira de Santana, Feira de Santana, BA, Brazil

[2] Instituto de Pesquisas Ambientais, Av. Miguel Stéfano, 3687 - CEP 04301902 - São Paulo, SP, Brazil

[3] Corresponding author's e-mail: ednlora@gmail.com

Abstract: In this work, we used previously published sequences available from the chloroplast of Lepidoziaceae and some new ones to estimate divergence dates into the subfamilies. Our focus is to discuss and understand the origin of diversity in lineages with a scarce fossil record using molecular phylogenetic methods to provide a means to estimate the time of divergence of leaves. The Lepidoziaceae originated in the Lower Cretaceous and later established major lineages in the Upper Cretaceous. This period of divergence is consistent with Cenozoic diversification for *Acromastigum*, *Bazzania*, *Lepidozia*, *Micropterygium* and *Telaranea*. Our evidence indicates that a similar pattern of origin was observed for the outgroup, as well as for other groups of liverworts. We indicate here that segmented leaves of Lepidoziaceae as seen in *Kurzia*, *Lepidozia*, *Telaranea* as plesiomorphic. The leaves which differ from the segmented pattern as the long, toothed leaves in *Bazzania* and *Acromastigum*, and the winged leaves in *Micropterygium* as apomorphy. Even though today's genera originated almost simultaneously on the Createaceous.

Key words: Divergence time, Liverworts, Molecular clock, Phylogeny, Plesiomorphic character.

Introduction

Associated with the great age of these plants and their extant diversity (von Konrat et al., 2010; Magill, 2010; Villarreal et al., 2010). Bryophytes have been the basis for several studies with hypotheses about evolutionary patterns and processes in these lineages. The vicariance process has been pointed by the transoceanic disjunctions, and the populations which show low levels of morphological divergence have been taken as evidence of low rates of evolution, for example, the genera *Kurzia* G. Martens and *Telaranea* Spruce ex Schiffn. with the restricted distribution around the world (Frey et al., 1999; Gradstein & Costa 2003; Peralta et al. 2022.).

The leafy liverwort Lepidoziaceae exhibits diverse morphology and widely disjunct geographic ranges within the North and Southern Hemisphere. The family presents the classic model of Gondwanan biogeographic distribution, with extant species ranges (Schuster, 1979, 1982, 1983; Frey et al., 1999; Cooper et al. 2012b).

The liverworts have a tetrahedral apical cell with one free face in its apical point of development that provides the leaves diversity of shapes evident in the group (Crandall-Stotler & Stotler, 2000). The leafy liverwort gametophytes have its body formed by stems, branches and leaves. Modification of these relatively simple structures gives rise to the entire morphological diversity of the lineage (Crandall-Stotler et al. 2008) and culminates in the recognition of 345 species morphologically distinct (ELPT database) (Söderström *et al*., 2016).

Nevertheless, the structural simplicity leads to increasing taxonomic difficulty, as can be seen in many groups of the liverworts (Heinrichs et al., 2011). Lepidoziaceae is a near cosmopolitan species-rich family of leafy liverworts, and the total of species number estimate is about 860 species of accepted today (ELPT database) (Söderström *et al*., 2016). Perhaps as much as 9-10% of the total liverworts species diversity. Schuster (1984,

2000) presented the family Lepidoziaceae as a complex of old and modern characteristics among the families of liverworts, which the evolutionary diversification occurred since Gondwana, differ of Lejeuneaceae since late Oligocene, a period where the continents had arrived at their current positions (Heinrichs et al., 2009; McLoughlin, 2001). In addition to being species-rich and exceptionally widespread, Lepidoziaceae also encompasses a large portion of the total morphological range covered by the liverworts. As well as the typical leafy morphology of the type genus, *Lepidozia* (Dumort.) Dumort., as segmented leaves. The family accommodates such discrepant morphotypes, as the simple thalloid morphology of the Metzgeriales, represented for *Pteropsiella* Spruce, *Protocephalozia* (Spruce) K. I. Goebel, and *Zoopsis* Hook.f. ex Gottsche with reduced or vestigial leaves. *Telaranea* Spruce ex Schfn. and *Kurzia* G.Martens, which resembles a charophycean alga with its branched filamentous protonema giving rise directly to the gynoecial and androecial branches, and the segmented leaves (Schuster, 2000). *Micropterygium* is characterized by winged leaves, *Lembidium* and *Mytilopsis* by the concave leaves, the diversity within Lepidoziaceae leaves is shown in Fig. 1.

Phylogenetic studies of the family always show its monophyly (Heslewood and Brown, 2007; Cooper et al., 2011; 2012a). However, several studies have presented incongruent topologies with the currently accepted subfamily and generic classifications (Engel and Merrill, 2004; Davis 2004; Renner et al., 2006; Heslewood and Brown, 2007; Cooper et al., 2011). The position of *Telaranea* based on morphological characters, led to an interpretation of the genus *Arachniopsis*. Other study indicated the paraphyly of *Zoopsis* and *Zoopsidella* even pointed out the morphological limitations to recover an accurate phylogeny (Engel & Merril, 2002, 2004; Renner et al. 2006).

We aim to test the hypothesis that simple leaves may be older than complex ones in the Lepidoziaceae family species. Our hypothesis follow the concept of the morphology change associated with the divergence time explored in the works of Hartmann *et al*., *Bryopteris* (2006); Feldberg *et al*., *Herbertus* (2007); Heinrichs *et al*., *Marchesinia* (2007, 2009); Newton *et al*., pleurocarpous mosses (2007); Wilson *et al*., liverworts under tertiary climatic fluctuations (2007); Devos & Vanderpoorten, *Leptoscyphus* (2009); Kreier *et al*., *Ptilidium* (2010); Cooper *et al*., *Lepidozia* (2011), Cooper *et al*., Lepidoziaceae (2012a).

In the study the Lepidoziaceae was analised based in morphological and evolutionary interpretation. The leaves and simple thalloid species aid to understanding the diversity and evolution of this family.

Materials and methods

Molecular methods

One nuclear and three chloroplast markers were sequenced (Table 1). For the new sequences included in the Genbank, we performed the DNA extraction using modifications of the CTAB protocol (Doyle & Doyle, 1987; Câmara, 2009). All PCR reactions were completed under standard conditions, each 10 µm reaction contained 0.5 µm each primer, 5 µm Top Taq, 3 µm of H2O. Genomic DNA was added as 0.5 µm to each reaction without standardizing concentration. A standard temperature profile was used: 95ºC for 2 min, then 30 cycles of 95º C for 1 min, 50º C for 1 min and 72º C for 1 min, followed by final extension step of 72º C for 10 min. The same primers were used for sequencing (Table 1).

