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NEW DATA ON THE GENUS *OXYRRHYNCHIUM* (BRACHYTHECIACEAE, BRYOPHYTA) IN THE RUSSIAN FAR EAST

НОВЫЕ ДАННЫЕ О ВИДАХ РОДА *OXYRRHYNCHIUM* (BRACHYTHECIACEAE, BRYOPHYTA) НА РОССИЙСКОМ ДАЛЬНЕМ ВОСТОКЕ

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Abstract

The genus *Oxyrrhynchium* was known in the Russian Far East as represented by a single species, *O. savatieri,* revealed recently in the Kuril Islands. The finding of *O. vagans*, a much more southern species, in Primorsky Territory was unexpected. When sporophytes are present, this species is easily differentiated from most other species of the genus by smooth, not rough setae. However, specimens with sporophytes are rare in *Oxyrrhynchium* and without sporophytes their identification often cannot be certain. Thus we sequenced nrITS of other collections from the Russian Far East and China that lack sporophytes. One another specimen of *O. vagans* has been found among them, from the Kuril Islands. *Oxyrrhynchium savatieri* is found in a sister position to the group of species with strong costa, previously segregated into the genus *Donrichardsia*. No one of Chinese specimens identified as *O. hians* was found in the clade with *O. hians* samples from North America and Europe.

Резюме

Видовое разнообразие рода *Oxyrrhynchium* на российском Дальнем Востоке было известно как представленное всего одним видом, *O. savatieri*, подтвержденным только по находкам с острова Шикотан на Курильских островах. Недавняя находка *O. vagans,* гораздо более южного вида, в Приморском крае оказалась неожиданной. Этот вид хорошо отличается от большинства видов рода гладкой ножкой. Без спорофитов, однако, уверенно различать виды *Oxyrrhynchium* не всегда возможно, в связи с чем видовую принадлежность таких образцов *Oxyrrhynchium* с Дальнего Востока мы проверили с помощью сиквенсов ДНК. В результате был выявлен еще один образец *O. vagans* с российского Дальнего Востока, с острова Шикотан. Образцы *Oxyrrhynchium savatieri* образуют граду к терминальной кладе гигрофильных представителей *Oxyrrhynchium* с мощной жилкой, которые ранее выделялись в особый род *Donrichardsia*. Ни один из образцов *O. hians* из Китая не оказался идентичным образцам этого вида из Европы и Северной Америки.

KEYWORDS: *Oxyrrhynchium savatieri,* nuclear ITS, East Asia, China, taxonomy, DNA-barcoding

INTRODUCTION

The moss family Brachytheciaceae includes many groups that are difficult for identification. The reason for that is the deficiency of characters useful for the species delimitation. One of the most widely used characters is the leaf shape: it is often the main distinction between species in the largest genera of the family, e.g. *Brachythecium, Sciuro-hypnum, Oxyrrhynchium, Rhynchostegium,* and *Rhynchostegiella*. At the same time, its variation is enormous, and the 'typical' shape, which has to be chosen when using a dichotomous key, often pose the problem of necessity of choice with quite low certainty.

Nevertheless, the leaf shape remains unavoidable in the Brachytheciaceae keys to identification, as species are numerous, while characters are few. The leaf shape appears to be helpful when a specimen is large and represent optimally developed plants. Most species in such condition can be named with a high confidence. Alternatively, few depauperate shoots of Brachytheciaceae, which regularly come to attention of bryologist from the collections gathered for vegetation relevees often cannot be identified for sure. In such cases, and especially if the identification is very important, the still expensive molecular barcoding approach might help. The present paper illustrates one of such cases with the genus *Oxyrrhynchium* in the Russian Far East.

