



Fig. 7. *Hagenia-Hypericum* forest at Karisoke showing large bryophyte cushions, 3100 m.



Fig. 8. A-B. *Hagenia-Hypericum* forest at Karisoke, 3100 m. **C.** Large bryophyte cushions, e.g. *Plicanthus giganteus*.



Fig. 9. A-C. Ericaceous shrub on Mt. Sabinyo, 3300 m.



Fig. 10. Ericaceous shrub **A-B.** Mt. Muhabura, 3400 m; **C-D.** Mt. Sabinyo, 3300 m.

4.2. The Virunga Volcanoes and their altitudinal zonation

The Virunga Volcanoes are situated on the borders of D.R. Congo, Uganda and Rwanda. Mt. Karisimbi, at 4507 m, is the highest peak in Rwanda. From 2700 to 3000 m, a secondary *Dombeya*-forest with scattered *Hagenia* is developed, followed by a *Hagenia-Hypericum* belt from 3000 to 3300 m, where large epiphytic moss cushions of *Antitricha kilimandscharica*, *Plicanthus giganteus* and *Plagiochila colorans* are found (Fig. 7, 8). On the saddle of Karisimbi at 3400 m, a moorland with the giant groundsel *Dendrosenecio erici-rosenii* and *Erica johnstonii* occurs. Around Lake Muderu and in the crater of Mt. Gahinga, a *Sphagnum* peat bog with *Carex runssorensis* is developed (Fig. 12, 13). Above 3400 m, a *Dendrosenecio erici-rosenii-Hypericum revolutum* subparamo can be observed. The paramo can be divided into two types: the *Dendrosenecio erici-rosenii-Lobelia stuhlmannii*-paramo from 3600 to 3900 m, and the *Dendrosenecio erici-rosenii-Lobelia wollastoni*-paramo from 3900 to 4200 m (Fig. 11). Above 4200 m, no giant groundsel is found, and nearly pure meadows of *Alchemilla johnstonii* are developed (Fig. 14). The summit at 4500 m is covered by an alpine desert, where bryophytes and lichens dominate (Fig. 14, 15). Important species are *Andreaea mildbraedii*, *Campylopus nivalis* or *Apomarsipella africana*. On Mt. Bisoke, reaching 3711 m, the *Hagenia-Hypericum* zone is followed by a *Hypericum-Lobelia gibberoa*-zone from 3200 to 3350 m. Above, a *Hypericum-Lobelia stuhlmannii*-subparamo is found which reaches about 3500 m altitude. The afroalpine vegetation on Mt. Bisoke is mainly composed of *Dendrosenecio erici-rosenii*, *Lobelia stuhlmannii*, *Deschampsia flexuosa* and *Huperzia saururus*. On Mt. Sabinoy (3634 m), Mt. Gahinga (3474 m) and Mt. Muhabura (4127 m) a distinct ericaceous scrub is developed with *Erica johnstonii* and *Erica arborea* reaching up to 10-15 m (Fig. 9, 10). Large cushions of *Plagiochila colorans*, *Herbertus dicranus* and *Tetralophozia cavallii* occur as epiphytes.

4.3. Savanna Vegetation

The eastern part of Rwanda is covered by a mosaic of dry forest and savanna. Rock outcrops are either ferricretes with *Craterostigma plantagineum*, *C. lanceolatum*, *Loudetia kagerensis* and *Microchloa kunthii* (Fig. 16), or quartzitic and granitic inselbergs (Fig. 17, 18). In small rock pools, a temporary vegetation with *Marsilea minuta*, *Rotala tenella*, *Schoenoplectus microglumis*, *Aponogeton stuhlmannii* and *A. vallisnerioides* is found, and numerous species of *Riccia* occur (Fischer, 1995). Large quartzitic outcrops can be observed in south-eastern Rwanda, where open rock surfaces and fissures are colonized by a diverse bryophyte and lichen flora (Fig. 18). Some specialists like the endemic *Streptocarpus bindseilii* and *Stemodiopsis ruandensis* and the shrubs *Parinari curatellifolia* and *Protea madiensis* are found. In rock fissures, *Targionia hypophylla* and *Exormotheca pustulosa* occur. The main part of the Akagera National Park is covered by tree savanna with *Acacia sieberiana* var. *kagerensis*, *A. senegal*, *Lannea humilis*, *L. stuhlmannii*, *Entada*

