

A REVISION OF THE GENUS *ORTHOTHECIUM* (PLAGIOTHECIACEAE, BRYOPHYTA)
IN NORTHERN EURASIA
РЕВИЗИЯ РОДА *ORTHOTHECIUM* (PLAGIOTHECIACEAE, BRYOPHYTA)
В СЕВЕРНОЙ ЕВРАЗИИ

MICHAEL S. IGNATOV^{1,2}, JAN KUČERA³, LARS HEDENÄS⁴, OXANA I. KUZNETSOVA¹
& ELENA A. IGNATOVA²

МИХАИЛ С. ИГНАТОВ^{1,2}, ЯН КУЧЕРА³, ЛАРС ХЕДЕНАС⁴, ОКСАНА И. КУЗНЕЦОВА¹,
ЕЛЕНА А. ИГНАТОВА²

Abstract

A revision of the genus *Orthothecium* involving a molecular phylogenetic approach was performed based on material from northern Eurasia with a particular focus on the territory of Russia. It showed that diversity of the genus in Asian Russia, and particularly in the permafrost regions of Siberia was strongly under-recorded if labelled with names of European species. While all five currently accepted European species occur in Asian Russia (although *O. rufescens* probably only reaches European-Asian borders), four additional species need to be described as new to science: *O. brunnescens*, *O. retroflexum*, *O. remotifolium* and *O. sibiricum*. The ranges of *O. lapponicum*, *O. chryseon*, *O. intricatum* and *O. rufescens* are discussed and revised. *Orthothecium strictum* and *O. intricatum* harbour a surprisingly high genetic diversification, however, the phylogenetic signal from analysed chloroplast and nuclear loci shows a reticulate pattern, which does not allow for drawing unequivocal taxonomic conclusions; moreover, the morphological characters are not fully consistent with the intraspecific molecular lineages and show mostly a clinal type of variation, hence we have refrained from description of additional species or intraspecific taxa. Incomplete lineage sorting has been documented in several cases between *O. sibiricum* and *O. lapponicum* and between *O. intricatum* and *O. rufescens*. Such specimens often show an intermediate morphology.

Резюме

Таксономическая ревизия рода *Orthothecium* с привлечением молекулярно-филогенетических методов проведена на материале из Северной Евразии, преимущественно с территории России. Показано, что видовое разнообразие этого рода в азиатской части России, особенно в районах распространения многолетней мерзлоты было сильно недооценено, как следствие того, что к растениям с этой территории применялись названия видов, описанных из Европы. В азиатской части России встречаются все пять европейских видов (хотя *O. rufescens*, по-видимому, едва заходит на восток от границы между Европой и Азией); кроме того, еще четыре вида необходимо описать как новые для науки: *O. brunnescens*, *O. retroflexum*, *O. remotifolium* и *O. sibiricum*. Обсуждается и уточняется распространение *O. lapponicum*, *O. chryseon*, *O. intricatum* и *O. rufescens*. У *Orthothecium strictum* и *O. intricatum* выявлено удивительно высокое генетическое разнообразие, однако филогенетический сигнал изученных хлоропластных и ядерных участков показывает ретикулятность, что не позволяет сделать однозначные таксономические заключения; более того, морфологические признаки не полностью соответствуют выделяемым по молекулярным маркерам внутривидовым группировкам и часто показывают клинальный тип варьирования; на этом основании мы воздерживаемся от описания дополнительных видов или внутривидовых таксонов. Неполная сортировка линий была выявлена в нескольких случаях между *O. sibiricum* и *O. lapponicum* и между *O. intricatum* и *O. rufescens*. У таких образцов часто имеются промежуточные морфологические признаки.

KEYWORDS: *Orthothecium*, Hypnales, taxonomy, molecular phylogeny, internal transcribed spacer, *trnF-trnS*, plastid, incomplete lineage sorting, homoplasy, phenotypic plasticity, distribution, Russia

¹ – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia – Россия 127276 Москва, Ботаническая 4, ГБС РАН; e-mails: misha_ignatov@list.ru; oikuznets@gmail.com

² – Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory 1-12, Moscow 119234 Russia – Москва, Ленинские горы 1 стр. 12, Московский государственный университет им. М.В. Ломоносова, Биологический факультет, кафедра экологии и географии растений; e-mails: misha_ignatov@list.ru; arctoa@list.ru

³ – University of South Bohemia, Faculty of Science, Department of Botany, Branišovská 1760, CZ–370 05 České Budějovice, Czech Republic; e-mail: kucera@prf.jcu.cz

⁴ – Swedish Museum of Natural History, Department of Botany, Box 50007, SE-104 05 Stockholm, Sweden; e-mail: lars.hedenas@nrm.se

INTRODUCTION

The genus *Orthothecium* Bruch, Schimp. & W. Gümbel was described in *Bryologia Europaea* (Bruch *et al.*, 1851), segregating a small group of mosses, characterized, among others, by lustrous plants of golden-green, reddish to purplish colour. Even after 170 years its delimitation has not been challenged; however, the species identification remains difficult due to the lack of invariable characters and the presence of transitional morphotypes.

Orthothecium has never been revised worldwide after Brotherus (1925) who assigned to it eight species in his monumental worldwide treatment for Engler's Pflanzenfamilien. Among them several were widely distributed in Europe and assigned to the genus upon its establishment, *O. rufescens* (Dicks. ex Brid.) Bruch, Schimp. & W. Gümbel, *O. chryseon* (Schwägr.) Bruch, Schimp. & W. Gümbel, and *O. intricatum* (Hartm.) Bruch, Schimp. & W. Gümbel, two species described by Lorentz (1864) from European Alps, *O. binervulum* Molendo and *O. strictum* Lorentz, then *O. acuminatum* Bryhn from Greenland and arctic Canada (Bryhn, 1906), the Chinese *O. catagonioides* Broth. (Lever, 1906), and the European *O. duri-aei* (Mont.) Besch. The two latter species were subsequently placed in other genera: *O. catagonioides* in *Isopterygiopsis* (Iwatsuki, 1970) and *O. duri-aei* in *Pseudorhynchostegiella* Ignatov & Vanderp. (Aigoin *et al.*, 2009).

Orthothecium binervulum Molendo was accepted in most floras and catalogues as a separate species in the 19th and first half of 20th centuries, but was later synonymised with *O. strictum* Lorentz by Steere (1947), who likely adopted the earlier suggestion by Grout (1928). *Orthothecium lapponicum* (Schimp.) C. Hartm. was combined to the genus by Hartman (1871), but it has not been accepted by Brotherus as a species and its resurrection has not occurred until the study of Hedenäs (1988).

Four historical names remaining in the genus *Orthothecium* in Tropicos database (<https://www.tropicos.org/nameSearch>, accessed 10 June 2020) have not yet been assigned to other genera, as only old incomplete data exist for them. None of these, however, seems to belong to the genus: (1) for *O. austrocatenulatum* (Müll. Hal.) Kindb. from southern South America, leaves with a percurrent costa are described; (2) *O. diminutivum* (Grout) H.A. Crum, Steere & L.E. Anderson, according to Redfearn Jr. (2014), putatively belongs in *Isopterygiopsis pulchella*; (3) *O. ovicarpum* (Dixon) W.R. Buck was placed in *Orthothecium* with the comment that it may not belong in the genus; the species epithet refers to a capsule shape which is unknown in other species of the genus; and (4) *O. schlagintweitii* (Sendtn. ex Müll. Hal.) Paris, from Central Europe, Carinthia, is likely also wrongly placed in the genus, as the protologue mentions a distinct costa.

Apart from the resurrected *O. lapponicum*, the first addition to the genus after Brotherus was thus *O. hya-*

lopiliferum Redf. & B.H. Allen, described from south-west China (Redfearn & Allen, 1991, 2005).

The recent study by Hedenäs *et al.* (2019) resulted in a considerable range extension for *O. lapponicum*: with the help of molecular markers its presence was confirmed in North-East Asia (Yakutia) and in the Arctic Archipelago of Canada. During that study, however, several studied specimens showed considerable inconsistencies between their morphology and position in the phylogenetic trees built on the nuclear ITS. In order to elucidate this enigma, we expanded the set of studied specimens in the present study and added the plastid region *trnF-trnS*, which contains variable *trnL-trnT* and *trnT-rps4* spacers, in addition to the commonly used *trnL-trnF* and *rps4-trnS* regions. The whole region appeared to be helpful in several pleurocarpous groups such as the closely related *Plagiothecium* (Wynns & Lange, 2014), but also in the Neckeraceae (Enroth *et al.*, 2019) and Anomodontaceae (Ignatov *et al.*, 2019).

MATERIALS AND METHODS

Sampling. Given the initial information from the study of Hedenäs *et al.* (2019), we at first concentrated at covering the observed morphological variability within Russian specimens labelled as *Orthothecium chryseon*, *O. rufescens* and *O. strictum*. The sampling for the study however developed on-the-go, having reflected the progress in understanding the variability of studied taxa. With respect to sampling of molecular loci, the initial decision was to sample the nuclear ribosomal ITS and chloroplast *atpB-rbcL* but we soon found that the variability in the latter locus is too low to yield a reasonable resolution and even for ITS, the locus obviously was unable to distinguish between morphologically extremely different plants (later identified with *O. chryseon* and the newly described *O. sibiricum*), while it showed an extreme diversity within specimens morphologically attributable to 'typical' *O. intricatum* or *O. strictum*. Therefore, we made a survey of variability within several loci investigated earlier in the study by Wynns & Lange (2014) and decided to employ the *trnL-rps4* and later even the whole *trnF-trnS* region for at least a subset of analysed specimens.

DNA isolation, PCR and sequencing. The samples were partly processed at the Tsitsin Main Botanical Garden in Moscow (isolates annotated as OK####, see Appendix) following the protocols described in Fedosov *et al.* (2016), and partly in the molecular laboratory of the Department of Botany at University of South Bohemia (isolates annotated as Ot####), following the protocols described in Kučera *et al.* (2019). These collections are marked in Appendix as deposited in CBFS. For the *trnL-rps4* region, we used the primers *rps4-166F* and *P6/7*, amplified as described in Wynns & Lange (2014).

Sequence editing, alignment and analysis. Raw sequence data were checked for sequencing errors and primer complements trimmed in BioEdit v.7.2.5 (Hall, 1999)

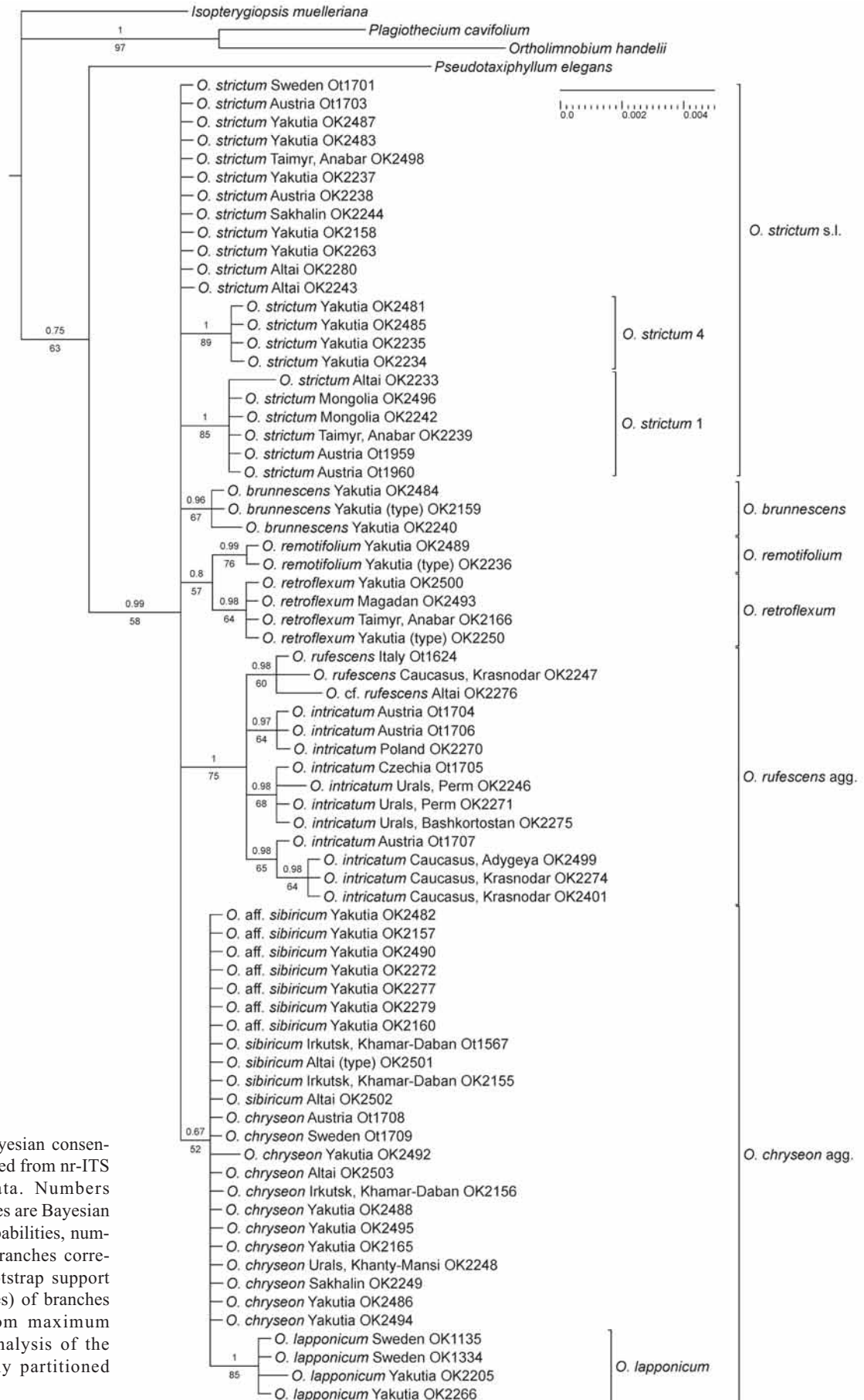
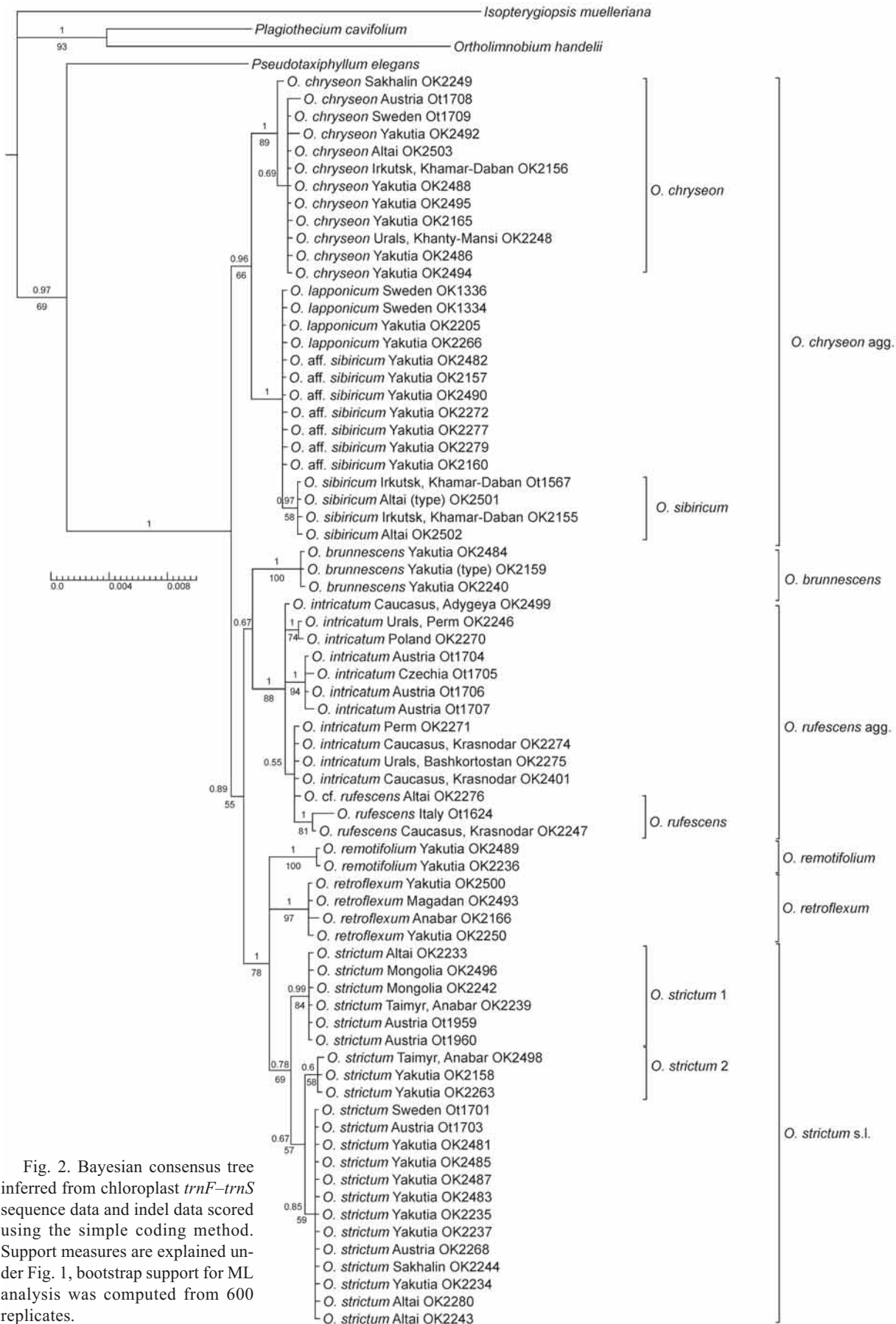


Fig. 1. Bayesian consensus tree inferred from nr-ITS sequence data. Numbers above branches are Bayesian posterior probabilities, numbers below branches correspond to bootstrap support (550 replicates) of branches obtained from maximum likelihood analysis of the same, equally partitioned dataset.



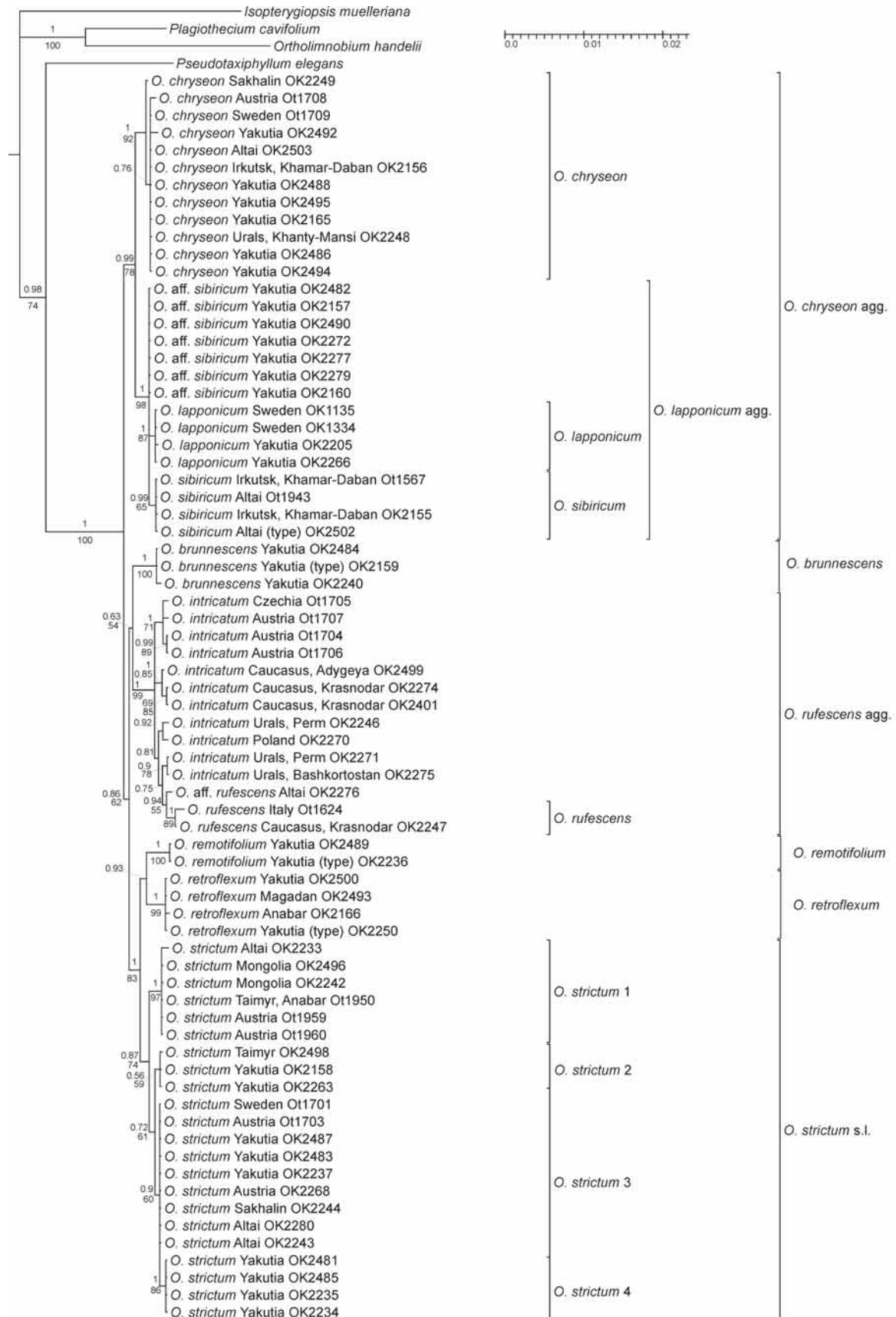


Fig. 3. Bayesian consensus tree inferred from concatenated nr-ITS and chloroplast *trnF-trnS* sequence data, partitioned according to genomic compartments (nuclear and concatenated chloroplast data, respectively). Indel data from the chloroplast partition were scored using the simple coding method. Support measures are explained under Fig. 1, bootstrap support for ML analysis was computed from 550 replicates.

and Geneious Prime 2020 (Biomatters Ltd., <http://www.geneious.com/>). Processed sequences were complemented with outgroup Plagiotheciaceae taxa (*Isopterygiopsis muelleriana* (Schimp.) Z. Iwats., *Plagiothecium cavifolium* (Brid.) Z. Iwats., *Ortholimnobia handelii* (Broth.) Schröck & J.T. Wynns and *Pseudotaxiphyllum elegans* (Brid.) Z. Iwats.) from the study by Wynns & Lange (2014). In total, we retrieved 81 ITS accessions (of which 15 were already published in the study of Hedenäs *et al.*, 2019) and 74 *trnL-rps4* accessions, of which 28 had the full sequence length with *trnF-trnL* and *rps4-trnS* ends; see Appendix for details and voucher information). For the final analyses, we used only accessions which had both ITS and *trnL-rps4* data (72 *Orthothecium* accessions and 4 outgroup taxa), the rest served the barcoding purpose. Sequences were aligned using MAFFT v. 7.470 (Katoh *et al.*, 2019) using the E-INS-i strategy and otherwise default parameters. Indel data were scored using the simple indel coding method (Simmons & Ochoterena, 2000), but as these only improved the tree resolution based on the chloroplast matrix, we only used them in the chloroplast partition, which was not further divided, based on the suggestion from the PartitionFinder2 software (Lanfear *et al.*, 2017). Separate analyses of chloroplast and ITS data yielded partly inconsistent results for a few accessions, and although we have not pruned them from the concatenated dataset, we discuss them in the light of possible gene flow among lineages and their incomplete sorting. The analyses included Bayesian Inference (BI) and Maximum Likelihood (ML), using the MrBayes 3.2.7a (Ronquist *et al.*, 2012) and RAxML v. 8.2.12 (Stamatakis, 2014) software packages run at the cluster computer facilities of MetaCentrum VO (see Acknowledgement). For the parameters of the analyses, see Kučera *et al.* (2019). TreeGraph 2 (Stöver & Müller, 2010) was finally used to summarise the topology and support from different analyses, and the resulting trees were then further edited graphically in the Inkscape v.0.92 program under the GPLv2+ licence.

RESULTS

Both analyses of individual genomic compartments (ITS, Fig. 1, and *trnF-trnS*, Fig. 2), and the concatenated matrix (Fig. 3) agree in a robust to maximal support for the monophyly of *Orthothecium*. ITS data (Fig. 1) resolved only three lineages with high support: (1) *O. rufescens* agg. containing *O. rufescens* and *O. intricatum* (PP 1 / BS 75; *O. rufescens* s. str. (PP 0.98 / BS 60) appears in a polytomy with three *O. intricatum* lineages), (2) *O. lapponicum* (PP 1 / BS 0.85), which however appears nested among accessions of *O. chryseon* and the newly recognised *O. sibiricum* s.l., and (3–4) two lineages of *O. strictum* s.l. (named here *O. strictum* 1 and 4, PP 1 / BS 85–89), leaving the rest of *O. strictum* s.l. accessions in a basal *Orthothecium* grade. The lineages of the newly described *O. brunnescens*, *O. retroflexum* and *O. remotifolium* appear monophyletic, albeit with a moderate to

weak support (PP 0.96–0.99 / BS 64–76). Accessions of *O. chryseon* and *O. sibiricum* s.l. (including *O. aff. sibiricum* differing in plastid data, as described below) not only appear unresolved but the individual lineages share completely some of their ribotypes; together they appear in a very weakly supported lineage (PP 0.67 / BS 52), which we designate here as *O. chryseon* agg.