The genus *Oxyrrhynchium* (Bruch, Schimp. & W. Gümbel) Warnst. was originally proposed as a subgenus of *Eurhynchium* (Bruch *et al*., 1854). It was elevated up to generic level about a hundred years ago, but shortly after that it had been returned to *Eurhynchium* as an infrageneric unit, and then resurrected only after molecu-

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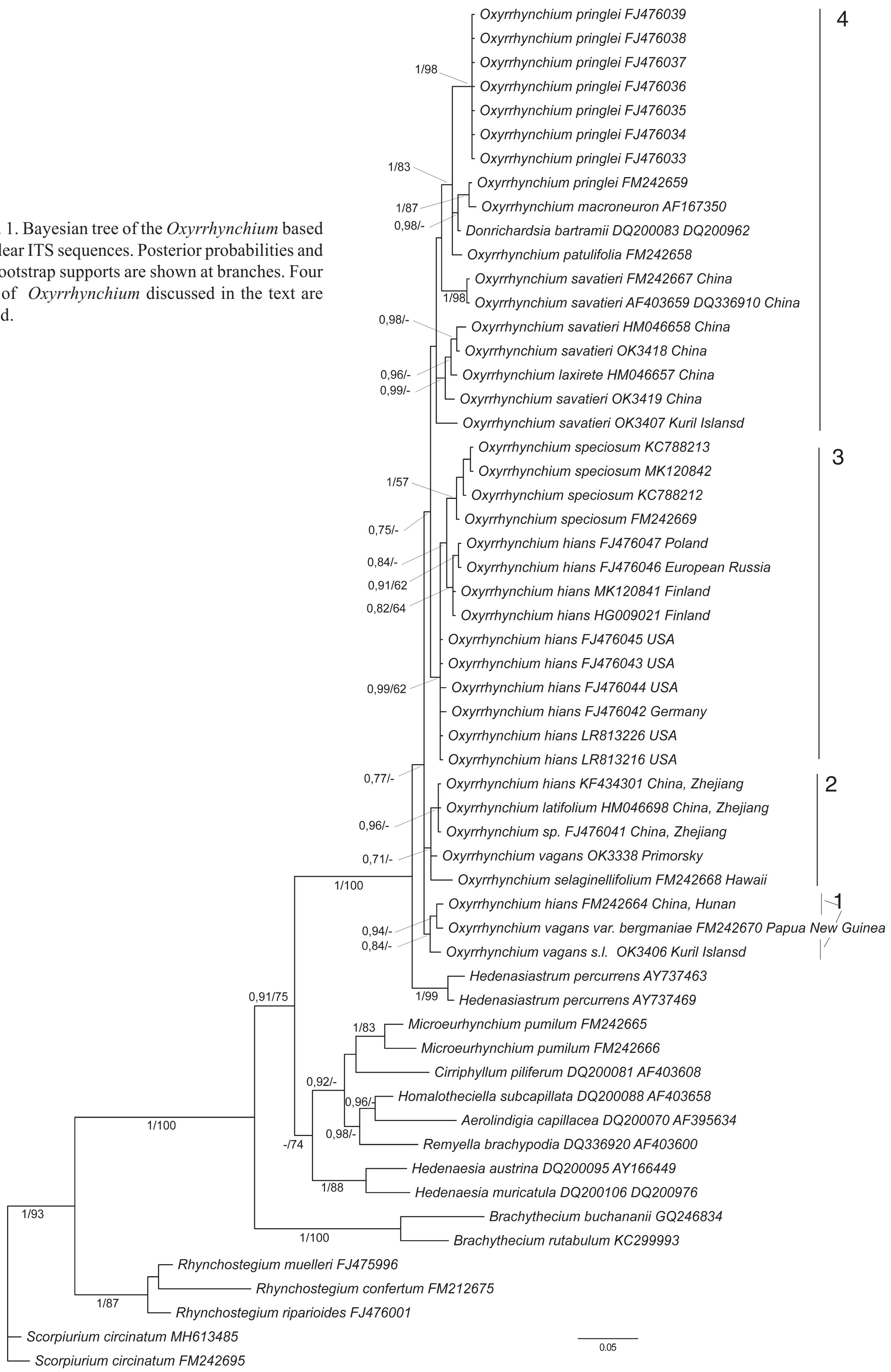

Fig. 1. Bayesian tree of the *Oxyrrhynchium* based on nuclear ITS sequences. Posterior probabilities and / MP bootstrap supports are shown at branches. Four clades of *Oxyrrhynchium* discussed in the text are labelled.

lar phylogenetic stidies found out that *Oxyrrhynchium* and *Eurhynchium* belong to different subfamilies of the Brachytheciaceae (Ignatov & Huttunen, 2002).

