

Wolfgang Frey (Editor)

# Syllabus of Plant Families

13<sup>th</sup> ed.

A. Engler's Syllabus der Pflanzenfamilien

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## 3 Bryophytes and seedless Vascular Plants



**Borntraeger**



# Syllabus of Plant Families

## Adolf Engler's Syllabus der Pflanzenfamilien

13<sup>th</sup> edition by Wolfgang Frey

### Part 3      Bryophytes and seedless Vascular Plants

Wolfgang Frey,  
Michael Stech

Marchantiophyta, Bryophyta, Anthocerotophyta

Eberhard Fischer

Protracheophyta (Horneophytosida)  
Tracheophyta p.p.: Rhyniophytina, Lycophytina,  
"Trimerophytina", Moniliformopses ("Pteridophyta"),  
Radiatopses (Progymnospermopsida)

With 72 illustrations prepared by H. Lünser (Bryophytes) and  
E. Fischer (seedless Vascular Plants)



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# Preface

Half a century ago, the 12<sup>th</sup> edition (vol. 1, 1954; vol. 2, 1964) of Adolf Engler's well-known "Syllabus der Pflanzenfamilien" ("Syllabus of Plant Families"), ed. by H. Melchior and E. Werdermann was published. Later, only a revision of the mosses (13<sup>th</sup> ed., Kapitel V,2 Bryophytina), by K. Walther, followed in 1983.

The advent of DNA sequencing and advances in phylogenetic analysis raised new interest in the relationships of Liverworts, Mosses, Hornworts, Ferns, and Fern allies as extant representatives of early land plant evolution. Numerous molecular analyses led to new insights and a better understanding of the evolution and systematics of these plant groups. On the other hand, "classical" morphological and taxonomical expertise is in decline, especially for less showy groups of organisms. We are convinced that in the "molecular times" there is an indispensable need to preserve the knowledge of the whole diversity and biology of organisms for the next generations. Otherwise, we will not be able to educate experts in the future who will maintain our knowledge of the full range of the biodiversity of our earth.

The present volume provides a basic treatment of the world-wide morphological and molecular diversity of a part of "lower" plants [Marchantiophyta, Bryophyta, Anthocerotophyta, Polysporangiomorpha, Protracheophytes, Rhyniophytina, Lycophytina, "Trimerophytina", Moniliformopses (Cladoxylopsida, Psilotopsida, Equisetopsida, Marattiopsida, Polypodiopsida)], and Radiatopses (Progymnospermopsida). Following the tradition of Engler, and incorporating latest results from molecular phylogenetics and phylogenomics, we hope to have created an up-to-date overview of families and genera that will serve as reference for a long time.

We are grateful to the publishers, Dr. E. Nägele and Dr. A. Nägele, for their understanding and cooperation and for realizing this volume. Moreover we would like to thank Mr. H. Lünser cordially for preparing the figures for the Bryophyte part.

Koblenz, Berlin, Leiden; October 2008

E. Fischer, W. Frey, M. Stech



# Contents

<b>Abbreviations, Symbols</b> .....	VII
<b>1 Introduction</b> .....	1
<b>2 Embryobionta</b> .....	6
<b>3 Bryophytes (Marchantiophyta, Bryophyta, Anthocerotophyta)</b> .....	9
<b>4 Marchantiophyta (Hepaticae, Liverworts)</b> .....	13
Characterization and relationships .....	13
Synopsis of classification .....	20
Systematic arrangement of taxa .....	23
Treubiopsida .....	23
Haplomitriopsida .....	24
Blasiopsida .....	25
Marchantiopsida .....	26
Sphaerocarpidae .....	27
Marchantiidae .....	28
Fossombroniopsida .....	36
Pallaviciniopsida .....	37
Pelliopsida .....	41
Jungermanniopsida .....	43
Jungermanniidae .....	43
Pleuroziidae .....	108
Metzgeriidae .....	109
<b>5 Bryophyta (Musci, Mosses)</b> .....	116
Characterization and relationships .....	116
Synopsis of classification .....	121
Systematic arrangement of taxa .....	124
<b>Takakiophytina</b> .....	124
Takakiopsida .....	124
<b>Sphagnophytina</b> .....	127
Sphagnopsida .....	128
<b>Bryophytina</b> .....	130
Andreaeopsida .....	138
Andreaeidae .....	138
Andreaebryidae .....	139
Oedipodiopsida .....	140
Tetraphidopsida .....	141
Polytrichopsida .....	142
Bryopsida .....	146
Buxbaumiidae .....	146
Diphysciidae .....	147

Timmiidae . . . . .	148
Encalyptidae . . . . .	149
Funariidae . . . . .	150
Gigaspermidae . . . . .	153
Dicranidae . . . . .	154
Bryidae . . . . .	185
<b>6 Anthocerotophyta . . . . .</b>	<b>258</b>
Characterization and relationships . . . . .	258
Systematic arrangement of taxa . . . . .	259
Leiosporocerotopsida . . . . .	259
Anthocerotopsida . . . . .	259
<b>7 Polysporangiomorpha . . . . .</b>	<b>264</b>
General remarks . . . . .	264
<b>8 "Protracheophytes" . . . . .</b>	<b>267</b>
Horneophytopsida . . . . .	267
<b>9 Tracheophyta . . . . .</b>	<b>270</b>
Characterization and relationships . . . . .	270
Systematic arrangement of taxa . . . . .	270
<b>Rhyniophytina . . . . .</b>	<b>272</b>
Rhyniopsida . . . . .	272
<b>Lycophytina . . . . .</b>	<b>275</b>
Characterization and relationships . . . . .	275
Synopsis of classification . . . . .	278
Systematic arrangement of taxa . . . . .	279
"Hsüa-Deuterophyton-group" . . . . .	279
Zosterophyllopsida . . . . .	281
Lycopsida . . . . .	290
<b>Euphyllophytina . . . . .</b>	<b>307</b>
"Trimerophytina" . . . . .	308
<b>Moniliformopses . . . . .</b>	<b>311</b>
Characterization and relationships . . . . .	311
Synopsis of classification . . . . .	316
Systematic arrangement of taxa . . . . .	317
"Cladoxylopsida" . . . . .	318
Psilotopsida . . . . .	329
Equisetopsida . . . . .	333
Marattiopsida . . . . .	340
Polypodiopsida . . . . .	344
<b>Radiatopses . . . . .</b>	<b>390</b>
Progymnospermopsida . . . . .	391
<b>Sources of Illustrations . . . . .</b>	<b>396</b>
<b>Index to Taxa . . . . .</b>	<b>400</b>

# Abbreviations/Symbols

acc.	according to
ACT	Australian Capital Territory
Afr.	Africa
alp.	alpine, alpine (geo)element
Am.	America
Am. south-temp.	American south-temperate
amphi-pacif.	amphipacific
antarct., Antarct.	antarctic, antarctic (geo)element, Antarctica
Archip.	Archipelago, archipelago
arct., Arct.	arctic, arctic (geo)element; Arctic
arct.-alp.	arctic-alpine, arctic-alpine (geo)element
asex.	asexual
asex. reprod.	asexual reproduction
atlant.	atlantic
Austr.	Australia
austral	southern Southern Hemisphere
bipol.	bipolar
bor.	boreal, boreal (geo)element
C	Central, central
c.	circa, about, approximately
cf.	confer, compare
circ.	circum
circ.-bor.	circumboreal
circ.-pol.	circumpolar
circ.-subantarct.	circumsubantarctic
circ.-teth.	circum-tethyan
cont.	continental
cosmopol.	cosmopolitan
cp	chloroplast
CS	cross-section
diam.	diameter
distr.	distribution
east.	eastern, east, resp. E (e.g., E Eur.)
e.g.	for example, <i>exempli gratia</i>
endem.	endemic
esp.	especially
Eur.	Europe
exc.	except
excl.	excluding
ext.	extending
fam.	family, families
gen.	genus, genera
Gondwan.	Gondwanan, Gondwanalandic
Hem.	Hemisphere
Holarct.	Holarctic region, holarctic
I., Is.	island, isle; islands, isles
i.e.	that is, <i>id est</i>

incl.	including
Indomal.	Indomalayan region
Indo-Malay.	Indo-Malaysia
inragen.	intrageneric
Lauras.	Laurasian region, Laurasia
l.c.	locus cited
lit. cit.	literature cited
loc.	locality, localities
LS	longitudinal section
Macaron.	Macaronesian, Macaronesia
Malay.	Malayan region
marit.	maritime
max.	maximal, maximally
medit., Medit.	mediterranean, Mediterranean region
mio.	million
mio.y	million years
monogen.	monogeneric
mont.	montane
mt	mitochondrial
mt(s), Mt(s).	mountain(s)
N Am.	North America
neotrop., Neotrop.	neotropical, Neotropics, Neotropical region
N Hem.	Northern Hemisphere
north.	northern, north, resp. N (e.g., N Eur.)
northernm.	northernmost
northw.	northward
northwest.	northwestern
NSW	New South Wales (Australia)
nuc	nuclear
N.Z.	New Zealand
occ.	occasional, occasionally
ocean.	oceanic
ord.	order, orders
orig.	originally
pacif.	pacific
palaearct.	palaeartic
palaeotrop., Palaeotrop.	palaeotropical, Palaeotropical region
palaeoaustr.	palaeoaustral
Pang.	Pangaeian
pantrop.	panropical, in all tropical areas
p.p.	pro parte
predom.	predominant, predominantly
prim.	primary, primarily
prob.	probably
prov.	province
Qld.	Queensland (Australia)
ref.	reference
rel.	relative, relatively
reprod.	reproduction, reproductive

resp.	respectively
s.	see
s.ab.	see above
S Am.	South America
s.bl.	see below
sex.	sexual
S Hem.	Southern Hemisphere
sing.	singular
s.l.	sensu lato
south.	southern, south, resp. S (e.g., S Eur.)
southernm.	southernmost
southw.	southward
south-temp.	south-temperate
spec., sp.	species
spp.	species (plural)
s.str.	sensu stricto
subalp.	subalpine
subantarct.	subantarctic, subantarctic (geo)element
subarct.	subarctic
subcosmopol.	subcosmopolitan
subfam.	subfamily, subfamilies
subgen., subg.	subgenus, subgenera
submont.	submontane
subocean.	suboceanic
subsp.	subspecies
subtrop.	subtropical, subtropics
syn.	synonym, synonymous
Tas.	Tasmania
temp.	temperate, in temperate zones
tert.	tertiary
trop., Trop.	tropical, tropics, Tropic (geo)element, Tropics
veg.	vegetative
Vic.	Victoria (Australia)
west.	western, west, resp. W (e.g., W Eur.)
y.	year, years
xerotherm.	xerothermic
(5)	number of species
±	more or less
∞	numerous
♂	male
♀	female
* *	in the Northern and Southern Hemisphere
* *	in the Northern Hemisphere
— *	in the Southern Hemisphere
(*)	scattered in the Northern Hemisphere
(*)	scattered in the Southern Hemisphere
E N S W	East, North, South, West



# 1 Introduction

## Advances in “Archegoniate” Systematics

The last two decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth, due to the dramatically increased amount of molecular data and advances in morphological-anatomical and palaeobotanical character interpretation. Land plants as a fundamental part of the tree of life have been steadily in the focus of research. Relationships between and within “early” land plants – the cryptogamous plants with a heteromorphic and heterophasic alternation of generations and the presence of an archegonium as main character (“Archegoniatae”), namely liverworts (Marchantiophyta), mosses (Bryophyta), hornworts (Anthocerotophyta), and ferns and their allies [Rhyniophytina, club mosses (Lycophytina) as well as horsetails, whisk ferns, and ferns (Moniliformopses)] – were considerably revised.

One of the most important insights from recent multigene phylogenies and phylogenomic evidence is a better understanding of the ancient split of archegoniate land plants in Late Silurian-Devonian time and their subsequent diversification (Fig. 2-1). “Bryophytes” are paraphyletic, and liverworts represent the earliest diverging lineage of extant embryophytes according to their basal position in molecular phylogenetic reconstructions and their fossil record, which is the oldest of all bryophyte groups. The age of the oldest liverwort fossil (*Pallaviciniites devonicus*, c. 380 mio.y) seems to be in good accordance with the age of the liverwort clade as inferred from molecular dating. Concerning the other two bryophyte groups, recent multigene phylogenies place hornworts sister to vascular plants and mosses sister to this hornwort-tracheophyte clade. This topology is supported by phylogenomic data, especially intron gains and losses in the mitochondrial and plastid genomes. A phylogenetic link between hornworts and tracheophytes is furthermore supported by, for example, similar cell wall xylans and the occurrence of haustorial placentas in hornworts, Psilotopsida, and leptosporangiate ferns.

A major achievement in understanding the evolution of vascular plants was the recognition of the polysporangiophyte clade (Polysporangiomorpha) and the protracheophyte grade below the point of diversification of all vascular plants (Figs. 2-1, 7-1). Polysporangiomorpha comprise early land plants with moss-like hydroids without secondary wall thickenings (Horneophytopsida) and all tracheophytes (Tracheophyta). The discovery of the polysporangiophyte clade implies that before acquisition of tracheids, the sporophyte was capable of enlargement and branching. This clade is characterized by the ability of the sporophytic plant to branch dichotomously in contrast to the ancestral unbranched condition in extant bryophyte groups. This achievement enabled the sporophyte to produce more sporangia, and perhaps to become larger.

