BioOne COMPLETE

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

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Lindbergia 41: linbg.01087, 2018
doi: 10.25227/linbg.01087
© 2018 The Authors. This is an Open Access article
Subject Editor and Editor-in-Chief: Nils Cronberg. Accepted 13 October 2017

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 cochleariform 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-cochleariform 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),

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <http://creativecommons.org/licenses/by/4.0/>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

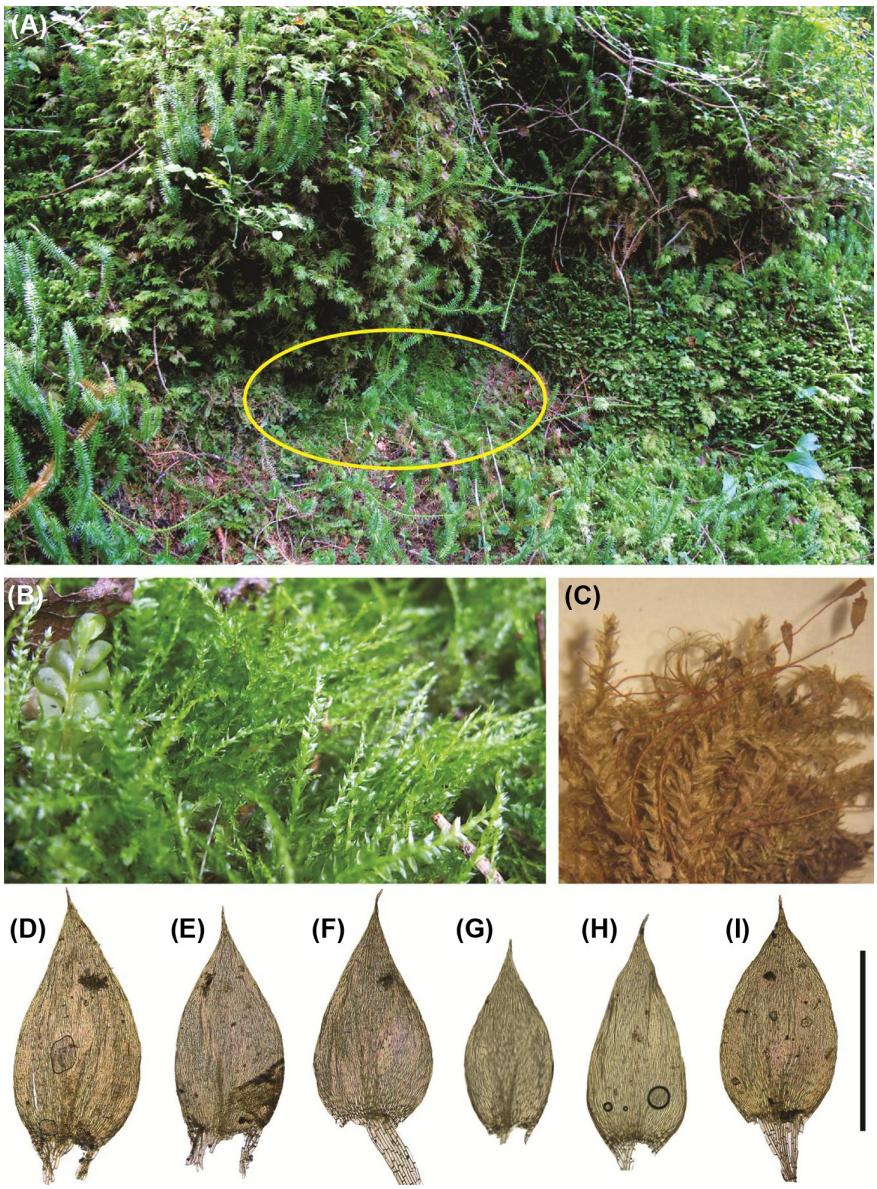


Figure 1. *Ortholimnobium handelii* (Broth.) C. Schröck & J.T. Wynns. (A) (in oval) and (B) in situ, Austria. (C) *Handel-Mazzetti 8314* (lectotype of *Plagiothecium handelii* Broth., S no. B160040). (D-I). Leaves: (D, E) *Handel-Mazzetti 7817*, Yunnan (syntype of *P. handelii*, S no. B160038); (F) *Long 34930*, Yunnan (E no. E00387864); (G) *Vajda s.n.*, Transylvania, Romania (C no. C-M-9099); (H) *Schröck 17477*, Austria (C no. CP0010623); (I) *Anderson 10524*, Tennessee, USA (DUKE no. 78480); scale bar = 1 mm.

