



## The genus *Cheilolejeunea* (Marchantiophyta: Lejeuneaceae) in tropical America

Cid José Passos Bastos<sup>1\*</sup> and S. Robbert Gradstein<sup>2</sup>

<sup>1</sup> Universidade Federal da Bahia, Instituto de Biologia, Laboratório de Taxonomia de Briófitas – BrioFLORA, Campus Universitário de Ondina, 40170-280 Salvador, Bahia, Brazil

<sup>2</sup> Department of Systematics, Biodiversity and Evolution of Plants, Albrecht von Haller Institute, University of Göttingen, 37073 Göttingen, Germany; Muséum National d'Histoire Naturelle, Institute de Systematique, Évolution, Biodiversité (UMR 7205), 75005 Paris, France

\* Corresponding author: cidbastos@gmail.com; cjbasto@ufba.br

With 3 figures

**Abstract:** *Cheilolejeunea* is one of the largest genera of Lejeuneaceae and is widely distributed in tropical and subtropical regions. We present an improved and updated taxonomic synthesis of the genus in Tropical America. Fifty-four species and six varieties are recognized, in seven sections; the number of accepted neotropical species is reduced about 20 percent. A key to neotropical taxa of *Cheilolejeunea* is provided and each species and variety is briefly described with data on differentiating characters, distribution and published illustrations. Sixteen new synonyms and two new lectotypifications are proposed; new names are: *C.* sect. *Trachylejeunea* (Spruce) C.J.Bastos & Gradst. comb. nov., *C. aneogyna* var. *riparia* (Steph.) C.J.Bastos & Gradst. comb. nov., *C. lobulata* (Lindenb.) Gradst. & C.J.Bastos comb. nov., *C. rigidula* var. *autoica* C.J.Bastos & Gradst. var. nov., *C. timboensis* C.J.Bastos & Gradst. sp. nov., *C. trifaria* var. *clausa* (Nees & Mont.) C.J.Bastos & Gradst. comb. nov.

**Key words:** liverworts; Neotropics; taxonomy

## Introduction

*Cheilolejeunea* (Spruce) Steph. is one of the largest genera of Lejeuneaceae with almost two hundred accepted species, mainly in tropical and subtropical regions (Söderström et al. 2016, Bastos 2017). The number of species may be lower, however, as the genus has not been monographed. A preliminary synthesis of the New World species, in the Portuguese language, was presented by Bastos (2017) who recognized 80 species, including 70 in the Neotropics and the remaining ones in southern South America (8) and North Amer-

ica (2). Two additional New World species have been added since, *Cheilolejeunea schiavoneana* M.E.Reiner & Gradst. (Gradstein & Reiner-Drehwald 2017) and *C. savannae* L.P.C.Macedo et al. (Macedo et al. 2020).

The taxonomic history and classification of *Cheilolejeunea* in the New World have been discussed by Bastos (2017). The genus is rather difficult to circumscribe, many of its morphological features are shared with other genera. The following combination of characters may serve to define the genus: (1) lobules usually strongly inflated, rarely reduced, with two teeth, second lobule tooth well developed, first lobule tooth usually reduced, when well-developed the two teeth positioned very close to each other; (2) hyaline papilla distal to the second tooth (Mizutani 1961); (3) leaf cells frequently mammillose and with conspicuous trigones, outer wall sometimes thickened and produced as a broad papilla; (4) oil bodies few per cell (1–5), usually large and coarsely segmented; (5) ocelli usually absent, present in *C. aneogyna* (Spruce) A.Evans, *C. urubuensis* (C.E.Zartman & I.L.Ackerman) R.L.Zhu & Y.M.Wei and in a few Asiatic species; (6) stem cells mostly thick-walled, hyalodermis usually absent (occasionally present); (7) perianths 4–5 keeled or terete, keels when present smooth or crenulate.

The purpose of this paper is to present an improved and updated taxonomic synthesis, in English language, of *Cheilolejeunea* in the New World, with a focus on the Neotropics. The status of the species accepted by Bastos (2017) has been critically reassessed, descriptions have been revised and a new and improved key to species and varieties has been prepared. The present treatment may contribute to improve our understanding of the diversity and distribution of the large genus *Cheilolejeunea* in the Neotropics.

## Materials and methods

The present account is based on the observations of Bastos (2017), who examined over one thousand specimens from 32 herbaria, supplemented with the results of study of new collections and of types not studied previously, as well as observations made by the second author in the framework of the forthcoming Flora of the Liverworts and Hornworts of Colombia and Ecuador (Gradstein in press). Based on these data, brief morphological descriptions of all accepted species and varieties of *Cheilolejeunea* in the Neotropics have been prepared together with characterizations of their geographical range. References to published descriptions and illustrations have been added, but type citations, synonyms and full bibliographic references of taxon names, for which see Bastos (2017) and Söderström et al. (2015, 2016), are omitted except for new synonymy and new nomenclature.

## Taxonomic treatment

### *Cheilolejeunea* (Spruce) Steph.

**Synonyms:** *Aureolejeunea* R.M.Schust., *Cyrtolejeunea* A.Evans, *Cystolejeunea* A.Evans, *Euosmolejeunea* (Spruce) Steph., *Leucolejeunea* A.Evans, *Omphalanthus* Lindenb. & Nees, *Omphalolejeunea* (Spruce) Lacout., *Peltolejeunea* (Spruce) Schiffn., *Potamolejeunea* (Spruce) Lacout., *Strepsilejeunea* (Spruce) Schiffn., *Trachylejeunea* (Spruce) Schiffn.

Plants 0.3–2.5 mm wide, green, pale green to grayish to brownish, or yellowish-green, prostrate, vegetative branches *Lejeunea*-type. Stem with ca. 7–24 epidermal cells and ca. 3–46 medullary cells, the cells mostly thick-walled, hyalodermis usually absent (present in sects. *Cheilolejeunea* and *Cyrtolejeunea*); ventral merophytes 2–12 cells wide. Leaves imbricate to contiguous, obliquely to widely spreading, sometimes falcate or squarrose; lobe ovate-orbicular to ovate-oblong, dorsal margin usually arched, entire or crenulate, rarely toothed or lacinate, apex rounded, obtuse, acute, apiculate to short-acuminate; leaf cells isodiametric and rounded to elongate-hexagonal, frequently mammillose and sometimes with a papilla on the dorsal surface, thin-walled to thick-walled, trigones usually produced, small or large, intermediate thickenings 0–2 per cell, rarely more, sometimes absent; ocelli usually absent; oil bodies 1–4(–5) per cell, usually large and coarsely segmented (*Calypogeia*-type or *Leucolejeunea*-type), rarely small and finely segmented (*Jungermannia*-type); lobule ovoid, triangular-ovoid, oblong to rectangular, free margin plane or incurved, with two teeth, the first tooth usually reduced, when well-developed the two teeth paired and very closely associated, second tooth usually well-developed, short or long, unicellular or multicellular; keel arched straight, smooth or crenate to papillose. Underleaves undivided or bifid, small or large, 1–7× stem width, margins usually entire, bases cuneate to rounded to auriculate, insertion line straight to deeply arched. Monoicous or dioicous. Androecia on main stem or on short or long branches, bracteoles restricted to the base of the male shoot or (less frequently) present throughout. Gynoecia on main stem or on short branches, bract lobes entire or toothed margins, apex rounded to acute to apiculate, innovations usually present, pycnolejeuneoid or lejeuneoid; perianths 4–5 keeled or terete, rarely pluriplicate, keels smooth to slightly crenate, beak short or long, sometimes absent. Vegetative reproduction by caducous leaves, caducous leaf lobes or caducous branches.

The present definition of *Cheilolejeunea* follows Ye et al. (2015) and others who showed, based on molecular evidence, that several previously accepted genera of Lejeuneaceae (e.g., *Aureolejeunea*, *Leucolejeunea*, *Cyrtolejeunea*, *Cystolejeunea*, *Omphalanthus*, *Trachylejeunea*) were nested in *Cheilolejeunea*. Fifty-four species and six varieties are accepted here in the Neotropics, or about 20% fewer species than recognized by Bastos (2017). Sixteen species are newly placed in synonymy and four additional ones are reduced to varietal level; one new species, *Cheilolejeunea timboensis* C.J.Bastos & Gradst., and one new variety, *C. rigidula* var. *autoica* C.J.Bastos & Gradst., are described.

The employed species and variety concepts follow Gradstein (1975) and Gradstein & Ilkiu-Borges (2015). Important criteria for the distinction of taxa in neotropical *Cheilole-*

*jeunea* include character states of the stem (with of the ventral merophyte), leaf lobes (margin, apex), lobules (size and shape, teeth), leaf cells (trigone size, papillae), oil bodies (number per cell, size, segmentation; but still unknown in many species!), underleaves (size and shape, depth of incision, apex, margins, bases), innovation type, number of perianth keels, and presence/absence of caducous leaves. Sexuality in neotropical *Cheilolejeunea* varies considerably and has been used as a “minor” taxonomic criterium at species and variety level, and only in combination with other morphological characters, following Bischler (1969) and Gradstein (1975). Twenty-six species are monoicous, twenty are dioicous (including ten probably dioicous, with sexual organs being unknown or known only in part) and seven are monoicous or dioicous (heteroicous). All neotropical sections of *Cheilolejeunea* (see below) have monoicous as well as dioicous species. Variation in sexuality has also been observed in other large genera of Lejeuneaceae, e.g. *Acrolejeunea* (Gradstein 1975), *Ceratolejeunea* (Dauphin 2003), *Cololejeunea* (Pócs et al. 2014), *Lejeunea* (Heinrichs et al. 2013), *Prionolejeunea* (Ilkiu-Borges 2016) and *Thysananthus* (Sukkharak & Gradstein 2014, 2017), and Heinrichs et al. (2013) found evidence for a rather frequent change of the sex system during the history of the genus *Lejeunea*, with a minimum number of changes in other character states.

The genus *Cheilolejeunea* has recently been subdivided into several sections based on integrated morphological and molecular evidence (Ye et al. 2015). Morphologically the sections are rather weakly defined, however, and as a consequence several neotropical species cannot be assigned to sections. Based on this classification the neotropical *Cheilolejeunea* species are arranged in seven sections. Morphologically, the sections are rather weakly defined and as a consequence nine neotropical species cannot be assigned to sections and are classified as “insertae sedis”.

*C. sect. Cheilolejeunea*: *C. adnata*, *C. decursiva*, *C. jamaicensis*, *C. lineata*, *C. schiavoneana*.

*C. sect. Cyrtolejeunea* (A.Evans) Ye et al.: *C. holostipa*, *C. insecta*.

*C. sect. Euosmolejeunea* (Spruce) Ye et al.: *C. savannae*, *C. discoidea*, *C. fragrantissima*, *C. intertexta*, *C. rigidula*, *C. trifaria*.

*C. sect. Leucolejeunea* (A.Evans) Ye et al.: *C. caducifolia*, *C. conchifolia*, *C. uncioba*, *C. xanthocarpa*.

*C. sect. Omphalanthus* (Nees) Ye et al.: *C. aurifera*, *C. baracoensis*, *C. filiformis*, *C. jackii*, *C. ovalis*, *C. paramicola*, *C. quinquecarinata*, *C. tonduzana*.

*C. sect. Strepsilejeunea* (Spruce) Ye et al.: *C. acutangula*, *C. amazonica*, *C. aracaensis*, *C. asperrima*, *C. choachina*, *C. comans*, *C. erostrata*, *C. grosseoleosa*, *C. inflexa*, *C. lobulata*, *C. ornata*, *C. timboensis*, *C. yanoae*.

*C. sect. Trachylejeunea* (Spruce) C.J.Bastos & Gradst., **comb. nov.** (*Lejeunea* subgen. *Trachylejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 180. 1884; *Trachylejeunea* (Spruce) Schiffn.). Characterized by lobules with a pair of closely associated teeth and gynoecea frequently without innovations. Seven species in the Neotropics: *C. acan-*

*thina*, *C. aneogyna*, *C. asperiflora*, *C. grandibracteata*, *C. neblinensis*, *C. papulosa*, *C. polystachya*.

Incertae sedis: *C. beyrichii*, *C. cuspidifera*, *C. lacerata*, *C. laciniata*, *C. laevicalyx*, *C. norisiae*, *C. revoluta*, *C. urubuensis*, *C. valenciae*. The sectional position of these nine species is unclear and needs further study.

**Key to the species of *Cheilolejeunea* in tropical America**

- 1. Underleaves undivided . . . . . 2
- 1. Underleaves bifid . . . . . 16
- 2. Plants very small, ca. 0.4–0.7 mm wide, ventral merophytes 2 cells wide. Underleaves small, distant, orbicular, insertion line straight. Leaf lobes suberect to obliquely spreading. Lobule tooth very long and sharp, consisting of a strongly elongate cell ca. 4× as long as wide . . . . *C. holostipa*
- 2. Plants larger, more than 1 mm wide, ventral merophytes 2–12 cells wide. Underleaves large, contiguous to imbricate, insertion line arched. Leaf lobes widely spreading. Lobule tooth consisting of 1–several short cells . . . . . 3
- 3. Plants producing caducous leaf lobes, stems and branches often denuded. Ventral merophytes 2 cells wide. Brazil . . . . . *C. caduciloba*
- 3. Plants not producing caducous leaf lobes. Ventral merophytes (2–)4–12 cells wide . . . . . 4
- 4. Lobules with a distinct, (1–)2–8 cell long tooth (but tooth sometimes inflexed) . . . . . 5
- 4. Lobules without distinct tooth . . . . . 8
- 5. Ventral margin of leaf lobes revolute. Leaves strongly convex . . . . . 6
- 5. Ventral margin of leaf lobes ± plane. Leaves plane or convex (but not strongly so) . . . . . 7
- 6. Lobules very large, ca. 2/3 of leaf length. Lobule tooth 3–6 cells long, clearly visible. Plants 0.7–1.2 mm wide. U.S.A., Brazil, Paraguay. . . . . *C. conchifolia*
- 6. Lobules smaller, ca. 1/2 of leaf length. Lobule tooth 1(–3) cells long, usually not well visible. Plants larger, 1.3–2.0 mm wide. Widespread . . . . . *C. xanthocarpa*
- 7. Plants pendent, brownish. Lobules 1/3 of leaf length, tooth 5–8 cells long. Underleaves very large, 0.6–0.7 mm wide, insertion line deeply arched. Only known from Cuba . . . . *C. baracoensis*
- 7. Plants creeping, pale-colored. Lobules larger, 1/2 of leaf length, tooth 2–4 cells long. Underleaves 4–5× stem width (0.3–0.5 mm wide), insertion line shallowly curved. Widespread. . . . . *C. uncioba*
- 8. Lobules maximally 1/3 of lobe length, subquadrate-trapezoid. Plants dioicous, yellowish-green to pale brown, never dark brown (former genus *Omphalanthus*) . . . . . 9
- 8. Lobules 2/5–1/2 of lobe length, (sub)rectangular. Plants autoicous, yellowish-green to dark brown (former genus *Aureolejeunea*) . . . . . 13
- 9. Underleaves orbicular or wider than long. Leaf apex rounded. Perianth usually terete and fully smooth, rarely keeled or angled . . . . . (*C. filiformis*) 10

9. Underleaves longer than wide. Leaf apex obtuse to acuminate. Perianth 5-keeled . . . . . 12
10. Perianth terete. Very common . . . . . *C. filiformis* var. *filiformis*
10. Perianth obtusely angled or sharply keeled, not terete. Rare . . . . . 11
11. Perianth obtusely 4-angled . . . . . *C. filiformis* var. *platycoleus*
11. Perianth sharply 5-keeled . . . . . *C. filiformis* var. *wallisii*
12. Leaf apex acuminate. Underleaves undivided to minutely bifid. Rare species, mainly in western Ecuador and the Galapagos Islands, in submontane forests below 1500 m . . . . . *C. jackii*
12. Leaf apex obtuse. Underleaves undivided. Widespread . . . . . *C. ovalis*
13. Leaf cells mammillose-papillose, the cells distinctly elevated and the outer wall strongly thickened, forming a large, tubercle-like papilla. In páramo of the northern Andes . . . . . *C. aurifera*
13. Leaf cells smooth or mammillose, not papillose. In montane forest and páramo . . . . . 14
14. Perianth with 2–5 narrow folds on the ventral surface and 1–3 narrow folds on the dorsal surface. Plants orange-brown to dark brown, ascending to pendent. Ventral merophytes on main stems 6–8 cells wide. In páramo . . . . . *C. paramicola*
14. Perianth sharply 5-keeled, or with 3–4 broadly rounded keels in the upper half (rarely without keels). Plants pale-colored to dark brown, creeping to ascending, not pendent. Ventral merophytes 2–6 cells wide . . . . . 15
15. Ventral merophytes on main stems 4–6 cells wide. Perianth with 3–4 low, rounded keels in the upper half, keels sometimes lacking. In montane forest and subpáramo . . . . . *C. tonduzana*
15. Ventral merophytes 2 cells wide. Perianth sharply 5-keeled. In páramo . . . *C. quinquecarinata*
16. Leaf margins toothed . . . . . 17
16. Leaf margins entire . . . . . 21
17. Underleaf margins toothed. Lobule apex with two long, closely associated teeth. Only known from the type from Peru . . . . . *C. acanthina*
17. Underleaf margins entire. Lobule apex with one tooth . . . . . 18
18. Keel with large papillae . . . . . 19
18. Keel without large papillae . . . . . 20
19. Leaf margins with 3–6 long, lacinate teeth. Underleaves ca. 2× stem width, apices rounded to obtuse. Panama, Cuba . . . . . *C. norisiae*
19. Leaf margins with 1–3 short teeth near apex. Underleaves larger, 3.5–4 × stem width, lobes cuspidate. Rare species from the tepuis of northern Brazil . . . . . *C. cuspidifera*
20. Dorsal leaf margin with coarse, 3–9 cell long teeth. Lobe apex shortly piliferous, terminating in a row of 2–4 cells. Underleaves imbricate, shallowly bifid, to 1/4–1/3 of underleaf length . . . . .  
. . . . . *C. laciniata*
20. Dorsal leaf margin with smaller, 1–2 cell long teeth. Lobe apex rounded to acute, not terminating in a row of cells. Underleaves distant, more deeply bifid, to 1/2 of underleaf length . . . . .  
. . . . . *C. lacerata*

