How molecular phylogenetics improve our understanding of bryophyte evolution, morphology and ecology – a tribute to the mossy side of Josef Poelt

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Abstract Molecular phylogenetics improved our understanding of bryophyte evolution and enabled the classification of numerous taxa, including those with untypical morphologies like *Tetraphis* and *Buxbaumia* (Bryophyta) or those poor in morphological traits like *Verdoornia* (Marchantiophyta). Highlighting the relevance of molecular biology for bryology, we summarize recent insights into liverwort and moss systematics, morphology and ecology. In the liverwort phylogeny, clear connections between the ecology of a species, including mycorrhiza-like associations and its systematic position exist. Ancient fungi like Glomeromycota or *Endogone*-like fungi are associated with ancient liverworts like Haplomitriopsida, whereas derived taxa are associated with Asco- or Basidiomycota. Concerning mosses and their backbone phylogeny, specific sporophyte architectures are crucial for classification and supported by molecular phylogenetics. Phylogenetically old taxa like *Takakia* or *Sphagnum* primarily lack peristomes, while taxa like *Polytrichum* have a nematodontous peristome. Mosses with arthrodontous peristomes represent 95 % of extant moss diversity. However, their speciation remains a central question of evolutionary biology. Josef Poelt described and re-classified four taxa within the arthrodontous moss genus *Schistidium*. As a tribute to his bryological work, the classifications of *Schistidium apocarpum* subsp. *papillosum* (Culm.) Poelt, *Schistidium boreale* Poelt, *Schistidium grande* Poelt and *Schistidium trichodon* (Brid.) Poelt are tested with molecular methods.

1. The impact of molecular phylogenetics on our understanding of bryophyte evolution

Due to the emergence of marker gene analyses and molecular phylogenetics, our knowledge about bryophyte evolution increased faster during the last two decades than during the last two centuries. Bryophyte phylogenies are often reflected by morphological and ecological characteristics of the taxa included. However, in some cases, the situation is not so clear. Especially secondary morphological reductions present in liverworts and mosses, and in the gametophyte as well as in the sporophyte, resulted in incorrect taxonomic classifications that require revisions with regard to molecular data. The genus *Verdoornia* (Marchantiophyta) with one endemic species in New Zealand was classified by Schuster (1963, 1984, 1999) as an ancient thalloid liverwort. This classification was based on the undifferentiated thallus that is, as we know nowadays, a result of secondary reduction. Recent molecular studies show that *Verdoornia* belongs to the family Aneuraceae, a derived family within thalloid liverworts (Stech & Frey 2001, Forrest & Crandall-Stotler 2004, Forrest et al. 2006). Later on, symbiosis with *Tulasnella* fungi, typical endophytes of Aneuraceae and Orchidaceae, were detected (Duckett & Ligrone 2008, Preussing et al. 2010a), providing further evidence for the classification of

Verdoornia as an Aneuraceae. In this case, the morphology of *Verdoornia* was misleading, while its ecology reflects the molecular phylogeny.

Not only in liverworts, but also in mosses, the morphology can be misleading in terms of taxonomic classifications. Within arthrodontous mosses, the presence of a peristome, the length of the seta or the general shape of the spore capsule are typical characteristics for taxonomic classifications. However, according to recent molecular analyses, reductions of sporophytic traits evolved several times within mosses and are often scattered across molecular phylogenies, thus rejecting sporophyte-based classification (McDaniel et al. 2010, Huttunen et al. 2012, Liu et al. 2012). In addition, hybrid species were detected, e.g. within the Funariaceae (Beike et al. 2014), indicating that hybridization might play an important role in speciation. In consequence, classifications based on morphological traits that do not necessarily reflect species evolution are also present in mosses. Molecular analyses enable a revision of these classifications and provide novel insights into underlying evolutionary processes.

Another advantage of molecular phylogenetics is the possibility to classify species with uncertain systematic position, such as *Buxbaumia*, *Diphyscium*, *Tetraphis* or *Schistostega* that have been excluded from systematics for many years due to their morphology (Frahm & Frey 1987: 507–510). Especially the lack of morphological characteristics or the presence of very different characteristics hinders an integration of these taxa into morphology-based systematics. Nowadays, these genera are included into the phylogeny of mosses with good support (Frey et al. 2009, Goffinet et al. 2009, Cox et al. 2010).

Furthermore, molecular data contribute to our understanding of moss and liverwort ecology in the context of evolution. The majority of ancient liverwort and moss taxa grows on mineral soil, whereas a few exceptions grow on peat or rock. With noteworthy exception of mosses, mycorrhiza-like associations occur in all major land plant lineages (Wang et al. 2010). However, mycorrhiza-like associations got lost in various groups. During the last years, associations of liverworts with ancient fungi like *Endogone* (Bidartondo et al. 2011, Desirò et al. 2013, Field et al. 2015) and Basidiomycota from the orders Sebacinales and Tulasnellales (Bidartondo et al. 2003, Kottke et al. 2003, Nebel et al. 2004, Preussing et al. 2010a, 2010b) attract scientific attention. Phylogenetically ancient liverworts (Haplomitriopsida, Marchantiopsida and Pelliidae) are associated with Glomeromycota, whereas Asco- and Basidiomycota occur in derived groups like Aneuraceae or Jungermanniales (Kottke & Nebel 2005, Pressel et al. 2010). In liverworts, fungal associations are often connected to the ecology and the systematic position of a certain species. Liverworts growing on mineral soil are usually associated with Glomeromycota, whereas species growing on wood or humus are rather associated with Asco- and Basidiomycota. Epiphytic species lack mycorrhiza-like associations in general. Epiphytism evolved several times independently during land

plant evolution within liverworts, mosses and ferns. Noticeably, it evolved in different groups during the same time around 150 million years ago and is correlated with the evolution of angiosperms that have barks suitable for epiphytes (Huttunen et al. 2004, Schneider et al. 2004, Feldberg et al. 2014).

