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FÚVIO RUBENS OLIVEIRA DA SILVA

REVISÃO TAXONÔMICA INTEGRATIVA DAS ESPÉCIES NEOTROPICAIS DE RADULACEAE (MARCHANTIOPHYTA)

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2024

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Tese de doutorado apresentado ao Curso de Pós-Graduação em Ciências Biológicas – Botânica Tropical da Universidade Federal Rural da Amazônia (UFRA)/ Museu Paraense Emílio Goeldi (MPEG), para defesa de doutorado.
Orientador: Dra. Anna Luiza Ilkiu Borges Benkendorff
(Museu Paraense Emílio Goeldi)
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Tese de doutorado apresentada ao Programa de Pós-Graduação em Ciências Biológicas, área de concentração Botânica Tropical, da Universidade Federal Rural da Amazônia e Museu Paraense Emílio Goeldi, para a obtenção do título de doutor.

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RESUMO

Radulaceae Müll. Frib. (Porellales Schljakov; Radulinae R.M.Schust.) é um grupo diverso, com mais de 300 espécies distribuídas no mundo e uma das linhagens mais isoladas das hepáticas folhosas (Marchantiophyta Stotl. & Crand.-Stotl.; Jungermanniidae Engl.). Características morfológicas diagnósticas da família incluem rizóides em tufos na superfície do lóbulo, ramos do tipo-*Radula*, oleocorpos grandes e marrons, ausência de anfigastros e periantos tubulares, achatados dorsiventralmente. O centro de diversidade das espécies está nas regiões tropicais úmidas, apesar de estarem distribuídas em todos os continentes, exceto na Antártica. A maioria das espécies cresce como epífita em florestas tropicais preservadas, desde as planícies até as florestas montanas acima de 4000 m de altitude. A família apresenta três gêneros (*Cladoradula*, *Dactyloradula* e *Radula*), mas a maioria das espécies pertencem ao gênero *Radula* Dumort., que é subdividido em cinco subgêneros: *Amentuloradula* Devos *et al.*, *Metaradula* R.M.Schust., *Odontoradula* K.Yamada, *Radula* e *Volutoradula* Devos *et al*. As circunscrições desses subgêneros são problemáticas e as divisões subgenéricas, suportadas apenas por dados moleculares, não são claras, especialmente entre as espécies neotropicais. As espécies de Radulaceae que ocorrem em florestas temperadas e nas regiões paleotropicais do mundo tiveram sua taxonomia revisada, restando uma lacuna de conhecimento taxonômico para as espécies da região neotropical, com mais de 140 nomes descritos e cerca de 75 espécies atualmente aceitas. Uma revisão preliminar das espécies de Radulaceae no Brasil mostrou que o número dessas espécies atualmente aceitas é provavelmente excessivo e que várias delas podem ser sinônimos, embora novas espécies ainda possam ser descobertas. O objetivo deste estudo é realizar uma revisão taxonômica integrativa das espécies neotropicais de Radulaceae, baseado no estudo abrangente de tipos, coleções adicionais de herbários e coletas em campo, usando evidências morfológicas, anatômicas, ecológicas e palinológicas. Logo no início desse estudo, foi possível identificar táxons novos com características marcantes como filídios bordeados (Capítulo I). Além da revisão das espécies da América tropical, foi feito uma revisão das espécies de Radulaceae da África tropical, em especial de Madagascar, o que resultou na descoberta de dois novos sinônimos de espécies neotropicais em um africano (Capítulo II). No âmbito da revisão taxonômica, foi dado atenção especial a características pouco estudadas que podem ser taxonomicamente informativas, como os esporos. No Capítulo III, foi realizada a primeira avaliação palinológica de dezesseis espécies de Radulaceae. Os dados palinológicos, especialmente a ornamentação dos esporos, podem ser uma contribuição importante para a taxonomia de Radulaceae na separação de espécies ou grupos de espécies. A partir da totalidade dos dados e do maior entendimento na circunscrição das espécies, a taxonomia de Radulaceae foi revisada, na qual são apresentadas descrições detalhadas das espécies, ilustrações de táxons selecionados, chave de identificação para todas as espécies e comentários sobre suas relações, distribuição geográfica (com mapas) e habitat (Capítulo IV). A revisão reconheceu 54 espécies e seis variedades, partindo de 75 espécies inicialmente aceitas para o Neotrópico. Três novas espécies foram descobertas e são descritas nesse último capítulo, bem como três táxons são restabelecidos, já que estavam como sinônimos de outras espécies; uma combinação nova foi proposta, assim como 27 novos sinônimos, 42 novos lectótipos, e seis espécies foram colocadas como duvidosas ou excluídas. A revisão taxonômica de Radulaceae na América tropical implicou no melhor entendimento sobre a circunscrição e distribuição os táxons, criando uma base segura que irá auxiliar a realização de futuros estudos.

Palavras-chave: América tropical, *Radula*, *Cladoradula*, hepáticas folhosas, taxonomia.

ABSTRACT

Integrative taxonomic revision of neotropical species of Radulaceae (Marchantiophyta)

Radulaceae Müll. Frib. (Porellales Schljakov; Radulinae R.M.Schust.) is a diverse group with more than 300 species distributed worldwide and one of the most isolated lineages of the leafy liverworts (Marchantiophyta Stotl. & Crand.-Stotl.; Jungermanniidae Engl.). Distinctive morphological diagnostics of the family include rhizoids in tufts on the lobule surface, *Radula*-type branches, large, brown oilbodies, absence of underleaves, and perianth tubular, dorsiventrally flattened. The center of diversity of the species is in the humid tropical regions, although they are distributed on all continents except Antarctica. Most species grow as epiphytes in preserved tropical forests, from the lowlands to montane forests above 4000 m altitude. The family has three genera (*Cladoradula*, *Dactyloradula* and *Radula*), but most species belong to the genus *Radula* Dumort., which is subdivided into five subgenera: *Amentuloradula* Devos *et al.*, *Metaradula* R.M.Schust., *Odontoradula* K.Yamada, *Radula* e *Volutoradula* Devos *et al*. Circunscriptions of these subgenera are problematic and the subgeneric divisions, supported only by molecular data, are unclear, especially among neotropical species. The species of Radulaceae that occur in temperate forests and in the paleotropical regions of the world have had their taxonomy reviewed, leaving a gap in taxonomic knowledge for the species of the neotropical region, with more than 140 names described and around 75 species currently accepted. A preliminary revision of the species of Radulaceae in Brazil showed that the number of these currently accepted species is probably excessive and that several of them may be synonyms, although new species may yet be discovered. The aim of this study is to carry out an integrative taxonomic revision of the neotropical species of Radulaceae, based on a comprehensive study of types, additional herbarium collections and field collections, using morphological, anatomical, ecological and palynological evidence. Early on in this study, it was possible to identify new taxa with striking features such as bordered leaves (Chapter I). In addition to the review of species from tropical America, a revision was made of Radulaceae species from tropical Africa, especially Madagascar, which resulted in the discovery of two new synonyms of neotropical species in one African (Chapter II). As part of the taxonomic revision, special attention was paid to little-studied characteristics that can be taxonomically informative, such as spores. In Chapter III, was carried out the first palynological assessment of sixteen species of Radulaceae. Palynological data, especially spore ornamentation, can be an important contribution to the taxonomy of Radulaceae in separating species or groups of species. From the totality of the data and the greater understanding in the circumscription of the species, the taxonomy of Radulaceae was revised, in which detailed descriptions of the species, illustrations of selected taxa, identification keys for all species and comments on their relationships, geographical distribution (with maps) and habitat are presented (Chapter IV). The revision recognized 54 species and six varieties, starting from 75 species initially accepted for the Neotropics. Three new species were discovered and are described in this last chapter, as well as three taxa were reinstated as synonyms of other species; a new combination was proposed, as well as 27 new synonyms, 42 new lectotypes, and six species were placed as doubtful or excluded. The taxonomic revision of Radulaceae in tropical America has led to a better understanding of the circumscription and distribution of the taxa, creating a secure base that will help in future studies.

Key words: Tropical America, *Radula*, *Cladoradula*, leafy liverworts, taxonomy.

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CONTEXTUALIZAÇÃO

Radulaceae

Hepáticas folhosas (Marchantiophyta: Jungermanniidae) com ca. de 5.000 espécies em ca. de 50 famílias é um dos grupos mais diversos das primeiras plantas terrestres, com uma longa história evolutiva (HEINRICHS *et al.*, 2006; CRANDALL-STOTLER *et al.*, 2009; FELDBERG *et al.*, 2014; BECHTELER *et al.*, 2023). Dentre eles, Radulaceae Müll. Frib. se destaca como uma das linhagens mais isoladas (filogeneticamente) e diversificadas de Porellales, uma ordem composta de seis grandes famílias tipicamente epifíticas e que tiveram seu sucesso evolutivo no estabelecimento das florestas tropicais dominadas por angiospermas (CRANDALL-STOTLER *et al.*, 2009; FELDBERG *et al.*, 2014).

Radulaceae, com mais de 800 binômios e cerca de 300 espécies no mundo (RENNER 2015), apresenta maior diversidade nas regiões tropicais do globo e a maioria das espécies crescem em florestas primárias ou secundárias tardias, em áreas de planície a montanas. Elas estão preferencialmente presentes em ambientes úmidos e sombreados, com alto nível de preservação (GRADSTEIN *et al.*, 2001; OLIVEIRA-DA-SILVA *et al.*, 2021). Devido a essa sensibilidade, Radulaceae pode ser considerada como um grupo indicador de ambientes preservados. A presença ou ausência de táxons ou grupos de táxons podem indicar o estado de conservação ou o potencial de diversidade de um local (ALVES *et al.*, 2016).

Traços morfológicos únicos da família, como os ramos tipo-*Radula* (ramo que se origina de uma célula epidérmica do caulídio e, portanto, associado a um filídio não modificado), ausência de anfigastros, presença de rizoides em tufos na superfície do lóbulo e perianto tubular, dorsiventralmente achatado, podem naturalmente distinguir Radulaceae dos outros grupos de hepáticas folhosas, especialmente as da mesma ordem e que de certa forma se assemelham pela cor e tamanho (SCHUSTER, 1980a; YAMADA, 1979; GRADSTEIN *et al.*, 2001; OLIVEIRA-DA-SILVA *et al.*, 2021). Estudos recentes (ASAKAWA *et al.*, 2020; HUSSAIN *et al.*, 2019) mostram que os oleocorpos de Radulaceae também são diferentes, morfologicamente e quimicamente, dos outros grupos de hepáticas. A maioria das espécies apresentam oleocorpos grandes e marrons, contendo principalmente bibenzil.

Vários dos componentes bibenzílicos apresentam atividades biológicas, como psicoatividade, antagonistas do receptor de vasopressina (VRAs), atividade antimicrobiana, antifúngica e inibidora da produção de NO (Óxido Nítrico), além de atividade citotóxica contra

linhas celulares de câncer humano (CHICCA *et al.*, 2018; ASAKAWA *et al.*, 2020; HUSSAIN *et al.*, 2019; FAN *et al.* 2021). Bibenzil cis-tetrahidrocanabinol e (-)-cis-perrottetineno foram isolados em três espécies de *Radula*, sendo uma delas neotropical. Esses compostos químicos se assemelham estruturalmente ao (-)-Δ9-trans-tetrahidrocanabinol encontrados somente na *Cannabis sativa* L. (CHICCA *et al.*, 2018).

Além da importância ecológica e química, Radulaceae tem sido modelo para a elucidação de padrões filogenéticos e biogeográficos das primeiras plantas terrestres. A família mostra uma intrigante variedade de padrões de distribuição intercontinental, incluindo faixas tropicais anfi-Atlântica e anfi-Pacífica (PATIÑO *et al.*, 2017).

Histórico

O histórico de Radulaceae nos neotrópicos está apresentado no capítulo IV deste documento, na seção “Historical Survey”.

Classificação tradicional

Diferentes sistemas de classificação para *Radula* foram propostos entre 1884 a 1980 (*e.g.* STEPHANI, 1884; 1910; SPRUCE, 1885; YAMADA, 1979; SCHUSTER, 1980a, b), todos baseados em caracteres morfológicos do gametófito. O primeiro a classificar *Radula* foi Stephani (1884), que reconheceu 92 espécies distribuídas em 12 táxons informais (não ranqueados) (*Acutifoliae*, *Macrolobae*, *Ampliatae*, *Communes*, *Javanicae*, *Micolobae*, *Plumulosae*, *Saccatilobae*, *Longilobae*, *Tumidae*, *Amentulosae* e *Cavifoliae*). O último autor incluiu características morfológicas, principalmente aquelas relacionadas aos lobos, lóbulos e ramos, para definir seus táxons. *Macrolobae*, por exemplo, incluía espécies que apresentavam lóbulos bem desenvolvidos, com base cobrindo o caulídio, como em *Radula voluta* Gottsche *et al*. e *R. quadrata* Gottsche.

Quase simultaneamente, Spruce (1885) propôs uma classificação infragenérica com base em 13 espécies e sete variedades de *Radula* coletadas em sua expedição à Amazônia e aos Andes, e as subdividiu em dois subgêneros, *Acroradula* e *Cladoradula*. Esse último subgênero compreendia apenas *Radula gottscheana* Taylor, reconhecida pela cápsula oblongo-globosa, perianto em ramos laterais curtos, com a boca larga e sem inovações, enquanto o subgênero típico *Acroradula* foi definido pela cápsula oblongo-cilíndrica, perianto em ramos terminais longos ou no ramo principal, boca do perianto estreita e ginoécio com inovação.

Em *Species Hepaticarum*, Stephani (1910) reconheceu 220 espécies de *Radula* para o globo, das quais 66 tiveram distribuição atribuída à América tropical e subtropical. Stephani (1910) não considerou a classificação de Spruce e apenas reduziu de 12 para sete os grupos não ranqueados já considerados em seu primeiro tratamento (*Acutifoliae*, *Appendiculatae*, *Ampliatae*, *Communes*, *Microlobae*, *Longilobae* e *Amentulosae*).

Após 26 anos, Hampstead Castle iniciou a revisão mundial do *Radula* publicando 11 artigos divididos em duas partes. A primeira englobando espécies *Radula* subg. *Cladoradula* (CASTLE, 1936; 15 espécies), e a segunda parte reunindo seções - em sua maioria propostas como grupos informais por Stephani (1884, 1910) - pertencentes a *Radula* subg. *Acroradula*, como *Epiphyllae* (CASTLE, 1938; 10 spp.), *Amentulosae* (CASTLE, 1950; 6 spp.), *Dichotomae* (CASTLE, 1959a; 22 spp.), *Marginatae* (CASTLE, 1959b; 2 spp.), *Lingulatae* (CASTLE, 1962; 4 spp.), *Saccatae* (CASTLE, 1963; 51 spp.), *Acutilobulae* (CASTLE, 1964; 11 spp.), *Densifoliae* (CASTLE, 1965; 29 spp.), *Ampliatae* (CASTLE, 1966; 35 spp.) e *Complanatae* (CASTLE, 1967; 44 spp.). Castle (1967) incluiu mais três espécies, como suplemento, que não pertenciam aquele subgênero ou seção: *Radula nigra* Person (sem subg.), *R. obiensis* Hattori (subg. *Cladoradula*) e *R. galapagona* Steph. (subg. *Acroradula* sect. *Ampliatae*).

Os subgêneros *Cladoradula* e *Radula* (= *Acroradula nom. ileg.*) e grupos/seções usadas no tratamento de Stephani e Castle foram a maioria formalizadas por Grolle (1970), que propôs diagnoses em latim e designou espécimes-tipo para cada uma delas. Essas classificações, todavia, foram fortemente criticadas por Jones (1977), que realizou um estudo taxonômico para as espécies de *Radula* do continente africano. Jones (1977) discutiu que essas seções eram puramente artificiais, na medida em que considerava espécies morfologicamente próximas em seções separadas.

O estudo de Jones (1977) foi o primeiro a chamar atenção para uma série de características morfológicas importantes que não eram usadas para a delimitação de grupos e na diferenciação de espécies, incluindo o formato da cápsula do esporófito, perianto e lóbulo, e anatomia do caulídio. Esse último caráter foi usado por Jones (1977) para identificar cinco grupos distintos na flora africana de *Radula*.

Um novo subgênero foi proposto por Yamada (1979) em seu tratamento para as espécies de *Radula* do continente asiático. *Radula* subg. *Odontoradula* K.Yamada (espécie tipo *Radula ocellata* K.Yamada) incluía espécies com uma morfologia única, especialmente pelos filídios

com ápice agudo a apiculado, margem usualmente denteadas, ginoécio terminal nos caulídios ou em ramos longos, com mais de um par de brácteas denteadas e perianto com boca denteada.

Desde a década de 80, Kohsaku Yamada dedicou-se somente aos estudos do gênero *Radula* em várias regiões do mundo, como Nova Caledônia (YAMADA, 1985), Queensland, na Austrália (YAMADA, 1984, 1987b), Península de Huon, em Papua-Nova Guiné (YAMADA; PIIPPO, 1989), Monte Kinabuli, na Malásia (YAMADA, 1989), Zaire e Rwanda (YAMADA, 1993b), Japão (YAMADA, 1996), e em países ou localidades nos Neotrópicos como Cuba (YAMADA, 1988), Ilha de Galápagos, no Equador (YAMADA; GRADSTEIN, 1991), Bolívia (YAMADA, 2000), e Brasil (YAMADA, em GRADSTEIN; COSTA, 2003). Este mesmo autor dedicou-se também a revisar os espécimes-tipo de *Radula* da América Latina (YAMADA, 1980, 1981, 1982a, 1987a, 1991, 1993a) e descrever novas espécies para a ciência, incluindo muitas para a América tropical (*e.g.* YAMADA, 1982b, 1982c, 1983, 1990).

Como consequência dos estudos sobre *Radula* na América do Norte, Schuster (1980b) propôs o quarto subgênero, Radula subg. *Metaradula* R.M.Schust. [espécie tipo *Radula buccinifera* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees], que foi validado quatro anos depois (SCHUSTER, 1984). *Radula* subg. *Metaradula* foi proposta com base em espécies que ocorriam sobre folhas (epífilas) e que apresentavam perigínio do tipo-*Isotachis* (estrutura tubular que envolve e protege o desenvolvimento do esporófito e que é derivada do tecido do caulídio; tipo-*Isotachis* = ereto). Assim como Jones (1977), Schuster (1980a, b) criticou as classificações propostas anteriormente para o gênero, destacando a falta de atenção no estudo de certas características morfológicas relevantes, como a morfologia e anatomia do esporófito.

Mediante os estudos tradicionais (Spruce 1885, Yamada 1979, Schuster 1980), o gênero *Radula* ficou dividido em quatro subgêneros, dos quais três (subg. *Cladoradula*, *Odontoradula* e *Metaradula*) segregavam espécies que apresentavam características morfológicas similares na formação de grupos, e apenas um (subg. *Radula*) contendo o restante e a maioria das espécies, refletindo ainda a falta de compreensão sobre a classificação infragenérica de *Radula*.

Estudos filogenéticos moleculares

Radulaceae foi alvo de estudos filogenéticos com base em dados moleculares (DEVOS *et al.*, 2011a,b; RENNER, 2014; RENNER *et al.*, 2013a,b,c; PATIÑO *et al.*, 2017; PROMMA *et al.*, 2018; ZANG *et al.*, 2021). Cerca de 100 espécies dessa família já foram sequenciadas e inseridas em análises filogenéticas. Essas investigações em Radulaceae foram baseadas em regiões de cloroplasto: *psbT-psbH*, *psb-trnH*, *rps4*, *atpB-rbcL*, *trnG* e *trnL-trnF*.

Devos *et al.* (2011b), que propuseram a primeira classificação subgenérica de *Radula* baseada em dados moleculares e morfológicos, testaram o monofiletismo dos subgêneros tradicionalmente conhecidos (*Radula*, *Cladoradula*, *Odontoradula* e *Metaradula*), incluindo em suas análises os espécimes-tipos de cada um, e encontrou clados bem suportados. Até mesmo o subgênero *Radula*, que continha o restante das espécies heterogêneas e que não se assemelhavam morfologicamente com os outros subgêneros, formou um clado bem suportado incluindo a espécie tipo do gênero, *Radula complanata*. Além disso, Devos *et al.* (2011b) reconheceram mais três linhagens distintas e propuseram três novos subgêneros: *Amentuloradula* Devos *et al.* [espécie tipo *Radula formosa* (Spreng.) Nees], *Dactyloradula* Devos *et al.* (*R. brunnea* Steph.) e *Volutoradula* Devos *et al.* (*R. voluta*).

Recentemente, Renner *et al.* (2022) elevaram os subgêneros *Cladoradula* (Spruce) M.A.M.Renner *et al.* e *Dactyloradula* (Devos *et al.*) M.A.M.Renner & Gradst. a nível de gênero. Os dois gêneros apresentaram-se como linhagens mais antigas e morfologicamente únicas dos demais grupos. As relações filogenéticas dos gêneros e subgêneros estão ilustradas na Figura 1.

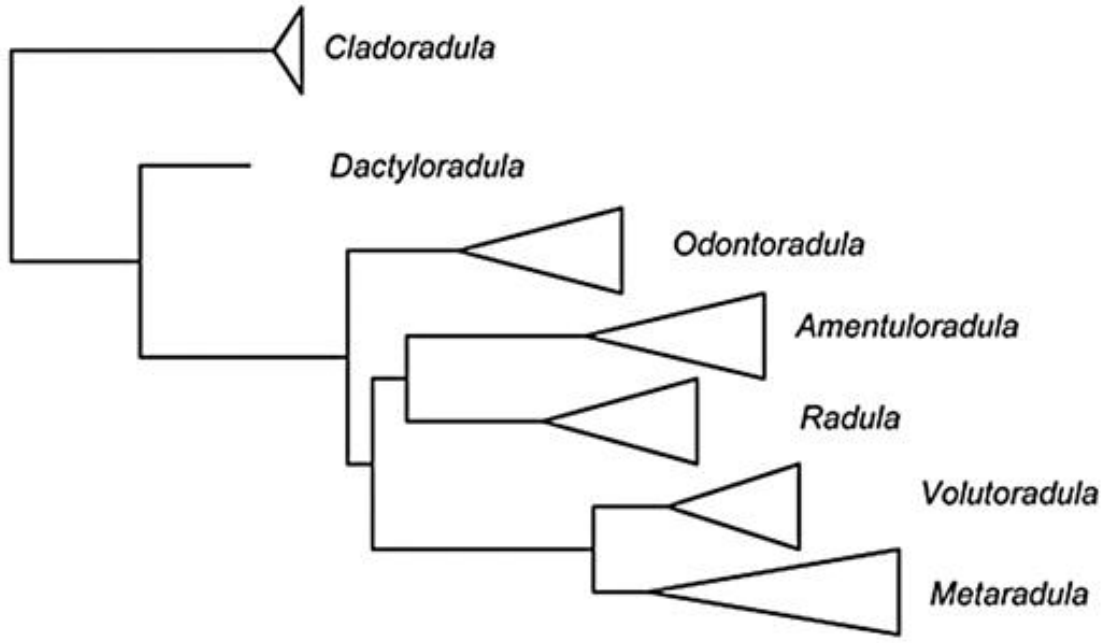

Figura 1. Relações filogenéticas entre os gêneros e subgêneros de Radulaceae. Fonte: Renner *et al.* (2013c).

Problemas e hipóteses

Apesar de morfologicamente distintos de outros grupos de hepáticas, os membros de Radulaceae não possuem muitas caraterísticas consideradas úteis na diferenciação entre as espécies (SCHUSTER, 1980a; RENNER; BRAGGINS, 2004). Não apresentam anfigastros, a maioria das espécies na América tropical apresenta filídios com ápice redondo a fracamente obtuso e margens inteiras, os periantos não variam consideravelmente e normalmente não apresentam estruturas como quilhas, dentes, cílios e lacínias e quase nenhuma espécie nos Neotropicos apresentam células especializadas (*e.g.* ocelos) ou claramente ornamentadas com papilas e mamilas. Além disso, características taxonomicamente importantes em Radulaceae como ramos micrófilos e/ou amentulosos e mais de um par de brácteas no ginoécio são raros nas espécies neotropicais, mas podem ser encontrados com frequência nas espécies de *Radula* que ocorrem em outras regiões do globo, especialmente Ásia e Austrália.

A escassez de caracteres morfológicos discrepantes entre os táxons, aliada a elevada plasticidade fenotípica encontrada em espécies neotropicais de Radulaceae [*e.g. R. javanica* Gottsche e *R. pallens* (Sw.) Mont.] são os grandes responsáveis pela dificuldade na identificação das espécies, podendo resultar em decisões taxonômicas equivocadas (SCHUSTER, 1980a, b). Alguns autores (*e.g.* SPRUCE, 1885; STEPHANI, 1910) tentaram lidar com a notável plasticidade fenotípica do gametófito de Radulaceae, descrevendo várias espécies cuja circunscrição se baseava em poucos caracteres e que ainda se sobrepunham. Com o avanço nos estudos da família, uma série de sinônimos foram propostos, mas algumas espécies ainda são extremamente duvidosas e pouco conhecidas (RENNER, 2016).

Radulaceae atualmente está dividida filogeneticamente e morfologicamente em três gêneros (RENNER *et al.*, 2022): *Cladoradula*, *Dactyloradula* e *Radula*. Todavia, a maioria das espécies pertencem a *Radula*. Esse último gênero contém cerca de 300 espécies em cinco subgêneros (DEVOS *et al.*, 2011b). Essa classificação subgenérica é baseada principalmente em dados moleculares e as definições morfológicas desses subgêneros permanecem problemáticas e a atribuição subgenérica de um número considerável de espécies ainda não é clara, especialmente das espécies que ocorrem na América tropical.

No "World Checklist of Hornworts and Liverworts" (RENNER, 2016), cerca de um terço das espécies neotropicais foram classificadas em nível subgenérico. As espécies restantes foram listadas como de afinidade subgenérica desconhecida "*Incertae sedis*". Isso ocorreu devido a pouca amostragem de espécies neotropicais nas reconstruções filogenéticas para o gênero (*e.g.* DEVOS *et al.*, 2011a,b; PATIÑO *et al.*, 2017).

Uma recente análise biogeográfica de Radulaceae (PATIÑO *et al.*, 2017) sugeriu um alto nível de endemismo das espécies que ocorrem na América Central e do Sul, especialmente em *Radula* subg. *Volutoradula.* Essa interessante hipótese biogeográfica, todavia, permanece sem fundamento à luz do conhecimento taxonômico, ainda incipiente, sobre as espécies da América tropical.

Revisões taxonômicas de Radulaceae se concentraram nas espécies que ocorrem em florestas temperadas e nas regiões paleotropicais do globo (*e.g.* YAMADA, 1979; JONES, 1977; SCHUSTER, 1980a; RENNER, 2005, 2014; RENNER *et al.*, 2013a,b,c; PROMMA; CHANTANAORRAPINT, 2015; SINGH *et al.*, 2016a, b), mas as espécies da região neotropical – um dos principais centros de diversidade do gênero com cerca de 75 espécies atualmente aceitas (RENNER, 2016; OLIVEIRA-DA-SILVA *et al.*, 2021; GRADSTEIN, 2021) – permanecem obscuramente delimitadas. As maiores contribuições para os Neotrópicos foram feitas por Castle (1936, 1939, 1959a, b, 1963, 1965, 1966, 1967) e Yamada (1980, 1981, 1982a, 1987a, 1991, 1993a). Todavia, a revisão mundial de Hempstead Castle é baseada em um número muito limitado de amostras e está desatualizada, enquanto as obras de Kohsaku Yamada foram restritas à revisão de espécimes tipo e descrições de novas espécies para a América Latina. Algumas listas e guias dispersos na região neotropical e que apresentam informações sobre o gênero são disponíveis para o Brasil (YAMADA, em GRADSTEIN; COSTA, 2003), Bolívia (YAMADA, 2000), Cuba (YAMADA, 1988), Equador (YAMADA; GRADSTEIN, 1991; GRADSTEIN, 2021), Guiana Francesa (GRADSTEIN; ILKIU-BORGES, 2009), México (FULFORD; SHARP, 1990), Colômbia (GRADSTEIN, 2021) e entre outros.

Estudos relacionados à taxonomia de Radulaceae ainda são um desafio. Schuster (1980a, b), Devos *et al.* (2011b) e Heinrichs *et al.* (2016) evidenciaram a necessidade de uma revisão substancial para esse grupo de hepáticas folhosas. Como mostrado anteriormente, as espécies exibem um padrão complexo de variação morfológica que confunde os limites entre as espécies e nenhuma sinapormofia real foi encontrada para os subgêneros de *Radula* atualmente aceitos.

Sinapomorfias reais provavelmente poderão ser encontradas através de estudo de características negligenciadas nos estudos de Radulaceae, e que taxonomicamente importantes para a definição de grupos em hepáticas, como: morfologia e quantidade de oleocorpos na célula, anatomia do caulídio, ornamentação da cutícula, estruturas de reprodução vegetativa, presença ou ausência de perigínio, e principalmente a morfologia e anatomia do esporófito

(SCHUSTER, 1980a, b; RENNER; BRAGGINS, 2004, 2005; DEVOS *et al.*, 2011b). Esse último inclui estudo dos esporos, elatérios, tamanho da seta, e morfologia e anatomia das células internas e externas das valvas.

Uma revisão taxonômica crítica das espécies neotropicais é extremamente necessária e preencheria uma importante lacuna de conhecimento. O autor desta tese, sob a mesma orientação, realizou uma revisão preliminar de Radulaceae no Brasil com base em evidências morfológicas e amostragem extensa (OLIVEIRA-DA-SILVA *et al.*, 2021). Os resultados mostraram que o número de espécies atualmente aceitas é provavelmente excessivo e que várias delas podem ser sinônimos, embora novas espécies ainda possam ser descobertas (OLIVEIRA-DA-SILVA; ILKIU-BORGES 2020, OLIVEIRA-DA-SILVA *et al.*, 2020).

Com base no conhecimento acumulado e no reconhecimento de suas lacunas, as seguintes questões foram formuladas: Qual a representatividade de Radulaceae nos Neotrópicos? Quais são as características que circunscrevem as espécies de Radulaceae nos Neotrópicos? Um novo olhar sobre caracteres gametofíticos e esporofíticos revelariam sinapomorfias que melhor sustentem as principais linhagens de *Radula*?

Com base nas questões formuladas, podemos inferir algumas hipóteses: 1) Radulaceae está subestimado e é insuficientemente conhecido na América tropical; 2) Devido a escassez de caracteres morfológicos taxonomicamente informativos aliados a elevada plasticidade fenotípica que algumas espécies apresentam, é necessário um conjunto maior de caracteres para delimitar as espécies de Radulaceae, em especial as espécies do gênero *Radula*; 3) A geração esporofítica fornecerá sinapomorfias definidoras de clados em *Radula* juntamente com caracteres gametofíticos que foram negligenciados na taxonomia do gênero.

Objetivo geral

O objetivo geral deste estudo é realizar uma revisão taxonômica integrativa das espécies neotropicais de Radulaceae, baseada no estudo abrangente de tipos, coleções adicionais de herbários e coletas em campo, usando evidências morfológicas, anatômicas, ecológicas e palinológicas.

Organização da tese

Esta tese está organizada em quatro capítulos:

Capítulo I: Two new Neotropical taxa of *Radula* Dumort. (Marchantiophyta: Radulaceae) with bordered leaves

Dois novos táxons foram descobertos durante o estudo das coleções de herbários internacionais. *Radula pallens* var. *marginata* e *R. smithii* (*Radula* subg. *Volutoradula*) foram recentemente descritos para as montanhas da Venezuela e Peru, respectivamente. Ambos os táxons se destacam pela presença de filídios bordeados por células diferenciadas. A nova variedade difere de *R. pallens* var. *pallens* pelo filídio bordeado por uma fileira de células incolores com trigonios salientes, enquanto *R. smithii* se destaca por uma fileira de 3 a 5 células de largura uniformemente espessas e borda de coloração marrom-avermelhada. Foram fornecidas uma descrição completa e ilustração dos dois novos táxons, bem como comentários sobre morfologia, taxonomia e distribuição (com mapas). Este manuscrito foi publicado a revista Phytotaxa.

Capítulo II: Afro-American Radulaceae (Marchantiophyta): Taxonomic Scrutiny Reveals New Synonymy in *Radula fulvifolia*

No decorrer do estudo taxonômicos sobre Radulaceae na América e na África tropical (GRADSTEIN *et al.*, 2022), notamos uma grande semelhança entre a espécie africana *Radula fulvifolia* e as neotropicais *R. galapagona* e *R. schaefer-verwimpii*. A observação dos espécimes tipos e coleções adicionais de vários herbários mostrou que essas três espécies são morfologicamente idênticas e constituem uma única espécie bastante polimórfica. Nosso estudo leva a um aumento adicional no número de táxons Afro-Americanos que emergem de trabalhos taxonômicos sobre hepáticas tropicais.

Capítulo III: Spores of Radulaceae (Marchantiophyta) exhibit a level of micromorphological diversity far beyond expectation

Este capítulo objetivou investigar os esporos de Radulaceae usando técnicas palinológicas padronizadas a fim de analisar a variação no tamanho e na ornamentação dos esporos e determinar se as circunscrições genéricas e subgenéricas são apoiadas pela morfologia dos mesmos. Os dados palinológicos, especialmente a ornamentação dos esporos, podem ser importantes para a taxonomia de Radulaceae na separação de espécies ou grupos de espécies. No entanto, esses grupos, não correspondem totalmente às circunscrições genéricas e infragenéricas, conforme sustentado por evidências filogenéticas moleculares. As informações

palinológicas sobre um número maior de espécies podem contribuir para uma compreensão mais clara das relações filogenéticas dentro da Radulaceae.

Capítulo IV: Taxonomic revision of Radulaceae (Machantiophyta: **Jungermanniidae) in tropical America**

Este capítulo teve como principal objetivo revisar a taxonomia das espécies neotropicais de Radulaceae a fim de contribuir para o entendimento de sua diversidade. Neste capítulo, são apresentadas descrições completas, chave, notas taxonômicas, incluindo as alterações e novidades taxonômicas necessárias, descrição de novas espécies, informações sobre distribuição geográfica (com mapas) e habitat, chave de identificação interativa, ilustrações e outros aspectos relevantes em uma revisão taxonômica.

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CAPÍTULO I

Título: Two new Neotropical taxa of *Radula* Dumort. (Marchantiophyta: Radulaceae) with bordered leaves

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Two new Neotropical taxa of *Radula* Dumort. (Marchantiophyta: Radulaceae) with bordered leaves

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Abstract

Radula pallens var. *marginata* and *R. smithii* (subg. *Volutoradula*) are newly described from montane forests of Venezuela and Peru, respectively. Both taxa stand out by the presence of bordered leaf lobes. The new variety differs from *R. pallens* var. *pallens* in its narrow leaf border of one row of colorless cells with bulging trigones, while *R. smithii* stands out by a broad, 3–5 cell rows wide, reddish-brown border made up of evenly thick-walled cells. A broad, pigmented leaf border of evenly thick-walled cells is also found in *R. ligula* from Brazil and Argentina, and in *R. marginata* (subg. *Amentuloradula*), from New Zealand, but the latter two species have very different lobules and stem anatomy. A full description and illustration of the two new taxa as well as comments on morphology, taxonomy and distribution are provided.

Key words. Liverworts, Neotropics, new species, new variety, *Radula* subg. *Volutoradula*, taxonomy

Introduction

Bordered leaves, characterized by leaf cell margins differentiated in cell shape, size, thickness, color or number of cell layers, are very common and characteristic in mosses, but much less in liverworts (Gradstein *et al.* 2001). In liverworts, they are commonly seen in species of *Adelanthus* Mitten (1864: 243), *Bazzania* Gray (1821: 704), *Calypogeia* Raddi (1818: 31), *Odontoschisma* (Dumortier 1831: 68) Dumortier (1835: 19), *Plagiochila* (Dumortier 1831: 42) Dumortier (1835: 14), *Scapania* (Dumortier 1831: 38) Dumortier (1835: 14) and a few genera of Lejeuneaceae Rostovzev (1913: 94). In other groups, leaf borders are absent or rare (*e.g.*, Paton 1999, Schuster 2000, 2002, Gradstein & Ilkiu-Borges 2015, Gradstein 2021). *Radula* Dumortier (1822: 112) is an example of a liverwort genus in which bordered leaves are an uncommon morphological feature (*e.g.*, Castle 1959, Yamada 1979, 1990, Renner & Braggins 2004, Oliveira-da-Silva *et al.* 2021). They occur in *R. wichurae* Stephani (1910: 168) from Macaronesia, which has leaf lobes bordered by one or more rows of small, thin-walled, hyaline cells, and in *R. marginata* Gottsche *et al.* (1845: 261) from New Zealand and *R. ligula* Stephani (1910: 228) from the Atlantic coast of Brazil and northern Argentina, which are characterized by a leaf border of small, thick-walled cells. In addition, a narrow border composed of 1–5 rows of thin-walled, hyaline cells is seen on the leaf lobules of *R. iwatsukii* Yamada (1979: 275) from Malesia, *R. scariosa* Mitten (1861: 367) from Fiji and *R. squarrosa* Yamada (1990: 1) from northern Australia.

During the ongoing project "Integrative taxonomic revision of *Radula* Dumort. (Marchantiophyta: Radulaceae) in the Neotropics" the authors came across two apparently undescribed taxa of *Radula* characterized by bordered leaves. One, collected in Venezuela by K. Mägdefrau in 1958 and kept in JE, was identical to *R. pallens* (Swartz 1788: 143) Montagne (1839: 71) except for the presence of a row of margin cells with larger, bulging trigones and a thickened outer wall. The specimen had been cited in Mägdefrau (1983) by K. Yamada, who believed that it belonged to an undescribed species, but the new taxon was not formally described. As the leaf border is the only feature separating the specimen from *R. pallens*, the plant is described here as a new variety of *R. pallens*. The other specimen, collected

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in Peru by D. Smith and kept in MO, had leaf lobes with a striking, reddish-brown border of thick-walled cells. A somewhat similar border is seen in *R. ligula* and *R. marginata*, but the latter two species have very different lobules and stem anatomy. The specimen also somewhat resembled *R. pallens*, but differed from the latter species in its leaf border and several other important aspects. Therefore, the Peruvian plant is described here as a new species.

The two new taxa are both members of *Radula* subg. *Volutoradula* Devos *et al.* (2011: 1629), characterized by a thick-walled, brownish stem epidermis and a thin-walled medulla and containing the majority of the Neotropical *Radula* species (Patiño *et al.* 2017). In some species of this subgenus both the inner and outer walls of the epidermis are thickened, in others the thickening is restricted to the outer epidermal wall. Both types of thickening are seen in the new taxa, the new species having thickened inner and outer epidermal walls while in the new variety only the outer wall of the epidermis is thickened.

Material and Methods

After moistening with water, specimens were observed and measured using a light microscope Leica EZ4 at the Laboratory of Bryology at the Museu Paraense Emílio Goeldi (MPEG). Measures represent the complete variation of the plants and were made using an eye-objective with a millimeter ruler calibrated with a millimeter glass-slide. Morphological descriptions of the gametophyte followed the model of Oliveira-da-Silva *et al.* (2021).

Illustrations were made using a light microscope Leica DM1000 with drawing tube. Photographs of the plants were taken at the Microscopy Laboratory of the MPEG using an optical microscope Leica DM6 B with an attached camera. The scanning electron microscopy (SEM) photographs were obtained at the Institutional SEM Laboratory of the MPEG, using a Tescan Mira 3 electron microscope with FEG (field emission gun) electron gun. For SEM preparation, specimens were placed on aluminum supports using conductive carbon tape and coated with gold in an Argon atmosphere at a pressure of 2.10-2 mbar for 2':30''. To obtain the images, a voltage acceleration of 5 kV and a working distance of 15 mm were used. The illustrations and photographs of the species were edited using the program Gimp 2.10.10.

Taxonomic treatment

Radula pallens var. ***marginata*** F.R.Oliveira-da-Silva, Gradst. & Ilk.-Borg., *var. nov.* (Fig. 1, 2A–C)

Radula maegdefrauí K.Yamada *nom. inval.* (Art. 38.1, Turland *et al.* 2018), in Mägdefrau, Nova Hedwigia 38: 20. 1983.

Type:—VENEZUELA. Maracay: "Nebelwald von Rancho Grande, am Weg zum Periquito," 1300 m, 25 February 1958, *K. Mägdefrau 363* (holotype JE!, isotype MG!).

Diagnosis:—Differs from *Radula pallens* (Sw.) Nees & Mont. var. *pallens* by the leaf lobes bordered by a row of thicker-walled cells with bulging trigones.

Description:—Dioicous. **Plants** 2–3 cm long, 1.7–2 mm wide, yellowish-green in herbarium specimens, irregularly pinnate, becoming dichotomous in upper stem portions below the gynoecia. **Branches** *Radula*-type or *Lejeunea*-type. **Stems** 170–220 µm diameter, in cross section with ca. 30 epidermal cells surrounding ca. 55 mostly larger medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, dark orange to brown, inner walls of the medullary cells thin-walled, yellowish. **Leaf lobes** widely spreading, imbricate, slightly convex, suborbicular, 0.9 –1.2 mm long, 0.7–1 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane to reflexed, entire to usually sinuous, bordered by one row of thick-walled cells; marginal cells isodiametric, 10–25 × 10–20 µm, median cells isodiametric to elongate, 10–20(–25) × 10–20 µm, basal cells elongate, 25–37 × 15–20 µm, cell walls thin, outer margin of the marginal cells strongly and evenly thickened, trigones small at leaf base becoming larger midleaf and bulging at the margin, cuticle smooth. **Lobules** distant, (sub)quadrate, 0.5–0.7 mm long, (0.3–)0.4–0.5 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area, insertion line almost straight, base plane, rounded to rarely angulate, covering up to 1/2 the stem, free margin plane, straight, apex plane to incurved, rounded to slightly obtuse, distal margin plane to incurved, straight, angle with the stem 50–60°, angle with the ventral margin of leaf lobe 160°–170°. **Rhizoids** colorless to brown, scanty, present on a few lobules. **Androecia** not seen. **Gynoecia** on long branches, with 1–2 innovations; bracts ovate, 0.8–1 mm long, 0.5–0.7 mm wide, apex rounded,

margin plane, entire to sinuous, lobule oblong, 1/2–1/3 of lobe length, apex rounded, keel convex. **Perianth** not seen. **Vegetative reproduction** by occasionally caducous leaf lobes.

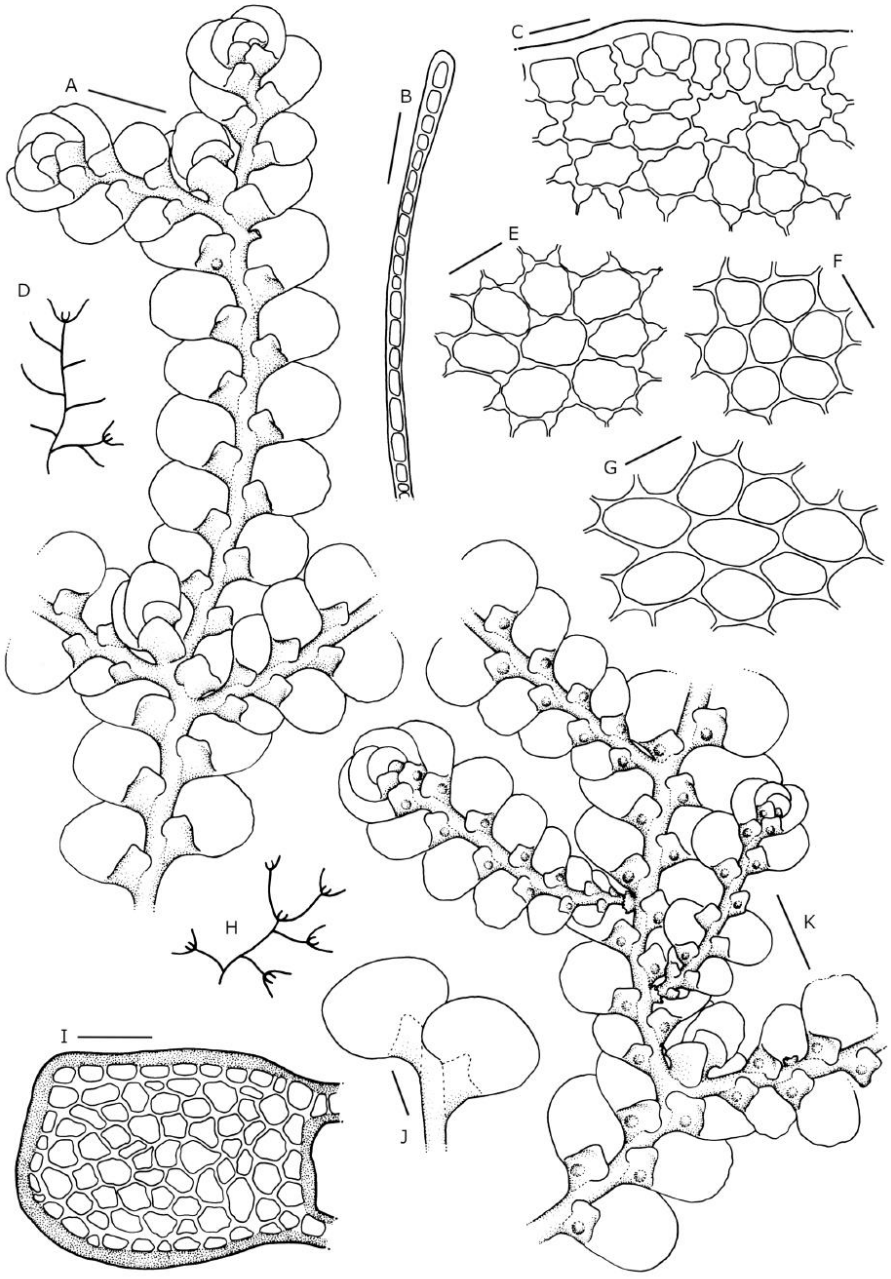

FIGURE 1. *Radula pallens* var. *marginata*. A, K. Habit with gynoecia, ventral view. B. Cross section of a leaf lobe, showing thick-walled cells at leaf margin. C. Marginal leaf cells. D, H. Cladographs of plants (U = gynoecia without perianths). E–F. Median leaf cells. G. Basal leaf cells. I. Cross section of a stem. J. Leaves in dorsal view (A, K= 1000 µm; B, I= 50 µm; C, E–G= 25 µm; H= 500 µm; A–K from the holotype). Drawing made by F. R. Oliveira-da-Silva and A. L. Ilkiu-Borges.

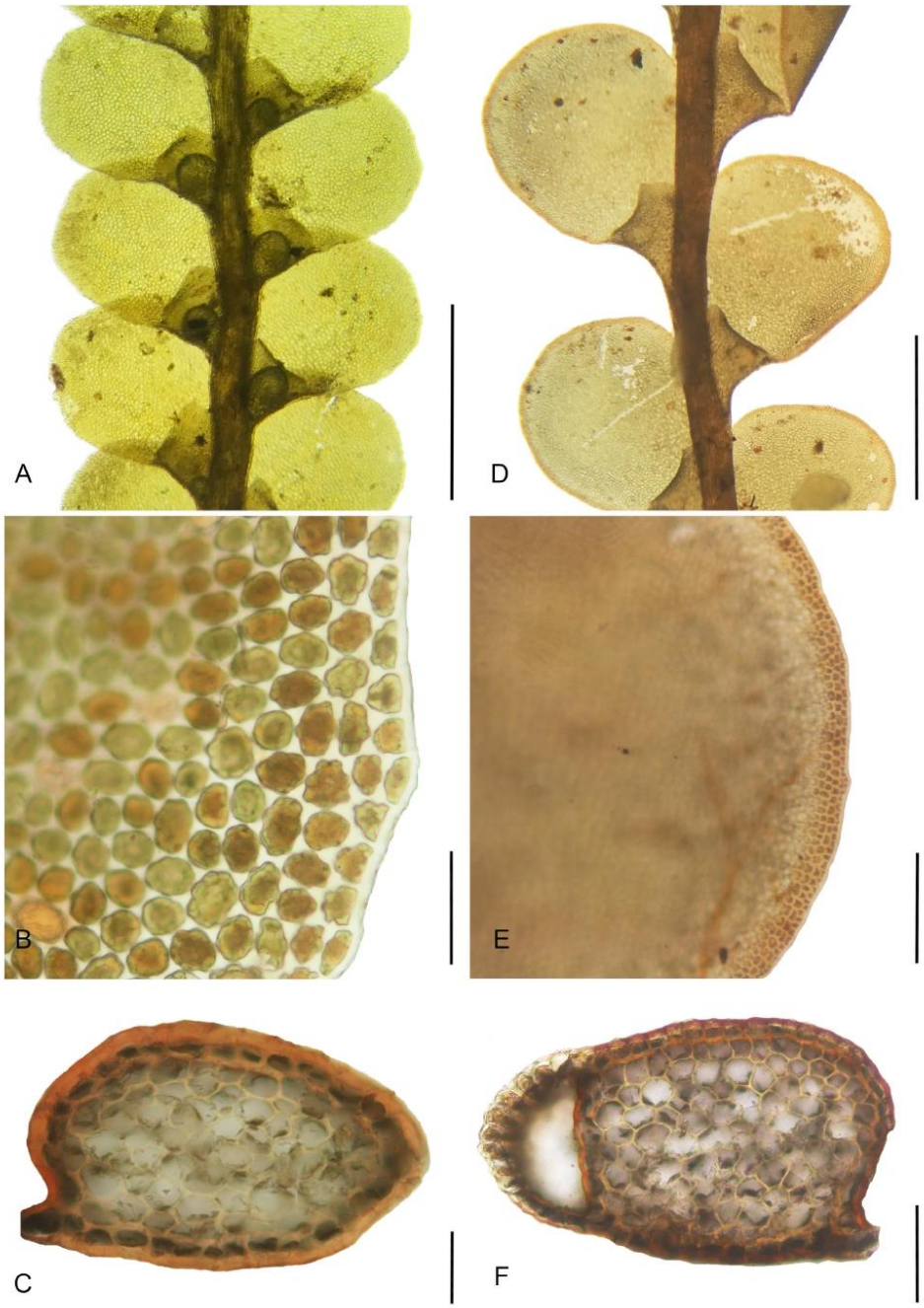

FIGURE 2. A–C. *Radula pallens* var. *marginata*. A. Habit, ventral view. B. Leaf lobe margin showing the border composed by thick-walled cells with large, bulging trigones. C. Cross section of stem. D–F. *Radula smithii*. D. Habit, ventral view. E. Leaf lobe margin showing the border composed of 3–4 rows of thick-walled, subquadrate to subrectangular or rounded cells. F. Cross section of stem (A, D= 1000µm; B–C= 50 µm; E= 200 µm; F= 100 µm; A–F from the holotype). Photograph taken by F. R. Oliveira-da-Silva.

Etymology:—The epithet of the new variety refers to the bordered leaf lobes.

Distribution and habitat:—*Radula pallens* var. *marginata* is only known from Rancho Grande in Henri Pittier National Park, northern Venezuela (Fig. 3). This species was collected growing on bark in montane cloud forest, at 1300 m.

Taxonomic notes:—*Radula pallens* var. *marginata* (subg. *Volutoradula*) differs from the typical variety by the presence of a narrow border on the leaf lobes composed of thicker-walled margin cells with larger, bulging trigones and a thickened outer wall (border absent in var. *pallens*). In addition, the leaf lobes in the new variety are sometimes caducous (caducous leaf lobes absent in var. *pallens*). The leaf border seen in *R. pallens* var. *marginata* is similar to that seen in some species of the genus *Odontoschisma* (Gradstein & Ilkiu-Borges 2015).

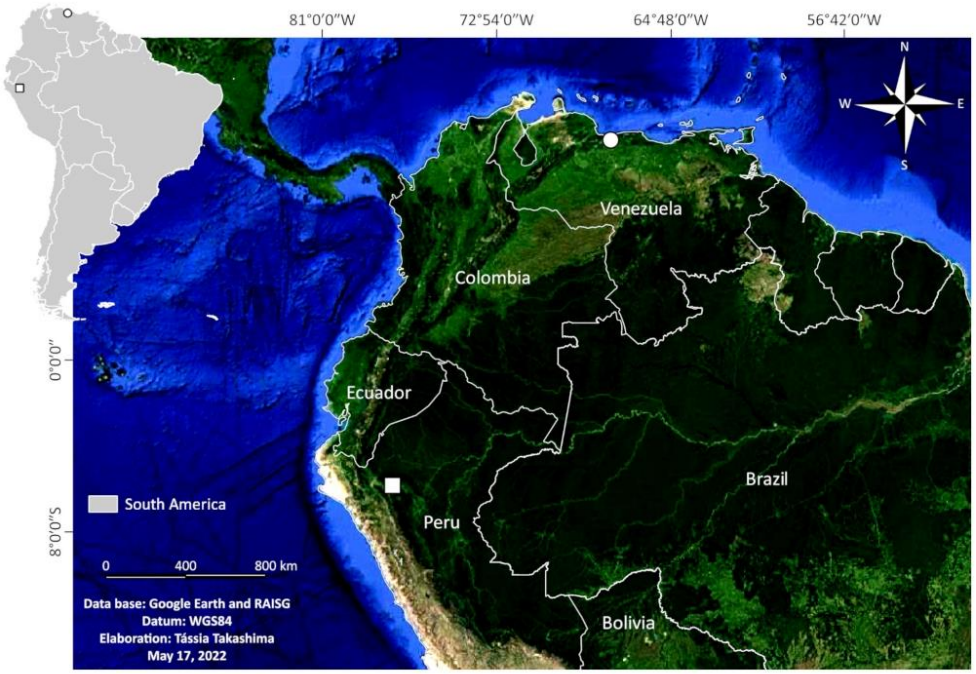

FIGURE 3. Localization map of *Radula pallens* var. *marginata* (dot) and *R. smithii* (square). Map made by T. T. G. Takashima-Oliveira.

Radula smithii F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., *sp. nov.* (Fig. 4, 5, 2D–F)

Type:—**PERU. San Martín:** Rioja, Venceremos, km 390, Pedro Ruíz—Moyobamba road, primary montane forest, on soil bank, 05°50'S, 077°45'W, 1750–2100 m, 27 July–9 August 1983, *D. N. Smith C-300* (holotype MO6968335!, isotype MG!).

Diagnosis:—Plants relatively robust, little branched. Leaf lobes distant, strongly convex, plane at the margin, the margin entire, bordered by 3-5 rows of thick-walled, reddish-brown cells. Lobules subquadrate with a rounded base covering 1/3(–1/2) of the stem and distal margin usually recurved.

Description:—Dioicous? **Plants** relatively robust, ca. 4 cm long, (2–)2.5–3 mm wide, yellowish-green to brown in herbarium, little branched, irregularly to dichotomous. **Branches** *Radula*-type, *Lejeunea*-type branches present on decapitated shoots. **Stems** 250–350 µm diameter, in cross section with 45–47 epidermal cells surrounding 98–100 mostly larger medullary cells, epidermal wall heavily and evenly thickened, brownish, inner walls of the medullary cells thin-walled, yellowish. **Leaf lobes** obliquely to widely spreading, distant, rarely contiguous, strongly convex, suborbicular, 1.7–2 mm long, 1.4–1.5 mm wide, dorsal base straight, not covering the stem, apex rounded, margins plane, entire; marginal cells subquadrate to subrectangular or rounded, 10–20 × 10–15 µm, median cells isodiametric

to elongate, 20–25 × 15–20 µm, basal cells elongate, 25–35 × 15–25 µm, cell walls thin at leaf base and in midleaf, evenly thickened and reddish-brown pigmented along the margin forming a broad, 3–5 cell rows wide border, trigones absent, cuticle finely papillose. **Lobules** distant, subquadrate, 0.8–1 mm long, 0.5–0.6 mm wide, 1/4–1/3 of lobe length, slightly inflated at the rhizoid area, insertion line almost straight, base plane, rounded, covering 1/3(–1/2) of the stem, free margin plane, straight, apex plane, rounded, distal margin incurved, straight, keel slightly convex, angle with the stem 50–60º, angle with the ventral margin of leaf lobe 150º–160º. **Rhizoids** brown, scanty, on a few lobules. **Sexual branches** not observed. **Vegetative reproduction** by stem fragmentation.

Etymology:—The new species is dedicated to its collector, Dr. David Nelson Smith.

Distribution and habitat:—The new species is only known from northern Peru (Department of San Martín), growing on soil or as an epiphyte in primary montane forest at 1750-2100 m (Fig. 3) together with *Radula episcia* Spruce (1885: 318).

Taxonomic notes:—*Radula smithii* (subg. *Volutoradula*) is distinguished by the leaf lobes bordered by 3–5 rows of thick-walled, reddish-brown cells, the border cells being strongly differentiated from those of the rest of the lobe. The border cells are distinctly pigmented and plane, while the rest of the leaf lobe cells are usually yellowish and strongly convex. The new species also stands out for the large, sparsely branched plants with very distant leaves.
Within *Radula*, a broad, pigmented leaf border of thick-walled cells otherwise occurs in *R. ligula* and *R. marginata*. The former species is widely distributed along the Atlantic coast of Brazil, with a single occurrence in Missiones, Argentina (Reiner-Drehwald 1994, Oliveira-da-Silva *et al.* 2021), and is possibly a member of subg. *Amentuloradula* Devos *et al.* (2011: 1630); the latter species is endemic to New Zealand and belongs to the subgenus *Amentuloradula* (Patiño *et al.* 2017). The border of *R. ligula* may be brownish in older leaves (Gradstein & Costa 2003) whereas that of *R. marginata* appears reddish in dorsal view (Renner & Braggins 2004). Both species have ligulate lobules, parallel and close to the stem, being very different from those of the new species, which has subquadrate lobules. The stem anatomy of *R. ligula* and *R. marginata* is also different, with the outer epidermal walls being heavily and evenly thickened, more so than the inner epidermal walls (similar to *R. pallens* var. *marginata*), while the inner epidermal cell wall and the medullary walls are thickened with concave trigones (Oliveira-da-Silva *et al.* 2021 erroneously described the medulla in *R. ligula* as being "thin-walled"). In *R. smithii*, in contrast, the epidermal cell walls are thickened whereas the medullary cells are thin-walled, without any trigones.

Radula smithii is similar to members of the former sect. *Dichotomae* Grolle (1970: 666) (= subg. *Volutoradula* p.p.) in the shape and areolation of the leaf lobe, the lobule and its dichotomous branching pattern. The new species may be confused with two widely distributed Neotropical members of this group, *R. pallens* and *R. episcia*. In both collections of the new species, the plants were growing mixed with *R. episcia*, which was immediately separated from *R. smithii* by the absence of a leaf border and by the more imbricate leaves. The scarcity of dichotomous branching in *R. smithii* and *R. episcia* separates these two species from *R. pallens*, which produce copious dichotomous branching in female plants, due to paired innovations.

The montane forests along the Pedro Ruíz – Moyobamba road, where the new species was detected in 1983, had already been inventoried a year earlier by a team of bryologists in the framework of the BRYOTROP project (Schultze-Motel & Menzel 1987), and 17 species of *Radula* has been collected there, including the new species *R. peruviana* Yamada in Schultze-Motel & Menzel (1987: 79). *Radula smithii,* however, was not found during the BRYOTROP expedition and this suggests that the species may be a rare taxon as the plants are robust and unlikely to be overlooked in the field.

Additional specimen examined (paratype):—**PERU. San Martín:** Rioja, km 390, Pedro Ruíz – Moyobamba road, primary montane forest, epiphyte, 05°50'S, 077°45'W, 1750–2100 m, 27 July – 9 August 1983, *D. N. Smith C-310* (MO6869091!, MG!).

Key to Neotropical species of *Radula* with bordered leaf lobes

1. Lobules ligulate ..... *R. ligula*
1. Lobules subquadrate 2
2. Leaf border reddish-brown, 3-5 cell rows wide, walls of the leaf border evenly thickened, without trigones. Leaves distant ..... *R. smithii*
2. Leaf border 1 cell row wide, walls of the leaf border thickened with bulging trigones. Leaves imbricate ..... *R. pallens* var. *marginata*

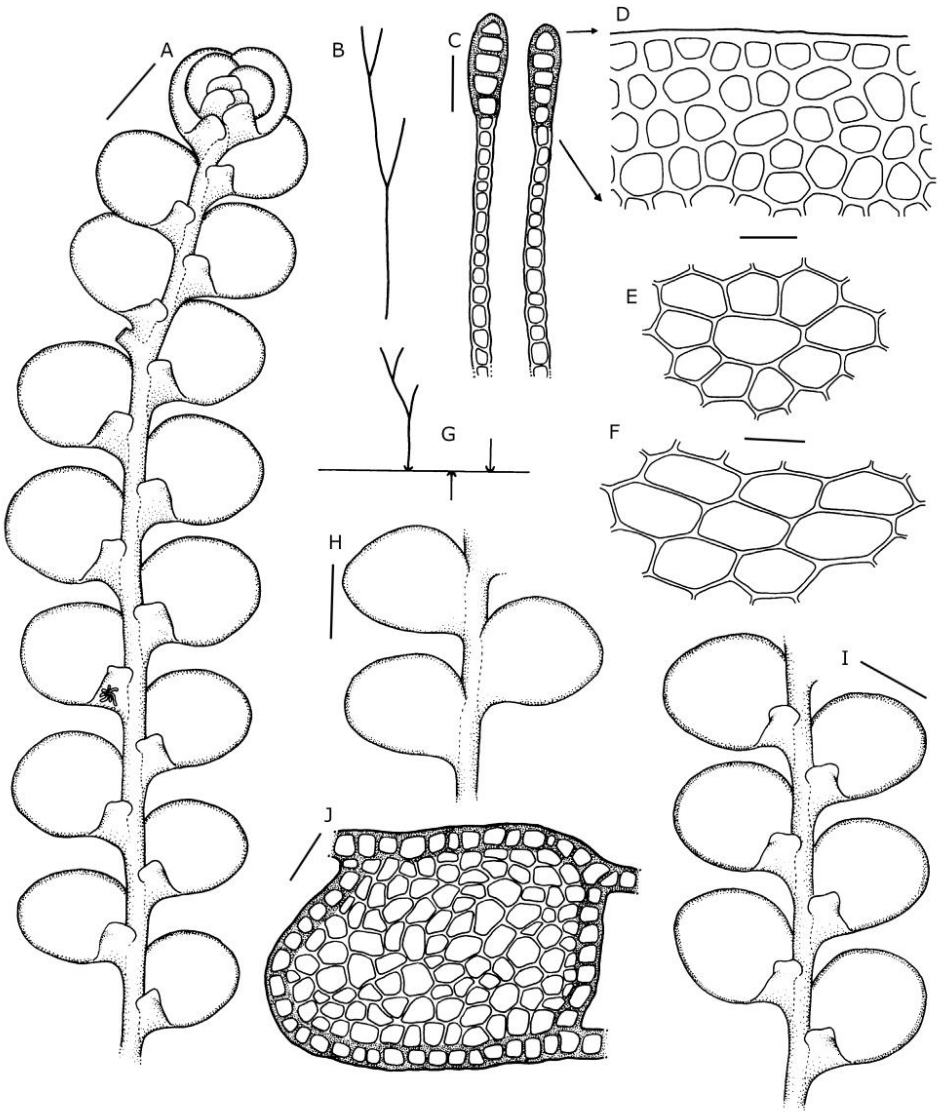

FIGURE 4. *Radula smithii*. A, I. Habit, ventral view. B, G. Cladographs of plants. C. Cross section of a leaf lobe, showing thick-walled, large, pigmented cells at leaf margin. D. Marginal leaf cells. E. Median leaf cells. F. Basal leaf cells. H. Leaves in dorsal view. J. Cross section of a stem (A, H, I= 1000 µm; C, J= 50 µm; D–F= 25 µm; A-J from the holotype). Drawing made by F. R. Oliveira-da-Silva and A. L. Ilkiu-Borges.

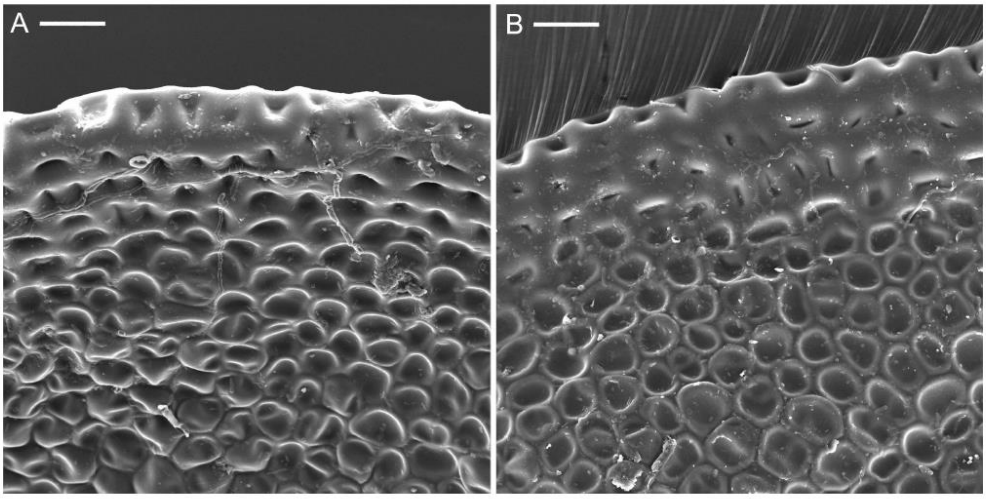

FIGURE 5. A–B. Scanning electron microscopy of the leaf lobe of *Radula smithii*, showing the difference between the border and the rest of the leaf lobe cells (A-B= 20 µm; A-B from the holotype). Photograph taken by H. T. Costi.

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CAPÍTULO II

Título: Afro-American Radulaceae (Marchantiophyta): Taxonomic Scrutiny Reveals New Synonymy in *Radula fulvifolia*

Autores: Fúvio Rubens Oliveira-da-Silva, Anna Luiza Ilkiu-Borges & S. Robbert Gradstein

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Afro-American Radulaceae (Marchantiophyta): Taxonomic Scrutiny Reveals New Synonymy in *Radula fulvifolia*

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Abstract

A taxonomic study on Radulaceae in tropical America and Africa shows that the names *Radula galapagona* and *R. schaefer-verwimpii* should be replaced by the older name *R. fulvifolia*. The species is delicate and stands out by fragile and highly denuded shoots due to the strongly caducous leaf lobes, ovate to falcate-ovate leaf lobes, thin-walled leaf cells usually without trigones, rhombic (rarely subquadrate) lobules with the base varying in size and shape but not fully covering the stem, and straight to concave keels. A lectotype is designated for the name *Radula fulvifolia*. Our study leads to a further increase in the number of Afro-American liverwort taxa.

Key-Words: Liverworts; *Radula*; tropical America; tropical Africa; taxonomy.

Introduction

The relationships of the bryophyte floras of tropical African and tropical America have frequently been discussed (e.g., Herzog 1926, Gradstein et al. 1983, Delgadillo 1993, Gradstein 2013), and numerous parallels and resemblances among the taxa of the two regions have been demonstrated. In a recent review of Afro-American liverworts, Gradstein (2013) listed 74 species occurring in tropical America and Africa, and not or very restrictedly elsewhere. Afro-American species constituted about 5% of the neotropical liverwort flora and 8% of the flora of Africa. Evidence from spore germination tests and molecular-phylogenetic analysis indicated

that the Afro-American species ranges probably resulted from long-distance dispersal events (van Zanten & Gradstein 1988, Heinrichs et al. 2009).

Recent taxonomic studies on tropical liverworts have led to a further increase in the number of Afro-American taxa (Gradstein & Ilkiu-Borges 2018, Gradstein & Reeb 2022, Gradstein et al. 2022). The latter authors showed that *Radula ankefinensis* Steph. from tropical Africa is a synonym of *R. mexicana* Lindenb. & Gottsche from tropical America, whereas the neotropical *R. gottscheana* Taylor is a synonym of the African *R. boryana* (F.Weber) Mont. (= *Cladoradula boryana* [F.Weber] M.A.M.Renner et al.; Renner et al. 2022). The conspecificty of *R. boryana* and *R. gottscheana* was already proposed by Castle (1936) in his world monograph of the genus *Radula*, but had been rejected by Yamada (1988).

The present paper focuses on Afro-American relationships in Radulaceae. Currently, five Afro-American species of Radulaceae are recognized: *Cladoradula boryana, Radula flaccida* Lindenb. & Gottsche, *R. mexicana, R. quadrata* Gottsche and *R. voluta* Gottsche et al. Of these, *Cladoradula boryana, Radula flaccida* and *R. mexicana* are limited to tropical America and Africa, *R. quadrata* and *R. voluta* extends to eastern North America and southern South America and *R. voluta* occurs also along the Atlantic coast of western Europe. In addition, *R. stenocalyx* Mont. and, possibly, *R. javanica* are distributed in tropical America and Africa, but these two species are also occur in tropical Asia and are pantropical taxa (Yamada 1979, Promma & Chantanaorrapint 2015).

In the course of our work on Radulaceae in tropical America and Africa, we noted a close resemblance between the African *Radula fulvifolia* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees and the neotropical *R. galapagona* Steph. and *R. schaefer-verwimpii* K.Yamada. *Radula fulvifolia* was first described in 1845, as *Jungermannia fulvifolia* Hook.f. & Taylor, based on a specimen from St. Helena, a remote volcanic tropical island in the southern Atlantic Ocean 1,950 km West of Africa and 4,000 km East of the coast of South America. The species was described and illustrated in detail by Müller et al. (2001), who reported new localities of the species from Ivory Coast, South Africa and Réunion. *Radula fulvifolia* was subsequently reported from many additional localities in continental and insular Africa by Grolle (2001), who found that it is one of the most common and widespread *Radula* species in Africa.

Radula galapagona, described by Stephani in 1910, is only known from the Galápagos Islands where it is a common and characteristic species of evergreen woodlands (Yamada & Gradstein 1991, Gradstein 2021). Full descriptions and illustrations of the species were provided by Castle (1967), Yamada (1991) and Yamada & Gradstein (1991).

Radula schaefer-verwimpii, finally, was described in 1990 from Brazil (Yamada 1990) and proved to be rather widespread in tropical South America where it occurs in submontane and montane forests, up to the shrubby páramo. The species was treated in detail by Yamada (1990) and Oliveira-da-Silva et al. (2021).

Our study of types and additional collections from various herbaria worldwide showed that *Radula fulvifolia*, *R. galapagona* and *R. schaefer-verwimpii* are morphologically identical and constitute a single, rather polymorphic species. The plants are delicate and stand out by the fragile and highly denuded shoots due to strongly caducous leaf lobes, ovate to falcate-ovate leaf lobes, thin-walled leaf cells usually without trigones, rhombic (rarely subquadrate) lobules with the base varying in size and shape but not fully covering the stem, and straight to concave keels. Our study leads to a further increase in the number of Afro-American taxa emerging from taxonomic work on tropical liverworts.

Taxonomic treatment

Radula fulvifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 261. 1845. *Jungermannia fulvifolia* Hook.f. & Taylor, London J. Bot. 4: 85. 1845. Type: St. Helena Island, 1 March 1843, *unknown collector*, in Dr. Greville's Herbarium (lectotype, E-00007234, **designated here**; isolectotypes, FH-00783498!, BM-000969264!, PC, W).

Fig. 1–2

= *Radula meyeri* Steph., Hedwigia 27: 62. 1888. syn. fide Grolle (2001).

= *Radula galapagona* Steph., Sp. Hepat. 4: 176. 1910. Type: Ecuador, Galápagos Island, s.d., *C. M. J. Andersson s.n.* (holotype, G-00112101!, scanty), ***syn. nov.***

= *Radula schaefer-verwimpii* K.Yamada, J. Jap. Bot. 65: 3. 1990. Type: Brazil, Minas Gerais, National Park Serra de Caparao, "auf schattigem Felsblock," 1360 m, 28 July 1987, *A. Schäfer-Verwimp 8989* (holotype, NICH; isotypes, G-00265052!, JE-04009540!, NY-01021153!, NY-01021154!, SP-383443!), ***syn. nov.***

Dioicous. **Plants** delicate, 1–2 mm wide, to 2 cm long, light green, yellowish-green to olive-green to brown in herbarium, irregularly to regularly pinnate. **Branches** *Radula*-type. **Stems** 100–180 μm in diameter, with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. **Leaf lobes** widely spreading,

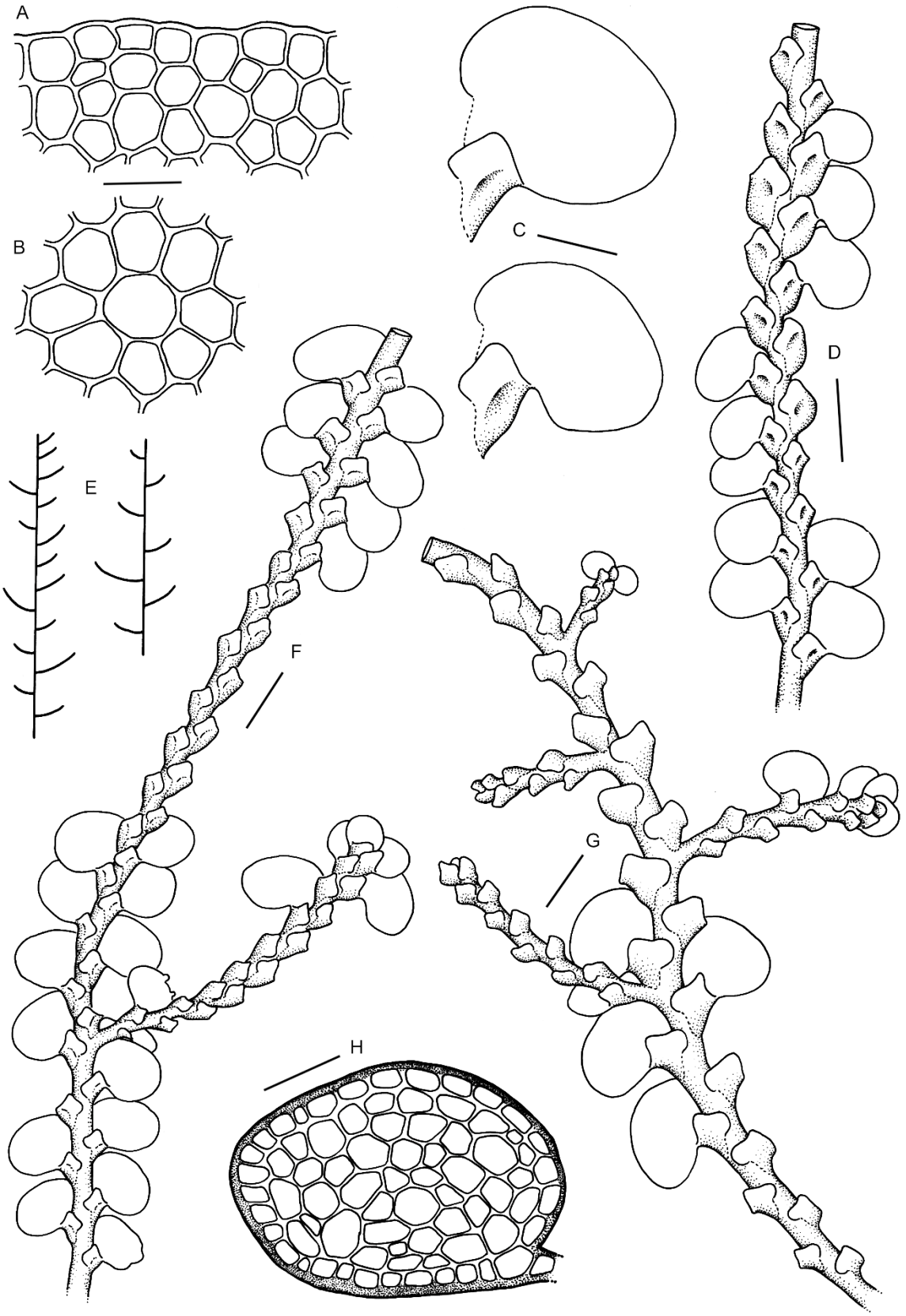

Figure 1. *Radula fulvifolia* – plants from Africa. A. Marginal leaf cells. B. Median leaf cells. C. Leaves. D, F–G. Habit. E. Cladographs. H. Cross section of stem (A–F, H from *Arts 11/14* and G from the isotype of *R. fulvifolia* in FH). Scale bars: A, B, H = 50 µm; C = 250 µm; D, F, G = 500 µm. Drawing by F. R. Oliveira-da-Silva and A. L. Ilkiu-Borges.

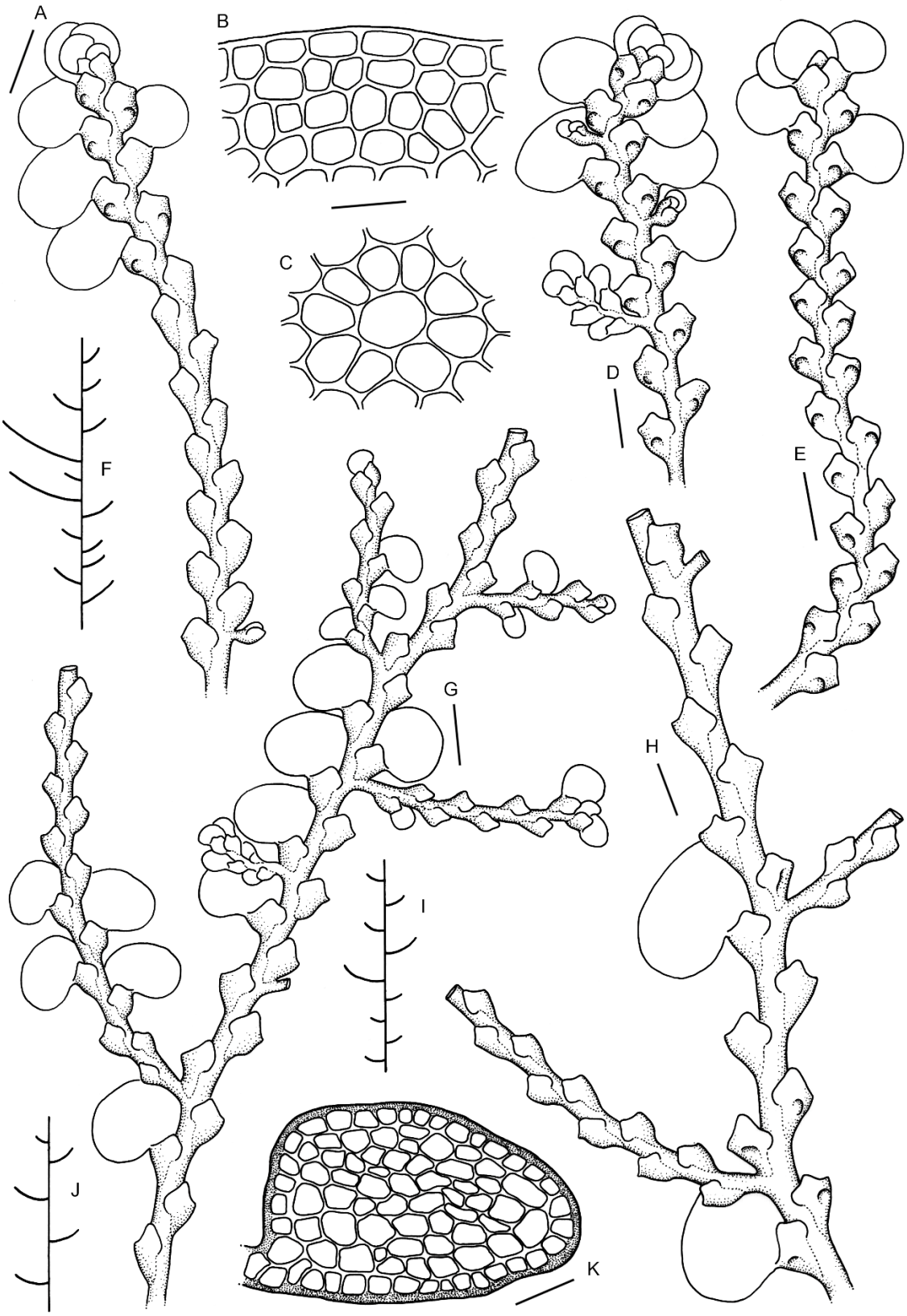

Figure 2. *Radula fulvifolia* - plants from Galápagos Islands. A, D–E. Habit (Isabela). B. Marginal leaf cells. C. Median leaf cells. F, I, J. Cladographs. G. Habit (San Cristobal). H. Habit (Santa Cruz). K. Cross section of stem. (A, D, J from *van der Werff 1436*; B, C, G, I from *Gradstein & Lanier H307/a*; E from *Gradstein* & *Weber H224*; F, H from *Gradstein et al. H52*). Scale bars: A, D, E, G, H = 500 µm; B, C = 25 µm; K = 50 µm. Drawing by F. R. Oliveira-da-Silva and A. L. Ilkiu-Borges.

distant to subimbricate, slightly convex, ovate to falcate-ovate, sometimes strongly falcate-ovate, 0.6–1.1 mm long, 0.4–0.8 mm wide, dorsal base rounded, covering 1/3–1/2 the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margins plane, entire; marginal cells subquadrate to subrectangular, 8–20 × 8–15 μm, median cells isodiametric to elongate, 15–25 × 10–20 μm, basal cells isodiametric to elongate, 20–30 × 15–20 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. **Lobules** distant to contiguous, usually rhombic, sometimes subquadrate, 0.3–0.6 mm long, 0.2–0.4 mm wide, 1/3–1/4 the lobe length, inflated at rhizoid area or along the keel, insertion 1–3× the base length, line of insertion slightly curved, base plane, rarely recurved, rounded to angulate, covering 1/3–2/3 the stem, rarely fully overlapping the stem, free margin plane, rarely recurved, almost straight, apex plane, rarely recurved, rounded to acute, distal margin straight, keel straight to concave, departing at rather narrow angles of 30–50º from the stem and forming an angle of 100–130º with the ventral leaf lobe margin, at its junction with the lobule. **Rhizoids** colorless, scanty, present on a few lobules. **Androecia** rare, intercalary on short branches, with 2–4 pairs of bracts, 0.7–1.1 mm wide; bracts distant to imbricate, ovate, 0.6–0.9 mm long, 0.25–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. **Gynoecia** rare, on short branches, with 2 innovations; bracts almost symmetrical, oblong-ovate, 0.7–0.85(–0.9) mm long, 0.3–0.4 mm wide, apex rounded, margin plane, entire, lobule symmetrical, oblong-rectangular, ca. 1/2 of lobe length, apex rounded to obtuse; perianth not developed. **Sporophytes** not observed. **Vegetative reproduction** by strongly caducous leaf lobes, producing completely denuded branches.

Distribution and habitat. Tropical America and Africa; in addition, recorded from tropical Asia by Yamada (1979, as *R. meyeri*), but the Asiatic plants were described as having a thin-walled stem epidermis and lacking caducous leaf lobes, and must therefore belong to some other species. *Radula fulvifolia* is most common in Africa, where it has been recorded from St. Helena, Ivory Coast, Ghana, Cameroun, Bioko, Central African Republic, Democratic Republic of the Congo, Rwanda, Uganda, Ethiopia, Kenya, Tanzania, Zimbabwe, South Africa, Comores, Madagascar (but see Gradstein et al. 2022), Réunion and Mauritius (Grolle 2001, Wigginton 2018) (Fig. 3). In tropical America the species is rare in Central America, where it known from Guatemala (Pérez 2009) and Costa Rica (new). It is more common in South America, where it occurs in Guyana, Venezuela, Colombia, Ecuador, Bolivia and the Atlantic

coastal region of Brazil (Gradstein 2021, Oliveira-da-Silva et al. 2021). The species grows on bark, rotten wood, rock or soil in humid submontane to montane forests up to the shrubby páramo, between 400–3700 m.

Figure 3. Distribution map of *Radula fulvifolia*. Specimens examined are marked by dots, additional literature reports by rings.

Additional specimens examined. ST. HELENA ISLAND. Diana's Peak, February 1840, *Hooker s.n.* (FH); without locality, s.d., *Burchell 206* (BM); "Leaph. Hanephton", s.d, *unknown collector* (BM). **GHANA.** Ankase river, on tree base, *Jones & Hall 1373b* (G). **CAMEROUN**. Bomanum, on tree trunks, 670 m, *Dusén 359* (G). **DEMOCRATIC REPUBLIC OF THE CONGO**. **LACS ÉDOUARD ET KIVU**: Kahuzi-Biega National Park, epiphyllous, 2470 m, *Fischer 8504* (G). **HAUT-KATANGA**: Plateau des Muhila, Laula river, *Malaisse 2006e*, *2083e* (BR). **RWANDA. LACS ÉDOUARD ET KIVU**: Nyungwe Forest, on bark, *Frey & Kürschner 7936* (G). **UGANDA.** Mawokota, on tree trunk, 1180 m, *Lye B299* (EGR). **SOUTH AFRICA. EASTERN CAPE**: Amathole Mts., Hogsback, on trunk base in forest, 1120 m, *Arts 21/08* (BR). **RÉUNION.** St. Philippe, Mare Longue Reserve, on rock, *Arts 11/14* (BR, MG). **COSTA RICA. ALAJUELA:** Piedades de San Ramón, 900 m, *Brenes 383* (MO). **GUYANA. UPPER MAZARUNI:** North slope of Mt. Roraima, mossy montane forest, on bark, 5°17'N, 60°43'W, 1200-1600 m, *Gradstein 5526* (GOET). **VENEZUELA. AMAZONAS:** Cerro Huachamacari,

Río Cunucunuma, montane rainforest, on tree trunk, 1200 m, *Marguire et al. 29913* (MG, NY). **ARAGUA**: Parque Nacional "H. Pittier", on branch, 1100 m, *Steyermark et al. 95843, 95846* (MG, NY). **COLOMBIA. RISARALDA:** Santa Rosa, near finca La Sierra, 3700 m, *Aguirre 1427* (GOET). **ECUADOR. Galápagos Islands:** Isabela, vulcan Alcedo, 1100 m, *van der Werff 1436* (GOET), ibid., *Gradstein* & *Weber H224* (L, MG); Santa Cruz, South slope of Mt. Crocker, on branches, ca. 800 m, *Gradstein et al. H52* (L, MG); San Cristobal, valley SW of El Junco, on trunk, 500 m, *Gradstein & Lanier H307/a* (L, MG). **BRAZIL**. **BAHIA:** Eunápolis, Estação Veracruz, on bark, 16°22' S, 39°10' W, *Vilas Bôas-Bastos & Bastos 354* (ALCB); Abaíra, Catolés, Serra do Barbado, Mata da Forquilha, on bark, 13°17'27"S, 41°54'0,15"W, 1594 m, *Bastos 5101* (ALCB). **ESPÍRITO SANTO:** Castelo, Parque Estadual do Forno Grande, 20°31'00"S, 41°05'14"W, 1250 m, *Peralta et al. 19216* (SP); Domingos Martins, Parque Estadual Pedra Azul, on wood, 5 August 2009, *Penha 440* (ALCB). **MINAS GERAIS:** Poços de Caldas, morro São Domigos, 1330 m, 21°47S, 46°33W, *Schäfer-Verwimp & Verwimp 7030* (SP); Catas Altas, Parque Natural do Caraça, on rock, 20°05'56" S, 43°29'17" W, 1280 m, *Peralta et al. 6406* (SP). **PARANÁ:** Morretes, Parque Estadual Pico do Marumbi, trilha do Olimpo, 25°27'10"S, 48°55'11"W, 1000–1200 m, *Peralta et al. 17704* (SP). **RIO DE JANEIRO:** National Park Itatiaia, Itatiaia, 1200 m, *Schäfer-Verwimp & Verwimp 9255* (SP); Teresópolis, Parque Nacional da Serra dos Órgãos, on rock, 22°27'33"S, 43°00'17"W, 1300-1500 m, *Peralta et al. 20403* (SP). **SÃO PAULO:** Guarulhos, 23°23'55"S, 46°29'55"W, 745 m, *Peralta & Fortes 13923* (SP); São José do Barreiro, fazenda pinheirinho, on roadside, 22°43'48"S, 44°38'38"W, 1400 m, *Peralta et al. 4988* (SP); Campos do Jordão, Parque Estadual de Campos do Jordão, sobre barranco, 22°41'15"S, 45°27'21"W, 1677 m, *Peralta et al. 21757* (SP); São Luiz do Piraitinga, Parque Estadual as Serra do Mar, Núcleo Santa Virgínia, on tree trunk, 23°20'45" S, 45°07'47" W, 956 m, *Peralta & Gugliota 13405* (SP).

Radula fulvifolia (subg. *Volutoradula*) is a rather polymorphic species recognized mainly by the delicate plants with pinnate branching and strongly caducous leaf lobes, producing almost completely naked branches. The species is also characterized by leaf lobes ovate to falcate-ovate, cells wall thin usually without trigones, and lobules rhombic (rarely subquadrate) with a rounded to angulate base covering 1/3–2/3 the stem, rarely fully overlapping, and keel straight to concave.

The lobule of the species varies considerably. Specimens from tropical America with a little expanded lobule base, covering only 1/3 of the stem, were described as *Radula schaefer-*

verwimpii, while specimens with a lobule base covering at least 1/2 of the stem were called *R. galapagona*. Gradstein (2021) suggested that these two species could be treated as subspecies, based on this single difference. However, the overlap in the variation observed in the studied specimens leads us to consider them as parts of one single taxon.

Considerable variation is also seen among the specimens from different islands of the Galapagos archipelago. The specimens from Santa Cruz are relatively robust with rhomboid lobules and with an angulate lobule base covering most of the stem (see Fig. 2H), while specimens from San Cristobal are smaller in all respects and similar to specimens called *Radula schaefer-verwimpii* (Fig. 2G). The specimens from Isabela are identical to the holotype of *R. galapagona*, as illustrated by Castle (1967) and Yamada (1991) (Fig. 2A, D, E), showing a convex lobule keel instead of a straight keel. This suggests that the specimen described by Stephani was probably collected on Isabela.

In Africa, *Radula fulvifolia* was long known as *R. meyeri* and there has been considerable confusion about the identity of the latter species (e.g., VandenBerghen 1972, Jones 1977), until Grolle (2001) showed its conspecificity with *R. fulvifolia*. By its strongly caducous leaf lobes and delicate statue, *R. fulvifolia* cannot be confused with any other African *Radula* species. In the Neotropics, however, several other *Radula* species have highly caducous leaf lobes, including *R. bischlerae* Gradst. & Ilk.-Borg., *R. pseudostachya* Spruce and *R. pocsii* K.Yamada. *Radula bischlerae*, endemic to páramo of Colombia, is easily recognized by its unusual, tubularly inflated lobules, whereas *R. pseudostachya*, an Amazonian species from Venezuela and Brazil, is very different from *R. fulvifolia* in its subrectangular lobules, leaf cells with large trigones, etc. The purely dichotomous branching and rather large trigones in the leaf cells of *R. pocsii*, finally, readily separate that species from *R. fulvifolia*.

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CAPÍTULO III

Título: Spores of Radulaceae (Marchantiophyta) exhibit a level of micromorphological diversity far beyond expectation

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Spores of Radulaceae (Marchantiophyta) exhibit a level of micromorphological diversity far beyond expectation

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Abstract

Radulaceae is one of the most isolated lineages of leafy liverworts. This family contains three genera and between 200 and 350 extant species worldwide. Most species belong to the genus *Radula*, which is subdivided in five subgenera and remains taxonomically challenging. In the framework of an integrative taxonomic revision of Radulaceae in tropical America we are paying special attention to little-studied features that may be taxonomically informative, such as spores. Here, we perform the first palynological evaluation of sixteen species of Radulaceae, including one in the genus *Cladoradula* and fifteen in *Radula*. The spores were processed by standard palynological techniques and described using light and electron microscopy. The spores of Radulaceae are isomorphic monads, apolar in species of the genus *Radula* and cryptopolar in *Cladoradula*, usually small to medium-sized (16.66–38.88 µm), rarely large (50.00–66.66 µm), inaperturate, with a circular to slightly elongated outline. The spore surface is ornamented with rounded elements, here called Granulate-type ornamentation, or with elongated elements, called Echinate-type ornamentation, and shows differences in each species. The palynological data, especially spore ornamentation, can make an important contribution to Radulaceae taxonomy for separating species or groups of species. The groups found here, however, do not fully correspond to generic and infrageneric circumscriptions as supported by molecular-phylogenetic evidence. Palynological information on a larger number of species might contribute to a clearer understanding of phylogenetic relationships within Radulaceae.

Key words. bryophytes, liverworts, *Radula*, *Cladoradula*, palynology, SEM, taxonomy

Introduction

Radulaceae Müll. Frib. (Porellales Schljakov suborder Radulinae R.M. Schust.) is one of the most isolated lineages of the leafy liverworts (Marchantiophyta Stotl. & Crand.-Stotl. subclass Jungermanniidae Engl.) (Crandall-Stotler *et al.* 2009). Distinctive morphological traits of the family include rhizoids in tufts on the lobule surface, *Radula*-type branches, very large, brown oil bodies, absence of underleaves, and tubular, dorsiventrally flattened perianths (Schuster 1980, Yamada 1979, Gradstein *et al.* 2001, Oliveira-da-Silva *et al.* 2021). The center of diversity is in the humid tropical to warm temperate regions, despite being distributed in all continents apart from Antarctica, and most species grow as epiphytes in moist tropical forests, from the lowlands to the upper montane belt (Gradstein *et al.* 2001).

Until very recently, Radulaceae has been considered a monogeneric family with only the genus *Radula* Dumort. Recently, Renner *et al.* (2022) proposed two small additional genera based on molecular and morphological evidence, *Cladoradula* (Spruce) M.A.M. Renner *et al.* with seven accepted species distributed throughout the Tropics and in eastern Asia and North America, and *Dactyloradula* (Devos *et al.*) M.A.M. Renner & Gradst. with only *D. brunnea* (Steph.) M.A.M. Renner & Gradst. in Japan, South Korea, Kuril Island, and British Columbia (Choi *et al.* 2021)[1]. The genus *Radula* alone contains between 200 and 350 species worldwide in five subgenera: *Amentuloradula* Devos *et al.*, *Metaradula* R.M. Schust., *Odontoradula* K.Yamada, *Radula*, and *Volutoradula* Devos *et al.* (Devos *et al.* 2011, Renner *et al.* 2022). The subgeneric classification is mostly based on molecular data; morphological definition of the subgenera remains problematic and the subgeneric assignment of a considerable number of species is still unclear.

An integrative taxonomic revision of Radulaceae in tropical America based on morphological and molecular evidence is under preparation by the first author. One of the specific objectives of this study is to pay attention to little-studied features that may be taxonomically informative, such as stem anatomy, oil bodies, cuticle ornamentation, asexual reproductive structures, presence/absence of stem perigynium, and characters of the sporophyte generation.

Sporophytes, although short-lived and rather rarely observed in *Radula*, produce spores which are the first cells of the gametophytic stage. Spores play a crucial role in dispersal (mainly by wind) and the establishment of new populations (Zanten & Pócs 1981, Medina & Estébanez

[1] Renner *et al.* (2022) erroneously cited *Radula brunnea* as being endemic to Japan.

2014, Glime 2015). In systematics, spore features such as germination, ornamentation shape and size, have allowed the identification of different bryophyte lineages (Bischler-Causse *et al.* 2005, Goffinet & Shaw 2009).

Various studies have reported data on size and ornamentation of spores of *Radula* species from Africa, Asia, North America, and Macaronesia (Erdtman 1957, 1965, Jones 1977, Yamada, 1979, Schuster 1980, Bourman & Dickse 1990). Jones (1977) was the first to propose the taxonomic usefulness of spore characteristics in *Radula* based on a study of the species from Africa. Schuster (1980) emphasized the general importance of sporophyte characters to unravel the taxonomy of *Radula*. One of the first detailed descriptions of *Radula* spores was presented by Udar & Kumar (1983) in their treatment of the new species *Radula pandei* Udar & Kumar. The latter authors distinguished the spores of the new species from those of *R. tasmanica* Steph. by means of scanning electron microscopy (SEM). SEM images were also used in the descriptions of the spores of *Radula complanata* (L.) Dumort. and *R. tabularis* Steph. by Udar & Srivastava (1984).

In a survey of morphological characters of the sporophytes of 28 Australasian *Radula* species, Renner & Braggins (2005) recognized seven different spore types based on their size and ornamentation, and emphasized the significance of spores in the taxonomy of Radulaceae. Further papers providing descriptions of *Radula* spores and highlighting their taxonomic significance include Renner (2006), Renner *et al.* (2010), Promma & Chantanaorrapint (2015) and Promma *et al.* (2018).

Information on Radulaceae spores in the literature is somewhat heterogeneous regarding the used descriptive terminology, complicating taxonomic interpretation. Here we use a standardized palynological approach in order to (1) analyze variation in spore size and spore ornamentation, and (2) determine whether generic and subgeneric circumscriptions are supported by spore morphology.

Material and Methods

Material

This study was based on herbarium material obtained on loan from the Federal University of Bahia (ALCB), University of Göttingen (GOET), Friedrich Schiller University Jena (JE), Missouri Botanical Garden (MO), New York Botanical Garden (NY) and

Environmental Research Institute of São Paulo (SP). Mature sporophytes are rare in Radulaceae as well as in many other families of leafy liverworts (*e.g.* Silva-e-Costa & Luizi-Ponzo 2019) and more than 1000 specimens were examined in search of sporophytes. In total, 25 specimens (16 species) with mature capsules in sufficient amount were examined for palynological analysis. The following species, arranged genus and subgenus, were analysed:

Cladoradula (Spruce) M.A.M. Renner *et al.*: *C. boryana* (F. Weber) M.A.M. Renner *et al.*

Radula subg. *Metaradula* R.M. Schust. (sect. *Epiphyllae* Grolle): *R. flaccida* Lindenb. & Gottsche, *R. mammosa* Spruce

Radula subg. *Odontoradula* K.Yamada: *R. decora* Steph.

Radula subg. *Radula*: *R. javanica* Gottsche

Radula subg. *Volutoradula* Devos *et al.*: *R. episcia* Spruce, *R. involvens* Spruce, *R. pallens* (Sw.) Mont., *R. sinuata* Steph., *R. subinflata* Lindenb. & Gottsche, *R. venezuelensis* K. Yamada, *R. voluta* Gottsche, Lindenb. & Nees, *R. xalapensis* Nees & Mont.

Subgenus unclear (species not yet sequenced): *Radula flavifolia* (Hook. f. & Taylor) Gottsche *et al.*, *R. ligula* Steph., *R. portoricensis* Steph. Of these three species, *R. ligula* might belong in subg. *Amentuloradula* due to morphological similarities with *R. marginata* Gottsche *et al.* and *R. lingulata* Gottsche (see Patiño *et al.* 2017, Oliveira-da-Silva *et al.* 2022), whereas *R. portoricensis* may be a member of subg. *Radula* as it resembles other species in that group. The subgeneric position of *R. flavifolia* remains fully unclear due to its unusual morphology.

Light microscopy - LM

Permanent spore slides were prepared at the Palynology Laboratory of the Museu Paraense Emílio Goeldi (MPEG) and photographs were taken in the Microscopy Laboratory of MPEG using a light microscope Leica DM6 B with camera. For observation of cellular content under light microscopy, spores were prepared according to the method of Wodehouse (1935) and the acetolysis method of Erdtman (1960), with modifications following Luizi-Ponzo & Melhem (2006).

The acetolysis method is a standard palynological preparation, which removes the cellular content and the intine. Thus, it allows a better visualization of the surface of the sporoderm under LM (Halbritter *et al.* 2018). It is widely used in palynology, both in studies dealing with pollen grains (*e.g.* Denk & Tekleva 2006, Martins *et al.* 2011, Matamoro-Vidal *et*

al. 2016, Mezzonato-Pires *et al.* 2018, Subasinghe Arachchige *et al.* 2022) and with spores of bryophytes (*e.g.* Luizi-Ponzo & Melhem 2006, Savaroglu & Erkara 2008, Caldeira *et al.* 2013, Luizi-Ponzo & Silva-e-Costa 2019, Passarella & Luizi-Ponzo 2022).

Spores were described using terminology and definitions of size classes proposed by Punt *et al.* (2007) and Erdtman (1952), respectively.

Scanning electron microscopy - SEM

Scanning electron microscopy (SEM) photographs were obtained at the Institutional SEM Laboratory of the MPEG, using a Tescan Mira 3 electron microscope with FEG (field emission gun) electron gun. For SEM preparation, spores were placed on aluminum supports using conductive carbon tape and coated with gold in an Argon atmosphere at a pressure of 2.10-2 mbar for 2':30''. To obtain the images, a voltage acceleration of 5 kV and a working distance of 15 mm were used. Photographs of the spores were edited using program Gimp 2.10.34.

Data analysis

Spores were measured under light microscopy using acetolyzed and non-acetolyzed material. Acetolysis was carried out on a single specimen per species (= reference specimen; RS); additional specimens of the species, when available, served as comparison specimens (CS). To estimate the diameter of the spores, 50 spores of the RS and 30 of CS were chosen randomly from three to five microscope slides for measurement and analysis. Descriptive statistics was done using Microsoft Excel (2016) and included size range (Xmin–Xmax), median, skewness, kurtosis, and values of 25 prcntil and 75 prcntil.

Kruskall Wallis test was applied to test the intraspecific variance of the morphometric data of acetolyzed spores (Hollander & Wolfe 1973), followed by the Wilcox test. Appropriate tests were applied for non-parametric data without normal distribution (Shapiro-Wilk test, $p < 0.05$) and homoscedasticity (Levene test, $p > 0.05$). Analysis and graphic presentation of the data was carried out with the R software system (version 4.3.2, R Core Team 2023).

To determine the similarity of the studied species, palynological, morphological, and ecological data were transformed into binary data (Supplementary material 1) and plotted in a matrix for hierarchical cluster analysis (Supplementary material 2). The "eclust" function of the

factoextra package (Kassambara & Mundt 2020) in R software system (version 4.3.2, R Core Team 2023) was used to perform k-means and h-clust clustering.

Results

Spores of Radulaceae are isomorphic monads, apolar in species of the genus *Radula* and, exceptionally, cryptopolar in *Cladoradula boryana*. They are usually small to medium-sized, 16.66–38.88 µm, rarely larger, 50.00–66.66 µm as in *Radula flavifolia*, inaperturate, with a circular to slightly elongate outline (Table 1, Figures 1, 2, 3). The ornamentation of the spore surface includes two distinct patterns: I) ornamentation with rounded elements, here called Granulate-type ornamentation, and II) ornamentation with elongate elements, here called Echinate-type ornamentation.

The Granulate-type ornamentation consists of granular projections, which are very close to each other and evenly distributed across the spore surface. The granules may be rough, being formed by union of nanogranules (Figures 2 and 3: A, C, D, H-J, L, M, O, P), or smooth (Fig. 2 and 3: G). Rough granules occurred in *Cladoradula boryana, Radula episcia*, *R. flaccida*, *R. javanica*, *R. ligula*, *R. mammosa*, *R. pallens*, *R. sinuata*, *R. subinflata*, *R. voluta* and *R. xalapensis*, whereas *R. javanica* had smooth granules.

Cladoradula boryana stands out by the occurrence of a small circular region of smaller granules on the spore surface (Figures 1 and 2: A). As this region is not associate with an aperture, the spores of *C. boryana* are characterized as being cryptopolar.

The spore ornamentation of *Radula episcia*, *R. mammosa*, *R. pallens*, and *R. subinflata* is very delicate, presenting a psilate appearance under light microscopy. However, under scanning electron microscopy, the nanogranules are regularly distributed and overlapping in *R. episcia*. *Radula pallens* and *R. mammosa* have spores with isolated nanogranules across the spore surface, and in *R. subinflata* occurs a fusion of nanogranules.

In *Radula sinuata* and *R. voluta*, the spore surface is formed by a continuous layer of partially fused nanogranules, presenting perforations. *Radula flaccida* is distinguished by nanogranules irregularly overlapping nanogranules on the spore surface. *Radula ligula* can be separated from other species by the scarcity of nanogranules over the spore surface whereas *R. xalapensis* differs in the large amount of nanogranules overlapping on the spore surface. In *R. javanica*, the spore surface is scabrate and the granules are smooth.

Table 1. Morphometric data of acetolyzed and non-acetolyzed spores of Radulaceae. Reference acetolyzed specimen indicated by an asterisk (n=50); comparison specimens (n=30).

