



The genus *Radula* Dumort. (Radulaceae, Marchantiophyta) in Brazil

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With 35 figures and 1 Appendix

Abstract: A taxonomic study of the liverwort genus *Radula* in Brazil based on morphological characters and on examination of types and over 1000 additional collections, leads to the recognition of 31 species and two varieties. A key to all species as well as descriptions, illustrations and comments on recognition, distribution and habitat of the recognized species are provided. One new species, *R. renneri*, is described and illustrated. *Radula longiloba*, *R. punctata* and *R. xalapensis* are new records for Brazil whereas the occurrence of *R. pseudostachya* and *R. subinflata* in Brazil is confirmed. *Radula elliottii*, *R. varilobula* and *R. wrightii* are excluded from the country and *R. marginata*, *R. microloba* and *R. saccatiloba* are doubtful records. Several new lectotypifications [for *R. flaccida*, *R. epiphylla* (= *R. flaccida*), *R. quadrata*, *R. stenocalyx*, *R. tectiloba* and *R. tenera*] and one new neotypification (for *R. yanoella*) are proposed. *Radula obovata* is proposed as a new synonym of *R. pallens*.

Keywords: bryophytes; hepatics; liverworts; morphology; Neotropics; taxonomy; tropical biodiversity

Introduction

Radula Dumort. is a large genus of leafy liverworts with about 200 species worldwide, most of them distributed in tropical and subtropical regions (Yamada 1979, 2003, Gradstein et al. 2001, Devos et al. 2011b, Patiño et al. 2017). The species occur from sea level to about 4000 m elevation and usually grow on bark, decaying wood, rock or living leaves, occasionally on soil (Gradstein et al. 2001).

Dumortier (1822) introduced the genus *Radula* based on eight species, including *Jungermannia complanata* L. [= *Radula complanata* (L.) Dumort.], which was conserved as the type of *Radula* (Grolle 1983). The genus is characterized by (1) terminal, *Radula*-type branches (originating from a stem epidermal cell and therefore associated with an unmodified leaf), (2) incubous, lobulate leaves, (3) underleaves absent, (4) rhizoids in tufts on lobule surface, and (5) perianth tubular, dorsiventrally flattened (Schuster 1980, Yamada 1979, 2003, Gradstein et al. 2001, Crandall-Stotler et al. 2009). *Radula* is well resolved in its own family and suborder, Radulaceae Müll.Frib. and Radulineae R.M.Schust., respectively (Crandall-Stotler et al. 2009). Based on morphological and molecular data, Devos et al. (2011a) subdivided the genus into seven subgenera: subg. *Amentuloradula* Devos et al., subg. *Dactyloradula* Devos et al., subg. *Cladoradula* Spruce, subg. *Metaradula* R.M.Schust., subg. *Odontoradula* K.Yamada, subg. *Radula*, and subg. *Volutoradula* Devos et al. The latter five subgenera occur in Brazil.

The genus *Radula* was first recorded from Brazil by Raddi (1823), who reported *R. complanata* and *R. pallens* (Sw.) Nees & Mont. from Rio de Janeiro State. Costa (2009), however, found that the record of *R. complanata* belonged to *R. voluta* Taylor while the collection of *R. pallens* was missing in the Raddi herbarium. Subsequently, many additional *Radula* species have been recorded from Brazil (e.g., Nees 1833, Spruce 1885, Stephani 1910, Dusén 1903, Castle 1959, 1962, 1963, 1964, Schiffner & Arnell 1964, Oliveira 1973). The latter author presented a key to the species of Rio Grande do Sul together with brief morphological descriptions and illustrations. Yano (1984, 1989, 1995) recorded 39 species of *Radula* in a checklist of liverworts and hornworts of Brazil, but only 27 were accepted by Yamada (2003) in a first taxonomic account of the genus for the country, with a key, comments on habitat and distribution, and illustrations of the species. In the latest version of the Brazil checklist, Yano (2008) listed 34 species for the country, including seven species excluded by Yamada (2003). Costa & Peralta (2015) considered Radulaceae the sixth most diverse liverwort family of Brazil, with 26 species including one endemic, *Radula brasiliica* K.Yamada. Recently, we described two new species and one new variety from Brazil, *Radula yamadae* F.R.Oliveira-da-Silva & Ilkiu-Borges (Oliveira-da-Silva & Ilkiu-Borges 2020), *R. bahiensis* F.R.Oliveira-da-Silva et al. and *R. fendleri* Steph. var. *paroica* Oliveira-da-Silva et al. (F.R.Oliveira-da-Silva et al. 2020).

Information on the Brazilian species of *Radula* is highly scattered across the literature. Besides the brief account of Yamada (2003), which lacks species descriptions, there is no comprehensive taxonomic treatment of the genus for the country. A taxonomic revision of the species of *Radula* of the world was carried out by Castle (1937, 1939, 1950, 1959a, 1959b, 1962, 1963, 1964, 1965, 1966, 1969) and useful accounts of selected Neotropical

species were published by Yamada (e.g., 1980, 1981, 1982, 1987, 1991, 1993a). In addition, brief treatments for Neotropical areas are available for Cuba (Yamada 1988), the Galápagos Islands (Yamada & Gradstein 1991) and French Guiana (Gradstein & Ilkiu-Borges 2009). Many Neotropical species, however, remain insufficiently known (Renner 2016).

The aim of this paper is to present a comprehensive taxonomic treatment of *Radula* in Brazil, based on study of type specimens and additional herbarium collections.

Materials and methods

Type specimens and over 1000 additional collections from 16 herbaria (ALCB, BM, G, GOET, HBRA, ICN, INPA, JE, MG, NICH, NY, PC, RB, S, SP, UFP) were examined. Leaf lobe and lobule, as well as details of the lobule, were measured as shown in Fig. 1. For taxonomic and geographical information on *Radula* species the main sources consulted were Castle (1937, 1939, 1950, 1959a, 1959b, 1962, 1963, 1964, 1965, 1966, 1969), Yamada (1979, 1980, 1981, 1982, 1983, 1987, 1990, 1991, 1993a, 1993b, 2003), Schuster (1980), Reiner-Drehwald (1994), Gradstein & Ilkiu-Borges (2009), Gradstein (in press), Tropicos (<http://www.tropicos.org/>), JSTOR Plant Sciences (<http://plants.jstor.org>) data on *Radula* in Brazil (<http://floradobrasil.jbrj.gov.br/>; <http://splink.cria.org.br/>) and biodiversity heritage library (<http://biodiversitylibrary.org>). Distribution maps were produced at the Space Analysis Laboratory (UAS/MPEG).

Results and discussion

In this study, 31 species and two varieties of *Radula* are recognized for Brazil. *Radula longiloba* K.Yamada, *R. punctata* Steph. and *R. xalapensis* Nees & Mont. are new to Brazil, while the occurrence of *R. pseudostachya* Spruce and *R. subinflata* Lindenb. & Gottsche in Brazil is confirmed. The latter two species had been reported from Brazil by Yano (1984), Yamada (1980) and Costa (1992), but were not included in recent lists (e.g., Yamada 2003, BFG 2018). *Radula wrightii* Castle, *R. varilobula* Castle and *R. elliotii* Castle are excluded from the Brazilian flora, and *R. marginata* Gottsche, Lindenb. & Nees, *R. microloba* Gottsche and *R. saccatiloba* Steph. are listed as doubtful records. *Radula wrightii* was firstly cited for Brazil (Minas Gerais) by Yano (1984) with erroneous reference to Ångström (1876); the latter author did not mention the species (which had in fact not yet been described in 1876). Further Brazilian records of *R. wrightii* could not be confirmed in this study, therefore the species is excluded from the Brazilian list. The Brazilian specimens of *R. varilobula* and *R. elliotii* proved to be misidentifications and belong to *R. schaefer-verwimpii* K.Yamada and *R. angulata* Steph., respectively. The first record for Brazil of *R. microloba* from Rio Grande do Sul (Lindman 1906) and of *R. saccatiloba* from Rio de Janeiro (Dusén 1903) were not found in herbaria. *Radula marginata*, firstly reported from Rio de Janeiro (Oliveira e Silva & Feitosa 1997) were not ex-

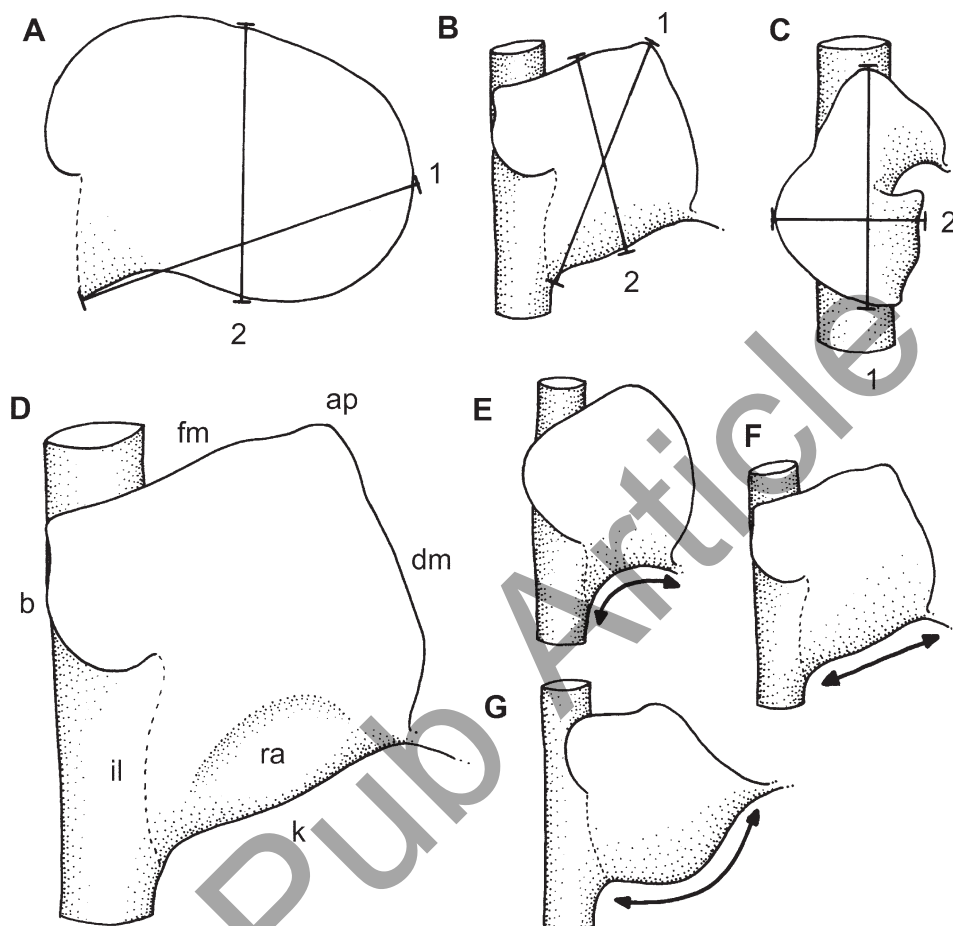


Fig. 1. A–G. Measurement and morphology of leaf lobes and lobules in *Radula*. A. Measurement of leaf lobes (1 = long; 2 = wide). B–C. Measurement of lobules (1 = long; 2 = wide). D. Lobule morphology (il = insertion line; b = base; fm = free margin; ap = apex; dm = distal margin; k = keel; ra = rhizoid area). E. Lobule with concave keel. F. Lobule with straight keel. G. Lobule with convex keel.

aminated and it is probably a misidentification (Reiner-Drehwald 1994, Yamada 2003). Since all other Brazilian collections of these three species proved to be misidentified, the occurrence of *R. marginata*, *R. microloba* and *R. saccatiloba* in Brazil is considered doubtful.

Concerning the worldwide distribution of Brazilian *Radula*, 13 species are widespread in tropical America, nine occur in tropical America and extend to subtropical and/or temperate regions of the continent, four species and one variety are endemic to Brazil, two are pantropical, one species is pantropical and occurs in northwestern Europe, one is Afro-American, and one occurs in tropical America and Macaronesia.

Widespread in tropical America: *Radula angulata*, *R. cubensis*, *R. fendleri* var. *fendleri*, *R. gottscheana*, *R. longiloba*, *R. mammosa*, *R. pallens*, *R. pocsii*, *R. pseudostachya*, *R. recubans*, *R. schaefer-verwimpitii*, *R. tenera*, *R. yanoella*.

Tropical America and subtropical and/or temperate regions of the continent: *Radula decora*, *R. ligula*, *R. mexicana*, *R. punctata*, *R. quadrata*, *R. sinuata*, *R. subinflata*, *R. tectiloba*, *R. xalapensis*.

Endemic to Brazil: *Radula bahiensis*, *R. brasilica*, *R. fendleri* var. *paroica*, *R. renneri*, *R. yamadae*.

Pantropical: *Radula javanica*, *R. stenocalyx*.

Pantropical and NW Europe: *Radula voluta*.

Afro-American: *Radula flaccida*.

Tropical America and Macaronesia: *Radula nudicaulis*.

Within Brazil, the Atlantic Forest region and Amazonia harbor the highest number of species. Few species occur in the Cerrado, Pampa and Caatinga domains, and no *Radula* species was recorded in Pantanal (Fig. 2). *Radula* species in Brazil occur from sea level to 2400 m elevation, growing on tree trunks, decaying wood and rock, occasionally on living leaves and soil. Six species (*R. flaccida*, *R. javanica*, *R. longiloba*, *R. stenocalyx*, *R. yamadae*, *R. yanoella*) occur on living leaves and four species (*R. convexa*, *R. javanica*, *R. fendleri*, *R. schaefer-verwimpitii*) on soil. The species prevail in humid, shaded places such as the understory of old-growth primary forests. Secondary forests harbor a relatively poor *Radula* flora.

Taxonomic treatment

***Radula* Dumort.**, Comment. Bot. 112. 1822.

Type: *Jungermannia complanata* L. [= *Radula complanata* (L.) Dumort.] (lectotype: OXF, designated by Grolle 1969).

Dioicous, rarely monoicous. PLANTS 0.8–3.5(–4) mm wide, green to yellowish-brown, brown in herbarium, rarely reddish-brown, regularly or irregularly (bi)pinnate to dichotomous branched. BRANCHES *Radula*-type, rarely *Lejeunea*-type. THALLUS absent, rarely present (*R. yanoella*). STEMS in cross section with 10–140 thin to thick-walled epidermal cells surrounding 5–200 thin to thick-walled medullary cells, rarely with a subepidermis (together with the epidermis forming a 2–4-layered, brownish cortex), medullary cells larger than epidermal cells or of the same size, epidermal and medullary cell walls colorless, yellowish or brown, trigones present or lacking, small to large when present. LEAVES incubous, divided into a large dorsal lobe and a smaller ventral lobe (=lobule), dorsal lobe obliquely to widely spreading, sometimes squarrose, distant to imbricate, plane to strongly concave, orbicular to oblong-ovate, sometimes falcate, 0.4–1.8 mm long, 0.3–1.7 mm

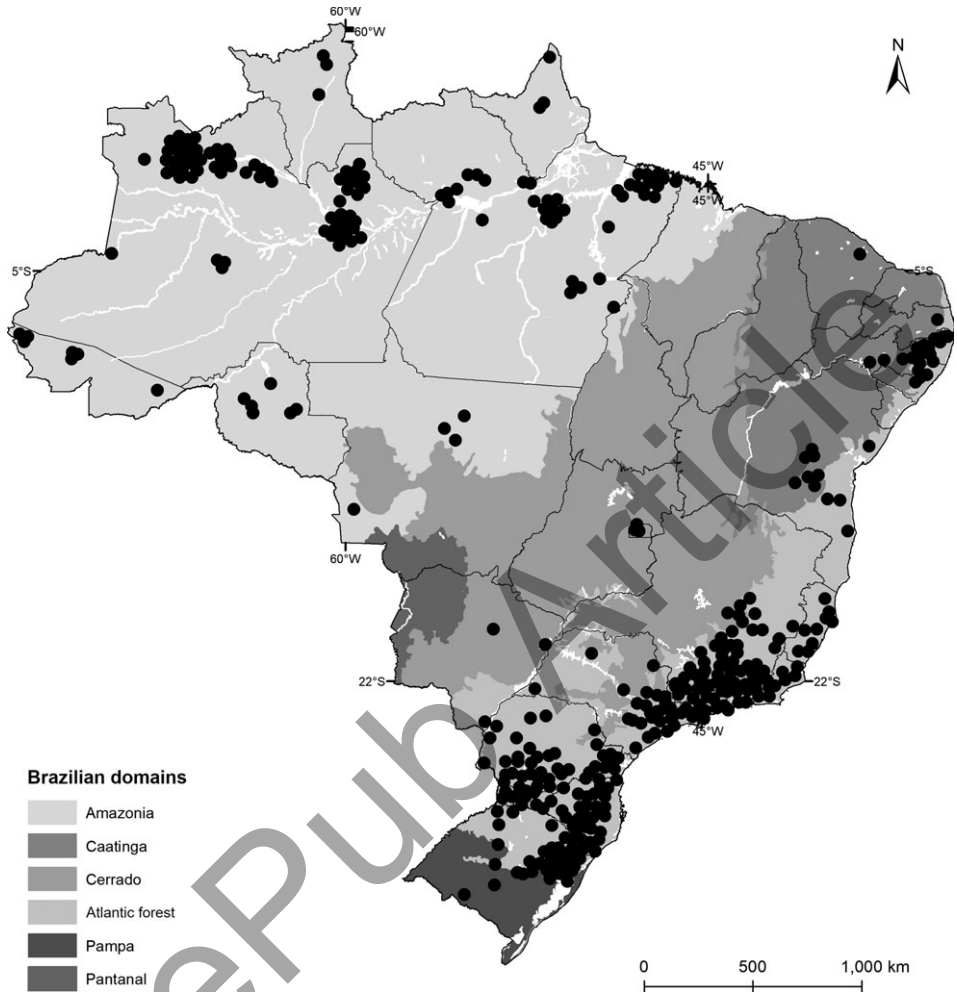


Fig. 2. Distribution of *Radula* species in Brazil and Brazilian domains.

wide, dorsal base rounded, overlapping the stem or not, apex rounded to subacute, margin plane to strongly recurved, entire to crenulate; marginal cells subquadrate to isodiametric, rarely rounded, $5\text{--}25 \times 5\text{--}20 \mu\text{m}$, median cells isodiametric to elongate, $12\text{--}25\text{--}(38) \times (8\text{--})10\text{--}25 \mu\text{m}$, basal cells isodiametric to elongate, $12\text{--}35\text{--}(40) \times (8\text{--})10\text{--}30 \mu\text{m}$, cell walls thin to evenly thickened, trigones small to large, sometimes increasing in size towards the margins, cuticle smooth, rarely finely papillose. LOBULES obliquely to widely spreading, distant to imbricate, quadrate to rectangular, orbicular to oblong, triangular-ovate to triangular-oblong or ligulate to folded-lunular, $0.14\text{--}1.2 \text{ mm}$ long, $0.1\text{--}1 \text{ mm}$ wide, $1/3\text{--}1/2$ the lobe length, inflated at the rhizoid area, along the keel or fully inflated, insertion line long to short, straight, arched, circinate or inverted J-shaped, base plane to

recurved, rounded to angulate, sometimes straight, occasionally auriculate, overlapping the stem or not, free margin plane to strongly recurved, straight to rounded, sometimes sinuate, apex plane to recurved or incurved, rounded to subacute, sometimes extended, distal margin straight to rounded, sometimes sinuate; keel straight to concave or convex, spreading at angles of 25–80° with the stem. RHIZOID in a fascicle from the lobules, colorless to brown, scanty to numerous, occasionally produced on a pronounced mammiliform swelling. ANDROECIA terminal or intercalary on short to long branches, sometimes preceding the gynoecia (in parocious plants), with 1–20 pairs of bracts, 0.3–1.7 mm wide; bracts imbricate, ovate, 0.25–1.2 mm long, 0.2–1 mm wide, apex rounded to obtuse, margin plane to recurved, entire, lobule hypostatic, imbricate, ovate to oblong, 1/2–3/4 of lobe length, base rounded to angulate, free margin straight to sinuate or recurved, apex rounded to subacute, keel convex, inflated. GYNOECIA on short to long branches, without or with 1–2 innovations, the innovations rarely rudimentary; bracts ovate to oblong-ovate, 0.45–1.7 mm long, 0.2–0.8 mm wide, apex rounded to obtuse, margin plane to recurved, entire, lobule usually oblong, rarely ovate, 1/3–1/2 of lobe length, apex rounded to obtuse. PERIANTHS campanulate to subcylindrical or trumpet-shaped, 1.4–4 mm long, 0.37–1.7 mm wide at apex, mouth entire to irregularly crenulate-undulate. VEGETATIVE REPRODUCTION by caducous leaf lobes, fragmentation of leaf lobes, fragmentation of main branches, caducous *Lejeunea*-type branches, regenerants, and by discoid gemmae (30–450 µm in diam.) produced on leaf margins, rarely on the perianth mouth or on (male or female) bracts.

Key to the species of *Radula* in Brazil

1. Plants growing on living leaves 2
1. Plants not growing on living leaves 8
2. Plants with persistent thallus (= persistent protonema) with short leafy shoots sprouting from thallus margins *R. yanoella*
2. Plants without a persistent thallus 3
3. Discoid gemmae produced on leaf margins 4
3. Gemmae lacking 5
4. Gemmae large (350–450 µm in diam.), base of gemmae deeply cordate-auriculate. Lobule apex extended towards an obtuse tip *R. flaccida*
4. Gemmae smaller (40–200 µm in diam.), base of gemmae not cordate-auriculate. Lobule apex rounded *R. stenocalyx*
5. Lobule keel straight. Rhizoid area inflated but not prominently projecting outwards *R. javanica*
5. Lobule keel strongly convex. Rhizoid area strongly inflated, prominently projecting outwards 6
6. Leaf apex rounded *R. mammosa*
6. Leaf apex obtuse to subacute 7

7. Lobules usually 1/3–1/4 the leaf length. Lobule base covering up to 1/3 the stem, keel straight (rarely slightly convex)	<i>R. longiloba</i>
7. Lobules usually 1/2–2/5 the leaf length. Lobule base covering 1/3 to fully overlapping the stem, keel strongly convex	<i>R. yamadae</i>
8. Discoid gemmae produced on leaf margins	9
8. Gemmae lacking	13
9. Plants 1–1.5 mm wide. Lobule base covering up to 1/2 the stem.	10
9. Plants 1.6–2.8 mm wide. Lobule base covering 1/2 to fully overlapping the stem	11
10. Plants without caducous leaves	4
10. Plants with caducous leaves	22
11. Lobules imbricate, base usually fully overlapping the stem.	<i>R. quadrata</i>
11. Lobules distant to subimbricate, base usually covering up to 2/3 the stem	12
12. Lobules distant. Lobule apex frequently somewhat extended, obtuse. Monoicous (paricous)	<i>R. renneri</i>
12. Lobules distant to subimbricate. Lobule apex not extended, rounded, rarely obtuse. Dioicous	<i>R. tectiloba</i>
13. Leaf lobes apex obtuse to subacute.	7
13. Leaf lobes apex rounded.	14
14. Lobule ligulate. Leaf lobes bordered by 3–4 rows of quadrate thick-walled cells.	<i>R. ligula</i>
14. Lobule not ligulate. Leaf lobes not bordered	15
15. Lobule folded and lunular.	<i>R. tenera</i>
15. Lobule not folded and lunular.	16
16. Lobule base auriculate	17
16. Lobule base not auriculate	20
17. Lobule base rounded to slightly auriculate, insertion line inverted J-shaped. Plants regularly pinnate.	<i>R. punctata</i>
17. Lobule base shortly to strongly auriculate, insertion line circinate. Plants irregularly pinnate	18
18. Auriculate base extending downwards beyond the keel. Keel short, 1/5–1/4 of leaf length	<i>R. gottscheana</i>
18. Auriculate base not extending downwards beyond the keel. Keel longer, 1/3–1/2 of leaf length	19
19. Lobule with strongly auriculate base, the base extending across and well beyond the stem and circinate coiled. Leaf cells with trigones small at leaf base increasing in size towards the margins, becoming bulging	<i>R. voluta</i>
19. Lobule with slightly auriculate base, the base not extending beyond the stem and not circinate coiled. Leaf cells without trigones	<i>R. sinuata</i>

20. Plants with caducous leaves 21

20. Plants without caducous leaves. 29

21. Plants 0.6–1.4 mm wide. Keel strongly convex 22

21. Plants 1–4 mm wide. Keel straight to slightly convex 23

22. Free margin of the lobules strongly recurved *R. brasiliica*

22. Free margin of the lobules plane. *R. schaefer-verwimpui*

23. Leaf lobes strongly recurved. Cells with trigones large, cuticle verruculose 24

23. Leaf lobes plane. Cells without or with trigones small, sometimes increasing in size from leaf base towards the margins, cuticle smooth. 25

24. Lobules distant, subrectangular (longer than wide). Lobule base covering up to 1/3 the stem *R. fendleri*

24. Lobules contiguous to subimbricate, usually subquadrate. Lobule base covering 1/2 to fully overlapping the stem. *R. pseudostachya*

25. Lobule base usually covering 3/4 to fully overlapping the stem 26

25. Lobule base usually covering up to 1/2 the stem 28

26. Plants 2.5–4 mm wide. Leaves distant to contiguous *R. xalapensis*

26. Plants 1–1.8 mm wide. Leaves subimbricate to imbricate 27

27. Leaf lobes ovate, margin entire. Cells with trigones small at leaf base increasing in size towards the margins. Keel spreading at angles of 60–70° with the stem *R. angulata*

27. Leaf lobes ovate to falcate-ovate (strongly falcate on branches), margin entire to weakly undulate. Cells without trigones. Keel spreading at angles of 40–50° with the stem. *R. cubensis*

28. Leaves distant to contiguous. Lobules rhombic *R. pocsii*

28. Leaves imbricate. Lobules (sub)quadrate *R. javanica*

29. Lobule with conspicuously extended, subacute apex 30

29. Lobule without conspicuously extended, subacute apex 31

30. Lobule base rounded to angulate, covering 3/4 to fully overlapping the stem. Leaf cells with trigones small at leaf base increasing in size towards the margins. Dioicous *R. angulata*

30. Lobule base rounded, covering up to 1/2 the stem. Leaf cells with trigones small or lacking. Monoicous. *R. mexicana*

31. Leaf lobes strongly convex 32

31. Leaf lobes plane to slightly convex 33

32. Lobules inflated at rhizoid area only. Leaf cells dorsally smooth *R. decora*

32. Lobules inflated along the keel, flattened above. Leaf cells dorsally mammillose *R. subinflata*

33. Lobules subrectangular (longer than wide). Monoicous (parocous) *R. fendleri* var. *parocous*

33. Lobules subquadrate. Dioicous. 34

34. Lobule base covering more than 1/2 to fully overlapping the stem 35
34. Lobule base covering up to 1/2 the stem (except on branches of *R. pallens*). 36
35. Plants irregularly branched. Leaf lobes oblong-ovate. Leaf cells with trigones small at leaf base increasing in size towards the margins, cuticle smooth *R. bahiensis*
35. Plants regularly branched. Leaf lobes ovate. Leaf cells with trigones small, cuticle verruculose *R. recubans*
36. Keel strongly convex. Rhizoid numerous on a pronounced mammiliform swelling of the lobule *R. mammosa*
36. Keel concave to straight. Rhizoid not as above 37
37. Leaves distant to contiguous. 38
37. Leaves imbricate. 39
38. Lobules rhombic, keel spreading at angles of 30–40° with the stem. Dorsal leaf base not overlapping the stem. Vegetative reproduction by caducous leaf lobes, producing almost completely naked branches *R. pocsii*
38. Lobules subquadrate, keel spreading at angles of 45–50° with the stem. Dorsal leaf base fully overlapping the stem. Vegetative reproduction absent *R. nudicaulis*
39. Leaves suborbicular. Keel straight to concave. Caducous leaf lobes absent *R. pallens*
39. Leaves ovate to falcate-ovate. Keel straight. Caducous leaf lobes present *R. javanica*

***Radula angulata* Steph.**, Hedwigia 23: 114. 1884.

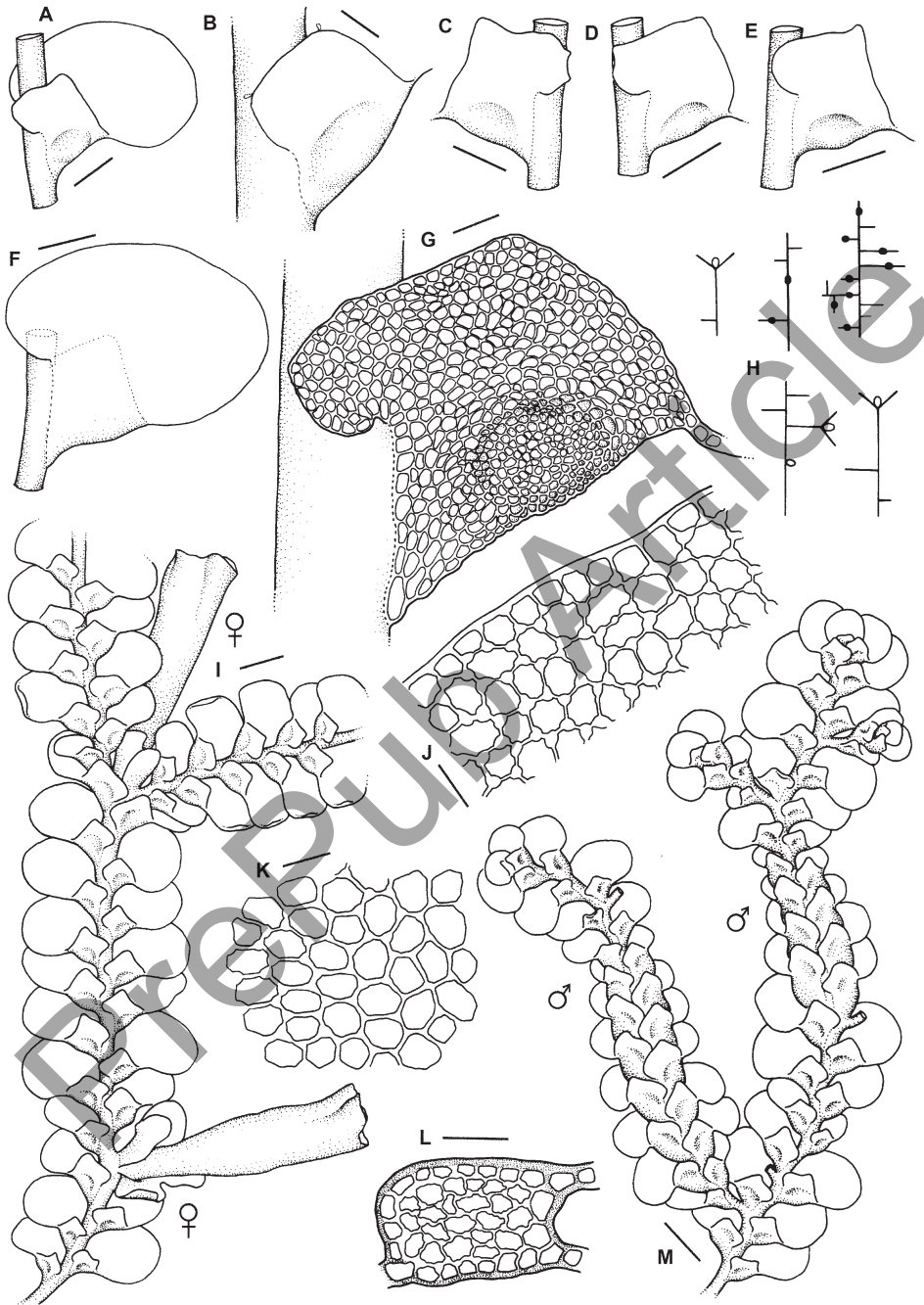
Fig. 3

Type: Venezuela, Caripe, *Moritz 152* (holotype: G-00043973!).

= *Radula korthalsii* Steph., Hedwigia 23: 133. 1884. Type: Venezuela, P. W. Korthals 184, ex hb. Sand. Lac. (lectotype: G-00283269!, designated by Yamada 1980). Venezuela. A. Fendler s.n., ex hb. Gottsche (syntype: G-00281267).

Dioicous. PLANTS 1.4–2 mm wide, yellowish-green to yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 20 thick-walled epidermal cells surrounding ca. 21 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones large. LEAVES obliquely to widely spreading, imbricate, slightly convex, ovate, 0.7–1.2 mm long, 0.65–0.9 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane, 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

Fig. 3. *Radula angulata* – A. Leaves, ventral view. B–E, G. Lobules. F. Leaf, dorsal view. H. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). I. Habit with gynoecia. J. Marginal leaf cells. K. Median leaf cells. L. Cross section of a stem. M. Habit with androecia. (A, C–F = 250 µm; B = 100 µm; G, L = 50 µm; I, M = 500 µm; J, K = 25 µm; A, C–F, J–L from the holotype in G; B, G–I, M from UFP-30030).



thin, trigones small at leaf base and midleaf, increasing in size towards the margins, cuticle smooth. LOBULES distant to contiguous, (sub)quadrate, 0.75–0.45 mm long, 0.35–0.55 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion line straight, base plane, rounded to angulate, covering 3/4 to fully overlapping the stem, free margin plane, straight, apex plane, acute to obtuse, distal margin straight; keel straight, spreading at angles of 50–70° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA terminal to intercalary on long branches, with 5–10 pairs of bracts, 0.8–1.1 mm wide; bracts 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. PERIANTHS subcylindrical, 2.4–2.8 mm long, 0.65–1.1 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by means of caducous leaf lobes and stem fragmentation.

Additional description and illustration: Castle (1964, p. 194–195, Fig. 4), Castle (1966, p. 8–10, Fig. 2 as *R. korthalsii*), Yamada (1980, p. 250–251, Fig. 6 as *R. korthalsii*, 1991, p. 87–88, Fig. 38).

Distribution and habitat: West Indies, Colombia, Venezuela, Brazil. In Brazil recorded from Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. The species grows in Atlantic forest, usually on tree trunks and decaying wood, at 670–1900 m elevation.

Taxonomic notes: *Radula angulata* is characterized by (1) plants irregularly pinnate; (2) leaf lobes ovate with entire margins, sometimes caducous; (3) leaf cell walls thin with small to large trigones increasing in size towards the margins; (4) lobules distant to contiguous, (sub)quadrate, base rounded to angulate, covering 3/4 to fully overlapping the stem, apex usually acute, and keel straight.

This species is similar to *R. cubensis*, especially in the lobule shape. *Radula cubensis*, however, has leaves ovate to strongly falcate-ovate, margin plane to undulate, cell walls thin, trigones lacking, and keel straight, spreading at angles of 40–50° with the stem (50–70° in *R. angulata*). *Radula angulata* may also be confused with *R. mexicana* but the latter species is monoicous, trigones are small or lacking, and the lobule base covers up to 1/2 the stem.

Selected examined specimens: BRAZIL. BAHIA: Abaíra, Mata da Serra do Rei, 14°16'N, 41°54'W, 1550–1650 m, 17 February 1992, Harley et al. 52108 (SP). ESPÍRITO SANTO: Domingos Martins, Reserva florestal “Pedra azul” östlich Venda Nova, 1200 m, 25 July 1987, Schäfer-Verwimp & Verwimp 8880 (MG). MINAS GERAIS: Parque Nacional do Itatiaia, along entry road near border of Rio de Janeiro, 22°22'S, 44°45'W, 1700–1900 m, 4 July 1991, Vital & Buck 19523 (NY). PARANÁ: Morretes, Parque Estadual Pico do Marumbi, 15 April 2015, Amélio 79 (SP). PERNAMBUCO: Caruaru, Brejo dos Cavalos, 27 August 1987, Pôrto s.n. (UFP). RIO DE JANEIRO: 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). RIO GRANDE DO SUL: Viamão, Parque Saint Hilaire, 28 August 1994, Michael

s.n. (ICN). SANTA CATARINA: Bergland bei Curitiba, 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, 23°26'38"S, 45°14'01"W, 867 m, 11 June 2013, Carmo & Peralta 588 (SP).

***Radula bahiensis* F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst.**, Phytotaxa 454(1): 25. 2020. Fig. 4

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, Vital & Buck 20271 (holotype: SP-353920!; isotype: MG!).