Although molecular phylogenetic studies improve our understanding of bryophyte evolution significantly, numerous questions are still unanswered, including e.g. phylogenetic reconstructions of species-rich families within arthrodontous mosses that contain taxa of difficult morphological classification. The species-rich moss genus *Schistidium* (Grimmiaceae) includes numerous species that are very difficult to classify. Blom (1996) provided a revision of the *Schistidium apocarpum* complex from Norway and Sweden. While the resulting narrow species concept has been subject of controversial discussions, molecular analyses confirmed his classification later on (Goryunov et al. 2007, Ignatova et al. 2009). Josef Poelt described two *Schistidium* species and re-classified two more species. Based on a phylogenetic analysis, his morphology-based classification of *Schistidium* is tested in this work.

2. Systematics and ecology of liverworts

Liverworts split off early during land plant evolution. Depending on the phylogenomic analysis, they cluster either in a sister group position to all remaining land plants (Qiu et al. 2006) or in a sister group position to mosses (Wickett et al. 2014). Within Marchantiophyta, the relationships between major clades are phylogenetically well supported (Forrest et al. 2006, Qiu et al. 2007). The liverwort cladogram presented here (Fig. 1a) is based on the list by Crandall-Stotler et al. (2009), which includes molecular and morphological data. *Haplomitrium* (Haplomitriidae) is with its rhizome-like thallus that lacks rhizoids closely connected to the soil. In contrast, the sister group *Treubia* (Treubiidae) has rhizoids at the ventral side of the thallus. All basal liverworts, including Marchantiopsida and Pelliidae, grow on soil, rarely on peat or rotten wood, and stick to the ground with their rhizoids (Kottke & Nebel 2005). Around 150 million years ago, strong plants, which lost direct soil contact and developed rarely rhizoids, evolved within numerous groups of liverworts. Species from the Metzgeriaceae were the first thalloid liverworts that became epiphytic and even epilithic (Feldberg et al. 2014). Aneuraceae, another family of Metzgeriales, grow preferentially on rotten wood and humus in a humid environment (Preussing et al. 2010a). Metzgeriidae are a sister group to folious liverworts (Jungermanniidae) with three orders (Fig. 1a). Ptilidiales contain only eight species that grow on humus, and are rarely epiphytic. In species-rich Porellales, the majority of species are epiphytes with few epilithic taxa. They contain 2,095 species (Nebel, unpublished), including taxa that evolved epiphylly (growth on living leaves) in the tropics. Jungermanniales are composed of soil-growing species as well as epiphytes that evolved sever-

al times independently (Feldberg et al. 2014). With 2,370 species in total (Nebel, unpublished), the Jungermanniales are the most species-rich order within liverworts.

3. Mycorrhiza-like associations in liverworts

During transition from water to land, land plants had to cope with numerous biotic and abiotic stresses, including the necessity of phosphorus uptake. In contrast to algae, nearly all major embryophyte lineages have genes required for mycorrhiza-like associations (Wang et al. 2010). In hornworts, liverworts, lycophytes, ferns and flowering plants, they are functional, whereas they are not functional in mosses that have been analyzed so far (Wang et al. 2010).

A mycorrhiza-like symbiosis between liverwort and fungi is given if (1) no injuries of the plant tissue are visible, (2) no defense reaction like e.g. cell wall thickenings are visible, (3) the cells associated with hyphae have intact cell membranes and organelles, and (4) plant cells remain stable in form and functionality after fungi association (Krause et al. 2011). In numerous liverworts, rhizoids with branched and swollen tips occur. These structures are often colonized by fungi (Paul 1916, Pocock et al. 1984, Pocock & Duckett 1985, Duckett et al. 1991, Read et al. 2000, Pressel et al. 2008, 2010). However, these structures are also formed by rhizoids that are not colonized by fungi (Pocock & Duckett 1985, Duckett et al. 1991). In the genus *Paraschistochila*, the rhizoids are not only branched and swollen, they furthermore develop apical thin-walled septae, induced by fungal colonization. Colonization by symbiotic fungal does not induce cell wall defense reactions, while colonization with non-symbiotic fungi induces rhizoid pegs as a defense reaction (Pressel et al. 2008).

The most ancient fungi that form symbioses with liverworts are *Endogone*-like fungi. The classification of fungi discussed here is based on James et al. (2006). Within liverworts, mycorrhiza-like associations with *Endogone* have been detected in Haplomitriopsida, Marchantiopsida, Pelliidae, Anthocerotophyta and Pteridophyta. In many cases, *Endogone* and Glomeromycota occur simultaneously. Due to its high phylogenetic age, *Endogone* is discussed as one of the oldest plant-associated fungi (Bidartondo et al. 2011, Desirò et al. 2013, Field et al. 2015).

All thalloid liverworts, with exception of Metzgeriales, form symbioses with Glomeromycota (Fig. 1b) via arbuscular mycorrhiza (AM) (Smith & Read 2008). In some taxa, usually pioneer plants like Ricciaceae, AM is secondarily reduced. Symbioses with Glomeromycota increase the photosynthesis rate and the growth of a plant as well as its fitness. These effects increase under conditions of elevated CO_2 concentrations, indicating that the advantages of mycorrhiza-like associations could have been even higher during the

Paleozoic (Humphreys et al. 2010). Until now, fungi from the genera *Glomus*, *Acaulospora* and *Ambispora* were molecularly identified to be liverwort symbionts (Ligrone et al. 2007, Bidartondo et al. 2011). In contrast, nine genera of Glomeromycota are described from hornworts, which contain considerably less species (Desirò et al. 2013). Since thalloid liverworts are phylogenetically older than the majority of extant land plant taxa, an origin of fungi-associations in the liverwort lineage seems likely, although this has not been proven yet. Mycorrhiza in liverworts might also represent a secondarily evolved association (Selosse 2005).

