#### Sporophyte

The young sporophyte is fully enveloped by the **calyptra** which derives from a fertilized archegonium. Some genera (e.g. *Adelanthus*) develop a shoot calyptra, i.e. a fleshy structure composed of stem and archegonial tissue. In several genera, tubular structures protecting the young sporophyte occur that entirely develop from stem tissue. This is called **perigynium** which may be erect (e.g. *Isotachis*) or pendent. If pendent, it is called **marsupium** (e.g. in *Calypogeia, Gongylanthus, Tylimanthus*). Then the perianth is usually reduced. The sporophyte consists of **foot**, **seta** and **capsule** (Fig. 29). The seta is colorless and ephemeral, and it rapidly elongates at capsule maturity. The capsule opens by four valves. Mature capsules contain spores and unicellular **elaters** (Fig. 29), which are elongated cells with one or more spirally thickened bands. They are hygroscopic and serve to loosen the spore mass.

#### Vegetative reproduction

Vegetative reproduction can be achieved by regeneration from leaf or stem cells, or by specialized diaspores (**gemmae**) produced on margin or surface of leaves. **Caducous leaves** regenerating to new plants are abundant in several taxa (e.g. *Lejeunea* spp., *Frullania* spp., *Bazzania* spp.) (Fig. 31).

### Thallose Liverworts

#### Habit and structure

A thallus is a vegetative plant structure that is not differentiated into stem and leaves, and thus resembles a green ribbon. The Marchantiopsida are entirely thallose, and the thallus is **anatomically complex** consisting of different types of tissue. The upper layers are usually of a green, chlorophyllose **assimilating tissue** mostly located in **air-chambers** that open by specialized **pores** (Fig. 32) on the upper surface of the thallus. **Oil bodies** are usually located in specialized cells in the middle thallus layers. On the ventral side **ventral scales** are present in two or more rows. In the Pallaviciniopsida and Jungermanniopsida subclass Metzgeriidae the thallus is **anatomically simple**, either multistratose throughout (*Aneura, Riccardia*) or with a specialized multistratose midrib and unistratose thallus wings (e.g. *Symphyogyna, Metzgeria*) (Fig. 32).

### Reproductive organs and sporophyte

**Antheridia** are produced on thallus surface either naked or surrounded by an involucre, orinside the thallus in specialized chambers. In *Marchantia* these chambers are located on stalked receptacles called **antheridiophores**. **Archegonia** are on thallus surface or embedded inside the thallus usually surrounded by an involucre. In *Asterella* and *Pallavicinia* there are two involucres around the archegonia, the inner one called **pseudoperianth** (Fig. 36). This structure only develops after fertilization and resembles the perianth of the Jungermanniopsida, but originates from the thallus and not from fused leaves. In *Aneura* and *Riccardia* the sporophyte

is surrounded by a fleshy **calyptra** (Fig. 33). In the Marchantiopsida the archegonia are located on lower surface of stalked **archegoniophores** (Fig. 35) or embedded in the thallus tissue (*Riccia*). The sporophyte consists of foot, seta and capsule (foot and seta lacking in *Riccia*). A shoot calyptra (see Leafy liverworts) is present in *Metzgeria*. The capsule opens by four valves in Metzgeridae, Fossombroniopsida and Pallaviciniopsida. In Marchantiopsida it usually opens by a disc-like operculum or irregularly. Spores are often richly ornamented on the outer (distal) surface (e.g. *Fossombronia, Riccia*) (Fig. 34) and provide important taxonomic characters.

### Vegetative reproduction

Often by specialized diaspores, e.g. gemmae on thallus surface (*Riccardia*, *Metzgeria*) or in cup-like structures (*Lunularia*, *Marchantia*) (Fig. 36).