Dioicous. PLANTS 2–3.5 mm wide, green to olive-green in herbarium, irregularly pinnately branched. STEMS in cross section with ca. 29 thick-walled epidermal cells surrounding ca. 47 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones small. LEAVES widely spreading, imbricate, slightly convex, oblong-ovate, 1–1.8 mm long, 0.6–1.1 mm wide, dorsal base rounded, overlapping the stem, apex rounded to obtuse, margin plane, entire to sinuate; 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, cuticle smooth. LOBULES distant to subimbricate, oblong, 0.7–0.9 mm long, 0.5–0.7 mm wide, ca. 1/2 of the lobe length, inflated along the keel, insertion line ± straight, base plane, rounded, covering 2/3 to fully overlapping the stem, free margin plane, straight, apex rounded to obtuse, distal margin ± straight to rounded; keel straight to sinuate-concave, spreading at angles of 40–50° with the stem. RHIZOIDS colorless, scanty. ANDROECIA terminal to intercalary on long branches, with 2–4 pairs of bracts, 1.1–1.4 mm wide; bracts ovate, 0.8–1 mm long, 0.3–0.5 mm wide, apex rounded, margin plane, entire to sinuate, lobule distant to contiguous, ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex rounded; keel convex, inflated. GYNOECIA on long branches, with one innovation; 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. PERIANTHS not seen. VEGETATIVE REPRODUCTION by stem fragmentation and caducous *Lejeunea*-type branches. (Oliveira-da-Silva et al. 2020).

Distribution and habitat: Only known from Bahia, occurring on tree trunks, at 50–200 m elevation.

Taxonomic notes: *Radula bahiensis* is recognized by (1) leaves widely spreading, oblong-ovate, apex rounded to obtuse, margin entire to shallowly sinuate; (2) leaf cells with small trigones at base increasing in size towards the leaf margins; (3) lobules oblong with base covering 2/3 to fully overlapping the stem, lobule apex rounded to obtuse, distal margin straight to rounded, and keel straight to sinuate-concave.

The species resembles robust *R. pallens* in leaves widely spreading, and keel straight to concave (Oliveira-da-Silva et al. 2020). *Radula pallens*, however, differs in leaves subor-

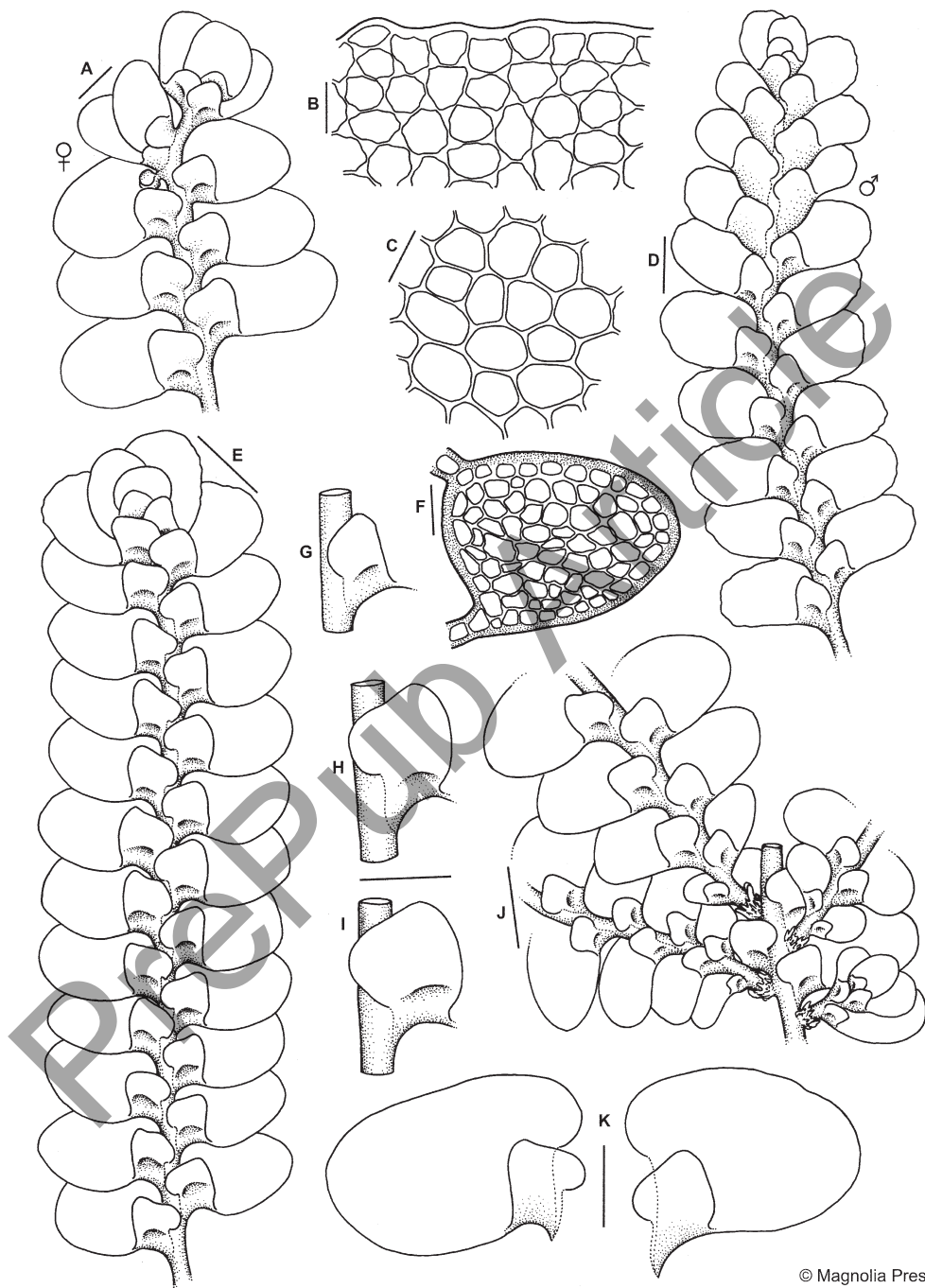


Fig. 4. *Radula bahiensis*. A. Habit with gynoecia. B. Marginal leaf cells. C. Median leaf cells. D. Habit with androecia. E, J. Habit. F. Cross section of a stem. G–I. Lobules. K. Leaves. (A, C, G, H, I, K = 500 μm ; B, D = 25 μm ; F = 50 μm ; E, J = 1000 μm ; A, E from the holotype in SP; D from the paratype in NY; B, C, F, G, H, I, J, K from the paratype in SP). From Oliveira-da-Silva et al. (2020), reproduced with permission from copyright holder.

bicular with broadly rounded apex, trigones usually lacking, and lobules (sub)quadrate with base covering 1/4–1/3 the stem.

Additional specimen examined: BRAZIL. BAHIA: Una, Maruim, border of the fazendas Maruim and Dois de Julho, 33 km SW of Olivença on road from Olivença to Burarema, Southern Bahian wet forest, epiphytic on tree, in full shade, 28 April 1981, Boom et al. 811 (paratype: NY).

Radula brasílica K.Yamada, J. Hattori Bot. Lab 74: 35. 1993.

Fig. 5

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, Schäfer-Verwimp & Verwimp 8484 (holotype: NICH-413169!).

Dioicous. PLANTS 0.8–1.4 mm wide, yellowish-green in herbarium, irregularly pinnate. STEMS in cross section with ca. 16 thick-walled epidermal cells surrounding ca. 16 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones lacking. LEAVES widely spreading to squarrose, imbricate, plane to slightly convex, ovate to strongly falcate-ovate, 0.4–0.55 mm long, 0.3–0.4 mm wide, dorsal base rounded, not overlapping the stem, apex rounded to obtuse, margin plane, entire to slightly crenulate; marginal cells subquadrate to isodiametric, 8–20 μm in diam., median cells and basal cells isodiametric to elongate, 15–25 \times 10–20 μm , cell walls thin, trigones small, cuticle smooth. LOBULES distant to contiguous, subquadrate, 0.14–0.5 mm long, 0.1–0.4 mm wide, 1/3–1/2 the lobe length, insertion line straight to arched, base 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 40–60° with the stem, lobule inflated along the keel. RHIZOIDS colorless, scanty. ANDROECIA terminal to intercalary on long branches, with 3–6 pairs of bracts, 0.65–0.7 mm wide; bracts 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 not seen. VEGETATIVE REPRODUCTION by caducous leaf lobes, producing almost completely naked branches, and by small discoid gemmae, ca. 40–65 μm in diam., produced on leaf margins.

Additional description and illustration: Yamada (1993b, p. 35–37, Fig. 1).

Distribution and habitat: Only known from the type from São Paulo State, in Atlantic forest, growing on decaying wood at 1850 m elevation.

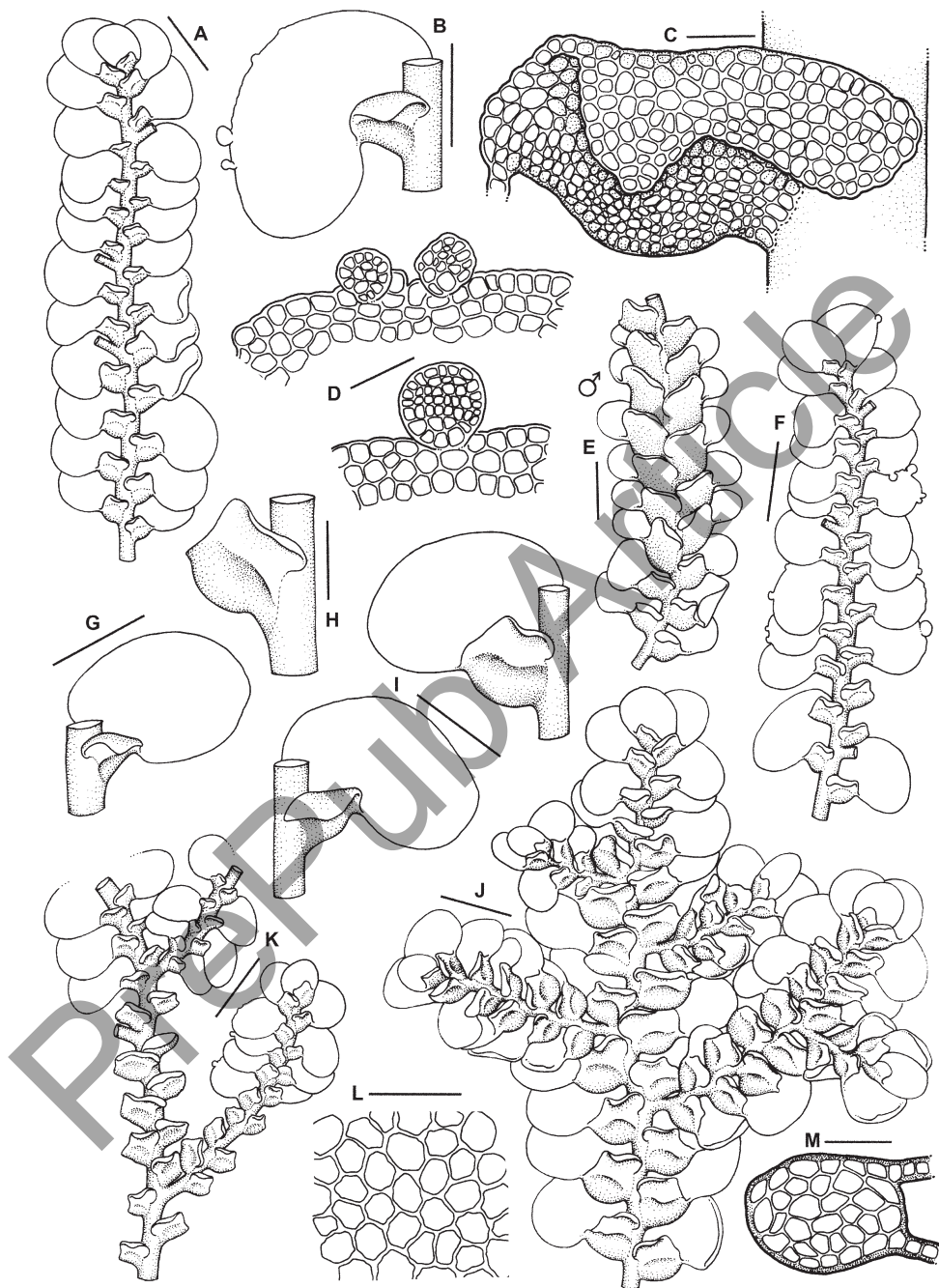


Fig. 5. *Radula brasiliica* – A, F, J, K. Habit. B, G, I. Leaves. C, H. Lobules. D. Leaf margin with regenerants. E. Habit with androecia. L. Median leaf cells. M. Cross section of a stem. (A, E, F, J, K = 500 µm; B, G, I = 250 µm; C, D, L, M = 50 µm; H = 100 µm; A–K from the holotype in NICH).

Taxonomic notes: *Radula brasiliica* differs from other *Radula* species in Brazil by (1) plants small (0.8–0.14 mm wide) and fragile due to caducous leaf lobes often resulting in almost naked branches; (2) leaf lobes ovate to falcate-ovate, with margins entire to slightly crenulate with regenerants; (3) lobules distant to contiguous, subquadrate, with base rounded, recurved, covering 1/3–1/2 the stem, free margin strongly recurved, and keel straight to strongly convex.

Due to the small and fragile plants (with caducous leaf lobes), and the strongly convex keel, *R. brasiliica* may be confused with *R. schaefer-verwimpii*. However, the latter species has subquadrate to rhombic lobules with the base covering only 1/5–1/3 the stem and free margin plane.

All studied specimens labelled as *R. brasiliica* in Brazilian herbaria proved to be misidentifications and mostly belong to *R. javanica*. Hitherto, *R. brasiliica* is only known from the type.

***Radula cubensis* K.Yamada**, J. Hattori Bot. Lab. 54: 241. 1983.

Fig. 6

Type: Cuba, Santiago de Cuba, Gran Piedra, on bark, 16 January 1979, D. Reyes M. 1621 (isotype: NICH-400980!).

Dioicous. PLANTS 1–1.7 mm wide, yellowish-green to green in herbarium, irregularly pinnate. STEMS in cross section with 10–12 thick-walled epidermal cells surrounding ca. 11 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish to colorless, trigones lacking. LEAVES widely spreading to squarrose, subimbricate, slightly convex, ovate to strongly falcate-ovate, 0.6–0.9 mm long, 0.4–0.5 mm wide, dorsal base rounded, not overlapping the stem, 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, cuticle smooth. LOBULES distant to contiguous, subquadrate, 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 line straight, base plane to slightly recurved, rounded to obtuse, covering 3/4 to fully overlapping the stem, free margin plane, straight to ± sinuate at middle, apex plane, rounded to obtuse, distal margin straight; keel straight, spreading at angles of 40–50° with the stem. RHIZOIDS colorless, scanty. ANDROECIA intercalary on long branches, with 2–4 pairs of bracts, 0.9–1.4 mm wide; bracts ovate, 0.7–1 mm long, 0.3–0.5 mm wide, margin entire, plane to recurved, apex obtuse, 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. PERIANTHS subcylindrical, ca. 1.9 µm long, ca. 0.8 µm wide at apex,

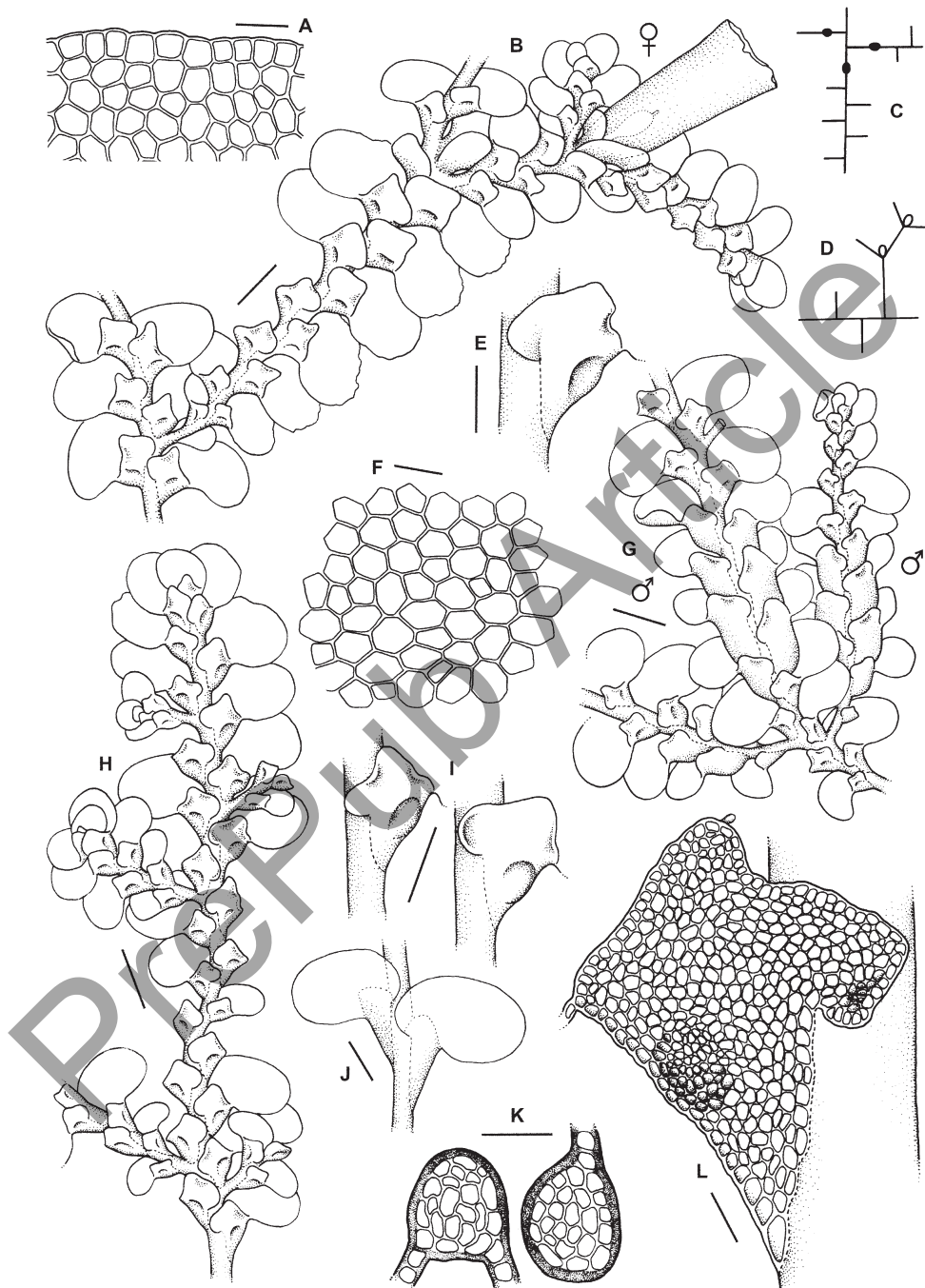


Fig. 6. *Radula cubensis* – A. Marginal leaf cells. B. Habit with gynoecia. C–D. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). E, I, L. Lobule. F. Median leaf cells. G. Habit with androecia. H. Habit. J. Habit, dorsal view. K. Cross section of a stem. (A, F = 25 µm; B, G, H = 500 µm; E, I, J = 250 µm; K–L = 50 µm; A, E, F, H–L from isotype in NICH; B, D from UFP-17966; C, G from SP-42291).

mouth irregularly undulate. VEGETATIVE REPRODUCTION by caducous leaf lobes, producing almost naked branches.

Additional description and illustration: Yamada (1983, p. 241–243, Fig. 1).

Distribution and habitat: Dominican Republic, Jamaica, Cuba, Ecuador, and Brazil. In Brazil recorded from Bahia, Espírito Santo, Minas Gerais, Pará, Paraná, Pernambuco, Rio Grande do Sul, Santa Catarina and São Paulo. This species usually colonizes tree trunks or decaying wood at 20–1250 m elevation.

Taxonomic notes: *Radula cubensis* presents the following diagnostic characters: (1) plants fragile, with almost naked branches due to caducous leaf lobes; (2) leaves ovate to strongly falcate-ovate with plane to weakly undulate margins; (3) leaf cell walls thin, trigones lacking; (4) lobule distant to contiguous, base plane to slightly recurved, rounded to obtuse, covering 3/4 to fully overlapping the stem, free margin straight to ± sinuate at middle, apex rounded to obtuse, and keel straight.

Radula cubensis is morphologically similar to *R. angulata*, especially in lobule shape (see discussion under *R. angulata*). The species also resembles *R. javanica* in the falcate-ovate leaves and absence of trigones. However, the latter species differs in the lobule apex varying from obtuse to (rarely) acute and lobule base rounded, covering up to 1/2 the stem.

Selected examined specimens: BRAZIL. BAHIA: Igrapiúna, Reserva Ecológica de Michelin, 13°48'S, 39°10'W, 15 February 2006, Bastos 4217 (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: Alto da Friburgo, estação de Theodoro de Oliveira, 1 May 1923, Vaughan Bandeira s.n. (RB). RIO GRANDE DO SUL: Viamão, Parque Saint Hilaire, 13 September 1969, Oliveira s.n. (ICN). SANTA CATARINA: Serra do Rio do Rastro, entre municípios Bom Jardim da Serra e Lauro Muller, 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).

Radula decora Steph., Hedwigia 23: 145. 1884.

Fig. 7

Type: Venezuela, Valencia, 1856, Fendler s.n., ex hb. Gottsche (lectotype: G-00121933!, designated by Yamada 1987).

Dioicous. PLANTS 1.3–1.7 mm wide, green to brownish in herbarium, irregularly pinnate branched. STEMS in cross section with ca. 15 thick-walled epidermal cells surrounding ca. 13 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls yellowish, trigones large. LEAVES obliquely to widely spreading, imbricate, strongly convex, suborbicular, 0.5–0.9 mm long, 0.4–0.7 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin entire, slightly recurved; marginal cells subquadrate, 10–12.5 μm in diam., median and basal cells isodiametric to elongate, 20–25 \times 10–20 μm , cell walls thin, trigones small at leaf base and midleaf, increasing in size towards the margins, cuticle smooth. LOBULES distant to contiguous, subquadrate, 0.75–0.45 mm long, 0.35–0.55 mm wide, ca. 1/2 the lobe length, inflated, insertion line \pm straight, base plane, rounded, covering 3/4 or less of the stem, free margin plane, straight, apex plane, rounded; keel convex, spreading at angles of 60–70° with the stem. RHIZOIDS colorless to brown, scanty. 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 \pm straight, apex obtuse. GYNOCIA not seen. VEGETATIVE REPRODUCTION not observed.

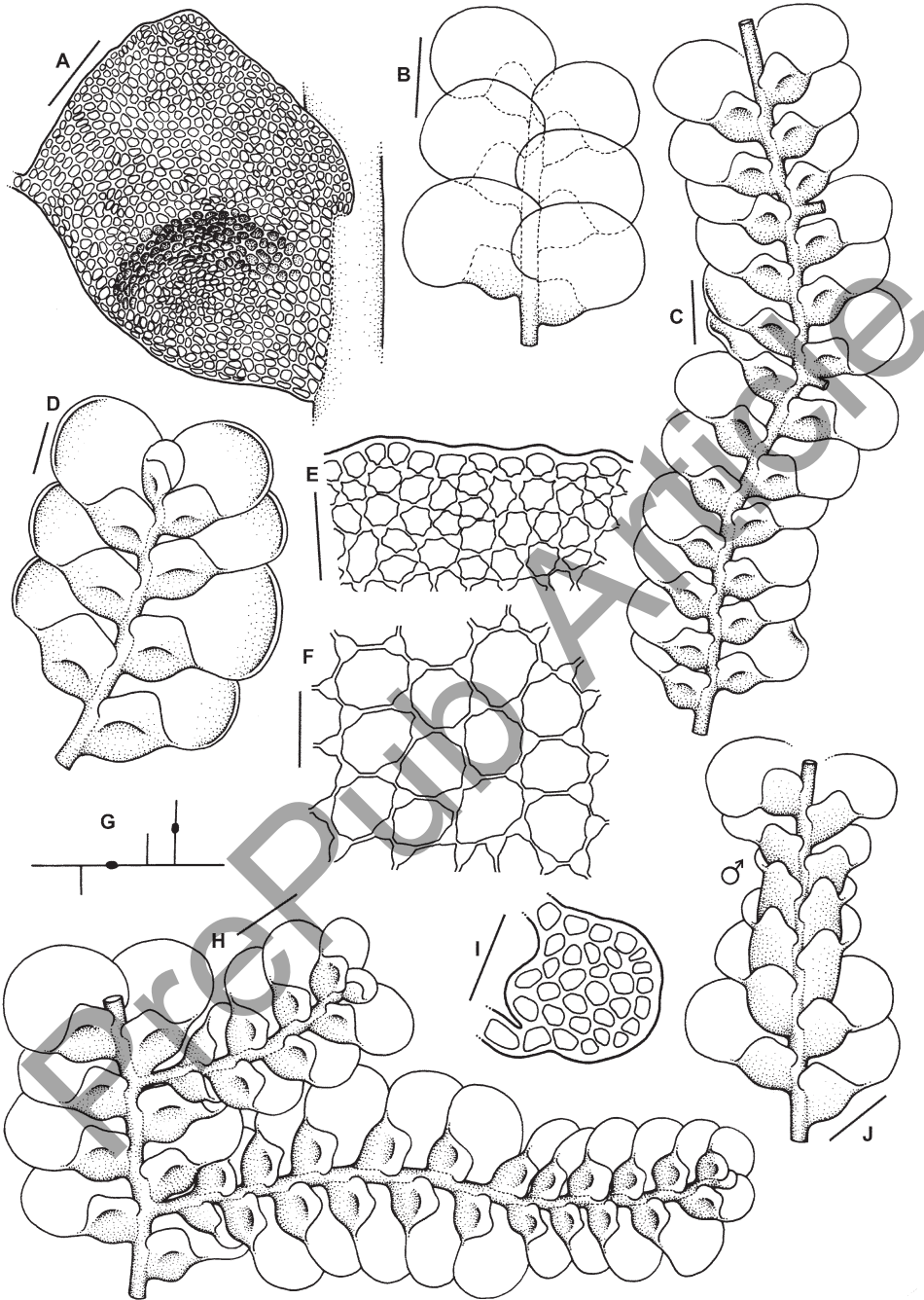
Additional description and illustration: Castle (1963, p. 15–17, Fig. 6), Solari (1978, p. 185–187, Fig. 3), Yamada (1987, p. 292–294, Figs. 33–34).

Distribution and habitat: Guadeloupe, Martinique, Ecuador, Venezuela, Brazil and Chile. In Brazil only known from Pernambuco and São Paulo, growing on bark of living trees and on rock at 50–900 m elevation.

Taxonomic notes: *Radula decora* is recognized by (1) leaves imbricate, strongly convex, suborbicular, with margin slightly recurved; (2) leaf cell walls thin, trigones small, increasing in size towards the leaf margins; (3) lobules subquadrate, inflated, with rounded base, covering up to 3/4 the stem, and keel convex. This is the only species of subg. *Odontoradula* in Brazil.

According to Yamada (1987), *Radula decora* is closely similar to *R. saccatiloba* (species excluded from Brazil), but the lobules in *R. saccatiloba* are narrowly inflated along the keel and flattened above while those in *R. decora* are completely inflated. Schiffner & Arnell (1964) recorded *R. decora* from São Paulo State; this record needs verification. From the specimens deposited in Brazilian herbaria as *R. decora*, only two collections,

Fig. 7. *Radula decora* – A. Lobule. B. Habit dorsal view. C, D, H. Habit. E. Marginal leaf cells. F. Median leaf cells. G. Cladograph of fertile plants (solid ellipse = androecia). I. Cross section of a stem. J. Habit with androecia. (A = 100 μm ; B, C, H, J = 500 μm ; D = 250 μm ; E, I = 50 μm ; F = 25 μm ; A, D, F, I from the lectotype in G; B, C, E, G, H from UFP-17962).



from Pernambuco and São Paulo, are *R. decora*. Others belong to *R. javanica*, *R. angulata* or *R. pallens*.

Selected examined specimens: BRAZIL. 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 fendleri* Steph. var. *fendleri, Hedwigia 23: 146. 1884.

Fig. 8

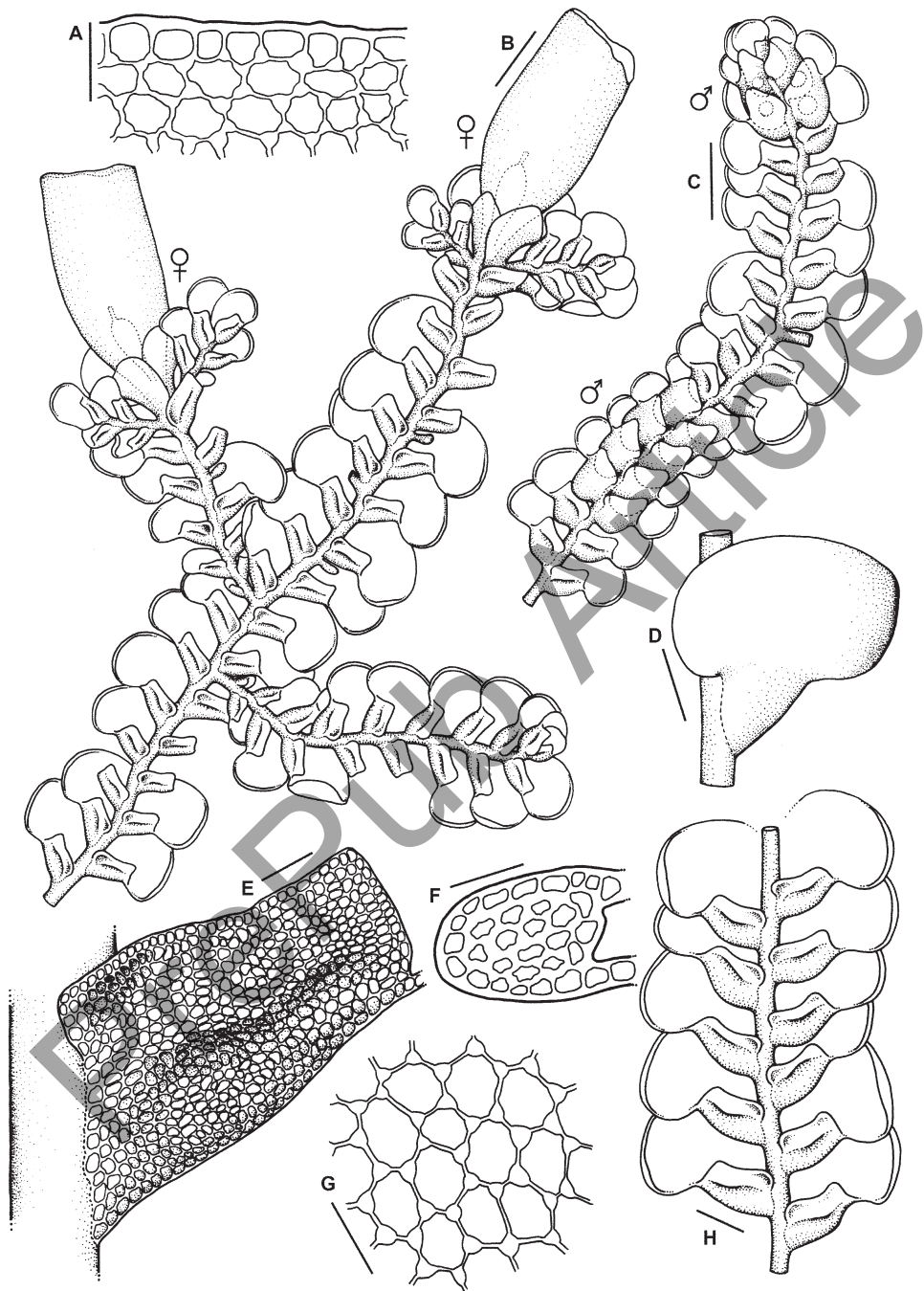
Type: Venezuela, Valencia, "in cortice repens," Fendler s.n. (lectotype: G-00121978!, designated by Yamada 1980). Guadeloupe, L'Herminier s.n., ex hb. Gottsche (syntype: G-00281263!).

Dioicous. PLANTS 1–1.8 mm wide, green to brownish in herbarium, irregularly pinnate. STEMS in cross section with ca. 17 thick-walled epidermal cells surrounding ca. 12 thick-walled medullary cells, epidermal and medullary cells of the same size, cell walls brown, trigones large. LEAVES 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, 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, cuticle verruculose. 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 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 50–60° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA terminal to intercalary on short branches, with 2–5 pairs of bracts, 0.8–0.9 mm wide; bracts 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 two innovations, innovations usually 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. PERIANTHS subcylindrical, 1.4–2.2 µm long, 0.7–0.8 µm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by caducous leaf lobes.

Additional description and illustration: Castle (1963, p. 5–7, Fig. 1), Yamada (1980, p. 244–246, Fig. 2).

Distribution and habitat: West Indies and tropical South America. In Brazil recorded from Bahia, Minas Gerais, Paraná, Rio Grande do Sul and São Paulo. The species grows in Atlantic forest, usually on tree trunks at 450–2400 m elevation.

Fig. 8. *Radula fendleri* var. *fendleri* – A. Marginal leaf cells. B. Habit with gynoecia. C. Habit with androecia. D. Leaf, dorsal view. E. Lobule. F. Cross section of a stem. G. Median leaf cells. H. Habit. (A, G = 25 µm; B, C = 500 µm; D, H = 250 µm; E, F = 50 µm; A, D–H from syntype in G; B from SP-395292; C from SP-280213).



Taxonomic notes: *Radula fendleri* is characterized by (1) caducous leaf lobes; (2) leaves ovate, strongly convex, with strongly recurved margin; (3) leaf cells with large trigones and cuticle verruculose; (4) lobules distant, subrectangular (longer than wide), inflated along the keel and flattened above, base covering ca. 1/3 the stem, apex rounded to obtuse.

This species resembles *R. pseudostachya* in the production of caducous leaf lobes, leaf margin strongly recurved, cells with large trigones, and cuticle verruculose. However, *R. pseudostachya* differs by lobule contiguous to subimbricate, 0.4–0.6 × 0.25–0.4 mm (0.3–0.5 × 0.1–0.25 mm in *R. fendleri*), and base covering 1/2 to fully overlapping the stem. Moreover, *R. fendleri* usually produces few caducous leaf lobes whereas in *R. pseudostachya* caducous leaves are produced in great abundance, leaving most branches almost completely naked.

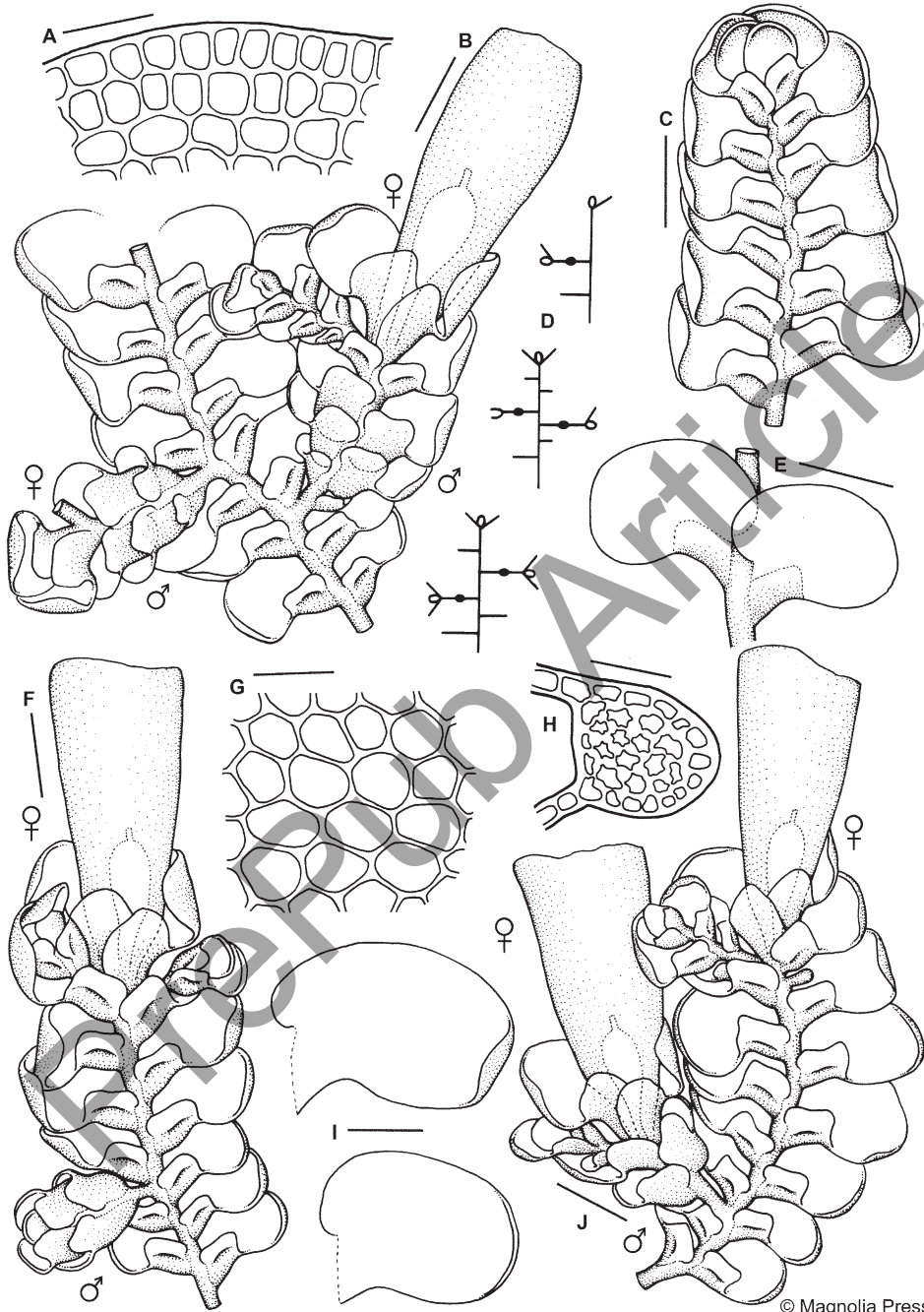
Selected examined specimens: BRAZIL. BAHIA: Abaíra, Campo de Ouro Fino (baixo), 13°15'N, 41°54'W, 1600–1700 m, 18 January 1992, Hind & Queiroz 50091 (SP). MINAS GERAIS: Nova Lima, Reserva Particular do Patrimônio Natural Parque Natural do Caraça, Trilha do Belchior, 20°05'43"S, 43°29'27"W, 1270 m, 27 July 2010, Peralta & Marcelli 11777 (SP). PARANÁ: Morretes, Parque Estadual Pico do Marumbi, Mata Atlântica, trilha entre a estação Marumbi e Cesário Lange, 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).