The genus *Oxyrrhynchium* was typified with *O. hians* (Ignatov & Isoviita, 2003), a species with a long history of taxonomic interpretations and confusion with '*Eurhynchium praelongum*', now in the genus *Kinbergia,* that belongs to the third subfamily of the Brachytheciaceae, i.e., other than *Eurhynchium* and *Oxyrrhynchium*.

Oxyrrhynchium hians is a widespread species in eastern North America and western half of Eurasia, while its East Asian distribution is not very well known. It was included in the floras of China (Wang & Hu, 2008; Ignatov *et al.*, 2005) and Japan (Noguchi *at al.*, 1991). It was reported from the Russian Far East by Lazarenko (1941), Bardunov & Cherdantseva (1982), and subsequent checklists (e.g., Ignatov *et al.*, 2006). However, the critical revision for the "Moss Flora of Russia" by Ignatov (2020) excluded it from the Russian Far East, finding reliable data on distribution eastwards only to Central Siberia. Most so-called collections from the Russian Far East appeared to be *Myuroclada longiramea*, the outstandingly protean species (Ignatov *et al.*, 2015).

Thus, the Moss Flora of Russia reported only one species of *Oxyrrhynchium* in the Russian Far East, *O. savatieri* Besch. This species has been described from Japan and reported also from China and Corea. Only two collections (both made by V.A. Bakalin) of this species from Russia are known, from two different localities in Shikotan Island, Kuril Islands (Ignatov, 2020).

The recent exploration of the moss flora of Ussurijsky State Nature Reserve in Primorsky Territory revealed *O. vagans* – the third species of *Oxyrrhynchium* for the moss flora of Russia (Ishchenko *et al.*, 2022). It is distinguished from *O. hians* and *O. savatieri* by having smooth setae. This finding was quite unexpected, as *O. vagans* is a much more southern, mainly tropical species. Suspecting that there could be more samples of *O. vagans* among herbarium collections, we applied the DNA barcoding for a search among specimens without sporophytes.

MATERIAL AND METHODS

The ITS sequences were used as they appeared to be most helpful for the taxonomy of Brachytheciaceae (Huttunen & Ignatov, 2004, 2010; Wynns *et al.*, 2009). Once the sequence of presumably *O. vagans* from the Russian Far East was obtained, the BLAST search selected the maximally similar sequences in GenBank, which were added to the analysis. In addition, few more samples from the Russian Far East and China available in MHA herbarium were sequenced. Newly obtained sequence data are provided in the Appendix 1.

We added to analysis the representatives of all three subfamilies of Brachytheciaceae (Huttunen *et al.*, 2015), with the better representation of Helicodontioideae where *Oxyrrhynchium* belongs to.

Sequences were aligned using MAFFT v. 7.402 (Katoh & Standley, 2013) with standard settings.

Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with 6 000 000 generations, and the chain temperature 0.02 in all analyses. Consensus trees were calculated after omitting the first 25% trees as burn-in.

Maximum parsimony analysis was performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 1000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

Morphological studies were conducted in a standard way. Illustrations were made under stereomicroscope Olympus SZX-7 (digital camera Infinity 8-8) and Olympus CX43 (digital camera Infinity 1-2), with Z-stacking in Helicon Software (Kozub *et al.*, 2008).

Amplification and sequencing protocols were essentially the same as in our previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005).

RESULTS

The Bayesian tree topology was found similar to previous analyses in separating three subfamilies. The Helicodontioideae taxa formed two clades, one (without support) includes a variety of genera: *Cirriphyllum, Hedenaesia, Remyella, Aerolindigia, Homalotheciella,* and *Microeurhynchium*, while another one, maximally supported (PP=1, BS=100) includes *Oxyrrhynchium* taxa and *Hedenasiastrum* as its sister group. The clade of the latter includes two samples (PP=1, BS=99), while the *Oxyrrhynchium* clade is almost unsupported (Fig. 1). However, its topology in the Bayesian analysis is identical with the strict consensus topology in the maximum parsimony analysis (not shown), segregating (with or without support) species and their groups that are essentially consistent with the morphology.

The *Oxyrrhynchium* clade includes the grade of the following subclades:

(1) 3 samples: a New Guinean sample of *O. vagans* var. *bergmaniae*, one sample from Kuril Islands, and one Chinese specimen (identified as *O. hians*).