Chloroplast data (Fig. 2) resolve most of the taxa which are described here as existing or new species except for *O. lapponicum* accessions which share the haplotype and appear in polytomy with accessions of most specimens of *O. sibiricum*, while four accessions of *O. sibiricum* s.str. form a moderately supported lineage (PP 0.97 / BS 58). Accessions of *O. strictum* s.l. cluster together in a weakly supported monophylum (PP 0.78 / BS 69), with one of the internal lineages (*O. strictum* 1, PP 0.99 / BS 84) being shared with the ITS data, while the other two lineages within the rest of *O. strictum* accessions are not reflected by the clustering based on ITS data; the specimens OK2158, 2263 and 2498 share a unique haplotype and are annotated as *O. strictum* 2 in Fig. 2. A similar pattern of non-matching internal diversification and clustering was resolved within *O. rufescens* agg., moreover one intermediate accession (*O. aff. rufescens*) approaching morphologically *O. intricatum* was resolved among *O. intricatum* accessions, although its haplotype is not completely identical to any of revealed haplotypes of *O. intricatum*. The affinities of *O. brunnescens* are unclear, while *O. remotifolium* and *O. retroflexum* appear in the well-supported clade with *O. strictum* s.l. The *Orthothecium chryseon* agg. received a moderate support (PP 0.96 / BS 66).

The concatenation (Fig. 3) largely reflects the results based on chloroplast matrix, with increased support values for the *O. chryseon* agg. (PP 0.99 / BS 78), *O. rufescens* agg. (PP 1 / BS 99) and *O. strictum* s.l. (PP 0.87 / BS 74), and adopting the clustering of *O. rufescens*, including *O. aff. rufescens* (yet with a weak support of PP 0.94 / BS 55), *O. lapponicum* (PP 1 / BS 0.87), *O. sibiricum* s.str. (PP 0.99 / BS 65) and *O. strictum* 2 and 4 from the analyses of individual partitions.

Morphological results are largely congruent with the results of the analysis of the concatenated matrix except for the impossibility of differentiation within *O. strictum* s.l. according to the molecular lineages 1 through 4, and similarly we were unable to clearly separate specimens of *O. sibiricum* s.str. with the unique chloroplast haplotype from the rest of *O. sibiricum* (*O. aff. sibiricum* in the tree) accessions, although generally the *O. sibiricum* s.str. plants are more robust, while the plants which share the haplotype with *O. lapponicum* are somewhat slenderer, although not enough to enable their morphological distinction (see below in Taxonomy section). At the same time, the plants of *O. lapponicum*, although only characterised molecularly by the nuclear data, show no morphological transition to *O. sibiricum* s.l.

DISCUSSION

Despite despite containing relatively few species, *Orthothecium* appeared to be a rather difficult genus for taxonomists due to the lack of invariable characters and the presence of transitional morphotypes among individual species. It is noteworthy that this is the only genus that was published twice in fasc. 48 (Margadant & van der Wijk, 1958) of *Bryologia Europaea*, in two versions. Each version has its own page numbering, and the first one in the order of the six-volumed edition includes three species, *O. rufescens*, *O. chryseon* and *O. intricatum*, while the second one includes only two species, *O. rufescens* and *O. chryseon*, and the description and illustrations of *O. chryseon* in this, obviously earlier version belong to another species, likely *Orthothecium intricatum* or *Isopterygiopsis pulchella* (small narrow-leaved plant with homomallous leaves). The later version with three species provides descriptions of *O. intricatum* and *O. chryseon* as they are understood now, with precise illustrations of their common phenotypes.

Traditionally, *Orthothecium* was subdivided into two informal groups (Brotherus, 1925). One included small plants with non-plicate leaves (*O. strictum* and *O. intricatum*), and the second group comprised larger plants with plicate leaves; the latter character was considered so important that *O. binervulum*, nowadays regarded synonymous with *O. strictum* was classified together with *O. chryseon* and *O. rufescens* because of biplicate leaves. The sixth species, *O. acuminatum*, was left by Brotherus unclassified as little known.

Molecular data prompted a radical change in taxonomic view of *Orthothecium* in several aspects. Unlike Brotherus's (1925) grouping, molecular data convincingly identified close phylogenetic affinities between *O. rufescens* and *O. intricatum*, as well as between *O. chryseon* and *O. lapponicum* (plus to-date undescribed taxa), while *O. strictum* represents yet another lineage, most closely related to two other yet undescribed taxa, of which the below described *O. retroflexum* is morphologically extremely similar to *O. chryseon*. The number of both molecularly and morphologically diagnosable lineages significantly exceeds the five species recognised so far in northern Eurasia, although it is consistent with the difficulties in which we encountered trying to identify Siberian collections with names based on European types. Another, probably even more interesting result, is the relatively small genetic differentiation between species of the genus as compared to the relatively substantial morphological differences between species, and sometimes even within species. It is unusual even among the generally young pleurocarpous species that the hyper-variable nuclear ribosomal ITS region is unable to barcode individual species. The most probable explanation of the close molecular affinity is the relatively young age of most *Orthothecium* taxa, which is further supported by the indications of incomplete lineage sorting among some of the species (see below).

Three of the below newly described species seem to be clearly defined both morphologically and molecularly. Of them, the species coined below as *O. brunnescens* is morphologically most distinct, reminding rather of a 'hypnoid' genus, such as, e.g., *Pseudohygrohypnum*, with respect to its homomallous, erect-spreading, hardly plicate and concave leaves and often brownish colouration, unusual in *Orthothecium*. The reason for its late discovery is probably in the relative scarcity of records and occurrence in remote, insufficiently explored regions of Asian Russia. *O. retroflexum* has the aspect of large *O. chryseon* and was previously identified so in collections from northern Asia and America. It can be viewed as a typical example of semi-cryptic species, in which the small yet stable morphological differences were only discovered in combination with molecular data. Similarly, the newly coined *O. remotifolium* shares the aspect of smaller morphs of *O. strictum* but can be safely distinguished by the characters specified below in the Taxonomy section. The generally plane margins, slightly serrulate in the upper part led us originally to the suspicion of identity with the North American *O. acuminatum*; however, that species is characterised by a rather dense, appressed foliation and production of stoloniferous minute branches which we have not observed in our material so far. Still, a close relationship between the two taxa is possible.

The other species except for *O. chryseon* seem to be taxonomically complicated, with possibly complex and ongoing speciation histories. The first such complex is *O. rufescens* agg. Although the typical and well-developed plants of *O. rufescens* and *O. intricatum* are extremely different in most aspects, we were able to reveal plants of variously intergrading morphologies in the Asian material (Figs. 25 & 26), and the specimen Ignatov & Ignatova 28-80 from Altaian Karakol lakes has ITS ribotype of *O. rufescens* and chloroplast haplotype falling within the (rather large) variability of *O. intricatum*. Given the generally rare to non-existent production of sporophytes in *Orthothecium*, this pattern of genetic information can probably rather be explained as the example of incomplete lineage sorting in young taxa. Such explanation is probably further supported by the extremely small genetic differentiation between *O. intricatum* and *O. rufescens* in combination with the relatively big diversification within *O. intricatum*. A similar case seems to exist in *O. lapponicum* agg. between that species and the newly described *O. sibiricum*. The two ITS ribotypes and two chloroplast haplotypes occur in three combinations; *O. lapponicum*-morphology is consistent with the presence of a unique ITS ribotype but the chloroplast haplotype of such plants is shared with plants approaching or sharing the morphology of the below described *O. sibiricum*. In a parallel way, a unique chloroplast haplotype is present in a smaller proportion of plants referable to *O. sibiricum*, mostly in the largest exemplars, morphologically approaching *O. chryseon* (yet with substantially less plicate leaves). Even here

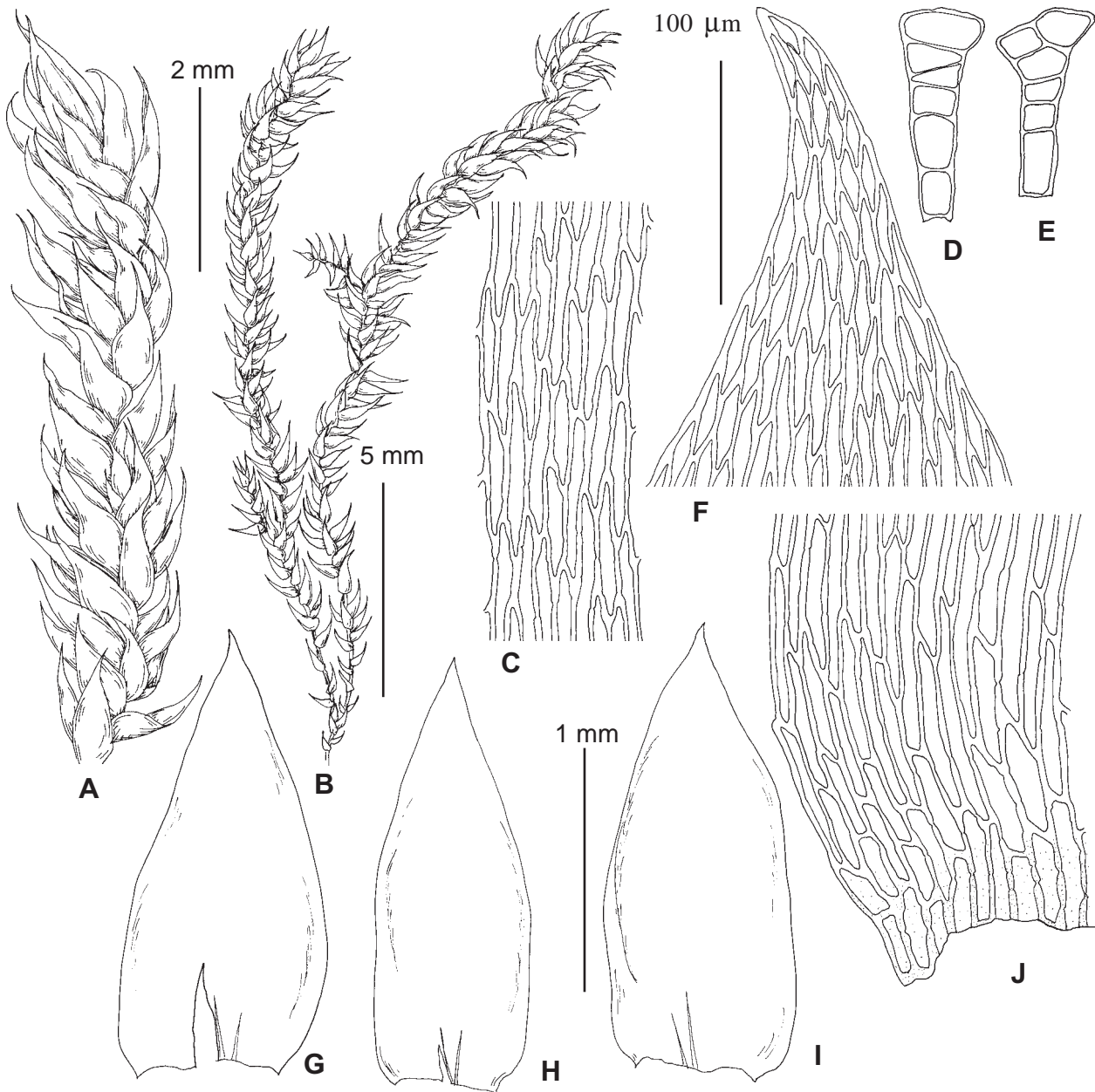


Fig. 4. *Orthothecium brunnescens* (A–C, F–J – from: Russia, Yakutia, Sette-Daban Mt. Range, *Bysyin* 17-482, MHA, OK 2159 & 2265 (holotype); D–E – from: Yakutia, Suntar-Khayata Range, At-Moole Creek, 22.VII.2003 *Ivanova & Zolotov s.n.*, MW 9049081). A–B: habit, dry; C: mid-leaf cells; D–E: gemmae; F: upper leaf cells; G–I – leaves; J – basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for G–I; 100 µm for D–F, J.

an explanation of the reticulate genotype patterns by hybridisation seems not very probable, as the sporophytes in either species are unknown, and moreover, the combination of ‘non-lapponicum’ ITS ribotype and ‘non-sibiricum’ chloroplast haplotype seems to be the most common case in *O. lapponicum* agg. We interpret such plants as *O. sibiricum* s.l. or *O. aff. sibiricum*. Morphologically they mostly have a look of stunted exemplars of *O. sibiricum*, and molecularly they are probably also best viewed as the result of incomplete lineage sorting between the two species. The most complicated case, which probably awaits further taxonomic elaboration is *O. strictum* s.l., which we discuss in detail in the Taxonomy section.

Considering the mismatch between morphological similarities and molecular affinities of the taxa, the species in the following account are arranged according to their morphology to facilitate the practical identification.

TAXONOMY

Orthothecium Bruch, Schimp. & W. Gümbel, *Bryol.*

Eur. 5: 105 (fasc. 48. Mon. 1), nom. cons.

Plants small to large, in loose tufts, golden-green, golden-yellow, bronze, brownish, dark-brown, brownish-red, wine-red or purple, glossy. *Stems* procumbent, ascending or erect, weakly or irregularly branched, terete-foliate, central strand present, hyalodermis absent,

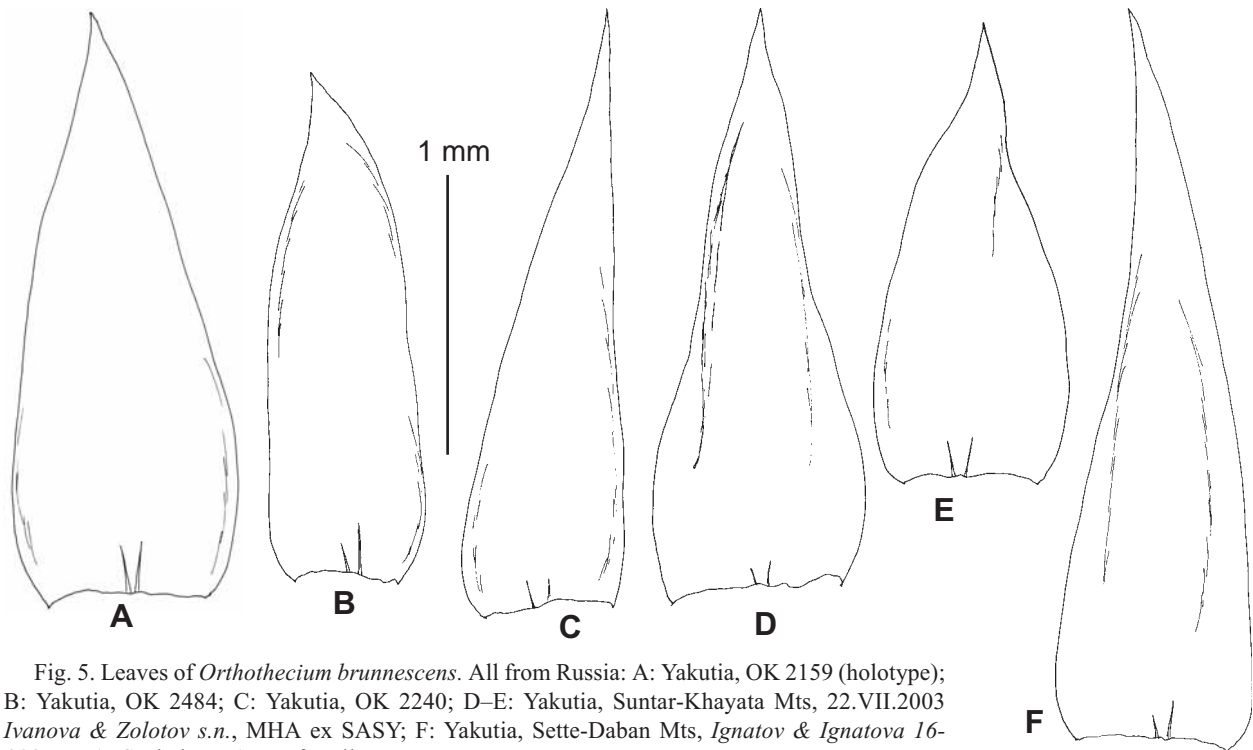


Fig. 5. Leaves of *Orthothecium brunnescens*. All from Russia: A: Yakutia, OK 2159 (holotype); B: Yakutia, OK 2484; C: Yakutia, OK 2240; D–E: Yakutia, Suntar-Khayata Mts, 22.VII.2003 Ivanova & Zolotov s.n., MHA ex SAS; F: Yakutia, Sette-Daban Mts, Ignatov & Ignatova 16-989, MHA. Scale bars: 1 mm for all.

rhizoids axillary. *Leaves* densely or, rarely, distantly arranged, erect-spreading, erect or appressed, occasionally secund, ovate, oblong-ovate, ovate-triangular, ovate-lanceolate, lanceolate or narrowly lanceolate, acute, acuminate or abruptly contracted into short, straight, flexuose or revolute apiculus, weakly narrowed or rounded to insertion, not decurrent or very shortly decurrent; margins entire or serrulate in upper part of acumina, plane or narrowly recurved; *costa* short, double or almost absent; *leaf cells* narrow linear, \pm thick-walled, scarcely or moderately porose; basal leaf cells shorter and wider, porose, alar cells not differentiated. *Specialized asexual reproduction* by axillary gemmae, occasionally present in almost all species, composed of one row of 3–5 cells and occasionally two cells wide at apex. *Dioicous*. *Sporophytes* rare, in some species unknown. *Capsules* erect or slightly inclined, straight or weakly curved. *Peristome* \pm perfect; exostome teeth pale, on dorsal surface striolate below, papillose above; endostome with high basal membrane, wide or narrow segments, cilia as long as segments or shorter. *Spores* 8–16 μ m.

Type: *Orthothecium rufescens* (Dicks. ex Brid.) Bruch, Schimp. & W. Gümbel. The genus includes at least 10 species in the Arctic and in the mountain regions of boreal and temperate zones of the Northern Hemisphere.

1. *Orthothecium brunnescens* Ignatova & Ignatov, sp. nov. Figs. 4–6.

Type: Asian Russia, Yakutia, Tomponsky District, near the pass between Kuraanakh and Dyby Rivers,

62°48'40"N, 139°00'30"E, alt. 1100 m, on cliffs in mountain tundra. 27 Aug 2017 N. Bysyin 17-482. Holotype MHA 9025568, isotypes MW, LE, CBFS. Figs. 4A–C, F–J; 5A; 6C–D. [DNA sequences: nuclear ITS MT681126, plastid *trnF*–*trnS* MT683698].

Diagnosis: *Orthothecium brunnescens* differs from the most similar species, *O. chryseon* and *O. sibiricum*, in having leaves homomallous to slightly falcate vs. straight, and plant colour olivaceous, brownish to dark brown vs. golden-yellow, bronze or vinaceous; additional distinctions from *O. chryseon* include erect-spreading to spreading vs. appressed leaves, not or scarcely plicate vs. strongly plicate leaves, and from *O. sibiricum* acute vs. narrowly acuminate/apiculate leaves.

Description: Plants medium-sized, olivaceous or yellowish-green, often with brownish tint, occasionally dark brown, glossy. Stems 2–6 cm long, 1.5–2.0 mm wide with leaves, terete-foliate. Leaves loosely or moderately densely arranged, erect-spreading to spreading, often slightly homomallous, 1.6–2.1(–2.6) \times 0.6–0.8 mm, ovate-lanceolate to oblong ovate, acute or short-acuminate, rounded at base, not decurrent, slightly concave, not plicate or, rarely, scarcely plicate; leaf margins plane or, rarely, weakly recurved at places, entire or slightly serrulate in apical part; laminal cells 50–80 \times 7–9 μ m. *Specialized asexual reproduction* by brood bodies 60–80 μ m long. *Gametangia* and *sporophytes* unknown.

Distribution and ecology. *Orthothecium brunnescens* is so far only known from several localities in the eastern Verkhoyansky Range, Yakutia, in the basins of Vostochnaya Khandyga and Maya Rivers. It was collected at al-



Fig. 6. *Orthothecium brunnescens*, showing variation in habit: A–B (shaded cliffs in forest): Yakutia, 22.VII.2003 Ivanova & Zolotov (MHA); C–D (exposed cliffs above solid timber-line): holotype: Yakutia, Bysyin 17-482, MHA, OK 2159 & 2265); E (cliffs along river, often flooded thus quite muddy): isolate OK2484; F (shaded cliffs in forest), Ignatov & Ignatova 16-989, MHA, plants with longer and narrower leaves. All scale bars are 1 mm.

titudes between 370–1100 m, on wet calcareous cliffs near waterfalls, at riverbanks, in niches and on ledges of cliffs in larch forest and in mountain tundra.

Additional specimens examined: RUSSIA: **Yakutia:** Tomponsky District: Suntar-Khayata Mts, “Suntar Khayata” protected area, 774 m alt., At-Moole brook, 22.VII.2003 Ivanova & Zolotov s.n. (MW 9049081); Sette Daban Mts, left bank of Vostochnaya Khandyga River opposite Segenyakh (Rosomakha) Creek mouth, 447 m alt., Ignatov & Ignatova 17-767 & 17-771 (MHA 9025345

& 9025340); Sette Daban Mts, western slope of Okraina Range, Nadezhda Creek, 500 m alt., Ignatov & Ignatova 16-989 (MHA 9022742).

Differentiation and variation. Superficially, *Orthothecium brunnescens* is not similar to any other species of the genus and can be confused in the field with *Pseudohygrohypnum* species, e.g. *P. subeugyrium* which is not rare on wet cliffs in Asian Russia. It differs, however, by undifferentiated alar cells and only slightly falcate leaves.

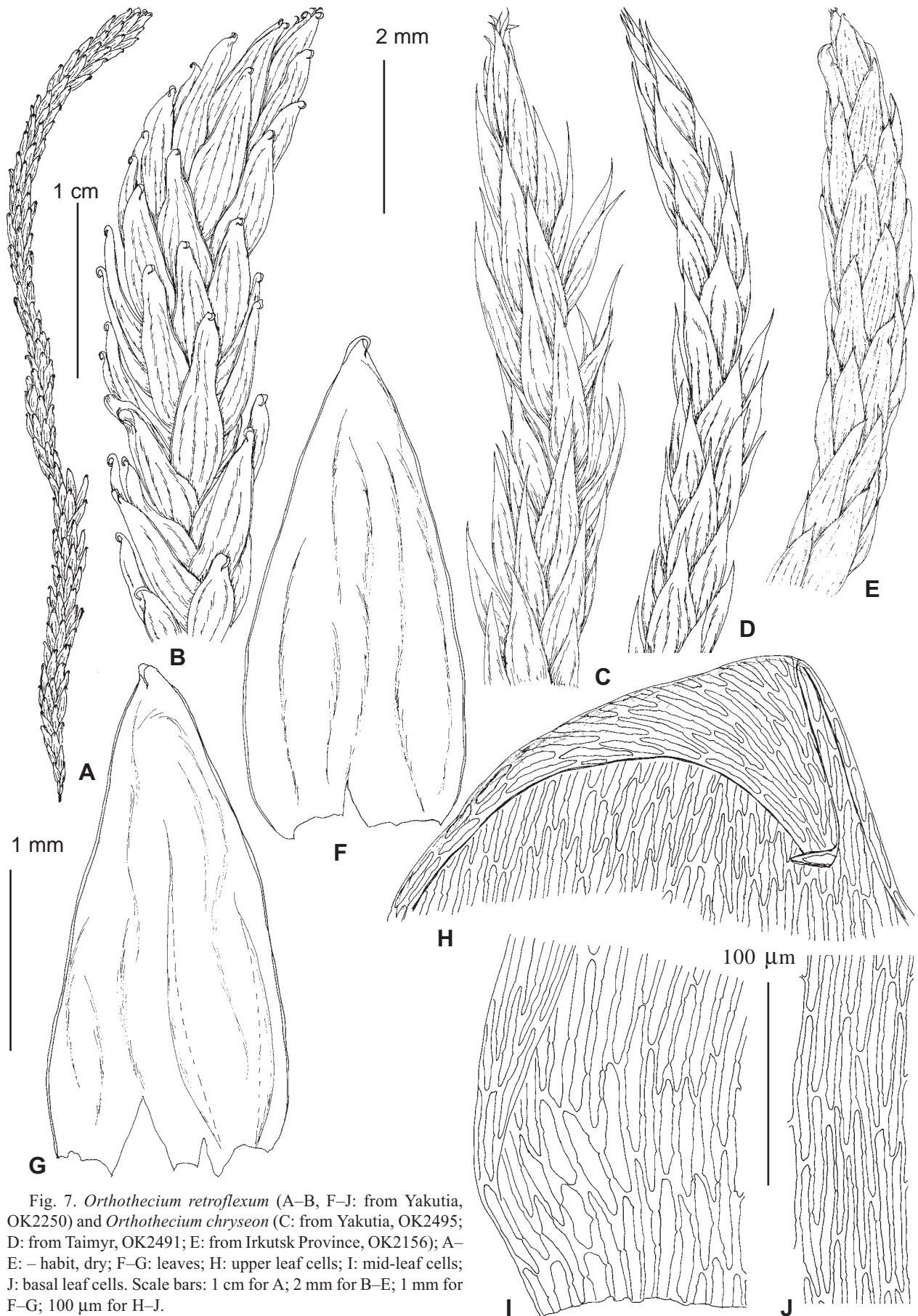


Fig. 7. *Orthothecium retroflexum* (A–B, F–J: from Yakutia, OK2250) and *Orthothecium chryseon* (C: from Yakutia, OK2495; D: from Taimyr, OK2491; E: from Irkutsk Province, OK2156); A–E: – habit, dry; F–G: leaves; H: upper leaf cells; I: mid-leaf cells; J: basal leaf cells. Scale bars: 1 cm for A; 2 mm for B–E; 1 mm for F–G; 100 μm for H–J.

