Range extensions for the rare moss Plagiothecium handelii, and its transfer to the resurrected genus Ortholimnobium

Authors: Wynns, Justin T., and Schröck, Christian

Source: Lindbergia, 41(1)

Published By: Dutch Bryological and Lichenological Society and Nordic Bryological Society

URL: https://doi.org/10.25227/linbg.01087
Range extensions for the rare moss *Plagiothecium handelii*, and its transfer to the resurrected genus *Ortholimnobium*

Justin T. Wynns and Christian Schröck

*J. T. Wynns (jwynns@hotmail.com), Natural History Museum of Denmark, Øster Farimagsgade 2D, opg. E, 3, DK-1353 Copenhagen, Denmark. – C. Schröck, Upper Austrian National Museum, Biology Center, Dept of Botany, Linz, Austria.*

*Plagiothecium handelii* is newly recorded for Europe (Austria and Romania) and eastern North America (Tennessee, USA). This dainty species was previously known only from Yunnan and Sichuan Provinces, China. Morphologically, the disjunctive populations belong to a single species. A 27-taxon phylogeny of *Plagiothecium* based on nuclear ITS and plastid *rpl*16 intron DNA sequence data resolved Austrian and Chinese populations of *P. handelii* as sisters, in a clade with *P. paleaceum*, a julaceous Himalayan species with cochlearsiform leaves. In contrast, *P. handelii* is a filiform plant with distant, ovate-acuminate leaves. In sequence identity the three terminals have a similar level of variation, suggesting that the geographic disjunction between the two populations of *P. handelii* is quite old. Morphologically and genetically the clade is a well defined lineage (*Ortholimnobium*) that is transitional between *Plagiothecium s.str.* and *Struckia*. The new combinations *O. paleaceum* and *O. handelii* are made. In Europe, *O. handelii* should be classified as vulnerable.

*Plagiothecium handelii* Broth. is a poorly known pleurocarpous moss. It was described by Brotherus (1929) from several collections made by Heinrich von Handel-Mazzetti in northwestern Yunnan Province, China, in 1915 and 1916. It resembles an etiolated form of *P. cavifolium* (Brid.) Z. Iwats. with concave, ovate-acuminate leaves with attenuate tips. It differs from the latter species in its pseudo-stipitate habit, narrower leaf cell net, and cortical hyalodermis composed of rectangular stem cells that detach with the leaves alongside the large leaf decurrencies that are typical of the genus (Fig. 1). In these respects, *P. handelii* also resembles an etiolated form of the closely related Sino-Himalayan species *P. paleaceum* (Mitt.) A. Jaeger, which differs in its slightly larger stature and broader, circular-ovate, concave-cochlearsiform leaves. The erect sporophytes of *P. handelii* and *P. paleaceum* are also very similar.

In the course of a recent phylogenetic study of *Plagiothecium* Bruch & Schimp. (Wynns et al. in press), the first author received several collections of a delicate, feltlike moss collected by the second author in Austria and identified by him as *Plagiothecium cavifolium* var. *gracile* Breidl. After comparison with several collections of *P. handelii* from Yunnan, China, including three syntypes, we identified the Austrian moss as the latter species. A herbarium study of global collections of *Plagiothecium* (Wynns 2015) uncovered additional specimens of *P. handelii* from Romania and the eastern United States.

Collections of *Plagiothecium handelii* from Austria and China were included in Wynns et al.’s molecular study of the genus. Here, we performed phylogenetic analyses of combined nuclear ITS and plastid *rpl*16 intron DNA sequence data from 27 collections of *Plagiothecium* and related pleurocarpous mosses (Table 1), in order to establish the conspecificity of Chinese and Austrian populations of *P. handelii*, and to place the species in a phylogenetic framework.

**Methods**

For the DNA analyses we included 20 collections of *Plagiothecium* (sensu Zuo et al. 2011), six collections of other Plagiotheciaceae (*Isopterygiopsis* Z. Iwats. and *Platydictya* Berk.), and one collection of *Fabronia pusilla* Raddi, which was used as the outgroup (Table 1). DNA extraction, PCR amplification and DNA sequencing were performed with the protocol of Wynns et al. (in press). Sequence alignment was performed manually in MEGA4 (Tamura et al. 2007). Next, indel data were generated for each alignment in SeqState ver. 1.4.1 (Müller 2005) using simple indel coding (Simmons and Ochoterena 2000). A single data file including both nucleotide and indel data for each DNA region was assembled in NEXUS format and analyzed by maximum parsimony (branch-and-bound search) in PAUP ver. 4.0.10b (Swofford 2002). A bootstrap (BS) analysis was also performed (2000 replicates) using branch-and-bound. A partition homogeneity test was performed (1000 branch-and-bound replicates),
to confirm that the two data sets were congruent and appropriate for a combined analysis.