Sequence alignment and evolution/phylogenetic analyses

The sequence alignments were produced using Muscle (Edgar, 2004) and edited in Mesquite (Maddison and Maddison, 2009).

The Lepidoziaceae genera was delimited over Cooper et al. (2013) and Söderström et al. (2016).

We compiled 60 taxon dataset for liverworts with seven species in outgroups and 12 Brazilian species (*Micropterygium* Lindenb. and *Lepidozia* Dumort.), and 41 from the published phylogenies by Heslewood & Brown (2007), Cooper et al. (2012), Cooper et al. (2013), including only those taxa for which 26S, rbcL, rps4 and trnl sequences were available (annex 1). The analyses were run with the data matrices and the topologies and divergence times compared to the estimates previously ran. The number of supported nodes (> 90% pp) were counted and, to visualize the effect of matrix incompleteness, we graphed node ages and their 95% highest posterior density (HPD) intervals against the 'best estimate' for these supported nodes.

BEAST analysis

BEAST was used to estimated the divergence times (Drummond et al., 2006; Drummond & Rambaut, 2007) using the uncorrelated lognormal relaxed clock to model rate heterogeneity and the mean rate was estimated during the analyses. Analyses were run using a Yule process as a tree prior. To test sensitivity to the Yule prior, an analysis of the complete data matrix including Lepidoziaceae and all calibration priors with a normal prior on the root was run using a birth–death process. The fossil calibration was adopted from the date to *Bazzania* (70 mya), *Lepidozia* (50 mya), Lepidozoideae (60 mya) and Lepidoziaceae (116 mya) as appointed by Cooper et al. (2013). Each gene partition was given its own substitution model and clock model. The same GTR + G + I substitution model was applied to each partition using the default prior values. Uninformative priors were used for the parameters of the clock model and the Yule birth rate. Each analysis was run for 12 million generations with parameters and treeslogged every 10000 generations. Based in the hypothesis that liverworts arose close to the earliest fossil record of land plants (Kenrick and Crane, 1997; Wellman et al., 2003, Sun et al., 2014),

The minimum age constraints were enforced at each calibration point by applying a uniform prior from the fossil age to 116 Mya (the root of Lepidoziaceae with the Crow maximum age). The final single tree visualized using FigTree v1.4.0., Mesquite and edited with Corel Draw.

Morphological data

A morphological dataset was obtained for this study in an attempt to define morphological synapomorphies for each genus (Appendix A). Multistate characters were scored for Lepidoziaceae and outgroup species. Structural elements characters were scored for these terminal taxa. All characters in both datasets were treated as unordered and unweighted (Fitch, 1971). The optimization was performed in Mesquite v.2.74 (Maddison and Maddison, 2010) using the likelihood method under the Mk1 model (Pagel, 1999). As a framework for character optimization, we used the BI consensus tree based on the combined 26S+rbcL+rps4+trnL-F sequence data in this analysis.

Morphological character scorings derived from the field and herbarium sources were compared with the taxonomic literature (e.g., Fulford, 1946, 1963, 1966; Gradstein & Costa 2003; Peralta et al. 2022) to ensure that all potentially informative characters were being considered for analysis. Scoring the morphological variation for the outgroup species relied mostly on literature sources and the online platform. Reconstruction of characters allowed the identification of potential synapomorphies for each of the Lepidoziacreae lineages.

Results

We listed 60 liverwort sequences derived from Lepidoziaceae. These sequences are either commonly used markers contributed by phylogenetic studies of specific genera or families or those contributed by a few broad phylogenetic studies of liverworts. The most common locus is the chloroplast *trn*L-*trn*F intergenic spacer (742 characters. The four loci used in the present study were amongst the most common with 1437 *rbc*L characters, and 824 to rps4 chloroplast genes and 1034 26Snuclear genes characters.

Deletion of up to 9.2% of characters from the data matrix resulted in topologies that are consistent with the phylogeny derived from our analysis of our complete dataset and that presented by Cooper et al. (2011, 2013).

Using the lognormal prior on the root age we estimated a crow node age of 116 (116-137) Mya for the Lepidoziaceae diversification (figure 1; table 1). Despite the morphological diversity presented in Lepidoziaceae, our analyzes present that the diversification of the leaves, as well as for the clades, happened simultaneously in several groups, as in *Bazzania*, *Micropterygium*, *Drucella* and *Telaranea* between 70 -75 Mya. Most genera showing segmented leaves would have diversified between 60-50 Mya as in *Kurzia*, *Lepidozia* and *Neogrella*. The conchifoliose aspect of the leaves, recognized for *Lembidium*-like would have diversified around 45 Mya.

We noticed that all expressed characters are indicated for the stem base of Lepidoziaceae (figure 3). Reinforcing that the speciation of the family occurred in a close period for the groups, as already indicated by Magallón & Hilu (2009) and Clarke, Warnock & Donoghue (2011).

Which indicates a period of extensive diversification among the bryophytes. Even though the groups diversified simultaneously, the segmented leaf present for instance in *Kurzia*, *Lepidozia*, *Telaranea* is indicated as the plesiomorphic character, its similarity with the outgroup. The lobulated character is indicated as a synapomorphy in *Acromastigum* and *Bazzania*. The conchifoliate leaves of *Lembidium*, as well as *Mytilopsis*, *Megalembidium*, *Isolembidium*, can also be interpreted as synapormorphic. The winged leaves of *Micropterygium* however are recognized only for this genus, occasionally, even among the liverworts, was considered as an apomorphy of the group.

Discussion

The Lepidoziaceae morphology is diverse and the gametophytes leaves express a total range of morphogenetic diversification that can be found throughout the Jungermanniales (Schuster, 2000). The phenotipic expression has been held to comprehend the expansion of this family and the variety of shapes. For instance, until the genera *Zoopsis* and *Pteropsiella* in which has a progressive evolution from a bilateral leafy archetype to a thallus were formally transferred to the Lepidoziaceae. *Kurzia*, *Telaranea* and *Lepidozia* where the leaves are segmented total or partially, *Micropterygium* with a great and complex wing, and *Bazzania* with the prostrate and falcate leaves specially to resist in dry environments.

The major limitations in molecular clock projects is the accurate calibration information. Three approaches have been used to calibrate Lepidoziaceae divergence times: the use of *Bazzania* fossil as minimum age consytraints (Hartmann et al. 2006; Heinrichs et al., 2006, 2007); divergence time estimates as secondary (Wilson et al., 2007; Heinrichs et al. 2009) calibrations; and the use of geological events (Devos & Vanderpoorten, 2009). Our approach to dating divergence in the Lepidoziaceae provides the use of secondary calibrations as an alternative, although the dataset results demand a long analysis run times, appropriate to run in an online service. Furthermore, unbalanced sampling might introduce biases into the estimation of branch lengths and, consequently, divergence times, requiring a great number of loci to an accurate relationship inference.