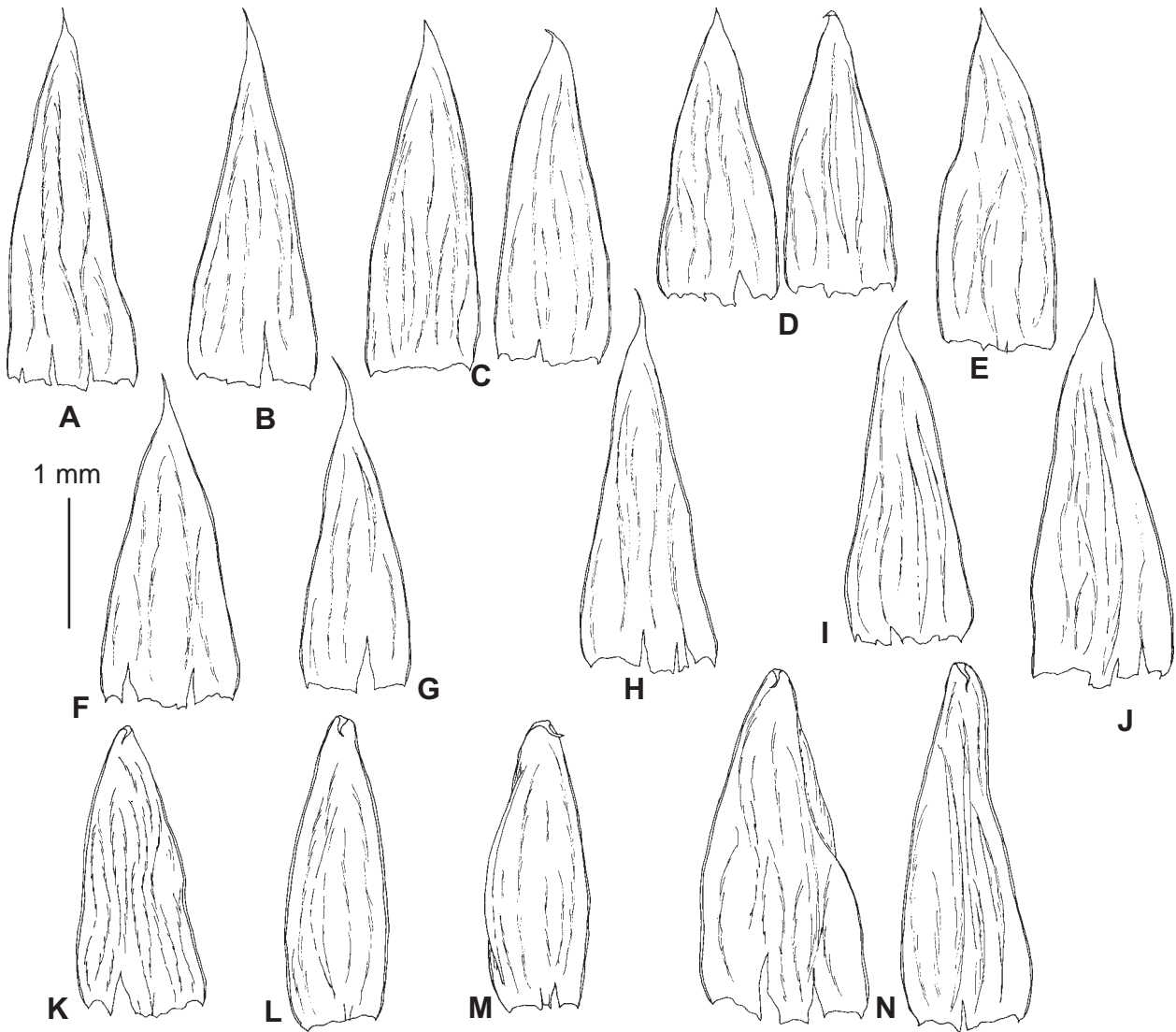


Fig. 8. Leaves of *Orthothecium chryseon* (A–J) and *O. retroflexum* (K–N). All from Russia: A: Sakhalin, OK 2249; B: Taimyr, OK 2491; C: Yakutia, OK 2495; D: Yakutia, OK 2492; E: Yakutia, OK 2486; F: Yakutia, OK 2165 & 2267; G: Altai, OK 2502; H: Altai, OK 2503; I: Yakutia, OK 2494; J: Khanty-Mansi Autonomous District, OK 2248; K: Taimyr, OK 2166; L: Magadan Province, OK 2493; M: Yakutia, OK 2500; N: Yakutia, OK 2250. Scale bar: 1 mm for all.

The combination of epicate leaves, medium-sized to large plants, homomallous to slightly falcate leaves and dark brownish, instead of reddish colour make *O. brunnescens* rather easy to identify, despite a rather variable leaf shape: plants from relatively dry and shaded cliffs in the forest have lanceolate leaves (Figs. 5F, 6F), while in wet sunny places leaves are broad (Figs. 5E, 6E). Large plants of *O. sibiricum* and *O. lapponicum* have straight, non-falcate leaves, and their reddish colour is conspicuous, especially in plants from exposed habitats, although it might disappear in not properly dried herbarium specimens. The colour of *O. brunnescens* is, however, variable: it is yellowish-green in shady habitats and usually with a brownish tint in exposed places (Fig. 6E). Large phenotypes of *O. strictum* might have a similar aspect, but their leaves are not homomallous (except for one case discussed under that species), and are generally considerably smaller,

having leaves $0.8\text{--}1.7 \times 0.2\text{--}0.6\ \mu\text{m}$ vs. $1.6\text{--}2.1\text{--}(2.6) \times 0.6\text{--}0.8\ \mu\text{m}$ in *O. brunnescens*. The leaf margins recurved for most of the leaf length are commonly present in *O. strictum*, but never in *O. brunnescens*.

2. *Orthothecium retroflexum* Ignatov & Ignatova, sp. nova. Figs. 7A–B, F–J, 8K–N, 9A–C.

Type: Asian Russia, Yakutia, Eveno-Bytantaysky Distr., Orulgan Range, upper course of Aenigan-Toloono Creek, $68^{\circ}14'N$, $128^{\circ}06'E$, alt. 900 m, wet cliffs, 7 Aug 2011 Ignatov 11-3974 (Holotype: MHA 9029736; isotypes MW, S, CBFS). Figs. 7A–B, F–G, 8N. [DNA sequences: nuclear ITS MN794387, plastid *trnL-rps4* MT683730].

Diagnosis: *Orthothecium retroflexum* is similar to *O. chryseon*, but differs in more broadly ovate leaves, abruptly contracted into a short, revolute or hooked apiculus.

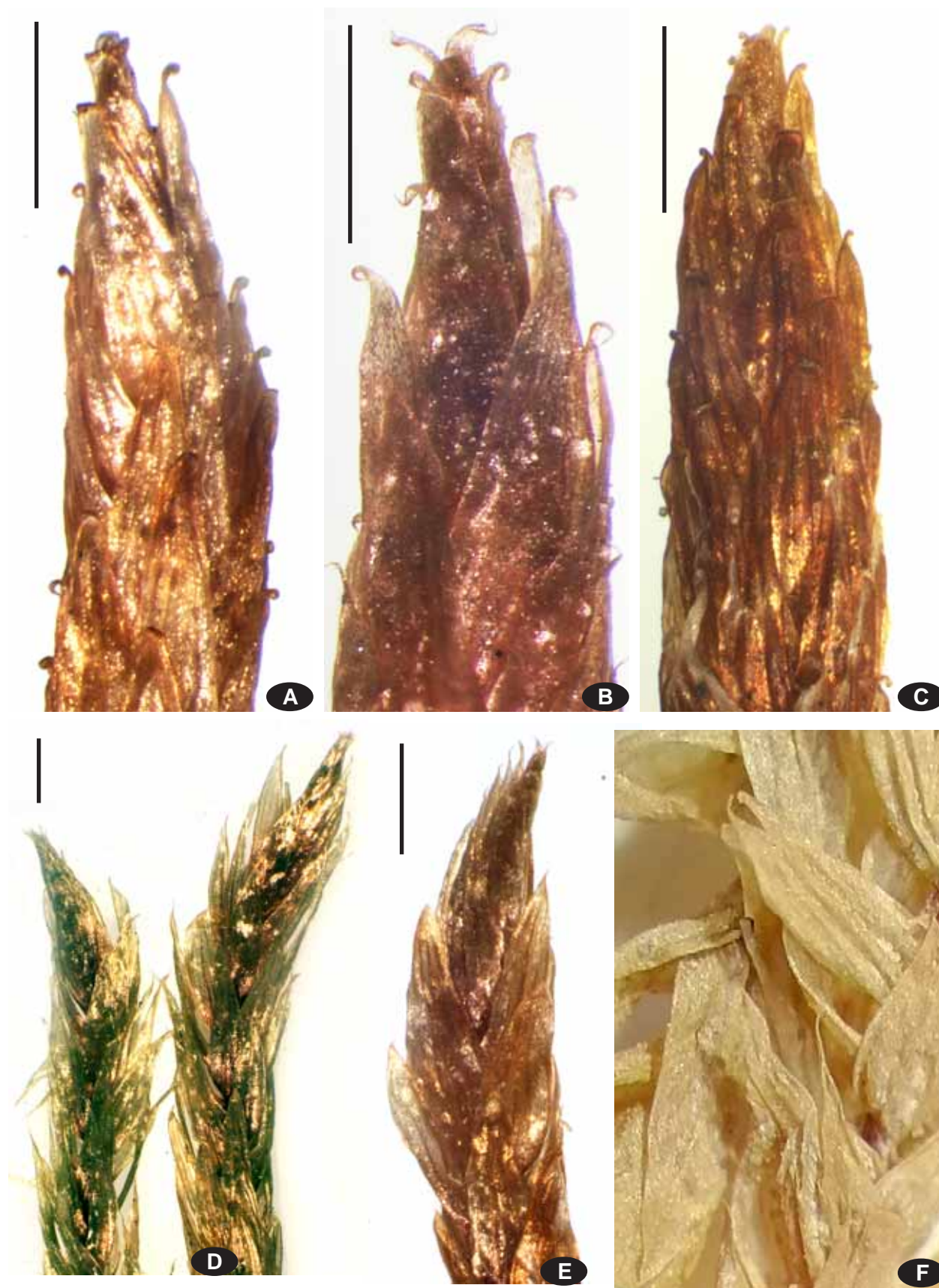


Fig. 9. Shoot tips of *Orthothecium retroflexum* (A–C) and *O. chryseon* (D–E), showing the differences in leaf apices. All from Russia: A: Taimyr, Anabar, OK2166; B: East Yakutia, Ignatov & Ignatova 18-870, MHA; C: SE Yakutia, OK 2500; D: Irkutsk Province, Slyudyanka, OK2156; E: East Yakutia, OK 2486; F – portion of holotype of *Leskea chrysea* var. *cochleariifolia* (H-SOL 1834001). All scale bars are 1 mm.

Description: Plants large, golden-green, reddish-green or bronze, glossy, in loose or dense tufts. Stems ascending to erect, 2–5(–10) cm long, not or weakly branched, terete-foliate. Leaves erect, appressed, imbricate, 2.1–2.7×0.8–1.2 mm, ovate, abruptly contracted into short, revolute or hooked apiculus, cochleariform, strongly plicate, slightly narrowed to the insertion, non-decurrent; margins narrowly recurved at most of leaf length; cells in the middle part of leaf 50–80×5–6 µm, thick-walled, porose; basal cells shorter and wider, strongly porose; alar cells not differentiated. Specialized vegetative reproduction unknown. Dioicous. Sporophytes unknown.

Distribution and ecology. *Orthothecium retroflexum* is widespread in Arctic regions of European and Asian Russia and in permafrost regions throughout Asian Russia. In southern Siberia it is known only from a single record in Eastern Sayan Mts, and the southernmost locality of this species is in Sakhalin Island. It was also revealed in collections from Alaska (see specimens examined), and likely is more widespread in the Arctic, although its distribution needs clarification. It is likely that *O. retroflexum* was previously reported from Russia under the name *O. chryseon*, while the records of *O. rufescens* from northern Russia mostly belong to *O. chryseon* (e.g., in Abramova *et al.*, 1961). The revision of herbarium collections (MHA, MW, and partly LE) revealed that the distributions of *O. chryseon* and *O. retroflexum* largely overlap. Both are widespread in the Arctic and permafrost areas and grow in similar habitats; however, *O. chryseon* has a wider distribution in the southern regions of Russia. In the northernmost Arctic areas, *O. retroflexum* often dominates in wet tundra. In permafrost areas of Siberia, it grows in mountain tundra, nival communities, near melting snow beds, along brooks and in creek valleys, on wet cliffs, most often on calcareous rocks. In Sakhalin Island, it was collected at an altitude of ca. 700 m, in a mossy tundra community and so far this is the southernmost locality of the species. While occurring in the Eastern Sayans in Baikal area, the species is seemingly absent from West Sayans and Altai, as well as from Caucasus, Urals and mountains of Central Europe.

Selected additional specimens examined: EUROPEAN RUSSIA: **Arkhangelsk Province**, Franz Josef Land: Hooker Island, 2.VIII.1930, V.P. Savicz *s.n.*, Hepaticae et Musci URSS Exsiccata Dec. I (1957) №10 (MHA, MW); Rudolf Island, 2.VIII.2012, Kholod *s.n.* (LE); Ziegler Island, Konoreva 911 (LE). ASIAN RUSSIA: **Krasnoyarsk Territory**: Taimyr Peninsula: near Dikson Town, Fedosov 17-2-12-18 (MW 9111718); Syrutaturku Lake, VIII.1994 Pospelova 94/85 (MW 9049063); lower course of Bikada River, 74°50'N. 106°10'E; 15.VIII.1989 Pospelova 37 (MW 9049066); upper course of Ereechka River, Fedosov 13-3-0019 (MW 9050854); middle course of Fomich River, 19.VIII.2003 Pospelov *s.n.* (MW 9050862). **Yakutia**: Novosibirskie Islands: Stolbovoy Island, Troeva *s.n.* (LE); Tomponsky District: Sette-Daban Mts, Sakkyryr River, Ivanov 17-624 (MW 9090216); Segenyakh Creek, Ignatov & Ignatova

va 17-879 (MW 9090286); Oymyakon District: Mus-Khaya Mt., Knoriy Creek, Ignatov & Ignatova 11-3050 (MHA); Ust-Maya District, Allakh-Yun settlement, 30.VIII.2000 Ivanova *s.n.*, Bryophyta Sibiriae Exsiccata, Fasc. I (2007) №38, MW 9049083); Novosibirskie Islands, Bolshoy Lyakhovsky Island, 5.VIII.1956 Aleksandrova *s.n.* (MHA); Mamsky District, Ulakhan-Chistai Range, Mramornaya Mt., Ignatov & Ignatova 18-1433 (MHA 9027927). **Chukotka**: Schmidt Cape, 29.VII.1965 Afonina *s.n.* (LE) **Magadan Province**: Ol'skoe Basalt Plateau in the upper course of Ola River, 11.VIII.2011, Malashkina MG-30-01-11 (MHA). **Buryatia**: Oka District, East Sayan Mts., Kitoy Range, 15.VIII.1960 Bardunov *s.n.*, Bryophyta Rossica et civitatum collimitaneorum Fasc. IX (2012), №380 (MW 9049072). **Sakhalinskaya Province**: Sakhalin Island, Smirnykhovsky District, protected area "Vaida Mountain", Ignatov & Teleganova 06-146 (MHA 9018693).

NORTH AMERICA: U.S.A., Alaska: Utukok River, 7.VII.1969 Steere, Holmen & Mårtensson *s.n.*, Bryophyta Arctica Exsiccata #46 (MW 049092); Point Barrow and vicinity, Steere 19054 (LE); East Oumalik and vicinity, Steere 16610 (LE).

Differentiation and variation. *Orthothecium retroflexum* differs from *O. chryseon* in having ovate vs. ovate-lanceolate or ovate-triangular leaves, cochleariform vs. moderately concave, and, most importantly, a hooked, revolute apiculus in all leaves in well-developed shoots (only in young shoots the leaves may have ± straight apices), whereas in *O. chryseon* the apical portions of leaves are straight or flexuose, only occasionally recurved at 90° in some leaves. This apiculus pattern in *O. retroflexum* is much alike that in *Plagiothecium berggrenianum* Frisvoll, where the hooked leaf apices are sufficient for species identification in the field. The leaf cells of *O. retroflexum* are generally thicker-walled and more strongly porose than in *O. chryseon*.

Orthothecium retroflexum is usually a tall, robust plant (stems with leaves ca. 2 mm wide when dry); however, slenderer morphotypes occasionally occur (stems with leaves 1–1.5 mm wide when dry). Leaf length and especially leaf width are also variable (2.1–2.7×0.8–1.2 mm), but the leaves keep their ovate shape with a short, strongly revolute apiculus; the latter character is present in most leaves, though the youngest leaves at some shoot tips may occasionally only be curved at right angle, as in *O. chryseon*.

The strongly concave, cochleariform leaves raised suspicions that *O. chryseon* var. *cochleariifolium* (Lindb.) Limpr. (Laubm. Deutschl. 3(27): 23. 1895. — *Leskea chrysea* var. *cochleariifolia* Lindberg, Öfvers. Kongl. Vetensk.-Akad. Förh. 23: 543. 1867) is the appropriate name for this taxon. Its range in North America is confined to the high Arctic (Redfearn Jr., 2014), which indirectly implies that our high Arctic plants may belong to this taxon. However, the type specimen in H-SOL ["*Orthothecium chryseum* var. *cochleariifolium* Lindb. 9 Febr. 67, Spitsbergen, Treurenbern bay, 1861, leg. Malmgren, H-SOL 1834001"!] belongs to *O. chryseon*, not to the species described here as *O. retroflexum*, and

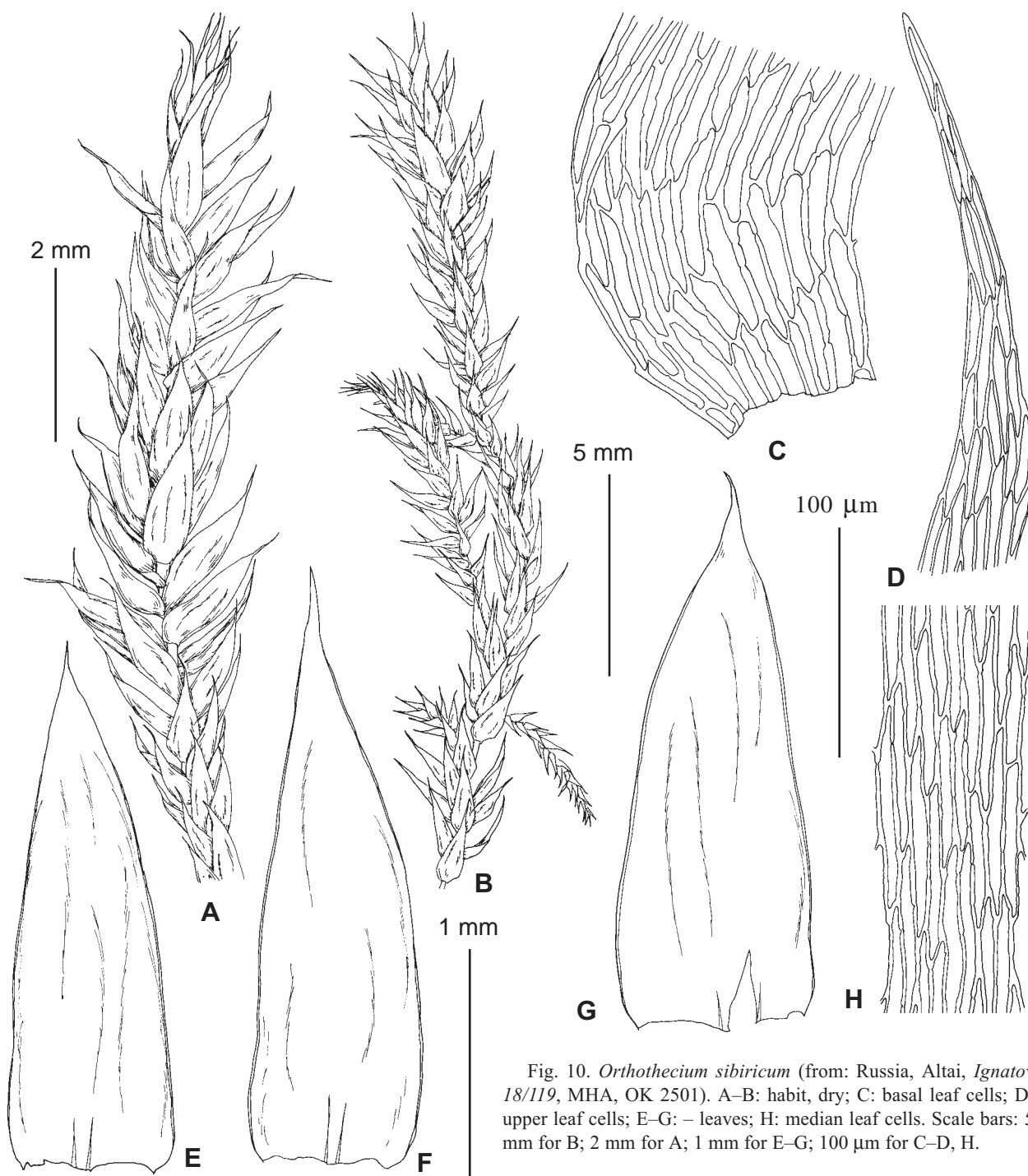


Fig. 10. *Orthothecium sibiricum* (from: Russia, Altai, Ignatov 18/119, MHA, OK 2501). A–B: habit, dry; C: basal leaf cells; D: upper leaf cells; E–G: – leaves; H: median leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for E–G; 100 µm for C–D, H.

lacks the characteristic hooked apiculus of the latter (cf. partial image of the holotype in Fig. (9F).

3. *Orthothecium chryseon* Bruch, Schimp. & W. Gümbel, Bryol. Eur. 5: 107. 1851. Figs. 8A–J; 9D–E.

Description: Plants large, goldish-, brownish- or red-dish-green, occasionally bronze or intense wine-red, glossy, in dense or loose tufts. Stems procumbent, ascending or erect (especially when growing in large, dense cushions), to 10 cm long. Leaves erect-spreading in upper parts of stems, appressed below, 2.1–2.9×0.8–1.0 mm, ovate-lanceolate or ovate-triangular, short or long acumi-

nate, upper part of narrow acumen straight, flexuose or, occasionally, in some leaves recurved or incurved at right angle, moderately concave, strongly plicate, slightly and gradually narrowed to insertion, very shortly decurrent; margins narrowly recurved from base and at most of leaf length; cells in mid-leaf 60–85×5–6(–7) µm, thick-walled, porose; basal leaf cells shorter and wider, strongly porose, alar cells not differentiated. Specialized vegetative reproduction unknown. Sporophytes rare. Setae 2.5 cm. Capsules pale, 2.5 mm long, cylindrical, erect, straight or slightly curved. Opercula conic, with small

apiculus. *Annulus* revoluble. *Peristome* \pm perfect; exostome teeth pale, striolate below on dorsal surface, papillose above; endostome basal membrane high, segments wide, cilia to 1/2 of segments length. *Spores* 11–16 μ m.

