



<https://doi.org/10.11646/bde.39.1.5>

A new species of *Cyclolejeunea* (Marchantiophyta: Lejeuneaceae) from the Chocó, Colombia

S. ROBBERT GRADSTEIN¹ & M. ELENA REINER-DREHWALD²

¹ Muséum National d'Histoire Naturelle, Département Systématique et Evolution, C.P. 39, 57 rue Cuvier, 75231 Paris cedex 05, France; email: gradstein@mnhn.fr

² Department of Systematics, Biodiversity and Evolution of Plants (with Herbarium), Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-Universität Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany; email: mreiner@uni-goettingen.de

Abstract

Cyclolejeunea is a small neotropical genus of six species and a common epiphyllous hepatic in lowland and montane rainforests. We describe the new species *Cyclolejeunea glimeana* M.E.Reiner & Gradst. from wet lowland rainforest along the Pacific coast of Colombia (Chocó). The new species is characterized by the absence of innovations, entire leaf margins, leaf lobules without any indication of a tooth, and ligulate, thalloid gemmae without rhizoids. The combination of morphological characters seen in *C. glimeana* sets this species well apart from the remaining members of the genus and warrants its placement in a separate subgenus, *C. subg. Chocolejeunea* M.E.Reiner & Gradst. *subg. nov.* Ecologically, the new species stands out by its preference for palm trunks. The new species is a further addition to the unusually rich flora of the Chocó region.

Key words: Chocó region, *Cyclolejeunea glimeana*, liverworts, morphology, lowland rainforest, Neotropics, *Prionolejeunea*, taxonomy, thalloid gemmae

Introduction

The Pacific coastal area of northern Southern America, known as the Chocó biogeographical region, is one of the world's major hotspots of biodiversity (Myers *et al.* 2000). Stretching from northern Peru through Ecuador, Colombia and Panama to southern Costa Rica, this area is known for its high species richness and strikingly high rates of endemism among flowering plants, birds, frogs, butterflies, etc. More than 5500 plant species have been recorded from the Chocó of Colombia and 16% of them are endemic (Bernal *et al.* 2016). There are at least two reasons for the exceptional biological diversity of the Chocó. First, this region has been separated from the rest of South America during several millions of years due to the uplift of the Andes in the Tertiary, allowing for many species to evolve in isolation. Furthermore, the area has some of the wettest rain forests of the world, with annual rainfall up to 12000 mm, in some places even up to 15000 mm (Frahm 2012).

The Chocó region is also a rich area for bryophytes, especially liverworts (Vasco *et al.* 2002; Gradstein & Uribe 2016). Almost two hundred species of liverworts have been reported from the Chocó of Colombia, including 13 endemic taxa. Some of the endemic bryophytes of the Chocó region, such as *Fulfordianthus pterobryoides* (Spruce 1884: 109) Gradstein (1992: 44), *Luteolejeunea herzogii* (Buchloh 1961: 515) Piippo (1986: 56) and *Symbiezidium dentatum* Herzog (1955: 57), all members of Lejeuneaceae Cavers (1910: 291), are surprisingly common and widespread in the region in spite of their absence elsewhere. A conservation icon in the Chocó bryophyte flora is *Spruceanthus theobromae* (Spruce 1884: 99) Gradstein (1985: 26), the single New World representative of the Asiatic-Australasian genus *Spruceanthus* (Lejeuneaceae) and only known from extensively managed cacao plantations, in a small area in western Ecuador (province Los Ríos). This species has been listed as critically endangered on the “World Red List of Bryophytes” (www.dbs.nus.edu.sg/lab/crypto-lab/WorldBryo.htm) and has featured as “Species of the Day” during the International Year of Biodiversity 2010 (www.iucnredlist.org/species-of-the-day).

