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WEISSIA EXSERTA (POTTIACEAE, BRYOPHYTA) IN RUSSIA

WEISSIA EXSERTA (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The present study deals with an identity of the rich and peculiar specimen of *Weissia* recently collected in the vicinity of Mondy settl. in Tunkinskaya valley of Buryatia. Morphologically it resembles *W. exserta* in possessing exserted cleistocarpous capsules with partly differentiated annuli, and opercula with long oblique beak; however, in having shorter leaves, cygneous setae and somewhat larger spores it differs from Japanese plants. Molecular barcoding with nrITS, cp *trn*L-F, rps4 and rbcL did not allow referring this specimen to any of the previously studied species, including *W. exserta*, represented in GenBank by Japanese specimens. Plants from Mondy are illustrated and compared with other Russian specimens assigned to *W. exserta*; their affinities are discussed.

Резюме

Обсуждается видовая принадлежность необычного образца *Weissia*, собранного недавно в окрестностях пос. Монды в Тункинской долине в Бурятии. Морфологически он похож на *W. exserta*, поскольку имеет поднятые над перихецием клейстокарпные коробочки с частично дифференцированным колечком и крышечкой с длинным косым клювиком, однако у него более короткие листья, дуговидно согнутая ножка и немного более крупные споры, что отличает его от растений из Японии. Молекулярное баркодирование с использованием nrITS, cp *trn*L-F, rps4 и *rbc*L не позволяет отнести этот образец ни к одному из ранее изученных с помощью этих маркеров видов, включая *W. exserta*, которая представлена в генбанке сиквенсами образцов из Японии. Для растения из Бурятии приведены иллюстрации и сравнение с другими образцами из России, отнесенными к *W. exserta*; обсуждаются их взаимоотношения с другими видами.

KEYWORDS: mosses, biodiversity, taxonomy, biogeography, Asia, DNA-barcoding

INTRODUCTION

DNA barcoding allows species identification in cases when underexplored morphological variability hampers fair assignment of specimen to any of the already known species, or supports a decision to describe a new species (Moritz & Cicero, 2004; Vijayan & Tsou, 2010; DeSalle & Goldstein, 2019). While collecting mosses in the foothills of Eastern Sayan Mountains (Southern Siberia, Republic of Buryatia), the first author met an unusual *Weissia*-like plants growing in abundance in dry steppe strongly disturbed by grazing (Fig. 1). In having exserted cleistocarpous capsules they resembled *W. levieri* (Limpr.) Kindb. and *W. exserta* (Broth.) P.C. Chen, especially the latter species, with which they share partly developed but not dehiscent opercula with long oblique beaks. However, due to the cygneous setae the plants from Sayan Mountains had an unusual appearance, first reminding *Microbryum curvicollum* (Hedw.) R.H. Zander. Microscopic studies also revealed that the plants from Sayan Mts have leaves shorter than in Japanese plants illustrated by Noguchi (1988), which are contorted rather than crisped when dry, and somewhat larger spores. Recent study by Inoue & Tsubota (2017) based on combination of rbcL and rps4, and Callaghan *et al*. (2019) based on combination of ITS and *trn*L-F showed a reasonable applicability of DNA markers for delimitation of cleistocarpous species of *Weissia*, at least while dealing with the regional selections of specimens. Therefore, we applied DNA barcoding to check the identity of these plants and assess a suitability of nuclear ITS and plastid *trn*LF, rps4 and *rbc*L markers in broader geographic context.

MATERIALS AND METHODS

Sequences for DNA barcoding were obtained according to the protocols described by Gardiner *et al*. (2005) for ITS, Fedosov *et al*. (2016) for *rbc*L and Hernández-Maqueda *et al*. (2009) for *trn*S-*trn*F, which includes gene rps4 and *trn*L-*trn*F region; in the latter case, primers trnaS and F were used for amplification and sequencing,

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and additionally an internal primer 166 for sequencing, that allowed obtaining the complete *trn*S-*trn*F sequence from the target specimen. No special molecular phylogenetic analyses were ran; to identify the closest sequences from those stored in GenBank, we used BLAST search and aligned results by the similarity. In addition, standard microscopic techniques were used to explore anatomy and morphology of the specimen and prepare its line drawings. The plants from Mondy settlement outskirts were also compared with three Russian specimens kept under the name *Weissia exserta* in Russian herbaria (all available specimens are kept in MW).