In addition to the parsimony analysis, a Bayesian analysis was performed using the program MrBayes ver. 3.2 (Ronquist et al. 2012). The data were divided into four partitions, two of nucleotide sequence data (rpl16 and ITS) and two respective partitions of binary indel data. The partitions were unlinked and were allowed to evolve at different rates. Based on the Akaike information criterion and the results of the hierarchical likelihood ratio tests, the program Modeltest ver. 3.06 (Posada and Crandall 1998), selected the K81uf+I+Γ (Kimura 1981) model of DNA sequence evolution. However, this model is not implemented in MrBayes, so for the nucleotide data partitions we used the GTR+I+Γ model (cf. Lecocq et al. 2013), which in fact had the best overall log likelihood score. For the indel data partitions the default model was used, a Γ-shaped rate variation was assumed (Yang 1993), and the coding bias was set to variable. A Markov chain Monte Carlo (MCMC) analysis was then run for 11 000 000 generations under the default settings. The results of the Bayesian analysis including posterior probability (PP) support values were visualized as a 50%-compromise phylogram based on average branch lengths using the program TreeGraph 2.1.0-386 beta (Stöver and Müller 2010).

Results

The rpl16 data set included 986 characters, of which 54 were indel characters. The ITS data set included 682 characters, of which 22 were indel characters. Thus, the molecular analyses included 1744 characters in total, of which 1668 were nucleotide characters and 76 were indel characters (4.4%);
Table 1. Specimens used in the DNA study. Barcode numbers are for the herbaria where the specimens are housed. Herbarium acronyms are from Index Herbariorum (Thiers, continuously updated). The last two columns are GenBank accession numbers. *We lacked an ITS sequence for Ortholimnobium paleaceum, and substituted a consensus of two Chinese O. paleaceum ITS sequences from GenBank.*

| Taxon | Collection number | Locality | Herb. | Barcode | ITS | rpl16 |
|-------|-------------------|----------|-------|---------|-----|-------|
| Fabronia pusilla Raddi | Hedenäs s.n. | Italy | S | B184347 | KY550326 | KY514032 |
| Isoterygiopsis alpicola (Lindb.) Hedenäs | Mogensen 90-65 | NU | C | KY997058 | MF001281 |
| l. muelleriana (Schimp.) Z. Iwats. | Frahm 2009593 | Austria | BONN | KY550334 | KY514040 |
| l. muelleriana (Schimp.) Z. Iwats. | Long 38040 | Scotland UK | E | E00387921 | KF882224 | KF882234 |
| l. muelleriana (Schimp.) Z. Iwats. | Wynns 3404 | NC USA | C | CP0010615 | KY550335 | KY514041 |
| l. pulchella (Hedw.) Z. Iwats. | Lenz 3027 | CA USA | UC | 1947397 | KY550336 | KY514042 |
| Ortholimnobium handelii (Broth.) n. comb. | Long 34930 | Yunnan China | E | E00387864 | KF882223 | KF882333 |
| O. handelii (Broth.) n. comb. | Schröck 17477 | Austria | C | CP0010623 | KY550290 | KY513995 |
| O. paleaceum (Mit.) n. comb. | Long 22443 | Sikkim India | E | E00387897 | HQ665452/3 | KY514020 |
| Plagiothecium caviolium (Brig.) Z. Iwats. | Wynns 2960 | Germany | C | CP0010620 | KF882226 | KF882236 |
| P. caviolium (Brig.) Z. Iwats. | Wynns 3313 | NC USA | C | CP0010618 | KY550269 | KY513974 |
| P. curvifolium Schleph. ex Limpr. | Wynns 1939 | Denmark | C | CP0010515 | KF882227 | KF882237 |
| P. denticulatum (Hedw.) Schimp. | Wynns 2081 | Denmark | C | CP0010611 | KF882229 | KF882239 |
| P. denticulatum var. obtusifolium (Turner) Moore | Wynns 2842 | Germany | C | CP0010626 | KF882230 | KF882330 |
| P. draytonii (Sull.) E.B. Bartram | Hoe 3557 | WI USA | C | KF882231 | KF882231 |
| P. eurypodium (Cardot & Thér.) Z. Iwats. | Mizutani 15227 | Japan | S | KY550289 | KY513994 |
| P. eurypodium (Cardot & Thér.) Z. Iwats., var. | Long 36218 | Yunnan China | E | E00387874 | KF882232 | KF882232 |
| P. laetum Schimp. | Wynns 2907 | Germany | C | CP0010628 | KF882234 | KF882234 |
| P. latebricola Wilson ex Schimp. | Goldberg s.n. | Denmark | C | KF882235 | KF882235 |
| P. neckeroides Schimp. | Schwarz 3783 | Philippines | BONN | KY550305 | KY514010 |
| P. neckeroides var. myurum Molendo | Shevock 26916 | Yunnan China | UC | 1921123 | KF882236 | KF882236 |
| P. undulantum (Hedw.) Schimp. | Wynns 2050 | Denmark | C | CP0010639 | KF882245 | KF882245 |
| Platyticta jungermannioides (Brig.) H.A. Crum | Shevock 32476 | CA USA | UC | 1933747 | KY550338 | KY514044 |
| Rectibezicum piliferum (Sw.) Hedenäs & Huttunen | Shevock 26205 | WA USA | UC | 1782403 | KF882240 | KF882340 |
| R. piliferum (Sw.) Hedenäs & Huttunen | B.R.C.C.E. 238 | Karelia Russia | Russia | KY550315 | KY514021 |
| Struckia argentata (Mitt.) Müll. Hal. | Shevock 25571 | Yunnan China | NY | KY550339 | KY514045 |
| S. enervis (Broth.) Ignatov, T.J. Kop. & D.G. Long | Moscos of USSR 15 | Altai Russia | NY | KY550340 | KY514046 |