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 (*rpl*16 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 hierarchichal 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 *rpl*16 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%);

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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
Isopterygiopsis alpicola (Lindb.) Hedenäs	Mogensen 90-65	NU	C		KY997058	MF001281
I. muelleriana (Schimp.) Z. Iwats.	Frahm 2009593	Austria	BONN		KY550334	KY514040
I. muelleriana (Schimp.) Z. Iwats.	Long 38040	Scotland UK	E	E00387921	KF882224	KF882324
I. muelleriana (Schimp.) Z. Iwats.	Wynns 3404	NC USA	C	CP0010615	KY550335	KY514041
I. pulchella (Hedw.) Z. Iwats.	Lenz 3027	CA USA	UC	1947397	KY550336	KY514042
Ortholimnobium handelii (Broth.) n. comb.	Long 34930	Yunnan China	E	E00387864	KF882233	KF882333
O. handelii (Broth.) n. comb.	Schröck 17477	Austria	C	CP0010623	KY550290	KY513995
O. paleaceum (Mitt.) n. comb.	Long 22443*	Sikkim India	E	E00387897	HQ665452/3	KY514020
Plagiothecium cavifolium (Brid.) Z. Iwats.	Wynns 2960	Germany	C	CP0010620	KF882226	KF882326
P. cavifolium (Brid.) Z. Iwats. s.l.	Wynns 3313	NC USA	C	CP0010618	KY550269	KY513974
P. curvifolium Schlieph. ex Limpr.	Wynns 1939	Denmark	C	CP0010515	KF882227	KF882327
P. denticulatum (Hedw.) Schimp.	Wynns 2081	Denmark	C	CP0010611	KF882229	KF882329
P. denticulatum var. obtusifolium (Turner) Moore	Wynns 2842	Germany	C	CP0010622	KF882230	KF882330
P. draytonii (Sull.) E.B. Bartram	Hoe 3557	HI USA	C		KF882231	KF882331
P. euryphyllum (Cardot & Thér.) Z. Iwats.	Mizutani 15227	Japan	S		KY550289	KY513994
P. euryphyllum (Cardot & Thér.) Z. Iwats., var.	Long 36218	Yunnan China	E	E00387874	KF882232	KF882332
P. laetum Schimp.	Wynns 2907	Germany	C	CP0010628	KF882234	KF882334
P. latebricola Wilson ex Schimp.	Goldberg s.n.	Denmark	C		KF882235	KF882335
P. neckeroideum Schimp.	Schwarz 3783	Philippines	BONN		KY550305	KY514010
P. neckeroideum var. myurum Molendo	Shevock 26916	Yunnan China	UC	1921123	KF882236	KF882336
P. undulatum (Hedw.) Schimp.	Wynns 2050	Denmark	C	CP0010639	KF882245	KF882345
Platydictya jungermannioides (Brid.) H.A. Crum	Shevock 32476	CA USA	UC	1933747	KY550338	KY514044
Rectithecium 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	BONN		KY550315	KY514021
Struckia argentata (Mitt.) Müll. Hal.	Shevock 25571	Yunnan China	NY		KY550339	KY514045
S. enervis (Broth.) Ignatov, T.J. Kop. & D.G. Long	Mosses 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 *rpl*16, the Chinese population had three autapomorphic changes (one transversion and two transitions) as well as three synapomorphic changes, while the Austrian population had a single autapomorphic transition. In the Chinese population, *rpl*16 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, *Isopterygiopsis 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 analogis eximia longitudine axium et internodiorum; cespite laxissimo, e caulibus prostratis pro maxima parte flagelliformibus contexto." Finally, Breidler (1892) described *P. roeseanum* 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. cavifolium* [= *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

