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Review Article

The phytogeography of European bryophytes

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ABSTRACT: A survey is given of the origin and distribution patterns of European bryophytes. The mixture of floristic elements is explained by the vegetation history of the Holocene, during which different floristic elements invaded under different climates. In contrast to other higher plants, the ranges of bryophytes are much wider and transcontinental, and relicts from the Tertiary and the ice ages play a more important role.

Key words: Bryophytes, Europe, phytogeography, endemism, disjunctions, relicts

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INTRODUCTION

Bryophyte geography is an important aspect of phytogeography because it differs from that of other organisms due to a different life cycle and Palaeozoic origin. The easy dispersal mainly by wind (not only by spores but also fragments of plants as demonstrated by the large ranges of totally sterile species) causes large ranges and facilitates a rapid adaptation to changing climates.

The latest treatment of European bryogeography was the textbook by Herzog (1926). The author treated Europe on 18 pages and gave a narrative or even poetic description of phytogeographical provinces with their characteristic elements without any numbers or evaluations, which is in part erroneous, includes unproved assertions or sometimes even nonsense (*Hyophila involuta* (Hooker) A. Jaeger as a Mediterranean element favoured by foehn winds). He did not discuss the origin of these elements under the light of fossil, palaeoclimatic and geotectonic data. The chapter bryogeography by Herzog (1932) in the Manual of Bryology is just a short revival of the book.

Fifty years later, Schuster (1984) gave the latest comprehensive treatment of bryogeography in the New Manual of Bryology. His merit is that he tried to explain distribution patterns first by plate tectonics, a hypothesis by the German climatologist Wegener, which was proved by the discovery of the submarine atlantic rim more than fifty years later. Secondly, he combined for the first time distribution patterns with phylogenetic aspects. Due to the global view of this contribution dealing mainly with types of distribution patterns, Europe is not treated in detail, only as part of Laurasia. Also the textbook by Schofield (1985) treats bryogeography in general without regard to single continents. An only very short account of European bryogeography is included in the textbook by the author (Frahm 2001). Therefore an attempt has been made here to provide a more detailed outline, which is still superficial due to the large amount of data involved but maybe useful due to the lack of any better treatment.

Origin of European species

About 60% of all bryophyte families have a world-wide distribution, which indicates a high phylogenetic age of this plant group. There are even genera of worldwide distribution. This has to be kept in mind when comparing the ranges of bryophytes with those of higher plants, which were not even evolved when most genera of bryophytes were already present.

The largest percentage of bryophytes in Europe belongs to the holarctic (laurasian) element. About two thirds of all species are identical in North America and Europe (Frahm & Vitt 1993). This is a fundamental difference between bryophytes and higher plants, that share only a few similarities on the genus level. The similarity between

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North America and Eurasia is especially strong in the arctic and boreal zones, still large in the temperate species but less developed in the southern elements. The reason for this correspondence of floras can be either the easy dispersal by spores or the possibility that the species are a result of the common stock of species from the Tertiary when North America and Europe were still connected. The problem can be solved only by molecular studies determining the genetical distances between the species in North America and Europe. Perhaps both explanations, gene exchange and long lasting separation can be taken into account, since genetic isolation of bryophytes over millions of years needs to result in speciation due to very low evolution rates of this ancient group of land plants.

Even older might be a stock of mainly xerotolerant species such as *Reboulia hemisphaerica* (L.) Raddi, or *Targionia hypophylla* L., which are widespread over large parts of the world and are interpreted as remnants of a pangaeic range.

Fossil records of bryophytes from the Tertiary are few. Dickson (1973) enumerated 40 species of bryophytes from Miocene deposits in Europe, 5 of them extinct today, and 79 species from Pliocene deposits, 5 of them extinct at present. Ochyra (1986, 1987) could show that *Sciaromiadelphus longifolius* Abramova & I.I. Abramov is identical with *Sciaromium bartlettii* H.A. Crum & Steere from the Carribbean and *Sciaromium laxirete* Abramova & I.I. Abramov is identical with *Platylomella lescurii* (Sull.) A.L. Andrews from North America. Genera such as *Echinodium* and *Gollania* resemble the flora of the Macaronesian islands, which survived on these islands but became extinct in Europe. The bryoflora of Europe suffered from regional extinction and some representatives survived only in the Macronesian Islands or the south coast of Portugal and Spain in Europe (e.g. *Tetrastichium virens* (Cardot) S.P. Churchill, *Claopodium whippleanum* (Sull.) Renauld & Cardot).

The climate change at the end of the Tertiary erased the tropical and subtropical elements in Central Europe, apparently suddenly. A reinvasion in later interglacials like with *Pterocarya* amongst the flowering plants is not proven. This is in contrast to North America, where a large deal of the tropical flora from the Tertiary could survive in refugia in the Southeast or in Central America. Fossils from the Pleistocene in North America show temperate species which are still present in Europe.

The bryoflora of the Tertiary in Europe was presumably less rich as compared with today. First of all, the relief was very different with peneplains, reducing much the variety of habitats. Habitats such as ravines, waterfalls, block streams or cliffs were not present due to the deep chemical decomposition under tropical climate conditions, although the precipitation was higher as today as seen by existence of swamp forests. The higher vegetation resembled that of south-eastern North America (with *Taxodium* swamps, *Tsuga* or *Pterocarya* forests) or Macaronesia (with *Persea*, *Laurus* and *Ilex*).

The first glaciations in Europe differed from the later ones by a warmer climate. Forests survived in southern Europe to a larger extend and allowed to survive some of the Pliocene elements amongst the flowering plants. This could be also true for bryophytes, however, fossils are not known from these periods There are also no records of fossil bryophytes from the first interglacials (Tegelen, Waal). The higher vegetation was dominated by *Pinus, Tsuga, Quercus, Ulmus, Pterocary, Carya* and *Sciadopytis* (Frenzel 1968). The first pleistocene records of bryophytes date from the Menap and Cromer interglacial (Dickson 1973). They consists of common temperate species. The vegetation of the Cromer interglacial consisted of *Quercus, Ulmus, Corylus* and *Tilia*, of the Holstein interglacial of *Carpinus, Picea, Abies, Juglans* still with *Carya* and *Pterocarya*. In Eem, the forests consisted of *Carpinus, Ulmus, Picea, Tilia* and *Quercus*. The very different forest types must have been accompanied by a very different bryoflora, with different species on the forest floor and as epiphytes. The deciduous forest reached much more further north as today, indicating a warmer and perhaps also more humid climate. As a consequence of the colder climates of the Saale glaciation, the forest refugia in southern Europe were no more continuous but split. They consisted of *Pinus*, *Picea, Abies, Rhamnus, Larix, Betula, Alnus* and *Salix*. The latter suggest refugia in valleys along rivers. *Quercus, Tilia* and *Ulmus* survied in the Carpathian mountains. The location of these refugia in *Artemisia* steppe suggests relative dry conditions and put the question where hygrophytes survived. In general, the bryoflora of the last glacial and interglacial periods was much the same as the present bryoflora.

Bryophyte flora as a result of vegetation history

Pre-Pleistocene elements. The pre-Pleistocene origin of the laurasian flora is doubtful. It could date back to the arcto-tertiary flora which was developed along the north coast of the continents. Its phanerogamic flora is preserved in fossils consisting of temperate elements (*Acer, Magnolia* pp.) and it can be assumed that the bryoflora of these forests was also temperate. Some Gondwana elements might have migrated from the south over the Central American land bridge or rafted across the Indian Ocean to India.