Rhyniophytes, formerly thought to be the forerunners of land plants, are now considered a blind branch in land plant evolution, as indicated by the occurrence of unique *S* (*Sennicaulis*)-type tracheids, known only from this extinct plant group. They are now separated from the remaining vascular plants on subdivision level (Rhyniophytina). Molecular phylogenetic studies confirm the basal split within the remaining vascular plants, i.e., between lycophytes (Lycophytina) and euphyllophytes (Euphyllophytina). Origin of lycopsid microphylls by sterilization of sporangia is a possible alternative to the enation and reduction hypothesis according to recent cladistic analyses.

Euphyllophytina are a well-supported group and comprise ferns and allies plus seed plants. They are of high morphological diversity, ranging from *Psilotum* and *Equisetum* to the most advanced angiosperm families such as Orchidaceae or Asteraceae. Cladistic analysis supports a basal dichotomy within the euphyllophytes, i.e., between taxa related to progymnosperms and seed plants (Radiatopses sensu Kenrick & Crane) and a fern clade (incl. Equisetopsida and Psilotopsida, Moniliformopses sensu Kenrick & Crane). The earliest megaphylls of *Eophyllophyton* support the hypothesis that the megaphyll has been derived from an axial branching system. Moniliformopses comprise all ferns s.str. (i.e., horsetails, whisk ferns, and all eusporangiate and leptosporangiate ferns) characterized by lateral root origin in the endodermis, usually mesarch protoxylem in axes, a pseudoendospore, plasmodial tapetum, and sperm cells with 30–1000 flagellae. They are sister to the spermatophytes within the Euphyllophytina.

Evolution of the heterophasic and heteromorphic alternation of generations of archegoniate plants could be demonstrated in the green algal model plant *Coleochaete*. In Coleochaetales and Charales the alternation of generations is initiated by a protected zygote, and in *Coleochaete* spp. by the division of the zygote into a 1–2-layered cell plate. This would support the antithetic hypothesis, which suggests that the algal ancestor of land plants lacked an alternation of generations and that the multicellular diploid spore-producing generation of land plants (the sporophyte) was generated by delaying zygotic meiosis in the life cycle of an alga similar to *Coleochaete* (Fig. 3-1.8). The nutritional and developmental interactions between zygotes (or “zygote fruits” with cortical cells) and gametophytes led to the evolution of the embryo and gametophyte-sporophyte junction, both characteristic features of embryophytic plants, and to an “embryophytic habit” of the young developing sporophyte (Fig. 3-1.9). At this evolutionary stage the diversification of terrestrial plant life started. But contrary to the antithetic hypothesis, fossil reconstructions of the gametophytes of the first polysporangiophytes like *Langiophyton* or *Lyonophyton* suggest that the transition to sporophyte dominance went through an isomorphic alternation of generations.

Molecular data in combination with analyses of morphological, anatomical, cytological and palaeobotanical characters also led to considerable systematic changes within the main groups of bryophytes and pteridophytes.

Former hypotheses of character evolution in liverworts, including the model of the ancestral liverwort prototype as an erect, radially symmetric plant are nowadays rejected in this broad sense. The archetype morphology is thought to be that of a prostrate, disymmetric, leafy plant, with the developmental and reproductive features of a simple thallose liverwort, derived from a hypothetical leafless ancestor. Few enigmatic extant taxa with different kinds of leaf-like lobes or lobules (Blasiaceae, *Fossombronia*, *Haplomitrium*, *Noteroclada*, *Phyllo-thallia*, *Pleurozia*, *Sphaerocarpos*, and *Treubiaceae*) are transitional between the thallose and

leafy conditions, and probably represent relics of the early liverwort diversification. Of these, Treubiaceae and *Haplomitrium* are sister groups and form the earliest diverging extant liverwort lineages in molecular phylogenetic reconstructions. Blasiaceae form a clade sister to marchantialean liverworts. Monophyly of the complex thallose Marchantiopsida as a fundamentally different liverwort group is supported by analyses of combined molecular and non-molecular data. The formerly thallose/semi-leafy Metzgeriidae s.l. (Jungermanniales anacrogynae) clearly are a paraphyletic assemblage. Molecular analyses indicate that the true simple thallose forms (e.g., *Metzgeria*, *Riccardia*), the semi-leafy Fossombronialean liverworts, and the leafy and thallose forms with a central strand (Pallaviciniaceae, Hymenophytaceae) represent different evolutionary lineages, of which Metzgeriidae s.str. (Aneurales and Metzgeriales) probably are a relatively young lineage of secondarily thallose forms. On the other hand, the leafy Jungermanniidae appear as monophyletic, except *Pleurozia*. *Pleurozia*, for a long time regarded as an isolated element of the leafy liverwort lineage, is resolved by molecular analyses as sister to Metzgeriidae and may have evolved independently from the Jungermanniidae as circumscribed here.

Mosses are monophyletic in all molecular phylogenetic reconstructions, including *Takakia*. *Takakia* was placed in the liverworts for more than 100 years but transferred to the mosses after the discovery of sporophytes. Phytochemical (flavonoid) and cytological data support an isolated position of the genus, which is, aside from some *Mniodendron* spp., obviously the only bryophyte taxon with a true haploid chromosome set. Molecular studies resolved either *Takakia* sister to all other mosses, or, more frequently, a sister clade of *Sphagnum* and *Takakia* basal within mosses. The two extant *Takakia* species may be considered stenotypic, extremely isolated relicts with a relict range, representing an isolated branch among ancestors of modern mosses. With respect to their fundamental morphological differences *Takakia*, Sphagnaceae, and "true" mosses are now treated as subdivisions Takakiophytina, Sphagnophytina, and Bryophytina, respectively. Considerable systematic changes within Bryophytina include, for example, recognition of morphologically and molecularly isolated basal lineages as separated from the arthrodontous mosses (Bryopsida), namely Andreaeopsida (with linear capsule dehiscence), the operculate but eperistomate Oedipodiopsida as well as Polytrichopsida and Tetrarhizopsida with nematodontous peristomes. Also within Bryopsida molecular data contributed to a better understanding of peristome evolution, e.g., by indicating that the haplolepideous peristome of the monophyletic Dicranidae evolved from a diplolepideous ancestor. Bryopsida are molecularly characterized, e.g., by the loss of the *rpoA* gene from the cp genome as a phylogenomic character (exc. Buxbaumiidae).

Within the polysporangiophyte clade, subsequent work showed that rhyniophytes and trimerophytes were unnatural groups. The extinct zosterophylls were shown to be monophyletic and form a clade together with lycopsids that is sister to all euphyllophytes (Fig. 2-1). Monophyly of Lycopsida is supported, and three major clades can be distinguished, a Drepanophycales-clade comprising the Early Devonian Drepanophycaceae (sensu Kenrick & Crane), a Lycopodiales clade with the extant Lycopodiaceae, and a Protolepidodendrales-Selaginellales-Isoetales clade which comprises the extinct Protolepidodendrales (isosporous, but ligulate), extant Selaginellaceae (heterosporous and ligulate), and the rhizomorphic lycopsids sensu DiMichele & Bateman (heterosporous and ligulate).

The systematic position of extant Psilotales has often been questioned ("thought to be the oldest living plants on earth"), indicating relationships to extinct "psilophytes" or lycopsids.

Today a close relationship with Ophioglossales and the sistergroup relationship of Psilotopsida to horsetails and all remaining extant ferns are generally accepted. The ophioglossoid ferns as part of the former eusporangiate ferns, now recognized as paraphyletic, have been assigned to different groups and even considered to be derived from progymnosperms. Recent studies showed that contradictory to various morphological hypotheses, ophioglossoid ferns, whisk ferns, horsetails and polypodioid ferns are monophyletic, and that heterosporous ferns, tree ferns and polypods are also resolved as monophyletic being sister group to adder-tongues, whisk ferns, horsetails and marattioid ferns. All leptosporangiate ferns form a monophyletic clade, while the traditional eusporangiate ferns appear in 2 different clades (ophioglossoid and marattioid ferns).

Finally, molecular data confirmed that the former “Hydropterides” or water ferns in fact form a monophyletic clade.

In this first part of the 13<sup>th</sup> edition of “Engler’s Syllabus of Plant Families” we present an up-to-date review of bryophyte and fern systematics and relationships on family and generic level, integrating morphological-anatomical and molecular data.

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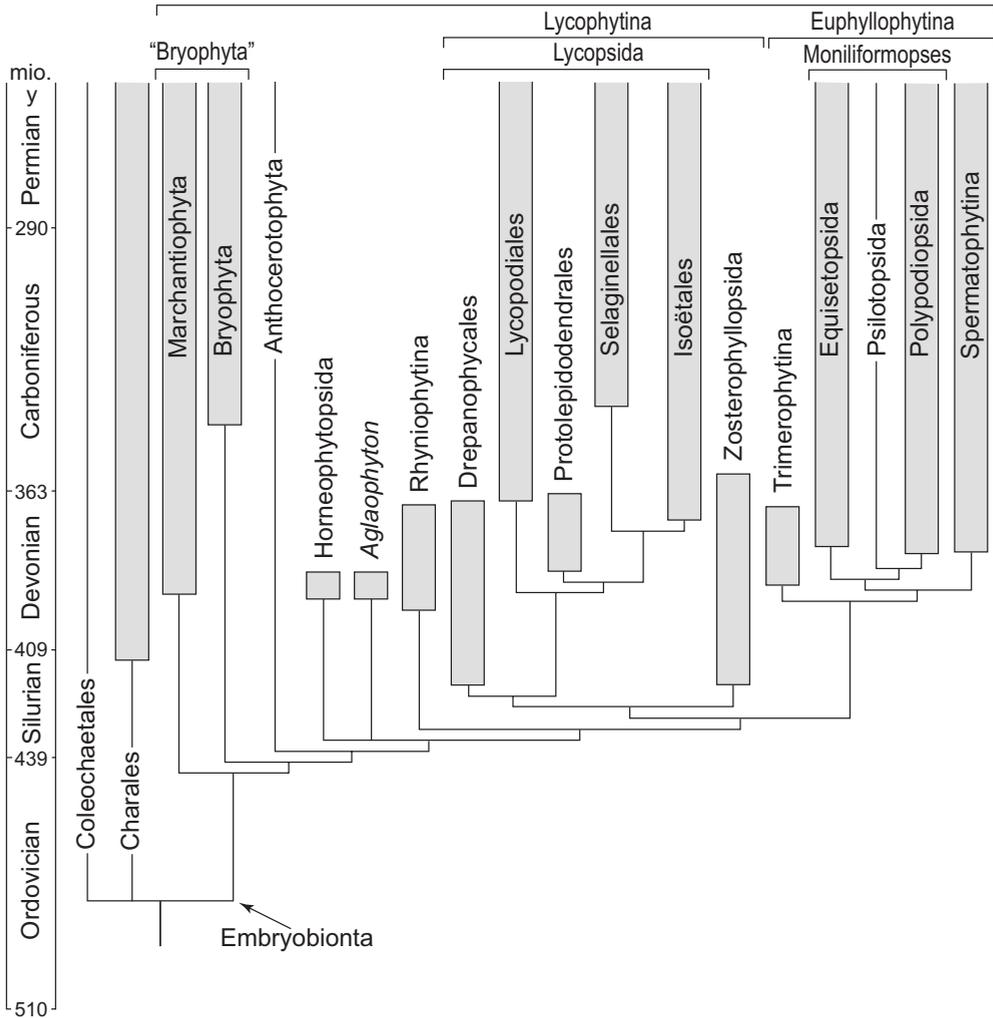
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## 2 Subkingdom **Embryobionta** Cronquist, Takht. & W.Zimm.

The **Embryobionta** (Embryophytes, subkingdom of the kingdom Eucarya) are classified in the divisions [phylum, phyla] Marchantiophyta (liverworts), Bryophyta (mosses), Anthocerotophyta (hornworts), “Protracheophyta” and Tracheophyta: [Rhyniophytina, Lycophytina and Euphyllophytina, the latter comprising Moniliformopses (horsetails, ferns) and Spermatophytina (seed plants)]. Comparative morphology and molecular data (e.g. Qiu et al. 2007) indicate unequivocally liverworts, mosses, hornworts, lycophytes, ferns and seed

Tab. 2-1. Classification of subkingdom Embryobionta.

Division (Phylum)	<b>Marchantiophyta</b> Hepaticae, Liverworts
Classes	Treubiopsida, Haplomitriopsida, Blasiopsida, Marchantiopsida, Fossombroniopsida, Pallaviciniopsida, Pelliopsida, Jungermanniopsida
Division	<b>Bryophyta</b> Musci, Mosses
Subdivision	Takakiophytina
Class	Takakiopsida
Subdivision	Sphagnophytina
Class	Sphagnopsida
Subdivision	Bryophytina
Classes	Andreaeopsida, Oedipodiopsida, Tetrarhizopsida, Polytrichopsida, Bryopsida
Division	<b>Anthocerotophyta</b> Hornworts
Classes	Leiosporocerotopsida, Anthocerotopsida
	<b>Polysporangiomorpha</b>
	<b>“Protracheophyta”</b>
Class	Horneophytopsida (extinct)
Division	<b>Tracheophyta</b>
Subdivision	<b>Rhyniophytina</b>
Class	Rhyniopsida (extinct)
Subdivision	<b>Lycophytina</b> Club mosses
Class	Zosterophylloids (extinct), Lycopsiads
Subdivision	<b>Euphyllophytina</b>
	<b>“Trimerophytina”</b>
Superclass	<b>Moniliformopses</b> (Horsetails, Ferns)
Classes	“Cladoxyloids” (extinct), Psilotopsida, Equisetopsida, Marattiopsida, Polypodiopsida
Superclass	<b>Radiatopses</b>
Class	Progymnospermopsida (extinct)
Subdivision	<b>Spermatophytina</b> Seed plants



**Fig. 2-1. Embryobionta.** Phylogenetic reconstruction showing the Late Silurian-Devonian split of embryophytic land plants based on megafossils (thick bars) and their minimum implied range extensions (thin lines). First records of Charophycean algae from Late Silurian (c. 410 mio.y.). Proposed similarities between living *Coleochaete* and Early Devonian *Parke* remain to be confirmed. Anthocerotalean fossils are first known from Cretaceous, probably Hepatic-like fossils from Lower Devonian (broken line; Edwards et al. 1995), earliest seed plant precursor *Runcaria* from Middle Devonian (Gerienne et al. 2004). Phylogenetic reconstruction based on Kenrick & Crane (1997) and Qiu et al. (2007).

plants representing strongly supported monophyletic groups. Three bryophyte lineages form a paraphyletic group to vascular plants, with liverworts representing the sister to all other land plants and hornworts being sister to vascular plants. Rhyniophytes and lycophytes (Lycophytina) are sisters to all other vascular plants, which are divided in two clades, Moniliformopses (horsetails, ferns) and Spermatophytina (“Euphyllophytina” sensu Kenrick & Crane 1997).

