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 The key to the genera of liverworts of Colombia (Uribe-M. & Aguirre-C. 1997) is out of date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 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. 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 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

Aytoniaceae

Asterella P.Beauv.

Plagiochasma Lehm. & Lindenb.

Corsiniaceae

Cronisia Berk.

Cyathodiaceae

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

Acrobolbus Nees Lethocolea Mitt.

Tylimanthus Mitt.

Adelanthaceae

Adelanthus Mitt.

Pseudomarsupidium Herzog

Arnelliaceae

Gongylanthus Nees

Balantiopsaceae

Isotachis Mitt.

Neesioscyphus Grolle

Ruizanthus R.M.Schust.

Calvpogeiaceae

Calypogeia Raddi

Cephaloziaceae

Alobiellopsis R.M.Schust.

Cephalozia (Dumort.) Dumort.

Fuscocephaloziopsis Fulford

Nowellia Mitt.

Odontoschisma (Dumort.) Dumort.

Cephaloziellaceae

Cephaloziella (Spruce) Schiffn.

Cephaloziopsis (Spruce) Schiffn.

Cylindrocolea 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) Schiffn. Drepanolejeunea (Spruce) Steph. Frullanoides Raddi Fulfordianthus Gradst. Harpalejeunea (Spruce) Schiffn. Lejeunea Lib. Lepidolejeunea R.M.Schust. Leptolejeunea (Spruce) Steph. Lindigianthus Kruijt & Gradst. Lopholejeunea (Spruce) Steph. Luteolejeunea Piippo Marchesinia Gray Mastigolejeunea (Spruce) Steph. Metalejeunea Grolle Microlejeunea (Spruce) Steph. Myriocoleopsis Schiffn. Neurolejeunea (Spruce) Schiffn. Odontolejeunea (Spruce) Schiffn. Otigoniolejeunea (Spruce) Schiffn. Otolejeunea Grolle & Tixier Pictolejeunea Grolle Prionolejeunea (Spruce) Schiffn. Pycnolejeunea (Spruce) Schiffn. Rectolejeunea A.Evans Schiffneriolejeunea Verd. Stictolejeunea (Spruce) Schiffn. 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

1.	Plants with stem and leaves
1.	Plants thalloid4
2.	Leaves divided into segments
	Jungermanniopsida: Key 2
2.	Leaves not divided into segments 3
3.	Leaves in 3 equal rows, leaf insertion
٥.	transcenses [Dlants arraying and from
	transverse. [Plants growing erect from
	a leafless rhizome, rhizoids absent].
	Known from Ecuador, to be expected
	in Colombia Haplomitrium blumei
	(Nees) R.M.Schust. (Haplomitriopsida)
3.	Leaves not in 3 equal rows (leaf insertion
	various) Jungermanniopsida: Key 2
4.	Thallus with air chambers (cross section)
	and numerous small pores on dorsal
	surface. Thallus underside with scales,
	at least near the tip. Antheridia and
	archegonia usually born in receptacles
4.	Thallus lacking air chambers and pores.
	Thallus underside with or without scales
	5
5.	Upper surface of the thallus with a
	median groove. Plants often growing
	in rosettes (loosely forked in aquatic
	plants). Sporophytes embedded in the
	thallus Ricciaceae: Key 1
5.	Upper surface of the thallus without
٥.	median groove. Plants not growing in
	rosettes. Sporophytes not embedded in
_	the thallus
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
- 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 Lindh
- 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
- 3. Gemma receptacles a lunate "scale"

 Lunularia cruciata (L.) Dumort.

- 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 ± dark-green and reticulate

- 6. Thallus thicker, not translucent. Ventral scales present throughout. Sporophytes not on the ventral thallus surface 7
- Air chambers without photosynthetic filaments. Female receptacles stalked..... 8
- 8. Pores surrounded by several rings of differentiated cells. Archegoniophore arising at the thallus apex on a 10-40 mm long stalk. Sporophyte surrounded by a large, conical, whitish or purplish pseudoperianth which hangs down beneath the receptacle and is split above into 8-16 narrow segments. Thallus glossy green to reddish Asterella

Plagiochasma rupestris (Forster) Steph.

9. Thallus bright light green, surface conspicuously reticulate, pores distinct. Ventral scales lanceolate, ± toothed, Key 2. Introductory key to Jungermanniopsida	
in several ill-defined rows, each scale 1. Plants with stem and leaves	2
with an ill-defined, linear-lanceolate 1. Plants thalloid	
appendage. Known from Ecuador (but 2. Plants robust, to 10 cm long a	
very rare), to be expected in Colombia mm wide, reddish or purplish.	
(Lindenb.) Müll.Frib. (Cleveaceae) clasping the stem, undivided	
10. Pores compound, barrel-shaped, formed margin with a conspicous white r	
of several layers of cells (cross-section). Underleaves absent. Perianth ter	_
Male and female receptacles stalked and plicate)	urozia
variously lobed	
10. Pores simple, of one layer of cells. 2. Plants different	
Receptacles sessile or only the female 3. Leaves undivided, succubous. Le	
receptacle stalked	s thin-
11. Thallus completely black when dry, walled, without trigones. Rhizoid	violet
margins and underside dark purplish- or colorless. Archegonia and ant	neridia
black. Ventral scales lanceolate, longer on dorsal surface of stem. On	soil or
than wide. Gemmae lacking. Sporophyte rock	Key 3
in a dark, swollen, mussel-like involucre 3. Leaves divided into segmen	ts or
below the thallus apex undivided, incubous, succubo	
	-
11. Thallus not black when dry, margins and cells thick. Cells thin-walled or	
underside green or tinged with purple. walled, often with trigones. R	
Ventral scales very broad, much wider not violet. Archegonia on apex of	
than long. Gemmae usually produced or short branch, antheridia in lea	
on thallus surface in a narrow, lunate On bark, living leaves, rotten	
receptacle. Sporophyte (very rare) on a rock and soil (Jungermanniidae –	
stalked receptacle liverworts)	
<i>Lunularia cruciata</i> (L.) Dumort. 4. Leaves with a ventral lobule (= s.	
12. Plants small, thallus segments less than large fold or sac appressed to the l	
0.5 cm wide, often in (partial) rosettes. the ventral side of leaf), incubous	
Thallus surface often with a median Porellales:	
groove	
12. Plants large, thallus segments 1-3 cm Jungermanniales:	
wide, never in rosettes. Thallus surface 5. Thallus unbranched or with a few	
without median groove	
whitish dots. Thallus margins undulate-	
crispate. Thallus without midrib Archegonia and antheridia on	
13. Thallus surface without whitish dots. siella serrulata Steph. (Lepidozia	-
Thallus margins plane. Thallus with a 5. Thallus variously branched.	
• •	halliis
narrow midrib formed by rhizoids on the margins without sausage-shaped	

