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NOTES ON THE GENUS *WEISSIA* IN RUSSIA FOCUSED MAINLY ON THE SPECIES FROM ASIAN RUSSIA

ЗАМЕТКИ О РОДЕ *WEISSIA* В РОССИИ, ПРЕИМУЩЕСТВЕННО О ВИДАХ ИЗ АЗИАТСКОЙ ЧАСТИ

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Abstract

A combined molecular phylogenetic and morphological approach was applied to the specimens of *Weissia* from the Russian Far East. *Weissia controversa* var. *sachalinensis* from Sakhalin and Kuril Islands was described as new for science. *S*pecimens from Asian Russia previously identified as *Weissia edentula* were referred to *W. newcomeri*. *Weissia planifolia* was found to be frequent in the southern Russian Far East; its assignment to the genus *Weissia* was confirmed. *Weissia rutilans* and *W. edentula* are excluded from the moss flora of Russia.

Резюме

Комбинированный молекулярно-филогенетический и морфологический подход был применен к образцам *Weissia* с российского Дальнего Востока. *Weissia controversa* var. *sachalinensis* с Сахалина и Курильских островов описана как новая для науки. Образцы из азиатской части России, ранее определенные как *Weissia edentula*, отнесены к *W. newcomeri*. *Weissia planifolia* является одним из наиболее частых видов рода на юге российского Дальнего Востока; подтверждено включение этого вида в род *Weissia*. *Weissia rutilans* и *W. edentula* исключены из списка видов флоры мхов России.

KEYWORDS: mosses, Pottiaceae, taxonomy, nrITS

Introduction

Weissia Hedw. is a comparatively large genus with a little less than 100 species distributed almost worldwide except Antarctica (Zander, 2007). It comprises tiny plants growing in small patches mainly on soil, often having persistent protonema. This genus is considered to be difficult for identification due to various reasons. First, presence of sporophytes is essential for *Weissia*, because they provide main diagnostic characters for species distinction. Traits of sporophyte reduction are characteristic for this genus, resulting in a great variety in seta length, an ability of capsule dehiscence, and peristome development (having stegocarpous capsules with a comparatively well-developed or reduced to totally absent peristome, or capsules with variously differentiated annulus but with persistent operculum, or totally cleistocarpous capsules). Mature sporophytes are not always present in collected specimens because of their short-term existence in many species. Identification of specimens without sporophytes is often impossible, and even when capsules are immature or old and disintegrated, it is very difficult to evaluate their distinctive characters, including spore size.

Another feature of the genus is a comparatively frequent occurrence of hybrids (Nicholson, 1905, 1906, 1910; Callaghan *et al*., 2019), which also hampers identification. Using molecular markers for species delimitation, which was successfully applied in many groups of mosses (e.g. Ignatova *et al*., 2010; Hedenäs, 2017; Cano *et al*., 2024, *etc.*), appeared to be less helpful in *Weissia*: it was demonstrated that some morphospecies are para- or polyphyletic (Werner *et al*., 2005; Callaghan *et al*., 2019).

There is also a problem of delimitation between *Weissia* and *Trichostomum* Bruch., as was pointed by Zander (1993, 2007). Species of *Weissia* are mainly monoicous, while most of *Trichostomum* species are dioicous, but there are exceptions in both cases. Many species of *Weissia* have leaves with tightly involute margins in their distal half, but species with almost plane leaf margins are also known in this genus. Most species of *Trichostomum* have plane leaf margins, but in *T. crispulum* Bruch the upper leaf margins are involute and leaf apices are cucullate. Close relationship between *Weissia* and *Trichostomum* was also confirmed by the molecular phylogeny of Trichostomoideae provided by Werner *et al*. (2007): *Trichostomum* was resolved as nested within *Weissia* in their

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analysis. However, both genera are still awaiting a worldwide revision.

Weissia was not in a focus of recent revisions for the moss flora of Russia. The last treatment of the genus for the USSR was provided by Savicz-Lyubitskaya & Smirnova (1970) who treated separately *Weissia* (with 6 species), *Astomum* Hampe (2 species), and *Hymenostomum* E. Brown. (5 species), altogether 13 species, but two of them being known only from Middle Asia, *i.e*. outside Russia. In the first check-list of mosses of the former USSR (Ignatov & Afonina, 1992), 9 species of *Weissia* (including *Hymenostomum*) and 2 of *Astomum* were listed for Russia, but such species present in Savicz-Lyubitskaya & Smirnova (1970) as *Astomum multicapsulare* (Sm.) Bruch, Schimp. & W. Gümbel, *Wessia squarrosa* (Nees & Hornsch.) Müll. Hal., and *W. tyrrhena* M. Fleisch. were excluded, *W. exserta* (Broth.) P.C. Chen was added, and *W. levieri* (Limpr.) Kindb. was considered at species level. In the second check-list (Ignatov *et al*., 2006), *Astomum* was included in *Weissia*, and the previous list was supplemented with *W. squarrosa* and *W. edentula* Mitt. Since then, only one species, *W. armata* (Thér. & Trab.) Fedosov, was added to this list (Fedosov, 2011). However, some uncertainty, concerning especially records of *Weissia* in the Russian Far East, remained. This paper presents the results of the combined molecular and morphological study of *Weissia* specimens from Russia, focused mainly on collections from the Russian Far East.

Material and methods

Morphological studies included specimens from MHA and MW, and duplicates from LE, VLA, NVS, UUH, and SASY.

Molecular studies started with ITS and *trn*L-F, but as many species has no differences in the latter plastid marker, we continued with ITS sequence data only, moreover the nuclear ITS is represented in GenBank better than any other molecular marker available for the genus. DNA extraction was done with the Qiagene Extractor. Primers L and B (White, 1990) were used for ITS amplification. The sequencing protocols were essentially the same as in our previous studies (Gardiner *et al.,* 2005). GenBank accession numbers and voucher data are giver in Appendix 1 for 48 samples sequenced de novo, mostly from Russia. Obtained sequences were aligned using MAFFT v. 7.487, E-INS-i strategy (Katoh & Standley, 2013).

Tree was rooted on species of *Trichostomum*, the genus closest to *Weissia* (Bechteler *et al*., 2023).

Maximum likelyhood analysis was performed at W-IQ-TREE server (Trifinopoulos *et al*., 2016), 1000 replications and otherwise default parameter, 1000 replications. Substitution models were selected by the server: ITS1: TNe+I+G4; 5.8S RNA gene K2P; ITS2: K2P+G4.

Results

Obtained ML tree includes the short basal grade with long branches and the long, poorly resolved terminal part, consisted of four not resolved polytomies, inserted into each other with few additional, weakly diverged and supported, nested clades. Such topology could be expected given an alignment, where most specimens differ from each other in few substitutions, while the samples of the basal grade are contrastingly more variable, sharing many indels and substitutions with *Trichostomum* species.

The samples from the basal grade belong to *W. squarrosa* and *W. rutilans* (all studied specimens of these two species), and also to *W. exserta* and *W. condensa*, but in case of the two latter species, the basal grade includes only a part of their samples involved in the analysis, whereas other samples (both downloaded from GenBank and originally obtained) were found in other parts of the tree.

