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A new key to the genera of liverworts of Colombia

Nueva clave para los géneros de Hepáticas de Colombia

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ABSTRACT

A key is presented to 130 liverwort genera recorded from Colombia. Some genera found in neighboring countries, but not yet in Colombia, are also included in the key.

Key words. Colombia, hepatics, identification, taxonomy.

RESUMEN

Se presenta una clave taxonómica para los 130 géneros de hepáticas registrados en Colombia. Algunos géneros registradas de países vecinos, pero aún no de Colombia, también son incluidos.

Palabras clave. Colombia, hepáticas, identificación, taxonomía.

INTRODUCTION

Colombia has a very rich liverwort flora. With about 715 accepted species, in 40 families, the country ranks second among the countries of tropical America, after Brazil with 725 species, and has more than half of the species recorded from tropical America (Gradstein & Uribe-M. 2016). Many species have been newly discovered in the country in recent years, and our knowledge of the liverwort flora of Colombia has been greatly improved by recent taxonomic revisions and monographs (e.g., Reiner-Drehwald & Goda 2000, Heinrichs 2002, Dauphin 2003, Váňa 2003, Bischler et al. 2005, Costa 2008, Uribe-M. 2008, Campos-Salazar & Uribe-M. 2012, Gradstein & Ilkiu-Borges 2015, Gradstein 2016, Ilkiu-Borges 2016). In spite of these studies and the availability of a modern catalogue (Gradstein & Uribe-M. 2016), identification of the liverworts of Colombia remains cumbersome. The key to the genera of liverworts of Colombia (Uribe-M. & Aguirre-C. 1997) is out of date

and keys to the species are very scattered in the literature and often difficult of access.

The lack of a modern means of identification has prompted the author to prepare an identification manual for the liverworts of Colombia (Gradstein in prep.). As a first step, a treatment of the genus Plagiochila (Dumort.) Dumort., the largest genus of the liverworts, was published (Gradstein 2016) and a revision of the large and troublesome genus Bazzania Gray is in preparation. The present paper presents a new key to the genera of liverworts of Colombia. Although 132 genera were listed in the recent catalogue (Gradstein & Uribe-M. 2016), several taxonomic changes have occurred since the publication of the catalogue leading to modification of the total number of liverwort genera in Colombia. Aureolejeunea R.M. Schust. and Omphalanthus Lindenb. & Nees have been transferred to Cheilolejeunea (Spruce) Steph. (We et al. 2015), Austrofossombronia R.M.Schust. is now included in Fossombronia Raddi (Stotler

et al. 2016), and Prionocolea R.M.Schust. and Taxilejeunea (Spruce) Steph. are synonyms of Lejeunea Lib. (Gradstein et al. 2016). On the other hand, Archilejeunea subgen. Dibrachiella (Spruce) Schiffn. with three species in Colombia was raised to genus level (Shi et al. 2015), Cololejeunea minutissima (Sm.) Schiffn. was transferred to Myriocoleopsis Schiffn. (Yu et al. 2015), a rare rheophytic genus previously unknown in Colombia, and Platycaulis R.M.Schust. was newly recorded from Colombia (Gil-Novoa et al. 2015). As a result, 130 genera are currently accepted for Colombia and are included in the key. Some genera known from neighboring areas but not yet from Colombia (e.g., Anthelia (Dumort.) Dumort., Clevea Lindb., Isopaches Buch, Lobatiriccardia Furuki. Nanomarsupella R.M.Schust. Schusteroleieunea Grolle. Spruceanthus Verdoorn) are also included. Genera with only one species in Colombia as well as a few other taxa are directly keyed to species.

CLASSIFICATION

The classification of the genera into families is according to Gradstein & Uribe-M. (2016) except for Stephaniella and Stephaniellidium, which are placed in a separate family, Stephaniellaceae, following Schuster (2002): see also Juárez-Martínez et al. (2016). Classification of the families into orders, subclasses and classes follows Crandall-Stotler et al. (2009) except for Pleuroziaceae which are placed in a separate subclass, Pleuroziidae, following Frey (2009). Author citations of the genera follow Söderström et al. (2016) but the use of "ex" (e.g., Gottsche ex Steph.) is omitted and only the second, validating author (in this case Steph.) is cited since the use of "ex" in author citation is not obligatory (McNeill et al. 2012).

MARCHANTIOPSIDA

Avtoniaceae Asterella P.Beauv. Plagiochasma Lehm. & Lindenb. Corsiniaceae Cronisia Berk Cvathodiaceae Cyathodium Kunze Dumortieraceae Dumortiera Nees Lunulariaceae Lunularia Adans. Marchantiaceae Marchantia L. Monocleaceae Monoclea Hook Ricciaceae Riccia L. Ricciocarpos Corda Targioniaceae Targionia L.

JUNGERMANNIOPSIDA

PELLIIDAE Fossombroniaceae Fossombronia Raddi Pallaviciniaceae Jensenia Lindb. Pallavicinia Gray Symphyogyna Nees & Mont. Pelliaceae Noteroclada Hook.f. & Wilson METZGERIIDAE Aneuraceae Aneura Dumort. Riccardia Gray Metzgeriaceae Metzgeria Raddi PLEUROZIIDAE Pleuroziaceae *Pleurozia* Dumort. JUNGERMANIIDAE 1. JUNGERMANNIALES

Acrobolbaceae Acroholbus Nees Lethocolea Mitt. Tvlimanthus Mitt. Adelanthaceae Adelanthus Mitt. Pseudomarsupidium Herzog Arnelliaceae Gongvlanthus Nees **Balantiopsaceae** Isotachis Mitt. Neesioscyphus Grolle Ruizanthus R.M.Schust. Calypogeiaceae Calypogeia Raddi Cephaloziaceae Alobiellopsis R.M.Schust. Cephalozia (Dumort.) Dumort. Fuscocephaloziopsis Fulford Nowellia Mitt. Odontoschisma (Dumort.) Dumort. Cephaloziellaceae Cephaloziella (Spruce) Schiffn. Cephaloziopsis (Spruce) Schiffn. Cvlindrocolea R.M.Schust. *Gymnocoleopsis* (R.M.Schust.) R.M.Schust. Kymatocalyx Herzog Gymnomitriaceae Gymnomitrion Corda Marsupella Dumort. Herbertaceae Herbertus Gray Triandrophyllum Fulford & Hatcher Jamesoniellaceae Syzygiella Spruce Jungermanniaceae Jungermannia L. Lepicoleaceae *Lepicolea* Dumort. Lepidoziaceae Bazzania Gray Kurzia G.Martens Lepidozia (Dumort.) Dumort. Micropterygium Gottsche *Monodactylopsis* (R.M.Schust.)