Cooper et al (2012a) appointed than Lepidoziaceae belongs to the Lophocoliineae which diverged from the Cephaloziineae and Jungermanniineae 198 Mya and the diversity time was 174 Mya. In the same study, Cooper et al. (2012b) indicated than Lepidoziaceae stem originated 137 Mya, but they started to diversify at 116 Mya. We present based on molecular phylogenetics techniques, deriving robust hypotheses of the relationship of the ambiguous morphological characters, convergent and parallel. Estimate phylogeny from morphology is difficult if not impossible as demonstrated by Renner (*et al.* 2011).

The morphological evolution in such organisms takes place within a limited time-space, in the Cenozoic. About this, some points are decisive (I) the morphological divergence between closely related species is low or absent, as presented in *Drucella*, *Kurzia*, *Lepidozia*, *Neogrella*, *Pseudocephalozia*; (II) the morphological divergence between closely related genera can appear to be comparatively large, as *Bazzania*, *Micropterygium*, *Paracromastigum*, *Lembidium*; and (III) the morphological phenotypic is derived independently as *Zoopsis*, *Zoopsidella*, and *Pteropsiella* although this was not sampled in this study and need to be investigated.

Acknowledgments

The authors are grateful to various colleagues LAMOL UEFS lab, for their help in fieldwork and/or discussions. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil (CAPES) for fellowships given.

References

Câmara, P. E. A. S. 2009. Métodos de extração de DNA de Bryophyta para análises filogenéticas. Heringeriana 3(2): 11-17.

Clarke, J.T., Warnock, R. C. M., Donoghue, P. C. J. 2011. Establishing a time-scale for plant evolution. New Phytologist 192: 266-301.

Cooper, E. D.; Shaw, A. J.; Shaw, B.; Henwood M. J.; Heslewood, M. M.; Brown, E. A. 2011. A multi-locus molecular phylogeny of the Lepidoziaceae: Laying the foundations for a stable classification. Molecular Phylogenetics and Evolution 59: 489-509.

Cooper, E. D., Henwood, M. J., Brown, E. 2012a. A molecular phylogeny of the Lepidozia generic complex supports re-circumscription of the Lepidozioideae. Molecular Phylogenetics and Evolution 65: 10-22.

Cooper, E. D.; Henwood, M. J.; Brown, E. A. 2012b. Are the liverworts really that old? Cretaceous origins and Cenozoic diversification in Lepidoziaceae reflect a recurrent theme in liverwort evolution. Biological Journal of the Linnean Society 07: 425-441.

Crandall-Stotler, B., Stotler R. E., Long D. G. 2008. Morphology and classification of the Marchantiophyta. p.p. 1–54. In: Goffinet B., Shaw A. J. (eds.) Bryophyte biology. New York, NY: Cambridge University Press.

Crandall-Stotler, B., Stotler, R. E. 2000. Morphology and classification of the Marchantiophyta. pp. 21-70. In: Shaw A.J., Goffinet B. (eds.) Bryophyte biology. Cambridge University Press, Cambridge.

Davis, E. C. 2004. A molecular phylogeny of leafy liverworts (Jungermaniidae: Marchantiophyta). pp. 61-86. In: Goffinet, B., Hollowell, V., Magill, R. (eds.). Molecular Systematics of Bryophytes. Missouri Botanical Garden Press, St. Louis, Missouri.

Devos, N., Vanderpoorten, A. 2009. Range disjunctions, speciation, and morphological transformation rates in the liverwort genus *Leptoscyphus*. Evolution 63: 779- 792.

Doyle, J. J.; Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemistry Bulletin 19: 11-15.

Drummond A. J, Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214.

Drummond, A. J., Ho, S. Y. W., Phillips, MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4: 699-710.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792-1797.

Engel, J. J.; Smith Merrill, G. L. 2004. Austral Hepaticae 35. A taxonomic and phylogenetic study of *Telaranea* (Lepidoziaceae), with a monograph of the genus in temperate Australasia and commentary on extra-Australasian taxa. Fieldiana, Bot. 44: 1-265.

Feldberg, K., Hentschel, J., Wilson, R., Rycroft, D. S., Glenny, D., Heinrichs, J. 2007. Phylogenetic biogeography of the leafy liverwort *Herbertus* (Jungermanniales, Herbertaceae) based on nuclear and chloroplast DNA sequence data: correlation between genetic variation and geographic distribution. Journal of Biogeography 34: 688-698.

Fitch, W. M. 1971. Towards defining the course of evolution: minimum change for a specific tree topology. Systematics Zoology 20, 406-416.

Frey, W., Stech, M., Meissner, K. 1999. Chloroplast DNA-relationship in palaeoaustral *Lopidium concinnum* (Hypopterygiaceae, Musci). An example of stenoevolution in mosses. Studies in austral temperate rain forest bryophytes 2. Plant Systematics and Evolution 218: 67-75.

Fulford, M. 1946. The genus *Bazzania* in Central and South America. Chronica Botanica Company. Waltham, Mass., U.S.A. pp. 187.

Fulford, M. 1963. Manual of the leafy Hepaticae of Latin America. Part I. Memoirs of Tthe New York Botanical Garden 11: 1–172.

Fulford, M. 1966. Manual of the leafy Hepaticae of Latin America. Part II. Memoirs of Tthe New York Botanical Garden 11: 173–276.

Gradstein, S. R.; Costa D. P. 2003. The Hepaticae and Anthocerotae of Brazil. Memoirs of The New York Botanical Garden 87: 1-318.

Hartmann, F. A., Wilson, R., Gradstein, S. R., Schneider, H., Heinrichs, J. 2006. Testing hypotheses on species delimitations and disjunctions in the liverwort *Bryopteris* (Jungermanniopsida: Lejeuneaceae). International Journal of Plant Sciences 167: 1205-1214.

Heinrichs, J., Lindner, M., Groth, H., Hentschel, J., Feldberg, K., Renker, C., Engel, J.J., von Konrat, M., Long, D.G., Schneider, H. 2006. Goodbye of welcome Gondwana? – insights into the phylogenetic biogeography of the leafy liverwort *Plagiochila* with a description of *Proskauera*, gen. nov. (Plagiochilaceae, Jungermanniales). Plant Systematics and Evolution 258: 227-250.

