

A REMARKABLE NEW SPECIES OF *CHEILOLEJEUNEA* (MARCHANTIOPHYTA: LEJEUNEACEAE) FROM COLOMBIA

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Summary: We describe the new liverwort species *Cheilolejeunea schiavoneana* M.E.Reiner & Gradst. from submontane rainforest in the Western Cordillera of Colombia. The new species is related to *C. adnata* (C. sect. *Cheilolejeunea*) but differs by larger plant, leaf and underleaf size, robust stems, a 5-6 cells wide ventral merophyte, abundance of microphyllous branches, and vegetative reproduction by caducous leaf lobes produced on flagelliform shoots. The latter feature is characteristic of the genus *Rectolejeunea* and its presence in *Cheilolejeunea* is apparently a case of parallel evolution. The discovery of *C. schiavoneana* adds a further endemic taxon to the rich flora of the Colombian Western Cordillera.

Key words: *Cheilolejeunea adnata*; *Cheilolejeunea schiavoneana*; *Cheilolejeunea* section *Cheilolejeunea*; Colombia; liverworts; morphology; taxonomy; Western Cordillera of Colombia.

Resumen: *Cheilolejeunea schiavoneana* (Marchantiophyta: Lejeuneaceae), una nueva especie de Colombia. Se describe la nueva especie *Cheilolejeunea schiavoneana* M.E.Reiner & Gradst., coleccionada en selva submontana de la Cordillera Occidental de Colombia. Este nuevo taxon está relacionado con *C. adnata* (C. sección *Cheilolejeunea*) pero difiere en el mayor tamaño de las plantas, hojas y anfigastrios, el ancho del merofito ventral (de 5-6 células), la abundancia de ramas microfilas, y la reproducción vegetativa por medio de lobos caducos producidos en tallos flagelíferos. Esta última propiedad es característica del género *Rectolejeunea*, y su presencia en *Cheilolejeunea* es aparentemente debida a evolución paralela. El descubrimiento de *C. schiavoneana* agrega otro taxon endémico a la gran diversidad de la flora en la Cordillera Occidental de Colombia.

Palabras clave: *Cheilolejeunea adnata*; *Cheilolejeunea schiavoneana*; *Cheilolejeunea* sección *Cheilolejeunea*; Colombia; hepáticas; morfología; taxonomía; Cordillera Occidental de Colombia.

INTRODUCTION

The Western Cordillera of the Andes of Colombia is a rich area for liverworts (Gradstein & Uribe, 2016). It is home to several rare or endemic species including *Drepanolejeunea pterocalyx* (Herzog) Bischl., *Fuscocephaloziopsis pulvinata* (Steph.) Fulf., *Lejeunea drehwaldii* Heinrichs & Schäf.-Verw. (= *Sphaerolejeunea umbilicata* Herzog), *Lepidozia pinnaticurris*

Steph., *Lepidolejeunea grossepapulosa* (Steph.) Piippo, *Micropterygium longicellulatum* Uribe & E.L.Linares, *Neesioscophus allionii* Steph., *Plagiochila fastigiata* Lindenb. & Gottsche, *Plagiochila rudischusteri* H.Rob., *Prionolejeunea arguta* (Nees) Steph., *P. magnistipula* Herzog and *Radula involvens* Spruce, and is the diversity center of the genus *Prionolejeunea* (Spruce) Schiffn. with ca. 40 % (10 spp.) of all *Prionolejeunea* species occurring in the area (Ilkui-Borges, 2016).

Here we describe a remarkable new species in the genus *Cheilolejeunea* (Spruce) Steph. from the Western Cordillera of Colombia. *Cheilolejeunea* is one of the largest genera of the liverwort family Lejeuneaceae, with a wide distribution throughout the Tropics and well into the temperate regions of the Southern Hemisphere. The main diagnostic feature of the genus is the distal hyaline papilla

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on the leaf lobule; other important characters include: 1) ventral merophyte 2-12 cells wide; 2) leaf margins usually entire; 3) leaf cells often with large trigones and without intermediate thickenings; 4) oil bodies few per cell, large, coarsely granular (rarely finely granular); 5) ocelli usually absent; 6) lobules never reduced; 7) underleaves undivided or bifid, with upright lobes; 8) vegetative reproduction rare, by caducous leaf-lobes; 9) spores ornamented by numerous rosettes (>10); 10) abundance of striatene-type sesquiterpenes and scarcity of flavonoids.