abyssinica, *Rhamnus staddo*, *Ozoroa reticulata*, *Albizia petersiana* and *Rhus natalensis*. Dominant grasses are *Hyparrhenia* spp., *Sporobolus infirmus* and *Themeda triandra*. Small hillsides are covered by dense dry forests which are rich in epiphytes (e.g. *Usnea* spp., *Ramalina hoehneliana*, and orchids like *Aerangis verdickii* and *Microcoelia globulosa*). Epiphytic bryophytes include *Acrolejeunea emergens*, *Frullania ericoides*, *Brachymenium* spp. and *Fabronia* spp. Dominant trees are *Haplocoelum gallaense*, *Strychnos usambarensis*, *Canthium lactescens* and *Nuxia congesta*.



Fig. 11. A. *Dendrosenecio* paramo on Mt. Gahinga showing cushions of *Antitricha kilimandscharica*, 3400 m. **B.** *Dendrosenecio-Lobelia wollastonii* paramo on Mt. Karisimbi, 3900 m, with Mt. Mikeno in the background.



Fig. 12. A-B. Swamp in crater of Mt. Gahinga, 3400 m.



Fig. 13. A. *Carex runssorensis*-swamp on crater rim of Mt. Bisoke, 3650 m. **B.** Swamp in crater of Mt. Gahinga showing *Sphagnum* spp. and *Breutelia* spp., 3400 m.



Fig. 14. A. *Alchemilla johnstonii*-tussock, Mt. Karisimbi, 4400 m. **B.** Alpine desert near summit of Mt. Karisimbi, 4450 m.



Fig. 15. A-B. Rocks near summit of Mt. Karisimbi showing cushions of bryophytes (*Andreaea mildbraedii*, *Campylopus nivalis*) and lichens (*Umbilicaria* spp.), 4500 m.

4.4. Gallery forests

Gallery forests are developed along Akagera river and its lakes in areas subject to regular inundation. This forest type has a biogeographical resemblance to lowland rainforests of Uganda and Congo. Large stands still exist in Akagera National Park and at Ibanda-Makera north of Rusumo, but the important forests of Kagitumba are now destroyed. Important trees of the gallery forests are *Phoenix reclinata*, *Markhamia lutea*, *Pancovia golungensis*, *Ekebergia capensis*, *Ficus vallis-choudae*, *Ficus lutea*, *Allophylus macrobotrys*, *A. africanus*, *Grewia platyclada* and *Mimusops bagshawei*. Epiphytes found here include *Porella subdentata* and *Plagiochila squamulosa*.

4.5. Agricultural landscape and plantations

More than 80% of the land area of Rwanda is under agricultural use or bears other anthropogenic vegetation generally poor in bryophytes. However, *Cupressus* or *Pinus* plantations often harbour interesting bryophyte populations (Petit & Symoens, 1974). *Frullania socotrana*, *Frullania cafraria*, *Frullania spongiosa*, and *Acanthocoleus madagascariensis* have been recorded only in these plantations or in agroforestry systems around Huye (Butare) (Fig. 18) and are highly endangered due to widespread logging. Roadsides are generally an interesting habitat for bryophytes as the grass is regularly cut and open soil is available for pioneer species. Another habitat that is often neglected is that of roadside trees and tree-lined roads.



Fig. 16. A-B. Lateritic outcrops in Akagera National Park, 1500 m.



Fig. 17. A-B. Quartzitic outcrops at Lutete, Bugesera, 1400 m.



Fig. 18. A. Quartzitic rocks at Nyarubuye, 1800 m. **B.** Trees with epiphytes in IRST-Park, Huye, 1700 m.

5. Diversity and phytogeography of bryophytes in Rwanda

Rwanda is situated in the Albertine Rift and harbours a very diverse flora and vegetation due to a considerable geodiversity and a climatic gradient from west to east. The number of vascular plants is estimated at around 3000 species, which originate from different biogeographical regions. The Albertine Rift includes the mountains along the Lakes Tanganyika, Kivu, Edward and Albert, situated in eastern D.R. Congo (Itombwe Mountains, Kahuzi-Biega National Park, Ruwenzori), Rwanda (Nyungwe National Park, Volcano National Park), Burundi (Kibira National Park, Bururi) and western Uganda (Bwindi Impenetrable Forest, Budongo Forest). The diversity of bryophytes is much less well known than that of the vascular plants and it is therefore often difficult to assess the distribution of species. However, several characteristic distribution patterns among the liverworts and hornworts of Rwanda can be distinguished.