Heinrichs J, Hentschel J, Wilson R, Feldberg K, Schneider H. 2007. Evolution of leafy liverworts (Jungermanniidae, Marchantiophyta): estimating divergence times from chloroplast DNA sequences using penalized likelihood with integrated fossil evidence. Taxon 56: 31-44.

Heinrichs, J., Klugmann, F., Hentschel, J., Schneider, H. 2009. DNA taxonomy, cryptic speciation and diversification of the Neotropical-African liverwort, *Marchesinia brachiata* (Lejeuneaceae, Porellales). Molecular Phylogenetics and Evolution 53: 113-121.

Heinrichs, J., Reiner-Drehwald, M. E., Feldberg, K., Grimaldi, D. A., Nascimbene, P. C., von Konrat, M., Schmidt, A. R. 2011. *Kaolakia borealis* nov. gen. et sp. (Porellales, Jungermanniopsida): a leafy liverwort from the Cretaceous of Alaska. Review of Palaeobotany and Palynology 165: 235-240.

Heslewood, M. M., Brown, E. A. 2007. A molecular phylogeny of the liverwort family Lepidoziaceae Limpr. in Australasia. Plant Systematics and Evolution. 265: 193-219.

Kenrick, P., Wellman, C.H., Schneider, H., Edgecombe, G.D. 2012. A timeline for terrestrialisation – consequences for the Carbon Cycle in the Palaeozoic. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 376: 519-536.

Kreier, H-P., Feldberg, K., Mahr, F., Bombosch, A., Schmidt, A.R., Zhu. R-L, von Konrat, M., Shaw, B., Shaw, A. J., Heinrichs, J. 2010. Phylogeny of the leafy liverwort *Ptilidium*: cryptic speciation and shared haplotypes between the Northern and Southern Hemispheres. Molecular Phylogenetics and Evolution 57: 1260-1267.

Maddison, W. P., Maddison, D. R. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.72. http://mesquiteproject.org.

Magallón, S., Hilu, K. W. 2009. Land plants (Embryophyta). p.p. 133–137. In: Hedges SB, Kumar S, (eds.). The timetree of life. Oxford: Oxford University Press.

Magill, R. E. 2010. Moss diversity: new look at old numbers. Phytotaxa 9: 167–174.

Newton, A. E., Wiksrtöm, N., Bell, N., Forrest, L.L., Ignatov. M. S. 2007. Dating the diversification of the pleurocarpous mosses. p.p.337-366. In: Newton, A.E., Tangney, R.S. (eds.). Pleurocarpous mosses: systematics and evolution. Boca Raton, FL: CRC Press.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematics Biology 48: 612–622.

Peralta, D.F.; Amelio, L.A.; Souza, A.M.; Carmo, D.M.; Santos, E.L.; Valente, E.B.; Oliveira, H.C.; Lima, J.S.; Prochazka, L.S. 2020. Lepidoziaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro.Available at: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB97671>. Accessed on: 03 fev. 2022

Renner, M. A. M., Brown, E. A., Glenny, D. 2006. Two new *Zoopsis* species and their relationships to other *Zoopsids* (Jungermanniopsida: Lepidoziaceae). Journal of Bryology 28: 331-334.

Renner, M. A. M. 2011. Morphological and molecular variation within the *Lejeunea tumida* Mitt. species group (Lejeuneaceae: Jungermanniopsida). Australian Systematic Botany Society Newsletter 146: 10-14.

Schuster, R. M. 1979. The phylogeny of the Hepaticae. pp. 41–82. In: Clarke G. C., Duckett J. G. (eds.) Bryophyte systematics, Systematics Association 14. Academic Press, London and New York.

Schuster, R. M. 1982. Generic and Familial Endemism in the Hepatic Flora of Gondwanaland: Origins and causes. Journal of the Hattori Botanical Laboratory 52: 3-35.

Schuster, R. M. 1984. Evolution, phylogeny and classification of the Hepaticae. pp. 892–1070. In: Schuster R. M. (ed.) New manual of bryology Vol. 2. Hattori Botanical Laboratory, Nichinan.

Schuster, R. M. 2000. Austral Hepaticae Part I. Nova Hedwigia 118: 1-524.

Schuster, R. M., Engel, J. J. 1983, Austral Hepaticae XVIII. Studies Toward a Revision of *Telaranea* subg. *Neolepidozia* (Lepidoziaceae). Field Museum of Natural History. New Series 14: 1-14.

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.; Xiaolan He; Heinrichs, 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.; Tiers, B.M.; Uribe, J.; Váňa, J.; Villarreal, J.C.; Wigginton, M.; Zhang, L.; Rui-Liang, Z. 2016. World checklist of hornworts and liverworts. PhytoKeys 59: 1-828.

Sun, Yu, He, X. Glenny, David. 2014. Transantarctic disjunctions in Schistochilaceae (Marchantiophyta) explained by early extinction events, post-Gondwanan radiations and palaeoclimatic changes. Molecular Phylogenetics and Evolution 76: 189-201.

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.

Von Konrat, M., Söderström, L., Renner M. A. M., Hagborg, A., Briscoe, L., Engel, J. J. 2010. Early Land Plants Today (ELPT): How many liverwort species are there? Phytotaxa 9: 22-40.

Wellman, C. H., Osterloff, P. L., Mohiuddin, U. 2003. Fragments of the earliest land plants. Nature 425: 282-285.

Wilson, R., Heinrichs, J., Hentschel, J., Gradstein, S.R., Schneider, H. 2007. Steady diversification of derived liverworts under tertiary climatic fluctuations. Biology Letters 3: 566-569.

Legends

Figure 1. Lepidoziaceae leaves diversity. A. *Acromastigum* A.Evans. B. *Micropterygium* Gottsche. C. *Pteropsiella* Spruce. D. *Zoopsis* Hook.f. ex Gottsche. E. *Telaranea* Spruce ex Schfn. F - G. *Bazzania* Gray. H - I. *Paracromastigum* Fulford & Taylor. J. *Drucella* E.A.Hodgs. K. *Kurzia* G.Martens L. *Lepidozia* (Dumort.) Dumort.