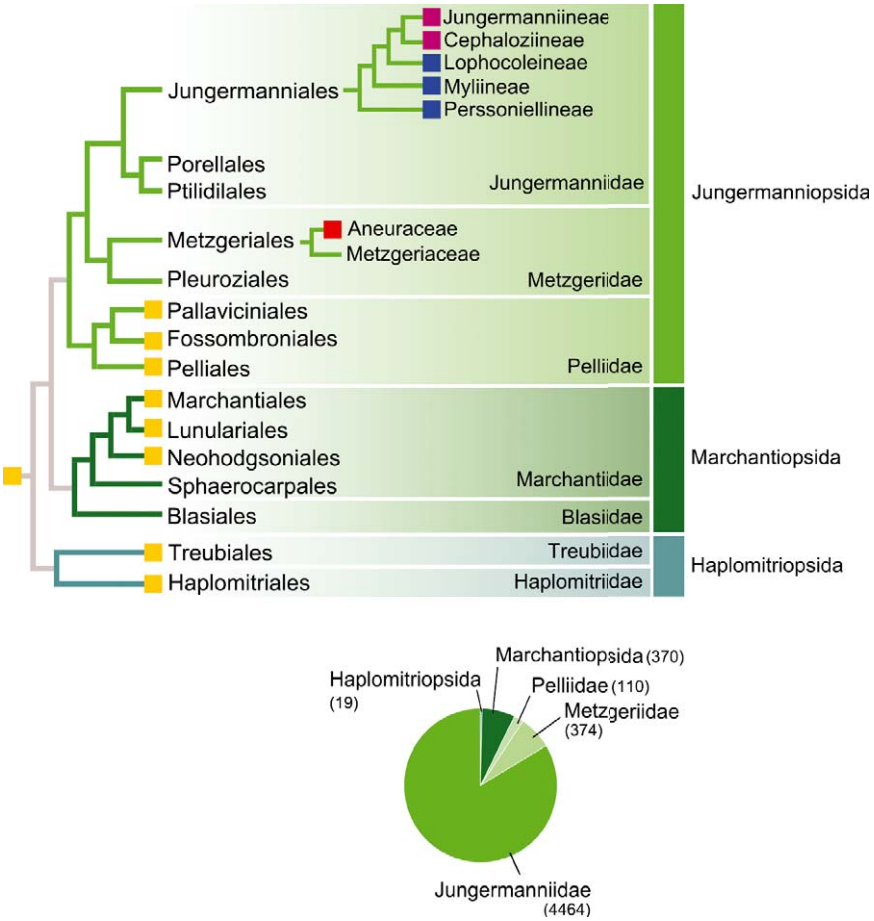

Fig. 1a: Species diversity and mycorrhiza-like associations in the context of the liverwort phylogeny – Liverworts (Marchantiophyta) represent early-diverged land plants that form mycorrhiza-like associations. The cladogram presented here is based on a list by Crandall-Stotler et al. (2009). The three liverwort classes Haplomitriopsida (turquoise), Marchantiopsida (dark green) and Jungermanniopsida (light green) are shown in a phylogenetic context. The occurrence of fungal associations is depicted with colored boxes at the respective branch. Mycorrhiza-like associations with Glomeromycota (yellow), Basidiomycota (red), Ascomycota (blue), and Asco- and Basidiomycota (magenta) are described from different liverwort lineages. Below, liverwort species numbers are depicted in a pie chart.