...... Dumortiera hirsuta

the thallus surface or in cavities, not on Archegonia in incisions of the thallus margin surrounded by numerous 6. Thallus midrib with a central strand. crowded, multicellular paraphyses, not Gametoecia on the dorsal side of the on branches. Known from Ecuador, to be midrib Pallaviciniaceae: Kev 3 expected in Colombia.... Lobatiriccardia Thallus 0.5-2(-3) mm wide, margins 6. Thallus midrib without central strand. or midrib absent Gametoecia on the with unicellular hairs (= rhizoids). ventral side of the midrib or at the thallus Midrib without central strand (cross margin Metzgeriidae: Key 3 section). Gametoecia on the ventral side Key 3. Metzgeriidae and Pelliidae Thallus usually more than 3 mm wide, margins without hairs. Midrib with (simple thalloid liverworts) central strand. Gametoecia on the dorsal 1. Plants with stem and leaves (Pelliidae). 2 side of the midrib (Pallaviciniaceae) 7 1. Plants thalloid (Metzgeriidae and Pellii-Thallus divided into lobes.....Symphyogyna 2. Rhizoids pale brown. Plants 4-10 mm wide, glaucous-green or deep green. Leaf Thallus ascendent to erect from a margins flat, entire Thallus prostrate or slightly ascendent, 2. Rhizoids purplish. Plants 2-4(-5) mm 9. Archegonia surrounded by a ring of wide. pale-green, usually forming rosettes. Leaf margins undulate, entire scales forming a cup-like involucre. After fertilization, a tubular pseudoperianth 3. Thallus simple or pinnate, without several times longer than the involucre developing from within the involucre.... midrib or with midrib only on branches.Jensenia Gametoecia on the thallus margin or on short lateral branche..... (Aneuraceae) 4 9. Archegonia merely with a small scale 3. Thallus simple or dichotomous, with a inserted behind them (= side directed midrib throughout. Gametoecia on the to the base of the thallus), cup-like involucre and pseudoperianth lacking.... 4. Thallus simple or scarcely branched,Symphyogyna more than 2 mm wide, prostrate. Oil 10. Thallus margins with scattered slime bodies 10-40 per cell. Male branches hairs 2-4 cells long. Midrib with 1 with antheridia in 2-6 rows...... Aneura central strand. Archegonia surrounded by a ring of scales forming a cup-like 4. Thallus distinctly branched (irregularly involucre. After fertilization, a tubular to regularly pinnate), 0.5-2(-8) mm wide, prostrate or erect. Oil bodies less pseudoperianth several times longer than 10 per cell. Male branches with than the involucre developing from within the involucre..... 5 Thallus 0.5 - 2mm wide. Pallavicinia lyellii (Hook.) Gray 1-3-pinnate with short or long branches. 10. Thallus margins without slime hairs.

Archegonia on short lateral branches,

with rather short and wide branches

(branches ca. $1-2\times$ as long as wide).

5. Thallus 2-8 mm wide, thallus 1-pinnate

Midrib with 1-3 central

Archegonia merely with a small scale

inserted behind them (= side directed

to the base of the thallus), cup-like

	involucre and pseudoperianth lacking Symphyogyna	6	conspicuously elongate near the ventral margin
	Key 4. Introductory key to	6.	Plants with 3 rows of leaves, moss- like. Perianth large, deeply plicate.
J	Jungermanniales (foliose liverworts I)		Minute whitish, prostrate liverwort from superpáramo of Ecuador, to be expected
1.	Leaves deeply divided into hair-like		in Colombia
	segments which are not more than 1-2		juratzkana (Limpr.) Trevis. (Antheliaceae)
	cells wide at base	6.	Plants with 2 rows of leaves (underleaves
1.	Leaves undivided or divided into		lacking). Perianth lacking or very small,
	segments which are more than 2 cells		inconspicuous
	wide at base		Gymnomitriaceae: Key 7
2.	Leaves divided to the base into 1-4	7.	Leaves with (1-)2 large, sausage-shaped
	filaments (= uniseriate segments),		slime papillae at the tips of the segments
	margins entire. Plants very small, alga-		or on the rounded margins. Plants very
2	like		small, less than 1 mm wide, whitish-
2.	Leaves divided into 4-9 segments,		green, the leaves almost longitudinally
	margins strongly ciliate. Plants larger,		inserted on the stem. On rotten wood,
3.	not alga-like	7.	soil and rock in rainforest Zoopsidella Leaves without large slime papillae at
٥.	into numerous ciliate parts, the plants	7.	the tips or on the margins
	strongly "hairy". Leaf cells with thin	8.	Leaves incubous 9
	or uniformly thickened walls, trigones	8.	Leaves succubous or transverse 16
	lacking. Underleaves smaller than lateral	9.	Underleaves and leaves of similar size,
	leaves. Plants whitish-green or brown		bifid or trifid (Herbertaceae) 10
		9.	Underleaves smaller than leaves 11
	Probably all <i>Trichocolea</i> species from		Leaves 2-3-lobed, without vitta. Leaf
	Colombia belong to <i>Leiomitra</i> but some		cells thin-walled to evenly thick-walled,
	poorly known species that are only		± without trigones
	known from sterile material have not yet		Triandrophyllum subtrifidum
	been transferred to Leiomitra.		(Hook.f. & Taylor) Fulford & Hatcher
3.	Leaves 4-lobed, the segments not split	10.	Leaves bifid, with a broad vitta of
	into numerous ciliate parts. Leaf cells		elongate cells. Leaf cells with large trigo-
	with large trigones. Underleaves as		nes
	large as lateral leaves. Plants gray-	11.	Leaves with 3 or more lobes or teeth
	green or brown	1.1	Lepidoziaceae: Key 8
1	Blepharostoma trichophyllum (L.)Dumort.		Leaves with 0-2 lobes or teeth
4.	Small whitish, worm-like plants with	12.	Rudimentary lobule (consisting of a
	densely imbricate leaves on soil in		few cells) present at ventral base of
4.	páramo		leaf. Stems fragile, ventral stem surface only 2-4 cells wide, hyalodermis often
4 . 5.			present. Ventral branches absent
٥.	Leafcells conspicuously elongate near the		Lejeu-
	ventral margin		neaceae (with reduced lobules): Key 12
	Arnelliaceae: Key 4b	12	Lobules completely lacking. Stems
5.	Leaves bifid, alternate. Leaf cells not		rigid, ventral stem surface more than 4
			<i>5,</i>

13.	cells wide, hyalodermis absent. Ventral branches frequently present		Key 4a. Jungermanniales - Leaves succubous or transverse, underleaves present
	on twigs near running water, with numerous clustered perianths on short lateral branches. Underleaves minute. Known from Ecuador, in rivers with	1.	Leaf margins toothed
	granite rocks and strongly fluctuating water levels, between 1200-1800 m, to	2.	Leaves not 4-lobed, underleaves smaller than leaves
	be expected in Colombia	3.	Leaves folded and usually keeled, at least above, the keel often winged
13.	Plants forked, irregularly branched or unbranched, not growing on twigs near running water, perianths lacking or on	3.	Leaves not folded, without winged keel4
	ventral side of stem (not clustered on short lateral branches). Underleaves well-developed	4.	Dorsal leaf base decurrent. Leaves asymmetrical, ventral margin arched, dorsal margin ± straight. Stems brown
14.	Stems forked, flagelliform ventral branches present. Leaf apex bifid or	4.	(or bluish), with thick-walled cortex Plagiochila Dorsal leaf base not decurrent. Leaves
14.	trifid (rarely entire)		± symmetrical. Thick-walled cortex lacking
15	Leaf apex entire or bifid	5.	Leaves ± transversely inserted, deeply concave. Branches originating from the ventral side of the stem <i>Isotachis</i>
13.	Underleaf cells very different from leaf cells (except in M . $nephrostipa$), conspicuously elongate, $2-5 \times$ as long	5.	Leaves ± longitudinally inserted, not deeply concave. Branches originating from the lateral and ventral side of the
	as wide, without chlorophyll, hyaline. Plants deep green to brown. Leaf apex entire. Oil bodies brownish, finely		teaves undivided
	granular. Vegetative reproduction by caducous leaves	7.	Leafy plants at the base arising from a leafless, stoloniform shoot
15.	Underleaves bifid. Underleaf cells similar to leaf cells, 1-2× as long as wide, with chlorophyll, not hyaline.		Leafy plants not arising from a leafless, stoloniform shoot
	Plants pale green to bluish green. Leaf apex usually bifid. Oil bodies colorless	8.	Ventral stolons present Leaf insertion reaching the dorsal midline of stem or not. Rhizoids scattered <i>Odontoschisma</i>
	or sepia, coarsely granular. Vegetative reproduction by gemmae produced on upright, flagelliform branches	8.	Ventral stolons lacking. Leaf insertion reaching the dorsal midline of stem.
	Underleaves present Key 4a Underleaves absent (or very small)	9.	Rhizoids scattered or in bundles 9 Underleaves entire, oblong-lanceolate. Rhizoids scattered. Plants green to
10.	Key 4b		reddish-brown or purple