***Radula fendleri* var. *paroica* F.R.Oliveira-da-Silva, Ilk.-Borg. & Gradst., Phytotaxa 454(1): 29. 2020.** Fig. 9

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 (paroicous). PLANTS 1–1.8 mm wide, brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 16 thick-walled epidermal cells surrounding ca. 13 thick-walled medullary cells, epidermal and medullary cells of the same size, cell walls brownish, trigones large. LEAVES widely spreading, imbricate, strongly convex, ovate to falcate-ovate, 0.6–0.8 mm long, 0.5–0.6 mm wide, dorsal base rounded, overlapping the stem, 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 lacking to small, cuticle verruculose. LOBULES distant, subrectan-

Fig. 9. *Radula fendleri* var. *paroica*. A. Marginal leaf cells. B, C, F, J. Habit. D. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). E. Leaf, dorsal view. G. Median leaf cells. H. Cross section of a stem. I. Leaf lobes. (A, G = 25 µm; B, C, E, F, J = 500 µm; H = 50 µm; I = 250 µm; A–J from the holotype in RB). From Oliveira-da-Silva et al. (2020), reproduced with permission from copyright holder.



gular, 0.3–0.5 mm long, 0.1–0.3 mm wide, ca. 1/2 the lobe-length, strongly inflated along the keel, 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 arched, spreading at angles of 45–60° with the stem. RHIZOIDS colorless, scanty. 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. PERIANTHS subcylindrical, 1.8–2.2 mm long, 0.65–0.9 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION not observed. (Oliveira-da-Silva et al. 2020).

Distribution and habitat: This variety is only known from the type from Rio de Janeiro State, growing on decaying wood in Atlantic forest.

Taxonomic notes: The new variety differs from the typical one by plants paroicous (dioicous in var. *fendleri*), leaf cells with small trigones or without trigones (large in var. *fendleri*), and absence of caducous leaves (caducous leaves present in var. *fendleri*) (Oliveira-da-Silva et al. 2020).

Radula flaccida Lindenb. & Gottsche, Syn. Hepat. 726. 1847.

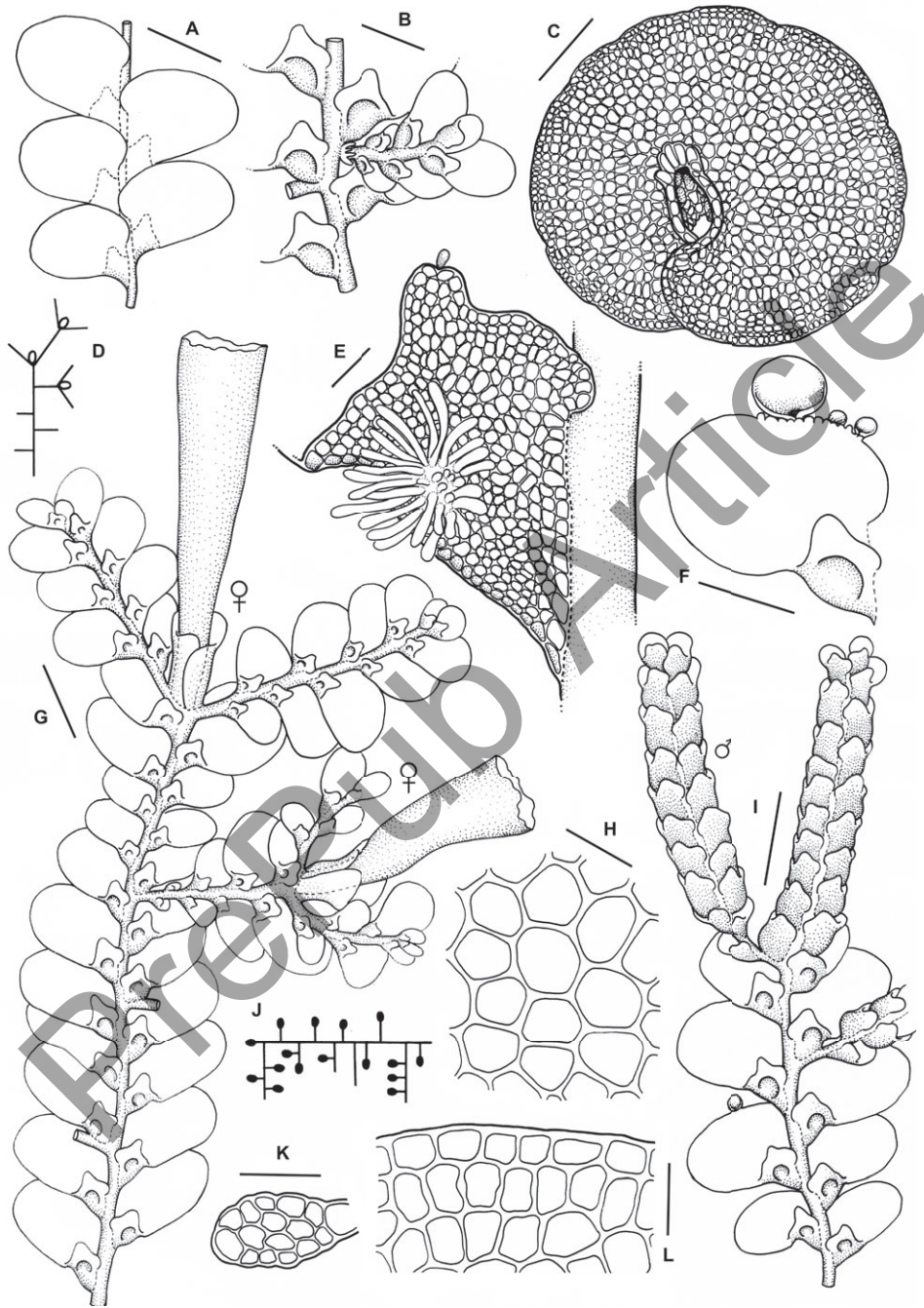
Fig. 10

Type: Mexico, “Prope Hacienda de Fovo foliis Psychotriae cuiusdam arcitissime irre-pens,” Liebmann s.n. (lectotype: BM-000969204!, designated here; isolectotypes: S-B43094!, S-B43089!).

= *Radula epiphylla* Mitt., Hedwigia 23: 151. 1884. Type: Niger, Barter s.n. (lectotype: NY-00831329!, designated here; isolectotypes: NY-00831330!, NY-00831331!).

Dioicous. PLANTS 1–1.5 mm wide, yellowish-green to green in herbarium, irregularly pinnate, rarely bipinnate. STEMS in cross section 9–11 thin-walled epidermal cells surrounding 3–4 thin-walled medullary cells, epidermal and medullary cells of the same size, cell walls colorless, trigones lacking. LEAVES obliquely to widely spreading, contiguous to subimbricate, slightly convex, ovate to ± obovate, 0.6–0.8 (–0.9) mm long, 0.35–0.65 mm wide, dorsal base rounded, not overlapping the stem, 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, cuticle smooth. LOBULES distant, (sub)quadrate, 0.15–

Fig. 10. *Radula flaccida* – A. Habit, dorsal view. B. Habit with *Lejeunea*-type branches. C. Gemmae. D, J. Cladograph of fertile plants (open ellipse = gynoecia, solid ellipse = androecia). E. Lobule. F. Leaf with gemmae. G. Habit with gynoecia. H. Median leaf cells. I. Habit with androecia. J. Cross section of a stem. L. Marginal leaf cells. (A, G, I = 500 µm; B, F = 250 µm; C = 100 µm; E, K = 50 µm; H, L = 25 µm; A, D, E, F, H, L from MG-171633; B, J from SP-433662; C, K from MG-174047; G, I from SP-134581).



0.3 (–0.4) mm long, 0.1–0.2 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion line \pm straight, base plane, covering 1/5–1/4 the stem, free margin plane, straight to sinuate, apex plane, extended towards an obtuse tip, distal margin straight; keel convex, spreading at angles of ca. 60° with the stem. RHIZOIDS colorless to brown, numerous on a pronounced mammiliform swelling. ANDROECIA intercalary to usually terminal on long branches, with 5–12 pairs of bracts, 0.3–0.4 mm wide; bracts ovate, 0.25–0.35 mm long, 0.1–0.25 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 to obtuse. GYNOCIA on long branches, with two 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. PERIANTHS trumpet-shaped, 2–2.5 mm long, 0.3–0.4 mm wide at apex, projected away from the substrate, mouth irregularly undulate. VEGETATIVE REPRODUCTION by caducous *Lejeunea*-type branches and by large discoid gemmae, produced on dorsal leaf margins, 1–3 per leaf, 0.35–0.45 mm in diam., base of gemmae deeply cordate-auriculate, opposite auricles touching to overlapping each other.

Additional description and illustration: Castle (1925, p. 441–445, Fig. 11, 1939, p. 28–32, Fig. 4), Schuster (1980, p. 648–651, Fig. 635), Zartman & Ilkiu-Borges (2007, p. 108 and 129, Fig. 21D–F), Gradstein & Ilkiu-Borges (2009, p. 40–41, Fig. 22D–G).

Distribution and habitat: Tropical America and Tropical Africa. In Brazil known from Acre, Alagoas, Amapá, Amazonas, Bahia, Espírito Santo, Minas Gerais, Mato Grosso, Pará, Paraíba, Pernambuco, Rondônia and Roraima. This species usually grows on living leaves, rarely on bark, at 30–550 m elevation.

Taxonomic notes: *Radula flaccida* is characterized by (1) plants forming rounded patches on the surface of living leaves; (2) lobules distant, (sub)quadrate with a pronounced mammiliform swelling at the rhizoidal area and apex extended towards an obtuse tip; (3) vegetative reproduction by large discoid gemmae with a deeply cordate-auriculate base, produced on dorsal leaf margins; (4) perianth trumpet-shaped, projected away from the substrate.

Radula flaccida shares the usual occurrence on living leaves and the production of discoid gemmae with *R. yanoella* and *R. stenocalyx*. However, gemmae in *R. flaccida* are very large, with a cordate-auriculate base, and are produced only on the dorsal leaf margin. In *R. yanoella* and *R. stenocalyx*, in contrast, gemmae are much smaller, not cordate-auriculate at base, and are produced all along the leaf margins.

Selected examined specimens: BRAZIL. ACRE: Rio Juruá, Juruá-Mirim, August 1901, Ule 568 (MG). ALAGOAS: Murici, 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). 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 Cientí-

fica Ferreira Penna, Caxiuana, várzea do furo do Camuim, 27 November 2000, Lisboa & Ilkiu-Borges 6911 (MG). PARAÍBA: Sapé, Reserva Particular do Patrimônio Natural Fazenda Pacatuba, 7°02'33"S, 35°09'24"W, 11 December 2009, Silva 530 (UFP). 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, 11°S, 64°W, 400 m, 15–22 March 1978, Reese 13467 (NY). RORAIMA: Rio Uraricoeara, vicinity of Uaica airstrip, 3 December 1978, Prance et al. 19991 (NY).

Radula gottscheana Taylor, London J. Bot. 5: 374. 1846.

Fig. 11

Type: Dominican Republic, St. Domingo, J. Dickson 1814 (isotypes: G-00265030!, S-B43095!, S-B43096!).

Dioicous. PLANTS 1.6–3 mm wide, green to brown in herbarium, irregularly bipinnate branched. STEMS with a cortex made up of ca. 140 rows of strongly thick-walled epidermal and subepidermal cells surrounding ca. 100 thin-walled rows of medullary cells, medullary cells larger than epidermal and subepidermal cells, epidermal and subepidermal cell walls brown, medullary cell walls yellowish, trigones lacking. LEAVES widely spreading, distant to contiguous, slightly convex, ovate to obovate, 0.7–1.5 mm long, 0.8–1.6 mm wide, dorsal base rounded to obtuse, overlapping the stem, apex obtuse to subacute, margin plane to irregularly recurved, entire; marginal cells subquadrate, 10–15 × 6–13 μm, median and basal cells isodiametric to elongate, 20–25 × 13–20 μm, cell walls thin, trigones large, cuticle smooth. LOBULES distant to subimbricate, triangular-ovate to triangular-oblong (sometimes subquadrate on branches), 0.35–0.8 mm long, 0.3–0.55 mm wide, ca. 1/2 the lobe length, not inflated, insertion line circinate, base plane, strongly auriculate, fully overlapping the stem, extending downwards and beyond the keel, free margin plane, rounded, apex plane, widely rounded to obtuse, distal margin straight to rounded; keel straight to slightly concave, spreading at angles of ca. 60–70° with the stem. RHIZOIDS not seen. ANDROECIA terminal to intercalary on long branches, with 3–6 pairs of bracts, 1.1–1.4 mm wide; lobes distant to contiguous, ovate, 0.7–1 mm long, 0.25–0.35 mm wide, apex rounded, margin plane, entire, lobules imbricate, oblong, ca. 5/6 the lobe length, base rounded to obtuse, free margin straight, apex obtuse. GYNOECIA and VEGETATIVE REPRODUCTION not seen.

Additional description and illustration: Yamada (1988, p. 389), Yamada & Gradstein (1991, p. 65).

Distribution and habitat: Tropical America. In Brazil recorded from Amazonas, Minas Gerais, Paraná, Rio de Janeiro and São Paulo. This species usually grows on bark of living trees and rock, at 450–1200 m elevation.

Taxonomic notes: *Radula gottscheana* has several distinct characters separating it from other *Radula* species in Brazil, including (1) stems with a thick-walled, brown, 2–4-layered cortex; (2) leaves with obtuse to subacute apex; (3) leaf cells with large trigones; (4) lobules with a strongly auriculate base extending downwards beyond the keel.

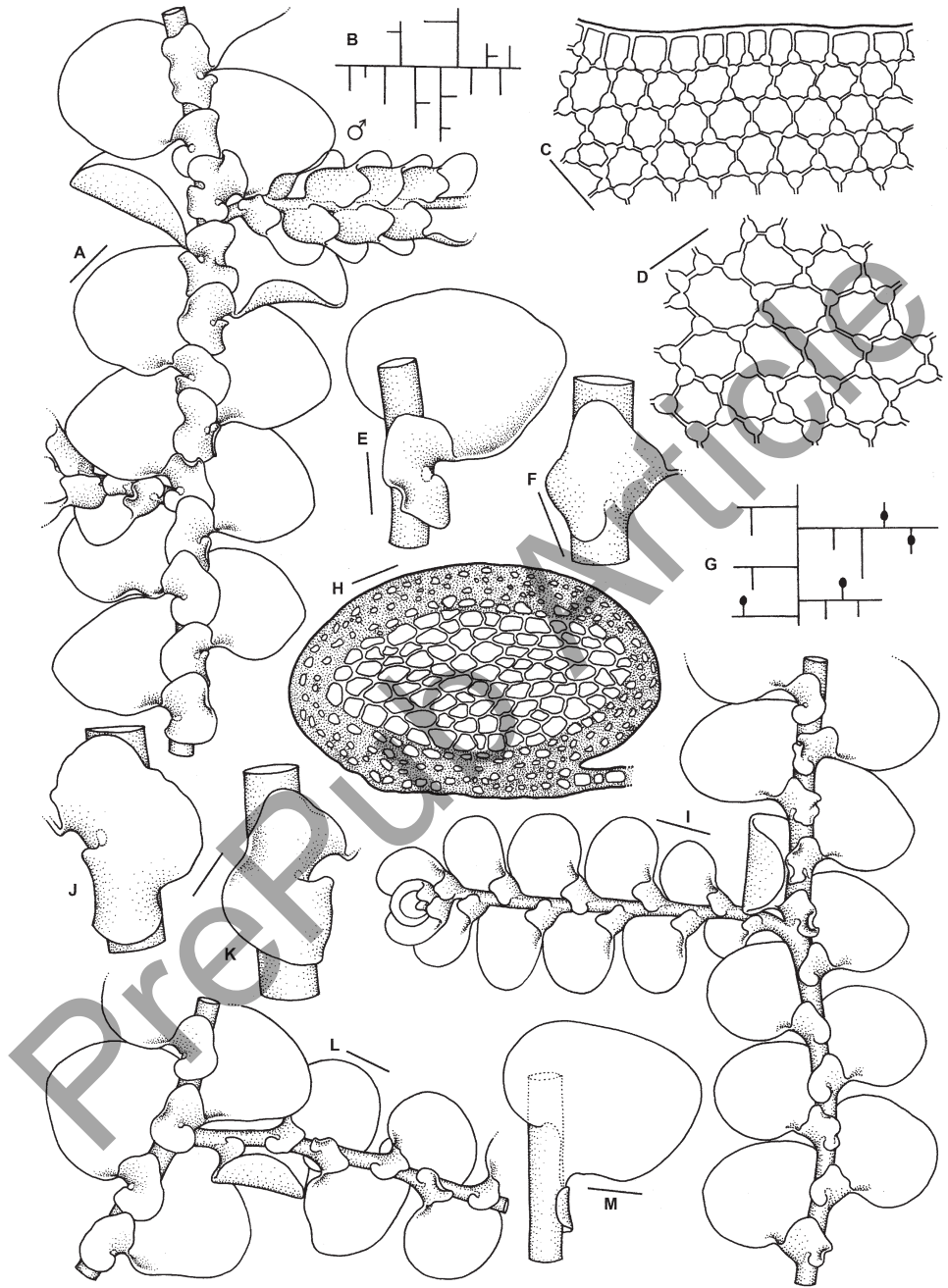


Fig. 11. *Radula gottscheana* – A. Habit with androecia. B, G. Cladograph of fertile plants (solid ellipse = androecia). C. Marginal leaf cells. D. Median leaf cells. E. Leave. F, J, K. Lobule. H. Cross section of a stem. I, L. Habit. M. Leaf dorsal view. (A, E, I, L, M = 500 µm; C, D = 25 µm; F, J, K = 250 µm; H = 50 µm; A from ICN-036937; B–H, J, K, M from isotype S-B43095; I, L from SP-284441).

Among Brazilian species, *R. gottscheana* can only be confused with *R. voluta*; both are large plants with strongly auriculate lobule bases. However, the keel in *R. voluta* is much longer than in *R. gottscheana* and the auriculate lobule base does not extend downwards beyond the keel.

Selected examined specimens: BRAZIL. AMAZONAS: Rio Negro, between Manaus and São Gabriel, Serra Curicuriari, 00°20'S, 66°50'W, 450 m, 9–12 July 1979, Schuster 79-15-580 (NY). MINAS GERAIS: Marmelópolis, Pousada Maeda, trilha das águas, 22°26'57"S, 45°09'55"W, 1500 m, 14 June 2006, Peralta 3584 (SP), PARANÁ: Morretes, Parque Estadual do Marumbi, trilha vermelha, 25°25'55"S, 48°54'54"W, 1200 m, 22 July 2014, Peralta et al. 15731 (SP). RIO DE JANEIRO: Teresópolis, Parque Nacional da Serra dos Orgãos, 21 October 1989, Yano & Costa 13551 (SP). 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).

***Radula javanica* Gottsche**, Syn. Hepat. 257. 1845.

Figs. 12–13

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; isolectotype: S-B43105!). Hawaii, Owaihi, hb. Hook. sub no. 56 as *R. boryana* (isosyntypes: S-B43103!, S-B43104!).

= *Radula amazonica* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 321. 1885. Type: Venezuela, “Ad. fl. Orinoco supra cataractas, in cortice,” Spruce s.n. (syntype: NY-01021079!).

= *Radula amazonica* var. *negrensis* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 322. 1885. Type: Venezuela, San Carlos del Rio Negro, Spruce s.n. (syntype: NY-01021080!).

= *Radula amazonica* var. *campanensis* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 322. 1885, fide Castle (1966).

= *Radula caldana* Ångström, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(7): 81. 1876[1877], fide Yamada in Reiner-Drehwald (1994) under *R. macrostachya*.

= *Radula macrostachya* Lindenb. & Gottsche, Syn. Hepat 726. 1847, fide Yamada (2000).

= *Radula surinamensis* Steph., Hedwigia 23: 136. 1884, fide Yamada (1989 under *R. caldana*).

For further synonymy see Yamada (1979) and So (2005, 2006).

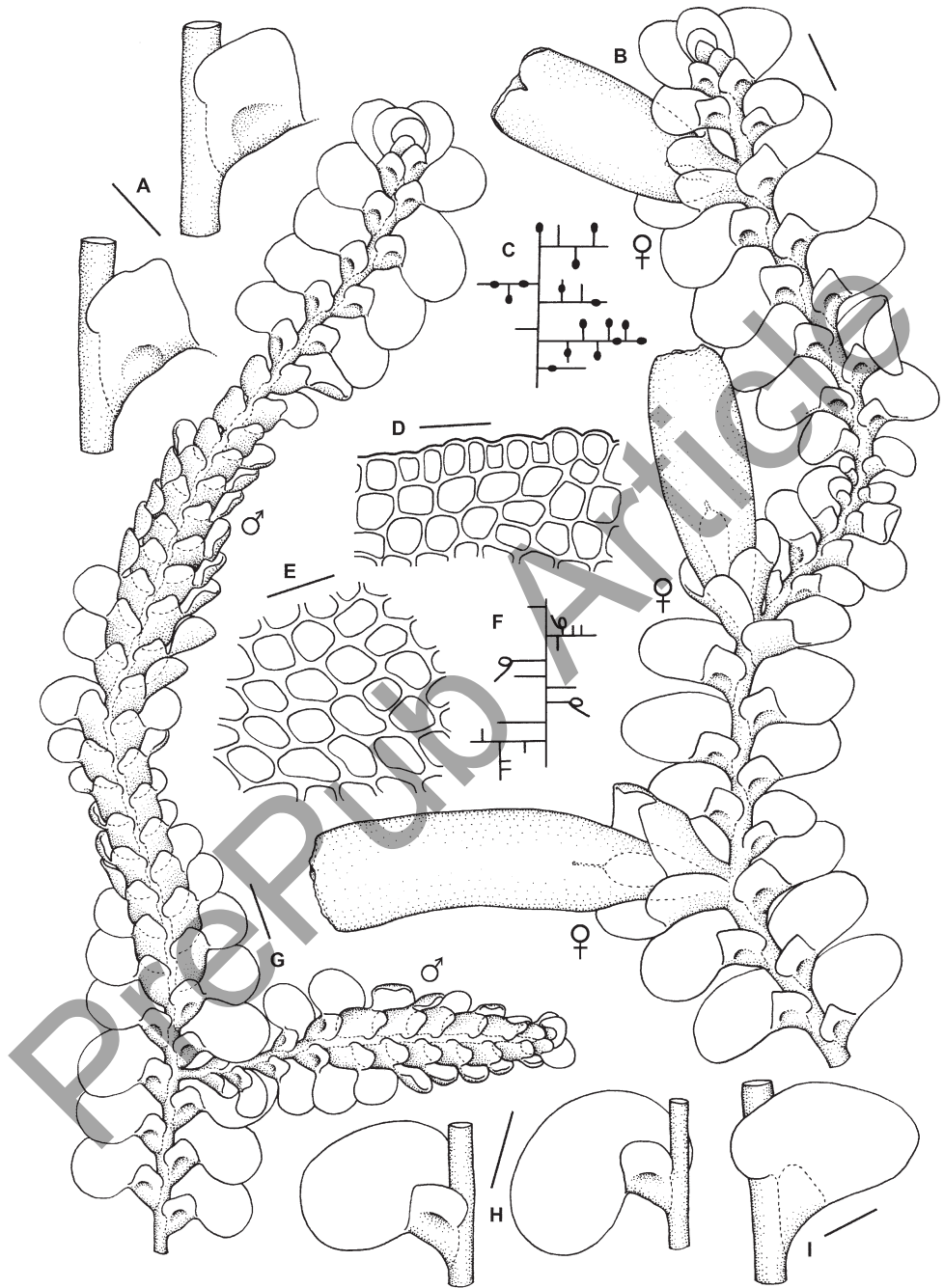


Fig. 12. *Radula javanica* – A. Lobule. B. Habit with gynoecia. C, F. Cladograph of fertile plants (open ellipse = gynoecia, solid ellipse = androecia). D. Marginal leaf cells. E. Median leaf cells. G. Habit with androecia. H. Leaves. I. Leaf, dorsal view. (A = 250 μ m; B, G, H, I = 500 μ m; D, E = 25 μ m; A from syntype G-265032; B, D, E, F, I from isosyntype S-B43104; C, G from INPA-83194; H from HBRA-8420).

Dioicous. PLANTS 1.8–3 mm wide, green to yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 21–62 thick-walled epidermal cells surrounding ca. 18–180 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls brown, trigones large. LEAVES obliquely to widely spreading, sometimes squarrose, distant to imbricate, slightly convex, ovate to falcate-

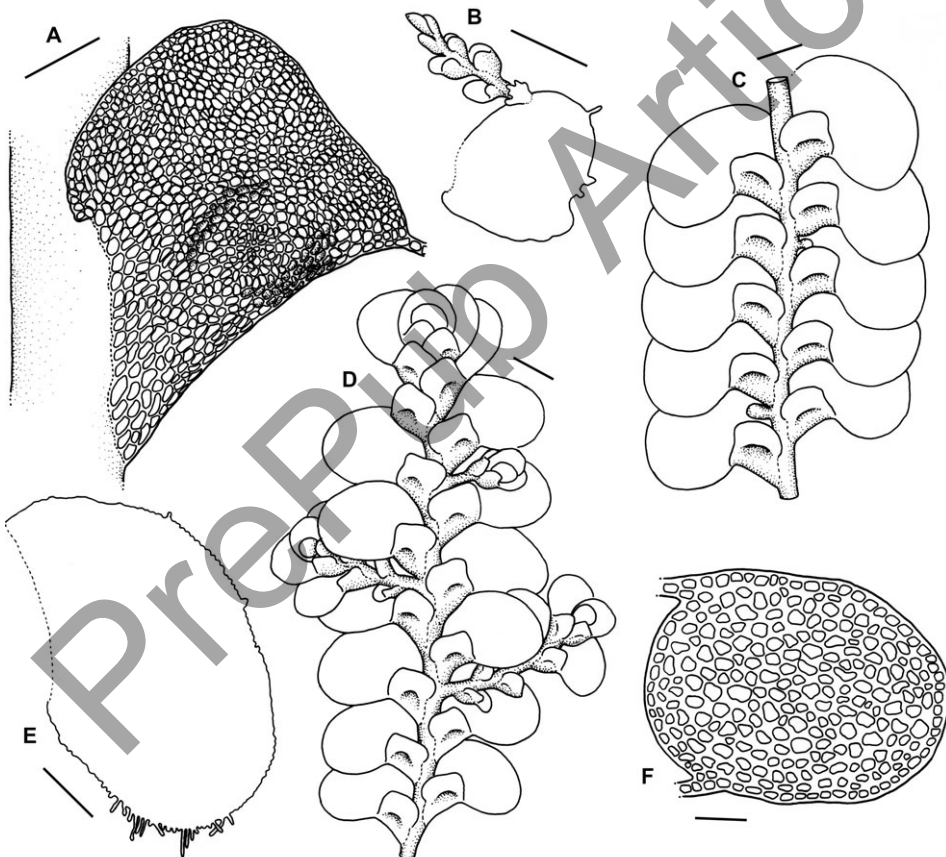


Fig. 13. *Radula javanica* – A. Lobule. B. Caducous leaf lobe with regnerants and rhizoids. C–D. Habitat. E. Caducous leaf lobes with rhizoids. F. Cross section of a stem. (A = 100 μ m; B, E = 250 μ m; C–D = 50 μ m; F = 50 μ m; A from the isosyntype S-B43102; B, D–E from SP-259307; C from HBRA-8420; F from the isosyntype S-B43105).

ovate, 0.8–1.5 mm long, 0.5–1 mm wide, dorsal base rounded, overlapping the stem, 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, cuticle smooth. LOBULES distant, (sub)quadrate, 0.5–0.8 mm long, 0.3–0.5 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion line straight, base plane, rounded, covering up to 1/2 the stem, free margin plane, straight, apex plane, rounded to subacute, distal margin straight; keel straight, rarely slightly convex, spreading at angles of 35–50° with the stem. RHIZOIDS colorless to brown, scanty. 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 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. PERIANTHS subcylindrical, 2.5–3.4 mm long, 0.85–1 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by means of caducous leaf lobes and regenerants.

Additional description and illustration: Castle (1966, p. 13–15, Fig. 4 as *R. elegans*, p. 15–17, Fig. 5 as *R. surinamensis*, p. 18–19, Fig. 6 as *R. caldana*, p. 19–22, Fig. 7 as *R. longifolia*, p. 22–25, Fig. 8 as *R. amazonica*, p. 58–61, Fig. 26 as *R. sandei*, p. 70–72, Fig. 32 as *R. cordiloba*, p. 72–75, Fig. 33 as *R. javanica*), Yamada (1979, p. 93–97, Figs. 42–45 as *R. surinamensis*, 2003 Fig. 83C), Lemos-Michel (2001, p. 160–162, Fig. 45 as *R. macrostachya*), So (2005, p. 187–188, 2006, p. 217–219), Renner (2005, p. 60–63, Figs. 47–51, 2014, p. 128–141, Figs. 8–17), Gradstein & Ilkiu-Borges (2009, p. 41–42, Fig. 23A–C).

Distribution and habitat: Pantropical. In Brazil known from Acre, Alagoas, Amapá, Amazonas, Bahia, Espírito Santo, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina and São Paulo. The species occurs in different domains in Brazil, mostly in the Atlantic Forest region and Amazonia, on tree trunks and decaying wood, rarely on rock, soil and living leaves, from sea level to 2000 m elevation.

Taxonomic notes: *Radula javanica* is characterized by (1) caducous leaf lobes; (2) leaves ovate to falcate-ovate; (3) lobules distant, (sub)quadrate with base covering up to 1/2 the stem, apex rounded to subacute, keel usually straight. Leaf shape and cell size are rather variable, and Yamada (2000) considered *R. javanica* “as one of the most plastic... species of *Radula*”. The variability of *R. javanica*, as defined by Yamada and other authors, probably explains its numerous synonyms (Castle 1966, Yamada, 1979, 2000, So 2005, 2006).

This species may be confused with several other *Radula* species in Brazil, especially with *R. brasiliica* and *R. recubans* (see comments under the latter species).

Selected specimens examined: 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). ESPÍRITO SANTO: Linhares, Reserva Florestal de Linhares, Acerro do Calimã, 17 January 1996, Costa et al. 2976 (RB). 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, Pietrobon et al. 8362 (HBRA). 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). 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: 2–4 km above the first rapids on the Rio Pacaas Novos, 15–22 March 1978, 400 m, Reese 3474 (MG). 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).

Radula ligula Steph., Sp. Hepat. 4: 228. 1910.

Fig. 14

Type: Brazil, Rio Grande, Lindmann “inter B 174” (holotype: G-00043905!).

Dioicous. PLANTS 1.2–2.8 mm wide, olive-green to brown in herbarium, irregularly pinnate, rarely bipinnate. STEMS in cross section with ca. 20 thick-walled epidermal cells surrounding 20–23 thin-walled medullary cells, epidermal and medullary cells of the same size, cell walls colorless, trigones large. LEAVES widely spreading, contiguous to imbricate, slightly convex, ovate, 0.75–1.3 mm long, 0.7–1 mm wide, dorsal base rounded, not overlapping the stem, 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 thick, trigones small to lacking, cuticle smooth. LOBULES distant, ligulate, 0.25–0.7 mm long, 0.15–0.3 mm wide, ca. 1/4 of the lobe length, inflated at rhizoid area, 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, lobules. RHIZOIDS colorless to brown, scanty. 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 usually rudimentary; bracts oblong-ovate, 1.6–1.7 mm long, 0.6–0.7 mm wide, apex rounded, margin recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS subcylindrical, 2.5–4 mm long, 0.7–1.1 mm wide at apex, mouth entire. VEGETATIVE REPRODUCTION not observed.

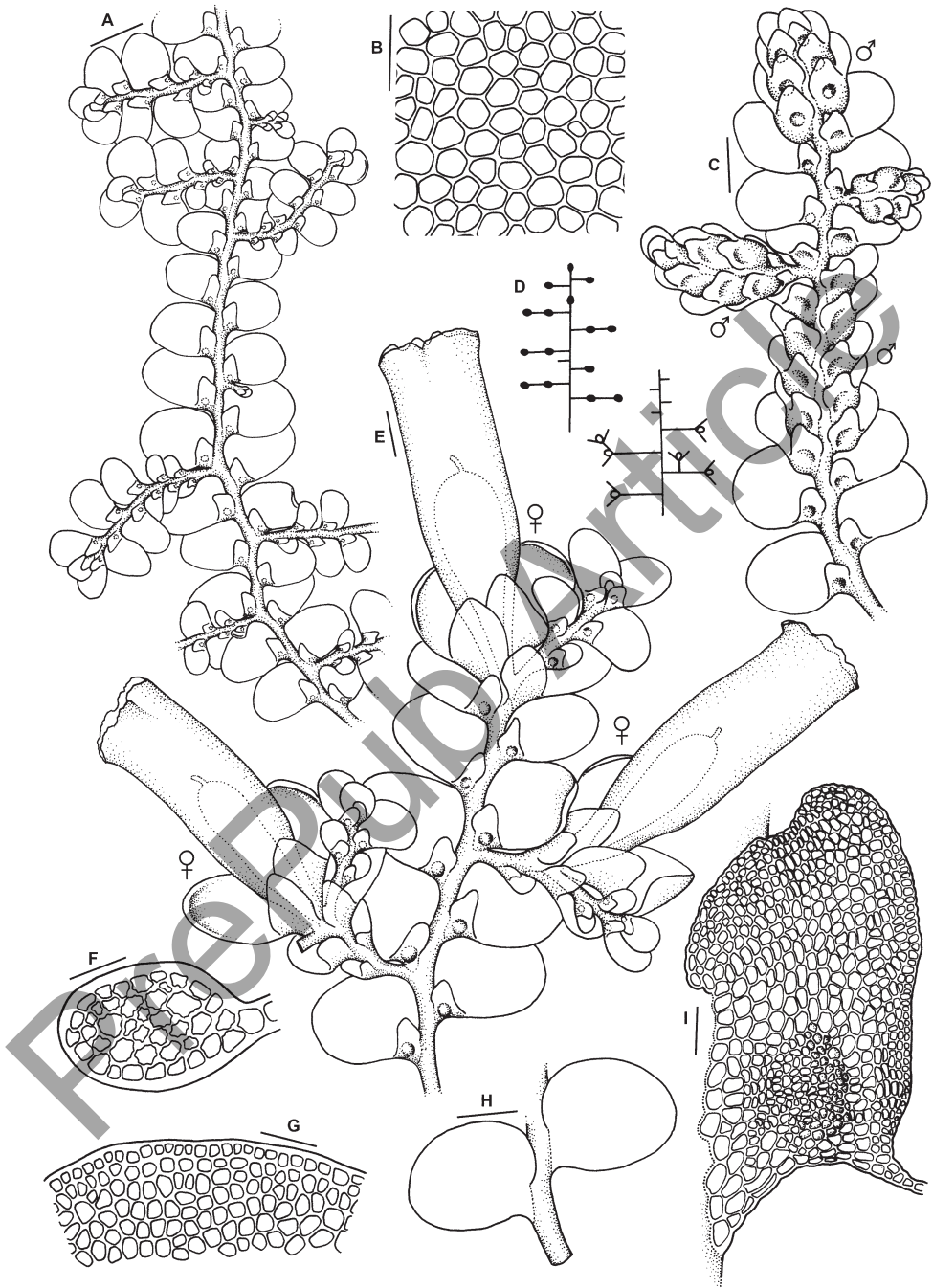


Fig. 14. *Radula ligula* – A. Habit. B. Median leaf cells. C. Habit with androecia. D. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). E. Habit with gynoecia. F. Cross section of a stem. G. Marginal leaf cells. H. Leaf, dorsal view. I. Lobule. (A = 1000 μm ; B, F, G, I = 50 μm ; C, E, H = 500 μm ; A, B, F–I from the holotype; C–E from ICN-39132).