21. Leaf lobes with a conspicuous row of 4–8 ocelli, the ocelli usually yellowish-brown. Amazonia, in the canopy of the rainforest . . . . . *C. urubuensis*

21. Leaf lobes without ocelli . . . . . 22

22. Underleaves shallowly bifid, to maximally 1/5(–1/4) of underleaf length . . . . . 23

22. Underleaves more deeply bifid (when in doubt try both leads) . . . . . 28

23. Plants very small, 0.25–0.45 mm wide. Underleaves 1.5–2.5× stem width, distant, insertion line straight. Leaf lobes suberect to obliquely spreading. Lobule tooth very long and sharp, consisting of a strongly elongate cell ca. 4× as long as wide. Bolivia and southern Brazil . . . . . *C. insecta*

23. Plants larger. Underleaves larger, contiguous to imbricate, insertion line arched. Leaf lobes widely spreading. Lobule tooth shorter . . . . . 24

24. Leaf apex acute-apiculate to acuminate . . . . . 25

24. Leaf apex rounded (to obtuse) . . . . . 26

25. Underleaves longer than wide, bases cuneate. Leaves ovate-lanceolate, apex acuminate, plane. Rare species, mainly in western Ecuador and the Galapagos Islands, in submontane forest below 1500 m . . . . . *C. jackii*

25. Underleaves wider than long, bases rounded. Leaves broadly ovate, apex acute-apiculate, recurved. Rare species in the high Andes, above 2500 m . . . . . *C. asperrima*

26. Ventral merophytes 2 cells wide . . . . . *C. fragrantissima*

26. Ventral merophytes broader, 4–7 cells wide . . . . . 27

27. Underleaf apex strongly recurved. Flagelliform branches usually present . . . . . *C. revoluta*

27. Underleaf apex plane. Flagelliform branches absent . . . . . *C. beyrichii*

28. Lobules globose, strongly swollen, free margin strongly involute. Perianths flat, without beak. Mostly in the West Indies, scattered elsewhere . . . . . *C. lineata*

28. Lobule not globose, swollen or not, free margin plane or incurved. Perianths inflated, with 4–5 smooth keels and with a beak . . . . . 29

29. Lobules strongly narrowed to the apex and decurved, apex almost touching the ventral margin of the lobe. Lobule apex with two tightly associated teeth . . . . . *C. neblinensis*

29. Lobules not decurved. Lobule apex with 1–2 teeth . . . . . 30

30. At least some leaf apices pointed (obtuse, acute, apiculate or acuminate) . . . . . 31

30. All leaf apices broadly rounded . . . . . 46

31. Keel with large, 7–12 µm high, tubercle-like papillae . . . . . 32

31. Keel without papilla or with a low, to maximally 3 µm high, lens-shaped papillae . . . . . 36

32. Lobule apex with two conspicuous, closely associated teeth . . . . . *C. aracaensis*

32. Lobule apex with one tooth . . . . . 33

33. Underleaves 3–5× stem width, bases rounded-cordate, insertion line arched. Plants 1–2 mm wide, autoicous . . . . . *C. inflexa*

33. Underleaves smaller, less than 3× stem width, bases cuneate, insertion line straight. Plants less than 1 mm wide, dioicous . . . . . 34
34. Underleaf lobes with rounded tips . . . . . *C. amazonica*
34. Underleaf lobes with acute tips . . . . . 35
35. Leaf cells with large trigones and with several oil bodies per cell. Eastern and northern Brazil and Ecuador . . . . . *C. ornata*
35. Leaf cells thin-walled, with very small trigones and with one very large oil body per cell. Only known from the type from southeastern Brazil (São Paulo State: Ilha de São Sebastião) . . . . .  
. . . . . *C. grosseoleosa*
36. Ventral merophytes on main stems more than 2 cells wide. [Dorsal leaf surface mammillose, outer cell walls thin. Perianth without keels, or with 3–4 low and broadly rounded keels. Innovations lejeuneoid. Above 2500 m in the Andes] . . . . . *C. laevecalyx*
36. Ventral merophytes 2 cells wide throughout . . . . . 37
37. Underleaf bases ± auriculate. Plants growing below 2000 m. Scattered in tropical America . . .  
. . . . . *C. comans*
37. Underleaf bases cuneate to rounded, not auriculate . . . . . 38
38. Underleaves 1.5–2.5× stem width . . . . . 39
38. Underleaves usually more than 2.5× stem width [when in doubt try both leads] . . . . . 43
39. Leaf apex acute to apiculate. Underleaves longer than wide. Rare species from Brazil and Bolivia . . . . . 40
39. Leaf apex obtuse to subacute. Underleaves as long as wide or wider than long . . . . . 41
40. Lobule tooth formed by 2 cells. Leaf lobes ovate. Bolivia (only known from the type) . . . . .  
. . . . . *C. yanoae*
40. Lobule tooth formed by one cell. Leaf lobes orbicular. Bahia (only known from the type) . . . .  
. . . . . *C. timboensis*
41. Leaf cells mammillose. Trigones well-developed. Lobules never reduced, with one short tooth. Caducous leaf lobes lacking. Widespread . . . . . 41a
41. Leaf cells not mammillose. Trigones lacking or very small. Lobules sometimes reduced, with two very small, paired teeth (teeth very closely side by side and sometimes overlapping). Plants sometimes with caducous leaf lobes. Common in Amazonia, rare elsewhere . . . (*C. aneogyna*) 42
- 41a. Leaf apex mostly obtuse to apiculate, few leaves with rounded tips. Microphyllous branches lacking. Perianth 5-keeled, dorsal keel present. Common in montane forest, 500–4000 m; occasionally found in the canopy of lowland rainforest . . . . . *C. lobulata*
- 41a. Leaf apex mostly rounded, few leaves with obtuse tips. Microphyllous branches present. Perianth 4-keeled, dorsal keel absent. In savannas and flooded forests of Eastern Amazonia from sea level to 120 m . . . . . *C. savannae*
42. Autoicous (but plants often sterile). Innovations lejeuneoid . . . . . *C. aneogyna* var. *aneogyna*
42. Dioicous. Innovations pycnolejeuneoid . . . . . *C. aneogyna* var. *riparia*



43. Leaf cells with small trigones. Dorsal leaf surface smooth, outer cell walls thin. Lobules with 2 long teeth. . . . . *C. grandibracteata*

43. Leaf cells with large, contiguous to confluent trigones. Dorsal leaf surface mammillose-papillose, outer cell walls thickened. Lobules with 0–1 teeth, occasionally with 2 very short teeth. . . 44

44. Lobules without distinct tooth. Perianth without beak. Innovations pycnolejeuneoid. Andes of Venezuela . . . . . *C. erostrata*

44. Lobules with a distinct tooth. Perianth beaked. Innovations lejeuneoid or pycnolejeuneoid . . 45

45. Innovations lejeuneoid. Apices of underleaf lobes rounded to obtuse. Leaves usually strongly convex. Above 2000 m, mostly in the Andes . . . . . *C. choachina*

45. Innovations pycnolejeuneoid. Apices of underleaf lobes acute. Leaves weakly convex. Below 2500 m, very common in Brazil . . . . . *C. acutangula*

46. Ventral merophytes on main stems 3–8 cells wide. Gynoecia without innovations . . . . . 47

46. Ventral merophytes 2 cells wide. Gynoecia with or without innovations . . . . . 50

47. Lobules large, 2/5–1/2 of leaf length, lobule apex with two teeth, the teeth closely associated and often overlapping. Northern Amazonia . . . . . *C. polystachya*

47. Lobules smaller, 1/6–1/3 of leaf length, apex with only one tooth . . . . . 48

48. Lobule tooth short, blunt. Caducous leaves absent. Rare, robust species from Venezuela and Nicaragua . . . . . *C. valenciae*

48. Lobule tooth long and sharp. Caducous leaves present or absent . . . . . 49

49. Plants with upright flagelliform shoots producing small caducous leaves. Dioicous (?). Western Colombia (only known from the type) . . . . . *C. schiavoneana*

49. Plants without upright flagelliform shoots, caducous leaves absent. Autoicous. Jamaica . . . . . *C. jamaicensis*

50. Lobule apex usually with two closely associated teeth, the two teeth often overlapping each other and sometimes inconspicuous (to be studied very carefully). Rare Amazonian species . . 51

50. Lobule apex with only one tooth, never with two teeth . . . . . 52

51. Keel rough by large, tubercle-like papillae. Cells with large trigones. Northern Amazonia . . . . . *C. asperiflora*

51. Keel not with large, tubercle-like papillae. Cells with very small trigones. Central Amazonia. . . . . *C. papulosa*

52. Lobules with a long and sharp tooth. Leaf cells with small trigones . . . . . 53

52. Lobules with a short tooth. Leaf cells with small or large trigones . . . . . 55

53. Plants producing caducous leaf lobes. Dioicous. Widespread in the Neotropics . . . . . *C. adnata* var. *adnata*

53. Plants not producing caducous leaf lobes. Autoicous. Very rare in the Neotropics (but common in the Paleotropics) . . . . . 54

54. Plants 0.4–0.7 mm wide. Leaves obliquely spreading, falcate. Gynoecia with pycnolejeuneoid innovations . . . . . *C. decursiva*
54. Plants larger, 0.7–1.0 mm wide. Leaves widely spreading, not falcate. Gynoecia without innovations . . . . . *C. adnata* var. *autoica*
55. Leaves suberect to obliquely spreading. Plants very small, 0.4–0.6 mm wide. Underleaves 1.5–2× stem width. Trigones minute. Innovations lejeuneoid. Autoicous. . . . . *C. discoidea*
55. Leaves widely spreading. Plants 0.5–2 mm wide. Underleaves 1.5–6× stem width. Trigones small or large. Innovations lejeuneoid or pycnolejeuneoid. Autoicous or dioicous . . . . . 56
56. Underleaves 1.5–3.5× stem width, distant to contiguous. Underleaf bases cuneate to slightly rounded . . . . . 57
56. Underleaves larger, 4–6× stem width, (sub)imbricate. Underleaf bases broadly rounded. . . . . (C. trifaria) 60
57. Monoicous (autoicous or paroicous), always fertile. Innovations pycnolejeuneoid . . . . . 58
57. Dioicous (very rarely autoicous), sterile or fertile. Innovations lejeuneoid . . . . (C. rigidula) 59
58. Leaf cells mammillose-papillose, frequently with a low lenticular papilla. Leaf lobes convex to squarrose. Perianth 4-keeled, dorsal keel absent. Bracteoles present throughout the male spike. In savannas and flooded forests of Eastern Amazonia from sea level to 120 m . . . . . *C. savannae*
58. Leaf cells mammillose only, papilla absent. Leaf lobes flat. Perianth 5-keeled, dorsal keel present. Bracteoles restricted to the base of the male spike. Widespread in the Paleotropics, rare in the Neotropics . . . . . *C. intertexta*
59. Male spikes short, with 2–4 pairs of bracts. Female bract lobes rounded. Dioicous. Common and widespread . . . . . *C. rigidula* var. *rigidula*
59. Male spikes longer, with 4–14 pairs of bracts. Female bract lobes apiculate. Autoicous. Very rare, only known from the type from the central Amazon region of Brazil. . . . . *C. rigidula* var. *autoica*
60. Underleaves usually wider than long, 1.0–1.5× wider than long, rarely orbicular. Autoicous, usually fertile. Very common . . . . . *C. trifaria* var. *trifaria*
60. Underleaves orbicular. Dioicous, mostly sterile. Not common . . . . . *C. trifaria* var. *clausa*

***Cheilolejeunea acanthina*** (Spruce) Gradst. & Ilk.-Borg.

**Description and illustration:** Bastos (2017).

**Distribution:** only known from the type from Peru.

**Comments:** *Cheilolejeunea acanthina* (sect. *Trachylejeunea*) is a very rare Peruvian species that is recognized by: 1) plants probably dioicous (androecia unknown), 0.8–0.9 mm wide, ventral merophytes 2 cells wide; 2) leaf lobe ovate, dorsal margin dentate-laciniate, ventral margin entire or dentate near apex, apex apiculate; 3) leaf cells mammillose and with a large papilla on the dorsal surface, trigones large, intermediate thickenings present; 4) lobules ovoid-rectangular, ca. 1/3 of leaf length, free margin plane or slightly incurved, apex with 2 sharp, closely associated teeth, keel straight, papillose; 5) underleaves broadly ovate to reniform, ca. 2.5–3.0× wider than the stem, bifid to 1/2, margins dentate-lacini-

ate, bases straight to cuneate, insertion line curved; 6) gynoecia on short branches, innovations absent, perianth not observed.

*Cheilolejeunea acanthina* is readily distinguished from all other neotropical *Cheilolejeunea* species by the dentate-laciniate underleaf margins.

***Cheilolejeunea acutangula*** (Nees) Grolle

*Jungermannia acutangula* Nees (*Strepsilejeunea acutangula* [Nees] Schiffn.). Type: Brazil, Minas Gerais, Martius s.n., c. gyn. (lectotype, designated by Gradstein (in press), STR-Nees!; isolectotype, PC-Mont.-MB1668!).

**Heterotypic synonyms:** *Lejeunea kunthiana* Lindenb. (*Strepsilejeunea kunthiana* [Lindenb.] Schiffn.). Type: Brazil, Rio de Janeiro, Gaudichaud s.n. (isotypes, PC-0103866!, PC-0103867!, PC-0103868!). *Lejeunea hieronymii* Spruce (*Strepsilejeunea hieronymii* [Spruce] Steph.), syn. nov. Type: Argentina, prov. Cordoba, Porto Alegre, 5 Febr. 1877, Hieronymus s.n. (isotype, G-00115836!, ster.).

**Description and illustration:** Bastos (2017).

**Distribution:** common in Brazil, scattered elsewhere in tropical America.

**Comments:** *Cheilolejeunea acutangula* (sect. *Strepsilejeunea*) is recognized by: 1) plants autoicous, 0.6–1.0 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, margins entire to crenulate, apex acute, mostly recurved; 3) leaf cells mammillose, trigones large, intermediate thickenings occasionally present, dorsal cell walls uniformly thickened and with a low, lenticular papilla, ventral cell walls thin; 4) lobules ca. 1/3 of leaf length, free margin involute, tooth long, obtuse to acute, keel slightly curved, crenulate by projecting mammillose cells; 5) underleaves ovate-orbicular, 2.5–4.0× stem width, distant to imbricate, bifid to 1/3–1/2, apices acute, sinus V-shaped to U-shaped, bases cuneate to slightly rounded, insertion line curved; 6) androecia on main stem or on short or long branches, with 2–6 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on main stem or on short branches, with 1–2 pycnolejeuneoid innovations, perianth sharply keeled, with a short beak.

*Cheilolejeunea acutangula* approaches *C. lobulata*, but the latter species has smaller underleaves (only 1.5–2× stem width) and obtuse to subacute leaf tips.

***Cheilolejeunea adnata*** (Lehm.) Grolle var. *adnata*

**Description and illustration:** Schuster (1980), Gradstein & Ilkiu-Borges (2009).

**Distribution:** throughout tropical America.

**Comments:** *Cheilolejeunea adnata* var. *adnata* (sect. *Cheilolejeunea*) is a common neotropical taxon that is characterized by: 1) plants dioicous, small, 0.7–1.0 mm wide, stem cells ± thin-walled, hyalodermis present, ventral merophytes 2 cells wide; 2) leaf lobes ovate-orbicular, margins entire but often with rhizoids, apex rounded; 3) leaf cells weakly mammillose, walls with small radiate trigones, intermediate thickenings present or ab-

sent; 4) lobules small, ca. 1/4 of leaf length, bottle-shaped (conspicuously constricted toward the mouth), strongly inflated, free margin involute, tooth very long and sharp, hyaline, keel arched, smooth; 5) underleaves small, ca. 1–2× stem width, ovate to suborbicular, distant, bifid to 1/3–1/2, sinus V-shaped, bases cuneate, insertion line shallowly curved; 6) androecia with bracteoles restricted to the base of the male spike; 7) gynoecia on main stem or on short branches, without or with one short lejeuneoid innovation, bract lobes with entire margins, apex rounded, perianth 4–5 keeled, beak short; 8) vegetative reproduction common, by caducous leaf lobes with marginal rhizoids.

*Cheilolejeunea adnata* var. *adnata* is easily recognized by the long, hyaline lobule tooth, occurrence of rhizoids on leaf margins and vegetative reproduction by caducous leaves. *Cheilolejeunea adnata* var. *adnata* approaches *C. schiavoneana*; for differences see under the latter species.