Distribution and ecology. *Orthothecium chryseon* has a broad arctic-alpine distribution. It is common in the Arctic, and in the high-Arctic region sometimes abundant or at places even dominating in tundra vegetation, e.g. in the Franz-Josef Land and Novaya Zemlya archipelagos. It occurs in various kinds of tundra vegetation north of the forest limit but is most frequent and abundant in areas with calcareous bedrock. In permafrost areas of Siberia *O. chryseon* is a constant component of rich fen vegetation, associated with *Paludella*, *Tomentypnum*, *Cinclidium*, *Catoscopium*, etc., it is not rare in nival communities, near melting snow beds, on brook banks, and hanging mires on steep slopes. In more southern regions, *O. chryseon* occurs only in the alpine to subnival belts of the mountains: Alps and Western Carpathians in Europe, Caucasus in Armenia. In all mountains of southern Siberia, it occurs in the alpine zone with tundra vegetation, but is more common on wet cliffs at all elevations; it occurs in Mongolia, but is absent from China, Japan, Korea, and most of the southern areas of the Russian Far East, where it is absent in continental area south of the Amur River and the Kuril Islands, although having a few localities in Sakhalin. In North America it extends southwards to Colorado. Contrasting with the wide distribution in Asian Russia, the southern limit of *O. chryseon* in European Russia is quite northern: the southernmost localities are in northern Karelia and in the Sub-Polar Urals in the Republic of Komi. In Europe, *O. chryseon* occurs in the Scandinavian countries, Iceland, and Central Europe where it is a rather rare species of the highest locations in the Alps and Western Carpathians. Plants with sporophytes are occasionally present in northern Scandinavia, but they are very rare in Russia: we collected them only once on a wall of rather soft schistose cliff with permanent seepage from melting permafrost, where the species formed a pure carpet.

Additional selected specimens examined: EUROPEAN RUSSIA: **Republic of Komi**, upper course of Grube-yu Creek, 14.VIII.1932 *Govorukhin s.n.* (MW 9050846). ASIAN RUSSIA: **Yamalo-Nenetsky Autonomous Area**, Polar Urals, Khadata Lake, 5.VIII.1964 *Filin s.n.* (MW 9050848). **Altai Republic**: Kosh-Agach District, Taldura River, *Ignatov & Ignatova 12-391* (MHA). **Krasnoyarsk Territory**: Severnaya Zemlya Archipelago, Sergey Kamenev Island, 26.VIII.1932 *Savicz 805* (MHA 9018699); Taimyr Peninsula: Afanasiyevskie Lakes, *Fedosov 06-13* (MW 9050858); Kotuykan River 4 km downstream Arbyn Creek mouth, *Fedosov 11-1265* (MW 9050856); Maimecha River, *Fedosov 09-173* (MW 9050863); Medusa Bay, Willem Barents biostation, 24.VII.2003 *Varlygina s.n.* (MW 9050860); Syrutaturku Lake, *Pospelova 94/75* (MW 9049061); Byrranga Range, Bolshaya Bootankaga River, 16.VII.1991 *Kuvaev 1786* (MW 9049055); Putorana Plateau, Glubokoe Lake, *Fedosov 15-0869* (MW 9050852); Putorana Plateau, Ayan

Lake, 16.VIII.1983, *Czernyadjeva 123* (LE). **Yakutia**: Oymyakon Distr., Suntar-Khayata Mt. Range, Mus-Khaya Mt., *Ignatov & Ignatova 11-3167* (MW 9049082); Tomponsky Distr., Sette-Daban Range: Segenyakh (Rosomakha) Creek, *Ignatov & Ignatova 15-531* (MW9049086); western slope of Okraina Range between Ulakh and Nadezhda Creeks, *Ignatov & Ignatova 16-887* (MHA 9022490); Momsky Distr., Ulakhan-Chistai Mt. Range, middle course of Tirekhtyakh River, *Ignatov & Ignatova 18-1575* (MHA 9027967). **Chukotka**: Krest Bay, Egvekinot Settlement, 26.VII.1969 *Afonina s.n.* (MW 9049091); Ioni Lake, 30.VI.1977 *Afonina s.n.* (MW 9049090); Bilibino Settlement, *Afonina s.n.*, Bryophyta Rossica et Civitatum Collimitaneorum Exsiccata, Fasc. V (2004) №152 (MW 9049089); Anadyr River basin, upper course of Yablon River, 7.VIII.1982 *Afonina s.n.* (LE); Anadyr Distr., upper course of Tanyurer River, Bezymyannoe Lake, 11.VII.1979 *Afonina s.n.* (LE); Vrangeli Island, Somnitel'naya Bay, 18.VIII.1985 *Afonina s.n.* (LE). **Kamchatsky Territory**: Northern Koryakia, Pekul'neyskoe Lake, 15.VIII.1984 *Afonina s.n.* (LE). **Irkutsk Province**: Usol'sk Distr., Kitoy River at Razdol'e Settl., 17.IX.1975, *Safonova s.n.* (LE). **Buryatia**: Oka District, Eastern Sayan Mts, Kitoy Range, upper course of Kitoy River, 15.VIII.1960 *Baranov s.n.*, Bryophyta Rossica et Civitatum Collimitaneorum Exsiccata, Fasc. IX (2012) #380 (MHA). **Khabarovsk Territory**: Verkhnebureinsky Distr., Bureinsky State Reserve, *Ignatov 97-331* (MHA 9018695). **Sakhalinskaya Province**: Sakhalin Island, East-Sakhalin Mountains, Balagan Mt., *Bakalin D#S-26-3-17* (MW9078378).

NORWAY: Svalbard, Hornsund, *Godzik & Grodzinska s.n.*, Bryophyta Svalbardensia Exsiccata, Fasc. IV (1987) №80 (MHA 9066908); Alpen Dovrefjeld, auf Felsen des Berges Knutsho, 24.VII.1907, *Bryhn s.n.*, E. Bauer, Musci europaei exsiccati #590 (MW 9050841). FINLAND: Kuusamo, Paana-järvi, Kuoppaoja, *Brotherus s.n.*, Bryotheca Fennica 261 (MW9050842). SWEDEN: Lule Lappmark, Kvikkjokk, Ruotnas, 2.IX.1837, *J. Ångström* (S, B32126); Jämtland, Åre, Silverfallet, 27.VIII.2011, *Hallingbäck TH 5661* (S, B217019); Jämtland, Undersåker, Norder-Tväråklumpen, Nordostbranten, 25.VII.2002, *Weibull TH 38249* (S, B217013); Torne lappmark, Jukkasjärvi, Kärketjärro, 19.VII.2005, *Hallingbäck TH 43113* (S, B217014).

Differentiation and variation. *Orthothecium chryseon* was most frequently misnamed in herbarium collections as *O. rufescens*. It is likely that the two large *Orthothecium* species common in Asian Arctic, i.e. *O. chryseon* and *O. retroflexum*, were assumed by bryologists as different, and having at hand two available names, i.e. *O. rufescens* and *O. chryseon*, they applied these names in a wrong way: *O. chryseon* was called *O. rufescens*, while *O. retroflexum* was called *O. chryseon*. Distinctions from *O. rufescens* and *O. retroflexum* are discussed under those species. *Orthothecium brunnescens* was also identified as *O. chryseon* due to a large size of plants; however, the former species has acute rather than acuminate leaves which are scarcely plicate and often homomallous to almost falcate-secund, while leaves of *O. chryseon* have narrower acumina, they are strongly plicate and terete, always erect to loosely appressed, with straight or flexuose, only occasionally (more often at shoot tips) curved at right angle in some leaves.

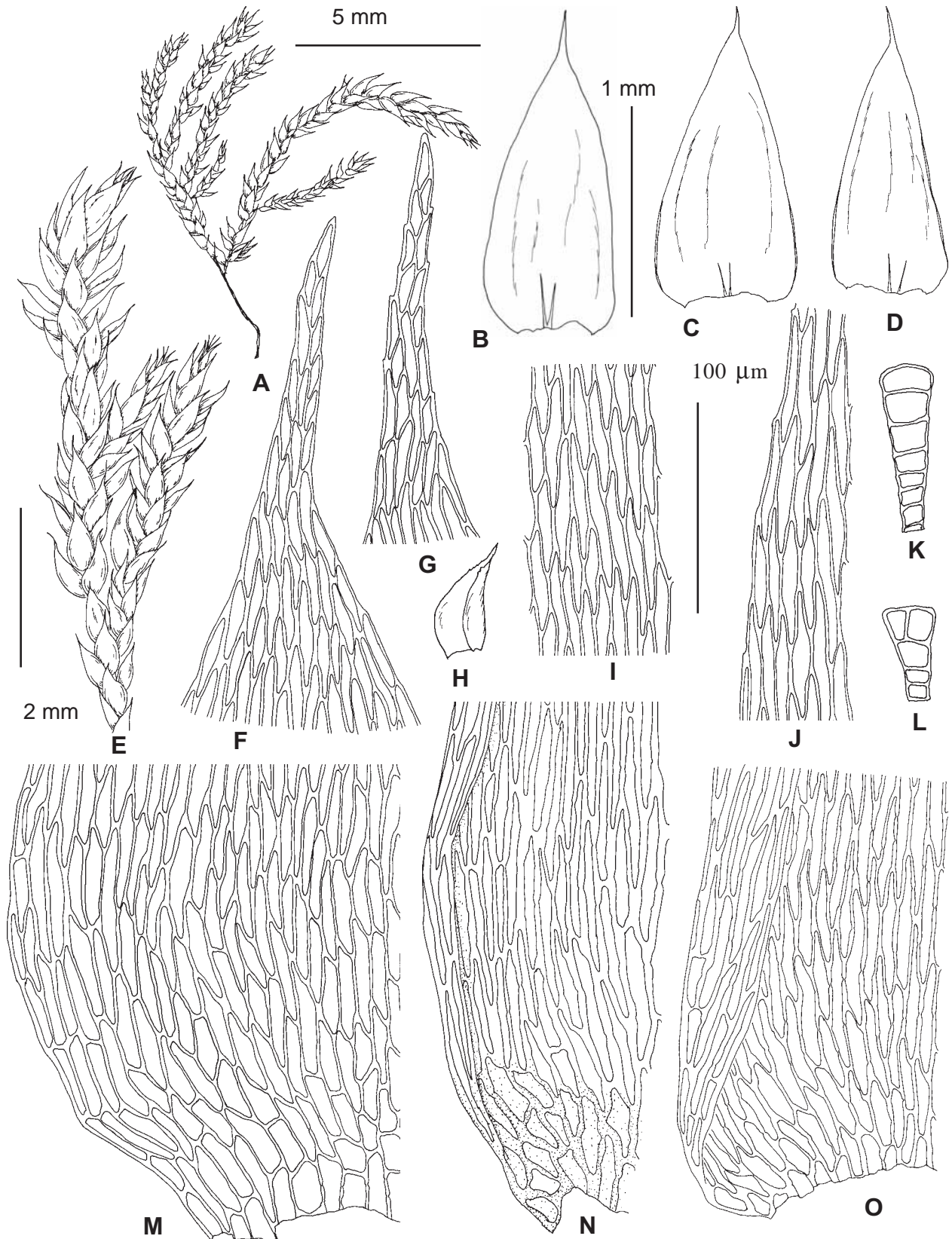


Рис. 11. *Orthothecium sibiricum* (A–F, I–J, M – from Yakutia, Ignatov & Ignatova 18-1441, OK2482; G–H, K–L – from: Yakutia, Sette-Daban Range, Ignatov & Ignatova 16-1277, MHA) and comparison of its leaf base with *O. chryseon*, from Taimyr, Kannukene s.n., OK2491 (N) and *O. rufescens*, from Krasnodar, Fisht, Ignatov s.n., OK2247 (O). A, E: habit, dry; B–D: leaves; F–G: upper leaf cells; H: perigonal leaf; I–J: median leaf cells; K–L: axillary gemmae; M–O: basal leaf cells. Scale bars: 5 mm for A; 2 mm for E; 1 mm for B–C, H; 100 µm for F–G, I–O.

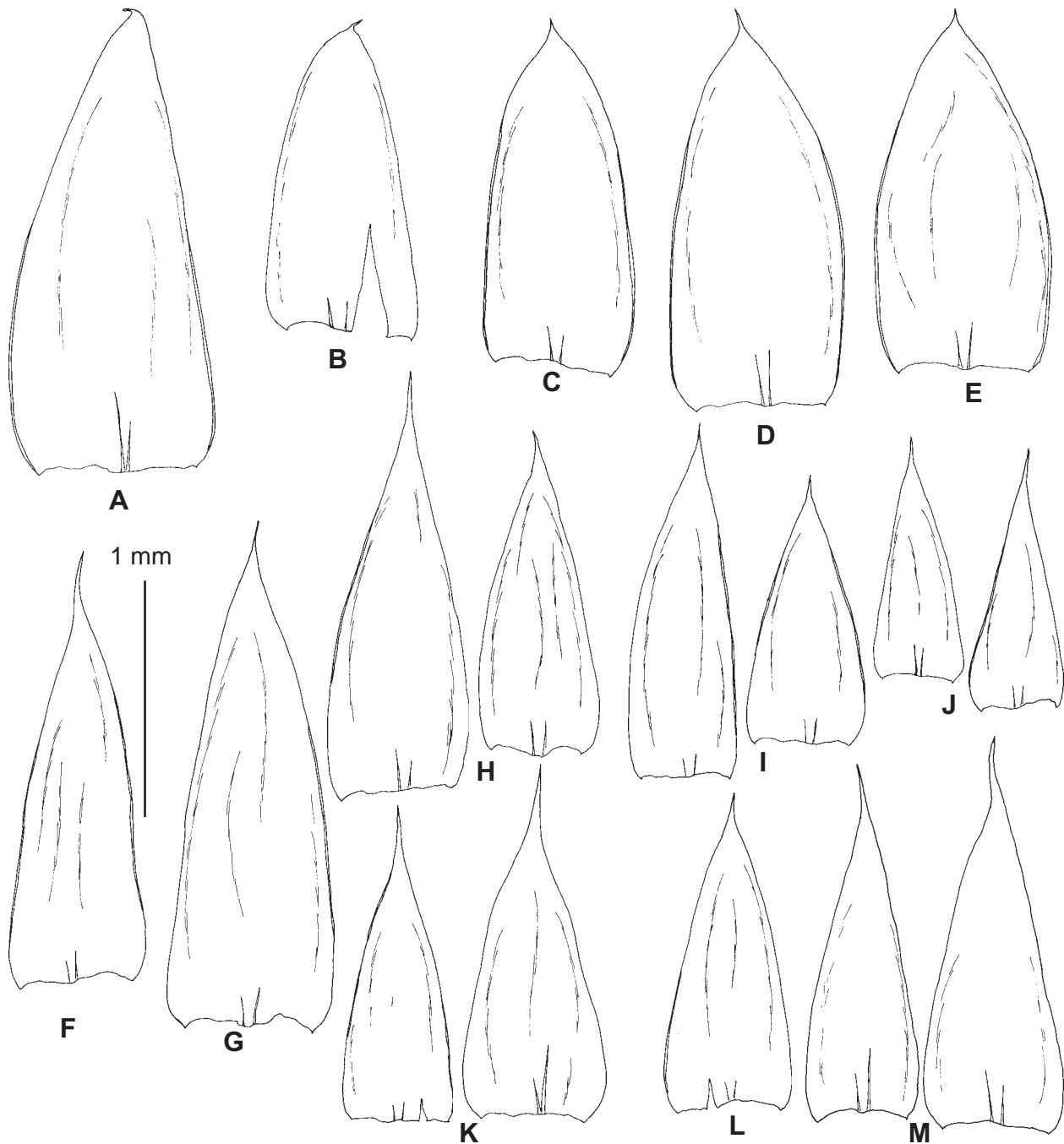


Fig. 12. Leaves of *Orthothecium lapponicum* (A–E) and *O. sibiricum* (F–M). A: Sweden, OK 1334; B: Sweden, OK 1335; C: Yakutia, OK 2205; D: Yakutia, OK 2266; E: Canada, OK 2402; F: Irkutsk Province, OK 2155; G: Altai, OK 2501; H: Yakutia, OK 1136; I: Yakutia, OK 2490; J: Yakutia, OK 2157; K: Yakutia, OK 2482; L: Yakutia, OK 2277; M: Yakutia, Oleneksky Distr., 22.VII.1957, Lukicheva & Samarina s.n., LE. Scale bars: 1 mm for all.

4. *Orthothecium sibiricum* Ignatov & Ignatova, sp. nova. Figs. 10, 11A–M, 12F–M, 13A–H.

Type: [Russia] USSR, Altai Mts., 51°44'N – 87°27'E, 470 m alt., Teletskoye Lake, Bolshoye Istyube Creek. Calcareous cliffs in deep canyon. 11 July 1991, Ignatov 18/119 (Holotype MHA 9029735, isotypes MW!, LE! CBFS!, and in other herbaria, exsiccata "Mosses of USSR" #166). Figs. 10, 12G, 13A–C. [DNA sequences: nuclear ITS MT681162, plastid *trnF-trnS* MT683739].

Diagnosis: *Orthothecium sibiricum* differs from *O. chryseon* in having slightly vs. strongly plicate leaves, more abruptly tapered to long and often piliferous acumens, more strongly rounded to base; from *O. lapponicum* by its smaller size, slightly plicate vs. smooth leaves, more gradually vs. abruptly acuminate leaves with longer acumina.

Description: Plants medium-sized, yellowish-green or brownish-green, glossy, in loose tufts. Stems ascend-



Fig. 13. Shoots of *Orthothecium sibiricum* (A–H) and *O. lapponicum* (I–J), showing variation in habit. A–C: Altai, Istyube, OK2501; D: Yakutia, OK1136; E–F: Irkutsk Province, Ot1567/OK2155; G: Yakutia, OK2482; H: Yakutia, Olenyoksky Distr., 20 July 1957 *Lukicheva & Samarica s.n.* (LE); I: Yakutia, OK2205; J: Canada, OK2402. All scale bars are 1 mm.

ing to erect, 2–4 cm long, terete-foliate, irregularly branched, branches 5–10 mm long. *Leaves* erect-spreading to loosely appressed, 1.0–1.8(–2.1)×0.4–0.7 mm, ovate-lanceolate, gradually acuminate, with long, narrow acumina, moderately concave, slightly plicate; margins narrowly recurved from near leaf base to above mid-leaf; *cells* 75–100×6–8 µm, in mid-leaf with moderately thickened, weakly porose walls, at basalmost part of leaf more thick-walled and strongly porose; alar cells not differentiated. *Specialized vegetative reproduction* by 4–5-celled clavate axillary gemmae. *Apparently dioicous*. *Gametangia* and *sporophytes* unknown.

Distribution and ecology. *Orthothecium sibiricum* is currently known from southern Siberia (Altai and Khamar-Daban mountains) and from several distant localities in Yakutia (Sette-Daban, Suntar-Khayata and Orulgan Ranges in Verkhoyansky System, Olenyokskiy District, Ulakhan-Chistai Range in Chersky System, Neryungri and Ust-Maya Districts in southern Yakutia) and the lower course of Lena River. It grows in mountain areas at altitudes of 470–1000 m, from the forest zone to the mountain tundra, on wet or damp calcareous cliffs, in niches of cliffs, between rocks and on rock outcrops on slopes.

Additional specimens examined: RUSSIA: **Yakutia:** Oymyakon District, Mus-Khaya Mt., Knoriy Creek, 14.VII.2011 *Ivanov s.n.* (MHA 9019891); Eveno-Bytantaysky District, Orulgan Range, upper course of Tumara River, *Ignatov 11-3874* (MHA 9019892); Neryngri District, Ivak River, 1.VIII.1987 *Volotovskiy s.n.* (MHA ex SASY); Olenyokskiy District, Sibikte River basin (tributary of Daldyn River, 20.VII.1957 *Lukicheva & Samarina s.n.* (LE). **Krasnoyarsk Territory:** Taimyr Peninsula, Anabar Plateau, Fomich River, *Fedosov 08-581* (MW 9045911). **Buryatia:** [Oka Distr.], East Sayan Mts, Bel'sky Range, Urik River at the mouth of Zegen-Gol Creek, 10.VIII.1959 *Bardunov & Vysokovskiy s.n.* (LE).

Differentiation and variation. Before molecular phylogenetic studies, the plants of *Orthothecium sibiricum* were identified partly as *O. chryseon* or *O. rufescens* (for larger plants) or *O. strictum* (for smaller plants). The larger plants, however, have only slightly plicate leaves (Fig. 10), and thus cannot be comfortably placed into the two former species. The leaves in larger plants of *O. sibiricum* are erect-spreading to spreading, whereas in *O. chryseon* they are usually appressed. Smaller plants (Fig. 11 A–M) have ovate to elliptic leaves and their size approaches the largest expressions of *O. strictum*, but differ in more strongly concave leaves, piliferous acumina, and leaf bases rather distinctly rounded towards insertion. The latter feature differentiates *O. sibiricum* from *O. chryseon* and *O. rufescens* as well (Fig. 11N–O): in the two latter species the leaves are not strongly rounded to the base.

Small plants of *O. sibiricum* approach *O. lapponicum*, but typical expressions of *O. lapponicum* are larger plants with leaves 1.0–2.3×0.5–0.9 mm vs. 1.0–2.1×0.4–0.7 mm in *O. sibiricum*, more abruptly and shorter acuminate.

Populations of *O. sibiricum* from southern Siberia comprise plants with larger leaves, 1.8–2.1×0.6–0.7 mm, while most of the Yakutian collections have leaves 1.0–1.8×0.4–0.6 mm. Molecularly, the plants named here *O. sibiricum* have two genotypes (see molecular results and discussion), the characteristic plastid haplotype is present only in a minority of mostly larger expressions, while most analysed plants share the plastid DNA with *O. lapponicum*. The morphologically distinct plants of the latter species, however, possess a distinct ITS ribotype.

5. *Orthothecium lapponicum* (Schimp.) C. Hartm., Handb. Skand. Fl. (ed. 10) 2: 29. 1871. — *Brachythecium lapponicum* Schimp., Syn. Musc. Eur. 697. 1860. — Figs. 12A–E, 13I–J.

Description. *Plants* in loose tufts, rather soft, golden yellow to yellow-brown to bright red, moderately lustrous. *Stems* to 5 cm long, ± julaceous, simple or occasionally irregularly branched. *Leaves* imbricate to slightly spreading, ovate, not or hardly decurrent, rather suddenly narrowed to acute or acuminate and mostly recurved apex, strongly concave and not or hardly plicate, 1.0–2.3×0.5–0.9 mm; leaf margins narrowly recurved from base nearly to apex, entire or finely denticulate just below leaf apex; median leaf cells 40–95×5–10 µm, slightly to strongly incrassate and porose; alar cells not differentiated. *Specialized vegetative reproduction* unknown. *Dioicous*. Only male plants seen. *Sporophytes* unknown.

Distribution and ecology. *Orthothecium lapponicum* is mostly found at elevations between 700 and 1240 m, with the lowest locality at 460 m. It most commonly grows in close proximity to late snow-beds, on slopes below these on wet soil or rocks, often with trickling meltwater, or sometimes at the margins of small brooklets. For more data see Hedenäs *et al.* (2019).

Differentiation and variation. *Orthothecium lapponicum* differs from the most closely related *O. sibiricum* in the relatively wider, more abruptly tapered and more concave leaves, which are somewhat less abruptly narrowed at their base (see above). It further differs from *O. strictum* in having mostly larger plants with concave, ovate leaves that are abruptly tapered to a very short acumens, versus moderately concave, ovate-lanceolate leaves that are more gradually tapered to a rather long acumens. *Orthothecium chryseon* usually has gradually tapered and markedly plicate leaves; it is generally a larger plant than *O. lapponicum*. Furthermore, the strongly concave leaves of the latter make its shoots tumid and sometimes wider than those of the appressed-leaved *O. chryseon*. Another good character is found in the mid-leaf cells; these are elongate, with a length to width ratio of 5–10:1 in *O. lapponicum* versus linear, and mostly 10–20:1 in *O. chryseon*. *Orthothecium retroflexum* is more similar to *O. lapponicum* in overall leaf shape, but its leaves are strongly plicate and have hooked leaf apices.