(2) 5 samples: Hawaiian *O. selaginellifolium*, Russian Far Eastern *O. vagans,* three samples from Zhejiang Province of China (deposited in GenBank as *O. hians*, *O. latifolium* and as *O.* sp. [*O.* sp. in Genbank and the respecive specimen in NY identified as *O. pringlei*]).

(3) 14 samples, including 10 specimens of *O. hians* and nested within them subslade of 4 specimens of *O. speciosum*. Interestingly, *O. hians* includes two subgroups: five samples from North America and one from Germany form a polytomy, with a nested clade of 4 specimens from Russia, Poland and Finland.

(4) 18 samples of 'the former *Donricharsia*' (an aquatic lineage of *Oxyrrhynchium*, characterized by species with stronger and longer costae) in terminal position and a grade to it formed by *O. savatieri* and one GenBank accession named *O. laxirete*.

The *'Donrichardsia'* clade (ten specimens of four species) is the only multispeciose clade in the present analysis which gained a high support (PP=1, BS=83). The

Fig. 2. *Oxyrrhynchium savatieri* from Russia, Kuril Islands, Shikotan Island, *Bakalin K-49-42-07,* MW9051874 (isolate OK3407). A–B: habit, dry; C: stem leaf; D: distal leaf cells; E: median laminal cells; F: habit, wet.

support of *O. hians*+*O. speciosum* clade is much lower (PP=0.99, BS=63).

DISCUSSION

The difficulties with the identification of poor collections of Brachytheciaceae were already mentioned in the introduction. This is the case of the present study: besides the recently collected perfect specimen of *Oxyrrhynchium vagans* with sporophytes, other collections available for this study are represented by few shoots each and lack sporophytes.

One of them, OK3407, identified as *O. savatieri,* has been confirmed in the present study by DNA sequence (Fig. 1). This is an important evidence because: (1) this is the only specimen definitely confirmed for Russia; (2) the specimen itself is rather poorly developed, and such traits as the conspicuous complanate foliage and a relatively long costa are not well expressed, posing a question on the specimen identity (Fig. 2). Its placement in *O. savatieri* was based on a relatively narrow laminal cells, narrower than usually in *O. hians*, and on a more triangular leaf shape (Fig. 2C) vs. more elliptic in branch leaves of *O. hians*.

We sequenced two specimens from China, Hunan Province, which were referred to *O. hians*, mostly because their branch leaves have no complanate aspect at all (Fig. 3A–B). The laminal cells are, however, long and narrow (Fig. 3E). The molecular phylogenetis analysis resolved them within *O. savatieri*-grade. This fact suggests reconsidering of the value of cell shape and complanate branch foliage, increasing the importance of the former and decsreasing a diagnositc value of the latter.

The costa in *O. savatieri* is usually longer than in *O. hians* s.l.; this is consistent with its sister position to the clade of species with strong costa, previously segregated into *Donrichardsia* (Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004; Wynns *et al*., 2009).

Only one specimen among *Oxyrrhynchium* samples related to ‘*Donrichardsia* clade’ has been deposited in