***Cheilolejeunea adnata* var. *autoica*** Gradst. & Ilk.-Borg.

**Synonyms:** *Cheilolejeunea larsenii* Mizut., syn. nov. (Type: see Shu et al. 2015). *Cheilolejeunea exinnovata* E.W. Jones (syn. fide Shu et al. 2015).

**Description and illustration:** Gradstein & Ilkiu-Borges (2009), Shu et al. (2015, as *C. larsenii*).

**Distribution:** pantropical.

**Comments:** similar to *C. adnata* var. *adnata*, but plants autoicous and caducous leaves usually absent. Shu et al. (2015) treated *Cheilolejeunea adnata* var. *autoica* as a separate species (*C. larsenii*), but we consider that the differences with *C. adnata* are too slight to warrant recognition at the species level. Moreover, we observed morphological overlap between the two varieties in Una Biological Reserve, Bahia, with some autoicous individuals showing vegetative reproduction by caducous leaves and producing rhizoids on leaf margins. We therefore consider that *C. larsenii* is a variety of *C. adnata* as proposed by Gradstein & Ilkiu-Borges (2009).

***Cheilolejeunea amazonica*** C.J.Bastos & C.E.Zartman

**Description and illustration:** Bastos & Zartman (2016).

**Distribution:** only known from the Amazon region of Brazil.

**Comments:** *Cheilolejeunea amazonica* (sect. *Strepsilejeunea*) is a rare Amazonian species that is recognized by: 1) plants dioicous (?), very small, ca. 0.4–0.6 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes triangularly ovate, margins strongly crenulate by projecting cells, apex obtuse to acute, recurved; 3) leaf cells strongly mammillose and with a large papilla on the projecting outer wall, trigones very large, intermediate thickenings occasionally present; 4) lobules ovoid-elongate, 1/3–2/5 of leaf length, free margin involute, tooth short, acute, keel arched, rough by large papillae; 5) underleaves distant, small, ca. 2× stem width, obovate-oblong, bifid to 1/3, apices rounded to truncate, sinus V-shaped, bases cuneate. Gametoecia not seen.

Because of the pointed leaf apex, large trigones, papillose leaf cells and bifid underleaves, *C. amazonica* is considered to be a member of sect. *Strepsilejeunea*. The species closely resembles *C. ornata* and *C. grosseoleosa*, but the underleaf tips in the latter two species are acute (rounded to truncate in *C. amazonica*).

***Cheilolejeunea aneogyna*** (Spruce) A.Evans var. *aneogyna*

**Synonym:** *Cheilolejeunea assurgens* (Spruce) Steph. (fide Bastos 2012c).

**Description and illustration:** Bastos (2012c).

**Distribution:** common and widespread in Amazonia, scattered elsewhere in tropical America.

**Comments:** *C. aneogyna* var. *aneogyna* (sect. *Trachylejeunea*) is a common Amazonian species that is characterized by: 1) plants autoicous, small, 0.8–1.1 mm wide, ventral merophytes two cells wide; 2) leaf lobes ovate-oblong, margins entire, apex rounded, plane; 3) leaf cells mammillose, thin-walled, trigones very small (usually) to medium-sized, intermediate thickenings 1–2 per cell, ocelli occasionally present, 2–3(–4) near the leaf base, larger than adjacent leaf cells (Moura 2010, Bastos 2012c); 4) lobules triangular-ovoid, small, 1/5–1/4 of leaf length, occasionally reduced, free margin involute, apex with two small, tightly associated teeth, keel straight; 5) underleaves distant, small, ca. 1.5–2.5× stem width, ovate to oblong-ovate, sinus V-shaped, bases cuneate, insertion line curved; 6) androecia on main stem or on short branches, with 3–4 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on main stem or on short branches, without innovations (usually) or occasionally with one lejeuneoid innovation, perianths 4-keeled, keels smooth, beak short; 8) vegetative reproduction by caducous leaves.

*Cheilolejeunea aneogyna* var. *aneogyna* closely resembles *C. rigidula*, but differs from the latter in autoicy and usual absence of gynoecial innovations (but plants often sterile), frequent presence of caducous leaves or caducous microphyllous branches, more obscure plant color, leaf cells more thin-walled (trigones usually very small), lobules smaller, to 1/4 of leaf length and sometimes reduced (never reduced in *C. rigidula*), and lobule apex with 2 very small, closely associated teeth. The paired lobule teeth are sometimes difficult to observe because the lobule apex is often incurved and the teeth may be overlapping each other. The occasional presence of ocelli in *C. aneogyna* (never present in *C. rigidula*) is a further difference between the two.

*Cheilolejeunea aneogyna* also approaches *C. polystachya*, but the latter species has broader, 4–6 cell wide ventral merophytes, recurved leaf apices, larger lobules (2/5–1/2 of leaf length) and no caducous leaves (He 2003).

***Cheilolejeunea aneogyna*** var. *riparia* (Steph.) C.J.Bastos & Gradst., **comb. nov.**

*Potamolejeunea riparia* Steph., Sp. Hepat. 5: 639. 1913 (*Cheilolejeunea riparia* [Steph.] M.E.Reiner). Type: Brazil, Amazonas, Rio Negro, Spruce L316 (lectotype, designated here, MANCH-CC 12923!; isolectotype, MANCH-CC 12922).

**Description and illustration:** Reiner-Drehwald (2000, as *Trachylejeunea riparia* [Steph.] M.E.Reiner), Bastos (2017, as *C. riparia*).

**Distribution:** only known from Amazonia.

**Comments:** differs from var. *aneogyna* in being dioicous and gynoecia with pycnolejeuneoid innovations.

*Cheilolejeunea aracaensis* C.J.Bastos et al.

**Description and illustration:** Bastos et al. (2016).

**Distribution:** only known from the Amazon region of Brazil.

**Comments:** *Cheilolejeunea aracaensis* (sect. *Strepsilejeunea*) is a rare Amazonian species that is characterized by: 1) plants autoicous, very small, ca. 0.5–0.6 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-falcate, margins crenulate, apex acute, mostly recurved; 3) leaf cells strongly papillose, with large trigones, intermediate thickenings scarce; 4) lobules ovoid, inflated, small, ca. 1/3 of leaf length, free margin involute, with 2 elongate, closely paired teeth that are often overlapping; 5) underleaves small, ca. 1.5–2.5× stem width, bifid to 1/3–1/2, sinus V-shaped to U-shaped, bases cuneate, insertion line curved; 6) androecia intercalary, with 3–4 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on main stem or on short branches, without innovations, perianths 4-keeled, keels crenulate, beak short, perianth cells smooth, without papillae.

*Cheilolejeunea aracaensis* resembles *C. asperiflora*, but the latter species differs in having rounded leaf tips, short-obtuse lobule teeth that are not overlapping, and papillose perianth cells (Bastos et al. 2016).

*Cheilolejeunea asperiflora* (Spruce) Gradst. & Ilk.-Borg.

**Description and illustration:** Bastos (2017).

**Distribution:** northern Amazonia (Brazil, Venezuela).

**Comments:** *Cheilolejeunea asperiflora* (sect. *Trachylejeunea*) is a rare Amazonian species that is characterized by: 1) plants autoicous, ca. 1 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, slightly falcate, margins crenulate, apex rounded, usually plane, occasionally recurved; 3) leaf cells strongly mammillose, each cell with a large papilla, trigones large, intermediate thickenings occasionally present; 4) lobules ovoid-triangular, small, ca. 1/3 of leaf length, free margin involute, apex with 2 closely associated teeth, the teeth short-obtuse and not overlapping, keel straight to slightly curved, strongly mammillose-papillose; 5) underleaves distant to contiguous, ovate-orbicular, 2.5–3.5× stem width, bifid to 1/3, sinus V-shaped, lobe apices acute, bases cuneate, insertion line curved; 6) androecia on short branches, with 3–4 pairs of bracts, bracteoles pre-

sent throughout the male spike; 7) gynoecia without innovations, perianths 5-keeled, perianth cells papillose.

*Cheilolejeunea asperiflora* resembles *Cheilolejeunea aracaensis*; for differences see under the latter species.

***Cheilolejeunea asperrima*** (Steph.) Grolle

**Description and illustration:** Stephani (1916, as *Taxilejeunea asperrima* Steph.), Bastos (2017), Gradstein (in press).

**Distribution:** tropical Andes (Venezuela, Colombia, Bolivia).

**Comments:** *Cheilolejeunea asperrima* (sect. *Strepsilejeunea*) is a rare Andean species that is characterized by: 1) plants dioicous, 1–1.5 mm wide, ventral merophyte 4–6 cells wide; 2) leaves strongly convex, broadly ovate, apex acute to apiculate, recurved; 3) leaf cells mammillose-papillose, with huge trigones; 4) lobules ca. 1/3 of leaf length, with a sharp tooth; 5) underleaves shallowly bifid (to 1/10–1/5), broad, ca. 5× stem width, apices rounded, sinus acute, bases broadly rounded (but not auriculate) and ± folded, insertion line deeply arched. Androecia and gynoecia not seen.

In general habit *C. asperrima* approaches members of sect. *Omphalanthus* (e.g. *C. filiformis*), but differs from the latter in the leaves with recurved, acute tips, mammillose-papillose leaf cells and very shallowly bifid underleaves (to 1/10–1/5) with rounded apices and broadly rounded bases.

***Cheilolejeunea aurifera*** (R.M.Schust.) W.Ye et al.

**Description and illustration:** Schuster (1987, as *Aureolejeunea aurifera* R.M.Schust.), Gradstein (in press).

**Distribution:** northern Andes, Costa Rica, Dominican Republic.

**Comments:** *Cheilolejeunea aurifera* (sect. *Omphalanthus*) is a rare páramo species that is recognized by: 1) plants autoicous, creeping, ca. 1–1.5 mm wide, glossy brown, ventral merophytes 4 cells wide; 2) leaf lobes convex, margins crenulate, apex rounded, recurved; 3) leaf cells mammillose and crowned by a low lenticular papilla on the outer walls, trigones large, swollen, intermediate thickenings absent; 4) lobules rectangular, 2/5–1/2 of leaf length, apex bluntly lobed or with a 2–3 cells long tooth; 5) underleaves distant to imbricate, large, 4–6× stem width, orbicular to reniform, undivided, apex usually narrowly recurved, bases broadly rounded, insertion line deeply arched; 6) androecia (Schuster 1987) on short branches, with 4–6 pairs of bracts, androecia restricted to the base of the spike; 7) perianths 5-keeled, with 1–2 lejeuneoid innovations.

*Cheilolejeunea aurifera* is very similar to *C. quinquecarinata*, but differs in having mammillose leaf cells crowned by a low lenticular papilla (papilla lacking in *C. quinquecarinata*), crenulate leaf margins and 4-cell wide ventral merophytes (2 cells wide in *C. quinquecarinata*).

*Cheilolejeunea baracoensis* (Mustelier et al.) W.Ye et al.

**Description and illustration:** Reiner-Drehwald et al. (2007, as *Omphalanthus baracoensis* Mustelier et al.).

**Distribution:** only known from Cuba.

**Comments:** *Cheilolejeunea baracoensis* (sect. *Omphalanthus*) is a rare, Cuban endemic that is distinguished by: 1) plants dioicous, 1.2–1.5 mm wide, ventral merophytes 4–6 cells wide; 2) leaf lobes ovate-orbicular, convex, margins entire, ventral margin  $\pm$  plane, apex rounded; 3) leaf cells with large trigones, intermediate thickenings 0–1 per cell; 4) lobules ca. 1/3 of leaf length, ovoid-subrectangular, inflated, free margin involute, tooth 5–8 cells long, mostly curved, keel curved; 5) underleaves imbricate, large, 5–6 $\times$  stem width, suborbicular, undivided, bases broadly rounded, insertion line deeply arched, ca. 175  $\mu$ m deep; 6) gynoecia with one lejeuneoid innovation, innovation usually fertile, perianths terete, beak short (Reiner-Drehwald et al. 2007). Androecia not seen.

*Cheilolejeunea baracoensis* is closely similar to *C. filiformis*, but differs from the latter species in the 5–8-cell long lobule tooth and gynoecia with fertile innovations.

*Cheilolejeunea beyrichii* (Lindenb.) M.E.Reiner

**Description and illustration:** Bastos & Gradstein (2006, as *Cheilolejeunea rupestris* C.J.Bastos & Gradst.), Reiner-Drehwald (2006).

**Distribution:** scattered in tropical America, known from Guatemala, the northern Andes (Venezuela to Ecuador), the Guayana Highland and Brazil.

**Comments:** *Cheilolejeunea beyrichii* (sect. unknown) is recognized by: 1) plants dioicous (?), 1.2–1.6 mm wide, ventral merophytes 4–6 cells wide; 2) leaf lobes convex, ovate-oblong, margins entire, apex obtuse, recurved; 3) leaf cells with large trigones; 4) lobules small, ca. 1/4 of leaf length, free margin involute, tooth short; 5) underleaves imbricate, reniform, 4–6 $\times$  stem width, shortly bifid to 1/5, sinus narrow. Gametoecia not observed.

*Cheilolejeunea beyrichii* is closely similar to *C. fragrantissima*; for differences see under the latter species.

*Cheilolejeunea caducifolia* (Gradst. & Schäf.-Verw.) W.Ye & R.L.Zhu

**Description and illustration:** Gradstein et al. (1993, as *Leucolejeunea caducifolia* Gradst. & Schäf.-Verw.), Bastos & Yano (2006, as *L. caducifolia*).

**Distribution:** southeastern and northeastern Brazil.

**Comments:** *Cheilolejeunea caducifolia* (sect. *Leucolejeunea*) is a characteristic Brazilian species that is recognized by: 1) plants dioicous, 1–2 mm wide, dull pale brown when dry, ventral merophytes 2 cells wide; 2) leaf lobes convex, ovate, margins entire, apex rounded to obtuse, plane to recurved; 3) leaf cells with distinct trigones, intermediate



thickenings occasionally present; 4) lobules large, rectangular, 1/3–1/2 of leaf length, tooth short; 5) underleaves imbricate to contiguous, small, 3–4× stem width, (sub)orbicular, undivided; 6) androecia intercalary on long shoots or on short branches, bracteoles limited to the base of the male spike; 7) gynoecia with one pycnolejeuneoid innovation (perianths not seen); 8) vegetative reproduction by caducous leaves.

*Cheilolejeunea caducifolia* is close to *C. uncioba*, but differs from the latter in the 2-cell wide ventral merophytes, the lobule with a short tooth, and vegetative reproduction by caducous leaves.

***Cheilolejeunea choachina*** (Gottsche) Gradst.

**Synonyms:** *Cheilolejeunea invaginata* R.M.Schust., syn. nov. Type: Venezuela, Tachira, S of Villa Paez, 2480 m, 2 March 1976, R.M. Schuster 76-2056a (holotype, F!). *Strepsilejeunea papulifolia* Steph., syn. nov. Type: Bolivia, Cordillera de Santa Cruz, 1913, Herzog 3915 (holotype, G-00069934!).

**Description and illustration:** Bastos (2016, as *C. invaginata*).

**Distribution:** tropical Andes (Venezuela, Colombia, Bolivia), usually above 2000 m.

**Comments:** *Cheilolejeunea choachina* (sect. *Strepsilejeunea*) is an uncommon Andean species that is recognized by: 1) plants autoicous, ca. 1 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes strongly convex, ovate, apex obtuse to subacute, widely recurved, margins entire; 3) leaf cells mammillose-papillose, with very large, often confluent trigones; 4) lobules ca. 1/3–2/5 of leaf length, free margin plane to slightly incurved and with 1(–2) short teeth, keel straight to slightly arched, crenulate; 5) underleaves distant, obovate, ca. 3–5× stem width, bifid to 1/3–1/2, apices rounded to obtuse to subacute, bases rounded, insertion line curved; 6) androecia intercalary or on short branches, with 4–6 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on main stem or on short branches, with 1–2 lejeuneoid innovations, perianths sharply keeled, beak very short or absent; 8) vegetative reproduction absent.

*Cheilolejeunea coachina* resembles *C. acutangula*, but differs from the latter in the strongly convex leaves with obtuse to subacute tips, lejeuneoid innovations and perianths without or with a very short beak. *Strepsilejeunea papulifolia* and *C. invaginata* are synonyms of *C. choachina*. Stephani (1916) illustrated a long perianth beak in *S. papulifolia*, but this seems to be an error as the perianths in the type material are beakless or with a very short beak.

***Cheilolejeunea comans*** (Spruce) R.M.Schust.

**Description and illustration:** Reiner-Drehwald (1998).

**Distribution:** scattered in tropical America (Argentina, Brazil, Jamaica, Panama, Venezuela).

**Comments:** *Cheilolejeunea comans* (sect. *Strepsilejeunea*) is an uncommon neotropical species that is distinguished by: 1) plants monoicous or dioicous, ca. 0.7–1.0 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, apex broad, rounded to shortly apiculate by 1–2 cells, plane or sometimes recurved; 3) leaf cells with large, swollen trigones (but cell-lumen oval, not angular), smooth or slightly convex, outer wall thin; 4) lobules small, 1/5–1/4 of leaf length, fully inflated, with a short blunt tooth, keel smooth,  $\pm$  straight, forming a wide angle with the ventral margin of the leaf lobe; 5) underleaves ovate-orbicular, 3–4 $\times$  stem width, bifid to 1/3(–1/2) with a rather narrow V-shaped sinus, apices obtuse to acute by one cell, bases auriculate (rarely rounded) with up to 50  $\mu$ m high auricles, insertion line arched; 6) androecia on short branches, with 2–4 pairs of bracts, bracteoles limited to the base of the male spike; 7) gynoecia with 1–2 lejeuneoid innovations, perianths sharply 5-keeled, keels smooth to crenate, beak long.