Most species in the tree were found to be polyphyletic. Some small highly supported clades include species that differ strongly from each other (Fig.1, red frames), e.g.:

— clade (BS=98) of one specimen of cleistocarpous *W. angustifolia*, one of gymnosomous *W. condensa* and two samples of perisomate *W. wimmeriana*;

— clade (BS=99) of one specimen of *W. condensa* and two of *W. wimmeriana*.

Some mixed clades, especially with GenBank data, may raise doubt in identification or else technical issues of aligning and analysis. However, at least several specially checked cases allow us to exclude artifacts (Fig. 1, green frames). Three examples are noteworthy:

— the clade of seven samples, six of *W. newcomeri* and one *W.* cf. *exserta*, with BS=98; the former species is one of the easiest to identify due to having long, delicate setae and broad, gymnostomous capsules (discussed in details below), while *W.* cf. *exserta* has cleistocarpous capsules emergent from perichaetial leaves on a short, curved setae;

— eight specimens of *W. planifolia* (with best developed peristome among our samples) together with another single specimen of *W.* cf. *exserta* appear in polytomy, having no common synanomorphies, but, at the same time, their sequences differ by only few substitutions/indels unique for each individual sample, excepting two sampes of *W. planifolia* that share one mutual substitution and thus form a bispecific clade;

— nine specimens of *Weissia* subg. *Astomum* with immersed capsules on very short setae (*W. longifolia, W. angustifolia, W. wilsonii*) form a clade (BS=97) with *W. rostellata,* a species with emergent capsules on the setae slightly longer than urn.

The latter cases are putatively caused by hybridization events, which can not be proved without other markers in addition to ITS and morphology.

Among an additional tests in this analysis, we tried to confirm the presence of *W. angustifolia* and *W. wilsonii* in Russia, based on their exhoustive descriptions by Callaghan *et al*. (2019). However, the samples from Russia best fitting these species morphologically appeared

to be among other species in the molecular-phylogenetic tree, not clustered with British specimens available in GenBank.

DISCUSSION

The obtained results make an interpretation of ITS variation somewhat vague, as some supported clades are formed by species with contrastingly different morphology (Fig. 1, red frames). However, *most,* 12 out of 18, small clades in our phylogenetic tree are unispecific, despite some species appear in more than one clade. This implies a certain usefulness of ITS for species delimitation or confirmation of their identity, at least in some cases. It seems that species are better defined in areas with fewer anthropogenic disturbance. In Russia, low populated areas in East Siberia and Far East probably provide a good example of an environment where the possibility for hybridization is lower than in denser populated areas in European part of the country. The subsequent discussion addresses several species of *Weissia* from the Russian Far East, for which ITS data appeared to be useful.

Weissia planifolia

Weissia planifolia was first recorded for the Russian Far East by Lazarenko (1940) under the name *W. platyphylla* Broth. (described from Hondo, Kumamoto Prefecture, Kyushu, Japan), which appeared to be illegitimate. Bardunov & Cherdantseva (1982) cited this record and characterized this species as a rare one, known in the south of Primorsky Territory from two localities (Chernigovka District and Popov Island near Vladivostok). Along with this species, *W. rutilans* (Hedw.) Lindb. was also listed both by Lazarenko (1940) and Bardunov & Cherdantseva (1982), and the latter species was considered as more frequent in this region. *Wessia planifo-*

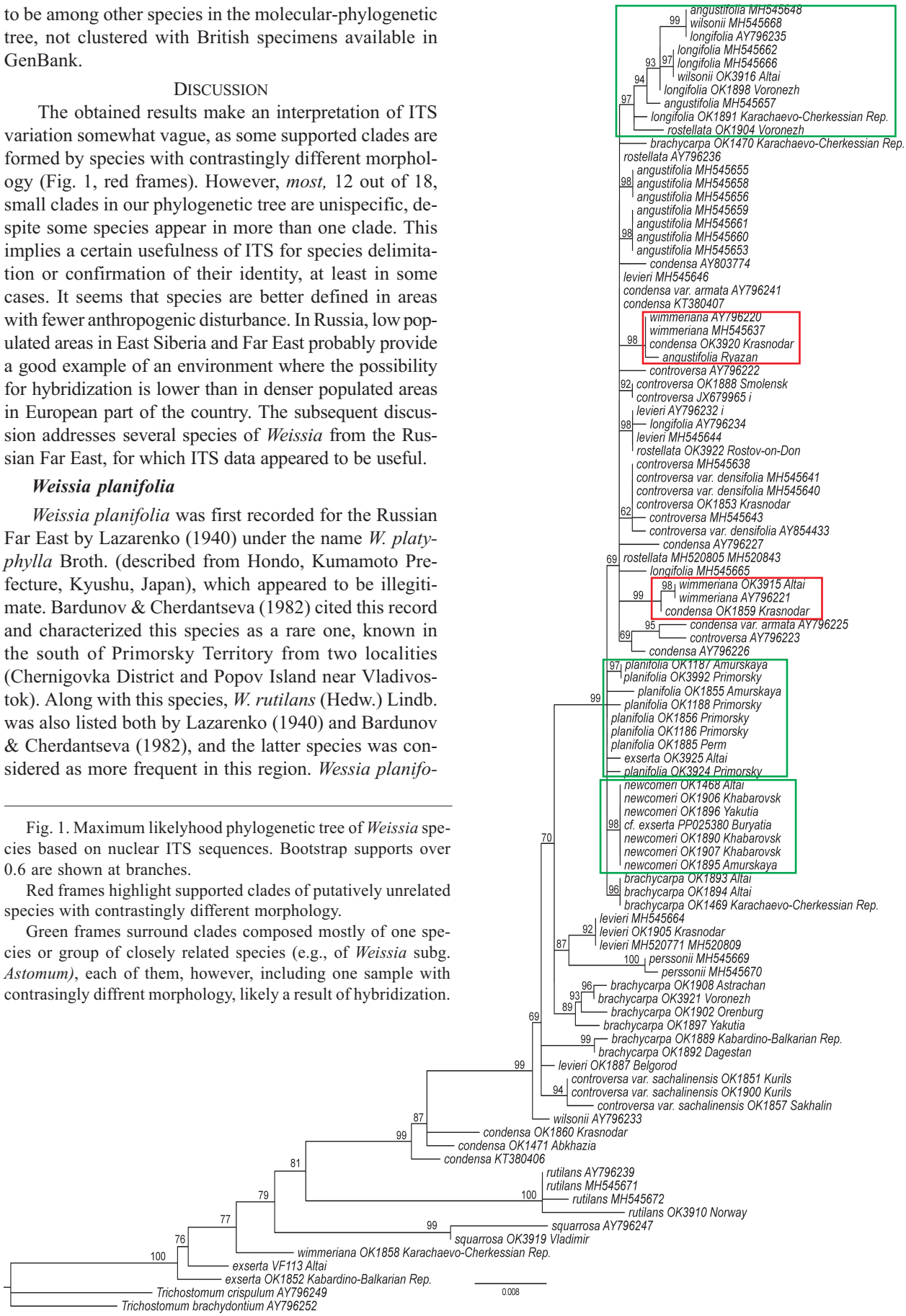

Fig. 1. Maximum likelyhood phylogenetic tree of *Weissia* species based on nuclear ITS sequences. Bootstrap supports over 0.6 are shown at branches.