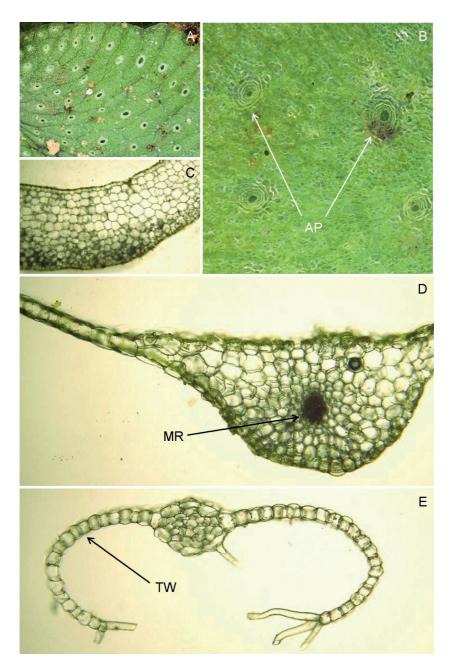
### Hornworts

## Habit and structure

The thallus is anatomically simple and consists of thin-walled cells with usually 1 chloroplast (occasionally 2-4 in *Megaceros*, not present in the area). Each chloroplast has a pyrenoid which is involved in the synthesis of starch. Oil bodies are lacking. The ventral side of the thallus bears air-chambers with pores and contains colonies of symbiotic cyanobacteria (*Nostoc*).

## **Reproductive structures and sporophyte**

**Gametangia** originate from subepidermal cells of thallus and not from epidermal cells as in liverworts and mosses. The **capsule** is elongate, slender and horn-like (Fig. 37), developing from an intercalary meristem. It bears **stomata** and lacks a seta. At first, the capsule is protected by a sheath-like involucre (Fig. 37), from which it emerges and elongates as it matures. The capsule has a central axis of sterile tissue called **columella** (Fig. 37) which is surrounded by sporogenous tissue. The **elaters** are unicellular or multicellular, then called **pseudoelaters** (Fig. 37). The capsule opens by 2 valves.



- Fig. 32. A. Marchantia pappeana. Thallus surface with air pores. B. Asterella abyssinica.
  Thallus surface with air pores. C. Aneura pinguis. Transversal section of thallus.
  D. Symphyogyna lehmanniana. Transversal section of thallus showing midrib.
  - **E.** *Metzgeria quadrifaria*. Transversal section of thallus. AP = air pores, MR = midrib,

TW = thallus wing.

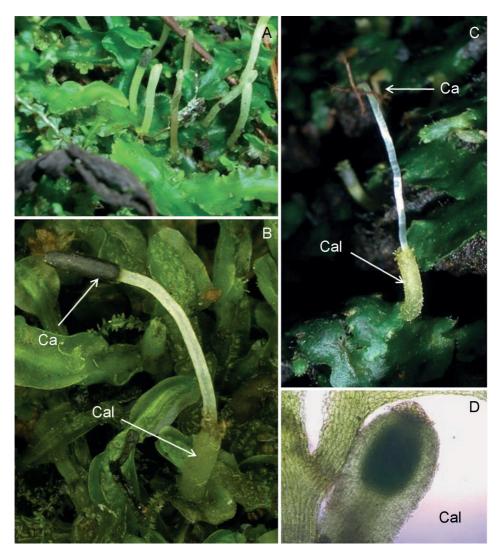


Fig. 33. Sporophytes of simple thallose liverworts. A-B. Symphyogyna lehmanniana.C. Aneura pseudopinguis. D. Riccardia amazonica. Ca = capsule. Cal = calyptra.



Fig. 34. Quillworts. A-B. Fossombronia pusilla. A. Thallus with sporophyte. B. Spore, distal face. C. Fossombronia rwandaensis with antheridia. Anth = antheridia, Ca = capsule, dis = distal, Th = thallus.

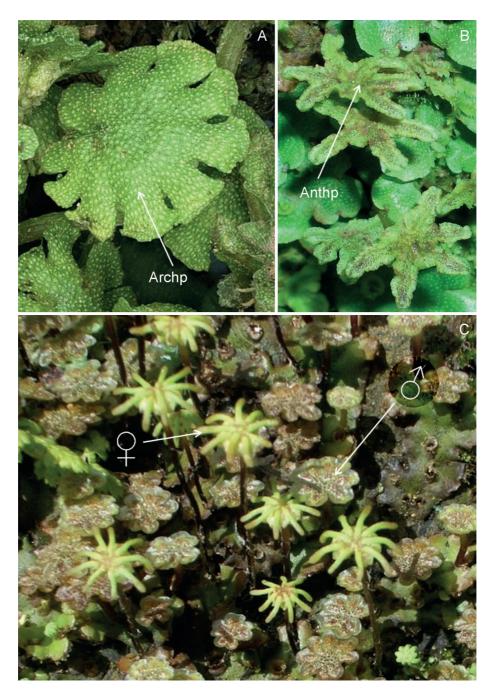


Fig. 35. A-B. *Marchantia pappeana*. A. Archegoniophore (Archp). B. Antheridiophore (Anthp). C. *Marchantia polymorpha* ssp. *ruderalis*, showing archegoniophores and antheridiophores.