Another element consists of presumably relicts from the Tertiary. These remnants have perhaps survived along the Atlantic coast and on the Macaronesian Islands and are oceanic in distribution. Such elements are all Sematophyllaceae, many Lejeuneaceae and the genera

Breutelia, *Ptychomitrium*, *Hyocomium*, *Leptodontium*, *Hookeria*, *Myurium*, *Pleurozia*, *Marchesinia*, *Mastigophora as* well as species of *Fissidens*, *Campylopus* and *Frullania*. This element includes many tropical species such as *Dumortiera hirsuta* (Swaegr.) Nees, *Metzgeria leptoneura* Spruce, *Anastrophyllum donianum* (Hook.) Schiffn., *Plagiochila carringtonii* (Balf.) Grolle and others *Acrobolbus wilsonii* Wils., *Adelanthus decipiens* (Hook.) Mitt., *Saccogyna viticulosa* (L.) Dumort., *Lepidozia cupressina* (Sw.) Lindenb., *Herbertus aduncus* (Dicks.) S.F. Gray, *Scapania gracilis* Lindb. , *Radula* spp., *Jubula hutchinsiae* (Hook.) Dumort., *Lejeunea* spp., *Colura calyptrifolia* (Hook.) Dumort., species of *Aphanolejeunea*, *Cheilolejeunea*, *Harpalejeunea* and *Drepanolejeunea*. It is, however, not known whether these species are true relicts. They could also have been dispersed from the tropics during the Holocene, at least in part. Schuster (1984) argued for the relict character for some of these species (for example *Anastrepta orcadensis* (Hook.) Schiffner, *Anastrophyllum donianum* (Hook.) Schiffn., *Scapania ornithopodioides* (With.) Pearson pp.), because they are sterile throughout their range, are unisexual and are found only in a single sex in parts of their ranges and have no known means of vegetative propagation.

The influence of ice ages. It has to be kept in mind that the ranges of the European bryophytes are in general not older than 12-14,000 years since the last glaciation has caused some kind of *tabula rasa* effect. The northern parts of Europe as well as the mountains in Central Europe higher than 1000 m were covered by ice shields, the region in between was tundra and south of it steppe. The present vegetation survived in local forest refugia in southern Europe, on the Macaronesian Islands, along the coast of the Atlantic or in ice free regions north of the ice shield. The long-lasting isolation of taxa in refugia has perhaps led to a micro-speciation. An example could be the *Hypnum cupressiforme* complex with its infraspecific taxa, which are lacking in North America but could have originated in different refugia in southern Europe by long-lasting isolation. A similar effect of speciation in refugia during glaciation is found in the avifauna (e.g. *Luscinia luscinia* Linnaeus, 1758 and *L. megarhynchos* Brehm, 1831, among others). Another refugium which is less considered was the ice-free coast of western Europe, where "small species" with an oceanic distribution such as *Oxystegus hibernicus* (Mitt.) Hilp., *Platyhypnidium lusitanicum* (Schimp.) Ochyra & Bednarek-Ochyra or *Isothecium holtii* Kindb. might have originated.

Examples of preservation of species north of the ice shield are few, since this refugium was only possible for cold adapted species. Some of these species stayed there until the present and were not able to extend southward (*Bryobrittonia longipes* (Mitten) D.G. Horton), others extended to northern Scandinavia (*Voitia hyperborea* Grev. & Arnott., *Schistidium holmenianum* Steere & Brassard, *Scapania spitsbergensis* (Lindb.) Müll.Frib.) but did not reach the southern high mountains such as the Alps. The flora of Europe is less rich than that in North America due to W-E stretching mountain ranges, causing the extinction rate amongst all plants to be much higher in Europe than in North America, where the vegetation could escape from the ice to the south in a broad front. The extinctions during the Pleistocene glaciations are proved by fossil records of species in Baltic amber (Grolle & Meister 2004, Frahm 2010), which are lacking in Europe but are still present in East Asia, for example the genera *Nipponolejeunea*, *Trocholejeunea* and *Trachycystis*.

The present vegetation including the bryoflora is a mixture composed of relicts from the tundra plus elements which came together in the Holocene over the past 12,000 years under different climatic conditions. Caused by climatic changes, whole biomes moved including higher plants, lower plants, vertebrate and invertebrate animals.

The postglacial period is characterized by continuous climatic changes, which resulted in severe changes of the bryoflora. Phases with continental climate (Boreal) showed the invasion of species with a continental type of distribution (*Sphagnum fuscum* (Schimp.) Klinggr. in bogs, *Mannia fragrans* (Balbis) Frye & Clark in chalk grasslands). Warmer periods as in the Atlanticum period allowed the immigration of Mediterranean elements northwards. The presence of *Pleurochaete squarrosa* (Brid.) Lindb., *Targionia hypophylla* and other species in Central Europe dates back to this event. Cooler periods such as the Subatlanticum allowed oceanic species such as *Lepidozia cupressina* (Hook.) Dumort., *Anastrepta orcadensis* or *Sematophyllum micans* (Mitt.) Braithw. to move from coastal regions eastwards. The fluctuation of species continued through the last centuries as seen by subfossil records of bryophytes from the Mid Age (Frahm & Wiethold 2004). Peat core studies reveal the change of *Sphagnum* species over time under different climatic regimes (Hölzer 2010).

The present climate change also has an influence on the extension of ranges and composition of local floras.

Phytogeographical arrangement

Zonal vegetation. The basic arrangement of zonal phytogeographical elements of bryophytes follows the threedimensional system of higher plants as well as animals. Thus we have in general the main N-S (arctic, boreal, temperate, Mediterranean), W-E (oceanic – continental) and vertical (planar, colline, montane, alpine) classification in bryophytes as in other groups of organisms.

The **arctic element** consists of relatively few species which are confined to the high arctic belt and do not show up in the Alps. Examples are *Voitia hyperborea*, *Seligeria polaris*, *Bryobrittonia longipes*, *Psilopilum* spp., *Arctoa hyperborea* (With.) Bruch & Schimp., *Haplodon wormskjoeldii* (Hornem.) R. Br., *Cyrtomnium hymenophyllum* (Bruch & Schimp.) Holm., *Kiaeria glacialis* (Berggr.) I. Hagen, *Andreaea blyttii* Schimp. and others. It is likely that these species survived the glaciations in ice-free areas north of the ice shield. Some of these species (*Bryobrittonia longipes*) and other species (*Andreaeobryum macrosporum* Steere & B. Murr.) are found in northern Alaska, which was also not glaciated. Apparently these species lost the ability to spread by their long isolation and still mark the icefree regions.

The origin of the arctic bryoflora is not known, since there are absolutely no fossils. Gams (1970) assumed its origin in the interior of Asia, since 94 species of the 147 common in the European arctic and the Alps are the same as in the Altai Mountains, however, a migration of the species from there is very unlikely. Arctic-alpine species are usually rock inhabiting species, which must have migrated through the Eurasian steppe. Northern Russia was occupied during the interglacials by taiga forests thus the arctic bryoflora must be of younger origin. The warmer climate during the first interglacials must have cause a much higher tree line and left hardly any space for an alpine flora. The first arctic species (*Distichium*, *Calliergon, Drepanocladus, Meesia, Mnium, Cimclidium, Paludella, Helodium, Scorpidium*) are known from deposits of the Saale glaciation, but there is no evidence where these species came from. The arctic bryoflora has, like the temperate element, undergone the widest migrations.