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

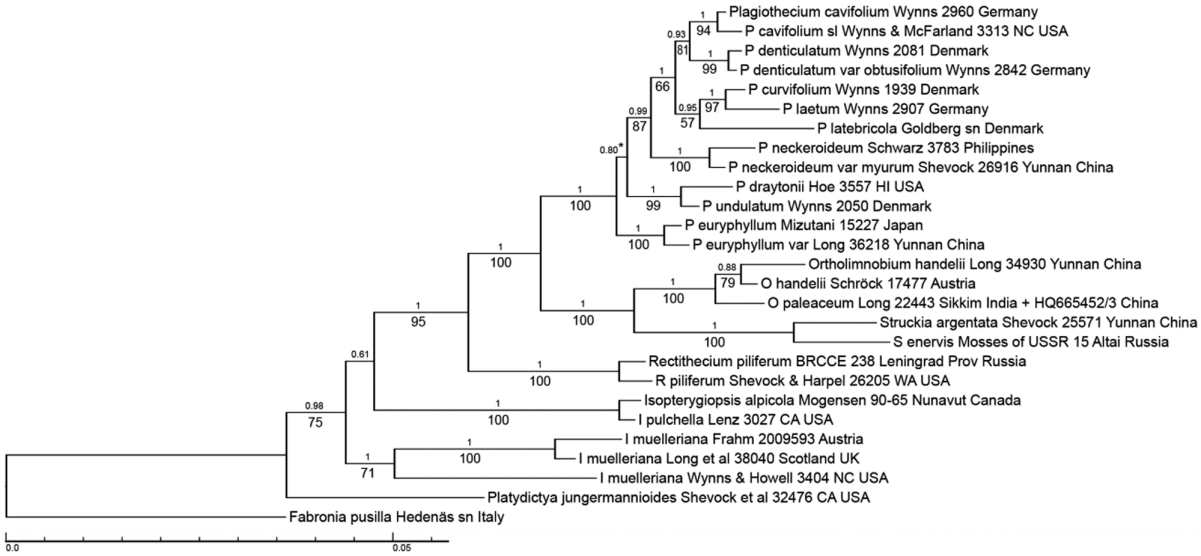


Figure 2. 50%-compromise phylogram based on average branch lengths generated from a Bayesian analysis of of plastid *rpl*16 intron and nuclear ribosomal ITS data from 27 collections of hypnalean mosses (Table 1). Gaps were coded as separate characters, using simple indel coding (Simmons and Ochoterena 2000). For *P. paleaceum*, we lacked an ITS sequence and substituted a consensus of two sequences from a public database (GenBank). Posterior probability support values are indicated above the branches, and bootstrap support values (2000 branch-and-bound replicates) from the parsimony analysis are indicated below the branches. The consensus parsimony tree (not shown) lacked one node (indicated with *), but was otherwise identical in topology. The node without a bootstrap value near the bottom of the tree was present in the parsimony tree but not in the bootstrap tree.

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., *Rhytidiadelphus loreus* (Hedw.) Warnst., *R. subpinnatus* (Lindb.) T.J. Kop., and *R. triquetrus* (Hedw.) Warnst. In contrast, *P. neckeroideum* Schimp., which also has a main distribution in Asia and occurs disjunctively in the Alps, grows in colder, more dynamic sites with larger boulders on the same mountainsides. Unlike *P. neckeroideum*, *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. neckeroideum*, *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 disjunctively in the eastern USA. Similarly, some bryophytes occur disjunctively between the eastern USA and southwest China, for example *Entodon macropodus* (Hedw.) Müll. Hal. (Iwatsuki and Sharp 1967), *Brothera leana* (Sull.) Müll. Hal., *Grimmia pilifera* P. Beauv. and *Acrobolbus ciliatus* (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 dioicous 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, Müller 1954, Schuster 1983, 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

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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 disjunctive 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 gemmae (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 epiphyty. 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 paleaceus* 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. Dajiuping, 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. 0156913), Sikkim, West Distr., Rathong Chhu Valley, on mossy boulder in *Quercus lamellosa* 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 Schiefer 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!, isolectotypes H no. H3112713, P no. PC0132634).

Syntypes: **CHINA**. NW Yunnan, In Tannenwäldern auf dem Nguka-la sw von Dschungdien ("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, 3800–4100 m, 17 Sep 1915, c. fr., Diar. Nr. 1502, *Handel-Mazzetti 8101* (H no. 3112712), An granit in der str. St. des birm. Mons. in der Seitenschlucht Naiwanglong des Djiou-djiang (e Irrawadi-Oberlaufes), 27°53′N, 2130 m, 5 July 1916, Diar. Nr. 1768, *Handel-Mazzetti 9339* (H no. 3112714).