R.M.Schust. Mytilopsis Spruce Paracromastigum Fulford & J.Taylor Pseudocephalozia R.M.Schust. Pteropsiella Spruce Telaranea Schiffn. Zoopsidella R.M.Schust. Lophocoleaceae Clasmatocolea Spruce Cryptolophocolea L.Söderstr. Heteroscyphus Schiffn. Leptoscyphus Mitt. Lophocolea (Dumort.) Dumort. Platycaulis R.M.Schust. Plagiochilaceae Plagiochila (Dumort.) Dumort. **Pseudolepicoleaceae** Blepharostoma (Dumort.) Dumort. Chaetocolea Spruce Temnoma Mitt. Scapaniaceae Anastrophyllum (Spruce) Steph. Diplophyllum (Dumort.) Dumort. Heterogemma (Jörg.) Konstant. & Vilnet Lophonardia R.M.Schust. Scapania (Dumort.) Dumort. Schistochilopsis (N.Kitag.) Konstant. Sphenolobus (Lindb.) Berggr. Solenostomataceae Nardia Grav Solenostoma Mitt. Stephaniellaceae Stephaniella J.B.Jack Stephaniellidium Grolle Trichocoleaceae *Leiomitra* Lindb. 2. PORELLALES Frullaniaceae Frullania Raddi Jubulaceae Jubula Dumort Lejeuneaceae Acanthocoleus R.M.Schust. Acrolejeunea (Spruce) Steph. Anoplolejeunea (Spruce) Schiffn. Archilejeunea (Spruce) Steph.

Blepharolejeunea S.W.Arnell Brachiolejeunea (Spruce) Schiffn. Bromeliophila R.M.Schust. Bryopteris (Nees) Lindenb. Caudaleieunea Schiffn. Ceratolejeunea (Spruce) J.B.Jack & Steph. Cheilolejeunea (Spruce) Steph. Cololejeunea (Spruce) Steph. Colura (Dumort.) Dumort. Cyclolejeunea A.Evans Dibrachiella (Spruce) X.Q.Shi et al. Dicranolejeunea (Spruce) Schiffn. Diplasiolejeunea (Spruce) So Drepanolejeunea (Spruce) S Frullanoides Raddi Fulfordianthus Gradst. Harpalejeunea (Spruce) Sch Lejeunea Lib. Lepidolejeunea R.M.Schust. Leptolejeunea (Spruce) Step Lindigianthus Kruijt & Grad Lopholejeunea (Spruce) Ster Luteolejeunea Piippo Marchesinia Gray Mastigolejeunea (Spruce) St Metalejeunea Grolle Microlejeunea (Spruce) Step Myriocoleopsis Schiffn. Neurolejeunea (Spruce) Schi Odontolejeunea (Spruce) Scl Otigoniolejeunea (Spruce) S Otolejeunea Grolle & Tixier Pictolejeunea Grolle Prionolejeunea (Spruce) Sch Pycnolejeunea (Spruce) Schi Rectolejeunea A.Evans Schiffneriolejeunea Verd. Stictolejeunea (Spruce) Schi Symbiezidium Trevis. Thysananthus Lindenb. Verdoornianthus Gradst. Xylolejeunea X.L.He & Grolle Porellaceae Porella L.

- Radulaceae
 - Radula Dumort.

KEY TO THE GENERA

The terminology used in the key follows the Guide to the Bryophytes of Tropical America (Gradstein et al. 2001). Users of the key are advised to consult the latter publication, especially the glossary, descriptions and illustrations, which might help in clarifying difficulties that may arise.

Introductory key

.....2

chiffn.	1.	Plants with stem and leaves 2
teph.	1.	Plants thalloid 4
-	2.	Leaves divided into segments
		Jungermanniopsida: Key 2
iffn.	2.	Leaves not divided into segments 3
	3.	Leaves in 3 equal rows, leaf insertion
		transverse. [Plants growing erect from
h.		a leafless rhizome, rhizoids absent].
lst.		Known from Ecuador, to be expected
oh.		in Colombia Haplomitrium blumei
•		(Nees) R.M.Schust. (Haplomitriopsida)
	3.	Leaves not in 3 equal rows (leaf insertion
eph.		various) Jungermanniopsida: Key 2
*	4.	Thallus with air chambers (cross section)
oh.		and numerous small pores on dorsal
		surface. Thallus underside with scales,
iffn.		at least near the tip. Antheridia and
hiffn.		archegonia usually born in receptacles
chiffn.		Marchantiopsida: Key 1
	4.	Thallus lacking air chambers and pores.
		Thallus underside with or without scales
niffn.		
iffn.	5.	Upper surface of the thallus with a
		median groove. Plants often growing
		in rosettes (loosely forked in aquatic
ffn.		plants). Sporophytes embedded in the
		thallus Ricciaceae: Key 1
	5.	Upper surface of the thallus without

- vithout Uppe median groove. Plants not growing in rosettes. Sporophytes not embedded in
- 6. Rhizoids papillose. Thallus large, 1-3 cm wide, surface uniformily green. Gametangia produced in rounded

receptacles with blacks hairs at the margin... Dumortiera hirsuta (Sw.) Nees

- 7. Thallus large, (0.5-)1-3 cm wide, without midrib, margins crispate-undulate, surface with numerous small whitish dots (fresh material). Antheridia produced in rounded or elongate receptacles on the thallus surface *Monoclea gottschei* Lindb.
- Thallus smaller, with or without midrib, margins plane or undulate, surface without small dots. Antheridia not produced in receptacles on the thallus surface Jungermanniopsida: Key 2 (couplets 5-6)