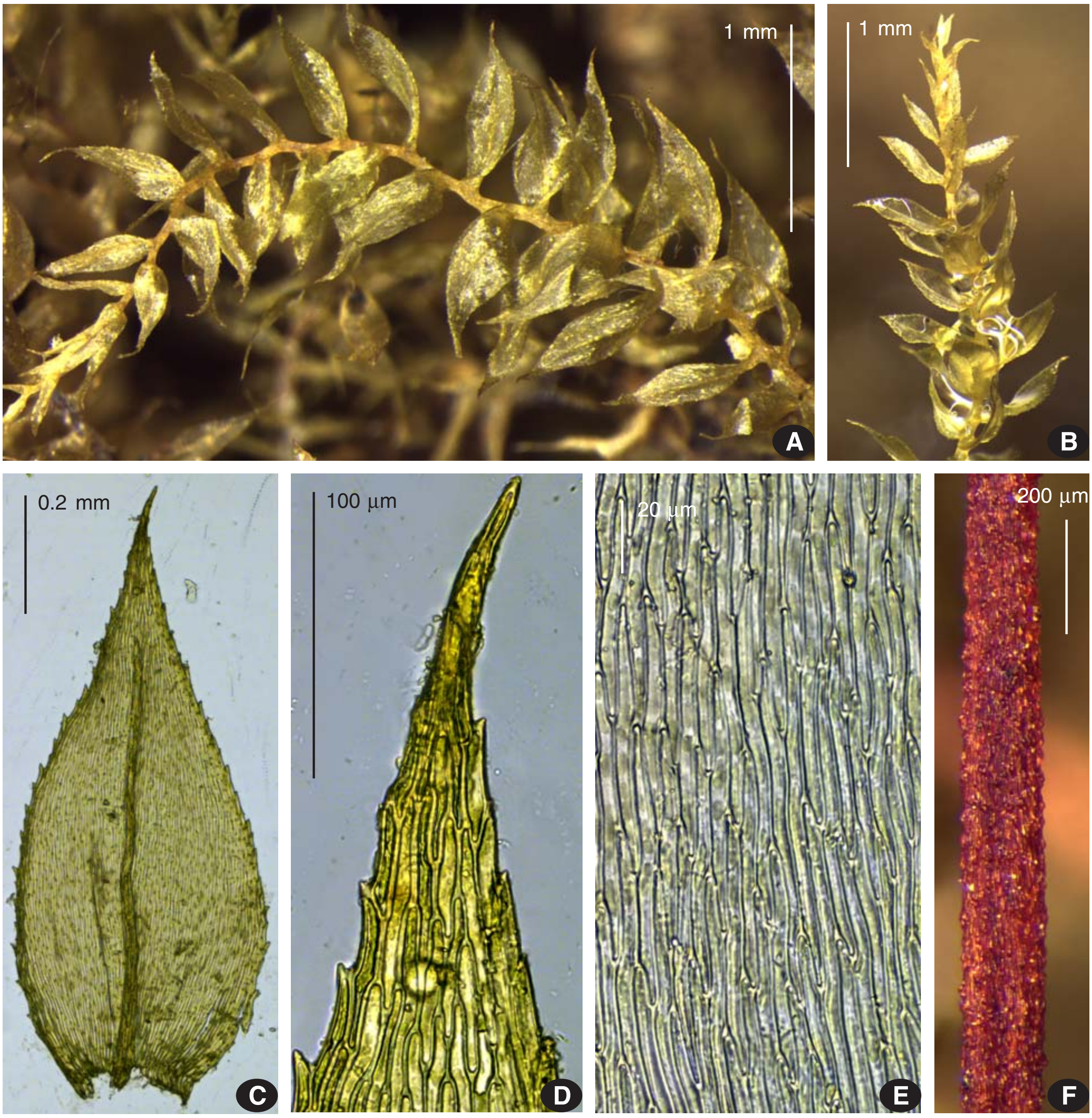

Fig. 3. *Oxyrrhynchium savatieri* from China, Hunan, Koponen *51808*, MHA9067103 (Isolate OK3418): A: habit, dry; B: habit, wet; C: stem leaf; D: distal leaf cells; E: median laminal cells; F: seta.

GenBank under the name other than *O. savatieri* (cf. Fig. 1): it is *O. laxirete*, a rather imperfectly known species, which main distinction from *O. savatieri* includes a somewhat broader cells and still longer costa (Takaki, 1956). Noguchi *et al*. (1991) accepted it as well, although mentioned that it is doubtly distinct from *O. savatieri.*

The current analysis shows that *O. hians* specimens from Europe and North America form a clade, albeit without support, that also includes *O. speciosum.* No one Chinese specimen referred to *O. hians* appeared within this clade. Interestingly, North American *O. hians* plus one specimen from Germany differ from Russian+ Polish+Finnish plants in one unique substitution in ITS1 region. The latter group of samples forms a nested clade within a polytomy of American (+ one Germanian) accessions, cf. Fig. 1. The strictly European subclade of *O. hians* is sister to *O. speciosum*, mainly European species, occurring also in West Asia and Macaronesia. Obviously, the phylogeography of *Oxyrrhynchium* is an intriguing matter for further studies based on expanded sampling.

Chinese *Oxyrrhynchium* specimens are especially thoublesome. The present analysis based on a relatively small sampling indicates that *Oxyrrhynchium hians* s.str., i.e., genetically similar to North American and European plants, is still not found in China. So-named specimens appeared to belong mainly to *O. savatieri*, which seems to be more common in East Asia.