Material	(X_{min}–X_{max})	Median	Skewness	Kurtosis	25 prcntil	75 prcntil
Cladoradula boryana (F.Weber) M.A.M.Renner *et. al.*						
Dauphin 1631 (MO) *	27.77 – 33.33	29.62	0.30	-1.14	27.77	31.48
Radula decora Steph.						
Zündorf 21137 (JE) *	31.48 – 37.03	33.33	0.69	-1.07	31.48	37.03
Radula episcia Spruce						
Dauphin 2117 (MO) *	20.37 – 24.07	22.22	-3.54E-14	-1.21	20.37	24.07
Topanta & Quishpe 669 (MO)	18.51 – 24.07	19.44	0.96	-0.60	18.51	20.83
Radula flaccida Lindenb. & Gottsche						
Caldwell & Baker 15423 (MO) *	20.37 – 25.92	22.22	0.21	-1.32	20.37	24.07
Pursell 11732 (MO)	16.66 – 20.37	18.51	-0.33	-1.49	16.66	20.37
Radula flavifolia (Hook.f. & Taylor) Gottsche *et al.*						
Zündorf 21341 (JE) *	40.74 – 66.66	55.55	-0.35	0.71	51.85	59.25
Zündorf 21139 (JE)	42.59 – 50.00	46.29	0.07	-1.21	43.98	50.00

Material	(X_{min}–X_{max})	Median	Skewness	Kurtosis	25 prcntil	75 prcntil
Radula involvens Spruce						
Topanta & Caranqui 1263 (MO) *	29.62 – 33.33	31.48	-0.19	-1.35	29.62	33.33
Radula javanica Gottsche						
Gómez 6577 (MO) *	29.62 – 35.18	31.48	0.50	-0.98	29.62	33.33
Montfoort & Ek 1117 (GOET)	25.92 – 29.62	27.77	-0.11	-1.09	27.31	29.62
Radula ligula Steph.						
Bastos 4311 (ALCB) *	20.37 – 24.07	22.22	0.17	-1.23	20.37	22.68
Radula mammosa Spruce						
Underwood 946a (NY) *	22.22 – 25.92	24.07	0.25	-1.31	22.22	24.53
Radula pallens (Sw.) Mont.						
Arroyo et al. 2590 (MO) *	20.37 – 29.62	24.07	1.02	0.88	24.07	25.92
Held & van Rhijn HH76 (GOET)	18.51 – 24.07	21.30	0.01	-1.39	18.51	22.68
Smith 10251 (MO)	18.51 – 24.07	20.37	0.10	-1.52	18.51	24.07
Radula portoricensis Steph.						
Breedlove 68131 (MO) *	25.92 – 31.48	27.77	0.33	-0.98	25.92	29.62

Material	(X_{min}–X_{max})	Median	Skewness	Kurtosis	25 prcntil	75 prcntil
Radula sinuata Steph.						
Yano & Peralta 28562 (SP) *	27.77 – 33.33	29.62	0.22	-1.40	27.77	31.48
Radula subinflata Lindenb. & Gottsche						
Allen 11916 (MO) *	22.22 – 27.77	25.00	-0.01	-1.29	24.07	27.77
Bastos 5251 (ALCB)	24.07 – 27.77	25.92	0.06	-1.23	24.07	27.77
Radula venezuelensis K.Yamada						
Maxon & Harvey 8455 (JE) *	31.48 – 37.03	37.03	-0.70	-1.33	33.33	37.03
Radula voluta Gottsche *et al.*						
Gradstein et al. 6852 (GOET) *	33.33 – 38.88	37.03	-0.24	-1.13	33.33	37.03
Herzog s.n. (JE)	24.07 – 33.33	27.77	0.42	-0.76	27.31	30.55
Schäefer-Verwimp *et al.* 24270 (MO)	29.62 – 33.33	29.62	1.11	-0.82	29.62	33.33
Radula xalapensis Nees & Mont.						
Marko Lewis 881742A (MO) *	22.22 – 25.92	24.07	-0.42	-1.26	24.07	25.92

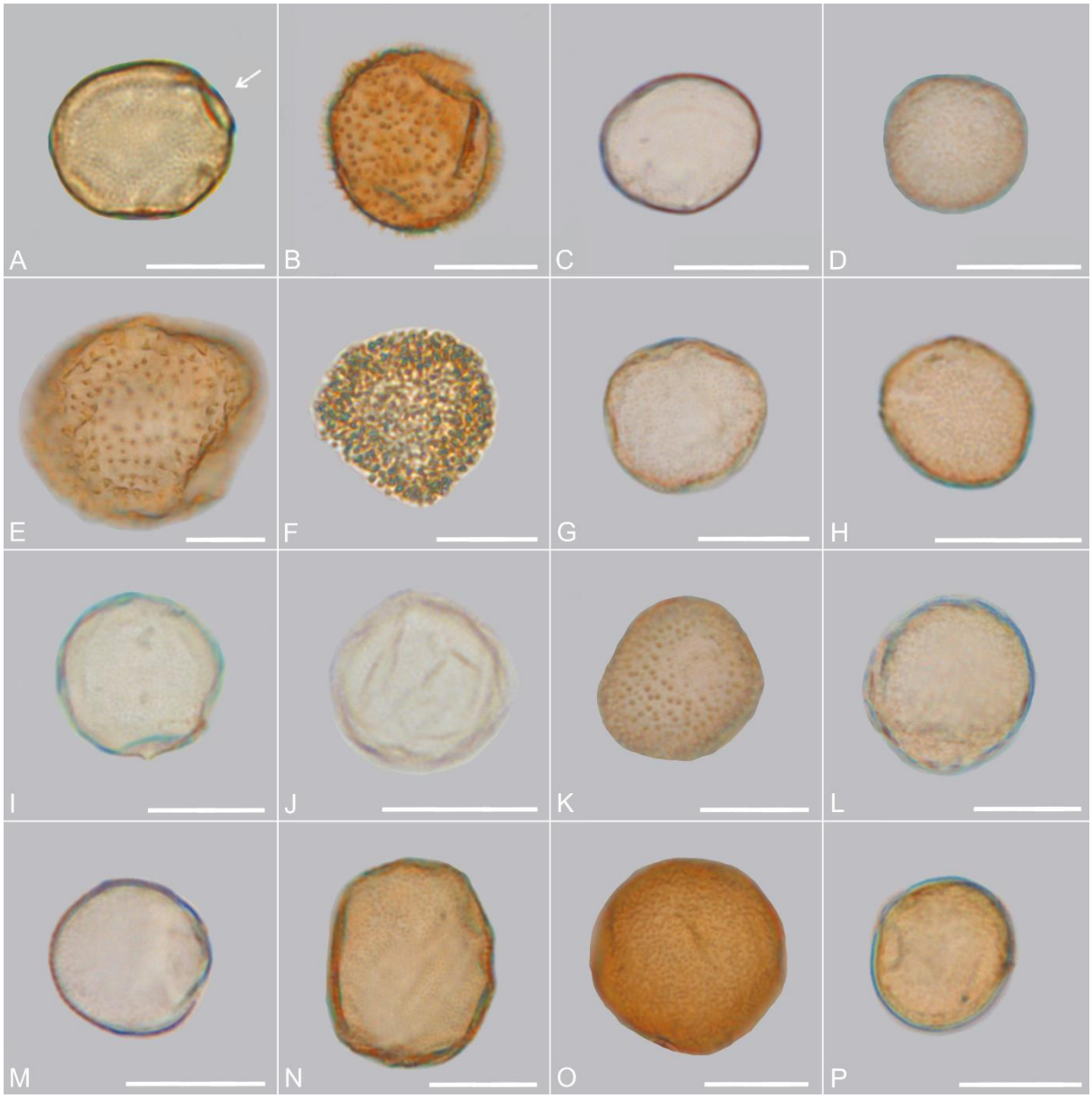

Figure 1. Photomicrographs of spores of species of Radulaceae under LM. **A.** *Cladoradula boryana*. **B.** *Radula decora*. **C.** *Radula episcia*. **D.** *R. flaccida*. **E.** *R. flavifolia*. **F.** *R. involvens*. **G.** *R. javanica*. **H.** *R. ligula*. **I.** *R. mammosa*. **J.** *R. pallens*. **K.** *R. portoricensis*. **L.** *R. sinuata*. **M.** *R. subinflata*. **N.** *R. venezuelensis*. **O.** *R. voluta*. **P.** *R. xalapensis*. Scale bar: 20 µm.

The Echinate-type ornamentation consists of blunt spiny projections, which may be distant or very close to each other, evenly or unevenly distributed across the spore surface. The spines may be smooth, distant to each other, and evenly distributed, as in *Radula decora*, *R. flavifolia*, and *R. portoricensis* (Figures 2 and 3: B, E, K), or rough, being formed by the union of nanogranules, very close to each other, and unevenly distributed, as in *Radula involvens* and *R. venezuelensis* (Figures 2 and 3: F and N).

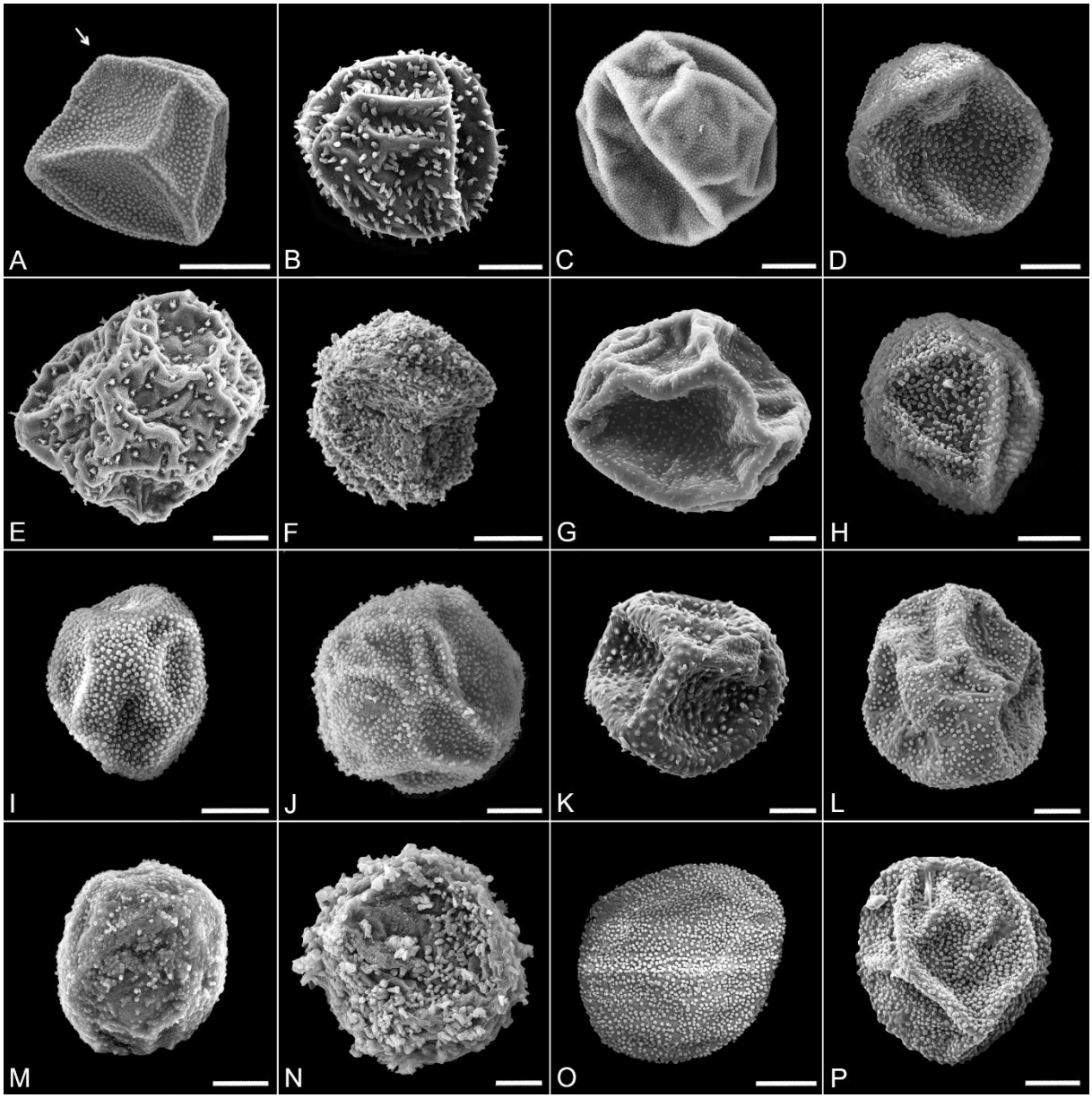

Figure 2. Electromicrographs of spores of species of Radulaceae under SEM. **A.** *Cladoradula boryana*. **B.** *Radula decora*. **C.** *R. episcia*. **D.** *R. flaccida*. **E.** *R. flavifolia*. **F.** *R. involvens*. **G.** *R. javanica*. **H.** *R. ligula*. **I.** *R. mammosa*. **J.** *R. pallens*. **K.** *R. portoricensis*. **L.** *R. sinuata*. **M.** *R. subinflata*. **N.** *R. venezuelensis*. **O.** *R. voluta*. **P.** *R. xalapensis*. Scale bar: A= 20µm; C-D, G-N, P = 5 µm; B, E-F, O = 10 µm.

Among the species with smooth spines, *Radula decora* and *R. flavifolia* have, in addition, elongate elements with ornamented apices. *Radula decora* has flattened apices, while *R. flavifolia* has barbed apices. In addition, the two species can be separated by the spore surface being covered by nanogranules in *R. decora* and by anastomosing nanogranules, presenting perforations, in *R. flavifolia*. *Radula portoricensis* differs by spore surface with striated exine and ornamentation elements heterogeneous in size and shape, some similar to verrucae, but predominantly elongate, resembling spines.

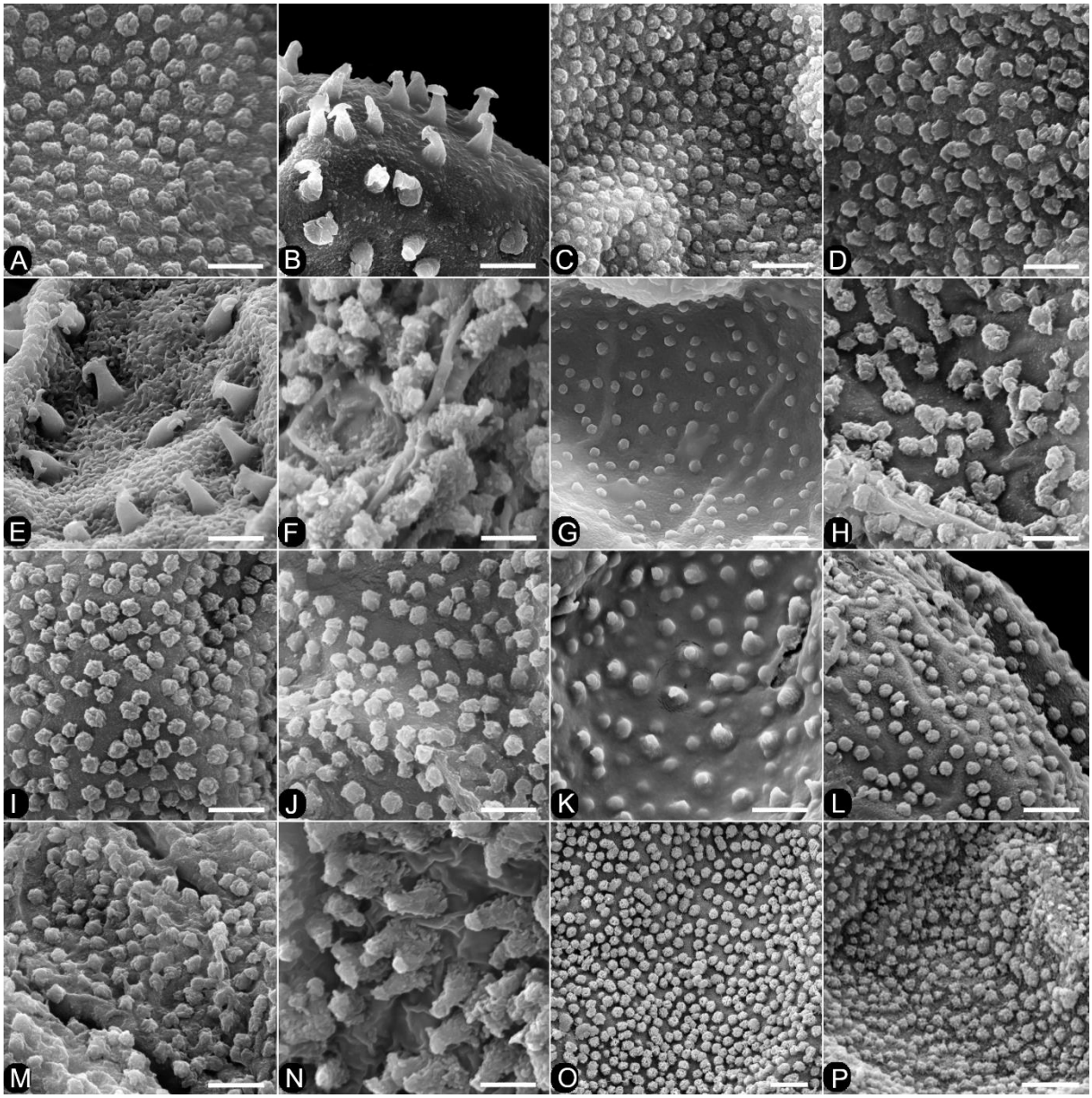

Figure 3. Electromicrographs of spore's ornamentation of species of Radulaceae under SEM. **A.** *Cladoradula boryana*. **B.** *Radula decora*. **C.** *Radula episcia*. **D.** *R. flaccida*. **E.** *R. flavifolia*. **F.** *R. involvens*. **G.** *R. javanica*. **H.** *R. ligula*. **I.** *R. mammosa*. **J.** *R. pallens*. **K.** *R. portoricensis*. **L.** *R. sinuata*. **M.** *R. subinflata*. **N.** *R. venezuelensis*. **O.** *R. voluta*. **P.** *R. xalapensis*.

Spore sizes in the species showed significant differences (chi-squared = 171.46, df = 19, p < 2.2e-16). The spores of *R. flavifolia* were significantly than those of the remaining species (Supplementary material 3, Figure 4) and were classified here as being "large", with 75% of the spores varying between 51.85 to 59.25 µm in diameter (Figure 4). *Radula portoricensis*, with spores classified here as "medium-sized" along with those of eight other species, had 75% of the spores ranging from 25.92 to 29.62 µm in diameter. In the remaining species significant differences in spore size were not observed, with spore sizes varying mainly between 22.22 to

27.77 µm in *Radula mammosa*, *R. pallens*, *R. subinflata* and *R. xalapensis*, as well as *R. episcia*, *R. flaccida* and *R. ligula*, and between 20.37 to 24.07 µm in *R. episcia*, *R. flaccida* and *R. ligula*.

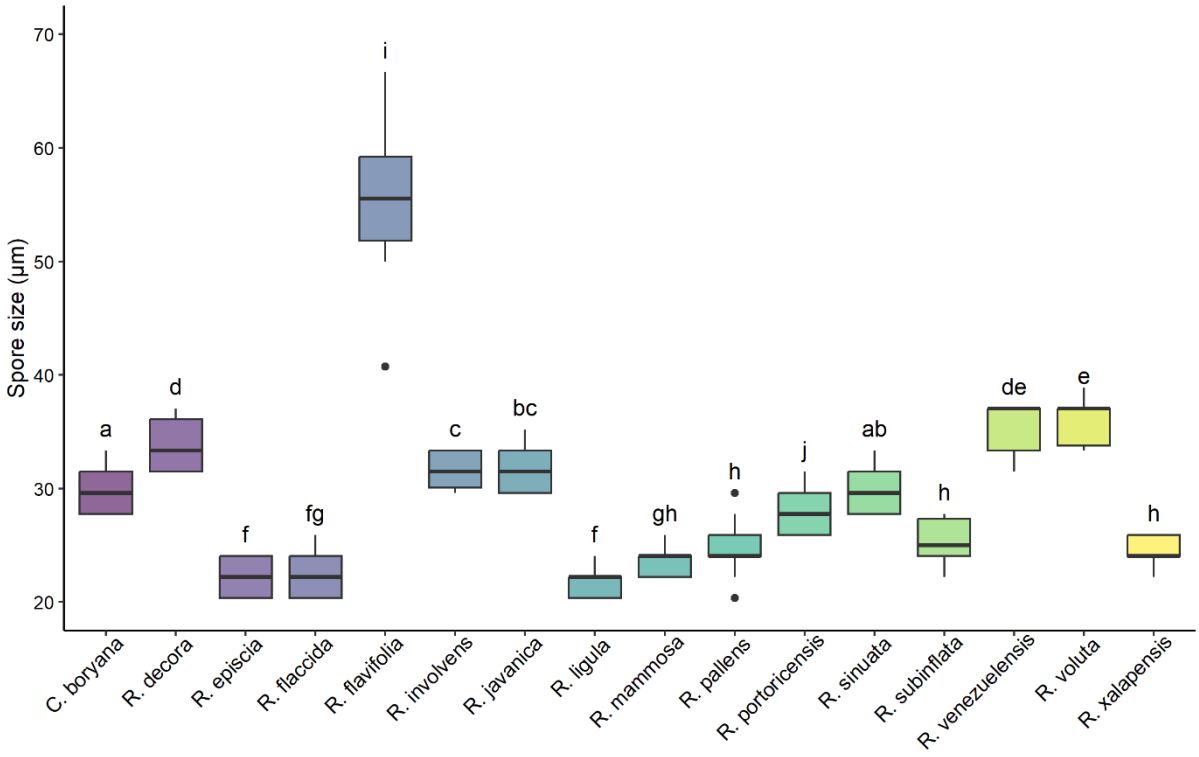

Figure 4. Boxplots representing the spore size distribution within Radulaceae.

The clustering of the species by the Kmean method revealed two groups with high intra-group similarity (Figure 5): a basal group (G1 in red) of species with Echinate-type spore ornamentation (pattern II), and a second group (G2 in blue) with Granulate-type spore ornamentation (pattern I).

Discussion

This is the first study on spores of Radulaceae using the standard palynological approach, unraveling polarity and presence or absence of apertures, and applying the standard palynological terminology for spore size classes and ornamentation patterns, including granule and spine morphology.

The results confirm the need to use LM as well as SEM for adequate palynological description (Luizi-Ponzo & Melhem 2006, Halbritter et al. 2018). LM observation of acetolyzed and non-acetolyzed spores allows for describing general characteristics such as spore size and

outline, apolar or cryptopolar condition, presence or absence of an aperture, and, to some extent, spore ornamentation. Description of ornamentation, however, is greatly enhanced with SEM, which allows to observe nanogranules, details of the exine, and ornamentation of the elements.

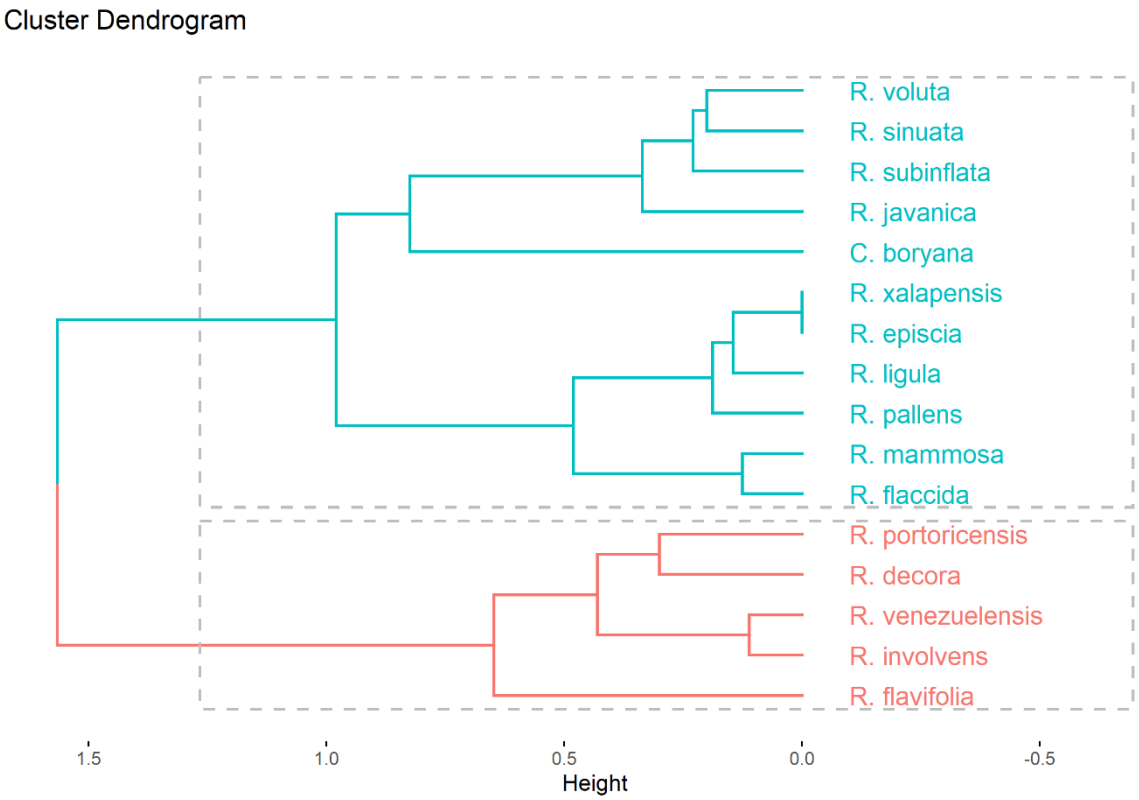

Figure 5. Detailed hierarchical clustering dendrogram of palynological, morphological and ecological data for Radulaceae species. The length of the vertical lines reflects the similarity between the groups (short lines are indicative of greater similarity).

Renner & Braggins (2005) investigated Radulaceae spores with SEM and using the terminology of Boros *et al.* (1993), adopting the term "echiane" instead of "bacula". The authors named different types of spores by using species epithets (*e.g. uvifera*-type). In the present study, however, spore types are named using morphological terms, with recognition of two main ornamentation types, the Granulate-type and the Echinate-type. Additionally, we describe the variation observed within the two ornamentation patterns. We believe that the use of morphological terms for the naming of spore types enhances their application to other taxa (*e.g.* families).

Thus far, spores of about 34 Radulaceae species had been studied (Erdtman 1957, 1965, Heckman 1970, Jones 1977, Schuster 1980, Udar & Kumar 1983, Udar & Srivastava 1984, Bourman & Dickse 1990, Renner & Braggins 2005, Renner 2006, Renner *et al.* 2010, Promma & Chantanaorrapint 2015, Promma *et al.* 2018). This number is very low, given that Radulaceae

has more than 200 species worldwide (Renner *et al.* 2022). In this study, spores of 16 species are comprehensively described for the first time, including 13 of which spores were unknown.

As pointed out by Renner & Braggins (2005), spores of Radulaceae show high micromorphological diversity, especially in ornamentation and size. Our findings lead to identifying polarity as a striking character separating the genera *Cladoradula* and *Radula* in the Neotropics and recognizing two patterns based on the spore ornamentation (Granulate-type and Echinate-type).

Cryptopolar spores were exclusively observed in the single neotropical species of *Cladoradula*, *C. boyana*, whereas apolar spores occurred in all species of *Radula* included in this study. *Cladoradula* was recently raised to generic level by Renner *et al.* (2022) based on molecular data and morphology, viz. (1) stems possessing a 1-3-layered subepidermis, (2) lobule insertion transverse to oblique, (3) gynoecia without innovation, and (4) capsules ovoid. The cryptopolar spores of *C. boryana* might be a further character separating *Cladoradula* from *Radula*. Spores of other *Cladoradula* species should be studied to verify its status as a diagnostic generic character.

Spore size in Radulaceae

In Radulaceae, spore size varies from 16.66 to 66.66 μm. According to Erdtman (1952), its classification ranges from small to large. Spore size of species appears to be independent of the size of the gametophyte. Thus, *Radula xalapensis* with plants measuring 2.5–4 mm wide and 5–8 cm long has smaller spores than *R. flavifolia* (1–1.2 mm wide and ca. 2 cm long) and similar in size to those of *R. mammosa* (1–2 mm wide and ca. 1 cm long).

Spores smaller than our findings were recorded for an African specimen of *Radula flaccida* (Jones 1977; at least 15 μm), for the Asiatic *R. gradilobula* Promma & Chantanaorr. (Promma & Chantanaorrapint 2015; at least 15 μm) and for the New Zealand *R. strangulata* Hook.f. & Taylor (as *R. silvosa* E.A. Hodgs. & Allison, in Renner & Braggins 2005; 11–12μm).

Radula flavifolia, so far, has spores with the largest diameter values recorded for Radulaceae, reaching 66.66 μm. Large spores have also been recorded for *R. aquilegia* (Hook. f. & Taylor) Gottsche et al. (44–50 μm) and *R. tabularis* Steph. (45–65 μm) (Jones 1977, Bourman & Dickse 1990, Udar & Kumar 1983). Jones (1977) also reported spore sizes of *Cladoradula boryana* (as *R. boryana* (F.Weber) Mont.; 30–35 μm), *R. flaccida* (15–18 μm) and

R.voluta (as *R. stipatiflora* Steph.; 22–27 µm). These measurements partially correspond to our findings for these species (see Table 1).

Renner & Braggins (2005) recognized three classes of spore size: spores smaller than 20 µm, between 20 and 30 µm (one species only), and larger than 30 µm in diameter. Our findings, however, reveal spores within two of these classes (*e.g. Cladoradula boryana*: 27.77–33.33 µm; *Radula flaccida*: 16.66–25.92 µm).

Spore ornamentation

Despite using other terminologies, published descriptions of spore ornamentation in Radulaceae present the two main types of ornamentation observed in this study, even with particularities (*i.e.* sub-categories). Few studies investigated spores using SEM techniques (*e.g.* Renner & Braggins 2005, Promma *et al.* 2018). The latter technique allows a much more detailed view of the spore surface. The difference between SEM and light microscope views is easily seen in Figures 1–3.

Spores ornamented by small, rounded granules formed by the union of nanogranules were described as tuberculate or "with tuberculate projections" by Renner & Braggins (2005). According to the latter authors, this type of ornamentation is found in members of at least three subgenera of *Radula*, including subg. *Amentuloradula* (*R. allamanoi* Gola, *R. buccinifera* [Hook.f. & Taylor] Gottsche *et al.*, *R. marginata* Gottsche *et al.*), subg. *Metaradula* (*R. strangulata*) and subg. *Odontoradula* (*R. allisonii* Castle). In the present study, this ornamentation type was found in species of subg. *Volutoradula* and in *Cladoradula*, thus being shared by old, basal lineages of Radulaceae (Patiño *et al.* 2017, Renner *et al.* 2022).

Udar & Krivastava (1984) and Promma *et al.* (2018) reported spores with a "papillate" ornamentation in *Radula complanata* and *R. deflexilobula*, respectively, but SEM pictures (Udar & Krivastava 1984: fig. 9; Promma *et al.* 2018: fig. 13-14) show smooth granules, similar to those found in *Radula javanica* in the present study. Interestingly, these three species are members of the same subgenus (subg. *Radula*). Further investigations on spore ornamentation of the species of subg. *Radula* should be carried out.

Spine projections barbed at apices in *Radula flavifolia* are striking similar in the spores of *Radula physoloba* Mont. (subg. *Amentuloradula*) and *R. uvifera* (Hook.f. & Taylor) Gottsche *et al.* reported by Renner & Braggins (2005). Spores ornamented by elongate elements with flattened apices found in *R. decora*, finally, are not yet known from other *Radula* species but

do occur in *Porella elegantula* (Mont.) E.A.Hodgs. (Renner & Braggins 2005, plate 10, fig. 58).

Spore ornamentation and habitat

Renner & Braggins (2005) found a partial correlation between spore ornamentation and habitats occupied by the species. In our findings, species with spores composed of elongated elements (Echinate-type) are typically corticolous, corroborating the observations of the latter authors. The echinate projections may assist in spore adherence to the surface of twigs and stems (Engel & Gradstein 2003). Spores ornamented with rounded elements (Granulate-type), on the other hand, occur in species with a broader habitat preference, including bark of trees, dead wood, living leaves, rock, and soil. Thus, *R. episcia* and *R. ligula* preferably grow on trees and wet rock while *R. flaccida* and *R. mammosa* are typically epiphyllous, growing on living leaves. Interestingly, the latter two species share a similar spore ornamentation with the epiphyllous *Radula buccinifera* from Australasia (Renner & Braggins 2005).

Conclusions

Palynological analysis can make an important contribution to taxonomic studies of Radulaceae. Spores provide valuable characters and high micromorphological diversity for separating species and groups of species. These groups, however, do not fully correspond to the generic and infrageneric circumscriptions in Radulaceae as supported by molecular evidence (*e.g.* Devos *et al.* 2011, Patiño *et al.* 2017). Spores in Radulaceae can be taxonomically valuable when dealing with closely similar taxa, or with taxa that are difficult to define. Cryptopolar spores found in a member of *Cladoradula* might be a new diagnostic generic feature in Radulaceae. Palynological information from a greater number of species might contribute to a clearer understanding of phylogenetic relationships within Radulaceae.

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Supplementary material

Supplementary material 1. Information on palynology, gametophyte morphology, and ecological aspects employed to perform cluster analysis.

Species	Type of spore	Spore Size	Spore Orn.	Type of granules	Apex of spine ornate	Heter. Orn.	Substrate preference	Stem subepid.	Gynoecial innovation	Asexual Reprod.	Auricle at lobule	Lobule insert	Leaf border	Trigones at leaf cells
Cladoradula boryana	Cryptopolar	Medium	Granulate	Granules with nanogranules	Absent	Present	Generalist	Present	Absent	Absent	Present	Transverse to oblique	Absent	Present
Radula decora	Apolar	Medium	Spine	Spine smooth	Present	Absent	Exclusive	Absent	Present	Absent	Absent	Longitudinal	Absent	Present
Radula episcia	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Absent	Absent	Longitudinal	Absent	Absent
Radula flaccida	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Exclusive	Absent	Present	Present	Absent	Longitudinal	Absent	Absent
Radula flavifolia	Apolar	Large	Spine	Spine smooth	Present	Absent	Generalist	Absent	Present	Absent	Absent	Longitudinal	Absent	Present
Radula involvens	Apolar	Medium	Spine	Spine with nanogranules	Absent	Absent	Exclusive	Absent	Present	Absent	Absent	Longitudinal	Absent	Present
Radula javanica	Apolar	Medium	Granulate	Granules smooth	Absent	Absent	Generalist	Absent	Present	Present	Absent	Longitudinal	Absent	Absent
Radula ligula	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Absent	Absent	Longitudinal	Present	Absent
Radula mammosa	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Exclusive	Absent	Present	Absent	Absent	Longitudinal	Absent	Absent
Radula pallens	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Present	Absent	Longitudinal	Absent	Absent
Radula portoricensis	Apolar	Medium	Spine	Spine smooth	Absent	Absent	Exclusive	Absent	Absent	Present	Absent	Longitudinal	Absent	Present
Radula sinuata	Apolar	Medium	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Present	Present	Longitudinal	Absent	Absent
Radula subinflata	Apolar	Medium	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Absent	Absent	Longitudinal	Absent	Absent
Radula venezuelensis	Apolar	Medium	Spine	Spine with nanogranules	Absent	Absent	Exclusive	Absent	Present	Present	Absent	Longitudinal	Absent	Present
Radula voluta	Apolar	Medium	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Absent	Present	Longitudinal	Absent	Present
Radula xalapensis	Apolar	Small	Granulate	Granules with nanogranules	Absent	Absent	Generalist	Absent	Present	Absent	Absent	Longitudinal	Absent	Absent

Supplementary material 2. Binary matrix based on the information employed to perform cluster analysis.

Species	TS.Crypt.	TS.Apolar	S.small	S.Med.	S.Large	O.Gran.	O.Spine	G.Smooth	G.nano	Sp.Smooth	Sp.Nan.	AG.Orna	H.Orn.	SP.gen	SP.exc	S.sub	Gyn.Ino	Ass.rep	Au.lob	LI.trans	LI.long	LB	TC
C._boryana	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1
R._decora	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	1
R._episcia	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0
R._flaccida	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0
R._flavifolia	0	1	0	0	1	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1
R._involvens	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1
R._javanica	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0
R._ligula	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
R._mammosa	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0
R._pallens	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	0
R._portoricensis	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1
R._sinuata	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	0
R._subinflata	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0
R._venezuelensis	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1
R._voluta	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1
R._xalapensis	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0

Supplementary material 3. Significance value according to the Wilcox test for interspecific morphometric variation of Radulaceae spores. Pink indicates a significant difference ($p<0.05$) and green not significant ($p>0.05$).

	C.boryana	R.decora	R.episcia	R.flaccida	R.flavifolia	R.involvens	R.javanica	R.ligula	R.mammosa	R.pallens	R.portoricensis	R.sinuata	R.subinflata	R.venezuelensis	R.voluta
R.decora	4.80E-09														
R.episcia	3.20E-16	2.60E-16													
R.flaccida	4.30E-16	3.40E-16	1												
R.flavifolia	5.20E-16	4.20E-16	4.00E-16	5.30E-16											
R.involvens	0.0041	0.00456	2.60E-16	3.40E-16	4.20E-16										
R.javanica	0.03399	0.00333	3.00E-16	4.00E-16	4.80E-16	1									
R.ligula	3.20E-16	2.60E-16	1	1	4.00E-16	2.60E-16	3.00E-16								
R.mammosa	3.30E-16	2.60E-16	0.00033	0.97706	4.10E-16	2.60E-16	3.00E-16	3.20E-05							
R.pallens	4.90E-13	2.00E-16	3.40E-07	0.01497	3.30E-16	1.40E-15	3.50E-15	4.70E-08	1						
R.portoricensis	0.00402	1.20E-14	3.10E-16	1.30E-14	5.10E-16	9.70E-11	1.90E-09	3.20E-16	3.10E-14	9.90E-10					
R.sinuata	1	1.40E-07	3.20E-16	4.30E-16	5.30E-16	0.04438	0.17457	3.30E-16	3.30E-16	4.70E-13	0.00257				
R.subinflata	1.10E-13	3.50E-16	2.20E-08	0.00017	5.40E-16	3.50E-16	4.00E-16	3.80E-09	0.14668	1	7.80E-08	1.50E-13			
R.venezuelensis	1.20E-12	0.07412	2.00E-16	2.00E-16	2.00E-16	7.40E-09	8.20E-09	2.00E-16	2.00E-16	2.00E-16	1.10E-15	9.10E-12	2.00E-16		
R.voluta	4.20E-15	6.20E-05	2.50E-16	3.40E-16	4.10E-16	1.30E-13	5.40E-12	2.50E-16	2.60E-16	2.00E-16	3.30E-16	1.20E-14	3.40E-16	1	
R.xalapensis	3.10E-16	2.50E-16	9.60E-08	0.00407	3.90E-16	2.50E-16	2.90E-16	1.40E-08	1	1	8.10E-13	3.10E-16	1	2.00E-16	2.40E-16

CAPÍTULO IV

Título: Taxonomic revision of Radulaceae (Machantiophyta: **Jungermanniidae) in tropical America**

Autores: Fúvio R. Oliveira-da-Silva, S. Robbert Gradstein, Anna Luiza Ilkiu-Borges

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Taxonomic revision of Radulaceae (Machantiophyta: Jungermanniidae) in tropical America

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ABSTRACT

A taxonomic revision of Radulaceae in tropical America based on a comprehensive study of types and over 5000 additional herbarium and fresh collections, and using morphological evidence, leads to the recognition of 54 species and six varieties in two genera, *Cladoradula* and *Radula*. *Cladoradula* has only one species, *C. boryana*. Three new species are described: *Radula sp. nov. 1* from Colombia and *R. sp. nov. 2* and *3* from Bolivia. *Radula dominicensis* and *R. macrostachya* are reinstated from the synonymy of *R. saccatiloba* and *R. javanica*, respectively, and *R. ramulina* var. *microphylla* from the synonymy of *R. voluta*, necessitating the new combination *R. voluta* var. *microphylla*. Twenty-seven names are proposed as new synonyms including the well-known names *R. mammosa*, *R. pocsii* and *R. tectiloba*. Forty-two new lectotypfications are proposed. Six species are considered as doubtful, excluded or erroneously reported taxa for tropical America. The majority of species of Radulaceae in tropical America grow as epiphytes; rock is the second-most colonized substrate. Most species show a wide altitudinal range but highest richness is found in submontane and lower montane forests. About 70% of the species occur exclusively in tropical America, while 30% reach other parts of the world. The northern Andes has the greatest diversity and endemism of Radulaceae species, followed by the Atlantic Coastal Region of Brazil and Central America. *Radula pallens* proved to heteroicous, being dioicous (usually) or monoicous (rarely). This is the second known heteroicous species in Radulaceae. This study includes full descriptions of the Neotropical species of Radulaceae, illustrations of selected taxa, an identification key for all species, and comments on their relationships, geographical distribution and habitat.

Keywords. Neotropics, leafy liverworts, *Radula*, *Cladoradula*, taxonomy.

INTRODUCTION

Leafy liverworts (Marchantiophyta Müll. Frib.: Jungermanniidae Engl.) are one of the most diverse groups of early land plants with numerous families with a long evolutionary history (Heinrichs *et al.* 2006, Crandall-Stotler *et al.* 2009, Feldberg *et al.* 2014, Bechteler *et al.* 2023). Among them, Radulaceae Müll. Frib. (Porellales Schljakov suborder Radulinae R.M.Schust.) is one of the most isolated lineages belonging to the order Porellales Schljakov and the only family within the suborder Radulinae (Crandall-Stotler *et al.* 2009). Radulaceae originated in the Cretaceous (Patiño *et al.* 2017), establishing in the angiosperm-dominated rainforests (Feldberg *et al.* 2014). Although its center of diversity is in humid tropical and warm temperate regions, the family is distributed across all continents of the globe (except Antarctica) and most species grow as epiphytes in lowland or montane rainforests (Gradstein *et al.* 2001). Radulaceae have distinctive morphological traits separating them from other liverwort families, including rhizoids in tufts on the lobule surface, terminal *Radula*-type branches, very large oil bodies, absence of underleaves, and tubular, dorsiventrally flattened perianths (Schuster 1980a, Yamada 1979, Gradstein *et al.* 2001, Crandall-Stotler *et al.* 2009, Oliveira-da-Silva *et al.* 2021). Radulaceae also are chemically distinct in producing bibenzyl cannabinoids and prenyl bibenzyl derivatives, as well as bis-bibenzyls (Chicca *et al.* 2018, Hussain *et al.* 2019, Asakawa *et al.* 2020).

With more than 800 binomials and between 200 and 350 species worldwide (Renner 2016), Radulaceae exhibit a wide range of morphologies and a considerable number of supraspecific taxa have been proposed to classify the species (*e.g.*, Stephani 1884, 1910, Spruce 1884, Castle 1936, Grolle 1970, Jones 1977, Yamada 1979, Schuster 1980a, Devos *et al.* 2011a, Renner *et al.* 2022).

Based on molecular, morphological and a divergence time analysis using fossil evidence evidence, Renner *et al.* (2022) recognized three genera within Radulaceae: *Cladoradula* M.A.M. Renner *et al.* with seven species distributed throughout the Tropics and in eastern Asia and North America, *Dactyloradula* (Devos *et al.*) M.A.M. Renner & Gradst. with only *D. brunnea* (Steph.) M.A.M. Renner & Gradst. in Japan, South Korea, Kuril Island and British Columbia, and *Radula* with between 200 and 350 species worldwide. The species of *Radula* are currently placed into five subgenera: *Amentuloradula* Devos *et al.*, *Metaradula* R.M. Schust., *Odontoradula* K.Yamada, *Radula* and *Volutoradula* Devos *et al.* (Devos *et al.* 2011,

Renner *et al.* 2022). The subgeneric classification is mostly based on molecular evidence; morphological circumscription of the subgenera remains problematic and the subgeneric assignment of a considerable number of species remains still unclear.

Taxonomic revisions are available for temperate and paleotropical Radulaceae species (*e.g.* Jones 1977, Yamada 1979, 1996, Schuster 1980a, Renner 2005, 2014, Renner *et al.* 2013a,b,c, Promma & Chantanaorrapint 2015, Shingh *et al.* 2016, Gradstein *et al.* 2022), but those of the Neotropics – one of the main diversity centers of the genus *Radula* with more than 70 accepted species (Oliveira-da-Silva *et al.* 2021, Gradstein 2021) – have not been monographed and remain insufficiently known. Important contributions to the taxonomy of the Neotropical taxa were made by Castle (1936, 1939, 1959a,b, 1963, 1965, 1966, 1967) and Yamada (*e.g.*, 1980, 1981, 1982a, 1987, 1991, 1993a), but these studies were mostly based on a limited sampling and are now largely outdated. In addition, keys and lists of species of Radulaceae have been provided for different countries of tropical America (*e.g.* Yamada 1988, 2000, Yamada & Gradstein 1991, Yamada 2003, Gradstein & Ilkiu-Borges 2009, Fulford & Sharp 1990, Gradstein 2021).

A critical taxonomic revision of the Neotropical species of Radulaceae is lacking and is urgently needed. The authors have done a preliminary revision of Radulaceae in Brazil based on morphological evidence and extensive sampling (Oliveira-da-Silva *et al.* 2021). The results showed that the number of currently accepted species is probably excessive and that several of them may be synonyms, even though new species may still be discovered (Oliveira-da-Silva & Ilkiu-Borges 2020, Oliveira-da-Silva *et al.* 2020).

The present study presents a taxonomic revision of Radulaceae in the Neotropics based on study of type specimens, additional herbarium collections and fresh material. Full species descriptions, an identification key, illustrations of selected taxa and comments on taxonomic relationships, geographical distribution and habitat are provided.

HISTORICAL SURVEY

The first description of a *Radula* species from the Neotropics was published by Swartz (1788) as *Jungermannia pallens* Sw. [=*Radula pallens* (Sw.) Mont.]. The species was collected in Jamaica by its author and considered endemic to Jamaica until recently. Gradstein (2021), however, found that *Radula pallens* was conspecific with *R. kegelii* Steph. and widespread in the Neotropics. Futher new species from tropical America were described by Nees & Montagne (1836: *Radula xalapensis*), Gottsche *et al.* (1844: *R. campanulata*), Gottsche *et al.* (1845: *R.*

quadrata), Gottsche *et al*. (1847: *R. affinis, R. conferta, R. flaccida, R. macrostachya, R. mollis,* and *R. subinflata*), Taylor (1846: *R. gottscheana, R. jamesonii, R. pocillifera, R. ramulina, R. recubans*), Taylor (1847: *R. grevilleana*), Montagne (1845: *R. stenocalyx*) Gottsche (1863: *R. mexicana, R. tenella,* and new varieties), and Ångström (1876: *R. caldana*).

The first major taxonomic treatment of *Radula* together with an infrageneric classification and descriptions of numerous new species was published by Stephani (1884). Seventeen species were newly described from tropical America, including *R. andicola, R. angulata, R. bogotensis, R. cordovana, R. decora, R. fendleri, R. gracilis, R. inflexa, R. kegelii, R. korthalsii, R. leiboldii, R. saccatiloba, R. subsimplex, R. surinamensis, R. taylorii, R. tenera,* and *R. tenerrima*. Based on shared morphological characteristics, Stephani (1884) proposed 12 species groups in Radulaceae: *Acutifoliae*, *Macrolobae*, *Ampliatae*, *Communes*, *Javanicae*, *Micolobae, Plumulosae, Saccatilobae*, *Longilobae*, *Tumidae*, *Amentulosae* and *Cavifoliae*.

Almost simultaneously, Spruce (1885) published an infrageneric classification of 13 species and seven varieties of *Radula* from the Amazon basin and the Andes, splitting them into two subgenera, *Acroradula* and *Cladoradula*. The latter subgenus comprised only *Radula gottscheana* Taylor, recognized by an oblong-globose capsule, gynoecia on short lateral branches without innovations, and a wide-mouthed perianth. The subg. *Acroradula* was defined by an oblong-cylindric capsule, gynoecia on long terminal branches or main stem and with two innovations, and a narrow-mouthed perianth. Spruce's work (Spruce 1884-1885) is one of the most important historical treatments of liverworts from tropical America, describing hundreds of new taxa including 11 new species of *Radula* and several new varieties, viz. *R. amazonica, R. amazonica var. campanensis, R. amazonica var. negrensis, R. cornucopiae, R. episcia, R. episcia var. opaciuscula, R. flaccida var. brachycalyx, R. involvens, R. pseudostachya, R. pusilla*, *R. riparia* and *R. viridiaurea*. Further new species for tropical America were described by Stephani (1888: *Radula eggersiana*, *R. portoricensis*, and *R. tectiloba*) and Spruce (1889: *R. aurantia*, 1890: *R. claviflora* and *R. mammosa*).

In his "Species Hepaticarum", Stephani (1910) recognized 220 species of Radulaceae worldwide, of which 66 were reported for tropical and subtropical America and 17 were described as new species: *Radula didrichsenii, R. elegans, R. falcifolia, R. frondescens, R. galapagona, R. glauca, R. guatemalensis, R. laxiramea, R. ligula, R. longifolia, R. montana, R. nudicaulis, R. obtusifolia, R. sinuata, R. sonsonensis, R. subtropica* and *R. uleana*. The genus was subdivided into seven sections, all of them previously proposed (Stephani 1884), viz. *Acutifolia, Appendiculatae, Ampliatae, Communes, Microlobae, Longilobae* and *Amentulosae*. The two subgenera recognized by Spruce (1885) were not taken into account.

Subsequently, Stephani (1916) described seven new species of *Radula* from Bolivia: *Radula appendiculata*, *R. boliviana*, *R. convexa*, *R. goebelii*, *R. grandiloba*, *R. longituba*, and *R. verrucifolia*, and three from various Neotropical countries: *R. arsenii* (Mexico), *R. dominicensis* (Dominica), and *R. sprucei* (Colombia) (Stephani 1924). A new species from Jamaica was described by Pearson (1931: *R. jamaicensis*)

In 1936, Hampstead Castle initiated a worldwide revision of *Radula* which resulted in 11 papers, divided in two parts. The first part concerned the species of *Radula* subg. *Cladoradula* (Castle 1936; 15 species) while the second part treated the species of subg. Acroradula, in ten sections (most of them recognized previously by Stephani 1884, 1910), including sect. *Epiphyllae* (Castle 1938; 10 spp.), *Amentulosae* (Castle 1950; 6 spp.), *Dichotomae* (Castle 1959a; 22 spp.), *Marginatae* (Castle 1959b; 2 spp.), *Lingulatae* (Castle 1962; 4 spp.), *Saccatae* (Castle 1963; 51 spp.), *Acutilobae* (Castle 1964; 11 spp.), *Densifoliae* (Castle 1965; 29 spp.), *Ampliatae* (Castle 1966; 35 spp.) and *Complanatae* (Castle 1967; 44 spp.). Two further species were added in a supplement (Castle 1967), resp. *Radula obiensis* Hattori (subg. *Cladoradula*) and *R. galapagona* Steph. (sect. *Ampliatae*).

Castle's treatment is one of the most important taxonomic works on Radulaceae. In addition to placing the species in subgenera and sections and providing detailed descriptions, llustrations, data on distribution and morphological discussions on the species, he also reported numerous new records, new synonyms and descriptions of new species, including 14 from tropical America: *Radula antilleana*, *R. dicksonii*, *R. elliottii*, *R. evansii*, *R. floridana*, *R. husnotii*, *R. lindigii*, *R. microlobula*, *R. neotropica*, *R. obovata*, *R. pagani*, *R. underwoodii*, *R. varilobula* and *R. wrightii*.

The subgenera and sections adopted in Castle's monograph were formalized by Grolle (1970), who provided Latin diagnoses and assigned type specimens to the infrageneric taxa. In addition, he described a new species from tropical America, *Radula castlei* Grolle.

Yamada (1979) published an oustanding taxonomic treatment of *Radula* from Asia and the Pacific region, and established a third subgenus, subg. *Odontoradula*. In the same year, Jans (1979) published a concise treatment of *Radula* from the high Andes of Colombia and described the new variety *Radula ramulina* var. *microphylla*.

Schuster (1984) described a remarkable new species of *Radula*, from the Amazonian rainforest, *R. yanoella*, characterized by a persistent, radially expanded thallus with leafy shoots sprouting from the thallus margin. Schuster (1984) also validated the subgenus *Metaradula* [type species *Radula buccinifera* (Hook.f. & Taylor) Gottsche *et al.*] proposed by Schuster (1980a), which included typically epiphyllous species of *Radula* characterized by

having an *Isotachis*-type perigynium (= tubular structure derived from stem tissue and surrounding and protecting the sporophyte).

From the 1980s onwards, important studies on *Radula* were conducted by Kohsaku Yamada. He published taxonomic treatments and species lists for different countries of the Neotropics, including Cuba (Yamada 1988), Galápagos Islands (Yamada & Gradstein 1991), Bolivia (Yamada 2000) and Brazil (Yamada 2003), a review of the type specimens of *Radula* from Latin America (Yamada 1980, 1981, 1982a, 1987, 1991, 1993a) and descriptions of numerous new species, including many from tropical America: *Radula brasilica*, *R. cochabambaensis*, *R. cubensis*, *R. eggersii*, *R. lewisii*, *R. longiloba*, *R. pocsii*, *R. schaefer-verwimpii*, *R. schofieldiana*, *R. sinskeana*, *R. tenuis*, *R. venezuelensis* (Yamada 1983, 1990, 1993b, 1997), *R. peruviana* (Yamada in Schultze-Motel & Menezes 1987), *R. gradsteinii*, *R. guyanensis*, *R. mazarunensis* (Yamada in Gradstein & Florschütz-de Waard 1989), and *R. santacruziana* (Yamada & Gradstein 1991).

Recently, the author together with his supervisors have published a taxonomic treatment of Radulaceae in Brazil, with the description of several new taxa: *Radula bahiensis*, *R. fendleri* var. *paroica*, *R. renneri* and *R. yamadae* (Oliveira-da-Silva & Ilkiu-Borges 2020, Oliveira-da-Silva *et al.* 2020, 2021). The Brazil treatment was the starting point of the present work. In addition, Gradstein (2021) provided a treatment of Radula in Colombia and Ecuador and together with A. L. Ilkiu-Borges described *R. bischlerae* sp. nov. from the Sierra Nevado del Cocuy, Colombia. Finally, *R. pallens* var. *marginata* was described from Venezuela and *R. smithii* from Peru were described by Oliveira-da-Silva *et al.* (2022), as the first results of the present treatment.

In recent years, Radulaceae have also been the subject of several molecular-phylogenetic studies (Devos *et al.* 2011a,b, Renner 2014, Renner *et al.* 2013a,b,c, Bechleler *et al.* 2017, Patiño *et al.* 2017, Promma *et al.* 2018, Zang *et al.* 2021). Around 120 specimens of Radulaceae have been included in phylogenetic analyses and more than 600 sequences, based on regions of chloroplast DNA such as *psbT-psbH*, *psb-trnH*, *rps4*, *atpB-rbcL*, *trnG* and *trnL-trnF*, were deposited in GenBank. Devos *et al.* (2011a) proposed the first subgeneric classification of *Radula* based on molecular and morphological traits. They tested the monophyly of four subgenera (*Radula*, *Cladoradula*, *Odontoradula* and *Metaradula*), including the type specimens of each in their analysis, and found them to be well-supported lineages. In addition, Devos *et al.* (2011a) recovered three additional lineages, which were formalised as subgenera: *Amentuloradula* [type species *Radula formosa* (Spreng.) Nees], *Dactyloradula* (*R. brunnea* Steph.) and *Volutoradula* (*R. voluta*). However, the authors found

only very few synapomorphies in these subgenera, resulting in problematic and contradictory circumscriptions of the lineages, generating homoplasies and allowing morphologically closely similar species to be assigned to different subgenera (Devos *et al.* 2011a).

The taxonomic status of the subgenus *Cladoradula* and *Dactyloradula* was recently reconsidered by Renner *et al.* (2022) based on a divergence time analysis using fossil evidence. These two subgenera appeared as significantly older lineages than the other subgenera of *Radula*, and their morphologies proved to be unusual as well. Because of this, Renner *et al.* (2022) raised these subgenera to genus level.

METHODOLOGY

This study was carried out based on the examination of about 6,000 specimens of Radulaceae, including types and additional collections from herbaria worldwide (ALCB, BM*, BR, F, FH*, G, GOET, ICN, INPA*, JE, L, MG*, MANCH*, MO, NICH, NY*, RB*, S, SP*, UFP and YU; acronyms are in accordance with the Index Herbariorum; herbaria signed with an asterisk were visited by the first author), as well as fresh material collected during field expeditions or requested from bryologists. Location of type specimens was based on the information available in the protologue, consulted in the original papers or websites online such as: Tropicos, Index Herbariorum, Biodiversity Heritage Library, JSTOR Plant Sciences, SpeciesLink and Reflora. When a type specimen could not be found, searches were made in the herbarium of the collector or the author of the species (Gradstein 2016).

The botanical nomenclature is in accordance with the rules and recommendations of the International Code of Nomenclature for Algae, Fungi and Plants (Turland *et al.* 2018). In taxon authorities, only the name of the validating author is cited and "ex" authors are omitted because their citation is not obligatory (Turland 2013). Author citations of species with more than three authors were abbreviated, with only the first one being spelled out and the remaining authors being cited as "*et al.*" [*e.g. Cladoradula* (Spruce) M.A.M.Renner *et al.*]., except in species headings.

Most of the Radulaceae species were examined and identified in the Bryology Laboratory (BRIOLAB) of the Museu Paraense Emílio Goeldi (MPEG). The species were identified on the basis of the original papers, comparison with the type specimen and/or specialized literature such as: Castle (1936, 1939, 1959a, 1963, 1965, 1966, 1967), Yamada (1979, 1980, 1981, 1982a, 1982b, 1987, 1991, 1993a, 2003), Schuster (1980a, b), Reiner-Drehwald (1994), Gradstein & Ilkiu-Borges (2009), Gradstein (2021), Oliveira-da-Silva *et al.* (2021), Gradstein

et al. (2022), Renner *et al.* (2022). The taxonomic classification to family is in accordance with Crandall-Stotler *et al.* (2009) and the generic and subgeneric classifications are in accordance with Devos *et al.* (2011a) and Renner *et al.* (2022).

Morphological and anatomical characters of the gametophyte and sporophyte were observed using a stereomicroscope Leica EZ4 and an optical microscope Leica DM500. Measures represent the complete variation of the plants and were made using an eye-objective with a millimeter ruler calibrated with a millimeter glass-slide. The anatomical cuts were made freehand using a scalpel. Illustrations carried out by the first and third author were made using a light microscope Leica DM1000 with drawing tube. Photographs of the plants were taken at the Microscopy Laboratory of the MPEG using an optical microscope Leica DM6 B with an attached camera. The illustrations and photographs of the species were edited using the software Gimp 2.10.34.

Distribution maps for the species were based on the species records, both of the specimens examined in this study and from records available in studies on Radulaceae (*e.g.* Castle revision and Yamada notes) or guides and catalogs for Neotropical countries (*e.g.* Stotler *et al.* 1998, Dauphin 2005, Pérez 2009, Gradstein & Ilkiu-Borges 2009, Schäfer-Verwimp 2010, Schäfer-Verwimp & van Melick 2016, Gradstein 2021). Morphological and anatomical descriptions followed the model adopted by Oliveira-da-Silva *et al.* (2021) and Renner & Braggins (2005) for the gametophyte and sporophyte, respectively, with modifications.

RSEULTS AND DISCUSSION
MORPHOLOGY AND ANATOMY

STEM ANATOMY

Stem anatomy is a significant taxonomic feature in Radulaceae (Jones 1977, Yamada 1979, Schuster 1980a, Renner & Braggins 2004) and is one of the most relevant morphological characteristics to support different phylogenetically well-defined lineages. In the present study, nine types of stem anatomy are recognized among 54 species and six varieties of Radulaceae recorded from tropical America (Table 1). Some stem anatomy types coincide with the subgenera as currently recognized based on molecular phylogeny. Nevertheless, we must be cautious to use stem anatomy as a subgeneric character in this study since most Neotropical species of Radulaceae have not yet been included in a molecular analysis.

Stem anatomy Type-1 (Figure 1A) is the only one with a subepidermis, an exclusive diagnostic feature of the genus *Cladoradula*. The majority of the species in tropical America has Type-2 (Figure 1B), which is characterized by the outer epidermal wall usually brownish, heavily and evenly thickened, more so than the inner epidermal wall. The only difference between the Type-2 and Type-3 (Figure 1C) is that the latter has both epidermal walls (outer and inner) heavily and evenly thickened. The only difference between Type-2 and Type-4 (Figure 1D) is the presence of thick-walled medullary cells by concave trigones (thin-walled in Type-2 and -3). Type-5 (Figure 1E) is anatomically identical to Type-2, differing by presenting the same color in epidermal and medullary cell walls, while Type-2, Type-3, and Type-4 have a distinct coloration of epidermal and medullary cell walls. Altogether, these four stem anatomy types (2, 3, 4, and 5) gather ca. 66 % of the species in tropical America, and part of these species are phylogenetically resolved in *Radula* subg. *Volutoradula*.

Stem anatomy Type-6 (Figure 1F) assembles species with thick-walled epidermal and medullary cells, cells uniform in size, and walls of the same color (colorless to brownish). Part of the species with stem anatomy Type-6 belong to *Radula* subg. *Radula*, and solely *R. saccatiloba* belongs to *Radula* subg. *Odontoradula* (Devos *et al.* 2011a).

Typically epiphyllous species of *Radula* subg. *Metaradula* sect. *Epiphyllae* have stem anatomy Type-7 (Figure 1G). The difference between Type-7 and Type-6 is the epidermal and medullary cells being thin-walled in Type-6, while being thick-walled in Type-7. In addition, the majority of the species with stem anatomy Type-7 have a small stem diameter, usually between 50 to 100 µm wide (except *R. grevilleana*), while species with Type-6 have a larger diameter, varying from (70–)100 to 360 µm.

Stem anatomy Type-8 (Figure 1H) and Type-9 (Figure 1I) are represented by one species each. *Radula wrightii* (Type-8) is the only species with epidermal cells larger than medullary cells, while *Radula ligula* (Type-9) has a set of diagnostic characteristics: thick-walled epidermal and medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, the cells of the same size, and walls of the same color (yellowish to brownish).

TABLE 1. Stem anatomy types in Neotropical Radulaceae.

TYPE	STEM ANATOMY	SPECIES
Type-1 (1sp.)	*Stems* 300–400 µm in diam., with a 3–4-layered cortex made up of rows of strongly thick-walled epidermal and subepidermal cells surrounding thin-walled medullary cells, medullary cells larger than epidermal and subepidermal cells, medullary walls colorless to yellowish, epidermal and subepidermal walls brown.	*Cladoradula boryana*
Type-2 (23 spp. + 4 varieties)	*Stems* 60–500 µm in diam., with thick-walled, brownish (rarely colorless to yellowish) epidermal cells surrounding mostly larger (rarely uniform in size), thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall.	*Radula bahiensis*, *R. brasilica*, *R. cochabambaensis*, *R. cubensis*, *R. eggersii*, *R. elliottii*, *R. episcia*, *R. fulvifolia*, *R. involvens*, *R. sp. nov. 2*, *R. macrostachya*, *R. sp. nov. 3*, *R. mexicana*, *R. nudicaulis*, *R. pallens* var. *pallens*, *R. pallens* var. *marginata*, *R. pusilla*, *R. santacruziana*, *R. sinuata*, *R. sonsonensis*, *R. venezuelensis*, *R. voluta var. voluta*, *R. voluta* var. *microphylla*, *R. xalapensis*, *R. yamadae*
Type-3 (4 spp.)	*Stems* 180–350 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, epidermal wall heavily and evenly thickened.	*Radula microlobula*, *R. recubans*, *R. smithii*, *R. underwoodii*
Type-4 (4 spp.)	*Stems* 90–170 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thick-walled (by concave trigones), yellowish	*Radula angulata*, *R. inflexa*, *R. leiboldii*, *R. subinflata*

	medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall.	
Type-5 (5 spp.)	*Stems* 80–150 µm in diam., with thick-walled epidermal cells surrounding mostly smaller or uniform in size, thin-walled medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls colorless to yellowish.	*Radula bischlerae, R. dominicensis R. sp. nov. 1, R. longiloba, R. tenuis*
Type-6 (10 spp. + 2 varieties)	*Stems* (70–)100–360 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless, yellowish or brownish.	*Radula fendleri* var. *fendleri, R. fendleri* var. *paroica, R. gradsteinii, R. javanica R. portoricensis, R. pseudostachya R. quadrata, R. renneri R. saccatiloba, R. taylorii, R. tenera*
Type-7 (4 spp.)	*Stems* 50–100(–200) µm in diam., with thin-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish.	*Radula flaccida, R. grevilleana, R. stenocalyx, R. yanoella*
Type-8 (1 spp.)	*Stems* 70–140 µm in diam., with thick-walled, epidermal cells surrounding mostly smaller, thick-walled (by concave trigones) medullary cells, outer epidermal wall heavily and evenly thickened, walls brownish	*Radula wrightii*
Type-9 (1 spp.)	*Stems* 150–170 µm in diam., with thick-walled, epidermal cells surrounding thick-walled (by concave trigones) medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, *Radula* the cells uniform in size, walls yellowish or brownish.	*Radula ligula*

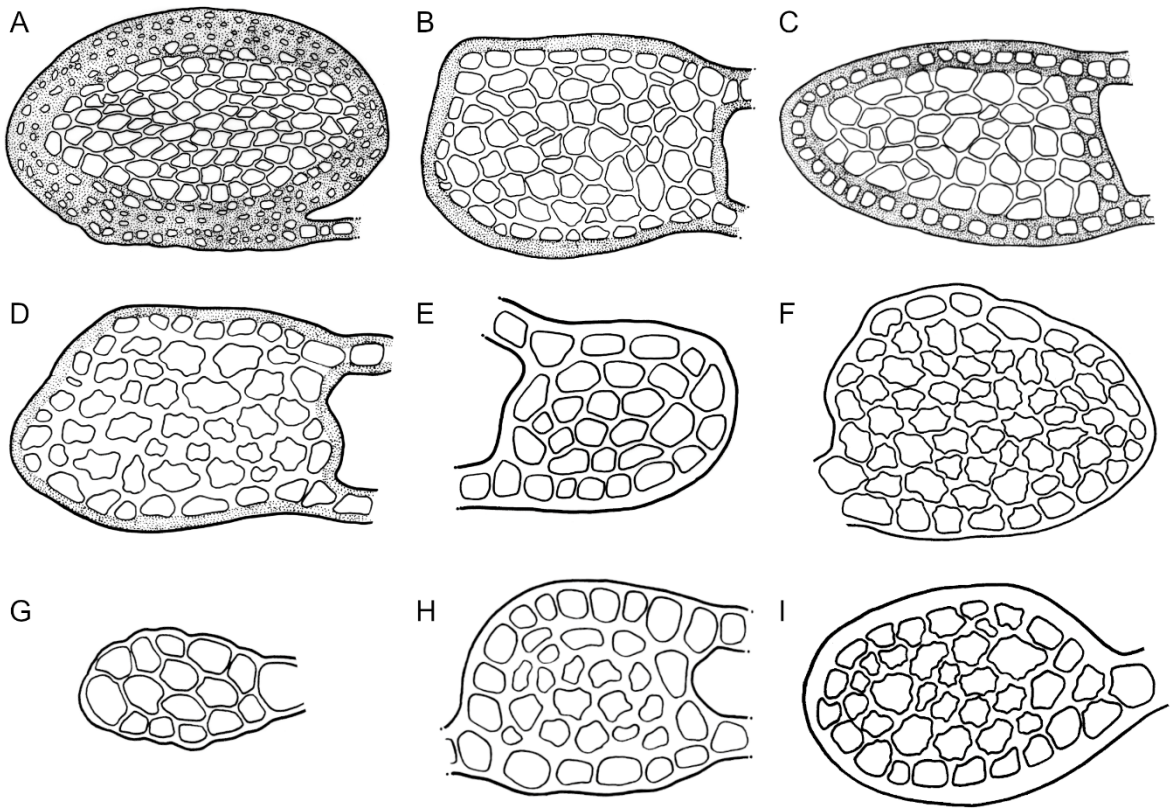

Figure 1. Types of stem anatomy. A. Type-1. B. Type-2. C. Type-3. D. Type-4. E. Type-5. F. Type-6. G. Type-7. H. Type-8. I. Type-9.

BRANCHING

Branching in Radulaceae is predominantly of the *Radula*-type, which originates from a stem epidermis cell and is therefore associated with an unmodified leaf (Crandall-Stotler 1969, Gradstein *et al.* 2001). The branch is produced at the base of the lobule keel of the associated leaf, without a basal collar. Sometimes, *Radula* species produce *Lejeunea*-type branches that originates from the lateral side of the stem, from behind the leaf, and have a distinct basal collar. Crandall (1969) was the first to report *Lejeunea*-type branches in Radulaceae, naming it "adventitious *Radula*-type" branches for *R. longituba* Steph. (= *R. grevilleana* Taylor) (see Crandall 1969, plate 19–21) and *Radula sp.* (plate 19). The latter author observed this type of branch associated with decapitated shoots. Renner & Braggins (2004) also suggested that *Lejeunea*-type branches occur in Radulaceae in response to damage. We observed *Lejeunea*-type branches on decapitated shoots in *Radula angulata*, *R. bahiensis*, *R. cochabambaensis*, *R. inflexa*, *R. javanica*, *R. mexicana*, *R. pallens*, *R. pusilla*, *R. recubans*, *R. saccatiloba*, *R. subinflata* and *R. tenuis*. They were common in *R. pallens* and *R. subinflata*, but rare in other species. In species of *Radula* subg. *Metaradula* (*Radula flaccida*, *R. grevilleana*, *R.*

stenocalyx), however, *Lejeunea*-type branches may occur without being associated with decapitated shoots (see Gradstein *et al.* 2022, Fig. 7I).

It is very common for the primary and secondary branches to be slightly smaller than the main stem in Radulaceae species. However, in *Radula eggersii*, *R. voluta* var. *microphylla* and fossil *R. steerei* branches are very small, being at least 3–4× smaller than the main stem. In this study, these reduced branches are described as "microphyllous" branches.

THALLUS

A thallus occurs in the Neotropical *Radula yanoella*. The thallus is closely attached to the substrate and difficult to detach. Usually, only a small part of the thallus can be detached for observation. The thallus is green to brownish, irregularly rounded, with lobes radially arranged, or narrowly irregularly elongate, with one layer of rectangular cells (20–40 × 6–20 µm). The thallus margin is entire, the cell walls are thickened without trigones, and the cuticle smooth. Short, sterile leafy shoots are sprouting from the thallus margin. The thallus is interpreted as a persistent protonema and is considered a neotenic feature of the species (Schuster 1991, Gradstein & Wilson 2009).

LEAVES

Leaves in Radulaceae, as well as in the other families of Porellales, are incubous and divided into a large dorsal lobe and a smaller ventral lobule. The leaf lobes are attached longitudinally to the stem along a straight insertion line. The insertion of the lobules, however, varies (see below).

The orientation of the leaf lobes varies from widely to (rarely) obliquely spreading and distant to strongly imbricate. The leaf lobes can be plane or strongly convex and vary in shape, from orbicular, suborbicular, ovate, oblong-ovate, falcate-ovate to oblong-falcate. The dorsal base is usually rounded (scarely so in *Radula smithii*), rarely auriculate (*R. sinuata*, *R. voluta* var. *voluta*, *R. voluta* var. *microphylla*, *R. yamadae*), and not covering the stem to fully overlapping. The leaf apex varies only little in Neotropical Radulaceae, being mostly rounded and, in a few species, obtuse to subacute. Leaf margins vary from plane to strongly recurved (both can occur on the same branch as in *R. involvens*, see Fig. XB), sometimes they are incurved or folded ventrally (in species from high elevations), and are entire to (rarely)

crenulate. Crenulate margins may result from the shape of the margin cells (*e.g. R. sonsonensis, R. venezuelensis*) or the production of gemmae (*e.g. R. quadrata, R. tectiloba*).

LEAF CELLS

Leaf cells may sometimes provide diagnostic characters for differentiating species. Marginal leaf cells are usually slightly smaller than median and basal cells, and median cells can be slightly smaller or the same size as basal cells. Concerning shape, marginal cells can be usually subquadrate to subrectangular, rarely rounded as in *Radula sonsonensis*, while median and basal cells vary from isodiametric to elongate. The cell walls vary from thin to evenly thickened, and without or with trigones and intermediate thickenings. In a few species the walls are thin at the leaf base and in midleaf, but evenly thickened along the margin resulting in a 1–4 cell rows wide border (*R. ligula*, *R. pallens* var. *marginata*, *R. smithii*). In species with trigones, margin cells are sometimes slightly more thick-walled than other leaf cells due to a slight and gradual increase of trigone size towards the margin, but without forming a distinct border. Intermediate thickenings are often seen in median and basal leaf cells of *Cladoradula boryana*, *R. gradsteinii*, *R. involvens*, *R. portoricensis*, *R. pseudostachya*, *R. santacruziana*, *R. taylorii* and *R. wrightii*.

Mammillose leaf cells were observed in a few Neotropical species only; their presence/absence varies with a plant and they are readily visible in dorsal view, without sectioning the leaf, when leaf margins are recurved. Leaf cross sections showed that mamillosity of cells usually occurs on the ventral and dorsal leaf surface (as in *Radula eggersii*, *R. sonsonensis*, *R. venezuelensis* and *R. voluta* var. *microphylla*), occasionally only on the dorsal surface (*R. dominicensis*, *R. subinflata*). In one specimen of *R. sonsonensis* (Cauca, Bischler 1060) a distinct papilla occurred on the mammillose cell surface, in the other collections of the species (including the type), papillae were absent.

The cuticle (term applied here to the outer cell surface) is smooth in the majority of the Neotropical Radulaceae species. Eight species and one variety had a finely verruculose cuticle (*Radula fendleri* var. *fendleri*, *R. fendleri* var. *paroica*, *R. gradsteinii*, *R. involvens*, *R. portoricensis*, *R. pseudostachya*, *R. pusilla*, *R. recubans*, *R. renneri*, *R. smithii*). The verrucosity of the cuticle varied, however, and sometimes the cuticle was (almost) smooth.

Oil bodies are important intracelular organelles only found in liverworts. They are highly distinctive and widely used in taxonomy (*e.g.* Gradstein 1978, He *et al.* 2013). Radulaceae stand out by usually having large, brown oil bodies containing mostly bibenzyls

(Asakawa *et al.* 2020). Most Neotropical species had one small to (usually) large oil body per cell (Figure 2). When large, the oil body occupied almost the whole lumen. One or two oil bodies per cell were observed in *Radula venezuelensis* and *R. voluta*; this variation occurred within a plant (see Fig. 2F-G). The oil bodies in the examined species were of the *Jungermannia*-type, spherical to ellipsoidal, light yellow to brown and smooth to slightly granular.

LOBULES

Shape and size of the lobule are key characters for species recognition in Radulaceae (Yamada 1979, Schuster 1980a, Renner & Braggins 2004, Oliveira-da-Silva *et al.* 2021). Lobules vary from small to large, and distant to imbricate. They can be very small in relation to the leaf lobe, such as in *Radula microlobula* (1/5–1/6 of lobe length), or very large and up to 2/3 of lobe length as in *R.* sp. nov. 1. Lobule shape is also highly variable; although being most frequently subquadrate to subrectangular, it can be oblong-rectangular (*Radula episcia*), oblong (*R. bahiensis*), oblong-ovate (*Cladoradula boryana*), suborbicular (*R. voluta*), subrhombic (*R. wrightii*), narrowly obtriangularly elongate (*R. bischlerae*), convolute and lunular (*R. tenera*), ligulate (*R. ligula*) or reniform (as in *R.* sp. nov. 3).

The insertion line of the lobule is useful for distinguishing genera in Radulaceae (Renner *et al.* 2022), species of *Cladoradula* having an oblique to transverse insertion line while *Radula* species are longitudinally inserted. The insertion can be short in both genera, but long only in species of *Radula*, such as in *R.* sp. nov. *2*. In some species of *Radula* the insertion line of the lobule is slightly extended near the lobule base, being circinnate in *R. sinuata* and *R. voluta*, and inverted J-shaped in *R.* sp. nov. 3, *R. quadrata* and *R. xalapensis*.

In addition to the insertion line, the present treatment recognizes the rhizoid area, the base, the free margin, the apex, the distal margin, and the keel of the lobule (see Oliveira-da-Silva *et al.* 2021, fig. 1D). The rhizoid area varies from plane to strongly inflated, especially in epiphyllous species. Regardless of the rhizoidal area, the lobule can be inflated along the keel and flattened above, as in *R. subinflata*, or fully inflated as in *R. saccatiloba*.

The lobule base is usually plane and shows different shapes, varying from rounded to subacute. In *Radula dominicensis* and *R.* sp. nov. 1, the base is exceptionally reduced. Some species have an auriculate lobule base that may be long, as in *Cladoradula boryana*, or short, as in *Radula sinuata*. The base may extend across a small part of the stem or can be strongly ampliate and cover the entire stem width.

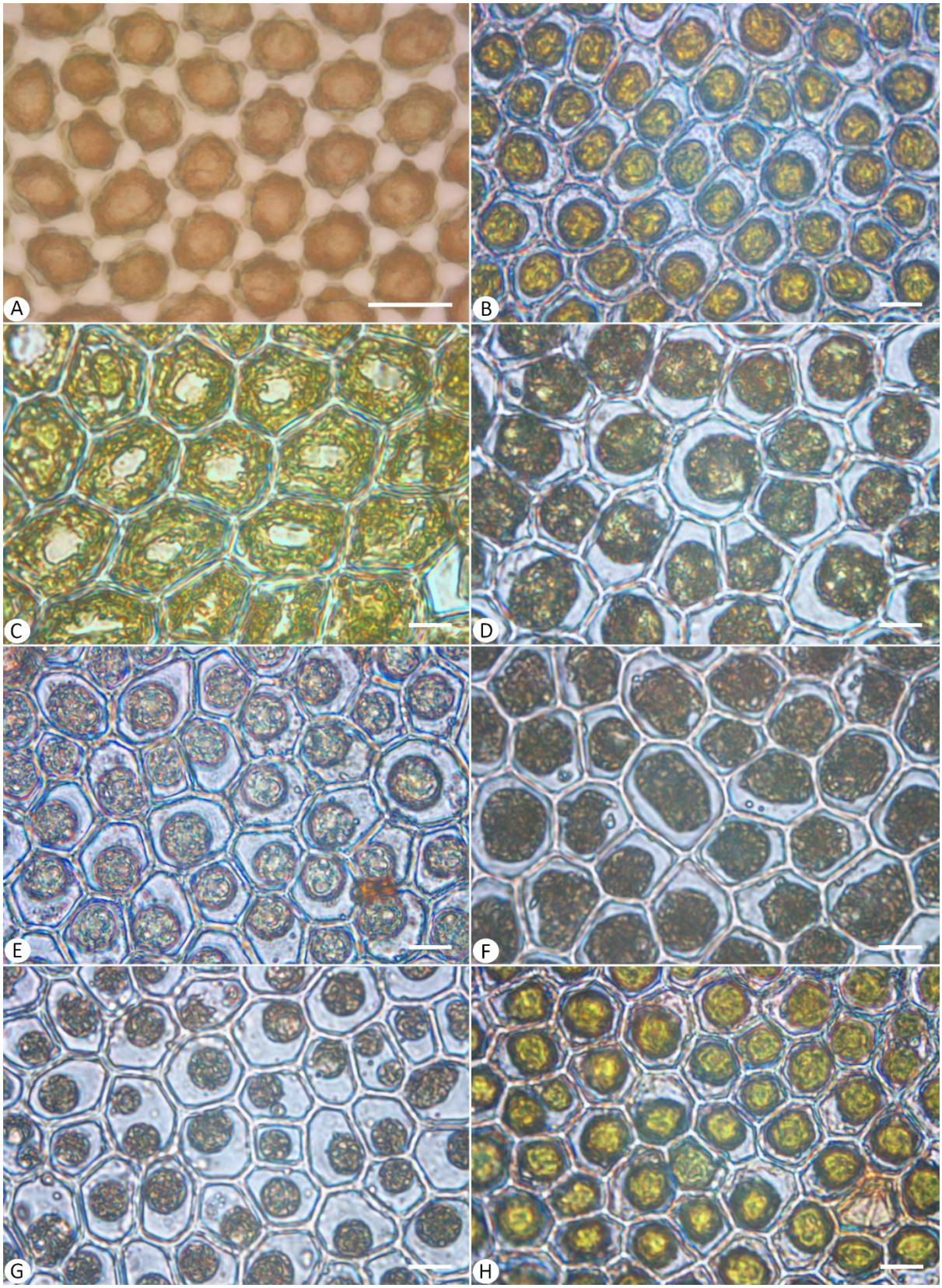

Figure 2. Oil-bodies of some species of Radulaceae. A. *Cladoradula boryana*. B. *Radula fendleri* var. *fendleri*. C. *Radula javanica*. D. *Radula pallens*. E. *Radula sinuata*. F-G. *Radula voluta* var. *voluta*. H. *Radula wrightii*. Scale bar: A= 20 µm; B-H= 10 µm.

The free margin of the lobule is usually plane, but in *Radula brasilica* it is strongly recurved. In the middle, the free margin can be straight, rounded or sinuate.

The lobule apex is plane in most species, but in *R. elliotii*, *R. episcia*, *R. nudicaulis*, *R. pallens*, *R. recubans*, *R. smithii* and *R. underwoodii* it is incurved, while in *R. brasilica*, it is recurved. The apex can be rounded to acute, sometimes prolonged in an obtuse to acute tip (*e.g. R. flaccida* and *R. tectiloba*).

The distal margin varies from straight to rounded or sinuate and its variation is without taxonomic significance. The outline of the keel, however, is taxonomically important and can be straight, concave or convex. In addition, the angle of the keel in relation to stem and to the ventral leaf lobe margin, at its junction with the lobule, are also good taxonomic characters.

RHIZOIDS

Rhizoids occur in tufts on the ventral lobule surface and are hyaline to brownish. In addition, they may occur on the margin of caducous leaf lobes, as in *Radula fulvifolia, R. javanica*, *R. pseudostachya*, and *R. tenuis*. Some species have only a few rhizoids, but epiphyllous plants usually produce a well-developed rhizoid-bundle consisting of numerous thizoids and sometimes arising from a pronounced mammiliform swelling of the mid-lobule surface (*R. flaccida*, *R. grevilleana*, *R. yanoella*). The large rhizoid bundles of epiphyllous plants is an adaptation to their growth on smooth leaf surfaces (Gradstein 1997). In many specimens, however, rhizoids were almost lacking. The lack of rhizoids may be a response to the growth form of the plants, such as being pendent, ascending, or creeping but partially attached to the substrate only.

SEX DISTRIBUTION

Most of Radulaceae species are dioicous; as shown by Devos *et al.* (2011b) less than 10% of the species worldwide are monoicous. In the Neotropics, *Radula cochabambaensis*, *R. fendleri* var. *paroica*, *R. mexicana* and *R. renneri* are the only monoicous taxa. The monoicous taxa are usually paroicous with exception of *R. mexicana* which is autoicous. *Radula pallens* proved to be heteroicous (=polyoicous), being usually dioicous but occasionally monoicous. This is the second heteroicous species known in Radulaceae, beside *R. obconica* Sullivant from North America (Castle 1925, 1967, Schuster 1980a). According to Schuster (1980a), the gynoecia of *R. obconica* may be preceded by male bracts or not, the plants being paroicous or

dioicous. The occurrence of dioicous and monoicous populations of a single species is not rare in many other families of bryophytes; in Lejeuneaceae, for example, it is fairly common (Gradstein 1994).

The sex distribution of *Radula bischlerae*, R. sp. nov. 3, *R. santacruziana* and *R. smithii* remains unclear.

Androecia

Androecia in Radulaceae are terminal or intercalary on short or long branches, sometimes preceding the gynoecia in paroicous plants. The androecia consist usually of 1–10(–12) pairs of bracts, except in *Radula* sp. nov. 1 which can reach up to 30 pairs of bracts, and in *R. javanica* to 20 pairs.

The bracts can be distant to imbricate and are without taxonomically significance. There are one or two antheridia in the axils of a male bract. The lobules are always hypostatic, distant to subimbricate, reaching 3/4 to 1/2 of the lobe length, varying from oblong to ovate with an obtuse to subacute apex, inflated, and with a strongly convex keel.

Gynoecia

Gynoecia of Radulaceae species occur terminal on main stem or on short to long branches, usually with one or two innovations. Innovations in *Radula ligula* and *R. fendleri* are sometimes rudimentary and gynoecia without innovations are observed in *Cladoradula boryana, Radula portoricensis* and *R. renneri*. The latter three species also stand out in having 2–3 pairs of bract-like leaves below the inner female bracts. The bracts vary from ovate to oblong-ovate with plane to recurved, and entire to (rarely) crenulate margins. Most of the species have symmetric bracts, but a few species have strongly asymmetrical ones (one bract larger than the other), such as *Radula venezuelensis*. The lobules of female bracts reach 1/3 to 1/2 of the lobe length and can be ovate to oblong.

Perianths in Radulaceae are of the *Scapania-Radula* type (Schuster 1966, p. 555), being formed by two coalesced, dorsiventrally compressed leaves, which are sharply folded. They are usually erect, rarely falcate, short to long, reaching to maximally 6 mm in *Radula eggersii* and *R. venezuelensis*. The perianth shape can be subcylindrical (perianth width almost uniform from base to apex), trumpet-shaped or campanulate. Trumpet-shaped perianths are usually very long and narrow and gradually become wider towards the apex, while campanulate perianths

are relatively short and wide, enlarging drastically from the base to the apex. The campanulate shape is sometimes age-related, being common in small, young perianths. *Radula pallens* may produce perianths of all three different forms.

The perianth mouth is usually entire to crenulate; the latter condition is sometimes due to the production of gemmae on the perianth mouth (*Radula quadrata*). The mouth can be plane to strongly undulate; the latter condition is characteristic of campanulate perianths. In *R. inflexa*, *R. portoricensis* and *R. voluta* perianth mouth is ventrally convolute, in *R. xalapensis* it is convolute towards the inner side of the perianth mouth, and in *R. stenocalyx* towards the outer side.

In transverse section, the perianth is usually unistratose throughout, but sometimes unistratose in the upper half (or near the perianth mouth), and 2–5-stratose in the lower half. Some species have slightly small longitudinal striae at the base or from the upper base to the middle. The calyptra wall can be unistratose throughout or only in the upper half, and 2–3-layered at the base. Most of the species have the perianth–calyptra fusion elevated above female bracts. The area between perianth-calyptra fusion and the female bract insertion elaborated into a low, fleshy, 2–6-layered tube within which the sporophyte foot is embedded. In *Radula flaccida, R. grevilleana, R. ligula, R. pallens* and *R. stenocalyx,* the multilayered tube extends upwards enveloping the sporophyte foot and part of the setae. The latter condition is referred to as a stem perigynium (Schuster 1980b).

SPOROPHYTE

The sporophyte is made up of foot, seta and capsule. Unlike the mosses, seta and capsule in leafy liverworts are fully enveloped within the calyptra, until cell division and the maturation of the spores are completed (Gradstein *et al.* 2001). The emergence of the sporophyte from the calyptra (and the perianth) is achieved by the elongation of the seta cells.

In Radulaceae, the sporophyte foot is beet-shaped and the seta is massive, being made up of many cell rows (Schuster 1984, Renner & Braggins 2005). Seta length after elongation varied from 1.5 to 2.5 mm in Neotropical species. The capsule shape ranges from ovoid in *Cladoradula boryana* to ellipsoid in *Radula* species. The capsule dehiscence lines are longitudinal, splitting the capsula in four valves. The valves in the Neotropical species are 2-layered and the cells of the valves are subquadrate, subrectangular, long-rectangular, or polymorphous (observed in the middle), and are furnished with wall thickenings. The

description of the thickenings of the valve cells in this work follows Renner and Braggins (2005) with slight modifications (seeTable 2 and 3, and Figures 3 and 4).

The elaters are yellowish to red-brown, 100 to 500 µm long and composed of two spiral bands with rounded ends. In most species the surface of the spiral bands is roughened, rarely smooth or finely granulate. Mature spores are isomorphic monads, apolar in species of the genus *Radula* and cryptopolar in *Cladoradula boryana*. They are small to medium-sized (16.66–38.88 µm), inaperturate, with a circular to slightly elongated outline. The ornamentation of the surface includes two patterns: ornamentation pattern I with rounded elements, here called Granulate-type, and ornamentation pattern II with elongated elements here called Echinate-type (for discussion and figures, see chapter 3).

VEGETATIVE REPRODUCTION

Almost 60% of Neotropical Radulaceae species exhibit asexual reproduction by specialized devices (= propagules). Some species can even display more than one type of propagule. The most common are caducous leaf lobes, being produced occasionally, as in *Radula angulata,* or profusely resulting in denuded branches, as in *Radula bischlerae*, *R. brasilica*, *R. fulvifolia*, *R. pseudostachya,* and *R. wrightii*. Caducous leaf lobes usually produce young plantlets (regenerants) on the margins; sometimes the regenerants appear while the leaf lobes are still attached to the stem. Regenerants are young plants that develop on the surface of a mature plant from an adult cell (Fulford 1956). Regenerants are sometimes confused with leaf-born gemmae, but differently from gemmae, regenerants are not detached from the leaves (Fulford 1956).

Vegetative reproduction may also occur by fragmentation by leaf lobes or stems. Fragmentation by leaf lobes is rare in Neotropical Radulaceae and is only seen in *R. voluta*. Fragmentation of stems, however, is more common and usually associated with the development of *Lejeunea*-type branches. In *Radula bahiensis, R. flaccida*, *R. pallens,* and *R. subinflata*, the *Lejeunea*-type branches may be caducous as well.

Vegetative reproduction by gemmae is important in Radulaceae. The gemmae are multicellular and discoid, and are usually produced on the margins of leaf lobes, varying in size and shape. The largest gemmae are found in *Radula flaccida,* They are exclusively produced on the dorsal leaf margin and are 350–450 µm in diameter, with a deeply cordate-auriculate base and with opposite auricles touching to overlapping each other (Williston 1912, Schuster 1980a). *Radula leiboldii, R. quadrata, R. renneri, R. santacruziana,* and *R. stenocalyx*

TABLE 2. Thickening types of outer cell walls of capsule valves.

TYPE	OUTER CELL WALL	SPECIES
Type-1	Cells with nodular thickenings, on every cell angle, sometimes on intermediate cell walls (Figure 3A).	*C. boryana*
Type-2	Cells with irregular linear thickenings, running the entire length of the wall, on every second longitudinal wall (Figure 3B).	*R. eggersii*, *R. flaccida*
Type-3	Cells with simple nodular thickenings, on every longitudinal wall, sometimes at the cell angles (Figure 3C).	*R. angulata*, *R. episcia*, *R. involvens*, *R. mexicana*, *R. pallens*, *R. quadrata*, *R. subinflata*
Type-4	Cells with simple nodular thickenings, on longitudinal wall of every second wall, sometimes at the cell angles (Figure 3D).	*R. javanica*, *R. sinuata*, *R. tenera*, *R. voluta*, *R. xalapensis*
Type-5	Cells with confluent adnate nodular thickenings, on every longitudinal wall (Figure 3E).	*R. grevilleana*, *R. leiboldii*
Type-6	Cells with confluent adnate nodular thickenings, on longitudinal wall of every second wall (Figure 3F).	*R. wrightii*

TABLE 3. Thickening types of inner cell walls of capsule valves.

TYPE	INNER CELL WALL	SPECIES
Type-1	Cells with nodular thickenings, irregularly distributed on the cell walls, 1–2 faint semi-annular bands per cell (Figure 4A).	*C. boryana*
Type-2	Cells with nodular thickening on the walls, semi-annular bands present, associated with the thickenings (Figure 4B).	*R. leiboldii*

Type-3	Cells without thickenings (Figure 4C).	*R. eggersii*, *R. flaccida*, *R. involvens*, *R. subinflata*, *R. tenera*, *R. voluta*, *R. xalapensis*
Type-4	Cells with confluent thickening on the walls (Figure 4D).	*R. angulata*, *R. episcia*, *R. grevilleana*, *R. javanica*, *R. mexicana*, *R. pallens*, *R. quadrata*, *R. sinuata*,

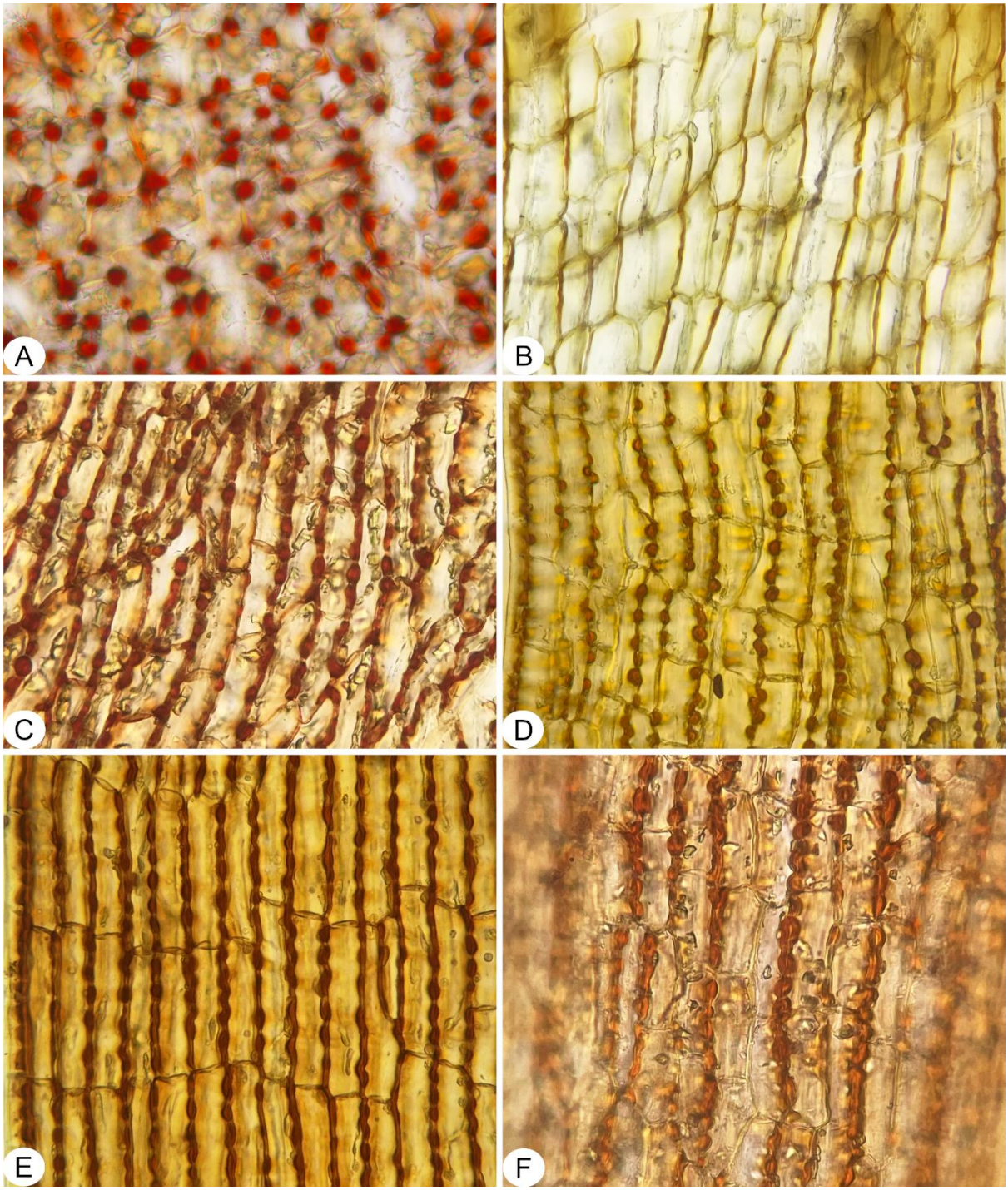

Figure 3. Anatomy of the outer layer cells of the capsule wall. A. Type-1. B. Type-2. C. Type-3. D. Type-4. E. Type-5. F. Type-6.

produce relatively small discoid gemmae along the dorsal leaf margin, and in *R. leiboldii* and *R. quadrata* also on the margins of the female bracts and perianth mouth. They are usually profusely produced except in *R. renneri* where gemmae are scarce.

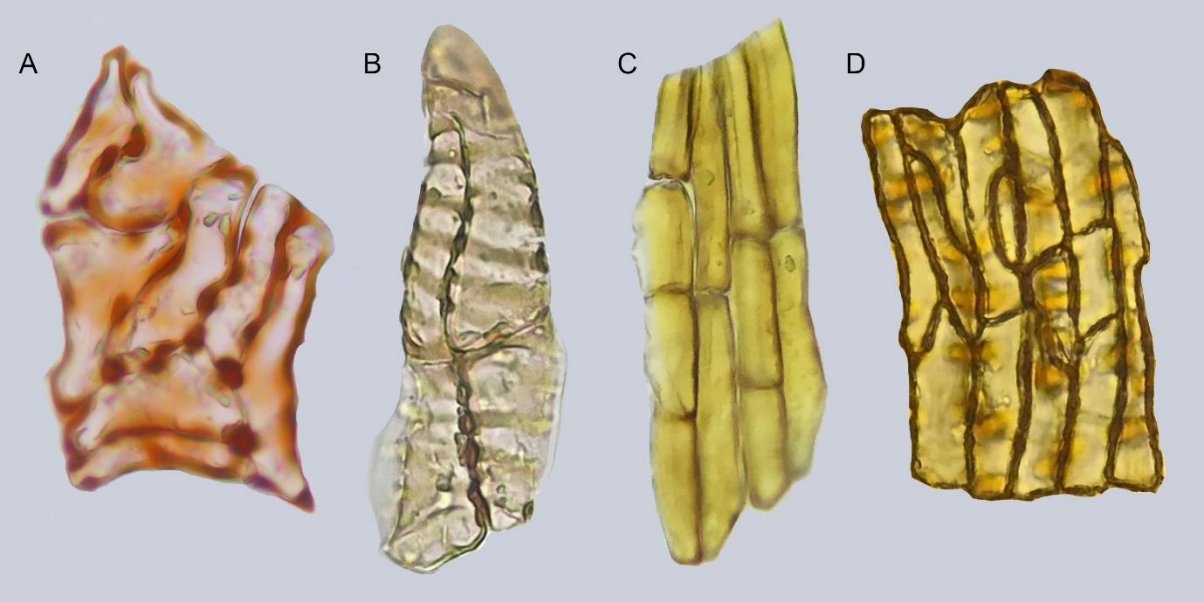

Figure 4. Anatomy of the inner layer cells of the capsule wall. A. Type-1. B. Type-2. C. Type-3. D-E. Type-4.

GROWTH HABIT

Radulaceae species of tropical America grow creeping or pendent, rarely ascending. The creeping growth habit is represented by plants which are partially or fully attached (=prostrate) to the substrate, forming flat, spacious to dense mats which increase in size depending on the degree of ramification. Epiphyllous species usually grow prostrate to the substrate (Figure 6 E-F). Plants with a pendent growth are generally long, loosely attached to the substrate and hanging downward (Figure 5 and 6).

Cladoradula boryana, in addition to the creeping and pendent habit, may also have an ascending habit when growing on the base of trees, roots, or on rock. Plants with the latter growth habit have the stem and branches pointing or arising obliquely upward, away from the substrate (see Renner *et al.* 2022, fig. 2).

PHYTOGEOGRAPHY

WORLDWIDE DISTRIBUTION

Radulaceae is a subcosmopolitan family, occurring in all floristic zones of the world, except for Antarctica (Jones 1977, Yamada 1979, Schuster 1984, Gradstein *et al.* 2001, Oliveira-da-Silva *et al.* 2021). Species that occur in tropical America were divided into six types of worldwide distribution (Table 4).

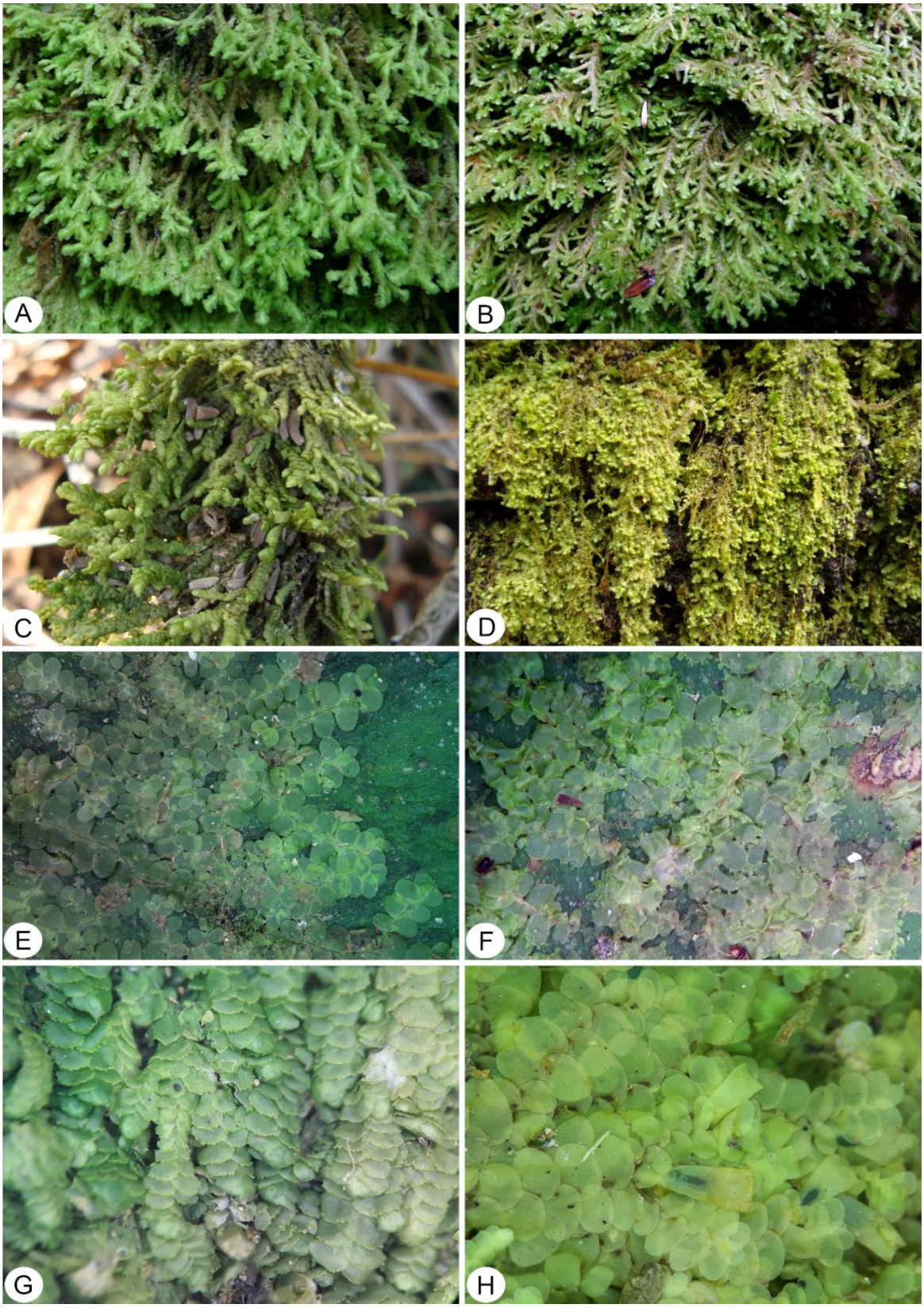

Figure 5. Radulaceae species on different substrates in Brazil. A. Female plants of *Radula pallens* on a tree (Teresópolis, Rio de Janeiro State). B. Male plants of *Radula pallens* on a tree (Teresópolis, Rio de Janeiro State). C. *Radula recubans* on tree (Cambará do Sul, Rio Grande do Sul State). D. *Radula fendleri* var. *fendleri* on ravine (Campos do Jordão, São Paulo State). E. *Radula flaccida* on leaves of vascular plants (Sooretama Biological Reserve, Espirito Santo State). F. *Radula stenocalyx* on leaves of vascular plants (Teresópolis, Rio de Janeiro State). G. *Radula quadrata* growing on tree (near Rio Turvo, São Paulo State). H. Female plants of *Radula sinuata* on tree (Urubici, Santa Catarina State). Photographs by Denilson F. Peralta.

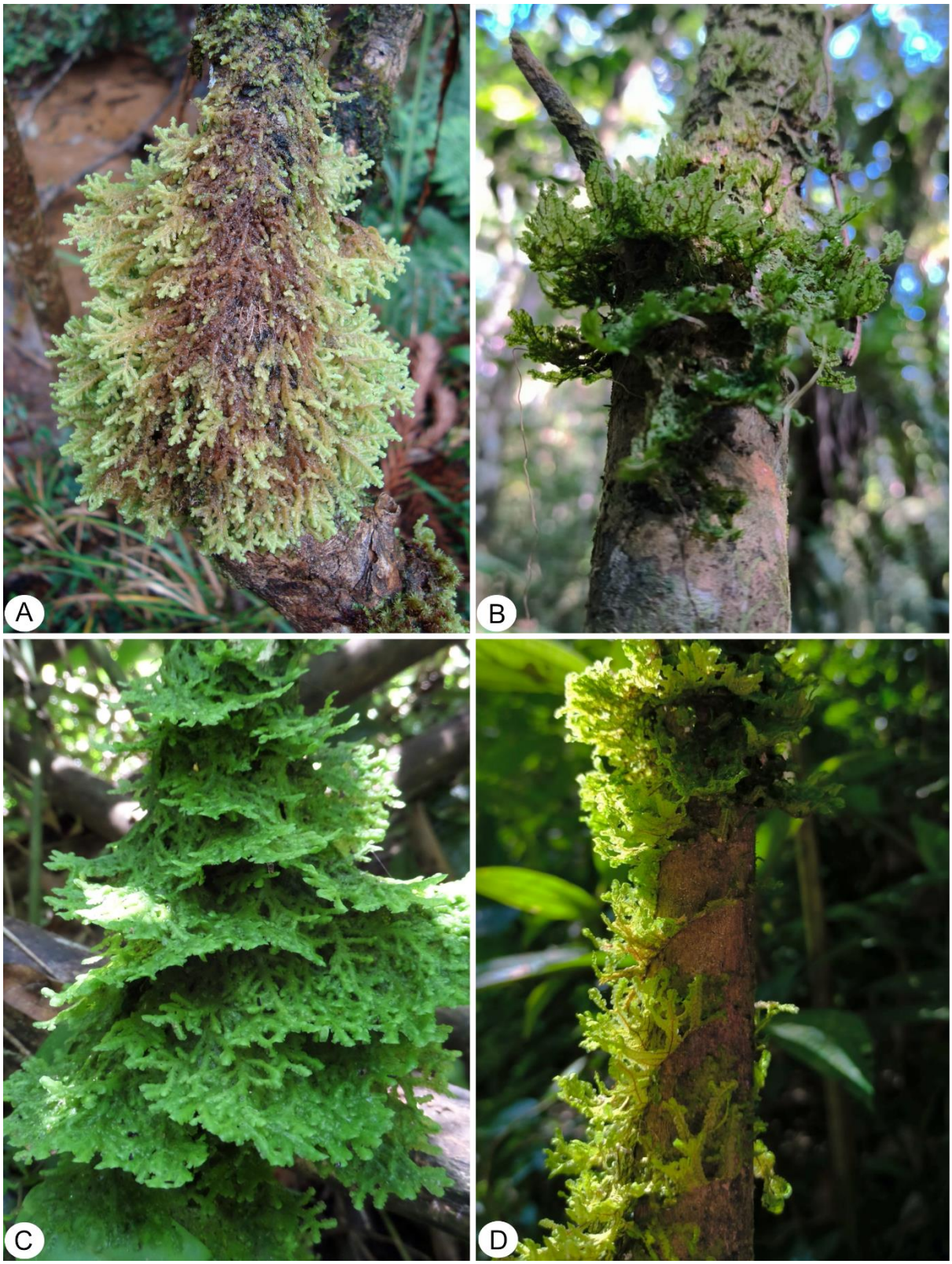

Figure 6. Radulaceae species of Brazil with a pendent habit. A. *Radula voluta* (Campos do Jordão, São Paulo State). B. *Radula pallens* (Parque das Neblinas, São Paulo State). C. *Radula javanica* (Serra do Mar, Paraná State). D. *Radula pallens* (Parque das Neblinas). Photographs A and C by Denilson F. Peralta, B and D by Matheus T. A. Gonçalves.