The circumscription of the genus was recently expanded based on molecular studies (Wilson *et al.*, 2007; Schäfer-Verwimp *et al.*, 2014; Ye *et al.*, 2015), which showed that several well-known genera of Lejeuneaceae, e.g. *Aureolejeunea* R.M.Schust., *Leucolejeunea* A.Evans, *Cyrtolejeunea* A.Evans, *Cystolejeunea* A.Evans, *Omphalanthus* Lindenb. & Nees and *Trachylejeunea* (Spruce) Steph., are part of *Cheilolejeunea*. As a result, the number of species assigned to the genus has risen to almost two hundred, in at least nine sections (Söderström *et al.*, 2016; Ye *et al.*, 2015). However, the real number of species in *Cheilolejeunea* may be much lower as the genus has not been monographed.

An unusual species of *Cheilolejeunea*, 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 the Pacific coast of Colombia (Frahm, 1994). The species differs from all members of the genus *Cheilolejeunea* by modified caducous leaf lobes produced on specialized flagelliform branches. It is our pleasure to dedicate this new species to Dr. María Magdalena (Magui) Schiavone, in honor of her important contributions to the bryology of South America.

RESULTS

Cheilolejeunea schiavoneana M.E.Reiner *et* Gradst., *sp. nov.* Fig. 1.

Diagnosis. *Plants 1.8-2.45 mm wide, irregularly 1-2-pinnate, with numerous microphyllous branches. Stems rigid, of 11-15 rows of epidermis*

cells and 20-25 rows of much narrower medullary cells, all stem cells slightly thick-walled; ventral merophyte on main stems 5-6 cells wide. Leaf apex rounded. Leaf cells large, 25-40 × 20-30 μm in midleaf, conspicuously smaller towards the margin, walls with triradiate trigones; ocelli not observed. Lobules shortly flask-shaped, 1/6-1/5 × leaf length, fully inflated, tooth long and sharp, lobule cells much smaller than leaf lobe cells. Underleaves broadly ovate, 2.5-3 × stem width, distant, bifid to 1/2, margins entire; ocelli not observed. Caducous leaves smaller than normal leaves, produced on short upright, flagelliform shoots, margins of caducous leaves with short rhizoids; underleaves on flagelliform branches imbricate, otherwise similar to normal underleaves.

Type. Colombia. Departamento Risaralda: western side of the Cordillera Occidental, municipio Mistrato, along the trail from Jeguadas to Puerto de Oro, ca. 5°45'N 76°01'W, on canopy branches in submontane rainforest, 1200 m, 27 July 1992, S.R. Gradstein 8591 (Holotype COL; Isotype GOET).

Plants to 2(-3) cm long, rather robust, 1.2-2.45 mm wide on stems, pale brown when dry, prostrate, irregularly and rather densely 1(-2)-pinnate, branches *Lejeunea*-type, frequently rather short and microphyllous with reduced leaf-lobes, microphyllous branches 0.3-0.4 mm wide. Stems 130-210 μm in diameter, pale brown, rigid, made up of 11-15 rows of epidermis cells (20-32 × 25-38 μm) surrounding 20-25 rows of much narrower medullary cells (12-15 × 17-20 μm), all stem cells slightly thick-walled; ventral merophyte 5-6 cells wide on main stems, 3-4 cells wide on branches. Leaves rather widely spreading, imbricate, leaf lobes convex, asymmetrically ovate with arched dorsal margin and ± straight ventral margin, not falcate, 0.7-1.35 mm long × 0.65-1.1 mm wide, leaf surface smooth, apex broadly rounded, plane or recurved, margins entire, plane or dorsal margin recurved on stem leaves, dorsal leaf base extending across and beyond the stem, length of dorsal insertion ca. 1/3 of leaf width. Cells of leaf lobe isodiametrical to elongate, 25-40 × 20-30 μm in midleaf, becoming larger to the base and conspicuously smaller towards the margin, forming a broad, ill-defined leaf border of several rows of