Fig. 36. A. Asterella abyssinica, archegoniophores with pseudoperianth (Pp).
B. Marchantia polymorpha ssp. montivagans. Cup with gemmae. C. Lunularia cruciata. Cup with gemmae. cp = cup, ge = gemmae.

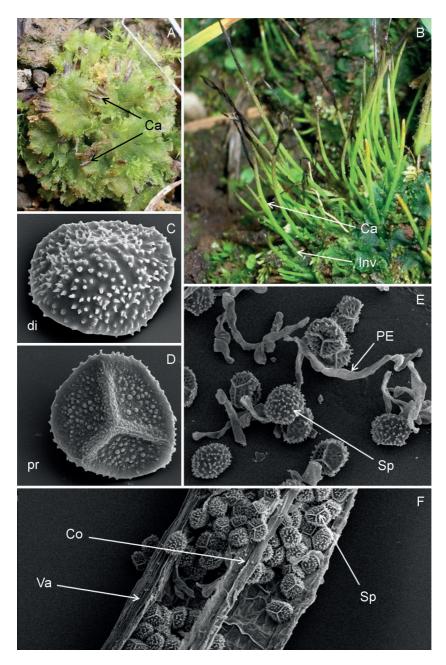


Fig. 37. Hornworts. A. Notothylas orbicularis, thallus with capsules. B. Anthoceros sambesianus, thallus with capsules. C-D. Phaeoceros carolinianus, spores. C. distal face (di). D. proximal face (pr). E-F. Anthoceros myriandroecius. E. Spores with pseudoelaters.
F. Longitudinal section of sporophyte. Ca = capsule, Co = columella, Inv = involucrum, PE = pseudoelaters, Sp = spore, Va = valve.

## 9. Artificial key to groups

1.	Thallose plants, not differentiated into stem and leaves2
1*.	Plants with stems and leaves, the leaves in two or three rows
2.	Thallus several cells thick over most of transverse section
2*.	Thallus one layer of cells thick, a pluristratose midrib clearly differentiated, thallus either dichotomously branched or resembling a filmy fern ( <i>Hymenophyllum</i> )
3.	One (-two) chloroplast per cell, colonies of cyanobacteria ( <i>Nostoc</i> ) present in the thallus, sporangium horn-like, long or short, dehiscing by longitudinal slits from the apex downwards <b>Hornworts - Anthocerotophyta</b> (p. 119)
3*.	Many chloroplasts per cell, <i>Nostoc</i> colonies always absent, sporangium ovate to spherical, dehiscing by four valves or irregularly
4.	Thallus with cavities (air chambers) or upper part with closely packed vertical filaments Complex thalloid liverworts - Marchantiopsida (p.110)
4*.	Thallus solid
5.	Thallus large, 8-10 mm x 40-100 mm, female inflorescences stalked
5*.	Thallus smaller, female inflorescence not stalked, sporangium on short seta, which elongates shortly before dehiscence, capsule opening with four valves, midrib poorly differentiated, thallus usually pinnately to bipinnately or palmately branched (except in <i>Aneura pseudopinguis</i> ), male and female inflorescences on very short lateral branches
6.	Inflorescence on short branches below the midrib, thallus not more than 2 mm wide, with distinct midrib up to 120 µm wide, formed of 2-4 rows of large cortical cells on dorsal side and 2-6 rows of similar cells on ventral side and 3-7 medullary cells, mainly epiphytic.

...... Simple thalloid liverworts - Metzgeriales (Metzgeriaceae) (p. 115)

6\*. Inflorescence on upper surface of thallus, midrib 300-600 μm wide, of 10-15 cell layers in transverse section, tapering gradually into unistratose wings ... Simple thalloid liverworts - Pallaviciniopsida (Pallaviciniaceae) (p. 112)

- Plants essentially leafy, the leaves free or united, thus reduced to dorsal, transverse, leaf-like lamellae, gynoecia dorsal on surface or on branches, without involucre...... Fossombroniaceae (Fossombronia) (p. 114)

- 8\*. Plants anisophyllous, prostrate to erect, with two obvious rows of lateral leaves and a third row of underleaves which may be reduced or lacking..... Leafy liverworts - Jungermanniopsida (p. 70)