Key 1. Marchantiopsida (complex thalloid liverworts)

- 2. Gemma receptacles absent 4

- 5. Plants floating on water (rarely on wet soil). Pores present, bounded by a ring

of cells. Ventral scales large, ligulate, with oil cells. Dorsal thallus surface \pm dark-green and reticulate

..... Ricciocarpos natans (L.) Corda

 Plants on soil, rarely in water (*Riccia* stenophylla). Pores ± absent, when present without ring of cells. Ventral scales usually absent, when present small and without oil cells. Dorsal thallus surface pale green to glaucous green, usually not reticulate Riccia

- 6. Thallus thicker, not translucent. Ventral scales present throughout. Sporophytes not on the ventral thallus surface 7
- 7. Air chambers without photosynthetic filaments. Female receptacles stalked..... 8

- Pores compound, barrel-shaped, formed of several layers of cells (cross-section). Male and female receptacles stalked and variously lobed Marchantia
- 11. Thallus completely black when dry, margins and underside dark purplishblack. Ventral scales lanceolate, longer than wide. Gemmae lacking. Sporophyte in a dark, swollen, mussel-like involucre below the thallus apex

..... Targionia hypophylla L.

11. Thallus not black when dry, margins and underside green or tinged with purple. Ventral scales very broad, much wider than long. Gemmae usually produced on thallus surface in a narrow, lunate receptacle. Sporophyte (very rare) on a stalked receptacle

..... *Lunularia cruciata* (L.) Dumort.

- 13. Thallus surface with numerous small whitish dots. Thallus margins undulatecrispate. Thallus without midrib

..... Monoclea gottschei

Key 2. Introductory key to Jungermanniopsida

- 1. Plants with stem and leaves 2
- 1. Plants thalloid 5
- 2. Plants different 3
- Leaves undivided, succubous. Leaf base several layers of cells thick. Cells thinwalled, without trigones. Rhizoids violet or colorless. Archegonia and antheridia on dorsal surface of stem. On soil or rock Pelliidae: Key 3
- 4. Leaves with a ventral lobule (= small or large fold or sac appressed to the leaf, on the ventral side of leaf), incubous

..... Porellales: Key 11

Leaves without lobule

.....Jungermanniales: Key 4

- 5. Thallus variously branched. Thallus margins without sausage-shaped slime papillae. Archegonia and antheridia on

- Thallus midrib with a central strand. Gametoecia on the dorsal side of the midrib Pallaviciniaceae: Key 3
- 6. Thallus midrib without central strand, or midrib absent. Gametoecia on the ventral side of the midrib or at the thallus margin Metzgeriidae: Key 3

Key 3. Metzgeriidae and Pelliidae (simple thalloid liverworts)

- 1. Plants with stem and leaves (Pelliidae). 2
- Rhizoids pale brown. Plants 4-10 mm wide, glaucous-green or deep green. Leaf margins flat, entire

..... Noteroclada confluens Taylor

- Rhizoids purplish. Plants 2-4(-5) mm wide, pale-green, usually forming rosettes. Leaf margins undulate, entire or toothed...... *Fossombronia*
- 3. Thallus simple or pinnate, without midrib or with midrib only on branches. Gametoecia on the thallus margin or on short lateral branche..... (Aneuraceae) 4
- 4. Thallus simple or scarcely branched, more than 2 mm wide, prostrate. Oil bodies 10-40 per cell. Male branches with antheridia in 2-6 rows...... *Aneura*

- 5. Thallus 2-8 mm wide, thallus 1-pinnate with rather short and wide branches (branches ca. 1-2× as long as wide).

Archegonia in incisions of the thallus margin surrounded by numerous crowded, multicellular paraphyses, not on branches. Known from Ecuador, to be expected in Colombia.... *Lobatiriccardia*

- 6. Thallus usually more than 3 mm wide, margins without hairs. Midrib with central strand. Gametoecia on the dorsal side of the midrib (Pallaviciniaceae) 7
- 7. Thallus divided into lobes.....

- 9. Archegonia surrounded by a ring of scales forming a cup-like involucre. After fertilization, a tubular pseudoperianth several times longer than the involucre developing from within the involucre....
 -Jensenia
- 9. Archegonia merely with a small scale inserted behind them (= side directed to the base of the thallus), cup-like involucre and pseudoperianth lacking....

..... Symphyogyna

10. Thallus margins with scattered slime hairs 2-4 cells long. Midrib with 1 central strand. Archegonia surrounded by a ring of scales forming a cup-like involucre. After fertilization, a tubular pseudoperianth several times longer than the involucre developing from within the involucre.

..... Pallavicinia lyellii (Hook.) Gray

 Thallus margins without slime hairs. Midrib with 1-3 central strands. Archegonia merely with a small scale inserted behind them (= side directed to the base of the thallus), cup-like

Key 4. Introductory key to Jungermanniales (foliose liverworts I)

- 5. Leaves bifid, alternate. Leaf cells not

conspicuously elongate near the ventral 6. Plants with 3 rows of leaves, mosslike. Perianth large, deeply plicate. Minute whitish, prostrate liverwort from superpáramo of Ecuador, to be expected in Colombia..... Anthelia *juratzkana* (Limpr.) Trevis. (Antheliaceae) 6. Plants with 2 rows of leaves (underleaves lacking). Perianth lacking or very small, inconspicuous..... Gymnomitriaceae: Kev 7 7. Leaves with (1-)2 large, sausage-shaped slime papillae at the tips of the segments or on the rounded margins. Plants very small, less than 1 mm wide, whitishgreen, the leaves almost longitudinally inserted on the stem. On rotten wood, soil and rock in rainforest ... Zoopsidella Leaves without large slime papillae at 7. 9. Underleaves and leaves of similar size, bifid or trifid...... (Herbertaceae) 10 9. Underleaves smaller than leaves...... 11 10. Leaves 2-3-lobed, without vitta. Leaf cells thin-walled to evenly thick-walled, ± without trigones..... Triandrophyllum subtrifidum (Hook.f. & Taylor) Fulford & Hatcher 10. Leaves bifid, with a broad vitta of elongate cells. Leaf cells with large trigones..... Herbertus 11. Leaves with 3 or more lobes or teeth..... Lepidozia 11. Leaves with 0-2 lobes or teeth...... 12 12. Rudimentary lobule (consisting of a few cells) present at ventral base of leaf. Stems fragile, ventral stem surface only 2-4 cells wide, hyalodermis often present. Ventral branches absentLejeuneaceae (with reduced lobules): Key 12