Guineo-Congolian: Species with predominantly western and central African distribution mainly found in lowland to mid-altitude rainforests: *Caudalejeunea yangambiensis*, *Ceratolejeunea diversicornua*, *Cololejeunea duvigneaudii*, *Cololejeunea obtusifolia*, *Cololejeunea pusilla*, *Colura digitalis*, *Cyathodium africanum*, *Lepidozia succida*, *Radula flaccida*, *Prionolejeunea grata*, *Odontolejeunea lunulata*.

Afromontane: Species occurring in the montane areas of tropical and South Africa, either restricted to East Africa or with disjunct distribution in the highlands of Cameroon and Eastern Africa: *Lethocolea congesta*, *Calypogeia afrocaerulea*, *Cephaloziella vaginans*, *Cylindrocolea gittinsii*, *Leptoscyphus hedbergii*, *Plagiochila colorans*, *Plagiochila ericicola*, *Herbertus dicranus*, *Andrewsianthus bilobus*, *Lophozia jamesonii*, *Plicanthus giganteus*, *Tetralophozia cavallii*, *Solenostoma mildbraedii*, *Syzygiella geminiflora*, *Cololejeunea grossepapillosa*, *Cololejeunea clavatopapillata*, *Caudalejeunea lewallei*, *Cheilolejeunea pocsii*, *Cololejeunea distalopapillata*, *Cololejeunea harrisii*, *Cololejeunea malanjae*, *Cololejeunea runssorensis*, *Cololejeunea zenkeri*, *Colura berghenii*, *Colura saroltae*, *Diplasiolejeunea aulae*, *Diplasiolejeunea deslooveri*, *Diplasiolejeunea kraussiana*, *Diplasiolejeunea runssorensis*, *Diplasiolejeunea symoensii*, *Phaeoceros fulvisporus*, *Anthoceros sambesianus*, *Anthoceros myriandroecius*, *Asterella abyssinica*, *Symphyogyna volkensii*, *Symphyogyna podophylla*, *Riccardia compacta*, *Telaranea trifida*, *Lepidozia pearsonii*, *Lepidozia stuhlmannii*, *Kurzia irregularis*, *Bazzana roccatii*, *Bazzana nitida*, *Bazzana decrescens*, *Mastigophora diclados*, *Microlejeunea kamerunensis*.

Afroalpine: Species occurring in the high mountains of Africa usually above 3000 m: *Apomarsupella africana*, *Marsupella subintegra*, *Anastrophyllum auritum*, *Diplophyllum africanum*, *Jensenia spinosa*, *Microlejeunea nyandaruenensis*.

Sudano-Zambezi: Species occurring mainly in savanna and dry forests from West Africa to East and South-East Africa, usually absent or rare in rainforests:

Riccia moenkemeyeri, *Riccia lanceolata*, *Riccia congoana*, *Riccia atropurpurea*, *Lejeunea rhodesiae*.

Sudano-Zambezian-Arabian: Species of Sudano-Zambezian distribution in continental Africa extending into the Arabian peninsula: *Riccia okahandjana*.

East Africa-Himalaya: Species occurring in the mountains of East Africa and in the Himalaya: *Asterella khasyana*.

East Africa-Madagascar: Species occurring in the mountains of East Africa and in Madagascar: *Cololejeunea capuronii*, *Solenostoma borgenii*, *Cheilolejeunea krakammae*, *Diplasiolejeunea cornuta*, *Frullania imerinensis*.

Palaeotropical: Species occurring in tropical Africa and Asia: *Mnioloma fuscum*, *Anastrophyllum piligerum*, *Plicanthus hirtellus*, *Acrolejeunea emergens*, *Cololejeunea hildebrandii*, *Cololejeunea tenella*, *Colura tenuicornis*.

Pantropical: Species occurring in the tropics of America, Africa and Asia: *Frullania ericoides*, *Frullania arecae*, *Chiloscyphus muricatus*, *Cololejeunea cardiocarpa*, *Cololejeunea platyneura*, *Cheilolejeunea xanthocarpa*.