10. 10.	entire. Rhizoids in bundles. Plants green to brown Lophocoleaceae: Key 9 Leaves divided into 3-5 lobes. Plants small, less than 2 mm wide, leafless stolons present or lacking		creeping, whitish in color. Leaves scarcely wider than the stem. On soil in superpáramo (above 4000 m). Known from Ecuador, to be expected in Colombia
	piliferous. On soil in superpáramo of the Sierra Nevada de Santa Marta]	17.	Leaves transverse, strongly concave. Sporophyte in a fleshy perigynium
11	Ruizanthus venezuelanus R.M.Schust. Underleaves similar to leaves (but	17	Leaves succubous. Sporophyte in a peri-
11.	sometimes smaller)	1/.	anth
12.	Leaves succubous. [Leaves palmate,	18.	Leaves and underleaves divided to the
	divided to ca. 1/2 into narrow lanceolate,		middle into 2-3 narrow lobes (some
	conspicuously diverging lobes]		3-lobed leaves always present). Rhizoids
12		10	in bundles
	Plants pale green, shallowly divided (to	10.	undivided, never 3-lobed, less deeply
15.	1/4 or less) into 3-4 triangular lobes. Stem		divided. Rhizoids scattered or in
	base stoloniform. Leaf cells thin-walled,		bundles
	cuticle smooth or sligthly papillose.	19.	Leaf insertion line not reaching dorsal
	Perianth on a short ventral branch,		midline of stem, dorsal side of stem
	3-keeled. In wet páramo		"leaf-free". Rhizoids scattered
	Pseudoce-		Cephaloziaceae: Key 5
1.2	phalozia quadriloba (Steph.) R.M.Schust.	19.	Leaf insertion line reaching dorsal
13.	Plants brownish, deeply divided (to	20	midline. Rhizoids in bundles
	3/4) into 3-4 stiff, subulate lobes. Stem base not stoloniform. Leaf cells thick-	20.	Plants often with some reddish coloration (especially in the rhioids).
	walled, cuticle strongly striate-papillose.		Branching purely ventral. Leaf cells
	Perianth on a long shoot. On rotten wood		narrowly rectangular, cuticle with
	in upper montane cloud forest		elongate papillae ("striate-papillose")
	Temnoma chaetophylla R.M.Schust.		Neesioscyphus
14.	Leaves in $3 \pm \text{equal rows}$, underleaves	20.	Plants without any reddish coloration.
	about as large as leaves		Branching lateral and ventral. Leaf cells
14.	Leaves not in 3 equal rows, underleaves		shorter, cuticle smooth or with small
1 5	smaller than leaves		rounded papillae
13.	Leaves distinctly elongate, (1.5-)2-7		Lophocoleaceae: Key 9
	times as long as wide. Leaves with a broad vitta of strongly elongate cells.		
	Trigones very large		
15.	Leaves shorter. Vitta absent. Trigones small or lacking		

6. Plants minute, less than 0.6 mm wide.

Leaf cells usually small, 8-25(-30) μm,

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

1. Plants densely pinnate, growing upright on twigs near running water, with numerous clustered perianths on short lateral branches, perianth beaked. Underleaves minute. Known from Ecuador in rivers with granite rocks and strongly fluctuating water levels, between 1200-1800 m, to be expected in Colombia. ————————————————————————————————————	
upright on twigs near running water, with numerous clustered perianths on short lateral branches, perianth beaked. Underleaves minute. Known from Ecuador in rivers with granite rocks and strongly fluctuating water levels, between 1200-1800 m, to be expected in Colombia. Columa irrorata (Lejeuneaceae) 7. Leaves opposite, dorsal leaf united	trian
short lateral branches, perianth beaked. Underleaves minute. Known from Ecuador in rivers with granite rocks and strongly fluctuating water levels, between 1200-1800 m, to be expected in Colombia	_
Ecuador in rivers with granite rocks and strongly fluctuating water levels, between 1200-1800 m, to be expected in Colombia	8
between 1200-1800 m, to be expected in Colombia	
1 D1 / 1'00 /	cells the small
 Plants different	ensely s not s the sually
 Plants not worm-like, never whitish, small or large, leaves less densely Plants with reddish or purple pig tation. Perianth inflated over its 	gmen- whole
imbricate	ourple
margin	dorsal Leaf
the ventral margin	11 ne or Leaf
4. Leaves alternate, the dorsal leaf bases tation. Perianth inflated over its	gmen-
not united, usually falcate. Stems on the dorsal side with green paraphyllia. Stems attached to soil by long stolons. Plants grayish to pale brown	giella purple wards
 5. Leaves plicate, with some longitudinal folds. Paraphyllia lanceolate. Sporophyte produced in a marsupium	when Leaf
5. Leaves smooth, without folds. Paraphyllia linear. Marsupium lacking, sporophyte surrounded by connate bracts	erous, in a iman-

12. Plants green or brown. Leaf apex various	brown when dry). Sporophyte in a
but usually not obliquely truncate-	marsupium
emarginate. Stems brown, darker than	19. Leaf cells smooth. Plants green to
leaves. Oil bodies colorless, not filling	reddish-brown to black. Sporophyte in a
cell-lumen. Sporophyte in a flattened	perianth
perianth	20. Leaves entire
13. Leaves several layers of cells thick near	20. Leaves 2(-3)-lobed
the base	21. Leaf cells conspicuously elongate
•	
13. Leaves only one layer of cells thick 14	towards the ventral margin. [Plants
14. Leafy plants arising from a creeping,	whitish-green to yellowish-green. Lea-
stolon-like shoot	ves tongue-shaped. Sporophyte in a
14. Leafy plants not arising from a creeping,	marsupium]
stolon-like shoot	Lethocolea glossophylla (Spruce) Grolle
15. Leaves transverse. [Dorsal margin	21. Leaf cells not elongate towards the
of leaves \pm inflexed (towards stem).	ventral margin. Sporophyte in a
Stem rigid, with thick-walled cortex.	perianth22
Gametoecia at stem base on abbreviated	22. Ventral stolons present. Leaf insertion
branches] (Adelanthaceae) 16	reaching dorsal midline of stem of stem
15. Leaves succubous	or not. Gemmae sometimes present.
16. Cells in the upper part of the leaf \pm	Gynoecia on a short ventral branch
evenly thick-walled, without distinct	Odontoschisma
trigones. Leaf base with a short vitta.	22. Ventral stolons absent. Leaf insertion
Stem cortex well-developed, brown, of	always reaching dorsal midline of stem
2-3 cell layers (cross-section)	of stem. Gemmae absent. Gynoecia
Adelanthus	terminal on the main stem or on a long
16. All leaf cells with distinct trigones, cells	branch 23
never evenly thick-walled. Vitta lacking.	23. Plants dark green to blackish-green,
Stem cortex poorly developed, pale-	growing on wet rock in rivers at high
colored, of 1 layer of cells	elevations, rather large, 1.5-2 mmm
	wide, leaves longer than wide. Leaf cells
17. Leaf cells small, less than 25 μm,	
	small, less than 30 µm long in mid-leaf,
without trigones. Plant less than 1 mm	thin-walled, trigones lacking or very
wide	small. Rhizoids few, not in bundles.
17. Leaf cells larger, with or without	Perigynium lacking (bracts not attached
trigones. Plants usually wider than 1 mm	to perianth base)
(rarely less than 1 mm)	mannia ovatotrigona (Steph.) Grolle
18. Leaf insertion line not reaching dorsal	23. Plants light green to reddish or brown,
midline of stem, dorsal side of stem	not growing on wet rock in rivers. Leaf
leaf-free. Plants frequently with upright	cells (20-)30-60 µm long in mid-leaf,
flagelliform branches producing gem-	trigones present or lacking. Rhzoids
mae Cephaloziaceae: Key 5	often numerous, sometimes in bundles.
18. Leaf insertion line reaching dorsal	Perigynium present (inner female bracts
midline of stem, dorsal side of stem not	attached to perianth base) Solenostoma
leaf-free. Plants without such gemmipa-	24. Stem with a hyalodermis
rous branches19	Cephaloziaceae: Key 5
19. Leaf cells papillose. Plants whitish-	24. Stem without hyalodermis
green to yellowish-green (sometimes	·