12. Lobules completely lacking. Stems rigid, ventral stem surface more than 4

(Spruce) Heinrichs et al. (Lejeuneaceae)

- 16. Underleaves present...... Key 4a16. Underleaves absent (or very small)......

Key 4a. Jungermanniales - Leaves succubous or transverse, underleaves present

1. 2. Leaves 4-lobed, underleaves as large as leaves..... Lepicolea Leaves not 4-lobed, underleaves smaller 3. Leaves folded and usually keeled, at least above, the keel often winged..... Lepidoziaceae: Key 8 3. Leaves not folded, without winged keel Dorsal leaf base decurrent. Leaves 4 asymmetrical, ventral margin arched, dorsal margin ± straight. Stems brown (or bluish), with thick-walled cortex..... 4. Dorsal leaf base not decurrent. Leaves \pm symmetrical. Thick-walled cortex 5. Leaves \pm transversely inserted, deeply concave. Branches originating from the ventral side of the stem...... Isotachis 5. Leaves \pm longitudinally inserted, not deeply concave. Branches originating from the lateral and ventral side of the stem...... Lophocoleaceae: Key 9 6. Leaves undivided.....7 7. Leafy plants at the base arising from a leafless, stoloniform shoot..... Lepidoziaceae: Key 8 7. Leafy plants not arising from a leafless, stoloniform shoot...... 8 8. Ventral stolons present Leaf insertion reaching the dorsal midline of stem or not. Rhizoids scattered.. Odontoschisma 8. Ventral stolons lacking. Leaf insertion reaching the dorsal midline of stem. Rhizoids scattered or in bundles........9 9. Underleaves entire, oblong-lanceolate. Rhizoids scattered. Plants green to reddish-brown or purple..... Nardia succulenta (Lehm.) Spruce

- 9. Underleaves bifid or toothed, rarely entire. Rhizoids in bundles. Plants green to brown...... Lophocoleaceae: Key 9

- 11. Underleaves similar to leaves (but sometimes smaller).....12

- Plants pale green, shallowly divided (to 1/4 or less) into 3-4 triangular lobes. Stem base stoloniform. Leaf cells thin-walled, cuticle smooth or sligthly papillose. Perianth on a short ventral branch, 3-keeled. In wet páramo......

.....Pseudoce-

phalozia quadriloba (Steph.) R.M.Schust.

- 17. Leaves transverse, strongly concave. Sporophyte in a fleshy perigynium...... *Isotachis*
- Leaves and underleaves divided to the middle into 2-3 narrow lobes (some 3-lobed leaves always present). Rhizoids in bundles..... Paracromastigum
- 19. Leaf insertion line not reaching dorsal midline of stem, dorsal side of stem "leaf-free". Rhizoids scattered.

..... Cephaloziaceae: Key 5

Key 4b. Jungermanniales - Leaves succubous or transverse, underleaves absent or minute

- Leaves bifid, alternate. Leaf cells not conspicuously elongate near the ventral margin....... Gymnomitriaceae: Key 7
- 4. Leaves opposite, the dosal leaf bases united, not falcate. Stems without paraphyllia. Stolons lacking. Plant green to brown to purplish or whitish.....

..... Gongylanthus

- Leaves plicate, with some longitudinal folds. Paraphyllia lanceolate. Sporophyte produced in a marsupium......... Stephaniellidium sleumeri (Müll.Frib.) Grolle

..... Cephaloziellaceae: Key 6

- 9. Plants with reddish or purple pigmentation. Perianth inflated over its whole length, with several plicae..... *Syzygiella*
- 9. Plants lacking reddish or purple pigmentation. Perianth flattened towards the mouth, with 2 keels...... *Plagiochila*
- Dorsal margin of leaves reflexed, dorsal leaf base distinctly decurrent. Leaf surface convex near dorsal margin and concave towards ventral margin....... 11

12. Plants green or brown. Leaf apex various but usually not obliquely truncateemarginate. Stems brown, darker than leaves. Oil bodies colorless, not filling cell-lumen. Sporophyte in a flattened perianth..... Plagiochila 13. Leaves several layers of cells thick near the base..... Pelliidae: Key 3 13. Leaves only one layer of cells thick. 14 14. Leafy plants arising from a creeping, stolon-like shoot......15 14. Leafy plants not arising from a creeping, 15. Leaves transverse. [Dorsal margin of leaves \pm inflexed (towards stem). Stem rigid, with thick-walled cortex. Gametoecia at stem base on abbreviated branches] (Adelanthaceae)......16 16. Cells in the upper part of the leaf \pm evenly thick-walled, without distinct trigones. Leaf base with a short vitta. Stem cortex well-developed, brown, of 2-3 cell layers (cross-section)..... Adelanthus 16. All leaf cells with distinct trigones, cells never evenly thick-walled. Vitta lacking. Stem cortex poorly developed, palecolored, of 1 layer of cells..... Pseudomarsupidium 17. Leaf cells small, less than 25 µm, without trigones. Plant less than 1 mm wide...... Kymatocalyx 17. Leaf cells larger, with or without trigones. Plants usually wider than 1 mm (rarely less than 1 mm)..... 18 18. Leaf insertion line not reaching dorsal midline of stem, dorsal side of stem leaf-free. Plants frequently with upright flagelliform branches producing gemmae..... Cephaloziaceae: Key 5 18. Leaf insertion line reaching dorsal midline of stem, dorsal side of stem not leaf-free. Plants without such gemmipa-