RESULTS

An obtained ITS sequence PP025380 (752 bp) nearly fully covers the ITS region (excepting 7 bases at the beginning of ITS1 and 9 bases at the and of ITS2. BLAST search suggests four sequences, two of *Weissia longifolia* var. *angustifolia* (Baumgartner) Crundw. & Nyholm (MH545658 and MH545655), one of *W. condensa* var. *armata* (Thér. & Trab.) M.J. Cano, Ros & J. Guerra (AY796241), and one of *Weissia sterilis* W.E. Nicholson (MH545673) as the most similar (99.6% similarity); three GenBank accessions referred to *W. levieri* (AY796232), *W. rostellata* (Brid.) Lindb. (AY796236) and *W. muhlenbergiana* (Sw.) W.D. Reese & B.A.E. Lemmon (AY796231) yielded similarity of 99.47%; other GenBank accessions show similarity of 99.34% and lower.

Blast search for the plastid *trn*L-F region of the specimen from Mondy outskirts, OR999103 (454 positions starting with *trn*F side, covering part of *trn*F gene, *trn*F-*trn*L spacer, second exon of *trn*L gene, intron in the *trn*L gene and part of the first exon of the *trn*L gene) revealed four identical sequences assigned in GenBank to *W. angustifolia* (Baumgartner) D.A. Callaghan (MH545578), *W. controversa* Hedw. (MH545601), *W. brachycarpa* var. *obliqua* (Nees & Hornsch.) M.O. Hill (MH545588), and *W. rostellata* (MH545587); all these sequences originate from the plants from UK.

Blast search for the plastid rps4 region of the specimen from Mondy outskirts, OR999101 (675 bp from the beginning of the rps4 gene up to the beginning of the *trn*S gene) revealed four identical sequences, three assigned to *W. controversa*, AF480976 (USA), AY950397 (USA), LC176284 (Japan), and one assigned to *W. exserta* (LC176285, Japan); somewhat lower similarity was found with the sequences of another specimen of *W. exserta* (LC769575, Japan), *W. longidens* Cardot (LC183827, Japan), *W.* sp. (LC183805, Japan) and one more specimen of *W. controvera* (LC183803, Japan).

Finally, Blast search for the plastid rbcL gene, OR999102 (1307 bp, incomplete from both ends) revealed three GenBank accessions of *W. controversa* (LC176261, LC183768, LC183766, all-three from Japan) with similarity 99.92 – 99.77% as the most similar to the one obtained from our specimen, while sequences assigned to *W. newcomeri* (E.B. Bartram) K. Saito, *W.* sp. and *W. longidens* had lower similarity, and both Japanese sequences of *W. exserta* have shown similarity of 99.46%.

The revision of the specimens referred to *W. exserta* from Russia – from Altai Mountains and Anabar Plateau (Ignatov *et al*., 2006; Fedosov *et al*., 2011) revealed that they differ from the specimen from Mondy settl. outskirts. Formally, one specimen from Altai (MW9069723) and one from Anabar (MW9069725) agree with the description of *W. exserta*; however, both specimens have young capsules, which do not allow a detailed comparison with the plant from Buryatia. Specimen from Anabar Plateau is represented by much smaller plants with very short leaves, and a degree of capsule development does not allow an estimation of the operculum differentiation and spore size. The second specimen from Anabar Plateau (MW9069725) was collected in the same place and date and thus tentatively referred to the same species despite the lack of sporophytes. Specimen from Altai agrees with plants from Buryatia in having rather short, curved to contorted leaves, and its sporophytic traits correspond well to *W. exserta*; their young setae are straight (curved in plants from Buryatia), while spores are unavailable for measurement. The second specimen of *W. exserta* from Altai Mountains, Ignatov 0/1627 (MHA) is too poor to assess its identity in detail.

DISCUSSION

The affinities of specimen from Mondy Settl. were resolved differently depending on the particular marker, which is partly explained by different representation of four used loci: ITS and *trn*L-F is available mostly for European accessions, while rps4 and rbcL – mostly for Asian ones. Nevertheless, no one of four markers (excepting rather conservative and thus non-informative rps4) revealed the affinities of the target specimen concordant with its morphology. According to the results of barcoding with ITS, the closest European taxon is *W. longifolia* var. *angustifolia* (= *W. angustifolia*); however, it has shorter setae and involute margins of perichaetial leaves (Callaghan *et al*., 2019); in *W. levieri* setae are also shorter than urn, and opercula often become detached from the mature capsules; *W. condensa* has stegocarpous capsules. *Trn*L-F region also reveals *W. angustifolia* and several species with stegocarpous capsules as closest relatives of our target specimen. The results obtained from these two markers can be explained by a strong geographical bias in representation of ITS, which remains unsampled for many Asian taxa, and by too low variability of *trn*L-F to distinguish species of the genus *Weissia.*