*Cheilolejeunea comans* is close to *C. acutangula*, but the underleaves bases in the latter species are cuneate, not auriculate, the outer wall of the leaf cells is thickened, and the innovations in *C. acutangula* are pycnolejeuneoid. Because the type material of *C. comans* is purely male, lacking gynoecia, the innovation type of this species cannot be determined on the type specimen.

*Cheilolejeunea conchifolia* (A.Evans) W.Ye & R.L.Zhu

**Description and illustration:** Schuster (1980, as *Leucolejeunea conchifolia* [A.Evans] A.Evans), Bastos & Vilas Bôas-Bastos (2000, as *L. conchifolia*).

**Distribution:** southeastern U.S.A., eastern Brazil (cerrado and caatinga region), Paraguay.

**Comments:** *Cheilolejeunea conchifolia* (sect. *Leucolejeunea*) is distinguished by: 1) plants autoicous or dioicous, 0.7–1.2 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes strongly convex, ovate, margins entire, ventral leaf margin and apex strongly revolute, apex rounded to obtuse; 3) leaf cells strongly mammillose, trigones small, intermediate thickenings scarce, dorsal cell wall thickened, with low, lens-shaped papillae; 4) lobules large, ca. 2/3 of leaf length, ovoid-oblong, free margin arched, plane to slightly incurved, tooth large and very well visible, 3–6 cells long, 2–3 cells wide at base, curved, keel straight, forming a straight line with the ventral leaf margin; 5) underleaves contiguous to imbricate, large, ca. 4 $\times$  stem width, suborbicular, undivided, bases rounded, insertion line curved; 6) androecia on short branches, with 2–4 pairs of bracts, bracteoles limited to the base of the male spike (Schuster 1980); 7) gynoecia on short branches, with one pycnolejeuneoid innovation, perianths 5-keeled, keels smooth.

*Cheilolejeunea conchifolia* resembles *C. xanthocarpa*, but the latter species differs from *C. conchifolia* in larger plant size (more than 1.3 mm wide), larger trigones and shorter lobules (1/2 of leaf length) with a short and rather inconspicuous, 1(–3) cell long tooth. *Cheilolejeunea conchifolia* is presumably autoicous (Schuster 1980) but androecia have not been observed in the South American plants.

*Cheilolejeunea cuspidifera* C.J.Bastos et al.

**Description and illustration:** Bastos et al. (2016).

**Distribution:** only known from the Guyana Highland of northern Brazil.

**Comments:** *Cheilolejeunea cuspidifera* (sect. unknown) is a rare Brazilian species that is recognized by: 1) plants dioicous (?) (androecia not observed), ca. 0.7 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes convex, ovate, margins with 1–3 teeth near the apex, apex acute to acuminate, recurved; 3) leaf cells mammillose-papillose, trigones large, intermediate thickenings absent; 4) lobules small, 1/3–1/4 of leaf length, free margin involute, tooth long and sharp, keel arched, strongly mammillose-papillose; 5) underleaves distant to contiguous, 3.5–4.0× stem width, longer than wide, bifid to 1/2, sinus U-shaped, lobes cuspidate, bases rounded, insertion line curved; 6) gynoecia with one pycnolejeuneoid innovation, perianths 4-keeled, keels crenulate, beak short. Androecia not observed.

*Cheilolejeunea cuspidifera* somewhat resembles the Brazilian *C. lacerata* C.J.Bastos & Gradst., but the latter species differs from *C. cuspidifera* by leaf cells without papillae, underleaf lobes obtuse, not cuspidate, lobule tooth short and blunt, and innovations lejeuneoid.

*Cheilolejeunea decursiva* (Sande Lac.) R.M.Schust.

**Synonym:** *Cheilolejeunea cyrtolejeuneoides* C.J.Bastos & Schäfer-Verw.

**Description and illustration:** Bastos & Schäfer-Verwimp (2017, as *C. cyrtolejeuneoides*).

**Distribution:** pantropical but very rare in the Neotropics (south and southeastern Brazil).

**Comments:** *Cheilolejeunea decursiva* (sect. *Cheilolejeunea*) is characterized by: 1) plants autoicous, very small, 0.4–0.7 mm wide, 2) stem epidermis cells ± thin-walled, hyalodermis present, ventral merophytes 2 cells wide; 3) ventral merophyte two cells wide; 3) leaf lobes ovate, obliquely spreading, ovate-falcate, margins entire, apex rounded; 4) leaf cells thin-walled with small trigones, intermediate thickenings mostly absent, oil bodies 2–3 per cell, coarsely segmented, filling the cell-lumen; 5) lobules large, ca. 1/2 of leaf length, ovoid, strongly inflated, free margin plane to slightly incurved, made up of elongate cells, tooth very long and sharp, curved, hyaline, keel arched; 6) underleaves distant, small, ca. 1.5–2.0× stem width, ovate-orbicular, bifid to 1/3–1/2, sinus acute, apices acute to obtuse, bases cuneate, insertion line curved; 7) androecia on main stem or on short branches, with 2–4 pairs of bracts, bracteoles restricted to the base of the male spike; 8) gynoecia on short branches, with one pycnolejeuneoid innovation, perianths 5-keeled, keels smooth, beak long.

*Cheilolejeunea decursiva* resembles *C. holostipa* and *C. insecta*, but differs from the latter two species in the more deeply bifid underleaves, the somewhat falcate leaves, the stems not zig-zag and the coarsely segmented oil bodies (Bastos & Schäfer-Verwimp 2017).

*Cheilolejeunea discoidea* (Lehm. & Lindenb.) Kachr. & R.M.Schust.

**Synonym:** *Cheilolejeunea myriantha* (Nees & Mont.) R.M.Schust.

**Description and illustration:** Schuster (1980, as *C. myriantha*).

**Distribution:** tropical and subtropical America.

**Comments:** *Cheilolejeunea discoidea* (sect. *Euosmolejeunea*) is recognized by: 1) plants autoicous, very small, ca. 0.5–0.6 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes suberect to obliquely spreading, ovate, margins entire, apex rounded; 3) leaf cells with very thin walls, trigones absent or minute, intermediate thickenings absent; 4) lobules small, ca. 1/3–1/2 of leaf length, ovoid, inflated, free margin involute, tooth short, obtuse, keel arched, smooth to slightly crenulate; 5) underleaves distant, small, ca. 1.5–2.0× stem width, ovate-oblong, bifid to 1/2, sinus acute, bases cuneate, insertion line almost straight; 6) androecia on main stem or on short branches, with 3–12 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia with 1–2 lejeuneoid innovations, perianths obovate, 5-keeled, keels smooth, beak short.

*Cheilolejeunea discoidea* approaches *C. rigidula*, but differs from the latter species in being much smaller, less than 0.6 mm wide, and autoicous. Moreover, the leaves in *C. discoidea* are suberect or obliquely spreading and the cell walls are very thin, without distinct trigones and intermediate thickenings. *Cheilolejeunea discoidea* has been confused with *C. savannae* (see under *C. savannae*).

*Cheilolejeunea erostrata* R.M.Schust.

**Description and illustration:** Bastos (2016).

**Distribution:** only known from the type from the Andes of Venezuela.

**Comments:** *Cheilolejeunea erostrata* (sect. *Strepsilejeunea*) is a very rare Andean species that is recognized by: 1) plants autoicous, rather large, 1.5–1.7 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, margins entire, apex acute to apiculate, recurved; 3) leaf cells mammillose-papillose, trigones large, intermediate thickenings ± absent; 4) lobules ca. 1/2 of leaf length, ovoid-rectangular, free margin involute, tooth very short, indistinct, keel straight to slightly curved; 5) underleaves large, ca. 4–5× stem width, ovate-orbicular, bifid to 1/3, sinus acute, bases rounded (but not auriculate), insertion line deep arched; 6) androecia on short branches, with 3–4 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia with 1–2 pycnolejeuneoid innovations, perianths oblong, 5-keeled, keels smooth, beak absent.

*Cheilolejeunea erostrata* differs from other neotropical members of sect. *Strepsilejeunea* in the large lobules (ca. 1/2 of leaf length) with a very short tooth, the large underleaves with a deeply arched insertion line, and the beakless perianth.

*Cheilolejeunea filiformis* (Sw.) W.Ye et al. var. *filiformis*

**Synonym:** *Lejeunea huanucensis* Gottsche (*Cheilolejeunea huanucensis* [Gottsche] W.Ye et al.), syn. nov. Type: Peru, “in cortice chinae”, Häcker s.n. (lectotype, designated here, G-00064388!; isolectotypes, W-Lindenberg 6265!, 6266!).

**Description and illustration:** Reiner-Drehwald (1993, as *Omphalanthus filiformis* [Sw.] Nees).

**Distribution:** throughout the mountains of tropical America.

**Comments:** *Cheilolejeunea filiformis* var. *filiformis* (sect. *Omphalanthus*) is a very common neotropical-montane taxon that is recognized by: 1) plants dioicous, rather large, 1.8–2.8 mm wide, ascending from the substrate or pendent; (2) stems rigid, of thick-walled cells, ventral merophytes 4–6 cells wide; 3) leaf lobes ovate-orbicular, obliquely to widely spreading, convex, apex broadly rounded, plane or recurved; 3) leaf cells usually mammillose, with large swollen trigones, intermediate thickenings absent; 4) lobules shortly trapezoidal, 1/4–1/3 of leaf length, free margin plane or somewhat incurved, with-out or with a very short tooth, keel arched; 5) underleaves imbricate, large, ca. 4–7× stem width, rounded to reniform, undivided, apex plane or recurved, bases rounded, insertion line deeply arched; 6) androecia on main stem or on short branches, with 2–5 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on short branches, with one sterile lejeuneoid innovation, perianths terete, beak short to inconspicuous.

Based on perianth shape, three varieties are recognized in *C. filiformis*, var. *filiformis* with a terete perianth, var. *platycoleus* with an obtusely 4-angled perianth, and var. *wallisii* with a sharply 5-keeled perianth. The var. *filiformis* is a very common, but the other two varieties are rare and largely restricted of the northern Andes.

*Cheilolejeunea huanucensis* is a phenotype of *C. filiformis* with recurved leaf and under-leaf apex.

*Cheilolejeunea filiformis* var. *platycoleus* (Herzog) W.Ye et al.

Fig. 1A

**Description and illustration:** Herzog (1955).

**Distribution:** tropical Andes (Colombia to Bolivia).

**Comments:** A rare Andean-Costa Rican taxon characterized by the obtusely 4-angled perianth. *Cheilolejeunea filiformis* var. *platycoleus* can be confused with *C. tonduzana*, but the latter species is autoicous (*C. filiformis* is dioicous) and the lobules in *C. tonduzana* are more elongate, 2/5–1/2 of lobe length.

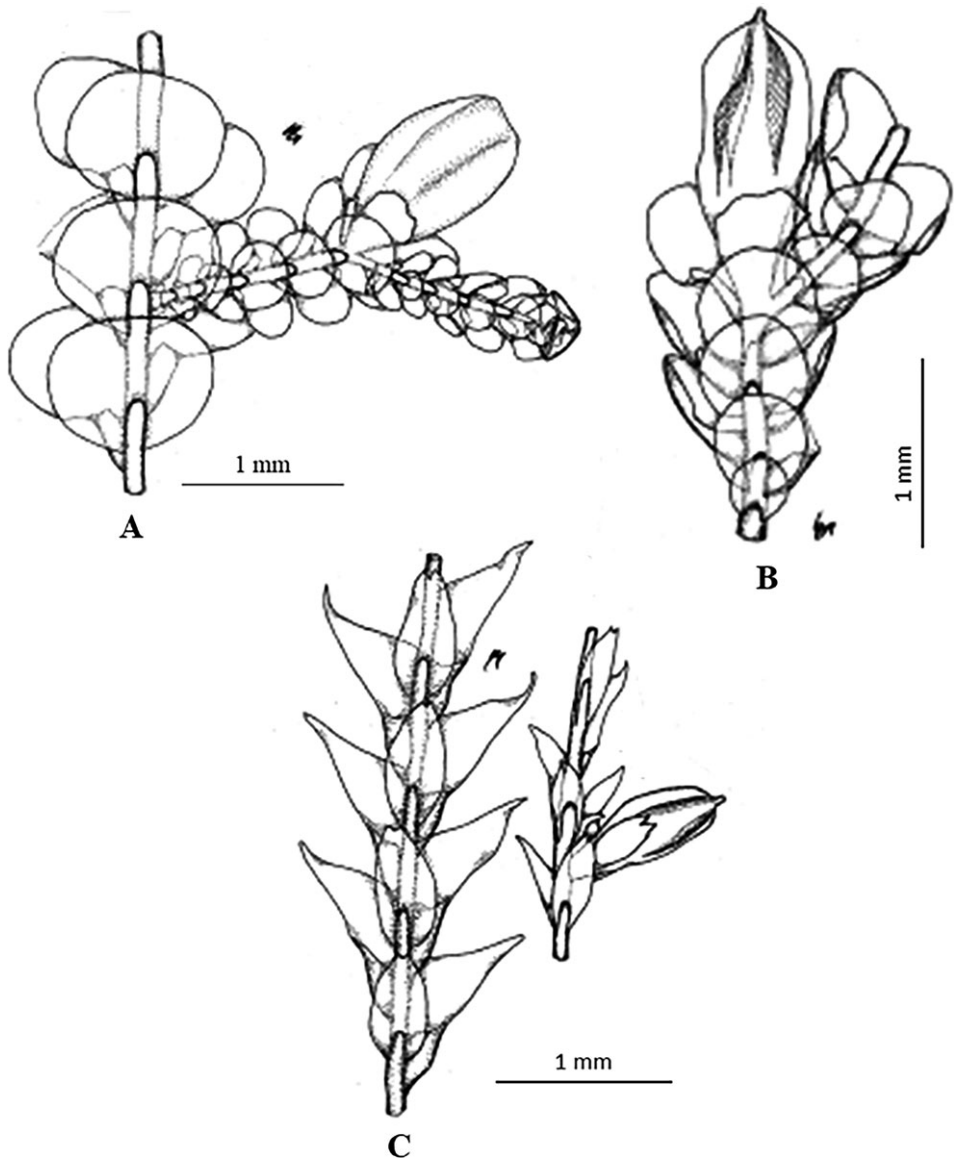
*Cheilolejeunea filiformis* var. *wallisii* (J.B.Jack & Steph.) W.Ye et al.

Fig. 1B

**Description:** Jack & Stephani (1892, as *Lejeunea wallisii* J.B.Jack & Steph.).

**Distribution:** northern Andes, Mexico.

**Comments:** A rare Andean-Mexican taxon characterized by the sharply 5-keeled perianth. In the shape of the perianth *C. filiformis* var. *wallisii* may be confused with *C. ovalis*



**Fig. 1.** A. *Cheilolejeunea filiformis* var. *platycoleus*, habit in ventral view. B. *Cheilolejeunea filiformis* var. *wallisii*, habit in ventral view. C. *Cheilolejeunea jackii*, habit in ventral view. A from the holotype (Colombia, Killip 7301, JE). B from the holotype (Colombia, Wallis s.n., G). C from Galápagos Islands, van der Werff 2362 (GOET). Drawings by Milena Malonek.

and *C. quinquecarinata*, but *C. ovalis* differs in having longer than wide underleaves (as long as wider or wide than long in *C. filiformis*) and an obtuse to subacute leaf apex (rounded in *C. filiformis*), whereas *C. quinquecarinata* differs in autoicous sexuality (dioicous in *C. filiformis*), ventral merophytes only 2 cells wide and lobules being more elongate,  $2/5$ – $1/2$  of lobe length.

***Cheilolejeunea fragrantissima*** (Spruce) R.M.Schust.

**Description and illustration:** Bastos (2017).

**Distribution:** northern South America, Dominican Republic.

**Comments:** *Cheilolejeunea fragrantissima* (sect. *Euosmolejeunea*) is a rare neotropical species that is distinguished by: 1) plants autoicous, to 1.6 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-oblong, margins entire, apex rounded, usually plane; 3) leaf cells mammillose, with large, confluent trigones and a smooth cuticle; 4) lobules very small,  $1/5$ – $1/6$  of leaf length, with a long and sharp tooth; 5) underleaves reniform,  $4$ – $6\times$  stem width, bifid to maximally  $1/5$ , bases cuneate to rounded; 6) androecia with  $8$ – $9$  pairs of bracts, bracteoles present throughout the male spike; 7) gynoecia with one lejeuneoid innovation, perianths obovate, 5-keeled, keels smooth, beak short.

*Cheilolejeunea fragrantissima* is very similar to *C. beyrichii*, but the ventral merophytes in the latter species are broader,  $4$ – $6$  cells wide, the leaf apex in *C. beyrichii* is obtuse and recurved, and the lobule tooth is short and blunt.