19. Leaf cells papillose. Plants whitishgreen to yellowish-green (sometimes

- 22. Ventral stolons present. Leaf insertion reaching dorsal midline of stem of stem or not. Gemmae sometimes present. Gynoecia on a short ventral branch....... *Odontoschisma*

- Plants light green to reddish or brown, not growing on wet rock in rivers. Leaf cells (20-)30-60 μm long in mid-leaf, trigones present or lacking. Rhzoids often numerous, sometimes in bundles. Perigynium present (inner female bracts attached to perianth base) *Solenostoma*

25. Leaves on sterile and male shoots with a very narrow base, the leaves 2-3× wider in the middle than at the base, caducousAcrobolbus cuneifolius (Steph.) Briscoe (= Acrobolbus caducifolius R.M.Schust. syn. nov.) 25. Leaves without very narrow base, not 26. Cuticle smooth.. Scapaniaceae: Key 10 27. Plants glossy whitish-green to light brown (never reddish or purple). Gemmae absent. Oil bodies brown......Acrobolbus 27. Plants greenish-brown to reddish or purple. Gemmae present or absent. Oil bodies colorless.....

..... Scapaniaceae: Key 10

Key 5. Cephaloziaceae

- Cells in midleaf 15-30(-40) μm long, trigones usually present (rarely lacking). Plants (0.5-)1-2 mm wide. On rotten wood, humus or rock, from sea level to páramo......Odontoschisma
- 3. Leaf base forming an inflated sac.....*Nowellia*
- 3. Leaf base not forming a sac...... 4
- 4. Leaves nearly longitudinally inserted, dorsal leaf base decurrent. Leaf apex shallowly retuse or bifid to 1/6-1/3 *.....Fuscocephaloziopsis*
- 4. Leaves subtransversely inserted, dorsal leaf base not decurrent. Leaf apex bifid to 1/3-1/2..... *Cephalozia*

Key 6. Cephaloziellaceae

- 1. Leaves undivided to retuse. Leafy stems erect, arising from creeping stolons...... 1. Leaves bifid to 1/3 or more. Leafy stems 2. Leaves obcuneate, widest above, apices rounded. Plants light green, without any pigmentation, minute, ca. 0.5 mm wide...Cephaloziopsis intertexta (Gottsche) R.M.Schust. 2. Leaves not obcuneate, apices acute or narrowly obtuse. Plants green to brown 3. Plants ca. 1 mm wide. Leaves distinctly concave, apices obtuse. Perianth terete. Only in páramo..... Gymnocoleopsis cvlindriformis (Mitt.) R.M.Schust. 3. Plants smaller, 0.3-0.6 mm wide. Leaves not concave, apices acute (rarely obtuse). Perianth plicate. Lowland, montane or páramo...... 4 4. Leaves subtransverse, hardly wider than the stem. Cells in midleaf very small,
- the stem. Cells in midlear very small, 8-15 μ m, thick-walled (rarely thinwalled). Leaf insertion reaching the dorsal midline of the stem. Occurring between ca. 500-4000 m... *Cephaloziella*
- Leaves distinctly succubous, distinctly wider than the stem. Cells in midleaf larger, 15-25 μm, thin-walled. Leaf insertion not reaching the dorsal midline of the stem. Below 1500 m.. *Cylindricola*

Key 7. Gymnomitriaceae

- 1. Plants larger, ascending to erect...... 3

- 3. Leaves strongly concave from base to apex (flattening of leaf impossible without tearing the leaf), very shallowly bifid to 1/8-1/5, with a broad, lunulate sinus and short, blunt tips....... *Gymnomitrion truncatoapiculatum* Herzog
- 4. Plants whitish to pale brown. Perianth lacking......*Gymnomitrion*
- 4. Plants green to brown to reddish, not whitish. Perianth present but very small, hidden between the bracts... *Marsupella*

Key 8. Lepidoziaceae

- Leaf cells very large, ca. 60-80 μm long in midleaf, thin-walled, without trigones. Leaf apex rounded to shortbifid, frequently with 1-2 large, sausageshaped slime papillae (rarely without)... Zoopsidella
- 4. Leaf cells smaller, usually with trigones. Leaf apex acute or divided into several

6. Leaves with 2-3 teeth at apex or

- 7. Leaves folded and usually keeled, at least above, the keel often winged...... 8
- 8. Leaf apex bifid to 1/4. Underleaves absent...... *Mytilopsis albifrons* Spruce
- 8. Leaf apex undivided or very short-bifid. Underleaves present (sometimes very small)......*Micropterygium*

- 10. Stem leaves 2-3-lobed. Stems with a stoloniferous base.... *Paracromastigum*

Key 9. Lophocoleaceae

- Underleaves variable, entire to bifid on the same stem and usually narrower than the stem. Plants pale green, small, less than 1.5 mm wide. Leaf cells thinwalled, ± without trigones. On moist soil and rock in or near running water.. *Clasmatocolea vermicularis* (Lehm.) Grolle
- Leaves ± transverse, strongly caducous. Plants minute, yellowish green, ca.
 0.5 mm wide. Tiny epiphyte in upper montane cloud forest and páramo.... Lophocolea fragmentissima R.M.Schust.