Cosmopolitan: Species distributed in extratropical and tropical regions all over the world: *Chiloscyphus coadunatus*, *Phaeoceros carolinianus*, *Anthoceros punctatus*, *Ricciocarpus natans*, *Lunularia cruciata*, *Marchantia polymorpha* ssp. *ruderalis*, *Pallavicinia lyellii*.

Mediterranean-Sudano-Zambezian: Species of Sudano-Zambezian distribution in continental Africa extending into the Mediterranean: *Targionia hypophylla*, *Exormotheca pustulosa*

South America Africa-Afromontane: Species of afromontane distribution in continental Africa extending into South America: *Isotachis aubertii*, *Chiloscyphus martianus*, *Syzygiella concreta*, *Tylimanthus laxus*, *Diplasiolejeunea cavifolia*, *Symphyogyna brasiliensis*, *Riccardia amazonica* (Gradstein et al., 1983).

Pantropical-Afromontane: Species of afromontane distribution in continental Africa also present in mountains of South America and Asia: *Haplomitrium blumei*.

Atlantic European-Afromontane: Species of afromontane distribution in continental Africa extending into Western Europe: *Adelanthus decipiens*, *Adelanthus lindenbergianus*, *Colura calyptrifolia*, *Cololejeunea minutissima*, *Cololejeunea microscopica*, *Gongylanthus ericetorum*, *Calypogeia arguta*, *Calypogeia fissa*, *Cephalozia bicuspidata*, *Leptoscyphus infuscatus*, *Blepharostoma trichophyllum*, *Solenostoma sphaerocarpum*, *Tritomaria exsecta*, *Lepidozia cupressina*.

Endemic: Species restricted to Rwanda: *Amphicephalozia africana*, *Riccia vulcanicola*, *Cololejeunea augieri*, *Cololejeunea frahmii*, *Cheilolejeunea omphalogastris*, *Cololejeunea cardiocarpoides*, *Cololejeunea magna*, *Diplasiolejeunea cyanguguensis*.

Fromontane-Albertine Rift Endemics: Species restricted to mountains of eastern Congo, western Uganda, Rwanda, Burundi, and western Tanzania: *Drepanolejeunea vandenberghenii*, *Omphalanthus roccatii*, *Schiffneriolejeunea altimontana*, *Harpalejeunea fischeri*, *Cephalozia africana*, *Chiloscyphus muhavurensis*, *Cololejeunea fischeri*, *Cololejeunea heterolobula*, *Cololejeunea parva*, *Cololejeunea pseudo-obliqua*, *Cololejeunea sphaerocarpa*, *Cololejeunea tenuiparietata*, *Fossombronia rwanadaensis*.