Here we describe a new species from the Chóco region in the genus *Cyclolejeunea* Evans (1904: 193). *Cyclolejeunea* is a small neotropical genus of Lejeuneaceae of six well-defined species and four doubtful ones (Söderström *et al.* 2016), and is one of the most common bryophyte genera in the Neotropics on living leaves (Bernecker-Lücking 1998;

Gradstein *et al.* 2001). Some species seem to be obligate epiphylls but at least three of them, *C. convexistipa* (Lehmann & Lindenberg, in Lehmann 1834: 43) Evans (1904: 198), *C. luteola* (Spruce 1884: 205) Grolle (1984: 761) and *C. peruviana* (Lehmann & Lindenberg, in Lehmann 1833: 18) Evans (1904: 196), may also grow on bark. Characteristic morphological features of *Cyclolejeunea* are the presence of ocelli at leaf base (absent only in *C. accedens*), a flattened, 2-keeled perianth with keels being expanded above into low auricles, gynoeceal innovations with pycnolejeuneoid leaf sequence (first leafy appendage is an underleaf), and vegetative reproduction by means of leafborn, multicellular gemmae with marginal rhizoids. Moreover, the leaf margins in *Cyclolejeunea* are usually toothed and the male bracteoles restricted to the base of the male spike (present throughout the spike in *C. convexistipa*).

Cyclolejeunea is sister to *Prionolejeunea* (Spruce 1884: 152) Schiffner (1893: 127), an Afro-American genus of 23 species (Ilkiu-Borges 2016), and the two genera have been classified in a separate subtribe, Lejeuneaceae subtribe Cyclolejeuneinae Gradstein (2013: 12). They share a flattened, obcordate-auriculate perianth, pycnolejeuneoid innovations and serrulate leaf margins, but *Prionolejeunea* lacks ocelli and does not produce gemmae with marginal rhizoids.

An unusual species of *Cyclolejeunea*, which appears to be undescribed, was detected by the second author among the collections made by the first author in the framework of an exploration of the bryophyte flora of the everwet rainforests along Pacific coast of Colombia (Frahm 1994). The new species differs from all known species of the genus by the absence of gynoeceal innovations, untoothed leaf margins, leaf lobules without any indication of a tooth, and ligulate, thalloid gemmae without rhizoids, born on decaying leaves. It is our pleasure to dedicate this remarkable new species to Dr. Janice Glime in honor of her important contributions to bryology.

Taxonomic treatment

Cyclolejeunea glimeana M.E.Reiner & Gradst., *spec. nov.* Fig. 1

DIAGNOSIS: Leaves with 2–3(–4) suprabasal ocelli. Leaf margins entire or slightly crenulate. Lobule without any indication of a tooth.

Underleaves bifid. Androecia on elongate branches with vegetative leaves, underleaves largely restricted to the base of the male shoot. Gynoeceal innovations lacking. Perianth obcordate, 2-keeled, keels expanded above into low auricles. Gemmae ligulate, without rhizoids, produced on decaying leaves of old shoots.

TYPE:—COLOMBIA. Departamento Chocó: municipio Nuquí, around Biological Station “El Amargal”, coastal lowland rainforest, ca. 30 m.s.m., growing in dense mats on palm trunks, 6 August 1992, S.R. Gradstein 8895 (holotype, COL!; isotypes, GOET!, PC!).

PARATYPE: *ibid.*, S.R. Gradstein 8849 (COL!, GOET!).