Main feature of embryophytic plants is the embryo, nourished by the mother plant, a universal feature of land plants. The evolution of an embryo is initiated in Coleochaetales and Charales by a protected zygote and the division of the zygote into a one or two-layered cell plate in *Coleochaete* spp. A gametophyte-sporophyte junction, often with transfer cells in the placenta, characterizes the connection zone between gametophyte and sporophyte in Marchantiophyta, Bryophyta, Anthocerotophyta, Lycophytina and Moniliformopses (horse-tails, ferns). In these plant groups a continuous development of the embryo is obvious leading without interruption to the sporophytic generation (sporophyte), whereas in Spermatophytina a dormancy period of the embryo sheltered by integuments is intercalated. In Marchantiophyta, Bryophyta and Anthocerotophyta, the gametophytic generation (gametophyte) predominates, in the Tracheophyta the sporophytic generation (sporophyte). The split and evolution of embryophytic land plant groups took place in Late Silurian-Devonian time. About 290 000 species. Tab. 2-1, Fig. 2-1.

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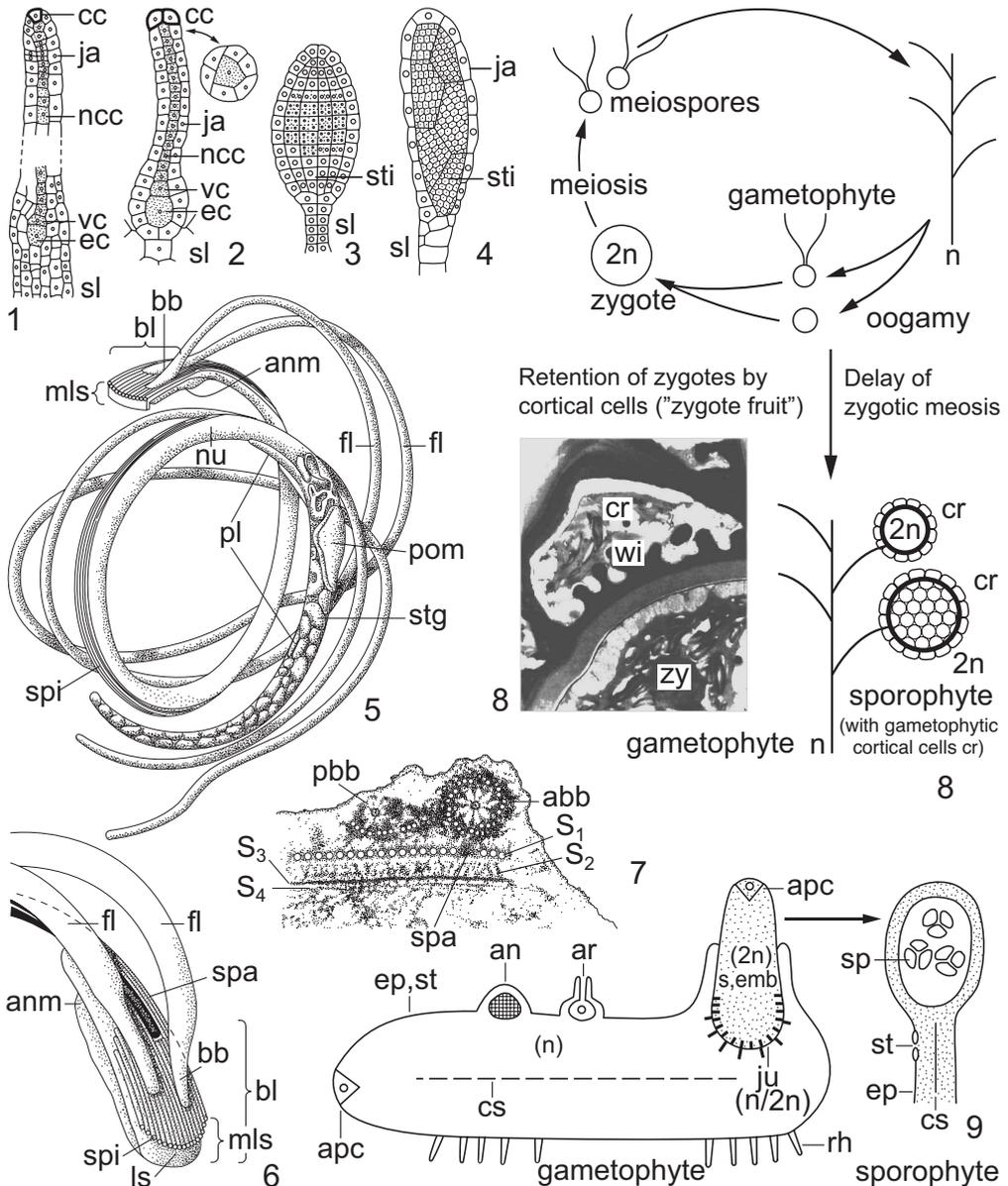
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### 3 Bryophytes (Marchantiophyta, Bryophyta, Anthocerotophyta)

**Bryophytes** (liverworts, mosses, and hornworts) are green embryophytic land plants with a regular alternation of a functionally haploid, conspicuous and usually dominant gametophytic generation and a functionally diploid sporophytic generation, connected by a gametophyte-sporophyte junction. The gametophytes are thallose or foliose [composed of a stem (cauloid) and leaves (phylloids)], without lignified tissue. Bryophytes colonize nearly all substrates (terricolous, epilithic, epiphytic and epiphyllous ones), with life forms ranging from dendroids and pendants to annuals. Figs. 2-1, 3-1, 4-1–9, 5-1–21.

General similarities of liverworts, hornworts, and mosses (plants rather simply structured, gametophyte dominant, sporophyte generally unbranched with a single sporangium) as well as fundamental characters of male gametogenesis indicated a monophyletic bryophyte clade (Bryophyta s.l.). Molecular data support liverworts, mosses, hornworts, and vascular plants each as monophyletic. However, “bryophytes” form a grade according to molecular phylogenies: a basal split of land plants into liverworts and a non-liverwort embryophyte clade is supported, e.g., by intron distributions in mt genes (cf. Groth-Maloney & Knoop 2005), cpITS sequences (Samigullin et al. 2002), and a multigene analysis of six cp, mt and nuc genes (Qiu et al. 2006). In these phylogenies, mosses incl. *Takakia* are placed between liverworts and hornworts, the latter being sister to vascular plants, whereas some earlier molecular analyses indicated a basal position of hornworts within land plants.

The early phylogenetic history of land plants is one of the major unresolved problems in palaeobiology. Bryophytes and other land plants seem to be derived from the Charophycean line in Silurian time (Fig. 2-1). The presently known fossil record does not contribute significantly to revealing the origin and diversification of the main bryophyte groups in Palaeophytic time, but Ordovician and Lower Devonian plant remnants (palynomorphs) seem to be of liverwort affinity and support a basalmost position of the hepatic lineage within land plants (Fig. 2-1). Different hypotheses have been presented to explain the Late Archaeophytic and Early Palaeophytic origin of the bryophytes resp. embryophytes. Two of them are of major importance. The **homologous hypothesis** is based on the premise that ancestors of embryophytes showed an alternation of isomorphic, free-living generations, similar to *Ulva*'s life cycle, and that the sporophyte became secondarily associated with the gametophytic generation with regard to nutritional and developmental interactions. However, this event is difficult to explain. In contrast, the **antithetic hypothesis** suggests that the algal ancestor of plants lacked an alternation of generations and that the multicellular diploid spore-producing generation of land plants (the sporophyte) was generated by delaying zygotic meiosis in the life cycle of an alga similar to *Coleochaete* (Fig. 3-1.8). The



**Fig. 3-1. Bryophytes (Marchantiophyta, Bryophyta). Gametangia, embryophytic plant evolution. 1–2.** Archegonia. 1. Bryopsida (x250). 2. Jungermanniidae (x200). 3–4. Antheridia. 3. Marchantiidae (x150). 4. Bryopsida (x190). 5. *Blasia pusilla*. Spermatozoid (x3,000). 6. *Marchantia polymorpha*. Blepharoplast morphology. Closed spline aperture (x3,000). 7. *Geothallus tuberosus*. Blepharoplast anatomy, CS in the region of the anterior end of the spline aperture. Anterior basal body with 9 triplets, posterial basal body: 3 triplet extensions associated with pbb; TEM micrograph (c.x50,000). 8. Anti-thetic hypothesis of embryophytic plant evolution. The hypothesis proposes that delay in meiosis occurred in the haplobiontic life cycle of an alga similar to *Coleochaete*, generating a small, multicellular diploid generation – a sporophyte. Retention of zygote and “zygote fruit” with gametophytic cortical cells upon parental thalli. TEM micrograph: junction between a cortical cell and a zygote of

nutritional and developmental interactions between zygotes (or “zygote fruits” with cortical cells) and gametophytes led to the evolution of the embryo and gametophyte-sporophyte junction, both characteristic features of embryophytic plants, and to an “embryophytic habit” of the young developing sporophyte (Fig. 3-1.9). At this evolutionary stage the diversification of terrestrial plant life started.

## Division **Marchantiophyta** Stotler & Crand.-Stotler Hepaticae, Liverworts

Thallose. Oil-bodies present. Gametangial ontogeny without apical cells. Seta present. Capsule without columella. Elaters unicellular. Stomata absent. Blepharoplast: plastid and associated posterior mitochondrion positioned at cell terminus. C. 5250 spp.

## Division **Bryophyta** Schimp. Musci, Mosses

Foliose. Gametangial ontogeny with apical cells. Seta present. Capsule with peristome and columella. Elaters absent. Sporophyte with stomata. Blepharoplast: plastid and associated posterior mitochondrion positioned along inner nuclear surface; occurrence of a stray microtubule. C. 12.500 spp.

## Division **Anthocerotophyta** Rothm. ex Stotler & Crand.-Stotl. Hornworts

Thallose. Thallus cells usually each with a single chloroplast containing a pyrenoid; oil-droplets present. Antheridia of endogenous origin. Archegonia single, embedded on dorsal thallus surface. Seta lacking. Sporophyte growing from base by indeterminate meristematic ac-

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*C. orbicularis* with wall-ingrowths. **9.** Schematic reconstruction of a hypothetical common ancestor of embryophytic land plants, a protracheophyte with an “embryophytic habit” of the young developing sporophyte. Apical cells, epidermis with thin cuticle and a central strand with hydroids and leptoids (protosteles) in both generations present. Gametophyte-sporophyte junction with transfer cells in the placenta. (2n diploid, abb anterior basal body, an antheridium, anm anterior mitochondrion, apc apical cell, ar archegonium, bb basal body, bl blepharoplast, cc cover cell, cr cortical cell, cs central strand, ec egg cell, emb embryo, ep epidermis, fl flagellum, ja jacket layer, ju gametophyte-sporophyte junction with placenta, ls lamellar strip, mls multilayered structure, n haploid, ncc neck canal cell, nu nucleus, pbb posterior basal body, pl plastid, pom posterior mitochondrion, rh rhizoid, s sporophyte, resp. sporangium, sl stalk, sp cutinized spores [tetrad], spa spline aperture, spi spline, st stoma, stg starch granule, sti spermatogenous tissue, S<sub>1</sub> spline [microtubular band], S<sub>1</sub>-S<sub>4</sub> = mls [multilayered structure, 4 layers], S<sub>2</sub>-S<sub>4</sub> lamellar strip, vc ventral canal cell, wi wall-ingrowth, zy zygote)

tivity, columella well or poorly defined. Pseudoelaters multi- or unicellular. Sporophyte with stomata. Blepharoplast: spline composed of 12 microtubules (inaperturate), lamellar strip rhomboidal, side by side orientation of the 2 basal bodies of equal size (as in Charophytes). C. 100–150 spp.

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## 4 Division **Marchantiophyta** Stotler & Crand.-Stotl. (Hepaticae, Liverworts)

### Characterization and relationships

**Marchantiophyta** (liverworts, hepatics) are supposed to be monophyletic, prob. represent the earliest diverging lineage of extant embryophytes, and show the oldest fossil record of all bryophyte groups. Liverworts are a highly diverse plant group with substantial morphological heterogeneity, comprising c. 5250 species in 8 classes, 32 orders, 89 families, and c. 380 genera including “complex thallose”, “simple thallose” and “leafy” liverworts. The majority of species (c. 82 %) belong to the Jungermanniidae, the leafy liverworts. Few taxa with leaf-like lobes are transitional between the thallose and leafy conditions. C. 150 genera (c. 40 %) are monospecific and relatively few genera (c. 14) contain more than 100 species, with the four largest genera being *Radula* (c. 150–200 spp.), *Cololejeunea* (c. 225 spp.), *Frullania* (c. 350 spp.), and *Plagiochila* (c. 425 spp.). C. 25 families are monospecific, c. 22 families contain fewer than 10 species, and c. 39 families are monogeneric. The Lejeuneaceae are the most species-rich family with c. 1280 species in 87 genera.