Red frames highlight supported clades of putatively unrelated species with contrastingly different morphology.

Green frames surround clades composed mostly of one species or group of closely related species (e.g., of *Weissia* subg. *Astomum)*, each of them, however, including one sample with contrasingly diffrent morphology, likely a result of hybridization.

lia and *W. rutilans* are similar in having leaves with almost plane or weakly incurved leaf margins in distal leaf portion and capsules with peristome. In the key to identification of *Weissia* species, Savicz-Lyubitskaya & Smirnova (1970) pointed that these species differ in leaf size and shape (leaves lanceolate from ovate, widened base, 2.0–2.7 mm long in *W. rutilans* vs. narrow lingulate from slightly widened base, to 1.2 mm long in *W. planifolia*), peristome color and structure (yellow, irregularly cleft, perforated, occasionally reduced vs. orange brown, short, entire or perforated peristome teeth), and spore size (20–27 μm vs. 17–20 μm). They characterized *W. planifolia* (as *W. platyphylla* Broth.) as a rare species occurring in Russia only in the Far East, while *W. rutilans* was recorded from European Russia, Caucasus, and Far East. We revisited all Far Eastern collections identified as *W. rutilans* and *W. planifolia* (as *W. platyphylla* Broth.) and found that they all belong to *W. planifolia*; it is also confirmed by the molecular phylogenetic analysis. These specimens are variable in leaf length and length/width ratio, but they are uniform in having almost plane leaf margins, peristome color (reddish brown) and structure (peristome teeth non-perforated, well developed, though variable in length, 50–90 μm long, erect to erect-spreading when dry), and spore size (16–20 μm). Actually, spore size is the most valuable character for distinguishing *W. planifolia* from *W. rutilans*, because they are very similar in gametophyte features, and even peristome of the latter species is described as variable, overlapping in length with *W. planifolia*: 40–60 μm long (Guerra *et al*., 2006) or even to 80 μm long (Smith, 2004), but occasionally strongly reduced. Thus, no wonder that specimens from the Russian Far East with shorter peristome teeth, ca. 50 μm long and leaves with flat margins were referred earlier to *W. rutilans*.

The only other species of *Weissia* with almost plane leaf margins in the Russian Far East is *W. newcomeri*, which is readily distinguished by eperistomate capsules. *Weissia planifolia* is the most frequent species of the genus in the Russian Far East, occurring both in its mainland part and the Kuril Islands.

Weissia planifolia is currently accepted as a member of the genus *Trichostomum*, where it was transferred by Zander (1993). It was reported for North America as *T. planifolium* (Dix.) R.H. Zander, who placed into its synonymy *Weissia sweetii* E.B. Bartram and *W. perligulata* H.A. Crum, both described from North America (Nevada and Utah, respectively). Illustrations of *W. sweetii* provided by Bartram (1945) and of *W. perligulata* by Flowers (1973) show oblong, oblong-lanceolae and long-spatulate leaves with costa percurrent or ending below leaf apex, obtuse apices, and almost plane or narrowly incurved margins. In illustration in Zander (2007), leaves of *Trichostomum planifolium* are oblong, costa percurrent, and uppermost leaf margins narrowly incurved. In the Moss flora of Mexico (Zander, 1994), leaves of *Weissia planifolia* are illustrated as oblong, with fairly plane margins and very shortly excurrent costa. In the description of Bartram (1945), the length of setae is given as 4–5 mm, and peristome teeth short. Flowers (1973) describes setae as 2.5–8 mm long, and peristome absent. Zander (2007) mentions that peristome of *T. planifolium* is absent or short-lanceolate, whereas Zander (1994) describes for *W. planifolia* setae 3.5–4.5 mm, and peristome teeth long-lingulate, irregularly cleft, ca. 130 μm long. For comparison, the plants of *W. planifolia* from the Russian Far East have oblong-lanceolate leaves with slightly widened bases but never spatulate, distal leaf margins plane or narrowly incurved, at least near apex, setae are longer, 5–9 mm, and peristome teeth are never reduced or cleft, 50–90 μm long. Similar plants are described and illustrated by Saito (1975). It seems unlikely that plants from Russia, Japan, and China (where from *Weissia planifolia* was described) are conspecific with North American ones. Furthermore, one North American specimen, under the name *Trichostomum sweetii* (E.B. Bartram) R.H. Zander, was included into the molecular phylogenetic study of Trichostomoideae by Werner *et al*. (2005), and it was resolved in a clade with *Trichostomum caespitosum* (Bruch ex Brid.) Jur. and *Weissia triumphans* (De Not. ex Schimp.) M.O. Hill, *i.e.* far from *Trichostomum brachydontium* Bruch*, T. crispulum* Bruch*,* and species of *Weissia*. Subsequently, Ros & Werner (2007) transferred the members of this clade into the genus *Pottiopsis* Blockeel & A.J.E. Sm. However, all sequenced specimens of *Weissia planifolia* from the Russian Far East in the present analysis were resolved within *Weissia*, thus challenging synonymization provided by Zander (1993). Thus, here we treat this species within the genus *Weissia*.

We do not confirm the presence of *W. rutilans* in Russia. Its records from Orenburg Province (South Urals) were based on misidentified specimens of *Trichostomum brachydontium* Bruch. No specimens from the Russian part of the Caucasus we also found.

Weissia controversa in the Russian Far East

This is the most widespread species of the genus, distributed nearly worldwide. In Russia, it is frequent in its European part, except its northern regions, known from the Caucasus, southern Siberia, and southern Far East in the Asian part of the country. Bardunov & Cherdantseva (1982) characterize it as a more or less common species in southern Primorje, often found with sporophytes. It was also recorded from Kamchatka, Amurskaya Province, Khabarovsk Territory, Sakhalin, and Kuril Islands (Cherdantseva *et al.*, 2018). *Weissia controversa* is recognized by combination of widely and tightly incurved margins in upper halves of leaves and peristomate capsules on long setae. Its peristome teeth are characterized as well developed, linear-lanceolate, papillose, or sometimes rudimentary (if *W. wimmeriana* **(**Sendtn.) Bruch,