Additional description and illustration: Castle (1962, p. 147–148, Fig. 3), Yamada (1981, p. 388–389, Fig. 13, 2003, Fig. 82A), Reiner-Drehwald (1994, p. 12–14, Fig. 3D–E).

Distribution and habitat: Brazil and Argentina (Reiner-Drehwald 1994). In Brazil known from Bahia, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. The species usually grows in humid rainforest, preferably near water bodies, on rock, tree trunks or decaying wood, at 30–1750 m elevation.

Taxonomic notes: *Radula ligula* is readily identified by (1) leaf lobes bordered by 3–4 rows of quadrate thick-walled cells; (2) lobules ligulate (parallel to the stem) with rounded apex; keel concave and inflated only at rhizoid area. These characters are unparalleled among *Radula* species in Brazil.

Selected examined specimens: 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, 39°03'W, 200 m, 17 July 1991, Vital & Buck 20271 (NY). 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). RIO GRANDE DO SUL: Viamão, Vianópolis, 05 October 1970, Oliveira s.n. (ICN). 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).

Radula longiloba K.Yamada, J. Hattori Bot. Lab. 54: 243. 1983.

Fig. 15

Type: Cuba, Santiago, Sierra de la Gran Piedra, near Finca Isabella, 1100 m, Pócs 9128/AR (isotype: NICH-400981!).

Dioicous. PLANTS 1.3–1.9 mm wide, yellowish-green in herbarium, irregularly pinnate to dichotomous. STEMS in cross section with ca. 14 thick-walled epidermal cells surrounding ca. 14 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls yellowish, trigones lacking. LEAVES widely spreading, imbricate, slightly convex, oblong to oblong-falcate, 0.6–0.95 mm long, 0.4–0.7 mm wide, dorsal base rounded, not overlapping the stem, apex obtuse to subacute, margin plane, entire; marginal cells subquadrate to isodiametric, 10–15 \times 8–12 μm , median and basal cells isodiametric to elongate, 20–25 \times 15–20 μm , cell walls thin, trigones small to

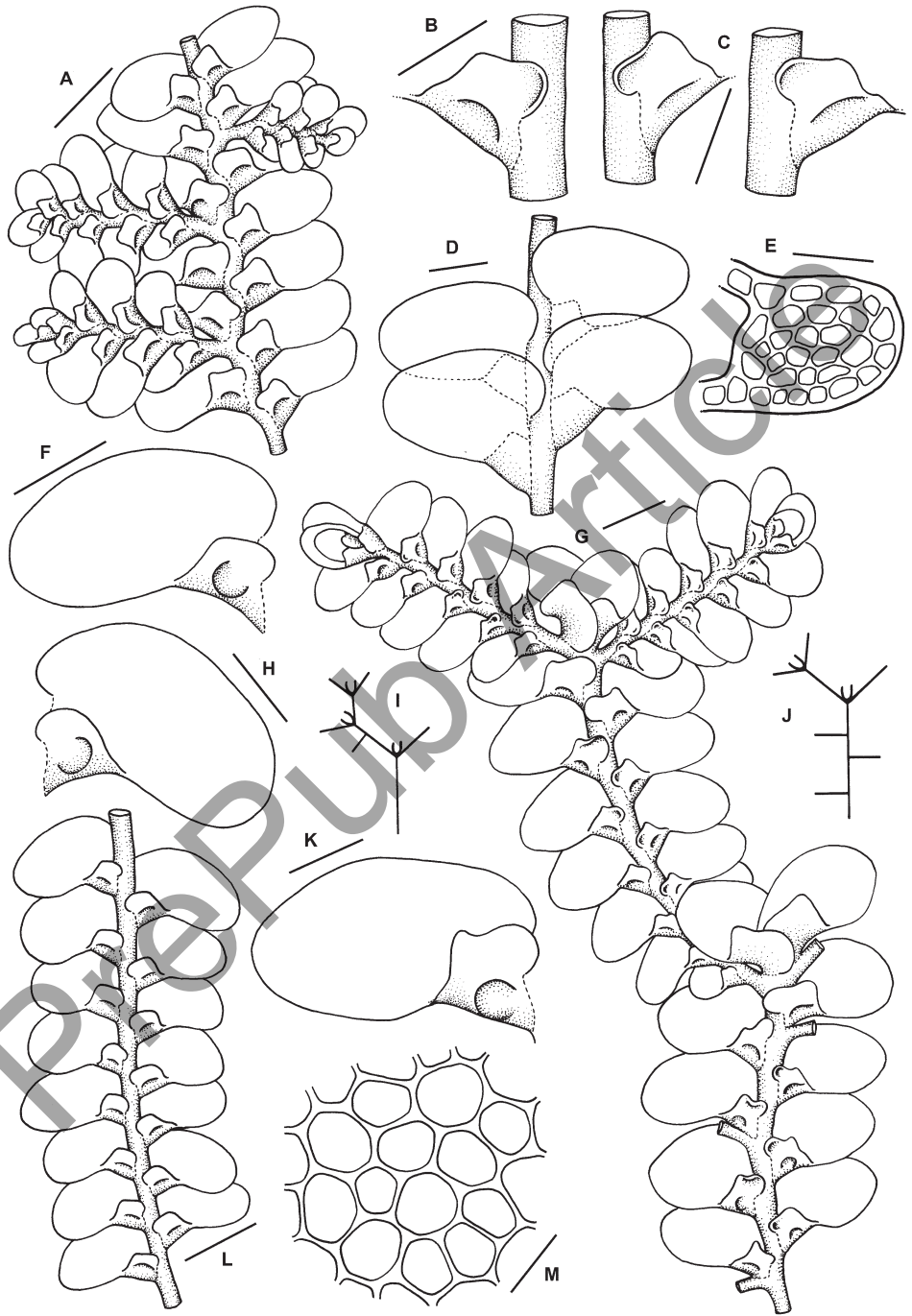


Fig. 15. *Radula longiloba* – A, G, L. Habit. B–C. Lobules. D. Habit, dorsal view. E. Cross section of a stem. F, H, K. Leaves. I–J. Cladograph of plants. M. Median leaf cells. (A, G, L = 500 μ m; B–D, F, H, K = 250 μ m; E = 50 μ m; M = 25 μ m; A, K from the holotype in NICH; B–J, L–M from SP-182102).

lacking, cuticle smooth. 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, insertion line straight to slightly arched, base plane to recurved, rounded, covering up to 1/3 the stem, free margin plane to slightly recurved, straight to sinuate, apex rounded to subacute, distal margin straight; keel straight, rarely slightly convex, spreading at angles of 50–60° with the stem. RHIZOIDS brownish, scanty. ANDROECIA not seen. GYNOECIA on long branches, with two innovation; 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. PERIANTHS and VEGETATIVE REPRODUCTION not seen.

Additional description and illustration: Yamada (1983, p. 243–245, Fig. 2).

Distribution and habitat: Cuba and Brazil. New to Brazil, from Rio Grande do Sul, where it grows on tree trunks in Atlantic forest.

Taxonomic notes: *Radula longiloba* is characterized by (1) stems slender with ca. 14 thick-walled epidermal cells surrounding ca. 14 thin-walled medullary cells; (2) leaves oblong to oblong-falcate with obtuse to subacute apex; (3) leaf cells with trigones small or lacking; (4) lobules distant, subquadrate with rounded base, covering up to 1/3 the stem, free margin straight to sinuate, and keel usually straight, rarely slightly convex, inflated at rhizoid area.

Radula longiloba shares similarities with *R. mexicana* and *R. pseudostachya*, but *R. mexicana* is autoicous and has ovate leaves with a rounded to obtuse apex, while *R. pseudostachya* has lobules contiguous to subimbricate with the base covering at least 1/2 the stem, and cells with large trigones and verruculose cuticle (Yamada 1983).

Radula longiloba is closely related to *R. yamadae* but differs from the latter mainly by leaves oblong and falcate, lobules distant, 1/3–1/2 the leaf length, lobule base covering up to 1/3 the stem, and keel straight to slightly convex. In *R. yamadae*, leaves are ovate and widely spreading but not falcate, lobules are distant to contiguous, rarely imbricate, 1/2–2/5 the lobe length, with lobule base covering 1/3 to fully overlapping the stem, and the keel is conspicuously convex (Oliveira-da-Silva & Ilkiu-Borges 2020).

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

Radula mammosa Spruce, Mem. Torrey Club 1: 127. 1890.

Fig. 16

Type: Bolivia, Yungas, “in Acrostichi frondibus cum Lejeuneis repens,” 4000 ft., 1885, Rusby 3025 p.p. (isotypes: NY-01021130!, G-00265038!).

Dioicous. PLANTS 1–1.6 mm wide, yellowish-green to pale green in herbarium, irregularly pinnate. STEMS in cross section with ca. 13 thin-walled epidermal cells surrounding ca. 9 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls yellowish to colorless, trigones lacking. LEAVES widely spreading, contiguous to shallowly imbricate, plane to slightly convex, ovate to falcate-ovate, 0.7–0.95 mm long, 0.4–0.7 mm wide, dorsal base rounded, not overlapping the stem, apex rounded, margin plane, entire; marginal cells subquadrate to isodiametric, $12\text{--}15 \times 10\text{--}12 \mu\text{m}$, median and basal cells isodiametric to elongate, $22\text{--}25 \times 12\text{--}17 \mu\text{m}$, cell walls thin, trigones lacking, cuticle smooth. LOBULES distant, subquadrate, 0.25–0.45 mm long, 0.2–0.35 mm wide, 1/3–1/2 the lobe length, strongly inflated at rhizoid area, insertion line straight to slightly arched, base plane, straight, not covering the stem, free margin plane, straight, apex plane, rounded, distal margin straight; keel strongly convex, rarely slightly straight on branches, spreading at angles ca. 60° with the stem. RHIZOIDS colorless to brown, numerous on a pronounced mammiliform swelling. ANDROECIA not seen. GYNOCIA on stems, with two innovations; bracts oblong-ovate, 0.9–1 mm long, 0.45–0.5 mm wide, apex rounded, margin plane, entire, lobule ca. 1/2 of lobe length, oblong, apex rounded to obtuse. PERIANTHS subcylindrical, 2.4–2.6 mm long, 0.45–0.8 mm wide at apex, mouth entire, undulate. VEGETATIVE REPRODUCTION not observed.

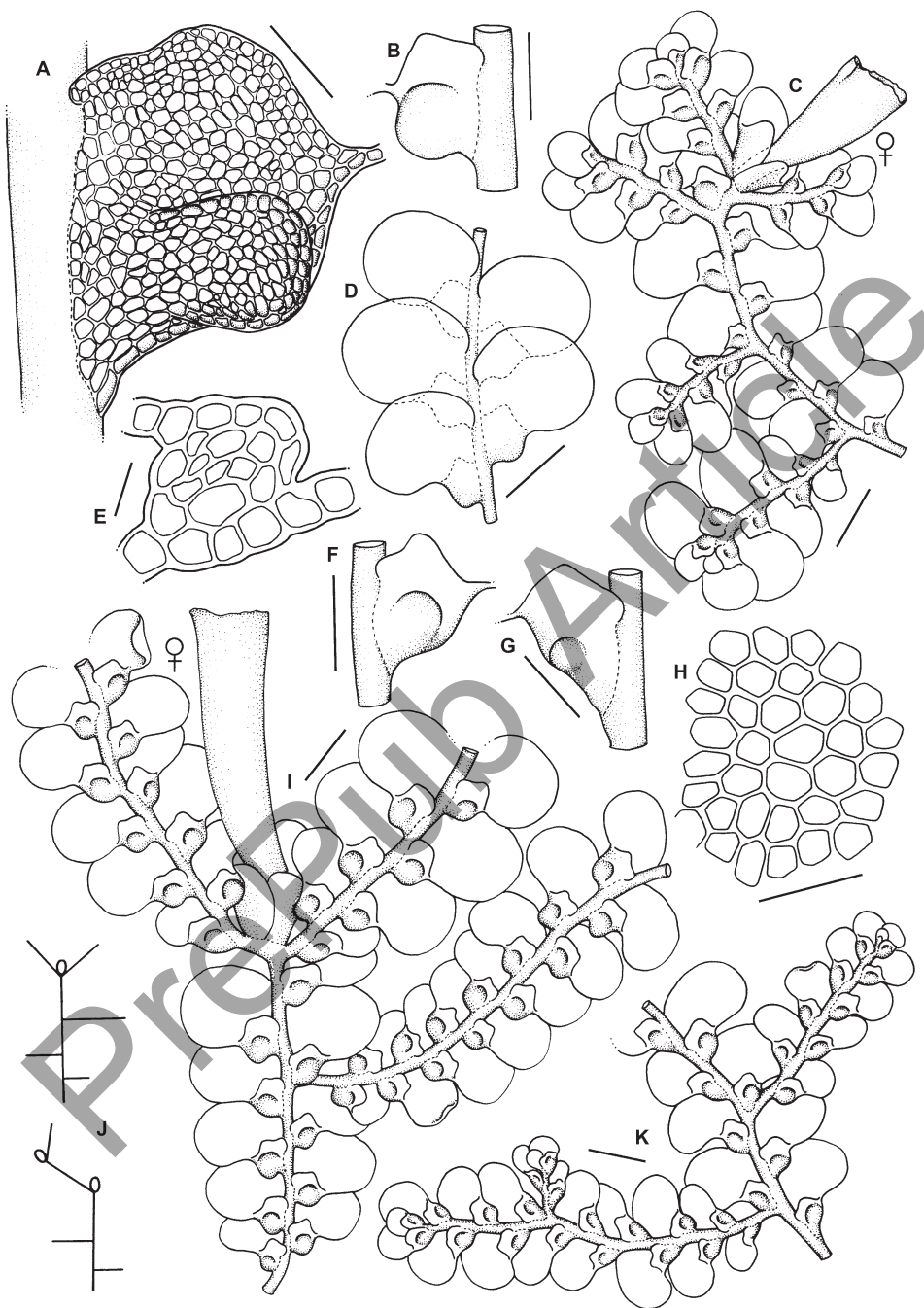
Additional description and illustration: Castle (1939, p. 24–26, Fig. 2), Yamada (1993a, p. 130–131, Fig. 50 based on the holotype of *R. verrucifolia*, 2003, Fig. 83E).

Distribution and habitat: Tropical America. In Brazil recorded from Pará, Paraná, Rio de Janeiro and São Paulo. The species usually occurs on living leaves, occasionally on bark or rock, at 500–1800 m elevation.

Taxonomic notes: *Radula mammosa* is characterized by (1) plants small, usually epiphyllous (occasionally occurring on bark or rock); (2) leaves ovate to falcate-ovate; (3) leaf cells without trigones; (4) lobule base straight, not covering the stem, keel strongly convex (rarely almost straight on branches), and with a pronounced mammiliform swelling at the rhizoid area; (5) gemmae absent.

This species resembles *R. flaccida* and *R. stenocalyx* by the epiphyllous plants with lobules strongly inflated at the rhizoid area. However, *R. mammosa* differs from the latter two species by the absence of gemmae and, additionally, from *R. flaccida* by the lobule base not covering the stem and lobule apex rounded (covering 1/5–1/4 the stem and lob-

Fig. 16. *Radula mammosa* – A–B, F, G. Lobule. C, I. Habit with gynoecia. D. Habit, dorsal view. E. Cross section of a stem. H. Median leaf cells. J. Cladograph of fertile plants (open ellipse = gynoecia with perianth). K. Habit. (A = 100 μm ; B, F, G = 250 μm ; C, D, I, K = 500 μm ; E = 25 μm ; H = 50 μm ; A–B, D–J from the isotype in G; C, K from SP-452187).



ule apex extended towards an obtuse tip in *R. flaccida*), and from *R. stenocalyx* by the subcylindrical perianth, 2.4–2.6 mm long and 0.45–0.8 mm wide at apex (trumpet-shaped to subcylindrical, 1.5–2 mm long and 0.2–0.3 mm wide at apex in *R. stenocalyx*). *Radula mammosa* also resembles *R. yamadae* but differs from the latter by leaf lobes with apex rounded and lobule base straight, not covering the stem. In *R. yamadae*, leaf apex is obtuse to subacute and the lobule base covers 1/3 to fully overlaps the stem (Oliveira-da-Silva & Ilkiu-Borges 2020).

Selected examined specimens: BRAZIL. PARÁ: São Geraldo do Araguaia, Serra dos Martírios-Andorinhas, Fazenda andorinhas, 6°10'2,8"S, 48°26'30,2"W, 18 December 2007, Lisboa & Barros 5703 (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. 15765 (SP). RIO DE JANEIRO: Nova Friburgo, 1600–1800 m, 10 October 1995, Costa et al. 1067 (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).

Radula mexicana Lindenb. & Gottsche, Mexik. Leverm. 150. 1863.

Fig. 17

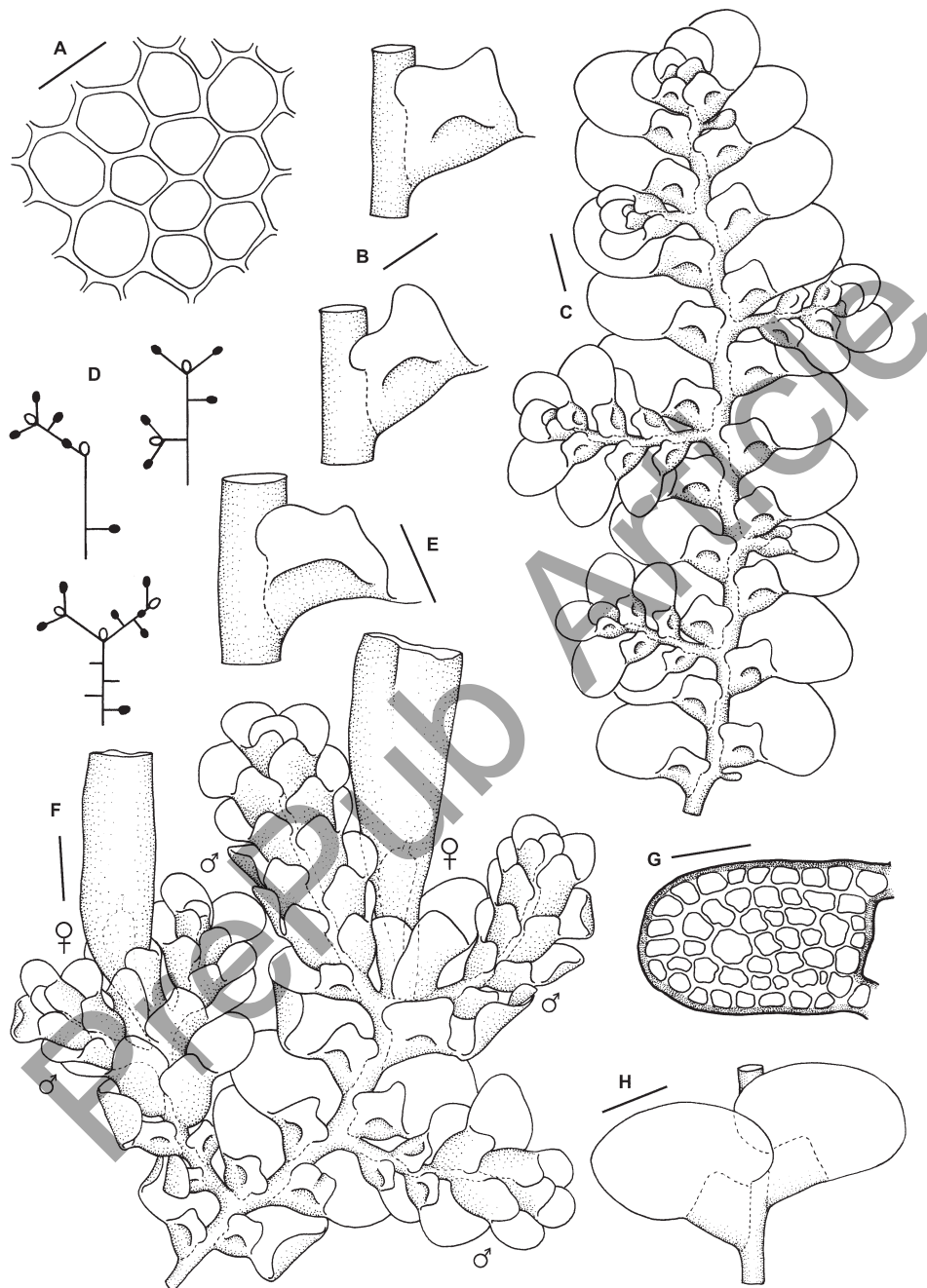
Type: Mexico, Veracruz, Hacienda Mirador, Liebmann 478 p.p. (n.v.).

= *Radula cordovana* Steph., Hedwigia 23: 163. 1884. Type: Brazil, Cordova, “in sylvis montosis,” Mohr 18, ex hb. Jack (holotype: G-00121976!).

= *Radula claviflora* Spruce, Mem. Torrey Club 1: 127. 1890. Type: Bolivia, Yungas, 6000 ft., 1885, Rusby 3034 (isotype: NY-01021107!).

Monoicous. PLANTS 1.5–2 mm wide, yellowish-green to yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 23 thick-walled epidermal cells surrounding ca. 25 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls yellowish, medullary cell walls colorless, trigones small. LEAVES obliquely to widely spreading, imbricate, slightly convex, ovate, 0.8–1.3 mm long, 0.6–0.9 mm wide, dorsal base rounded, overlapping the stem, apex rounded to obtuse, margin plane to incurved, entire; marginal cells subquadrate to isodiametric, 10–15 × 8–10 µm, median and basal cells isodiametric to elongate, 15–20(–25) × 10–15 µm, cell walls thin, trigones small to lacking, cuticle smooth. LOBULES distant, (sub)quadrate, 0.3–0.6 mm long, 0.2–0.45 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, insertion line ± straight, base plane, rounded, covering up to 1/3 (rarely 1/2) the stem, free margin plane, straight, apex plane, rounded to acute, rarely obtuse, distal margin straight; keel straight, spreading at angles of 40–50° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA terminal on short branches, with 1–5 pairs of bracts, 0.7–1 mm wide; bracts distant to

Fig. 17. *Radula mexicana* – A Median leaf cells. B, E. Lobule. C. Habit. D. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). F. Habit with gynoecia and androecia. G. Cross section of a stem. H. Leaf, dorsal view. (A = 25 µm; B, E = 250 µm; C, F, H = 500 µm; G = 50 µm; A–H from the holotype of *R. cordovana*).



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. GYNOECIA on short 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. PERIANTHS subcylindrical, 2–3 mm long, 0.6–0.8 mm wide at apex, mouth entire to slightly irregularly undulate. VEGETATIVE REPRODUCTION by stem fragmentation.

Additional description and illustration: Castle (1964, p. 192–194, Fig. 3), Yamada (1993a, p. 131–133, Fig. 51 based on the holotype of *R. cordovana*).

Distribution and habitat: Tropical and subtropical America. In Brazil, it occurs in Espírito Santo, Pernambuco and Rio Grande do Sul. This is an uncommon species that grows on tree trunks and decaying wood in Atlantic forest.

Taxonomic notes: *Radula mexicana* is characterized by (1) plants monoicous; (2) lobules distant, (sub)quadrate, base rounded, covering up to 1/3 (rarely 1/2) the stem, apex rounded to acute, rarely obtuse, keel straight.

Radula mexicana resembles *Radula angulata* in the lobule apex and leaf shape, but differs from the latter by lobule base covering up to 1/3 (rarely 1/2) the stem (covering 1/2 to fully overlapping the stem in *R. angulata*), plants monoicous (dioicous in *R. angulata*), and leaf cells without trigones (trigones small at leaf base and increasing in size towards the margin in *R. angulata*). *Radula mexicana* was long considered the only monoicous *Radula* species in Brazil but in this study, two further monoicous taxa were detected, *R. fendleri* var. *paroica* and *R. renneri*.

Selected examined specimens: 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).

Radula nudicaulis Steph., Sp. Hepat. 4: 174. 1910.

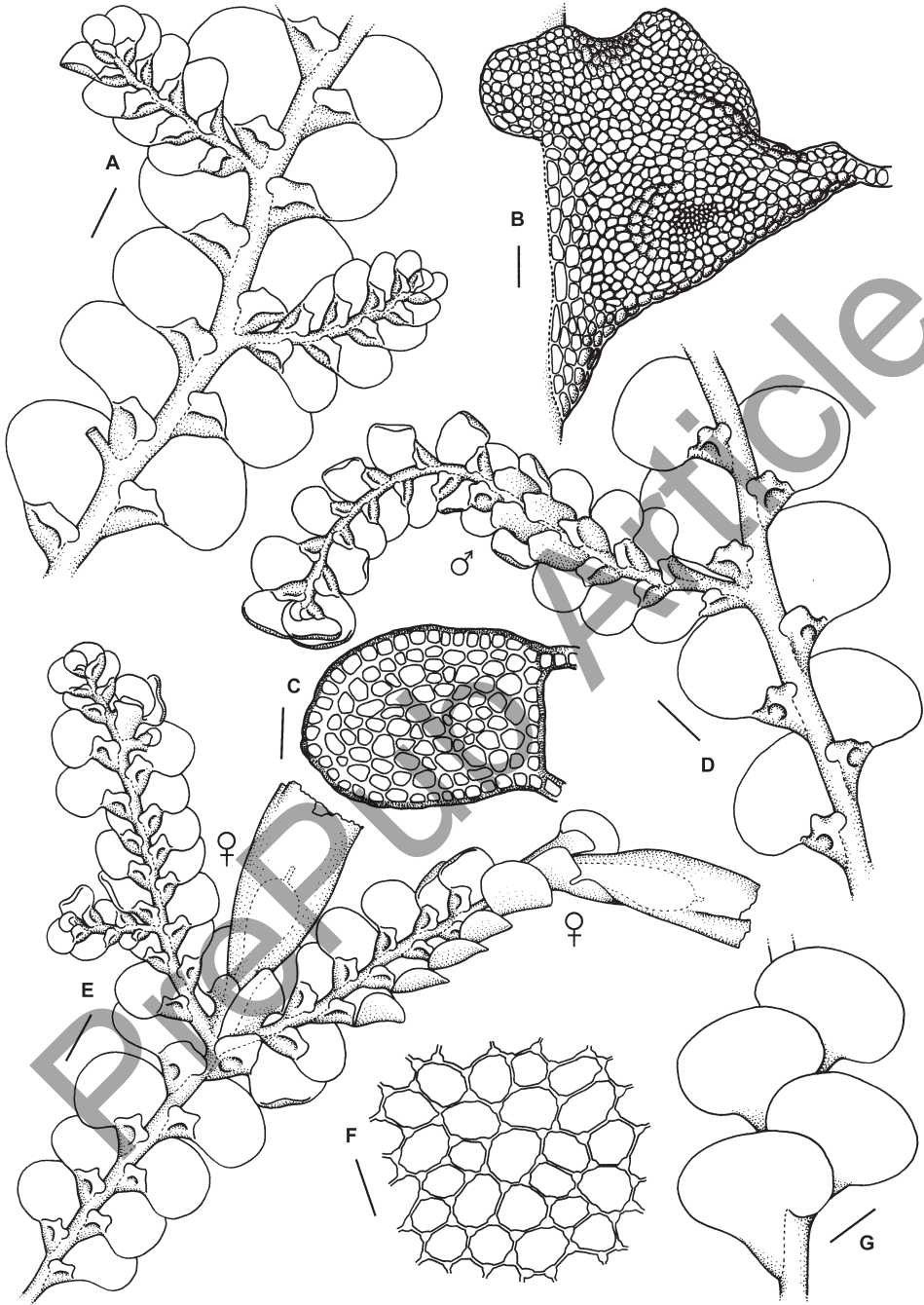
Fig. 18

Type: Brazil, Serra do Itatiaia, 1894, Ule 436 (holotype: G-00043871!).

= *Radula goebelii* Steph., Biblioth. Bot. 87: 232. 1916. Type: Bolivia, San Mateo, Sunchal, Herzog 4458 (holotype: G-00043890!).

Dioicous. PLANTS 1.9–2.5 (–3) mm wide, yellowish-brown to reddish-brown in herbarium, regularly pinnate. STEMS in cross section with ca. 40 thick-walled epidermal cells surrounding ca. 71 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls colorless, trigones lacking.

Fig. 18. *Radula nudicaulis* – A. Habit. B. Lobule. C. Cross section of a stem. D. Habit with androecia. E. Habit with gynoecia. F. Median leaf cells. G. Habit, dorsal view (A, D, E, F = 500 µm; B, C = 50 µm; F = 25 µm; A, C, G from the holotype in G; B, D, E, F from RB-284180).



LEAVES widely spreading, distant to contiguous, convex, ovate, 0.9–1.2 (–1.5) mm long, 0.7–1 (–1.2) mm wide, dorsal base rounded, overlapping the stem, 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, cuticle smooth. LOBULES distant, (sub)quadrate, 0.5–0.7 mm long, 0.3–0.5 mm wide, 1/3–1/2 the lobe length, inflated along the keel and at rhizoid area, insertion line straight, base plane, rounded, covering up to 1/2 the stem, free margin sinuate-plicate in the middle, apex plane to incurved, rounded, distal margin sinuate; keel straight to convex, spreading at angles of 40–50° with the stem. RHIZOIDS colorless, scanty. ANDROECIA terminal to intercalary on long branches, with 2–6 pairs of bracts, 0.9–1.1 mm wide; bracts 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. GYNOCIA on long branches, with two 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 ca. 1/2 of lobe length, oblong, apex rounded. PERIANTHS subcylindrical, 2–2.8 mm long, 0.7–1.1 mm wide at apex, mouth irregularly undulate. VEGETATIVE REPRODUCTION not observed.

Additional description and illustration: Castle (1967, p. 33–35, Fig. 13), Jans (1979, p. 425–426, Fig. 1i), Yamada (1982, p. 458–461, Figs. 28–29, 2003, Fig. 84D), Bouman & Dirkse (1990, p. 122–123, Fig. 3).

Distribution and habitat: Costa Rica, Ecuador, Colombia, Bolivia, Brazil and Macaronesia (Azores and Madeira). In Brazil known from Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina and São Paulo. The species grows on trunks of living trees, decaying wood and rock, in humid places at 125–2020 m elevation.

Taxonomic notes: *Radula nudicaulis* is characterized by (1) plants regularly pinnate; (2) leaves distant to contiguous, convex, ovate; (3) lobules distant, (sub)quadrate, base rounded, covering up to 1/2 the stem, free margin usually sinuate-plicate in the middle, keel straight to convex, spreading at angles of 40–50° with the stem.

Radula nudicaulis resembles *R. pallens* in lobule shape, but the latter differs by irregularly pinnate to dichotomous branching, leaves imbricate, and keel straight to concave, spreading at angles of 60–70° with the stem.

Selected examined specimens: 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). 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). RIO GRANDE DO SUL: Viamão, Parque Saint Hilaire, 9 June 1994, Reschke s.n. (ICN); Cambará do Sul, Itaim-bezinho, 3 October 1976, Vianna 3258 (ICN). RONDÔNIA: Ariquemes, Alto Condeias, Mi-brasa Tin Mine, 10°35'S, 63°35'W, 200 m, 17 May 1982, Fife et al. 4178 (INPA). Ro-

RAIMA: 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).

***Radula pallens* (Sw.) Nees & Mont.**, Voy. Amér. Mérid., Bot. 71. 1839. Fig. 19

Jungermannia pallens Sw., Prodr. 143. 1788. Type: Jamaica, Swartz s.n. (holotype: S-B28464!).

= *Radula didrichsenii* Steph., Sp. Hepat. 4: 818. 1912, fide Castle (1959a).

= *Radula kegelii* Steph., Hedwigia 23: 152. 1884. Type: Suriname, Near Maricpaston, 1846, Kegel 1412 (lectotype: G-00121979!, designated by Gradstein in press; isolectotypes: G-00264270!, G-0026471!). Brazil, Santa Catarina, 1847, Pabst 886 (syntype: G-00264272!).

= *Radula obovata* Castle, J. Hattori Bot. Lab. 21: 16. 1959. SYN. NOV. Type: Dominica, on leaves, head of Castle Bruce River, 1896, W.R. Elliott 1657, as *R. pallens* (holotype: BM). Guadeloupe. L'Herminier 14, Hep. Eur. Exsicc. 564 (ed. Gottsche & Rabenhorst as *R. pallens*) (paratypes: JE-04007822!, JE-04007823!, JE-04007824!).

Dioicous. PLANTS 1.5–3 mm wide, olive-green to brown in herbarium, irregularly pinnate to dichotomous. STEMS in cross section with ca. 35 thick-walled epidermal cells surrounding ca. 68 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones small to lacking. LEAVES widely spreading, imbricate, slightly convex, suborbicular, 1.1–1.6 mm long, 0.8–1.1 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane, entire; marginal cells subquadrate to isodiametric, 15–20 × 10–15 µm, median and basal cells isodiametric, 15–20 µm, cell walls thin, trigones small to usually lacking, cuticle smooth. LOBULES distant, (sub)quadrate, 0.3–0.6 mm long, 0.2–0.5 mm wide, 1/4–1/3 the lobe length, inflated at rhizoid area, insertion line straight, base plane to recurved, rounded, covering 1/2 the stem, rarely fully overlapping the stem on branches, free margin plane, ± straight, apex plane to sometimes incurved, rounded to ± obtuse, distal margin straight; keel straight to concave, spreading at angles of 60–70° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA terminal to intercalary on long branches, with 3–6 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 rarely recurved, entire, lobule ovate, ca. 3/4 of lobe length, base rounded to obtuse, free margin ± straight, apex rounded. GYNOCIA on long branches, with 1–2 innovations; bracts ovate, 1–1.3 mm long, 0.5–0.8 mm wide, apex rounded, margin plane, entire, lobule oblong, 1/2–1/3 of lobe length, apex rounded. PERIANTHS subcylindrical, 2.3–4 mm long, 1–1.4 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by regenerants on leaf margins and leaf surfaces, caducous *Lejeunea*-type branches and stem fragmentation.