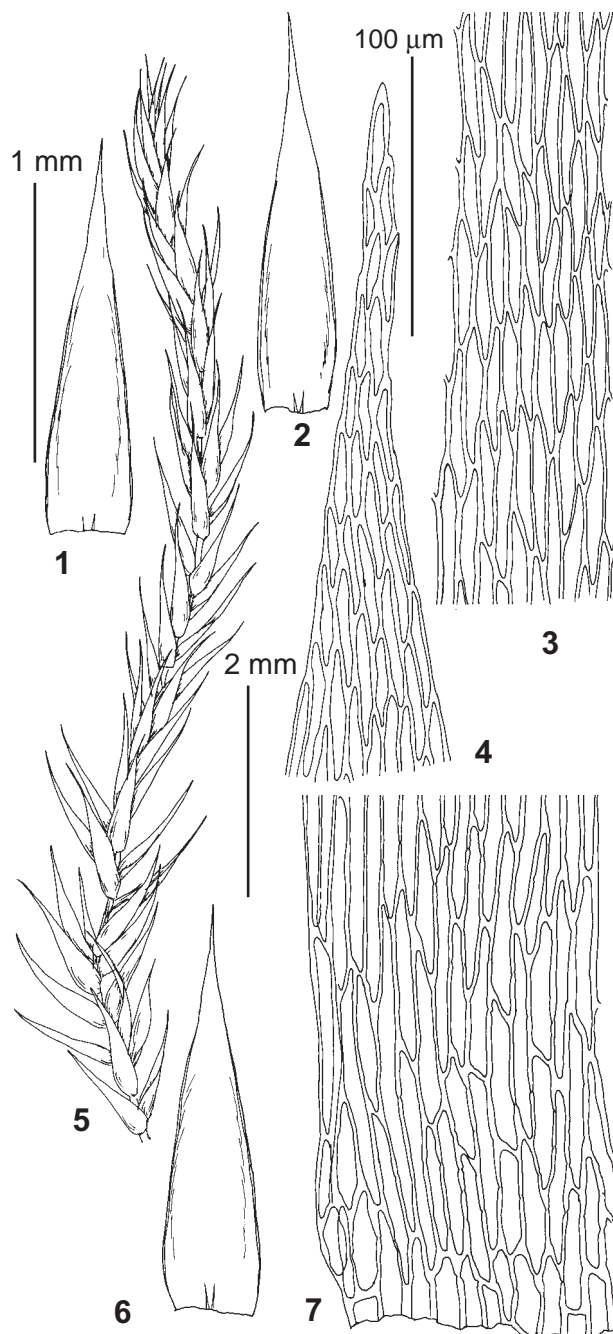


Fig. 14. *Orthothecium strictum* [clade 1] (Altai, Ignatov & Ignatova 12-495, OK 2233). 1–2, 6 – leaves; 3 – mid-leaf cells; 4 – upper leaf cells; 5 – habit, dry; 7 – basal leaf cells. Scale bars: 2 mm for 5; 1 mm for 1–2, 6; 100 µm for 3–4, 7.

6. *Orthothecium strictum* Lorentz, Moosstudien, 122. 5d. 1864. — *O. rubellum* (Mitt.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 46. 1883. — *Stereodon rubellus* Mitt., J. Proc. Linn. Soc., Bot. 8: 40. 1864. — *O. binervulum* Molendo in Lorentz, Moosstudien, 120. 1864. — Figs. 14–16, 17B–V, 18–21, 22C–D.

Plants small, rarely medium-sized, golden-, brownish- or reddish-green, glossy. *Stems* procumbent or ascending, to 2.5 cm long, terete-foliate, irregularly branched. *Leaves* erect-spreading or appressed (exceptional-

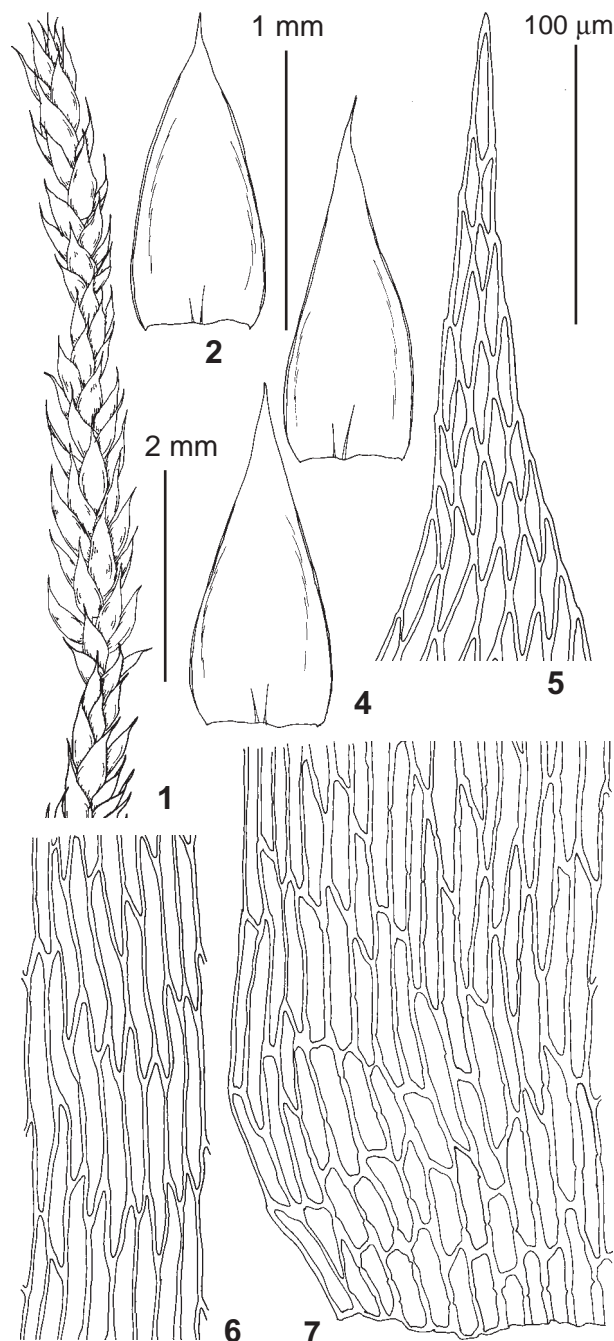


Fig. 15. *Orthothecium strictum* [grade 3] (from: Austria, Köckinger 15145, Ot1703). 1 – habit, dry; 2–4 – leaves; 5 – upper leaf cells; 6 – mid-leaf cells; 7 – basal leaf cells. Scale bars: 2 mm for 1; 1 mm for 2–4; 100 µm for 5–7.

ly homomallous, see discussion of OK2481 below), 0.8–1.7(–2.2)×0.2–0.6 mm, ovate-lanceolate or lanceolate, acuminate, slightly narrowed to insertion, not decurrent, moderately concave, non-plicate or slightly plicate in some leaves, especially in younger parts of plants; margins narrowly recurved for most of leaf length on both sides, rarely only in one side; *cells* in mid-leaf (40–)50–85×5–9 µm, with moderately thickened, weakly porose walls; basal leaf cells in 1–2 rows shorter and wider, porose, alar cells not differentiated. *Specialized asexual*



Fig. 16. Habit of *Orthothecium strictum*, showing variation: A: Mongolia, OK2496; B: Yakutia, OK 2237; C–D: Altai, OK2280. All scale bars are 1 mm.

reproduction by axillary gemmae rarely present, gemmae $60\text{--}85 \times 12\text{--}18\ \mu\text{m}$. *Sporophytes* very rare (described here for first time based on specimen OK2481, with anomalous gametophyte morphology, Fig. 21). *Setae* ca. 1 cm. *Capsules* short cylindrical, $0.9\text{--}1.1\ \text{mm}$ long, slightly inclined, slightly curved. *Exostome teeth* ca. $300\ \mu\text{m}$ long, whitish or yellowish-white, striolate below, papillose above; *endostome* with basal membrane ca. $150\ \mu\text{m}$ high, segments narrow, perforate, cilia 2, nodose. *Spores* $12\text{--}15\ \mu\text{m}$.

Distribution and ecology. *Orthothecium strictum* is a circum-Holarctic arctic-alpine species. It penetrates southward in Eurasia to Central Europe, Mongolia and Tibet, in North America to Colorado. In European Russia it occurs in northern regions where rocky substrates are abundant, and in the North Urals; in Asian Russia it is widespread in the mountains and in Arctic regions; in the south of the Russian Far East it was found only in Sakhalin Island. It occurs in a wide altitudinal range, from the sea level (in Kamchatka) to $2800\ \text{m}$ (in Altai Mts), and $5400\text{--}5800\ \text{m}$ in Tibet, growing on wet, shady limestone and gypsum cliffs and rock outcrops, arctic and mountain tundra, in niches between rocks of rock-fields.

Additional selected specimens examined: EUROPEAN RUSSIA: **Arkhangelsk Province:** Franz Josef Land: Hooker Island, Sedov Cape, 1929, *I.M. Ivanov s.n.* (LE); Alexandra Land Island, south of Nagurskaya station, 29.VII.2012, *Kholod II* (LE); Fersman Island, 7.VIII.2012, *Kholod s.n.* (LE); Georg V Land Island, *Kholod s.n.* (LE); ASIAN RUSSIA: Yamalo-Nenetsky Autonomous District: Yunto Lake, 12.VIII.1994, *Czernyadjeva 93* (LE); same place, 10.VIII.1993, *Czernyadjeva 58* (LE). **Krasnoyarsk Territory:** Vise Island, 14.VIII.1932 *V.P. Savicz 1562* (MHA, LE); Jenisei, Mjelnitsa, 13.VII.2876, *Arnell s.n.* (S, B213763); Taimyrsky Autonomous District, Kayak Settl., Kotui River, *Fedosov 07-830* (MW 9075084); western Taimyr, right bank of Pyasina River near Tareya Settl., 15.VII.1966, *Matveeva s.n.* (MW 9075083). **Yakutia:** Lensk District, Pilka River basin, 25.VII.1999, *E.I. Ivanova s.n.* (MHA ex SASY); Olenyokskiy Distr., Daldyn River basin, 29.VI.1956, *Lukicheva & Zagrebina s.n.* (LE); Tomponsky Distr., Sette-Daban Mt. Range, Segenyakh (Rosomakha) Creek, *Ignatov & Ignatova 15-586* (MHA 9029737); Eveno-Bytantaysky Distr., Orulgan Mt. Range, Enigan-Toolono Creek, 8.VIII.2011, *Isakova 439* (MHA ex SASY); Khangalassky Distr., Lenskie Stolby near Labydja Creek mouth, *Ignatov 00-223* (MHA); Oymyakon Distr., Suntar-Khayata Mt. Range, Mus-Khaya Mt., *Ignatov & Ivanov 11-3535* (MHA). **Altai Republic:** Ak-Turu, 19.VII.1966, *Bardunov s.n.* (MHA); Kuraiskij Mt. Range north of Kosh-Agach, 1.VIII.1992, *Ignatov 31/183* (MHA).

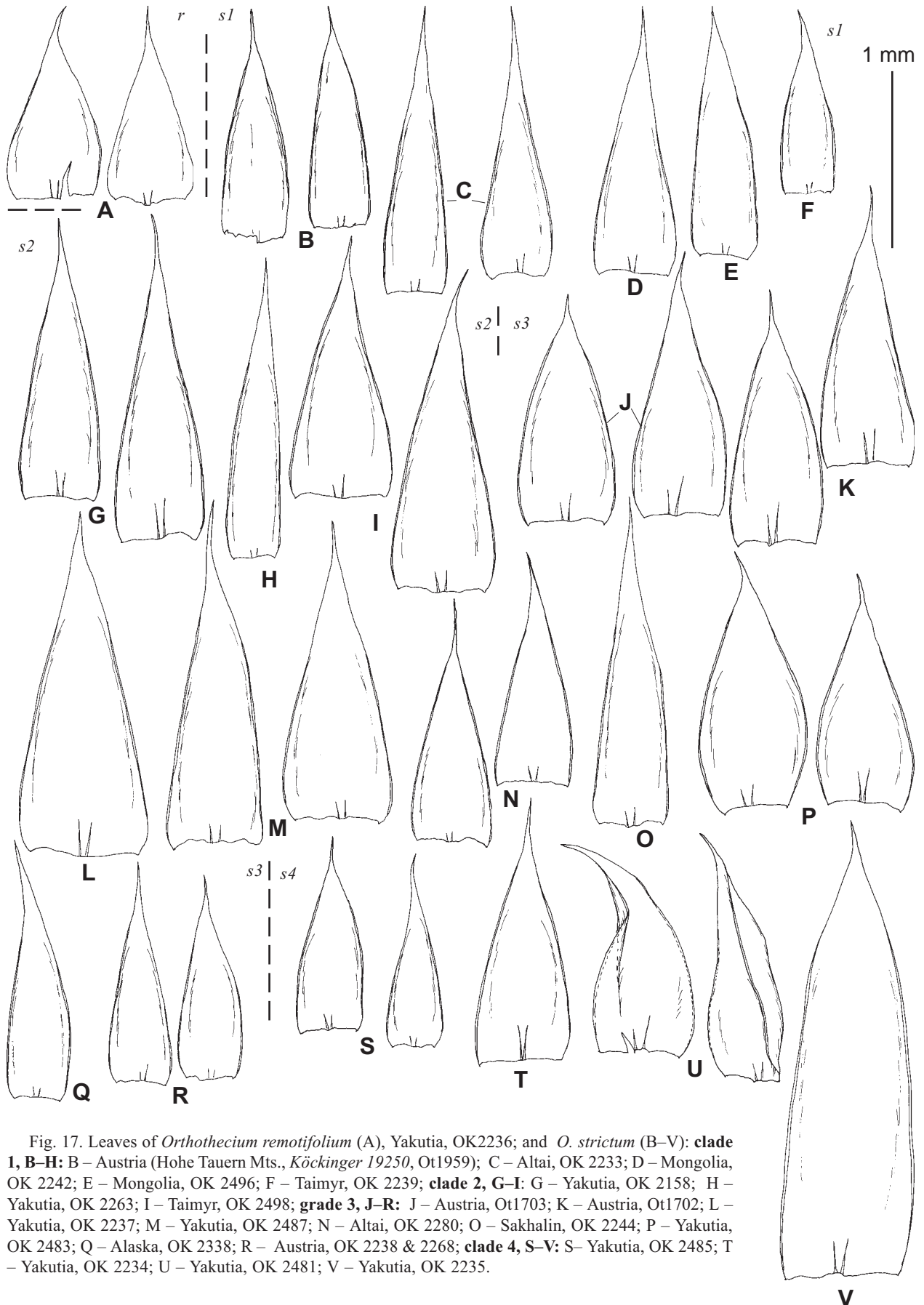


Fig. 17. Leaves of *Orthothecium remotifolium* (A), Yakutia, OK2236; and *O. strictum* (B–V): **clade 1, B–H**: B – Austria (Hohe Tauern Mts., Köckinger 19250, Ot1959); C – Altai, OK 2233; D – Mongolia, OK 2242; E – Mongolia, OK 2496; F – Taimyr, OK 2239; **clade 2, G–I**: G – Yakutia, OK 2158; H – Yakutia, OK 2263; I – Taimyr, OK 2498; **grade 3, J–R**: J – Austria, Ot1703; K – Austria, Ot1702; L – Yakutia, OK 2237; M – Yakutia, OK 2487; N – Altai, OK 2280; O – Sakhalin, OK 2244; P – Yakutia, OK 2483; Q – Alaska, OK 2338; R – Austria, OK 2238 & 2268; **clade 4, S–V**: S – Yakutia, OK 2485; T – Yakutia, OK 2234; U – Yakutia, OK 2481; V – Yakutia, OK 2235.

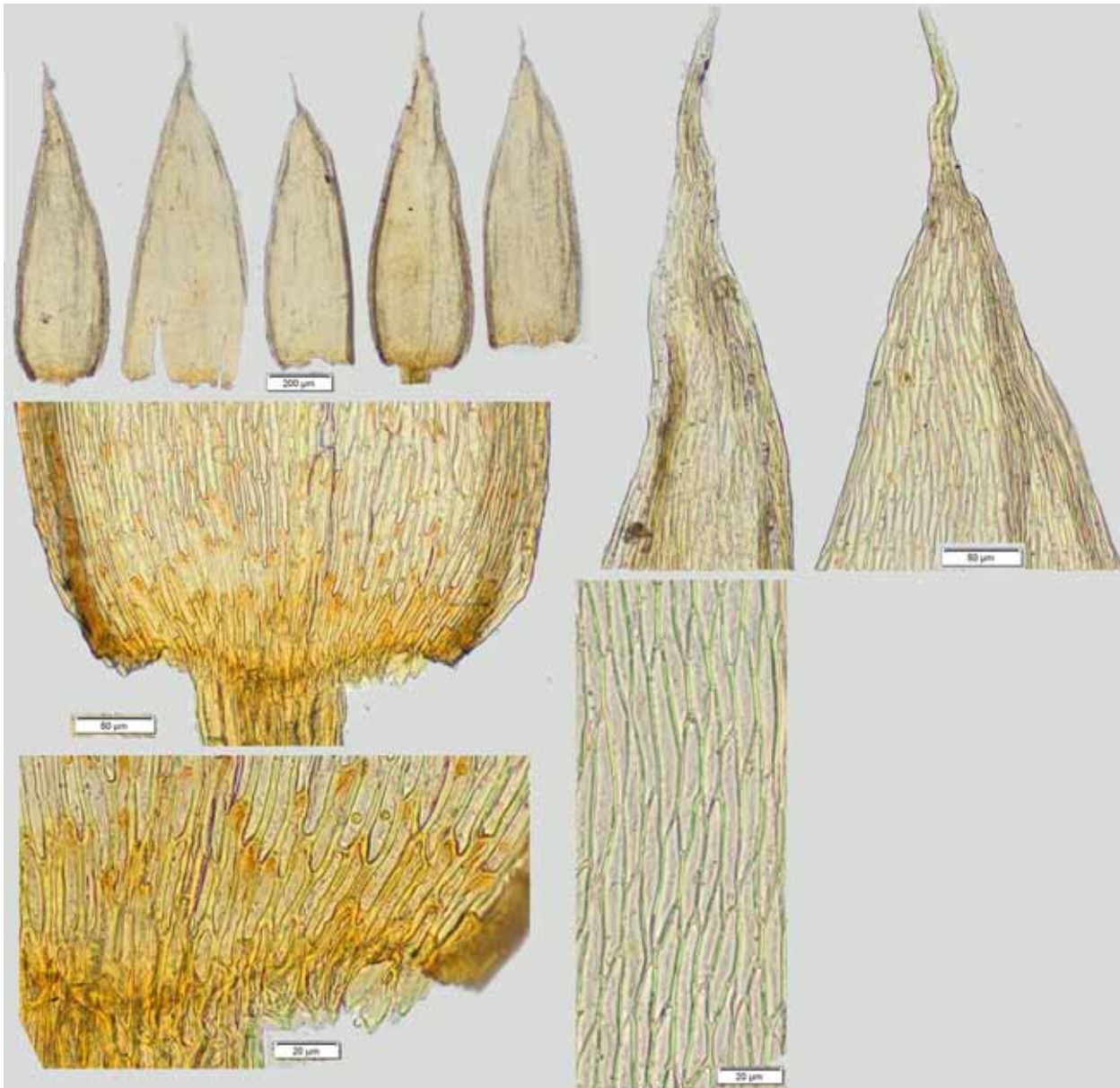


Fig. 18. Isotype of *Orthothecium strictum* Lorentz (S-B171896): Austria, Hohe Tauern Mts., Pasterze glacier, 1861, P.G. Lorentz.

EUROPE: **Norway:** Nord-Trøndelag Province, Røyrvik Distr., 18.VII.2014, *Hedenäs s.n.* (S, B205284); Svalbard, Advent Bay, 1926, *Lagerkranz s.n.* (S, B213723). **Sweden:** Jämtland Province, 19.VII.1882, *Adlerz s.n.* (S, B213525); Torne lappmark Province, Jukkasjärvi, VII.1944, *Hülphers s.n.* (S, B213631); Lule lappmark Province, Kivickjock, Kaddepakti, 29.VII.1867, *Holmgren s.n.* (S, B213549); Lycksele lappmark Province, Tärna, *Hülphers s.n.* (S, B213540). **Finland:** Koillismaa Province, Kuusamo Distr., VIII.1883, *Brotherus s.n.* (S, B213709). **Italy:** Veneto Province, Belluno Distr., 25.VIII.1907, *Pampanini 889* (S, B213762). **Switzerland:** Graubünden, Rhaetia Val Duana, 20.VII.1868, *Pfeffer s.n.* (S, B213769).

NORTH AMERICA: **Canada:** Northwest Territories, Ellesmere Island, 0.VIII.1967, *Brassard 3236* (S, B213888); Yukon Territory, 8.VII.1973, *Vitt 7978* (S, B213887). **Greenland:** Narssaq, 26.VIII.1962, *Steere 62-1153* (S, B213886). **U.S.A.:** Alaska, Umiat and vicinity, Colville River, 21-26.VII.1951, *Steere 17145* (S, B213954).

Differentiation and variation. *Orthothecium strictum* is distinguished by a combination of the following characters: small size of plants; terete foliate stems; erect to erect-spreading leaves, occasionally appressed or widely spreading, lanceolate or ovate-lanceolate, not or weakly plicate [when dry], narrowly acute or acuminate; leaf margins entire or weakly serrulate near apex, and narrowly recurved for most of leaf length or partly so. Its differences from *O. brunnescens* and *O. remotifolium* are discussed under those species. *Orthothecium intricatum* is similar to *O. strictum* (especially to its narrow-leaved morphs) in its plant and leaf size but has usually slightly homomallous leaves and flat leaf margins. Homomallous leaves are rare in *O. strictum* except for specimens collected at one locality in Yakutia, Ulakhan-Chistay Mt. Range, which have falcate-secund leaves with narrowly recurved margins (isolate OK 2481; Fig. 21). This is the

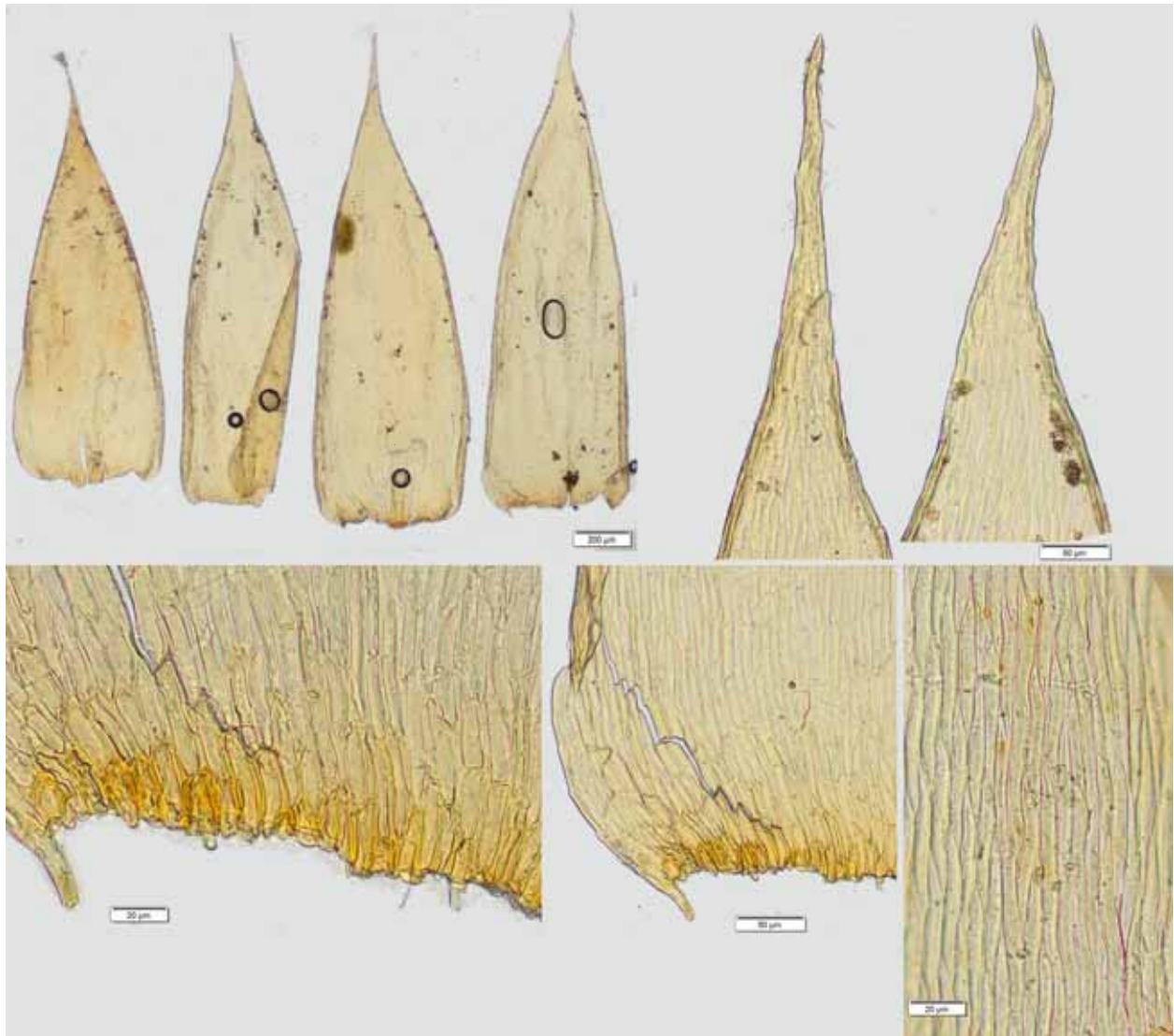


Fig. 19. Syntype of *Orthothecium binervulum* Molendo (S-B171895): Germany, Bavaria superior, Bernadeinalpe bei Partenkirchen, 1850 m. 1862. Coll. Molendo.

only known collection of this species with sporophytes.