The **boreal element** inhabits the boreal forest and the (high) montane region of the higher mountains in Central Europe. It consists of frequent species growing in conifer forests such as *Hylocomium splendens* (Hedw.) Schimp., *Ptilium crista-castrensis* (Hedw.) De Not., *Catoscopium nigritum* (Hedw.) Brid., *Helodium blandowii* (F.Weber & D.Mohr) Warnst., *Meesia* ssp., *Cinclidium* spp., *Tetraplodon* spp., and *Splachnum luteum* Hedw.. Most of them are holarctic boreal, also found in northern Canada and northern Russia. The extension of the boreal zone (forests plus bogs) in the holarctic is larger than the tropical rainforests (most cartographic projections show these regions to be smaller than they are) and the phytomass of that biome is larger than that of the tropical rain forests, especially due to the masses of peat. Therefore *Hylocomium splendens*, which covers the ground of the forest is possibly the moss species with the largest phytomass in the world. The boreal element has possibly survived the glaciations in Siberia, which was not glaciated and is a refugium for the conifer forest.

The term "boreo-alpine" is misleading, because "alpine" would mean to occur above the forest line, but in this case alpine means occurring in the Alps, which is also not true, since these species are found also outside the Alps at higher elevations. In fact this element is just the boreal element, which shows up in Central Europe at higher elevation, similar to the arctic element, which shows up in Central Europe above the forest line.

There is no direct indication where the boreal bryoflora came from. However, it is known that northern Russia was covered by *Pinus-Larix-Picea*-forests in Pliocene (Frenzel 1968) and that this taiga type forest is the origin of the boreal bryoflora. Thus, we can assume that the bryophytes in the forests have undergone the same history. The boreal element is therefore of Pleistocene age. It is the element which is less affected by climate changes and which shares the most species with North America.

To the **temperate** element belong common species such as *Mnium hornum* Hedw., *Atrichun undulatum* (Hedw.) T.J.Kop., *Polytrichastrum formosum* (Hedw.) G. L. Sm. etc. They have survived the glaciations in forest refugia in southern Europe. The origin of the temperate species is perhaps the arcto-tertiary flora (a misleading term, which has nothing to do with arctic flora but concerns a fossil temperate flora in the presently arctic regions). There is hardly any fossil evidence for bryophytes from this period, except for eocene bryophytes in amber, which were present in a subtropical oak-pine forest south of the arcto-tertiary forest.

The temperate element was severely affected by the Pleistocene climate changes, by migration and survival during glacial periods in various forest refugia. The isolation in different refugia could have also resulted in genetic changes, e.g. the high genetic variability of *Hypnum cupressiforme*.

The **Mediterranean element** consists of species such as *Pleucochaete squarrosa* (Brid.) Lindb., *Crossidium squamiferum* (Viv.) Jur., *Tortula atrovirens* (Sm.) Lindb., *T. inermis* (Brid.) Mont., *Syntrichia princes* (De Not.) Mitt., *Pterygoneurum lamellatum* (Lindb.) Jur., *Entosthodon muhlenbergii* (Turner) Fife, *Bryum torquescens* Bruch & Schimp., *Habrodon perpusillus* (De Not.) Lindb., *Scorpiurium circinatum* (Bruch) M.Fleisch. & Loeske, *Scleropodium illecebrum* Schimp., predominantly acrocarps with a high percentage of Pottiaceae. It is composed of several distribution types. Another part of the Mediterranean species is part of the sino-saharian element, which stretches from North Africa through the desert regions in Arabia and Iran to Turan. Examples are especially dry adapted Pottiaceae such as *Crossidium*, *Aloina*, species of *Tortula*, *Pterygoneurum* etc.

At least there are many cosmopolitan species in the Mediterranean such as *Trichostomum brachydontium*

Bruch, *Reboulia hemisphaerica*, *Targionia hypophylla*, which are found around the world. Whether these species go back to pangaeic ranges is a matter of discussion.

Some Mediterranean species show up not only in Europe and North America but also in the southern hemisphere (Chile, New Zealand, southern Australia). These regions share a Mediterranean type of higher (sclerophyll) vegetation, which is composed of higher plants of totally different systematic origin but share certain bryophyte species such as *Bartramia stricta* Brid., *Crossidium geheebii* Milde, *Syntrichia princeps*, *Aloina ambigua* (Bruch & Schimp.) Limpr. and others. Therefore, Frey (1990) interpreted them as pangaean element. These species could have been evolved during the Mesozoic under arid conditions and persisted since. This could be the oldest floristic element. Since this element includes dry adapted Pottiaceae (e.g. *Tortula atrovirens*), Frey & Kürschner (1988) called it the "xeropottoid life syndrom". However, the floristic element includes many other non-xerophytic and non-pottioid species as well (e.g. *Homalothecium aureum* (Spruce) H. Rob., *Anacolia webbii*, *Bartramia stricta*, *Claopodium whippleanum*)

The question is, whether these species have their origin in the northern hemisphere and were able to cross the equator, are relicts of a pangaean range or were introduced e.g. by viniculture, which matches the ranges of these species. Mediterranean elements occur in the warmer parts of Central Europe (upper Rhône valley, Rhine and Moselle valley etc.), where they are interpreted as relics from the postglacial temperature optimum. They can, however, also be dispersed at any time later. Their occurrence together with Mediterranean lizards, grasshoppers, snakes and other animals suggests that they were part of Mediterranean ecosystems which moved northwards during warmer periods and stayed in microclimatic habitats which correspond to the present Mediterranean climate.

Part of the Mediterranean bryoflora is found in warmer regions of Central Europe. Under the climatic conditions of the postglacial temperature optimum (6000-8000 years b.p.), which resulted in an increase of the main temperature of up to 3°C, the Mediterranean fauna and flora moved northwards using river valleys (Danube, Rhône, Saône, Rhine, Moselle) as routes. They are supposed to have survived later colder climatic periods in special habitats such as S-exposed rocks and slopes, where the microclimate still resembled the meso-climate of their Mediterranean origin.

The **atlantic element** is confined to western Europe; some species are restricted to coastal areas (eu-atlantic species such as *Breutelia chrysocoma* (Hedw.) Lindb., *Pleurozia purpurea* Lind. and others listed under the chapter **Origin of European species**), others extend more to the East such as *Hyocomium armoricum* (Brid.) Wijk & Margad. (Fig. 1), *Lepidozia cupressina*, *Scapania compacta* (Roth) Dumort., *Ptychomitrium polyphyllum* (Sw.) Bruch & Schimp. (Fig. 1) or even to the 1°C January isotherm (subatlantic species such as *Plagiothecium undulatum* (Hedw.) Schimp.). It consists of heterogeneous elements:

1. Part of the species shows also up along the east coast of North America (e.g. *Sphagnum pylaisii* Brid., *Diphyscium foliosum* (Hedw.) D.Mohr, Fig. 2). They are amphi-atlantic species. The species may have developed when the Atlantic Ocean started to open in the Tertiary and the species remained separated along the east coast of North America and the west coast of Europe. They could also be dispersed with the west wind drift from North America to Europe. Other species are disjunct between the west coast of North America and the west coast of Europe. Examples are *Plagiothecium undulatum* (Hedw.) Schimp. (Fig. 3), and *Antitrichia curtipendula* (Timm ex Hedw.)