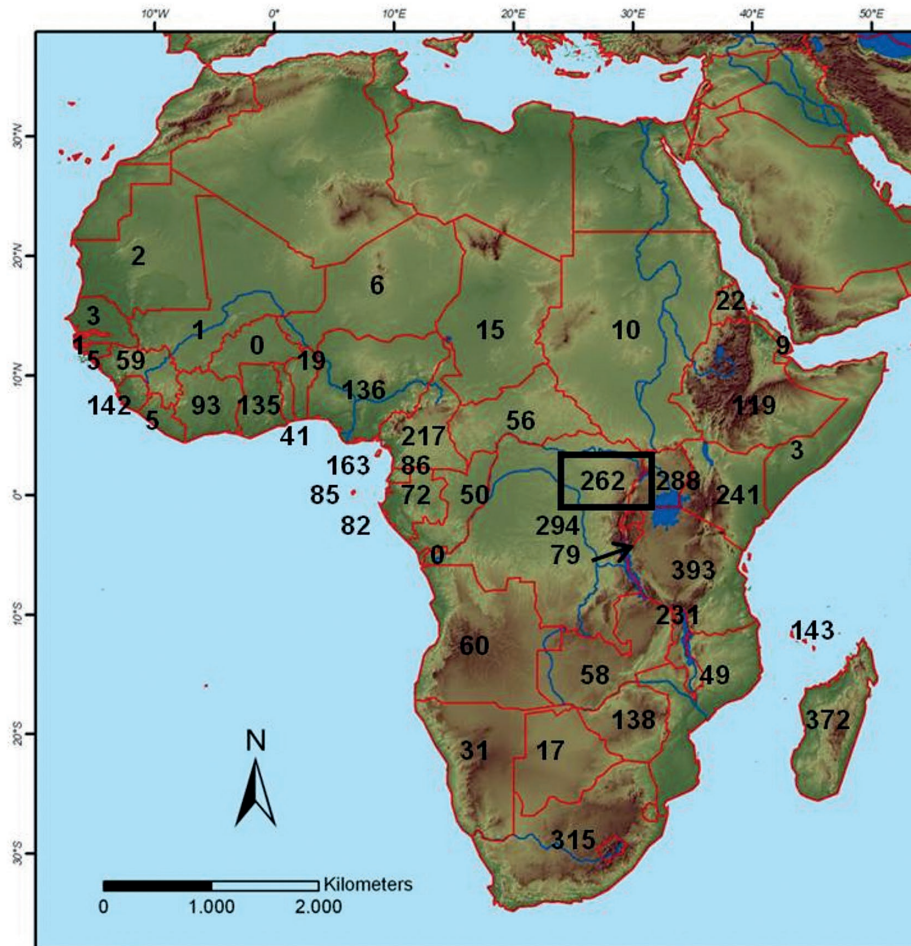


Fig. 19. Species numbers of liverworts and hornworts from Subsaharan Africa. Rwanda is indicated by bold rectangle. Numbers mainly after Wigginton (2009).

Rwanda is one of the bryologically better known African countries (see also Chapter 3), and 262 liverwort and hornwort species have so far been recorded. For an area not exceeding 27,000 km², this high number is remarkable and reflects the wide habitat diversity ranging from mid-altitude and montane rainforest to alpine habitats, and various savanna and dry forest types with lateritic outcrops.

In comparison, from the countries of the moist tropics in western Africa from Senegal to Cameroon covering more than 2.8 million km², only 292 species are known (Wigginton, 2004). With 262 liverwort and hornwort species (Fig. 19), Rwanda is among the 5 most species-rich countries in continental Africa, in current knowledge only exceeded by Uganda with 288, D.R. Congo with 294, South Africa with 315 and Tanzania with 393 species (Wigginton, 2009). These numbers, however, reflect the different degree of exploration. In Uganda, numerous new records have been provided by expeditions of the British Bryological Society (e.g. Wigginton *et al.*, 1999; Pócs & Lye, 1999). D.R Congo is underexplored, and the species-rich eastern parts of the Albertine Rift are still difficult to access due to political instability. The high number for Tanzania reflects the fact that T. Pócs lived there for many years and contributed numerous records (e.g. Pócs, 1985, 1990). The adjacent country of Burundi, also part of the Albertine Rift centre of endemism, is a good example of a much underexplored area, with only 79 species of liverworts and hornworts recorded (Wigginton, 2009). However, the habitat diversity is almost the same as in Rwanda, only lacking alpine habitats and providing Miombo-dry forests instead, and an estimated number of 230-250 hepatic species is likely to occur.

6. Systematics of Liverworts and Hornworts

The bryophytes consist of three major divisions, i.e. Marchantiophyta (liverworts), Anthocerotophyta (hornworts) and Bryophyta (mosses) (Frey *et al.*, 2009). Here we give an overview of the systematics of liverworts and hornworts, as the arrangement in the main part is mainly pragmatic, distinguishing thallose liverworts, foliose liverworts and hornworts. The systematic list provides information on families and genera recorded from Rwanda.

Division Marchantiophyta Stotler & Crand.-Stotl.

Class Haplomitriopsida Stotler & Crand.-Stotl.
Order Haplomitriales H.Buch ex Schljakov
Haplomitriaceae Dédecěk
Haplomitrium Nees

Class Marchantiopsida Cronquist, Takht. & W.Zimm.
Subclass Marchantiidae Engl.
Order Lunulariales D.G.Long
Lunulariaceae Klinggr.
Lunularia Adans.