Additional description and illustration: Castle (1959a, p. 39–42, Fig. 18 as *R. kegelii*, 1960, 1967, p. 30–32, Fig. 12), Yamada (1980, p. 248–250, Fig. 5 as *R. kegelii*), Reiner-

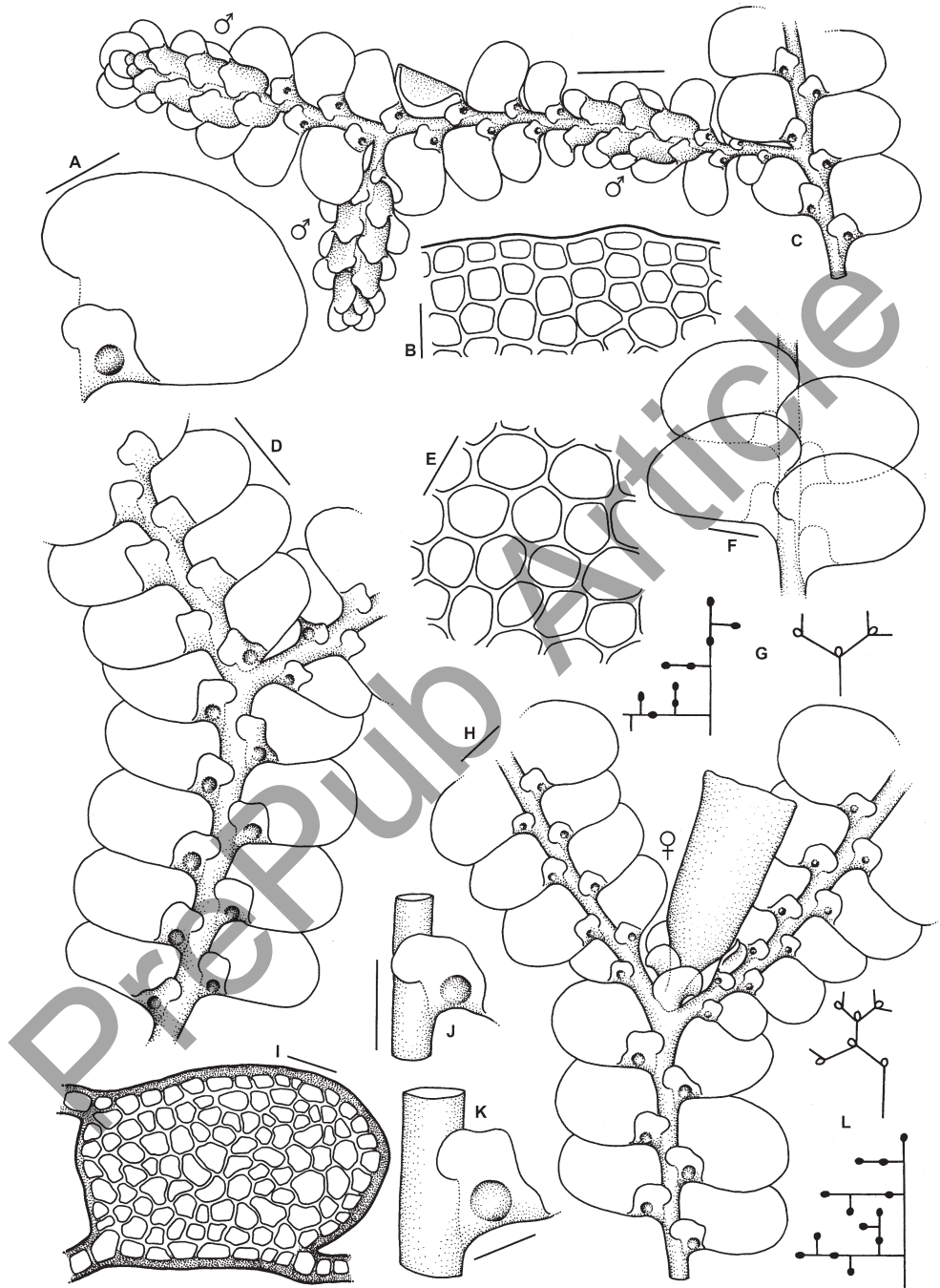


Fig. 19. *Radula pallens* – A. Leaf. B. Marginal leaf cells. C. Habit with androecia. D. Habit. E. Median leaf cells. F. Habit, dorsal view. G, L. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). H. Habit with gynoecia. I. Cross section of a stem. J, K. Lobule. (A, F, H, I = 500 μ m; B, E = 25 μ m; C, D = 1000 μ m; J = 44 μ m; K = 250 μ m; A, B, D–F, J, K from the isoelectotype G-00264270 of *R. kegelii*; C, G, H, I, L, from SP-449510).

Drehwald (1994, p. 10–12, Fig. 2B as *R. kegelii*), Lemos-Michel (2001, p. 157–159, Fig. 44 as *R. kegelii*), Gradstein & Ilkiu-Borges (2009, p. 40–41, Fig. 22I–K as *R. kegelii*).

Distribution and habitat: Widespread in tropical America. In Brazil recorded from Acre, Alagoas, Amazonas, Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. The species usually grows on bark and decaying wood, from sea level to 1560 m elevation.

Taxonomic notes: *Radula pallens* is characterized by (1) plants irregularly pinnate to dichotomous; (2) leaves suborbicular with entire margins and broadly rounded apex; (3) leaf cells small, 15–20 μ m in midleaf, thin-walled, trigones small or lacking, cuticle smooth; (4) lobules distant, parallel to stem, (sub)quadrate, base rounded, covering up to 1/2 the stem (rarely fully overlapping the stem on branches), apex rounded to obtuse, keel straight to concave.

The species was considered endemic to Jamaica by Castle (1960), but Gradstein (in press) based on study of the types found that it is conspecific with *R. kegelii*, a species widely distributed in the Neotropics. *Radula pallens* is also conspecific with *R. obovata*, a species recorded from Mexico, West Indies (Castle 1959a) and Brazil (Yamada 2003).

Selected examined specimens: 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, 59°50'W, 24 August 1979, Buck 3102 (NY). BAHIA: Santa Teresinha, Serra da Jibóia, ca. 800 m, 16 December 2003, Valente 308 (UFP). 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 Timbui, 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, Pietrobon et al. 10032 (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, 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 Ecológica Aracuri, 30 July 1982, Bueno 1720 (ICN). SANTA CATARINA: Santa Cecília, km 122 da BR 116, 28 April 1983, Yano & Pirani 7116 (SP). 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).

Radula pocsii K.Yamada, J. Hattori Bot. Lab. 54: 245. 1983.

Fig. 20

Type: Cuba, Santiago, Sierra de la Gran Piedra, Finca Isabelica, 1100 m, 30 October 1980, Pócs & Caduf 9199/AQ (isotype: NICH-400982!).

Dioicous. PLANTS 1.5–2 mm wide, green to yellowish-green in herbarium, dichotomous. STEMS in cross section with ca. 17 thick-walled epidermal cells surrounding ca. 18 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls brown, trigones large. LEAVES 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, not overlapping the stem, apex rounded, 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, increasing in size towards the margins, cuticle smooth. LOBULES distant, rhombic, 0.5–0.8 mm long, 0.25–0.5 mm wide, 1/3–1/2 the lobe length, inflated at rhizoid area, 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 to slightly sinuate; keel straight, spreading at angles of 30–40° with the stem. RHIZOIDS not seen. ANDROECIA not seen. GYNOECIA on long branches, with 1–2 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. PERIANTHS not seen. VEGETATIVE REPRODUCTION by caducous leaf lobes and regenerants.

Additional description and illustration: Yamada (1983, p. 245–247, Fig. 3).

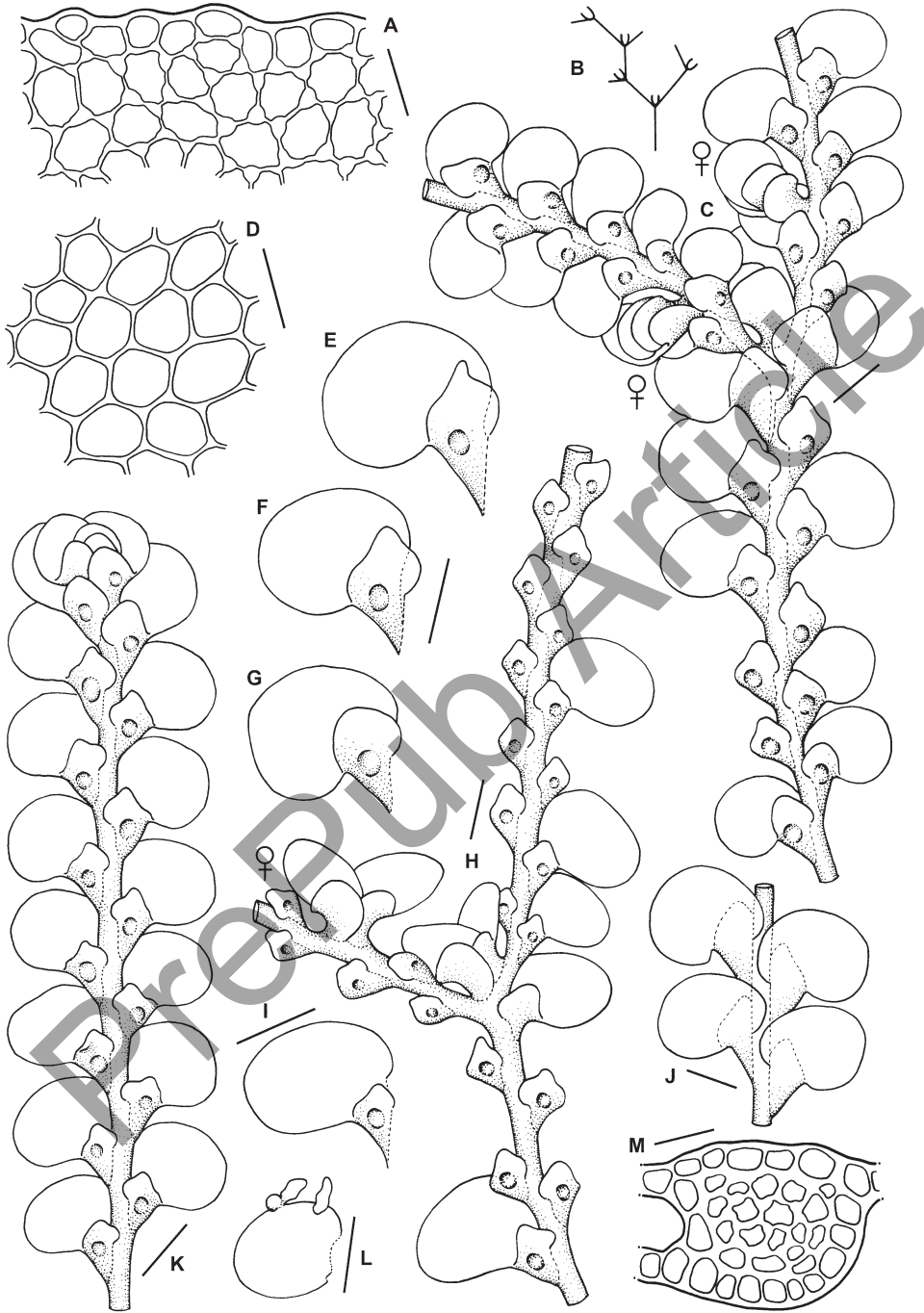
Distribution and habitat: Cuba and Brazil. In Brazil recorded from Paraná, Rio de Janeiro, Rio Grande do Sul and São Paulo. The species grows in Atlantic forest on tree trunks and rock, usually in humid places, at 650–1700 m elevation.

Taxonomic notes: *Radula pocsii* is characterized by (1) plants dichotomous; (2) leaves distant to contiguous, convex, ovate to usually falcate-ovate; (3) leaf cells with trigones small at leaf base increasing in size towards the margins; (4) lobules distant, rhombic, with base rounded, covering 1/3–1/2 the stem, apex rounded, keel straight (long), spreading at angles of 30–40° with the stem, lobule inflated at rhizoid area.

The species resembles *R. javanica* but the latter species is irregularly pinnate (dichotomous in *R. pocsii*), without or with small trigones, which do not increase in size towards the leaf margin (increasing in size towards the margins in *R. pocsii*), and lobules 0.2–0.45 × 0.1–0.25 mm (0.5–0.8 × 0.25–0.5 mm in *R. pocsii*).

Selected examined specimens: BRAZIL. PARANÁ: Morretes, Parque Estadual do Marumbi, trilha vermelha, 25°26'55"S, 48°54'54"W, 1200 m, 22 July 2014, Peralta et al.

Fig. 20. *Radula pocsii* – A. Marginal leaf cells. B. Cladograph of plants (U = gynoecia without perianth). C, H, K. Habit, ventral view. D. Median leaf cells. E–G, I. Leaves. J. Habit, dorsal view. L. Leaf with regenerants. M. Cross section of a stem. (A, D = 25 µm; C, E–L = 500 µm; M = 50 µm; A, D, K from SP-452239; B–C, E–J, L–M from the isotype in NICH).



15804 (SP). RIO DE JANEIRO: Serra do Itatiaia, Resende, 1520 m, 20 April 1987, Schäfer-Verwimp & Verwimp 8395 (MG). 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).

***Radula pseudostachya* Spruce**, Trans. & Proc. Bot. Soc. Edinburgh 15: 319. 1885.

Fig. 21

Type: Venezuela, Amazonas, San Carlos de Rio Negro, “ad arborum ramulus in sylvis,” Spruce s.n. (isotype: G-00047738!).

Diocious. PLANTS 1.3–2 mm wide, yellowish to yellowish-brown in herbarium, regularly pinnate. STEMS in cross section with ca. 19 thick-walled epidermal cells surrounding ca. 14 thick-walled medullary cells, epidermal and medullary cells of the same size, cell walls yellowish to brown, trigones large. LEAVES widely spreading, contiguous to subimbricate, convex, falcate-ovate, 0.8–1.1 mm long, 0.5–0.7 mm wide, dorsal base rounded, overlapping the stem, 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, cuticle verruculose. LOBULES contiguous to subimbricate, subquadrate to 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 line arched, base plane, rounded, covering 1/2 to fully overlapping the stem, free margin plane, straight, apex plane, rounded, distal margin straight; keel convex, spreading at angles of 50–60° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA not seen. 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. PERIANTHS not seen. VEGETATIVE REPRODUCTION by caducous leaf lobes, producing almost completely naked branches.

Additional description and illustration: Castle (1967, p. 21–22, Fig. 8), Yamada (1980, p. 251–252, Fig. 7).

Distribution and habitat: Venezuela and Brazil. In Brazil only known from Amazonas, where it was found growing on bark. The type is from Venezuela, not from Brazil (Castle 1967, Yamada 1980).

Taxonomic notes: *Radula pseudostachya* is characterized by (1) plants with strongly caducous leaf lobes, branches often almost denuded; (2) leaves falcate-ovate, convex with strongly recurved margins; (3) cell with large trigones and verruculose cuticle; (4) lobules contiguous to subimbricate, subquadrate to subrectangular, base covering 1/2 to fully overlapping the stem, keel convex, strongly inflated along the keel.

This species is closely related to *R. fendleri* var. *fendleri*; for differences see under the latter.

Selected examined specimens: BRAZIL. AMAZONAS: Manaus, Manaus-Caracarai road, km 45, caatinga on white sand, on tree trunk, 5 April 1971, Prance et al. 11384 (INPA).

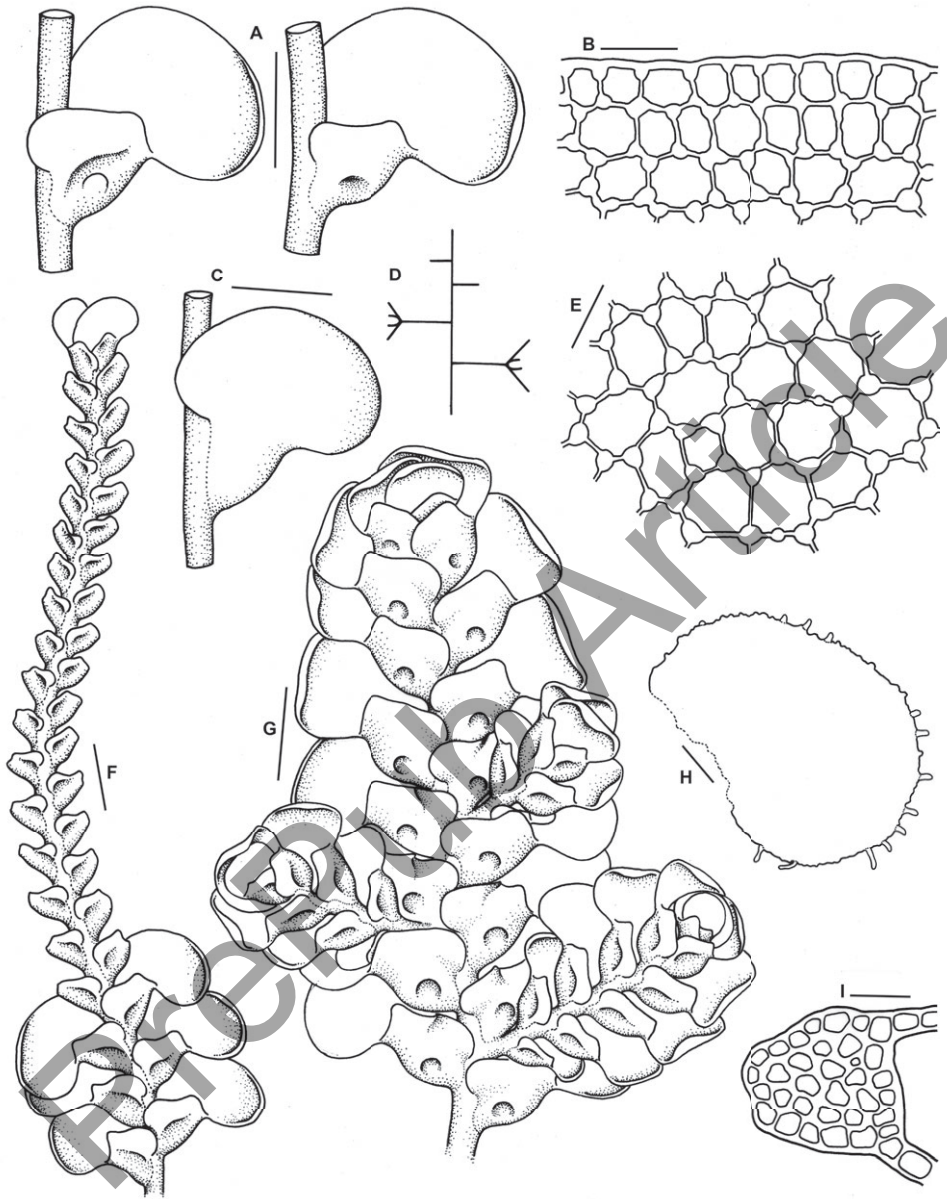


Fig. 21. *Radula pseudostachya* – A. Leaves. B. Marginal leaf cells. C. Leaf dorsal view. D. Cladograph of plants. E. Median leaf cells. F–G. Habit. H. Caducous leaf with rhizoids on margin. I. Cross section of a stem. (A, C, F, G = 500 μ m; B, E = 25 μ m; H = 100 μ m; I = 50 μ m; A–I from INPA-51640).

***Radula punctata* Steph.**, Hedwigia 23: 135. 1884.

Fig. 22

Type: Chile, Krause s.n., ex hb. Sande Lacoste (holotype: G-00112207!).

= *Radula plumosa* Steph., Hedwigia 23: 154. 1884, fide Castle (1937 "1936").

Dioicous. PLANTS 2–3.2 mm wide, green to brown in herbarium, regularly pinnate. STEMS in cross section with ca. 60 thick-walled epidermal cells surrounding ca. 200 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones small to lacking. LEAVES widely spreading, shallowly imbricate, slightly convex, ovate, 1–1.5 mm long, 0.7–1.3 mm wide, dorsal base shallowly auriculate, overlapping the stem, apex rounded, margin plane, entire; marginal cells subquadrate, 10–15 × 8–10 μm, median and basal cells isodiametric to elongate, 15–25(–30) × 10–15(–20) μm, cell walls thickened, trigones small at leaf base increasing in size towards the margins, cuticle smooth. LOBULES distant to contiguous, subquadrate, 0.6–1 mm long, 0.4–0.7 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, insertion line inverted J-shaped, base plane on main stem, shallowly recurved on branches, rounded to slightly auriculate, covering 1/2 to fully overlapping the stem, free margin plane, straight to sinuate, apex rounded, distal margin ± straight; keel straight, spreading at angles of 50–90° with the stem. RHIZOIDS colorless to brown, numerous. ANDROECIA not seen. GYNOCIA on long branches, with 2 innovations; bracts ovate, 2.5–3.3 mm long, 0.6–0.7 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded. PERIANTHS subcylindrical, 2.4–2.8 mm long, 1.3–1.5 mm wide at apex, mouth irregularly undulate. VEGETATIVE REPRODUCTION not observed.

Additional description and illustration: Castle (1937, p. 30–33, Fig. 5), Solari (1978, p. 197–199, Fig. 9), Yamada (1981, p. 390–393, Figs. 15–17 as *R. plumosa*).

Distribution and habitat: Brazil, Argentina, Chile. New to Brazil, collected in Atlantic forest in Rio de Janeiro and Santa Catarina, growing on rock at 280–1010 m elevation.

Taxonomic notes: *Radula punctata* is characterized by (1) plants relatively large and regularly pinnate; (2) stem with ca. 260 cells in cross section (epidermal plus medullary cells); (3) leaf lobes shallowly imbricate, ovate; (3) lobule distant, subquadrate with slightly auriculate base, covering 1/2 to fully overlapping the stem, free margin ± straight to sinuate, apex rounded, keel ± straight, inflated at rhizoid area.

Radula punctata resembles *R. recubans* but the latter species differs in plants regularly pinnate, cuticle verruculose (smooth in *R. punctata*) and lobule with a rounded base and straight insertion line (with auriculate base and an inverted J-shaped insertion line in *R. punctata*). Váňa & Engel (2013) suggested that *R. punctata* should be called *R. plumosa* but the name *R. punctata* is older (Gradstein in press).

Examined specimens: BRAZIL. PARANÁ: Morretes, Serra da Graciosa, 14 October 1990, Xavier-Santos 5 (UFP). RIO DE JANEIRO: Itatiaia, Parque Nacional do Itatiaia, °26'22"S, 44°36'7"W, 1010 m, 22 August 2014, Rezende & Costa 297 (RB). SANTA CATARINA: Blumenau, Nova Rússia, 27°03'7"S, 49°05'16"W, 281 m, 17 November 2003, Costa et al. 4382 (RB).

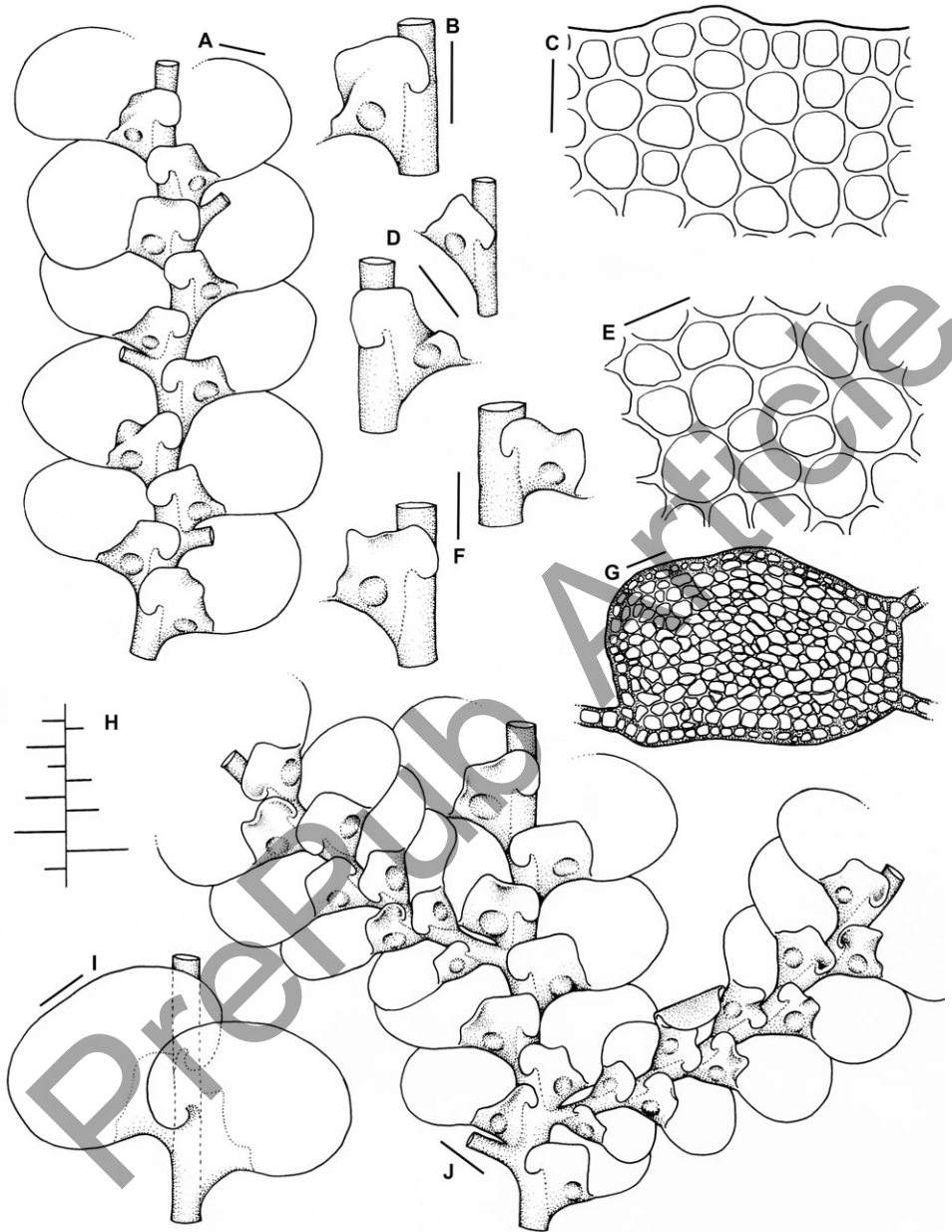


Fig. 22. *Radula punctata* – A, J. Habit. B, D, F. Lobules. C. Marginal leaf cells. E. Median leaf cells. G. Cross section of a stem. H. Cladograph of plants. I. Leaf dorsal view. (A, B, D, F, I, J = 500 μ m; C, E = 25 μ m; G = 50 μ m; A–J from RB-629672).

Radula quadrata Gottsche, Syn. Hepat. 255. 1845.

Fig. 23

Type: Mexico, Jalapa, unknown collector (lectotype: G-00116228!, designated here).

= *Radula mollis* Lindenb. & Gottsche, Syn. Hepat. 725. 1847, fide Yamada & Gradstein (1991).

= *Radula glauca* Steph., Sp. Hepat. 4: 175. 1910, fide Yamada (1993a).

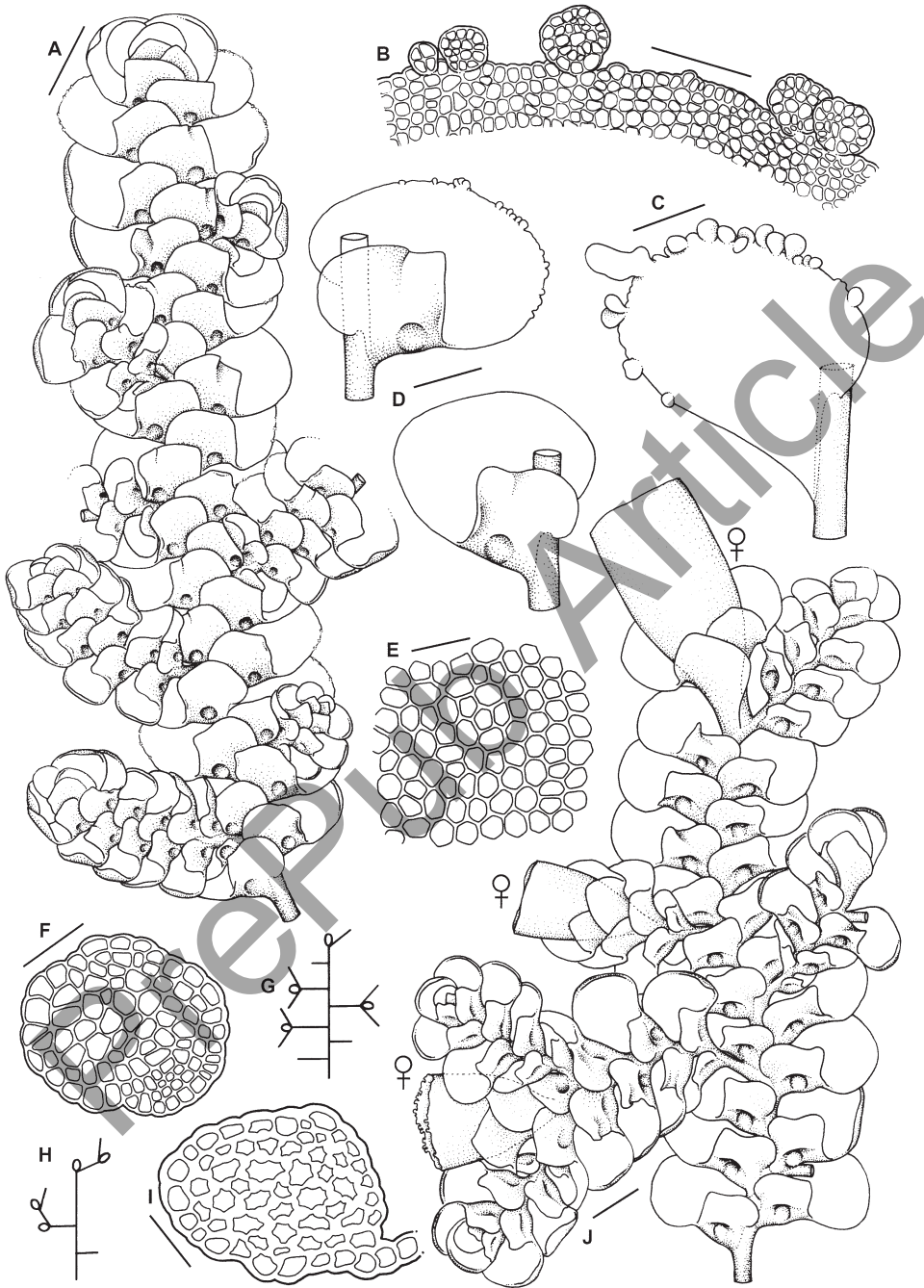
Diocious. PLANTS 2–2.8 mm wide, yellowish-green to brownish in herbarium, irregularly pinnate. STEMS in cross section with ca. 21–25 thick-walled epidermal cells surrounding ca. 20–32 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones large. LEAVES widely spreading, imbricate, slightly convex, ovate, 1.4–1.6 mm long, 1–1.3 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane to recurved, entire to strongly crenulate when with gemmae; marginal cells subquadrate to rounded, 9–18 μm , median and basal cells isodiametric (–10)20–28 μm , cell walls evenly thickened, trigones small, cuticle smooth. LOBULES widely spreading, contiguous to imbricate, subquadrate, 0.85–1 mm long, 0.7–0.75 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area and along the keel, insertion line \pm straight, base plane, rounded, fully 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. RHIZOIDS colorless to brown, scanty. ANDROECIA not seen. GYNOCIA 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. PERIANTHS subcylindrical, 1.6–2.5 mm long, 0.8–1.1 mm wide at apex, mouth entire, irregularly undulate. VEGETATIVE REPRODUCTION by small discoid gemmae, ca. 60–150 μm in diam., copiously produced on the margins of leaves, perianths and bracts.

Additional description and illustration: Castle (1965, p. 332–334, Fig. 1, p. 334–338, Fig. 2 as *R. mollis*), Schuster (1980, p. 615–621, Figs. 626–627 as *R. mollis*), Yamada & Gradstein (1991, p. 65 and 67), Yamada (1993a, p. 133–135, Fig. 52).

Distribution and habitat: Tropical and subtropical America, ranging northwards into warm-temperate, southeastern U.S.A. In Brazil collected in Bahia, Distrito Federal, Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. The species usually grows on bark, at 10–1100 m elevation.

Taxonomic notes: *Radula quadrata* is recognized by (1) leaves convex with margins plane to recurved, entire or strongly crenulate when with gemmae; (2) lobule large, im-

Fig. 23. *Radula quadrata* – A. Habit. B. Leaf margin with gemmae. C. Dorsal leaf margin with gemmae. D. Leaves. E. Median leaf cells. F. Gemma. G–H. Cladograph of fertile plants (open ellipse = gynocia with perianth). I. Cross section of a stem. J. Habit with gynocia (A = 1000 μm ; B = 100 μm ; C = 250 μm ; D, J = 500 μm ; E, F, I = 50 μm ; A, D from the lectotype in G; B, C, E, F, I from MG-130705; G, H, J from SP-181497).



bricate, subquadrate with rounded base, fully overlapping the stem, keel straight, inflated along the keel and at rhizoid area. Besides on leaf lobes, discoid gemmae are also produced on the perianth mouth and bract margins.

Radula quadrata resembles *R. tectiloba* by leaves ovate with margin entire to crenulate with numerous small discoid gemmae, and lobules subquadrate. However, *R. quadrata* differs by lobules $0.85\text{--}1 \times 0.7\text{--}0.75$ mm, imbricate (lobules $0.5\text{--}0.8 \times 0.3\text{--}0.5$ mm, distant to subimbricate in *R. tectiloba*) and lobule base fully overlapping the stem (usually covering 1/2 the stem in *R. tectiloba*, rarely fully overlapping).

Selected examined specimens: BRAZIL. BAHIA: Ilhéus, área da CEPEC, km 22 da rodovia Ilhéus/Itabuna, BR 415, $14^{\circ}47'20''\text{S}$, $39^{\circ}02'58''\text{W}$, 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 Iguaçu, 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, $22^{\circ}32'74''\text{S}$, $43^{\circ}03'79''\text{W}$, 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). SANTA CATARINA: Araranguá, Morro dos Conventos, 18 November 1969, Oliveira s.n. (ICN). SÃO PAULO: Peruibe, Guaraú, Estação Ecológica de Jureia, $24^{\circ}19'12''\text{S}$, $46^{\circ}59'54''\text{W}$, 10 m, 2 July 1988, Yano et al. 11465 (SP).

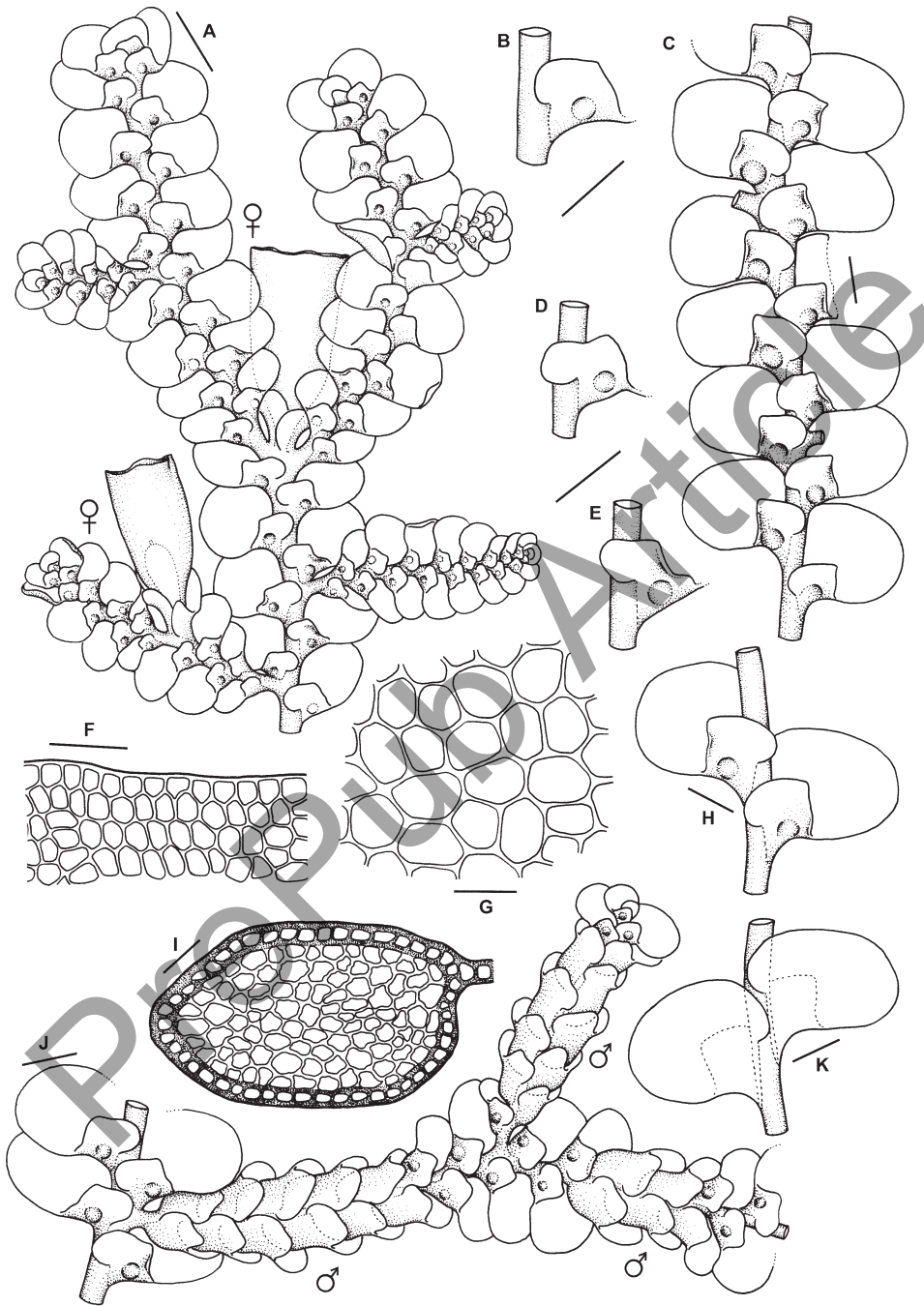
Radula recubans Taylor, London J. Bot. 5: 376. 1846.

Fig. 24

Type: Guyana, Georgetown, Demerara, ex hb. Greville (isotypes: G-00265045!, NY-01021152!).