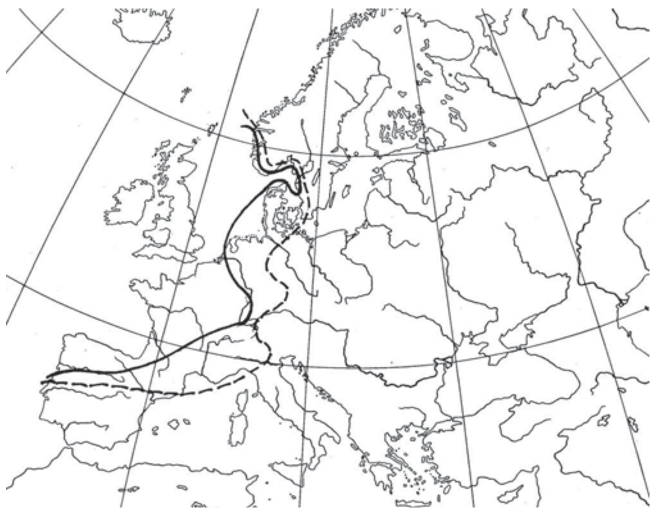

Fig. 1. Eastern border line of *Hyocomium armoricum* (full line) and *Ptychomitrium polyphyllum* (dashed line), as examples of Atlantic distribution type.

Fig. 2. Distribution range of *Diphyscium foliosum,* as an example of amphi-nord-atlantic disjunction.

Fig. 3. Distribution range of *Plagiothecium undulatum,* as an example of western-North America and Western Europe disjunction.

Fig. 4. Laurasian disjunction of *Campylopus atrovirens.*

Brid. amongst others. They are holarctic species which depend on high oceanic climate.

2. Another part of the species are tropical (predominantly neotropical) elements, which show up in the Macaronesian islands but part of them also in Ireland and Scotland, some to SW Norway or even the Faroe Islands. Examples are *Campylopus shawii* Wilson, *Frullania teneriffae* (F. Weber) Nees, *Leptoscyphus cuneifolius* (Hook.) Mitt. etc. As always in such cases, their occurrence in Europe can be explained by either long-distance dispersal or relicts. Long-distance dispersal is not possible under present climatic conditions (the direction of dispersal is against the trade winds) but must have happened earlier under a different global wind system, perhaps during the Pleistocene. The relict hypothesis means that these species (or part of them) were present in Europe in the Tertiary, colonized the young volcanic islands after their origin and stayed on these islands when Europe underwent the glaciations. Another possibility is that these species survived the glaciations in ice-free regions along the coast of the Atlantic. It has to be kept in mind that the sea level was 170 m lower at that time and large parts of the European shelf were land, providing refugia. After the steady rise of the sea level in the Holocene these species migrated to their present regions. Thus, these species are not true relicts because they survived in other places but migration relicts, which reached their final destination later.

3. A third group is disjunct in the Himalayas (or adjacent Yunnan), the Alps, and the oceanic west coasts of the Atlantic. This group consists of 16 species of hepatics, for example *Pleurozia purpurea*, *Anastrophyllum joergensenii* Schiffner, *Herbertus sendtneri* (Nees) Lindb., and *Plagiochila carringtonii* (Balf.) Grolle, as well as numerous mosses such as *Campylopus atrovirens* De Not. (Fig. 4), *Dicranodontium uncinatum* (Harv.) A. Jaeger, *D. subporodictyon* Broth., *Paraleptodontium recurvifolium* (Taylor) D.G. Long. and others.

The **continental element** consists of species that have predominantly a higher frequency in eastern Europe and also a western border in Central Europe. Examples are *Heterophyllium haldanianum* (Grev.) H.A.Crum and *Polytrichastrum pallidisetum* (Funck) G.L.Sm. Such species occur in North America in the eastern part. This element includes steppe species from southern Russia (Pontian element) and Inner Asia such as *Mannia fragrans* and *Hilpertia velenovskyi* (Schiffn.) R.H.Zander, which could be relicts from the Boreal period, when a steppe flora with species of *Stipa*, *Adonis vernalis* L. etc. invaded Central Europe or later spore dispersal. They are highly xeromorphic and grow in xerothermic habitats. Therefore they are easily taken to be Mediterranean elements, with which they grow together.

Arctic-alpine Elements (Fig. 5) are found in the higher mountains of Central Europe as well as in northern Europe. In contrast to true arctic elements, these species have survived the glaciations in ice-free regions south of the northern ice shield and migrated later northwards in the present arctic regions and southwards to the alpine mountains. Examples are *Andreaea* ssp., *Gymnomitrium* ssp., *Marsupella* ssp., *Hygrohypnum* spp., *Conostomum*

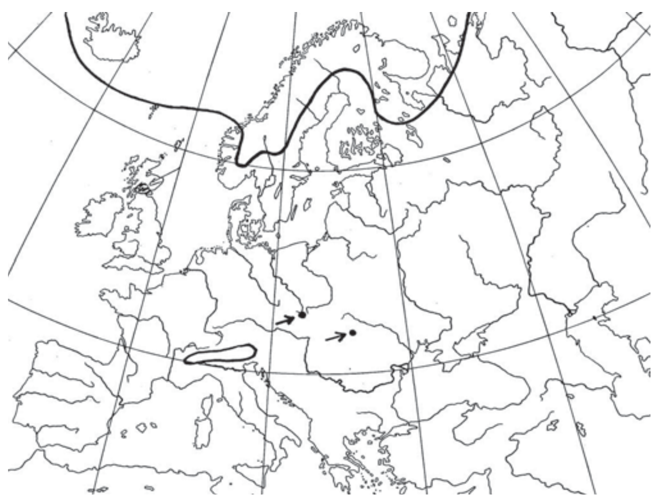

Fig. 5. Distribution range of *Tayloria lingulata* (Dicks.) Lindb.*,* as an example of arcto-alpine species/disjunction.

boreale Sw. (syn *C. tetragonum* (Hedw.) Lindb.), *Polytrichastrum sexangulare* (Brid.) G.L.Sm., *Amphidium lapponicum* (Hedw.) Schimp., *Mniobryum albicans* (Wahlenb.) Limpr., var. *glaciale* (Brod.) Limpr., *Anthelia julacea* (L.) Dumort., *Pleurocladula albescens* (Hook.) Grolle., *Arnellia fennica* (Gott.) Lindb., *Hydrogrimmia mollis* (Bruch & Schimp.) Loeske, *Aongstroemia julacea* (Hook.) Mitt., *Pohlia cucullata* (Schwaegr.) Lindb., *Bryum blindii* Bruch & Schimp., *Brachythecium glaciale* Schimp., *Chandonanthus setiformis* (Ehrh.) Lindb., species of *Stegonia* and *Desmatodon* etc. Their origin is not clear. Herzog (1926) lists examples of alpine species "deren Herkunft nicht feststeht". The alpine species are cold-adapted which limits their presence in the Alps to the Pleistocene. However, alpine species must have existed before the glaciation period. Only rarely have attempts been made at explanation, which are highly hypothetical. For instance Gams (1970) proposed an antarctic origin of these species, which seems quite unlikely. („So lässt sich für viele der höchststeigenden Flechten und Moose zeigen, daß ihre ursprüngliche Heimat um Umkreis der größten Eismasse der Erde, der Antarktis liegt, von wo auch Arten mit vorwiegend ozeanischen Ansprüchen über die nordamerikanischen und europäischen Westküsten bis Skandinavien und in die Alpen gekommen sind.")