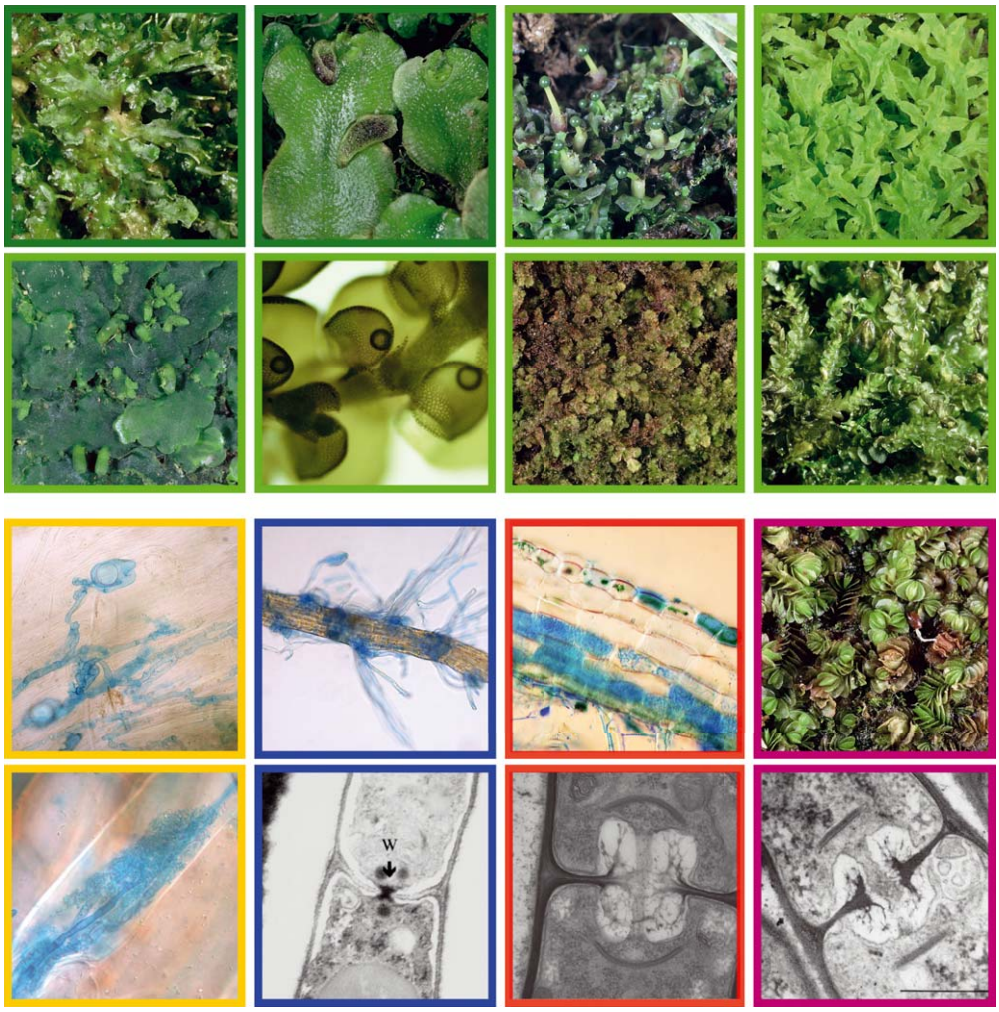

Fig. 1b: **Typical representatives of the liverwort-subclasses and fungal symbionts**. Corresponding to the color code of figure 1a, typical representatives of the liverwort sub-classes are shown. From the upper left to the lower right: *Blasia pusilla, Lunularia cruciata, Pellia endiviifolia, Metzgeria pubescens, Aneura pinguis, Frullania dilatata, Ptilidium pulcherrimum* and *Jungermannia atrovirens*. Below liverwort-associated fungi are shown, namely Glomeromycota (yellow), Ascomycota (blue), Basidiomycota (*Tulasnella*) (red, Preussing et al. 2010a) and Ascomycota (*Sebacina*) (magenta). For *Sebacina*-associations, the liverwort *Gongylanthus granatensis* is shown above the porus (Kottke et al. 2003).

Ascomycota symbionts (Fig. 1b) are restricted to Jungermanniales (as compiled by Nebel et al. 2004). Most evidence for Ascomycota in liverworts has been achieved with fluorescence microscopy (Duckett & Read 1991), whereas ultrastructural analyses are rare (Read et al. 2000, Kottke et al. 2003, Pressel et al. 2008). On molecular level, *Rhizoscyphus ericae* has been detected in *Cephaloziella* (Chambers et al. 1999, Upson et al. 2007) and *Paraschistochila*

(Pressel et al. 2008). As *Paraschistochila* is phylogenetically older than ferns and flowering plants, which form symbioses with Ascomycota, the authors concluded that Ascomycota-symbioses evolved here. However, also a secondary colonization cannot be excluded.

Until now, Basidiomycota that associate with liverworts as non-parasitic endophytes are only described from the genera *Tulasnella* and *Sebacina*, that both belong to the basal Hymenomycetes. Both are characterized by a doliporus with imperforate parenthesome (Weiss et al. 2004). Aneuraceae grow basically on rotten wood and humus and form symbioses with Tulasnellales (Fig. 1b). First ultrastructural evidence of *Tulasnella* endosymbionts in Aneuraceae was given by analyses of *Aneura* (= *Cryptothallus*) *mirabilis* and *Aneura pinguis* (Pocock & Duckett 1984, Ligrone et al. 1993), followed by molecular evidence from *Aneura mirabilis* (Bidartondo et al. 2003). Symbioses between Aneuraceae and Tulasnellales represent the most frequently analyzed mycorrhiza-like associations in liverworts. Tulasnellales-associations occur in all Aneuraceae genera, namely *Aneura*, *Lobatiriccardia*, *Riccardia* and *Verdoornia* (Duckett & Ligrone 2008, Preussing et al. 2010b). On molecular level, Sebacinales are also frequently detected in Aneuraceae (Duckett & Ligrone 2008, Bidartondo & Duckett 2010, Preussing et al. 2010a). However, the colonization of intact Aneuraceae cells by *Sebacina* has not been shown on ultrastructural level yet. In consequence, it remains unclear whether this is symbiosis or not. Transmission electron microscopy of *Tulasnella* in Aneuraceae showed a cup-shaped parenthesome (Fig. 1b) and slime bodies in the cell walls (Ligrone et al. 1993, Krause et al. 2011). Structures like these are typically known from *Tulasnella* fungi.

As shown via ultrastructural analyses, Sebacinales (Fig. 1b) form symbioses with Jungermanniales (Read et al. 2000, Kottke et al. 2003, Nebel et al. 2004, Duckett et al. 2006). The parenthesome of the doliporus is almost straight in cross-section (Fig. 1b). Furthermore, there are several molecular studies that identified Sebacinales fungi from Jungermanniales (Kottke et al. 2003, Nebel et al. 2004, Bidartondo & Duckett 2010, Newsham & Bridge 2010). Based on a recent molecular phylogeny of Jungermanniales, this order is subdivided into five sub-orders (Shaw et al. 2015). When mapping the fungal symbionts detected so far onto the phylogeny, it becomes evident that symbioses in the three more basal sub-orders Perssonniellineae, Myliineae and Lophocoleineae are formed with Ascomycota only, while Sebacinales are found in addition to Ascomycota in Cephaloziineae (Scapaniaceae only) and in different families of Jungermanniineae (Fig. 1a, b). Hence, *Sebacina*-symbioses are found in derived sub-orders so far. Based on this, Sebacinales-symbioses evolved comparably late.

4. Sporophyte architecture reflects the backbone phylogeny of mosses

With around 12,500 species (Frey et al. 2009), mosses are the second largest group of land plants. The rise of molecular phylogenetics boosted our knowledge about moss systematics and evolution during the last decades and yielded numerous re-classifications in various groups. Including taxa like *Buxbaumia* or *Tetraphis*, which have morphological traits difficult to interpret (Frahm & Frey 1987: 507–510), the backbone phylogeny of mosses is nowadays well supported with molecular data (e.g. Cox et al. 2004, 2010). The moss cladogram presented here (Fig. 2a) is based on the list by Goffinet et al. (2009) that considers morphological and molecular data. In the context of moss evolution, the architecture of the sporophyte is one of the very changeable morphological characteristics highlighted in the following. In the most ancient and unusual moss *Takakia*, the mature spore capsule opens along a diagonal split and releases the spores (Fig. 2b). In *Sphagnum* (peat mosses, Fig. 2b), the lid of the capsule is blown off under considerable air pressure hurling the spores out. In *Andreaea* (Fig. 2b), the spore capsule has four, rarely eight splits. The opening mechanism of these splits depends on shrinking of the columella during maturity and dryness. At high humidity, the capsules close again due to swellings of the columella. The spore capsules of these moss groups have initially no peristome teeth (Fig. 2b). With around 395 species in total, *Takakia*, *Sphagnum* and *Andreaea* represent 3.2 % of moss species diversity (Frey et al. 2009). Two major types of peristomes evolved during moss evolution, the nematodontous peristome and the arthrodontous peristome. A nematodontous peristome is ancestral in peristomate mosses and built from teeth of whole, elongated dead cells (Cox et al. 2004). Typical nematodontous mosses are *Polytrichum* or *Tetraphis* (Fig. 2a, b). In *Polytrichum* (Fig. 2b), the rigid peristome teeth are connected to a membrane (epiphragm). Mature *Polytrichum* capsules release their spores like saltshakers, as their peristomes are not hygroscopic like in arthrodontous mosses. As the names suggest, *Tetraphis* (Fig. 2b) and *Tetradontium* have four nematodontous teeth. With around 235 species, nematodontous mosses account for 1.9 % of extant moss diversity.