Liverworts are widely distributed on earth, in all environments, except in marine ones; from the arctic to the subantarctic/antarctic regions, with high cover values mainly in tropical cloud forests and temperate rain forests, but also in desert crusts. They colonize a wide range of substrates, terrestrial, epilithic, epiphytic and epiphyllous ones (even leaves of other bryophytes), only a few are growing in aquatic environments. Figs. 2-1, 3-1, 4-1–4-9.

**Alternation of generations.** Regular alternation between a usually perennial, seldom annual, functionally haploid and usually dominant gametophyte generation, and a very short-lived functionally diploid sporophyte generation (heteromorphic, heterophasic). **Gametophytes.** Plants thallose, semi-leafy or leafy, growing from a single 2–4-sided apical cell giving rise to thallus or stem tissue and in leafy liverworts to 3, resp. 2 rows of leaves, lacking stomata. In advanced taxa there is a short-lived and often unbranched protonemal stage giving rise to only a single plant, in some relatively generalized groups branched filamentous protonemata occur, each of the branches is potentially capable of producing a plant. Leaves are usually one layer of cells thick, undivided or divided into segments; a midrib is lacking. “Complex thallose” liverworts usually possess air chambers with dorsal pores and differentiated internal tissues, restricted to the monophyletic Marchantiopsida. The true “simple thallose” forms (e.g., *Metzgeria*, *Riccardia*), the “semi-leafy” fossombronialean liverworts and the thallose forms with a central strand (Pallaviciniaceae, Hymenophytaceae) are resolved as paraphyletic and obviously represent different evolutionary lineages. “Leafy liverworts” range

from polysymmetric with three rows of morphologically similar leaves (isophyllous) to monosymmetric with 2 rows of lateral leaves and an additional row of reduced to absent postical amphigastria (underleaves) (anisophyllous). Obviously leaves, leaf-like lobes or lobules have evolved in every major group. Chlorophyllose cells contain numerous lenticular chloroplasts, lacking pyrenoids. Homogeneous or segmented membrane-bound oil bodies, accumulating lipophilic terpenoids and aromatic compounds, are present in c. 90% of all taxa, and the size, shape, colour and number per cell is often taxa specific. Oil-cells, containing a single large oil droplet, occur in some thallose liverworts. Rhizoids originate from the ventral/postical side of plant, rarely from the postical lobes (*Radula*) or from thallus margins (*Metzgeria*), are unicellular (very rarely of several cells) and commonly present, smooth; in Marchantiopsida tuberculate. In epiphyllous taxa, rhizoids often fuse together to form a secondary rhizoid disk. Water-conducting cells (central strand) with cell walls perforated by plasmodesmata-derived pores are restricted to the gametophytic generation, occurring in *Haplomitrium* and Pallaviciniales. In simple and thallose liverworts uniseriate to branched slime papillae (mucilage-secreting hairs) surround and protect meristematic regions. Slime papillae, flattened multicellular scales with marginal papillae as protective structures occur in *Blasia*, *Cavicularia* and complex thallose liverworts.

**Sexual reproduction.** Archegonial and antheridial ontogeny exogenous from superficial cells, without apical cells. Gametangia with sterile jacket layer, stalked. Antheridia usually short-ovoid or spherical and stalked, with unistratose jacket, enclosing the spermatogenous tissue (spermatid mother-cells, each with 2 plastids); 1 to several in axils of leaf-like bracts or on the thallus surface. Oblique division of the spermatid mother cell in two uniplastidic spermatids (immature spermatozooids). Spermatozooids (antherozoids) biflagellated, asymmetric, sinistrally coiled. Blepharoplast (locomotory apparatus): staggered arrangement of dimorphic basal bodies (also in lycopods), basal bodies markedly different in length, spline (microtubular band) composed of 16–104 microtubules; spline aperture closed or open. Position of the plastid and associated posterior mitochondrion at cell terminus. Spermatozooids motile, swimming to the egg through the film of water left by rain or dew, following an increasing gradient of chemical attractant secreted by either the mature archegonium or the egg. Archegonia flask-shaped, with a free jacket layer; a multistratose venter containing an egg cell, a ventral canal cell and a unistratose neck with (3–)4–8–16(–40) neck canal cells (Archegoniatae). Disintegration of neck canal cells and ventral canal cell before fertilization. One to several archegonia surrounded by leaf-like bracts/leaves (“perianth”) (leafy plants) or an involucre (thallose plants). (Fig. 3-1.2–3, 5–7.)

Distribution of gametangia: dioicous (unisexual), monoicous (autoicous, paroicous, heteroicous or synoicous [bisexual]). Position of archegonia: acrogynous (“Jungermanniales acrogynae”), anacrogynous (“Jungermanniales anacrogynae”).

**Sporophytes.** The first division of the zygote is transverse, producing an epibasal (→ foot, seta, capsule) and a hypobasal cell (→ haustorium); the further mitotic divisions lead to an embryo. Sporophytes grow by an apical cell, and are entirely surrounded during development by a calyptra (wall of the venter; ruptures as the seta lengthens, leaving only a basal collar), resp. stem-calyptra, syn. shoot-calyptra (a hollow fleshy structure, derived from both stem and archegonium tissue; it has the same function as a perianth and bracts). They are usually surrounded by additional protective structures: a perianth, a coelocaul [an extreme form of a stem(shoot)-calyptra, derived only from stem tissue; a type of a perigynium], a perigynium s.str. (a tubular extension of the stem tissue, elevating the ♀ bracts and perianth, if present) or a marsupium (a highly elongated marsupium is sometimes called a marsupid-

ium) in leafy liverworts; an involucre/um (strictly, a sheath growing from a thallus and protecting the archegonia in hornworts and marchantialean liverworts; often loosely applied to the pseudoperianth of the metzgerialean liverworts and the ♀ bracts and bracteoles of the Jungermanniidae), or a pseudoperianth (a membranous tubular sheath that surrounds the sporophyte, in double involucre, inner involucre = pseudoperianth) in thallose liverworts. Sporophytes are non-photosynthetic, short-living, unbranched and monosporangiate, strictly determinate in growth; differentiated into a usually dark brown capsule (= theca), a usually colourless, delicate seta (elongation after spore maturation), and a foot (absorbing organ). In marchantioid taxa (e.g., *Riccia*, *Corsinia*) the seta is vestigial or lacking. Stomata are lacking. Sporophytes are attached by a foot (gametophyte-sporophyte junction, s.bl.) to the gametophyte and nutritional dependent on it (gonotrophy) throughout life time. Capsules are spherical or ellipsoid, consisting of a wall of sterile cells derived from the amphithecium, and a spore sac derived from the endothecium; lacking columella, peristome, and stomata. They dehisce normally into 4 valves, rarely into 2 to 12–14 (*Phyllohallia*) valves to irregular fragments or plates; they are rarely cleistocarpous or dehiscence takes place by an apical lid. Each archesporium cell divides unequally into a spore mother cell (sporocyte) and an elater-mother cell (elaterocyte). Spores are produced by meiosis (meiospores); each diploid spore mother cell is divided into 4 haploid spores (a tetrad). Monoplastidic meiosis (as in all mosses and hornworts) occurs in basal liverwort taxa (*Monoclea*, *Blasia*, *Cavicularia*, *Haplomitrium*) and in *Wiesnerella*, *Lunularia*, *Dumortiera* and *Marchantia*, other are polyplastidic. Spore maturation is synchronous, before elongation of seta. Spores are uni- or multicellular, isosporous, Ø range from 6–200 µm; the spore coat is cutinized. Spore germination is exosporic or endosporic; the latter type of germination is particularly characteristic of epiphytes (*Plagiochila* spp., *Radula* spp., Jubulaceae, Lejeuneaceae). The diploid elaters are unicellular, narrowly elongated, and provided mostly with one or more helical thickened bands, interspersed among spores to facilitate their separation and dispersal by hygroscopic movement. Spore-elater ratio 4:1 to 46–58:1, in *Schistochila* c. 200:1 (over 5 mio. spores per capsule). Elaterophores are sterile tissue structures at the base or apex of the capsules of some liverworts, where elaters are attached.

**Chromosome sets** (all numbers refer to gametophytic chromosome numbers). Chromosome sets are aneuploid, primary diploid and secondary polyploid ( $n = 6–48$ ) by aneuploidy, autopolyploidy, or allpolyploidy. It is assumed that the basic chromosome number in liverworts is  $x = 5$ , not present in extant taxa. The predominant aneuploid set of chromosomes with  $n = 9$  (functionally haploid) must have appeared before the liverworts began to evolve by autopolyploidy and aneuploidy;  $n = 8$  and  $n = 12, 16, 18, 20, 22, 27, 36, 48$  being derived numbers. Gametophytes are quasi diploid (functionally haploid), sporophytes quasi tetraploid (functionally diploid) (as in mosses, exc. *Takakia* and some *Mniodendron* spp.).

**Gametophyte-sporophyte junction.** A clear-cut demarcation zone between the gametophyte and the sporophyte placental layers, a placental space, as in mosses, is apparent. In many taxa the placental space is filled with residues of collapsed cells of gametophytic origin. Intermingling, resp. interdigitating of sporophytic and gametophytic placental cells as in hornworts and Psilotopsida does not occur.

**Chemical constitution.** There is almost no chemical affinity between Marchantiophyta, Bryophyta and Anthocerotophyta, except for common sterols. The Marchantiophyta are chemically quite complex. Most of the liverworts elaborate a number of terpenes (mono- and sesquiterpenes are characteristic; triterpenes are lacking). Lunularic acid and its decarboxylation product, lunularin, and their

derivates are widespread. Sesquiterpenoids occur in oil-bodies. Biflavonoids are lacking. Several of the cell constituents have been shown to possess antibacterial, antifungal and/or antitumorogenic activities. The active constituents belong to non-ionized organic acids, alkanes, phenolics, bibenzyls, sesquiterpenoids, flavonoids and related compounds.

**Asexual reproduction.** Gametophytes of liverworts commonly reproduce asexually (vegetatively). 1. Asex. reprod. s.str.: Reprod. by  $\pm$  specialized caducous organs [stems, branches, leaves, leaf apices, leaf fragments, shoot apices, bulbils, cladia (brood branchlets), regenerants of leaf margins, perianths] or by specialized propagules (brood cells, gemmae, rhizoidal tubers), and gemmae on young regenerants [unique in *Chiloscyphus perpusillus* (Hook.f. & Taylor) J.J.Engel]. 2. Clonal reprod.: Buds on protone-ma, decaying and dissolving of stem and thallus parts, aerial shoots from stoloniferous or rhizome-like shoots, shoots from rhizoid wicks, innovations from shoot or branch buds, basitonic innovations, fragmentation (dividuals generally called ramets).

**Fungal associations. Mykorrhiza-like associations** occur in gametophytic tissue of thallose liverwort groups with Glomeromycota, except Blasiales, Sphaerocarpaceae, Ricciales, Metzgeriales and *Pleurozia*; *Monoclea* shows symbiosis with *Acaulospora*, Aneuraceae with *Tulasnella*, leafy liverworts p.p. (Jungermanniales, Lepicoleales p.p.) symbiosis with *Sebacina* and/or *Hymenoscyphus*; symbiosis does not occur in epiphytic Radulales, Porellales and Lepicoleales p.p. About 350 species of Ascomycetes are known to be restricted to the gametophytes of hepatics and mosses (**bryophilous Ascomycetes**), forming ascomata (fruit-bodies of Ascomycetes) at distinct and species-specific microsites, e.g., perianths, leaf border or axils, or even individual cells (one of the most typical strategies is leaf perforation) in foliose liverworts. Ascomata immersed in the thalli are typical for marchantialean hosts. Niche selection is a typical, often diagnostic feature of bryophilous ascomycetes. The **cyanobacterial symbiosis** is not well examined in liverworts and mosses, e.g., the ventral "auricles" of *Blasia pusilla* L. are filled with *Nostoc* colonies.

**Molecular phylogeny.** Marchantiophyta represent the earliest diverging lineage of extant embryophytes and are sister to all other land plants in molecular phylogenies (e.g., Qiu et al. 2006, 2007) (Fig. 2-1). Treubiaceae and *Haplomitrium* are resolved as sister groups and form the earliest diverging lineages within liverworts. *Blasia* and *Cavicularia* form an own clade sister to marchantialean liverworts. Monophyly of the complex thallose Marchantiopsida as a fundamentally different liverwort group is supported by analyses of combined molecular and non-molecular markers. The formerly thallose/semi-leafy Metzgeriidae s.l. group (Jungermanniales anacrogynae) is clearly a paraphyletic assemblage. Combined molecular analyses indicate that the true simple thallose forms (e.g., *Metzgeria*, *Riccardia*), the semi-leafy Fossombronialean liverworts, and the leafy and thallose forms with a central strand (Pallaviciniaceae, Hymenophytaceae) represent different evolutionary lineages. On the other hand, the leafy Jungermanniidae (exc. *Pleurozia*) appear as monophyletic. Despite considerable progress in understanding their evolutionary history based on molecular analyses relationships within this group are still incompletely resolved. The prevailing hypotheses of character evolution in hepatics, including the model of the ancestral liverwort prototype as an erect, radially symmetric plant is rejected in this broad sense. The archetype morphology is thought to be that of a prostrate, dissymmetric, leafy plant, with the developmental and reproductive features of a simple thallose liverwort (Crandall-Stotler et al. 2005), derived from a hypothetical leafless ancestor (cf. Héban 1977; Frey & Losch 2004, Fig. 5-15; Fig. 3-1.9).