The majority of the species (70%) occur esclusively in the Neotropics, followed by eight species in tropical and subtropical America, four Afro-American species, two Pantropical and two in America continent and tropical Africa, and *Radula nudicaulis* in tropical America and Macaronesia.

Radula australis Austin, *R. complanata* (L.) Dumort., *R. obconica* Sull., and *R. sullivantii* Austin were registered in Florida (USA) (Castle 1925, Schuster 1980a), still in the neotropical region. However, we decided that it would be better not to include these species, as their distribution is more linked to the Horlactic than tropical America.

NEOTROPICAL DISTRIBUTION

We followed the subdivision of tropical America adopted by Gradstein *et al.* (2001), with modifications based on a few more recent studies (*e.g.* Gradstein & Costa 2003, Désamoré *et al*. 2010, Ilkiu-Borges 2016). The subdivision is presented in Table 5.

ALTITUDINAL DISTRIBUTION

M Most of Radulaceae species have a wide altitudinal range in tropical America (Figure 7). Few species have a limited elevational occurrence and the altitudinal ranges of *Radula inflexa*, *R. macrostachya*, and *R. taylorii* remain unclear. We recognize five types of tropical forest belts according to Frahm & Gradstein (1991) and Gradstein *et al.* (2001): lowland forest, submontane forest, lower montane forest, upper montane forest and subalpine forest (Table 6).

Lowland forests are found from sea level to the foot of the mountains up to 500 m. This tropical environment consists of different types of forests such those found in Amazonia. The diversity of Radulaceae in this altitudinal belt is made up of 21 species, with *Radula pseudostachya* being restricted to lowlands. *Radula flaccida*, *R. javanica* and *R. yanoella* are very common in lowland forests, but may occur rarely in higher forest belts.

Submontane (=premontane) forests are confined to the lower slopes of the mountains, usually from 500 to 1400 m. Its is the most speciose elevational belt for Radulaceae, with 38 recorded species and four varieties, and eight taxa being restricted to this belt: *Radula cochabambaensis*, *R. gradsteinii*, *R. longiloba*, *R. pallens* var. *marginata*, *R. renneri*, *R. santacruziana*, *R. tenuis*, and *R. yamadae*. The appearance of montane species and the influence of mist and lower temperatures are the main reasons why the bryophyte flora of submontane forest differs from lowland forest.

TABLE 4. Worldwide distribution of Neotropical Radulaceae.

DISTRIBUTION	COMMENTS	SPECIES
Tropical America (38 spp. + 4 varieties)	These species occur only in the Neotropics. Most of these species are known only from the type locality, or have few occurrences, or even have a more restricted distribution to a certain location or enviroment.	*R. angulata*, *R. bahiensis*, *R. bischlerae*, *R. brasilica*, *R. cochabambaensis*, *R. cubensis*, *R. dominicensis*, *R. eggersii*, *R. elliottii*, *R. fendleri* var. *fendleri*, *R. fendleri* var. *paroica*, *R. gradsteinii*, *R. sp. nov. 1*, *R. inflexa*, *R. involvens*, *R. ligula*, *R. sp. nov. 2*, *R. longiloba*, *R. macrostachya*, *R. sp. nov. 3*, *R. microlobula*, *R. pallens* var. *marginata*, *R. portoricensis*, *R. pseudostachya*, *R. pusilla*, *R. recubans*, *R. renneri*, *R. santacruziana*, *R. smithii*, *R. sonsonensis*, *R. taylorii*, *R. tenera*, *R. tenuis*, *R. underwoodii*, *R. venezuelensis*, *R. voluta var. microphylla*, *R. wrightii*, *R. yamadae*, *R. yanoella*
Tropical and subtropical America (8 spp.)	Besides the Neotropical region, these species may occur in southern South America (Chile and Argentina).	*R. episcia*, *R. grevilleana*, *R. leiboldii*, *R. pallens*, *R. saccatiloba*, *R. sinuata*, *R. subinflata*, *Radula xalapensis*
Pantropical (2 spp.)	Species which occur in all tropic of the globe. *Radula javanica* also occur in southern South America.	*R. javanica*, *R. stenocalyx*
Tropical America + Macaronesia (1 sp.)	Besides the Neotropical region, the species also occurs at the Azores and Madeira Islands.	*R. nudicaulis*
Afro-American (4 spp.)	Species with disjunct distribution in tropical America and Africa	*C. boryana*, *Radula flaccida*, *R. fulvifolia*, *R. mexicana*

America + tropical Africa (2 spp.)	Species that occur from the eastern North America to southern South America, and also in tropical Africa. *Radula voluta* also occurs along the Atlantic coast of western Europe.	*Radula quadrata* and *R. voluta*

TABLE 5. Regional distribution of Neotropical Radulaceae. Species in bold are endemic to the phytogeographic region.

PHYTOGEOGRAPHIC REGION	COMMENTS	SPECIES
Mexico (12 spp.)	This region includes Mexico only, which is located in the limits of Neotropical forests, on the border with the Northern Hemisphere.	*C. boryana, R. angulata, R. flaccida, R. javanica, R. leiboldii, R. macrostachya, R. mexicana, R. pallens, R. portoricensis, R. quadrata, R. subinflata, R. voluta*
Central America (30 spp.)	This region includes Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica (including Cocos Is.), and Panama. It is the second richest phytogeographic region for liverworts and the third for Radulaceae. Of the species that occur in Central America, more than 70% can be found in Costa Rica, including nine endemic species.	*C. boryana, R. angulata, R. cochabambaensis, R. elliottii, R. episcia, R. fendleri, R. fulvifolia, R. flaccida, R. grevilleana, R. involvens, R. javanica, R. leiboldii, R. mexicana, R. microlobula, R. nudicaulis, R. pallens, R. portoricensis, R. pusilla, R. quadrata, R. recubans, R. saccatiloba, R. sinuata, R. stenocalyx, R. subinflata, R. tenera, R. venezuelensis, R. voluta, R. wrightii, R. xalapensis, R. yanoella*
West Indies (28 spp.)	This region is divided into two subregions: the Greater Antilles with the Bahamas (comprising Cuba, Jamaica,	*C. boryana, R. angulata, R. cubensis, R. dominicensis, R. elliottii, R. episcia, R. fendleri, R. flaccida, R. grevilleana,* ***R.***

	the Dominican Republic, Puerto Rico, and the Virgin Islands) and the Lesser Antilles [comprise the Leeward Islands (30+ Is.), Windward Islands (7 Is.), Trinidad and Tobago, and the southern Dutch Antilles (3 Is.)].	***inflexa***, *R. involvens*, *R. javanica*, *R. leiboldii*, *R. longiloba*, *R. macrostachya*, *R. microlobula*, *R. pallens*, *R. portoricensis*, *R. pusilla*, *R. quadrata*, *R. saccatiloba*, *R. stenocalyx*, *R. taylorii*, ***R. tenuis***, ***R. underwoodii***, *R. venezuelensis*, *R. voluta*, *R. wrightii*, *R. yanoella*
Chocó (11 spp.)	This is the wettest region of the Neotropics, which includes lowlands areas up to 500 m. The Chocó is located along the Pacific coast of Colombia and Ecuador. Most of the Radulaceae records in Chocó were based on the study by Gradstein (2021).	*R. cubensis*, *R. dominicensis*, *R. episcia*, *R. fendleri*, *R. involvens*, *R. javanica*, *R. grevilleana*, *R. mexicana*, *R. nudicaulis*, *R. stenocalyx*, *R. subinflata*
Northern Andes (34 spp. + 4 varieties)	This region includes the Andean mountains of eastern Venezuela, Colombia, Ecuador (including the Galápagos Islands), and northern Peru (north of 8°S). Because of the climate and altitudinal range, the northern Andes have a highly diverse bryophyte flora, with many endemic taxa (Gradstein *et al.* 2001). This is evident in this study.	*C. boryana*, *R. angulata*, ***R. bischlerae***, *R. cubensis*, *R. dominicensis*, ***R. eggersii***, *R. episcia*, *R. fendleri*, *R. flaccida*, *R. fulvifolia*, *R. grevilleana*, ***R. sp. nov. 1***, *R. involvens*, *R. javanica*, *R. leiboldii*, *R. mexicana*, *R. nudicaulis*, *R. pallens* var. *pallens*, ***R. pallens* var. *marginata***, *R. portoricensis*, *R. pusilla*, *R. quadrata*, *R. recubans*, *R. saccatiloba*, ***R. santacruziana***, *R. sinuata*, ***R. smithii***, ***R. sonsonensis***, *R. stenocalyx*, *R. subinflata*, *R. tenera*, *R. venezuelensis*, *R. voluta* var. *voluta*, ***R. voluta* var. *microphylla***, *R. xalapensis*, *R. yanoella*

Central Andes (24 spp.)	This region includes Andean mountains of southern Peru (south of 8°S), Bolivia, and northern Chile/Argentina.	*C. boryana*, *R. cochabambaensis*, *R. cubensis*, *R. episcia*, *R. flaccida*, *R. fulvifolia*, *R. grevilleana*, *R. involvens*, *R. javanica*, *R. leiboldii*, ***R. sp. nov. 2***, ***R. sp. nov. 3***, *R. mexicana*, *R. nudicaulis*, *R. pallens*, *R. quadrata*, *R. sinuata*, *R. sonsonensis*, *R. stenocalyx*, *R. subinflata*, *R. voluta*, *R. wrightii*, *R. xalapensis*, *R. yanoella*
Amazonia (16 spp.)	Vast lowlands areas (below 500 m) drained by the Amazon and Orinoco River systems, including particularly upland forests, daily or periodically flooded forests, white-sand vegetation and savanna. Amazonia covers part of Brazil, Venezuela, Colombia, Ecuador, Peru, Bolivia, Guyana, Surimame, and French Guiana.	*C. boryana*, *R. cubensis*, *R. flaccida*, *R. fulvifolia*, *R. grevilleana*, *R. javanica*, *R. leiboldii*, *R. nudicaulis*, *R. pallens*, ***R. pseudostachya***, *R. quadrata*, *R. recubans*, *R. sinuata*, *R. stenocalyx*, *R. taylorii*, *R. yanoella*
Guyana Highlands (6 spp.)	This region is made up of large table mountains or tepuis (ca. 1000-3000 m), which isolated and almost inaccessible. They are underlain by Proterozoic sandstones of the Roraima Group that extensively cover the Precambian Guiana Shield, across southern Venezuela, northern Brazil (Amazonas and Roraima) and northwestern Guyana.	*R. flaccida*, ***R. gradsteinii***, *R. involvens*, *R. javanica*, *R. pallens*, *R. pusilla*
Brazilian Planalto (10 spp.)	This region includes especially two large Brazilian domains: Cerrado and Caatinga (between Amazonia and	*R. angulata*, *R. bahiensis*, *R. fendleri*, *R. flaccida*, *R. javanica*, *R. leiboldii*, *R. pallens*, *R. quadrata*, *R. quadrata*, *R. tenera*

	the Atlantic Coastal Region). The Brazilian planalto is relatively low in elevation and because of the dry climate, the region is relatively poor in liverworts. The species of *Radula* observed in this region were largely linked to the transition zone between Amazonia-Cerrado, Altantic Forest-Cerrado or Altantic Forest-Caatinga.	
Atlantic Coastal Region of Brazil (31 spp. + 2 varieties)	The Atlantic forest extends from Rio Grande do Norte (northeastern Brazil) to Rio Grande do Sul (southern Brazil), occurring in coastal and from the interior over mountains and plateaus. This region has several mountain ranges with cloud forest, *Araucária* forest, and high-elevation grasslands (*Campos de altitude*). The Brazilian Atlantic forest harbors a rich bryophyte flora, being the third in importance of the Neotropics.	*C. boryana*, *R. angulata*, ***R. bahiensis***, ***R. brasilica***, *R. cubensis*, *R. elliottii*, *R. episcia*, *R. fendleri* var. *fendleri*, ***R. fendleri* var. *paroica***, *R. flaccida*, *R. fulvifolia*, *R. grevilleana*, *R. javanica*, *R. leiboldii*, ***R. ligula***, *R. longiloba*, *R. mexicana*, *R. nudicaulis*, *R. pallens*, *R. quadrata*, *R. recubans*, ***R. renneri***, *R. saccatiloba*, *R. sinuata*, *R. stenocalyx*, *R. subinflata*, *R. tenera*, R. *voluta*, *R. wrightii*, *R. xalapensis*, ***R. yamadae***, *R. yanoella*

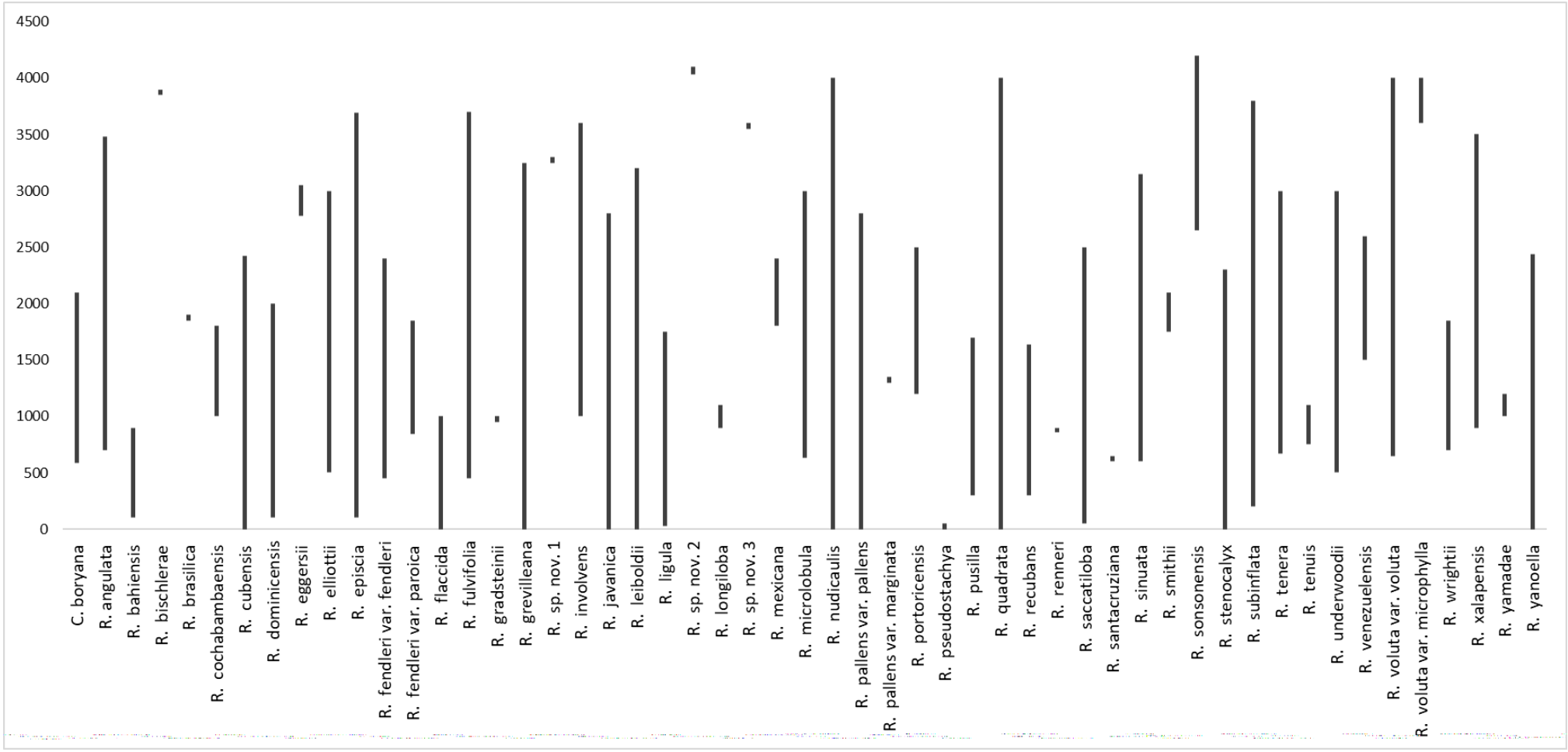

Figure 7. Altitudinal distribution of species of Radulaceae in tropical America.

Lower montane forest occurs at 1400 to 2000 m and is recognized by having much more luxuriant bryophyte species than lowland and submontane forests. However, the diversity of Radulaceae in this forest belt is lower than in submontane forest, with 31 species and two varieties, and no exclusive species.

The upper montane forest occurs from 2000 to near the forest line at 3000-4000 m. This type of forest is mainly found in the high Andes and high mountains of Central America. The diversity of Radulaceae in this altitudinal belt is 29 species, without restricted species.

Tropical subalpine forests are dwarf forests near the timberline and occur above 3000 m, while alpine formations include the páramo of the northern Andes (from Venezuela to northern Peru). Subalpine forest has the lowest number of species (17 spp.), some of which are restricted to these forests: *Radula bischlerae, R.* sp. nov. 1, *R.* sp. nov. 2, *R.* sp. nov. 3, and *R. voluta* var. *microphylla*.

TABLE 6. Altitudinal distribution of Neotropical Radulaceae.

TROPICAL FOREST BELTS	ELEVATION (METERS)	N° OF SPECIES	N° OF EXCLUSIVE
Lowland Forest	< 500	21 spp.	1 sp.
Submontane forest	500 – 1400	38 spp. + 4 var.	7 spp. + 1 var.
Lower montane forest	1400 – 2000	31 spp. + 2 var.	0
Upper montane forest	2000– 3000(-4000)	29 spp.	0
Subalpine forest	> 3000	17 spp.	4 spp. + 1 var.

SUBSTRATE

The majority of Neotropical Radulaceae grow as epiphytes on the bark of trees and shrubs (Table 7). Forty-three corticolous species were recorded, of which 12 are exclusive to this substrate. These results were to be expected since Porellales are predominantly composed of epiphytes (*e.g.* Feldberg *et al.* 2014).

Surprisingly, rock is the second-most colonized substrate of Radulaceae. We recorded 31 saxicolous taxa, including *Radula* sp. nov. 2 exclusive to rock, *R. javanica*, *R. ligula*, *R. nudicaulis* and *R. pallens* being common on rock and *R. wrightii* rather frequent. The colonization of this substrate by Radulaceae seems to be linked to high humidity.

Dead trees or rotten logs are further important substrates for Radulaceae. The epixylic members of *Radula* total 21 species, and *R. brasilica* and *R. fendleri* var. *paroica*, both restricted to the Atlantic Coastal Region of Brazil, are exclusive to this substrate. Nevertheless,

a recent study (Lima *et al.* 2023) considered epixylic bryophytes as generalists and colonizers of different substrates.

Soil is the fourth most colonized substrate by Radulaceae, with 15 species. *Radula bischlerae* is the only species exclusive to this substrate, but it is only known from the type specimen.

Few Radulaceae species grow exclusively on leaf surfaces of vascular plants (13 spp.). Epiphyllous species may occur also on other substrates. Based on their habitat preference, a distinction is made between "typical epiphylls" and "facultative epiphylls" (Gradstein 1997). Typical epiphylls occur mostly, or exclusively, on living leaves, rarely on other substrates and include *Radula flaccida*, *R. grevilleana*, *R. stenocalyx* and *R. yanoella*. Characteristic is their flat, appressed growth and pronounced rhizoidal area with a thick rhizoid bundle that functions as an adhesive disc, allowing the plants to firmly adhere to the substrate (Winkler 1967). Facultative epiphylls, in contrast, occur commonly on other substrates as well such as bark, rotten logs, soil or rock. In tropical America, *R. bahiensis, R. episcia, R. javanica*, *R. pallens* var. *pallens*, *R. pusilla*, *R. subinflata* and *R. xalapensis* are facultative epiphylls. *Radula yamadae* is known from only two records, one on leaves and the other on rock.

TABLE 7. Substrate preference of Neotropical Radulaceae based on data retrieved from the specimen labels (many examined specimens lacked substrate information). * Including branches, twigs, pole, lianas and roots; ** Including standing or fallen trees.

SPECIES	SUBSTRATES				
	TREE*	DEAD TREE/ROTTEN LOGS**	LEAVES	ROCK	SOIL
Cladoradula boryana	20	1		9	
Radula angulata	85	19		3	
Radula bahiensis	98	1	2	5	
Radula bischlerae					1
Radula brasilica		1			
Radula cochabambaensis	2				
Radula cubensis	31	10		6	
Radula eggersii	2				
Radula elliottii	3			2	

Radula episcia	15	1	2	14	2
Radula fendleri var. *fendleri*	27				2
Radula fendleri var. *paroica*		1			
Radula flaccida	19	4	209	1	
Radula fulvifolia	10	3		4	3
Radula gradsteinii	2				
Radula grevilleana	1		20	3	3
Radula involvens	6			1	
Radula javanica	284	51	4	24	8
Radula leiboldii	152	9		5	2
Radula ligula	19	6		17	
Radula sp. nov. 2				1	
Radula longiloba	1			1	
Radula sp. nov. 3	2				
Radula mexicana	3	2			
Radula microlobula	1	1		1	
Radula nudicaulis	16	1		17	4
Radula pallens var. pallens	175	26	1	51	1
Radula portoricensis	3				
Radula pseudostachya	10				
Radula pusilla	3		1	1	
Radula quadrata	25	1	1	5	2
Radula recubans	13	1		1	
Radula renneri	1				
Radula saccatiloba	2			1	
Radula santacruziana	1				
Radula sinuata	45	3		3	
Radula smithii	1				1
Radula sonsonensis	2			1	1
Radula stenocalyx			14	1	
Radula subinflata	42	7	1	3	
Radula tenera	17				
Radula tenuis	2				

Radula underwoodii	1			2	1
Radula venezuelensis	3				
Radula voluta var. *voluta*	54	3		9	3
Radula voluta var. *microphylla*	2				
Radula wrightii	6			10	
Radula xalapensis	15		1	1	5
Radula yamadae			1	1	
Radula yanoella			9		
TOTAL SPECIES	43	21	13	31	15
TOTAL SPECIMENS	1222	152	266	204	39

SYSTEMATIC TREATMENT

Radulaceae Müll. Frib., Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz 1: 404. 1909.

Dioicous, rarely monoicous (paroicous or autoicous). *Plants* 0.5–4.5(–5) mm wide on main stem, 1–5(–8–10) cm long, light green to olive-green or yellowish in field, whitish, light green to olive-green, yellowish to brown, rarely reddish-brown in herbarium, regularly 1–2-pinnate to irregularly pinnate, dichotomous in female plants by (sometimes repeatedly) fertile paired innovation, rarely purely dichotomous. *Branches Radula*-type, rarely *Lejeunea*-type, usually on decapitated shoots; microphyllous branches absent, rarely present (*R. eggersii*, *R. steerei*, *R. voluta var. microphylla*). *Thallus* absent, rarely present (*R. yanoella*). *Stems* 50–500 μm in diam., with thin to thick-walled, colorless to brownish epidermal cells surrounding larger, smaller or uniform in size, thin to thick-walled (sometimes by concave trigones), colorless to brownish medullary cells, rarely with a subepidermis (together with the epidermis forming a 2–4-layered, brownish cortex), outer epidermal wall often heavily and evenly thickened, sometimes more so than the inner epidermal wall. *Leaves* incubous, divided into a large dorsal lobe and a smaller ventral lobule. *Leaf lobes* widely to obliquely spreading, distant to imbricate, plane to strongly convex, orbicular to oblong-ovate to falcate-ovate or (rarely) oblong-falcate, 0.3–2.7 mm long, 0.2–2.3 mm wide, dorsal base rounded, rarely straight, rarely auriculate, overlapping or not the stem, dorsal margin rounded, ventral margin straight to rounded, apex rounded to subacute, margins plane to strongly recurved, sometimes incurved or folded ventrally, entire to crenulate; marginal cells subquadrate to subrectangular, rarely rounded, (5–

)7–25(–30) × (5–)7–20 µm, median cells isodiametric to elongate, 15–40 × 8–25 µm, basal cells isodiamentric to elongate, 20–40 × (8–)10–25 µm, leaf cells smooth to mammillose on ventral and dorsal surface, rarely on dorsal surface only, cell walls thin to evenly thickened, sometimes thickened along the margin forming a 3–4 cell rows wide border, trigones lacking to large, sometimes increasing in size towards the margins, intermediate thickening lacking or rarely present, cuticle smooth, rarely verruculose; oil bodies 1(–2) per cell, spherical to ellipsoidal, light yellow to brown, smooth to slightly granular, (5–)8–23 × 5–15 µm. *Lobules* distant to imbricate, variable (subquadrate, subrectangular, oblong-rectangular, oblong, oblong-ovate, suborbicular, subrhombic, narrowly obtriangularly elongate, convolute and lunular, ligulate, or reniform), 0.1–1.6 mm long, 0.1–1.6 mm wide, 1/6–2/3 the lobe length, flat or inflated at rhizoid area and/or along the keel, sometimes inflated throughout or strongly inflated along the keel covering the apex, free margin and apex, insertion short to long, 1–10× or 1/4–1/2 the base length, insertion line straight to curved, sometimes circinate or inverted in a small J-shaped, base plane, rarely recurved, rounded to angulate, sometimes straight to absent, rarely auriculate, overlapping the stem or not, auricle (when present) smaller or as large as the lobule, extending downward up to the keel or far beyond the keel, free margin plane, rarely strongly recurved, straight to rounded, sometimes sinuate, apex plane, rarely strongly recurved or incurved, rounded to acute, sometimes extended, distal margin straight to rounded, sometimes sinuate, keel concave to strongly convex, spreading at 20–70º with the stem, 50–180º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty to numerous, sometimes numerous on a pronounced mammiliform swelling, present on a few or numerous lobules. *Androecia* terminal to intercalary on short or long branches, sometimes preceding the gynoecia (in paroicous plants), with 1–20(–30) pairs of bracts, 0.3–1.7 mm wide; bracts distant to imbricate, ovate, 0.25–1 mm long, 0.1–0.6 mm wide, apex rounded, margin plane to recurved, entire to sinuate, lobules hypostatic, distant to imbricate, ovate to oblong, 3/4–1/2 the lobe length, base straight, rounded to obtuse, free margin straight (recurved in *R. brasilica*), apex obtuse, rarely subacute. *Gynoecia* on short or long branches, 0–2 innovations, innovations sometimes rudimentary; when without innovation, 2–3 pairs of bract-like bellow the bracts; bracts ovate to oblong-ovate, 0.5–1.7 mm long, 0.15–0.9 mm wide, apex rounded, margin plane to recurved, entire, sometimes slightly crenulate, lobule ovate to oblong, 1/3–1/2 of lobe length, apex rounded to obtuse. *Perianth* erect to falcate, subcylindrical to trumpet-shaped (sometimes inflated at middle), rarely campanulate, 0.6–6 mm long, 0.1–0.6 mm wide at base, 0.3–1.6 mm wide at middle, 0.3–1.7 mm wide at apex, mouth entire to sometimes crenulate, plane to strongly undulate, sometimes convolute to the

ventral surface, or inrolling to inside or outside the perianth; perianth wall 1–5-stratose in the lower base, 1–3-stratose from the upper base to the middle or unistratose from the upper base to the apex, sometimes with small longitudinal striae at base or from the upper base to the middle; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–6-layered tube within which the sporophyte foot, sometimes part of seta (perigynium), is embedded. *Calyptra* wall 1–3-layered at the base, 1 cell layer thick above, unfertilized archegonia elevated on the outer surface of the thickened base of the calyptra. *Seta* 1.5–2.5 mm long. *Capsule* ovoid (genus *Cladoradula*) to long-cylindrical (genus *Radula*), 0.8–1 mm in diam., ca. 0.2 mm wide, 4-valved to base, valves 0.7–2.6 mm long, 0.07–0.8 mm wide at middle, with 2 layers of cells, secondary thickenings variable (see Table 2 and 3). *Elaters* yellowish to red-brown, 100–500 µm long, smooth, rough or finely granulate. *Spores* spherical, 16.66–38.88 µm in diam., granulate or spiculate, granules or spine smooth or composed by nanogranules. *Vegetative reproduction* by caducous leaf lobes, sometimes producing completely denuded branches, fragmentation of leaf lobes, fragmentation of main branches, caducous *Lejeunea*-type branches, regenerants, discoid gemmae, 30–450 µm in diam, produced on leaf margin, rarely on the perianth mouth or bracts.

Idnetification Key to the Genera of Radulaceae in tropical America

1. Lobule insertion transverse to oblique. Stem with a brown, 2–3-layered subepidermis between epidermis and medulla. Spores cryptopolar .....*Cladoradula*
1’. Lobule insertion longitudinal. Stem without subepidermis. Spores apolar..... *Radula*

Cladoradula (Spruce) M.A.M.Renner, Gradst., Ilk.-Borg. & F.R.Oliveira-da-Silva. Bryoph. Div. Evol. 45: 105. 2022. *Radula* subg. *Cladoradula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 315. 1885. Type: *Radula gottscheana* Taylor [=*Cladoradula boryana* (F.Weber) M.A.M.Renner, Gradst., Ilk.-Borg. & F.R.Oliveira-da-Silva].

Plants robust, regularly 2-pinnate. *Stem* rigid, possessing 1–3 layered subepidermis, which contributes to a multistratose, heavily-thickened and brown-pigmented stem cortex. Lobule insertion transverse to oblique. Gynoecia without innovation (a single exception is seen

in *C tenax* (Lindb.) Renner *et al.* which produces innovations). Perianth short, rare. Capsule ovoid. Spores cryptopolar.

1. Cladoradula boryana (F.Weber) M.A.M.Renner, Gradst., Ilk.-Borg. & F.R.Oliveira-da-Silva, Bryoph. Div. Evol. 45: 105. 2022. *Jungermannia boryana* F.Weber, Hist. Musc. Hepat. Prodr. 58: 1815. *Radula boryana* (F.Weber) Mont., Ann. Sci. Nat., Bot., sér. 2, 18: 13. 1842. Type: Réunion, *Bory s.n.* (lectotype, S-B25055!, selected by Renner *et al.*, 2022: 108; isolectotypes, BM, S-B25054, W).

Fig. 8-9

Radula gottscheana Taylor, London J. Bot. 5: 374. 1846. Type: Dominican Republic, St. Domingo, 1814, *J. Dickson s.n.* (lectotype, FH-00965761!, c. andr., **designated here**; isolectotypes, S-B43095!, S-B43096!, c. andr., G-00265030!), syn. fide Castle (1936).

Dioicous. *Plants* 2.5–3 mm wide on main stem, to 10 cm long, olive-green to brown in herbarium, regularly 2-pinnate. *Branches Radula*-type. *Stems* 300–400 μm in diam., with a 3–4-layered cortex made up of rows of strongly thick-walled epidermal and subepidermal cells surrounding thin-walled medullary cells, medullary cells larger than epidermal and subepidermal cells, medullary walls colorless to yellowish, epidermal and subepidermal walls brown. *Leaf lobes* widely spreading, contiguous to subimbricate, slightly convex, ovate to suborbicular, 1.1–1.3 mm long, 1.1–1.4 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to subacute, margins plane to irregularly recurved, entire; marginal cells subquadrate, 10–15 × 8–15 μm, median cells isodiametric to elongate, 15–25 × 15–20 μm, basal cells elongate, 20–30 × 15–20 μm, cell walls thin, trigones large, intermediate thickening present on median and basal cells, cuticle smooth; oil bodies 1 per cell, spherical to ellipsoidal, light yellow to brown, slightly granular, 15–23 × 12–15 μm. *Lobules* on main stem, contiguous to subimbricate, oblong-ovate, 0.6–0.9 mm long, 0.4–0.7 mm wide, 1/3–1/2 the lobe length, flat, insertion ca. 1/4 the base length, insertion line circinate, base plane to irregularly undulate, rounded, strongly auriculate, auricle as large as the lobule or slightly smaller, overlapping the stem, extending downward far beyond the keel, free margin rounded, apex widely rounded to obtuse, distal margin almost straight to rounded, keel straight to slightly concave, spreading at 60–70º with the stem, 120–130º with the ventral leaf lobe margin, at its junction with the lobule; lobules on primary branches, distant to contiguous, oblong-ovate to triangular-ovate, 0.4–0.6 mm long, 0.4–0.5 mm wide, 1/3–1/2

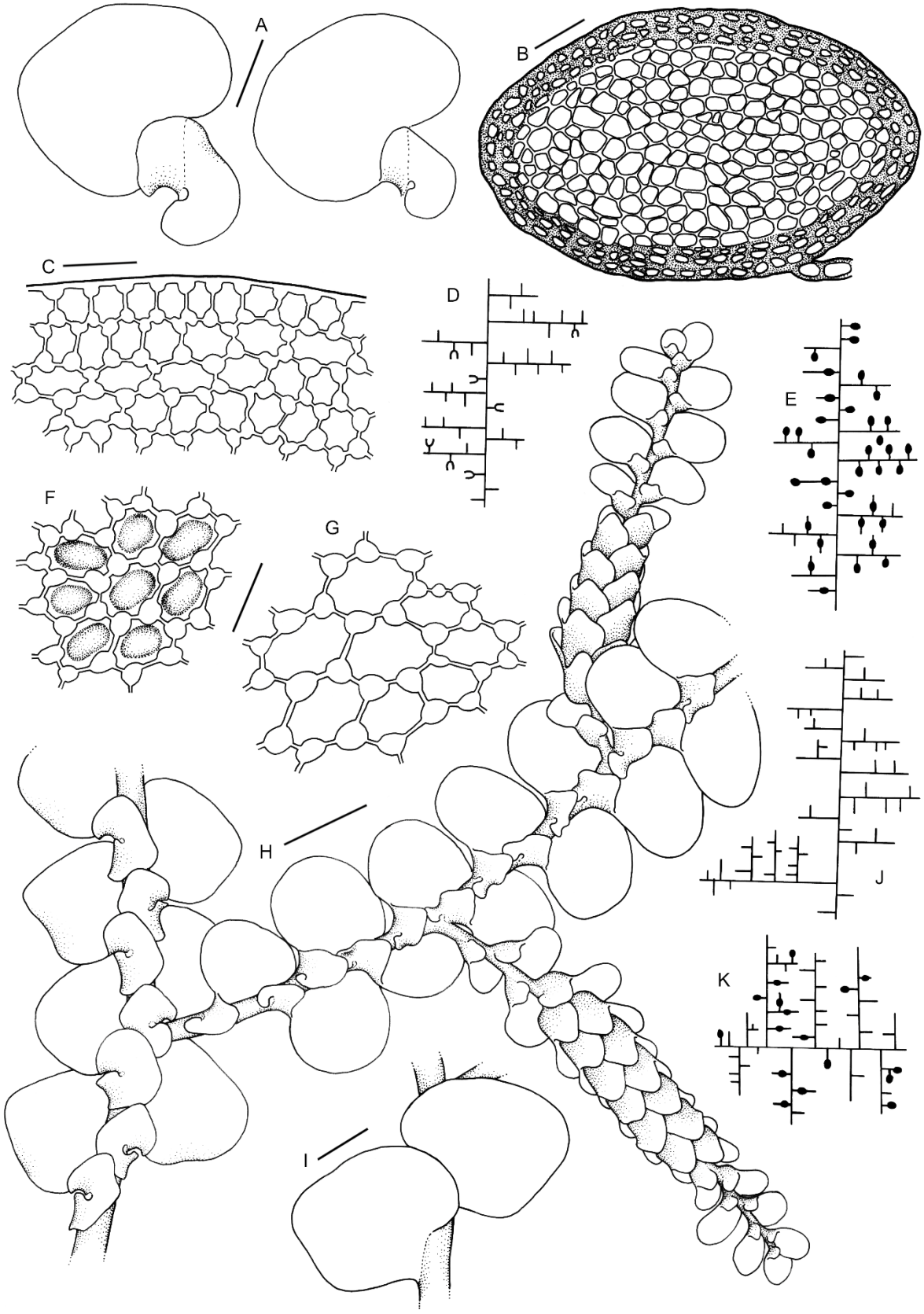

Figure 8. *Cladoradula boryana*. A. Leaves. B. Cross section of main stem. C. Marginal leaf cells. D−E, J−K. Cladographs of fertile and non-fertile plants (black dots = androecia, U = gynoecia without perianth). F. Median leaf cells with oil bodies. G. Basal leaf cells. H. Habit with androecia, showing morphological differentiation of branch and stem lobules. I. Leaves in dorsal view (A, I= 500 µm; B= 50 µm; C, F, G= 25 µm; H= 1000 µm; A, B, D and J from *A. Schäfer-Verwimp 19906*; C, E−I and K from *G. Dauphin 1631*).

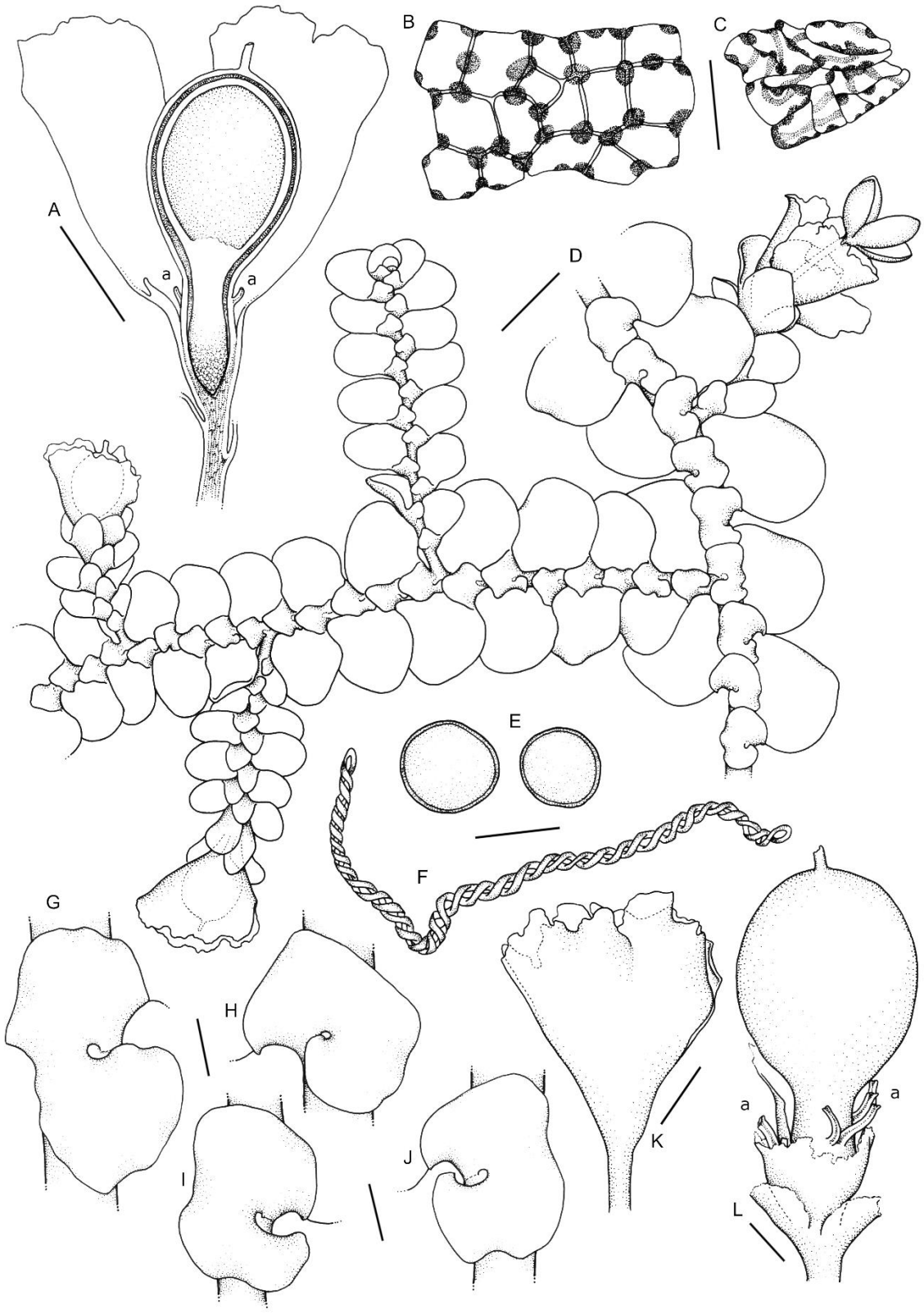

Figure 9. *Cladoradula boryana*. A. Longitudinal section of perianth, calyptra and young sporophyte, showing foot penetrated into the stem and low shoot calyptra with two archegonia (a= archegonia). B. Outer cell layer of capsule wall. C. Inner cell layer of capsule wall. D. Habit with gynoecia and dehisced sporophyte. E. Spores. F. Elater. G–J. Lobules of main stem, showing variation in size and shape of auricle. K. Perianth. L. Sporophyte covered by the calyptra with archegonia on the base; perianth removed (A, K= 500 μm; B, C= 50 μm; D= 1000 μm; E, F= 25 μm; G–J, L= 250 μm; A–F and K–L from *G. Dauphin 1631*; H-I from *D. F. Peralta et al. 3206*; J from *R. Liesner et al. 12930*).

of lobe length, auricle fully overlapping the stem and extending downward to just beyond the keel, free margin almost straight to rounded, apex widely rounded to obtuse, distal margin almost straight, keel straight to slightly concave, spreading at 40–50º with the stem, 120–140º with the ventral leaf lobe margin, at its junction with the lobule; lobules on secondary branches distant, subquadrate, 0.2–0.3 mm long, 0.1–0.2 mm wide, 1/4–1/3 of lobe length, slightly inflated, insertion line slightly curved, base plane, not auriculate, covering 2/3 to overlapping the stem, margins almost straight, apex obtuse, keel straight, spreading at 50–70º with the stem, 140–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* terminal to intercalary on long branches, with 2–8 pairs of bracts, 1.1–1.4 mm wide; bracts distant to contiguous, ovate, 0.7–1 mm long, 0.25–0.35 mm wide, apex rounded, margin plane, entire, lobules imbricate, oblong, ca. 3/4 the lobe length, base rounded to obtuse, free margin straight, apex obtuse. *Gynoecia* on very short branches, with 1 pair of bracts, 2–3 pairs of bract-like bellow the bracts, innovations absent; bracts oblong-ovate, 0.9–1.1 mm long, 0.5–0.7 mm wide, apex rounded to acute, margin plane to recurved, entire, lobules oblong-ovate, ca. 1/2 of lobe length, apex obtuse. *Perianth* erect, campanulate, 1.4–1.7 mm long, 0.3–0.5 mm wide at base, 0.8–1.1 mm wide at middle, 1–1.6 mm wide at apex, mouth irregularly entire, undulate; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to the apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 4–6-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 2-layered at the base, 1 cell layer thick above. *Seta* ca. 1.5 mm long. *Capsule* 0.8–1 mm in diam., valves ca. 0.8 mm long, ca. 0.2 mm wide at middle, with 2 layers of cells, outer layer cells subquadrate to polygonal, nodular thickenings reddish-brown, at every cell angle, sometimes on intermediate cell walls, inner layer cells polymorphous, nodular thickenings reddish-brown, irregularly distributed on cell walls, 1–2 faint semi-annular bands per cell. *Elaters* 150–300 µm long, smooth. *Spores* spherical, 27.77–33.33 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* not observed.

Distribution and habitat. Widespread in tropical Africa and tropical America. In addition to the specimens examined in this study, *Cladoradula boryana* has also been recorded in Ecuador, Peru and Bolivia (Yamada 2000, Graham *et al.* 2016, Gradstein 2021; also included in the distribution map). This species grows creeping in dense or sparse clumps, sometimes pendernt, rarely ascending, on tree trunks (including roots and lianas) and moist rock, rarely on fallen trees. Most of the rupicolous specimens were collected in the Atlantic Coastal Region

of Brazil. *Cladoradula boryana* can be found in sunny or shaded environments, in undisturbed or disturbed submontane to upper montane tropical forests, at 590–2100 m elevation.

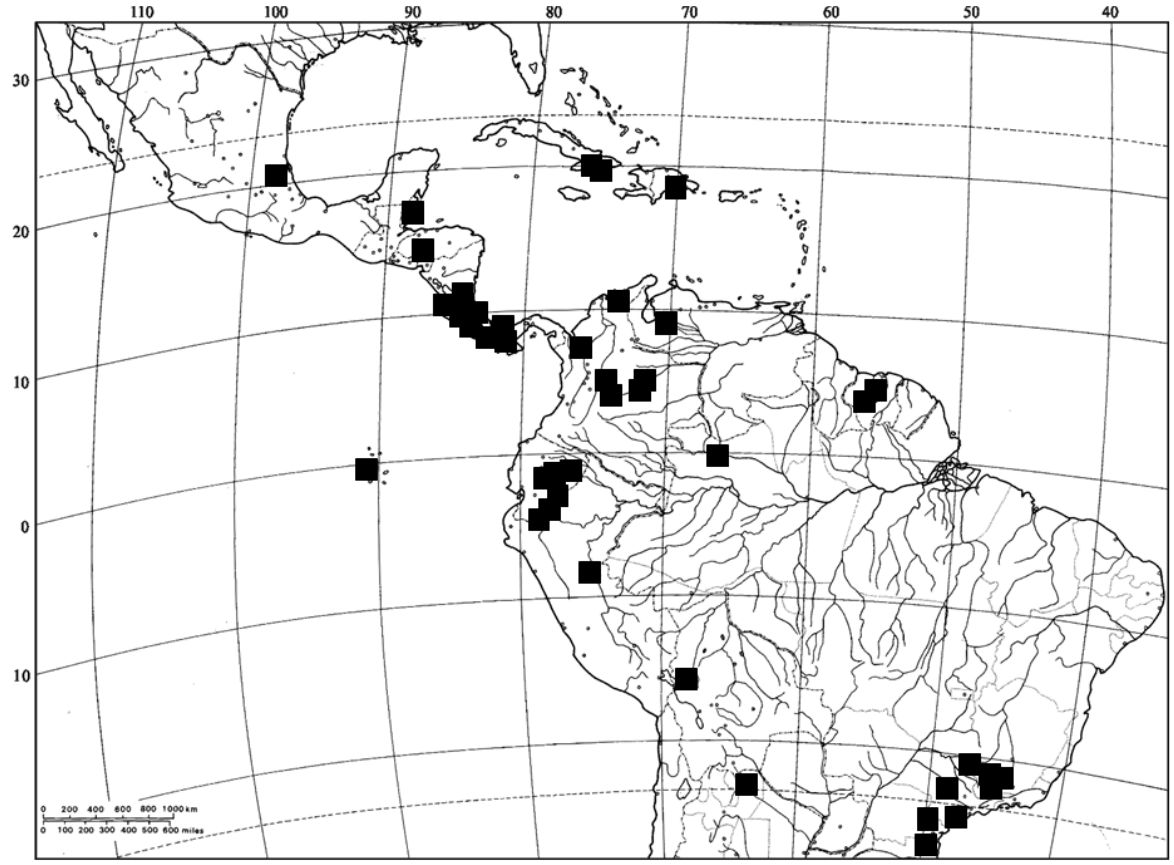

Figure 10. Distribution of *Cladoradula boryana*.

Additional specimens examined. MEXICO. VENADITO: Staat Coahuila, *Stahl s.n.* (JE).

BELIZE. TOLEDO: Columbia River Forest Reserve, on buttress root, 16°22’59”N, 89°07’18”W, 705 m, 12 February 1997, *Allen 18598* (MO).

HONDURAS. COMAYAGUA: vicinity of Siguatepeque, moist shaded bank, 1080-1400 m, *Standley 56340* (JE).

COSTA RICA. Without locality, s.d., *James s.n.* (MO6169776). **ALAJUELA:** Angeles, R.B. Alberto Manuel Brenes, Estacion Rio San Lorenzo, sobre tronco vivo expuesto a luz, 800 m, 6 May 1996, *Trana 4* (MO). **CARTAGO:** vicinity of Pejivalle, 900 m, *Standley & Valerio 46972, 46984* (JE). **HEREDIA:** Vara Blanca, between Poás and barba volcanos, 1600-1700 m, 22 July 1923, *Maxon & Harvey 8333a* (JE). **PUNTARENAS:** Monteverde, Atlantic slope, Monteverde Cloud Forest Preserve, on tree trunk, 10°18’N, 84°47’W, 1600 m, 4 March 1992, *Lyon 157* (MO). Monteverde Reserve, in leeward cloud forest, epiphytic, 10°18’N, 84°48’W, 1500-1550 m, 20 February 1992, *Stephen et al. 1370* (MO). Potrero Grande, P.N. La Amistad,

Cerro Bioley, sobre tronco a la sombra, 09°02’20”N, 83°00’30”W, 1650 m, 25 February 1995, *Dauphin 1631* (MO). Distrito Pittier, Laguna Gamboa, Fila Cruces, San Visto, epífito semicolgante, 8°57’00”N, 83°04’20”W, 300-400 m, 7 June 1995, *Dauphin 1719* (MO). Distrito Pittier, Estacion Pittier, Santa Maria de Pittier, epífito sobre tronco de Ficus en potrero expuesto al sol, 9°01’30”N, 82°57’40”W, 1600-1700 m, 4 February 1995, *Dauphin 1418* (MO). Distrito Pittier, Fila Tigra, Palmira de Gutierrez Braun Area de bosque de roble secundario, sobre corteza a la sombra, 8°56’40”N, 82°53’30”W, 1100-1200 m, 26 October 1995, *Dauphin 1984, 1985* (MO). Along road between La Union (Border of Panama) and Coton, between Rio Negro and Rio Coto Brus, growing in dense clump on tree trunk, 9 August 1974, *Croat 26680* (MO). Reserva Biologica Monteverde, undisturbed cloud forest, on trunk and lianas at edge of forest gap, 1550 m, 22 September 1994, *Gradstein & Mues 9680* (GOET). Reserva Biologica Monteverde, undisturbed cloud forest, on exposed trunk at edge of gap, 1550 m, 11 November 1993, *Gradstein 9615* (GOET). Ibid., pendent from treelet, *Gradstein 9577* (GOET). Monteverde Reserve, in cloud forest, epiphytic on bark, 1500-1550 m, 21 November 1992, *Ingram & Ferrell-Ingram 1765* (GOET). Chimongo trail near Monteverde, rain forest near top divide, 15 March 1971, *James s.n.* (MO6169785). Jungle forest near Monteverde, June 1962, *James s.n.* (MO61699783). **SAN JOSÉ:** Vicinity of Santa María de Dota, on tree, 1500-1800 m, *Standley 41696* (JE).

PANAMA. BOCAS DEL TORO: Campamento la pasta del Cedro, Bosque nuboso muy humedo, crescendo sobre arbol caido, 9°03’N, 82°43’W, 1525 m, 8 March 2004, *Alfaro & Monro 5440* (MO). **CHIRIQUI:** Res. Forestal Fortunato an der Straβe von Chiriqui nach Chiriqui Grande, an Baumbasis und an Weghang im Nebelwald oberhalb der Finca La Suiza, Mun. Gualaca, 8°39’N, 82°11’W, 1660 m, 30 March 2013, *Schäfer-Verwimp & Verwimp 34424* (MO). Cordillera Talamanca, Straβe von El Vocan nach Rio Sereno, auf Felsblock an Bach in Regenwald bei Santa Clara, 8°49’N, 82°44’W, 1200 m, 3 April 2013, *Schäfer-Verwimp & Verwimp 34712* (MO). Holcomb trail, April 1918, *Cornman 3129, 3198* (MO). Near Manniche’s, *LCornman 3055* (MO).

CUBA. SANTIAGO DE CUBA: Sierra Maestra, El Uvero, em el caminho de la costa a El Manguito, 400-600 m, 1969, *Bisse & Lippold 014503/a* (JE). Sierra Maestra, 1300-1500 m, 1969, *Bisse & Lippold 14617/b* (JE).

DOMINICAN REPUBLIC. ST. DOMINGO: The type of *Radula gottscheana* (FH, S, G).

SURIMAN. In montibus, qui dicuntur Emmaketen, mountain savanna-forest on almost bare granite, between Gonggrijptop and Hendriktop, 600 m, 22 August 1959, *Daniëls & Jonker*

1010 (GOET). Lely Mts., SW plateaus covered ferro-bauxite, forest on plateau, epiphytic, 550-710 m, 25 September 1975, *Lindeman et al. 354a* (GOET).

VENEZUELA. TRUJILLO: 15 km East South East of Bocono, 1 km west of Guaramecal, primary forest and river edge, epiphyte, 9°11'N, 70°09'W, 1600 m, 16 March 1982, *Liesner et al. 12930* (MO).

COLOMBIA. ANTIOQUIA: Amalfi, 8-15 km de Amalfi a Rumazon, sítios "Salazar" y "La Playa" Cordillera Central, 6°56'N, 75°04'W, 1550 m, 28 September 1988, *Betancur et al. 753* (MO). **CASANARE:** Sácama, 1450 m, *Aguirre et al. 3025* (GOET). **CUNDINAMARCA:** Bosque subandino, epilítica, 2100 m, 29 April 1973, *Cleef 9691* (MO, BM).

BRAZIL. AMAZONAS: Rio Negro, between Manaus and São Gabriel, Serra Curicuriari, 00°20'S, 66º50'W, 450 m, 9–12 July 1979, *Schuster 79-15-580* (NY). **MINAS GERAIS:** Marmelópolis, Pousada Maeda, trilha das águas, sobre rocha na margem da trilha, 22°26'57"S, 45°09'55"W, 1500 m, 14 June 2006, *Peralta 3584* (SP). Lima Duarte, Parque Estadual do Ibitipoca, na base do tronco de árvore na matinha da baixada, mata de galeria, 21°43'32" S, 43°52'35" W, 11 November 1987, *Sousa s.n.* (SP). **PARANÁ:** Morretes, Parque Estadual do Marumbi, trilha vermelha, caminho para ponta do tigre, Mata Atlântica com afloramento rochosos, sobre rocha, 25°25'55" S, 48°54'54" W, 1200 m, 22 July 2014, *Peralta et al. 15731, 16364* (SP). **RIO DE JANEIRO:** Teresópolis, Parque Nacional da Serra dos Orgãos, 21 October 1989, *Yano & Costa 13551* (SP). Itatiaia, Picada Watotei, 03 February 1967, *Vianna 3937, 3956* (ICN, SP). Resende, Parque Nacional do Itatiaia, picada Véu de Noiva, paredão úmido, 22°28'08"S, 44°26'48"W, 1165 m, 20 June 1983, *Yano & Santos 7488* (SP, MO). Parati, Bairro do Curisco, na margem do riacho sobre rocha, 23°13'04" S, 44°42'47" W, 5 m, 23 October 1988, *Vital s.n.* (SP374706); Parque Nacional do Itatiaia, Véu de Noiva, sobre pedra úmida na cachoeira, 1200 m, 30 September 1995, *Yano & Zaidan 24262* (SP). **SANTA CATARINA:** Jaraguá do Sul, 450 m, *Carl 144* (JE). **SÃO PAULO:** Moji das Cruzes, Parque Municipal da Serra de Itapety, 23°31'22"S, 46°11'18"W, 1000 m, 22 October 2005, *Peralta & Cunha 3206* (SP, MO). Serra da Cantareira, virgin forest, on fern leaf, 1200 m, 18 July 1960, *Eiten et al. 2187A* (BM).

ARGENTINA. SALTA: Departamento Orán, Reserva San Andrés, pr. Río Blanquito, epífita, 23°12'S, 64°43'W, 590-950 m, 17 Jun 2008, *Fuertes s.n.* (MO6895384).

Cladoradula boryana is a distinct species recognized by the large 2(–3)-pinnate plants with a rigid stem, which in cross section is composed by a thick-walled, brownish cortex of 3–4 cell-layers surrounding a yellowish to colorless, thin-walled medulla. It also has diagnostic

leaf cells with large trigones, somewhat bulging, and lobules with a strongly auriculate base extending downward beyond the keel. Lobules from branches are smaller than those of the main stem and auricles are small and absent on primary and secondary branches, respectively.

Cladoradula was firstly described as a subgenus of *Radula* by Spruce (1885), but Renner *et al.* (2022) raised the subgenus to a genus level because of its unique morphology and phylogenetic old age. Further information about this species is given by Gradstein *et al.* (2022) and Renner *et al.* (2022).

Radula Dumort., Comment. Bot. 112. 1822. *nom. cons.* Type: *Jungermannia complanata* L. [=*Radula complanata* (L.) Dumort.].

Plants small to robust, irregularly to regularly 1–2-pinnate, purely dichotomous or dichotomy exclusive to female plants by fertile paired innovation. *Stem* thin to rigid, without subepidermis, variable anatomically. Lobule longitudinal. Gynoecia (0–)1–2 innovations. Perianth short to long, rare to frequent. Capsule long-cylindrical. Spores apolar.

Identification key to the species of *Radula* in the tropical America

1. Plants with persistent thallus, with short leafy shoots sprouting from thallus margins. Vegetative reproduction present (small discoid gemmae) ..... *R. yanoella*
1. Plants without a persistent thallus. Vegetative reproduction present (various) or lacking 2
2. Plants with microphyllous branches (branches 3–4× smaller than the main stem, regularly pinnate, and arranged very close to each other) 3
2. Plants without microphyllous branches 5
3. Microphyllous branches arranged distant to each other. Fossil species (Dominican amber) ..... *R. steerei*
3. Microphyllous branches arranged very close to each other. Extant species 4
4. Lobules with a voluted auricle. Microphyllous branches always associated with a lobule keel ..... *R. voluta* var. *microphylla*
4. Lobules without auricle. Microphyllous branches at each 1–2(–3) leaves on the main stem ..... *R. eggersii*
5. Leaf bordered by 3–5 rows of thick-walled cells 6
5. Leaf without border of thick-walled cells 7

6. Leaf border distinctly reddish-brown. Lobules subquadrate .....*R. smithii*

6. Leaf border colorless or sometimes brownish. Lobules ligulate ..... *R. ligula*

7. Lobule base auriculate (auricle downward).....8

7. Lobule not auriculate 11

8. Lobule coiled auriculate. Insertion line circinate.....9

8. Lobule not coiled auriculate. Insertion line straight to inverted in small J-shaped 10

9. Coiled auricle small, not extending downward, partially covering the ventral stem surface. .....*R. sinuata*

9. Coiled auricle large, extending downward and usually reaching the keel, covering almost the whole ventral stem surface .....*R. voluta*

10. Lobule subquadrate. Lobule base covering 1/2–2/3 to (rarely) fully overlapping the stem.. .....*R. xalapensis*

10. Lobule reniform. Lobule base fully overlapping and extending beyond the stem .... *R. sp. nov. 3*

11. Discoid gemmae present, produced on leaf margin.....12

11. Discoid gemmae absent 17

12. Gemmae very large, 350–450 µm in diameter, base deeply cordate-auriculate, produced exclusively on dorsal leaf margin.....*R. flaccida*

12. Gemmae small to medium-sized, 30–200 µm in diameter, base not cordate-auriculate, produced along the leaf margin 13

13. Plants typically epiphyllous, 0.9–1.4 mm wide. .....*R. stenocalyx*

13. Plants typically corticolous, 1.6–2.8 mm wide.....14

14. Leaf margin occasionally producing gemmae. Plants monoicous. Perianth usually without innovation.....*R. renneri*

14. Leaf margin always producing numerous gemmae. Plants dioicous. Perianth with 1–2 innovation.....15

15. Lobule base not ampliate. Endemic to Santa Cruz (Galápagos Islands) ....*R. santacruziana*

15. Lobule base ampliate, covering 1/2 to fully overlapping the stem. Widely distributed in tropical America 16

16. Lobules usually imbricate, base extending fully across and beyond the stem....*R. quadrata*

16. Lobules distant to subimbricate, base covering 1/2 to rarely fully overlapping the stem .... *R. leiboldii*

17. Plants with strongly caducous leaf lobes, producing almost completely denuded branches 18

17. Plants without or with occasionally caducous leaf lobes 22
18. Lobules subrectangular. Leaf cells with large trigones ..... *R. pseudostachya*
18. Lobules various, not subrectangular. Leaf cells without or with small trigones 19
19. Lobules narrowly obtriangularly elongate, tubularly inflated, 2.5–4× longer than wide ..... *R. bischlerae*
19. Lobules subquadrate to subrhombic, not tubularly inflated, ca. 2× longer than wide 20
20. Lobules subquadrate with free margin strongly recurved ..... *R. brasilica*
20. Lobules usually subrhombic with free margin plane 21
21. Plants purelly dichotomous. Usually fertile ..... *R. wrightii*
21. Plants regularly to irregularly pinnate. Rarely fertile ..... *R. fulvifolia*
22. Lobules imbricate, base covering the entire stem, stem surface hardly visible 23
22. Lobules distant to contiguous, base not or covering the entire stem, stem surface clearly visible 24
23. Leaves densely imbricate. Lobules spreading at angles of 50–60º with the stem. Plant endemic to tepuis ..... *R. gradsteinii*
23. Leaves imbricate. Lobules spreading at angles of 30–40º with the stem ..... *R. taylorii*
24. Lobule strongly inflated along the keel, inflated portion of lobule curved, becoming convolute and lunular in shape 25
24. Lobule plane to strongly inflated along the keel, inflated portion of lobule not curved, not becoming convolute and lunular in shape 26
25. Plants small, 1–1.4 mm wide, densely branched. Leaf lobes ovate, strongly convex ..... *R. tenera*
25. Plants large, 1.8–2.2 mm wide, sparsely branched. Leaf lobes strongly falcate-ovate, slightly convex ..... *R. involvens*
26. Lobule subrectangular (longer than wide) 27
26. Lobule not subrectangular 30
27. Plants densely branched. Leaf margin crenulate. Leaf cells mammillose on ventral and dorsal surface ..... *R. venezuelensis*
27. Plants sparsely branched. Leaf margin entire. Leaf cells smooth 28
28. Plants > 1.8 mm wide, regularly pinnate. Gynoecia on small branches without innovation ..... *R. portoricensis*
28. Plants < 1.8 mm wide, irregularly pinnate. Gynoecia on long branches with 1-2 innovation 29

29. Plants dioicous. Leaf cells with large trigones. Vegetative reproduction by caducous leaf lobes.....*R. fendleri* var. *fendleri*

29. Plants monoicous (paroicous). Leaf cells without or with small trigones. Vegetative reproduction absent.....*R. fendleri* var. *paroica*

30. Lobule keel convex.....31

30. Lobule keel concave to straight.....40

31. Leaf cells without or with small trigones.....32

31. Leaf cells with medium-sized to large trigones.....36

32. Plants < 1 mm wide. Leaf lobes oblong-ovate.....*R. sp. nov. 1*

32. Plants > 1 mm wide. Leaf lobes ovate to falcate-ovate.....33

33. Plants purelly dichotomous.....*R. elliottii*

33. Plants regularly to irregularly pinnate.....34

34. Plant corticolous, never growing as epiphyll. Lobules subrhombic.....*R. tenuis*

34. Plant epiphyll, but also grows on others substrates. Lobules subquadrate.....34

35. Leaves contiguous to subimbricate. Leaf apex rounded.....*R. grevilleana*

35. Leaves imbricate. Leaf apex obtuse to subacute.....*R. yamadae*

36. Leaf lobe suborbicular. Lobule inflated throughout, sometimes also inflated at rhizoid area .....*R. saccatiloba*

36. Leaf lobe ovate to falcate-ovate. Lobule inflated along the keel, flattened above, also at rhizoid area 37

37. Leaves strongly imbricate. Leaf cells conspicuously mammillose on the ventral and dorsal surface of the lobe, often with a distinct papilla. Lobule keel sometimes crenulated by mammillose cells.....*R. sonsonensis*

37. Leaves contiguous to imbricate. Leaf cells smooth (except on dorsal surface of *R. dominicensis*). Lobule keel entire.....38

38. Lobule keel strongly convex.....*R. dominicensis*

38. Lobule keel straight to slightly convex.....39

39. Leaf lobe ovate. Lobule slightly inflated along the keel.....*R. inflexa*

39. Leaf lobe falcate-ovate. Lobule strongly inflated along the keel.....*R. involvens*

40. Lobule 1/6–1/5 the lobe length.....*R. microlobula*

40. Lobule 1/4–1/2 the lobe length.....41

41. Lobule narrowly obtriangularly elongate.....*R. sp. nov. 2*

41. Lobules not obtriangularly elongate.....42

42. Lobules with conspicuously extended apex.....43

42. Lobules without extended apex 47
43. Leaves usually distant to contiguous. Leaf lobe ventral margin straigth. Lobule base covering up to 1/3 the stem ..... *R. macrostachya*
43. Leaves subimbricate. Leaf lobe ventral margin straight to rounded. Lobule base covering more than 1/3 the stem 44
44. Leaf cells with distinct trigones, increasing in size towards the margins ..... *R. angulata*
44. Leaf cells trigones lacking or not increasing in size towards the margins 45
45. Leaf lobes ovate to falcate-ovate (strongly falcate on branches), margin entire to weakly undulate. Caducous leaf lobes present. Plants dioicous ..... *R. cubensis*
45. Leaf lobes ovate, margin entire to crenulate. Caducous leaf lobes absent. Plants monoicous 46
46. Plants essentially paroicous. Gynoecia usually whithout innovation. Gemmae present along the leaf margin. Endemic to Brazil ..... *R. renneri*
46. Plants essentially autoicous. Gynoecia with 1–2 innovations. Gemmae lacking. Afro-American species ..... *R. mexicana*
47. Lobule base covering more than 1/2 to fully overlapping the stem 48
47. Lobule base covering up to 1/2 the stem (except in few cases of *R. pallens* and *R. javanica*) 50
48. Lobules oblong. Leaf cells with distinct trigones ..... *R. bahiensis*
48. Lobules subquadrate. Leaf cells without or with small (rarely medium-sized) trigones ... 49
49. Plants yellowish to yellowish-brown, densely 1–2-pinnate, up to 8 cm long. Cuticle smooth. Occurs usually at high elevation ..... *R. xalapensis*
49. Plants green to olive-green, not densely 1–2-pinnate, up to 2 cm long. Cuticle smooth to verruculose. Occurs usually at low elevation ..... *R. recubans*
50. Lobules rectangular to oblong-rectangular (wider than long) 51
50. Lobules subquadrate to subrhombic 52
51. Leaves distant to contiguous, widely spreading. Leaf lobe orbicular ..... *R. episcia*
51. Leaves strongly distant, obliquely spreading, rarely widely spreading. Leaf lobe oblong-ovate ..... *R. underwoodii*
52. Lobule base covering up to 1/4 the stem ..... *R. pusilla*
52. Lobule covering more than 1/4 the stem 53
53. Plants with caducous leaf lobes 54
53. Plants without caducous leaf lobes 55
54. Plants purelly dichotomous. Lobules subquadrate to subrhombic ..... *R. wrightii*

54. Plants regularly to irregularly pinnate (dichotomy restricted to female branches with paired innovations). Lobules subquadrate ..... *R. javanica*
55. Plants monoicous. Lobule apex on a depressed line between the free margin and the distal margin of the lobule ..... *R. cochabambaensis*
55. Plants dioicous. Lobules apex not on a depressed line 56
56. Lobules inflated at rhizoid area 57
56. Lobules conspicuosly inflated along the keel, flattened above 58
57. Leaf lobe margin composed of thin-walled cells without trigones .... *R. pallens* var. *pallens*
57. Leaf lobe margin composed of thick-walled cells with larger, bulging trigones and a thickened outer wall ..... *R. pallens* var. *marginata*
58. Leaf lobe oblong to oblong-falcate (longer than wide) ..... *R. longiloba*
58. Leaf ovate to falcate-ovate 59
59. Leaf margin crenulate, usually recurved. Leaf cells sometimes mammillose on dorsal surface. Stem in cross section with thick-walled medullary cells ..... *R. subinflata*
59. Leaf margin entire, usually plane, rarely recurved. Leaf cells smooth (never mammillose). Stem in cross section with thin-walled medullary cells ..... *R. nudicaulis*

1. Radula angulata Steph., Hedwigia 23: 114. 1884. Type: Venezuela, Caripe, *J. W. K. Moritz 152* (lectotype, G-00043973!, c. andr., **designated here**; isolectotype, G-00121223!, c. andr., BM-000969188!, c. andr., BM-000969189!, c. andr.).

Radula bogotensis Steph., Hedwigia 23: 115. 1884. Type: Colombia, Bogotá, Azerradero, 2500 m, 1860, *A. Lindig 1738* (lectotype, G-00043906!, selected by Gradstein, 2021: 623; isolectotypes, G-00265022!, G-00265923!, BM-000969190!, BM-000969191!, BM-000969192!), syn. fide Gradstein (2021).

Radula korthalsii Steph., Hedwigia 23: 133. 1884. Type: Venezuela, *P. W. Korthals 184*, ex hb. Sande Lacoste (lectotype, G-00283269!, c. gyn., selected by Yamada, 1980: 251); Venezuela, *A. Fendler s.n.*, ex hb. Gottsche (syntype, G-00281267!), syn. fide Yamada (1991).

Dioicous. *Plants* 1.4–2 mm wide, to 1.5 cm long, light green to yellowish-green in field, yellowish-green to yellowish-brown in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on

decapitated shoots. *Stems* 100–170 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thick-walled (by concave trigones), yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, slightly convex, ovate, rarely falcate-ovate, 0.7–1.2 mm long, 0.65–0.9 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane, sometimes recurved, entire; marginal cells subquadrate to isodiametric, 10–20 × 7–10 µm, median cells isodiametric to elongate, 15–25 × 10–15 µm, basal cells elongate, 20–30 × 10–15 µm, cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, subquadrate, 0.45–0.75 mm long, 0.35–0.55 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion ca. 1× the base length, insertion line straight, base plane, rounded to usually strongly angulate, covering 1/2 to fully overlapping the stem, free margin plane, straight, apex plane, narrowly rounded to acute, distal margin straight, keel straight, spreading at angles of 50–70º with the stem, 150–170º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 5–10 pairs of bracts, 0.8–1.1 mm wide; bracts distant to imbricate, ovate, 0.7–1 mm long, 0.35–0.55 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to angulate, free margin straight, apex obtuse, rarely subacute. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.9–1.1 mm long, 0.4–0.45 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical to trumpet-shaped, 2.4–3.1 mm long, 0.3–0.5 mm wide at base, 0.7–0.8 mm wide at middle, 0.8–1.1 mm wide at apex, mouth entire, plane to undulate; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* ca. 2.5 mm long. *Capsule* ca. 1 mm long, ca. 0.2 mm wide, valves ca. 1.25 mm long, ca. 0.25 mm wide at middle, outer layer cells subrectangular to long-rectangular, simple nodular thickenings yellowish-brown, on every longitudinal wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* and *Spores* not observed. *Vegetative reproduction* by means of caducous leaf lobes and stem fragmentation.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habitat. Tropical America. Besides the countries listed in the additional specimens examined, *Radula angulata* has been reported from Guadeloupe (Stephani 1884, as *R. korthalsii*, Pagán 1942, as *R. korthalsii*), Dominica (Schäfer-Verwimp 2010) and Haiti (Yamada 1988a, as *R. korthalsii*) (Figure 11). We are reporting the species for the first time from Mexico, Trinidad and Tobago, and Ecuador. *Radula angulata* forms dense mats usually on trees or palm trees (including roots), sometimes on rotten logs, rarely on rock, in humid and shaded places in submontane and montane forests, rarely in subalpine forests, at 700–3480 m elevation. The species has also been collected in pasture woods and *Araucaria* forest in Southern Brazil.

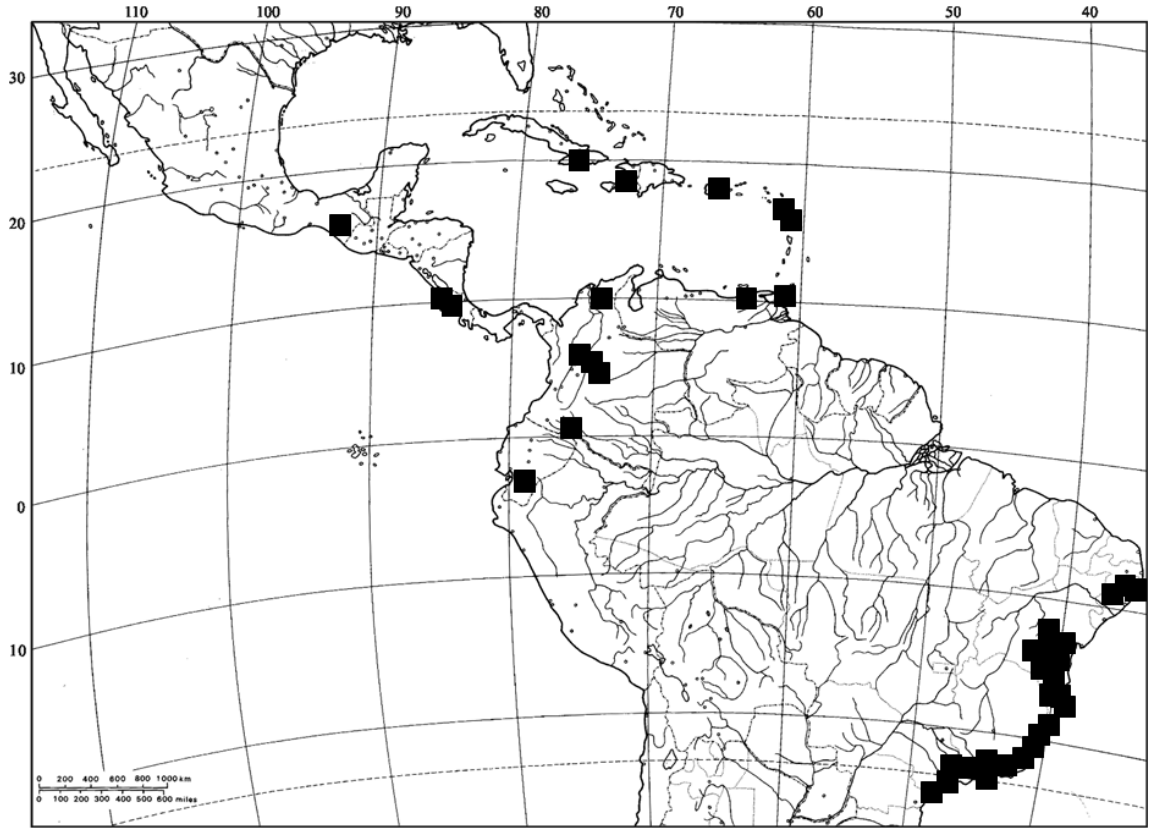

Figure 11. Distribution of *Radula angulata*.

Additional examined specimens. MEXICO. CHIAPAS: La Trinitaria, Cinco Lagunas, Lagos de Montebello National Park, growing on trunk, 1600 m, 24 May 1988, *Breedlove 68621* (MO).

COSTA RICA. GUANACASTE: Monteverde Biological Reserve, on tree, 10°15'N, 84°45'W, 5 August 1993, *Timme 11441* (MO). Monteverde, February 1963, *James 63B14*

(MO). Monteverde, pasture woods, 17 March 1965, *James 89* (MO). Monteverde, along path spring, 10 March 1965, *James 47* (MO).

CUBA. SANTIAGO DE CUBA: Sierra Maestra de la Gran Piedra, in pluviisilvis montanis, in cortice, 1100 m, 1969, *Borhidi & Muniz 5366* (JE).

PUERTO RICO. MARICAO: December 1962, *Manuel & Diaz 130A* (MO).

TRINIDAD AND TOBAGO. Without locality, 1974, *Crüger s.n.* (JE-H1363). Without locality, s.d., *Crüger s.n.* (FH-00965703).

VENEZUELA. The Type of *R. angulata* and *R. korthalsii* (G)

COLOMBIA. ANTIOQUIA: Nova Granada, s.d., *unknown collector* (FH-00965683).

ECUADOR. AZUAY: Sevilla de Oro, 3480 m, 1947, *G. Harling 2325 pp.* (JE).

BRAZIL. BAHIA: Abaíra, Mata da Serra do Rei, sobre tronco de árvore, 14°16'N, 41°54'W, 1550–1650 m, 17 February 1992, *Harley et al. 52108* (SP). Eunápolis, Estação Veracruz, trilha Pau-Brasil, Floresta Atlântica, corticícola, 16°22'S, 39°10'W, 9 September 1999, *Vilas Bôas-Bastos & Bastos 1234, 1285, 1378, 1599, 1615* (ALCB). Camacã, Serra Bonita, corticícola, 15°23'S, 39°43'W, 853 m, 24 February 2015, *Costa 4* (ALCB). Wenceslau Guimarães, Estação Ecológica Estadual de Wenceslau Guimarães, Floresta Atlântica, corticícola, 13°32'S, 39°42'W, 16 January 2011, *Reis 577* (ALCB). Santa Cruz Cabrália, Fragmento Cara-branca, Floresta ombrófila Atlântica, epíxila, 16°22'S, 39°08'W, 9 March 2001, *Bastos 2594* (ALCB). Santa Teresinha, Povoado de Pedra Branca, Serra da Jibóia, Morro da Pioneira, em floresta ombrófila montana, corticícola, 13°50'55,3"S, 39°28'34,2"W, 786 m, 18 September 2015, *Rodrigues 182, 231, 259, 312* (ALCB). **ESPÍRITO SANTO:** Domingos Martins, Reserva florestal "Pedra azul" östlich Venda Nova, 1200 m, 25 July 1987, *Schäfer-Verwimp & Verwimp 8880* (MG, ALCB). Santa Teresa, Reserva Biológica Augusto Ruschi, sobre tronco, February 2003, *Rissini et al. 240, 250* (SP); Ibid., base de uma palmeira, December 2002, *Rissini et al. 129, 146* (SP). **MINAS GERAIS:** Parque Nacional do Itatiaia, 22°22'S, 44º45'W, 1700–1900 m, 4 July 1991, *Vital & Buck 19523* (NY). Passa Quatro,1921, *Zikán 273/a* (JE). Camanducaia, tronco vivo na margem da estrada, 22°45'19" S, 46°08'41" W, 1050 m, 14 January 2006, *Peralta et al. 3420* (SP). **PARANÁ:** Morretes, Parque Estadual Pico do Marumbi, 15 April 2015, *Amélio 79, 89* (SP). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, sobre tronco de árvore, 27 August 1987, *Pôrto s.n.* (UFP). Taguaritinga do Norte, sobre rochas graníticas na mata, 24 Aug 1980, *Yano & Lima 2636* (SP). **RIO DE JANEIRO:** Resende, Parque Nacional do Itatiaia, na lateral do abrigo Água Branca, 22°26'2"S, 44°38'25"W, 1701 m, 9 April 2014, *Rezende & Costa 163* (RB). Teresópolis, Parque Nacional da Serra dos Órgãos, sobre rocha, 22°27'33" S, 43°00'17" W, 1300-1500 m, 21 March 2017,

Peralta et al. 20403 (SP). **RIO GRANDE DO SUL:** Viamão, Parque Saint Hilaire, 28 August 1994, *Michael s.n.* (ICN). Sapiranga, arredores, sobre rochas, 7 September 2000, *Azevedo et al. 2* (SP). **SANTA CATARINA:** Bergland bei Curitibanos, 1030 m, 13 October 1987, *Schäfer-Verwimp & Verwimp 9136* (MG). **SÃO PAULO:** Natividade da Serra, Parque Estadual da Serra do Mar, Núcleo de Santa Virgínia, corticícola, 23°26'38"S, 45°14'01"W, 867 m, 11 June 2013, *Carmo & Peralta 588* (SP). Alto da Serra, 1921, *A. Gehrt 344/a, 4* (JE). Ilhabela, caminho para cachoeira da Toca, sobre pedra na mata úmida, 31 December 1982, *Yano 5119* (SP).

Radula angulata (subg. *Volutoradula*?) is recognized by leaves usually ovate, somewhat fragile by caducous leaf lobes, leaf cells with conspicuous trigones that increase in size towards the margins. Besides, it has lobules subquadrate on which the base varies in form and size (along the stem), although usually angulate, covering 1/2 to fully overlapping the stem, apex narrowly rounded to acute.

This species resembles the Afro-American *Radula mexicana* in lobule shape. However, the latter species is monoicous (essentially autoicous) and has thin-walled leaf cells without distinct trigones. *Radula angulata* is also similar to *R. cubensis* in lobule shape, but the latter has leaves ovate to usually strongly falcate-ovate, leaf cell walls without trigones and lobule keel spreading at the angle of 40–50° with the stem (50–70º in *R. angulata*).

2. Radula bahiensis F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., Phytotaxa 454(1): 25. 2020. Type: Brazil, Bahia, Uruçuca, 6.2 Km N of town of Serra Grande, ca. 40 Km N of Ilhéus along coast, wet tropical forest with small stream in ravine, 14°26'S, 39°03'W, 200 m, 17 July 1991, *D. M. Vital & W. R. Buck 20271* (holotype, SP-353920!; isotypes, NY!, MG!).

Dioicous. *Plants* 2–3.5 mm wide, to 2 cm long, green to olive-green in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on decapitated shoots. *Stems* 200–250 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, slightly convex, oblong-ovate, 1–1.8 mm long, 0.6–1.1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded to obtuse, margin plane, rarely incurved, entire to sinuose; marginal cells subquadrate, 12–20(–30) × 10–15 µm, median and

basal cells isodiametric to elongate, 20–25(–30) × 15–20 μm, cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, oblong, 0.7–0.9 mm long, 0.5–0.7 mm wide, ca. 1/3 of the lobe length, inflated along the keel, insertion 1× the base length, insertion line almost straight, base plane, rounded, covering 2/3 to fully overlapping the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin almost straight to rounded, keel straight to concave, spreading at angles of 40–50º with the stem, 140–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 2–4 pairs of bracts, 1.1–1.4 mm wide; bracts distant, ovate, 0.8–1 mm long, 0.3–0.5 mm wide, apex rounded, margin plane, entire to sinuate, lobule contiguous to subimbricate, ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex rounded. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 1–1.3 mm long, 0.6–0.8 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 1/3 of lobe length, apex rounded. *Perianth* and *Sporophyte* not observed. *Vegetative reproduction* by stem fragmentation and caducous *Lejeunea*-type branches.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habitat. This species is only known in the state of Bahia, northeastern Brazil (Figure 12), where it grows on trees, rarely on rock, fern leaves, and rotten logs. *Radula bahiensis* occurs in shaded and humid places, in the lowland to submontane Atlantic forest, with few records in the transition zone between Atlantic Coastal Region and Caatinga, 100–900 m.

Additional examined specimens. BRAZIL. BAHIA: Una, Maruim, border of the fazendas Maruim and Dois de Julho, wet forest, epiphytic on tree, in full shade, 28 April 1981, *Boom et al. 811* (paratype NY). Ubaíra, Reserva do Timbó, Floresta Atlântica, corticícola, 14°07’19,4”S, 39°39’34,7”W, 20 November 2011, *Reis 4618* (ALCB). Camacã, Serra Bonita, trilha das Bromélias, corticícola, 15°23’S, 39°43’W, 853 m, 24 February 2015, *Costa 4* (ALCB). Wenceslau Guimarães, comunidade quilombola de Nova Esperança, Estação Ecológica Estadual de Wenceslau Guimarães, trilha Água Vermelha, rupícola, 13°34’42”S, 39°42’28”W, 29 September 2017, *Vilas Bôas-Bastos 3210* (ALCB). Igrapiúna, Reserva Ecológica da Michelin, fragmento Pacangê, corticícola, 11°48’S, 39°10’W, 11 August 2006,

Bastos 4647 (ALCB). Santa Teresinha, Povoado de Pedra Branca, Serra da Jibóia, Morro da Pioneira, Caatinga, em floresta ombrófila montana, interior da mata, corticícola, 12°51'20,8"S, 39°28'32,1"W, 800 m, 17 September 2015, *Rodrigues 166* (ALCB).

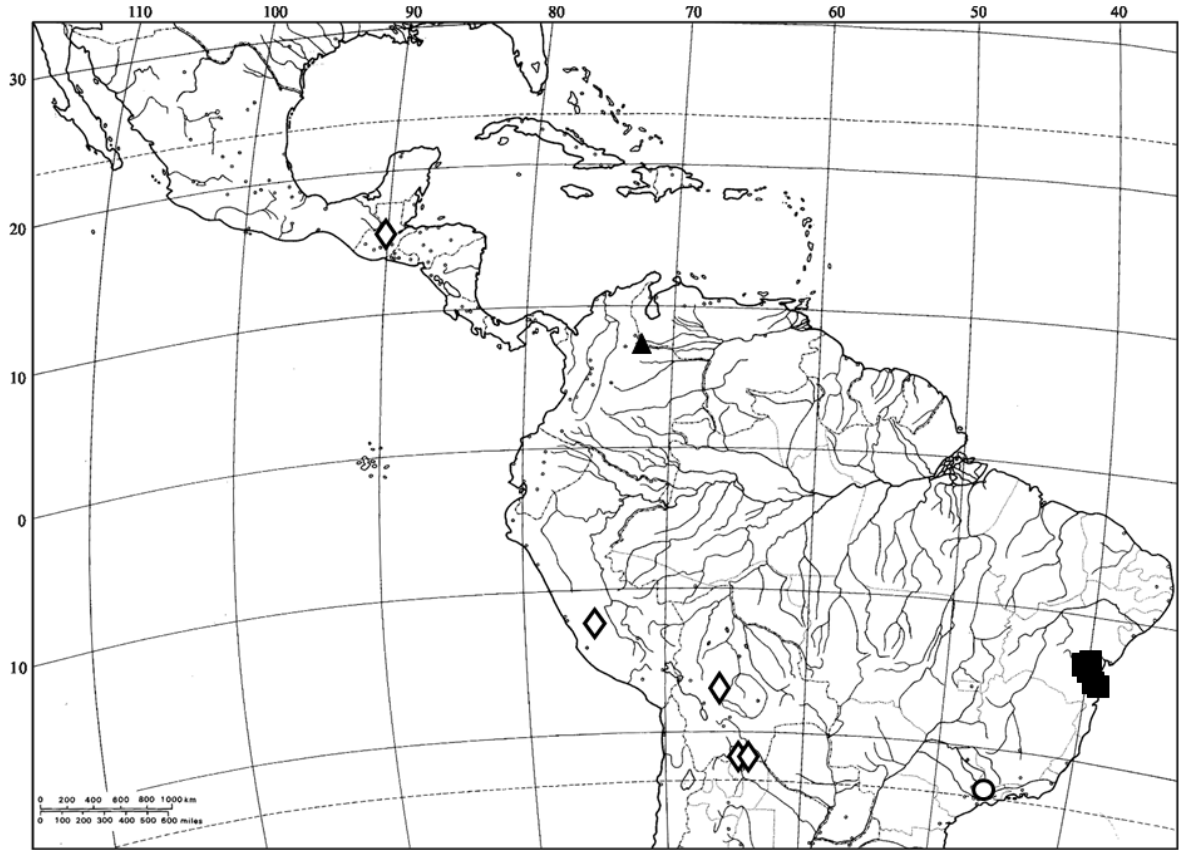

Figure 12. Distribution of *Radula bahiensis* (black square), *R. bischlerae* (black triangle), *R. brasilica* (white circle), and *R. cochabambaensis* (white rhombus).

Radula bahiensis (subg. *Volutoradula*?) is a large plant (up to 3.5 wide) with oblong-ovate leaves with rounded to obtuse apex, entire to slightly sinuose margins, and cells with distinct trigones, especially at the margin. This species has oblong lobules, usually contiguous, with base covering 2/3 to fully overlapping the stem, apex rounded to obtuse, distal margin straight to rounded, and keel straight to usually sinuose-concave.

The species resembles *Radula pallens* var. *pallens*, but the latter has usually suborbicular leaves, cells without trigones and subquadrate lobules, clearly distant.

3. Radula bischlerae Gradst. & Ilk.-Borg., Mem. New York Bot. Gard. 121: 623. 2021. Type: Colombia, Boyacá, Sierra Nevado del Cocuy, Guicán, Corralitos, 3900 m, on soil in páramo, 10 June 1959, *H. Bischler 2894* (holotype, COL; isotypes, PC, MG-238829!).

Dioicous? *Plants* 1–1.5(–2) mm wide, to 1 cm long, brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 100–120 µm in diam., with thick-walled epidermal cells surrounding thin-walled medullary cells, the cells uniform in size, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls yellowish. *Leaf lobes* widely spreading, imbricate, plane to slightly convex, ovate to strongly falcate-ovate, 0.6–0.7 mm long, 0.5–0.6 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to slightly obtuse, margin plane, subentire to crenulate; marginal cells subquadrate, 14–20 × 8–15 µm, median and basal cells isodiametric to elongate, 20–25 × 15–20 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, narrowly obtriangularly elongate, 0.25–0.5 mm long, 0.1–0.25 mm wide, ca. 1/4 of the lobe length, inflated along the keel, insertion ca. 3× the base length, insertion line slightly curved, base plane, rounded to obtuse, covering 1/3–2/3 the stem, free margin plane, straight, apex plane, obtuse, distal margin almost straight to slightly rounded, keel straight to slightly convex, spreading at angles of 25–40º with the stem, 50–60º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids*, *Sexual organs* and *Sporophyte* not observed. *Vegetative reproduction* by strongly caducous leaf lobes and regenerants.

Illustration. Gradstein (2021).

Distribution and habit. This species is only known from the type locality in Boyacá, Colombia (Figure 12), where it was growing on soil in páramo, at 3900 m.

Examined specimens. COLOMBIA. BOYACÁ: The type of *Radula bischlerae* (MG).

Radula bischlerae (subg. *Volutoradula*?) is recognized by the very fragile, highly denuded shoots with strongly caducous leaf lobes and by the elongate, tubularly inflated lobules, 2.5–4× longer than wide.

The lobule shape of *Radula bischlerae* is almost similar to that of *Radula* sp. nov. 2, and by its size and strongly caducous leaf lobes the species resembles *R. fulvifolia*. For differences see under *R.* sp. nov. 2 and *R. fulvifolia*.

4. Radula brasilica K.Yamada, J. Hattori Bot. Lab 74: 35. 1993. Type: Brazil, São Paulo, Serra de Mantiqueira, Campos do Jordão, "auf morschem Holz im Regenwald am Pico do Itapeva," 1850 m, 22°45'S, 45°31'W, 13 June 1987, *A. Schäfer-Verwimp & Verwimp 8484* (holotype, NICH-413169!).

Dioicous. *Plants* 0.8–1.4 mm wide, to 1 cm long, yellowish-green in herbarium, irregularly pinnate. *Branches Radula*-type. *Stems* 60–75 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger (or uniform in size), thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, plane to slightly convex, strongly falcate-ovate, rarely ovate, 0.4–0.55 mm long, 0.3–0.4 mm wide, dorsal base rounded, covering 2/3 to overlapping the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded to obtuse, margin plane, entire to slightly crenulate with the presence of small regenerants; marginal cells subquadrate, 8–20 µm in diam., median and basal cells isodiametric to elongate, 15–25 × 10–20 µm, cell walls thin, trigones small, intermediate thickening absent, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, subquadrate to almost ovate, 0.14–0.5 mm long, 0.1–0.4 mm wide, 1/3–1/2 the lobe length, inflated along the keel, insertion 1–2× the base length, insertion line straight to curved, base strongly recurved, rounded, covering 1/3–1/2 the stem, free margin strongly recurved, apex recurved, rounded to obtuse, distal margin straight, keel straight to strongly convex, spreading at angles of 40–60º with the stem, 80–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on few lobules. *Androecia* terminal to intercalary on long branches, with 3–6 pairs of bracts, 0.65–0.7 mm wide; bracts contiguous to subimbricate, ovate, 0.7–0.8 mm long, 0.25–0.4 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 3/4 of lobe length, base obtuse, free margin recurved, apex obtuse. *Gynoecia* and *Sporophyte* not observed. *Vegetative reproduction* by caducous leaf lobes, producing almost completely denuded branches, the caducous leaf lobes often with regenerants on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. This species is only known from the type locality in the Serra de Mantiqueira, São Paulo State, Brazil (Figure 12). This species was collected in lower montane Atlantic forest growing on a rotten log, at 1850 m.

Specimens examined. BRAZIL. SÃO PAULO: The type of *Radula brasilica* (NICH).

The main diagnostic character of *Radula brasilica* is the strongly recurved free margin of the lobule, which separates it from all other Neotropical species. This species also stands out by plants being very small (0.8–1.4 mm wide) with fragile leaf lobes, often resulting in almost denuded branches, and the leaf lobes being usually falcate-ovate with margins entire to slightly crenulate and with regenerants. The lobules of this plant show a large variation, from small and distant with an almost straight keel to large and contiguous with a strongly convex keel.

Radula brasilica is similar to *R. fulvifolia* in the small plants with caducous leaf lobes and a convex keel, but the latter species has subrhombic lobules with the free margin always plane. Oliveira-da-Silva *et al.* (2021) erroneously described the regenerants in this species (and in *R. schaefer-verwimpii = R. fulvifolia*) as discoid gemmae.

5. Radula cochabambaensis K.Yamada, J. Hattori Bot. Lab. 74: 37. 1993. Type: Bolivia, Cochabamba, Chapare, road Cochabamba villa Tunari Ian 112, cloud forest, on trunk, 65°44'W, 17°09'S, 1850 m, 8-13 November 1989, *S. R. Gradstein 7590* (holotype, U!; isotype, NICH-432554!).

Fig. 13

Monoicous. *Plants* 2.3–2.8 mm wide, to 1 cm long, yellowish-brown to olive-green in herbarium, regularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or rarely *Lejeunea*-type. *Stems* 140–250 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, rarely subimbricate, slightly convex, ovate to falcate-ovate, 1.2–1.5 mm long, 0.7–1 mm wide, dorsal base rounded, covering 2/3 to overlapping the stem, dorsal margin rounded, ventral margin slightly rounded, apex rounded, margin plane to recurved, entire; marginal cells subquadrate, 10–20 μm in diam., median and basal cells isodiametric to elongate, 20–25 × 15–20 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical to ellipsoidal, light yellow, smooth to slightly granular, 13–21 × 10–15 μm. *Lobules* distant, subquadrate, 0.5–0.7 mm long, 0.5–0.6 mm wide, ca. 1/3 the lobe length, inflated at rhizoid area or along the keel, insertion 2–3× the base length, insertion line straight, base plane, rounded, covering 1/2–2/3 the stem, free margin plane, almost straight to usually rounded, apex

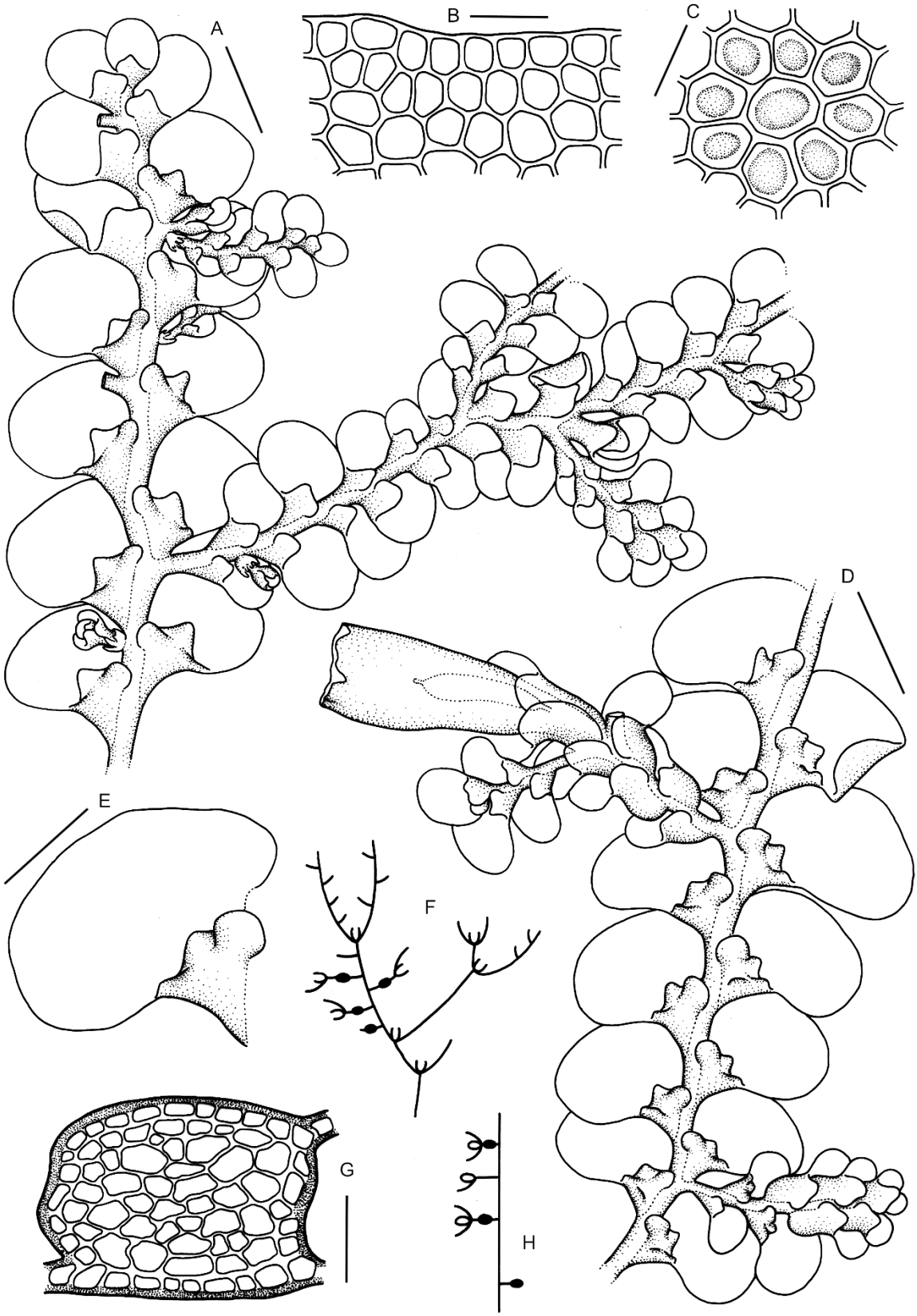

Figure 13. *Radula cochabambaensis*. A. Habit with androecia, gynoecia and *Lejeunea*-type branches. B. Marginal leaf cells. C. Median leaf cells with oil bodies. D. Habit with androecia and perianth. E. Leaf. F, H. Cladograph of plants (black dots = androecia, white dots = gynoecia with perianth, U = gynoecia without perianth). G. Cross section of stem (A, D= 1000 µm; B, C= 25 µm; E= 500 µm; G= 50 µm; A from *Buchtien 15 pp.*, B-E, G-H from the isotype in NICH, F from *Churchill 23454*).

plane, rounded to obtuse, positioned on a depressed line between the free margin and the distal margin, distal margin straight to sinuouse, keel straight to slightly concave, spreading at angles of 40–50º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brown, scanty, present on a few lobules. *Androecia* terminal or preceding the gynoecia on short branches, with 1–3 pairs of bracts, 1–1.2 mm wide; bracts distant to contiguous, ovate, 0.9–1 mm long, 0.4–0.5 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex rounded to obtuse. *Gynoecia* on short or long branches, with 1–2 innovations; bracts oblong-ovate, 1–1.1 mm long, 0.4–0.5 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to acute. *Perianth* erect to falcate, trumpet-shaped, 1.7–2.4 mm long, 0.25–0.4 mm wide at base, 0.5–0.7 mm wide at middle, 0.7–0.8 mm wide at apex, mouth entire, plane; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Distribution and habit. *Radula cochabambaensis* was only known from the type locality in Bolivia, but in this study its distribution is extended to Guatemala and Peru, and to other localities in Bolivia (Figure 12). The species grows on trees in lower montane forest and cloud forest, 1000–1850 m.

Additional specimens examined. GUATEMALA. ALTA VERA PAZ: Without locality, October 1887, *Türckheim s.n.* (FH).

PERU. JUNÍN: Tarma, Ort. Bei der Brucke “Pan de Azugar”, 12 km von San Ramón in Richtung Tarma, Fels, 1000 m, 13 June 1977, *Hegewald 8557* (MO).

BOLIVIA. Palopolo bei Coroiko, n. Yungas, 1300 m, October 1912, *Buchtien 15 pp.* (JE). **COCHABAMBA:** The Type of *Radula cochabambaensis* (NICH). **TARIJA:** Arce, Padcaya, Cantón Emborozú, Reserva Natural Alarachi, Zona Cayotal, Río Emborozú Chico, bosque premontano Tucumano-Boliviano, sobre tronco de árbol, poco sol, 22°14’18”S, 64°34’19”W, 1220 m, 21 September 2004, *Churchill 23454* (MO).

Radula cochabambaensis (subg. *Volutoradula*?) is characterized by the monoicous plants with regularly pinnate branching, leaf lobes ovate to falcate-ovate, leaf cells without or with small trigones, lobule subquadrate with base rounded that cover usually 1/2 the stem, line between the free margin and the distal margin usually depressed, lobule apex rounded to

obtuse, and keel straight to slightly concave. One specimen from Bolivia (*Buchtien 15 pp.*, JE) excepcionally possessed *Lejeunea*-type branches not associated with decapitated shoots.

This species resembles *Radula episcia*, but the latter is dioicous and has purely dichotomous branching.

6. Radula cubensis K.Yamada, J. Hattori Bot. Lab. 54: 241. 1983. Type: Cuba, Santiago de Cuba, Gran Piedra, on bark, 16 January 1979, *D. Reyes 1621* (holotype, HAC; isotypes, EGR, NICH-400980!).

Fig. X

Dioicous. *Plants* 1–1.7 mm wide, to 2 cm long, green to yellowish-green in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches* *Radula*-type. *Stems* 80–100 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger (or uniform in size), thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, subimbricate, slightly convex, ovate to strongly falcate-ovate, 0.6–0.9 mm long, 0.4–0.5 mm wide, dorsal base rounded, covering 1/2 to overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margin plane or weakly undulate; marginal cells subquadrate, 10–15 µm in diam., median and basal cells isodiametric to elongate, 17.5–25 × 12.5–15 µm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, subquadrate to usually subrhombic, 0.35–0.45 mm long, 0.25–0.35 mm wide, 1/3–1/2 of the lobe length, inflated at rhizoid area, insertion ca. 2× the base length, insertion line straight, base plane to slightly convex, rounded to obtuse, covering 3/4 to overlapping the stem, free margin plane, straight to sinuose at middle, apex plane, rounded to obtuse, distal margin straight, keel straight, spreading at angles of 40–50º with the stem, 100–120º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* intercalary on long branches, with 2–4 pairs of bracts, 0.9–1.4 mm wide; bracts distant, ovate, 0.7–1 mm long, 0.3–0.5 mm wide, apex obtuse, margin plane to recurved, entire, lobule ovate, ca. 3/4 of lobe length, base acute to obtuse, free margin straight, apex obtuse, rarely subacute. *Gynoecia* on long branches, with 2 innovations; bracts ovate, 0.8–1 mm long, 0.4–0.5 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 the lobe length, apex rounded to obtuse. *Perianth* erect, trumpet-shaped, ca. 1.9 mm long, ca. 0.5 mm wide at base, ca. 0.6 mm wide at middle, ca. 0.8 mm wide at apex, mouth entire, plane to irregularly undulate;

perianth wall unistratose. *Calyptra* and *Sporophyte* not observed. *Vegetative reproduction* by caducous leaf lobes, sometimes producing almost completely denuded branches.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. A rather scattered Neotropical species, reported for Jamaica (Schäfer-Verwimp & van Melick 2016), Cuba, Ecuador (Gradstein 2021), Colombia, Brazil and Bolivia (Figure 14). This species colonizes trees, sometimes dead trees or rotten logs, rarely rock, in humid places in lowland and montane forests, from sea level to 2420 m.

Additional specimens examined. CUBA. GUANTÁNAMO: Monte Cristo, 1968, *Urban 776-b* (JE). **SANTIAGO DE CUBA:** The type of *R. cubensis* (NICH).

DOMINICAN REPUBLIC. PEDERNALES: Las Abejas, 55 km N of porto f Cabo Rojo on Alcoa Road, humid broadleaf forest, 3600 m, 5 May 1982, *Steere 22827* (NY).