Both ITS and chloroplast data agree on the support for the lineage, annotated as *O. strictum* 1 in the phylogenetic trees. The plants with this multilocus genotype are morphologically rather homogeneous, corresponding perfectly to the description of *O. strictum* (Lorentz, 1864) as small, high-alpine cryophilous plants, occurring in corresponding biotopes throughout the Northern Hemisphere. Most of the molecularly barcoded specimens of *O. strictum* 1 lineage are from the region extending from Alaska through Magadan Province and Yakutia to Mongolian and Altaian highlands, and also in Anabar Plateau in the southern Taimyr. However, two specimens of the same genotype were discovered in high-alpine regions of Austria, with one them even from the same mountain range where the type locality of *O. strictum* occurs (*Köckinger* 15250, isolate Ot1959: Austria: Tyrol, Hohe Tauern, Mt Säulkopf, Fig. 17B). The plants match mor-

phologically the isotype of *O. strictum* (Fig. 18). However, we are at present not able to distinguish such plants morphologically from small plants belonging to the other three lineages within *O. strictum* s.l., although these lineages often contain markedly more robust plants, with leaves often at least slightly plicate and having sometimes markedly remote-leaved foliage.

It is not impossible that *O. binervulum* can be resurrected for plants belonging to the grade annotated here as *O. strictum* 3 (containing, e.g., the specimen from Austria: Upper Austria, Hochschwab Mts, Rinnerhütte, coll. *Köckinger* 15250, isolate Ot1703, Fig. 17J). The morphology of these plants agrees with two available syntypes from Austria and Italy (Figs. 19, 20), although unfortunately, both syntype specimens and the recent Austrian collections from Austrian Alps rather represent the smaller expressions while all robust, morphologically distinct plants originate from northeast-Asian collec-

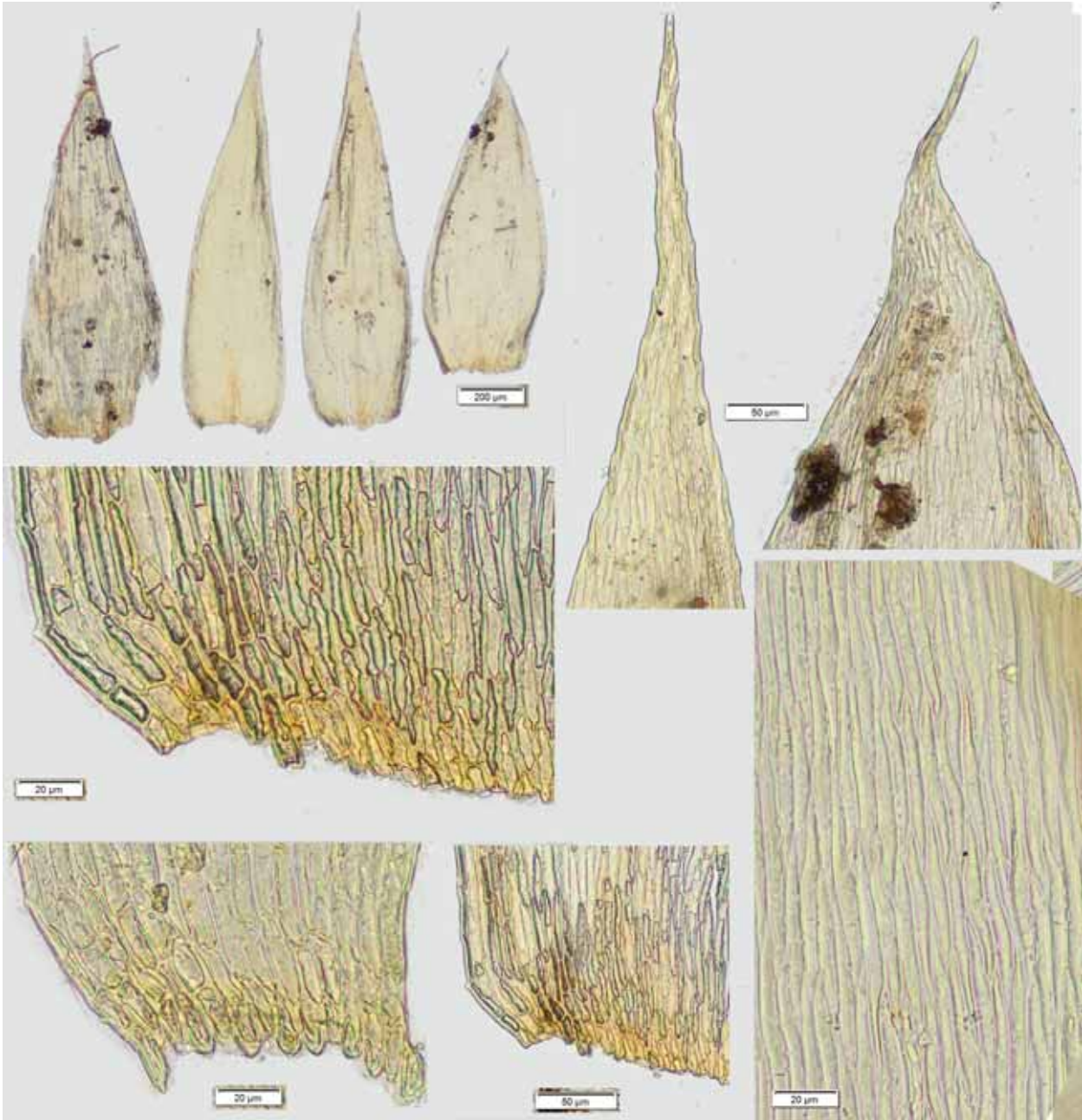


Fig. 20. Syntype of *Orthothecium binervulum* Molendo (S-B171894): Italy, Trentino-Alto Adige, Marmolada in Val Fredda, 5600'. 1863. Coll. Molendo.

tions. *Orthothecium binervulum* was moreover described from four different localities in the peripheral ranges of the Alps, although in all cases from markedly less cryophilous conditions and in all cases from calcareous substrates, in contrast to the crystalline rocks of the Hohe Tauern Mts in the close proximity of Pasterze glacier at the type locality of *O. strictum* (H. Köckinger, pers. comm.). Whether the match with habitat and the slight morphological differentiation is fully consistent across the distribution range of the species, needs to be confirmed, however it is noteworthy that the Asian barcoded collections of *O. strictum* 1 also mostly originated from non-calcareous areas.

With respect to the enormous morphological plasticity within *O. strictum* 2–4 lineages and the relatively small amount of molecularly barcoded material, it would be premature to suggest any taxonomic consequences from the molecular resolution within *O. strictum* s.l., as the observed differences could not be used for practical identification. For example, the leaf shape seems to form a continuum among the lineages (Fig. 17), although the specimens from clade 1 (Fig. 17B–F) have rather small, narrow-leaved plants with leaves lanceolate, 0.6–1.4×0.2–0.4 mm. Representatives of clade 2 (Fig. 17G–I) have mostly longer and relatively narrow-leaved plants with leaves 1.4–1.8×0.3–0.6 mm, approaching in leaf length

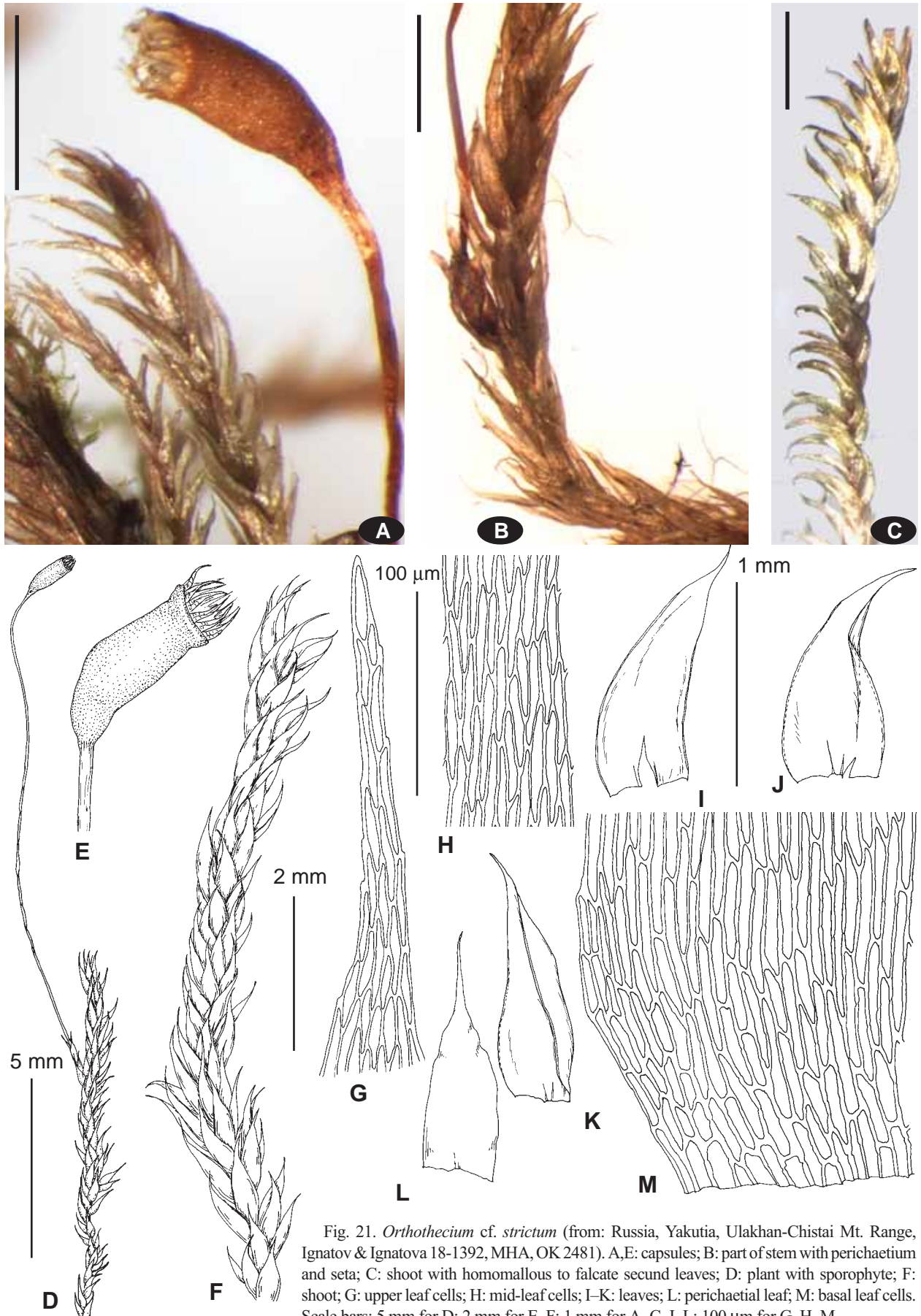


Fig. 21. *Orthothecium* cf. *strictum* (from: Russia, Yakutia, Ulakhan-Chistai Mt. Range, Ignatov & Ignatova 18-1392, MHA, OK 2481). A, E: capsules; B: part of stem with perichaetium and seta; C: shoot with homomallous to falcate second leaves; D: plant with sporophyte; F: shoot; G: upper leaf cells; H: mid-leaf cells; I-K: leaves; L: perichaetial leaf; M: basal leaf cells. Scale bars: 5 mm for D; 2 mm for E-F; 1 mm for A-C, I-L; 100 µm for G, H, M.

to plants of the grade 3. The most common grade (polytomy) 3 (Fig. 17J–R) is especially variable: some plants comprise phenotypes with ovate-lanceolate leaves (Fig. 17J–K) 1.1–1.4×0.45–0.50 mm, similar to the type material of *O. binervulum* (Figs. 19, 20), while others comprise plants with leaves very variable in shape and size (Fig. 17L–R): ovate-lanceolate, triangular-lanceolate and lanceolate, 1.1–1.7×0.3–0.6 mm. Four specimens of clade 4 (Fig. 17S–V) are also extremely variable, comprising plants with the smallest and the largest leaves (Fig. 17S & V), as well as a fertile specimen with falcate-secund leaves (Fig. 17U); leaf size in this clade is the most variable, 0.9–2.2×0.3–0.6 mm (Fig. 17S–V).

The lectotypification of *O. binervulum* requires special attention, as Molendo in his original description (Lorentz, 1864) mentioned that the leaves of *O. binervulum* are shorter than leaves of *O. strictum*, whereas Limpricht (1895) mentioned that *O. binervulum* has larger leaves, up to 2(–3) mm long, matching our interpretation of the types. It is likely that Limpricht's opinion convinced many later authors (Brotherus, 1925; Podpěra, 1953) to accept this taxon.

There are morphotypes of *O. strictum* that have some aspects of *O. intricatum*, including poorly expressed recurved leaf margins, very narrow leaves, but the most unusual plants were found in Yakutia, in the foothills of Mramornaya mountain, a giant marble monolith piece, and one of two areas where *Andreaeobryum macrosporum* Steere & B.M. Murray was found in Eurasia (Ignatov *et al.*, 2018). Several specimens were collected in very close proximity; they were named in the field as *Hygrohypnum luridum* due to falcate-secund leaves and numerous sporophytes. However, closer examination revealed undifferentiated alar cells, a dioicous sexual con-

dition, and axillary rhizoids, and molecular data pointed at an affinity with *Orthothecium strictum*. It is noteworthy that curved and inclined capsules are unique in *Orthothecium*: its generic name refers to straight, erect capsules which are often present in European collections of *O. rufescens* and *O. intricatum*.

7. *Orthothecium remotifolium* Ignatov & Ignatova, sp. nova. Figs. 22A,B, 23–24.

Type: Russia: Yakutia, Eveno-Bytantaysky District, Orulgan Range, upper course of Aenigan-Toloono Creek, 68°14'N, 128°06'E, alt. 600 m, boggy hummock on rarely flooded creek bank, 8.VIII.2011, Ignatov 11-4134 (Holotype: MHA 9029738), isotype: MW 9049153, <https://plant.depo.msu.ru/public/scan.jpg?pcode=MW9049153>. Figs. 22A, 23A–J, 24A–D. [DNA sequences: nuclear ITS MT681154, plastid *trnF-trnS* MT683729].

Diagnosis: *Orthothecium remotifolium* differs from *O. strictum* in a more broadly triangular leaf shape vs. lanceolate to ovate-lanceolate, leaf margin serrulate below mid-leaf vs. entire to serrulate only near apex, and incurved, flat or occasionally recurved vs. usually recurved, rarely almost flat leaf margins; from *O. acuminatum* it differs in the more gradual tapering of leaf to apex vs. leaves more abruptly contracted to apex in *O. acuminatum* and leaves erect to spreading vs. commonly tightly appressed.

Description: Plants small, slender, light-green or yellowish-green, glossy. Stems 1–3 cm long, loosely to densely terete-foliate, loosely fasciculate branched to almost unbranched. Leaves erect-spreading, occasionally slightly secund, 0.7–1.2×0.3–0.4 mm, ovate-triangular, gradually tapered into short, narrow acumen, slightly narrowed at base, not decurrent, moderately concave, epligate to weakly plicate; margins flat, incurved or in some leaves recurved in upper half, rarely recurved at larger distance, often on one side; cells 30–50×7–9 µm. Gemmae up to 100 µm long, of 5–6 cells in one row, except the top where cells occasionally are two. Sporophytes unknown.

Distribution and ecology. This species was collected in Eurasia so far in a few places: two times in Yakutia, Orulgan Range, 68°N, at 600 and 800 m alt., at and above “tree-line” (where 3 m tall *Salix* and *Larix* can grow) in that area, in wet tundra, at a brook bank; once in southern Taimyr, Anabar Plateau, 71°N, ca. 400 m, in a crevice of dolomite cliff; and also it was found in two collections from the Franz Josef Land (80°N), near a pool on terrace of N-facing slope, and inexact habitat close to shore of the Bay Tikhaya.

Additional specimens examined: EUROPEAN RUSSIA: **Arkhangelsk Province:** Franz Josef Land: insula Scott Keltie, 25.VII.1933, V.P. Savicz 888 (LE); Hooker Island, 1-3.VII.1929, I.M. Ivanov s.n. (LE). **ASIAN RUSSIA: Krasnoyarsk Territory,** Anabar Plateau, slope of height 424 to Kotuykan River valley, Fedosov 07-305 (MW9110081).

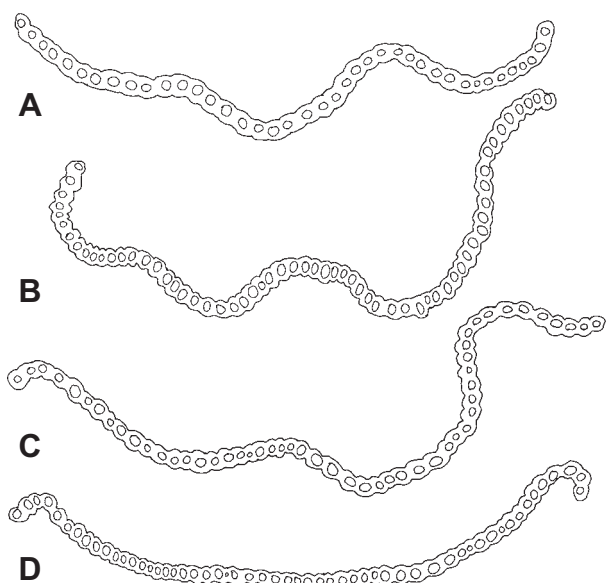


Fig. 22. *Orthothecium remotifolium*, A (Yakutia, OK2489), B (Yakutia, OK2236) and *O. strictum*, C (Austria, OK2591, Ot1703), D (Altai, OK2233). Scale bar 100 µm for all.

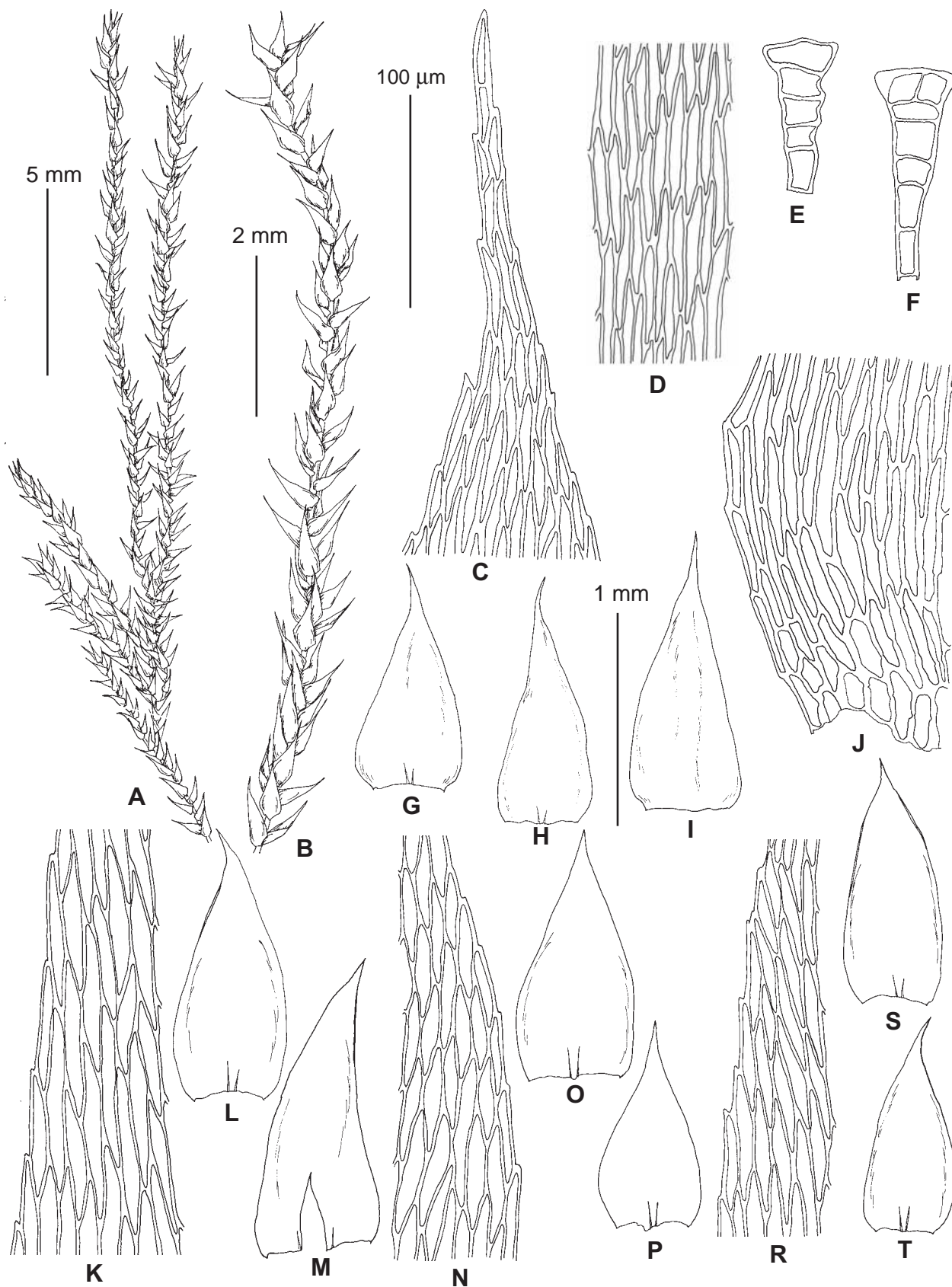


Fig. 23. *Orthothecium remotifolium* (A-J: Yakutia, OK2236; K-M: Taimyr, Fedosov 07-305, MW9110081; N-P: Franz Josef Land, 1-3.VIII.1929, I.M. Ivanov s.n., LE; R-T: Franz Josef Land, 25.VII.1933, V.P. Savicz 888, LE). A-B: habit, dry; C: upper leaf cells; D, K, N, R: mid-leaf cells; E-F: gemmae; G-I, L-M, O-P, S-T: leaves; J: basal leaf cells. Scale bars: 5 mm for A; 2 mm for B; 1 mm for G-I, L-M, O-P, S-T; 100 µm for C-F, J, K, N, R.



Fig. 24. *Orthothecium remotifolium*: A–D: from Yakutia, OK2236 (holotype); E–F, H: from Franz Josef Land, Scott Keltie Island, 25.VII.1933, V.P. Savicz 888 (LE); G: from Franz Josef Land, Hooker Island, 1–3.VII.1929, I.M. Ivanov s.n. (LE). Scale bars for A–C & E: 1 mm, for D, F–H: 0.5 mm.

Differentiation and variation. *Orthothecium remotifolium* looks like a small morph of *O. strictum*, differing in the long, evenly foliated shoots with distantly arranged, erect-spreading to widely spreading, quite con-

cave leaves that are relatively broader and shorter and mostly also smaller ($0.7\text{--}1.2 \times 0.3\text{--}0.4$ mm vs. most commonly $0.8\text{--}1.8 \times 0.3\text{--}0.6$ mm in *O. strictum*). Habitually, this species is not distinct from some morphs of *O. stric-*

tum, and we realised and properly evaluated the microscopic differences only after we retrieved the molecular data which showed a strong differentiation from *O. strictum*.

The most arguable decision was the possible identity of this species with *Orthothecium acuminatum*. That species was described from Greenland and Ellesmere Island in high arctic Canada, and later lectotypified with a specimen from Greenland (Grout, 1928). In the end of detailed Latin description, Bryhn (1906) provided a short summary in Danish: “This new species that in habit mostly looks like *Orthothecium strictum*, differs from the latter – and all the other species of *Orthothecium* – by the peculiar leaf shape and toothed leaf borders” (translation by Irina Goldberg). According to the description, leaf shape is ovate-triangular, abruptly contracted to the acumen. The description also mentioned plane leaf margins.

Courtesy of Siri Rui (herbarium O), we were able to study high resolution scanned images of the type material, including the lectotype of *Orthothecium acuminatum* (“Bryophyta in itinere polari Norvegorum secunda collectum # 2786, *Orthothecium acuminatum* Bryhn sp.n., America arctica, Kong Oscars Land, Gaasefjord, Lat. sept. circiter 76°30', Mense Junis Anni 1901, legit Herm. S. Simmons, Determ. N. Bryhn” O-B-100188).

Leaf details were not seen in these scans, however the lectotype and two syntypes studied contain plants with a julaceous foliage that is very distinct not only from the type material of *O. remotifolium* and other Yakutian collections, which are typically rather distantly foliate and their leaves are spreading at wide angle (Figs. 23, 24) but also from plants from more northern parts of Eurasia, Taimyr and Franz Josef Land which in different shoots vary from imbricate (Fig. 24E) to erect (Fig. 24G) and spreading foliage (Fig. 24F, H). Unfortunately, the fresh material from European and North American Arctic was unavailable for molecular studies, which leaves the confirmation of molecular distinctness between *O. remotifolium* and *O. acuminatum* pending to the future studies.