Barcoding based on rps4 sequences revealed one of specimens of *W. exserta* as identical with the target specimen, but it also found three specimens of *W. controversa* identical with these two. Such result allows considering our plant as *W. exserta*, but it also likely suggests that the latter species has a hybridogeneous origin with *W. controversa* being the mother. Widespread hybridiza-

Fig. 1. Habit of *Weissia exserta* (Russia, Buryatia, foothills of Tunkinskie Goltsy Range, Mondy Settl. outskrits).

tion between Japanese *Weissia* was supposed by Inoue & Tsubota (2017) to be responsible for the origin of two endemic Japanese species with cleistocarpous capsules. However, the second specimen of *W. exserta* has a different rps4 sequence. Finally, rbcL found no identical specimens in an available for comparison Asian selection of taxa, and it suggests higher similarity of specimen from Mondy settl. outskirts with Asian lineages of *W. controversa* rather than with *W. exserta*; the latter species represented by two Japanese accessions has clear molecular synapomorphies, which differentiate it's sequences from one obtained from our specimen.

Although a recent spread of integrative taxonomic framework allowed resolving system in many problematic groups of living beings, where traditional approach has failed, in several groups molecular data revealed patterns, which cannot be addressed in a traditional way. In particular, within several species complexes morphological variability is not correlated with molecular data (cf. Wiens & Penkrot, 2002). The genus *Weissia* appeared among such groups (Werner *et al.*, 2005). Although on the regional selections of taxa molecular data allow determining most specimens of *Weissia* with cleistocarpous capsules in Japan (Inoue & Tsubota, 2017) and at least several species of the genus in UK (Callaghan, 2019), at broader geographical sampling the boundaries between morphotypes assigned to different species disappear (Werner *et al.*, 2005).

The generitype of the genus *Weissia, W. controversa* appeared most problematic in all reconstructions; it could be considered as polyphyletic according to reconstructions published by both Werner *et al.* (2005) and Inoue & Tsubota (2017), if the backbone phylogeny of the genus was better resolved and supported, or at least as paraphyletic. Lack of molecular synapomorphies and remarkable divergence of geographically isolated lineages assigned to the same species based on morphological ground hampers the use of DNA barcoding for segregating species as they are currently recognized. Moreover, in such cases cladistic approach does not allow formal recognition even for advanced lineages, which possess both molecular and morphological synapomorphies (Hörandl & Stuessy, 2010; Maltseva *et al.*, 2023). If in case of *Tortula acaulon*/ *Phascum cuspidatum* (cf. Zander, 1993) an estimation of advanced morphological traits is a matter of classification, in case of the genus *Weissia* this would affect a species recognition, leading to underestimation of biodiversity. Moreover, topologies where the advanced lineages appeared nested within the polymorphic ancestral species often originate due to various effects, such as hybridization, ILS, *etc*. Therefore, many authors assume that phylogenetic relationships in complexes of closely related species cannot be represented as a dichotomic tree and suggest to implement alternative approaches, such as haplotype networks (Clements *et al.*, 2000; Dos Santos *et al.*, 2016) and splits trees (Huson & Bryant, 2006) for revealing and/or visualizing the affinities between species. Employing such an approach in case of unique morphology and ambiguous results of DNA barcoding, we could describe the plant from Mondy settl. outscirts as a new species. However, until just a single specimen is available, its variation and morphological differentiation from *W. exserta* cannot be established. On the other hand, Callaghan *et al.* (2019) recognize morphologically distinct species represented by series of haplotypes overlapping with those of the other morphospe-