- 7. Leaf apex bifid...... Lophocolea
- Leaf apex with 3 or more cilia (rarely only 2)..... Leptoscyphus

- Gametangia on very short ventral branches, hidden under the leaves. Perianth without keels.... *Heteroscyphus*
- 10. Leaves bifid..... Cryptolophocolea
- Leaves with 4-15 cilia, not bifid. Leptoscyphus trapezoides (Mont.) L.Söderstr.
- Underleaves attached to leaves on one side only. Leaf apex entire or with 2-3 obtuse lobes...... *Heteroscyphus contortuplicatus* (Nees & Mont.) Grolle

- 12. Leaf apex with 2 teeth. Underleaves with 2-6 teeth or cilia (rarely more)...... *Cryptolophocolea*
- 12. Leaf apex with 3 or more teeth or cilia. Underleaves with numerous cilia...... 13
- Underleaves small, 2-3× wider than the stem, subquadrate, deeply bifid. Dioicous...... *Leptoscyphus trapezoides*
- Underleaves larger, 3-5× wider than the stem, reniform, not or shallowly bifid. Monoicous or dioicous... *Heteroscyphus*

Key 10. Scapaniaceae

- Leaf margins on sterile stems toothed. Leaf cells large, 30-60 μm in midleaf, thin-walled, with very small trigones. 4
- 4. Ventral stolons present..... Lophonardia

- Leaf cells smaller, 30-40 μm in midleaf. Stem epidermis cells less than 4× longer than wide. Gemmae presen....... Schistochilopsis incisa (Schrad.) Konstant.
- Trigones large. Leaf apex acute to acuminate. Plants reddish-brown or purple, rarely green..... Anastrophyllum

- Leaf cells with ± uniformly thickened walls, trigones inconspicuous. Ventral stolons absent. Gemmae present or absent. Rare species of (super)páramo. 8
- Leaves distant or laxly imbricate, leaf apices acute or obtuse. Leaf cells smaller, 15-20 μm in midleaf. Plants dioicous, frequently sterile, without resin smell. Gemmae absent or reddish-brown......9
- Leaves succubous, leaf apices obtuse. Plants greenish-brown, ca. 1 mm wide. Perianth eplicate, completely smooth.....

cylindriformis (Cephaloziellaceae)

- *ylinarijormis* (Cephaloziellaceae)
- 9. Leaves transverse, leaf apices (sub)acute. Plants reddish or greenish-brown, 0.5-1 mm wide. Perianth plicate, sometimes with a white mouth...... **Sphenolobus**

Key 11. Introductory key to Porellales (foliose liverworts II)

- 4. Plants pure green, without any trace of reddish pigmentation. Leaf margins toothed. Lobules very small, attached to the ventral margin of the lobe, at some distance from the stem.....

..... Jubula bogotensis Steph.

- Stems fragile, epidermis of only 5-6 rows of cells. Rhizoids from ventral surface of stem. Lobules very narrowly attached to stem (by only 1-4 cells). Plants very small, usually less than 1 mm wide. Leaf cells with many small, colorless oil bodies......

..... Lejeuneaceae: Key 12

Key 12. Lejeuneaceae

- 4. Underleaves undivided to weakly
- 4. Underleaves bifid..... Key 12b

Key 12a. Lejeuneaceae with undivided underleaves

- 1. Leaf margins toothed, at least near apex 2
- 2. Ventral merophyte 4 or more cells wide
- 2. Ventral merophyte 2(-3) cells wide.... 11
- Width of the ventral merophyte is measured by the number of epidermis cells across the ventral stem surface (= area between where the underleaves are attached, but not in the direct neighborhood of the underleaf base because there the number of epidermis cells is variable).
- Leaf cells with evenly thickened walls, trigones lacking. Lobules with a very long, curved tooth (5-10 cells long). Underleaves toothed, emarginate. *Fulfordianthus pterobryoides* (Spruce) Gradst.

- 6. Plants pinnate or dichotomous, branches predominantly *Frullania*-type. Innovations lacking...... *Bryopteris*
- Lobules with 7-9 teeth. Underleaf apex ± rounded, base auriculate. Perianth 8-10-keeled, with innovations. High Andes of Peru and Ecuador, to be expected in Colombia....... *Frullanoides laciniatiflora* (Loitl.) van Slageren.
- Lobules with 1-3 teeth. Underleaf apex emarginate, base not auriculate. Perianth 3-keeled, without innovations. Throughout tropical America.. *Caudalejeunea lehmanniana* (Gottsche) A. Evans
- Underleaf insertion line ± straight. Plants 1.5-2 mm wide. Perianth with two ventral keels, innovations lacking.... Lopholejeunea nigricans (Lindenb.) Schiffn.

- 10. Lobules strongly inflated-rounded, small (hidden behind the underleaves),

 \pm without teeth. Perianth on a very short branch, with one short innovation or without innovation..... Symbiezidium dentatum Herzog 11. Underleaves very large, 6-10× stem width, apex very short-bifid. Perianth terete, without keels..... Lejeunea sulphurea (Lehm. & Lindenb.) Spruce 11. Underleaves smaller, apex undivided (emarginate in Harpalejeunea). Perianth 12. Plants pale green. Disciform gemmae usually produced on dorsal leaf margins. Underleaf apex truncate... Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans 12. Plants brownish green. Disciform 13. Leaves with (5-)7-25 teeth. Underleaves toothed or entire. On living leaves or bark Odontolejeunea 13. Leaves with 1-5 teeth. Underleaves entire. On bark or rock..... 14 14. Branches predominantly Frullania-type. Female bracteole toothed. Dicranolejeunea axillaris (Nees & Mont.) Schiffn. 14. Branches predominantly Lejeunea-type. Female bracteole entire. Acanthocoleus aberrans (Lindenb. & Gottsche) Kruijt 16. Leaves with ocelli (scattered, in a row or 1-2 ocelli near leaf base)..... 17 17. Ocelli in a row or 1-2 near leaf base. 18 18. Row of ocelli 7-22 cells long. Ventral merophyte 4-6 cells wide. Lobule tooth 3-5 cells long. Canopy epiphyte in lowland rainforest of Brazil; to be expected in the Colombian Amazon. Neurolejeunea seminervis (Spruce) Schiffn. 18. Row of ocelli 1-6 cells long. Ventral merophyte 2(-3) cells wide. Lobule tooth 1 cell long 19 19. Lobule fully inflated, bottle-shaped, with a long, falcate tooth. Perianth sharply

