Are there endemic bryophyte species in the Alps? - The range of Brotherella lorentziana (Lor.) Loeske

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Abstract: In the past, many bryophyte species were regarded as endemic to the Alps. Hserzog listed more than 70 examples. Many of them are micro-endemisms or merely alpine forms of other species (Leptodontium styriacum) and not of taxanomic value, or considered as relics from the last interglacial period, although the Alps were covered by glaciers during the last ice age, which made a survival almost impossible, especially for forest species and epiphytes. Several of these species turned out to occur as well in Asia (Distichophyllum carinatum) or were described from there under a different name (Tayloria rudolphiana as T. delavayi). So far, one important species, Brotherella lorentziana, remained unsolved. A recent study revealed that this species is present in Asia, where it is known as B. henonii. At the present state of knowledge, five species namely Herbertus sendtneri, Riccia breidleri, Barbula bicolor, Marsupella ramosa and Trochobryum carniolicum must still be considered as endemic.

In his famous book "Geographie der Moose", Herzog (1926) listed about 70 species as alpine endemisms. His enumeration included:
B. flavipes = Barbula enderesii, which is Eurasian in distribution.
Barbula kneuckeri – a dubious taxon which is placed as variety either to Barbula fallax, B. asperifolius, B. reflexa, B. rufa or Didymodon ferrugineus.
Brachythecium ruebelii = B. velutinum
Bryum opalinii = B. alpinum var.
Cephaloziella integerrima – also in North America.
Cephaloziella obtusa = no legetimate species.
Didymodon giganteus*
Didymodon Lamyi = dubious taxon
Ditrichum nivale = Ditrichum pusillum var.
Encalypta longicolla = also in North America
Grimmia andreaeoides = Didymodon subandreaoides, also Russia and North America.
Grimmia triformis = also in Russia and North America.
Hygrohypnum styriacum = also in North America.
Hymenostomum meylanii = Weissia squarrosa
Leptodontium styriacum = L. flexifolium
Marsupella pygmaea = no legetimate species.
Merceya ligulata*
Mnium nivale = Mnium ambiguum
Molendoa hornschuchiana*

Orthotrichum juranum = O. cupulatum var.
Plagiothecium noricum = P. neckeroideum ssp., the latter also in Asia.
Pohlia berninae = Pohlia polymorpha ssp.
Racomitrium mollissimum = Racomitrium canescens fo.
Schistidium tarentasiense = S. apocarpum var.
Streblotrichum flavipes = Barbula enderesii
Streblotrichum helveticum = no legetimate species.
Trichostomum muticum = T, crispulum var.
Webera ambigua = Pohlia elongata
Zygodon dentatus *
plus 31 more Brya* Species with a wider distribution, erroneously cited by Herzog.
Most of the species are merely alpine forms of more widespread species.
Several are erroneously listed in this context, because the worldwide distribution was not known to him. And many of these so called endemic species were described by Herzog himself, who seemed to be much in favour with this concept.
Beside of the species mentioned above, some other species such as Voitia nivalis or Oreas martiana were said to be alpine endemics but were later found in Asia. Except for the unsufficient exploration of Asia, it was not considered (or known) that Asia was not affected by the pleistocene glaciations, and served as a refuge for the species in Europe, especially for the alpine flora.
The older literature is full of speculations about the reasons for the endemicity of bryophyte species endemic to the Alps. Herzog (1926) called Brotherella lorentziana, Distichophyllum carinatum and Tayloria rudolphiana "arktotertiäre Relikte, die möglicherweise unweit ihren heutigen Standorten aushielten oder nur wenig verdrängt wurden". He does not explain how an epiphyte such as Tayloria rudolphiana or a forest moss such as Brotherella lorentziana could survive in their present habitats. Gams (1928, 1955) regarded them as relics from the last interglacial, which survived in ice free regions within the Alps. The explanations of the ranges by Gams (1928, 1930, 1932, 1955) can be regarded as historical and influenced by former phytogeographical opinions such as the nunatakker theory. Long distance dispersal is not considered but relic hypotheses are stressed
Although several bryophyte species were and are still regarded as endemic to the Alps, there is a considerable doubt in many cases. Such doubts specially concern forest species, since the Alps were glaciated until 12.000 years b.p. and the origin of new endemic species is as unlikely as a survival of the last glaciation.