***Cheilolejeunea grandibracteata*** Steph.

**Synonym:** *Cheilolejeunea gottscheana* C.J.Bastos ( $\equiv$  *Strepsilejeunea lindenbergii* Steph.), syn. nov. (Type: see Bastos 2012b, 2017).

**Description and illustration:** Bastos (2012b).

**Distribution:** only known from southeastern Brazil.

**Comments:** *Cheilolejeunea grandibracteata* (sect. *Trachylejeunea*) is a rare Brazilian species that is characterized by: 1) plants dioicous (?),  $0.7$ – $0.8$  mm wide, ventral merophytes 2 cells wide; 2) leaves slightly convex, ovate, margins entire, apex narrowly rounded to obtuse, mostly recurved; 3) leaf cells with small trigones, intermediate thickenings  $\pm$  absent; 4) lobules small,  $1/4$ – $1/3$  of leaf length, ovoid, inflated, free margin plane to involute, with 2 long, closely associated, curved teeth, keel arched; 5) underleaves distant, small,  $2.5$ – $3\times$  stem width, ovate-orbicular, bifid to  $1/2$ , sinus acute, apices obtuse, bases cuneate, insertion line curved; 6) gynoecia on a short branch, with one lejeuneoid innovation, perianths keeled, keels smooth, beak short. Androecia not observed.

The distinctive characters of *C. grandibracteata* are the narrowly rounded to obtuse, recurved leaf apex, the small distant underleaves and the lobules with two long and sharp, paired teeth (like in members of the former genus *Trachylejeunea*). The species resembles *C. neblinensis* in the narrowly rounded to obtuse and usually recurved leaf apex, but *C.*

*neblinensis* clearly differs from *C. grandibracteata* in having decurved lobules, being strongly narrowed to the apex and curved towards the keel, and leaf cells with large trigones.

*Cheilolejeunea gottscheana* ( $\equiv$  *Strepsilejeunea lindenbergii*) is morphologically identical to *C. grandibracteata* and a synonym of the latter.

***Cheilolejeunea grosseoleosa*** C.J.Bastos & Schäf.-Verw.

**Description and illustration:** Bastos & Schäfer-Verwimp (2017).

**Distribution:** only known from the type from southeastern Brazil (São Paulo state: Ilha de São Paulo).

**Comments:** *Cheilolejeunea grosseoleosa* (sect. *Strepsilejeunea*) is a rare Brazilian species that is recognized by: 1) plants dioicous (?), very small, ca. 0.37–0.47 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, falcate, margins crenulate, apex acute to shortly apiculate, mostly recurved; 3) leaf cells mammillose, each cell with a large papilla, trigones very small, intermediate thickenings scarce, oil bodies one per cell, very large, coarsely segmented; 4) lobules small, up to 1/3 of leaf length, strongly inflated, ovoid, free margin involute, tooth short and acute, keel arched, strongly papillose; 5) underleaves distant, very small, 1.5–2.0 $\times$  stem width, ovate-orbicular, bifid to 1/2, apices acute, bases cuneate, insertion line curved; 6) gynoecia with one pycnolejeuneoid innovation, perianths 5-keeled, beak short. Androecia not seen.

*Cheilolejeunea grosseoleosa* is close to *C. lobulata* and *C. ornata*, but *C. lobulata* differs in having obtuse tips of leaves and underleaves, larger trigones and smaller papillae, whereas *C. ornata* differs in larger trigones and leaf cells with several oil bodies per cell.

***Cheilolejeunea holostipa*** (Spruce) Grolle & R.L.Zhu

**Description and illustration:** Evans (1903, as *Cyrtolejeunea holostipa* [Spruce] A.Evans), Grolle et al. (2001).

**Distribution:** scattered throughout tropical America.

**Comments:** *Cheilolejeunea holostipa* (sect. *Cyrtolejeunea*) is a rather common neotropical species that is easily recognized by: 1) plants autoicous, very small, ca. 0.4–0.7 mm wide; 2) stems zig-zag, epidermis cells  $\pm$  thin-walled, hyalodermis present, ventral merophytes 2 cells wide; 3) leaf lobes suberect to obliquely spreading, strongly convex, ovate-orbicular, margins entire, apex rounded; 4) leaf cells with small trigones, intermediate thickenings occasionally present, oil bodies 2–5 per cell, small, finely granular; 5) lobules large, 1/2 of leaf length, ovoid, strongly inflated, free margin plane to slightly incurved, tooth very long and sharp, falcate, hyaline, keel arched, smooth; 6) underleaves distant, very small, 1.5–2.0 $\times$  stem width, orbicular, undivided, bases cuneate, insertion line slightly curved; 7) androecia on a short branch, with 3–4 pairs of bracts, bracteoles restricted to the base of the male spike; 8) gynoecia on elongate shoots, with one short pycnolejeuneoid innovation, perianths sharply 5-keeled in the upper half, beak long.



By the very small plants with suberect to obliquely spreading leaves, zig-zag stems, large lobules with a very long, falcate tooth, leaf cells with small trigones and finely granular oil bodies, as well as small, orbicular, undivided underleaves, *C. holostipa* cannot be confused with any other neotropical *Cheilolejeunea* species except perhaps *C. insecta*. However, the latter species has shallowly bifid underleaves and bracteoles present throughout the male spike (Grolle et al. 2001).

***Cheilolejeunea inflexa*** (Lehm.) Grolle

**Description and illustration:** Gradstein & Ilkiu-Borges (2009), Ye & Zhu (2009), Bastos (2016).

**Distribution:** scattered in tropical America.

**Comments:** *Cheilolejeunea inflexa* (sect. *Strepsilejeunea*) is a characteristic neotropical-montane species that is distinguished by: 1) plants autoicous, more than 1 mm wide, ventral merophytes 2 cells wide; 2) leaves convex, ovate, margins crenulate, apex sharply acute-acuminate, recurved; 3) leaf cells on the dorsal leaf surface and keel mammillose and with a huge, rounded papillae, the papilla about half the diameter of the cell (or more), trigones large, intermediate thickenings occasionally present; 4) lobules small, ca. 1/2 of leaf length, ovoid, inflated, free margin involute, tooth acute, keel arched, strongly papillose; 5) underleaves (sub)imbricate, large, 3–5× stem width, bifid to 1/3, tips and sinus acute, bases cordate to rounded, insertion line arched; 6) androecia intercalary on long shoots or on a short branch, with 2–3 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on a short branch, with one pycnolejeuneoid innovation, perianths 5-keeled, keels smooth to crenulate, beak short.

*Cheilolejeunea inflexa* is unmistakable in having a recurved, acute-acuminate leaf apex, bifid underleaves with a cordate base, and the leaf keel with huge papillae, each papilla measuring about half the diameter of the cell lumen (or more).

***Cheilolejeunea insecta*** Grolle & Gradst.

**Description and illustration:** Grolle et al. (2001).

**Distribution:** subtropical South America (Bolivia, southern Brazil).

**Comments:** *Cheilolejeunea insecta* (sect. *Cyrtolejeunea*) is characterized by: 1) plants dioicous, very small, 0.25–0.45 mm wide, stem epidermis cells ± thin-walled, hyalodermis present, ventral merophytes 2 cells wide; 2) leaf lobes suberect to obliquely spreading, obovate, margins entire, apex rounded, ± decurved; 3) leaf cells with small to large trigones, intermediate thickenings ± absent; 4) lobules large, ca. 1/2–2/3 of leaf length, ovoid, strongly inflated, free margin involute, plane at apex, tooth very long and sharp, falcate, hyaline, keel arched, smooth; 5) underleaves distant, small, 1.5–2.5× stem width, orbicular, short-bifid to 1/10–1/5, bases cuneate, insertion line slightly curved to straight; 6) androecia on main stem or a long branch, usually intercalary, with 2–3 pairs of bracts, bracteoles present throughout the male spike; 7) gynoecia on main stem or a short branch,

with 1–2 pycnolejeuneoid innovation, perianths 5-keeled, keels smooth, beak 5–10 cells long (Grolle et al. 2001).

*Cheilolejeunea insecta* closely resembles *C. holostipa*, but differs from the latter species in the short-bifid underleaves (bifid to 1/10–1/5 of underleaf length) and the presence of bracteoles throughout the male spike.

*Cheilolejeunea intertexta* (Lindenb.) Steph.

**Description and illustration:** Mizutani (1982), Bastos (2012a).

**Distribution:** pantropical but rare in tropical America.

**Comments:** *Cheilolejeunea intertexta* (sect. *Euosmolejeunea*) is a widespread pantropical species that is recognized by: 1) plants paroicous, occasionally autoicous, very small, 0.5–0.8 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes widely spreading, ovate, margins entire, apex rounded; 3) leaf cells mammillose, thin-walled, trigones small, intermediate thickenings occasionally present; 4) lobules small, ca. 1/3 of leaf length, ovoid, inflated, free margin involute, tooth short, obtuse, keel straight to slightly arched, smooth to slightly crenulate; 5) underleaves distant, small, ca. 2.0–2.5× stem width, ovate-orbicular, bifid to 1/2, sinus acute, bases cuneate to rounded, insertion line curved; 6) androecia usually below the gynoecia, occasionally on short separate branches, with 2–3 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia with one pycnolejeuneoid innovation, perianths obovate, 5-keeled, keels smooth, beak short.

*Cheilolejeunea intertexta* is the only neotropical *Cheilolejeunea* species with paroicous sexuality. The species resembles *C. discoidea* and *C. savannae*, but the latter two species are autoicous, never paroicous. Moreover, *C. savannae* has convex to squarrose leaf lobes, mammillose-papillose cells with thickened walls, a 4-keeled perianth and male bracteoles throughout the male spike, whereas *C. discoidea* differs in having suberect to obliquely spreading leaves, smaller underleaves (less than 2× stem width) and lejeuneoid innovations.

*Cheilolejeunea jackii* (Prantl) W.Ye et al.

Fig. 1C

**Distribution:** Bolivia, Ecuador, Nicaragua; the record from Peru is erroneous (Gradstein in press).

**Comments:** *Cheilolejeunea jackii* (sect. *Omphalanthus*) is a submontane Andean species that is rather common in the western foothills of the Ecuadorian Andes and the Galápagos Islands. The species is readily distinguished by: 1) plants dioicous (but male and female plants sometimes growing mixed), growing long-pendent, pale green to yellowish-green, ventral merophytes 4–6 cells wide; 2) leaves ovate-lanceolate, obliquely spreading, margins entire, apex acuminate; 3) leaf cells ± mammillose, trigones distinct, intermediate thickenings absent; 4) lobules small, 1/4–1/3 of leaf length, trapezoid, free margin involute, tooth reduced, keel straight, smooth; 5) underleaves narrowly oblong, 2–3× longer

than wide, apex minutely bifid or undivided, bases cuneate, insertion line deeply arched. Gametoecia similar to those of *C. ovalis*.

*Cheilolejeunea jackii* is close to *C. ovalis*, but differs from the latter species in the acuminate leaf tips (obtuse to subacute in *C. ovata*) and more strongly elongate underleaves, with undivided to slightly bifid apex.

***Cheilolejeunea jamaicensis* Steph.**

**Description and illustration:** Bastos (2017).

**Distribution:** only known from Jamaica.

**Comments:** *Cheilolejeunea jamaicensis* (sect. *Cheilolejeunea*) is a rare Jamaican species that is recognized by: 1) plants autoicous, 0.9–1.2 mm wide, stem cells ± thick-walled, ventral merophytes 3–4 cells wide; 2) leaves ovate, apex rounded, margins entire; 3) leaf cells with large, bulging trigones, which are touching each other (but without becoming confluent), intermediate thickenings scarce; 4) lobules ca. 1/4–1/3 of leaf length, tooth very long, hyaline; 5) underleaves distant, small, ca. 1.5–2.0× stem width, orbicular, bifid to 1/3, bases cuneate; 6) androecia on main stem or on short branches, with 2–5 pairs of bracts, bracteoles limited to the base of the male spike; 7) gynoecia without true innovations, but sometimes with pseudo-innovations (= subgynoecial *Lejeunea*-type branches), bract lobes acute to apiculate, perianths obovate, sharply keeled, with a short beak.

*Cheilolejeunea jamaicensis* is close to *C. adnata*, especially its var. *autoica*, but differs from the latter in the thicker, fleshy stems without hyalodermis, the 3–4 cells wide ventral merophytes, the leaf cells with large bulging trigones and the female bract lobes with an acute to shortly apiculate apex.

***Cheilolejeunea lacerata* C.J.Bastos & Gradst.**

**Description and illustration:** Bastos & Gradstein (2006).

**Distribution:** only known from the type from Brazil.

**Comments:** *Cheilolejeunea lacerata* (sect. unknown) is a rare Brazilian species that is characterized by: 1) plants autoicous, 0.7–1.0 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, margins irregularly toothed by triangular teeth, the teeth 2 cells long and 2–3 cells wide at base, apex rounded to acute, usually recurved; 3) leaf cells strongly mammillose, trigones large, intermediate thickenings scarce, oil bodies very large, 1–2 per cell, coarsely segmented; 4) lobule ca. 1/3 of leaf length, ovoid, inflated, free margin involute, tooth short and blunt, keel arched, crenulate; 5) underleaves distant, ovate-orbicular, ca. 2× stem width, bifid to 1/2, sinus V-shaped, bases cuneate to rounded, insertion line curved; 6) androecia on short branches, with 2–3 pairs of bracts, bracteoles present throughout the male spike; 7) gynoecia with one lejeuneoid innovation, perianths 5-keeled, beak short.

*Cheilolejeunea lacerata* approaches *C. laciniata* but the latter species differs in the much more strongly toothed leaf margins, the piliferous leaf apex, less deeply bifid underleaves and strongly lacinate perianth keels.

*Cheilolejeunea laciniata* D.F.Peralta & M.E.Reiner

**Description and illustration:** Peralta & Reiner-Drehwald (2013).

**Distribution:** only known from the type from Minas Gerais, Brazil.

**Comments:** *Cheilolejeunea laciniata* (sect. unknown) is a rare Brazilian species that is characterized by: 1) plants autoicous, very small, 0.4–0.7 mm wide, ventral merophytes 2 cells wide, all stem cells thick-walled; 2) leaf lobes ovate, highly asymmetrical, dorsal leaf margin strongly arched and irregularly dentate-lacinate, the teeth (2–)3–9 cells long and 2–3 cells wide at base, ventral leaf margin slightly curved and  $\pm$  entire, leaf apex shortly piliferous, terminating in a row of 2–4 cells, often recurved; 3) leaf cells mammillose (but without papilla), trigones large, intermediate thickenings lacking; 4) leaf lobules triangular-ovoid, ca. 1/3–1/5 of leaf length, free margin incurved, tooth short,  $\pm$  falcate, keel arched, crenulate; 5) underleaves imbricate to contiguous, large, ca. 3–4 $\times$  stem width, wider than long, reniform to suborbicular, bifid to 1/4–1/3, sinus V-shaped to U-shaped, bases cuneate, insertion line curved; 6) androecia on short branches, with 2–5 pairs of bracts, bracteoles present throughout the male branches (see comment below); 7) gynoecia on main stem or on short branches, with one lejeuneoid innovation, perianths 5-keeled, keels irregularly lacinate above, beak 5–6 cells long (Peralta & Reiner-Drehwald 2013).

By the very small, autoicous plants with longly dentate-lacinate dorsal leaf margins, piliferous leaf tips, shallowly bifid underleaves and lacinate perianth keels, this species is unmistakable. Peralta & Reiner-Drehwald (2013) described the male bracteoles as being restricted to the base of the male branches but in the illustrations the male bracteoles are present throughout the branches.

*Cheilolejeunea laevicalyx* (J.B.Jack & Steph.) Grolle

**Description and illustration:** Zhu (2006).

**Distribution:** northern Andes, above 2500 m.

**Comments:** *Cheilolejeunea laevicalyx* (sect. unknown) is an uncommon Andean species that is distinguished by: 1) plants autoicous, 1.0–1.6 mm wide, ventral merophytes on main stems (2–)3–4 cells wide; 2) leaf lobes convex, ovate, margins entire, apex obtuse to acute, usually broadly recurved; 3) leaf cells mammillose, smooth, trigones small, intermediate thickenings absent; 4) lobules ovate-oblong, 1/3–2/5 of leaf length, strongly inflated, free margin plane, tooth usually indistinct, keel straight to slightly curved; 5) underleaves large, 3–6 $\times$  stem width, suborbicular,  $\pm$  longer than wide, bifid to 1/4–1/3, apices rounded, bases cuneate to rounded, insertion line arched; 6) androecia on main stem or on short branches, with 1–3 pairs of bracts, bracteoles restricted to the base of the

male spike; 7) gynoecia with 1–2 lejeuneoid innovations, perianths terete or slightly keeled with 3–4 short, rounded to obtuse keels, beak absent or rudimentary (based on Zhu 2006).

*Cheilolejeunea laevicalyx* approaches *C. choachina*, but the latter species has more strongly convex leaves, much larger trigones and sharply keeled perianths. Both species occur in the high Andes above 2000 m.

***Cheilolejeunea lineata*** (Lehm. & Lindenb.) Schiffn.

**Description and illustration:** Evans (1906, as *Cystolejeunea lineata* [Lehm. & Lindenb.] A.Evans), Gradstein & Ilkiu-Borges (2009).