5-keeled, the keels smooth or toothed, never extending into inflated horns...... Harpalejeunea 19. Lobule inflated in the lower half, flattened above, rectangular, with a short, blunt tooth. Perianth 4-keeled, the keels smooth and extended into inflated horns..... Ceratolejeunea 20. Ventral merophyte 4 or more cells wide.. 20. Ventral merophyte 2-3 cells wide (see note in couplet 2)..... 22 21. Underleaf apex undivided. Frullaniatype branches present. Leaf apex rounded Stictolejeunea 21. Underleaf apex emarginate. Frullaniatype branches lacking. Leaf apex acute, rarely rounded...... Lepi-

- Leaf cells with minute trigones. Ocelli inconspicuous, equal in size to or smaller than other leaf cells. Epidermal cells thin-walled. Lobules straight or somewhat curved upwards....... Lepidolejeunea sullivantii (Gottsche) E.Reiner
- 23. Ventral merophyte 4 or more cells wide 24

- 26. Plants dark green to brown to blackish, rather robust, 2-3.5 mm wide, leaves when dry strongly convolute. Stems rigid, without hyalodermis, ventral

- 27. Lobules with 0-2 teeth (occasionally 3 teeth: *Mastigolejeunea innovans*)...... 30
- Plants blackish in older stem portions. Perianth with 5-10 keels, with innovations *Frullanoides*
- Plants not blackish. Perianths with 3-10 keels, innovations present or absent......
 29
- 29. Underleaf insertion line slightly curved, underleaf base plane. Perianth with 5-10 keels, innovations lacking. Flagelliform branches (producing caducous leaves) frequently present. Lowlands (0-800 m) *Acroleieunea*
- Ventral epidermis cells not or scarcely larger than medulla cells (stem crosssection). Medulla cells thick-walled. Plants brown-green to blackish-green. 31

- 34. First lobule tooth short, incurved and blunt, second tooth long, pointing outwards, sharp. Lobule truncate. Leaves not squarrose when moist. Upper montane (above 2000 m).....

..... Blepharolejeunea

 Lobule teeth equal or the first tooth larger than the second. Lobule oblique or truncate. Leaves squarrose when moist. Lowland and montane (300-2000 m)....

.....Brachiolejeunea

- 36. Lobules with 2-4 teeth...... 37
- 36. Lobules with 0-1 tooth...... 40
- Leaf apex strongly and broadly recurved, acute. Epidermal cells thin-walled. Plants glossy brown. Above 2000 m...... *Lindigianthus cipaconeus* (Gottsche) Kruijt & Gradst.
- 37. Leaf apex ± plane, rounded or acuteacuminate. Epidermal cells thick-walled
 38
- 38. Insertion line of underleaves deeply arched (more than 100 μm deep). Ventral merophyte 6-12 cells wide. Plants more than 2 mm wide, often black. Perianth without ventral keels........ Marchesinia
- 38. Insertion of underleaves straight or shallowly curved. Ventral merophyte 4 cells wide. Plants smaller, never black. Perianth with two ventral keels....... 39

- 41. Lobules less than 1/4 leaf length. Leaf cells with radiate trigones. Perianth on a very short branch (appearing lateral on the stem), keels ciliate-laciniate. Lowland and montane.... *Symbiezidium*
- 41. Lobules 1/4-1/2× leaf length. Leaf cells usually with large bulging trigones. Perianth on an elongate shoot, keels smooth. Exclusively montane.....

.. Cheilolejeunea (sect. Omphalanthus)

- 44. Epidermis cells distinctly larger than medulla cells (stem cross-section).

- 45. Innovations lacking. Free margin of lobule incurved, at least near apex. Leaves when moist obliquely spreading, ± squarrose. Amazonia *Verdoornianthus*
- 45. Innovations present. Free margin plane. Leaves when moist widely spreading, not squarrose. Widespread, common. 46
- 46. At least some lobules reduced. Underleaves 2-4× stem width, distant to subimbricate. Innovations lejeuneoid (basal leaf on innovation is a lateral leaf: see Gradstein *et al.* 2001: Fig. 4J). Autoicous. Plants pale-green to greenish-brown to black.... *Dibrachiella*
- Lobules strongly swollen, ball-shaped, free margin inrolled 2-3 times. *Anoplolejeunea conferta* (Meissn.) A. Evans

- 48. *Frullania*-type branches lacking. Lobules with 1 tooth. Plants pale green... 49
- 49. Plants tiny, 0.4-0.7 mm wide. Leaf lobes suberect to obliquely spreading. Lobule tooth long-acute, consisting of a strongly elongate cell (at least 4× as long as wide). Hyaline papilla distal to the

49. Plants larger. Leaves wide-spreading. Lobule tooth blunt or acute, short. Hyaline papilla proximal to the tooth (except in *L. herminieri* (Steph.) R.L.Zhu). Underleaves larger.. *Lejeunea*

Key 12b. Lejeuneaceae with bifid underleaves

- 1. Leaves highly specialized, upper part forming an inflated sac...... *Colura*

- 3. Plants growing upright or pendent from a rhizome-like base. Lobules lacking on upright or pendent stems. Leaves transversely inserted, insertion line very short. Underleaves minute. Paroicous; antheridia in axils of female bracts........ *Colura irrorata* (= *Myriocolea irrorata*)
- 3. Plants creeping or pendent, without rhizome-like base. Lobules present. Leaves longitudinally inserted, insertion line long. Underleaves well-developed. Autoicous; antheridia on separate

branches..... .. Lejeunea (subg. Neopotamolejeunea) 4. Underleaf lobes conspicuously diverging Underleaf lobes not conspicuously 4. diverging......13 5. One underleaf to each leaf, the underleaves usually densely overlapping. Leaf apex rounded..... Diplasiolejeunea 5. One underleaf to every alternate leaf, the underleaves usually distant. Leaf apex 6 Underleaf lobes mostly 1 cell wide (except at the base), apex acute......7 6. Underleaf lobes broader, apex blunt... 10 7. 8. Lobule tooth short and blunt, not falcate. Ocellus near leaf base very large. 2.5- $4 \times$ longer than adjacent leaf cells. Gynoecium without innovation..... Leptolejeunea Lobule tooth elongate, falcate. Ocellus 8. near leaf base smaller, maximally $2 \times$ longer than adjacent leaf cells. Gynoecium with innovation. In lowland rainforest..... Drepanolejeunea polyrhiza (Nees) Grolle & R.L.Zhu Ocellus near leaf base very large, 2.5-9. $4 \times$ longer than surrounding leaf cells. Lobule tooth short and blunt, not falcate. Gynoecium without innovation..... Leptolejeunea 9. Ocellus at leaf base smaller, $1-2 \times \text{longer}$ than surrounding leaf cells, or lacking. Lobules with a long, falcate tooth (rarely short and blunt). Gynoecium usually with innovation (rarely without)..... Drepanolejeunea