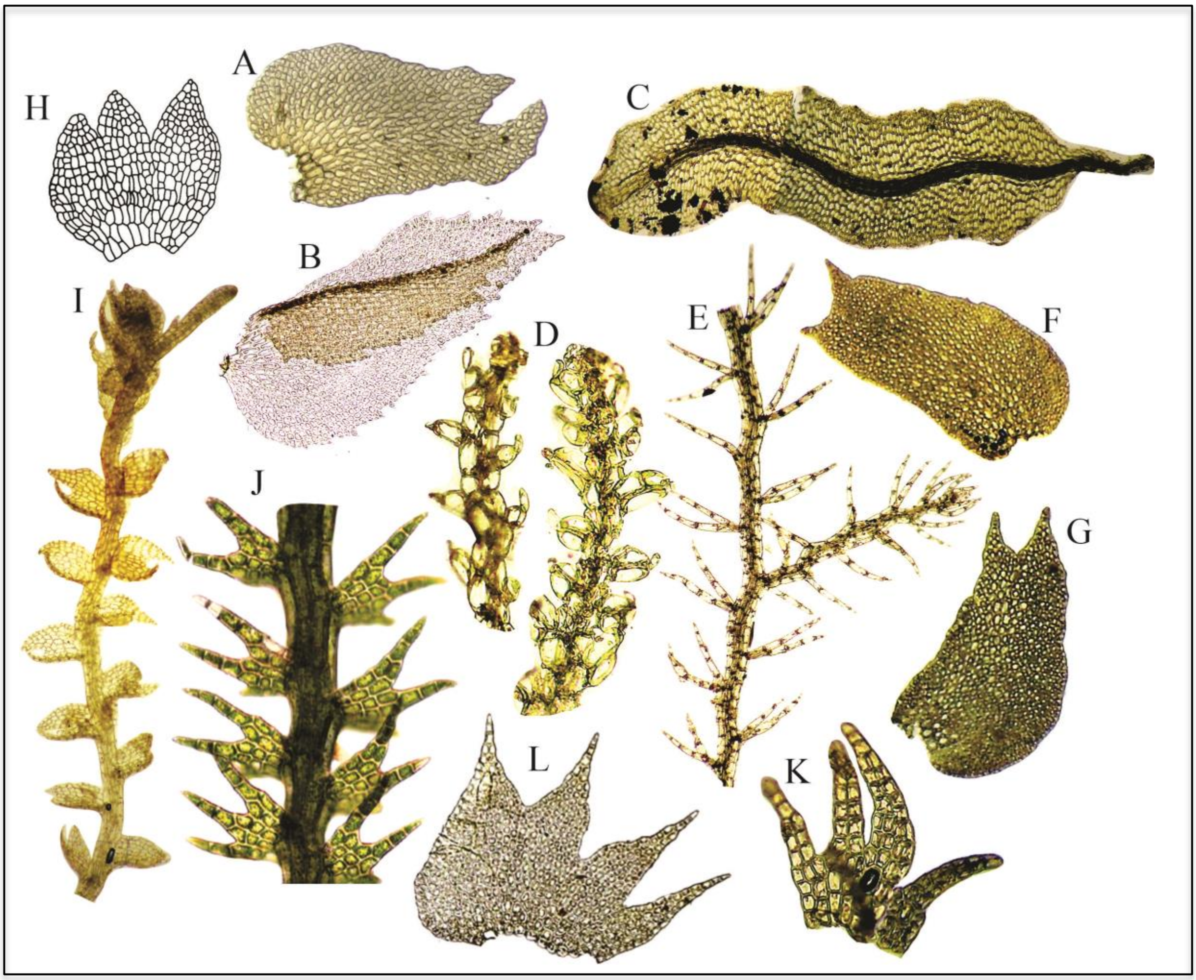


Figure 2. Chronogram of the Lepidoziaceae. The maximum clade credibility tree from Bayesian analysis of four loci (26S, rbcL, rps4, trnL-F) assuming an uncorrelated lognormal relaxed clock is shown. Branches are drawn proportional to geological time and the timescale in millions of years before present is shown below the tree. The 95% highest probability density interval on node age is indicated by horizontal light blue bars for those nodes with posterior probabilities > 0.9. Sequences provided for this study were selected in the box. * Represent the *Bazzania* calibration fossil.

Figure 3. Ancestral state estimates of morphological characters reconstructed on the fifty percent majority rule consensus tree derived from the Bayesian inference (BI) total evidence analysis (26S+rbcL+rps4+trnL+trnF) showing the relationships among Lepidoziaceae genera and outgroups. The proportional likelihoods are reported in square brackets for each synapomorphic character. Character state numbers are listed in Appendix A.

Figure 2.