Plants to 1–1.5 cm long, 0.6–0.9 mm wide on stems, glistening pale yellowish when dry, very transparent, creeping and forming dense flat mats on bark, irregularly branched, branches *Lejeunea*-type with large collars, sometimes caducous, innovations absent. Stems ca. 50–80 μm in diameter, pale brown, made up of 8 rows of epidermis cells surrounding 10 rows of smaller and thinner-walled medullary cells, epidermis cells ca. 25 \times 40 μm , with slightly thickened walls, medullary cells ca. 20 μm in diameter, thin-walled; epidermis cells in optical view quadrate to subrectangular, arranged in straight longitudinal rows; ventral merophyte 2 cells wide on stems and branches. Surfaces of leaves and underleaves smooth. Leaves widely spreading, slightly imbricate, leaf lobe convex, asymmetrically ovate-suborbicular, not falcate, 0.35–0.5 mm long \times 0.25–0.35 mm wide, leaf apex broadly rounded, margins entire to slightly crenulate, without teeth, dorsal leaf base extending across but beyond the stem, dorsal insertion ca. 1.5 mm long. Leaf cells usually isodiametrical-hexagonal, occasionally elongate, 20–25(–30) \times 20–25 μm in midleaf, margin cells slightly smaller, quadrate to subrectangular, 15–20 μm high; cell walls with very small trigones, trigones usually somewhat elongate and extending along the longer wall, intermediate thickenings absent or very small, elliptical; cuticle smooth; oil bodies not observed; ocelli present, 2–3(–4) suprabasal and side by side, brown, rectangular, 38–45 \times 17–25 μm , larger than adjacent lamina cells. Lobules shortly ovate, 1/3 of leaf length, 120–150 \times 70–120 μm , strongly inflated in the lower 2/3, flattened towards the free margin, lobule obliquely truncate along the apical margin (between apex and lobule tip), apical margin not or very shortly continuing into the ventral leaf margin, forming a sharp angle with the keel, the keel strongly arched, crenulate; free margin plane, bordered by six to eight somewhat larger, subquadrate cells from the base of the lobule to the tip, apex bluntly angled, formed by two free margin cells, tooth reduced to blunt cells at the lobule apex, hyaline papilla hanging down from the margin (from a minute sinus) between the two cells at the apex, on the inner side of the lobule (proximal to the cell that might have given rise to a tooth); lobule cells similar to leaf lobe cells. Underleaves distant, slightly concave, obovate-obcuneate, 150–160 μm long \times 140–150 μm wide,