25. Leaves on sterile and male shoots with a very narrow base, the leaves 2-3× wider	Key 6. Cepha	aloziellaceae
in the middle than at the base, caducous	Leaves undivided a erect, arising from	to retuse. Leafy stems creeping stolons
cuneifolius (Steph.) Briscoe (= Acrobol-		Kymatocalyx
bus caducifolius R.M.Schust. syn. nov.) 25. Leaves without very narrow base, not		or more. Leafy stems acking2
caducous	2. Leaves obcuneate,	widest above, apices
26. Cuticle smooth Scapaniaceae: Key 10		th green, without any
26. Cuticle finely papillose		ute, ca. 0.5 mm wide
brown (never reddish or purple).	ziopsis intertexta (Gottsche) R.M.Schust.
Gemmae absent. Oil bodies brown		eate, apices acute or
27. Plants greenish-brown to reddish or		Plants green to brown 3
purple. Gemmae present or absent. Oil	3. Plants ca. 1 mm w	ride. Leaves distinctly
bodies colorlessScapaniaceae: Key 10		otuse. Perianth terete <i>Gymnocoleop-</i>
Scapamaceae. Key 10		(Mitt.) R.M.Schust.
Key 5. Cephaloziaceae	3. Plants smaller, 0.3-	-0.6 mm wide. Leaves
1. Leaves undivided. Stem without		s acute (rarely obtuse). Lowland, montane or
hyalodermis. Ventral stolons usually	páramo	4
present		rse, hardly wider than
Leaves shallowly or deeply bifid. Stem with hyalodermis. Ventral stolons		midleaf very small, walled (rarely thin-
lacking	walled). Leaf ins	sertion reaching the
2. Cells in midleaf 40-100 µm long, cell		the stem. Occurring 000 m <i>Cephaloziella</i>
walls without trigones. Plants less than 1 mm wide. On bare clay soil below 2000		succubous, distinctly
m	wider than the ste	em. Cells in midleaf
<i>opsis dominicensis</i> (Spruce) Fulford2. Cells in midleaf 15-30(-40) μm long,		n, thin-walled. Leaf ing the dorsal midline
trigones usually present (rarely lacking).		1500 m <i>Cylindricola</i>
Plants (0.5-)1-2 mm wide. On rotten		
wood, humus or rock, from sea level to páramo	Key 7. Gymn	omitriaceae
3. Leaf base forming an inflated sac	1. Plants minute, fil	iform, 0.1-0.2(-0.35)
Nowellia	mm wide, creeping	g 2
3. Leaf base not forming a sac		and stem epidermis
dorsal leaf base decurrent. Leaf apex		(one large, rounded
shallowly retuse or bifid to 1/6-1/3		Plants usually pale-
4. Leaves subtransversely inserted, dorsal		er dry superpáramo. zuela and Ecuador, to
leaf base not decurrent. Leaf apex bifid	be expected in Col	ombia
to 1/3-1/2	Nanomarsupella x	enophylla R.M.Schust.

2.	Cells of leaves and stem epidermis		teeth or lobes, without sausage-shaped
	smooth or somewhat mamillose, papillae		papillae5
	lacking. Plants purplish to blackish	5.	Leaves incubous
	Gymnomitrion atrofilum Váňa	5.	Leaves succubous or transverse 7
3.	Leaves strongly concave from base	6.	Leaves divided into 4-6 lobes. Branching
	to apex (flattening of leaf impossible		(bi)pinnate. Ventral flagellae usually
	without tearing the leaf), very shallowly		absent. Plants 0.5-1.5 mm wide
	bifid to 1/8-1/5, with a broad, lunulate		Lepidozia
	sinus and short, blunt tips <i>Gymno</i> -	6.	Leaves with 2-3 teeth at apex or
	mitrion truncatoapiculatum Herzog	0.	undivided. Branching forked or ventral.
2	-		Ventral flagellae common. Plants 1-6
3.	,		_
	flattened towards the apex, more deeply	-	mm wide
	bifid, sinus rounded to acute (not broadly	7.	,
	lunulate)	_	least above, the keel often winged 8
4.	Plants whitish to pale brown. Perianth	7.	,
	lacking	8.	Leaf apex bifid to 1/4. Underleaves
4.	2		absent
	whitish. Perianth present but very small,	8.	Leaf apex undivided or very short-bifid.
	hidden between the bracts Marsupella		Underleaves present (sometimes very
			small)
	Key 8. Lepidoziaceae	9.	Leaves and underleaves shallowly
			divided (to 1/4 or less) into 3-4 triangular
1.	Plants consisting of a small thallus with		lobes. Plants growing upright from a
	a narrow midrib and unistratose wings.		stoloniferous base. In páramo
	Amazonia		Pseudocephalozia quadriloba
1.	Plants not thalloid	9.	
2.	Plants consisting of minute shoots (less		divided. Plants creeping or ascending,
	than 0.2 mm wide), 2 cells wide, with		stoloniferous stem base present or
	rudimentary leaves, each leaf consisting		absent
	of 1-2 cells with a slime papilla on top.	10	Stem leaves 2-3-lobed. Stems with a
	In lowland rainforest		stoloniferous base Paracromastigum
	lopsis monodactyla (Spruce) R.M.Schust.	10	Stem leaves 4-lobed. Stems without
2.	Plants larger, leaves not rudimentary,	10.	stoloniferous base
	made up of more than 2 cells		storomicrous ouse
3.	Leaves hair-like, consisting of 1-4		Key 9. Lophocoleaceae
٥.	uniseriate filaments, undivided, leaf		Key 7. Eophocoleaceae
	lamina lacking	1	Leaf surface covered by numerous
2	=	1.	
٥.	Leaves not hair-like, with a short or long		small, spinose teeth
1	lamina	1	Lophocolea muricata (Lehm.) Nees
4.	Leaf cells very large, ca. 60-80 µm	1.	Leaf surface smooth
	long in midleaf, thin-walled, without	2.	Leaves apex entire
	trigones. Leaf apex rounded to short-	2.	Leaf apex toothed
	bifid, frequently with 1-2 large, sausage-	3.	Leaves broadly reniform, almost twice
	shaped slime papillae (rarely without)		as wide as long, stiffly appressed to each
	Zoopsidella		other. Plants brown. In páramo bogs,
4.	Leaf cells smaller, usually with trigones.		rare <i>Platycaulis renifolia</i> R.M.Schust.
	I and amore nauta are divided into accord		

Leaf apex acute or divided into several

3.	Leaves ovate-orbicular to oblong, as wide as long or longer than wide,	12.	Leaf apex with 2 teeth. Underleaves with 2-6 teeth or cilia (rarely more)
	appressed or spreading		Cryptolophocolea
4.	Underleaves variable, entire to bifid on	12.	Leaf apex with 3 or more teeth or cilia.
•••	the same stem and usually narrower		Underleaves with numerous cilia 13
	than the stem. Plants pale green, small,	13	Underleaves small, 2-3× wider than
	less than 1.5 mm wide. Leaf cells thin-	13.	the stem, subquadrate, deeply bifid.
	walled, ± without trigones. On moist soil		Dioicous Leptoscyphus trapezoides
	and rock in or near running water <i>Clas</i> -	13	Underleaves larger, 3-5× wider than the
	matocolea vermicularis (Lehm.) Grolle	13.	stem, reniform, not or shallowly bifid.
1	Underleaves not entire and bifid on the		Monoicous or dioicous <i>Heteroscyphus</i>
4.			Wiolioicous of dioicous Heteroscyphus
	same stem. Plants green to brown, small		Var. 10. Saananiaaaaa
	or large. Leaf cells usually with trigo-		Key 10. Scapaniaceae
_	nes	1	T 45-14-4 194 11 4 1 1-1
5.	Leaves ± transverse, strongly caducous.	1.	Leaves divided into a small dorsal lobe
	Plants minute, yellowish green, ca.	1	and a large ventral lobe
	0.5 mm wide. Tiny epiphyte in upper	1.	Leaves not divided into a small dorsal
	montane cloud forest and páramo Lo-		lobe and a large ventral lobe. Mostly in
_	phocolea fragmentissima R.M.Schust.	2	páramo
5.	Leaves distinctly succubous, not	2.	Ventral leaf-lobe 2× longer than wide.
	caducous. Plants different		Plants small, 1-1.5 mm wide, creeping
6.	Underleaves free from the leaves 7		on soil. Perianth inflated, plicate
6.	Underleaves connate with leaf bases on	2	
_	one or both sides	2.	Ventral leaf-lobe 1-1.5× longer than
7.	Leaf apex bifid		wide. Plants 1.5-5 mm wide. Perianth
7.	Leaf apex with 3 or more cilia (rarely	2	flat, smooth
0	only 2)	3.	Leaf margins on sterile stems toothed.
8.	Plants fertile 9		Leaf cells large, 30-60 µm in midleaf,
8.	Plants sterile	2	thin-walled, with very small trigones. 4
9.	Gametangia on very short ventral	3.	Leaf margins on sterile stems entire. Leaf cells smaller
	branches, hidden under the leaves.	4.	Ventral stolons present <i>Lophonardia</i>
9.	Perianth without keels <i>Heteroscyphus</i> Gametangia on long branches, not	4. 4.	Ventral stolons absent
7.	hidden under the leaves. Perianth 2-3-	5.	Leaf cells very large, 40-60 µm in
	keeled	٥.	midleaf. Stem epidermis cells 4-8×
10	Leaves bifid		longer than wide. Gemmae lacking. In
	Leaves with 4-15 cilia, not bifid. <i>Leptos</i> -		páramo bogs, very rare
10.	cyphus trapezoides (Mont.) L.Söderstr.		
11	Underleaves attached to leaves on one		(Herzog & Grolle) L. Söderstr. & Váňa
11.	side only. Leaf apex entire or with 2-3	5.	Leaf cells smaller, 30-40 µm in midleaf.
	obtuse lobes	٥.	Stem epidermis cells less than 4× longer
	contortuplicatus (Nees & Mont.) Grolle		than wide. Gemmae presen Schis-
11	Underleaves attached to leaves on both		tochilopsis incisa (Schrad.) Konstant.
11.	sides. Leaf apex with (0-)2-4 sharp teeth	6.	Trigones large. Leaf apex acute to
		٥.	acuminate. Plants reddish-brown or
	12		purple, rarely green Anastrophyllum