The present results also show that the *Oxyrrhynchium* species with smooth setae, the *O. vagans* group, are likely more widespread than previously thought. Specimens with sporophytes are very easy to refer to this group. However, sporophytes are rare in most species of the genus, and in some species even unknown, e.g. in East Aisan *Oxyrrhynchium latifolium* (*Eurhynchium latifolium*) and Hawaiian *O. selaginellifolium*. Thus, the fact that the particular specimen belongs to *O. vagans* group is difficult to confirm. Some keys, e.g. in Ignatov *et al.* (2005) highlight the long laminal cells (>100 µm) as an important character for *O. vagans* (cf. Fig. 3). However, the long laminal cells seem to correlate with the general plant stature: the robust plants have laminal cells reaching 140–150 µm in Papua New Guinea (Ignatov *et al.*, 1999), in Hunan Province of China (Ignatov *et al.*, 2005), and in recent cellections from Primorsky Territory of Russia (Fig. 4).

Oppositely, there are descriptions of *O. vagans* where leaf cells are reported to be only up to 95–100 µm long, i.e., as in *O. savatieri*. Such shorter cell length for *O. vagans* is reported for Taiwan, to 100 µm (Takaki, 1956); for China [Sichuan and Yannan], to 100 µm (Wang & Hu, 2008); for Papua New Guinea, for *O. vagans* var. *vagans*, to 100 µm (Ignatov *et al.*, 1999); and for the original material from India (Ignatov *et al.*, 1999).

There is another species with the smooth setae in China, *Oxyrrhynchium protractum* (Müll. Hal.) Broth. It is a little known species described from Shaanxi Province (Müller, 1896), and definitely known by the type only. Ignatov *et al.* (2005) synonymized with question mark with *O. protractum* two taxa, *Rhynchostegium leptomitophyllum* Müll. Hal. and *Rhynchostegium subspeciosum* var. *filiforme* Müll. Hal. Both of them were described from Tsin-lin Mountains in Shaanxi Province and never recorded since the end of 19th century. The question mark was put for them because of sporophyte absence and paucity of material. Laminal cells in *O. protractum* are up to 90 µm long (Ignatov *et al.*, 2005), and plants in the above mentioned collections are quite slender.

One more rather short-celled representative of the *O. vagans* group is the specimen from Kuril Islands, Shikotan Island, shown in Fig. 5. Its assignment to this group is based on the present molecular phylogenetic studies (Fig. 1), which resolve it in a clade with *O. vagans* var. *bergmaniae* from Papua New Guinea and GenBank specimen '*O. hians* FM242664 from China [Hunan, Koponen 53740, H, det. Ignatov]'. Only two specimens out of 31 identified as *O. hians* from Hunan had sporophytes, thus short-celled morphotypes were referred to *O. hians* 'by default': as differing from *O. savatieri* in non-complanate aspect, and from *O. vagans* in short cells.

Three samples from the *Oxyrrhynchium* clade first emerging in its phylogenetic tree are not similar morphologically: Papua New Guinean one is a robust plant and has long laminal cells, whereas Russian and Chinese plants are slender and short-celled (cf. Fig. 5).

Another clade comrising plants with smooth setae occurs next in the grade after the specimens described above (Fig. 1). It includes five samples, three of which were taken from GenBank, and their morphology remains unknown for us. The Hawaiian *O. selaginellifolium* is a robust plant with long cells (sporophyte unknown), and the Russian Far Eastern *O. vagans* c. fr. is similar to it in the mentioned traits (Fig. 4).

The finding of *Oxyrrhynchium vagans* in the Russian Far East is fairly unexpected. This species was described from the Himalayas in India and later found in many areas of Indochina, Malaysia, Indonesia, Papua New Guinea, Philippines, and Oceania (Hawaii). It was reported in the Moss Flora of China (Wang & Hu, 2008) in Sichuan and Yunnan only, and later added to the flora of Hunan Province by Ignatov *et al.* (2005). Earlier, Takaki (1956) also cited this species for Taiwan.

In Japan *Oxyrrhynchium vagans* has not been reported by Takaki (1956) and Noguchi *et al.* (1991), but later Iwatsuki (2004) listed it from Ryukyu.