Order Marchantiales Limpr. in Cohn
 Suborder Marchantiinae H.Buch ex Schljakov
 Aytoniaceae Cavers
 Asterella P.Beauv.; *Mannia* Opiz; *Plagiochasma*
 Lehm. & Lindenb.
 Dumortieraceae D.G.Long
 Dumortiera Nees
 Exormothecaceae Müll.Frib. ex Grolle
 Exormotheca Mitt.
 Marchantiaceae Lindl.
 Marchantia L.
 Suborder Corsiniinae R.M.Schuster ex Schljakov
 Cyathodiaceae Stotler & Crand.-Stotl.
 Cyathodium Kunze
 Suborder Targioniinae R.M.Schust. ex Schljakov
 Targioniaceae Dumort.
 Targionia L.
 Order Ricciales Schljakov
 Riccaceae Rchb.
 Riccia L.; *Ricciocarpus* Corda

Class Fossombroniopsida W.Frey & Hilger
 Order Fossombroniales Schljakov
 Fossombroniaceae Hazsl.
 Fossombronia Raddi

Class Pallaviciniopsida W.Frey & Stech
 Order Pallaviciniales W.Frey & Stech
 Pallaviciniaceae Mig.
 Jensenia Lindb.; *Pallavicinia* Gray; *Symphyogyna*
 Nees & Mont.

Class Jungermanniopsida Stotler & Crand.-Stotl.
 Subclass Jungermanniidae Engl.
 Superorder Jungermannianae Schljakov
 Order Perssoniellales Schljakov
 Schistochilaceae H.Buch
 Schistochila Dumort. (incl. *Gottschea* Nees ex Mont.)
 Order Jungermanniales H.Klinggr.
 Suborder Balantiopsineae R.M.Schust.
 Balantiopsaceae H.Buch
 Isotachis Mitt.
 Suborder Jungermanniinae R.M.Schust.
 Acrobolbaceae E.A.Hodgs.
 Lethocolea Mitt.; *Tylimanthus* Mitt.
 Calypogeiaceae Arnell
 Calypogeia Raddi; *Mnioloma* Herzog
 Gymnomitriaceae H.Klinggr.
 Apomarsupella R.M.Schust.; *Gymnomitrium* Corda;
 Marsupella Dumort.

- Jungermanniaceae Rchb.
 - Solenostoma* Mitt.; *Notoscyphus* Mitt.
- Order Jamesoniellales W.Frey & Stech
 - Adelanthaceae Grolle
 - Adelanthus* Mitt.
 - Jamesoniellaceae He-Nygrén *et al.*
 - Jamesoniella* (Spruce) F.Lees; *Syzygiella* Spruce
- Order Lophoziales Schljakov
 - Suborder Cephaloziineae Schljakov
 - Cephaloziaceae Mig.
 - Cephalozia* (Dumort.) Dumort.
 - Cephaloziellaceae Douin
 - Amphicephalozia* R.M.Schust.; *Cephalojonesia* Grolle; *Cephaloziella* (Spruce) Schiffn.; *Cylindrocolea* R.M.Schust.
 - Suborder Lophoziineae Schljakov
 - Lophoziaceae Cavers
 - Anastrophyllum* (Spruce) Steph.; *Andrewsianthus* R.M.Schust.; *Lophozia* (Dumort.) Dumort.; *Plicanthus* R.M.Schust.; *Tetralophozia* (R.M.Schust.) Schljakov.; *Tritomaria* Schiffn.
- Order Trichocoleales W.Frey & Stech
 - Blepharostomataceae W.Frey & Stech
 - Blepharostoma* (Dumort.) Dumort.
- Order Lepidoziales Schljakov
 - Lepidoziaceae Limpr.
 - Bazzania* Gray; *Kurzia* G.Martens; *Lepidozia* (Dumort.) Dumort. (incl. *Sprucella* Steph.); *Telaranea* Spruce ex Schiffn. (incl. *Arachniopsis* Spruce)
- Order Lepicoleales Stotler & Crand.-Stotl.
 - Herbertaceae Müll.Frib. ex Fulford & Hatcher
 - Herbertus* Gray
 - Mastigophoraceae R.M.Schust.
 - Mastigophora* Nees
- Order Lophocoleales W.Frey & Stech
 - Arnelliaceae Nakai
 - Gongylanthus* Nees
 - Lophocoleaceae Vanden Berghen
 - Leptoscyphus* Mitt.; *Chiloscyphus* Corda (incl. *Lophocolea* (Dumort.) Dumort.); *Clasmatocolea* Spruce
 - Plagiochilaceae Müll.Frib.
 - Plagiochila* (Dumort.) Dumort.
- Superorder Porellanae W.Frey & Stech
 - Order Porellales Schljakov
 - Porellaceae Cavers
 - Porella* L.
 - Order Radulales Stotler & Crand.-Stotl.
 - Radulaceae Müll.Frib.
 - Radula* Dumort.