**Characters of Marchantiophyta unique in plant kingdom.** Archegonial and antheridial ontogeny without an apical cell, unequal division of the archesporangium into a spore mother cell and an elater cell, presence of oil bodies (unique organelles of the liverworts, lacking in any other plant group), and lunularic acid.

**Life form.** The habit of a plant in harmony with its life conditions, i.e. growth-form, assemblage of individuals and the influence of external factors. **Annuals:** life cycle within a year, only sex. reprod., no regenerative shoots; e.g., *Riccia glauca*; **short turfs:** orthotropic; shoots < 1cm high, with regenerative shoots; pauciennial, e.g., *Gymnomitrium corallioides*; **tall turfs:** orthotropic; shoots up to 15 cm high, often with acrotonous branching; perennial, e.g., *Herbertus sendtneri*; **mats:** plagiotropic; main and lateral shoots/thallus close to substrate; usually perennial, e.g., *Radula complanata*; **wefts:** plagiotropic; shoots grow loosely through one another; perennial, e.g., *Trichocolea tomentella*; **pendents:** epiphytic; main shoots hanging down (comb mosses); pauciennial or perennial, e.g., *Frullania atrata*; **thread:** tiny, solitary, growing or among turfs and wefts; pauciennial or perennial, e.g., *Drepanolejeunea bidens*; **tails:** shoots stand out from substrate and are slightly branched or unbranched; perennial, e.g., *Schistochila rubriseta*; **fans:** creeping on vertical substrate, shoots branching towards one another; perennial, e.g., *Bryopteris filicina*; **dendroids:** orthotropic; shoots with a tuft of large leaves or lateral shoots at top; perennial, e.g., *Hymenophyton* spp.

**Life-strategy.** Complex of co-evolved adaptive traits, i.e. life span, life form, reprod. behaviour and dispersal behaviour. **Annual shuttle species:** short life span (annual), sex. reproductive effort high, no asex. reprod., short-range dispersal of spores (shuttle), e.g., *Riccia glauca*; **short-lived shuttle species:** pauciennial, sex. reproductive effort high, asex. reprod. infrequent, short-range dispersal of spores (shuttle), e.g., *Targionia hypophylla*; **colonists:** pauciennial, sex. reproductive effort high, asex. reprod. partly frequent, long-range dispersal of spores, e.g., *Marchantia polymorpha*; **perennial shuttle species:** perennial, sex. reproductive effort high, asex. reprod. frequent, short-range dispersal of spores (shuttle), e.g., *Frullania dilatata*; **perennial stayers:** perennial, sex. and asex. reprod. frequent or partly frequent, different dispersal types, e.g., *Bazzania trilobata*.

**Zoophagy.** Evidence of zoophagy in *Colura* and *Pleurozia* with trap-like structures in the water sacs of leaves.

**Fossil history.** Palaeophytic records: Assignable Devonian-Carboniferous-Permian hepatic fossils: *Grisellatheca salopensis* Edwards et al., Lower Devonian, first known fossil with hepatic features. Enigmatic Lower Devonian microfossils (epidermal surface tissues, rhizoids) may be the remains of early marchantioid liverworts. *Metzgeriothallus sharonae* VanAller Hernick et al., upper Middle Devonian, N Am. and *Pallaviciniites devonicus* (Hueber) R.M.Schust., lowermost Upper Devonian, N Am., the first known true bryophyte fossils, comparable to the Pallaviciniaceae. *Treubiites kidstonii* (J.Walton) R.M.Schust., Upper Carboniferous, Scotland is rejected as presumable precursor of Treubiopsida due to ventral scales (as in *Blasia*) and is thought to be precursor of Blasiopsida. *Blasiites lobatus* (J.Waton) R.M.Schust., Upper Carboniferous, Scotland, "similarity" to *Blasia* prob. purely superficial, assignable to Pelliaceae. *Metzgeriothallus metzgerioides* (J.Walton) R.M.Schust., Upper Carboniferous, England, similar to *Riccardia*; *Hepaticites langii* J.Walton, England, superficially similar to *Aneura* or *Riccardia*. *Gessella* Poulsen (2), Lower Permian, Denmark, of Haplomitrialean affinity. Apparently no convincingly true marchantioid fossils (Marchantiidae) are known from Palaeophytic time (except the uncertain Lower Permian *Marchantites loreus* Zalesky from the Ural), and there is a total lack of evidence of leafy Jungermanniidae.

Mesophytic records: Prob. Jungermannialean leafy *Jungermannites keuperianus* (De Gasparis) Oostendorp, Upper Triassic, Germany. *Marchantites cyathoides* (Townrow) H.M.Anderson and *M. temantii* H.M.Anderson from Middle Triassic of S Afr., Marchantiidae. The more derivative Marchantiopsida did not arise, prob. before the start of the relatively arid Mesophytic. *Naiadita lanceolata* P.B.Brodie, Upper Triassic of S England, is discussed to belong to the Sphaerocarpidae or Haplomitriopsida. *Jungermannites gracilis* (T.Halle) Oostendorp, Middle Jurassic, Graham Land, Antarct., first authenticated case of a member of the Jungermanniales and *Cheirorhiza brittae* Krassilov, Upper Jurassic of Russia. *Laticaulina papillosa* Krassilov, Upper Jurassic of Russia, with affinities to the Pallaviciniopsida (*Symphyogyne*). *Diettertia montanensis* J.T.Br. & Robinson, Lower Cretaceous, with disymmetric organization. *Marchantites* spp. and *Thallites* spp., Alexander I., Antarct. Only very few

Mesozoic fossils belong to Jungermanniidae. To date, the fossil records up to Cretaceous time have not provided unequivocal answers to questions about phylogenetic relationships among liverworts.

Neophytic fossil records: The most diverse Palaeogene bryoflora has been authenticated by study of specimens of Baltic (Eocene, 54.8–34 mio.y), Bitterfeld (Germany) (Oligocene, 23.8–25.3 mio.y), Dominican (Miocene, 35–25 mio.y) and Mexican (Miocene, 35–25 mio.y) amber (e.g., Gradstein 1993, Grolle & Meister 2004). The liverworts are exclusively represented by leafy liverworts (Jungermanniidae). Structures similar to thallose liverworts have been proved as artefacts (pseudofossils). There are reports of 26 spp. of 17 modern genera (e.g., *Frullania*, *Jungermannia*, *Radula*) from Baltic and Bitterfeld amber, 20 spp. of 17 modern gen. of Dominican and 1 sp. of Mexican amber (mainly Lejeuneaceae). 7 amber hepatics (all Lejeuneaceae), e.g., *Nipponolejeunea subalpina* (Horik.) S. Hatt., Baltic and Bitterfeld amber; extant: humid subalp. E Asia (Zaowan, Japan) and *Mastigolejeunea auriculata* (Wils.) Schiffn., Dominican amber; extant: pantrop., are presently the oldest known bryophyte fossil representatives conspecific with extant species. They are most convincing examples for steno-evolution (steno-evolutionary taxa, i.e., taxa without or with only little genetic divergence, low evolution rates, and no speciation after separation or extinction of populations in geological times; extant taxa, e.g., *Pallavicinia xiphoides*) (Frey et al. 1999). Preservation of Neogene fossils is usually good.

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- For meaning of terms see Malcolm & Malcolm (2006).

## Synopsis of classification of the Marchantiophyta Stotler & Crand.-Stotl.

### Superclass I

Class **Treubiopsida** Stech, J.-P.Frahm, Hilger & W.Frey  
 Order **Treubiales** Schljakov  
**Treubiaceae** Verd.

Class **Haplomitriopsida** Stotler & Crand.-Stotl.  
 Order **Haplomitriales** H.Buch ex Schljakov  
**Haplomitriaceae** Dědeček

### Superclass II

Class **Blasiopsida** Stech & W.Frey  
 Order **Blasiales** Stotler & Crand.-Stotl.  
**Blasiaceae** H.Klinggr.

Class **Marchantiopsida** Cronquist, Takht. & W.Zimm.  
 Subclass **Sphaerocarpidae** Stotler & Crand.-Stotl.  
 Order **Sphaerocarpales** Cavers  
 Suborder **Sphaerocarpineae** R.M.Schust. ex Stotler & Crand.-Stotl.  
**Sphaerocarpaceae** Heeg  
 Suborder **Riellineae** R.M.Schust. ex Stotler & Crand.-Stotl.  
**Riellaceae** Engl.  
 Subclass **Marchantiidae** Engl.  
 Order **Monocleales** R.M.Schust.  
**Monocleaceae** A.B.Frank  
 Order **Neohodgsoniales** D.G.Long  
**Neohodgsoniaceae** D.G.Long  
 Order **Lunulariales** D.G.Long  
**Lunulariaceae** Klinggr.  
 Order **Marchantiales** Limpr. in Cohn  
 Suborder **Marchantiineae** Buch ex Schljakov  
**Aytoniaceae** Cavers, **Cleveaceae** Cavers, **Conocephalaceae** Müll.Frib. ex Grolle,  
**Dumortieraceae** D.G.Long, **Exormothecaceae** Müll.Frib. ex Grolle, **Marchan-**  
**tiaceae** Lindl., **Monosoleniaceae** Inoue, **Wiesnerellaceae** Inoue  
 Suborder **Corsiniineae** R.M.Schust. ex Schljakov  
**Corsiniaceae** Engl., **Cyathodiaceae** Stotler & Crand.-Stotl.  
 Suborder **Monocarpineae** R.M.Schust.  
**Monocarpaceae** D.J.Carr ex Schelpe  
 Suborder **Targioniineae** R.M.Schust. ex Schljakov  
**Targioniaceae** Dumort.

Order **Ricciales** Schljakov  
**Oxymitraceae** Müll.Frib. ex Grolle, **Ricciaceae** Rchb.

### Superclass III

Class **Fossombroniopsida** W.Frey & Hilger  
 Order **Fossombroniales** Schljakov  
**Allisoniaceae** Schljakov, **Fossombroniaceae** Hazsl., **Makinoaceae** Nakai, **Petalophyllaceae** Stotler & Crand.-Stotl., **Sandeothallaceae** R.M.Schust.

Class **Pallaviciniopsida** W.Frey & Stech  
 Order **Phyllothalliales** Schljakov  
**Phyllothalliaceae** E.A.Hodgs.  
 Order **Pallaviciniales** W.Frey & Stech  
**Moerckiaceae** Stotler & Crand.-Stotl., **Pallaviciniaceae** Mig.  
 Order **Hymenophytales** W.Frey & Stech  
**Hymenophytaceae** R.M.Schust.

Class **Pelliopsida** W.Frey & Stech  
 Order **Noterocladales** W.Frey & Stech  
**Noterocladaceae** W.Frey & Stech  
 Order **Pelliales** He-Nygrén, Juslén, Ahonen, Glenny & Piippo  
**Pelliaceae** H.Klinggr.

### Superclass IV

Class **Jungermanniopsida** Stotler & Crand.-Stotl.

Subclass **Jungermanniidae** Engl. (Jungermanniales acrogynae)

Superorder **Jungermannianae** Schljakov  
 Order **Perssoniellales** Schljakov  
**Perssoniellaceae** R.M.Schust. ex Grolle, **Schistochilaceae** H.Buch

Order **Jungermanniales** H.Klinggr.  
 Suborder **Balantiopsineae** R.M.Schust.  
**Balantiopsaceae** H.Buch, **Trichotemnomaceae** R.M.Schust.  
 Suborder **Jungermanniineae** R.M.Schust. ex Stotler & Crand.-Stotl.  
**Acrobolbaceae** E.A.Hodgs., **Antheliaceae** R.M.Schust., **Calypogeiaceae** Arnell,  
**Gymnomitriaceae** H.Klinggr., **Jungermanniaceae** Rchb., **Mesoptychiaceae**  
 I noue & Steere, **Myliaceae** Schljakov, **Stephaniellaceae** R.M.Schust.

Suborder **Brevianthineae** J.J.Engel & R.M.Schust.  
**Brevianthaceae** J.J.Engel & R.M.Schust., **Chonecoleaceae** R.M.Schust. ex Grolle

Suborder “**Geocalycineae** s.str.”  
**Geocalycaceae** H.Klinggr., **Gyrothyraceae** R.M.Schust.

Order **Jamesoniellales** W.Frey & Stech  
**Adelanthaceae** Grolle, **Jamesoniellaceae** He-Nygrén, Juslén, Ahonen, Glenny & Piippo

- Order **Lophoziales** Schljakov
  - Suborder **Cephaloziineae** Schljakov
    - Cephaloziaceae** Mig., **Cephaloziellaceae** Douin, **Jackiellaceae** R.M.Schust.
  - Suborder **Lophoziineae** Schljakov
    - Blepharidophyllaceae** R.M.Schust., **Chaetophyllopsaceae** R.M.Schust., **Delavayellaceae** R.M.Schust., **Lophoziaceae** Cavers, **Scapaniaceae** Mig.
- Order **Trichocoleales** W.Frey & Stech
  - Blepharostomataceae** W.Frey & Stech, **Trichocoleaceae** Nakai
- Order **Lepidoziales** Schljakov
  - Lepidoziaceae** Limpr., **Neogrolleaceae** J.J.Engel & Braggins, **Phycolepidoziaceae** R.M.Schust.
- Order **Lepicoleales** Stotler & Crand.-Stotl.
  - Suborder **Lepicoleineae** R.M.Schust.
    - Lepicoleaceae** R.M.Schust., **Vetaformaceae** Fulford & J.Taylor
  - Suborder **Herbertineae** R.M.Schust.
    - Grolleaceae** Solari ex R.M.Schust., **Herbertaceae** Müll.Frib. ex Fulford & Hatcher, **Mastigophoraceae** R.M.Schust.
- Order **Pseudolepicoleales** W.Frey & Stech
  - Pseudolepicoleaceae** Fulford & J.Taylor
- Order **Lophocoleales** W.Frey & Stech
  - Arnelliaceae** Nakai, **Lophocoleaceae** Vanden Berghen, **Plagiochilaceae** Müll.Frib.
  