**Distribution:** West Indies, northern South America, southeastern Brazil, at low elevations (below 1000 m).

**Comments:** *Cheilolejeunea lineata* (sect. *Cheilolejeunea*) is a very distinct neotropical species that is characterized by: 1) plants dioicous, rather robust, 1.5–2.5 mm wide, sometimes pendent, stem epidermis cells  $\pm$  thin-walled, hyalodermis present, ventral merophytes 2 cells wide; 2) leaf lobes wide-spreading, convex, ovate-oblong, apex rounded to obtuse-apiculate, margins entire, sinuate; 3) leaf cells mammillose, outer wall thickened and with a low lens-shaped papilla, trigones large, swollen, intermediate thickenings  $\pm$  absent, oil bodies very large, 2–3 per cell, coarsely segmented; 4) lobules ovoid to ball-shaped, ca. 1/3 of leaf length, free margin strongly involute-inrolled, tooth obtuse, usually invisible due to inrolled free margin, keel arched; 5) underleaves distant, small, ca. 2 $\times$  stem width, suborbicular, bifid to 1/3, apices obtuse, bases cuneate to rounded, insertion line curved; 6) androecia on main stem or on short branches, with 4–5 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on very short or elongate branches, without innovations, perianths flattened, without beak; 8) vegetative reproduction by caducous leaf lobes.

By the ball-shaped lobules with strongly inrolled free margin, the mammillose leaf cells with large, bulging trigones and a lens-shaped papilla on the outer surface, the small, bifid underleaves with obtuse apices, the gynoecia without innovations and the flat perianths without beak, this species cannot be confused with any other member of the genus *Cheilolejeunea*. The lobules of *C. lineata* somewhat resemble those of *Anoplolejeunea conferta* (Spreng.) A.Evans, but the latter species is a smaller plant (1.0–1.5 mm wide) with undivided underleaves, small trigones and 5-keeled perianths with innovations.

***Cheilolejeunea lobulata*** (Lindenb.) Gradst. & C.J.Bastos, **comb. nov.**

*Lejeunea lobulata* Lindenb., Syn. Hepat. 353. 1845 (*Strepsilejeunea lobulata* [Lindenb.] Steph.). Type: St. Kitts (“St. Christopher”), Breutel s.n. (isotype, G-00069933! c. andr.).

**Heterotypic synonyms:** *Cheilolejeunea aciculifera* R.M.Schust., syn. nov. Type: Jamaica, trail to Caledonia peak, R.M. Schuster 67-125e (holotype, F!). *Cheilolejeunea herzogiana* Steph., syn. nov. Type: Bolivia, Cerro Pampalargo bei Vallegrande, 2220 m,

Herzog 4139 (holotype, G-00112344!). *Cheilolejeunea nana* R.M.Schust., syn. nov. Type: Venezuela, Estado Tachira, S. of Villa Paez, 2560 m, 2 March 1976, R.M. Schuster 76-2061b (holotype, F!). *Cheilolejeunea oncophylla* (Ångstr.) Grolle & M.E.Reiner (*Lejeunea oncophylla* Ångstr.), syn. nov. Type: see Grolle & Reiner-Drehwald (1997). *Strepsilejeunea obtusistipula* Steph., syn. nov. Type: Bolivia, “Cuchicancha (3000 m)”, Herzog 4164 (holotype, G-00069931!).

**Description and illustration:** Grolle & Reiner-Drehwald (1997, as *C. oncophylla*).

**Distribution:** rather widespread in tropical America, but apparently rare in the West Indies.

**Comments:** *Cheilolejeunea lobulata* (sect. *Strepsilejeunea*) is characterized by: 1) plants heteroicous (usually autoicous, sometimes dioicous), rather small, 0.45–1.0 mm wide, ventral merophytes 2 cell wide; 2) leaf lobes convex, ovate, margins entire or crenulate, apex mostly obtuse, sometimes rounded or bluntly apiculate, plane or recurved; 3) leaf cells mammillose, trigones large, intermediate thickenings occasionally present, dorsal cell walls uniformly thickened and frequently with a low, lenticular papilla, ventral cell wall thin, oil-bodies 1(–4) per cell, coarsely segmented; 4) lobules ovoid-elongate, ca. 1/3–2/5 of leaf length, never reduced, inflated, free margin involute, tooth long and sharp, keel arched, crenate; 5) underleaves distant, small, 1.5–2.5× stem width, ovate-obovate, deeply bifid to 1/2–2/3, sinus acute, apices narrowly rounded to obtuse, bases cuneate, insertion line curved; 6) androecia on short branches, with 2–3 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on long or short branches, with one pycnolejeuneoid innovation, perianths sharply 5-keeled; 8) vegetative reproduction occasionally present, by caducous leaf lobes and cladia (Grolle & Reiner-Drehwald, 1997 as *C. oncophylla*).

*Cheilolejeunea lobulata* was usually called *C. oncophylla*, but the name *C. lobulata* has priority. Grolle (1979) treated *C. lobulata* (= *Strepsilejeunea lobulata*) as a synonym of *C. acutangula*, but examination of the type material of *C. lobulata* revealed that the tips of leaves and underleaves are obtuse and the underleaves only 2× wider than stem, like in *C. oncophylla*. In *C. acutangula* the tips of leaves and underleaves are acute and the underleaves are larger, 2.5–4× stem width. *Cheilolejeunea lobulata* is also close to *C. ornata*, but the latter species has leaf cells with a very large papilla on the dorsal leaf surface and keel (see under *C. ornata*). In *C. oncophylla* the leaf cells have low, lenticular papilla on the dorsal leaf surface and keel, or lack a papilla.

*Cheilolejeunea herzogiana* and *C. nana* are female, unisexual populations of *C. lobulata*, *C. aciculifera* is a sterile population with very large, confluent trigones and *Strepsilejeunea obtusistipula* is a phenotype with strongly convex leaves and recurved leaf apices. The latter plants resemble *C. choachina*, but the underleaves in *C. choachina* are larger (3–4× stem width) and the innovations lejeuneoid.

*Cheilolejeunea neblinensis* Ilk.-Borg. & Gradst.

**Description and illustration:** Ilkiu-Borges & Gradstein (2008).

**Distribution:** northern Amazonia (Brazil, Venezuela, Colombia) and Bahia (Brazil).

**Comments:** *Cheilolejeunea neblinensis* (sect. *Trachylejeunea*) is an Amazonian species that is characterized by: 1) plants dioicous, 8.0–1.0 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-oblong, convex, margins entire, apex rounded to subacute; 3) leaf cells mammillose, trigones large, 0–1 intermediate thickenings per cell; 4) lobule triangular-ovoid, ca. 1/2–2/3 of leaf length, strongly narrowed to the apex and decurved towards the keel, free margin plane, apex with a pair of sharp teeth, keel arched, crenulate, sometimes with enlarged cells; 5) underleaves contiguous to imbricate, 3.0–3.5× stem width, suborbicular to reniform, bifid to 1/3, sinus acute, bases cuneate, insertion line curved; 6) androecia on a short branch, with 2 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia with 1–2 pycnolejeuneoid innovations, perianths 5-keeled, keels smooth, beak short.

*Cheilolejeunea neblinensis* is readily recognized by the triangular-ovoid, decurved lobule, which is strongly narrowed to the apex and curved towards the keel, and the presence of a pair of sharp teeth at the lobule apex. A further characteristic feature, seen in the type specimen from Cerro de la Neblina, are the enlarged cells along the lobule keel (Ilkiu-Borges & Gradstein 2008). In the populations from the Colombian Amazon and Bahia, however, the cells along the keel are usually not enlarged.

*Cheilolejeunea norisiae* G.Dauphin & Gradst.

**Description and illustration:** Dauphin & Gradstein (2003).

**Distribution:** Panama, Cuba (Mustelier-Martinez 2012).

**Comments:** *Cheilolejeunea norisiae* (sect. unknown) is a rare Panamanian species that is characterized by: 1) plants dioicous (?), very small, 0.5–0.7 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-falcate, apex acute-acuminate, asymmetrical, ventral margin curved, entire, dorsal margin arched, dentate-laciniate, with 3–6 coarse teeth, the teeth 1–6 cells long, and 1–4 cells wide at base; 3) leaf cells unipapillose, cell walls strongly thickened, oil bodies 1–4 per cell, very large, coarsely segmented; 4) lobules ovoid, strongly inflated, 1/3–2/3 of leaf length (larger on branches), free margin involute, tooth acute, keel strongly papillose, keel apex with a 1–2 cell long pre-apical tooth; 5) underleaves distant, small, ca. 2× stem width, orbicular-obovate, bifid to 1/3, apices rounded to obtuse, bases cuneate, insertion line curved. Gametocia not seen.

By the laciniate dorsal leaf margins *C. norisiae* is similar to *C. laciniata* from eastern Brazil, but the leaf cells and keel in the latter species are not papillose and the underleaves are larger, imbricate.

***Cheilolejeunea ornata*** C.J.Bastos

**Synonym:** *Cheilolejeunea caracariensis* C.J.Bastos et al., syn. nov. Type: Brazil, Roraima, Caracarái, Serra da Mocidade, 600 m, 29 January 2016, M.H.T. Araújo 1217a (holotype, ALCB!; isotype, INPA).

**Description and illustration:** Bastos (2011).

**Distribution:** eastern and northern Brazil (Bahia, Amazonia), Ecuador (Gradstein & Benitez 2017).

**Comments:** *Cheilolejeunea ornata* (sect. *Strepsilejeunea*) is a rare tropical South American species that is recognized by: 1) plants dioicous (?), very small, ca. 400 µm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-oblong to triangular-ovate, falcate, margins crenate by projecting mammillose-papillose cells, apex obtuse to acute to apiculate, mostly recurved; 3) leaf cells unipapillose, the papillae large, 8–10 µm high, trigones large, intermediate thickenings occasionally present, oil bodies several per cell, coarsely segmented; 4) lobule ± ovoid, 1/3–1/2 of leaf length, free margin involute, tooth acute, keel arched, strongly roughened by projecting papillose cells; 5) underleaves distant, small, 1.5–2.0× stem width, (ob)ovate-oblong, longer than wide, bifid to 1/2, apices acute, bases cuneate, insertion line straight; 6) androecia on short branches, with 2–3 pairs of bracts, bracteoles restricted to the base of the male spike. Gynoecia not observed.

This species is habitually similar to *C. lobulata*, but is distinguished from the latter by the large, 8–10 µm high papillae on leaf cells (Bastos 2011). In *C. lobulata* the papillae are low, lens-shaped, 2–3 µm high. Moreover, *C. ornata* is probably dioicous (gynoecia not seen) whereas *C. lobulata* is autoicous. *Cheilolejeunea ornata* also resembles *C. grosseoleosa*, but the latter species has leaf cells with small trigones and a single huge oil body per cell. *Cheilolejeunea caracariensis* is a phenotype of *C. ornata* with triangular-ovate leaf lobes and conical lobules.

***Cheilolejeunea ovalis*** (Lindenb. & Gottsche) W.Ye et al.

**Description and illustration:** Gradstein (in press).

**Distribution:** scattered in tropical America.

**Comments:** *Cheilolejeunea ovalis* (sect. *Omphalanthus*) is recognized by: 1) plants dioicous, ca. 1.0–1.2 mm wide, ventral merophytes 6–8 cells wide; 2) leaf lobes ovate, dorsal margin arched, entire, ventral margin straight, curved, apex obtuse to subacute; 3) leaf cells mammillose, trigones distinct, intermediate thickenings absent; 4) lobules small, 1/4–1/3 of leaf length, trapezoid, free margin involute, tooth reduced, keel straight, smooth; 5) underleaves undivided, large, ca. 2.5–3.5× stem width, longer than wide, oblong-ovate, bases auriculate, insertion line deeply arched; 6) gynoecia on a short branch, with one lejeuneoid innovation, perianths obovate, 5-keeled, beak short. Androecia not seen.

*Cheilolejeunea ovalis* is habitually similar to *C. filiformis*, but differs in the longer than wide underleaves (as long as wide or wider than long in *C. filiformis*) and the obtuse to



subacute leaf apex (broadly rounded in *C. filiformis*). Moreover, the perianth in *C. ovalis* is 5-keeled, while being mostly terete in *C. filiformis* (5-keeled in the rare *C. filiformis* var. *wallisii*). On the Galápagos Islands *C. ovalis* and *C. filiformis* are very common and sometimes grow intermingled.

***Cheilolejeunea papulosa*** Schiffn.

**Description and illustration:** Reiner-Drehwald & Grolle (2012, illustration only), Bastos (2017, description only).

**Distribution:** central Amazon region of Brazil.

**Comments:** *Cheilolejeunea papulosa* (sect. *Trachylejeunea*) is a rare central Amazonian species that is distinguished by: 1) plants dioicous (?), very small, 0.5–0.6 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate, margins crenulate by projecting mammillose cells, apex rounded, recurved to plane; 3) leaf cells strongly mammillose, trigones very small, intermediate thickenings absent; 4) lobules ovoid, inflated, small, ca. 1/3 of leaf length, free margin involute, with two closely associated, obtuse teeth, the first tooth shorter than the second tooth and sometimes reduced, keel arched, crenulate; 5) underleaves distant, small, 2.0–2.5× stem width, ovate to orbicular, bifid to 1/2, bases cuneate, insertion line curved; 6) gynoecia on main stem or on short branch, without true, *Radula*-type innovations, but sometimes with pseudo-innovations (= subgynoecial *Lejeunea*-type branches). Perianths and androecia not observed.

*Cheilolejeunea papulosa* is close to *C. aneogyna*, but differs from the latter species in leaf margins and keel crenulate, leaf cells strongly mammillose, lobule teeth differing in length (first lobule tooth shorter than second tooth and sometimes reduced) and gynoecia without true innovations.

***Cheilolejeunea paramicola*** (Herzog) W.Ye et al.

**Description and illustration:** Schuster (1987, as *Aureolejeunea paramicola* [Herzog] R.M.Schust.), Bastos (2017).

**Distribution:** northern Andes.

**Comments:** *Cheilolejeunea paramicola* (sect. *Omphalanthus*) is an uncommon northern Andean species that is distinguished by: 1) plants autoicous, rather large, 1.6–1.8 mm wide, brown to glossy orange-brown plants, creeping to ascending to pendent, ventral merophytes 6–8 cells wide; 2) leaf lobes ovate, margins entire, apex rounded, recurved, rare plane; 3) leaf cells mammillose, trigones large, intermediate thickenings ± absent; 4) lobules large, 1/2–2/3 of leaf length, rectangular, free margin involute, tooth short, obtuse, keel straight to slightly arched; 5) underleaves large, ca. 4.0–5.0× stem width, undivided, ovate to orbicular, contiguous to slightly imbricate, bases straight, insertion line deeply arched; 6) androecia on short branches, with 4–5 pairs of bracts, bracteoles limited to the base of the male spike; 7) gynoecia on main stem, with 1–2 lejeuneoid innovations, peri-

anths pluriplicate, with 4–8 narrow folds, 3–5 folds on the ventral perianth surface (mostly on the broad ventral keel) and 1–3 in the dorsal surface, beak short.

*Cheilolejeunea paramicola* is close to *C. aurifera*, *C. quinquecarinata* and *C. tonduzana*; for differences see the key.

***Cheilolejeunea polystachya*** (Spruce) Gradst. & Ilk.-Borg.

**Description and illustration:** Reiner-Drehwald (2000, as *Trachylejeunea polystachya* [Spruce] Steph.).

**Distribution:** northern Amazonia (upper Rio Negro and Rio Uaupés region, Brazil).

**Comments:** *Cheilolejeunea polystachya* (sect. *Trachylejeunea*) is a rare Amazonian species that is recognized by: 1) plants autoicous, 0.9–1.0 mm wide, ventral merophytes 4–6 cells wide; 2) leaf lobes ovate, margins entire, apex rounded, mostly recurved; 3) leaf cells mammillose, trigones small, intermediate thickenings scarce; 4) lobules large, 2/5–1/2 of leaf length, rectangular, free margin plane, apex with two short, but distinct, closely associated teeth, keel straight to slightly arched; 5) underleaves distant, ovate-orbicular, slightly longer than wide, 2–3× stem width, bifid to 1/2, sinus V-shaped, bases cuneate, insertion line curved; 6) androecia on short branches, with 2–3 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia without innovations, perianths (Reiner-Drehwald 2000) 4-keeled, beak short.

*Cheilolejeunea polystachya* is close to *C. aneogyna*, but the ventral merophytes in the latter species are only 2 cells wide, the leaf apex is plane, the lobules are much smaller (maximally 1/4 of leaf length) and the leaves in *C. aneogyna* are frequently caducous.

***Cheilolejeunea quinquecarinata*** (R.M.Schust.) W.Ye et al.

**Description and illustrations:** Schuster (1987, as *Aureolejeunea quinquecarinata* R.M.Schust.), Bastos (2017).

**Distribution:** northern Andes, Guyana Highland, Dominican Republic.

**Comments:** *Cheilolejeunea quinquecarinata* (sect. *Omphalanthus*) is an uncommon páramo species that is distinguished by: 1) plants autoicous (Schuster 1987), creeping, ca. 1–1.5 mm wide, glossy brown, ventral merophytes 2 cells wide; 2) leaf lobes convex, margins entire, apex rounded, broadly recurved; 3) leaf cells mammillose (but without papilla), with large swollen trigones, intermediate thickenings absent; 4) lobules rectangular, 2/5–1/2 of leaf length, tooth multicellular, 2–3 cells long; 5) underleaves imbricate, large, 4–5× stem width, orbicular or slightly wider than long, undivided, margins often narrowly recurved, bases broadly rounded, insertion line deeply arched; 6) perianths sharply 5-keeled, with 1–2 lejeuneoid innovations. Androecia not seen.