Dioicous. PLANTS 1.5–2.5 mm wide, olive-green to brown in herbarium, regularly pinnate. STEMS in cross section with ca. 48 thick-walled epidermal cells surrounding ca. 94 thin-walled medullary cells, medullary cells large than epidermal cells, epidermal cell walls brown, medullary cell walls yellowish, trigones small. LEAVES widely spreading, contiguous to subimbricate, slightly convex, ovate, 1–1.6 mm long, 0.75–1.2 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane, entire; marginal cells subquadrate, $12\text{--}18 \times 10\text{--}13$ μm , median cells isodiametric to elongate, $22\text{--}30 \times 12\text{--}18$ μm , basal cells elongate, $25\text{--}35 \times 12\text{--}18$ μm , cell walls thin, trigones small, cuticle verruculose. LOBULES obliquely to widely spreading, distant to contiguous, subquadrate, 0.4–0.9 (–1) mm long, 0.3–0.75 mm wide, ca. 1/2 of the lobe length, inflated at rhizoid

Fig. 24. *Radula recubans* – A. Habit with gynoecia. B, D–E. Lobule. C. Habit. F. Marginal leaf cells. G. Median leaf cells. H. Habit, ventral view. I. Cross section of a stem. J. Habit with androecia. K. Habit, dorsal view. (A = 1000 μm ; B, C, D, E, H, J, K = 500 μm ; F = 25 μm ; G, I = 50 μm ; A, B, D, E, G, I, J from SP-436494; C, F, H, K from the isotype in G).



area, insertion line straight, base plane, rounded, covering 2/3 to fully overlapping the stem, free margin plane, straight, apex plane, sometimes incurved, rounded to obtuse, distal margin sinuate; keel straight to slightly concave, spreading at angles of 40° with the stem. RHIZOIDS not seen. ANDROECIA terminal to intercalary on long branches, with 2–8 pairs of bracts, 0.75–1.1 mm wide; bracts 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. PERIANTHS subcylindrical, 2.5–2.9 mm long, 1–1.4 mm wide at apex, mouth entire, undulate. VEGETATIVE REPRODUCTION not observed.

Additional description and illustration: Castle (1966, p. 11–13, Fig. 3), Yamada (1980, p. 252–254, Fig. 8, 2003, Fig. 84A).

Distribution and habitat: Guatemala, Venezuela, Guyana, Brazil. In Brazil recorded in Amazonas, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul and São Paulo. The species has been collected on tree trunks, decaying wood and rock, usually in humid places, at 300–1640 m elevation.

Taxonomic notes: *Radula recubans* is recognized by (1) plants regularly pinnate; (2) lobes widely spreading, ovate; (3) cells thin-walled, with small trigones and verruculose cuticle; (4) lobules distant to contiguous, subquadrate with rounded base, covering 2/3 to fully overlapping the stem, distal margin usually sinuose and inflated at rhizoid area. *Radula recubans* resembles *R. punctata*; for differences see under *R. punctata*.

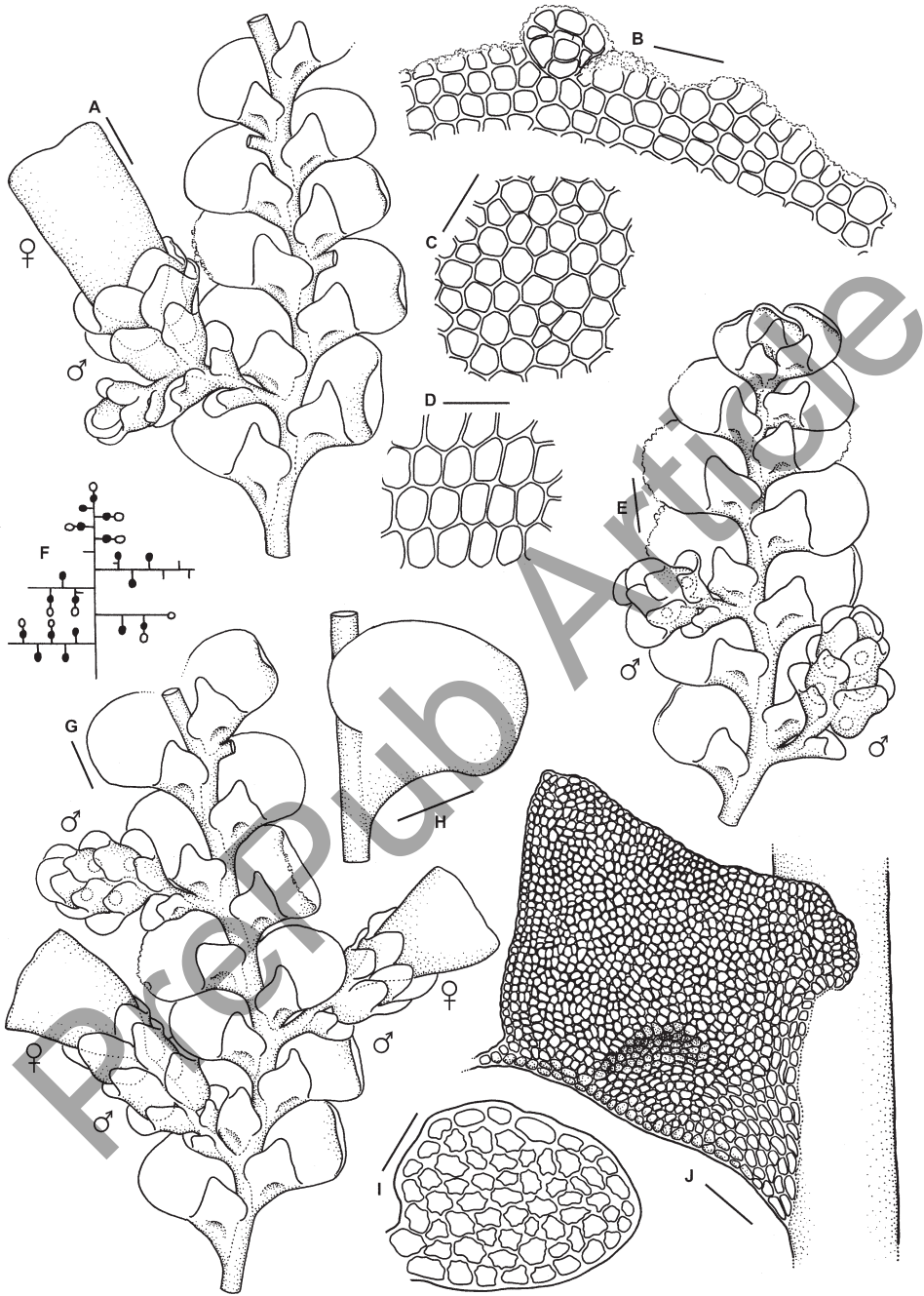
Selected examined specimens: BRAZIL. AMAZONAS: São Gabriel da Cachoeira, Serra Curicuriari, 0°20'S, 66°50'W, 450 m, 9 July 1979, Schuster 79-15-576 (INPA). ESPÍRITO SANTO: Castelo, Parque Estadual do Forno Grande, 20°31'00"S, 41°05'14"W, 1250 m, 1 October 2016, Peralta et al. 19277 (SP). MINAS GERAIS: Lima Duarte, Parque Estadual do Ibitipoca, Rego Seco, 1550 m, 9 August 1993, Yano et al. 20365 (SP). PARANÁ: Morretes, Estação Marumbi, 13 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). SÃO PAULO: Campos do Jordão, 22°43'06"S, 45°32'03"W, 1640 m, 13 September 2012, Gibertoni 52 (SP).

***Radula renneri* F.R.Oliveira-da-Silva, Ilk.-Borg., Gradst. sp. nov.**

Fig. 25

Diagnosis: Paroicous. Leaves ovate, margins entire to crenulate in gemmate leaves. Leaf cell walls thin, with very small trigones. Lobules subquadrate to rhombic, apex usually

Fig. 25. *Radula renneri* – A, E, G. Habit. B. Leaf margin with gemma. C. Median leaf cells. D. Basal leaf cells. F. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). H. Leaf, dorsal view. I. Cross section of a stem. J. Lobule. (A, E, G, H = 500 µm; B, C, D, J = 50 µm; I = 100 µm; A–J from RB-00709793).



extended, obtuse to acute (ending in one cell), base rounded, usually covering 1/2 the stem. Gynoecia usually without innovations, rarely one. Vegetative reproduction by means of small discoid gemmae produced on leaf margins.

Type: Brazil, Rio de Janeiro, Teresópolis, “bairro Quebra Frascos, sobre tronco vivo, na sombra, vegetação de capoeira”, 23 March 1926, Vaughan Bandeira s.n. (holotype: RB-00709793!; isotype: MG!).

Etymology: The new species is dedicated to Matthew A. M. Renner, renowned expert of *Radula*.

PAROICOUS. PLANTS 1.7–2.2 mm wide, yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 23 thick-walled epidermal cells surrounding ca. 40 thick-walled medullary cells, epidermal and medullary cells of the same size, cell walls yellowish, trigones large. LEAVES obliquely to widely spreading, subimbricate, convex, ovate, 1–1.8 mm long, 0.8–1.7 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane to slightly recurved, entire to crenulate in gemmate leaves; 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 very small, cuticle finely papillose. LOBULES distant, subquadrate to rhombic, 0.5–0.9 mm long, 0.45–0.8 mm wide, 2/5–1/2 the lobe length, insertion line straight, base plane, rounded, covering 1/2 the stem, rarely more, free margin plane, straight, apex plane, usually elongate, obtuse to acute (ending in one cell), distal margin straight; keel straight, spreading at angles of 45–65° with the stem, lobules inflated at rhizoid area. RHIZOIDS colorless, scanty. ANDROECIA on short branches, terminal or preceding the gynoecia, with 1–3 pairs of bracts, 1–1.3 mm wide; bracts 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. PERIANTHS trumpet-shaped to subcylindrical, 1.4–2.3 mm long, 1–1.5 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by small discoid gemmae, ca. 65 µm in diam., produced on leaf margins.

Distribution and habitat: The new species is in Brazil only known from Rio de Janeiro State. The species was growing on a living tree trunk in a secondary, Atlantic rainforest in the surroundings of Teresópolis.

Taxonomic notes: *Radula renneri* is recognized by its paroicous condition, leaf margins entire to crenulate in gemmate leaves, leaf cell walls thin, with very small trigones, lobules subquadrate to rhombic, with a usually extended, obtuse to acute (ending in one cell) apex and a rounded base, the base covering ± 1/2 the stem width (rarely more), gynoecia with 0(–1) innovation, and vegetative reproduction by means of small discoid gemmae produced on leaf margins.

The new species was initially thought to be *Radula complanata*, which has been reported several times from Brazil as well as from other tropical and subtropical regions, but all

these records are erroneous or highly doubtful (Yamada 1979, 2003). *Radula renneri* and *R. complanata* share parioicous sexuality and the presence of small discoid gemmae on leaf margins. However, *R. complanata* differs in the smooth cuticle and narrowly rounded to obtuse lobule apex (very rarely subacute). Additionally, *R. complanata* has slightly smaller lobules. The new species is also similar to *R. tectiloba* in lobule shape and presence of discoid gemmae on leaf margins, but the latter species differs in dioicous sexuality and slightly smaller lobules with the apex not extended and usually rounded (rarely obtuse).

Before this study, *Radula mexicana* was the only monoicous species registered from Brazil (Yamada 2003, BFG 2018). This latter species, however, is autoicous, produces innovations (usually two per gynoeceium) and lacks gemmae.

***Radula schaefer-verwimpii* K. Yamada**, J. Jap. Bot. 65: 3. 1990. Fig. 26

Type: Brazil, Minas Gerais, National Park Serra do Caparaó, “auf schattigem Felsblock,” 1360 m, 28 July 1987, Schäfer-Verwimp 8989 (isotypes: G-00265052!, SP-383443!, NY-01021153!, NY-01021154!, GOET-012152!, GOET-012153!).

Dioicous. PLANTS 0.6–1.2 mm wide, green to olive-green in herbarium, irregularly pinnate. STEMS in cross section with ca. 16 thick-walled epidermal cells surrounding ca. 12 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls colorless, trigones lacking. LEAVES widely spreading, distant to contiguous, convex, ovate to falcate-ovate, 0.6–0.9 mm long, 0.4–0.7 mm wide, dorsal base rounded, not overlapping the stem, apex obtuse, margin plane, entire; marginal cells isodiametric, 8–15 µm in diam., median cells isodiametric to elongate, 15–20 × 10–15 µm, basal cells isodiametric to elongate, 20–25 × 10–15 µm wide, cell walls thin, trigones lacking, cuticle smooth. LOBULES distant, subquadrate to rhombic, 0.3–0.5 mm long, 0.15–0.25 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, insertion line arched, base plane, rounded, covering 1/5–1/3 the stem, free margin plane, straight, apex plane, rounded to obtuse, distal margin straight; keel strongly convex, spreading at angles of 30–40° with the stem. RHIZOIDS colorless, scanty. ANDROECIA intercalary on short branches, with 2–4 pairs of bracts, 0.7–1.1 mm wide; bracts 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 on short branches, with two innovations; bracts oblong-ovate, 0.7–0.85(–0.9) mm long, 0.3–0.4 mm wide, apex rounded, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS not seen. VEGETATIVE REPRODUCTION by caducous leaf lobes, producing completely denuded branches, and by discoid gemmae, 50–130 µm in diam., produced on leaf margins.

Additional description and illustration: Yamada (1990, p. 3–6, Fig. 2).

Distribution and habitat: Guyana, Venezuela, Colombia, Ecuador, Bolivia and Brazil. In Brazil recorded in Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro and São Paulo. The species usually grows on rock and soil, rarely on tree trunks, in Atlantic forest, at 1000–2400 m elevation.

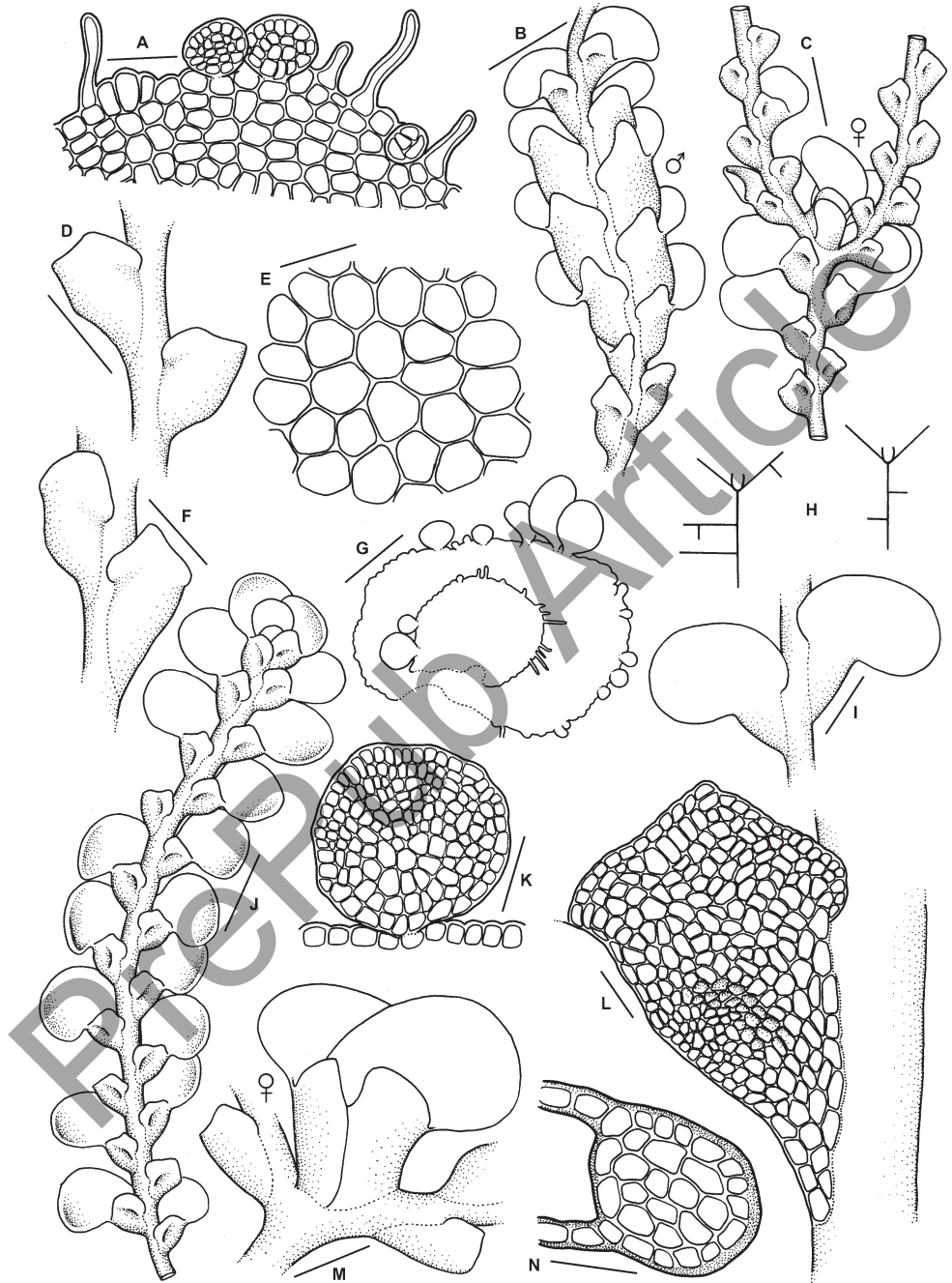


Fig. 26. *Radula schaefer-verwimpii* – A. Marginal leaf cells with regenerants and rhizoids. B. Habit with androecia. C. Habit with gynoecia. D, F, L. Lobules. E. Median leaf cells. G. Caducous leaf with regenerants and rhizoids on margin. H. Cladograph of plants (U = gynoecia without perianths). I. Leaf dorsal view. J. Habit. K. Regenerants. M. Bracts. N. Cross section of a stem. (A, J, K, L, N = 50 µm; B, C, J = 500 µm; D, G, I, M = 250 µm; E = 25 µm; F = 200 µm; A, F, G, K, L from isotype G00265052; C, D, E, H, I, M, N from the isotype in SP; B from SP-43401; J from SP-461245).

Taxonomic notes: *Radula schaefer-verwimpii* differs from other Brazilian species of *Radula* in the following combination of characters: (1) plants with strongly caducous leaf lobes; (2) leaves ovate to falcate-ovate with rounded apex; (3) lobules small, distant, subquadrate to rhombic, base covering only 1/5–1/3 the stem, keel convex. This is the most fragile species among Brazilian *Radulas*; the branches are usually devoid of leaf lobes.

This species resembles *R. pocsii* by caducous leaf lobes, producing almost completely denuded branches, leaves ovate to falcate-ovate, and lobule shape with keel straight, spreading at angles of 30–40° with the stem. However, *R. schaefer-verwimpii* differs by the stem anatomy, plants usually 0.6–1.2 mm wide (1.5–2 mm in *R. pocsii*), and leaf cells without trigones (trigones small at leaf base and increasing in size towards the margins in *R. pocsii*). *Radula schaefer-verwimpii* also resembles *R. brasílica*; differences are given under *R. brasílica* and in the key.

Selected examined specimens: BRAZIL. ESPÍRITO SANTO: Castelo, Parque Estadual do Forno Grande, 20°31'00"S, 41°05'14"W, 1250 m, 1 October 2016, Peralta et al. 19216 (SP). MINAS GERAIS: Poços de Caldas, morro São Domingos, 1330 m, 21°47'S, 46°33'W, 24 May 1986, Schäfer-Verwimp & Verwimp 7030 (SP). PARANÁ: Morretes, Parque Estadual Pico do Marumbi, trilha do Olimpo, 25°27'10"S, 48°55'11"W, 1000–1200 m, 16 October 2015, Peralta et al. 17704 (SP). RIO DE JANEIRO: National Park Itatiaia, Itatiaia, 1200 m, 1 November 1987, Schäfer-Verwimp & Verwimp 9255 (SP). SÃO PAULO: Guarulhos, 23°23'55"S, 46°29'55"W, 745 m, 26 April 2013, Peralta & Fortes 13923 (SP).

Radula sinuata Steph., Sp. Hepat. 4: 161. 1910.

Fig. 27

Type: Brazil, Minas Gerais, Caldas, 1854, Lindberg s.n. (lectotype: G-00282150!, designated by Yamada 1987; isolectotype: G-00282151!).

= *Radula montana* Steph., Sp. Hepat. 4: 176. 1910. Type: Brazil, Paraná, Serra do Mar, 29 January 1907, Dusén 3478 (lectotype: G-00043901!, designated by Yamada 1987).

= *Radula obtusifolia* Steph., Sp. Hepat. 4: 178. 1910, fide Castle (1965).

Dioicous. PLANTS 1.3–2.2 mm wide, yellow to yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 41 thick-walled epidermal cells surrounding ca. 75 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones lacking. LEAVES obliquely to widely spreading, imbricate, convex, ovate to falcate-ovate, 0.8–1 mm long, 0.6–0.9 mm

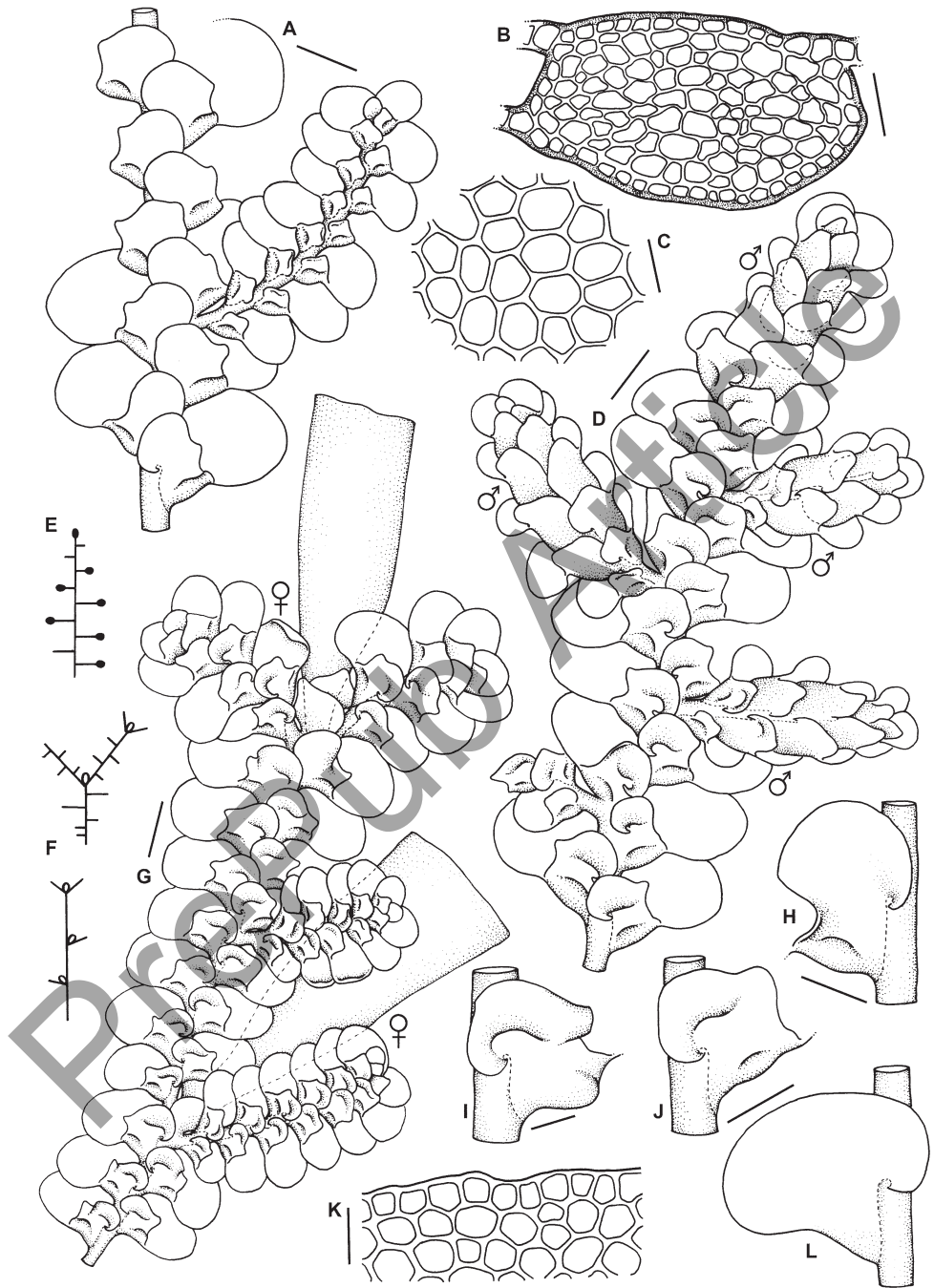


Fig. 27. *Radula sinuata* – A. Habit. B. Cross section of a stem. C. Median leaf cells. D. Habit with androecia. E–F. Cladograph of fertile plants (open ellipse = gynoecea with perianth; solid ellipse = androecia). G. Habit with gynoecea. H–J. Lobule. K. Marginal leaf cells. L. Leaf, dorsal view. (A, D, G, J, L = 500 μ m; B = 50 μ m; C, K = 25 μ m; H = 250 μ m; I = 162 μ m; A from SP-379616; B–C, I–L from the lectotype in G; D–E from SP-455594; F–G from SP-407257; H from SP-280499).

wide, dorsal base rounded to shallowly auriculate, overlapping the stem, apex rounded, margin plane to recurved, entire; marginal cells subquadrate to isodiametric, 8–15 μ m in diam., median and basal cells isodiametric to elongate, 20–25 \times 15–20 μ m, cell walls thin, trigones lacking, cuticle smooth. LOBULES contiguous to imbricate, subquadrate, 0.5–0.8 mm long, 0.5–0.8 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, insertion line circinate, base plane, short-auriculate, covering 3/4 to fully overlapping the stem, free margin plane to incurved, broadly rounded, apex plane, rounded to obtuse, distal margin sinuate; keel \pm straight to convex, spreading at angles of 60° with the stem. RHIZOIDS colorless, scanty. 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 imbricate, oblong, ca. 3/4 of lobe length, base rounded, free margin \pm 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. PERIANTHS subcylindrical, 3.3–4 mm long, 1.2–1.7 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by caducous leaves (rare) and regenerants.

Additional description and illustration: Castle (1965, p. 345–348, Fig. 5 as *R. montana*, p. 348–350, Fig. 6), Yamada (1987, p. 294–295, Fig. 35 as *R. montana*, p. 297–298, Fig. 37, 2003, Fig. 83D), Reiner-Drehwald (1994, p. 16–17, Fig. 1A as *R. montana*), Lemos-Michel (2001, p. 162–165, Fig. 46 as *R. montana*).

Distribution and habitat: Costa Rica to Bolivia, Brazil and Argentina. In Brazil registered from Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. This species is usually found growing on bark, rarely on rock or decaying wood, at 600–1900 m elevation.

Taxonomic notes: *Radula sinuata* is easily recognized by lobules contiguous to imbricate, subquadrate, insertion line circinate, base short-auriculate, frequently fully overlapping the stem, free margin broadly rounded, apex broadly rounded to obtuse, distal margin sinuate, keel \pm straight to convex.

Radula sinuata resembles *R. voluta* in stem anatomy, leaf shape and the auriculate lobule base. However, *R. sinuata* differs by lobule base short-auriculate (strongly auriculate or circinate to coiled in *R. voluta*) and cells without trigones (trigones small at leaf base and increasing in size towards the margins, becoming bulging, in *R. voluta*).

Selected examined specimens: 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, 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). 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). SANTA CATARINA: Lajes, along the BR 116, ca. 19 km S, 11 March 1976, Vital 5647 (SP). SÃO PAULO: Serra do Paranapiacaba, near Apiai, 930 m, 3 May 1987, Schäfer-Verwimp & Verwimp 8447 (SP).

***Radula stenocalyx* Mont.**, Ann. Sci. Nat., Bot., sér. 4, 3: 315. 1855.

Fig. 28

Type: French Guiana, Cayenne, “ad folia filicum,” Leprieur 1395 (lectotype: PC-Montagne-069928!, designated here; isolectotype: BM-000969242!).

= *Radula tenella* Gottsche, Mexik. Leverm. 149. 1863. Type: Trinidad and Tobago, without locality, H. Crüger s.n. (isotype: G-00281383!).

Dioicous. PLANTS 0.9–1.4 mm wide, yellowish-green to brown in herbarium, irregularly pinnate. STEMS in cross section ca. 10 thin-walled epidermal cells surrounding ca. 5 thin-walled medullary cells, epidermal and medullary cells of the same size, cell walls colorless, trigones lacking. LEAVES widely spreading, contiguous, slightly convex, ovate, 0.6–1 mm long, 0.5–0.7 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin plane, sometimes slightly recurved, entire to strongly crenulate when 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, cuticle smooth. LOBULES distant, subquadrate, 0.3–0.4 mm long, 0.2–0.3 mm wide, ca. 1/3 of the lobe length, strongly inflated at rhizoid area, insertion line straight, base plane, not covering the stem, free margin plane, straight, apex plane, rounded, distal margin straight to sinuose; keel convex, spreading at angles of ca. 50° with the stem. RHIZOIDS colorless to brown, numerous on a pronounced mammiliform swelling. ANDROECIA terminal on long branches, with 2–10 pairs of bracts, 300–400 µm wide; bracts 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. PERIANTHS trumpet-shaped to subcylindrical, 1.5–2 mm long, 0.2–0.3 mm wide at apex, mouth irregularly undulate to entire. VEGETATIVE REPRODUCTION by discoid gemmae, 44–200 µm in diam., produced on leaf margins.

Additional description and illustration: Castle (1939, p. 36–39, Fig. 6), Yamada (1993a, p. 135–136, Fig. 53 based on isotype of *R. tenella*), Promma & Chantanaorrapint (2015, p. 229–230, Figs. 64–83).

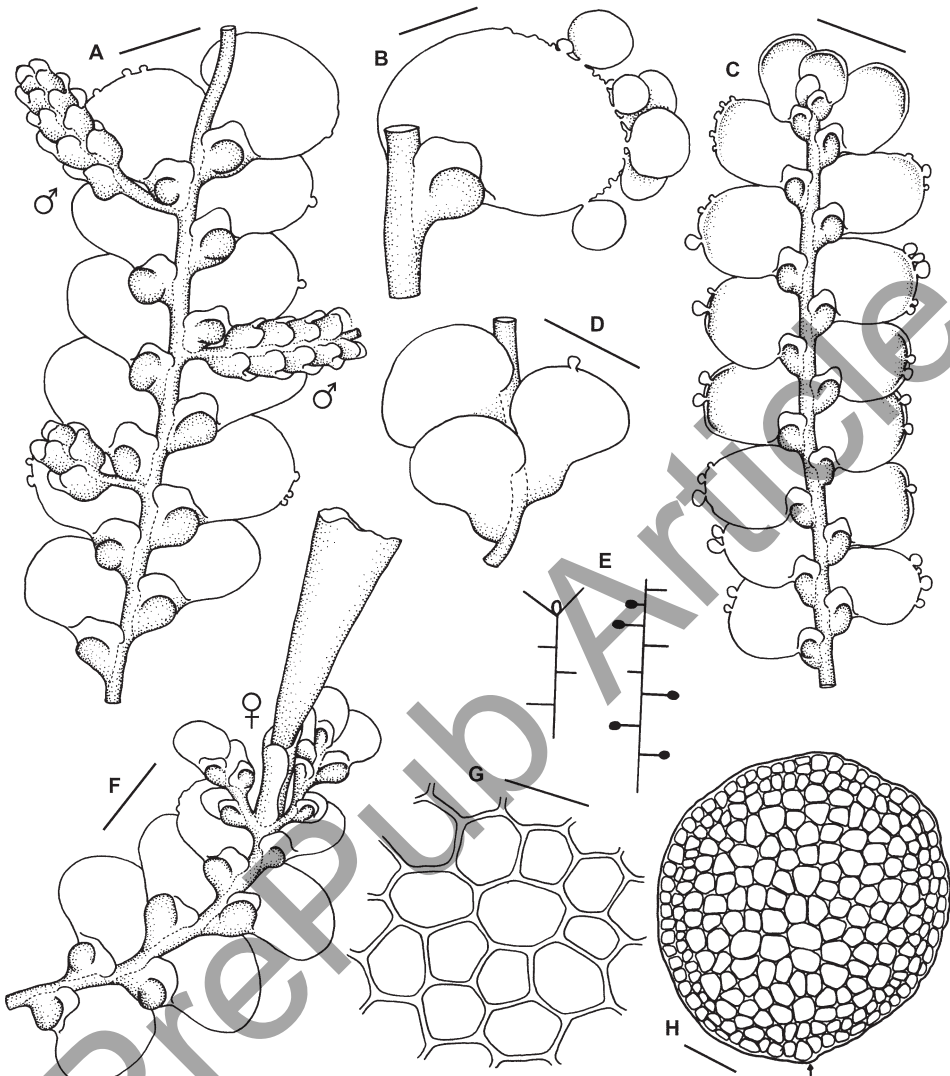


Fig. 28. *Radula stenocalyx* – A. Habit with adroecia. B. Leaf with gemmae. C. Habit. D. Habit, dorsal view. E. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). F. Habit with gynoecia. G. Median leaf cells. H. Gemma. (A, C, D, F = 500 µm; B = 250 µm; G = 25 µm; H = 50 µm; A, D–H from the isolectotype in BM; B–C from MG-130703).

Distribution and habitat: Tropical America, tropical Africa, Asia. In Brazil it occurs in Amazonas, Pará, Paraná, Rio de Janeiro and São Paulo. The species usually grows on living leaves, at 300–1100 m elevation.

Taxonomic notes: *Radula stenocalyx* is characterized by (1) plants epiphyllous; (2) leaves widely spreading with numerous small, discoid gemmae on the margins; (3) leaf cells without trigones; (4) lobules distant, subquadrate, base not covering the stem, apex usually rounded, keel convex, and with a pronounced mammiliform swelling at rhizoid area.

Radula stenocalyx resembles *R. flaccida* and *R. yanoella*; for differences see under *R. flaccida*.

Selected examined specimens: BRAZIL. AMAZONAS: Rio Negro, between Manaus and São Gabriel, south slope of Morro Ximaio, 00°45'–50'S, 66°50'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, 44°36'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).

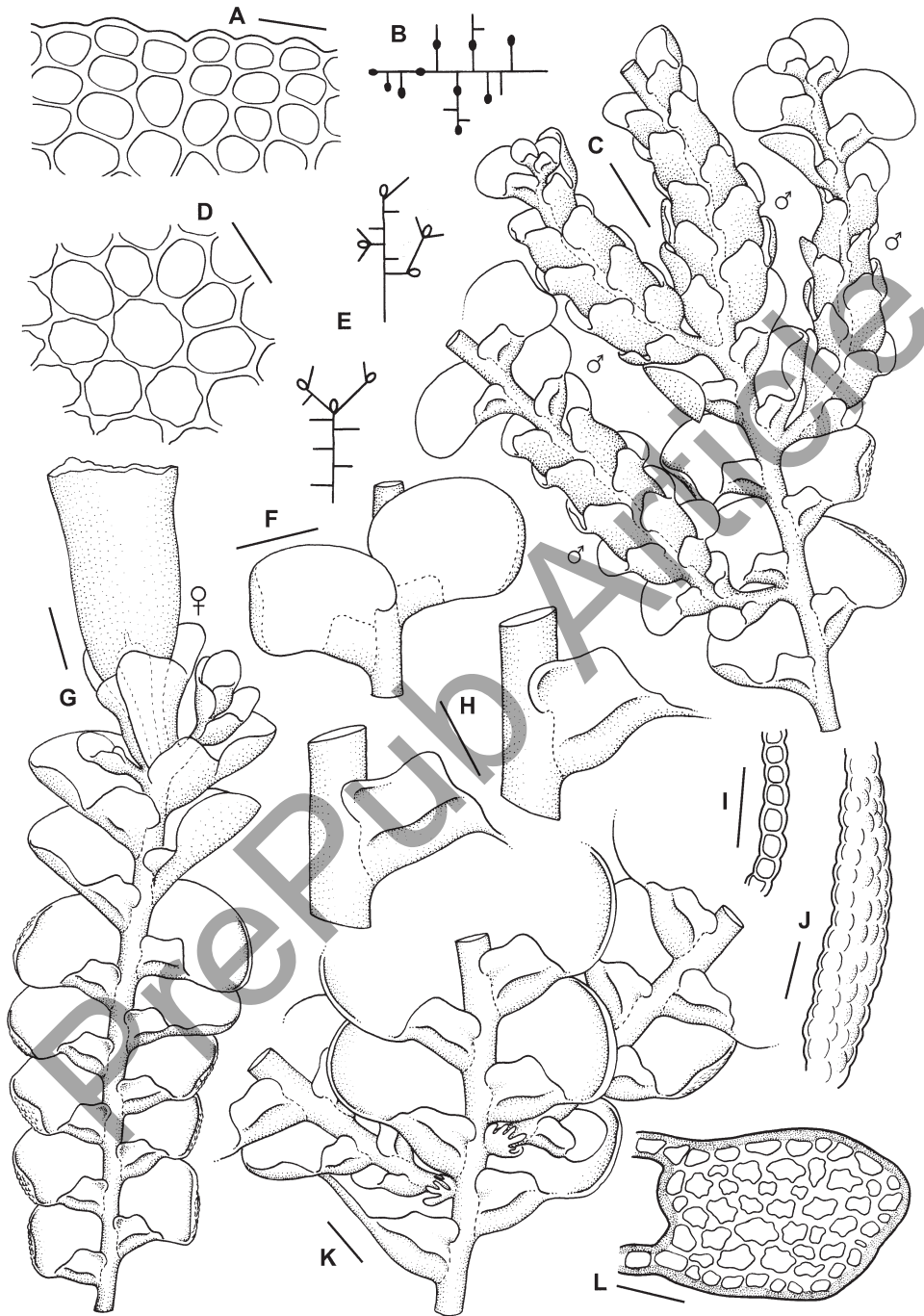
Radula subinflata Lindenb. & Gottsche, Syn. Hepat. 724. 1847.