1384 characters were constant, 153 were variable but not parsimony-informative and 207 were parsimony-informative (20.6% variable characters). The strict consensus of two equally-parsimonious trees of 550 steps was well-resolved, with consistency index (CI, Kluge and Farris 1969) = 0.735, CI excluding uninformative characters = 0.627, retention index = 0.790, and rescaled consistency index = 0.581 (Farris 1989). The 50%-compromise Bayesian tree (Fig. 2) was identical to the parsimony tree in topology, with an additional unsupported node. The results of the partition homogeneity test (p = 0.190) indicated that the plastid and nuclear data sets reflect the same underlying phylogeny.

The two populations of Plagiothecium handelii formed a clade (BS = 79, PP = 0.88) that was sister to P. paleaceum (BS = 100; PP = 1). This clade was sister (BS = 100, PP = 1) to a Struckia Müll. Hal. sensu Ignatov et al. (2007) clade. The branches leading to these clades were relatively long (Fig. 2). All together, this early-diverging clade (Struckia sensu Huttunen et al. 2013) was intercalated between P. piliferum (Sw.) Schimp. and the rest of Plagiothecium.

The two populations of Plagiothecium handelii had some variation in both DNA regions (cf. Fig. 2). In ITS, the Chinese population had two autapomorphic transitions and four synapomorphic changes, while the Austrian population had a single synapomorphic transversion. In rpl16, the Chinese population had three autapomorphic changes (one transversion and two transitions) as well as two synapomorphic changes, while the Austrian population had a single autapomorphic transition. In the Chinese population, rpl16 included a variable 10–21 base pair insertion that was also present in P. laetum Schimp., P. draytonii (Sull.) E.B. Bartram, P. paleaceum, P. piliferum from Russia, Isoterygiopsis pulchella (Hedw.) Z. Iwats. and I. alpicola (Lindb.) Hedenäs (Table 1).

Discussion

When Brotherus (1929) described Plagiothecium handelii from Yunnan, he was not aware that the same plant had been recorded much earlier from the Alps by Lorentz (1860: 24), who described a delicate, distinctly flagelliform form of P. sylvaticum (Brid.) Schimp. growing in dark fissures, with narrow, almost knife-shaped leaves. Subsequently, Molendo (1865: 173) described P. sylvaticum var. laxum from Zwingsteg, Freiberg near Oberstdorf, Germany: “Forma cavernarum ut in omnibus analogous eximia longitudine axium et internodiorum; cespite laxissimo, e caulibus pro maxima parte flagelliformibus contexto.” Finally, Breidler (1892) described P. roeseanum (Brid.) Schimp. growing in dark fissures, with narrow, almost knife-shaped leaves. Subsequently, Molendo (1885) described P. sylvaticum var. gracile growing between boulders in Alpine woods and cited numerous Austrian localities. Plagiothecium handelii has concave leaves and microscopically could be taken for a small form of the polymorphic, circumboreal species P. caviolium [= P. roeseanum Schimp., P. sylvaticum (Brid.) Schimp. pro parte]. This similarity is apparently the reason that P. handelii has been overlooked in Europe.

In Austria, Plagiothecium handelii colonizes humus-rich, cool and moist scree slopes in the montane belt dominated by spruce forests. It occurs in small cavities filled by humus under boulders (Fig. 1, A). The bedrock is mostly...
granite, gneiss or schist. Other plants found at these sites include ferns, Lycopodium annotinum L., Vaccinium myrtillus L., and bryophytes characteristic of montane boulder-rich forests such as Hylocomium splendens (Hedw.) Schimp., Plagiochila asplenioides (L.) Dumort., P. porelloides (Torr. ex Nees) Lindenb., Polytrichum formosum Hedw., P. longisetum Sw. ex Brid., Plagiothecium denticulatum (Hedw.) Schimp., P. succulentum (Wils.) Lindb., Rhytidium rugosum (L.) Warnst., R. subpinnatum (Lindb.) T.J. Kop., and R. triguestrus (Hedw.) Warnst. In contrast, P. neckeroides Schimp., which also has a main distribution in Asia and occurs disjunctly in the Alps, grows in colder, more dynamic sites with larger boulders on the same mountainsides. Unlike P. neckeroides, P. handelii also grows on (less acidic) shale, and thus the distribution of P. handelii in Europe is likely to be slightly wider.