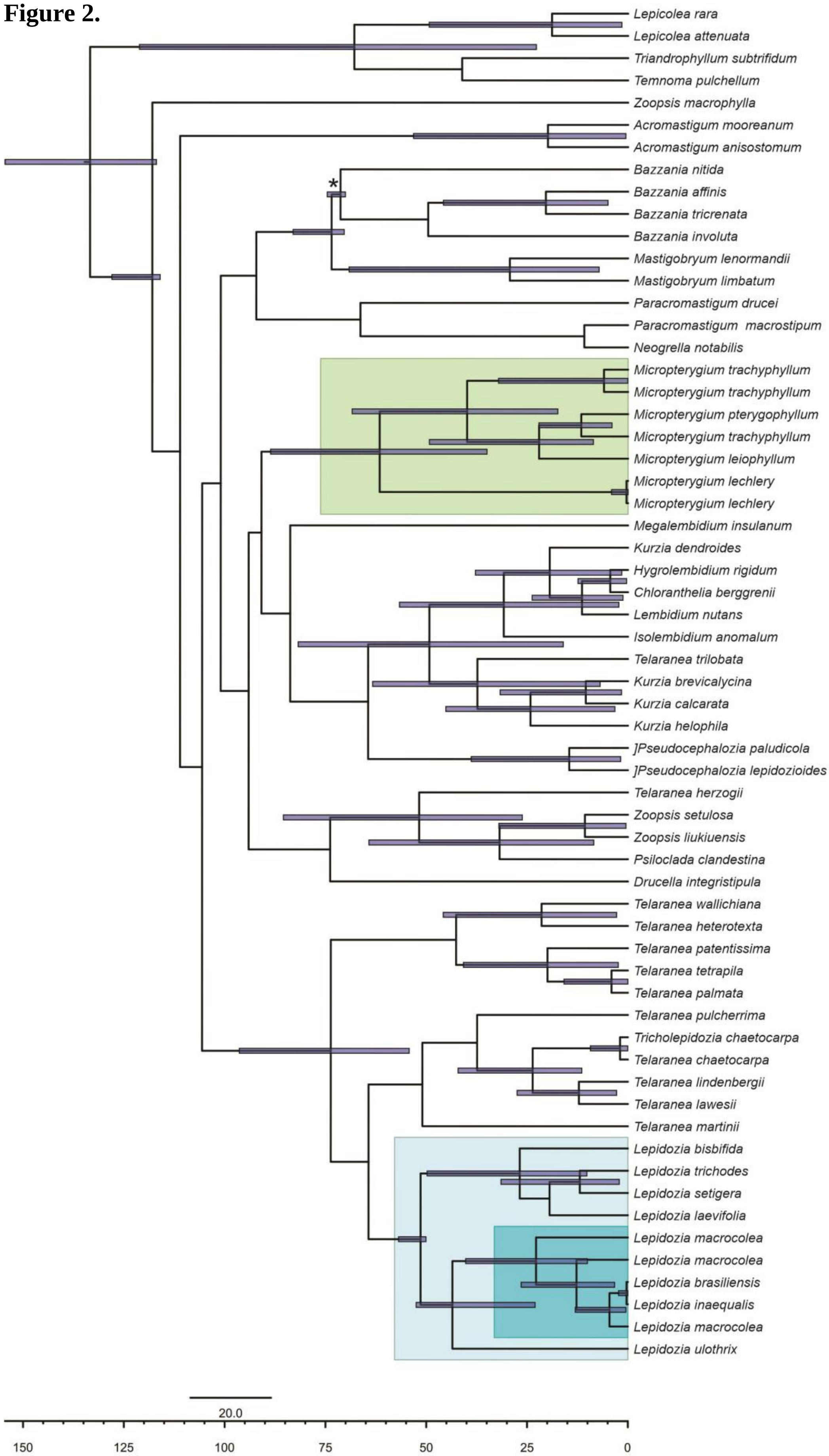

Lepicolea rara
Lepicolea attenuata
Triandrophyllum subtrifidum
Temnoma pulchellum
Zoopsis macrophylla
Acromastigum mooreanum
Acromastigum anisostomum
Bazzania nitida
Bazzania affinis
Bazzania tricrenata
Bazzania involuta
Mastigobryum lenormandii
Mastigobryum limbatum
Paracromastigum drucei
Paracromastigum macrostipum
Neogrella notabilis
Micropterygium trachyphyllum
Micropterygium trachyphyllum
Micropterygium pterygophyllum
Micropterygium trachyphyllum
Micropterygium leiophyllum
Micropterygium lechlery
Micropterygium lechlery
Megalembidium insulanum
Kurzia dendroides
Hygrolembidium rigidum
Chloranthelia berggrenii
Lembidium nutans
Isolembidium anomalum
Telaranea trilobata
Kurzia brevicalycina
Kurzia calcarata
Kurzia helophila
]Pseudocephalozia paludicola
]Pseudocephalozia lepidozioides
Telaranea herzogii
Zoopsis setulosa
Zoopsis liukiuensis
Psiloclada clandestina
Drucella integristipula
Telaranea wallichiana
Telaranea heterotexta
Telaranea patentissima
Telaranea tetrapila
Telaranea palmata
Telaranea pulcherrima
Tricholepidozia chaetocarpa
Telaranea chaetocarpa
Telaranea lindenbergii
Telaranea lawesii
Telaranea martinii
Lepidozia bisbifida
Lepidozia trichodes
Lepidozia setigera
Lepidozia laevifolia
Lepidozia macrocolea
Lepidozia macrocolea
Lepidozia brasiliensis
Lepidozia inaequalis
Lepidozia macrocolea
Lepidozia ulothrix
*
20.0
150
125
100
75
50
25
0

Figure 3.