*Cheilolejeunea quinquecarinata* is closely related to *C. aurifera*, *C. paramicola* and *C. tonduzana*; for differences see the key.

***Cheilolejeunea revoluta*** (Herzog) Gradst. & Grolle**Description and illustration:** Gradstein et al. (1993).**Distribution:** southeastern Brazil, northern Andes, Costa Rica.

**Comments:** *Cheilolejeunea revoluta* (sect. unknown) is an uncommon neotropical species that is characterized by: 1) plants dioicous, relatively robust, 1.3–2.5 mm wide, ventral merophytes on main stems 6–7 cells wide; 2) leaf lobes asymmetrically ovate-orbicular, margins entire, apex rounded to obtuse; 3) leaf cells mammillose, trigones large, intermediate thickenings scarce; 4) lobules very small, 1/6–1/4 of leaf length, flask-shaped, free margin involute, tooth short, obtuse, keel straight to slightly curved; 5) underleaves imbricate, large, 4–5× stem width, reniform, shallowly bifid to 1/5–1/4, sinus widely acute, apical margin revolute, bases cuneate, insertion line deeply arched; 6) androecia on main stem or on branches, with 2–6 pairs of bracts, bracteoles present throughout the male spike; 7) gynoecia with 1–2 pycnolejeuneoid innovations, perianths sharply 5-keeled, beak short, 3–4 cells long.

By the robust shoots with 6–7 cell wide ventral merophytes, the very small lobules, and the large, shallowly bifid underleaves with revolute apical margin this species is unmistakable.

***Cheilolejeunea rigidula*** (Mont.) R.M.Schust. var. *rigidula*

**Synonyms:** *Cheilolejeunea brunella* Steph., syn. nov. Type: French Guiana, Leprieur s.n. (holotype, G-00060750!). *Cheilolejeunea ovistipula* Steph., syn. nov. Type: Guadeloupe, L'Herminier s.n. (holotype, G-00112875!). *Cheilolejeunea polyantha* A.Evans, syn. nov. Type: U.S.A., Florida, Underwood 1380 p.p. (isotype, JE!). *Lejeunea brunella* Steph. Type: Suriname, Splitgerber s.n. (holotype, G-00112872!). For further synonyms see Schuster (1980) and Bastos (2017).

**Description and illustration:** Schuster (1980), Reiner-Drehwald (1998), Gradstein & Ilkiu-Borges (2009), Bastos (2017, also as *C. ovistipula*).

**Distribution:** tropical America and Africa, very common.

**Comments:** *Cheilolejeunea rigidula* (sect. *Euosmolejeunea*) is a very common species that is distinguished by: 1) plants dioicous, 0.8–1.2 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes orbicular-ovate to ovate, margins entire, apex rounded, usually plane; 3) leaf cells mammillose, trigones small to large, intermediate thickenings scarce, oil bodies 2–4 per cell, large, coarsely segmented; 4) lobules ca. 1/4–1/3 of leaf length, never reduced, ovoid, inflated, free margin involute, tooth obtuse, short to long, oblong, keel arched; 5) underleaves distant, obovate, small, 2–3(–3.5)× stem width, bifid to 1/2, sinus V-shaped, apices obtuse to acute, bases cuneate to slightly rounded, not auriculate, insertion line slightly curved; 6) androecia on long shoots or on short branches, with 2–4 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia with 1–2 lejeuneoid innovations, perianths 4-keeled, beak short; 8) vegetative reproduction by caducous leaves very rare (usually absent).

Robust phenotypes of *C. rigidula* with slightly rounded underleaf bases may be confused with *C. clausa*. However, the underleaves of *C. clausa* are 4–6× stem width and contiguous to imbricate, while those of *C. rigidula* are less than 4× stem width (usually 2–3× stem width) and usually distant. Small phenotypes of *C. rigidula* may be confused with *C. discoidea* and *C. intertexta*, but the latter two species are monoicous and have pycnolejeuneoid innovations. For further differences see the key and under *C. intertexta*. *Cheilolejeunea rigidula* may also be confused with *C. aneogyna* (see under *C. aneogyna*).

*Cheilolejeunea polyantha* A.Evans, including its variety *caduciloba* R.M.Schust., are synonyms of *C. rigidula*. As indicated by Schuster (1980), the characters of *C. polyantha* and *C. rigidula* completely overlap. *Cheilolejeunea brunella*, a species described from French Guiana and represented by only one single shoot almost devoid of leaves, was treated as a synonym of *C. discoidea* by Gradstein & Hekking (1989). We have reexamined the material and conclude that it is a poorly developed specimen of *C. rigidula*.

***Cheilolejeunea rigidula* var. *autoica* C.J.Bastos & Gradst., var. nov.**

**Type:** Brazil, Amazonas, Rio Negro, São Gabriel, “in cortice”, R. Spruce s.n. (holotype, MANCH-0004811!).

**Diagnosis:** Plants 0.6–0.8 mm wide, ventral merophytes two cells wide, medullary cells strongly thick-walled; lobe ovoid, margins entire, apex rounded; lobule small, ca. 1/3–1/4 of leaf length, free margin involute, tooth short, oblong, keel arched; underleaves distant, small, 1.5–2.0× stem width, ovate to suborbicular, bifid to 1/2, sinus V-shaped. Autoicous. Androecia intercalary on main stem or on short or long branches, with 4–14 pairs of bracts, bracteoles restricted to the base of the male spike. Gynoecia on main stem or on short branches, with one lejeuneoid innovation, bract lobes (ob)ovate, margins entire, apex apiculate; perianths 5-keeled, keels smooth, beak short, 2–3 cells long. Vegetative reproduction by caducous leaves.

**Comments:** this new variety differs from *C. rigidula* var. *rigidula* in autoicous sexuality (var. *rigidula* is dioicous), the longer male spikes with 4–14 pairs of bracts (2–4 pairs in var. *rigidula*) and the shortly apiculate female bract lobes (rounded in var. *rigidula*). It might merit recognition as a new species; however as it is only known from one collection and very similar to *C. rigidula*, we prefer describing it as a variety of the latter.

***Cheilolejeunea savannae* L.P.C.Macedo et al.**

**Description and illustration:** Macedo et al. (2020).

**Distribution:** In savannas and flooded forests of Eastern Amazonia from sea level to 120 m.

**Comments:** *Cheilolejeunea savannae* (sect. *Euosmolejeunea*) is recognized by: 1) plants autoicous, profusely branched and with microphyllous branches, very small, 0.5–0.7 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes widely spreading, convex to squarrose, obovate to suborbicular, margins slightly crenulate, apex rounded to obtuse, plane to

recurved; 3) leaf cells mammillose on the dorsal surface of the leaf lobe, outer wall thickened and often with a low, lenticular papilla, trigones small, intermediate thickenings absent; 4) lobules 1/3–2/5 of leaf length, ovoid, inflated, free margin involute, tooth short, obtuse to acute, keel arched, crenulate; 5) underleaves distant, 1.5–3× stem width, ovate-orbicular, bifid to 1/3, lobes acute, bases cuneate to rounded, insertion line curved; 6) androecia on short male branches, with 2 pairs of bracts, bracteoles present throughout the male spike; 7) gynoecia with 1–2 pycnolejeuneoid innovations, perianths obovate, 4-keeled (dorsal keel absent), keels smooth, beak very short.

*Cheilolejeunea savannae* stands out among the neotropical members of sect. *Euosmolejeunea* by having leaf cells with a dorsal papilla and androecia with bracteoles throughout the spike. The species has been confused with *C. discoidea* (see Macedo et al. 2020), but the latter species has suberect to obliquely spreading leaves, leaf cells without papilla, lejeuneoid innovations, 5-keeled perianths and androecia with bracteoles restricted to the base of the male spike. *Cheilolejeunea savannae* is also close to *C. intertexta* but the latter species differs in being frequently parocious, absence of microphyllous branches, flat leaves and leaf cells without papilla, perianths 5-keeled and male bracteoles restricted to the base of the spike.

***Cheilolejeunea schiavoneana*** M.E.Reiner & Gradst.

**Description and illustration:** Gradstein & Reiner-Drehwald (2017).

**Distribution:** only known from the type from the Western Cordillera of Colombia.

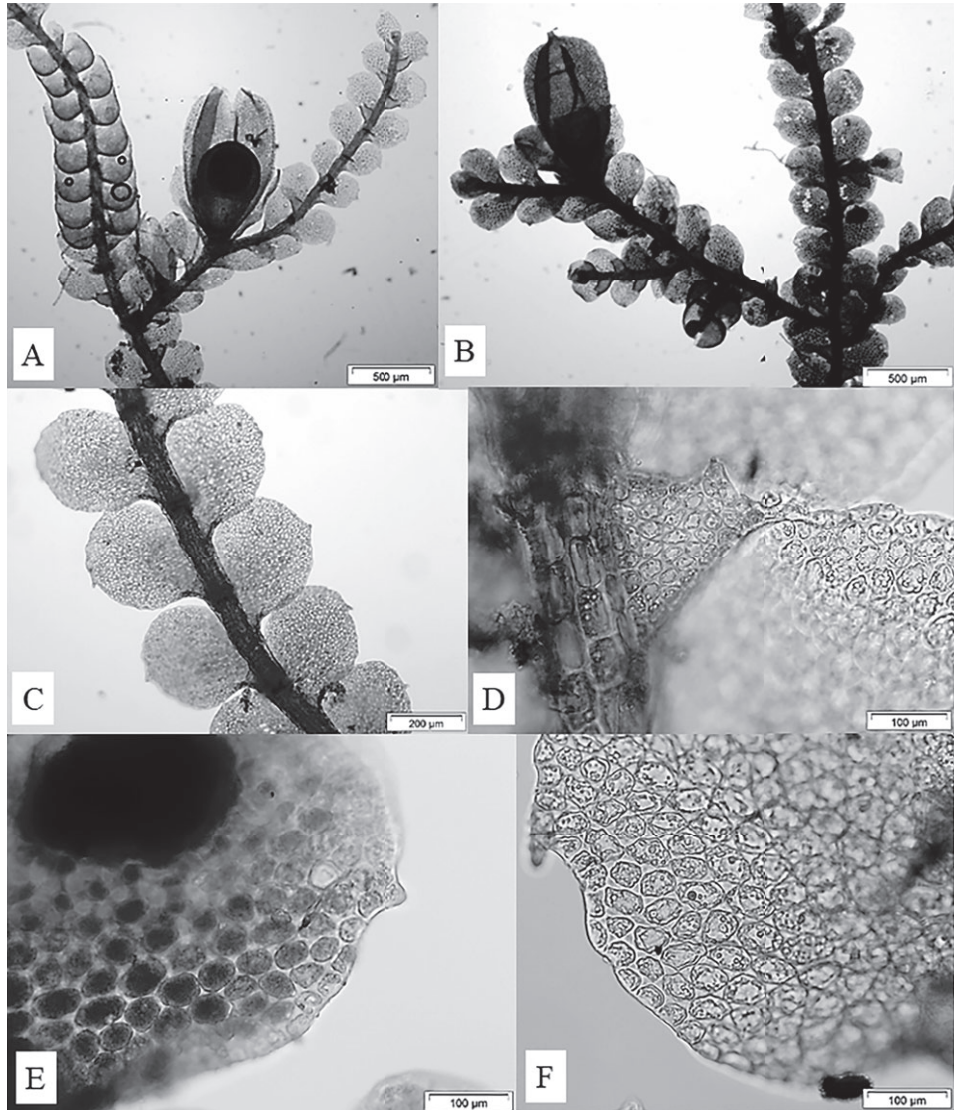
**Comments:** *Cheilolejeunea schiavoneana* (sect. *Cheilolejeunea* ?) is a very rare Colombian species that is characterized by: 1) plants dioicous (?), 1.8–2.4 mm wide, with numerous microphyllous branches; 2) stem cells ± thin-walled, hyalodermis present, ventral merophytes 5–6 cells wide; 3) leaves ovate, apex rounded, margins entire; 4) cells 25–40 × 20–30 μm in midleaf, conspicuously smaller toward the margin, walls with small triradiate trigones and 0–2 intermediate thickenings; 5) lobules shortly flask-shaped, 1/6–1/4 of leaf length, fully inflated, with a long and thin tooth, lobule cells much smaller than lobe cells; 6) underleaves distant, 2.5–3.0× stem width, bifid to 1/2, margins entire, bases cuneate; 7) caducous leaf lobes produced on short upright, flagelliform shoots with densely imbricate underleaves, caducous leaf lobes smaller than normal leaf lobes and with short marginal rhizoids. Gametoecia not observed.

By the presence of a hyalodermis, leaf cells with small radiate trigones, bottle-shaped lobules with a long and thin tooth, and caducous leaves, *Cheilolejeunea schiavoneana* approaches *C. adnata*, but the latter species differs in smaller plant size, thinner stems with 2-cell wide ventral merophytes, absence of microphyllous branches, and caducous leaf lobes produced on ordinary leafy shoots, not on flagelliform shoots, and not smaller than normal leaf lobes.

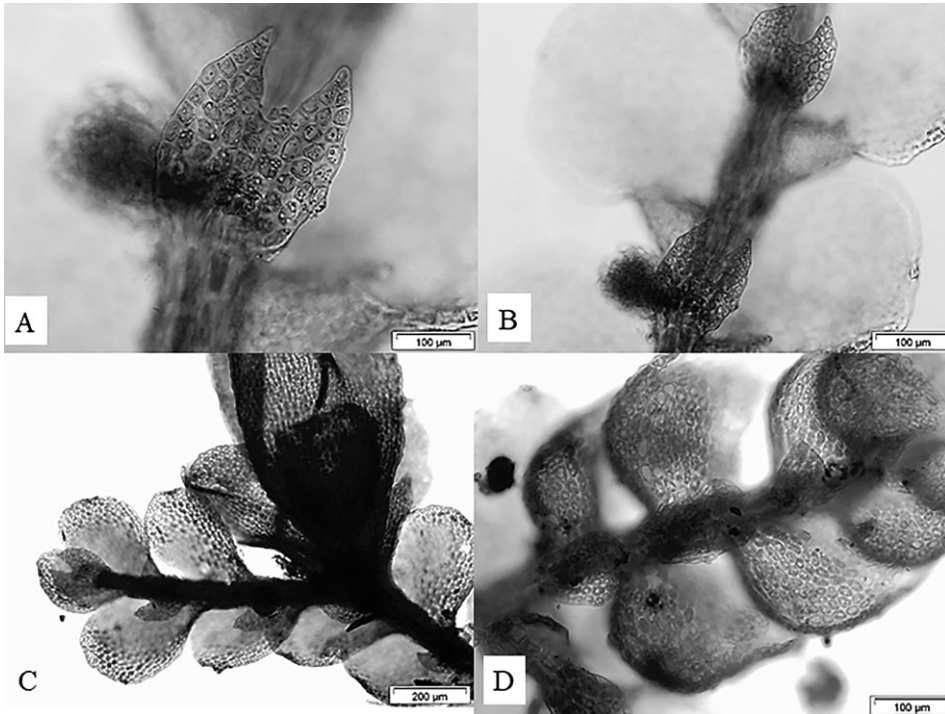
*Cheilolejeunea timboensis* C.J.Bastos & Gradst., **spec. nov.**

Figs. 2–3

**Diagnosis:** Plants autoicous, 0.63–0.67 mm wide, ventral merophytes 2 cells wide. Leaf lobes (sub)orbicular, margins crenulate, apex shortly apiculate, plane or recurved. Leaf cells mammillose, with large trigones and 1–2 intermediate thickenings per cell. Leaf



**Fig. 2.** *Cheilolejeunea timboensis*. A, B. Gametophyte with androecia and gynoecium with perianth, ventral view. C. Part of gametophyte, ventral view. D. Leaf lobule. E, F. Leaf lobes apices (all from holotype). Photographs by Cid J.P. Bastos.



**Fig. 3.** *Cheilolejeunea timboensis*. A, B. Underleaves. C. Gynoecium with lejeuneoid innovation, ventral view. D. Male branch showing bracteoles present throughout the male spike (all from holotype). Photographs by Cid J.P. Bastos.

lobules ca. 1/3 of leaf length, ovoid, free margin involute, tooth short, obtuse, keel straight to slightly curved. Underleaves 1.5–2.0× stem width, (ob)ovate, bifid to 1/2, lobes acute, bases cuneate, insertion line curved. Androecia on short or long branches, with 3–8 pairs of bracts, bracteoles present throughout the male spike. Gynoecia with one lejeuneoid innovation, perianths 5-keeled, keels smooth, beak short.

**Type:** Brazil, Bahia, Amargosa, Refúgio da Vida Silvestre de Amargosa, Serra do Timbó, 13°07'19"S, 39°39'34"W, on tree trunk, 880 m, 16 November 2011, L.C. Reis 4505 (holotype: ALCB).