The sister relationship between the Chinese and Austrian populations of Plagiothecium handelii that was found in the molecular analyses (Fig. 2) corroborates their conspecificity. Although the populations from Romania and USA were not included in the molecular sampling, the unusual growth form of this species (felt-like mats of etiolated stems, cf. Fig. 1, A, B) is quite easy to recognize, so we have confidence in their identity. Plagiothecium handelii thus has an unusual distribution pattern. While there are several bryophytes that occur disjunctively between the Alps and the Sino-Himalayan region, including P. neckeroides, Distichophyllum carinatum Dixon & W.E. Nicholson (Dixon and Nicholson 1909, Redfearn et al. 1994), Tayloria rudolphiana (Garov.) Bruch & Schimp. (Koponen 1992), and (possibly) Brotherella lorentziana (Molendo ex Lorentz) Loeske (Frahm 2013), none of these species occur disjunctly in the eastern USA. Similarly, some bryophytes occur disjunctly between the eastern USA and southwest China, for example Entodon macropodus (Hedw.) Müll. Hal. (Iwatsuki and Sharp 1967), Brotherella leana (Sull.) Müll. Hal., Grimmia pilifera P. Beauv. and Acroprosopsis ciliata (Mitt.) Schiffn. (Iwatsuki 1972), but these species are not found in Europe. This suggests either the European or American populations of P. handelii may have arisen through long-distance dispersal (cf. Frahm 2013).

On the other hand, Plagiothecium handelii is a dioicus species that is seldom collected in fruit, reducing the likelihood of dispersal by spores. Furthermore, it is restricted to pristine habitats which apparently have a similar ecology at all of the stations. Also, the plants occur in discontinuous localities, both in Europe and America. Last, the relatively large genetic divergence (Fig. 2) between Austrian and Chinese collections is suggestive of a very old disjunction. These facts support a hypothesis that extant populations of P. handelii are relicts of a pre-Pleistocene flora that once had a much broader distribution (Steere 1937, Iwatsuki 1972, Schuster and Damsholt 1974, Manos and Stanford 2001, Hedenäs 2008, Patiño et al. 2016). We believe this explanation is more likely. Many authors (Herzog 1926, Schuster 1983, Schönswetter et al. 2005, Müller 1994, Schönswetter et al. 2005, Damsholt 2013) suggest that certain small Alpine localities must have remained uncovered during the Pleistocene glaciations and thus served as refugia for older floras.

Phylogenetic position of Plagiothecium handelii

The sister relationship between Plagiothecium handelii and P. paleaceum was first identified by Zuo et al. (2011), as was the sister relationship between this lineage and Struckia. Huttunen et al. (2013) subsequently transferred P. handelii and P. paleaceum to Struckia. Wynns et al. (in press) found P. handelii and P. paleaceum morphologically closer to
Plagiothecium than to Struckia, and like Zuo et al. they included Struckia in Plagiothecium.

Struckia sensu Ignatov et al. (2007) includes two species. Struckia argentata (Mitt.) Müll. Hal. is not uncommon on tree trunks in the Sino-Himalayan region, while S. enervis (Broth.) Ignatov, T.J. Kop. & D.G. Long occurs on rocks, and has a restricted distribution in boreal Asia with a discontinuous occurrence in southwest China (Tan et al. 1990, Hedenäs 1996). Struckia differs from Plagiothecium in several respects. In general, species of Plagiothecium are prostrate satiny mosses with spreading leaves, whereas both species of Struckia are small erect mosses with appressed leaves and a shaggy appearance (produced by the long-attenuate leaf tips). Microscopically, the leaves are hardly decurrent in Struckia, while this is a defining feature of Plagiothecium. Also unlike Plagiothecium, the leaves in Struckia have a large number of quadrate alar cells (reminiscent of Entodon Müll. Hal.). Struckia argentata further differs from Plagiothecium in its epiphytic habit, denticulate upper leaf margins, and shiny, small-mouthed capsules with conic-mammillate opercula. On the other hand, S. argentata resembles the sympatric species P. handelii and P. paleaceum in having short erect capsules and ovate-acuminate, concave, subplicate leaves that are often subtended by cells of the cortical hyalodermis when detached.

Struckia enervis is peculiar in that it forms erect defoliated shoots topped with clusters of shortly ligulate, costate gamommae (reduced leaves) (cf. Abramova and Abramov 1981). The specialized morphology of S. enervis promotes vegetative spread and probably arose with the transition away from the epiphytic habitat. It is presumably the more derived species of Struckia (Tan et al. 1990).

Paraphyletic taxa are the real result of evolution (Hörandl 2006) and should not automatically be rejected as the basis for names. In this case Plagiothecium would be rendered paraphyletic by retaining P. handelii and P. paleaceum but excluding Struckia as a distinct genus that evolved rapidly under adaptive pressures associated with a change to epiphytic. This is a plausible hypothesis that is consistent with the morphological and genetic (Fig. 2) differences between Plagiothecium and Struckia. However, this classification hides the close relationship between the P. handelii + P. paleaceum clade and Struckia. Morphologically P. handelii and P. paleaceum share features of both genera and are clearly a transitional taxon that can itself be treated as a distinct genus. The type of the genus Ortholimnobium Dixon belongs to P. paleaceum (Enroth et al. 1992), so this name is available.