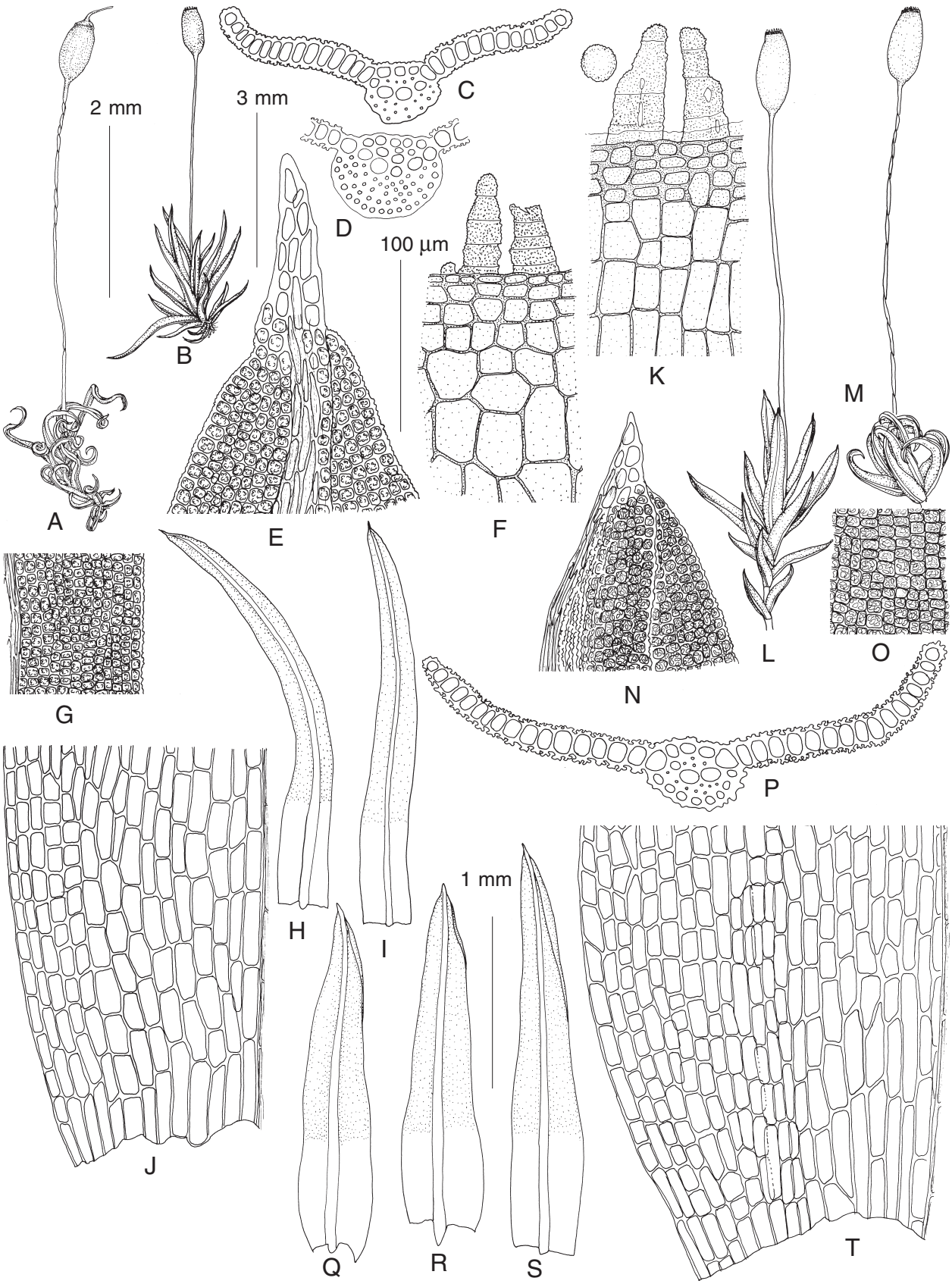

Fig. 2. *Weissia planifolia* (from Russia, Primorsky Territory: A–I: Partisansk Distr., Olkhovaya Mt., *Ignatov & Ignatova 06-2861*, MHA9102668; K–T: Khasansky Distr., Ryazanovka, *Ignatov s.n.*, MHA9111946). A, M: habit, dry; B, L: habit, wet; C–D, P: leaf transverse sections; E, N: upper leaf cells; F, K: peristome teeth; G, O: mid-leaf cells; H–I, Q–S: leaves; J, T: basal leaf cells. Scale bars: 3 mm for B; 2 mm for A, L–M; 1 mm for H–U, Q–S; 100 µm for C–G, J–K, N, O–P, T.

Schimp. & W. Gümbel is treated as a variety of *W. controversa*). Its spore size is described more or less uniformly in Floras of various regions: 16–20 μm (Smith, 2004), 18–20 μm (Guerra *et al*., 2006), 17–20 μm (Savicz-Lyubitskaya & Smirnova, 1970); 15–20 μm (Saito, 1975), 14–22 μm (Crum & Anderson, 1981). In the course of present study, three specimens from Sakhalin and Kuril Islands identified as *W. controversa* took our attention. The molecular phylogenetic analysis resolved them in a separate, highly supported clade. *Weissia controversa,* as well as most other widespread species of *Weissia*, was found to be polyphyletic by Werner *et al*. (2005) and in our analysis, based on sequences of ITS1–2 region. The main morphological characters of plants from Sakhalin and Kuril Islands, such as leaves with incurved upper margins and capsules on long setae with lanceolate, entire peristome teeth are in agreement with *W. controversa*; however, some differences are also observed: their leaf margins are narrower incurved, and its spores are larger, (19–)21–25 μm. We consider that these differences, as well as a separate position in the molecular phylogenetic tree allow us to describe these plants as a variety of *W. controversa.*

Eperistomate Weissia in the Russian Far East

Weissia edentula has been first recorded in Russia from Bureinsky Nature Reserve in Khabarovsk Territory (Ignatov *et al*., 2000). Later specimens of *Weissia* with long setae and eperistomate capsules were collected in other localities in the southern Russian Far East, from Zeya Reserve in Amurskaya Province to Primorsky Territory and Kuril Islands, the northernmost one in Kamchatka Peninsula; they were also identified as *W. edentula*. This species was described from Madras, India and is also known from China, Japan, Vietnam, Thailand, the Philippines, Papua New Guinea, Africa, and Australia (Li *et al*., 2001; Brinda & Atwood, 2024). Its presence in SE Russia did not look impossible, likely representing populations on the northern boundary of its range. However, in the course of preparation the treatment of *Weissia* for the ongoing volume of the Moss Flora of Russia, we found that the plants from Russia called *W. edentula* do not fit comfortably the description of this species provided by Saito (1975) and Li *et al*. (2001) and especially its illustrations in Saito (2005) and Gao (1996). In these illustrations, leaves of *W. edentula* are shown as linear-lanceolate, narrowly acuminate, with more or less strongly involute upper margins, whereas plants from Russia have shorter and wider leaves, with lower length/width ratio, with much narrower and weaker incurved margins, and obtuse apices (Fig. 4). In Japan, there are two other eperistomate species of *Weissia*, i.e. *W. atrocaulis* K. Saito and *W. newcomeri* (E.B. Bartram) K. Saito, both having oblong leaves with obtuse apices (Saito, 1975; Noguchi & Iwatzuki, 1988). However, *W. atrocaulis* has totally plane leaf margins, percurrent costa, and longer capsules; furthermore, it is described as a robust plant with black stems to 3 cm long. The plants from the Russian Far East lack this combination of characters. *Weissia atrocaulis* is currently treated in *Trichostomum* where it was transferred by R.H. Zander. At the same time, the plants in question from the Russian Far East (Fig. 4) are very similar to *W. newcomeri,* as it is illustrated and described by Saito (1975). They have oblong leaves with length/width ratio 4–6:1, with slightly and narrowly incurved margins, obtuse apices, and shortly excurrent costa. All other morphological characters of plants from Russia fit well the description of this species. So we only with a little hesitation refer the plants from the Russian Far East not to *W. edentula* but to *W. newcomeri*, keeping in mind that it should be tested with molecular methods, if the specimens of *W. newcomeri* from Japan and *W. edentula* from East Asia will be available.