Alpine elements are confined to the Alps, but do not occur in the arctic. Examples are *Leptodontium styriacum* (Jur.) Limpr., *Riccia breidleri* Jur., *Trochobryum carniolicum* Breidl. & Beck and *Molendoa hornschuchiana* (Hook.) Lindb. ex Limpr.. Herzog (1926) lists many other species but most of them turned out to occur elsewhere and many are of doubtful taxonomic value and/or are no more accepted as species. At the present state of knowledge, *Brotherella lorentziana* (Molendo ex Lorentz) Loeske ex M.Fleisch. and *Tayloria rudolphiana* (Garov.) Bruch & Schimp. are worldwide confined to the (northern) Alps, which is difficult to explain, because these species are forest species and these regions were glaciated until 10,000 years ago. It might be that they occur elsewhere in the world as in the case of *Distichophyllum carinatum* Dixon & W.E.Nicholson, which was described as endemic to the northern Alps but occurs in China as well as in Japan.

Some species regarded as alpine endemics may turn out to occur elsewhere in the world. This might also be an explanation for *Zygodon gracilis* Wilson which is so far known only from the northern Alps and in a very limited area in England.

More numerous are oreophytes, which occur also in other parts of the world, especially in the Himalayas. Examples are *Geheebia gigantea* (Funck) Boulay, *Voitia nivalis* Hornsch., *Campylopus schimperi* Hammar, *Merceya ligulata* (Spruce) Schimp., *Mielichhoferia elongata* (Hoppe & Hornsch. ex Hook.) Hornsch., and the genera *Oreoweisa*, *Molendoa* and *Pleuroweisia*. Their origin is not clear. The Alps were glaciated and it is difficult to assume that these species survived the glaciation on ice free mountain peaks (nunatakker). The only logical explanation is that they must have reached the Alps in the Holocene by long-distance dispersal.

Endemism

Possibly as a result of the easier dispersal, endemism is much lower in bryophytes as compared with phanerogams. Therefore we have only few endemics on the genus level in Europe (*Cinclidotus*, *Scorpiurium*, *Hyocomium*, *Pleuroweisia* and *Trochobryum*). An example for an endemic species is *Encalypta streptocarpa* Hedw.. More examples of endemism in Europe turned out to be wrong, when the species were discovered elsewhere in the world, such as species of the *Bryum bicolor* complex (Vanderpoorten & Zertman 2002). *Bruchia trobasiana* De Not.and *B. vogesiaca* Nestl. ex Schwaegr. were regarded as European endemics but turned out to occur in Asia and North America (Rushing 1986).

Relicts

The term relicts has to be used with caution, because an isolated occurrence outside the main range can also be explained by long-distance dispersal, which has to be presented by molecular studies.

Arctic-alpine relicts. Relicts from the tundra vegetation of the latest ice age remained in open habitats, which were no more covered by forests. These are species such as *Chandonanthus setiformis* (Ehrh.) Lindb., *Tetraplodon angustatus* (Hedw.) Bruch & Schimp. or *Andreaea rothii* F. Weber & D. Mohr growing on rock and in rocky streams, *Jungermannia cordifolia* Hook. surviving in cold streams. The kar vegetation includes such species as *Polytrichum alpinum* Hedw., *Scapania uliginosa* (Sw. ex Lindenb.) Dumort., *Marsupella sparsifolia* (Lindb.) Dum., and rich fens (*Meesia triquetra* (L. ex Jolycl.) Angstr., *Paludella squarrosa* (Hedw.) Brid., *Helodium blandowii*, *Tomenthypnum nitens* (Hedw.) Loeske, *Scorpidium turgescens* (T.Jensen) Loeske, *Cinclidium stygium* Sw., *Pseudobryum cinclidioides* (Huebener) T.J.Kop. etc.). However, we can never exclude that species arrived later by spores, as shown for *Paludella squarrosa*, which is more frequent in northern Europe but found only in a few places in the Alps (Herzog 1926, Fig. 97). A relict status is not the case in so called glacial relicts in raised bogs, because they developed later and offered no consistent habitat since the time of glaciation. Also species growing in dry habitats can be arctic relicts, because some of these habitats remained open since the last glaciation and were not covered by forests. Such an example is *Athalamya hyalina* (Sommerf.) Hattori. *Rhytidium rugosum* (Hedw.) Kindb. is a tundra species, but grows in Central Europe on dry chalk grasslands as well. According to results of molecular studies, its sterile scattered populations can be considered as relicts (Sabovljevic & Frahm 2011).

Xerothermic relicts. Open habitats not covered by forests allowed species from the Mediterranean as well as continental steppes to survive. They are interpreted as relicts from the postglacial temperature optimum (6000 – 7800 y.b.p.), when the temperatures were 2-3°C higher. Examples are *Pleurochaete squarrosa*, *Targionia hypophylla*, *Pterygoneuron* spp., *Pottia* spp., *Bryum torquescens*, *Tortula atrovirens*, *T. inermis*, *T. canescens* Mont., *Syntrichia princeps*, *Rhynchostregiella tenella* (Dicks.) Limpr., *Sphaerocarpus texanus* Austin, etc.

Tertiary relicts. There are three groups of bryophyte species, which are interpreted as relicts from the Tertiary.

1. Species occurring in the tropics as well as in the eu-atlantic parts of western Europe are interpreted as relicts from tropical climates in the Tertiary. Examples are *Leptoscyphus cuneifolius* (Hook.) Mitt., *Adelanthus decipiens* (Hook.) Mitt., *A. lindenbergianus* (Lehm.) Mitt., *Teleranea nematodes* (Aust.) Howe., *Lepidozia cupressina* (Sw.) Lindenb., *Plagiochila bifaria* (Sw.) Lindenb., *Campylopus shawii*, *Harpalejeunea molleri* (Steph.) Grolle., *Drepanoclolejeunea hamatifolia* (Hook.) Schiffn., *Colura calyptrifolia* (Hook.) Dumort., *Jubula hutchinsiae* and others. These species are said to have survived the glaciations along the Atlantic coast, not necessarily along the present coastline but also in regions below, since the sea level was ca. 150 m lower and large parts of the shelf were land. It can, however, not be excluded that these species or part of them arrived later by spore dispersal.

2. Some species, which are more widely distributed in the world, are confined in Europe to the southern Alps, usually to a few localities. Examples are *Braunia alopecura* (Brid.) Limpr., *Haplohymenium triste* (Ces. In De Not.) Kindb., or *Haplocladium angustifolium* (Hampe & Müll. Hal.) Broth..

Other species such as *Campylopus oerstedianus* (Müll. Hal.) Mitt. (Sabovljevic & Frahm 2008), *Frullania inflata* Gottsche, *F. riparia* Lehm. and *F. parvistipula* Steph. are found in the southern Alps as well as in the Pyrenees and other parts of the northern Mediterranean region. They usually occur also in East Asia and in part also in North America.

The extraordinary distribution of these species has not received much attention. Herzog (1926) lists species such as *Braunia alopecura* simply as Mediterranean elements. *Frullania riparia* is called a Mediterranean element on one page and Eastern North American element on another page. The extraordinary disjunction of these species is not discussed. A hypothesis is that these species were part of the bryoflora in the Tertiary and survived glaciation in the southern Alps. The habitats, however, are situated in former glacier valleys and – if this hypothesis is maintained, these species must have survived above the glacier, which is not unlikely because glacier valleys in Alaska or New Zealand show forest above the ice. The alternative hypothesis is, as ever, long-distance dispersal. This can be excluded in the case of *Campylopus oerstedianus*, which is worldwide known only in the sterile state. The distributions in the Pyrenees, the southern Alps and northern Greece (as well as in Costa Rica and North Carolina) are arranged along the northern shore of the former Tethys Ocean and suggest a relictness (Sabovljevic and Frahm 2008).