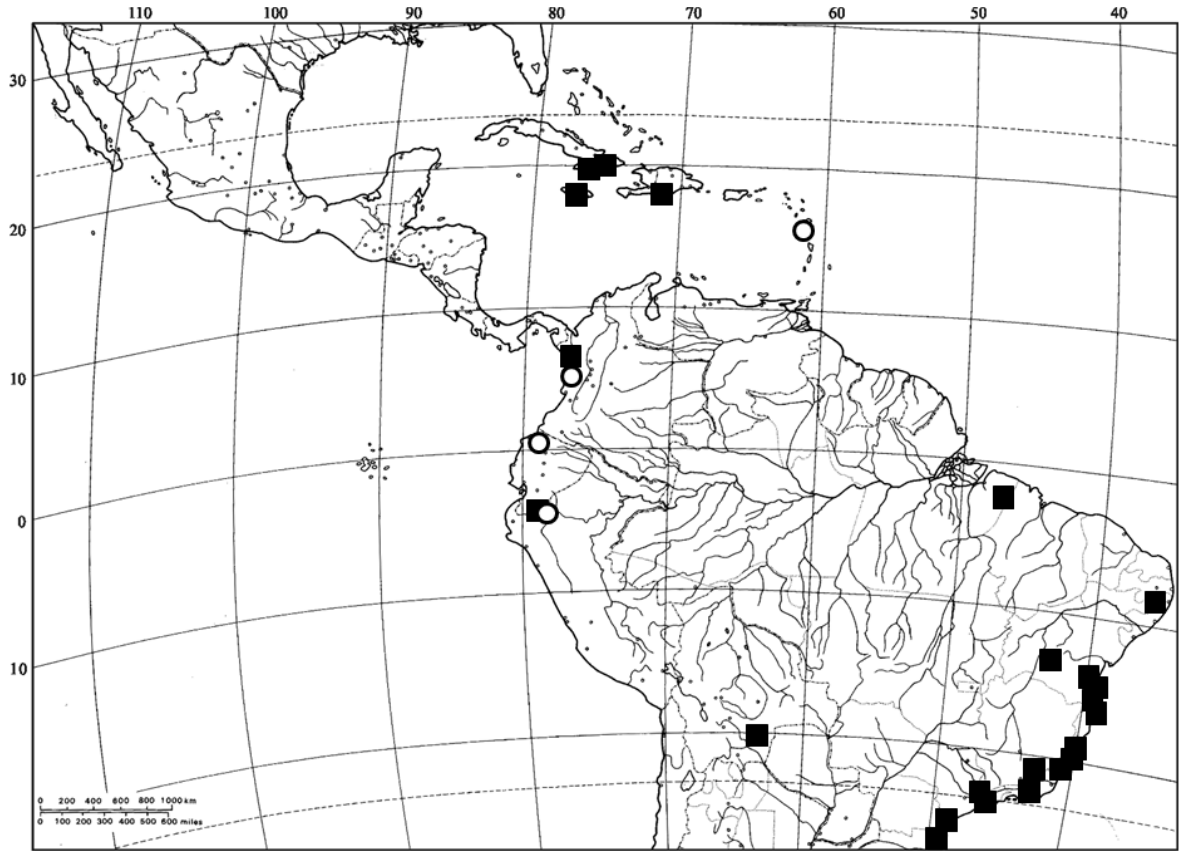

Figure 14. Distribution of *Radula cubensis* (black square) and *R. dominicensis* (white circle).

COLOMBIA. CASANARE: Sácama, camino que va desde el municipio hasta la Quebrada Macueque, pasando por el Río Sácama, 1200 m, 17 August 1982, *Aguirre et al. 3113* (GOET).

BRAZIL. BAHIA: Igrapiúna, Reserva Ecológica de Michelin, 13°48'S, 39°10'W, 15 February 2006, *Bastos 4217* (ALCB). Eunápolis, Estação Veracruz, trilha Pau-Brasil, Floresta Atlântica, corticícola, 16°22'S, 39°10'W, 9 September 1999, *Vilas Bôas-Bastos & Bastos 1268, 1253, 1256, 1378, 1318* (ALCB). Abaíra, Catolés, Serra do Barbado, Mata do Cigano, floresta estacional Montana, corticícola, 13°16'47,7"S, 41°54'14,9"W, 1734 m, 5 September 2008, *Vilas Bôas-Bastos 2399, 2382* (ALCB). **ESPÍRITO SANTO:** Linhares, Reserva Florestal de Linhares, 16 January 1996, *Costa et al. 2964* (RB**). MINAS GERAIS:** Alto do Alto do Caparaó, Parque Nacional do Caparaó, 20°26'00"S, 41°52'06"W, 1000 m, 30 October 1994, *Visnadi & Vital 2652* (SP). **PARÁ:** São Domingos do Capim, Sítio Santa Joana, Mata de Igapó, Igarapé Catita, 1°50'02"S, 47°44'57"W, 20 m, 5 November 2012, *Lopes 163* (SP). **PARANÁ:** Tijucas do Sul, 25°51'07"S, 49°14'48"W, 1100 m, 6 June 1998, *Shirata 3536* (SP). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 11 August 1987, *Pôrto s.n.* (UFP). **RIO DE JANEIRO:** Nova Friburgo, Estação Theodoro de Oliveira, 1 May 1923, *Vaughan Bandeira s.n.* (RB). Santa Maria Madalena, PE do Desengano, sobre tronco de árvore na mata após o córrego, 21°52'81"S, 41°54'98"W, 1156 m, 15 May 2007, *Santos et al. 821* (RB). **RIO GRANDE DO SUL:** Viamão, Parque Saint Hilaire, 13 September 1969, *Oliveira s.n.* (ICN). Cambará do Sul, Parque Nacional Aparados da Serra, sobre tronco vivo, 29°09'58" S, 50°05'19" W, 1030 m, 16 April 2010, *Peralta et al. 10750* (SP). **SANTA CATARINA:** Serra do Rio do Rastro, sobre paredão de pedra, 28°23'56"S, 49°32'59"W, 1254 m, 15 November 2003, *Costa et al. 4358* (RB). **SÃO PAULO:** Pico do Jaraguá, 850 m, 24 August 1986, *Schäfer-Verwimp & Verwimp 7536* (SP). Praia Grande, Fortaleza de Itaipu, Morro do Xixová, sobre pedra úmida na picada do morro, 16 July 1994, *Yano et al. 23034* (SP).

BOLIVIA. CHUQUISACA: Belisario Boeto, al lado de Río Alisos, ca. 19 km Villa Serrano por Nuevo Mundo, bosque montano de Tucumano-Boliviano, sobre tronco de árbol, 19°00'26"S, 64°18'53"W, 2420 m, 20 July 2004, *Churchill et al. 23086* (MO).

Radula cubensis (subg. *Volutoradula*) is characterized by leaves ovate to usually falcate-ovate, with margins plane to weakly undulate, leaf cell walls without trigones, and lobules subquadrate to usually subrhombic, base plane to slightly convex, rounded to obtuse, covering 3/4 to fully overlapping the stem, apex rounded to usually obtuse (narrowly elongate) and keel straight.

This species resembles *Radula angulata* in several respects; differences are discussed under the latter species. The falcate, caducous leaf lobes of *Radula cubensis* are similar to those of *R. javanica* but the latter has lobules subquadrate with apex rounded (not narrowly elongate) and lobule base usually covering up to 1/2 the stem, rarely more (never extending fully across the stem as in *R. cubensis*).

7. Radula dominicensis Steph., Sp. Hepat. 6: 507. 1924. Type: Dominica, *W. R. Elliott 1924 p.p* (lectotype, G-00043880!, selected by Castle, 1963: 20; isolectotype, FH!). Dominica, *W. R. Elliott 1239 p.p* (remmaning syntype, G-00281268).

Dioicous. *Plants* 1–1.5 mm wide, to 1 cm long, brown in herbarium, regularly pinnate to dichotomous in female plants by repeatedly fertile paired innovation. *Branches Radula*-type. *Stems* 110–150 µm in diam., with thick-walled epidermal cells surrounding mostly smaller or uniform in size, thin-walled medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls yellowish to brownish. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate, 0.5–0.9 mm long, 0.3–0.7 mm wide, dorsal base rounded, covering 1/2 to overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margin recurved, rarely plane, entire to slightly crenulate; marginal cells subquadrate, 10–15 × 8–11 µm, median and basal cells isodiametric to elongate, 15–25 × 15–20 µm, leaf cells sometimes mammillose on dorsal surface, cell walls evenly thickened, trigones medium-sized to large, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.3–0.4 mm long, 0.2–0.3 mm wide, ca. 1/3 the lobe length, strongly inflated along the keel, insertion line straight to curved in the inflated area, base not developed, free margin plane, almost straight, apex plane, rounded, distal margin straight to sinuate, keel convex to strongly convex, spreading at angles of 40–60º with the stem, 120–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long branches, with 2 innovations; bracts symmetrical, ovate, 1–1.3 mm long, 0.7–0.8 mm wide, apex rounded, margin plane to recurved, entire, lobule symmetrical, subquadrate, ca. 1/2 of lobe length, apex rounded, keel straight. *Perianth* erect, trumpet-shaped, ca. 4.7 mm long, ca. 0.5 mm wide at base, ca. 0.9 mm wide at middle, ca. 1.1 mm wide at apex, mouth entire, plane; perianth wall not observed. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Yamada (1987, as *R. saccatiloba*).

Distribution and habit. Scattered in tropical America (see Castle 1963, and Gradstein 2021, as *R. saccatiloba*). This species occurs on trees and rock from lowland to alpine elevations, 100–4500 m (Castle 1963, Gradstein 2021). In the distribution map we did not include the locations reported by Castle (1963), since the latter author treated *R. dominicensis* as a synonym of *R. saccatiloba* (Figure 14).

Specimens examined. DOMINICA. The type of *Radula dominicensis* (G, FH).

Radula dominicensis (subg. *Volutoradula*?) is recognized by leaf lobes strongly convex with recurved margin, lobules as long as wide, strongly inflated along the strongly convex keel, and leaf cells thickened with small to medium-sized trigones. We observed mammillose cells on the dorsal surface of some leaf lobes, which were not mentioned in previous descriptions (*e.g.* Castle 1963 and Yamada 1987, as *R. saccatiloba*).

This species was synonymized under *R. saccatiloba* by Castle (1963). However, examination of the type specimen deposited in herbarium G revealed characters separating these two species, especially the lobule shape. *Radula dominicensis* has lobules strongly inflated along the keel (flattened above) and without an expanded base as well as a strongly convex keel, whereas in *R. saccatiloba* the lobule base is slightly expanded, covering up to 1/3 the stem, inflated on the rhizoid area or completely inflated, and a slightly convex keel (not strongly so). In addition, the stem anatomy differs in both species. *Radula dominicensis* has outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, while *R. saccatiloba* has the epidermal and medullary cells equally thickened.

8. Radula eggersii K.Yamada, J. Hattori Bot. Lab. 82: 339. 1997. Type: Ecuador, Loja, ea. 50krn N of Loja near Tcanama, 2950-3050 m, pasture with spots of forest, epiphytic, 8 March 1994, *J. Eggers ECU 6/14* (holotype, NICH-432555!, c. per. + spor.)

Fig. 15

Dioicous. *Plants* 2.4–3 mm wide, to 4 cm long, yellowish-brown in herbarium, dichotomous in female plants by repeatedly fertile paired innovation. *Branches Radula*-type; microphyllous branches present, at each 1–2(–3) leaves on the main stem, regularly pinnate, 0.5–1.5 mm wide, 3–11 pairs of reduced leaf, unbranched. *Stems* 100–300 µm in diam., with thick-walled,

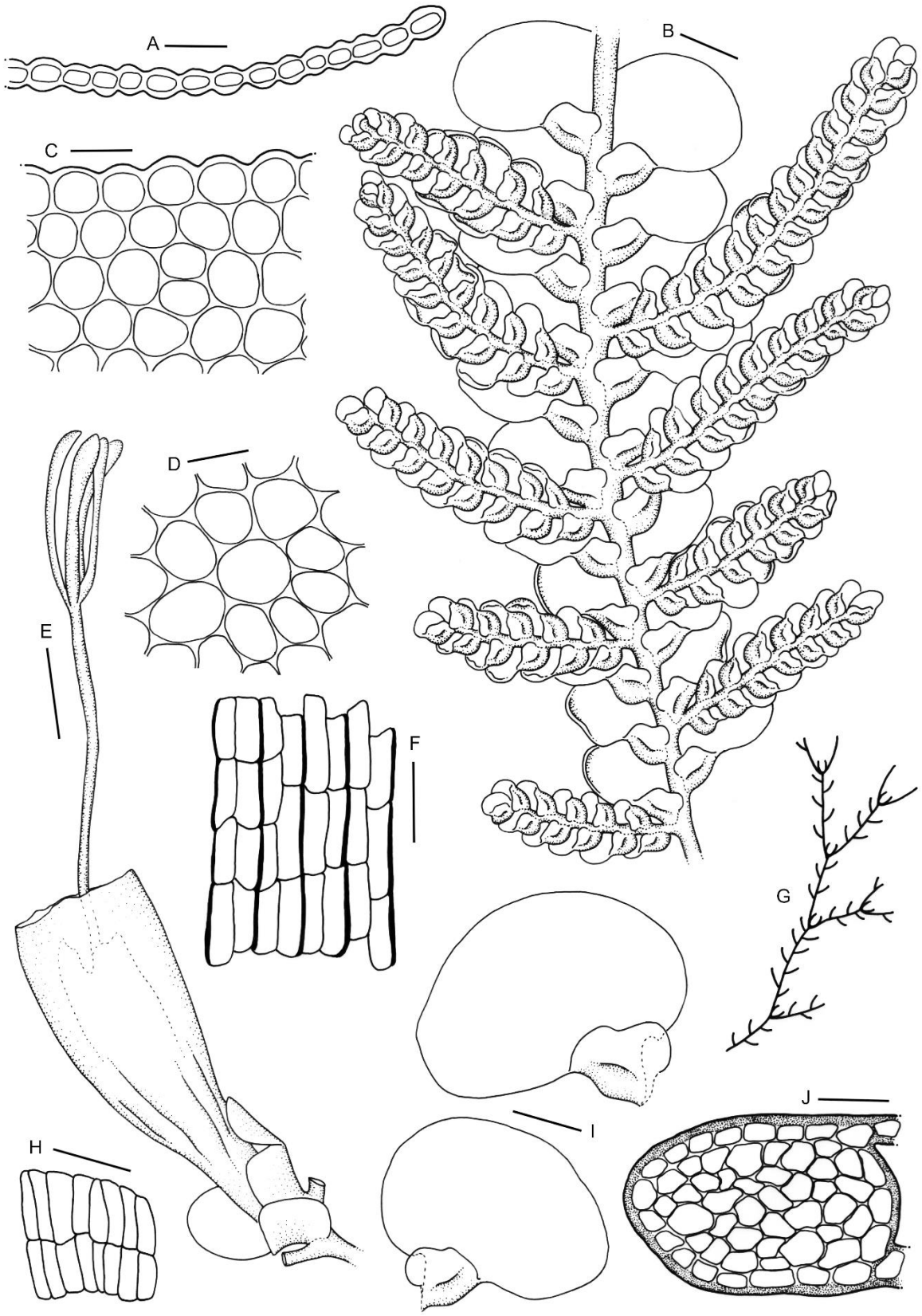

Figure 15. *Radula eggersii*. A. Cross section of leaf. B. Habit. C. Marginal leaf cells. D. Median leaf cells. E. Perianth with sporophyte. F. Outer cell layer of capsule wall. G. Cladograph of plants (U = gynoecia without perianth). H. Inner cell layer of capsule wall. I. Leaves. J. Cross section of stem (A, F, H, J = 50 µm, B, I = 500 µm, C, D = 25 µm, E = 1000 µm; All from the holotype).

brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, subimbricate, convex, ovate to oblong-ovate, 1.1–1.4 mm long, 0.7–1.3 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded to obtuse, margin plane to recurved, crenulate; marginal cells rounded to subquadrate, 10–15 × 12–20 μm, median and basal cells isodiametric to slightly elongate, 20–30 × 15–25 μm, leaf cells mammillose on ventral and dorsal surface, cell walls thin, trigones medium-sized, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.5–0.7 mm long, 0.2–0.5 mm wide, ca. 1/3 the lobe length, inflated along the keel, insertion ca. 1× the base length, insertion line curved, base plane, rounded, covering 1/2–2/3 the stem, free margin plane, almost straight to sinuouse, apex plane, rounded to obtuse, distal margin straight to rounded, keel straight, rarely convex, spreading at angles of 50–60º with the stem, 130–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long branches, with 2 innovations; bracts obong-ovate, 1.3–2 mm long, 0.9–1.2 mm wide, apex rounded, margin plane to recurved, crenulate, lobule oblong, 1/3–1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, trumpet-shaped, 3.2–6 mm long, 0.5–0.6 mm wide at base, 1.1–1.6 mm wide at middle, 1.5–1.7 mm wide at apex, mouth entire to slightly crenulate, plane; perianth wall 3–5-stratose in the lower base, 2–3-stratose from the upper base to the middle, unistratose at apex, with longitudinal striae from the upper base to the middle; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 5–8-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–3-layered at the base, 1 cell layer thick above. *Seta* 7–8 mm long. *Capsule* 1–1.8 mm long, 0.5–0.7 mm wide, valves ca. 2 mm long, ca. 0.2 mm wide at middle, outer layer cells subrectangular, irregular linear thickenings reddish-brown, running the entire length of the wall, on every second longitudinal wall, inner layer cells rectangular to long-rectangular, thickenings absent. *Elaters*, *Spores* and *Vegetative reproduction* not observed.

Distribution and habit. This species is only known from province of Loja (type locality, Yamada 1997) and Zamora-Chinchipe (Lüth & Schäfer-Verwimp 2004), southern Ecuador (Figure 16). *Radula eggersii* was collected growing on remnant trees in pasture and on branch of shrub in humid scrub, at 2780–3050 m.

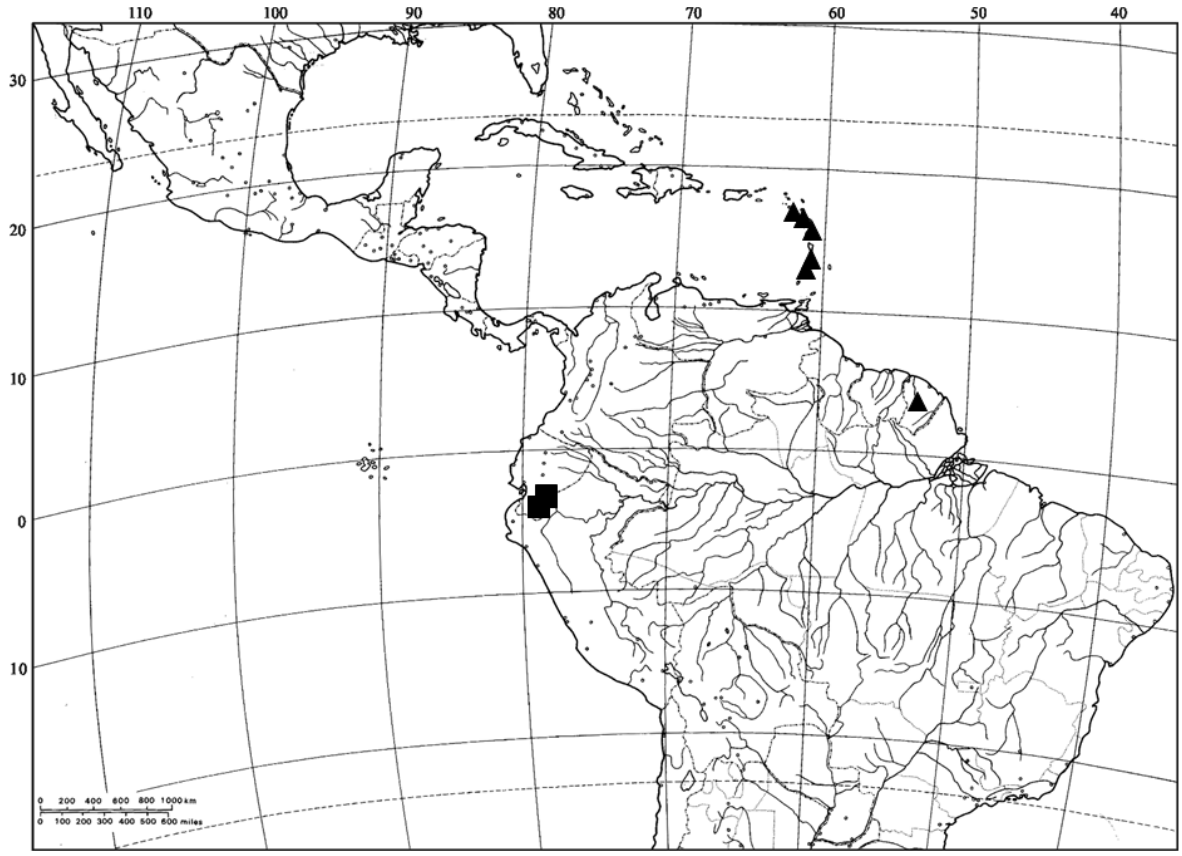

Figure 16. Distribution of *Radula eggersii* (black square) and *R. elliottii* (black triangle).

Specimens examined. ECUADOR. LOJA: The type of *Radula eggersii* (NICH).

The main diagnostic character of *Radula eggersii* (subg. *Volutoradula*) is the presence of reduced axes (microphyllous branches), which distinguishes it from all other species of the genus in tropical America. These branches are 3–4× smaller than the main stem and regularly pinnate, arranged very close to each other, with only 1–2(–3) leaves on the main stem between the side branches. The species also stands out by the leaf margin crenulate, presence of mammillose cells on ventral and dorsal leaf surface, leaf cell wall thin with medium-sized trigones, lobule subquadrate, inflated along the keel, lobule keel of the main stem straight to rarely convex, lobule keel of the branches strongly convex, and a long perianth, up to 6 mm long.

The mammillose leaf cells were not given due attention in the original description, yet are clearly visible, especially on recurved leaf margins on the branches.

Annother character that was incorrectly described was the capsule wall. Yamada (1997) described it as being thin with poorly developed thickenings, but we observed irregularly linear

thickenings on the outer cells, running along the entire length of the wall on every second longitudinal wall, and no thickenings on the inner cells.

9. Radula elliottii Castle, J. Hattori Bot. Lab. 21: 12. 1959. Type: Dominica, Morne Micotrin, 3500 m, 1896, *W. R. Elliott 1133*, as "*Radula pallens* Nees" (holotype, BM-000969198!, c. per. + andr.; isotype, JE-04003707!, c. andr.).

Radula varilobula Castle, J. Hattori Bot. Lab. 21: 19. 1959. Type: Dominica, windward slope of Morne Diablotin, on rock and trees, 25-3000 m, 17.3.1896, *W. R. Elliott 2151*, as "*Radula pallens*" (holotype, BM, not found; lectotype, YU-169881!, **designated here**, c. andr.), ***syn. nov.***

Dioicous. *Plants* 1.5–2.1 mm wide, to 3 cm long, green to yellowish-green in herbarium, purely dichotomous. *Branches Radula*-type. *Stems* 140–180 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous, rarely distant, convex, ovate, 0.8–1.2 mm long, 0.5–0.8 mm wide, dorsal base almost rounded, covering up to 1/4 the stem, dorsal margin rounded, ventral margin straight, apex rounded, margin plane, entire, rarely recurved; marginal cells subquadrate, 15–20 × 12–15 µm, median and basal cells isodiametric to elongate, 25–40 × 15–22 µm, cell walls thin at leaf base to middle becoming a little thick at the margin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.4–0.55 mm long, 0.3–0.4 mm wide, ca. 1/3 the lobe length, inflated along the keel, rarely in rhizoid area, insertion 2× the base length, insertion line curved, base plane, rounded, covering up to 1/4 the stem, free margin plane, straight, apex plane to slightly incurved, rounded, distal margin straight, keel convex, rarely almost straight, spreading at angles of 40–60º with the stem, 130–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* intercalary on long branches, with 3–5 pairs of bracts, 1.2–1.5 mm wide; bracts distant, ovate, 0.9–1 mm long, 0.4–0.6 mm wide, apex rounded, margin plane to recurved, entire, lobule distant to subimbricate, ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. *Gynoecia* on long branches, with 2 innovations; bracts ovate, 1–1.3 mm long, ca. 0.7 mm wide, apex rounded, margin plane, entire, lobule subquadrate, ca. 1/2 of lobe length, apex rounded, keel straight. *Perianth* erect,

subcylindrical, ca. 3.6 mm long, ca. 0.5 mm wide at base, ca. 0.8 mm wide at middle, ca. 1 mm wide at apex, mouth entire, plane; perianth unistratose. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Castle (1959).

Distribution and habit. St. Kitts (new record), Guadeloupe, Dominica, St. Vincent, St. Lucia, French Guiana (new record), Venezuela and Brazil (new record) (Castle 1959) (Figure 16). Records from Venezuela and Brazil were not included in the distribution map due to lack of information. *Radula elliottii* occurs on bark and rock in submontane and montane forests, at 500–3000 m.

Additional specimens examined. ST. KITTS. Without locality, 1841, *Breutel s.n.* (FH).

GUADELOUPE. In silvis montosis, *P. Duchassaing s.n.*, as "*R. pallens* sub. nomine *R. xalapensis*" (paratype of *Radula varilobula*, YU-24220).

DOMINICA. Windward slope of Morne Diablotin, on rock and trees, 2500-3000 m, 17 March 1896, *Elliott 2109* (paratype of *Radula varilobula*, YU-169882).

ST. LUCIA. Without locality and collector, June 1902, ex. hb. Mitten (paratype of *Radula varilobula*, YU-169883).

FRENCH GUIANA. SAÜL: ridge of Mont Galbao, mixed forest, on pole, 500 m, 23-30 June 1986, *Gradstein 6208* (GOET).

BRAZIL. Without locality, 1902, *P. Dusén s.n.* (JE).

Radula elliotti (subg. *Volutoradula*?) is characterized by purely dichotomous branching, leaf lobes convex, lobule base partially extending across the stem allowing the stem to be clearly visible, and lobule keel usually convex. According to Castle (1959), herbarium specimens of *R. elliottii* were often identified as *R. pallens*. The latter species is very similar to *R. elliotti*, but *R. pallens* has branching in part irregularly pinnate, leaf lobes rather plane, lobule base covering usually 1/2 of the stem (or more) and keel straight to concave. In addition, the stem of *Radula elliottii* is slightly thinner (140–180 μm) than that of *R. pallens* (180–280 μm).

In sect. *Dichotomae*, Castle (1959) described *Radula elliottii* and *R. varilobula* from Dominica based on a collection of W. R. Elliott. After careful examination of the types deposited in the Hampstead Castle herbarium (YU), *Radula elliottii* and *R. varilobula* proved to be conspecific. The specimen sequenced by Devos *et al.* (2011a) as *Radula varilobula* (*Hill*

21274, NY!) belongs to *R. javanica* and clustered with another specimen of *R. javanica* in the molecular tree.

10. Radula episcia Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 318. 1885. Type: Ecuador, "Hab. ad fluvium Pastasa Andium Quitensium, in rupibus umbrosis humectatis ad fl. Verde ostia," 1400 m, *R. Spruce s.n.* (lectotype, MANCH-13579!, **designated here**; isolectotypes, BM-000969199!, BM-000969200!, NY-01021082!). Ecuador, "in spelunca Sicsihuaíco dicta," 1800 m, *R. Spruce s.n.* (synnot found).

Radula antilleana Castle, J. Hattori Bot. Lab. 21: 48. 1959. Type: Puerto Rico, Monte Montoso, on rock, 13 February 1915, *N. L. Britton & J. F. Cowell 4166* (lectotype, YU-242211!, **designated here**, c. per. + spor.), syn. fide Gradstein (2021).

Radula cornucopiae Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 318. 1885. Type: Ecuador, "in montis Chimborazo devexis sylvaticis, 1200 m, e ramulis pendula," *R. Spruce s.n.* (lectotype, MANCH-11952!, **designated here**, c. per.; isolectotypes, MANCH-11951!, MANCH-11947!, YU-169865!, slide, c. per.), syn. fide Yamada & Gradstein (1991).

Radula opaciuscula (Spruce) Castle, J. Hattori Bot. Lab. 21: 22. 1959. *Radula episcia* var. *opaciuscula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 319. 1885. Type: Peru, Mt. Campana, *R. Spruce s.n.* (holotype, MANCH-13578!), syn. fide Gradstein (2021).

Radula paganii Castle, J. Hattori Bot. Lab. 21: 33. 1959. Type: Puerto Rico, on rock and living trees, Mt. Guilarte, Adjuntas, 3690 m, 8 August 1937, *F. M. Pagán 440* (holotype, YU-241478!, c. andr. + per.), ***syn. nov***.

Dioicous. *Plants* 2.3–4 mm wide, to 5 cm long, olive-green, yellowish to brown in herbarium, purely dichotomous. *Branches Radula*-type, sometimes *Lejeunea*-type on decapitated shoots. *Stems* 180–350 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, rarely subimbricate, slightly convex, orbicular, 1.2–1.7 mm long, 1–1.8 mm wide, dorsal base rounded, covering ca. 1/2 the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margin plane to slightly incurved, entire, rarely crenulate; marginal cells subquadrate, 10–12 × 8–10 μm, median and basal cells isodiametric to elongate, 20–30 × 15–20 μm, cell walls thin, trigones small to lacking, intermediate

thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical to ellipsoidal, light yellow, smooth, 10–15 × 7–10 µm. *Lobules* distant, rectangular to oblong-rectangular, 0.1–0.4 mm long, 0.6–1.1 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area or not, insertion 5–6× the base length, insertion line straight, base plane, rounded, covering 1/5–2/3 the stem, free margin plane, rounded, apex plane to incurved, rounded, distal margin straight, keel straight to almost concave, spreading at angles of 30–50º with the stem, 120–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 5–10 pairs of bracts, 1–1.4 mm wide; bracts distant to subimbricate, ovate, 0.7–0.9 mm long, 0.3–0.5 mm wide, apex rounded, margin plane to recurved, entire, lobule contiguous to subimbricate, ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin almost straight, apex rounded. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.9–1.2 mm long, 0.5–0.9 mm wide, apex rounded, margin plane, entire, lobule oblong, 1/2–1/3 of lobe length, apex rounded. *Perianth* erect or falcate, trumpet-shaped or campanulate, 3.4–4.5 mm long, 0.3–0.6 mm wide at base, ca. 0.8 mm wide at middle, 1–1.2 mm wide at apex, mouth entire, plane to strongly undulate; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall unistratose. *Seta* 4.5–5.5 mm long. *Capsule* ca. 1.8 mm long, ca. 0.4 mm wide, valves 1.6–2 mm long, 0.2–0.35 mm wide at middle, with 2 layers of cells, outer layer cells subquadrate to polygonal, nodular thickenings reddish-brown, on every longitudinal wall, inner layer cells polymorphous, confluent thickening on the walls. *Elaters* 200–350 µm long, rough. *Spores* 18.51–24.07 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* rarely by regenerants.

Illustration. Reiner-Drehwald (1994)

Distribution and habit. Widespread in tropical America; newly recorded here from southern Brazil (Figure 17). *Radula episcia* grows loosely creeping or pendent on horizontal or vertical surfaces of wet rock or on bark, rarely on soil, rotten logs and leaves of vascular plants. The species is commonly found in shaded places, with few records from exposed sites, in lowland, montane and subalpine forests, 100–3690 m.

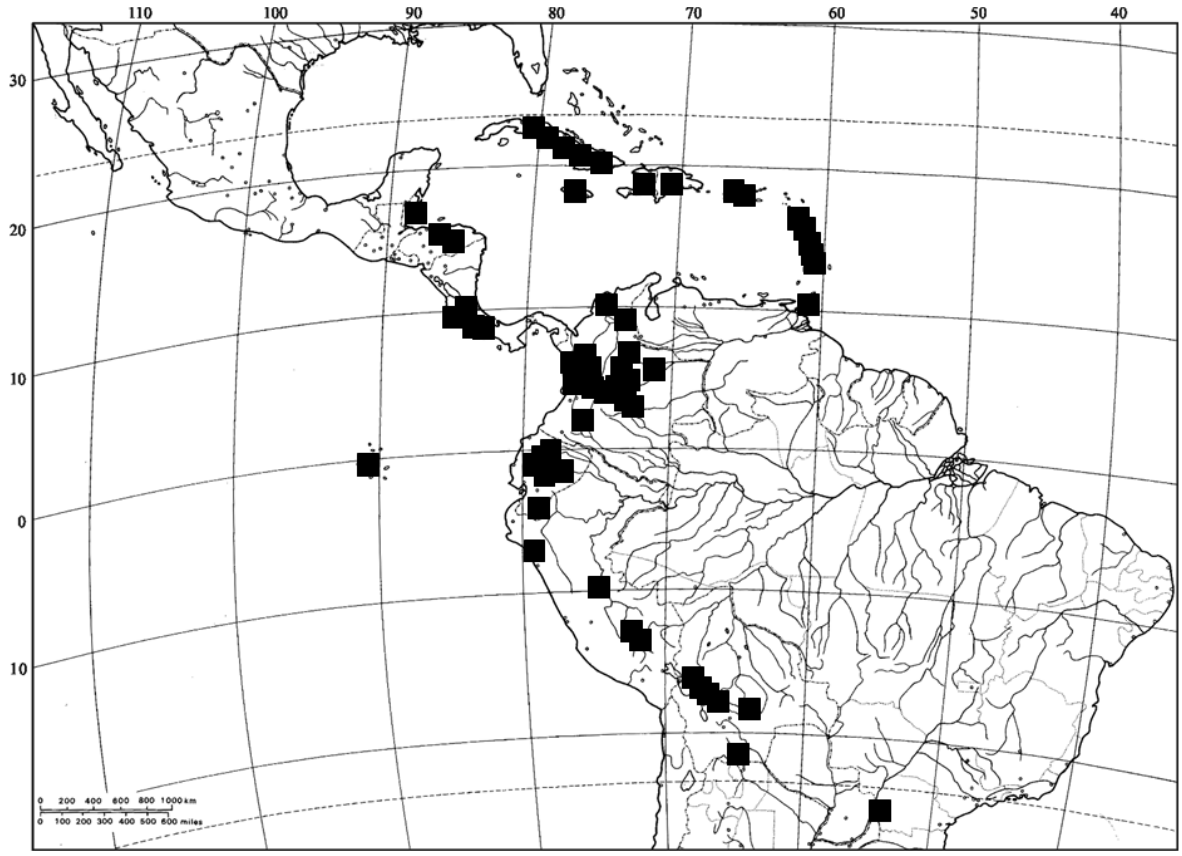

Figure 17. Distribution of *Radula episcia.*

Additional examined specimens. BELIZE. TOLEDO: Columbia River Forest Reserve, on limestone outcrop in sink, 16°22'N, 89°07'W, 700 m, 13 February 1997, *Allen 18680* (MO).

HONDURAS. OLANCHO: Sierra de Algalta, La Chorrera, Rio Lara below Montana Babilonia, on rock face by waterfall, 14°59'N, 85°56'W, 1100-1800 m, 30 May 1992, *Allen 12578* (MO). **YORO:** Cordilera Nombre de Dios, ridge between Rio Guán and Quebrada, on boulder in forest, 15°30'N, 87°28'W, 100-300 m, 4 March 1993, *Allen 13492* (MO); Ibid., on boulder at edge of stream, 6 March 1993, *Allen 13671* (MO).

COSTA RICA. ALAJUELA: Río Cuarto, R.V.S. Bosque Alegre, Laguna Hule, area de bosque alterado, sobre tronco expuesto, 10°17'N, 84°12'W, 700 m, 12 January 1996, *Dauphin 2117* (MO). **GUANACASTE:** Monteverde Biological Preserve, epiphyll, 10°15'N, 84°45'W, 5 August 1993, *Timme 11396* (MO). Santa Elena Biological Preserve, on tree trunk, 10°15'N, 84°45'W, 4 August 1993, *Timme 11345a* (MO). **PUNTARENAS:** Reserva Biologica Monteverde, undisturbed cloud forest, on bark, 1550 m, 9 November 1993, *Gradstein 9448* (GOET). Monteverde Cloud Forest Preserve, TSC Reserch area, pacific slope, pre-montane wet forest, on branches, 10°18'N, 84°48'W, 1500 m, 21 March 1992, *Lyon 404* (MO). Monteverde pacific slope, on trail from ridge NE of entrance to Monteverde Cloud Forest

Reseve, 10°18'N, 84°48'W, 1500 m, 24 February 1992, *Lyon 2* (MO). Pittier, Cerro Paraguas, San Vito, Fila Cruces, bosque primário alterado en ladera y bordes de camino, sobre talud pedregoso a la sombra, 08°57'00"N, 83°04'20"W, 1410-1520 m, 10 June 1994, *Dauphin 1795* (MO).

BERMUDA. Without locality, 1873, *Moseley JE-H1366* (JE).

CUBA. Without locality, 1863, *Wright s.n.* (JE).

JAMAICA. Without locality, s.d., *unknown collector*, ex hb. Richard in PC (YU). **PARISH ST. THOMAS:** zwischen Portland Gap und Blue Mountain Peak, 1700-1850 m, 31 October 1973, *Hegewald 8020* (MO).

PUERTO RICO. Shaded vertical rock , just below summit of La Torrecilla, NW of Barranquitas, 27 October 1939, *Steere 4536* (JE). Canóvanas, Torito Mt., Cubuy Bo., on living tree, 2600 m, July 22, 1937, *Pagán 264a, 268,* (YU). Ibid., on moist shady rock , *Pagán 269, 280* (YU). Mount Morales, near Utuado, near summit, March 15, 1906, *Howe 811, 1116* (YU).

ST. KITTS. Without locality, s.d., *unknown collector*, as *R. pallens*, ex hb. Bossier in G (YU).

GUADELOUPE. Lesser Antilles, s.d., *l'Herminier JE-H1364* (JE). Without locality, s.d., *l'Herminier s.n.*, as *R. pallens*, ex hb. PC (YU), ex hb. Spruce in MANCH (YU).

DOMINICA. Morne Micotrin, on trees, 2000-4000 m, 1892, *Elliott 69, 99* (YU). On fern leaf, windward slope Diablotin, 2000-2500 m, 1896, *Elliott 2164* (YU). Mountain lake, *Armitage s.n.* (YU).

MARTINIQUE. Without locality, s.d, *Belanger 863* (YU). Without locality, s.d, *l'Herminier s.n.* (YU). Mt. Pelée, on trees, August-September 1901, *Duss 613* (YU).

ST. VICENT. Without locality, s.d., *unknown collector*, as *Jung. pallens*, ex hb. Kew (YU-167860, YU-167861). Common on mountain tops, inter allis muscos, 2500-3300 m, *H. H. Smith 1384*, as *R. pallens*, ex. hb. K (YU).

COLOMBIA. ANTIOQUIA: 9.5 km E de Sonsón, sobre carretera a Argelia/Nariño, bosque pluvial montano, 05°40'N, 75°17'W, 2660 m, 22 June 1985, *Churchill & Sastre-de-Jesus 12929* (MO). **RISARALDA:** West side of Cordillera Occidental, above the village of Jeguadas, W of Mistrato, submontane relatively open rainforest on steep slope with low cover of dry adapted species, on shaded rock, 800 m, 29 July 1992, *Gradstein 8607* (GOET). **CUDINAMARCA:** San Antonio de Tena, Parque Montanes de Chicaque, on base of shaded rock in secondary forest, 2200 m, 28 May 1991, *Linares & Gradstein 3523* (GOET).

ECUADOR. Confluence of River Toachi and Piloton, on branch, 3000 m, 4 April 1951, *Bell 328A* (BM). **GALÁPAGOS ISLAND:** San Cristobal, gorge west of El Junco, on shaded,

humose soil under treeferns, 21 May 1976, *Gradstein & Lanier H269* (MG, MO). **IMBABURA:** Cotacachi, Intag, comuna Santa Rosa de Pucura, Reserva Intag, Bosque Montano no intervenido, sendero ecológico, sobre corteza, tronco caído, 00°22'S, 78°28'W, 2200 m, 7 March 2002, *Caranqui 945* (MO). **LOS RIOS:** Hacienda La Clementina, virgin forest, 750 m, 24 March 1947, *Harling 2162/d, 2133/a, 2145/d* (JE). **PICHINCHA:** Los Bancos, Mindo, Centro de Educación Ambiental, boque maduro montano bajo, caminho al bosque protector, sobre ramas de arbusto, pendiente, mucha luz, 00°00'S, 78°45'W, 1680 m, 7 August 2000, *Toapanta & Quishpe 669* (MO).

PERU. CUZCO: Madre de Dios, October 1893, *Jay 66* (YU). Torontoy, Urubamba Valley, 2400 m, 5 June 1915, *Cook & Gilbert 1105* (YU). **LORETO:** Panguana am Rio Yuyapichis, 9°37'S, 74°56'W, 260 m, 1978, *Schlüter 257* (MO).

BRAZIL. PARANÁ: Iguazú, in den feuchten, Schludhten des National Park des Río Iguazú im Urwald, epiph., 16 July 1933, *Hosseus 77* (JE).

BOLIVIA. PADCAYA: Cantón Emborozú, Reserva Natural Alarachi, Zona Cayotal, río Emborozú Chico, bosque premontano Tucumano-Boliviano, sobre roca vertical, poco sol, 22°14'18"S, 64°34'19"W, 1220 m, 21 september 2004, *Churchill 23450* (JE). **LA PAZ:** Nor Yungas, Parque Nacional Cotapata, Estación Biológica Tunquini, a lo largo del río, Stamm, 16°11'44" S, 67°52'03" W, 1553 m, 20 August 2001, *Drehwald & Drehwald 10386* (GOET); Ibid., auf Fels, aromatischer Geruch, *Drehwald & Drehwald 10299* (GOET). Franz Tamayo, Parque Nacional Madidi, Río Mojos, bosque de Yungas subandino superior, estacional, humedo, en pared rocosa, 14°33'27"S, 68°49'57"W, 1500 m, 5 July 2005, *Fuentes et al. 9743* (MO). Franz Tamayo, Parque Nacional Madidi, sector Coranara, al lado del Río Pelechuco, mancha de bosque montano inferior estacional primário, 14°46'21"S, 68°59'11"W, 2290 m, *Fuentes & Huaylla 13123A* (MO). Franz Tamayo, Parque Nacional Madidi, entre Virgen del Rosario y Pata, bosques ralos de cerrado y bosque semideciduo hacia los falderios, sobre substrato arenoso, 14°36'48"S, 68°40'59"W, 1000-1300 m, *Fuentes & Cuevas 6243* (MO). Franz Tamayo, Parque Nacional Madidi, Chiriuno, bosque montano húmedo com Podocarpus, 14°30'00"S, 68°13'58"W, 1850 m, 1 July 2002, *Fuentes 4958* (MO). Franz Tamayo, Santo Domingo, sector cabeceras Arroyo Tintaya, bosque de Yungas basimontano pluvial, sobre fuste de arbolito, 14°46'24"S, 68°35'16"W, 1450 m, 25 October 2006, *Fuentes et al. 11299* (MO). **SANTA CRUZ:** Florida, Samaipata, bosque montano de Tucumano-Boliviano, poco seco, sobre roca vertical em la sombra, 18°15'45"S, 63°39'59"W, 1450-1550 m, 11 December 2004, *Churchill et al. 23708* (MO).

Radula episcia (subg. *Volutoradula*) is distinguished by sparsely and purely dichotomously branching, leaf lobes distant to contiguous and orbicular, lobules rectangular to oblong-rectangular (being wider than long), base of lobule variable in width but usually covering only 1/4 the stem (rarely to 2/3), and insertion line long, 5–6× base length.

The species is often confused with the common Neotropical *Radula pallens*, but the latter has suborbicular leaf lobes with ventral margins usually straight, and subquadrate lobules with an insertion line 1–3× the base length. *Radula episcia* also shares similarities with the recently described *R. smithii*, but the latter has leaf lobes bordered by 3–5 rows of cells differentiated in size, shape and color, and subquadrate lobules. *Radula episcia*, *R. pallens* and *R. smithii* can occur together.

The lobe shape of *R. episcia* is also seen in *R. underwoodii*, but the latter has very distant and usually obliquely spreading leaves, and leaf lobes oblong-ovate.

Radula paganii is a new synonym of *R. episcia*. Castle (1959) compared *Radula paganii* with *R. cornucopiae* (=*R. episcia*), but except for plant length, the species are fully identical.

Gradstein (2021) synonymized *Radula antilleana* with *R. episcia* based on the description and illustration of Castle (1959). The lectotype of *R. antilleana* is indeed identical to *R. episcia*, but many of the paratypes cited by Castle (1959) belong to *R. pallens*. In the original description of *Radula antilleana*, Castle (1959) indicated that the type was deposited in NY and YU, without designating a holotype. As no type specimen was found in NY, the type material in YU is here designated here as the lectotype.

11. Radula fendleri Steph. var. **fendleri**, Hedwigia 23: 146. 1884. Type: Venezuela, Valencia, "in cortice repens," *A. Fendler s.n.* (lectotype, G-00121978!, **designated here**; isolectotypes, G-00282114, BM-000969201!, FH!). Guadeloupe, *l'Herminier s.n.*, ex hb. Gottsche (syntypes, G-00281263!, G-00281262, BM-000969203!, BM-00096202!).

Radula gracilis Steph., Hedwigia 23: 147. 1884. Type: Colombia, Andes bogotensis, *J. Weir s.n.* ["Weverley"] (lectotype, NY-01021112!, designated by Castle, 1967: 20; isolectotype, G-00042688!), ***syn. nov.***

Dioicous. *Plants* 1–1.8 mm wide, to 1 cm long, light green to olive green in field, light green to brownish in herbarium, irregularly pinnate. *Branches Radula*-type. *Stems* 70–110 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls

brownish. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate to falcate-ovate, 0.7–1 mm long, 0.5–0.7 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margin strongly recurved, entire; marginal cells subquadrate, 5–15 μm in diam., median and basal cells isodiametric, 20–25 × 15–20 μm, cell walls thin, trigones large, intermediate thickening rare, cuticle smooth to verruculose; oil bodies not observed. *Lobules* distant, subrectangular, 0.3–0.5 mm long, 0.1–0.25 mm wide, ca. 1/2 the lobe length, inflated along the keel, insertion 2× the base length, insertion line slightly arched, base plane, rounded, covering 1/3(–1/2) the stem, free margin plane, straight, apex plane, rounded, rarely obtuse, distal margin straight, keel convex, spreading at angles of 50–60º with the stem, 130–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on short branches, with 2–5 pairs of bracts, 0.8–0.9 mm wide; bracts subimbricate, ovate, 0.4–0.6 mm long, 0.2–0.3 mm wide, apex rounded, margin strongly recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin straight, apex rounded to obtuse. *Gynoecia* on long branches, with 2 innovations, innovations sometimes rudimentary; bracts ovate, 0.7–0.9 mm long, 0.4–0.5 mm wide, apex rounded, margin recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex obtuse. *Perianth* erect, subcylindrical, 1.4–2.2 mm long, 0.3–0.4 mm wide at base, 0.7–0.8 mm wide at middle, 0.7–1 mm wide at apex, mouth entire, plane to undulate; perianth wall 2–4-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base; perianth-calyptra not fusion. *Calyptra* wall unistratose. *Sporophyte* not observed. *Vegetative reproduction* by caducous leaf lobes, often with regenerants on the margins of caducous leaves.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Tropical America. Besides the countries listed in the specimens examined section, *Radula fendleri* var. *fendleri* was additionally reported for Martinique and Suriname by Castle (1963), from Cuba by Yamada (1988) (Figure 18), and from Hawaii and Java by Stephani in his *Icones Hepaticarum* (So 2005). The latter two are considered doubtful records and need verification. The species usually grows on bark, rarely on soil, in montane forests, 450–2400 m. *Radula fendleri* var. *fendleri* is more common in the Atlantic Coastal Region of Brazil, where it can be collected in different environments, including “campos de altitude”, dense ombrophilous forests, *Araucaria* forests and seasonal montane forests. The species forms small, dense, prostrate mats on vertical surfaces.

Additional specimens examined. NICARAGUA. JINOTEGA: Macizos de Peñas Blancas, top and N slope of steep ridge SW of finca of Manuel Estrada (El Cielo), S of Río Gusaneras, cloud forest on steep slope, relatively dry, 13°15'N, 85°42'W, 1200-1330 m, 16 January 1979, *Stevens 11626 p.p.* (MO).

GUADELOUPE. The Type of *R. fendleri* (G).

FRENCH GUIANA. SAÜL: 8.5 km nord de Saut Mais, epiphyte sur arbre em sous bois, 18 January 1980, unknown collector (GOET).

VENEZUELA. The Type of *R. fendleri* (G, FH).

COLOMBIA. The Type of *R. gracilis* (G).

ECUADOR. SUCUMBÍOS: Cantón Gonzalo Pizarro, 3.3 km N of Puerto Libre, little disturbed, premontane forest, corticolous, 0°13'22.71"N, 29°17'17.29"W, 760 m, 10 October 2013, *Burghardt et al. MB8363* (JE).

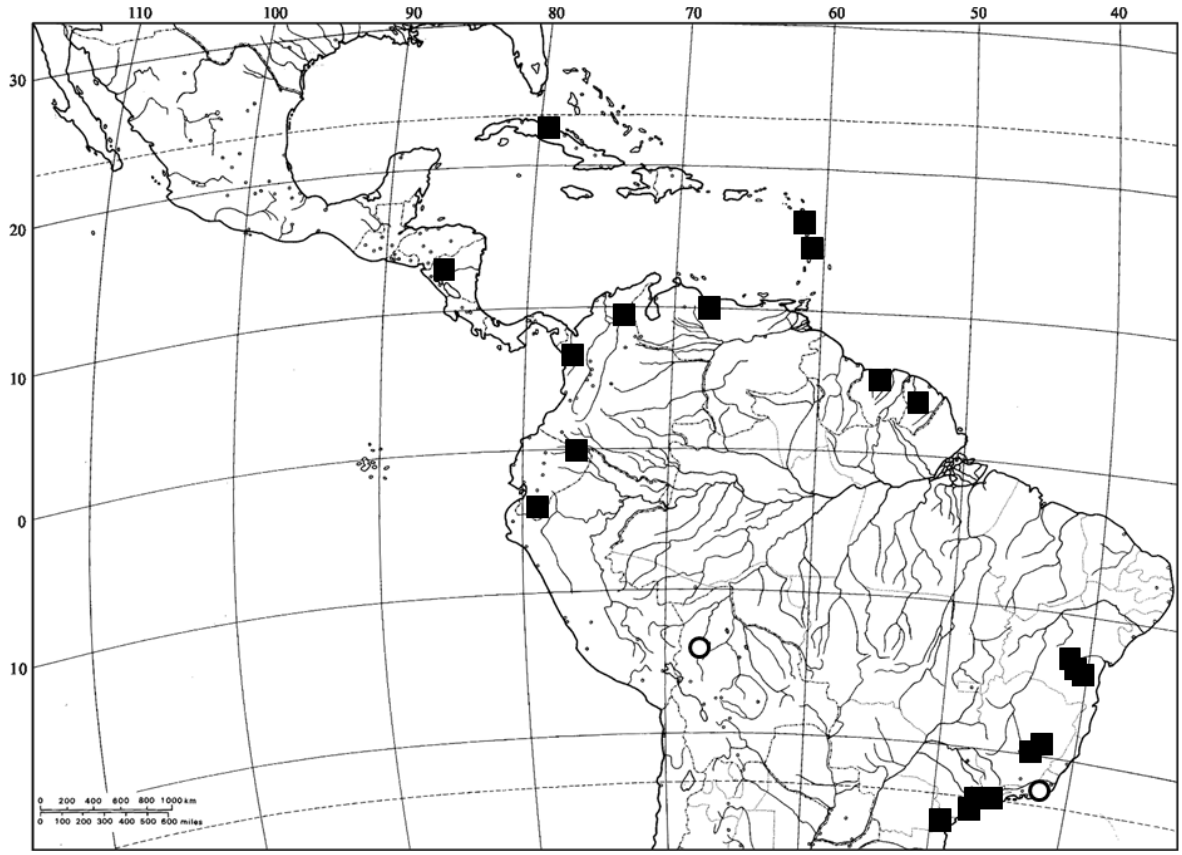

Figure 18. Distribution of *Radula fendleri var. fendleri* (black square) and *R. fendleri var. paroica* (white circle).

BRAZIL. BAHIA: Abaíra, Campo de Ouro Fino (baixo), 13°15'N, 41°54'W, 1600–1700 m, 18 January 1992, *Hind & Queiroz 50091* (SP). Abaíra, Catolés, Serra do Barbado, Mata da

Forquilha, floresta estacional Montana, corticícola na borda da mata, 13°17’27” S, 41°54’0,15”W, 1594 m, 5 September 2008, *Bastos 5162, 5156, 5146* (ALCB); Ibid., *Vilas Bôas-Bastos 2377, 2371* (ALCB). Santa Teresinha, Povoado de Pedra Branca, Serra da Jibóia, Morro da Pioneira, em floresta ombrófila, corticícola, 12°51’20,8” S, 39°28’32,1” W, 800 m, 17 September 2015, *Rodrigues 166* (ALCB). **MINAS GERAIS:** Nova Lima, Reserva Particular do Patrimônio Natural Parque Natural do Caraça, Trilha do Belchior, 20°05’43”S, 43°29’27”W, 1270 m, 27 July 2010, *Peralta & Marcelli 11777* (SP). Santa Bárbara, Parque Natural do Caraça, sobre tronco de arbusto na trilha, 1270 m, 4 December 1993, *Yano et al. 21924* (SP). Itamonte, sobre tronco vivo, 22°21’ S, 44°48’ W, 20 May 1988, *Vital 15871* (SP). Lima Duarte, Parque Estadual do Ibitipoca, em tronco de árvore, 21°43’32” S, 43°52’35” W, 27 August 1987, *Sousa s.n.* (SP). **PARANÁ:** Morretes, Parque Estadual Pico do Marumbi, Mata Atlântica, 25°26’09”S, 48°55’03”W, 450 m, 17 June 2015, *Peralta et al. 17837* (SP). **RIO GRANDE DO SUL:** Planalto, Parque Florestal Estadual de Nonoai, 2 May 1996, *Lemos-Michel 3490* (SP). **SÃO PAULO:** Moji das Cruzes, Parque Municipal da Serra de Itapety, Mata Atlântica, 23°31’22”S, 46°11’18”W, 742 m, 25 August 2005, *Yano et al. 28409* (SP). Distrito de Palheiros, estrada Tadão Inoue, base do tronco de árvore, 16 October 2007, *Yano & Kanashiro 30191* (SP). São Luiz do Paraitinga, Parque Estadual Serra do Mar, Núcleo Santa Virgínia, sobre tronco vivo, 23°20’45” S, 45°07’47” W, 956 m, 17 April 2013, *Peralta & Gugliota 13555, 13602* (SP). Natividade da Serra, Bairro Vargem Grande, Parque Estadual da Serra do Mar, Núcleo Santa Virgini, Trilha do Pico do Corcovado, Mata Atlântica com mata Nebular, sobre tronco vivo, 23°26’50” S, 45°11’30” W, 1100 m, *Peralta et al. 9225* (SP). Piquete, trilha de acesso ao Pico dos Marins, vegetação de mata nebular e campo de altitude, sobre barranco, 22°36’50” S, 45°10’33” W, 2000-2400 m, 24 October 2008, *Peralta & Barros 7069* (SP). Campos do Jordão, Parque Estadual Campos do Jordão, mata ombrófila mista com Araucária, corticícola, 22°42’25” S, 47°27’59” W, 1670 m, 1 October 2017, *Amélio 406* (SP).

Radula fendleri var. *fendleri* (subg. *Radula*) is recognized by the small plants with strongly convex and occasionally caducous leaf lobes, usually recurved leaf margins, leaf cells with large trigones and finely verruculose cuticle (rarely smooth), and lobules subrectangular (longer than wide), inflated along the keel. The species resembles the Amazonian endemic *R. pseudostachya*, but the latter has lobules contiguous to subimbricate with the base covering 1/2 to fully overlapping the stem, and profusely caducous leaf lobes, leaving the branches almost completely denuded. *Radula fendleri* var. *fendleri*, instead, produces only few caducous leaf lobes.

Gradstein (2021) synonymized *Radula gracilis* under *R. javanica*. However, examination of the type revealed that *R. gracilis* is conspecific with *R. fendleri* var. *fendleri*; both have subrectangular lobules (longer than wide), leaf lobes strongly convex and leaf cells with large trigonen, while *R. javanica* has subquadrate lobules, leaf lobes plane to slightly convex and leaf cells without trigones. There has been some confusion about the type citation of *R. gracilis*. Castle (1967, p. 20-21) concluded that it should be "Colombia, Andes Bogotensis, *Weverley s.n.*" although the label of the type mentions 'Aries Bogoh, *Weir s.n.*', and designated material in the Mitten herbarium as the lectotype (NY-01021112!). So (2005, p. 185-187), however, considered a specimen in the Stephani's herbarium (G-00042688!) labeled "Aries Bogoh, *leg. Weverley*" as the holotype but cited it as "Patria ignota [Hawaii]. *Weverley s.n.*", since Stephani illustrated material from Hawaii and Indonesia (Java) in his *Icones Hepaticarum*. Since Mitten and Stephani described many species of bryophytes based on collections made by John Weir in "Andes Bogotensis", we consider that the type collection of *R. fendleri* var. *fendleri* is from Colombia, being collected by Weir. Material from Hawaii and Java has not been seen and these records are considered doubtful.

12. Radula fendleri var. **paroica** F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., Phytotaxa 454(1): 29. 2020. Type: Brazil, Rio de Janeiro, Nova Friburgo, "Estrada para Teresópolis, sobre pau podre na capoeira," 6 May 1927, *M. C. Vaughan Bandeira s.n.* (holotype, RB-99454!).

Monoicous. *Plants* 1–1.8 mm wide, to 1 cm long, brown in herbarium, irregularly pinnate. *Branches Radula*-type. *Stems* ca. 100 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls brownish. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate to falcate-ovate, 0.6–0.8 mm long, 0.5–0.6 mm wide, dorsal base rounded, covering the entire stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margin strongly recurved, entire; marginal cells subquadrate, 7–10 µm in diam., median and basal cells isodiametric to elongate, 15–25 × 10–15 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle verruculose; oil bodies not observed. *Lobules* distant, subrectangular, 0.3–0.5 mm long, 0.1–0.3 mm wide, ca. 1/2 the lobe-length, strongly inflated along the keel, insertion 1× the base length, insertion line slightly curved, base plane, rounded, covering 1/3(–1/2) the stem, free margin plane, almost straight, apex plane, rounded, rarely obtuse, distal margin straight, keel straight, spreading at angles of 45–60º with the stem, 110–150º with the ventral leaf lobe margin, at its junction with the lobule.

Rhizoids colorless, scanty, present on a few lobules. *Androecia* terminal or preceding the gynoecia, on short branches, with 1–3 pairs of bracts, 0.55–1 mm wide; bracts ovate, 0.45–0.75 mm long, 0.2–0.4 mm wide, apex rounded, margin strongly recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin ± straight, apex rounded to obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.75–1 mm long, 0.55–0.6 mm wide, apex rounded, margin recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex obtuse, keel straight to concave. *Perianth* erect, subcylindrical, 1.8–2.2 mm long, 0.3–0.4 mm wide at base, 0.6–0.8 mm wide at middle, 0.65–0.9 mm wide at apex, mouth entire, plane; perianth wall not observed. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Brazil and a new record for Bolivia (Figure 18). *Radula fendleri* var. *paroica* grows on dead trees, in humid submontane forest, 846–1850 m.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: the type.

BOLIVIA. LA PAZ: Franz Tamayo, Parque Nacional Madidi, Chiriuno, bosque montano húmedo com Podocarpus, 14°30’00”S, 68°13’58”W, 1850 m, 1 July 2002, *Fuentes 4958* (MO).

Radula fendleri var *paroica* differs from the typical variety by monoicous sexuality (dioicous in var. *fendleri*), leaf cells without or with small trigones (large trigones in var. *fendleri*) and absence of caducous leaf lobes (present in var. *fendleri*).

13. Radula flaccida Lindenb. & Gottsche, Syn. Hepat. 726. 1847. Type: Mexico, “Prope Hacienda de Fovo foliis Psychotriae cuiusdam arctissime irrepens,” *F. M. Liebmann s.n.* (lectotype, BM-000969204!, c. andr., selected by Oliveira-da-Silva *et al.*, 2021: 94; isolectotypes, S-B43094!, S-B43089!).

Radula flaccida var. *brachycalyx* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 321. 1885. Type: Silva Amazonica, Rio Negro, *R. Spruce 1442* (lectotype, MANCH-13590!, **designated here**; isolectotype, MANCH-13591!). Silva Amazonica, Rio Negro, *R. Spruce 1448* (syntype, MANCH-13595!), ***syn. nov.***

Radula flaccida var. *propagulifera* Gottsche, Mexik. Leverm. 148: 244. 1863. Type: Mexico, "i Naerheden af Santa Maria Tlapacoyo i Departementa Vera Cruz i Skovene paa Hacienda de Jovo (2000') paa et Psychotria-Blad," *F. M. Liebmann 533* (not found), ***syn. nov.***

Dioicous. *Plants* 1–1.5 mm wide, to 2 cm long, light green in field, yellowish-green, green or olive green in herbarium, irregularly 1–2-pinnate, sometimes dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type. *Stems* 50–60 µm in diam., with thin-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish. *Leaf lobes* obliquely to widely spreading, contiguous to subimbricate, plane to slightly convex, ovate to suborbicular, 0.6–0.8(–0.9) mm long, 0.3–0.6 mm wide, dorsal base rounded, covering up to 1/3 the stem, dorsal margin rounded, ventral margin straight to rounded, apex rounded, margin plane, entire to strongly crenulate on dorsal margin when with gemmae; marginal cells subquadrate, 5–12 µm in diam., median and basal cells isodiametric to elongate, 25–38 × 12–25 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate to subrhombic, 0.15–0.3(–0.4) mm long, 0.1–0.2 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion 1–2× the base length, insertion line almost straight, base plane, rounded, covering 1/5–1/4 the stem, free margin plane, straight to sinuose, apex plane, usually extended towards an obtuse tip, distal margin almost straight, keel convex, rarely straight, spreading at angles of ca. 60º with the stem, 130–170º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, numerous on a pronounced mammiliform swelling, present on numerous lobules. *Androecia* intercalary to usually terminal on long branches, with 5–12 pairs of bracts, 0.3–0.4 mm wide; bracts imbricate, ovate, 0.25–0.35 mm long, 0.1–0.25 mm wide, apex rounded, margin recurved, entire, lobule ovate, ca. 3/4 of lobe length, base slightly rounded to straight, free margin straight, apex rounded to obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 0.5–0.6 mm long, 0.15–0.2 mm wide, apex rounded to obtuse, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, trumpet-shaped, sometimes strongly inflated at middle, 2–2.5 mm long, 0.1–0.2 mm wide at base, 0.3–0.4 mm wide at middle, 0.3–0.6 mm wide at apex, mouth plane, entire to irregularly undulate; perianth wall 2–3-stratose at base, unistratose from the middle to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–5-layered tube (perigynium) within which the sporophyte foot and part of the Seta is

embedded. *Calyptra* wall 1–2-layered at the base, unistratose above. *Seta* 3.5–4.6 mm long. *Capsule* 0.5–0.7 mm long, ca. 0.2 mm wide, valves 0.7–1 mm long, 0.07–0.1 mm wide at middle, outer layer cells subrectangular, irregular linear thickenings reddish-brown, running the entire length of the wall, on every second longitudinal wall, inner layer cells rectangular to long-rectangular, thickenings absent, rarely faint on some walls. *Elaters* 100–200 µm long, rough. *Spores* 16.16–25.92 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by caducous *Lejeunea*-type branches and by large discoid gemmae, produced on dorsal leaf margins, 1–3 per leaf, 350–450 µm in diam., base of gemmae deeply cordate-auriculate, opposite auricles touching to overlapping each other.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Widespread in tropical Africa and tropical America. In addition to the countries of tropical America listed in the additional examined specimens section, *Radula flaccida* has been reported from the United States (Flórida), Guatemala, Costa Rica, Puerto Rico, Dominica, Colombia and Peru (see Castle 1939, Dauphin 2005, Graham *et al.* 2016, Gradstein 2021) (Figure 19). The species usually grows on leaves of vascular plants, sometimes on bark, rarely on rotten logs and rock (*Bastos 4108*, ALCB), in humid lowland and submontane forests, rarely in montane forest, from sea level to 1000 m. The species forms small to large, flat, prostrate and sometimes rounded mats.

Additional specimens examined. MEXICO. The Type of *R. flaccida* (BM, S).

HONDURAS. ATLÁNTIDA: Lancetilla Valley, near Tela, on leaves, 600 m, 1927-1928, *Standley 55624, 55662, 54861, 54792, 54846, 54854, 54847, 55652, 56890, 54834* (JE).

NICARAGUA. Atlántico Norte, along Río Waspuk ca. 1 km upstream from confluence of Río Pis Pis, river margin, second growth around plantations and tall evergreen forests, stems and leaves of small tree of Violaceae, 14°15'N, 84°36'W, 70-100 m, 1 March 1979, *Stevens 13105* (MO).

PANAMA. PANAMÁ: Canal Zone, Barro Colorado Island, Shannon Creek, on living leaves in virgin lowland rain forest, 9°10'N, 79°50'W, 150 m, October 1993, *Salazar Allen & Gradstein 15145* (MO, JE, MG, GOET). Barro Colorado Island, Tom Barbour Trail, on leaves, 200-300 m, 23 November 1948, *Killip 39971, 39972* (MO). Canal Area, Drowned forest of upper Río Pequení between Salamanca Hydro-Graphic Station and Río Boqueron, on leaves,

9°21’N, 79°34’W, 70 m, *Allen 17277A* (MO). Westerly arm of Quebrada Salamanca, 70 m, 16 December 1934, *Dodge 17014* (MO).

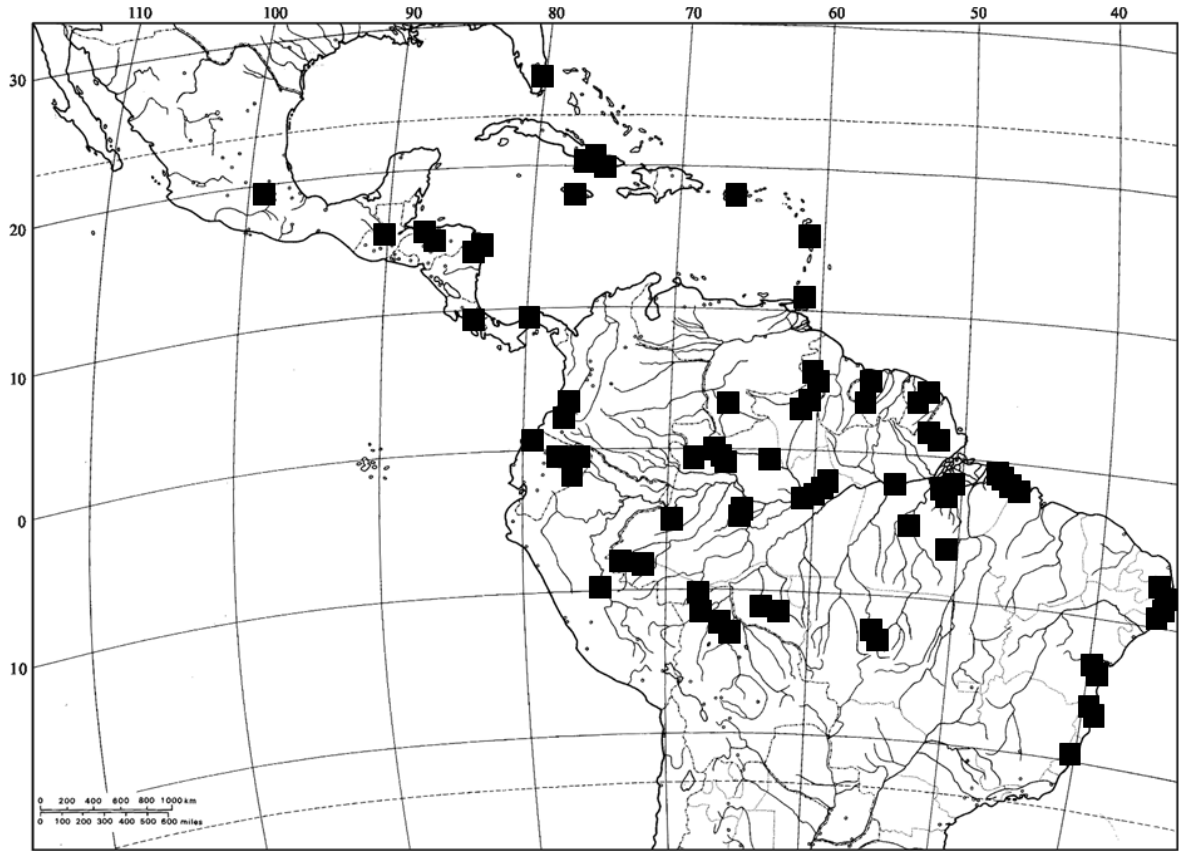

Figure 19. Distribution of *Radula flaccida.*

CUBA. Without locality, s.d., *Wright s.n.* (MO). Santa Catalina, W Cuba, January – February 1907, *Caldwell & Baker 15422*, *15423* (MO). Hills of Tabajo, Base of El Yunque, Oriente, on fern and “Parna Rosa”, 1-2 December 1910, *Shafer 8377* (MO). **GRANMA:** Sierra Maestra, firme de la Sierra entre Alcarraza y Punta de Lanza, 800-1000 m, *Bisse & Lippold 14225/a* (JE).

JAMAICA. On living leaves, 31 July 1903, *Evans 332* (FH).

TRINIDAD AND TOBAGO. Without locality, 1912, *Thaxter s.n.* (FH-00965721, FH-00965722). On palm leaf, forest, for miles east of Arima, 15 March 1920, *Britton et al. 641* (FH).

FRENCH GUIANA. CAYENNE: Montagnes de Kaw, upper slope forest on shallow laterite soil, epiphyllous, 52°15' W, 4°33' N, 200-300 m, March 1985, *Gradstein 5875* (GOET). **SAÜL:** 2 km SW of the village, “sentier limonade”, lowland moist forest on laterictic soil, epiphytic on tree base, 03°32’ N, 53°12 W, 180-210 m, 5 July 1986, *Montfoort & Ek 1103* (GOET).

SURINAM. SIPALIWINI: NICKERIE: area of kabelebo Dam project, near camp road km 23, line on westbordes of river kabalebo rainforest, on bark of living tree, 150 m, 6 November 1981, *Bekker 1340b* (GOET). **SIPALIWINI:** Blanche Marie valley, on bark, 04°44' N, 56°53' W, 100 m, *Muñoz 98-83* (MO, GOET). El Dorado Falls, ca. 3 km NE of Blanche Marie guest houses, epiphyllous, 4°45'N, 56°53'W, 50-100 m, 10 June 1997, *Pursell 11732* (MO).

GUYANA. UPPER MAZARUNI: Jawalla, at confluence of Kukui River and Mazaruni River, virgin forest, epiphyll, 500 m, 6-7 February 1985, *Gradstein 4862* (GOET).

VENEZUELA. AMAZONAS: Rio Cassiquiare, 04 October 1928, *P. Lützelburg 22617* (JE). Rio Cassiquiare, 02 October 1928, *Lützelburg 23114* (JE).

ECUADOR. ESMERALDAS: Straβe Ibarra – San Lorenzo, feuchte Sekundärvegetation am Rio Lita bei Lita, epiphyll am Flussufer, 500 m, 20 August 2004, *Schäfer-Verwimp et al. 24422* (MO).

BRAZIL. ACRE: Rio Juruá, Juruá-Mirim, August 1901, *Ule 568* (MG). **ALAGOAS:** Muricí, Estação Ecológica de Murici, 9°11'05"–9°16'48"S, 35°45'20"– 35°55'12"W, 555 m, 2 December 2004, *Pôrto s.n.* (UFP). **AMAPÁ:** Serra do Navio, Parque Natural Municipal do Cancão, 00°55'22,7"N, 052°00'11,9"W, 140 m, 7 September 2012, *Gentil 349* (MG). **AMAZONAS:** Santa Isabel do Rio Negro, 0°25'S, 65°31'W, 100 m, 2 July 1979, *Schuster 79-9-225* (INPA). Barcelos, Acânga, 01°10' S, 61°30' W, 27 June 1979, *Schuster 79-3-46* (SP). Manaus, regenwald am Oberlauf des Rio Janauaca, ca. 50 km sudwestich der Stadt, epiphyll, 3°23'S, 60°16'W, 50 m, 21 July 1986, *Schäefer-Verwimp & Verwimp 7294* (SP, JE). Manaus, Flores, 16 August 1928, *Lützelburg 22004* (JE). Rio Cauaburi, cachoeira do caranguejo, sobre folhas vivas, 3 July 1979, *Yano 1628* (INPA). **BAHIA:** Eunápolis, Estação Veracruz, trilha Pau-Brasil, Floresta Atlântica, corticícola, 16°22' S, 39°10' W, 8 September 1999, *C. Bastos & S.B. Vilas Bôas-Bastos 1574* (ALCB). Igrapiúna, Reserva Ecológica da Michelin, Mata da Vila Cinco, epíxila, 13°48' S, 39°10'W, 14 fevereiro 2006, *S.B. Vilas Bôas-Bastos 1848, 1893* (ALCB). **ESPÍRITO SANTO:** Linhares, Reserva Florestal da Vale do Rio Doce, 15 May 1992, *Yano & Windisch 17328* (SP). **MATO GROSSO:** Cláudia, Parcela Permanente de Biodiversidade, 11°34'54"S, 55°17'15"W, 300 m, 2 September 2011, *Peralta & Borges 12409* (SP). **PARÁ:** Melgaço, Estação Cientifica Ferreira Penna, Caxiuanã, várzea do furo do Camuim, 27 November 2000, *Lisboa & Ilkiu-Borges 6911* (MG). Parauapebas, Serra dos Carajás, Serra Norte, em mata alta sobre solo aurífero, sobre folhas vivas, *Lisboa et al. 1649* (MG). **PARAÍBA:** Sapé, Reserva Particular do Patrimônio Natural Fazenda Pacatuba, 7°02'33"S, 35°09'24"W, 11 December 2009, *Silva 530* (UFP). Primavera, margem da PA 446 para primavera, Retiro dois Irmãos, capoeira alta, epifila no interior da mata, 00°58'32" S, 47°09'57,4" W, 2 April

2011, *Pietrobom et al. 8457* (SP). Nova Timboteua, floresta de igapó, epifila no interior da mata, 01°12'12" S, 47°25'42" W, 17 May 2011, *Pietrobom et al. 8467* (SP). **PERNAMBUCO:** São Lourenço da Mata, Engenho São Bento, Estação Ecológica de Tapacurá, Mato Toró-Cuieira, 26 August 1980, *Yano & Lima 2659* (SP). **RONDÔNIA:** 2–4 km above the first rapids on the Rio Pacaás Novos, epiphyll over stream, 11°S, 64ºW, 400 m, 15–22 March 1978, *Reese 13467* (NY, JE). Ji-Paraná, on leaves of treelets, along a shallow and narrow stream, in primary forest, 10°08' S, 61°53' W, 13 October 1986, *Vital 14416* (SP). **RORAIMA:** Rio Uraricoeara, vicinity of Uaica airstrip, forest on terra firme, growing on living tree, 3 December 1978, *Prance et al. 19991* (NY, INPA).

BOLIVIA. BENI: Vicinity of Guayaramerín, dense mature forest on sandy soil, gentle slope to a swampy stream bottom, epiphyll on Apocynaceae, 24-25 January 1978, *Reese 12764* (JE). **PANDO:** Gral. Frederico Roman, Santos Marcado, Loma Alta, a 5 km por el caminho que va a reserva, bosque amazónico de tierra firme, cresce sobre hoja de Araceae, 10°45'27"S, 65°57'40"W, 143 m, 5 November 2012, *Linneo & Araujo 3234* (MO).

Radula flaccida (subg. *Metaradula* sect. *Epiphyllae*) is recognized by the large discoid gemmae with a deeply cordate-auriculate base, produced on dorsal leaf margins (1–3 per leaf). The huge, disciform gemmae are unique to Radulaceae and are commonly produced in this species. Further diagnostic features of *Radula flaccida* are the small, distant, subsquadrate to subrhombic lobules with a pronunced rhizoidal area with a large bundle of numerous rhizoids, and apex elongate toward an obtuse tip. The species is easily recognized in the field by the epiphyllous plants with a glistening green color and the very large, discoid gemmae. When fertile, the trumpet-shaped perianths of *Radula flaccida* arise perpendicularly from the prostrate plants.

Radula flaccida is morphologicalloy most similar to *R. stenocalyx* and *R. yanoella*. However, the latter two species produce much smaller gemmae, without cordate-auriculate base. In addtion, *R. yanoella* stands out by its small thallus with short leafy shoots arising from the margin.

14. Radula fulvifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 261. 1845. *Jungermannia fulvifolia* Hook.f. & Taylor, London J. Bot. 4: 85. 1845. Type: St. Helena Island, 1 March 1843, *unknow collector*, in Dr. Greville's Herbarium (lectotype, E-00007234, selected by Oliveira-da-Silva *et al.* in press; isolectotypes, FH-00783498!, BM-000969264!, PC, W).

Fig. 20

Radula galapagona Steph., Sp. Hepat. 4: 176. 1910. Type: Ecuador, Galápagos Island, s.d., *C. M. J. Anderson s.n.* (lectotype, G-00112101!, scanty, selected by Yamada 1991:89), syn. fide Oliveira-da-Silva *et al.* (in press).

Radula schaefer-verwimpii K.Yamada, J. Jap. Bot. 65: 3. 1990. Type: Brazil, Minas Gerais, National Park Serra de Caparao, "auf schattigem Felsblock," 1360 m, 28 July 1987, *A. Schäfer-Verwimp 8989* (holotype, NICH; isotypes, G-00265052!, JE-04009540!, NY-01021153!, NY-01021154!, SP-383443!), syn. fide Oliveira-da-Silva *et al.* (in press).

Dioicous. *Plants* 1–2 mm wide, to 2 cm long, light green, yellowish-green to olive-green to brown in herbarium, irregularly to regularly pinnate. *Branches Radula*-type. *Stems* 100–180 µm in diameter, with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to subimbricate, slightly convex, ovate to falcate-ovate, sometimes strongly falcate-ovate, 0.6–1.1 mm long, 0.4–0.8 mm wide, dorsal base rounded, covering 1/3–1/2 the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margins plane, entire; marginal cells subquadrate to subrectangular, 8–20 × 8–15 µm, median cells isodiametric to elongate, 15–25 × 10–20 µm, basal cells isodiametric to elongate, 20–30 × 15–20 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, usually subrhombic, sometimes subquadrate, 0.3–0.6 mm long, 0.2–0.4 mm wide, 1/3–1/4 the lobe length, inflated at rhizoid area or along the keel, insertion 1–3× the base length, insertion line slightly curved, base plane, rarely recurved, rounded to angulate, covering 1/3–2/3 the stem, rarely fully overlapping the stem, free margin plane, rarely recurved, almost straight, apex plane, rarely recurved, rounded to acute, distal margin straight, keel straight to concave, departing at rather narrow angles of 30–50º from the stem and forming an angle of 100–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* intercalary on short branches, with 2–4 pairs of bracts, 0.7–1.1 mm wide; bracts distant to imbricate, ovate, 0.6–0.9 mm long, 0.25–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate, ca. 3/4 of lobe

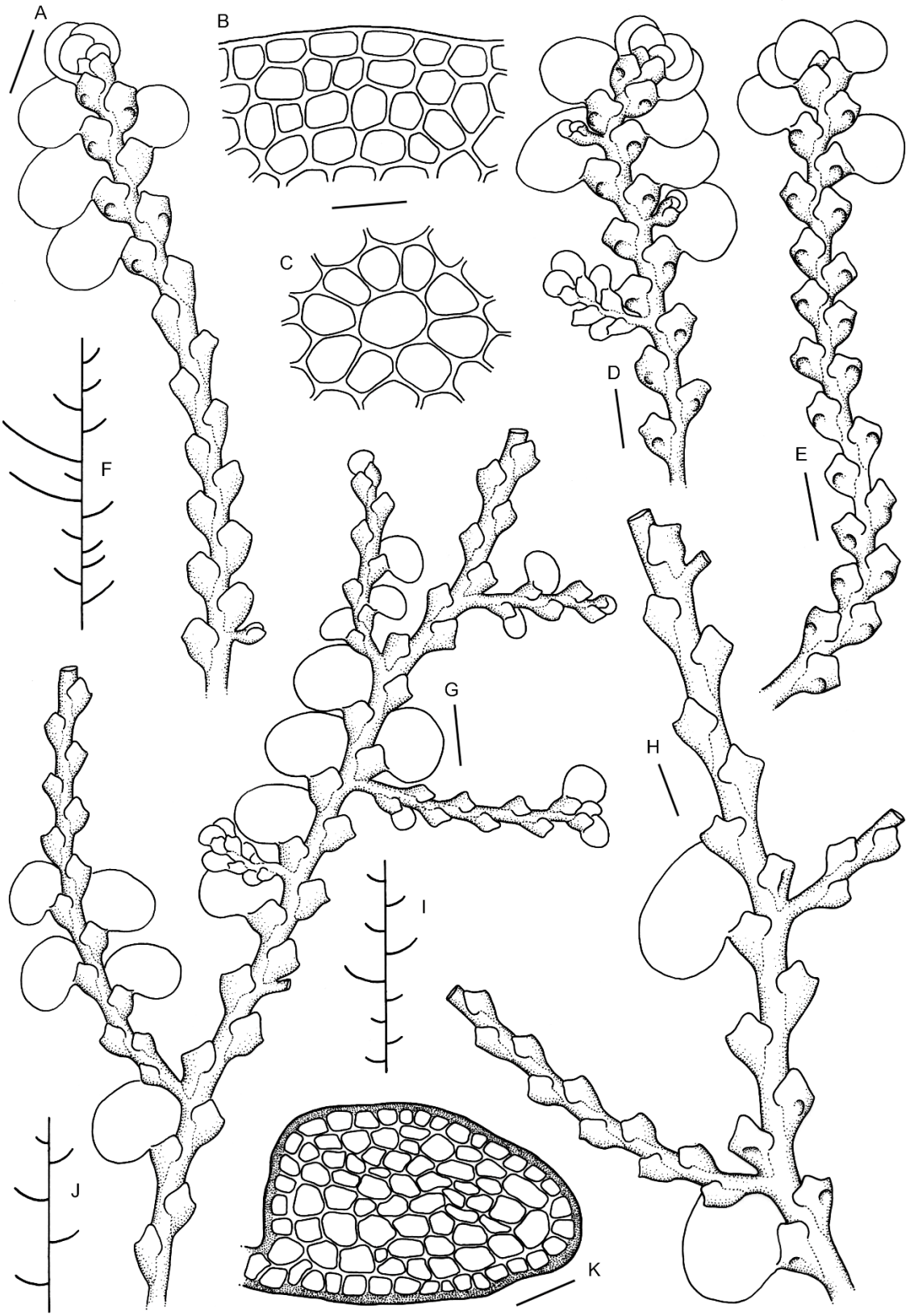

Figure 20. *Radula fulvifolia* - plants from Galápagos Islands. A, D–E. Habit (Isabela). B. Marginal leaf cells. C. Median leaf cells. F, I, J. Cladographs. G. Habit (San Cristobal). H. Habit (Santa Cruz). K. Cross section of stem. (A, D, J from *van der Werff 1436*; B, C, G, I from *Gradstein & Lanier H307/a*; E from *Gradstein* & *Weber H224*; F, H from *Gradstein et al. H52*). Scale bars: A, D, E, G, H = 500 µm; B, C = 25 µm; K = 50 µm.

length, base rounded, free margin straight, apex obtuse. *Gynoecia* on short branches, with 2 innovations; bracts almost symmetrical, oblong-ovate, 0.7–0.85(–0.9) mm long, 0.3–0.4 mm wide, apex rounded, margin plane, entire, lobule symmetrical, oblong-rectangular, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* and *Sporophyte* not observed. *Vegetative reproduction* by strongly caducous leaf lobes, producing completely denuded branches, often with regenerants on the margins of caducous leaves.

Distribution and habit. Tropical America and Africa. *Radula fulvifolia* is rare in Central America, where it is known from Guatemala (Pérez 2009) and Costa Rica. It is more common in South America, where it occurs in Guyana, Venezuela, Colombia, Ecuador, Bolivia and the Atlantic Coastal Region of Brazil (Gradstein 2021, Oliveira-da-Silva *et al.* 2021) (Figure 21). The species grows on trees, rotten logs, rock or soil, in humid submontane to montane forests up to the shrubby páramo, 400–3700 m.

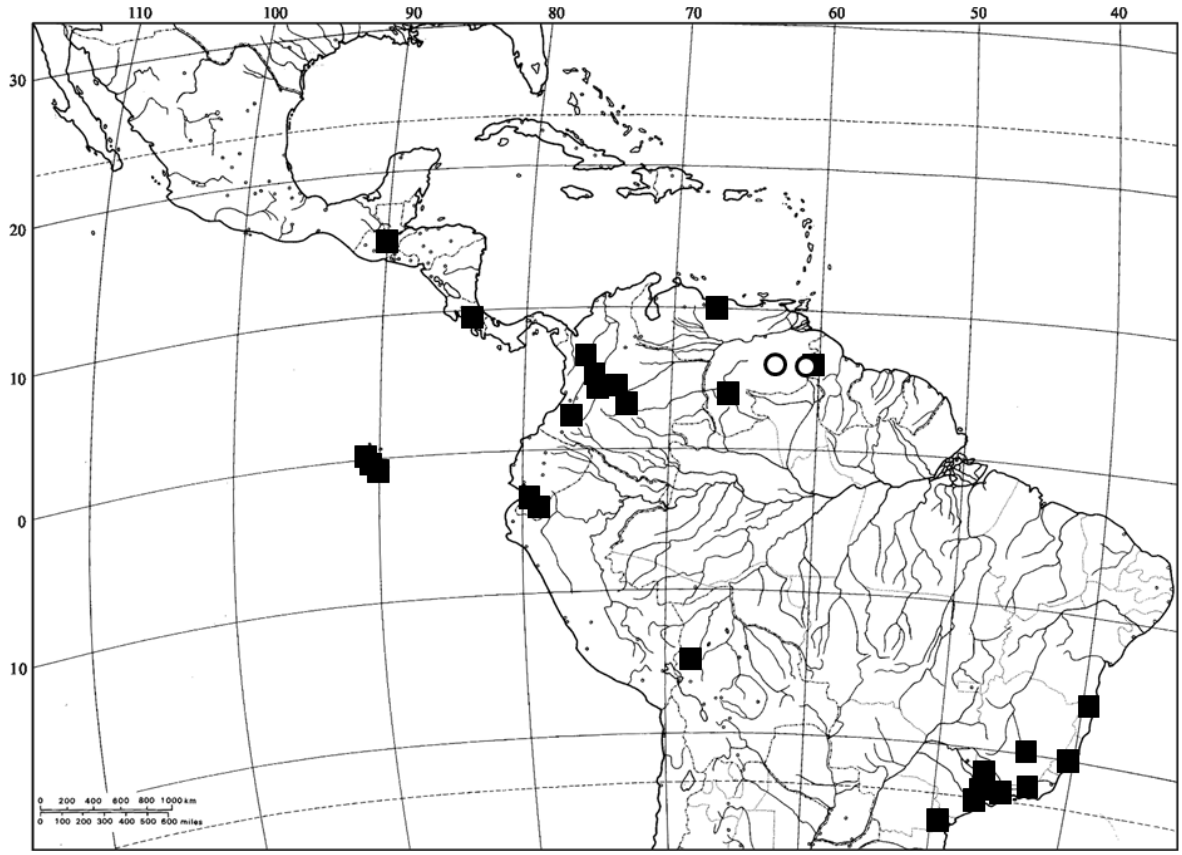

Figure 21. Distribution of *Radula fulvifolia* (black square) and *R. gradsteinii* (white circle).

Additional specimens examined. COSTA RICA. ALAJUELA: Piedades de San Ramón, 900 m, *Brenes 383* (MO).

GUYANA. UPPER MAZARUNI: North slope of Mt. Roraima, mossy montane forest, on bark, 5°17'N, 60°43'W, 1200-1600 m, *Gradstein 5526* (GOET).

VENEZUELA. AMAZONAS: Cerro Huachamacari, Río Cunucunuma, montane rainforest, on tree trunk, 1200 m, *Marguire et al. 29913* (MG, NY). **ARAGUA**: Parque Nacional "H. Pittier", on branch, 1100 m, *Steyermark et al. 95843*, *95846* (MG, NY).

COLOMBIA. RISARALDA: Santa Rosa, near finca La Sierra, 3700 m, *Aguirre 1427* (GOET).

ECUADOR. Galápagos Islands: Isabela, vulcan Alcedo, 1100 m, *van der Werff 1436* (GOET), ibid., *Gradstein* & *Weber H224* (L, MG); Santa Cruz, South slope of Mt. Crocker, on branches, ca. 800 m, *Gradstein et al. H52* (L, MG); San Cristobal, valley SW of El Junco, on trunk, 500 m, *Gradstein & Lanier H307/a* (L, MG).

BRAZIL. **BAHIA:** Eunápolis, Estação Veracruz, on bark, 16°22' S, 39°10' W, *Vilas Bôas-Bastos & Bastos 354* (ALCB); Abaíra, Catolés, Serra do Barbado, Mata da Forquilha, on bark, 13°17'27"S, 41°54'0,15"W, 1594 m, *Bastos 5101* (ALCB). **ESPÍRITO SANTO:** Castelo, Parque Estadual do Forno Grande, 20°31'00"S, 41°05'14"W, 1250 m, *Peralta et al. 19216* (SP); Domingos Martins, Parque Estadual Pedra Azul, on wood, 5 August 2009, *Penha 440* (ALCB). **MINAS GERAIS:** Poços de Caldas, morro São Domigos, 1330 m, 21°47S, 46°33W, *Schäfer-Verwimp & Verwimp 7030* (SP); Catas Altas, Parque Natural do Caraça, on rock, 20°05'56" S, 43°29'17" W, 1280 m, *Peralta et al. 6406* (SP). **PARANÁ:** Morretes, Parque Estadual Pico do Marumbi, trilha do Olimpo, 25°27'10"S, 48°55'11"W, 1000–1200 m, *Peralta et al. 17704* (SP). **RIO DE JANEIRO:** National Park Itatiaia, Itatiaia, 1200 m, *Schäfer-Verwimp & Verwimp 9255* (SP); Teresópolis, Parque Nacional da Serra dos Órgãos, on rock, 22°27'33"S, 43°00'17"W, 1300-1500 m, *Peralta et al. 20403* (SP). **SÃO PAULO:** Guarulhos, 23°23'55"S, 46°29'55"W, 745 m, *Peralta & Fortes 13923* (SP); São José do Barreiro, fazenda pinheirinho, on roadside, 22°43'48"S, 44°38'38"W, 1400 m, *Peralta et al. 4988* (SP); Campos do Jordão, Parque Estadual de Campos do Jordão, sobre barranco, 22°41'15"S, 45°27'21"W, 1677 m, *Peralta et al. 21757* (SP); São Luiz do Piraitinga, Parque Estadual as Serra do Mar, Núcleo Santa Virgínia, on tree trunk, 23°20'45" S, 45°07'47" W, 956 m, *Peralta & Gugliota 13405* (SP).

Radula fulvifolia (subg. *Volutoradula*) is a rather polymorphic species recognized by the strongly caducous leaf lobes, producing almost completely naked branches, leaf lobes ovate to falcate-ovate, cell walls thin usually without trigones, and lobules rhombic (rarely subquadrate) with a rounded to angulate base covering 1/3–2/3 the stem, rarely fully

overlapping it and keel straight to concave. The species is discussed in detail by Oliveira-da-Silva *et al.* (in press).

15. Radula gradsteinii K.Yamada, in Gradstein & Florschütz-de Waard, Trop. Bryol. 1: 37. 1989. Type: Guyana, Mount Roraima, summit of Mt. Latipu, ca. 8 km. north of Kamarang, on poles in scrubby vegetation, 5°57'N, 60°38'W, 1000 m, 25 February 1985, *S. R. Gradstein 5608* (holotype, U!; isotypes, NICH, GOET!).

Fig. 22

Dioicous. *Plants* 1.6–2.5 mm wide, to 1.5 cm long, yellowish brown in herbarium, regularly to irregularly pinnate. *Branches Radula*-type. *Stems* 100–150 μm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate, 1–1.2 mm long, 0.7–1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin almost straight, apex rounded, margins recurved, slightly crenulate; marginal cells subquadrate, 10–20 × 10–15 μm, median cells isodiametric to elongated, 20–25 × 15–20 μm, basal cells elongate, 30–40 × 15–20(–25) μm, cell walls thin, trigones large, intermediate thickening present, cuticle verruculose; oil bodies not observed. *Lobules* imbricate, subrectangular, 0.6–0.7(–8) mm long, 0.3–0.4(–5) mm wide, ca. 1/2 the lobe length, inflated at rhizoid area and along the keel, insertion 1× the base length, insertion line slightly curved, base plane, rounded, overlapping the stem (stem surface hardly visible), free margin plane, rounded to almost straight, apex plane, obtuse, prolonged, rarely rounded, distal margin curved, keel almost straight, spreading at 50–60º with the stem, 120–170º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long or short branches, with 1–2 innovations; bracts oblong-ovate, 1–1.2 mm long, 0.6–0.7 mm wide, apex rounded, margin strongly recurved, slightly crenulate, lobules oblong-ovate, ca. 1/2 of lobe length, apex acute. *Perianth* erect, subcylindrical, ca. 2 mm long, ca. 0.7 wide at base, ca. 1.1 mm wide at middle, ca. 0.7 mm wide at apex, mouth irregularly entire, plane; perianth wall unistratose. *Calyptra*, *Sporophyte* and *vegetative reproduction* not observed.

Distribution and habit. Endemic to the tepuis of Venezuela and Guyana (Figure 21), growing as epiphyte in scrub vegetation, in submontane tropical forest, 950–1000 m.

Additional specimens examined. GUYANA. UPPER MAZARUNI: The type.

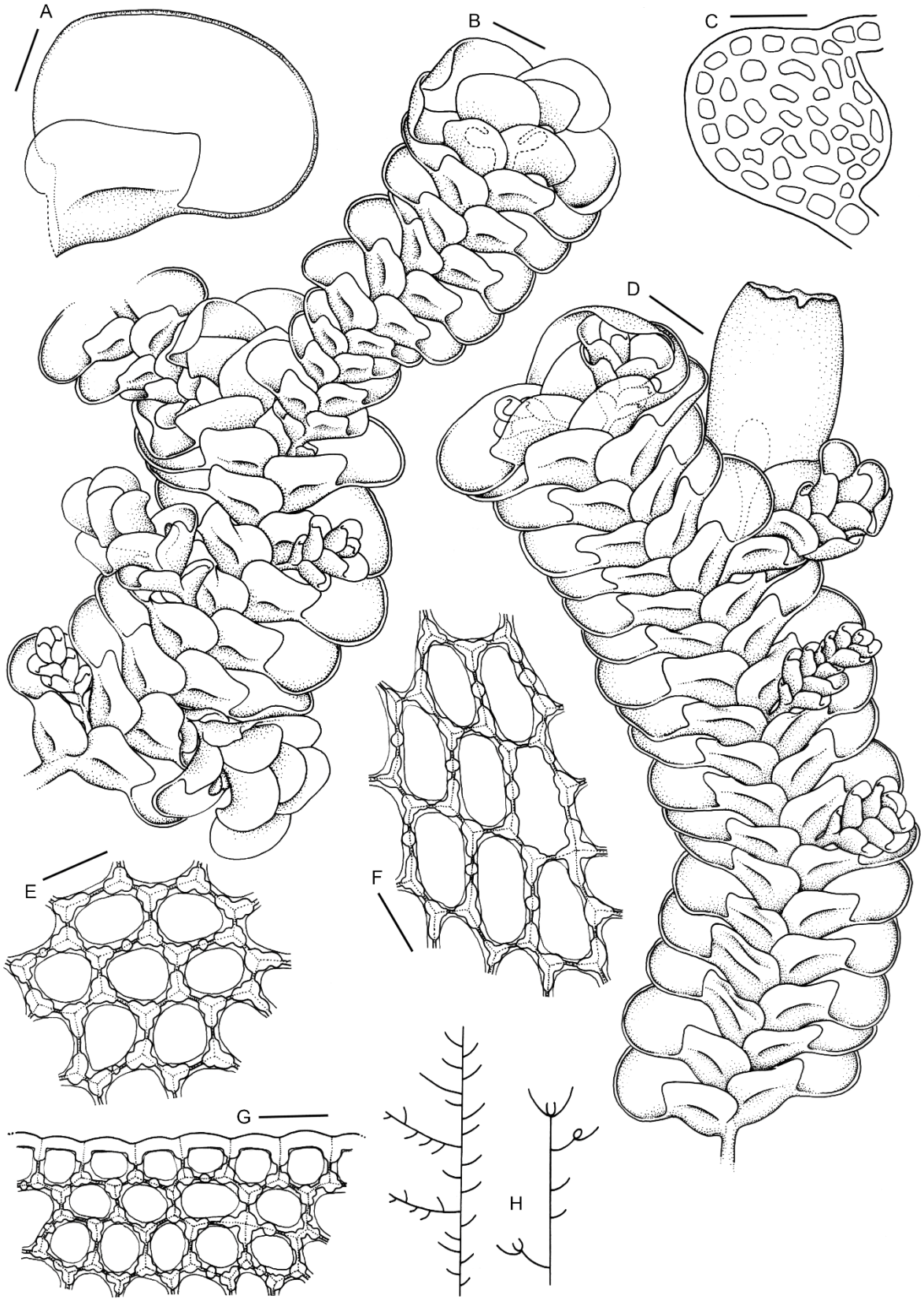

Figure 22. *Radula gradsteinii*. A. Leaf. B. Habit with gynoecia. C. Cross section of stem. D. Habit with perianth. E. Median leaf cells. F. Basal leaf cells. G. Marginal leaf cells. H. Cladograph of plants (white dots = gynoecia with perianth, U = gynoecia without perianth) (A = 250 µm, B, D = 500 µm, C = 50 µm, E-G = 25 µm; A-C, E-H from the isotype in GOET, D from *Sipman 26644*).

VENEZUELA. BOLIVAR: Cerro Guaiquinima, in central part of upper plateau (near camp 4), low mossy forest on rocky sandstone slope towards stream, epiphytic, 5°40'N, 63°34'W, 950 m, 6 February 1990, *Sipman 26644* (GOET).

Radula gradsteinii (subg. *Radula*) is a rare and distinct species characterized by densely pinnate plants with imbricate, strongly convex leaves with recurved margins, leaf cell walls with large, nodulose trigones, cuticle distinct verruculose and lobules imbricate with a base covering the entire stem and a prolonged, usually obtuse apex.

This species may be confused with *R. quadrata* by its similar lobule shape, but the latter species produces small discoid gemmae on the leaf margins (gemmae absent in *R. gradsteinii*) and has leaf cell walls without trigones (with large, nodulose trigones in *R. gradsteinii*) and a smooth cuticle (verruculose in *R. gradsteinii*).

The type of *Radula gradsteinii* has female branches (without perianths), although they were not described in the protologue. The additional specimen from Venezuela consists of female plants with a robust, subcylindrical perianth. The Venezuelan material was annotated by K. Yamada, but was not published.

16. Radula grevilleana Taylor, Ann. Mag. Nat. Hist. 20: 380. 1847. Type: Jamaica, on leaves of *Danaea alata* Sm., *unknown collector*, in Dr. Greville's Herbarium (lectotype, FH-00783525!, c. andr.+ per.+ spor., **designated here**; isolectotypes E-00002899, G, NY-01041812!, NY-01041813!).

Radula evansii Castle, Ann. Bryol. 11: 37. 1938. Type: Dominica, Laudat village, 1903, *F. E. Lloyd 106* (types NY and YU, not found), ***syn. nov.***

Radula longituba Steph., in Herzog, Biblioth. Bot. 87: 233. 1916. Type: Bolivia, Tablas, 1800 m, *T. C. J. Herzog 4559* (type, G, not found), syn. fide Castle (1939, under *R. mammosa*).

Radula mammosa Spruce, Mem. Torrey Club 1: 127. 1890. Type: Bolivia, Yungas, "in Acrostichi frondibus cum Lejeuneis repens," 4000 ft., 1885, *H. H. Rusby 3025 p.p.* (type, MANCH not found; lectotype, G-00265038!, c. per., **designated here**; isolectotype, NY-01021130!), ***syn. nov.***

Radula verrucifolia Steph., in Herzog, Biblioth. Bot. 87: 233. 1916. Type: Bolivia, Tablas, 1800 m, *T. C. J. Herzog 4557* (lectotype, G-00043872!, c. per., selected by Yamada, 1993: 131; isolectotype, MANCH-15378!), syn. fide Castle (1939, under *R. mammosa*).

Dioicous. *Plants* 1–2 mm wide, to 1 cm long., light-green, pale green to yellowish-green in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type, rarely *Lejeunea*-type. *Stems* 100–200 µm in diam., with thin-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish. *Leaf lobes* widely spreading, contiguous to slightly imbricate, plane to slightly convex, ovate to falcate-ovate, 0.7–1.3 mm long, 0.4–0.9 mm wide, dorsal base rounded, not covering the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded, margin plane to sometimes recurved, entire; marginal cells subquadrate to isodiametric, 12–15 × 10–12 µm, median and basal cells isodiametric to elongate, 22–25 × 12–17 µm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.25–0.5 mm long, 0.2–0.4 mm wide, ca. 1/3 the lobe length, strongly inflated at rhizoid area, insertion 3–4× the base length, insertion line straight to slightly arched, base plane, rounded, covering up to 1/5 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin straight, keel straight to strongly convex, spreading at angles ca. 60º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, numerous on a pronounced mammiliform swelling, present on a few or usually on numeros lobules. *Androecia* not seen. *Gynoecia* terminal on main stems or long branches, with 1–2 innovations; bracts oblong-ovate, 0.9–1 mm long, 0.45–0.5 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, ovate to oblong-ovate, apex rounded to obtuse. *Perianth* erect, rarely falcate, subcylindrical to trumpet-shaped, sometimes strongly inflated at middle, 1.2–4.2 mm long, 0.2–0.5 mm wide at base, 0.3–1 mm wide at middle, 0.4–1.7 mm wide at apex, mouth entire, plane to undulate; perianth wall 2–4-stratose at base, unistratose from the middle to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–5-layered tube (perigynium) within which the sporophyte foot and part of the Seta is embedded. *Calyptra* wall 1–2-layered at the base, unistratose above. *Seta* 1.9–4 mm long. *Capsule* 0.4–1.5 mm long, 0.2–0.5 mm wide, valves 0.6–1.2 mm long, 0.1–0.2 mm wide at middle, outer layer cells subrectangular, confluent adnate nodular thickenings reddish-brown, on every longitudinal wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* 150–310 µm long, rough. *Spores* 22.22–25.92 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by occasionaly caducous leaf lobes and regenerants (according to Castle 1939; not observed in this study).

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Widespread in tropical America, with few records from subtropical America. In addition to the countries listed in the additional examined specimens section, *Radula grevilleana* was reported from Dominica, Colombia, Ecuador, Chile (see Caste 1939, Gradstein 2021) and Peru (Pócs *et al.* 2022, Graham *et al.* 2022) (Figure 23). This species grows usually on leaves of angiosperms and ferns, rarely on bark, rock and soil, in humid and shaded places in lowland and montane forests, from sea level to 3250 m.

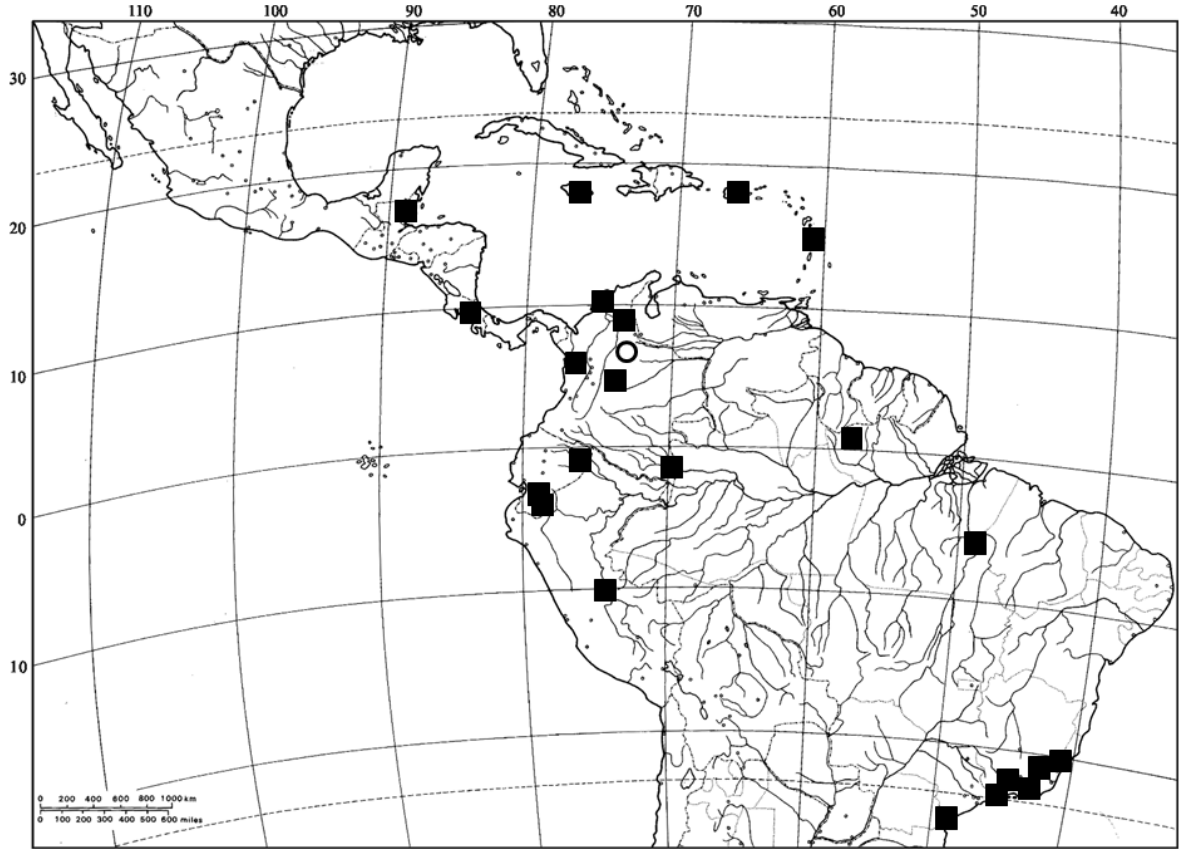

Figure 23. Distribution of *Radula grevilleana* (black square) and *R. sp. nov. 1* (white circle).

Additional specimens examined. BELIZE. CAYO: in forest along ridge and along small stream just below ridge in vicinity of Doyle's Delight, southern Maya Mountains, on boulder by river, 16°30'N, 89°06'W, 1098 m, 5 December 1993, *Allen 15157* (MO).