Taxonomy

Weissia planifolia Dixon, Rev. Bryol., n. s. 1: 179. f. 1. 1928. — *Trichostomum planifolium* (Dixon) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 92. 1993. Fig. 2.

Plants in small, dense or lax patches, yellowish-green. *Stems* 1–2(–4) mm long. *Leaves* crispate when dry, erect-spreading to patent when moist, 1.1–2.5×0.25–0.45 (–0.5) mm, with length:width ratio 4–8:1, becoming longer distally, lanceolate to oblong-lanceolate, canaliculate distally, margins almost plane in midleaf, narrowly incurved in the upper third or near apex, apices slightly cucullate, base slightly widened; *costa* strong, 50–70 μm wide at base, excurrent into short mucro, in transverse section with one row of guide cells, ventral band of 1(2) layers of substereids, dorsal band of 2–4 layers of stereids, ventral epidermis differentiated, dorsal epidermis not or slightly differentiated, cells on dorsal surface of costa linear or elongate rectangular, smooth or with scarce papillae in middle part; *cells* in the middle and upper part of lamina quadrate, thin-walled, 9–12×9–12 μm, with 3–4 papillae per cell, papillae low, simple and bifid, obscuring cell walls; basal laminal cells rectangular, smooth, yellowish or hyaline, with moderately thickened walls, 30–80×11–15 μm. *Autoicous*. *Perichaetial leaves* similar to upper stem leaves. *Setae* 5–9 mm, pale yellowish. *Urns* 0.7–1.1 mm long, light-brownish, cylindrical, not or weakly narrowed to the mouth. *Exothecial cells* thin-walled. *Annuli* differentiated, persistent, *operculum* falling off, low conic, with long, narrow, straight or oblique beaks ca. 0.5 mm long. *Peristome* well developed, teeth erect or erect-spreading when dry, subobtuse at tips, 50–90 μm long, reddish-brown or brownish, densely papillose. *Spores* 16–20 μm.

***Distribution and ecology*.** This is the most frequent species of *Weissia* in the southern Russian Far East (Amur Province, south of Khabarovsk and Primorsky Territories, and South Kuril Islands). In grows on soil banks along roads, in dry *Quercus mongolica* forests on slopes, in ravines, at edges of arable fields, and in flood-valley stands (willow, poplar, and alder).

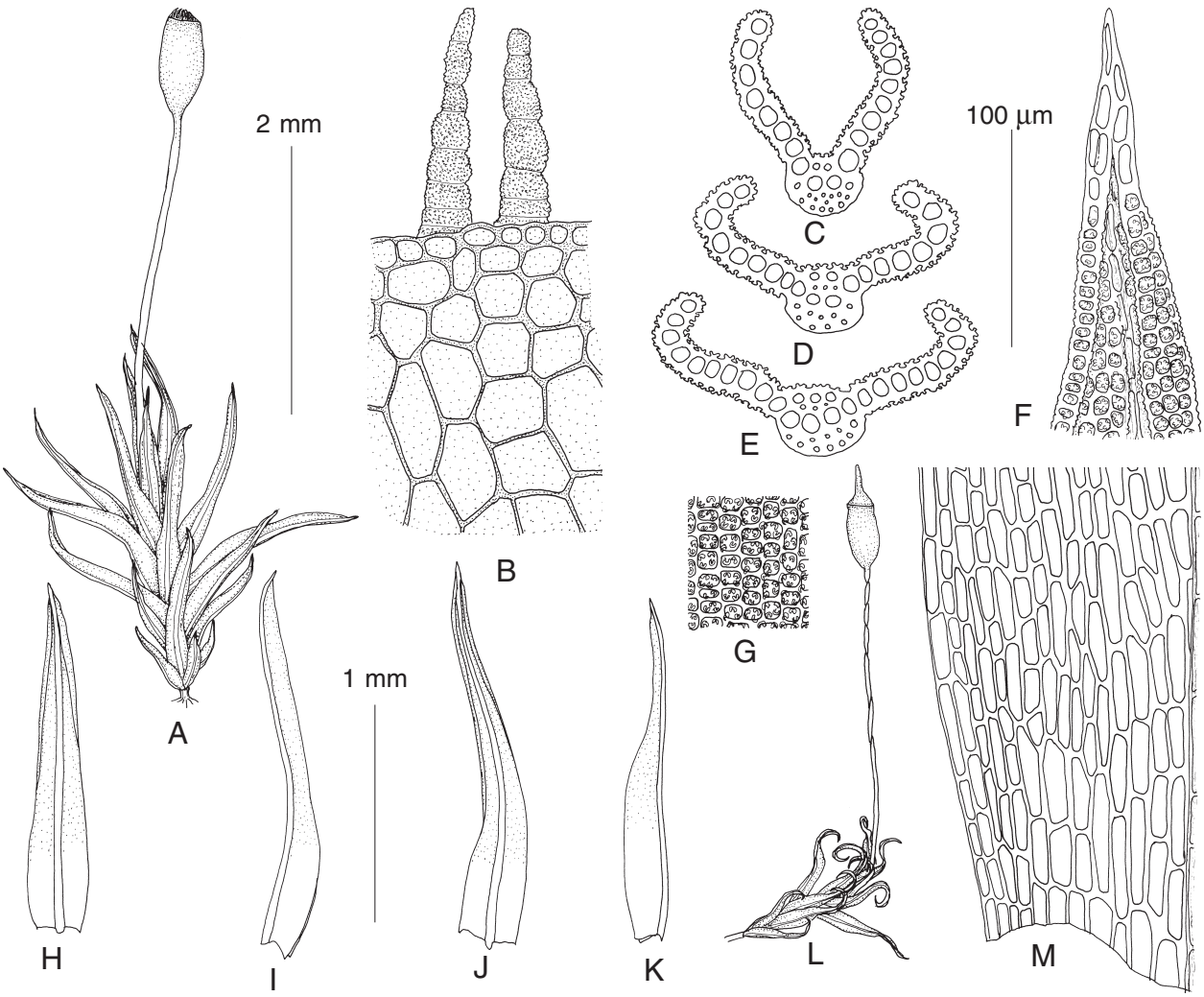

Fig. 3. *Weissia controversa* var. *sachalinensis* (from holotype). A: habit, wet; B: peristome teeth; C–E: leaf transverse sections; F: upper leaf cells; G: mid-leaf cells; H–K: leaves; L: habit, dry; M: basal leaf cells. Scale bars: 2 mm for A, L; 1 mm for H–K; 100 µm for B–G, M.