## 9.1. Jungermanniopsida – Key to Families and Genera in Rwanda

1.	Leaves divided to base or nearly to base into 2-4 straight segments, the segments sometimes laciniate or branched, not more than 1-2 cells wide at base, underleaves similar to leaves
1*.	Leaves undivided or divided into segments (not to base) which are wider than 1-2 cells, underleaves present or absent, if present usually different from leaves
2.	Perianth at apex of short ventral branch, terminal or ventral flagellae usually present, plants delicate to robust, trigones absent
2*.	Perianth at apex of elongated lateral branch, flagellae absent, plants delicate, cells distinctly thickened at angles
3.	Leaves (3-)4(-5)-lobed from 1/4 to more than half their length; usually robust plants
3*.	Leaves undivided, or simply 2-lobed or divided into a dorsal and a ventral lobe
4.	Pinnately or bipinnately branched with attenuate branches
4*.	Branching not pinnate

5.	Leaves transversely inserted, underleaves bilobed with additional laciniae, sexual organs at apex of non-specialized elongated branches with leaves
5*.	Leaves incubous, underleaves 4-lobed, without paraphyllia, female and often male sexual organs on specialized short branches, usually of ventral origin Lepidoziaceae (Lepidozia)
6.	Leaves asymmetrically 3(-4)-lobed, obliquely inserted; leaf cells with large, bulging trigones Lophoziaceae ( <i>Plicanthus</i> )
6*.	Leaves symmetrically 4-lobed, transversely inserted; leaf cells with indistinct trigones Lophoziaceae ( <i>Tetralophozia</i> )
7.	Leaves with a complex structure, the lobe fused above to form a terminal sac or inflated horn, the base of the sac closed by a mobile valve
7*.	Leaves simple or complex, with or without lobule but never with terminal inflated sac
8.	Leaves divided into two often unequal parts (dorsal lobe and ventral lobule), lobule sometimes reduced to few cells or transformed to an open sac 9
8*.	Leaves not divided into dorsal lobe and ventral lobule15
9.	Dorsal part of leaf (lobe) as large as ventral part or smaller, ventral part (lobule) never formed into a sac-like structure
9*.	Dorsal part of leaf (lobe) distinctly larger than ventral part (lobule), lobule sometimes formed into a sac-like structure
10.	Leaves dentate, with a mostly winged keel resulting from plication between lobe and lobule <b>Schistochilaceae (Schistochila)</b>
10*.	Leaves not dentate, keel not winged, perianth usually dorsiventrally compressed <b>Scapaniaceae (Diplophyllum)</b>
11.	Underleaves absent12
11*.	Underleaves present13
12.	Lobules broadly attached to stem; rhizoids on ventral lobule of leaves, not on stems, perianth with large apex Radulaceae (Radula)
12*.	Lobules narrowly attached to stem by only 1-4 cells; rhizoids on stems, perianth with constricted apex

13.	Ventral lobule attached to lobe by a keel equal in length to the lobule (or nearly so), lobule sometimes reduced to few cells, only one archegonium per inflorescence Lejeuneaceae
13*.	Ventral lobule attached to lobe by a straight peduncle, several archegonia per inflorescence
14.	Lobule usually helmet-like or cup-like, sometimes reduced to a ventrally concave lobe, underleaves bilobed or bidentate. <b>Frullaniaceae</b> ( <i>Frullania</i> )
14*.	Lobule plane or with revolute and decurrent margin, underleaves entire or irregularly dentate Porellaceae (Porella)
15.	Leaves incubous (upper margin of a leaf covers lower part of leaf situated immediately above), underleaves present
15*.	Leaves succubous (lower margin of leaf covers upper part of leaf situated immediately below), or transversly inserted on stem, underleaves present or absent
16.	Leaves entire or shortly bidentate at apex, underleaves usually bilobed or bidentate or entire with an irregularly dentate margin, sporophyte developing in an hypogeic marsupium
	Leave with the second control of a leave to the second control of
16*.	Leaves with truncate, shallowly 2-3-lobed or truncate apices or entire, in that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae ( <i>Bazzania</i> )
16*. 17.	that case underleaves bilobed or not, but at least 2 x as large as the stem,
	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae (Bazzania)
17.	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae ( <i>Bazzania</i> ) Underleaves present
17. 17*.	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae (Bazzania) Underleaves present
17. 17*. 18.	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae (Bazzania) Underleaves present
17. 17*. 18. 18*.	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae (Bazzania) Underleaves present
17. 17*. 18. 18*. 19.	that case underleaves bilobed or not, but at least 2 x as large as the stem, marsupium lacking Lepidoziaceae (Bazzania) Underleaves present