3. A few species of tropical distribution such as *Trematodon longicollis* Michx. and *Calymperes erosum* Müll. Hal. are found at fumaroles in Italy and were also interpreted as relicts. *T. longicollis* as well as *Jungermannia handelii* (Schiffn.) Amak. and the fern *Woodwardia radicans* (L.) Sm. grow together in Crete and may have survived there during glaciation, although *T. longicollis* is a colonist on ephemeral habitats and may have also been dispersed later.

Subtropical relicts are presumably of Tertiary origin, which could survive in Europe in the Mediterranean and western Europe. Examples are *Tetrastichium virens*, *Daltonia splachnoides* (Sm.) Hook. & Taylor, *Colura calyptrifolia* (Hook.) Dumort., *Lejeunea holtii* Spruce and others. Their relict status is, however hypothetical. Species of tropical genera such as *Breutelia chrysocoma* are only found in Europe, which is an argument that they survived here and were not dispersed later by long distance dispersal. Other species show strange disjunctions (*Leptodontium flexifolium* (Dicks.) Hampe in New Guinea, Central America and western Europe), indicating either a former continuous range in Tertiary or later dispersal during the Holocene, perhaps due to volcanic eruptions.

Long-distance dispersals

Several bryophyte species which are frequent in North America show up in Europe in very limited regions. Examples are *Bryhnia novae angliae* auct. eur. non (Sull. & Lesq.) Grout, *Frullania oakesiana* Austin or *Dichelyma falcatum* (Hedw.) Myrin. The limited range suggests a spore dispersal from overseas.

Even tropical bryophytes are found in Central Europe (except for those found in western Europe, see under chapter **Origin of European species**). *Heterophyllium affine* (Hook. in Kunth) Fleisch. is native in northern South and Central America and was found in the 19th Century in southern Germany, Austria and the Carpathians. Later, it became extinct. The location and restriction of records suggests that the species arrived by a spore shower from overseas but could not establish itself for a longer period of time.

Hyophila involuta (Hook.) Jaeg. is a pantropical weed growing on humid rocks and asphalt, but is found in Europe along the shores of some Swiss lakes, the Lake Constance and the rivers of Aare and upper Rhine, however in the splash zone of the water. A relict can be excluded since these lakes are glacial lakes. The limited unnatural range suggests an introduction or long-distance dispersal. *Anacolia laevisphaera* (Taylor) Flowers is widespread in the tropical mountains, especially the Andes, but has been found about a dozen times in natural habitats in a small area in the Moselle region of Germany. Their presence in Europe can hardly be explained other than by spore dispersal, perhaps in combination with volcanic eruptions.

Neophytes

Compared with higher plants, the percentage of neophytes is comparably very low amongst bryophytes. Except for local introductions of species in Britain or on imported tree fern trunks in Ireland, we have only a few species, which are widespread and have successfully established in Europe: the mosses *Orthodontium lineare* Schwaegr. from South Africa and New Zealand, *Campylopus introflexus* (Hedw.) Brid. from the temperate southern hemisphere, *Phascum leptophyllum* (Müll. Hal.) J. Guerra & M. J. Cano from South Africa and the liverwort *Lophocolea semiteres* (Lehm.) Mitt. from New Zealand, which showed up in Europe during the past hundred years. All these neophytes came from the southern hemisphere. The reason is that there is a common stock of species of bryophytes in the holarctic and thus no potential for introductions. In contrast, the main source for neophytic phanerogams is North America with a similar climate as in Europe. Since it is almost impossible for spore plants to cross the innertropical convergence, introductions of bryophytes happened only from the southern hemisphere. Only two species from North America, *Tortula amplexa* (Lesq.) Steere and *Hennediella standfordensis* (Steere) Blockeel, showed up locally in England. The status of other species such as the heavy metal moss *Scopelophila cataractae* (Mitt.) Broth., first recognized in Europe in 1967 in Wales is not clear because it was later found in abandoned mines from the 19th Century also in Germany. More species could have arrived before 1800, before bryological exploration started. This concerns *Tortula pagorum* (Milde) De Not., which is known with both sexes in Australia but in Europe with only males, in North America with only females, and *Tortula papillosa* Wilson, which is sterile in the northern hemisphere and produces sporophytes only in the southern hemisphere. Hill *et al.* (2006) give 21 moss species non native in Europe, introduced by human agency.

Global Disjunctions

North America – Europe. Although North America and Europe share a large percentage of bryophyte species, some of them have a distinctly uneven distribution. There are only a few examples of species that are more frequent in Europe as compared with North America (e.g. *Rhodobryum roseum* (Hedw.) Limpr., *Calliergonella cuspidata* (Hedw.) Loeske), but most are more frequent in North America. Examples are *Bryhnia novae-angliae* and *Frullania bolanderi* Austin, which are found in Europe solely in southern Norway and adjacent Sweden. Since these regions in Europe were glaciated, they must have been dispersed during the Holocene. More frequent are examples in the Mediterranean bryoflora. Certain species (*Tortula papillosissima* (Copp.) Broth., *Pterygoneurum ovatum* (Hedw.) Dixon, *P. subsessile* (Brid.) Jur., *Entosthodon muehlenbergii* pp.) are found in North America (California, Arizona) and Europe. It can be supposed that these species were already present in the Tertiary, when the northern continents were still connected. This separation for 50 million years has perhaps led to the evolution of species pairs (e.g. *Anacolia webbii* (Mont.) Schimp. – *A. menziesii* (Turner) Paris). Subsequent long-distance dispersal has led to *A. menziesii* coming to the Mediterranean. Long-distance dispersal with prevailing western winds is perhaps due to the presence of species common in North American which are rarely and locally found in the Mediterranean such as *Claopodium whippleanum* (Sull.) Renauld & Cardot. They could be interpreted as relicts from a time when North America and Europe were still connected, though their rarity in Europe suggests a spore dispersal.

Himalayas – western North America – western Europe – Alps. Sixteen species of liverworts and several species of mosses (e.g. *Dicranodontium subporodictyon* Broth., *D. uncinatum* (Harv.) A. Jaeger, *Campylopus gracilis* (Mitt.) A. Jaeger, *Leptodontium recurvifolium* (Dicks.) Boulay) are known to occur in Europe as well as along the west coast of North America and the Himalayas. Part of them (*Herbertus sendtneri*, *Anastrophyllum assimile* (Mitt.) Steph., *A. donianum* (Hook.) Schiffn. and *Frullania parvistipula*) are also found in the Alps. As these were glaciated during the Pleistocene, their occurrence must be due to long-distance dispersal. Both species of *Anastrophyllum* as well as *Pleurozia purpurea* and *Mastigophora woodsii* (Hooker) Nees are also found in western North America. *Tetralophozia filiformis* (Steph.) Urmi is found as well as in the Himalayas, also in China, Japan, Alaska, British Columbia, and in Europe only in a single locality in Cantabria. This might indicate that this group of species is heterogeneous and consists of relicts (in formerly ice-free regions) as well as species with long-distance dispersal.