- Leaf lobes with an unbroken row of 4-8 ocelli, ocelli usually glossy yellowishbrown. In the outer canopy of Amazonian rainforest...... *Cheilolejeunea urubuensis* (Zartman & I.L.Ackerman) Wei *et al.*
- 10. Leaf lobes with a broken or unbroken row of (1-)2-3 ocelli in the lower half,

	the ocelli colorless or grayish. Lowland
	and montane11
11.	Ocelli in a broken row

- Drepanolejeunea
- Innovations pycnolejeuneoid (basal leaf on innovation is an underleaf; see Gradstein *et al.* 2001: Fig. 4I). Cells on dorsal leaf surface mamillose, thick-walled, with a broad, lens-shaped papilla. Lobule with or without pre-apical tooth (= tooth situated at the distal end of the lobule, at the junction with the ventral leaf margin)...... *Drepanolejeunea*

- 13. Underleaves smaller..... 15
- 14. Leaf cells uniformly thin-walled or with small trigones. Lobules often reduced; hyaline papilla proximal to the tooth at the lobule apex (see Gradstein *et al.* 2001: Fig. 4G). Plants glistening pale green, yellowish-green or whitish (stems often long and slender, pendent). Oil bodies small, numerous per cell, finely granular or homogeneous...... Lejeunea
- 14. Leaf cells with conspicuous trigones. Lobules not reduced; hyaline papilla distal to the tooth at the lobule apex (see Gradstein *et al.* 2001: Fig. 4H). Plants dull pale green to olive green. Oil bodies very large, 1-3 per cell, sausage-shaped, coarsely granular.

..... Cheilolejeunea

15. Lobules when well-developed very large, 3/5-4/5 of lobe length. Leaves usually suberect, almost parallel to the stem. Plants minute, 0.2-0.6 mm wide.... 16

- 16. Plants dioicous. Leaves usually with 1 or more ocelli (at the base or scattered in the leaf). Innovations lejeuneoid (basal leaf on innovation is a lateral leaf; see Gradstein *et al.* 2001: Fig. 4J).....

.....Microlejeunea

- 17. Ocelli present in leaves...... 18

- 18. Ocelli lacking in underleaves...... 21
- Ocelli reddish or brown. Leaf cells with a broad papilla or smooth. Caducous leaves absent. Gynoecia on a very short branch, without innovations.....

..... Pictolejeunea

- 23. Plants brown or brownish-green. Walls of leaf cells ± pale brown, trigones radiate (or lacking). Branch bases sometimes with a huge, strongly inflated lobule ("utricle"). Perianth usually with inflated horns (horns sometimes absent...

..... Ceratolejeunea

- 24. Leaf lobes not with an unbroken row of 4-8 ocelli. Lowland and montane...... 25
- 25. Underleaf margins denticulate to crenulate to subentire. Gemmae usually present on leaf margins. Perianth flattened, 2-keeled, the keels expanded above into short auricles. On living leaves, occasionally on bark or rock......

Cyclolejeunea

- Plants very small, less than 0.7 mm wide. Leaves suberect or obliquely spreading. Ocelli grayish or brown..*Microlejeunea*

...... *Otigoniolejeunea huctumalcensis* (Lindenb. & Gottsche) Y.M.Wei *et al.*

- Leaf margins (and sometimes the entire dorsal leaf surface) toothed by conically projecting cells with thick-walled tips ...
 31

- Dorsal leaf surface smooth or papillose, not spinose. Perianth flattened, with 2 keels Prionolejeuna
- 32. Vegetative reproduction by means of large, multicellular, rounded or elongate gemmae from leaf margins. [Plants usually growing on living leaves.

Margins of leaves and underleaves ± toothed] *Cyclolejeunea*

- 36. Leaves less elongate...... 40
- 37. Leaves suberect, apex acute-acuminate.. *Drepanolejeunea*

- 39. In wet leaf axils of tank bromeliads. Midleaf cells in elongate leaves 35-70 μm long, 1.5-4× longer than wide. Perianth inflated, 5-keeled, keels not expanded into auricles.....

..... Bromeliophila helenae Gradst.

- On living leaves in lowland rainforest. Midleaf cells smaller, 20-30 μm long, subisodiametrical. Perianth flattened, 2-keeled, keels expanded into large auricles...... Otolejeunea schellii Tixier
- 40. Walls of leaf cells ± pale brown, trigones radiate (or lacking). Branch bases sometimes with a huge, strongly inflated lobule (= utricle). Perianth usually with horns. Plants brown or brownish-green..

..... Ceratolejeunea

- 41. Trigones large or small. Lobules never reduced, always strongly inflated. Oil bodies large (more than 1/2 the cell lumen in length), coarsely segmented. Hyaline papilla distal to the lobule tooth (or between 2 small, closely associated teeth at the leaf apex) (see Gradstein *et al.* 2001: Fig. 4H)....... *Cheilolejeunea*
- 41. Trigones lacking or very small. Lobules sometimes reduced, inflated or not inflated. Oil bodies smaller (less than 1/4 the cell lumen in length), finely segmented or smooth. Hyaline papilla proximal to the lobule tooth (see Gradstein *et al.* 2001: Fig. 4G).....

..... Lejeunea

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