0.	obtuse to subacute. Plants green or brownish, rarely purplish (Sphenolobus	2.	lacking or indistict. Lobule parallel to the stem or weakly spreading
7.	austroamericanus)	3.	Underleaves undivided. Lobules plane, with rounded apex, margins of lobule often dentate to laciniate, at least near the base. Plants green to brown, robust,
7	Loof colls with the informaly thickened	2	3-7 mm wide
 7. 8. 	Leaf cells with ± uniformly thickened walls, trigones inconspicuous. Ventral stolons absent. Gemmae present or absent. Rare species of (super)páramo. 8 Leaves densily imbricate, leaf apices	3.	Underleaves divided (rarely undivided). Lobules inflated, sac-like (or plane, then with acute apex), margins of lobule ± entire. Plants green to reddish or purple, 0.5-2.5 mm wide
0.	acute. Leaf cells 20-30 µm in midleaf. Plants brownish, with a strong resin smell, paroicous, usually copiously fertile. Gemmae reddish. In superpáramo above 4000 m, known from Ecuador, to be expected in Colombia	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
8.	<i>Isopaches bicrenatus</i> (Hoffm.) H.Buch 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.	4.	Plants usually with reddish pigmentation, rarely pure green. Leaf margins entire (rarely toothed). Lobules usually very close to the stem (at some distance from stem in the <i>Diastaloba</i> group: small
9.	Gemmae absent or reddish-brown 9 Leaves succubous, leaf apices obtuse. Plants greenish-brown, ca. 1 mm wide. Perianth eplicate, completely smooth Gymnocoleopsis	5.	reddish plants)
9.	cylindriformis (Cephaloziellaceae) Leaves transverse, leaf apices (sub)acute. Plants reddish or greenish-brown, 0.5-1 mm wide. Perianth plicate, sometimes with a white mouth Sphenolobus	5.	Plants very small, usually less than 1 mm wide. Leaf cells with many small, colorless oil bodies
L	Key 11. Introductory key to Porellales		thick-walled cells. Rhizoids in bundles from the surface of the lobule. Lobules
Г	(foliose liverworts II)		more broadly attached to stem. Plants usually larger. Leaf cells with 1-2 large,
1.	Underleaves present		brownish oil bodies
2.	Lobule for most of its length attached to the lobe along a keel. Keel and lobule		Key 12. Lejeuneaceae
	usually widely spreading from stem. Plants variously colored but never red or purple Lejeuneaceae: Key 12	1.	Leaves highly specialized, distal part forming an inflated sac (= extension of the lobule)

1.	Leaves less specialized, distal part not	4.	ξ , ξ
	forming an inflated sac		cordate5
2.	Underleaves lacking	4.	Median leaf cells isodiametric, trigones
2.			various, not cordate
	small)4	5.	Underleaves toothed
3.	Plants growing upright from a	5.	Underleaves entire
	stoloniferous base, in or near running	6.	Plants pinnate or dichotomous,
	water. Stems rigid, of thick-walled cells.		branches predominantly Frullania-type.
	Known from Ecuador, to be expected in		Innovations lacking Bryopteris
	Colombia	6.	Plants irregularly branched, branches
	coleopsis gymnocolea E.Reiner &		predominantly Lejeunea-type. Innova-
	Gradst.		tions present
3.	Plants creeping, without stoloniferous		nanthus amazonicus (Spruce) Schiffn.
	base. Stems fragile, of thin-walled cells	7.	Lobules with 7-9 teeth. Underleaf apex
	Cololejeunea		± rounded, base auriculate. Perianth
4.	Underleaves undivided to weakly		8-10-keeled, with innovations. High
	emarginate Key 12a		Andes of Peru and Ecuador, to be
4.			expected in Colombia Frullanoi-
	•		des laciniatiflora (Loitl.) van Slageren.
	Key 12a. Lejeuneaceae with	7.	Lobules with 1-3 teeth. Underleaf
	undivided underleaves		apex emarginate, base not auriculate.
			Perianth 3-keeled, without innovations.
1.	Leaf margins toothed, at least near apex		Throughout tropical America Caudale-
	2		jeunea lehmanniana (Gottsche) A. Evans
1.	Leaf margins entire	8.	Underleaf insertion line ± straight.
2.	Ventral merophyte 4 or more cells wide		Plants 1.5-2 mm wide. Perianth with two
	3		ventral keels, innovations lacking Lo-
2.	Ventral merophyte 2(-3) cells wide 11		pholejeunea nigricans (Lindenb.) Schiffn.
	Width of the ventral merophyte is	8.	Underleaf insertion line deeply arched.
	measured by the number of epidermis		Plants usually more than 2 mm
	cells across the ventral stem surface (=		wide. Perianth without ventral keels,
	area between where the underleaves		innovations present or absent
	are attached, but not in the direct	9.	Apical portion of leaf broadly recurved.
	neighborhood of the underleaf base		Ventral merophyte 4 cells wide,
	because there the number of epidermis		epidermal cells thin-walled. Plants
	cells is variable).		glossy brown
3.	Leaf cells with evenly thickened walls,		gianthus cipaconeus Kruijt & Gradst.
	trigones lacking. Lobules with a very	9.	Leaf ± plane. Ventral merophyte more
	long, curved tooth (5-10 cells long).		than 4 cells wide, epidermal cells thick-
	Underleaves toothed, emarginate. Fulfor-		walled
	dianthus pterobryoides (Spruce) Gradst.	10.	Lobules plane, with (1-)2-4 teeth.
3.	2 /		Perianth terminal on main stem or
	thickened. Lobules with a shorter tooth		elongated branches, with two long
	(less than 5 cells long) or with several		innovations
	teeth (or without tooth). Underleaves	10.	Lobules strongly inflated-rounded,
	entire or toothed4		small (hidden behind the underleaves),