Bryophyte vegetation as a composition of different phytogeographical elements

In nature, species of many different phytogeographical elements are intermingled in the same region or at the same habitat. For example, the Ruhr valley in the Eifel Mountains (continuation of the Belgian Ardennes) is composed of boreal species (*Jungermannia cordifolia, Andreaea rothii*), which perhaps remained from the tundra vegetation of the last glaciation in this damp, rocky cool valley. The Atlantic species *Hookeria lucens* (Hedw.) Sm., *Trichocolea tomentella* (Ehrh.) Dumort., *Isothecium holtii* Kindb. (relict status proved by molecular studies, Sabovljevic *et al.* 2005), and *Hyocomium armoricum* (Brid.) Wijk & Margad. are relicts from cooler humid periods. *Hylocomium splendens*, *Ptilium crista-castrensis* are boreal species, which invaded with conifer forests. The bryophyte flora of the Mosel valley in Germany consists - beside the main stock of zonal temperate species - of tundra relicts (*Rhytidium rugosum*), assumed Mediterranean relicts (*Targionia hypophylla*, *Trichostomum brachydontium*, *Pleurochaete squarrosa*), steppe elements (*Mannia fragrans*), a neophyte (*Campylopus introflexus*) and dispersal from overseas (*Anacolia laevisphaera*). With the exception of the latter, the composition of the phanerogamic flora is similar.

Concluding remarks

Knowledge of the phytogeography of bryophytes in Europe has much increased over time owing to a better floristic exploration, resulting in detailed checklists (e.g. Hill *et al.* 2006). Increased taxonomic studies Worldwide, revisions of genera and the discovery of many synonyms have contributed much to a more exact base for phytogeographical discussions. In spite of better information concerning climate history or plate tectonics, the interpretation of ranges remains still speculative. The only way to come to secure results are fossil records, which are limited due to the poor preservation of bryophyte material, and especially molecular studies determining genetic distances between populations.

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Botanica SERBICA

REZIME

Fitogeografija evropskih briofita

Jan-Peter Frahm

U radu se daje pregled porekla i obrazaca distribucije evropskih briofita. Mešavina florističkih elemenata objašnjava se istorijom vegatacijskih promena u Holocenu, tokom kojeg su različiti floristički elementi širili ili skupljali areale pod uticajem klimatskih promena. Za razliku od drugih viših biljaka, briofite imaju znatno šire i transkontinentalne areale, a relikti Tercijara i ledena doba igraju značajnu ulogu u razumevanju recentnog rasprostranjenja briofita.

Ključne reči: briofite, Evropa, fitogeografija, endemizam, disjunkcije, relikti

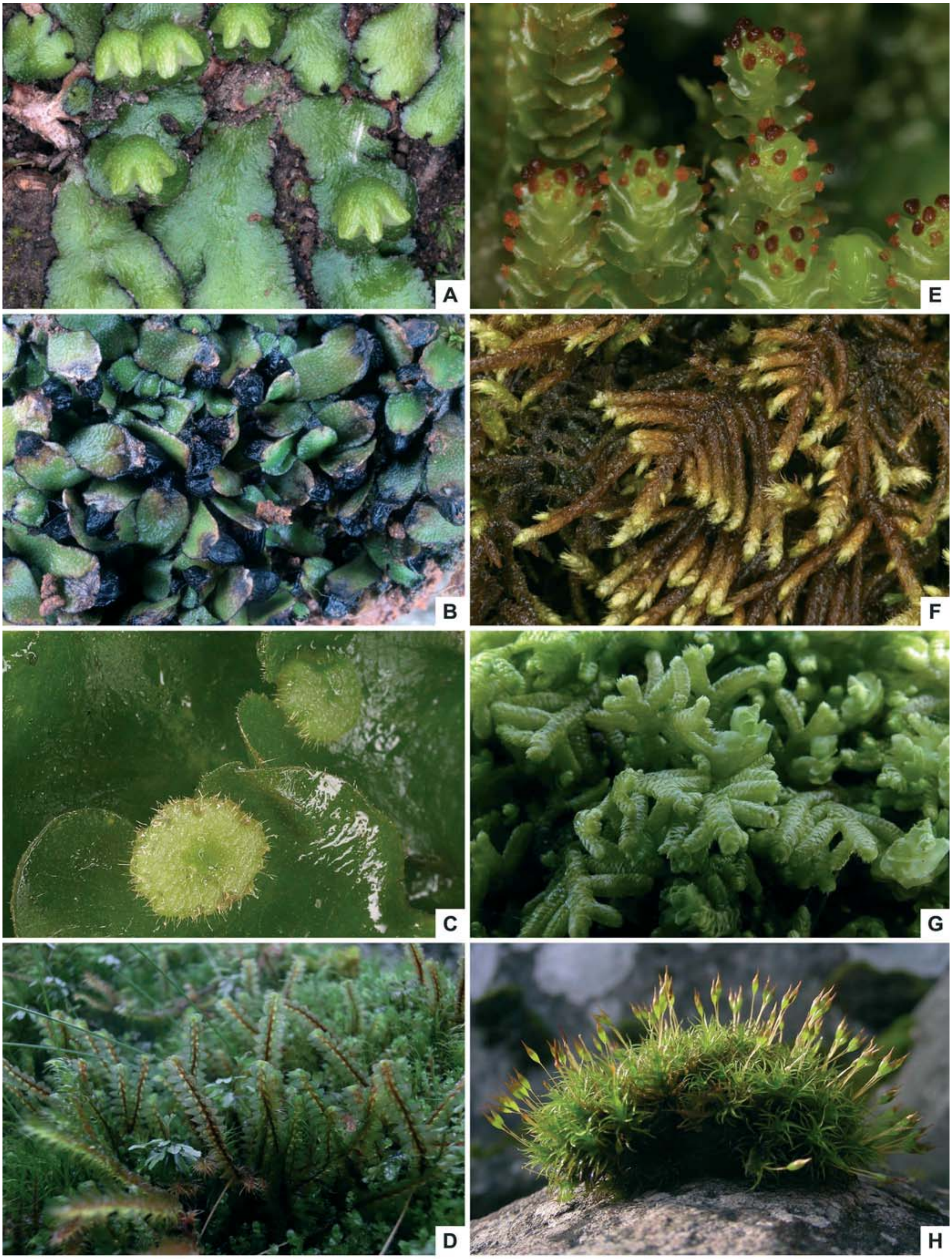

Table I. A) *Reboulia hemisphaerica*, **B)** *Targionia hypophylla*, **C)** *Dumortiera hirsuta*, **D)** *Scapania ornithopodioides*, **E)** *Anastrepta orcadensis*, **F)** *Hyocomium armoricum*, **G)** *Lepidozia cupressina*, **H)** *Ptychomitrium polyphyllum*