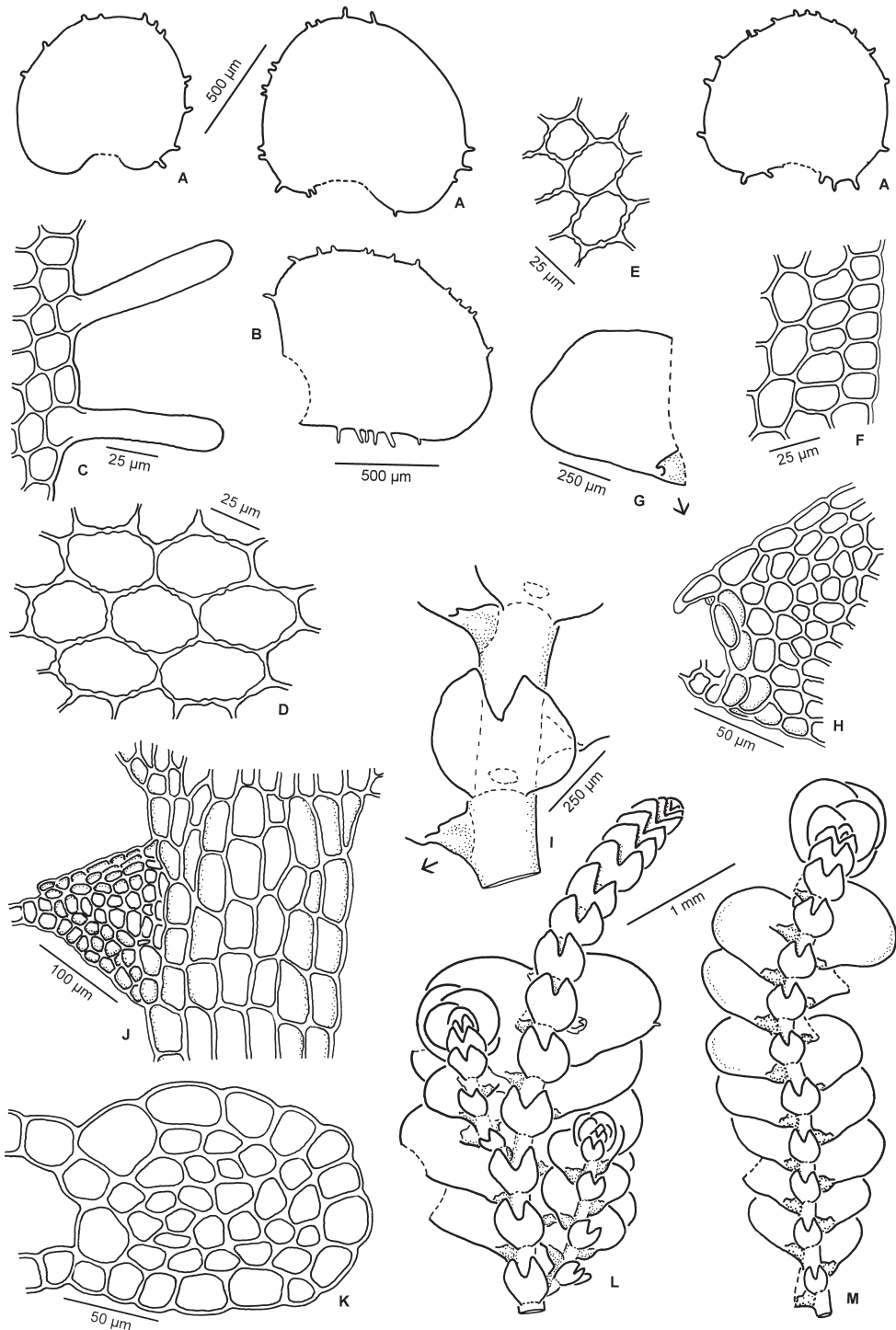


Fig. 1. *Cheilolejeunea schiavoneana*. **A, B:** Caducous leaf lobes. **C:** Margin of caducous leaf lobe with rhizoids. **D:** Median cells of caducous leaf lobe. **E:** Median cells of leaf lobe. **F:** Marginal cells of leaf lobe. **G:** Leaf. **H:** Apex of leaf lobule (detail of fig. G). **I:** Shoot sector. **J:** Stem and leaf lobule in situ. **K:** Cross section of stem. **L:** Habit, with flagelliform shoot at apex. **M:** Habit. (All drawn from the type).