	± without teeth. Perianth on a very short		5-keeled, the keels smooth or toothed
	branch, with one short innovation or		never extending into inflated horns
	without innovation	10	
	Symbiezidium dentatum Herzog	19.	Lobule inflated in the lower half
11.	Underleaves very large, 6-10× stem		flattened above, rectangular, with a
	width, apex very short-bifid. Perianth		short, blunt tooth. Perianth 4-keeled, the
	terete, without keels		keels smooth and extended into inflated
	sulphurea (Lehm. & Lindenb.) Spruce		horns
11.	Underleaves smaller, apex undivided	20.	Ventral merophyte 4 or more cells wide.
	(emarginate in Harpalejeunea). Perianth		21
	with keels12	20.	Ventral merophyte 2-3 cells wide (see
12.	Plants pale green. Disciform gemmae		note in couplet 2)22
	usually produced on dorsal leaf margins.	21.	Underleaf apex undivided. Frullania-
	Underleaf apex truncate Cyclolejeunea		type branches present. Leaf apex roun-
	convexistipa (Lehm. & Lindenb.) A.Evans		ded
12	Plants brownish green. Disciform	21	Underleaf apex emarginate. Frullania-
	gemmae lacking	21.	type branches lacking. Leaf apex acute
13	Leaves with (5-)7-25 teeth. Underleaves		rarely rounded
15.	toothed or entire. On living leaves or bark		dolejeunea eluta (Nees) R.M.Schust.
		22	Leaf cells with large trigones. Ocell
12	Leaves with 1-5 teeth. Underleaves	22.	
13.			conspicuous, usually larger than green
1 4	entire. On bark or rock		leaf cells. Epidermal cells thick-walled
14.	Branches predominantly <i>Frullania</i> -type.		Lobules curved downward
	Female bracteole toothed. <i>Dicranolejeu</i> -		teolejeunea herzogii (Buchloh) Piippo
	nea axillaris (Nees & Mont.) Schiffn.	22.	Leaf cells with minute trigones. Ocell
14.	Branches predominantly <i>Lejeunea</i> -type.		inconspicuous, equal in size to or
	Female bracteole entire. <i>Acanthocoleus</i>		smaller than other leaf cells. Epiderma
	aberrans (Lindenb. & Gottsche) Kruijt		cells thin-walled. Lobules straight or
15.	Underleaves toothed		somewhat curved upwards Lepido-
15.	Underleaves entire		lejeunea sullivantii (Gottsche) E.Reiner
16.	Leaves with ocelli (scattered, in a row or	23.	Ventral merophyte 4 or more cells wide
	1-2 ocelli near leaf base)		24
16.	Leaves without ocelli	23.	Ventral merophyte 2 cells wide (see note
17.	Ocelli in a row or 1-2 near leaf base 18		in couplet 2)
	Ocelli scattered	24.	Trigones ± cordate. Leaves convolute
	Row of ocelli 7-22 cells long. Ventral		when dry (rarely plane)25
	merophyte 4-6 cells wide. Lobule tooth	24.	Trigones various but not cordate. Leaves
	3-5 cells long. Canopy epiphyte in low-		spreading when dry (rarely slightly
	land rainforest of Brazil; to be expec-		convolute)
	ted in the Colombian Amazon. Neu-	25	Underleaf apex emarginate
	rolejeunea seminervis (Spruce) Schiffn.		Underleaf apex rounded or truncate, no
1 Ω	Row of ocelli 1-6 cells long. Ventral	25.	emarginate
10.	merophyte 2(-3) cells wide. Lobule	26	Plants dark green to brown to blackish
	tooth 1 cell long	20.	
10			rather robust, 2-3.5 mm wide, leaves
19.	Lobule fully inflated, bottle-shaped, with		when dry strongly convolute. Stems
	a long, falcate tooth. Perianth sharply		rigid, without hyalodermis, ventra

	merophyte 8 cells wide. Perianth with innovations	32.	Plants turning dark-brown to black. Innovations present. Female bract apices
	Thysananthus amazonicus		rounded
26.	Plants light green to pale yellowish-	33.	Lobules mostly reduced
	brown, smaller, 1.5-2 mm wide, leaves		Acanthocoleus aberrans
	usually not convolute. Stems flaccid,	33.	Lobules well-developed, never reduced,
	with a distinct hyalodermis, ventral		with two teeth
	merophyte 4 cells wide. Perianth without	34.	First lobule tooth short, incurved and
	innovations		blunt, second tooth long, pointing
	Caudalejeunea lehmanniana		outwards, sharp. Lobule truncate.
27.	Lobules with 3-10 teeth (the teeth		Leaves not squarrose when moist. Upper
	sometimes inflexed)		montane (above 2000 m)
27.	Lobules with 0-2 teeth (occasionally 3		Blepharolejeunea
	teeth: Mastigolejeunea innovans) 30	34.	Lobule teeth equal or the first tooth
28.	Plants blackish in older stem portions.		larger than the second. Lobule oblique or
	Perianth with 5-10 keels, with inno-		truncate. Leaves squarrose when moist.
	vations Frullanoides		Lowland and montane (300-2000 m)
28.	Plants not blackish. Perianths with 3-10		Brachiolejeunea
	keels, innovations present or absent	35.	Median leaf cells distinctly elongate,
	29		ca. $2 \times longer$ than wide. [Plants robust.
29.	Underleaf insertion line slightly curved,		Ventral merophyte more than 10 cells
	underleaf base plane. Perianth with 5-10		wide. Lobules often reduced. Perianth
	keels, innovations lacking. Flagelliform		with 5-8 keels]. In cacao plantations of
	branches (producing caducous leaves)		western Ecuador, not yet known from
	frequently present. Lowlands (0-800 m)		Colombia
20		2.5	ceanthus theobromae (Spruce) Gradst.
29.	Underleaf insertion line deeply arched, underleaf bases folded. Perianth with	<i>3</i> 3.	Median leaf cells isodiametrical or
		26	slightly elongate
	3(-4) keels, innovations present. Flagelliform branches lacking. Montane		Lobules with 0-1 tooth
	(300-2000 m)		Leaf apex strongly and broadly recurved
30	Ventral epidermis cells not or scarcely	57.	acute. Epidermal cells thin-walled
50.	larger than medulla cells (stem cross-		Plants glossy brown. Above 2000 m
	section). Medulla cells thick-walled.		Lindigianthus
	Plants brown-green to blackish-green. 31		cipaconeus (Gottsche) Kruijt & Gradst.
30.	Ventral epidermis cells distinctly larger	37.	Leaf apex ± plane, rounded or acute-
	than medulla cells. Medulla cells thin-		acuminate. Epidermal cells thick-walled
	walled		
31.	Leaf apex acute. Female bracts and	38.	Insertion line of underleaves deeply
	bracteole toothed. Amazonia		arched (more than 100 µm deep). Ventral
	Thysananthus amazonicus		merophyte 6-12 cells wide. Plants more
31.	Leaf apex rounded. Female bracts and		than 2 mm wide, often black. Perianth
2.0	bracteole without teeth	2.0	without ventral keels Marchesinia
32.	Plants turning olive- to reddish-brown.	38.	Insertion of underleaves straight or
	Innovations lacking. Female bract apices		shallowly curved. Ventral merophyte 4
	acute-acuminate		cells wide. Plants smaller, never black. Perianth with two ventral keels 39
	Schiinerioieieunea		i ciianui wiui two venuai keeis 39