Of the species which are commonly regarded as endemic to the Alps, the following turned out to be alpine forms of common or more widespread species:

Leptodontium styriacum (Jur. ex Geh.) Limpr.
Herzog (1926) regarded it as a presumable relic (from what?) "Zu den Relikten ist vielleicht auch das in den Alpen umgewandelte Leptodontium styriacum zu rechnen."
This species was generally regarded as distinct and differing from L. flexifolium by the prfesence of beood bodies, a hyaline apical cell at the leaves and larger laminal cells. Brood bodies, however, are also found outside the Alps, some collections of Leptodontium in the Alps showed no hyaline apical cell and a difference in the size of the laminal cells could not be confirmed that L. sytriacum was synonymised with L. flexifolium (Frahm 2012). After publication of this synonymy, I found an earlier but less noted support in the Russian literature. Interestingly, L. flexifolium was found in Mongolia (Abramov & Abramova 1983). The authors compared it with L. styriacum and concluded that they were identical. They wrote: "The genus Leptodontium (C. Müll.) Hampe is represented in Mongolia by one species – L. flexifolium (With.) Hampe. We were confirmed in this conviction after very careful comparison of Mongolian specimens with European and East Asian materials of this genus. Until recently, brood bodies have not been

known in L. flexifolium, and its specific distinguishing feature differing it from the closely related species L. styriacum refers just to brood bodies. Moreover, both species are said to differ in the leaf shapes, type of denticulation and size of laminal cells. All these characters are, however, very variable. Having examined many European collections of L. flexifolium we found in leaf angles axillary gemmae. Form and shape of the gemmae vary considerably in European and Mongolian plants. They can be elliptic, claviform to fusiform and all these forms can be found at the same time in one plant or even in one cluster. Usually they are 3-5-celled but there are also multicellular gtemmae observed. Therefore, the understanding of L. flexifolium has basically changed and there is a need of critical study of Eurasian species of the genus Leptodontium. Zander (1972) stated that L. styriacum occurs only in Central Europe and differs from the closely related L. flexifolium in having acute leaves and fusiform gemmae." (Translated from Russian). They illustrated material which refers to L. flexfolium. Even if the Mongolian plants would be referred to L. styriacum, the latter would no more endemic to the Alps. With regard to the presence in Mongolia, the Alps and the oceanic parts of Europe, L. flexifolium has a range which can be compared with Campylopus gracilis (schwarzii), Dicranodontium asperulum, D. uncinatum and others.

Tayloria rudolphiana (Garov.) Bruch & Schimp.

This species is an epiphyte mainly on Acer pseudoplatanus in parts of the Alp in Germany, Austria and Switzerland and considered as European endemic. The status as en epiphyte corroborates the status as endemic species of the Alps, because in this case it must have been originated after the reforestation of the Alps or must have survived the glaciations in forest refugia in southern Europe, which is both very much unlikely.
Already Brotherus (1926) listed the species together with Tayloria delavayi (Besch.) Besch. without giving a difference. Gams (1932) regarded T. rudolphiana as close to Tayloria delavayi. He wrote that „unser Endemit der Nordalpen ist wohl gleich dem Schisma in Tirol und gleich der Breutelia um den Vierwaldstättersee ein Interglazialrelikt ozeanischer Herkunft". (cf. also Gams 1930) because „alle heutigen Fundorte …. liegen in während der letzten Eiszeit wenig vergletscherten …. Gebieten." At least, Gams admits that Tayloria rudolphiana occurs in other regions as Breutelia arcuata and Distichophyllum carinatum, which he regards as relics, too, but concludes that Tayloria has only survived on the warmest nunatakker (as an epiphyte!). He mentions a story, that the species was found on a human sceleton, however, the herbarium specimen in the Botanical Institute in Innsbruck consists – according to Thomas Kiebacher – of Tetraplodon angustatus. Anyway, the story is so remarkable that it is cited here :
„Den ersten Fund machte Arnold 1874 auf einem Holzdach in Habichen im Oetztal bei ca. 850m, den anderen im Mai 1929 ein Innsbrucker Gerichtsmediziner auf der Winkleralm über Absam bei Hall ca. 1400m. Ich erhielt von diesem einen menschlichen Oberarmknochen von einem dort gefundenem Skelett mit der Bitte, mit Hilfe der darauf gewachsenen Moose zu bestimmen, wie lange die Leiche dort gelegen hat. Neben spärlichen Resten von Funaria hygrometrica und Ceratodon purpureus fand ich einen großen, prächtig fruchtenden Rasen von Tayloria rudolphiana. Da diese Moose ihre optimale Entwicklung gewöhnlich im Jahr nach ihrer Ansiedlung erlangen und dieses Optimum offenbar im Vorjahr eingetreten war, schloss ich, dass die Blosslegung des Knochens durch Raubwild und wohl auch der vorangegangene Unfall oder Mord 1927 stattgefunden haben muss."
Finally, Koponen (1992) synonymized this species with T. rudolphiana "on morphological basis". Tayloria delavayi is found in Yunnan on trunks of oak in elevations between 3800 und 4400 m. Gams (1932) cites the collector v. Handel-Mazetti from a letter to him "auf Laubbäumen in 2200 – 3800 m Höhe). Koponen, however, regarded the disjunction as "remnants of an earlier wider range", thus coming back the relic theory of Gams and Herzog. She did not consider that the Alps were glaciated but Yunnan not.