8. *Orthothecium rufescens* (Dicks. ex Brid.) Bruch, Schimp. & W. Gümbel, Bryol. Eur. 5: 107. 1851. — *Hypnum rufescens* Dicks. ex Brid., Muscol. Recent. 2(2): 139. 1801. Fig. 25 A, H, 26 A–B, D–E.

Description: Plants large, cherry-red, moderately to slightly glossy when dry. Stems procumbent to ascending, 2–10 cm long, irregularly branched. Leaves erect-spreading, often slightly secund, 2.0–4.5×0.5–1.0 mm, narrowly lanceolate-triangular, tapering from near base to long and narrow acumen, scarcely narrowed to insertion, “truncate” at base, with small and sharp rounding at leaf angles, not decurrent, weakly concave, strongly plicate; margins narrowly recurved almost from base at most of leaf length; cells in mid-leaf 50–150×5–8 (–10) µm, with moderately thickened, weakly porose walls; basal leaf cells shorter and wider, thick-walled,

porose, alar cells not differentiated. *Specialized asexual reproduction* by axillary gemmae rarely present. *Sporophytes* rare, unknown in Russia. *Setae* 2–3.5 cm long. *Capsules* ca. 3 mm long, cylindrical, erect or slightly inclined, straight or almost so. *Opercula* highly conic to shortly rostrate. *Annulus* revoluble. *Peristome* ± reduced: exostome teeth narrow, pale, striolate below on dorsal surface, finely papillose above; endostome basal membrane 1/4 of peristome height, segments narrow, cilia absent or rudimentary. *Spores* 10–14 µm [sporophyte features based on material from Scandinavia and the European Alps].

Distribution and ecology. *Orthothecium rufescens* is known from most European countries, Caucasus and Western Asia. In Russia it was reported from many areas, including the Arctic; however, these records were based on misidentifications of *O. chryseon*. *Orthothecium rufescens* only occurs in few localities in the Russian part of Caucasus and in a single locality in NW European Russia. We also confirm its occurrence in North Urals (Perm Province). In Caucasus it occurs in the alpine zone, being abundant at places on wet, shady calcareous rocks, near entrances into karst caves, etc. In Karelia it was also collected on wet calcareous cliffs near a waterfall.

Specimens examined: EUROPEAN RUSSIA: **Karelia:** Kuusamo, Paanajärvi, Kulmakkapuro, 31.VIII.1933, *Kotilainen s.n.* (LE); same place, Sovajärvi, 8.VIII.1936, *Kotilainen s.n.* (LE). **Perm Territory:** Chusovskoy Distr., left bank of Chusovaya river, 16.VII.2017, *Bezgodov 213* (MW 9090558).

EUROPE: Romania: Transsilvania, distr. Năsăud, 2.VII.1918, *Peterfi s.n.*, Flora Romaniae Exsiccata #1136 (MHA 9066913). **Slovakia:** mont. Mala Tatra, prope Terchova, IX.1988, *Pilous s.n.* (MHA 9066909). **Poland:** Tatra Mts, SW of Zakopane, 10.III.1995, *Ignatov & Ochrya s.n.* (MHA 9066910). **Switzerland:** Neuchâtel, 29.IX.2017, *Hedenäs s.n.* (S, B262945). **Austria:** Schneeberg Mt., *Ignatov & Schanzer 05-5007* (MHA 9066911); Salzburg, VIII.1907, *Klaus s.n.*, E. Bauer, Musci europaei exsiccati #591 (MW 9091881). **Croatia:** Plitvice, 20.IV.1954, *Een Cr044* (S, B22282). **France:** Midi-Pyrénées Province, Hautes-Pyrénées, 4.VIII.1959, *Een F367* (S, B33705); **Germany:** Bayern, VII.1886, *Haussknecht s.n.* (S, B289705). **Italy:** Lombardia, Como, 4.VIII.1895, *Artaria s.n.* (S, B214468). **Norway:** Nord-Trøndelag, Røyrvik, 19.VII.2014, *Hedenäs s.n.* (S, B205394). **Sweden:** Dalsland, Dalskog, 25.X.1975, *Hallingbäck TH 44309* (S, B217040); Torne lappmark, Jukkasjärvi, 10.VIII.1983, *Hedenäs s.n.* (S, B295979); Pite lappmark, Arjeplog, 16.VII.1932, *T. & A. Arwidsson s.n.* (S, B113369). **United Kingdom:** Scotland, 27.VII.1956, *Een UK184* (S, B24278).

Differentiation and variation. *Orthothecium rufescens* is somewhat similar to *O. chryseon* in leaf shape and a strong plication, which has caused confusion. However, they differ in habit: *O. rufescens* always has stiff, erect-spreading, often somewhat secund leaves, which are gradually tapered almost from the base, whereas the leaves of *O. chryseon* are loosely appressed, softer, never secund, and ovate-lanceolate. Furthermore, the recurvation of leaf margins in *O. rufescens* ends slightly above

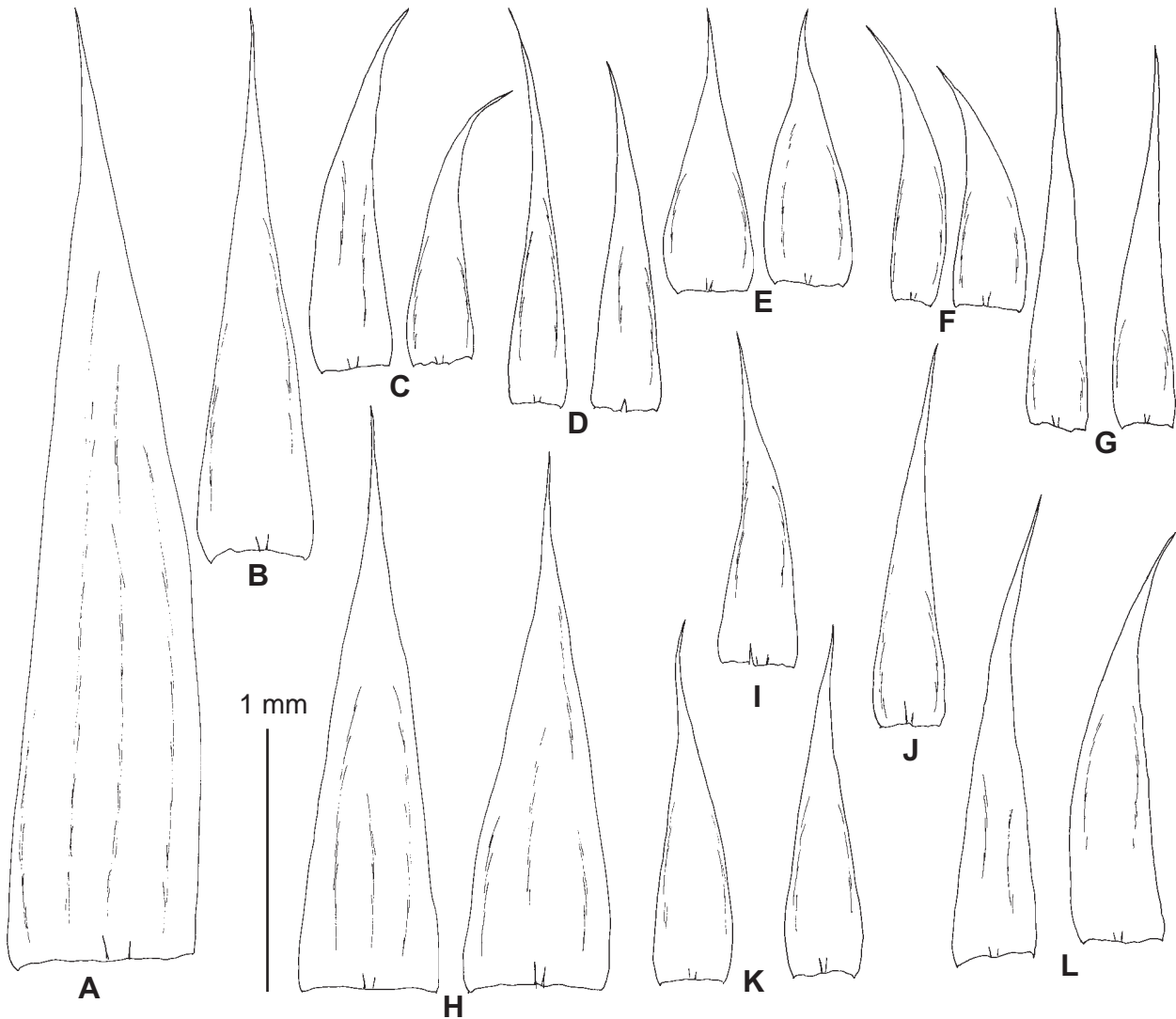


Fig. 25. Leaves of *Orthothecium rufescens* (A), *O. aff. rufescens* (H) and *O. intricatum* (B–G, I–L). A: Krasnodar Territory, OK 2247; B: Czech Republic, OK 2588; C: Poland, OK 2270; D: Krasnodar Territory, OK 2274; E: Republic of Adygea, OK 2499; F: Austria, OK 2592; G: Bashkortostan, OK 2275; H: Altai, OK 2276; I: Altai, OK 2245; J: Perm Province, OK 2271; K: Perm Province, OK 2246; L: Dagestan, OK 2273. Scale bars: 1 mm for all.

the leaf insertion, so small portion in the leaf angles are flat, whereas in the leaves of *O. chryseon* the margins are recurved to the lowermost leaf portion, including the short decurrencies. Also, the leaves of *O. rufescens* are longer acuminate.

One enigmatic specimen, *O. aff. rufescens*, OK2276, collected on wet cliffs in the subalpine zone of Altai, was resolved as *O. rufescens* in the ITS analysis, and among *O. intricatum* accessions in the plastid tree. It is intermediate in morphology: the leaves are the largest among *O. intricatum* included in this study (Fig. 25H), but unlike *O. rufescens* (Fig. 26A,D) the leaves in the Altaian plants are appressed to somewhat erect (Fig. 26B, E), similar to some plants of *O. intricatum*, especially those from the eastern part of its Eurasian distribution (Fig. 26C, F) and unlike western populations, where the leaves are homomallous-spreading (Fig. 26G, H). They are terete in the specimen from Altai.

9. *Orthothecium intricatum* (Hartm.) Bruch, Schimp. & W. Gümbel, Bryol. Eur. 5: 108. 1851. — *Leskea intricata* Hartm., Handb. Skand. Fl. (ed. 5) 336. 1849. Figs. 25 B–G, I–L, 26 C, F–H.

Description: Plants small, brownish-green or reddish-golden, glossy. Stems 1.0–1.5 cm long. Leaves erect, appressed or erect-spreading, terete or slightly secund, (1.5–) 1.7–2.0×0.3–0.4 mm, lanceolate or narrow lanceolate, gradually tapered to narrow acumens, scarcely narrowed to insertion, not decurrent, smooth; margins plane or weakly recurved at places; cells in mid-leaf 45–80×5–6 µm, ± thin-walled, not porose, basal cells in 1–2 rows shorter and wider, with thicker, porose walls, alar cells not differentiated. Specialized asexual reproduction by axillary gemmae often present, gemmae 60–80×10–17 µm. Sporophytes rare [unknown in Russia]. Setae 1–2 cm. Capsules 1.4 mm long, erect or slightly inclined, oblong or shortly cylindric. Opercula conical, with short



Fig. 26. *Orthothecium rufescens*, Caucasus, Krasnodar Territory, OK2247 (A, D), *O. aff. rufescens*, Altai, 2276 (B, E), *O. intricatum*, Urals, Perm Province, OK 2246 (C, F); *O. intricatum*, Czech Republic, OK 2588 (G, H). All scale bars are 1 mm.

obtuse apex. *Annuli* revoluble. *Peristome* slightly reduced; exostome teeth narrow and short, pale, striolate below on dorsal surface, finely papillose close to apex; endostome basal membrane 1/3 of peristome height, segments narrow and sometimes short, cilia absent or up to 3/4 of segment length. *Spores* 8–12 µm [sporophyte features based on material from Scandinavia].

Distribution and ecology. *Orthothecium intricatum* is mainly a montane species, known also from Svalbard, Greenland and Arctic Canada. It occurs in most mountain areas of Europe, northern Africa, Caucasus, Crimea, the mountains of Middle Asia, Himalayas, and Japan, but the southernmost localities in North America are in Quebec. In European Russia its distribution is confined to the mountain regions of Caucasus, South and North Urals, and Kola Peninsula. In Asian Russia it occurs only in southern Siberia. Its records from northern areas of Asian Russia were based on misidentified specimens, mainly of *O. strictum*. It grows on calcareous cliffs and rock outcrops, often in crevices and cavities and also often near waterfalls and on sites with seeping water.

Selected specimens examined: RUSSIA: **Karachaevo-Circassian Republic:** Teberda Nature Reserve, Amanauz Creek, *Ignatov & Ignatova* 05-3488 (MHA). **Crimea:** Plateau Chatyrdag (between Simferopol and Alushta, 18.VIII.1995 *Ignatov s.n.* (MHA). **Republic of Altai:** left branch of Kayra Creek near Kayrabazhi Peak, 14.VII.1991 *Ignatov* 13/193 (MHA); Altaisky Nature Reserve, Teletskoye Lake, Kamga Creek, 6.VI.1989 *Ignatov* 0/1022 (MHA). [**Krasnoyarsk Territory**], Western Sayan Mts, Olen'ya Rechka, 21.VI.1968 *Bardunov s.n.* (MHA ex IRK).

EUROPE: **Norway:** Hordaland, Ullensvang, 15.VIII.1992, *Hedenäs s.n.* (S, B295978). **Sweden:** Jämtland, Berg, Hoverberget, Rämnan, 13.VI.1996, *Hallingbäck TH* 45376 (S, B217022); Härjedalen, Storsjö, Mt. Skarsfjället, 8.VII.2002, *Hedenäs s.n.* (S, B74649); Norrbotten, Tärendö, 20.VI.1962, *Lönnqvist* 952 (S, B181125); Gotland, Kräklingbo, 19.IX.1987, *Hedenäs s.n.* (S, B147848). **United Kingdom:** Scotland, Inverness, 27.VII.1956, *Een UK175* (S, B24281); England, Westmorland, 17.IX.1958, *Perry s.n.* (S, B24280).

Differentiation: *Orthothecium intricatum* can most likely be confused with narrow-leaved morphotypes of the very variable *O. strictum* (Fig. 17C, H, O). In such cases flat vs. narrowly recurved leaf margins and secund vs. terete leaves are helpful for their recognition. However, a specimen with characters of both these species (i.e., falcate-secund leaves with narrowly recurved margins) was once collected in Ulakhan-Chistai Mt. Range in Yakutia (Fig. 21) and is discussed under *O. strictum*. The differentiation from *O. aff. rufescens* from Altai is discussed under the latter species.

KEY TO IDENTIFICATION OF THE SPECIES OF ORTHOTHECIUM IN NORTHERN EURASIA

(see also Fig. 27 for synopsis of the most common leaf shape and relative size in the species)

1. Plants small; leaves 0.3–0.5(–0.6) mm wide, not or weakly plicate 2
- Plants large or medium-sized; leaves (0.5–)0.6–1.2

- mm wide, plicate or rarely not plicate 5
2. Leaves rounded at base, more or less abruptly acuminate 7. *O. sibiricum* p.p.
- Leaves slightly narrowed at base, narrowly acute or gradually acuminate 3
3. Leaves 0.7–1.2×0.3–0.4 mm, often distantly arranged, ovate-triangular; leaf margins serrulate, flat or, occasionally, incurved or recurved at places 4. *O. remotifolium*
- Leaves 0.8–1.4(–2.1)×0.2–0.5(–0.6) mm, closely arranged; leaf margins entire or serrulate near apex, narrowly recurved or flat 4
4. Leaf margins narrowly recurved; leaves lanceolate or ovate-lanceolate, usually erect, very rarely falcate-secund 5. *O. strictum*
- Leaf margins flat; leaves lanceolate or narrow lanceolate, often slightly secund 2. *O. intricatum*
- 5(1). Leaves oblong-ovate, ovate-lanceolate or broadly ovate, not or weakly plicate 6
- Leaves ovate-lanceolate to ovate, plicate (only narrow leaves of imperfectly developed morphs are eplicate) 7
6. Shoots moderately densely foliate; leaves homomalous to slightly falcate, ovate-lanceolate to oblong-ovate, slightly to moderately concave, acute or acuminate, not or weakly plicate; leaf margins flat; plants olivaceous or yellowish-green, often with brownish tint, occasionally dark brown 3. *O. brunnescens*
- Shoots densely foliate, terete; leaves ovate to broadly ovate, strongly concave, abruptly apiculate, not plicate; leaf margins narrowly recurved; living plants often red, plants in herbarium collections yellow-green or golden-yellow 6. *O. lapponicum*
7. Leaves weakly plicate, rounded at base 7. *O. sibiricum* p.p.
- Leaves strongly plicate, slightly narrowed at base 8
8. Plants purple-reddish; leaves erect all along the stem, straight or, occasionally, homomalous, lanceolate, moderately to longly tapered, not especially concave; leaf margin recurved nearly to the base, except the small part in leaf corners, where leaf is abruptly rounded; decurrencies absent or inconspicuous; laminal cells 50–150 µm long 1. *O. rufescens*
- Plants golden-green, bronze to deeply vinaceous red; stems terete-foliate; leaves straight, with distal parts appressed or erect, ovate to lanceolate, moderately to longly tapered or abruptly apiculate and with reflexed apiculus; leaf margin recurved to the base extending to short decurrency, only slightly rounded to base; laminal cells 50–85 µm long 8
9. Leaves ovate-lanceolate to lanceolate, ending in short, straight, flexuose, occasionally incurved or recurved apiculus 7. *O. chryseon*
- Leaves ovate to broadly oblong-ovate, ending in strongly revolute apiculus 8. *O. retroflexum*

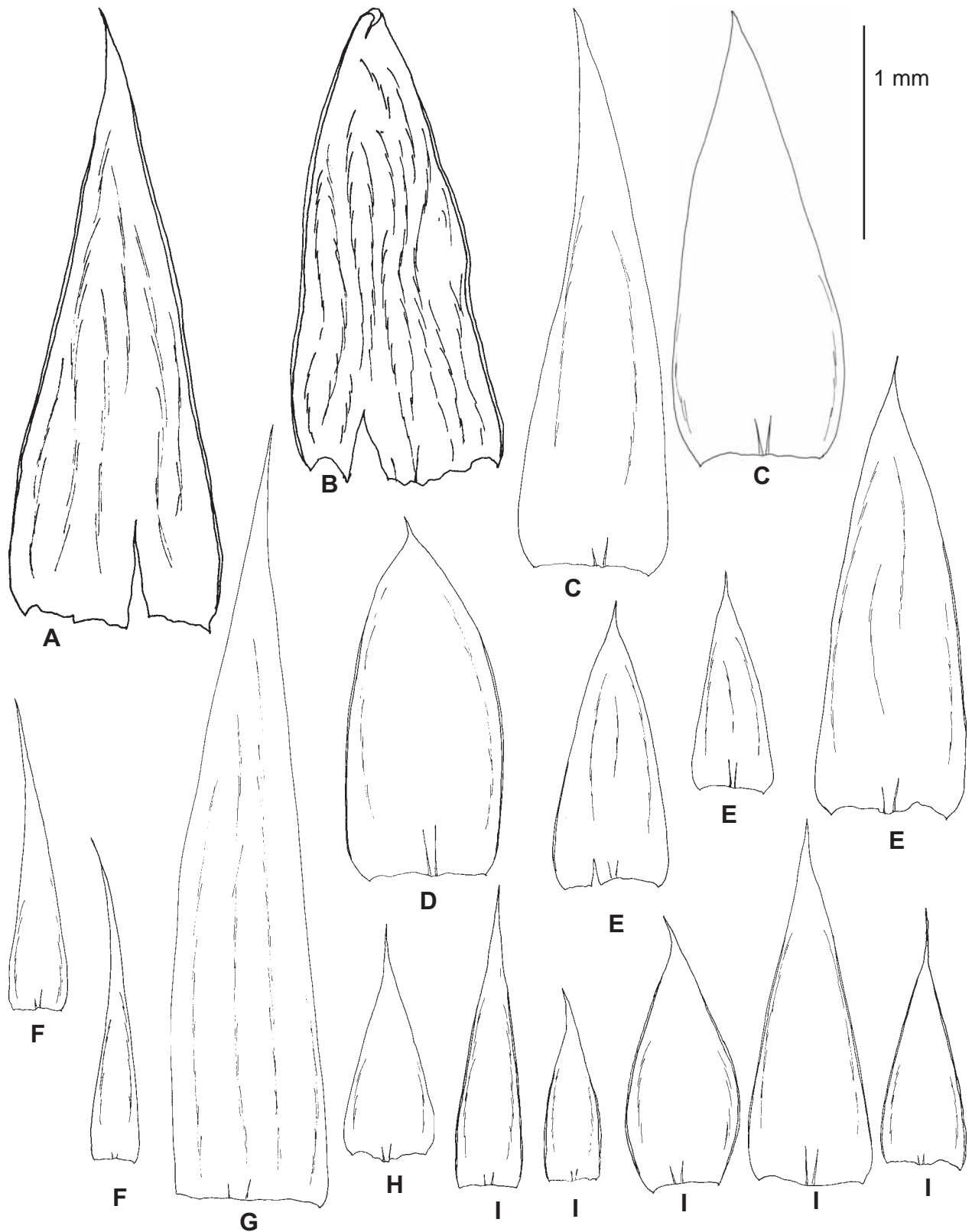


Fig. 27. Leaves of *Orthothecium* species occurring in North Eurasia: A: *O. chryseon* (Taimyr, OK 2491); B: *O. retroflexum* (Taimyr, OK 2166); C: *O. brunnescens* (Yakutia, Ignatov & Ignatova 16-989 & Yakutia, OK 2159); D: *O. lapponicum* (Yakutia, OK 2266); E: *O. sibiricum* (Yakutia, OK 2277; Yakutia, OK 2157; Altai, OK 2501); F: *O. intricatum* (Perm Province, OK 2271; Krasnodar Territory, OK 2274); G: *O. rufescens* (Krasnodar Territory, OK 2247); H: *O. remotifolium* (Yakutia, OK 2236); I – *O. strictum* (Altai, OK 2233; Taimyr, OK 2239; Yakutia, OK 2483; Yakutia, OK 2237; Altai, OK 2280). Scale bars: 1 mm for all.

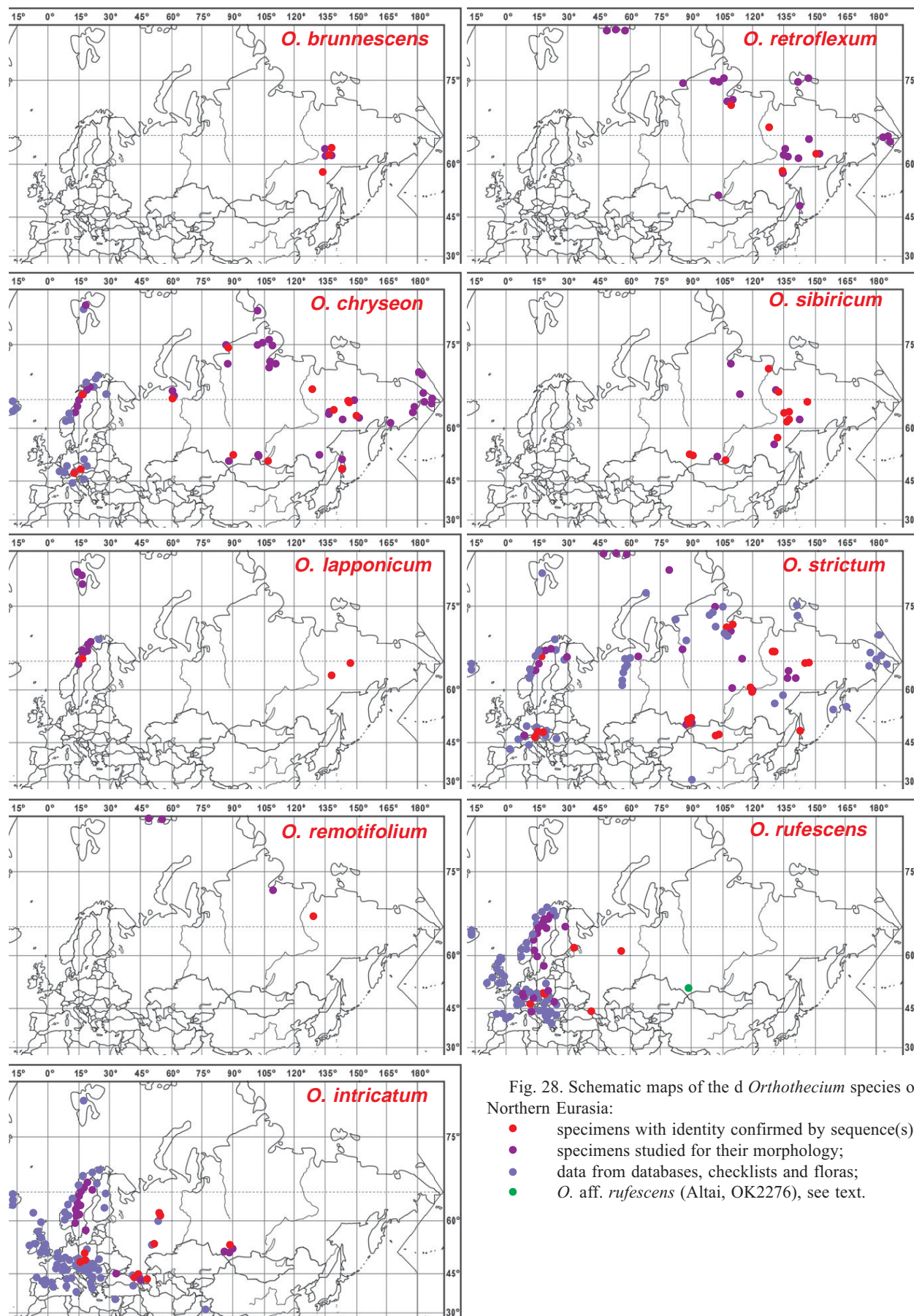


Fig. 28. Schematic maps of the distribution of *Orthothecium* species of Northern Eurasia:

- specimens with identity confirmed by sequence(s);
- specimens studied for their morphology;
- data from databases, checklists and floras;
- *O. aff. rufescens* (Altai, OK2276), see text.