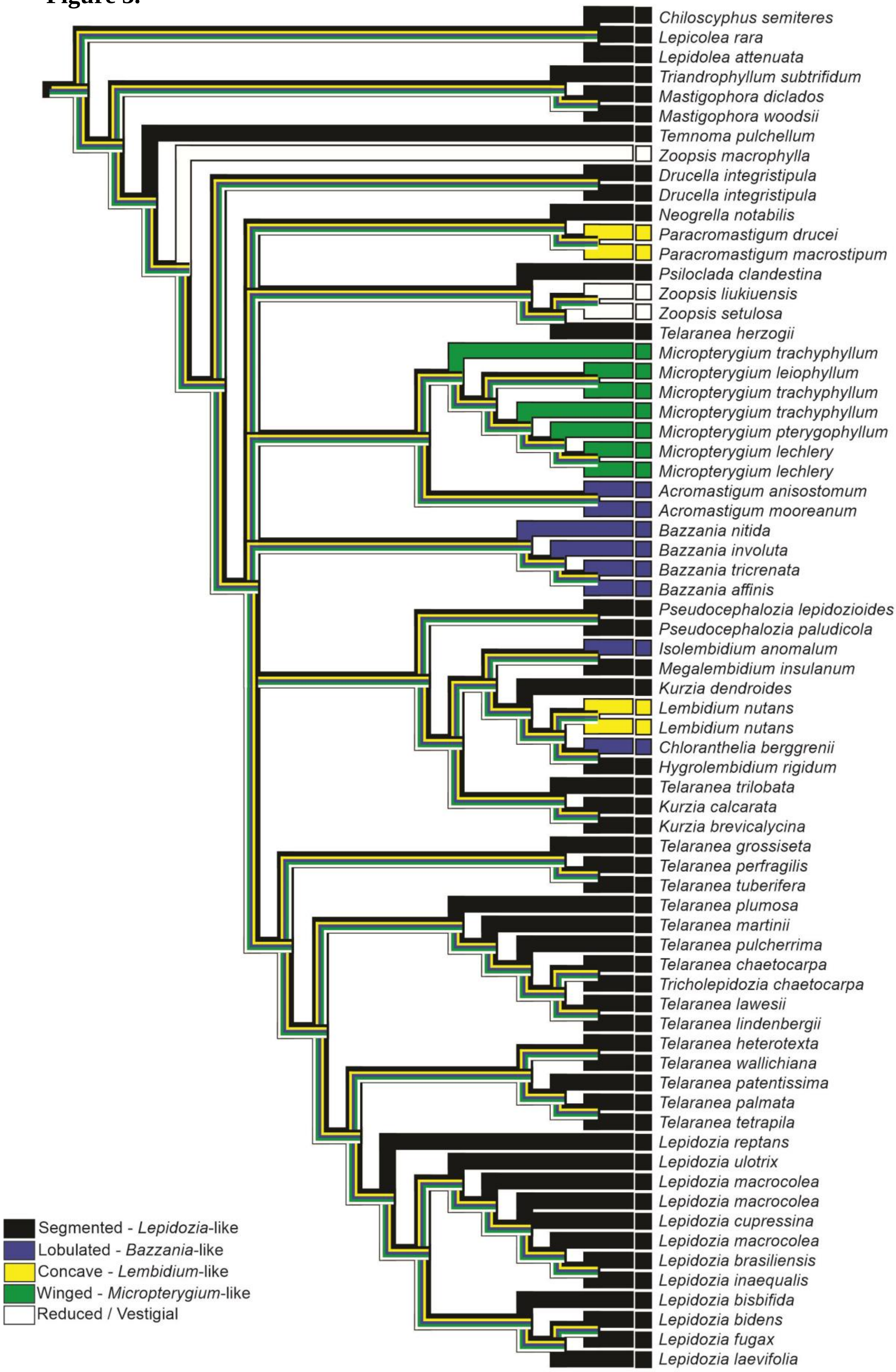

Chiloscyphus semiteres
Lepicolea rara
Lepidolea attenuata
Triandrophyllum subtrifidum
Mastigophora diclados
Mastigophora woodsii
Temnoma pulchellum
Zoopsis macrophylla
Drucella integristipula
Drucella integristipula
Neogrella notabilis
Paracromastigum drucei
Paracromastigum macrostipum
Psiloclada clandestina
Zoopsis liukiuensis
Zoopsis setulosa
Telaranea herzogii
Micropterygium trachyphyllum
Micropterygium leiophyllum
Micropterygium trachyphyllum
Micropterygium trachyphyllum
Micropterygium pterygophyllum
Micropterygium lechlery
Micropterygium lechlery
Acromastigum anisostomum
Acromastigum mooreanum
Bazzania nitida
Bazzania involuta
Bazzania tricrenata
Bazzania affinis
Pseudocephalozia lepidozioides
Pseudocephalozia paludicola
Isolembidium anomalum
Megalembidium insulanum
Kurzia dendroides
Lembidium nutans
Lembidium nutans
Chloranthelia berggrenii
Hygrolembidium rigidum
Telaranea trilobata
Kurzia calcarata
Kurzia brevicalycina
Telaranea grossiseta
Telaranea perfragilis
Telaranea tuberifera
Telaranea plumosa
Telaranea martinii
Telaranea pulcherrima
Telaranea chaetocarpa
Tricholepidozia chaetocarpa
Telaranea lawesii
Telaranea lindenbergii
Telaranea heterotexta
Telaranea wallichiana
Telaranea patentissima
Telaranea palmata
Telaranea tetrapila
Lepidozia reptans
Lepidozia ulotrix
Lepidozia macrocolea
Lepidozia macrocolea
Lepidozia cupressina
Lepidozia macrocolea
Lepidozia brasiliensis
Lepidozia inaequalis
Lepidozia bisbifida
Lepidozia bidens
Lepidozia fugax
Lepidozia laevifolia
Segmented - Lepidozia-like
Lobulated - Bazzania-like
Concave - Lembidium-like
Winged - Micropterygium-like
Reduced / Vestigial

Table 1. Details of markers used in this study

Marker	Genome	Primer [sequence 5'-3']	Reference:
nr26S	nuclear	LS0F[ACCCGCTGTTTAAGCATAT]	Shaw 2000
		LS12R[ATCGCCAGTTCTGCTTACCA]	Shaw 2000
rbcL	chloroplast	mtrnRR[GCTCTAATCCACTGAGCTAC]	Cox *et al*., 2001
		nm34[GTTGTTGGGATTTAAAGCTGGTGTT]	Cox *et al*., 2001
		rcbL1[GGGATTTATGTCACCACAAACAGA]	Gadek & Quinn 1993
		rbcL2 [GATCTCCTTCCATACTTCACAAGC]	Gadek & Quinn 1993
rps4	chloroplast	rps5 [ATGTCCCGTTATCGAGGACCT]	Nadot *et al*. 1994
		trnas [TACCGAGGGTTCGAATC]	Souza-Chies *et al.* 1997
trnL-trnF	chloroplast	trnF [ATTTGAACTGGTGACACGAG]	Taberlet *et al.* 1991
		trnC [CGAAATCGGTAGACGCTACG]	Taberlet *et al.* 1991

Appendix

1. Genbank accesion numbers for sequences used in this study.

Taxon	***nr26S***	***rbcL***	***rps4***	***trnL-trnF***
Acromastigum anisostomum (Lehm. Et Lindenb.) A. Evans	JF316097	JF316321	JF316457	JF316588
Acromastigum mooreanum (Steph.) E. A. Hodgs.	JF315904	JF316318	JF316455	JF316587
Bazzania affinis (Lindenb. & Gottsche) Trevis.	AY608200	DQ439680	AY608048	JF316633
Bazzania involuta (Mont.) Trevis	JF315915	JF316323	JF316448	JF316631
Bazzania nitida (F. Weber) Grolle	JF315919	JF316322	JF316444	JF316630
Bazzania tricrenata (Wahlenb.)Lindenb.	JF315877	JF316310	JF316451	JF316635
Chloranthelia berggrenii (Herzog) R. M. Schust.	JF315931	JF316296	JF316423	JF316601
Drucella integristipula (Steph.) E. A. Hodgs.	JF315897	JF316287	JF316436	JF316576
Hygrolembidium rigidum R. M. Schust. & J. J. Engel	JF315932	JF316299	JF316422	JF316602
Isolembidium anomalum (Rodway) Grolle	JF315926	JF316294	JF316416	JF316600
Kurzia brevicalycina (Steph.) Grolle	JF315918	EF100993	JF316427	EF101102
Kurzia calcarata (Steph.) Grolle	JF315921	JF316301	JF316428	JF316596
Kurzia dendroides (Carrington & Person) Grolle	JF315920	EF100996	JF316418	EF101105
Kurzia helophila R. M. Schust.	JF315923	JF316300	JF316431	JF316597
Lembidium nutans (Hook. F & Taylor) Mitt. ex A. Evans	JF315922	EF100992	JF316419	EF101046
Lepidozia bisbifida Steph.	JF315940	JF316305	JF316480	JF316627
Lepidozia brasiliensis Steph.	*new*	*new*	*new*	*new*
Lepidozia inaequalis (Lehm. & Lindenb.) Lehm. & Lindenb.	*new*	*new*	*new*	*new*
Lepidozia laevifolia (Hook. & Taylor) Gottsche, Lindenb & Ness	JF315906	EF101000	JF316472	EF101109
Lepidozia macrocolea Spruce	*new*	*new*	*new*	*new*
Lepidozia setigera Steph.	JF315907	JF316326	JF316471	JF316625
Lepidozia trichodes (Reinw. ex Blume & Nees) Gottsche	JF315898	JF316324	JF316479	JF316624
Lepidozia ulothrix (Schwägr.) Lindenb.	JF315939	JF316306	JF316473	JF316626
Mastigobryum lenormandii Steph.	JF315916	EF100989	JF316449	EF101096
Mastigobryum limbatum Steph.	JF315908	EF100990	JF316446	EF101097
Megalembidium insulanum (W. Martin & E. A. Hodgs)	JF315925	EF101005	JF316417	EF101115
Micropterygium lechleri Reimers	*new*	*new*	*new*	*new*
Micropterygium lechleri Reimers	*new*	*new*	*new*	*new*
Micropterygium leiophyllum Spruce	*new*	*new*	*new*	*new*
Micropterygium pterygophyllum (Nees) Trevis.	*new*	*new*	*new*	*new*
Micropterygium trachyphyllum Reimers	*new*	*new*	*new*	*new*
Micropterygium trachyphyllum Reimers	*new*	*new*	*new*	*new*
Micropterygium trachyphyllum Reimers	*new*	*new*	*new*	*new*