Around 95 % of extant moss species have arthrodontous peristomes that open or close the mouth of spore capsules via hygroscopic movements and contribute to climate- or water-dependent spore release. In contrast to the nematodontous peristomes, the arthrodontous peristomes are hygroscopic. The cells of the arthrodontous peristome are thickened and only the outer cell wall is thin. In turgescent cells, the outer cell wall is stretched and the capsules remain closed. Under dry conditions, the peristome teeth open the capsule mouth and release the spores. At the basis of arthrodontous mosses, different peristome types evolved. In principal, they are composed of two rows of teeth with different characteristics. The exostome usually consists of cellular teeth, while the endostome consists of segments or cilia. First arthrodontous peri-

stomes with two rows are present in *Buxbaumia* and *Diphyscium* (Fig. 2b). In the Funariidae, a diplolepidous arthrodontous peristome is present as well. In the Funariaceae (*Funaria hygrometrica*, Fig. 2b), the teeth are arranged in an opposite position and their peristome is classified as diplolepidous-opposite. Buxbaumiidae, Diphysciidae, Timmiidae (*Timmia bavarica*, Fig. 2b) and Funariidae represent 2.6 % of mosses with around 326 species.

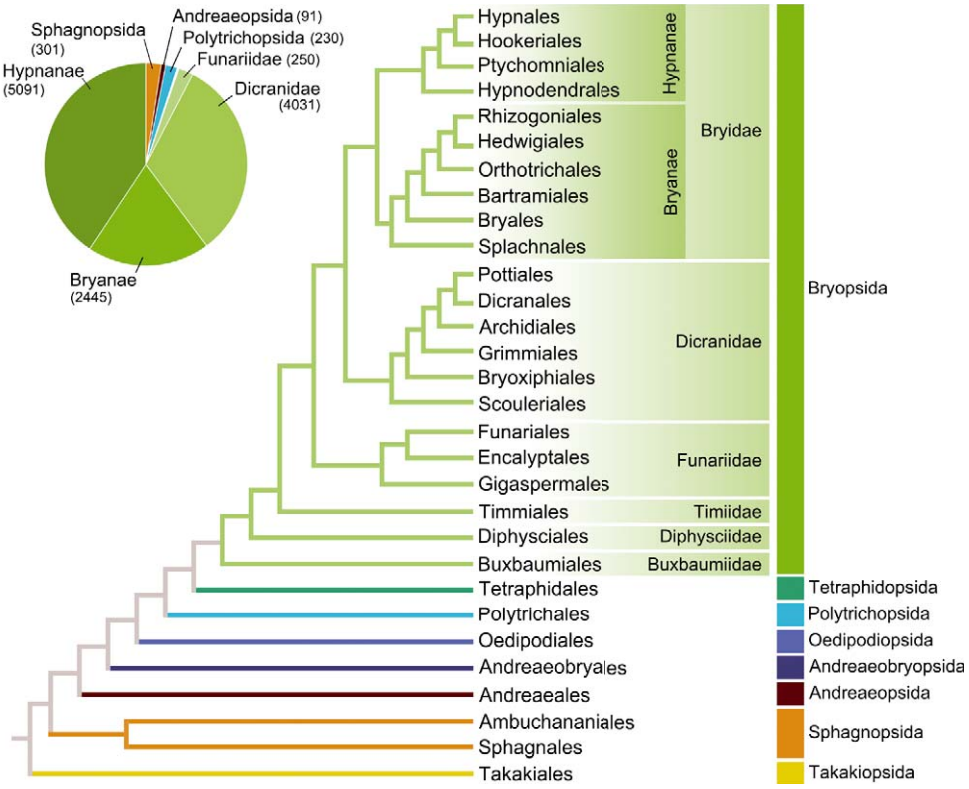

Fig. 2a: Species diversity and sporophyte architecture in the context of the moss phylogeny. With around 12,500 species, mosses (Bryophyta) are the largest group of haploid-dominant land plants. The moss cladogram shown here is based on Goffinet et al. (2009). On the right the eight moss classes, Takakiopsida (yellow), Sphagnopsida (orange), Andreaeopsida (brown), Andreaeobryopsida (dark blue), Oedipodiopsida (light blue), Polytrichopsida (turquoise), Tetraphidopsida (dark green) and Bryopsida (light green) are depicted. The species numbers are shown on the upper left.

By reduction of the exostome, the haplolepidous peristome (*Schistidium crassipilum*, Fig. 2b) of Dicranidae evolved. Dicranidae contain species-rich moss families like *Grimmiaceae*, *Dicranaceae* and *Pottiaceae* and represent around one third of extant moss biodiversity with 4,031 species (Fig. 2a). In numerous clades of the haplolepidous mosses, but also within the diplolepidous-opposite Funariaceae, reduction of sporophytic characteristics up to clei-

stocarpy occurs. In cleistocarpic species like e.g. the model organism *Physcomitrella patens*, the capsule opens by disintegration or the capsule itself is the distribution unit.