- 21. Perianth laterally compressed, the ventral face narrow, leaves and underleaves often with spiniform teeth, plants ± brownish to fuscous pigmented ...... Lophocoleaceae (Leptoscyphus)

- 26. Perianth absent or strongly reduced, not exceeding the involucral bracts, leaf insertion like a closed V, the two parts of leaf approached to each other, worm-like plants from alpine habitats ...... **Gymnomitriaceae**

28.	Outermost stem cells in transverse section distinctly larger than inner cells (hyalodermis), cells without trigones <b>Cephaloziaceae (Cephalozia)</b>
28*.	Outermost stem cells not distinctly larger than inner cells, cells with trigones
29.	Leaves asymmetrically 2-(3)-lobed, gemmae present at leaf margin
29*.	Leaves ± symmetrically bilobed
30.	Leafy shoots frequently becoming flagelliform, microphyllous, stoloniform distally; branches arising from dorsal side of stem ( <i>Anomoclada</i> -type) Lophoziaceae ( <i>Andrewsianthus</i> )
30*.	Leafy shoots not becoming flagelliform and microphyllous; branches lateral or ventral, rarely dorsal
31.	Leaf insertion transverse (except decurrent part), plants usually brownish . 
31*.	Leaf insertion oblique, succubous, plants usually green to yellowish green
32.	Perianths absent, marsupium terminal, long and cylindric, cells conspicuously elongate along ventral margin of leaf, plants prostrate, usually yellow-greenish
32*.	Perianths present, cells not elongate along ventral margin of leaf, plants prostrate to ascending or erect, colour various
33.	Leaves opposite, eventually connate dorsally or ventrally, rhizoids on stem in tufts
33*.	Leaves alternate, not connate, rhizoids on stem dispersed
34.	Perianth well developed, exceeding involucral bracts distinctly, sporophyte at apex of stem, leaves entire or paucidentate near apex, ovate-triangular or ovate-oblong
34*.	Perianth much shorter than involucral bracts, sporophyte developing in a subcylindric hypogeic pocket (marsupium), leaves entire, suborbicular to ovate Arnelliaceae (Gongylanthus)
35.	Leaf margin usually dentate, with at least 1-3 teeth
35*.	Leaf margin entire

- 36. Leaves longly or shortly decurrent in upper and lower part, subentire to irregularly dentate, inflorescence terminal on leafy main stem or branches, perianth compressed laterally in upper part.**Plagiochilaceae** (*Plagiochila*)

- 37\*. Leaves spreading, leaf margins not incurved, usually with numerous rhizoids, underleaves bilobed or absent ...... Jungermanniaceae

# 9.2. Families of Leafy liverworts with ≥ two genera in Rwanda – Keys to Genera in Rwanda

## Acrobolbaceae

- 1. Leaves entire, with entire margin, plants prostrate, usually yellow-greenish *Lethocolea*

### Calypogeiaceae

### Cephaloziellaceae

- 2. Leaves incubous, dentate, sometimes 3-lobed ...... Cephalojonesia
- 3. Underleaves conspicuous, undivided, perianths clavate, widest in upper third, mouth constricted, vegetative reproduction by gemmae at leaf-tips ... *Amphicephalozia africana*
- 3\*. Underleaves minute or absent, perianths cylindrical to obconical, mouth wide or narrowed, vegetative reproduction not known ...... *Cylindrocolea*

#### Gymnomitriaceae

1.	Plants greyish- to whitish-green, glaucous or pale brownish, shoots
	julaceous to nearly filiform, leaves appressed, rarely squarrose, leaf cells
	thick-walled, with absent or small trigones, perianth lacking, replaced by
	scales or laciniae Gymnomitrium

- 2. Leaf margin revolute, leaves bilobed, leaflobes blunt, perianth absent ...... *Apomarsupella*

#### Jamesoniellaceae

1.	eaves distinctly opposite with the leaf bases united dorsally and ventrally	
	Syzygiella	Э