COSTA RICA. SAN JOSÉ: Cordillera Talamanca, Cerro de la Muerte, Páramo Buena Vista at Panamerican Highway, km 87, S of Highway, at edge of Páramo formation, small rivulet, growing in cushions in a spring, 83°45'W, 09°34'N, 3250 m, 20 January 2000, *Holz*

CR 00-187 (JE, MO). Distrito Páramo, base del Cerro Asuncion, Buenavista, sobre roca a la sombra, 09°36’00”S, 83°46’00”W, 3000 m, 26 February 1996, *Dauphin 2221* (MO).

JAMAICA. ST. THOMAS: Blue Mountains, S-Abhang bei der wildflower Lodge oberhalb Epping Farm, Weg zum PortlandGap, Regenwald, epiphyll auf Farnwedel, 18°03,1’N, 76°36,1’W, 1620 m, 14 December 2013, *Schäfer-Verwimp 35358* (MO, topotype of *Radula grevilleana*).

PUERTO RICO. Cordillera Central, above Vilalba, Doña Juana recreation area, leeward slope, lower montane wet forest, 800-1000 m, 2 June 1988, *Thiers 5304* (NY).

BRAZIL. ESPÍRITO SANTO: Município de Domingos Martins, Parque Estadual Pedra Azul, Trilha das Piscinas, Mata Atlântica, terrícola, 28 outubro 2009, *Penha 654* (ALCB). **MINAS GERAIS:** Alto do Caparaó, Parque Nacional do Caparaó, Cachoeira Bonita, 20°26’07”S, 41°47’57”W, 1750 m, 11 July 2009, *Bordin et al. 1619* (SP). **PARÁ:** São Geraldo do Araguaia, Serra dos Martírios-Andorinhas, 6°10’2,8”S, 48°26’30,2”W, 18 December 2007, *Lisboa & Barros 5703* (MG). Oriximiná, ESEC do Grão-Pará, Serra do Acari, floresta de terra firme submontana aberta, sobre folha próximo ao igarapé, 1°16’16,8”S, 58°48’0,6”W, 501 m, 4 September 2008, *Pietrobom & Maciel 8060* (SP). **PARANÁ:** Morretes, Parque Estadual do Marumbi, trilha vermelha, 25°26’55”S, 48°54’54”W, 1200 m, 22 July 2014, *Peralta et al. 15765* (SP). Morretes, Estação Murumbi, Pico do Murumbi, epifila sobre pteridófita, 750 m, 5 July 1991, *Yano et al. 15457* (SP). **RIO DE JANEIRO:** Nova Friburgo, floresta ombrófila, sobre solo, 1600–1800 m, 10 October 1995, *Costa et al. 1067* (RB). Parque Nacional do Itatiaia, epifila, 22°25’7” S, 44°37’12” W, 1041 m, 22 August 2014, *Rezende & Costa 269* (RB). **SÃO PAULO:** Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, 23°26’02”S, 45°04’16”W, 23 October 1988, *Visnadi & Vital 4035* (SP).

BOLIVIA. Types of *R. mammosa*, *R. longituba* and *R. verrucifolia*.

Radula grevilleana (subg. *Metaradula* sect. *Epiphyllae*) is a typically epiphyllous species recognized by the lobule with a strongly protruding rhizoidal area and base usually not covering the stem, and the very thin-walled leaf cells. The species lacks gemmae, which separates it from the other Neotropical species of the sect. *Epiphyllae* (*e.g., R. flaccida*, *R. stenocalyx*). The lobule keel of *R. grevilleana* varies from straight to strongly convex. A specimen from Puerto Rico (*Thiers 5304*, NY) has rhizoids on the margins of caducous leaf lobes, whereas *Lejeunea*-type branches not associated with decapitated shoots were seen in a few specimens.

Radula grevilleana has long been considered endemic to Jamaica (Castle 1939, Schäfer-Verwimp & Van Melick 2016), but examination of the type in the Taylor herbarium (FH) showed that the species is conspecific with *R. mammosa* and the little-known *R. evansii*.

17. Radula sp. nov. 1 F.R.Oliveira-da-Silva, ***sp. nov.*** Type: Colombia, Santander, Valle de San José, 3250 m, 11 September 1957, *P. J. Grubb & D. A. Guymer B 446 B* (holotype, BM-013763001!; isotype MG!).

Fig. 24

Dioicous. *Plants* 0.5–0.7 mm wide, to 1 cm long, yellowish to brownish in herbarium, regularly pinnate. *Branches Radula*-type. *Stem* 80–100 µm in diam., with thick-walled epidermal cells surrounding mostly smaller or uniform in size, thin-walled medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls yellowish. *Leaf lobes* obliquely to widely spreading, distant, convex, oblong-ovate, 0.3–0.5 mm long, 0.2–0.3 mm wide, dorsal base rounded, covering up to 1/3 the stem, dorsal margin slightly rounded, ventral margin straight to slightly rounded, apex rounded, margin plane, entire; marginal cells subquadrate to subrectangular, 11–18 × 7–11 µm, median and basal cells isodiametric to elongated, 15–22 × 8–15 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical to ellipsoidal, yellow, smooth, 8–16 × 8–10 µm. *Lobules* distant, subrectangular, 0.25–0.3 mm long, 0.1–0.14 mm wide, ca. 2/3 the lobe length, strongly inflated along the keel, insertion line curved, base not developed, free margin plane, straight to sinuose, apex plane, rounded to slightly obtuse, distal margin straight to sinuose, keel convex, spreading at angles of 35–45º with the stem, 160–180º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, long, scanty, present on a few lobules. *Androecia* terminal on long branches, with 15–30 pairs of bracts, ca. 0.2 mm wide; bracts contiguous to imbricate, oblong-ovate, ca. 0.3 mm long, ca. 0.1 mm wide, apex rounded, margin plane, entire, lobule distant to contiguous, oblong-ovate, ca. 3/4 of lobe length, base straight, free margin straight, apex rounded. *Gynoecia* and *Vegetative reproduction* not observed.

Distribution and Ecology. The new species is only known from its type locality in Valle de San José, Department of Santander, Colombia (Figure 23), where it was collected at 3250 m elevation.

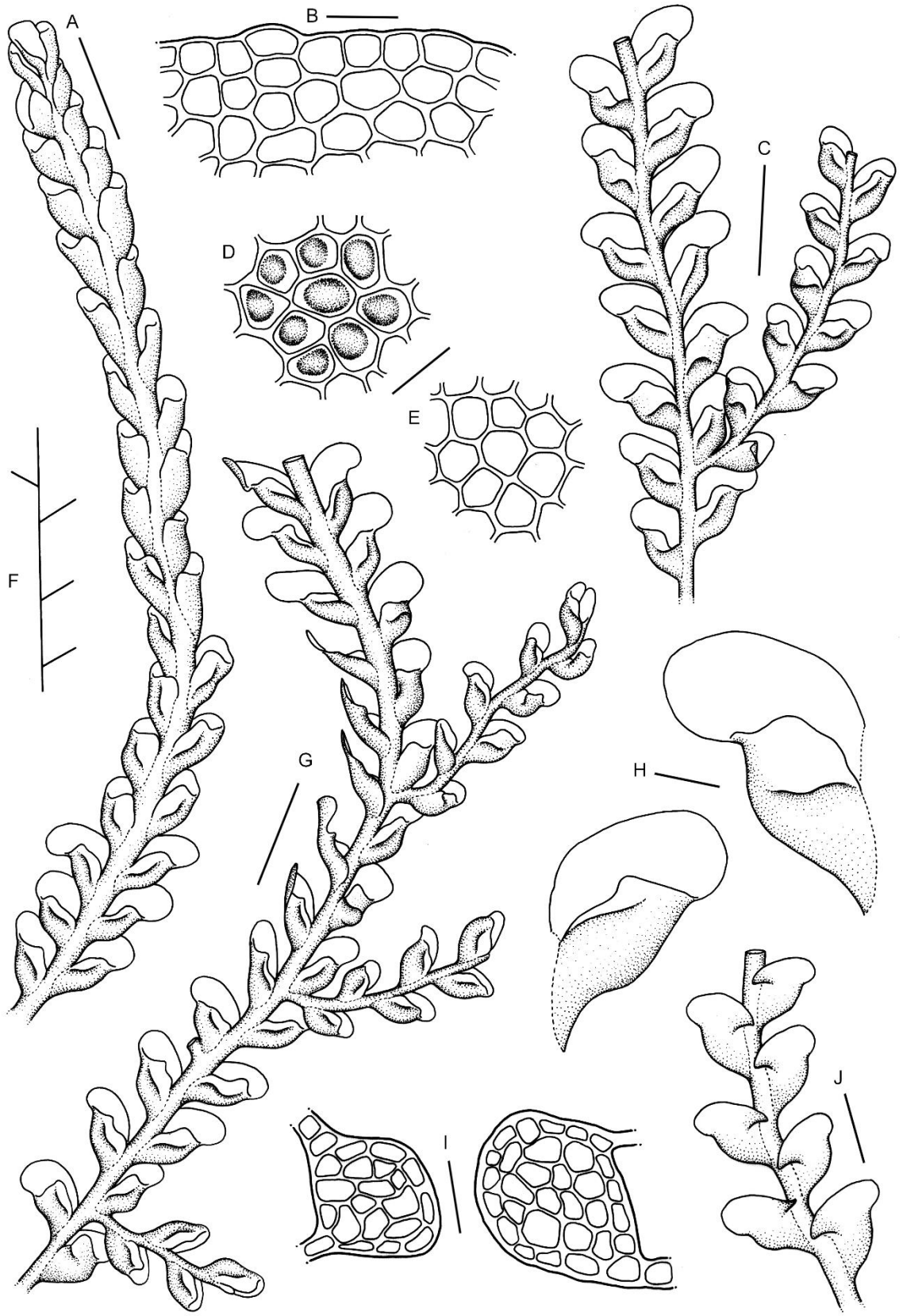

Figura 24. *Radula sp. nov. 1.* A. Habit with androecia. B. Marginal leaf cells. C. Habit. D. Median leaf cell with oil bodies. E. Median leaf cells. F. Cladograph of plants. G. Habit. H. Leaves. I. Cross section of stem. J. Habit in dorsal view (A, C, G = 500 µm, B, D, E = 25 µm, H = 100 µm, I = 50 µm, J = 250 µm; All from the holotype).

Radula sp. nov. 1 (subg. *Volutoradula*?) is the smallest Neotropical *Radula* species, with shoots 0.5–0.7 mm wide and up to 1 cm long. The new species is readly distinguished by the usually widely spreading, oblong-ovate leaf lobes and the unusually large lobules, ca. 2/3 the lobe length, subquadrate and strongly inflated along the keel.

By its very small size *Radula* sp. nov. 1 is somewhat similar to *R. brasilica* (0.8–1.4 mm wide), but the latter is morphologically different from the new species in many respects (see under *R. brasilica*). The diagnostic characters of *Radula* sp. nov. 1 are unparalleled among the *Radula* species from tropical America.

At a first glance, *Radula* sp. nov. 1 resembles *Cololejeunea* (Lejeuneaceae), but in the latter genus rhizoids are produced on the stem (not on the lobule surface) and the stem epidermis cells are thin-walled.

18. Radula inflexa Steph., Hedwigia 23: 148. 1884. Type: Guadeloupe, s.d., *l'Herminier s.n.* (lectotype, G-00121996!, c. per + andr., selected by Yamada, 1980: 247; isotype, NY-00562168!, scanty, BM-000969215!, BM-000969216!).

Dioicous. *Plants* 1.3–2.2 mm wide, to 5 cm long, yellowish brown to reddish brown in herbarium, irregularly pinnate to dichotomous in female plants by repeatedly fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on decapitated shoots. *Stems* 132–170 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thick-walled (by concave trigones), yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, convex to strongly convex, ovate, 0.9–1.1 mm long, 0.6–0.7 mm wide, dorsal base rounded, covering the entire stem, dorsal margin rounded, ventral margin rounded to almost straight, apex rounded to obtuse, margins strongly recurved, rarely plane, entire; marginal cells subquadrate, 10–15 × 8–10 µm, median and basal cells isodiametric to elongated, 20–25 × 12–15 µm, cell walls thin, trigones large, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, rarely subrectangular, 0.4–0.6 mm long, 0.25–0.4 mm wide, ca. (–1/2)1/3 the lobe length, inflated along the keel, insertion ca. 2× the base length, insertion line curved, base plane, rounded, covering 1/5–1/3 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margim almost straight, keel slightly convex to almost straight, spreading at 50–80º with the stem, 130–150º with the ventral leaf

lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* intercalary on long branches, with 3–4 pairs of bracts, 0.8–1 mm wide; bracts imbricate, ovate, 0.7–0.8 mm long, 0.35–0.5 mm wide, apex rounded, margin slightly recurved, entire, lobule oblong-ovate, ca. 1/2 of lobe length, base slightly rounded, free margin straight, apex rounded to obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 1.1–1.5 mm long, 0.6–0.7 mm wide, apex rounded, margin plane to strongly recurved, entire, lobules oblong-ovate, ca. 1/2 of lobe length, apex rounded. *Perianth* erect, subcylindrical to trumpet-shaped, 2.7–5.2 mm long, 0.3–0.6 mm wide at base, 0.9–1.5 mm wide at middle, 0.9–1.6 mm wide at apex, mouth entire, plane to undulate, sometimes convolute ventrally; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–4-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 2-layered at the base, 1 cell layer thick above. *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Yamada (1980).

Distribution and habit. Scattered in the West Indies (Figure 25). In addition, Castle (1963) recorded the species from Guatemala and Brazil; these records are considered dubious and require confirmation. *Radula inflexa* grows on bark and rock (Castle 1963).

Specimens examined. JAMAICA. Slope of Sir John's Peak, Blue Mountains, 5 October 1908, *Britton 1187* (NY).

PUERTO RICO. Whitout locality, s.d., *Iduvanecke s.n.* (BM).

GUADELOUPE. The type of *Radula inflexa* (G, NY).

MARTINIQUE. Whitout locality, s.d., *Duss s.n.* (BM).

Radula inflexa (subg. *Volutoradula*?) is a rare species recognized by the yellowish brown to reddish brown plants with densely, irregularly pinnate to dichotomous branching; the dichotomous branching occurs in female plants and is due to repeatedly fertile, paired innovation. Itn addition, the species stands out by ovate, strongly convex leaf lobes with ventral margin strongly recurved, leaf cells with large, bulging trigones, and lobules usually subquadrate with the base scarcely covering the stem (1/5–1/3).

This species is similar to *R. involvens* in the leaf lobes strongly recurved and leaf cells with large, bulging trigones. However, the latter species has leaf lobes strongly falcate-ovate and lobules subrectangular to lunular, narrowly inflated along the keel. Moreover, *R. involvens* has few branches, while *R. inflexa* is densely branched.

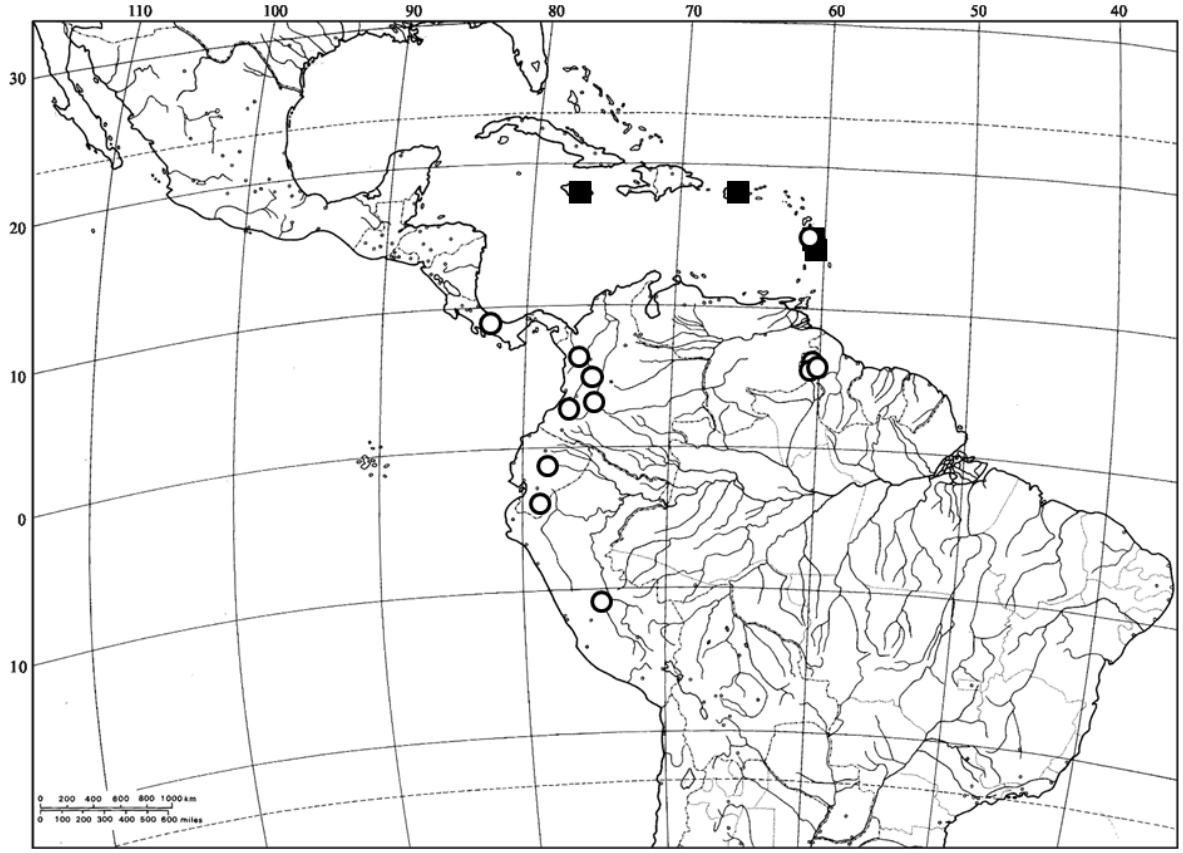

Figure 25. Distribution of *Radula inflexa* (black square) and *R. involvens* (white circle).

19. Radula involvens Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 325. 1885. Type: Ecuador, "in Silva Canelos," *R. Spruce s.n.* (lectotype, MANCH-13616!, **designated here**; isolectotypes, MANCH-13617!, G-00121957!, scanty).

Fig. 26-27

Dioicous. *Plants* 1.8–2.2 mm wide, to 5 cm long, yellowish brown in herbarium, regularly to irregularly pinnate. *Branches Radula*-type. *Stems* 200–400 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to imbricate, plane to slightly convex, strongly falcate-ovate, 1.2–1.5 mm long, 0.7–0.8 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margins strongly recurved,

sometimes convolute ventrally, rarely plane, entire; marginal cells subquadrate, 15–20 × 10–15 µm, median cells isodiametric to elongated, 20–25 × 15–20 µm, basal cells elongate, 30–35 × 15–20(–25) µm, cell walls thin, trigones large, intermediate thickening present on basal cells, cuticle smooth to finelly verruculose; oil bodies 1 per cell, spherical to ellipsoidal, light yellow, slightly granular, 10–25 × 8–15 µm. *Lobules* distant, subrectangular to convolute and lunular, 0.4–0.6(–0.7) mm long, 0.1–0.3 mm wide, ca. 1/3 the lobe length, strongly inflated along the keel, insertion 2–3× the base length, insertion line straight to curved, base plane, rounded, covering up to 1/5 the stem, free margin plane, almost straight, sometimes covered by the inflated keel, apex plane, rounded, distal margin almost straight, apex and distal margin also covered by the inflated keel, keel concave to convex, spreading at 30–60º with the stem, 120–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* terminal to intercalary on long branches, with 7–12 pairs of bracts, 1–1.3 mm wide; bracts distant, ovate, 0.7–0.9 mm long, 0.4–0.5 mm wide, apex rounded, margin recurved, entire, lobule ovate, ca. 1/2 of lobe length, base straight to almost rounded, free margin straight, apex rounded. *Gynoecia* on long branches, with 2 innovations; bracts oblong-ovate, ca. 1.4 mm long, 0.6–0.7 mm wide, apex rounded, margin plane to recurved, sligltly crenulate, lobules oblong-ovate, ca. 1/2 of lobe length, apex rounded. *Perianth* erect or falcate, trumpet-shaped, 3.5–5 mm long, 0.3–0.5 mm wide at base, 0.8–1.1 mm wide at middle, 1.1–1.7 mm wide at apex, mouth entire, plane; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–5-layered tube within which the sporophyte foot is embedded. *Calyptra* 2–3-layered at the base, 1 cell layer thick above. *Capsule* 1200–1500 µm long, 350–380 µm wide, valves ca. 1.5 mm long, ca. 0.5 mm wide at middle, outer layer cells rectangular to long-rectangular, simple nodular thickenings reddish-brown, on cell angles and evenly spaced along every longitudinal wall, inner layer cells long-rectangular, nodular thickenings absent. *Elaters* 250–300 µm long, finely granulate. *Spores* 29.62–33.33 µm in diam., espiculate, spine composed by nanogranules. *Vegetative reproduction* not observed.

Distribution and habit. Scattered in the Neotropics. Previosly known only from Guyana, Colombia, Ecuador and Peru (Castle 1959, Yamada 1980, Gradstein 2021, Graham *et al.* 2016); new to Panama and Dominica, extending its distribution to Central America and the West Indies (Figure 25). *Radula involvens* is usually found on trees, rarely on rock, in montane forests and páramo at 1000–3600 m.

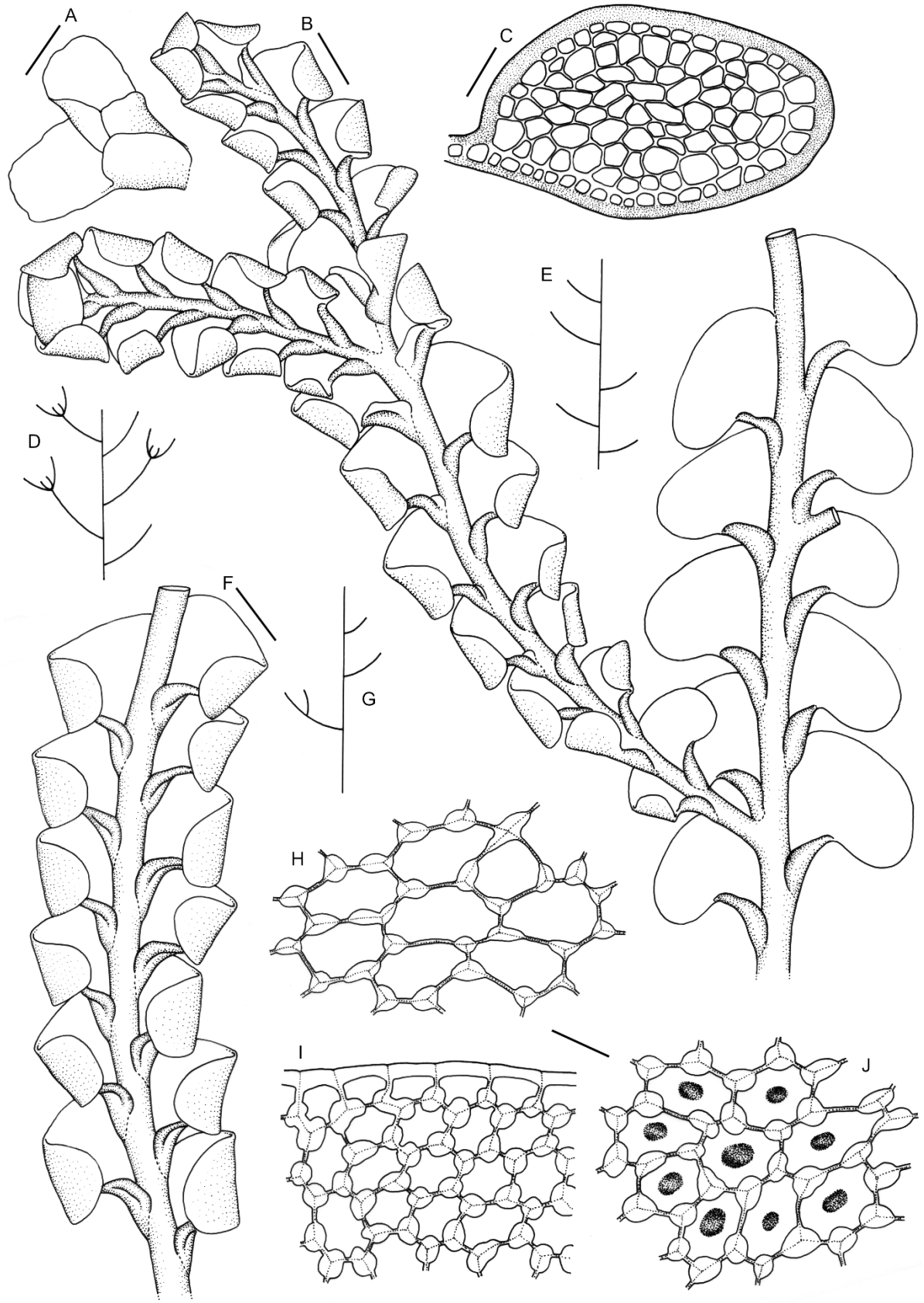

Figure 26. *Radula involvens*. A. Female bracts. B. Habit with gynoecia. C. Cross section of stem. D, E, G. Cladograph of plants (U = gynoecia without perianth). F. Habit. H. Basal leaf cells. I. Marginal leaf cells. J. Median leaf cells (A, B, F = 500 µm, C = 50 µm, H-J = 25 µm; A-D, F from *Gradstein 8358*, E, G, H-J from *Gradstein 5787*).

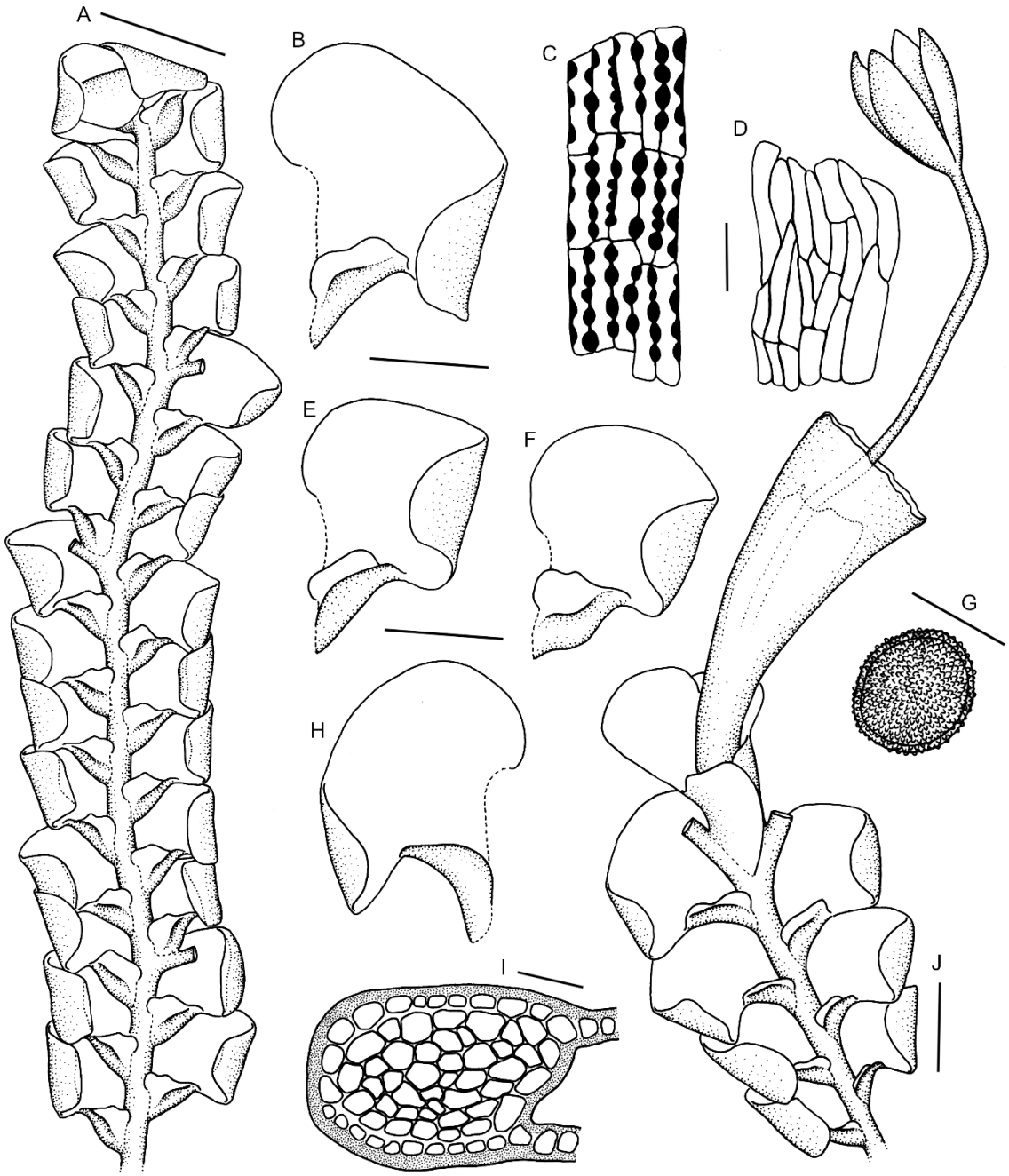

Figure 27. *Radula involvens*. A. Habit. B, E, F, H. Leaves. C. Outer cell layer of capsule wall. D. Inner cell layer of capsule wall. G. Spore. I. Cross section of stem. J. Habit with perianth and sporophyte (A, J = 1000 µm; B, E, F, H = 500 µm, C-D, I = 50 µm, G = 25 µm; A, E, F, I from *Gradstein 5287*, B, H from *Gradstein 8358*, C, D, G, J from *Toapanta & Caranqui 1263*).

Additional specimens examined. PANAMA. BOCAS DE TORO: Parque La Amistad, Valle libre at border Chiriqui, 2470 m, 13 February 1994, *Sallazar-Allen s.n.* (GOET).

DOMINICA. SAINT GEORGE: Trail to sumit of Morne Anglais from Giraudel, mostly in ridgeline elfin cloud forest, old volcanic peak, epiphyte on wet tree trunks along ridge north summit, 15°17'N, 61°20'W, 3000-3600 m, 2 June 1996, *Hill 28082* (MO).

GUYANA. UPPER MAZARUNI: North slope of mout Roraima, ca. 25 m tall, mixed, humid, mossy forest on steep N-facing slope, on poles + logs, 5°17'N, 60°43'W, 1200-1600 m, 14-18 February 1985, *Gradstein 5287, 5441* (GOET); Ibid., on rock, *Gradstein 5391* (GOET); Ibid., on smooth trunk, high up, *Gradstein 5199* (GOET); Ibid., on sapling, *Gradstein 5452* (U, JE).

COLOMBIA. CHOCÓ: West side of Cordillera Occidental, along trail from Jeguadas of Puerto de Oro, W of Mistrato, lower montane rainforest, canopy of the tree ca. 15 m, 1500 m, 25 July 1992, *Gradstein 8358* (GOET).

ECUADOR. TUNGURAHUA: Baños Cantón, El Topo, Parque Nacional Llanganates, bosque primário, bosque siempre verde montano alto, 01°21'S, 78°08'W, 2740 m, 28 November 2001, *Toapanta & Caranqui 1263* (MO).

Radula involvens (subg. *Volutoradula*) is an uncommon and distinct species recognized by the glossy yellowish-brown plants with leaf lobe strongly falcate-ovate, apex usually recurved, leaf cells with large, bulging trigones, and lobules subrectangular to lunular, narrowly inflated along the keel. Specimens from Guyana and Ecuador show a golden coloration at the leaf lobe base, while the specimen from Colombia has a reddish leaf base.

The species is very similar to the rare *R. venezuelensis*, but the latter species differs in having crenulate leaf margins and mammillose leaf cells. Yamada (1982b) suggested that the two species also differ in plant length and leaf apex shape, but these characters seem to overlap. *Radula involvens* may also be confused with *R. tenera* by its yellowish-brown plant color and the convolute, lunulate lobules. However, in the latter species the plants are densely branched and leaf lobes ovate and strongly convex, while *R. involvens* has plants little branched and leaf lobes strongly falcate-ovate and only slightly convex. In addition, *R. tenera* is a smaller plant (only 1–1.4 mm wide).

20. Radula javanica Gottsche, Syn. Hepat. 257. 1845. Type: Caroline Islands, Kusaie (Ualan/Strong Island), "as *R. boryana*, misit Kunth 1833," 1825, *R. P. Lesson s.n.* (lectotype, PC-0031658!, designated by Castle 1966: 73; isolectotype, S-B43105!). Hawaii, Owaihi, hb. Hook. sub. no. 56 as *R. boryana* (isosyntypes, S-B43103!, S-B43104!). India, "Nilgherries," hb. Montagne as *R. boryana*, *Perottet s.n.* (isosyntypes, BM, S-B43099!, S-B43100!). Indonesia, Java, "insula ad Sadjra Prov. Bantam," *Blume s.n.* (isosyntype, S-B43101!, S-B43102!). Mauritius, hb. Sieber as *R. boryana* (isosyntype, G-00265032!).

Radula amazonica Spruce var. *amazonica*, Trans. & Proc. Bot. Soc. Edinburgh 321. 1885. Type: Brazil, Pará, Caripi, "ad rupes maritimas," *R. Spruce s.n.* (syntype, n.v.). Venezuela, "San Carlos, aliisque locis secus fl. Negro, in cortice," *R. Spruce s.n.* (syntype, n.v.). Venezuela, "Ad. fl. Orinoco supra cataractas, in cortice," *R. Spruce s.n.* (syntype, n.v.), syn. fide Yamada (1991, under *R. surinamensis*).

Radula amazonica var. *campanensis* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 322. 1885. Type: Peru, Mt. Campana, "in cortice," 1200 m, *R. Spruce 1446* (lectotype, MANCH-13445A!, **designated here**, c. per.; isolectotypes, BM!, BM! ex K), syn. fide Castle (1966, under *R. amazonica* var. *amazonica*).

Radula amazonica var. *negrensis* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 322. 1885. Type: Venezuela, San Carlos del Rio Negro, *R. Spruce 1443* (lectotype, MANCH-13446!, **designated here**; isolectotypes, NY-01021080!, BM-000969301!, BM-000969302!, BM-000969303!), syn. fide Castle (1966, under *R. amazonica* var. *amazonica*).

Radula conferta Lindenb. & Gottsche var. *conferta*, Syn. Hepat. 729. 1847. Type: Mexico, Mirador, *F. M. Liebmann 332* (lectotype, W!, hb. Lindenberg n° 5544, **designated here**; isolectotype, G-00121982!), ***syn. nov.***

Radula conferta var. *laxior* Gottsche, Mexik. Leverm. 150 (246). 1863. Type: Mexico, April Hacienda de Mirador, hb. *F. M. F. M. Liebmann 9* (not found), ***syn. nov.***

Radula convexa Steph., in Herzog, Biblioth. Bot. 87: 232. 1916. Type: Bolivia, "Nebewald über Comarapa," 2600 m, April 1911, *T. C. J. Herzog 4272* (lectotype, G-00043882!, selected by Yamada, 1982: 451; isolectotype, JE-04003682!), syn. fide Yamada (2000).

Radula elegans Steph., Sp. Hepat. 4: 172. 1910. Type: Panamá, Chiriqui, *Frere Helion s.n.* (lectotype, G-00043875!; selected by Castle, 1966: 15; isolectotype FH!), syn. fide Yamada (1991, under *R. surinamensis*).

Radula falcifolia Steph., Sp. Hepat. 4: 174. 1910. Type: Costa Rica, Carrisal, 1889, 2800 m, *H. Pittier 6013b* (lectotype, G-00042622!, scanty, selected by Castle, 1967: 19; isolectotype, FH!, scanty), syn. fide Yamada (1991, under *R. surinamensis*).

Radula floridana Castle, Rev. Bryol. Lichénol. 36(1–2): 1–4. 1968[1969]. Type: United States, Florida, Timms Hammock, Dade County, 18 March 1915, *J. K. Small & C. A. Moisier 5296* (holotype, NY-00239607; isotype, YU-241687!), syn. fide Yamada (1991, under *R. surinamensis*).

Radula lewisii K.Yamada, J. Hattori Bot. Lab. 74: 39. 1993. Type: Bolivia, Cochabamba, Provo Chapare, "Foothills Chapare", Foothills 8W of Villa Tunari, ca. 20 lan, along

Chapare Highway, 17°00'8, 65°38'W, on rock along the trail, ca. 650111, 4 April 1983, Marko Lewis 83- 1408 (holotype, LPB; isotype, NICH-432556!, scanty), ***syn. nov.***

Radula longifolia Steph., Sp. Hepat. 4: 181. 1910. Type: Guadeloupe, s.d., *A. Duss 128* (lectotype, G-00043904!, selected by Castle, 1966: 21; isolectotype FH!, BM-000969226!), syn. fide Yamada (1991, under *R. surinamensis*).

Radula surinamensis Steph., Hedwigia 23: 136. 1884. Type: Surinam, s.d., *unknown collector*, ex hb. Sande-Lacoste (lectotype, G-00281419!, designated by Yamada 1991: 94; isolectotypes G-00281418!, G-00281420!, G-00113195!), syn. fide Yamada (1989, under *R. caldana*).

Dioicous. *Plants* 1.8–3 mm wide, to 3 cm long, green to yellowish-brown in herbarium, regularly to irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type, rarely *Lejeunea*-type present on decapitated shoots. *Stems* 170–300 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls yellowish to brownish. *Leaf lobes* obliquely to widely spreading, distant to imbricate, slightly convex, rarely strongly convex, ovate to strongly falcate-ovate, 0.8–1.5 mm long, 0.5–1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to rounded, apex rounded, margin plane to slightly recurved, entire; marginal cells subquadrate, 10–15 × 8–12 µm, median and basal cells isodiametric to elongate, 15–30 × 8–15 µm, cell walls thin, trigones small to usually lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, ellipsoidal, light yellow, smooth, 9–10.5 × 5–7.8 µm. *Lobules* distant to contiguous, subquadrate, 0.5–0.8 mm long, 0.3–0.5 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area or along the keel, insertion 1× the base length, insertion line straight to curved, base plane, rounded, covering up to 1/2 the stem, rarely 2/3 or more, free margin plane, straight to slightly rounded, apex plane, rounded to subacute, distal margin straight, keel straight to slightly convex, spreading at angles of 35–50º with the stem, 90–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 3–20 pairs of bracts, 0.8–1.7 mm wide; bracts distant to imbricate, ovate, 0.7–1 mm long, 0.3–0.5 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate, 3/4–1/2 of lobe length, base rounded, free margin straight, apex rounded to obtuse. *Gynoecia* on long or rarely short branches, with 1–2 innovations; bracts ovate, 1–1.3 mm long, 0.5–0.7 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, rarely falcate, subcylindricalal to trumpet-shaped, sometimes

campanulate, 2.5–4.2 mm long, 0.5–0.8 mm wide at base, 0.8–1.1 mm wide at middle, 0.8–1.5 mm wide at apex, mouth entire, plane to irregularly undulate; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall unistratose. *Seta* ca. 6.3 mm long. *Capsule* ca. 1 mm long, 0.25–0.6 mm wide, valves 1.1–1.8 mm long, ca. 0.3 mm wide at middle, outer layer cells subquadrate, simple nodular thickenings reddish-brown, on longitudinal wall of every second wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* 100–300 µm long, rough. *Spores* 25.92–35.18 µm in diam., granulate, granules smooth. *Vegetative reproduction* by means of caducous leaf lobes and regenerants.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Pantropical species, with some records from subtropical regions. *Radula javanica* is very common and widely distributed in tropical America, especially in the lowlands of Amazonia (Figure 28). This species grows creeping to pendent, forming dense to spaced mats on many substrates, usually on trees, but sometimes on dead trees or on rotten logs and rock, rarely on leaves and soil, in shaded, humid habitats in lowland and montane forests, from sea level to 2800 m. This species has also been collected in exposed and disturbed environments, such as managed or depleted forests.

Additional specimens examined. UNITED STATES. FLORIDA: everglade keys, tropical Florida, 21 June 1915, *Small & Moiser 6237* (FH). Ibid., 16 March 1915, *Small & Moiser 5249* (FH). Ferns Grottos, Pineola, on trees and rock, 1937, *Blomquist et al. 8883* (FH). Miami, 26 January 1916, *Lowe s.n.* (FH).

MEXICO. Vera Cruz: Los Tuxlas, 33 km N of Catemaco, on soil along road to the station, 18°34’ N, 96°05’ W, 140 m, 28 September 2004, *Burghardt 4447* (GOET).

BELIZE. BELIZE: in vicinity of Tropical Education Center Mile 28-29 on western higway, on ground, 17°21’N, 88°32’W, 10 m, 5 December 1996, *Allen 17958* (MO). **CAYO:** Limestone sink vicinity of Las Cuevas Field Station, on bark of tree trunk, 16°44’N, 88°59’W, 550 m, 8 December 1996, *Allen 18134* (MO). In forest along ridge, near ridge top camp in vicinity of Doyle’s Delight, southern Maya Mountains, on tree trunk, 16°30’N, 89°03’W, 1098 m, 8 December 1993, *Allen 15124, 15272* (MO).

GUATEMALA. ALTA VERAPAZ: 9 mi up road to Oxec along gravel road which turns N of hwy 7E between Tucuru and El Estor, ca. 6 km NE of Panzós, 800 m, 20 July 1977, *Croat 41665* (MO). **PETÉN:** Tikal National Park, en el tronco de un Ramon, February-March 1959, *Morgan 21* (MO).

HONDURAS. ATLÁNTIDA: La Ceiba, Pico Bonito National Park, in vicinity of UNAH-CURLA campamento, on boulders, 15°42'N, 86°51'W, 95 m, 27 April 1996, *Allen 17652* (MO). **COPÁN:** Copán Ruinas, disturbed primary forest, ca. 18 km north of Copan Ruinas along to Agua Calient at El Zapote, on tree trunk, 14°58'N, 89°10'W, 900-1000 m, 30 April 1996, *Allen 17761* (MO).

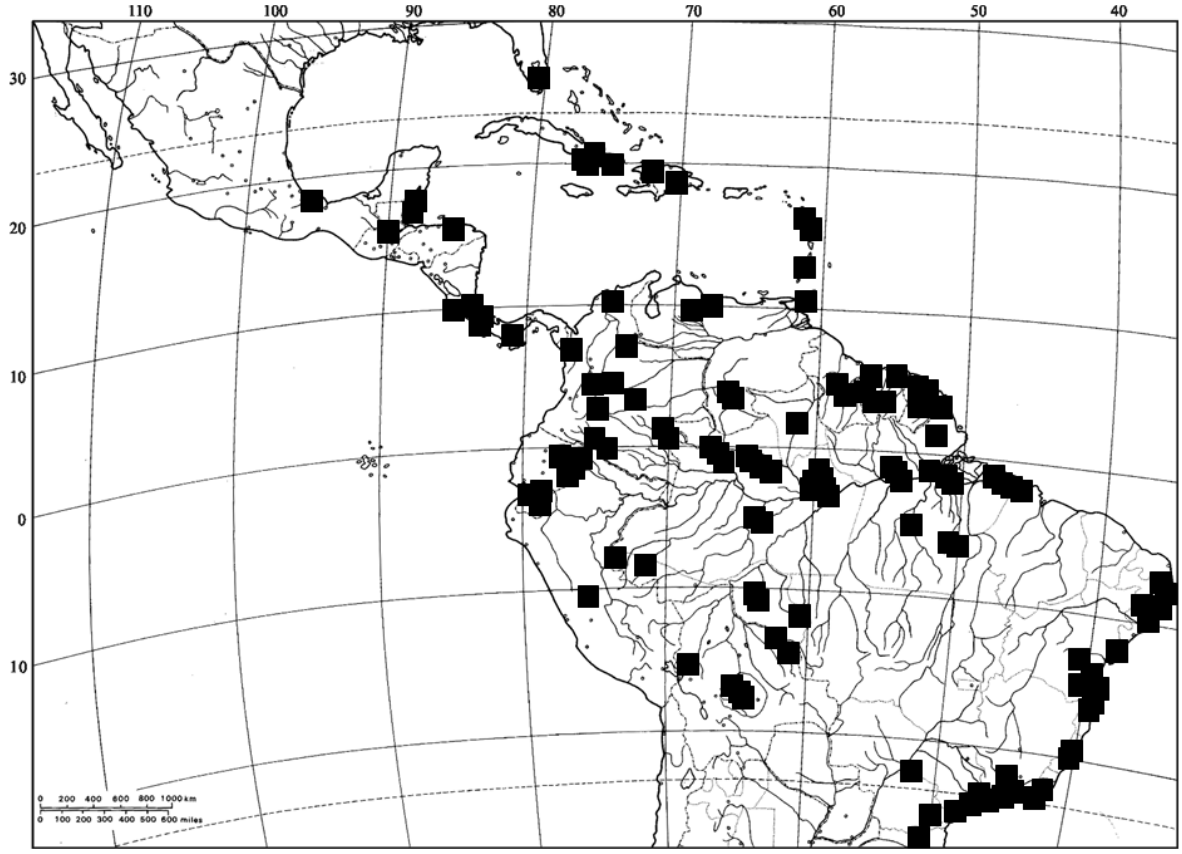

Figure 28. Distribution of *Radula javanica.*

COSTA RICA. CARTAGO: Vicinity of pejivalle, on tree, 900 m, 7-8 February 1926, *Standley & Valerio 47134* (JE). Cerro de La Carpintera, on tree, 1500-1850 m, *Standley 34346* (JE). **GUANACASTE:** Monteverde Biological Preserve, epiphyll, 10°15'N, 84°45'W, 5 August 1993, *Timme 11396* (MO). **LIMÓN:** Tortuguero, lowland Caribbean rainforest, on tree trunk along Rio Mora, 10°31'N, 83°32'W, 2 August 1993, *Timme 11254* (MO). **PUNTARENAS:** Monteverde, October 1969, *James s.n.* (MO). Monteverde, Pacific Slope, Monteverde Cloud Forest Preserve, research area, lower montane wet forest, on fallen small branch, 10°18'N,

84°48'W, 1500 m, 7 March 1992, *Lyon 174* (MO). **SAN JOSÉ:** Isla Cocos, region de Bahia Yglesias, 50 m, February 1976, *Gómez 6577* (MO).

PANAMA. VERAGUAS: lower montane wet forest, 6-7 km W of Santa Fé, on new road past agricultural school, 2900 m, 18 February 1974, *Nee 9860* (MO).

CUBA. Without locality, s.d., *Wright s.n.* (FH-00965704). **HOLGÍN:** Moa, La Melba, valle de Juguani em la zona de la reservación, pluviosa, 3 January 1969, *Bisse & Lippold 011740a, 011741a* (JE). Camino desde Moa hacia La Melba, cerca de 10 km, 30 January 1969, *Lippold 012298a* (JE). **GUANTÁNAMO:** Forallones of La Perla, north of Jaguey, on tree trunk of a rocky wooded slope, 585 m, 1907, *Maxon s.n.* (FH). **SANTIAGO DE CUBA:** falda este de Gran Piedra, pluviosa, 26 April 1969, *Bisse & Lippold 015028a* (JE).

HAITI. Vicinity of St. Louis du Nord, 7April – 30 March 1929, *Leonard & Leonard 14203* (JE). **DU NORD:** Vicinity of Marmelade, on tree, 800 m, *Leonard 8103* (JE). Vicinity of Plaisance, rotten log in dense thicket, 400 m, *Leonard 9333b* (JE).

DOMINICAN REPUBLIC. ST. DOMINGO: Pedernales, Las Abejas, Sierra de Baoruco, on fallen branches on forest floor, 1200 m, 8 November 1979, *Smith 10056* (MO).

GUADELOUPE. Without locality, s.d., *l'Herminier s.n.* (JE, FH-00965699, FH-00965700, FH-00965701, FH-00965741). Without locality, 1973, *l'Herminier s.n.* [Gottsche & Rabenh., Hep. Eur. Exs. 564 as *R. pallens*] (JE).

DOMINICA. SAINT PAUL PARISH: between park trail boundary and Middleham Falls, montane forest above paved road NE of Cochrane, on volcanic bedrock at falls, 2200 m, 20 March 1990, *Hill 21274* (MO). **SAINT JOHN PARISH:** Syndicate Estate, south of Northern Forest Reserve, near base of trail to Morne Diablotins summit, trail to parrot overlook in reserve, in primary rainforest on trunks, 2000 m, 17 March 1991, *Hill 22056* (MO).

MARTINIQUE. Auf morschem Holz beim Forsthaus, Balata, März 1952, *Hürlimann T 1258 II* (GOET).

ST. VINCENT. Without locality, March 1890, *Smith & Smith 1385* (FH).

TRINIDAD AND TOBAGO. Without locality, s.d., *Crüger s.n.* (FH-00965703). Long stretch via Valencia, on rotten wood, 18 May 1923, *Broadway 7505* (MO). **TUNAPURNA PIACO:** Caura, on wet shaded ground, 11 January 1929, *Broadway 7077* (MO).

FRENCH GUIANA. ROURA: Emerald Jungle Village, secondary moist forest, bark, 4°17'11" N, 52°25'38" W, 60 m, 11 September 200, *Holz FG 00-62* (GOET). **CAYENNE:** Ct. de Approuague-Kaw, Pic Matécho, camp side, primary moist forest, bark, 3°45' N, 53°03' W, 500 m, 17 September 2000, *Holz FG 00-0197* (GOET). **SAÜL:** mixed forest "Sentier Limonade", south of the village, on pole, 23-30 June 1986, *Gradstein 6169* (GOET). Ibid., on

treelet, *Gradstein 6173, 6170* (GOET). Moist forest south of the village, epiphytic, 23-30 June 1986, *Gradstein 6084* (GOET). 2 km SW of the village, "sentier limonade", lowland moist forest on laterictic soil, epiphytic on upper trunk, 03°32' N, 53°12 W, 180-210 m, 13 August 1986, *Montfoort & Ek 1117, 1120* (GOET). Primary forest near Boeuf Mort, on buttresses, 53°12' W, 3°38' N, 200-300 m, March 1985, *A. Artroot 15310* (GOET).

SURINAME. Brownsberg, November 1975, *Florschütz s.n.* (GOET). **NICKERIE:** area of Kabalebo Dam project, near camp road km 23, line on westbordes of river kabalebo rainforest, on bark of living tree, 150 m, 6 November 1981, *Bekker 1327* (GOET). Area of Kabalebo Dam project, line W from road km 34, on Marshforest, on feet of tree near water, 2 November 1981, *Bekker 1185* (GOET). Area of Kabalebo Dam project, line E from road km 80, on rainforest, on a rotting log, 10 November 1981, *Bekker 1413* (GOET). **SIPALIWINI:** El Dorado Falls, small stream feeding Nickerie River, 3 km NE of Blanche Marie Guest House, on trunk of fallen tree, 4°45'N, 56°53'W, 50-100 m, 10 June 1997, *Allen 19240* (MO). Blanche Marie valley, bark, 4°44'N, 56°53'W, 100 m, 2-7 February 1998, *Muñoz 98-21*, *98-52* (MO). Vicinity of Blanches Marie guest houses on Nickerie River, on tree limb by river, 4°45'N, 56°52'W, 50 m, 8 June 1997, *Pursell 11688* (MO). Ibid., on loose tree bark, along trail to waterfalls, 7 June 1997, *Pursell 11631* (MO). Vicinity of Blanches Marie Falls, along the Nickerie River, on bark, 50-60 m, 7 June 1997, *Price 208* (MO).

GUYANA. Mabura Hill, 180 km SSE of Georgetown, dry, evergreen forest on white sand, on lower canopy branches, 5°20' N, 58°40' W, 50 m, 27 March 1985, *Cornelissen & ter Steege C592* (GOET). Ibid., on trunk of fallen tree on trail, 2 March 1985, *Cornelissen & ter Steege C067* (GOET). Mabura Hill, 180 km S of Georgetown, on decaying log in dry evergreen "wallaba" forest on white sand, 5°20' N, 58°40' W, 0-50 m, 16 April 1985, *Cornelissen & ter Steege c217* (MG, MO). Junction of Mazaruni and Cuyuni Rivers, 6 July, *Graham 165a* (MO).

VENEZUELA. AMAZONAS: Cerro Huachamacari, Río Cunucunuma, Montane rainforest near camp II, on trunk of leaving tree, 1200 m, 12 December 1950, *Marguire et al. 29913* (MG, NY). Atabapo, 2 km east of Culebra on Río Cunucunuma, 3°44'N, 65°44'W, 210-300 m, 17 February 1985, *Liesner 17904* (MO). **ARAGUA:** Maracay, Rancho Grande, puerto chuelo, Ocumare, 1000 m, 27 February 1958, *Mägdefrau 433* (JE). **YARACUY:** Hacienda Guaquira, Cerro Zapatero, sobre arbol, 10°15'N, 68°38'W, 17 June 2008, *Morales et al. 1359* (MO).

COLOMBIA. Cassiquiare, Capiguara, 120 m, 27 January 1958, *Mägdefrau 194A* (JE). **SANTANDER:** western slope of Páramo de las Puentes above La Baja, oak forest, on tree, 3300-

3400 m, 25-31 January 1927, *Killip & Smith 18172* (JE). **PUTUMAYO:** Mocoa, Vereda Alto Campucana, finca "La Mariposa", epífito, 21 April – 1 May 1994, *Giraldo-Cañas 2052* (MO).

ECUADOR. ZAMORA CHINCHIPE: 600 m, *Harling 2259/a pp., 2256 pp., 2257 pp.* (JE). El Pangui, región de la Cordillera del Cóndor, cuenca del Río Tundayme, 14 km SO de campamento de Mirador, bosque montano bajo, sobre tronco de arbolito, poco sol, 3°37'19"S, 78°28'54"W, 1480-1520 m, 9 December 2005, *Churchill et al. 24534* (MO).

PERU. HUÁNUCO: Leoncio Prado, 660 m, 21 October 1973, *Hegwald 7776* (MO).

BRAZIL. ACRE: Vicinity Serra da Moa, 24 April 1971, *Prance et al. 12429* (NY). **ALAGOAS:** Murici, Estação Ecológica de Murici, 9°11'05"S, 35°45'20"W, 24 March 2006, *Alvarenga s.n.* (UFP). **AMAPÁ:** Oiapoque, BR156, 109 km SSE of Oiapoque on road between Oiapoque and Calçoene, 3°0'N, 51°30'W, 6 December 1984, *Mori et al. 17221* (MG). **AMAZONAS:** Manaus, Reserva Florestal Ducke, 2 April 1971, *Prance et al. 11311* (NY). Barcelos, Acânga, 01°10' S, 61°30' W, 27 June 1979, *Schuster 79-3-90* (SP). São Gabriel da Cachoeira, Serra do Curicuriari, from Igarapé Arabú on Rio Curicuriari to summit, 00°20' S, 66°50' W, 450 m, 9 July 1979, *Schuster 79-15-567, 79-15-706, 79-15-576* (SP). Presidente Figueiredo, cachoeira de Iracema, ca. 800 km de Manaus, no paredão úmido da trilha, 5 September 2010, *Yano & Zartman 32710* (SP). Rio Negro, Ilha Acaburu, sobre pau podre, 00°40' S, 66°40' W, 4 July 1979, *Yano 1663* (SP). **BAHIA:** Santa Teresinha, Povoado de Pedra Branca, Serra da Jibóia, Morro da Pioneira, Caatinga, em floresta ombrófila, corticícola, 12°50'58"S, 39°28'33"W, 791 m, 6 October 2016, *Bastos 5801* (ALCB). Boa Nova, recanto dos Pássaros, floresta ombrófila densa, terrícola, 26 June 2013, *Souza et al. 561* (SP). Uruçuca, Serra Grande, Mata Atlântica, na base de um tronco cortado, 14°35'35"S, 39°17'04"W, 100 m, 17 July 1991, *Vital s.n.* (SP). **ESPÍRITO SANTO:** Linhares, Reserva Florestal de Linhares, Acerro do Calimã, 17 January 1996, *Costa et al. 2976* (RB). Linhares, Reserva Natural do Vale do Rio Doce, 19 October 2000, *Yano et al. 26585, 26394, 26449* (SP). **MINAS GERAIS:** Lima Duarte, Parque Estadual do Ibitipoca, 1400 m, 9 August 1993, *Yano et al. 20266* (SP). **PARÁ:** Bragança, Rodovia PA 112, comunidade do km 20, 1°11'55,4"S, 46°05'40,6"W, 16 June 2010, *Pietrobom et al. 8362* (HBRA). Almerim, FLOTA do Paru, próximo ao rio Parú, floresta de terra firme alterada, epífita na base de tronco vivo próximo ao rio, 00°57'19,9"N, 53°14'44"W, 70 m, 6 December 2008, *Pietrobom & Marciel 8171* (SP). Tracuateua, Vila Fátima, floresta de terra firme, epífita na base de tronco vivo no interior da mata, 01°11'16,6"S, 47°00'28"W, 22 June 2011, *Lima et al. 200, 201* (SP). Belém, Reserva do Mocambo, mata de terra firme, lugar muito úmido, sobre tronco vivo, 9 June 1982, *Lisboa 661* (SP). Capanema, balneário toca do índio, próximo a BR 308, km 4, floresta de igapó, epífita na base de tronco vivo, 01°12'40,9"

S, 47°08’06,3” W, 1 December 2010, *Ferreira & Brito 4* (SP). Serra do Cachimbo, Base aérea do Cachimbo, km 780-820 on Cuiabá-Santarém highway (BR 163), ca. 20 km N of border of Mato Grosso, Sandy plain with sandestone exposures, on small tree uin forest along Rio Braço Norte, 9°22’S, 54°54’W, 25-30 April 1983, *Reese 16412* (MO). **PARAÍBA:** Sapé, Reserva Particular do Patrimônio Natural Fazenda Pacatuba, 7°02’33”S, 35°09’24”W, 11 December 2009, *Silva & Oliveira 511* (UFP). **PARANÁ:** Lapa, Reserva Particular do Patrimônio Natural Uru, 25°48’35”S, 49°41’05”W, 855 m, 11 December 2013, *Ristow & Santos 3711* (SP). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 27 August 1987, *Pôrto 2583* (UFP). São Vicente Férrer, complexo da Serra dos Macarenhas, epífita sobre tronco vivo, 07°35’00”S, 35°30’00”W, 600-650 m, 22 February 1999, *Pietrobom-Silva 4534* (SP). **RIO DE JANEIRO:** Nova Friburgo, 790 m, 5 May 1988, *Costa et al. 675* (RB). **RIO GRANDE DO SUL:** Cambará do Sul, Fortaleza dos Aparados, 23 November 1995, *Lemos-Michel 3024* (SP). **RONDÔNIA:** along rio Pacaás Novos, between its confluence with the Rio Mamoré and the first rapids, várzea forest, on small tree, 8-13 March 1978, *Reese 13301* (JE). 2-4 km above the first rapids on the Rio Pacaas Novos, 15–22 March 1978, 400 m, *Reese 13474* (MG, JE). **RORAIMA:** Br 174, vicinity of army base, acampamento do 6° BEC-Jundia, 100 m, 16–17 November 1977, *Buck et al. 1842* (INPA). **SANTA CATARINA:** Lajes, Morro do Pinheiro Seco, 950 m, 14 July 1963, *Reitz & Klein 15791* (SP). **SÃO PAULO:** Ubatuba, Parque Estadual Serra do Mar, Núcleo Picinguaba, 23°26’02”S, 45°04’16”W, 10 m, 4 October 1988, *Vital & Visnadi 16354* (SP). Peruibe, Estação Ecológica da Juréia, sobre casca de tronco vivo, 24°33’S, 47°14’W, 20 November 1987, *Vital 15714* (SP). Natividade da Serra, on leaves of treelets, in a small area of residual Atlantic forest, 23°20’ S, 45°27’ W, 17 August 1987, *Vital 15179* (SP); Teodoro Sampaio, região do pontal do Paranapanema, Parque Estadual Morro do Diabo, terrestre, 22°32’S, 52°11’W, 250-350 m, 11 January 1995, *Silva 1552* (SP). Cananeia, Ilha do Cardoso, growing 1m upo n tree trunk in a swampy gallery forest, 24 May 1974, *Vital 3208* (SP); Praia Grande, lado direito do Palácio São Francisco de Assis, na base do tronco de arbusto na restinga da Cidade Ocean, 8 November 1992, *Yano & Marcelli 17614* (SP). Im Wald der Morre do Jaguará, 30 April 1921, *Hoehne 240* (JE). Jaraguá, 21 June 1921, *Hoehne 409/b, 13* (JE). Moji das Cruzes, Parque Municipal da Serra do Itapety, mata Atlântica, sobre tronco caído, área aberta, 23°31’22”S, 46°11’18”W, 1000 m, *Peralta & Cunha 3181* (SP, MO). Teodoro Sampaio, região do Pontal do Paranapanema, Parque Estadual Morro do Diabo, terrestre em barranco com solo úmido e sombreado, 16 January 1995, *Silva 1552* (MO).

BOLIVIA. BENI: Itenez, caminho a Mategua, 65 km de Tiquin em línea recta, más de 25 km después de la Concesión Forestal San Luis de ida a Aproon Patuju, segundo puete de

palos, boque amazónico-chiquitano, intervenido, 13°27’28”S, 62°32’18”W, 174 m, 17 September 2012, *Linneo & Rossell 2956A* (MO). **COCHABAMBA:** Chapare, Paque Machia, cerca Villa Tunari, Bosque subandino em transición com amazónico, sobre raiz de palma, 16°58’S, 65°24’W, 240 m, 31 October 2002, *Churchill et al. 22173, 22187* (MO). Chapare, Parque Nacional de Carrasco, Santuario de Los Guácharos, al lado de Río San Mateo, bosque amazónico premontano, sobre tronco de árbol, 17°06’08”S, 65°30’46”W, 615 m, 9 December 2007, *Costa et al. 4893* (MO). Carrasco, Estación Experimental Sacta, bosque amazónico, sobre tronco de árbol, poco sol, 17°04’56”S, 64°30’26”W, 220 m, 18 June 2004, *Churchill 23014* (MO). Carrasco, Pojo, Estación Experimental Sacta, Sandero que va a la parcela permanente de Fambo, boque amazónico, sobre tronco de arbolito, 17°05’S, 64°46’W, 250 m, *Churchill & Arroyo 21637* (MO). Tiraque, Shinaota, km 280 carretera Cochabamba – Santa Cruz, siguiendo senda que continua a la avenida Busch, boque premontano húmedo, sobre tronco de árbol, 16°59’S, 65°14’W, 450 m, 6 August 1992, *Fuentes 118* (MO). **LA PAZ:** Franz Tamayo, village Ilipana Yuyo, 32 km S de Apolo, bosque yungueño, cresciendo sobre árbol, 14°43’02”S, 68°24’51”W, 1447 m, *Inturias et al. 335* (MO). **SANTA CRUZ:** Velasco, entrando por Santa Rosa de la Roca em la localidad de Cerro Pelao, bosque amazónico-chiquitano, cresce em corteza, 14°22’19”S, 61°37’15”W, 235 m, 18-25 May 2012, *Linneo 2896* (MO). Velasco, Parque Nacional Noel Kempff Mercado, parcela permanente de estúdio Los Fierros, bosque humedo Chiquitano, sobre tronco de arbolito, 14°32’S, 60°48’W, 250 m, 3 June 2001, *Churchill et al. 20506* (MO).

Radula javanica (subg. *Radula*) is a very polymorphic species and has been described under many different names (see *e.g.* Yamada 1979, 1991, 2000, So 2005, 2006, Oliveira-da-Silva *et al.* 2021). The main characters are plants irregularly pinnate, leaf lobes distant to imbricate, ovate to strongly falcate-ovate, frequently caducous, leaf cells usually without trigones, lobules distant to contiguous, subquadrate, apex rounded to subacute, base rounded, covering up to 1/2 of stem width, rarely more, and keel straight to slightly convex.

This species may be confused with several species but especially with *Radula recubans*. The latter species, however, differs in stem anatomy and in the widely rounded lobule base, covering 2/3 to overlapping the entire stem. In addition, some specimens of *R. recubans* have leaf cells with verruculose cuticle, which was not seen in Neotropical *R. javanica*.

Radula conferta and *R. lewisii* are new synonyms of *R. javanica.* The former species was well described and illustrated by Castle (1966) and Yamada (1980). No morphological differences distinguishing it from *R. javanica* were mentioned by the latter authors. However,

in Castle and Yamada's illustration it is possible to observe that the innovation does not appear (even though it is mentioned in the description) and the leaves below the female bracts are strongly imbricated and of the same size as the bracts (or even larger). This characteristic gives the impression that the gynoecia is composed by a set of more than one pair of bracts. In our observations of the type specimen, however, we recognized rudimentary innovations and that only a few gynoecia had 2–3 pairs of bracts-like below the innovations. The type material of *R. conferta* in W is designated as the lectotype since this herbarium holds the Lindenberg collections (*e.g.* Gradstein 2016).

21. Radula leiboldii Steph., Hedwigia 23: 116. 1884. Type: Mexico, without locality, s.d., *F. E. Leibold s.n.* (lectotype, G-00043903!, c. per., selected by Castle 1963: 27).

Radula arsenii Steph., Sp. Hepat. 6: 505. 1924. Type: Mexico, without locality, s.d., *G. J. B. Arsène 7800* (lectotype, G-00067964!, selected by Castle, 1964: 188), syn. fide Castle (1964).

Radula aurantii Spruce, Bull. Soc. Bot. France 36 (Suppl. Congrés Bot. 1889): CXCIV. 1889[1890]. Type: Paraguay, Guarapi, "sur le tronc des orangers," 1884, *B. Balansa 3715* (lectotype, G-00047494!, c. per. + spor., **designated here**; isolectotypes, G-00124017!, c. per. + spor., G-00124018!, c. per. + spor., BM!, c. per. + spor.). Paraguay, Cordillere de Péribebuy, 1879, *B. Balansa 4248* (syntype, G-00124020!), syn. fide Yamada (1981).

Radula uleana Steph., Sp. Hepat. 4: 201. 1910. Type: Brazil, without locality, s.d., *E. H. G. Ule 244* (lectotype, G-00043874!, c. per. + spor., selected by Yamada, 1981: 397; isolectotype, JE-04003675!, c per. + spor.). Brazil, without locality, s.d., *E. H. G. Ule 348* (syntype, G-00264265), syn. fide Castle (1964, under *R. aurantii*).

Radula tectiloba Steph., Hedwigia 27: 298. 1888. Type: Puerto Rico, without locality, s.d., "in cortice," *P. E. E. Sintenis 65* (lectotype, G-00043865!, selected by Oliveira-da-Silva *et al.* 2021: 141; isolectotypes, G-00281377!, FH!, BM-000969247!, BM-000969248!), ***syn. nov.***

Dioicous. *Plants* 1.6–2 mm wide, to 1 cm long, yellowish-green to yellowish-brown or green to olive green in herbarium, regularly to irregularly pinnate. *Branches Radula*-type. *Stems* 90–160 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thick-walled (by concave trigones), yellowish medullary cells, outer epidermal wall

heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, convex, ovate, 0.6–1.1 mm long, 0.5–0.8 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to recurved, entire to crenulate with gemmae; marginal cells subquadrate to rounded, 12–25 μm in diam., median cells and basal cells isodiametric to elongate, 20–30 × 15–25 μm, cell walls thin, trigones small to medium-sized, cuticle smooth; oil bodies not observed. *Lobules* distant to subimbricate, subquadrate, 0.5–0.8 mm long, 0.3–0.5 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area and along the keel, insertion ca. 2× the base length, insertion line straight, base plane, rounded, covering ca. 1/2 the stem, rarely overlapping, free margin plane, rarely recurved, straight, apex rounded to obtuse, sometimes angular-obtuse, distal margin straight, keel concave to convex, spreading at angles of 50–60º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 4–8 pairs of bracts, 0.6–0.8 mm wide; bracts distant to subimbricate, ovate, 0.4–0.5 μm long, 0.25–0.3 mm wide, apex rounded, margin recurved, entire to crenulate, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.8–0.9 mm long, 0.5–0.6 mm wide, apex rounded, margin recurved, entire to crenulate with gemmae, lobule oblong-ovate, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical, 1.7–2.2 mm long, 0.7–0.8 mm wide at base, 1–1.2 mm wide at middle, 0.8–1.1 mm wide at apex, mouth entire to crenulate with gemmae, plane to slightly undulate; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall unistratose. *Seta* 2–2.7 mm long *Capsule* ca. 0.8 mm long, ca. 0.5 mm wide, valves 0.7–0.8 mm long, 0.1–0.2 mm wide at middle, outer layer cells subquadrate to subrectangular, confluent adnate nodular thickenings reddish-brown, on every longitudinal wall, inner layer cells long-rectangular to polymorphous, nodular thickening on the walls, semi-annular bands present, associated with the thickenings. *Elaters* and *Spores* not observed. *Vegetative reproduction* by numerous small discoid gemmae, 30–60 μm in diam., produced on the margins of leaves, perianths and bracts.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Tropical and subtropical America. In addition to the countries mentioned in the additional examined specimens section, *Radula leiboldii* was reported from Jamaica, Costa Rica and French Guiana (see Castle 1964, as *R. tectiloba*, Gradstein & Ilkiu-Borges 2009, as *R. aurantii*, Schäfer-Verwimp & Melick 2016, as *R. tectiloba*) (Figure 29). This species usually grows on trees, rarely on rotten logs, rock or soil, in humid lowland to montane forest, rarely in subalpine forest, from sea level to 3200 m. In Brazil, *R. tectiloba* is very common in the Atlantic Coastal Region, especially in *Araucaria* forests in southern Brazil. The species forms large, dense mats that may be prostrate or pendent.

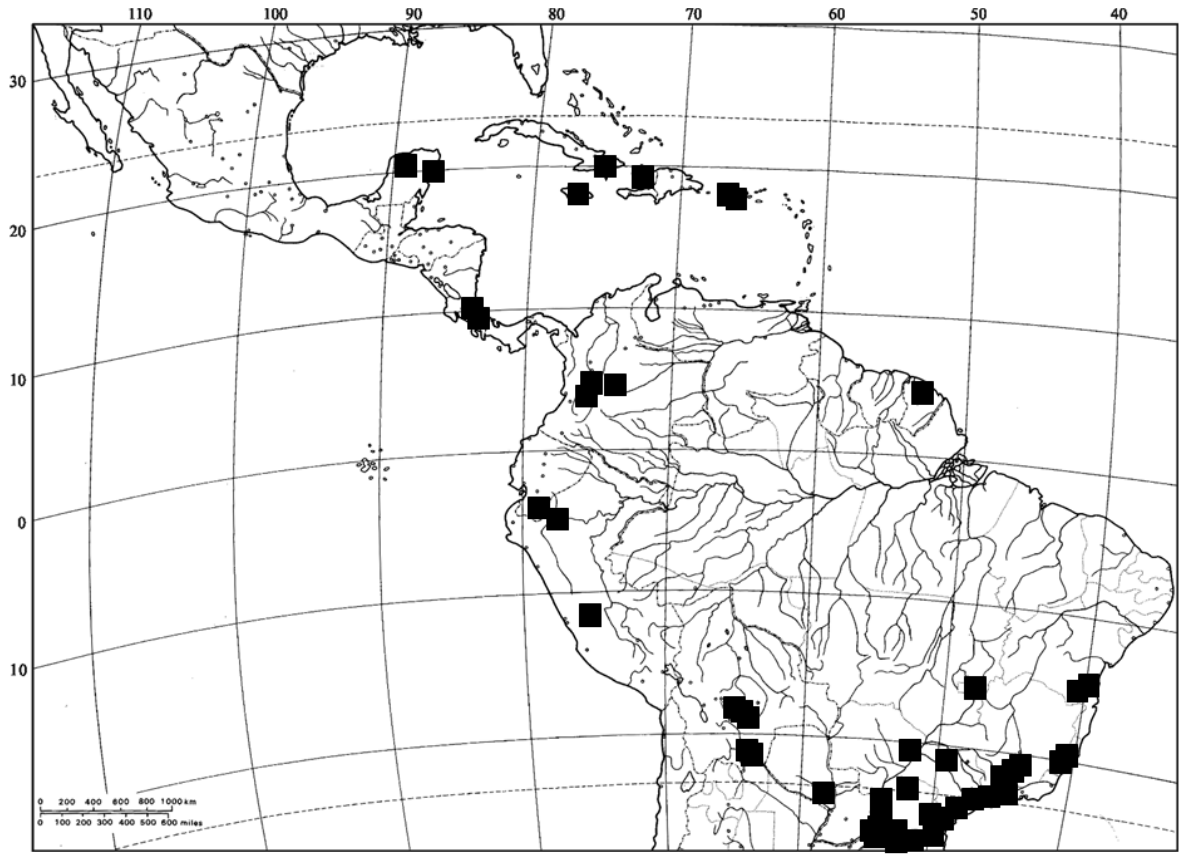

Figure 29. Distribution of *Radula leiboldii.*

Additional specimens examined. MEXICO. Types of *Radula arsenii* and *R. leiboldii* (G).

CUBA. GUANTÁNAMO: La Municion, Yateras, *Schubert M199-b* (JE). **VILLA CLARA:** 5 km westlich Topes de Collantes, *Schubert M376-b* (JE).

HAITI. L'ARTIBONITE: summit east of Ennery, 325-900 m, *Leonard 9004, 9006a* (JE).

PUERTO RICO. Type of *Radula tectiloba* (G).

COLOMBIA. BOGOTÁ: Boquerón, 3200 m, 1929, *Troll 2198* (JE). **TOLIMA:** Santa Isabel, Finca El Ochoral, 2960 m, 28 July 1980, *Aguirre 1572* (GOET).

ECUADOR. ZAMORA-CHINCHIPE: Reserva Biológica San Francisco 30 km from Loja, 3°58'18" S, 79°04'44" W, 1800-3150 m, *Nöske 1003* (GOET).

PERU. PASCO: 2-4 km east of Oxapampa, 10°36'S, 75°23'W, 1820-1920 m, *Smith C-404* (MO). **AMAZONAS:** Bagua chica, 1200 m, *Hegewald 7143* (MO).

BRAZIL. **BAHIA:** Itabuna, nas plantações de Cacau da CEPLAC, 24 January 1980, *Vital 8697* (SP). Itambé, em fragmento florestal, Floresta estacional semidecídua, corticícola, 15°10'58" S, 40°20'28" W, 28 Abril 2011, *Reis 2761* (ALCB). **DISTRITO FEDERAL:** Brasília, no km 38,5 da BR 040, Reserva Ecológica do IBGE/Recor, Ponte do Corujão, 15°56'14"S, 47°53'09"W, 12 March 2016, *Yano & Kirizawa 34081* (SP). **ESPÍRITO SANTO:** Castelo, Parque Estadual do Forno Grande, 20°31'00"S, 41°05'14"W, 1250 m, 1 October 2016, *Peralta et al. 19270* (SP). Domingos Martins, Reserva Florestal Pedra Azul, in kleiner Bachschlucht epiphytish, 27°25'S, 41°01'W, 9 October 1988, *Schäfer-Verwimp & Verwimp 10119* (JE). Vagem Alta, feuchte Sekundärvegetation in kleiner Bachschlucht hinter dem Hotel Cheminé, epiphytisch, 20°40'S, 41°01'W, 700 m, 15 October 1988, *Schäfer-Verwimp & Verwimp 10367* (JE). **MATO GROSSO DO SUL:** Mundo Novo, perto da cachoeira, 18 March 1982, *Yano 4033* (SP). Três Lagoas, reserva agroflorestal, sobre tronco de árvore, 230 m, 12 September 1992, *Yano & Marcelli 17073* (SP). **MINAS GERAIS:** Três Corações, margem do Rio Santa Fé, 25 September 2008, *Yano & Kirizawa 31316* (SP). Serra da Mantiqueira, Camanducaia, na Strauch an der Straβe zur Hotel Fazenda Serra Negra, 1240 m, 16 July 1991, *Schäfer-Verwimp & Verwimp 14699/A* (JE). Serra de São José, estrada para o Calçadão, sobre tronco de arbusto na trilha, 21°5' S, 44°5' W, 800 m, 3 December 1993, *Yano et al. 21793* (SP). Caldas, sobre tronco de árvore, mata ciliar, 960-1105 m, 14 April 2017, *Yano & Lopes 34191* (SP). Nepomuceno, Km 647 da BR Fernão Dias, sobre tronco de árvore viva na mata, 18 Mar 1983, *Yano & Santos 6198* (SP). Coronel Pacheco, Km 63 da BR 133, sobre tronco vivo, mata secundária, 26 May 1983, *Yano & Pirani 7251* (SP). **PARANÁ:** Pinhais, Centro Paranaense de Referência em Agroecologia, Jardim Boa Vista, 25°23'20"S, 49°07'01"W, 900 m, 14 October 2013, *Ristow & Picote 3552* (SP). Curitiba, Stadtzentrum, epiphytisch an Alleebaum in der Umgebung der Praça Ten. E. Vidal, 25°25,9'S, 49°15,3'W, 915 m, 20 November 2012, *Schäfer-Verwimp 34060* (MO). Serra do Mar, nordlich Curitiba, Capivari Grande, Sekundarvegetation unterhalb der Antennen, epiphytisch, 25°07,2'S, 48°49,6'W, 1108 m, 17 November 2012, *Schäfer-Verwimp 33857* (JE). Kolonie Iguazú, in der feuchter Schluchten des Nationalparks des Río Iguazú, im Urwald, 16 July 1933, *Hosseus 4B* (JE). General Carneiro, Km 520 da BR 153, sobre árvore viva, mata de Araucária, 20 April 1983, *Yano & Pirani 6507* (SP). Pato Branco, Rio Pato Branco na BR 280, sobre tronco de árvore viva na mata ciliar, 15

Jan 1983, *Yano et al. 5435* (SP). Guaraniçu, BR 277, Km 321, hanging from branches and trunks of trees, 14 March 1976, *Vital 5777* (SP). Realeza, sobre tronco de árvore, 15 January 1983, *Yano et al 5474* (SP). **RIO DE JANEIRO:** Itatiaia, Serra do Itatiaia, Brejo da Lapa, 26 November 2012, *Yano & Morretes 33376* (SP). **RIO GRANDE DO SUL:** Caxias do Sul, 780 m, 25 September 2005, *Bordin 140c* (SP). Caxias do Sul, bairro Cinquentenário, sobre muro de pedra, 780 m, 9 February 2006, *Bordin & Sartori 422* (HUCS, MO). Campus da UCS, sobre tronco na mata ao lado da creche, 780 m, 17 January 2006, *Bordin & Pasini 298* (HUCS, MO). Serra Gaúcha, Gramado, Park Knorr, epiphytisch, 850 m, 19 January 1987, *Schäfer-Verwimp & Verwimp 8197* (JE). Montenegro, an Zypresse, 1952, *Warnke 6* (JE). Colônia nova Wuttenburg, 450 m, 15 August 1905, *Bornmüller s.n.* (JE). Porto Alegre, 9 July 1897, *Reineck s.n.* (JE). **SANTA CATARINA:** Chapecó, Ecoparque, 27°05'10"S, 52°37'02"W, 660 m, 31 July 2013, *Villagra 695* (SP). São Miguel D'Oeste, perímetro urbano, sobre tronco vivo, 16 January 1983, *Yano et al. 5502* (SP). Jaborá, 5 Km antes da cidade, sobre tronco vivo, 22 April 1983, *Yano & Pirani 6702* (SP). Lages, praça João da Costa, sobre tronco vivo, 28 April 1983, *Yano & Pirani 7102* (SP). Berland bei Fraiburgo, feuchter Wald im Park des Hotels Renar, an Kiefernborke, 27°01'S, 50°52'W, 1100 m, 11 October 1987, *Schäfer-Verwimp & Verwimp 9099* (JE). **SÃO PAULO:** Campos do Jordão, Parque Estadual de Campos do Jordão, caminho para Mirante das Cachoeiras, 1350 m, 22 June 1993, *Yano & Marcelli 19466* (SP). Teodoro Sampaio, ca. 700 km westlich von São Paulo, Primärwald am Morro do Diabo, epiphytish im Gipfelbereich, 22°31'S, 52°18'W, 570 m, 14 February 1988, *Schäfer-Verwimp & Verwimp 9459/B* (JE). Galeriewald an der Raposo Tavares, km 501, ca. 65 km östlich von Presidente Prudente, epiphytisch, 350 m, 13 February 1988, *Schäfer-Verwimp & Verwimp 9435* (JE). Piraju, in a cerrado vegetation, on bark of tree trunk, 23°17'S, 49°16'W, 30 December 1977, *Vital 7842, 7844* (JE). Near top of Morro Pedolo, on base of tree trunk, 1974, *Vital 4820* (JE). Serra da Paranapiacaba, Fazenda Intervales sudlich Capão Bonito, epiphytisch in lichtem Sekundärwald am Weg zum Morro do Mirante, 24°16'S, 48°25'W, 950 m, 20-22 April 1990, *Schäfer-Verwimp & Verwimp 12624* (JE). Ilha de Santo Amaro, Mangrove-Vegetation am Kanal von Bertioga, epiphytisch, 23°52'S, 46°09'W, 2 m, 22 November 1991, *Schäfer-Verwimp & Verwimp 15064* (JE).

BOLIVIA. CHUQUISACA: Belisario Boeto, al lado de Río Alisos, Nuevo Mundo, ca. 22 km Villa Serrano por Nuevo Mundo, bosque montano de Tucumano-Boliviano, sobre ramas de arbolito, 19°00'00"S, 64°18'50"W, 2300 m, 19 July 2004, *S. Churchill et al. 23051, 23060* (MO). **SANTA CRUZ:** Vallegrande, caminho de Vallegrande hacia Las Pampitas, El Rodeo, a 16.9 km al norte de Villegrande, caminho antigua de las rutas del Che. Prepuna, borde de

caminho, sobre arbol, 18°37’22”S, 64°07’32”W, 2786 m, 24 August 2011, *S. Carreño & M. Huanca 1436* (JE, MO). Vallegrande, Guadalupe, boque montano de Tucumano-Boliviano, sobre árbol, 18°33’43”S, 64°06’28”W, 2385 m, 23 July 2011, *Inturias et al. 403B, 497* (MO). Vallegrande, Huasacañada, 5 km al norte de Vallegrande, vales internos andinos com vegetación degradada, sobre ramas secas em bosquecillo de quebrada, 18°26’S, 64°05’W, 2000 m, 3 November 1993, *Fuentes & Vargas 236* (MO). Vallegrande, 7 km norte de Postrer Valle, caminho a Tierras Nuevas, Bosque Tucumano-Boliviano, sobre ramas de árbol, 18°28’59”S, 63°51’57”W, 2240 m, 13 September 2006, *Churchill & Linneo 24553* (MO). Vallegrande, Loma Larga, a 26 km al Sur de Vallegrande, formaciones vegetales de bosque montane de Tucumano-Boliviano, sobre tronco em decomposición, 18°46’26”S, 63°53’42”W, 1874 m, 14 April 2011, *Carreño & Linneo 635* (MO). Vallegrande, Cincho Redondo, Tucarillo Moro Moro, habicado a 7 km de Moro Moro, ubicado al lado noroeste de Vallegrande a 28 km, predominan las formaciones de Prepuna, cresce sobre roca, 18°21’10”S, 64°20’30”W, 2555 m, 10 April 2011, *Carreño & Linneo 410* (MO). Vallegrande, Kasamonte, a 20 km al sur de Vallegrande, caminho Vallegrande y Loma Larga desvio al lado derecho, bosque montano de Tucumano-Boliviano, sobre ramitas de arbol, 18°42’40”S, 64°01’27”W, 2175 m, 23 August 2011, *Carreño & Huanca 1263B* (MO). Vallegrande, Guapural, ca. 41 km sur de Vallegrande caminho a Gualase, bosque Yungas, sobre arbolito, 18°40’S, 64°01’W, 2150 m, 27 February 2002, *Churchill & Arroyo 21223* (MO). Florida, a 1 km de la catarata La Pajcha, valle seco interandino, sobre árbol, 18°29’10”S, 63°49’22”W, 1825 m, 24 September 2009, *Inturias et al. 258* (MO). Florida, colecta sobre la catarata La Pajcha, boque Tucumano-Boliviano, sobre suelo, 18°29’10”S, 63°49’22”W, 23 September 2009, *Inturias et al. 252* (MO). Florida, Canton Samaipata, entre Bermejo y Laguna Volcan, Bosque Montano de Tucumano-Boliviano, sobre tronco de árbol, 18°07’S, 63°38’W, 900 m, 22 August 2001, *Churchill et al. 20883* (MO). **TARIJA:** Gran Chaco, Bolsa Chica, a 6 km al SE de Nazareno, bajando por la antigua senda hacia el puesto Sanandita, bosque premontano Tucumano-Boliviano, sobre corteza de árbol, 21°39’58”S, 63°39’30”W, 1200 m, 3 October 2007, *Apaza et al. 33* (MO). Arce, Padcaya, Cantón Emborozú, Reserva Natural Alarachi, Zona Alarachi, al lado de Río Bermejo, sobre tronco, 22°12’18”S, 64°37’47”W, 1140 m, 12 September 2004, *Churchill et al. 23295* (MO). Arce, Reserva Natural Alarachi, Zona Alarachi, La Lima, aguas arriba de la Quebrada Los Pinos, bosque semideciduo, estacional Tucumano-Boliviano, 22°10’59”S, 64°37’46”W, 1300 m, 12 September 2004, *Churchill et al. 23249* (MO). O’Connor, road Tarija-Entre Rios, headwaters Rio Tambo, degraded Podocarpus woodland, on bark, 64°20’ W, 21°25’ S, 2100 m, 15-18 November 1989, *Gradstein 7625* (GOET).

PARAGUAY. ALTO PARANÁ: Ciudad Pte. Stroessner, Salto Monday, sobre corteza, 4 September 1987, *Drehwald 2378* (GOET). Puerto Franco, Salto de Monday ca. 10 km südlich von Pto. Stroessner, epiphytish, 160 m, 5 February 1988, *Schäfer-Verwimp & Verwimp 9379* (MO). Sekundärwald bei Hernandarias ca. 20 km nördlich von Puerto Stroessner, epiphytisch, 220 m, 5 February 1988, *Schäfer-Verwimp & Verwimp 9356* (JE). Puerto Franco, Salto de Monday ca. 10 km südlich von Pto. Stroessner, epiphytisch, 160 m, 5 February 1988, *Schäfer-Verwimp & Verwimp 9379* (JE). Stadtpark von Puerto Stroessner, epiphytisch, 160 m, 5 February 1988, *Schäfer-Verwimp & Verwimp 9367* (JE). **PRESIDENTE HAYES:** Route Fortín General Bruguez, entre km 50-55, Chaco, bosques secos simi-decíduos e savanas inundadas en argilas, epífita em troco de árvore, 25 July 1995, *Pietrobom da Silva & Zardini 2185* (MO).

Radula leiboldii (subg. *Radula*?) is recognized by the numerous small discoid gemmae produced along the leaf margins, and distant to subimbricate, quadrate to subrectangular lobule with a rounded to obtuse apex, sometimes angular-obtuse, covering usually ca. 1/2 the stem. Further significant morphological features are the leaf cells with small to medium-sized trigones and the presence of discoid gemmae on the margins of bracts and perianth mouth. The species shares similarities with the Afro-American *Radula quadrata*, especially in the production of numerous small discoid gemmae. However, the latter species differs in the larger, imbricate lobules with the base extending fully across and beyond the stem.

Radula leiboldii has long been considered endemic to Mexico (Castle 1963, Fulford & Sharp 1990, Yamada 1991), but examination of the lectotype in G showed that the species is conspecific with the widespread *R. tectiloba*. The lectotype of *R. leiboldii* is mixed with a few female and many male plants of *R. quadrata*, whereas the isolectotypes in BM and YU are mixed with male *R. quadrata*. Castle (1963) reported gemmae in *R. leiboldii*, but Yamada (1991) did not observe them and suggested that the gemmae observed by Castle (1963) belonged in fact to *R. quadrata*. However, we confirm the occurrence of gemmae in the type of *R. leiboldii*. Castle (1963) and Yamada (1991) described androecia in their treatments of *R. leiboldii*, but we believe that they belonged to *R. quadrata*.

Radula aurantii Spruce was described based on three different collections made by Balansa (1284, 3715, 4248) in Paraguay. The Spruce's herbarium in MANCH holds four specimens of *R. aurantii* marked as "type" without information on locality, date and collector. In contrast, isosyntype specimens in G and BM hold the complete label information of the protologue. Moreover, the latter specimens are fertile, having androecia, perianths and

sporophytes, while those in MANCH are sterile. Therefore, the specimen G-00047494 is selected here as the lectotype of *R. aurantii*.

22. Radula ligula Steph., Sp. Hepat. 4: 228. 1910. Type: Brazil, Rio Grande, *C. A. M. Lindmann "inter B 174"* (lectotype, G-00043905!, selected by Castle, 1962: 148; isotype, BM-00969225!).

Dioicous. *Plants* 1.2–2.8 mm wide, to 2 cm long, green to olive-green in field, olive-green to brown in herbarium, irregularly pinnate. *Branches Radula*-type. *Stems* 150–170 μm in diam., with thick-walled, epidermal cells surrounding thick-walled (by concave trigones) medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, the cells uniform in size, walls yellowish or brownish. *Leaf lobes* widely spreading, contiguous to subimbricate, convex, ovate, 0.75–1.3 mm long, 0.7–1 mm wide, dorsal base rounded, covering 1/2 the stem, dorsal margin rounded, ventral margin slightly rounded to almost straight, apex rounded, margin plane, entire; marginal cells quadrate, 5–12 μm in diam., median cells isodiametric, 12–25 μm in diam., basal cells isodiametric to elongate, 20–35 × 12–20 μm, cell walls thin at leaf base and in midleaf, evenly thickened (colorless or sometimes brownish) along the margin forming a broad, 3–4 cell rows wide border, trigones lacking, intermediate thicking lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, ligulate, 0.25–0.7 mm long, 0.15–0.3 mm wide, ca. 1/4 the lobe length, inflated at rhizoid area, insertion 2× the base length, insertion line straight, base plane, rounded, covering 1/5 the stem, free margin plane, rounded, arching towards base, apex plane, rounded to obtuse, distal margin straight to rounded, keel concave, spreading at angles of 70–80° with the stem, 150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few or numerous lobules. *Androecia* terminal to intercalary on short branches, with 2–4 pairs of bracts, 0.55–1 mm wide; bracts distant to imbricate, ovate, 0.45–0.9 mm long, 0.35–0.55 mm wide, apex rounded, margin plane or recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. *Gynoecia* on short branches, with 1–2 innovations, innovations sometimes rudimentary; bracts oblong-ovate, 1.6–1.7 mm long, 0.6–0.7 mm wide, apex rounded, margin recurved, entire, lobule oblong, 1/3–1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical, 2.5–4 mm long, 0.3–0.6 mm wide at base, 0.9–1 mm wide at middle and apex, 0.7–1.1 mm wide at apex, mouth entire to irregularly crenulate, plane; perianth wall 4–6-stratose at base, unistratose from the middle to apex;

perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–8-layered tube (perigynium) within which the sporophyte foot and part of the Seta is embedded. *Calyptra* wall 2–3-layered at the base, 1 cell layer thick above. *Elaters* 150–310 µm long, rough. *Spores* 22.22–25.92 µm in diam., granulate, granules composed by nanogranules. *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Atlantic Coastal Region of Brazil and Argentina (Missiones) (Figure 30). This species grows in humid rainforest, near water bodies such as rivers and waterfalls, on trees and rock, sometimes on rotten logs, in lowland, submontane and lower montane forests, at 30–1750 m.

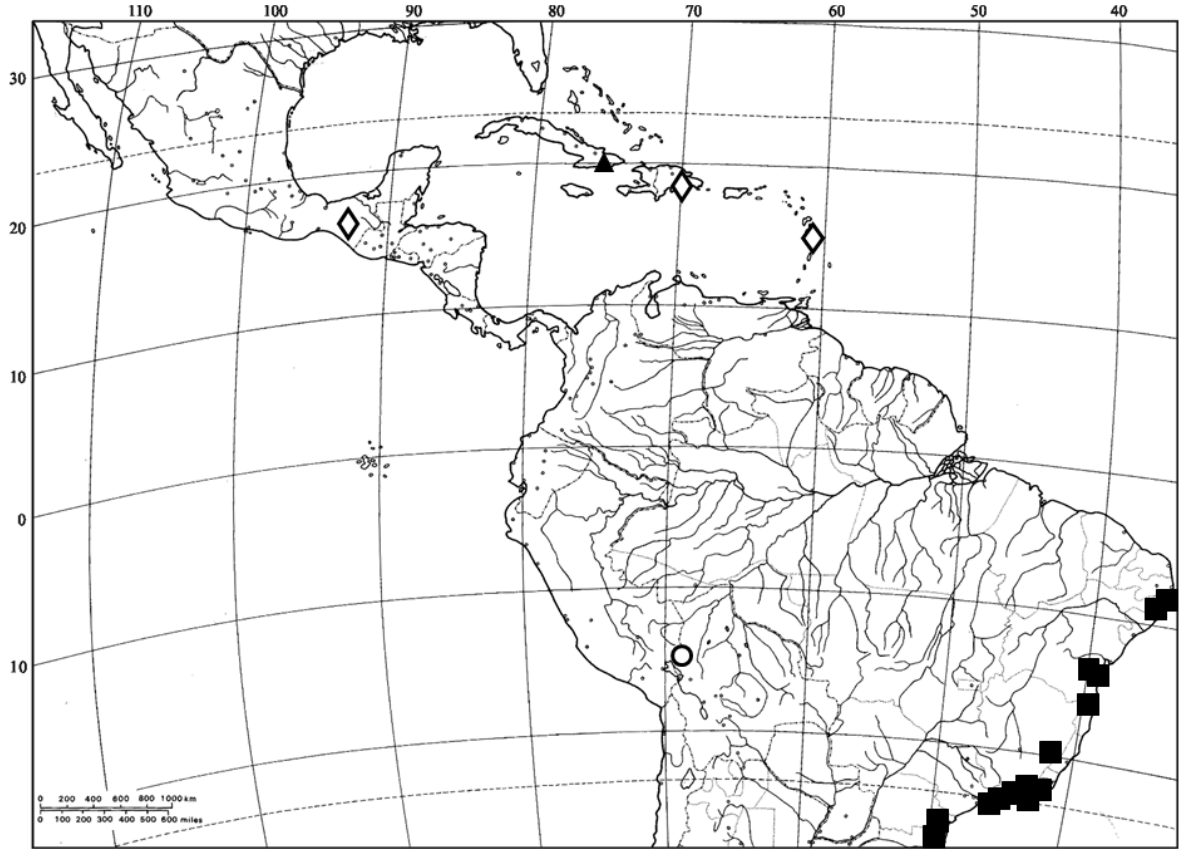

Figure 30. Distribution of *Radula ligula* (black square), *R. sp. nov. 2* (white circle), *R. longiloba* (black triangle), and *R. macrostachya* (white rhombus).

Additional specimens examined. BRAZIL. BAHIA: Uruçuca, 6,2 km N of town of Serra Grande, ca. 40 km N of Ilhéus along coast, ca. 200 m, 14°26’S, 39º03’W, 200 m, 17 July

1991, *Vital & Buck 20271* (NY, isotype of *Radula bahiensis*). Eunápolis, Estação Veracruz, trilha Pau-Brasil, Floresta Atlântica, corticícola, 16°22’ S, 39°10’ W, 9 September 1999, *Bastos & Vilas Bôas-Bastos 1323* (ALCB). Wenceslau Guimarães, Povoado de Nova Esperança, Estação Ecológica Estadual de Wenceslau Guimarães, corticícola, Floresta Atlântica, 13°34’42” S, 39°42’28” W, 443 m, 29 setembro 2017, *Bastos 6057, 6067, 6079, 6112* (ALCB). Igrapiúna, Reserva Ecológica da Michelin, Mata da Vila Cinco, trilha do Guigó a direita, floresta ombrófila, rupícola, 13°48’ S, 39°10’W, 15 fevereiro 2006, *Bastos 4084, 4089, 4269, 4311* (ALCB). **MINAS GERAIS:** Alto do Caparaó, Parque Nacional do Caparaó, Cachoeira Bonita, 20°26’07”S, 41°47’57”W, 1750 m, 11 July 2009, *Bordin et al. 1619* (SP). **PARANÁ:** Morretes, Parque Estadual do Marumbi, trilha do Olimpo, 25°26’58”S, 48°55’40”W, 940 m, 24 July 2014, *Peralta et al. 16365* (SP). **PERNAMBUCO:** São Vicente Ferrer, Serra do Mascarenhas, Mata do Estado, 7°36’58”S, 35°30’34”W, 23 March 2010, *Silva 307* (UFP). **RIO DE JANEIRO:** Parque Nacional da Tijuca, 350 m, 8 June 2000, *Costa & Gradstein s.n.* (RB). Angra dos Reis, Ilha Grande, sobre tronco caído no caminho, 600-1110 m, *Yano et al. 23653* (SP). Parque Nacional do Itatiaia, Mata Ombrófila Densa, Mata Atlântica, sobre rocha, 22°25’25” S, 49°36’24” W, 1200 m, 6 May 2016, *Peralta & Gissi 18395, 18399* (SP). **RIO GRANDE DO SUL:** Viamão, Vianópolis, 05 October 1970, *Oliveira s.n.* (ICN, SP). Sapiranga, Picada São Jacó, Mata Atlântica, tronco de árvore vivo no interior da mata, 29°38’17” S, 51°00’25” W, 600 m, 11 December 2005, *Peralta et al. 3272* (SP). **SANTA CATARINA:** Corupá, 26°12’04”S, 49°07’48”W, 1000 m, 29 December 2012, *Dias-Melo 1031* (SP). **SÃO PAULO:** Mogi das Cruzes, Biritiba Mirim, Fazenda Casa Verde, 23°39’26”S, 46°01’54”W, 980 m, 15 June 2007, *Peralta et al. 5083* (SP). Salvador do Sul, sobre pedra, 22 April 1982, *Bueno 1501* (SP). Ubatuba, Serra do Mar, Núcleo Picinguaba, floresta de terras baixas, sobre tronco de árvore, 23°33’72” S, 44°85’3” W, 30-50 m, *Costa et al. 5087* (RB).

Radula ligula (subg. *Amentuloradula*?) is easily recognized by the leaf lobe bordered by 3–4 rows of quadrate thick-walled cells and lobule ligulate (parallel to the stem) with a rounded to obtuse apex. The same type of border is found in *R. smithii* from Peru, but the border of the latter species is distinctly pigmented (reddish-brown) and the lobule is subquadrate. Yamada (2003) reported a brownish border in older leaves of *R. ligula*, but in this study, this was not observed.

Radula ligula resembles *R. marginata* Gottsche *et al.* from New Zealand, but the latter species has larger, ovate-ligulate leaf lobules (Castle 1959, Hodson *et al.* 1994).

23. Radula sp. nov. 2 F.R.Oliveira-da-Silva, ***sp. nov.*** Type: Bolivia, La Paz, Franz Tamayo, Area Natural de Manejo Integrado Apolobamba, Queara, Supay Cocha, fragmento relicto del bosque de yungas altoandino com *Polylepsis* y *Gynoxys*, sobre roca em sombra, 14°43'40" S, 69°04'16" W, 4040 m, 17 April 2008, *A. Fuentes et al. 12708* (holotype, MO-6097704!, c. gyn.; isotype, MG!).

Fig. 31

Dioicous. *Plants* 2.5–3 mm wide, to 2 cm long, green to yellowish-green in herbarium, regularly pinnate. *Branches Radula*-type. *Stem* ca. 200 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, subimbricate on branches, plane, orbicular to falcate-ovate, 1.5–1.8 mm long, 1.1–1.4 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margin plane, entire; marginal cells subquadrate to subrectangular, 10–15 × 8–10 µm, median cells isodiametric to elongated, 15–20(–22) × 12–20 µm, basal cells isodiametric to elongate, 20–25 × 15–20 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, narrowly obtriangularly elongate, 0.7–1.1 mm long, 0.4–0.5 mm wide, ca. 1/3 the lobe length, flat, insertion 4–6× the base length, insertion line straight, base plane, rounded, covering ca. 1/2 the stem, free margin plane, straight, apex plane, rounded to slightly obtuse, distal margin straight, keel straight, convex on lobules of the branches, spreading at angles of 20–30º with the stem, 90–110º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long branches, with 2 innovations; bracts ovate, 0.9–1.2 mm long, 0.6–0.7 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, 1/3–1/2 of lobe length, apex acute. *Perianth*, *Sporophyte* and *Vegetative reproduction* not observed.

Distribution and Ecology. The new species is only known from its type locality in province of Franz Tamayo, Department of La Paz, Bolivia (Figure 30). *Radula sp .nov. 2* was collected on shaded rock in a fragment of the high Andean yungas forest with *Polylepsis* sp. and *Gynoxys* sp., at 4040 m.

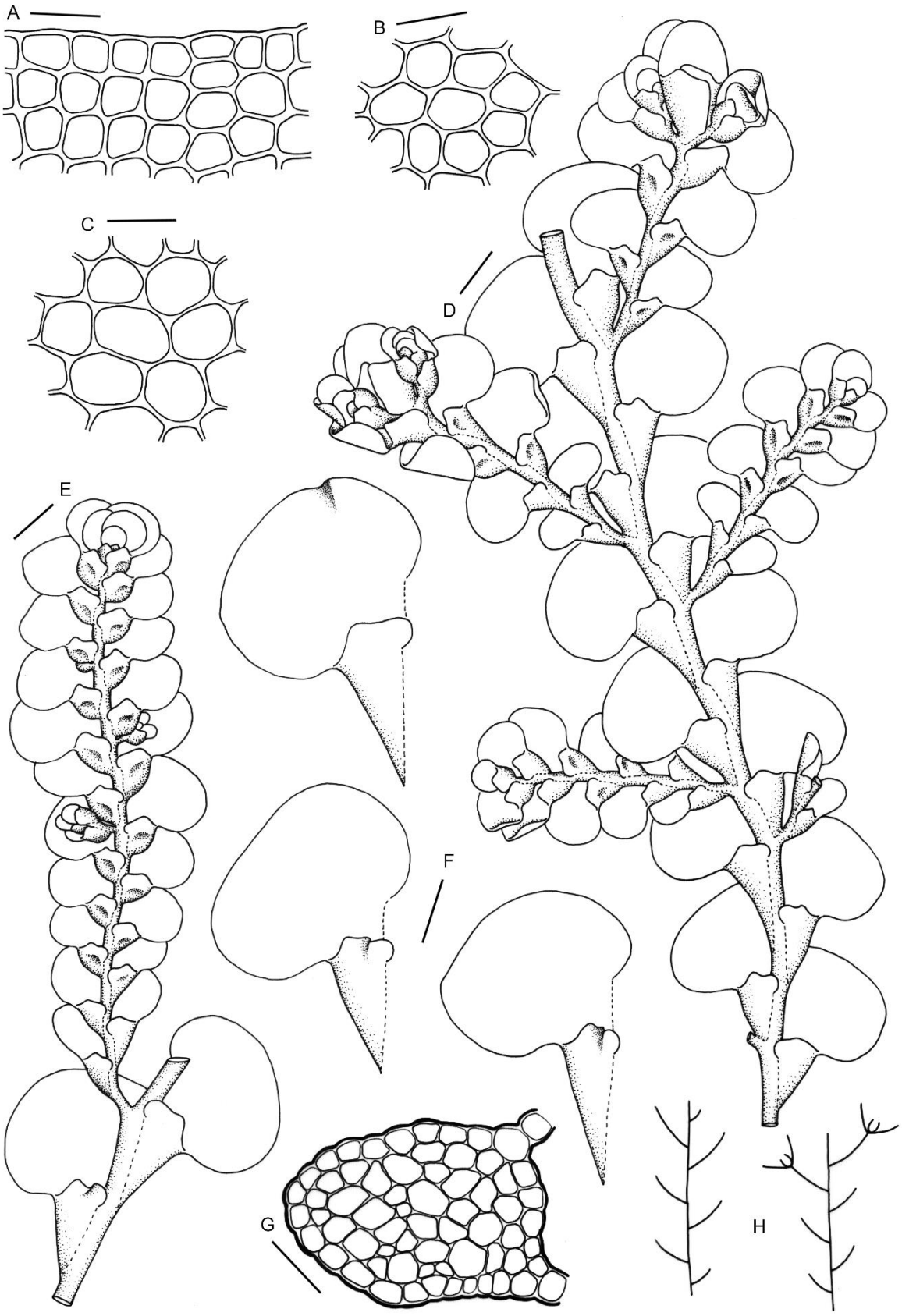

Figura 31. *Radula sp. nov. 2*. A. Marginal leaf cells. B. Median leaf cells. C. Basal leaf cells. D. Habit with gynoecia. E. Habit. F. Leaves. G. Cross section of stem. H. Cladograph of plants (U = gynoecia without perianth) (A-C, G = 50 µm, D-F = 500 µm; All from the holotype).

Radula sp. nov. 2 (subg. *Volutoradula*?) is recognized by the regularly pinnate plants with distant to contiguous leaves, lobules narrowly obtriangularly elongate, 3–4× longer than wide and flat, insertion line straight, 4–6× the base length, and keel long and straight. Branches may have shorter, subquadrate to obconic lobules which are strongly inflated along the keel or not and with a straight to concave keel.

The new species resembles *Radula bischlerae* from Colombia by the obtriangularly elongate lobule, which is much longer than wide; both species occur at high, alpine elevations in the tropical Andes. However, *R. bischlerae* is a very fragile plant with strongly caducous leaf lobes and lobules tubularly inflated lobules with a curved insertion line. In *R.* sp. nov. 2 caducous leaves are lacking and the lobules are plane, with a straight line of insertion. The relationship of these two species deserves further study based on additional material.

24. Radula longiloba K.Yamada, J. Hattori Bot. Lab. 54: 243. 1983. Type: Cuba, Santiago de Cuba, Sierra de la Gran Piedra, epifilos em el bosque nublando cerca Finca Isabelica, 1100 m, *T. Pócs 9128/AR* (holotype, HAC; isotypes, NICH-400981!, EGR).