Fig. 29

Type: Mexico, Sempoaltepec, Liebmann s.n. (isotype: G-00124238!).

Dioicous. PLANTS 1.3–2.4 mm wide, green to yellowish-green in herbarium, irregularly pinnate. STEMS in cross section with ca. 25 thick-walled epidermal cells surrounding ca. 26 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones large. LEAVES widely spreading, contiguous to imbricate, strongly convex, ovate to falcate-ovate, 0.7–1 mm long, 0.45–0.8 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin recurved, slightly crenulate; marginal cells isodiametric, 8–10 µm in diam., median and basal cells isodiametric to elongate, 10–15 × 15–25 µm, cell walls thin, mammillose on the dorsal lobe surface, trigones small, cuticle smooth. LOBULES distant, (sub)quadrate, 0.4–0.5 mm long, 0.3–0.4 mm wide, 1/3–1/2 the lobe length, strongly inflated along the keel, insertion line ± straight, base plane to slightly recurved, rounded, covering up to 1/4 the stem, free margin plane to sinuate, straight, apex rounded, distal margin ± straight;

Fig. 29. *Radula subinflata* – A. Marginal leaf cells. B, E. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). C. Habit with androecia. D. Median leaf cells. F. Leaves, dorsal view. G. Habit with gynoecia. H. Lobules. I. Cross section of a leaf. J. Dorsal leaf with mammillose cells. K. Habit. L. Cross section of a stem (A, D = 25 µm; C, F, G, K = 500 µm; H = 250 µm; I, J, L = 50 µm; A, D–L from MG-130701; B–C from SP-407308).



keel straight to slightly convex, spreading at angles of 40–60° with the stem. RHIZOIDS colorless, scanty. ANDROECIA terminal to intercalary on long branches, with 3–6 pairs of bracts, 0.8–1 mm wide; bracts ovate, 0.6–0.7 mm long, 0.3–0.35 mm wide, margin recurved, entire, apex rounded, lobule ovate, ca. 3/4 of lobe length, base rounded, free margin straight, apex obtuse, keel convex, inflated. GYNOECIA on long branches, with 1–2 innovations; bracts ovate, 1–1.2 mm long, 0.6–0.7 mm wide, margin recurved, entire, apex rounded, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS subcylindrical, 2–3.5 mm long, 0.9–1.1 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by stem fragmentation and caducous *Lejeunea*-type branches.

Additional description and illustration: Castle (1963, p. 13–15, Fig. 5), Yamada & Gradstein (1991, p. 67–68).

Distribution and habitat: Tropical and subtropical America. In Brazil occurring in Bahia, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. The species grows in Atlantic forest, usually on tree trunks and decaying wood, rarely on rock, at 1000–2500 m elevation.

Taxonomic notes: *Radula subinflata* is readily recognized by (1) leaves widely spreading, ovate to falcate-ovate, convex, margins crenulate and recurved; (2) leaf cells dorsally mammillose; (3) lobules distant, (sub)quadrate, with base plane to slightly recurved, covering up to 1/4 the stem, keel straight to slightly convex, lobule strongly inflated along the keel.

Radula subinflata is similar to *R. javanica* in the shape of leaf lobes (ovate to falcate-ovate) and lobules (sub)quadrate. It differs from *R. javanica*, however, in the lobule inflated along the keel (lobule inflated only in rhizoid area in *R. javanica*). Moreover, *R. subinflata* is the only Brazilian species with leaf cells conspicuously mammillose dorsally and leaf margins crenulate without occurrence of gemmae. In other *Radula* species in Brazil, crenulate leaf margins are only seen in connection with presence of gemmae.

Selected examined specimens: BRAZIL. BAHIA: Abaíra, mata Serra do Rei, 4°16'N, 41°54'W, 1550–1650 m, 17 February 1992, Harley et al. 52110 (SP). MINAS GERAIS: Lima Duarte, Parque Estadual do Ibitipoca, Gruta do Cruzeiro, 1530 m, 28 November 1993, Yano et al. 21600 (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. 15827 (SP). RIO DE JANEIRO: Resende, 1 km após o Hotel Alsene, 2500 m, 24 November 1993, Yano et al. 21357 (SP). 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).

Radula tectiloba Steph., Hedwigia 27: 298. 1888.

Fig. 30

Type: Puerto Rico, “in cortice,” Sintenis 65 (lectotype: G-00043865!, designated here; isolectotype: G-00281377!).

= *Radula arsenii* Steph., Sp. Hepat. 6: 505. 1924. Type: Mexico, Arsène 7800 (holotype: G-00067964!).

= *Radula aurantii* Spruce, Bull. Soc. Bot. France 36 (Suppl. Congrès Bot. 1889): CXCIV. 1889[1890], fide Yamada (1981).

= *Radula uleana* Steph., Sp. Hepat. 4: 201. 1910. Type: Brazil, without locality, Ule 244 (holotype: G-00043874!).

Dioicous. PLANTS 1.6–2 mm wide, yellowish-green to yellowish-brown in herbarium, irregularly pinnate. STEMS in cross section with ca. 18 thick-walled epidermal cells surrounding ca. 15 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones large. LEAVES obliquely to widely spreading, imbricate, convex, ovate, 0.6–1.1 mm long, 0.5–0.8 mm wide, dorsal base rounded, overlapping the stem, apex rounded, margin recurved, entire to crenulate when 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, cuticle smooth. LOBULES distant to subimbricate, subquadrate to subrectangular, 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 line straight, base plane, rounded, covering ca. 1/2 the stem, rarely overlapping, free margin plane or recurved, straight, apex rounded, rarely obtuse, distal margin straight; keel concave to convex, spreading at angles of 50–60° with the stem. RHIZOIDS colorless to brown, scanty. 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 mm long, 0.25–0.3 mm wide, apex rounded, margin recurved, entire to crenulate, lobule ovate, 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, lobule oblong-ovate, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS subcylindrical, 1.7–2.2 mm long, 0.9–1.1 mm wide at apex, mouth entire to irregularly undulate-crenulate. VEGETATIVE REPRODUCTION by numerous small discoid gemmae, 30–60 µm in diam., produced on the margins of leaves, perianths and bracts.

Additional description and illustration: Castle (1964, p. 187–190, Fig. 1), Yamada (1981, p. 395–398, Figs. 20–22, 2003, Fig. 82F), Reiner-Drehwald (1994, p. 15–16, Fig. 2C–D as *R. aurantii*), Lemos-Michel (2001, p. 165–167, Fig. 47), Gradstein & Ilkiu-Borges (2009, p. 40–41, Fig. 22H as *R. aurantii*).

Distribution and habitat: Tropical and subtropical America. In Brazil registered from Bahia, Espírito Santo, Goiás, Mato Grosso do Sul, Paraná, Rio Grande do Sul, Santa Catarina and São Paulo. The species colonizes bark of living trees, rotten wood and rock, in *Araucaria* and Atlantic forests, at 50–1600 m elevation.

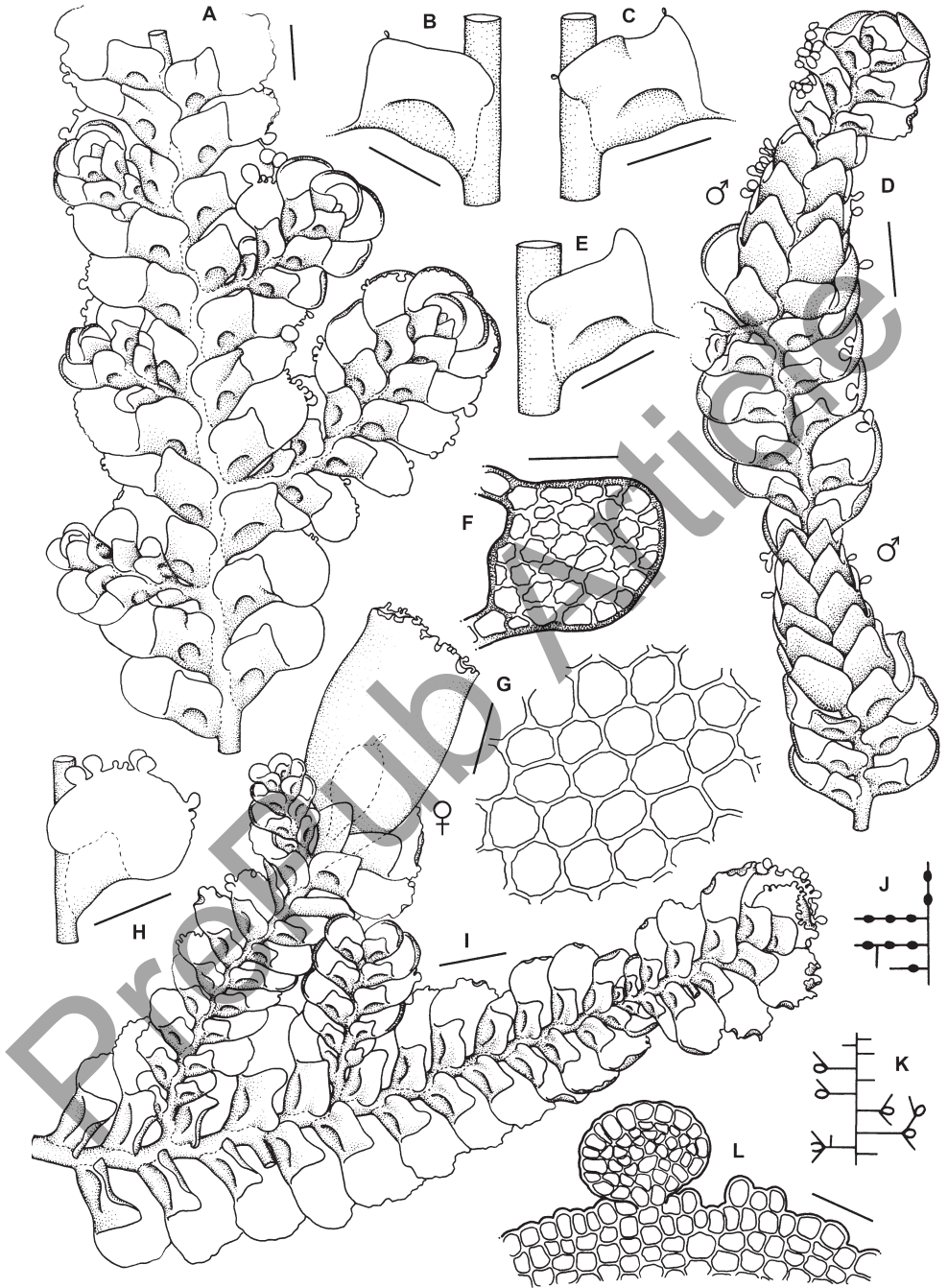


Fig. 30. *Radula tectiloba* – A. Habit. B, C, E. Lobule. D. Habit with androecia. F. Cross section of a stem. G. Median leaf cells. H. Leaf, dorsal view. I. Habit with gynoecia. J–K. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). L. Marginal leaf cells with gemma. (A, D, H, I = 500 µm; B–C, E = 250 µm; F, L = 50 µm; G = 25 µm; A, B–C, E, F–H, K from the isoelectotype in G; D, J from ICN-010297; I, K from ICN-11469).

Taxonomic notes: *Radula tectiloba* is characterized by (1) leaf apex recurved, margin entire, or crenulate when producing gemmae; (2) lobules distant to subimbricate, sub-quadrate to subrectangular, with apex rounded to acute, rarely obtuse, base covering ca. 1/2 the stem, rarely fully overlapping the stem; (3) plants with numerous small discoid gemmae, especially on leaf margins. This species is highly variable morphologically, especially its lobules. In Brazil it may be confused with *R. quadrata* (see comments under *R. quadrata*). The species is also similar to *R. renneri* (see under the latter species).

Yamada (1981) considered *R. aurantii* conspecific with *R. tectiloba* whereas Reiner-Drehwald (1994) recognized the two as distinct species. The latter author pointed out that *R. aurantii* has widely spreading leaves, keel usually concave (“incurved”), and lobule free margin convex in the lower half, while *R. tectiloba* has leaves obliquely spreading, keel usually convex and free margin plane throughout. In our study, however, we found that leaves in *R. tectiloba* vary from obliquely to widely spreading, the keel varies from concave to straight to convex and the lobule free margin from plane to recurved. Therefore, we treat *R. aurantii* as a synonym of *R. tectiloba* following Yamada (1981).

Selected specimens examined: BRAZIL. BAHIA: Itabuna, nas plantações de Cacau da CEPLAC, 24 January 1980, Vital 8697 (SP). 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). MATO GROSSO DO SUL: Mundo Novo, perto da cachoeira, 18 March 1982, Yano 4033 (SP). MINAS GERAIS: Três Corações, margem do Rio Santa Fé, 25 September 2008, Yano & Kirizawa 31316 (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). 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). SANTA CATARINA: Chapecó, Ecoparque, 27°05'10"S, 52°37'02"W, 660 m, 31 July 2013, Villagra 695 (SP). 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).

Radula tenera Steph., Hedwigia 23: 149. 1884.

Fig. 31

Type: Brazil, without locality, Sowerby s.n. (lectotype: NY-01021198!, designated here; isoelectotypes: G-00265058!, NY-01021201!, NY-01021199!).

Dioicous. PLANTS 1–1.8 mm wide, yellowish-green to yellowish-brown in herbarium, regularly pinnate. STEMS in cross section with ca. 27 thick-walled epidermal cells surrounding

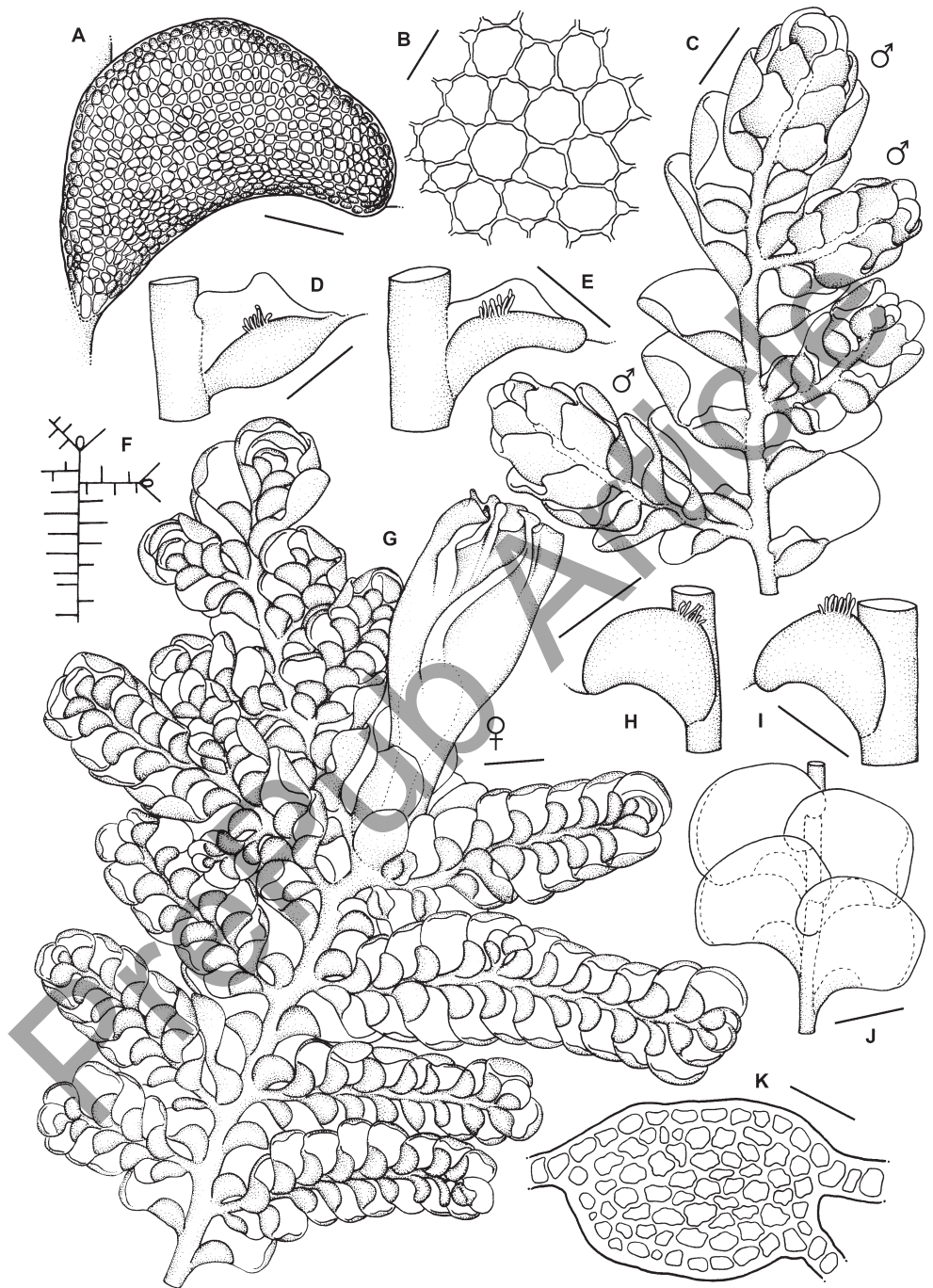


Fig. 31. *Radula tenera* – A, D–E, H–I. Lobule. B. Median leaf cells. C. Habit with androecia. F. Cladograph of fertile plants (open ellipse = gynoecia with perianth). G. Habit with gynoecia. J. Habit, dorsal view. K. Cross section of a stem. (A = 100 µm; B = 25 µm; C, G, J = 500 µm; D–E, H–I = 250 µm; K = 50 µm; A–B, E–K from lectotype in NY; C–D from SP-449003).

ca. 42 thick-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell and medullary cell walls yellowish, trigones large. LEAVES widely spreading, imbricate, strongly convex, ovate, 0.7–1.2 mm long, 0.4–1 mm wide, dorsal base rounded, overlapping the stem, 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, cuticle smooth. LOBULES distant to contiguous, usually folded and lunular, rarely subquadrate to subrectangular, 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 line straight, short, base plane, straight, not covering the stem, free margin plane, ± 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 40–50° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA terminal to intercalary on short branches, with 2–4 pairs of bracts, 0.7–1 mm wide; bracts 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 ± 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. PERIANTHS trumped-shaped, 2.4–3.6 mm long, 1–1.1 mm wide at apex, mouth entire, strongly undulate. VEGETATIVE REPRODUCTION not observed.

Additional description and illustration: Castle (1963, p. 11–13, Fig. 4), Yamada (1980, p. 255–256, Fig. 10, 2003, Fig. 82B).

Distribution and habitat: Costa Rica, Ecuador, Colombia, Guyana and Brazil. In Brazil registered from Espírito Santo, Paraná, Rio de Janeiro and Rio Grande do Sul. The species grows in Atlantic and *Araucaria* forest, usually on bark of living trees, at 670–1550 m elevation.

Taxonomic notes: *Radula tenera* strikingly differs from other *Radula* species in Brazil by lobules usually folded and lunular with a short insertion line and a strongly and narrowly inflated carinal region, lobule base not covering the stem, keel concave, as well as leaves ovate and strongly convex with a strongly recurved margin.

Selected examined specimens: BRAZIL. 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, Dusén 2584 (NY). 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, 50°05'W, 1000 m, 26 September 1984, Vital & Buck 12232 (NY).

Radula voluta Taylor, Syn. Hepat. 255. 1845.

Fig. 32

Type: Ireland, Kings Co., Dunkerron, Taylor in hb. Gottsche (isoelectotype: PC-Mont.!, designated by Grolle 2001).

= *Radula ramulina* Taylor, London J. Bot. 5: 374. 1846, fide Yamada & Gradstein (1991).

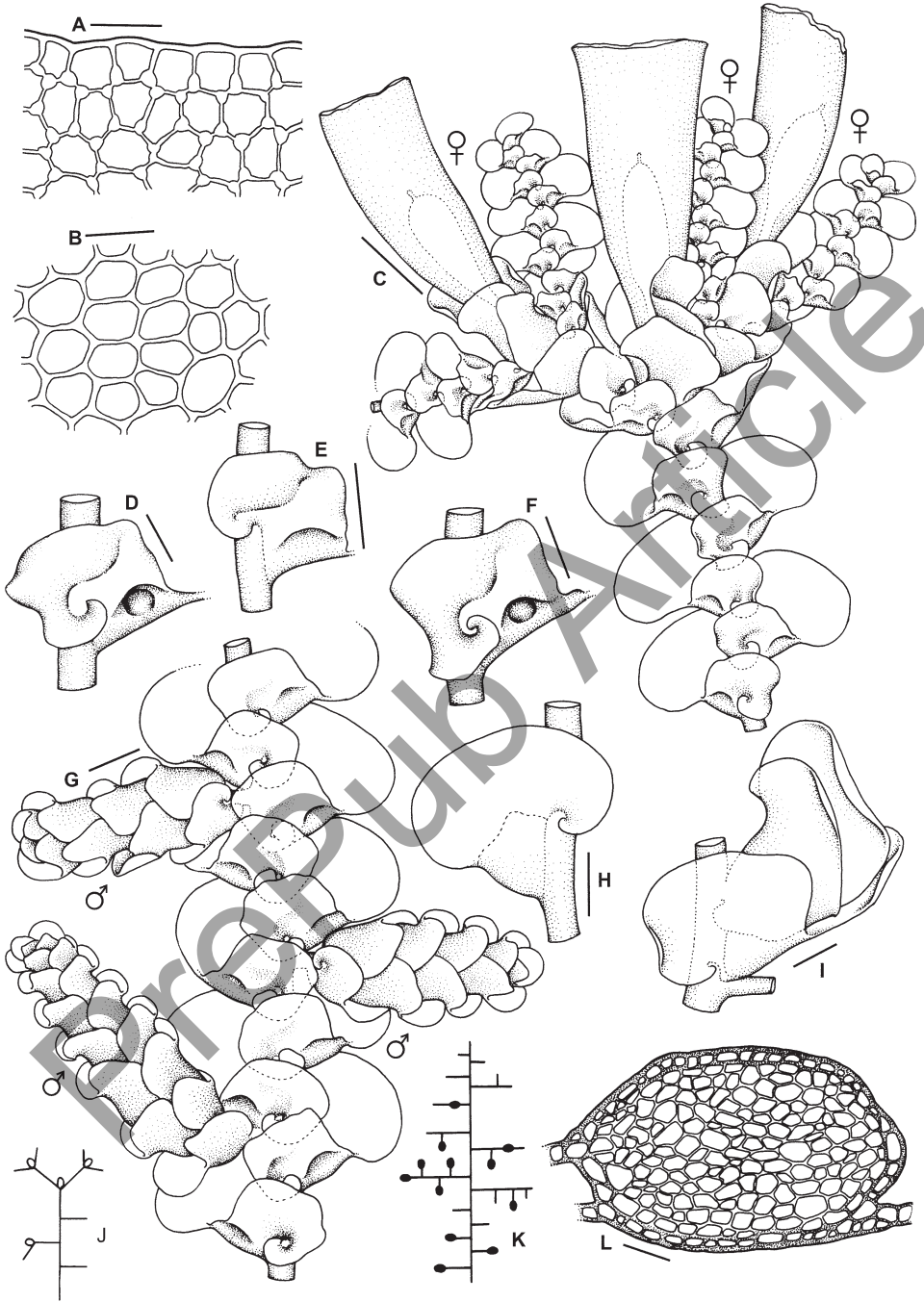
= *Radula subtropica* Steph., Sp. Hepat. 4: 162. 1910, fide Castle (1965).

Diocious. PLANTS 1.8–2.8 mm wide, yellowish-green to yellowish-brown in herbarium, regularly pinnate, rarely bipinnate. STEMS in cross section with ca. 48 thick-walled epidermal cells surrounding ca. 150 thin-walled medullary cells, medullary cells larger than epidermal cells, epidermal cell walls brown, medullary cell walls yellowish, trigones lacking. LEAVES obliquely to widely spreading, distant to contiguous, slightly convex, orbicular to ovate, sometimes falcate-ovate, 0.8–1.4 mm long, 0.6–1.2 mm wide, dorsal base auriculate, overlapping the stem, apex rounded to \pm obtuse, margin plane, entire; marginal cells subquadrate, $10\text{--}15 \times 8\text{--}10 \mu\text{m}$, median and basal cells isodiametric to elongate, $20\text{--}25 \times 15\text{--}20 \mu\text{m}$, cell walls thin, trigones small at leaf base increasing in size towards the margins, cuticle smooth. LOBULES contiguous to imbricate, subquadrate to suborbicular, 0.5–1 mm long, 0.6–1 mm wide, ca. 1/2 the lobe length, inflated at rhizoid area, insertion line circinate, base plane, fully overlapping and extending beyond the stem, strongly auriculate, the auricle circinately coiled, reaching downwards maximally to the keel (not beyond the keel), free margin plane, straight to \pm rounded, apex plane, rounded to obtuse, distal margin straight to sinuate; keel straight, spreading at angles of $55\text{--}75^\circ$ with the stem. RHIZOIDS colorless, scanty. ANDROECIA terminal to intercalary on short branches, with 3–8 pairs of bracts, 0.7–1.2 mm wide; bracts ovate, 0.7–1 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 \pm straight, apex obtuse. GYNOECIA on long branches, with two innovations; bracts 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. PERIANTHS subcylindrical, 3.5–4.2 mm long, 1–1.5 mm wide at apex, mouth entire to irregularly crenulate. VEGETATIVE REPRODUCTION by fragmentation of leaf lobes.

Additional description and illustration: Castle (1965, p. 339–343, Fig. 3, as *Radula ramulina*, p. 352–355, Fig. 8), Jans (1979, p. 427–428 as *R. ramulina*, p. 428–429 as *R. ramulina* var. *microphylla*), Schuster (1980, p. 622–627, Fig. 628), Yamada & Gradstein (1991, p. 68), Reiner-Drehwald (1994, p. 18–20, Fig. 3A–C), Lemos-Michel (2001, p. 168–170, Fig. 48).

Distribution and habitat: Pantropical and northwestern Europe. In Brazil recorded from Espirito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul and Santa Catarina. This species usually grows on bark and rock in Atlantic forest, at 900–1550 m elevation.

Fig. 32. *Radula voluta* – A. Marginal leaf cells. B. Median leaf cells. C. Habit with gynoecia. D–F. Lobules. G. Habit with androecia. H. Leaf dorsal view. I. Bracts. J–K. Cladograph of fertile plants (open ellipse = gynoecia with perianth; solid ellipse = androecia). L. Cross section of a stem. (A–B = 25 μm ; C = 1000 μm ; D–E, I = 250 μm ; F–H = 500 μm ; L = 50 μm ; A–F, H–J, L from RB-486885; G, K from SP-131758).



Taxonomic notes: *Radula voluta* is characterized by (1) plants regularly (bi)pinnate; (2) stem with ca. 200 cells in cross section (epidermal plus medullary cells); (3) leaves distant to contiguous, orbicular to ovate, sometimes falcate-ovate; (4) lobule contiguous to imbricate, subquadrate to suborbicular, free margin \pm straight to rounded, arching towards the large auriculate base, which is circinately coiled across and beyond the stem and reaches downwards maximally to the keel (not beyond the keel), apex rounded to obtuse, keel straight, inflated.

Radula voluta resembles *R. sinuata* and *R. gottscheana* in the auriculate lobule base, but strikingly differs in other aspects (see comments under the latter two species). Castle (1965) described vegetative reproduction in *R. voluta* by means of regeneration from the dorsal leaf lobe, which he considered occasionally caducous. Schuster (1980), however, described and illustrated *R. voluta* with small discoid gemmae on leaf margins (p. 625, Fig. 628 2–4). Reiner-Drehwald (1994), instead, observed that the gemmae reported by Schuster were early stages of regenerant development and that vegetative reproduction in *R. voluta* is usually by means of leaf lobe fragmentation. Our study of the species in Brazil and in the Andes confirms the latter observation.

Selected examined specimens: BRAZIL. ESPÍRITO SANTO: Alfredo Chaves, São Bento da Ucrânia, 900–1000 m, 19 October 2000, Hatschbach et al. 71460 (SP). MINAS GERAIS: Itamonte, Parque Nacional do Itatiaia, 22°22'07"S, 44°44'43"W, 2000 m, 8 July 2015, Peralta et al. 16841 (SP). PARANÁ: Guaraniçu, BR 277, km 321, 14 March 1976, Vital 5777 (SP). RIO GRANDE DO SUL: Esmeralda, Estação Ecológica Aracuri, 30 June 1983, Bueno 3129 (ICN). RIO DE JANEIRO: Nova Friburgo, 05 May 1957, Sehnem 7153 (ICN). SANTA CATARINA: Urubici, cachoeira do Avenal, 28°02'33"S, 49°37'1"W, 1481 m, 14 November 2003, Costa et al. 4289 (RB).

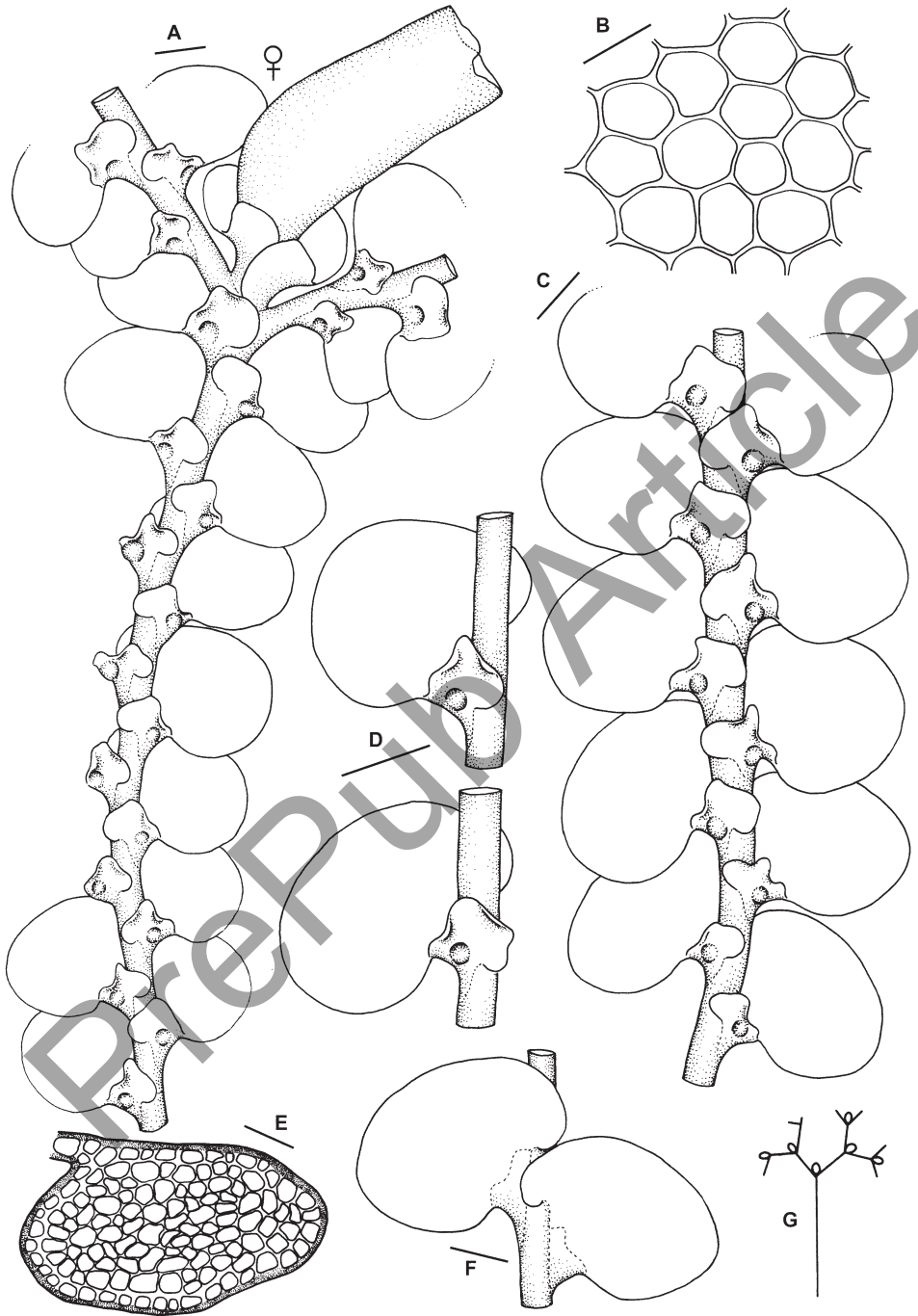
Radula xalapensis Nees & Mont., Ann. Sci. Nat., Bot., sér. 2, 5: 56. 1836. Fig. 33

Type: Peru, “ad Stictam cometiam repens,” d’Orbigny 213 (lectotype: PC-0723919!, designated by Gradstein et al. 2016; isolectotype: PC-0723920!).

= *Radula frondescens* Steph., Sp. Hepat. 4: 181. 1910. Type: Peru, Sandia, 3000 m, Weberbauer 807, 1902 (holotype: G-00043885!).

Dioicous. PLANTS 2.5–3.5(–4) mm wide, yellowish-brown in herbarium, regularly pinnate to dichotomous. STEMS in cross section with ca. 39 thick-walled epidermal cells surrounding ca. 84 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal cell walls brown, medullary cell walls yellowish, trigones lacking. LEAVES widely spreading to squarrose, distant to contiguous, slightly convex, ovate to falcate-ovate, 1.2–1.5 mm long, 1–1.3 mm wide, dorsal base rounded, overlapping the stem, apex rounded to

Fig. 33. *Radula xalapensis* – A. Habit with gynoecia. B. Median leaf cells. C. Habit. D. Leaves. E. Cross section of a stem. F. Habit, dorsal view. G. Cladograph of fertile plants (open ellipse = gynoecia with perianth) (A, C–D, F = 500 μ m; B = 25 μ m; E = 50 μ m; A–G from RB-347475).



obtuse, margin plane, entire; marginal cells subquadrate to isodiametric, 15–20 × 10–12 µm, median and basal cells isodiametric to elongate, 20–30 × 15–20 µm, cell walls thin, trigones small to lacking, cuticle smooth. LOBULES distant to contiguous, (sub)quadrate, 0.5–0.8 mm long, 0.3–0.5 mm wide, ca. 1/3 the lobe length, inflated at rhizoid area, insertion line straight, base plane, rounded, covering 3/4 to usually fully overlapping the stem, free margin plane, straight to incurved, apex plane to incurved, rounded to obtuse, distal margin usually incurved; keel concave, rarely straight, spreading at angles of 25–40° with the stem. RHIZOIDS colorless to brown, scanty. ANDROECIA not seen. GYNOECIA on long branches, with 1–2 innovations; bracts ovate, 1.3–1.4 mm long, 0.7–0.8 mm wide, apex rounded, margin plane to recurved, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS subcylindrical, 2.3–3.5 mm long, 1–1.1 mm wide at apex, mouth entire to irregularly undulate. VEGETATIVE REPRODUCTION by caducous leaf lobes.

Additional description and illustration: Castle (1966, p. 35–38, Fig. 14), Yamada (1982, p. 453–454, Fig. 25 as *R. frondescens*).

Distribution and habitat: Ecuador, Colombia, Peru, Bolivia, Brazil, Chile. The species is a new record for Brazil (Rio de Janeiro), occurring on rocks near a water course in Atlantic forest, at 900 m elevation.

Taxonomic notes: *Radula xalapensis* is characterized by (1) plants robust (2500–4000 µm wide), regularly 1–2-pinnate (see Gradstein et al. 2016); (2) leaves widely spreading to squarrose, distant to contiguous, ovate to falcate-ovate; (3) lobules distant to contiguous, (sub)quadrate, base rounded and sometimes slightly coiled, covering 3/4 to fully overlapping the stem, free margin and distal margin incurved, rarely plane, apex rounded to obtuse, and keel straight to concave.