## Jungermanniaceae

1.	Bilobed underleaves present Notoscyphus
1*.	Underleaves lacking or very small, subulate Jungermannia
Leje	uneaceae
1.	Underleaves lacking 2
1*.	Underleaves present
2.	Lobule usually small compared with the lobe, not exceeding half of lobe surface, reduced leaves absent or rare, innovations of the Lejeunea-type (with basal collar), small or medium-sized plants
2*.	Lobule large compared with the lobe, usually exceeding half of lobe, reduced leaves frequent, innovations without basal collar, very small delicate plants <b>Cololejeuna subg. Aphanolejeunea</b>
3.	One amphigastrium per leaf 4
3*.	One amphigastrium per leaf pair5
4.	Leaves with an inflated cylindric prolongation of the lobule, the opening of the pocket formed by the lobe closed by a moveable valvular cap, ocelli absent
4*.	Leaves (lobes and lobule) not inflated, without inflated prolongation and valvular cap, with normal lobe and lobule, sometimes ocelli present
5.	Plants usually robust, underleaves entire, sometimes slightly retuse or emarginated at apex, never bilobed
5*.	Plants generally small, underleaves all distinctly bilobed or bidentate 17
6.	Hyaline papilla distal to the apical tooth7
6*.	Hyaline papilla proximal to or behind the apical tooth8
7.	Gynoecium without innovations beneath it, immersed in the cucullate bracts, underleaves inserted on four or more rows of stem cells, lobule subquadrangular, its free margin not incurved, not strongly constricted just below the apex, subalpine
7*.	Gynoecium with innovations, underleaves inserted on two rows of stem- cells, lobule strongly inflated with free margin incurved, sharply contracted below the mouth, submontane to montane <i>Cheilolejeunea montagnei</i>

8.	Female inflorescence without innovations below it
8*.	Female inflorescence with one or two innovations below it, becoming lateral or between dichotomic branches
9.	Perianth with two lateral and two ventral keels, all, but the lateral keels, with dentate or laciniate wings, trigones triconvex or triconcave, cell walls brown, glossy brown or blackish plants Lopholejeunea
9*.	Perianth different, trigones with one face concave and two faces convex, green or brown to blackish plants
10.	Perianth compressed, with lateral keels only, or trigonous with an additional ventral keel, with a dentate or laciniate wing around apex, female bracts and bracteoles dentate, green plants with dimorphic shoots, fertile shoots ascending from sterile creeping shoots, leaves and underleaves usually dentate
10*.	Perianth cylindric or pyriform, bracteole sometimes notched at apex but otherwise female bracts, bracteoles and underleaves entire, mostly brown or blackish plants
11.	Perianth with 5-10 longitudinal keels or folds, lobule with two or more teeth, oil bodies simple, male bracts weakly saccate, outermost cells of stem thin-walled, pale
11*.	Perianth inflated, without keel or with 1-5 keels, lobule with one tooth, oil bodies compound, male bracts strongly saccate, outermost cells of stem thick-walled, becoming brownish
12.	Underleaves entire, leaves entire, sometimes with a few obscure teeth near apex, apex rounded or acuminate
12*.	Underleaves dentate, leaves apiculate or dentate, female bracts dentate .16
13.	Perianth compressed, biconvex in transverse section, with two keels 14
13*.	Perianth with four or more keels15
14.	Perianth margins keeled but entire, not winged, underleaves inserted on 4-10 rows of stem cells, two innovations below female inflorescence
14*.	Perianth with a laciniate wing around apex, sometimes reduced to a few short laciniae or teeth, underleaves inserted on two rows of stem-cells <i>Acanthocoleus</i>

- 20. Delicate thread-like plants with only three medullary cells in transverse section of stem, leaves distant, lobule large, inflated, nearly equalling or exceeding in area the free part of the lobe, apical tooth long, curved ....... *Microlejeunea*
- 20\*. Plants more robust, stem with more than three medullary cells in transverse section, lobule much smaller, apical tooth smaller, usually not curved ..... 21
- 21. Perianth strongly compressed, obcordate, without ventral or dorsal keels, borne on a very short lateral branch without any innovations below gynoecium ...... *Prionolejeunea*
- 21\*. Perianth not compressed or if compressed with dorsal and ventral keels, or with innovations below gynoecium ...... *Lejeunea* s.l.
- 22\*. Perianths single or maximally 2 in a row on lateral branches ....... Lejeunea

#### Lepidoziaceae