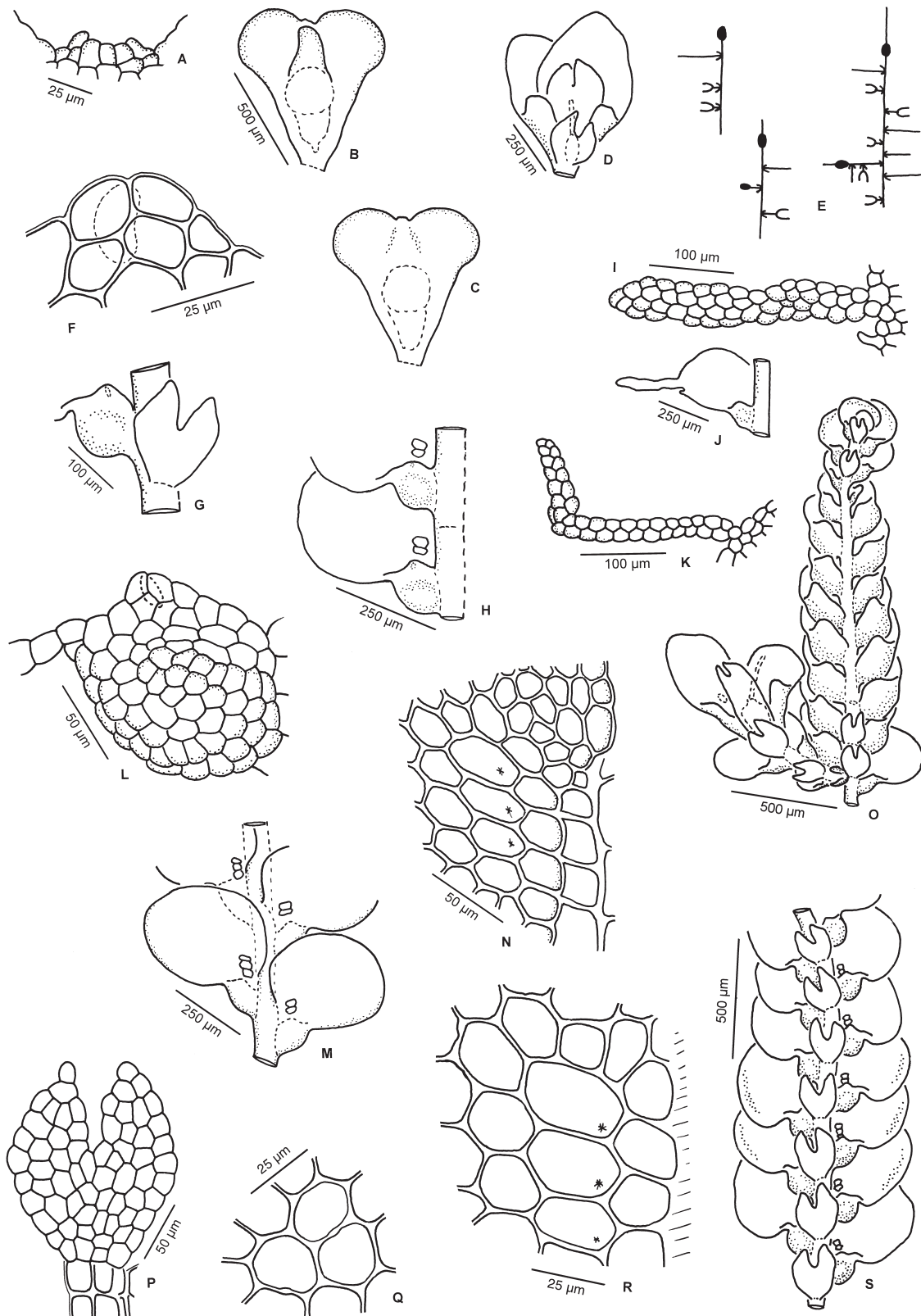


FIGURE 1. *Cyclolejeunea glimeana*. A. Beak. B. Perianth in ventral view. C. Perianth in dorsal view. D. Gynoeceum, ventral view. E. Cladographs showing gametoeical arrangement (solid ellipses indicating male branches, U indicating gynoecea). F. Lobule apex, showing ental hyaline papilla. G. Shoot sector with lobule and underleaf. H. Shoot sector, ocelli indicated. I, K. Gemmae. J. Leaf with gemma. L. Lobule. M. Shoot sector, ocelli indicated, dorsal view. N. Basal leaf-lobe cells, right stem sector (* = ocelli). O. Habit, with intercalary male branch and terminal gynoeceum, ventral view. P. Underleaf. Q. Median leaf-lobe cells. R. Basal leaf-lobe cells. S. Habit, ventral view. All drawn from the holotype.

2–2.5× stem width (ca. 3× branch width), bifid to 1/2, lobes 4–6 cells wide at base, apex subacute, of a row of 1(–2) cells, sinus rather narrowly V-shaped, margins plane, entire or crenulate, sometimes bluntly angled in the middle but without tooth, bases cuneate, insertion line straight; underleaf cells as in the leaves but walls slightly evenly thickened, ocelli lacking; rhizoid disc small, rhizoids few, colorless, underleaf attached to the stem by two U-shaped cells (seen in transverse section).

Autoicous. Androecia terminal or intercalary on short or long leafy branches with vegetative leaves (not on short-specialized branches), bracts in 3–7 pairs, with enlarged, fully swollen lobules ca. 1/2× lobe length, lobules epistatic when distant but becoming hypostatic when imbricate, with two antheridia; male bracteoles mostly restricted to the base of the male shoot, sometimes a small bracteole developed halfway the male shoot. Gynoecia on short branches without innovation (sometimes with a short *Lejeunea*-type pseudo-innovation originating below the bract), with 1–3 series of vegetative leaves and underleaves and one series of much larger female bracts and bracteole, the bracts and bracteole free, not connate; bract lobe obliquely spreading, convex, oblong, ca. 0.6–0.7 × 0.3–0.4 mm, with 10–14 brown ocelli in the lower half, ocelli adjacent or scattered, lobe apex rounded, margins entire or crenulate; bract lobule oblong, ca. 2/3× bract length, slightly extended beyond the keel, apex rounded to retuse, margins entire; keel ± straight, without wing; bracteole strongly concave, oblong, 0.4 × 0.2 mm, 2/3× bract length, apex bifid to 1/3, lobes rounded to obtuse, touching each other, sinus very narrow, margins entire, ocelli lacking. Perianth slightly emergent beyond the obliquely spreading bracts, obcordate and somewhat flattened, ca. 0.7–0.8 mm long, 0.6–0.7 mm wide above, without ocelli, conspicuously narrowed to the base, with 2 lateral keels, dorsal and ventral keels lacking but ventral perianth surface slightly swollen; lateral keels expanded above into a broad and low, smooth auricle with entire or slightly crenulate margin, the auricles slightly extended beyond the perianth apex and widely diverging, leaving a wide, shallow sinus; beak absent or rudimentary. Sporophyte immature.