Ignatov *et al.* (1999) studied rich collections of T.J. Koponen and D.H. Norris expeditions to Papua New Guinea and found that *Oxyrrhynchium* (that time *Eurhynchium*) with smooth setae is represented there by at least two taxa, which were referred to two varieties of *Oxyrrhynchium vagans*. A moderately small plants were referred to *O. vagans* var. *vagans,* whereas a robust morphotype was named *O.* (as *Eurhynchium*) *vagans* var. *bergmaniae* (based one *E. bergmaniae* E.B. Bartram, described from Indonesian part of New Guinea).

Ignatov *et al.* (1999) found that in Papua New Guinea var. *vagans* and var. *bergmaniae* differ in plant size, the latter being much more robust. However, they accepted them as merely varieties because in other areas, e.g. in Philippines, there are plants with intermediate morphology. In Russian specimens the morphology is opposite: small plants are in the clade with robust Papua New Guinean var. *bergmaniae*, whereas the robust morphotype from Russia is in another clade. The present results challenges the differentiation of two these varieties of *O. vagans*.

At the same time, all these eight samples from first and second clades differ from all other studied species of *Oxyrrhynchium* (*O. hians, O. speciosum, O. savatieri,* and *O. laxifolium*) in one substitution in ITS1. One specimen from China, Hunan, referred by us to *O. vagans* (Ignatov *et al*., 2005) was sequenced (FM242671). It is not included in the molecular phylogenetic tree (Fig. 1), due to incomplete reading, but the mentioned substitution confirms its position in *O. vagans*.

Thus, we see that all samples (albeit only two) with smooth setae occur in the first and second clade of the basal grade in the phylogenetic tree of *Oxyrrhynchium*. Further on in the tree all species have rough setae, and wherever this was checked, there was no exceptions.

We may tentatively propose that some or all specimens found in the first and second clade belong to *O. vagans*

Fig. 4. *Oxyrrhynchium vagans* (from: Russia, Primorsky Territory, Ussurijsky Reserve, *Ishchenko*, MHA (isolate OK3338). A–C: habit (A–B: dry, C: wet), D: plant with sporophyte (showing smooth seta); E: stem leaf; F: distal leaf cells; G: median laminal cells.