Taxonomy

Ortholimnobium Dixon. J. Bombay Nat. Hist. Soc. 39: 787. 1937.

Type species: O. borii Dixon. J. Bombay Nat. Hist. Soc. 39: 788, pl. 1, f. 15. 1937. Type: INDIA. Assam, Aka Hills, Piri, 2300 m, 17 November 1934, N. L. Bor 252 (BM).

Plants glossy, pseudo-stipitate; branches more or less terete, with cortical hyalodermis; leaves imbricate to distant, symmetric, ovate-acuminate, concave, weakly plicate, decurrent, with short narrow cells; capsules short, erect.

Included species:

Ortholimnobium paleaceum (Mitt.) C. Schröck & J.T. Wynns, comb. nov. Basionym: Stereodon paleacus Mitt. J. Proc. Linn. Soc., Botany, Suppl. 1: 103. 1859. Plagiothecium paleaceum (Mitt.) A. Jaeger. Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1876–77: 452 (Gen. Sp. Musc. 2: 518). 1878. Struckia paleacea (Mitt.) Hedenäs & Huttunen. Bot. J. Linn. Soc. 171(2): 344. 2013.

Lectotype (designated by Enroth et al. 1992). CHINA. Thibet, Yatsen tebo, 17000 ft., J. D. Hooker 1075, ex herb. Mitten (NY no. 00913410).

Syntypes: INDIA. Himalaya, Sikkim, Tonglo, 7–8000 ft., Hooker 1006, ex herb. Mitten (NY nos. 00913411, 00913412), Singalehah, 11000 ft., Hooker 1007 (NY nos. 00913413, 00913414, P no. PC0132613).

Enroth et al. (1992) reported that the lectotype specimen was probably collected by T. Thomsen, not J. D. Hooker. Here we have simply followed the information given by Mitten (1859), which corresponds with the label data.

Additional specimens examined: CHINA. Yunnan, Yangbi Co., vic. Dajuaping, on shaded boulder in ravine in mixed broadleaf-evergreen forest, 25.50°N, 99.59°E, 2800 m, 1 July 2004, P. L. Redfearn & Y.-G. Su 950 (ex SMS, DUKE no. 0156745, NY no. 1596230). INDIA. NO-Indien, Darjeeling, Tiger Hill, an Felsen, 2800 m, 18 March 1909, M. Fleischer B 3270 p.p. (ex B, DUKE no. 0159613), Sikkim, West Distr., Rathong Chhu Valley, on mossy boulder in Quercus lamelloa forest, 27°24′N, 88°12′E, ca. 2315 m, 8 July 1992, D. G. Long 22443 (E no. E00387897).

NEPAL. Sankhuwasabha Distr., E bank of Saldim Khola, near bridge, on bank under stump in mossy Tsuga forest, 27°46′N, 87°16′E, ca. 2920 m, 12 Oct 1991, D. G. Long 21152 (E no. E00387890).

Ortholimnobium handelii (Broth.) C. Schröck & J.T. Wynns, comb. nov. Basionym: Plagiothecium handelii Broth. Symbolae Sinicae 4: 115. 1929. Struckia handelii (Broth.) Huttunen & Hedenäs. Bot. J. Linn. Soc. 171(2): 344. 2013.

Lectotype (designated here): CHINA. NW Yunnan, Am Wegrand auf Schieber im tp. Regenwalde des Doyon-lumba am Salwin, 28°2’, 3150 m, 23 Sep 1915, c. fr., Diar. Nr. 1536, H. F. von Handel-Mazzetti 8314 (S no. B160040!, islectotypes H no. H3112713, P no. PC0132634).

Syntypes: CHINA. NW Yunnan, In Tannenwäldern auf dem Nguka-la sw von Dschungden ("Chungtien") auf Diabas, 3750–3800 m, 25 Aug 1915, Diar. Nr. 1429, Handel-Mazzetti 7817 (E no. E00049113!, H no. H3112711, P no. PC0132633, S nos. B160036!, B160038!, US no. 00070394), In Tannenwäldern der ktp. St. unter dem Doker-la an der tibetischen Grenze auf Granit, 28°15′N, 28°15′W, Wegrand auf Schiefer im tp. Regenwalde des Doyon-lumba, 27°30′N, 27°49′E, ca. 2920 m, 5 July 1916, Diar. Nr. 1768, Handel-Mazzetti 9339 (H no. H3112714).
Plagiothecium roeseanum var. gracile Breidl. Mitteilungen der Naturwissenschaftlichen Vereines für Steiermark 28: 195. 1891. Plagiothecium roeseanum fo. gracile (Breidl.) Jedl. Spisy Vydávané Přírodovědeckou Fakultou Masarykova University 308: 37. 1948.