Fig. 2b: Corresponding to the color code of figure 2a, two images are shown per moss species. On top a picture of the gametophyte is shown, below a picture of the capsules with focus on the presence or absence of a peristome. From the upper left to the lower right: *Takakia ceratophylla* (Flora of North America, www.efloras.org), *Sphagnum squarrosum, Andreaea rothii, Polytrichum formosum, Tetraphis pellucida, Diphyscium foliosum, Timmia bavarica, Funaria hygrometrica, Schistidium crassipilum* and *Hypnum cupressiforme*. Images of *Andreaea rothii, Tetraphis pellucida* and *Diphyscium foliosum* by Michael Lüth.

Within Bryidae, the peristome is diplolepidous (*Hypnum andoi*, Fig. 2b), but the two rows of teeth are in an alternate position. The exostome is composed of teeth that develop from one cell, the endostome is composed of cilia composed by two cells. The diplolepidous-alternate peristome is found in two-thirds (60.2 %) of extant moss diversity with 7,536 species (Fig. 2a). Also in the sub-class of Bryidae reductions of sporophytes are observed. Molecular analyses of Neckeraceae and Lembophyllaceae indicate an adaptive evolution upon habitat shift, but provide evidence for potential genetic or developmental pathways yielding comparable phenotypes (Huttunen et al. 2012).

5. *Schistidium* – the mossy side of Josef Poelt

The genus *Schistidium* belongs to the family Grimmiaceae (Dicranidae). *Schistidium* and *Grimmia* are closely related. Molecular studies revealed that *Schistidium* is monophyletic and clusters within *Grimmia*, hence *Grimmia* is paraphyletic (Hernández-Maqueda et al. 2008a, 2008b). All 110 *Schistidium* species worldwide grow on rock. Since monographies from the high mountains, including the Alps, are lacking, the species number is likely underestimated at present. Blom (1996) wrote a monography about Norwegian and Swedish species of the *Schistidium apocarpum* complex. From 31 species subdivided into 36 taxa (including subspecies and varieties), 13 species and 17 taxa were newly described, including *Schistidium poeltii* H.H. Blom. His taxonomic classification and the species concept is well supported by molecular data (Goryunov et al. 2007, Ignatova et al. 2009). Josef Poelt described two novel species in the genus *Schistidium*, namely *Schistidium boreale* Poelt (Poelt 1953) and *Schistidium grande* Poelt (Poelt 1955). Furthermore, he re-classified *Schistidium papillosum* Culm. as *Schistidium apocarpum* subsp. *papillosum* (Culm.) Poelt and *Grimmia trichodon* Brid. to *Schistidium trichodon* (Brid.) Poelt (Poelt 1953). Poelt's interest in the genera *Grimmia* and *Schistidium* was likely connected to the habitat of these mosses, growing on rock in close proximity to rock-inhabiting lichens. The molecular phylogeny presented in this work includes all *Schistidium* species described and classified by Poelt (Fig. 3). Based on a phylogenetic analysis of the internal transcribed spacer region (White et al. 1990), his classification of *S. grande* is well supported. *S. grande* is closely related to the two analyzed subspecies of *Schistidium brunnescens*, *S. brunnescens* subsp. *griseum* and *S. brunnescens* subsp. *brunnescens.* Concerning *S. boreale* and *S. trichodon*, the situation is not clear yet. Poelt's re-classification of *S. trichodon* from *G. trichodon* is clearly supported, however *S. boreale* and S. *trichodon* are not unambiguously separated and further molecular analyses would be required to clarify the range of both taxa. Concerning *S. apocarpum* subsp. *papillosum*, the molecular data reject a classification as a subspecies. In fact, *S. apocarpum* subsp. *papillosum* is closely related to *S. apocarpum*, but it clusters in a sister group position, clearly separated (Fig. 3). Hence, a classification as a species, *S. papillosum* Culm., rather than a subspecies is conclusive.

As a namesake of *S. poeltii* Josef Poelt's importance for bryological research has been once more shown and acknowledged. With his excellent species knowledge, Poelt made major contributions to bryology and enriched our knowledge about species diversity and classification. His work forms a scientific basis for generations of bryologists.