Dioicous. *Plants* 1.3–1.9 mm wide, to 1 cm long, yellowish-green in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type. *Stems* ca. 100 µm in diam., with thick-walled epidermal cells surrounding mostly smaller or uniform in size, thin-walled medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls colorless to yellowish. *Leaf lobes* widely spreading, imbricate, slightly convex, oblong to oblong-falcate, 0.6–1 mm long, 0.4–0.7 mm wide, dorsal base rounded, covering 1/2–3/4 the stem, dorsal margin rounded, ventral margin slightly rounded, apex obtuse to subacute, margin plane, entire; marginal cells subquadrate to isodiametric, 10–15 × 8–12 µm, median and basal cells isodiametric to elongate, 20–25 × 15–20 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.2–0.3 mm long, 0.15–0.2 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area and along the keel, insertion 1× the base length, insertion line straight to slightly arched, base plane to slightly convex, rounded, covering ca. 1/2 the stem, free margin plane to slightly convex, straight to sinuose, apex plane, rounded to subacute, distal margin straight, keel straight, spreading at angles of 50–60º with the stem, (130–)150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brownish, scanty, present on a few lobules. *Androecia* not observed. *Gynoecia* on

long branches, with 2 innovations; bracts oblong-ovate, 0.75–0.85 mm long, 0.4–0.5 mm wide, apex rounded to obtuse, margin plane, entire, lobule oblong, ca. 1/2 the lobe length, apex obtuse to subacute. *Perianth*, *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Cuba and Brazil (Figure 30). This rare species grows on fern fronds and tree trunks, in cloud forest, at ca. 1100 m.

Additional specimens examined. CUBA. SANTIAGO DE CUBA: The Type (NICH).

BRAZIL. RIO GRANDE DO SUL: Cambará do Sul, Parque Nacional de Aparados da Serra, sobre tronco vivo, 27 April 1983, *Yano & Pirani 7028* (SP).

Radula longiloba is recognized by delicate plants with subimbricate, oblong to oblong-falcate (longer than wide) leaf lobes with a rounded to obtuse apex, leaf cells usually without trigones and lobules subquadrate with a rounded to subacute apex.

This species is closely similar to *R. yamadae* from Brazil, but in the latter species the leaves are ovate, not falcate, lobules distant to contiguous, rarely imbricate, ca. 1/2 the lobe length (ca. 1/3 in *R. longiloba*), lobule bases covering 1/3 to fully overlapping the stem (ca. 1/2 in *R. longiloba*), and keels conspicuously convex (straight to slightly convex in *R. longiloba*).

25. Radula macrostachya Lindenb. & Gottsche, Syn. Hepat. 726. 1847. Type: Mexico, "In regno Mexicano apud Havienda de Fovo, ibique lecta est mense," May 1841, *F. M. Liebmann 568* (lectotype, W!, hb. Lindenberg n° 5511, **designated here**).

Radula caldana Ångström, Öfvers. För. Kongl. Svenska Vetensk.-Akad. 33(7): 81. 1876 [1877]. Type: Brazil, Caldas, *J. F. Widgren donavit s.n.* (type, S, not found), syn. fide Yamada in Reiner-Drehwald (1994, under *R. macrostachya*).

Radula eggersiana Steph., Hedwigia 27: 302. 1888. Type: Dominican Republic, St. Domingo, *H. F. A. Eggers 21* (lectotype, G-00043877!, selected by Yamada, 1982a: 458; isolectotype, FH!), syn. fide Castle (1967).

Radula tenerrima Steph., Hedwigia 23: 136. 1884. Type: Venezuela, "in Bryopteride repens", *unknown collector*, ex. hb. Sande-Lacoste (type, G, not found), syn. fide Castle (1967).

Dioicous. *Plants* 1.5–1.8 mm wide, to 1 cm long, yellowish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 120–180 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, convex, ovate, 0.8–1 mm long, 0.5–0.75 mm wide, dorsal base rounded, covering 1/2 of the stem, dorsal margin rounded, ventral margin straight, sometimes almost rounded, apex rounded to obtuse, margins plane, entire; marginal cells subquadrate, 10–15 × 8–15 μm, median and basal cells isodiametric to elongated, 20–30 × 15–25 μm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate-subrhombic, 0.4–0.5 mm long, 0.2–0.3 mm wide, 1/4–1/3 the lobe length, slightly inflated at rhizoid area, insertion 3–4× the base length, insertion line slightly curved, base plane, covering up to 1/3 the stem, free margin plane, straight, apex plane, obtuse, prolonged, rarely rounded, distal margin straight, keel straight, spreading at 30–50º with the stem, 120–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Sexual organs* and *Vegetative reproduction* not observed.

Illustration. Yamada (1982).

Distribution and Habit. Reported by Castle (1967) from Mexico, West Indies and Venezuela (Figure 30), growing on bark and rock, at relatively low elevation.

Additional specimens examined. MEXICO. Type of *Radula macrostachya* (W).
DOMINICAN REPUBLIC. Type of *Radula eggersiana* (G).
MARTINIQUE. "Bois du Lorrani", 1899, *Duss 152* (NY).

Radula macrostachya (subg. *Volutoradula*) is recognized by plants regularly pinnate with leaves usually distant to contiguous, ovate with ventral margin straight and apex usually obtuse, lobules distant, subquadrate-subrhombic, apex obtuse, prolonged, lobule base not or little covering the stem (up to 1/3) and keel straight.

This species resembles *Radula pusilla* in lobule shape. However, *Radula pusilla* has leaf lobes with a broadly rounded apex and ventral margin, and keels at a narrow angle (90–110º) with the ventral leaf lobe margin, while *R. macrostachya* has leaflobes with an obtuse apex and

straight ventral margin, and keels at a wider angle (120–150º) with the ventral leaf lobe margin. Moreover, *Radula pusilla* has a rounded, non-prolonged lobule apex, while in *R. macrostachya* the lobule apex is obtuse and prolonged. *Radula macrostachya* also resembles *R. wrightii*, but the latter species has purely dichotomous branching.

Radula macrostachya was synonymized under *R. javanica* by Yamada (2000), but examination of the types of the two species showed that the two differ in stem anatomy and lobule shape, and belong to different subgenera. *Radula javanica* (subg. *Radula*) has stems with thick-walled epidermal and medullary cells, the stem cells being uniform in size and color. *Radula macrostachya* (subg. *Volutoradula*) in contrast, has stems with thick-walled, brownish epidermal cells and thin-walled, colorless to yellowish medullary cells; the epidermal cells are mostly smaller than the medullary cells. Moreover, lobules of *R. javanica* are subquadrate with the base usually covering 1/2 of the stem, while *R. macrostachya* has subquadrate to subrhombic lobules with the base not or little covering the stem, to maximally 1/3 the stem.

Radula caldana was synonymized with *R. macrostachya* by Yamada in Reiner-Drehwald (1994). We did not have the opportunity to examine the type of *R. caldana*, and follow Yamada's opinion. Castle (1966) did not observe the type of *R. caldana* but his description and illustration of the species, which were based on plants from Brazil (leg. Regnell), seem to refer to *R. javanica*. This needs future study.

26. Radula sp. nov. 3 F.R.Oliveira-da-Silva, ***sp. nov.*** Type: Bolivia, Departamento La Paz, Província Inquisivi, Camillaya, western slope of Cerro Kharrata SSE Camillaya, Polylepsis-forest, on trunk, 3550–3600 m, 30 September 1997, *J. Heinrichs & J. Müller JH 4039* (holotype, JE!; isotypes, LPB, MO-5131314!).

Fig. 32

Dioicous? Plants 3–4.5(–5) mm wide, to 5 cm long, yellowish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stem* 300–500 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant, plane, oblong-ovate, 2.3–2.7 mm long, 2–2.3 mm wide, dorsal base rounded, covering up to 1/2 the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margin plane to irregularly undulate, sometimes convolute ventrally, entire; marginal cells subquadrate, 10–17 × 8–10 µm, median cells

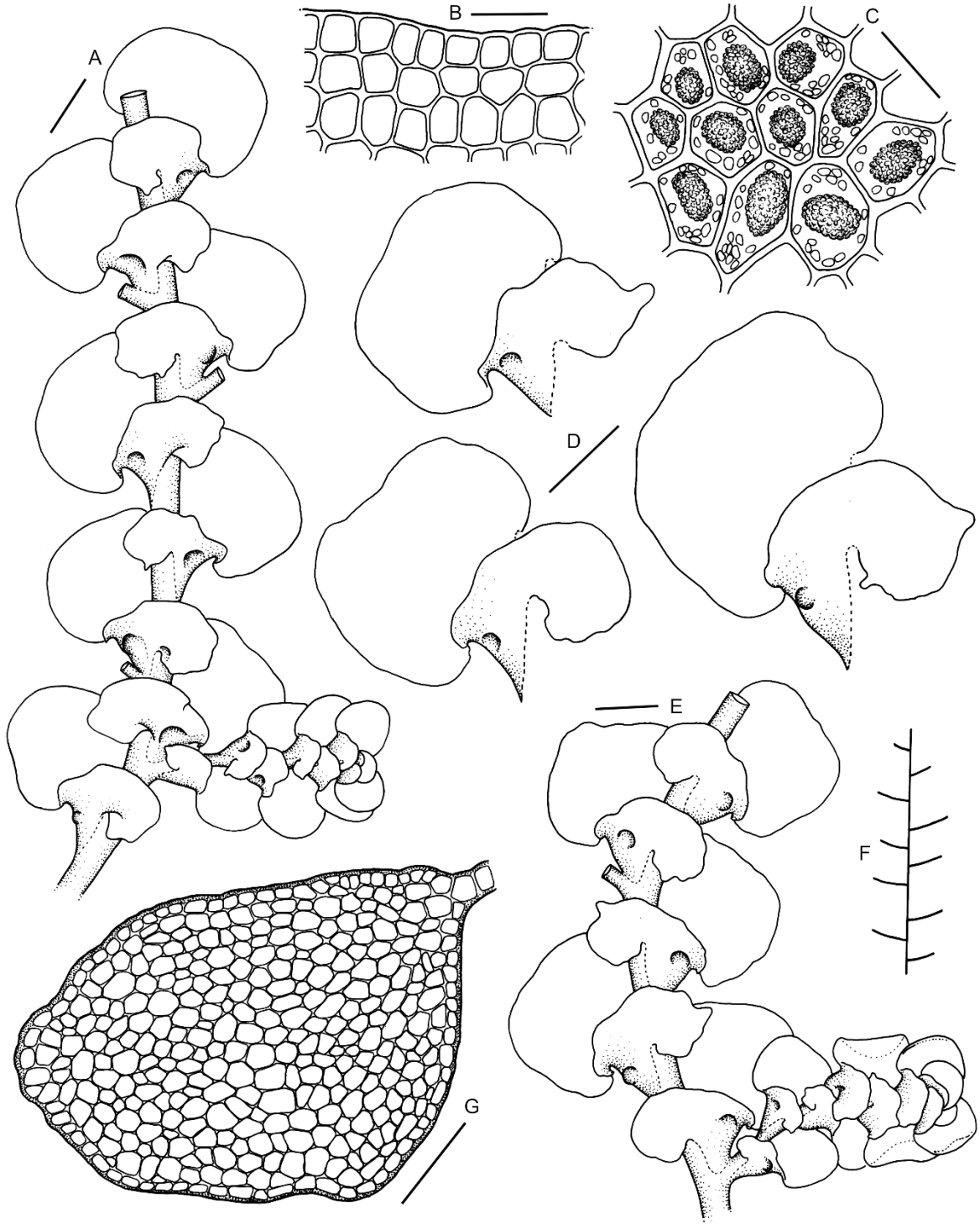

Figura 32. *Radula sp. nov. 3*. A. Habit. B. Marginal leaf cells. C. Median leaf cells with oil bodies. D. Leaves. E. Habit. F. Cladograph of plants. G. Cross section of stem (A, D, E = 500 µm, B, C = 25 µm, G = 100 µm; All from the holotype).

isodiametric to elongate, 20–30 × 17–25 µm, median cells isodiametric to elongate, 30–40 ×20–25 µm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, ellipsoidal, brownish, granular, 10–18 × 7–13 µm. *Lobules* distant,

reniform, 1.4–1.6 mm long, 1.5–1.6 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, slightly inflated along the keel, insertion 1× the base length, insertion line inverted small J-shaped, base plane, irregularly rounded, sometimes with 1–2 short lacinia, fully overlapping, extending beyond the stem, short auriculate, free margin plane, irregularly rounded, apex plane, irregularly rounded to obtuse, distal margin almost straight to rounded, keel straight, spreading at angles of 40–50º with the stem, 40–80º with the ventral leaf margin at the junction with the lobule. *Rhizoids, Sexual organs* and *Vegetative reproduction* not observed.

Distribution and habit. The new species is only known from the type from the high Andes of Bolivia (Figure 33). It was found growing on a trunk of *Polylepis* sp. (Rosaceae) in subalpine dwarf forests, at 3550–4040 m.

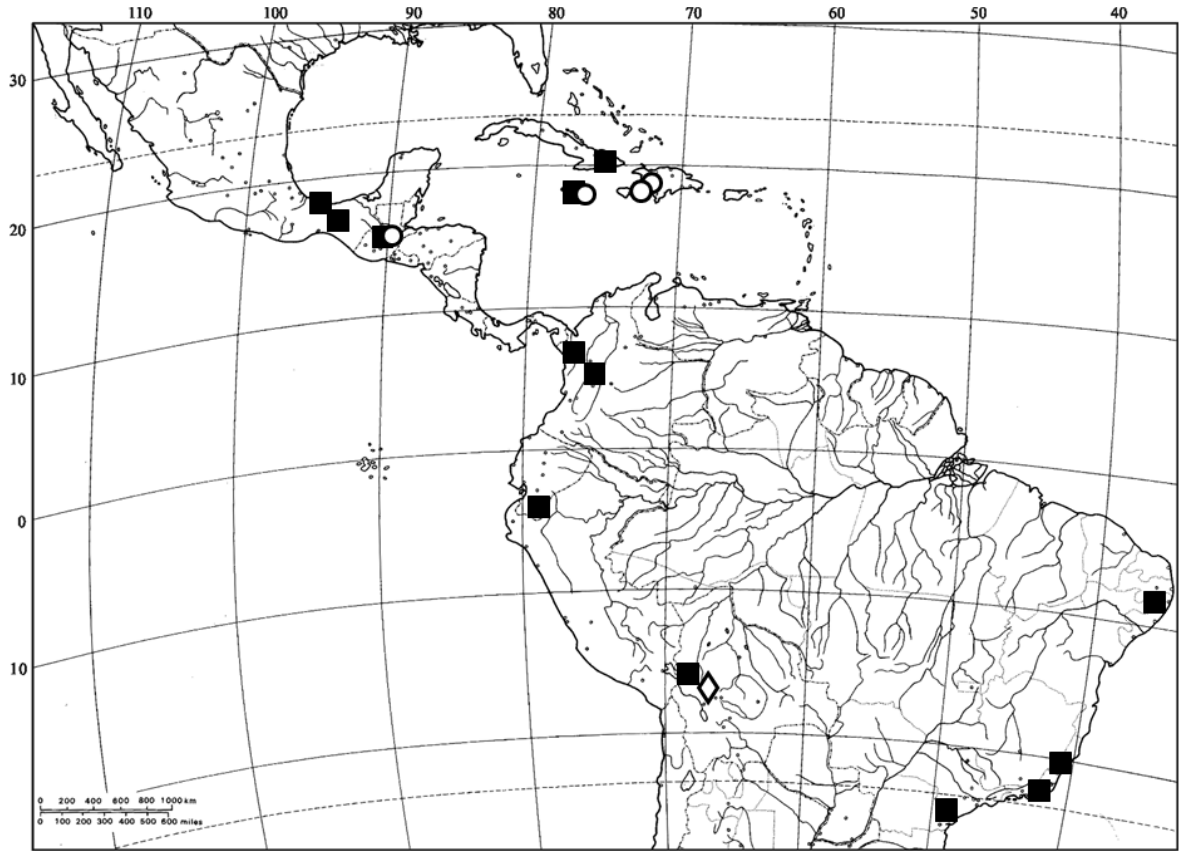

Figure 33. Distribution of *Radula sp. nov. 3* (white rhombus), *R. mexicana* (black square), and *R. microlobula* (white circle).

Additional specimens examined. BOLIVIA. LA PAZ: Franz Tamayo, Area Natural de Manejo Integrado Apolobamba, Queara, fragmento relicto del bosque de yungas altoandino, sobre *Polylepis pepei* B.B.Simpson, 14°43’41”S, 69°04’16”W, 4040 m, *Fuentes et al. 12701* (paratype MO).

Radula sp. nov. 3 (subg. *Volutoradula*?) is characterized by robust plants (3–5 mm wide) with regularly pinnate branches, leaves distant, and lobules reniform with a broad base, fully overlapping and extending beyond the stem. The leaf margins of this plant are plane to slightly irregularly undulate, sometimes convolute ventrally. One or two short lacinia are sometimes seen on the free margin of the lobule near the base (see Fig. XD). Another striking feature of the new species is the very narrow angle between the lobule keel and the ventral leaf margin (40–80º).

The material of *Radula* sp. nov. 3 was originally named *R. voluta*. At first glance, the new species indeed resembles *R. voluta* due to the robust plant size and the broad lobule base. However, the lobule in *R. voluta* has a large voluted auricle, being circinately coiled and reaching downwards (maximally to the keel) and having a short, circinate line of insertion. *Radula* sp. nov. 3, in contrast, has a small auricle, which is not circinately coiled and has a much longer insertion line. In addition, the dorsal leaf base in *R. voluta* is auriculate and fully overlaps the stem, while in the new species it is not auriculate and does not fully overlap the stem (covering only up to 1/2 the stem).

27. Radula mexicana Lindenb. & Gottsche, in Gottsche, Mexik. Leverm. 150. 1863. Type: Mexico, Veracruz, Hacienda Mirador, *F. M. Liebmann 478 p.p.* (n.v.).

Radula cordovana Steph., Hedwigia 23: 163. 1884. Type: Brazil, Cordova, "in follis in sylvis montosis," *C. T. Mohr 18*, ex hb. Jack (lectotype, G-00121976!, **designated here**, c. per + andr.; isolectotype, G-00282115!, c. per + andr.), syn. fide Castle (1964).

Radula claviflora Spruce, Mem. Torrey Club 1: 127. 1890. Type: Bolivia, Yungas, 6000 ft., 1885, *H. H. Rusby 3034* (holotype, MANCH, not found; lectotype, NY-01021107!, **designated here**), syn. fide Castle (1964).

Monoicous. *Plants* 1.3–2.1 mm wide, to 1 cm long, yellowish-green to yellowish-brown in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type, rarely *Lejeunea*-type present on decapitated shoots. *Stems* 100–200 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to imbricate,

slightly convex, ovate, 0.8–1.3 mm long, 0.6–0.9 mm wide, dorsal base rounded, covering 2/3 to overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to recurved, entire, rarely irregularly crenulate; marginal cells subquadrate to isodiametric, 10–15 × 8–10 µm, median and basal cells isodiametric to elongate, 15–25 × 10–15 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1–2 per cell, spherical, light yellow, smooth to slightly granular, 10–15 µm in diam. *Lobules* distant, subquadrate, 0.3–0.6 mm long, 0.2–0.45 mm wide, 1/3–2/5 the lobe length, slightly inflated at rhizoid area, insertion 1× the base length, insertion line almost straight, base plane, rounded, rarely angulate, covering 1/3–1/2 the stem, rarely overlapping the stem, free margin plane, straight, apex plane, rounded to acute, sometimes prolonged, distal margin straight to sinuose, keel straight, spreading at angles of 40–60º with the stem, 140–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long or short branches, with 1–5 pairs of bracts, 0.7–1.1 mm wide; bracts distant to imbricate, ovate, 0.7–0.9 mm long, 0.3–0.4 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex rounded to obtuse. *Gynoecia* on short or long branches, with 1–2 innovations; bracts ovate, 1–1.1 mm long, 0.5–0.6 mm wide, apex rounded, margin plane to incurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to acute. *Perianth* erect or falcate, subcylindrical to trumpet-shaped, sometimes campanulate (when young), 1.3–3 mm long, 0.2–0.4 mm wide at base, 0.5–0.9 mm wide at middle, 0.6–1 mm wide at apex, mouth entire to irregularly crenulate, plane to strongly undulate; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with longitudinal striae at base or middle; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–4-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* ca. 3.2 mm long. *Capsule* 0.5–1 mm long, 0.25–0.4 mm wide, valves ca. 1.2 mm long, ca. 0.3 mm wide at middle, outer layer cells subrectangular, simple nodular thickenings reddish-brown, on every longitudinal wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* and *Spores* not observed. *Vegetative reproduction* by stem fragmentation.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. A widespread, Afro-American species (Gradstein *et al.* 2022). In tropical America, *Radula mexicana* has a wide distribution but is rare. Besides the countries listed in the additional specimens examined, this species has been reported from Guatemala, Cuba, Jamaica and Ecuador (Castle 1964, Yamada 1988, Gradstein 2021) (Figure 33). Gradstein et al. (2022) reported the species new to Africa, where it was called *R. akefinensis* Gottsche. *Radula mexicana* grows on barks and dead trees, usually in shaded places in montane rainforest, at 1800–2400 m.

Additional specimens examined. MEXICO. VERACRUZ: The Type.

COLOMBIA. ANTIOQUIA: Belmira, 1.5 km de las partidas entre Entrerrios y Belmira, creciendo sobre rastrojo en la sombra, 2400 m, 5 November 1989, *Escobar 8706* (MO).

BRAZIL. ESPÍRITO SANTO: Itapecoá, Iconha, Est. do Espírito Santo, 18 April 1965, *Vital 376* (SP). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 18 August 1987, *Pôrto 2046h* (UFP). **RIO GRANDE DO SUL:** Torres, 08 July 1977, *Vianna 3287* (ICN). Viamão, Viamópolis, 05 October 1970, *Oliveira s.n* (ICN). **SÃO PAULO:** Apiaí, s.d., *Puiggari s.n.* (FH-00965697).

BOLIVIA. SANTA CRUZ: Florida, Samaipata, Parque Nacional Amboró, Barrientos, 5.5 km NE de carretera Santa Cruz-Cochabamba, bosque montano, sobre base de árbol en la sombra, 18°06'S, 63°68'W, 2020 m, 23 Agosto 2002, *Churchill & Vásquez 21778* (MO).

Radula mexicana (subg. *Volutoradula*) is one of the few monoicous species (autoicous, rarely paroicous) reported from tropical America. The plants are typically yellowish-green to yellowish-brown and usually fertile, with ovate leaf lobes, thin-walled leaf cells without trigones, and subquadrate lobules with a rounded to acute (somentimes prolonged) apex and a straight keel. The lobule base varies from rounded to angulate (obtuse to acute) and covers ca. 1/3 the width of the stem. Moreover, perianths are erect to (rarely) falcate (*e.g.*, Colombia, *Escobar 8706*), subcylindrical to trumpet-shaped, sometimes campanulate (when young), unistratose or 2–3-stratose in the lower half and unistratose in the upper half, and sometimes with a few longitudinal striae. In African specimens, Gradstein *et al.* (2022) also found short, four cells high wings in the upper half of the perianths.

Radula mexicana resembles *R. angulata*; differences are given under the latter species. *Radula claviflora* Spruce, a synonym of *R. mexicana*, was described based on a collection made by H. Rusby in Bolivia. As the type specimen is lacking in the Spruce herbarium (MANCH), an isotype in NY is designated as the lectotype.

28. Radula microlobula Castle, J. Hattori Bot. Lab. 21: 35. 1959. Type: Jamaica, on tree, Maybess River, July 25, 1903, *A. W. Evans 299* (holotype, YU-169885!).

Fig. 34

Dioicous. *Plants* 1.5–2(–2.2) mm wide, to 3 cm long, yellowish-green to olive-green in herbarium, purely dichotomous. *Branches Radula*-type. *Stems* 180–250 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, epidermal wall heavily and evenly thickened. *Leaf lobes* widely spreading, distant to subimbricate, convex, ovate, 0.9–1.2 mm long, 0.7–1 mm wide, dorsal base rounded, covering the entire stem, dorsal margin rounded, ventral margin rounded, apex rounded to obtuse, margin plane to incurved, entire; marginal cells subquadrate, 8–10 × 5–10 µm, median cells isodiametric to elongate, 15–25 × 10–15 µm, basal cells elongate, 20–35 × 15–20 µm, cell walls thin at the base to middle becoming a little thick at the margin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, irregularly ellipsoidal, light yellow, slightly granular, 10–14 × 6–9 µm. *Lobules* distant, subrhombic, 0.4–0.5 mm long, 0.1–0.2 mm wide, 1/6–1/5 the lobe length, slightly inflated at rhizoid area, insertion 3–6× the base length, insertion line straight, base plane, rounded, covering up to 1/3 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin sinuose, keel straight to slightly convex, spreading at 60–70º with the stem, 120–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brown, scanty, present on a few lobules. *Androecia* not seen. *Gynoecia* on long branches, with 2 innovations; bracts oblong-ovate, 0.7–0.9 mm long, 0.4–0.5 mm wide, apex rounded, margin plane, entire, lobules oblong-ovate, 1/3–1/2 of lobe length, apex rounded. *Perianth* erect, campanulate to trumpet-shaped (in the original description), 0.6–0.7 mm long, 0.8–0.9 mm wide at apex (2.4 mm long, 1.2 mm wide at the apex in the original description), mouth irregularly entire, undulate-crisped. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Distribution and habit. Haiti, Jamaica and Guatemala (new record) (Figure 33). The species grows on trees, rotten logs and rock, in shaded habitats in submontane and montane forests, near rivers, at 630–3000 m. In the protologue of *Radula microlobula*, Castle (1959) cited a specimen from Cuba (paratype YU-199884!), but this specimen belongs to *R. pallens* (Cañiza Ovelar & Oliveira-da-Silva 2022).

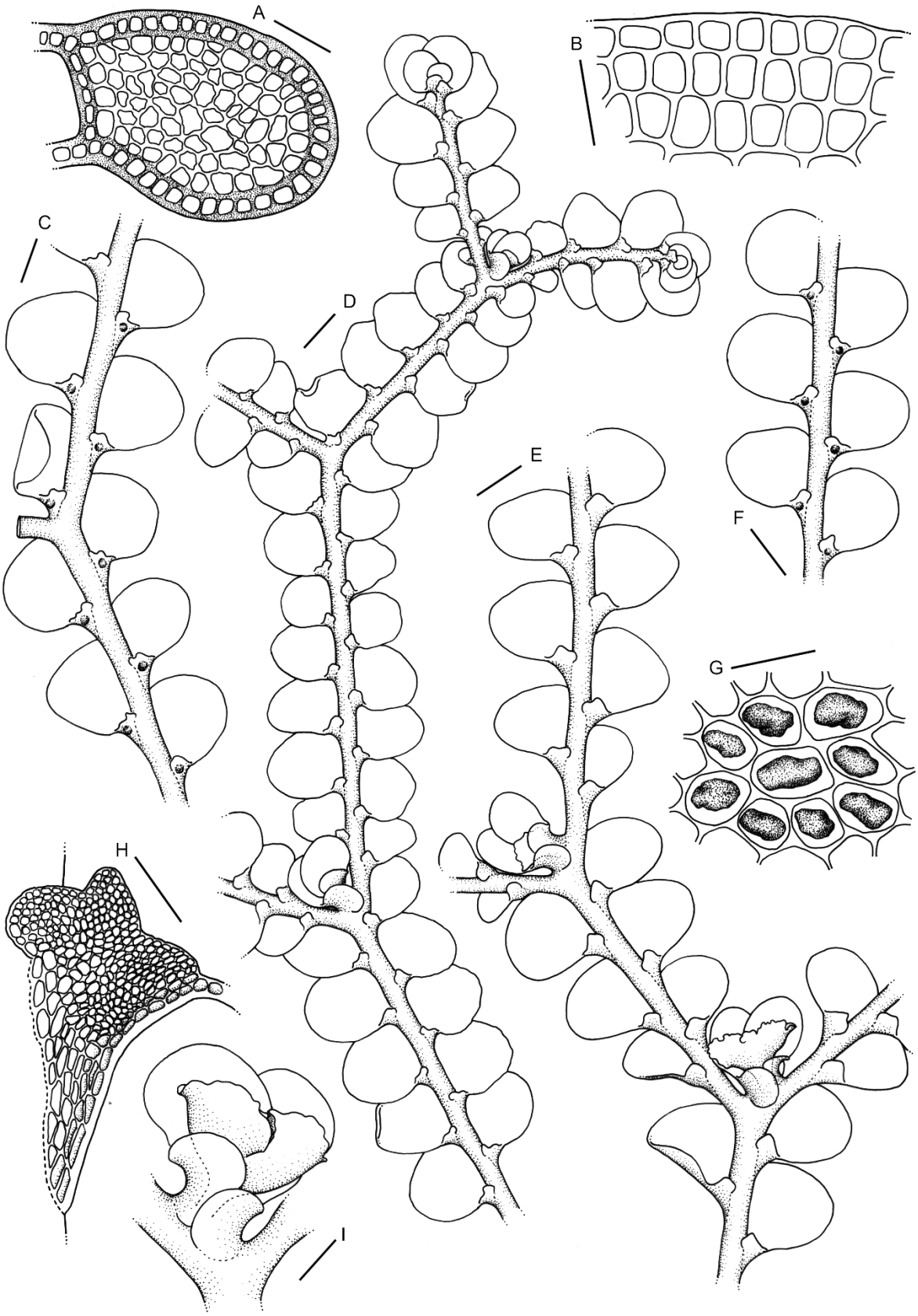

Figure 34. *Radula microlobula*. A. Cross section of stem. B. Marginal leaf cells. C, F. Habit. D. Habit with gynoecia. E. Habit with perianth. G. Median leaf cells with oil bodies. H. Lobule. I. Perianth (A = 50 µm, B, G = 25 µm, C-F = 500 µm, H = 100 µm, I = 250 µm; A-C, E-I from the holotype, D from *Leonard & Leonard 15156*).

Additional specimens examined. GUATEMALA. ALTA VERA PAZ: February 1886, *Türckheim s.n.* (FH-00965711, FH-00965712).

HAITI. Road from camp n. 1 to La Barriére Couchant, 2800 m, 17 July 1905, *Nash & Taylor 1105* (paratype YU). Vicinity of Bassin Bleu, Haut Piton summit, on rock, 630-1500 m, 14-27 April 1929, *Leonard & Leonard 15156* (JE).

JAMAICA. On trees, banks of Manbath River, 3000 m, 2 September 1903, *Rehder s.n.*, comm. W. Monkemeyer (paratype YU). On dead tree, Maybess River, July 25, 1903, *Evans 281* (paratype YU).

The unique feature of *R. microlobula* (subg. *Volutoradula*) is the very small lobule (relative to the size of the leaf lobe). The species shows a great variability in the the leaf lobes, which are distant to contiguous with broadly rounded apex (rarely obtuse) in the specimens from Jamaica (including the holotype; Fig. 34F), but subimbricate with a narrow, obtuse apex subimbricate leaves with obtuse apex in plants from Haiti (Fig. 34D). Some specimens show a faintly reddish coloration of the basal cells of the leaf lobes.

According to Castle (1959) the perianths are ca. 2.4 mm long and 1.2 mm wide at the apex, and the androecia have 4–6 pairs of bracts (see Castle 1959, p. 36, fig. 16). In the holotype, however, androecia are absent and perianths are mostly rudimentary (0.6–0.7 mm long, 0.8–0.9 mm wide at apex), being shorter than the bracts.

29. Radula nudicaulis Steph., Sp. Hepat. 4: 174. 1910. Type: Brazil, Serra do Itatiaia, 1894, *E. H. G. Ule 436* (lectotype, G-00043871!, selected by Castle, 1967: 34).

Radula goebelii Steph., in Herzog, Biblioth. Bot. 87: 232. 1916. Type: Bolivia, San Mateo, Sunchal, *T. C. J. Herzog 4458* (lectotype, G-00043890!, selected by Castle, 1967: 34), syn. fide Castle (1967).

Dioicous. *Plants* 2–2.5(–3) mm wide, to 3 cm long, yellowish-brown to reddish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 220–250 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to subimbricate, convex, ovate, 0.9–1.2(–1.5) mm long, 0.7–1(–1.2) mm wide, dorsal base rounded, overlapping the stem, dorsal margin

rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to slightly recurved, entire; marginal cells subquadrate to rounded, 15–20 × 10–15 μm, median and basal cells isodiametric, 20–25 × 15–20 μm, cell walls thin, trigones small to medium sized, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.5–0.7 mm long, 0.3–0.5 mm wide, ca. 1/3 the lobe length, inflated along the keel and at rhizoid area, insertion 2(–3)× the base length, insertion line almost straight, base plane, rounded, covering up to 1/2 the stem, free margin sinuose-plicate in the middle, apex plane to incurved, rounded, distal margin sinuose, keel straight to convex, spreading at angles of 40–50º with the stem, 110–170º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 2–6 pairs of bracts, 0.9–1.1 mm wide; bracts subimbricate, ovate, 0.7–0.8 mm long, 0.2–0.25 mm wide, apex rounded, margin recurved, entire, lobule ovate, ca. 5/6 of lobe length, base rounded, free margin straight, apex rounded to obtuse. *Gynoecia* on long branches, with 2 innovations; bracts oblong-ovate, 0.9–1 mm long, 0.6–0.7 mm wide, apex rounded to obtuse, margin plane to ± recurved, entire, lobules oblong, ca. 1/2 of lobe length, apex rounded. *Perianth* erect, subcylindrical to trumpet-shaped, 2–2.8 mm long, 0.3–0.4 mm wide at base, 0.6–0.8 mm wide at middle, 0.7–1.1 mm wide at apex, mouth entire, plane to undulate; perianth wall not observed. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Costa Rica, Ecuador, Colombia, Brazil, Bolivia and Macaronesia (Azores and Madeira) (Bouman & Dickse 1990, Gradstein 2021, Oliveira-da-Silva *et al.* 2021) (Figure 35). This species grows on tree and rock, rarely on dead tree and soil, in humid and shaded places, in lowland to montane forest up to páramo, from sea level to 4000 m.

Additional specimens examined. COSTA RICA. SAN JOSÉ: Cordillera Talamanca, San Gerardo de Dota, Quercus copeyensis-Primärwald auf Erde, 2900 m, 14 February 2000, *Holz CR 00-0663* (GOET). Copey, P.N. Tapantí-Macizo de La Muerte, área de bosque de roble, primário alterado y borde de caminho, a la base de tronco, 2600 m, 11 July 1996, *Dauphin 2621* (MO).

BRAZIL. ESPÍRITO SANTO: National Park Serra do Caparaó, 2020 m, 27 July 1987, *Schäfer-Verwimp & Verwimp 8928* (MG). **MINAS GERAIS:** National Park Serra do Caparaó, trail to Pico da Bandeira, 2680 m, 27 July 1987, *Schäfer-Verwimp & Verwimp 8980* (MG). **PARANÁ:** Pato Branco, Rio Pato Branco na BR 280, 15 January 1983, *Yano et al. 5435* (SP).

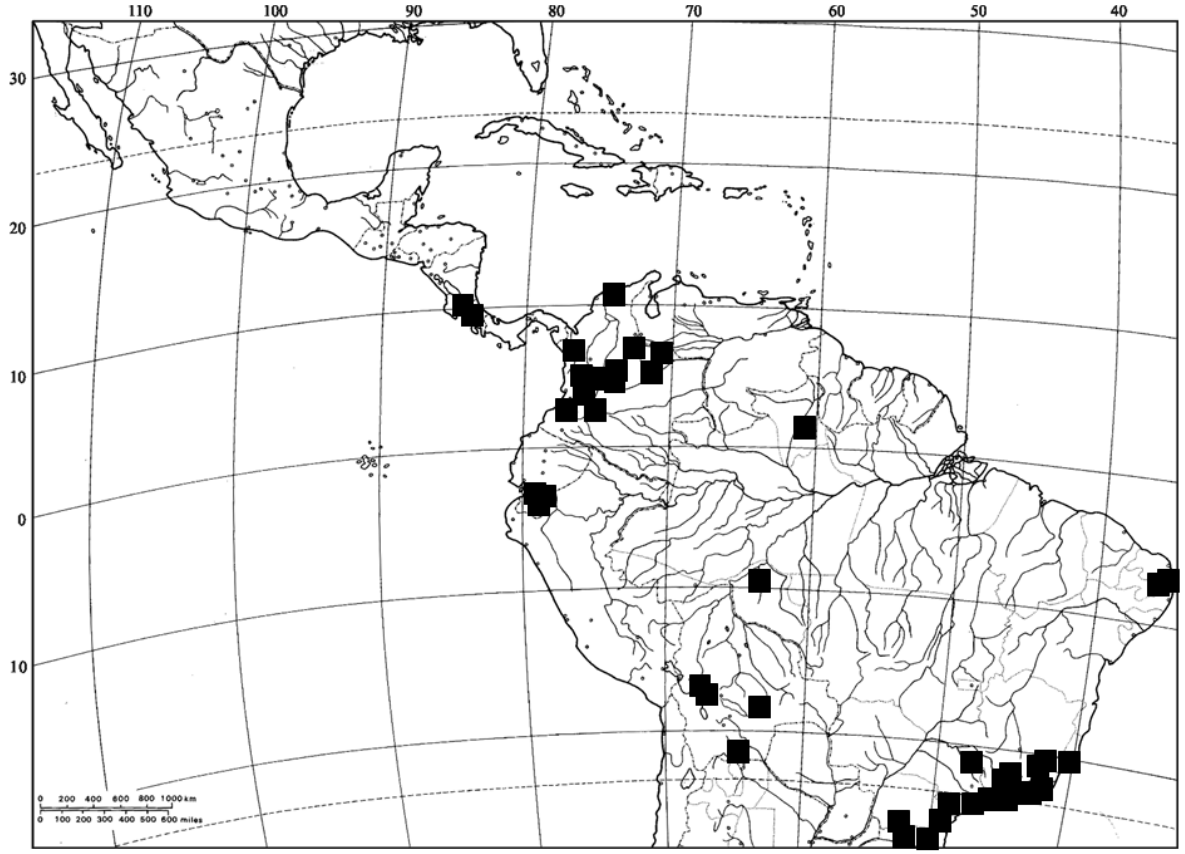

Figure 35. Distribution of *Radula nudicaulis.*

PERNAMBUCO: São Lourenço da Mata, Tapacurá, 4 February 1988, *Yano & Mariz 11262* (SP). **RIO DE JANEIRO:** Santa Maria Madalena, 21°57'54"S, 41°51'28"W, 125 m, 14 May 2007, *Costa 4816* (RB). Serra do Itatiaia, 2200 m, 15 May 1902, *P. Dusén 366* (JE). **RIO GRANDE DO SUL:** Viamão, Parque Saint Hilaire, 9 June 1994, *Reschke s.n.* (ICN); Cambará do Sul, Itaimbezinho, 3 October 1976, *Vianna 3258* (ICN). **RONDÔNIA:** Ariquemes, Alto Condeias, Mibrasa Tin Mine, 10°35'S, 63°35'W, 200 m, 17 May 1982, *Fife et al. 4178* (INPA). **RORAIMA:** 10 km of Serra da Lua, 2°25–29'N, 60°11–14'W, 19 January 1969, *Prance et al. 9352* (INPA). **SANTA CATARINA:** Xanxerê, 21 April 1983, *Yano & Pirani 6611* (SP). **SÃO PAULO:** Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, 23°33'72"S, 44°85'3"W, 30–50 m, 28 October 2009, *Costa et al. 5061* (RB). Barra do Turvo, fazenda Sanharao, 1973, *Vital 2789* (JE).

BOLIVIA. Palopolo bei Coroiko, n. Yungas, 1300 m, October 1912, *Buchtien 15 pp.* (JE). **LA PAZ:** Nor Yungas, Parque Nacional Cotapata, Estacion Biológica Tunquini, caminho al palmar, 16°11'44"S, 67°52'03"W, 1600-1900 m, 21 August 2001, *Drehwald & Drehwald 10489* (GOET). Franz Tamayo, along the trail between Pelechuco and Pata, along the Rio Pelechuco, downstream from Pelechuco at altitudes between, dense, humid forests, at base of boulder, 14°46'S, 69°01'W, 2900 m, 14 November 1988, *Lewis 88-1815* (MO). **SANTA CRUZ:** Vallegrande, bosque montano de Tucumano-Boliviano, dosel bajo, epifita creciendo sobre *Ilex argentina*, 18°34'44"S, 63°46'31"W, 2168 m, 29 July 2011, *Inturias et al. 899* (MO).

Radula nudicaulis (subg. *Volutoradula*) is recognized by plants large (2–3 mm wide), regularly pinnate, leaf lobe distant to subimbricate, slightly convex, ovate, leaf cells with minute to medium-sized trigones, lobules distant, rather small, subquadrate, usually inflated along the keel, lobule base rounded, covering ca. 1/2 of stem width, and free margin conspicuously sinuose-plicate. Some authors reported caducous leaf lobes (*e.g.* Bouman & Dickse 1990, Gradstein 2021) and small discoid gemmae (Jans 1979) in *R. nudicaulis*, but we did not observe vegetative reproduction in the species. Gradstein (2021) suggested that the discoid gemmae reported by Jans (1979) may have been regenerants, which may resemble gemmae when juvenile.

Radula nudicaulis resembles the common Neotropical *R. pallens* in lobule shape, but the latter has irregularly to dichotomous branching, leaves usually imbricate, and lobule keel spreading at a wider angle, of 60–70°, with the stem (40–50° in *R. nudicaulis*).

30. Radula pallens (Sw.) Mont. var. **pallens**, Voy. Amér. Mérid., Bot. 71. 1839. *Jungermannia pallens* Sw., Prodr. 143. 1788. Type: Jamaica, s.d., *O. Swartz s.n.* (holotype, S-B28464!).

Radula campanulata Lindenb. & Gottsche, Syn. Hepat. 256. 1844. Type: Dominican Republic, St. Domingo, *Thouin s.n.* (lectotype, W!, hb. Lindenberg n° 5518, **designated here**; isolectotypes, W!, hb. Lindenberg n° 5517, G-00281252!, scanty, BM!), ***syn. nov.***

Radula didrichsenii Steph., Sp. Hepat. 4: 818. 1910. Type: Brazil, Rio de Janeiro, Petrópolis, *F. Didrichsen s.n.* "Diedrichsen" (lectotype, G-00113194!, **designated here**). Brazil, Paraná, Serra do Mar, 5 IV 1904, *P. Dusén 4398* (syntype, G-00281300!). "Brasilia", *E. H. G. Ule 135* (syntype, G-00281301). "Brasilia", Serra do Itatiaia, *E. H. G. Ule 483*

(syntype, G-00113193!). Brazil, Rio de Janeiro, *K. C. Kindberg s.n.* (syntype, G-00113192), syn. fide Castle (1959, under *R. kegelii*).

Radula husnotii Castle, J. Hattori Bot. Lab. 21: 45. 1959. Type: Guadeloupe, Pl. des Antilles, sur la terre, Le Matouba, on soil, 700 m, 1868, *T. Husnot 251*, as *R. pallens* (lectotype, YU-242192!, **designated here**; isolectotypes, YU-242193!, YU-242194!, YU-242195!, BM-000969213!, BM-000969214!), ***syn. nov.***

Radula jamaicensis Pearson, Ann. Bryol. 4: 103. 1931. Type: Jamaica, Chinchona, 4000-5000 ft., August 1909, *F. O. Bower 811a* (lectotype, MANCH-13618!, **designated here**, c. andr.; isolectotype, MANCH-13619!, c. andr.), ***syn. nov.***

Radula kegelii Steph., Hedwigia 23: 152. 1884. Type: Surinam, Near Mariepaston, 1846, *H. Kegel 1412* (lectotype G-00121979!, selected by Gradstein, 2021: 633; isolectotypes G-00264270!, c. gyn., G-0026471!, FH-00965693!). Brazil, Santa Catarina, 1847, *Pabst 886* (syntypes, G-00264272!, FH-00965694!), syn. fide Gradstein (2021).

Radula laxiramea Steph., Sp. Hepat. 4: 178. 1910. Type: Panama, Chirique, *F. Hélion 412* (lectotype, G-00112206, selected by Yamada, 1991: 90), ***syn. nov.***

Radula lindigii Castle, J. Hattori Bot. Lab. 21: 29. 1959. Type: Colombia, on the roots of trees in forest, 1800 m, 1860, *A. Lindig s.n.*, as *R. pallens*, in hb. Hampe (holotype, BM-000969308!, c. andr.; isotype, JE-04007825!, c. andr.), ***syn. nov.***

Radula neotropica Castle, J. Hattori Bot. Lab. 21: 31. 1959. Type: Dominica, on trees, windward slope of Morne Diablotin, 2500-3000 m, 1896, *W. R. Elliott 2191*, as *R. pallens* (holotype, BM, not found; lectotype, YU-167872!, **designated here**, c. andr. + gyn.), ***syn. nov.***

Radula obovata Castle, J. Hattori Bot. Lab. 21: 16. 1959. Type: Dominica, on leaves, head of Castle Bruce River, 1896, *W. R. Elliott 1657*, as *R. pallens* (holotype, BM, not found). Morne Micotrin, 1896, *W. R. Elliott 1119* (lectotype, BM!, c. per. + spor., **designated here**; isolectotype, JE!, c. per.). Guadeloupe. *l'Herminier 14*, Hep. Eur. Exsicc. 564 (ed. Gottsche & Rabenhorst as *R. pallens*) (paratypes, JE-04007822!, c. gyn., JE-04007823!, c. per., JE-04007824!, c. per.), syn. fide Oliveira-da-Silva *et al.* (2021).

Radula pocillifera Taylor, London J. Bot. 5: 377. 1846. Type: Dominican Republic, St. Domingo, 1814, *Dickson s.n.*, ex hb. Pearson (lectotype, MANCH-15315!, **designated here**, c. per.), syn. fide Castle (1968 [1969], under *R. campanulata*).

Radula subsimplex Steph., Hedwigia 23: 130. 1884. Type: Guadeloupe, *C. l'Herminier s.n.* (lectotype, G-00043857!, c. andr., selected by Yamada, 1980: 254; isolectotype, BM-000969246!, c. andr.), syn. fide Gradstein & Lavocat Bernard (2020).

Dioicous, rarely monoicous. *Plants* 1.5–3 mm wide, to 5 cm long, green to yellowish in field, olive-green to brown in herbarium, irregularly pinnate to dichotomous in female plants by repeatedly fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on decapitated shoots. *Stems* 180–280 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to imbricate, rarely distant, slightly convex, suborbicular, sometimes falcate-ovate, 0.9–1.6 mm long, 0.5–1.2 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight, rarely slightly rounded, apex rounded, margin plane, incurved or recurved, entire; marginal cells subquadrate to subrectangular, 10–20 × 8–15 μm, median cells isodiametric to elongate, 15–25 × 15–20 μm, basal cells isodiametric to elongate, 20–30 × 15–20 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical to ellipsoidal, light yellow, smooth to slightly granular, 12.5–18 × 10–15 μm. *Lobules* distant, quadrate to subquadrate, 0.3–0.6 mm long, 0.2–0.5 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area, insertion 1–2× the base length, insertion line straight to slightly curved, base plane, rounded, covering ca. 1/2 the stem, rarely overlapping the stem, free margin plane, almost straight, apex plane, sometimes incurved, rounded to obtuse, distal margin straight, keel straight to almost concave, spreading at angles of 60–70º with the stem, 140–180º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty to numerous, present on a few or numerous lobules. *Androecia* terminal to intercalary on long branches, with 3–10 pairs of bracts, 0.9–1.4 mm wide; bracts distant to subimbricate, ovate, 0.8–1 mm long, 0.3–0.6 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin almost straight, apex rounded. *Gynoecia* on short or long branches, with 1–2 innovations; bracts ovate, 1–1.3 mm long, 0.5–0.8 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, 1/2–1/3 of lobe length, apex rounded, keel straight to concave. *Perianth* erect, subcylindrical, trumpet-shaped or campanulate, 2.3–4 mm long, 0.2–0.3 mm wide at base, 0.7–0.9 mm wide at middle, 0.9–1.4 mm wide at apex, mouth entire, plane to strongly undulate; perianth wall 2–5-stratose in the lower base, unistratose from the upper base to apex, rarely with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–8-layered tube within which the sporophyte foot, sometimes part of the seta (perigynium), is embedded. *Calyptra* wall 2–3-layered at the base, 1 cell layer

thick above. *Seta* 4–8 mm long. *Capsule* 1–1.6 mm long, 0.2–0.5 mm wide, valves 1.1–1.8 mm long, 0.2–0.4 mm wide at middle, outer layer cells subquadrate, simple nodular thickenings reddish-brown, on every longitudinal wall and on some cells angle, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* 200–300 µm long, rough. *Spores* 18.51–29.62 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by regenerants on leaf margins and leaf surfaces, caducous *Lejeunea*-type branches and stem fragmentation.

Distribution and habit. Widespread in Tropical America; in addition, in southern South America (Chile and Argentina) (Figure 36). *Radula pallens* grows on various substrates, usually trunks of living trees and on rotten logs, rarely on leaves, rock and soil, in lowland andf montane forests, from sea level to 2800 m elevation. The species usually has prostrate growth, rarely pendent, forming dense to sparse mats.

Illustration. Oliveira-da-Silva *et al.* (2021).

Additional specimens examined. MEXICO. CHIAPAS: 1 km West of Tziscao, 55 km east of Comitán, epiphyte on trunk in cloud forest, 1250 m, 16 May 1973, *den Held & van Rhijn HH76* (GOET). **VERA CRUZ:** Los Tuxlas, way to "Cerro Vigia", on rock in little disturbed lowland rainforest, 18°34' N, 96°5' W, 150 m, 27 September 2004, *Burghardt 4444* (GOET).

BELIZE. CAYO: In forest along ridge and along small stream just below ridge in vicinity of Doyle's Delight, southern Maya Mountains, on ground, 16°30'N, 89°03'W, 1098 m, 5 December 1993, *Allen 15110* (MO).

GUATEMALA. ALTA VERAPAZ: 4 mi up road to Oxec along road which turns N of hwy 7E to El Estor, ca. 6 km NE of Panzos, disturbed steeps slopes above road, 500 m, 20 July 1977, *Croat 41601* (GOET, MO). Cobán, 1600 m, January 1908, *Türckheim s.n.* (FH).

HONDURAS. ATLÁNTIDA: Lancetilla Valley, near Tela, on tree trunk, 20-600 m, 6 December 1927 – 20 March 1928, *Standley 55813* (JE). La Ceiba, Pico Bonito National Park, east side of Rio Bonito, on boulder, 15°42'N, 86°51'W, 110 m, 12 April 1996, *Allen 17331, 17233* (MO). Ibid., UNAH-CURLA campamento, on boulder, 95 m, 27 April 1996, *Allen 17641* (MO). **LEMPIRA:** Montana de Celaque, Quebrada below Camp Don Tomas along Rio Naranjo, 10 km SW of Gracias, on Boulder by stream, 1900 m, 11 May 1992, *Allen 11935* (MO).

EL SALVADOR. SAN VICENTE: Volcán de San Vicente, 1200-1500 m, 7-8 March 1922, *Standley 21573* (MO, FH).

NICARAGUA. ALTÂNTICO NORTE: along Caño Majagua, on rock, 13°45'N, 85°00'W, 750-850 m, 10-11 March 1978, *Stevens 6947* (MO). **GRANADA:** Lado NW del Volcan Mambacho, finca "San Joaquin", 11°50'N, 85°59'W, 800-1000 m, 15 May 1981, *Moreno 8537* (MO).

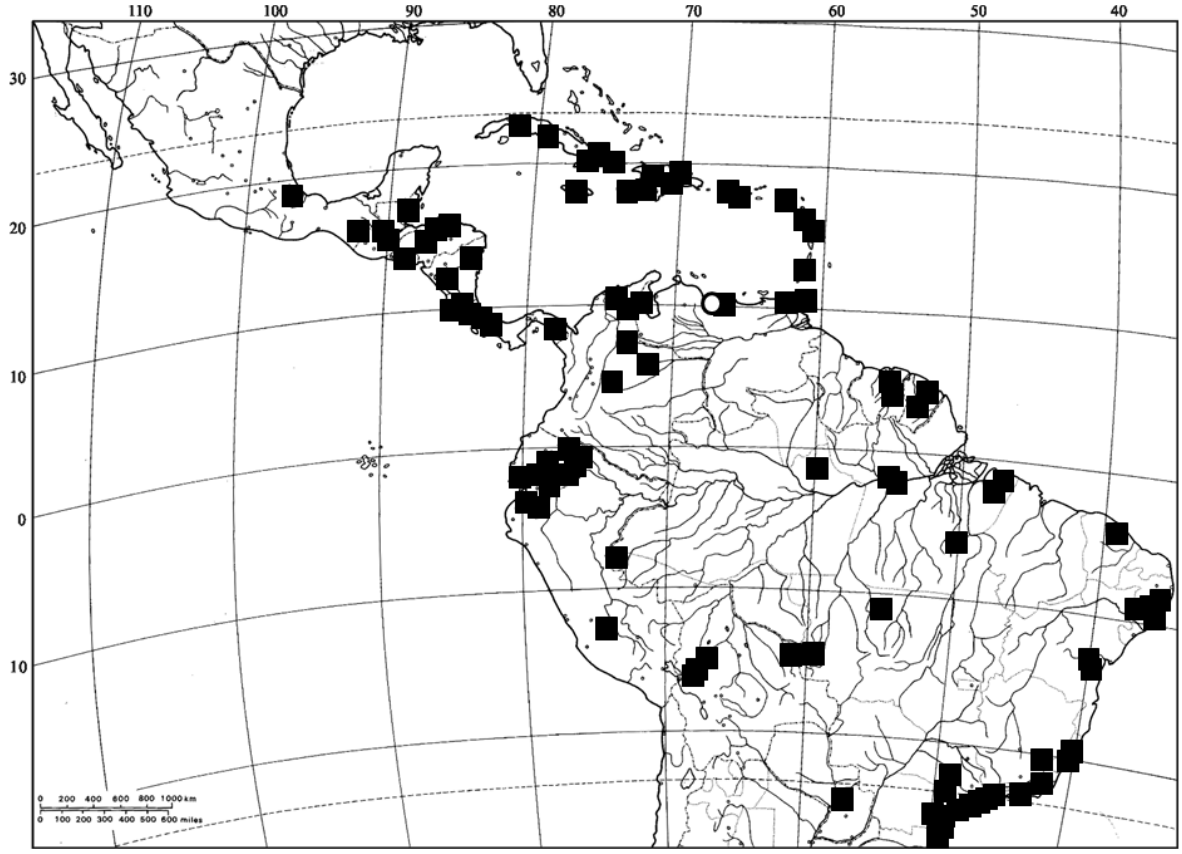

Figure 36. Distribution of *Radula pallens* var. *pallens* (black square) and *R. pallens* var. *marginata* (white circle).

COSTA RICA. ALAJUELA: along road from San Ramon N-ward through balsa, 13,8 km N of bridge over Quegrada Volio, 4,6 km N of bridge over Rio Balsa, epiphyte, 10°12'N, 84°31'W, 900-1000 m, 29 August 1979, *Stevens 13720, 13723, 13728, 13731* (MO). Río Cuarto, R.V.S. Bosque Alegre, Laguna Hule, area de bosque alterado, sobre tronco expuesto, 10°17'N, 84°12'W, 700 m, 12 January 1996, *Dauphin 2117* (MO). **CARTAGO:** Vicinity of Pejivalle, on tree, 900 m, 7-8 February 1926, *Standley & Valerio 46897* (JE). Vicinity of Orost, on tree, 30 March 1924, *Standley 39746* (JE). Catie, 3 km E of Turrialba, "los Espaveles" nature trail, on rock, 09°54'N, 83°39'W, 600 m, 9 May 1983, *Liesner 15264* (MO). **HEREDIA:** Yerba Buena, on tree, 2000 m, 22-28 February 1926, *Standley & Valerio 49937* (JE). Cerro de

las Caricias, on wet rock , 2000-2400 m, *Standley & Valerio 51990* (JE). **GUANACASTE:** Monteverde Biological Preserve, on tree trunk, 10°15'N, 84°45'W, 5 August 1993, *Timme 11427* (MO). La Cruz, P.N. Guanacaste, sobre roca a la sombra, 11°00'N, 85°33'W, 600-1145 m, 10 June 1996, *Dauphin 2520, 2529* (MO). **LIMON:** Llanuras de Santa Clara near Rio Agua Frio, 16 Airline mi NE of Guapiles, base of large tree, 10°23'N, 83°45'W, 100-150 m, 1-7 April 1954, *Daly 16, 43B, 44* (MO). **SAN JOSÉ:** in dense oak and bamboo forest near Laguna de la Escuadra, northeast of El Copey, on tree, 2000-2200 m, 16 December 1925, *Standley 41926, 42017* (JE). La Hondura, on tree, 1300-1700 m, 2-4 March 1924, *Standley 36204, 37826* (JE). **PUNTARENAS:** Reserva Biológica Monteverde, undisturbed cloud forest, on trunks and branches in forest understorey, 1550 m, 22 September 1994, *Gradstein & Mues 9681* (GOET). Monteverde, on trees near Motas, 4 April 1969, *James 1969-92* (MO). Monteverde, 20 January 1971, *James s.n.* (MO6169777). Monteverde Cloud Forest Preserve, Atlantic slope, on tree trunk, 10°18'N, 84°47'W, 1600 m, 4 March 1992, *Lyon 157* (MO). Ibid., Pacific slope, pre-montane wet forest, on tree trunk, 10°18'N, 84°47'W, 1500 m, 21 March 1992, *Lyon 422* (MO). Potrero Grande, P.N. La Amistad, Cerro Bioley, sobre piedra, 09°02'N, 83°00'W, 1500-1766 m, 25 February 1995, *Dauphin 1628* (MO).

PANAMA. DÁRIEN: Estación Pirre de Inrenare, em las faldas del Cerro Pirre, sobre corteza de árbol, 100 m, 5 June 1991, *Salazar Allen & Gradstein 9228* (GOET). **PANAMÁ:** Barro Colorado Island, Canal Zone, trail Shannon Creek, on palm base, 9°10' N, 79°10' W, October 1993, *Gradstein & Salazar Allen 15133* (GOET). Drowned forest of Quebrada Ancha, 75 m, 21 December 1934, *Steyermark 17122, 17133* (MO).

BERMUDA. Church Cave, Juckers Joun, 31 August – 20 September 1905, *Britton 327* (MO, FH). On moist rock at the mouth of Church Cave, in the Hamilton district, April 1911, *Rugg s.n.* (FH).

CUBA. Without locality, s.d., *Wright s.n.* (JE-H1367, MO-5374254, MO-5374250, MO-444008, FH-00965736). **CIENFUEGOS:** Soledad Mina Carlota, tree trunk in moist shaded ravine, 1948, *Welch 9417, 9426* (JE). Sierra del Escambray, cafetal de San Blas, 400-500 m, 1 March 1969, *Bisse & Lippold 13077/b* (JE). **HABANA:** Isla de Pinos, Nueva Gerona, Sierra la Cañada, 300 m, 26 December 1966, *Bisse 763, 745/c* (JE). **HOLGÍN:** Moa, La Melba, 3 January 1969, *Bisse & Lippold 11240/c, 011738/a, 011739/a* (JE). Camino desde Moa hacia La Melba, 4 February 1969, *Lippold 12244/a* (JE). **GUANTÁNAMO:** Baracoa, pluviosa al sur de la Loma del Yunque, 300-400 m, June 1967, *Bisse & Rojas 2714/d, 2719/a* (JE). Monte Verde, 600-700 m, 1 noviembre 1968, *Bisse & Lippold 10136/a* (JE). Sierra Maestra, 1100 m, 1969, *Borhidi & Muniz 5380* (JE). Monte Cristo, 1968, *Urban 776/c* (JE). Monte Cristo, 1968, *Hadac F16*

(JE). Monte Cristo, 700 m, 1968, *Samek et al. Cr47/b* (JE). Forest de la Perla, 600 m, August 1913, *León s.n.* (FH). **SANCTI SPÍRITUS:** 5 km westlich Topes de Collantes, 20 February 1968, *Schubert M399* (JE). Topes de Collantes, falda norte y cima del Pico Potrerillo, 600-930 m, 6 May 1977, *Lepper 34956* (JE). **SANTIAGO DE CUBA:** falda este de Gran Piedra, pluviosilva, 26 Abril 1969, *Bisse & Lippold 15009/d, 15031/a, 15049/a, 15050/a, 15132/a, 15136/a, 15137/a, 15138/a* (JE). Sierra de la Gran Piedra, 1980, *Pócs & Caluff 9199-EF* (1980). Sierra Maestra de la Gran Piedra, in pluviisilvis montanis, in cortice, 1100 m, 1969, *Borhidi & Muniz 5389* (JE). Sierra Maestra de la Gran Piedra, in pluviisilvis stacion, submontanis as Brazo Escondido prope pag. Filé, 500 m, 1969, *Borhidi & Muniz 5105* (JE).

JAMAICA. Without locality, s.d., *Wolle s.n.* (MO-4421557).

HAITI. Vicinity of St. Louis du Nord, on damp surface of rocks, mountain slope, 30 March – 7 April 1929, *Leonard & Leonard 14149* (JE). Vicinity of St. Louis du Nord, on trunk of trees, 30 March – 7 April 1929, *Leonard & Leonard 14565* (JE). Vicinity of St. Louis du Nord, on rocks and rotten stump, summit southwest of city, 30 March – 7 April 1929, *Leonard & Leonard 14474* (JE). **L'ARTIBONITE:** vicinity of Ennery, 325-900 m, 23 January 1926, *Leonard 9123, 9135a* (JE). Vicinity of Ennery, 325-900 m, 5 February 1926, *Leonard 9535, 9542* (JE). **DU NORD:** vicinity of Plaisance, 400 m, 28 January 1926, *Leonard 9382* (JE). Vicinity of Marmelade, on rock, 800 m, 19 December 1925, *Leonard 8126b* (JE). Vicinity of Marmelade, steep grassy slope, 800 m, 19 December 1925, *Leonard 8148a, 8150b* (JE).

DOMINICAN REPUBLIC. ST. DOMINGO: Samana, Parque Nacional Los Haitises, dense humid forest along trail of Naranjo, on tree roots, 20 January 1980, *Smith 10429* (MO). Pedernales, Las Abejas, Sierra de Baoruco, on bark of living tree, wet broad-leaf forest in ravine, 1200 m, 8 November 1979, *Smith 10058* (MO). Estrelleta, Sierra de Neiba, at height of land along Carretera Internacional, dense humid broad-leaf forest, on liana, 1800 m, 27 November 1979, *Smith 10251* (MO).

PUERTO RICO. On most cliff along trail, hills E of Matrullas Resevoir, Toro Negro Purchase Unit, Cordillera Central, 19 March 1940, *Pagán 6826* (JE). Utuado, 1887, *Sintenis H143* (JE). Without locality, 25 March 1886, *Sintenis 55* (MO). Without locality, 25 March 1887, *Sintenis 143* (MO). **ADJUNTAS:** Reserva Florestal Guilarte, lower slopes of Monte Guilarte, on rotten log, 9 August 1966, *Stimson 3894A* (MO). **LUQUILLO:** Caribbean National Forest, Sierra de Luquillo, 4 December 1973, *Redfearn 29247* (MO).

ST. KITTS. Without locality, s.d., *Breutel s.n.* (JE).

GUADELOUPE. Without locality, s.d., *l'Herminier s.n.* (FH-00965700, JE). Without locality, s.d., *l'Herminier 14*, Hep. Eur. Exsicc. 564 (ed. Gottsche & Rabenhorst as *R. pallens*)

(paratypes of *Radula obovata*, JE-04007822, JE-04007823, JE-04007824). Le Matouba, sur la terre, 700 m, 1868, *Husnot s.n.* (FH).

DOMINICA. SAINT PATRICK PARISH: trail to Sari-Sari Falls, along Sari-Sari River from La Plaine, wet lowland rainforest, epiphyte, 1100-1300 m, 31 May 1994, *Hill et al. 25719* (MO). Morne Micotrin, 1896, *Elliott 1119* (JE, paratype of *Radula obovata* Castle).

ST. VINCENT. Without locality, March 1890, *Smith & Smith 1384, 1385* (FH).

TRINIDAD AND TOBAGO. Without locality, s.d., *unknown collector* (JE).

FRENCH GUIANA. CAYENNE: Montagnes de Cacao, dense forest, epiphytic, 52°28' W, 4°35' N, 150 m, March 1985, *Aptroot 15570* (GOET). **SAÜL:** mixed forest "Sentier Limonade", south of the village, on rough bark of old trunk, plants pendulous, 23-30 June 1986, *Gradstein 6171* (GOET). Trail to Mt. Galbao, creek forest at mountain foot, east side, on palm stem, 23-30 June 1986, *Gradstein 6204* (GOET). Trail close to village of Saül, secondary moist forest, on tree trunk, 3°37'55" N, 53°12'16" W, 200 m, 25 September 2000, *Holz FG 00-328* (GOET). 2 km SW of the village, "Sentier Limonade", mixed forest on lateritic soil, epiphytic on tree base, 03°32' N, 53°12' W, 180-210 m, 27 August 1986, *Montfoort & Ek 412* (GOET).

SURINAME. BROKOPONDO: Brownsberg, trail to Witie creek, dry ridge forest on east-slope, on trunk base, 55°11' W, 4°56' N, 300-400 m, 25-29 January 1985, *Gradstein 4646* (GOET).

VENEZUELA. MIRANDA: Cerros del Bachiller, near east endvirgin forest evergreen forest, lower slopes and stream margins of Quebrada Corozal, south of Santa Cruz, 10°9' N, 65°48' W, 20-65 m, 16-17 March 1978, *Steyermark & Davidse 116287B* (GOET). **SUCRE :** Cerro Patao, Norte de Puerto de Hierro, Noroeste de Guiria, quebrada pedregosa (esquisto de Mica), on boulders by stream bed, 100-300 m, 23 July 1962, *Steyermark & Agostini 91249* (MG, NY). **ZULIA:** Valley of the río Socuy, in cloud forest above large pastureland, the "Gran Sabana", on tree trunk, 2400-2800 m, *Griffin III 221* (GOET).

COLOMBIA. CASANARE: Sácama, caminho que va desde el município hasta la Quebrada Macueque, passando por el río Sácama, 1220 m, 17 August 1982, *Aguirre C. et al. 3110* (GOET). **MAGDALENA:** Sierra Nevada de Santa Marta, transecto del Buritaca, selva cálido-tropical, sobre roca, 500 m, 30 August 1977, *Rangel & van der Hammen 1227* (GOET).

ECUADOR. **ORELLANA:** Yasuni National Park, abundant on tree trunks in varzea forest near Tiputini Biodiversity Station, 200 m, 30 October 2018, *Gradstein 12814* (MG, QCA). **SANTIAGO-MENDEZ:** 700 m, 1947, *Harling 2228 pp.* (JE). **SUCUMBIOS:** Shushufindi, Secoya San Pablo de Cantesiayá, bosque tierras bajas, várzea-igapó, epífita a la sombra, 00°15'58"S, 76°27'33"W, 300 m, 4 April 2008 *Cerón & Reyes 61844* (MO). **ZAMORA CHINCHIPE:** 600 m,

Harling 2259/a pp. (JE). Zamora, Reserva Biológica San Francisco, al lado Río San Francisco, bosque montano bajo, sobre hojarasca, em roca vertical a la sombra, 03°58'17"S, 79°04'39"W, 1860 m, 24 November 2005, *Churchill & Jaramillo 24116* (MO).

PERU. JUNÍN: Ort. Bei der Brucke "Pan de Azugar", 12 km von San Ramón in Richtung Tarma, 1000 m, 13 June 1977, *Hegewald 8535* (MO).

BRAZIL. **ACRE:** Rio Moa between Republica & Serra da Moa, 19 April 1971, *Prance et al. 12095* (NY). **ALAGOAS:** Murici, Estação Ecológica de Murici, 2 December 2004, *Pôrto s.n.* (UFP). **AMAZONAS:** along W shore of Rio Uatumã at junction of Rio Pitinga, 01°31'S, 59º50'W, 24 August 1979, *Buck 3102* (NY). **BAHIA:** Santa Teresinha, Serra da Jibóia, ca. 800 m, 16 December 2003, *Valente 308* (UFP). Estação Ecológica Estadual de Wenceslau Guimarães, trilha Água Vermelha, corticícola, floresta ombrófila, 13°34'42" S, 39°42'28" W, 443 m, 29 September 2017, *Bastos 6067* (ALCB). Reserva Ecológica da Michelin, Pancada Grande, Trilha Corte Alto, floresta ombrófila, corticícola, 13°48' S, 39°10' W, 21 April 2006, *Bastos 4413* (ALCB). **CEARÁ:** Pacatuba, Serra do Pacatuba, 3°50'S, 38°47'W, 22 July 1997, *Almeida-Neto et al. 223* (SP). **ESPÍRITO SANTO:** Santa Teresa, Rio Timbuí, 5 July 1981, *Yano 3622* (SP). **MATO GROSSO:** Vila Bela da Santíssima Trindade, Serra Ricardo Franco, 23°S, 60°W, 300–400 m, 22 March 1978, *Windisch 1806* (SP). **MINAS GERAIS:** Serra do Caparaó, 20°25'S, 41°50'W, 1350 m, 28 July 1987, *Schäfer-Verwimp & Verwimp 8988* (SP). **PARÁ:** São Miguel do Guamá, 01°35'10,1"S, 47°31'39,5"W, 22 November 2014, *Pietrobom et al. 10032* (SP). **PARANÁ:** Serra da Esperança, 8 km west of junction with BR 277 to Irati on BR 373, Km 119, 980 m, 11 September 1977, *Vitt 21400* (JE). Iguaçú, in der feuchter Schluchten des National Parks des Río Iguaçú im Urwald, epiph., 16 July 1933, *Hosseus 29A, 29B, 52* (JE). Tijucas do Sul, 25°51'07" S, 49°14'48" W, 1100 m, 6 June 1998, *Shirata 3610* (SP, JE). Tijucas do Sul, distrito de Lagoa, Vivat Floresta Sistemas Ecológicos, sobre galho de arbusto, 03°58'17"S, 79°04'39"W, 880 m, 13 July 2004, *Yano & Shirata 28031* (MO). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 26 August 1987, *Pôrto 2063* (UFP). **RIO DE JANEIRO:** Nova Friburgo, Macaé de cima, Rio das Flores, 1100–1200 m, 26 November 1986, *Santos et al. 355* (RB). **RIO GRANDE DO SUL:** Esmeralda, Estação Ecologica Aracuri, 30 July 1982, *Bueno 1720* (ICN). Nova Roma do Sul, perto da cachoeira do Rio das Antas, sobre pedra no barranco perto da estrada, 24 November 2009, *Yano et al. 32055* (SP, JE). Flores da Cunha, cachoeira Menegon, sobre rochas, 750 m, 2 July 2005, *Marchett 300* (MO). Caxias do Sul, Vila Seca, sobre caule, 5 May 2007, *Sartori 162* (MO). **SANTA CATARINA:** Santa Cecília, km 122 da BR 116, 28 April 1983, *Yano & Pirani 7116* (SP). Blumenau, 1889, *Ule s.n.* (FH-00965702, FH-00965716). **SÃO PAULO:** Natividade da Serra, Parque Estadual da Serra do Mar, Núcleo de

Santa Virgínia, 23°26’38”S, 45°14’01”W, 867 m, 11 June 2013, *Carmo & Peralta 588* (SP). Itupeba, fazenda Rio das Pedras, 7 January 1895, *J. Puiggari 450* (JE). Butantan, 31 August 1920, *Hoehne 100* (JE). Distrito de Palheiros, São Lourenço, Rodoanel trecho sul 4, sobre tronco de árvore, mata úmida, 13 November 2007, *Yano 30545* (SP, JE). São Paulo, Palheiros, São Lourenço, Rodoanel trecho sul 4, sobre tronco de árvore, mata úmida, 13 November 2007, *Yano 30424* (MO). São Luiz do Paraitinga, Fazenda Rio das Flores, na base do tronco perto do rio, 23°13’18”S, 45°18’36”W, 11 June 1982, *Yano & Lopes 4304* (MO). Sorocaba, March 1875, *Mosén 86* (FH).

BOLIVIA. Yungas, 1300 m, October 1912, *Buchtien 207* (JE). **Beni:** Ballivian, Serrania del Pilon Lagas, river valley and submontane forest, on trunk, 67°2’W, 15°11’S, 850 m, 30 October – 3 November 1989, *Gradstein 7174* (GOET). **La Paz:** Caranavi, bosque ribereño del río Caripo, sobre árbol, 15°19’17”S, 61°05’12”W, 500 m, 17 July 2002, *Arroyo et al. 2590* (MO). **Santa Cruz:** Velasco, Parque National Noel Kempff Mercado, catarata El Encanto, al SE de Los Fierros, bosque alto subhúmedo pluviestacional, 14°37’S, 60°42’W, 300 m, 28 September 1995, *Fuentes 1083-E* (MO).

PARAGUAY. Paraguarí: Mbatoví, 25°15’S, 57°07’W, 199 m, 29 October 2000, *Fretes & Rempel LF172* (MO).

Radula pallens (subg. *Volutoradula*) normally has widely spreading, suborbicular leaf lobes with a broadly rounded apex, lobules distant, quadrate to subquadrate with rounded to obtuse (not elongate), lobule base usually covering up to 1/2 of the width of the main stem, and keel straight to slightly concave, spreading at angles of 60–70º with the stem, and 140–180º with the ventral leaf lobe margin, at its junction with the lobule. In some specimens the lobule base may cover the entire stem, especially on branches.

Radula pallens may be confused with *R. episcia*, but the latter has purely dichotomous branching, orbicular leaf lobes (with a rounded ventral margin), and wider than long lobules with a long insertion line, 5–6× base length (1–2× base length in *R. pallens*).

Radula campanulata, *R. husnotii*, *R. jamaicensis*, *R. laxiramea*, *R. lindigii* and *R. neotropica* are new synonyms of *R. pallens*. A short, cup-shaped (campanulate) perianth is typical of *R. campanulata*, but as noted by Castle (1959) it is an early developmental stage of the perianth and has no taxonomic value. *Radula husnotii* and *R. jamaicensis* are small phenotypes of *R. pallens* with distant to contiguous leaves, while *R. laxiramea* is a robust phenotype with subimbricate leaves and a longly campanulate perianth. Except for plant length and leaf spacing, these species are fully identical.

Radula lindigii has been erroneously considered a synonym of *R. mammosa* (= *R. grevilleana*) (Gradstein *et al.* 2003, Gradstein & Costa 2003). Examination of the type showded that the plants fully identical to *R. pallens.*

Stephani (1910) described *Radula didrichsenii* based on several collections made by various collectors in Brazil (*e.g.* Didrichsen, Dusén, Ule). The specimen collected by F. Didrichsen is designated here as the lectotype.

31. Radula pallens var. **marginata** F.R.Oliveira-da-Silva, Gradst. & Ilk.-Borg., Phytotaxa 564: 96. 2022. *Radula maegdefraui* K.Yamada, in Mägdefrau, Nova Hedwigia 38: 20. 1983, nom. inval. Type: Venezuela, Maracay, Nebelwald von Rancho Grande, am Weg zum Periquito, 1300 m, 25 February 1958, *K. Mägdefrau 363* (holotype, JE!; isotype, MG!).

Fig. 37

Dioicous. *Plants* 1.7–2 mm wide, 2–3 cm long, yellowish-green in herbarium, irregularly pinnate to dichotomous in female plants by repeatedly fertile paired innovation. *Branches* *Radula*-type or *Lejeunea*-type. *Stems* 170–220 µm diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, slightly convex, suborbicular, 0.9 –1.2 mm long, 0.7–1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin almost straight, apex rounded, margin plane to incurved, entire to sinuouse, bordered by one row of thick-walled cells; marginal cells subquadrate to subrectangular, 10–25 × 10–20 µm, median cells isodiametric to elongate, 10–20(–25) × 10–20 µm, basal cells elongate, 25–37 × 15–20 µm, cell walls thin, outer margin of the marginal cells strongly and evenly thickened, trigones small at leaf base, increasing in size from midleaf towards to the margins, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.5–0.7 mm long, (0.3–)0.4–0.5 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area, insertion 1–2× the base length, insertion line straight to slightly curved, base plane, rounded, rarely angulate, covering up to 1/2 the stem, free margin plane, straight, apex plane to incurved, rounded to slightly obtuse, distal margin plane to incurved, straight, keel straight to almost concave, spreading at angles of 50–60º with the stem, 160–170º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few

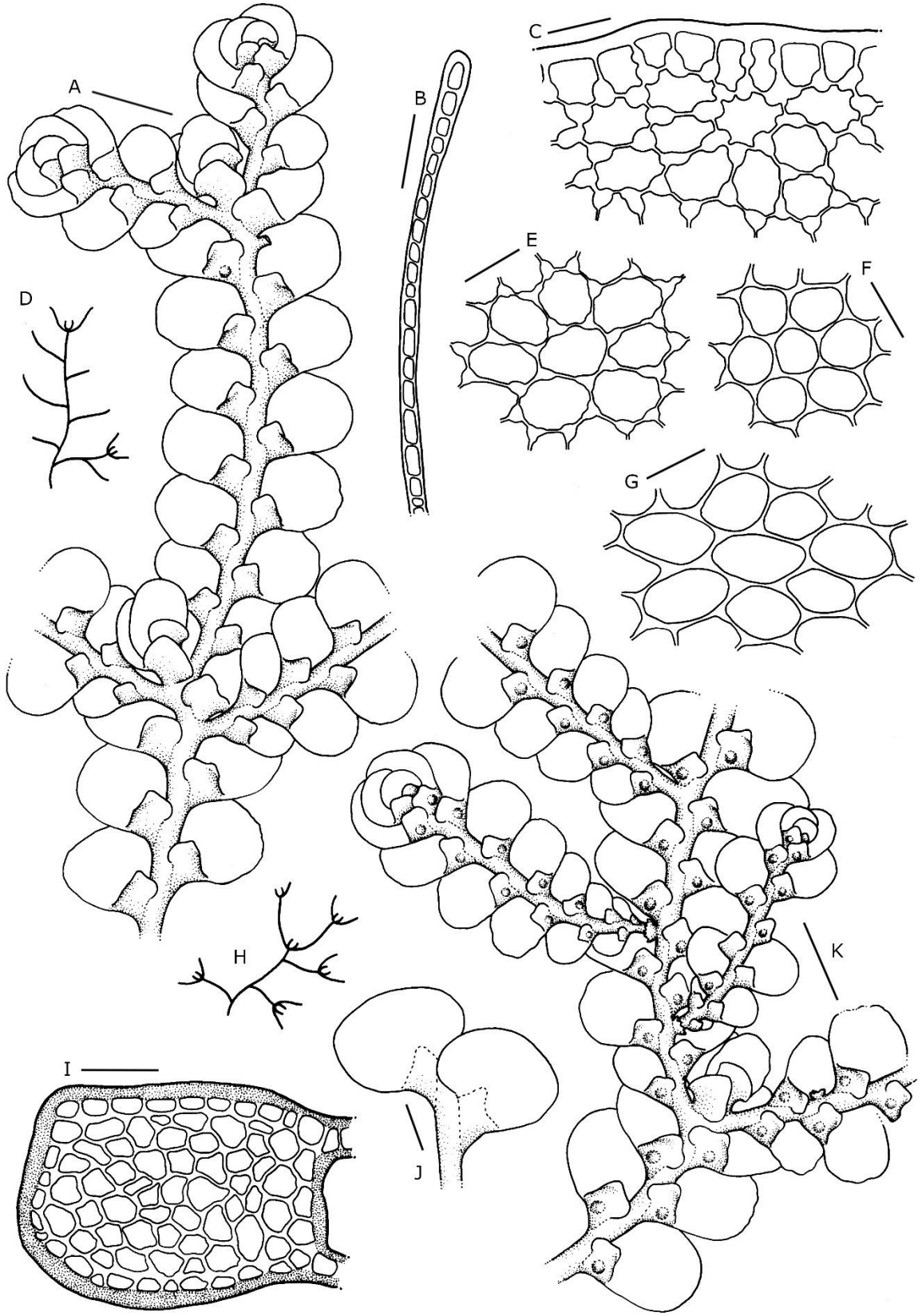

Figure 37. *Radula pallens* var. *marginata*. A, K. Habit with gynoecia, ventral view. B. Cross section of a leaf lobe, showing thick-walled cells at leaf margin. C. Marginal leaf cells. D, H. Cladographs of plants (U = gynoecia without perianths). E–F. Median leaf cells. G. Basal leaf cells. I. Cross section of a stem. J. Leaves in dorsal view (A, K= 1000 μm; B, I= 50 μm; C, E–G= 25 μm; H= 500 μm; A–K from the holotype).

lobules. *Androecia* not seen. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.8–1 mm long, 0.5–0.7 mm wide, apex rounded, margin plane, entire to sinuouse, lobule oblong, 1/2–1/3 of lobe length, apex rounded. *Perianth* and *Sporophyte* not observed. *Vegetative reproduction* by occasionally caducous leaf lobes.

Distribution and habit. Only known from the type locality in Rancho Grande (Henri Pittier National Park), northern Venezuela (Figure 36). *Radula pallens* var. *marginata* was collected from bark in montane cloud forest, at 1300 m elevation.

Specimens examined. VENEZUELA. ARAGUÁ: the type.

Radula pallens var. *marginata* (subg. *Volutoradula*) differs from the typical variety by the presence of a narrow border on the leaf lobes composed of thicker-walled margin cells with larger, bulging trigones and a thickened outer wall (border absent in var. *pallens*). The variety occasionally produces caducous leaf lobes, a character not founded in var. *pallens*.

32. Radula portoricensis Steph., Hedwigia 27: 298. 1888. Type: Puerto Rico, Sierra de Luquillo, 13 July 1885, *P. E. E. Sintenis 75* (lectotype, G-00043948, selected by Yamada, 1981: 395; isolectotype, YU-212925!).

Fig. 38

Radula guatemalensis Steph., Sp. Hepat. 4: 198. 1910. Type: Guatemala, Alta Verapas, 400m, September 1096, *H. Türkhein 6329* (lectotype, G-00112156!, selected by Castle, 1936: 50), syn. fide Yamada (1981).

Dioicous. *Plants* 1.8–2.5 mm wide, to 1 cm long, yellowish to brownish in herbarium, regularly pinnate, sometimes irregularly pinnate. *Stems* 180–200 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls yellowish. *Leaf lobes* widely spreading, contiguous to imbricate, rarely distant, strongly convex, ovate, 1–1.5 mm long, 0.8–1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded to almost straight, apex rounded, margin plane, rarely recurved, entire; marginal cells subquadrate, 10–12 × 0.8–12 µm, median and basal cells isodiametric to elongate, 15–25 × 10–15 µm, cell walls thin, trigones large, intermediate thickening present, rare, cuticle smooth to

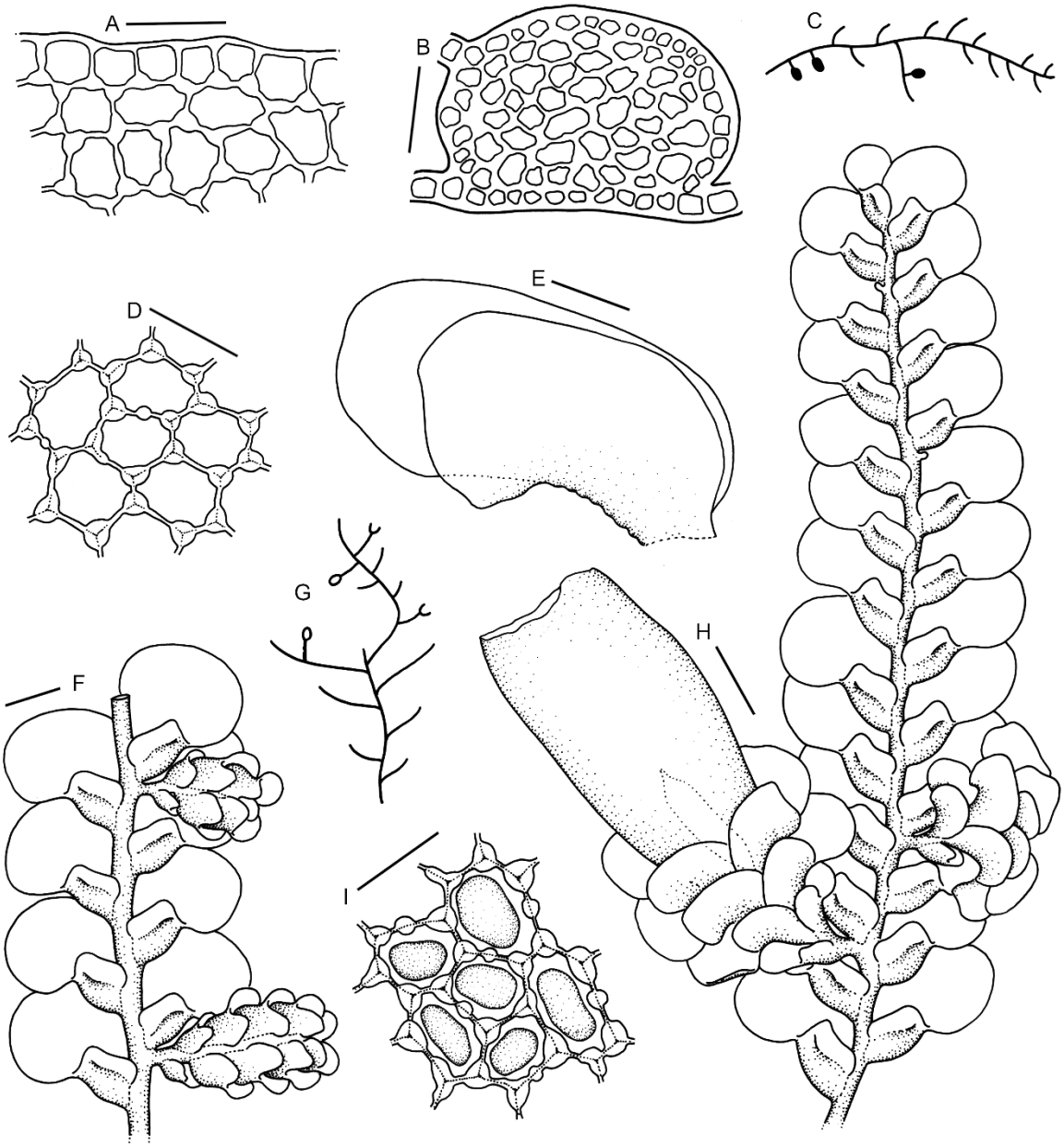

Figure 38. *Radula portoricensis*. A. Marginal leaf cells. B. Cross section of stem. C, G. Cladograph of plants (black dots = androecia, white dots = gynoecia with perianth). D. Median leaf cells. E. Female bract. F. Habit with androecia. H. Habit with perianth. I. Basal leaf cells with oil bodies (A, D, I = 25 µm, B = 50 µm, E, F, H = 500 µm; All from *Standley & Valerio 48089*).

finelly verruculose; oil bodies 1 per cell, spherical to ellipsoidal, light yellow, slightly granular, 5–20 × 5–15 µm. *Lobules* distant, subrectangular, 0.6–0.7 mm long, 0.3–0.4 mm wide, ca. 1/3 the lobe length, inflated along the keel, insertion 1–2× the base length, insertion line curved, base plane, rounded, covering up to 1/3 the stem, free margin plane, straight to slightly sinuose in the middle, apex plane, rounded to obtuse, distal margin straight, keel convex, spreading at angles of 40–45º with the stem, 90–120º with the ventral leaf lobe margin, at its junction with

the lobule. *Rhizoids* colorless, scanty, rarely numerous on a few lobules. *Androecia* terminal on short branches, with 4–6 pairs of bracts, 0.7–0.8 mm wide; bracts distant to subimbricate, ovate, 0.5–0.6 mm long, 0.3–0.4 mm wide, apex rounded, margin plane to slightly recurved, entire, lobule oblong-ovate, ca. 3/4 of lobe length, base rounded, free margin ± straight, apex rounded. *Gynoecia* on very short branches, with 1 pair of bracts, 2–3 pairs of bract-like bellow the bracts, innovations absent; bracts oblong-rectangular, 1–2.5 mm long, 0.5–1 mm wide, apex obtuse to subacute, margin plane, entire, lobule oblong-rectangular, ca. 2/3 of lobe length, apex obtuse to subacute. *Perianth* erect, subcylindrical, 2.7–3 mm long, 0.6–0.8 mm at base, 1–1.2 mm wide at middle, 0.8–0.9 mm wide at apex, mouth entire, plane to convolute ventrally; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 2-layered at the base, 1 cell layer thick above. *Sporophyte* not observed. *Elaters* 180–300 µm long, rough. *Spores* 25.92–31.48 µm in diam., espiculate, spine smooth. *Vegetative reproduction* by caducous leaf lobes.

Distribution and habit. Mexico (new record), Guatemala, Nicaragua (new record), Costa Rica, Jamaica, Dominican Republic, Puerto Rico, Guadeloupe and Colombia (new record) (Figure 39). *Radula portoricensis* grows on bark of trees in submontane and montane forests, at 1200–2500 m.

Additional specimens examined. MEXICO. CHIAPAS: Zinacantan, Slope with evergreen cloud forest near summit of Cerro Muktavits, growing on trunk, 2740 m, 17 May 1988, *Breedlove 68131* (MO).

GUATEMALA. The type of *Radula guatemalensis* (G)

NICARAGUA. GRANADA: W slope of volcan Mombacho, road and trail above Finca Santa Ana, epiphytic, 11°50'N, 85°58'W, 950-1150 m, 1 October 1977, *Stevens 4383* (MO).

COSTA RICA. SAN JOSÉ: Zurquí, on tree, 2000-2500 m, 13 February 1926, *Standley & Valerio 48089* (JE). **CARTAGO:** Cerro de La Carpintera, on tree, 1500-1850 m, *Standley 34346* (JE).

PUERTO RICO. The type of *Radula portoricensis* (G).

COLOMBIA. CASANARE: Sácama, camino que va desde el municipio hasta la Quebrada Macueque, pasando por el Río Sácama, 1200 m, 17 August 1982, *Aguirre et al. 3113* (GOET).

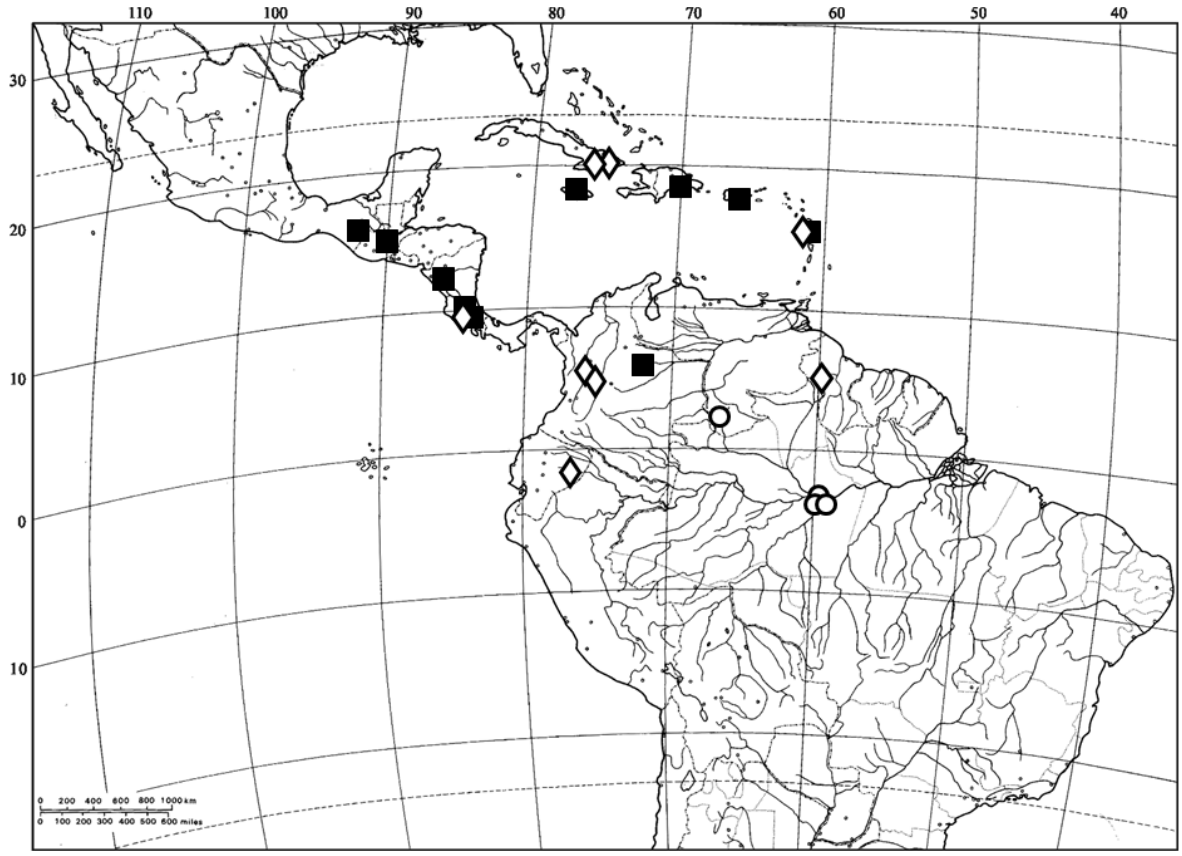

Figure 39. Distribution of *Radula portoricensis* (black square), *R. pseudostachya*, (white circle) and *R. pusilla* (white rhombus).

Radula portoricensis (subg. *Radula*?) is recognized by plants frequently with caducous leaves, lobules subrectangular, inflated along the keel, and gynoecia on very short branches without innovations. Absence of innovation is also observed in *Radula renneri*, but the latter species is monoicous and has subquadrate lobules with a prolonged apex. Sterile plants of *R. portoricensis* may be confused with *R. fendleri* (as noted by Castle 1936) but *R. fendleri* is a slightly smaller, more compact and usually green plant with branches irregularly pinnate. *Radula portoricensis*, in contrast, is usually yellowish to brownish with branches regularly pinnate (especially on male or sterile plants), rarely irregularly pinnate.

Stephani (1888) described *Radula portoricensis* based on three collections (Sintenis 75, 108, 109). One nrs. 75 and 108 (two collection) are present in G (see online catalogue of G). Examination of the material revealed that only nr. 75 belongs to *Radula portoricensis*. The two collections of *Sintenis 108* belong to, respectively, *R. elliotii* (not seen; fide Yamada 1981 as *R. varilobula*) and *R. wrightii* (G-00281392!).

33. Radula pseudostachya Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 319. 1885. Type: Venezuela, Amazonas, San Carlos del Rio Negro, "ad arborum ramulus in sylvis," *R. Spruce s.n.* (lectotype, MANCH-15319!, **designated here**; isolectype, G-00047738!).

Dioicous. *Plants* 1.3–2 mm wide, to 1 cm long, yellowish to yellowish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* ca. 140 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless. *Leaf lobes* widely spreading, contiguous to subimbricate, strongly convex, falcate-ovate, 0.8–1.1 mm long, 0.5–0.7 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight, apex rounded, margin recurved, entire; marginal cells subquadrate, 10–15 × 5–10 µm, median cells isodiametric, 15–30 µm in diam., basal cells elongate, 30–35 × 15–25 µm, cell walls thin, trigones large, intermediate thickening present, cuticle verruculose; oil bodies not observed. *Lobules* contiguous to subimbricate, subrectangular, 0.4–0.6 mm long, 0.25–0.4 mm wide, ca. 1/2 the lobe length, strongly inflated along the keel, insertion ca. 1× the base length, insertion line curved, base plane, rounded, covering 1/2 to overlapping the stem, free margin plane, straight, apex plane, rounded, distal margin straight, keel convex, spreading at angles of 50–60º with the stem, 90–120º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* not observed. *Gynoecia* on short branches, with 2 innovations; bracts ovate, 0.6–0.8 mm long, 0.3–0.45 mm wide, margin entire, plane to recurved, apex rounded, lobule oblong, ca. 1/2 of lobe length, apex obtuse. *Perianth* not observed. *Vegetative reproduction* by caducous leaf lobes, producing almost completely denuded branches, the caducous leaf lobes often with regenerants on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Venezuela and Brazil (Figure 39). This rare Amazonian species grows on tree trunks in lowland rainforest or white sand vegetation, at sea level.

Additional specimens examined. VENEZUELA. AMAZONAS: The type.

BRAZIL. **AMAZONAS:** Manaus, Manaus-Caracarai road, km 45, on white sand, on tree trunk, 5 April 1971, *Prance et al. 11384* (INPA29784, INPA29771). Reserva Biológica de

Campina, Estrada Manaus-Caracaraí, Km 61, sobre galhos, Jul 1974, *Griffin III et al. 544* (INPA51640).

Radula pseudostachya (subg. *Radula*?) is recognized by the strongly caducous leaf lobes, causing branches to be almost denuded. Further characteristics include the falcate-ovate, strongly convex leaf lobes with strongly recurved margins, leaf cells with large trigones and cuticle verruculose, lobules contiguous to subimbricate, subquadrate to subrectangular, base covering 1/2 to fully overlapping the stem, and keel convex and strongly inflated.

This species is closely related to *R. fendleri* var. *fendleri*; for differences see under the latter. Caducous leaf lobes producing almost completely naked branches are also observed in *R. bischlerae*, *R. fulvifolia* and R. *wrightii*, but these species are otherwise very different from *R. pseudostachya* (Oliveira-da-Silva *et al.* in press).

34. Radula pusilla Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 320. 1885. Type: Ecuador, "Andes quitenses ad flum. Bombonasa," *R. Spruce s.n.* (lectotype, MACH-15320!, c. per., **designated here**; isolectotype, MANCH-15321!).

Fig. 40

Radula guyanensis K.Yamada, in Gradstein & Florschütz-de Waard, Trop. Bryol. 1: 38. f. 5. 1989. Type: Guyana, Mount Roraima, Jawalla village at confluence of Kukui river and Mazaruni river, on roots in rainforest, 500 m, 6-7 February 1985, *S. R. Gradstein 4859* (holotype, U; isotypes, NICH, GOET!, c. gyn.), ***syn. nov.***

Radula mazarunensis K.Yamada, in Gradstein & Florschütz-de Waard, Trop. Bryol. 1: 38. 1989. Type: Guyana, upper Mazaruni district, Mt. Latipu, ca. 8 km N of Kamarang, on rough bark of trunk, 5°57'N, 60°38'W, 600 m, 24 February 1985, *S. R. Gradstein 5548* (holotype, U; isotypes, GOET!, c. per., NICH), syn. fide Gradstein (2021).

Dioicous. *Plants* 1.4–2 mm wide, to 2 cm long, green to yellowish brown in herbarium, regularly to irregularly pinnate or dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on decapitated shoots. *Stems* 150–180 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to subimbricate, slightly convex, ovate to falcate-ovate, 0.8–1 mm long, 0.6–0.7 mm wide, dorsal

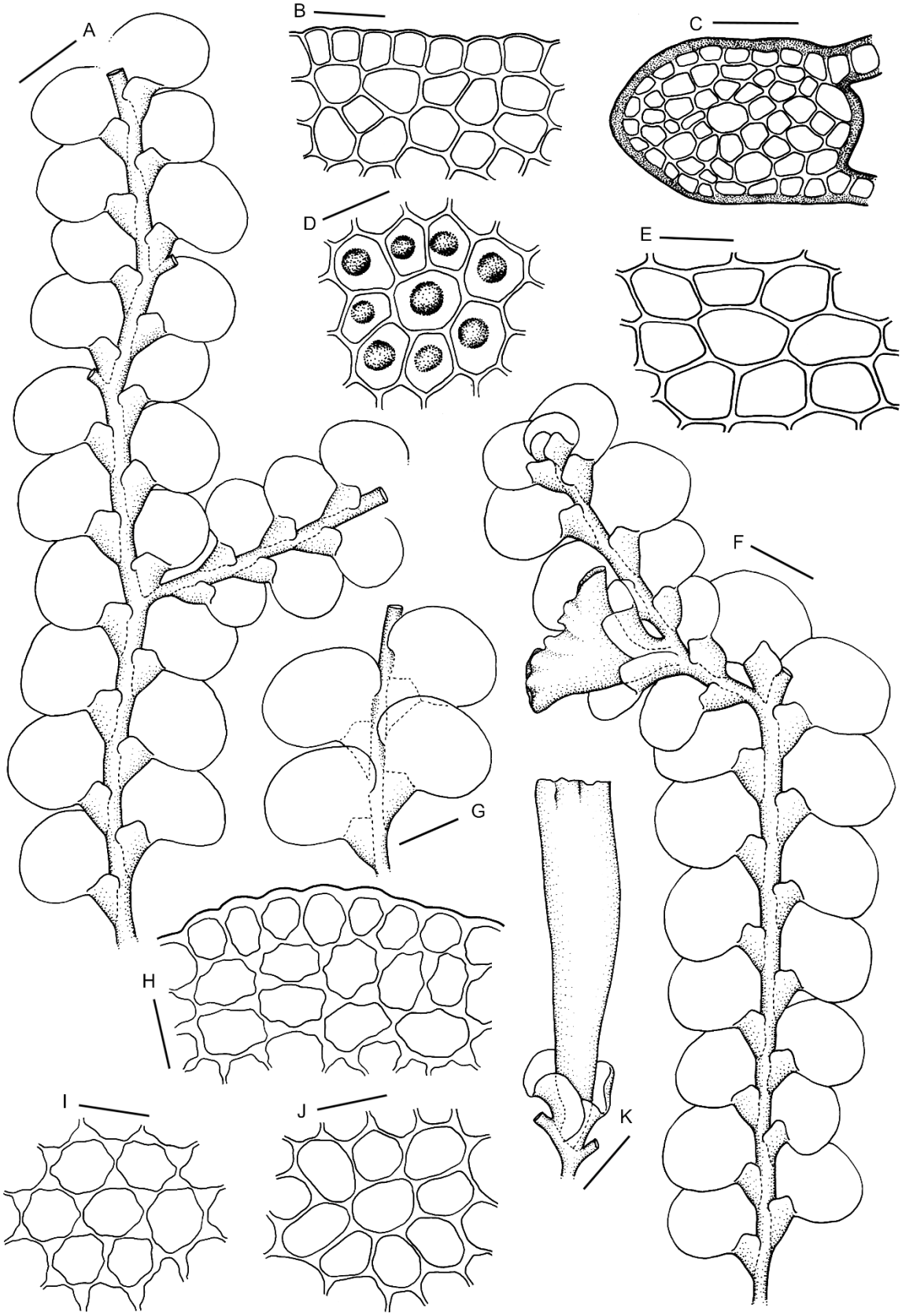

Figura 40. *Radula pusilla*. A. Habit. B. Marginal leaf cells. C. Cross section of stem. D. Median leaf cells with oil bodies. E. Basal leaf cells. F. Habit with perianth. G. Habit in dorsal view. H. Marginal leaf cells. I. Median leaf cells. J. Basal leaf cells. K. Perianth (A, F, G, K = 500 µm, B, D, E, H, I, J = 25 µm, C = 50 µm; All from the isotype of *Radula mazarunensis*).

base rounded, covering 1/2 the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margins plane, entire to slightly crenulate; marginal cells subquadrate, 10–15 × 8–15 μm, median cells isodiametric to elongated, 20–22 × 15–20 μm, basal cells elongate, 20–30 × 15–20 μm, cell walls thin, trigones small to large, intermediate thickening lacking, cuticle smooth to slightly verruculose; oil bodies 1 per cell, spherical, light yellow, slightly granular, 8–10 μm in diam. *Lobules* distant, subquadrate to subrhombic, 0.4–0.5 mm long, 0.3–0.4 mm wide, 1/4–1/3 the lobe length, slightly inflated at rhizoid area, insertion 3–4× the base length, insertion line slightly curved, base plane, not or covering up to 1/4 the stem, free margin plane, straight, apex plane, rounded, distal margin straight, keel straight, spreading at 30–40º with the stem, 90–110º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* not observed. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 0.7–0.8 mm long, 0.3–0.5 mm wide, apex rounded, margin plane, slightly crenulate, lobules oblong-ovate, 1/2–2/3 of lobe length, apex acute. *Perianth* erect, campanulate to trumpet-shaped, 0.9–2.7 mm long, 0.2–0.3 mm wide at base, 0.6–0.5 mm wide at middle, 0.6–1.1 mm wide at apex, mouth entire, plane to strongly undulate; perianth wall not observed. *Calyptra* and *Sporophyte* not observed. *Vegetative reproduction* by occasionaly regenerants on leaf margin.

Distribution and habit. Costa Rica, Cuba, Puerto Rico (new record), Dominica, French Guiana (new record), Guyana, Colombia and Ecuador (Gradstein 2021, Cañiza Ovelar & Oliveira-da-Silva 2022) (Figure 39). *Radula pusilla* occurs on bark, rarely on rock and leaves of vascular plants, in lowland, submontane to lower montane forest, at 300–1700 m.

Additional specimens examined. COSTA RICA. CARTAGO: Vicinity of Pejivalle, on tree, 900 m, 7-8 February 1926, *Standley & Valerio 46897* (JE).

CUBA. GUANTÁNAMO: Baracoa, pluviosa en las cabezas del río Naranjo, 300 m, 6 August 1975, *Meyer 27841* (JE). **SANTIAGO DE CUBA:** Sierra Maestra de la Gran Piedra, in pluviisilvis montanis, in rupibus andesiticis, 1200 m, 1969, *Borhidi & Muniz 5063, 5065* (JE).

PUERTO RICO. MARICAO: Monte del estado de Maricao, 31 December 1962, *Manuel & Diaz-Piferrer 136, 137, 138, 139, 164* (MO).

FRENCH GUIANA. CAYENNE: Montane de Kaw, 2 km north camp Caiman, on trunk of treelet, in low rainforest on rock soil, 52°12’ W, 4°34’ N, 200-300 m, 15 May 1985, *ter Steege & Cornelissen C0330a* (GOET). **SAÜL:** Primary Forest near Boeuf Mort, on buttresses, 53°12’ W, 3°38’ N, 200-300 m, March 1985, *Artroot 15310* (GOET).