39. Plants whitish, pale yellowish or grayish. Perianth keels ciliate-laciniate, in	
Oil bodies 1-2(-3) per leaf cell, very vations lacking. Plants glossy blac	k or
large, filling up the cell lumen. Second dark-brown, rarely green. Oil bo	dies
lobule tooth much larger than the first homogeneous	nea
tooth. Androecia on short-specialized 44. Epidermis cells not or little larger	
branches, male bracteoles reduced medulla cells. Perianth keels smoot	
Cheilolejeunea (sect. Leucolejeunea) denticulate, innovations present, ra	
39. Plants pale green to brown. Oil bodies lacking. Plants green or brown.	
more than 3 per leaf cell, rather small, bodies granular	
not filling up the cell lumen. Lobule 45. Innovations lacking. Free margin	
teeth identical or the first tooth larger lobule incurved, at least near a	
than the second tooth. Androecia on Leaves when moist obliquely spread	
elongate shoots, male bracteoles not ± squarrose. Amazonia <i>Verdoornian</i>	_
reduced	
40. Underleaf insertion line deeply arched, Leaves when moist widely spread	
over 100 µm deep	_
40. Underleaf insertion line straight or 46. Lobules never reduced. Underleaf	
shallowly curved	
41. Lobules less than 1/4 leaf length. Leaf Innovations pycnolejeuneoid (b	
cells with radiate trigones. Perianth on leaf on innovation is an underleaf:	
a very short branch (appearing lateral Gradstein et al. 2001: Fig. 4I). Dioie	
on the stem), keels ciliate-laciniate. (rarely paroicous). Plants yellow-br	
Lowland and montane Symbiezidium to dark brown	
41. Lobules 1/4-1/2× leaf length. Leaf cells 46. At least some lobules redu	
usually with large bulging trigones. Underleaves 2-4× stem width, dis	
Perianth on an elongate shoot, keels to subimbricate. Innovations lejeun	
smooth. Exclusively montane (basal leaf on innovation is a la	
Cheilolejeunea (sect. Omphalanthus) leaf: see Gradstein et al. 2001:	
42. Plants whitish, pale-yellowish or 4J). Autoicous. Plants pale-greer	_
grayish. Oil bodies 1-2(-3) per leaf cell, greenish-brown to black <i>Dibrach</i>	
very large, filling up the cell lumen 47. Lobules strongly swollen, ball-sha	
Cheilolejeunea (sect. Leucolejeunea) free margin inrolled 2-3 times. Anop	_
42. Plants darker: green, brown or black. Oil <i>lejeunea conferta</i> (Meissn.) A. Ev	
bodies more than 3 per leaf cell, smaller, 47. Lobules not ball-shaped, free ma	
not filling up the cell lumen	_
43. Midleaf cells small, 10-20 μm in dia- 48. <i>Frullania</i> -type branches pre	
meter, trigones confluent, walls almost (sometimes only few). Lobules w	
evenly thickened. Lobules flask-shaped, well-developed with 2 teeth. Pl	
often darker than the leaf-lobe. Plants greenish-brown	
usually blackish	
43. Midleaf cells larger, trigones not Lobules with 1 tooth. Plants pale gre	_
confluent, walls not evenly thickened.	
Lobules not flask-shaped, not darker 49. Plants tiny, 0.4-0.7 mm wide.	
than the leaf-lobe. Plants green, brown lobes suberect to obliquely spread	
	of a

strongly elongate cell (at least 4× as long

as wide). Hyaline papilla distal to the

44. Epidermis cells distinctly larger than

medulla cells (stem cross-section).

	tooth. Underleaves very small, 1.5-2×		branches
	stem width, orbicular		Lejeunea (subg. Neopotamolejeunea)
	Cheilolejeuna	4.	Underleaf lobes conspicuously diverging
	holostipa (Spruce) Grolle & R.L.Zhu		(spreading outwards)5
49.	Plants larger. Leaves wide-spreading.	4.	Underleaf lobes not conspicuously
	Lobule tooth blunt or acute, short.		diverging
	Hyaline papilla proximal to the tooth	5.	One underleaf to each leaf, the
	(except in L. herminieri (Steph.)	٥.	underleaves usually densely overlapping.
	R.L.Zhu). Underleaves larger <i>Lejeunea</i>		Leaf apex rounded <i>Diplasiolejeunea</i>
	R.L.Zhu). Ondericaves larger Lejeuneu	5.	
	V 12h I -:	٥.	,
	Key 12b. Lejeuneaceae with bifid		underleaves usually distant. Leaf apex
	underleaves		acute-acuminate to rounded
		6	Underleaf lobes mostly 1 cell wide
1.	Leaves highly specialized, upper part		(except at the base), apex acute
	forming an inflated sac	6.	Underleaf lobes broader, apex blunt 10
1.	Leaves less specialized, upper part not	7.	Leaf apex rounded 8
	forming an inflated sac	7.	Leaf apex acute or acuminate
2.	Plants densely pinnate, growing in or	8.	Lobule tooth short and blunt, not falcate.
	near running water, with numerous short		Ocellus near leaf base very large, 2.5-
	sexual branches. Stems robust, ventral		4× longer than adjacent leaf cells.
	merophyte (4-)6-14 cells wide. Known		Gynoecium without innovation
	from Ecuador and Brazil, to be expected		Leptolejeunea
	in Colombia	8.	
2.	Plants not densely pinnate. Stems		near leaf base smaller, maximally
	thinner, ventral merophyte 2(-6) cells		2× longer than adjacent leaf cells.
	wide		Gynoecium with innovation. In lowland
	Width of the ventral merophyte is		rainforest
	measured by the number of epidermis		nea polyrhiza (Nees) Grolle & R.L.Zhu
	cells across the ventral stem surface (=	9.	Ocellus near leaf base very large, 2.5-
	area between where the underleaves	٦.	
			4× longer than surrounding leaf cells.
	are attached, but not in the direct		Lobule tooth short and blunt, not falcate.
	neighborhood of the underleaf base		Gynoecium without innovation
	because there the number of epidermis	0	Leptolejeunea
•	cells is variable).	9.	Ocellus at leaf base smaller, 1-2× longer
3.	Plants growing upright or pendent from		than surrounding leaf cells, or lacking.
	a rhizome-like base. Lobules lacking		Lobules with a long, falcate tooth (rarely
	on upright or pendent stems. Leaves		short and blunt). Gynoecium usually
	transversely inserted, insertion line very		with innovation (rarely without)
	short. Underleaves minute. Paroicous;		Drepanolejeunea
	antheridia in axils of female bracts	10.	Leaf lobes with an unbroken row of 4-8
	Colura irrorata (= Myriocolea irrorata)		ocelli, ocelli usually glossy yellowish-
3.	Plants creeping or pendent, without		brown. In the outer canopy of Amazonian
	rhizome-like base. Lobules present.		rainforest Cheilolejeunea urubuen-
	Leaves longitudinally inserted, insertion		sis (Zartman & I.L.Ackerman) Wei et al.
	line long. Underleaves well-developed.	10.	Leaf lobes with a broken or unbroken
	Autoicous; antheridia on separate		row of (1-)2-3 ocelli in the lower half,
			* /

	the ocein coloriess of grayish. Lowland	15. Loddies smaller. Leaves spreading.
	and montane	Plants small or large
11.	Ocelli in a broken row	16. Plants monoicous. Leaves without
	Drepanolejeunea	ocelli. Innovations pycnolejeuneoid
	Ocelli in an unbroken row	(basal leaf on innovation is an underleaf;
12.	Innovations pycnolejeuneoid (basal	see Gradstein et al. 2001: Fig. 4I)
	leaf on innovation is an underleaf; see	Metale-
	Gradstein et al. 2001: Fig. 4I). Cells on	jeunea cucullata (Reinw. et al.) Grolle
	dorsal leaf surface mamillose, thick-	16. Plants dioicous. Leaves usually with 1 or
	walled, with a broad, lens-shaped papilla.	more ocelli (at the base or scattered in
	Lobule with or without pre-apical tooth	the leaf). Innovations lejeuneoid (basal
	(= tooth situated at the distal end of the	leaf on innovation is a lateral leaf; see
	lobule, at the junction with the ventral	Gradstein <i>et al.</i> 2001: Fig. 4J)
	leaf margin)	Microlejeunea
12.	Innovations lejeuneoid (basal leaf on	17. Ocelli present in leaves
	innovation is a lateral leaf; see Gradstein	17. Ocelli lacking in leaves
	et al. 2001: Fig. 4G). Cells on dorsal	18. Ocelli present in underleaves
	leaf surface smooth, thin-walled (rarely	18. Ocelli lacking in underleaves
	thick-walled and with a conical papilla:	19. Ocelli reddish or brown. Leaf cells with
	H. scabra). Lobule without pre-apical	a broad papilla or smooth. Caducous
	tooth Harpalejeunea	leaves absent. Gynoecia on a very short
13.	Underleaves very large, at least 6× wider	branch, without innovations
	than the stem	Pictolejeunea
	Underleaves smaller	19. Ocelli colorless or gray. Leaf cells
14.	Leaf cells uniformly thin-walled or with	smooth. Caducous leaves present or
	small trigones. Lobules often reduced;	absent. Gynoecia on long shoots, with
	hyaline papilla proximal to the tooth	1-2 innovations
	at the lobule apex (see Gradstein et al.	20. Caducous leaves present, produced on
	2001: Fig. 4G). Plants glistening pale	flagelliform branches
	green, yellowish-green or whitish (stems	jeunea emarginiflora (Schiffn.) A. Evans
	often long and slender, pendent). Oil	20. Caducous leaves absent or present, when
	bodies small, numerous per cell, finely	present not produced on flagelliform
	granular or homogeneous Lejeunea	branches
14.	Leaf cells with conspicuous trigones.	21. Underleaf lobes broadly rounded.
	Lobules not reduced; hyaline papilla	[Ocelli 2-3 in an unbroken row in the
	distal to the tooth at the lobule apex (see	lower half of the leaf]12
	Gradstein et al. 2001: Fig. 4H). Plants	21. Underleaf lobes (sub)acute to
	dull pale green to olive green. Oil bodies	acuminate
	very large, 1-3 per cell, sausage-shaped,	22. Leaves with a very large ocellus near
	coarsely granular	the base, the basal ocellus $2.5-4 \times larger$
	Cheilolejeunea	than adjacent leaf cells. Underleaf
15.	Lobules when well-developed very	lobes subulate (1-2 cells wide), inserted
	large, 3/5-4/5 of lobe length. Leaves	at the outer edges of the underleaf.
	usually suberect, almost parallel to the	Underleaf margins bordered by large
	stem. Plants minute, 0.2-0.6 mm wide	cells Leptolejeunea
	16	