rather small cells, margin cells ca. 12-16 μm high; cell walls with conspicuous triradiate trigones and 0-2 rounded to elongate intermediate thickenings, cuticle smooth; oil bodies not observed; ocelli not seen. Lobules ovate, shortly flask-shaped, on stems $1/6-1/5 \times$ leaf length, on microphyllous branches ca. $2/3 \times$ leaf length, 0.15-0.3 mm long \times 0.12-0.2 mm wide, strongly inflated, free margin incurved, not or very shortly continuing into the ventral leaf margin, lobule apex obliquely truncate, with a long and sharp tooth, the tooth, 25-40 μm long and 10 μm wide, 2.5-4 \times longer than wide, \pm straight, with a conspicuously thickened tip; hyaline papilla in a small notch distal to the tooth; keel smooth and straight on stem leaves (arched and crenate on microphyllous branch leaves), forming an almost straight line with the ventral leaf margin; lobule cells much smaller than leaf cells, subisodiametrical, 12-20 μm long, walls with triradiate thickenings, free margin cells in the upper half of the lobule covered by a broad, colorless layer of thickening. Underleaves distant to contiguous, plane, broadly ovate, 0.3-0.5 mm long \times 0.35-0.6 mm wide, 2-3 \times stem width, bifid to $1/2-3/5$, lobes broad, ca. 13-16 cells wide at base, apex obtuse or narrowly rounded, incision rather widely V-shaped, sinus narrowly rounded, margins plane, entire, sometimes bluntly angled in the middle, bases cuneate to rounded, insertion line curved; underleaf cells smaller than the leaf lobe cells, oil bodies and ocelli not observed; rhizoid disc small, rhizoids few, colorless.

Dioicous? (Gametocia not seen). Vegetative reproduction by caducous leaf lobes produced on ascending, flagelliform prolongations of prostrate branches, the ascending shoots ca. 4-15 leaf cycles long, with tiny leaf lobules and densely imbricate, appressed to subsquarrose underleaves, shoot apex usually with a few closely appressed, undetached leaf lobes; caducous leaf lobes suborbicular to broadly ovate, slightly smaller than normal leaves, ca. 0.75-0.9 mm long \times 0.75-1 mm wide, insertion line subtransverse, margin with 5-30 scattered rhizoids, the rhizoids short, (10-)20-80(-120) μm long; cells of caducous leaf lobes 35-65 \times 20-30 μm in midleaf, as large as or somewhat larger than those of normal leaf lobe cells, not or scarcely larger at leaf base, smaller at the margin; ocelli not observed; gemmalings developing from leaf surface, 1-3 per leaf.

Distribution and habitat. *Cheilolejeunea schiavoneana* is only known from the type locality in submontane rainforest at ca. 1200 m in the Western Cordillera of Colombia, on the western slope of the Andes bordering the wet Pacific coastal lowland rainforests of the Chocó Department. The new species was growing in loose mats on branches in the forest canopy together with several other members of Lejeuneaceae, including *Bryopteris filicina* (Sw.) Nees, *Ceratolejeunea cornuta* (Lindenb.) Steph., *Cyclolejeunea peruviana* (Lehm. & Lindenb.) A.Evans, *Drepanolejeunea biocellata* A.Evans, *Lejeunea flava* (Sw.) Nees, *Lepidolejeunea cordifissa* (Taylor) M.E.Reiner, *L. involuta* (Gottsche) Grolle, *Microlejeunea acutifolia* Steph., *Stictolejeunea squamata* (Willd.) Schiffn. and an undescribed species of the genus *Rectolejeunea* A.Evans (Gradstein, in prep.).

Observations. *Cheilolejeunea schiavoneana* is a member of the genus *Cheilolejeunea* (Lejeuneaceae subtribe Cheilolejeuneinae Gradst.) because of the lobule with a distal hyaline papilla (Fig. 1H). Within this genus, the new species stands out by the robust stems, being 5-6 cells wide across the ventral stem surface, the presence of numerous small, microphyllous branches, triradiate trigones and, especially, by vegetative reproduction by means of caducous leaf lobes falling off from small, upright flagelliform shoots. The caducous leaf lobes are somewhat smaller than normal leaf lobes and are typically broader than long, with a rather short, subtransverse insertion and numerous short rhizoids on the margins. The flagelliform shoots are largely devoid of lateral leaves except for the small, persistent lobules; in addition, a few undetached leaf lobes may be present at the tips of the shoots. The underleaves of the flagelliform shoots are densely imbricate due to shortening of the merophytes of the shoots. In contrast, underleaves on normal shoots are usually widely spatiated and distant.