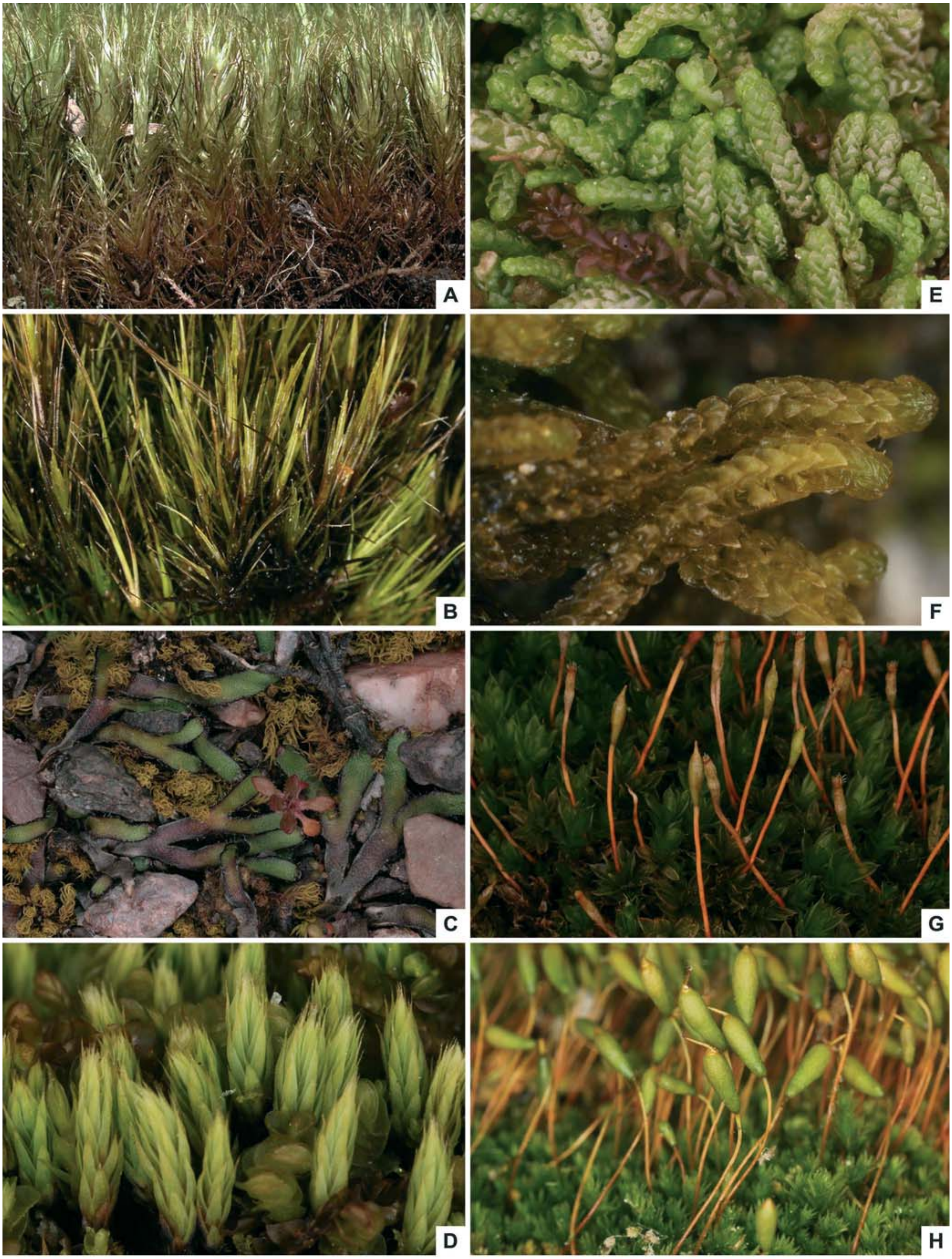

Table II. A) *Campylopus shawii*, **B)** *Campylopus atrovirens*, **C)** *Mannia fragrans*, **D)** *Conostomum boreale*, **E)** *Pleurocladula albescens*, **F)** *Chandonanthus setiformis*, **G)** *Tayloria rudolphiana*, **H)** *Mielichhoferia elongata*

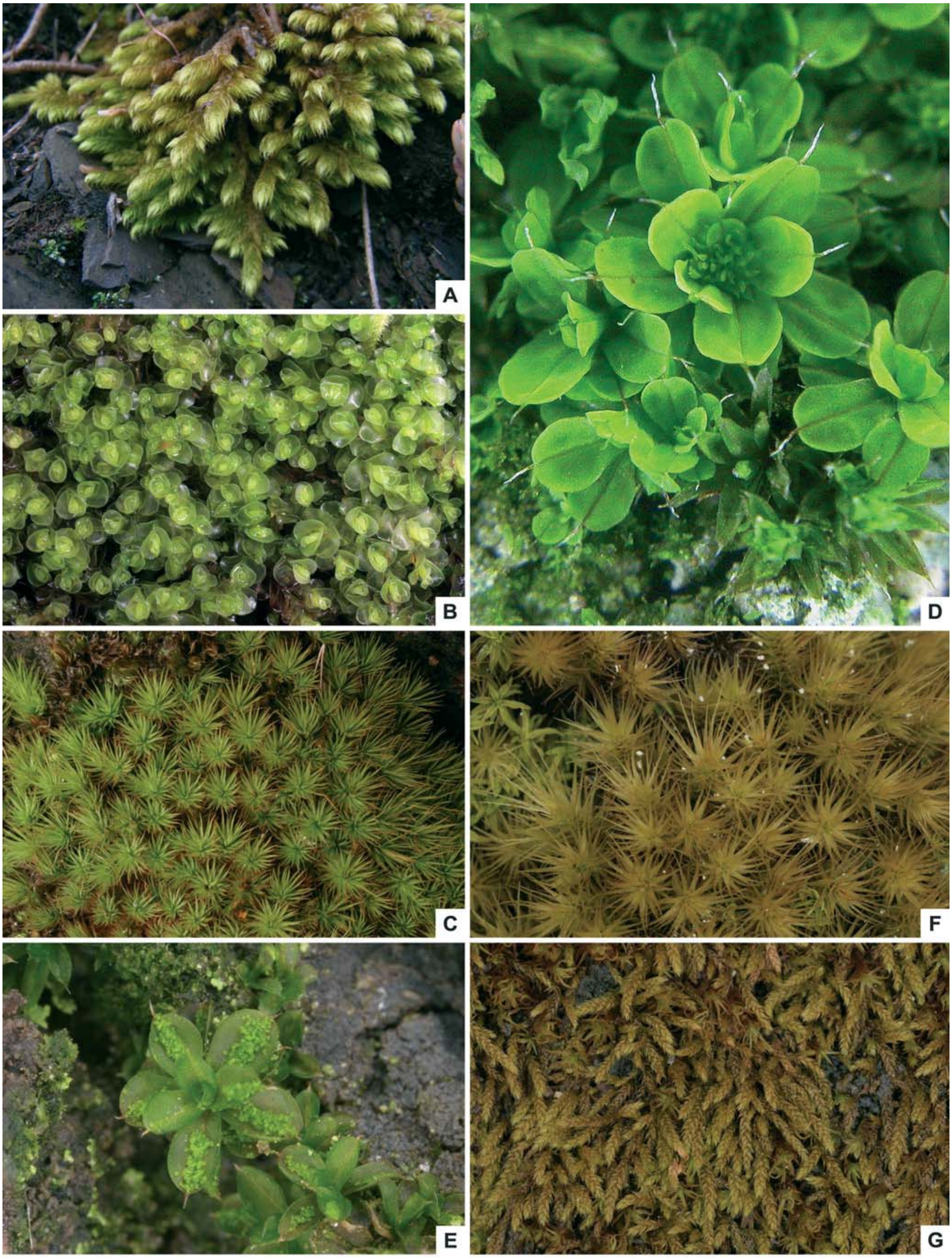

Table III. A) *Rhytidium rugosum*, **B)** *Jungermannia handelii*, **C)** *Anacolia laevisphaera*, **D)** *Tortula pagorum*, **E.)** *Tortula papillosa*, **F)** *Anacolia webbii*, **G)** *Claopodium whippleanum*