Lectotype (designated here): AUSTRIA. Steiermark, bei Schladming, Wäld am Rissachfall [Riesachfall], 1080 m, 30 July 1876, sub P. denticulatum, P. roeseanum var. gracile (GJO 0071175).

Syntypes (all leg. and det. J. Breidler as P. roeseanum var. gracile): AUSTRIA. Salzburg, Pinzgau, 12–1500 m, Wäld am Krinmler Fall, 1879, sub P. denticulatum (GJO 0071166), Felstrümmerwerk im Walde in der Ammerthaler Öd n. Mittersill, 1884, leg. P. roeseanum var. tenellum (GJO 0071164), Steiermark, bei Schladming. Wäld unterhalb der Ursprunghal in der Sölk, 2100 m, 1884, leg. J. Breidler, sub P. roeseanum var. tenellum (GJO 0071173), Ostabdachung des Knallstein in der Sölk, 2100 m, 1884, leg. J. Breidler, sub P. roeseanum fo. erecta (GJO 0071156), Vorarlberg, Montafon, NW-hang, Fichtenwald, Blockwerk, Silikat, 46.96°N, 10.08°E, ca 1372 m, 10 Aug 2010, C. Schröck 17477 (C no. CP0010623), Allgäuer Alpen, Kleinwalsertal, valley of the Wildenhorn, 2011, C. Schröck 20284. CHINA: Yunnan Prov., Pe yen tsin, 3000 m, 1922, S. Ten s.n., sub P. paleaevum var. laxirete Dix. (S no. B192147), Fugong Co., E slope of Gaoligong Shan (Nu Jiang catchment), in mossy litter under bamboo, 27°03’14.6’’N, 98°45’10.7’’E, 3190 m, 13 Aug 2005, D. G. Long 34719 (E no. E00387866), N bank of North Fork Yamu River, between Shibali and Yaping Pass, steep hillside with dense Abies-Rhododendron-bamboo forest, on rotten stump, 27°12’03.4’’N, 98°42’48.3’’E, 3230 m, 17 Aug 2005, D. G. Long 34930 (E no. E00387860). ROMANIA: Transylvania, montes Biharegység, in rubus umbrosis vallis Drăgăneșului par. pag. Poieni, L. Vajda s.n., 6 July 1963, sub P. roeseanum fo. tense Jedl. (C no. C-M-9099). UNITED STATES: Tennessee, Roane Co., Cumberland Plateau, Rockwood, Mammys Creek, on peaty soil, 1500 ft., 6 Oct 1929, A. J. Sharp 36, sub P. roeseanum, ex hb. Grout (DUKE no. 78475), Sevier Co., Great Smoky Mountains National Park, Clingmans Dome, on humus of forest floor, 21 July 1959, L. E. Anderson 10524, sub P. cavifolium (DUKE no. 78480).

Additional specimens examined (in herb. Schröck where not otherwise indicated): AUSTRIA. Kärnten, Gössgraben, Karnthen, leg. J. Breidler, 1880, sub P. roeseanum var. tenellum, P. roeseanum var. gracile (GJO 0071168), Ritteralpbachfall, leg. J. Glowacki, 1903, sub P. roeseanum var. gracile (GJO 0071152), Niederösterreich, Aspanger Klause, 1882, leg. K. Fehlner, sub P. nitidulum (GJO 0071165), Salzburg, Pinzgau, Hohe Tauern, Venediger-Gruppe, Krinmler Wasserfälle, 1999, C. Schröck 2456, Habichtal, Blockwerk, Humus, 47.19’’N, 12.35’’E, ca 1360–1500 m, 2000, C. Schröck 9209, 9375, Untersulzbachtal, 2001, C. Schröck 10944, 14499, 14502, 14503, 14504, 2014, C. Schröck s.n., Goldberg-Gruppe, Seidlwinkl, 1999, C. Schröck 2637, 4258, Granatspitz-Gruppe, Stubachtal, Ödbachtal, Blockwerk, Spalten, Gneis, 47.20’’N, 12.59’’E, ca 1050 m, 25 Aug 2000, C. Schröck 7920, Dorfer Öd, Blockwerk, Gneis, 47.18’’N, 12.58’’E, ca 1300–1400 m, 25 Aug 2000, C. Schröck 7921 (NY no. 02467330), Ammertherd Öd, Felstrümmerwerk im Walde, 1879, leg. J. Breidler, sub P. denticulatum, P. roeseanum var. tenellum (GJO 0071163), Zillertaler Alpen, Wildgerlosalt, 2001, C. Schröck 14500, Steiermark, Preuneggthal bei Schladming. Wäld unterhalb der Ursprungalm, 1880, leg. J. Breidler, sub P. roeseanum var. tenellum (GJO 0071173), Obstachung des Knallstein in der Sölk, 2100 m, 1884, leg. J. Breidler, sub P. roeseanum fo. erecta (GJO 0071156), Vorarlberg, Montafon, NW-hang, Fichtenwald, Blockwerk, Silikat, 46.96’’N, 10.08’’E, ca 1372 m, 10 Aug 2010, C. Schröck 17477 (C no. CP0010623), Allgäuer Alpen, Kleinwalsertal, valley of the Wildenhorn, 2011, C. Schröck 20284.