Caducous leaf lobes are uncommon in the genus *Cheilolejeunea*; when present, they are always produced on normal leafy shoots (e.g. in *C. adnata* (Lehm.) Grolle, *C. aneogyna* (Spruce) A. Evans and *C. caducifolia* (Grolle & Gradst.) Yet *et al.*), never on upright flagelliform shoots. Such specialized flagelliform shoots are quite characteristic of the genus *Rectolejeunea* (Reiner-

Drehwald & Grolle, 2012), but are unknown in *Cheilolejeunea*, and the new species was therefore initially believed to be an undescribed member of *Rectolejeunea*. However, the absence of ocelli, the leaf cells with trigones and, especially, the distal hyaline papilla clearly separate *C. schiavoneana* from *Rectolejeunea*. The latter genus is a member of Lejeuneaceae subtribe Lepidolejeuneinae Gradst. and phylogenetically quite distant from *Cheilolejeunea* (Heinrichs *et al.*, 2015; Bechteler *et al.*, 2016). We therefore suggest that the presence of vegetative reproduction by means of caducous leaf lobes produced on specialized flagelliform branches in *C. schiavoneana* may be interpreted as a case of parallel evolution between *Rectolejeunea* and *Cheilolejeunea*.

Within *Cheilolejeunea*, the new species seems to be most closely related to *C. adnata*, a species widespread in tropical America and type of the genus *Cheilolejeunea*; for descriptions see Evans (1906, as *C. decidua* [Spruce] A. Evans), Schuster (1980) and Gradstein & Ilkiu-Borges (2009). The two species share several distinct features, such as: 1) smooth leaves with a rounded apex; 2) leaf cells with small, triradiate trigones and intermediate thickenings; 3) bottle-shaped lobules with a long and thin tooth, and the hyaline papilla positioned in a small notch distal to the tooth; 4)

distant underleaves bifid to 1/2 and with a cuneate base; 5) vegetative reproduction by caducous leaf lobes with short rhizoids on the margins. They clearly differ, however, in size, branching pattern, stem structure and vegetative reproduction; differences are shown in Table 1. The most striking differences are undoubtedly the more robust stems of *R. schiavoneana* with a 5-6 cells wide ventral merophyte, and caducous leaf lobes produced on upright flagelliform shoots.

Because of its similarity to *C. adnata*, *C. schiavoneana* may be placed in *C.* sect. *Cheilolejeunea*. The latter is a small group of about five species, including *C. adnata* (neotropical), *C. larsenii* Mizut. (pantropical), *C. lineata* Steph. (neotropical), and possibly *C. albovirens* (Hook. f. & Taylor) E.A. Hodgs. (Australasia) and *C. verrucosa* Steph. (Asia) (Ye *et al.*, 2015). Characters of this section include the long and thin lobule tooth, presence of a hyalodermis and absence of gynoecial innovations. *Cheilolejeunea schiavoneana* clearly differs from the members in this section by the robust stem and the peculiar flagelliform branches. As the material was sterile, absence of gynoecial innovation in *C. schiavoneana* could not be verified. We suggest that the phylogenetic relationships of this remarkable species be clarified based on fertile plants and DNA analysis.

Table 1. A comparison of *Cheilolejeunea adnata* and *C. schiavoneana*.

	<i>C. adnata</i>	<i>C. schiavoneana</i>
Plant width	0.7-1.2 mm	1.2-2.45 mm
Microphyllous branches	absent	present
Stem	85-120 µm thick; ca. 7 rows of epidermal cells and 10 rows of medullary cells	130-210 µm thick; 11-15 rows of epidermal cells and 20-25 rows of medullary cells
Ventral merophyte on stem	2 cells wide	5-6 cells wide
Stem leaves	0.6-0.7 mm long	0.7-1.35 mm long
Caducous leaf lobes	as large as normal leaf lobes, produced on normal shoots	smaller than normal leaf lobes, produced on specialized, upright flagelliform shoots
Leaf cells	with small triradiate trigones and intermediate thickenings	with small triradiate trigones and intermediate thickenings
Lobules	1/4-1/3× leaf length, bottle-shaped, with a long and sharp tooth	1/6-1/5× leaf length, bottle-shaped, with a long and sharp tooth
Underleaves	1.5-2× stem width	2-3× stem width