Vegetative reproduction by caducous branches and by ligulate, thalloid gemmae produced on the surfaces and margins of decaying leaves, in old, brownish-colored, decaying portions of the plants; gemmae soon becoming detached, 4–15× longer than wide, 0.2–0.8 mm long, 25–50 µm wide (2–4 cells), simple or sometimes branched, margins crenate, without rhizoids; new plantlets (gemmae) sprouting from tips or margins of gemmae.

DISTRIBUTION AND HABITAT: *Cyclolejeunea glimeana* is only known from the type locality in everwet lowland rainforest along the Pacific coast of Colombia. The terrain is undulating, rainfall is very high (to 12000 mm annually) and the forest is densely clad in cloud during early morning. Bryophyte diversity (mostly epiphytic) is very high, with almost fifty species of liverworts recorded from a 20 x 20 m plot in the forest understory (the canopy was not inventoried), on earth, rotten wood, living leaves, shrubs and lower portions of tree trunks to 3 m height (Gradstein unpubl.). The forest seems to be representative of tropical lowland cloud forest, described from French Guiana and characterized by high epiphyte diversity (Gradstein *et al.* 2010; Gehrig-Downie *et al.* 2013).

Cyclolejeunea glimeana was exclusively found on the trunks of *Welfia regia* André (1871: 93), a common and characteristic subcanopy palm in the rainforests of the Chocó region (Galeano & Bernal 2010). The surface of the trunk is rather smooth and finely structured in this species, consisting of a dense network of microscopically small fibres. Under the dissecting microscope, it appeared that the old, brownish-colored shoots of *Cyclolejeunea glimeana* were densely intertwined with the palm fibres.

Discussion

Cyclolejeunea glimeana is readily recognized as a member of *Cyclolejeunea* by the leaves with 2–3(–4) suprabasal ocelli, the smooth, thin-walled leaf cells, the 2-keeled, obcordate perianth with the keels expanded above into low auricles, and by the presence of multicellular gemmae. Unique features of *C. glimeana*, separating it from other species of *Cyclolejeunea* are: 1) leaf margins entire to slightly crenulate, without any teeth; 2) lobules with any indication of a tooth; 3) absence of gynoecial innovations; 4) long, ligulate, thalloid gemmae without any rhizoids on margins, produced on decaying leaves of old shoots. The thalloid gemmae of *C. glimeana* are quite different from those seen in other species of *Cyclolejeunea*, which are usually disciform (rarely elongate; *C. luteola*), have rhizoids and are produced on ascending branches, on the margins and surfaces of strongly toothed, gemmiparous leaves. The gemmae of *C. glimeana* are strikingly similar to the thalloid gemmae of *Prionolejeunea* (Ilkiu-Borges 2016) and the former genus *Stenolejeunea* from Asia and Australasia (Grolle 1966; Schuster 2000). However, it seems that gemmae in the latter two genera are freely produced on vigorous leaves, not only on old, decaying leaves.

By the lack of innovations and the presence of ligulate gemmae without rhizoids, *Cyclolejeunea glimeana* is more

similar to *Prionolejeunea* than *Cyclolejeunea*. However, the presence of ocelli readily separates it from *Prionolejeunea*, which lacks them. Also, the entire leaf margins of the new species are quite atypical for *Prionolejeunea*.