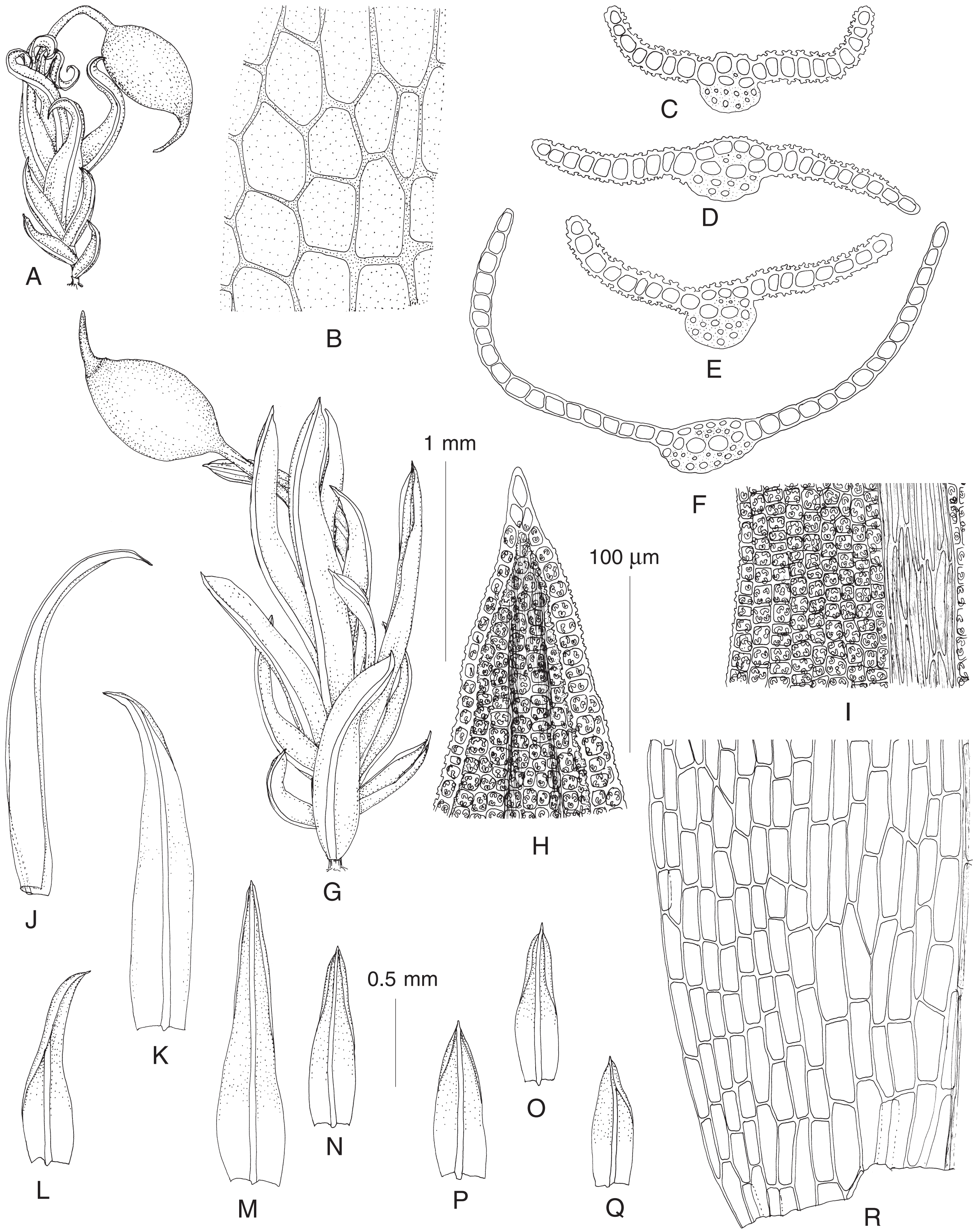

Fig. 2. *Weissia exserta* (from Russia, Buryatia, Mondy Settl. outskirts, *Fedosov* 11.VII.2023, MW). A: habit, dry. B: exothecial cells; C–F: leaf transverse sections; G: habit, wet; H: upper leaf cells; I: mid-leaf cells; J, K: perichaetial leaves; L–Q: stem leaves; R: basal laminal cells. Scale bars: 1 mm for A, G; 0.5 mm for J–Q; 100 µm for B–F, H–I, R.

cies. At the moment we see no better decision than following this practice. At the same time, below we provide descriptions and illustrations of the plant from Buryatia as a reference to be considered along with the set of barcoding sequences available in GenBank for the further study of Asian *Weissia* taxonomy, which is especially important since no one specimen referred to *W. exserta* from inland Asia has been studied with molecular data so far.

TAXONOMY

Weissia exserta (Broth.) P.C. Chen, Hedwigia 80: 158. 1941. – *Astomum exsertum* Broth., Hedwigia 38: 212. 1899. – *Hymenostomum exsertum* (Broth.) Broth., Die Natürlichen Pflanzenfamilien I(3): 386. 1902).