Neogrollea notabilis E. A. Hodgs	JF315891	JF316288	JF316443	JF316605
Paracromastigum drucei (R. M. Schust.) R. M. Schust.	JF315887	JF316283	JF316461	JF316586
Paracromastigum macrostipum (Steph.) R. M. Schust.	JF315874	JF316303	JF316434	JF316628
Pseudocephalozia lepidozioides R. M. Schust.	JF315893	JF316289	JF316413	JF316593
Pseudocephalozia paludicola R. M. Schust.	JF315894	JF316290	JF316414	JF316594
Psiloclada clandestina Mitt.	JF315868	EF101007	JF316458	EF101116
Telaranea chaetocarpa (Pearson) Grolle	JF315886	EF101011	JF316462	EF101120
Telaranea herzogii (E. A. Hodgs.) E. A. Hodgs.	JF315903	JF316309	JF316440	JF316639
Telaranea heterotexta (Steph.) J. J. Engel & G. L. Merr.	JF315910	EF101012	JF316464	EF101121
Telaranea lawesii (Steph.) Grolle	JF315885	JF316332	JF316469	JF316606
Telaranea lindenbergii (Gottsche) J. J. Engle & G. L. Merr.	JF315884	JF316316	JF316482	JF316608
Telaranea martinii (E. A. Hodgs.) R. M. Schust.	JF315936	JF316330	JF316484	JF316615
Telaranea palmata J. J. Engel & G. L. Merr.	JF315914	JF316317	JF316468	JF316612
Telaranea patentissima (Hook. & Taylor) E. A. Hodgs.	JF315867	EF101016	JF316465	EF101125
Telaranea pulcherrima (Steph.) R. M. Schust.	AY608256	DQ439704	AY608114	JF316618
Telaranea tetrapila (Hook. & Taylor) J. J. Engel & G. L. Merr.	JF315913	JF316329	JF316467	JF316611
Telaranea trilobata (R. M. Schust.) J. J. Engel & G. L. Merr.	JF315917	JF316293	JF316429	JF316599
Telaranea wallichiana (Gottsche) R. M. Schust.	JF315892	JF316328	JF316463	JF316609
Tricholepidozia chaetocarpa (Pearson) E.D. Cooper	JF315886	EF101011	JF316462	EF101120
Zoopsis liukiuensis Horik.	JF315911	EF101024	JF316441	EF101134
Zoopsis macrophylla R. M. Schust.	JF315882	JF316286	JF316433	JF316574
Zoopsis setulosa Leitg.	JF315912	EF101025	JF316525	EF101135
Lepicolea attenuata (Miit.) Steph.	DQ268888	AY507410	AY507452	AY507540
Lepicolea rara (Steph.) Grolle	AY608227	DQ439691	AY608081	JF316579
Temnoma pulchellum (Hook.) Mitt. ex. Bastow	AY608257	DQ439705	AY608115	JF316575
Triandrophyllum subtrifidum (Hook & Taylor) Fulford & Hatcher	AY608259	DQ439706	AY608117	JF316580

2. Morphological characters combined of the Lepidoziaceae and out group.

		Planta dicotomata	Planta sub dicotomata	Filídios	Filídios segmentado	Filídio lobulado	Filídios com dentes	Filídios com vitta	Filídios com asa	Filídios sucubos	Filídios planos	Margem do filídio - denteada/lisa	Anfigastro
Bazzanioideae Rodway	*Acromastigum* A.Evans	1	0	1	0	1	0	0	0	1	0	0	1
	Bazzania Gray	1	0	1	0	1	1	1	0	0	1	0	1
	Micropterygium Gottsche	1	0	1	0	0	1	0	0		1	0	1
Drucelloideae R.M.Schust.	*Drucella* E.A.Hodgs.	1	0	0	0	0	0	0	0	0	1	0	0
Lembidioideae R.M.Schust.	*Hygrolembidium* R.M.Schust.	1	0	2	0	1	1	0	0	1	0	1	1
	Isolembidium R.M.Schust.	0	1	2	0	1	0	0	0	1	0	1	1
	Kurzia G.Martens	1	0	0	1	0	0	0	0	0	0	1	2
	Lembidium Mitt.	1	0	2	0	1	0	0	1	1	0	1	1
	Megalembidium R.M.Schust.	1	0	2	0	1	1	0	0	1	0	1	1
	Pseudocephalozia R.M.Schust.	1	0	0	0	0	0	0	0	0	1	0	1
Lepidozioideae Müll.Frib.	*Lepidozia* (Dumort.) Dumort.	1	0	0	0	0	0	1	0	0	1	0	0
	Tricholepidozia (R.M.Schust.) E.D.Cooper	1	1	0	0	0	0	1	0	1	0	0	0
Zoopsidoideae R.M.Schust.	*Neogrollea* E.A.Hodgs.	1	0	0	0	0	1	0	0	1	0	1	0
	Paracromastigum Fulford et J.Taylor	1	0	1	0	0	0	0	0	1	0	1	1
	Psiloclada Mitt.	1	0	0	1	0	0	0	0	1	0	1	1
	Telaranea Spruce ex Schfn.	1	0	0	1	0	0	0	0	0	0	1	2
	Zoopsis Hook.f. ex Gottsche	1	0	4	0	1	0	0	0	0	0	1	2
Out group	*Lepicolea* Dumort.	1	0	0	1	0	1	0	0	1	0	0	0
	Mastigophora Nees.	1	0	0	1	0	1	0	0	1	0	0	0
	Temnoma Mitt.	1	0	0	1	0	1	0	0	1	0	0	0
	Triandrophyllum Fulford & Hatcher	1	0	0	1	0	1	0	0	1	0	0	0