The theory of a postglacial immigration from China is supported by the fact that the species lacks in the southern Alps and has a very uneven distribution in the northern Alps, is rare and lacks in many potential habitats. A long distance dispersal from China (which was not glaciated in the Pleistocene) is also supported by the relatively small range in the Alps. The alpine range is even smaller in other examples of disjunctions China – Alps such as Voitia nivalis, Tayloria hornschuchiana, or species with only local occurrence such as Dicranodontium asperulum, D. uncinatum, Campylopus gracilis, C. schimperi and others.

Distichophyllum carinatum Dix. & Nichols.

This species was collected by the authors in 1908 in the Zinkenbachklamm, a valley at the Wolfgangsee in Austria (Dixon 1908). They realized the floristic connections between the Alps and the Himalayas but were not able to identify their material with one of the Asian species of Distichophyllum. Interestingly, they just described this species as new and although they realized the tropical affiliation of the species, they avoided any speculations about its origin.
Loeske (cited after Gams 1928) supposed a distribution with volcanic dust, and Gams (1928) proposed the Azores as origin. In fact, the species was new to science and not described from any other place in the world. In 1952, Josef Futschig discovered this species in three nearby localities in the Alps of the Allgäu (Futschig 1954), where it still exists, whereas the species has no more be found since 1978 in Austria. Additionally it was found once in Switzerland (cf. Grims 1999) and thus is one of the rarest species in Europe. For more than sixty years it was regarded as species endemic to the Alps. later, it was reported from Japan (Takaki 1951 cf. Grims 1999) and China (Redfearn et al. 1994, Lin & Tan 1995).

Brotherella lorentziana (Lor.) Loeske

This species was discovered by Molendo in three localities in the northern Alps and described by Lorentz as Hypnum lorentzianum. Later the species was collected in Austria, too. Its systematic placement is still discussed, at first by Herzog (1920), who published a discussion which was as long as useless. It was placed in Heterophyllium by Roth, by Kindberg in Rhaphidostegium, by Brotherus in Stereodon und recently by Buck in Pylaisiadelpha. Loeske transferred it to Brotherella. The species was almost forgotten until Herzog (1920) collected it in several additional sites in the northern Alps and in one locality in the Black Forest. Lotto & Lotto (1973) added many new records. Ochsner (1951) reported the species for Switzerland.
Considering the fact that Tayloria rudolphiana as well as Distichophyllum carinatum occur not only in the Alps but also in China, the “Moss Flora of China” (Wu et al. 2008) has been used to identify material of Brotherella lorentziana from the Alps. The identification ended with Brotherella henonii (Duby) Fleisch., which could be confirmed by comparison with herbarium material. The species is widespread from Japan to the Himalaya on soil covered rocks, soil and rotten log. Brotherella henonii was described as Hypnum henonii in 1877. Therefore B. lorentziana has priority (as in the cases of Distichophyllum carinatum and Tayloria rudolphiana reflecting the earlier exploration of the Alps. An official synonymization is not made since the type of B. henonii has not be studied. Interestingly the plants from Asia look somewhat different, more compact, in appearance much like Hypnum cupressiforme, however, the anatomical details of the leaves are fully identical (see figs. 1-2). A similar effect was reported by Koponen (1992) comparing Tayloria rudolphiana and T. delevayi, which may reflect differences between the populations due to a long lasting separation.

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Fig. 1 (top): Brotherella henonii, Higuchi 13213 (HIRO, hb. Frahm BONN).
Fig. 2 (below): Brotherella lorentziana, Frahm 9.9..73 s.n. (hb Frahm BONN)

At the present state of knowledge, the following species are still known as endemic in the Alps:

Barbula bicolor
Marsupella ramosa
~~Trochobryum carniolicum,~~

Herbertus sendtneri (Nees) Lindb.
Like Tayloria rudolphiana or Brotherella lorentziana, this species was also regarded as relic from the last interglacial period (Gams 1930). The present localities are interpreted as nunatakker, since the species is not found in valleys. The explanation of the range is highly hypothetical ("Die Einwanderungsgeschichte….stelle ich mir so vor…".) and long distance dispersal generally is neglected. Frey (in Frey et al. 2006) calls it a "interglacial relict of last glacial period" (whatever this means, possibly a relic from the last interglacial). Considering the discovery of Herbertus stramineus in Alaska and the synonymization of H. borealis with H. delavayi from the Himalaya, it cannot b e excluded that H. sendtneri occurs somewhere else in the world.