Fig. 1, 2.

Plants in loose tufts, yellow-green to brownish. *Stems* 2.0–3.5 mm long, simple or branched, with well developed central strand and cortical cells very weakly delimited from underlying parenchimatose cells, with a little smaller lumens and thicker cell walls. *Leaves* loosely contorted when dry, spreading when wet, 1.2–1.8×0.25–0.4 mm, widest a little above base, ovate-lanceolate in lower part of stem, gradually becoming longer distally, upper leaves lanceolate to linear-lanceolate, acute to short acuminate, strongly concave distally, with cucullate apices; margins entire, flat or narrowly incurved distally; costa strong, 1/6–1/7 of leaf base width, 50–60 µm wide at base, yellowish to brownish, shortly excurrent as a brownish mucro, with two stereid bands divided by 4–5 guide cells, and papillose ventral epidermis; lamina unistratose, upper laminal cells 6–13×8–10 µm, subquadrate to hexagonal, transverse-rectangular or irregular in shape, thin-walled, with numerous low, massive papillae, 4–8 per cell; basal cells (12–)15–32(–40)×9–15 µm, rectangular, moderately thick-walled, smooth, hyaline to yellowish, translucent, gradually becoming shorter distally, or abruptly becoming quadrate in midleaf, boundary between smooth basal leaf cells and papillose distal leaf cells straight or V-shaped, papillose upper leaf portion occupies ca. 2/3 of the total leaf length. *Autoicous*, sporophytes abundant, single per perichaetium. *Perichaetial leaves* with somewhat wider base and longer distal portion, acute to short acuminate. Setae (1.2–)1.5–2 mm, cygneous when capsules are mature, rarer flexuose, pale. *Capsules* exserted, cleistocarpous, 0.6–0.8 mm long, elliptical, pale; exothecial cells isodiametric, moderately thick-walled. *Annuli* partly differentiated. *Opercula* partly differentiated, not dehiscent, with long, oblique beak. *Spores* 21–25 µm, brownish, verrucose. *Calyptrae* ca. 1 mm, cucullate.

Specimens examined: RUSSIA: **Buryatia Republic**, East Sayan Mountains, Tunkinsky Distr., "Tunkinskaya valley" National Park, vicinity of Mondy settl., 51.681617°N, 100.975603°E, 1363 m alt., open steppe community, 11.VII.2023, *Fedosov* (MW). **Altai Republic**, Ongudai Distr., ca. 50°30'N, 86°35'E, 1500 m alt., rock outcrops on the mountain eastwards of Malyi Yaloman settl., 4.VIII.2000 *Ignatova* (MW9069723). **Krasnoyarsk Territory**, Taimyrsky Municipal Distr., 70.9978°N, 102.699°E, ca. 50 m alt., Kysyl-Khaya calcareous rock outcrops on the right bank of Kotuy River, on loamy ground, 14.VII.2005 *Fedosov 05-500* (MW9069724).

Distribution. *Weissia exserta* was described from Japan; it occurs in Honshu, Shikoku and Kyushu (Inoue & Tsubota, 2017). Also, this species is believed to be widespread in China excepting its poorer sampled NW provinces, and also occurs in India (Li *et al*., 2001). However, an affinity between Chinese plants assigned to *W. exserta* and Japanese specimens has not been so far tested with molecular markers. Thus, this question, as well as an identity of Russian material needs in specially focused study with wider sampling in many lineages of Asian *Weissia*. Several findings made in the vicinity of Mondy settlement, such as *Indusiella thianschanica* Broth. & Müll. Hal., *Jaffueliobryum latifolium* Lindb. & Arnell ex Thér., and *Aongstroemia julacea* (Hook.) Mitt., represent predominantly Central Asian phytogeographical element that agrees with dry continental climate of Mondy Settlement area. However, *Aongstroemia julacea* (= A. *fuji-alpina* (Takaki) Takaki) is also known from Japan, thus further phytogeographical implication would better based on integrative floristic approach (Fedosov *et al*., 2022).

Differentiation. Morphological circumscription of *W. exserta* accepted here in accordance with Brotherus (1899), Noguchi *et al*. (1988), and Inoue & Tsubota (2017) is based on combination of exserted cleistocarpous capsules with partly differentiated annuli and opercula with long oblique beaks. In possessing setae remarkably longer than capsules and long beak, it differs from all other cleistocarpous species of the genus *Weissia*.

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