- Superorder **Porellanae** W.Frey & Stech
  - Order **Ptilidiales** Schljakov
    - Neotrichocoleaceae** Inoue, **Ptilidiaceae** H.Klinggr.
  - Order **Porellales** Schljakov
    - Suborder **Lepidolaenineae** R.M.Schust.
      - Goebeliellaceae** Verd., **Jubulopsaceae** R.M.Schust., **Lepidolaenaceae** Nakai
    - Suborder **Porellineae** R.M.Schust.
      - Porellaceae** Cavers
  - Order **Radulales** Stotler & Crand.-Stotl.
    - Radulaceae** Müll.Frib.
  - Order **Jubulales** W.Frey & Stech
    - Frullaniaceae** Lorch, **Jubulaceae** H.Klinggr., **Lejeuneaceae** Casares-Gil
  
- Subclass **Pleuroziidae** W.Frey & Stech
  - Order **Pleuroziales** Schljakov
    - Pleuroziaceae** Müll.Frib.
  
- Subclass **Metzgeriidae** Barthol.-Began (Jungermanniales anacrogynae p.p.)
  - Order **Aneurales** W.Frey & Stech
    - Aneuraceae** H.Klinggr., **Mizutaniaceae** Furuki & Z.Iwats., **Verdoorniaceae** Inoue
  - Order **Metzgeriales** Chalaud
    - Metzgeriaceae** H.Klinggr.

## Systematic arrangement of taxa

Species numbers are provisional. Reliable taxonomic concepts until June 2008.

### Superclass I

#### Class **Treubiopsida** Stech, J.-P.Frahm, Hilger & W.Frey

##### Order **Treubiales** Schljakov

Fam. **Treubiaceae** Verd. Anacrogynous. Unique “leafy” growth form with 2 lateral rows of alternate, succubous lobes and transversely oriented dorsal lobules (scales). Dimorphic leaf cells: scattered cells with 1 large oil-body, other cells only with chloroplasts. Slime papillae on ventral surface, producing a thick covering of mucilage. Axis with a central strand of parenchymatous cells, with intra- and intercellular infection by a glomerophycotean fungus. Gametangia in axils of dorsal lobules in *Treubia*. Blepharoplast: lamellar strip (spline) with up to 104 microtubules, open spline aperture, overlap between anterior and posterior basal bodies. Gametophyte-sporophyte junction either resembling that one of Jungermanniopsida (*Apotreubia*) or similar to *Haplomitrium* and *Fossombronia* (*Treubia*). Di- or monoicous. Asex. reprod. by stalked gemmae in the axils of the dorsal lobules. Single sporophyte per gynoeceium. Stem(shoot)-calyptra present. Spores 21–26 µm in Ø. n = 9. 2 gen. (11), distrib. pattern orig. Pangaeen. Fig. 4-1.1–3.

*Apotreubia* S.Hatt. & Mizut. (4), predom. Lauras. Branches terminal and pseudodichotomous. – *Treubia* K.I.Goebel (7), basically Gondwan.; Malesia, Australasia, Oceania (S Pacific), Chile (1); not in Afr. Branches lateral-intercalary.

Based on morphological characters the two extant genera *Treubia* and *Apotreubia* may be regarded as the most archaic living liverworts. In molecular trees either Treubiopsida are resolved as sister to all other liverworts (Blasiopsida – Jungermanniopsida), or Treubiopsida and Haplomitriopsida together form the earliest diverging liverwort lineage, similar to cladistic analyses based on male gametogenesis. Both groups share following common features: e.g., tetrahedral apical cells, mucilage secreting from epidermal cells, leaf-wing origin from a single leaf initial, anacrogynous gametangial position, well-developed stem(shoot)-calyptra, massive seta, massive blepharoplasts and spermatozoids. But due to the divergent evolution since presumably Carboniferous time, the classes Treubiopsida and Haplomitriopsida are maintained and included in one informal superclass.

No fossil records known. The Upper Carboniferous *Treubiites* R.M.Schust. is rejected as presumable precursor of Treubiopsida due to lateral succubously shingled “leaves” and ventral scales (as in *Blasia*).

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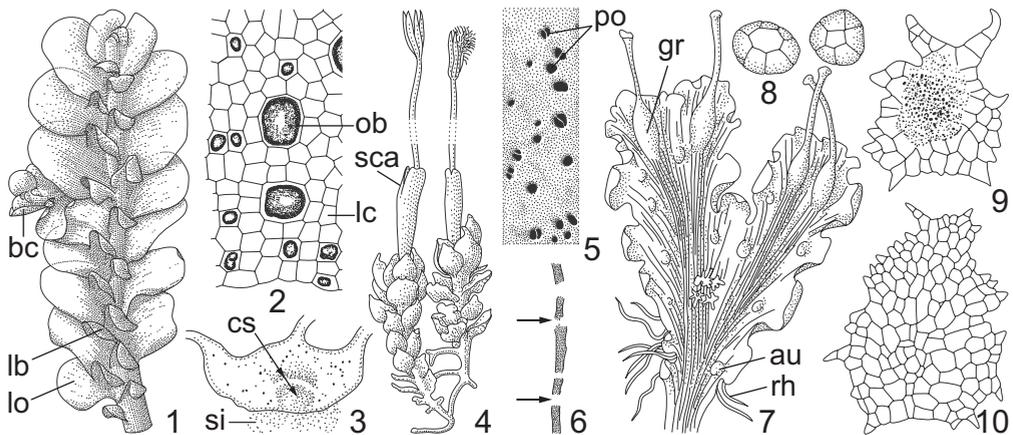
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## Class Haplomitriopsida Stotler & Crand.-Stotl.

### Order Haplomitriales H.Buch ex Schljakov

Fam. **Haplomitriaceae** Dědeček Upright habit. Subterranean creeping axis (“rhizome”) with endophytic aseptate fungi (*Glomus*). Mostly “isophyllous”, transversely inserted “leaves”. Rhizoids lacking. Central strand present, with axially slightly elongated, thin-walled water-conducting cells, with numerous perforations (pores) ( $\text{\O}$  0,3–0,5  $\mu\text{m}$ ) in the transverse or only slightly oblique end walls (originating from plasmodesmata). Di- or monoicous. Scattered gametangia in diffuse groups laterally along the stem without specialized protective bracts. Seta massive; stem-calyptra extensive. Blepharoplast: lamellar strip (spline) with up to 90 microtubules, spline aperture on the left side. Gametophyte-sporophyte junction: 1–2



**Fig. 4-1. Marchantiophyta.** Treubiopsida, Haplomitriopsida, Blasiopsida. Treubiopsida: 1–2. *Treubia lacunosa*. 1. Upper part of a plant, with lateral succubous lobes, 2 rows of dorsal lobules (scales) and a lateral intercalary branch (x2.5). 2. Marginal cells of thallus with oil-bodies (oil-cells), where present; chloroplasts not drawn (x120). 3. *T. tasmanica*. CS of axis, with central strand and oil-cells (indicated) (x12). Haplomitriopsida: 4–6. *Haplomitrium*. 4. *H. hookeri*. ♀ plant with mature sporophytes and stem-calyptra (x8). 5–6. *H. gibbsiae*. 5. SEM micrograph of an transverse wall between two water-conducting cells with pores (x5850). 6. TEM micrograph of a CS through a transverse wall (x9000). Blasiopsida: 7–10. *Blasia pusilla*. 7. Thallus with flask-shaped gemma-receptacles and *Nostoc*-filled “auricles” (x3.5). 8. Gemmae from gemma-receptacle (x80). 9. Stellate gemma (x100). 10. Dentate ventral scale (x200). (arrow: pore, au auricle, bc branch, cs central strand, gr gemma receptacle, lb lobule, lc lamina cell, lo lobe, ob oil-body, po pore, rh rhizoid, sca stem-calyptra, si slime).

sporophyte and 2–3 gametophyte placental cell layers; gametophyte transfer cells with highly branched and thin, long wall ingrowths. Multiple sporophyte production per gynoeceum. Capsule ellipsoid-cylindrical, dehiscent by 4 valves; walls unistratose, with unique secondary thickenings. Elaterophore basal. Elaters filamentous. Asex. reprod. lacking.  $n = 9$ ; 8. Fig. 4-1.4–6.

*Haplomitrium* Nees (9),  $\frac{*}{*}$ , basically Gondwan., centre of diversity Australasia.

**Fossil records:** No true haplomitrialean fossils have been found (cf. fossil history).

*Haplomitrium* is morphologically and anatomically isolated by a “series of fundamental criteria” (s.ab.) and regarded as an early-diverging lineage within liverworts, prob. existing since at least Carboniferous time.

The precise placement of *Haplomitrium* in molecular trees is still problematic and varies depending on taxon sampling. Cladistic analyses of male gametogenesis characters and recent combined molecular analyses revealed that *Haplomitrium* plus *Treubia* (superclass I) form a clade sister to all other liverwort groups. Cf. Treubiopsida.

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## Superclass II

### 1. Class **Blasiopsida** Stech & W.Frey

#### Order **Blasiales** Stotler & Crand.-Stotl.

Fam. **Blasiaceae** H.Klinggr. Thalli with ill-defined midrib grading into unistratose wings (leafy habit). Air-chambers and gametangiophores lacking. 2 rows of flattened multicellular scales (as in complex thallose liverworts), on ventral surface of thallus. Small ventral hemispherical “auricles” filled with *Nostoc* colonies and unique, flanked-shaped gemmae-receptacles present (unique in liverworts). Stellate gemmae often present near apex on dorsal surface. Dioicous. Antheridia solitary in dorsal antheridial cavities (*Blasia*) or single in tubular involucres at axis apices (*Cavicularia*). Archegonia dorsal, naked, behind apex. Marchantialean blepharoplast-type. Gametophyte-sporophyte junction: 1 sporophyte (*Cavicularia* several layers) and 2–3 gametophyte placental cells layers with marchantialean-type wall ingrowths. Capsule dehiscent by 4(–6) valves. Elaters 2-helical. Elaterophore basal, rudimentary. Spores 35–55  $\mu\text{m}$  in  $\varnothing$ .  $n = 5$  or 6?; 8, 9. Figs. 3-1.5, 4-1.7–10. 2 monospecific gen.

*Blasia* L. *B. pusilla* L., circ.-bor. Capsule valves 2-stratose. Stellate and ovoid gemmae present. Oil bodies lacking. On mineral soil, colonist. – *Cavicularia* Steph., *C. densa* Steph., endemic., Japan. Capsule valves 2–3- to 3–4-stratose. Gemmae ventral.

*Blasia* was traditionally included in the metzgerialean group, but blepharoplast ultrastructure and a marchantialean-type gametophyte-sporophyte junction assign it to the Marchantiopsida. Similarly, molecular results resolve *Blasia* and *Cavicularia* as sister to the Marchantiopsida.

The Upper Carboniferous *Blasiites lobatus* (J.Walton) R.M.Schust. is supposed to be an ancestor of the extant taxa (however, see Pelliopsida). The Carboniferous *Treubiites kidstonii* (J.Walton) R.M.Schust. with lateral succubously shingled leaves and ventral scales (as in *Blasia*) is rejected as presumable precursor of Treubiopsida, but serves as a model from which the more frondose, semithallose extant *Blasia* may be derived.

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## 2. Class Marchantiopsida Cronquist, Takht. & W.Zimm.

### Complex thallose liverworts

19 fam., 32 gen., c. 380 spp. Plants thallose, often with marked tissue differentiation. Air-chambers and air-pores often present. Rhizoids usually dimorphic, smooth or tuberculate. Single oil-bodies restricted to scattered oil-cells without chloroplasts. Monoicy frequent. Antheridia scattered or in groups, sunken in the thallus or on sessile or stalked receptacles (antheridiophores). Archegonia with 6 rows of neck cells, usually in groups, usually surrounded by an involucre. After fertilization, archegonia are elevated in some genera on stalked receptacles (archegoniophores) bearing the archegonia (and sporophytes) in a carpocephalum (apical part of the archegoniophore), less often on the thallus surface, or within thallus cavities or immersed in the thallus. Blepharoplast structure uniform; closed apertures, three spline microtubules wide. Gametophyte-sporophyte junction: 1–2 sporophyte and 2–4 gametophyte placental cell layers; cells of both layers with characteristic wall ingrowths (marchantiopsidalean type). Seta not or hardly elongating (exc. *Monoclea*). Dehiscence of capsule by (3–)4–8 irregular valves or fragments (exc. *Lunularia*), by a lid (operculum, operculate) in Aytoniaceae, by a longitudinal slit (*Monoclea*) or capsule cleistocarpous; wall unistratose. Spores 8–175(–200)  $\mu\text{m}$  in  $\emptyset$ ; germinating with germ tube and germ rhi-

zoid. Usually 4:1 spore-elater ratio. Spore number 25 to >10,000 per capsule. Elaters unicellular, 2-or more helical or ehelical. Predom. set of chromosomes  $n = 9$ , other numbers derived, see orders. Specialized propagules lacking, exc. in *Marchantia*, *Neohodgsonia*, and *Lunularia* (pluricellular discoid gemmae) and *Cyathodium* and *Conocephalum* (tubers). Terrestrial or saxicolous, from Arctic (Svalbard) to Antarctic (Antarct. Peninsula). Perennial or pauciennial xerophytes or short-lived “annuals”. Figs. 3-1.3, 6-7; 4-2.1-22.