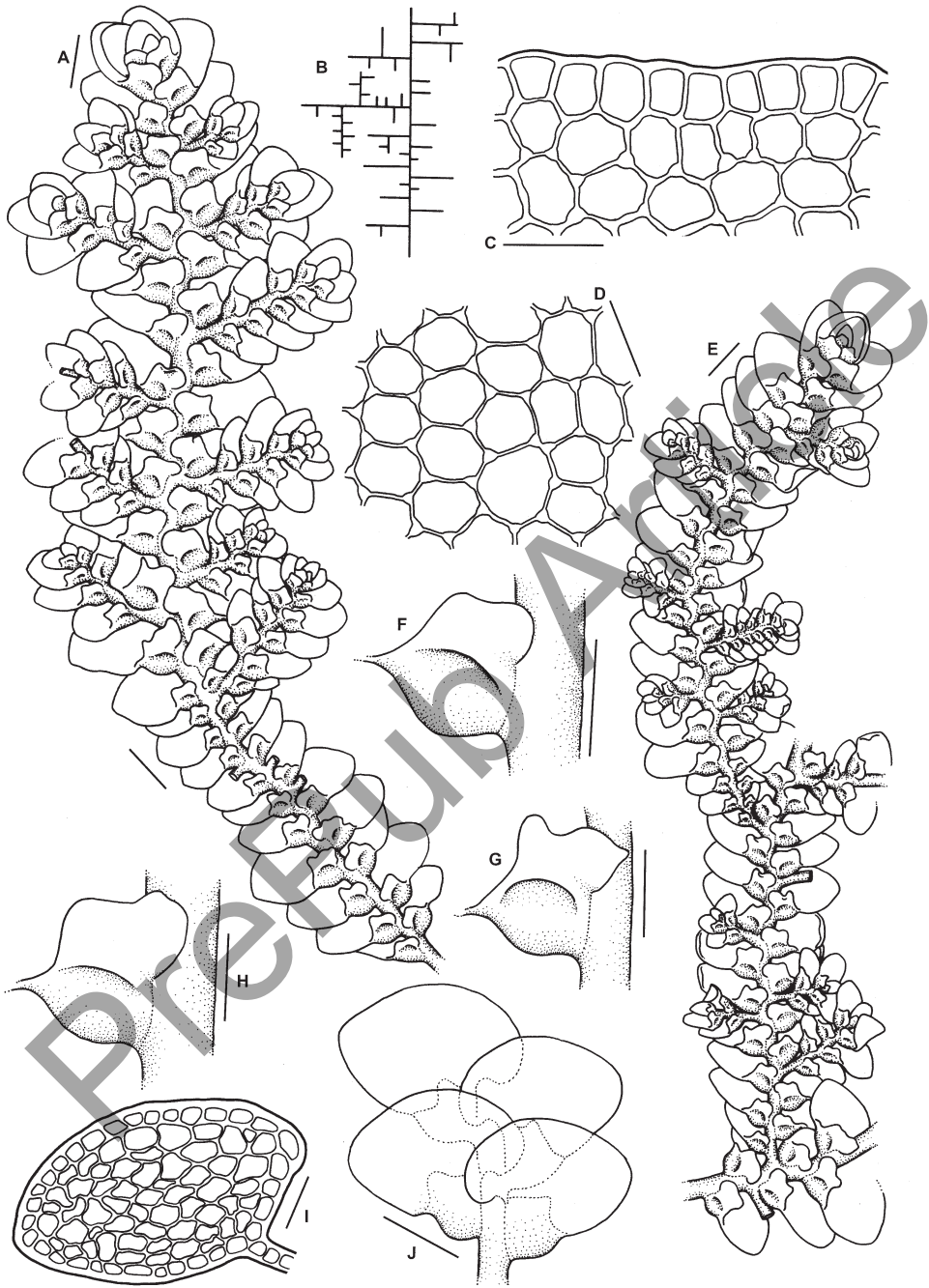
In the large habit and regularly 1–2-pinnate branching *R. xalapensis* resembles *R. voluta*, but the lobules in the latter species are larger, imbricate and the base of the lobule is much more expanded, extending far across and beyond the stem and being more strongly coiled.

Examined specimen: BRAZIL. RIO DE JANEIRO: Parque Nacional do Itatiaia, riacho de uma propriedade particular a direita da estrada para Maromba e Véu de Noiva, na estrada logo após a entrada da administração, sobre pedra a beira do riacho, 900 m, 10 April 2000, Costa & Gradstein 3724 (RB).

Radula yamadae F.R.Oliveira-da-Silva & Ilk.-Borg., Nova Hedwigia 110(3–4): 288, 1. 2020. Fig. 34

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, Peralta & Carmo 14155 (holotype: SP-438627!).

Fig. 34. *Radula yamadae* – A, E. Habit, ventral view. B. Cladograph of plants. C. Marginal leaf cells. D. Median leaf cells. F–H. Lobules. I. Cross section of a stem. J. Habit, dorsal view. (A, E, J = 500 µm; C, D = 25 µm; F–H = 250 µm; I = 50 µm; A–J from the holotype in SP). From Oliveira-da-Silva & Ilkiu-Borges (2020) (www.borntraeger-cramer.de/journals/nova_hedwigia).



Dioicous. PLANTS 1–2(–2.5) mm wide, yellowish-green to pale green in herbarium, densely regularly to irregularly pinnate. STEMS in cross section with ca. 30 thick-walled epidermal cells surrounding ca. 60 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls colorless, trigones lacking. LEAVES widely spreading, imbricate, slightly convex, ovate, 0.7–1.2 mm long, 0.5–0.8 mm wide, dorsal base rounded, auriculate, overlapping the stem, apex obtuse to subacute, margin plane, entire; marginal cells subquadrate to isodiametric, $12\text{--}17 \times 10\text{--}12 \mu\text{m}$, median and basal cells isodiametric to elongate, $12\text{--}22 \times 10\text{--}15 \mu\text{m}$, cell walls thin, trigones small to lacking, cuticle smooth. LOBULES distant to contiguous, rarely imbricate, subquadrate, 0.3–0.6 mm long, 0.25–0.5 mm wide, $1/2\text{--}2/5$ the lobe length, strongly inflated at rhizoid area and along the keel, insertion line arched, base plane, rounded to obtuse, covering $1/3$ to fully overlapping the stem, free margin plane, straight to sinuate, apex rounded to obtuse, distal margin \pm straight; keel conspicuously convex, spreading at angles of 60° with the stem. RHIZOIDS colorless to brown, numerous. GAMETOECIA and VEGETATIVE REPRODUCTION not observed (Oliveira-da-Silva & Ilkiu-Borges 2020).

Distribution and habitat: Brazil. The species is known from Paraná and São Paulo, growing on living leaves and rock in Atlantic forest, at 1000–1200 m elevation

Taxonomic notes: *Radula yamadae* is diagnosed by (1) plants densely branched; (2) stem consisting of ca. 90 cells in cross section (epidermal plus medullary cells); (3) leaf lobes ovate with obtuse to subacute apex; (4) cell with small trigones; (5) lobules distant to contiguous, rarely imbricate, subquadrate, $1/2\text{--}2/5$ the lobe length, base rounded to obtuse, covering $1/3$ to fully overlapping the stem, keel conspicuously convex, strongly inflated at rhizoid area and along the keel (Oliveira & Ilkiu-Borges 2020). The species is close to *R. longiloba* (see comments under the latter species).

Additional examined specimens: BRAZIL. PARANÁ: Morretes, Parque Estadual do Marumbi, trilha vermelha, caminho para a ponta do tigre, Mata Atlântica com afloramentos rochosos, sobre rocha, $25^\circ 26' 55''\text{S}$, $48^\circ 54' 54''\text{W}$, 1200 m, 22 July 2014, Peralta et al. 15877 (SP, MG).

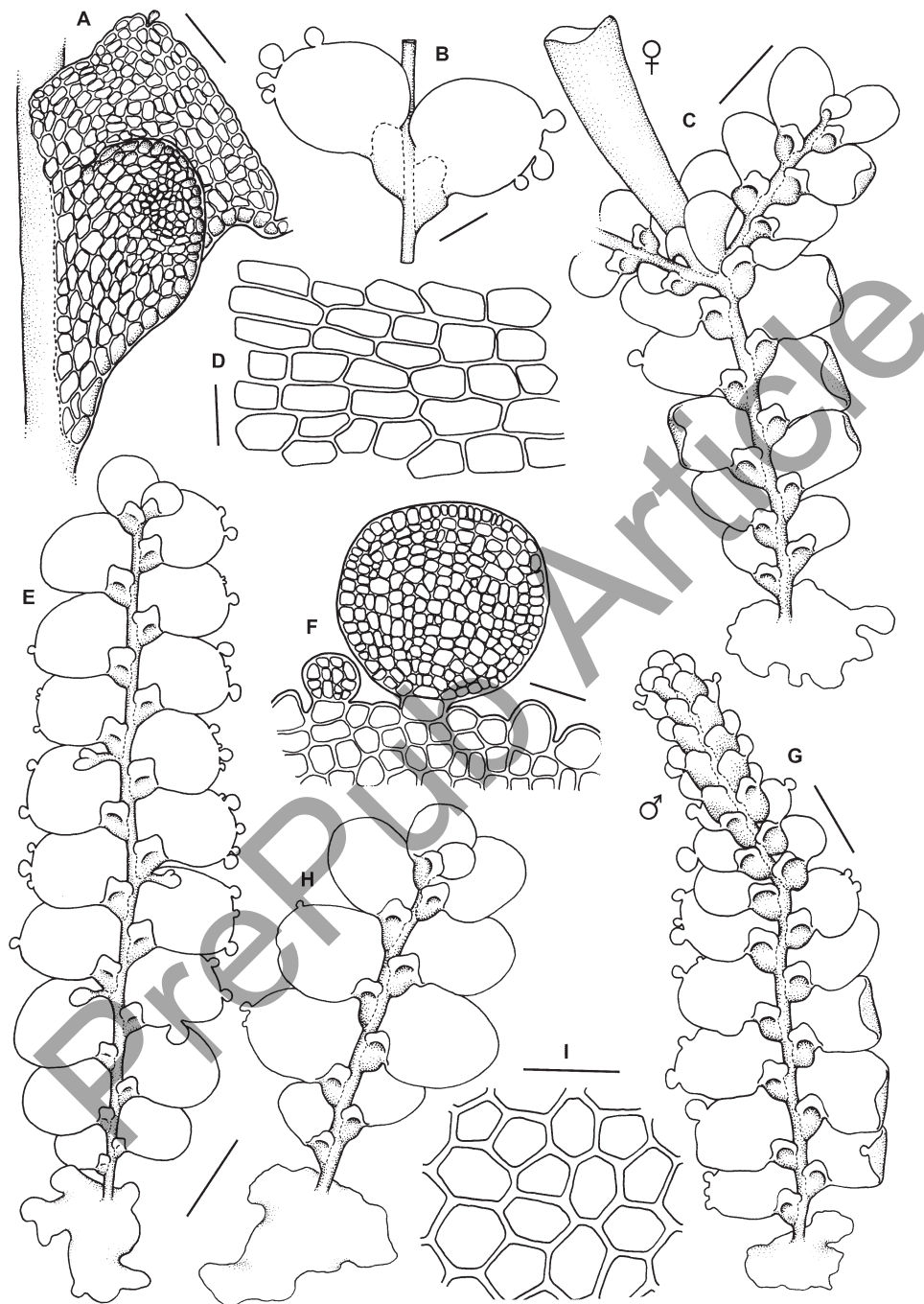
Radula yanoella R.M.Schust., Phytologia 56: 72. 1984.

Fig. 35

Type: Brazil, Amazonas, Rio Negro, near São Gabriel, from Igarapé Arabú on Rio Curicuriari to summit of Serra Curicuriari, $00^\circ 20'\text{S}$, $66^\circ 50'\text{W}$, 450 m, 9–12 July 1979, R. M. Schuster 79-15-627#2 (neotype: NY-00840786!, designated here), *ibid.*, 79-15-627 (isoneotype: NY-00840787!).

Dioicous. PLANTS 0.9–1.1 mm wide, green to pale green in herbarium, consisting of a small, irregularly pinnate, rosette-like thallus with leafy shoots sprouting from the thallus

Fig. 35. *Radula yanoella* – A. Lobule. B. Habit, dorsal view. C. Habit with gynoecia. D. Cells of thallus. E, H. Habit. F. Gemmae. G. Habit with androecia. I. Median leaf cells. (A = 50 μm ; B = 250 μm ; C, E, G, H = 500 μm ; D, F, I = 25 μm ; A, D, H–I from the neotype in NY; B, C, G from HBRA-8439; E–F from SP-182539).



margins, leafy shoots usually unbranched. THALLUS to ca. 1 μm wide, of 1 layer of rectangular cells, 20–40 \times 6–20 μm , thallus margins irregularly rounded, entire, producing leafy branches, cell walls thick, trigones lacking, cuticle smooth. STEMS in cross section with 10–13 thin-walled epidermal cells surrounding 4–5 thin-walled medullary cells, epidermal and medullary cells of the same size, epidermal and medullary cell walls colorless, trigones lacking. LEAVES 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 overlapping the stem, apex rounded, margin plane, entire to crenulate when with gemmae; marginal cells subquadrate to isodiametric, 10–12 \times 7–10 μm , median and basal cells isodiametric, 12–20 μm in diam., cell walls thin, trigones small to lacking, cuticle smooth. 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, inflated at rhizoid area, insertion line \pm arched, base plane, \pm rounded, covering 1/3–1/2 the stem, free margin plane, straight, apex rounded to obtuse, distal margin straight; keel \pm straight to convex, spreading at angles 45–50° with the stem. Rhizoids colorless, numerous on a pronounced mammiliform swelling. ANDROECIA terminal on long branches, with 3–6 pairs of bracts, 0.4–0.5 mm wide; bracts ovate, 0.34–0.38 mm long, 0.14–0.2 mm wide, apex rounded, margin plane, entire, lobule ovate, ca. 5/6 of lobe length, base \pm rounded to straight, free margin straight, apex rounded. GYNOECIA on long branches, with two innovations; bracts oblong-ovate, ca. 0.7 mm long, 0.4 mm wide, apex rounded to obtuse, margin plane, entire, lobule oblong, ca. 1/2 of lobe length, apex rounded to obtuse. PERIANTHS subcylindrical, ca. 1.8 mm long, ca. 0.48 mm wide at apex, mouth entire, undulate. VEGETATIVE REPRODUCTION by small discoid gemmae, ca. 100 μm in diam., produced on leaf margins.

Additional description and illustration: Schuster (1991, p. 59–61, Fig. 2), Gradstein & Ilkiu-Borges (2009, p. 41–43, Fig. 23D–H).

Distribution and habitat: Costa Rica, Ecuador, French Guiana, Brazil. In Brazil *Radula yanoella* has for a long time been known from the Amazon basin (Amazonas, Pará); here the species is newly reported from the Atlantic Forest region (Rio de Janeiro) where it seems to be very rare. The species grows on living leaves at 400–600 m elevation.

Taxonomic notes: *Radula yanoella* is a neotenic species characterized by (1) plants small, epiphyllous, consisting of a rosette-like thallus (=persistent protonema) with short leafy shoots sprouting from the thallus margins; (2) leaf lobes with small discoid gemmae on the margins. *Radula yanoella* somewhat resembles *R. flaccida* and *R. stenocalyx* but the latter species lack a persistent thallus (see also comments under these species).

Radula yanoella was described by Schuster (1984) based on a specimen collected in Serra Curicuriari, Amazonas, Brazil, and numbered Schuster 80-1691 in the protologue. Schuster (1991) indicated that the plants were growing on fern fronds and that the type was deposited in NY with a duplicate to his personal herbarium (currently in F). However, this collection was not found in F or NY. As Schuster's collections are usually numbered by year of collecting and as the expedition to Serra Curicuriari took place in 1979 (Costa et al. 2017), the collection number is presumably erroneous. Instead, the specimen in NY of *R. yanoella* labelled "isotype" (NY-1021204!) bears the number Schuster 79-15-691

(with a note indicating that this is the correct number of the type). However, this specimen contains only *R. flaccida*, not *R. yanoella*, and the substrate is not fern frond. According to Dr. Matt von Konrat (pers. com.), the duplicate of this specimen in the Schuster herbarium contains only various species of Lejeuneaceae, no *Radula*. Nonetheless, studying further material in NY from the Curicuriari expedition, two duplicate specimens were found containing *Radula yanoella* growing on a fern frond, Schuster 79-15-627 (NY-00840787!) and 79-15-627#2 (NY-00840786!). Both contain an annotation in Dr. Schuster's handwriting, indicating that they are the type of *Radula yanoella*. As the specimen with the original collection number cannot be found, the specimen 79-15-627#2 is designated here as neotype (ICN Art. 9.8) and 79-15-627 as isoneotype.

Selected examined specimens: BRAZIL. AMAZONAS: São Gabriel, Serra Curicuriari, from Igarapé Arabú on Rio Curicuriari to summit, 00°20'S, 66°50'W, 450 m, 9 July 1979, Schuster 79-15-725 (INPA). PARÁ: Oriximiná, ESEC do Grão Pará, Serra do Acari, 407–600 m, 28 August 2008, Pietrobom & Maciel 7838 (HBRA). RIO DE JANEIRO: Resende, Parque Nacional do Itatiaia, junto do Véu de Noiva, 20 June 1983, Yano & Santos 7481 (SP).

Excluded records

Radula elliottii Castle: This species was recorded from Brazil by Schäfer-Verwimp & Vital (1989) based on a specimen from Serra do Mar, São Paulo State (Schäfer-Verwimp 7634, SP-386118!). Our study of the specimen revealed that it belongs to *R. angulata*. Further specimens in Brazilian herbaria identified as *R. elliottii* proved to be *R. javanica* or *R. pocsii*.

Radula varilobula Castle: The species was recorded by Schäfer-Verwimp & Vital (1989) from Poços de Caldas, Minas Gerais (Schäfer-Verwimp & Verwimp 7030, SP-386069!). The record – the only report of the species from Brazil – was confirmed by Yano (1995) and Yamada (2003). Our study of the material revealed that it belongs to *R. schaefer-verwimpii*.

Radula wrightii Castle: All collections from Brazil identified as *R. wrightii* proved to belong to *R. pallens* or *R. javanica*. *Radula wrightii* is apparently restricted to Cuba (Castle 1959a).

Doubtful records

Radula marginata Gottsche, Lindenb. & Nees: This species, endemic to New Zealand, was first reported in Brazil from a collection Teresópolis, Rio de Janeiro State, by Oliveira e Silva & Feitosa (1997); the collection was not examined and it is probably a misidentification (see Reiner-Drehwald 1994, Yamada 2003). The description and illus-

tration of Oliveira e Silva & Feitosa (1997) lead to *Radula ligula*, resembling *R. marginata* by ligulate lobules and differentiated marginal leaf cells.

Radula microloba Gottsche: This Chilean species was first reported for Brazil from Rio Grande do Sul by Lindman (1906); the collection was not found. All further collections from Brazil identified as *R. microloba* proved to belong to *R. pallens* or *R. javanica*.

Radula saccatiloba Steph.: First recorded for Brazil by Dusén (1903) from Rio de Janeiro; the specimen was not located and further collections from Brazil identified as *R. saccatiloba* belong to *R. javanica*, *R. decora* or *R. subinflata*. The species is known from Central America, West Indies and northern Andes.

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Appendix

List of additional examined collections: *Radula angulata*: Sehnem 13310 (ICN); Vianna 7718 (ICN); Schäfer-Verwimp & Verwimp 8447 (MG); Costa & Caruso Gomes 995 (RB); Costa et al. 4954 (RB); Santos et al. 635 (RB); Vervloet & Costa 955 (RB); Amélio 89 (SP); Azevedo et al. 2 (SP); Peralta et al. 3420, 20403, 3420 (SP); Rissini et al. 129, 146, 240, 250 (SP); Schäfer-Verwimp & Verwimp 9136 (SP); Yano & Lima 2636 (SP); Yano & Pôrto 33109 (SP); Yano & Visnadi 9875, 9949 (SP); Yano 5119 (SP); Yano et al. 25559, 29657 (SP); Campelo 106, 115 (UFP); Pôrto 1497, 1831c, 1838, 1860, 1872, 1978, 1979, 1987, 1988, 1994, 1998, 2003, 2025, 2028, 2065, 2082, 2106, 2145, 2178, 2179, 2368, 2414, 2417, 2473, 2487, 2499, 2513, 2524, 2542, 2544, 2582b, 2608, 2614, 2622, 2634, 2643a, 2649, 2660, 2680 (UFP); Pôrto s.n. (UFP27256, UFP60011, UFP21396, UFP21739, UFP27269, UFP20387, UFP21494, UFP21501, UFP27258, UFP27259, UFP30030, UFP23105, UFP27558, UFP21529, UFP21488, UFP23048, UFP20619, UFP23108, UFP60009, UFP21489, UFP23106, UFP22555, UFP22540, UFP21461). *Radula bahiensis*: Vital s.n. (SP). *Radula cubensis*: Lemos 284 (ICN); Santos et al. 821 (RB); Peralta et al. 10750 (SP); Vianna 460 (SP); Yano et al. 23034 (SP); Pôrto 2598a, 2582b, 2634, 2642, 2649, 2574, 2566, 1860, 2463, 2522, 2141, 2178, 2106, 2063 (UFP); Pôrto s.n. (UFP21539, UFP27256, UFP25018, UFP21487, UFP60009); Sá s.n. (UFP10492, UFP10539, UFP10547, UFP10594, UFP10590, UFP10630, UFP10597). *Radula decora*: Pôrto 2046h (UFP). *Radula fendleri* var. *fendleri*: Amélio 406 (SP); Peralta & Barros 7069 (SP); Peralta & Gugliotta 13602, 13555 (SP); Peralta et al. 9225 (SP); Sousa s.n. (SP); Vital 7708, 15871 (SP); Yano & Kanashiro 30191 (SP); Yano et al. 21924 (SP). *Radula flaccida*: Ferreira & Brito 4 (HBRA); Arévalo 591, 600, 609, 617, 626, 634, 664, 667, 679, 703, 718 (INPA); Buck 2864, 2879 (INPA); Flores 463, 468 (INPA); Griffin III et al. s.n. (INPA); Lisbôa & Lisbôa 929 (INPA); Prance et al. 19991 (INPA); Schuster 79-15-640, 79-18-946, 79-14-425, 79-10-296, 79-14-441, 79-21-1098, 79-18-910, 79-10-221, 79-13-402, 79-3-46, 79-21-1113, 79-18-894, 79-20-1060, 79-18-913, 79-21-1141 (INPA); Yano 1591, 1628, 1737, 2013, 2020 (INPA); Zartman 1814, 1879, 1883, 1884, 1885, 1912 (INPA); Alvarenga 281, 287, 515, 541, 213, 495 (MG); Gentil 371, 410 (MG); Lisboa et al. 1649 (MG); Moraes et al. 2639, 2649, 2670, 2655, 2674, 2675, 3005, 3090 (MG); Buck 2864, 2879 (NY); Nelson 695 (NY); Schuster 79-3-69, 79-3-92, 79-21-1150, 79-21-1141, 79-21-1113, 79-18-913, 79-18-946, 79-18-910, 79-13-402, 79-15-707A, 79-15-723 (NY); Costa et al. 2697 (RB); Dias & Dias-Melo 579e (SP); Griffin III et al. 143, 208 (SP); Pedro & Macêdo 109 (SP); Pietroboim et al. 8457, 8467 (SP); Schäfer-Verwimp & Verwimp 7217, 7294 (SP); Schuster 79-3-46 (SP); Souza & Pietroboim 1252 (SP); Vital 14416 (SP); Yano & Cruz 14547 (SP); Yano & Lima 2662 (SP); Yano 1482, 2013, 2020 (SP); Germano s.n. (UFP61051, UFP61050). *Radula gottscheana*: Peralta et al. 16364 (SP); Sousa s.n. (SP); Vianna 3937, 3956 (ICN); Vital s.n. (SP); Yano & Santos 7488 (SP); Yano & Zaidan 24262 (SP). *Radula javanica*: Santos 5289 (ALCB); Pietroboim & Maciel 8229, 8230, 8171 (HBRA); Pietroboim et al. 8369 (HBRA); Silva et al. 142 (HBRA); Souza 618 (HBRA); Buck 3121, 2362, 2737 (INPA); Maia et al. 314 (INPA); Schuster 79-14-462, 79-9-248, 79-3-90, 79-15-657, 79-15-720a, 79-15-728 (INPA); Farias s.n. (ICN); Lindeman 6627 (ICN); Sehnem 5613 (ICN); Vianna

765, 3258 (ICN); Alvarenga 346 (MG); Buck 3121, 2362 (MG); Gentil 384, 459, 479, 490 (MG); Ilkiu-Borges et al. 2882 (MG); Lisboa & Rosa 6459 (MG); Lisboa 340, 7056, 7213 (MG); Lisboa et al. 717 (MG); Sales & Rosário 510, 1259 (MG); Salomão et al. 213 (MG); Santos et al. 1792 (MG); Silva & Rosário 6249 (MG); Strudwick & Sobel 3425 (MG); Alencar 314 (NY); Buck 2362, 2737, 2865A, 3060A, 3121, 3127 (NY); Reese 13455 (NY); Schuster 79-20-1048, 79-3-101, 79-9-201, 79-9-203a, 79-9-216, 79-9-220, 79-9-224, 79-9-248, 79-9-249, 79-14-462, 79-15-531, 79-15-543, 79-15-566, 79-15-578, 79-15-728 (NY); Strudwick & Sobel 3425, 3952 (NY); Vital & Buck 20330B (NY); Costa & Aguiar 8 (RB); Costa et al. 2938, 2760 (RB); Rezende & Costa 157 (RB); Ferreira & Brito 4 (SP); Lima et al. 200, 201 (SP); Lisboa 620, 661 (SP); Pietrobon & Maciel 8171 (SP); Pietrobon et al. 8362 (SP); Pietrobon-Silva 4534 (SP); Schuster 79-3-90, 79-9-201, 79-15-567, 79-15-706, 79-15-576, 79-3-101 (SP); Silva 1552 (SP); Visnadi & Vital 1487 (SP); Vital 3208, 15714, 15179 (SP); Yano & Marcelli 17614 (SP); Yano & Prado 24660 (SP); Yano & Windisch 17353 (SP); Yano & Zartman 32710 (SP); Yano 1837, 1663 (SP); Yano et al. 23491, 26449, 26394, 26585 (SP); Campelo 125 (UFP); Pôrto 2574, 2647, 2535, 2639, 2624i (UFP); Sá s.n. (UFP13909, UFP13911). *Radula ligula*: Bueno 1501 (ICN); Costa et al. 1181, 5087 (RB); Oliveira s.n. (SP); Peralta & Gissi 18395, 18399 (SP); Peralta et al. 3272 (SP); Yano et al. 23653 (SP); Sá s.n. (UFP10524, UFP10483, UFP13896). *Radula mammosa*: Rezende & Costa 269 (RB); Pietrobon & Maciel 8060 (SP); Yano et al. 15457 (SP). *Radula mexicana*: Oliveira s.n. (ICN); Pôrto s.n. (UFP); Pôrto 2584d (UFP). *Radula nudicaulis*: Bueno 1095, 326 (ICN); Oliveira s.n. (ICN); Sehnem 5250 (ICN); Yano & Visnadi 9875 (INPA); Schäfer-Verwimp & Verwimp 8944 (MG); Costa et al. 647, 4114 (RB); Santos et al. 103 (RB); Dias & Sylvestre 688 (SP); Hoehne 254 (SP); Lemos-Michel 3024 (SP); Loefgren 450 (SP); Peralta & Barros 7882 (SP); Peralta & Huaman 2670 (SP); Peralta et al. 4500, 7527, 17357 (SP); Pietrobon-Silva et al. s.n. (SP); Vital 15216, 15235, 2819 (SP); Yano & Gradstein 24708 (SP); Yano & Kirizawa 30898, 31939 (SP); Yano & Prado 26186 (SP); Yano & Yano 22708 (SP); Yano & Zaidan 24279 (SP); Yano et al. 19373, 12502, 21506, 32055 (SP). *Radula pallens*: Abreu 302 (HBRA); Souza & Teixeira 406 (HBRA); Michel s.n. (ICN); Vianna 44 (ICN); Glaziov 18027 (NY); Vital & Buck 20271 (NY); Costa et al. 798 (RB); Amélio 100 (SP); Bordin et al. s.n. (SP); Bueno 1720, 2504 (SP); Colletes et al. 181 (SP); Dias & Dias-Melo 483b (SP); Germano s.n. (SP); Kuniyoshi s.n. (SP); Melo et al. 2419 (SP); Moura s.n. (SP); Peralta & Gugliotta 13405 (SP); Peralta et al. 5053, 20868, 5696 (SP); Pietrobon-Silva 5249a, 5249, 5439 (SP); Pietrobon-Silva et al. 5028, 5237 (SP); Puigari 450 (SP); Rossini et al. 195, 146 (SP); Schäfer-Verwimp 33822 (SP); Souza & Teixeira 406 (SP); Vianna 2474 (SP); Visnadi & Vital 1424, 1352 (SP); Vital & Buck 12441 (SP); Vital 447, 665, 919, 13601 (SP); Wasum et al. s.n. (SP); Yano & Cordeiro 25675 (SP); Yano & Costa 22496 (SP); Yano & Lima 2583, 2582 (SP); Yano & Marcelli 20997, 18872, 19282 (SP); Yano & Mello 11556, 23077 (SP); Yano & Pôrto 33103 (SP); Yano & Shirata 27844 (SP); Yano 2890, 30545, 3087 (SP); Yano et al. 27224, 30383, 7992, 14803, 15449, 15666, 15461, 23595, 23746 (SP); Alvarenga s.n. (UFP50946, UFP50946, UFP50937); Germano s.n. (UFP); Pôrto s.n. (UFP48848, UFP48855, UFP48796, UFP45851, UFP49220); Pôrto EPX072 (UFP); Valente 235 (UFP); Sá s.n. (UFP10590, UFP10527, UFP10536, UFP13906, UFP13909, UFP13921, UFP13893, UFP13905,

UFP10483, UFP10460, UFP10498); Silva 223, 226, 252, 243 (UFP); Silva & Silva s.n. (UFP). *Radula pocsii*: Oliveira s.n. (ICN); Costa et al. 257, 4158, 4954 (RB); Peralta et al. 15817 (SP); Schäfer-Verwimp & Verwimp 8395 (SP); Yano & Melo 12648 (SP). *Radula pseudostachya*: Griffin III et al. 544 (INPA); Prance et al. 11371 (INPA); Nelson 5 (NY); Prance 11371, 11384 (NY); Griffin III et al. 544 (SP); Yano & Lima 14679 (SP). *Radula quadrata*: Bueno 1310 (ICN); Sehnem 2174, 3636 (ICN); Vianna 1469 (ICN); Schäfer-Verwimp & Verwimp 8521 (MG); Costa et al. 5178 (RB); Peralta et al. 10416a (SP); Ristow 1187 (SP); Vital 8846 (SP); Yano & Lima 2662, 2929 (SP); Yano & Peralta 26684 (SP); Yano & Pirani 6561, 5843 (SP); Yano & Santos 6065 (SP); Yano et al. 11513, 18584 (SP). ***Radula recubans***: Vianna 57 (ICN); Buck 2362, 2737 (INPA); Lisboa 368 (INPA); Maia et al. 314 (INPA); Yano 2038, 1837 (INPA); Santos et al. 597, 821 (RB); Yano & Marcelli 11160 (SP); Yano & Pirani 7349 (SP); Yano & Visnadi 9875 (SP); Yano et al. 20381 (SP). ***Radula schaefer-verwimpii***: Vital & Buck 19768 (NY); Peralta et al. 17704, 21757, 6406, 20403, 4988 (SP); Peralta & Gugliotta 13405 (SP); Schäfer-Verwimp & Verwimp 9255 (SP). ***Radula sinuata***: Baptista s.n. (ICN); Bueno 502 (ICN); Oliveira s.n. (ICN); Sehnem 7681 (ICN); Vianna 400, 772, 765, 1137 (ICN); Yano & Visnadi 9875 (INPA); Schäfer-Verwimp 8342 (MG); Vital & Buck 12185, 19482, 19496 (NY); Berger 162 (RB); Costa & Gradstein 3847 (RB); Vaughan Bandeira s.n. (RB); Bordin & Pasini 488, 568 (SP); Bueno 4885 (SP); Klein 4836 (SP); Lemos-Michel 3196 (SP); Leoni 1919 (SP); Loefgren 450 (SP); Peralta & Barros 7923 (SP); Peralta et al. 3440, 4547, 4518, 3285, 21070, 19221, 6576 (SP); Reitz & Klein 15587, 15791 (SP); Ristow & Picote 3552 (SP); Ristow & Ristow 3569, 1804 (SP); Ristow & Santos 3710 (SP); Ristow et al. 2785, 3127 (SP); Ropelato 9 (SP); Schäfer-Verwimp 6885, 8342, 33856 (SP); Visnadi & Vital 4805 (SP); Vital 9352, 9411, 13601 (SP); Wasum 4487 (SP); Yano & Kirizawa 33241 (SP); Yano & Marcelli 15733, 19466 (SP); Yano & Pirani 6507, 7040, 7028 (SP); Yano 28562 (SP); Yano et al. 5396, 5435, 22268, 22235, 15666, 16651 (SP); Oliveira 209 (UFP). ***Radula stenocalyx***: Pietrobom & Maciel 8062 (HBRA); Peralta & Gissi 18304 (SP); Schäfer-Verwimp & Verwimp 8435 (SP); Visnadi & Vital 5199 (SP); Vital & Buck 19974 (SP). ***Radula subinflata***: Schäfer-Verwimp & Verwimp 8389 (MG); Dusén 76 (NY); Vital & Buck 19489, 19562 (NY); Costa 4698, 4780 (RB); Costa et al. (RB); Santos et al. 684, 476 (RB); Kuniyoshi s.n. (SP); Peralta & Marcelli 11777 (SP); Peralta 5576 (SP); Peralta et al. 6627 (SP); Petean 953 (SP); Ristow & Santos 4316 (SP); Ristow et al. 2380 (SP); Vital & Buck 19919 (SP); Vital 15850 (SP); Yano & Marcelli 13320 (SP); Yano & Peralta 28586 (SP); Yano & Pirani 7116 (SP); Yano 33322 (SP). ***Radula tectiloba***: Bueno 281 (ICN); Lemos 351 (ICN). Lorscheitter & Baptista s.n. (ICN); Lorscheitter s.n. (ICN); Canêz & Spielmann s.n. (SP); Lemos-Michel 2266 (SP); Peralta 21283 (SP); Peralta et al. 5460, 12735, 21187 (SP); Ristow & Villagra 3491 (SP); Schäfer-Verwimp et al. 33767 (SP); Schäfer-Verwimp & Verwimp 9344 (SP); Vianna 460, 3823, 7718 (SP); Visnadi 3302 (SP); Vital 5777, 14652, 5717, 10568, 10661, 15113 (SP); Wasum 4487 (SP); Yano & Lopes 34191 (SP); Yano & Marcelli 17073, 19608 (SP); Yano & Michel 17287 (SP); Yano & Morretes 33352, 33047 (SP); Yano & Peralta 29699, 26694, 403226 (SP); Yano & Pirani 7054, 7147, 7131, 5889, 7125, 7120, 6674, 6702, 6529, 6892, 6953, 5781, 7028, 6927, 7102, 6742, 7251, 6849, 650, 6495, 6489 (SP); Yano & Santos 6198 (SP); Yano & Shirata 11346, 28062, 15045 (SP); Yano & Silva 11310, 13516

(SP); Yano & Yano-Kida 33755 (SP); Yano 3964, 3981 (SP); Yano et al. 5474, 22313, 12514a, 5432, 5461, 22235, 5580, 15415, 18027, 18108, 29795, 5548, 5502, 5435, 21793, 18457, 22146, 22189 (SP). ***Radula tenera***: Vital & Buck 12239 (NY); Canestraro & Lozano 1161 (SP); Peralta et al. 17928 (SP); Schäfer-Verwimp et al. 33892 (SP). ***Radula voluta***: Sehnem 6049 (ICN); Costa et al. 4288 (RB); Lemos-Michel 3580 (SP); Peralta et al. 19357 (SP); Schäfer-Verwimp & Verwimp 7049 (SP); Vital 9438 (SP); Yano & Pirani 6380 (SP); Yano et al. 20379 (SP). ***Radula yanoella***: Pietrobon & Maciel 7838 (SP); Schuster 79-10-296 (SP).

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