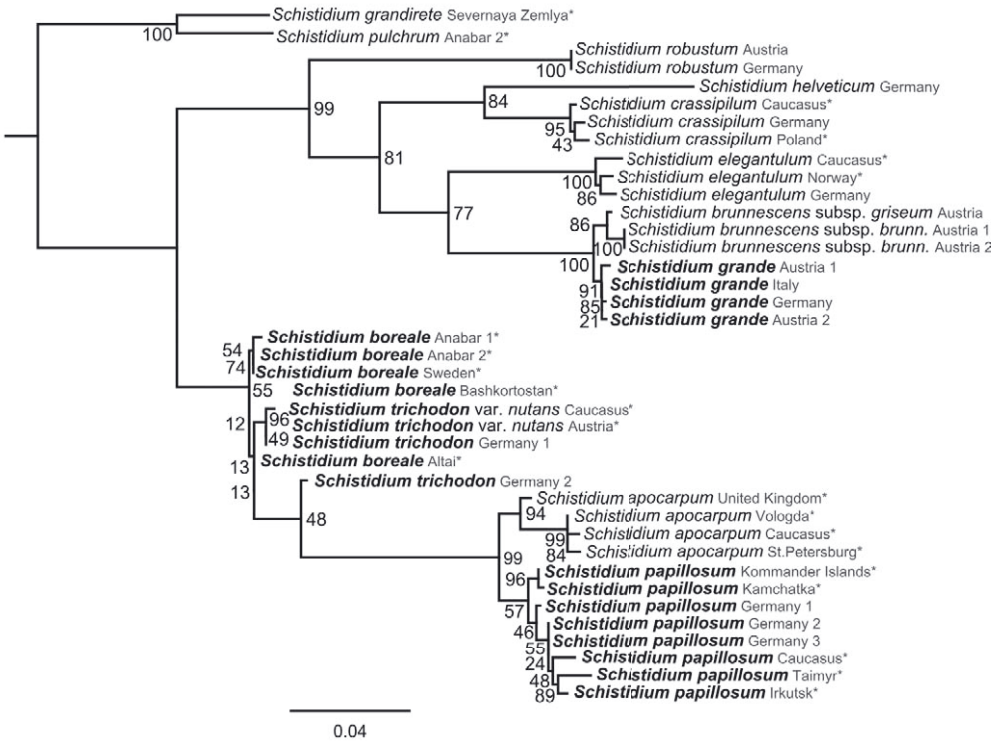

Fig. 3: Phylogenetic analysis of *Schistidium* species classified by Josef Poelt. The internal transcribed spacer region (ITS1-ITS2) was amplified from 17 *Schistidium* samples representing eight species and two sub-species. Including sequences from Goryunov et al. (2007), Ignatova et al. (2009) and Miliutina et al. (2010) (highlighted with stars), the phylogenetic tree was calculated with Maximum Likelihood (1,000 replicates). The support values show Maximum Likelihood bootstrapping values. The scale bar depicts substitutions per site. Species classified by Poelt are highlighted in bold.

6. Conclusions and final remarks

The relevance of marker gene analyses for the reconstruction of phylogenies and the identification of symbionts improved our understanding of bryophyte evolution. Still, there are many central questions unanswered, including e.g. the taxonomic classification within genera or families that include taxa difficult to classify due to variations of sporophytic traits. With regard to lacking *Schistidium* monographies of the high mountains, the species diversity is likely underestimated at present and should be characterized with a combination of classical and molecular methods. The identification of bryophyte symbionts is also a promising branch of research. A much higher species diversity of Glomeromycota-symbionts in liverworts can be expected considering the symbiont diversity in hornworts. Furthermore, the relevance of Ascomycota as symbionts of Jungermanniales requires further clarification on molecular and ultrastructural level. Associations of Jungermanniales with

Sebacinales (Basidiomycota) might represent phylogenetically young symbioses. A distribution of typical symbionts in Jungermanniales, but also in liverworts in general, are required to receive insights into the evolution of symbioses in basal land plants.

7. References

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8. Appendix

DNA extraction, internal transcribed spacer (ITS) amplification and phylogenetic analysis

From each herbarium sample, dried tissue was disrupted in a Tissue Lyser (Qiagen, Hilden, Germany) for 2 min at 20 Hz. Genomic DNA was extracted from 2–10 mg dry weight using the Genomic DNA from Plant Kit II (Macherey-Nagel GmbH & Co. KG, Düren, Germany) according to the manufacturer's protocol. The internal transcribed spacer regions ITS1-ITS2 (White et al. 1990) were amplified using the primers from Spagnuolo et al. (1999): 5'-GGAGAAGTCGTAACAAGGTTTCCG-3' and Stech et al. (2003): 5'-TCCTCCGCTTAGTGATATGC-3'. The PCR was done in a reaction volume of 25 µL [2.5 µL 10×DreamTaq Green Buffer (Thermo Scientific, St. Leon-Rot, Germany), 2.5 µL deoxyribonucleotide triphosphates (dNTPs, 2 mM, Thermo Scientific, St. Leon-Rot, Germany), 0.2 µL DreamTaq polymerase (5 U/µl, Thermo Scientific, St. Leon-Rot, Germany), 0.5 µL of each primer (10 pmol/µL), 1 µL genomic DNA]. After an initial denaturation at 94 °C for 5 min, the cycling conditions consisted of a denaturation step of 45 sec at 94 °C, an annealing step at 55 °C for 45 sec and elongation step for 1 min at 72 °C for 32 cycles. For final elongation, the reaction was incubated at 72° C for 5 min. The PCR was controlled via agarose gel electrophoresis and the samples were sent for sequencing to LGC genomics (Berlin, Germany).

Additional sequences of *Schistidium* species of interest were downloaded from Goryunov et al. (2007), Ignatova et al. (2009) and Miliutina et al. (2010). The sequence were analyzed and aligned with MAFFT (Katoh & Standley 2013) using the Geneious 8.0.5 software (Kearse et al. 2012). Maximum Likelihood analysis was done with RAxML 7.2.8 (Stamatakis 2006) using the GTR gamma nucleotide model and a rapid bootstrapping analysis of 1,000 replicates. The phylogenetic tree was visualized with Geneious and the final figure was generated using Inkscape (www.inkscape.org).

Taxon set and Genbank identifiers

The species, subspecies and varieties analyzed in this work are listed on the left. The region as depicted in the tree and the voucher are included for each sample. The Genbank identifier (ID) is listed on the right. Sequences downloaded from Goryunov et al. (2007), Ignatova et al. (2009) and Miliutina et al. (2010) are marked with a *.

Species	Region (tree)	Voucher	Genbank ID (reference)
Schistidium apocarpum (Hedw.) Bruch & Schimp.	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3764 (MW)	DQ822033/HM031074 *
Schistidium apocarpum (Hedw.) Bruch & Schimp.	St. Petersburg	Russia, St.-Petersburg, 25.10.1996, Ignatov s.n. (MHA)	DQ822034/HM031075 *
Schistidium apocarpum (Hedw.) Bruch & Schimp.	United Kingdom	United Kingdom, 08.09.2004, Ignatov s.n. (MHA)	HM031076 *
Schistidium apocarpum (Hedw.) Bruch & Schimp.	Vologda	Russia, Vologda Province, 14.08.2001, Ignatov & Ignatova s.n. (MHA)	DQ822035/HM031077 *
Schistidium boreale Poelt	Altai	Russia, Altai, Ignatov #0/285 (MHA)	DQ822025/HM031060 *
Schistidium boreale Poelt	Anabar 1	Russia, Anabar Plateau, Fedosov #06-208 (MW)	HM053888 *
Schistidium boreale Poelt	Anabar 2	Russia, Anabar Plateau, Fedosov #06-694 (MW)	HM053889 *
Schistidium boreale Poelt	Bashkortostan	Russia, Bashkortostan, 06.2000, Martynenko #14 (MW)	DQ822024/HM031069 *
Schistidium boreale Poelt	Sweden	Sweden, 20.07.1990, Hedenäs & Aronsson #B1748 (S)	HM053890 *
Schistidium brunnescens Limpr. subsp. *griseum* (Nees & Hornsch.) H.H. Blom	Austria	Austria, Steiermark, Eisenerzer Alpen, Köckinger, 10.02.1993, Köckinger, 93-05 (Herbarium Köckinger)	KT715466
Schistidium brunnescens Limpr. subsp. *brunnescens*	Austria 1	Austria, Kärnten, Hohe Tauern, Köckinger, 10.10.1995, 95-763 (Herbarium Köckinger)	KT715465