GUYANA. UPPER MAZARUNI: The Type of *Radula guyanensis* and *R. mazarunensis* (GOET).

ECUADOR. ZAMORA-CHINCHIPE: Reserva Biológica San Francisco, 30 km from Loja and Zamora, at the Northern limit of the Parque Nacional de Podocarpus, montane tropical rainforest, on tree trunk, 3°58'18" S, 79°04'44" W, 1800-3150 m, 2 August 2001, *Nöske 1028* (GOET).

Radula pusilla (subg. *Volutoradula*) is distinguished by plants flaccid and sparsely branched, leaves contiguous to subimbricate, ovate to falcate-ovate with apex broadly rounded, margins entire to slightly crenulate, lobules small, distant, subquadrate to subrhombic with base not or little covering the stem (up to 1/4 the stem width) and keel straight. The leaf cells usually lack trigones, occasionally have distinct trigones (e.g. type of *R. mazarunensis*).

Radula pusilla may be confused with the widespread *R. pallens*, but the latter species has more rigid stems, imbricate, suborbicular leaf lobes, and lobule base covering 1/2 the stem or more. *Radula pusilla* also resembles *R. macrostachya*; differences are given under the latter species.

35. Radula quadrata Gottsche, Syn. Hepat. 255. 1845. Type: Mexico, Jalapa, s.d., unknown collector (lectotype, G-00116228!, selected by Oliveira-da-Silva *et al.*, 2021: 124, scanty).

Radula affinis Lindenb. & Gottsche, Syn. Hepat. 725. 1847. Type: Mexico, Mirador, February 1842, *F. M. Liebmann 284* (lectotype, W!, hb. Lindenberg n° 2477, **designated here**; isolectotype, G-000121956, FH!), syn fide Yamada (1993a).

Radula andicola Steph., Hedwigia 23: 114. 1884. Type: Ecuador, on *Pilotrichum tetragonum*, under *R. sinuata*, s.d., *Krause s.n.*, ex hb. Jack (lectotype, G-00281264!, **designated here**; isolectotype, G-00043974, BM-000969187!). Silla de Caracas, *Birschall s.n.* (synnot found). Brazil, Rio de Janeiro, *J. Deventer s.n.*, ex hb. Sande-Lacoste (syntype not founf), syn. fide Castle (1965, under *R. mollis*).

Radula calcarata Steph., Rev. Bryol. 36: 140. 1909. Type: Mexico, State of Puebla, Honey Station, 7000 ft, June 11, 1908, *C. G. Pringle 15340* (lectotype, G-00043911!, **designated here**; isolectotypes, G-00043910, UVMVT-053099, FH-00509578!, YU-241598!), syn. fide Yamada (1993a).

Radula quadrata var. *fusca* Gottsche, Syn. Hep. 225. 1845. Type: Mexico, "voxe i Oajacas oslige District Chinautla," s.d., *F. M. Liebman 411* (lectotype, BM-000969234!, **designated here**), syn. fide Castle (1965).

Radula quadrata var. *propagulifera* Gottsche, Mexik. Leverm. 144 (240). 1863. Type: Mexico, "paa Xalapa …, og paa Plantagen Hacienda de Mirador", s.d., *F. M. Liebman* 41 b, 102, 116b, 133 (syntypes not found), ***syn. nov.***

Radula quadrata var. *manzanensis* Gottsche, Ann. Sc. Nat., Bot., sér. 5, 1: 143. 1864. Type: Colombia, Bogotá, "ad Manzanos," 2700 m, december 1860, *A. Lindig 1740* (lectotype, BM-000969236!, c. andr. + per. + spor., **designated here**; isolectotype, BM-000969235!, c. andr. + per. + spor.), ***syn. nov.***

Radula glauca Steph., Sp. Hepat. 4: 175. 1910. Type: Brazil, Serra do Itatiaia, "sylva 2000 m, an Zweigen," March 1894, *E. H. G. Ule 459* (lectotype, G-00043889!, selected by Castle, 1965: 338; isotypes, BM-000969205!, FH!), syn. fide Castle (1965, under *R. mollis*).

Radula mollis Lindenb. & Gottsche, Syn. Hepat. 725. 1847. Type: Mexico, Pico de Orizaba, September 1842, *F. M. Liebman 151* (lectotype, W!, hb. Lindenberg n° 5471, **designated here**; type in G, according to Castle 1965, not found), syn. fide Yamada & Gradstein (1991).

Radula viridiaurea Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 324. 1885. Type: Ecuador, "Andes Quitenses, ad pedem montis Tunguragua, juxta pagum Baños, in cortice", *R. Spruce s.n.* (type MANCH not found, lectotype, G-00265060!, **designated here**), syn. fide Castle (1965, under *R. mollis*).

Dioicous. *Plants* 2–2.8 mm wide, to 2 cm long, light green in field, green, yellowish-green to brownish in herbarium, regularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type. *Stems* 120–175 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless, yellowish or brownish. *Leaf lobes* widely spreading, imbricate, slightly convex, ovate, 1.4–1.6 mm long, 1–1.3 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to recurved, entire to strongly crenulate when with gemmae; marginal cells subquadrate to rounded, 9–18 µm in diam., median and basal cells isodiametric (–10)20–28 µm, cell walls evenly thickened, trigones small, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* widely spreading, subimbricate to imbricate, subquadrate, 0.85–1 mm long, 0.7–0.75 mm wide, 1/2 the lobe length, inflated at rhizoid area and along the keel, insertion 1× the base length, insertion

line straight or inverted small J-shaped, base plane, rounded, overlapping the stem, free margin plane, straight to sinuose, apex plane, rounded to obtuse, distal margin straight to sinuose, keel straight, spreading at angles of 60–80° with the stem, 140–180º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on few or numerous lobules. *Androecia* not observed. Gynoecia on short branches, with 1–2 innovations; bracts ovate to oblong, 1–1.5 mm long, 0.5–0.8 mm wide, apex rounded, margin recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindricalal, rarely trumpet-shaped, 1.6–2.7 mm long, 0.5–0.8 mm wide at base, 0.8–1.1 mm wide at middle, 0.8–1.1 mm wide at apex, mouth entire to irregularly crenulate with gemmae, plane; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small wings in the lower half; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 4–5-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* ca. 1.5 mm long. *Capsule* ca. 0.6 mm long, 0.1 mm wide, valves ca. 1.2 mm long, ca. 0.2 mm wide at middle, outer layer cells subrectangular, simple nodular thickenings reddish-brown, on every longitudinal wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* and *Spores* not observed. *Vegetative reproduction* by small discoid gemmae, 60–150 μm in diam., copiously produced on the margins of leaves, perianths and bracts.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Tropical and subtropical America (Figure 41), ranging northwards into warm-temperate, southeastern U.S.A; also in Africa. This species grows on bark, rarely on dead trees, rock, soil and leaves, in lowland and montane rainforests up to the páramo and in plantations, in shaded or occasionally exposed places, from sea level to 4000 m.

Additional specimens examined. MEXICO. MEXICO: Bachschuchtwald oberhalb des Valle de Bravo-Strausees, auf Erde im Bergwald, Kalk, 1800 m, 22 October 1966, *Düll A-62* (JE). **OXACA:** Sierra Juarez, Km 81, epiphytenreicher Bergwald, 2820 m, 2 October 1966, *Düll A-59* (JE).

GUATEMALA. ALTA VERA PAZ: Cobán, 1350 m, August 1906, *Türckheim s.n.* (FH-00965734, FH-00965735).

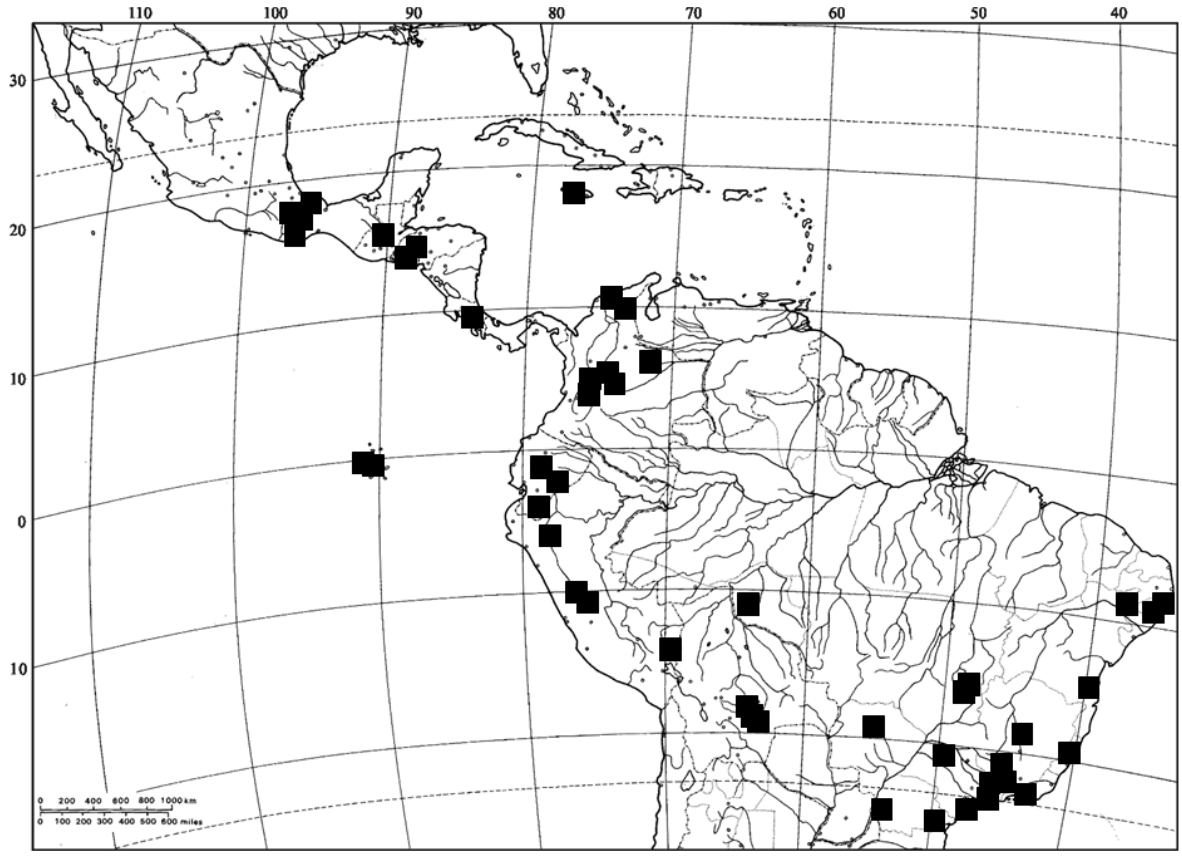

Figure 41. Distribution of *Radula quadrata.*

EL SALVADOR. SAN SALVADOR: Volcan San Salvador, El Boqueron, on a rock, 13°45’50”N, 89°16’15”W, 1650-1800 m, 4 February 1998, *Davidse 2248* (MO).

HONDURAS. LEMPIRA: Montana de Celaque, La Planta Electrica Stacione, ca. 7,5 km SW of Gracias, on tree trunk, 1400 m, 9 May 1992, *Allen 11827* (MO).

COSTA RICA. CARTAGO: Orori, P.N. Tapantí-Macizo de La Muerte, Paramo, C. de la Muerte, base del paramo Buenavista, al lado de la Carretera Interamericana, km 90, sobre arbusto em sitio expuesto, 9°35’30”N, 83°45’30”W, 3000-3300 m, 2 November 1995, *Dauphin 2080* (MO).

CUBA. Arroyo Gallego, “in saxis sylvarum,” 500 m, 1889, *Eggers 4653c* (BM).

COLOMBIA. BOGOTÁ: Cerro de Guadeloupe, 2700-3200 m, 1929, *Troll 2059, 2056/a* (JE). **CASANARE:** Sácama, camino que va desde el municipio hasta la Quebrada Macueque, pasando por el Río Sácama, 1270 m, 17 August 1982, *Aguirre C. et al. 3087* (GOET).

ECUADOR. GALAPAGOS ISLAND: Isabela, Rim of Volcano Alcedo, SE side flat patches on rock and stems of *Zanthoxylum sp.* in shade, 1100-1200 m, 10-12 May 1976, *Gradstein H231* (GOET). Florena, Cerro “Wittmer” above the spring, 450-550 m, 26 April 1976, *Gradstein H172* (GOET). Pinta, S-exposed slope of the highest volcano, rather open, on dead,

horizontal *Pisonia sp.* stem, 400-550 m, 8-10 July 1976, *Gradstein et al. H523* (GOET). **ZAMORA-CHINCHIPE:** Reserva Biologica San Francisco, 30 km from Loja and Zamora, at the Northern limit of Parque Nacional de Podocarpus, montane tropical rain forest, 3°58'18" S, 79°04'44" W, 1800-3150 m, 16 August 2001, *Nöske 1239* (GOET). Reserva Biológica San Francisco, al lado Río Francisco, bosque montano bajo, sobre roca em la sombra, 3°58'17"S, 79°04'39"W, 1860 m, 24 November 2005, *Churchill & Jaramillo 24122* (MO).

PERU. AMAZONAS: Bongara, Laguna Pomacochas, 2220 m, 1 September 1973, *Hegewald 7056* (MO). **CUZCO:** Quispicanchis, between Marcapata and Achubamba, on rock along trail in "Ceja de Selva" zone, 2800 m, 13 September 1984, *Inoue 872* (JE, MO). Urubamba, Machu Picchu, Inkapfad, Beim Tor, 2450 m, 29 June 1977, *Hegewald 8815* (MO). **HUÁNUCO:** Cochabamba, Torontoy Valley, 2200 m, 1927, *Herrera 1596* (JE). **PASCO:** Oxapampa, Piña Flor 12 km von Oxapampa in Richtung Tarma, 11 June 1977, *Hegewald 8417* (MO). Oxapampa, 2 km von Oxapampa-Ortsmitte in Richtung Tarma, 1780 m, 12 June 1977, *Hegewald 8461* (MO).

BRAZIL. **BAHIA:** Ilhéus, área da CEPEC, km 22 da rodovia Ilhéus/Itabuna, BR 415, 14°47'20"S, 39°02'58"W, 50 m, 15 July 1991, *Vital s.n.* (SP). **DISTRITO FEDERAL:** Rio Sobradinho, immediately west of Sobradinho, 1100 m, 10 February 1971, *Irwin et al. 33244* (NY). **ESPÍRITO SANTO:** Linhares, Reserva Natural Vale do Rio Doce, estrada Macanaíba, 19 October 2000, *Yano et al. 26584* (SP). **MATO GROSSO DO SUL:** Camapuã, ca. 5 km of Costa Rica Village, 22 May 1976, *Vital 6397* (SP). **MINAS GERAIS:** Serra da Mantiqueira, Pouso Alto, 900 m, 6 April 1986, *Schäfer-Verwimp 6824* (MG). **PARANÁ:** Foz do Iguaçú, Pricada Poço Preto, sede do Parque Nacional do Iguaçu, 14 July 1968, *Vianna 238* (ICN). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 25 August 1987, *Pôrto 2463* (UFP). **RIO DE JANEIRO:** Magé, RPPN El Nagual, 22°32'74"S, 43°03'79"W, 190 m, 28 February 2005, *Santos et al. 103* (RB). **RIO GRANDE DO SUL:** Viamão, Parque Saint Hilaire, 1 November 1994, *Michel s.n.* (ICN). **RONDÔNIA:** Seringal São Luis, just below the first rapids on the Rio Pacaás Novos, mature forest with some sandstone exposures, on tree base, 30-31 March 1978, *Reese 13737* (JE). **SANTA CATARINA:** Araranguá, Morro dos Conventos, 18 November 1969, *Oliveira s.n.* (ICN). **SÃO PAULO:** Peruibe, Guaraú, Estação Ecológica de Juréia, 24°19'12"S, 46°59'54"W, 10 m, 2 July 1988, *Yano et al. 11465* (SP).

BOLIVIA. SANTA CRUZ: Vallegrande, San Lorenzo, bosque Tucumano-Boliviano, epífita, 18°40'36"S, 63°55'01"W, 2378 m, 11 April 2011, *Inturias et al. 648* (MO). Florida, Samaipata, ca. 1 km sur de La Negra, bosque Tucumano-Boliviano secundario, 18°08'S, 63°41'W, 1090 m, 26 May 2002, *Churchill et al. 21666* (MO). Florida, Canton Samaipata,

Cerro Esculpido de Samaipata, bosque montano secundário, sobre rama de arbol, 18°10'S, 63°49'W, 1900 m, 1 November 2001, *Churchill 20989* (MO). Florida, Canton Samaipata, El Fuerte, Cerro Esculpido de Samaipata, bosque de Tucumano-Boliviano secundário, em suelo sobre roca, com sol, 18°10'S, 63°42'W, 1900 m, 29 August 2010, *Calzadilla et al. 472* (MO).

Radula quadrata (subg. *Radula*) is recognized by having numerous small discoid gemmae produced on leaf margins (sometimes also on perianth mouth and bracts margins) and large, imbricate lobules with a widely arched base, covering the entire stem and sometimes extending beyond the stem width. The species is closely similar to *R. tectiloba*, but the lobules in the latter species are distant to subimbricate (not densely imbricate) and the lobule base usually covers only part of the stem, rarely the entire stem width.

As the type of *Radula viridiaurea* Spruce lacks in MANCH, the isotype in G is designated as the lectotype.

36. Radula recubans Taylor, London J. Bot. 5: 376. 1846. Type: Guyana, Demerara, *unknown collector*, in Dr. Greville's Herbarium (lectotype, FH-00965762!, **designated here**; isolectotypes, G-00265045!, NY-01021152!).

Radula sinskeana K.Yamada, J. Hattori Bot. Lab. 74: 41. 1993. Type: Ecuador, Pichincha, Tinalandia estate, about 18 km E of St. Domingo de los Colorados, 830 m, on liana, 18 July 1991, *T. Arts 18/047b* (holotype, BR-5040318001356; isotypes, QCA, NICH-432558!, c. per.), ***syn. nov.***

Dioicous. *Plants* 1.5–3 mm wide, to 2 cm long, green to olive-green in herbarium, regularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type, rarely *Lejeunea*-type present on decapitated shoots. *Stems* 280–320 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, epidermal wall heavily and evenly thickened. *Leaf lobes* widely spreading, contiguous to subimbricate, slightly convex, ovate, rarely falcate-ovate, 1–1.6 mm long, 0.75–1.2 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded, margin plane, entire; marginal cells subquadrate, 12–18 × 10–13 µm, median cells isodiametric to elongate, 22–30 × 12–18 µm, basal cells elongate, 25–35 × 12–18 µm, cell walls thin, trigones small, intermediate thickening lacking, cuticle smooth to verruculose; oil bodies not observed. *Lobules* widely spreading,

distant to contiguous, subquadrate, 0.4–0.9(–1) mm long, 0.3–0.75 mm wide, (–1/4)1/3–1/2 of the lobe length, inflated at rhizoid area, insertion ca. 1× the base length, insertion line straight, base plane, rounded, covering 2/3 to overlapping the stem, free margin plane, slightly rounded to straight, apex plane, sometimes incurved, rounded to obtuse, distal margin straight to sinuose, keel straight to slightly concave, spreading at angles of 50–60º with the stem, 150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* terminal to intercalary on long branches, with 2–8 pairs of bracts, 0.75–1.1 mm wide; bracts distant to subimbricate, ovate, 0.55–0.95 mm long, 0.2–0.4 mm wide, apex rounded, margin plane, rarely recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.9–1.1 mm long, 0.35–0.45 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical to trumpet-shaped, 2.5–2.9 mm long, 0.5–0.7 mm wide at base, 1–1.2 mm wide at middle, 1–1.4 mm wide at apex, mouth entire, plane to slightly undulate; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base. *Calyptra* and *sporophyte* not observed. *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Guatemala, Ecuador, Venezuela, Guyana and Brazil (Figura 42). The species grows on bark, dead trees and rock, usually in humid places, in lowland to montane forest, at 300–1640 m.

Additional specimens examined. GUYANA. The type of *R. recubans* (FH, G, NY).

ECUADOR. The type of *R. sinskeana* (NICH).

BRAZIL. Without locality, s.d., *unknown collector* (FH-00965707). **AMAZONAS:** São Gabriel da Cachoeira, Serra Curicuriari, 0°20’S, 66°50’W, 450 m, 9 July 1979, *Schuster 79-15-576* (INPA). **ESPÍRITO SANTO:** Castelo, Parque Estadual do Forno Grande, 20°31’00”S, 41°05’14”W, 1250 m, 1 October 2016, *Peralta et al. 19277* (SP). Domingos Martins, Parque Estadual Pedra Azul, Trilha Pedra das Flores, Mata Atlântica, corticícola, 5 agosto 2009, *Penha 454* (ALCB). Ibid., Trilha das Piscinas, 7 março 2009, *Penha 214* (ALCB). **MINAS GERAIS:** Lima Duarte, Parque Estadual do Ibitipoca, Rego Seco, 1550 m, 9 August 1993, *Yano et al. 20365* (SP). Passa quatro, 1921, *Zikán 435* (JE). **PARANÁ:** Morretes, Estação Marumbi, 13

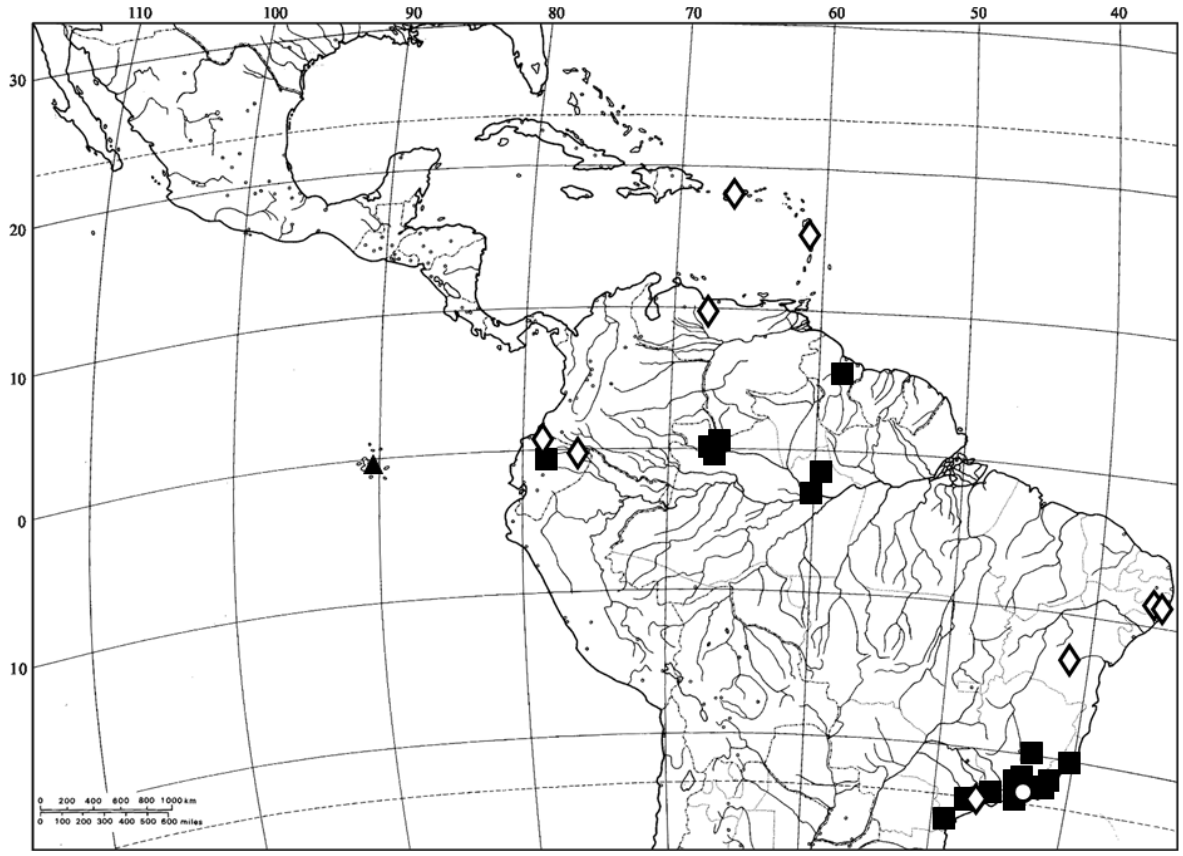

Figure 42. Distribution of *Radula recubans* (black square), *R. renneri* (white circle), *R. saccatiloba* (white rhombus), and *R. santacruziana* (black triangle).

February 1992, *Hatschbach & Barboza 56377* (SP). **RIO DE JANEIRO:** Parque Nacional da Tijuca, pedra da Gávea, 22°59'44"S, 43°47'18"W, 377 m, 8 February 2007, *Santos et al. 704* (RB). **RIO GRANDE DO SUL:** Cambará do Sul, Itaimbezinho, 3 October 1976, *Vianna 3209* (ICN). **SANTA CATARINA:** Urubici, Parque Nacional São Joaquim, mata Nebular e campo de altitude, estrada de acesso ao morro da igreja, sobre tronco vivo, 28°07'12" S, 49°28'44" W, 1400-1600 m, 11 Mar 2009, *Peralta & Barros 7882* (JE). **SÃO PAULO:** Campos do Jordão, 22°43'06"S, 45°32'03"W, 1640 m, 13 September 2012, *Gibertoni 52* (SP). Ibiuna, bairro Sorocabuçu, sobre tronco vivo na mata secundária úmida, 15 January 1988, *Yano & Marcelli 11160* (SP).

Radula recubans (subg. *Volutoradula*) is characterized by plants regularly pinnate to dichotomous in female plants by fertile paired innovations, leaves widely spreading, ovate to rarely elongate, falcate-ovate, leaf cells without trigones, cuticle smooth to verruculose, and lobules subquadrate with deeply rounded base, covering 2/3 to overlapping the entire stem.

Castle (1966) recorded the occasional occurrence of caducous leaves in *R. recubans* (not observed in this study).

This species is similar to *R. javanica*; for differences see under the latter species.

Examination of the type of *R. sinskeana* deposited in NICH herbarium shows that the species is coespecific with *R. recubans*. The only difference is the shape of the leaf lobes, wich vary from narrowly ovate to falcate-ovate in *R. sinskeana* (see description of Yamada 1993b) and is ovate in *R. recubans*. However, this feature commonly overlaps in *Radula* (*e.g. R. fulvifolia, R. javanica, R. pallens* and *R. xalapensis*). The dichotomous branches reported in *R. sinskeana* by Yamada (1993b) are due to exclusively female plants (with perianth) exhibiting repeated pairs of innovations, as in *R. recubans*.

37. Radula renneri F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., Nova Hedwigia 112: 128. 2020[2021]. Type: Brazil, Rio de Janeiro, Teresópolis, "bairro Quebra Frascos, sobre tronco vivo, na sombra, vegetação de capoeira", 23 March 1926, *M. C. Vaughan Bandeira s.n.* (holotype, RB-00709793!, c. andr. + per. + spor.; isotype, MG!, c. andr. + per. + spor.).

Monoicous. *Plants* 1.7–2.2 mm wide, to 2 cm long, yellowish-brown in herbarium, irregularly pinnate. *Branches Radula*-type. *Stems* ca. 360 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless, yellowish or brownish. *Leaf lobes* widely spreading, subimbricate, convex, ovate, 1–1.8 mm long, 0.8–1.7 mm wide, dorsal base rounded, overlappimg the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to slightly recurved, entire to crenulate with gemmae; marginal cells subquadrate to isodiametric, 10–15 × 8–10 µm, median cells isodiametric, 20–25 µm in diam., basal cells elongate, 25–35(–40) × 20–30 µm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle finely verruculose; oil bodies not observed. *Lobules* distant, subquadrate to almost subrhombic, 0.5–0.9 mm long, 0.45–0.8 mm wide, 2/5–1/2 the lobe length, inflated at rhizoid area, insertion ca. 2× the base length, insertion line straight, base plane, rounded, covering 1/2 the stem, rarely more, free margin plane, straight, apex plane, elongate, obtuse to acute (ending in one cell), distal margin straight, keel straight, spreading at angles of 45–65° with the stem, 150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few or numerous lobules. *Androecia* on short branches, terminal or preceding the gynoecia, with 1–3 pairs of bracts, 1–1.3 mm wide; bracts imbricate, ovate, 0.8–1 mm long, 0.5–0.65 mm wide, apex

rounded, margin plane to recurved, entire, lobule ovate, 3/4 of the lobe-length, base rounded to obtuse, free margin straight, apex rounded to obtuse. *Gynoecia* on short branches, with 0(–1) innovation; bracts ovate, 0.9–1.1 mm long, 0.5–0.8 mm wide, apex rounded, margin plane, entire, lobule oblong, 1/3–1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, campanulate to subcylindrical, 1.4–2.3 mm long, 0.5–1.5 mm wide at base, 0.8–1.5 mm wide at middle, 1–1.5 mm wide at apex, mouth entire, plane; perianth wall not observed. *Calyptra* and *Sporophyte* not observed. *Vegetative reproduction* occasionally by small discoid gemmae, ca. 65 µm in diam., produced on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Only known from the state of Rio de Janeiro, southeastern Brazil (Figura 42). *Radula renneri* was found growing on tree in a secondary Atlantic rainforest in the surroundings of Teresópolis, at about 871 m.

Radula renneri is easily recognized by its paroicous condition, leaf margins entire to crenulate in gemmate leaves, lobules subquadrate to almost subrhombic, with a usually extended, obtuse to acute (ending in one cell) apex and a rounded base, the base usually covering 1/2 the stem width, gynoecia with 0(–1) innovation, and vegetative reproduction by means of small discoid gemmae produced on leaf margins.

By its monoicous sexuality and obtuse to acute lobule apex, the species approaches *R. mexicana* but the latter is essentially autoicous (paroicous in *R. renneri*), has usually two innovations and lacks gemmae. *Radula renneri* also resembles the holarctic *Radula complanata* (L.) Dumort.; for differences see Oliveira-da-Silva *et al.* (2021).

38. Radula saccatiloba Steph., Hedwigia 23: 129. 1884. Type: Guadeloupe, s.d., *l'Herminier s.n.* (lectotype, G-00043863!, **designated here**; isolectotype, G-00283276!, scanty).

Radula decora Steph., Hedwigia 23: 145. 1884. Type: Venezuela, Valencia, 1856, *A. Fendler s.n.*, ex hb. Gottsche (lectotype G-00121933!, selected by Yamada, 1987: 293). Chile, s.d., *Spencer s.n.* (syntype, BM, not found), ***syn. nov.***

Dioicous. *Plants* 1.3–1.7 mm wide, to 2 cm long, green to brownish in herbarium, irregularly pinnate branched. *Branches Radula*-type. *Stems* 80–240 µm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls colorless, yellowish or brownish. *Leaf lobes* widely spreading, subimbricate, convex to strongly convex, suborbicular, 0.5–0.9 mm long, 0.4–0.7 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin entire, plane to slightly recurved; marginal cells subquadrate, 10–12.5 µm in diam., median and basal cells isodiametric to elongate, 20–25 × 10–20 µm, cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, subquadrate, 0.75–0.45 mm long, 0.35–0.55 mm wide, ca. 1/2 the lobe length, inflated throughout, sometimes also inflated at rhizoid area, insertion line almost straight, base plane, rounded, covering up to 1/4 the stem, free margin plane, straight, apex plane, rounded, distal margin straight, keel convex, spreading at angles of 60–70º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules. *Androecia* terminal to intercalary on long branches, with 2–3 pairs of bracts, 0.8–1 mm wide; bracts distant to imbricate, ovate, 0.6–0.8 mm long, 0.3–0.4 mm wide, margin entire, plane, rarely recurved, apex rounded, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin ± straight, apex obtuse. *Gynoecia, Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021, as *R. decora*).

Distribution and habit. Puerto Rico, Venezuela, Ecuador (Gradstein 2021), Atlantic Coastal Region of Brazil (Figure 42), and Chile where it is common. The species occurs on bark, rarely on rock, in lowland and montane rainforests, 50–2500 m.

Additional specimens examined. PUERTO RICO. On wet rock near Mt. Torito, Canóvanas, 2500 m, 22 July 1937, *Pagán 294* (FH).

GUADELOUPE. The type of *Radula saccatiloba* (G).

VENEZUELA. The type of *Radula decora* (G).

BRAZIL. BAHIA: Abaíra, Catolés, Serra do Barbado, Mata do Cigano, floresta estacional Montana, corticícola, 13°16’47,7” S, 41°54’14,9” W, 1734 m, 6 setembro 2008, *Bastos 5247* (ALCB). **PERNAMBUCO:** Caruaru, Brejo dos Cavalos, 27 August 1987, *Pôrto 2624i* (UFP). **SÃO PAULO:** Mogi das Cruzes, propriedade da Suzano, Mata Atlântica, base do

morro Pedra do Garrafão, 23°39’26”S, 46°01’54”W, 980 m, 15 June 2007, *Peralta et al. 5053* (SP).

Radula saccatiloba (subg. *Odontoradula*) is distinguished by suborbicular leaf lobes with slightly to strongly recurved margins (rarely plane), lobules rather large (ca. 1/2 lobe length), subquadrate, inflated throughout or inflated at rhizoid area, base scarcely covering the stem (up to 1/3 of stem width), apex broadly rounded and keel convex. Leaf cells have small to large trigones (sometimes absent according to Yamada 1987).

Radula decora is a new synonym of *R. saccatiloba*. Both species were described by Stephani in the same year, but the name *Radula saccatiloba* is slightly older having been published in September 1884 (Hedwigia 23, fasc. 9: 129), while the name *R. decora* was published in October 1884 (Hedwigia 23, fasc. 10: 145). Yamada (1987) separated *R. decora* from *R. saccatiloba* mainly by the inflation of the lobule (fully inflated in *R. decora*, flattened above in *R. saccatiloba*), but his interpretation of the latter species refers to *R. dominicensis*, which is reinstated in this study. Recent interpretations of *R. saccatiloba* usually follow Yamada (1987) and refer to *R. dominicensis* (*e.g.* Gradstein 2021, Oliveira-da-Silva *et al.* 2021).

Specimen G-00043863 is selected here as the lectotype of *R. saccatloba* as it is more copious that the other syntype in G.

39. Radula santacruziana K.Yamada & Gradst., Trop. Bryol. 4: 67. 1991. Type: Ecuador, Galápagos Islands, Santa Cruz, *Miconia* scrub around Media Luna, loosely creeping with long slender stems on *Miconia* branches, 600-650 m, April 17, 1976, *S. R. Gradstein & W. A. Weber H104* (holotype, U; isotype, NICH-417138!).

Fig. 43

Dioicous? *Plants* 1.6–2.7 mm wide, to 1.5 cm long, yellowish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 180–250 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, slightly convex, ovate, 1–1.4 mm long, 0.75–1.7 mm wide, dorsal base rounded, covering 1/2 to overlapping the stem, dorsal margin rounded, ventral margin slightly rounded, apex rounded, margin plane, entire to crenulate with gemmae; marginal cells subquadrate, 10–15 × 10–12 μm, median cells elongate,

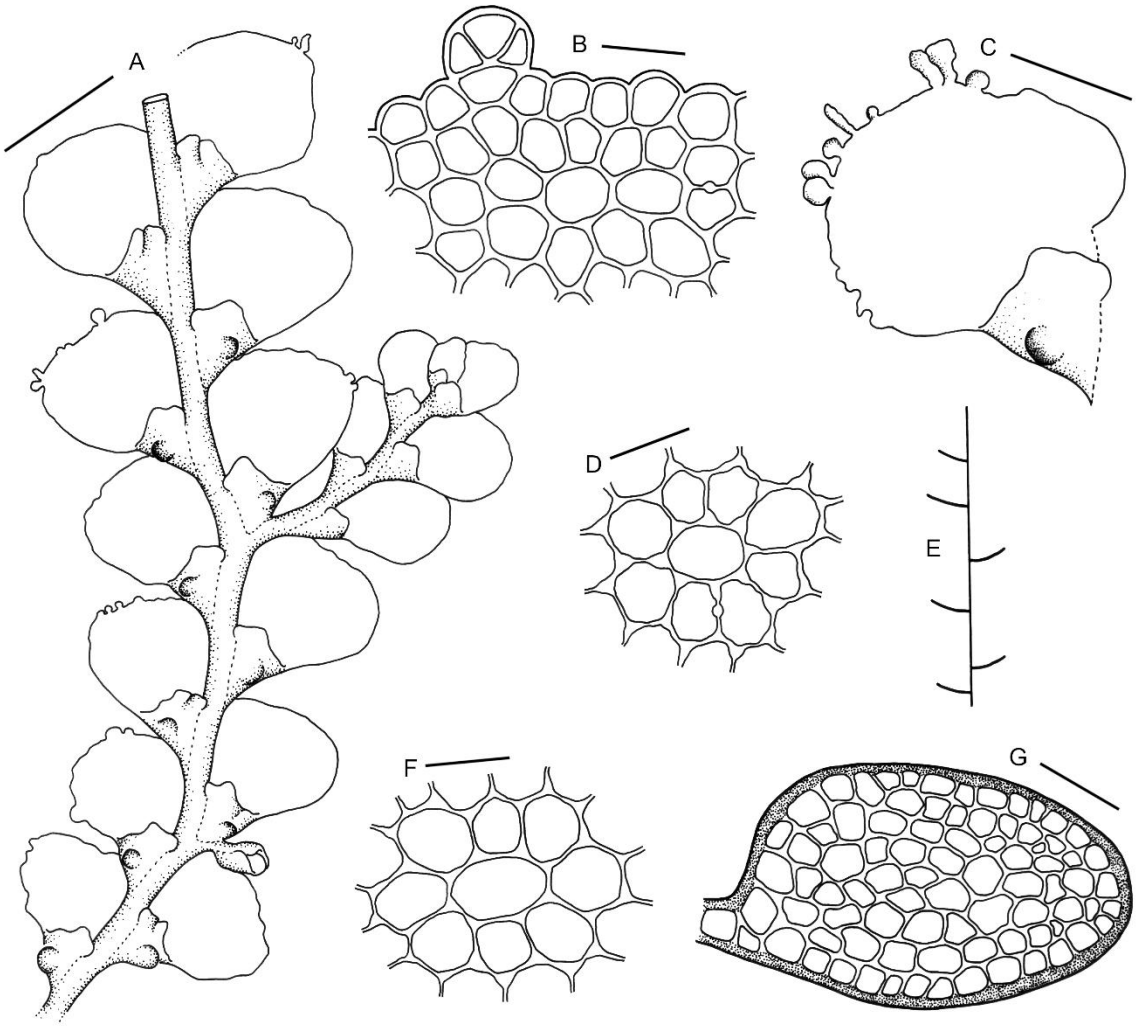

Figura 43. *Radula santacruziana*. A. Habit, B. Marginal leaf cells. C. Leaf with gemmae. D. Median leaf cells. E. Cladograph of plants. F. Basal leaf cells. G. Cross section of stem (A = 1000 µm, B, D, F = 25 µm, C = 500 µm, G = 50 µm; All from the isotype in NICH).

15–22 × 10–15 µm, basal cells elongate, 15–30 × 10–20 µm, cell walls thin at the base to middle becoming a little thick at the margin, trigones small to large, intermediate thickening present, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.5–0.7 mm long, 0.3–0.5 mm wide, ca. 1/3 the lobe length, slightly inflated along the keel, insertion 3–5× the base length, insertion line straight, base plane, slightly rounded to straight, not covering the stem, free margin plane, straight, apex plane, rounded, distal margin straight, keel straight, spreading at angles of ca. 50º with the stem, 150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Sexual organs* not observed. *Vegetative reproduction* by numerous gemmae produced along the margin of the leaf lobe.

Distribution and habit. Only known from the type locality in the Galápagos Islands (Figure 42), Ecuador, where it was found growing on bark of *Miconia robinsoniana* at 600 to 650 m.

Diagnostic features of *Radula santacruziana* (subg. *Volutoradula*?) are the small and numerous gemmae along the leaf margins and subquadrate lobules without ampliated base. Similar gemmae also occur in *Radula tectiloba* and *R. quadrata*, but the latter two species have an ampliate lobule base covering partially or entirely the stem width.

40. Radula sinuata Steph., Sp. Hepat. 4: 161. 1910. Type: Brazil, Minas Gerais, Caldas, June 1854, *G. A. Lindberg s.n.* (lectotype G-00282150!, c. gyn., **designated here**; isolectotypes, G-00282151!, BM-000969238!, BM-000969239!, BM-000969240!, BM-000969241!).

Radula montana Steph., Sp. Hepat. 4: 176. 1910. Type: Brazil, Paraná, Serra do Mar, 29 January 1907, *P. Dusén 3578* (lectotype, G-00043901!, selected by Castle, 1965: 347), syn. fide Yamada (2000).

Radula obtusifolia Steph., Sp. Hepat. 4: 178. 1910. Type: Brazil, Santa Catarina, "Apiaphy," 1891, *E. H. G. Ule 337* (lectotype, G-00043870, selected by Castle, 1965: 347) syn. fide Castle (1965, under *Radula montana*).

Dioicous. *Plants* 1.3–2.2 mm wide, to 2 cm long, green to yellowish in field, yellow to yellowish-brown in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type. *Stems* 150–270 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, convex, ovate to falcate-ovate, 0.8–1 mm long, 0.6–0.9 mm wide, dorsal base rounded, slighlty auriculate, overlapping the stem, dorsal margin rounded, ventral margin straight to slightly rounded, apex rounded, margin plane to recurved, entire; marginal cells subquadrate to isodiametric, 8–15 μm in diam., median and basal cells isodiametric to elongate, 20–25 × 15–20 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* contiguous to imbricate, subquadrate to oblong, 0.5–0.8 mm long, 0.5–0.8 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, along the keel and in the free margin, insertion 1× the base length, insertion line circinate, base plane, rounded, shorthly auriculate, covering 3/4 to

overlapping the stem, free margin plane to incurved, broadly rounded, apex plane, rounded to obtuse, distal margin sinuose, keel straight to slightly convex, spreading at angles of 50–60º with the stem, 140–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* terminal on short branches, with 2–6 pairs of bracts, 1–1.5 mm wide; bracts distant to imbricate, ovate, 0.8–1 mm long, 0.25–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 3/4 of lobe length, base rounded, free margin ± straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 1–1.4 mm long, 0.5–0.6 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex obtuse to subacute. *Perianth* erect, subcylindrical to trumpet-shaped, 2.5–4.3 mm long, 0.2–0.3 mm wide at base, 0.6–0.8 mm wide at middle, 1.2–1.7 mm wide at apex, mouth entire, plane to slightly undulate; perianth wall unistratose; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2-layered tube within which the sporophyte foot is embedded. *Calyptra* unistratose. *Seta* 4.7–6.2 mm long. *Capsule* 1.1–1.3 mm long, 0.3–0.6 mm wide, valves 1.5–1.6 mm long, 0.3–0.4 mm wide at middle, outer layer cells subquadrate to subrectangular, simple nodular thickenings reddish-brown, on longitudinal wall of every second wall, inner layer cells long-rectangular to polymorphous, confluent thickening on the walls. *Elaters* 190–250 µm long, rough. *Spores* 27.77–33.33 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by occasionaly caducous leaf lobes, the caducous leaf lobes often with regenerants on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Rare in Central America, with a few records from Guatemala and Costa Rica (Castle 1965, under *R. montana*); more common in South America, especially along the Atlantic Coastal Region of Brazil. In addition to the countries listed below, *Radula sinuata* has been reported from Colombia, Peru and Argentina (Castle 1965, under *R. montana*, Gradstein 2021) (Figure 44). This species occurs on bark, rarely on dead trees and rock, in submontane and montane forests, at 600–3150 m.

Additional specimens examined. SURINAME. Without locality, s.d., *Kegel s.n.* (FH).

ECUADOR. ZAMORA-CHINCHIPE: Reserva Biológica San Francisco, 30 km from Loja and Zamora, at the Northern limito d the Parque Nacional de Podocarpus, montane tropical rain forest, 3°58'18" S, 79°04'44" W, 1800-3150 m, 16 October 2001, *Nöske 1367* (GOET).

BRAZIL. BAHIA: Rio de Contas, topo do Pico das Almas, 13°31'19"S, 41°57'44"W, 1870 m, 27 October 1994, *Visnadi & Vital 2605* (SP). **ESPÍRITO SANTO:** Domingos Martins,

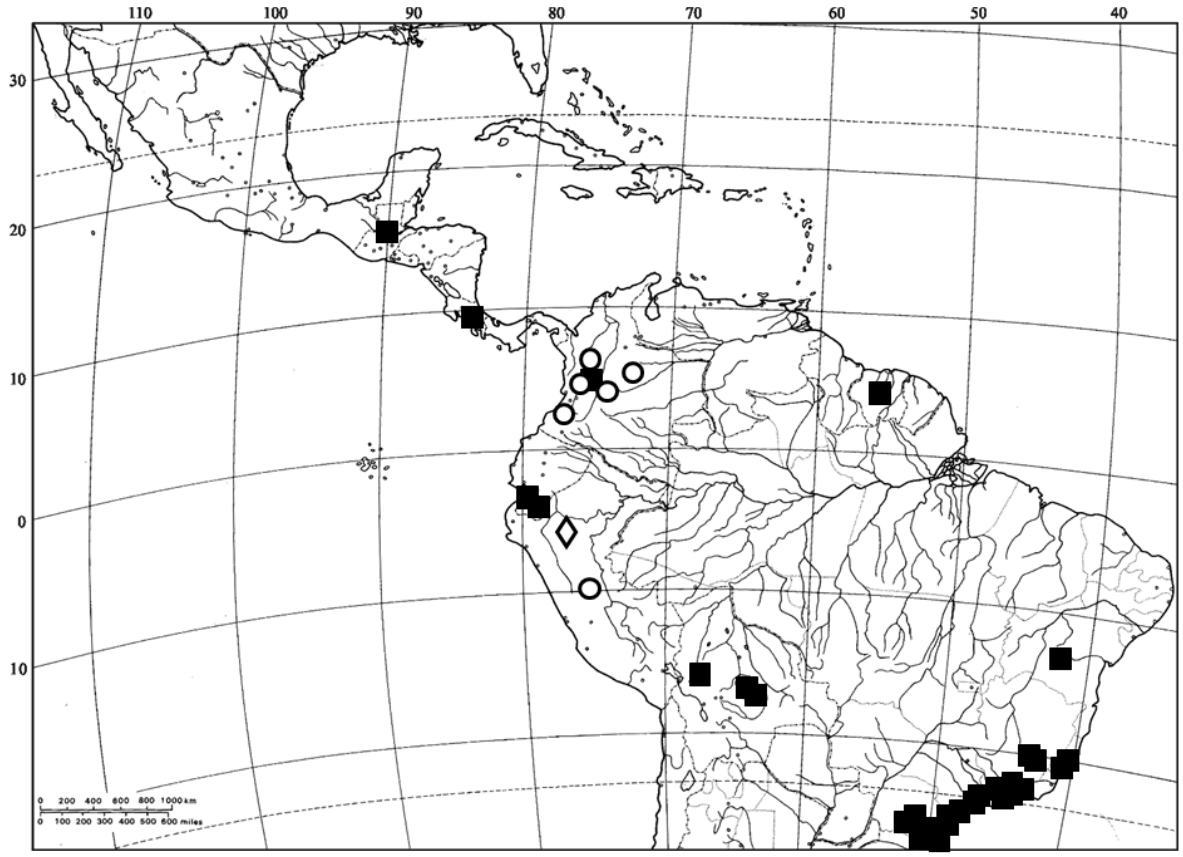

Figure 44. Distribution of *Radula sinuata* (black square), *R. smithii* (white rhombus), and *R. sonsonensis* (white circle).

Parque Estadual da Pedra Azul, 20°23'57"S, 41°01'14"W, 1360 m, 2 October 2016, *Peralta et al. 19507* (SP). **MINAS GERAIS:** Serra da Mantiqueira, Piranguçu, Campos do Jordão, 1450 m, 19 April 1986, *Schäfer-Verwimp 6885* (MG). **PARANÁ:** São José dos Pinhais, Campo Largo da Roseira, 25°40'26"S, 49°12'33"W, 21 May 2011, *Machado et al. 25* (SP). Serra da Esperança, 29 km West of junction with BR 277, Km 140, 1150 m, 11 September 1977, *Vitt 21368* (JE). **RIO DE JANEIRO:** Serra do Itatiaia, caminho dos 3 picos, 18 October 1926, *Vaughan Bandeira s.n.* (RB). **RIO GRANDE DO SUL:** Serra Gaúcho, near Canela, 730 m, 20 January 1987, *Schäfer-Verwimp & Verwimp 8206* (MG). Caxias do Sul, Jardim Botânico, na beira da mata, sobre tronco, 780 m, 18 April 2006, *Bordin & Pasini 488* (MO). **SANTA CATARINA:** Lajes, along the BR 116, ca. 19 km S, 11 March 1976, *Vital 5647* (SP). Bom

Retiro, epiphytic, 1220 m, *Shafer-Verwimp 13448-b* (JE). **SÃO PAULO:** Serra do Paranapiacaba, near Apiai, 930 m, 3 May 1987, *Schäfer-Verwimp & Verwimp 8447* (SP). Estrada Vergueiro, Alto da Serra, December 1920, *Hoehne 120* (JE).

BOLIVIA. SANTA CRUZ: Vallegrande, bosque montano de Tucumano-Boliviano, cresciendo sobre *Ilex argentina*, 2150 m, 30 July 2011, *Inturias et al. 973A* (MO). Florida, Mairana, 23 km nordeste de Mairana, bosque nublado secundário, com arbustos, poco helecho arbóreo, sobre arbusto, 18°03'S, 63°54'W, 2100-2300 m, 30 March 2002, *Churchill et al. 21420* (MO).

Radula sinuata (subg. *Volutoradula*?) is easily recognized by the lobule shape with a line of circinate insertion, base short-auriculate, frequently fully orverlapping the stem, and free margin slightly to strongly rounded. The lobules are subquadrate to oblong with free margin strongly rounded, and inflated at rhizoid area, along the keel and free margin.

This species is similar to *Radula voluta* in the stem anatomy, leaf shape and auriculate lobule base. However, the lobule base of *R. voluta* is strongly auriculate or circinately coiled, while in *R. sinuata* the lobule base is only shortly auriculate. The two species also differ in size and vegetative reproduction, with *R. voluta* being a larger plant without caducous leaves.

Oliveira-da-Silva *et al.* (2021) erroneously cited Yamada (1987) in the designation of the lectotype of *R. montana* (which was selected by Castle 1965).

41. Radula smithii F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., Phytotaxa 564: 99. 2022. Type: Peru, San Martín, Rioja, Venceremos, km 390, Pedro Ruíz – Moyobamba road, primary montane forest, on soil bank, 05°50'S, 077°45'W, 1750–2100 m, 27 July – 9 August 1983, *D. N. Smith C-300* (holotype, MO-6968335!; isotype, MG!).

Fig. 45

Dioicous? *Plants* (2–)2.5–3 mm wide, to 4 cm long, yellowish-green to brown in herbarium, irregularly pinnate to dichotomous. *Branches Radula*-type or *Lejeunea*-type branches present on decapitated shoots. *Stems* 250–350 μm diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, epidermal wall heavily and evenly thickened. *Leaf lobes* obliquely to widely spreading, distant, rarely contiguous, strongly convex, orbicular, 1.7–2 mm long, 1.4–1.5 mm wide, dorsal base almost absent, not covering the stem, dorsal margin rounded, ventral margin rounded, apex rounded,

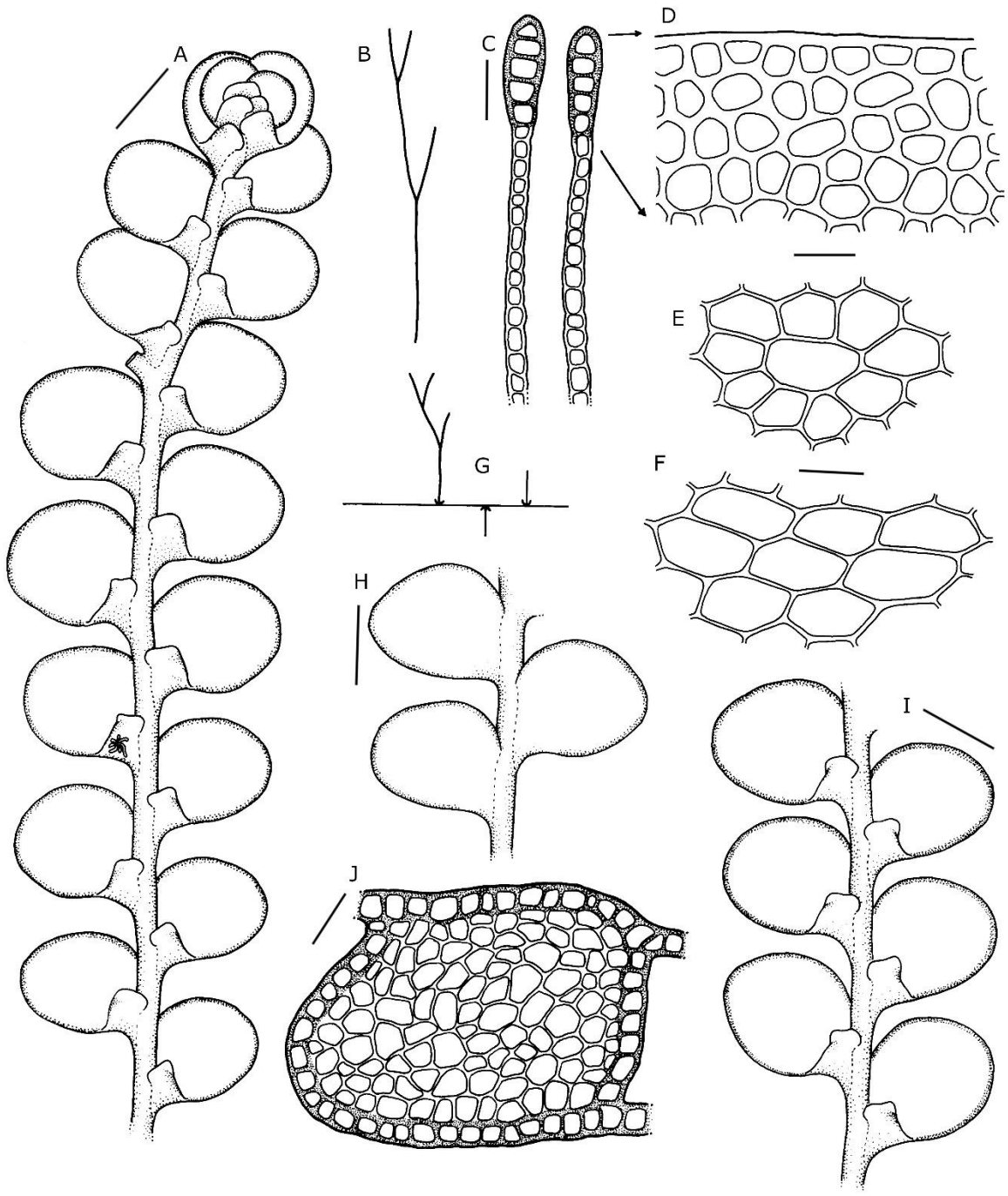

Figure 45. *Radula smithii*. A, I. Habit, ventral view. B, G. Cladographs of plants. C. Cross section of a leaf lobe, showing thick-walled, large, pigmented cells at leaf margin. D. Marginal leaf cells. E. Median leaf cells. F. Basal leaf cells. H. Leaves in dorsal view. J. Cross section of a stem (A, H, I= 1000 μm; C, J= 50 μm; D–F= 25 μm; A-J from the holotype).

margins plane, entire; marginal cells subquadrate to subrectangular or rounded, 10–20 × 10–15 μm, median cells isodiametric to elongate, 20–25 × 15–20 μm, basal cells elongate, 25–35 × 15–25 μm, cell walls thin at leaf base and in midleaf, evenly thickened and distinctly reddish-brown along the margin forming a broad, 3–5 cell rows wide border, trigones lacking, cuticle finely verruculose; oil bodies not observed. *Lobules* distant, subquadrate, 0.8–1 mm long, 0.5–

0.6 mm wide, 1/4–1/3 of lobe length, slightly inflated at rhizoid area, insertion 2× the base length, insertion line almost straight, base plane, rounded, covering 1/3(–1/2) the stem, free margin plane, straight, apex plane, rounded, distal margin incurved, straight, keel slightly convex, spreading at angles of 50–60º with the stem, 150–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brown, scanty, present on a few lobules. *Sexual branches* not observed. *Vegetative reproduction* by stem fragmentation.

Distribution and habit. Only known from the type locality in northern Peru (Dept. San Martín) (Figure 44), growing on soil or as an epiphyte in primary lower montane forest, at 1750–2100 m.

Additional specimens examined. PERU. SAN MARTÍN: Rioja, km 390, Pedro Ruíz – Moyobamba road, primary montane forest, epiphyte, 05°50’ S, 077°45’ W, 1750-2100 m, 27 July - 9 August 1983, *D. N. Smith C-310* (paratypes MO-6869091, MG).

Radula smithii (subg. *Volutoradula*) is a distinct species recognized by the large, sparsely branched plants with highly distant leaves and leaf lobes with a broad, 3–5 cell rows wide, reddish-brown border made up of evenly thick-walled cells (Oliveira-da-Silva *et al.* 2022). Bordered leaves are also found in *R. ligula*; for differences see under the latter species.

42. Radula sonsonensis Steph., Sp. Hepat. 4: 201. 1910. Type: Colombia, Antioquía, Páramo de Sonsón, 1872, *G. Wallis s.n.* (lectotype, G-00043860!, scanty, c. per., selected by Castle, 1963: 9; isolectotype, FH!).

Fig. 46

Dioicous. *Plants* 0.8–1.2 mm wide, to 1 cm long, yellowish-brown in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type. *Stems* 100–150 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal along the keel, insertion 2–3× the base length, insertion line almost straight, base plane, rounded, not or scacely covering the stem, rarely overlapping the stem, free margin plane, wall wide, dorsal base rounded, covering 2/3 to overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margin plane to recurved, crenulate; marginal cells

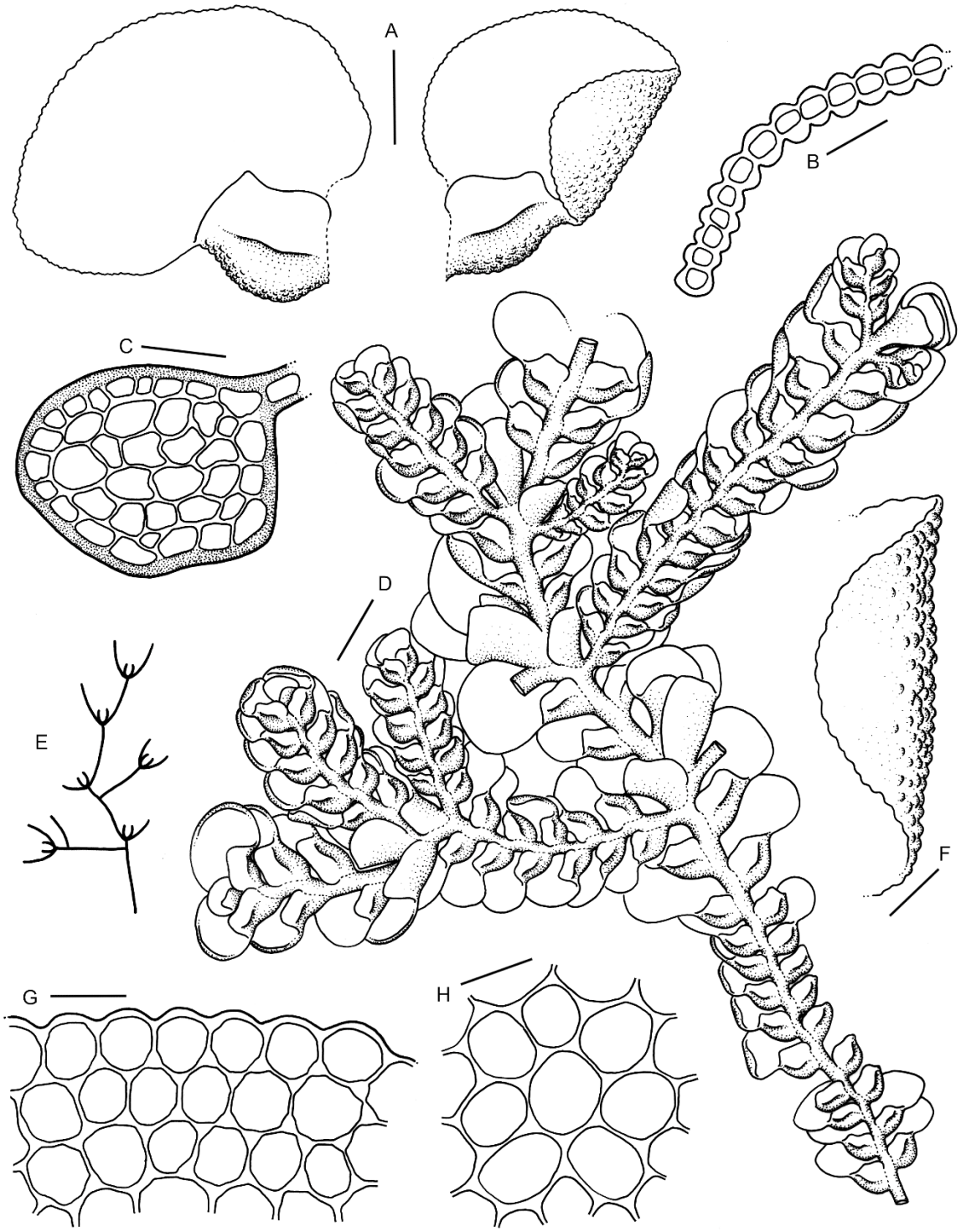

Figura 46. *Radula sonsonensis*. A. Leaves. B. Cross section of leaf. C. Cross section of stem. D. Habit with gynoecia. E. Cladograph of plants (U = gynoecia without perianth). F. Leaf margin, showing the mammillose cells on dorsal surface. G. Marginal leaf cells. H. Median leaf cells (A = 250 µm, B, C = 50 µm, D = 500 µm, F = 100 µm, G, H = 25 µm; All from *Bischler 1060*).

heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate to falcate-ovate, 0.5–0.9 mm long, 0.3–0.7 mm

subquadrate to rounded, 15–20 × 12–15 µm, median and basal cells isodiametric to elongate, 20–30 × 15–25 µm, leaf cells mammillose on the ventral and dorsal surface, often with a distinct papilla, cell walls thin, trigones medium-sized, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* contiguous to imbricate, subquadrate, rarely subrectangular, 0.3–0.5 mm long, 0.2–0.3 mm wide, 1/3–1/2 the lobe length, strongly inflated straight, apex plane, rounded to obtuse, distal margin straight, keel strongly convex, sometimes crenulate by mammillose cells, spreading at angles of 50–60º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long branches, with 2 innovations; bracts oblong, 0.9–1.3 mm long, 0.5–0.8 mm wide, apex rounded to slightly obtuse, margin plane to recurved, crenulate, lobule oblong, ca. 1/2 of lobe length, apex obtuse. *Perianth* erect, trumpet-shaped, ca. 3.3 mm long, 0.3 mm wide at base, ca. 0.5 mm wide at middle, ca. 0.7 mm wide at apex, mouth crenulate, plane; perianth wall unistratose. *Calyptra* and *sporophte* not observed. *Vegetative reproduction* occasionally by caducous leaf lobes.

Distribution and habit. Rather rare Andean species found in Colombia (see Castle 1963, Jans 1979, Gradstein 2021) and once in Peru (Graham *et al.* 2016) (Figure 44). *Radula sonsonensis* grows on bark, rock (volcanic, limestone, sandstone) and soil in upper montane cloud forest and humid páramo, at 2650–3850(–4200) m.

Additional specimens examined. COLOMBIA. ANTIOQUÍA: The type of *Radula sonsonensis* (G). **BOYACÁ:** Páramos al NW de Belén, cabeceras Quebrada Minas, 600 m al NE de la laguna El Alcohol, on soil in humid páramo vegetation, 3850 m, 2 March 1972, *Cleef 2137c* (GOET, U, MG). **CAUCA:** Valle de las Papas, near Valencia, epiphyte, in small cushions, 2910 m, September – October 1958, *Bischler 1060* (U, MG). **RISARALDA:** St. Rosa de Cabal, subandean forest belt, between Termales and Volcano Otún, on bark of Miconia in low bush, 2650 m, 16-19 July 1980, Gradstein 3583 (GOET). **TOLIMA:** Nevado del Tolima, S slope, along trail to La Cueva, on rock in cloud forest, 3200 m, 12 August 1975, Van der Hammen & Jaramillo 3347 (U, MG).

Radula sonsonensis (subg. *Volutoradula*?) is recognized by the small plants (0.8–1.2 mm wide) with irregularly pinnate to dichotomous (in female plants) branching, leaves strongly imbricate, ovate to falcate-ovate with apex usually recurved and crenulate margins, leaf cells conspicuously mammillose on the ventral and dorsal surface of the lobe (seen mainly on the

dorsal surface due to recurved margin) and sometimes with a distinct papilla (*Bischler 1060*), lobules strongly inflated along the keel, base not or scarcely covering the stem, and keel strongly convex, sometimes crenulate by mammillose cells.

The species resembles *Radula brasilica* by the small plants with imbricate, ovate to falcate-ovate leaf lobes and a strongly convex keel (see Oliveira-da-Silva *et al.* 2021, Fig. 5J). The latter species, however, has the lobule free margin strongly recurved and leaf lobes often strongly caducous, resulting in almost naked branches. In *R. sonsonensis* the lobule free margin is plane and caducous leaf lobes occur only occasionally, and do not result in naked branches.

Types and additional collections of *Radula sonsonensis* (mostly checked by Jans and Yamada) were scanty.

43. Radula stenocalyx Mont., Ann. Sci. Nat., Bot., sér. 4, 3: 315. 1855. Type: French Guiana, Cayenne, "ad folia filicum," *M. Leprieur 1395* (lectotype, PC-Montagne-069928!, designated by Oliveira-da-Silva *et al.* 2021: 136; isolectotype, BM-000969242!, c. per. + andr.).

Radula tenella Gottsche, Mexik. Leverm. 149. 1863. Type: Trinidad and Tobago, 8 May 1847, *H. Crüger 159* (holotype, B, not found; lectotype, G-00281258!, **designated here**; isolectotypes, G-00281383!, FH!), syn. fide Castle (1939).

Dioicous. *Plants* 0.9–1.4 mm wide, to 1 cm long, light green in field, pale green to yellowish-brown in herbarium, irregularly pinnate. *Branches Radula*-type, rarely *Lejeunea*-type. *Stems* 80–100 μm in diam., with thin-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish. *Leaf lobes* obliquely to widely spreading, contiguous, slightly convex, ovate, 0.6–1 mm long, 0.5–0.7 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight to rounded, apex rounded, margin plane, sometimes slightly recurved, entire to strongly crenulate with gemmae; marginal cells subquadrate, 10–15 μm in diam., median and basal cells isodiametric to elongate, 20–25 × 15–20 μm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.3–0.4 mm long, 0.2–0.3 mm wide, ca. 1/3 the lobe length, strongly inflated at rhizoid area, insertion ca. 2× the base length, insertion line straight, base plane, covering up to 1/3 the stem, free margin plane, straight, apex plane, rounded, distal margin straight to sinuose, keel straight to convex, spreading at angles of 50–70º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule.

Rhizoids colorless to brown, numerous on a pronounced mammiliform swelling, present on numerous lobules. *Androecia* terminal on long branches, with 2–10 pairs of bracts, 0.3–0.4 mm wide; bracts contiguous to imbricate, ovate, 0.2–0.3 mm long, 0.1–0.2 mm wide, apex rounded, margin recurved, entire, lobule ovate, ca. 5/6 of lobe length, base slightly rounded to straight, free margin straight, apex rounded. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong, 0.5–0.6 mm long, 0.2–0.3 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded. *Perianth* erect to falcate, campanulate when young to trumpet-shaped, 0.8–2 mm long, ca. 0.1 mm wide at base, 0.3–0.6 mm wide at middle, 0.2–0.3 mm wide at apex, mouth entire, plane to undulate, rarely inrolling to outside of the perianth; perianth wall 2–3-stratose at base, unistratose from the middle to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 3–5-layered tube (perigynium) within which the sporophyte foot and part of the Seta is embedded. *Calyptra* wall 1–2-layered at the base, unistratose above. *Sporophyte* not observed. *Vegetative reproduction* by few to numerous, small to large discoid gemmae, 44–200 μm in diam., produced on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Widespread in tropical America and Africa; also in tropical Asia (Thailand, China, India). In addition to the countries of tropical America mentioned in the additional examined specimens section, *Radula stenocalyx* has been reported for Cuba, Dominica, Venezuela, Ecuador and Peru (Castle 1939, Martínez 2012, Gradstein 2021, Graham *et al.* 2023) (Figure 47). The species usually grows on leaves of vascular plants; one record is from rock (*Peralta et al. 17816*) and is found in humid, undisturbed lowland and montane forests, from sea level to 2300 m (to 2550 m in Asia; Promma & Chantanaorrapint 2015).

Additional specimens examined. COSTA RICA. PUNTARENAS: Reserva Biológica Monteverde, undisturbed cloud forest, on fern fronds, 1550 m, 9 November 1993, *Gradstein 9454a* (GOET).

TRINIDAD AND TOBAGO. The type of *Radula tenella* (FH, G).

FRENCH GUIANA. The type of *Radula stenocalyx* (PC, BM).

COLOMBIA. CAUCA: Gorgona I., virgin rain forest on wet side of the island, on living leaves in river valley, 12-13 August 2006, *Gradstein & Varon 11071* (GOET).

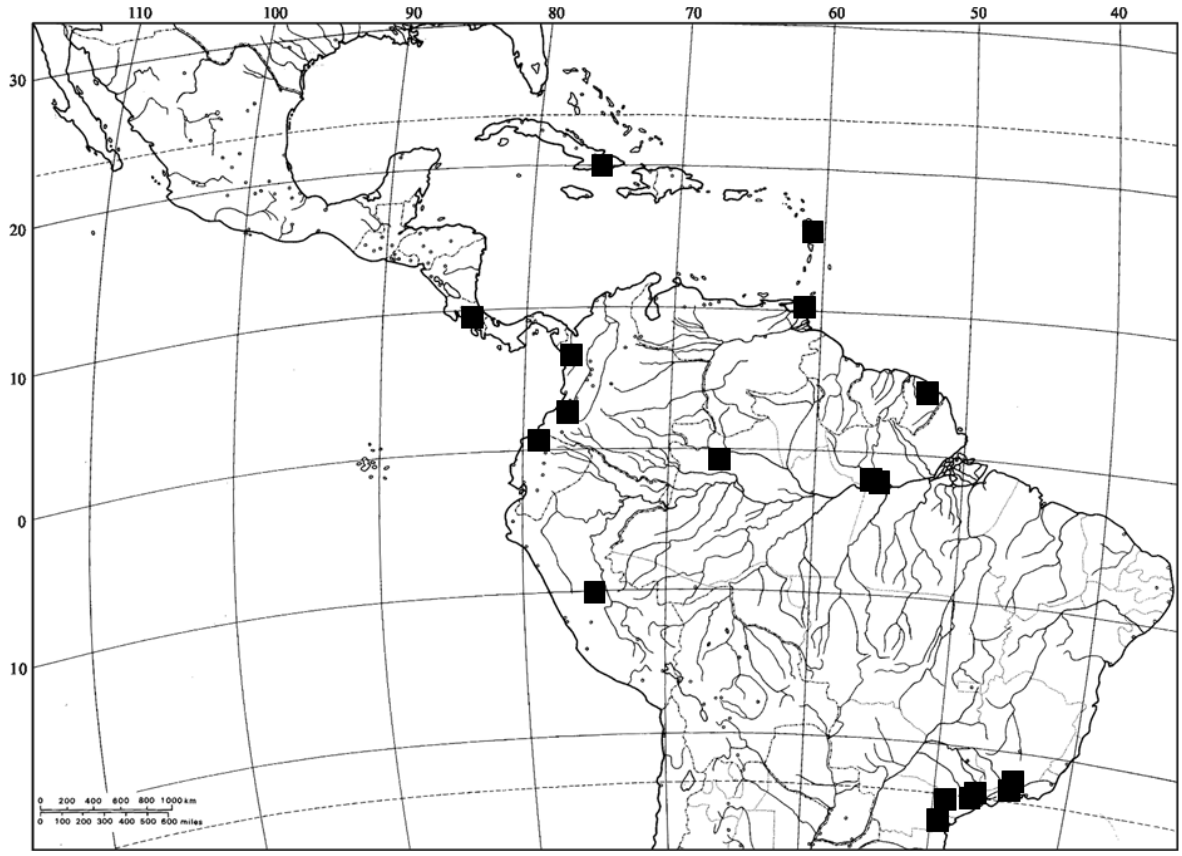

Figure 47. Distribution of *Radula stenocalyx.*

BRAZIL. AMAZONAS: Rio Negro, between Manaus and São Gabriel, south slope of Morro Ximaio, 00°45–50'S, 66º50'W, 7 July 1979, *Schuster 79-14-425* (NY). **PARÁ:** Oriximiná, ESEC do Grão Pará, Serra do Acari, 1°16'47,4"S, 58°41'28,5"W, 475 m, 30 August 2008, *Pietrobom & Maciel 8230* (HBRA). **PARANÁ:** Morretes, Parque Estadual Pico do Marumbi, 25°26'09"S, 48°55'03"W, 450 m, 17 July 2015, *Peralta et al. 17816* (SP). **RIO DE JANEIRO:** Parque Nacional do Itatiaia, along trail to Veu de Noiva and Itaporani, ca. 13,5 km, 22°25'S, 44º36'W, 9 July 1991, *Vital & Buck 19974* (NY). **SÃO PAULO:** Serra de Paranapicaba, between Apiai and Iporanga, 300 m, 1 May 1987, *Schäfer-Verwimp & Verwimp 8435* (MG, SP). Guapiara, Parque Estadual Intervales, sobre folhas, 24°11'06"S, 48°31'58"W, 700 m, 24 July 1991, *Visnadi & Vital 5199* (SP). Estação Biológica Campo Grande, 1 May 1923, *Hoehne 655, 14, 655/r* (JE). Litoral Norte, Ilha de São Sebastião, Mata Atlântica am Westabhang, epiphyll, 23°51'S, 45°21'W, 440 m, 27 July 1986, *Schäfer-Verwimp & Verwimp 7312* (MO).

Radula stenocalyx (subg. *Metaradula* sect. *Epiphyllae*) is recognized by the small epiphyllous plants with few to numerous discoid gemmae produced on dorsal leaf margins and subquadrate lobules, which are strongly inflated at the rhizoid area. The leaves are obliquely

to widely spreading and plane to slightly convex (Oliveira-da-Silva *et al.* 2021, Fig. 28A and C). Promma & Chantanaorrapint (2015) reported the occurrence of gemmae also on perianth mouth and margins of male bracts.

Radula stenocalyx is closely similar to *R. flaccida*; for differences see under the latter species.

44. Radula subinflata Lindenb. & Gottsche, Syn. Hepat. 724. 1847. Type: Mexico, Sempoaltepec, 1842, *F. M. Liebmann s.n.* (lectotype, W!, hb. Lindenberg n° 5456, **designated here**).

Dioicous. *Plants* 1.3–2.4 mm wide, to 2 cm long, green to yellowish-green in herbarium, irregularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type, rarely *Lejeunea*-type present on decapitated shoots. *Stems* 180–230 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thick-walled (by concave trigones), yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to imbricate, slightly convex, ovate to slightly falcate-ovate, 0.7–1 mm long, 0.45–0.8 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin slightly rounded, apex rounded, margin recurved, rarely plane, slightly crenulate; marginal cells subquadrate to almost rounded, 8–10 µm in diam., median and basal cells isodiametric to elongate, 10–15 × 15–25 µm, leaf cells mammillose on the dorsal surface, cell walls thin, trigones small to medium-sized, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.4–0.5 mm long, 0.3–0.4 µm wide, 1/3 the lobe length, inflated along the keel, insertion 1–2× the base length, insertion line curved, base plane to slightly recurved, rounded, covering up to 1/2 the stem, free margin plane to sinuose, straight, apex plane, rounded, distal margin straight, keel straight to slightly convex, spreading at angles of 40–60º with the stem, 120–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty. *Androecia* terminal to intercalary on long branches, with 3–6 pairs of bracts, 0.8–1 mm wide; bracts distant to contiguous, ovate, 0.6–0.7 mm long, 0.3–0.35 mm wide, apex rounded, margin recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 1–1.2 mm long, 0.6–0.7 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical, 2–3.7 mm long, 0.2–0.3 mm wide at base, 0.7–1 mm wide at middle, 0.9–1.1 mm wide at apex,

mouth entire, plane to undulate; perianth wall unistratose, sometimes with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2-layered tube within which the sporophyte foot is embedded. *Calyptra* wall unistratose. *Seta* ca. 4.5 mm long. *Capsule* 1.1–1.2 mm long, 0.25–0.3 mm wide, valves ca. 1.5 mm long, 0.25–0.3 mm wide at middle, outer layer cells rectangular to long-rectangular, simple nodular thickenings reddish-brown, on cell angles and evenly spaced along every longitudinal wall, inner layer cells long-rectangular, nodular thickenings absent. *Elaters* 200–500 µm long, rough. *Spores* 22.22–27.77 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by stem fragmentation and caducous *Lejeunea*-type branches.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Tropical and subtropical America (Figure 48). In addition to the countries listed in the additional specimens examined, Castle (1963) reported this species for Guatemala; we report it for the first time from Honduras and Bolivia. *Radula subinflata* grows usually on trees, rarely on rotten logs, rock and leaves of vascular plants, in lowland to montane forests, at 200–2168 m. Gradstein (2021) recorded it from páramo up to 3800 m. The species is very common in the Atlantic Coastal Region of Brazil, but uncommon elsewhere in tropical America.

Additional specimens examined. MEXICO. The type of *Radula subinflata* (W).

HONDURAS. LEMPIRA: Montana de Celaque, quebrada below camp Don Tomas along Rio Naranjo, 10 km SW of Gracias, on leaves of small tree by stream, 1900 m, 11 May 1992, *Allen 11916* (MO).

COLOMBIA. CHOCÓ: Road Sta. Cecilia, Tadó 40 km W of Sta. Cecilia, on rotten wood, 200 m, 1 August 1992, *Gradstein 8738* (GOET).

ECUADOR. PICHINCHA: Quito, s.d., *Jameson s.n.* (FH-00965709).

BRAZIL. BAHIA: Abaíra, mata Serra do Rei, 4°16'N, 41°54'W, 1550–1650 m, 17 February 1992, *Harley et al. 52110* (SP). Abaíra, Catolés, Serra do Barbado, Mata do Cigano, floresta estacional Montana, corticícola, 13°16'47,7" S, 41°54'14,9" W, 1734 m, 5 setembro 2008, *Vilas Bôas-Bastos 2399, 2475* (ALCB). Eunápolis, Estação Veracruz, trilha tropical, Floresta Atlântica, corticícola, 16°22' S, 39°10' W, *Vilas Bôas-Bastos & Bastos 337* (ALCB). **ESPIRITO SANTO:** Município de Domingos Martins, Parque Estadual Pedra Azul, Trilha das

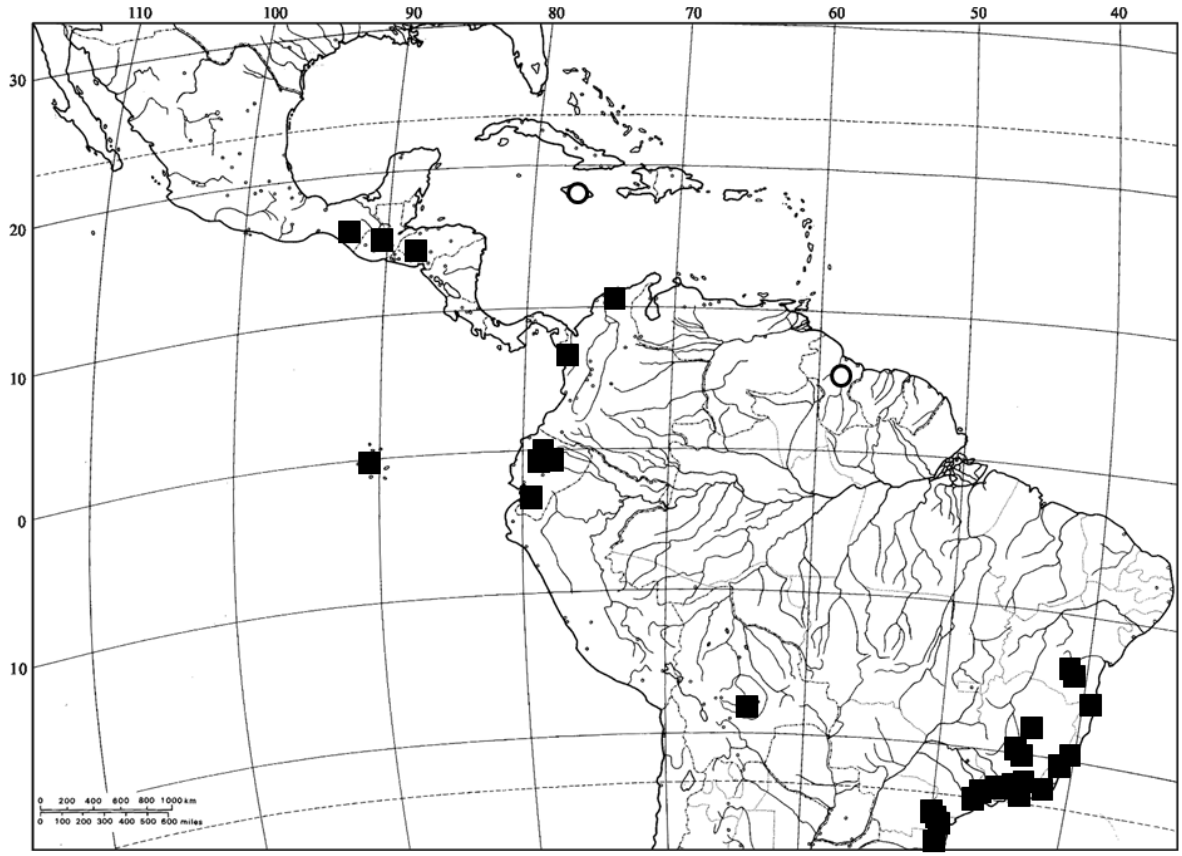

Figure 48. Distribution of *Radula subinflata* (black square) and *R. taylorii* (white circle).

Piscinas, Floresta Montana, epíxila, 6 agosto 2009, *L.T. Penha 584* (ALCB). **MINAS GERAIS:** Lima Duarte, Parque Estadual do Ibitipoca, Gruta do Cruzeiro, 1530 m, 28 November 1993, *Yano et al. 21600* (SP). Parque Nacional do Itatiaia, along entry road near border of Rio de Janeiro, between km 1.5 and km 3, humid montane forest, 1700-1900 m, 4 July 1991, *Vital & Buck 19489* (NY, MG). **PARANÁ:** Morretes, Parque Estadual do Marumbi, trilha vermelha, 25°26'55"S, 48°54'54"W, 1200 m, 22 July 2014, *Peralta et al. 15827* (SP). **RIO DE JANEIRO:** Resende, 1 km após o Hotel Alsene, 2500 m, 24 November 1993, *Yano et al. 21357* (SP). Parque Nacional do Itatiaia, Pico das Agulhas Negras, N of Engo Passos, 17.5 km NE of União, in alpine tussock grassland with large composites e bamboo-type shrubs, on granitic rock and on soil in crevices between rock, 2300 m, 14 September 1977, *Vitt 21492* (JE). **RIO GRANDE DO SUL:** Cambará do Sul, Parque Nacional Aparados da Serra, 29°00'00"S, 49°59'15"W, 994 m, 28 August 2017, *Peralta et al. 20925* (SP). **SANTA CATARINA:** Bom Retiro, Campos dos padres, 18 January 1957, *Sehnem 7047* (ICN). **SÃO PAULO:** São José do Barreiro, fazenda floresta pousada Recanto da Floresta, 22°42'52"S, 44°35'33"W, 1900–2090 m, 15 May 2007, *Peralta et al. 4791* (SP). Estação Biológica Alto da Serra, 1920, *Gert 105, 492* (JE). Estação Biológica Alto da Serra, epiphyll, October 1922, *Hoehne 657 pp.* (JE).

BOLIVIA. SANTA CRUZ: Vallegrande, bosque montano de Tucumano-Boliviano, dossel bajo 12-14 m de altura, crescendo sobre *Weinmannia*, 18°34’44”S, 63°46’31”W, 2168 m, 29 July 2011, *Inturias et al. 852* (MO).

Radula subinflata (subg. *Volutoradula*?) is recognized by the convex, ovate to slightly falcate-ovate leaf lobes with a rounded apex, slightly crenulate and recurved leaf margins (rarely plane), leaf cells not or slightly mammillose on the dorsal lobe surface, trigones small to medium-sized, and lobules subquadrate with rounded base, covering up to 1/2 the stem, and conspicuously inflated along the keel.

This species is very similar to *Radula venezuelensis*, especially in lobule shape. However, *R. venezuelensis* has thin-walled medullary cells, leaf lobes strongly falcate-ovate with an obtuse to subacute apex, and leaf cells conspicuously mammillose and with bulging trigones; in *R. subinflata* the medullary cells are thick-walled with large trigones, leaf lobes are ovate to slightly falcate-ovate with a rounded apex, and the leaf cells are scarcely mammillose and with small to medium-sized trigones. In addition, the spores of both species are different, being composed of rounded elements in *R. subinflata* and of elongate elements in *R. venezuelensis*.

45. Radula steerei Grolle, Mem. New York Bot. Gard. 45: 259. 1987. Type: Inclusion in Dominican amber, Museum für Naturkunde Berlin (Paläontologische Museum) Inventory no. 1985/a (holotype), Inventory no. 1985/a (paratype).

Description and Illustration. Grolle (1987).
Distribution. Dominican Republic, in amber from the Miocene.

Radula steerei was described by Grolle (1987) based on two sterile fragments preserved in amber. The plants are very small, 1.58–0.71 mm long and 0.38–0.46 mm wide, and the branches are mostly of the *Radula*-type, rarely *Lejeunea*-type. In addition, the species produces microphyllous branches, 3–4 × smaller than the main stem. The leaves are obliquely spreading, contiguous, ovate, with dorsal margin rounded and ventral margin almost straight, and the leaf cells are thin-walled, without trigones and with a smooth cuticle. The lobules are distant, subrectangular, 1/2 the lobe length and inflated at the rhizoid area, with a rounded base covering the stem to about 2/5, a straight free margin, rounded apex, and slightly convex keel.

According to Grolle (1987) the most remarkable characteristics of this species are the microphyllous branches, justifying its placement in the Asiatic section *Faurianae* with the single extant species, *R. fauriana* Steph. (Yamada 1979).

46. Radula taylorii Steph., Hedwigia 23: 133, 156. 1884. Type: Guyana, Demerara, s.d., *unknown collector*, ex hb. Gottsche, sub "*Jung. pallens Sw.*", mist T. Taylor (lectotype, G-00112216!, scanty, c. per., selected by Yamada 1991: 98).

Dioicous. *Plants* 2.1–2.9 mm wide, to 2 cm long, olive green to brownish in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 200–250 μm in diam., with thick-walled epidermal and medullary cells, the cells uniform in size, walls brown. *Leaf lobes* widely spreading, imbricate, distant to contiguous on branches, strongly convex, ovate, 1.3–1.9 mm long, 0.9–1.1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded to slightly obtuse, margin plane to recurved, entire; marginal cells subquadrate, 8–10× 5–8 μm, median cells isodiametric to elongate, 15–20× 10–15 μm, basal cells isodiametric to usually elongate, 20–35 × 15–30 μm, cell walls thin to medium-sized, trigones large, intermediate thickening present, cuticle smooth; oil bodies not observed. *Lobules* contiguous to subimbricate, oblong, 0.7–0.9 mm long, 0.5–0.6 mm wide, 1/3 the lobe length, slightly inflated at rhizoid area, insertion ca. 1/2 the base length, insertion line almost straight, base plane, rounded, covering 2/3 to overlapping the stem (stem surface hardly visible), free margin plane, straight to rounded, apex rounded to obtuse, distal margin straight, keel straight to slightly convex, spreading at angles of 30–40º with the stem, 120–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on long branches, with 1 innovation; bracts ovate, 1.2–1.5 mm long, 0.6–0.8 mm wide, apex rounded, margin recurved, entire, lobule oblong to almost subuadrate, ca. 1/2 of lobe length, apex rounded. *Perianth* erect, subcylindricalal, ca. 3.8 mm long, 0.4–0.5 mm wide at base, 1.2–1.3 mm wide at middleto the apex, mouth entire plane; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, with small longitudinal striae at base. *Calyptra, Sporophyte* and *Vegetative reproduction* not observed.

Illustration. Yamada (1991).

Distribution and habit. *Radula taylorii* was only known from the type locality in Guyana; here its distribution is extended to Jamaica (Figure 48). Informationon on the habitat of the species is lacking.

Additional specimens examined. JAMAICA. Whitout locality, s.d, *Lehman s.n.*, hb. Sullivant (FH).

GUYANA. The type of *Radula taylorii* (G).

Radula taylorii (subg. *Radula*?) is recognized by strongly convex leaves with a rounded to obtuse apex and usually recurved ventral margin, leaf cells with large trigones, and lobules oblong, imbricate (distant to contiguous on branches), with the base covering 2/3 to the entire stem, and the keel spreading at an angle of 30–40º with the stem. The species resembles *R. javanica*, but the latter has leaf cells without trigones and distant lobules with the base covering usually 1/2 the stem. The type specimen of *R. taylorii* contains two short, brownish shoots, one with perianth. The specimen from Jamaica, instead, consists of long, olive-green shoots with long and regularly pinnate branching.

47. Radula tenera Steph., Hedwigia 23: 149. 1884. Type: Brazil, without locality, *Sowerby s.n.*, hb. Mitten (lectotype, NY-01021198!, c. per., selected by Oliveira-da-Silva *et al.*, 2021: 143; isolectotypes, G-00265058!, scanty, NY-01021201!, NY-01021199!).

Dioicous. *Plants* 1–1.4 mm wide, to 2 cm long., yellowish-green to yellowish-brown in herbarium, regularly pinnate. *Branches Radula*-type. *Stems* 170–200 µm in diam., with epidermis and medulla thick-walled, the cells uniform in size, walls colorless. *Leaf lobes* widely spreading, imbricate, strongly convex, ovate, 0.7–1.2 mm long, 0.4–1 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin straight, apex rounded to obtuse, margin strongly recurved, entire; marginal cells subquadrate, 10–18 × 8–12 µm, median and basal cells isodiametric to elongate, 15–25(–30) × 10–20 µm, cell walls thin, trigones large, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, convolute and lunular, rarely subquadrate, 0.3–0.5 mm long, 0.1–0.25 mm wide, ca. 1/2 the lobe length, strongly and narrowly inflated along the keel, insertion very short, insertion line curved, base plane, straight, not covering the stem, free margin plane, almost straight, usually covered by the inflated keel, apex plane, obtuse, usually covered by the inflated keel, distal margin straight, keel concave, rarely straight, spreading at

angles of 40–50º with the stem, 50–80º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty to numerous, present on a few lobules. *Androecia* terminal to intercalary on short branches, with 2–4 pairs of bracts, 0.7–1 mm wide; bracts imbricate, ovate, 0.5–0.9 mm long, 0.25–0.4 mm wide, apex rounded, margin strongly recurved, entire, lobule ovate, ca. 3/4 of lobe length, base straight, free margin almost straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 1–1.2 mm long, 0.5–0.6 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate to oblong, ca. 1/2–1/3 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical, 2.4–3.6 mm long, 0.4–0.5 mm wide at base, ca. 1 mm wide at middle, 1–1.1 mm wide at apex, mouth entire, strongly undulate; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–5-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 2–3-layered at the base, 1 cell layer thick above. *Seta* ca. 3 mm long. *Capsule* ca. 2 mm long, ca. 5 mm wide, valves ca. 2 mm long, 0.3–0.5 mm wide at middle, outer layer cells subquadrate to almost rectangular, simple nodular thickenings yellowish, on cell angles and longitudinal wall of every second wall, inner layer cells rectangular to long-rectangular, nodular thickenings absent. *Elaters* and *Spores* not observed. *Vegetative reproduction* by caducous leaf lobes on specialized upright, lagelliform shoots (see Gradstein 2021).

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Costa Rica, Ecuador, Colombia and Brazil (Dauphin 2005, Gradstein 2021) (Figure 49). This species grows on bark of trees and shrubs in montane forests up to the páramo, at 670–3200 m.

Additional specimens examined. ECUADOR. LOJA: Cordillera Oriental, Parque Nacional Podocarpus, Cachunuma, páramo vegetation, on twigs of shrubs, 3200 m, 8 August 2003, *Gradstein & Mandl 10156* (GOET). **ZAMORA-CHINCHIPE:** road Loja-Zamora 30 km, NE slope of Cordillera Numbala, Reserva Biológica San Francisco, trail to summit, in wet, shrubby subpáramo vegetation, growing on twigs of isolated shrubs, 3°58’N, 79°04’W, 2800-3000 m, 30 September 2002, *Gradstein & Nöske 10095* (GOET).

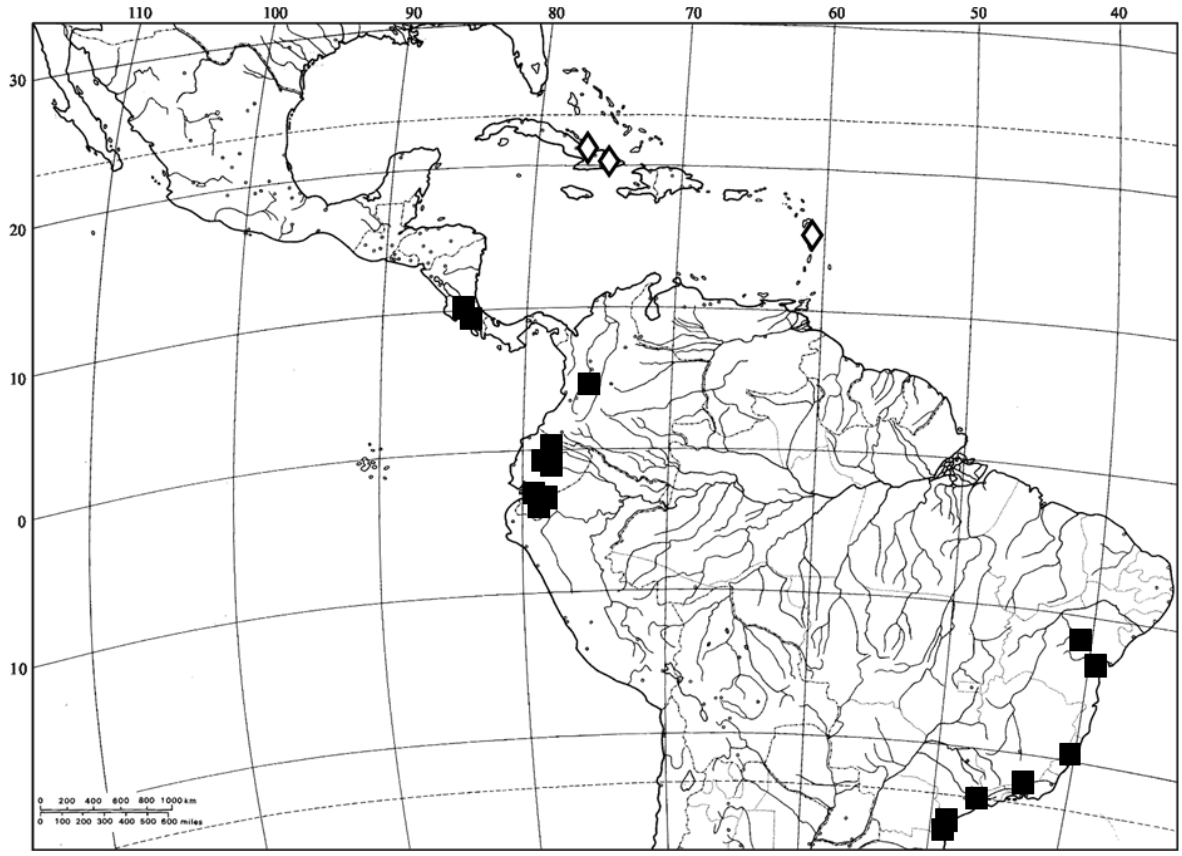

Figure 49. Distribution of *Radula tenera* (black square) and *R. tenuis* (white rhombus).

BRAZIL. BAHIA: Santa Teresinha, Povoado de Pedra Branca, Serra da Jibóia, Morro da Pioneira, Caatinga, em floresta ombrófila, corticícola, 12°51'19,7"S, 39°28'30,6"W, 810 m, 17 September 2015, *C. Bastos 5659-A* (ALCB). Miguel Calmon, Parque Estadual Sete Passagens, Mata do Dandá, floresta estacional, corticícola, 11°25'S, 40°35'W, 1000-1200 m, 17 december 2005, *Ballejos 150, 157* (ALCB). **ESPÍRITO SANTO:** Santa Tereza, Santa Lúcia, trilha Indaia-Açú, 19°57'52"S, 40°32'23"W, 670 m, 18 September 2002, *Vervloet & Costa 963* (RB). **PARANÁ:** Serra do Mar, 29 January 1904, *P. Dusén 2584* (NY). Serra do Mar, nordlich Curitiba, Capivari Grande, Rand des Nebelwaldes im Gipfelbereich, epiphytisch na Strauch, 25°07,9'S, 48°49,2'W, 1550 m, 17 November 2012, *Schäefer-Verwimp et al. 33892* (SP, MO). Piraquara, Parque Estadual Pico do Marumbi, Mata Atlântica Nebular com afloramentos rochosos, sobre tronco vivo, 25°30'55"S, 48°58'58"W, 1200-1300 m, 18 July 2015, *Peralta et al. 17928* (SP). Morretes, Estrada Graciosa, Rio Taquari, floresta ombrófila densa montana, sobre tronco vivo, 25°18'40"S, 48°56'00"W, 4 January 2018, *Canestraro & Lozano 1161* (SP). **RIO DE JANEIRO:** Itatiaia, Abrigo Rebouças, 03 February 1967, *Vianna 3939* (ICN). **RIO GRANDE DO SUL:** Cambará do Sul, Parque Nacional de Aparados da Serra,

near Itaimbezinho, 29°08’S, 50º05’W, 1000 m, 26 September 1984, *Vital & Buck 12232* (NY). **SÃO PAULO:** Estação Biológica, 29 November 1920, *A. Geht s.n.* (JE).

Diagnostic features of *Radula tenera* (subg. *Volutoradula*) are the small (1–1.4 mm wide, to 2 cm long), densely branched plants with convolute, lunular lobules with a short insertion line and a strongly and narrowly inflated rhizoid area. The keel is concave and the leaf lobes are strongly convex, with a recurved margin. A similar lobule shape occurs in *Radula involvens*, but the latter species differs in its larger size (1.8–2.2 mm wide, to 5 cm long), sparse branching and strongly falcate-ovate leaf lobes (ovate in *R. tenera*), which are only slightly convex (strongly convex in *R. tenera*).

48. Radula tenuis K.Yamada, J. Hattori Bot. Lab. 54: 247. 1983. Type: Cuba, Prov. Holguín, Cuchillas de Moa, la ladera NO del Pico El Toldo, 1000-1100 m, *T. Pócs 9177/Q* (holotype, HAC; isotypes, EGR, NICH-432556!, c. gyn.).

Dioicous. *Plants* 1.3–1.4 mm wide, to 1 cm long, yellowish-green in herbarium, regularly pinnate to dichotomous in female plants by fertile paired innovation. *Branches Radula*-type or *Lejeunea*-type present on decapitated shoots. *Stems* 80–90 µm in diam., with thick-walled epidermal cells surrounding mostly smaller or uniform in size, thin-walled medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall, walls colorless to yellowish. *Leaf lobes* widely spreading, distant to contiguous, convex, ovate to falcate-ovate, 0.7–0.9 mm long, 0.45–0.6 mm wide, dorsal base rounded, covering ca. 1/2 the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded to obtuse, margin plane to recurved, entire; marginal cells subquadrate to subrectangular, 11–22 × 10–13 µm, median and basal cells isodiametric to elongate, 22–37 × 14–22 µm, cell walls thin, trigones lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical, light yellow, slightly granular, 7–11 µm in diam. *Lobules* distant, subhombic, 0.4–0.6 mm long, 0.2–0.3 mm wide, 1/2 the lobe length, inflated at rhizoid area, insertion 9–10× the base length, insertion line almost straight to curved, base plane, rounded, covering up to 1/5 the stem, free margin plane, straight, apex plane, rounded, distal margin plane, straight, keel convex, spreading at angles of 30–50º with the stem, 130–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, scanty, present on a few lobules and leaf lobes. *Androecia* not observed. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, ca. 0.6 mm long, ca. 0.3 mm wide, apex rounded, margin plane to

recurved, entire, lobules ovate, ca. 1/2 of lobe length, apex rounded. *Perianth* and *Sporophyte* not observed. *Vegetative reproduction* by occasionaly caducous leaf lobes.

Illustration. Yamada (1983).

Distribution and habit. Cuba and Dominica (Schäfer-Verwimp 1999) (Figure 49). *Radula tenuis* grows on bark in submontane rainforest, at 750–1100 m.

Additional specimens examined. CUBA. GUANTÁNAMO: Bach tal 5 km östlich Campamento Gupeyal, 23 January 1968, *Schubert M 246* (JE). **HOLGÍN:** Moa, La Melba, falda este de la Sierra de Moa, pluviosa, 800-1000 m, 23 December 1968, *Bisse & Lippold 11200* (JE).

Radula tenuis (subg. *Volutoradula*?) is recognized by the small, flaccid, yellowish-green plants with subrhombic lobules with a narrow base, which usually does not cover the stem (or covering the stem to maximally 2/5), and a convex keel, spreading at angles of 30–50º with the stem. Additional important features include regularly pinnate branching, leaf lobes convex and ovate to falcate-ovate, and leaf cells without trigones. Some specimens have rhizoids on the margin of the caducous leaf lobes.

Radula tenuis resembles *R. wrightii*, which is widespread in Cuba, but the latter species has purelly dichotomous branching, leaf cells with small trigones at the leaf base and increasing in size towards the margins, and lobules with a long, straight keel (rarely slightly convex in the Costa Rican specimens).

49. Radula underwoodii Castle, J. Hattori Bot. Lab. 21: 37. 1959. Type: Jamaica, Mt. Diabolo, 2000 m, *L. M. Underwood 1854* (holotype, YU-169890!).

Fig. 50

Dioicous. *Plants* 1.5–2(–2.2) mm wide, to 6 cm long, olive-green in herbarium, purely dichotomous. *Branches Radula*-type. *Stems* 150–200 μm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, epidermal wall heavily and evenly thickened. *Leaf lobes* obliquely spreading, rarely widely

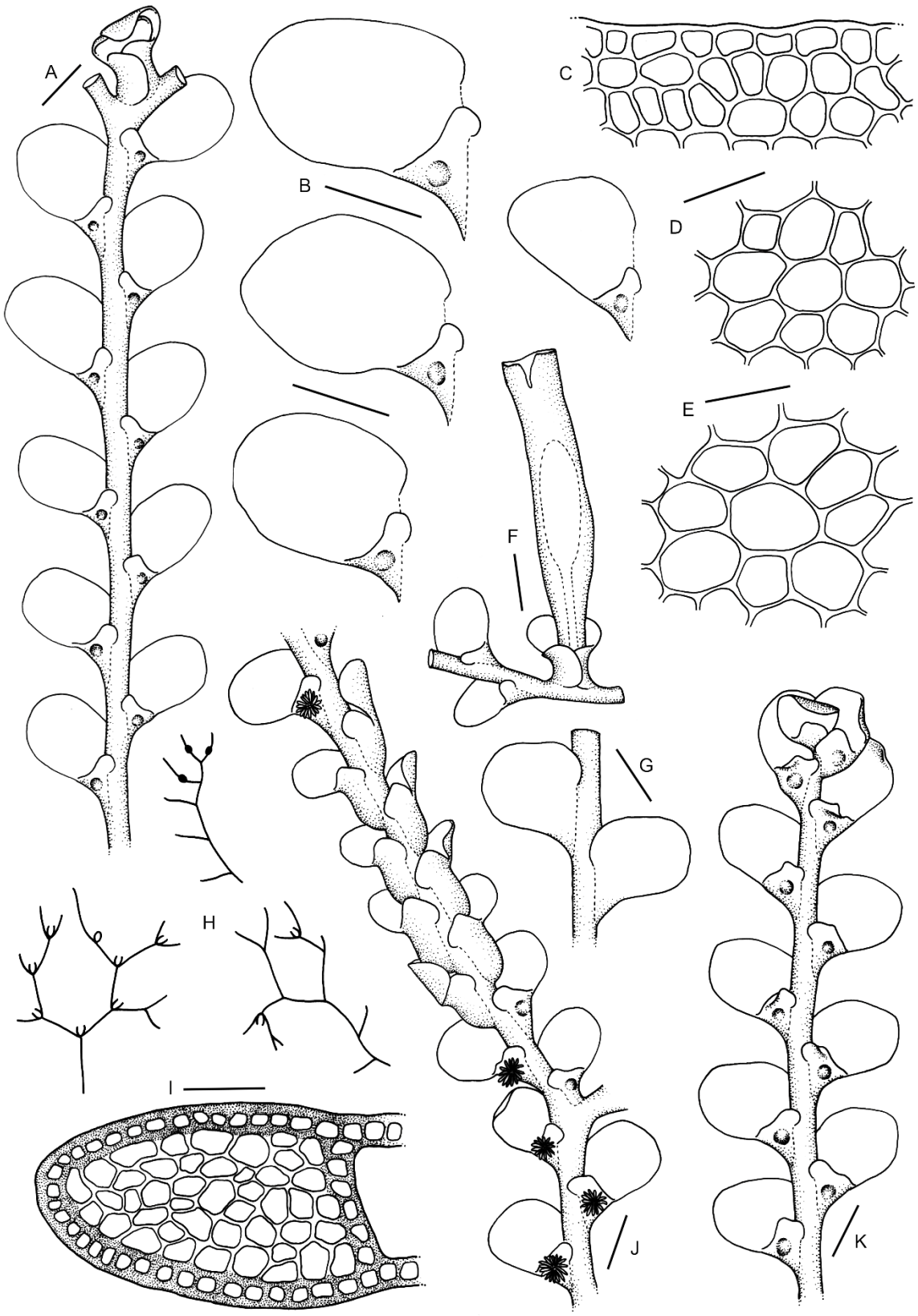

Figure 50. *Radula underwoodii*. A. Habit with gynoecia. B. Leaves. C. Marginal leaf cells. D. Median leaf cells. E. Basal leaf cells. F. Habit with perianth. G. Habit in dorsal view. H. Cladograph of plants (black dots = androecia, white dots = gynoecia with perianth, U = gynoecia without perianth). I. Cross section of stem. J. Habit with androecia. K. Habit (A, B, F, G, J, K = 500 µm, C-E = 25 µm, I = 50 µm; All from the holotype).

spreading, strongly distant, convex, oblong-ovate, 1–1.2 mm long, 0.7–0.8 mm wide, dorsal base rounded, covering ca. 1/3 the stem, dorsal margin rounded, ventral margin straight, apex rounded to obtuse, margin plane, entire; marginal cells subquadrate to subrectangular, 10–15 × 8–10 μm, median cells isodiametric to elongate, 15–20 × 10–15 μm, basal cells elongate, 20–25 × 12–15 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate to subrectangular, 0.3–0.7 mm long, 0.2–0.4 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area, insertion 2–3× the base length, insertion line straight to slightly curved, base plane, rounded, covering up to 1/3 the stem, free margin plane, almost straight to rounded, apex incurved, rarely plane, rounded, distal margin incurved, straight, keel straight to slightly concave, spreading at angles of 45–55º with the stem, 160–180º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* brown, scanty to numerous, present on a few or numerous lobules. *Androecia* intercalary on long branches, with 3–6 pairs of bracts, 1–1.2 mm wide; bracts distant, ovate, 0.8–1 mm long, 0.3–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong-ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts ovate, 0.6–0.7 mm long, 0.3–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobules ovate, ca. 1/2 the lobe length, apex rounded. *Perianth* erect, subcylindrical, ca. 3 mm long, ca. 0.3 mm wide at base, ca. 0.5 mm wide at middle, ca. 0.5 mm wide at mouth, mouth entire, plane; perianth wall unistratose. *Calyptra*, *Sporophyte* and *Vegetative reproduction* not observed.