ACKNOWLEDGEMENTS

We are grateful to Heribert Köckinger for helpful criticism; to staffs of H (Xiao-lan He) and O (Siri Rui) for making available images of the original collections, to Irina Goldberg for information and images of collection from C. J. Kučera acknowledges the laboratory work of Alžběta Manukjanová in the Plant Molecular Laboratory at his workplace. Financial support for molecular analyses of JK was provided from the institutional resources at the Faculty of Science, University of South Bohemia. Computational resources ('Metacentrum VO') were supplied by the Ministry of Education, Youth and Sports of the Czech Republic under the Projects CESNET (Project No. LM2015042) and CERIT-Scientific Cloud (Project No. LM2015085) provided within the program Projects of Large Research, Development and Innovations Infrastructures. MI and OK thank RSF 18-14-00121 for support of molecular studies. Work of EI was conducted under institutional project AAAA-A16-116021660039-1.

LITERATURE CITED

- [ABRAMOVA, A.L., L.I. SAVICZ-LJUBITSKAYA & Z.N. SMIRNOVA] АБРАМОВА А.Л., Л.И. САВИЧ-ЛЮБИЦКАЯ, З.Н. СМИРНОВА. 1961. Определитель листостебельных мхов Арктики СССР. – [Handbook of mosses of Arctic of the USSR] *Л., Изд-во АН СССР [Leningrad, Izd. Akad. Nauk SSSR]*, 716 pp.
- AIGOIN, D.A., S. HUTTUNEN, M.S. IGNATOV, G.M. DIRKSE & A. VANDERPOORTEN. 2009. *Rhynchostegiella* (Brachytheciaceae): molecular re-circumscription of a convenient taxonomic repository. – *Journal of Bryology* **31**: 213–221.
- BROTHERUS, V. F. 1925. Musci. – In: Engler, A. & Prantl, K. (eds.). *Die Natürlichen Pflanzenfamilien*, ed. 2, W. Engelmann, Leipzig, **11**: 1–522.
- BRUCH, P., W.P. SCHIMPER & W.T. GÜMBEL. 1851. *Bryologia Europaea*. vol. 5. – Stuttgart, E. Schweizerbart.
- BRYHN, N. 1906. Bryophyta in itinere polari Norvagorum Secundo collecta. 11. – In: *Report of the Second Norwegian Arctic Expedition in the 'Fram' 1898–1902*. A. W. Broegger, Kristiania, 260 pp.
- ENROTH, J., S. OLSSON, S. HUTTUNEN, V. BUCHBENDER, R., TANGNEY, M. STECH, L. HEDENÄS & D. QUANDT. 2019. Orthotrichaceae fam. nov. and other novelties in pleurocarpous mosses revealed by phylogenetic analyses. – *The Bryologist* **122**(2): 219–245.
- FEDOSOV, V.E., A.V. FEDOROVA, A.E. FEDOSOV & M.S. IGNATOV. 2016. Phylogenetic inference and peristome evolution in haplolepidous mosses, focusing on Pseudoditrichaceae and Ditrichaceae s. l. – *Botanical Journal of the Linnean Society* **181**(2): 139–155. <https://doi.org/10.1093/sysbio/49.2.369>
- GROUT, A.J. 1928. Moss flora of North America north of Mexico. Vol. 3. – Published by the author, New-York, pp. 63–114 + pl. 16–29.
- HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucleic Acids Symposium Series* **41**: 95–98.
- HARTMAN, C.J. 1871. Mossor. 2. – In: *Handbok i Skandnaviens Flora, Tonde Upplagan* (ed. 10). Stockholm. Zacharias Haeggströms Förlag, pp. xxviii + 1–179.
- HEDENÄS, L. 1988. The status of *Orthothecium lapponicum* and *O. complanatum* (Musci, Plagiotheciaceae). – *Annales Botanici Fennici* **25**: 153–157.
- HEDENÄS, L., T. HEDDERSON, O.I. KUZNETSOVA, E.I. IVANOVA & M.S. IGNATOV. 2019. *Orthothecium lapponicum*: a disjunctive Circum-Holarctic species. – *Arctoa* **28**: 159–166.
- IGNATOV, M.S., A.V. FEDOROVA & V.E. FEDOSOV. 2019. On the taxonomy of Anomodontaceae and *Heterocladium* (Bryophyta). – *Arctoa* **28**(1): 75–102.
- IGNATOV, M.S., E.A. IGNATOVA, E.I. IVANOVA, O.V. IVANOV & N.A. BYSYIN. 2018. On the distribution of *Andreaeobryum* in Russia. – *Arctoa* **27**(2): 112–118.
- IWATSUKI, Z. 1970. A revision of *Plagiothecium* and its related genera from Japan and her adjacent areas, I. – *Journal of the Hattori Botanical Laboratory* **33**: 331–380.
- KATOH, K. & J. ROZEWICKI & K. YAMADA, KAZUNORI. 2019. MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. – *Briefings in bioinformatics* **20**(4): 1160–1166. DOI: <https://doi.org/10.1093/bib/bbx108>
- KUČERA, J., O.I. KUZNETSOVA, A. MANUKJANOVA & M.S. IGNATOV. 2019. A phylogenetic revision of the genus *Hypnum*: towards completion. – *Taxon* **68**(4): 628–660.
- LANFEAR, R., P.B. FRANDSEN, A.M. WRIGHT, T. SENFELD, B. CALCOTT. 2017. PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. – *Molecular Biology and Evolution* **34**(3): 772–773. DOI: 10.1093/molbev/msw260
- LEVIER, É. 1906. Muscinee raccolte nello Schen-si (China) dal Rev. Giuseppe Giraldi. – *Nuovo Giornale Botanico Italiano, Nuova Serie* **13**: 237–280.
- LIMPRICHT, K.G. 1895. Die Laubmoose. – In: Rabenhorst, L. (ed.) *Kryptogamen-flora von Deutschland, Oesterreich und der Schweiz*, fasc. 26, Leipzig, Eduard Kummer: 769–853.
- LORENTZ, P. G. 1864. Moosstudien. – Leipzig, Wilhelm Engelmann, 171 pp.
- MARGADANT, W.D. & R. VAN DER WIJK. 1958. The citation of the "Bryologia Europaea". – *Taxon* **7**: 97–103.
- PODPĚRA, J. 1954. Conspectus Muscorum Europaeorum. – *Nakladatelství Československé akademie věd, Praha*, 697 pp.
- REDFEARN Jr., P.L. & B.H. ALLEN. 1991. *Orthothecium hyalopiliferum* (Musci: Hypnaceae) a new species from Sichuan, China. – *The Bryologist* **94**: 449–451.
- REDFEARN Jr., P.L. & B.H. ALLEN. 2005. A re-examination of *Orthothecium hyalopiliferum* (Hypnales). – *The Bryologist* **108**: 406–411.
- REDFEARN Jr., P.L. 2014. *Orthothecium*. – In: *Flora of North America Editorial Committee* (eds). *Flora of North America* **28**: 554–557.
- RONQUIST, F., M. TESLENKO, P. MARK. VAN DER, D.L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J.P. HUELSENBECK. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systems Biology* **61**: 539–542. DOI: 10.1093/sysbio/sys029
- SIMMONS, M.P. & H. OCHOTERENA. 2000. Gaps as characters in sequence-based phylogenetic analyses. – *Systems Biology* **49**: 349–381.
- STAMATAKIS, A. 2014. RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics* **30**(9): 1312–1313. DOI: 10.1093/bioinformatics/btu033
- STÖVER, B.C. & K.F. MÜLLER. 2010. TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. – *B. M. C. Bioinformatics* **11**: 7. DOI: 10.1186/1471-2105-11-7
- STEERE, W.C. 1947. Musci [In: N. Polunin, Botany of the Canadian Eastern Arctic. Part II. Thallophyta and Bryophyta]. – *Bulletin of the National Museum of Canada* **97**: 370–490.
- WYNNS, J.T. & C.B.A. LANGE. 2014. A comparison of 16 DNA regions for use as phylogenetic markers in the pleurocarpous moss genus *Plagiothecium* (Hypnales). – *American Journal of Botany* **101**(4): 652–669.

Table 1. Vouchers and GenBank accession numbers.

Species	Provenance	Specimen voucher	Isolate MHA	isolate CBFS	ITS	tnf-trnL	trnL-rps4	rps4
<i>Isopterygiopsis muelleriana</i>	Scotland, UK	D. G. Long et al. 38040 (E)			KF882224	KF882174	KF882374	KF882349
<i>Ortholimnobia handelii</i>	Yunnan, China	D. G. Long 34930 (E)			KF882233	KF882183	KF882383	KF882358
<i>O. brunnescens</i>	Russia: Yakutia, Dyby Pass	Bysylin 17-482 (MHA:9025568)	OK2159,2265	Otl1944	MT681126	MT683698	MT683698	MT683698
<i>O. brunnescens</i>	Russia: Yakutia, Yúgorenok	Ignatov 00-218 (MHA)	OK2240		MT681127	–	MT683696	–
<i>O. brunnescens</i>	Russia: Yakutia, Segenyakh Creek	Ivanov 17-746 (MHA)	OK2484	Otl1930	MT681128	–	MT683697	MT683697
<i>O. chryseon</i>	Austria: Tyrol, Hohe Tauern, Mt Schinal	CBFS: Kučera 6093		Otl1956	–	MT683711	MT683711	–
<i>O. chryseon</i>	Russia: Irkutsk Province, Slyudyanka	Ignatov et al. 18-4355 (MHA:9027444)	OK2156	Otl1952	MT681129	MT683708	MT683708	MT683708
<i>O. chryseon</i>	Russia: Yakutia, Mus-Khaya Mt.	Ignatov & Ignatova 11-3062a (MHA)	OK2165,2267		MT681130	–	MT683699	–
<i>O. chryseon</i>	Russia: Khanty-Mansi Autonomous District, Urals	Lapshina 1351, 5-Aug-2015 (MHA)	OK2248		MT681131	–	MT683700	–
<i>O. chryseon</i>	Russia: Sakhalin Province, Sakhalin, Vaida Mt.	Ignatov & Teleganova 06-145 (MHA)	OK2249		MT681132	–	MT683701	–
<i>O. chryseon</i>	Russia: Yakutia, Moma District, Kyttysh Kuel	Ignatov & Ignatova 18-2414 (MHA)	OK2486		MT681133	–	MT683702	–
<i>O. chryseon</i>	Russia: Yakutia, Moma District	Ignatov & Ignatova 18-1486 (MHA)	OK2488	Otl1953	MT681134	MT683709	MT683709	MT683709
<i>O. chryseon</i>	Russia: Taimyr District, Uboinaya River	Kannukene 14940 (MHA)	OK2491		MT681135	–	–	–
<i>O. chryseon</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4329 (MHA)	OK2492	Otl1941	MT681136	MT683706	MT683706	–
<i>O. chryseon</i>	Russia: Yakutia, Ust-Nera, Tas-Kystabyt	Ignatov & Ignatova 15-1364 (MHA)	OK2494		MT681137	–	MT683703	–
<i>O. chryseon</i>	Russia: Yakutia, Segenyakh	Ignatov & Ignatova 15-531 (MHA)	OK2495	Otl1954	MT681138	MT683710	MT683710	MT683710
<i>O. chryseon</i>	Russia: Altai Republic, Kaira River	Ignatov 13-39 (MHA)	OK2503	Otl1942	MT681139	MT683707	MT683707	MT683707
<i>O. chryseon</i>	Austria: Styria, Schladinger Tauern, Mt Hochwildstelle	CBFS: Kučera 10215	OK2586	Otl1708	MT681140	MT683704	MT683704	MT683704
<i>O. chryseon</i>	Sweden: Lule Lappmark, Mt Stuur Dijder	CBFS: Kučera 19691	OK2587	Otl1709	MT681141	MT683705	MT683705	MT683705
<i>O. intricatum</i>	Russia: Altai Republic, Teletskoye Lake	Ignatov 0-1021 (MHA)	OK2245		MT681142	–	–	–
<i>O. intricatum</i>	Russia: Perm Province, Vishera Nature Reserve	Bezgodov 477, 17-Aug-2014 (MHA)	OK2246	Otl1946	MN794398	MT683723	MT683723	MT683723
<i>O. intricatum</i>	Poland: Tatra Mts, Zakopane	Ignatov & Ochrya 10.III.1995 (MHA)	OK2270		MN794399	–	MT683712	–
<i>O. intricatum</i>	Russia: Perm Province, Vishera Nature Reserve	Bezgodov 30.VII.2017 #384611 (MHA)	OK2271		MT681143	–	MT683713	–
<i>O. intricatum</i>	Russia: Dagestan, Gunib	Ignatov & Ignatova 09-390 (MHA)	OK2273	–	–	MT683714	–	–
<i>O. intricatum</i>	Russia: Krasnodar Territory: Khosta	Ignatov & Ignatova 8.VIII.2002 (MHA)	OK2274		MT681144	–	MT683715	–
<i>O. intricatum</i>	Russia: Bashkortostan Republic,	Baisheva 135-07 (MHA ex UFA)	OK2275		MN794397	–	MT683716	–
<i>O. intricatum</i>	Russia: Krasnodar Territory: Fisht Mt.	Ignatov 19-Aug-1999 (MHA)	OK2401		MT681145	–	MT683717	–
<i>O. intricatum</i>	Russia: Adygeya Republic, Oshten Upland	Ignatov 17-Aug-1999 (MHA)	OK2499	Otl1934	MT681146	MT683722	MT683722	–
<i>O. intricatum</i>	Austria: Salzburg, Radstädter Tauern, Mt Weissgrubenkopf	CBFS: Kučera 12197	OK2585	Otl1707	MT681150	MT683721	MT683721	MT683721
<i>O. intricatum</i>	Czech Republic, Křížlice	CBFS: Kučera 14749	OK2588	Otl1705	MT681148	MT683719	MT683719	MT683719
<i>O. intricatum</i>	Austria: Salzburg, Hohe Tauern, Mt Bratschenkopf	CBFS: Kučera 12758	OK2589	Otl1706	MT681149	MT683720	MT683720	MT683720
<i>O. lapponicum</i>	Austria: Salzburg, Schladinger Tauern, Göriachbach	CBFS: Kučera 9297	OK2592	Otl1704	MT681147	MT683718	MT683718	MT683718
<i>O. lapponicum</i>	Sweden: Pite Lappmark	Hedenäs 9-Aug-2015 (S:B227367)	OK1135,1336		MN794385	–	MT683726	–
<i>O. lapponicum</i>	Sweden: Torne Lappmark	Hedenäs 14-Aug-1990 (S:B236586)	OK1334		MT681151	–	MT683725	–
<i>O. lapponicum</i>	Russia: Yakutia, Mramornaya Mt	Ignatov & Ignatova 18-1535 (MHA)	OK2205	Otl1947	MT681153	MT683727	MT683727	MT683727
<i>O. lapponicum</i>	Russia: Yakutia, Suntar-Khayata Range	Ermakov et al. 8-Jul-2005 (MHA)	OK2266,297		MT681152	–	MT683724	–
<i>O. lapponicum</i>	Canada: Nunavut, Ellesmere Island	Hedderston 8-Aug-1988 (NFLD)	OK2402		MN794386	–	–	–
<i>O. remotifolium</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4134 (MHA)	OK2236,2269	Otl1948	MT681154	MT683729	MT683729	MT683729
<i>O. remotifolium</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4458 (MHA)	OK2489	Otl1929	MT681155	MT683728	MT683728	MT683728
<i>O. retroflexum</i>	Russia: Taimyr District, Anabar Plateau	Fedosov 08-54 (MHA)	OK2166	Otl1945	MN794388	MT683733	MT683733	MT683733
<i>O. retroflexum</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-3974 (MHA)	OK2250		MN794387	–	MT683730	–

Table 1. Vouchers and GenBank accession numbers.

Species	Provenance	Specimen voucher	Isolate MHA	isolate CBFS	ITS	tnfF-tnlL	tnlL-rps4	rps4
<i>O. retroflexum</i>	Russia: Magadan Province, Seimchan	Mochalova 08-6 (MHA)	OK2493	Otl932	MT681156	MT683732	MT683732	–
<i>O. retroflexum</i>	Russia: Yakutia, Allakh-Yun	Ignatov 00-205 (MHA)	OK2500	Otl931	MT681157	–	MT683731	–
<i>O. rufescens</i>	Italy: Kreuzbergpass	CBFS: Kučera 7259	–	Otl624	MT681158	–	MT683734	MT683734
<i>O. rufescens</i>	Russia: Krasnodar Territory, Fisht Mt.	Ignatov 19-Aug-1999 (MHA)	OK2247	Otl949	MN794396	MT683735	MT683735	MT683735
<i>O. aff. rufescens</i>	Russia: Altai Republic, Karakolskie Ozera	Ignatov & Ignatova 28-80 (MHA)	OK2276	Otl951	MT681119	MT683688	MT683688	MT683688
<i>O. sibiricum</i>	Russia: Irkutsk Province, Snezhnaya River	CBFS: Kučera 20667	–	Otl567	MT681161	MT683738	MT683738	–
<i>O. sibiricum</i>	Russia: Irkutsk Province, Slyudyanka	Ignatov et al. 18-4501 (MHA:9027563)	OK2155	–	MT681159	–	MT683736	–
<i>O. sibiricum</i>	Russia: Altai Republic, Teletskoe Lake, Bolshoe Isube	Ignatov 18-119 (MHA)	OK2501	Otl943	MT681162	MT683739	MT683739	–
<i>O. sibiricum</i>	Russia: Altai Republic, Bolshoi Shaltan Creek	Ignatov 0-641 (MHA)	OK2502	–	MT681160	–	MT683737	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Suntar-Khayata Range	Ignatov & Ignatova 15-362 (MHA)	OK1136	–	MT681120	–	–	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Sakkyryr River	Ignatov & Ignatova 17-635 (MHA:9025425)	OK2157,2264	Otl957	MN794395	MT683694	MT683694	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Segenyakh Creek	Ignatov & Ignatova 16-1293 (MHA)	OK2160	–	MT681121	–	MT683689	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Allakh-Yun	Ignatov 00-217 (MHA)	OK2241	–	MT681122	–	–	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Yugorenok	Ignatov 00-216 (MHA)	OK2272	–	MT681123	–	MT683690	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Kharullakh Range	Pisarenko 01053 (MHA)	OK2277	–	MN794393	–	MT683691	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4526 (MHA)	OK2279	–	MN794394	–	MT683692	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Mramornaya Mt.	Ignatov & Ignatova 18-1441 (MHA)	OK2482	Otl940	MT681125	MT683693	MT683693	–
<i>O. aff. sibiricum</i>	Russia: Yakutia, Suntar-Khayata, Sukhaya Creek	Ignatov & Ignatova 15-122 (MHA)	OK2490	Otl958	MT681124	MT683695	MT683695	MT683695
<i>O. strictum</i>	Sweden: Lule Lappmark, Väisäloukta	CBFS: Kučera 19649	–	Otl701	MT681176	MT683750	MT683750	MT683750
<i>O. strictum</i>	Austria: Tyrol, Hohe Tauern, Mt Säulkopf	CBFS: Köckinger 15250	–	Otl959	MT681182	MT683760	MT683760	MT683760
<i>O. strictum</i>	Austria: Styria, Niedere Tauern, Hornfeldspitze	CBFS: Köckinger 15249	–	Otl960	MT681183	MT683761	MT683761	MT683761
<i>O. strictum</i>	Russia: Yakutia, Lenskie Stolby	Ignatov & Ignatova 16-487 (MHA)	OK2158	–	MN794391	–	MT683740	–
<i>O. strictum</i>	Russia: Altai Republic, Taldura	Ignatov & Ignatova 12-495 (MHA)	OK2233	–	MT681163	–	MT683741	–
<i>O. strictum</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-3874 (MHA)	OK2234	–	MT681164	–	MT683742	–
<i>O. strictum</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4361 (MHA)	OK2235	Otl955	MT681165	MT683759	MT683759	–
<i>O. strictum</i>	Russia: Yakutia, Orulgan Range	Ignatov 11-4361 (MHA)	OK2237	–	MT681166	–	MT683743	–
<i>O. strictum</i>	Austria: Lower Austria, Mt Schneeberg	Ignatov & Schanzer 05-5018 (MHA)	OK2238,2268	–	MT681167	–	MT683744	–
<i>O. strictum</i>	Russia: Taimyr District, Anabar Plateau	Fedosov 05-133 (MHA)	OK2239	Otl950	MN794390	MT683758	MT683758	–
<i>O. strictum</i>	Mongolia: Mongolian Altai Range, Gikhgenii Nuruu	Ignatov 01-75 (MHA)	OK2242	–	MT681168	–	MT683745	–
<i>O. strictum</i>	Russia: Altai Republic, Tokpak	Ignatov 36-42 (MHA)	OK2243	–	MN794389	–	MT683746	–
<i>O. strictum</i>	Russia: Sakhalin Province, Sakhalin, Vaida Mt.	Ignatov & Teleganova 06-150 (MHA)	OK2244	–	MT681169	–	MT683747	–
<i>O. strictum</i>	Russia: Yakutia, Ulahan Chistai Range	Ignatov & Ignatova 18-2702 (MHA)	OK2263	–	MT681170	–	MT683748	–
<i>O. strictum</i>	Russia: Altai Republic, Kukol	Ignatov 0/1020 (MHA)	OK2280	–	MN794392	–	MT683749	–
<i>O. strictum</i>	U.S.A.: Alaska, Beechey Point Quadrangle	Buck 8926 (MHA ex NY692838)	OK2338	–	MT681171	–	–	–
<i>O. strictum</i>	U.S.A.: Alaska, St. Matthew Island	Schofield 108784 (MHA ex NY580681)	OK2339	–	MT681172	–	–	–
<i>O. strictum</i>	Russia: Yakutia, Mramornaya Mt.	Ignatov & Ignatova 18-1392 (MHA)	OK2481	Otl935	MT681179	–	MT683753	MT683753
<i>O. strictum</i>	Russia: Yakutia, Mramornaya Mt.	Ignatov & Ignatova 18-1424 (MHA)	OK2483	Otl938	MT681173	–	MT683756	–
<i>O. strictum</i>	Russia: Yakutia, Mramornaya Mt.	Ignatov & Ignatova 18-1427 (MHA)	OK2485	Otl936	MT681174	–	MT683754	MT683754
<i>O. strictum</i>	Russia: Yakutia, Tit-Ary	Ignatov & Ignatova 16-192 (MHA)	OK2487	Otl937	MT681180	MT683755	MT683755	–
<i>O. strictum</i>	Mongolia: Mongolian Altai: Gikhgenii Nuruu	Ignatov 01-76 (MHA)	OK2496	Otl933	MT681175	MT683752	MT683752	–
<i>O. strictum</i>	Russia: Taimyr District, Anabar Plateau, Fomich River	Fedosov 08-3 (MHA)	OK2498	Otl939	MT681181	MT683757	MT683757	MT683757
<i>O. strictum</i>	Austria: Styria, Hochschwab Mts, Moosloch	CBFS: Köckinger 15144	OK2590	Otl702	MT681177	–	–	–
<i>O. strictum</i>	Austria: Upper Austria, Hochschwab Mts, Rimmerhütte	CBFS: Köckinger 15145	OK2591	Otl703	MT681178	MT683751	MT683751	MT683751
<i>Plagiothecium cavifolium</i>	Denmark	J. T. Wynns 1885 (CP)	–	–	KF882225	KF882175	KF882375	KF882350
<i>Pseudotaxiphyllum elegans</i>	Germany	J. T. Wynns 3061 (CP)	–	–	KF882246	KF882196	KF882396	KF882371