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

= *Plagiothecium roeseanum* var. *gracile* Breidl. Mitteilungen der Naturwissenschaftlichen Vereines für Steiermark 28: 195. 1891. *Plagiothecium roeseanum* fo. *gracile* (Breidl.) Jedl. Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 37. 1948.

Lectotype (designated here): **AUSTRIA**. Steiermark, bei Schladming, Wald 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, Wald am Krimmler Fall, 1879, sub *P. denticulatum* (GJO 0071166!), Felstrümmerwerk im Walde in der Ammerthaler Öd n. Mittersill, 1879, sub *P. denticulatum* (GJO 0071164!), Steiermark, bei Schladming, Wald unterhalb der Ursprungalm im Preuneggthal, 1880 (GJO 0071157!), ca. 1300 m, 7 Aug 1876, sub *P. denticulatum* (GJO 0071174!), Unterthal, 1870, sub *P. sylvaticum* (GJO 0071171!), Felstrümmer beim Kreutzsteg [Kreuzsteg südlich Bräualm] b. St. Nikolai in der Sölk, 1200 m, 1883, sub *P. roeseanum* var. *tenellum* (GJO 0071176!), Seewieggraben bei Aich, 8–900 m, 1888, sub *P. roeseanum* var. *tenellum* (GJO 0071172!).

=? *Plagiothecium sylvaticum* var. *laxum* Molendo. Bericht des Naturhistorischen Vereins in Augsburg 18: 173. 1865.

Syntypes: **GERMANY**. Algäu, in Sandsteinklüften beim Zwingsteg 3100' nw. und am Freiberge 2800' nö, leg. *Molendo* [?].

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* distant, or somewhat overlapping, 1–1.4 × 0.35–0.65 mm, concave, erect-spreading, twisted when dry, shortly ovate- to oblong-lanceolate, 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, flanking thin-walled rectangular stem cortical cells that detach with leaves. Dioicous [fide Brotherus 1929]. *Seta* orangish- or reddish-brown. *Capsules* erect or slightly inclined, cylindric, slightly constricted below mouth, not or weakly furrowed when dry, ca 1 mm long without lid. *Operculum* shortly rostrate. *Annulus* present.

Additional specimens examined (in herb. Schröck where not otherwise indicated): **AUSTRIA**. Kärnten, Gössgraben, Kärnthen, 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, Krimmler Wasserfälle, 1999, *C. Schröck 2456*, Habachtal, 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, Seidlwinkltal, 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 7902*, Dorfer Öd, Blockwerk, Gneis, 47.18°N, 12.58°E, ca 1300–1400 m, 25 Aug 2000, *C. Schröck 7921* (NY no. 02467330), Ammerthaler Öd, Felstrümmerwerk im Walde, 1879, leg. *J. Breidler*, sub *P. denticulatum*, *P. roeseanum var. tenellum* (GJO 0071163), Zillertaler Alpen, Wildgerlostal, 2001, *C. Schröck 14500*, Steiermark, Preuneggthal bei Schladming, Wald unterhalb der Ursprungalm, 1880, 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 Wildenbach, 2011, *C. Schröck 20284*. **CHINA**: Yunnan Prov., Pe yen tsin, 3000 m, 1922, *S. Ten s.n.*, sub *P. paleaceum* 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. E00387864). **ROMANIA**: Transylvania, montes Biharhegység, in rupibus umbrosis vallis Drágánvölgy pr. pag. Poieni, *L. Vajda s.n.*, 6 July 1963, sub *P. roeseanum* fo. *tenue* 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).

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 neckeroideum*, 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

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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 endemicis URSS. 1. *Cephalocladium 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 *Ortholimnobium*. – 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). – Bot. J. Linn. Soc. 156: 341–354.

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

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

Huttunen, 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. Taxonomy 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 phyletics 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. Pattens of genetic and reproductive traits differentiation in mainland vs Corsican populations of bumblebees. – PloS One 8(6): e65642.

Lorentz, P. G. 1860. Beiträge 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.): S77–S93.

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. Abtlg., 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., Stehlik, I., 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 *Cephalocladium* Lazar. (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.

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

Wynns, 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/cla.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.

Downloaded From: https://complete.bioone.org/journals/Lindbergia on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use