Distribution and habit. Scattered in the West Indies: Bermuda, Cuba, Jamaica, Puerto Rico (new record) and Trinidad and Tobago (Figure 51). The species usually grows on wet rock, rarely on soil, in montane forests, at 500–3000 m.

Additional specimens examined. BERMUDA. Harrington House, on rock at mouth of cave, February 10 – March 9, 1908, *Brown 554*, as *Radula pallens* (paratype YU-169894).

CUBA. GUANTÁNAMO: Yunque, Mt. Baracoa, March, 1903, *Underwood & Earle s.n.* (paratype YU-169895, YU-169896, YU-169897).

JAMAICA. Without locality, 1885, *unknown collector*, as *R. pallens*, ex hb. Person in BM (paratype YU-169889). Hollymount, 19-20 September 1906, *Underwood 3445* (paratype YU-169893). Doll Wood, near Silver Hill Gap, on wet rock , 3000 m, 16 April 1903, *Maxon 1171* (paratype YU-169891). **PORTLAND:** Blue Mountains, B1 unweit nordlich Hardwar Gap,

feuchter Hang and der Straβe, 18°05,2'N, 76°43,3'W, 3 December 2013, *Schäfer-Verwimp 34963* (MO).

PUERTO RICO. MARICAO: On steep moist bank along new trail, CCC #1, from Maricao-to-Maricao insular forest, south, 20 December 1939, *Pagán 5547* (JE).

TRINIDAD AND TOBAGO. Heights of Aripo, 16 March 1921, *Britton 2394* (FH).

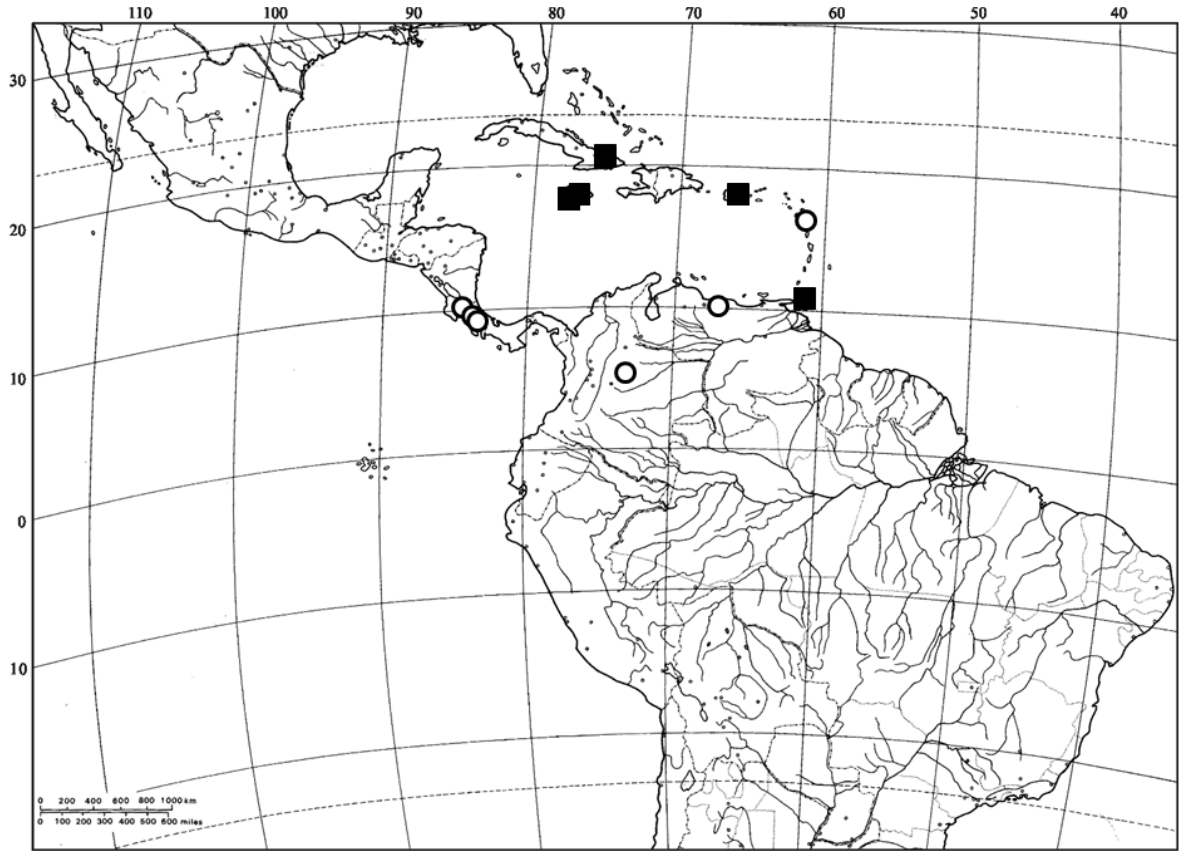

Figure 51. Distribution of *Radula underwoodii* (black square) and *R. venezuelensis* (white circle).

Characteristic of *Radula underwoodii* (subg. *Volutoradula*?) are the long (up to 6 cm), dichotomously branched, olive-green plants with brown, rigid stemsd and obliquely spreading, very distant, ovate to oblong-ovate leaf lobes. The angle of the lobule keel with the ventral leaf lobe margin, at its junction with the lobule, is the broadest (up to 180º) among Neotropical Radulaceae.

Radula underwoodii is rather similar to the common Neotropical *R. episcia*, especially in the shape of the lobule; for differences see under the latter species.

50. Radula venezuelensis K.Yamada, Misc. Bryol. Lichenol. 9: 122. 1982. Type: Venezuela, Aragua, Maracay, Parque Nacional Henry Pittier, Regrecava de Diables,

arbre de forêt humide, 1630 m, 13 June 1978, *M. Onraedt 78/V/4553* (holotype, BR-5040245483737; isotype, NICH-400978!).

Fig. 52

Dioicous. *Plants* 1.3–3 mm wide, to ca. 2 cm long, yellowish brown in herbarium, regularly to irregularly pinnate, sometimes dichotomous above in female plants by fertile paired innovation. *Branches Radula*-type. *Stems* 200–300 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, contiguous to imbricate, convex, strongly falcate-ovate, 1.2–1.8 mm long, 0.7–1.2 mm wide, dorsal base rounded, overlapping the stem, entire or with 1–2 short lacinia, dorsal margin rounded, ventral margin rounded, apex obtuse to subacute, margins plane to strongly recurved, rarely convolute ventrally, crenulate to irregularly crenulate; marginal cells subquadrate, 10–15 × 8–15 µm, median cells isodiametric to elongated, 20–25 × 15–20 µm, basal cells elongate, 25–30 × 20–25 µm, leaf cells mammillose on ventral and dorsal surface, cell walls thin, trigones large, intermediate thickening lacking, cuticle smooth; oil bodies 1–2 per cell, spherical, light yellow, slightly granular, ca. 10 µm in diam. *Lobules* distant, subrectangular, 0.7–0.8 mm long, 0.3–0.5 mm wide, ca. 1/3 the lobe length, strongly inflated along the keel, insertion 1–2× the base length, insertion line slightly curved, base plane, rounded, covering up to 1/3 the stem, free margin plane, almost straight, apex plane, rounded, distal almost straigh, covered by the inflated keel, keel straight to convex, spreading at 50–60º with the stem, 90–110º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* and *Androecia* not observed. *Gynoecia* on main stem or on long branches, with 1–2 innovations; bracts oblong-ovate, 1.7–1.8 mm long, 0.9–1 mm wide, apex rounded, margin plane to usually recurved, crenulate, lobules oblong-ovate, 1/3–1/2 of lobe length, apex rounded, keel concave. *Perianth* erect, trumpet-shaped, 2.1–6 mm long, 0.5–0.6 mm wide at base, 0.8–1 mm wide at middle, 0.9–1.3 mm at apex, mouth entire, plane; perianth wall 2–4-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 4–6-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 2-layered at the base, 1 cell layer thick above. *Capsule* (young) ca. 2.4 mm long, ca. 0.5 mm wide. *Elaters* 200–300 µm long, rough. *Spores* 31.48–37.03 µm in diam.,

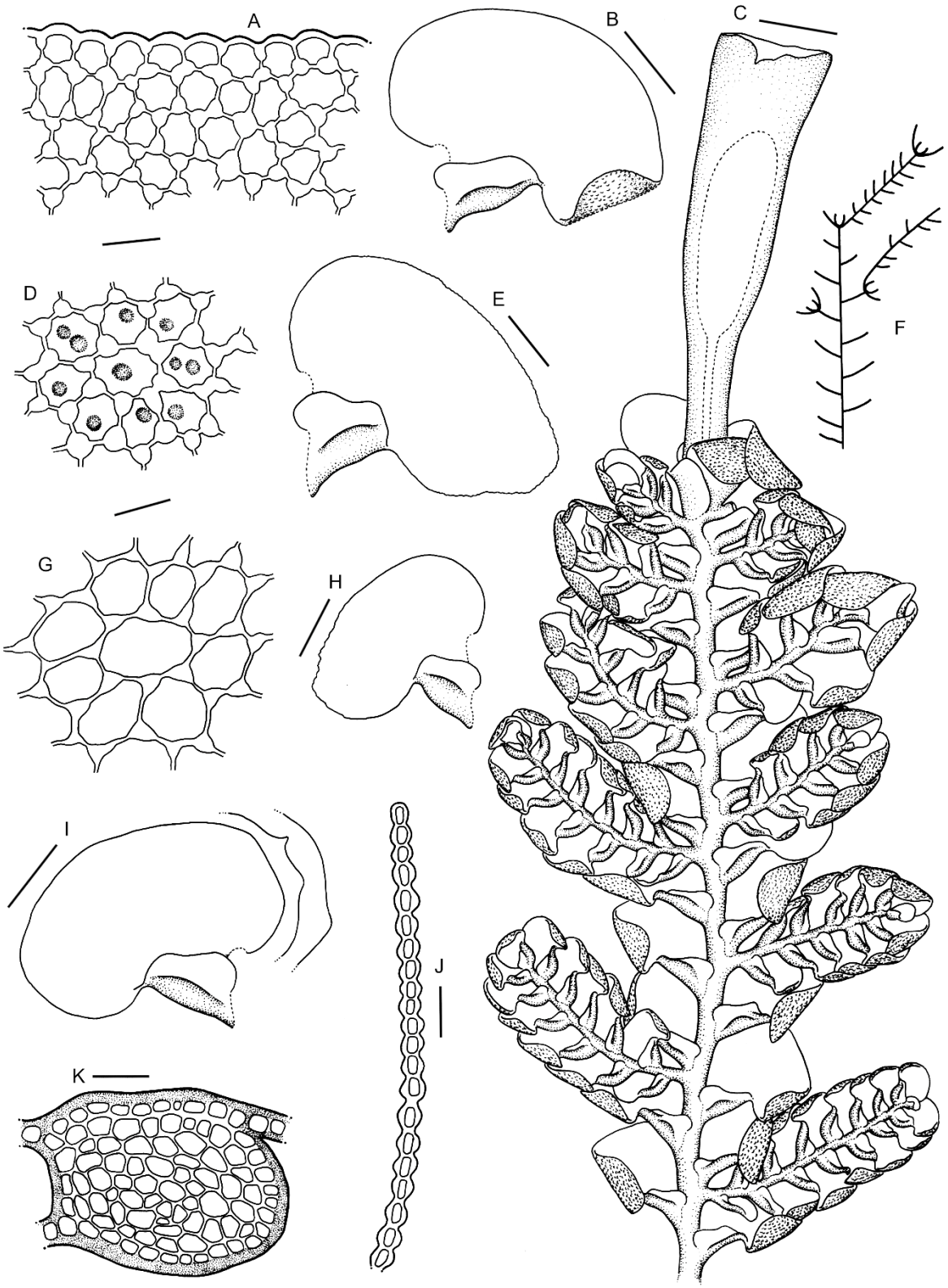

Figure 52. *Radula venezuelensis*. A. Marginal leaf cells. B. Leaf. C. Habit with perianth. D. Median leaf cells. E. Leaf. F. Cladograph of plants (U = gynoecia without perianth). G. Basal leaf cells. H-I. Leaf. J. Cross section of leaf. K. Cross section of stem (A, D, G = 25 µm, B, I= 500 µm, C= 1000 µm, H, E = 250 µm, J, K = 50 µm; A, D-H from the isotype, B, C, I, J, K from *Maxon & Harvey 8455*).

espiculate, spine composed by nanogranules. *Sporophyte* and *Vegetative reproduction* not observed.

Distribution and habit. *Radula venezuelensis* was only knonw from the type locality from Venezuela, but is newly registered here from Costa Rica, Guadeloupe and Colombia (Figure 51). The species occurs on tree trunks in lower and upper montane forest, at 1500–2600 m.

Additional specimens examined. COSTA RICA. CARTAGO: Cordillera Talamanca, 2600 m, 3 January 2000, *Holz & Schäfer-Verwimp CR 00-0124* (GOET). **HEREDIA:** Along the cart-road from Vara Blanca (between Poás and Barba Volcanoes) to La Concordia, on tree trunk, 1600-1950 m, 23 July 1923, *Maxon & Harvey 8455* (JE). **PUNTARENAS:** Vicinity of La Palma, on the road to La Hondura, on tree trunk, 1500-1700 m, 17-18 July 1923, *Maxon & Harvey 7870* (JE).

GUADELOUPE. Without locality, s.d., *l'Herminier s.n.* (FH-00965707).

VENEZUELA. ARAGUA: The type of *Radula venezuelensis* (NICH).

COLOMBIA. BOYACÁ: road Sogamoso to Pajarito, in most forest along Río Cusiana, 2000 m, epiphytic, 4 February 1959, *Bischler 1792, 1795* (COL, GOET).

Radula venezuelensis (subg. *Volutoradula*?) is recognized by the leaf lobes usually strongly falcate-ovate with apex obtuse to subacute, margins plane to strongly recurved, rarely convolute, crenulate, and leaf cells with large, bulging trigones, mammillose on the ventral and dorsal leaf surface (more clearly visible on the dorsal leaf surface due to the recurved margins).

The type of *R. venezuelensis* has plane leaf margins while specimens from Costa Rica and Guadeloupe have leaves with strongly recurved to convolute leaf margins. A collection from Costa Rica (*Maxon & Harvey 7870*) had unusually long perianths, reaching to 6 mm long.

Radula venezuelensi resembles *R. involvens* and *R. subinflata*; differences are given under the latter species.

51. Radula voluta Gottsche, Lindenb. & Nees var. **voluta**, Syn. Hepat. 255. 1845. Type: Ireland, Kings Co., "in Hibernia, prope Dunkerron," Taylor in hb. Gottsche (lectotype, W, selected by Grolle, 2001: 66; isolectotypes, PC-Mont.!, G-00281315!).

Radula appendiculata Steph., in Herzorg, Biblioth. Bot. 87: 231. 1916. Type: Bolivia, Comarapa, 2600 m, *T. C. J. Herzog 4321* (lectotype, G-00043909, selected by Castle, 1965: 342). Corani Valley, *T. C. J. Herzog 4746* (syntype, G-00121236!), syn. fide Castle (1965, under *Radula ramulina*).

Radula boliviana Steph., in Herzog, Biblioth. Bot. 87: 231. 1916. Type: Bolivia, Corani Valley, 2600 m, *T. C. J. Herzog 5079* (lectotype, G-00043913!, selected by Castle, 1965: 342). Locotal, 1800 m (syntype, G, not found). Pocona, 2800 m (syntype, G, not found), syn. fide Castle (1965, under *Radula ramulina*).

Radula castlei Grolle, The Bryologist 73: 662. 1970. Type: Venezuela, Merida, E1 Valle nördlich Merida, Gehölz bei etwa 2600 m, *Oberwinkler & Poelt HV69-52* (holotype, JE-04003708!, c. andr.; isotype, NY), ***syn. nov.***

Radula dicksonii Castle, Rev. Bryol. Lichénol. 33: 343. 1965. Type: Dominican Republic, St. Domingo, 1814, *J. Dickson s.n.* (holotype, BM-000969254!, scanty), syn fide Yamada (2000).

Radula grandiloba Steph., in Herzorg, Biblioth. Bot. 87: 232. 1916. Type: Bolivia, Incacorral, 2200 m, *T. C. J. Herzog 5097* (lectotype, G-00043888, selected by Castle, 1956: 342; isolectotype, JE-04003664!, c. per.), syn. fide Castle (1965, under *Radula ramulina*).

Radula ramulina Taylor, London J. Bot. 5: 374. 1846. Type: Ecuador, Cayambe, on trunks of tree, "13,500 feet high," 20 October 1827, *W. Jameson s.n.* (lectotype, FH-!, c. per. + spor., **designated here**; isolectotypes, E, MANCH, NY). Pinchincha, *W. Jameson s.n.* (syntype, FH-00783497!), syn. fide Yamada & Gradstein (1991).

Radula subtropica Steph., Sp. Hepat. 4: 162. 1910. Type: Brazil, "Hab Brasilia, valde communis," *E. H. G. Ule 245* (lectotype, G-00064717!, c. per., selected by Castle, 1965: 341). Minas Gerais, Caldas, "ad margines aquaeductus," 25 August 1873, *C. Mosén s.n.* (syntype, FH-00965987!), syn. fide Castle (1965, under *Radula ramulina*).

Dioicous. *Plants* 2–3.5(–4) mm wide, to 3 cm long, yellowish-green to yellowish-brown in herbarium, regularly 1–2-pinnate, dichotomous in female plants by fertile paired innovation. *Branches Radula*-type. *Stem* 250–400 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, slightly convex, orbicular to ovate, sometimes falcate-ovate, 0.8–2 mm long, 0.6–1.7 mm wide, dorsal base rounded, auriculate, overlapping the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded, margin plane

to strongly recuved, sometimes convolute ventrally, entire; marginal cells subquadrate, 10–15 × 8–10 µm, median and basal cells isodiametric to elongate, 20–25 × 15–20 µm, cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, spherical to irregularly ellipsoidal, brownish, slightly granular, 14–22 × 11–12 µm. *Lobules* contiguous to imbricate, subquadrate to suborbicular, 0.5–1.3 mm long, 0.6–1.2 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, insertion 1/3–1/2 the base length, insertion line circinate, base plane, rounded, fully overlapping, extending beyond the stem, strongly auriculate, the auricle circinately coiled, extending downward maximally to the keel, free margin plane, straight to rounded, apex plane, rounded to obtuse, distal margin straight to sinuose, keel straight, spreading at angles of 55–75º with the stem, 130–160º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* terminal to intercalary on short branches, with 3–8 pairs of bracts, 0.7–1.2 mm wide; bracts contiguous to imbricate, oblong-ovate, 0.7–1 mm long, 0.25–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong-ovate, ca. 3/4 of lobe length, base rounded, free margin almost straight, apex obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 1–1.5 mm long, 0.4–0.7 mm wide, apex rounded, margin recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded. *Perianth* erect, subcylindrical to trumpet-shaped, 3.5–4.5 mm long, 0.5–0.8 mm wide at base, 1–1.5 mm wide at middle, 1–1.7 mm wide at apex, mouth entire to irregularly crenulate, plane to convolute ventrally; perianth wall 2–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–5-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* 3.6–7 mm long. *Capsule* 1–2 mm long, 0.7–0.8 mm wide, valves 2.2–2.6 mm long, 0.5–0.8 mm wide at middle, outer layer cells subquadrate to subrectangular, simple nodular thickenings reddish-brown, on longitudinal wall of every second wall, inner layer cells long-rectangular to polymorphous, thickening absent. *Elaters* 200–500 µm long, rough. *Spores* 24.07–38.88 µm in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by occasionaly fragmentation of leaf lobes.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Tropical and subtropical America (from southeastern USA to Chile) (Figure 53), Africa and western Europe. In tropical South America, *Radula voluta* is very common in montane forests of the Andes and the Atlantic Coastal Region. This species is uncommon in Central America and very rare in West Indies, with only one record from the Dominican Republic. *Radula voluta* grows usually on bark, occasionally on dead trees, rock or soil, in montane forests up to the páramo, at 650–4000 m. The species growns prostrate or pendent, forming loose to dense mats.

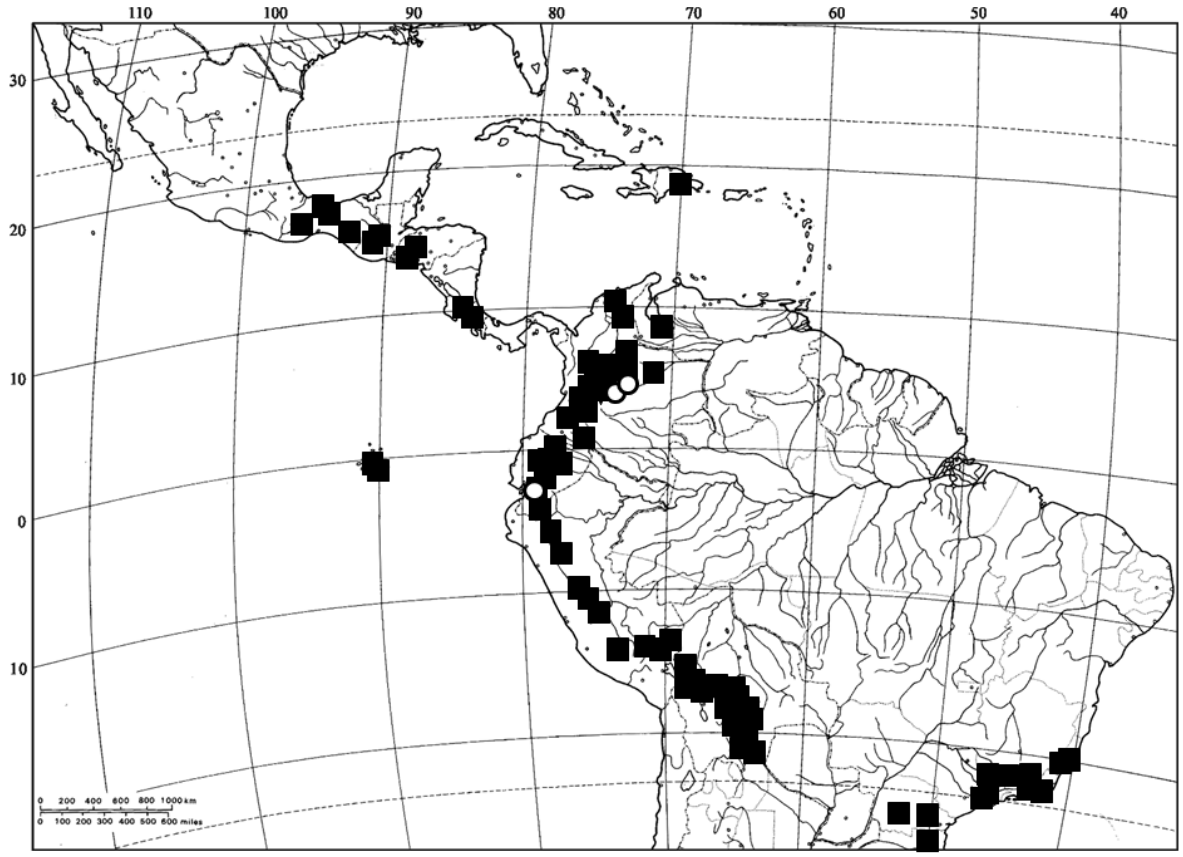

Figure 53. Distribution of *Radula voluta* var. *voluta* (black square) and *R. voluta* var. *microphylla* (white circle).

Additional specimens examined. MEXICO. CHIAPAS: Tenejapa, evergreen Cloud Forest, growing on trunk, 2740 m, 19 May 1988, *Breedlove 68485* (MO). **OAXACA:** Str. Oaxaca-Tuxtepec, bei km 96, im epiphytenreichen Bergwald, am Borke, 2700 m, 2 October 1966, *Düll A101* (JE). **VERACRUZ:** am Faβ Porto de Aire, ca. 10 km vor Acultzingo, Bergnebelwald, 2300 m, 21 August 1975, *Düll 2/237* (JE). 3 km W Villa Juarez im Bergwald, 9 September 1966, *R. Düll A110* (JE). Near Jalapa, 25 June 1908, *Pringle 15331* (FH).

GUATEMALA. ALTA VERA PAZ: Cobán, in arboribus, 1350 m, December 1906, *Türckheim s.n.* (FH). **HUEHUETENANGO:** Cordillera Los Cuchumatanes, northwest portion of

Guatemala, noth of San Mateo Ixtatan, mixed hardwood forest with pines, on hardwood trunk in dense forest, 15°51'45,1"N, 91°30'52,1"W, 9200 feet, 11 April 2007, *Laeger 3704* (MO).

HONDURAS. LEMPIRA: Montana de Celaque, trail from camp Don Tomas to first ridge, on tree trunk, 2350 m, 13 November 1991, *Allen 11283* (MO).

EL SALVADOR. Trail up to the top of Monte Cristo Montane Cloud Forest, on vine, 2478 m, 26 October 1977, *Watson ES-0032* (MO).

COSTA RICA. Treeless windy mountains top, March 1963, *James s.n.* (MO). Forest du Rancho Flores, 2043 m, 22 February 1890, *Tonduz 2147a* (JE). **ALAJUELA:** vicinity of Fraijanes, 1500-1700 m, 12-13 February 1926, *Standley & Torres 47496* (JE). **CARTAGO:** Orori, P.N. Tapantí-Macizo de La Muerte, Paramo Buenavista, epífito sobre ramas finas, expuesto, 09°36'05"N, 83°45'48"W, 3300 m, 26 February 1996, *Dauphin 2229* (MO).

DOMINICAN REPUBLIC. ST. DOMINGO: Paravia, Cordillera Central, on roadside bank, 2320 m, 6 December 1979, *Smith 10339* (MO).

VENEZUELA. MÉRIDA: The Type of *Radula castlei* (JE).

COLOMBIA. ANTIOQUIA: La Ceja, 5.5 km OE de La Ceja, carretera a La Unión, bosque montano secundário, 06°00'N, 75°20'W, 2420 m, 21 June 1985, *Churchill 12853B* (MO). **BOGOTÁ:** Tequendama, 2200-2400 m, 1929, *Troll 2120* (JE). Boquerón, Vorpostenstamme na der Waldgrenze, 3200 m, 1929, *Troll 2198* (JE). **CUNDINAMARCA:** Páramo de Palacio, Cabeceiras Rio Negro, km 19 de la carretera, 3370 m, *Cleef 5150* (JE). Guasca, March 1932, *Pérez 2211* (JE). Sabana de Bogotá, páramo de Cruz Verde, on twigs in thickets, 2700 m, May 1951, *Schultes 12162, 12184* (FH). Subachoque, el Tablazo, north of Bogota, 05°00'N, 74°00'W, 3500 m, November 1988, *Allen 9994* (MO). **PUTUMAYO:** Colón, quebrada Siguichica, sobre tronco, 2400 m, 28 March 1991, *Ramírez 3272* (MO). **RISARALDA:** Santa Rosa de Cabal, West slope central cordillera, *Polylepsis* dwarf forest, epiphyte, 4°49' N, 75°28' W, 4130 m, 26 August 1990, *Wolf 1604* (GOET). Santa Rosa de Cabal, Valle de la Quebrada Betánia, Fda. La Sierra, Bosque alto-andino, 3755 m, 23 January 1980, *van Reenen & Cleef 913* (GOET).

ECUADOR. El Altar, Paramo region, 4000 m, 1903, *Meyer 4205* (JE). **AZUAY:** 30 km W of Cuenca, N-facing slope of EW valley to the N of Lake Toredora, epiphytic at base of *Polylepsis*, 3600-4000 m, 15-18 September 1995, *Price 36* (MO). **CARCHI:** road Tulcan to Madonado, páramo El Angel, east of the pass near the Lagunas, 30 km from Tulcan, mossy dwarf forest of Polylepsis-Compositae, 3900 m, 5-6 October 1988, *Gradstein et al. 6854, 6852, 6867* (GOET). **GALÁPAGOS ISLAND:** Pinta, S-exposed slope of the highest volcano, moist zone, dense, old, *Zanthoxylum* woodland, mats on rotting bark, 550-600 m, 8-10 July 1976,

Gradstein et al. 10166 (GOET). Santa Cruz, betweem Puntudo and Mt. Crocker, Pedulous on dead *Scalesia pedunculata* Hook. f. stem, 650-750 m, 14 April 1976, *Gradstein & Weber H15* (GOET). **NAPO:** Papallacta-pass zwischen Quito und Baeza, Res. Ecologica Cayambe-Coca, Paramo de La Virgen nordöstlich der Passhöhe, na Sträuchern, 4000 m, 15 August 2004, *Schäfer-Verwimp et al. 24270* (MO). **TUNGURAGUA:** Upper Pastaza region, Río Machay, trail from the mouth of the river to Cascade de Tucan, moist lower montane forest, on tree trunk, 1500-1900 m, 24 July 2003, *Gradstein 10166* (GOET). **ZAMORA-CHINCHIPE:** Reserva Biológica San Francisco, 30 km from Loja and Zamora, at northern limit of the Parque Nacional de Podocarpus, montane tropical rainforest, on tree trunk, 3°58'18" S, 79°04'44" W, 1800-3150 m, 19 October 2001, *Nöske 1790* (GOET). Along road between Zamora and Romerillos Alto, 23.9 km E of Río Bombuscaro bridge in Zamora, 11.1 km E of Pituca, on ground, 04°13'21"S, 78°56'24"W, 1457 m, *Croat 91584* (MO).

PERU. AMAZONAS: Bongará, Zwischen Ingenio und Pomacocha, 1 September 1973, *Hegewald 7113* (MO). Chachapoyas, Calla Calla zwischen Balsas und Leimebamba, 3100 m, 31 August 1973, *Hegewald 6916* (MO). **AYACUCHO:** Huanta, 25 km von paβ Tapuna in Richtung Ayna, 5 July 1977, *Hegewald 9026, 9027, 9006* (MO). **CUZCO:** Urubamba, Muchu Picchu, Felsritzen der Ruinen, 2400 m, 6 May 1973, *Hegewald 5580* (MO). Urubamba, Aguas calientes bei Muchu Picchu, Fels, 2100 m, 26 June 1977, *Hegewald 8739* (MO). Quispicanchis, between Marcapata and Achubamba, on moist rock in wet forest in "Ceja de Selva" zone, 2800 m, 13 September 1984, *Inoue 873* (JE, MO). **HUANUCO:** vicinity of Mito, 20 km N of Huanuco, 9000 feet, April 1923, *Bryan 217* (MO). **JUNÍN:** Huancayo, 56 km von Huancayo in Richtung Parihuanca, 14 km vor Chilifruta, Rohhumus, 3000 m, 8 July 1977, *Hegewald 9225* (MO). Schunke hacienda, above San Ramón, dense forest, 1300-1700 m, August-October 1923, *Schunke A126* (JE). **LA LIBERDAD:** Bolivar, Ucuncha, southwestern side of Cerro Fila de Andosa, on top of karst boulder, 07°07'14"S, 77°49'23"W, 3900 m, 14 November 2013, *Bussmann et al. 18333* (MO). **PASCO:** Oxapampa, Piña Flor 12 km vor Oxapampa aus der Richtung von San Ramon, Baum, 1750 m, 11 June 1977, *Hegewald 8416* (MO). Oxapampa, 5 km SE of Oxapampa, advanced second growth with a few primary forest treesremaing in the stand, epiphytic on branch, 1850 m, 9 April 1983, *Smith C-260A* (MO).

BRAZIL. ESPÍRITO SANTO: Alfredo Chaves, São Bento da Ucrânia, 900–1000 m, 19 October 2000, *Hatschbach et al. 71460* (SP). Castelo, Parque Estadual Forno Grande, Mata Atlântica com afloramentos rochosos, sobre tronco vivo, 20°30'56"S, 41°05'31"W, 1380 m, 1 October 2016, *Peralta et al. 19357* (SP). Domingos Martins, Parque Estadual Pedra Azul, Trilha Pedra das Flores, Mata Atlântica, corticícola, 5 August 2009, *Penha 533*, 542 (ALCB).

MINAS GERAIS: Itamonte, Parque Nacional do Itatiaia, sobre tronco vivo, 22°22'07"S, 44°44'43"W, 2000 m, 8 July 2015, *Peralta et al. 16841* (SP). Caldas, Pocinhos do Rio Verde, bergwald am waserfall A. Moreiro, epiphytisch, 1050 m, *Schäefer-Verwimp & Verwimp 7049* (SP), Lima Duarte, Parque Estadual do Ibitipoca, sobre tronco de arbusto na mata, 1550 m, 9 August 1993, *Yano et al. 20379* (SP). **PARANÁ:** Guaraniçu, BR 277, km 321, 14 March 1976, *Vital 5777* (SP). Imbituva, margem do rio Ribeira, sobre tronco vivo na mata ciliar, 19 April 1983, *Yano & Pirani* 6380 (SP). **RIO GRANDE DO SUL:** Esmeralda, Estação Ecologica Aracuri, 30 June 1983, *Bueno 3129* (ICN). Caxias do Sul, sobre troncos na beira da mata, 780 m, 12 April 2006, *Bordin et al. 461* (MO). Barracão, Parque Florestal Espigão Alto, sobre tronco de Araucária, 21 June 1996, *Lemos-Michel 3580* (SP). **RIO DE JANEIRO:** Nova Friburgo, 05 May 1957, *Sehnem 7153* (ICN). Paratí, Serra entre Cunha e Paratí, 1963, *Hell 489* (JE). **SANTA CATARINA:** Urubici, cachoeira do Avenal, 28°02'33"S, 49°37'1"W, 1481 m, 14 November 2003, *Costa et al. 4289, 4288* (RB). Jaraguá do Sul, 450 m, 3 August 1937, *Carl 122* (JE). Curitibanos, sobre tronco ao longo de um riacho, 27°17' S, 50°27' W, 22 July 1980, *Vital 9438* (SP). **SÃO PAULO:** S. Francisco dos Campos, *Loefgren 33146* (JE). Campos do Jordão, Serra da Mantiqueira, 1700 m, 19 September 1923, *Hoehne 623* (JE). Campo Limpo, Jundiaí, 1918, *Wacket & Decker 776/b* (JE).

BOLIVIA. Without locality, May 1911, *Herzog 4613* (JE). Casana im Tipnamital, 1400 m, 1922-1923, *Buchtien 254* (JE). **CHUQUISACA:** Belisario Boeto, al lado de Río Alisos, 22 km Villa Serrano por Nuevo Mundo, bosque montano de Tucumano-Boliviano, sobre base de árbol, 19°00'00"S, 64°18'50"W, 2300 m, 19 July 2004, *Churchill et al. 23064* (MO). Hernando Siles, Cañón Lacayotal, area de transición seco a húmedo, bosque premontano de Tucumano-Boliviano, sobre corteza, 20°19'21"S, 64°02'00"W, 1450 m, 25 December 2004, *Lozano et al. 1727* (MO). **COCHABAMBA:** Ayopaya, Cocapata, comunidad de Altamachi, Ceja de bosque yungueño, sobre corteza, 16°55'40"S, 66°19'35"W, 3534 m, 4 April 2012, *Linneo & Jaimes 2646, 2768* (MO); Ibid., cresce em suelo, 16°56'13"S, 66°20'52"W, 3584 m, 5 April 2012, *Linneo & Jaimes 2789C* (MO). Independencia, al frente de la comunidad de Sivingani, Cerro Isapo arriba de Zapanana, bosque montano nublado de yungas, 16°57'30"S, 66°52'12"W, 18 April 2010, *Linneo & Salinas 2026* (MO). Independencia, comunidad de Chuchuani, vagetación yungueña em transición a puneña, 16°56'04"S, 66°50'00"W, 3500 m, 23 April 2010, *Linneo 2267* (MO). Independencia, Sivingani, alredor del caminho y bordes del rio, vegetación ribereña, sobre corteza, 16°56'59"S, 66°52'01"W, 2880 m, 22 April 2010, *Linneo & Salinas 2183A* (MO). Carrasco. Serranía de Siberia, camino Pojo-Churo, bosque montano de Yungas, sobre tronco de arbolito, 17°45'50"S, 64°48'53"W, 2570 m, 14 December

2009, *Churchill et al. 24959, 24956* (MO). Carrasco, Serranía de Siberia, 11 km oeste de El Churo, bosque montano nublado, sobre tronco de árbol em la sombra, 17°45'S, 64°48'W, 2500 m, 20 May 2003, *Churchill et al. 22567* (MO). Carrasco, 9.4 km oeste de El Churo, bosque montano nublado de Serranias de Siberia, perturbado, sobre tronco de arbolito, 17°46'S, 64°48'W, 2580 m, 9 September 2002, *Churchill et al. 22004* (MO). Chapare, Villa Tunari, bosque montano bajo, sobre tronco em decomposición em la sombra, 17°07'S, 65°42'W, 1140 m, 4 July 2002, *Churchill & del Ortiz-Gentry 21764* (MO). **LA PAZ:** Franz Tamayo, Area Natural de Manejo Integrado Apolobamba, Piara hacia Pelechuco, bosque de Yungas montano superior pluvial transicionando a ceja de monte, epífita, 14°47'48"S, 69°00'52"W, 2700-2900 m, 17 April 2006, *Fuentes et al. 10191* (MO). Franz Tamayo, Parque Nacional Madidi, Queara, Tolca Cocha, fragmento relicto del bosque de yungas, sobre tronco, 14°41'13"S, 69°05'17"W, 4037 m, 12 April 2007, *Fuentes 12472* (MO). Nor Yungas, Parque Nacional Cotapata, Laguna Chaco Khota, Sanjapamapa a 4.5 km al NO de Chucura desviando del Choro, Páramo yungueño, sobre roca, 16°14'39"S, 68°02'26"W, 4020 m, 14 May 2005, *Aldana 164* (MO). Nor Yungas, Parque Nacional Cotapata, Estación Biológica Tunquini, caminho al palmar, epiphytisch, 16°11'42" S, 67°51'31" W, 2000 m, 21 August 2001, *Drehwald & Drehwald 10527* (GOET). **SANTA CRUZ:** Manoel Maria Caballero, Serranía de Siberia, cerca El Empalme, caminho al San Mateo, bosque montano yungas, sobre tronco de árbol inclinado, 17°49'20"S, 64°42'45"W, 2440 m, 13 December 2009, *Churchill et al. 24916* (MO). Manoel Maria Caballero, Serranía de Siberia, Lagunas cerca de caminho, bosque montano nublado muy humedo, sobre ramas, poco sol, 17°50'S, 64°45'W, 2900 m, 10 April 2003, *Churchill et al. 22373* (MO). Manoel Maria Caballero, 11 km este de Siberia, 1 km por San Mateo, em caminho nuevo, bosque montano nublado muy humedo, sobre ramas, 17°50'S, 64°41'W, 2540 m, 8 September 2002, *Churchill et al. 21894* (MO). Manoel Maria Caballero, 15 km este de Siberia por Comarapa, bosque montano nublado de Serranias de Siberia, muy humedo, sobre arbusto, 17°49'S, 64°40'W, 2500 m, 9 September 2002, *Churchill et al. 21957* (MO). Manoel Maria Caballero, Parque Nacional Amboró, Cerro Bravo, juntas del Río Alizar y Amparo, bosque nublado, epífita, 17°57'S, 64°24'W, 2000 m, 7 June 1992, *Vargas et al. 1483-E* (MO). Florida, Quirusillas, a redores de la Laguna Esmeralda, bosque Tucumano-Boliviano, sobre árbol, 18°21'00"S, 63°55'25"W, 1650 m, 20 November 2008, *Inturias & Carreño 126* (MO). Florida, Cerro Herrandura, 5 km este-nordest de Bermejo, montano abierto secundário, con hierbas, sobre roca em suelo, 18°07'S, 63°36'W, 1400 m, 23 March 2002, *Churchill et al. 21329* (MO). Florida, entre 21-23 km nordeste de Mairana, Area Natural de Manejo Integrado Amboró, bosque nublado de montano, yuñgas, 18°03'32"S, 63°54'33"W, 2100-2300 m, 25

Agosto 2005, *Churchill et al. 23928* (MO). Vallegrande, Abra, bosque montano de Tucumano-Boliviano, epífita, 18°33’30”S, 63°46’44”W, 2150 m, 30 July 2011, *Inturias et al. 848, 892, 908, 991, 1007* (MO). Vallegrande, Sauhintal, bosque montano de Tucumano-Boliviano, sobre solo y roca, 18°33’30”S, 63°46’44”W, 2150 m, 30 July 2011, *Inturias et al. 440* (MO). Vallegrande, caminho de Loma Larga a Cerro Bacón, bosque Tucumano-Boliviano, com neblina, epifita, 18°50’48”S, 63°51’32”W, 1900 m, 7 April 2011, *Inturias et al. 528, 529* (MO). Vallegrande, San Lorenzo, bosque montano Tucumano-Boliviano, com suelo com algunas rocas, epífita, 18°40’36”S, 63°55’01”W, 2378 m, 11 April 2011, *Inturias et al. 649* (MO). Vallegrande, entre Mosquera-Petacas, bosque chiquitano del subandino, sobre arbol, 18°42’10”S, 63°39’29”W, 720 m, 10 May 2012, *Inturias et al. 1303* (MO). Vallegrande, Las bateas, a 16 km de Vallegrande caminho hacia Masicurí, bosque boliviano-tucumano, sobre árbol, 18°34’27”S, 64°02’36”W, 2385 m, 31 January 2013, *Inturias et al. 1350* (MO). Vallegrande, caminho de Vallegrande a Loma Larga, 26 km al norte, Cerro Bocon situado a 18 km sur de Loma Larga, bosque Tucumano-Boliviano, borde de caminho, sobre corteza de árbol, 18°52’32”S, 63°51’27”W, 1770 m, 19 August 2011, *Carreño & Huanca 872* (MO). Comarapa, 2600 m, April 1911, *Herzog s.n.* (JE). **TARIJA:** Arce, Reserva Natural Alarachi, Zona Alarachi, Pendiente media del Cerro Los Tajerinas, bosque montano Tucumano-Boliviano, sobre tronco de árbol, bastante sol, 22°11’13”S, 64°36’27”W, 2200 m, 16 September 2004, *Churchill et al. 23366* (MO, GOET). Arce, Padacaya, Parque Nacional Tariquia û RNFFT, Camino al lado de Río Aliso, bosque montano de Tucumano-Boliviano, húmido, sobre roca en la sombra, 22°00’38”S, 64°35’32”W, 2300 m, 11 November 2004, *Churchill et al. 23569* (MO). Arce, Padacaya, Parque Nacional Tariquia û RNFFT, Achirales, Lomo Laja, quebrada de Arbolito, bosque premontano de Tucumano-Boliviano, húmido, sobre tronco de árbol, poco sol, 22°02’05”S, 64°31’32”W, 1720 m, 13 November 2004, *Churchill et al. 23642* (MO). O’Connor, Entre Ríos, San Mateo, pasando río Saldito, subiendo a antiguo pozo petrolero, bosque Tucumano-Boliviano, cresce em suelo, 21°40’13”S, 64°16’21”W, 1413 m, 18 April 2014, *Linneo et al. 3936, 3936B* (MO).

Radula voluta (subg. *Volutoradula*) is recognized by the rather robust plants with regularly 1–2-pinnate branching and large lobules with a voluted, circinately coiled auricle, extending across and beyond the stem and downwards to the keel (not beyond the keel as in *Cladoradula boryana*). The species resembles *R. sinuata* in the auriculate lobule base and in stem anatomy; for differences see under the latter species.

Radula castlei is a new synonym of *R. voluta*; the two species are fully identical. Castle (1969) treated *R. grandiloba* as a synonym of *R. ramulina* (= *R. voluta*), but Yamada (1987) considered *R. grandiloba* a synonym of *R sinuata*. Based on our examination of the type of *R. grandiloba*, we agree with the opinion of Castle (1969).

52. Radula voluta var. **microphylla** F.R.Oliveira-da-Silva, ***comb. nov.*** *Radula ramulina* Taylor var. *microphylla* Jans, Proc. Kon. Ned. Akad. Wetensch., C 82: 428. 1979. Type: Colombia, Meta, Páramo de Sumapaz, Hoya Sitiales, Laguna La Primavera y alredores, pedregal 300 m al NW de la laguna com um matorral de *Hypericum* sp., 3580 m, 25 January 1972, *A. M. Cleef 969* (holotype, COL; isotype, JE-04008913!, GOET!, U, F).

Fig. 54

Dioicous. *Plants* 3–4(–4.5) mm wide on main stems, to 5 cm long, yellowish-green in herbarium, regularly 2-pinnate. *Branches Radula*-type; microphyllous branches present, regularly pinnate, each branch associated with a lobule, 0.6–2 mm wide, 2–8 pairs of reduced leaf, 1-branched. *Stem* 300–500 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless to yellowish medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, plane to slightly convex, orbicular to ovate, 1.6–3 mm long, 1.1–2 mm wide, dorsal base auriculate, overlapping the stem, dorsal margin rounded, ventral margin straight to rounded, apex rounded, margin plane to strongly recurved on branches, entire; marginal cells subquadrate, 10–15(–20) × 10–15 µm, median and basal cells isodiametric to elongated, 20–25 × 15–20 µm, leaf cells mammillose on ventral and dorsal surface, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies 1 per cell, irregularly ellipsoidal, brownish, slightly granular, 13–18 × 8–12 µm. *Lobules* distant to contiguous, assymetrically subquadrate to suborbicular, 1.2–1.6 mm long, 2–1.2 mm wide, ca. 1/2 the lobe length, strongly inflated at rhizoid area, insertion ca. 1/2 the base length, insertion line circinate, base plane, rounded, fully overlapping, extending beyond the stem, strongly auriculate, the auricle circinately coiled, reaching downwards maximally to the keel, free margin plane, rounded, apex plane, rounded to slightly obtuse, distal margin straight to sinuose, keel straight to slightly convex, spreading at angles of 40–60º with the stem, 140–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brownish, numerous, present on a few lobules. *Androecia* not observed. *Gynoecia*

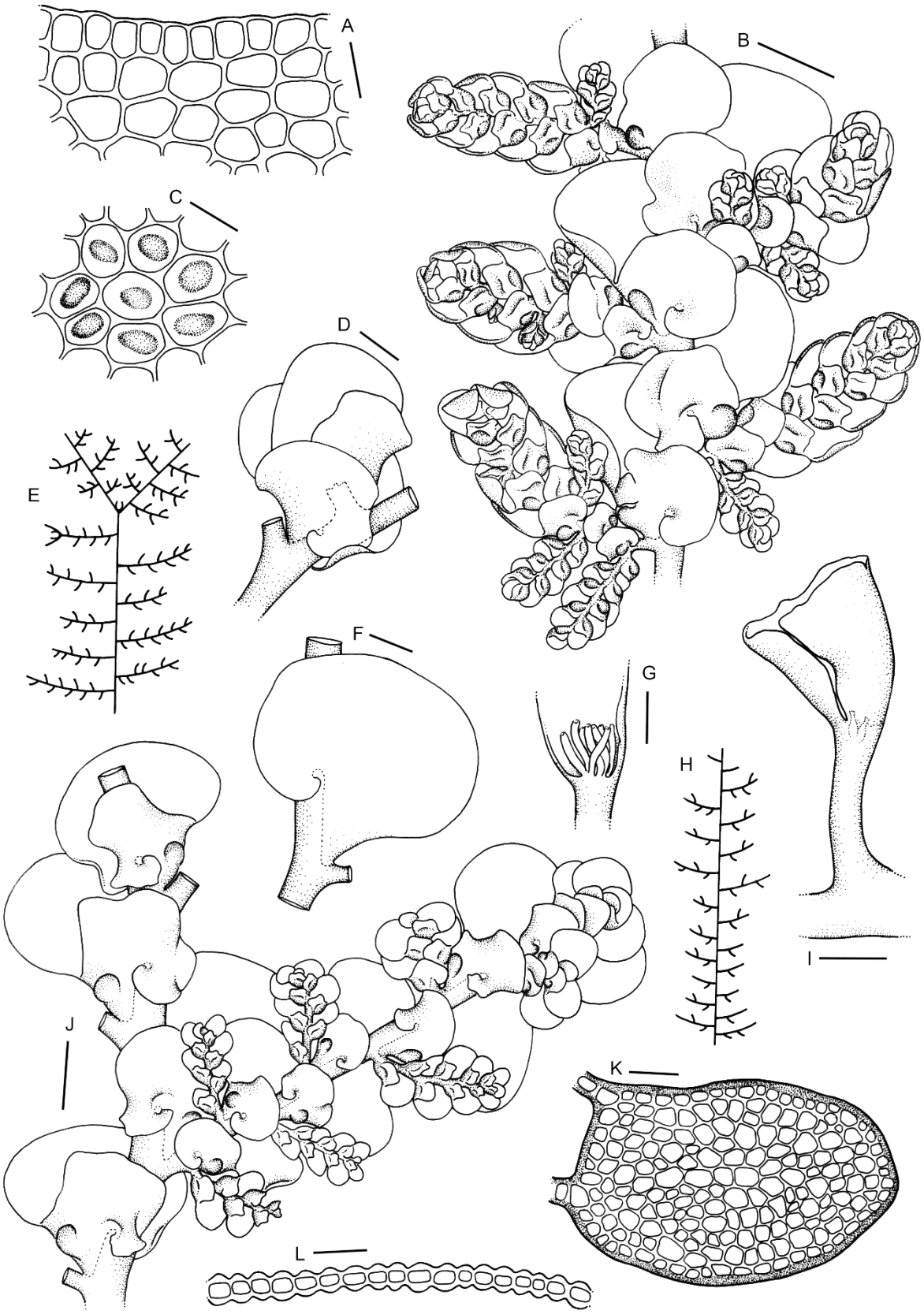

Figura 54. *Radula voluta* var. *microphylla*. A. Marginal leaf cells. B. Habit. C. Median leaf cells. D. Gynoecia. E, H. Cladograph of plants (U = gynoecia without perianth). F. Leaf, dorsal view. G. Achegonia. I. Perianth. J. Habit. K. Cross section of stem. L. Cross section of leaf (A, C = 25 µm, B, J = 1000 µm, D, F, I = 500 µm, G = 250 µm, K, L= 50 µm; All from *Price 48a*).

on long branches, with 1–2 innovations; bracts oblong-ovate, 2–2.5 mm long, 1.4–1.5 mm wide, apex rounded, margin plane to recurved, entire, lobule ovate, ca. 1/2 of lobe length, apex rounded. *Perianth* erect, stipitate, trumpet-shaped, ca. 2.2 mm long, ca. 0.5 mm wide at base, ca. 0.7 mm wide at middle, ca. 1 mm wide at apex, mouth entire, undulate; perianth wall not observed. *Calyptra* and *Sporophyte* not observed. *Vegetative reproduction* not observed.

Distribution and Ecology. *Radula voluta* var. *microphylla* is known from the páramo of Colombia (Departament of Cudinamarca and Meta) and Ecuador (Departament of Azuay) (Figure 53). This species was collected as epiphytic in subalpine forests, at 3400-4200 m.

Additional specimens examined. COLOMBIA. META: The type of *Radula voluta* var. *microphylla* (GOET, JE).

ECUADOR. AZUAY: on SSW slope of E-W ridge parallel with road through park, below peak Portada de Burn, epiphytic, 3700-4200 m, 14-29 October 1995, *Price 16* (MO). 30 km W of Cuenca, N-facing slope of EW valley to the N of Lake Toredora, epiphytic, 3600-4000 m, 15-18 September 1995, *Price 48a* (MO).

Radula voluta var. *microphylla* (subg. *Volutoradula*) differs from the typical variety by long plants (ca. 5 cm long) with microphyllous branches 3–4× smaller than the main stem, regularly pinnate, arranged very close to each other and each branch associated with a lobule. Besides, it has leaf cells slightly mammillose on ventral and dorsal surfaces (more visible on dorsal leaf surface due to the recurved margin), and perianth long and stipitate.

This species was originally described as a variety of *Radula ramulina* Taylor. However, the latter species was reduced to a synonym of *R. voluta* by Yamada & Gradstein (1991). Therefore, *Radula ramulina* var. *microphylla* has also been considered a synonym of *R. voluta* in succeding studies (*e.g.* Yamada 2000, Gradstein 2021).

53. Radula wrightii Castle, J. Hattori Bot. Lab. 21: 15. 1959. Type: Cuba, as *R. pallens* var. *brasiliensis*, Hep. Cub. Wright, in part, *C. Wright s.n.* (lectotype, YU-169877!, c. per., **designated here**; isolectotype, YU-169876!, scanty, slide).

Radula pocsii K.Yamada, J. Hattori Bot. Lab. 54: 245. 1983. Type: Cuba, Santiago, Sierra de la Gran Piedra, Bosque nublado detrás Finca Isabelica, 1100 m, 30 October 1980, *T. Pócs & Caduf 9199/AQ* (holotype, HAC; isotype NICH-400982!, c. gyn.). ***syn. nov.***

Radula schofieldiana K.Yamada, J. Hattori Bot. Lab. 82: 337. 1997. Type: Costa Rica, La Palma, Prov. San José, 1600m, March 17, 1924. *P. C. Standley 37992* (holotype, JE; isotype, NICH-432557!, c. gyn.), ***syn. nov.***

Dioicous. *Plants* 1.5–2 mm wide, to 3 cm long, green to yellowish-brown in herbarium, purely dichotomous. *Branches Radula*-type, rarely *Lejeunea*-type. *Stems* 70–140 μm in diam., with thick-walled, epidermal cells surrounding mostly smaller, thick-walled (by concave trigones) medullary cells, outer epidermal wall heavily and evenly thickened, walls brownish. *Leaf lobes* widely spreading, distant to contiguous, convex, ovate to falcate-ovate, 0.9–1.2 mm long, 0.6–0.9 mm wide, dorsal base rounded, covering 1/3–2/3 the stem, dorsal margin rounded, ventral margin rounded, apex rounded, rarely obtuse, margin plane, entire; marginal cells subquadrate, 10–12 × 8–10 μm, median and basal cells isodiametric to elongate, 20–35 × 15–20 μm, cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, intermediate thickening present, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate to subrhombic, 0.5–0.8 mm long, 0.25–0.5 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion 3–4× the base length, insertion line straight, base plane, rounded, covering 1/3–1/2 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin straight, keel straight, spreading at angles of 30–50º with the stem, 110–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* not observed. *Androecia* terminal to intercalary on long branches, with 2–8 pairs of bracts, 0.7–1.2 mm wide; bracts distant to subimbricate, ovate, 0.7–0.9 mm long, 0.3–0.4 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin almost straight, apex rounded to obtuse. *Gynoecia* on long branches, with 2 innovations; bracts ovate to oblong, 0.8–1 mm long, 0.4–0.65 mm wide, apex rounded to obtuse, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. *Perianth* erect, subcylindrical to trumpet-shaped, 1.9–2.8 mm long, 0.3–0.4 mm wide at base, 0.7–0.8 mm wide at middle, 0.9–1 mm wide at apex, mouth entire, plane to undulate; perianth wall 1–2-stratose in the lower base, unistratose from the upper base to apex; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–3-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* ca. 2.7 mm long. *Capsule* 0.7–0.9 mm long,

0.2–0.3 mm wide, valves ca. 0.9 mm long, ca. 0.2 mm wide at middle, outer layer cells subquadrate to subrectangular, confluent adnate nodular thickenings reddish-brown, on longitudinal wall of every second wall, inner layer cells long-rectangular to polymorphous, continuous faint thickening on every wall. *Elaters* and *Spores* not observed. *Vegetative reproduction* by caducous leaf lobes, sometimes producing almost completely denuded branches, the caducous leaf lobes often with regenerants on leaf margins.

Illustration. Oliveira-da-Silva *et al.* (2021, as *R. pocsii*).

Distribution and habit. Previously known from Cuba and Brazil (Oliveira-da-Silva *et al.* 2021, as *R. pocsii*). Here, its distribution is extended to Costa Rica, Haiti, Puerto Rico, and Bolivia, where it is rare (Figure 55). *Radula wrightii* grows on rock and bark in submontane and lower montane forests, in humid places, at 700–1850 m.

Additional specimens examined. COSTA RICA. The type of *Radula schofieldiana* (NICH).

CUBA. Without locality, s.d., *Wright s.n.*, as "*Radula eggersiana*", ex hb. Stephani (paratype, YU-169878). Without locality, s.d., *Wright s.n.* (MO5277269, MO5285940). **CIENDUEGOS:** Sierra del Escambray, falda norte del Pico Potrerillo, 800 m, 6 November 1968, *Bisse & Lippold 10067, 10392a* (JE). **HOLGÍN:** Moa, camino desde Moa hacia La Melba, ca. 10 km, 30 January 1969, *Lippold 012298/b* (JE). Moa, La Melba, falda este de la Sierra de Moa, pluviosa, 800-1000 m, 1968, *Bisse & Lippold 11181/b* (JE). **GUANTÁNAMO:** Monte Cristo, 700 m, 1968, *Samek et al. Cr23* (JE). Monte Cristo, 1968, *Urban 776-b* (JE). 3 km nördlich Campamento Gupeyal, 12 January 1968, *Schubert M173* (JE). 5 km ördlich Campamento Gupeyal, 23 January 1968, *Schubert M249* (JE). Imías, Sierra de Imias, 16 April 1984, *G. Arnold s.n.* (JE). **SANTIAGO DE CUBA:** Sierra Maestra, Pico Tuquino, on tree trunk, 1850 m, 1915, *Ekman 5462/b* (JE). Sierra Maestra, alto de la Maestriza, monte nublado, 1300-1400 m, 10 April 1969, *Bisse & Lippold 014466/a* (JE). Sierra Maestra, Pico Palma Mocha, monte nublado, 1300-1400 m, 18 May 1971, *Lippold 019211/b, 19214/b* (JE). Sierra Maestra, El Uvero, Loma Siberia, monte nublado, 1300 m, 29 March 1969, *Bisse & Lippold 13668/b* (JE).

HAITI. Vicinity of St. Louis du Nord, on rock and rotten stump, summit southwest of city, 30 March – 7 April 1929, *Leonard & Leonard 14425* (JE).

PUERTO RICO. LUQUILLO: Sierra de Luquillo, *Sintenis 108* (G, as syntype of *Radula portoricensis*).

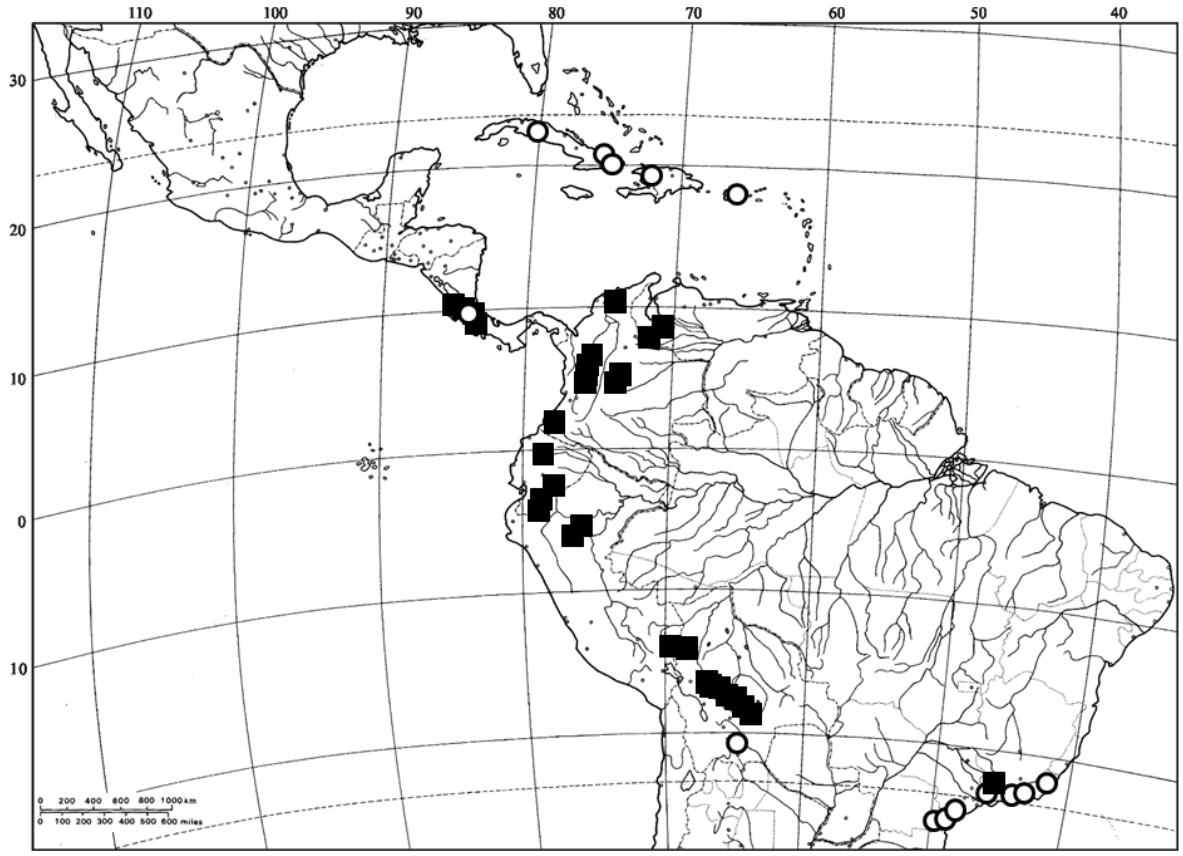

Figure 55. Distribution of *Radula wrightii* (white circle) and *R. xalapensis* (black square)

BRAZIL. **PARANÁ:** Morretes, Parque Estadual do Marumbi, trilha vermelha, sobre rocha, 25°26’55”S, 48°54’54”W, 1200 m, 22 July 2014, *Peralta et al. 15804* (SP). Morretes, Parque Estadual do Murumbi, trilha vermelha, caminho para ponta do tigre, Mata Atlântica com afloramentos rochosos, sobre rocha, 25°26’55”S, 48°54’54”W, 1200 m, 22 July 2014, *Peralta et al. 15817* (SP). **RIO DE JANEIRO:** Serra do Itatiaia, Resende, 1520 m, 20 April 1987, *Schäfer-Verwimp & Verwimp 8395* (MG, SP). Nova Friburgo, parque de furnas, rupícola, em local úmido, 650 m, 3 June 1987, *Costa et al. 257* (RB). Correias, Parque Nacional Serra dos Órgãos, sobre paredão de pedra, 22°28’40”S, 43°04’38”W, 1549 m, *Costa et al. 4158* (RB). Santa Maria Madalena, PE desengano, rancho da Mata Atlântica, trilha da pedra do desengano, 21°53’86”S, 41°54’70”W, 1700 m, *Costa et al. 4954* (RB). **RIO GRANDE DO SUL:** Gramado, 15 May 1965, *Vianna 400* (ICN). **SÃO PAULO:** Serra da Mantiqueira, Campos do Jordão, 1680 m, 14 June 1987, *Schäfer-Verwimp & Verwimp 8513* (MG). Peruíbe, Estação Ecológica de Juréia, morro Guarau, na base do tronco vivo, mata úmidado morro, 24°31’S, 47°16’W, 22 April 1989, *Yano & Melo 12648* (SP).

BOLIVIA. TARIJA: Arce, Padcaya, Cantón Emborozú, Reserva Natural Alarachi, Zona Cayotal, Río Emborozú Chico, Bosque premontano de Tucumano-Boliviano, sobre roca arenoso vertical, 22°14'18"S, 64°34'19"W, 1120 m, 20 September 2004, *Churchill 23444* (JE, MO).

Radula wrightii (subg. *Volutoradula*) is characterized by plants purely dichotomous plants with ovate to falcate-ovate leaf lobes, leaf cells with small trigones at leaf base increasing in size towards the margins, lobules subquadrate to subrhombic, with a long insertion line (3–4× the base length), and a long and straight keel, spreading at an angle of 30–50º with the stem. This species is usually fertile and female; a specimen from Santiago de Cuba (*Bisse & Lipold 014466/a,* JE) stood out by consisting of of long, male plants with numerous *Lejeunea*-type branches.

Radula wrightii was a poorly known species, considered endemic to Cuba (Castle 1959, Yamada 1988), but examination of the types in YU and NICH showed that the species is conspecific with the rather widespread *R. pocsii*, which was described from the same type locality (Yamada 1983). All the avowed differences between the two species, discussed by Yamada (1988), overlap.

Radula schofieldiana is a further new synonym of *R. wrightii*; presumed differences with *R. wrightii* (Yamada 1997) overlap. The isotype of *R. schofieldiana* in NICH is very poor, consisting of a single shoot of *R. schofieldiana* and five shoots of *R. javanica*.

54. Radula xalapensis Nees & Mont., Ann. Sci. Nat., Bot., sér. 2, 5: 56. 1836. Type: Peru, "ad Stictam cometiam repens," *d'Orbigny 213* (lectotype, PC-0723919!, selected by Gradstein *et al.* 2016: 471; isolectotype, PC-0723920!).

Radula frondescens Steph., Sp. Hepat. 4: 181. 1910. Type: Peru, Sandia, 3000 m, 1902, *A. Weberbauer 807* (lectotype, G-00043885!, c. andr. + per. + spor., selected by Castle, 1966: 31; isolectotype, FH!), syn. fide Gradstein *et al.* (2016).

Radula jamesonii Taylor, London J. Bot. 5: 375. 1846. Type: Ecuador, "Woods on Pinchincha," *W. Jameson 335*, ex. hb. Hook. (lectotype, FH-00290650!, **designated here**), ***syn. nov.***

Radula peruviana K.Yamada, in Schultze-Motel & Menezes, Nova Hedwigia Beiheft 88: 79. 1987. Type: Peru, San Martin, Rioja, "Straβe Chachapoyas-Moyobamba, am Paβ

zwischen Rioja and Balsapata, oberer Bergregenwald mit Baumfarnen," 2300 m, 10 Sept. 1982, *J.-P. Frahm et al. 2200* (holotype, B; isotype, NICH-411176!), ***syn. nov.***

Radula riparia Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 322. 1885. Type: Peru, "Hab. Tarapoto Andium Peruviae, ad rupes umbrosas in rivuli ripis," *R. Spruce s.n.* (lectotype, MANCH-11949!, **designated here**, c. andr.; isolectotype, MANCH-11950!), syn. fide Castle (1966).

Radula sprucei Steph., Sp. Hepat. 6: 515. 1924. Type: Colombia, 1912, *E. Irmscher 26* (lectotype, G-00043858!, c. gyn., selected by Castle 1966: 29), syn. fide Castle (1966, under *R. jamesonii*).

Dioicous. *Plants* 2.5–4 mm wide, to 5(–8) cm long, yellowish to yellowish-brown in herbarium, regularly 1–2-pinnate. *Branches Radula*-type. *Stem* 300–400 µm in diam., with thick-walled, brownish epidermal cells surrounding mostly larger, thin-walled, colorless medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, distant to contiguous, slightly convex, ovate to falcate-ovate, 1.3–1.7 mm long, 1.4–1.7 mm wide, dorsal base rounded, overlapping the stem, dorsal margin rounded, ventral margin rounded, apex rounded, margin plane to sometimes recuved, entire; marginal cells subquadrate to subrectangular, 8–10 × 10–15 µm, median and basal cells isodiametric to elongate, 20–30 × 20–15 µm, cell walls thin to medium-sized, trigones medium-sized to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate, 0.5–0.8 mm long, 0.3–0.5 mm wide, 1/4–1/3 the lobe length, inflated along the keel or at rhizoid area, insertion 1(–2)× the base length, insertion line straight to inverted small J-shaped, base plane, rounded, covering 1/2–2/3 the stem, rarely overlapping the stem, free margin plane, sinuose or incurved, straight to almost rounded, apex plane to incurved, rounded to obtuse, distal margin straight to sinuose, keel straight to usually concave, spreading at angles of 40–60º with the stem, 110–140º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, scanty, present on a few lobules. *Androecia* terminal to intercalary on short or long branches, with 3–7 pairs of bracts, 0.7–1.7 mm wide; bracts contiguous, oblong-ovate, 0.8–1.1 mm long, 0.3–0.4 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong-ovate, ca. 3/4 of lobe length, base rounded, free margin almost straight, apex rounded to obtuse. *Gynoecia* on long branches, with 1–2 innovations; bracts oblong-ovate, 1.2–1.5 mm long, 0.5–1 mm wide, apex rounded, margin plane to usually recurved, entire, lobule oblong, 1/2–1/3 of lobe length, apex rounded. *Perianth* erect, rarely falcate, trumpet-shaped, 1.9–5 mm long, 0.3–0.4 mm wide at base, 0.7–0.9 mm

wide at middle, 0.8–1.3 mm wide at apex, mouth entire to irregularly crenulate, plane or inrolling to inside of the perianth; perianth wall 1–3-stratose in the lower base, unistratose from the upper base to apex, sometimes with small longitudinal striae at base; perianth–calyptra fusion elevated above female bracts, area between perianth-calyptra fusion and female bract insertion elaborated into a low, fleshy, 2–5-layered tube within which the sporophyte foot is embedded. *Calyptra* wall 1–2-layered at the base, 1 cell layer thick above. *Seta* 5–5.2 mm long. *Capsule* ca. 2 mm long, ca. 0.7 mm wide, valves 2–2.1 mm long, 0.2–0.4 mm wide at middle, outer layer cells subrectangular, simple nodular thickenings reddish-brown, on longitudinal wall of every second wall, inner layer cells long-rectangular to polymorphous, thickenings absent. *Elaters* 250–500 µm long, rough to finely granulate. *Spores* 22.22–25.92 in diam., granulate, granules composed by nanogranules. *Vegetative reproduction* by occasionally caducous leaf lobes.

Illustration. Yamada (1982, as *R. frondescens* and *R. jamesonii*).

Distribution and habit. Costa Rica, tropical Andes (Venezuela, Ecuador, Colombia, Peru and Bolivia), southeastern Brazil (rare) and Chile (rare) (Figure 55). *Radula xalapensis* grows on bark, rarely on rock and soil; one collection is from fern leaves (*Lewis 881742A*). The species grows prostrate or pendent, usually in dense mats, in montane and subalpine forests, at 900–3500 m.

Additional specimens examined. COSTA RICA. SAN JOSÉ: La Hondura, on tree, 1300-1400 m, 1924, *Standley 36319 pp.* (JE). Cordillera Talamanca, San Geraldo de Dota, Paradeo Lacustre 'Los Ranchos', Sendero 'El Riachuelo', Sekundärwald am Bach epiphytisch, Stamm, 2000 m, 14 March 2000, *Holz CR 00-774B* (GOET). **CARTAGO:** Cordillera Talamanca, Villa Mills, CATIE-Station 'Siberia' Interam, Sur km 100, Sendero Ecologico, Stamm, 2700 m, 28 February 2000, *Holz CR 00-0493* (GOET). **PUNTARENAS:** Reserva Biológica Monteverde, undisturbed cloud forest, very common on bark, 1550 m, 9 November 1993, *Gradstein 9443* (GOET).

VENEZUELA. MÉRIDA: Sierra de St. Domingo, Páramo de Mucuchies, 3500 m, 1969, *Oberwinkler & Poelt HV69-51* (JE). **TÁCHIRA:** Jauregui, páramo El Rosal, between La Grita and San José de Bolívar, sobre ramas, August 1975, *Griffin III et al. 619* (GOET).

COLOMBIA. ANTIOQUIA: Urrao, road between Urrao and Caicedo, epiphytic, 06°23'N, 76°03'W, 2570 m, 27 February 1989, *MacDougal et al. 4234* (MO). **BOYACÁ:**

Carretera Chiquinquirá-Pauna, más allá del Boqueron, debajo de “Santo Antonio”, 2300 m, 3 September 1967, *Hammen et al. 2471* (GOET). **NARIÑO:** Pasto, km 16 Pasto-Chachagui, La Josefina, 2640 m, 14 March 1991, *Ramírez 3243* (MO). **RISARALDA:** Santa Rosa, 3140 m, 20 July 1980, *Aguirre 1277* (GOET).

ECUADOR. MORONA-SANTIAGO: between Gualaceo and General L. Plaza, eastern Cordillera, western slope, on litter, 3000 m, 30 July 1991, *Arts 30/001* (JE).

PERU. The Type of *R. frondescens*, *R. peruviana*, *R. riparia* and *R. xalapensis*.

BRAZIL. **RIO DE JANEIRO:** Parque Nacional do Itatiaia, sobre pedra a beira do riacho, 900 m, 10 April 2000, *Costa & Gradstein 3724* (RB).

BOLIVIA. COCHABAMBA: Chapare, road Cochabamba-Villa Tunari km 112, cloud forest, on trunk, 65°44’ W, 17°09’ S, 1850 m, 8-13 November 1989, *Gradstein 7583* (GOET). Carrasco, 9.4 km oeste de El Churo, bosque montano nublado de Serrnias de Siberia, perturbado, sobre hojarasca em la sombra, 17°46’S, 64°48’W, 2580 m, 9 September 2002, *Churchill et al. 21982-B* (MO). Carrasco, 11 km oeste de El Churo, bosque montano nublado, sobre tronco de arbolito em la sombra, 17°45’S, 64°48’W, 2740 m, 21 May 2003, *Churchill et al. 22603* (MO). Chapare, Cañodon, carretera nuevo Cochabamba – Villa Tunari, bosque ceja de montano, Yungas, barranco sobre hojarasca, 17°12’42”S, 65°53’18”W, 3200 m, 8 December 2007, *Churchill et al. 24789* (MO). Chapare, Por Tables Monte, ca. 8 km norte de carretera nuevo Cochabamba – Villa Tunari, bosque montano, Yungas, secundário, sobre tronco de árbol, 17°09’30”S, 65°54’17”W, 2600 m, 8 December 2007, *Costa et al. 4872* (MO). Chapare, Parque Nacional de Carrasco, cordillera El Ronco, caminho antigua Chapare, por El Limbo, Cochabamba – Villa Tunari, bosque montano de Yungas, sobre tronco de árbol, 17°11’45”S, 65°41’16”W, 3400 m, 7 December 2007, *Churchill et al. 24758* (MO). Chapare, 76 km de Villa Tunari, entre Locatal – Corani, carretera nuevo Cochabamba – Santa Cruz, bosque montano secundário, sobre hojarasca, poco sol, 17°11’S, 65°56’W, 2200 m, 29 October 2002, *Churchill et al. 22122* (MO). **La Paz:** Franz Tamayo, along trail between Pelechuco and Pata, along the Río Pelechuco, on fern, 14°45’S, 69°00’W, 2500-2650 m, 18 November 1988, *Lewis 881742A* (MO). Franz Tamayo, Parque Nacional Madidi, Tokoaque, por el camino entre Keara y Mojos, bosque montano pluvial de Yungas, sobre árbol, 14°36’58”S, 68°57’14”W, 2400 m, 8 November 2007, *Araújo M. 256A* (MO). Franz Tamayo, area Natural de Manejo Integrado Apolobamba, entre Selumacan y antiguo puente Corapara, al lado del Río Pelechuco, bosque montano superior estacional-pluvial, 14°46’20”S, 68°00’01”W, 2420 m, 14 June 2008, *Fuentes & Huaylla 13050* (MO). **Santa Cruz:** San Lorenzo a 22 km al norte de Vallegrande, camino entre Vallegrande a Loma Larga, bosque montano de Tucumano-boliviano, borde de

caminho, sobre corteza de árbol, 18°39’57”S, 63°55’25”W, 2316 m, 20 August 2011, *Carreño & Huanca 986* (MO). Vallegrande, Abra, bosque montano de Tucumano-Boliviano, epífita, 18°33’30”S, 63°46’44”W, 2150 m, 30 July 2011, *Inturias et al. 1007* (MO). Manuel Maria Caballero, Serranía de Siberia, Cerca El Empalpe, camino al San Mateo, bosque montano Yungas, sobre tronco de árbol inclinado, 17°49’20”S, 64°42’45”W, 2440 m, 13 December 2009, *Churchill et al. 24916* (MO). Manuel Maria Caballero, 11 km este de Siberia, 4 km en camino nuevo por San Mateo, bosque montano nublado muy humedo, sobre tronco de árbol, 17°49’S, 64°42’W, 2280 m, 8 September 2002, *Churchill et al. 21941* (MO).

Radula xalapensis (subg. *Volutoradula*) is characterized by plants rather robust, 2.5–4 mm wide, regularly 1–2-pinnate, leaf lobes ovate to falcate-ovate, leaf cells with small to large trigones, lobules small (1/4–1/3 the lobe length), distant, subquadrate, insertion line straight to inverted small J-shaped, free margin slightly sinuose, plane or incurved, base rounded, extending widely across the stem, usually 1/2–2/3 of stem width, rarely more, and keel straight to usually concave. The shape of the leaf lobe, trigones and size of the lobule base vary greatly.

This species is similar to *Radula voluta* by large plants with regular 1–2-pinnate branching. However, *R. voluta* strikingly differs in the large lobules with a voluted auricle, which is circinately coiled, reaching downwards to the keel (lobules small and without auricle in *R. xalapensis)*. *Radula xalapensis* also resembles the Chilean *R. hastata* Steph. differing mainly in stem anatomy; this relationship needs future study.

Radula jamesonii and *R. peruviana* are new synonyms of *R. xalapensis*. The former species is a robust phenotype of *R. xalapensis,* with strongly falcate-ovate leaf lobes and large trigones in the leaf cells, while *R. peruviana* is a small phenotype with ovate leaf lobe and small trigones. Yamada (1982a) and Yamada in Schultze-Motel & Menzel (1987) reported irregularly pinnate branching in *R. jamesonii* and *R. peruvian*a, but branching in the types of these two species is regularly and densely pinnate.

For a detailed discussion of the type of *R. xalapensis* see Gradstein *et al.* (2016).

55. Radula yamadae F.R.Oliveira-da-Silva & Ilk.-Borg., Nova Hedwigia 110(3–4): 288, 1. 2020. Type: Brazil, São Paulo, São Luiz do Piraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, “trilha do Corcovado, Mata Atlântica, sobre folhas,” 23°24’07”S, 45°11’33”W, 981 m, 11 June 2013, *D. F. Peralta & D. M. Carmo 14155* (holotype, SP-438627!).

Dioicous. *Plants* 1–2(–2.5) mm wide, to 1.5 cm long, green to pale green in herbarium, regularly to irregularly pinnate. *Branches Radula*-type. *Stems* 130–150 μm in diam., with thick-walled, colorless to yellowish epidermal cells surrounding mostly larger, thin-walled, colorless medullary cells, outer epidermal wall heavily and evenly thickened, more so than the inner epidermal wall. *Leaf lobes* widely spreading, imbricate, convex, ovate, 0.7–1.2 mm long, 0.5–0.8 mm wide, dorsal base rounded, auriculate, covering the entire stem, dorsal margin rounded, ventral margin almost straight, apex obtuse to subacute, margin plane, entire; marginal cells subquadrate to isodiametric, 12–17 × 10–12 μm, median and basal cells isodiametric to elongate, 12–22 × 10–15 μm, cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant to contiguous, rarely imbricate, subquadrate, 0.3–0.6 mm long, 0.25–0.5 mm wide, 1/2–2/5 the lobe length, strongly inflated at rhizoid area and along the keel, insertion 1× the base length, insertion line curved, base plane, rounded to obtuse, covering 1/3 to overlapping the stem, free margin plane, straight to sinuose, apex plane, rounded to obtuse, distal margin almost straight, keel conspicuously convex, spreading at angles of 60º with the stem, 130–150º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless to brown, numerous. *Sexual organs* and *Vegetative reproduction* not observed.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. *Radula yamadae* is only known from Paraná and São Paulo State, southern and southeastern Brazil (Figure 56), respectively, growing on leaves and rock in submontane forests, 1000–1200 m.

Additional specimens examined. BRAZIL. PARANÁ: Morretes, Parque Estadual do Marumbi, Mata Atlântica com afloramentos rochosos, sobre rocha, 25°26’55”S, 48°54’54”W, 1200 m, 22 July 2014, *D. F. Peralta et al. 15877* (paratype SP, MG).

Radula yamadae is characterized by the densely branched plants with ovate leaf lobes with an obtuse to subacute apex, lobules distant to contiguous, subquadrate, with base rounded to obtuse, covering 1/3 to fully overlapping the stem, strongly inflated at the rhizoid area and along the convex keel. The species is morphologically close to *R. longiloba* (see discussion under the latter species).

Epiphyllous specimens of *R. yamadae* grow in rounded, whitish patches, while saxicolous plants form dense, dark mats.

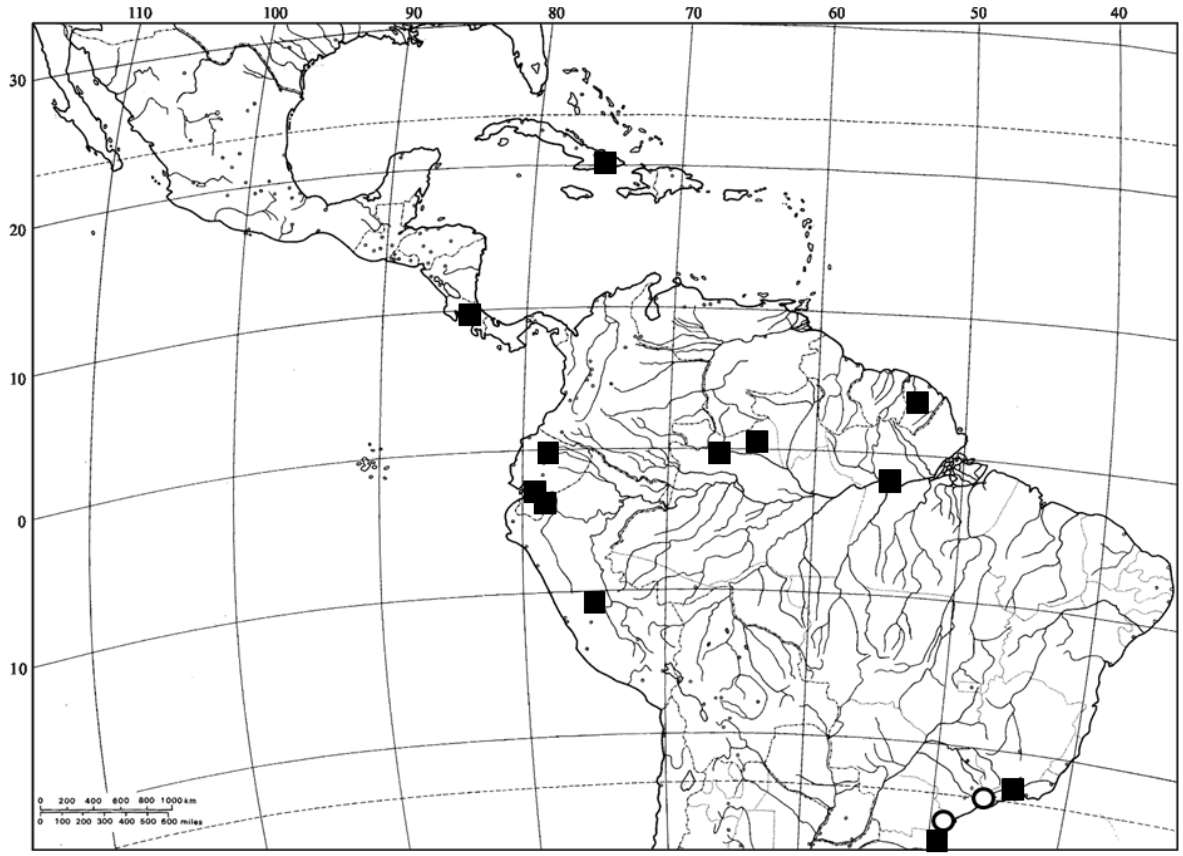

Figure 56. Distribution of *Radula yamadae* (white circle) and *R. yanoella* (black square).

56. Radula yanoella R.M.Schust., Phytologia 56: 72. 1984. Type: Brazil, Amazonas, Rio Negro, near São Gabriel, from Igarapé Arabú on Rio Curicuriari to summit of Serra Curicuriari, 00°20’S, 66º50’W, 450 m, 9–12 July 1979, *R. M. Schuster 79-15-627#2* (neotype, NY-00840786!, selected by Oliveira-da-Silva *et al.*, 2020: 152), ibid., *R. M. Schuster 79-15-627* (isoneotype, NY-00840787!).

Radula aguirrei M.A.M.Renner, Phytotaxa 202(1): 70. 2015. *Radula aguirrei* R.M.Schust., J. Hattori Bot. Lab. 70: 56. 1991, *nom. inval.* Type: Colombia, Isla Gorgona, on trail just below El Mirador, trail to Laguna, southern half of island, *R. M. Schuster 88-1620a* (holotype, F), syn. fide Pócs *et al.* (2022).

Dioicous. *Plants* 0.9–1.1 mm wide, green to pale green in herbarium, consisting of a small, irregularly pinnate thallus with leafy shoots sprouting from the thallus margins, leafy shoots usually unbranched. *Thallus* to ca. 1 μm wide, of 1 layer of rectangular cells, 20–40 ×

6–20 µm, thallus margins irregularly rounded to narrowly elongated, entire, producing leafy branches, cell walls thick, trigones lacking, cuticle smooth. *Stems* 80–120 µm in diam., with thin-walled epidermal and medullary cells, the cells uniform in size, walls colorless to yellowish. *Leaf lobes* obliquely to widely spreading, contiguous to subimbricate, slightly convex, ovate to falcate-ovate, 0.55–0.75 mm long, 0.4–0.55 mm wide, dorsal base rounded, not covering the stem, dorsal margin rounded, ventral margin almost straight to rounded, apex rounded, margin plane to sometimes recurved, entire to crenulate with gemmae; marginal cells subquadrate to isodiametric, 10–12 × 7–10 µm, median and basal cells isodiametric, 12–20 µm in diam., cell walls thin, trigones small to lacking, intermediate thickening lacking, cuticle smooth; oil bodies not observed. *Lobules* distant, subquadrate to ovate-subquadrate, 0.15–0.3 mm long, 0.1–0.15(–0.2) mm wide, 1/4–1/3 the lobe length, slightly to strongly inflated at rhizoid area, insertion 3–4× the base length, insertion line almost straight, base plane, rounded to almost straight, covering 1/3–1/2 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin straight, keel straight to strongly convex, spreading at angles 45–50º with the stem, 90–130º with the ventral leaf lobe margin, at its junction with the lobule. *Rhizoids* colorless, numerous on a pronounced mammiliform swelling, present on a few or numerous lobules. *Androecia* on main stem, with 3–6 pairs of bracts, 0.4–0.5 mm wide; bracts imbricate, ovate, ca. 0.3 mm long, 0.1–0.2 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 5/6 of lobe length, base almost rounded to straight, free margin straight, apex rounded. *Gynoecia* on main stem, with 2 innovations; bracts oblong-ovate, ca. 0.7 mm long, ca. 0.4 mm wide, apex rounded to obtuse, margin plane, entire, lobule oblong, ca. 2/3 of lobe length, apex rounded to obtuse. *Perianth* erect, trumpet-shaped, ca. 1.8 mm long, ca. 0.1 mm wide at base, ca. 0.3 mm wide at middle, ca. 0.5 mm wide at apex, mouth entire, plane; perianth wall unistratose. *Calyptra* and *Sporophyte* not observed. *Vegetative reproduction* by small discoid gemmae, ca. 100 µm in diam., produced along the leaf lobe margins.

Illustration. Oliveira-da-Silva *et al.* (2021).

Distribution and habit. Costa Rica, Cuba, French Guiana, Ecuador, Peru and Brazil (Figure 56). *Radula yanoella* was long considered endemic to Amazonia with one disjunct record in Costa Rica. Recently, the species was found in the Atlantic forest of Rio de Janeiro State (Oliveira-da-Silva *et al.* 2021), the Peruvian Andes (Pócs *et al.* 2022) and the West Indies (Cañiza Ovelar & Oliveira-da-Silva 2022), where it seems to be very rare. *Radula yanoella* usually forms minute pachtes on living leaves of ferns and angiosperms, in shaded habitats, in

lowland, submontane and lower montane rainforests, rarely in upper montane forests, near rivers, lakes and waterfalls, from sea level to ca. 2450 m.

Additional specimens examined. CUBA. GUANTÁNAMO: Baracoa, pluvisilva en las cabezadas del río Naranjo, 300 m., on fern fronds, 06 August 1975, *Meyer HFC 27828* (JE).

FRENCH GUIANA. SAÜL: Base of Mont Galbao, along upper part of la Mana Fleuve, primary moist tropical forest along small stream with several tree falls, 3°37'N, 53°17'W, 380 m, 15 November 1997, *Buck 33404* (NY).

BRAZIL. **AMAZONAS:** São Gabriel, Serra Curicuriari, from Igarapé Arabú on Rio Curicuriari to summit, 00°20'S, 66º50'W, 450 m, 9 July 1979, *Schuster 79-15-725* (INPA). Santa Isabel do Rio Negro, Rio Cauaburi, 0°15' S, 65°55' W, 3 July 1979, *Schuster 79-10-296* (SP). **PARÁ:** Oriximiná, ESEC do Grão Pará, Serra do Acari, 407–600 m, 28 August 2008, *Pietrobom & Maciel 7838* (SP, HBRA). **RIO DE JANEIRO:** Resende, Parque Nacional do Itatiaia, junto do Véu de Noiva, 20 June 1983, *Yano & Santos 7481* (SP). **SANTA CATARINA:** Blumenau, 1889, *Ule 186* (FH).

Radula yanoella (subg. *Metaradula* sect. *Epiphyllae*) is a peculiar, typically epiphyllous species characterized by a small thallus with short, little branched leafy shoots arising from the thallus margins, producing small discoid gemmae on lobes margins. The thallus is interpreted as a persistent protonema, and a neotenic feature of the plants (Schuster 1991, Gradstein & Wilson 2009). The thallus of *Radula yanoella* is very difficult to detach from the substrate and usually only a small portion can be removed. *Radula aguirrei* was separated from *R. yanoella* by its pinnate branching and lobule keel (Schuster 1991), but Pócs *et al.* (2022) found overlap in the avowed differences nd reduced *R. aguirrei* to synonymy under *R. yanoella*.

Radula yanoella resembles *R. flaccida* and *R. stenocalyx*, but the latter two species lack a persistent thalloid protonema and the gemmae in *R. flaccida* are much larger and with a deeply cordate-auriculate base.

INVALID NAMES

Jungermannia portoricensis Sprengel, Syst. Veg. 4(1): 226. 1827. Material: Puerto Rico, on stones, *Bertero s.n.* (G) = *Radula pallens* (see *R. kegelii* in Castle 1959, p. 40) = ***Radula pallens*** (Sw.) Nees & Mont.

Radula bursata Lindenb, in Duss, Énum. Musc. Ant. Franç. 1: 17. 1903, nom. inval. (Art. 38.1, Turland *et al.* 2018). Material: Guadeloupe, Sur les arbres, Bouillante, bois du Trou-aux-Trois-Diables, 430 m, *Duss 425* (FR). Martinique, Montagne Pelée, 910 m, *Duss 245* (FR).

Radula divaricata Lindenb., in Duss, Énum. Musc. Ant. Franç. 1: 17. 1903, nom. inval. (Art. 38.1, Turland *et al.* 2018). Material: Guadeloupe, sur les arbres, Bois du Matelyane, 880 m, 30 May 1898, *Duss 298* (NY!, YU-242216!, FR) = ***Radula elliottii*** Castle

Radula grateloupii Mont., in Duss, Énum. Musc. Ant. Franç. 1: 18. 1903, nom. inval. (Art. 38.1, Turland *et al.* 2018). Material: Guadeloupe, Sur les arbres, Bois du Lorrain, entre le Champflore et la route de la Trace, 620 m, *Duss 286, 287* (FR).

DOUBTFUL AND EXCLUDED TAXA

Radula carringtonii Jack – North Atlantic endemic. This species was registered in tropical America (Costa Rica and Bolivia) by Yamada (1995, 2000). Patiño *et al.* (2013) pointed out differences in leaf cell size and keel suggesting that the Neotropical material of *R. carringtonii* was misidentified. The Neotropical specimens were not examined but judging by the illustration of Yamada (1995) we believe that they are a phenotype of *R. javanica* with gynoecia on short branches.

Radula costaricensis Gottsche – According to the protologue, this species was collected in 1875 by Helmuth Polakowski n° 120A in Alajuela, Costa Rica. The type was not found and is probably lost since Stephani did not treat *Radula costaricensis* in his Species Hepaticarum, neither did Castle in his world review of *Radula* and Yamada in his numerous notes on Latin American *Radula*.

Radula marginata Gottsche et al. – New Zealandic endemic. Recorded in Brazil by Oliveira e Silva & Feitosa (1997), which is probably a misidentification (Reiner-Drehald 1994, Gradstein & Costa 2003, Oliveira-da-Silva *et al.* 2021). The Brazilian record may belong to *Radula ligula*, which is a well-distributed species along the Atlantic Coastal Region of Brazil (Oliveira-da-Silva *et al.* 2021).

Radula microloba Gottsche – Chilean species. The records from Brazil belongs to *R. pallens* var. *pallens* and *R. javanica* (Oliveira-da-Silva *et al.* 2021).

Radula punctata Steph. – Occurs in southern South America (Chile and Argentina). This species was registered in Colombia by Wolf (1993), but it is probably a misidentification according to Gradstein (2021). *Radula punctata* was reported for southern and southeastern Brazil by Oliveira-da-Silva *et al.* (2021), but all records belong to *R. xalapensis*. The latter species shows wide morphological variation, especially in plant size, leaf shape, and in the presence/absence of trigones in leaf cells.

Radula retroflexa Taylor – Paleotropical species. The record from Galápagos Islands, Ecuador (León-Yánez *et al.* 2006) is considered erroneous (Gradstein 2021).

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CONSIDERAÇÕES FINAIS

Neste estudo foram reconhecidas 54 espécies e seis variedades de Radulaceae para a América tropical, baseados na análise dos tipos nomenclaturais e extenso número de amostras depositadas em herbários. Foram descritos cinco táxons novos de *Radula*, dos quais *R. pallens* var. *marginata* e *R. smithii* foram previamente publicadas (Capítulo I: Oliveira-da-Silva *et al.* 2022), e *Radula sp. nov. 1, 2 e 3* serão publicadas na revisão taxonômica (Capítulo IV). *Radula dominicensis*, *R. macrostachya* e *R. ramulina* var. *microphylla* são reintegradas a partir dos sinônimos de *R. saccatiloba*, *R. javanica* e *R. voluta*, respectivamente. Uma nova combinação foi necessária de *R. ramulina* var. *microphylla* para *R. voluta* var. *microphylla*.

Um dos resultados mais importantes foi o refinamento da lista de espécies, o que gerou 27 novos sinônimos. Esse dado reforça a hipótese de que o número de espécies estava subestimado e excessivo. Além disso, 42 novos lectótipos são propostos, mostrando o avanço e estabilização da nomenclatura dos nomes.

Muitas espécies tiveram sua distribuição expandida, incluindo as que eram conhecidas apenas para sua localidade tipo (*e.g. Radula cochabambaensis* e *R. venezuelensis*), assim como informações ecológicas como preferência por substratos e zonas de altitude. A maioria das espécies de Radulaceae são encontradas sobre troncos de árvores vivas, seguido de rochas, em florestas úmidas, sombreadas e preservadas. Poucas espécies ocorrem em áreas mais abertas e expostas, ou até mesmo em áreas que foram impactadas. As espécies apresentam uma ampla faixa altitudinal, mas a maioria ocorre em florestas submontanas a baixa montana, que varia de 500 a 2000 metros de altitude. Cerca de 70% das espécies ocorrem exclusivamente na América tropical, e os outros 30% podem ocorrer em outras regiões do mundo. O norte dos Andes apresenta a maior diversidade de espécies de Radulaceae, bem como o maior número de espécies endêmicas, seguido da Mata Atlântica e América Central.

O estudo de caracteres negligenciados e que são taxonomicamente importantes para a definição de grupos em hepáticas (*e.g.*, morfologia e anatomia do esporófito) se mostrou importante em Radulaceae para nível específico, porém não corroboram com a classificação subgenérica proposta por evidencias moleculares (veja Capítulo III). A anatomia do caulídio é uma característica importante na definição das diferentes linhagens de Radulaceae, em especial dos subgêneros de *Radula*. Todavia, o estudo molecular ainda se faz necessário, visto que poucas espécies estão inseridas nas reconstruções filogenéticas propostas.

A proposta inicial deste projeto era incluir, além do estudo morfológico, anatômico, ecológico e palinológico, o estudo filogenético molecular. Na verdade, o estudo molecular foi

realizado durante o doutorado, mas não está finalizado. O DNA de mais de 100 espécimes de *Radula* foram extraídos, das quais 70 amostras foram bem sucedidas. Essas amostras já passaram pela amplificação das seis regiões dos cloroplastos conhecidos para o grupo. Todavia, devido a problemas técnicos no laboratório de biologia molecular do Museu Goeldi, ainda não foi possível sequenciar a maioria das amostras. Mais de 400 sequências serão geradas e, juntamente com as sequências baixadas no GenBank, resultará em uma futura e robusta filogenia para a família, reconhecida aqui como um resultado direto dessa revisão, mesmo que seja produzida posteriormente.

Durante o doutorado, o discente foi convidado para colaborar em outros manuscritos sobre Radulaceae em Cuba (CAÑIZA OVELAR; OLIVEIRA-DA-SILVA 2022), Madagascar (GRADSTEIN *et al.*, 2022) e artigo filogenético molecular (RENNER *et al.*, 2022) que culminou no reconhecimento de três gêneros na família (ver anexos). O estudo de Radulaceae na África tropical que está sendo realizado pelo orientador do discente foi essencial para a produção do Capítulo II deste projeto. Esses são resultados indiretos da presente tese.

APÊNDICES

Nova Hedwigia, Vol. 115 (2022), Issue 1-2, 47–55 Article
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Notes on the genus *Radula* Dumort. (Radulaceae, Marchantiophyta) in Cuba: new, excluded and doubtful records

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With 3 figures

Abstract: Cuba, an archipelago located in the Caribbean Sea, is famous for its richness in bryophyte species, especially leafy liverworts. In this paper, we report two rare and interesting *Radula* species collected in the eastern region of Cuba, on the banks of the Naranjo River: *Radula pusilla* Spruce (subg. *Volutoradula* Devos et al.) and *R. yanoella* R.M.Schust. (subg. *Metaradula* R.M.Schust., sect. *Epiphyllae* Grolle). Both species are new records for Cuba, and *R. yanoella* is reported for the first time for the West Indies. *Radula pusilla* is a little-known neotropical species recorded for Dominica, Costa Rica, Guyana, Colombia and Ecuador. *Radula yanoella* is a neotenic species reported for Costa Rica, Ecuador, Peru, French Guiana and Brazil. We provide a note on the species along with brief descriptions, illustrations and comments on its morphology, distribution and habitat. Furthermore, *Radula microlobula* Castle is excluded from the Cuban flora, and *R. complanata* (L.) Dumort. and *R. pseudostachya* Spruce are highly doubtful records.

Key words: Bryophytes; liverwort; West Indies; taxonomy; tropical America

Introduction

Cuba, an archipelago consisting of two major and more than 1500 small islands located in the Caribbean Sea, is famous for its richness in bryophytes species, especially rare and/or endemic leafy liverworts, e.g., *Ceratolejeunea baracoensis* G.Dauphin et al., *Diplasiolejeunea grolleana* Reyes, *Drepanolejeunea senticosa* Bischl., *Nowellia wrightii* (Spruce) Steph. and *Radula wrightii* Castle (Castle 1959, Reyes 1982, Pócs 1988, Dau-

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Article

The genus *Radula* Dumort. (Marchantiophyta: Radulaceae) in Madagascar, with a key to the tropical African species

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With 8 figures

Abstract: A taxonomic study of the Radulaceae from Madagascar leads to the recognition of thirteen species, in five subgenera. *Radula evelynae*, *R. lindenbergiana* and *R. retroflexa* are new to Madagascar, *R. fulvifolia* is excluded from the Madagascan flora and *R. javanica* is considered a doubtful record. *Radula ankefinensis* is a new synonym of *R. mexicana* and its distribution is extended to the Neotropics, *R. silvestris* and *R. comorensis* are new synonyms of *R. appressa*, and *R. bipinnata* and the neotropical *R. gottscheana* are placed in the synonymy of *R. boryana* following Castle (1936). Four new lectotypfications are proposed. The species usually grow as epiphytes in mid-elevation forests, more rarely in lowland forests; one species, the Holarctic *R. lindenbergiana*, is restricted to the upper montane belt. *Radula marojezica* and *R. pinnata* are endemic to Madagascar and about 70% of the species have wide, intercontinental ranges. The commonness of intercontinental ranges in Madagascan *Radula* may be explained by the old age of the *Radula* lineages, their good dispersibility and habitat preferences. Descriptions and selected illustrations of the species are provided together with a key to the *Radula* species of tropical Africa. Surface wax, observed on the leaves of *R. appressa*, is reported for the first time in the family Radulaceae.

Key words: biogeography; bryophytes; liverworts; morphology; Africa; taxonomy; tropical biodiversity

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Molecular and morphological evidence support the recognition of three genera within Radulaceae (Porellales: Marchantiophyta)

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Abstract

The discovery of new fossil bryophytes allows refined estimates of divergence times when the fossils have unambiguous synapomorphies enabling their confident assignment to nodes within molecular phylogenies. We use two fossil *Radula* species from Cretaceous age Burmese amber to estimate divergence times for *Radula*. One of these fossils, *R. cretacea* which has synapomorphies of subg. *Odontoradula,* has been used previously; the other, with relative synapomorphies of subg. *Amentuloradula*, has not. In combination these two fossils, when used to constrain the crown node age of their respective subgenera, result in median age estimates for the *Radula* crown node of 263 million years, under our preferred time-calibration scenario where subgeneric crown-node fossil assignments are coupled with a secondary maximum age constraint on the Porellales crown node. We explore other time-calibration scenarios, including deeper fossil assignments, and conclude that, under all, *Radula* as currently circumscribed is an outlier among land plant genera on the basis of its age. While this violates no established norms regarding how old genera should be, the absolute age, the relative ages of other families within Porellales, and the morphological distinctiveness of the two serial sister lineages, subg. *Cladoradula,* with seven species, and subg. *Dactyloradula* with one species, motivates our proposal to elevate these two subgenera to generic rank, resulting in three genera within the family Radulaceae. We provide diagnoses for genera, new combinations for species, and an emended circumscription for *Radula,* that reflect this change.

Introduction

Fossils provide critical insight into past diversity. DNA sequences do not record their own rate of evolutionary divergence, meaning the absolute time course of divergence among sequences must be calibrated from another data source (Ho & Phillips 2009; Sauquet *et al.* 2012). Fossils can be used to calibrate diversification timelines by constraining the age of particular divergence events. However, identifying the node to which a particular fossil may tie into a phylogeny containing only extant species is sometimes challenging, and always requires careful justification (Gandolfo *et al.* 2004). Divergence time estimates can be highly sensitive to small differences in node assignment of fossil taxa, as well as to sampling density (Cusimano & Renner 2010).

The discovery of new fossil bryophytes allows refined estimates of divergence times when the fossils have unambiguous synapomorphies enabling their confident assignment to nodes within molecular phylogenies. Here, we use new fossil evidence to revisit divergence time estimations for the liverwort genus *Radula* Dumortier (1822: 112). *Radula* (Radulaceae) with anywhere between 200 and 350 species worldwide (Yamada 1979; Renner 2016) is a highly distinctive, monophyletic, phylogenetically isolated leafy liverwort genus (Devos *et al.* 2011a,b; Patiño *et al.* 2017). It is the only genus in the family Radulaceae, and the suborder Radulineae (Crandall-Stotler *et al.* 2009). The phylogenetic isolation of *Radula* is reflected in its unusual morphology including a ventral merophyte that does

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