**Etymology:** named after the type locality (Serra do Timbó).

Plants 0.63–0.67 mm wide, prostrate, pale green to brownish. Stems ca. 80 µm in diameter, in cross section with 7 epidermal cells and 8 medullary cells, all cells thick-walled; ventral merophytes 2 cells wide. Leaves spreading, contiguous to imbricate; lobes orbicular, 270–300 µm long × 280–300 µm wide, dorsal margin entire to crenulate, ventral margin entire, apex shortly apiculate, terminating in a row of 1–2 cells, plane or recurved; leaf cells hexagonal to isodiametric, 23–38 × 18–20 µm, mammillose, trigones large,

sometimes confluent, intermediate thickenings 1–2 per cell; oil bodies not seen; ocelli absent; lobules ovoid, inflated, 100–120  $\mu\text{m}$  long  $\times$  80–100  $\mu\text{m}$  wide, ca. 1/3 of leaf length, occasionally reduced, free margin involute, tooth short, obtuse, hyaline papilla at the distal base of the tooth, keel straight to slightly curved, weakly crenulate. Underleaves distant, small, 100–170  $\mu\text{m}$  long  $\times$  110–150  $\mu\text{m}$  wide, ca. 1.5–2.0 $\times$  stem width, ovate to suborbicular, rarely obovate, bifid to 1/2, lobes acute, sinus V-shaped to U-shaped, bases cuneate, insertion line curved. Autoicous. Androecia terminal or intercalary on short or long branches, with 3–8 pairs of bracts, bracteoles present throughout the male spike. Gynoecia on main stem or on short branches, with one lejeuneoid innovation, bract lobes obovate-oblong, ca. 460  $\mu\text{m}$  long  $\times$  280  $\mu\text{m}$  wide, margins entire to crenulate, apex short-apiculate, lobules oblong to obovate, apex acute, bracteoles narrowly obovate-oblong, ca. 530  $\mu\text{m}$  long  $\times$  190  $\mu\text{m}$  wide, bifid, sinus narrowed, margins entire. Perianths obovate, 5-keeled, 0.9–1.0 mm long  $\times$  0.6 mm wide, beak short, ca. 50  $\mu\text{m}$  long.

**Distribution and habitat:** *Cheilolejeunea timboensis* is so far known from two collections from Bahia (northeastern Brazil), at elevations between 540–880 m, growing in rainforest on tree trunks mixed with other bryophytes.

**Comments:** *Cheilolejeunea timboensis* is presumably a member of the section *Strepsilejeunea*. Within this group the new species stands out by the presence of bracteoles throughout the male spike. In all other neotropical species of sect. *Strepsilejeunea* the male bracteoles are restricted to the base of the spike. *Cheilolejeunea timboensis* resembles some phenotypes of *C. acutangula* and *C. lobulata* in the large trigones and rather small underleaves, but the latter two species have pycnolejeuneoid innovations and bracteoles restricted to the base of the male spike. By the lejeuneoid innovations *C. timboensis* approaches *C. comans*, but the latter species is a larger plant with larger, (sub)auriculate underleaves and ovate leaf lobes.

**Additional specimen examined:** BRAZIL. Bahia: Wenceslau Guimarães, Estação Ecológica de Wenceslau Guimarães, 13°33'14"S, 39°42'07"W, 543 m, on tree trunk, 18 January 2011, L.C. Reis 534 (ALCB).

*Cheilolejeunea tonduzana* (Steph.) W.Ye et al.

**Description and illustration:** Schuster (1987, as *Aureolejeunea fulva* R.M.Schust.), Bastos (2017).

**Distribution:** Mexico to Bolivia, Southeastern and Northeastern Brazil, Lesser Antilles.

**Comments:** *Cheilolejeunea tonduzana* (sect. *Omphalanthus*) is recognized by: 1) plants autoicous, creeping to ascending, ca. 1.4–1.7 mm wide, pale brown, ventral merophytes 4–6 cells wide; 2) leaf lobes ovate, margins entire, apex rounded; 3) leaf cells mammillose, trigones large, intermediate thickenings present, 1–2 per cell; 4) lobules large, 2/5–1/2 of leaf length,  $\pm$  rectangular, free margin involute, tooth short, keel straight to slightly arched; 5) underleaves contiguous to imbricate, large, ca. 5–6 $\times$  stem width, suborbicular to reniform, undivided, bases cuneate, insertion line deeply arched; 6) androecia on short branches, with 3–4 pairs of bracts, bracteoles limited to the base of the male spike; 7)



gynoecia with one lejeuneoid innovation, perianths 3–4 keeled to almost terete, beak very short to  $\pm$  absent.

*Cheilolejeunea tonduzana* resembles the common *C. filiformis*, but differs in the longer, rectangular lobules, autoicous sexuality and more brownish color.

***Cheilolejeunea trifaria*** (Reinw. et al.) Mizut. var. *trifaria*

**Synonym:** *Cheilolejeunea azureomontana* C.J.Bastos & Schäf.-Verw., syn. nov. Type: see Bastos & Schäfer-Verwimp (2017).

**Description and illustration:** Mizutani (1982), Reiner-Drehwald (1998), Gradstein & Ilkiu-Borges (2009), Bastos & Schäfer-Verwimp (2017, as *C. azureomontana*).

**Distribution:** pantropical, very common.

**Comments:** *Cheilolejeunea trifaria* (sect. *Euosmolejeunea*) is a very common tropical species that is recognized by: 1) plants autoicous, 1.5–1.7 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-orbicular, margins entire, apex rounded, plane or recurved; 3) leaf cells mammillose (without papilla), trigones usually large, intermediate thickenings scarce; 4) lobules ca. 1/4–1/3 of leaf length, never reduced, ovoid, free margin involute, tooth short, obtuse, keel arched, smooth; 5) underleaves contiguous to imbricate, broadly ovate to suborbicular, usually wider than long (rarely as wide as long), ca. 4–6 $\times$  stem width, bifid to 1/5–1/3, sinus V-shaped, apices acute, bases rounded to somewhat auriculate, insertion line arched; 6) androecia intercalary on main stem or on short branches, with 4–5 pairs of bracts, bracteoles limited to the base of the male spike; 7) gynoecia with 1–2 lejeuneoid innovations, perianths 5-keeled, keels smooth, beak short.

Characteristics of *C. trifaria* are the autoicous plants with rounded leaf tips and large underleaves that are 4–6 $\times$  stem width and usually wider than long, rarely as wide as long. The latter plants were described as *C. azureomontana*.

*Cheilolejeunea trifaria* is very similar to *C. rigidula*, but the latter species is a smaller plant with smaller underleaves (2–3.5 $\times$  stem width) with cuneate to slightly rounded bases.

***Cheilolejeunea trifaria* var. *clausa*** (Nees & Mont.) C.J.Bastos & Gradst. **comb. nov.**

*Lejeunea clausa* Nees & Mont., Ann. Sci. Nat. Bot. ser. 2, 14: 337. 1840 (*Cheilolejeunea clausa* [Nees & Mont.] R.M.Schust.).

**Description and illustration (all as *C. clausa*):** Schuster (1980), Reiner-Drehwald (1998), Campos et al. (2014).

**Distribution:** scattered in tropical and subtropical America.

**Comments:** *Cheilolejeunea trifaria* var. *clausa* differs from var. *trifaria* in being dioicous. In addition, the underleaves of var. *clausa* are rounded whereas in var. *trifaria* they are mostly wider than long, rarely rounded. The existence of autoicous *C. trifaria* with

rounded underleaves (described as *C. azureomontana*) indicates that *C. clausa* must be a variety of *C. trifaria*, not a separate species.

***Cheilolejeunea uncioloba*** (Lindenb.) Malombe

**Description and illustration:** Schuster (1980, as *Leucolejeunea uncioloba* [Lindenberg] A.Evans).

**Distribution:** tropical and subtropical America, Africa, rather common.

**Comments:** *Cheilolejeunea uncioloba* (sect. *Leucolejeunea*) is characterized by: 1) plants autoicous, 1.3–1.9 mm wide, very pale-colored, ventral merophytes 4 cells wide; 2) leaf lobes ovate, convex, slightly falcate, margins entire, plane, apex rounded, plane or slightly recurved; 3) leaf cells slightly mammillose, trigones small, intermediate thickenings indistinct, dorsal wall of leaf cells thin-walled; 4) lobules large, ca. 1/2 of leaf length, oblong-rectangular, free margin incurved or plane, tooth long and sharp, curved, multicellular, 2–4 cells long, 2 cells wide at the base, keel straight; 5) underleaves contiguous to imbricate, large, ca. 4–5× stem width, orbicular to reniform, undivided, bases rounded, insertion line shallowly curved; 6) androecia on main stem or on short branches, with 2–4 pairs of bracts, bracteoles limited to the base of the male spike; 7) gynoecia with one pycnolejeuneoid innovation, perianths 5-keeled, beak short.

*Cheilolejeunea uncioloba* is close to *C. xanthocarpa*, but the latter species differs in the strongly revolute ventral and apical leaf margins, the unicellular lobule tooth, and more strongly mammillose leaf cells with thickened dorsal cell walls.

***Cheilolejeunea urubuensis*** (C.E.Zartman & I.L.Ackerman) R.L.Zhu & Y.M.Wei

**Description and illustration:** Zartman & Ackerman (2002, as *Vitalianthus urubuensis* C.E.Zartman & I.L.Ackerman), Campos et al. (2014, as *V. urubuensis*).

**Distribution:** Amazon region of Brazil and Colombia.

**Comments:** *Cheilolejeunea urubuensis* (sect. unknown) is a canopy species in Amazonian rainforests that is readily recognized by: 1) plants autoicous, small, 0.5–0.65 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate to ovate-oblong, with a conspicuous row of 4–8 yellowish to yellowish-brown ocelli, margins entire to crenulate, apex rounded, plane to slightly recurved; 3) leaf cells with evenly thickened walls, trigones and intermediate thickenings absent, ocelli present (see above); 4) lobules very large, 1/2–2/3 of leaf length, free margin plane, tooth long and curved, multicellular, keel straight to slightly arched; 5) underleaves small, 1.5–2.0× stem width, deeply bifid to more than 1/2, lobes slightly divergent, blunt, bases cuneate, insertion line straight; 6) androecia on long or short branches, with 2–4 pairs of bracts, bracteoles limited at the base of the male spike; 7) gynoecia on short branches with 1–2 pycnolejeuneoid innovations, perianths obconical, 4-keeled, apex truncate (Zartman & Ackerman 2002).

*Cheilolejeunea urubuensis* is readily recognized by the leaf lobes with a row of yellowish to yellowish-brown ocelli. It is the only neotropical species in the genus *Cheilolejeunea* with ocelli always present.

***Cheilolejeunea valenciae*** (Steph.) X.L.He

**Description and illustration:** He (1996).

**Distribution:** Venezuela, Nicaragua.

**Comments:** *Cheilolejeunea valenciae* (sect. unknown) is a rare neotropical species that is characterized by: 1) plants dioicous, large, 2–3 mm wide, ventral merophytes 4–8 cells wide; 2) leaf lobes ovate, convex, margins entire, apex rounded; 3) leaf cells mammillose, trigones large, intermediate thickenings present, one per cell; 4) lobules very small, ca. 1/6–1/5 of leaf length, ovoid, free margin plane to slightly incurved, tooth very short, obtuse, keel straight; 5) underleaves contiguous to distant, 2–3× stem width, orbicular to suborbicular, sinus V-shaped, apices acute, bases cuneate to rounded, insertion line arched; 6) androecia on main stem or on short branches, with 3–6 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia on short branches, without innovation, perianths 4-keeled, beak short.

By the large plants (2–3 mm wide) with broad, 4–8 cell wide ventral merophytes, very small leaf lobules (ca. 1/6–1/5 of leaf length) with a short, obtuse tooth, and absence of innovations, *Cheilolejeunea valenciae* is unmistakable.

***Cheilolejeunea xanthocarpa*** (Lehm. & Lindenb.) Malombe

**Description and illustration:** Schuster (1980, as *Leucolejeunea xanthocarpa* [Lehm. & Lindenb.] A.Evans).

**Distribution:** pantropical.

**Comments:** *Cheilolejeunea xanthocarpa* (sect. *Leucolejeunea*) is a common pantropical species that is distinguished by: 1) plants autoicous, 1.3–1.9 mm wide, ventral merophytes 4 cells wide; 2) leaf lobe ovate, convex, margins entire, ventral and apical margin strongly revolute, apex rounded; 3) leaf cells strongly mammillose, trigones large, intermediate thickenings present, dorsal cell wall thickened, with low, lens-shaped papilla (one per cell); 4) lobules large, ca. 1/2 of leaf length, rectangular, free margin incurved or plane, tooth short and usually rather inconspicuous, 1(–3) cells long, obtuse, keel straight; 5) underleaves contiguous to imbricate, large, 3–4× stem width, suborbicular to reniform, undivided, bases rounded, insertion line curved; 6) androecia on short branches, with 2–5 pairs of bracts, bracteoles restricted to the base of the male spike; 7) gynoecia without innovation or with 1–2 pycnolejeuneoid innovations, perianths 5-keeled, beak short.

*Cheilolejeunea xanthocarpa* is close to *C. conchifolia* and *C. uncioloba*, for differences see under the latter two species.

***Cheilolejeunea yanoae*** C.J.Bastos

**Replaced name:** *Strepsilejeunea muscicola* Herzog

**Description and illustration:** Bastos (2015).

**Distribution:** only known the type from Bolivia.

**Comments:** *Cheilolejeunea yanoae* (sect. *Strepsilejeunea*) is a rare Bolivian species that is characterized by: 1) plants dioicous (?), small, 0.8–1.1 mm wide, ventral merophytes 2 cells wide; 2) leaf lobes ovate-falcate, margins entire, apex acute to apiculate, mostly recurved; 3) leaf cells mammillose, trigones large, intermediate thickenings  $\pm$  absent; 4) lobules ovoid-triangular, ca. 1/3 of leaf length, free margin incurved or plane, tooth elongate, obtuse, formed by two cells, keel straight; 5) underleaves distant, small, ca. 2–3 $\times$  stem width, longer than wide, bifid to 1/3, sinus V-shaped, bases cuneate, insertion line curved. Gametoeceia not observed.

*Cheilolejeunea yanoae* resembles *C. acutangula*, but in the latter species the lobule tooth consists of only one cell, not two, and the underleaves are wider than long or as long as wide (not longer than wide).

## Doubtful species

*Cheilolejeunea tenerrima* (Steph.) C.J.Bastos

**Description and illustration:** Bastos (2012b).

**Distribution:** only known from the type from São Paulo State (leg. Puiggari).

**Comments:** *Cheilolejeunea tenerrima* (sect. *Strepsilejeunea*) is characterized by: 1) plants dioicous (?) (gynoecia not observed), 0.8–1.2 mm wide, ventral merophytes 2 cells wide; 2) stems in cross section made up of only 7 epidermal cells and 3 medullary cells, all stem cells thick-walled; 3) leaf lobes ovate, slightly falcate, margins entire, apex acute to short-apiculate; 4) leaf cells with very small trigones, intermediate thickenings  $\pm$  absent; 4) lobules triangular-ovoid, ca. 1/3 of leaf length, free margin incurved, tooth short, acute, keel straight; 5) underleaves distant, small, ca. 1.5–2.0 $\times$  stem width, longer than wide, ovate-oblong, bifid to 1/2, sinus V-shaped, bases cuneate, insertion line arched; 6) androecia on short or long branches, with 6–10 pairs of bracts, bracteoles restricted to the base of the male spike. Gynoecia not observed.

*Cheilolejeunea tenerrima* closely resembles *C. acutangula* and is perhaps a weak and poorly developed phenotype of the latter, but differs in the stems with only 3 rows of medullary cells (more than 3 medullary cell rows in *C. acutangula*), acute to shortly apiculate leaf tips (acute in *C. acutangula*) and a short lobule tooth (tooth long in *C. acutangula*). The species is known only from the type from the State of São Paulo and has not been found in recent collections.

## Excluded records

*Cheilolejeunea curvatiloba* (Herzog) Grolle (*Harpalejeunea curvatiloba* Herzog) — Colombia: Val (Herzog 1955). Not a good taxon and presumably a synonym, even though it is not clear to which species it belongs (R. L. Zhu, pers. comm.); the record is therefore excluded here.

*Cheilolejeunea rufescens* (Lindenb.) Grolle (*Lejeunea rufescens* Lindenb.) — Brazil, without locality, Burchell 59A2-2 (NY). A rare species from southern Argentina (Staten Island) and South Africa. The Brazilian record is probably based on an erroneous label (Bastos 2017) and is therefore excluded here.

## New synonyms

*Cheilolejeunea aciculifera* = *C. lobulata*

*Cheilolejeunea azureomontana* = *C. trifaria* var. *trifaria*

*Cheilolejeunea brunella* = *C. rigidula* var. *rigidula*

*Cheilolejeunea caracariensis* = *C. ornata*

*Cheilolejeunea gottscheana* = *C. grandibracteata*

*Cheilolejeunea herzogiana* = *C. lobulata*

*Cheilolejeunea huanucensis* = *C. filiformis* var. *filiformis*

*Cheilolejeunea invaginata* = *C. choachina*

*Cheilolejeunea larsenii* = *C. adnata* var. *autoica*

*Cheilolejeunea nana* = *C. lobulata*

*Cheilolejeunea oncophylla* = *C. lobulata*

*Cheilolejeunea ovistipula* = *C. rigidula* var. *rigidula*

*Cheilolejeunea polyantha* = *C. rigidula* var. *rigidula*

*Strepsilejeunea hieronymii* = *C. acutangula*

*Strepsilejeunea obtusistipula* = *C. lobulata*

*Strepsilejeunea papulifolia* = *C. choachina*

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