Monophyly of the Marchantiopsida is strongly supported by all molecular analyses.

**Fossil records:** Some enigmatic Lower Devonian microfossils (epidermal surface tissues, rhizoids) may be regarded as remains of early marchantioid liverworts. Convincing marchantioid fossils unknown from Lower Palaeophytic, starting with the Lower Permian *Marchantites loreus* Zalessky (incertae sedis), the unequivocal Middle Triassic *Marchantites cyathoides* (Townrow) H.M.Anderson and *M. tennantii* H.M.Anderson, and becoming rel. species-rich from Triassic to Eocene. Prob. the initial diversification of the Marchantiopsida took place at the beginning of the rel. arid Mesophytic, followed by a rapid radiation of marchantioid taxa coincident with the extreme conditions and ecological reorganisation in Upper Permo-Triassic time.

## 1. Subclass **Sphaerocarpidae** Stotler & Crand.-Stotl.

### Order **Sphaerocarpaceae** Cavers

Thalli rosette-like, lobed or stem-like axes with unistratose undulate wings or leaf-like lobes. Air-chambers, mucilage cells and pores lacking. Archegonia and sporophytes in pear-shaped involucre on dorsal side of thallus. Rhizoids smooth. Seta remaining very short. Capsule spherical, cleistocarpous, at maturity with permanent tetrads of spores, and green nutritive cells. Elaters lacking. Stenotypic. Fig. 4-2.1-3.

Molecular studies (Forrest et al. 2006, He-Nygrén et al. 2006) indicate nesting of Sphaerocarpaceae within the Marchantiidae. Until further studies substantiate this statement, the subclass Sphaerocarpidae is maintained.

*Naiadita lanceolata* P.B.Brodie, Upper Triassic of England, is discussed to belong to the Sphaerocarpaceae.

### 1. Suborder **Sphaerocarpaceae** R.M.Schust. ex Stotler & Crand.-Stotl.

Fam. **Sphaerocarpaceae** Heeg Thalli lobed; multistratose in the middle, becoming unistratose in the lobes. Oil-bodies lacking. Dioicous. Marchantialean blepharoplast type and gametophyte-sporophyte junction. Capsule cleistocarpous or opening irregularly (*Geothallus*). Spore tetrads 60–185  $\mu\text{m}$  in  $\varnothing$ . Sex-correlated chromosomes first discovered in plants.  $n = 8$ , 16. 2 gen. (c. 8–10). Fig. 4-2.2-3.

*Sphaerocarpos* Boehm. (8–9), pacif. N Am., south. N and south. S Am., Macaron.-medit.-atlant., S Afr., SE Austr. Plants winter-annual or ephemeral, heterothallic. Lobes subfoliose and succubous. On damp soil. – *Geothallus* Campb. (1). *G. tuberosus* Campb., S California. Thalli *Fossombronia*-like (“stem” and succubous “leaves”). Perennating tubers present. On soil around vernal pools and wet depressions.

## 2. Suborder **Riellineae** R.M.Schust. ex Stotler & Crand.-Stotl.

Fam. **Riellaceae** Engl. Thalli ± erect; stem-like axes with undulate wings. Leaf-like appendages (wings) present on ventral and lateral side of axes. Antheridia in seriate chambers along thallus margin. Oil-bodies solitary, in scattered cells. Spores 60–130 µm Ø. Di- or monoicous. Asex. reprod. rare, by gemmae. In shallow water or creeping on muddy soil. n = 9. Fig. 4-2.1.

*Riella* Mont. (18), in warm and rather dry climates. Medit., Canary Is., N Afr., S Afr. (centres of diversification), N Am., south. S Am., SE Austr., India, Caucasus, C Asia.

## 2. Subclass **Marchantiidae** Engl.

Plants thallose, often with marked tissue differentiation: chlorenchyma and storage parenchyma. Air-pores (cells usually lacking chloroplasts) and air-chambers usually present. Storage parenchyma (containing starch grains) with scattered isolated cells with single large compound oil-bodies or occ. mucilage. Ventral surface of thalli with smooth and tuberculate rhizoids in midrib region. Usually 2, or more rows of ventral scales. Antheridia and archegonia borne in receptacles on modified branches (gametangiophores: ♀ archegoniophore, ♂ antheridiophore) with similar internal structure to thallus, or immersed in dorsal surface of thallus. Marchantialean blepharoplast-type. Multilayered structure contains a lamellar strip with a right-hand notch. Capsule with or without elaters. Spores strongly polar, with 3 flat inner faces separated by triradial ridges. Fig. 4-2.4–22.

### 1. Order **Monocleales** R.M.Schust.

Fam. **Monocleaceae** A.B.Frank Thalli homogeneous, without midrib, air-pores, and air-chambers; among the largest liverworts. Dimorphic thallus cells: scattered oil-cells with single oil bodies still retaining chloroplasts, and cells with chloroplasts only. Ventral scales lacking. Rhizoids dimorphic, thick-walled and smooth; few tuberculate, and thin-walled and smooth. Dioicous. Antheridia sunken in dorsal cavities, aggregated into sessile receptacles along the median portion of thallus. Archegonia at base of involucre near thallus apex. Often (2–)3–4 sporophytes per involucre. Seta massive, elongate. Capsule elongate-ellipsoid, dehiscing by 1 longitudinal slit. Spores 15–20 µm in Ø. Spore/elater ratio 2:1. Elaters 1–2-helical. n = 9. Restricted to hyperhygric habitats. Fig. 4-2.4.

*Monoclea* Hook. (2), Gondwan. *M. forsteri* Hook., N.Z., Auckland Is. *M. gottschei* Lindb., S and C Am.

No fossils known. Marchantialean blepharoplast structure and gametophyte-sporophyte junction as well as molecular data (*Monoclea* as sister to *Dumortiera*) indicate inclusion of *Monoclea* in the Marchantiales. Due to isolate position and the evolution in former Gondwanaland the order Monocleales is retained at present.

## 2. Order **Neohodgsoniales** D.G.Long

Fam. **Neohodgsoniaceae** D.G.Long Air-chambers without chlorophyllose filaments. Rhizoids smooth. Ventral scales lacking appendages. Archegoniophores branched. Spores 22–24  $\mu\text{m}$  in  $\emptyset$ . Asex. reprod. by gemmae (only one growing point).

*Neohodgsonia* Perss. (1). *N. mirabilis* (Perss.) Perss., N.Z., Tristan da Cunha, Gough I. Mont. forests.

Molecular results (Forrest et al. 2006) resolved *Neohodgsonia* as sister to all other complex thallose liverworts.

## 3. Order **Lunulariales** D.G.Long

Fam. **Lunulariaceae** H.Klinggr. Air-pores elevated, volcano-shaped. Dioicous. Stalk of ♀ receptacle without rhizoid furrow. Seta massive, elongate, exerted from a tubular involucre. Capsule opening by a lid and 4 valves. Spores 18–24  $\mu\text{m}$  in  $\emptyset$ . Asex. reprod. by discoid gemmae; gemma-cups crescent-shaped.  $n = 9$ . Fig. 4-2.5.

*Lunularia* Adans. (1). *L. cruciata* (L.) Lindb., nearly cosmopol., in temp. to warm-temp. climates, 62°N to 45°S; synanthropic.

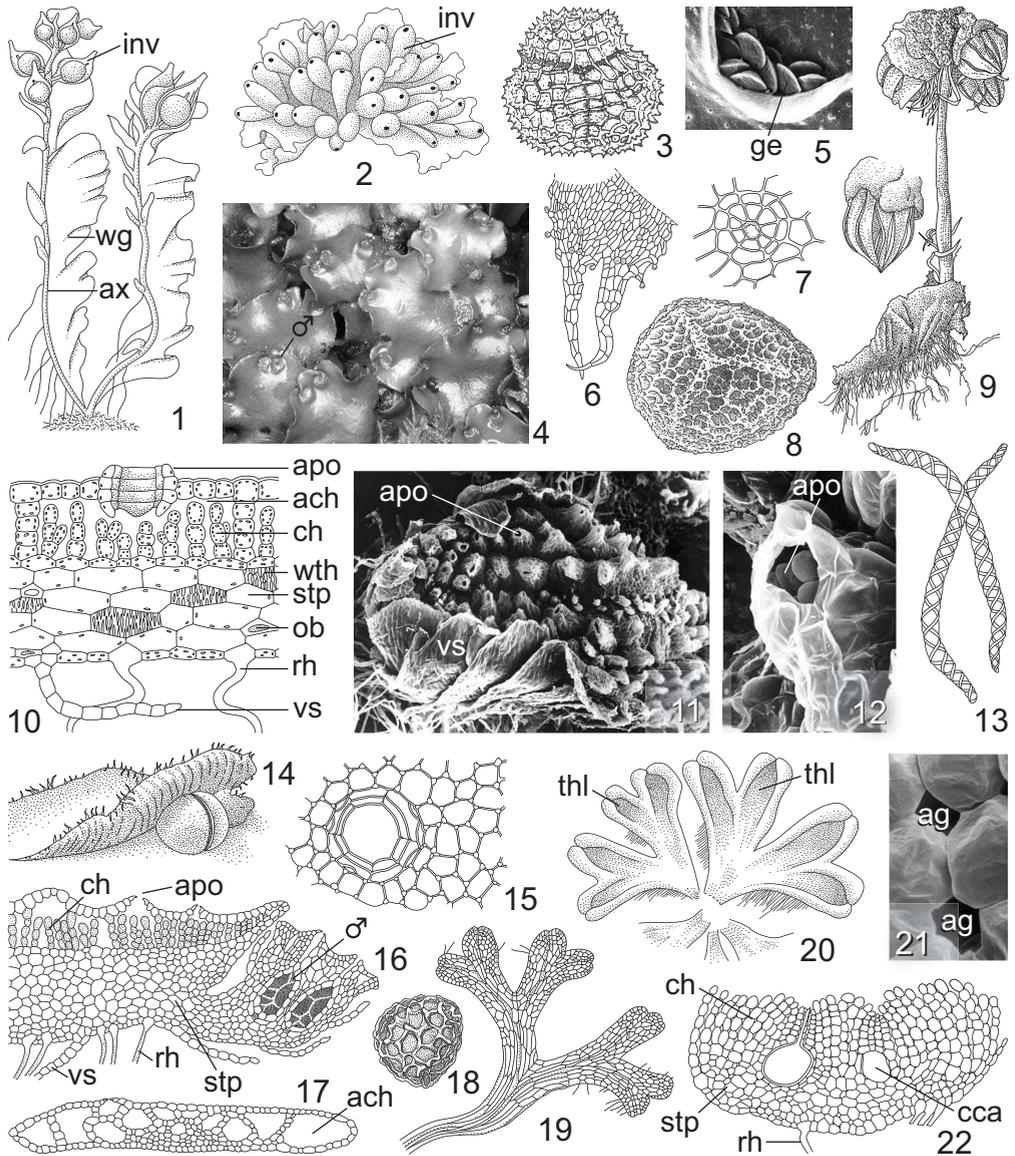
Ordinal rank for Lunulariaceae is well-supported by molecular data (Forrest et al. 2006).

## 4. Order **Marchantiales** Limpr. in Cohn

Plants thallose. Air-pores surrounded by 2 or more rings of differentiated concentric or superposed rings of cells. Air-chambers usually with chlorophyllose filaments. Compact, generally colourless ventral tissue (storage parenchyma). Di- or monoicous. Sessile or stalked discoid receptacles with antheridia (antheridiophores). Stalked entire or variously lobed receptacle with archegonia (archegoniophores) (sessile in *Corsinia*, *Cronisia*, *Cyathodium* and *Targionia*). Archegonia usually surrounded by an involucre. Pseudoperianths occ. present. Ventral scales usually present. Rhizoids usually typically dimorphic (tuberculate, smooth). Sporophyte on ventral surface of receptacle. Seta short, not or hardly elongating. Foot bulbous. Spore-elater ratio usually 4:1. Elaters usually 2–3-helical.  $n = 9$ ; other numbers:  $n = 8, 16, 18, 24, 27, 32, 36$  derived. 12 fam., 25 gen. (c. 180),  $\frac{*}{*}$ . Fig. 4-2.6–16.

At present, molecular results about relationships within the marchantialean liverworts are tentative. Taxa which have their sporophytes elevated on a carpocephalum are supported as one clade. Extant acarpocephalate taxa are derived from carpocephalate forms. There is strong implication that, within the carpocephalate clade, tolerance of extreme seasonality is the primitive condition, whereas taxa with large thalli and small spores, such as *Dumortiera* and *Marchantia*, are morphologically derived. Primary of xeromorphic nature.

Primitive taxa of Xerothermic Pangaeian origin, known from the Triassic period (form-species of *Marchantites*) to the present (*Marchantia* spp. from the Tertiary period). Fossil records see also Marchantiopsida.