Cyclolejeunea glimeana is monoicous (most *Cyclolejeunea* species are dioicous) and the plants were copiously fertile, with numerous gynoecial branches and androecia. However, almost all gynoecia in our material were immature, containing unfertilized archegonia and lacking well-developed perianths. Upon carefully searching of the material, however, we were able to detect a few mature gynoecia with well-developed, obcordate-auriculate perianths, as typical of *Cyclolejeunea*.

Grolle (1984) classified the species of *Cyclolejeunea* in three different subgenera: 1) subg. *Hyalolejeunea* Grolle (1984: 763), characterized by papillose leaf cells, lack of ocelli, disciform gemmae and monoicy, and containing *C. accedens* (Gottsche, in Gottsche *et al.* 1845: 339) Evans (1904: 201); 2) subg. *Nephrolejeunea* Grolle (1984: 763), characterized by smooth leaf cells, presence of ocelli, elongate gemmae (with rhizoids) and dioicy, and containing *C. luteola*; and 3) subg. *Cyclolejeunea*, with the same characters as *Nephrolejeunea* but gemmae disciform, containing the rest of the species. A recent molecular analysis of *Cyclolejeunea* resolved the three subgenera as monophyletic (Heinrichs *et al.* 2014). Morphologically, *Cyclolejeunea glimeana* does not fit in any of the subgenera. Although superficially similar to *C. luteola* in having elongate gemmae, the gemmae in these two species are quite dissimilar in other respects, as discussed above. Moreover, *C. glimeana* differs from *C. luteola* in important traits such as the lack of innovations, entire leaf margins, lobules without any indication of a tooth, and monoicy. As the combination of characters seen in *C. glimeana* sets this species well apart from the remaining members of the genus, we propose its placement in a subgenus of its own, as follows:

Cyclolejeunea* subg. *Chocolejeunea* M.E.Reiner & Gradst., *subg. nov.

Type: *C. glimeana* M.E.Reiner & Gradst.

Leaf margins entire to slightly crenulate. Leaf cells smooth. Lobule without tooth. Monoicous. Innovations lacking. Gemmae ligulate, without rhizoids, produced on old, decaying shoots.

Key to the species of *Cyclolejeunea*

Three species described in *Cyclolejeunea*, *C. ecuadorensis* Steph., *C. integerrima* (Steph.) Steph. and *C. spectabilis* Steph., are of doubtful status (Söderström *et al.* 2016) and are omitted here. A further dubious species of *Cyclolejeunea* described as *Prionolejeunea maculata* Herzog (Ilkiu-Borges 2016, Söderström *et al.* 2016) is also excluded from the key. Judging from their original descriptions and illustrations, these four taxa are quite different from *Cyclolejeunea glimeana*.

- 1. Underleaves undivided *C. convexistipa*
- Underleaves bifid 2
- 2. Underleaves of creeping stems shallowly bifid (1/6–1/4), underleaf lobes rounded or apiculate, margins entire. Gemmae wider than long (reniform) *C. chitonia* (Taylor) A.Evans
- Underleaves of creeping stems more deeply divided, underleaf lobes acute, margins entire or toothed. Gemmae rounded or longer than wide 3
- 3. Plants 1.5–3 mm wide. Leaf margins of creeping stems sharply toothed, the teeth 1-4 cells long. Lobule tooth \pm reduced, obtuse *C. peruviana*
- Plants smaller, 0.5–1.5(–1.7) mm wide. Leaf margins of creeping stems entire or toothed, the teeth not more than 1 cell long. Lobule tooth reduced or well-developed 4
- 4. Cells of leaf margin and dorsal leaf surface mamilllose and with a broad papilla. Ocelli lacking. Gemmae orbicular .. *C. accedens*
- Cells of leaf margin and dorsal leaf surface smooth, not mamilllose, without papilla. Ocelli present at leaf base. Gemmae orbicular or elongate 5
- 5. Lobule tooth well-developed, acute. Gemmae elongate, with rhizoids *C. luteola*
- Lobule tooth small and obtuse, or absent. Gemmae orbicular, or elongate without rhizoids 6
- 6. Leaf margins \pm toothed. Lobule with a small tooth. Innovations present. Gemmae orbicular, with rhizoids, produced on sharply toothed branch leaves. Androecia on short branches without vegetative leaves *C. foliorum*
- Leaf margins entire or crenulate. Lobule without tooth. Innovations lacking. Gemmae ligulate, without rhizoids, produced on old, decaying shoots. Androecia on elongate branches with vegetative leaves *C. glimeana*