Species	Region (tree)	Voucher	Genbank ID (reference)
Schistidium brunnescens Limpr. subsp. *brunnescens*	Austria 2	Austria, Steiermark, Eisenerzer Alpen, Köckinger, 13.06.2005, 14980 (Herbarium Köckinger)	KT715464
Schistidium crassipilum H.H. Blom	Caucasus	Russia, Krasnodar Territory, Seregin #M-564 (MW)	DQ822021/HM031070 *
Schistidium crassipilum H.H. Blom	Germany	Germany, Baden-Württemberg, Bodenseegebiet, Schäfer-Verwimp, 14.06.2009, 30679 (STU)	KT715462
Schistidium crassipilum H.H. Blom	Poland	Poland, 10.03.1995 Ignatov & Ochyra, s.n. (MHA)	DQ822020/HM031073 *
Schistidium elegantulum H.H. Blom	Caucasus	Russia, Krasnodar Territory, 05.08.2002, Ignatov &Ignatova s.n. (MHA)	DQ822022/HM031071 *
Schistidium elegantulum H.H. Blom	Germany	Germany, Niedersachsen, Harz, Preußing, 15.09.2003, MP04414 (STU)	KT715473
Schistidium elegantulum H.H. Blom	Norway	Norway, Bergen, 2002 Ignatov & Ignatova #06-5062 (MW)	DQ822023/HM031072 *
Schistidium grande Poelt	Austria 1	Austria, Kärnten, Nockberge, Köckinger, 30.07.2004, 14982 (Herbarium Köckinger)	KT715470
Schistidium grande Poelt	Austria 2	Austria, Tirol, Hohe Tauern, Köckinger, 10.09.2000, 14981 (Herbarium Köckinger)	KT715469
Schistidium grande Poelt	Germany	Germany, Wettersteingebirge, Zugspitze, Preußing, 05.09.1997, 630, Topotypus (Herbarium Köckinger)	KT715468

Species	Region (tree)	Voucher	Genbank ID (reference)
Schistidium grande Poelt	Italy	Italy, Trentino, Dolomiten, Schütz & Preußing, 07.09.2001, MP010062 (STU)	KT715467
Schistidium grandirete H.H. Blom	Severnaya Zemlya	Russia, Severnaya Zemlya, 04.08.2000, Matveeva s.n. (LE)	HM053911 *
Schistidium helveticum (Schkuhr) Deguchi	Germany	Germany, Baden-Württemberg, Neckarbecken, Nebel, 21.03.2013, MN132170 (STU)	KT715463
Schistidium papillosum Culm.	Caucasus	Russia, Kabardino-Balkaria, 27.07.2004, Ignatov & Ignatova s.n. (MW)	DQ822012/HM031061 *
Schistidium papillosum Culm.	Germany 1	Germany, Baden-Württemberg, Schwarzwald, Holz & Lüth, 08.05.1998, IH98039 (STU)	KT715460
Schistidium papillosum Culm.	Germany 2	Germany, Baden-Württemberg, Schwarzwald, Nebel & Sauer, 20.09.1997, NS97133 (STU)	KT715461
Schistidium papillosum Culm.	Germany 3	Germany, Baden-Württemberg, Randen, Nebel, Sauer & Holz, 13.06.1997, IH97059 (STU)	KT715459
Schistidium papillosum Culm.	Irkutsk	Russia, Irkutsk Province, 08.06.2005, Ignatov & Kazanovsky s.n. (MHA)	DQ822013/HM031062 *
Schistidium papillosum Culm.	Kamchatka	Russia, Kamchatka, 31.08.2003, Czernyadjeva #120 (MW)	DQ822014/HM031063 *
Schistidium papillosum Culm.	Kommander Islands	Russia, Kommander Islands, Bering Island, Fedosov #1-3-177 (MW)	HQ890520 *

Species	Region (tree)	Voucher	Genbank ID (reference)
Schistidium papillosum Culm.	Taimyr	Russia, Taimyr, 15.06.2004, Fedosov #Sch7 (MW)	DQ822015/HM031065 *
Schistidium pulchrum H.H. Blom	Anabar 2	Russia, Taimyr, 18. 08. 2004, Fedosov #HK-9 (MW)	HQ890521 *
Schistidium robustum (Nees & Honsch.) H.H. Blom	Austria	Austria, Kärnten, Südwestlich Villach, Schütt, Koperski, 07.09.2003 (STU)	KT715471
Schistidium robustum (Nees & Honsch.) H.H. Blom	Germany	Germany, Baden-Württemberg, Schwäbische Alb, Wental, Nebel, 24.04.2001, MN1012 (STU)	KT715472
Schistidium trichodon (Brid.) Poelt	Germany 1	Germany, Bayern, Allgäuer Alpen, Schäfer-Verwimp, 27.09.2009, 30584 (STU)	KT715457
Schistidium trichodon (Brid.) Poelt	Germany 2	Germany, Baden-Württemberg, Schwäbische Alb, Nebel, 24.04.2001, MN1010 (STU)	KT715458
Schistidium trichodon var. *nutans* H.H. Blom	Austria	Austria, Köckinger #12261 (MW)	HM053953 *
Schistidium trichodon var. *nutans* H.H. Blom	Caucasus	Russia, Kabardino-Balkaria, Kharzinov #1721 (MW)	HM053954 *

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