Riccia breidleri Jur.
This species characteristic for alpine lakes seems to be a true alpine endemic species but one can imagine that it can also occur e.g. in Mongolia or the Altai region, from where many bryophytes and especially Higher Plants colonized the Alps after the last glaciation.

In contrast to Distichophyllum carinatum, Brotherella lorentziana or Tayloria rudolphiana, the latter species are true alpine and not montane species. Generally, a time span of 10.000 years seems not sufficient to generate an endemic species, in the Alps or wherever else, considering the age of bryophyte species, with present species known in Dominican and Baltic amber with an age of 20-45 mio years. The fact that most so called species endemic to the Alps have a wider range in Asia raises the question how and when these species were dispersed. The fact that the Alps were glaciated and Asia not allows the conclusion that the dispersal went from East to West, however, when and how remains unsolved. Gams postulated a migration of rock inhabiting alpine species from the interior of Asia through the steppe regions along soil cliffs of rivers without considering long distance dispersal.

Literature

Abramov, J.J., Abramova, A.L. 1983. Conspectus of the Moss Flora of Mongolia. Leningrad (in Russian).
Brotherus, V.F. 1926. Laubmoose in: Die Natürlichen Pflanzenfamilien Bd. 10, Jena.
Dixon, H.N. 1909. Distichophyllum carinatum Dixon et Nicholson, a species and genus of Mosses new to Europe. Revue bryol. 36: 21-26.
Frahm, J.-P. 2012. The taxonomic status of Leptodontium styriacum (Jur. ex Geh.) Limpr. Archive for Bryology 141: 1-4.
Frey, W. 2006. Liverworts in: Frey, W., Frahm, J.-P., Fischer, E., Lobin, W. The liverworts, Mosses and Ferns of Europe. Martins (Harley Books).
Futschig, J. 1954. Distichophyllum carinatum Dixon et Nicholson in den Allgäuer Alpen. Ber. Bayer. Bot. Ges. XXX (1954): 15-18.
Gams, H. 1928. Brotherella lorentziana (Molendo) Loeske und Distichophyllum carinatum Dixon et Nicholson. Ein Beitrag zur kausalen Erfassung engbegrenzter Moosareale. Annales Bryologici 1: 69-78.

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Gams, H. 1930. Schisma sendtneri, Breutelia arcuata und das Rhacomitrietum lanuginosi als ozeanische Elemente in den Nordalpen. Beiträge zur analytischen Behandlung von Moosarealen III. Revue Bryologique N.S. 3: 12-19.

Gams, H. 1932. Die Verbreitung einiger Splachnaceen und des Oreas martiana in den Alpen.. Annales Bryologici 5: 51-68.

Gams, H. 1955. Zur Arealgeschichte der arktischen und arktisch-oreophytischen Moose. Feddes Repertorium 58: 80-92.

Grims, F. 1999. Die Laubmoose Österreichs. Cataklogus Florae Austriae II. Bryophyten (Moose) Heft 1 Musci. Österr. Akad. Wiss. Wien, 419 pp.

Herzog, Th. 1920. Hypnum lorentzianum, eine bryogeographische Skizze. Kryptogamische Forschungen (München) 1 (1): 345-353.

Herzog, Th. 1926. Geographie der Moose. Jena.

Koponen, A. 1992. European Asiatic connections in Tayloria (Splachnaceae, Musci). Bryobrothera 1: 57-62.

Lin, P.J. & Tan, B.C. 1995. Contribution to the bryoflora of China (12): a taxonomic revision of Chinese Hookeriaceae (Musci). Harvard Papers in Botany 7: 25-68. 39 fig.

Lotto, H., Lotto, R. 1973. Zur Verbreitung von Brotherella (Mol.) Loeske in der Bundesrepublik und in Österreich. Herzogia 3: 61-74.

Ochsner, F. 1951. Le Brotherella lorentziana (Mol.) Loeske en Suisse. Revue Bryol. Lichénol. 20: 299.

Redfearn, P.L. Jr., Allen, B. & He, S. 1994. New distributional records for Chinese Mosses. The Bryologist 97(3): 275-276.

Wu, P.-C., Crosby, M.R., He, S. 2008. Moss Flora of China, English Version. Vol. 8. – Bejing & St. Louis.

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