Acknowledgments

Fieldwork in the Chocó of Colombia by the first author was supported by the National Geographic Society (grant # 46 91-91 to J.-P. Frahm). We express our gratitude to Anna Luiza Ilkiu-Borges and Tamás Pócs for corrections on the manuscript.

References

- André, E. (1871) *Welfia regia* H. Wendland. *L'illustration horticole* 168: 92–94, Pl. LXII.
- Bernecker-Lücking, A. (1998) The genus *Cyclolejeunea* A. Evans (Hepaticae, Lejeuneaceae) in Costa Rica. *Phyton* 38: 175–193.
- Bernal, R., Gradstein, S.R. & Celis, M. (Eds.) (2016) *Catálogo de Plantas y Líquenes de Colombia*. Universidad Nacional de Colombia, Bogotá, 3060 pp.
- Buchloh, G. (1961) Einige species novae und Neufunde von Moosen aus den Anden von Peru. *Nova Hedwigia* 3: 507–516.
- Cavers, F. (1910) The interrelationships of the Bryophyta. *New Phytologist* 9: 269–304.
- Evans, A.W. (1904) Hepaticae of Puerto Rico. IV. *Odontolejeunea*, *Cyclolejeunea* and *Prionolejeunea*. *Bulletin of the Torrey Botanical Club* 31: 183–226.
<https://doi.org/10.2307/2478687>
- Frahm, J.-P. (1994) A contribution to the bryoflora of the Chocó region, Colombia. I. Mosses. *Tropical Bryology* 9: 89–110.
- Frahm, J.-P. (2012) Mosses and liverworts of the Chocó region, Colombia. *Archives for Bryology* 123: 1–14. Available from: <http://www.archive-for-bryology.com/Archive%20123.pdf> (accessed 1 June 2017)
- Galeano, G. & Bernal, R. (2010) *Palmas de Colombia: guía de campo*. Universidad Nacional de Colombia, Bogotá, 688 pp.
- Gehrig-Downie, C., Obregón A., Bendix, J. & Gradstein, S.R. (2013) Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Journal of Bryology* 35: 243–254.
<https://doi.org/10.1179/1743282013Y.0000000070>
- Gottsche, C.M., Lindenberg, J.B.G. & Nees von Esenbeck, C.G. (1845) *Synopsis Hepaticarum*, 2: 145–304. Meissner, Hamburg.
- Gradstein, S.R. (1985) A guide to the holostipous Lejeuneaceae. *Beihefte zur Nova Hedwigia* 80: 13–30.
- Gradstein, S.R. (1992) The genera *Thysananthus*, *Dendrolejeunea*, and *Fulfordianthus* gen. nov. (Studies on Lejeuneaceae subfamily Ptychanthoideae XXI). *The Bryologist* 95: 42–51.
<https://doi.org/10.2307/3243784>
- Gradstein, S.R. (2013) A classification of Lejeuneaceae (Marchantiophyta) based on molecular and morphological evidence. *Phytotaxa* 100: 6–20.
<https://doi.org/10.11646/phytotaxa.100.1.2>
- Gradstein, S.R. & Uribe, J. (2016) Marchantiophyta. In: Bernal, R., Gradstein, S.R. & Celis, M. (Eds.) *Catálogo de plantas y líquenes de Colombia*. Universidad Nacional de Colombia Press, Bogotá, pp. 282–352.
- Gradstein, S.R., Churchill, S.P. & Salazar Allen, N. (2001) Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* 86: 1–577.
- Gradstein, S.R., Obregon, A., Gehrig, C. & Bendix, J. (2010) The tropical lowland cloud forest – a neglected forest type. In: Bruijnzeel, L.E., Scatena, F.N. & Hamilton, L.S. (Eds.) *The Tropical Montane Cloud Forest*. Cambridge University Press, Cambridge, U.K., pp. 130–133.