Differentiation. *Weissia planifolia* is recognized by having leaves with almost plane or weakly and narrowly incurved margins in distal part; long and thin setae; and well developed, erect or slightly spreading, reddish-brown peristome teeth. In some specimens, costa is weakly papillose on dorsal surface in mid-leaf. This character is considered as diagnostic for the Japanese species *W. deciduifolia* K. Saito (*Trichostomum deciduifolium* (K. Saito) R.H. Zander); however, its costa is much denser papillose, and its leaves are strongly deciduous. The distinctions of *W. planifolia* from *W. controversa* var. *controversa* include weakly and narrowly vs. tightly and widely incurved leaf margins, and from *W. controversa* var. *sachalinensis* in weaker incurved leaf margins and smaller spores (16–20 µm vs. (19–)21–25 µm).

Weissia controversa var. **sachalinensis** Ignatova & Ignatov, var. nova. Fig. 3.

Diagnosis. The new variety differs from the type variety by narrower incurved upper leaf margins and larger spores, (19–)21–25 µm vs. 16–20 µm.

Type: Russia, Sakhalin Island, Korsakovo District, Tonino-Anivsky Peninsula, outskirts of Novikovo Settlement, 46°21'N, 143°22'E, 10 m alt. N-faced rock outcrops along a stream. 15.IX.2009. Coll O.Yu. Pisarenko op03797. Holotype MHA9102705, isotype NSK2003797.

Etymology. The name of variety points its distribution in Sakhalin Province of Russia (Sakhalin and Kuril Islands).

Plants in small, more or less dense patches, yellowish-green. *Stems* 1–2(–4) mm long. *Leaves* crisped when dry, erect-spreading when wet, 1.4–2.2×0.25–0.35 mm, becoming larger distally, lanceolate to linear-lanceolate, with margins narrowly but strongly incurved in distal halves, slightly cucullate distally, with slightly widened bases; *costa* 35–50 µm wide at base, excurrent into a short mucro, smooth dorsally, ventral stereid band 1–2-layered, dorsal stereid band 2–3-layered, dorsal epidermis not differentiated; upper and median laminal *cells* quadrate and shortly transverse rectangular, moderately thick-walled, 6–9×9–11 µm, papillae 3–4(–5) per cell,

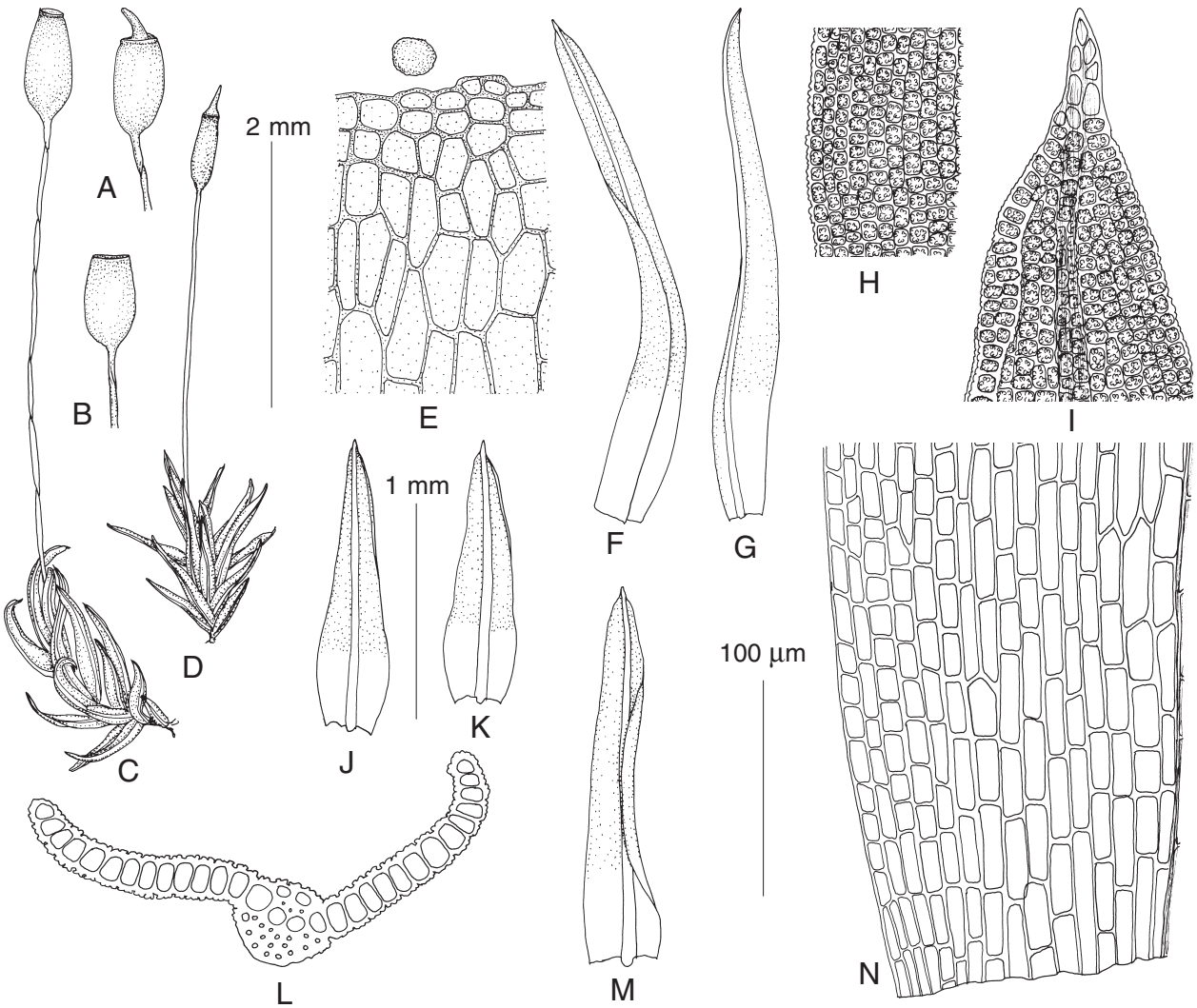

Fig. 4. *Weissia newcomeri* (from: Russia, Khabarovsk Territory, Bureinsky Nature Reserve, Bureya, *Ignatov 97-1262*, MHA). A–B: capsules; C: habit, dry; D: habit, wet; E: exothecium at urn mouth and spore; F–G: upper stem leaves; H: mid-leaf cells; I: upper leaf cells; J–K, M: lower stem leaves; L: leaf transverse section; N: basal leaf cells. Scale bars: 2 mm for A–D; 1 mm for F–G, J–K, M; 100 µm for E, H–I, L, N.

low, simple and bifid, obscuring cell walls; basal laminal cells rectangular, smooth, yellowish or hyaline, with moderately thickened walls, 25–60×8–11 µm. *Autoicous*. *Perichaetial leaves* similar to upper stem leaves. *Setae* 3–4 mm, yellowish to light brownish when mature. *Urns* 0.7–1.2 mm long, light-brown, cylindrical, weakly narrowed to the mouth. *Exothecial cells* thin-walled. *Annuli* differentiated, *opercula* falling off, low conic and with narrow, straight or oblique beaks ca. 0.5 mm long. *Peristome* well developed, peristome teeth erect when dry, lanceolate, obtuse, 90–100 µm long, reddish-brown, densely papillose. *Spores* (19–)21–25 µm.