**Fig. 4-2. Marchantiophyta.** Marchantiopsida. Sphaerocarpaceae: **1.** *Riella helicophylla*. ♀ plant with axes and wings, sporophytes with involucre (x3). **2-3.** *Sphaerocarpos michelii*. **2.** ♀ thallus with archeogonia in involucre (x4.5). **3.** Spore tetrad (x190). Marchantiidae. Monocleales: **4.** *Monoclea forsteri*. ♂ plant with receptacles (x0.4); light micrograph. Lunulariales: **5.** *Lunularia cruciata*. Semi-lunar gemmae cup with gemmae (x2.5). Marchantiales: **6-9.** *Asterella persica*. **6.** Ventral scale (x30). **7.** Air-pore (x200). **8.** Spore, proximal surface (x230). **9.** Archegoniophore with carpocephala (x5). **10.** *Marchantia polymorpha*. CS of thallus (x120). **11-12.** *Exormotheca pustulosa*. **11.** Thallus with ventral scales and chimney-like air-chambers (x30). **12.** Air-chamber with air-pore and apical cells of chlorophyllose filaments (x170). **13-16.** *Targionia hypophylla*. **13.** Elaters (x320). **14.** Part of thallus with envelope-like involucre opening by 2 valves (x5.5). **15.** Air-pore and epidermal cells (x130). **16.** CS of thallus with air-pores, air-chambers, chlorophyllose filaments and storage parenchyma; right-hand: antheridial

## 1. Suborder **Marchantiineae** Buch ex Schljakov

Fam. **Aytoniaceae** Cavers Thalli often drought-tolerant. Air-chambers in 2 or more layers, without true chlorophyllose filaments. Ventral scales with 1–3 appendages. Monoicous, rarely dioicous (in *Mannia*). ♂ receptacles on dorsal surface of midrib. ♀ receptacles with one rhizoid furrow. Pseudoperianths lacking, except in *Asterella*. Dehiscence of the capsule by a lid (operculum). Spores 35–120 µm in Ø. Elaters 2–4-helical. n = 9, 18. 5 gen. (c. 85), in areas with medit.-type climate; isolated spp. of *Asterella* and *Mannia* in alp. and arct. regions. Fig. 4-2.6–9.

*Asterella* P. Beauv. (45–50), almost cosmopol., to the Arct., warm and temp. habitats; N Am. (7), C, S Am. (13), Eur. (4), Asia incl. Malesia (14), Afr. (10), Austr., N.Z. (6), Oceania (3). Deeply divided pseudoperianth present. Paraphyletic. Usually on soil or rock. – *Cryptomitrium* Austin ex Underw. (3), disjunct in N, C and S Am., Himalayas, SE Afr. Involucre bilabiate. On rock outcrops and rock crevices. – *Mannia* Opiz [= *Grimaldia* Raddi] (16), medit.-type climate, to the Arct.; absent from SE Asia and Australasia. ♀ receptacles with 3–4 bell-shaped involucre (involucral skirts). On rocky soil or in rock crevices. – *Plagiogchasma* Lehm. & Lindenb. (c. 16), cosmopol., in warm areas; Am. (9), Eur. (2), Afr. (5), Asia and Oceania (6), Austr., N.Z. (1). Thalli green or blue-green. Archegoniophores dorsal. – *Reboulia* Raddi (1–4), *R. hemisphaerica* (L.) Raddi, subcosmopol., exc. subantarct./antarct. and subarct./arct. regions. Polymorphic sp. with 4 genetically distinct entities. Air-pores surrounded by 3–5 concentric rings of cells. On dry soil and rock crevices.

Fam. **Wiesnerellaceae** Inoue Air-pores with 3–5 rings of 6–8 cells. Monoicous. Antheridia and archegonia in terminal cushions. n = 9.

*Wiesnerella* Schiffn. (1). *W. denudata* (Mitt.) Steph., Himalayas, SE Asia, E-Afghanistan, trop. Asiatic Is., Réunion. Rock crevices, in constantly moist habitats.

Fam. **Conocephalaceae** Müll.Frib. ex Grolle. Thalli reticulate, drought-intolerant. Air-pores volcano-shaped. Dioicous. ♀ receptacles conical, stalk with one rhizoid furrow, at apices of thallus branches. Spores 70–100 µm in Ø, pluricellular. n = 9; 8. Asex. reprod. by fragments, tubers and apical bulbils. N Hem., temp. and cold regions; often weedy.

*Conocephalum* Hill (3). *C. conicum* (L.) Underwood, circ.-bor. Calicicole; damp, wet habitats.

Fam. **Marchantiaceae** Lindl. Thalli drought-intolerant. Air-pores elevated, barrel-shaped or lacking. Ventral scales in 2, 4 or 4–10 rows. Di- or monoicous. Receptacles arising at thallus apices; ♀ 4–16-lobed. Pseudoperianths present. Spores 8–80 µm in Ø. Spore/elater ratio > 4:1. Elaters 2–4-helical. n = 9, 18, 27. Asex. reprod. by discoid gemmae in *Marchantia*, developing in cup-shaped gemma-cups on dorsal side of thallus. 3 gen. (c. 38),  $\frac{\ast}{\ast}$ . Fig. 4-2.10.

*Bucegia* Radian (1). *B. romanica* Radian, disjunct E, SE Eur., N Siberia, Canadian Rocky Mts.; Tertiary relict sp. Rocky, mont. habitats. – *Marchantia* L. (36),  $\frac{\ast}{\ast}$ ; N Am. (3), C, S Am.

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receptacles (x35). Riccials: **17–19**. *Riccia fluitans*. 17. CS of thallus with air-chambers (x35). 18. Spore (x200). 19. Thallus lobes (x3.5). **20**. *R. beyrichiana*. Thallus lobes (x3.5). **21**. *R. lamellosa*. Apical cells of cell columns and air-gaps (x380). **22**. *R. gothica*. CS of thallus (x50). 5, 11, 12, 21 SEM micrographs. (♂ male receptacle, antheridium resp., ach air-chamber, ag air-gap, apo air-pore, ax axis, cca capsule cave, ch chlorenchyma, ge gemma, inv involucre, ob oil-body, rh rhizoid, stp storage parenchyma, thl thallus lobe, vs ventral scale, wg wing, wth wall thickenings of water storage cells)

(9), Eur. (2), Afr., E Afr. Is. (6), Asia, Oceania (30), Austr., N.Z. (5); in humid-temp. subtrop. and trop. climates, rare in areas with dry seasons; some spp. to Arct. and Antarct. (e.g., *M. berteriana* Lehm. & Lindenb., *M. polymorpha* L.). Gametangiophores with 2 or 4 rhizoid furrows. ♂ receptacles lobed or palmate. Spores 8–41 µm in Ø. 3 subgen. Exposed, bare and rocky soil, often on man-made habitats. *M. polymorpha* L., cosmopol. In damp and wet habitats; subsp. *ruderalis* Bischl. & Boisselier often weedy. – *Preissia* Corda (1). *P. quadrata* (Scop.) Nees, circ.-bor. Ventral scales in 4 rows, the laminal scales inconspicuous. Spores 55–80 µm in Ø. Cold-tolerant; calcareous rocks and outcrops, shaded and moist habitats.

Fam. **Dumortieraceae** D.G.Long. Thalli drought-intolerant. Air-chambers (assimilatory layer) lacking or vestigial. Presence of “bristles” (in addition to rhizoids) on ventral surface of thallus and gametangiophores. Monoicous. Pseudoperianths lacking. Tubular bristly involucre opening by a slit. Spores 20–35 µm in Ø.

*Dumortiera* Nees (1). *D. hirsuta* (Sw.) Nees, ocean. distr. (50°N to 40°S). In shaded and humid habitats.

Several cytotypes known. In molecular trees not closely related to marchantiacean taxa.

Fam. **Monosoleniaceae** Inoue. *Monosolenium* Griff. (1). *M. tenerum* Griff., Himalayas, China, Japan. Thalli drought-intolerant. Air-pores and air-chambers lacking. Monoicous. Sessile antheridial cushions. Archegoniophores shortly elongated, with 2 rhizoid furrows. Spores 50–60 µm in Ø. n = 9. Mesic habitats.

*Peltolepis* Lindb. (2), arct.-alp., cont. <sup>\*</sup>. Air-pores slightly elevated, radial walls thickened. 2–3 layers of empty air-chambers. Scales in several, ill-defined rows. Antheridia in cushions with peripheral scales. Spores 40–70 µm in Ø. n = 9, 18. Rock crevices, on soil over limestone, calcareous snow beds.

Usually included in the Cleveaceae but appears in molecular trees separated from *Athalamia* and *Sauteria*.

Fam. **Cleveaceae** Cavers Air-pores stellate, radial walls thin or thickened. Air-chambers lacking chlorophyllose filaments. Ventral scales in ill-defined rows. Monoicous. Archegoniophores with scales at top. Spores 40–80 µm in Ø. Mostly in arct. and alp. areas. 2 gen. (c. 20).

*Athalamia* Falc. (12–15), <sup>\*</sup>/<sub>\*</sub>, worldwide in cold and temp. areas. Archegoniophores dorsal on main thallus, without rhizoid furrows. n = 9, 18. Rocky habitats. – *Sauteria* Nees (c. 7), arct.-alp., N Hem., Andes, Galapagos, Malawi. Ventral scales with oil-cells. n = 36. Rock crevices and rock outcrops.

Fam. **Exormothecaceae** Müll.Frib. ex Grolle Chimney-like or inflated bladder-like air-chambers elevated; air-pores thin walled; often perennating by tuberous apices or tubers. Di- or monoicous. Antheridia embedded in dorsal groove along thallus midline, single or in 2–3 irregular rows. Spores 40–150 µm in Ø. n = 8, 9, 16. 3 gen. (10). Fig. 4-2.11–12.

*Aitchisoniella* Kashyap (1). *A. himalayensis* Kashyap, W Himalayas. Thalli purple tinged. Archegoniophores connected with posterior edge of thallus. Elaters 3-helical. Dry, rocky, exposed habitats. – *Exormotheca* Mitt. (8), medit.-type climates from 43°N to 33°S; in Eurasia E to China. ♀ receptacles spherical, shortly stalked or nearly sessile. Spores 50–150 µm in Ø. Dry exposed rock outcrops and rocky soil. – *Stephensoniella* Kashyap (1). *S. brevipend-*

*unculata* Kashyap, W Himalayas. Air-pores wide. Antheridia embedded in dorsal groove along thallus midline. n = 8, 9. Dry, exposed rock outcrops in mont. habitats.

## 2. Suborder **Corsiniineae** R.M.Schust. ex Schljakov

Fam. **Cyathodiaceae** Stotler & Crand.-Stotl. Thalli drought-intolerant, perennating by tubers. Air-pores with 1 ring of 5–21 cells, wide open. Air-chambers without chlorophyllose filaments. Di- or monoicous. Antheridia embedded in small ventral or apical branches with large scales. Archegonia in terminal archegonial cavities. Capsule opening by a lid and 6–8 irregular valves. Spore/elater ratio > 4:1. Spores 25–85 µm in Ø. n = 9.

*Cyathodium* Kunze (12), pantrop., to W Austr., S Japan, E Afr., S Eur. (S Italy, pre-glacial relict). In low light intensities; on rocks and soil, occ. weedy.

Fam. **Corsiniaceae** Engl. Thalli drought-tolerant. Air-pores hardly elevated. Air-chambers in 1(–2) layers. Ventral median portion of thallus keel-like. Di- or monoicous. Antheridia embedded in dorsal groove on median part of thallus. Archegonia in dorsal cavities. Sporophytes sessile. Capsule cleistocarpous. 2 gen. (3).

*Corsinia* Raddi (1). *C. coriandrina* (Spreng.) Lindb., warm-temp. areas with mediterranean-type climate; circ.-teth. Eur. and N Afr., Macaron., N Am. (Texas, ?Louisiana), S Am. (Brazil, Argentina, Chile). Involucral scales thick, pluristratose. Spores 90–150 µm in Ø. n = 8, 16. On warm, non-calcareous soil and humus. – *Cronisia* Berk. (2), Neotrop., winter-dry savannas in C and S Am. Involucral scales involute around archegonia. Spores 60–97 µm in Ø. Elaters 1-helical. n = 9.

## 3. Suborder **Monocarpineae** R.M.Schust.

Fam. **Monocarpaceae** D.J.Carr ex Schelpe Plants minute, delicate. Air-chambers wide open (no epidermal air-pores present), without chlorophyllose filaments. Ventral scales and mucilage papillae lacking. Rhizoids smooth. Monoicous. Antheridia 1–2, in open air-chambers. ♀ receptacle short-stalked, without rhizoid furrow. 1 sporophyte per involucre. Seta short. Capsule cleistocarpous. Spores 39–60 µm in Ø. Elaters lacking. Sterile cells among spores. n = 9.

*Monocarpus* D.J.Carr (1). *M. sphaerocarpus* D.J.Carr, ephemeral; in desert salt pans of W and S Austr., Tas., south. S Afr.

## 4. Suborder **Targioniineae** R.M.Schust. ex Schljakov

Fam. **Targioniaceae** Dumort. Thalli drought-tolerant. Air-pores elevated (80–170 µm in Ø). Air-chambers in 1 layer. Ventral scales violet to purple-red. Monoicous, occ. dioicous. ♂ receptacles dorsal or terminal on main thallus or on short lateral branches. ♀ receptacles sessile on ventral side of thallus apex in coriaceous envelope opening by 2 valves. Spores 50–100 µm in Ø. Capsule dehiscing by irregular breaking up of the upper part. n = 9, 27. Xerotherm.-pang., warm-temp. regions between 55°N and 42°S. Fig. 4-2.13–16.

*Targionia* L. (3–4), warmer areas with dry season, absent in humid and warm trop. regions. Rock crevices and rock outcrops. *T. hypophylla* L., widespread in warm dry regions.