- Grolle, R. (1966) Lebermoose aus Neuguinea. 3. *Stenolejeunea*. *Journal of the Hattori Botanical Laboratory* 29: 75–78.
- Grolle, R. (1984) Zur Kenntnis der Lejeuneoideae in Cuba (1): *Cyclolejeunea*. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Naturwissenschaftliche Reihe* 33: 759–764.
- Heinrichs, J., Czumaj, A., Dong, S.S., Scheben, A., Schäfer-Verwimp, A., Peralta, D.F., Feldberg, K., Schmidt, A.R. & Schneider, H. (2014) The Bromeliaceae tank dweller *Bromeliophila* (Lejeuneaceae, Porellales) is a member of the *Cyclolejeunea-Prionolejeunea* clade. *Plant Systematics and Evolution* 300: 63–73.
<https://doi.org/10.1007/s00606-013-0860-4>
- Herzog, T. (1955) Hepaticae aus Columbia und Peru. *Feddes Repertorium Specierum Novarum Regni Vegetabilis* 57: 156–203.
<https://doi.org/10.1002/fedr.4880570105>
- Ilkiu-Borges, A.L. (2016) *Prionolejeunea*. *Flora Neotropica Monograph* 116: 1–126.
- Lehmann, J.G.C. (1833) *Novarum et minus cognitarum stirpium pugillus quintus*. Meissner, Hamburg. 28 pp.
- Lehmann, J.G.C. (1834) *Novarum et minus cognitarum stirpium pugillus sextus*. Meissner, Hamburg. 72 pp.
- Lehmann, J.G.C. (1844) *Novarum et minus cognitarum stirpium pugillus octavus*. Meissner, Hamburg. 56 pp.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
<https://doi.org/10.1038/35002501>
- Piippo, S. (1986) A monograph of *Lepidolejeunea* and *Luteolejeunea* (Lejeuneaceae: Hepaticae). *Acta Botanica Fennica* 132: 1–69.
- Schiffner, V. (1893) Hepaticae. In: Engler, A. & Prantl, K. (Eds.) *Die Natürlichen Pflanzenfamilien I, vol. 3*. Engelmann, Leipzig, pp. 1–141.
- Schuster, R.M. (2000) Studies on Lejeuneaceae, III. Revisionary studies on *Stenolejeunea* Schust. *Journal of the Hattori Botanical*

Laboratory 89: 151–171.

Söderström, L., Hagborg, A., von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D.C., Costa, D.P., Crandall-Stotler, B.J., Cooper, E.D., Dauphin, G., Engel, J., Feldberg, K., Glenny, D., Gradstein, S.R., He, X.-L., Heinrichs, J., Hentschel, J., Ilkiu-Borges, A.L., Katagiri, T., Konstantinova, N.A., Larrain, J., Long, D.G., Nebel, M., Pócs, T., Puche, F., Reiner-Drehwald, E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Moragues, J.G.S., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J., Váña, J., Villarreal, J.C., Wigginton, M., Zhang, L. & Zhu, R.-L. (2016) World checklist of hornworts and liverworts. *PhytoKeys* 59: 1–828.

<https://doi.org/10.3897/phytokeys.59.6261>

Spruce, R. (1884) Hepaticae amazonicae et andinae. I. *Transactions and Proceedings of the Botanical Society of Edinburgh* 15: 1–308.

Vasco, A.M., Cobos, R. & Uribe, J. (2002) Las hepáticas (Marchantiophyta) del departamento del Chocó, Colombia. *Biota Colombiana* 3: 149–162.