Plants bright green, delicate, pseudo-stipitate, in loose trailing felt-like mats over rock or humus. Rhizoids fasciculate, smooth, reddish-brown. Stems with cortical hyalodermis, often etiolated and threadlike with leaves poorly developed, or appearing thickened by small clasping leaves; branches frequent, somewhat flattened. Leaves distinct, or somewhat overlapping, 1–1.4 × 0.35–0.65 mm, concave, erect-spread, twisted when dry, shortly ovate-oblanceolate, weakly striate, acuminate with slender tip, clasping at base, decurrent; leaf margins entire, erect toward base; median leaf cells narrow, (75)85–125 × 7.5–10 µm; basal cells sometimes brownish; decurrent cells inflated, ovoid-rectangular, irregularly thick-walled, flaking thin-walled rectangular stem cortical cells that detach with leaves. Dioicus [fide Brothers 1929]. Seta orangish- or reddish-brown. Capsule erect or slightly inclined, cylindric, slightly constricted below mouth, not or weakly furrowed when dry, ca 1 mm long without lid. Operculum shortly rostrate. Annuulus present.

Variation

In general Ortholimnobium handelii is quite stenotypic. However, a form with wider cells occurs at high elevations. We noticed this both in Austrian (Breidler s.n., 2100 m, GJO 0071156) and American (Anderson 10524, ca 2000 m, DUKE no. 78480) populations. Occasional collections of most species of Plagiothecium s.l. have a laxer leaf areolation, perhaps in response to environmental factors.

Conservation

In Austria, Ortholimnobium handelii is apparently rare to scattered in mountainous areas with siliceous bedrock. It has a wider distribution than the sympatric Plagiothecium neckeroides, which is rare or absent in the western Alps. Most populations of O. handelii are not currently threatened, but the complex local climate of scree slopes can certainly be disturbed by road construction and logging. Although numerical population data are missing, O. handelii can be
categorized as VU D1 (Vulnerable) under current IUCN criteria, on the basis of small population sizes. Now that O. handelii is known to occur in Europe, future floristic studies should improve our knowledge of the frequency and distribution of this species.

Acknowledgements — We thank Kell Damsholt and Ken McFarland for providing information on bryophyte geography, and Conny Asmussen Lange, who supervised the first author’s PhD study in which the DNA sequence data were obtained. We also thank Derick Poindexter for helpful suggestions to improve the manuscript.

References

Abramova, A. L. and Abramov, I. I. 1981. De muscis endemicos URSS. 1. *Cephalodium zerovii* Lazar. – Novosti Sist. Nizsh. Rast. 18: 179–187.

Breidler, J. 1892. Die Laubmoose Steiermarks und ihre Verbreitung. – Mitt. Naturwiss. Vereines Steiermark 28: 3–234.

Brotherus, V. F. 1929. Musci. Symbolae Sinicae 4. – J. Springer.

Damsholt, K. 2013. The liverworts of Greenland. – Nordic Bryological Society.

Dixon, H. N. and Nicholson, W. E. 1909. *Distichophyllum carinatum* Dixon et Nicholson, a species and genus of mosses new to Europe. – Rev. Bryol. 36: 21–26.

Enroth, J., Koponen, T. and Li, X.-J. 1992. Contributions to the bryoflora of China 1. Taxonomic status of *Orbuloimmobium*. – Ann. Bot. Fenn. 29: 315–318.

Farris, J. S. 1989. The retention index and the rescaled consistency index. – Cladistics 5: 417–419.

Frahm, J. P. 2013. Are there endemic bryophyte species in the Alps? – The range of *Brotherella lorentziana* (Lor.) Loeske. – Arch. Bryol. 183: 1–7.

Hedenäs, L. 1996. On the taxonomic position of *Struckia* C. Müll. – J. Hattori Bot. Lab. 80: 241–245.

Hedenäs, L. 2008. Molecular variation and speciation in *Antitrichia curtipendula* s.l. (Leucodontaceae, Bryophyta). – J. Linn. Soc. 156: 341–345.

Hertog, T. 1926. Geographie der Moose. – Gustav Fischer.

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa—evolutionary versus cladistic classification. – Taxon 55: 564–570.

Huhtunen, S., Ignatov, M. S., Quandt, D. et al. 2013. Phylogenetic position and delimitation of the moss family Plagiotheciaceae in the order Hypnales. – Bot. J. Linn. Soc. 171: 330–353.

Ignatov, M. S., Milyutina, I. A., Koponen, T. et al. 2007. Taxyonomy of *Struckia* (Plagiotheciaceae, Bryophyta) based on morphological and molecular data. – Chenia 9: 117–125.

Iwatsuki, Z. 1972. Distribution of bryophytes common to Japan and the United States – In: Graham, A. (ed.), Floristics and Paleofloristics of Asia and eastern North America. – Elsevier.

