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

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*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 *rpl16* 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. caviolium* (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 caviolium* 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 *rpl16* 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 Ortholimnobium ITS sequences from GenBank.

<table>
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<th>Taxon</th>
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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 Struckcia 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 (BS = 100, PP = 1) was sister (BS = 0.88) that was sister to a clade identified as P. sylvaticum 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 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 transition. In rp16, 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, rp16 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. pillerium from Russia, Isotheriopygia 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 caulius 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. cavitulum [= 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 Hylcomium splendens (Hedw.) Schimp., Plagiochila asplenioides (L.) Dumort., P. pellorooides (Torr. ex Nees) Lindenb., Polytrichum formosum Hedw., P. longisetum Sw. ex Brid., Plagiochilium denticulatum (Hedw.) Schimp., P. succulentum (Wils.) Lindb., Rhytiadiadelphus loreus (Hedw.) Warnst., R. subpinnatus (Lindb.) T.J. Kop., and R. triquestrus (Hedw.) Warnst. In contrast, P. nekeroidesum 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 mountain sides. Unlike P. nekeroidesum, 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 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. nekeroidesum, Distichophyllum carinatum (Dixon and 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 Acroblousciated (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 un covered 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 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 gamomae (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**


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:


Syntypes: INDIA. Himalaya, Sikkim, Tonglo, 7–8000 ft., Hooker 1006, ex herb. Mitten (NY nos. 00913411, 00913412), Singalehah, 11000 ft., Hooker 1007 (NY nos. 01596313, 01596314, 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.


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 0071166), Seewieggrab bei Aich, 8–900 m, 1888, sub P. roeseanum var. tenellum (GJO 0071172).


Syntypes: GERMANY. Algäu, in Sandsteinklüften beim Zwintegste 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 distinct, 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. 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. Annulus 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.

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