22. Basal ocellus smaller, maximally 2× larger than adjacent leaf cells. Underleaf lobes wider, not inserted at outer edges of underleaf. Underleaf margins not bordered by large cells	 26. Caducous leaves present or absent, when present not smaller than ordinary leaves. Leaf cells larger. Lobule tooth short, not falcate
23. Plants brown or brownish-green. Walls of leaf cells ± pale brown, trigones	Leaves suberect or obliquely spreading. Ocelli grayish or brown <i>Microlejeunea</i>
radiate (or lacking). Branch bases sometimes with a huge, strongly inflated	27. Plants larger. Leaves wide-spreading. Ocelli colorless or grayish
lobule ("utricle"). Perianth usually with	28. Epidermis cells thin-walled. Lobules
inflated horns (horns sometimes absent Ceratolejeunea	sometimes reduced. Underleaves distant. Perianth with flat, antler-like lacinia near
23. Plants green or whitish (rarely brown).	apex
Walls of leaf cells colorless, trigones	Otigoniolejeunea huctumalcensis
not radiate. Utricles lacking. Perianth	(Lindenb. & Gottsche) Y.M.Wei et al.
without inflated horns	28. Epidermis cells thick-walled. Lobules
24. Leaf lobes with a long, unbroken row	never reduced. Underleaves distant or
of 4-8 ocelli, the ocelli usually glossy	imbricate. Perianth without antler-like
yellowish-brown. In the canopy of	lacinia
Amazonian rainforest	29. Underleaves distant. Leaf cells thin-
Cheilolejeunea urubuensis	walled, without or with very small
24. Leaf lobes not with an unbroken row of	trigones. Leaf base with two transversal
4-8 ocelli. Lowland and montane 25	rows of larger, elongate cells, the
25. Underleaf margins denticulate to	upper, suprabasal row consisting of 2-5
crenulate to subentire. Gemmae usually	adjacent ocelli
present on leaf margins. Perianth flattened, 2-keeled, the keels expanded	29. Underleaves (sub)imbricate. Leaf cells with conspicuous trigones. Leaf base not
above into short auricles. On living	with two transversal rows of elongate
leaves, occasionally on bark or rock	cells, the ocelli 2-20 per leaf, adjacent or
Cyclolejeunea	scattered
25. Underleaf margins entire (sometimes	30. Leaf margins (and sometimes the entire
with a small tooth: Xylolejeunea).	dorsal leaf surface) toothed by conically
Gemmae lacking. Perianth 3-5-keeled	projecting cells with thick-walled tips
in the upper half, the keels not expanded	31
into auricles. On bark or rotten wood	30. Leaf margins entire or \pm toothed, but
26	not toothed by conically projecting cells
26. Caducous leaves present, very small,	with thick-walled tips
much smaller than ordinary leaves,	31. Dorsal leaf surface spinose. Perianth
produced on flagelliform branches.	inflated, with 5 keels
Leaf cells very small, 14-18 μm long in the middle of the lobe, walls thin or	31. Dorsal leaf surface smooth or papillose,
uniformly thickened, without trigones.	not spinose. Perianth flattened, with 2 keels
Lobules usually with a long, falcate	32. Vegetative reproduction by means of
tooth. [Plants less than 1 mm wide; leaves	large, multicellular, rounded or elongate
wide-spreading]	gemmae from leaf margins. [Plants
Rectolejeunea	usually growing on living leaves.

	Margins of leaves and underleaves ±	Bromeliophila helenae Gradst.
	toothed] Cyclolejeunea	39. On living leaves in lowland rainforest.
32.	No vegetative reproduction by means of	Midleaf cells smaller, 20-30 µm long,
	multicellular gemmae	subisodiametrical. Perianth flattened,
33.	Vegetative reproduction by means of	2-keeled, keels expanded into large
	caducous leaves	auricles Otolejeunea schellii Tixier
33.	No vegetative reproduction by caducous	40. Walls of leaf cells \pm pale brown, trigones
	leaves	radiate (or lacking). Branch bases
34.	Leaf cells small, less than 20 µm in	sometimes with a huge, strongly inflated
	diameter, trigones lacking. Caducous	lobule (= utricle). Perianth usually with
	leaves much smaller than ordinary	horns. Plants brown or brownish-green
	leaves, usually produced on special fla-	Ceratolejeunea
	gelliform branches	40. Walls of leaf cells colorless, trigones
34.	Leaf cells larger, trigones present or	not radiate. Utricles lacking. Perianth
	absent. Caducous leaves not smaller	without horns. Plants green or whitish,
	than ordinary leaves, special flagelliform	rarely greenish-brown
	branches usually lacking	41. Trigones large or small. Lobules never
35.	Lobule tooth long and sharp, hyaline	reduced, always strongly inflated. Oil
	papilla distal to the tooth. Lobules not	bodies large (more than 1/2 the cell
	reduced	lumen in length), coarsely segmented.
	Cheilolejeunea adnata (Kunze) Grolle	Hyaline papilla distal to the lobule tooth
35.	Lobule tooth short and blunt, hyaline	(or between 2 small, closely associated
	papilla proximal to the tooth. Lobules	teeth at the leaf apex) (see Gradstein et
	sometimes reduced	al. 2001: Fig. 4H) Cheilolejeunea
36.	All or part of the leaves conspicuously	41. Trigones lacking or very small. Lobules
	elongate, (1.2-)2-4 times longer than	sometimes reduced, inflated or not
	wide	inflated. Oil bodies smaller (less than
36.	Leaves less elongate	1/4 the cell lumen in length), finely
	Leaves suberect, apex acute-acuminate	segmented or smooth. Hyaline papilla
	Drepanolejeunea	proximal to the lobule tooth (see
37.	Leaves obliquely to widely spreading,	Gradstein et al. 2001: Fig. 4G)
	apex rounded	Lejeunea
38.	Leaves with very short insertion,	
	attached to the stem by only 2-3 cells.	LITERATURE CITED
	Lobules ± ligulate, flat, standing upright	
	almost parallel to the stem, keel very	BISCHLER, H., S.R. GRADSTEIN, S. JOVET-AST,
	short. Plants rheophytic (growing in	D.G. Long & N. SALAZAR ALLEN. 2005.
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	terolejeunea inundata (Spruce) Grolle	Taxonomic revision of Balantiopsaceae
38.	Leaves with a longer insertion. Plants	(Marchantiophyta) of Colombia. Hedwigia 94:
	not rheophytic39	94-127.
39.	In wet leaf axils of tank bromeliads.	COSTA, D.P. 2008. Metzgeriaceae (Hepaticae). Flora Neotropica Monograph 102: 1-170.
	Midleaf cells in elongate leaves 35-	Crandall-Stotler, B.J., R.E. Stotler & D.G.
	70 μ m long, 1.5-4 \times longer than wide.	Long. 2009. Phylogeny and classification of

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Perianth inflated, 5-keeled, keels not

expanded into auricles.....

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