Iwatsuki, Z. and Sharp, A. J. 1967. The bryogeographical relationships between eastern Asia and North America. – J. Hattori Bot. Lab. 30: 152–170.

Kimura, M. 1981. Estimation of evolutionary distances between homologous nucleotide sequences. – Proc. Natl Acad. Sci. USA 78: 454–458.

Kluge, A. G. and Farris, J. S. 1969. Quantitative phylogenetics and the evolution of anurans. – Syst. Zool. 18: 1–32.

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

Lecocq, T., Vereecken, N. J., Michez, D. et al. 2013. Patterns of genetic and reproductive traits differentiation in mainland vs Corsican populations of bumblebees, – PloS One 8(6): e65642.

Lorentz, P. G. 1860. Beitrage zur Biologie und Geographie der Laubmoose. – PhD thesis, Univ. of Munich.

Manos, P. S. and Stanford, A. M. 2001. The historical biogeography of Fagaceae: tracking the Tertiary history of temperate and subtropical forests in the Northern Hemisphere. – Int. J. Plant Sci. 162(6 suppl.): 577–593.

Mitten, W. 1859. Musci Indiae Orientalis, an enumeration of the mosses of the East Indies. – J. Proc. Linn. Soc., Bot., suppl. 1: 1–171.

Molendo, L. 1865. Moos-Studien aus den Allgäuer Alpen. Beiträge zur Phytogeographie. – Ber. Naturhist. Vereins Augsburg 18: 77–240.

Müller, Kai 2005. SeqState – primer design and sequence statistics for phylogenetic DNA data sets. – Appl. Bioinf. 4: 65–69.

Müller, Karl 1954. Die Lebermoose. – In: Dr. L. Rabenhorst’s Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, VI. Band, 1. Abgl., 3. Auflage. – Geest & Portig.

Patiño, J., Goffinet, B., Sim-Sim, M. and Vanderpoorten, A. 2016. Is the sword moss (*Bryoxiphium*) a preglacial Tertiary relict? – Mol. Phylogen. Evol. 96: 200–206.

Posada, D. and Crandall, K. A. 1998. Modeltest: testing the model of DNA substitution. – Bioinformatics 14: 817–818.

Redfearn, P. L., Jr., Allen, B. and He, S. 1994. New distributional records for Chinese mosses. – Bryologist 97: 275–276.

Ronquist, F., Teslenko, M., van der Mark, P et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – Syst. Biol. 61: 539–542.

Schuster, R. M. 1983. Phytogeography of the Bryophyta. – In: Schuster, R. M. (ed.), New manual of Bryology, vol. 1. – Hattori Bot. Lab.

Schuster, R. M. and Damsholt, K. 1974. The Hepaticae of West Greenland from ca 66°N to 72°N. – Meddel. Grønland 199: 1–373.

Schönswetter, P., Stehlík, L., Holderegger, R. et al. 2005. Molecular evidence for glacial refugia of mountain plants in the European Alps. – Mol. Ecol. 14: 3547–3555.

Simmons, M. P. and Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. – Syst. Biol. 49: 369–381.

Steere, W. C. 1937. *Bryoxiphium norvegicum*, the sword moss, as a preglacial and interglacial relict. – Ecology 18: 346–358.

Stöver, B. C. and Müller, K. F. 2010. TreeGraph2: combining and visualizing evidence from different phylogenetic analyses. – BMC Bioinf. 11: 7.

Swofford, D. L. 2002. PAUP* – Phylogenetic analysis using parsimony (*) and other methods) version 4.0.10b. – Sinauer.

Tamura, K., Dudley, J., Nei, M. et al. 2007. MEGA4: molecular evolutionary genetics analysis (MEGA) software ver. 4.0. – Mol. Biol. Evol. 24: 1596–1599.

Tan, B. C., Buck, W. R. and Ignatov, M. S. 1990. On the Himalayan *Struckia* C. Muell. and the Russian *Cephalodium Lazr.* (Musci, Hypnaceae). – Lindbergia 16: 100–104.

Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. <www.sweetgum.nybg.org/science/ih/> accessed 15 September 2017.

Wynnns, J. T. 2015. Molecular phylogeny and systematic revision of the pleurocarpous moss genus *Plagiothecium*. – PhD thesis, Univ. of Copenhagen.

Wynnns, J. T., Munk, K. R. and Lange, C. B. A. Molecular phylogeny of *Plagiothecium* and similar hypnalean mosses, with a revised sectional classification of *Plagiothecium*. – Cladistics doi: 10.1111/cl.12210.

Yang, Z. 1993. Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates differ over sites. – Mol. Biol. Evol. 10: 1396–1401.

Zuo, Q., Higuchi, M., Wang, Y.-F. et al. 2011. The status of *Struckia Müll.* Hal. (Plagiotheciaceae, Bryopsida) inferred from multiple nuclear and chloroplast loci. – J. Bryol. 33: 221–228.