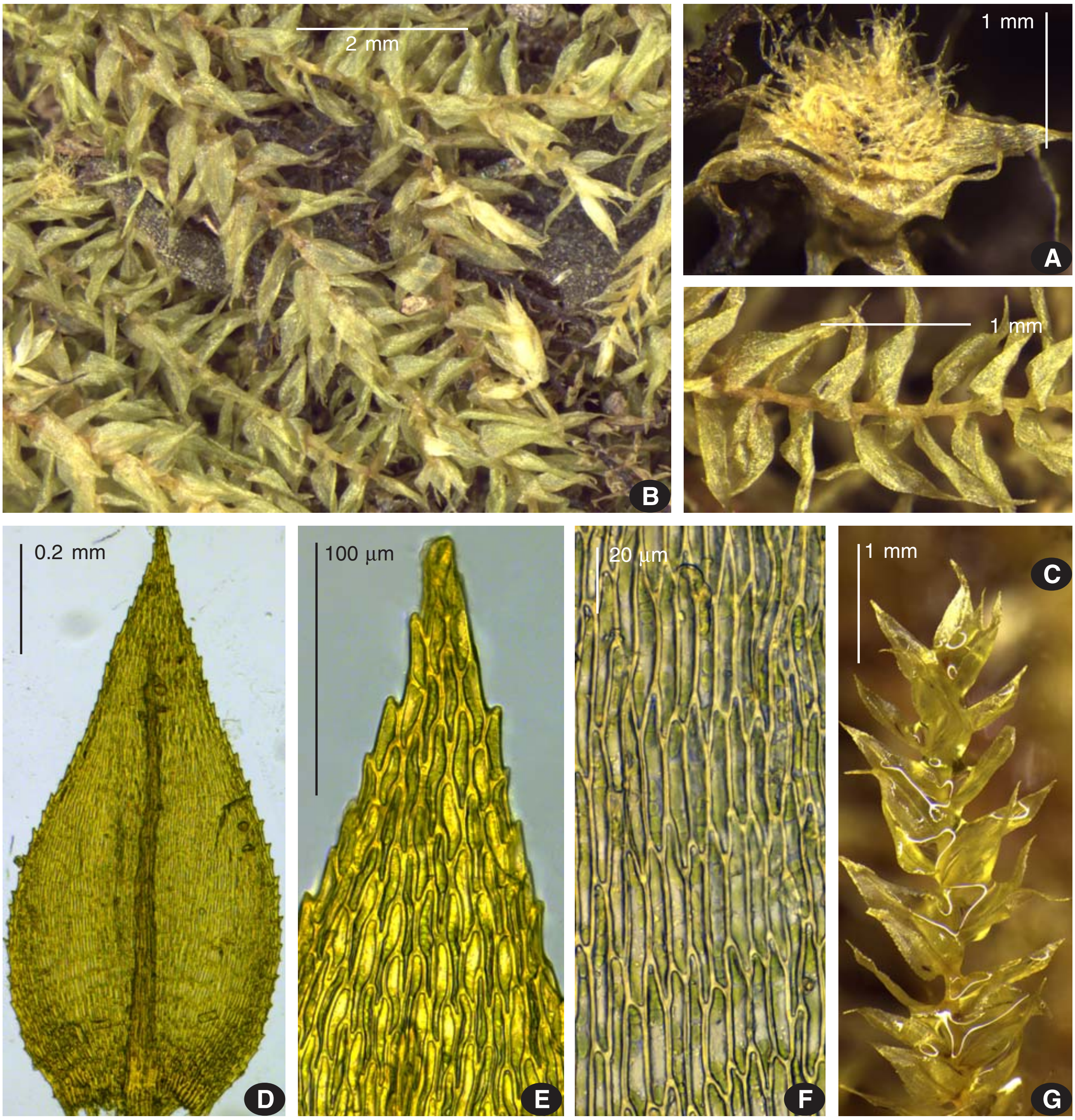

Fig. 5. *Oxyrrhynchium vagans* s.l. from: Russia, Kuril Islands, Shikotan, *Bakalin K-49-42-07,* MW9051874 (isolate OK3406). A: perichaetium with numerous paraphyses; B–C: habit, dry; D: stem leaf; E: distal leaf cells; F: median laminal cells; G: habit, wet.

group. However, the variation in sequences is still not fully understood, thus we are pending the question of the species identity for specimens not studied by us.

As the Shikotan specimen (Fig. 5) has no sporophytes, its assignment to *O. vagans* is also easy to oppose. At the same time, though lacking setae, the specimen has perichaetia with very long, abundant paraphyses (Fig. 5A).

Regarding varieties of *O. vagans*, we can only conclude that the genetic differentiation found in the present study seems to be too subtile for their segregation. There is no one position in alignment where three samples of the first clade differ from all five samples of the second clade in Fig. 1. Therefore, we accept two Russian samples of *O. vagans* s.l. without recognition of any taxononic units, unlike previously proposed segregation of *O. bergmaniae* (Huttunen & Ignatov, 2010), partly based on plastid *trn*T-*trn*E marker. Further study of *O. vagans*-group with expanded sampling and additional markers is required.

Regardless the taxonomic problems, the finding of *O. vagans* s.l. in Russia looks odd, considering much more southern distribution of this species. Overlooking and undercollecting are, of course, always a possible explanation. However, a possibility of the recent expansion of *O. vagans* should be also considered. Current global climatic changes result in more numerous and more severe cyclons affecting the hemiboreal and even boreal vegetation of the Russian Far East as described recently by Korznikov *et al*. (2022).

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Appendix 1. Newly sequenced specimen vauchers and GenBank accession numbers.

Oxyrrhynchium vagans OK3338	Russia: Primorsky Territory, Ussuriisky Reserve, *Ishchenko,* MHA	OP998265
Oxyrrhynchium vagans OK3406	Russia: Kuril I., Shikotan, *Bakalin K-49-42-07*, MW9051874	OP998266
Oxyrrhynchium savatieri OK3407	Russia: Kuril I., Shikotan, *Bakalin K-50-20-07*, MW9051875	OP998267
Oxyrrhynchium savatieri OK3418	China: Hunan, *Koponen 51808*, MHA9067103 (det. Ignatov as *O. hians*)	OP998268
Oxyrrhynchium savatieri OK3419	China: Hunan, *Koponen 31742*, MHA9067096 (det. Ignatov as *O. hians*)	OP998269

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