Distribution and ecology. The variety is known only from Sakhalin, Shikotan, and Kunashir Islands (see specimen data in Appendix 1). It was collected on rock outcrops along a stream, on small rocks under high grasses and in rock crevices at sea coast. The type variety was also reported to grow occasionally on rock substrates, but more frequently it grows on various soil banks.

Differentiation. The distinctions from the type variety are given in the diagnosis. Another Far Eastern species with narrowly incurved leaf margins and well developed peristome is *W. planifolia*; it differs by having leaves with wider, subobtuse apices, weaker incurved leaf margins, longer setae (5–9 mm vs. 3–4 mm), and smaller spores (16–20 µm vs. (19–)21–25 µm).

Weissia newcomeri (E.B. Bartram) K. Saito, J. Hattori Bot. Lab. 39: 423. 1975. — Bryologist 50: 162. f. f–h. 1947. Fig. 4.

Plants in small, more or less dense patches, green or yellowish-green. *Stems* 1–5(–10) mm long. *Leaves* contorted and incurved or crisped when dry, erect-spreading to spreading when wet, 1.4–2.5×0.3–0.45 mm, lanceolate or oblong, with length/width ratio 4–6(8):1, with upper leaf margins narrowly and weakly incurved, slightly cucullate at apices, lower leaves with hardly widened bases, upper leaves with slightly widened bases; *costa* 40–60

(–90) μm wide at base, excurrent into short, smooth mucro, smooth dorsally, ventral stereid band 1–2-layered, dorsal stereid band 2–3-layered, dorsal epidermis not or slightly differentiated; upper and mid-leaf *cells* quadrate and rounded-hexagonal, thin- or moderately thick-walled, 6–9×7–11 μm, papillae 3–4(–5) per cell, low, simple and bifid; basal leaf cells rectangular, smooth, yellowish, with moderately thickened walls, 20–50×8–12 μm. *Autoicous*. *Perichaetial leaves* similar to upper stem leaves, with slightly wider bases. *Setae* (4–) 5–6 mm, yellowish, later becoming light-brownish. *Urns* ca. 1 mm long, cylindrical, weakly narrowed to mouth. *Exothecial cells* thin-walled. *Annuli* differentiated, *opercula* falling off, low conic and with narrow, straight or oblique beaks ca. 0.5 mm long. *Peristome* absent. *Spores* (15–)18–21 μm.

***Distribution and ecology*.** Until recently, this species was considered to be an endemic of Japan, were it is distributed in Honshu, Kyushu, Sikoku, and Okinawa. In Russia it occurs in the southern Far East (Amurskaya Province, Khabarovsk and Primorsky Territories), and in one locality in Kamchatka (Klyuchevskie volcanoes). It grows in forests on soil banks on slopes, along roads and streams, and on rocks and cliffs.

***Differentiation*.** Leaves with obtuse apices and weakly, narrowly incurved upper margins make this species similar to *W. planifolia,* but the latter species is readily distinguished by having a well developed peristome. Other eperistomate species of *Weissia* with long setae occurring in Russia are *W. condensa* (Voit) Lindb. and *W. brachycarpa* (Nees & Hornsch.) Jur. The former species has leaves with stronger involute margins and stronger costae; its distribution in Russia is restricted to the European part. *Weissia brachycarpa* also has stronger incurved leaf margins, shorter setae, and urns clearly narrowed to the mouths.

KEY TO IDENTIFICATION OF *WEISSIA* SPECIES OCCURRING IN RUSSIA[1]

1. Upper and median leaf cells bulging on both surfaces, with 1–2 high, strongly branched papillae per cell ..... *W. armata*
— Upper and median leaf cells not bulging or slightly bulging only on ventral surface, with 3–5 low, simple and bifid papillae per cell 2
2. Setae shorter than urns, capsules immersed into perichaetial leaves 3
— Setae as long as urns or longer, capsules emergent or exserted above perichaetial leaves 6
3. Annuli not differentiated 4
— Annuli differentiated, consisting of few rows of small cells; opercula persistent or falling off 5
4. Capsules round, obtuse, abruptly narrowed into short beaks ..... *W. longifolia*
— Capsules short ellipsoidal, gradually narrowed into low conic, strait or oblique beaks ..... *W. wilsonii*
5. Perichaetial leaves with almost flat or weakly incurved upper margins; opercula often fall off in nature ..... *W. levieri*
— Perichaetial leaves with strongly involute upper margins; opercula usually do not fall off in nature .... *W. angustifolia*

6(2). Capsules on long setae; opercula fall off easily; peristome present, well developed or short 7
— Capsules on short or long setae; opercula fall off easily or can be removed only with special effort; peristome absent 10
7. Anteridia naked, in leaf axils close to archegonia; peristome usually short, occasionally strongly reduced ..... *W. wimmeriana*
— Perigonia bud-like, on stems below perichaetia; peristome well developed 8
8. Upper leaf margins almost flat or weakly incurved; peristome teeth reddish-brown, erect to slightly reclined when dry ..... *W. planifolia*
— Upper leaf margins tightly incurved; peristome teeth pale reddish or yellowish, erect when dry 9
9. Upper leaf margins widely incurved; spores 15–20 μm; widespread .. *W. controversa* var. *controversa*
— Upper leaf margins narrowly incurved; spores (19–) 21–25 μm; Russian Far East .... *W. controversa* var. *sachalinensis*

10(6). Setae 1–3 mm long; capsules cleistocarpous or with differentiated annulus but with opercula persistent in nature 11
— Setae 3–8 mm long; capsules stegocarpous 14
11. Setae as long as urn; capsules emergent .... *W. rostellata*
— Setae 2–3 times longer than urns; capsules exserted 12
12. Perichaetial leaves with tightly involute upper margins; spores 16–21 μm ..... *W. exserta*
— Perichaetial leaves with weakly incurved upper margins; spores 20–25 μm 13
13. Setae straight; opercula falling off, but epiphragm remaining at mouth, so spores are released through breaks of capsule walls ..... *W. squarrosa*
— Setae arcuate when wet; opercula differentiated but persistent, not falling off in mature capsules .... *W.* cf. *exserta* (cf. Fedosov *et al*., 2023.)

14(10). Leaf margins plane or weakly incurved in distal portion; urns hardy narrowed to the mouths .... *W. newcomeri*
— Upper leaf margins widely and tightly involute; urns narrowed to the mouths 15

[1] – The key includes *W. wilsonii* and *W. angustifolia* based on their circumscriptions of Callaghan *et al*. (2019). Few specimens from Russia studied by us appeared to be not genetically similar to so-called specimens from outside Russia. However, our data are so far too few for certain conclusion, hence we call for attention of collectors from Russia to plants with such features.