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BIBLIOGRAPHY

- BECHTELER, J., G. E. LEE, A. SCHÄFER-VERWIMP, T. PÓCS, D. F. PERALTA, M. A. M. RENNER, H. SCHNEIDER & J. HEINRICHS. 2016. Towards a monophyletic classification of Lejeuneaceae IV: reinstatement of *Allorgella*, transfer of *Microlejeunea aphanella* to *Vitalianthus* and refinements of the subtribal classification. *Plant Syst. Evol.* 302: 187-201.
- EVANS, A. W. 1906. Hepaticae of Puerto Rico VI. *Cheilolejeunea*, *Rectolejeunea*, *Cystolejeunea* and *Pycnolejeunea*. *Bull. Torrey Bot. Club* 33: 1-25.
- FRAHM, J.-P. 1994. A contribution to the bryoflora of the Chocó region, Colombia. I. Mosses. *Trop. Bryol.* 9: 89-110.
- GRADSTEIN, S. R. & A. L. ILKIU-BORGES. 2009. Guide to the Plants of Central French Guiana. Part IV. Liverworts and Hornworts. *Mem. N. Y. Bot. Gard.* 76, 4: 1-140.
- GRADSTEIN, S. R. & J. URIBE M. 2016. Marchantiophyta. Pages 282-352 in R. Bernal, S.R. Gradstein & M. Celis (eds.), *Catálogo de plantas y líquenes de Colombia*. Universidad Nacional de Colombia Press, Bogotá.
- HEINRICHS, J., K. FELDBERG, J. BECHTELER, A. SCHEBEN, A. CZUMAJ, T. PÓCS, H. SCHNEIDER & A. SCHÄFER-VERWIMP. 2015. Integrative taxonomy of *Lepidolejeunea* (Jungermanniopsida: Porellales): Ocelli allow the recognition of two neglected species. *Taxon* 64: 216-228.
- ILKIU-BORGES, A. L. 2016. *Prionolejeunea*. *Flora Neotropical Monograph* 116: 1-131.
- REINER-DREHWALD, M. E. & R. GROLLE. 2012. Review of the genus *Rectolejeunea* (Lejeuneaceae, Marchantiophyta). *Nova Hedwigia* 95: 451-482.
- SCHÄFER-VERWIMP, A. K. FELDBERG, S. DONG, H. VAN MELICK, D. F. PERALTA, A. R. SCHMIDT, H. SCHNEIDER & J. HEINRICHS. 2014. Towards a monophyletic classification of Lejeuneaceae III: the systematic position of *Leiolejeunea*. *Phytotaxa* 170: 187-198.
- SCHUSTER, R. M. 1980. *The Hepaticae and Anthocerotae of North America* IV. Columbia Univ. Press, New York.
- SÖDERSTRÖM, L., A. HAGBORG, M. VON KONRAT, S. BARTHOLOMEW-BEGAN, D. BELL, L. BRISCOE, E. BROWN, D. C. CARGILL, D. P. COSTA, B.J. CRANDALL-STOTLER, E. D. COOPER, G. DAUPHIN, J. J. ENGEL, K. FELDBERG, D. GLENNY, S. R. GRADSTEIN, X. L. HE, J. HEINRICHS, J. HENTSCHEL, A. L. ILKIU-BORGES, T. KATAGIRI, N. A. KONSTANTINOVA, J. LARRAIN, D. G. LONG, M. NEBEL, T. PÓCS, F. FELISA PUCHE, E. REINER-DREHWALD, M. A. M. RENNER, A. SASS-GYARMATI, A. SCHÄFER-VERWIMP, J. G. SEGARRA MORAGUES, R. E. STOTLER, P. SUKKHARAK, B. M. THIERS, J. URIBE, J. VÁÑA, J. C. VILLARREAL, M. WIGGINTON, L. ZHANG & R. L. ZHU. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-821.
- WILSON, R., S. R. GRADSTEIN, H. SCHNEIDER & J. HEINRICHS. 2007. Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): evidence for four main lineages. *Molec. Phylog. Evol.* 43: 270-282.
- YE, W., S. R. GRADSTEIN, J. A. SHAW, B. SHAW, B. C. HO, A. SCHÄFER-VERWIMP, T. PÓCS, J. HEINRICHS & R. L. ZHU. 2015. Phylogeny and classification of Lejeuneaceae subtribe *Cheilolejeuneinae* (Marchantiophyta) based on nuclear and plastid molecular markers. *Cryptog., Bryol.* 36: 313-333.

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