15. Spores 14–16(–20) µm; costae 60–80(–100) µm wide ..... *W. condensa*
— Spores 16–24 µm; costae 30–50 µm wide .... *W. brachycarpa*

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Appendix 1. Voucher data and GenBank accession numbers for newly sequenced specimens.

Species	Isolate	Locality	Voucher data	ITS, GenBank
Weissia angustifolia	OK3917	Russia: Ryazan Prov.	Volosnova s.n., 21 June 2001, MW9069726	PQ069236
W. brachycarpa	OK1469	Russia: Karachaevo-Cherkessian Rep.	Ignatov & Ignatova 05-3689, MHA	PQ069237
W. brachycarpa	OK1889	Russia: Kabardino-Balkarian Rep.	Ignatov et al. 05-1580, MHA	PQ069238
W. brachycarpa	OK1892	Russia: Dagestan Rep.	Ignatov & Ignatova 09-362, MHA	PQ069239
W. brachycarpa	OK1893	Russia: Altai Rep.	Ignatov 36/365, MHA	PQ069240
W. brachycarpa	OK1894	Russia: Altai Rep.	Ignatov 8/297, MHA	PQ069241
W. brachycarpa	OK1897	Russia: Yakutia Rep.	Ivanova s.n. 12 July 2007, MHA	PQ069242
W. brachycarpa	OK1902	Russia: Orenburg Prov.	Spirina & Zolotov s.n., 1 June 2004, MHA	PQ069243
W. brachycarpa	OK1908	Russia: Astrachan Prov.	Suragina s.n., 5 May 2002, MHA	PQ069244
W. brachycarpa	OK3921	Russia: Voronezh Prov.	Popova, 29 May 2014 #28, MHA9111891	PQ069245
W. brachycarpa	OK1470	Russia: Karachaevo-Cherkessian Rep.	Ignatov & Ignatova 05-1087, MHA	PQ069246
W. condensa	OK1860	Russia: Krasnodar Terr.	Ignatov & Ignatova 05-121, MHA	PQ069235
W. condensa	OK1859	Russia: Krasnodar Terr.	Ignatov & Ignatova 05-101, MHA	PQ069247
W. condensa	OK1471	Georgia: Abkhazia	Teplov KUT-MHA-04-005A, MHA	PQ069248
W. condensa	OK3920	Russia: Krasnodar Terr.	Ignatov & Ignatova s.n., 3 May 2005. MHA9102723	PQ069249
W. controversa	OK1853	Russia: Krasnodar Terr.	Ignatov Ignatova 05-560, MHA	PQ069250
W. controversa	OK1888	Russia: Smolensk Prov.	Ignatov s.n., 16 July 2004, MHA	PQ069251
W. controversa var. *sachalinensis*	OK1851	Russia: Kuril Islands	Barkalov K-52-6-07, MHA	PQ069275
W. controversa var. *sachalinensis*	OK1900	Russia: Kuril Islands	Ignatov 06-1413, MHA	PQ069276
W. controversa var. *sachalinensis*	OK1857	Russia: Sakhalin Island	Pisarenko 03797, MHA ex NVS	PQ069277
W. exserta	OK3925	Russia: Altai Rep.	Ignatov 0/1627, MHA	PQ069258
W. exserta	VF113	Russia: Altai Rep.	Ignatova s.n., 4 Aug 2000, MW9069723	PQ069234
W. exserta	OK1852	Russia: Kabardino-Balkarian Rep.	Ignatov et al. s.n., 3 Aug 2004, MHA	PQ069232
W. levieri	OK1887	Russia: Belgorod Prov.	Ignatov s.n., 3 June 2006, MHA	PQ069259
W. levieri	OK1905	Russia: Caucasus, Krasnodar Terr.	Ignatov & Ignatova 05-666, MHA	PQ069260
W. longifolia	OK1898	Russia: Voronezh Prov.	Popova s.n., 29 May 2014, MHA	PQ069261
W. longifolia	OK1891	Russia: Karachaevo-Cherkessian Rep.	Ignatov & Ignatova 05-3697, MHA	PQ069262
W. newcomeri	OK1468	Russia: Altai Rep.	Ignatov 0/1625, MHA	PQ069252
W. newcomeri	OK1890	Russia: Khabarovsk Terr.	Ignatov 97-1266, MHA	PQ069253
W. newcomeri	OK1895	Russia: Amurskaya Prov.	Bezgodov, 9 July 2010 #353, MHA	PQ069254
W. newcomeri	OK1896	Russia: Yakutia Rep.	Ignatov & Ignatova 11-3470, MHA	PQ069255
W. newcomeri	OK1906	Russia: Khabarovsk Terr.	Ignatov & Ignatova 13-986, MHA	PQ069256
W. newcomeri	OK1907	Russia: Khabarovsk Terr.	Ignatov 97-1262, MHA	PQ069257
W. planifolia	OK1186	Russia: Primorsky Terr.	Ignatov 08-335, MHA	PQ069264
W. planifolia	OK1187	Russia: Amurskaya Prov.	Bezgodov, 10 June 2011 #81, MHA	PQ069265
W. planifolia	OK1188	Russia: Primorsky Terr.	Ignatov 08-374, MHA	PQ069266
W. planifolia	OK1855	Russia: Amurskaya Prov.	Bezgodov, 13 June 2011 #190a, MHA	PQ069267
W. planifolia	OK1856	Russia: Primorsky Terr.	Malashkina & Ivanov Pr-6-4-13, MHA	PQ069268
W. planifolia	OK1885	Russia: Perm Terr.	Bezgodov, 10 Aug 2005 #120, MHA	PQ069269
W. planifolia	OK3924	Russia: Primorsky Terr.	Ignatov et al. 06-2861, MW9069749	PQ069270
W. planifolia	OK3992	Russia: Primorsky Terr.	Ignatov, 14 Sept 1985 #47, MHA9111947	PQ069271
W. rostellata	OK1904	Russia: Voronezh Prov.	Popova s.n., 29 May 2014, MHA	PQ069272
W. rostellata	OK3922	Russia: Rostov-on-Don Prov.	Babenko 831 MHA9111954	PQ069273
W. rutilans	OK3910	Norway	Ignatov & Ignatova 06-5071, MW9069754	PQ069274
W. squarrosa	OK3919	Russia: Vladimir Prov.	Kokoshnikova s.n., 8 June 2007, MW9069758	PQ069233
W. wilsonii	OK3916	Russia: Altai Rep.	Pisarenko s.n., 20 June 1995, MHA9111940	PQ069263
W. wimmeriana	OK3915	Russia: Altai Rep.	Pisarenko s.n., 19 July 2000, MHA9111959	PQ069278
W. wimmeriana	OK1858	Russia: Karachaevo-Cherkessian Rep.	Ignatov & Ignatova 05-3100, MHA	PQ069231

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